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No. 3

NEW ZEALAND POLLEN STUDIES
THE MONOCOTYLEDONS

BY
LUCY M. CRANWELL, F.L.S., F.R.S.N.Z.

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AUCKLAND INSTITUTE AND MUSEUM
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THE MONOCOTYLEDONS

LAKE MATHESON AND MOUNT TASMAN (11,467 FEET), WESTLAND

Under still waters and in peats lie clues to the past. Time is the warp on which their pollen layers thread the weft of forest and climate history. Here, near sea-level, *Phormium* fringes the podocarp forest at the foot of the Southern Alps.

Photograph by courtesy of White's Aviation, Ltd., Auckland.

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A COMPARATIVE ACCOUNT

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LUCY M. CRANWELL

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INTRODUCTION

Before an instrument is put to use, its form and construction should be tried. It is a principle that applies, even more than to mechanical and physical devices, when the instrument is knowledge itself used as a theoretical basis for interpretation of related phenomena.

Recognition of the principle was implied, when, in 1935, under the guidance of Professor L. von Post, Lucy M. Cranwell entered upon the examination, description and systematic review of New Zealand pollen types, as a preliminary to palaeoecological and palaeoclimatological research based on the then rapidly developing methods of pollen analysis.

In this Bulletin, after an interval of several years, she presents the results of a further stage, more particularly in morphology. We of the Auckland Institute and Museum welcome in this account of the Monocotyledons, the return of a former colleague to active participation in our research program. We share the conviction of the author that identification and interpretation in the difficult but rewarding discipline of pollen analysis may be a mere fumbling in the dark without sound systematic and ecological preparation.

It is perhaps unnecessary to point out that these studies should eventually have a wide application in taxonomy, and in the economic fields of hayfever and honey studies.

This monograph is issued jointly by the Harvard University Press and the Auckland Institute and Museum. We gratefully acknowledge the pleasure we have in this association with Harvard University, as we also thank the Harvard University Press for its helpful collaboration in publication and distribution.

GILBERT ARCHY
*Director, Auckland
Institute and Museum*

Auckland, 1952

FOREWORD

THROUGH the kindness of the Director and Council of the Auckland Institute and Museum, of whose staff I was a member until coming to the United States in 1944, I am now able to bring out a further part of my New Zealand pollen studies.

Although appearing as a separate Museum Bulletin, this account is to be considered a direct continuation of the long-planned and long-promised pollen studies that began with records of grains of native gymnosperms and beeches in particular (Cranwell and von Post, 1936; Cranwell, 1939, 1940), and found expression in a single much condensed wartime paper, containing a key to the pollen types of the flora as a whole (Cranwell, 1942).

With more material available, and with direct access to the wealth of pollen literature in American libraries, especially those of Harvard University, this section should have benefited somewhat by the delay. It is admitted, however, that gaps still exist, and not every

useful source of literature has been traced: pollen references tend to crop up belatedly in all directions, like stones in a New England field.

The New Zealand flowering plants point the necessity to seek widely in the literature. To know a species or its pollen fully, one must of course see it in relation to other genera and other pollen types: hence a time-consuming checking of other floras for descriptions and theories, and for material. Of the hundred-odd native families, none is endemic, and since many have very few representatives, one may need to search far afield for comparative pollen material and for published work upon it. The Burmanniales, for instance, have in New Zealand one exceedingly rare member, whose nearest relatives are in Tasmania and Illinois. What has been written about them? What has been written about other branches of the family? Often nothing can be traced, but the search must go on hopefully.

Cambridge, Massachusetts
August, 1952

LUCY M. CRANWELL
(MRS. WATSON SMITH)
*Honorary Botanist, Auckland
Institute and Museum*

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Others associated with Harvard University who have helped in various ways with material, literature, and much kindness have been Dr. E. Barghoorn (Biological Laboratories), Dr. R. C. Rollins, Dr. Robert C. Foster and Dr. Bernice Schubert of Gray Herbarium; Mr. C. Schweinfurth of the Oakes Ames Orchid Herbarium; Dr. J. O. Brew and Professor H. L. Movius of the Peabody Museum; Professor L. Cleveland and Mr. Francis W. Hunnewell, the last two named having collected with me in Auckland in the mid-thirties. During stays in other parts of the United States assistance was given by the following: Dr. and Mrs. Paul A. Vestal, of Rollins College, Winter Park, Florida; Dr. Harold S. Colton, of the Museum of Northern Arizona, Flagstaff, Arizona; Dr. Alexander Wetmore, of the Smithsonian Institution, Washington; Mr. Egbert H. Walker and Mrs. Agnes Chase, of the U. S. National Herbarium, Washington; Miss Marie Neal, of the Bernice P. Bishop Museum, Honolulu; and Miss Annetta Carter of the Botany Department, University of California, Berkeley. In addition, much help was given by Miss Ruth Sanderson and Miss Margery Stone, Miss Constance Ashenden, Miss Margaret Currier, Miss E. Ingalls and Miss Margaret Titcomb, librarians at the Gray and Farlow Herbaria, Peabody Museum, Harvard Biological Laboratories, and B. P. Bishop Museum, respectively.

Thanks to Dr. W. A. Sledge of Leeds University, and to those mentioned below, numerous species have recently been added to the collection. *Dunedin*: Dr. G. Baylis and the late Mr. George Simpson; *Wellington*: Miss Lucy B. Moore, Miss Ruth Mason, Messrs. W. F. Harris, A. J. Healy, N. T. Moar, A. P. Druce.

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Swedish friends, notably Dr. C. Skottsberg and Dr. B. Lindquist of Gothenburg, have forwarded some rare species, while Dr. E. G. Erdtman (Bromma) and Dr. R. P. Wodehouse (New York), veteran pollen workers, as also Dr. F. Verdoorn, have given much kindly advice.

In all cases collectors are mentioned further with the detailed text. Where not otherwise indicated the material has been derived from the rich collections of the Auckland Institute and Museum.

As in earlier papers, I offer thanks to Dr. H. H. Allan, who, while Director of the Botany Division, sponsored a most encouraging Department of Scientific and Industrial Research grant (1937-1939) for part-time assistance and materials. Mr. W. F. Harris, followed in 1940 by Miss B. Molesworth (thanks to help from Sir Frank Mappin and Sir Carrick Robertson, members of the Auckland Institute and Museum Council), assisted in this project.

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Miss Cordelia Galt, Editor, Peabody Museum, has most generously assisted with the preparation of the manuscript for the press. Finally, I offer my grateful thanks to my mother, Mrs. Marian Cranwell, of Auckland, and to my husband, Watson Smith, who has helped along the project in many ways during these last itinerant years since leaving New Zealand.

ON THE NATURE AND USES OF MONOCOTYLEDONOUS POLLEN

FOR the monocotyledons, "modern" pollen records begin with Nehemiah Grew in 1682 and Malpighi in 1686; after them came occasional notes which trickled slowly along with the main stream of pollen observations until the early nineteenth-century work of Purkinje, Fritzsche, and Mohl. Interest surged anew with Fischer's contribution, became quiescent again, and then mounted with the expanding hayfever studies of Wodehouse, of pollen in honey by Armbruster, Oenike and Zander, and of fossil pollen by von Post, Erdtman, Firbas, Potonié, Selling, and many others, pub-

lished in a hundred journals and almost a score of tongues.

It seems typical of the pollen morphologist that he should feel compelled to scour far beyond the bounds of his immediate needs, to seek records bearing in even the most tenuous way on his subject. Such records range from those exquisite stone murals of Nineveh, showing the pollination of the date palm by gods or priests, to the newest descriptions of X-ray elucidation of exine structure, which open a new world of vision beyond that for which visual light has until now been the only tool.

CEREMONIAL AND OTHER USES

POLLEN, to the Navaho and many other American Indians, who seem to have understood its function in fertilisation, and have developed what may be termed a "pollen cult" based on the use of cattail (*Typha*) and corn pollen in particular, is "an emblem of peace, of happiness, of prosperity, and its use is supposed to bring these blessings." (Matthews, 1902, 42.) An enemy who can be induced to put his feet down in pollen is thereby constrained to peace; the ordinary devotee pleads, "May my trail be in pollen."

There appears to be nothing mytho-therapeutic of this kind recorded in Polynesian lore, but considerable use was once made of *Typha* pollen ("*pungapunga*") by the primitive New Zealanders. Bucketsful were beaten out gently from the spikes, according to Colenso (1880, 28), who wrote: "In appearance in its raw state it exactly resembles the ground yellow mustard of commerce. . . . To use it as food it is mixed up with water into cakes and baked. It is sweetish and light and reminds one strongly of London gingerbread."

Colenso sent some samples to Kew, and was informed by Sir J. D. Hooker that natives of Scinde, in India, used it in exactly the same way. In the galleries of the Auckland Museum there has long been an exhibit of a rufous cake of *pungapunga*, collected by Sir James Hector in 1870.

Pollination of the Date Palm

Probably the earliest account showing some conception of the function of pollen is given

by Pliny (23-79 A.D.), who fancifully described the process of fertilisation in a date grove in these words: "Many ladies stand around each man and bend their branches smiling against him. The man stretches his branches stiff upwards and fecundates the female through his fragrance . . . or through the powder which he sends to them. If the male tree is cut, the females are standing sterile like widows, so strong is the feeling of love in these trees." (Täckholm and Drar, 1950, 217).

Theophrastus had referred to it also, while about 3000 years before him, according to the same authors, among others, the process was depicted in early Babylonian, and especially in Assyrian and Hittite art, as accomplished by winged gods.

Pollen Harvests: Ancient and Modern

The "vast tonnage" of wind-borne pollen (Durham, 1951, 277) yields a bulk trade worth over \$80,000 annually in the United States alone, where several million people suffer from pollen and fungal spore allergies. Grasses, of course, are best known as the source and potential cure for this "pollinosis," but other monocotyledons, such as palm and cattail, occasionally cause irritation, Durham (1951, 238) stating that the latter finds a few buyers at 50 cents per gram. Apache-Navaho trade also absorbs cattail pollen at about 25 cents per teaspoonful.

Studies of pollen in honey (see p. 38) have been intensive in Germany (cf. Zander, 1935-1949), cited in the law courts in England, but only barely touched in New Zealand, mainly

in a brief but interesting paper by Harris and Filmer (1948).

Pollen as a Climate Index

Of less obvious economic value is a rapidly growing discipline to whose ends the morphological part of this paper is largely directed. This is pollen analysis, an interpretative study of past vegetation- and climate-change, which, based most firmly on pollen sequences of post-Pleistocene lake and bog deposits, is now being extended to older strata as well. In what follows I hope I have pressed sufficiently von Post's postulates of lapidary skill and caution in identification, linked with the bold concepts of the ecologist in interpretation.

The Use of Pollen Characters in Taxonomy

As Maheshwari (1945) stresses, ". . . if we assume phyletic trends in the external morphology of the flower it is only natural to expect them also in such internal structures as

pollen grains, . . ." This view has been held for over one hundred years by pollen morphologists, from Brown, Guillemin, and Lindley onward to Wodehouse and Erdtman at the present time. Wodehouse in particular has been the champion of this use of pollen grains. Unfortunately, very few accounts of the pollen grains accompany descriptions of new species, especially with regard to the monocotyledons. Skottsberg, however, refers to the pollen of *Astelia* in his treatment of the genus, while Occhioni (1948) describes and figures material of a new South American Iridaceous species, but on the whole, pollen types are better known to peat and hayfever specialists than they are to the systematists, who could use them to equal advantage.

With the evolution of a fairly stable terminology, it is possible that pollen work will again be as important in classification as it was in the Hookers' day.

GENERAL DISCUSSION

Monocotyledonous pollen grains can usually be recognized as such, but their narrow range of diagnostic characters may often make intergeneric and even interfamilial differentiation impossible. In addition, there are likenesses to monolete and trilete bryophyte and pteridophyte spores to increase the difficulties of identification.

Various authors have referred to the types of pollen found in the group, and many, including Hofmeister, Wille, Juel, Rosenberg, Erdtman, and Wodehouse have worked on developmental or morphological problems. Apparently, Malpighi was the first to notice single-furrowed grains.

Basic Types of Grains

Essentially, there are two types of grains: (A) those with bilateral symmetry, characterized by a single furrow or pore; and (B) those (usually spheroidal) with no recognizable aperture. The latter are regarded as derived from the aperture type. Of the few variants known, *Alisma* is many-pored: some have two apertures, but, as Professor I. W. Bailey has recently stressed, none has three.

Two of the three most typical pollen features, namely, distal position of the furrow and successive meiosis, are bound up with development and can be distinguished only in the

early stages in the pollen mother cell, or if the grains remain permanently in tetrads.

First, as to polarity: it was Goebel (1923, 1938) who first demonstrated orientation in monolete grains by showing that the furrows of *Pinus Mugo* var. *Pumilio* (= *P. Pumilio*) were turned outward and at right angles to the polar axis during tetrad formation. Newman (1928) showed that it was distal also in the Australian *Doryanthes*, but it was Pohl (1928) who, in describing tetrads of *Molineria* (Text fig. 1), advanced the theory that the furrow in

FIG. 1. Young *Molineria* tetrads: lateral and end views. After Pohl (1928). Furrows occur on distal ("Basis") side.

the monocotyledons is homologous with that in the gymnosperms.

Wunderlich (1936) and others have confirmed this orientation in many genera, while Wodehouse (1935), Swamy (1949), and others have recorded it for certain dicotyledons

as well. As a result, it has been assumed too readily that the furrow is distal in all monocolpate grains. Professor Bailey and his co-workers (1943, 1950), however, have proved that it may exceptionally be proximal, as in *Asimina* and *Amborella*. Fritzsche (1837) had figured this position for the aperture in *Annona Cherimolia* (*A. tripetala*), and it was finally confirmed for Annonaceous tetrads by Dr. S. J. Golub, one of Professor Bailey's associates.

A list of dicotyledonous families (all with Ralian affinities), which may have monocolpate or derived types of pollen, will be found in Bailey and Nast (1943, 341). New Zealand genera in this category (cf. Cranwell, 1942), are as follows: *Ascarina*, *Beilschmiedia*, *Cassytha*, *Hedycarya*, *Laurelia*, *Litsea*, *Macropiper*, *Peperomia*, and *Pseudowintera* (cf. Table 1). The only other native dicotyledons with even superficially comparable pollen grains are the acolpate *Aleurites*, the obscurely pored forms of *Drapetes*, and an occasional monoporate *Fuchsia* or *Epilobium*.

Secondly, successive meiosis has been considered as essential a feature in the monocotyledons as simultaneous division in the dicotyledons. However, it is now clear from the work of Hofmeister, Guignard, Rosenberg, and various others (cf. Schnarf, 1929), that although most of the families are uniform in this respect, some, especially sedges, rushes, and orchids, are characterized by simultaneous division, while both types may occur in such homogeneous families as the Amaryllidaceae and Palmae, or even, as in *Aponogeton*, in the same pollen sac. On the other hand, successive division has also been traced in the Ralian group (Polycarpicae) already mentioned (e.g., in *Cinnamomum*: Täckholm and Söderberg, 1917). The association of the single furrow with successive division in this group is of special interest. There is no agreement as to which type of division may be the more advanced.

Thirdly, the furrow of the monocolpate grain never encloses a pore; and finally, the furrow margins are rarely thickened, the exine pattern often extending with little modification over the furrow membrane. Furrows of this type are found only occasionally in the tricolpate and derived dicotyledonous types, but they do occur fairly freely in the Polycarpicae. Wodehouse (1936, 495), in discussing the grains of *Ranunculus*, for instance, considers this poreless furrow "of profound phylogenetic

significance." The tendency to elimination of the furrow is also discussed by him (1935, 1937). In the native flora, *Hectorella* (Caryophyllaceae: aberrant), the Cruciferae, *Teucrium* (Pl. 1, fig. 14) in the Verbenaceae), and a few other genera in the Ranunculaceae in particular, share this type of furrow.

Aberrant Types

Continuous or Twinned Furrows. Aberrant or imperfectly understood types include those with merged (fused) furrows, usually separable into two elements, *zonate* if running around the equator, and *dicolpate* if running meridionally. The presence of two apertures has frequently been reported for the monocotyledons, as by Fritzsche, Zander, Erdtman, and Wodehouse, but little detail has been available. The most penetrating discussion of the condition is that of Money, Bailey, and Swamy (1950), in relation to Ralian families. They see in *Austrobaileya* and the Laurelieae, of the key family Monimiaceae, a possible "transitional series between a primitive monocolpate and a derived dicolpate condition. . . ." Swamy (1949, cf. Text fig. 2), had previously shown that the ends of the single furrow, which are often broadened (as in some monocotyledons), were both exceedingly long and broad in the Degeneriaceae, and that a constriction occurred in the middle of the furrow around the distal pole: further, the pollen tube was seen to emerge from one of the broadened ends, i.e., near the equator. Money, Bailey, and Swamy followed up with the study of the Monimiaceae already mentioned. *Laurelia* was shown to have a furrow even longer than in the Degeneriaceae, and equally constricted over the poles: *Doryphora* (see Text fig. 3), moreover, with dicolpate grains, had no trace of furrow over the poles.

FIG. 2. *Laurelia novae-zelandiae*. FIG. 3. *Doryphora Sassafras*. Furrow outlines are dotted on undersurface of grains. After Money, Bailey and Swamy, 1950, figs. 15, 16 respectively.

These researches are particularly important with regard to the monocotyledons, as they indicate how two diametrically opposed pores, as in *Nidularium* (Bromeliaceae), might arise through reduction of meridional furrows. They also trace the evolution of a very unexpected change in orientation of monocotyledonous furrows.

Diporate grains occur in other dicotyledonous groups, as in *Fuchsia*, in which, very rarely, dwarfed monoporate grains will be found (Pl. 2: 2-4). Money, Bailey, and Swamy (1950, 401) emphasize, however, that "Although the end-products of specialization . . . of monocolpate and tricolpate pollen may at times be somewhat similar, they arise by entirely different phylogenetic modifications."

The Divided or "Y" Furrow. Furrows of this nature were first mentioned by Fritzsche (1832). Wodehouse (1935) indicated that they were essentially monocolpate in origin, and Erdtman (1944b, 166) listed a number of species, all in the lily and palm families, in which they are found. Erdtman's illustrations, as well as almost all the material I have seen, seem to support his view that mechanical factors may be responsible for their formation: there is certainly an equivalence between the number of angles on the equator and the number of forkings of the furrow. In trilete spores (Erdtman, 1947b, figs. 3-7) the outlines are more often rounded, and the proximal scar is rigid and thickened on the rims, while in the angiosperms concerned the furrow membrane (distal) is usually much wider, very distensible, and unthickened on the rims. For pollen analysis, these differences have practical value comparable with those existing between monocolpate grains and monolete spores (cf. Selling, 1947).

It is clear that the comparative rarity of this furrow gives it phylogenetic significance. In the Liliaceae it appears to be restricted to the Asphodeloideae (e.g., *Arnocrinum*, *Dianella*, *Johnsonia*, and *Streptopus*). Its constancy in *Phormium*, even in hybrid material, seems to be the most valid reason for retaining this isolated genus in the family. In the palm family it has been recorded by Erdtman (1944b) and Selling (1947): it is also occasional in *Rhopalostylis*. Its derivation from the single furrow is clearly traceable in this family. In *Thelymitra*

and other orchids and in *Laurelia*, its origin is less obvious. In the former it may be shown to represent proximal facets left weak after the separation of the components of a loose tetrad. The possibility of proximal orientation in grains which are always "trichotomocolpate" (e.g., *Phormium*) should not be overlooked.

Areas of this crestlike or triradiate type, regardless of orientation, have also been described as "Y"-shaped (Potonié, 1934) for trilete spores in particular; "3-armed" (Cranwell, 1942); "3-slit" (Erdtman, 1944b; 1945b); and finally Erdtman's "trichotomocolpate" has been promoted to "trichotomosulcate" by Selling (1947).

Confusion with fused furrows might occur, as with grains of *Liparophyllum* (Pl. 8, fig. 18), *Elytranthe* (Pl. 8, fig. 19), and the Myrtaceae. In these types, however, the furrows run meridionally, in true dicotyledonous fashion; further, where they fuse they form "islands" of ectexine over the poles.

COHERENT UNITS

Permanent Tetrads

Many ripe grains remain in groups of four, and a wide literature beyond what is mentioned here is available (cf. Wodehouse, 1935; Levan, 1942; Faegri and Iversen, 1950). Erdtman (1945b) has listed seven monocotyledonous families with variously united grains: only 3 of these occurring in New Zealand have local tetrad-bearing members. The advance suggested by these aggregations has been stressed by Wille (1886), Pohl (1929), and Ames (1946). A special type, the concealed tetrad (the "pseudomonad" of Selling, 1947) is typical of the Cyperaceae.

Barber (1942, Tab. 3) gives a useful graphic survey of tetrad types: this has been too little quoted. His discovery of interactions between synchronous units not separated by a cuticularized wall (i.e., exine) is mentioned again on page 67: his work carries on from Wille's (see particularly 1866, 38-41).

In view of the double duty served by the term (cf. Erdtman, 1945b), an alternative should be available for these permanent tetrads. Pohl (1929) uses "Vierling": the translation "fourling," or the term "quad" might prove acceptable in English.

Most of the New Zealand families characterized by tetrads were mentioned by the writer (1942): a few more records are added in this paper.

Dyads

No obligate dyad arrangements were noted. A few, perhaps temporary, arrangements of this type were noted in the orchids (cf. *Thelymitra*) but all were abnormally small and seemingly imperfect.

COLOUR RANGE AND POLLINATION

Pale yellow is the commonest pollen colour, but a wide range has been noted, blue and green probably being the rarest.

Blue: *Agapanthus* ("Himmelblau," Fischer, 1890, 12).
Green: *Bomarea*; sulphur—green; *Alstroemeria* (various shades are recorded for this genus in Curtis's *Botanical Magazine*).

Yellow: *Dianella* (pale); *Xeronema* (rich); orchids (single grains and pollinia).

Orange: various lilies; *Phormium*; brownish-orange: some lilies.

Whitish or colourless: *Astelia* spp., *Bilbergia cruenta*, *Freycinetia* (greyish-white), *Ruppia* (white).

Blackish: *Tulipa Gesneriana*.

When acetolysed (EM) the exine layers may show characteristic colour differences of some value in identification.

Pollination

This subject has been so fully explored by nineteenth-century botanists in particular that it is unnecessary to outline more than the main methods, with apparent modification of sculptural features of the pollen, that are exemplified by the native flora. Each family is considered further in the systematic part of this account. For a general reference, Svensson's summary (1936) will be found most useful. Further, the distinguishing characteristics of anemophilous, entomophilous, and hydrophilous pollen is described in detail by Wodehouse in a number of papers. He considers wind-pollination "the most ancient and primitive method . . .," but one to which many genera have returned. Transitional types can be recognized (e.g., the willows, and a few members of the lily and screw-pine families) but the direction of modification can only be surmised. Few families are as uniform with regard to pollina-

tion as the orchids. While they are almost completely entomophilous and considered very advanced, the grasses, also considered very advanced by some systematists, are by contrast, as fully anemophilous.

For the New Zealand flora generally the most important work has been done by Cheeseman, whose early orchid observations are especially interesting, but there are, in addition, useful notes by Thomson (1927), Laing and Blackwell (1927), and Miss Heine (1937). Much, of course, remains to be done.

Wind-pollination is very common, being about 29 per cent as compared with 21 and 23 per cent for the German and Swedish floras respectively. Amongst the monocotyledons, about 74 per cent of the genera are wind-pollinated, with at least 69 genera and 290 species involved. Overlapping of methods is indicated in the following lists, but it is clear that the families of greatest ecological importance, especially those of open formations such as bog, swamp, and grassland, are anemophilous.

It is reported that anthesis in rushes may occur briefly on one day only, whereas in some orchids it may last for over two months. Some interest has centred in the sun orchids (*Thelymitra*), but there are very few Australasian records of this type for the monocotyledons.

Entomophilous families. Pollen often strongly sculptured and sticky. Amaryllidaceae (Hypoxis), Burmanniaceae (Thismia), Iridaceae (Libertia), Lemnaceae (most genera), Orchidaceae (all genera), Palmae (Rhopalostylis), Pandanaceae (Freycinetia).

Ornithophilous groups. Pollen coherent.

Liliaceae (Phormium); Freycinetia.

Chirophilous groups: Freycinetia (?).

Some bats are known to be pollen-eaters.

Anemophilous families. Pollen smooth, or with little sculpture.

Typical: Centrolepidaceae, Cyperaceae, Gramineae, Juncaceae, Potamogetonaceae (all Potamogetonoideae), Restionaceae, Sparganiaceae, Typhaceae.

Occasional: Liliaceae (Astelia, Collospermum, Ripogonum), Palmae (Rhopalostylis).

Hydrophilous groups. Pollen typically lacking exine.

Potamogetonaceae (Zannichellia, Zostera).

Self-pollinated groups.

Occasional: Gramineae, Juncaceae, Orchidaceae (Dendrobium, Spiranthes, etc.).

Members of the small Ralanian group already mentioned may also be anemophilous, or in a transitional state. Many have small

dull-coloured flowers, as in Ascarina, Hedy-carya, Laurelia, Macropiper, and Peperomia. The gymnosperms, also distinguished by monocolpate or apparently derived types of grains, are all wind-pollinated,* with the possible exception of *Gnetum* (not native) which has more or less spiny or papillate pollen.

MORPHOLOGY AND METHOD

It must be remembered . . . that the shape of the pollen grain is also dependent on its history and on the treatment it has received . . .

— Christensen (1946, 12).

Shape Classes

As already indicated, most monocotyledonous grains are ellipsoidal or globular, with or without a depression on one side when unexpanded: only a few are pear-shaped or tetrahedral. Many are rotation ellipsoids, with the polar axis in the shorter dimension, hence the terms oblate, peroblate, etc., are applicable. However, as Erdtman (1943, 46) points out, these designations are best reserved for the pollen grains of the dicotyledons: in the latter, whatever the comparative length of the polar and the equatorial axes, the furrows tend to run meridionally between the poles. In the monocotyledons, on the other hand, the furrow is intersected by the polar axis.

Shape, in conjunction with other characters, may be of great value in the identification of pollen grains.

Size Classes

Erdtman's grouping (1945a, 191) has been adopted here, since it is now in fairly general use:

Very small		less than 10 μ
Small		10–25 μ
Medium		25–50 μ
Large		50–100 μ
Very large		more than 100 μ

With the exception of the pollen of *Zostera*, which is *sui generis*, almost all the material studied lies between 15 and 80 μ . Very small grains, unless possibly dwarfed, are not found in the monocotyledons. Those of *Lemna*, *Thismia*, a few species of *Astelia*, and of or-

chids, lie at the lower limit. While Fischer (1890) recorded very large grains for *Musa ensete* (180 μ), later writers give much lower figures, e.g., 90 μ (Armbruster and Oenike, 1927).

Measurements and Types of Preparation

Varying methods of preparation, of course, have much to do with results, fresh material being especially distensible. Some Scandinavian workers even reject the acetolysis method since it induces unequal swelling in fresh and fossilized material. Christensen (1946, 17), however, seeks to modify it, urging the prior use of KOH, since the former method has so much in general to recommend it. Since very refined measurements were not sought in this work, the writer was able to utilize several types of preparation, in order to become familiar with the grains in different stages of expansion.

In spite of so much elasticity, good use can be made of size characters, even in very uniform types. Firbas (cf. p. 37), using the KOH method, has perhaps been most successful: he discovered that the pollen grains of European cereals and wild grasses can be separated since their size curves are bimodal.

As in earlier work, use was made of material (fresh, dried, and fossilized) prepared by acetolysis, by heating briefly in 10-per cent KOH or in lactic acid, or by mounting, after staining, in glycerine jelly. Such diversity has many advantages when a collection is not intended for palynological work only. In measuring, a minimum of 10 grains was used:

up through the pollination fluid in the micropylar canal of an inverted ovule, and tend to orient them with the germinal furrow in contact with the nucellus."

*A blow to preconceived ideas about the function of the air sacs of the Coniferales is struck by Doyle (1945, 61), who asserts that they are not essentially for airfloatation, but are "devices which float the grains

dwarfed, over-distended, or torn material was not included. Total measurements include the exine (apart from spines). By subtraction of exine thickness, the lumen figures are easily available.

Where orientation is doubtful the main diameters are given, but where 3 axes can be recognised, the dimensions are given as for the native podocarps (Cranwell, 1940), noting *length* (L) for the longitudinal axis, *width* (W) for the short (transverse) axis crossing the equatorial plane, and *depth* (D) for the vertical or polar axis. *Length over-all* may include projections from the ectexine. In tetrahedral grains (e.g., *Phormium*), the measurement of one side of the equatorial triangle is given, usually followed by the width from apex to the side first measured: the depth between the poles is often given as well.

Exine standards have been retained much as in Cranwell (1942, 284):

Exceedingly thin	less than 0.5 μ
Very thin	up to 1 μ
Thin	up to 1.5 μ
Moderately thick	ca. 2 μ
Thick	2-3 μ
Very thick	over 3 μ

IDENTIFICATION

Shape and size being protean, there is all the more need to approach identification with caution. However, just as one can recognise the familiar face in the crowd, so can one pick out the grains of certain genera in some atmospheric or even fossil preparations, for instance. *Freycinetia*, *Phormium*, *Chrysobactron*, grains of the *Astelia* complex, and various others, have this quality in common. Difficulties increase with older fossil material as it is bound to comprise forms already extinct as well as others with possibly identical pollen but vastly different ecological significance.

Dr. Isabel Cookson (1947, 134) has shown caution to a marked degree in dealing with graminoid-type grains (l.c., Pl. 15, figs. 41, 42) in lignites from Kerguelen Island. Couper (1951a, fig. 2), on the other hand, is rather more confident with identifications of New Zealand microspores as far back as the Cretaceous.

Most baffling to identify, especially from peats, etc., are the one-furrowed types, as in

the Ranales (p. 73), Liliiflorae (p. 76) and Principes (p. 64). Note, for example, the grain with wide furrow-ends figured by Dr. Virkki (1946, Pl. 3, fig. 35) from Indian beds: this might well be placed with palms of a warm climate, from the Miocene to the present day, whereas it is some unknown representative of the ancient, and cold, *Glossopteris* flora!

NOMENCLATURE

The families are given very much as by Skottsberg (1940), who was much influenced by Wettstein (1935). The latter made three main groups, not in lineal sequence, but considered to be quite possibly from a common stock: (1) Helobiae, (2) Liliiflorae and allies (these having Ranalian affinities), and (3), the group of the Pandanales and Spadiciflorae (= Spathiflorae). The writer follows Skottsberg in transposing groups 2 and 3, but treats the Palmae near the Liliiflorae in order to stress the continuity of their pollen types. Should these furrowed groups be taken first, all the typically inaperturate or monoporate groups (many with tetrads) would be isolated. Hutchinson's system, placing the Glumiflorae highest in the evolutionary scale, parallels this arrangement to some extent. Since it is not really known whether pores are more "advanced" than furrows, or tetrads than single grains, a more conservative path is followed in placing the orchids at the end of the series.

However, attention is given to Hutchinson's views throughout, since many of his innovations, while revolutionary, are pollen-morphologically attractive, as in the isolation of *Cordyline* and *Phormium* (in particular) from the rest of the Liliaceae, and the placing of the palms near the Agavaceae (see p. 54).

Minor groupings are mainly as in Engler and Diels (1936), or in Krause (1936).

Many references to Cheeseman's Manual (1925) will be found, and a number of gaps are filled from more recent papers, or from personal observations on distribution and autecology. The advice of Dr. H. H. Allan has been followed in a number of spellings and name-changes.

All systems offer difficulties; hence, it seems best to offer the following systematic account without over-much discussion and leave the data to be sifted by eventually pollen-conscious systematists.

GLOSSARY OF POLLEN TERMS

- An asterisk denotes that the term was used by the writer in her key (1942). *Abbreviations*: C. (Cranwell, 1942); E. (Erdtman); F. & I. (Faegri and Iversen, 1950); I. & T.-S. (Iversen and Troels-Smith, 1950); P. (Potonié, 1934); W. (Wodehouse, 1935); S. (Selling, 1947).
- Acolpate***: W. 1935, lacking furrows and pores — inaperturate (F. & I.; I. & T.-S.); non-aperturate. (E., 1943; S., 1947).
- Alete**: (spore): lacking tetrad scar (E., 1943).
- Annulus***: a ring-like (halonate) area around a pore, as in *Gramineae*.
- Apiculate**: poles (or ends, e.g., *Freycinetia*) protruding slightly (F. & I.).
- Baculate** (sculpturing): P., 1934; F. & I.; I. & T.-S.; rod-like elements, neither conical nor club-shaped.
- Cell contents***: occasionally of importance in study of fresh material (e.g., starch grains of *Agathis*, *Thismia*; hyaline plugs of *Juncaceae*, etc.); usually destroyed in fossil grains, and in material prepared for their comparative study. Occasionally, the interior may be infested by fungal hyphae (as in *Agathis australis*).
- Clavate** (sculpturing): F. & I., p. 27: like baculate, but club-shaped.
- Columella** (structure): F. & I.; I. & T.-S.; rod-like granules supporting the tectum (q.v.). For digitate and fused types, cf. F. & I., Pl. I.
- Colpus (colpi)**: W., 1935, cf. Furrow (germinal).
- Colpate***: Possessing furrows and/or pores (W., 1935; C., 1942, 284). Now kept for grains with meridional furrows only (E., 1943; S., 1947), or for all furrowed grains without reference to orientation (F. & I.; I. & T.-S.; C., this paper). Prefixes: mono-, di-, tri-, etc. There seems to be no more satisfactory term than colpate for grains with one aperture, whether the furrow is distal (or rarely, proximal) and sharply defined, or of a transitional furrow-pore type.
- Dicolporate**: S., 1947. With two pores per furrow (see *Myoporum* (Pl. I, fig. 18).
- Dicolpate (disulcate)**: E., 1943, 51, "encircled by a single furrow . . . dicolpate or zonate." "Zonate" seems preferable for this condition, as otherwise both proximal and distal furrows must be assumed (but see p. 11).
- Diporate**: two-pored. Aberrant types only in monocots (cf. E., 1944a, for cereal grains with more than one pore). Triporate grains unknown outside dicotyledons (but see *Cyperaceae*).
- Dorsal***: W., 1935, cf. proximal.
- Dyad**: Reichenbach, 1852 (see E., 1945b), twinned grains formed by one mother cell. No recorded examples in New Zealand flora.
- Echinate*** (sculpturing): elements pointed, e.g., *Astelia* spp.
- Exine***: the outer (1-2-layered) membrane of a pollen grain. Resistant to most acids. (In baculate, gemmate, echinate, and verrucate — warty — types greatest diameter of granule is less than twice the smallest.)
- Endexine***: inner homogeneous layer, where two present.
- Ektexine**: outer layer, with granules embedded in, or projecting from matrix.
- Exit, exitus**: the part of the aperture through which the pollen tube leaves the grain. P., 1934; S., 1947; F. & I., 1950; etc.
- Fenestrate** (sculpturing): F. & I., p. 17. Used tentatively here for larger meshes of *Phormium* spp. (p. 52).
- Flecked*** (structural): W., 1943, a useful term where detail is obscure at ordinary working magnifications (about 400 X).
- Fossulate**: E. — surface grooved, e.g., *Centrolepidaceae*.
- Foveolate** (sculpturing): E., 1947; F. & I., 27 (pitted, diameter of pits more than 1 μ).
- Furrow***: a very old term, covering active and inactive germinal grooves and their membranes. Normally elongate (length about twice width) but with many transitions to short or even ragged porelike areas (cf. colpi, sulci, rugae).
- Furrow membrane**: typically distensible, with more or less ektexinous "pattern."
- Gemmate**: F. & I., 27. Diameter of base of granule greater than height, constricted at base.
- Germinal furrow***: W., 1935 (cf. exit and furrow): in the monocotyledons it serves "directly as the place of emission of the pollen tube" and as a harmomegathus (W., 1935), a furrow which functions strongly in volume changes.
- Halonate**: Purkinje 1830, annular.
- Inaperturate**: F. & I. (replacing nonaperturate, E.; S.), e.g., *Ruppia*.
- Intectate**: "ektexine elements, if present, are free and isolated (*Ilex*) or form an open pattern (*Armeria*)," F. & I.
- Intine***: essential membrane of a pollen grain: occurring without exine covering in *Zostera*; acts as temporal furrow in *Potamogeton* (inaperturate), W., 1935.
- Intra-baculate**: with rods (columellae) under surface of the exine, e.g., *Astelia*.
- Intra-reticulate**: with reticulum beneath the surface.
- Lacuna (Lacunae)***: "regularly distributed large openings in the ektexine," F. & I., e.g., *Phormium*. W. uses the term in a wider sense, e.g., for mesh of reticulate *Liliaceae* generally.

