

ON A CONIFER FROM THE JURASSIC OF EAST ANTARCTICA

By

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(With one plate and five text figures.)

ABSTRACT

The genus *Nothodacrium* gen nov. is described, with one species, *N. warrenii* sp. nov., from the uppermost Beacon Group, of Jurassic age. Also described is the pollen cone *Masculostrobilus warrenii* sp. nov., which may belong with *N. warrenii*. These fossils are ascribed to the Podocarpaceae, and their position in the Family is discussed.

INTRODUCTION

During the 1964-65 New Zealand Antarctic Research Programme the plant fossil locality at Carapace Nunatak was revisited and more material collected, part of which is dealt with here. The material consists of a cutinised shoot, an attached seed cone, not cutinised, and an isolated pollen cone, containing poorly preserved pollen grains similar to, but probably distinct from, *Tsugaepollenites trilobatus* (Balme) Dettmann. On the evidence of the seed cone and shoot, these two are believed to be podocarpaceous, and their structure, complementing that of *Rissikia* and *Mataia*, dealt with in the first of these notes on early mesozoic southern conifers, suggests one (but not necessarily the only) manner in which the non-epimatial podocarp seed cone may have evolved.

DESCRIPTIONS

Family PODOCARPACEAE

Genus **NOTHODACRIUM** nov.Type species *Nothodacrium warrenii* sp. nov.

Diagnosis. Conifers, with terminal shoot systems not showing divisions into long and short shoots, each shoot showing distinct terminal bud. Shoots slightly flattened into one plane, branching more or less pinnate, but probably ultimately spiral. Diameter of terminal shoots (including decurrent leaf leaves) about 1.5 mm. Leaves borne spirally, all of one sort, directed forwards and diverging from the shoot at an angle of 10-30°. Leaves about 3 mm. long, 1.5 mm. wide and 1 mm. thick, more or less rhomboidal in section, often slightly falcate, (presumably) with one vein. Leaf bases strongly decurrent, down to next leaf on same side of the shoot, phylotaxis probably 3/8.

Cuticle similar all over the leaf, cells more or less rectangular, in rows, but narrower at the leaf margins, and over midrib. Stomata lying on four flanks of the leaf, in (probably) single rows, and about equally numerous all over. Cell outlines pierced by holes, but otherwise more or less

straight; cells away from margin and midrib often bearing solid or hollow papillae, especially towards the leaf base. Stomata mono- or incompletely dicyclic, longitudinally or obliquely or transversely orientated, with guard cells sunken in a more or less rectangular pit, with walls formed by the subsidiary cells. Lateral subsidiary cells two to four, generally smooth, but rarely bearing a low and obscure Florin Ring (cutin thickening round the stomatal pit). Guard cells feebly cutinised.

Seed cone terminal on a branch of normal form, bearing leaves as on vegetative branches. Cone elongated, spike-like, consisting of 10-15 units. Units consisting of spirally inserted bracts and axillary cone scales free from each other. Bracts about 2 mm. long, and 0.5 mm. wide, simple, probably more or less strongly flattened bifacially. Cone scale flattened, consisting of three pointed lobes, about 2 mm. long, with the three points either bluntly or sharply pointed. Scale bearing single seed (as far as can be seen), about 1 mm. long and a little less at its widest; seed stalk (probably) adnate to scale, and seed (probably) inverted. Seed borne about centrally on cone scale. (Cuticle of seed cone unknown).

Nothodacrium warrenii sp. nov.

Pl. 1A, B, D. Figs. 1A-D; 2A-E; 3B-D.

1913 *Sphenolepidium oregonense* Halle, non Fontaine pp. 80-81, pl. 9, figs. 5b, 9-11 (shoots) and ?13 (cone). Hope Bay Graham Land.?1913 *Conites* sp. Halle, pp. 81-82, pl. 9, figs. 12, 12a; seed cone. Hope Bay Graham Land.1940 *Sphenolepidium oregonense* Florin non Fontaine, pp. 72-73. Discussion of Halle's material.1947 *Elatocladus* sp. Jones and de Jersey, p. 9, figs. 15-17. Shoots from the Brighton Beds, Queensland.1962 *Brachyphyllum* cf. *B. expansum* Plumstead non Sternberg, pp. 88-90, pl. 22, figs. 3 and 4.1962 *Pagiophyllum* cf. *P. peregrinum* Plumstead non Lindley and Hutton, pp. 90-91, pl. 22, figs. 5 and 6.1962 *Elatocladus* cf. *E. heterophylla* Plumstead non Halle, pp. 90-93, pl. 22, figs. 7-10. Material from Carapace Nunatak.

Type specimen. B 1012/10. New Zealand Geological Survey; see Plumstead (1962) pl. 22, fig. 3.

Locus typicus. Carapace Nunatak, E. Antarctica; Beacon Group, Jurassic.

