

The Mesozoic megafossil genus *Linguifolium* Arber 1917

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ABSTRACT. The plant megafossil genus *Linguifolium* Arber 1917 is chiefly known from the Middle and Upper Triassic of Gondwana. The range of *Linguifolium* extended beyond Gondwana by the Late Triassic, persisting there through the earliest Jurassic (Hettangian). The parent plants probably grew in a well-watered, canopied environment.

Diagnoses of the genus and four of its species – *Linguifolium tenison-woodsii* (Shirley 1898) Retallack 1980, *L. waitakiense* Bell in Bell et al. 1956, *L. parvum* Holmes & Anderson in Holmes et al. 2010, and *L. steinmannii* (Solms-Laubach 1899) Arber 1917 – are emended with particular reference to venation and leaf morphology; consequently, the stratigraphic ranges of the species have been more precisely defined.

Coalescent venation has previously been reported in some species of *Linguifolium* and is identified in new material described herein. Although the vast majority of specimens assigned to the genus are from the Upper Triassic, none shows coalescent venation. This character is entirely restricted to the Middle Triassic, in particular to two species: *L. waitakiense* and *L. parvum*.

Linguifolium tenison-woodsii is restricted to the Carnian–lowermost Norian of Australia and South Africa and is recorded here for the first time from the Tarong Basin (upper Carnian), Queensland. Confusion regarding assignment of specimens to this species from the Middle Jurassic of Queensland is resolved.

KEYWORDS: *Linguifolium*, Gondwana, Triassic, Hettangian, Queensland, Ipswich Basin, Tarong Basin

INTRODUCTION

Linguifolium Arber 1917 comprises obovate-linear-ovate leaves with entire margins and prominent midribs. Venation generally arises very acutely from the midrib, curves away from the midrib, commonly forking once and in some species occasionally twice. Nearly all material has been described from the Triassic (Anisian–lowermost Norian) of Australia, New Zealand and South Africa; several specimens have also been recorded from Antarctica and South America. The genus is not known from the Indian Triassic but material from the Middle–Upper Jurassic of the subcontinent has been referred to the genus, albeit doubtfully. *Linguifolium* has been recorded from

the extra-Gondwanan Upper Triassic and lowermost Jurassic (Hettangian of the Russian far east).

Most material referred to the genus has been assigned to one species, *Linguifolium tenison-woodsii* (Shirley 1898) Retallack 1980 emend. Pattemore & Rigby herein (or to its junior synonym, *L. gracile* Anderson & Anderson 1989). Other species are only known from several specimens, but these include almost-complete leaves, viz. *L. parvum* Holmes & Anderson in Holmes et al. 2010, *L. waitakiense* Bell in Bell et al. 1956, and *L. steinmannii* (Solms-Laubach 1899) Arber 1917, all emended herein. The majority of specimens attributed

to the type species (*L. lillieanum* Arber 1917) are fragmentary. Retallack (1980, fig. 8) constructed a histogram of leaf widths in order to segregate species; however, considerably more is known now regarding defining characters of individual species, thereby enabling their stratigraphic ranges to be better constrained. Retallack's specimens were mostly small fragments and thus his histogram method was practical at that time for speciation.

Anderson and Anderson's (1989) treatment of the genus was based chiefly on specimens from the Carnian of South Africa attributed to one species, *L. gracile*. All other species were only briefly discussed; their nomenclature, descriptions and figures essentially followed Retallack (1980, 1981, 1983, 1985). Anderson and Anderson (1989) suggested that the genus may be represented by a 'single polymorphic species'. However, the impression of a morphological continuum among species is an artefact of Retallack's (1980) speciation method (above) which, by its design, establishes that continuum.

It has been speculated since the erection of *Linguifolium* that some specimens attributed to various species of the genus possess coalescent venation. In these, two or three veins merge but remain discrete from adjacent veins and thus are not consistently networked (i.e. anastomosing). Although coalescent venation may be regarded as a subset of anastomosis, the latter term is avoided with regard to *Linguifolium* so as not to imply an extensively reticulate pattern.

Arber (1913, 1917) noted apparent merging of veins in specimens from the Middle Triassic (Ladinian) of New Zealand; these specimens formed the basis of the type species but that author regarded the coalescence as an artefact of preservation or due to damage. He explicitly excluded anastomosis in his diagnosis of the genus. Seward (1914) disagreed; he re-examined Arber's (1913) specimens and regarded the coalescence as genuine.

Subsequently, specimens have been identified from the Australasian (i.e. Australia and New Zealand) Middle Triassic that clearly conform with previous diagnoses of *Linguifolium* except that they include occasional coalescence of veins. Bell et al. (1956) reported coalescent venation in a specimen from the Middle Triassic (Ladinian) of South Island, New Zealand. Likewise, Holmes et al. (2010) identified this character in specimens from the Middle

Triassic (Anisian) of New South Wales (Nymboida Sub-Basin).

Retallack (1980) assigned numerous specimens from South Island, New Zealand (Ladinian) to various *Linguifolium* species. His emendation of the genus did not explicitly exclude coalescent or otherwise anastomosing venation. New material described herein from the Middle Triassic (Anisian) of Queensland (Esk Trough) features coalescent venation and is included in *L. waitakiense*. Significantly, this character has only been recorded in specimens from the Middle Triassic despite the vast majority of attributions to the genus occurring in the Upper Triassic. This paper describes new material from the Anisian–lowermost Norian of Australia and reviews the genus.

MATERIAL AND METHODS

All specimens described herein are held in the Queensland Museum, Brisbane and are distributed among three collections therein: Queensland Museum (QMF), Geological Survey of Queensland (GSQF), and The University of Queensland (UQF). The new material comprises previously undescribed specimens from the Queensland Museum and one specimen that was collected from the Meandu Mine, Tarong Basin (Fig. 1; co-ordinates given below) by one of us [GAP]. That specimen was recovered from a fresh spoil heap with the assistance of mine staff (see Acknowledgements). All other specimens are from well-known fossil sites in southeast Queensland as indicated in the text and Figure 1.

The specimens described herein are preserved as compressions or impressions and, unless otherwise stated, lack carbonaceous material. Venation density was measured parallel to the midrib and approximately halfway between midrib and margin. Some specimens show a line (ridge or depression) central to the midrib or veins that is probably due to the desiccation phase of fossilization. Although the character is described herein, it is not regarded as diagnostically important.

SYSTEMATIC PALAEOBOTANY

Division: ? Pteridospermophyta

Family: ? Matatiellaceae Anderson
& Anderson 2003

Genus: *Linguifolium* Arber 1917 emend.
Pattimore & Rigby herein

Type species. *Linguifolium lillieanum* Arber 1917; Mount Potts Group (Ladinian),

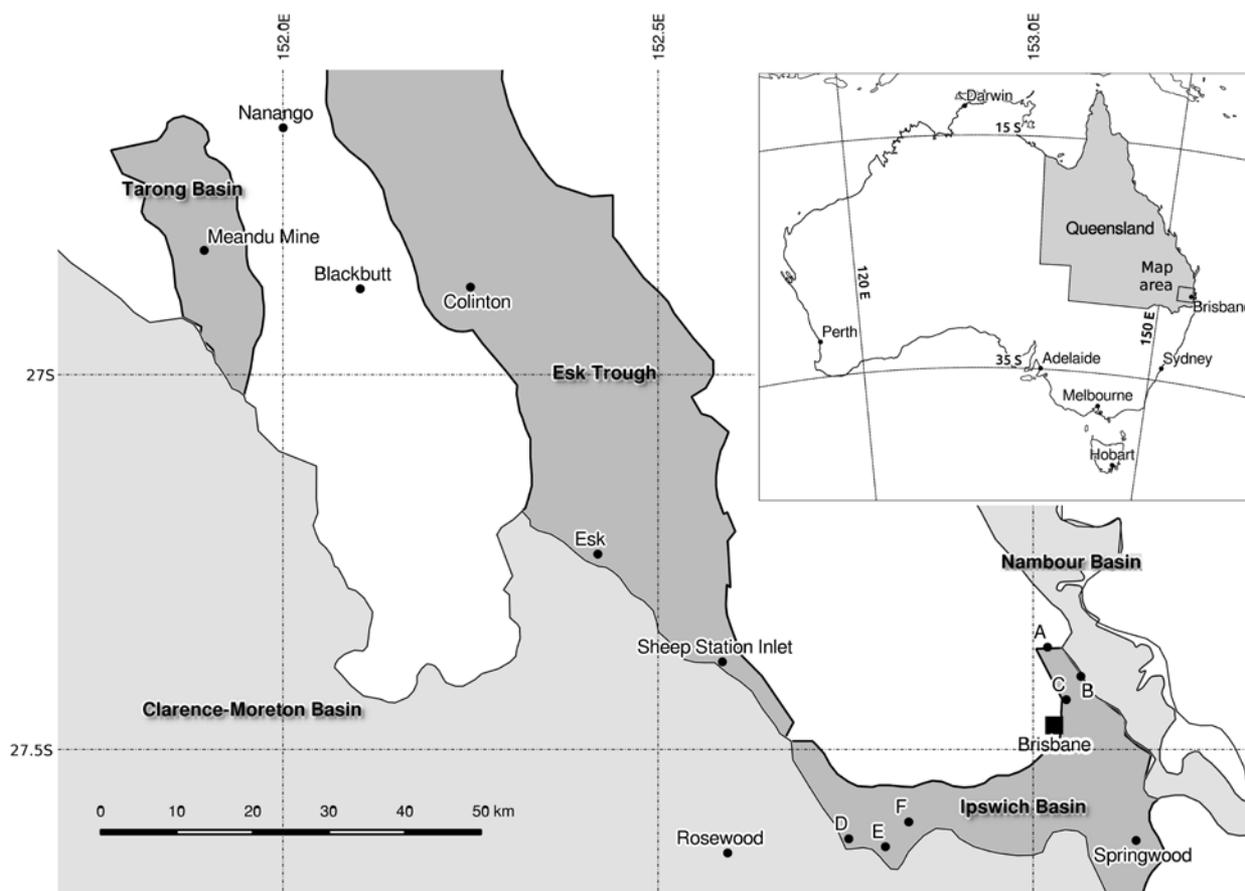


Fig. 1. Triassic and Jurassic basins of southeast Queensland, Australia: Esk Trough (Anisian); Ipswich Basin (Carnian–lowermost Norian); Tarong Basin (upper Carnian); northeastern Clarence-Moreton Basin (Rhaetian–Middle Jurassic) and southern Nambour Basin (Rhaetian–Lower Jurassic). Key to locations: **A** – Aspley; **B** – Nundah; **C** – Albion; **D** – Denmark Hill; **E** – Blackstone; **F** – Dinmore

South Island, New Zealand (Arber 1917, Retallack 1980, 1981, Retallack & Ryburn 1982).

Emended diagnosis. Leaves linear-obovate-ovate, entire, simple. Leaf apices acute–obtuse. Leaf bases attenuate–obtuse, symmetrical or asymmetrical either side of midrib. Midrib prominent but may become very thin apically. Venation branched acutely from midrib (usually less acute apically), then curving toward leaf margin (usually neither apically nor basally), may curve distally toward leaf apex (usually not apically). Veins approach margin acutely (commonly with greater angle apically). Venation either unforked or once- or twice-forked, almost parallel for the most part, may be sparsely coalescent.