Lumen (Lumina): mesh of a coarse reticulum.

Also used (see p. 15) for measurement of grain, as contained by the exine.

Matrix*: Homogeneous ground-substance of the exine (cf. F. & I., 10, 34).

Monad: Reichenbach, 1852, any grain occurring singly (cf. dyad, tetrad): to be distinguished from "pseudomonad" (Selling), signifying a grain whose development is known to have been compound, e.g., *Carex*, *Oreobolus* — typical of the pollen of the Cyperaceae, but not always recognizable as such.

Monocolpate*: W., 1935, one-furrowed. Typically distal in the monocotyledons and a few dicotyledons; (Selling, 1947, reserves use for odd aberrant grains where one furrow supersedes the three typical meridional furrows, e.g., *Gunnera petaloidea*.)

Monolete: spore with single tetrad scar (on proximal side).

Monoporate: with one pore, independent of a furrow, e.g., *Freyinetia*, all grasses.

Palynology: a term introduced in Wales, in 1944, by Hyde and Williams, to embrace all pollen and spore studies.

Pattern*: appearance of sculpture and/or structure.

Pits*, pitted*: previously used both for a perforate tectum and for a finely reticulate pattern. See foveolate.

Pore*: in monocotyledons, an aperture occurring independently of a furrow; serves for emission of pollen tube, as a rule.

Proximal*: E., 1943, side of grain turned inward in tetrad formation.

Pseudomonad: see Monad.

Psilate*: W., perfectly smooth (*Thismia*) or with minute pits or grooves (F. & I.)

Reticulate*: columellae forming a mesh.

Rugulate: irregular elongate ridges: see Pl. 5 (8).

Scabrate (sculpturing): F. & I., p. 27; radial elements "isodiametric," with no dimension more than $1\ \mu$ (papillate*).

Sculpturing*: F. & I., p. 25, "those elements which project beyond an imaginary surface, either the endexine in intectate pollen or an imaginary surface touching the lower-most parts of the tectum."

Structure (= texture): pattern of granules endemic within the ectexine.

Sulcus: originally used for grooves in a grain (e.g., Lindley, 1848) but used tentatively by Erdtman and adopted by Selling, 1947, for a straight or triradiate furrow on the distal side of a pollen grain. Disulcate: two on one side, or zonate (cf. dicolpate, E., 1943).

Taxa (Taxon sing.): taxonomic groups of varied rank.

Tectum, tectate: F. & I., 17, membrane of ectexine, often supported by rods.

Tetrad: a unit of 4 grains formed by one mother cell, or, a union of 4 grains which function independently.

Fig. 4 (after Erdtman, 1945b, and Potonié, 1934).

I, Tetrahedral; II, cross; III, square or tetragonal; IV, rhomboidal.

Texture*: see Structure.

Vesiculate: winged gymnosperm grains.

Zonate: see p. 11.

ABBREVIATIONS

Those referring to authorship of morphological terms will be found in the glossary.

Collectors: C. Sg. — Dr. C. Skottsberg; H. H. A. — Dr. H. H. Allan; L. B. M. — Miss Lucy B. Moore; L. M. C. — Lucy M. Cranwell (Mrs. Watson Smith).

Localities, etc.: Auck. — Auckland; Aust. — Australia; Bot. Div., D.S.I.R. — Botany Division, Department

of Scientific and Industrial Research, Wellington (Wgtn.); N.Z. — New Zealand; Tas. — Tasmania.

Methods & stains: EM — Dr. G. Erdtman's method of acetolysis; F — Basic fuchsin; GV — Gentian violet; KOH — Potassium hydroxide (von Post's method); L, Lp — Lactic acid, Lactophenol (as with safranin); MG — Methyl green; S — Safranin.

Measurements: μ — micron (Greek symbol); $1/1000$ in. = ca. $25.4\ \mu$.

MASTER KEY TO THE MAIN POLLEN CLASSES IN THE FLORA

A. POLLEN GRAINS UNITED (coherent)

1. Contact faces distinct
 - A. Units formed by 2 grains **Dyads** (1)
 - B. Units formed by 4 grains **Tetrads** (2), Text-fig. 3; Pl. 1 (1-5); Pl. 8 (21-23)
 - C. Units (as above) loosely grouped, in massulae, or in a common envelope **Pollinia**, Text-fig. 66; Pl. 7 (14-15)
2. Contact faces lacking,¹ exits usually present **Reduced tetrads: Pseudomonads** (3), Pl. 1 (6)
Cyperaceae
Leucopogon Frazeri (*Epacridaceae*)

B. GRAINS OCCURRING SINGLY, OR VERY LOOSELY ASSOCIATED

1. Exits lacking or obscure **Monads** (4)
2. Exits clearly defined **Inaperturate**, Pl. 1 (7)
Aperturate, See Pl. 1 & Pl. 2
Colpate
Vesiculate (Podocarps only), Pl. 1 (8-10)
Monocolpate, Pl. 1 (11)
Dicolpate (see *syncolpate*, *zonate*) Pl. 1 (12)
Tricolpate — *stephanocolpate*, etc.
Colporate, Pl. 1 (15-19)
Porate, Pl. 2
Monoporate, Pl. 2 (1, 2, 4a)
Diporate, Pl. 2 (2-3)
Triporate (Dicots only), Pl. 2 (5-7)
Tetraporate — *polyporate*, etc.
- A. Without pores: furrows present
 1. With 2-3 air-sacs; furrow elongate or triangular
 2. Without air-sacs
 - a. One furrow, simple or forked
 - b. Two furrows, sometimes fused
 - c. Three or more meridional furrows
- B. With pores
 1. Pores associated with furrows²
 2. Pores not associated with furrows
 - a. With one pore
 - b. With two pores
 - c. With three pores
 - d. With more than three pores

KEY TO THE POLLEN GRAINS OF THE MONOCOTYLEDONS

(* = with more than one entry in the keys)

1. **DYADS**. (Dwarfed grains only,³ 7-10 μ) **Orchidaceae** * e.g., *Thelymitra*
2. **TETRADS** **Liliaceae** * e.g., *Chrysobactron*
- A. Inaperturate, or seeming so
 1. Free: contact faces (of intine) weak; almost completely smooth; 25-52 μ .. **Juncaceae**,*⁴ Pl. 4 (6, 7); see Table 1
 2. In pollinia: contact faces distinct; tetrads 30-70 μ **Orchidaceae**,*⁵ (Acrotonae); see Table 1 & Pl. 7 (3-15)
(Polychondreae *)
e.g., *Pterostylis* type, Pl. 7 (12-14)
e.g., *Gastrodia* type, Pl. 7 (15)
Kerosphaereae, e.g., *Earina* type
- B. Aperturate
 1. Exits distinct: grouping irregular **Gramineae** * (rare), Pl. 4 (4)
 2. Exits weakly defined **Juncaceae**,* Table 1
Polychondreae, Pl. 7 (9)

3. **REDUCED TETRADES** — "Pseudomonads." * Compounding of grains indicated by several exits (up to 4, elongate or rounded). Exine tectate, smooth, but rough over exits; rod-layer distinctive; 25–55 μ

Cyperaceae,* pp. 42–47

4. MONADS

I. INAPERTURATE, or seeming so

1. Exine discontinuous or lacking

A. Grains filiform, ca. 2000 μ ; no exine

Zostera, Text-fig. 7a–c; p. 25

B. Grains spheroidal, under 50 μ

1. Under 30 μ

Zannichellia palustris, p. 26

2. 30 μ or over

Lepilaena, p. 26

2. Exine continuous; grains under 80 μ

A. Spinulose; about 20 μ

Lemnaceae,* p. 27

B. Reticulate

1. Subcylindric or $\pm$ arcuate, 50–70 μ

Ruppia spiralis, p. 24

2. Spheroidal, up to 36 μ

a. Rods rather indistinct; ca. 24 μ

Triglochin, Pl. 3 (2, 3); p. 22

b. Rods clavate, mesh even; 20–30 μ

Potamogeton, Pl. 3 (1); p. 22

c. Rods straight or clavate, usually open on one side, otherwise covered by tectum; 14–36 μ

Orchidaceae (Polychondreae)*⁸
Orthoceras type, Pl. 7 (10); see
Table 1, p. 77

C. Psilate (almost or completely smooth)

1. Without exine pattern: 17 $\times$ 12 μ

Thismia Rodwayi, Pl. 7 (2); p. 65

2. With rods (granules); mainly tectate

a. Globular or pear-shaped; often with pore traces; 25–55 μ

Cyperaceae,* Pl. 4 (8–16); p. 43

b. Spheroidal, intectate part usually with bolder mesh; 12–30 μ

Orchidaceae,*⁸ (as above)
e.g., Corybas type

II. APERTURATE

A. Pored Grains

1. Monoporate

A. Spinulose, pore often obscure, ratio 1:5; ca. 20 μ

Lemnaceae,* p. 27

B. Reticulate; grains globular, under 30 μ

1. Mesh open, rods straight; ca. 23 μ . Pore-ratio 1:7–1:4

Sparganium subglobosum, Pl. 3
(5, 6); p. 30

2. Mesh irregular (rugulate) in high focus, rods clavate, touching around pores; ca. 27 μ . Pore-ratio 1:4

Typha angustifolia var.
Pl. 3 (7, 8); p. 29

C. Psilate

1. Pore distinct, halonate

a. Annulus conspicuous; grains globular or ovoid, 20–70 μ ; exine pattern obscure as a rule. Pore-ratio mainly 1:8–1:10

Gramineae,* Pl. 4 (1–5); p. 38;
see Table 1

b. Annulus not conspicuous; grains plano-convex, 16–26 μ ; pattern lacking. Pore-ratio 1:3–1:2

Freycinetia Banksii, Pl. 3 (1–5);
p. 31

2. Pore diffuse "basal," with granular membrane, (ratio 1:3–1:4): rest of grain psilate, tectate

Cyperaceae,* see Table 1; p. 43
Enantioblastae⁷

D. Foveolate, the pits often slanting or linked. Pore-ratio 1:3–5:7; 25–55 μ ..

1. Mainly over 36 μ ; pouch-shaped, or collapsed over pore; exine often coarsely fragmented around and over pore

a. Pits under 1 μ across, crowded (under 2 μ apart); exine thin; 36–46 (50) μ

Restionaceae

b. Pits up to 1.5 μ across, not crowded

Lepyrodia Traversii, Text-fig.
12a, b; p. 34

(1) Strongly pouched, exine over 2 μ thick; pits 2–6 μ apart; 42–55 μ

Hypolaena lateriflora, Pl. 3 (16,
17); Text-fig. 14a–d; p. 35

(2) Ellipsoidal or slightly pouched; exine under 2 μ , pits 2–4 μ apart; 27–35 (40) μ

Leptocarpus simplex, Pl. 3 (14);
Text-fig. 13a, b; p. 34

2. Mainly under $36\ \mu$, often flatter over exits; pits ca. $1.5\ \mu$ (or enlarged by linking)
- Surface quite rough; $28-34\ \mu$
 - Surface slightly rough; pits mainly $1-3\ \mu$ apart
 - $23-28\ \mu$; exit rigid, splitting widely
 - $30-36\ \mu$; exit circular or appearing forked when crumpled ..
2. With several (up to 4) elongate pores scattered over broader part of grain
- B. Monocolpate**
- Furrow forked (triradiate), rims unthickened; grains tetrahedral, $20-40\ \mu$..

A. Pattern lacking over exit

 - Strongly reticulate, part or all tectate; $30-40\ \mu$
 - Faintly textured all over, $20-29\ \mu$

B. Pattern continuous, the lumina graded in size; $24-32\ \mu$
 - Furrow simple, occasionally oblique or encircling; membrane usually very distensible

A. Furrow conspicuous; rod layer present

 - Sculpture lacking; texture fine
 - Exine up to $3.3\ \mu$ (for roughening, *see* p. 64); $40-70\ \mu$
 - Exine exceedingly thin; $28-34 \times 16-24\ \mu$
 - Sculpture distinct
 - Basically reticulate
 - Concavo-convex to biconvex; rod-layer continuous over furrow
 - Surface rugulate
 - Under $36\ \mu$; ridges delicate; ca. $28 \times 16\ \mu$
 - Over $36\ \mu$
 - Ridges very coarse; $36 \times 26\ \mu$
 - Ridges coarse; $48 \times 31\ \mu$
 - Surface not rugulate
 - Mesh graded, lumina up to $3\ \mu$; $44 \times 33\ \mu$
 - Mesh more uniform; lumina up to $1.5\ \mu$.
 - Averaging $56 \times 26\ \mu$
 - Averaging $36 \times 26\ \mu$
 - Proximally flattened; under $40\ \mu$
 - Surface very rough; exine very thick; ca. $34 \times 24 \times 24\ \mu$
 - Surface comparatively smooth; ca. $34 \times 22 \times 22\ \mu$
 - Exine fairly thick
 - Exine not thick
 - Not reticulate
 - Evenly spinulose; $13-45\ \mu$
 - Spines irregular or lacking; furrow rimmed with granules
 - Projections (spiny) present; ca. $40 \times 30 \times 24\ \mu$
 - Projections absent; ca. $42 \times 30 \times 20\ \mu$
- Centrolepidaceae**, Text-figs. 15-17; p. 35
Pseudalepyrum, p. 36
- Centrolepis strigosa**, Pl. 3 (18); p. 35
Gaimardia setacea, Pl. 3 (19, 20); p. 36
Cyperaceae,* *see* Table 1; Pl. 4 (11-16); pp. 43-44
- Liliaceae** *⁸
- Phormium**, Pl. 6 (2-6); p. 53
P. tenax, Pl. 6 (2-4)
P. Colensoi, Pl. 6 (5)
cf. Fossil, Pl. 6 (6)
Dianella intermedia var. *norfolkensis*, Pl. 6 (1); p. 52
Herpolirion novae-zelandiae, Pl. 6 (7-9); p. 50
- Rhopalostylis sapida**, Pl. 6 (15), Pl. 7 (1); p. 64
Libertia, Pl. 6 (14); p. 62
- Iphigenia novae-zelandiae**, Text-fig. 36; p. 48
- Chrysobactron Rossii**
C. Hookeri, Pl. 5 (8); p. 50
- Xeronema Callistemon**, Pl. 5 (4-7); p. 49
- Arthropodium cirrhatum**, Pl. 5 (1-3); p. 48
A. candidum, p. 49
Cordyline, p. 54
C. indivisa, Pl. 5 (10)
C. australis
C. Banksii, Pl. 5 (11); **C. pumilio**, Pl. 5 (9)
- Astelia**,* Pl. 5 (12); Text-figs. 52, 53; p. 56
Collosperrum
C. hastatum, Pl. 5 (13, 14); p. 57
C. microspermum, Text-fig. 46; p. 57

- (3) Psilate (possibly reticulate?) over body of grain, but scabrate over furrow, which is often irregular; ⁹ 23–33 μ **Hypoxis pusilla**,* Pl. 6 (12, 13); p. 60
- A. Furrow riftlike or weakly indicated; grains spheroidal
1. Spinulose; 13–45 μ **Astelia**,* p. 56
 2. Minutely reticulate, more or less smooth
 - a. Rods straight, exine ca. 2 μ ; furrow wide; 36 (34–50) $\times$ 25 μ **Luzuriaga marginata**, Pl. 6 (10); Text-fig. 54; p. 58
 - b. Rods clavate, exine under 2 μ ; furrow riftlike; 30–35 $\times$ 25 μ **Ripogonum scandens**, Pl. 6 (11); Text-fig. 55; p. 59
- C. *Dicolpate*. Furrows continuous, or irregular; ⁹ about 32 μ **Hypoxis pusilla*** (see p. 20)

Footnotes for Keys: 1–9

¹ An academic distinction as far as the identification of isolated material is concerned. See under *monads*. When contact faces consist of intine only (as in the *Juncaceae*) they may disappear as during acetolysis.

² Normally with one pore per furrow, but two occur in the *Myoporaceae* (Cranwell, 1942, Selling, 1947): see Pl. 1 (18).

⁴ Cf. footnote 1. The exine may survive KOH treatment; both wall and contents are retained in ordinary glycerine preparations (e.g., MG).

⁸ Arrangements in twos, or in threes (triads) may indicate meiotic disturbances, or merely, as in the

orchids, the partial separation of grains from an unstable tetrad.

⁶ Rarely, if ever, found in peats, etc. It is possible, however, that whole pollina might yet be recognised.

⁹ Weak areas are usually not evident before the tetrad breaks up.

⁷ Difficult but rewarding material. *Lepyrodia*, if it can be separated with confidence from *Hypolaena* in particular, has special value as a climate-indicator.

⁸ Found occasionally in *Chrysobactron*, *Rhopalostylis*, etc. Possibly proximal (cf. *Phormium*).

⁹ More material needed for study of furrow.

ORDER 1: POTAMOGETONALES

The difficulties of classification in this order are clearly stated by Miki (1937), and an excellent summary of researches and views about the pollen types found in it is offered by Wodehouse (1935, 81, 297), who disagrees with Fritzsche (1837) about the status of the group: on the pollen evidence Wodehouse (l.c., 299) considers the families advanced, at least "higher than the palms," which also have simple grains, but of the monocolpate type which he considers truly primitive. Wodehouse stresses the relationship between type of pollination and condition of the exine, the grains of genera which emerge their flowers for wind-pollination having exine (e.g., *Potamogeton*, *Ruppia*) while those pollinated under water have none, or only the merest vestiges (e.g., *Zannichellia*, *Zostera*). Further, the intine in the latter type is very thin, but is protected and floated by a coating of oil.

Miki (1937, 478) also considers these plants advanced; from his study of *Potamogeton* he comes to the conclusion that the monocotyledons are quite probably biphyletic in origin, as already held by Lotsy (1911) in particular, and vigorously contested by Maheshwari (1939, 418). Kinship with Synanthae or Pandanales is suggested for *Potamogeton* by

Miki (1937, 472, 473) who also refers (from fossil remains in the genus) to a possible connection with the Spadiciflorae (= *Spathiflorae*).

Pollen type: Grains single, inaperturate, spheroidal, with very thin, easily collapsed, essentially reticulate exine, or traces of granules only if exine lacking; intine very thin, or with local thickening, the "temporal furrow" of Wodehouse (1935, 300); hyaline bodies present.

The following key is given, with little change, from Cranwell (1942, 290, 291, 293);

1. Exine discontinuous or lacking
 - a) Grains elongate, 50 μ or more long
Filiform, 2550 μ , no exine
Zostera
Arcuate, 50–70 μ ; exine reticulate
Ruppia
 - b) Grains spheroidal, under 50 μ
Exine meshed; 30 μ or more
Lepilaena bilocularis
Exine vestigial; under 30 μ
Zannichellia palustris
2. Exine continuous, finely reticulate
About 20–30 μ
Potamogeton Cheesemanii,
natans, *ochreatus*.
About 24 μ ; granules obscure
Triglochin striata

POTAMOGETONACEAE: PONDWEED FAMILY

It is granted here that *Triglochin* is really inaperturate, but with a "temporal furrow" (seen only where contents are preserved) sometimes lying in a fold that simulates a furrow. As already indicated, the temporal furrow, while of no value for identification of fossil material, is important for the study of affinities and of trends towards anemophily. As stated by DeCandolle (1878), cf. p. 59, and Wodehouse (1935) reduction of exine sculpture and exits is characteristic of wind-pollinated plants, while complete loss of both is seen in hydrophilous genera.

TRIGLOCHINOIDEAE

TRIGLOCHIN L.

As in *Lilaea* (Fischer, 1890, 21) and *Tetroncium* (Auer, 1933, Abb. 55, figs. 30, 31) a finely reticulate exine is typical. In *Scheuchzeria* dyads occur; with the exclusion of this genus from the family (Wettstein, 1935), all remaining members are seen to have grains occurring singly. Zander (1935, 112) chiefly quotes from Warnstorf (in Knuth, 1904, 408), giving the pollen of *T. palustris* as $31\ \mu$, with *T. maritima* $25\text{--}31\ \mu$, and yellowish-white in colour. A more detailed account is given by Faegri and Iversen (1950, 134) who state that the sculpturing is reticulate-clavate, and uniform, with closely spaced "imperceptible" granules distinct from those in the mesh of *Potamogeton*.

Although wind-pollinated, *Triglochin* has rarely been recognized from peats or from atmospheric collections; Hyde (1950, 409), however, identified a single grain (as compared with 84,254 grains of grasses) from eight British collecting stations during 1943.

Twelve species are known from salty or fresh marshes of both hemispheres: of these, only two occur in New Zealand.

T. striata Ruiz & Pav. var. *filifolium* Buch.

Pl. 3 (2, 3).

Grains spheroidal or collapsed on one side, averaging $24\ \mu$; exine almost smooth, evenly reticulate, the lacunae very small and columellae obscure. Intine thickened under crescentic fold.

Material: Auckland, L. M. C.; MG. C. Skottsberg, Oct., 1938; GV.

Range, etc.: Coastal in four main islands, or by

thermal pools from Te Aroha to Taupo district; also in Australia, Tasmania, and Chile (Cheeseman, 1925, 125).

T. palustris L.: Native material not seen.

Various measurements have been given (e.g., Edgeworth, 1877, 15 and fig. 36, about $17\text{--}22\ \mu$; Zander, 1935, 112 ca. $31\ \mu$).

Range, etc.: Montane and local in Canterbury and Otago (Cheeseman, 1925, 126).

TEXT FIG. 5. *Potamogeton natans*. Grain in optical section, showing "temporal furrow," indicated by (a) thicker intine, and (b) hyaline body.

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POTAMOGETONOIDEAE

POTAMOGETON L.

The pollen grains of this genus are very uniform, as shown by Schumann (1844, col. 684), by Fischer (1890, 21), who was followed by Zander (1941, 15, Abb. 5) for *P. natans*, and by Erdtman (1943, 63; Pl. II; figs. 20, 21) who gave a measurement of $25\ \mu$ for *P. perfoliatus*. A few more-detailed accounts stress similarity with *Triglochin* in particular, e.g., Wodehouse (1935; 1943, 6) and Faegri and Iversen (1950, 134). Edgeworth (1877, fig. 29, a, b) must have overlooked the meshed nature of the exine as he figured, and mentioned, small spines instead of the connected rods of the muri; he also indicated a fold in one grain, but this is lacking in a second, more expanded grain.

Most authors describe the grains as more or less globular, with changes in shape due to the state of expansion, but Miki (1937) distinguished between "globular" grains of *Eupotamogeton* and "oblong" ones in *Coleogeton* (e.g., *P. pectinatus*). Faegri and Iversen (1950, 134), however, hold that both sections of the genus are subspheroidal, with reticulate-clavate sculpture, as in *Ruppia* and *Triglochin*, the granules being widely separated and reticulum indistinct in *Coleogeton*, but clearly spaced and more distinct in *Eupotamogeton*.

It is clear that the identification of these grains may be difficult, especially from fossil deposits. They have been isolated from peats, e.g., by Meinke (1927) and by Iversen (1946), and from Tertiary oil shales by Wodehouse (1933). No special indicator-value is attached to them, apparently, but they are usually found in eutrophic sediments, as in bottom layers of raised bogs.

As is well known, the pollen may be freed both above and below water. Details of pollination in the family as a whole will be found in Kerner and Oliver (1895), Pohl (1929), and Svensson (1936).

The following description for the family is taken from Wodehouse (1935, 299): "Grains, when moist and expanded, ellipsoidal or approximately spheroidal, 25 to 31 μ in diameter. Exine covered with delicate reticulate thickenings throughout, resembling a foam pattern of varying mesh and similar to that of *Typha*. Intine of most of the grain thin but greatly thickened in a longitudinal strip on one side." Measurements as high as 40 μ have been noted.

Hybridism occurs freely in the northern hemisphere species at least, as shown by Taylor and Sledge (1944) and by Praeger (1951, 12-13), among others, the latter listing nine Irish crosses, including *crispus*, *natans*, and *perfoliatus* among the parents.

The New Zealand material has been referred to by the writer (1942, 291), who gave a measurement of 26 μ and compared the grains with the smaller ones of *Peperomia* (9-14 μ). Notes on three of the five species are given here. One introduced species, *P. crispus*, is now acclimatized. The following may also be foreign.

P. natans L.: Pondweed

Text-fig. 5 (after Wodehouse).

Grains reticulate and inaperturate, "tending

to be ellipsoidal or globular, 21 to 31 μ in diameter. . ." according to Wodehouse (1935, 300), who gives excellent illustrations (Pl. IV, 8, and text fig. 84), the latter, reproduced here, showing the "temporal furrow" of thick intine. Zander (1941, 15, Abb. 5) states that the grains average 33.8 x 20 μ when dry and 29 x 25 μ when moist.

Material: Foreign pollen studied: Quebec (Harvard Pollen Collection: lactic acid preparation), measuring about 26.5 x 21 μ , lacunae angled, mainly about 1 μ in diameter.

Range, etc.: Rare, according to Cheeseman (1925, 127); occurring outside New Zealand in Europe, Asia, and America. Iversen (1946) has reported *Potamogeton* pollen similar to this from a late-glacial dwelling-place near Bromme in Denmark.

P. ochreatus Raoul

Grains about 24-30 μ in diameter, often collapsed; exine thin, intectate, weak, delicately reticulate, the muri closer than in *Triglochin*, and slightly roughening the surface; columellae clavate.

Material: Waihi Stream, Waikato; T. F. C.; MG.

Range, etc.: Both main islands, apparently not abundant. Summer-flowering.

P. Cheesemanii A. Bennett: Manihi.

Pl. 3(1).

As in the preceding species but smaller, about 24 x 17 μ ; exine evenly reticulate; columellae baculate.

Material: Waikato; T. F. C.; MG. Chelsea; L. M. C., October, 1938; EM.

Range, etc.: "universally distributed throughout the Dominion. Sea-level to 3000 ft." Cheeseman (1925).

Useful notes on *Potamogeton* and *Ruppia* are given by Miss Mason (1949, 11, 12).

FIG. 6. *Ruppia maritima*. Sketch showing closed mesh, thinning out to isolated rods over unshaded parts.—FIG. 7: *Zostera marina*. (a) end of bundle of parallel pollen strands; (b) end of strand with swelling; (c) branched strand. After Fritzsche, 1837, Taf. XII, fig. 4; Taf. III, figs. 1, 2, 4, respectively.

RUPPIA L.

The pollen of this very small brackish-water genus is well known from the full description and much-copied figure given by Fritzsche (1837, 708, and Taf. XII, Fig. 4). On the basis of this work, the grains are described as uniform, but range in size may be considerable, Fritzsche himself stating that the width varied from $1/50$ to $1/16$ of the length. He placed *R. maritima* amongst grains without preformed openings, stating that it was a very isolated and interesting form: "Ein schlauchartiges, in einem stumpfen Winkel in der Mitte knieförmig gebogenes Korn. . .," the exine at first glance appearing cellular (in his opinion), this reticulation being more difficult to trace over the ends and over the kneelike swelling.

Later, Hooker (1855-1860, 42; 1867, 279) merely referred to "polline trihedro" and later described it as "a long curved cell," while Schumann (1894, col. 698 and Tab. CXXI) gave a good sketch, noting that the pollen was yellow and "arcuato-curvata" (also described as "curvata subutriculosa" in his key), with the exine "reticulato-granulata," but he interpreted the

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Fig. 8. *R. maritima* (Queensland, C. T. White, ex Gray Herb.; lactic). Sketch to show dense starch grains (to right) and reduction of mesh over three projecting areas. $70 \times 30 \mu$.

blunt ends as two pores. Fischer (1890, 33, followed by Zander, 1941, 113, 142), on the other hand, had described *Ruppia* pollen as monocolpate. Wodehouse (1935, 301, Text fig. 85 and Pl. IV, fig. 7) summarized much of the literature and gave excellent illustrations of the pollen of the following species (about 61μ long in his material). Faegri and Iversen (1950, 134) refer to Wodehouse, and state that the exine is reticulate-clavate, as in *Potamogeton* and *Triglochin*.

In addition, Goebel (1921, 1711) had stated that *Ruppia* pollen sank in water.

Since forms of *R. maritima* have often been confused in literature and in collections (vide Mason, 1950, 240) the writer has decided to give a general note, based on the studies quoted, leaving a detailed description of the form, or forms, found in New Zealand, until more material is available. Small differences in shape, and type of reticulation emerge, but these may be due in part to methods of preparation, or may be paralleled in foreign material also.

R. maritima L.: Ditch Grass (*sensu lato*)

Text figs. 6, 8.

Grains arcuate, typically $50-75 \mu$ long and $1/4$ to $1/3$ as wide, bulging slightly at ends, and on one side, occasionally adhering loosely. Exine finely reticulate with the open mesh reduced or perhaps lacking over bulging areas of grain. Intine (according to Wodehouse, 1935, 300, and Fig. 85) "rather thick and slightly further thickened in the swollen regions where the exine is defective. . ."

Comparative material: Utah (14,005, Harvard pollen collection; lactic acid): grains irregular, yet typically arcuate, larger than normal, about $105 \times 20 \mu$.

R. spiralis L.: Horse's Mane

Pl. 3(4).

Grains tending to be more cylindric; mesh very broken over thin area.

Material: Lake Hayes; B. E. G. Molesworth, March 16, 1941; MG. Washdyke (per L.B.M., 1952): pollen friable, white.

Range, etc.: Abundant in North and South Islands, mainly in brackish water (Cheeseman, 1925, 129). At the present time *Ruppia* is wide-spread in the Pacific, occurring even in the crater lake on Niauofu Island (Gray Herbarium specimen !); probably bird-carried over vast areas of ocean.

Records from lignite: Whangamarino (Waikato), in Pliocene material (allochthonous) collected by the writer. Grains measuring $55-75 \times 23-40 \mu$; very similar to living *Ruppia* pollen.

ZOSTEROIDEAE

ZOSTERA L.

Few descriptions and illustrations of *Zostera* pollen equal those of Fritzsche (1837), who worked with material kept fresh for 17 days in moss after being collected at Kiel. He con-

sidered the grains exceptional in their great length and likeness to the pollen tubes of other plants. He described them as very long ($2550 \times 3.7 \mu$), clear yellow, simple, one-walled "zart und fein" threads arranged in parallel masses equalling the anther in length, and tending to become very tangled when disturbed. Branched filaments (l.c., Taf. III, fig. 4) and a streaming movement of granules in the tubes were also observed. Threads comparable with these are reported for *Posidonia* and *Cymodocea*, but they develop on germination of the grains (see Svensson, 1936, 309, and Fig. 236, respectively, the latter after Borner).

Schnitzlein (1843-1846, 71, Fig. 8) illustrated tangled threads of "*Z. minor*," while Cheeseman, Hutchinson, Fernald, and others have referred mainly to the filiform ("confer-void") shape of the grains. Wodehouse (1935), paid tribute to Fritzsche's work, while Rosenberg (1901, quoted by Svensson, 1936, 308 and Knuth, 1904, 46) described their elusive tetrad division for the first time. His measurements ($2000 \times 8 \mu$) are often quoted (e.g., by Potonié, 1934, 8).

Since writing the above, I have seen some of the rarer *Zostera* papers. Most important is the second by Rosenberg (1901b), who corrects his own, and Hofmeister's, statements that tetrads are lacking. He shows that division (successive) is very late, occurring after the pollen mother cells (PMC) have grown from 70μ to 450μ in length: as in *Najas*, there are 6 chromosomes in the pollen grain or "thread."

These remarkable grains appear to be produced in abundance, but many forms do not have flowers regularly, if at all. Tutin (1936, 229) reports further that there is a tendency for the anthers to fall as soon as the pollen is shed (*Z. marina*), but in *Z. nana* they may persist for a short time. Naturally, there are no pollen records from peats, etc.

As stated (1942), the writer and Miss Moore once collected male flowers at Doubtful Sound, but lost them before preparations could be made.

The New Zealand species are imperfectly known, as stated by Setchell (1933, 814, 816) who described the new species, *Z. novae-landica*, for material previously grouped with the Australian *Z. Muelleri*: he also gives *Z. capricorni* ("a taller, sterile plant") as a possible member of the flora.

Flowers of *Z. novae-landica* (collected at Bluff, S. Is., by the late Professor and Mrs. W. A. Setchell, March 11th., 1927, and forwarded to me by Miss Annetta Carter, of the Herbarium of the University of California, at Berkeley) yielded typically twisted pollen strands. No description has therefore been attempted.

NAJADACEAE

ZANNICHELLIOIDEAE

ZANNICHELLIA and LEPILAENA

References to the pollen of this sub-family are few, chief being those of Fritzsche (1837), who showed that the grains of *Z. pedunculata* (closely allied to the native species) were to be classed with the inaperturate, exineless, seemingly primitive ones of *Caulinia* and *Zostera*. Fischer (1890, 21) merely added that the grains of *Z. palustris* were completely smooth, while Campbell (1897, 42), whom Wodehouse (1935, 301) also quotes, described them as small (about $25-27.5 \mu$, according to his illustrations on Pl. IV, fig. 92, a, b), globular, lacking in exine, with starch grains abundant at maturity. He also refers to a "conducting tissue" which appears to nourish the grains during their passage through the canal of the style. It is interesting to note that Campbell refers frequently in this paper on *Zannichellia* and *Najas* to a possible connection between the monocotyledons and pteridophytes such as *Isoetes* and *Equisetum*.