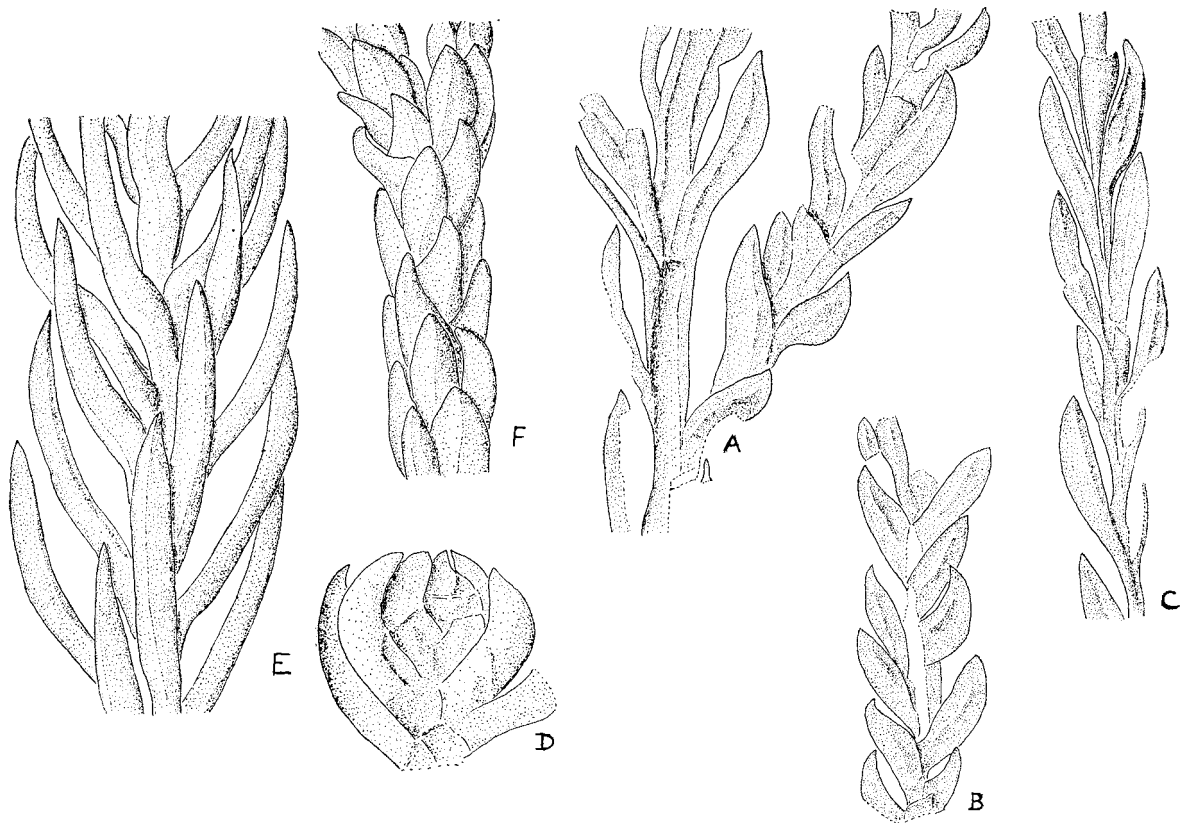


FIG. 1.—*Nothodacrydium warrenii* A-D: *Dacrydium novoguineense*, E, F.

A-D: Parts of shoots showing a branching (A), a bud (D) and various forms of leaves; all x 7. A-C B1012/10, D1012/21. E, F: Parts of shoots with juvenile (E) and adult (F) leaves. x 7. Herb. C.S.I.R.O. Robbins 183.

Diagnosis. Terminal shoots about 1.5 mm. diameter, bearing more or less falcate leaves 1.5-3.5 mm. long, and 0.75-1.5 mms. wide and about 1 mm. thick at the base. Midrib generally visible as a raised line on the lower leaf surface, but upper leaf surface more or less flat. Leaf apex acute. Cuticle about 4μ thick, showing cells about 120μ long ($80-150\mu$) and 40μ wide ($20-65\mu$); outlines about 4μ wide. Stomata well separated from one another by about 8 (4-12) cells, including terminal encircling cells. Stomatal pit rectangular, about $60\mu \times 25\mu$, bounded at least laterally by a strong cutin rim. Papillae mostly solid, about 10μ high.

Cone (single specimen) 1.25 cms. long, those units (flowers) borne laterally lying about 1.5 mm. apart, but strongly decurrent. Bract and cone scale about 2 mm. long, seed scale complex about 0.5 mm. wide, bearing (presumed) seed about 0.25 from base of complex. Three points to cone scale free for usually less than half total length of scale. Cone axis about 1 mm. wide at base of cone.

Description.

(1) *The Carapace Nunatak locality.* On Carapace Nunatak the plants, with conchostracans, are found in narrow shale or cherty bands underlying, and also interleaved with, a basalt flow (see Gunn and Warren 1962, p. 111). The degree of silicification increases nearing the basalt. Counting down from the base of the solid basalt, most plants come from the fourth and fifth shale bands, but isolated blocks of chert, probably from a higher band, have yielded plants. The material described by Plumstead (1962) came, in part, from a nearby moraine, but I surmise that most also originated in the fourth or fifth shale band. The plants are preserved in an unusual way. They may either be naturally macerated, or else not much compressed, and with the internal substance replaced by a siliceous mineral. At times, and in the material from (presumably) higher bands, the plant matter is entirely replaced by mineral. However, though indeterminate coniferous type petrified wood is present, the shoots are not petrifications. The conditions of deposition are discussed by Gunn and Warren (1962) who believed following Plumstead (1962) that the plant beds were Lower Jurassic, but they may be younger than this.

(2) *The Material.* The material examined consists of B.697/1, 2 and 5, figured by Plumstead (1962, pl. 22) and this has no cuticle, and also B.1012/10, a cutinised shoot with B.1012/21 an uncutinised shoot with cone attached. This further material was collected by the Allan Nunatak Party, N.Z.A.R.P. 1964-65; the whole is now in the collections of the Geological Survey of New Zealand.

The small ultimate shoots are, so far as can be seen, all alike (Pl. IB and see Plumstead 1962, pl. 22, fig. 7), and visible on a number of them is a cluster of leaves, as over an apical bud (e.g. Fig. 1D). This suggests that, as in *Dacrydium cupressinum* for example, there was no division into long (main) shoots, and lateral (short) ones. However, the branches all emerge from the side, or near the side, of the parent shoot (Pl. IB, Fig. 1A and see Plumstead 1962, pl. 22 figs. 4, 8), suggesting that the whole shoot system may have been flattened somewhat as in *Podocarpus dacrydioides* (juvenile) and similar species.

The leaves are shown in Figs. 1A-D. They now lie all round the shoot, and since no twisting of cell rows at the leaf base can be seen, were so borne in life. Compressed laterally, the leaves show a median ridge (Fig. 1A, B) appearing in the cuticle as a zone of much elongated narrow cells (Fig. 2A right), interpreted as a thin, angular, but not scarious margin. Compressed dorsi-ventrally, the lower (abaxial) surface shows a raised area, sometimes sharp but more often not, over the midrib (Fig. 1C right), while the impression of the upper (abaxial) leaf surface shows an even less prominent ridge (Fig. 1C left). Again, in the cuticle there is a rather vague zone of narrow cells over the midrib (Pl. ID left), but from the absence of folding in the cuticle, it is supposed that the leaf, though rhombic in section, showed only a slightly projecting midrib on each surface. In shape it is reconstructed as being close to *Dacrydium novoguineense* Gibbs (Fig. 1E, F), only without the scarious margin of that species.

The leaf shape varies considerably even on one shoot, and it is possible that some of this variation may be seasonal, small leaves tending to occur at branch bases, or over the buds. The midrib cannot be seen on the lower surface.

The cuticle, as with other Carapace Nunatak material, was already largely macerated, and about an hour in dilute nitric acid followed by very dilute ammonia was sufficient treatment. Only small fragments covering both surfaces of the leaf could be obtained. However, on these fragments (Fig. 2A, C) the cuticle was similar all over, and in the larger isolated fragments, there was, with one possible exception, no distinction visible into an upper and lower cuticle. The exception is that on some pieces stomata were very few indeed, or even absent, and it is possible that rather more stomata lay on one pair of flanks than on the other. The difference, if any, was slight.

As noted, both margins and midrib were visible on the cuticle. The cells lay in more or less regular rows, except at the leaf base, where, on the upper surface, the cells were irregularly set. The papillae (Fig. 2) were seen on most cells, about, but not always, centrally on a cell. The stomata are shown in Figs. 2B, D, E. In most the guard

cells' cuticle has vanished, but in a few, the stomatal aperture is seen to be parallel with the long axis of the pit. This was variably orientated, though most often more or less longitudinal, and presumably the guard cells were also variably orientated. In most stomata the subsidiary cell surface is smooth (Fig. 2B, E), but in some three or four a low obscure Florin ring, like that in e.g. *Dacrydium cupressinum* could be seen (Fig. 2D). In one place a cutinised hypodermis seems to be visible.

