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Palissya – absolutely incomprehensible or surprisingly interpretable: a new morphological model, affiliations and phylogenetic insights

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ABSTRACT. The morphology of the adaxial structures of cones belonging to *Palissya* Endlicher 1847 emend. nov. are reinterpreted based on exquisitely preserved permineralised material from the Lower Cretaceous of Queensland. Although the material was not found *in situ*, it likely derives from the Orallo Formation, which is Valanginian in age. The cones have dual vascular bundles in each bract/scale complex, and the different tissue types in the bract and ovule/scale complex support interpretation of the cone as a compound structure.

Since the early twentieth century it has been widely accepted that each ovule is surrounded by a cup-shaped structure, but the detailed morphology of the "cup" has hitherto been unclear. These new three-dimensionally preserved specimens with *in situ* ovules are described as *Palissya tillackiorum* sp. nov. This study demonstrates that the "cup" is formed from a pair of thin scales that subtend but are not fused to each ovule; each pair of scales comprises a thicker outer and thinner inner scale. The organographic relationships among ovules and scales in *Palissya* show a high degree of synorganisation. The adaxial surface of the bract/scale complex has 2–6 pairs of erect (orthotropous) ovules. The ovule/scale units are arranged symmetrically in two parallel rows on either side of the midline of the bract/scale. Individual ovule/scale units are comparable to those seen in extant Podocarpaceae and Taxaceae. The ovules are thin-walled and are interpreted to have a single integument and a non-thickened (non-lignified) micropyle. These new insights allow reinterpretation of material previously referred to *Palissya*. A new species is described from Yorkshire, England, as *P. harrisii* C.R. Hill ex Pattemore & Rozefelds sp. nov. All species based on well preserved cones are reconsidered herein: *P. sphenolepis* (Braun 1843) Nathorst 1908 emend. Florin 1958, *P. elegans* Parris, Drinnan & Cantrill 1995 emend. nov., *P. bartrumii* Edwards 1934 emend. nov., *P. antarctica* Cantrill 2000 and *P. hunanensis* Wang 2012.

Palissya ovalis Parris et al. 1995 differs structurally from *Palissya* and is transferred to *Knezourocarpon* Pattemore 2000 emend. nov. Representatives of this genus may superficially resemble those of *Palissya* in compressions and impressions, and their congeneric status has been previously suggested; hence its inclusion in this study. *Knezourocarpon* has adaxial processes that are positioned in two parallel rows but it lacks ovules and paired lateral scales that formed a cup-shape, and its processes attach directly to a central vascular trace. The improved understanding of *Palissya*'s morphology allows for definite separation of these genera, although the higher-order affiliation of *Knezourocarpon* remains unclear.

KEYWORDS: *Palissya*, *Knezourocarpon*, Lower Cretaceous, Valanginian, Orallo Formation, Surat Basin, Queensland

INTRODUCTION

Fructifications assigned to *Palissya* Endlicher 1847 emend. nov. have been reported from the Upper Triassic–Middle Jurassic of the Northern Hemisphere and the Middle Jurassic–Lower Cretaceous of the Southern Hemisphere (Parris et al. 1995, Schweitzer & Kirchner 1996, Wang 2012, Pattemore et al. 2014). Florin's (1958: 267, 268) generic emendation explicitly recognised the compound structure of the cone. He erected Palissyaceae and included *Stachyotaxus* Nathorst 1886 from the Rhaetian of Greenland and Sweden (Florin 1958: 375). The cones *Metridiostrobus* Delevoryas & Hope 1981 from the Upper Triassic of North Carolina, USA, and *Knezourocarpon* Pattemore 2000 emend. nov. from the Australian Lower Jurassic also share characters with *Palissya*; in particular, helically arranged lateral appendages and adaxial organs positioned in two symmetric, parallel rows.

Palissya remains poorly understood despite being recorded from several localities in both hemispheres during the past 170 years (Pattemore et al. 2014). There is broad agreement that *Palissya* cones are lax and the lateral appendages are helically arranged, but many different and often conflicting interpretations of cone structure have been proposed. Varying terminology, often based on assumptions about relationships, has influenced the description of these cones; this remains an ongoing challenge (Tab. 1). Until the morphology of the cones is resolved, it will not be possible to understand their phylogenetic relationships. The key questions that need resolving are whether the cones are compound or simple, ovulate or microsporangiate, and the structure and purpose of the adaxial components on the lateral appendages of the cones.

OVULATE OR MICROSPORANGIATE STRUCTURE?

Nearly all researchers have accepted the cones as being ovulate, and the scales were interpreted as winged seeds by Schenk (1867). Florin (1958) described seeds from the type species, but evidence of seeds has been largely missing or not recorded for all other species (Tab. 1). Schweitzer & Kirchner (1996) interpreted both *Metridiostrobus* and *Palissya* as microsporangiate cones, emending the diagnosis of Palissyaceae to include both microsporangiate and ovulate cones. They erected *P. oleschinskii* based on cones from the Rhaetian–Lower Jurassic of Zangerud, Iran, which have adaxial, alternate to sub-opposite, biseriate pollen sacs mounted on a sporophyll. Their assignment to *Palissya* was questioned (Wang 2012, Pattemore et al. 2014), as the cones lack the cup-like structures that surround ovules or ovule attachment scars.

COMPOUND OR SIMPLE CONES?

There has been uncertainty about whether *Palissya* cones are compound or simple structures (Tab. 1). Saporta (1884: pl. 197, fig. 2a–d) interpreted ovule/scales belonging to the type species of *Palissya* as having an ovule attached on either side of each lobe of a pinnate-like structure – akin to a modified fern frond. This was apparently based on his view of cone development (Schenk 1890); his interpretation of the cones as simple was supported by Solms-Laubach (1891) and Seward (1919). Nathorst's (1908) study, based on fragmentary impressions and compressions, focused on the adaxial structures, but his description of a Hauptleitbundel (main vascular bundle) on the adaxial surface of the lateral appendages may suggest a structural separation of organs (i.e. a bract/scale complex). Florin (1944: pl.184, figs 20–22, 1958) interpreted the bract as having two distinct vascular traces extending from the cone axis into a Deckschuppe (sporophyll/bract) and Samenschuppe (or ovule/scale complex). Parris et al. (1995) questioned Florin's (1944, 1958) interpretation of the cones as compound (Tab. 1). Their study of Nathorst's (1908) Swedish specimens and material from Victoria and New Zealand (Parris et al. 1995) was based upon impressions and compressions that show little evidence of preserved vasculature.

WHAT ARE THE ADAXIAL STRUCTURES ON THE BRACTS OF THE CONE?

Seeds are extremely rare, but a circular scar in the centre of cup-like structures has been interpreted as an ovule attachment point in the type species *Palissya sphenolepis* (Braun 1843) Nathorst 1908 emend. Florin 1958, *P. elegans* Parris, Drinnan & Cantrill 1995 emend. nov., *P. antarctica* Cantrill 2000, and *P. hunanensis* Wang 2012 (Tab. 1). On the adaxial surface of the bracts are structures that have been variously referred to as winged seeds, seed cups, epimatia, arils, or cup-like collars or processes (Tab. 1). Nathorst (1908) recognised that the adaxial structures formed cup shapes around the ovules. Most researchers have accepted this generalised description and have interpreted the "cup" as a single structure (Tab. 1), although Nathorst (1908), Florin (1958) and Parris et al. (1995) recognised that each "cup" is asymmetrical, with its height varying from one side to the other. Its surface has a striated appearance,

Table 1. *Palissya*: previous and current terminology. Translations follow context and are not necessarily literal. Selected studies are limited to those where *Palissya* material was directly examined by the authors and the cone structure was described

Author	Fructification/Cone	Lateral appendage	Adaxial structures on lateral appendages
Schenk (1867)	Ovulate fructification or cone (weiblichen Blüthenständen or Zapfen)	Scale (Schuppe). Brief description, no distinction in terminology between ovuliferous scale and bract	Winged seeds (Samen, geflügelt)
Saporta (1884)	Ovulate (strobili foeminei), simple	Scale and bract (squamis or bractare) formed from a single pinnate-like structure	Pinnate-like (lobed) ovuliferous scale bearing an inverted winged ovule on either side of each lobe (Saporta 1884: pl. 197, fig. 2a–d)
Schenk (1884, 1890)	Ovulate cone (Zapfen), compound	Cone scale (Schuppe or Zapfenschuppe) comprising a bract (Bractee, Deckschuppe, Lamelle) and ovuliferous scale (Samenschuppe or Fruchtblätte). Separation of ovule/scale and bract implied in the terminology	Ovules (Samen) on the margin of an ovule/scale
Nathorst (1886)	Cone (kottar)	Ovuliferous scale (fröfjället) [used Schenk's (1884) terminology]	Wing/skin-like cone scales (fritt vingelikt, kottefjällen)
Solms-Laubach (1891)	Ovulate, probably simple	Fertile scale and bract scale, but doubted that sporophylls are formed from two separate parts	Lobe-like projections
Nathorst (1908)	Ovulate (weiblich Zapfen)	Cone scales (Zapfenschuppen), bulged or keeled on their abaxial surface (Rückseite gekielt) and having a protruding central vascular bundle (Hauptleitbündel) on their adaxial surface. However, there is no clear distinction in his terminology between ovule/scale and bract. Nathorst's description is based on isolated lateral appendages of fragmented cones, hence his focus on the adaxial structures	Thin-walled lamella (Lamella) forming a cup-like organ (schalen- oder becher-förmigen Organen); also, Becher, Samenbecher (seed cup), or Cupula. Nathorst (1908: 7, 8) noted that the height of the cup varied from one side of the cup to the other. He suggested that each cup-like structure may be an epimatium. However, the term "cup" (a single structure) was used in preference to "epimatium" to avoid biased terminology
Seward (1919)	Ovulate (megastrobilus), probably simple	Scale, cone scale, seed-bearing scale or sporophyll (no distinction between ovuliferous scale and sporophyll). Reiterated Solms-Laubach's (1891) view that cones are unlikely to be compound	Cup-like basal investments, cupules
Hirmer (1936)	Ovulate (weiblich Zapfen), compound	Bract (Deckschuppe) and ovule/scale (Fruchtschuppe) differentiated but not demonstrated	Epimatium (single structure)
Florin (1944)	Ovulate (weiblich Zapfen), compound	Bract/scale complex (Samenschuppenkomplex), comprising bract (Deckschuppe) and ovuliferous scale (Samenschuppe oder Makrosporophyll) Dual vascular bundles were demonstrated (Florin 1944: pl. 184, figs 20–22) and interpreted as a compound structure	Cup-like aril (arillus) being an annular outgrowth (ringförmigen Auswuchs) from the base of the seed
Florin (1951)	Ovulate cone, compound	Bract and seed/scale complex. Seed/scale complex comprises 10 "megasporophylls", each having a terminal ovule	Cup-shaped aril (single structure), free above chalaza
Florin (1958)	Ovulate cone, compound	Cone scale, comprising bract and axillary seed/scale complex (ovuliferous scale). Each seed scale bears a terminal ovule with an aril	Cup-like aril (single structure)
Hill (1974)	Ovulate cone, compound	Cone-scale with bract and ovule/scale	Cup-like aril (single structure)
Parris et al. (1995)	Probably ovulate	Stalked sporophylls. Doubted that the cone is compound (see text)	Cup-like process (single structure)
Schweitzer & Kirchner (1996)	Microsporangiate cone, simple	Interpreted as microsporangiate (see text)	Pollen sacs
Wang (2012)	Ovulate, compound	Bract and female dwarf shoots	Cup- or barrel-shaped scale enclosing ovule (single structure)
Present study	Ovulate, compound	Bract/scale complex comprising a bract fused (or adpressed) to an ovule/scale complex	Major and minor paired scales forming a cup-shaped structure surrounding and subtending an ovule

with radiating lines extending to the margin of the "cup" in *P. sphenolepis* (Nathorst 1908: pl. 1, figs 3–5, Parris et al. 1995: fig. 13E), *P. elegans* (Parris et al. 1995: fig. 5A, B, 6), *P. hunanensis* (Wang 2012: fig. 3C) and specimens belonging to *Palissya* from Yorkshire, England (Hill 1974 and Fig. 12 herein). The "cups" have also been interpreted as arils or epimatia by various researchers (Nathorst 1908, Hirmer 1936, Florin 1944, 1954, 1958, Hill 1974), which suggests links to conifer families such as Podocarpaceae and Taxaceae. Recent research has referred to these structures as processes (Parris et al. 1995) or scales (Wang 2012). These different interpretations of the "cup" have made comparisons with other groups of plants difficult, resulting in uncertainty about the phylogenetic placement of *Palissya*. This is due in part to the paucity of detailed studies, and also the difficulties of interpreting impression and compression material, which is all that has been available.

Much of the early research on *Palissya* suggested a resemblance to extant members of Cupressales (e.g. Schenk 1884). Nathorst (1908: 10) questioned links with extant conifers, although he noted a broad similarity of *Stachyotaxus* with extant representatives of the Podocarpaceae. Seward (1919) and many subsequent authors have attributed *Palissya* to "Coniferales", which is equivalent to Pinales Gorozh. (sensu Christenhusz et al. 2011: 59). Florin (1958: 375) regarded the ovule/scale complex in Palissyaceae as unlike that of any extant conifer family; he had earlier suggested that *Palissya* evolved from voltzialean conifers (Florin 1944). Meyen (1984: 87, 90) also placed Palissyaceae within Pinales but regarded the family as "absolutely incomprehensible", a comment that presumably relates to the lack of clear homologies with other gymnosperms. Stewart & Rothwell (1993: 433) suggested links with the early evolution of Cephalotaxaceae (Cupressales). Parris et al. (1995) concluded that *Palissya* cones are not compound structures but rather sporophylls, suggesting possible affinities with pteridosperms. The phylogenetic placement of *Palissya* therefore remains equivocal, and this uncertainty about the very basic structure of the *Palissya* cone resulted in Miller (1999), in part influenced by the comments of Parris et al. (1995), excluding the genus from his review of fossil conifers. There has also been uncertainty as to whether Gondwanan specimens should be considered congeneric with those of Eurasia (Parris et al. 1995, Pattemore et al. 2014).

Most leaves assigned to *Palissya* are not considered to belong to the genus (Parris et al. 1995, Schweitzer & Kirchner 1996, Pattemore et al. 2014), including leaves from the Lower Cretaceous Stanwell Coal Measures, Queensland (Shirley 1902). Hill (1974) indicated that leaves are possibly attached basally on one of the cones from Hasty Bank, Yorkshire, England; the co-preservation of *Elatocladus*-like leaves and cones at the site, along with cuticular evidence from these organs, suggests that they are from the same plant. However, no compelling new evidence regarding leaf affiliation has been advanced since Florin (1958) and Hill (1974).

In this paper we assess the age of the permineralised floras in south-eastern Queensland (Figs 1, 2) in which these new *Palissya* cones have been found. These cones provide an opportunity to resolve the morphology of *Palissya*, and the ovule/scale arrangement and the bract/scale complex are described in detail. A new model for the ovule/scale complex is proposed and the phylogenetic relationships of *Palissya* are reconsidered. Consequently, compression and impression specimens assigned previously to several species of *Palissya* were re-examined. This also necessitated a review of *Knezourocarpon*, which has been considered as possibly synonymous with *Palissya* (McLoughlin et al. 2002).

MATERIAL AND METHODS

The new specimens described herein are held in the Queensland Museum, Brisbane (QMF and UQF). Previously reported material from Australasia (including types) described by McLoughlin & Drinnan (1995), Parris et al. (1995), Pattemore (2000), Jansson et al. (2008) and Pattemore et al. (2014) in the Queensland Museum and Museum Victoria, Melbourne (MVP), were also re-examined. One author (AR) also examined material, including types, from Yorkshire, England, and New Zealand in the Natural History Museum, London (BMV), that were described by Hill (1974) and Edwards (1934) respectively.

