

Middle Triassic megafossil plants from Long Gully, near Otematata, north Otago, New Zealand

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The Long Gully Formation of the Corbies Creek Group contains abundant remains of the low-diversity coastal vegetation characteristic of the Middle and Late Triassic Pacific margins of Gondwana. The plant-bearing rocks in Long Gully conformably overlie fossiliferous deltaic and marine Ladinian rocks (Kaihikuan local stage).

A variety of fossil fructifications were found, allowing better understanding of the botanical affinities of the plants. Fertile remains referred to *Todites maoricus* sp. nov., indicate osmundalean affinities for one common kind of sphenopterid fern frond. *Townrovia petasata* gen. et sp. nov. is the likely microsporophyll and ?*Peltaspermum* sp. indet. the likely megasporophyll of seed fern leaves referred to *Pachydermophyllum*, represented at Long Gully by *P. dubium* (Burgess) comb. nov. and *P. praecordilleriae* (Frenguelli) comb. nov. The ovulate voltziacean conifer cone *Telemachus lignosus* sp. nov. and "unidentified cone B" may be fructifications of a species also producing leaves referred to *Heidiphyllum elongatum* (Morris) gen. et comb. nov., including leaves widespread in Triassic rocks of Gondwana formerly referred to *Phoenicopsis*, *Podozamites* and *Desmiophyllum*. The ginkgoalean ovulate cone *Karkeniania secunda* sp. nov. and "unidentified cone A" may have been produced by the same species as the leaves *Sphenobaiera robusta* (Arber) Florin.

INTRODUCTION

In Long Gully, near Otematata, north Otago, terrestrial sedimentary rocks conformably overlying marine Ladinian rocks (Kaihikuan local stage), contain abundant megafossil plants (Retallack and Ryburn, in press). Many of these are identical to fossil plants in the Tank Gully Coal Measures of the lower Mt Potts Group, which conformably underlie Ladinian (Kaihikuan) marine rocks (discussed by Retallack, 1979, 1980). Thus fossil plants from Long Gully also serve to establish a correlation between the provincial ecostratigraphy and biostratigraphy of Gondwana (as proposed by Retallack, 1977) and the international geological time scale, largely based on the biostratigraphy of marine fossils.

As discussed elsewhere (Retallack and Ryburn, in press), the plants preserved in the Long Gully Formation of the upper Corbies Creek Group in Long Gully, probably vegetated delta plains and the margins of interdistributary bays and coastal lagoons. Abundant fructifications have been found at several localities in Long Gully. Considering the low diversity of these coastal plant associations, I here make some suggestions regarding the various organs attributable to the same ancient species and their more precise botanical affinities. Unfortunately, detailed anatomical analysis to support these observations of close association is not possible. The sediments show low-grade metamorphism corresponding to the prehnite-pumpellyite facies. These rocks have also been deeply weathered and almost entirely leached of carbonaceous material, possibly because of their position in the core of a gently plunging, upright isoclinal syncline (Retallack and Ryburn, in press, fig. 2).

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Fossil plants from Long Gully have only been cursorily mentioned (Gair, Gregg and Speden, 1962; Mutch, 1963; Townrow in Ryburn, 1967; Campbell and Warren, 1965; and Force, 1974). I could not locate any of the collections on which these identifications were based. Apart from one specimen of *Ginkgophytopsis lacerata*, I collected all the material described here during the summers of 1975 and 1976 (Retallack and Ryburn, in press). There is no convincing evidence of the genus *Dicroidium* in my collections from Long Gully, and I have assumed that previous records of this genus from Long Gully were misidentified *Pachydermophyllum* leaves. Similarly, earlier records of species of *Cladophlebis* are probably apical fragments of *Todites maoricus* and records of "*Stenopteris*" are more likely roots (cf. Fig. 10A). Other previous records differ from those given here because of emendations proposed here and previously (Retallack, 1980).

The suprageneric classification used here is adapted from that of Harland *et al.* (1967). Fossil numbers prefixed by B are housed in the collections of the Geological Survey of New Zealand, Lower Hutt; those prefixed by OU in the Geology Department, Otago University, Dunedin. Fossil localities are cited in the code of the New Zealand Fossil Record File based on both the 1:63,360 and the metric 1:50,000 map series. MMF specimens are in the Mining Museum of the Geological Survey of New South Wales, Sydney.

Division: Pteridophyta

Class: Pteropsida

Order: Osmundales

Family: Osmundaceae

Genus: *Todites* Seward emend. Harris 1961: 75.

***Todites maoricus* sp. nov. (Figs. 1A-C, 11A-B)**

1980 *Sphenopteris* sp. indet., Retallack, p. 33, figs. 1A-B.

Holotype: Fertile specimen B1087.40, N.Z. Geological Survey.

Type locality: S117/f754, in road cutting along Backyards to Otematata River road, Long Gully, near Otematata, north Otago, New Zealand (see Retallack and Ryburn, in press): Long Gully Formation, upper Corbies Creek Group, Ladinian or late Middle Triassic (Kaihikuan local stage).

Derivation: The specific epithet has been Latinized from the New Zealand word *maori*, used in its broader sense of "belonging to New Zealand".

Diagnosis: Tripinnatifid fronds, probably over 60 cm long; primary rachis bulging abaxially, flat to sulcate adaxially, often with a narrow laminar flange; pinna rachis similar; pinnae up to 15 cm long, catadromic, tapering gently towards the apex; pinnules up to 18 mm long by 5 mm wide, divided laterally into 4 or 5 subrectangular lobes, each lobe supplied by a single set of clearly marked, doubly-forking secondary veins; well-preserved pinnules flat, with thin and delicate leaf substance, showing obscure, random cellular outlines; other fronds apparently more coriaceous with strongly recurved pinnules, transversely wrinkled around the lobes; apical pinnules of the pinna cladophleboid.

Fertile fronds with more strongly recurved pinnules, covered abaxially by contiguous, exindusiate sori; approximately 9 sporangia per sorus in a loose, radial arrangement; sporangia measuring about 400 by 300 μm ; with extensively thickened apical cells; body of sporangium tapering down from thickened apex to a very short stalk; stomium vertical and penetrating the thickened apical cells.

Description: The largest fragment of a frond found (B1087.51) is 123 mm long and shows slightly shorter pinnae apically. The longest pinna observed (B1087.52) is about 150 mm long. Assuming a lenticular frond outline attaining twice the width of the longest observed pinna at the centre and tapering at the observed rate, the whole frond was probably over 600 mm long.

The primary and secondary rachides are strongly curved abaxially but flat or slightly sulcate adaxially. Coal cleat and fine fossil rootlets penetrating the matrix and fossils made it difficult to be certain whether these rachides were pubescent.

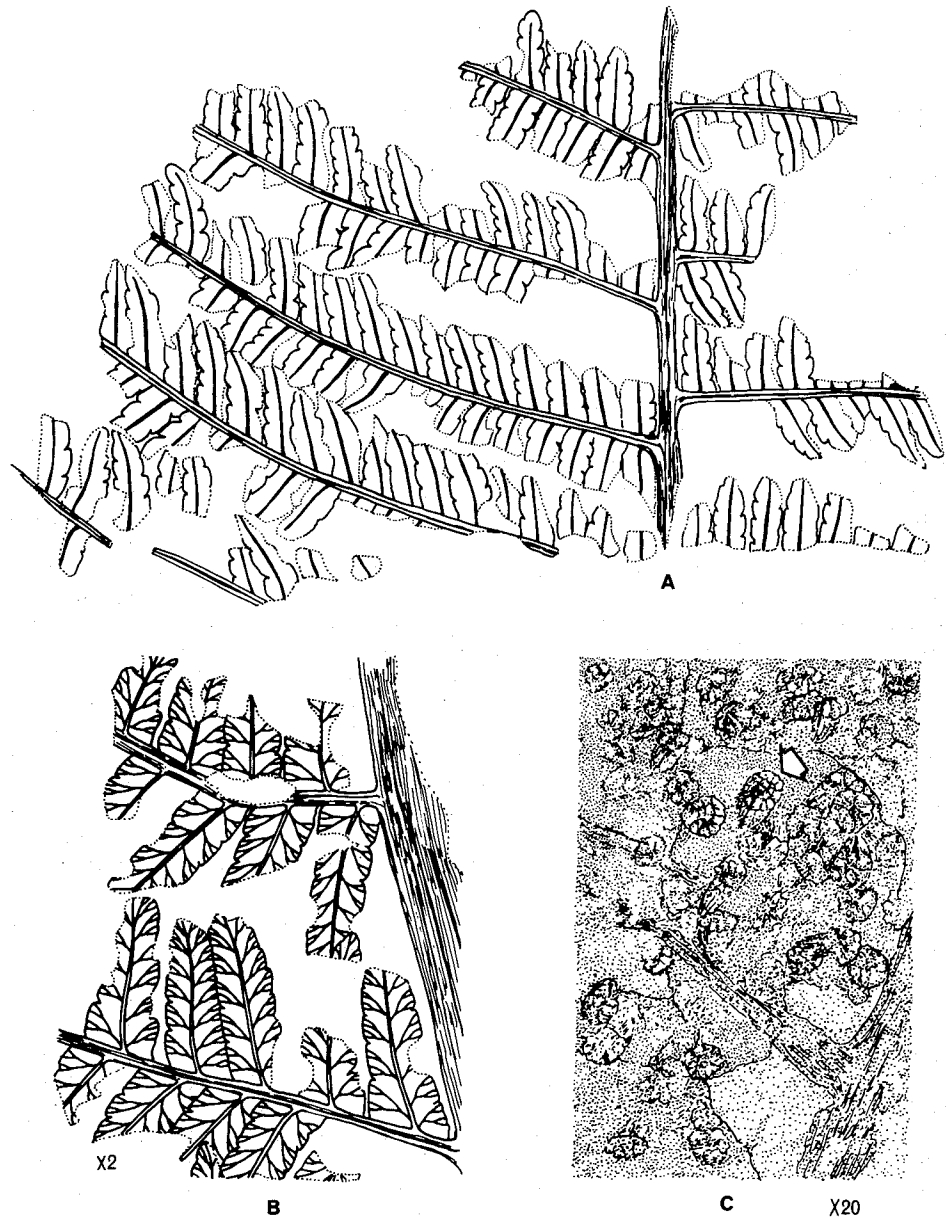


Fig. 1—*Todites mauricus*; A, portion of frond, natural size, B1088.1; B, detail of venation, twice natural size, B1087.22; C, portion of fertile pinnule, arrow indicates well-preserved sporangium, twenty times natural size, B1087.40.

The pinnules are arranged catadromically on the pinna. There are a few falcate cladophleboid pinnules at the pinna apex but most are lobate and sphenopteroid. Each of the pinnule lobes is supplied by a single set of lateral veins. These veins are strongly lignified in the thin leaf substance of better preserved specimens. A single lateral vein arises from the pinna rachis and forks twice before reaching the pinnule margin. Each fork of the lateral veins is strictly dichotomous with the branches directed away from each other immediately after the fork, and then bending back toward the margin. The leaf, when well preserved, is flat, with no carbonaceous film and with fine, irregular cell outlines. Other remains may have recurved pinnules, which may give the lobes a misleading rounded appearance. Extremely recurved and

transversely wrinkled pinnules may have a misleading cladophleboid appearance, because lobes of the pinnules curve away into the matrix.

Few fertile fronds were found. Only one specimen had distinct and complete sporangia (arrowed in Figs. 1C, 11B). Most of the apical cells of the sporangium are thickened. From this thickened disc (annulus) the body of the sporangium tapers gradually until basally constricted at a short stalk. The stomium runs the whole length of the sporangium and also appears to penetrate the apical thickened cells. Tearing along this apical extension of the stomium may explain the more irregularly shaped impressions of sporangia. About 9 sporangia in a loose radial arrangement form each sorus. Contiguous sori cover most of the pinnule surface. Fertile pinnules are usually recurved, so that little of the leaf margin may be visible on natural fracture surfaces exposing the fertile abaxial surface.

Dimensions of the holotype: Width of primary rachis = 3.9 mm; width of pinna rachis = 0.8 mm; length of longest pinnule = 11.4 mm; width of widest pinnule = 3.2 mm; diameter of sorus (Fig. 11B) = 1.5 mm; dimension of best-preserved sporangium (arrowed in Figs. 1C, 11B) = 400 by 300 μm .