Though coming from one specimen the cuticle shows variation, especially in cell size and shape and in form of papillae as well as in the number of holes through the outline (Figs. 2A, B), such holes causing the cell outlines to appear sinuous at low magnification. The cuticle is in places damaged by re-crystallised silica grains.

The seed cone, as noted, is not preserved with cuticle. The mineral infilling indeed tends to blur the outlines of the parts, though examined under kerosene these can still be made out. However, parts (e.g. possibly seeds) can be lifted out, probably intact, so that the material can be, in a way of speaking, dissected apart.

The cone is in contact with more shoots (Pl. IA), though the extent of contact is not large, and for this reason one name is used for both shoot and cone. These shoots though uncutinised show the features of the other material of *N. warrenii* other than cuticular and the branch bearing the cone has leaves towards its base like those on other branches. The fertile branch was like an ordinary vegetative branch.

The units (flowers or seed scale complexes with their bracts) stand out at about 70° from the shoot. The bract is seen compressed laterally in Fig. 3C, and in this view looks much like a vegetative leaf. In Fig. 3D two are seen probably compressed more or less dorsi-ventrally, and here, though the lower surface is raised, the bract does not show the midrib as clearly as the leaves do. Presumably it was more flattened. In several places the cone scale is seen to end in three distinct points (Pl. IA and Figs. 3B, C, D). The whole structure is now flattened on the rock, and may have been flattened in life, for turned-in edges (*cf. Rissikia*) are not seen. The points, however, may be obtuse (Fig. 3D) or acute (Fig. 3C). The nature of the seed is still uncertain. In a number of places (Figs. 3C, D) there is either a hollow, or a raised piece of matter, which can be lifted out intact which looks as if it contained, or was, the seed. On this view there was only one per complex. The narrow end of this putative seed pointed towards the cone axis, seen especially clearly when the unit is compressed laterally (Fig. 3D), and from this it is deduced that the seed was inverted. In one unit compressed laterally (Fig. 3B) there is a deep trench between the seed and the scale, and this may represent the position of a free stalk. On the other hand, in other places (e.g. Fig. 3D, shown by lines) there are wisps of tissue showing elongated cells, and these wisps are connected with the scale below. On the whole, I think it is more likely that the seed stalk was adnate to the scale, and the trench referred to might be caused by the inrolling of a laterally compressed structure. The matter must remain open. There is no evidence on the venation of the seed scale complex.

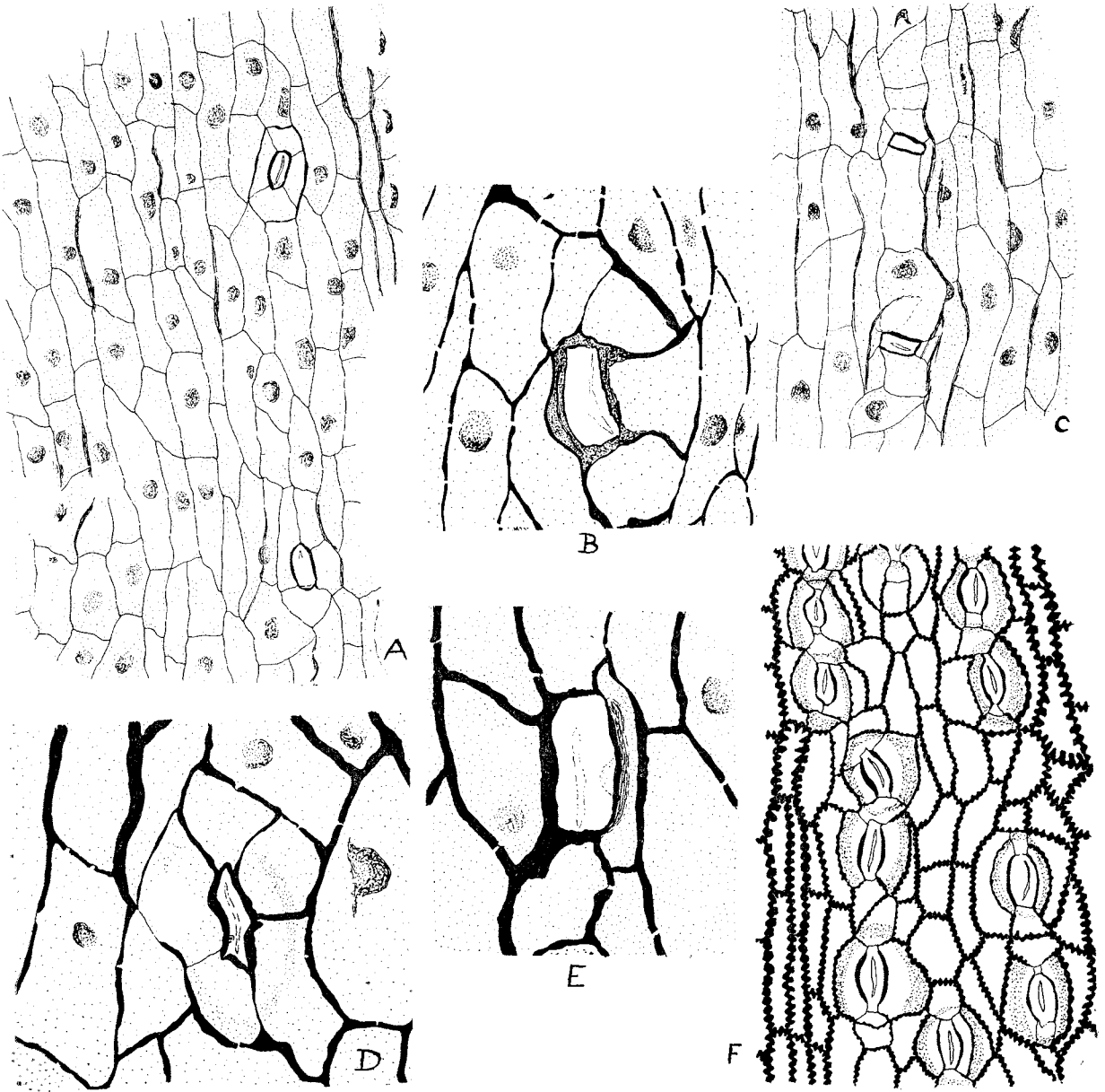


FIG. 2.—*Nothodacrium warrenii* A-E; *Dacrydium araucarioides*, F.

A, C: Cuticle from the plants of the leaf, showing stomata and papillae. x 300. B1012/10. B-E: Three stomata, obscure Florin Ring (D) x 600. B1012/10. F: Cuticle showing a few stomata not strictly aligned. x 300. Nat. Herb. Melbourne.