The new Australian permineralised (siliceous) specimens are from an agricultural property called Brig-O-Doon, near Wandoan, Queensland (25.922947°S, 149.575461°E; Figs 1 and 2, site A). The surface geology (Figs 1, 2) at this site and the surrounding region, the stratigraphy, and the age of the specimens are based on data provided by the Queensland Department of Natural Resources, Mines and Energy (McKellar 2013, Cranfield 2017, DNRME 2018). Specimens were preserved within a single, smooth, well-rounded silcrete

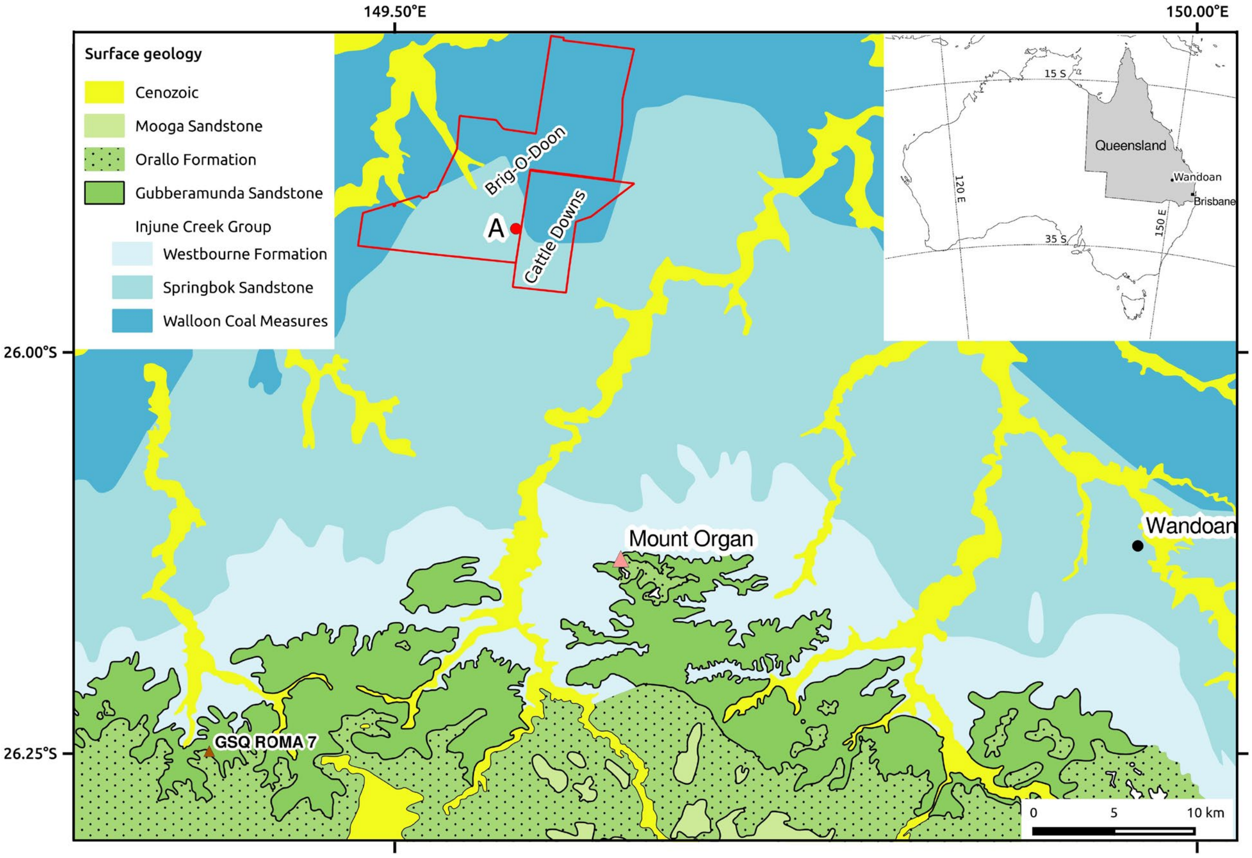

Fig. 1. Surat Basin surface geology in the Wandoan area of Queensland. **A**: specimen collection site. Property boundaries outlined in red. Stratigraphic well GSQ ROMA 7 (see Swarbrick 1973, Cranfield 2017). Other features and scale as marked. Geology from DNRME (2018)

rock (~110 mm × 110 mm × 230 mm) which was found within the soil profile (i.e. not *in situ*). The weathered exterior showed no indication of included specimens, the cones only being discovered after the rock had been cut with a diamond saw into slabs ~10 mm thick, which resulted in sections that were not true longitudinal or transverse sections. The slabs were further cut to isolate identified specimens, and thin sections were prepared from a single cone using standard sectioning techniques in order to study the internal structure of the lateral appendages of the cones in more detail. Sectioning was restricted to a single specimen because a limited number of cones were available.

Selected specimens were photographed with (1) a thin application of vegetable oil using a generic USB microscope (Figs 3, 4, 5B, 6B–D); or (2) under alcohol with a Canon DSLR camera and processed with Zerene stacker software (http://www.zerenesystems.com) and a Visionary Digital Photographic System (Figs 5A, C, D, 6A, 7F, G); or (3) thin sections (Fig. 7A–E) were photographed using the photographic system in (2) above. The permineralised specimens were also checked for photoluminescence under UV light but there was no observable fluorescence. An attempt to image permineralised specimens using the Imaging and Medical Beamline at the Australian Synchrotron, Melbourne, failed to produce usable results because X-ray absorption was excessive in one dimension and possibly due to a lack of density differentiation between matrix and plant material. Specimens from Yorkshire and New Zealand were photographed by staff of the Natural History Museum, London (Figs 10–12). All other specimens were photographed using a Pentax DSLR camera without any special sample preparation. Interpretation is based on detailed examination of the cones, and a model was generated using 3D animation software (blender.org).

No organic connection with leaves has been identified in the present study, with the possible exception of one of Hill's (1974) specimens from the Jurassic of Yorkshire as noted by that author. The few identifiable leaves preserved with the cones from Brig-O-Doon are fern-like but are too degraded to allow generic assignment or useful description.

TERMINOLOGY

As noted above, various terms have been used to describe the cone morphology of *Palissya* (Tab. 1). The key challenges in this project were to determine if the cones are ovulate or microsporangiate, compound or simple, and to resolve the nature of the cup-like structures surrounding the ovules. It is shown herein that these cup-like structures are formed from a pair of scales that subtend each ovule. Historically the term "scale", as applied to *Palissya* (Tab. 1) and conifers generally, has been

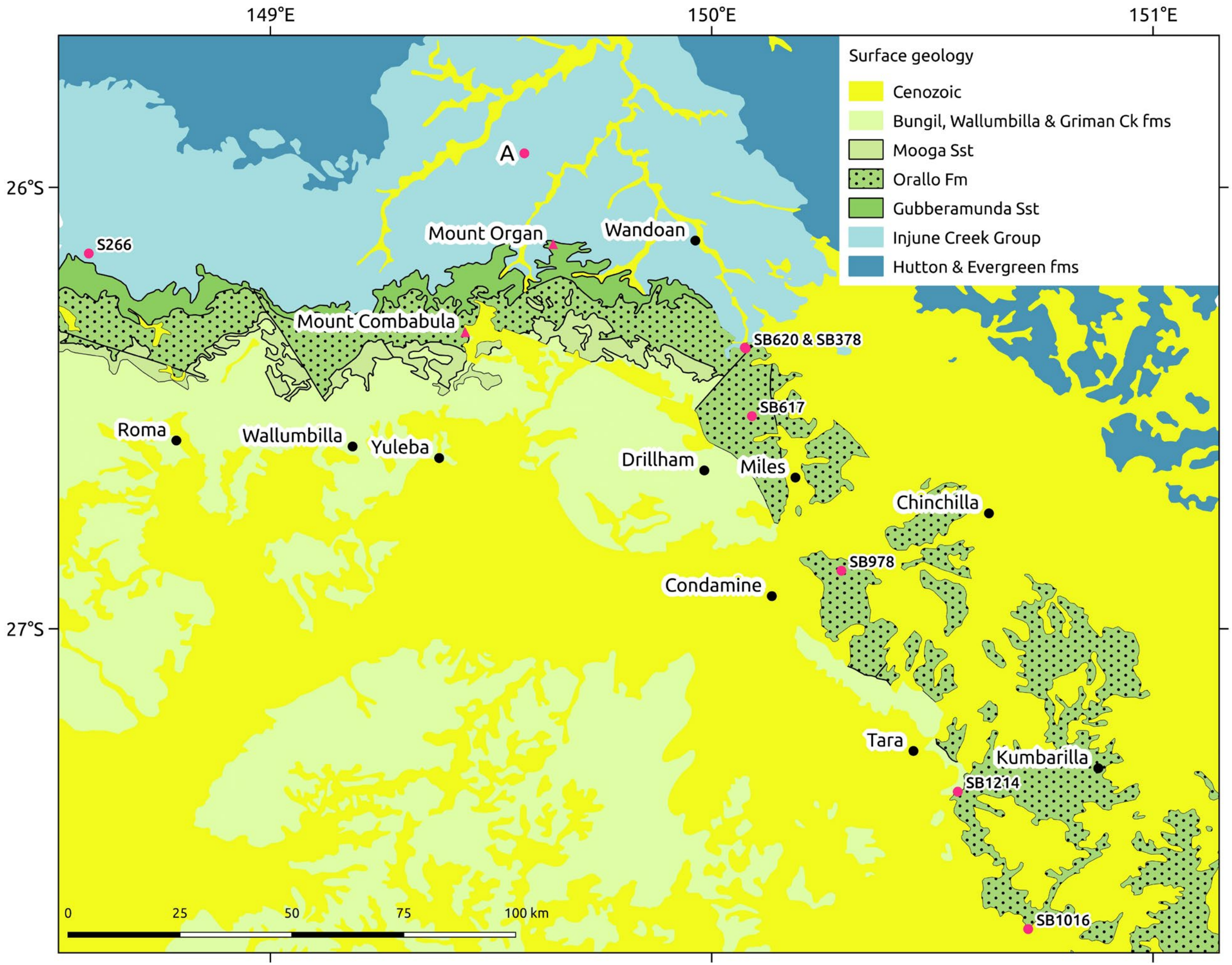

Fig. 2. Surat Basin surface geology in the Roma–Chinchilla area of Queensland (only main outcrops shown; see Fig. 1 for detailed map). **A**: specimen collection site. Sites prefixed "S" are those reported by White (1967a, b). Other features and scale as marked. Geology from DNRME (2018)

used to refer to an individual scale (that subtends an ovule), or in a collective sense for an individual ovule/scale unit, or applied to the whole ovule/scale complex.

For clarity the present study applies the following terminology to *Palissya*.

a) The axis has lateral, helically arranged appendages, each comprising a bract fused (or adpressed) to an ovule/scale complex. The entire lateral appendage is referred to as a bract/scale complex.

b) The ovule/scale complex comprises several ovule/scale units in two parallel rows. Each ovule/scale unit comprises (i) an ovule attached to (ii) the scale-vasculature with (iii) the ovule subtended by a pair of scales.

Scales are colour-coded in some figures to clearly illustrate the precise organographic relationship between the scales and ovules. The term "cup" is used in the limited sense of referring to the 3-dimensional cup-shaped structure formed by the arrangement of paired scales. The descriptive portion of this work uses the term "ovule" but the terms "ovule" and "seed" are applied interchangeably elsewhere in the paper. *Knezourocarpon* is interpreted herein as being a microsporangiate cone, but as this genus is less well understood than *Palissya*, descriptive unbiased terminology is applied. It has lateral appendages that are described as laminae, each having several adaxially mounted processes. Classification above the level of family follows Christenhusz et al. (2011).

LOCATION AND GEOLOGY OF THE NEW PERMINERALISED MATERIAL

The fossil site at Brig-O-Doon is located on a SSW-trending ridge and within outcropping Springbok Sandstone of the Injune Creek Group, Surat Basin (Fig. 1, site A: DNRME 2018). All permineralised plant material collected from this and adjoining properties was found on the surface of agricultural fields (Tidwell & Rozefelds 1990, Tidwell & Clifford

1995, Tidwell et al. 2013); that is, they were not found *in situ*, and the rocks containing the specimens are well-rounded, commonly occurring with other similarly rounded pebble- and cobble-sized rocks within drainage features and palaeostream deposits (A. Rozefelds, pers. obs.). Almost all of the permineralised plants described from this region (Fig. 2) were not found *in situ* (White 1967a, Tidwell & Rozefelds 1990, 1991, Tidwell & Clifford 1995, Clifford & Carney 1994, Clifford 1995, Tidwell et al. 2013) or such information was not recorded (Sahni 1920, Gould 1973). *In situ* permineralised remains in this region occur in the Orallo Formation (White 1967b, Exon 1976: fig. 40, see Fig. 2, SB617 herein). The stratigraphy and location of permineralised ferns from Mount Organ Station (Gould 1973) are unknown, but the property includes outcropping strata of the Orallo Formation (Fig. 1). Previous researchers therefore either assumed that the silicified plants were derived from, and are the same age as, the sediments in which they occur, or inferred an origin from topographically higher strata that are no longer in place locally. In neither case were attempts made to identify the likely source of silica responsible for the preservation of these plant remains. Rare occurrences of fossil wood are known from the Springbok Sandstone in the Chinchilla area but, unlike the specimens from Brig-O-Doon, these are preserved in a strongly lateritised sandstone matrix (Cranfield 2017).

The Surat Basin of southern Queensland includes extensive flat-lying Mesozoic strata of the Injune Creek Group (including the Springbok Sandstone) that lie stratigraphically below the Gubberamunda Sandstone and Orallo Formation (Tab. 2). These latter two units outcrop ~20 km south of the fossil site (Figs 1, 2) along the above-noted SSW-oriented ridge. Despite the poor weathering resistance of some components of the Orallo Formation (Exon 1976), it represents a topographical high, forming part of the Great Dividing Range within the map area (Fig. 1).

The permineralised material shows no evidence of water-related sedimentary processes being involved in preservation. There are no included clasts and no indication that a sediment matrix was deposited amongst the vegetative matter. The vegetation is not aligned in a particular direction and is loosely stratified, but has minimal or no observable compression and appears to be preserved as an undisturbed collection of vegetative fragments, suggesting rapid terrestrial burial by volcaniclastics. There is a strong correlation between the colour of the preserved vegetation and its degree of decay, lighter-coloured specimens being more degraded; white, cloudy or filamentous fungi are present throughout the cut slabs (e.g. QMF58804, Fig. 6D; QMF58813C, Fig. 7D, labelled Mx). Thus, the specimens from Brig-O-Doon are interpreted as thick forest floor leaf litter consisting of wood, fragments of leaves,

Table 2. Stratigraphy and plant remains in the Roma–Wandoan–Chinchilla area of Queensland. Based on Exon (1976, 1980), Cook et al. (2013), McKellar (2013) and Cranfield (2017); see Figures 1, 2 herein

Surat Basin unit	Depositional environment and chronostratigraphic range	Notes
Bungil, Wallumbilla & Griman Creek fms	Chiefly marine Lower Cretaceous (Hauterivian–Albian)	Either lacking plant fossils or with unidentified fragments (impressions)
Mooga Sst	Fluvial Lower Cretaceous (uppermost Valanginian)	Plant impressions. No permineralised preservation
Orallo Fm	Fluvial, riparian Lower Cretaceous (uppermost Berriasian–Valanginian)	Permineralised and compressional remains. Largely volcanic sediment source with both fluvial and ash-fall (tuff) deposition. *In situ* preservation of tree trunk. Widespread permineralised wood and other plant organs. Probable source of permineralised specimens described as *Palissya tillackiorum* herein
Gubberumunda Sst	Fluvial lowermost Cretaceous (chiefly, Berriasian)	Poorly preserved unidentified plant fragments. No recorded permineralised preservation
Westbourne Fm & Springbok Sst (Injune Creek Group)	Fluvial, lacustrine, paludal uppermost Jurassic (chiefly, Tithonian)	Either lacking plant fossils or very poorly preserved unidentified plant impressions. Rare minor coal seams occur in both units and sporadic occurrences of fossil wood are known in the Springbok Sst along the Condamine River in the Chinchilla area (Cranfield 2017: 43, pl. 13)

rare seeds and cones, all in varying states of pre-preservational decay.

The sediments that gave rise to the Orallo Formation were chiefly volcanic and were from an unknown distal source (Exon 1976: 104, Cook et al. 2013: 538). The formation includes sandstone, carbonaceous siltstone and layers of tuff (some weathered, forming bentonite up to 2 m thick). This volcaniclastic material was the likely source of silica in the subsequent permineralisation process and explains the exquisite preservation of some of this material. This also indicates that the abundant vegetative litter is autochthonous and has not been transported; hence the widely used informal name "Forest Floor" is appropriate to describe this material (Clifford 1995: 419). As the simple fabric of the silcrete lacks any formational structure or ripening sequences, this indicates a non-pedogenic formation (Ullyott & Nash 2016: tab. 1, Taylor & Eggleton 2017).

The Orallo Formation includes *in situ* permineralised plants, whereas permineralised specimens attributed to other stratigraphic units in the general area were found as "floaters" in soil or creek beds. The plant fossils recorded from the Orallo Formation include tree trunks, abundant fossil wood, and impressions of bennettitaleans, ferns, equisetaleans and conifer leaves (Day 1964, White 1967a, b, 1969, Exon 1976). Silicified taxa described from the formation are mostly fern stems (Gould 1973, Tidwell & Rozefelds 1990, 1991, Tidwell & Clifford 1995) and an unusual cupulate fructification (Clifford 1995), and cannot be easily compared with the impression floras known from elsewhere in the formation, although permineralised *Cladophlebis*-like leaves are known (A. Rozefelds pers. obs. 2017). A large permineralised plant fossil assemblage (White 1967a, locality S266) which was thought to be derived from the Doncaster Member of the Wallumbilla Formation is also more likely to be from the Orallo Formation. The Wallumbilla Formation is a marine deposit which does not have recorded permineralised plants (Tab. 2).