Comparison: I have here followed Harris (1931, 1961) in using *Todites* for fertile osmundalean fronds with laminar ultimate segments, unlike the filiform ultimate segments of *Osmundopsis*. Most species of *Todites* (described by Harris, 1931, 1961; Ash, 1969; Andrews, *et al.*, 1970; Schorokova, 1975) have cladophleboid, pectopteroid or neuropteroid pinnules, unlike *T. maoricus*. *Todites giganteus* (Oishi) Schorokova 1975 and *T. pseudoraciborskii* (Srebrodol'skaya) Schorokova 1975 have a secondary venation and slightly undulose margins comparable to the more pronounced lobation of *T. maoricus*. The pinnules of *T. kamyschbachensis* Brik (Krischtovich, 1957: 241) are also similar but have more irregularly shaped, apically directed lobes, each with more copiously branching venation. Sphenopteroid pinnules are also found in *T. sibiricus* (Schmalhausen) Radchenko 1955, *T. evenkensis* Radchenko 1955, *T. berekensis* Stanislavsky 1976 and *T. princeps* (see Harris, 1931, 1961), but the pinnules of all these species are shorter, more tapered and have rounder pinnule lobes and simpler venation than does *T. maoricus*. The small sphenopteroid fragment which Barnard (1965) called *T. crenatus* has more dentate and rounded lobes, a distinctive zig-zag midrib in its pinnules and more complex lateral venation than *T. maoricus*. Mature pinnules of *Cladophlebis mesozoica* (Geinitz) Frenguelli 1947 may be similar to those of *T. maoricus* but have more rounded pinnule lobes and greater proportion of cladophleboid pinnules on the frond.

Remarks: *Todites maoricus* and *Cladophlebis* sp. cf. *C. takezakii* described here are most similar to *Todites giganteus* and *T. pseudoraciborskii* from the Late Triassic of the far eastern U.S.S.R. Like other Triassic species of *Todites* (described by Ash, 1969, and Harris, 1931), they have a more extensive apical annulus than found in younger fossil and modern Osmundaceae. An extensive apical annulus is also seen in the possible osmundalean sporangium figured by Gould and Delevoryas (1977, Fig. 9E) from a late Permian petrified peat in Queensland which has also yielded abundant osmundalean trunks (*Palaeosmunda*) and sphenopteroid foliage (Gould, 1970). Like other Permian and Triassic *Todites*, Permian impressions from central Siberia and the Sayano-Altai, U.S.S.R., also have sphenopteroid foliage, but details of their sporangia are not clear (Radchenko, 1955). Several European Permian and Carboniferous compressed sporangia with even more massive apical annuli have been discussed by Miller (1971) and Andrews *et al.*, (1970). Some of these with more elongate or apically constricted sporangia have been referred to the Schizaeaceae (Andrews *et al.*, 1970). It is known that some Carboniferous ferns whose sporangia had massive apical annuli, also had abaxially-oriented, gutter-like petiole traces (*Anachoropteris* of Phillips and Andrews, 1965), and others had petiole traces "H" shaped in cross-section (Tedeaceae of Eggert and Taylor, 1966). This is unknown even in the oldest recognized osmundalean trunks or their possible ancestors (Miller, 1971) and appears to have characterized extinct families of ferns with horizontally oblique annuli, such as the Euramerican Carboniferous Sermayaceae (possibly including several supposed Carboniferous Gleicheniaceae; Eggert and Delevoryas, 1967; Rothwell, 1978). The extinct Damudopteridaceae from the Permian of Gondwana (Pant and Khare, 1974; Pant, 1977; possibly including other sporangia figured by Gould and Delevoryas, 1977, Figs.

9A-B) may also be allied to the Sermayaceae. Plants with massive apical annuli and protostelic pinna traces (e.g. *Norwoodia* of Rothwell, 1976) appear more likely osmundalean ancestors, considering their anatomy and the direction of sporangial evolution indicated by Permian and Triassic *Todites*. However, the early evolution of osmundaleans will not be clear until more plants classified according to their stem anatomy (as outlined by Phillips, 1974) are reassessed according to their attached sporangia.

Occurrence: Fertile *Todites maoricus* is only known from Long Gully (S117/f754) and near Benmore Dam (S117/f50, specimens B42.74, B42.37), both near Otematata, New Zealand. Identical large fragments of sterile fronds have been found in Long Gully (S117/f631; S117/f751-753) and in Tank Gully (*Sphenopteris* sp. indet. of Retallack, 1979, 1980). Similar sterile fragments have also been found in marine rocks of the Murihiku Supergroup in Southland near Gore (S170/f552, at grid reference 076346, specimens B30.1, B30.3, B30.4), near Maitara (S182/f551, g.r. 720978, OU3963, OU3965, OU3967) and along Beers Track near Dipton (S169/f1016, g.r. 492596, B1077.1 and S169/f1017, g.r. 492596, B1076.4, B1076.5). These extend the range of *Todites maoricus* to include the Anisian as well as the Ladinian, and thus embrace the whole Middle Triassic.

Order: incertae sedis

Genus: *Cladophlebis* Brongniart emend. Frenguelli 1947:12.

Cladophlebis sp. cf. *C. takezakii* Oishi 1940 (Fig. 2)



Fig. 2—*Cladophlebis* sp. cf. *C. takezakii*, pinna fragment, natural size, B1087.21.

Description: Only one fragmentary pinna of this cladophleboid frond was found, so higher order branching is unknown. Pinnules are up to 32 mm long by 7 mm wide. They are lobed, almost dentate near their subacute apex, parallel-sided for about half their length and slightly constricted basally. Secondary venation is twice forked with all forking very close to the midrib so that the branch veins run parallel for most of their length toward the margin.

Comparison: The species of *Cladophlebis* have been reviewed by Frenguelli (1947), Herbst (1971) and Boureau and Doubinger (1975), and additional species were discussed by Oishi (1940), Oishi and Huzioka (1938), McQueen (1956), Harris (1961) and Kimura (1976). Of these, the fragment from Long Gully is most like *Cladophlebis takezakii* Oishi 1940 (see also Kimura and Kansha, 1978). This species is most like *Cladophlebis raphaeliaeformis* (Boureau and Doubinger, 1975, fig. 190), which has shorter and dentate, rather than lobed, pinnules. The constriction of the bases of the pinnules in these two species is not as extreme as in the form genera *Raphaelia* (see Kimura and Sekido, 1976) and *Stormbergia* (Seward, 1911). Most other large species of *Cladophlebis* with non-falcate pinnules and at least twice-forked secondary veins do not have

constricted pinnule bases. Of these, *C. lenaensis*, *C. aldanensis* (Lebedev, 1965) and *C. aktashensis* (Harris, 1961) all have entire pinnules. The lobation of the pinnules in *C. haiburnensis* (in the sense of Harris, 1961, who includes *C. ingens* and *C. spectabilis* in that species) and "*C. gigantea*" (now *Todites giganteus* (Oishi) Schorokhova 1975) and the apical denticulation of *C. raciborskii* (Frenguelli, 1947) are not as deeply incised as the lobation of *C. takezaki*. Other large cladophleboid fronds, such as *C. halleiana* and *C. fukiensis*, are distinguished by having secondary veins which fork three times throughout the pinnules (Frenguelli, 1947).

Remarks: This fragment from Long Gully shows some general resemblance to *Todites maoricus* although it is twice as large and has narrower pinnule lobes, and also to *Todites giganteus* (Oishi) Schorokhova 1975. It may also prove to be osmundalean when found fertile.

Occurrence: The single specimen from Long Gully was found at locality S117/f754. *Cladophlebis takezaki* is known from several Early Cretaceous localities in Japan (Oishi, 1940, p. 290; Kimura and Kansha, 1978).

Division: Gymnospermophyta

Class: Pteridospermopsida

Order: Peltaspermales

Family: Peltaspermaceae

Genus: *Townrovia* gen. nov.

Type species: Townrovia petasata comb. nov.

Diagnosis: Pinnate, unforked microsporophyll; pinnae simple or forked; sporangial heads with an irregular, adaxial, laminar wing and a median, elongate, fleshy receptacle, to which are attached numerous, unilocular, spathuloid pollen sacs in two or three irregular rows; stomata of sporangial head surrounded by a relatively even ring of (usually) five subsidiary cells, each bearing a papilla which overhangs the stomatal opening; pollen disaccate and colpate.

Derivation: This genus is named after Dr J. A. Townrow in honour of his many contributions to the understanding of Mesozoic pteridosperms.

Comparison: Comparable Palaeozoic pteridosperm pollen organs are reviewed by Millay and Taylor (1979). Many of these have sporangia attached radially at the end of branch systems and bear pseudosaccate, trilete or monolete prepollen, unlike *Townrovia*. Many are planated, but few have any terminal leaf-life structures like the sporangial heads of *Townrovia*. In *Feraxotheca*, a genus based on petrified material similar to the widespread compression fossils referred to *Crossotheca*, the sporangia are in two rows, pendant from an elongate terminal head. The poorly known Permian compression fossil *Psaliangium* may have been similar. Unlike *Townrovia*, *Feraxotheca* did not have a marginal flange on the sporangial receptacle, had higher orders of branching and trilete prepollen. The true pollen of the Callistophytacean genera *Idanothekion* and *Callandrium* are superficially similar to the disaccate pollen of *Townrovia* but have a girdling monosaccus and leptoma. Callistophytacean microsporophylls also differ from *Townrovia* in having many radial aggregates of pollen sacs attached abaxially to unmodified sphenopterid foliage.

Caytonanthus, the microsporophyll of the caytonialeans, is also very different from *Townrovia*. In *Caytonanthus* the pollen sacs are arranged in radial groups on the abaxial surface, near the ends of pinnately-arranged reduced segments. The stomata of *Caytonanthus* are anomocytic (haplocheilic) but lack papillae on the subsidiary cells (Harris, 1964) and its pollen are disaccate but leptomatous (Townrow, 1965). The impression fossil *Perezlaria oaxacensis* Delevoryas and Gould 1971, is superficially similar to *Caytonanthus*, but it is uncertain whether it bore seeds or pollen.

Several other little known Mesozoic and Palaeozoic pollen organs differ from *Townrovia* either in the helical arrangement of their sporangial heads, their radially-arranged pollen sacs, anomocytic (haplocheilic) stomata without papillae overhanging the stomatal pit, leptomatous disaccate pollen (see Townrow, 1965), or a combination of these features. These include *Jongmansensis transvaalensis* (Plumstead, 1961, 1963), "*Pteruchus*" *indicus* Pant and Basu 1973, "*P.*" *nidpurensis* Srivastava 1974, *Pramelreuthia haberfelneri* Krasser (Kräusel 1948), *Stachyopitys edwardsii* (Thomas) Townrow 1962a and "*S. cfr annularoides*" (Halle, 1913).

The microsporophyll of crustosperm pteridosperms, *Pteruchus*, could be confused with *Townrovia*, but in *Pteruchus* the pollen sacs are attached to the lateral margins rather than a median receptacle. The pollen of *Pteruchus* is also disaccate colpate (Townrow, 1962a, 1962b, 1965), but its stomata are laterocytic (in the sense of den Hartog—van ter Tholen and Baas, 1978, or pseudosyndetocheilic of Retallack, 1977), and have non-papillate subsidiary cells. *Pteruchus* is the likely microsporophyll of a variety of leaves widespread in Gondwanaland, referred to the genera *Dicroidium*, *Xylopteris* and *Johnstonia* (Townrow, 1962a; Retallack, 1977).