The impressions considered to be the marks left by seeds vary in size, being smaller than the dimensions cited above towards the base of the cone. One explanation is that, as in *Dacrydium franklinii* today, not every ovule ripened (Fig. 5).

The name is compounded of *nothos* = false and *-dacrium* shortened from *Dacrydium*.

(3) *Specific comparisons.* The material figured by Plumstead (1962) does vary considerably in leaf shape, but so does mine (cf. Figs. 2B-D and Plumstead 1962, pl. 22); one fragment (Fig. 1B) showing especially short wide leaves is seen to be identical on its cuticle. The total variation is, however, scarcely more than one would find in a living tree with similar sorts of leaves, and though identity of Plumstead's material with mine cannot be absolutely proved, in absence of cuticle, I believe it is extremely likely that it does all belong to one species. It all differs from *Brachyphyllum expansum* and *Pagiophyllum peregrinum*, with which she compared some, though without referring to the recent revisions of these species (Kendall, 1948, 1949).

The identity of Halle's (1913) material from Graham Land and of Jones and de Jersey's (1947) from Queensland with *N. warrenii* is open to question, for details are not available for it. However, in size, leaf and shape and, less certainly, cone form, it agrees, and is therefore identified. Halle's figures, however, show less richly branched shoots.

The name is given for Mr. Guyon Warren, who discovered the Carapace Nunatak locality, and the first material. He also organised the project to re-explore the area, and it was a great pity that he was prevented from taking part by an unfortunate accident. The least I can do is to name the material after him.

There would seem to be only one species with which *N. warrenii* could be confused, and that is *Elatocladus heterophylla* Halle (1913, see discussion by Florin, 1940). This species lacks cuticle details, but can be distinguished because its parts are about twice as large as those of *N. warrenii*. Going on figures only, it seems to show a distinct tendency to produce long and short shoots (Halle 1913 pl. 8, figs. 13, 14, text fig. 18), and on some of the short shoots the leaves are interpreted by Florin as bilaterally flattened (pl. 18, figs. 18, 20, 22a, text fig. 18), whereas in *N. warrenii* any flattening is bifacial. Menendez (1957) figures a small shoot, with cuticle, but no stomata. In cell shape and arrangement the cuticle is much like that of *N. warrenii*. Florin (1940) states that *E. heterophylla* is much like *Podocarpus* Section *Dacrycarpus*, however *N. warrenii* foliage is more like *Dacrydium* group B. The cone of *E. heterophylla* is unknown.

(4) *Generic comparison.* In both foliage and cone *Nothodacrydium* closely approaches *Dacrydium*, especially *D. elatum*, *D. cupressinum* and their allies (Group B of Florin 1931). The general outline, and branching pattern of the shoots is however not entirely the same as this group of *Dacrydium*, but the leaf form is close. The cuticle differs, notably in showing stomata of variable orientation, (though *D. araucarioides* may show a slight approach Fig. 2F), in having papillae, and in lacking (in most stomata) the Florin ring (see Florin 1931 and

Figs. 2B, E). The cone is less easy to compare, since a number of points are uncertain. However, accepting the reconstruction offered here, the long rather loose form of the cone can be matched in *D. franklinii*, where, however, the cone is smaller. The division of the cone scale into three points is also sometimes seen in *D. franklinii*, though the points there are very much smaller and, rarely, also in *D. laxifolium*. The (probably) inverted seed, unenclosed by an epimatium, is not found in living *Dacrydium* species, but in ontogeny, the ovule of *D. cupressinum* starts inverted, and only later becomes partially upright.

It is, in fact, so easy to interpret the cone and foliage of *Nothodacrydium* in terms of *Dacrydium*, that *Nothodacrydium* is placed in the Podocaraceae with some assurance. However, the differences just outlined make it undesirable to include it in *Dacrydium*, which is in any case inconveniently heterogeneous.

Tricanolepis monosperma Roselt (1958) comes close to *Nothodacrydium*, but differs in that the bract is adnate to the cone scale, the cone has many more units, and the stalk of the units is longer.

(5) *Morphology of the seed cone.* As noted, the seed cone is readily to be described in terms of the seed cone of *Dacrydium*, especially *D. franklinii*. The differences are essentially that the cone is larger, and the cone scale more complicated. The difference, on the other side, between *D. franklinii* and *D. cupressinum*, for example, is that the cone of *D. cupressinum* is reduced to one fertile unit, and the cone scale to a small unlobed frill at the base of the seed. There is thus a series, partly also a series in time, from *Nothodacrydium* to species such as *D. cupressinum*. I interpret this as a series, illustrating evolution in the female cone.

However, it is also easy to describe *Nothodacrydium* (Jurassic) in terms of *Rissikia* (Triassic). The chief difference between the two in their seed cones lies in this. *R. media* has two seeds associated with each of the three free lobes of the cone scale, but *Nothodacrydium* shows adnation between the three lobes of the complex, and has lost five out of the six seeds. *R. apiculata* to some extent bridges the gap, since it has (as far as can be made out) only three, or even fewer, seeds per unit.

? PODOCARPACIAE

Organ Genus *MASCULOSTROBUS* Seward

Masculostrobus warrenii sp. nov.

Pl. 1C, Figs. 3A, E; 4B, D, E.

Holotype: B 1012; 19 Geological Survey of New Zealand, Pl. 1C.

Type locality: Carapace Nunatak, E. Antarctica; Beacon Group, Jurassic.

(1) *Diagnosis:* Conifer pollen cone, 8 mms. long, oblong, 5 mm. wide at widest part, bearing (estimated) 30 sporophylls. Cone base showing three sterile leaves, 2 mm. long 0.25 mm. wide, rhomboidal in cross-section but cone not showing a stalk. Cone axis stout 1-5 mms. in diameter at base, showing elongated cells. Sporophylls emerging at about 110° at cone base, decreasing to about 45° at cone apex; each sporophyll consisting of connective, about 0.5 mm. in diameter showing