Discussion. *Linguifolium* was named and figured by Arber (1913). Later, Arber (1917) provided a diagnosis and description of the genus and type species, thus validating the genus (ICN: McNeill et al. 2012, Articles 33.1, 38.5, 38.7 and 38.8). Retallack (1980) emended Arber’s (1917) generic diagnosis by providing

a more detailed circumscription, chiefly based on specimens from the Ladinian of New Zealand. The emended diagnosis proposed herein augments Retallack’s (1980) emendation to include coalescent venation.

Bomfleur et al. (2011b) speculated that *Linguifolium*, *Dejerseya* Herbst 1977 emend. Bomfleur et al. 2011b and *Pachydermophyllum* Thomas & Bose 1955 may form an intergradational foliar series and that they possibly belong to the Matatiellaceae; hence the tentative attribution of *Linguifolium* to this family herein. The suggested foliar series was based on megascopic form and cuticle. However, cuticle of *Linguifolium* is known from only ten specimens of a single species, all collected from one site (discussed below). Neither fructifications nor stems have been found in biological connection with *Linguifolium*. Retallack (1980) suggested an association with the ovule *Carpolithus mackayii* Arber 1917, which he indicated was always found preserved with *Linguifolium*. Subsequent reports from the Ladinian of New Zealand (Retallack 1981,

1983) supported that scenario. However, the association has not been reported from the Upper Triassic of New Zealand (Retallack 1985), nor from elsewhere in the Gondwanan Middle and Upper Triassic.

Linguifolium tenison-woodsii (Shirley 1898) Retallack 1980 emend. Pattemore & Rigby herein

Figs 2, 3

Synonymy.

- 1898 *Taeniopteris Tenison-Woodsii* (Eth. fil.) Shirley, p. 23, pl. 9, fig. 2.
 1917 *Taeniopteris tenison woodsii* Etheridge Jr; Walkom, pp. 32–34, text-fig. 9.
 1947 *Doratophyllum tenison-woodsii* (Etheridge); Jones & de Jersey, pp. 37–39, pl. 6, fig. 1.
 1965 *Doratophyllum tenison-woodsii* (Etheridge) Jones & de Jersey; Hill et al., pl. T8, fig. 1.
 1980 *Linguifolium tenison-woodsii* (Etheridge); Retallack, pp. 50–51.
 1980 *Linguifolium tenison-woodsii* (Etheridge); Webb, pl. 20, figs 2–4, pl. 21, figs 1–7, 9–11, 14, 15 [unpublished].
 1989 *Linguifolium gracile*; Anderson & Anderson, p. 521 (incl. text-figs 1–18), pls 311–314 (all figs).
 2005 *Linguifolium tenison-woodsii* (Etheridge in Jack & Etheridge 1892) Retallack 1980; Pattemore & Rigby, pp. 338–340, fig. 7C, D.

Emended diagnosis. Leaf narrow, linear. Apex acute to obtuse. Base attenuate. Midrib wide, striated, with or without central line. Laminae laterally attached. Venation branching from midrib very acutely, generally curving toward margin, then usually curving toward apex near leaf margin (uncommon apically), thus approaching margin very acutely (angles commonly greater apically). Veins commonly bifurcate once, usually near midrib. Quantitative characters given in Table 6.

Basionym. Shirley (1898, p. 23, pl. IX, fig. 2); GSQF396, lectotype designated herein.

Material. All types listed below are designated herein.

Lectotype. GSQF396, described and figured by Shirley (1898, p. 23, pl. IX, fig. 2) and herein (Fig. 3); Denmark Hill, Ipswich, Queensland (Blackstone Formation, Brassall Subgroup, Ipswich Basin; Carnian–lowermost Norian).

Syntypes. GSQF14501, UQF2293 (6 fragments), UQF12694, UQF20624, UQF43870–UQF43871 (previously S37 and S66 of Simmonds's collection; Fig. 3B, C herein),

UQF82583A/B (part and counterpart), UQF82596; Denmark Hill, Ipswich, Queensland (Blackstone Formation, Brassall Subgroup, Ipswich Basin; Carnian–lowermost Norian).

Syntype. QMF57875; Meandu Mine, Tarong Basin (upper Carnian). Figured herein (Fig. 2C, D). Co-ordinates: lat., 26.836346°S; long., 151.894089°E (Fig. 1).

Syntypes. UQF82574–UQF82575; New Aberdare East No. 3 Colliery, Blackstone, Ipswich, Queensland (Blackstone Formation, Brassall Subgroup, Ipswich Basin; Carnian–lowermost Norian).

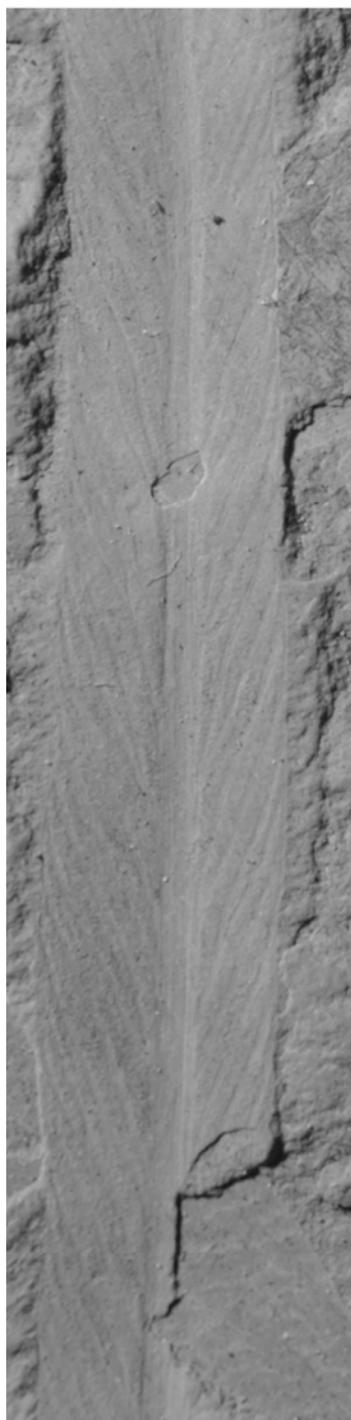
Syntypes. QMF42415–QMF42418, QMF42487–QMF42489, QMF42524, UQF64538, UQF82578A/B (part and counterpart), UQF82580–UQF82582; Dinmore Quarry, Dinmore, Queensland (upper Tivoli Formation, Brassall Subgroup, Ipswich Basin; Carnian–lowermost Norian). Venation in specimen QMF42487 is figured herein (Fig. 2A, B); the complete specimen was figured by Pattemore and Rigby (2005, fig. 7D).

Occurrence. Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian) and Tarong Basin (upper Carnian), Queensland; Molteno Formation (Carnian), South Africa.

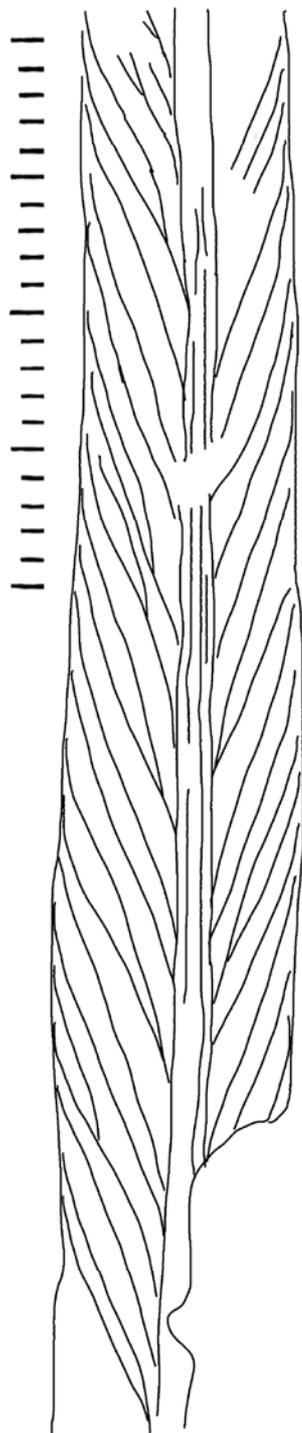
Description. Largest specimen 205 mm long (incomplete); leaf width 7–9 mm. Venation branching from midrib acutely (10°–40°, mostly < 30°); but commonly at a greater angle near apex (> 60°). Veins usually arching away from the midrib; commonly bifurcating once near the midrib. Near margin, veins commonly curve toward apex, approaching margin acutely (< 30°), but less acutely near apex. Midrib striated, some specimens having prominent central line. Midrib 0.5–1.1 mm wide for most of its length, narrowing to ~0.2 mm apically and extending to leaf tip. Leaf apices acute to obtuse. Venation density: 6–16 veins per 10 mm, increasing toward apex.



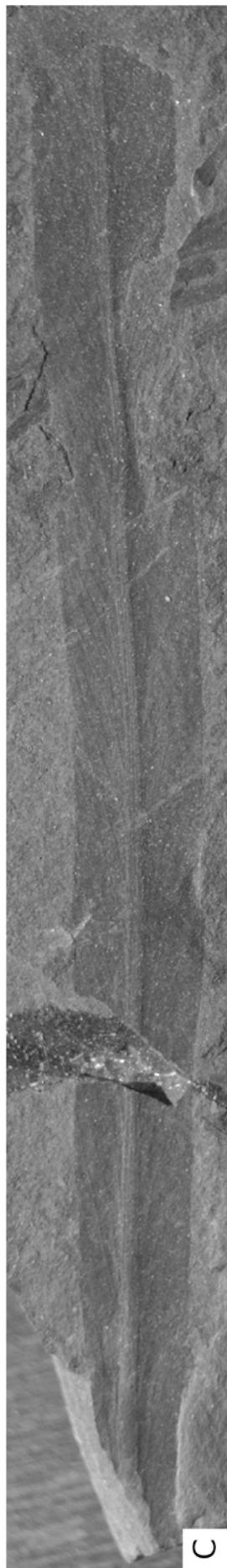
Fig. 2. *Linguifolium tenison-woodsii* (Shirley 1898) Retallack 1980 emend. Pattemore & Rigby herein. **A** – QMF42487 (syntype), Dinmore Quarry, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian), Queensland. **B** – QMF42487, camera lucida image. **C** – QMF57875 (syntype), Meandu Mine, Tarong Basin, Queensland (upper Carnian). **D** – QMF57875, camera lucida image. Scale: A–B, 1 cm in 0.5 mm increments; C–D, 1 cm in 1 mm increments