Thus, the permineralised specimens from Brig-O-Doon, Cattle Downs and elsewhere in the Surat Basin (Fig. 2) are interpreted as weather-resistant remnants of eroded strata of the Orallo Formation. Clifford and Carney (1994) and Clifford (1995) similarly assumed that the silicified fructifications they studied were eroded from the "Forest Floor" or "Fossil Wood Beds" of the Kumbarilla beds in the Surat Basin, which are now regarded as part of the Lower Cretaceous Orallo Formation (Cook et al. 2013). This silicified vegetation is broadly contemporaneous with floral assemblages reported by Parris et al. (1995) from the Gippsland Basin, Victoria (Pattemore et al. 2015: fig.1).

Palynological studies of the Orallo Formation suggested an earliest Cretaceous age (latest Berriasian–Valanginian: McKellar 2013, Cranfield 2017). Current research by Jennifer Cooling (pers. comm. 2018) on the Upper Jurassic–Lower Cretaceous of the Surat Basin has recorded pollen belonging to a diverse assemblage of gymnosperms including bennettitaleans, conifers (Araucariaceae, Cheirolepidaceae, Podocarpaceae, ?Pinaceae, Cupressaceae), ginkgoaleans, gnetaleans and unnamed angiosperm pollen. No palynomorphs have been recorded from fossiliferous silcrete of the region, precluding a palynological comparison with other records from the Orallo Formation.

RESULTS AND SYSTEMATIC PALAEOBOTANY

Class: PINOPSIDA Burnett 1835

Order: PALISSYALES Doweld 2001

The present study supports the widely held view that *Palissya* is a conifer cone (Tab. 1). However, the affinities of *Palissya* remain uncertain and Doweld's (2001) Palissyales is adopted herein, being placed within Pinopsida following Meyen (1984) and Anderson et al. (2007).

Family: PALISSYACEAE Florin 1958

Diagnosis. See Florin (1958: 276).

Genus: ***Palissya*** Endlicher 1847 emend. nov.

Emended diagnosis. Cones woody, compound, ovulate, slender, with helically arranged lateral appendages (bract/scale complexes), each comprising an abaxial bract with an adaxial ovule/scale complex; the bract and ovule/scale complex have separate vascular bundles and they differ in their internal structure. Ovule/scale complex, highly synorganised, comprising symmetrically arranged pairs of ovule/scale units positioned in two parallel rows on either side of the midline of the ovule/scale complex. Each ovule terminates a vascular trace and is subtended by, but not fused to, a pair of transversally arranged scales which formed a cup-shaped structure surrounding the basal portion of the ovule and extending toward the ovule's apex. Scales comprise parenchymatous tissue, lacking vasculature, and have a striated surface. Ovules are erect (orthotropous) more or less at right angles to the bract/scale complex (not inverted), and have a single integument and a short micropyle.

Type species. *Palissya sphenolepis* (Braun 1843) Nathorst 1908 emend. Florin 1958, its lectotype (Braun 1843: pl. 13, fig. 19) being designated by Florin (1958). The genus was erected by Endlicher (1847) – for nomenclatural detail see Pattemore et al. (2014: 51).

Palissya tillackiorum sp. nov.

Figs 3–8

Diagnosis. Cone >60 mm long, 10–15 mm wide (Fig. 3). Axis <2.5 mm wide, endarch, consisting of radially arranged tracheids and a pith of parenchyma and fibres, with foliar organs having abundant sclereids. Lateral appendages (bract/scale complex) helically inserted and sub-perpendicular on the axis, ~6 mm wide, ~8 mm long, each appendage consisting of an outer (abaxial) sclerenchymatous layer with abundant sclereids (bract) and an adaxial layer of longitudinally arranged, parenchymatous tissue with adaxially placed ovule/scale complex (Fig. 7A). Bract and ovule/scale complex tightly integrated, each having separate but fused or adpressed vascular bundles. Bract gradually tapering basally, commonly bending sub-perpendicularly toward the axis along ~1/3 its length. Bract apically tapering to an acute apex (acuminate) and commonly curving outward (abaxially) near the tip. Abaxial surface of bract strongly rugose, with two parallel, sharply pointed ridges positioned immediately either side of the bract's longitudinal midline, ~0.6 mm high above the surface of the bract and 0.5 mm wide basally (Fig. 7C, D). Internal structure of bract has strongly pigmented sclerenchymatous cells.

The ovule/scale complex comprises two parallel rows of 3 or 4 ovule/scale units, each being formed from an ovule mounted apically on a vascular trace with a pair of scales. Mature ovule not winged, symmetrical, ~2 mm long, ~0.9 mm wide, integument ~70 µm thick. Immature ovule symmetrical, not winged, 0.7 mm long, 0.5 mm wide, micropyle ~70 µm wide. Each ovule subtended by a pair of parenchymatous scales and the facing (internal) surface of the scales is radially striated. The scales are free from the ovule and extend up to ~3/4 the length of the ovule. Each pair of scales comprising a single major (outer, distal) scale, 1.7 mm long (laterally), <0.6 mm thick and rising to 1.5 mm high, and a minor (inner, proximal) scale, 1.1 mm long (laterally), <0.4 mm thick and 1.2 mm high; both scales are free distally but they abut (or possibly merge) basally. The major and minor scale pair forms a cup-like structure ~1.0–1.3 mm in diameter at its widest point, and a circular ovule attachment scar <0.5 mm diameter occupies a central position in the cup. The vascular trace to each ovule is ~0.2 mm in diameter (Fig. 7B). The circular ovule attachment point is surrounded by a series of ~12–18 (interpolated from partial count) very small and evenly spaced ?abscission scars (Fig. 5B, Vc), each being at a consistent radius of ~0.3 mm from the centre of the circular ovule attachment scar.

Type specimens. The holotype QMF58817 (Figs 3, 4) and paratypes QMF58813A–C (sectioned specimen: longitudinal thin-section, Fig. 7A, B; transverse thin-section, Fig. 7C–E), QMF58816 (Figs 5A, B, 7F, G), QMF58820 (Fig. 5C, D) are all designated herein and are from Brig-O-Doon, ~40 km northwest of Wandoan, Queensland, Australia. Type stratum (inferred): Lower Cretaceous (Valanginian) Orallo Formation, Surat Basin, Queensland.

Material examined. All the above-designated types and QMF58802, QMF58804 (Fig. 6D), QMF58805, QMF58806, QMF58807 (Fig. 6B, C), QMF58810–QMF58812, QMF58814, QMF58815, QMF58818, QMF58819, QMF58821, QMF59019 (Fig. 6A), QMF59018A–G. All specimens are from the type locality.

Etymology. The species was named in honour of the donors of the specimens, Ron & Linda Tillack.

Remarks. The permineralised specimens from Brig-a-Doon provide significant new insights into the morphology of the genus. They possess a suite of new characters and also provide greater detail and further clarity on the morphology of previously reported structures in compressions and impressions assigned to the genus.

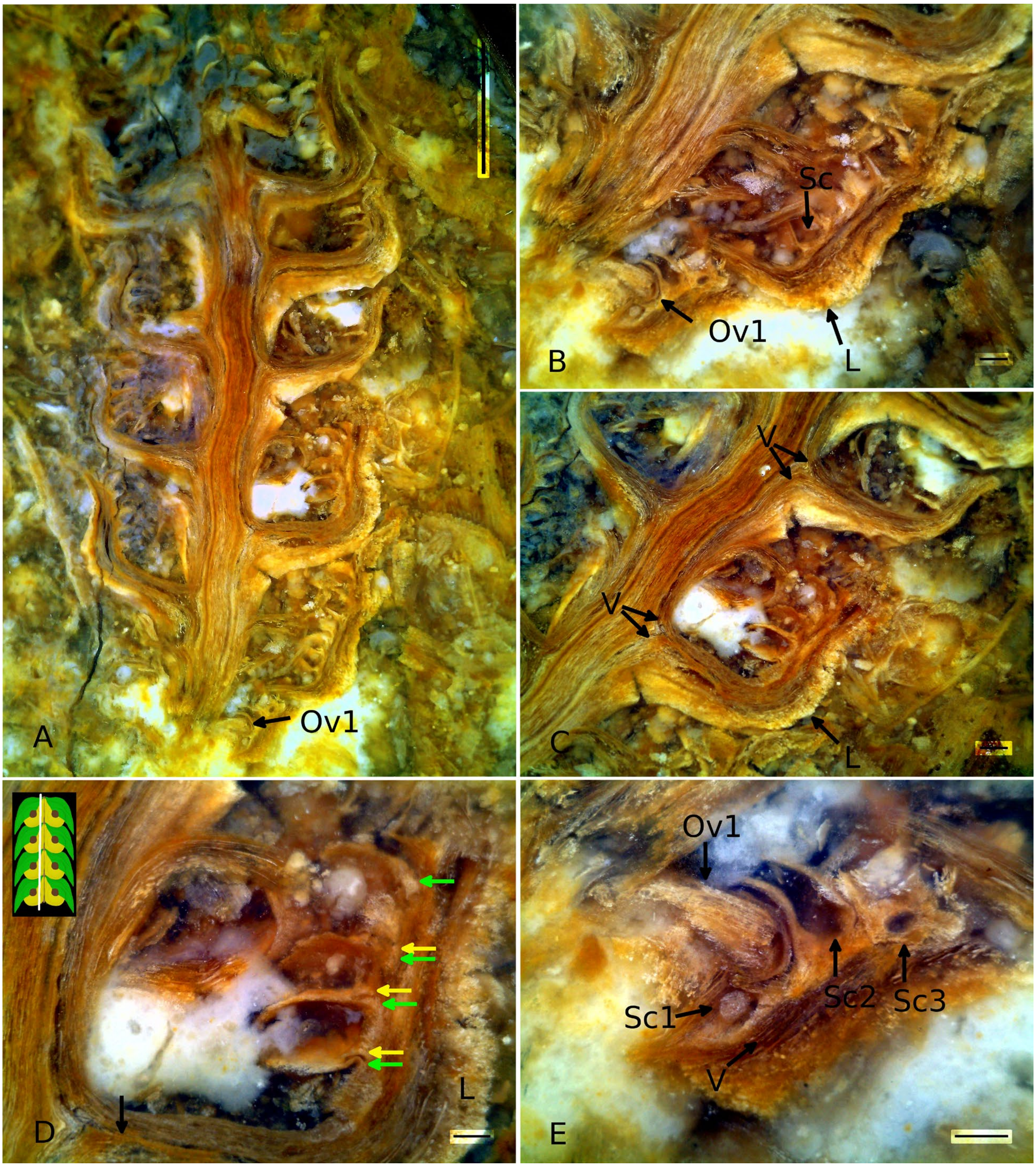

Fig. 3. **A–E**: *Palissya tillackiorum* sp. nov. (QMF58817: holotype designated herein); Brig-O-Doon, near Wandoan, Queensland (Valanginian Orallo Formation, Surat Basin). **A**: longitudinal section of cone. **B–E**: detail of cone shown in A. **B**: two partially preserved bract/scale complexes showing an ovule (**Ov1**), rugose abaxial surface of bract (**L**), adaxial scales, ovule attachment scar (**Sc**). **C**: detail of cone showing separate vascular traces (**V**) for bract and ovule/scale complex; rugose abaxial surface texture of bract (**L**). **D**: the major scale (green arrows) and minor scale (yellow arrows) pairs are indicated, with black arrow marking distict separation of bract and ovule/scale complex. **D** (inset): conceptual planar view showing inferred position of cross-sectional cut. **E**: Ovule attachment scars Sc1, Sc2 and ovule Ov1 are aligned on one side of the midline of the ovule/scale complex; Sc3 is positioned on the opposite side of the midline and includes remnant scales; arrow V indicates vascular traces within truncated portion of bract. Key: L, bract (abaxial surface); **Ov1** – ovule; **Sc** – ovule attachment scar; **V** – vascular bundles/traces. Scale: A = 5 mm; B, C = 1 mm; D, E = 0.5 mm

The cones have a well-defined bract/scale complex which is tightly integrated with two zones of tissue. The abaxial part of the bract/scale complex is interpreted as the bract, which is composed of dark-coloured fibres and sclereids, with the abaxial surface being strongly rugose (Fig. 7A, B). One cone has an abaxial surface texture which may have preferentially degraded relative to other fibrous parts of the cone (Fig. 3B–D, labelled L). Prominent

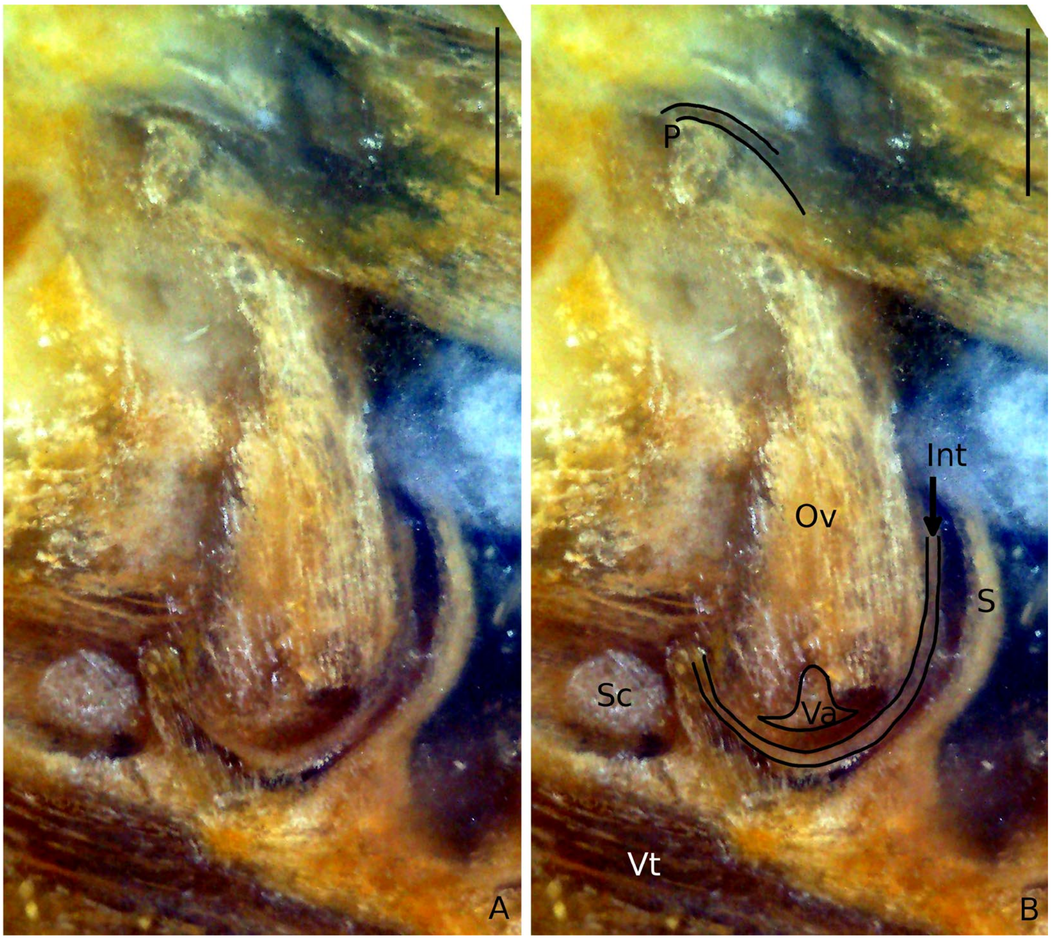

Fig. 4. **A**, **B**: *Palissya tillackiorum* sp. nov. (QMF58817: holotype designated herein); Brig-O-Doon, near Wandoan, Queensland (Valanginian Orallo Formation, Surat Basin). **A**: attached ovule with subtending scale. **B**: camera lucida overlay of ovule shown in A. Key: **Vt** – vascular tissue; **S** – scale; **Ov** – ovule; **Va** – vascular attachment (tracheidal pad); **P** – probable position of micropyle; **Int** – integument; **Sc** – attachment scar with dehisced seed. Scale: A, B = 0.5 mm

parallel longitudinally paired abaxial ridges occur along the midline of the bracts (Fig. 7C, D) but the interpretation of the smaller adaxial ridges is less clear (Fig. 7D, labelled R). The ovule/scale complex is fused or adpressed to the bract's adaxial surface and is lighter-coloured, having longitudinally arranged parenchymatous tissue; it is interpreted as being formed by scale tissue of each ovule/scale unit.

Two ovules have been identified *in situ* in separate cones (Figs 3–5). The ovule/scale complex has three to four pairs of ovules and associated scales arranged in parallel rows either side of the midline of the ovule/scale complex. The ovules are subtended by scales and were attached by a slightly raised circular platform (Fig. 3E), and the position of the vascular trace (Fig. 7B, labelled V) and a series of small ?abscission scars (Fig. 5B, labelled Vc) suggests that it supplied an ovule within the cup-shaped structure formed by the subtending scales. A small conical structure within the basal portion of the ovule (Fig. 4B, marked Va) is likely related to ovule attachment (tracheidal pad).

