

# The structure of umkomasiacean fructifications from the Triassic of Queensland

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Received 15 October 2015, accepted for publication 7 December 2015

**ABSTRACT.** The plant fossil genera *Umkomasia* Thomas 1933 and *Pteruchus* Thomas 1933 emend. Townrow 1962 are known chiefly from the Middle and Upper Triassic of Gondwana. The structure of these fructifications has been conjectural, some being identified as pinnate, others as helically arranged. Specimens from the Ladinian–lower Norian of Queensland (northeastern Australia) show that the female and male fructifications – *U. geminata* (Shirley 1898) Rigby in Playford et al. 1982 emend. nov. and *P. dubius* Thomas 1933 emend. Townrow 1962, respectively – have a bipinnate structure. Those fructifications and the bipinnate leaf, *Dicroidium feistmantelii* (Johnston 1894) Gothan 1912, probably all belonged to the same parent plant. It was first suggested by John Townrow in 1962 that the sporangial heads of *P. dubius* have a pinnate structure; this character is confirmed herein. *Pteruchus* is recorded for the first time from the Carnian Tarong Basin, Queensland.

The holotype of *Stachyopitys simmondsii* Shirley 1898 is shown to be ovuliferous. The species is recombined as *Umkomasia simmondsii* (Shirley 1898) comb. et emend. nov. Genuine male fructifications, previously identified as *S. simmondsii*, and later as *Pteruchus simmondsii* (Shirley 1898) Jones and de Jersey 1947, are assigned to *P. minor* Thomas 1933. That species comprises the smallest fructifications of the genus. *Townrovia polaris* Bomfleur et al. 2011 and *Stachyopitys lacrisporangia* Anderson & Anderson 2003 are identified as junior synonyms to *P. minor*. The diagnosis of *Townrovia* Retallack 1981 is inaccurate and the genus is insufficiently distinguished from *Pteruchus*.

**KEYWORDS:** Gondwana, Triassic, Queensland, Esk Trough, Ipswich Basin, Tarong Basin

## INTRODUCTION

The family Umkomasiaceae Petriella 1981 is chiefly represented in the Anisian through Norian of Gondwana and has been rarely reported from beyond Gondwana (Pattemore et al. 2015a). There have been widely divergent opinions and taxonomy regarding leaves assigned to the family (cf. Retallack 1977, Anderson & Anderson 1983) and on the structure of its fructifications (Townrow 1962a, Yao et al. 1995, Petriella 1980, Taylor et al. 1984, Holmes 1987, Klavins et al. 2002, Anderson & Anderson 2003, Pattemore & Rigby 2005). Predominately, the family includes the female and male fructifications – *Umkomasia* Thomas 1933 and *Pteruchus* Thomas 1933 emend. Townrow 1962a, respectively (discussed below) – and the foliate *Dicroidium* Gothan 1912 emend. Townrow

1957, but several other genera have also been allied with the family (Pattemore et al. 2015a). The morphology of the parent plants of some species and their position in the ecosystem are known in some detail (Axsmith et al. 2000, Cúneo et al. 2003, Taylor et al. 2006). However, phylogenetic relationships both within the family and more broadly are poorly understood (Pattemore et al. 2015a). Previous studies include Meyen (1984), Crane (1985), Retallack & Dilcher (1988) and Gordenko & Broushkin (2015). The umkomasiacean lineage probably terminated globally near the end-Triassic (Pattemore et al. 2015a); specimens reported by Kirchner & Müller (1992) from the Liassic of Germany are doubtful representatives of the family (below).

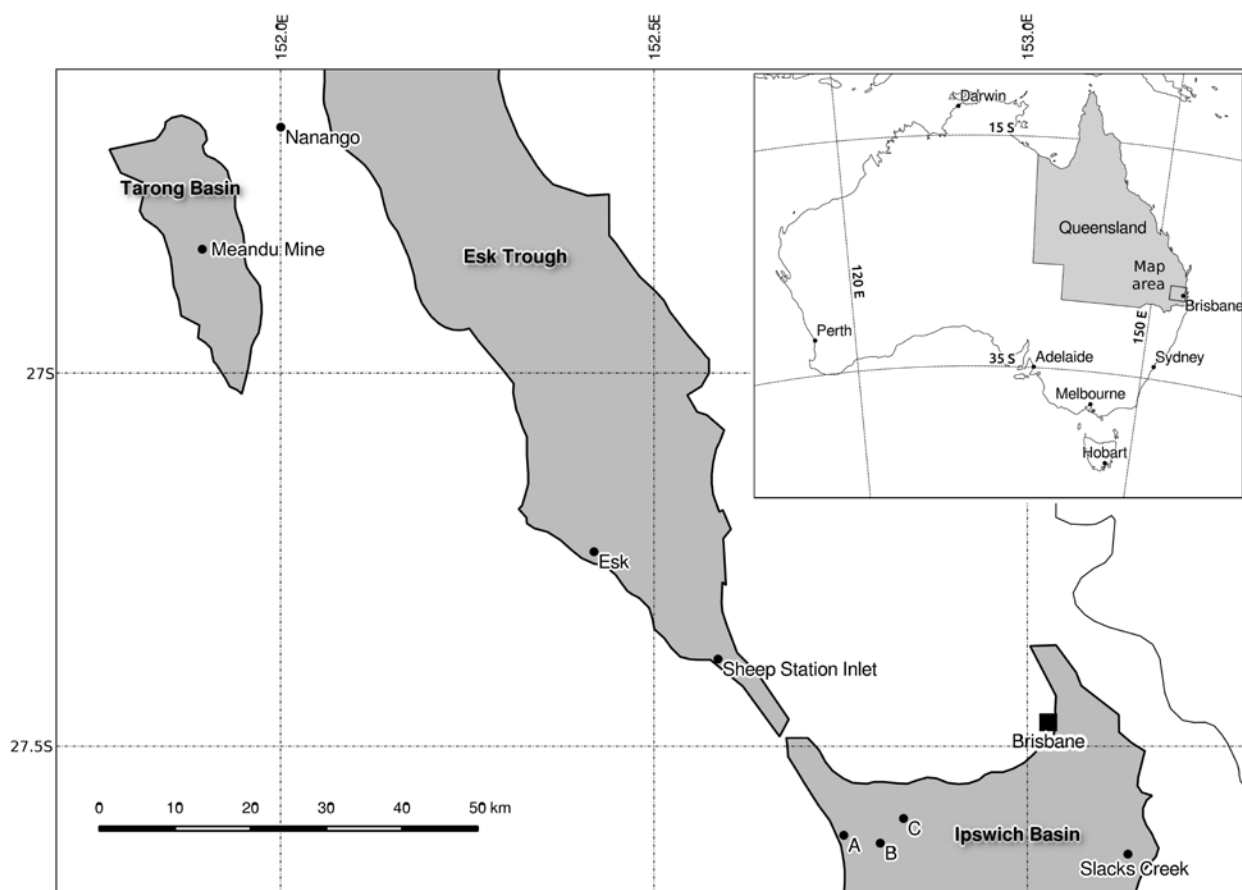
Structural detail of umkomasiacean fructifications from the Triassic of Queensland (Fig. 1) is advanced herein. Results of this study suggest that the interpretation and taxonomy of several specimens attributed to this family from Gondwana and beyond require reconsideration.

## 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). New material comprises previously undescribed specimens from the Queensland Museum and specimens collected from the Meandu Mine (lat., 26.836346°S; long., 151.894089°E), Tarong Basin (Fig. 1). Mine specimens were recovered from a fresh spoil heap by or with the assistance of mine staff (see acknowledgements). Specimens examined herein from the Moolayember Formation, Bowen Basin, Queensland, were first reported by Playford et al. (1982) from north of Injune, Queensland. All other specimens are from well-known fossil sites in southeast Queensland as

indicated in the text and Fig. 1. Specimens are preserved as compressions or impressions and, unless otherwise stated, are not carbonaceous.

Umkomasiaceans have been allied with the class Ginkgoopsida (Meyen 1984, Gordenko & Broushkin 2015). Ginkgoalean long and short shoots are well understood botanically and terminology applied herein follows Leigh et al. (2011) and Little et al. (2013). Terminology applied to umkomasiacean fructifications has been complicated as a result of conflicting views on attachment mode (above). Helically arranged fructifications comprise several fertile structures, each branched individually from an axis and with each branch constituting a separate sporophyll (e.g. Yao et al. 1995). In contrast, pinnate fructifications comprise a rachis bearing fertile structures that are branched in a single plane, oppositely–alternately (e.g. Townrow 1962a, b); the entire structure, including the rachis, is a single sporophyll. Townrow's (1962a) study was the first comprehensive analysis of the structure of umkomasiacean fructifications. His interpretation is confirmed herein. Indeed, the fructifications are based on a pinnate plan resembling that of the frond *Dicroidium*. Thus, the terminology applied by Townrow (1962a) is adopted herein. More generally, pinnate morphological terminology follows Andrews (1990, pp. xiii–xx) and Vasco et al. (2013). All references to the ICN are based on McNeill et al. (2012).



**Fig. 1.** Triassic basins of southeast Queensland, Australia: Esk Trough (Anisian), Ipswich Basin (Carnian–lowermost Norian), Tarong Basin (upper Carnian). Key to locations: **A** – Denmark Hill; **B** – Blackstone Hill; **C** – Dinmore. Co-ordinates in decimal degrees

## SYSTEMATIC PALAEOBOTANY

Class: **Ginkgoopsida**Order: **Peltaspermales**Family: **Umkomasiaceae** Petriella 1981

**Discussion.** Representatives of the Umkomasiaceae and their speciation and phylogeny have been discussed by Petriella (1981), Meyen (1984), Pattemore et al. (2015a) and references therein. Higher systematic placement herein follows Meyen (1984).

Genus: **Umkomasia** Thomas 1933

**Type species.** *Umkomasia macleanii* Thomas 1933 by original designation. Type specimen figured by Thomas (1933, pl. 23, fig. 56), Klavins et al. (2002, fig. 16) and Anderson & Anderson (2003, pl. 82, fig. 8).

**Discussion.** Thomas (1933) erected *Umkomasia* and *Pilophorosperma* which he largely differentiated using cupule structure but these genera have subsequently been regarded as synonymous (Holmes 1987, Klavins et al. 2002). Both genera were diagnosed with bilateral branching. Thomas (1933) also erected *Spermatocodon* for specimens with helical branching but which otherwise resemble *Umkomasia*. *Spermatocodon* was based on only two fragments, although they were reportedly well preserved. Apart from branching arrangement, Thomas separated the aforementioned three genera based on cupule characters and cuticle. Anderson and Anderson (2003) regarded Thomas's (1933) figured specimens – those variously assigned to one of the above three genera – as belonging to the type species of *Umkomasia*.

Holmes (1987) regarded *Spermatocodon* as distinct from *Umkomasia* but emended the diagnosis of the latter genus to include helical branching. Likewise, Klavins et al. (2002) did not include *Spermatocodon* in *Umkomasia* but emended the diagnosis of the latter genus, removing reference to bilateral branching and explicitly identifying spiral arrangement in ultimate branches. The generic emendation by Klavins et al. (2002) followed the discovery by Axsmith et al. (2000) of a specimen from near the Shackleton Glacier in the Ladinian–Carnian of the Central Transantarctic Mountains, Antarctica, that has biologically

connected organs resembling *Umkomasia* and *Dicroidium*. Their ovulate fructifications, assigned to *U. uniramia* Axsmith et al. 2000, have an unusual whorled arrangement which is unlike that of other representatives of the genus. Their attribution to *Umkomasia* and the reported organic connection has been questioned by Anderson and Anderson (2003), Holmes and Anderson (2005), and Anderson et al. (2008) on the basis of long and short shoot development. However, their reasoning was shown to be doubtful using an example from a living *Ginkgo biloba* L. (Axsmith et al. 2007); that species has complex and highly variable shoot development that is strongly influenced by environmental conditions (Leigh et al. 2011, Little et al. 2013). The suggestion by Artabe and Brea (2003) that the specimen assigned to *U. uniramia* by Axsmith et al. (2000) does not have organically connected organs was refuted by Axsmith et al. (2007). Artabe and Brea (2007) regarded *U. uniramia* as structurally distinct from the umkomasiaceans. Arce and Lutz (2010) offered no new insight.

Species now included in *Umkomasia* have a variety of reported branching arrangements: (1) bilateral, opposite to subopposite [*U. polycarpa* Holmes 1987]; (2) bilateral, alternate [*U. macleanii*]; (3) helical [*U. distans* Holmes 1987, *U. resinosa* Klavins et al. 2002]. Anderson and Anderson (2003, p. 240) noted the diversity of branching mode that has been included in the genus. Klavins et al. (2002, pp. 670, 672) suggested that specimens preserved as compressions and having apparently opposite or alternate bilateral arrangement have been misinterpreted because they lack three-dimensional detail, implying that all species are helically arranged; hence, their proposed generic emendation. Stem twist recorded in vascular traces of specimens described herein does not support this view, rather indicating that fructifications were pinnate or bipinnate. *Umkomasia geminata* (Shirley 1898) Rigby in Playford et al. 1982 had been regarded as helically (Playford et al. 1982, pl. 5, fig. 2) or irregularly arranged (Pattemore & Rigby 2005); all specimens from both of these collections are re-assessed herein. Previously considered to represent single fructifications, they are re-interpreted as pinnate fructifications emerging from small short shoots (discussed below). What had been regarded as the main axis of a single fructification is shown to be a long shoot. This interpretation may also

apply to other species: e.g. *U. polycarpa* Holmes 1987 and *U. quadripartita* Anderson & Anderson 2003.

Representatives of *Umkomasia* evidently had most of their total weight distributed among their numerous cupulate ovules and, in life, were probably pendulous open panicles. Most recorded specimens have a disturbed and fragmented preservation that probably resulted from ovules being disarranged during burial. Thus, in permineralized specimens, analysed using sectioning, it is not surprising to find ovules arranged around a stem in a manner suggesting a mode other than pinnate. Moreover, absent systematic sectioning, stem twist or damage may not be observed.

Pattemore et al. (2015a) noted that variation in branching mode recorded in species assigned to the Umkomasiaceae suggests that the family is not monophyletic. Organs described herein that probably belonged to the same plant (see below: *Umkomasia geminata*, *Pteruchus dubius*, *Dicroidium feistmantelii*) all have a bipinnate structure. Specimens possessing genuine helical branching are probably taxonomically distinct from *Umkomasia* and the Umkomasiaceae. The genus has been reported from outside Gondwana (Pattemore et al. 2015a and references therein).