Most similar to *Townrovia* are the pollen organs of peltasperm pteridosperms, *Antevsia*, the likely microsporophyll of plants producing leaves of *Lepidopteris* (Townrow, 1960) and *Pteroma*, the likely microsporophyll of plants producing leaves of *Pachydermophyllum papillosum* (Harris, 1964). These two microsporophylls and their likely leaves all have anomocytic stomata more or less overhung by papillae on each of the subsidiary cells, and disaccate, colpate pollen like *Townrovia*. *Pteroma* differs fundamentally from *Townrovia* as its sporangial heads are fused discoidal synangiate structures, with the embedded elongate sporangia in two rows and dehiscing by a longitudinal abaxial slit. *Antevsia* differs from *Townrovia* in having monocolpate pollen and in the weakly-alate receptacle of its sporangial head. The structure of the ultimate fertile units of *Harrisiothecium* (Harris, 1932b, Lundblad, 1961) are most like those of *Pteroma*, but the discoidal synangium is folded longitudinally into a saddle-like shape. *Harrisiothecium* is probably also a peltasperm microsporophyll, but its likely leaves, *Ptilozamites* (see Harris, 1932a) have odontopteroid venation, unlike any other peltasperm, even in the broadest sense outlined by Dobruskina (1975). Heavily cutinized anomocytic stomata without papillate subsidiary cells are most common in *Harrisiothecium* and *Ptilozamites*. This and the leptomatous pollen of *Harrisiothecium* (see Townrow, 1962b, 1965) set these apart from other peltasperm remains.

Botanical affinities: *Townrovia* is most similar to microsporophylls of the seed fern family Peltaspermaeae, especially considering the attachment of its pollen sacs to an elongate receptacle, the cuticle of its sporangial heads and its likely leaf "*Pachypteris crassa*", characterized by anomocytic (haplocheilic) stomata with papillate subsidiary cells. The leaves "*Pachypteris crassa*" are quite different in age and morphology from all the specimens synonymized with them by Townrow (1965), and, considering their cuticle, are perhaps better regarded as a new species of *Lepidopteris* with relatively broad pinnules.

Related leaves: Townrow (1965) did not mention that other pteridosperms, including *Dicroidium*, have also been found in the Langloh Mine with "*pachypteris crassa*" and *Townrovia petasata* (see for example, specimen MMF16361a). Nevertheless, *Dicroidium* has a different cuticle, and Townrow's arguments for regarding "*Pachypteris crassa*" and *Townrovia petasata* as parts of the same plant species are convincing. In Long Gully (S117/f754), where *Townrovia* was found, the only pteridosperm leaves found have been referred to the genus *Pachydermophyllum*, also of likely peltasperm affinities.

Townrovia petasata (Townrow) comb. nov. (Figs. 3C, 11E)

1965 *Pteruchus petasatus*, Townrow, p. 506, figs. 3J, 4, 5E, 6A-H, pl. 1B, D-E.

Holotype: "*Pteruchus petasatus*" specimen 81940 figured by Townrow (1965, pl. 1B): collections of the Geology Department, University of Tasmania, Hobart, Tasmania.



Fig. 3—Fructifications; A, unidentified cone A, OU14231; B, (?) *Peltaspermum* sp. indet, B1087.27; C, *Townrovia petasata*, B1087.24. All three times natural size.

Type Locality: Shale bed in the worked seam, Langloh Coal Mine, Hamilton, Tasmania; Newtown Coal Measures or earlier Feldspathic Sandstone (Townrow, 1965).

Description: The best example of this species found in Long Gully (Figs. 4C, 11E) shows the impression of several sporangial heads, stalks and axes irregularly exposed on a muddy solution plane of rock. The sporangial heads are up to 15 mm long. Each has about 20 spathuloid pollen sacs, 3-4 mm long, attached to a fleshy receptacle about 1 mm wide. There are some indications of laminate adaxial flanges on the receptacles, but these are not all evident, partly because of poor preservation and partly because the sporangial heads have preferentially split along the plane of the pollen sacs.

Occurrence: This species has only been found in Langloh Coal Mine, Tasmania (Townrow, 1965) and at S117/f754, in Long Gully, New Zealand. Both are most likely Middle Triassic (Retallack, 1977).

Genus: *Peltaspermum* Harris emend. Townrow 1960:353.

(?) *Peltaspermum* sp. indet. (Fig. 3B)

Remarks: A single natural group of seeds from Long Gully S117/f754 (Fig. 3B) was referred here because some of the seeds form a radial group. The seeds are leached and

both the compressed exterior and natural longitudinal sections of the seeds can be seen. Some appear to have had a broadly triradiate sclerotesta. It is not certain whether the associated axes were attached to these seeds.

Genus: *Pachydermophyllum* Thomas and Bose 1955

Type species: Pachydermophyllum papillosum Thomas and Bose 1955.

Comparison: As discussed elsewhere (Retallack, 1977: 264), the genus *Pachydermophyllum* has been submerged by some authors within the genus *Pachypteris*, which has since become very unwieldy, including remains formerly referred to *Stenopteris*, *Cycadopteris* and *Thinnfeldia* (Harris, 1964; Boureau and Doubinger, 1975). The type species of *Pachypteris* (*P. lanceolata*; Thomas, 1954, and Harris, 1964) is bipinnate with hypostomatic cuticle and haplocheilic (or anomocytic in the terminology of Dilcher, 1974) stomata. However, the type species of *Pachydermophyllum* is unipinnate with amphistomatic cuticle. Its stomata are also anomocytic, but each of the subsidiary cells bears a papilla overhanging the stomatal pit (Thomas and Bose, 1955; Harris, 1964). The type species of *Thinnfeldia* has a cuticle very similar to that of *Pachypteris* and was rightly transferred there by Doludenko (1971). However other species formerly referred to *Thinnfeldia*, especially those with a tight, narrow ring of subsidiary cells (Gothan, 1912; Antevs, 1914), probably form a separate genus.

Jones and de Jersey (1947) and Douglas (1969) have both confused *Pachydermophyllum* leaves with *Rienitsia* Walkom 1932. Jones and de Jersey argued that the uncutinized fertile type specimen of *Rienitsia* was a bennettitalean microsporophyll like *Wonnacottia*. However, *Wonnacottia* has quite different sporangia to *Rienitsia spathulata* Walkom 1932, and a very different cuticle to the fossils identified as "*Rienitsia*" by Jones and de Jersey (1947) and Douglas (1969). Finally, *Wonnacottia* is now believed to be an insect-eaten and galled leaf of *Anomozamites nilssonii*, containing drift pollen in the gall pouches (Harris, 1969: 82). The type specimen of *Rienitsia spathulata* (MMF2487) is a pinnatifid, fertile marattiaceous fern, as also suspected by Townrow (1957) and indicated by Herbst (1977). I disagree with Townrow and feel that *Rienitsia* should not be included within *Asterotheca fuchsii* (Herbst, 1977). Coalescence of the lamina has proved an important evolutionary process in the Marattiaceae (Mamay, 1950), and wider recognition of *Rienitsia* may have stratigraphic value.

Jones and de Jersey (1947) also obtained *Pachydermophyllum*-like cuticle from entire leaves which they referred to the genus *Doratophyllum*. This cuticle is quite unlike that found in *Doratophyllum* (as described by Harris, 1932a), which is hypostomatic and has about eight thickly cutinized subsidiary cells around the stomatal opening. Jones and de Jersey indicated that some of their "*Doratophyllum*" leaves had straighter secondary veins at an acute angle to the midrib and others had strongly curved veins. The former are most likely uncuticularized remains of *Linguifolium tenison-woodsii* (Etheridge) Retallack 1980, and the others are better referred to *Dejerseya lobata* (Jones and de Jersey) Herbst 1977. However, the other species of *Dejerseya* are here included within *Pachydermophyllum*, their senior synonym, as their venation and cuticle are indistinguishable and their gross form differs only in insignificant detail.

Dobruskina (1975) has discussed the large number of seed fern leaves which have a cuticular structure similar to *Pachydermophyllum*. Of these, only *Compsopteris* is unipinnate and has a relatively simple secondary venation like *Pachydermophyllum*. However, *Compsopteris* includes larger leaves, with less persistent pinna midribs and secondary venation at a more acute angle to the pinna midrib than in *Pachydermophyllum*.

Species: I here list five recognized species of *Pachydermophyllum*, with more details on those species not found in the Triassic of New Zealand.

Pachydermophyllum dubium (Burgess) comb. nov. has pinnae two to three times as long as wide and often coalescing at their base. It is found in the Early to Late Triassic of Tasmania, New South Wales, Queensland and New Zealand.

Pachydermophyllum sp. (unnamed new species) has small, thick, coriaceous pinnae, lanceolate to subrhombic, contracted at their bases and reaching their maximum width at about half their length. It is found in the Middle and Late Triassic of Tasmania and Argentina. It is based on the "*Pachypteris pinnata*", specimen 89775c of Townrow and Jones (1969, figs 1E, 2A, 3C) as holotype and also includes "*Dicroidium* sp." of Archangelsky (1968a, fig. 1C, excluding the top left-hand two specimens).

Pachydermophyllum papillosum Thomas and Bose 1955 has thick, coriaceous, lanceolate to ovate pinnae, contracted at the base, reaching their maximum width a short distance from the base and tapering towards a subacute apex. It is found in the Late Triassic of Argentina and the Middle Jurassic of England. This species is based on "*Pachydermophyllum papillosum*" specimen v31551 of Thomas and Bose (1955, fig. 1A) and includes "*Pachypteris papillosa*" of Harris (1964, figs. 51H, I, 52-54; pl. 5, figs. 7, 10-13, pl. 6, fig. 7). "*Pachypteris papillosa*" of Boureau and Doubinger (1975: 685, fig. 585) and (in part) "*Thinnfeldia praecordilleriae*" of Frenguelli (1944b: 511, pl. 1, fig. 1, pl. 2, fig. 1, pl. 3, figs. 1-2, pl. 4 only).

Pachydermophyllum pinnatum (Walkom) comb. nov. has more or less equant pinnae, not coalescing at the base and erect on the rachis. It is found in the later Triassic to Early Cretaceous of eastern Australia, New Zealand and Argentina. The species is based on the specimen of "*Thinnfeldia pinnata*" figured by Walkom (1921, pl. 2, figs. 1-2) and includes "*Rienitsia ? variabilis*" of Douglas (1969, p. 25, figs. 1, 12-24, pl. 4, figs. 1-3, pl. 5, figs. 1-5, pl. 6, figs. 1, 4, 5) and possibly also "*Pecopteris subtenera*" of Shirley (1898, p. 22, pl. 17, fig. 2) (in part) "*Microphylopteris pectinata*" of Arber (1917, p. 40, pl. 2, fig. 10, pl. 7, figs. 3, 4, 6, 8, 10, 11 only), "*Microphylopteris pectinata*" of Walkom (1919, p. 186, pl. 8, figs. 1, 4), "*Todites williamsoni*" of Jones (1948, p. 103, pl. 1, figs. 3-4), "*Dicroidium odontopteroides*" of Medwell (1954, pl. 94), (in part) "*Thinnfeldia praecordilleriae*" of Jain and Delevoryas (1967, pl. 90, fig. 8 only), and *Dejerseya variabilis* of Herbst (1977, p. 22); but not the Tasmanian material of Townrow and Jones (1969), here regarded as a new unnamed species of *Pachydermophyllum*.

Pachydermophyllum praecordilleriae (Frenguelli) comb. nov. has elongate, parallel-sided pinnae with rounded apices. It is found in the Middle Triassic of New Zealand, Late Triassic of Argentina and possibly also in the latest Permian or Early Triassic of India.

Botanical affinities: There is little doubt from its morphology and cuticular structure that *Pachydermophyllum* is the leaf of a seed fern. Dobruskina (1975) has grouped a large number of later Palaeozoic and early Mesozoic pteridosperm leaves with a similar cuticular structure into the family Peltaspermaeae. This is supported to a limited extent by the reproductive structures attributed to some of these leaves.

***Pachydermophyllum dubium* (Burges) comb. nov. (Fig. 4B)**

- ?1886 *Pecopteris caudata*, Johnston: 373, in part.
- ?1896 *Pecopteris caudata*, Johnston: 61, fig. 4.
- 1935 *Odontopteris dubiae*, Burges: 261, figs. 6, 6a.
- 1947 *Reinitsia incisa*, Jones and de Jersey: 43, figs. 35-36, pl. 9, figs. 2-3.
- 1965 *Reinitsia incisa*, Jones and de Jersey; Hill, Playford and Woods: pl. T9, fig. 9.
- 1977 *Dejerseya incisa* (Jones and de Jersey); Herbst: 22.

Holotype: Specimen SUGD2007, figured as "*Odontopteris dubiae*" by Burges (1935, figs. 6, 6a); housed in the Department of Geology and Geophysics, University of Sydney, Australia.

