

Middle Triassic Megafossil Plants and Trace Fossils from Tank Gully, Canterbury, New Zealand

G. J. RETALLACK
Indiana University

[Received by the Editor, 19 September 1978; as revised, 13 July 1979]

Abstract

Coal measures conformably underlying marine rocks of Ladinian age in Tank Gully have yielded a diverse assemblage of fossil plants. The presence of *Dicroidium* and *Johnstonia* leaves and corytosperm fructifications, supported by other remains (*Neocalamites*, *Cladophlebis*, *Lobifolia* and *Sphenobaiera*), indicate correlation of the flora with the *Dicroidium odontopteroides* zone of Late Anisian to Ladinian age.

Several taxonomic changes are proposed. The ginkgoalean affinities of "*Phoenicopsis*" *elongatus* seem more remote than ever, so it is transferred to the non-committal genus *Desmiophyllum*. A re-organization of palaeophyllalean form-genera and of the species of *Ginkgophytopsis* is proposed to include remains formerly referred to *Chiropteris*. Glossopteridalean affinities are suggested for the redefined species of *Linguifolium* and their likely seeds, *Carpolithus mackayi*.

The following new combinations are proposed: *Desmiophyllum elongatum* (Morris), *Ginkgophytopsis cuneata* (Carruthers), *G. lacerata* (Arber), *G. tasmanica* (Walkom), and *Linguifolium tenison-woodsii* (Etheridge).

Dwelling burrows (*Macanopsis erewhonensis* sp. nov.) found in coastal lagoonal deposits in Tank Gully are ornamented with several types of scratch marks suggesting that they were inhabited by natantid crustaceans.

INTRODUCTION

Diverse megafossil plant remains from coal measures conformably underlying Ladinian (Kaihikuan local stage) marine rocks in Tank Gully occupy a key position in the international correlation of the provincial floras of Gondwanaland. The fossil plants are not well preserved, having been changed to graphitic material during low-grade burial metamorphism and often leached of any organic material. Nevertheless, the variety of corytosperm leaves and fructifications, supported by other taxa, suggest correlation with the *Dicroidium odontopteroides* zone of Late Anisian to Ladinian age (Retallack 1977b). Different localities of this age in Tank Gully have yielded both the *Linguifolium* and *Dicroidium odontopteroides* fossil plant associations (of Retallack 1977b). The palaeoecology and geology of the plant localities in Tank Gully have been discussed elsewhere (Retallack 1979).

Megafossil plants from Tank Gully were last described by Arber (1917), who apparently had a mixed collection, including some fossils from Jurassic localities in the Clent Hills, only 29 km east of Tank Gully along the road to Christchurch. The Clent Hill fossils have a very similar, carbonaceous argillite matrix to those from Tank Gully, and include the following species which have never been found in collections from Tank Gully after Arber's record: *Equisetites minutus* (Arber) Townrow 1955, *Dictyophyllum "acutilobum"* (Braun) Schenk 1867 (see Oishi and Yamasita 1936, p. 154), *Taeniopteris thomsoniana* Arber 1917 (see Blaschke and Grant-Mackie 1976), and *Mataia podocarpoides* (Ettingshausen) Townrow 1967. These species are also found in Middle Jurassic rocks of the Murihiku Supergroup in Southland, where they are securely dated by associated marine fossils (Speden 1958; Arber 1917). None of these Jurassic species are discussed further here.

The suprageneric classification 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 the 1:63 360 and 50 000 map series. Localities mentioned are Tank Gully except where noted otherwise.

Kingdom: Plantae
 Division: PTERIDOPHYTA
 Class: SPHENOPSIDA
 Family: Apocalamitaceae
 Genus: *Neocalamites* Halle 1908

Neocalamites carrerei (Zeiller) Halle 1908 (Figs. 1F, 10A)

DESCRIPTION: Narrow leaflets associated with these remains and apparently attached to some nodes (Fig. 1F) are free to their bases and 0.6 to 1.5 mm wide. On the external surface of the axes, the finer striae are grouped into broad, shallow grooves from 1.5 to 3 mm wide. The pith casts show clear, undifferentiated striations.

COMPARISON: The only other species of *Neocalamites* described from Gondwanaland are *N. ramaccionii* Frenguelli 1944a, *N. ischigualastii* Frenguelli 1944b, and various remains which have been referred to *N. hoerensis* (Schimper) Halle 1908. Harris (1961) doubts that these last-mentioned remains are conspecific with the European type material of *N. hoerensis* and indicates several different features in the material from Gondwanaland. According to Jones and de Jersey (1947), such remains have much broader leaflets (1-2.5 mm) than *Neocalamites carrerei*. Townrow (1955) transferred some of these broader leaved *Neocalamites* to *Phyllothea brookvalensis*. The remainder have a less strongly sulcate axis than *P. brookvalensis* and constitute a new, un-named species of *Neocalamites* (including material described by Du Toit 1927, pp. 315, 396; Walkom 1924, 1925c; Jain and Delevoryas 1967; Retallack 1973). *Neocalamites ischigualastii*, like *N. carcinoides* Harris 1931, appears to be an intermediate between *Neocalamites* and *Schizoneura*, because some of its leaflets are laterally fused. The exterior of *N. ramaccionii* is more coarsely sulcate than that of *N. carrerei*. End members of large populations of both *N. ramaccionii* and *N. ischigualastii* may be difficult to distinguish from *N. carrerei* (de Cabrera 1971).

Few other species of *Neocalamites* have leaflets as narrow as those of *N. carrerei*. Of these, *N. issykulensis* (see Boureau 1964) and *N. muratae* Kon'no 1973, bear abundant branch scars. Kon'no (1973) has imperfectly characterized his species *N. superpermicus*, but it appears to have a more finely and less regularly striated pith cast, and its exterior surface is without broad sulci. *Neocalamites pinitoides* (Chachlov) Prynada 1962 is based on relatively slender and herbaceous remains, with irregular and less lignified ribbing on its pith case and a smoother exterior surface than *N. carrerei*.

OCCURRENCE: Tank Gully locality S72/f569. Accepting the ages of formations proposed by Retallack (1977b), *Neocalamites carrerei* is also found in Late Anisian to Norian rocks of Argentina (de Cabrera 1971), South Africa (Anderson 1974) and Queensland (Jones and de Jersey 1947). Records of it from older formations in Gondwanaland are more likely based on specimens of the very similar un-named species with broader leaflets (discussed above), which appears to have survived into the Middle and Late Triassic, and possibly into the Albian (Walkom 1919; Gould 1976). *Neocalamites carrerei* flourished in Japan during the Ladinian and Carnian but was rare in the Liassic (Kon'no 1962). It penetrated Siberia during the Carnian and was widespread in southeast Asia and Mexico during the Late Triassic (Bureau

1964), reaching Uzbekistan, Europe and Greenland by the Liassic (Harris 1946; Sixtel *et al.* 1971).

Class: PTEROPSIDA

Order: *incertae sedis*

Genus: **Sphenopteris** Brongniart *sensu* Seward 1910:529

Sphenopteris sp. indet. (Figs. 1A-B)

These sterile frond fragments are provisionally referred to the form genus *Sphenopteris*. They are evidently identical (Retallack 1977a) to more abundant sterile and

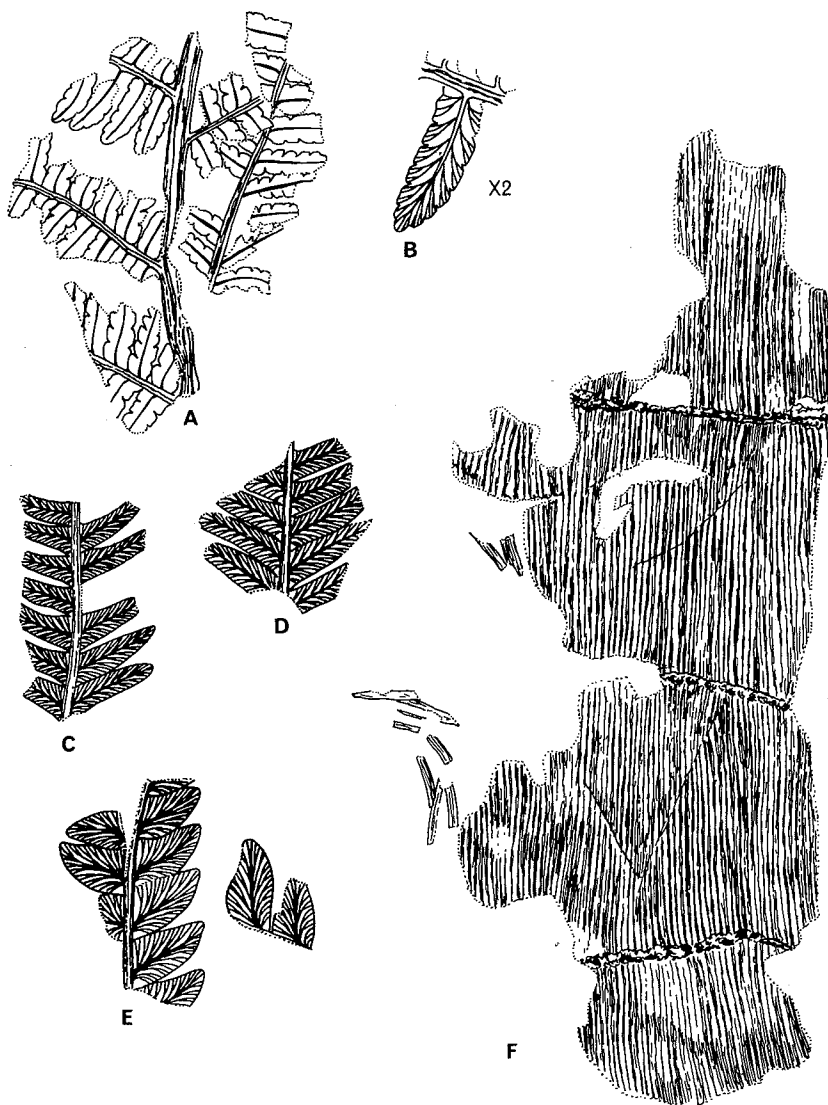


FIG. 1. — Pteridophytes, A-B, *Sphenopteris* sp. B1092.6; A, frond fragment; B, pinnule from upper left hand pinna, twice natural size; C-D, *Cladophlebis indica*, two fragments on the same slab, B1091.38; E, *Lobifolia dejerseyi*, B121.15; F, *Neocalamites carrerei*, large axis with associated leaflets, B1091.18. All natural size unless otherwise indicated.

fertile material of a new species of Triassic fern from Long Gully, North Otago, yet to be described.

S72/f569, S72/f573.

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

Cladophlebis indica (Oldham and Morris) Sahni and Rao 1933 (Figs. 1C-D, 10A)

DESCRIPTION: Several examples of pinna fragments have been found lying parallel on the same slabs, which suggests that they belong to a bipinnate frond. The pinnules are falcate, strongly tapered towards the apex, and often have slightly recurved margins. Their lateral veins are singly forking throughout.

COMPARISON: Most species of *Cladophlebis* have been discussed in reviews by Frenguelli (1947), Herbst (1971) and Boureau and Doubinger (1975), and others by Oishi (1940), Oishi and Huzioka (1938), McQueen (1956), Harris (1961) and Kimura (1976). The leaves of only a few resemble *C. indica* in having singly-forked lateral veins and entire, falcate pinnules. *Cladophlebis acuta* has more acute pinnule apices than *C. indica*. *Cladophlebis grahamii* is distinguished by the subauriculate basal acroscopic margins of its pinnules and the occasional double forking of the basal lateral veins. Unfortunately, the type of *C. nebbensis* is very poorly preserved, but following Frenguelli's (1947) understanding of this species, the pinnules are less falcate, less tapered, and more obtusely pointed than those of *C. indica*. From Halle's (1913) figures of the type material, *C. oblonga* does not necessarily have the blunt, subrectangular pinnules usually taken as representing it. *Cladophlebis oblonga* is the most similar species, differing only in its less-tapered pinnule apices.

REMARKS: *Cladophlebis indica* has been transferred to *Todites indicus* by Bose and Shah (1968). According to article 69 of the International Code of Botanical Nomenclature this must be considered a separate taxon from *C. indica*. *Todites indicus* is best used only for Indian leaves, and a new specific epithet of *Cladophlebis* is not needed for the various sterile non-Indian fronds. These New Zealand fronds are indistinguishable from the sterile Indian type material figured by Oldham and Morris (1862, pl. 27) and when fertile fronds are found may also prove to be osmundalean. Sharma (1971) has proposed that the sterile fronds of *Todites indicus* be transferred to *Cladophlebis denticulata*, intended in the unrealistically broad sense of Seward (1910). However, the pinnule apices of *C. denticulata* are dentate, unlike those of *C. indica*.

OCCURRENCE: In New Zealand, S72/f569. Frenguelli (1947) records *C. indica* from Paso Flores and Malacara, Argentina, of Rhaetian age (Retallack 1977b). *Cladophlebis indica* in the El Tranquilo Basin of Argentina (Herbst 1971) could be of any age within the Triassic period (Retallack 1975). In India, *Todites indicus* is found in both Jurassic and Cretaceous rocks (Sukh-Dev 1974). Although Frenguelli (1947) accepted the Sri Lankan Jurassic fragment figured by Seward and Holtum (1922) as a valid record of *C. indica*, that fragment does not show the characteristic tapered pinnules of *C. indica*.

Genus: *Lobifolia* Rasskazova and Lebedev 1968

Lobifolia dejerseyi Retallack (in Retallack *et al.* 1977) (Fig. 1E)

These small fragments of pinnae are identical with remains discussed more fully by Retallack *et al.* (1977); the basal margin of the pinnules is constricted basiscopically and flared acroscopically. The strong midvein dissolves towards the apex. The secondary venation is twice forking.

S72/f569.



FIG. 2. — *Dicroidium* leaves, A-B, *Dicroidium dubium* var. *tasmaniense*; A, B1091.4; B, B1091.5; C, *Dicroidium incisum*, B1091.61; D-E, *Dicroidium eskense*; D, B1091.42; E, B1095.12; F-G, *Dicroidium lancifolium* var. *lancifolium*; F, B1091.13; G, B1091.30. All natural size.

Division: GYMNOSPERMOPHYTA
 Class: PTERIDOSPERMOPSIDA
 Order: Corystospermales
 Family: Corystospermaceae
 Genus: *Dicroidium* Gothan emend. Townrow 1957:26



FIG. 3. — *Dicroidium* and *Johnstonia* leaves, A-B, *Dicroidium prolungatum*; A, B1091.30; B, B1091.44; C-E, *Dicroidium odontopteroides* var. *argenteum*; C, B1095.10; D, holotype B1095.1; E, B1091.12; F-G, *Dicroidium odontopteroides* var. *moltenense*; F, B1091.15; G, B1091.7; H-I, *Dicroidium odontopteroides* var. *odontopteroides*; H, B1091.2; I, B1091.32; J-K, *Dicroidium odontopteroides* var. *remotum*; J, B1091.14; K, B1095.15; L, *Johnstonia stelzneriana* var. *stelzneriana*, B1091.22; M, *Johnstonia dutoitii*, B1091.3. All natural size.

The various taxa of *Dicroidium* described here are based on my (1977b) revision of the taxonomy and distribution of the genus.

Dicroidium dubium* var. *tasmaniense (Anderson and Anderson) Retallack (in Retallack *et al.* 1977) (Figs. 2A-B)

Two specimens were found with rounded pinna lobes and thin leaf substance, clearly showing the secondary venation. One (Fig. 2A) shows two branches of the rachis converging towards a concealed dichotomy.

S72/f569.

Dicroidium eskense (Walkom) Jacob and Jacob 1950 (Figs. 2D-E)

This unipinnate species has a deep sinus in the basal acroscopic margin of the pinna and secondary venation at a very acute angle to the pinna midrib.

S72/f569, S72/f573.

Dicroidium incisum (Frenguelli) Anderson and Anderson 1970 (Fig. 2C)

This is a pinnatifid species with constricted pinna bases and secondary venation at an acute angle to the pinna midrib. The details of the pinna margin of a specimen from Tank Gully figured by Arber (1913, p. 346, pl. 8, fig. 7; 1917, p. 49, pl. 5, fig. 1, as "*Thinnfeldia lancifolia*") are unclear owing to the recurved nature of the leaf, but it, also, most likely belongs to *D. incisum*.

S72/f569.

Dicroidium lancifolium* var. *lancifolium (Morris) Gothan 1912 (Figs. 2F-G)

These are small to medium-sized unipinnate fronds, with relatively tapered pinnae, though not as tapered and well spaced as those of *D. lancifolium* var. *lineatum*.