Schumann (1894, Pl. 122) was obviously dealing with dicotyledonous material when he ascribed three-pored pollen with arci to *Zannichellia*. Hutchinson's contribution (1934, 50), on the other hand, is valuable, in that he uses pollen characters in keying the genera: "A. Pollen sphaeroid; plants of fresh or brackish water. . . . *Lepilaena* (Austral., N. Zeal.) *Althenia* (Mediterr.) *Zannichellia* (Cosmopolitan) AA. Pollen thread-like; marine plants. . . . *Diplanthera* . . ." Fernald (1950) and others have also referred briefly to the pollen in their diagnoses.

The genus is ignored by peat specialists, Faegri and Iversen (1950, 134) merely indicating that hydrogamous species, because of lack of exine, are unsuitable for pollen analysis. Identification for any purposes would of course be made more difficult, if, as Kerner and Oliver (1895, 105) indicate, the grains change from

spherical or ellipsoidal to tubelike when they are freed.

ZANNICHELLIA L.

Z. palustris L.: Horned Pondweed

Grains as in *Potamogeton*, but mainly smaller, and with exine almost or completely lost: about $24\ \mu$ in diameter; exine sometimes represented by odd granules.

Material: Waikato River; T. F. C., May, 1884; MG.

Comparative material: Lactic acid preparation of material from New Brunswick (Harvard pollen collection). Grain more swollen ($24\text{--}28\ \mu$); exine granules present.

Range, etc.: In fresh and brackish water from Waikato southwards, with one station in Otago; flowering, Dec.–May (Cheeseman, 1925, 129).

LEPILAENA F. Muell.

Pollen almost identical with that of *Zannichellia*, with some difference in size and degree of retention of exine to be expected. *Althenia* is grouped with *Lepilaena* by some systematists.

L. bilocularis T. Kirk

Grains about $28\text{--}32\ \mu$ in diameter, often angled under pressure; a few fine exine granules present; starch grains and hyaline bodies conspicuous.

Material: Lake Waiholo; D. Petris, Feb. 2, 1891; MG.

Range, etc.: "Lagoons at Palliser Bay . . . V. D. Zotov! The first record for North Island . . ." (Allan, 1935, 231); occurring locally in Canterbury and Otago: "A very curious little plant. . . ." (Cheeseman, 1925, 131).

L. Preissii F. Muell.

No pollen available from Kirk's original collection (represented in both Auckland Museum and Gray Herbaria) which Cheeseman considers may really be *Zannichellia*. Australian material (ex Gray Herbarium, collected in Melbourne by Mueller) yielded so few grains that the following notes should be accepted with some reserve: grains spheroidal, about $28\ \mu$ in diameter; exine lacking; intine greatly thickened on one side only, as in *Potamogeton*.

ORDER 2: SPATHIFLORAE

LEMNACEAE: DUCKWEED FAMILY

LEMNOIDEAE

In 1942, having failed to secure *Lemna* material, the writer keyed its pollen (Cranwell, p. 293) tentatively as spherical and acolpate, with spinulose and possibly discontinuous exine: had the exine been uniform, and the intine thin, the position would have changed slightly (l.c., 282), and the grains would have been contrasted with those of the Lauraceae. The description attempted was based on Hegelmaier's monograph (1868, 142; t. 9, 10), but it was also in conformity with the work of a number of investigators, for instance, Schnitzlein, Engler (1887, 154), Goebel (1921, 24), Cheeseman (1925, 283; probably derived from Hegelmaier, 1868), and Giardelli. Schnitzlein (1843-1870) had dealt with *Lemna gibba* and *Pistia occidentalis* (now in Araceae), while Hegelmaier, who considered the pollen grains important in diagnosis, gave the following family description in "Flora Brasiliensis" (1878-1882, col. 1-2): "Pollinis cellulae globosae, exine tenuissime spinosa vel verruculosa," *Wolffia* being verruculose and *L. minor* and *L. gibba* minutely spiny. *Wolffiella* flowers have not been described (Fernald, 1950, 60).

Giardelli (1937, 99) figured a single inaperturate grain ($\times 265$) of his new Argentine species, *L. Parodiana* (affinities with *L. gibba* and *L. disperma*), and gave the following note: "Pollen globosa y espinosa, de $20\ \mu$ de diámetro." Faegri and Iversen (1950, 135), however, indicate that *Lemna* is truly aperturate, with a single pore and uniform projections (spines) $1\frac{1}{2}\ \mu$ long.

Probably because of the insignificance of the plants, it would seem that their pollen has rarely been examined with care. It is interesting to note that the size of the microspore in flowering plants bears no relation to the size of the plant, but most monocotyledons have grains slightly larger than those of *Lemna*.

The family comprises about 25 species (13 of *Lemna* and *Spirodela*, 12 of *Wolffiella* and *Wolffia*, the smallest known flowering plants). As noted for *Pistia* (which has more scattered spines), the pollen of the Lemnaceae may well be compared with that of the Araceae on the one hand (cf. Selling, 1947, Pl. 54, fig. 873) for *Colocasia antiquorum* var. *esculentum*

(spiny, and with one aperture), and with the poreless Lauraceae (Cranwell, 1942, 290) and *Astelia* (l.c., 293), which have the same size-range and type of sculpture. Taro (*Colocasia*) has been cultivated for hundreds of years in northern New Zealand but it flowers so rarely that it is unlikely to yield any pollen record of its history and should therefore offer no source of confusion with *Lemna*.

LEMNA L.

Ecologically, these species seem to be indicators of almost uniformly eutrophic (nutrient-rich) waters. They have thus some significance for future palynological work. It might even be possible to trace their introduction into New Zealand, if, as has been suggested, they may all be foreign. Hicks (1932, 239), in his studies of *Lemna* in Ohio, found that most species were found between pH 5.8 and pH 8.8: very few tolerated acidity as high as pH 4.4.

Three species are known from New Zealand. Although the cosmopolitan *L. gibba* and *minor* were collected by Hooker as early as 1854, Allan (1940, 305) considers that all may have been introduced. The discovery of the third species, the Asian *L. oligorrhiza*, by the late Professor T. L. Lancaster in a pond near Palmerston North, seems to support this view, but it is possible that the others (like *Wolffia*, newly reported by Miss Ruth Mason in 1949) were merely overlooked.

L. minor L.: Duckweed

Grains monoporate (Faegri and Iversen, 1950, 135), globular, about $20\ \mu$ in diameter, minutely spiny, the spines about $1\frac{1}{2}\ \mu$ long. Pore circular, about $4\ \mu$ across.

Material: No local pollen seen. The following notes are based on material provided by Professor B. Lindquist, and collected by H. A. Fröding at Tveta, in Värmland. Grains $17-20\ \mu$ (KOH); pores about $4\ \mu$ in diameter; spines delicate (finer than in *Astelia*).

Range, etc.: Sea level to 2000 feet altitude, in neutral to base-rich waters.

L. gibba L.

Pollen not seen. According to Dr. Erdtman (personal communication, 1951), the grains average about $22\ \mu$ (EM) and the pore is "ulceroid, often difficult to trace, . . ." He compares them with the grains of the Araceae.

ORDER 3: PANDANALES

TYPHACEAE AND SPARGANIACEAE

In these small monogeneric families, both wind-pollinated, there are strikingly uniform spheroidal pollen grains with a single pore and a thin, delicately reticulate exine. The description offered for *Typha Domingensis*, *T. angustifolia*, and *T. latifolia* by Kronfeld (1894, col. 638) in "Flora Brasiliensis" is probably the most succinct: "Polline simplici vel conglobato 4-dymo, plerumque sarciniformi, granis 20-40 μ in diam." Kronfeld did not refer to pores: neither did Mohl (1834, 79) for *Sparganium simplex* (also p. 36) and for *Typha minima*, although he recognized them in *S. ramosum* and *T. angustifolia*.

In *Sparganium* the grains are monadal, whereas, in *Typha*, as stated above, they occur either singly, as in *T. angustifolia* and *T. Domingensis*, or in tetrads, as in *T. latifolia*, *T. minima*, *T. Shuttleworthii* (Goebel, 1923, 1705), and *T. angustata*.

The pollen of most of these species has received fleeting attention, because of an apparent simplicity, based however on reduction.

The grains of the cosmopolitan *T. angustifolia* have been treated by (among others) Mohl (1834, 52, 79): "Kugelig, mit einem rundem Nabel"; by Schnitzlein (1843-1846, 73; fig. 6, showing 3 irregularly shaped grains, and fig. 7, one grain in section); by Kronfeld; by Fischer (1890, 23) in his group with one "Austrittsstelle"—"kugelig, auch oval, mit fein und dicht netziger Exine, an der eine kleine, rundliche, unregelmässig begrenzte Stelle von der Skulptur frei, nur ganz fein körnig punktiert ist-"; by Wodehouse (1935, 297; 1945, 33, and 34—"18 to 30 μ in diameter"); by Cranwell (1942, 294); by Erdtman (1943, 64, Pl. III, fig. 32, illustrating the proximal side of a grain 31 by 23 μ); and, most recently, by Faegri and Iversen (1950, 134). According to Kronfeld (l.c., 642) and Pl. 115, fig. 9, showing 3 grains with elliptic slits), the grains of *T. Domingensis* are 20-26 μ in diameter.

Mohl (l.c., 80) referred to the tetrads of *T. minima*, while Firbas (1934) dealt with *T. Shuttleworthii* as well. Most attention has been devoted to *T. latifolia* (e.g., Koelreuter, 1811, quoting Delile), LeMaout, and DeCaisne (1868, 628 and figure showing 3 tetrads with pores placed in the middle of each grain), and Edgeworth [1877, reprinted 1879, with figs. 26a & b of dry and expanded grains 9/6000 in. in diameter (ca. 38 μ), interpreted by the writer as "subglobular, with 4 valves," while *a* is one of the most bizarre of the type of sketch

already criticized by Wodehouse (1935, 92)]. Fischer (1890, 17) was quick to realize that only the fact of union distinguished the individual grains of a tetrad from those of *T. angustifolia*; he stated further that they were slightly flattened by mutual pressure, with the germ pores directed outwards. Zander (1941, Abb. 3a) illustrated a tetrad of this type and added two linear arrangements, stating (l.c., 14) that the grains are yellow with a beaded ("geperlte") surface.

Graebner (1900, 5) referred merely to the distribution of single and united grains, stating that *T. angustifolia*, *T. angustata* (!) and *T. Laxmannii* have solitary grains. Wodehouse however, added solidly to the work of Fischer; while Pohl (1929, 279, 285) followed up Wille's (1886, 38) interpretation of the tetrad condition as a fairly new development, a "reduziertes Stadium," seen in advanced species, although it is pointed out that some entomophilous ancestors (unspecified) had also developed it. Wodehouse (1935, 296-297) also stressed its importance: he figured "all possible tetrad arrangements" save tetrahedral, and states that square, tetragonal, and rhomboidal forms predominate. He also discusses the reduced reticulum with traces of buttressing, and the ragged pores, as probable anemophilous adaptations. His concern for a closely related entomophilous form (lacking in the American flora) is perhaps answered in the Pandanaceae, which are both wind and insect-pollinated—typically *Freycinetia* has psilate grains but those of *Pandanus* and *Sararanga* are more or less spiny.

Wodehouse shows also that the pores are anomalous in that they have no fixed position on the outer walls of the tetrad, and he stresses that the pore membrane is inactive; as with many thin-walled spheroidal grains, the walls, when dry, will "collapse quite irregularly without reference to the pore." Erdtman (1943, 64 and Pl. III, fig. 33) follows Wodehouse's excellent description, and compares the continuous reticulum with that stretching from grain to grain in dyads of *Scheuchzeria*.

Measurements of *T. angustifolia* range from 19.4-26.2 μ (Wodehouse) to 31 x 23 μ (Erdtman) and 26-33 μ (Kronfeld). New Zealand material described by the writer (1942) is within this range. Tetrads (measurements based on compact types) range from about 37.60-42 μ (*T. latifolia*, Erdtman, 1943, 64). In peats, etc., these tetrads should be

easy to identify. For instance, Wilson and Webster (1946, 272, fig. 17) have described and figured grains of an Eocene *Typha* (*T. latifolipites* from Montana: tetrads 50 μ , component grains about 22 μ) which they consider "in all respects identical with those of the pollen of *T. latifolia*."

Almost inseparable from some of the monads in the Typhaceae, however, are the pollen grains of some species of *Sparganium* (Faegri and Iversen, 1950, 134). Fortunately, those of the native species are fairly distinctive.

Various authors have reported *Typha* pollen (type unspecified). In the Americas, Deevey (1944, 143) reports it (with the first finding of fossil maize and agave pollen) from the Valley of Mexico, while Hansen (1942) shows that it occurs in several profiles from Lower Klamath Lake: in Table 29 (Klamath Falls) *Typha* is reported from all save one of the 13 spectra. Although not accepted in the pollen sum, it may have value in reconstructing the history of a deposit and eventually of the surrounding area. In New Zealand it is an indicator of entrophic deposits so it may be lacking over the wide areas characterized by an acid substratum.

Although pollen production is copious and wind-carriage efficient for miles (Wodehouse 1945, 33),¹ these grains are rarely found abundantly in deposits, but records from Scandinavia and Europe usually refer to odd grains; while from New Zealand, for instance, Harris and Filmer (1946, 12) have reported three grains of *Typha* in a swamp deposit. Couper (1951a, 13) caps this meagre sub-fossil record with continuous representation in deposits right back to the beginning of the Miocene.

Many references to both *Typha* and *Sparganium* pollen can be traced through the literature reviews prepared by Erdtman (e.g., 1951, Grana Palynologica, 6).

TYPHA (Tourn.) L.

As the grains are so well known, the family description is given very briefly: monoporate, spheroidal or compressed, monadal or in linear, rhomboidal, tetragonal (square), or rarely tetrahedral tetrads; components 18–33 μ in greatest diameter. Exine thin, finely reticulate, the lacunae of different sizes, partly buttressed. Pore rounded, edged with open lacunae.

According to Wodehouse (1935, 295), the pore membrane bears a few scattered flecks.

¹ Pohl (1937, 395) estimates that *T. angustifolia* produces about 174 million grains per plant.

Wodehouse (l.c., 296), on pollen evidence, would place this family higher in the evolutionary scale than the palms. Hutchinson (1934, 125), without reference to the pollen, also gave it higher rank, and isolated the Pandanaceae as even more advanced.

The following measurements, etc., apply only to the New Zealand material. These grains differ slightly in size from those of forms discussed elsewhere, but the small size of the lacunae appear to be more significant. Miss Mason (1950, 228) refers the native material to *T. Muelleri*.

T. angustifolia L.: Raupo.

Pl. 3(7–8); text fig. 10.

As in family outline: occurring singly. Typically spheroidal, averaging 27.5 x 22 (24–31 x 17.15–27.5 μ). Exine less than 1 μ thick, weak, reticulate-clavate, the lacunae small (ca. 1 μ) in proportion to the width of the rugulate ridges between them, sometimes as small as 0.5 μ , giving a beaded, roughened appearance, smoothest where tectate near pore. Pore irregular in outline, about 6 μ in diameter; membrane smooth, sometimes flecked. Pore-ratio about 1:4. Intine fairly thick.

Material: Hanmer, T. F. C.; GV. Takanini, Mrs. H. Jones (Naera Mackie), 1932; KOH.

Comparative material: *T. angustata*: mainly square tetrads, about 48 x 43 μ over-all, with finer reticulation and smoother surface. Greece, ex Gray Herbarium; MG.

Range, etc.: Occurring in two (edaphic?) forms, Kermadecs to Canterbury, lowlands; summer flowering, the yellow pollen so profuse that it was formerly collected to make the Maori *punga punga* or bread, as in the exhibit in Auckland Institute and Museum, 270, presented by Sir James Hector, 1870.

Fossil Record: *T. robusta*, described by W. R. B. Oliver (1936, 289) from leaf fragments, Kaikorai, Tertiary.

Pollen: Harris and Filmer (l.c.), and Couper (l.c.).

FIG. 9: *Sparganium subglobosum* (sect.); FIG. 10: *Typha angustifolia* var. *Muelleri* (?), exine at mid-focus; FIG. 11: *Freycinetia Banksii*, (a) surface, (b) sect., showing protruding contents. $\times 1000$.

SPARGANIACEAE: BURR REED FAMILY

References to *Sparganium* pollen tend to be even briefer than for *Typha*. In the opinion of Mohl the genus had representatives in two groups (a) *S. ramosum* (1834, 79) "mit einem rundem Nabel," classed with *T. angustifolia* and the grasses, and (b) *S. simplex* (l.c., 36), associated with the distinctly granular "in-aperturate" grains of the tetrads of *T. minima*.

As usual, Schnitzlein's (1843-1846) figures of *S. ramosum* add little, but Fischer (1890, 23) corrects Mohl, stating that the grains of both species mentioned have a pore, and he remarks on their similarity to the grains of *Restio squarrosus*. Wodehouse (1935, 204) merely groups *Sparganium* with the Typhaceae in his key, while Zander (1941, 108, 112, 151, 160) mainly follows Fischer, after (1935, 112) describing strongly granular, layered grains of *S. simplex*, ranging from $21.6 \times 16.2 \mu$ (dry) to $25.4 \times 23.4 \mu$ (expanded), while his illustration (Pl. II, fig. 8) shows clearly a thickening of the intine below a weakly indicated pore. Erdtman (1943, 64 and figs. 30, 31) followed with detailed sketches of the grains of *S. minimum* ($27 \times 22 \mu$) and *S. ramosum* ($34 \times 29 \mu$) and showed that there were significant differences in reticulation.

Fægri and Iversen (1950, 135) treat *Sparganium* and *Typha* together in their key, and emphasize in a footnote that the grains of some species of the former are "extremely difficult" to separate from those of *T. angustifolia* in peats and recent sediments. Older material has been identified by Thiergart (1937, 307, quoted by Erdtman, 1943, 220; "Sparganiaceae—pollenites polygonalis. . .") and by Wilson and Webster (1946, 276, fig. 17) who based a new species, *S. globipites* from the Eocene of Montana, on pollen material: "grains spherical; single germ pore, circular to irregular, 7-8 microns in diameter; exine 1-1.5

microns thick, delicately and irregularly reticulate; diameter 28-30 microns."

Ten or more species exist today, only one, common to New Zealand and eastern Australia, being found south of the equator. Its grains were keyed by the writer (Cranwell, 1942, 294) with those of *Typha angustifolia* and *Freycinetia Banksii*. The following account is based on the same material.

SPARGANIUM L.

S. subglobosum Graebn.: Burr Reed

Pl. 3(5-6); text fig. 9.

Grains monoporate, spheroidal, or bulging around the pore, averaging $23 \times 20 \mu$ ($20-28 \times 17-24 \mu$), occasionally ellipsoidal when unexpanded. Exine delicately reticulate over whole surface, the lumina (mesh) rounded, up to 1.5μ in diameter, their muri made up of slender rods (columellae) which roughen the surface; pattern closed around the pores, which are rounded, ca. $3.5-6 \mu$ in diameter, with slightly projecting smooth membranes. Pore-ratio 1:7-1:4. Intine thicker under pore.

Material: Lake St. John, T.F.C., 1919; F.

Range, etc.: A lowland semi-aquatic herb found with *Typha* from north Cape to Cook Strait; rare in South Island (Picton and Methven); see Cheeseman, 1925; and Wall (1935, 110) for Pegasus Bay. Also self-pollinating (Pohl, 1929, 260). Potentially valuable as an indicator species if found in peats, etc.

Important material collected at the Bay of Islands by U. S. Exploring Expedition (Wilkes) was seen at the Gray Herbarium but male flowers had apparently been shed before the material was collected. The remainder of the inflorescence matched the common form.

Comparative material: *S. hypoboreum*, Newfoundland. Grains more rounded, averaging 28.5μ (swollen in lactic acid), evenly reticulate, exine tending to be thicker on one side; no pore seen.

PANDANACEAE: SCREWPIKE FAMILY

Of the same general type as in the preceding genera, but with more specialized and more distinctive pore apparatus, are the grains of the Pandanaceae, one of its two commoner genera being represented in New Zealand by an endemic *Freycinetia*. A survey of much of the literature is given by Selling, who reveals mainly the paucity of earlier information with

regard to both genera. Persistent references to a furrow in the family (as erroneous as for the grasses described by Malpighi, 1686) seem to stem from the statement of Mohl (1834, 35) who described an unidentified species of *Pandanus* in this way. This was accepted without question by Edgeworth, Fischer, Pohl, Zander, and others. Schnitzlein (1843-

1846, Tab. 74, fig. 8), in figuring 3 ellipsoidal grains of *Freycinetia Arnottii*, also suggested furrows: these in their turn bear a striking resemblance to those in the Atlas of Gaudichaud (1841-52, Pl. 36, figs. 11, 12) for the same species. The latter shows elongate grains with a single line representing either a furrow or a fold, and this is repeated in a larger drawing which seems to interpret correctly a single lateral pore as well, possibly with an operculum or thickened membrane. Fischer (1890, 59) showed that a single rounded pore occurred in *Pandanus*, free on the surface of the grain, but described an apical position for it in *P. furcatus*, and stated that its exine was covered with fine warty granules. This sculpture appears to be typical for the genus (e.g., Warburg, 1900, 44: "pollinis granula saepe tuberculata," or p. 14: "der Pollen ist elliptisch und mit feinen Papillen bedeckt. . . ."; his figure 26 shows a grain of *Sararanga*, also spiny, extruding its contents). Selling (1947, 341) refers to "warts or spines" for the Hawaiian variety of *P. tectorius*. Solms-Laubach, (1878, 1) noted banding which has never been confirmed, and Hofmann (1948, 89, Abb. 17, 18) referred briefly to equally anomalous 3- to 4-pored grains in *P. utilis*. Her measurements for this species were 32-33 μ , and for *P. furcatus*, 23-33 μ ; sculpture was not mentioned. Comparison of figure 18 (with 3-4 pores) with figure 22 in the same paper suggests myrsinaceous pollen instead of *Pandanus*.

Selling's description of var. *sandwicensis* is brief and clear but the pores "at one of the short ends" do not show very well in any of the photomicrographs (Pl. 54, figs. 879-882).

A brief note by Endlicher (1833, 25) that the pollen of *F. Baueriana* is "pallide sulphureum" appears to be the earliest for the pollen of this family.

FREYCINETIA Gaud.

The varying references already made to *Freycinetia*, coupled with notes by Cranwell (1942, 294) for *F. Banksii* and by Selling (1947, 341, 342) for *F. arborea*, make it clear that it is set apart, morphologically, because of its distinctive pore. Cranwell placed these small, clinging grains with those of *Typha* and *Sparganium* on the one hand, and with the highly specialized, strikingly rimmed grass pollen on the other. Thick intine underlying

the pore was mentioned for the New Zealand material: this was interpreted as the possible position of a furrow, of which the pore would then be the greatly modified vestige.

F. Banksii A. Cunn.: Kiekie

Pl. 3, (9-13), text fig. 11a,b.

Grains monoporate, ellipsoidal to globular, but frequently flattened and with a single fold on one side; mainly 16-20 μ in greatest diameter. Pore circular or elliptic, about 6 μ in diameter, typically lateral, with a distensible glassy membrane of ectexine, a brilliant thickening of endexine, and traces of vestibule and operculum. Exine thin, about 1 μ thick over most of grain, psilate, and only very obscurely flecked with granules. Intine thicker under pores. Pore-ratio 1:3-1:2.

Material: Waitakere Range, K. Thompson, September, 1938; F; GV. Ohacawai, S. Berggren, ca. 1874 (ex herb. Gothenburg Botanical Garden); KOH.

Range, etc.: A root-climber and rock-scrambler which grows to great heights on podocarps in particular. Typical of lowlands, but ascending in the north to over 2600 feet above sea level. Abundant in rain-forest of North Island, and as far south as Marlborough, Nelson, and the West Coast Fiords. Spring-flowering: pollen a dirty white, copiously produced and tending to cling, but probably carried by wind as well as by insects, rats, and birds visiting the succulent bracts.

Comparative: *F. Elmeri*, Leyte: collected by C. A. Wenzl, November 8, 1914 (ex Gray Herbarium); see Table 1.

Comparative: *Pandanus tectorius*, A. C. Smith, 1281, Kanibaru, Fiji (ex Bishop Museum and Gray Herbarium); Lactic acid. This slide was made for a comparison of exine structure. Quite apart from the sculptural elements (widely separated spines), there is a flecking or pitting of the matrix of the exine which is quite unlike that of grains of *Freycinetia Banksii*.

Selling reports *Freycinetia* pollen in abundance from Hawaiian peats, the species concerned growing around the bogs, or even in acid (though not peat-forming) *Sphagnum* cushions, as in the Kohala mountains, Hawaii. The New Zealand species does not belong to the bog communities, so its pollen should reach acid deposits only through distance-carriage by wind. It does grow on *Podocarpus dacrydioides* hummocks in swamp-forest, however, and should be well represented in less acid sequences during which this species has dominated. It has thus a considerable value as an indicator of both edaphic and climatic conditions.

ORDER 4: ENANTIOBLASTAE

CENTROLEPIDACEAE AND RESTIONACEAE

The pollen grains of these families are essentially alike. Mohl (1834, 52, 77) placed *Restio fruticosus* in the same group with the grasses and *Typha angustifolia*: "Oval, äussere Haut punktiert, mit einem Nabel." Schnitzlein (1843-46, 45, fig. 10) illustrated spherical dry and moist grains of *R. tectorum*, but these told little, while Hooker (1855-1860) offered only a trace of an aperture for *Trithuria* (Hydattella). Fischer (1890, 23) made the same grouping as Mohl, referring to the exit of *R. squarrosus* as an "Austrittsstelle," and also stressing the likeness of its grains to those of the Sparganiaceae. Later, Edgeworth (1877), Pohl (1930), and Zander (1941, 112, 151, 160) referred mainly to Mohl or Fischer, but Cranwell and Erdtman offered their original and independent observations.

Cranwell (1942, 293) showed that all the New Zealand representatives were monocolpate, but had vestigial furrows (*sensu* Wodehouse, 1935) "reduced to a porelike area, or indicated only by a rift in the exine," grains of *Leptocarpus* and the Centrolepidaceae being spheroidal with their exine finely pitted, while those of the latter family was sculptured as well. The grains of the other two New Zealand members of the Restionaceae were shown to be "typically pouch-shaped, the 'pores' constricted by coarsely granular collars; exine characterized by brilliant embedded and additional surface granules. Exine very thick; 40 μ . . . *Calorophus* (*Hypolaena*). Exine thin, pattern bold, continuous; 32 to 40 μ ," or alternatively, "Pattern weak all over" (as may occur) — *Lepyrodia* (*Sporadanthus*). Three genera of the Centrolepidaceae with members in New Zealand were shown to differ in their smaller-sized grains (averages of 24-34 μ) and characteristic exine patterns. In the disappointingly short space available for the 1942 key, it was of course impossible to describe these important grains very adequately.

Erdtman turned frequently to both families. In 1943, 55, he mentions the "exit" of *Gaimardia setacea* (shown in his Pl. 1, fig. 5) and refers to *Centrolepis* (*C. aristata*, "*Desvauxia billardieri*" and "*D. strigosa*"), stating: "There is evident a gradual transition from the irregular exit of this pollen type to the well-defined pore in the pollen grains of some plants belonging to the Restionaceae." *Lepyrodia An-*

arthria (1943, 63; Pl. II, fig. 25), in his opinion, illustrates the most advanced type in this transition, while the South African *Hypodiscus aristatus* and the West Australian *Ecdeio-colea monostachya* approach more closely to the "grass pollen type with a contracted and well defined pore." Later (1944b, 167), he referred to the "graminoid pollen grains" of the Flagellariaceae as well, and again suggested the Centrolepidaceae-Restionaceae-Gramineae sequence. Selling (1947, 350) also refers to pore similarity between the Flagellariaceae (*Joinvillea*) and the Gramineae. A study of the annular constrictions around the pores in these groups is bound to prove useful.

According to van Zinderen Bakkers's illustration (1951, fig. 10, 3) of a grain of *Restio major* (measuring ca. 43 x 35 μ) from the Southwest Cape District (S. Africa), it is of the *Hypodiscus* type.

As far as is known, the exine matrix in both families is essentially pitted: according to Erdtman the pitting becomes progressively weaker in the sequence already mentioned, ending in the characteristic and very delicate pattern of the Gramineae. Erdtman does not refer particularly to the bold fragmentation found in these families. Pohl (1929, 256, 259) states in his summary that both are probably completely wind-pollinated: perhaps the granules are vestiges from an earlier entomophilous condition.

Pollen production is high in *Leptocarpus*, but much sparser in the other native genera. Marloth (1915, 58), however, states for "*Dovea tectorum*" that it sheds "clouds of pollen." Pollen of other African species is mentioned briefly by Masters (1865, 220).

All members of these families are found on wet or boggy ground, and are characteristically selective in their requirements. This fact, coupled with their strong present anemophily, should make their grains of value as indicators in peats everywhere. *Hypolaena lateriflora* pollen was first recorded from New Zealand deposits by Cranwell and von Post (1936, 317). The smaller grains of bog Centrolepidaceae were recognized by the junior author while doing the analyses, but not recorded separately. Harris and Filmer (1946, 12) have since found unspecified Restionaceous pollen highly represented in Hauraki peats, north of the area in which the writer worked until 1940

FIGS. 12-14: RESTIONACEAE. FIGS. 15-17: CENTROLEPIDACEAE.

The sketches show the tendency of coarse granular masses to fragment around or over the rigid exits. $\times$ ca. 1000, except for 12 a and 14 b, c.

12: *Lepyrodia Traversii*, a exit ruptured (EM), $46\ \mu$; b expanded grain, less pouchlike than usual. 13: *Leptocarpus simplex*, ruptured grains, a rod layer shown, b lumina at mid focus. 14: *Hypolaena lateriflora*, a, c expanded grains, strongly pouchlike; b exit ruptured (EM); d polar view with "fragmentation area" shaded, $49\ \mu$ (from Waikato peat). 15: *Pseudalepyrum ciliatum* var. *genuinum*, exit unruptured. 16: *P. pallidum*. 17: *Gaiarddia setacea*, pore area distorted.

(results unpublished). Similar records are to be expected from acid deposits in particular in Australia and Tasmania, and to some extent in South Africa.

Reference should be made to Hutchinson's (1934, 190) map showing the circumpolar emphasis in the Restionaceae, the only northern outlier being *Leptocarpus disjunctus* (Indo-Malaya to Philippines). Hutchinson (l.c., 193) restricts *Hypolaena* to Australia. As has been shown, the pollen grains of the Restionaceae bear out Hutchinson's contention that this is an advanced family. According to Skottsberg (1940, 635), both families may be of Antarctic origin.

RESTIONACEAE

About 300 species have been recorded, mainly from South Africa and Australia, with a few species in southern South America and in New Zealand. The three New Zealand species are endemic, *Hypolaena* and *Lepyrodia* being tied to acid seepages or true bogs (Cranwell, 1952), while the halophytic *Leptocarpus simplex* is rarely found away from the coast-line.

LEPYRODIA R. Br.

L. Traversii, F. v. Muell: Tassel Top

Pl. 3 (15); text figs. 12a, b.

Grains monoporate, typically spheroidal, and usually pouchlike because of constricting ring of granules around the pore; averaging $45 \times 37 \mu$ (40–50 μ , acetolysed). Exine tectate, under 1.8 μ thick, distinguished by a delicate but brilliantly foveolate ("pitted") appearance, the lumina distinctive because they penetrate the endexine, hence their brilliance:¹ about 1.6–2 μ apart, and less than 1 μ in diameter, the muri wide, with wavy outline roughening the surface; further, the lumina are joined by slanting passages of the same diameter, giving the middle of the exine a curiously eroded appearance.

Pore 12 μ at the least, often torn open as wide as the grain when it is fully expanded; rounded or merely riftlike in outline, covered with a more or less disorganized ectexine pattern, with scattered verrucae as around the constricting margins. Verrucae up to 3 μ in diameter, brilliant. Pore without graminoid "collar" or annulus. Intine thick.

The pollen grains of this species are very like those

¹Erdtman (1952, 376, fig. 22) indicates that the endexine in this order is of normal type, not perforate, as I have stated.

of *L. Amarthria*, as described and illustrated by Erdtman (1943, 63: "41 by 32 μ ," and Pl. II, fig. 25, showing a lateral view of a grain after loss of pore membrane), but it exhibits the complicated horizontal pitting reported elsewhere in the order only for species of *Centrolepis* (Erdtman, l.c., 55). If we follow Erdtman, *Lepyrodia* combines simple and advanced characteristics; however, the pitting is quite distinct from anything recorded in the Gramineae.

Material: Ohaupo, south end of Rukuhia Bog, Waikato, D. Petrie, ex Kew Herbarium; EM, KOH. Grains pale yellow when acetolysed, the endexine a little lighter in colour.

North of Lake Tangonge, near Kaitaia, H. B. Marthews, 1913; acetolysed (material kindly prepared by Miss Teresa LeCroix, Harvard Biological Laboratories, 1952).

Range, etc.: A tall herb (up to 10 feet) restricted to bogs (neutral to very acid) of Middle Waikato and interior of Chatham Islands. In the Waikato communities it is best preserved on Tuatua moana (Moanatuatua) where thousands of acres of irregularly domed blanket bog are still dominated by it, despite burning and marginal draining. Its great recuperative power was over-tested at Tangonge in North Auckland, so only pollen in the peat remains to prove it grew there until recently. As long as the water level is high in a bog, the plant recovers rapidly after flash fires; surface parts are provided with protection from water-logging (as the peat grows upwards) by a collar of spongy air-tissue.

Flowering takes place late in September: pollen fairly abundant.

Fossil: Abundant, with pollen of the associated *Hypolaena*, in Middle Waikato peats. Distinguished from the latter by thinner exine and much smaller pits. The records by Harris and Filmer (1946, 12) should refer to these species, as *Leptocarpus* is strictly coastal in this district.

LEPTOCARPUS R. Br.

Pollen undescribed. Material previously keyed (Cranwell, 1942) proved to belong to the Cyperaceae, the pollen being intrusive on herbarium inflorescences. The following description is based on fresh material, collected at anthesis by the writer. The grains are seen to be typical of the family.

L. simplex A. Rich.: Jointed Rush; Oioi

Pl. 3 (14); text figs. 13a, b.