Type locality: Unspecified locality in the sea cliffs between Long Reef and Palm Beach, north of Sydney; Newport Formation, Narrabeen Group, Sydney Basin, late Scythian to early Anisian or latest Early to earliest Middle Triassic (see Retallack, 1977).

Description: Only a single specimen was found at Long Gully (Fig. 4B). It is very similar to the holotype and to specimens with cuticle described by Jones and de Jersey (1947).

Remarks: The type specimen is a slightly asymmetric leaf and has markedly smaller pinnules towards the base, indicating that it was unipinnate. Cuticle is preserved only in very small patches on the type specimen, but is well known in material described by Jones and de Jersey (1947).



Fig. 4—*Pachydermophyllum* leaves; A, C-F, *Pachydermophyllum praecordillerae*; A, OU14232; C, OU14229; D, OU14230; E, B1087.20; F, B1087.49; B, *Pachydermophyllum dubium*, OU14229. All figures natural size.

The name "*Pecopteris caudata*" of Johnston (1886, 1896) cannot be regarded as a valid senior synonym for the specific epithet of *Pachydermophyllum dubium*, because he included a great variety of plants within "*Pecopteris caudata*", his drawings are sketchy and the specimens can no longer be found in the Tasmanian Art Gallery and Museum, Hobart.

Occurrence: *Pachydermophyllum dubium* has been found at locality H39/β3, in Long Gully, New Zealand, in the Newport Formation of New South Wales (Burgess, 1935), in the Ipswich Coal Measures of southeastern Queensland (Jones and de Jersey, 1947; Hill *et al.*, 1965) and possibly also occurs in the Triassic of Tasmania (Johnston, 1886, 1896). According to the ages of these formations proposed by Retallack (1977), it has a mid-Scythian to Norian range.

Pachydermophyllum praecordillerae (Frenguelli) comb. nov. (Figs. 4A, C-F)

?1902 *Neuropteris punctata* Shirley: 11, pl. 7.

1944b *Thinnfeldia praecordillerae* Frenguelli: 511, pl. 1, fig. 2, pl. 2, figs. 2-3, pl. 3, fig. 3 only.

- 1956 *Thinnfeldia lancifolia* (Morris); Bell, in Bell *et al.*: 669, fig. 4.4.
 1957 *Dicroidium odontopteroides* (Morris) Gothan cf. *Odontopteris dubiae* Burges; Townrow, 33, figs. 3B, 4H, 5D, 6M.
 ?1961 *Danaeopsis gracilis*, Lele: 74, figs. 4-6, pl. 2, figs. 18-20.
 1967 *Thinnfeldia praecordillerae* Frenguelli; Jain and Delevoryas: 570, pl. 90, fig. 7 only.
 ?1967 *Thinnfeldia* sp., Orlando: 10, fig. 4.
 ?1968 *Thinnfeldia* sp., Orlando: 8, fig. 4.
 1975 *Pachypteris praecordillerae* (Frenguelli); Boureau and Doubinger: 687.

Lectotype: Selected here, "*Thinnfeldia praecordillerae*" specimen 10.127, figured by Frenguelli (1944b, pl. 1, fig. 2, specimen lying from upper left to lower right); housed in the Museo de La Plata, La Plata, Argentina.

Type Locality: Behind the old building of the Y.P.F. administration, Cacheuta, Argentina; Potrerillos Formation, Cacheuta Group (see Frenguelli, 1948; Stipanovic, 1969).

Description: The size and texture of these leaves is quite variable. From the largest specimen found (Fig. 4F) the leaf appears to have had a lanceolate general outline about 20 cm long and 8 cm wide. There are also varying degrees of clarity of secondary venation and transverse wrinkling of the pinnae. This variation is comparable to that seen in much larger collections of this species from near Benmore Dam, north of Otematata, New Zealand (for example, specimens OU14198, OU14200, OU14207, B1085.1, B1085.8, B42.26).

Remarks: I have selected the lectotype from Frenguelli's specimens from Cacheuta, as his specimens from Ischigualasto appear indistinguishable from *Pachydermophyllum papillosum*. Unfortunately, the cuticle of these fossil leaves from Ischigualasto is unknown, although Archangelsky (1968a) isolated cuticle from slightly different Ischigualasto leaves here assigned to an unnamed new species of *Pachydermophyllum*. Townrow (1957) has described the cuticle of an Argentine leaf morphologically identical to *Pachydermophyllum praecordillerae*.

"*Neuropteris punctata*" of Shirley (1898, 1902) has been discussed by Walkom (1917: 43), who points out that two quite dissimilar fragments have been referred to this species, neither being nominated as holotype. Possible records of *Pachydermophyllum praecordillerae* by Lele (1961) and by Orlando (1967, 1968), cited tentatively in the synonymy, are represented by a few fragmentary specimens, without cuticle.

Occurrence: *Pachydermophyllum praecordillerae* has been found at H39/f3, S117/f754 and S117/f755 in Long Gully and also at several localities near Benmore Dam, north of Otematata (S117/f756, S117/f664, S117/f665, S117/f50 and H39/f2), north Otago, New Zealand. This species is best known from the Potrerillos Formation, Cacheuta Group, in Argentina (Frenguelli, 1944b, Jain and Delevoryas, 1967; Stipanovic, 1969). Similar, but fragmentary, remains have also been found in marine rocks of the Murihiku Supergroup in Kaihiku Gorge, southwest of Balclutha (S179/f499, grid ref. 360200, specimen B130.10) and North Etal Creek, southwest of Mossburn (S159/f482, grid. ref. 280600, B109.3), New Zealand, in the Ipswich Coal Measures of southeastern Queensland (Shirley, 1902), on Livingston Island near the Antarctic Peninsula (Orlando, 1967, 1968) and near Beli, India (Lele, 1961). According to the ages of these deposits and localities proposed by Retallack (1977), *Pachydermophyllum praecordillerae* has a Middle to Late Triassic range, possibly extending also into the Early Triassic.

Class: Coniferopsida

Order: Coniferales

Family: Voltziaceae

Genus: *Telemachus* Anderson 1978

Type species: Telemachus elongatus Anderson 1978.

Diagnosis: Ovulate cones with numerous cone units, arranged in a well-spaced helix, cone scale and bract scale fused for most of their length, diverging distally; bract entire or weakly dentate, elongate, acutely pointed, with wide central midrib, oriented distally at various angles, horizontal or reflexed towards the base of the cone; cone scale divided distally into five free lobes, each acutely pointed, stiff and spreading, oriented outwards (distally) and upwards (towards the apex of the cone); ovules inverted, two or three per cone scale, attached adaxially in the angle of the diverging free lobes.

Comparison: Conifer cones with multilobed cone scales are found in the families Voltziaceae, Podocarpaceae and Taxodiaceae (as understood by Miller, 1977). The spiny projections on the cone scales of some Taxodiaceae (such as *Cryptomeria*, see Dallimore *et al.*, 1966: 183) are not as conspicuous as those of *Telemachus*. Furthermore, the Taxodiaceae are characterized by more complete fusion of the bract and cone scales and by a markedly thickened outer portion of the cone unit (Miller, 1975). Some early Mesozoic conifers assigned to the modern family Podocarpaceae (such as *Rissikia*, see Townrow, 1967a, 1969; Miller, 1977) have strongly lobed cone scales and so appear to be transitional between the Podocarpaceae and the extinct Voltziaceae. These remains differ from the Voltziaceae in general and from *Telemachus* in particular, in having ovules borne well out on the lobes of the cone scale.

As understood by Miller (1977), the Voltziaceae are an exceedingly diverse group including fossil plants formerly classified (by Harland *et al.*, 1967) in three separate families, Voltziaceae, Cycadocarpidiaceae and Cheirolepidaceae. Plants of this last group (regarded as the subfamily Hirmerelloideae by Miller, 1977), also have lobed cone units. The lobed ovulate structure was not fused to the adjacent bract scale and is commonly found separately, unlike the cone unit of *Telemachus*. In some cheirolepidacean or hirmerelloid conifers, the ovules are also protected by additional adaxial tissue (Archangelsky, 1968b; Harris, 1979), not evident in *Telemachus*.

Cycadocarpidium has been placed in its own family, the Cycadocarpidiaceae (by Harland *et al.*, 1967) or included within the Voltziaceae (by Miller, 1977). As interpreted by Florin (1953) and Kon'no (1961), *Cycadocarpidium* has cone units including one large leafy sterile bract with parallel venation and two or three reduced cone scale lobes, each bearing an inverted ovule. *Borysthenia* (Stanislavsky, 1976) is similar in having three inverted ovules borne on reduced cone scale lobes and in its elongate bract scale, although the bract differs in being narrow and linear. These features distinguish these two genera readily from all other Voltziaceae including *Telemachus*. Organs superficially similar to the bract of *Cycadocarpidium* cone units are also seen in *Dechellyia* (Ash, 1972) and *Fraxinopsis* (Jain and Delevoryas, 1967), and serve to distinguish these genera from *Telemachus*, but the exact homology of these organs and their botanical affinities remain unsettled.

From petrified cones, Schweitzer (1963) reinterpreted the cone unit of *Pseudovoltzia* as a basally fused, dorsiventral structure diverging apically into a pointed bract scale and five adaxial, radially arranged ovuliferous lobes. This has also been reported in *Voltzia* (Delevoryas and Hope, 1975), *Voltziopsis* (Townrow, 1967b) and *Swedenborgia* (Harris, 1935) and is also applicable to *Telemachus*. This structure appears to have been more typical of the Voltziaceae than the dwarf shoot interpretation of Florin (1944). The main generic differences within the Voltziaceae are the number and relative size of the bract and cone scale lobes. Relatively few voltziacean conifers have cone scales with fewer than five lobes, differing in this respect from *Telemachus*. These include *Tricranolepis* (Roselt, 1958) with one or three seeds on three-lobed cone scales, *Schizolepis* (in the sense of Roselt, 1958; see also Harris, 1979) with two ovules on two lobed cone scales, *Pachylepis* (Krausel, 1952) with five ovules on a very weakly lobed, almost-peltate cone scale, *Ullmania* with a single ovule on a large orbicular cone scale and *Drepanolepis* with a single ovule on an acutely pointed cone scale (see Miller, 1977). Among the remaining voltziacean genera, *Voltziopsis* (see Townrow, 1967b), *Swedenborgia* (Harris, 1935) and *Aethophyllum* (Grauvogel-Stamm and Grauvogel, 1975) all have cone scales with five lobes, but differ from *Telemachus* in having five seeds per

cone scale and also in the nature of their bract scales which may be reduced to a stump (in *Swedenborgia*), be long and bifid (in *Voltziopsis*) or no longer than the lobes of the cone scale (*Aethophyllum*). *Telemachus* is most similar to *Pseudovoltzia*, with five-lobed cone scales bearing three ovules and to *Glyptolepis* with five- and six-lobed cone scales and two ovules (see Florin, 1951; Schweitzer, 1963). In both *Pseudovoltzia* and *Glyptolepis* the bract scale is generally shorter than the cone scale lobes, but in some species of *Glyptolepis* it may be a little longer (Miller, 1977), although never as prominent as in *Telemachus*.

Botanical affinities: From the foregoing comparisons it is apparent that the affinities of *Telemachus* lie with the Voltziaceae *sensu stricto*, such as the Permian and Triassic genera *Glyptolepis* and *Pseudovoltzia*.

The large bract scale of *Telemachus* could be regarded as morphologically intermediate between forms like *Glyptolepis* and *Pseudovoltzia* and later Triassic and Jurassic conifers, such as *Borysthenia* and *Cycadocarpidium*. *Telemachus* has been found in Ladinian, and possibly also Carnian and Anisian, rocks in South Africa and New Zealand. *Cycadocarpidium* has a Carnian to Jurassic range and is widely distributed throughout Laurasia (Jongmans and Dijkstra, 1959; Kon'no, 1961; Harland *et al.*, 1967; Anderson, 1978). Several Triassic species of *Cycadocarpidium* have shorter bract scales and three prominent ovuliferous scales, although better known later Triassic and Jurassic species have long bract scales and only two small ovuliferous scales (Stanislavsky, 1976). *Borysthenia* has been found at the late Norian Garzhova locality in the Protopivskaya Suite of the Donetz Basin, north of the Sea of Azov, southeastern U.S.S.R. (Stanislavsky, 1976). It has more linear bract scales and lobes of the ovuliferous scales, but is otherwise similar to associated three-ovulate *Cycadocarpidium* cone units. Thus both the meagre morphological and stratigraphical evidence at hand support the idea that *Telemachus* was related to an intermediate group of voltziacean plants ancestral to *Cycadocarpidium* and allied plants.