The ovules have a single integument and their internal structure consists of poorly preserved thin-walled parenchymatous cells (Fig. 4). The ovule in the holotype (QMF58817: Fig. 4) is missing most of its distal end, thus the micropyle is not preserved. An immature ovule is preserved in specimen QMF58820 (Fig. 5C, D), which has an ovule beak (0.1 mm long) and, although internal details are limited, lineations suggest the micropyle is ~0.2 mm long (including beak) and ~70 µm wide. These small seeds were shed from the cone and probably were anemochorus, based on a comparison with extant gymnosperms (Leslie et al. 2017). The number of cones in the silica block suggests that the cones were shed as a unit from the parent tree after the seeds were released.

The scales subtending the ovules are transversally and precisely arranged: a thicker major scale (Figs 3D, 6C, 7, 8: colour-coded green) partially surrounds the distal and outer side of the

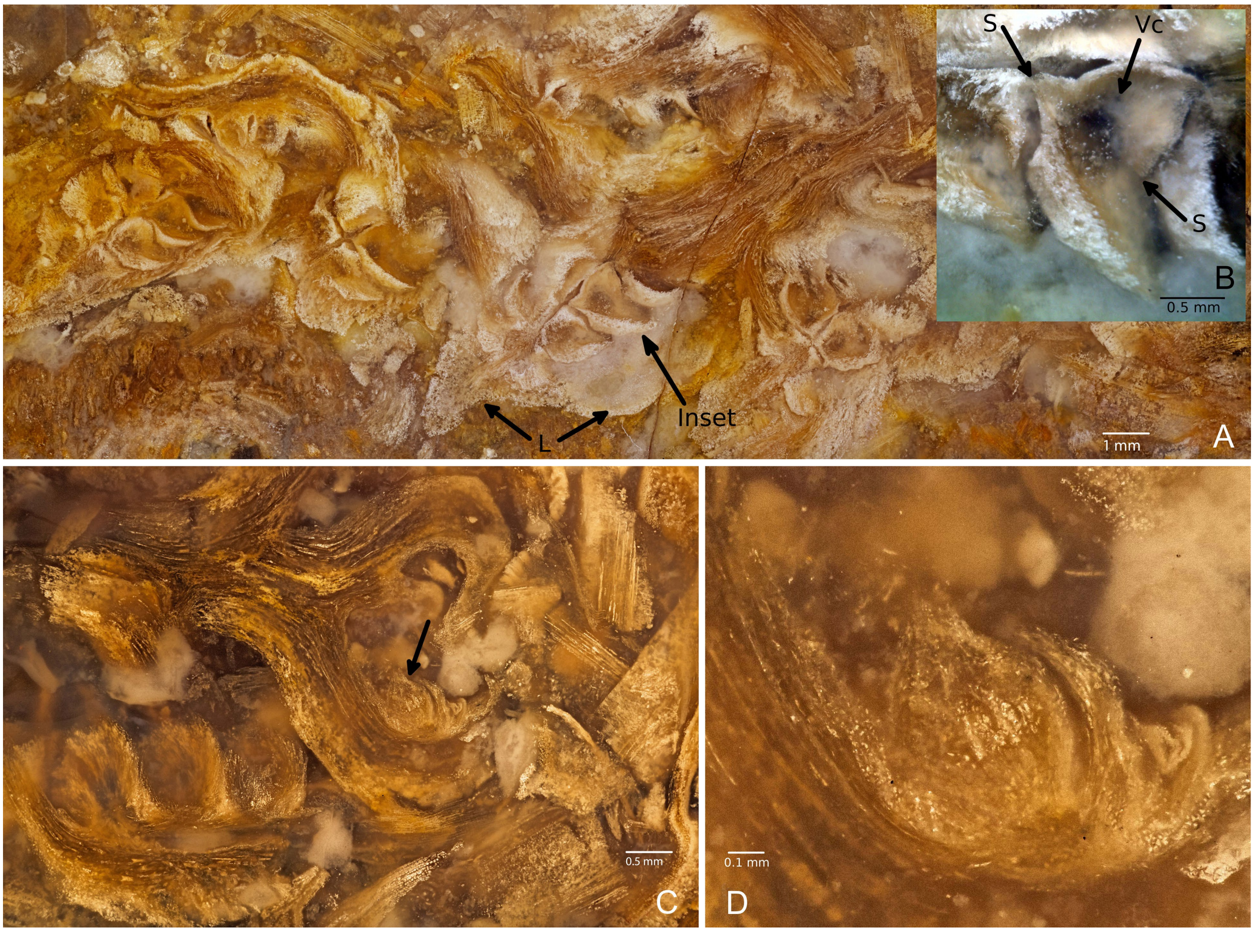

Fig. 5. **A–D**: Section through silcrete rock showing plant material and *Palissya tillackiorum* sp. nov. cones from Brig-O-Doon, near Wandoan, Queensland (Valanginian Orallo Formation, Surat Basin). **A**, **B**: QMF58816 (paratype designated herein), adaxial side of bract/scale complex showing cup-shaped structures, with each "cup" having a pair of scales and ovule attachment scar; arrow indicates position of inset (**B**); "L" indicates outline of bract margin. **B** (inset): detail of scales and circular ovule attachment scar; arrows marked "S" indicate separation between major and minor scales; arrow marked "Vc" indicates ring of small abscission marks. **C**, **D**: QMF58820 (paratype designated herein), cone tip with developing ovule and scales; arrow indicates position of ovule that is enlarged in D and white filamentous material (fungal hyphae). Scale as shown

ovule, whereas a narrow and attenuate minor scale (Figs 3D, 6C, 7, 8: colour-coded yellow) is positioned on the proximal and inner side. Detailed examination of many sections of ovule/scale complexes and scales shows that each major and minor scale pair is discrete but may abut basally (Figs 3D, 5B, 6C, 7B) or possibly even merge (Figs 3E, Sc3); they are interpreted as being formed from separate primordia. The scales comprise parenchyma tissue having no obvious vascular traces. They probably were relatively soft, thin structures; despite this, some are preserved in remarkable detail (Figs 3–7).

Four partially closed cones were identified (QMF58808, QMF58809, QMF58814, QMF58822), but only one of these shows an adaxial pattern on one bract, albeit degraded (QMF58814), resembling those of specimens assigned to *Palissya tillackiorum*. Another strongly degraded cone (QMF58803) has an axis and remnants of appendages but it is insufficiently preserved for identification or further description. Cone QMF59019 is possibly microsporangiate but it is also strongly degraded and lacks any clearly preserved adaxial structure; the patterns on some laminae suggest indifferently preserved remnants of scales (Fig. 6A, arrows). The remainder of the plant material in the slabs comprises unidentifiable, strongly degraded vegetative matter including stems of various sizes (~3–70 mm in cross section). Other plants recorded from elsewhere in the Orallo Formation are discussed above.

Palissya elegans
Parris, Drinnan & Cantrill 1995 emend. nov.

Fig. 9

Synonymy.

1995 *Palissya elegans* Parris, Drinnan & Cantrill, pp. 90–95, figs 3–6.

2002 *Palissya elegans* Parris, Drinnan & Cantrill 1995; McLoughlin et al., pp. 76–77, fig. 49A, B.

Fig. 6. **A–D**: *Palissya tillackiorum* sp. nov.; Brig-O-Doon, near Wandoan, Queensland (Valanginian Orallo Formation, Surat Basin). **A**: QMF59019, possible male cone; however, the patterns on two lateral appendages (arrows) suggest that the cone may be a degraded female cone. **B**, **C**: QMF58807, bract/scale complex with camera lucida overlay in C indicating major (green) and minor scales (yellow); note the much wider margin of the bract relative to that of the ovule scale complex. **D**: QMF58804, bract and scales in cross section, missing ovules; probable fungal hyphae in and around the structure (white filamentous material); inset indicating orientation of cross-sectional cut through ovule/scale structures. Scale: A = 10 mm, B, C = 1 mm, D = 0.5 mm

Emended diagnosis. Cone >115 mm long, 10–13 mm wide. Cone axis up to 1.5 mm wide, bearing acutely to sub-perpendicularly attached, overlapping lateral appendages (bract/scale complexes). Each bract/scale complex petiolate, obovate to almost circular, ~5 mm wide, ~5 mm long (~7 mm long including stalk), tapering to acutely pointed apex (acuminate). Apical portion of bracts curving outward (abaxially). Ovule/scale complex bears 2 or 3 pairs of ovule/scale units positioned along either side of the midline of the ovule/scale complex. Each ovule 2.5 mm long, 1.1 mm wide, with longitudinal striations surrounded by a cup-like structure formed from a pair of scales with radiating striations on their inner surface, and a circular slightly raised scar (~0.4 mm diameter) occurs at the base of the cup-shaped structure.

Type specimen. Holotype (MVP182805: Fig. 9 herein) by original designation (Parris et al. 1995: 90, figs 3A–D, 6A) from the Lower

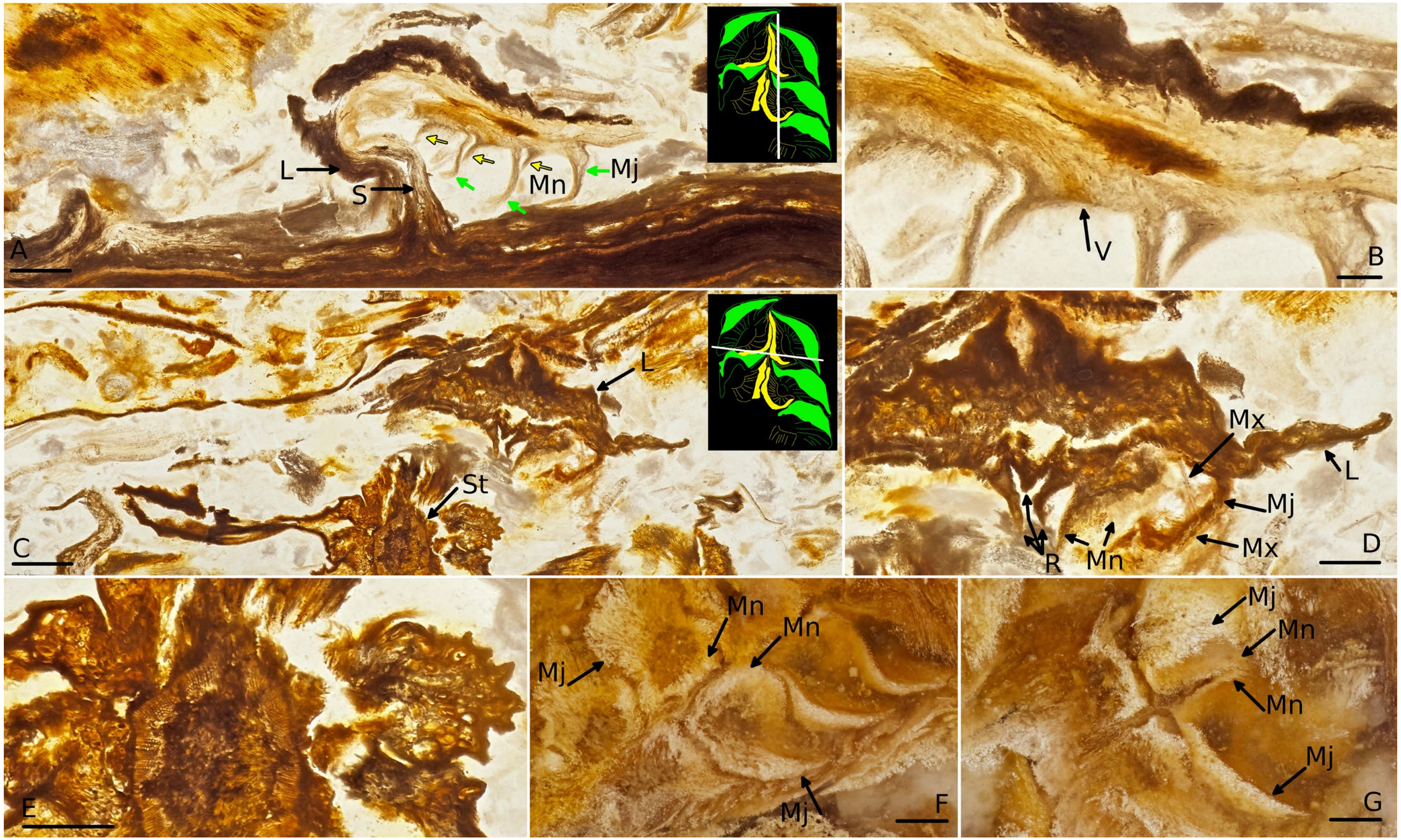

Fig. 7. **A–E**: *Palissya tillackiorum* sp. nov., thin sections; Brig-O-Doon, near Wandoan, Queensland (Valanginian Orallo Formation, Surat Basin). **A**: QMF58813B (paratype designated herein), longitudinal section of cone through axis and attached bract scale complex, showing the different components of the bract and ovule/scale complex with separate vascular traces, major (green arrows) and minor scales (yellow arrows), and the ridges and rugose texture on the abaxial surface of the bract; inset indicating inferred orientation and position of cross-sectional cut. **B**: QMF58813B (paratype designated herein), detail of bract scale complex in A, showing vascular trace which is interpreted to be the ovule attachment site. **C**: QMF58813C (paratype designated herein), transverse section through same cone as in A, showing cross section through axis and bract of cone scale or foliar organ; inset indicating inferred orientation of cross-sectional cut through bract and ovule/scale complex. **D**: QMF58813C detail of cross section through bract in C. **E**: QMF58813C, enlargement of cross section through axis in C, showing detail of tracheids and central pith of parenchymatous cells; the lateral appendages have conspicuous sclereids with concentric lamellae. **F**, **G**: *Palissya tillackiorum* sp. nov., QMF58816 (paratype designated herein), enlargement of ovule/scale complex (complete specimen: Fig 5 herein) in planar view – cf. similar features shown in C and D. Annotation: **L** – bract; **Mj** – major scale (green); **Mn** – minor scale (yellow); **Mx** – segmented hypha (~18 µm diameter) attached to mycelial node embedded in major scale; **R** – ridges on adaxial surface of bract; **S** – vascular trace of ovule/scale complex; **St** – fructification axis; **V** – vascular connection to ovule attachment point. Scale: A, C = 1 mm; B = 0.25 mm, D–G = 0.5 mm

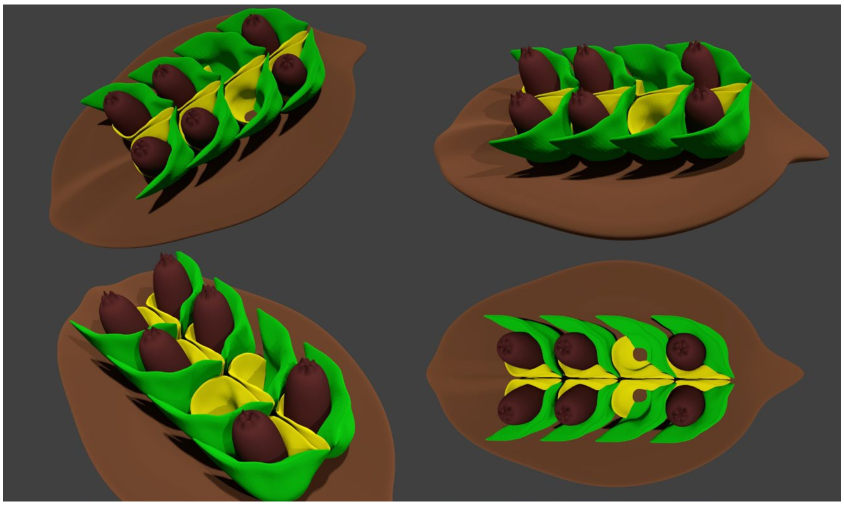

Fig. 8. *Palissya tillackiorum* sp. nov., reconstruction. Connection to axis on left-hand side of bracts. Based on Figs 3–7 with the apical portion of seeds modelled on Fig. 5D. Legend: green (major scale), yellow (minor scale), brown (bract). Scale: ovule ~2 mm long

Table 3. *Palissya* and *Knezourocarpon*: records of detailed cone morphology. Excludes Schweitzer & Kirchner's (1996) *P. oleschinskii* (see text)

Epoch	Stage/Age	Species	Location	References
Early Cretaceous	Aptian	*P. antarctica* Cantrill 2000	Antarctic Peninsula	Cantrill (2000)
	Aptian	*Palissya* sp. "Koonwarra"	Victoria, Australia	Drinnan & Chambers (1986), Parris et al. (1995), Pattemore et al. (2014) McLoughlin & Pott (2019)
	Valanginian	*P. tillackiorum* sp. nov.	Queensland, Australia	Herein
	Valanginian	*P. elegans* Parris et al. 1995 emend. nov.	Victoria, Australia	Parris et al. (1995), McLoughlin et al. (2002), herein
?Late Jurassic	?Tithonian	*P. bartrumii* Edwards 1934 emend. nov. (Huriwai Stream specimen)	North Island, New Zealand	Bartrum (1921), Edwards (1934), Parris et al. (1995), Pattemore et al. (2014)
Middle Jurassic	Callovian	*P. bartrumi*i Edwards 1934 emend. nov.	South Island, New Zealand	Edwards (1934), Parris et al. (1995), herein
	Bathonian	*K. ovalis* Parris et al. 1995 comb. et emend. nov.	Queensland, Australia	McLoughlin & Drinnan (1995), Parris et al. (1995)
Middle Jurassic	Bathonian	*Knezourocarpon* sp. cf. *K. narangbaensis* by Pattemore et al.(2014) – see synonymy for previously used nomenclature	New South Wales, Australia	White (1986), Parris et al. (1995) Pattemore et al. (2014), Pattemore (2016b: 235)
Middle Jurassic	Aalenian	*P. harrisii* C.R. Hill ex Pattemore & Rozefelds sp. nov.	Yorkshire, England	Hill & van Konijnenburg-van Cittert (1973), Hill (1974), herein
Early Jurassic	Toarcian	*K. narangbaensis* Pattemore 2000 emend. nov. [type species]	Queensland, Australia	Pattemore (2000, 2016b), Pattemore et al. (2014), herein
Late Triassic–Early Jurassic	Rhaetian–Hettangian [sensu stricto, lower Liassic]	*P. sphenolepis* (Braun 1843) Nathorst 1908 emend. Florin 1958 [type species]	Franconia, Germany & Stabbarp, Sweden	Braun (1843), Schenk (1867, 1884, 1890), Saporta (1884), Nathorst (1886, 1908), Hirmer (1936), Florin (1944, 1958), Parris et al. (1995)
Late Triassic	Rhaetian	*P. hunanensis* Wang 2012	Hunan Province, China	Wang (2012)

Cretaceous (Valanginian), Locmany Member of the Rintoul Creek Formation, Gippsland Basin at the Boola Boola State Forest, Victoria, Australia.