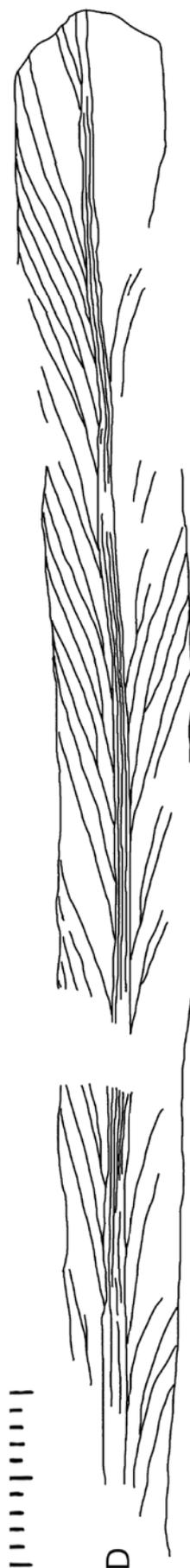
A



B



C



D

Table 1. Nomenclatural history relating to Middle Jurassic specimens from Rosewood (west of Ipswich), Queensland, which were referred to *Angiopteridium tenison-woodsii* Etheridge in Jack & Etheridge 1892

Reference	Notes
Oldham & Morris (1863, pp. 35–36, pl. VI, figs 8–10)	<i>Stangerites ensis</i> Oldham in Oldham & Morris 1863 was established for specimens from Burio, Moorcha Pass (also Murcha or Morcha; alternate spelling used by later authors), Rajmahal Hills, Bengal, India (Lower Cretaceous: Banerji 1992, 2004). Bornemann (1856, p. 59–60) established <i>Stangerites</i> . That author used the orthography <i>Strangerites</i> , apparently a misspelling (Seward, 1895, p. 16)
Schimper (1869, p. 606)	<i>Stangerites ensis</i> re-combined as <i>Angiopteridium ensis</i> (Oldham in Oldham & Morris 1863) Schimper 1869
Feistmantel (1876, p. 40)	The name ' <i>Taeniopteris (Angiopteridium) ensis</i> Oldham & Morris' was used for specimens from the Godavari District, India (Upper Jurassic: Lakhanpal et al. 1976)
Feistmantel (1877b, p. 173, pl. I, figs 6a, 7a)	<i>Angiopteridium ensis</i> (Oldham in Oldham & Morris 1863) Schimper 1869 was used for specimens from the Godavari District, India (Upper Jurassic: Lakhanpal et al. 1976). Discussed but not figured by Feistmantel (1877a, pp. 97–98) and Feistmantel (1881, pp. 190–191)
Tenison-Woods (1883, p. 119)	Specimens from Rosewood, Queensland (Middle Jurassic, Walloon Coal Measures, Clarence-Moreton Basin) were referred to <i>Angiopteridium ensis</i> . These were not figured and no museum reference numbers were provided; held in the Macleay collection, University of Sydney. Discussed but not figured by Feistmantel (1890a, p. 116)
Jack & Etheridge (1892, p. 375)	The Rosewood specimens (above) were regarded as distinct from the Indian material and <i>Angiopteridium tenison-woodsii</i> Etheridge in Jack & Etheridge 1892 was erected based solely on the Rosewood specimens. Venation described as 'very oblique to the midrib' and 'almost straight'. The specimens unfigured; no museum catalogue numbers provided
Shirley (1898, p. 23, pl. IX, fig. 2)	<i>Angiopteridium tenison-woodsii</i> re-combined as <i>Taeniopteris tenison-woodsii</i> (Etheridge in Jack & Etheridge 1892) Shirley 1898; new material added from Denmark Hill, Ipswich (Blackstone Formation, Ipswich Basin; Carnian–lowermost Norian). Specimen re-figured herein (Fig. 3A). At that time little geological distinction was drawn between the Ipswich Coal Measures and the Walloon Coal Measures; Rosewood is only several kilometres west of Ipswich. <i>Taeniopteris tenison-woodsii</i> was discussed but not figured by Dun (1898)
Retallack (1980)	<i>Angiopteridium tenison-woodsii</i> re-combined as <i>Linguifolium tenison-woodsii</i> (Etheridge in Jack & Etheridge 1892) Retallack 1980. One of Tenison-Woods's (1883) Rosewood specimens (purportedly SUMM30) selected as lectotype but not figured. Retallack (1980) considered, without explanation, the type locality to be the Aberdare Mine, Ipswich Coal Measures, Queensland. Additional material from Tank Gully, South Island, New Zealand (Ladinian); synonymy list includes Middle and Late Triassic specimens from Australasia and South America
Webb (1980) [unpublished]	Combination proposed as ' <i>Linguifolium tenison-woodsii</i> '; one of Tenison-Woods's (1883) Rosewood specimens (purportedly SUMM61b) selected as lectotype and other specimens (SUMM4 and SUMM61c) assigned to this 'species'. The proposed lectotype was figured (Webb 1980, text-fig. 41p) and considered to be from Denmark Hill, Ipswich, Queensland (Blackstone Formation, Ipswich Basin; Carnian–lowermost Norian). Additional material was included from several eastern Australian localities (Anisian–Sinemurian; Tab. 2). Synonymy list includes Middle and Late Triassic specimens from Australasia and South America

Discussion. The nomenclatural history of *Linguifolium tenison-woodsii* is somewhat confused by the fact that it is based upon Middle Jurassic specimens from the Walloon Coal Measures, Clarence-Moreton Basin (Tab. 1). *Linguifolium* species are otherwise unknown from the Walloon Coal Measures (Gould 1974, 1980, Rigby 1978, McLoughlin & Drinnan 1995, Turner et al. 2009; also collections by one of us [GAP] that are currently being investigated). There is little doubt that the Middle Jurassic specimens assigned to *Angiopteridium ensis* (Oldham in Oldham & Morris 1863) Schimper 1869 by Tenison-Woods (1883) and to *A. tenison-woodsii* Etheridge in Jack and Etheridge 1892 by Jack and Etheridge (1892) are in fact from Rosewood. That location was well known at the time Tenison-Woods (1883) described the material. However, because the

original Rosewood specimens were neither numbered nor figured, considerable doubt exists as to which specimens in the Macleay Collection are in fact Tenison-Woods's (1883) specimens assigned to *A. ensis* (Tab. 1). Both Retallack (1980) and Webb (1980) specified different specimen numbers for these specimens; both suggested that the material was not from Rosewood and proposed differing Ipswich Basin locations for the material's probable collection site. Given the lack of published figures and uncertainty regarding Tenison-Woods's (1883) actual specimens, *A. tenison-woodsii* is of doubtful validity. In an unpublished thesis, Webb (1980) included a line-drawing of a specimen (Tab. 1) that was purportedly one of Tenison-Woods's (1883) specimens assigned to *A. ensis*, but as noted above, this is uncertain. Webb's (1980, text-fig. 41p) figure is not

consistent with the venation that was described by Jack & Etheridge (1892) as ‘very oblique to the midrib’. The brief description provided by the latter authors is suggestive of a taeniopterid leaf, indeed a far more probable identification for a specimen collected from Rosewood.

The confusion of the Middle Jurassic Rosewood and Triassic Ipswich Basin collections began when Shirley (1898) proposed the combination *Taeniopteris tenison-woodsii* because he also assigned Ipswich Basin specimens to the species (Tab. 1; Fig. 3); thereafter, all new material added to this species (and subsequently to *Linguifolium tenison-woodsii*) is Anisian–Norian in age.

Although Shirley (1898) applied the combination *Taeniopteris tenison-woodsii*, he was clearly describing a known Carnian–lowermost Norian specimen (GSQF396) with a known collection location (Denmark Hill, Ipswich; >10 km east of Rosewood). It is proposed herein that:

1. *Angiopteridium tenison-woodsii* Etheridge in Jack & Etheridge 1892 be retained for the Middle Jurassic Rosewood specimens of Tenison-Woods (1883) and Jack & Etheridge (1892) that were originally ascribed to *Angiopteridium ensis* by Tenison-Woods (1883); and,

2. *Linguifolium tenison-woodsii* (Shirley 1898) Retallack 1980 emend. Pattermore & Rigby herein be retained for Carnian–lowermost Norian specimens previously ascribed to *L. tenison-woodsii*, *Doratophyllum tenison-woodsii* and *T. tenison-woodsii* as listed in the above synonymy but not the material included in *Angiopteridium tenison-woodsii* by Etheridge in Jack and Etheridge (1892).

The type of Retallack’s (1980) binomial combination *Linguifolium tenison-woodsii* is explicitly excluded herein from that species, because the specimens attributed to *Angiopteridium ensis* by Tenison-Woods (1883), and subsequently to *Angiopteridium tenison-woodsii* by Etheridge in Jack and Etheridge (1892), have been excluded. Thus, *Taeniopteris tenison-woodsii* Shirley 1898 is the basionym of *L. tenison-woodsii*, and being a later homonym, Shirley (1898) is cited as the original author (ICN, McNeill et al. 2012, Article 48). His specimen (GSQF396; Fig. 3A) is the default lectotype designated herein. Additionally, several syntypes are designated (above).

Angiopteridium ensis (Tab. 1) is a petiolate leaf with a distinctly thinning midrib,

but unlike *Linguifolium* its venation extends toward the margin at a much larger angle (50°–85°), generally intersecting with the margin at >45° and tending to bifurcate near the margin (Oldham & Morris 1863, pl. VI, figs 8–10; Feistmantel 1877b, pl. I, figs 6a, 7a). These distinctive characters were also noted by Menéndez (1951, p. 186), and more generally, distinction of *Linguifolium* and taeniopterid leaves and/or various post-Triassic ferns were discussed by Arber (1917), Walkom (1919), Medwell (1954), Retallack (1980), and Webb (1980).

The figured specimen (Fig. 3A; GSQF396, the lectotype designated herein) from the Ipswich Basin was attributed to *Taeniopteris tenison-woodsii* by Shirley (1898) but now lacks the leaf apex. Venation, although generally poorly preserved, can be seen in places branching acutely from the midrib (<30°), but less acutely toward the apex. Near the margin, venation is less clear, but in places curves toward the apex to meet the margin acutely. The midrib (0.6–1.1 mm wide) is faintly striated.

Walkom (1917) included several specimens in *Taeniopteris tenison-woodsii* (Fig. 3B, C); three are accepted as belonging to *Linguifolium tenison-woodsii* herein (GSQF396, UQF43870, UQF43871). His specimen GSQF399 from the Esk Trough (Anisian), Queensland, is too poorly preserved for positive generic identification. Specimens identified as *T. tenison-woodsii* by Walkom (1924b, 1928) from the Esk Trough were only briefly described and not figured.

Arber (1917) proposed the combination *Linguifolium feistmantelii* (Etheridge 1892) Arber 1917, but this was not supported by Walkom (1919). Etheridge’s (1892) original specimen was collected from a location ~200 km north of the Leigh Creek Coalfield (Brown 1892). The specimen is not Triassic in age but is probably from post-Jurassic strata (Callen et al. 1995). Etheridge (1892) compared this specimen to material from the Cretaceous of Queensland. Likewise, specimens used to establish *L. kurtzii* Frenguelli 1941 from the uppermost Triassic–Lower Jurassic of Argentina are reportedly not attributable to *Linguifolium* (Herbst 1966, Retallack 1980).