Related leaves: Both the morphology of *Heidiphyllum elongatum* comb. nov. and its widespread association with *Telemachus* cones are evidence that these organs were produced by the same species of voltziacean conifer. Anderson (1978) has documented the widespread association of *Heidiphyllum elongatum* and *Telemachus elongatus* at nine localities in the Molteno Formation of South Africa. Several of these localities contain few kinds of leaves other than *Heidiphyllum elongatum*, which is one of the most common fossils in the Molteno Formation. Unfortunately, the cuticular anatomy of *Telemachus* is not yet known for comparison with *Heidiphyllum*. *Heidiphyllum* is one of very few conifer-like leaves in the Molteno Formation which could be attributed to the conifer cone *Telemachus* (see Townrow, 1967a; Anderson, 1974).

Although *Telemachus lignosus* has been found at only one place in New Zealand, the botanical affinities of the rest of the low-diversity Middle Triassic vegetation of New Zealand are sufficiently well understood, so that *Heidiphyllum elongatum* is the only likely leaf to have been produced by a plant with *Telemachus* cones. The locality for all the specimens of *Telemachus lignosus* (S117/f754) has also yielded *Todites maoricus*, *Cladophlebis* sp. cf. *C. takezakii*, *Townrovia petasata*, *Peltaspermum* sp. indet., *Pachydermophyllum praecordillerae*, *Heidiphyllum elongatum*, *Sphenobaiera robusta*, *Linguifolium arctum*, *L. lilleanum*, *L. steinmannii*, *L. tenison-woodsii*, *Carpolithus mackayi* and an indeterminate cone. As discussed here and elsewhere (Retallack, 1980), *Carpolithus mackayi* is the likely seed of *Linguifolium* spp.; *Karkeniania secunda*, the likely ovuliferous cone of *Sphenobaiera robusta*; *Peltaspermum*, the likely megasporophyll of *Pachydermophyllum praecordillerae* or *P. dubium* or both; *Todites maoricus* is an osmundalean fern; and *Cladophlebis* sp. cf. *C. takezakii* is also likely to be a true fern. Of the remaining fossil leaves in the Middle Triassic flora of New Zealand, the seed fern *Dicroidium* has corystosperm megasporophylls and *Ginkgophytopsis* is probably pteridophytic.

Other comparable conifers which probably also had similar elongate, simple leaves include *Aethophyllum* (Grauvogel-Stamm and Grauvogel, 1975) and *Borysthenia* (Stanislavsky, 1976).

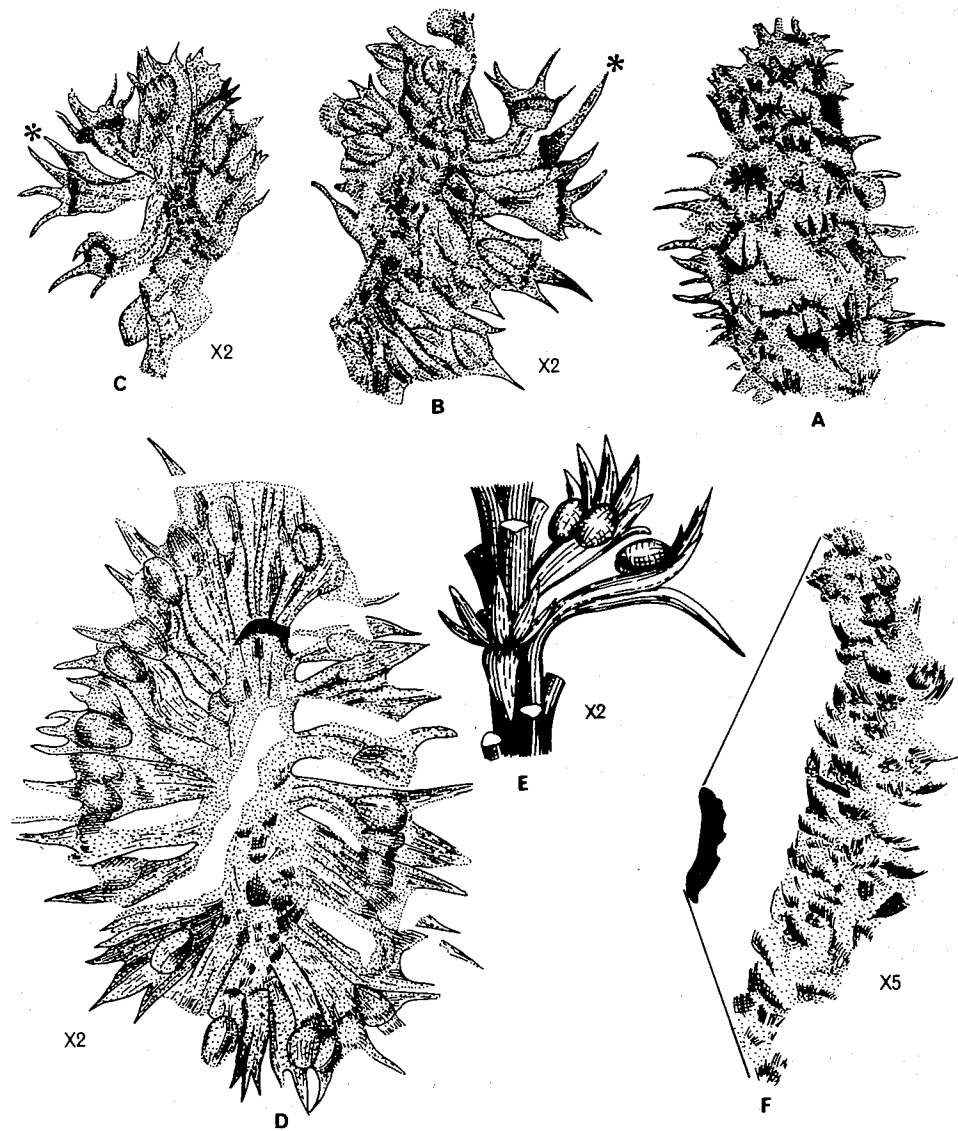


Fig. 5—Fertile cones; A-E, *Telemachus lignosus*; A, exterior view of entire cone, natural size, B1087.2; B, C, part and counterpart of the holotype, a natural oblique section of a cone, twice natural size, asterisks indicate part and counterpart of the same spine; B, 1087.3; C, 1087.4; D, natural oblique section of a cone, twice natural size, composite of specimens B1087.7 (lower right) and B1087.8 (upper left); E, reconstruction of several cone units, twice natural size; F, unidentified cone B, five times natural size, silhouette indicates natural size, B1087.22.

Occurrence: *Telemachus* is only known from the Long Gully Formation, upper Corbies Creek Group, of Ladinian or later Middle Triassic age, New Zealand, and in rocks of the same age, possibly extending into the Anisian (earlier Middle Triassic) and Carnian (earliest Late Triassic), in the Molteno Formation in South Africa (Anderson, 1978; Retallack, 1977).

Telemachus lignosus sp. nov. (Figs. 5A-E, 11J-L)

Holotype: Specimen B1087.3 and B1087.4 (part and counterpart), natural oblique sections of a cone (Figs 5B-C, 11J-K); in the collections of the Geological Survey of New Zealand, Lower Hutt.

Type Locality: S117/t754, in cuttings along the Backyards to Otematata River road, in Long Gully, New Zealand: Long Gully Formation, upper Corbies Creek Group, Ladinian age (Kaihikuan local stage).

Derivation: The specific epithet is from the Latin *lignosus*, meaning woody, and refers to the strongly coalified and longitudinally striated cone units.

Diagnosis: *Telemachus* cones up to 60 mm long and 23 mm in diameter; cone units arranged in a well-spaced helix around a woody axis about 5 mm in diameter. Fused portion of cone scale 8 mm long, expanding from 3 mm wide near the cone axis to 5 mm wide distally; cone scale lobes spinous, stiff, up to 5 mm long; bract scale lobe up to 7 mm long, with pronounced central midrib and obscure parallel venation; two or three inverted ovules per scale, ovules ovoid, 3-4 mm long by 2-3 mm wide.

Description: The size and shape of these cones shows some variation, which could prove to characterize more than one species. Some (Figs. 5A, 11L) are ovoid in outline and 52 mm long by 25 mm in diameter, others (B1087.19) are more elongate and parallel sided, more than 52 mm long but only 11 mm in diameter.

The cone axis is about 5 mm in diameter and has a very irregular shape, due to the robust decurrent bases of the cone units. The cone units had a relatively equant cross-section at the base, with a strong abaxial rib and rounded lateral margins.

The structure of the cone units has been reconstructed (Fig. 5E) from parts and counterparts of several natural oblique sections of cones. A thick covering of mineralized and cleated coal was scraped out to reveal impressions of the cone units. This may show only one surface of the cone unit, but more commonly the individual cone units have broken obliquely to reveal both bract and lobes of the same cone unit on one surface. In one specimen (Fig. 5D) the cone tapers towards an apex, which is exposed on the side of the slab. Natural fracture through the cone units has thus revealed partial impressions of their adaxial surfaces, including impressions of the ovules. Two or three of these appear to have been borne at the bases of the diverging spines of each cone scale.

The nature of the ovules is difficult to assess from the poor impressions available. They are ovoid in outline, presumably with the micropyle at the pointed end, which is directed towards the cone axis. A thin fleshy outer layer is evident on some of the seeds, but no further details could be gained from their coalified interior.

Dimensions of the holotype: Cone diameter (calculated) = 20 mm; cone axis diameter = 5.2 mm; cone unit below asterisk (Figs 5B-C; 11J-K), length = 7.4 mm, maximum width = 4.2 mm, width at base = 1.5 mm; thickness of cone unit above asterisk = 1.3 mm; seed (second cone unit below asterisk), length = 3.9 mm, width = 2.3 mm.

Comparison: The only other species of *Telemachus* known is *T. elongatus* Anderson 1978. This differs from *Telemachus lignosus* principally in the large size of its bract scale, up to 30 mm long. This difference is not believed to be merely a different maturation state of a single species, because specimens of the two species are of comparable size and because the New Zealand cones appear to have been at least equally robust and woody.

Occurrence: *Telemachus lignosus* has only been found at the type locality.

Genus: Heidiphyllum gen. nov.

Type species: Heidiphyllum elongatum (Morris) comb. nov.

Diagnosis: Leaves, elongate, linear-elliptic to linear-oblongate. Leaf base apetiolate, gradually tapering; leaf apex subacute to obtusely rounded; veins parallel,

well-spaced, often with conspicuous interveinal striae; converging near the apex; each of 2-4 basal veins forking once or twice only near the base of the leaf.

Cuticle delicate, hypostomatic; epidermal cells seldom more than twice as long as wide, crudely aligned with venation; stomata with five to six radially arranged subsidiary cells, each papillate and strongly cutinized around the stomatal pit; stomata randomly oriented within poorly-defined interveinal zones.

Derivation: This genus is named after Dr Heidi M. Anderson, in honour of her continuing research on the Triassic fossil flora of the Molteno Formation of South Africa.

Comparison: Since last writing about these leaves, so common and widespread in Gondwana (Retallack, 1980), both their cuticle and likely cones have been reported by Anderson (1978). Her data allow more detailed comparison than possible previously.