Material examined. The holotype, MVP198371 and MVP198375, all from the type locality. Figured by Parris et al. (1995: figs 3, 4D, 4E, 5D).

Occurrence. Recorded only from the type locality (but excludes the nearby younger and indifferently preserved "Koonwarra" specimens: Tab. 3).

Table 4. Comparison of the characters of *Palissya* and *Knezourocarpon* fructifications. Full botanical names including author attribution are listed in Table 3

Region	Eurasia	Eurasia	Eurasia	Eastern Gondwana	Eastern Gondwana	Eastern Gondwana	Eastern Gondwana	Eastern Gondwana	Eastern Gondwana
Series	uppermost Triassic–lowermost Jurassic	uppermost Triassic	Middle Jurassic	Middle–?Upper Jurassic	Lower Cretaceous	Lower Cretaceous	Lower Cretaceous	Lower Jurassic	Middle Jurassic
Species	*P. sphenolepis* [type species]	*P. hunanensis*	*P. harrisii* C.R. Hill ex Pattemore & Rozefelds sp. nov.	*P. bartrumii* emend. nov.	*P. elegans* emend. nov.	*P. tillackiorum* sp. nov.	*P. antarctica*	*K. narangbaensis* emend. nov.	*K. ovalis* comb. et emend. nov.
Preservation C = compression I = impression P = permineralised	C/I	C (coalified)	C	C	C/I	P	C	I	I
Type & other material examined herein	N	N	Y	Y	Y	Y	N	Y	Y
Cone length	< 100 mm	< 80 mm	> 45 mm	> 120 mm	> 115 mm	> 60 mm	< 25 mm	~75 mm	> 120 mm
Cone diameter	15–30 mm	< 17 mm	10–15 mm	10–18 mm	10–13 mm	10–15 mm	10 mm	~15 mm	~15 mm
Cone axis width (max.)	3 mm	2 mm	2 mm	2.5 mm	1.5 mm	2.5 mm	2 mm	1.5 mm	2.5 mm
Bract length	10–15 mm, sessile	~8.5 mm, sessile	6–10 mm sessile (?short stalk)	7–10 mm inc. 2 mm stalk	~7 mm inc. short stalk	~8 mm ?sessile /?short stalk	< 6 mm inc. ~1 mm stalk	< 8 mm inc. ~1 mm stalk	< 12 mm inc. 3–4 mm stalk
Bract width	2–4 mm	~2 mm	4–5 mm	3–4 mm	~5 mm	~6 mm	2–3.1 mm	2–3 mm	3–5 mm
Bract shape	linear/lanceolate	linear/lanceolate	obovate	elliptic	obovate–subcircular	obovate	elliptic	elliptic	elliptic
Pairs of cup-shaped [3D] or (sub)circular [2D] structures, each formed from 2 scales which encompass an ovule	5 or 6	3–5	2–(4, 5)	3 or 4	(2) or 3	3 or 4	up to 3	–	–
Ovule size	2.5 × 2 mm	~1mm (?subspherical)	scar only	scar only	2.5 × 1.1 mm	2 mm × 0.9 mm	scar only	–	–
Pairs of adaxial processes (lacking cup-like structures)	–	–	–	–	–	–	–	4	4–(5, 6)–?7

Remarks. The holotype (MVP182805) designated by Parris et al. (1995) appears to be nearly complete and is well preserved as a mineral-stained impression (with some 3-dimensional structure preserved). Those authors did not identify ovules or ovule attachment points in the holotype but they tentatively did in other less well preserved specimens (Parris et al. 1995: fig. 5A, B, D). Examination of the holotype herein has identified another possible ovule preserved *in situ* (Fig. 9B, Ov1) which is consistent in size and shape with those reported by Parris et al. (1995), and a possible minor scale is shown in Figure 9B (yellow arrows); other adjacent features are more difficult to interpret and may be a truncated amalgam of compressed scales and possibly other ovules. Parris et al. (1995: fig. 5) figured other cup-shaped structures which we interpret as pairs of scales subtending ovules; these have striations radiating from the circular ovule attachment scar. The holotype also shows the adaxial side of bract and ovule/scale complexes, and although lacking ovules (e.g. Fig. 9C), the very faint marking indicates that remnants of the ovule/scale unit are consistent with those seen in *Palissya tillackorium* sp. nov. (Tab. 4). The original diagnosis is brief (Parris et al. 1995); new information identified herein, particularly that relating to the ovule/scale complex, prompted emendation of the diagnosis.

Axes and attachment of lateral appendages in representatives of the species are either obscured or not well enough preserved to confidently determine if the attachment includes separate vascular bundles for a bract and an ovule/scale complex. A recent addition to the species by Poropat et al. (2018: fig. 7B) from the Victorian Cretaceous does not show identifiable ovule/scale complexes.

Palissya bartrumii

Edwards 1934 emend. nov.

Fig. 10

Synonymy.

1917 *Stachyotaxus* (?) sp.; Arber, p. 61, pl. 13, fig. 7.

1921 ?*Stachyotaxus* cf. *S. elegans* Nath.; Bartrum, p. 258.

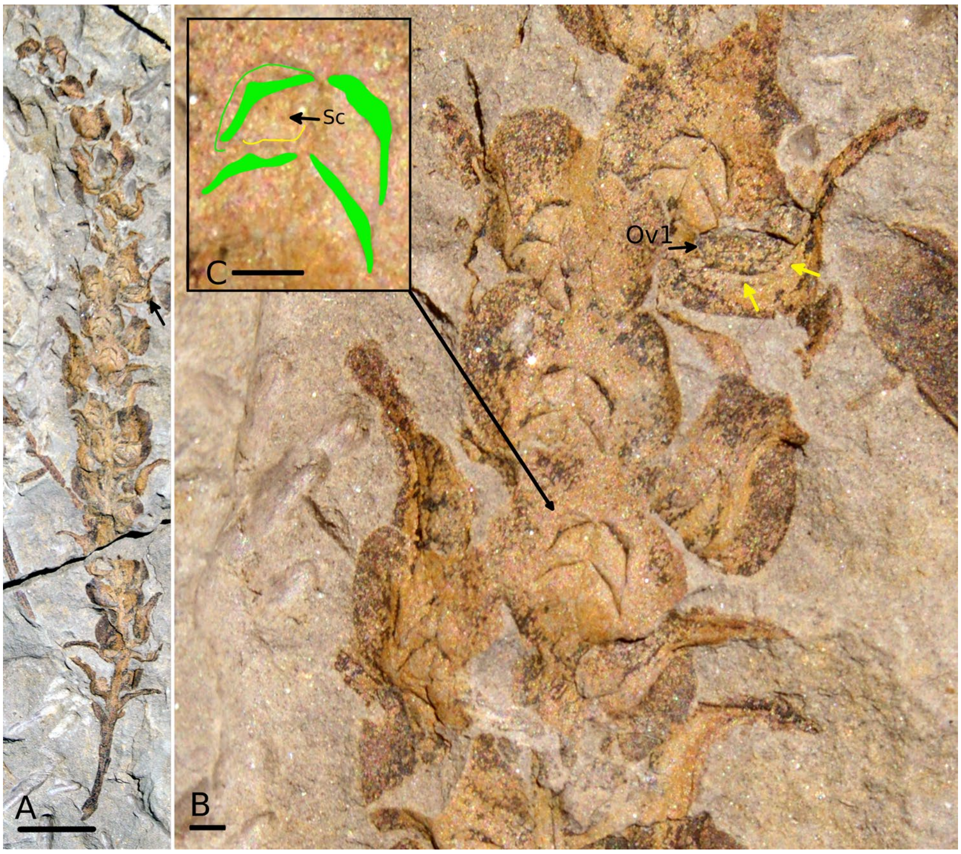

Fig. 9. **A–C**: *Palissya elegans* Parris et al. 1995 emend. nov. (MVP182805: holotype); Boola Boola State Forest, Victoria (Valanginian Locmany Member of the Rintoul Creek Formation, Gippsland Basin). **A**: cone with arrow indicating the position of an ovule (Ov1). **B**: detail showing ovule and possible scale (yellow arrows). **C**: detail with camera lucida overlay indicating major (green) and minor (yellow) scales and a possible faint ovule attachment scar (Sc); other cup-shaped structures were figured by Parris et al. (1995, fig. 5A, B). Annotation: **Ov1** – ovule; **Mj** (green) – major scale (outer); **Mn** (yellow) – minor scale (inner). Scale: A = 10 mm; B, C = 1 mm

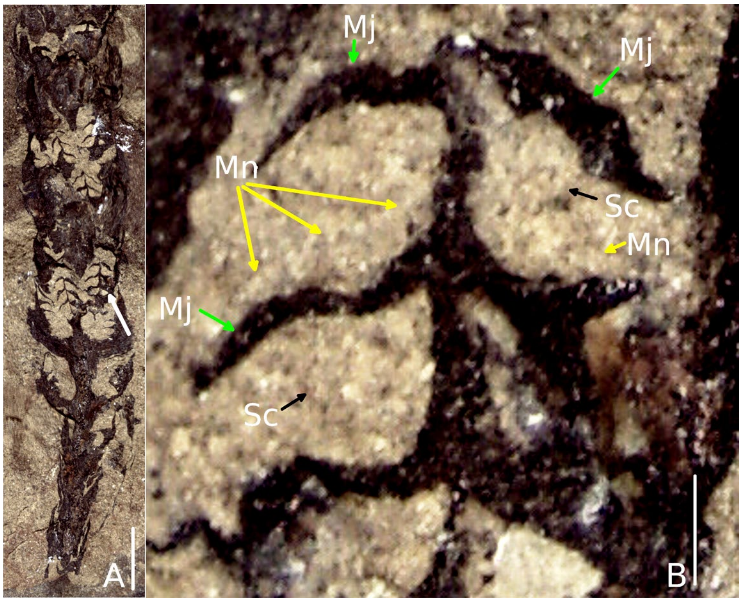

Fig. 10. **A**, **B**: *Palissya bartrumii* Edwards 1934 emend. nov. (BMV15787, holotype); Curio Bay, South Island, New Zealand (Callovian, Middle Jurassic). **A**: enlarged proximal portion of cone; specimen partially figured by Edwards (1934: pl. 5, fig. 5) and entire specimen figured by Parris et al. (1995: fig. 11A); arrow indicates area of enlargement shown in B. **B**: detail of adaxial scales, with faint impression of parts of minor scales and ovule attachment scars. Annotation: **Mj** – major scale; **Mn** – minor scale; **Sc** – ovule attachment scar. Photographs provided by P. Hayes, Natural History Museum, London. Scale: A = 5 mm; B = 0.5 mm

1934 *Palissya bartrumi* Edwards, p. 100, pl. 5, figs 5, 6. [basionym]

1995 *Palissya bartrumi* Edwards 1934; Parris et al., pp. 99–101, figs 11, 12.

Emended diagnosis. Cone >120 mm long, 10–18 mm wide. Cone axis <2.5 mm wide, bearing sub-perpendicular bract/scale complexes. Bract/scale complex elliptic, petiolate, with rugose abaxial surface, ~3–4 mm wide, ~7–10 mm long including stalk 2 mm long, tapering to acutely pointed apex (acuminate). Ovule/scale complex bears 3–4 pairs of ovule/scale units positioned oppositely along either side of the longitudinal midline of the ovule/scale complex. Each ovule/scale unit is formed from major and minor scales which encompass a circular ovule attachment scar (~0.25 mm diameter).

Type specimen. Holotype (BMV15787: Fig. 10 herein) by original designation (Edwards 1934: 100, pl. 5 fig. 5), from the Middle Jurassic (Callovian: Pole 2004), Murihiku Terrane at Curio Bay (Waikawa), South Island, New Zealand (Arber 1917).

Material examined. The holotype and BMV15786 also from the type locality: previously figured by Parris et al. (1995: fig. 11).

BMV15751A/B and BMV15752A/B from Mokoia, near Gore, South Island, New Zealand, within Middle Jurassic (Callovian), Murihiku Terrane (Pattemore et al. 2014). Specimen BMV15751 was figured by Parris et al. (1995: fig. 12).

BMV23293 from the mouth of Huriwai Stream, south of Waikato Head, North Island, New Zealand (Bartrum 1921); ?Upper Jurassic, ?Murihiku Terrane (see Pattemore et al. 2014: 55). Figured by Edwards (1934: pl. 5, fig. 6).

Occurrence. Middle Jurassic (Callovian)–?Upper Jurassic, Murihiku Terrane, New Zealand.

Remarks. Re-examination of the holotype and other material suggests that the ovule/scale units (Fig. 10) are formed from two scales that surround an ovule as seen in *Palissya tillackiorum* and that the specimens have the dendroid pattern seen in *P. elegans* (resulting from the relative size and arrangement of ovule scales; discussed below); hence the emended diagnosis. Very faint ovule attachment scars and the outline of minor scales are visible in the type specimen (Fig. 10B). The ovule/scale units in the holotype are slightly smaller than those belonging to *P. elegans* emend. nov. and *P. tillackiorum* sp. nov.

The larger specimens from Mokoia (BMV15751, BMV15752) are degraded and have unclear adaxial organs. However, their size suggests that the holotype may be a smaller example of the species. Likewise, Bartrum's (1921) specimen from near Waikato Head (BMV23293) is indifferently preserved.

Palissya harrisii C.R. Hill ex Pattemore & Rozefelds sp. nov.

Figs 11, 12

Synonymy.

1973 *Palissya* sp. nov.; Hill & van Konijnenburg-van Cittert, p. 62. [unfigured and unnamed]

1974 *Palissya harrisii* Hill, pp. 165–173, pls 24–26. [unpublished thesis]

Diagnosis. Cone borne singly at the end of a leafy shoot, >45 mm long, 10–15 mm wide, axis 1–2 mm wide. Bract/scale complex obovate, entire, up to 10 mm long, ~4–5 mm wide, mounted at 30°–70° angle to the axis and having a narrow apical projection (acuminate), tapering basally to decurrent attachment on the axis, sessile or shortly petiolate. Ovule/scale complex adpressed to and occupying the proximal portion (~3/4 of length) of the underlying bract and bearing 2–5 (commonly 4–5) pairs of ovule/scale units positioned along either side of the longitudinal midline of the underlying bract. Each ovule/scale unit in planar view has an irregular circular outline formed from two scales: a major (lateral) scale 1.1 mm high, and minor (inner) scale 0.9 mm high, which together surround the circular ovule scar (~0.2 mm diameter). Scales radially striated, extending laterally from central circular scar 0.3–0.9 mm (in compressed condition).

Type specimen. Holotype (BMV61495a/b: Figs 11, 12) from Hasty Bank, Yorkshire, England (Hill 1974), and from the Middle Jurassic (Aalenian), Saltwick Formation, Cleveland Basin (Slater & Wellman 2015). This specimen was selected as the type by Hill (1974, pls 24, 25; identified as specimen B1) and is designated as the holotype herein.