***Umkomasia simmondsii*** (Shirley 1898)  
comb. et emend. nov.

Fig. 2

**Synonymy.**

- 1898 *Stachyopitys Simmondsi* Shirley, p. 13, pl. 18, fig. 2.  
1917 *Stachyopitys Simmondsi* Shirley; Walkom, p. 13 (not figured).  
1947 *Pteruchus simmondsi* (Shirley) Thomas; Jones & de Jersey, p. 55 (not figured).  
1962a *Pteruchus simmondsi* (Shirley) Thomas; Townrow, pl. 24, fig. 2 only.

**Emended diagnosis.** Small pinnate ovuliferous fructification arising from bulbous short shoot. Short shoot 1.8 mm wide, 1.5 mm long. Scale-like appendages ca 1.5 mm long, 0.4 mm wide also arising from short shoot (?bases of other rachides). Rachis slender, <0.4 mm wide, >19 mm long, probably having 5 or more oppositely attached pedicel pairs. Pedicels ca 2.5 mm long, extending around cupule and attached near uppermost point. Ovules cupulate, ca 1 mm wide, ca 1.4 mm long. Cupule ca 0.1 mm thick, apparently covering most (?all) of ovule.

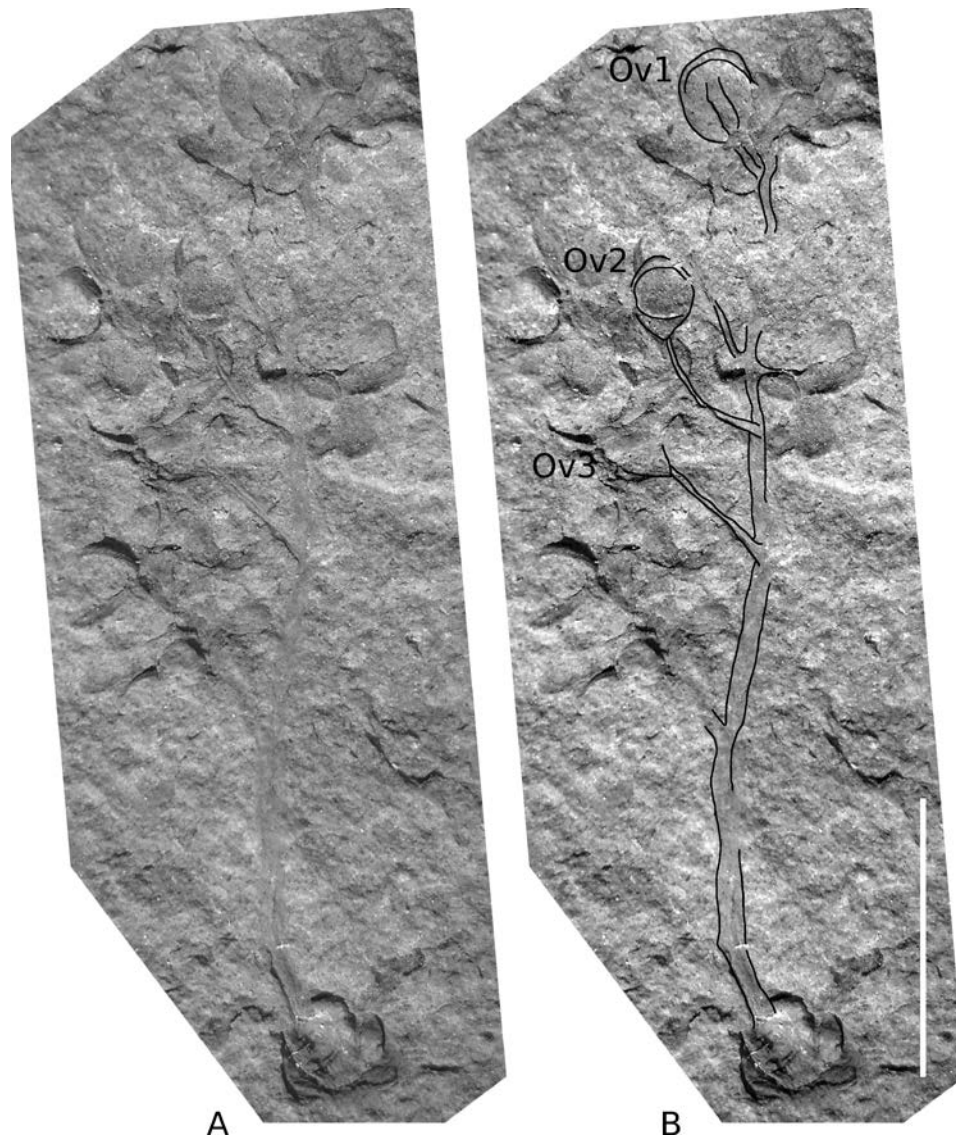
**Type material.** Shirley (1898, p. 13, pl. 18, fig. 2), GSQF256, holotype by effective original designation (ICN, Article 9.1, Note 1): Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013).

**Material.** GSQF256 (holotype): Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Line-drawn by Shirley (1898, pl. 18, fig. 2) as *Stachyopitys simmondsii* Shirley 1898. Small photographic figure provided by Townrow (1962a, pl. 24 fig. 2). Fig. 2 herein.

**Occurrence.** Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian).

**Discussion.** Specimen GSQF256 was first described by Shirley (1898) as *Stachyopitys simmondsii*. It is very small and unattached debris resembling fragments of *Antevsia extans* (Frenguelli 1944) Townrow 1960 are scattered amongst the fructification, thus suggesting that it is a male fructification (hence Shirley's interpretation). Indeed, it was recombined as *Pteruchus simmondsii* (Shirley 1898) Jones & de Jersey 1947 [author attribution: ICN, Article 41.3] and this was later supported by Townrow (1962a) and Retallack (1977). Attribution to *Pteruchus* had earlier been suggested provisionally by Thomas (1933, p. 244); he indicated that several characters required clarification before the "generic identity can be regarded as established". Anderson and Anderson (2003, p. 217) stated that "... *S. [stachyopitys] simmondsii* from Queensland, based on a complete strobilus, is accepted by us as a valid species".

Specimen GSQF256 is re-figured herein (Fig. 2) at considerably higher resolution than was previously available, revealing that the only clearly attached reproductive parts are ovuliferous and, although very small, they resemble cupulate ovules of *Umkomasia*. The fructification was preserved in such a way that pinnae have mostly been swept to one side of the rachis (Fig. 2A, B). Ovules (Fig. 2B) are attached: ovule Ov2 shows that they are cupulate; ovule Ov3 is incomplete and has a feathered edge due to a thin band of white mineralization through that part of the rock slab. Another ovule with probable but obscured attachment (Fig. 2B, Ov1) shows a pedicel positioned at the back of an ovule such that the micropyle would be



**Fig. 2. A, B:** *Umkomasia simmondsii* (Shirley 1898) comb. et emend. nov.; GSQF256 (holotype); Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). **A** – fructification and short shoot; **B** – modification of A with enhanced contrast and camera lucida overlay. Ov1–3 indicate ovules. Scale: A as for B; B – 5 mm

oriented toward the rachis. The specimen lacks the scale-like appendages that both subtend pinnae and are paired on pinnae in representatives of the type species (Thomas 1933, Anderson & Anderson 2003). If not for the absence of these scales in specimen GSQF256, the combination proposed herein would invoke synonymy with *U. macleanii* [type species].

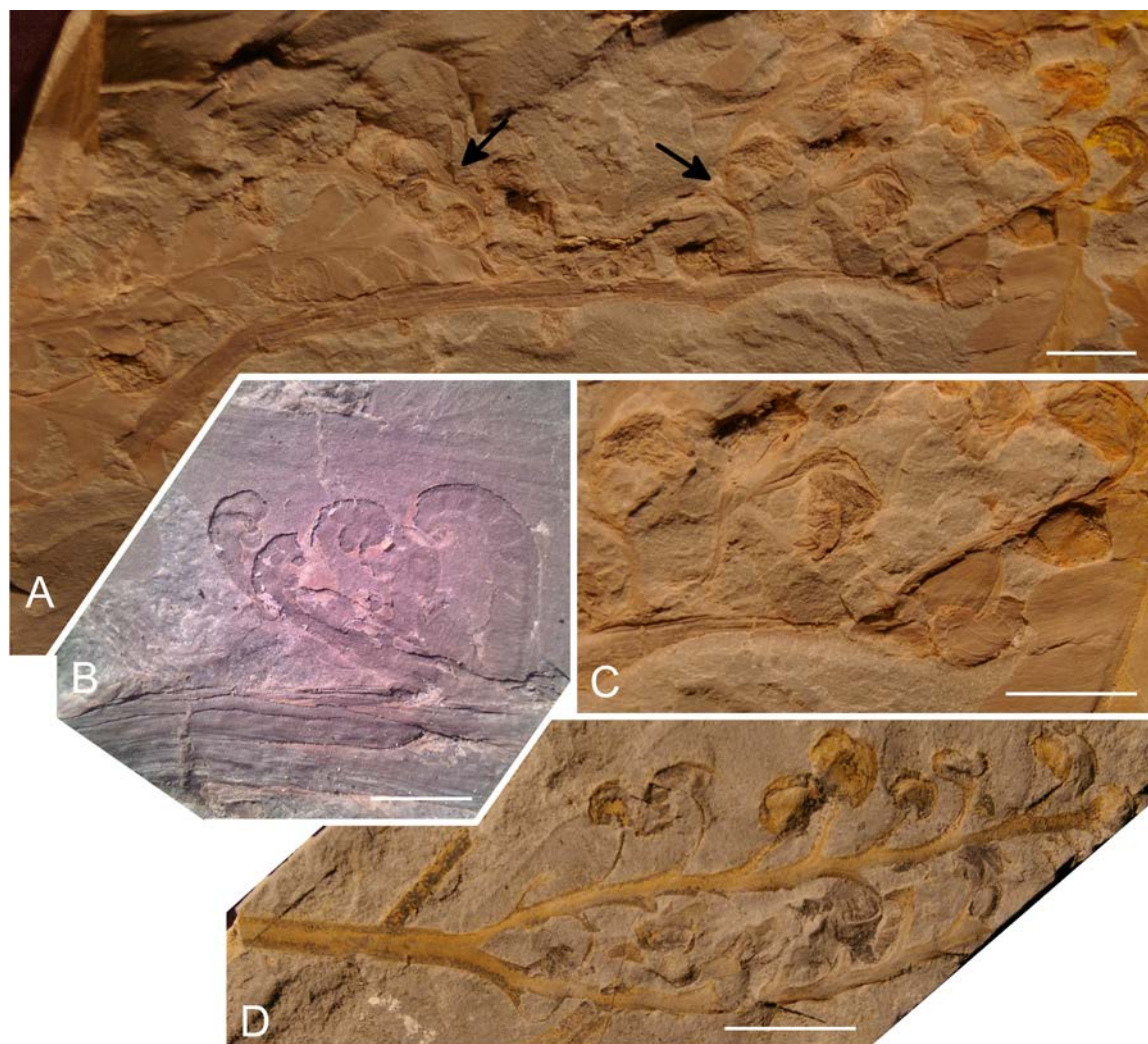
***Umkomasia geminata*** (Shirley 1898) Rigby in Playford et al. 1982 emend. nov.

Figs 3, 4

Synonymy. See Pattemore & Rigby (2005, p. 333).

Emended diagnosis. Megasporophyll borne on short shoot. Several short shoots per

long shoot, irregularly (?bilaterally) arranged, some bearing leaves. Long shoot ca 5 mm wide, >130 mm long (probably substantially longer). Short shoot, very small, ca 5 mm wide, 1–3 mm long. Megasporophyll pinnate, >50 mm long, some with bifurcating rachides, generally having paired opposite–subopposite cupulate ovules (1-pinnate) or pinnately branched, attaching an ovule pair (2-pinnate). Rachis 1–2.5 mm wide. Pedicels short, <5 mm long, <1 mm wide (not including portion curled around cupule). Pedicel curling around cupule such that vascular connection with cupule is farthest from rachis; thus, micropyle directed inwardly. Curled section of pedicel adpressed on cupule but having distinct vascular bundle. Cupulate ovules elliptical, varying in size from 5 × 4.5 mm to 17 × 11 mm.



**Fig. 3. A–D** – *Umkomasia geminata* (Shirley 1898) Rigby in Playford et al. 1982 emend. nov. **A–C** – QMF42583; Blackstone Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian); **A** – entire specimen including long shoot, several attached megasporophylls (arrows indicate possible rachis bifurcations) and foliar crozier; **B** – foliar crozier; **C** – right-hand section of long shoot; collected by R. Knezour; **D** – UQF59912B; former State Quarry, Slacks Creek, Brisbane; Tingalpa Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian); bifurcating megasporophyll. Scale: A, C, D – 1 cm; B – 5 mm

Type material. Shirley (1898, p. 16–17, pl. 20, figs 1–5), GSQF103 (lectotype designated by Rigby in Playford et al. 1982, p. 8, pl. 5, fig. 8): Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013).

Material. GSQF103 (lectotype): Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Figured by Shirley (1898, pl. 20, fig. 1a), Walkom (1917, pl. 8, fig. 9) and Playford et al. (1982, p. 8, pl. 5, fig. 8).

QMF42528–42531 (counterparts 42532–42535 respectively), 42536–42538, 42540–42543, 42544, 42583, 42589 (counterpart 42593): Blackstone Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin

(Carnian–lowermost Norian). Specimen QMF42544 was figured by Pattemore & Rigby (2005, fig. 3B); QMF42583 figured herein (Fig. 3A–C).

UQF59907A and counterpart UQF59907B, UQF59912B: former State Quarry, Slacks Creek, Brisbane; Tingalpa Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013, Purdy & Cranfield 2013). Site geology was discussed by Pattemore et al. (2015b, tab. 2). Specimen UQF59912B figured herein (Fig. 3D).

UQF72940: Spring Creek, north of Injune, Queensland; Moolayember Formation (Ladinian: Fergusson & Henderson 2013, fig. 3.110), Bowen Basin. Figured by Playford et al. (1982, pl. 5, figs 1, 2) and herein (Fig. 4).