Heidiphyllum leaves have in the past most commonly been referred to *Phoenicopsis*, a genus for fossil impressions, without cuticle, of elongate, simple ginkgoalean leaves, commonly found in brachyblast groups (see Samylina, 1970; Krassilov, 1970). Although exceedingly common in some localities (Anderson, 1978; Retallack, 1977), these so-called "*Phoenicopsis*" leaves have never been found in brachyblast groups in Gondwana. Discovery of the cuticle of *Heidiphyllum* confirms that it was a quite different plant, as its cuticle is different from that of all six genera of *Phoenicopsis*-like leaves based on cuticular features (see Florin, 1936a, 1936b; Tralau, 1968; Harris, Millington and Miller, 1974). Many of these genera also differ from *Heidiphyllum* in their common occurrence in brachyblast groups (*Stephenophyllum*, *Windwardia*, *Culgoweria*, *Torellia*), in their more straight-sided, cuneate outline and abruptly rounded or truncate apices (*Stephenophyllum*, *Culgoweria*, *Windwardia*), in their long petiole-like bases (*Eretmophyllum*) and in having only a single vein at the base of the leaf (*Stephenophyllum*, *Windwardia*). The stomata of *Heidiphyllum* are typically gymnospermous, but not diagnostic of a particular order of plants. They have a strongly-cutinized rim around the stomatal pit formed by the inner walls of bulging, weakly-papillate subsidiary cells. Similar stomata are found in pteridosperms (such as "*Thinnfeldia*" *callipteroides*, see Townrow, 1966b), ginkgoaleans (such as *Torellia rigida* and *Stephenophyllum solmsii*, see Florin, 1936a; and *Baiera furcata* see Harris *et al.*, 1974) and conifers (such as *Palissyia sphenolepis* and *Elatocladus speciosus*, see Florin, 1958). The development of the papillae on the subsidiary cells of these plants is not so extreme as to cover much of the stomatal opening, as in many ginkgoaleans (such as *Pseudotorellia minuta* Lundblad 1957 and several species of *Ginkgo* described by Tralau, 1968) and most peltasperm pteridosperms (such as the leaves and fructifications discussed by Townrow, 1960, 1965, 1966b). The cuticles of those ginkgoalean leaves which are superficially similar to *Heidiphyllum*, differ largely in the distribution and orientation of the stomata, which may be amphistomatic (*Culgoweria*, *Windwardia*, *Eretmophyllum*), have unusually elongate epidermal cells between the stomatiferous zones (*Stephenophyllum*, *Windwardia*), have stomata arranged in longitudinal rows (*Torellia*, *Pseudotorellia*, *Culgoweria*), or have stomatal openings oriented longitudinally (*Culgoweria*, *Pseudotorellia*).

Glossophyllum (Kräusel, 1943) has been considered ginkgoalean (Tralau, 1968). It differs from *Heidiphyllum* in its elongate, narrow leaf bases, amphistomatic cuticle and strongly developed papillae on the subsidiary cells overarching the stomatal opening.

The conifer foliage referred to *Araucariodendron* by Krassilov (1967) is superficially similar to *Heidiphyllum*, but differs in having the parallel venation of the leaves arise by unequal dichotomy within two marginal veins and in having anomocytic stomata with a conspicuously narrow ring of subsidiary cells and with the stomatal openings oriented longitudinally.

Feistmantel (1889), Frenguelli (1937), and Anderson (1978) have referred *Heidiphyllum* leaves to *Podozamites*, a genus of largely Laurasian late Triassic and Jurassic leaves of plants believed to have produced the conifer cones *Cycadocarpidium* and

Swedenborgia (Harris, 1935; Florin, 1953). Although *Heidiphyllum* was probably also produced by a conifer, whose cones are here referred to *Telemachus*, their assignment to the genus *Podozamites* was unsatisfactory for several reasons. The apetiolate leaf bases of *Heidiphyllum* are unlike the narrow petiolate leaf bases of *Podozamites* (Harris, 1935, Seward, 1919). Despite the local abundance of *Heidiphyllum* in Gondwana (Anderson, 1978; Retallack, 1977), only one case of a natural group of leaves (Frenguelli, 1937) and two cases of possible attachment (Tenison-Woods, 1883; Retallack, 1980) have been reported. It seems probable that the leaves of *Heidiphyllum* were completely deciduous, whereas other conifers with similar foliage, such as *Podozamites* and

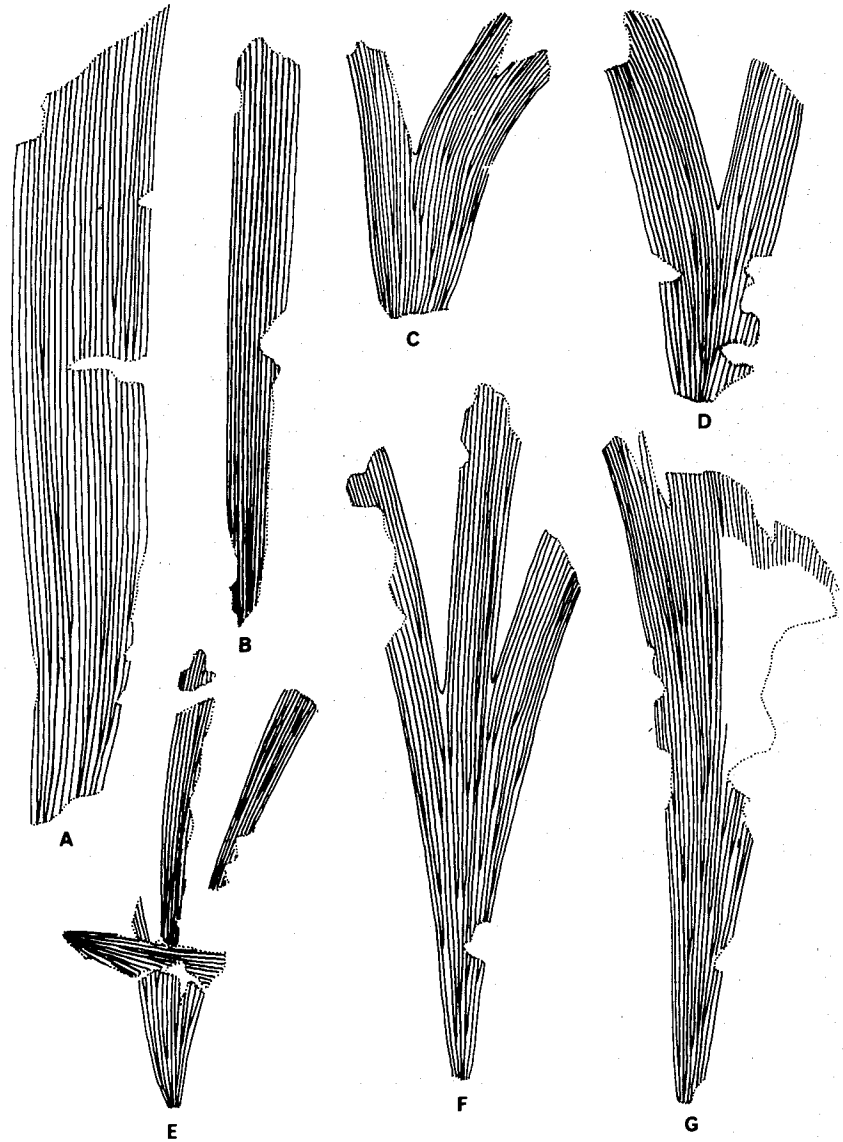


Fig. 6—*Sphenobaiera*, *Heidiphyllum* and *Desmiophyllum* leaves: A, *Desmiophyllum* sp., B1087.48; B, *Heidiphyllum elongatum*, B1090.5; C-G, *Sphenobaiera robusta*; C, B1087.43; D, B1087.42; E, OU14230; F, B1090.15; G, B1090.4. All natural size.

Lindleycladus dropped some leaves but also numerous leafy shoots. The various styles of leaf dropping in modern conifers are discussed by Harris (1976). Additional differences between *Heidiphyllum* and these superficially similar Laurasian leaves are readily apparent from their cuticles. The leaves of *Podozamites* (including its type species) are hypostomatic, with longitudinally oriented cells and paracytic (syndetocheilic) stomata arranged in files and almost all transversely oriented (Florin, 1953; Doludenko, 1967; Harris, 1935, several species excepting "*Podozamites*" *stewartensis*). The leaves of the morphologically similar *Lindleycladus* are also hypostomatic, with longitudinally oriented cells and stomata in files, but its paracytic and laterocytic (syndetocheilic and pseudosyndetocheilic) stomata are oriented longitudinally (Harris, 1979; this genus possibly also includes "*Podozamites*" *stewartensis* of Harris, 1935). Both these genera have a more regular arrangement of the stomata and more symmetrical arrangement of the subsidiary cells than known in *Heidiphyllum*.

Occurrence: As for the only species recognized to date, *Heidiphyllum elongatum*.

***Heidiphyllum elongatum* (Morris) comb. nov. (Fig. 6B)**

Holotype: "*Zeugophyllites elongatus*" Morris 1845, pl. 6, figs. 5, 5a; v 7512 in the British Museum (Natural History), London.

Type locality: "Jerusalem Basin", Tasmania. According to Townrow (1966a), other fossils described from the same area and in the same paper probably came from Triassic sandstone cropping out along the bank of the Coal River, 1 km east of Lowdina Homestead, Campania (42° 36' 20" S and 147° 20' 30" E). However, the type specimen of *Heidiphyllum elongatum* is one of a number of black impressions on a slab of grey shale, and, although probably from nearby, evidently came from a different locality.

Emended Diagnosis: *Heidiphyllum* leaves linear elliptic to linear-oblongate, 58-170 mm long (average 140 mm), 7-16 mm wide (av. 10 mm) at widest point; venation parallel; 8-12 veins, spaced about 1 mm apart; forking once or twice only near the base of the leaf; only 2-4 basal veins; veins converging towards the apex.

Leaf hypostomatic; upper cuticle with square to rectangular epidermal cell outlines, 20-60 μ m long, arranged in crude longitudinal rows, lower cuticle strongly papillate; stomata anomocytic (haplocheilic), with 5-6 subsidiary cells; stomatal pit strongly cutinized, outlined by low papillae or a continuous cutin lappet on the adjacent subsidiary cells; stomatal openings irregularly oriented within poorly-defined zones.

Remarks: This species has been discussed by many authors under the generic names *Podozamites* (Feistmantel, 1889; Frenguelli, 1937; Anderson, 1978) and *Phoenicopsis* (Seward, 1919; du Toit, 1927). The old generic name *Zeugophyllites* used by Morris (1845) for the holotype of *Heidiphyllum elongatum* is regarded as a *nomen nudum*, as Brongniart (1828) did not figure the type species, *Z. calamoides*. This was probably an unrelated plant, possibly *Noeggerathiopsis*, as the type specimen came from the "mines de houille de l'Inde" (Brongniart, 1828: 120) of probable Permian age (Seward, 1919: 74).

Considering the delicate cuticles of *Heidiphyllum* (Anderson, 1978), and its common occurrence in sandy facies (Retallack, 1977), a restriction of the genus *Heidiphyllum* to specimens with cuticle would prove impractical and obscure its evident prominence in Middle Triassic vegetation of Gondwana. Unless specimens agree in all respects with known specimens of *Heidiphyllum*, they are better assigned to the non-committal genus *Desmiophyllum*, as broadly similar leaves can be produced by araucariacean and cycadocarpidiacean conifers, cordaitaleans and ginkgoaleans (Sahni, 1928; Seward, 1919). Such leaves, now regarded as distinct from *Heidiphyllum*, include the narrower leaves figured by Seward (1934) and Kurtz (1921), leaves with more closely spaced venation described by Lele (1961) and Barnard (1965), smaller leaves such as *Desmiophyllum indicum* Sahni 1928 (see also Retallack, 1980) and leaves with veins

forking at various distances from the base of the leaf (discussed here and by Retallack, 1980).

Occurrence: In New Zealand this species is found in Tank Gully (Retallack, 1980) and Long Gully (S117/f631, S117/f751-755) in Torlesse rocks and near Gore (S170/f560, grid ref. 798471, specimen NZGSB31.63) and in Wairoa Gorge, near Nelson (S20/f499, grid. ref. 476140, NZGSB136.2) in the Murihiku Supergroup. *Heidiphyllum elongatum* is widespread in Middle and Late Triassic rocks of Gondwana (see Retallack *et al.*, 1977, for more detailed occurrences).

Order: Ginkgoales

Family: Karkeniaceae

Genus: *Karkenia* Archangelsky 1965

***Karkenia fecunda* sp. nov. (Figs. 7A-B, 11G-H)**

Holotype: Specimen OU14233 and OU14234, part and counterpart in the collections of the Geology Department, Otago University, Dunedin, New Zealand.