S72/f569.

Dicroidium odontopteroides* var. *argenteum Retallack 1977b (Figs. 3C-E, 10F)

I take this opportunity to figure the varietal type (Figs. 3D, 10F) more adequately. There is some variation in these fronds, but all are unipinnate, and have constricted pinna bases. All are distinguished from *D. odontopteroides* var. *crassum* by their rounded and more erect pinnae.

S72/f569, S72/f573.

Dicroidium odontopteroides* var. *moltenense Retallack 1977b (Figs. 3F-G, 10E)

These have the characteristic subtriangular pinnae but are rather smaller than usual for this variety.

S72/f569, S72/f573.

Dicroidium odontopteroides* var. *odontopteroides (Morris) Gothan 1912 (Figs. 3H-I)

These are rather smaller than usual for this variety and also show an impersistent midrib. The midrib is not as well developed, nor are the pinnae as long, as those of *Dicroidium lancifolium*.

S72/f569.

Dicroidium odontopteroides* var. *remotum (Szajnocha) Retallack (in Retallack *et al.* 1977) (Figs. 3J-K)

This material is not well preserved, but it shows many of the distinctive features of this variety — cordate and subtriangular pinnae below the fork of the rachis, elongate, overlapping pinnae with rounded apices on the outside of the rachis above the fork, and narrow, acutely-angled, inside pinnae.

S72/f569, S72/f573.

Dicroidium prolongatum (Menendez) Retallack 1977b (Figs. 3A-B)

The two specimens found in Tank Gully are of quite different sizes, though not approaching either the maximum or minimum for this variety. Their pinnules are subrhombic, with numerous irregularities including undulation, lobation, and splitting. These poorly-preserved and leached remains convey the impression that the living leaves were relatively thin with strongly-lignified secondary venation.

S72/f569.

Dicroidium zuberi var. **papillatum** (Townrow) Retallack 1977b (Figs. 4C-D)

The two specimens found in Tank Gully are of quite different sizes, though

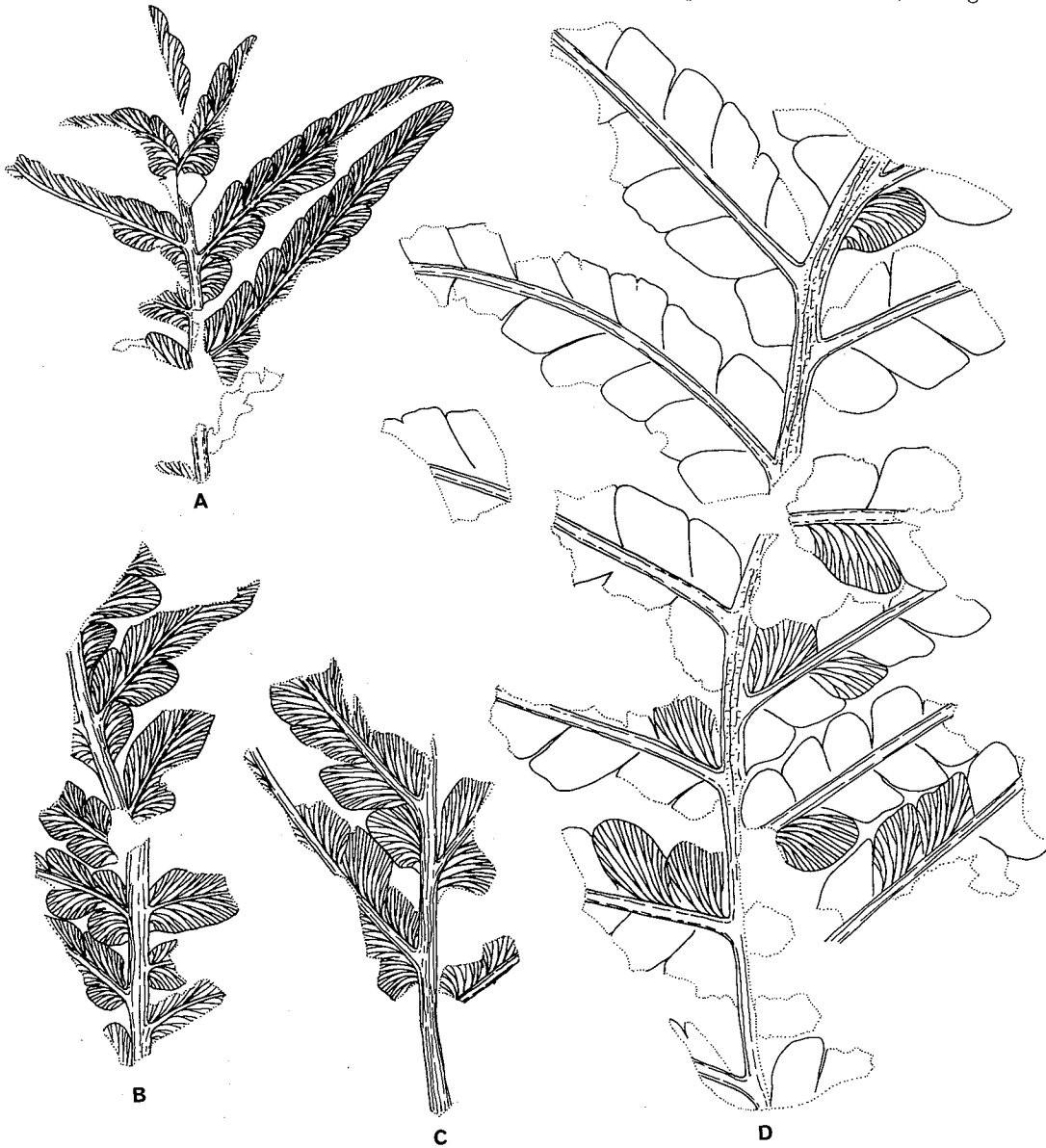


FIG. 4. — *Dicroidium zuberi* leaves, A-B, *Dicroidium zuberi* var. *sahnii*; A, B1091.58; B, B1091.26; C-D, *Dicroidium zuberi* var. *papillatum*; C, B1091.39; D, B1091.29. All natural size.

not approaching either the maximum or minimum for this variety. Their pinnules are subrhombic, with numerous irregularities including undulation, lobation, and splitting. These poorly-preserved and leached remains convey the impression that the living leaves were relatively thin with strongly-lignified secondary venation.

S72/f569.

Dicroidium zuberi var. **sahnii** (Seward) Retallack 1977b (Figs. 4A-B)

The semi-pinnatifid pinnae are typical of this variety but the remains are smaller and have more pointed pinnules than the varietal type material of Seward (1933). The modified pinnae on the right-hand side of one of the specimens from Tank Gully (Fig. 4B) were probably inside and close to the fork of the rachis.

S72/f569.

Genus: **Johnstonia** Walkom emend. Frenguelli 1943:314

Johnstonia dutoitii (Townrow) Retallack 1977b (Fig. 3M)

The single specimen found in Tank Gully is rather more deeply incised below the fork of the rachis than is usual. The branches of the rachis after the fork are shorter than the length of the rachis below the fork, as is common in *Johnstonia* with broader leaves, such as *J. coriacea* var. *obesa*. This specimen is very similar to the "*Dicroidium odontopteroides*" of Jain and Delevoryas (1967, p. 571, pl. 90, fig. 3).

S72/f569.

Johnstonia stelzneriana var. **stelzneriana** (Geinitz) Retallack 1977b (Fig. 3L)

Although only a small fragment was found, it shows a distinct curvature of the rachis and an asymmetry, indicating that it belonged to a forking frond. The lobes are narrow, deeply incised, and supplied with secondary veins which arise from the rachis well below the segment in which they end. The fragment appears to have been a robust and coriaceous leaf, like the varietal type material (Geinitz 1876, pl. 2, figs. 7-8).

S72/f569.

Genus: **Pteruchus** Thomas emend. Townrow 1962a:289

Pteruchus johnstonii (Feistmantel) Townrow 1962b (Figs. 5A, 10B)

Only one specimen of this well-known corystosperm microsporophyll was found in Tank Gully. Its sporangial heads are rectangular with numerous pendent pollen sacs. The stalks of the sporangial heads are shorter and stouter than is usual in this species. I have given a more detailed discussion of this and related species in Retallack *et al.* (1977).

S72/f569.

Genus: **Pilophorosperma** Thomas 1933

Pilophorosperma sp. cf. **costulatum** Thomas 1933 (Figs. 5B, 10C)

A single specimen is preserved as a curved natural cast containing some graphitic material. Judging from the relief in this fossil, it was probably a solid woody structure. The entire-margined cupule contains a protruding seed, as in *P. costulatum*, but the cupule is more reflexed than usual, as in *P.* sp. type B of Thomas (1933). The species of *Pilophorosperma* are still unsatisfactorily organized (see discussion in Retallack *et al.* 1977).

S72/f569.

Pilophorosperma sp. A. (Figs. 5C-D, 10D)

I have chosen this non-committal term for several isolated cupules found in Tank Gully (S72/f569) and near Benmore Dam (Retallack 1977a, 1977b), New Zealand, and for more complete remains from the Ipswich Coal Measures, southeastern Queensland. These are characterized by large, smooth or finely-pitted cupules. Usually the cupule is irregularly wrinkled, and the organ was probably fleshy in life. All the New Zealand specimens consist of isolated cupules, often with traces of the stalk. More complete Queensland specimens have been figured by Shirley (1898, p. 16, pl. 20) and Walkom (1917b, p. 26, pl. 8, figs. 6, 7, 9 only) as "*Beania geminata*". These remains lack the distally-expanded cone units of *Beania* (see Sporne 1969, fig. 20). Paired, pinnately-arranged bodies are common in *Pilophorosperma*, and the slightly fused, apparently-paired bodies of "*Beania geminata*" (Shirley 1898, pl. 20, fig. 3) are best compared with those of *Pilophorosperma geminatum* Thomas 1933 (fig. 14a). I am not convinced by the explanation offered by Thomas (1933) that this last structure is formed by two partially fused cupules. Judging from the branching pattern of Thomas's specimens, this structure is more likely a dehisced, bivalved cupule. No cuticle is preserved on either the New Zealand or Queensland specimens of this fructification, so the interpretation of these various remains will remain unclear until better-preserved material is discovered.

Class: CONIFEROPSIDA

Order: Ginkgoales

Genus: **Sphenobaiera** Florin 1936**Sphenobaiera robusta** (Arber) Florin 1936 (Figs. 6G-I, 10H)1913 *Baiera* cf. *paucipartita* Arber, p. 346, pl. 7, figs 1-3.1917 *Baiera robusta* Arber, p. 56, pl. 11, figs 3-4.1936 *Sphenobaiera robusta* (Arber); Florin, p. 108.

HOLOTYPE: The specimen figured by Arber (1913, pl. 7, fig. 3; 1917, pl. 11, fig. 4), in the British Museum (Natural History).

TYPE LOCALITY: Tank Gully, New Zealand (S72/f569); Tank Gully Coal Measures, Mt Potts Group, Kaihikuan Stage.

DESCRIPTION: The newly collected material includes several more complete remains than those figured by Arber (1913, 1917). These leaves are relatively narrow and cuneate. Usually two deep divisions of the lamina extend from the apex down to the same level at about one half the length of the leaf. Thus there is a long

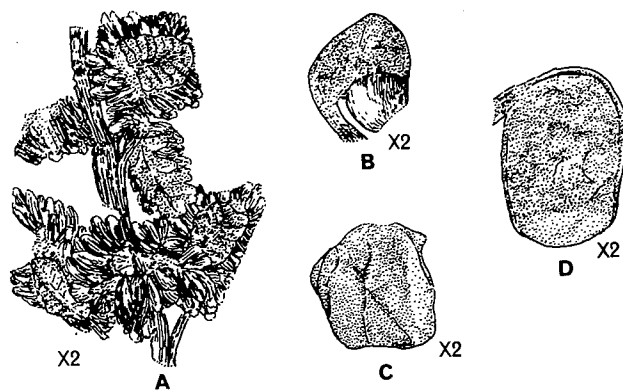


FIG. 5. — Corystosperm fructifications, A, *Pteruchus johnstonii*, B1095.3; B, *Pilophorosperma* sp. cf. *P. costulatum*, B1091.41; C-D, *Pilophorosperma* sp. A; C, B1091.36; D, B1091.62. All twice natural size.

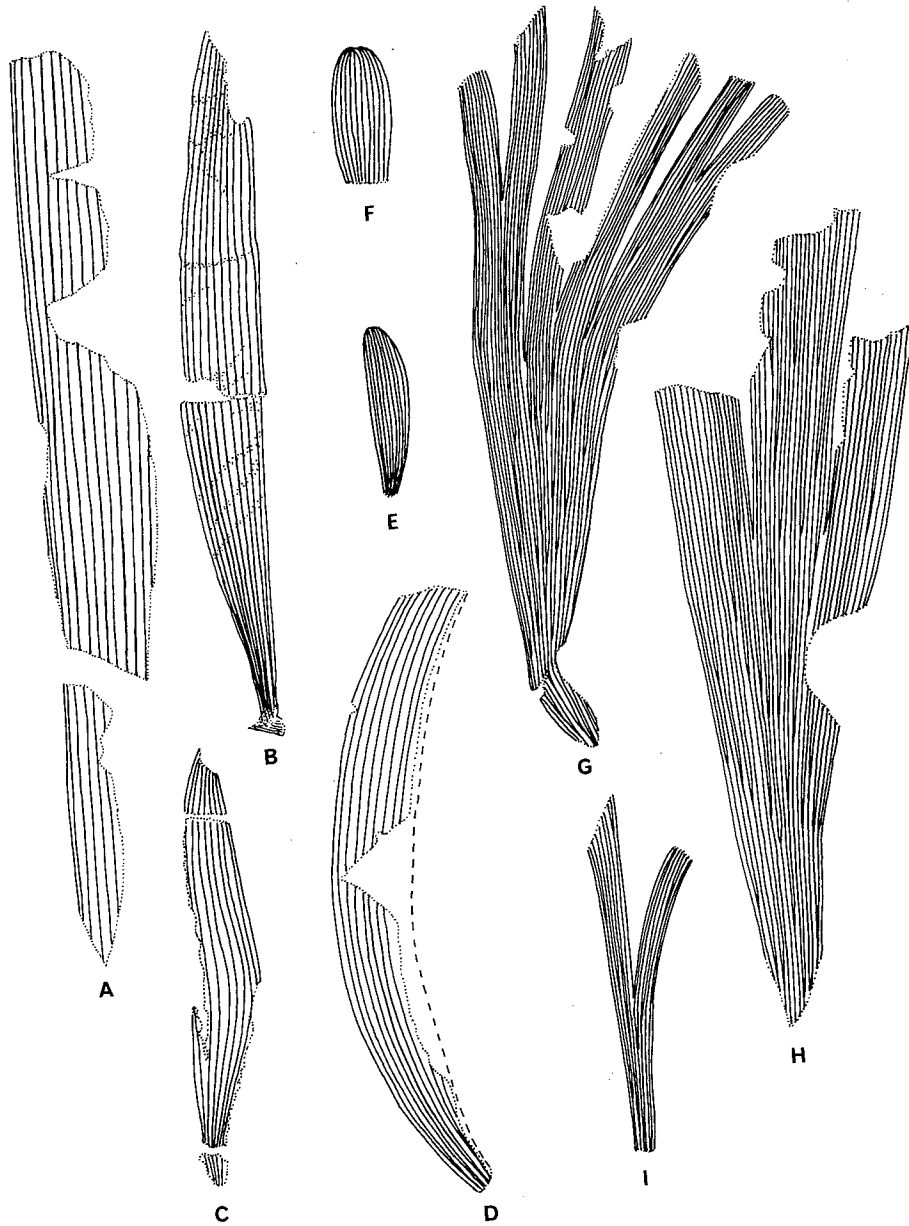


FIG. 6. — *Desmiophyllum* and *Sphenobaiera* leaves, A, *Desmiophyllum* sp., B1091.57; B-D, *Desmiophyllum elongatum*; B, B1068.17; C, B1091.11; D, B1091.25; E-F, *Desmiophyllum* sp. cf. *D. indicum*; E, B1091.60; F, B1091.27; G-I, *Sphenobaiera robusta*; G, B1091.25; H, B1091.43; I, presumed apical fragment, B1091.25. All natural size.

undivided leaf base. No complete leaf base was found, so the number of veins there (important taxonomically) could not be examined. A small, once-forked fragment (Fig. 6I), is here regarded as a broken apical segment of this species.