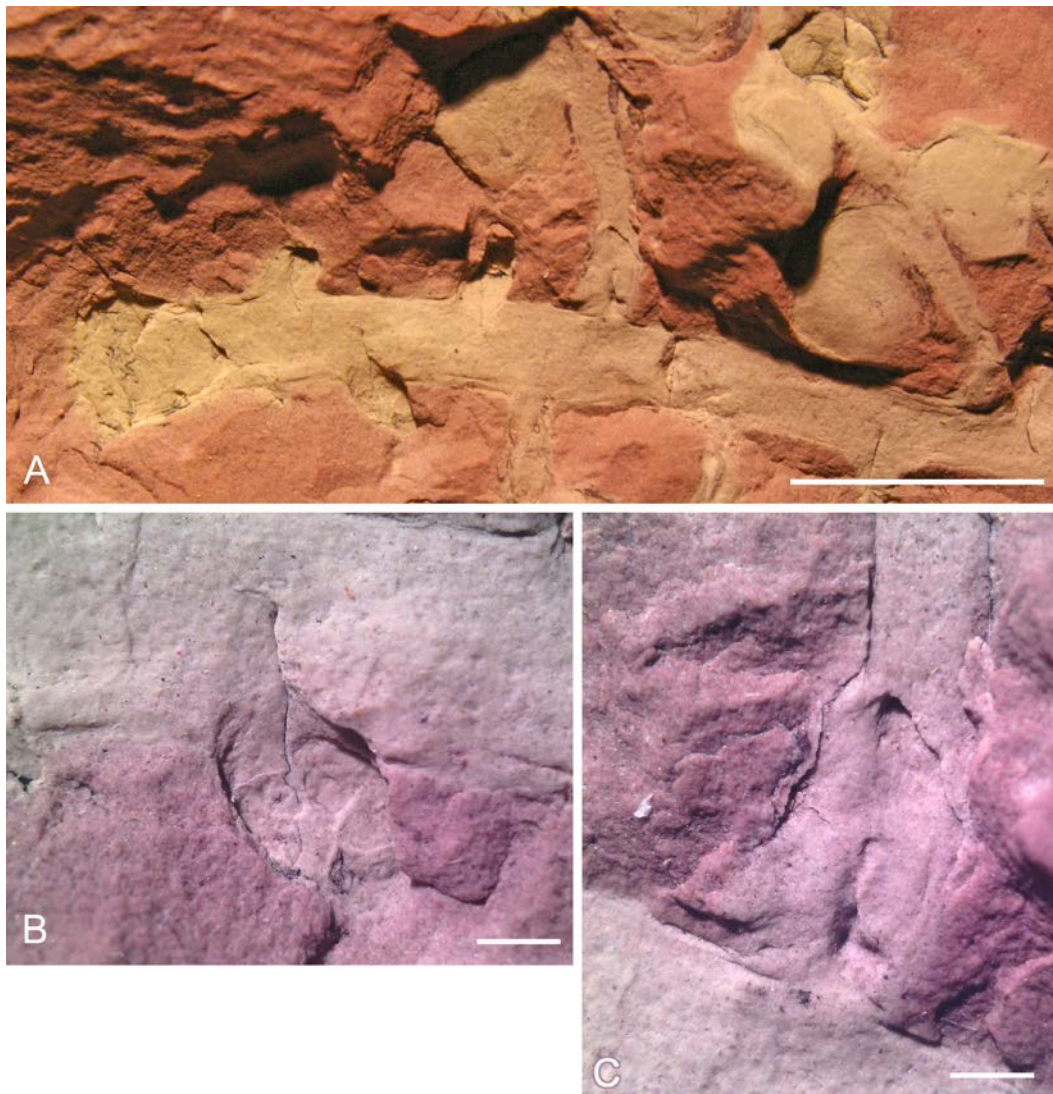
**Occurrence.** Blackstone and Tingalpa formations, Brassall Subgroup, Ipswich Basin (Carbonian–lowermost Norian). Moolayember Formation (Ladinian), Bowen Basin, Queensland.

**Discussion.** Specimen QMF42583 comprises a long shoot bearing several small short shoots. Fructifications resembling *Umkomasia geminata* arise from most short shoots, but one has an emergent vegetative crozier (Fig. 3A, B). That specimen was previously regarded as a single fructification with irregular branching (Pattemore & Rigby 2005). The vegetative crozier arises from a short shoot that resembles those attaching adjacent pinnate fructifications. Today croziers are predominantly restricted to the ferns, although leaves of some cycads also form in this manner (Vasco et al. 2013). The

short shoots in specimens from the Ipswich Basin are very small, rising 1–2 mm above the surface of the long shoot. Thus, the short shoots are difficult to recognize without the diversity of attached organs; they could easily be mistaken for branching within a single fructification.

The long shoot comprises a section (130 mm long) of what was probably a much longer branch. One end of the long shoot is partially obscured by sediment; however, where visible, stem thickness evidently varies little from one end to the other.

Croziers, albeit small and partially formed, are fern-like (Fig. 3A, B) and probably represent juvenile fronds belonging to *Dicroidium feistmantelii* (Johnston 1894) Gothan 1912, a bipinnate species. Many specimens from the same location were assigned to *D. feistmantelii*



**Fig. 4. A–C:** *Umkomasia geminata* (Shirley 1898) Rigby in Playford et al. 1982 emend. nov.; UQF72940; Spring Creek, north of Injune, Queensland; Moolayember Formation, Bowen Basin (Ladinian). **A** – long shoot with several lateral short shoots. **B** – short shoot without attached parts. **C** – short shoot with attached megasporophyll. Scale: A – 1 cm; B, C – 1 mm. Entire specimen figured by Playford et al. (1982, pl. 5, figs 1, 2)

by Pattemore & Rigby (2005). Interpretation of this crozier as a developing ovulate fructification is doubtful. Basal pinnules show venation resembling that of *Dicroidium*, including vein dichotomy. That pattern is unknown in cupules of *Umkomasia* (Fig. 3 herein; Anderson & Anderson 2003, pls 82–89) and there is no indication of structures resembling ovules.

Fructifications arising from the short shoots have pinnately (commonly opposite–subopposite) attached ovules. However, some specimens (e.g. the lectotype and QMF42544) indicate higher-order branching (bipinnate), with pinnae probably consisting of no more than a single pair of cupulate ovules. Specimen UQF59912B (Fig. 3D) has a bifurcating rachis, and others (e.g. QMF42583: Fig. 3A, arrowed) have divided segments that are both equal and sufficiently wide to suggest they represent rachis bifurcations rather than pinnate branching. The bipinnate structure indicates modification from bipinnate vegetative fronds such as *Dicroidium feistmantelii*. This is also consistent with reinterpretation of their probable associated male fructifications assigned to *Pteruchus dubius* Thomas 1933 emend. Townrow 1962a. The male fructification is shown below to have a bipinnate structure. The frond (*D. feistmantelii*) and the fructifications (*Umkomasia geminata* and *P. dubius*) were all found preserved together abundantly (Pattemore & Rigby 2005).

Specimen UQF72940 from the Moolayember Formation, Bowen Basin (Ladinian) was assigned to *Umkomasia geminata* by Rigby in Playford et al. (1982). In light of the above finding regarding this species, their specimen was re-examined herein. It is preserved as a white stained impression. It has apparent helical branching (Playford et al. 1982, pl. 5, figs 1, 2) and its base is slightly expanded, suggesting that the entire structure issues from a short shoot. It is unclear if this expanded base represents a short shoot: it shows no abscission marks; but cf. arrangement of long and short shoots in *Ginkgo biloba* (Little et al. 2013, fig. 13). However, many of the “branches” have expanded bases that resemble small short shoots (Fig. 4B, C). Like that of specimen QMF42583 above, this specimen probably represents a long shoot with several pinnate fructifications arising individually from short shoots (Fig. 4). It differs from the Ipswich Basin specimens (QMF42583 and

QMF42588) in having slightly longer short shoots (ca 3 mm: Fig. 4) but it is otherwise consistent with those and other specimens listed above. Specimen UQF72940 from the Bowen Basin is approximately 10–15 Myr older than the Ipswich Basin specimens.

Holmes (1987) erected *Umkomasia polycarpa* with a single specimen from the Esk Trough (Anisian), Queensland; it is re-examined herein (UQF81139: includes part and counterpart and associated fragments; formerly UQF73298 and UQF73299; also figured by Cook & Rozefelds 2015, p. 88). It is a carbonaceous impression but the “branches” have a thick coal-like structure and lack definition. However, a “branch” preserved on one of the associated fragments appears to be a bifurcating rachis with attached ovules. Furthermore, the rachis emerges from almost the same point as a second rachis, suggesting that they both emerge from an individual short shoot.

It seems possible that some specimens figured by Anderson and Anderson (2003, e.g. pl. 84, figs 1, 5 and pl. 85, fig. 1) as representatives of *Umkomasia* similarly represent long shoots bearing small short shoots which attach pinnate fructifications and the reported “bracteoles” at the bases of “branches” are in fact part of, or associated with, short shoots. Some of these specimens may be attributable to *U. geminata*.

Genus: *Pteruchus* Thomas 1933 emend.  
Townrow 1962a

Type species. *Pteruchus johnstonii* by subsequent designation (Townrow 1962b).

Discussion. The pollen-bearing structures of *Pteruchus* have been variously reported as pinnately (Townrow 1962a, b, Petriella 1980, Taylor et al. 1984) or helically arranged (Pant & Basu 1973, 1979, Yao et al. 1995). Thomas’s (1933) diagnosis included dichotomous, alternate and opposite branching, although the only reported rachis bifurcation was regarded as uncertain (discussed below). One species, *Pteruchus edwardsii* Thomas 1933, was identified as having genuine helical branching (Thomas 1933, Townrow 1962a) and was recombined as *Stachyopitys edwardsii* by Townrow (1962a), albeit reservedly. Although he distinguished the single specimen from *Pteruchus*, he was ambivalent about its attribution to *Stachyopitys* Schenk 1867. Anderson and Anderson (2003, p. 151) indicated that the specimen



probably belongs to *Peltaspermum* Harris 1937 emend. Townrow 1960.

Four helically arranged species identified from the Triassic (?Permian) of India (Pant & Basu 1979) are doubtful representatives of the genus (discussed below). Sections through a single permineralized fructification assigned to the genus from Antarctica suggested helical arrangement (Yao et al. 1995: see below), and Anderson & Anderson (2003) tentatively suggested that all species of the genus reported from the Upper Triassic (Carnian) of South Africa are helically arranged. Townrow (1962a, b) examined Australian and South African specimens, including many type specimens, and considered the type species and others to be pinnate.

*Pteruchus barrealsensis* (Frenguelli 1942) Holmes & Ash 1979 has been recorded from the Lorne Basin (uppermost Lower Triassic: Pattemore et al. 2015a), Australia, and the Barreal Formation (Retallack 1977, Petriella 1980), Barreal-Rincón Blanco Basin, Argentina (Middle Triassic: Morel et al. 2003). This pinnate species (Petriella 1980) has the largest sporangial heads recorded in the genus (up to 80 mm long: Frenguelli 1942, Holmes & Ash 1979). Townrow (1962a) re-assigned Frenguelli's (1942) original specimens – those attributed to *Pterorrachis barrealsensis* Frenguelli 1942 – as *Pteruchus dubius* Thomas 1933 emend. Townrow 1962a, but they were regarded as distinct from that species by Holmes and Ash (1979). On this point, Petriella (1980) largely agreed with Townrow (1962a) but considered the larger size of Frenguelli's specimens as an important character; thus Petriella erected *Pteruchus dubius* var. *barrealsensis*. Frenguelli's (1944b, fig. 12) reconstruction of the fructification included a bifurcating rachis; however, there is no evidence for this character (Townrow 1962a, Petriella 1980). The reconstruction also indicates the pollen sacs entirely covered the sporangial head (i.e. both upper and lower surfaces) but again this seems doubtful: cf. reconstruction of the species by Retallack (1977, fig. 7), which was supported by Petriella (1980). *Pteruchus barrealsensis* is known only from the uppermost Lower Triassic through Middle Triassic of Australia and South America.

Four *Pteruchus* species were identified as spirally arranged by Pant & Basu (1979, table 1); all were reported from the Nidhpuri (=Nidpur) locality (near the Gopad River),

Madhya Pradesh, India. This area has complex geology, and differentiation between Permian and Triassic strata is not always clear (Pant & Pant 1987, Pattemore et al. 2015a). *Pteruchus nidpurensis* Srivastava 1974 was based on isolated sporangial heads and thus branching arrangement is unknown (Srivastava 1974, Pant & Basu 1979). Retallack (2002) suggested that this species may belong to *Permotheca* Zalessky 1929. The other three Indian species – *Pteruchus indicus* Pant & Basu 1973, *P. thomasi* Pant & Basu 1979, and *P. gopadensis* Pant & Basu 1979 – are characterised by their very small sporangial heads and short pedicels. All of the sporangial heads are about the same width, or considerably smaller than, the fructifications' main axis. These three species are structurally unlike *Pteruchus* and almost certainly belong to *Permotheca*: cf. reconstruction of a representative of the latter genus by Krassilov et al. (1999, text-fig. 2). Accordingly, the generic emendation of *Pteruchus* by Pant and Basu (1973) is not followed herein. *Permotheca* is known chiefly from beyond Gondwana (Zalessky 1929, Gomankov & Meyen 1986, Krassilov et al. 1999, Naugolnykh 2013) but has been identified from near the Permo–Triassic boundary in the Sydney Basin, Australia (Retallack 2002, Pattemore et al. 2015a).

Kirchner and Müller (1992) erected *Pteruchus septentrionalis* from the Lower Jurassic (*sensu stricto*, Liassic) of Germany. They interpreted the branching arrangement as probably spiral on the basis of vascular traces in the axis. Like that of the Indian specimens (above), the axis is wide relative to the size of the microsporophylls – much more so than Gondwanan specimens reliably attributed to the genus. Anderson and Anderson (2003) regarded the German specimens as distinct from *Pteruchus* and assignable to a new genus. I agree with those authors that the German specimens do not resemble *Pteruchus*, particularly regarding the figured axis with branched microsporophylls (Kirchner & Müller 1992, pl. 3. fig. 2). Kirchner and Müller (1992) suggested that their specimens are similar to *Pteroma* Harris 1964 but apparently lack the embedded pollen sacs that are characteristic of the genus (Harris 1964). The youngest specimen attributed to *Permotheca*, as noted above, is from near the Permo–Triassic boundary (Retallack 2002, Pattemore et al. 2015a).

Following the erection of *Pteruchus fremouwensis* Yao et al. 1995, based on permineralized specimens from the Middle Triassic of Queen Alexandra Range, Central Antarctic Mountains, some authors have suggested that all representatives of the genus are helically arranged (e.g. Anderson & Anderson 2003, Bomfleur et al. 2011). The specimens reported by Yao et al. (1995) were described as having “helically and alternately” mounted microsporophylls. They identified two axes; only one figure shows actual branching from an axis (Yao et al. 1995, fig. 1) and that does not show branching arrangement. The axis in that figure was transversely sectioned and the wood structure and apparent arrangement of stems around the axis (Yao et al. 1995, fig. 4) were regarded as implying helical insertion. It is unclear how the reported alternate branching arrangement was determined. The in-situ pollen identified by those authors and examined by Osborne and Taylor (1993), were regarded as strongly degraded by Balme (1995). Sporangial sacs were shown to be mounted in rows along either side of oppositely arranged veins on the sporangial head (Yao et al. 1995). This is supported by the discovery of a pinnate structure within the sporangial head in specimens assigned to *P. dubius* herein.