Material examined. The holotype, BMV61478a/b, BMV61484a/b, BMV61488a/b, BMV61489a/b, BMV61491a/b, BMV61492a/b (Hill's 1974: pl. 26 specimen B16), BMV61494a/b. All specimens are from the type locality.

Occurrence. Recorded only from the type locality.

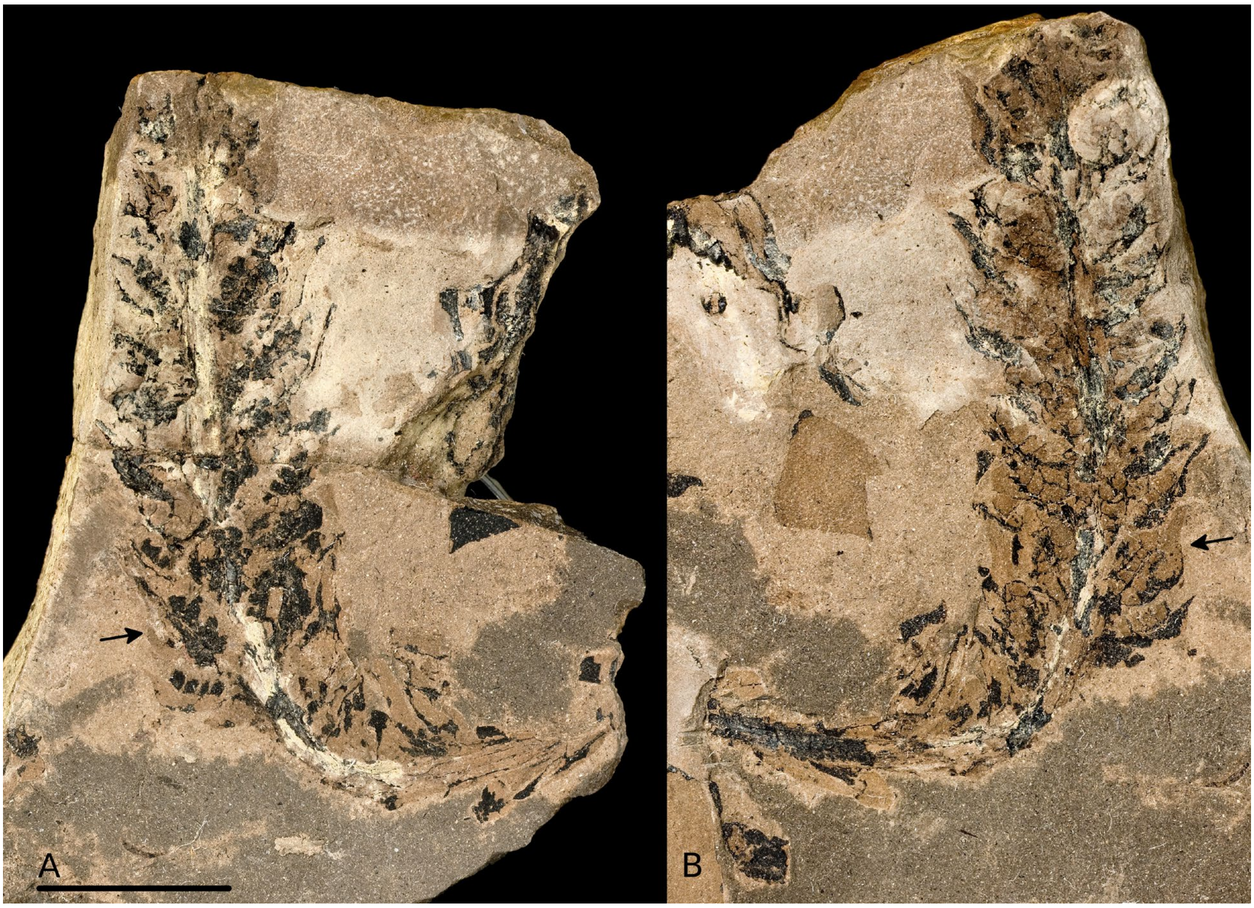

Fig. 11. **A**, **B**: *Palissya harrisii* C.R. Hill ex Pattemore & Rozefelds sp. nov. from the Middle Jurassic of Yorkshire, England; holotype (BMV61495A,B), originally identified as specimen B1 by Hill (1974: 165–173, pls 24, 25). **A**, **B**: arrows on part and counterpart show the shape of a bract (obovate) with its associated adaxial ovule/scale complex. **B**: arrow indicates the area enlarged in Fig. 12. Specimen examined by ACR and photographs provided by P. Hayes, Natural History Museum, London. Scale: 10 mm, applies to A and B

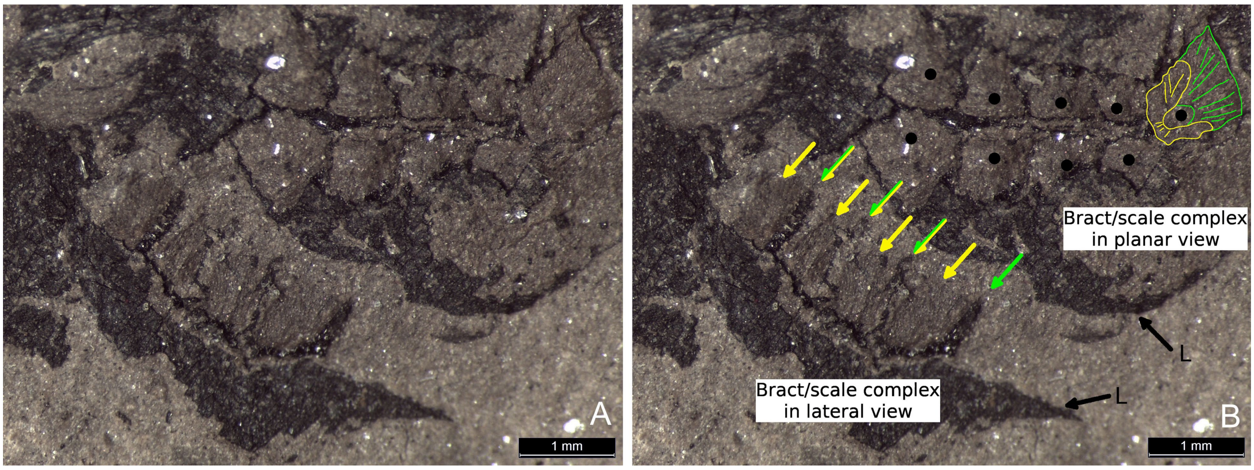

Fig. 12. A, **B**: *Palissya harrisii* C.R. Hill ex Pattemore & Rozefelds sp. nov. from the Middle Jurassic of Yorkshire, England. **A**, **B**: detail of portion of BMV61495B (holotype: Fig. 11 herein), showing adaxial surface of bract/scale complexes in planar and lateral views. **B**: specimen shown in A with interpretive overlay. Arrows/lines: major scale (green); minor scale (yellow); major and/or minor scales (green & yellow). Circles: ovule attachment scars (black). Annotation: **L** – bract. Specimen examined by ACR and photograph provided by Dr P. Hayes, Natural History Museum, London. Scale: as marked

Remarks. Hill & van Konijnenburg-van Cittert (1973) recorded this material as *Palissya* sp., and later it was recorded (Hill 1974) under the unpublished name "*Palissya harrisii*", which is formally erected herein. *Palissya harrisii* sp. nov. differs from the Northern Hemisphere species *P. sphenolepis* and *P. hunanensis* in having smaller cones with obovate rather than lanceolate bracts (Tab. 4). The obovate shape of the bract also distinguishes this species from *P. antarctica* and *P. bartrumii*, which have elliptical bracts, and from *P. elegans* in typically having 4–5 pairs of ovule/scale units (Tab. 4).

There is clear differentiation in the components that make up the bract/scale complex, which supports Hill's (1974) interpretation of the cone as compound, consisting of a bract and ovule/scale complex; this supports affinity with conifers (Fig. 12A, B). Hill (1974) reported abundant small resinous cell-casts in leaves and noted that the cell structure resembles that of conifers.

Hill's (1974) material comprises unattached leaves and cones, and as noted by that author, one specimen has possible leaves (or sterile bracts) attached at the base of a cone (BMV61495a/b: Hill 1974, pls 24, 25; and Fig. 11 herein). The cuticle that he extracted from the cones lacks stomata but he noted that other epidermal characters suggest that the leaves and cones are from the same plant. *Palissya harrisii* sp. nov. is diagnosed herein from fructifications only.

As interpreted by Hill (1974), the adaxial processes likely formed a cup shape that surrounded an ovule (Hill used the term "aril"). These "cups" are interpreted herein to be formed from a pair of scales (Fig. 12B), differing from species of the Southern Hemisphere in the circular pattern they preserve, in contrast to the branched "dendroid" pattern commonly seen in Gondwanan material; this difference may be due to differences in the relative thickness of the major and minor scales in Gondwanan and European specimens (discussed below).

The lower bract/scale complex in Figure 12B shows a lateral view of the adaxial elements marked by arrows; being a compression, not a section, it is likely that some overlap of major and minor scales has occurred. The upper bract/scale complex in Figure 12B shows a planar view with a major (outer) scale being the most distal on the bract/scale complex (outlined in green), which is consistent with other species of *Palissya*. Therefore in lateral view the dark carbonaceous band marked with a solid green arrow is interpreted as the remnant of a distal major scale. This darker band is slightly higher than the adjacent area marked with a yellow arrow, supporting the notion that it is the remnant of a major scale. Following from this, the lateral view also shows a repetition of such bands (green/yellow arrows) which likely resulted from a combination of adpressed adjacent major and minor scales preserved side-on. Spanning the gaps between these bands (yellow arrows) are remnants that are interpreted chiefly as minor scales, being generally shorter in height.

The bract/scale complex presented in planar view (Fig. 12B) shows that there are five pairs of ovule/scale units either side of the midline of the ovule/scale complex, having small, circular, more or less central scars located in each of the ovule/scale units. Another (fainter) concentric mark around these scars probably reflects the basal attachment of the major and minor scales, suggesting that these paired scales subtend the ovule. The upper right ovule/scale unit in planar view (outlined in green and yellow: that is, the most distal cup-like structure) is apparently almost completely preserved, showing the striated inner surface of the cup (cf. Parris et al. 1995: fig. 5A, B). Permineralised specimens assigned to *Palissya tillackiorum* sp. nov., being viewed only in uncompressed section, do not show this compressed and splayed planar view of scales.

Bracts commonly appear to have a lanceolate shape, as was recorded by Hill (1974). This is because the area covered by the adaxial ovule/scale complex, which is lanceolate in broad outline, is the thickest element in planar carbonaceous preservation and therefore forms the darkest outline in preservation. However, the much fainter outline of the bract is obovate, not lanceolate (Fig. 11, arrows). *Palissya* sp. 'Sofiero' from Sofiero, Sweden, apparently also has oval-shaped bracts (Parris et al. 1995).

Hill (1974) did not identify pollen adhering to or otherwise associated with the material that he assigned to *Palissya*. Subsequently, monosulcate pollen was reported from his specimens, located on cuticle in macerated samples, and these were regarded as *in situ* (van Konijnenburg-van Cittert 2008 and pers. comm.), based on the assumption that the cone is microsporangiate, a view that was influenced by Schweitzer & Kirchner's (1996) erroneous reinterpretation of the genus (discussed below). Thus, there is no compelling reason to attribute this pollen type to these ovulate cones. *Palissya harrisii* sp. nov. was collected from the lower claystone section of the Hasty Bank plant bed, which is dominated by conifer pollen (~70% of recorded microflora) but with monosulcate pollen comprising up to ~10% of the total palynomorph count (Slater & Wellman 2015).

Stachyotaxus is recorded to have monosulcate pollen and is widely thought to belong to the Palissyales (Balme 1995). Grains were identified as structurally atypical by Frederiksen (1980: 3) but without explanation, and were excluded from his study of monosulcate pollen for that reason. Pollen located on Hill's (1974) specimens differs from that of *Stachyotaxus* in lacking striations, and some grains have folds near the sulcus (Tekleva & Roghi 2018: 15). Monoaperturate pollen (monosulcate or monocolpate: see definitions by Traverse 2007: 146) are rare in conifers but not unknown, being reported from the Mesozoic of China and the USA in representatives of Podocarpaceae and Pinaceae (Balme 1995, Gandolfo et al. 2001, Taylor et al. 2009: 838, 866).

Class: ?PINOPSIDA Burnett 1835

Order: ?PALISSYALES Doweld 2001

Family: KNEZOUROCARPONACEAE Pattemore, Rigby & Playford 2014

Genus: ***Knezourocarpon*** Pattemore 2000 emend. nov.

Emended diagnosis. Cone microsporangiate, elongate, with lateral appendages helically arranged on a central axis. Each appendage comprises a lamina bearing adaxial processes attached in opposite–subopposite pairs to the lamina's central vascular bundle. Processes are thin lamina-like structures, commonly curved and longitudinally striated. Processes on each side of the midrib are commonly imbricate, each process being overlapped on its outer surface by its more distal neighbour.

Remarks. The genus was erected monotypically based on the specific diagnosis of the type species, *Knezourocarpon narangbaensis* Pattemore 2000. The discovery of well-preserved permineralised specimens of *Palissya* from the Lower Cretaceous of the Surat Basin and the proposal to place *Palissya ovalis* Parris et al. 1995 in *Knezourocarpon* required a reconsideration of both the morphology of the cones assigned to the genus and the generic limits of these taxa; hence the emended generic status.

Our tentative placement of *Knezourocarpon* within Palissyales in the present study is based on the broad structural resemblance of its two species with those of *Palissya* – in particular, the symmetrical and imbricate arrangement of adaxial processes that are positioned in two parallel rows either side of the midline. The previous interpretation of specimens assigned to the type species of *Knezourocarpon* included ovulate and microsporangiate cones; however, our re-examination of the material has found no evidence of ovules or ovulate structures (discussed below).

Fig. 13. **A–F**. *Knezourocarpon narangbaensis* Pattemore 2000 emend. nov. from Narangba, north of Brisbane, Queensland (Toarcian Landsborough Sandstone, Marburg Subgroup, Nambour Basin). **A**: QMF39226 (holotype), originally figured by Pattemore (2000, fig. 5.1); arrows indicate adaxial processes that were interpreted as ovules by Pattemore (2000) but are reassessed herein as deformed processes that have been adpressed together. **B**: QMF39240 (paratype), arrows indicate helically attached lateral appendages having a single vascular bundle for the overlying lamina and adaxial processes (i.e. a simple cone); the complete specimen was figured by Pattemore et al. (2014, fig. 8B). **C**: QMF39242 (paratype), arrow indicates abaxial surface with a prominent midrib and sub-parallel lineations (?vascular traces). **D**: QMF39263 (paratype), having sub-opposite processes; arrow marks abaxial surface of lamina with an impression of a midrib, and adjacent parallel ?ridges or other surface texture. **E**: QMF39246 (paratype), arrows indicate opposite process with a small portion of the overlying lamina retained. **F**: QMF39236 (paratype), arrows show process attachment and the imbricate arrangement of processes; complete specimen was figured by Pattemore et al. (2014, fig. 8F). Scale: A, B, C, F = 5 mm; D, E = 2 mm

Knezourocarpon differs from *Palissya* in lacking (1) pairs of scales that form (2) a cup-like structure, and (3) ovules or ovule attachment scars (Figs 13–15). The ovule/scale unit attachment in *Palissya* is considerably offset from the central vasculature, whereas the processes of *Knezourocarpon* attach directly to the central vasculature and, given that the processes resemble thin laminae, they are interpreted to be microsporangiate surfaces. Furthermore, it appears likely that the cones had a simple structure, as there is no clear evidence of dual vascular traces (Fig. 13) despite having well-preserved vasculature in some specimens.

No co-preservation of *Palissya* and *Knezourocarpon* has been recorded. The oldest recorded cone attributable to *Palissya* in Eastern Gondwana is from the Callovian of New Zealand (*P. bartrumii* Edwards 1934 emend. nov.), whereas the youngest records of *Knezourocarpon* are from the Bathonian of Queensland and New South Wales (*K. ovalis* comb. et emend. nov. and *Knezourocarpon* sp. cf. *K. narangbaensis*: Tab. 3) – see the palaeogeographic reconstruction by Pattemore et al. (2014: fig. 4). Thus the genera are spatio-temporally separated.

The processes (probable sporangiophores) in *Knezourocarpon* are located on the adaxial surface. Pattemore (2000) suggested that in life *Knezourocarpon* was catkin-like because its elongate cones would doubtfully have been able to support themselves in any other orientation; in this position the processes would be pendulous. Extant microsporangiate conifer cones are either peri- or hypo-sporangiate, the latter having their sporangiophores restricted to the abaxial surface of the cones' lateral appendages (Dörken et al. 2011). However, Mesozoic conifers variously had abaxial and adaxial sporangiophores (Grauvogel-Stamm & Galtier 1998).