Chapman and Cookson (1926) compared one specimen from the Leigh Creek Coal Measures, South Australia to *Taeniopteris tenison-woodsii*. Its poor preservation hinders confident attribution to *Linguifolium tenison-woodsii*;

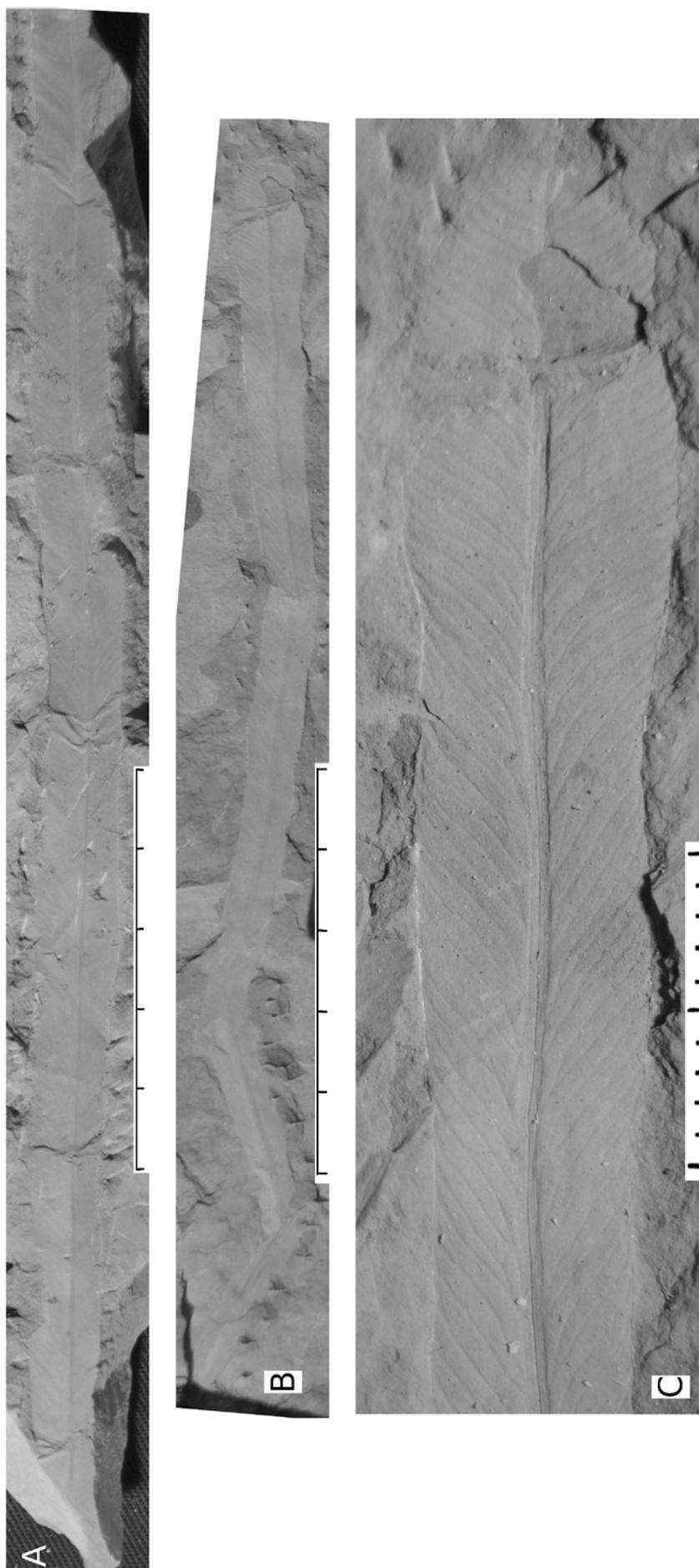


Fig. 3. *Linguifolium tenison-woodsii* (Shirley 1898) Retallack 1980 emend. Pattenmore & Rigby herein. **A** – GSQF396 (lectotype), figured by Shirley (1898, pl. IX, fig. 2) as *Taeniopteris Tenison-Woodsi* Eth. fil. **B** – UQF43870 (syntype; formerly, Simmonds's collection S37), figured by Walkom (1917, text fig. 9) as *Taeniopteris tenison-woodsii*. **C** – UQF43870, enlarged apical portion. Scale: A–B, 5 cm in 1 cm increments; C, 1 cm in 1 mm increments

the collection location is imprecisely known but it would probably be associated with coal-bearing strata (Anisian–lower Norian: Kwitko 1995). Hill (1930) and Houston (1967) listed locations of specimens assigned to *Linguifolium*/*Taeniopteris* from the general areas of Brisbane, Ipswich and Esk, Queensland but the specimens were not figured or described.

Webb (1980) indicated that *Linguifolium tenison-woodsii* ranged from the Middle Triassic through Early Jurassic (Tab. 2). His uppermost Triassic (and younger) specimens are almost certainly from the Ipswich Basin (Carnian–lowermost Norian). He was unable to extract cuticle from several Australian specimens identified as *Linguifolium tenison-woodsii* and *L. lillieanum*. Jones & de Jersey (1947, pp. 37–38, pl. 10, fig. 1) described cuticle from a specimen that they assigned

to *Doratophyllum tenison-woodsii* from the Ipswich Basin. However, Webb (1980, p. 179) regarded that specimen as representative of *Dejerseya*.

Although cuticle is not known from the type species, it has been reported from South African specimens (Molteno Formation; Carnian) identified as *Linguifolium gracile* Anderson & Anderson 1989; this species is herein regarded as a junior synonym of *L. tenison-woodsii*. Anderson and Anderson (1989) described ten cuticular specimens from one locality (Little Switzerland, western KwaZulu-Natal, South Africa). Pattemore and Rigby (2005) suggested that *L. gracile* is synonymous with *L. tenison-woodsii*, the two species having previously been separated on venation density and other minor geometric details. Those authors showed that *L. tenison-woodsii*

Table 2. Figured Queensland specimens assigned to *Linguifolium tenison-woodsii* by Webb (1980)

Figure in Webb (1980)	Reported geological unit	Reported age	Assessed age	Remarks and attribution herein
pl. 21, fig. 8	Upper Ripley Road Sandstone–lower Gatton Sandstone, Woogaroo Subgroup, Clarence-Moreton Basin [inferred from reported co-ordinates]	Sinemurian [inferred]	? Carnian	Specimen not collected by Webb (1980) and locality co-ordinates probably incorrect. Webb (1980) gave two differing co-ordinates for this specimen and both differ from that of the Museum record; an author [GAP] of the present contribution was unable to locate the specimen. <i>Linguifolium</i> is otherwise unknown from these units. Specimen almost certainly from Ipswich Coal Measures. Secondary venation distally recurved. Attribution: ? <i>L. tenison-woodsii</i>
pl. 20, figs 2, 4; pl. 21, figs 4, 5, 7, 10, 11, 15	Aberdare Conglomerate and Raceview Fm, Woogaroo Subgroup, Clarence-Moreton Basin [Springwood area, southern Brisbane]	Rhaetian	Carnian–lowermost Norian	All these specimens are from localities close to (<1.2 km) and including the Light Street locality (former State quarry) reported by Barone-Nugent et al. (2003); Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Gould (1967) considered the quarry and surrounding areas to comprise two Mesozoic stratigraphic units: Tingalpa (lower) and Moorooka (upper) fms; he suggested the two were separated by an unconformity but did not establish that the upper unit was unrelated to the Ipswich Basin despite his assignment of the unit to the Moorooka Fm. Webb (1980) apparently regarded this reported unconformity as the contact with the Clarence-Moreton/Nambour Basin. A typical Ipswich Basin megafloreal assemblage was reported from both these units at several sites in the immediate area by Gould (1965, 1967). Webb's (1980) figured specimens from this area are almost certainly Carnian–lowermost Norian in age. Most show distal recurvature of secondary venation. Attribution: <i>L. tenison-woodsii</i>
pl. 21, figs 1–3, 6, 9, 14	Blackstone Fm, Brassall Subgroup, Ipswich Basin	Carnian	Carnian–lowermost Norian	Most show distal recurvature of secondary venation. Attribution: <i>L. tenison-woodsii</i>
pl. 21, fig. 12	Mt. Crosby Fm, Kholo Subgroup Ipswich Basin	Carnian	Carnian	Weak distal recurvature of secondary venation, lamina strongly asymmetric about midrib. Attribution: <i>Linguifolium</i> sp.
pl. 21, fig. 13	Bryden Fm, Esk Trough	Anisian	Anisian	No distal recurvature of venation, some veins bifurcate twice and possible coalescence of two veins; original specimen unable to be located. Attribution: <i>L. waitakiense</i>

has considerable variation in venation density and branching angle from the midrib (Tab. 6). Specimens attributable to *Linguifolium* were collected from the Little Switzerland locality by GAP and were regarded as indistinguishable (Pattimore 1998, pp. 108–109) from specimens collected from the Ipswich Basin, later referred to *L. tenison-woodsii* (Pattimore & Rigby 2005). Specimens from the Carnian–lowermost Norian of Queensland examined in this work are non-cuticular, with the possible exception of QMF57875 which has a thin carbonaceous film. This is the only known *Linguifolium* specimen from the Tarong Basin (upper Carnian); hence, no destructive analysis was attempted.

Several specimens were identified as *Linguifolium tenison-woodsii* (Tab. 3) from the Ladinian of South Island, New Zealand. All of are evidently poorly preserved and their venation does not curve distally toward the apex, a character considered specifically important herein (Tab. 6). Middle Triassic specimens previously identified as *L. tenison-woodsii* are re-assigned to *L. waitakiense* (below).

Retallack's (1980) synonymy list for his combination *Linguifolium tenison-woodsii*

included a specimen attributed to *Pecopteris caudata* Johnston 1885 by Johnston (1888, pl. 26, fig. 1) from the Triassic of Tasmania (probably Carnian–lower Norian: Reid et al. 2014). Johnston (1888) did not describe the specimen and his line-drawing lacks sufficient detail for confident assignment to *Linguifolium*. The same specimen (almost complete but very small) was figured by Feistmantel (1890b, pl. 8, fig. 13) who referred it to *Thinnfeldia Ettingshausen* 1852. Feistmantel's (1890b) specimens are held by the Národní Muzeum, Prague and recent examination of this collection [JFR] found the specimen in question to be too poorly preserved for confident attribution to *Linguifolium*. Walkom (1924a) tentatively included both figures of the specimen in his synonymy list for *L. diemenense* Walkom 1924a. He re-examined several specimens previously described by Johnston (presumably some of those described by Johnston 1885, 1886, 1888, 1893, 1895), but the locality information for most specimens had evidently been lost (Walkom 1924a, p. 73). Given this, and the fact that *L. diemenense* is figured only by hand drawings of very small apical fragments, the species is of doubtful validity and can only be