COMPARISON: Florin (1936) used *Sphenobaiera* for cuneate apetiolate leaves, divided apically so that the ultimate segments contain more than four veins. Krassilov (1970) noted other distinctive features of the genus, including twin veins throughout the narrowest portions of the leaf base, the nature of resin bodies and cuticular features.

Other *Sphenobaiera*-like leaves from Gondwanaland all differ in being more deeply dissected on a strictly dichotomous plan and in having more widely-spreading segments. These include *Sphenobaiera schenkii* (Feistmantel) Florin 1936, "*Ginkgo*" *taeniata* Frenguelli 1937, "*Baiera*" *cuyana* Frenguelli 1942c, "*Baiera*" *rolleri* Frenguelli 1946 and "*Ginkgoites*" *ipsviciensis* (Shirley) Florin 1936. It is not known whether some of these were petiolate or apetiolate. "*Baierophyllites florinii*" Jain and Delevoryas 1967 (which I have seen) is more likely a very coriaceous and lignified frond of *Johnstonia coriacea* var. *coriacea* (as described by Retallack 1977b), a conclusion also supported by its cuticle. Its once-forked, narrow leaf is quite unlike *Sphenobaiera robusta*. Both *S. argentiniae* (Kurtz) Frenguelli 1946 and "*Ginkgoidium*" *bifidum* Frenguelli 1946 differ from *S. robusta* in having only one division of the leaf. *Sphenobaiera stormbergensis* (Seward) Frenguelli 1948 is a larger and more robust leaf with widely-spreading segments and a pleated appearance owing to the copious development of woody interveinal striae. The fragment referred to "*Ginkgo*" *crassipes* by Frenguelli (1937) could be a leaf base of *Sphenobaiera robusta*, but it appears to taper more rapidly towards the base than do the New Zealand specimens.

Externally *Sphenobaiera robusta* is most similar to northern-hemisphere species, such as *S. paucipartita* (Lundblad 1959) and *S. spectabilis* (Harris 1935). However, these leaves are now defined on cuticular characters, unknown in *S. robusta*, and they also have one central division of the leaf which is deeper than any other division.

OCCURRENCE: This species is only known from Kaihikuan (approximately equivalent to Ladinian) coal measures at Tank Gully (S72/f569) and Long Gully (near Otematata, see Retallack 1977a, 1977b), New Zealand.

Plantae incertae sedis

Genus: *Desmiophyllum* Lesquereux emend. Solms-Laubach 1904:3

This is a non-committal name for strap-shaped leaves with parallel venation.

Desmiophyllum elongatum (Morris) comb. nov. (Figs. 6B-D)

These common Gondwanaland leaves are discussed by Retallack *et al.* (1977). They are narrow, lanceolate and have a rounded apex. The veins are well spaced, parallel and fork only at the base of the leaf. One specimen (Fig. 6B) shows possible attachment of a leaf to a slender axis by a broad apetiolate base with about half the number of veins compared to the rest of the leaf. This is quite distinct from the narrow petiolate base of *Podozamites* and *Nageiopsis*. This is also distinct from the "ginkgoalean" *Phoenicopsis*, which is commonly found in brachyblast groups (Samylina 1970; Krassilov 1970). *Desmiophyllum elongatum* is similar — in the shape and arrangement of its leaves — to *Glossophyllum florinii* Kräusel 1943 and *Phyllotenia longifolia* Salfeld 1909, although both these species have a narrower, more tapered leaf base attached to axes thicker than those of *Desmiophyllum elongatum*. However, fossils like *Pelourdea*, also known in Gondwanaland (Frenguelli 1942b), have broader and more closely-spaced leaf-bases attached to thicker axes.

S72/f569, S72/f571-f574.

Desmiophyllum sp. cf. **indicum** Sahnı 1928 (Figs. 6E-F)

These two leaves are distinguished by their small size and by their reaching their maximum width at about two-thirds of their length from base to apex. Although identical with leaves described as *Desmiophyllum indicum* by Lele (1961, p. 80, pl. 4, figs. 42-44), all these remains are shorter and more spatulate than the cutinized type material of *D. indicum* Sahnı 1928 (p. 8, pl. 5, figs 61-64). The cuticles of Lele's and these New Zealand leaves are not known, and as there are only three specimens, it seems premature to create a new species of *Desmiophyllum*.

S72/f569.

Desmiophyllum sp. (Fig. 6A)

Some large, wide, *Desmiophyllum* leaves were also found. As they are incomplete it is impossible to know whether they had tapered and obtuse apices like the smaller leaves of *Desmiophyllum elongatum*.

S72/f569.

Genus: **Ginkgophytopsis** (Høeg) emend. nov.

TYPE SPECIES: *G. flabellata* (Lindley and Hutton) Høeg 1967.

LECTOTYPE: Specimen in the Sunderland Museum, Newcastle, figured by Arber (1912, pl. 42, fig. 3, pl. 43, fig. 7, pl. 44, fig. 8), Seward (1919, fig. 666) and Høeg (1967, figs 270-271).

EMENDED DIAGNOSIS: Leaves cuneate, divided or frayed at the apex. Venation dense, anastomosing and dichotomizing, evenly radiating from base to apex, often obscured by copious, woody interveinal striae. Leaf bases narrow apetiolate, passing decurrently into slender woody axes, on which they are helically arranged.

DISTRIBUTION: Cosmopolitan, ranging from the Late Carboniferous to the end of the Triassic.

COMPARISON: In 1912, Arber established the order Palaeophyllales for leaves of ginkgoalean appearance but uncertain botanical affinities. The palaeophylls are all wedge- or fan-shaped and attached without modification by long, apetiolate, sheathing bases to helically arranged ridges on slender woody axes. Variable features of the palaeophylls are the presence or absence of anastomoses between the veins, the development of woody interveinal striae, and the longitudinal division of the apical margin. Høeg (1967) regarded this last feature as the most important for distinguishing the various palaeophyll genera. In practice it is the most difficult to use, because leaves become split and frayed along the veins during transport and deposition. I prefer to emphasize anastomosing venation, a feature which has always been regarded as of generic importance in all plant groups in which it occurs, including filicaleans, pteridosperms, cycadophytes, glossopterids, and angiosperms. Reconsidering the type species of the various palaeophyll genera on this basis gives the following generic classification:

Flabellifolium (type species, *F. brownianum* (Dawson) Stone 1973) includes palaeophylls with clear, well-spaced evenly dichotomizing venation and with few or no woody interveinal striae.

Ginkgophytopsis (type species, *G. flabellata* (Lindley and Hutton) Høeg 1967) includes palaeophylls with dense dichotomizing venation, with anastomoses, often obscured by woody interveinal striae.

Ginkgophyllum (type species, *G. grassertii* Saporta 1875) includes palaeophylls with dense dichotomizing venation, without anastomoses, often obscured by woody interveinal striae.

The New Zealand Triassic species of *Ginkgophytopsis*, described here, were previously included in the very similar *Chiropteris* by Arber (1917). This genus is now a rather heterogeneous group of leaves with anastomosing venation, all of which differ from *Ginkgophytopsis* in having long, woody petioles. Unlike *Ginkgophytopsis*, *Chiropteris* has never been found attached to woody axes. The type species of *Chiropteris*, *C. lacerata* (Quenstedt) Rühle von Lilienstern 1931, includes coriaceous, palmatifid leaves deeply dissected into cuneate segments and commonly rolled longitudinally into the form of a funnel. The *reniformis* species group of *Chiropteris* are relatively undissected, reniform or cordate leaves with dense venation. These include *Chiropteris reniformis* Kawasaki 1925, *C. kawasakii* Kon'no 1939 and *C. harrisii* Archangelsky 1960.

The *zeileri* species group are also cordate or semi-circular, but they have relatively open venation, characteristically without any anastomoses between a central pair of veins. These include *Chiropteris barrealensis* Frenguelli 1942d and *C. zeileri* Seward 1903. Thus each of these various groups of *Chiropteris* leaves has other features also distinguishing them from *Ginkgophytopsis*.

Gondwanophyton (Maithy 1974) may be allied with the palaeophylls but is distinguished by its more broadly sheathing and cordate leaf base.

BOTANICAL AFFINITIES: Considering present views on the evolution of ginkgoaleans (Tralau 1968; Krassilov 1970) and the distinctive apetiolate attachment of *Ginkgophytopsis* to slender axes, ginkgoalean affinities for the palaeophylls are most unlikely.

Rühle von Lilienstern (1931) considered the superficially similar *Chiropteris* a dipteridacean fern. Heavily cutinized and lignified fossil Dipteridaceae are known (Sukh-Dev 1972). However, the mesh pattern of *Chiropteris* and *Ginkgophytopsis* is quite unlike that of the Dipteridaceae and the supposed sori of *Chiropteris* (described by Rühle von Lilienstern) are more likely fungal infestations or insect domatia, like those discussed by Stace (1965).

It seems more likely that the palaeophylls belonged to an extinct pteridophytic group, such as the progymnosperms. Palaeophylls have been found attached to woody axes and commonly contain interveinal striae, which suggests that they belong to a woody plant. The genus *Eddyia* (of Beck 1967) has *Ginkgophytopsis*-like leaves, which I have examined, attached to structurally-preserved progymnosperm wood of the *Callixylon* type, but this could be regarded as a juvenile plant of *Archaeopteris*. Pteridophytic fructifications of *Enigmophyton* have been found in very close association with leaves of the *Platyphyllum* type (by Høeg 1942; 1967, p. 416).

SPECIES: At present six are recognized:

Ginkgophytopsis flabellata (Lindley & Hutton) Høeg 1967 has long, narrow leaf bases and lateral margins curving outwards to a wide and irregularly lacinate apical margin. It is found in the Late Carboniferous of England.

"Ginkgophyllum" scoticum (Wilson) Høeg 1967 also has anastomosing venation and is better regarded as an additional species of *Ginkgophytopsis*. These remains from the Late Carboniferous of Scotland include narrow cuneate leaves, divided into two segments.

Ginkgophytopsis kidstonii (Seward) Høeg 1967 (also figured by Le Roux 1970, as "*Ginkgoites* sp. types A and B", "*Pygmyphyllum kidstonii*" and "*P. sp.*"; and by Dun 1911, as *Rhipidopsis ginkgoides* var. "*sussmilchii*" and emended by Maithy 1974, to "*Ginkgophyllum kidstonii*") has small, narrow, spatulate to cuneate leaves, with lateral margins converging slightly towards the apex, very short leaf bases, and large leaves deeply divided into two segments. This species has been found in the later Early Permian of South Africa and the latest Permian of New South Wales.

Ginkgophytopsis lacerata (Arber) comb. nov. (discussed below) has small to medium-sized, broadly cuneate fronds with concave lateral margins and the apical margin divided into two or more spreading segments. It is found in Middle to Late Triassic rocks of Australia, New Zealand, Chile, Argentina and South Africa.

Ginkgophytopsis cuneata (Carruthers) comb. nov. (for "*Cyclopteris cuneata*" of Carruthers 1872, p. 355, pl. 27, fig. 5; and similar leaves described by many authors) has small to large, narrow, cuneate to spatulate leaves, entire or irregularly split and frayed along the apical margin. It is found in Early to Late Triassic rocks of Australia, Chile, South Africa, and possibly also in Argentina.

Ginkgophytopsis tasmanica (Waikom) comb. nov. (for "*Chiropteris tasmanica*" of Walkom 1925b, p. 72, pl. 9, fig. 2; also including "*Sagenopteris salisburioides*" of Etheridge 1894, and (in part), "*Chiropteris barrealensis*" of Frenguelli 1942d, fig. 1 only) has small (probably; juvenile), deltoid or broadly obovate, entire leaves. It has been found in Early to Late Triassic rocks of Tasmania, New South Wales and Argentina.

A more detailed discussion of *Ginkgophytopsis cuneata* and *C. tasmanica* is intended for a future publication on the megafossil flora from near Benmore Dam, North Otago.

***Ginkgophytopsis lacerata* (Arber) comb. nov. (Figs. 9A-C, 10J)**

- ?1887 *Ginkgophyllum australe* Johnston, p. 178.
- 1913 *Chiropteris lacerata* Arber, p. 346, pl. 8, fig. 6.
- 1917 *Chiropteris lacerata* Arber, p. 27, pl. 3, fig. 8.
- 1927 *Chiropteris copiapensis* Solms-Laubach; Du Toit, p. 324, fig. 3D only.
- 1931 *Chiropteris arberi* Rühle von Lilienstern, p. 266.
- 1932 *Chiropteris arberi* Rühle von Lilienstern, p. 230.
- 1932 *Chiropteris copiapensis* Solms-Laubach; Rühle von Lilienstern, p. 230.
- ?1947 ?*Ctenis* sp. 1 Jones and de Jersey, p. 39, figs 27-28.
- ?1947 ?*Ctenis* sp. 2 Jones and de Jersey, p. 40, fig. 29.

- 1951 *Chiropteris copiapensis* Solms-Laubach; Menendez, p. 171, pl. 3, figs 1-4.
 1956 *Chiropteris biloba* Bell, in Bell *et al.*, p. 667, figs 4.11-12.
 1956 *Chiropteris waitakiensis* Bell, in Bell *et al.*, p. 669, figs 4.10,14.
 1956 *Ginkgo digitata* (Brongniart); Bell, in Bell *et al.*, p. 671, fig. 4.16.
 1967 ?*Chiropteris* sp. Gould, p. 129.
 1969 *Chiropteris copiapensis* Solms-Laubach; Stipanovic and Bonetti, p. 1093.
 1974 *Chiropteris lacerata* Arber; Anderson, table 3.
 1974 *Chiropteris biloba* Bell; Anderson, table 3.
 1974 *Chiropteris waitakiensis* Bell; Anderson, table 3.
 1975 *Chiropteris* sp. Flint and Gould, p. 71.

HOLOTYPE: "*Chiropteris lacerata*" of Arber (1913, pl. 8, fig. 6; 1917, pl. 3, fig. 8) in the British Museum (Natural History).

TYPE LOCALITY: Tank Gully near Erewhon homestead, Canterbury, New Zealand (S72/f569); Tank Gully Coal Measures, Mt Potts Group, Kaihikuan Stage.

DESCRIPTION: These remains show even more clearly than the holotype that the apical margin of the leaf was deeply incised. None has been preserved as far as the second dichotomy of the lamina; all are less than 5 cm long, so speciation based on number of divisions (Bell *et al.* 1956) is impractical. Natural groups of such leaves (Fig. 9C) spirally arranged around slender axes, were mistaken for single *Ginkgo*-like leaves (Bell *et al.* 1956). Venation is of variable clarity and spacing, becoming more obscure in leaves more copiously ramified by woody interveinal striae.

OCCURRENCE: Tank Gully localities S72/f569, S72/f572. *Ginkgophytopsis lacerata* is best known from Tank Gully (Arber 1913, 1917), Benmore Dam (Bell *et al.* 1956) and Long Gully, in Torlesse rocks and near Highfield, Lake Gunn and Taylors Creek, in the Murihiku Supergroup (N.Z. Geological Survey collections), New Zealand; from the upper Chihuiu and Tronquimalal Formations, Llantenes Group, Argentina (Menendez 1951; Stipanovic 1969); from cycles 2-4 or zone D of the Molteno Formation, Karroo Basin, South Africa (Du Toit 1927; Anderson 1974) and the Moorooka Formation near Brisbane, Queensland (Gould 1967). There are also less reliable records of the species from the "Feldspathic Sandstone Series", at New Town, Tasmania (Johnston 1887), from the Ipswich Coal Measures, Queensland (Jones and de Jersey 1947) and from the Barreal Group and Cacheuta and Potrerillos Formations, Cacheuta Group (Stipanovic 1969; Stipanovic and Bonetti 1969). Accepting the ages of these formations proposed here and by Retallack (1977b), this species has a Ladinian to Rhaetian range.

Genus: *Linguifolium* Arber emend. nov.

TYPE SPECIES: *Linguifolium lilleanum* Arber 1913.

EMENDED DIAGNOSIS: Simple, entire leaves; linear, spatulate, lanceolate or ovate; apices subacute to rounded; bases gently tapering. Midrib strong and wide at the base, tapering and persistent to the apex. Secondary veins arising at a very acute angle to the midrib, arching outwards to meet the leaf margin at an acute angle; usually forking only once, sometimes one of these branches forking again; most forkings of the secondary veins within the inner third of their length. Cuticle unknown.

DISTRIBUTION: Restricted to Middle and Late Triassic rocks of the Pacific margin of Gondwanaland.