Knezourocarpon narangbaensis
Pattemore 2000 emend. nov.

Fig. 13A–F

Synonymy.

2000 *Knezourocarpon narangbaensis* Pattemore, pp. 189–192, figs 3–6. [basionym]
2008 *Caytonia cucullata* McLoughlin in Jansson et al., p. 16, fig. 8A–F.
2014 *Knezourocarpon narangbaensis*; Pattemore et al., pp. 57–59, fig. 8A–F.
2016b *Knezourocarpon narangbaensis*; Pattemore, pp. 230–234, fig. 6.8A–F.

Emended diagnosis. Cone ~75 mm long, ~15 mm wide, axis up to 1.5 mm wide. Lamina-like lateral appendages petiolate, up to 8 mm long (including ~1 mm stalk), 2–3 mm wide, entire, elliptic, commonly having long (1–3 mm) pointed acute apex (acuminate), bearing adaxial processes arranged in 4 opposite–subopposite pairs either side of a central vascular bundle. Processes ~2 mm long, ~0.6 mm wide, <0.1 mm thick, faintly striated longitudinally, apices acute to truncate. Process bases cuneate–obtuse, commonly symmetric, having vascular attachment stalk ~0.15 mm wide, near-sessile to 0.2 mm long, attached directly to the adaxial or lateral surface of the central vascular bundle.

Type specimen. Holotype (QMF39226: Fig. 13A) by original designation (Pattemore 2000: 192, fig. 5.1) from Narangba Quarry, Narangba, north of Brisbane, Queensland, within the Lower Jurassic (Toarcian) Landsborough Sandstone, Marburg Subgroup, Nambour Basin.

Material examined. The holotype, paratypes QMF39229A,B (counterpart, previously registered as QMF39232: Pattemore 2000, fig. 5.2, 5.3), QMF39236 (Fig. 13F), QMF39237; QMF39240 (Fig. 13B), QMF39241, QMF39242 (Fig. 13C), QMF39245, QMF39246 (Fig. 13E), QMF39248, QMF39258, QMF39259, QMF39262, QMF39263 (Fig. 13D), QMF39264, QMF39265–QMF39267, QMF39276A and its counterpart QMF39276B (counterpart previously registered as QMF39277), QMF39318 and other specimens QMF39315, QMF42597–QMF42599, QMF54881, QMF54885–QMF54888. All are from the type locality.

Specimens QMF50949, QMF50950, and QMF50955 from the Inverleigh Quarry, near Warwick, Queensland, from within ?Pliensbachian–Toarcian upper Gatton Sandstone, Marburg Subgroup, Clarence-Moreton Basin. These were assigned to *Caytonia cucullata* by Jansson et al. (2008) but were subsequently attributed to *Knezourocarpon narangbaensis* by Pattemore et al. (2014).

Occurrence. Recorded only from the Lower Jurassic (?Pliensbachian–Toarcian) of the Nambour and Clarence-Moreton basins, southeast Queensland (Pattemore 2000, 2016b, Pattemore et al. 2014).

Remarks. In the original diagnosis of the species, lateral appendages were tentatively identified as bilaterally arranged, and a pteridosperm affiliation was suggested (Pattemore 2000). The cones are elongate and were evidently delicate and flexible, readily deforming to suit the bedding plane during deposition; hence the apparent bilateral arrangement commonly observed in specimens. All specimens previously assigned to the species are re-assessed herein, and the vascular detail preserved in a few specimens (QMF39236, QMF39240, QMF50949) clearly shows that the lateral appendages are helically arranged (e.g. Fig. 13B).

At the erection of the species, both ovulate and microsporangiate fructifications were thought to be present (Pattemore 2000). The “ovulate” cones were a minor component of the entire collection – three specimens, QMF39226 (holotype: Fig. 13A), QMF39229A/B and QMF39233 – and these were less well preserved than others in the collection. They were originally interpreted as having a single large inverted ovule beneath each lamina-like lateral appendage, but our re-examination of the specimens suggests that these structures are not ovules but are probably damaged and overlapping adaxial processes, bent over and adpressed against the underside of the lateral appendages (type specimen, QMF39226: Fig. 13A, arrows). The micropyle that was identified in the type specimen probably is a cleft formed between two adaxial processes. Specimen QMF39233 comprises a collection of indifferently preserved flat processes, but they are not biologically connected to each other or to an axis.

Thus, no characters clearly separate the specimens identified as ovulate and microsporangiate by Pattemore (2000). Several specimens (QMF39236, QMF39242, QMF39246, QMF39248, QMF39263; Fig. 13C–F) show that the processes were thin, commonly curved, lamina-like structures that are interpreted herein as sporangiophores. No cup-like structures, circular ovule attachment scars or ovules have been identified. There is no indication of separate vascular bundles for lamina and processes (Fig. 13B, E, F, marked with arrows) – the processes are attached to the adaxial or lateral side of the lamina’s vascular bundle.

Knezourocarpon ovalis (Parris et al. 1995) comb. et emend. nov.

Fig. 14A–C

Synonymy.

1995 *Palissya ovalis* Parris, Drinnan & Cantrill, pp. 96, 98, fig. 9. [basionym]

1995 *Palissya ovalis* Parris, Drinnan & Cantrill; McLoughlin & Drinnan, pp. 267–269, fig. 6A–I.

Emended diagnosis. Cone >120 mm long, ~15 mm wide, axis up to 2.5 mm wide. Lamina-like lateral appendages petiolate, up to 12 mm long (including 3–4 mm stalk), 3–5 mm wide, entire, elliptic, apex obtuse or rounded, bearing processes arranged commonly in 5 or 6 opposite–subopposite pairs, each being 1.5–2 mm long, ~0.5–1 mm wide, thin, faintly striated longitudinally and having truncate apices with undulating margins. Processes basally asymmetric, each having its attachment considerably offset and connected via a narrow wedge-shaped stalk up to 0.75 mm long and ~0.1 mm wide, imbricately arranged, and strongly angled back toward the cone axis.

Type specimen. Holotype QMF17170 (Fig. 14A), by original designation (Parris et al. 1995, fig. 9C, D) from Reynolds Creek, Queensland, and from the Middle Jurassic (Bathonian) Walloon Coal Measures, Clarence-Moreton Basin.

Material examined. The holotype and QMF17167, QMF17168A/B, QMF28444, QMF28445, UQF31693–UQF31695, all from the type locality.

Specimen QMF 17174 from Kalbar, Queensland (Pattemore 2016a: fig. 2) and from the Middle Jurassic (Bathonian) Walloon Coal Measures, Clarence-Moreton Basin.

Specimens UQF79671, UQF79678, UQF79682, UQF79685, UQF79695 (Fig. 14B, C), UQF79697, UQF79698, UQF79701–UQF79703, UQF79722, UQF79727 from Mutdapilly, Queensland (Pattemore 2016a: fig. 2), and from the Middle Jurassic (Bathonian) Walloon Coal Measures, Clarence-Moreton Basin.

Occurrence. Recorded only from the Middle Jurassic (Bathonian) Walloon Coal Measures, Clarence-Moreton Basin.

Remarks. Attribution of this material to *Palissya* by Parris et al. (1995) and McLoughlin & Drinnan (1995) was no doubt influenced by the symmetrical, paired and imbricate arrangement of processes somewhat resembling major scales in representatives of *Palissya*. However, the processes are tightly arranged on either side of the lamina’s midline in only one direction and there are no minor processes or indication of cup-like structures. Furthermore, no ovules or ovule attachment scars were identified in the specimens by Parris et al. (1995) or McLoughlin & Drinnan (1995) or in the present study. Previously unpublished material from the Reynolds Creek locality (UQF31693–95) likewise shows imbricate, lamina-like processes, but they also lack evidence of ovule attachment or paired elements that form

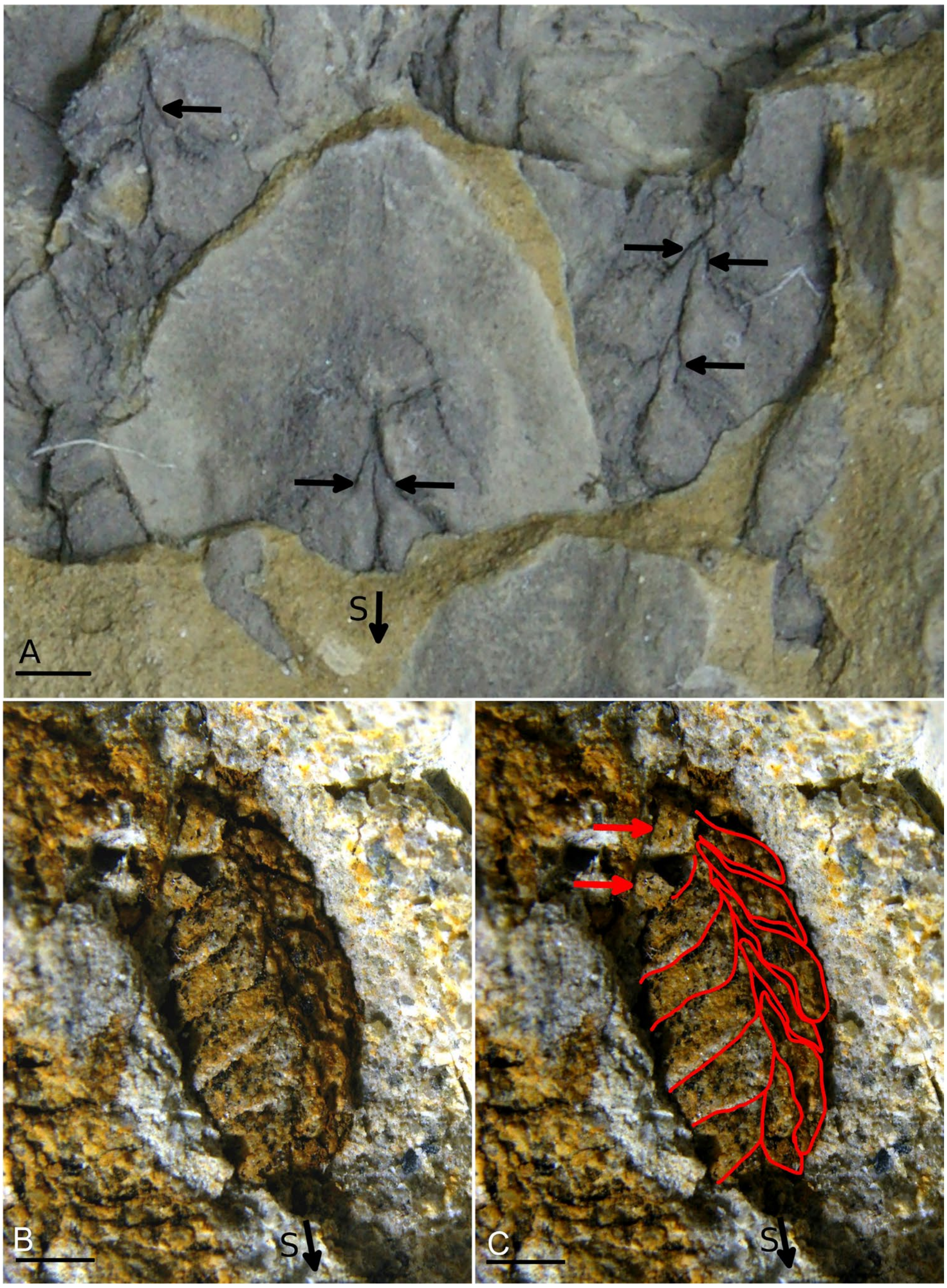

Fig. 14. **A–C**. *Knezourocarpon ovalis* (Parris et al. 1995) comb. et emend. nov.; Middle Jurassic (Bathonian) Walloon Coal Measures, Clarence-Moreton Basin. **A**: Reynolds Creek (3–4 km WSW of Kalbar), Queensland. **B**, **C**: Mutdapilly (22 km north of Kalbar), Queensland. **A**: QMF17170 (holotype), arrows indicate offset process stalk connecting adaxial processes with vascular bundle; complete specimen figured by Parris et al. (1995: fig. 9C, D). **B**: UQF79695, detail of imbricate adaxial processes and offset connection (overlying lamina missing); the complete specimen was figured by McLoughlin & Drinnan (1995: fig. 6B, H). **C**: UQF79695 with camera lucida overlay showing processes and their offset attachment stalks; red arrows indicate broken and dislodged process. Legend: **S** – direction of connection to axis. Scale: A–C = 1 mm

a cup-shaped structure. No specimens indicate that dual vascular bundles extended into each lateral appendage.

Knezourocarpon ovalis (Parris et al. 1995) comb. et emend. nov. is distinguished from the type species in being generally more robust, having a larger number of adaxial process, and in the geometry of process attachment. The processes are connected via a long wedge-shaped stalk that is significantly offset from the midline of the process (Fig. 14A, C). This results in the processes of *K. ovalis* being strongly imbricate and commonly tightly layered. In contrast, the processes in representatives of the type species are more loosely imbricate.

McLoughlin & Drinnan (1995) identified 7–8 pairs of processes in specimens from Mutdapilly; however, this may have resulted from including processes from both sides of the lamina's midline in their count. Most laminae from that site have six pairs of processes (e.g. Fig. 14B, C); possibly a diminutive seventh pair may be present in some specimens.

THE MORPHOLOGY OF *PALISSYA*

Palissya is interpreted as a compound, woody, catkin-like, ovulate cone with helically inserted bract/scale complexes comprising a bract and an ovule/scale complex, each having separate vascular traces (Figs 3C, 3D, 7A). The ovule/scale complex has two rows of conspicuously arranged ovule/scale units. Ovules are inserted on the adaxial surface and apically on individual ovule/scale units; this is tightly integrated with the bract, which forms the abaxial component. Lateral appendages show varying degrees of degradation, with some perhaps separating along zones of differing tissue (Fig. 3A–C). In thin-section, vascular traces extend from the axis through to the point of ovule attachment (Fig. 7A, B). This structural arrangement of vascular bundles resembles that identified by Florin (1944: pl. 184, figs 20–22) in the type species. Vascular detail is less clear in Hill's (1974) specimens, but distinct separation of bract and ovule/scale complex is evident in some bract/scale complexes (e.g. Fig. 12, lower bract/scale complex). Unfortunately there is little detail of vascular structure visible in *Palissya elegans* and *P. bartrumii*. Parris et al. (1995) doubted that *Palissya* represents a compound cone, which is understandable due to the state of preservation of their specimens.

Palissya cones have been almost invariably interpreted as ovulate (Tab. 1), although evidence of seeds is rare (Florin 1958). The permineralised material assigned to *P. tillackiorum* shows that the cones are ovulate, the seeds being thin-walled and apparently not strongly lignified; thus, they likely had a short viability period. Seeds were apparently shed from the mature cone; their small size and the lack of any evidence of specialisation favouring zoochory indicate that they were anemochorus (Leslie et al. 2017, McLoughlin & Pott 2019). The pollination mechanism and the pollen that fertilised *Palissya* ovules are unknown. The previously reported association with monosulcate grains (van Konijnenburg-van Cittert 2008) is shown herein to be doubtful.

The organographic relationship among elements within the ovule/scale complex is difficult to interpret in compressions and impressions; it has been interpreted in various ways and probably is the most contentious element of these cones (Tab. 1). Most researchers have treated the cup-like structure as a single, somewhat asymmetrical element, largely based on studies by Nathorst (1908) and Florin (1944, 1958).

The permineralised cones of *Palissya tillackiorum* sp. nov. show that the "cup" is formed from a pair of lateral scales that subtend the ovule. They occupy a transversal position, and it seems likely they were initiated separately but as paired structures, although the outer scale (which is in a lateral position) is consistently larger (thicker and slightly taller) than the inner scale (which occupies a mesial position), and this gives the "cup" a degree of asymmetry, as was noted by Nathorst (1908), Florin (1958) and Parris et al. (1995). In specimens preserved as impressions or compressions the "cups" appear as circular features with near-concentric attachment scars. In such specimens it usually is impossible to confirm that the "cups" are formed from two separate elements; however, as shown herein, evidence of such structures is preserved in several specimens. Nathorst's (1908: pl. 1, fig. 4) line-drawn figure (specimen S50006, Swedish Museum of Natural History), reproduced by Parris et al. (1995: fig. 14C, marked "p"), shows a break or overlap of scales with a distinct change in the direction of striations at the point where a major and minor scale would meet. Recent photographs of specimen S50006 provided by the Swedish Museum of Natural History (S. McLoughlin pers. comm. 2019) confirm the accuracy of Nathorst's line drawing.