Table 3. Figured specimens from New Zealand attributed to *Linguifolium* species

Reference	Age	Designation	Assessment herein
Arber (1913, 1917)	Ladinian	<i>L. lillieanum</i>	<i>L. lillieanum</i>
McQueen (1954, pl. 12, fig. 8)	?	<i>Linguifolium</i> sp.	? (doubtful specimen; Retallack 1980)
Bell et al. (1956, text fig. 4 (6, 7))	Ladinian	<i>L. waitakiense</i>	<i>L. waitakiense</i>
Bell et al. (1956, text fig. 4 (8, 9))	Ladinian	<i>L. lillieanum</i>	<i>L. lillieanum</i>
Retallack (1980, fig. 7 A, B) Retallack (1981, fig. 9 A, B) Retallack (1983, fig. 8 A)	Ladinian	<i>L. lillieanum</i>	<i>L. lillieanum</i>
Retallack (1980, figs 7 C, 7D, 10 I) Retallack (1981, fig. 9 C–E) Retallack (1983, figs 8 B, 8C, 10 E)	Ladinian	<i>L. steinmannii</i>	<i>L. parvum</i>
Retallack (1980, fig. 7 E) Retallack (1981, fig. 9 F–H) Retallack (1983, fig. 8 D)	Ladinian	<i>L. arctum</i>	<i>L. waitakiense</i>
Retallack (1980, fig. 7 F–H) Retallack (1981, fig. 9 I–K) Retallack (1983, figs 8 E–H, 10 D) Retallack (1985, fig. 8 C(2))	Ladinian	<i>L. tenison-woodsii</i>	<i>L. waitakiense</i>
Retallack (1985, fig. 8 F)	middle–late Norian	<i>L. lillieanum</i>	<i>L. lillieanum</i>
Retallack (1985, fig. 9 A(2))	middle–late Norian	<i>L. arctum</i>	<i>Linguifolium</i> sp.; very small fragment with insufficient detail
Retallack (1985, fig. 9 A(3))	middle–late Norian	<i>Linguifolium</i> sp.	<i>Linguifolium</i> sp.
Retallack (1985, fig. 9 C(5))	Rhaetian	<i>L. lillieanum</i>	<i>Linguifolium</i> sp.; very small fragment with insufficient detail
Retallack (1985, figs 9 B(4), 9 C(3, 4, 6), 10 I)	Rhaetian	<i>L. steinmannii</i>	<i>Linguifolium</i> sp.; insufficient detail
Retallack (1985, fig. 9 B(5, 6))	Rhaetian	<i>L. arctum</i>	<i>Linguifolium</i> sp.; very small fragments

regarded as indicative of the occurrence of *Linguifolium* in the Triassic of Tasmania.

Menéndez (1951) assigned specimens to *Linguifolium diemenense* from the Llantenes Formation of Argentina (? Norian: Morel et al. 2003) but noted that Walkom's (1924a) specific diagnosis was insufficient for direct comparison. Those specimens were included in *L. tenison-woodsii* by Retallack (1980); however, some veins fork twice and there is no indication that veins curve toward the apex near the leaf margin. The specimens identified as *L. diemenense* by Menéndez (1951) are fragmentary; one is 15 mm wide and the other two are much narrower, suggesting they may be basal or apical fragments. They were differentiated by Menéndez (1951) from other material assigned to the genus chiefly because of their acute apices. He erected *L. arctum* and *L. llantenense* and the specimens he attributed to *L. diemenense* are probably within the natural variation of one or both of those species.

Several specimens from the Upper Triassic of Argentina and Chile have been assigned to *Linguifolium tenison-woodsii* and to other species of the genus (Artabe et al. 1998, Gnaedinger & Herbst 1998, Morel et al. 1999, Herbst et al. 2005, Leppe 2005, Herbst & Troncoso 2012). None of the specimens figured as *L. tenison-woodsii* nor their descriptions by those authors indicate any degree of venation curvature near the margin resembling that of this species from the Carnian–lowermost Norian of Australia and South Africa. Furthermore, some figured specimens show vein bifurcation mostly close to the margin (e.g. Gnaedinger & Herbst 1998, fig. 2f), which is unlike that of *L. tenison-woodsii*. Most South American specimens are Norian in age, but some are only datable broadly as Late Triassic–earliest Jurassic. *Linguifolium llantenense* Menéndez 1951, reported by its author from the Llantenes Formation (? Norian: Morel et al. 2003), Argentina, apparently does possess venation that distally curves toward the leaf apex (Tabs 5, 6).

Linguifolium is reportedly abundant in the Upper Triassic of Antarctica (Bomfleur et al. 2007, 2011a). However, there has been only limited systematic treatment of representatives of the genus from that continent (Escapa et al. 2011, Cantrill & Poole 2012, and references therein). Bomfleur et al. (2011a) figured but did not describe a specimen assigned to *L. tenison-woodsii* from the Section Peak

Formation (Upper Triassic) of the Vulcan Hills, North Victoria Land; the specimen is falcate (perhaps a preservational effect) and lacks venation detail. Tessensohn and Mädler (1987) identified two specimens from the same locality as *Linguifolium* sp., but the venation is unclear and the description inadequate for specific assignment; however, the leaf shape is not like *L. tenison-woodsii*.

Linguifolium waitakiense Bell in Bell et al. 1956 emend. Pattermore & Rigby herein

Figs 4, 5

Synonymy.

- 1956 *Linguifolium waitakiense* Bell in Bell et al., p. 670, text-fig. 4(6, 7).
 1980 *Linguifolium tenison-woodsii* (Etheridge); Retallack, fig. 7F–H.
 1980 *Linguifolium arctum* Menendez 1951; Retallack, fig. 7E.
 1980 *Linguifolium tenison-woodsii* (Etheridge); Webb, pl. 21, fig. 13 [unpublished].
 1981 *Linguifolium tenison-woodsii* (Etheridge) Retallack 1980; Retallack, fig. 9I–K.
 1981 *Linguifolium arctum* Menendez 1951; Retallack, fig. 9F–H.
 1983 *Linguifolium tenison-woodsii* (Etheridge) Retallack 1980; Retallack, figs 8E–H, 10D.
 1983 *Linguifolium arctum* Menendez 1951; Retallack, fig. 8D.
 1985 *Linguifolium tenison-woodsii*; Retallack, fig. 8C(2).
 2010 *Linguifolium tenison-woodsii* (Jack and Etheridge 1892) Retallack 1980; Holmes et al., p. 7, fig. 8B, C.

Emended diagnosis. Leaf linear, apex acute to obtuse, base attenuate, petiole long and slender. Midrib wide, striated. Laminae laterally attached. Venation branching from midrib very acutely but with greater angle apically, then curving toward margin. Some veins curving toward the apex but only very close to margin (<0.3 mm). Most veins bifurcating once, rarely twice, commonly near midrib. Veins rarely coalescing. Quantitative characters given in Table 6.

Material. All types listed below are designated herein.

Paratypes. Paratypes: UQF23630, UQF23632–UQF23634 and UQF82590–UQF82592 on same slab; Ottaba, north of Esk, Queensland (Esk Formation, Esk Trough; Anisian). Paratypes: UQF82587, UQF82588, UQF82595; Sheep Station Inlet (formerly

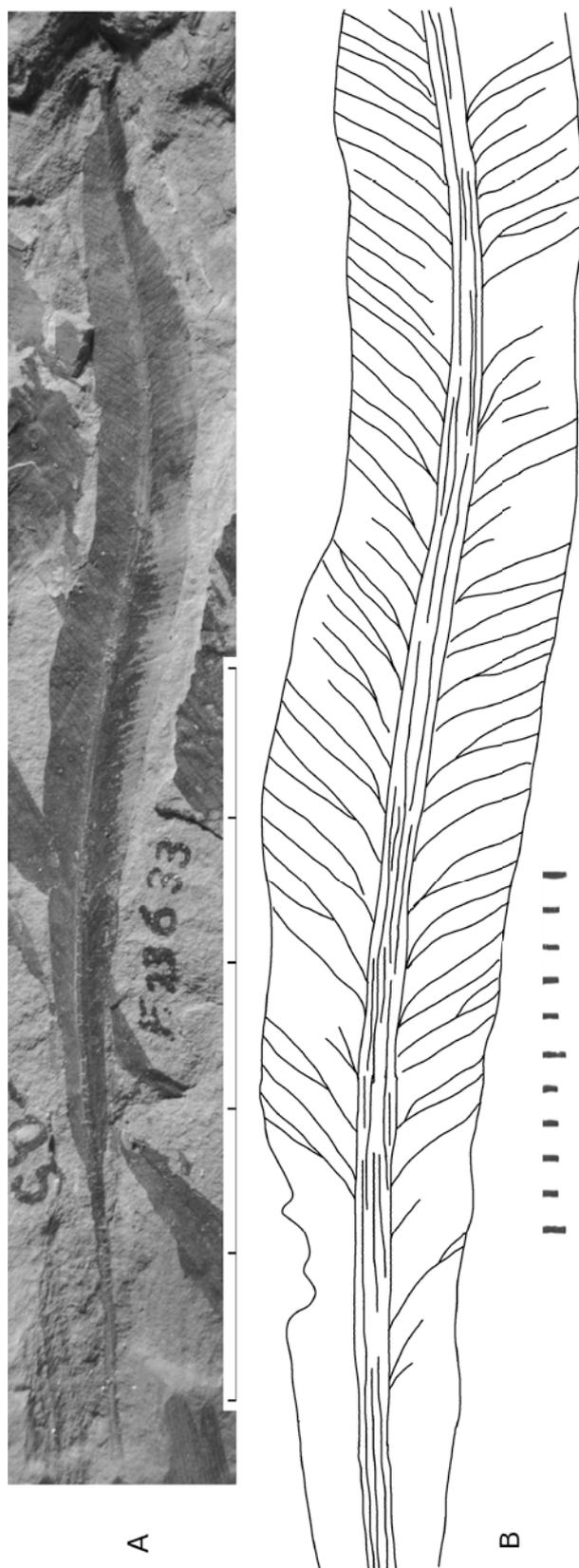


Fig. 4. *Linguifolium waitakiense* Bell in Bell et al. 1956 emend. Pattemore & Rigby herein. **A** – UQF23633 (paratype), Ottaba, north of Esk, Queensland (Esk Formation, Esk Trough; Anisian). **B** – UQF23633, camera lucida image. Scale: A, 5 cm in 1 cm increments; B, 1 cm in 1 mm increments

Sheep Station Creek, now submerged), by Wivenhoe Dam, Queensland (Esk Formation, Esk Trough; Anisian). UQF23633 is figured herein (Figs 4, 5).

Occurrence. Basin Creek Formation, Nymboida Sub-Basin, New South Wales (Anisian); Toogoolawah Group, Esk Trough, Queensland (Anisian); South Island, New Zealand (Ladinian).

Description. Largest specimen 110 mm long, almost complete); leaf width 7–10 mm. Venation branching acutely from midrib (10° – 40° , mostly $<30^{\circ}$) but up to 60° apically. Veins arching away from midrib but less curved apically; most bifurcating once, commonly near midrib, rarely twice-forked, uncommonly coalescing. Within 0.3 mm of margin, some veins curving toward apex, approaching margin acutely (20° – 60°). Midrib striated, 0.5–1.0 mm wide for most of its length, reducing to ~ 0.2 mm wide apically, probably extending to the leaf tip. Some midribs with prominent central line. Leaf apices acute to obtuse. Petiole 21 mm long, 0.8 mm wide, slightly expanded basally (0.9 mm wide). Venation density: 8–12 veins per 10 mm basally; 16–20 veins per 10 mm apically.