Grains closest to those of *Lepyrodia*, but significantly smaller, ranging from 27–35 (40) μ and averaging $32 \times 26 \mu$, ellipsoidal to weakly pouch-shaped, the exits less symmetrically placed, about 6–10 μ wide, projecting little beyond the body of the grain. Exine under 2 μ thick, smooth, strongly pitted (foveolate), the pits vertical (or sometimes slanting), from 2–4 μ apart and about 1.3–1.5 μ in diameter.

Material: Manapouri, November 18th., 1949; Watson and Lucy Smith (L. M. C.); lactophenol with various stains; M.G.

Range, etc.: A stiff, jointed, rushlike herb found in the lowlands of the four main islands, mainly coastal, but found inland at Rotorua (thermal area) and at Lake Manapouri, for instance, probably carried there on muddy feet of sea-birds. In spite of these records, high frequencies of pollen will probably have valuable indicator-value in the study of shore-level changes, etc. In the Hauraki area, for instance, it grows at present only within touch of tide-water, while *Hypolaena* and *Lepyrodia* are restricted to neutral or very acid bogs inland to the south. Flowers spring to early summer; pollen pale yellow, more abundant than in the above-mentioned species.

Fossil: To be expected especially in submerged peats of the Auckland Isthmus, and in the Far North. Abundant, for example, in fibrous (sedge) peat collected at Rangiputa for the author by the late Mr. E. T. Frost.

HYPOLAENA R. Br.: "Bog Rush"

H. lateriflora Benth. (*Calorophus elongatus* Labill.)

Pl. 3 (16, 17); Text figs. 14a-d.

As in the preceding species, but larger and more uniformly pouched. Grains ca. $48 \times 41 \mu$, with extreme range of $36-56 \times 34-48 \mu$, with exit included. Exine rigid, up to 3μ thick, dense, smooth, tectate-foveolate, the pits or lumina (some slanting) about 1.5μ across and separated by wide muri ($3-4.3 \mu$). Exits wide, with ragged margins, rimmed by granules up to 1.7μ in diameter which separate widely on distension or rupture of the pore-membrane. Constriction below rim very characteristic.

Material: Ex Gray Herbarium; G. Einar DuRietz, (collected 1928); E.M. Tauhei (Waikato); R. A. S. Browne, Sept. 28, 1939; iodine. Freestone Hill (Manapouri district); L. B. M. and L. M. C., Dec. 29, 1939; GV, lactophenol with various stains.

Range, etc.: From North Cape southwards, from sea level to over 5000 feet, extending to Stewart Island and Chathams, as also to Australia and Tasmania (Cheeseman, 1925, 286): grows on acid peat or mineral ground (e.g., eruptive material from Volcanic Plateau mountains), and is destroyed by burning and draining, as formerly at Lake St. John, Auckland. Flowers sparsely, Sept.-March, according to locality and altitude. A small, possibly edaphic form, var. *minor*, occurs at high elevations.

Fossil: First recorded by Cranwell and von Post (1936, 317), with high frequencies for the pollen reported from most of the southern peats investigated.

Some Centrolepidaceous grains may have been included in these totals, but these can usually be identified separately. The pollen has also been observed by the writer in Waikato peats.

CENTROLEPIDACEAE

Hieronymous (1873, 192, 205) noted a mesh of ridges ("Leisten") in the exine (cf. *Centrolepis* below), and described the pollen as "globosum, sublaeve vel subtilissime areolatum, uniporosum. . ." He considered that the pore membranes, which were retracted when dry, lacked exine.

As already indicated, the pollen is monoporate, and very similar to that of the previous family. The grains are spheroidal when expanded, from $20-40 \mu$ in diameter, usually more elongate when unexpanded and then flattened on the weaker (distal) side. Pore or exit circular or compressed (text figs. 15-17), lacking the constriction seen in the Restionaceae. Exine smooth, tectate, reticulate-foveolate (pitted), tending to be thick and rigid, but tearing around the exit area like an eggshell.

Their shape, smaller average size, less clearly defined pores, and particularly the character of the exine, separates them from the Restionaceous pollen described. Erdtman (1943, 55; Pl. I, fig. 5) has given descriptions of *Gaimardia* and *Centrolepis* pollen and has figured a grain (lateral view) of *G. setacea*. Descriptions of the pollen of South American species of *Gaimardia* (*G. boliviana* occurring as a northern outlier at 5000 metres altitude) are not available, but Castellanos (1945, Tab. II, fig. I) gives a useful map for world distribution of the family.

No published records for fossil pollen in the family are known to the writer.

CENTROLEPIS Labill.

Erdtman (1943, 55) was the first to observe that the lumina or pits "are connected by shallow grooves" (cf. Restionaceae). This is a very important feature in this group, and of great potential value for pollen analysis.

C. strigosa Roem. and Schult.

Pl. 3(18).

Grains $23-28 \times 16 \mu$, often flattened; exine fragmented over the pore membrane, and tending to split widely and characteristically when over-expanded: lumina vertical or slanting, about 1.5μ in diameter, and about $1-3 \mu$ apart.

Material: Bluff Hill, T. Kirk; F.

Range, etc.: Confined in New Zealand to Bluff Hill and Oreti Beach, Otago. Abundant in Australia and Tasmania. Flowering in summer.

PSEUDALEPYRUM (Hieron.) Dandy

This genus is said to be very close to *Centrolepis*, and has much the same range, being found in colder parts of New Zealand and its dependencies, as also in Tasmania. Gilg-Benedict (1930, 32) treated the following species in *Alepyrum*, while Cheeseman (1925, 288) kept them in *Gaimardia*. Dandy's classification is followed here.

P. ciliatum (Hook.f.) Dandy var. *genuinum* Dandy (*Gaimardia ciliata*)

Text fig. 15.

As in *Centrolepis*, but larger, averaging 33 μ ; pattern coarser and continuous over the whole surface.

Material: Mt. Arthur, T.F.C.; GV.

Range, etc.: Occasional in North Island bogs, around 5000 feet altitude; abundant in South Island, Stewart Island, and the Auckland and Campbell Islands; often at sea level in bleaker areas. Summer flowering.

P. pallidum (Hook.f.) Dandy

Text fig. 16.

Grains spheroidal to ellipsoidal, about 28–34 μ in diameter; exit about 20 μ in diameter, with granular rims; exine 1.5 μ thick, with distinctive pitting, the lumina larger than in *Lepyrodia*; very brilliant clavate columellae. Pits larger under tectum, often coalescing.

Material: Blue Mountains, Otago; D. Petrie; acid Fuchsin.

Range, etc.: Occurring sparsely from Volcanic Plateau mountains southward to Blue Mountains, and on Campbell Island (Cheeseman 1925, 289, under *G. pallida*).

GAIMARDIA Gaud.

G. setacea Hook.f.

Pl. 3 (19, 20); text fig. 17.

Slightly larger than in the preceding, 30–36 μ in diameter; exine weaker, easily crumpled, the walls often folding over the pore area to make it appear three-armed (trichotomosulcate). Pits crowded, 1 μ or more in diameter, often linked.

Erdtman (1943, 55), figures a grain measuring 35 x 31 μ , and mentions the fine pitting of the exine.

Material: Arthurs Pass, 1949, C. Skottsberg; EM.

Range, etc.: Mountain bogs of South and Stewart Island; flowering in late summer.

HYDATELLA Diels

H. inconspicua Cheesem.

Pollen not seen. According to Cheeseman (1925, 287) male flowers have not been collected. It is hoped that material may be found as Mason et al., 1950, 84) have recently found the plant in swampy areas near Auckland: according to one of the authors (Robert Cooper, private communication) flowers should probably be sought for in spring.

The only references to *Hydatella* pollen known to me are those of Hooker (1855–1860, p. 78, Pl. 138), who shows three small ellipsoidal grains of "*Trithuria submersa*" (*H. inconspicua*), all marked with a suggested fold or exit: he states that the pollen is globose.

Range, etc.: North Cape district (Cheeseman, 1925, 287); also near Kaipara Heads (Mason et al., 1950).

ORDER 5: GLUMIFLORAE

GRAMINEAE: GRASS FAMILY

The pollen grains in this very large group are typically spheroidal, mainly under $40\ \mu$, with a thin featureless exine of reduced type. Thus far, the description fits the sedges as well, but similarity ends here. First, all the grasses are equipped with a highly specialized and very conspicuously ringed pore of a type most nearly approached by that of the Flagellariaceae (Juncaceae); and secondly, they are free, whereas the Cyperaceae all exhibit a curious compounding distinct from that in normal tetrads, so that up to four ragged pores appear on the one grain.

Morphologically, therefore, there is strong pollen evidence in favour of separating these two major families, as has been done by Wettstein (1935), Skottsberg (1940), and others.

The grasses have received increasing attention over the last 100 years. Fritzsche (1832, 22, 39) was apparently the first to report the single pore, referring to both pre-formed exits and canoe-shaped furrows (the latter opinion relinquished by 1837, 726), and describing a faint granulation of the exine. Malpighi (1686) had seen the same fold, and reference to it as an essential feature of the grain crops up persistently in the literature.

Purkinje (1830, 28, 33–34) dealt with several genera but merely noted that their pollen was “pellucid.” Mohl’s descriptions (1834, 52, 77) referred especially to granulation (?), and to the projecting pore with its thickening. Edgeworth (1877, 10) failed to find a pore in *Lagurus ovatus* but gave measurements ($7\text{--}8/6000$ inch = ca. $29.6\text{--}33.9\ \mu$).

Finally, Fischer (1890, 23), and Wodehouse (1935) in particular, dealt in detail with the unique pore-apparatus, and the latter writer provided numerous descriptions and illustrations of grains as well as doing much research into the rôle of grasses in causing hayfever.

Division is of the successive type. According to Schnarf (1931, 266), development and position of the pollen mother cells are very unusual, since these lie like sectors of a circle around the mid-point of a young anther, as seen in cross-section. The walls are lost even before the pores appear on the young grains, all of which are strung in their tetrads along the wall of the anther. Drahowzal (1936) confirmed these observations in her studies of 3

grasses, amongst them *Avenastrum decorum*, in which (l.c., Abb. 11, b) the crowded lateral position of the grains, with their pores touching the walls, is clearly seen. The polarity of the grains is not clear: Miss Drahowzal states that it is unique in being independent of the plane of division of the pollen mother cell, but that there exists a relationship (possibly nutritional?) between pore position and an inner layer of the anther sac.

Pollen type: Monoporate, only exceptionally multiporate; globular to ovoidal, often collapsed when unexpanded; mainly under $35\ \mu$ in diameter, with extreme range of about $14\ \mu$ to $111\ \mu$ or more. Pore rounded, protruding, 2 to $9\ \mu$ in diameter, halonate; pore membrane smooth, thin, sometimes flecked, moat-like around a small operculum. Exine tough, thin (rarely $2\ \mu$), very distensible, psilate-scabrate, flecked with faint reticulation. Intine thickest at pore end of grain. Contents granular with hyaline bodies lying opposite the pores.

Size may vary but it tends to be uniform for any one method of preparation, unless aberrant grains are present (see Firbas, 1937, Tab. 1 and Abb. 1): Erdtman (1944a, 77) describes 5-pored grains of the hybrid cereal *Triticale Rimpau* which are 91 by $78\ \mu$,

whereas normal grains are as small as $39\ \mu$ in diameter.

Text fig. 18. After Erdtman, 1944a, Fig. 1, 11.

Giant grain of *Triticale Rimpau* with four supernumerary pores.

Firbas (1937, 454) gives very low average figures for *Zea Mays* ($66.5\ \mu$, KOH), whereas Erdtman (1943, 58) reports $111\ \mu$ for the same species (acetolysed), but is eclipsed by Hindenburg’s (1897, 164) and Pope’s (1925, 65) measurements of $135\ \mu$ and $160\ \mu$, respectively. Excessive size here appears to be linked with gross distension of the membranes.

Firbas (l.c., 448) showed further (from the study of 215 species) that the grains of wild and cereal types may be separated on the basis

of size and exine thickness, and this has proved of great significance in separation of cultural and wild grassland phases in earlier vegetation in the Northern Hemisphere. Welten (1944, 44; Abb. 11) found cereal (but cf. *Elymus*) pollen from as early as 2500 B.C., based on the chronology of the laminated Faulensee sediments in Switzerland.

In an earlier paper (Cranwell and von Post, 1936, 317) it was shown that the grains of the dominant southern grasses could be separated to some extent on size and pore characters: "(a) the *Danthonia Raoulii* type, representing tall tussock grassland of cold wet areas, and (b) the *Poa caespitosa* and *Festuca novae-zelandiae* (type), the dominants of existing dry steppe. . . ." Identification of fossil grains is of course a different matter, since many unknowns with quite different ecological requirements could very well have identical types of pollen. Geisler (1945), who set herself the task of approaching the problem from a knowledge of a large series of grasses from different ecological settings, was still unable to make much use of size as a distinguishing factor within the series. Striking differences were noted, but whereas most of the aquatic species, for instance, had small grains, these were paralleled by *Sporobolus* and *Koeleria* of the prairie, while the single large-grained example, *Zizania aquatica*, was also matched by several of the prairie species. The tendency to larger size in the latter at least led to the conclusion that "if the peaks fall into the lower range of grass pollens, i.e., 19-39 microns, prairie conditions can hardly be associated." The difficulties met by American workers in trying to trace climate changes as possibly indicated by fossil grass pollen frequencies is discussed by Erdtman (1943, 62), amongst others.

The grasses are all wind-pollinated, apart from cleistogamic exceptions such as are mentioned by Hackel (1887, 8), Wodehouse (1945, 36), and Werth (1911), who dealt with Antarctic species whose florets may never open on sunless islands. Vast quantities of pollen are produced, and in some species the grains are highly toxic, even if, as in maize, they are rarely known to cause hayfever.

Grass pollen is sought by bees: of 1000 honey samples studied by Zander (1935, 114), for instance, almost 50 per cent had this impurity: even the heavy maize pollen was represented.

Pollen production in maize, according to

Kirchner (1911, 32) is estimated at 50 million grains per plant. According to Wodehouse (1945, 36), the pollen grains of most, if not all of the 4500 species, "appear to be capable of sensitizing hayfever patients . . .," the common characteristics (i.e., 5) being "buoyancy, abundance and allergenic toxicity."

Vast quantities of pollen in the air may settle and be sealed in lakes, swamps, and bogs: as already indicated the resistant exines may survive in perfect condition. Very many references to fossil or sub-fossil grass pollen have been made during the last 25 years and they have world-wide range, Couper (1951b, fig. 2) giving New Zealand records back into the Eocene.

NEW ZEALAND GRASSES

These have been briefly referred to by Cranwell (1942, 294), considerable size-range being recorded from acetolysed and other material (28-70 μ): some genera at least are therefore characterized by grains as large as those of the cereals. Grass pollen was caught on atmospheric slides during 1937-1938 but no identifications were made. In addition to native grasses, there are many introduced species, including most of the major sources of hayfever (e.g., Timothy, Kentucky Bluegrass, and Red-top).

Range of size is given for 30 species in the tables. Much more work could be done on size of pore membrane and annulus, and ratio between size of grain and pore.

See Table 1, pp. 74-75.

The pollen grains of the following species are taken as the "type" for the family in New Zealand.

Arundo Kakaho Steud. (*A. conspicua* Forst.): Toetoe (cf. Cranwell, 1942)

Pl. 2(1), Pl. 4(1-5); text fig. 21.

Grains monoporate, 36-46 μ , broadly ovoidal to spheroidal when moderately expanded, the walls often folded. Exine thin but firm and elastic, with a fine rod-layer and slight roughening of surface. Pore at broader end, or asymmetrically placed, up to 5 μ over-all, including the 3.4-4 μ -wide pore membrane.

Material: Collected by H. Carse, 1913; EM, MG.

Range, etc.: The tallest native grass, up to 10 feet high; often confused with the taller, denser Pampas grass (now naturalized in the North). Common in wet patches and swamps of the 4 main islands and the Three Kings Islands. Summer-flowering.

ORDER 6: JUNCALES

JUNCACEAE: RUSH FAMILY

According to Wodehouse (1935, 322), the rushes are so isolated and so reduced that it is difficult to know what affinities their pollen grains may show. The reduction of exine and aperture characteristic of the family is usually traceable to anemophily, but Pohl (1929, 258, 281) states that still other agents are involved. Werth (1911, 292) also refers to cleistogamy, linked with excessively low pollen production, for the Antarctic *Juncus pallidus*.

While Wodehouse, Pohl, and Hutchinson, working from rather different angles, consider the family advanced, Erdtman (1944b, 167) would seem to place the weakly pored tetrad-bearing Thurniaceae and Juncaceae as a "primitive link" with the rare members of the Cyperaceae which have specialized pores of rather graminoid appearance.

Juncaceous pollen has a rich literature and is well known from many floras. Briefly, it may be described as follows: Grains inaperturate, occurring in medium-sized tetrads, typically tetrahedral, rarely of cross or rhomboidal type; components enclosed in a continuous envelope of exine, but lacking exine on the contact walls. Exine thin, smooth, very distensible around the rudimentary pores (distal) which may be indicated mainly by the position of hyaline bodies below or by local protrusion or collapse of the exine. Intine thick.

An interesting feature of these Juncaceous tetrads is the absence of exine on the cross-walls. The outer wall of the tetrad, as in the Cyperales, is derived from the original mother cell, as shown first by Wille (1882), and is thus continuous from one component to the next. In this family, however, the inner walls are not absorbed, as in the Cyperales, to form "pseudomonads."

The early investigators failed to find pores (Fritzsche, 1832, 29; Mohl, 1834, 37, 77; Aldridge, 1842, 592; Schnitzlein, 1843-1846, see fig. 4, showing outlines of typical cross and tetrahedral tetrads; Fischer, 1890, 21), but Edgeworth (1877, 5), who was familiar with *Juncus effusus* alone, recognized them, as did Wille (1886). Most investigators now describe and figure some break or depression, e.g., Sears (1930, 103), who refers to a "faintly broken area as in *Carex*," and Wodehouse (1935, 320, who emphasizes that the porelike area is derived from a furrow. As in the sedges, the tetrad walls are provided by the pollen mother cell: both families are linked in addition by

simultaneous division, seen also according to Täckholm and Söderberg (1917, 7), in the Liliaceae, Iridaceae, Commelinaceae, and Orchidaceae, and a few other families. The same authors quote the view of Lubimenko and Maige (1907) that successive division, so common in the monocotyledons, is older, and they state their own conclusion that simultaneous division in the Enantioblastae, Cyperales, and the orchids is of secondary development, as also in irises, rushes, and asphodels.

Zander (1935) gives excellent photomicrographs of tetrads of *Luzula pilosa* (Pl. 5, figs. 30, 31) measuring $33.2 \times 30 \mu$ dry, and $38.2 \times 35.7 \mu$ moist, and of *Juncus acutifolius* (Pl. 5, fig. 32), while in figs. 30, 33, and 35 of tetrads in Bavarian honey the hyaline bodies pressing behind the "pores" are very clear. Selling (1947, 348, and Pl. 54, fig. 891) also gives a photomicrograph of *L. hawaiiensis* and provides a wide survey of the literature.

Selling (l.c., 349) found no fossil pollen of this family in Hawaiian peats. The delicate grains, or their cross walls, may have been destroyed by acetolysis, but Conway (1947, 181) suggests another explanation in reporting high frequencies of pollen of this type (at 180 cm.) from Ringinglow Bog, near Sheffield. She found that the grains were best preserved in peat which had grown rapidly, without setbacks from humification. Faegri and Iversen (1950, 133) do not refer to preservation specifically, but key rush pollen amongst inaperturate grains.

No tetrads of this type have been reported (as such) from New Zealand peats.

Hafsten (1951) has also failed to find them in Tristan da Cunha deposits. Couper (1951a, fig. 2), however, gives *Juncus*, at least, a long fossil record in New Zealand.

The few references to strictly native material are derived mainly from Hooker's "Flora Antarctica" (1847), viz., for *Rostkovia* (*R. magellanica*, p. 81, "Pollen tetragonum, intus 3-4-granulosum, flavum. . . ." and *R. gracilis*, p. 83, "Pollen flavum, obtuse tetragonum. . . ."), and for *Luzula crinita*, with three (yellow-tinted) tetrads figured, though only three of the components appear to have been recognized by Hooker (Pl. 48, figs. 5, 6): "Pollen stramineum, globosum, immatureum trigonum, hyalinum, nucleo opaco, intus tripartito." His figure 6 of a grain with tripartite banding is of the type referred to by Bennett

(1875, 115), Schnitzlein (1843-1846, fig. 4), Edgeworth (1877), Buchenau (1888, fig. 1, E, a), and others familiar with the curious appearance of fresh material in which the thick inner walls of intine are always very striking.

Cranwell (1942, 307) described the tetrads as follows: Components with one furrow-pore area, tetrahedral; "pore," circular, distensible, reinforced by hyaline bodies. Exine almost or quite patternless. . . Over $50\ \mu$ — *Juncus* spp.; $36\ \mu$ or less (organization clear) — *Luzula* and some grains of *Rostkovia*; organization obscure — *J. maritimus* and *Rostkovia*. It was also pointed out that *Juncus* and *Hedycarya* (Monimiaceae) tetrads might sometimes merge with the acolpate (inaperturate) class.

LUZULA DC.

The grains of this genus will not be described further in general terms except to record size, as in *L. campestris* (Hansgirg, 1897, 19: tetrads $40-50\ \mu$, components $15-20\ \mu$ [the latter figure seemingly inaccurate]; Wodehouse, 1935, 321: $25.1-29.6\ \mu$ for individual cells and $38\ \mu$ for a tetrad [Pl. 5, fig. 7], and further, $36-41\ \mu$ [1943, 7]). For *L. hawaiiensis*, Selling (1947, 349) records an average of $42\ \mu$.

L. campestris DC. var. *australasica* Buch.: Woodrush

Pl. 4, fig. 6.

As for the genus: tetrads tetrahedral and conglobate, $34-36-40\ \mu$ over-all, components $28 \times 20\ \mu$, often rhomboidal or crossed ("paarweise gekreuzt," Buchenau, 1906, 4, and fig. 7, C), components of the latter measuring about $34\ \mu$ in polar depth by about $12\ \mu$ on narrow contact faces. Exine exceedingly thin, perfectly smooth, tectate, minutely "pitted," appearing faintly granular under high powers, but showing on immersion a pattern of crowded straight rods opening up slightly to about $0.5\ \mu$ apart over the distal faces. Pore areas indicated chiefly by the beading of the exine and by depression of the surface, but also, where contents are preserved, by one or more shining plugs about $4\ \mu$ in diameter. Intine very thick around but not under the "pore," and between the components, giving in section the crested appearance commonly seen in older illustrations.

Material: MG. The size of the plugs is of course dependent on the state of expansion of the grain.*

Range, etc.: The species, in its many forms, is widely spread from the Three Kings (Oliver, 1948, 219) to

*Fritzsche (1832, Fig. 12) gives an interesting illustration of the escape of the pear-shaped hyaline bodies from the distal side of each grain of a tetrad of *Luzula campestris*, swollen in acid and seemingly subjected to pressure.

the subantarctic islands (var. *crinita*). Cheeseman (1925, 301) gives 8 species but stresses close intergrading. *L. hawaiiensis* also belongs to the *campestris* assemblage.

Pollen of another species (unidentified), prepared in the same way, had thinner exine (about $0.5\ \mu$), pattern unmodified over whole surface, and larger plugs. Despite differences of this kind, it would be very difficult to distinguish between tetrads of different species in atmospheric or peat studies.

JUNCUS L.

J. antarcticus Hook. f.: Rush

Tetrads spheroidal, tetrahedral, about $50\ \mu$ in diameter, the components fitting snugly together, about $30-36 \times 25\ \mu$. Exine very thin, tectate, smooth, vaguely pitted (psilate) over whole surface.

Material: G. E. DuRietz #1353; KOH.

Range, etc.: Montane, from Volcanic Plateau southwards to Otago, descending there to sea level, as also on the Auckland and Campbell Islands. A very distinct species, according to Cheeseman (1925, 298).

J. maritimus Lam. var. *australiensis* Buch. Pl. 4(7).

As in the preceding, but with smaller tetrads ($36\ \mu$) and thinner exine. Components often difficult to distinguish.

Material: Thames, T. F. Cheeseman; MG.

Range, etc.: Coastal, or occasionally by inland thermal waters: North Cape to Westland and Canterbury.

Interesting notes on the sparse yellow pollen and self-pollination of the subantarctic *J. pusillus* (also native to New Zealand) are given by Werth (1911, 292, 293; Taf. 24; 14).

ROSTKOVIA Desv.

The pollen notes on both species by Hooker (1847), who did not refer to the tetrads as such, have already been mentioned, together with the writer's notes on size and the obscure organization of the components as seen in some grains (1942, 307).

R. gracilis Hook. f.

Tetrads consistently rounded, typically tetrahedral, much as in *Luzula* and *Juncus*, but occasionally cohering, averaging about $36\ \mu$ in diameter; exine perhaps thinner, completely smooth, the faint structural rod pattern clearly perceptible only with oil immersion. Pores obscure. Intine mainly thin; hyaline plugs present but not very conspicuous.

Material: Campbell Island, T. Kirk; GV ($34-40\ \mu$). Hollyford Valley, J. E. Holloway, ex Herbarium Botany Division, D. S. I. R., Wgtn.; MG ($36-38\ \mu$).

Range, etc.: South Island, Auckland and Campbell Islands; usually at high altitudes. Summer-flowering.

FIGS. 19-21: GRAMINEAE. FIG. 22: JUNCACEAE. FIGS. 23-34: CYPERACEAE.
 $\times$ ca. 900 unless other measurements given.

19: *Danthonia australis*, a, c lateral, b, polar view, 36 μ . 20: *Agrostis Dyeri*, 24 μ . 21: *Arundo Kakabo*, pore in section, operculum retracted ($\times 1125$). 22: *Rostkovia magellanica*, 44 μ . 23, a-d: *Oreobolus pectinatus*, a unexpanded; b-d expanded, showing intine, contents and hyaline bodies. 24: *O. strictus*, expanded (note crushed sister cells). 25: *Carex secta*. 26: *C. appressa*. 27: *Uncinia unciniata*. 28: *U. riparia*. 29: *Scirpus nodosus*, a surface, b lateral section, showing contents (stippled) and sister cells cut off by "callus" of intine. 30: *Carpha alpina*, showing dominant pore; tectum indicated. 31: *Schoenus pauciflorus*, pore area depressed; note long "furrows" (an unusually large grain). 32: *Vauthiera australis*, showing smooth tectum (diagrammatic). 33: *Cladium complanatum*, with rods projecting over 4 or 5 areas. 34: *C. Sinclairii*, 30 μ , see p. 46.

R. magellanica Hook f.

Text fig. 22.

Much as in *R. gracilis*, but not identical: Grains about 44 μ (spheroidal) to 50 x 30 μ ; tetrads variously arranged. Exine exceedingly thin, foveolate, slightly roughened. Pores fairly conspicuous, underlain by hyaline bodies.

Material: East Falkland (Falkland Islands), C. Sg., 1907; MG. Ex herb. Gothenburg Botanical Garden.

Range, etc.: Auckland and Campbell Islands, the island of South Georgia, Tierra del Fuego, and alpine Ecuador (Castellanos, 1945). The preceding species is sometimes referred with two others in this genus, to *Marsippospermum*, leaving *R. magellanica* to form a monotypic genus.

ORDER 7: CYPERALES

CYPERACEAE: SEDGE FAMILY

The divergent nature of Cyperaceous pollen was described by Elfving (1878), Wille (1882, 1886), and Juel (1900), and it has been found to be uniform in the order. The "grain" is really a degraded tetrad, contained (as in the rushes) by the wall of the pollen mother cell, in which, in *Carex*, for example (Juel, l.c.), the three smaller of the four free nuclei are crowded into one end of the mother cell and there degenerate, leaving the fourth nucleus.

and others consider this tetrad-equivalence as strong support for closer relationship between this order and the Juncales.

Erdtman (1943, 46), in emphasizing that the pollen is "not homologous with ordinary pollen grains but with pollen mother cells instead. . .," shows that orientation, in consequence, cannot be designated as distal or proximal in the usual sense. His text figure 3 (1,2) shows these truly compound grains compared with a tetrahedral tetrad (unspecified): the comparison would be especially striking if made with a *Pseudowintera* tetrad, since it is characterized by monoporate components, as in the rushes. As has been seen, the rushes develop cross walls, but may have even further reduced pores.

Historically, there has been a long sequence of references to the pollen, beginning with those of Purkinje (1830, 29, 34), descriptive of the acuminate grains common in the family ("caudulata *Scirpi*"), followed by those of Fritzsche (1832, 11, 32) who found no preformed exits at all, and Mohl (1834, 47), who elegantly figured three grains with more or less "vorstehende Warze" instead of a pore, these projections being classed by Esenbeck (1842, col. 1-2) as "rimula simplici." Edgeworth (1877, 5) followed up the droplike type and added an unusually perceptive comment for *Carex*: "somewhat prismatic with a pore in each facet, which is the form of the Junaceae." His figures for *Carex* and *Cyperus* suggest long-furrowed forms which occur in the family (cf. Text figs. 29-31).

Fischer (1890, 26) made a great advance, distinguishing the granular exits, and noting that they occurred regularly scattered over the surface; he also pointed out that the intine was thin under the exits, but thick in the "angles" of the grain. Caul-like deviations in *Cladium Mariscus* were indicated (cf. Erdtman's figure, in press).

FIG. 35. *Scirpus lacustris*: emergence of strong and weak nuclei (a-c), the latter sealed off by intine (d, e). After Piech (1924): see also Schnarf (1929, Abb. 3).

A type of simultaneous division has taken place, but anything in the nature of a plate is soon reabsorbed. The monadal appearance that results cannot be confused with that of any other monocotyledonous pollen as long as the pores (up to the four of a normal type of tetrad) can be traced. Skottsberg (1940, 654)

The development of sedge pollen is its most distinctive feature; owing to reduction connected with anemophily the grains may be bafflingly nondescript. They may be placed in their family in peat studies, but generic identifications are usually difficult, or impossible. In *Carex* and *Oreobolus* the 4 vestigial pores, indicated by roughened areas of the exine, may be quite distinct, especially after staining, but many other genera appear to be either completely poreless or else monoporate, with the pore at the broad end in more or less graminoid fashion (Erdtman, 1944b, 167). Cranwell (1942, 294) attempted to key the New Zealand genera but found the range of furrow-pore or vaguely porelike areas very elusive as a basis for classification. Selling (1947, 7, 59), dealing with most of the same genera, but with the addition of *Rhynchospora*, keyed their pollen (a) amongst "apparent" inaperturate monads, and (b) more precisely, in his pseudomonad group, characterized by "a few, often indistinct exits of diffuse margins. . . ." Faegri and Iversen (1950, 134) found the first grouping practical for pollen-analytical work in northwestern Europe.

Wodehouse (1935, 351) noted adaptive likenesses between anemophilous grains of ash, poplars and sedges, and Iversen (1946, 198) assures us that the last two groups have been confused in some peat studies.

Cranwell and von Post (1936, 317) also warn against confusion of sedge grains (*Uncinia* type) with those of *Nothofagus Menziesii*. For a wealth of references to sedge pollen in fossil and sub-fossil deposits attention should be given to reviews of the literature by Gams and by Erdtman. Recognizing the family's ecological importance, especially as an indicator (with the grasses) of open country, von Post was quick to admit sedge pollen to the percentage sum in pollen statistics and this course is now widely followed. Cranwell and von Post (1936, 319, 321), for instance, use the predominance of grass-sedge pollen in southern New Zealand to delimit Zone I, the period of grassland dominance after the retreat of the glaciers, and before the return in force of either podocarps (Period II), or of beeches (Period III). Reference to distinctive features in *Carex* and in *Carphe* (whose pearlike grains had already been figured by Auer, 1933, Abb. 55, figs. 33, 34) was made in the same paper.

As already stated, most of the genera represented in New Zealand have received attention elsewhere, but there are very few pollen

notes on the native material. The first to publish descriptions was Hooker (1844-1847) who described the pollen of *Oreobolus pectinatus* as "hyalinum, stramineum, tri-tetragonum, angulis obtusis, intus granulis opacis tot quot angulis. . . ." while Cranwell (1942, 294) later referred to this genus, together with *Carex*, *Carphe*, *Cladium*, *Eleocharis*, *Desmoschoenus*, *Lepidosperma*, *Mariscus*, *Schoenus*, *Uncinia*, and *Fimbristylis* (l.c., 293).

Over 3000 species are known, and of these about 120 are found in New Zealand, *Uncinia* and *Carex* being especially richly represented. Pollen from each genus was sought, but it was not possible to study very many species in detail. The individuality of certain minor types noted here may thus be overstressed through lack of study of the intermediates which undoubtedly occur. It is clear, however, that there is a certain narrow range of difference which should repay intensive study.

Pollen types: Pollen units spheroidal to gourd-shaped, medium-sized, 30 to 60 μ ; exine very thin to thin, pale in colour (acetolysed), faintly granular to foveolate, often with larger gemmae associated with the exits. Pores (exits) weak or obscure. Intine very thick at broad end and in "angles" of grain.

It is too early to offer a key to all genera and species, but the following groupings should prove useful as a guide to future work.

Pollen characters of 28 native species are summarized on p. 75 (Table 1), under both "inaperturate" and "pores rudimentary."

KEY TO POLLEN TYPES IN THE NATIVE CYPERACEAE

1. Grains pear-shaped or paraboloid
 - All pores developed (Type A)
 - Oreobolus pectinatus* 27-37 μ
 - O. strictus* 45 x 30 μ
 - Basal pore dominant (Type A-B)
 - O. Pumilio* 38 x 21 μ
 - Carex* spp. 27-50 μ
 - Uncinia* spp. 26-40 μ
 - Scirpus nodosus* 30 μ
 - S. frondosus* 40 x 28 μ
 - Eleocharis gracilis* 32 μ
 - Pores lacking or obscure (Type B)
 - E. sphacelata* 50 x 46 μ
 - S. sulcatus* var. 26 x 22 μ
 - S. medianus* * 40 x 36 μ
 - Gabnia lacera* 36 x 26 μ
 - Carphe alpina* 34-50 μ
 - Schoenus apogon* 37 x 30 μ
 - S. pauciflorus* 40 x 20 μ
 - O. strictus* * 45 x 30 μ
 - Carex* spp. 27-50 μ

2. Grains spheroidal

Pores clear, 4 or more (Type C)

Pores 4-(5 rare)

*Cladium complanatum*28 μ

Pores 4 only

*C. articulatum*23-33 μ

Pores lacking or obscure (Type D)

Pattern fine

*C. teretifolium*23 μ *C. Sinclairii*25 μ *Vauthiera australis*32 μ *Mariscus ustulatus*33 μ *Lepidosperma* (2 spp.)32-45 μ *Scirpus* spp.26-40 μ

Pattern coarse

*Fimbristylis*27 x 30 μ

* variable.