***Pteruchus johnstonii*** (Feistmantel 1890)  
Townrow 1962b

Figs 5–7

**Synonymy.**

- 1888 *Baiera tenuifolia* (R.M. Johnston); Johnston, pl. 2D, E (fructification only).  
 1890 *Trichopitys Johnstoni* Feistmantel, pp. 113–114, pl. 10, fig. 5 (fructification only).  
 1892 *Phyllothea* sp. ind.; Etheridge in Jack & Etheridge, pp. 365–366, pl. 42, fig. 1.  
 1898 *Stachyopitys annularioides* Shirley, p. 13, pl. 18, fig. 1.  
 1917 *Stachyopitys annularioides* Shirley; Walkom, p. 13, pl. 4, fig. 6.  
 1924 *Baiera tenuifolia* Johnston; Walkom, pp. 85–86, figs 15, 16 (fructification only).  
 1933 *Pteruchus africanus* Thomas, pp. 235–237, p. 24, figs 71, 72, text-figs 34, 35.  
 1962a *Pteruchus africanus* Thomas; Townrow, pp. 297–300, pl. 24, fig. 4, pl. 25, figs 1, 2, pl. 26, figs 2, 4–11, text-figs 1–3, 6–10.  
 1962b *Pteruchus johnstoni* (Feistmantel) Townrow, pp. 91–93, figs A–C.  
 1965 *Pteruchus johnstoni* (Feistmantel) Townrow; Hill et al., pl. T6, fig. 4.  
 1977 *Pteruchus johnstonii* (Feistmantel) Townrow 1962; Retallack et al., p. 98, fig. 8C.  
 1980 *Pteruchus johnstonii* (Feistmantel) Townrow 1962; Retallack, p. 39, figs 5A, 10B.  
 1982 *Pteruchus johnstonii* (Feistmantel) Townrow 1962; Holmes, pp. 15, 17, fig. 7E, F.  
 2003 *Pteruchus africanus* H.H. Thomas 1933; Anderson & Anderson, p. 254, pl. 90, figs 1–9.

**Diagnosis.** See Townrow (1962b, pp. 92–93).

**Type material.** Feistmantel (1890, pp. 113–114, pl. 10, fig. 5), Tasmanian Museum specimen B1049, holotype designated by Townrow (1962b); Lord’s Hill (Upper Triassic: Reid et al. 2014), Hobart, Tasmania.

**Material.** GSQF536: Borehole Colliery, Bundamba, Ipswich; Blackstone Formation (Denmead 1955, Denaro et al. 2013), Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013). Identified as *Phyllothea* sp. by Etheridge in Jack & Etheridge (1892, pp. 365–366, pl. 42, fig. 1).

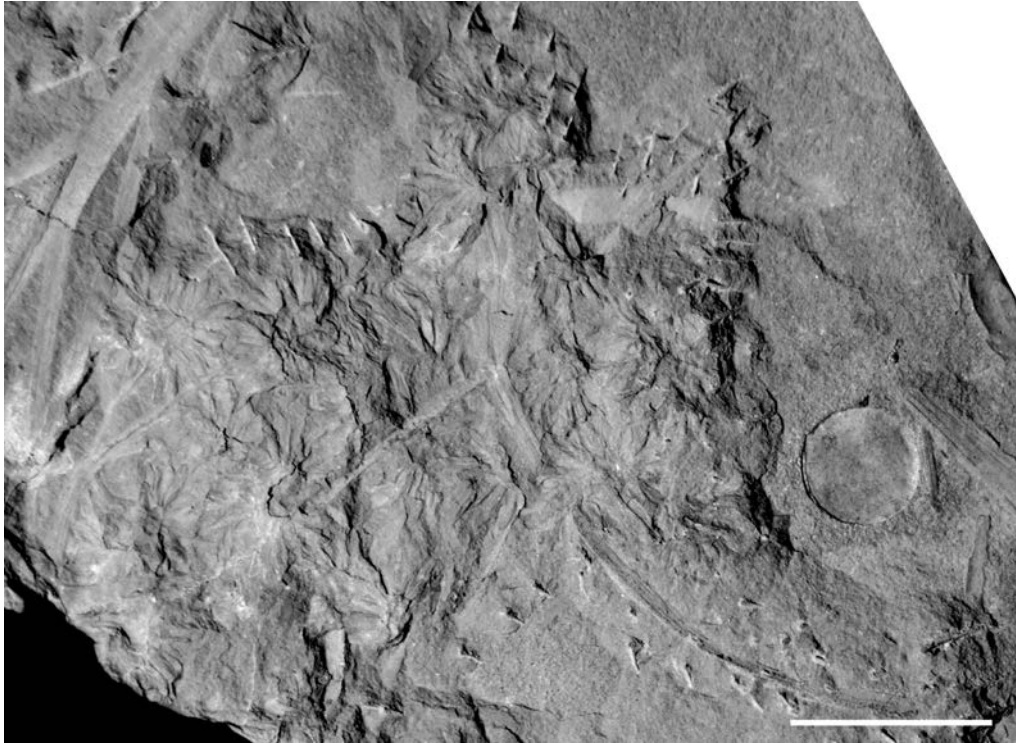
GSQF142: Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013). Identified by Shirley (1898, p. 13, pl. 18, fig. 1) as *Stachyopitys annularioides* Shirley 1898. Figured herein (Figs 5, 6).

UQF2077 (part and counterpart), UQF82589: Sheep Station Inlet (formerly Sheep Station Creek, now submerged), Wivenhoe Dam, Queensland; Esk Formation, Esk Trough (Anisian: Purdy 2013). Both figured herein (Fig. 7).

**Occurrence.** Upper Triassic: coal measures (Lord’s Hill, Hobart), Upper Parmeener Supergroup, Tasmania Basin (Reid et al. 2014); Brassall and Kholo subgroups, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013, Purdy & Cranfield 2013); Molteno Formation (Carnian: Anderson & Anderson 2003), South Africa.

Middle Triassic: Napperby Formation (Anisian: Holmes 1982, Cameron et al. 1999), Gunnedah Basin, New South Wales. Basin Creek and Cloughers Creek formations, Nymboida Sub-Basin (Anisian: Purdy 2013, Purdy & Cranfield 2013), New South Wales. Esk Formation, Esk Trough (Anisian: Purdy 2013), Queensland. Torlesse Supergroup, South Island, New Zealand (Ladinian: Retallack 1980, 1987).

**Description.** Microsporophyll ?pinnate. Axis striated, up to 60 mm long, 1–2 mm wide. Several microsporangial pinnae per axis, branching at 20°–40°. Pinnae up to 6 mm long



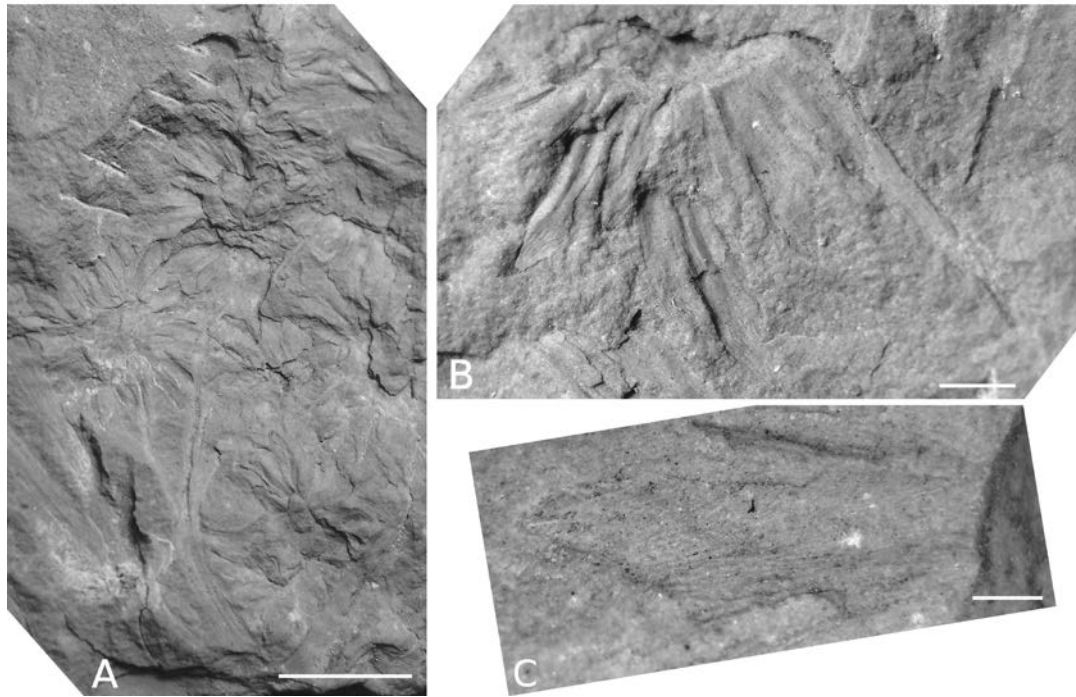
**Fig. 5.** *Pteruchus johnstonii* (Feistmantel 1890) Townrow 1962b. GSQF142: Denmark Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Contrast enhanced. Line-drawn by Shirley (1898, pl. 18, fig. 1) as *Stachyopitys annularioides* Shirley 1898. Scale: 1 cm

(excluding sporangial head), ca 0.4 mm wide, each bearing a single terminal sporangial head. Pinnae tightly curved through ca 80° near connection with sporangial head. Sporangial head with rugose texture on one side, lacking pollen sacs, subcircular–obovate, 2.5–3.5 mm long and ca 2.5 mm wide (up to 7 mm long and 5 mm wide including marginal pollen sacs); other side crowded with pollen sacs, covering entire surface. Sporangial heads from the Esk Trough are smaller (0.5–2 mm long) but all are probably incomplete. Pollen sacs elliptical–oblanceolate, apices pointed, 2–5 mm long, 1–1.5 mm wide, longitudinally striated.

**Discussion.** Thomas (1933) erected *Pteruchus* and several of its species based on specimens from the Molteno Formation (Carnian), South Africa. Townrow (1962a) re-examined Thomas's material and described more specimens from the latter author's original collection site: the Umkomaas Valley, western kwaZulu-Natal, South Africa; site Umk111 of Anderson and Anderson (2003). Townrow's (1962a) generic and specific emendations added considerable detail vis-à-vis morphology, cuticle and pollen. He regarded many of Thomas's (1933) species as junior synonyms of *P. africanus* Thomas 1933 emend. Townrow 1962a.

That species had hitherto been regarded as the type species (Thomas 1933, Townrow 1962a). However, Townrow (1962b) re-examined specimens used to erect *Trichopitys johnstonii* Feistmantel 1890 from the Tasmanian Upper Triassic, and *Stachyopitys annularioides* Shirley 1898 (Figs 5–6 herein) from the Ipswich Basin (Carnian–lowermost Norian), Queensland. He regarded these as indistinguishable from the South African *P. africanus*. Thus, by priority, Townrow (1962b) identified *P. africanus* as a junior synonym of *P. johnstonii*. The latter name has now been widely adopted (e.g. Meyen 1984, Retallack & Dilcher 1988, see above synonymy). Pollen belonging to the type species were described by Balme (1995) and references therein.

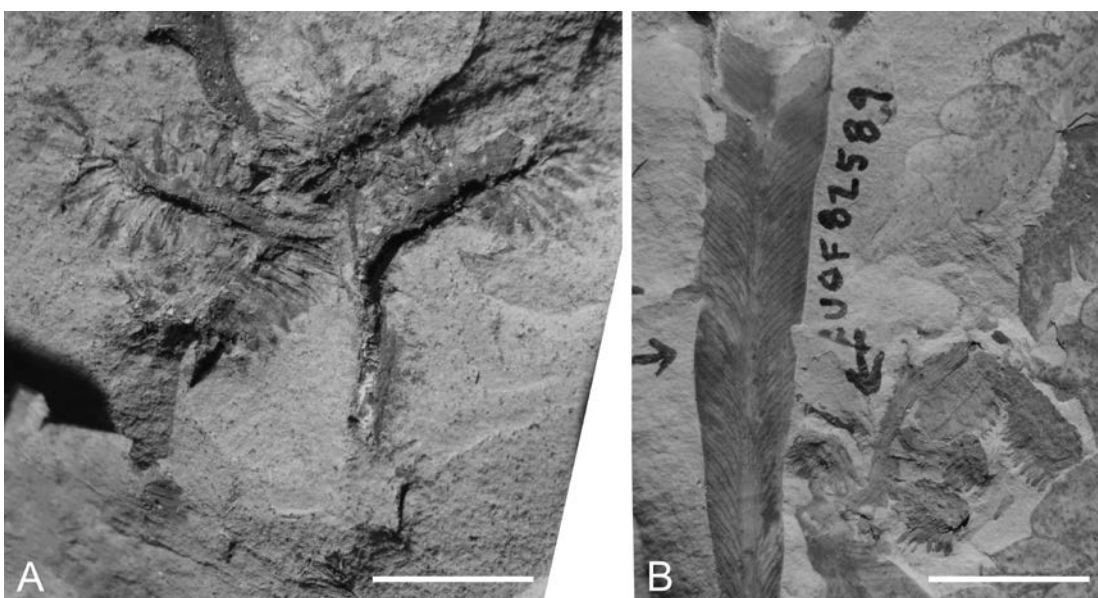
Feistmantel (1890) suggested that the fructification *Trichopitys johnstonii* was biologically attached to an adjacent leaf. Johnston (1888) erected *Baiera tenuifolia* for the leaf but he did not name the fructification. However, the specimen was re-examined by Walkom (1924) who doubted attachment and Townrow (1962b) confirmed that no attachment exists – indeed, he noted that the fructification and foliage are oriented in opposite directions and are preserved in different layers within the slab. Anderson and Anderson (2003, p. 250)



**Fig. 6. A–C** – *Pteruchus johnstonii* (Feistmantel 1890) Townrow 1962b; GSQF142; Denmark Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). **A** – microsporophyll with attached sporangial heads. **B** – side view of sporangial head. **C** – pollen sac with longitudinal striation. Line-drawn by Shirley (1898, pl. 18, fig. 1) as *Stachyopitys annularioides* Shirley 1898. Scales: A – 5 mm; B – 1 mm; C – 0.5 mm

identified Johnston's specimen (more accurately attributable to Feistmantel 1890) as *Pteruchus africanus* and they suggested that it is the youngest record of the genus. Thus, despite disregarding priority, Anderson and Anderson (2003) apparently agreed with Townrow's (1962b) conclusion that *Trichopitys johnstonii* and *P. africanus* are synonymous.