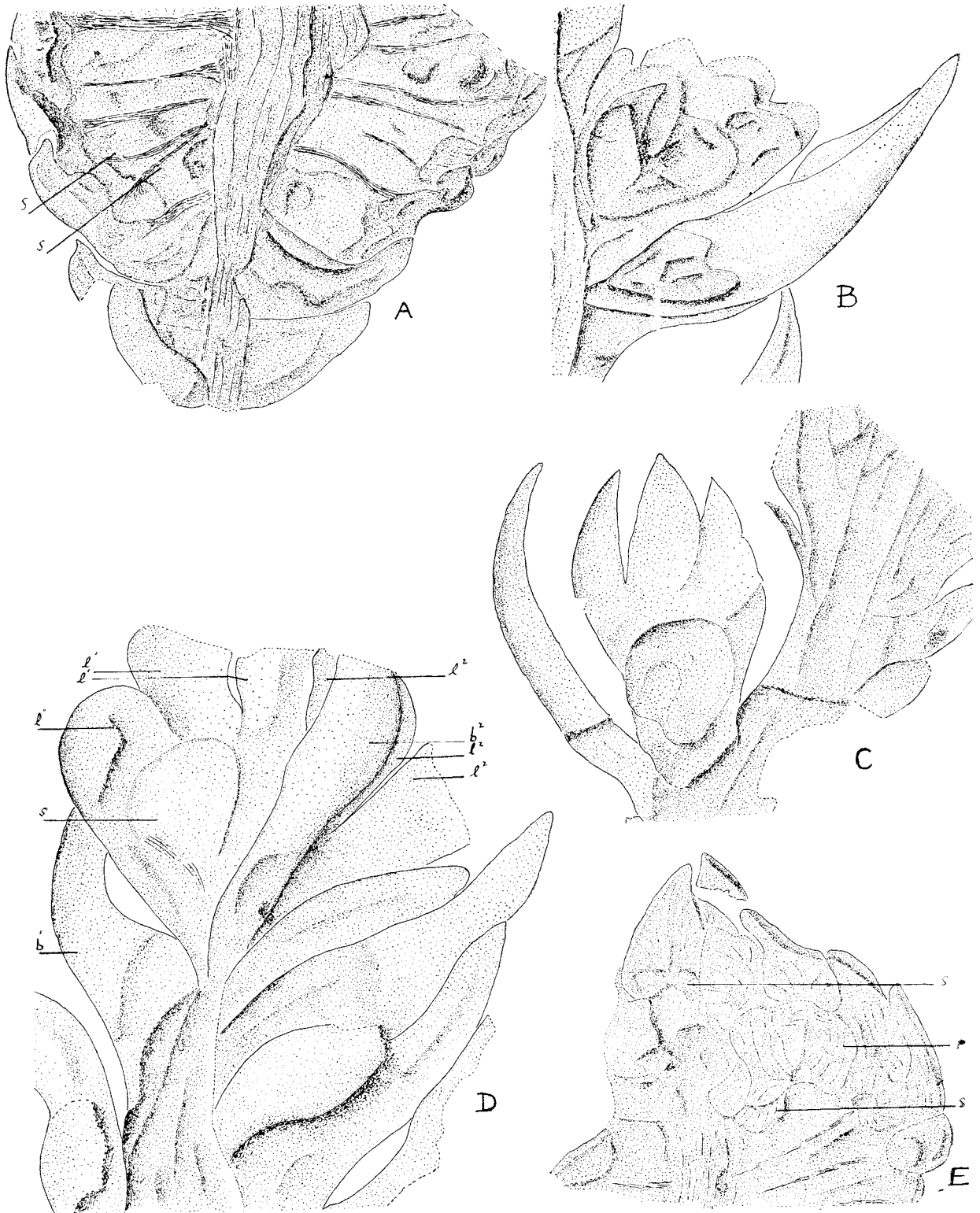


FIG. 3.—*Nothodacrium warrenii* B-D; *Masculostrobus warrenii*, A, E.

A: Base of the cone, showing leaves like leaves on shoot of *N. warrenii* at base. x 10 B.1012/15. B, C: Part (C) and counterpart (B) of same cone unit. x 7. D: Apex of the cone, b^1, b^2 —bract of units 1 and 2; l^1, l^2 —lobes of cone scale of units 1 and 2; s = seed (lines indicate region where elongated cells are present). x 7. B.1012/21. E: Apex of the cone, s = imprint of pollen sac, P = scale x 10. B.1012/15.

elongated cells, peltate scale, triangular in shape, attached to connective a little below the mid-point, about 1.5 mm. high and 0.5 mm. wide, and (probably) two pollen sacs. Apex of peltate scale more or less pointed, outward surface showing rows of cells radiating out from point of connection with connective, scale margin ragged by reason of ex-current cell rows. Scale not connected to pollen sacs. Pollen sacs about 1 mm. deep, probably connected along whole length of connective. Cuticle unknown.

Pollen of more or less rounded outline, diameter about 110μ (78μ to 153μ), amb equilateral triangular, but with well rounded corners, of side about 88μ (62μ to 110μ), and usually reaching outside edge of grain at three places. Grain with three sacci, rarely confluent. Sacci about 16μ (3μ to 24μ) wide, not always of equal size. Sacci sometimes showing small radial foldings. Exine of amb 1.5μ thick, at saccus edge (exoexine) 2μ ; sometimes very faintly showing more or less reticulate pattern, and sometimes faint triradiate mark, with arms running more or less straight and reaching almost to the equator.

(2) *Descriptions and Discussion*: The material consists of a single cone, part and incomplete counterpart, coming from the same shale band (and within a few feet of) some of the material of *Nothodacrium*. Unluckily replacement has gone so far that all efforts to obtain cuticle were unsuccessful, though cells can still be seen, under kerosene, and in one pollen preparation elongated cells possibly of a pollen sac could be made out. It is possible that the cone had shed most of its pollen before fossilisation, for mineral matter occupies the space on most sporophylls where the pollen sacs should be.

Just as in *N. warrenii* the sterile leaves show a ridge down the mid-line whether viewed laterally or from upper or lower surface (Fig. 3A). This presumably means they were rhomboidal in section.

The form of the scale is given as peltate, and not attached to the pollen sacs because in several sporophylls, viewed from the outside, there is a depression from which cell rows radiate, just as over the point of attachment of connective and scale in a living conifer, and this depression is set some way from the base of the scale (Fig. 3E). Further, the scale overlaps, at a different level, the pollen sac (Fig. 3E). The reason for thinking that there are only two pollen sacs is that two depressions flank the point of attachment of the connective (Fig. 3E). It is not clear, however, what the shape of the pollen sacs is, from the sac at *s* in Fig. 3A it is thought that they probably extended the whole length of the connective.

By analogy with living podocarps having the male cone terminal on a normal branch (e.g. *Dacrydium*, or *Microcachrys* (Fig. 4G) I think it probable that *M. warrenii* was also terminal on a normal leafy shoot. For in the living species the cone tends to disarticulate leaving no stalk, but carrying with it three or four scales of form similar to the ordinary leaves, but often slightly smaller. In species such as *P. lawrencei* Hook. or *Saxegothea* Lindl., the scales tend to be left behind. Three sterile scales are seen in *M. warrenii*.

The pollen proved troublesome to prepare. Finally, pieces of mineral matter replacing the pollen sacs were removed and treated on a plastic side with HF to spread the siliceous matter, followed by a mixture of equal parts of water, HF, HNO₃ (as for *N. warrenii*). This gave modest success, but the grains are not well preserved.

A variety of pollen was found, namely two lycopside microspores, two grains referable to a species of *Classopollis* Pflug, one cycad-like, as well as sixteen grains closely resembling *Tsugaepollenites* Potonié. The *Tsugaepollenites* grains are considered to belong to the cone because (a) they are the most numerous sort seen, and (b) seven are still united in tetrads. This evidence is not very satisfactory.