Discussion. Few complete or almost-complete specimens have been assigned to *Linguifolium* from the Anisian of Gondwana (Holmes et al. 2010, and herein). Specimen UQF23633 (Figs 4, 5) from the Esk Trough (Anisian) is the only almost complete specimen attributed to *L. waitakiense*. Importantly, it shows that the species is petiolate, includes coalescent venation, and was long and narrow. A faint line central to each vein (Fig. 5) is an artefact of reflected photographic lighting and probably represents a small ridge or depression (possibly caused during the desiccation phase of fossilization). In this figure, the central lines appear to join near the margin, suggesting a full vascular merger; however, vascular bundle detail is unclear because of the sandy rock matrix. Bell et al. (p. 670, text-fig. 4(7)) figured coalescent veins in this species. Coalescent venation has not been reported in *L. tenison-woodsii* nor in any other specimen attributed to the genus from the Upper Triassic, despite most specimens identified with the genus occurring in that interval.

Nearly all specimens listed in the above synonymy are not photographically figured and all



Fig. 5. *Linguifolium waitakiense* Bell in Bell et al. 1956 emend. Pattemore & Rigby herein. Enlargement of coalescent venation in UQF23633 (paratype), Ottaba, north of Esk, Queensland (Esk Formation, Esk Trough; Anisian). Scale bar: 1 mm

are fragmentary. Several of Retallack's (1980, 1981, 1983) line-drawn specimens suggest, but do not confirm, the presence of coalescent veins. The Ladinian specimens described in his papers are very poorly preserved, having reportedly undergone low-grade metamorphism and varying degrees of distortion. Hence, sparse vein coalescence may be under-represented in the published record, but it has been recorded in specimens assigned to another species (*Linguifolium parvum*) which is known only from the Eastern Gondwanan Middle Triassic.

The specimen reported by Bell et al. (1956) with coalescent veins was assigned by Retallack (1980) to *Linguifolium arctum* but without reference to the venation. He may have regarded the coalescence of veins as an aberration or not of diagnostic consequence. Menéndez (1951) established *L. arctum* based on specimens from the Llantenes Formation, Mendoza Province, Argentina (? Norian; Morel et al. 2003). The various figures and descriptions of that species (Tab. 5) suggest only singly-bifurcating venation, with no indication of coalescence.

Retallack (1985) assigned several foliar fragments to *Linguifolium* from a number of sites in the Upper Triassic of New Zealand (Tab. 3); only one was photographically figured (Retallack 1985, fig. 10I) and its venation is unclear. His other figured specimens (small fragments) are illustrated by line-drawings that depict only a single bifurcation except for one showing twice-bifurcation (Retallack 1985, fig. 9B(4)). His most complete figured specimen, assigned to *L. lillieanum*, was accompanied by marine invertebrate fossils (Retallack

1985, fig. 8F, from his Otamita Stream locality; Norian).

Cúneo et al. (2003, pl. 2, fig. 1) figured specimens that were included in *Dicroidium* Gothan 1912 emend. Townrow 1957 from the upper Fremouw Formation, Central Transantarctic Mountains, Antarctica (Middle Triassic). A fragment on the same slab (not identified by those authors) is the distal portion of a very narrow leaf, possibly attributable to *Linguifolium waitakiense*.

Two linear leaves preserved parallel and adjacent to each other were tentatively assigned to *Taeniopteris tenison-woodsii* by Walkom (1925) from the Newport Formation, Narrabeen Group, Sydney Basin, New South Wales (uppermost Olenekian; Metcalfe et al. 2015). They may be representative of *Linguifolium waitakiense* but the figure (Walkom 1925, pl. xxix, fig. 1) is insufficient for confident identification.

Strzeleckia Johnston 1895, a poorly understood genus, was established with material from the Tasmanian Triassic. Megascopically, it resembles *Linguifolium* except that it has no obvious midrib; instead, it has a series of closely parallel central veins (Holmes 1982). Some of Johnston's (1895) figured specimens have been re-assigned to *Linguifolium* (Walkom 1924a, Retallack 1980). Holmes (1982) reported *Strzeleckia gangamopteroides* Johnston 1895 from the Middle Triassic of the Gunnedah Basin, New South Wales. A very narrow leaf figured by Johnston (1895, fig. 8) as *Strzeleckia tenuifolia* Johnston 1895 was tentatively included by Walkom (1924a) in his genus *Johnstonia*.

***Linguifolium parvum* Holmes & Anderson**
in Holmes et al. 2010 emend. Pattemore
& Rigby herein

Fig. 6

Synonymy.

- 1980 *Linguifolium steinmannii* (Solms-Laubach) Frenguelli 1941; Retallack, figs 7C, 7D, 10I.
- 1980 *Linguifolium ascium*; Webb, text-fig. 44a–e, pl. 24, figs 1–3 [unpublished].
- 1981 *Linguifolium steinmannii* (Solms-Laubach) Frenguelli 1941; Retallack, fig. 9C–E.
- 1983 *Linguifolium steinmannii* (Solms-Laubach) Frenguelli 1941; Retallack, figs 8B, 8C, 10E.
- 2010 *Linguifolium parvum* Holmes and Anderson in Holmes et al., p. 7, pl. 9A–E.

Emended diagnosis. Leaves obovate, sessile. Midrib striated. Veins branching from

the midrib very acutely, curving toward margin, approaching margin acutely. Most veins bifurcating once (rarely twice) usually near midrib; uncommonly coalescing. Quantitative characters given in Table 6.

Material. UQF72597; east of Blackbutt, Queensland (Esk Formation, Esk Trough; Anisian). This site is near the Collinton site of Walkom (1917).

Occurrence. Basin Creek Formation, Nymboida Sub-Basin, New South Wales (Anisian); Toogoolawah Group, Esk Trough, Queensland (Anisian); South Island, New Zealand (Ladinian).

Description. Small fragment (35 mm long, 20 mm wide) of an obovate leaf. Venation branched from midrib acutely, curving toward the margin; bifurcating once, mostly near the

midrib. Midrib prominent, with median line, but thinning and less prominent apically.

Discussion. Holmes et al. (2010) erected *Linguifolium parvum* with material from the Middle Triassic of New South Wales (Nymboida Sub-Basin; Anisian). They recorded coalescent veins in some specimens (e.g. Holmes et al. 2010, fig. 9B), and included this character in their specific diagnosis. As noted previously, coalescent venation is unknown from the Gondwanan Upper Triassic despite a substantially larger collection having accrued from that interval.

Webb (1980) named a new (but unpublished) species, *Linguifolium ascium*, based on specimens from the Middle Triassic of Queensland (Anisian; Esk Trough). His figured specimens (including UQF72597, re-examined herein; Fig. 6) conform with *L. parvum*.

Holmes et al. (2010) recorded one specimen of *Linguifolium* as 'sp. A'. This small apical fragment has a finely toothed margin with veins apparently extending appreciably beyond the margin. A residual pattern of venation is discernible on the sediment surface adjacent to the specimen (Holmes et al. 2010, fig. 8e), indicating that the toothed margin and the extension of venation beyond the margin may be an artefact of the cleavage plane and that a significant amount of marginal lamina is missing. If this interpretation were confirmed the specimen may well belong to *L. parvum*.

Playford et al. (1982) assigned a specimen to *Linguifolium* sp. from the Moolayember Formation (upper Anisian–Ladinian; Draper 2013), Bowen Basin, Queensland, which apparently has anastomosing venation. This specimen has since been tentatively referred to *Gontriglossa* by Anderson and Anderson (1989). The venation (Playford et al. 1982, pl. 5, fig. 5) shows greater density of anastomosing veins to the left of the midrib. The specimen was re-examined in this study and some of these linked veins may be attributable to the residual impression of overlaying plant debris. The venation on the right-hand side of the midrib is possibly a closer representation of the original leaf. However, without better preserved specimens this remains conjectural. The specimen has a prominently striated midrib that probably extended to the leaf tip. The leaf lamina on the right-hand side of the midrib and in the basal portion of the specimen



Fig. 6. *Linguifolium parvum* Holmes & Anderson in Holmes et al. 2010 emend. Pattemore & Rigby herein. UQF72597, east of Blackbutt, Queensland (Esk Formation, Esk Trough; Anisian), Queensland. Scale: 1 cm in 1 mm increments

includes numerous coalescing veins, many more than are known in any *Linguifolium* species. The specimen possibly represents a sport.

Linguifolium steinmannii

(Solms-Laubach 1899) Arber 1917 emend.
Pattimore & Rigby herein

Synonymy.

1899 *Lesleya Steinmanni* Solms; Solms-Laubach, pp. 596–597, pl. XIII, figs 5–7.

1917 *Linguifolium Steinmanni* (Solms); Arber, p. 37.

1973 (?) *Linguifolium* sp.; Krassilov & Shorokhova, p. 25, pl. V, fig. 4, pl. VI, fig. 2.

Emended diagnosis. Leaves oblong-ovate, shortly petiolate. Apex narrowly obtuse or broadly rounded. Leaf base obtuse, asymmetric. Midrib prominent basally, thinning apically. Quantitative characters given in Table 6.

Occurrence. Western Gondwana and north-east Asia: Upper Triassic–lowermost Jurassic (imprecisely dated) of Region III, Chile; Lower Jurassic (Hettangian), Schitukhe Formation of eastern Russia (east of Vladivostok: Salyukova et al. 2013).

Discussion. Solms-Laubach (1899) assigned material from northwest of Copiapó, Chile (near Cerro La Ternera in Region III) to *Lesleya steinmannii* Solms-Laubach 1899. The locality, described by Steinmann (1899) and Frenguelli (1941), exposes a thick (>1800 m) sedimentary succession dated only broadly as Late Triassic–earliest Jurassic (Paulina et al. 2003, Charrier et al. 2007). Plant fossils from this same general area have also been reported by Herbst et al. (1998), Troncoso & Herbst (1999) and Gnaedinger & Herbst (2004). Solms-Laubach's (1899) figured specimens are three small fragments: the leaf is consistent with *Linguifolium* but differs from other species of the genus in being oblong with an obtuse base. All other species of *Linguifolium* have distinctly attenuate leaf bases (Tab. 6). Arber (1917, p. 37) recombined *Lesleya steinmannii* as *Linguifolium steinmannii* (as noted by Frenguelli 1941, p. 428; but cf. Retallack 1980, p. 50). It has been suggested that the obtuse leaf base figured by Solms-Laubach (1899, pl. XIII, fig. 5) resulted from physical damage (Retallack 1980); however, only one side of the midrib appears damaged and this is insufficient to regard the base as anything other than obtuse.

Krassilov and Shorokhova (1973) assigned complete leaves to *Linguifolium* sp. from the

Schitukhe Formation (Hettangian) to the east of Vladivostok; the geology and megafloora were subsequently discussed by Salyukova et al. (2013). Krassilov and Shorokhova's (1973) figures only show broad leaf detail; however, their description indicates the leaves resemble Solms-Laubach's (1899) foliar fragments in all but leaf width. The latter specimens are no wider than 20 mm, whereas the Russian specimens are larger (27–35 mm wide). Given the small and fragmentary nature of Solms-Laubach's material, the reported width is probably an underestimate. The most distinctive feature of both the Chilean and Russian specimens is the asymmetrically obtuse leaf bases.