While these groupings are elastic, it is clear that two main types occur. Overswelling of the grain may cause the pore areas to appear more prominent, as in Plate 4 (12), showing a pseudomonad of *Oreobolus* overexpanded in KOH.

Of the following, *Oreobolus*, *Carex*, *Uncinia*, *Carpha*, *Schoenus*, and *Cladium* are of most importance for pollen analysis. However, none of these genera are referred to by Harris and Filmer (1946, 12), who give high frequencies for sedge pollen from Hauraki peats: neither does Couper (1951a, fig. 2) indicate the types met in extending the record in New Zealand as far back as to the Cretaceous.

OREOBOLUS R. Br.

As already mentioned, the pollen of New Zealand members of this genus has been mentioned by Hooker, and by Cranwell (1942, 294). Auer (1933) and Selling (1947) failed to describe or recognize *Oreobolus* pollen in peat studies in Tierra del Fuego and Hawaii respectively, and there are no published notes on the pollen of the New Guinea form. All of the species are peat-formers. Pollen of *Oreobolus* type occurs freely in New Zealand peats.

Pollen type (A-B). Pseudomonads, typically pear-shaped, but sometimes spheroidal; inaperturate, or more commonly with 4 roughened pore areas, one at the "base" and the other 3 near the middle of the grain. Exine tectate, under 1 μ thick, the delicate rods all lying within the tectum, but free, or joined in pairs over the pore membrane. Intine very thin, enclosing strong hyaline bodies at angles of grain.

O. pectinatus, Hook. f.

Pls. 1(6), 4(11-12); text figs. 23a-d.

Pollen as above, the grains measuring 27-30 x 18-25 μ (EM); 32-42, or up to 50 μ (KOH, excessively expanded): both slides from material collected by Dr. Greta Cone, on Mount Maungatua, near Dunedin, Sept. 15th, 1945.

Range, etc.: Cushion-plants; found isolated in north on subalpine sloping (soligenous) bogs of Te Moehau (just under 3000 feet altitude), and then abundant on acid substrata from Hikurangi and Maungapohatu southwards to the Auckland and Campbell Islands; descending to sea level in bleaker areas. Able to colonise acid soil directly, where there is sufficient rainfall, as on volcanic ash of Tongariro National Park and Mount Egmont, or on slopes near Lumsden, they are especially important as members of blanket and raised bog communities, but are not leading peat-formers, as only the small tough rootlets resist humification. Selling (1947, 351) assigns a much more important role to *O. furcatus* in Hawaiian montane bogs.

O. strictus Berggr.

Pl. 4(10); text fig. 24.

Grains more irregular, about 40-54 x 26-36 μ , tending to be drawn out in gourd fashion. Basal pore conspicuous, with larger rods (about 1 μ apart) than over lateral pores. Exine very thin, perforate over pores. Hyaline bodies very large and distinct in fresh material, one filling the narrow end almost completely, while two flank the basal pore in typical Cyperaceous fashion. Intine very thin.

Material: Waimarino, on peaty ground; collected by C. Sg. and L. M. C., Oct., 1938; GV.

Range, etc.: Tongariro National Park (as above) and Ruahine Range to Stewart Island, mainly montane and rarely common. Closely allied to the following, but with distinct pollen.

O. Pumilio R. Br.

Grains ovoidal (38 x 31 μ); smaller than in *O. strictus*, with thinner exine (0.5 μ over structureless areas) and finer, more crowded rods over the pores, only the basal pore being very clearly defined. Intine exceedingly thin; hyaline bodies barely indicated.

Material: Oct., 1938, C. Sg.; F.

Range, etc.: Local, from West Nelson to Otago; montane.

Comparative: *O. furcatus* Mann. About 34 μ . Maui, C. N. Forbes (Bishop Museum), March 8, 1919, KOH.

CAREX L.

Over 50 species are native, according to Cheeseman (1925). Their ecological importance may be judged from the writings of Cockayne (1928). Values as high as 48 per cent and 55 per cent of the percentage sum have been given for sedge pollen by Cranwell and von Post (1936, 336-347). These comprise records for *Carex* as also for some *Carpha*, *Oreobolus*, and *Uncinia*. In identification, shape, rather large size, "basal" pore (tending to be smoother in *Carex* than in *Uncinia*), and exine pattern, are taken into account. *Carex stricta*, described by Wodehouse (1935, 320), and *C. montis-Eke*, with measurements and illustrations in Selling (1947, 352; Pl. 55, figs. 901, 902) appear much the same.

C. dissita Sol.: A-B type

Pollen pear-shaped, about 48×33 ($36-56 \times 26-36$), with little trace of pores except at the broad end where the tectum of the very thin, delicate psilate exine tends to fragment, freeing numerous more or less coarse granules.

Material: Palmerston North, H. H. Allan, 1935 (pollen sample only); EM.

Range, etc.: Three main islands, often in montane bogs.

C. appressa R. Br.: averaging smaller, about 36μ ; more rounded with slightly stronger texture. Pollen slide ex Botany Division, D. S. I. R., Wgtn. *Text fig. 26*.

Range, etc.: Allied to *C. secta* (see tables) and *C. virgata*, but southern, from Banks Peninsula to subantarctic islands.

C. ternaria Forst.: pear-shaped, $33 \times 28 \mu$; pattern obscure; intine showing very strongly in GV preparation. *Pl. 4 (9)*.

UNCINIA Pers.

U. uncinata (L.f.) Kuekenh. *U. australis* Pers.

Text fig. 27.

As in *Carex dissita*, about $39 \times 32 \mu$, with weaker, collapsing exine and faintly but uniformly roughened surface. Pores obscure.

Material: Dr. A. Sinclair, Canterbury?; MG, and ex Herb. Bot. Div., D.S.I.R.; KOH.

Range, etc.: Widely distributed in different forms (cf. Cheeseman, 1925, 247). A good photomicrographic illustration of the pollen of Hawaiian form of the species by Mr. K. E. Samuelsson is given in Selling (1947, Pl. 55, fig. 900).

SCIRPUS L. (*sensu lato*)

Grains of A-B types, but usually paraboloid, with basal pore most conspicuous; size ranging from $26-68 \mu$ long (largest grains possibly aberrant) by $22-40 \mu$ at base. Exine exceedingly thin, patterned in rod-layer.

S. nodosus Rottb.

Text fig. 29a, b.

As above, $32 \times 25 \mu$; tectum persisting over pore area and tending to fragment without freeing the inner granules. Hyaline body, in thick intine, closed off by a non-exinous wall at narrow end of grain (cf. *Oreobolus*).

Material: Piha, L. M. C., Nov., 1938; GV.

Range, etc.: Abundant as far south as Stewart Island.

S. sulcatus Thouars var. *distigmata* C. B. Clarke.

Type B, paraboloid, $26 \times 22 \mu$, granules exceedingly fine; hyaline bodies discrete.

Material: North Ruahines, in bog at 2200 feet. A. P. Druce, Jan. 19th, 1946; Lp & S.

Range, etc.: Hokianga southward to Ashburton (Cheeseman, 1925, 223).

S. frondosus Banks and Sol.: Pingao

Pl. 4 (13-16).

As in *S. nodosus*, $40 \times 28 \mu$.

Material: Piha, L. M. C., Oct. 1938; GV.

Range, etc.: On foredunes of coasts of the 3 main islands and Chathams. Endemic.

GAHNIA Forst.

Pollen undescribed by Cranwell (1942) and by Selling (1947). The anthers are very papery and fugacious: pollen rather sparse.

G. lacera Steud. Cutty-grass.

Type B; grains ovoid, about $36 \times 27 \mu$, faintly patterned, with surface slightly roughened at most.

Material: Waitakere Range, 800 feet, L. M. C., Nov., 1938; MG ($34 \times 27 \mu$), Lp, and S ($34 \times 22 \mu$).

Range, etc.: Lowlands of North Island, flowering in winter and spring.

ELEOCHARIS R. Br.

The pollen has been described by various authors, amongst them Miss Kuprianova (1945, 44*) who described that of *E. acicularis* from the Volga area as $28.6-57.9 \mu$ and sometimes egg-shaped.

For an early paper on *Eleocharis* (and *Carex*) development, see Wille (1886, 46).

E. gracilis R. Br. (= *E. Cunninghamii* Boeck.)

Type A; grains pear-shaped, about 32μ long, with pores set near base.

Material: Riverhead (Auckland), C. Sg., Nov., 1938.

Range, etc.: Much as in *sphacelata*.

E. sphacelata R. Br.

Type B; $44-56 \times 45-50 \mu$; pores eliminated, or one at base of grain.

Material: Piha, L. M. C., Nov., 1938; GV.

Range, etc.: Margins of eutrophic waters in North Islands, local as far south as Stewart Island.

CARPHA R. Br.

The single native species, found also in Tasmania, eastern Australia, and the high mountains of New Guinea, is limited to acid

*I am indebted to Mrs. William Chamberlin, of Cambridge, for translating this Russian paper. It deals with about 50 monocots from the Volga area, or, in some cases, from Tashkent. Sedge- and grass-grain measurements are the chief original contributions.

substrata. As stated earlier, Auer (1933) has figured the pear-shaped grains of *C. schoenoides* in their fossilized condition. The writer studied fresh material of *alpina* as early as 1935: much pollen of its type was found in southern peats (Cranwell and von Post, 1936, 317). In Cranwell (1942, 294) the grains were first described as elongate ("curved at narrow end"); with flecked, i.e., granular, exine, etc. The size given, 46–56 μ , is higher than has been obtained from other material.

C. alpina R. Br. Text fig. 30.

Type B, 34–46 μ or more; pear- or gourd-shaped, sometimes ovoid, but usually asymmetrical. Exine granular.

Material: (a) ex Kew Herbarium (1935); KOH (46–56 μ), (b) Tararua Range, J. E. Attwood, Jan., 1933; GV (34–36 μ), KOH (43 x 37 μ).

Range, etc.: Common on true bogs of the three main islands. Mainly montane, but descending to sea level in the south, and on Auckland Island.

SCHOENUS L.

Three of the 70-odd species known are native. The relationship to the preceding is close. The grains are of type B, paraboloid, narrower than in *Carex*, with a delicate rod-layer: hyaline bodies may lie at the apex.

S. pauciflorus Hook. f. 40 x 20 (35–45 x 26–32) μ . Text fig. 31.

Material: Westport, T. F. Cheeseman; GV. Hollyford Valley, A. L. Poole, December 1939; Lp with S.

Range, etc.: Much as in the preceding, with southern limit in Stewart Island; endemic.

S. apogon Roem. and Schult.; 32–38 x 28 μ .

Material and Range: Ex pollen collection of Botanical Division; KOH. Smaller than the preceding, found mainly north of Bay of Plenty, but recorded also from Kowai Pass, low in the Southern Alps.

CLADIUM P. Browne

Many references to the pollen grains of this genus occur, Mohl (1834, Tab. VI, fig. 33), for instance, figuring a droplike grain of *C. germanicum* (cf. p. 42): Erdtman's most recent illustration of an aberrant grain of *C. Mariscus* has also been mentioned. The native species all appear to be of the same type as in *C. angustifolium* of Hawaiian bog margins (cf. Selling, 1947, Pl. 55, photomicrographic fig. 895), or with the pores lacking or obscure, i.e., types C and D. The exine is exceedingly thin, with delicate rods. Rounded hyaline bodies embedded in intine tend to push out under the pore membranes and elsewhere on the surface.

C. complanatum Berggr.

Text fig. 33. 26 μ , globular; pores 4 (or more?). Type C.

Material: Lake Waihi (Huntly), V. J. Cook, Sept., 1946; F, MG.

Range, etc.: Northwards from Whangarei, very local (Cheeseman, 1925, 232); endemic.

C. teretifolium R. Br.

About 23 μ , 4 pores only.

Material: From Collingwood, Nelson, N. Potts (cult. in Opotiki), Oct., 1948; F, GV.

Range, etc.: Lowlands of the 2 main islands, abundant in peaty ground. E. Australia and Tasmania also.

C. articulatum R. Br.; 23–27 μ ; as in *teretifolium*.

Material: Piha, Oct., 1938; L. M. C.; Lp and S.

Range, etc.: Lowlands to north of Hawkes Bay; in Australia, New Caledonia and New Hebrides also.

C. Sinclairii Hook. f. As in the other species, but with pores lacking or very obscure; 26–31 μ ; exine more faintly patterned. Hyaline bodies numerous.

Text fig. 34: showing large hyaline bodies.

Material: Waitakere Range, L. M. C. and C. Sg., Nov., 1938; GV.

Range, etc.: North Island only, mainly on wet cliffs, especially "papa" (sedimentary) formations. Flowers in spring and summer.

VAUTHIERA R. Br.

V. australis A. Rich. (= *C. Vauthiera* C. B. Clarke)

Text figs. 32a, b.

Type C–D, i.e., as in *Cladium*, spheroidal, 24–35 μ , averaging 31 x 29 μ ; pores obscure, if present. Exine faintly patterned.

Material: Botany Division, D. S. I. R. (Herb. 33, 903); (F).

Range, etc.: Lowlands of the 3 main islands; summer-flowering.

MARISCUS Gaertn.

M. ustulatus C. B. Clarke: Cutty-grass.

Type B–D, ovoid or globular, about 30–36 μ long. Tectum continuous except over vague pores where openly spaced granules reach the surface; pattern delicate.

Material: Poor Knights Islands, L. B. M. and L. M. C., Nov. 19th, 1933; Lp and S (31 x 24 μ), B. C. Aston; MG (30–36 x 24 μ).

Range, etc.: Lowlands and coastal: Kermadecs, Three Kings (Oliver, 1948, under *Cyperus*), and as far south as Stewart Island. Flowers in late spring and summer.

FIMBRISTYLIS Vahl.

F. squarrosus Vahl. var. *velata* C. B. Clarke. 27–30 μ , spheroidal or ellipsoidal (unexpanded), with obscure exits; C–D type. Exine very thin, reticulate, with a beaded surface due to clavate elements in the exine.

Material: Rotorua, T. F. Cheeseman, Jan., 1887; MG.

Range, etc.: North Island, local as far south as Rotorua lakes. Found in Australia also. Summer-

flowering. The grains seem quite distinct from any in the family. In an earlier paper (1942) I mistook a fold in the exine for a single furrow.

LEPIDOSPERMA Labill.

L. laterale R. Br. Pl. 4(8).

Material and Range, etc.: *L. laterale* R. Br. — Spirits Bay, D. Petrie (Dominion Museum Herbarium); MG. Auckland Province only, as far south as Upper Waikato, usually on podsolised soils. Also in Australia and Tasmania. *L. filiforme* Labill. (GV). On similar soils far north of Auckland, and in Australia.

ORDER 8: LILIIFLORAE

1. LILIACEAE, 2. AMARYLLIDACEAE,
3. IRIDACEAE

Although not restricted to a single "pollen species," there is nevertheless great uniformity in the major units comprising this order, especially with the exclusion of the Juncaceae, as in Hutchinson (1934, 1948), in Skottsberg (1940) and others. First, there is a predominant and apparently simple type of monocolpate grain which is morphologically if not phylogenetically identical with that of the palms and certain gymnosperms; aberrant furrow shapes are merely derivatives of this basic type. Secondly, most have a reticulate exine (first considered by Fritzsche, 1837, p. 709 and Taf. VIII, figs. 4 and 7 for *Lilium candidum* and *Pancratium* respectively, to be cellular) or vestiges of this pattern; spines are rare apart from certain Liliaceous genera in which a transition from entomophily or ornithophily to anemophily can be traced, the spines being vestigial where the leaning towards wind-pollination is strongest. Finally, tetrads are very rare in the group.

As has been stressed by Hutchinson (1934) and Skottsberg (l.c.), it is difficult to set the limits between the Liliaceae and the Amaryllidaceae on floral characters: the former author makes use of vegetative characters as well, grouping *Cordyline*, *Phormium*, *Yucca*, and other arborescent or coarse forms in the Agavales, which he suggests is "a half-way house between the Liliaceous stock and the climax group of the Palmae. . . ." As far as is known to the writer, who followed Hutchinson in an earlier paper, there seem to be points of similarity in the grains of this group, but unfortunately Hutchinson's classification leaves *Agapanthus*, whose grains may be compared with those of *Cordyline*, very far removed.

LILIACEAE: LILY FAMILY

As Selling (1947, 352) has remarked, there has been no comprehensive pollen survey of this huge and rather unwieldy family. Erdtman (1944b, 166) in particular considers there is sufficient diversity of pollen type in the Liliaceae (as in the Palmae) for use "in delimiting and characterizing different subdivisions" of these families.

The earliest mention of Liliaceous pollen is that of Grew (1682, 168) who considered the "Particles" from the "Male Attire" (anthers) as serving to "discharge some redundant part of the Sap." He figured (l.c., Pl. 58) a cylindrical grain and described it as "In Orange Lilly, Oval, . . . like an Ants-Egg." Purkinje (1830, 13) remarked on the absence of a true "hila" or pore, but did not refer to a furrow or fold; Fritzsche (1832, 7, 21, 22, 26) however, described the single-furrowed type in *Arthropodium*, identical with that of *Amaryllis nutilans* (l.c., fig. 18), and stated his view that the triangular grains of *Dianella* "mit drei übergeschlagenen Lappen" were merely modifications of the former type. Hassall (1841, 96, 98) usually a sturdily independent worker, followed Fritzsche (1837) in considering reticulation in the order as cellular; he referred also to the black pollen of *Tulipa Gesneriana*, a species in which Fischer (1890) later claimed to have found three furrows. This statement, although frequently quoted, has never been confirmed. Edgeworth (1877) referred to a number of genera, both from the literature and from personal experience, and gave some useful measurements. He also stated that *Tulipa* might have 2 to 3 furrows. Fischer gave a detailed account of varying shape, size, aperture number, and exine character. He referred (l.c., p. 21) to globular inaperturate grains covered with fine "warts" (*Lapageria*, *Smilax*,

Trillium), and to spiny-warty grains with smooth bands (*Aphyllanthes monspeliensis*, see also Erdtman 1944b, 165, and fig. 6), and to a second class (l.c., p. 32) with one usually ill-defined furrow, and paid great attention to the granular, coarsely warty, or reticulate exine patterns. He stressed that the mesh is always greatest on the backs of the grains, and diminishes steadily towards the furrows (i.e., on distal side).

Armbruster and Oenike (1929) and Zander (1935, et seq.) made full use of Fischer's classification, the former adding some excellent illustrations (l.c., Taf. 14-16), e.g., *Agapanthus*, 50 μ , while Zander stated that all members of the family, with the possible exception of *Tulipa*, were monocolpate: his own illustrations of *Tulipa* do not reveal any exits at all. Amongst a wealth of details he refers to range of size in the sub-families, the Lilioideae and Asphodeloideae having the largest grains and the Asparagoideae the smallest. Later (1941, 114) Zander gave 17 to 90 μ as the size-range in the family, and provided a number of illustrations, those of expanded grains showing excellently the part played by the intine in the swelling of the grains. He had suggested (1935) that *Tofieldia* had two furrows; this was not specifically confirmed by Wunderlich (1936, 35), who does, however, mention Geitler's (1935) statement that *Uvularia grandiflora* grains are dicolpate. Zander (1941, 19, 22), in making further references to dicolpate grains in *Tofieldia* and *Crinum*, provides sketches which suggest that this is really a modified monocolpate or zonate furrow, as in *Laurelia* (Cranwell, 1942).

VERATROIDEAE

IPHIGENIA Kunth

As to the single endemic New Zealand species, Cranwell (1942, 292) has given brief notes, amplified below, contrasting the grains with those of *Hypoxis* (about 33 μ , with stronger pits) and *Libertia* (about the same size, with thinner, psilate exine) in particular. Comparison should also be made with the much larger grains of *Arthropodium*. No other descriptions have been noted by the author. Thanks to the kindness of Professor I. W. Bailey, material of *I. indica* from Corcan, India (lactic acid preparation) was made available. As will be seen, the pollen of the two species is almost identical, although the shape differs because of great expansion in lactic acid compared

with the unexpanded or only moderately expanded condition of the native material.

I. novae-zealandiae Bak.

Text figs. 36a, b.

Grains monocolpate, spheroidal, or ellipsoidal, about 20 to 30 by 16 μ , mainly 28 μ long. Furrow long and clearly defined, sunken when grain unexpanded but with membrane protruding on expansion, and then about 8 μ wide. Exine up to 2 μ thick, smooth, intectate, reticulate, with narrow lumina and rugulate ridges.

Material: Burnham, Canterbury, T. Kirk; MG.

Range, etc.: South Island only (swamps from near Christchurch to Otago), found up to 2500 ft. altitude. Flowering in early summer (see Cheeseman, 1925, 326). Other species occur in Australia, Africa, Madagascar (1 each), and India (2).

Comparative material: *I. indica*. As in the preceding, but globular in lactic acid, with long widely stretched furrow with ragged edges; exine less than 1.5 μ thick, finely reticulate all over, averaging about 27.5 μ in diameter. Corcan, India.

ASPHODELOIDEAE

ARTHROPODIUM, R. Br.

Fritzsche (1832, 21) briefly described the pollen of *A. fimbriatum* as oval when dry, "mit zwei übergeschlagenen Lappen welche eine scheinbare Furche bilden." Edgeworth (1877, 13) and Hansgirg (1897, 21) gave measurements of 10/6000 inch (ca. 42.3 μ) and 50 to 60 μ by 25 to 40 μ , respectively — neither referred to the furrow. These figures for length agree with the average of 55 μ for *A. cirrhatum* given by the author (1942, 293).²

A. cirrhatum R. Br.: Renga Lily; Rock Lily

Pl. 5 (1-3); text fig. 37.

Grains monocolpate, averaging 56 by 26 (51-62 x 22-34) μ , rarely below 20 μ in width or depth, ellipsoidal (acetolysed) to spheroidal, with truncate ends, usually slightly flattened dorsally and with deeply channelled furrow when unexpanded; more rounded when expanded but with little protrusion of furrow. Exine partly tectate, very thin (under 1.25 μ), with fine, even, and characteristic reticulation, the rounded-hexagonal lumina smaller on surface of exine, ranging from 1 to

² Through a typographical and proof-reading error, the text for *Xeronema* was allotted to *Arthropodium* and that for the latter ("Size about 55 μ ; pits uniform. . .") omitted altogether. A printed correction was made at the time, but the slips may not have been inserted in some copies sent out during the war.

1.5 μ in diameter in middle of proximal side, and only slightly smaller on and adjacent to the furrow; rod simple, clavate. Furrow very long, running more than half-way around the grain, opening to about 12 μ , but with margins almost touching in middle when unexpanded and tending to leave the ends very widely exposed. Furrow membrane covered by ektexine only, psilate, marginally delimited by the endexine. Intine thick under furrow.

At very high magnifications the lumina are seen, at mid-focus, to be pebbled with shorter, straight rods.

Material: Ellerslie (cult.), L.M.C., Nov., 1937; EM.

Range, etc.: A showy herb common in North Island; also found on Three Kings and in Nelson and Marlborough. Mainly coastal. Entomophilous, flowering Nov.-Dec.; pollen yellow. Endemic.

A. candidum Raoul

Grains distinguished from the preceding by smaller size, averaging 36 by 26 (34-38 x 16-28) μ , and with smoother, tectate, much more finely reticulate, intrabaculate, exine.

Material: Wakatipu, George Simpson, Nov., 1938; EM, MG; (size differing only very slightly).

Range, etc.: From Little Barrier Island (in two forms) and Cape Colville to Foveaux Strait, up to 3500 feet altitude (Cheeseman, 1925, 324). Entomophilous, flowering Nov.-Jan. Endemic.

The pollen grains of these two species are fairly distinctive because of their uniform and continuous pattern, which is much more delicate than in *Xeronema*; the larger grains may be compared with those of *Rhopalostylis* and *Chrysobactron* (exine thicker in both) and the smaller with *Hypoxis*, *Iphigenia*, and *Libertia*.

XERONEMA Brogn. et Gris.

Cranwell (1942, 293, see below) offers the only description of the pollen grains of this genus, which has one endemic species in New Zealand, and one in New Caledonia. An interesting account of the very recent discovery of the native species is to be found in Oliver (1925, 1926): see also notes by Cranwell (1933).

As already stated (see p. 48), through an error, the name *Arthropodium* replaced that of *Xeronema* in the key while the *Arthropodium* line was omitted altogether. Briefly, the grains were stated to be of the same general type as in *Rhopalostylis* and *Chrysobactron* (*Bulbinella*), but with narrower furrows and ill-defined margins ("unthickened"). I should like to add now, as for others in these groups, that the mode of preparation alters the furrows so much that width is not a very satisfactory criterion unless both expanded and unexpanded conditions are known.

X. Callistemon W. R. B. Oliver: Poor Knights Lily.

Pl. 5(4-7); text figs. 38a, b.

Grains as in *Arthropodium*: monocolpate, ranging from 44 (36-48) μ by about 30 μ wide and 34 μ deep in the boat-shaped and slightly channelled unexpanded condition, but becoming spheroidal (or practically globular, as in lactic acid) when expanded. Proximal side usually somewhat flattened and ends apiculate when unexpanded. Furrow shorter than long axis, fairly narrow (up to 7 μ wide) unless over-expanded, with marked reduction in size of lumina approaching it, as on the rather inactive furrow membrane.

Exine fairly thick (1.8-2 μ on proximal side), tectate, the reticulation exceedingly characteristic in size and disposition, being coarse and open where thickest, and very fine (foveolate) on the opposite side of grain. Furrow membrane psilate. Ektexine, with rough-ended surface continuous over furrow, the lumina more elongate than in *Arthropodium*, ranging from 1.5 to 3 μ on one side to ca. 1 μ , on the furrow. Lumina smaller in surface than in basal measurement; muri very narrow on proximal side, but comparatively wide on distal side. Intine about 1.5 μ thick.

Aberrant forms occur: see Pl. 5(5, 6).

Material: St. Heliers Bay, Auckland, A. T. Pycroft (cult.), Nov., 1937; EM. Poor Knights Island, L. B. M. and L. M. C., 19-11-33; MG, GV, lactic (41 x 35 μ), Lactophenol with safranin (37.7 x 24 μ), unexpanded.

Range, etc.: A showy plant with swordlike leaves and profuse crimson flowers; pollen abundant, crimson. Probably both insect and bird-pollinated. Confined to Poor Knights group (lat. 35° 30' South, long. 170° 45' East) and Taranga Island, from spray-zone to summit of Tawhiti Rahi in former group, and from higher cliffs to about 1000 feet altitude in latter. Found as drift only on shores of Chickens Islands.

Comparative Material: X. *Moorei* Brogn. et Gris.

As in the preceding; 37-42 x 24-34 μ (Lp) Endemic to New Caledonia. Collected at 800 m. by Mrs. (?) Koglin, March, 1929 (material from Gray Herbarium).

CHRYSOBACTRON Hook f.

This endemic entomophilous genus, which has at times been included in both *Anthericum* and *Bulbinella*, comprises three species, the two whose pollen is discussed below, and a third, the little-known Stewart Island *C. Gibbsii*.

The pollen of *C. Rossii* was described by Hooker (1844-1847, 72) as follows: "Pollen flavum, ovoideum, longitudinaliter bi- vel trisulcatum." The magnificent double colour-plate (*l.c.*, Tab. 44, 45; fig. 4), showing the habit of the plant, includes small outlines of two

pale yellow, ellipsoidal grains, shaded to indicate smooth-membraned sulci or furrows. The extra furrows are obviously to be explained by folding of the exine.

Much later, Cranwell (1942, 292) showed that the grains were of the monocolpate type dominant in the lily and palm families. They were described as about $50\ \mu$ in greatest diameter, with a clearly defined and vigorous furrow, patternless furrow-membrane, and rather thick, "granular-pitted" exine. This description was based on *C. Hookeri* alone. In the following account the sculpture is termed rugulate (see Faegri and Iversen, 1951, Pl. II, fig. 2).

C. Hookeri Benth. and Hook.

Pl. 5(8); text figs. 39, 57

Grains monocolpate or occasionally trichotomocolpate, ellipsoidal, often asymmetrical, being wider at one end, or flattened proximally, and protruding over furrow area when expanded. Size range considerable, up to $55\ \mu$ long by $34\ \mu$ wide, but averaging 48 by $31\ \mu$ (acetolysed). Furrow very long, typically confined to one side of grain, often running obliquely, about 7 to $10\ \mu$ across at widest point, closing tightly when unexpanded. Furrow membrane psilate. Exine reticulate, about $2.5\ \mu$, smooth where tectate, with slightly uneven surface and rugulate sculpture.

Material: Wellington (cult.); L. M. C., 1937; EM (smallest grains $36 \times 22\ \mu$; mainly $44\text{--}51 \times 30\text{--}34\ \mu$); ex Gray Herbarium, GV ($48 \times 24 \times 24\ \mu$), KOH ($40 \times 30\ \mu$), furrow opening almost as wide as grain when prepared in this way.

Range, etc.: A stout herb found on sour soil, spreading rapidly after fire. Abundant in high or cold districts in both main islands and in Stewart Island. Spring- and summer-flowering.

C. Rossii Hook. f.

Text fig. 40.

Grains similar, but distinguished by very coarsely rugulate sculpture and smaller size, most measuring $36\text{--}40 \times 26\ \mu$ when acetolysed. Exine appearing very thick all over because of granular or beaded projections of the ridges (vallae), which are crowded closely, irregularly spaced, and about twice as long as broad. Lumina very narrow.

Material: J. D. Hooker (Auckland or Campbell Islands: locality not stated); ex Gray Herb.; KOH. Dunedin (cult.), Marie C. Neal, December, 1925; ex Herb. B. P. Bishop Museum; GV.

Range, etc.: A large peat-forming herb up to 4 feet tall, found only on Auckland and Campbell Islands, and flowering so profusely that "its presence can be observed at a distance of more than a mile from the shore. . . ." (Cheeseman, 1925, 322).

Forked furrows occur in *Chrysobactron*, as also in the closely related South African *Bulbinella*. In *B. setosa*, for example (material from Harvard Pollen Collection), the broad furrow is drawn out towards the angles (3 to 4) of the grain. Early stresses within the grains seem to effect this relationship between the number of angles and the forkings of the furrow area.

HERPOLIRION Hook. f.

Cranwell (1942, 292) refers the pollen of this monotypic genus to the small group (with a well-defined but sharply 3-armed crestlike furrow) which includes *Dianella*, *Phormium*, and others mentioned earlier. Further, the grain is stated to be angled, about $27\ \mu$, with "pitted" (i.e., finely reticulate) exine. The genus is confined to New Zealand, Tasmania, and southeastern Australia. Entomophilous. The following notes are those on which the brief statement noted above was based.

H. novae-zelandiae Hook. f.

Pl. 6(7-9); text figs. 45a, b.

Grains almost indistinguishable from those of *Dianella*; tetrahedral. More or less angled in equatorial outline, measuring 24 to $28\ \mu$ in greatest diameter, by $18\ \mu$ between the poles, one of which lies in the middle of the typically three-armed ("trichotomosulcate") furrow area. Arms of furrow reaching to equator, sometimes vaguely defined at tips; margins broadest near middle. Exine psilate, finely reticulate, with crowded clavate rods bordering narrow lumina which are smallest near the furrow margins.

Material: Pukemako, King Country, V. Fisher, Nov. 21, 1930; MG. Mossburn Bog, L. M. C., Dec. 26, 1939; GV, Lactic. Waipori Valley, W. A. Sledge, 1929; KOH.

Range, etc.: A small lilac-blue or white-flowered herb found mainly in montane areas, from Waitomo to Stewart Island, especially in bogs. Entomophilous, flowering in early summer. The grains might possibly be confused with aberrant ones of *Hypoxis*.

DIANELLA Lam.

The distinctive pollen grains of *Dianella* claimed early attention. Fritzsche (1832, 22,

FIGS. 36-55: LILIACEAE, $\times$ ca. 900, except for detail sketches (with 44, 50, 51, 55), and 47 (left) and 54, which are at lower magnifications.
 36: *Ipbigenia novae-zelandiae*. 37: *Artibropodium cirrhatum*. 38: *Xeronema Callistemon*, a much expanded, b lateral view. 39: *Chrysobacron Hookeri*, edge of endoxine dotted; 41: *var. angustifolia*; 40: *C. Rossii*, proximal view. 42-44: *Cordylina* — 42: *C. pumilio*; 43: *C. Banksii*; 44: *C. indicisa*, b mesh at mid-focus. 45: *Herpolirion novae-zelandiae*. 46: *Dianella intermedia* (in 45 and 46, edges of endoxine are dotted). 47-49: *Phorrium* — 47: *Phorrium* — 47: slit in endoxine shown opposite furrow. 48: "square" grain; 49: slit in endoxine shown opposite furrow. 50: *Collospermum bastatum*, showing ruptured furrow and exine pattern at mid and low focus, and in optical section. 51: *C. microsperrum*, rods as in 50. 52: *Aselia Banksii*, furrow open. 53: *A. nervosa*, furrow closed. 54: *Luzuriaga marginata*, a dyad, b lateral view. 55: *Ripogonum scandens*, furrow closed.

26) stated that *D. caerulea* and *D. nemorosa* have triangular grains when dry with three "Lappen" (lobes of the furrow) meeting in the middle, and he stressed that the triangular form is only a modification of the *Amaryllis* type (l.c., fig. 18), shared also by *Arthropodium fimbriatum*, whose furrow he described as having two folded lobes which contain an apparent furrow.

Edgeworth's (1877, 13) description of *D. caerulea* and *D. laevis* (*strumosa*), measuring 6 and 5/6000 in. (25 and 21 μ)* respectively, as "Trigonus cocked hats" is especially effective. The illustrations of *D. laevis* grains (fig. 12) dry (three-cornered), and expanded in oil, differ little; it cannot be determined from them whether the nature of the furrow was understood.

Fischer (1890, 30) merely placed *Dianella* together with *Cordyline congesta* and others amongst the one-furrowed grains with weakly granular to "runzlig" (wrinkled or reticulate?) exine. Schittler's monograph on the genus yields only this disappointingly brief statement: that the grains are at first tetrahedral, but later rounded, with smooth surface, colour yellow to whitish. Cranwell (1942, 292) gave original descriptions of the grains of the single variety found in New Zealand, describing them as angular, flattened; furrow sharply 3-armed ("crestlike"), about 32 μ , lacking pattern (i.e., sculpture). Erdtman (1944b) in discussing these "three-slit" openings, as he terms them, shows that they are aberrant forms of monocolpate grains and that both types may occur in the same species.

Erdtman had studied *D. sandwicensis* (one of three Hawaiian species) in particular, from material collected by Selling, who in turn (l.c., 354, and Pl. 55, figs. 903-905) described it more fully, using his term "trichotomosulcate" (as for *Cocos*) instead of the brief "three-armed" or "three-slit," already mentioned. Selling gives the average size (acetolysed) as 23 by 30 μ , and states that the exine is about 2 μ thick, smooth, and with a faint granular or reticulate texture. No fossil records are given.