The pollen is closely similar to *Tsugaepollenites trilobatus* (Balme) Dettmann (see Balme 1957, Dettmann 1963, full account with further references). Thanks to the kindness of Dr. B. E. Balme, and of Dr. M. Dettmann, I was able to examine material of *T. trilobatus* and also of the similar *T. dampieri* which has fully confluent sacci. Most grains were like the ones shown in Figs. 4B, D, but others (Fig. 4E) show only very faint sacci, and a nearly perfectly circular outline, while others again show more or less confluent sacci. A feature sometimes seen in my material, and not plainly seen in material of *T. trilobatus* is the numerous small radial folds rather like those seen in e.g. *Dacrydium cupressinum* (Fig. 4B, but see Dettmann 1963 pl. 24 figs. 7 and 8). Also the extine ornament is not seen in my material, it is too ill preserved. However, when all this is said, correspondence is close in general form, dimensions and in such detail is visible, including triradiate mark.

I do not identify the grains with *T. trilobatus* because there do seem to be some definite differences (e.g. the folding of the saccus) and some of the features upon which the diagnosis of *T. trilobatus* depends are not visible.

Gamerro (1965) has found *T. trilobatus* in a cone belonging to *Apterocladus lanceolatus* Archangelsky, and has shown that *T. trilobatus* and *T. dampieri* (Balme) Dettmann are identical. This material comes from the Lower Cretaceous of the Argentine. Archangelsky and Gamerro consider that *Apterocladus* belonged to the Podocarpaceae, and for *M. warrenii* I agree that *Tsugaepollenites trilobatus* (with *T. dampieri*) is most probably podocarpaceous (below).

Cranwell (1961) raises the possibility that in the Podocarpaceae the single encircling saccus is the primitive form of the saccus. It is certainly an ancient form, but I do not think original in the Podocarpaceae, since *Rissikia* has disaccate grains. In this connection it is of great interest to find that *Acmopyle*, usually disaccate, does sometimes produce trisaccate grains, with sacci still separate (Cranwell *loc. cit.*). The encircling saccus in the Podocarpaceae is here regarded as derived, from either a di- or a trisaccate original.

It seems possible that the tri- to monosaccate grains of the *T. trilobatus* sort are to be compared most closely with the fully trisaccate grains of *Podocarpus* of the Section *Dacrycarpus*, differing in that the sacci become confluent and smaller. In *P. dacrydioides*, for example (Cranwell 1961), grains

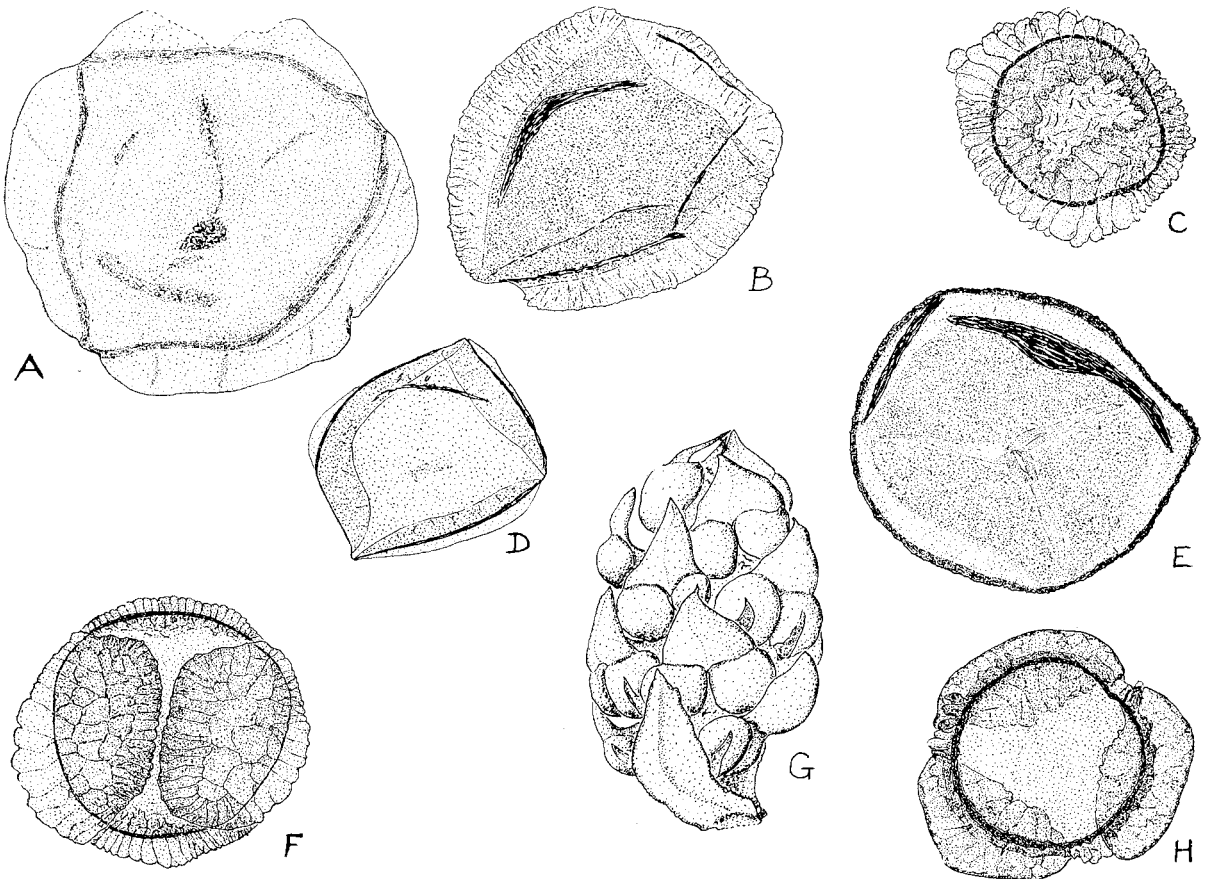


FIG. 4.—*Tsugapollenites trilobatus* A; pollen from *Masculostrobus warrenii* B, D, E; *Dacrydium araucarioides*, C; *D. cupressinum*, F; *Microcachrys tetragona* G; *Podocarpus dacrydioides* H.