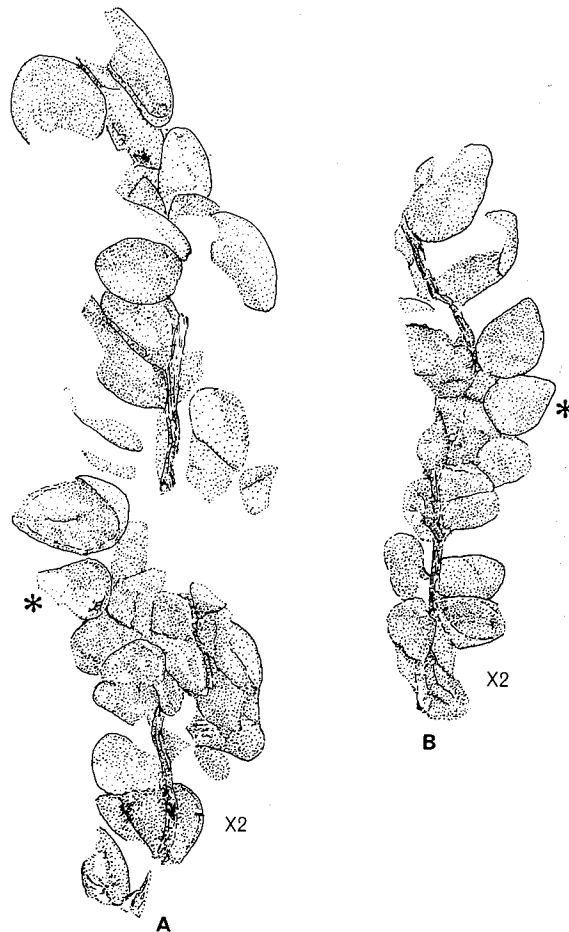


Fig. 7—*Karkenia fecunda*, a lax ovulate cone; A, OU14234; B, OU14233. Part and counterpart of holotype, twice natural size. Asterisks indicate part and counterpart of the same ovule.

Type locality: H39/f3, in cuttings along the Backyards to Otematata River road, in Long Gully, near Otematata, New Zealand; Long Gully Formation, upper Corbies Creek Group, Ladinian (Kaihikuan local stage) or later Middle Triassic (see Retallack and Ryburn, in press).

Derivation: The specific epithet is from the Latin *fecundus*, meaning fruitful.

Diagnosis: Elongate ovulate cones, 13 mm in diameter and over 50 mm long, consisting of 50 or more stalked ovules arranged helically on a slender (0.7 mm) cone axis; ovules inverted, ovoid, 4 mm in diameter and 8 mm long, attached by short stalk which is contiguous with the sarcotesta along the basal half of the ovule; outermost layer of ovule appearing smooth and waxy with some irregular bumps and striations, possibly due to hairs and resin bodies; sclerotesta with a coarsely pitted outer surface, often coalified with a well-developed cleat, its broader, subtriangular base tapering towards the apex; apex of the ovule with large (1.5 mm diameter) shallow pit, defined by prominent rounded margin, tapering into narrow micropylar opening through the innermost sclerotesta; nucule not observed.

Description: In all the specimens of *Karkenina fecunda*, ovules cover much of the rock surface. Many of these are aggregated into cones with clear cone axes, but others are evidently loose. Thirty-nine ovules were counted on the holotype cone (Figs. 7A, 11G) and 27 on another cone (spec. OU14235). Taking into account ovules not seen on these natural oblique sections, it is likely that there were at least 50 ovules per cone.

The ovules are inverted on short, terete stalks. As can be seen from twisted ovules (Fig. 7B), the stalk is free in its proximal half, but adnate to the sarcotesta in the distal portion along the basal half of the ovule.

The ovules are ovoid, 4 mm in diameter and 8 mm long. The outermost surface of the ovule is characteristically light brown or yellow and relatively smooth and shiny, so may have been waxy. This contrasts with the dull greenish-grey matrix. This outer surface also shows fine longitudinal cellular striation, some irregular deeper furrows (possibly remains of hairs) and scattered round lumps (possibly from resin bodies in the underlying sarcotesta). The sarcotesta is usually compressed to a very thin coaly layer with weakly-developed coal cleat. The outermost surface of the sclerotesta, exposed on many specimens, is dull, gray and deeply pitted. The ovoid shape of the ovule is slightly modified by the subtriangular base of the sclerotesta. From this base, three weakly-defined broad ribs run towards the slightly tapered apex of the sclerotesta. At the apex these symmetrically disposed ribs fuse laterally to form a broad ring encircling a shallow pit, about 1.5 mm in diameter, which tapers inward into a narrow micropylar opening. The sclerotesta is usually strongly coalified, with a mineralized coal cleat which obscures the inner structure of the ovules.

Dimensions of the holotype: Preserved length of cone = 38.9 mm; diameter of cone = 14.8 mm; diameter of cone axis = 0.7 mm; diameter of stalks = 0.3 mm; length of stalk from axis to opposite micropyle of ovule = 1.1 mm; diameter of most apical ovule (Fig. 7B) = 4.3 mm; length of most apical ovule = 7.5 mm.

Comparison: *Karkenina fecunda* is very similar to *K. incurva* Archangelsky 1965, which has more and smaller ovules on a comparably sized cone and a striated, rather than pitted, sclerotesta. The micropylar opening of *Karkenina incurva* is in the convex apex of the ovule, rather than in a flattened or depressed area as in *K. fecunda*. In *Karkenina asiatica* Krassilov 1972 the ovules are borne erect or only slightly incurved, quite different from both *K. incurva* and *K. fecunda*.

Karkenina may also prove to include *Strobilites milleri* Seward and Bancroft 1913, which has a more lax arrangement of ovule-like structures than *Karkenina fecunda*, and possibly also the small "megasporophylls with seeds, Type 3" of Douglas (1969: 246). The poorly known ovuliferous cone *Ontheostrobos* (Ganju, 1947) is superficially similar to *Karkenina*, but apparently the chalazal ends of the ovules are sessile in membranous cupules on the cone axis.

Remarks: The family Karkeniaceae was proposed by Krassilov (1970), and is most convenient for *Sphenobaiera robusta* leaves and *Karkenina fecunda* cones. These two fossils are believed to have been produced by one species because of their close association and similarities with other remains referred to the Karkeniaceae. There are only a limited number of seed plants in the Middle Triassic vegetation of New Zealand, most of these occurring with *Karkenina fecunda* at H39/f3 in Long Gully (see Retallack and Ryburn, in

press). The strobilar shape of *Karckenia* is most unlike a pteridosperm ovulate fructification, so is unlikely to be related to *Pachydermophyllum* and *Dicroidium*. *Carpolithus mackayi* is most likely the seed of *Linguifolium* spp. (Retallack, 1980). *Heidiphyllum elongatum* is the only conifer-like foliage which could be attributed to the voltziacean ovulate cone *Telemachus lignosus*.

Krassilov (1972) also argues, from close association and from similarity of pollen in pollen chambers of ovules and adhering to the surface of leaves, that *Karckenia asiatica* was the ovulate cone of a species with leaves of *Sphenobaiera ulmatensis*. From close association in low-diversity assemblages, Archangelsky (1965) suggested that *Karckenia incurva* was the ovulate fructification of a plant with "*Ginkgoites*" *tigrensis* leaves. The relatively short "petiole", amphistomatic cuticle, fusiform resin bodies and twin veins in the "petiole" of "*G.*" *tigrensis* all indicate that it may be better referred to *Sphenobaiera* than *Ginkgoites*, according to the scheme proposed by Krassilov (1970: 14, 17).

Occurrence: *Karckenia fecunda* has only been found at the type locality.

Genus: *Sphenobaiera* Florin 1936a: 105.

Sphenobaiera robusta (Arber) Florin 1936a (Figs. 6C-G)

Remarks: Like the specimens from Tank Gully described previously (Retallack, 1980), these also have three deep apical clefts reaching almost to the same level of the frond. One specimen (Fig. 6G) appears to be almost entire and another (Fig. 6D) divided only once, like *Sphenobaiera argentiniae* (Kurtz) Frenguelli 1946. Such fragmentary remains are insufficient to characterize additional species.

Occurrence: *Sphenobaiera robusta* occurs at Long Gully localities H39/f3, S117/f754 and S117/f751, and in the Tank Gully Coal Measures at Tank Gully, Canterbury, New Zealand (Retallack, 1980).

Class: Cycadopsida

Order: incertae sedis

Genus: *Taeniopteris* Brongniart emend. Harris 1932a:33.

Taeniopteris sp. indet. (Fig. 8)

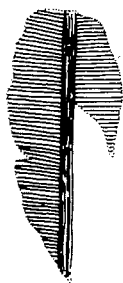


Fig. 8—*Taeniopteris* sp. indet., natural size, B1090.13.

Remarks: This non-committal name is used for a single *Nilssonia*-like fragment from Long Gully locality S117/f751. The midrib is 1.5 mm wide and so clearly defined that it is likely that the impression is the underside of a leaf in which the lamina is attached to the top of the midrib. The right half of the leaf is 10.6 mm wide. The secondary venation is almost erect, parallel, unforked and has a density of 20 per cm at the margin.

This fragment is similar to remains referred to "*Nilssonia* sp." by Solms-Laubach (1899: 603, pl. 14, fig. 7), by Frenguelli (1944a: 297, pl. 4, figs. 1-2) and by Menendez (1951: 201, pl. 12, fig. 7). Some larger taeniopterid leaves from Gondwana are similar to these fragments in their erect, dense venation and apparent attachment of the lamina on one side of the rachis. These include *Taeniopteris wianamattae* (Feistmantel) Walkom

1917, *T. lata* Oldham and Morris 1862 and *T. nilssonoides* Zeiller 1903 (as discussed by du Toit, 1927: 350 and probably also including remains compared with "*Nilssonia princeps*" by Menendez 1951 and Flint and Gould, 1975). The true nature of these various remains has yet to be established by work on their cuticles.

Plantae: incertae sedis

Genus: *Desmiophyllum* Lesquereux emend. Solms-Laubach 1904: 8.

Desmiophyllum sp. indet. (Fig. 6A)

Remarks: This specimen from Long Gully locality S117/f754 is similar to one from Tank Gully, New Zealand (Retallack, 1980). It is very wide and venation includes dichotomies at all levels in the leaf, unlike *Heidiphyllum elongatum*.

Genus: *Ginkgophytopsis* Høeg emend. Retallack 1980: 43

Ginkgophytopsis lacerata (Arber) Retallack 1980 (Fig. 10C)

Remarks: Although badly torn, this fragment shows part of one dichotomy of the leaf and very clear anastomosing venation. The specimen was collected from an unspecified locality in the road cuttings in Long Gully (S117/f631).

Genus: *Linguifolium* Arber emend. Retallack 1980: 45

Linguifolium arctum Menendez 1951 (Figs. 9F-H)

Remarks: Several specimens of the usual width of this species were found, some of them relatively complete. Their apices are broadly lanceolate rather than spatulate, but they still reach their maximum width at well beyond half their length. This species was found at Long Gully localities H39/f3, S117/f755, S117/f754 and S117/f751.

Linguifolium lilleanum Arber 1913 (Figs. 9A-B)

Remarks: None of the wide obovate leaves more typical of this species was found. These specimens are more oblanceolate than usual for *Linguifolium steinmannii*, but could be considered end members of a population of that species. This species was found at Long Gully localities S117/f754, S117/f752 and S117/f751.

Linguifolium steinmannii (Solms-Laubach) Frenguelli 1941 (Figs. 9C-E)

Remarks: One specimen (Fig. 9C) has exceptionally clear and photogenic venation and can be considered the most accurate of my sketches of venation. Some of these leaves (for example Fig. 9E) have been deformed by lateral shear which has opened out the venation on one side of the midrib and closed it towards the midrib on the other side. This species was found at Long Gully H39/f3, S117/f754, S117/f753 and S117/f751.

Linguifolium tenison-woodsii (Etheridge) Retallack 1980 (Figs. 9I-K)

Remarks: These specimens demonstrate more clearly than those from Tank Gully (Retallack, 1980) the tapered base and subacute apex of these leaves; they were found in Long Gully localities H39/f3, S117/f754, S117/f753, S117/f751, S117/f631.