D. intermedia Endl. var. *norfolkiensis* F. D. H. Brown: Turutu.

Pl. 6(1); text figs. 46a, b (detail).

Grains tetrahedral with furrow up to 3-6 μ wide, running 3-armed from the distal pole (i.e., on the rounded side of grain), averaging

* 4/6000 in. (17 μ), on p. 71 (l.c.).

24 (20-32) μ ; depth of polar axis about 22 μ ; furrow area lacking endexine (?), more or less regular in shape, but tending to split widely when expanded at one or other corner of the grain. Exine under 1 μ , minutely reticulate, with only local roughening of surface.

Range, etc.: A grassy herb found from Three Kings Island to Foveaux Straits, most abundant in dryish heath or forest of lowlands, Oct.-Dec. Pollen yellow.

Material: Kaitaia, H. B. Matthews; MG.

Comparative material: (*Herpolirion* and *Phormium*.) *D. tasmanica* grains almost identical with the preceding, about 23 μ in diameter, with narrow furrow and less tendency to shed ectexine; grown by Mrs. A. Skeates, Auckland, Sept., 1940; MG.

HEMEROCALLIDEAE

PHORMIUM Forst.

The grains of this genus, although they possess a triradial furrow and angular outline, as in *Dianella* and *Herpolirion* (Cranwell, 1942, 292; see also Erdtman, 1944b, Figs. 7, a, b, for distal and proximal views of grains of *P. Colensoi*) are still unique because of the combination of a distinctive sculpture and structure with this unusual configuration.

Pollen type: Grains trichotomocolpate, tetrahedral, oblate, medium-sized, sharply angled when unexpanded, flattened (or rounded) on proximal side, rounded to bulging on distal side, especially when expanded. Furrow triradial (i.e., forked over distal pole). Exine thick, tectate-foveolate to reticulate, the holes in the tectum very small at angles of grain and toward furrow margins, but more or less "fenestrate" on proximal surface and in middle of areas between the forks or arms of the furrow, the bubble-like reticulation further characterized by interstitial lumina; muri exceedingly narrow, composed of long rods which cause some granulation of the surface. Intine very thick in a triangular plate under and around the furrow area.

Two species are known, one endemic, and the other, the "flax" or "New Zealand hemp" of commerce, found also on Norfolk Island. Both species have been reported again recently from the Three Kings Islets (Oliver, 1948, 219).

Pollination is mainly by birds, although insects play some part, beetle-visitors being reported for *P. Colensoi* by Miss Heine (1937, 139, 142). Thomson (1927, 106, 110) goes into more detail for *P. tenax*, stressing the "immense quantities of honey" produced, and listing the

"honey-eaters" (tui, bell-bird, stitch-bird, white-eyes), parrots, and paroquets that commonly visit them. Nectar shakes freely from the flowers while the birds' bodies pick up masses of adhesive orange pollen that show up clearly at a distance.

P. tenax Forst.: Harakeke, "Flax"

Pl. 6(2-6).

As in generic description, averaging about $36\ \mu$ in greater diameter ($34 \times 36 \times 30\ \mu$), often quite symmetrical in polar view, with the very long furrow arms extending beyond the angles of the grain, their margins almost meeting when unexpanded, but $5\ \mu$ or more wide when moderately expanded. On over-expansion considerable swelling of the smooth furrow membrane occurs at mid-points in each arm of the furrow. Exine up to $2\ \mu$ thick on strongly meshed areas, thinning at margins and lacking ektextine on membranes. Largest lacunae are about $4\ \mu$ in diameter, often confluent ($6.5\ \mu$ or more), smallest less than $1\ \mu$ in diameter. Rods broadest at base (see figure below).

Left (FIG. 56): *P. tenax*. Oblique view of lumen.

Right (FIG. 57): *Chrysobactron Hookeri*. Lumina at mid-focus, showing rods scattered over whole surface (muri shaded). *Diagrammatic*.

Material: Auckland Domain; W. F. H.; GV. Colombia, S. Am., (cult.), Feb. 3, 1949, collected by H. Gareja-Barriga (ex U.S. National Herb.); EM (slide prepared by Miss Teresa LaCroix). $12-38\ \mu$ (many abnormal); mesh ca. $1\ \mu$.

Range, etc.: Abundant in lowlands of the four main islands, especially at sea level and on hummocks in eutrophic deposits, as in the Waikato; found also on Norfolk, Three Kings, and Campbell Islands. Flowering early October (occasional) to January, according to latitude. At montane limits (about 4500 feet) I have usually found it on over-dried and eroding peat, as on the Blue Mountains, Tapanui (Cranwell, 1952, in press). It is frequently confused in the literature with the following species.

Fossil: A single grain of *Phormium* (probably of this species) was reported by Harris and Filmer (1946, 12) from Hauraki peats. Couper (1951a, 11) has since reported the genus from fossil measures, and the writer has found odd grains as from Pyramid Valley [Pl. 6 (6)] in 1940.

P. Colensoi Hook, f.: Wharariki

Pl. 6(5); text fig. 47.

Grains very similar, symmetrical, but perhaps consistently distinguishable because of more rounded outlines, especially at the angles, rather smaller, averaging about $30-32\ \mu$ in greatest diameter, but very distensible and therefore unreliable for comparative measurements in some types of preparation; furrow arms shorter, reticulation less coarse, with lacunae mainly about $3\ \mu$ in diameter over back and sides of grain.

Occasionally rhomboidal grains ($32 \times 32\ \mu$) were found; in these the furrow area was four-armed.

Material: G. Einar DuRietz, 1928, # 783; KOH. Westland, 4000 ft., 1935, F. W. Hunnewell; Lp & S. F. S. Ellerslie (cult.); L. M. C., Nov., 1937; EM.

Range, etc.: A weaker-fibred plant found mainly on coasts and in the mountains, on rocky or peaty soil, though not a member of acid bog communities, as a rule, probably because of lack of aeration for the roots. Flowering November to January.

Hybrids. Text figs. 48, 49.

The two species cross freely, sometimes producing modified sex organs which may continue vegetative growth independently (Allan and Cranwell, 1942) as "vivipars." Viable as well as sterile pollen may be produced.

Material: Wild (Wellington Heads, H. H. Allan), originally discovered by A. J. Healy, 1937, EM; cultivated (Diocesan High School, Auckland), L. M. C., 1932, and Henderson, L. M. C., 1941, EM.

DRACAENOIDEAE: DRACAENEAE

CORDYLINE Comm. ex Juss.

About twenty species of *Cordyline* are known, four endemic in New Zealand, one in South America, and the others mainly in and around the Pacific, with *C. terminalis* ranging westward through Queensland, New Guinea, Malaya, and India. All the native species appear to be entomophilous and heavily scented, Thomson (1927, 110) reporting pollination by beetles for *C. australis* and *C. Banksii*, while Heine (1937, 141) mentions diptera on flowers of the latter.

Much of the literature has been summarized by Selling (1947, 354), whose original contribution is a description of the pollen of the "ti" (*C. terminalis*), a plant tied to migrations in Polynesia, and found even as far south as North Auckland.

It is included here for comparative purposes and for its slight potential value as an indicator of the duration of Maori occupation.

Fischer's description (1890, 31) of the sculpture of *C. congesta* (given as a *Dracaena*) as "fein runzlig mit übergang in rundmaschignetzformige Zeichnung" is typical of a number of members of the Liliaceae (*Anthericum*, *Agapanthus*, etc.); he also mentioned the stronger mesh of the proximal sides of the grains.

Cranwell (1942, 292, 293) added details about several New Zealand species, *C. indivisa* being grouped with ellipsoidal monocolpates with very long, wide, well-defined furrows, and thick, reticulate or "pitted" exine.

The polyploid nature of *C. australis* was discussed by Matsura and Sutô (1935, 67) who found that its chromosome numbers were higher than any hitherto noted in the family. Wunderlich (1950, 493-495) gave pollen notes in her survey of the group forming Hutchinson's Agavaceae, but could offer nothing conclusive about the position of *Cordyline* and *Phormium*. Tests for steroid saponins (a type found only in the monocotyledons), as suggested by Briggs (1947, 173), might help prove whether these baffling genera should be allied with the agaves and yuccas.

Pollen type: Monocolpate, oblate, proximally flattened, bulging on furrow side except when acetolysed, under 40 μ , the furrow exceeding the length of the long axis of the grain. Exine coarsely reticulate as a rule, surface roughened, especially on proximal side. Intine thick under furrow. Yellow or yellowish-white; insect- or bird-carried.

The vigorous protrusion of the distal side of similar grains with thick intine is well illustrated by Zander (1935, Taf. 7, abb. 50; 1937, Taf. 22, abb. 98) in his photomicrograph and sketch of pollen of *Yucca filamentosa*, which belongs to this sub-family. These grains are also strongly flattened on the proximal side.

As the illustrations show, the pollen of *C. indivisa*, while adhering to the generic type, is unique in the flora. In it is seen an exaggeration of shape and exine characters common to the cordylines. Differences between the other species appear to be very slight, and have not received more detailed study at present as they have almost the same indicator-value, ecologically, for possible peat studies.

In the following tables only slight differences in average size are shown as resulting from different methods of preparation, apart from those excessively expanded in lactic acid. The measurements are in microns.

1	2	3	4	5
Species	Method	Length	Width	Depth
<i>indivisa</i>	EM	34	24	24
	KOH	30	26	27
	GV	28	24	27
<i>australis</i>	EM	34	22	21
	GV	33	22	21
	MG	29	22	22
	Lactic *	44	30	30
<i>Banksii</i>	EM	35	24	24
<i>pumilio</i>	KOH	32	21	21
	MG	34	21	22
<i>terminalis</i> (Selling, 1947)	EM	36	22	22

* Great expansion results from the use of the lactic method, but exine features show up particularly clearly, and the typical flattening of the proximal side of the grain is retained.

C. indivisa Steud.: Toii, Mountain Cabbage Tree.

Pl. 5 (10); text figs. 44a, b.

Grains averaging 30 x 26 x 20 μ (KOH), spheroidal when most expanded, but more typically flattened on proximal side, traversed on domed side by a long, wide furrow, which causes deep channelling when unexpanded. Exine beaded on surface, very thick (averaging 3.5 μ) and coarsely meshed over middle of proximal side, the lacunae deep and small in proportion to the muri between, diminishing to pits over the distal side of grain and especially towards the furrow margins.

Material: Dominion Museum Flower Show, 1937; L. M. C.; EM. Mount Egmont (cult.), T. Kirk; KOH, GV.

Range, etc.: A bulky tree of montane districts from Coromandel Peninsula (mainly destroyed by goats and cattle) to Banks Peninsula and Dusky Sound. Spring-flowering. Insect- and bird-pollinated, with wind possibly playing some part, as the huge inflorescences are held high and free in the air. Pollen yellowish-white, copious.

C. australis Hook. f.: Ti, Cabbage Tree.

Grains more conspicuously flattened, averaging 34 x 22 x 21 μ (acetolysed) with narrower, shorter furrows, of the same general shape, forming a rift with unthickened rims. Exine under 2 μ , with finer reticulation on both sides of the grain, the columellae about 1 μ long where exine is thickest.

Material: Waikowhai; L. M. C., October, 1931; EM. Palmerston North; H. H. A.; EM. Auckland; C. J. Burgess; MG, F, lactic. Waiheke Island, Auckland; T. Kirk; KOH (Botany Department, Otago University, per G. Baylis).

Range, etc.: Both this and the following species are tall shrubs or trees common in lowlands in both main islands, increasing after disturbance in the forest. Often an early coloniser after fire. Spring-flowering, e.g., late September–November, in Auckland. The yellow colour of the pollen of this species was referred to by W. J. Hooker (1828).

C. Banksii Hook. f.: Ti-ngahere

Pl. 5 (11); text fig. 43.

Grains much as in *australis*, about $35 \times 24 \times 24 \mu$ (EM); exine thinner.

Material: Egmont; L. M. C., 1932; EM, Waiheke Island, Auckland; T. Kirk; KOH, MG.

Range, etc.: A smaller tree than the preceding, with similar distribution in the north, but not extending beyond Marlborough and Westland. Hybrids frequent. Flowers in late spring and early summer.

C. pumilio Hook. f.: Ti-rauriki, Dwarf Cabbage Tree

Pl. 5 (9); text fig. 42.

Grains as in *australis* and *Banksii*, averaging $32 \times 21 \times 21 \mu$ (KOH), or $34 \times 21 \times 22 \mu$ (MG); exine as in the latter (ca. 1.3μ).

Material: Waiheke Island, Auckland; T. Kirk; KOH, MG. Campbell's Bay, Auckland, G. T. S. Baylis, December, 1929; KOH, GV, MG.

Range, etc.: In lowlands from North Cape to Wellington; also recorded from Banks Peninsula (Wall, 1935); "rare and local to the south of the East Cape. . ." (Cheeseman, 1925, 312); common on North Auckland "gumfields." Flowering in early summer.

C. terminalis Knuth: Ti-pore

Edgeworth (1877, 13) referred to grains from about 6/6000 to 8/6000 inch long (ca. 25 to 39 μ) in "*C. Rodii*" (horticultural?) and *Dracaena magnifica* (*C. terminalis*) respectively, only the latter being repeated in his 1879 reprint. The measurements for "*C. Rodii*" agree best with those for the above species as given by Selling (1947, 355), who also provided excellent illustrations (Pl. 55; figs. 906–910) of unexpanded grains very similar to those of the *C. australis* type, averaging $36 \times 22 \times 22 \mu$, with very long furrows, which sometimes widen towards the ends, and thick exine (2.5–3 μ), the ectexine being of "distinct, granular or reticulate texture." He compared it with *Sisyrinchium* and *Pritchardia*.

Material: Native pollen not seen.

Range, etc.: Kermadecs (Sunday Island); North Auckland, still occasionally found lingering on sites of Maori plantations. Flowering July to September (Cheeseman, 1925, 310). Widely spread to the west of Polynesia.

MILLIGANIEAE

The setting up of the new genus *Collosperrum* by Skottsberg (1934b, 37) leaves *Astelia* with very uniform pollen, judging from the South American, Hawaiian, and New Zealand material I have seen. However, *Collosperrum* grains are very similar, differing chiefly in greater size, more irregular and vigorous furrow area, and more distinctive sculpture.

ASTELIA and COLLOSPERMUM

Fortunately, the published notes on *Astelia* (in a wide sense) are not as scant as indicated by Selling (1947, 356), who quoted the generic description by J. D. Hooker (1844, 76), here translated: *pollen* ovoid or angular, granular or minutely echinulate, excavated on one side: but overlooked his use of pollen characters in attempting to show the affinities of the genus within the family, as also his excellent little sketches of 3 spiny grains of *A. pumila* (1847, Pl. 127, fig. 3), showing a long irregular furrow in one, whereas the others are in lateral view, or split. Hooker (1853; 1860) also stated that the Tasmanian *Milligania* (2 species) had sub-globose pollen: Skottsberg (1934b, 10) has since emphasized the likeness between *Milligania* and *Astelia*, especially because of the peculiar scales common to them.

Edgeworth (1877, 71, fig. 14, a–d) followed with figures, all except *d* showing a furrow, and the sculpture was stated to be "obtusely spiny"; the grains measured 1/1000 inch (25.40 μ). Some doubt arises about the identity of Edgeworth's *Astelia*, given as *A. Cunninghamii* (now *A. Solanderi*, see p. 57), as this species has often been confused with *A. trinervia* and even with *A. Banksii*. This is to be regretted as the figures compare favourably with those of Hooker's, a rare circumstance with this author.

Schnitzlein (1843–1846, Tab. 51a, fig. 8) gives two typical grains with rimmed furrow uppermost and a third with half of the furrow showing on one side, all expanded. The species is stated to be *A. montana*, but this identification appears to be dubious (Skottsberg, 1934a). Selling (1947) interprets the furrow rims as marking two furrows on one of the grains. McCarthy (1928, 351 and fig. 12) correctly

A. Cockaynei Cheesem.

Grains of similar size-range, $30-34 \times 24-27 \times 18 \mu$, with thinner exine and smaller, narrower spines, their tips $1-2.5 \mu$ apart; exine rods finer.

Material: Arthurs Pass, W. A. Sledge, 1929; M.G.

Range, etc.: Subalpine in the 3 main islands, mainly from East Cape southward (cf. Skottsberg, 1934, 64-67, and map, Fig. 272). Apparently closely related to *A. nervosa* var. *sylvestris*, and belonging to the same subgenus, *Tricella*, in which hybridism is rife. Flowers in November (Cockayne, 1928) and later.

A. trinervia Kirk (Pl. 5, fig. 12), and **A. Solanderi** A. Cunn. (= **A. Cunninghamii** Hook. f.)

Grains mainly $23 \times 18 \times 13 \mu$ in *trinervia* ("Kauri Grass") and $23 \times 20 \times 17 \mu$ in *Solanderi*. Both have a long wide furrow, a fine rod-layer and small narrow-based spines.

Material: *trinervia* (Trounson Kauri Park, G. E. DuRietz, #2821, May 24th, 1927; KOH); *Solanderi* (Nelson, George Simpson; EM).

Range, etc.: These 2 species are very often confused in herbaria. The former, with crimson berries, makes a rank, erect cover in *Agathis* forest, hence its popular name: its presence in a few areas beyond the present range of this type of forest may indicate earlier limits in fairly recent times. The latter species, with varicoloured and often stippled berries, is lax, commonly epiphytic, and widely spread in the North Island, but less common in northern parts of the South Island (cf. Skottsberg, 1934b, 36-46).

A. Banksii A. Cunn.

Text fig. 52.

Grains smaller, $18-20 \times 13-18 \times 10-16 \mu$ (unexpanded), or about 20μ (expanded).

Material: (a) Waitemata, T. Kirk; KOH. (b) Russell, "in aërohyaline belt," G. E. DuRietz, April 30th, 1927; KOH. Sample ex herbarium, Gothenburg Botanical Garden.

Range, etc.: Mainly rupestral (or in crotches of pohutukawa by sea), most common from Coromandel and Auckland shorelines northward (cf. Cheeseman, 1925, 316). I have seen it at high elevations only where exposed to salt winds.

A. linearis Hook. f.: Bog *Astelia*

Grains distinguished by small size, about $16 \times 20 \times 10 \mu$, or, when globular, 16μ , and by exceedingly thin exine with delicate rod-layer and minute, closely crowded, rounded projections with tips about 1.5μ apart. Furrow elongate, or rounded, up to 10μ wide in greatly expanded grains.

Material: Auckland Island, J. F. Findlay, forwarded by Miss L. B. Moore, Botany Division, D.S.I.R.; KOH.

Range, etc.: A montane peat-forming herb — "East Cape and Ruapehu southwards" (Cheeseman, 1925): apparently very abundant in subantarctic islands.

Very similar but rather larger grains ($19 \times 16 \times 15 \mu$) characterized a larger form collected by Miss L. B. Moore and the writer on Key Summit, near Homer Tunnel. This is possibly a variety or a hybrid form. As to the pollen of that remarkable plant, *A. subulata*, with its "panicle" of one flower (Skottsberg, 1934b, 34) nothing is known. Judging by my own collecting on Stewart Is. bogs (fruit only), its season must be early: Mr. B. C. Aston collected it Port Ross on Jan. 8th, 1909 (Skottsberg, l.c., 34).

COLLOSPERMUM Skottsberg.

Of the 5 known members of this closely-knit genus, 3 are found in New Zealand, one in Fiji, and one in Samoa. The pollen, being smooth and uniformly larger than in *Astelia*, is quite distinct, appearing well-suited to anemophily, though insect visitors are common.

C. hastatum (Col.) Skottsberg. (= **A. Solanderi** *sensu* Hook. f.)

Pl. 5(13, 14); text figs. 50, a-d.

Grains irregularly spheroidal on expansion, or ellipsoidal, with one broad end; commonly $40 \times 38 \times 24 \mu$. Exine a little over 1μ thick, with a rod-layer overlain by pointed granules from $2-4 \mu$ apart, which very slightly roughen the tectate surface. Furrow very long, wide, and active, causing bending of the proximal, and deep invagination of the distal side of the grain; furrow membrane granular, and rimmed by coarser granules; the rod-layer, as in *Astelia*, lacking over this area. Intine about 6μ thick, capable of great swelling to rupture the tough furrow membrane either at a mid-point, or along the edges.

Material: Auckland, Nov., 1938, L. M. C.; GV.

Range, etc.: Nest epiphytes (with tank leaf-bases); sometimes rupestral on exposed rocks. Pollen copious; main flowering in late summer. With *Freycinetia*, this plant gives much of its tropical aspect to podocarp-broadleaf forest of the North Island and warmer parts of the South Island. Pollen not yet recorded from peats.

C. microspermum (Col.) Skottsberg.

Text fig. 51.

Grains $38-48 \times 26-32 \times 17-30 \mu$, differing from the preceding mainly in their perfectly smooth exine, and more distinctive rod-layer.

Material: ex Gray Herbarium, determined by L. M. C. One grain (38μ) with 3-slit furrow seen; KOH.

Range, etc.: Much smaller and narrower-leaved than *hastatum*. North Island only (cf. Skottsberg, 1934b).

Comparative: *C. samoënsis* Skottsb. $35-45 \times 34 \mu$; large-grained and smooth as in the preceding species, but with a few coarse granules at one end of the wide furrow (17μ), exine about 1.5μ .

Material: Savaii, Samoa (above Matavanu Crater), altitude 1500 meters, epiphytic in wet forest, collected by Dr. E. Christophersen and E. P. Hume, July 30th, 1931; GV. Endemic in Samoa. Material by courtesy of Miss Marie P. Neal, B. P. Bishop Museum, Honolulu.

THE TASMANIAN MILLIGANIA

Comparative: The pollen grains of *Milligania densiflora*, already referred to by Hooker, are elongate, long-furrowed, and rather small, as in *Astelia*, measuring about $27 \times 14 \mu$, but they are of the spineless type typical of *Collosperrum*. The species is endemic to Tasmania.

Material: ex Gray Herbarium, collected by R. G. Gunn; Gly. jelly with GV.

LUZURIAGOIDEAE

Notes on pollen morphology in this small Austral sub-family are few, but they indicate a striking lack of uniformity. As already mentioned, Fischer (1890, 21) placed *Lapageria rosea* (Chilean) with *Smilax* and *Trillium* amongst spherical grains with scattered fine "warts," while Auer (1933, Abb. 55, fig. 35) figured a similar grain of *Philesia buxifolia* (= *magellanica*), though obviously spiny, and measuring about 45μ in diameter (excluding the 3μ -long crooked spines) from South American peat, and Erdtman (1944b, fig. 2, 8) followed up with a larger grain of the same species, measuring about 80 by 70μ . No exits are indicated in any of this material. The single New Zealand member, on the other hand, is definitely monocolpate, although the furrow is considerably reduced; it lacks all trace of spines or projections and is very finely "pitted" (Cranwell 1942, 293). The writer keyed its grains with those of *Ripogonum*; there is a very striking resemblance, especially in the nature of the ectexine. The pattern in the latter, however, is much stronger. In the previous paper the writer gave 40μ as an average figure, as against 33μ for *Ripogonum*. Study of further material, however, made up in different ways, has proved that the figures are not altogether dependable. Whereas *Luzuriaga* appears to have swelled further (up to 50μ) in the first preparations, fresh material from the herbarium of Mr. F. W. Hunnewell of Wellesley Hills, Mass., prepared by the KOH method, averaged only 35 by 26.5μ .

The strong development of spines, among other features, in one section of the sub-family, adds evidence in favour of splitting. With one sweep, Hutchinson (1934, 113) removed all members from the Liliaceae, without regard for the different pollen types still associated in the resultant Philesiaceae, but much earlier Lindley (1848) had thought *Philesia* distinct, while Goodspeed (1944, 34) had stated his view that *Lapageria* would eventually be removed to some "allied group."

LUZURIAGA Ruiz et Pav.

The native species extends to Patagonia, Tierra del Fuego, and the Falklands. Distribution for the sub-family (which is much as for the Milliganieae) is given by Krause (1930) and by Hutchinson (1934: map, p. 115).

L. marginata (Gärtn.) Benth. et Hook. f.

Enargea parviflora Skbg.

Pl. 6(10); text fig. 54.

Grains monocolpate, as in *Ripogonum* almost globular when greatly expanded ($38-50 \mu$), but with a characteristic unexpanded condition: spheroidal, or rather elongate, with the furrow side flattened, and occupied almost wholly by the furrow area, the size over-all about 34 to 38 by 20.5 to 28μ . Exine up to 2μ thick (KOH), with a very faint but characteristic reticulate pattern, the lumina about 1μ in diameter, the muri built up of crowded slender rods which cause a very slight roughening of the surface. Furrow often 30μ , and about 15μ wide (unexpanded), covered with modified ectexine, the tectum apparently torn apart so that the individual granules of the reticulum are revealed more clearly, especially when the grain is over-distended.

Material: Mount Egmont, Jan. 14th., 1935, F. W. Hunnewell; KOH. Wgmt., Dec., 1937, L. M. C.; F.

Range, etc.: A small montane herb found from Te Moehau summit southward. Spring-summer flowering; entomophilous.

Comparative: *Luzuriaga radicans* Ruiz et Pav. (large-flowered), Andes, Captain Reynolds, ex Gray Herbarium. Grains quite distinct from the preceding, though of same general type: averaging about 27 by 24μ , flattened on one side, completely smooth, and with granulation mainly on furrow membrane.

SMILACOIDEAE

Concerning the pollen of *Smilax*, which has been found both in recently formed peat and in Tertiary deposits (see Selling, 1947, 359),

Mohl (1834, 78) stated that *S. aspera* had granular monocolpate grains with a non-granular furrow, while Selling (l.c.) found *S. sandwicensis* to be furrowless and globular, with distinctive "angular projections" on the exine. DeCandolle (1878, 213) described the grains of "Smilaceae" rather similarly as "siccum ellipsoideum, in aqua sphaericum, papillis brevissimis undique vestitum. . . ."

Further, DeCandolle (l.c., 27) considered the papillate grains of *Smilax* to be less airworthy than the smoother ones of *Ripogonum*.

RIPOGONUM Forst.

The writer (1942, 293) placed the pollen of the only native member with monocolpates such as *Astelia* and *Luzuriaga*, characterized by more or less weakly defined or vestigial furrows, unthickened rims, and very thin granular-flecked exine (also under the superior heading, l.c., 292, of "reticulate or pitted"): the average size was given as 33 μ , a little larger than in most of the preceding species, and larger also than in the Hawaiian *Smilax* (22–28 μ , according to Selling, l.c., 359). Judging from the known records, the reduced condi-

tion of the grains would seem to favour Hutchinson's view (1934, 109) that this is a "considerably advanced" group. *Ripogonum* itself is a very small genus restricted to New Zealand, Australia, and New Guinea.

R. scandens Forst.: Supplejack, Kareao

Pl. 6(11); text fig. 55.

Grains monocolpate, ellipsoidal to spheroidal, but usually flattened on one side, measuring about 34 by 25.7 (30.8–35 x 23.8–29.2) μ . Furrow typically vestigial, occurring as a more or less well-marked rift in the exine, usually shorter than the long axis of the grain. Furrow membrane uniform with rest of grain, or psilate, with scattered granules marking the rift in the ectexine. Exine tectate, about 1.5 μ thick, minutely foveolate (i.e., "pitted"), the lacunae rounded to slightly elongate, rimmed with clavate granules whose tips give a distinctively brilliant appearance to the slightly roughened surface of the exine.

Material: Kaitia, 1913, H. B. Matthews; KOH.

Range, etc.: A high-climbing liane found in lowland forests of all four of the main islands. Insect- or wind-pollinated, flowering in early summer: pollen production sparse.

AMARYLLIDACEAE: AMARYLLIS FAMILY

The Amaryllidaceae, even in the wider sense, as accepted by Mohl, Fischer, Engler and Diels, Skottsberg (1940, 675), and many others is not very rich in pollen types. Zander (1941, 115, etc.) gives examples, partly from the literature: (a) single cells (*monocolpate*), 20–100 μ in diameter, with smooth or reticulate exine, e.g., *Agave*, *Amaryllis*, *Clivia*; *dicolpate* — *Crinum*, *Podocrinum*; and (b) loose tetrads — *Fourcroya* (after Schacht, 1860, 189). His illustrations of *Crinum* (l.c., 22, Abb. 13; 142, Abb. 123) suggest that one very long single furrow, rather than two short furrows, one at each end of the grain, is involved (cf. Iridaceae). The only common type is therefore an ellipsoidal or chisel-shaped (Mohl, 1834) monocolpate grain of Liliaceous type characterised by a long, broad, active furrow, rather smooth exine, granular to spiny (?) or reticulate, and with considerable range in size.

The exine may be reticulate over the whole surface, as in *Agave americana* (Fischer, 1890, 31) or diminish in coarseness toward the fur-

row membrane, as in *Agapanthus umbellatus* — if Hutchinson's classification can be accepted — (see Zander, 1937, Taf. I, Abb. I: an excellent photomicrographic illustration), or be lacking altogether on the membrane, as in *Pancratium* (Fritzsche, 1837, 134 and Taf. VIII, 7), whose reticulation was apparently first noted by Purkinje (1830, 29).

HYPOXIDIOIDEAE

Whereas Mohl and Baker (1878) separate *Hypoxis* and its allies from the Amaryllidaceae, Hutchinson (1934, 129) goes much further, excluding the Agaveae as well, for example, but including the Allieae and Agapantheae, stating that *Agapanthus*, usually included in the Liliaceae, is the most primitive genus in the family. His researches emphasize the difficulty of separating the Liliaceae and the Amaryllidaceae, whether on ovary characters or on the arrangement of the inflorescence and its bracts. Fischer (1890, 31) and others have drawn attention to the similarity between the pollen grains in the two families.

HYPOXIS L.

Hutchinson (l.c., 163), in removing the Hypoxidaceae (*Campynema*, *Campynemanthe*, *Hypoxis*, *Paurida*, and *Curculigo*) to the Haemodoriales, places the family near the Apostasiaceae, and states boldly that this is a stock which "has probably given rise to the Orchidaceae." It should be noted that the diandrous orchids, the most primitive, also have single monocolpate grains with little pattern.

Purkinje (1830, Tab. II, 7a) provided an early illustration of a single elongate grain, shaded but nondescript, of *H. prolifera* (*sobolifera*?), while Mohl (1834, 38, 77) described the ellipsoidal grains of *H. elegans* and *H. juncea* as having one long furrow, a smooth granular exine, and a non-granular furrow membrane, contrasting with the granular membrane of *Curculigo recurvata* in the same group. Mohl's comparison of *Hypoxis* with *Smilax aspera* (l.c., 77) and *Pandanus* does not seem valid (although Selling 1947, 340, accepts them without criticism) since *Pandanus* is pored, any furrowlike depression being merely a fold in the exine, and *Smilax* lacks both pore and furrow.

Minute sketches of two grains of *H. villosa* merely hinting at a furrow (Schnitzlein, 1843-1846, Tab. 63, fig. 9) add little to the picture but Wunderlich (1936, Abb. 3, fig. 12) provides a cross-section of a grain of *H. sobolifera*, showing the typical outline, and the thinning of the exine over the pointed ends of the grain. For *Zephyranthes* (Amaryllidaceae proper), she notes a much thicker exine and states that the grains tend to germinate in the anthers. Pohl (1928) has placed the Hypoxidaceae with Pandanaceae (certainly following

Mohl) amongst "einfaltige" types: Zander (1935, 58) quotes this without comment.

There is thus little information about these rather featureless grains. Cranwell (1942, 292), however, treated the New Zealand species rather more fully, considering the space limitations of the key. Its grains were shown to be comparable with the rather smaller ones of *Iphigenia novae-zelandiae* and *Libertia*.

About 100 species of *Hypoxis* are known: they are entomophilous (Pohl, 1928). In the following account three-slit furrows in the genus are mentioned for the first time.

H. pusilla Hook. f.

Pl. 6 (12, 13); text figs. 58 a, b.

Grains monocolpate (or occasionally with forked furrows), about 23-33 μ in greatest length, typically ellipsoidal when unexpanded, irregularly spheroidal when expanded, more or less angled when possessing divided furrow; tending to fold and collapse because of weakness of the exine. Furrow long, typically 3-4 μ wide, or roughly triangular in outline; rims usually roughened. Exine very thin (about 0.5 μ), rather strongly flecked (reticulate?), scabrate on furrow membrane.

Material: #1184: Wairau River, Marlborough, on sandy ground; collected by J. H. MacMahon; GV, EM.

Range, etc.: A small, rather rare herb, spring-flow-ering; found also in Victoria and Tasmania. Entomophilous. One record in North Island (Hawkes Bay-Colenso); South Island: Wairau River mouth; Banks Peninsula; Canterbury Plains (Cheeseman, 1925).

The most recent record is from Wither Hills, Blenheim, where it was found by Miss L. B. Moore (1949, 15) in September, 1948.

IRIDACEAE: IRIS FAMILY

The Iris family is a large and widely dispersed entomophilous family centered in South Africa and South America, and with only one genus, *Libertia*, represented in New Zealand.

From almost the earliest accounts it became clear that there existed a considerable range of pollen types in this family. Mohl (1834, 77), for instance, described spherical granular grains of *Crocus* spp., either acolpate, or "in gewundene Streifen getheilt," and ellipsoidal grains with a single longitudinal furrow, the exine granular ("punktirt") over the whole

surface (*Ixia*) or with pattern lacking over the furrow (*Sisyrinchium*), and reticulate in *Iris*, while *Tigridia Pavonia*, also with reticulate exine, was considered, with a few others, to have two longitudinal furrows. Fritzsche (1832, 22) has described pollen grains of a *Sisyrinchium* exactly as for *Arthropodium fimbriatum*: oval when dry, "mit zwei übergeschlagenen Lappen welche eine scheinbare Furche bilden," and in 1837 (p. 711 and Tab. XI, fig. I) had discussed and beautifully figured the pollen of *Tigridia Pavonia*, with its coarsely reticulate exine, thickened by rods.

FIG. 58: AMARYLLIDACEAE. FIG. 59: PALMAE. FIGS. 60-65: ORCHIDACEAE.
 × ca. 900 unless otherwise indicated.

58: *Hypoxis pusilla*, showing single, forked, and confluent furrows; *b* (lower) exine pattern indicated, 30-34 μ .
 59: *Rhopalostylis sapida*, *a-d* smooth grains, mainly tectate (expanded, with contents); *a* lateral view (section);
b distal view; *c* and *d* end views, exine coarser; *e* distal view, furrow closed, 55 μ ; *f* lateral view, furrow retract-
 ed (endexine black), 60 μ . 60: *Thelymitra venosa* var. *typica*, *a* tetrad opening up; *b* dyad; *c* exine detail at
 mid focus (× 1125). 61: *Adenochilus gracilis*. 62: *Chiloglottis cornuta*. 63: *Pterostylis venosa*. 64: *Petalochilus*
calyciformis, showing elongate and angled furrow areas. 65: *Earina autumnalis*, *a* edge of pollinium; *b*, separated
 tetrads (both at low magnifications); *c* two views of tetrads.

and scattered granules on the floor of each of the lacunae ("Felder"). It is clear that Fritzsche accepted the presence of two furrows, although he stated that they were derived from a single furrow.