A: Pollen grain in polar view. *Dettmann* Kopperamame Bore 2970 ft. D 2346. B: Grain with sacci well seen, sacci showing many small radial folds. D: Grain with distinct sacci folded in over corpus (Several grains seen deformed so). E: grain with very obscure sacci, but showing triradiate mark. C, F: Grain in distal polar view, sacci to left and right. G: A cone, disarticulated to carry with it the (two in *M. tetragona*) leaf-like scales at base (cf. Fig. 3A) $\times 7$. H: grain in proximal polar view, showing sacci continuous round equator. All pollens $\times 600$. B, D, E B 1021/15. C, Bucholz 1059; F, Dominion Museum No. 2; H, *Smith* 78627, Herb. DSIR, New Zealand.

can be found not uncommonly in which the sacci are confluent in the equatorial region (Fig. 4H); and in this species also a triradiate mark may be found (*Cranwell loc cit.*). There is moreover a partial analogy in some species of *Dacrydium*, from *D. cupressinum* (Fig. 4F) with connected but large sacci, via *D. araucarioides* or *D. balansae* in which the sacci are smaller and connected by a wide frill (Fig. 4C) to *D. guilleaunii* Bucholz in which the frill-like saccus is the same width all the way round the grain (*Erdtman* 1957, figs. 25 and 26). The analogy is only partial because these grains are essentially di- not tri- saccate, and the sacci are strongly offset distally, and are not equatorial.

This view has nothing to say on the ultimate origin of the saccus, which *Gamerro (loc cit. following Wodehouse)* considers arose through a separation of extine and intine around the colpus.

Masculostrobus warrenii is thought to belong to the Podocarpaceae. This is because there are, as far as can be seen, only two pollen sacs, possibly attached along the whole length of the connective: the form of the scale recalls *Rissikia* and also some living podocarps, e.g. *D. cupressinum*, and the supposed pollen as noted, is more like that of members of the Podocarpaceae than other conifers. The manner of disarticulation is also consistent with the view that it is podocarpaceous.

There is a strong possibility the *M. warrenii* is the pollen cone of *Nothodacrium*. The chief evidence is that the sterile scales at the base of the cone are of the same shape as, and slightly smaller than the leaves of *Nothodacrium*. The size of the cone stalk is, also, the same size as the axis of the ultimate branchlets of *Nothodacrium*. Also, as noted, the two are associated. Without agreement

in microscopic detail it would be wrong to call them by the same name. It might be argued that *Nothodacrium* should be referred to *Apterocladus*, but this is not done, largely because it is not certain that *M. warrenii* does belong with *Nothodacrium*, and because *Nothodacrium* is largely defined on its seed cone characters, unavailable to Gamero, and the leaves differ.

GENERAL DISCUSSION

As it is interpreted, the cone scale of *Nothodacrium* is like that of *Rissikia* on the one hand, especially *R. apiculata*, and *Dacrydium franklinii* with *D. cupressinum* on the other. In Fig. 5 this series is shown. I suggest that this series might be regarded as an evolutionary one, indicating how the non-epimatial sort of cone scale arose, though no claim is made that this is the only possible scheme, or the only set of changes that has taken place.

Taking the position here suggested, *Mataia* and *Nothodacrium* complement one another, and both point back to the *Rissikia* seed cone scale unit as being an original form which most (not all) cone scales of the living Podocarpaceae can fairly simply be derived. In the epimatial unit, it is possible that one of the three lobes of the *Rissikia* unit is retained, originally with two seeds, (*Mataia*), later with one only (*Podocarpus*): while in the non-epimatial unit it may be that all three lobes of the *Rissikia* unit are retained, but reduced in size finally to a small frill, while the seeds are reduced to three (*R. apiculata*, probably) then one (*Nothodacrium* and *Dacrydium*).

It is very interesting that the genus *Tricanolepis* Roselt (1958) shows a set of changes very similar to those observed between *Rissikia* and *Nothodacrium*, as well as showing their essentially trimerous symmetry. This may be a case of parallel evolution, but to me suggests that *Tricanolepis* should be placed with *Rissikia* and *Nothodacrium* in the Podocarpaceae, not the Taxodiaceae (Roselt *loc. cit.*). If so, this is evidence in addition to pollen (e.g. Gamero 1965) that at some stages in the Mesozoic the Podocarpaceae were world wide (but see Florin 1963).

Assuming that *Masculostrobos warrenii* belongs with *Nothodacrium warrenii*, the fossil shows points recalling three groups of podocarps. It has the pinnate branching pattern, flat subsidiary cells and (as it is argued) a similar pollen organisation to *Podocarpus* Sect. *Dacrycarpus*. The rather simple arrangement of subsidiary and encircling cells also recalls *Dacrycarpus*. However, in that the ultimate shoots are of unlimited growth, and in the leaf shape *Dacrydium* group B (*D. elatum*, *D. cupressinum* and their allies) is recalled. This group, unlike *Dacrycarpus* has non-epimatial cone scales, one fertile cone scale per cone. *Dacrydium franklinii* is recalled in that the spike-like cone consists of several fertile units, and each cone scale is trifold. However, in other available features *N. warrenii* diverges from *D. franklinii*, and I am inclined to minimise the resemblances since, as above, three lobes per cone scale seems to be basic to the Podocarpaceae, and the reduction from several to one fertile unit has almost certainly proceeded at least twice independently (in *Podocarpus* Section

Stachycarpus, and in *D. franklinii* versus *D. laxifolium*). In having (as it is thought) an inverted seed *N. warrenii* comes perhaps closer to *D. cupressinum*, in which the seed is first inverted, but in ontogeny becomes semi-upright, than to *D. franklinii* in which, as far as is known, this change does not take place. The pollen cone does not especially recall any of the above groups showing points of resemblance to all, and a single terminal cone on an ordinary branch, as *M. warrenii* is thought to have been, is found in all three.

It seems therefore, that the two groups particularly recalled are *Podocarpus* Section *Dacrycarpus* and *Dacrydium* group B, and except for the more doubtful case of *D. franklinii*, no others seem to be concerned. This is interesting, for Hair (1963) has shown that *Dacrycarpus* and *Dacrydium* Group B have particularly similar chromosomes, and he tentatively groups them together. It seems that the fossil evidence offers a little support to Hair's view.