COMPARISON: The genus was founded by Arber (1913, 1917) for leaves superficially similar to *Glossopteris* but without anastomosing secondary venation. Such leaves had previously been referred to *Phyllopteris*, but Arber showed that *Phyllopteris* was the junior synonym of *Sagenopteris*, which (along with *Pseudosagenopteris* and *Dactylopteris*) differs from *Linguifolium* in having four, five, or more (respectively) palmately compound, commonly asymmetric, leaflets, each with reticulate venation and a less persistent midrib (see Frenguelli 1941). Unlike Arber (1917), I believe that

neither *Copiapaea* nor *Blechnoxylon* should be included within *Linguifolium*. *Copiapaea* has strong, erect, well-spaced, lateral venation giving it a distinctive pleated appearance (Solms-Laubach 1899; see also Frenguelli 1941; Menendez 1951). *Blechnoxylon* has small leaves arranged in whorls along with coriaceous triangular scales (Etheridge 1899). Unlike *Linguifolium*, it has well-spaced, less acute, secondary venation, a strongly revolute margin, and a pilose abaxial surface.

Medwell (1954a, 1954b) transferred some Australian remains, formerly referred to *Phyllopteris*, to a new genus, *Phyllopteroides*. These have more symmetrical leaflets than *Linguifolium*, commonly reaching their maximum width half-way along their length and arranged pinnately on slender axes. Their secondary veins are forked up to four times so that the venation is much denser at the margin than near the midrib. *Tatarina* (including *Pursongia*) includes leaves with a band of hypodermal tissue, rather than a true midrib, and whose cuticle is similar to that described by Meyen (1969a, 1969b). *Protophyllocladus* has a thick, coriaceous, lanceolate leaf, its midrib dissolves at one half to two thirds of its length from base to apex, and its secondary venation is straight and unforked. Its type species is palmately trifoliate (Berry 1903).

According to Frenguelli (1941), *Lesleya* is larger and has finer, more numerous and more copiously forked secondary veins than *Linguifolium*. His genus *Velisia* is more regularly lanceolate, with undulose margins and very dense secondary venation, few forkings, and commonly about three woody striae between veins. *Palaevittaria* differs from *Linguifolium* in having a midrib only at the base (Chandra 1974). Johnston (1896) described some specimens, under the name *Strzeleckia*, as similar to *Ganagamopteris* but lacking anastomoses. After examining Johnston's collections, Walkom (1925a) concluded that the central series of veins in these leaves could be regarded as a midrib, and so synonymized them with *Linguifolium*. Unfortunately the specimens have been lost from the Tasmanian Museum and Art Gallery, and the status of this possible senior synonym of *Linguifolium* remains uncertain. Finally, a great variety of taeniopterid leaves (including *Taeniopteris*, *Nilssoniopteris*, *Doratophyllum* and *Nipaniophyllum*) may be distinguished from *Linguifolium* by having more erect secondary venation.

SPECIES: In the past the species of *Linguifolium* have been distinguished on the basis of supposedly cordate shape (more likely poor preservation), the leaf outline, the shape of the apex and strength of the midrib within the apex. With large collections of leaves available, I have found it difficult to accept these distinctions and have been tempted to include all the specimens in one species. This problem is common to many form genera, such as *Cladophlebis* and *Dicroidium*, where we can only guess at the significance of characters used for taxonomy.

Leaf width is the most easily observed feature. The histograms (Fig. 8) include measurements of leaves from Tank Gully, Long Gully and near Benmore Dam (N.Z. Geological Survey specimens). Such histograms alone are not adequate to distinguish species (Retallack 1975, p. 10), but these species separated by size also show other distinctive characters. For example, *L. tenison-woodsii* has elongate, linear-lanceolate leaves with acute apices. *Linguifolium arctum* is elongate, linear-spathulate, with rounded or obtusely pointed apices and a very narrow apical midrib. *Linguifolium steinmanii* is more or less lanceolate with a subacute apex, and *L. lilleanum* is lanceolate, oblanceolate or obovate, with a subacute to rounded apex and very narrow apical midrib. Although all the species occur in New Zealand at each locality (Fig. 8), only one or two species are found at any given *Linguifolium* locality in Australia, Chile and Argentina. Until the meaning of this distribution becomes clear, the width classification is adopted for convenience.

PROBLEMATICAL REMAINS: In order to substantiate the restricted distribution

of *Linguifolium* proposed here, several poorly-known remains must be excluded from the genus.

I have not considered uncertain and unillustrated records of *Linguifolium* by Stipanovic (1957) and Fleming (in Houston 1967), and regard "*Linguifolium deguistoi*" (Archangelsky 1965) as a *nomen nudum*.

The fragment referred to *Linguifolium* by McQueen (1954), which I have seen, is covered with a thick mineralized crust obscuring the venation and has certainly been distorted by shearing. It is indeterminable, and could equally belong to *Taeniopteris*, *Rhabdotaenia*, *Palaeovittaria* or *Glossopteris*.

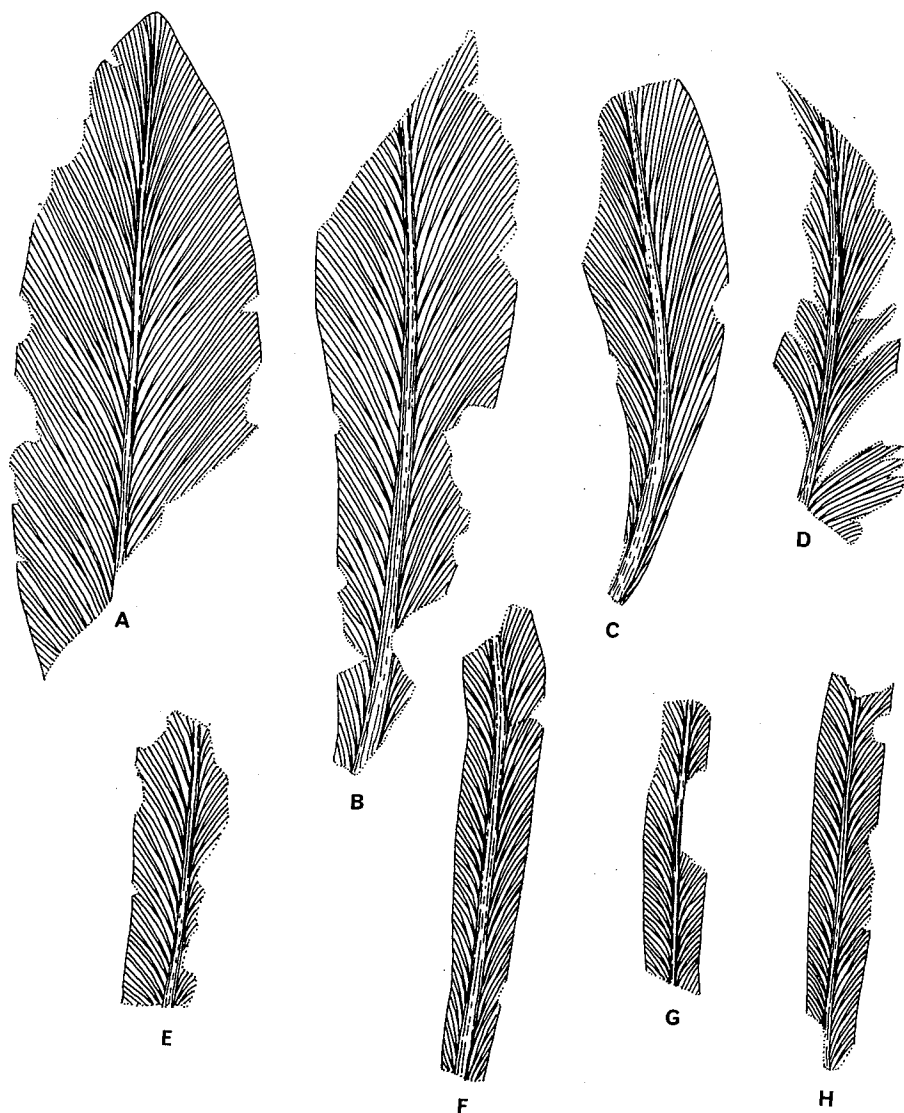


FIG. 7. — *Linguifolium* leaves, A-B, *Linguifolium lilleanum*; A, B1095.5; B, B1091.48; C-D, *Linguifolium steinmannii*; C, B1091.25; D, OU3961; E, *Linguifolium arctum*, B1092.1; F-H, *Linguifolium tenison-woodsii*; F, B1091.53; G, B1091.40; H, B1091.2. Plant drawings all natural size.

Herbst (1966 p. 43) has re-examined the specimens of "*Linguifolium kurtzii*" Frenguelli 1941, and found them to be *Sagenopteris rhoifolia*.

Several other leaves which have been confused with *Linguifolium* would be better identified with *Phyllopteroides*, as discussed above. These include "*Thimfeldia* sp." of Seward (1904, p. 175, pl. 17, fig. 27), and "*Stangerites (Taeniopteris) ensis*" of Oldham and Morris (1862, p. 35, pl. 6, figs 8-10).

Frenguelli (1937, 1941) regarded "*Taeniopteris morrisii*" (Oldham and Morris 1862, p. 43, pl. 3, fig. 1, pl. 4, fig. 3) as a *Linguifolium* leaf. Compared to *Linguifolium*, its secondary venation is more dense, straighter in its course and forms a more open angle to a more prominent but narrower midrib.

All these features also serve to distinguish "*Phyllopteris plumula*" (Saporta 1873, p. 450, pl. 63, fig. 6) from *Linguifolium*. In addition, Saporta's small fragment has split and undulose lateral margins.

I do not accept records of *Linguifolium* at the plant localities of Malvern Hills (Arber 1917) and Clent Hills (N.Z. Geological Survey collection B69). The mixing of fossil collections from Tank Gully and Clent Hills was discussed at the beginning of this paper. The supposed Clent Hills specimens of *Linguifolium* (B69.33, B69.34, B69.56, B69.58) have a matrix and style of preservation more like that of Tank Gully than Clent Hills. There are no other fossil species on these slabs. The record of *Linguifolium* from Malvern Hills (Arber 1917) is also uncertain, as no such specimens could be found in the collections of the Canterbury Museum (Mrs. M. Bradshaw, pers. comm. 1977).

Linguifolium arctum Menendez 1951 (Fig. 7E)

1898 *Taeniopteris Tenison-Woodsii* (Etheridge); Shirley, p. 23, pl. 9, fig. 2 only.

1917a *Taeniopteris Tenison-Woodsii* (Etheridge); Walkom, p. 32, fig. 9, left hand specimen only.

1947 *Doratophyllum tenison-woodsii* (Etheridge); Jones and de Jersey, p. 37, excluding narrower and cuticularized specimens in description.

1951 *Linguifolium arctum* Menendez, p., 182, pl. 6, figs 1-5.

1951 *Linguifolium llantenense* Menendez, p. 185, pl. 7, figs 1-4.

1956 *Linguifolium waitakiense* Bell, in Bell *et al.*, p. 670, figs 4, 7 only.

1956 *Linguifolium lilleanum* Arber; Bell, in Bell *et al.*, p. 670, specimens 1.2 cm wide mentioned in description.

LECTOTYPE: Selected here, *Linguifolium arctum* of Menendez (1951, pl. 6, figs 2, 5); specimens 4831/4837 (part/counterpart) in the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina.

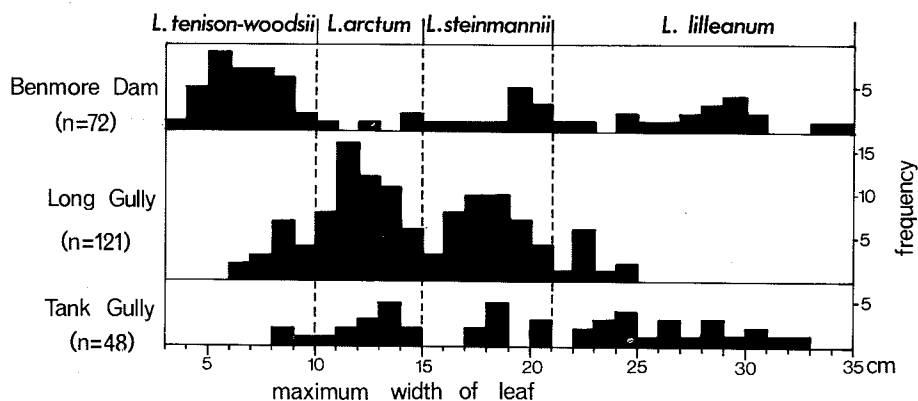


FIG. 8. — Frequency histogram of leaf width in *Linguifolium* leaves from Tank Gully, Long Gully and near Benmore Dam, New Zealand (New Zealand Geological Survey collections).

TYPE LOCALITY: Locality 6(?), Upper Chihui Formation, Llantenes Group, Argentina (Menendez 1951; Stipanovic 1969).

DISTINGUISHING FEATURES: *Linguifolium* leaves, 10-14 mm wide; usually elongate, linear-spathulate, with a rounded or obtusely pointed apex, and relatively narrow apical midrib.

DESCRIPTION: Leaves of this species from Tank Gully are all very imperfectly preserved.

REMARKS: Menendez (1951) characterized *Linguifolium llantenense* by its spatulate outline, well-spaced lateral venation and thick midrib. However, these differences from *L. arctum* are not prominent in the figures of his fragmentary specimens. Jones and de Jersey (1947) assigned leaves of this species and of *L. tenison-woodsii* to *Doratophyllum*, on the basis of their supposed cuticle. This cuticle is quite unlike that of *Doratophyllum* (described by Harris 1932) and most likely belongs to a very similar pteridosperm leaf, unrelated to *Linguifolium*. Jones and de Jersey called these pteridosperm leaves "Reinitsia". Bell (in Bell *et al.* 1956) was evidently unaware of the work of Menendez (1951) when she proposed the name "*Linguifolium waitakiense*".

OCCURRENCE: Tank Gully localities S72/f569, S72/f571-f572. This species also occurs at Long Gully and near Benmore Dam (in Torlesse rocks, near Otamatata), and in Wairoa Gorge and near Highfield homestead (in the Murikuku Supergroup, near Nelson), New Zealand (N.Z. Geological Survey collections). It has been found in the Ipswich Coal Measures of southeastern Queensland (Jones and de Jersey 1947) and in the Llantenes Group of Argentina (Menendez 1951; Stipanovic 1969). In New Zealand it has a Ladinian to Rhaetian range (Retallack 1977a), and following Retallack (1977b), is found in Carnian to Norian rocks elsewhere.

Linguifolium lilleanum Arber 1913 (Figs. 7A-B)

- 1913 *Linguifolium lilleanum* Arber, p. 346, pl. 7, figs 1, 4, wider forms only.
 1917 *Linguifolium lilleanum* Arber, p. 38, pl. 3, figs 1, 7, wider forms only.
 1920 *Linguifolium lilleanum* Arber; Steinmann, p. 350, fig. 1.
 1925b *Linguifolium lilleanum* Arber; Walkom, pp. 64, 67.
 ?1926 *Phyllopteris Feistmanteli* Etheridge; Chapman and Cookson, p. 171, pl. 23, fig. 19.
 1941 *Linguifolium lilleanum* Arber; Frenguelli, p. 428.
 1945 *Lesleya Steinmannii* (Solms-Laubach); Berry, p. 187.
 1947 *Linguifolium lilleanum* Arber; Jones and de Jersey, p. 48.
 1956 *Linguifolium lilleanum* Arber; Bell, in Bell *et al.*, p. 670, figs 4. 8-9.
 ?1965 *Linguifolium lilleanum* Arber; Archangelsky, p. 279.
 ?1967 *Linguifolium lilleanum* Arber; Fleming, in Houston, p. 15.

LECTOTYPE: Selected here, the specimen of "*Linguifolium lilleanum*" figured by Arber (1913, pl. 7, fig. 1; 1917, pl. 3, fig. 1), in the British Museum (Natural History).

TYPE LOCALITY: Tank Gully, near Erewhon homestead, Canterbury, New Zealand; Tank Gully Coal Measures, Mt Potts Group, Kaihikuan Stage.

DISTINGUISHING FEATURES: *Linguifolium* leaves, 21-35 mm wide, usually lanceolate to oblanceolate or obovate, with subacute to rounded apex and relatively narrow apical midrib.

DESCRIPTION: The leaves collected in Tank Gully have apices ranging from rounded to bluntly pointed. They are widest at a point well beyond half their length.