Other early records are brief, from Koelreuter (1811, 182) for *Sisyrinchium Bermudianum* and Purkinje (1830, Tab. II, figs. 2, 3) for *S. palmifolium* and *Iris florentina* ("Pollen maximum") respectively, to Schnitzlein (1843-1870, 61): "Pollen plerumque ellipticum, granulatum," (with figures 7-8 showing two dry and one moist ruptured grain) and Edgeworth (1877, 17), partly in summary of early papers, but giving an original measurement of *S. magellanicum* (cf. Auer, 1933, Abb. 56, figs. 69-71, showing the monocolpate grains in different positions).

Fischer (1890) followed with more detailed notes on furrowed and furrowless types, on exine characters (smooth, warty, reticulate with high rods ["Stäbchen"] as in *Tigridia* [8 μ high], and so forth). Most genera appeared to have one furrow, but he confirms the earlier descriptions of two-furrowed grains (l.c., 33), and of some with spiral furrows. Many were shown to be large (150 μ , or rarely 250 μ in *Iris squalens*). Zander (1935), following on the work of Mohl and Fischer, made two main divisions, acolpate, spherical, up to 137 μ in diameter in *Crocus*, and monocolpate, ellipsoidal (as in Liliaceae and Amaryllidaceae); and he points out, as had Griebel (1930, 1931) that it is difficult to separate this type of pollen in overseas honey from that of genera such as *Liriodendron*. Later (1941, 115), Zander mentioned in addition the double-spiral furrow of *Crocus* spp. and gave useful sketches of grains of *Iris pseudacorus* (Abb. 14) and *I. reticulata* (Abb. 15) whose monocolpate, reticulate grains are described more fully by Erdtman (1943, 63, Pl. III, fig. 28). Zander follows Armbruster and Oenike (1929) in interpreting two-furrow types as monocolpate in origin. Selling (1947, 363) adds the first description of the pollen of *Sisyrinchium acre* (E. Maui and Hawaii), while Cranwell (1942, 292) had already given a brief outline for the

nearly related *Libertia*, apparently the first, as Schnitzlein had neglected *L. ixioides* in his Brazilian diagnoses.

SISYRINCHIEAE

Hutchinson (1934, 135) considers that the characters of the Iridaceae are largely those of the Liliales hence similarities in the pollen grains are to be expected. He considers that *Sisyrinchieae* contain the most simple and primitive forms, but the comparison of *Libertia* with *Sagittaria graminea* that he suggests is not fortified by pollen-morphological characters, as the grains of *Sagittaria* are spiny and have 12-15 pores.

LIBERTIA Spreng.

L. grandiflora Sweet: Tukauki, Native Iris Pl. 6(14).

Grains monocolpate, about 30-33 x 20-25 μ (acetolysed), ellipsoidal to pear-shaped when not fully expanded, with the furrow closing tightly at the ends and only about 3.3 μ wide in the middle: otherwise more rounded when expanded, often slightly flattened proximally, the furrow opening to about 10 μ on the rounded distal side. Furrow running length of grain, or reaching onto other side, often oblique. Exine very thin, psilate, with obscure rod pattern.

Material: Auckland, Sept. 20th, 1937, L. M. C.; EM.

Range, etc.: A tufted herb very closely allied to the following: found throughout both main islands.

L. ixioides Spreng.; 30-33 x 20 x 20 μ . Wgtn., L. M. C., 1937; EM.

L. peregrinans Ckne.; 26-34 x 16 x 16 μ . Dunedin, L. M. C., 1949; KOH.

Range, etc.: Both are lowland species, *ixioides* being found in the 4 main islands. Miss Heine (1937, 142) records a burrowing bee as a pollinating agent for *ixioides*.

Comparative Material: *L. paniculata*, N. S. W., ex Gray Herbarium. Grains about 34 x 27 μ , with wide furrow; EM.

L. coerulescens, Chile, ex Gray Herbarium. About 28-32 x 24 x 24 μ : almost textureless.

ORDER 9: PRINCIPES

PALMAE: PALM FAMILY

The Palmae, with 1500 odd species, exhibit both anemophily and entomophily (see Hansgirg, 1897; Pohl 1930, 259; Skottsberg, 1940, 620). Some produce nectar and are scented: the pollen may stick together or separate freely. Drar (in Täckholm and Drar, 1950) gives a full account of hand-pollination of the date palm, mentioning that insects, etc., are relied upon in only a few areas. This pollen, when stored, may remain viable for at least a year.

While one-furrowed grains are typical of the family, it is interesting to note that a single aberrant type has been reported by Erdtman (1944b, 165) who figures characteristic "three-slit" furrow areas for *Acanthorhiza Mocinni* and *Euterpe oleracea* (also monocolpate) and mentions 7 other genera in which this shape is typical or occasional. Selling (1947, 337) adds *Cocos nucifera* to the list: "rarely trichotomosulcate (one grain seen, . . .)." This furrow-form, noted first by Fritzsche (1832) for *Dianella*, may perhaps suggest a further link between the Palmae and the Liliaceae (cf. Erdtman, l.c., 166), but it is not confined to them, being found as far afield as in *Laurelia novae-zelandiae*.

If these rather rare grains are excluded, the pollen type for the family appears very uniform: a monocolpate (monosulcate) grain, occurring singly, ellipsoidal, and often proximally flattened when unexpanded, almost globular when expanded, ranging from 15–70 μ . Furrow wide, very long, usually widening at the tips, very active in volume-change. Furrow membrane thin-walled, very distensible, bulging greatly on expansion of the grain. Exine rather thick, smooth, or roughened, the pattern granular, more or less reticulate, or spiny. Intine thickest under furrow.

In recent years consideration of the almost exclusively monocolpate condition of these pollen grains has given rise to sharply divergent views. Wodehouse (1935, 236, 303), on the one hand, states that the type is "unquestionably primitive," only the almost complete closure of the more elongate furrow setting

it above the grains of primitive gymnosperms such as *Cycas* and *Ginkgo*. He sees "great stability and persistence" of this type of furrow running through the Cycadales, many monocotyledons, and some "primitive" dicotyledons: "Indeed" it "appears to have been the starting point from which the many elaborate and varied forms of grain of both angiosperms and gymnosperms have evolved." Erdtman (l.c., 166) vehemently rejects this linking of the palms with the gymnosperms.

Wodehouse treated the family as quite isolated, making no comparison with the grains of the Liliaceae, Hypoxidaceae, and Iridaceae as was later done by the writer (Cranwell, 1942, 292) who, for instance, paired *Rhopalostylis* with *Chrysobactron* (*Bulbinella*) in the key. Whatever the true relationships of the Palmae, it is difficult to explain why the single furrow occurs as it does—so commonly in gymnosperms and monocotyledons (though only proximally in the Orchidaceae), and so rarely in the dictotyledons, e.g., *Ascarina* (Chloranthaceae), *Laurelia* (Monimiaceae), and *Macropiper* (Piperaceae), to mention only New Zealand examples (l.c., 292–293): see p. 11 and Table 1, p. 73.

The most recent and detailed work on palm pollen has been mentioned but many have made small contributions, beginning with Purkinje (1830, Tab. IV, 7a, showing a small spherical grain of *Chamaerops Palmetto*); Mohl (1834, 79 for *C. humilis*—"ellipsoidisch, eine Langefürche, Streifen punctirt"); Gaudichaud (Plates: 1866, Pl. 14, fig. 10), who figured grains of *Phytelephas Ruizii* and (Pl. 6) two curious spiny units of three grains for *Nipa frutescens*, apparently drawn to suggest adherence in a tetrad; Schnitzlein (1843–70, 75a, 6), who also referred to *C. humilis*, while Drude (1881, p. 253) added a brief family description and referred to spiny grains in *Mauritia*. Fischer (1890, 30) added a warty-punctate type. Wodehouse (1943, 7) gives size-details, etc., of small wind-carried grains (only 10–25 μ), while Zander's honey work (1941, 16, 108, 112, 141, 160, etc.) has been rich in

comment, especially as he studied *Phoenix* pollen in connection with analyses of Egyptian mummy honey.

The Fossil Record

Authentic fossil records of palm pollen are few. Selling (1947, 336), after finally managing to distinguish *Pritchardia* grains from monolete spores of pteridophytes, reports up to seven per cent of these grains from recent Hawaiian peats. As *Pritchardia* grows on the bogs (e.g., Kohala mountains), it is probable that both forest and bog species have contributed to the fossil pollen picture.

Miocene records of pollen and wood of the same taxon (Sabaleae) are given by German workers, and for *Cocos zeylanica* Berry (Ceroxyloideae) from Cooper's Beach, North Auckland—a valuable record also backed by remains of nuts (see note by Berry, 1926 on *Cocos* and *Phymatocaryon* from this deposit). Couper (1951a, Fig. 2) also reports "Nikau" pollen through the Miocene to the present day.

CEROXYLOIDEAE : ARECEAE

RHOPALOSTYLIS Wendl. et Drude

Two endemic species of *Rhopalostylis* occur in New Zealand, and of these the mainland one (*R. sapida*) has the most southerly distribution of any palm in the world. Three other species are known, one from Norfolk Island, and two from Polynesia.

Small yellow-tinted grains of *R. sapida* figured by Hooker (1853, 262, tt. 59, 60) showed vague traces of furrow while Edgeworth (1877, fig. 27) gave unusually clear sketches of grains of *R. Baueri* (Norfolk Is.): "eye-shaped, smooth, . . ." when unexpanded, but rounded and "somewhat echinulate" (!) in water. His measurement of 12/6000 in (= ca. 50 μ) coincides with averages for unexpanded grains of the native species.

He did not stress the presence of an apparent furrow indicated in the sketch of an unexpanded grain. The following description of *R. sapida* grains is amplified from the earlier description in Cranwell (1942, 292), and *R. Cheesemanii* is added.

R. sapida Wendl. et Drude: Nikau
Pl. 6(15), Pl. 7(7); text figs. 59a-f.

Grains monocolpate, rather large, averaging 50 μ (40–70 μ in extreme size-range), ellipsoidal, and deeply channelled (like a date-stone) when unexpanded, and ellipsoidal to irregularly rounded, or globose when expanded, the proximal side usually flatter than the distal (furrow-bearing side) at all times. Furrow very long, markedly broader at the ends, rather variable in appearance; furrow membrane very distensible, but delicate, tending to rupture. Exine almost smooth, fairly thick (1.5–3.3 μ), ectexine brownish (acetolysed), with small radial elements forming a fine reticulum of crowded, $\pm$ clavate rods, coarsest on proximal side,¹ endexine colourless, extending over the furrow membrane. Intine slightly thickened under furrow; cell contents finely granular, capable of great distension.

Material: Waitakere Range, Auckland, L. M. C., (a) June, 1936; EM; (b) June, 1937, EM, MG.

Range, etc.: A graceful tall palm abundant in lowlands of North Island and occurring as far south as Banks Peninsula and Ross (south of Hokitika, as given by Cheeseman, 1925, 282); also in Chatham Islands. Flowering mainly in mid- or late-summer. Pollen copious, whitish in colour. Probably carried both by wind and by insects, etc.

Fossil: Rangiputa, N. Auckland (from coastal sedge peat collected by Mr. E. T. Frost): *probably* this species.

R. Cheesemanii Beccari:² Kermadec Nikau

As in the preceding species, measuring about 46 x 36 x 34 μ (KOH).

Material: Auckland (cultivated), collected by Mrs. D. Clark, June 13th., 1951; L, KOH & acid Fuchsin.

Range, etc.: Kermadec Islands, about 300 miles north of mainland: Sunday Island, abundant from sea-level to the tops of the hills, altitude 1500 ft., . . ." (Cheeseman, 1925, 282).

¹ Irregularities (contrast figs. 59a and f from different samples) may be due to development of texture or to abnormal divisions.

² Identification tentative as the fruit has some of the characters of *R. Baueri*.

ORDER 10: BURMANNIALES

BURMANNIACEAE

This small saprophytic family of about 125 species is so reduced that it is difficult to see where its affinities lie. It has been placed near the orchids (Bentham and Hooker, 1865; Engler, 1889a; Hutchinson, 1934, 175) but Jonker (1938, 7) holds that only the small size of the seeds of this "somewhat derived and undoubtedly very old" family favour this position. Like Lindley (quoted by Jonker, l.c., 5), he sees some likeness to the Iridaceae and considers that the Amaryllidaceae and Taccaceae are perhaps related. On the grounds of pollen morphology alone, there would seem to be little connection with the Taccaceae, which have much larger, clearly one-furrowed grains with rather thick exine. As will be shown, hints of furrows or pores are known in the Burmanniaceae, and Dr. Orville Dahl has informed me (private communication, July 3, 1945) that he has seen *Apteria setacea*¹ material in which "the essentially smooth pollen grains are borne in basically tetragonal tetrads." Small or absent apertures, and the presence of tetrads, are characteristics which link up perhaps more closely with certain groups of orchids than with any of the families mentioned.

Hutchinson (l.c., 177) considered the group as a whole "remarkable and very advanced" and placed it near the *Hypoxidaceae* (*Curculigo*): he made 3 divisions, his *Thismiaceae* being "much more modified from the orthodox type of Monocotyledon" than his Burmanniaceae. He followed Schlechter (1921) in placing the New Zealand species in *Sarcosiphon* (*Thismia*), although Cheeseman (1925, 330) had preferred to retain *Bagnisia*, merging with *Thismia* being a "retrograde" step, in his opinion. Jonker, however, treated it as identical with the Tasmanian species, and showed that, with *T. americana* (found only on the outskirts of Chicago) it formed the strangely discontinuous section *Rodwaya* Schltr.

None of these systematic accounts gave notes on pollen morphology, and they are omitted even in recent exhaustive surveys of Malaysian genera.

Mohl (1834, 77) had described the grains of a *Burmattia* (*Tripterella violacea*:¹ see Edgeworth, 1877) as "Rundlich oval, auf einer Seite starker gekrümmt, an beiden Polen ein kleiner Nabel . . ." *Polen* should probably be treated here as "ends" of the grain), while Schnitzlein (1834-1846, fig. 60) showed 7

minute grains of *Burmattia bicolor*, some with suggestions of a furrow or fold at one end.

Von Mueller (1891, 235; fig. 5) illustrated three bean-shaped pollen grains of *Thismia Rodwayi*, stating in an appendix to his diagnosis for the species, that they were "whitish when moist, almost dimidiate globular." Miss Pfeiffer (1914, 130; fig. 29) also indicated a very reduced type in her account of *T. americana*:

"In mature stages the pollen grains are slightly oval. They are very pale, almost transparent, with a pale green cast, due to little bodies, probably fat, . . . The microspores are loose and free, . . . Before shedding, the generative nucleus divides (fig. 29). A granular mass in the spore suggests the presence of a prothallial cell, . . ." No mention is made of the exine. In the New Zealand material I have observed unequal massing of the contents and have tentatively interpreted the smaller mass as a hyaline body underlying a weak "apical" exit.

In the writer's key (Cranwell, 1942, 291), Cheeseman's nomenclature was followed, and the pollen of the native species placed amongst acolpate types: "Grain 'humped' on one side, flat on the other; 17 by 12 μ , patternless." The following description, based on the same material, gives consideration to weaknesses in the exine not mentioned above, but further work is needed to ascertain whether the grains may bear a true furrow area on the flattened side rather than a pore at one end.

THISMIA Griffith

T. Rodwayi, F. v. Muell.

Pl. 7(2).

Grains mainly seeming inaperturate, about 17 x 12 μ , asymmetrical, usually humped on one side, the flattened (distal?) side opposite often channelled, with extremities distinctly apiculate, a slight break in the exine suggesting the aperture of a small vestibule. Exine very thin, psilate; intine rather thin over most of the grain but thickening greatly at one beaked end, thus probably causing distension and bursting of the weak spot; contents packed with starch granules.

Material: Specimens collected by Mr. E. S. West in the area in which the plant was first discovered by H. Hill; MG.

Range, etc.: New Zealand: Only at Opepe, near Taupo, at 2000 feet above sea level, where it grows under *Podocarpus dacrydioides* and other trees; flowering in January. Tasmania: first reported by Mueller (1891) from collections made by L. Rodway at Derwent, and later, on Mt. Wellington.

¹See also (a) Seubert (1847, 57-58) for *Apteria* (coherent) and *Dictyostegia* ("subceraceum"); and (b) Martius (1824, 10; fig. 5) for *B. bicolor*.

ORDER 11: ORCHIDALES

ORCHIDACEAE: ORCHID FAMILY

In the early period of orchid development, many millions of years ago, there were six anther-bearing stamens in the flower and the pollen was composed of loose, separable grains. Then a reduction in the number of pollen-bearing stamens took place—when or why we do not know—and the pollen grains began to cohere together, first in fours (tetrads), and later became compacted into definite masses of varying texture and different form . . . —Oakes Ames (1946, 21).

The evolution of massulae and pollinia indicated above is paralleled only in the Asclepiadaceae and the Mimosaceae. While now considered a most efficient method of effecting pollination, it was thought most baffling by Darwin, who at first failed to balance the apparent waste of hundreds of thousands of grains against the vast numbers of ovules (sometimes millions) to be fertilized in each flower: "I never was more interested in any subject in my life . . ." wrote Darwin to Sir Joseph Hooker in 1861 (cf. Ames, 1948).

The earliest studies of the pollen apparatus in orchids appear to have been those of Trew, Brogniart, Lindley, Robert Brown, and Bauer, Brown in 1831 being the first to puzzle out the structure of the flower as a whole. Countless papers have since mentioned the pollinia in particular, Lindley, in 1830, making full use of them as a basis of classification of the subfamilies. Pfitzer (1889) and others shifted emphasis to the vegetative features, but Schlechter (1926) reasserted the taxonomic value of both the free and coherent types of grains.

Against the criticism that pollinia are fugacious should be set the fact that, under moist conditions generally, and especially in montane mossy forest in hot countries, the orchids tend strongly toward self-pollination, or even cleistogamy. This anomaly in a family conspicuously adapted to insect-pollination has been noted by Cheeseman (1892, 295), Schlechter (1914), and others.

Since the pollen is rarely, if ever, recovered from fossil deposits, from atmospheric collections, or from honeys, its study has had little practical value. Descriptions are thus mainly confined to pollinia types, or developmental stages, such as those in *Vanilla*, etc., by Swamy (1947, 1948). Mohl (1834) and Fischer (1890, 18, 19, 32), gave useful groupings, the former, however, referring to 2-furrowed grains, while the latter stated that a single furrow occurred on the outer (i.e., distal) side of each grain of a tetrad. Selling (1947, 367), in the absence of free grains in the Hawaiian species he investigated, appears to have followed Fischer in deciding that "Monads (monosulcate) are of

rare occurrences . . ."; that grains retained in tetrads do not bear furrows, and that those deep within the pollinia lack sculpture (*sensu lato*) as well.

In the Australasian material at least it is clear (1) that free grains (monads) are very common; (2) that their weak areas are proximal* (judging from their position in young or unstable tetrads); (3) that no comparable weak areas exist on the distal sides of stable tetrads whether free or aggregated; and (4) that none of the interior tetrads in pollinia are wholly lacking in sculpture.

THE NEW ZEALAND MATERIAL

Bauer (1830–1838), noted for his illustrations of pollen grains and for a curious theory of orchid fertilization (questioned at once by Lindley), appears to have provided the first figure of native orchid pollen (see *Pterostylis Banksii*, p. 69). Others, referring to "pollen," have invariably meant aggregations of grains. The individual grains have gone almost unnoticed, except by Cranwell (1942, 308), who, however, selected only one free "type" (*Orthoceras*) and a few typically tetrad-bearing "types" (*Chiloglottis*, *Earina*, *Pterostylis*) with component grains about 16–26 μ long.

It is beyond the scope of this paper to dwell on the pollinia. It is well known that they may be free, or attached to the rostellum by cement, or by discs: this cement has been known since Purkinje's time (1830) to occur in the form of threads (as in *Epilobium*), as an envelope around the grains, or as a central axis, sometimes elongated into a caudicle with an elastic core different from the other sterile material. Perhaps because of this coating and embedding substance the germination of pollinia may take ten times as long as for free tetrads (cf. Godfrey, 1933, 19). Brief descriptions of the pollinia of New Zealand orchids will be found in Cheeseman (1925) and earlier authors.

* As in *Acacia* massulae, which have no furrows on the distal side, but weak proximal sides from which the pollen tubes emerge (Newman, 1934, 279).

Fig. 66. *Prasophyllum patens* R. Br. Material from South Australia, from the Oakes Ames Orchid Herbarium.
It is generally held that dwarfs among united grains are sterile, but Barber (1942, 101), in his important paper on the orchids, shows that where contact faces are uncuticularized (as apparently in the tightly cohering massulae figured above) division is synchronous, all grains are viable, and the deficiency of one nucleus is made good by the others.

Schlechter's classification, followed here, places all the native genera (all monandrous) in the Acrotonae (a): Pollinia granular, soft — *Polychondreae*; (b): Pollinia smooth, waxy, or cartilaginous — *Kerosphaerae*.

Because of conflicting statements as to the furrow (or sulcus), the following account is based entirely on New Zealand and Australian material.

Pollen types: Tetrads permanent or unstable, 15–70 μ , mainly rhomboidal, apparently furrowless when coherent, but with weak proximal facets. Components (in twos [rare], eights, or multiples, as well as in fours) or free grains very small (7–9 μ) to medium-sized (36 μ), mainly 18–25 μ ; variable in size and shape due to compression, but mainly spheroidal (expanded) or grooved or faceted (unexpanded) on weaker side. Exine usually in-tectate (reticulate), but with a smooth or pitted tectum over distal side of grain. Columellae straight or clavate.

In some sub-families the exine pattern is very distinctive and should have some value in classification.

In the condensed systematic part to follow, only two genera are missing; much detail will be found in the tables. About half of the native species are found also in Australia or Tasmania, New Guinea perhaps being the centre of distribution for a few such as *Bulbophyllum* (N. G. 500: N. Z. 2). Only one genus, *Spiranthes*, is cosmopolitan.

Polychondreae

THELYMITRA Forst.

... an orchid with regular flowers persisting to the present day ... — Godfery (1933, 5).

The beautiful sun orchids form a genus of under 50 species, mainly in Australia and New Zealand, but extending as far north as the Philippines. Hutchinson (1934) especially sees in their actinomorphic flowers one of the "missing links" provided by the monocotyledons of the Southern Hemisphere. The high incidence of free grains is certainly reminiscent of supposedly ancestral orchid forms such as *Cephalanthera* (Fischer, 1890, 33; Godfery, 1933, 46) which lack a rostellum, but both permanent and unstable tetrads are also found in *Thelymitra*.

As already stressed, the putative furrow is proximal. In over-expanded grains (L) the membrane is convex and is delimited only by the change from its thinner, open-reticulate surface to the denser and more or less tectate

cover of the rest of the grain. In less expanded grains (MG, GV) the weak area is depressed and more clearly indicated.

The following generic description is based on the following species: *caesia*, *decora*, *ixioides*, *longifolia*, *pachyphylla*, *uniflora*, and *venosa*.

Pollen type: Grains uniform, 22–34 μ , mainly free, or in rather loose tetrads (IV: up to 60 x 50 μ ; also types I, II). Exine reticulate, lumina 2–4 μ in diameter, often smaller over contact areas. See Table I.

Many grains may be compressed or defective (e.g., dyads of small size). Rhomboidal tetrads in particular tend to produce paired grains of two sizes and shapes, the larger pair having elongate furrows and the smaller more strongly faceted ones marking the contact faces. Paired grains have also been reported from hybrid *Funaria* by Wettstein (1924), but here disparity is explained by crossing of parents with different-sized spores.

Disparate pairs of spores have also been observed by the writer in native *Psilotum nudum*.

ORTHOCERAS R. Br.

O. strictum R. Br.

Pl. 7(10).

Grains free, spheroidal, or angled, 25–28 μ , rarely elongate (39 x 20 μ); sometimes in loose rhomboidal tetrads. Exine about 1.5 μ thick, mainly tectate-perforate, the lumina larger (reticulate) beneath surface and over furrow areas; muri delicate, variable in width, with clavate rods fused top and bottom, or sometimes free on floor of the 2 μ -wide lumina.

Material: Great Barrier Island; MG.

Range, etc.: Lowlands of both main islands, as far south as Nelson Province; found also in east and south Australia. Genus monotypic.

MICROTIS R. Br.: PRASOPHYLLUM R. Br.

The grains of these genera appear to be distinguished to some extent by size, the former being about 30 μ singly, or 40–60 μ in tetrads (Type IV), while the latter are smaller, as in *P. pumilum*, or in dense tetrads of 48 x 30 μ (*rufum*). Further, *Prasophyllum* was seen to have irregularly compressed tetrads in mas-sulae of 8, or more.

W. J. Hooker (1835, *Botanical Magazine*, IX, n.s.) illustrated pollinia and both square and rhomboidal tetrads of *M. Banksii* (now *M. porrifolia*).

See Table I, p. 77. For range, etc., see recent helpful papers by Mr. E. D. Hatch. **Illustrations:** *M. unifolia* (Forst. f.) Reichb. — Pl. 7 (8); *P. Colensoi* — Pl. 7 (6); *P. patens* (not native) — text fig. 66.

CHILOGLOTTIS R. Br.

A genus of 3 species, with 2 common to Australia and New Zealand: tetrads of the following were described by Cranwell (1942, 308).

C. cornuta Hook. f.

Text fig. 62.

Tetrads stable, about $38\ \mu$ (I), or $52\text{--}65 \times 32\ \mu$ (IV); components or free grains (occasional) about $30 \times 16\ \mu$; contact faces angled, reticulate; exine of rest of grain slightly rough, with smaller lumina.

Material: (a) Devonport, L. M. C.; EM. (b) Ex Botany Division, D. S. I. R.; GV.

Range, etc.: North Auckland to subantarctic islands.

Comparative Material: *C. diphylla* [Tas., collected by R. C. Gunn, 15th May, 1844 (ex Oakes Ames Herbarium); GV]. Tetrads smaller and more compact, $30 \times 21\ \mu$; exine with smaller lumina.

ACIANTHEAE AND CALADENIEAE

The pollen grains of this rather uniform group appear to have escaped attention.

Pollen type: Grains mainly free, from $18\text{--}25\ \mu$, but with tetrads more typical of some (e.g., *Aporostylis*, Type I, and *Caladenia Lyallii*). Exine sometimes reticulate, but more commonly tectate-perforate and smooth over greater part of grain, the rods clavate at tips, or at both ends (*Aporostylis*), thus reducing size of lumina: weaker side of grain reticulate, lacking tectum.

Acianthus — *Lyperanthus*, See Table I, p. 77.

As will be seen, *Lyperanthus* is set apart by a very distinctive exine pattern which is not duplicated, as far as I know, in any of the orchids. *Calochilus*, placed in the Thelymitreae by Schlechter and in the Caladenieae by Rupp, has characters common to both groups, judging by the incidence of free grains, size (about $16\text{--}32\ \mu$), and psilate to foveolate exine (as in *Robertsonii* = *campestris*), or reticulate, or patchily devoid of sculpture, as in the loosely cohering grains of *paludosus*. Details of a selection of my material are given below, and in the tables.

Acianthus reniformis (R. Br.) Schltr. var. *oblongus* (Hook. f.) Rupp and Hatch = *Cyrtostylis oblonga* Hook. f.

Grains mainly free, variously shaped, often flattened on one side, from $20\text{--}28 \times 15\text{--}25\ \mu$. Exine coarsely reticulate over whole surface, forming a characteristic pattern of deep-walled, irregularly shaped lumina up to $4.5\ \mu$ in diameter, and with chains of much smaller lumina set in their walls; exine rods about 1.5

μ high, tips projecting to roughen surface. Pattern weaker on compressed (proximal) side.

Material: Rangitoto Island, W. A. Sledge; F.

Range, etc.: North and South Islands: flowering in winter and spring.

Adenochilus gracilis Hook. f.

Text fig. 61.

Grains free, irregular, with size-range as in the preceding species, $20\text{--}24 \times 18\ \mu$. Exine tectate and smooth, however, except over furrow.

Material: South Westland, Ruth Mason, Dec. 29th, 1948; KOH.

Range, etc.: Both main islands, endemic. Hatch's statement (1947) that the "pollen" is granular obviously refers to the nature of the pollinia, not to the exine of the grains.

Lyperanthus antarcticus Hook. f.

Grains free, $20\text{--}27 \times 18\text{--}21\ \mu$, ellipsoidal, or with one flattened side containing the furrow. Exine almost $2\ \mu$ thick (perforate), foveolate to reticulate, the lumina usually larger below the surface, about $1\text{--}2\ \mu$ across, forming a somewhat rugulate surface, with channels between.

Material: Mount Dennan (3500 feet), Tararua Range, L. B. M. and L. M. C., Jan., 1933; MG.

Range, etc.: From the above area southward to Auckland Island, apparently not common; endemic. Four other endemics occur in Australia, and one in New Caledonia.

PETALOCILUS Rogers

This endemic genus of 2 very local species, first described in 1924, was considered by Mr. Rogers to be perhaps more nearly related to *Caladenia* and *Glossodia* than *Thelymitra*, hence its position in this account. Further, because of their fine exine pattern, the pollen grains are in keeping with this grouping; however, the pollen evidence offers nothing conclusive.

P. calyciformis Rogers

Text fig. 64a-c.

Tetrads in dense masses, mainly separating, the individual grains broadly ellipsoidal, about $23 \times 17\ \mu$ (unexpanded), traversed by a broad proximal furrow depression about $11\ \mu$ wide. Exine intectate, psilate, less than $1\ \mu$ thick.

Material: Ex Botany Division Herbarium, collected by H. B. Matthews.

Range, etc.: Known only from a small area, now disturbed, near Kaitia, north Auckland. Not seen alive recently (Rogers, 1924, 65).

CORYBAS Salisb.

The pollen grains are smaller than in most of the groups already described. They may be free, as in *Pogonia* (cf. Ames, 1947, Pl. IX, fig. 7), or they may be in tetrads. The following description is based on the species listed in the tables.

Grains mainly 14–17 μ , or as little as 10 μ (empty ?); perhaps typically free, separating into unstable tetrads. Exine psilate, with delicate structural pattern; intine thick; hyaline bodies sometimes present (*macranthus*).

Range, etc.: cf. Cheeseman (1925, under *Corysanthes*) and Hatch (1947).

PTEROSTYLIS R. Br.: Hooded Orchids

Over 50 species are known, the majority being native to Australia (over 40): 4 outliers occur in New Guinea and New Caledonia. Recent notes on the genus will be found in Hatch (1950). The following account is based on 9 of the 14 native species, viz. *Banksii*, *barbata*, *graminea*, *micromega*, *nana* (*puberula*), *mutica*, *nutans* (the last 2 from Australian specimens from the Oakes Ames Herbarium), *venosa* and *trullifolia*.

As early as 1832, Bauer had referred with wonder to the presence of solitary grains in *Banksii* (Curtis' *Botanical Magazine*, #3172): "These grains, in their ordinary form, consist of three- or four-celled corpuscles, or as Botanists express it, 'e sphaerulis quaternis conflatis' (see Brown, Prodr. p. 310). I therefore send you herewith, a sketch of some grains of your plant, which are represented as seen under water, except that at A, which is in a dry state, when it appears collapsed. This I consider an important circumstance, and could not be detected by Botanists possessed only of glasses of moderate power." His figure 10 gives tinted reticulate grains, 4 of them with traces of an elongate exit. His somewhat ambiguous remarks have already led to misunderstanding (cf. Wodehouse, 1935). It seems clear to me that his "ordinary form" refers only to the tetrads long known to be common in the family.

Lindley (1839) next described the pollen of *barbata* as powdery and referred to the pollinia (erroneously) as waxy. The writer's reference to pollen of "*Pterostylis* type" (Cranwell, 1942, 308) as "acolate; reticulate; tetrads compact; components 20 μ ," was based on *trullifolia*.

Pollen type: Grains typically free, but often (in some species) occurring in more or less stable rhomboidal tetrads. Exine reticulate; rod structure usually clavate, the muri diminishing towards or over proximal facets.

P. venosa Col. Text fig. 63.

P. trullifolia Hook. f.

Pl. 7(11–14).

As in generic description: tetrads (Types IV, I, III) sometimes separating in part at maturity; components about 17 x 21 x 13 μ ; tetrads 40 μ . Exine about 1.5 μ ; lumina roughly hexagonal, up to 3 μ across; rods clavate.

Material: Swanson, W. F. Harris; EM, MG.

Range, etc.: Lowlands from Three Kings and North Island to Marlborough; endemic. For details of fertilization in the genus, see Cheeseman (1873).

GASTRODIA R. Br.

The pollen apparatus of *G. sesamoides* was described by Hooker (1855, 263) as: "Pollen-masses 4, united in pairs, curved, free, composed of very large grains . . ." and on page 31: "e granulis magnis elastice cohaerentibus." His illustrations (l.c., Pl. 126, figs. 4, 5, 6) show the distinctive pollinia and a spherical brownish "grain." Rogers (1927) also refers to the pollinia, significantly comparing them with those of *Prasophyllum*, but failing as apparently Hooker had done, to recognize that these large "grains" were really tight massulae or aggregations of grains.

These round or elongate massulae, arranged around a central axis, and with a common membrane, occur also in *Cunninghamii*, and probably in *minor*, the only other native species. They are large (about 170 x 120 μ in *sesamoides*) and packed about with sterile matter. The grains occur in tetrads (rhomboidal, square, or more rarely tetrahedral), ranging from 28–40 μ , the components being uniformly about 18 μ , and finely reticulate.

G. sesamoides R. Br. Pl. 7(15).

Material: N.S.W., E. Cheel, Oct. 1902 (ex Oakes Ames Herb.); KOH.

Range, etc.: local in N.Z.: also Aust. and Tas.

SPIRANTHES L. C. Rich.

This is "One of the few orchid genera with round-the-world distribution, occurring in North and South America, the British Isles, Europe, Asia, the East Indies, Japan, Australia, Tasmania, and New Zealand. . . ." (Blanche Ames, 1947, 70).

Pollen grains of various species have been described, amongst them *speciosa*, as by Bauer (1830–1838, Tab. IV, fig. 13), who shows 4 square or rhomboidal tetrads, some with furrow-like areas around the contact faces, these areas being, apparently, the ones that Lindley failed to see at the time. The various species illustrated by Blanche Ames (l.c.) are all

shown to have reticulate exine and the same types of tetrads. The following is the only member in Australia and New Zealand.