Shirley's (1898) specimen (GSQF142) comprises at least two overlying fructifications, both attributable to the type species. This specimen and others examined herein do not clearly show branching mode. Thus, Townrow's (1962b) assessment that the type species is pinnate rather than helically arranged is followed herein.



**Fig. 7. A, B** – *Pteruchus johnstonii* (Feistmantel 1890) Townrow 1962b. **A** – UQF2077. **B** – UQF82589; leaf on left (UQF82595) identified as *Linguifolium waitakiense* Bell in Bell et al. 1956 emend. Pattemore & Rigby in Pattemore et al. 2015b; leaf shown above (UQF20594) is part of a large bifurcating frond attributable to *Dicroidium feistmantelii* (Johnston 1894) Gothan 1912; Sheep Station Inlet, by Wivenhoe Dam, Queensland; Esk Formation (Anisian), Esk Trough. Scale: A, B – 1 cm

Chatterjee et al. (2013) recorded an indifferently preserved specimen as *Pteruchus* sp. from the Allan Hills (Middle and Upper Triassic: Pattemore et al. 2015a), South Victoria Land, Antarctica. It may belong to the type species but the apparently incomplete sporangial head could simply represent a portion of a larger fructification (e.g. *P. dubius*).

Specimens recorded by Jones (1948) in a core sample from an unidentified well near Cracow, Queensland, included an unnamed, small (ca 10 mm long, ca 3 mm wide) detached strobilus. Its generic identity is uncertain, being only figured by line-drawn interpretation (Jones 1948, pl. 1, fig. 15) and it was apparently not retained in a permanent collection. Furthermore, the well's exact location and the core recovery depth were unrecorded but it almost certainly penetrated Permo-Triassic strata of the Bowen Basin. Cracow is located close to the basin's eastern boundary and to younger strata of the Surat Basin (Draper 2013). Some specimens recorded by Jones (1948) possibly resemble those of Playford et al. (1982) from the Ladinian Moolayember Formation, Bowen Basin.

***Pteruchus dubius* Thomas 1933 emend.  
Townrow 1962a**

Figs 8C–G, 9A–C

**Synonymy.**

- 1933 *Pteruchus dubius* Thomas, pp. 241–242, figs 44, 45.  
 1947 *Pteruchus* cf. *africanus* Thomas; Jones & de Jersey, p. 55, text-fig. 51.  
 1962a *Pteruchus dubius* Thomas; Townrow, pp. 300–302, pl. 24, figs 5, 6, pl. 25, fig. 3, pl. 26, fig. 1, text-figs 1e, 4b, c, 7b, 8d, 10a–c, 11a, b.  
 1965 *Pteruchus dubius* Thomas; Hill et al., pl. T6, fig. 3.  
 1984 *Pteruchus dubius*; Taylor et al. 1984, pl. 1, figs 1, 2.  
 1995 *Pteruchus dubius* Thomas 1933 emend. Townrow 1962; Cantrill et al., pp. 55–57, fig. 5a–g.  
 2005 *Pteruchus dubius* Thomas 1933 emend. Townrow 1962; Pattemore & Rigby, pp. 333–334, fig. 3a.

**Diagnosis.** See Townrow (1962a, pp. 300–301).

**Type material.** Thomas (1933, pp. 241–242, fig. 44): Umkomaas Valley, western kwaZulu-Natal, South Africa; Molteno Formation (Carnian), Karoo Basin.

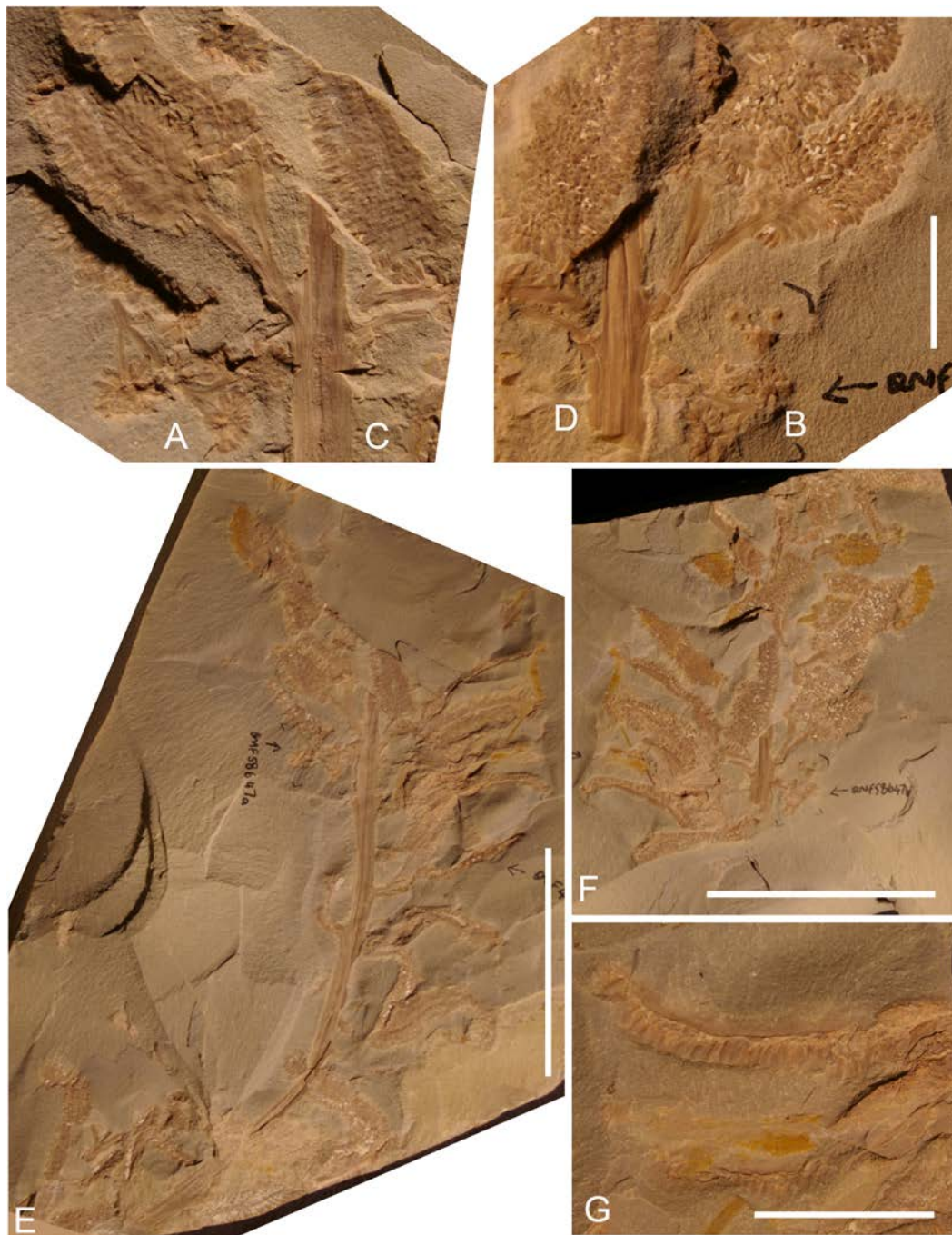
**Material.** QMF42547 (counterpart 42576), 42548 (counterpart 42550) [Figs 8C, 8D, 9A–C herein], 42557 (counterpart 42558), 42567 (counterpart 42568), 42574 (counterpart 42575): Blackstone Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013, Purdy & Cranfield 2013).

UQF28090A/B (part and counterpart): Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). UQF28090B was figured by Hill et al. (1965, pl. 6, fig. 3).

**Occurrence.** Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian); Molteno Formation (Carnian: Anderson & Anderson 2003); Flagstone Bench Formation, Prince Charles Mountains, East Antarctica (Norian: McLoughlin & Drinnan 1997).

**Description.** Microsporophyll pinnate. Rachis >200 mm long, up to ca 4.5 mm wide. Pinnae commonly subopposite, branching at 50–80°, ca 13 mm long (not including sporangial head), 0.5–1.5 mm wide, commonly subtended by a cataphyll. Pinnae commonly bifurcating <5 mm from rachis, each with terminal sporangial head. Cataphyll 7–9 mm long, 1–1.5 mm wide. Sporangial head 15–38 mm long, 5–8 mm wide, comprising three distinct layers: (1) a thin rugose lamina forming probable upper surface, overlying (2) a thin pinnate lamina to which (3) pollen sacs are attached, probably pendulously. Pinnate lamina approximately same overall size as overlaying lamina. Pinnules linear but slightly curved with faint costule, 15–20 each side of pinna-rachis (probably less in smaller specimens). Pollen sacs crowded, attached in ?pairs laterally along pinnae, ca 5 sac pairs per pinnule; thus >200 pollen sacs in total per sporangial head. Pollen sacs commonly oblanceolate, pointed–rounded apically and pointed at their attachment, 1.5–2.5 mm long, 0.5–0.8 mm wide, longitudinally striated (ca 35 per mm).

**Discussion.** The specimens listed above from Blackstone Hill were first described by Pattemore and Rigby (2005) as *Pteruchus dubius*. Extending their description, in particular, the microsporophyll is indeed pinnate but some sporangial heads show a previously unidentified distinct lamina to which the sporangial sacs are attached (Fig. 9A, B). This lamina is pinnate, thus indicating that the entire

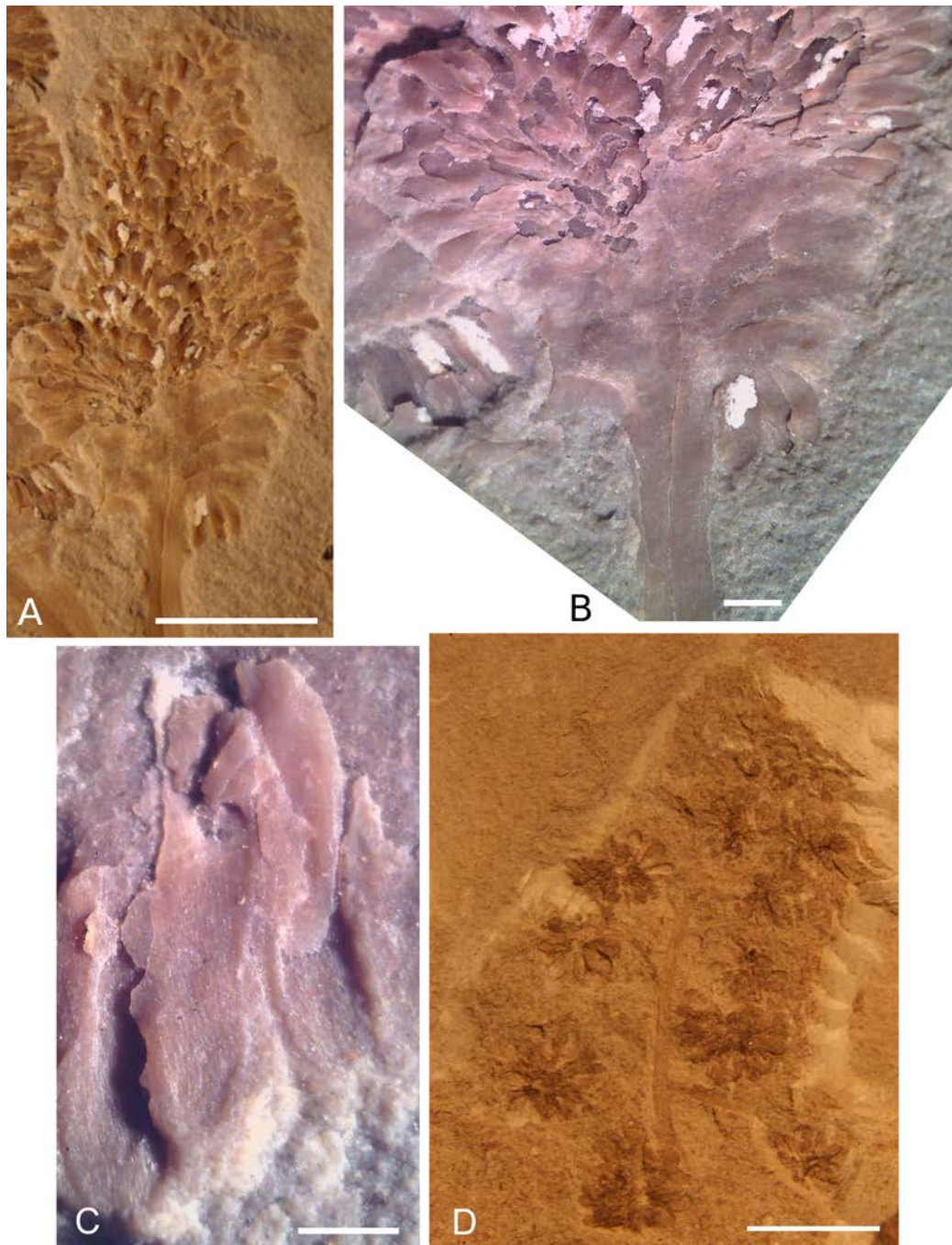


**Fig. 8.** **A, B** – *Pteruchus minor* Thomas 1933; QMF58647 (part and counterpart). **C, D** – *Pteruchus dubius* Thomas 1933 emend. Townrow 1962a; QMF42548 and counterpart QMF42550 respectively. Blackstone Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). **E, F** – *Pteruchus dubius* Thomas 1933 emend. Townrow 1962a; entire specimen with part (E: QMF42548) and counterpart (F: QMF42550) vertically aligned. **G** – *Pteruchus dubius* Thomas 1933 emend. Townrow 1962a; side view of sporangial heads, QMF42548. Collected by R. Knezour. Scale: A–D – 1 cm; E, F – 5 cm; G – 1 cm

fructification represents a modified bipinnate leaf. Townrow (1962a, p. 294) first suggested that the sporangial heads belonging to this and other species of *Pteruchus* probably have a pinnate structure. Pattemore & Rigby (2005) considered *P. dubius* to be associated with the bipinnate leaf *Dicroidium feistmantelii* (Johnston 1894) Gothan 1912 based on their frequent preservation at the same locality. Cook

and Rozefelds (2015, p. 88) figured *P. dubius* (QMF58599) from the same locality.