OCCURRENCE: Tank Gully localities S72/f569, S72/f570, S72/f573. Also found at Long Gully and near Benmore Dam (in Torlesse rocks) and near Otamita Stream (Southland) and Highfield homestead (near Nelson, also in the Murihiku Supergroup) in New Zealand (N.Z. Geological Survey and Otago University collections). Also found in the Ipswich Coal Measures of southeastern Queensland (Jones and de Jersey 1947), in the "Feldspathic Sandstone Series" of Tasmania (Walkom 1925b) and near Talcamavede (personal examination of material discussed by Berry 1945, in U.S. National Museum, Washington, D.C.) and on the Bio Bio River (Steinmann 1920) in Chile. It may also occur in the Tingalpa Formation, near Brisbane,

Queensland (Fleming, in Houston 1967), in the Leigh Creek Coal Measures, South Australia (Chapman and Cookson 1926) and the El Tranquilo Basin, Argentina (Archangelsky 1965). The Ladinian to Rhaetian range of this species in New Zealand is not contradicted or amplified by its occurrence elsewhere.

Linguifolium steinmannii (Solms-Laubach) Frenguelli 1941 (Figs. 7C-D, 10I)

- ?1896 *Strzeleckia gangamopteroides* Johnston, p. 58, figs 5-7, also discussed by Walkom (1925a).
 1899 *Lesleya Steinmanni* Solms-Laubach, p. 596, pl. 13, figs 5-7.
 1917 *Linguifolium lilleanum* Arber, p. 38, narrower forms of description.
 1941 *Linguifolium Steinmanni* (Solms-Laubach); Frenguelli, p. 428.
 1945 *Lesleya Steinmanni* (Solms-Laubach); Berry, p. 187.
 1947 *Linguifolium denmeadi* Jones and de Jersey, p. 49, fig. 40, pl. 4, fig. 4.
 1965 *Linguifolium denmeadi* Jones and de Jersey; Hill, Playford and Woods, pl. T8, fig. 2.
 ?1967 *Linguifolium denmeadi* Jones and de Jersey; Gould, p. 129.
 ?1967 *Linguifolium denmeadi* Jones and de Jersey; Fleming, in Houston, pp. 15, 82.
 ?1975 *Linguifolium denmeadi* Jones and de Jersey; Flint and Gould, p. 71.

LECTOTYPE: Selected here, the specimen of "*Lesleya Steinmanni*" figured by Solms-Laubach (1899, pl. 13, fig. 6), in the Strasburg Museum, Germany.

TYPE LOCALITY: Reddish-brown clay ironstone in the lower portion of a 30 to 40 m thick coal-bearing shale and clay-ironstone unit, beside the road leading up the ravine near the coal mine (of 1899), Quebrada La Ternera, near Copiapó, Chile (Steinmann 1899).

DISTINGUISHING FEATURES: *Linguifolium* leaves 15-20 mm wide, usually lanceolate with a subacute apex.

DESCRIPTION: This species is usually the most completely preserved of *Linguifolium* leaves from Tank Gully, presumably because it is not as elongate nor as large as other species and so is less easily broken in transport. One specimen (Fig. 7D) found in a sandstone matrix has been deeply split along the veins, probably during turbulent and abrasive conditions of deposition.

REMARKS: Solms-Laubach (1899) thought that this species had a cordate leaf base and a short petiole. As Menendez (1951) observes, it seems more likely that the single specimen on which this idea was based (Solms-Laubach 1899, pl. 13, fig. 5) was curled and broken at the base, as the basal third of one of the secondary veins has been truncated. If this difference is disregarded then *Linguifolium denmeadii* Jones and de Jersey 1947 becomes a junior synonym of *Linguifolium steinmannii*.

OCCURRENCE: Tank Gully localities S72/f569, S72/f570, S72/f573-574, S72/f552. This species has also been found in Long Gully and near Benmore Dam (in Torlesse rocks) and near Highfield homestead (in the Murihiku Supergroup, near Nelson) in New Zealand (N.Z. Geological Survey collections), in the Ipswich Coal Measures, southeastern Queensland (Jones and de Jersey 1947), and near La Ternera and Talcamavide, in Chile (Solms-Laubach 1899; Berry 1945). It may also occur in the Moorooka and Tingalpa Formations, near Brisbane, Queensland (Fleming, in Houston 1967; Gould 1967), in the Red Cliff Coal Measures of northeastern New South Wales (Flint and Gould 1975) and in the "Feldspathic Sandstone Series" at Mt Nichols, Tasmania (Johnstone 1896). The Ladinian to Rhaetian range of this species in New Zealand is not contradicted or amplified by its occurrence elsewhere.

Linguifolium tenison-woodsii (Etheridge) comb. nov. (Figs. 7F-H)

- 1883 *Angiopteridium ensis* Tenison-Woods, p. 119.
 ?1888 *Pecopteris caudata* Johnston, pl. 26, fig. 1.
 ?1890a *Thinnfeldia saligna* Schenk; Feistmantel, p. 97, pl. 8, fig. 13.
 1890b *Angiopteridium ensis* Tenison-Woods; Feistmantel, p. 116.
 1892 *Angiopteridium Tenison-Woodsi* Etheridge, in Jack and Etheridge, p. 375.
 ?1896 *Strzeleckia tenuifolia* Johnston, p. 58, fig. 8.
 1898 *Taeniopteris (Angiopteridium) ensis* (Tenison-Woods) Dun, p. 375.

- 1898 *Taeniopteris Tenison-Woodsii* (Etheridge); Shirley, p. 23, narrower forms in description only.
 1917a *Taeniopteris Tenison-Woodsii* (Etheridge); Walkom, p. 32, fig. 9, right hand specimen only.
 1925a *Linguifolium diemenense* Walkom, p. 81, fig. 11
 ?1926 *Taeniopteris* cf. *Tenison-Woodsii* (Etheridge); Chapman and Cookson, p. 169, pl. 21, fig. 13.
 1930 *Taeniopteris tenison-woodsii* (Etheridge); Hill, p. 184.
 1947 *Doratophyllum tenison-woodsii* (Etheridge); Jones and de Jersey, p. 37, pl. 6, fig. 1 only.
 1951 *Linguifolium diemenense* Walkom; Menendez, p. 183, pl. 7, figs 6-8.
 1956 *Linguifolium waitakiense* Bell, in Bell *et al.*, p. 670, fig. 4.6 only.
 1965 *Doratophyllum tenison-woodsii* (Etheridge); Hill, Playford and Woods, pl. T8, fig. 1.
 1965 *Linguifolium diemenense* Walkom; Archangelsky, p. 279.
 1967 *Linguifolium diemenense* Walkom; Fleming, in Houston, pp. 15, 17.
 1967 *Doratophyllum tenison-woodsii* (Etheridge); Gould, p. 124.
 1970 *Johnstonia coriacea* (Johnston); Azcárate and Fasola, p. 259, fig. 5.

LECTOTYPE: Selected here from specimens mentioned by Tenison-Woods (1883, p. 83) and Etheridge (in Jack and Etheridge 1892, p. 375); no. 30 of the Macleay Collection in the Department of Geology and Geophysics, University of Sydney, Australia.

TYPE LOCALITY: Aberdare Mine, Ipswich Coal Measures, southeastern Queensland.

DISTINGUISHING FEATURES: *Linguifolium* leaves 2-9 mm wide; usually linear-lanceolate with a subacute, tapering apex.

DESCRIPTION: Only fragments of this species were found at Tank Gully, but in these the gentle basal and apical taper of these leaves can be seen.

REMARKS: The specimens which Johnston (1896, fig. 8) called "*Strezleckia tenuifolia*" could be conspecific with *Linguifolium tenison-woodsii* if these unconnected and crossing leaf bases are correctly drawn. Unfortunately the specimens are lost from the Tasmanian Museum and Art Gallery, and there is no way of distinguishing these fragments from those of *Johnstonia coriacea* (Johnston) Walkom 1925a. There is, however, a sufficient length of the specimen identified with this latter species by Azcárate and Fasola (1970) for it to be recognizable as *Linguifolium tenison-woodsii*. Most of the confusion concerning *L. tenison-woodsii* arose from a sketch of "*Taeniopteris Tenison-Woodsii*" by Walkom (1917a, fig. 9). The secondary venation in this sketch is not at as acute an angle to the midrib as is usual in *Linguifolium*, and it is difficult to decide whether it is a poor drawing or a different fossil, perhaps a pteridosperm fragment. The type material of *Linguifolium tenison-woodsii* (which I have examined) certainly has secondary venation at an acute angle to the midrib, but this was not suspected by those who established the junior synonyms *Linguifolium diemenense* Walkom 1925a and *L. waitakiense* Bell (in Bell *et al.* 1956). A previously proposed transferral of *Linguifolium tenison-woodsii* to the genus *Doratophyllum* has already been discussed in so far as it relates also to *Linguifolium arctum*.

OCCURRENCE: Tank Gully localities S72/f569, S72/f571-f572, S72/f574. *Linguifolium tenison-woodsii* has also been found at Long Gully (in Torlesse rocks near Otematata) and in North Etal Creek (in the Murihiku Supergroup, near Mossburn) in New Zealand (N.Z. Geological Survey collections), in the Ipswich Coal Measures and Moorooka and Tingalpa Formations, and in the Toogoolawah Group, southeastern Queensland (Jones and de Jersey, 1947; Fleming, in Houston 1967; Gould 1967; Hill 1930), in the "Feldspathic Sandstone Series" of Tasmania (Walkom 1925a), in the Llantenes and El Tranquilo Groups, Argentina (Archangelsky 1965; Menendez 1951; Stipanovic 1969) and at Los Molles, Chile (Azcárate and Fasola 1970). It may also occur in the Leigh Creek Coal Measures, South Australia (Chapman and Cookson 1926). This species is only found in the Ladinian rocks of New Zealand, but accepting the ages of formations proposed by Retallack (1977b), it ranged from the Late Anisian to Norian elsewhere.

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

***Carpolithus mackayi* Arber 1917 (Figs. 9F-I)**

1917 *Carpolithus McKayi* Arber, p. 64, pl. 11, fig. 6.
 ?1965 gymnospermous seed Hill *et al.* pl. T8, fig. 8.

HOLOTYPE; The specimen figured by Arber (1917, pl. 11, fig. 6); no. B59.1, N.Z. Geological Survey, Lower Hutt, New Zealand.

TYPE LOCALITY: "Wairoa Gorge", locality S20/f499, near Nelson, New Zealand.

DESCRIPTION: Twenty of these common seeds from various New Zealand localities average 11.3 mm (8.9-15.4 mm; standard deviation = 0.19) long by 7.99 mm

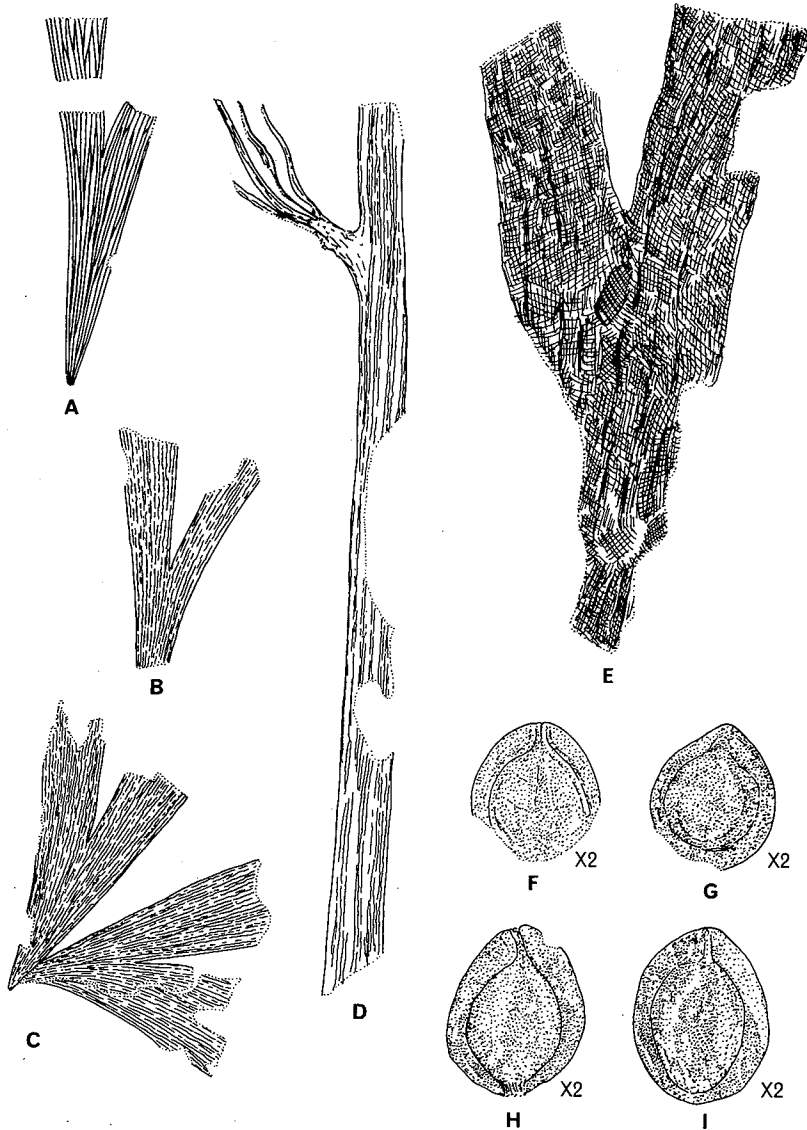


FIG. 9. — Plants of uncertain taxonomic position, A-C, *Ginkgoephytopsis lacerata*; A-B, B1094.1; C, leaf group, B1068.23; D, thick root with bundle of adventitious rootlets, like "*Czekanowskia rigali*", B1091.34; E, forked, coarsely-ribbed, stem, possibly *Rhexoxylon*, B1091.55; F-I, *Carpolithus mackayi*, twice natural size; F, B1092.4; G, B1092.3; H, B1091.65; I, B1091.66. All natural size unless otherwise indicated.

(6.5-11.4 mm; s.d. = 0.13) wide. They are ovate in compressed outline and show a clearly-differentiated integument and nucule. Integument is differentiated into an outer fleshy sarcotesta and an inner coalified sclerotesta. Irregular creases in the sarcotesta may result from compression onto the harder inner layers of the seed, but finer markings may also result from secretory canals or vascular strands within the sarcotesta. Seeds commonly show one or two longitudinal ridges, probably compressed triradiate ribs of the sclerotesta. The presence of an endotesta in the integument could not be established. The integument appears completely separated from the nucule, except at the very base. Nucule averages 9 mm (6.3-13.5 mm; s.d. = 0.11) long by 6.2 mm (4-8.4 mm; s.d. = 0.12) wide, is widest near the base and tapered towards the apex, more distinctly ovate than the outline of the seed as a whole. The nucule is firmly attached to the base of the seed by a thick woody peduncle. Details of the micropyle are unclear, but there is commonly some loose, irregular tissue just inside the micropylar opening, possibly an extension of the nucellus forming a pollen chamber. The micropylar opening through the integument is sometimes collinear with the long axis of the seed, but more often curved to one side. The surface of the nucule may show several fine striations, which suggests the nucellus was vascularized.

REMARKS: The non-committal genus name *Carpolithus* was retained for this species, as it is still poorly understood. Little would be gained by transferring it to *Samaropsis* despite its similarity to several species of that genus. In any case the longitudinal ribbing of this seed may indicate radiospermy, rather than platyspermy generally accepted for *Samaropsis*. (I have corrected Arber's spelling of the species name in accordance with Recommendation 73C of the International Code of Botanical Nomenclature.)

BOTANICAL AFFINITIES: *Carpolithus mackayi* is clearly the seed of a woody gymnosperm. The asymmetric micropylar opening suggests that they were borne laterally or aggregated into infructescences, rather than solitary and erect.

Comparison with other fossil seeds also gives some idea of botanical affinities. Amongst compressions, *Carpolithus mackayi* most resembles several species of *Samaropsis*. Sukhov (1969) describes several such species intimately associated with cordaitalean remains in the Russian Permian. *Samaropsis drupaeformis* differs largely in its wider sarcotesta. *Samaropsis mungatica*, *S. moracia*, and *S. siberiana* all lack ribs like those of *Carpolithus mackayi*. Similar compressed seeds are also widely associated with glossopteridalean remains in Gondwanaland (Walkom 1921; Maithy 1964; Millan 1969). Of these, *Samaropsis barcellosa*, *S. moreiana* and *Nummulospermum bowenense* all have a much thicker sarcotesta in the apical than basal region. Also unlike *Carpolithus mackayi*, *Samaropsis ganjrensis* and *S. goraiensis* have incompletely enclosing outer integuments.