S. sinensis (Pers.) Ames

Tetrads mainly rhomboidal, $35 \times 22 \mu$ (components $18-24 \mu$), closely massed but irregular in outline. Exine foveolate.

Material: Tangonge, North Auckland, H. B. Matthews; Lp.

Range, etc.: Lowlands of both main islands, mainly on acid soil.

Comparative Material: Specimens from Myponga, South Australia, collected Jan., 1909, by Dr. and Mrs. R. S. Rogers (ex Oakes Ames Herbarium); GV. Tetrads differing in size ($38 \times 24-54 \times 28 \mu$: Type IV, or rarely $65 \times 20 \mu$ for square tetrads of unusual type, ellipsoidal in outline (as if solitary), or clearly of 4 components, each about $32 \times 10 \times 10 \mu$, arranged like pairs of link sausages; lumina of exine about 2μ across.

Kerosphaereae

DENDROBIUM Swartz

While notes on the paired pollinia of this huge genus of about 1000 species are quite common (cf. Gaudichaud, 1829, 423; Richard, 1818), references to the pollen grains themselves are very rare, the first apparently being to those of a species from Ceylon by Bauer (1830-1838) who figured numerous tetrads of 3 types, some with threadlike processes and others with obscure markings suggestive of the distal apertures Bauer reported (erroneously) for certain other genera; over 100 years later brief notes on the following endemic (and only) native species were published (Cranwell, 1942, 308).

D. Cunninghamii Lindl.

Pollinia waxy, the massulae like fingers. Tetrads mainly rhomboidal, about $30 \times 21 \mu$, the components very irregular, about 17μ at most, or as small as 6μ when dwarfed through pressure. Exine smooth, thickest over outer walls; pattern faint.

Material: (a) Waitakere Range, B. Molesworth; EM. (b) Huia Dam, K. Thompson, Dec. 12th, 1950; KOH, GV.

Range, etc.: Epiphytic (or less often rupestral) in 3 main islands. Dec.-Feb., fragrant. *Fertilization* (cf. Thomson, 1879).

EARINA Lindl.

A Pacific genus of 7-8 species with two endemic and widely spread throughout New Zealand. Pollinia and tetrads as in *Dendrobium*, the tetrads being larger in Type IV; components more rounded and elongate, about $17 \times 14 \mu$, or dwarfed, 8μ . Exine smooth or very slightly roughened. Intine very thick on outside of grain.

E. mucronata Lindl. See Table I, p. 78.

E. autumnalis Hook. f. See Table I; text fig. 65.

Material: *mucronata* — Wgtn., L. M. C., 1937; EM. *Autumnalis* — Waitakere Range, April, 1949, Egbert Walker; MG.

Range, etc.: Epiphytic in lowlands throughout, *mucronata* extending to the Chathams.

Source of Material

Where not otherwise indicated the orchid material has been obtained from the herbarium of the Botany Division, D. S. I. R., Wellington, and has been checked by Mr. A. P. Druce and Miss L. B. Moore.

NOTE ON VIABILITY

Strong ties between New Zealand and Australian orchids, in particular, suggest that pollen or seeds might come to New Zealand with the prevailing winds that sometimes coat New Zealand glaciers with red Australian dust. Hafsten (1951) and Polunin (1951, 352) give records of air carriage to Tristan da Cunha and the Polar regions, respectively, the latter suggesting that variation in grasses, sedges and rushes might be due to such movements of pollen. The orchids are not plastic and their pollen is not well suited to wind carriage, but the possibility should not be ruled out.

TABLE 1: SALIENT POLLEN CHARACTERS OF NEW ZEALAND MONOCOTYLEDONS

with comparative data for some closely allied or little-known Pacific species, and for lower native spermatophyte taxa with comparable microspores.

The families and genera are arranged as in the systematic account. Foreign species are in italics and possible pre-European introductions marked with an asterisk. Sources of information about foreign material are indicated.

Grains with a triangular weak area are marked by Δ. The type of meiotic division in the family is given as follows: successive (‡), simultaneous (‡‡).

The measurements are of unexpanded to moderately expanded material.

For the sake of brevity grains with faint texture or sculpture over pore areas (cf. Cyperaceae) are merely termed "± smooth."

Families, etc.	Inaperturate (or seeming so)	Aperturate Monocolpate	Aperturate Monoporate	Size in μ	Exine
A: LOWER TAXA ¹					
CONIFERALES					
<i>Agathis australis</i>	X	...	...	42-52	Baculate (granular) ²
<i>Dacrydium</i> (7 spp.) ³	...	X	...	33-53	Psilate-reticulate
<i>Libocedrus</i> (2 spp.)	X	...	...	24-34	Flecked; wrinkled
<i>Phyllocladus</i> (3 spp.) ³	...	X	...	21-30	Psilate
<i>Podocarpus</i> (7 spp.) ³	...	X	...	30-58	Psilate-reticulate
(<i>dacrydioides</i>)	...	Δ	...	42-52	Psilate-reticulate
DICOTYLEDONES					
<i>Ranales</i> (Polycarpicae) ‡, ‡‡					
<i>Ascarina</i> (2 spp.)	...	X	...	23-26	Clavate; thick
<i>Beilschmiedia</i> (2 spp.)	X	...	...	26-42	Spiny; very thin
<i>Cassytha paniculata</i>	X	...	...	20-26	Warty; very thin
<i>Hedycarya Cunninghamii</i> ⁴	?	Zonate?	...	30-42	Psilate
<i>Laurelia novae-zelandiae</i>	...	1-2; zonate	...	40-24	Reticulate; 2.5 μ .
<i>Litsea calicaris</i>	X	...	...	20-33	Spiny; very thin
<i>Macropiper excelsum</i>	...	X	...	10-16	Furrow warty
<i>Peperomia tetraphylla</i>	X	...	...	14	Warty
<i>Urvilleana</i>	X	...	...	11	Warty
<i>Pseudowintera</i> (3 spp.) ⁴	...	...	X	33-50	Reticulate
<i>Non-Ranalian</i>					
Convolvulaceae ‡‡					
<i>Ipomoea palmata</i> (aberrant) ⁴	X	...	...	ca. 130	Reticulate
Euphorbiaceae ‡‡					
<i>Aleurites moluccana</i> *	X	...	...	36-50	Reticulate?
Gentianaceae ‡‡					
<i>Liparophyllum Gunnii</i> ⁵	...	(3-4 exits)	...	28	Striate
Myrtaceae ⁵ pl. 8 (14, 15) ‡‡	...	(3 exits)	...	10-30	Psilate
Oenotheraceae ‡‡					
<i>Epilobium</i> spp. (aberrant)	...	...	X	(Dwarf)	Psilate
<i>Fuchsia</i> spp. (aberrant)	...	...	X	(Dwarf)	Psilate
Thymelaeaceae ‡‡					
<i>Drapetes</i> spp. ⁶	X	...	...	30	Reticulate; thick
<i>Pimelea</i> spp. ⁶	X	...	...	40	" "
B: MONOCOTYLEDONES					
POTAMOGETONALES ‡					
Potamogetonaceae					
<i>Triglochin palustris</i>	X	...	...	30	Reticulate
striata <i>var. filifolium</i>	X	...	...	24	"
<i>Potamogeton Cheesemanii</i>	X	...	...	24×17	"
<i>natans</i> (W. 1935)	X	...	...	20-34	"
<i>ochreatus</i>	X	...	...	24-30	"
<i>Ruppia</i>	X	...	...	50-75×20	"
<i>Zostera nova-zelandica</i>	X	...	...	?	Absent
<i>marina</i>	X	...	...	ca. 2000	"
Najadaceae					
<i>Zannichellia palustris</i>	X	...	...	24	Absent, or flecked
<i>Lepilaena bilocularis</i> , <i>Preissii</i>	X	...	...	28-32	" " "

Families, etc.	Inaperturate (or seeming so)	Aperturate Monocolpate	Aperturate Monoporate	Size in μ	Exine
SPATHIFLORAE ‡					
Araceae					
Colocasia antiquorum <i>var.</i> esculentum * (Java), S; 1947	...	X	(?)	20×25	Spiny
Lemnaceae					
Lemna * etc., see text	...	...	X	18-23	Minutely spiny
PANDANALES ‡					
Typhaceae					
Typha angustifolia <i>var.</i>	...	...	X	27×22	Reticulate
Sparganiaceae					
Sparganium subglobosum	...	...	X	23-30	Reticulate
Pandanaceae					
Freycinetia Banksii	...	...	X	16-20	Psilate
Elmeri (Leyte, Philippines)	...	...	X	10-12	Reticulate-spiny
ENANTIOBLASTAE ‡‡					
Restionaceae					
Lepyrodia Traversii *	...	...	X	36-46-52	Finely foveolate
Leptocarpus simplex	...	...	X	30-40	Foveolate
Hypolaena lateriflora	...	...	X	40-53	Foveolate, thick
Centrolepidaceae					
Centrolepis strigosa	...	...	X	20-28×16	Foveolate
Pseudalepyrum ciliatum	...	...	X	30-33	"
pallidum	...	...	X	28-34	"
Gaimardia setacea	...	...	X	30-36	"
GLUMIFLOREAE ‡					
Gramineae				Pore size in brackets	"psilate-scabrate" F.&I., (1950)
Pooideae					
Festuceae					
Festuca rubra	...	...	X	34×31	Smooth
rubra (W., 1935)	...	...	X	31-36.5 (2.6-4.5)	"
novae-zelandiae	...	...	X	26-36	"
Poa anceps	...	...	X	20	"
caespitosa	...	...	X	28	"
Colensoi	...	...	X	22	"
Hordeae					
Agropyron scabrum	...	...	X	51	"
repens, Smithii, (W., 1935)	...	...	X	47-52	"
Arundineae					
Arundo Kakaho (= conspicua)	...	...	X	46 (4)	"
Eragosteae					
Eleusine indica	...	...	X	26-34 (3.5)	"
Aveneae					
Danthonia australis	...	...	X	36-48 (4)	"
flavescens	...	...	X	38-48 (3.4)	"
gracilis (semiannularis)	...	...	X	34×31 (4.5)	"
Deschampsia gracillima	...	...	X	26-32 (3)	"
australis (Hawaii, S., 1947)	...	...	X	34-41 (3×5)	"
Trisetum antarcticum	...	...	X	30×27 (3.5)	"
spicatum	...	...	X	31 (3.6)	"
Agrosteae					
Agrostis Dyeri	...	...	X	20-24 (1.4)	"
magellanica	...	...	X	30	"
Alopecurus geniculatus	...	...	X	32 (2)	"
Deyeuxia avenoides	...	...	X	35	"
quadriseta	...	...	X	29 (3.5)	"
Dichelachne crinita	...	...	X	30 (4)	"
Echinopogon ovatus	...	...	X	26-32 (4)	"

Families, etc.	Inaperturate (or seeming so)	Aperturate		Size in μ	Exine
		Monocolpate	Monoporate		
<i>Phalarideae</i>					
Ehrharta Colensoi (Petriella Colensoi)	...	...	X	33 (3.3)	Smooth
Hierochloe antarctica	...	...	X	42-54 (4)	"
Microlaena avenacea var. Carsei	...	...	X	25-30	"
Colensoi	...	...	X	34 (3.6)	"
<i>Panicoideae</i>					
Cenchrus calyculatus	...	...	X	42 (5.6)	"
Isachne globosa	...	...	X	21	"
Oplismenus undulatifolius	...	...	X	38	"
Paspalum distichum	...	...	X	36 (4.5)	"
Spinifex hirsutus	...	...	X	40-52 (4-6)	"

Families, etc.	Inaperturate	Pores rudimentary	Size of tetrads	Exine
JUNCALES				
<i>Juncaceae</i> ⁴ _{††}				
Luzula campestris var.	X.....X		34-40	± Smooth
hawaiiensis (S., 1947)	X.....X		39-45	"
Juncus antarcticus	X.....X		50	"
maritimus var.	X.....X		36	"
Rostkovia gracilis	X.....X		36	"
magellanica	X.....X		44	"
CYPERALES _{††}				
<i>Cyperaceae</i> ⁹				
<i>Cypereae</i>				
Mariscus ustulatus	X.....X		33×27	"
<i>Scirpeae</i>				
Eleocharis acuta	X.....X		40×28	"
gracilis	X.....X		32	"
sphacelata	X.....X		50×46	"
Fimbristylis squarrosa	X.....?		27×30	"
Scirpus frondosus	X.....X		42×28	"
medianus	X.....X		40×36	"
nodosus	X.....X		32×25	"
sulcatus var.	X.....X		26×22	"
Isolepis crassiuscula?	X.....X		32	"
<i>Rhynchosporae</i>				
Carpha alpina	X.....X		34-50	"
Schoenus apogon	X.....X		36×20	"
pauciflorus	X.....X		40×26	"
Cladium articulatum	X.....X		25	"
complanatum	X.....X		25	"
Sinclairii	X.....X		30	"
teretifolium	X.....X		23	"
Vauthiera australis	X.....X		32	"
Lepidosperma filiforme	X.....X		37-45	"
laterale	X.....X		32	"
Gahnia lacera	X.....X		36×27	"
Oreobolus pectinatus	X.....X		30-36	"
pumilio	X.....X		30-36	"
strictus	X.....X		45×30	"
furcatus (Maui) КОИ	X.....X		ca. 34	"
<i>Cariceae</i>				
Uncinia				
riparia	X.....X		28-35	"
uncinata	X.....X		36-40	"
Carex				
dissita	X.....X		50	"
secta	X.....X		28×26	"

Families, etc.	Inaperturate (or seeming so)	Aperturate Monocolpate	Monoporate	Size in μ	Exine
LILIIFLORAE †, ††					
Liliaceae					
<i>Veratroideae</i>					
<i>Iphigenia novae-zelandiae</i>	...	X	...	28×16	Reticulate-rugulate
<i>indica</i> (India) L	...	X	...	27.5	
<i>Asphodeloideae</i>					
<i>Arthropodium candidum</i>	...	X	...	36×26	Reticulate
<i>cirrhatum</i>	...	X	...	56×26	Rod-pattern coarser
<i>Xeronema Callistemon</i>	...	X	...	44×30	Reticulate; up to 2 μ
<i>Moorei</i> (New Caledonia)	...	X	...	38×28	Reticulate
<i>Chrysobactron Hookeri</i>	...	X	...	48×31	Rugulate-reticulate
<i>Rossii</i>	...	X	...	36–40	Warty-reticulate
<i>Herpolirion novae-zelandiae</i>	...	ΔX	...	24–28	Finely reticulate
<i>Dianella intermedia</i> var.	...	Δ	...	20–29	Psilate; very thin
<i>Hemerocallideae</i>					
<i>Phormium</i> ¹¹	...	Δ	...	28–42	Reticulate
<i>Colensoi</i>	...	Δ	...	31×31	Rods fine
<i>tenax</i>	...	Δ	...	34×36	Rods coarser
(hybrid pollen)	...	Δ ¹⁰	...	30–38; Dwarf: 20×24×15	
<i>Dracaenoideae</i>					
<i>Cordyline</i> ¹¹	...	X	...	ca. 26–36	Psilate to warty-reticulate
<i>Milliganieae</i> ¹²					
<i>Astelia</i> (see text key)	...	X	...	ca. 13–45	Spinulose; intra-baculate
<i>veratroides</i> (Oahu) MG	...	X	...	25×15	Spinulose
<i>Collospermum hastatum</i>	...	X	...	40×38×24	Roughened; intra-baculate
<i>microspermum</i>	...	X	...	42×30×20	Spineless
<i>samoënsis</i> (Samoa)	...	X	...	40×38	"
<i>Luzuriagoideae</i>					
<i>Luzuriaga marginata</i>	...	X	...	36×25	Thick, rods fine
<i>radicans</i> (Andean)	...	X	...	24×27	Smother
<i>Smilacoideae</i>					
<i>Ripogonum scandens</i>	...	X	...	34×26	Psilate-clavate
Amaryllidaceae					
<i>Hypoxis pusilla</i>	...	X	...	23–33	Smooth; furrow scabrate
Iridaceae					
<i>Libertia</i> (see p. 62)	...	X	...	28–34×16–24	Completely smooth
<i>coerulescens</i> (Chile)	...	X	...	28–31×24×24	" "
<i>paniculata</i> (Aust.)	...	X	...	34×27	" "
PRINCIPES †, ††					
Palmae					
<i>Rhopalostylis sapida</i>	...	X	...	40–50 (70)	Psilate; 1.5–3.3 μ
<i>Cheesemanii</i>	...	X	...	46×36×34	" "
<i>Baueri</i> (Norfolk Is.)	...	...	...	ca. 50	...
Edgeworth, 1877					
BURMANNIALES ††					
Burmanniaceae					
<i>Thismia Rodwayi</i>	?	?	?	17×12	Patternless
(<i>Bagnisia Hillii</i>)					

Families, etc.	Aperture ¹³	Status A free B tetrads	Free grains	SIZE	Tetrads	Exine
ORCHIDALES ‡‡¹⁸						
Orchidaceae						
POLYCHRONDREAE						
<i>Position uncertain</i>						
Petalochilus calyciformis	X....A (B)		21-24×14-17	...		Psilate
Calochilus Robertsoni	X....A		18-24×14	...		Foveolate
paludosus	?....A (B)		31×18	unstable		Reticulate
<i>Thelymitreae</i>						
Thelymitra caesia	X....A B		24-34×14-24	IV, (I, III)		Reticulate
decora	X....A (B)		26-34×24×24	65×24 (IV)		"
ixioides	X....B A		25-29×23×23	55×42 (IV)		"
	X....B		24×15×15	31-51×32 (III-IV); 35 (I)		"
longifolia	X....A (B)		24-30×24×20	56×50 (I)		"
pachyphylla	X....A		28-32×24×22	...		"
pulchella	X....A (B)		24-34×24×24	50×48		"
uniflora	X....B		22-26×16	48×32 (IV); 27(III); 30(I)		"
venosa	X....A (B)		24-32×20×18	42		"
<i>Diurideae</i>						
Orthoceras strictum	X....A (B)		25-28	...		"
<i>Prasophylleae</i>						
Microtis unifolia	?....B		...	...		"
Prasophyllum Colensoi	?....B		...	40-60×35 (IV)		"
pumilum	X....A		18×15	...		"
"rufum"	X....B		...	48×30		Foveolate-reticulate
<i>Drakaeae</i>						
Chiloglottis cornuta	X....B (A)		30×16	55 (IV); 38 (I)		Reticulate
<i>Aciantheae & Caladenieae</i>						
Acianthus reniformis var. oblongus	X....A (B)		25×20	...		"
Adenochilus gracilis	X....A		22×18	...		Psilate
Aporostylis bifolia	X....A (B)		21×18	30 (I)		Psilate (perforate)
Caladenia Lyallii	X....A (B)		28×20	unstable		Psilate-foveolate
Lyperanthus antarcticus	X....A		25×20	...		Foveolate-reticulate
<i>Pogonieae</i>						
Corybas (= Corysanthes)						
macranthus	X....A (B)		16×16	...		Psilate-foveolate
Matthewsii	X....A		17	...		" "
rivularis	?....A		16×12	...		" "
rotundifolius	X....A		14×12	...		" "
<i>Pterostylideae</i>						
Pterostylis Banksii	X....A (B)		...	I, II, III, IV		Reticulate; intectate
barbata	X....A		25×19	...		" "
graminea	X....A		18×15	...		" "
micromega	X....A		20×18×14	...		" "
nana	X....A		20×20×25 (L)	...		" "
venosa	X....B		24×14	31×28 (IV)		Reticulate; tectate
trullifolia	?....A (B)		22×18	...		Reticulate
	?....B		18×13	40×25 (IV), II, III		"
<i>Gastrodieae</i>						
Gastrodia Cunninghamii	?....B		18×16×17	40×20 (IV)		"
sesamoides	?....B		20	40×20		"
<i>Spirantheae</i>						
Spiranthes sinensis	X....B		18-24	35×22 (III-IV)		"

Families, etc.	Aperture ¹³	Status ¹⁴ A free B tetrads	Free grains	SIZE	Tetrads	Exine
KEROSPHAERAEAE						
<i>Dendrobieae</i>						
<i>Dendrobium Cunninghamii</i>	B		(6)-17		28 (I); 30×21 (IV)	Psilate
<i>Glomereae</i>						
<i>Earina autumnalis</i>	B		(8×8); 17×14		17 (I); 30×19 (IV)	"
<i>mucronata</i>	B		(10); 19×17		27 (III); 30×14 (IV)	"
<i>Bulbophylleae</i>						
<i>Bulbophyllum tuberculatum</i>	X....A				...	?
<i>Sarcantheae</i>						
<i>Sarcochilus adversus</i>	?B		16×23×14 30		54 (I)	?
(material poor)						

FOOTNOTES

¹ See glossary.² Cookson (1947, 131) points out that *Agathis* pollen is granular, not "pitted," as I at first thought (Cranwell, 1940).³ Vesiculate (i.e., with air-sacs).⁴ Tetrads. In *Pseudowintera* the components are monoporate and may occasionally occur singly.⁵ Tricolporate grains whose furrows isolate triangular "islands" over the poles.⁶ Basically with numerous small pores.⁷ I understand that the name *Muelleri* was reinstated, but the position is still not clear.⁸ Dr. H. H. Allan (private communication, 1952)informs me that he intends to revert to the use of *Sporadanthus* in his coming revision of Cheeseman's *Manual of the New Zealand Flora*.⁹ Reduced tetrads (cf. "Pseudomonads" in glossary). For practical purposes these grains must be classed as monads.¹⁰ This material shows that the weak area is probably proximal, as a single furrow has been found on the opposite side.¹¹ Position uncertain.¹² Hutchinson (1934).¹³ Weak areas proximal.¹⁴ Status: less common form bracketed.

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COLLOTYPE PLATES 1-8

For most of the photomicrographs the following equipment was used by the writer: an $8\times$ periplanar ocular, a $97\times$ oil immersion lens (n.a. 1.25), and a Leitz "Micam" photographic attachment (horizontal model). Greater depth of focus and higher magnifications were obtained in some cases through the assistance of Professor I. W. Bailey (Pl. 1, figs. 8-10) and Professor L. Cleveland (Pl. 3, figs. 8-13; Pl. 4, fig. 7), using their specialized equipment with extensible bellows.

Mounting of cut prints is responsible for faint margins on Pl. 2, fig. 15, Pl. 5, fig. 12, Pl. 6, fig. 14, Pl. 7, figs. 12-14.

PLATE 1, FIGS. 1-19. Types of grains (see Master Key). Tetrads (1-6); monads (7-19).

1-6: (1-2) *Pentachondra pumila* (Epacridaceae), F, $\times 480$. (1) Tetrahedral, (2) cross tetrads; (3) *Drosera binata* (Droseraceae), EM, $\times 750$; tetrahedral; spines on limb not clear. (4) *Ipomoea palmata*, GV, $\times 230$; spineless aberrant form. (5) *Epilobium macropus* (Oenotheraceae), F, $\times 480$; square tetrad. (6) *Oreobolus pectinatus* (Cyperaceae); reduced tetrad: see Plate 4.

7: *Agathis australis*, EM, $\times 750$. Inaperturate. Sect., surface granules almost out of focus.

8-14: Colpate: (8-10, vesiculate, $\times 750$, distal views); (8) *Dacrydium Bidwillii*, EM; (9) *Podocarpus ferrugineus*, F; (10) *P. dacrydioides*, EM; (11) *Chrysobactron Hookeri*: see Plate 5; (12) *Laurelia novae-zelandiae*, GV, $\times 230$, dicolpate: lateral views; (13) *Ranunculus Lyallii*, F, $\times 480$, lateral and polar views; (14) *Teucrium parvifolium* (Verbenaceae), EM, $\times 480$, lateral views.

15-19: Colporate: (15) *Alseuosmia macrophylla* (Caprifoliaceae), GV, $\times 480$, polar view, sect., contents dense; (16) *Avicennia officinalis* (Verbenaceae), EM, 28 μ , lateral view, showing large pore; (17) *Entelea arborescens* (Tiliaceae), EM, $\times 480$; lateral view; (18) *Myoporum laetum* (Myoporaceae), MG, $\times 480$; note transverse furrow above; (19) *Ixerba brexioides* (Escalloniaceae), EM, 32 μ , polar view.

PLATE 2, FIGS. 1-16. Types of grains (see Master Key). One- to many-pored types (1-14).

1: Monoporate, *Arundo Kakaho*: see Plate 4. 2-5: Sometimes monoporate. *Fuchsia excorticata*, $\times 480$, (2) dwarfs with 1 pore at right, MG, $\times 480$; (3) diporate, sect., EM; (4, 5) *Epilobium pedunculare* var. *brunnescens*, F, $\times 230$; (4) one-pored; (5) normal grains, polar view, sect.

6-9: Pores slitlike, meridional, $\times 480$. (6) *Geranium Traversii* var. *elegans* (Geraniaceae), EM; (7-9) Haloragidaceae; (7) *Gunnera arenaria*, EM; (8) *Haloragis cartilaginea*, EM; (9) *H. procumbens*, F. 10: *Nothofagus fusca* (Fagaceae), EM, 38μ .

11-14: Many-pored. (11) *Pimelea longifolia*, EM, $\times 480$; (12-14) Malvaceae: *Hibiscus trionum*, EM, $\times 480$; (12) surface view, rod tips bright; (13) lower focus on rods, now dark; (14) *H. diversifolius*, EM, $\times 230$; spineless, (a rare condition), showing tectum in section and rod layer below.

15-16: Exine detail. (15) scabrate — *Nothofagus Menziesii*, EM, $\times 750$, surface view near equator; (16) reticulate — *Xeronema Callistemon*, surface view.

PLATE 3, FIGS. 1-20. Potamogetonaceae (1-4); Sparganiaceae (5-6); Typhaceae (7-8); Pandanaceae (9-13); Restionaceae (14-17); Centrolepidaceae (18-20).

1-4: (1) *Potamogeton Cheesemani*, GV, $\times 300$. Note "temporal furrow" (intine). (2, 3) *Triglochin striata*, F, (2), $\times 300$; (3) $\times 900$; sect., rods just perceptible; intine and contents shown. (4) *Ruppia spiralis*, EM, $\times 480$; mesh rather even. 5-6: *Sparganium subglobosum*, F, (5) wall folded, $\times 300$; (6) pores showing, $\times 480$. 7-8: *Typha angustifolia*, EM, (7) sect., lateral view of pore, $\times 1100$. Note clavate and fused rods; (8) surface; rugulate ridges of reticulum, at high focus, $\times 1500$. 9-13: *Freycinetia Banksii*, GV, (9) $\times 180$; (10) showing range in shape, thickening of intine, and mottled contents, $\times 480$; (11) pore in lateral view, $\times 900$. Membrane unexpanded; (12) lateral view, showing intine and textureless exine, $\times 2000$; (13) lateral; pore in higher focus, $\times 2500$. 14-17: *Leptocarpus simplex* (14), EM, $\times 480$, sect., lateral view; (15) *Lepyrodia Traversii*, EM, $\times 480$, lateral; (16-17) *Hypolaena lateriflora*, $\times 480$, (16) F, exine deeply stained around pore; (17), EM, lateral view: pore ruptured; in high focus, exine pits showing dark. 18-20: (18) *Centrolepis strigosa*, F, lateral view, sect.; (19-20) *Gaimardia setacea*, F, distal views, (19), $\times 300$, (20), $\times 900$.

PLATE 4, FIGS. 1-16. Gramineae (1-5); Juncaceae (6-7); Cyperaceae (8-16).

1-5: *Arundo Kakaho*, EM, $\times 480$ (excluding fig. 3, $\times 500$ — operculum detail, surface view). 4: Sect., tetrad arrangement persisting in almost mature grains (rare): the artifacts are crystals. Note pores on some of the grains. Normal grain to left (same preparation).

6: *Luzula campestris*, MG, $\times 480$, sect., Tetrahedral tetrad; rounded hyaline bodies present. 7: *Juncus maritimus*, MG, $\times 480$, sect. Rhomboidal tetrad.

8: *Lepidosperma laterale*, MG, $\times 480$, sect. Intine thick, contents dense. 9: *Carex ternaria*, GV, $\times 480$, sect. Contents dense; broad end depressed. 10: *Oreobolus strictus*, F, $\times 480$. 11-12: *O. pectinatus*, F & KOH (over-expanded); $\times 900$. (11) surface view, showing 3 of the 4 pores; (12) another grain at lower focus, showing sterile part at narrow end. 13-16: *Scirpus frondosus*, F & KOH, $\times 480$. (13) pores rupturing (over-expanded?); less expanded grain: dark mass of degenerate sister cells lies at narrow end; (15-16), sect.; intine plates shown cutting off narrow end of grain.

PLATE 5, FIGS. 1-14. Liliaceae: Arthropodium-Collospermum.

1-3: *Arthropodium cirrhatum*, EM, (1) lateral view of 2 grains, furrows facing, unexpanded; $\times 480$; (2) proximal (polar) view of grain, unexpanded, with truncate (ruptured) furrow ends; $\times 300$; (3) lateral view, EM, $\times 390$.

4-7: *Xeronema Callistemon*, (4) lateral view, EM, $\times 480$, showing graded mesh; (5, 6) sketches of aberrant grains, upper in distal, lower in lateral view; (7) distal surface view of expanded grain, showing furrow area with smaller mesh: dark rod tips show faintly at angles of mesh: Lp & Saf, $\times 2500$.

8: *Chrysobactron Hookeri*, EM (unexpanded), $\times 550$, sect.; exine in low focus below surface also.

9-11: *Cordyline*. (9) *C. pumilio*, MG, $\times 230$; oblique lateral view, with part of furrow showing; (10) *C. indivisa*, EM (unexpanded), $\times 480$; sect.; exine in low focus; (11) *C. Banksii*, EM (unexpanded), $\times 480$; sect., exine in low focus.

12: *Astelia trinervia*, EM, $\times 1100$, 5 grains (unexpanded), with furrows clear in two. 13, 14: *Collospermum hastatum*, GV, $\times 390$. Distal views, sect. and part surface.

PLATE 6, FIGS. 1-15. Liliaceae (1-11); Amaryllidaceae (12-13); Iridaceae (14); Palmae (15).

1: *Dianella intermedia* var. *norfolkiensis*, MG, $\times 480$. Distal view, upper fork of furrow ruptured. 2-6: *Phormium*, $\times 480$. *P. tenax*, GV. (2): grains in distal and lateral views, furrows closed; (3, 4) more expanded grain, showing mesh in equat. section, and in low surface focus. *P. Colensoi*, Lp & Saf, (5) left greatly and right less expanded, truncate on equator. Proximal views. (6) Fossil grain, MG, $\times 390$ (Pyramid Valley, 1940). Lateral view, showing typical appearance when ruptured.

7-9: *Herpolirion novae-zelandiae*, EM, distal and lateral views; (7) $\times 300$; (8-9) $\times 480$. Texture shown on some grains.

10: *Luzuriaga marginata*, F, $\times 480$, lateral view, furrow membrane showing at top. 11: *Ripogonum scandens*, EM, $\times 480$, unexpanded grains. Upper left in distal, right in proximal, and lower grains in lateral views.

12-13: *Hypoxis pusilla*, GV, $\times 480$. Lateral and distal views, sect. and part surface. 14: *Libertia grandiflora*, EM, $\times 1000$, sect., equat., with furrows faintly indicated on upper surface. 15: *Rhopalostylis sapida*, EM, $\times 480$. Distal view; furrow closed. Exine at low focus.

PLATE 7, FIGS. 1-15. Palmae continued (1); Burmanniaceae (2); Orchidaceae (3-15).

1: *Rhopalostylis sapida*; unexpanded sterile grain enclosed by persistent mother cell wall (sketch). 2: *Thismia Rodwayi*, EM, $\times 1700$. Sect., showing contents and thick intine.

3-5: *Acianthus reniformis* var. *oblongus*, F; (3) $\times 480$; (4, 5) sketches showing coarse pattern of the exine. 6: *Prasophyllum Colensoi*, GV, $\times 300$. 7: *Caladenia Lyallii*, F, $\times 480$. Monad; contact face marked by fold at one end. 8: *Microtis unifolia*, MG, $\times 230$; tetrads in different positions. 9: *Thelymitra ixioides*, GV, $\times 480$. Furrowlike contact faces shown by grains separating from tetrad under pressure. 10: *Orthoceras strictum*, EM, $\times 500$. Monads. 11-14: *Pterostylis trullifolia* tetrads, MG; (11) lateral view, $\times 300$; (12, 13) surface views, high and low focus respectively, $\times 900$; (14) loosely cohering tetrads, with two completely free on left. 15: *Gastrodia sesamoides*, GV, $\times 90$. Tetrads occurring in tight masses (massulae).

PLATE 8, FIGS. 1-23. Post-Pleistocene peat deposit (1). Microspores comparable with those of monocotyledons (cf. Table 1): pollen grains (2-10, 12-15, 18-23); pteridophyte spores (11, 16, 17).

1: Rain-fed (ombrogenous) montane bog, Blue Mts., near Tapanui, N. Z. Eroded and drying surface favouring tussock grasses and *Phormium tenax* (intrusive). *Dracophyllum* stumps exposed above *Sphagnum* layer. L. B. Moore & A. L. Poole beside pond. 1940, Photo., L.M.C.

2-5, 9-10: (2-3) *Aleurites moluccana*, GV, $\times 480$, (2) sect., (3) surface view in low focus. (4) *Litsea calicaris*, GV, $\times 230$; folded. (5) *Peperomia Urvilleana* (sketch). (9) *Drapetes Dieffenbachii*, EM, $\times 480$. (10) *Pimelea Traversii*, EM, $\times 390$. 6-13 (One exit): *Macropiper excelsum* (6-8), sketches; lat. (exp. & unexp.) and polar views. (11) *Pyrrosia serpens* (Polypodiaceae), EM, $\times 390$, sect., lat.; exospore knobby. (12) *Ascarina lucida*, F, $\times 390$; sect.; furrows unexp., rather oblique. (13) *A. lanceolata*, EM, $\times 390$. 14-20 (Forked scars or furrows): (14) *Eugenia Maire*, EM, $\times 480$. (15) fossil type (Myrtaceous), unknown in living flora (Waikato peats); EM, $\times 480$. (16, 17) *Lycopodium Drummondii*, MG, $\times 390$. (18) *Liparophyllum Gunnii*, GV, $\times 480$. (19) *Elytranthe Colensoi* (Loranthaceae) EM, $\times 480$. Furrow torn open on one side. (20) *Laurelia novae-zelandiae*, GV, $\times 390$. 21-23 (Tetrads): (21) *Carpodetus serratus* (Escalloniaceae?), EM, sect., note furrows. (22) *Epacris pauciflora* and (23) *Dracophyllum latifolium* (Epacridaceae); all $\times 480$.

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