Many pinnae are subtended by a cataphyll. Townrow (1962a, p. 292) reported rare “vegetative pinnules” in one specimen assigned to *Pteruchus dubius* and in specimens attributed to two other species but he noted that they did not subtend any structure. Anderson and Anderson (2003) identified paired sporangial



**Fig. 9.** A–C – *Pteruchus dubius* Thomas 1933 emend. Townrow 1962a; QMF42548 and counterpart QMF42550. A, B – QMF42550. C – QMF42548; pollen sac. Blackstone Hill, Ipswich, Queensland; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian); collected by R. Knezour. D – *Pteruchus minor* Thomas 1933; UQF16609; Petrie’s Quarry, Albion, Brisbane, Queensland; Aspley Formation, Kholo Subgroup, Ipswich Basin (Carnian–lowermost Norian). Scale: A, D – 5 mm; B, C – 1 mm

heads, each mounted terminally on a singly bifurcated pedicel that is subtended by a cataphyll (termed bracteole) in specimens referred to their species *P. matatimajor*. Cataphylls in the specimens examined herein were probably thin laminae but lack visible venation. They appear to have been easily lost or shed (Anderson & Anderson 2003, p. 250) or perhaps did not always develop.

Anderson and Anderson (2003) tentatively

regarded all *Pteruchus* species from the Molteno Formation, South Africa as having irregular helical branching; that viewpoint was apparently influenced by the discovery of the supposedly helically arranged *P. fremouwensis* from the Triassic of Antarctica (discussed above). The specimens figured as *P. matatimajor* by Anderson and Anderson (2003, pls 92–94) suggest that species is probably a junior synonym of *P. dubius*.

Specimens termed *Pteruchus* sp. cf. *P. matatimajor* by Holmes and Anderson (2005, p. 11, fig. 23A–E) from the Nymboida Sub-Basin (Anisian) display a range of sporangial head sizes like that of specimens attributed to *P. dubius* by Pattemore and Rigby (2005). Holmes and Anderson's (2005) figured specimens may be attributable to that species. The Nymboida Sub-Basin is approximately coeval (Purdy & Cranfield 2013) with the Esk Trough (Anisian: Purdy 2013); a Ladinian age has also been suggested (Holmes & Anderson 2013). A single specimen figured as *Pteruchus* sp. A by Holmes and Anderson (2005, pl. 23, fig. F) may represent overlying sporangial heads rather than a single forked head, which is unknown in the genus.

Townrow (1962a) tentatively indicated that pollen sacs of *Pteruchus dubius* may completely encompass the head, i.e. covering both upper and lower surfaces. The specimens examined herein clearly show that one side (probably the upper surface) lacks pollen sacs (Fig. 8G). This surface is bract- or leaf-like and its rugose texture probably resulted from a combination of the underlying pinnate lamina and the crowded pollen sacs. Likewise, the slightly crenulate margin of the non-sporangial surface probably represents the apical portion of pinnules in the underlying layer. Restriction of sporangial sacs to one side of the head was also noted by Cantrill et al. (1995) based on specimens from the Flagstone Bench Formation (Norian), Prince Charles Mountains, East Antarctica.

A specimen attributed to *Pteruchus dubius* by Taylor et al. (1984, pl. 1, figs 1–2) was apparently collected from Dinmore Quarry, Queensland (Zavada & Crepet 1985, Osborn & Taylor 1993, p. 206); thus it is probably from the Tivoli Formation (Pattemore & Rigby 2005, but Blackstone Formation and of Norian age according to Raven et al. 2015), Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013). Retallack (1983) reported *P. dubius* from the Ladinian of the South Island, New Zealand; however, the single indifferently preserved fragment is very small and insufficient for specific identification. Pollen obtained from representatives of the species have been described by Townrow (1962a), Taylor et al. (1984), Zavada and Crepet (1985), Balme (1995) and Cantrill et al. (1995) and resemble the dispersed pollen genus *Falcisporites* Leschik 1956 emend. Klaus 1963.

### *Pteruchus minor* Thomas 1933

Figs 8A, 8B, 9D

#### Synonymy.

- 1903 *Stachyopitys* sp.; Seward, pp. 66–67, pl. 9, figs 2, 2a.  
 1933 *Pteruchus minor* Thomas, pp. 242–243, pl. 24, fig. 76.  
 1944a *Stachyopitys anthoides* Frenguelli, pp. 385–392, fig. 1, pls 1–2.  
 1947 *Pteruchus annularoides* (Shirley) Thomas; Jones & de Jersey, p. 55, text-fig. 38 (fructification only).  
 1947 *Pteruchus simmondsi* (Shirley) Thomas; Jones & de Jersey, p. 55 (not figured).  
 1962a *Pteruchus simmondsi* (Shirley) Thomas; Townrow, pp. 303–305, pl. 24, figs 1, 3, pl. 26, figs 3, 12, text-figs 2a–c, 4a, 4d–h, 6j, 6k, 7d, 8a, 8e, 11c, 11d.  
 1965 *Pteruchus simmondsi* Thomas; Hill et al., pl. T6, fig. 5.  
 1967 *Pteruchus rhaetica* (Geinitz); Jain & Delevoryas, pp. 572–573, pl. 90, fig. 15.  
 1980 *Pteruchus simmondsi* (Shirley) Thomas em. Townrow 1962; Petriella, pp. 172–174, pl. 2, figs 1–3.  
 2003 *Stachyopitys lacrisporangia* Anderson & Anderson, p. 220, pl. 76, figs 1–16; pl. 77, figs 1–5; pl. 78, figs 1–12; pl. 81, figs 1–6.  
 2011 *Townrovia polaris* Bomfleur et al. 2011, pp. 818–820, fig. 8.  
 2013 *Townrovia polaris* Bomfleur et al. 2011; Chatterjee et al., p. 217, fig. 5C.

Diagnosis. See Thomas (1933, p. 242).

Material. QMF58647(a, b) part and counterpart: Blackstone Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian: McKellar 2013). Fig. 8A, B herein.

UQF16609: Petrie's Quarry (west side of Bartley's Hill), Albion, Brisbane, Queensland; Aspley Formation, Kholo Subgroup, Ipswich Basin (Carnian–lowermost Norian). Figured by Hill et al. (1965, pl. 6, fig. 5) as *Pteruchus simmondsii*. Fig. 9D herein.

UQF82572, UQF82573: Denmark Hill, Ipswich; Blackstone Formation, Brassall Subgroup, Ipswich Basin (Carnian–lowermost Norian). Specimen UQF82573 is located on the same slab as a ginkgoalean leaf (UQF2037) that was assigned to *Czekanowskia tenuifolia* Johnston 1886 by Jones and de Jersey (1947).

Occurrence. Kholo and Brassall subgroups, Ipswich Basin (Carnian–lowermost



Norian: McKellar 2013, Purdy & Cranfield 2013). Molteno Formation (Carnian: Anderson & Anderson 2003), South Africa. Potrerillos and Cacheuta formations, Cuyo Basin, Argentina (uppermost Ladinian–lowermost Norian: Morel et al. 2003). Falla Formation (Upper Triassic: Bomfleur et al. 2011), Victoria Group, Queen Alexandra Range, Central Transantarctic Mountains, Antarctica. Upper Lashly Formation (Middle or Upper Triassic: Pattemore et al. 2015a), Allan Hills, South Victoria Land, Antarctica.

**Description.** Small incomplete open panicle, 15 mm long, 10 mm wide, bilaterally branched, opposite–alternate. Rachis 0.8 mm wide. Pinnae branching at 30°–70° with pinna stem ca 4 mm long, <0.5 mm wide, bearing a single terminal subcircular–elliptical sporangial head (1.5–2 mm diameter; 3–4.5 mm including marginal pollen sacs). Pollen sacs probably covering entire head (i.e. both upper and lower sides); total number of sacs per head unclear, but up to 14 visible around margin. Sacs oblan-ceolate–obovate, 1–2 mm long, 0.4–0.7 mm wide; apices rounded or pointed (obtuse–acute). Sacs pointed at their attachment.

**Discussion.** These specimens would have been attributed to *Pteruchus simmondsii* (Shirley 1898) Jones & de Jersey 1947 emend. Townrow 1962a. However, the type specimen (GSQF256) of that species is shown herein to be ovuliferous and therefore not representative of *Pteruchus* – it is now identified as *Umkomasia simmondsii* (above).

*Pteruchus minor* was diagnosed by Thomas (1933) as having a bilateral and alternate branching habit. The type specimen is a very small fragment (Thomas 1933, pl. 24, fig. 76, Anderson & Anderson 2003, p. 255, text-fig. 9) comprising only three sporangial heads. Thomas (1933) indicated that a possible fork in the rachis may actually be a branch, thus suggesting opposite–alternate branching. This seems probable, as a forked rachis is otherwise unknown in the genus: cf. *P. barrealensis* (discussed above). Specimens described herein have pinnate, opposite–alternate branching (Figs 8A, 8B, 9D). Several specimens previously attributed to *P. simmondsii* are assigned to *P. minor* herein. Townrow (1962a, p. 294) noted that ridges on the head of one specimen assigned to *P. simmondsii* suggested that the head has a pinnate structure. That character

is confirmed for *P. dubius* (above) and supports the view that *P. minor* is consistent with *Pteruchus*.

Specimen QMF58647 (part and counterpart) suggests that the head was possibly fully covered with pollen sacs (i.e. both upper and lower surfaces: Fig. 8A, B). However, the pollen sacs are sufficiently large relative to the size of the head that some sacs may have flexed around the head during burial, thus giving the impression of sac attachment to both surfaces. The specimen is preserved adjacent to a large fructification (QMF42548) that was assigned to *Pteruchus dubius* by Pattemore and Rigby (2005) and is re-examined herein (above). The pollen sacs in specimen QMF58647 appear fully developed and of similar size to those of *P. dubius* and other species of the genus. The holotype of *P. minor* is an impression without a counterpart. Thomas's (1933, fig. 46) line-drawn interpretation also suggests the possibility that sacs covered the entire head.

The male fructification *Townrovia* Retallack 1981 is remarkably similar to *Pteruchus*. It was based on specimens from the Middle Triassic of New Zealand and the Upper Triassic of Tasmania. The type specimens (Tasmanian) were originally included in *Pteruchus* (Townrow 1965, Retallack 1981). The basis for separation of those genera is doubtful. In defining *Townrovia*, Retallack (1981) stated that "... in *Pteruchus* the pollen sacs are attached to the lateral margins rather than a median receptacle". This misrepresents the genus; all genuine *Pteruchus* species discussed herein have pollen sacs crowded below the lamina, covering most or all of that surface. This is clearly indicated in Townrow's (1962a) emendation of the genus. Pollen sacs only appear restricted to the margin when obscured by an overlying lamina. Specimens attributed to *P. dubius* (Fig. 9A, B) show the structural arrangement of pollen sac attachment covering the entire surface beneath the lamina. Townrow's (1965) specimens assigned to his species *P. petasata* provided the basis for *Townrovia* and are Carnian–Norian in age (Pattemore et al. 2015a). He regarded that species as most similar to *P. dubius*, being chiefly separated by the number of rows of pollen sacs and a laminar head that has a marginal rim lacking pollen sacs. These differences were not considered to be of generic significance by Townrow (1965). He regarded the lamina head to be unambiguously leaf-like, not stem-like.

Retallack (1981) included material from the Ladinian of the South Island, New Zealand in his recombination, *T. petasata* (monotypic); his specimens are small, indifferently preserved fragments with no indication of a rim lacking pollen sacs.

Bomfleur et al. (2011, table 2) assumed that *Pteruchus* is helically arranged, and this was identified as a significant character distinguishing that genus from *Townrovia*. Those authors also separated the genera by pollen sac shape and cuticle. Pollen sacs of *Pteruchus* were regarded by Bomfleur et al. (2011, table 2) as fusiform (elongate or narrowly elliptical with tapered apices) and those of *Townrovia* as clavate (oblanceolate–obovate with rounded apices): however, their diagnosis of *T. polaris* includes elliptical sacs. The type material of *Townrovia* (Townrow 1965, figs 4, 6) indicates that sacs are oblanceolate–obovate with rounded to pointed apices. *Pteruchus* includes elliptical–oblanceolate–obovate sacs with rounded to pointed apices: see herein and diagnoses of various *Pteruchus* species by Thomas (1933) and Cantrill et al. (1995). Thus, generic differentiation based on this character is doubtful. Furthermore, it is a character that would probably be somewhat dependent on the condition and maturity of the plant organ at its time of preservation.

Bomfleur et al. (2011, table 2) also indicated that subsidiary cells in representatives of *Townrovia* are papillate, whereas those of *Pteruchus* are non-papillate. This apparently is based on Retallack's (1981) diagnosis of *Townrovia* that states incorrectly that subsidiary cells are papillate. Stomata and subsidiary cells in representatives of the genus are known only from Townrow's (1965) description of *P. petasatus*, as Retallack (1981) did not describe epidermal detail and Bomfleur et al. (2011) only described epidermis devoid of stomata. Townrow (1965) identified only five stomata and four papillate cells – in total – from a few minute fragments obtained from various parts of the microsporophyll; it is unclear what proportion of cells are papillate. He did not describe subsidiary cells as papillate but, rather more generally, he indicated the epidermis has solid or hollow papillae. Otherwise, his epidermal description is consistent with other species of *Pteruchus*. Papillae were considered rare in the genus by Townrow (1962a) but they are not unknown. Thomas (1933) erected

*P. papillatus* but representatives of this species were not microscopically examined by Townrow (1962a); pollen from the type specimen of that species were described by Zavada and Crepet (1985). Thus, *P. petasatus* and *P. papillatus* differ from other representatives of the genus in apparently having more commonly occurring papillae, but this is of dubious generic import. The number and position of papillae is affected by environmental conditions and other non-genetic factors (Barclay et al. 2007, tab. 1). Thus, it is doubtful that a sufficiently objective basis has been established to differentiate *Townrovia* from *Pteruchus*.

*Townrovia polaris* – regarded as a junior synonym to *P. minor* herein – was based on specimens from the Upper Triassic of Antarctica and included part and counterparts. The counterparts are small fragments; they were not figured but were used to extract pollen. Like that of *Pteruchus*, in-situ pollen identified from the type specimen of *T. polaris* resemble the dispersed pollen genus *Falcisporites*. Pollen were also identified by Bomfleur et al. (2011) within the micropylar canal of some ovules assigned to *Matatiella dejerseyi* (erected by those authors); they considered that organ as probably belonging to the same parent plant as *T. polaris*. However, pollen grains identified in those micropylar canals were only tentatively regarded as resembling *Falcisporites* (Bomfleur et al. 2011, p. 818).