It is difficult to be certain enough of the internal structure of *Carpolithus mackayi* to compare it with better preserved, cutinized and petrified fossil seeds. With these reservations, it seems that *C. mackayi* has an organization broadly similar to seeds of glossopteridaleans (Gould and Delevoryas 1977), medullosaceans (Taylor 1962, 1967), peltaspermaceans, corystospermaceans, caytoniaceans and pentoxylaceans (Sporne 1969; Harris 1954). Cordaitalean seeds are also similar but usually platyspermic (Seward 1917; Taylor and Stewart 1964). Callistophytacean seeds are platyspermic and have distinctive vascular blades in the sarcotesta and a vascular disc at the base of an otherwise unvascularized nucellus (Stidd and Hall 1970). Bennettitalean seeds are distinguished by elaborate micropylar beaks, and in cycadalean, ginkgoalean and many conifer seeds the nucule is largely fused to the integument (Harris 1954).

I further assume that *Carpolithus mackayi* is the seed of *Linguifolium*. This seed has never been found in fossil assemblages without *Linguifolium*. At Tank Gully lo-

cality S72/f570, *Carpolithus mackayi* is associated with only *Linguifolium* spp. and *Sphenopteris* sp. Fertile leaves of this species of *Sphenopteris* have been found at Long Gully, near Otematata, New Zealand (Retallack 1977a), showing that it is a true fern. At Wairoa Gorge locality S20/f499, *Carpolithus mackayi* is associated with *Linguifolium* spp., *Taeniopteris* sp., and *Desmiophyllum elongatum*. This last is probably a primitive conifer with quite distinctive seed cones (Retallack 1977a, 1977b). The particular form of *Taeniopteris* is very rare, poorly known and nowhere else associated with *Carpolithus mackayi*. Of the remaining Middle Triassic fossil plants from New Zealand, *Sphenobaiera robusta* is most likely a karkeniacean (Retallack 1977a, 1977b). The likely fructifications of various pteridosperm fronds and the possible pteridophytic nature of *Ginkgophytopsis* have already been discussed.

If *Carpolithus mackayi* was the seed of *Linguifolium* spp., the seed and leaf combination would suggest the Pentoxylales or Glossopteridales more than any other gymnospermous group with which *C. mackayi* shows similarities. Considering the likely deciduous nature of *Linguifolium* (Retallack 1979), its southern distribution, and the pycnoxylic wood commonly associated with *Linguifolium*-dominated assemblages, then it is more likely that *Carpolithus mackayi* and *Linguifolium* are survivors of the Glossopteridales than ancestral Pentoxylales.

OCCURRENCE: Tank Gully localities S72/f569-570, S72/f573. *Carpolithus mackayi* has also been found in Long Gully and near Benmore Dam (in Torlesse rocks near Otematata) and in Wairoa Gorge (in the Murihiku Supergroup, near Nelson) in New Zealand (N.Z. Geological Survey collections). It may also occur in the Ipswich Coal Measures of southeastern Queensland (Hill *et. al.* 1965).

Logs and smaller axes (Fig. 9E)

Large compressed logs are commonly found in the Bench Sandstone and upper Tank Gully Coal Measures, where *Linguifolium* is also most common. Some of these logs are up to 27 cm wide (the original diameter according to Walton's (1936) compression theory). A heavily limonitized fragment found in the lower Bench Sandstone showed growth rings, like a better-preserved specimen from Long Gully (NZGS BI090.6).

An unusual coalified axis (Fig. 9E) was found in boulders of the gully bed (S72/f569) in a massive mudstone matrix more typical of the lower than upper Tank Gully Coal Measures. This shows a dichotomous branch and several strong longitudinal furrows. These furrows may outline sectors of woody tissue, like those of *Rhexoxylon* trunks described by Brett (1968). Considering the nature of this axis and remains associated with it, it could be the stem of *Dicroidium*. Archangelsky (1968) has argued that *Rhexoxylon* is the trunk of *Dicroidium*.

Carbonized roots (Fig. 9D)

Much of the Tank Gully Coal Measures contains fossil roots, some of them penetrating up to 90 cm of sediment. One distinctive type of fossil root (Fig. 9D) consists of thick axes bearing lateral, possibly spirally-arranged, bundles of adventitious rootlets. Similar remains, referred to "*Czekanowskia rigali*" by Frenguelli (1942a), are common in Triassic rocks of Gondwanaland (Retallack *et al.* 1977).

S72/f569.

Trace fossil

Genus: *Macanopsis* Macsotay 1967

Macanopsis erwhonensis sp. nov. (Figs. 11-12)

HOLOTYPE: Specimen OU 14191, a burrow entrance just below the sandstone-shale interface (Figs. 11D-E, 12B); housed in the Geology Department, Otago University, Dunedin, New Zealand.

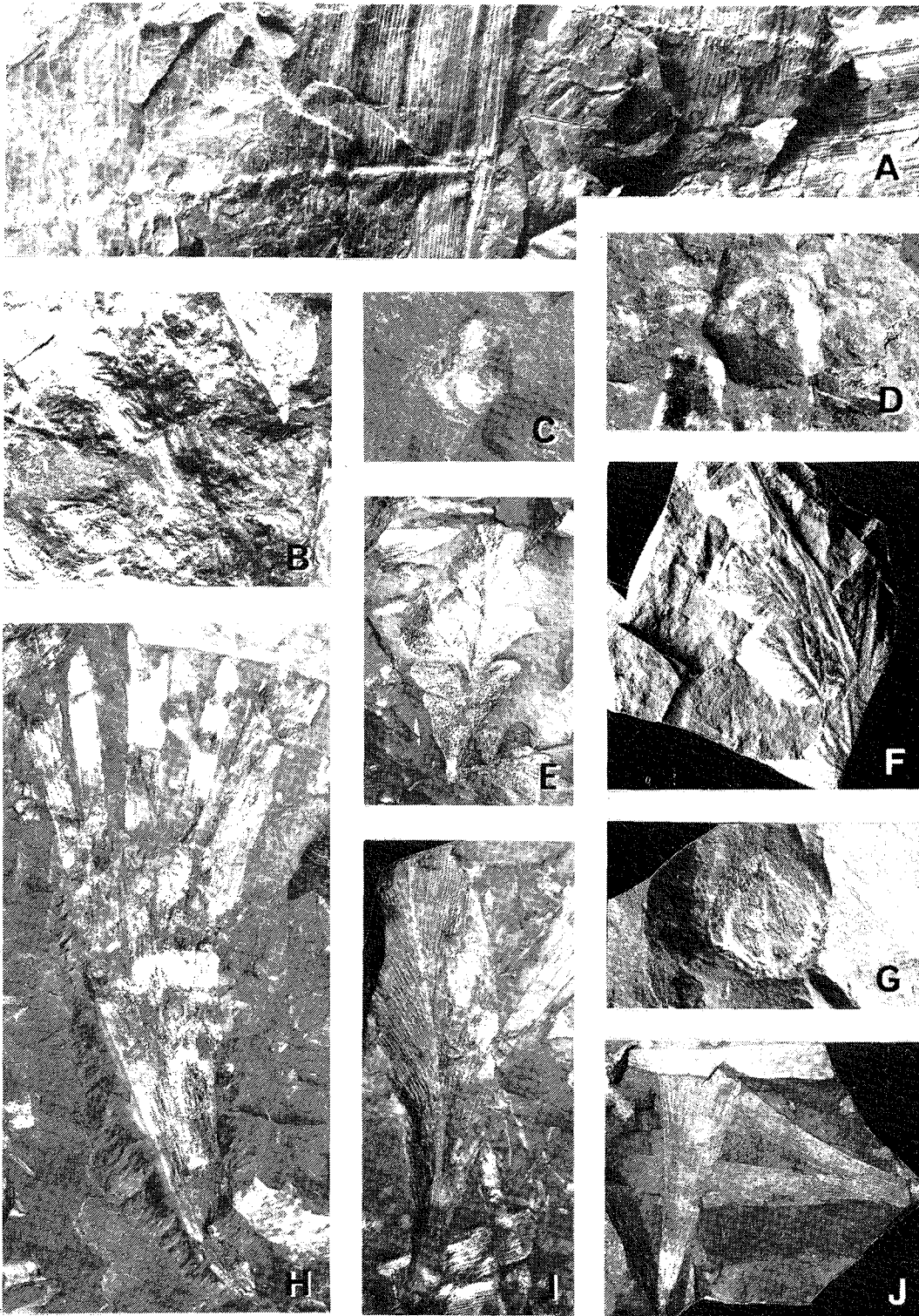


FIG. 10. — Megafossil plants, A, *Neocalamites carrerei* (striated stems) and *Cladophlebis indica* (fern fragments), B1091.21; B, *Pteruchus johnstonii*, twice natural size, B1095.3; C, *Pilophorosperma* sp. cf. *P. costulatum*, twice natural size, B1091.41; D, *Pilophorosperma* sp. A, twice natural size, B1091.36; E, *Dicroidium odontopteroides* var. *moltenense*, B1091.16; F, *Dicroidium odontopteroides* var. *argenteum*, holotype, B1095.1; G, *Carpolithus mackayi*, B1092.4; H, *Sphenobaiera robusta*, B1091.25; I, *Linguifolium steinmannii*, B1091.25; J, *Ginkgophytopsis lacerata*, B1094.1. All natural size unless otherwise indicated.

TYPE LOCALITY: Locality J35/f2, interbedded shale and sandstone at the base of Nowhere Formation, northern bank of central Tank Gully, New Zealand; Mt Potts Group, Kaihikuan Stage.

DERIVATION: The specific name is after Erewhon homestead, near the type locality.

DIAGNOSIS: *Macanopsis* with a short, steeply dipping entrance burrow opening out into a larger, horizontal, ellipsoidal living chamber. Median ridge on floor of entrance burrow separating broad, transverse scratch marks which terminate at a thin longitudinal furrow about half way up the burrow wall. Living chambers also bearing broad scratch marks.

DESCRIPTION: Subvertical entrance burrows are much more common at the type locality than horizontal living chambers. The fossils are exposed in a thin layer of shale adhering to the soles of weather-resistant sandstone layers, so that most of the living chambers have been eroded away. All these trace fossils are epichnia of Martinsson (1970) or domichnial vollformen of Seilacher (1964). They were evidently preserved in the shale by filling from overlying sandstone layers.

The entrance burrows are 8-13 mm wide, more or less tubular and dip steeply across bedding. The holotype measures 8.7 by 6 mm in section. It shows several features suggesting that the animal escaped as sand filled the burrow. The floor of the burrow is marked by a median ridge and transverse scratch marks on either side (Fig. 11E). These scratch marks are 0.5 to 0.8 mm wide and run at a much less oblique angle to the axis of the burrow than cleavage (the deep cracks in Figs 11E, 12B). Another natural oblique section of an entrance burrow (Fig. 11A) shows the median ridge and crude transverse spreiten. The holotype shows a narrow furrow along each side of the entrance burrow which separates the scratched floor from the smoother roof.

The holotype also shows three, oval seams within the sand fill (Fig. 11D). These may mark the junction between sand entering around the body and around flailing appendages of the escaping animal, and later fill of sand.

The entrance burrows curve into the horizontal plane as they pass into the larger living chamber. These are 3-4 cm long by 2-3 cm wide. They are irregular in shape,

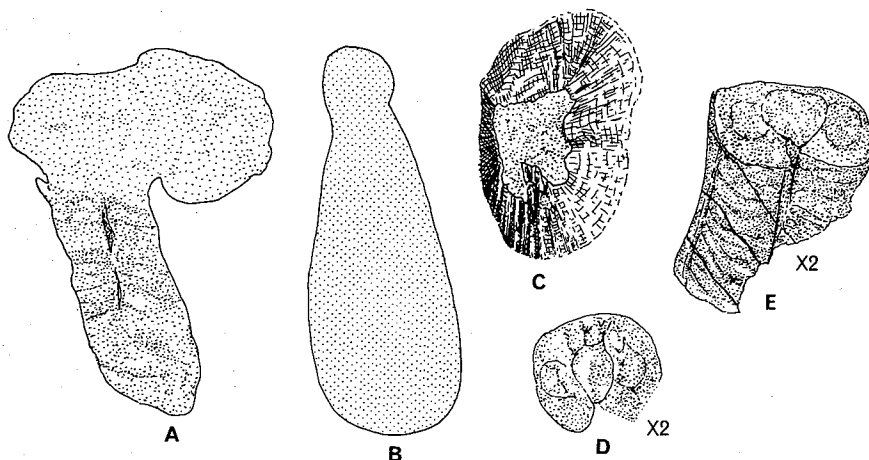


FIG. 11. — The trace fossil *Macanopsis erewhonensis*, A, entrance burrow, with irregular spreiten and portion of the ventral ridge (below) opening into living chamber (above), OU 14187; B, living chamber, from a field sketch; C, lower side of living chamber, showing scratching on the innermost ventral wall, OU 14190; D-E, natural cast of entrance burrow (holotype), in oblique (E) and axial (D) view, twice natural size. All natural size unless otherwise indicated.

generally more or less oval. One of these (Figs 11C, 12C) shows scratching on its innermost ventral wall. These scratches are of a similar width and type to the transverse scratches on the holotype entrance burrow (Figs 11E, 12B).

COMPARISON: *Macanopsis* is most similar to the trace fossil genus *Pholeus*, which has at least two subvertical entrance burrows to the living chamber (Häntzschel 1975). Frey (1970) describes how young crabs (*Ocypode*) form burrows like *Skolithus* when young, *Pholeus* burrows when older and the largest crabs inhabit burrows like *Macanopsis erewhonensis*. The entrance burrow of *Macanopsis pagueyi* Macsotay 1967 is longer and its living chamber shorter and more spherical than that of *M. erewhonensis*.

THE BURROWING ORGANISM: Several assumptions can be made about the likely organism inhabiting these burrows. It was most likely of comparable size to the living chamber with all its appendages on a comfortable position. Judging from the markings on the entrance burrow, it could barely squeeze out. The internal seams in the sand fill and the median ridge of the holotype entrance burrow indicate that the creature was bilaterally symmetrical with two rows of ventro-lateral appendages. These were evidently separated from the smoother dorsal surface of the animal by some sort of narrow flange or spine which incised a groove along each side of the burrow. The scratch marks on the entrance burrow and the innermost ventral wall of the living chamber are relatively broad, suggesting that at least the posterior appendages of the animal were rounded swimmerets, rather than clawed, spiny or hairy appendages. Finally, these creatures evidently lived in a brackish marine environment. Their burrows are associated with marine shell fragments, underlie beach sandstone of the Nowhere Formation and overlie lagoonal, allochthonous coal of the Tank Gully Coal Measures.

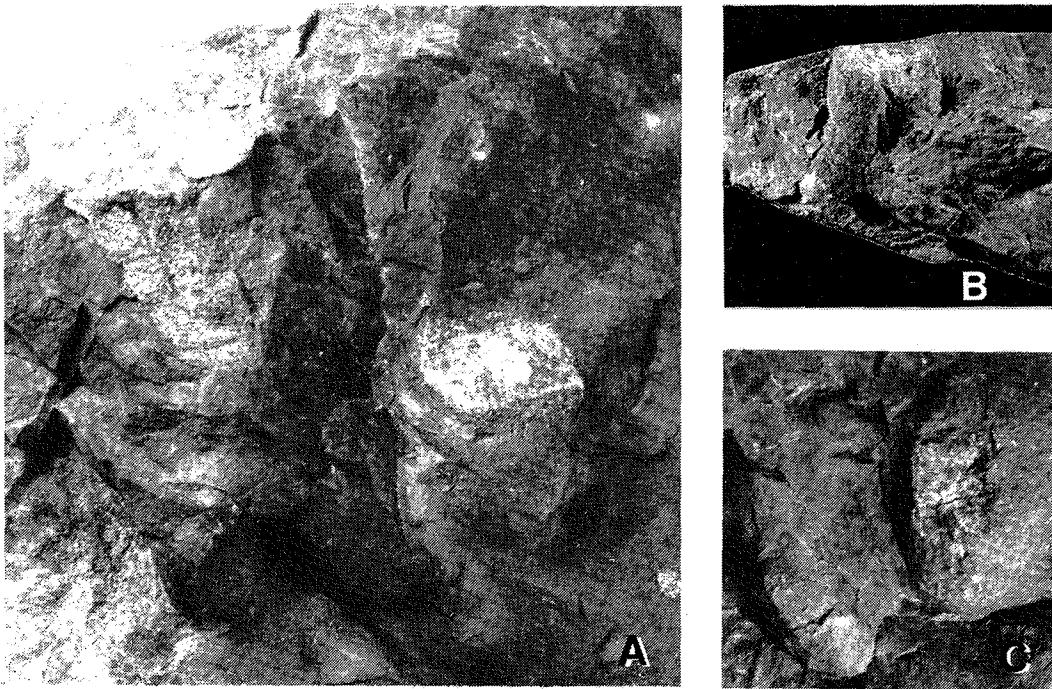


FIG. 12. — The trace fossil *Macanopsis erewhonensis*, A, two living chambers, one (to left) with an entrance burrow, OU 14187; B, oblique view of natural cast of entrance burrow, holotype; C, entrance burrow (to left) and living chamber (to right), OU 14190.