Genus: *Carpolithus* Linnaeus emend. Seward 1917: 364.

Carpolithus mackayi Arber 1917 (Figs. 10D-G, 11I)

Remarks: This species has been discussed more fully elsewhere (Retallack, 1980). In Long Gully it was found in H39/f3 and S117/f754.

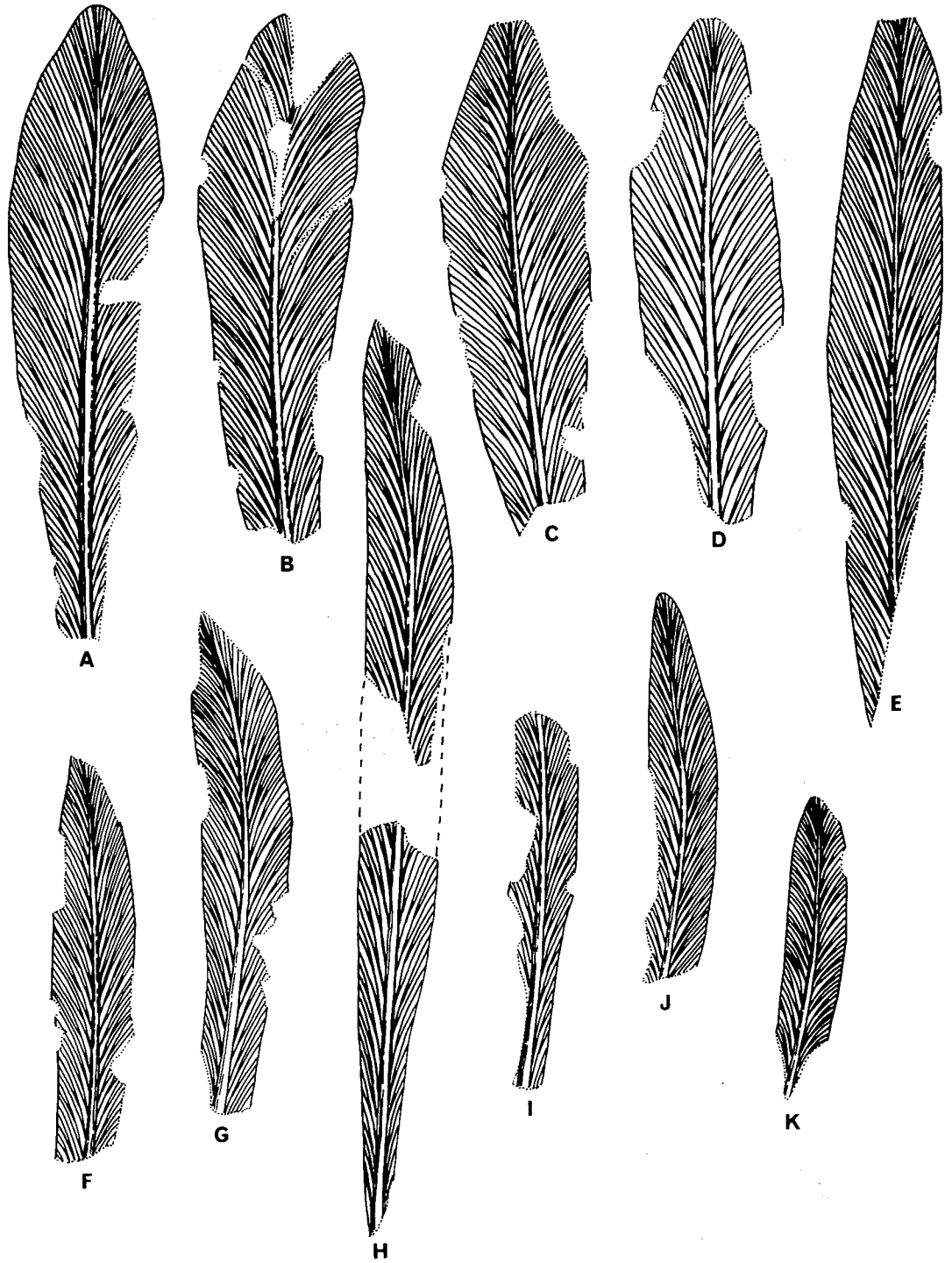


Fig. 9—*Linguifolium* leaves from Long Gully. A-B, *Linguifolium lilleanum*; A, B1090.13; B, B1089.4; C-E, *Linguifolium steinmannii*; C, B1087.45; D, B1088.3; E, B1090.7; F-H, *Linguifolium arctum*; F, B1090.11; G, B1090.10; H, B1090.14; I-K, *Linguifolium tenison-woodsii*; I, B1090.12; J, B1087.43; K, B1090.9. All natural size.

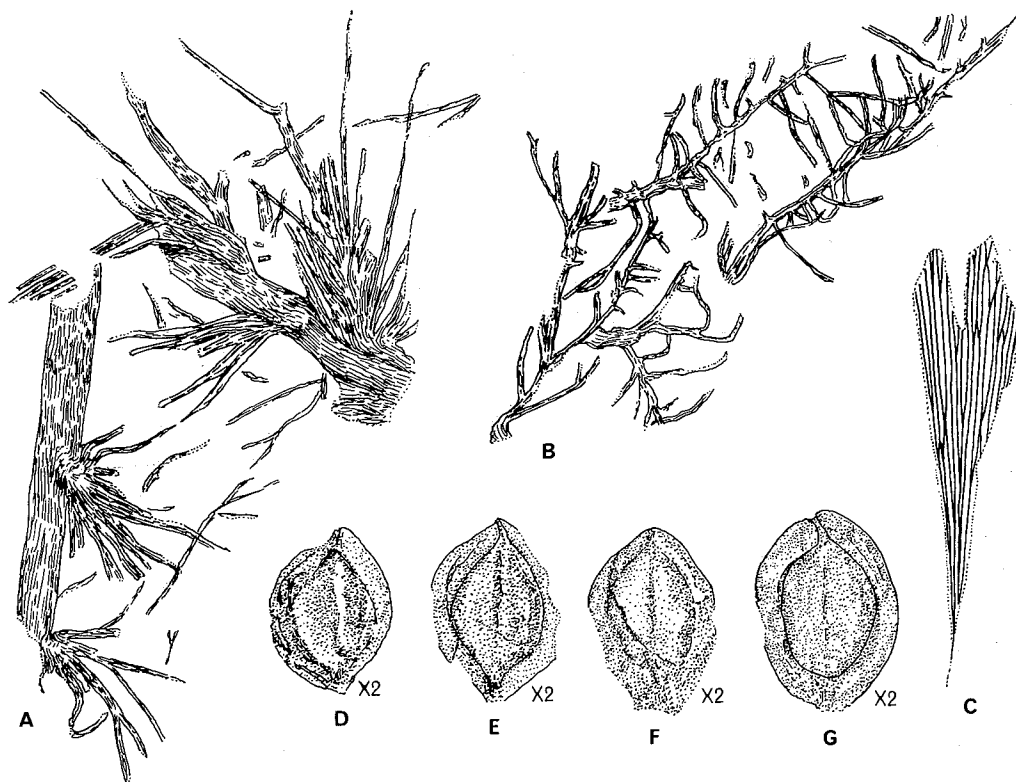


Fig. 10—Plants of uncertain taxonomic position; A, thick roots with bundles of adventitious rootlets, like "*Czekanowskia rigali*"; B1090.16; B, roots with helically arranged lateral rootlets, B1087.25; C, *Ginkgophytopsis lacerata*, OU14205; D-G, *Carpolithus mackayi*, all natural size; D, B1087.31; E, B1087.47; F, B1087.28; G, B1087.32. All natural size unless otherwise indicated.

Unidentified cone A (Figs. 3A, 11D)

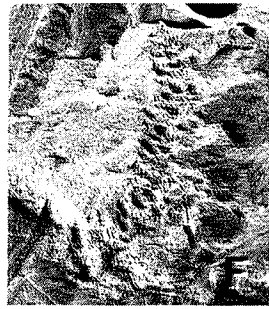
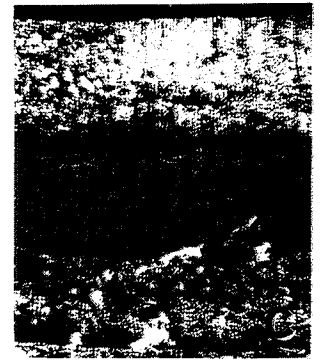
Remarks: This fragment of a small lax cone has a series of slender, flexuous appendages, arranged helically, each terminating in (at least) one ovoid body. These terminal bodies have a longitudinal striation, as if they were pollen sacs. However, the strong curvature of split or doubled bodies and their high relief in the rock matrix indicates that they were more robust than is usual for pollen sacs.

It is difficult to compare this with other fossils without a more detailed understanding of its structure. However, it does have superficial similarities with supposed ginkgoalean pollen organs, such as those described by Kräusel (1943). Such affinities would also be compatible with its occurrence in the same bed with *Karkeniania secunda* and *Sphenobaiera robusta* at locality H39/f3 in Long Gully.

Unidentified cone B (Figs. 5F, 11F)

Remarks: This small coalified and mineralized fragment is probably an elongate pollen cone. The helically-arranged cone units have been weathered out of the matrix. Impressions around the base of these are probably sporangia. However, the shape of the cone scales, the number of sporangia and their attachment to the cone scales cannot be determined.

Superficially, this cone is like various conifer pollen cones, such as *Masculostrobus* (Seward emend. Barnard, 1968), *Podostrobus* (Rao and Bose, 1971) and *Darneya* (Schaarschmidt and Maubeuge, 1969). Coniferalean affinities are compatible with the



occurrence of this cone in the same bed with *Heidiphyllum elongatum* and all the cones of *Telemachus lignosus* at S117/f754 in Long Gully. *Cladostrobus* (Maheshwari and Meyen, 1975) is another superficially similar pollen cone of a plant whose foliage was *Desmiophyllum*-like.

Logs and stems Fig. 11C

Remarks: Compressed logs were seen throughout the outcrops of the Long Gully Formation in Long Gully. One of these from S117/f751 was thin-sectioned. The limonitized fragment of a log was evidently more than 13 cm in original diameter. Unfortunately, few cell outlines could be seen because of ferruginization. There are, however, clear growth rings, often with two minor rings within the major banding (Fig. 11C). These could represent a three-year cycle of very severe winters but are more likely due to prolonged periods of stormy weather during the growing season.

Carbonized roots Figs. 10A-B

Remarks: Two distinct kinds of fossil roots were found. Firstly, thick roots with bundles of adventitious rootlets (Fig. 10A from locality S117/f751) are similar to those found in Tank Gully (Retallack, 1980) and elsewhere (Retallack *et al.*, 1977). Secondly, long slender roots with helically-arranged rootlets are also common (Fig. 10B from S117/f754). I have seen similar remains from the Brookvale shale lens of the Hawkesbury Sandstone (Australian Museum AMF39397 and Sydney University SUGD13036, figured by Townrow, 1967a, as "*Rissikia apiculata*") and from the Newport Formation, Narrabeen Group (Retallack, 1973), both in the Sydney Basin.

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Fig. 11—Fossil plants from Long Gully; A-B, *Todites maoricus*; A, detail of frond, twice natural size, B1087.22; B, sorus of fertile pinnule, sporangia arrowed, ten times natural size, B1087.40; C, transverse section of ferruginized wood, showing dense winter wood (below) and open summer wood (above) of a growth ring, ten times natural size, B1090.6; D, unidentified cone A, twice natural size, OU14231; E, *Townrovia petasata*, twice natural size; B1087.24; F, unidentified cone B, twice natural size, B1087.22; G-H, *Karkeniania fecunda* part and counterpart of holotype, twice natural size; G, OU14234; H, OU14233; I, *Carpolithus mackayi*, twice natural size, B1087.47; J-L, *Telemachus lignosus*; J-K oblique natural section of holotype, part and counterpart, asterisks indicate part and counterpart of the same spine, twice natural size, J, B1087.4; K, B1087.3; L, exterior view of entire cone, natural size, B1087.2.

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