*Stachyopitys lacrisporangia* Anderson & Anderson 2003 is also identified herein as a junior synonym of *Pteruchus minor*. One specimen assigned to *S. lacrisporangia* by Anderson and Anderson (2003, pl. 81) has a bulbous base. A narrow strap-like appendage is also evidently attached to that same base and was interpreted by those authors to be a leaf resembling *Sphenobaiera* Florin 1936. The appendage is very small: ca 30 mm long, 0.7 mm wide near its base, apparently broadening to ca 2 mm wide distally; however, the distal portion may represent two adjacent but separate specimens (Anderson & Anderson 2003, pl. 81, fig. 1). The appendage lacks venation and its basal width corresponds to that of the adjacent fructification's stem. Anderson and Anderson's (2003, p. 220, fig. 10a) line-drawing implies that the appendage is distally complete (not discussed by those authors). Their interpretation of this appendage is doubtful, being apparently based entirely on its distal

portion somewhat resembling a single terminal division in a ginkgoalean leaf. Their purported evidence is insufficient to establish an organic connection between *Sphenobaiera* and the fructification.

The reconstruction of the fructification by Anderson and Anderson (2003, p. 220, text-fig. 5) suggests that pollen sacs in representatives of *Stachyopitys lacrisporangia* encompassed the entire sporangial head. Bomfleur et al. (2011) first indicated that *Townrovia polaris* and *S. lacrisporangia* may be synonymous.

*Stachyopitys* is a ginkgoalean fructification, and unlike *Pteruchus* it contains monosulcate pollen (van Konijnenburg-van Cittert 2010). Pollen is unknown from specimens assigned to *Stachyopitys* from the Middle and Upper Triassic of Gondwana (most specimens have been reported by Anderson and Anderson 2003). Gondwanan specimens attributed to *Stachyopitys* differ from those of well-understood species of the Northern Hemisphere in having a simpler branching pattern and in the number and the mode of attachment of pollen sacs (van Konijnenburg-van Cittert 2010, Bomfleur et al. 2011). Furthermore, based on Anderson and Anderson (2003, pls 72–81) it seems

possible that Gondwanan specimens assigned to *Stachyopitys* may have a pinnate structure.

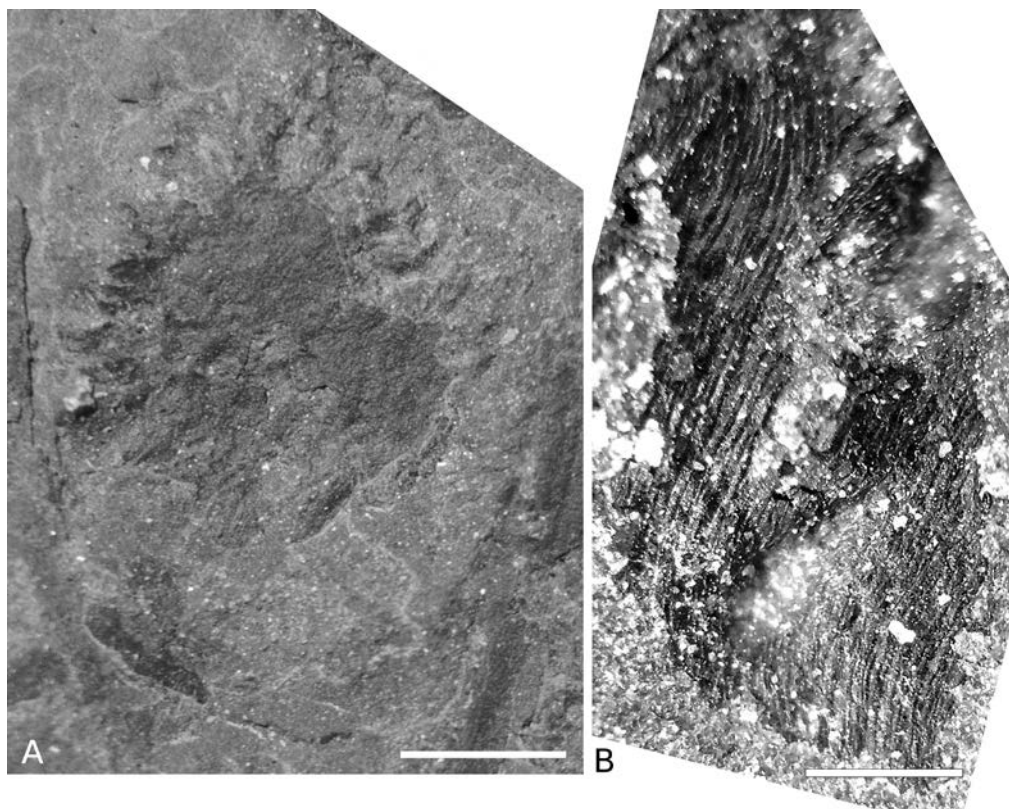
A specimen (UQF72911) assigned to *Pteruchus simmondsii* by Playford et al. (1982, pl. 2, fig. 6) from the Ladinian Moolayember Formation, Bowen Basin, Queensland was re-examined herein. However, it appears to have degraded since it was originally figured and its generic identity could not be confirmed. *Sphenolepis rhaetica* was erected by Geinitz (1876) for very small fructifications described as spirally arranged cones with woody scales. These may be identified as *Pteruchus minor* but Geinitz's description and line-drawings are insufficient for generic identification. If they belong to the same species then Geinitz's (1876) nomenclature has priority.

### *Pteruchus* sp.

Figs 10–12

**Material.** QMF57869: Meandu Mine, Tarong Basin (upper Carnian: McKellar 2013), Queensland, Australia.

**Description.** Microsporophyll head incomplete, 10 mm long, ca 7 mm wide (not including pollen sacs around margin) with rugose texture.



**Fig. 10.** A, B – *Pteruchus* sp.; QMF57844; Meandu Mine; Tarong Basin (upper Carnian), Queensland. A – sporangial head; see also Fig. 11j herein. B – pollen sac. Scale: A – 5 mm; B – 0.5 mm



**Fig. 11.** Short shoot with camera lucida overlay: Meandu Mine, Tarong Basin (upper Carnian), Queensland; **a** – long shoot; **b** – short shoot, QMF57870 (Fig. 12 herein); **c–i** – ginkgoalean leaf fragments; **j** – *Pteruchus* sp., QMF57844, Fig. 10 herein; **k–l** – shoots. Scale: 1 cm



Pollen sacs numerous, slender, <2.5 mm long and <1 mm wide, finely striated longitudinally (ca 40 striations per mm).

**Discussion.** The fructification (QMF57869) is located within 19 mm of a short shoot (QMF57870; Figs 11b, 12) but they are not organically connected. Both the general form of the fructification (Figs 10A, 11j) and its pollen sacs (Fig. 10B) resemble *Pteruchus*; however, its indifferent preservation disallows specific identification. No structure is visible within the head. The shoot includes ginkgoalean-like foliage fragments that are either attached or otherwise clearly associated based on their orientation (Fig. 11c–i). Small curved features are present near the apex of the short shoot (Figs 11k, 11l, 12).

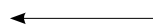
The ginkgoalean-like leaves are incomplete. They are fan-shaped and have parallel venation (Figure 11c, d and g). Other leaves resembling *Sphenobaiera* Florin 1936 are preserved separately on the same slab (QMF57871, QMF57872) and elsewhere in the collection. All other leaves in the collection are attributable to either *Linguifolium* Arber 1917 emend. Pattemore & Rigby in Pattemore et al. 2015b, *Xylopteris* Frenguelli 1943 or *Dicroidium* (the latter two are currently being investigated).

## CONCLUSIONS

1. *Umkomasia geminata* is bipinnate and arises from small short shoots. The species has been recorded from the Ladinian–lowermost Norian of Australia but it probably had a wider geographic distribution during that interval.

2. *Pteruchus dubius* has a bipinnate structure. Townrow (1962a) suggested that the sporangial heads in representatives of this species are based on a pinnate plan and this is confirmed herein. Pollen sacs are attached to a pinnate lamina.

3. The bipinnate structure of *Umkomasia geminata*, *Pteruchus dubius* and *Dicroidium feistmantelii* further supports the view that they belonged to the same parent plant. Moreover, it strongly indicates that specimens with genuine helical branching are taxonomically



**Fig. 12.** Short shoot, QMF57870: Meandu Mine, Tarong Basin (upper Carnian), Queensland. See also Fig. 11b herein. Scale: 5 mm

distinct from those genera and probably from the Umkomasiaceae.

4. The type specimen of *Stachyopitys simmondsii* Shirley 1898, subsequently identified as *Pteruchus simmondsii* (Shirley 1898) Jones & de Jersey 1947, is shown to be ovuliferous. The species, newly combined herein with *Umkomasia* as *U. simmondsii*, may be synonymous with the type species of the genus.

5. Several specimens previously identified as *Pteruchus simmondsii* from the Gondwanan Middle and Upper Triassic are assigned to *P. minor*. *Townrovia polaris* and *Stachyopitys lacrisporangia* from the same interval are identified as junior synonyms of *P. minor*.

6. *Townrovia* is not regarded as convincingly distinguished from *Pteruchus*.

7. *Pteruchus* is recorded for the first time from the Carnian Tarong Basin, Queensland.

#### ACKNOWLEDGEMENTS

This work is part of a research project funded by an Australian Postgraduate Award (to GAP). Prof. G.E. Webb of The University of Queensland (UQ) has helped with the establishment and progress of this project. Prof. G. Playford (UQ) and J.F. Rigby (Queensland University of Technology) provided constructive advice on the manuscript. Helpful comments by Dr. Heidi Anderson (University of Witwatersrand, South Africa) and another (anonymous) reviewer are gratefully acknowledged.

N. Ferdinands, Senior Coal Geologist, Stanwell Corporation Limited and D. Edwards and E. Mills, Mining Engineers, Downer Corporation assisted with collection of fossil material from the Meandu Mine, Nanango, Queensland. Specimens described herein from Blackstone Hill were collected by R. Knezour, Ipswich, Queensland.

Dr. A. Rozefelds and K. Spring, Queensland Museum assisted with locating museum specimens and assigning specimen numbers and were most accommodating during several visits to the museum. Map data were provided by Geoscience Australia and Queensland Department of Natural Resources and were distributed under Creative Commons Attribution 3.0 – Australia.

#### REFERENCES

- ANDERSON H.M., HOLMES W.B.K. & FITNESS L.A. 2008. Stems with attached *Dicroidium* leaves from the Ipswich Coal Measures, Queensland, Australia. *Mem. Qd Mus.*, 52(2): 1–12.
- ANDERSON J.M. & ANDERSON H.M. 1983. Palaeoflora of Southern Africa: Moltano Formation (Triassic): Vol. 1: Part 1 Introduction. Part 2 *Dicroidium*. A.A. Balkema, Rotterdam.
- ANDERSON J.M. & ANDERSON H.M. 2003. Heyday of the gymnosperms: systematics and diversity of the Late Triassic Moltano fructifications. *Strelitzia*, 15: i–viii + 1–398.
- ANDREWS S.B. 1990. Ferns of Queensland: a handbook to the ferns and fern allies. Queensland Herbarium and Dept. of Primary Industries, Brisbane.
- ARCE F.E. & LUTZ A.I. 2010. Fructificaciones de la Formación Los Rastros, triásico superior, Provincia de San Juan, Argentina. *Rev. Mex. Cienc. Geol.*, 27: 31–42.
- ARTABE A. & BREA M. 2003. A new approach to *Corystospermales* based on Triassic permineralized stems from Argentina. *Alcheringa*, 27: 209–229.
- ARTABE A. & BREA M. 2007. Réplica al trabajo de Axsmith et al. (2007) publicado en *Ameghiniana* 44: 223–230: “The ‘new approach to *Corystospermales*’ and the Antarctic fossil record: a critique”. *Ameghiniana*, 44: 739–746.
- AXSMITH B.J., TAYLOR E.L. & TAYLOR T.N. 2007. The “new approach to *Corystospermales*” and the Antarctic fossil record: a critique. *Ameghiniana*, 44: 223–230.
- AXSMITH B.J., TAYLOR E.L., TAYLOR T.N. & CÚNEO N.R. 2000. New perspectives on the Mesozoic seed fern order *Corystospermales* based on attached organs from the Triassic of Antarctica. *Amer. J. Bot.*, 87: 757–768.
- BALME B.E. 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Rev. Palaeobot. Palynol.*, 87: 81–323.
- BARCLAY R., McELWAIN J., DILCHER D. & SAGEMAN B. 2007. The cuticle database: developing an interactive tool for taxonomic and paleoenvironmental study of the fossil cuticle record. *Courier Forschungs-Institut Senckenberg*, 258: 39–55.
- BOMFLEUR B., TAYLOR E.L., TAYLOR T.N., SERBET R., KRINGS M. & KERP H. 2011. Systematics and paleoecology of a new peltaspermealean seed fern from the Triassic polar vegetation of Gondwana. *Int. J. Plant Sci.*, 172: 807–835.
- CAMERON R.G., MEAKIN N.S., POGSON D.J., COLQUHOUN G.P., YOO E.K., HENDERSON G.A.M., WARREN A.Y.E. & MORGAN E.J. 1999. Sydney–Gunnedah Basin: 281–312. In: Facer R.A. & Stewart J.R. (eds), *Explanatory notes. Dubbo 1:250 000 geological sheet SI/55-4*, 2nd ed. Geological Survey of New South Wales and Australian Geological Survey Organisation.
- CANTRILL D.J., DRINNAN A.N. & WEBB J.A. 1995. Late Triassic plant fossils from the Prince Charles Mountains, East Antarctica. *Antarctic Sci.*, 7: 51–62.
- CHATTERJEE S., TEWARI R. & AGNIHOTRI D.A. 2013. *Dicroidium* flora from the Triassic of Allan Hills, South Victoria Land, Transantarctic Mountains, Antarctica. *Alcheringa*, 37: 209–221.
- COOK A. & ROZEFELDS A.C.F. 2015. In search of ancient Queensland. Queensland Museum, Brisbane.
- CRANE P.R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. Missouri Bot. Gard.*, 72: 716–793.