Taking this into account, *Macanopsis erewhonensis* was most likely excavated by crustaceans, such as swimming prawns (*Natantia s. l.* of Glaessner 1969) or mantis shrimps (Stomatopoda of Holthius and Manning 1969). According to Dakin (1966, p. 175-176), swimming prawns migrate into estuaries to breed and are commonly found half-buried in the bottom sediments. Some are permanent estuarine burrowers. Stomatopoda also form permanent burrows below tide mark (Dakin 1966, p. 200-201). The oldest stomatopods known are the Late Jurassic Sculcidae, which have spiny exopods. Squillid stomatopods, with rounded swimmerets, do not appear until the Cretaceous (Holthius and Manning 1969). *Macanopsis erewhonensis* was more likely excavated by a prawn, such as the Permian to Cretaceous cosmopolitan genus *Antrimpos* (figured by Glaessner 1969). This is the creature depicted in my reconstruction (Retallack 1979, fig. 6).

OCCURRENCE: *Macanopsis erewhonensis* has only been found at the type locality. As Frey (1970) has observed similar modern burrows, this and similar trace fossils may prove to be widespread in both time and space.

ACKNOWLEDGMENTS

I thank Drs D. C. Mildenhall and W. A. Watters (Geological Survey, New Zealand), R. E. Gould (Geology Department, University of New England) and D. L. Dilcher and Mr S. R. Manchester (Biology Department, Indiana University) for helpful discussions and editorial assistance, and Dr D. C. Mildenhall and Sir Charles Fleming (Geological Survey, New Zealand) for curating and shipping my fossil collections and for access to files and other fossil collections in the Geological Survey of New Zealand. The project was funded by a Commonwealth Postgraduate Award tenable at the University of New England, Armidale, New South Wales, Australia.

REFERENCES

- ANDERSON, H. M. 1974. A brief review of the flora of the Molteno "Formation" (Triassic), South Africa. *Palaeontographica Africana* 17: 1-10.
- ANDERSON, H. M., and ANDERSON, J. M. 1970. A preliminary review of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. *Palaeontographica Africana, Supplement 13*.
- ARBER, E. A. N. 1912. On *Psygmoxyllum majus* sp. nov. from the Lower Carboniferous rocks of Newfoundland, together with a revision of the genus and remarks on its affinities. *Transactions of the Linnean Society of London* 7: 391-407.
- 1913. A preliminary note on the fossil plants of the Mt Potts Beds, New Zealand, collected by Mr. D. G. Lillie, biologist to Captain Scott's Antarctic Expedition in the "Terra Nova". *Proceedings of the Royal Society of London* B86: 344-347.
- 1917. Earlier Mesozoic floras of New Zealand. *N.Z. Geological Survey Palaeontological Bulletin* 6.
- ARCHANGELSKY, S. 1960. "*Chiropteris harrisi*" nueva especie de la Serie La Golondrina, Provincia de Santa Cruz. *Acta Geologica Lilloana* 3: 289-293.
- 1965. Tafofloras paleozoicas y eomesozoicas de Argentina. Analisis de sus componentes y vinculaciones con otras tafofloras coetáneas extra-argentinas. *Boletin Sociedad Argentino Botanico* 10: 247-291.
- 1968. Studies on Triassic fossil plants from Argentina. IV. The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems. *Palaeontology* 11: 500-512.
- AZCARATE, V., and FASOLA, A. 1970. Sobre formas nuevas para la flora triasica de Los Molles. *Boletin del Museo Nacional de Historia Natural de Chile* 29: 249-269.
- BECK, C. B. 1967. *Eddyia sullivanensis*, gen. et sp. nov., a plant of gymnospermic morphology from the Devonian of New York. *Palaeontographica* B121: 1-22.
- BELL, S.; HARRINGTON, H. J.; MCKELLAR, I. C. 1956. Lower Mesozoic plant fossils from Black Jacks, Waitaki River, South Canterbury. *Transactions of the Royal Society of N.Z.* 83: 663-678.
- BERRY, E. W. 1903. The American species referred to *Thinnfeldia*. *Bulletin of the Torrey Botanical Club* 30: 438-445.
- 1945. The genus *Linguifolium* of Arber. *Johns Hopkins University, Studies in Geology* 14: 187-190.
- BLASCHKE, P. M., and GRANT-MACKIE, J. A. 1976. Mesozoic leaf genus *Taeniopteris* at Port Waikato and Clent Hills, New Zealand. *N.Z. Journal of Geology and Geophysics* 19: 933-941.
- BOSE, M. N., and SHAH, S. C. D. 1968. Some pteridophytic remains from the Rajmahal Hills, Bihar. *Palaeobotanist* 16: 12-28.
- BOUREAU, E. 1964. *Traité de paléobotanique. III. Sphenophyta, Noeggerathiophyta*. Masson: Paris.
- BOUREAU, E., and DOUBINGER, J. 1975. *Traité de paléobotanique. IV(2). Pteridophylla (prem. part.)*. Masson: Paris.

- BRETT, D. W. 1968. Studies on Triassic plants from Argentina. III. The trunk of *Rhexoxylon*. *Palaeontology* 11: 236-245.
- CARRUTHERS, W. 1872. Notes on fossil plants from Queensland, Australia. *Quarterly Journal of the Geological Society of London* 28: 350-359.
- CHANDRA, S. 1974. *Glossopteris* and allied genera — morphological studies, in Surange, K. R.; Lakhanpal, R. N.; and Bharadwaj, D. C. (Eds). *Aspects and Appraisal of Indian Palaeobotany*. Birbal Sahni Institute of Paleobotany, Lucknow, 126-143.
- CHAPMAN, F., and COOKSON, I. C. 1926. A revision of the Sweet Collection of Triassic plant remains from Leigh Creek, South Australia. *Transactions of the Royal Society of South Australia* 50: 163-178.
- DAKIN, W. J. 1966. *Australian Seashores*. Angus and Robertson: Sydney.
- DAWSON, J. W. 1882. *The fossil plants of the Erian (Devonian) and Upper Silurian formations of Canada. Part 2*. Geological Survey of Canada, Montreal.
- DE CABRERA, J. D. 1971. Estudio de algunos ejemplares del genero *Neocalamites* en el Triasico de la Republica Argentina. *Acta Geologica Lilloana* 11: 111-124.
- DUN, W. S. 1898. Notes on the Australian Taeniopteridae. *Report of the 7th Meeting of the Australasian Association for the Advancement of Science Sydney*: 384-400.
- 1911. Notes on some fossil plants from the roof of the coal seam in the Sydney Harbour Colliery. *Journal and Proceedings of the Royal Society of New South Wales* 44: 615-619.
- DU TOIT, A. L. 1927. The fossil flora of the upper Karroo Beds. *Annals of the South African Museum* 22: 289-420.
- ETHERIDGE, R. 1894. Palaeontologia Novae Cambriae Meridionalis, Descriptions of New South Wales fossils, no. 1. *Records of the Geological Survey of New South Wales* 4: 32-38.
- 1899. On a fern (*Blechnoxylon talbragarensis*), with secondary wood, forming a new genus from the coal measures of the Talbragar district. *Records of the Australian Museum* 3: 125-147.
- FEISTMANTEL, O. 1889. Die Karroo-Formation und die dieselbe unterlagernden Schichten. *Böhmische Gesellschaft der Wissenschaften in Prague Abhandlung, Mathematische-Naturwissenschaftlichen Klasse* 3(6): 89p.
- 1890a. *Uhlonosné útvary v Tasmanii*. Královské České Společnosti Náuk, Prague.
- 1890b. Geological and palaeontological relations of the coal and plant-bearing beds of Palaeozoic and Mesozoic age in eastern Australia. *Memoir of the Geological Survey of New South Wales Palaeontology* 3.
- FLINT, J. C. E., and GOULD, R. E. 1975. A note on the fossil megaflores of the Nymboida and Red Cliff Coal Measures, southern Clarence-Moreton Basin. *Journal and Proceedings of the Royal Society of New South Wales* 108: 70-74.
- FLORIN, R. 1936. Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Eroterungen über vermeintlichen Cordaitales mesozoischen Alters. *Palaeontographica* B81: 173p.
- FRENGUELLI, J. 1937. La florula jurásica de Paso Flores en el Neuquen, con referencias a la de Piedra Pintada y otras floras jurásicas argentinas. *Revista del Museo de La Plata 1 Paleontologia* 1: 67-108.
- 1941. *Sagenopteris* y *Linguifolium*. *Notas del Museo de La Plata 6 Paleontologia* 34: 405-437.
- 1942a. Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina. III. *Czekanowskia rigali* n. sp. *Notas del Museo de La Plata 7 Paleontologia* 44: 287-291.
- 1942b. Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina. IV. *Pelourdea polyphylla* n. sp. *Notas del Museo de La Plata 7 Paleontologia* 45: 293-295.
- 1942c. Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina. V. *Baiera cuyana* n. sp. *Notas del Museo de La Plata 7 Paleontologia* 46: 297-303.
- 1942d. Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina. X. *Chiropteris barrealensis* n. sp. *Notas del Museo de La Plata 7 Paleontologia* 51: 341-353.
- 1943. Reseña crítica de los géneros atribuidos a la "Serie de *Thinnfeldia*". *Revista del Museo de La Plata 2 Paleontologia* 12: 225-336.
- 1944a. Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina. XXI. *Neocalamites ramaccionii* n. sp. *Notas del Museo de La Plata 9 Paleontologia* 70: 479-485.
- 1944b. Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina. XXII. *Neocalamites ischigualastii* n. sp. *Notas del Museo de La Plata 9 Paleontologia* 71: 487-492.
- 1946. Contribuciones al conocimiento de la flora del Gondwana Superior en la Argentina. XXXIII. "Ginkgoales" de los Estratos de Potrerillos en la Precordillera de Mendoza. *Notas del Museo de La Plata 11 Paleontologia* 87: 100-127.
- 1947. El genero *Cladophlebis* y sus representantes en la Argentina. *Anales del Museo de La Plata B2(2)*.
- 1948. Estratigrafía y edad del llamado Retico en la Argentina. *Gaea, Buenos Aires* 8: 159-309.
- FREY, R. W. 1970. Environmental significance of recent marine lebensspuren near Beaufort, North Carolina. *Journal of Paleontology* 44: 507-517.
- GEINITZ, H. B. 1876. Über rhätische Pflanzen und Tierreste in den argentinischen Provinzen La Rioja, San Juan und Mendoza. *Palaeontographica Supplement* 3.
- GLAESSNER, M. F. 1969. Decapoda. In Moore, R. C. (Ed). *Treatise on Invertebrate Paleontology. Arthropoda* 4(2). Geological Society of America and University of Kansas, Boulder and Lawrence, R399-R533.
- GOTHAN, W. 1912. Über die Gattung *Thinnfeldia* Ettingshausen. *Abhandlung der Naturhistorische Gesellschaft zu Nürnberg* 19: 67-80.

- GOULD, R. E. 1967. The geology of the Slack's Creek area, southeast Queensland. *Papers of the Department of Geology, University of Queensland* 6(5): 115-144.
- 1976. The succession of Australian pre-Tertiary megafossil floras. *Botanical Reviews* 41: 453-483.
- GOULD, R. E., and DELEVORYAS, T. 1977. The biology of *Glossopteris*: evidence from petrified seed- and pollen-bearing organs. *Alcheringa* 1: 387-399.
- HALLE, T. G. 1908. Zur Kenntnis der mesozoischen Equisetales Schwedens. *Kungliga Svenska Vetenskaps Akademiens Handlingar* 43.
- 1913. The Mesozoic flora of Graham Land. *Wissenschaftliche Ergebnisse der Schwedische Südpolar Expedition, 1901-1903* 3(14): 123p.
- HÄNTZSCHEL, W. 1975. *Treatise on Invertebrate Paleontology. Part W. Miscellaneous. Supplement 1. Trace Fossils and Problematica*. Geological Society of America and University of Kansas: Boulder and Lawrence, 269 p.
- HARLAND, W. B.; HOLLAND, C. H.; HOUSE, M. R.; HUGHES, N. F.; REYNOLDS, A. B.; RUDWICK, M. J. S.; SATTERTHWAITHE, G. E.; TARLO, L. B. H.; WILLEY, E. C. 1967. *The Fossil Record: A Symposium with Documentation*. Geological Society of London: London.
- HARRIS, T. M. 1931. The fossil flora of Scoresby Sound, East Greenland. Part 1. Cryptogams (exclusive of Lycopodiales). *Meddelelser om Grønland* 85(2): 104 p.
- 1932. The fossil flora of Scoresby Sound, East Greenland. Part 2. Descriptions of seed plants *incertae sedis*, together with a discussion of certain cycadophyte cuticles. *Meddelelser om Grønland* 85(3): 112 p.
- 1935. The fossil flora of Scoresby Sound, East Greenland. Part 4. Ginkgoales, Coniferales, Lycopodiales and isolated fructifications. *Meddelelser om Grønland* 112(1): 176 p.
- 1946. Liassic and Rhaetic plants from East Greenland. *Meddelelser om Grønland* 114(9): 38 p.
- 1954. Mesozoic seed cuticles. *Svensk Botanisk Tidskrift* 48: 281-291.
- 1961. *The Yorkshire Jurassic Flora, I. Thallophtya-Pteridophyta*. British Museum (Natural History), London.
- HERBST, R. 1966. Revisión de la flora liásica de Piedra Pintada, provincia de Neuquen, Argentina. *Revista del Museo de La Plata Paleontología* 5: 27-53.
- 1971. Revision de las especies argentinas del genero *Cladophlebis*. *Ameghiniana* 8: 265-281.
- HILL, D. 1930. The stratigraphical relationship of the shales about Esk to the sediments of the Ipswich Basin. *Proceedings of the Royal Society of Queensland* 41: 162-191.
- HILL, D.; PLAYFORD, G.; WOODS, J. T. 1965. *Triassic Fossils of Queensland*. Queensland Palaeontographical Society, Brisbane.
- HØEG, O. A. 1942. The Downtonian and Devonian flora of Spitsbergen, *Skrifter Norges Svalbard- og Ishavsundersøkelser* 83: 228p.
- 1967. Ordre *incertae sedis* des Palaeophyllales. In Boureau, E. (Ed.), *Traité de Paléobotanique. II. Bryophyta, Psilophyta, Lycophyta*. Masson, Paris, 362-399.
- HOLTHIUS, L. B., and MANNING, R. B. 1969. Stomatopoda, In Moore, R. C. (Ed.), *Treatise on Invertebrate Paleontology. Arthropoda* 4(2). Geological Society of America and University of Kansas, Boulder and Lawrence, R353-552.
- HOUSTON, B. R. 1967. Geology of the city of Brisbane. Part II. The post-Palaeozoic sediments and volcanics. *Publications of the Geological Survey of Queensland* 324: 7-86.
- JACK, R., and ETHERIDGE, R. 1892. The geology and palaeontology of Queensland and New Guinea. *Publications of the Geological Survey of Queensland* 92: 768p.
- JACOB, K., and JACOB, C. 1950. A preliminary account of the structure of the cuticles of *Dicroidium* (*Thinnfeldia*) fronds from the Mesozoic of Australia, *Proceedings of the National Institute of Sciences India* 16: 101-126.
- JAIN, R. K., and DELEVORYAS, T. 1967. A middle Triassic flora from the Cacheuta Formation, Minas de Petroleo, Argentina. *Palaentology* 10: 564-589.
- JOHNSTON, R. M. 1887. Fresh contribution to our knowledge of the plants of Mesozoic age in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania for 1886*: 160-179.
- 1888. *The Geology of Tasmania*. Government Printer: Hobart.
- 1896. Further contributions to the history of the fossil flora of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania for 1895*: 57-63.
- JONES, O. A., and DE JERSEY, N. J. 1947. The flora of the Ipswich Coal Measures — morphology and floral succession. *Papers of the Department of Geology, University of Queensland* 3(3).
- KAWASAKI, S. 1925. Some older Mesozoic plants in Korea. *Bulletin of the Geological Survey of Chosen* 4(1).
- KIMURA, T. 1976. Mesozoic plants from the Yatsushino Formation (Albian), Kumamoto Prefecture, Kyushu, southwest Japan. *Bulletin of the National Science Museum, Tokyo* C2(4): 179-208.
- KON'NO, E. 1939. A new *Chiropteris* and other fossil plants from the Heian System, Korea. *Japanese Journal of Geology and Geography* 16: 105-114.
- 1962. Some species of *Neocalamites* and *Equisetites* in Japan and Korea. *Science Report Tohoku University* 5: 21-47.
- 1973. New species of *Pleuromeia* and *Neocalamites* from the upper Scythian bed in the Kitakami Massif, Japan. *Science Report Tohoku University* 43: 99-115.
- KRASSILOV, V. A. 1970. Approach to the classification of Mesozoic "ginkgoalean" plants from Siberia. *Palaebotanist* 18: 12-19.