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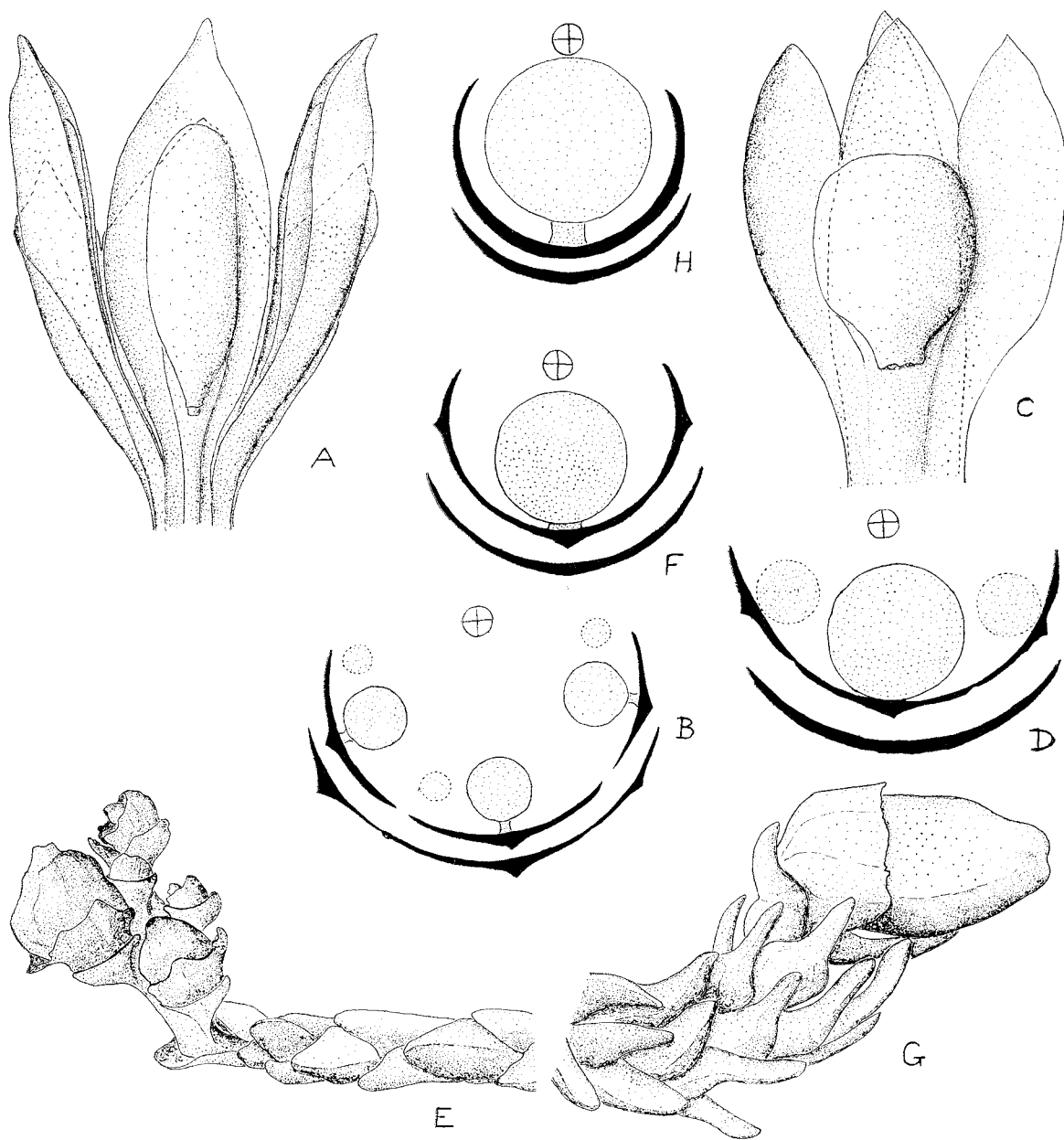


FIG. 5.—A: *Rissikia apiculata*, reconstruction in adaxial view of one unit (cone scale and bract) x ca. 18. B: *R. apiculata*, floral diagram (using Florin's terminology) of unit in 5A. C, D: *Nothodacrium warrenii*, reconstructions as in 5A, B. E: *Dacrydium franklinii*, a cone, x 7, and F: floral diagram. F, G: *D. cupressinum*, floral diagram and cone.

NOTE: seeds shown dotted in B and D are those supposed lost as between *Rissikia media* and *R. apiculata* (B), and *R. apiculata* and *Nothodacrium* (D). No effort is made to interpret the cones in terms of their (supposed) original radial symmetry.

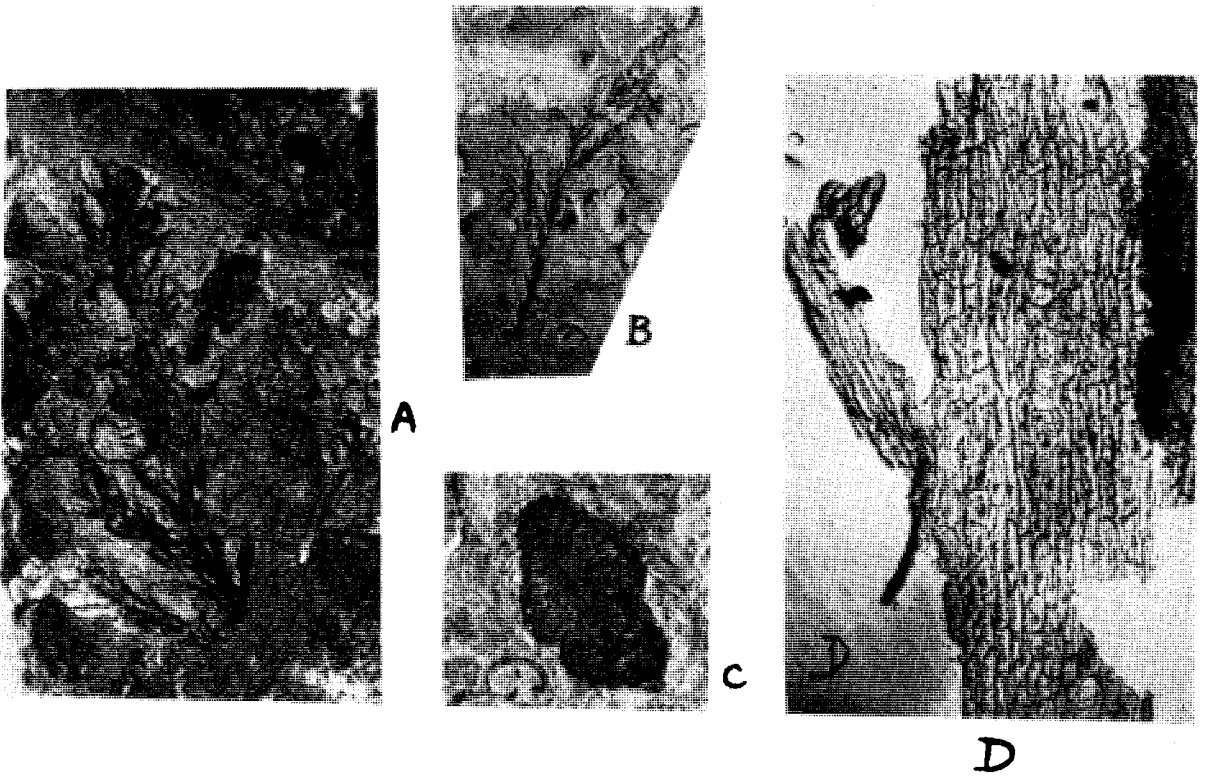


PLATE I.—A: *Nothodacrium warrenii*, shoot with base of the seed cone, B1012/21 x 2. B: *N. warrenii*, cutinised shoot x 1, B1012/10. C: *Masculostrobus warrenii*, the cone B1012/15, x 1.25. D: cuticle cells papillae and stomata. B1012/10, x 50.