Retallack (1980, 1981, 1983, 1985) assigned numerous specimens from the New Zealand Ladinian and Rhaetian to *Linguifolium steinmannii* (Tab. 3). His figured specimens that include leaf bases (two specimens: one Ladinian, the other Rhaetian) are both attenuate.

Specimens identified as *L. steinmannii* by Artabe et al. (1998), Gnaedinger and Herbst (1998), D'Angelo et al. (2011), and Morel et al. (2011) from the Upper Triassic of Argentina are assignable to either *L. arctum* or *L. lillianum*; leaf bases (where preserved) are attenuate and leaf shape is obovate or oblanceolate. A leaf assigned to *L. steinmannii* by Nielsen (2005, fig. 7(5)) from the Santa Juana Formation, Chile (Upper Triassic: Charrier et al. 2007) lacks both base and apex but its shape suggests it was probably an oblanceolate leaf with an attenuate base. In an unpublished thesis, Leppe (2005, pl. 20d, pl. 21a) attributed an ovate leaf to *L. steinmannii* from the Santa Juana Formation that apparently has an obtuse base and a width of ~60 mm. Although the specimen is much wider than other representatives of *L. steinmannii*, it otherwise appears consistent with the species. The figured leaf margin (Leppe 2005, pl. 20d) is unclear, but if confirmed it suggests the species attained considerably greater size than is indicated in Table 6.

From the Upper Triassic of Germany Kelber (1998) attributed a single apical portion of a leaf to an unnamed species of *Linguifolium*. Although seemingly conformable with the genus, the specimen is insufficient for specific identity, though it does suggest that the genus had dispersed beyond Gondwana by the Late Triassic.

Linguifolium curvatum Bose & Banerji 1984, from the Indian Middle–Upper Jurassic, represents the first report of this genus from the subcontinent (Bose & Banerji 1984). The species diverges considerably from others of the genus. Remains are fragmentary, lacking both apices and bases; the most complete specimens are curved and strongly asymmetric about the midrib in both leaf width and venation morphology. These specimens possibly belong to *Phyllopteroides* Medwell 1954.

The reconstruction of a *Linguifolium* leaf by Steinmann (1921, fig. 1) was based on several specimens from New Zealand (Ladinian) and Chile (Upper Triassic–lowermost Jurassic) and is not representative of an individual species. Indifferently preserved apical leaf fragments from Chubut Province, Argentina, assigned to *L. steinmannii* by Feruglio (1934, pl. 1, fig. 1 [lower left], fig. 2), are doubtful representatives of the genus; they were possibly collected from the Cañadón Asfalto Formation (Upper Jurassic: Cabaleri & Armella 2005).

Linguifolium sp. cf. *L. lillieanum*

Arber 1917

Synonymy.

1947 *Linguifolium denmeadi* Jones & de Jersey, p. 49, pl. iv, fig. 4, text-fig. 40.

1965 *Linguifolium denmeadi* Jones and de Jersey; Hill et al., pl. T8, fig. 2.

1980 *Linguifolium lillieanum* Arber 1913; Webb, pl. 20, figs 5–11, text-figs 40a–i [unpublished].

Material. GSQF604 and GSQF14503 (both on same slab); Nundah Colliery, Kedron Brook, Brisbane, Queensland (Aspley Formation, Kholo Subgroup, Ipswich Basin; Carnian).

UQF7636; Denmark Hill, Ipswich, Queensland (Blackstone Formation, Brassall Subgroup, Ipswich Basin; Carnian–lowermost Norian).

UQF13382; Petrie's Quarry (west side of Bartley's Hill), Albion, Brisbane, Queensland (Aspley Formation, Kholo Subgroup, Ipswich Basin; Carnian).

Description. Largest specimen 65 mm long (incomplete). Leaf obovate, up to 20 mm wide. Veins branching from midrib acutely (10°–40°), some curving away from midrib and slightly curving toward the apex near the margin, approaching margin acutely; most bifurcating once. Midrib 0.7–1.0 mm wide for most of its length, but apically very thin, extending to

rounded leaf apex. Venation density ~8 veins per 10 mm.

Occurrence. See specimen locations (above). Occurrence of *Linguifolium lillieanum*: Ladinian and Norian of New Zealand (Tab. 3); Norian of South America (Tab. 4); Carnian–lower Norian of Australia (Queensland and Tasmania: Webb 1980).

Discussion. Arber (1913, p. 345, footnote) noted that New Zealand Ladinian specimens of *Linguifolium lillieanum* appear to have a small number of coalescent veins. He did not regard this as true venation but rather a result of preservation or later damage. Arber (1917) reasserted this view and suggested that Seward's (1914, p. 38) contrary opinion was incorrect. Neither Bell et al. (1956) nor Retallack (1980, 1981, 1983) reported coalescent venation in specimens they assigned to this species; however, this character was recorded by Bell et al. (1956) in material referred to *L. waitakiense* (above).

Like *Linguifolium tenison-woodsii*, venation in *L. lillieanum* curves toward the apex (near the margin) and approaches the margin acutely, but this is apparently much less pronounced in the latter species. Arber's (1917) diagnosis stated '...veins arising at an acute angle to the midrib, arching upwards and then bending to the margin...'. Curving of venation distally, toward the apex, is only barely perceptible in Arber's (1913, 1917) figured specimens and seems to be absent apically. Presumably this is the 'bending' to which Arber (1917) was referring, as no other distal curvature of venation is discernible in his figures. In fact, no other figured specimens assigned to *L. lillieanum* nor to any other *Linguifolium* species from New Zealand show this feature; however, most specimens assigned to the genus from New Zealand are indifferently preserved (discussed above). Notably, only Arber's (1913, 1917) reports include photographs of *L. lillieanum* from New Zealand; all other figured specimens are reportedly poor, with line-drawn illustrations only.

Bell et al. (1956) and Retallack (1980, 1981, 1983, 1985) referred several specimens to *Linguifolium lillieanum* from the Middle and Upper Triassic of New Zealand (Tab. 3). The latter author's Ladinian and Norian specimens do not show venation curving toward the apex (near the margin) but they otherwise appear consistent with the type species. The

Table 4. Reports of *Linguifolium lillieanum* from South America

Reference	Formation/Group	Age
Gnaedinger & Herbst (1998)	El Tranquilo Group, Argentina	late Carnian–Norian (Gnaedinger & Herbst 1998, Morel et al. 2003)
Troncoso & Herbst (2000)	Cajón de Troncoso Beds, Maule region, Chile	Late Triassic (Charrier et al. 2007)
Gnaedinger & Herbst (2004)	La Ternera Fm, Chile	Norian–earliest Jurassic (Paulina et al. 2003, Charrier et al. 2007)
Herbst et al. (2005)	Panguipulli Fm, Chile	? Carnian–Norian (Herbst et al. 2005)
Tavera-Jerez (1960) Leppe (2005) Moisan et al. (2010)	Santa Juana Fm, Chile	Late Triassic (Charrier et al. 2007)
Morel et al. (2011)	Rio Blanco Fm, Argentina	? Norian (Morel et al. 2003)

figured specimen attributed to *L. lillieanum* by Retallack (1985, fig. 9C(5)), reportedly from the Rhaetian of New Zealand, is a very small fragment with insufficient detail for specific assignment. The type species has been reported from several Upper Triassic locations in South America (Tab. 4). Some figured specimens show slight distal curvature of venation resembling that figured by Arber (1913, 1917).

Specimens examined herein show venation curving toward the leaf apex near the leaf margin but only weakly and not apically or basally; in other features they are consistent with Arber's (1917) diagnosis. Jones and de Jersey (1947) assigned the apical portion of a leaf to their species *Linguifolium denmeadii*; this specimen (UQF7636) was also figured by Hill et al. (1965). As indicated above, the apical portion of specimens assigned to *L. tenisonwoodsii* and *L. lillieanum* (and other species; Tab. 6) is of doubtful diagnostic significance. Specimen UQF7636 is almost certainly a *Linguifolium* leaf; in the absence of more complete specimens we regard it as probably within the range of natural variation of the type species. Webb (1980) also ascribed this specimen to the type species.

Flint and Gould (1975) identified *Linguifolium denmeadii* from the Red Cliff Coal Measures, New South Wales (Anisian) but it was not described or figured, nor apparently retained institutionally; furthermore, no specific collection location was indicated. A specimen attributed to *L. denmeadii* by White (1961, pl. 5, fig. 3) from the Western Australian Cretaceous was referred by McLoughlin (1996) to his species *Phyllopteroides westralensis*. Retallack (1995) noted that specimens attributed to *Linguifolium* by White (1961) – presumably those identified as *Linguifolium* sp., from the Culvida Sandstone (Olenekian–Anisian), Canning

Basin, Western Australia – are assignable to *Dicroidium*. A specimen was reported by White (1963, 1964) from the Blantyre Sandstone, Eromanga Basin, Queensland (Middle–Late Jurassic: Cook et al. 2013) as possibly assignable to *Linguifolium*; it was not figured and she considered it too fragmentary for confident generic identification.

Walkom (1917) and Webb (1980) assigned specimen GSQF604 from the Ipswich Basin to *Taeniopteris tenisonwoodsii* and to *Linguifolium tenisonwoodsii* respectively. The leaf shape and width suggest resemblance to the type species. The only specimen explicitly identified by Jones and de Jersey (1947) as *L. lillieanum* (GSQF7635 but not figured by those authors) could not be located during the present study.

Figured specimens assigned to *Linguifolium lillieanum* by Webb (1980) show no indication that veins curve toward the apex, except perhaps very weakly in the apical portion of one specimen (Webb 1980, pl. 20, fig. 11, from the Aspley Formation, Kholo Subgroup, Ipswich Basin; Carnian). All but one of Webb's (1980) figures (pl. 20, fig. 5) suggest the midrib is very weak or absent apically. His figured specimens are from Barber's Mine, near Fingal, Tasmania (Carnian–lower Norian: Reid et al. 2014) and Campbell's Quarry, Albion, Brisbane, Queensland (Aspley Formation, Kholo Subgroup, Ipswich Basin; Carnian). The Queensland specimens were unavailable for re-examination.