- KRAUSEL, R. 1943. Die Ginkgophyten der Trias von Lunz in Nieder-Osterreich und von Neue Welt bei Basel. *Palaeontographica* B87: 59-93.
- LELE, K. M. 1961. Studies in the Indian Middle Gondwana flora. 2. Plant fossils from the South Rewa Gondwana Basin. *Palaeobotanist* 10: 69-83.
- LE ROUX, S. F. 1970. Some fossil ginkgophytes and a possible voynovskya element from the *Glossopteris* flora of Vereeniging, Transvaal. *Palaeontographica Africana* 13: 1-13.
- LUNDBLAD, A. B. 1959. Studies in the Rhaeto-Liassic floras of Sweden. II(1). Ginkgophyta from the mining district of NW Scania. *Kungliga Svenska Vetenskaps Akademiens Handlingar* 6(2).
- MACSOTAY, O. 1967. Huellas problematicas y su valor paleoecologico en Venezuela. *Geos* 16: 7-79.
- MAITHY, P. K. 1964. Studies in the *Glossopteris* flora of India. 18. Gymnospermic seeds and seed-bearing organs from the Karharbari Beds of Giridh Coalfield, Bihar. *Palaeobotanist* 13: 45-56.
- 1974. Studies in the *Glossopteris* flora of India. 41. *Gondwanophyton* gen. nov., with a revision of allied plant fossils from the Lower Gondwana of India. *Palaeobotanist* 21: 298-304.
- MARTINSSON, A. 1970. Toponomy of trace fossils. In Crimes, T. P. and Harper, J. L. (Eds.), Trace fossils. *Special Issue Journal of Geology* 3: 323-330.
- MCQUEEN, D. R. 1954. Upper Palaeozoic plant fossils from the South Island, New Zealand. *Transactions of the Royal Society of New Zealand* 82: 231-236.
- 1956. Leaves of Middle and Upper Cretaceous pteridophytes and cycads from New Zealand. *Transactions of the Royal Society of New Zealand* 83: 673-685.
- MEDWELL, L. M. 1954a. A review and revision of the flora of the Victorian Lower Jurassic. *Proceedings of the Royal Society of Victoria* 65: 63-111.
- 1954b. Fossil plants from Killara near Casterton, Victoria. *Proceedings of the Royal Society of Victoria* 66: 16-23.
- MENENDEZ, C. A. 1951. La flora mesozoica de la Formacion Llantenes (Provincia Mendoza). *Revista del Museo Argentino de Ciencias Naturales "Bernadino Rivadavia"*, *Institucion Nacional de Investigaciones de Ciencias Naturales, Ciencias Botanicas* 2: 147-261.
- MEYEN, S. V. 1969a. New data on relationship between Angara and Gondwana late Palaeozoic floras. *Gondwana Stratigraphy, Proceedings of the 1st IUGS Gondwana Symposium, Buenos Aires*. UNESCO, Paris, 139-157.
- 1969b. O rode *Zamipteris* Schmalhausen i ego sootnoshenii s nekotorymi smezyimi ordam (On the genus *Zamipteris* Schmalhausen and its relation to similar genera). *Trudy Instituta Geologicheskikh Nauk, Moskva* 190: 59-84.
- MILLAN, J. H. 1969. The gymnospermic and platyspermic seeds of the *Glossopteris* flora of Brazil and correlated foreign regions. *Gondwana Stratigraphy, Proceedings of the 1st IUGS Gondwana Symposium, Buenos Aires*, UNESCO, Paris, 107-120.
- OISHI, S. 1940. The Mesozoic floras of Japan. *Journal of the Faculty of Science Hokkaido University 4th series, Geology and Mineralogy* 5 (2-3): 1-480.
- OISHI, S., and HUZIOKA, K. 1938. Fossil plants from Nariwa. A supplement. *Journal of the Faculty of Science, Hokkaido University, 4th Series, Geology and Mineralogy* 4: 69-101.
- OISHI, S., and YAMASITA, K. 1936. On the fossil Dipteridaceae. *Journal of the Faculty of Science, Hokkaido University, 4th Series, Geology and Mineralogy* 3: 135-184.
- OLDHAM, T., and MORRIS, J. 1862. The fossil flora of the Rajmahal Series, Rajmahal Hills, Bengal. *Memoir of the Geological Survey of India, Palaeontologia Indica* 1.
- PRYNADA, V. C. 1962. *Mezozoiskaya flora vostochnoi sibirii i zabaikalaya (Mesozoic floras of eastern Siberia and Zabaikal)*. Irkutskoe Geologicheskikh Upravlenie, Moskva.
- RASSKAZOVA, E. S., and LEBEDEV, Y. L. 1968. Novy rod Mezozyskikh paparotnikov *Lobifolia* (A new genus of Mesozoic ferns *Lobifolia*). *Trudy Akademii Nauk SSR, Geologicheskikh Instituta* 191: 56-69.
- RETALLACK, G. J. 1973. Stratigraphy, Palaeobotany and Environmental Analysis of an Area Around Pittwater, N.S.W. Unpublished BSc Honours thesis, University of New England, Armidale, New South Wales.
- 1975. The life and times of a Triassic lycopod. *Alcheringa* 1: 3-29.
- 1977a. A Biostratigraphy for Terrestrial Triassic Rocks of Gondwanaland. Unpublished Ph.D. thesis, University of New England, Armidale, New South Wales.
- 1977b. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa* 1: 247-277.
- 1979. Middle Triassic coastal outwash plain deposits in Tank Gully. Canterbury, New Zealand. *Journal of the Royal Society of N.Z.* 9: 397-414.
- RETALLACK, G. J.; GOULD, R. E.; RUNNEGAR, B. 1977. Isotopic dating of a Middle Triassic megafossil flora from near Nymboida, northeastern New South Wales. *Proceedings of the Linnean Society of New South Wales* 101: 77-113.
- RÜHLE VON LILIENSTERN, H. 1931. Über *Chiropteris*. *Paläontologische Zeitschrift* 13: 253-277.
- 1932. Nachtrag zu meiner Arbeit über *Chiropteris* Kurr. *Paläontologische Zeitschrift* 14: 229-232.
- SAHNI, B. 1928. Revision of Indian fossil plants. Part 1, Coniferales, (a) Impressions and encrustations. *Memoir of the Geological Survey of India, Palaeontologia Indica* 11: 1-49.
- SAHNI, B., and RAO, A. R. 1933. On some Jurassic plants from the Rajmahal Hills. *Journal of the Asiatic Society of Bengal* 27: 183-208.
- SALFELD, H. 1909. Beiträge zur Kenntniss jurassischer Pflanzenreste aus Norddeutschland. *Palaeontographica* 56: 1-34.

- SAMYLYNA, V. A. 1970. Ginkgos and czezanowskias. *Paleontological Journal* 4: 397-405.
- SAPORTA, G. 1873. *Plantes jurassiques. I. Algues, Equisétacées, Characées, Fougères*. Masson, Paris.
- 1875. Sur la découverte de deux types nouveaux de Conifères dans les schistes Permien de Lodève (Hérault). *Comptes Rendus, Académie des Sciences, Paris* 80: 1017-1022.
- SCHENK, A. 1867. *Die fossile Flora der Grenzschichten der Keuper und Lias Frankens*. Kreidel: Wiesbaden.
- SEILACHER, A. 1964. Sedimentological classification and nomenclature of trace fossils. *Sedimentology* 3: 253-256.
- SEWARD, A. C. 1900. *The Jurassic Flora. I. Catalogue of the Mesozoic Plants in the Department of Geology, British Museum*. British Museum (Natural History): London.
- 1903. Fossil flora of Cape Colony. *Annals of the South African Museum* 4: 1-122.
- 1904. On a collection of fossil plants from Victoria. *Records of the Geological Survey of Victoria* 1: 155-187.
- 1910. *Fossil Plants. II. Sphenophyllales (cont.), Psilotales, Lycopodiales, Filicales, Pteridosperms (incertae sedis)*. Cambridge University Press, Cambridge.
- 1917. *Fossil plants. III. Pteridosperms, Cycadofilicales, Cordaitales, Cycadophytes*. Cambridge University Press: Cambridge.
- 1919. *Fossil plants. IV. Ginkgoales, conifer-like incertae sedis, Coniferales, Gnetales*. Cambridge University Press: Cambridge.
- 1933. On some fossils from the Parsora Stage, Rewa. *Records of the Geological Survey of India* 66: 235-243.
- SEWARD, A. C., and HOLTUM, R. E. 1922. Jurassic plants from Ceylon. *Quarterly Journal of the Geological Society of London* 78: 271-277.
- SHARMA, B. D. 1971. Further studies on fossil pteridophytic fronds collected from the Middle Jurassic rocks of Dhokuti in the Rajmahal Hills, India. *Palaeontographica* B133: 61-71.
- SHIRLEY, J. 1898. Additions to the fossil flora of Queensland. *Bulletin of the Geological Survey of Queensland* 7: 9-25.
- SIXTEL, T. A.; SAVISAKAYA, L. N.; KHUBAIBERDYEV, R. Kh.; LOSEVA, N. M.; BURAKOVA, A. T.; IMINOV, Y. A. Kh. 1971. Yurskoi rastenya iz opornykh razrezov kulitanga i shuraba (Early Jurassic plants from Kulitanga and Shuraba). In Shaykuboe, T. Sh.; Subsmely, T. A.; Krymdolyts, G. Ya.; Kum, A. N.; Repman, E. A. (Eds.), *Paleontologicheskoe obosnovanie opornykh razrezov yurskoi systemi uzbekistana i sopredelynyx raionov* (Paleontological evidence bearing on the basal section of the Jurassic System of Uzbekistan and adjacent districts). *Sbornik Ministerstvo Geologicheskikh Uzbekistan S.S.R., Tashkent* 10: 164-206.
- SOLMS-LAUBACH, H. G. 1899. Das Auftreten und die Flora der rhätischen Kohlschichten von La Ternera (Chile). 2. Beschreibung der Pflanzenreste von La Ternera. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Beilage Band* 12: 593-608.
- 1904. Die Strukturbietenden Pflanzengesteine von Franz Josefs Land. *Kungliga Svenska Vetenskaps Akademien Handlingar* 37(7).
- SPEDEN, I. G. 1958. A note on the age of the Jurassic flora of Owaka Creek, southeast Otago. *N.Z. Journal of Geology and Geophysics* 1: 530-532.
- SPORNE, K. R. 1969. *The Morphology of Gymnosperms*. Hutchinson: London.
- STACE, C. A. 1965. Cuticular studies as an aid to plant taxonomy. *Bulletin of the British Museum of Natural History, Botany* 4(1).
- STEINMANN, G. 1899. Das Auftreten und die Flora der rhätischen Kohlschichten von La Ternera (Chile). 1. Das Auftreten der Kohlschichten von La Ternera in der Cordillere von Copaipó. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Beilage Band* 12: 581-592.
- 1920. Rhätische Floran und Landverbindungen auf der Südhalbkugel. *Geologische Rundschau* 11: 350-354.
- STIDD, B. M., and HALL, J. W. 1970. The natural affinity of the Carboniferous seed *Callospermion*. *American Journal of Botany* 57: 827-836.
- STIPANICIC, P. N. 1957. El sistema Triásico en la Argentina. *Proceedings of the 21st International Geological Congress, Mexico, Section 2*: 73-112.
- 1969. Las sucesiones triásicas argentinas. *Gondwana Stratigraphy, Proceedings of the 1st IUGS Gondwana Symposium, Buenos Aires, UNESCO, Paris*, 1121-1149.
- STIPANICIC, P. N., and BONETTI, M. I. R. 1969. Consideraciones sobre la cronología de los terrenos triásicos argentinas. *Gondwana Stratigraphy, Proceedings of the 1st IUGS Gondwana Symposium, Buenos Aires, UNESCO, Paris*, 1081-1119.
- STONE, J. L. 1973. Problems with the name "Platyphyllum". *Taxon* 22: 105-108.
- SUKH-DEV 1972. Ferns from the Cretaceous of Madhya Pradesh. 3. Dipteridaceae — *Hausmannia pachyderma* n. sp. *Palaeobotanist* 19: 281-291.
- 1974. Mesozoic pteridophytes. In Surange, K. R.; Lakhanpal, R. N.; Bharadwaj, D. C. (Eds.), *Aspects and Appraisal of Indian Palaeobotany*. Birbal Sahni Institute of Paleobotany: Lucknow. Pp. 73-76.
- SUKHOV, S. V. 1969. Semena pozdnepaleozoiskikh rastenii srednei sibiri (Seeds of the late Paleozoic plants of central Siberia). *Trudy Instituta Geologicheskikh Geofizi Sibirskoe Otdelenie* 64.
- TAYLOR, T. N. 1962. Additional observations on *Stephanospermum ovoides*, a Middle Pennsylvanian seed. *American Journal of Botany* 49: 794-800.

- 1967. Palaeozoic seed studies: on the structure of *Conostoma leptospermum* n. sp. and *Albertlongia incostata* n. gen. et sp. *Palaeontographica* B121: 23-29.
- TAYLOR, T. N., and STEWART, W. N. 1964. The Palaeozoic seed *Mitrospermum* in American coal balls. *Palaeontographica* B115: 51-58.
- TENISON-WOODS, J. 1883. On the fossil flora of the coal deposits of Australia. *Proceedings of the Linnean Society of New South Wales* 8: 37-100.
- THOMAS, H. H. 1933. On some pteridospermous plants from the Mesozoic rocks of South Africa. *Philosophical Transactions of the Royal Society of London* B222: 193-265.
- TOWNROW, J. A. 1955. On some species of *Phyllothea*. *Journal and Proceedings of the Royal Society of New South Wales* 89: 39-63.
- 1957. On *Dicroidium*, probably a pteridospermous leaf, and other leaves now removed from this genus. *Transactions of the Geological Society of South Africa* 60: 21-60.
- 1962a. On *Pteruchus*, the microsporophyll of the *Corystospermaceae*. *Bulletin of the British Museum of Natural History, Geology* 6: 285-316.
- 1962b. On the nomenclature of *Pteruchus johnstoni* (Feistmantel) com. nov. *Papers and Proceedings of the Royal Society of Tasmania* 96: 91-93.
- 1967. On *Rissikia* and *Mataia*, podocarpaceous conifers from the Lower Mesozoic of southern lands. *Papers and Proceedings of the Royal Society of Tasmania* 101: 103-136.
- TRALAU, H. 1968. Evolutionary trends in the genus *Ginkgo*. *Lethaia* 1: 63-101.
- WALKOM, A. B. 1917a. Mesozoic floras of Queensland. Part 1 (cont.). The flora of the Ipswich and Walloon Series (c) Filicales, etc. *Publications of the Geological Survey of Queensland* 257.
- 1917b. Mesozoic floras of Queensland. Part 1 (concluded). The flora of the Ipswich and Walloon Series, (d) Ginkgoales, (e) Cycadophyta, (f) Coniferales. *Publications of the Geological Survey of Queensland* 259.
- 1919. Mesozoic floras of Queensland. Parts 3 and 4. The floras of the Burrum and Styx River Series. *Publications of the Geological Survey of Queensland* 263.
- 1921. *Nummulospermum bowenense* gen. et sp. nov. *Quarterly Journal of the Geological Society of London* 77: 289-295.
- 1924. On fossil plants from Bellevue near Esk. *Memoir of the Queensland Museum* 8: 77-92.
- 1925a. Notes on some Tasmanian Mesozoic plants. Part 1. *Papers and Proceedings of the Royal Society of Tasmania for 1924*: 73-89.
- 1925b. Notes on some Tasmanian Mesozoic plants. Part II. *Papers and Proceedings of the Royal Society of Tasmania for 1925*: 63-74.
- 1925c. Fossil plants from the Narrabeen Stage of the Hawkesbury Series. *Proceedings of the Linnean Society of New South Wales* 50: 215-224.
- WALTON, J. 1936. On the factors which influence the external form of fossil plants; with descriptions of some species of the Paleozoic equisetalean genus *Annularia* Sternberg. *Philosophical Transactions of the Royal Society of London* B226: 219-237.

DR. G. J. RETALLACK
Department of Biology
Indiana University
Bloomington
Indiana 47405
U.S.A.