- CÚNEO N.R., TAYLOR E.L., TAYLOR T.N. & KRINGS M. 2003. In situ fossil forest from the upper Fremouw Formation (Triassic) of Antarctica: paleoenvironmental setting and paleoclimate analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 197: 239–261.
- DENARO T.J., RANDALL R.E. & SMITH R.J. 2013. Mineral and energy resources: 687–762. In: Jell P.A. (ed.), *Geology of Queensland*. Geological Survey of Queensland, Brisbane.
- DENMEAD A.K. 1955. The West Moreton (Ipswich) coalfield. *Publ. Geol. Surv. Qd*, 279: i–vi + 1–114.
- DRAPER J.J. 2013. Bowen Basin: 371–384. In: Jell P.A. (ed.), *Geology of Queensland*. Geological Survey of Queensland, Brisbane.
- FEISTMANTEL O. 1890. Uhlonosné útvary v Tasmánii. Spisův počtých Jubilejní cenou královské české společnosti nauk v Praze, 3(7): i–xiii + 1–162 + plates I–X [in Czech].
- FERGUSON C.L. & HENDERSON R.A. 2013. Thomson Orogen: 113–224. In: Jell P.A. (ed.), *Geology of Queensland*. Geological Survey of Queensland, Brisbane.
- FRENGUELLI J. 1942. Contribuciones al conocimiento de la Flora del Gondwana superior en la Argentina. VI. *Pterorrachis* n. gen. *Not. Mus. La Plata Paleontol.*, 7(47): 303–313.
- FRENGUELLI J. 1944a. Contribución al conocimiento de la flora del Gondwana Superior en la Argentina, XVII *Stachyopitys anthoides* n. sp. *Not. Mus. La Plata Paleontol.*, 9(65): 385–392.
- FRENGUELLI J. 1944b. Las especies del género *Zuberia* en la Argentina. *An. Mus. La Plata n.s. Paleontol. Paleobot.*, B 2(1): 1–30.
- GEINITZ H.B. 1876. Ueber Rhaetische Pflanzen und Thierreste in den Argentinischen Provinzen La Roija, San Juan und Mendoza. *Palaeontogr. Supp.*, 3(2): 1–14.
- GOMANKOV A.V. & MEYEN S.V. 1986. Tatarina flora (composition and distribution in the Late Permian of Eurasia). *Trudy Acad. Sci. SSSR*, 401: 1–174 [in Russian].
- GORDENKO N.V. & BROUSHKIN A.V. 2015. Ginkgoales: some problems of systematics and phylogeny. *Paleontol. J.*, 49: 546–551.
- HARRIS T.M. 1964. The Yorkshire Jurassic flora. II Caytoniales, Cycadales & pteridosperms. *Brit. Mus. (Nat. Hist.)*, Lond.: 1–191.
- HILL D., PLAYFORD G. & WOODS J.T. (eds) 1965. *Triassic fossils of Queensland*. Queensland Palaeontographical Society, Brisbane.
- HOLMES W.B.K. 1982. The Middle Triassic flora from Benolong, near Dubbo, central-western New South Wales. *Alcheringa*, 6: 1–33.
- HOLMES W.B.K. 1987. New corystosperm ovulate fructifications from the Middle Triassic of eastern Australia. *Alcheringa*, 11: 165–173.
- HOLMES W.B.K. & ANDERSON H.M. 2005. The Middle Triassic megafossil flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 4. *Umkomasiaceae. Dicroidium* and affiliated fructifications. *Proc. Linn. Soc. N.S.W.*, 126: 1–37.
- HOLMES W.B.K. & ANDERSON H.M. 2013. A synthesis of the rich Gondwana Triassic megafossil flora from Nymboida, Australia: 296–305. In: Tanner L.H., Spielmann J.A. & Lucas S.G. (eds), *The Triassic system*. B. New Mex. Mus. Nat. Hist. Sci., 61.
- HOLMES W.B.K. & ASH S.R. 1979. An Early Triassic megafossil flora from the Lorne Basin. *Proc. Linn. Soc. N.S.W.*, 103: 47–70.
- JACK R.L. & ETHERIDGE R. 1892. Geology and palaeontology of Queensland and New Guinea. *Publ. Geol. Surv. Qd*, 92: i–xxxi + 1–768 + plates 1–68 + maps 1–6.
- JAIN R.K. & DELEVORYAS T. 1967. A Middle Jurassic flora from the Cacheuta Formation, Minas de Petroleo, Argentina. *Palaeontology*, 10: 564–589.
- JOHNSTON R.M. 1888. Systematic account of the geology of Tasmania. W.T. Strutt, Hobart.
- JONES O.A. 1948. Triassic plants from Cracow. *Proc. R. Soc. Qd*, 59: 101–103.
- JONES O.A. & de JERSEY N.J. 1947. The flora of the Ipswich Coal Measures: morphology and floral succession. *Pap. Dep. Geol. Univ. Qd*, 3(3): 1–88.
- KIRCHNER M. & MÜLLER A. 1992. *Umkomasia franconica* n. sp. und *Pteruchus septentrionalis* n. sp., Fruktifikationen von *Thinnfeldia* Ettinghausen. *Palaeontographica*, B, 224(1–3): 63–73.
- KLAVINS S.D., TAYLOR T.N. & TAYLOR E.L. 2002. Anatomy of *Umkomasia* (Corystospermales) from the Triassic of Antarctica. *Amer. J. Bot.*, 89: 664–676.
- KRASSILOV V.A., AFONIN S.A. & NAUGOLNYKH S.V. 1999. *Permotheca* with in situ pollen grains from the Lower Permian of the Urals. *Palaeobotanist*, 48: 19–25.
- LEIGH A., ZWIENIECKI M.A., ROCKWELL F.E., BOYCE C.K., NICOTRA A.B. & HOLBROOK N.M. 2011. Structural and hydraulic correlates of heterophylly in *Ginkgo biloba*. *N. Phytol.*, 189: 459–470.
- LITTLE S.A., JACOBS B., McKECHNIE S.J., COOPER R.L., CHRISTIANSON M.L. & JERNSTEDT J.A. 2013. Branch architecture in *Ginkgo biloba*: Wood anatomy and long shoot-short shoot interactions. *Amer. J. Bot.*, 100: 1923–1935.
- McKELLAR J.L. 2013. Fig. 7.2. Detailed correlation chart across main Queensland basins of the Great Australian Superbasin and comparison of their stratigraphic columns to the international standard and to Australian zonal schemes: 518–519. In: Jell P.A. (ed.), *Geology of Queensland*. Geological Survey of Queensland, Brisbane.
- McLOUGHLIN S. & DRINNAN A.N. 1997. Revised stratigraphy of the Permian Bainmedart Coal Measures, northern Prince Charles Mountains, East Antarctica. *Geol. Mag.*, 134: 335–353.

- McNEILL J., BARRIE F.R., BUCK W.R., DEMOULIN V., GREUTER W., HAWKSWORTH D.L., HERENDEEN P.S., KNAPP S., MARHOLD K., PRADO J., PRUD'HOMME van REINE W.F., SMITH G.F., WIERSEMA J.H. & TURLAND N.J. (eds), 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code), adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. *Regnum Vegetabile* 154. Koeltz Scientific Books, Königstein, <http://www.iapt-taxon.org/nomen/main.php>.
- MEYEN S.V. 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. *Bot. Rev.*, 50: 1–111.
- MOREL E.M., ARTABE A.E. & SPALLETTI L.A. 2003. Triassic floras of Argentina: biostratigraphy, floristic events and comparison with other areas of Gondwana and Laurasia. *Alcheringa*, 27: 231–243.
- NAUGOLNYKH S.V. 2013. New male reproductive organs of gymnosperms *Permotheca colovratuca* sp. nov. from the Lower Permian of the Ural Mountains. *Paleontol. J.*, 47(1): 114–126.
- OSBORN J.M. & TAYLOR T.N. 1993. Pollen morphology and ultrastructure of the *Corystospermales*: permineralized in situ grains from the Triassic of Antarctica. *Rev. Palaeobot. Palynol.*, 79: 205–219.
- PANT D.D. & BASU N. 1973. *Pteruchus indicus* sp. nov. from the Triassic of Nidpur, India. *Palaeontographica*, B, 144(1–2): 11–24.
- PANT D.D. & BASU N. 1979. Some further remains of fructifications from the Triassic of Nidpur, India. *Palaeontographica*, B, 168(4–6): 129–146.
- PANT D.D. & PANT R. 1987. Some *Glossopteris* leaves from Indian Triassic beds *Palaeontogr. Abt. B*, 205(1–6): 165–178.
- PATTEMORE G.A. & RIGBY J.F. 2005. Fructifications and foliage from the Mesozoic of southeast Queensland. *Mem. Qd Mus.*, 50(2): 329–345.
- PATTEMORE G.A., RIGBY J.F. & PLAYFORD G. 2015a. Triassic–Jurassic pteridosperms of Australasia: speciation, diversity and decline. *Boletín Geológico y Minero*, 126: 689–722.
- PATTEMORE G.A., RIGBY J.F. & PLAYFORD G. 2015b. The Mesozoic megafossil genus *Linguifolium* Arber 1917. *Acta Palaeobot.* 55(2): 123–147. DOI: 10.1515/acpa-2015-0009
- PETRIELLA B. 1980. Sinopsis de las *Corystospermaceae* (*Corystospermales*, *Pteridospermophyta*) de Argentina. II. Estructuras fértiles. *Ameghiniana*, 17: 166–180.
- PETRIELLA B. 1981. Sistemática y vinculaciones de las *Corystospermaceae* H. Thomas. *Ameghiniana*, 18: 221–234.
- PLAYFORD G., RIGBY J.F. & ARCHIBALD D.C. 1982. A Middle Triassic flora from the Moolayember Formation, Bowen Basin, Queensland. *Publ. Geol. Surv. Qd*, 380: 1–52.
- PURDY D.J. 2013. Esk Trough: 387–391. In: Jell P.A. (ed.), *Geology of Queensland*. Geological Survey of Queensland, Brisbane.
- PURDY D.J. & CRANFIELD L.C. 2013. Ipswich Basin: 391–396. In: Jell P.A. (ed.), *Geology of Queensland*. Geological Survey of Queensland, Brisbane.
- RAVEN R.J., JELL P.A. & KNEZOUR R.A. 2015. *Edwa maryae* gen. et sp. nov. in the Norian Blackstone Formation of the Ipswich Basin - the first Triassic spider (*Mygalomorphae*) from Australia. *Alcheringa*, 39: 259–263.
- REID C.M., FORSYTH S.M., CLARKE M.J. & BACON C. 2014. The Parmeener Supergroup – late Carboniferous to Triassic: 363–384. In: Corbett K.D., Quilty P.G. & Calver C.R. (eds), *Geological evolution of Tasmania*. Spec. Publ. Geol. Soc. Aust., Tasm. Div., 24.
- RETALLACK G.J. 1977. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa*, 1: 247–278 + microfiche frames G1–J17.
- RETALLACK G.J. 1980. Middle Triassic megafossil plants and trace fossils from Tank Gully, Canterbury, New Zealand. *J. R. Soc. N.Z.*, 10: 31–63.
- RETALLACK G.J. 1981. Middle Triassic megafossil plants from Long Gully, near Otematata, north Otago, New Zealand. *J. R. Soc. N.Z.*, 11: 167–200.
- RETALLACK G.J. 1983. Middle Triassic megafossil marine algae and land plants from near Benmore Dam, southern Canterbury, New Zealand. *J. R. Soc. N.Z.*, 13: 129–154.
- RETALLACK G.J. 1987. Triassic vegetation and geography of the New Zealand portion of the Gondwana supercontinent: 29–39. In: McKenzie G.D. (ed.), *Gondwana Six: Stratigraphy, Sedimentology, and Paleontology*. Geophysical Monograph Series, American Geophysical Union, 41.
- RETALLACK G.J. 2002. *Lepidopteris callipteroides*, an earliest Triassic seed fern of the Sydney Basin, southeastern Australia. *Alcheringa*, 26: 475–500.
- RETALLACK G.J. & DILCHER D.L. 1988. Reconstructions of selected seed ferns. *Ann. Missouri Bot. Gard.*, 75: 1010–1057.
- SEWARD A.C. 1903. Fossil floras of Cape Colony. *An. S. Afric. Mus.*, 4: 1–122.
- SHIRLEY J. 1898. Additions to the fossil flora of Queensland. *Publ. Geol. Surv. Qd*, 128 [Bulletin 7]: 1–25.
- SRIVASTAVA S.C. 1974. Pteridospermic remains from the Triassic of Nidpur, Madhya Pradesh, India. *Geophytology*, 4: 54–59.
- TAYLOR E.L., TAYLOR T.N., KERP H. & HERMSEN E.J. 2006. Mesozoic seed ferns: old paradigms, new discoveries. *J. Torrey Bot. Soc.*, 133: 62–82.
- TAYLOR T.N., CICHAN M.A. & BALDONI A.M. 1984. The ultrastructure of Mesozoic pollen: *Pteruchus dubius* (Thomas) Townrow. *Rev. Palaeobot. Palynol.*, 41: 319–327.

- THOMAS H.H. 1933. On some pteridospermous plants from the Mesozoic rocks of South Africa. *Philos. Trans. R. Soc. Lond. (B)*, 222(489): 193–265.
- TOWNROW J.A. 1962a. On *Pteruchus*, a microsporophyll of the *Corystospermaceae*. *B. Brit. Mus. (Nat. Hist.), Geology*, 6(2): 287–320.
- TOWNROW J.A. 1962b. On the nomenclature of *Pteruchus johnstoni* (Feistmantel) *com. nov.* *Pap. Proc. R. Soc. Tasm.*, 96: 91–94.
- TOWNROW J.A. 1965. A new member of the *Corystospermaceae* Thomas. *Ann. Bot.*, 29, 495–511.
- van KONIJNENBURG-van CITTERT J.H.A. 2010. The Early Jurassic male ginkgoalean inflorescence *Stachyopitys preslii* Schenk and its in situ pollen. *Scripta Geologica Special Issue*, 7: 141–149.
- VASCO A., MORAN R.C. & AMBROSE B.A. 2013. The evolution, morphology, and development of fern leaves. *Frontiers in Plant Science*, 4(345): 16 pp.
- WALKOM A.B. 1917. Mesozoic floras of Queensland. Part 1 (concluded): The flora of the Ipswich and Walloon series. (d) Ginkgoales, (e) Cycadophyta, (f) Coniferales. *Publ. Geol. Surv. Qd*, 259: 1–49.
- WALKOM A.B. 1924. Notes on some Tasmanian Mesozoic plants. Part I. *Pap. Proc. R. Soc. Tasm.*, 1924: 73–87.
- YAO XUANLI, TAYLOR T.N. & TAYLOR E.L. 1995. The corystosperm pollen organ *Pteruchus* from the Triassic of Antarctica. *Amer. J. Bot.*, 82: 535–546.
- ZALESSKY M.D. 1929. Sur des débris de nouvelles plantes permienes. *B. Russ. Acad. Sci., Phys.-Math. Ser.*, 7(6): 677–689.
- ZAVADA M.S. & CREPET W.L. 1985. Pollen wall ultrastructure of the type material of *Pteruchus africanus*, *P. dubius* and *P. papillatus*. *Pollen Spores*, 27: 271–276.