Specimen UQF13382 from the Aspley Formation, Kholo Subgroup, Ipswich Basin (Carnian) is a basal fragment of a *Linguifolium* leaf. It is the only specimen examined herein from the Carnian–lowermost Norian of Queensland that shows twice-forked veins; such venation was not identified in any specimen from

Table 5. *Linguifolium*: key specimens

Species	Stratigraphic interval	Key figured specimens and remarks
<i>L. steinmannii</i> (Solms-Laubach 1899) Arber 1917 emend. Pattenmore & Rigby herein	Upper Triassic–Hettangian	Solms-Laubach (1899, pl. XIII, figs 5–7); Krasilov & Shorokhova (1973, pl. V, fig. 4, pl. VI, fig. 2). Complete leaves from the Hettangian of Russia. Chilean material is fragmentary and age imprecisely known (Upper Triassic–lowermost Jurassic)
<i>L. arctum</i> Menéndez 1951	?Norian	Menéndez (1951, pl. VI); Artabe et al. (1998, fig. 5e); Morel et al. (1999, fig. 5e). Poorly understood; limited to several South American specimens. <i>Linguifolium patagonicum</i> Gnaedinger & Herbst 1998 may be a junior synonym of this species; it has a smaller angle between venation and midrib in the apical portion of the leaf
<i>L. llantenense</i> Menéndez 1951	?Norian	Menéndez (1951, pl. VII, figs 1–4). Poorly understood; limited to a few South American specimens. Retallack (1980) considered this species to be a junior synonym of <i>L. arctum</i> . Secondary veins form an ‘S’ curve across the lamina (Menéndez 1951)
<i>L. tenison-woodsii</i> (Shirley 1898) Retallack 1980 emend. Pattenmore & Rigby herein	Carnian–lowermost Norian	Figs 2, 3 herein; Anderson & Anderson (1989, pl. 311–314); Pattenmore & Rigby (2005, fig. 7C, D). The majority of specimens attributed to <i>Linguifolium</i> have been referred to this species. Cuticle described from South Africa (10 specimens; Anderson & Anderson 1989)
<i>L. lillieanum</i> Arber 1917 [type species]	Ladinian–Norian	Arber (1913, pl. 7, figs 1, 4); Arber (1917, pl. III, figs 1, 7); Tavera-Jerez (1960, pls 1–3). Species poorly understood. Chiefly identified from New Zealand (Tab. 3) and South America (Tab. 4) but most indifferently preserved. The published record is insufficient to allow a detailed comparison of Ladinian and post-Ladinian specimens assigned to this species. Largest specimens, >40 mm wide, from the Upper Triassic of Chile (Tavera-Jerez 1960, Troncoso & Herbst 2000, Leppe 2005). Specimens from the Ladinian–Norian of New Zealand are <36 mm wide but are fragmentary (Retallack 1980), and those from the Carnian–lower Norian of Australia are <45 mm wide (Webb 1980)
<i>L. waitakiense</i> Bell in Bell et al. 1956 emend. Pattenmore & Rigby herein	Anisian–Ladinian	Figs 4, 5 herein. Known from almost-complete leaf and several fragments
<i>L. parvum</i> Holmes & Anderson in Holmes et al. 2010 emend. Pattenmore & Rigby herein	Anisian–Ladinian	Fig. 6 herein; Retallack (1980, fig. 10I); Holmes et al. (2010, fig. 9A–E). Known from almost-complete leaves

the Brassal Subgroup, Ipswich Basin (stratigraphically above the Kholo Subgroup: Purdy & Cranfield 2013). However, being only a basal leaf fragment, it could not be identified confidently at specific level.

Linguifolium lillieanum is an uncommon component of Gondwanan floral assemblages. The type species is poorly understood, being based mainly on only a few incomplete specimens, mostly from New Zealand and South America (Tabs 3, 4, 5). The largest and most complete leaves have been reported by Tavera-Jerez (1960) and Leppe (2005) from the Santa Juana Formation, Chile (Upper Triassic: Charrier et al. 2007).

Only a few reports illustrate material that clearly shows venation curved toward the apex (near the margin), as originally figured and diagnosed by Arber (1917). Insufficient information exists to definitively compare Middle

and Upper Triassic specimens assigned to the type species (Tabs 5, 6). Seward’s (1914) suggestion that the type material includes coalescent venation has not been confirmed.

DISCUSSION

The Triassic megafloal assemblages of southeast Queensland and New Zealand were located near the Eastern Gondwanan margin at high latitude (>50°S: Golonka 2007, Sun et al. 2012). Temperatures in the Early Triassic were elevated globally; equatorial temperatures exceeded the tolerance threshold of many plant and animal groups, resulting in sustained suppression of the ecosystem, but conditions at higher latitudes were more equable (Sun et al. 2012, 2013, Metcalfe et al. 2013, Haig et al. 2015). The extreme climate resulted

Table 6. *Linguifolium*: species comparison

Taxon		<i>L. parvum</i>	<i>L. waitakiense</i>	<i>L. lillieanum</i> [type species]	<i>L. tenison-woodsii</i>	<i>L. llantenense</i>	<i>L. arctum</i>	<i>L. steinmannii</i>
Stratigraphic interval		Anisian–Ladinian	Anisian–Ladinian	Ladinian–Norian	Carnian–lowermost Norian	?Norian	?Norian	?Upper Triassic–Hettangian
Leaf character	Shape	Obovate	Linear	Obovate	Linear	Oblanceolate	Oblanceolate	Oblong-ovate
	Apex	Acute–obtuse	Acute–obtuse	Acute–obtuse	Acute–obtuse	Obtuse	Acute–obtuse	Obtuse
	Base	Asymmetric, attenuate	Asymmetric, attenuate	Asymmetric, attenuate	Attenuate	Attenuate	Attenuate	Asymmetric, obtuse
	Maximum length (mm)	~110	~140	>200	>200	~100	~100	~90
	Width (mm)	<22	6–14	17–60	<10	<~15	<~15	20–35
	Petiole	sessile	Slender, 20 mm long, 0.8 mm wide	Stout, ~10 mm long, 2 mm wide	?	?	?	Stout, <~5 mm long, 2–3 mm wide
Leaf venation	Midrib width	~1.5 mm, <0.3 mm apically	~1.0 mm, 0.2 mm apically	1–2 mm but weak apically	<1.1 mm, 0.2 mm apically	<1.5 mm basally	~1 mm basally	Prominent, weak apically
	Branching angle	<40°	<40°, <60° apically	<40°	<40°, commonly exceeded apically	<10° basally, <40° apically	<10° basally, ~35° apically	20°–40°
	Distally curving toward tip	None visible	No or slight (<0.3 mm from margin)	No or slight	Commonly, but usually not apically	Yes	No	No
	Bifurcation	Nil or 1, rarely 2	Nil or 1, rarely 2	Nil, 1 or 2	Nil or 1	Nil, 1 or 2	Nil or 1	Nil, 1 or 2
	Density (veins/10 mm)	8–18, increasing apically	8–20: 8–12 basally, 16–20 apically	8–16	6–16, increasing apically	~10	~14	?
	Coalescent	+	+	–	–	–	–	–
Cuticle described		–	–	–	+	–	–	–

in a global ‘coal gap’ through the Early Triassic (Retallack et al. 1996, Metcalfe et al. 2015). Global temperatures declined late in the Early Triassic, thus facilitating the development of extensive peat-forming environments during the Middle and Late Triassic.

Historically, speciation in *Linguifolium* has been problematic, having been determined largely on leaf size (e.g. Retallack 1980). Species as defined above and in Table 6 are not diagnosed differentially on leaf size alone. For example, excluding leaf size, *L. waitakiense* and *L. parvum* are separated by two (possibly three) characters; and *L. waitakiense* and *L. tenison-woodsii* are separated with three characters. Importantly, these characters also show that most species occur in more restricted stratigraphic intervals than previously acknowledged. This degree of well defined speciation has not been achieved in many Triassic genera, including those of the

umkomasiaceans (Pattemore et al. in press). Variation in leaf size should of course be expected in any plant population, fossil or otherwise, due to growth stage (ontogeny), degree of sun exposure, and other environmental factors. Among species of most plant genera, the spread of leaf sizes and other characters is not only a challenge restricted to palaeobotany but is equally a matter of consideration and debate regarding extant plant genera (e.g. Parnell et al. 2006). The type species of *Linguifolium* and species recorded from South America are less well understood than others of the genus (Tabs 5, 6); however, of these, only *L. arctum* and *L. llantenense* are not convincingly separated. They are regarded herein as distinct species based on Menéndez’s (1951) specification of venation differences (Tab. 5). However, as suggested by Retallack (1980), the latter may be a junior synonym of the former.

Coalescent venation occurs in two species of *Linguifolium* (Tab. 6) and, notably, both are restricted to the Middle Triassic. Seward (1914) suggested that veins coalesce in the type specimens (Ladinian) of the type species but this remains unconfirmed. In all specimens with coalescent veins, merging only occurs once or twice per leaf. Although relatively few specimens have been attributed to *Linguifolium* from the Middle Triassic, coalescent venation is known in a number of these. In contrast, the vast majority of specimens assigned to *Linguifolium* are from the Upper Triassic but none possesses coalescent venation. The genus is best known from the Carnian–lowermost Norian; numerous Australian and South African specimens from that stratigraphic interval have been attributed to *L. tenison-woodsii*. Moreover, apart from catalogued specimens, many slabs from the Ipswich Basin held in the Queensland Museum include fragments attributable to *L. tenison-woodsii*. Despite the large number of available specimens, none has coalescent venation.

Generally, the trend from netted to more or less parallel venation results in a lower vein length per unit area (VLA). Representatives of *Linguifolium* figured by Holmes et al. (2010), Retallack (1980, 1981, 1983, 1985) and herein all have a very low VLA (1–2.4 mm/mm²). The leaf shape, size and very low VLA in *Linguifolium* species is most advantageous in a well-watered, canopied environment (Sack & Scofoni 2013). No correlation between VLA and age is evident in our specimens, nor in illustrated Australasian specimens, many of which are interpretive as they were hand-drawn. Moreover, VLA varies significantly along the leaf in species of the genus (lower basally–higher apically), so a much larger dataset is required for a reliable comparison of VLA amongst species. The consistently very low VLA suggests the host plants' preferred habitat did not vary significantly through the Middle and Late Triassic.

Linguifolium is not recorded from the Lower Triassic. Although there has been speculation that the genus derived from the Permian glossopterids (Seward 1914, Berry 1945, Bell et al. 1956), support for this was only based on net venation in both groups. Recapitulation of glossopterid-like leaf morphology is known in unrelated species from the post-Permian (Rigby 1984). Net venation has since been reported in

several plant groups from the Gondwanan Triassic (Anderson & Anderson 2003).

Linguifolium dispersed beyond Gondwana by the Late Triassic, where it persisted in the earliest Jurassic (Hettangian). The genus may have also remained in Western Gondwana through the earliest Jurassic. In Australasia, and probably elsewhere in Eastern Gondwana, the genus was extinct by the end-Triassic.

CONCLUSIONS

1. Speciation of *Linguifolium tenison-woodsii*, *L. waitakiense*, *L. parvum*, and *L. steinmannii* is now well defined on characters other than leaf size.

2. The earliest record of *Linguifolium* is from the Anisian of Eastern Gondwana, and the genus probably became extinct in Gondwana by the end-Triassic but possibly continued in Western Gondwana through the earliest Jurassic. The genus dispersed beyond Gondwana by the Late Triassic and persisted there in the Early Jurassic (Hettangian).

3. *Linguifolium* specimens with coalescent venation are restricted to the Middle Triassic of Australasia.

4. *Linguifolium tenison-woodsii* is restricted to the Carnian–lowermost Norian of Australia and South Africa, and is recorded for the first time from the Tarong Basin (upper Carnian), Queensland.

5. The parent plants that bore *Linguifolium* leaves probably inhabited well-watered, canopied environments. The higher taxonomic affinity of the genus is uncertain.

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