The scales that subtend the ovules are parenchymatous, lack a vascular trace, and have been consistently described as having a striated appearance (Nathorst 1908, Hill 1974, Parris et al. 1995). As a result, the scales have been interpreted as winged seeds, arils, epimatia, or processes (Tab. 1). In the permineralised specimens of *Palissya tillackiorum* the scales are not fleshy, the parenchymatous cells are not enlarged, as seems to be the case for epimatia or arils (Dörken et al. 2018), and they form relatively thin, bract-like structures around the seeds (Fig. 6B–D). The scales are not attached to the seed, as noted by Florin (1951), and our studies show that they are separate from the ovary at the chalazal level and that they subtend the ovule (Fig. 4). Florin thought they might be outgrowths from the sporophyll and therefore an organ *sui generis*, but as they are separate from, and subtend, the ovule, we interpret them as scales or modified leaves (bracts) of the ovule/scale unit which is a modified ovulate short shoot.

DIFFERENTIATING THE SPECIES OF *PALISSYA*

Despite their differing preservation, specimens assigned to *Palissya tillackiorum* sp. nov. resemble approximately coeval Victorian cones belonging to *P. elegans* that are described from compressions and impressions. The circular attachment points in representatives of *P. elegans* (e.g. Parris et al. 1995: fig. 5A, B) are similar in size (~0.4 mm diameter) to those in the specimens assigned to *P. tillackiorum*, and both species have fine lineations radiating from the circular attachment points. These characters are also known in *Palissya* from the Northern Hemisphere (Tab. 4). However, much greater detail is available in specimens assigned to *P. tillackiorum*.

All species of *Palissya* appear to have ovules with subtending pairs of scales, although the differences in preservation between species make comparisons difficult (Tab. 4). In Gondwanan compression fossils, where the cleavage plane is near-parallel to the plane of the bract/scale complex, a dendroid pattern is commonly produced (e.g. Figs 9C, 10; and see Edwards 1934, Parris et al. 1995, Cantrill 2000): "branches" of the dendroid pattern resulted from the remnants of major scales, and the central "stem" of the pattern is formed from abutting minor scales. Where major and minor scales abut, usually it is difficult to differentiate the two elements. This organographic relationship is also evident in permineralised specimens (e.g. Fig. 6B). In compression fossils from Europe the carbonaceous remnants form a near-complete circle, generally without any obvious extra thickening at any point (e.g. Fig. 12; and see Parris et al. 1995: figs 13, 14b, c). The ovule/scale units typically exhibit a series of circles either side of the midline rather than a dendroid pattern as seen in Gondwanan specimens. This variation in appearance probably results from the Gondwanan specimens having much thicker major scales; hence the dendroid pattern. In this limited sense, and allowing for the differences in preservation, the Gondwanan species *P. tillackiorum* sp. nov., *P. elegans* Parris et al. 1995 emend. nov., *P. antarctica* Cantrill 2000 and *P. bartrumii* Edwards 1934 emend. nov. form a particularly cohesive group, as noted by Parris et al. (1995) and Pattemore et al. (2014).

Wang (2012: fig. 3A–H) figured the microscopic detail of ovules and scales from a coalified specimen attributed to *Palissya hunanensis*; it provides an unusual perspective, requiring careful comparison with other representatives of the genus. The figured specimens show scales and ovules, some with their connecting stalk (Wang 2012: fig. 3A, C, D, I). Macerated specimens show a side view of scales (Wang 2012: fig. 3F, G). It is difficult to confidently interpret the morphology of the figured microscopic specimens, but they show scales partially encompassing ovules, circular ovule attachment scars, and a compound bract/scale structure. Wang (2012: fig. 3C) also figured longitudinal lineations on scales resembling those observed in Hill's (1974) specimens (e.g. Fig. 12 herein) and in a representative of the type species from Stabbarp, Sweden (S50006; Parris et al. 1995: fig. 13E). Such lineations have been recorded on scales in specimens assigned to *Palissya* from the Lower Cretaceous of Queensland (Figs 5B, 6B, C) and Victoria (Parris et al. 1995: fig. 5A, B).

Wang's (2012: fig. 4) camera lucida sketch includes features that may be interpretative errors, possibly resulting from incomplete preservation. For example, the vascular bundle of the ovule/scale complex shown on the lower right of the sketch extends beyond the ultimate ovule/scale unit, a feature unknown in other representatives of the genus. This apparently extended portion of the bundle probably belongs to the partially preserved underlying bract. Furthermore, the lateral attachment of scales to the vascular bundle on the lower right of the sketch seems inconsistent with his figured specimens.

Palissya hunanensis appears to most closely resemble the type species, as noted by Wang (2012). It is difficult to confidently interpret the morphology based on his figures and line drawings, but they appear to have elongate bract/scale complexes in open cones and scales with radiating striations, possible ovules, and circular ovule scars. The "stalk" illustrated by Wang (2012) may be part of the vascular

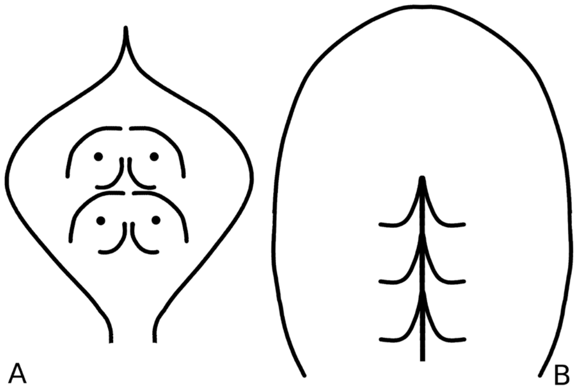

Fig. 15. Stylised line drawing comparing arrangement of adaxial elements of (**A**) *Palissya elegans* Parris et al. 1995 emend. nov. (based on holotype shown in Fig. 9B, C) and (**B**) *Knezourocarpon ovalis* (Parris et al. 1995) comb. et emend. nov. (based on holotype shown in Fig. 14A). Both A and B are based on impressions that show adaxial detail in planar view. Note that *Palissya* (A) has ovule attachment (dots) offset from the central vasculature, whereas the attachment of processes in *Knezourocarpon* (B) is directly along the central vascular trace. Scale: width of bract (A) and lamina (B) ~4–5 mm

trace and possibly is enhanced by differential shrinkage or loss of the coalified material around the trace, but similar structures have not been observed in any other species of *Palissya*, as also noted by Wang (2012). Vaez-Javadi (2011, Fig. 9E,F, 12A) described and illustrated a partial cone as *Palissya* sp. from the early Middle Jurassic Dansirit Formation in Iran that was interpreted as having circular cup-shaped structures, but the photographs and line drawings are difficult to interpret and compare with the better-known species.

The previously suggested synonymy of *Knezourocarpon* and *Palissya* (McLoughlin et al. 2002) cannot be supported. *Knezourocarpon* lacks cup-like structures and ovules, and its adaxial processes (probable sporangiophores) attach directly to the central vascular bundle – the arrangement of adaxial elements differs markedly from that of *Palissya* (Fig. 15). Its adaxial processes are lamina-like and, despite the presence of well-preserved vascular traces in some specimens, there is no evidence that appendages have dual vascular bundles.

COMPARISON WITH OTHER FOSSIL TAXA

Palissya first appeared in the latest Triassic and is unrecorded after the Aptian (Tab. 3), approximately the time of marked angiosperm radiation (Doyle 2012). Its origins are obscure but affinity with Palaeozoic voltzialeans was suggested by Florin (1944), and the Mesozoic genera *Stachyotaxus* and *Metridiostrobus* have been included in Palissyaceae (Florin 1958, Delevoryas & Hope 1981). Its apparent disappearance after the Aptian may also suggest that it was outcompeted by these new groups of flowering plants that were emerging at this time. Several gymnosperms have paired ovules positioned either side of the midline of the bract.

Representatives of *Stachyotaxus* apparently are restricted to the Rhaetian of Greenland and Sweden, and the genus has been allied with *Palissya* (Hirmer 1936, Florin 1944, 1958, Pott & McLoughlin 2011, Pattemore et al. 2014). *Stachyotaxus* is known from leaves, cuticle, pollen, and microsporangiate and ovulate cones (Nathorst 1886, 1908, Harris 1935, Florin 1944, Balme 1995, Arndt 2002, Pott & McLoughlin 2011). In ovulate cones of the genus, each lateral appendage has only a single pair of erect ovules (Nathorst 1908, Hirmer 1936, Florin 1944), whereas those of *Palissya* have 2–6 pairs of ovules.

Delevoryas & Hope (1981) erected *Metridiostrobus* with specimens from the Upper Triassic of North America. Their interpretation of *Metridiostrobus* has sessile ovules oriented outward (laterally, toward the bract's margin) from a central vascular bundle, lacking associated processes, and having ovules more or less lying on the surface of the bract. *Compsostrobus*, also from the Upper Triassic of North America, has paired inverted ovules, resembling extant representatives of Pinaceae (Delevoryas & Hope 1987, Tomlinson & Takaso 2002: tab. 3). The ovules in *Palissya* are erect (orthotropous) and therefore differ from those in *Compsostrobus* and *Metridiostrobus*.

Schweitzer and Kirchener (1996) interpreted both *Metridiostrobus* and *Palissya* as microsporangiate cones, emending the diagnosis of Palissyaceae to include both microsporangiate and ovulate cones resembling *Metridiostrobus* and *Compsostrobus* respectively. They erected *Palissya oleschinskii* from the Rhaetian–Lower Jurassic of Zangerud, Iran, interpreting it as being a helically arranged, compound cone having alternate to subopposite biseriate pollen sacs mounted adaxially on bracts. Recent photographs of the holotype, provided by the Swedish Museum of Natural History (S. McLoughlin pers. comm. 2019), were examined in this study. The specimen lacks major and minor scale pairs, ovules or evidence of ovules, and therefore are not referable to *Palissya*. The adaxial structures are also unlike the uniform, leaf-like adaxial processes found in species of *Knezourocarpon*.

RELATIONSHIPS TO EXTANT AND FOSSIL SEED PLANTS

The interpretation of the scales in *Palissya* as epimatia or arils (Nathorst 1908, Florin 1958) suggests possible links to representatives of Taxaceae or other conifer families with fleshy-fruited cones that have been interpreted as reduced (Stützel & Röwekamp 1999, Farjon 2010). The terms "aril" and "epimatium" are used for a range of structures associated with seeds that are not homologous (Silveira et al. 2016: 2), and the question of the organ(s) from which these fleshy parts are derived remains controversial in extant Taxaceae (Dörken et al. 2018). The aril/arillode is an enation or fleshy outgrowth from a seed, commonly distinctly coloured, typically involved in biotic seed dispersal (Lovisetto et al. 2012, Silveira et al. 2016), and is derived from the integument (Farjon 2010) or funicle (Bell 1991). An epimatium is an outer layer of tissue that partially covers the seed in many representatives of Podocarpaceae, and is a specialised modification of the ovule/scale structure (Farjon 2010, Dörken et al. 2018). In both cases the aril/epimatium covers part of the seed and is shed with the seed. As the seed in *Palissya* is shed separately from the major and minor scales that subtend the ovule, it appears unlikely that scales developed from any part of the ovule. Thus, the terms "aril" and "epimatium" are inappropriate and should not be used to describe these structures in *Palissya* (cf. Florin 1958, Hill 1974).

Generally there appears to have been a significant evolutionary advantage for seed plants to shift the reproductive function away from the ovule and abiotic dispersal toward extra-ovulate tissue and biotic dispersal (Leslie & Boyce 2012). Mack (2000) considered that fruit-like parts evolve initially to protect the seed from attack by pathogens, fungi, dessication and seed predators, and that they only subsequently evolve to exploit that part for biotic dispersal. As noted above, *Palissya* seeds are thin-walled and appear not to be strongly lignified, suggesting that they probably had a short period of viability; therefore, protection of the seed until its dispersal would have offered an advantage for the species. Scales would have served to protect the seed prior to dispersal but are not likely to have functioned as a biotic attractant to aid dispersal.

Dörken et al. (2018) noted the similarity of the epimatium in some Podocarpaceae (*Phyllocladus*) to the aril of *Pseudotaxus*, and Tomlinson & Takaso (1989) observed that two lateral initials form lobes on the collar in *Phyllocladus*. Dörken et al. (2018) studied the ontogeny of arils in representatives of *Taxus* and *Pseudotaxus* (both in Taxaceae), which are broadly homologous to the cup-like structures in *Palissya*, except in those extant genera the twin primordia generally merge into a ring primordia in very early stages of development, and the primordia may have initiated from different organs. Those authors also examined teratological specimens belonging to *Pseudotaxus* where the ring primordia failed to form, the arils instead remaining as twin scales (fleshy arils) forming a cup shape. This supported their hypothesis that the aril in *Pseudotaxus* may be a modified scale leaf rather than being an outgrowth of the ovule/scale, shoot axis, funicle or integument. In the above-noted conifers these paired structures have been variously referred to as scales, scale leaves or bracts, and in some modern genera the scales become fleshy and have been described as arils or epimatia. In different genera of Taxaceae the arils are either free or strongly fused to the ovule (Dörken et al. 2018).

It is somewhat ironic, then, that previous researchers have suggested that the scales in *Palissya* are arils or epimatia (Nathorst 1908, Florin 1944, 1958, Hill 1974: see Tab. 1). With the recognition of paired lateral scales subtending the ovule in *Palissya* it is possible to compare the cones of *Palissya* with those of modern conifer families. The ovule/scale units of *Palissya* are organographically comparable to those seen in extant members of Taxaceae and Podocarpaceae, in that the scales are formed from two initials (Tab. 5; and cf. Dörken et al. 2018). *Palissya* has ovules in pairs, and some Taxales also have paired ovules: *Cephalotaxus* and occasional specimens of *Pseudotaxus* (Lang et al. 2013, Dörken et al. 2018; see Tab. 5).

A depression in the basal portion of dispersed fossil seeds belonging to Ephedrales was figured by Rydin et al. (2006); it may

Table 5. Character comparison: *Palissya* and selected extant gymnosperms. Based on Price (1996), Farjon (2010), Rydin et al. (2010) and Leslie et al. (2017). *Palissya* has unspecialised seeds (sensu Leslie et al. 2017); such seeds do not have features that encourage zoochory and are largely wind-dispersed

	Palissya	Podocarpaceae	Taxaceae	Ephedrales
Ratio of median seed volume to that of *Palissya* (0.85 mm^3)	1	1 (for species with unspecialised seeds only)	10–1000 for seeds having arils (i.e. not unspecialised)	~30 (for species with unspecialised seeds only)
Ovule	orthotropous	Mostly anatropous, but some orthotropous	orthotropous	orthotropous
Single integument	Y	Y	Y	Y
Micropyle lignified	N	N	N	Y
Seed envelope	N	N	N	Y
Seed arrangement	Two parallel rows either side of midline	Usually single and terminal	Single or paired	Single, two or rarely three
Ovule/scale complex	Present	Absent	Reduced or absent	Absent
Ovule placement	Adaxial	Terminal	Terminal	Terminal
Scales	Transversal	Transversal	Decussate	Decussate arrangement or in whorls of three
Mature fruits	Not fleshy	Not fleshy, or having fleshy epimatium	Fleshy aril	Not fleshy, or having fleshy/scaly bracts

structurally resemble a small conical feature at the base of the *Palissya* ovule (Fig. 4B, Va). This depression is not recorded in extant Ephedrales (Rydin et al. 2010) or conifers (Farjon 2010). Seeds of extant Ephedrales are also surrounded by several decussate bracts, and they have a seed envelope surrounding the integument. This envelope has not been recorded in fossil Ephedrales but its existence has been inferred (Rydin et al. 2010: 422). No such seed envelope has been observed in *Palissya* seeds (Figs 4, 5D). Thus, affiliation of *Palissya* with Ephedrales is less convincing (Tab. 5).

Taylor et al. (2009) hypothesised that the aril in the Taxales may be derived from sterile scales of an ovule-carrying short shoot, and although *Palissya* may not be closely related to families of this order, the complex cones in *Palissya* may represent a possible model for the precursors of ovulate cones in some of these families that are modified for zoochory. The evolution of fruit-like parts in these conifers has been interpreted as resulting from a shift from abiotic to biotic dispersal, and these fruit characters are therefore derived. This is not surprising, because seeds with fleshy fruit-like organs have arisen many times in unrelated seed plants, including the Taxales, and this has been shown to be controlled by a suite of MADS-box genes (Lovisetto et al. 2012). Fossil groups that also have extra ovular protective organs include the Erdtmanithecales, Caytoniales, glossopterids and Bennettitales (Friis et al. 2007, Doyle 2008), but no convincing links have been identified with *Palissya*.

The bract/scale complex in extant Taxaceae has been interpreted as being reduced in size and complexity (discussed above), in some cases to only a single terminal ovule, and all members of Taxaceae lack a distinct bract/scale complex (Dörken et al. 2018), so a detailed comparison with *Palissya* is not possible. The insertion of ovules on the adaxial surface of the cone scale, rather than the axil, is also known from some early fossil Cupressaceae (e.g. Spencer et al. 2015), which are sister to Taxaceae. Representatives of Voltziaceae also have seeds inserted on the adaxial surface, but they and members of Cupressaceae differ from *Palissya* in having a different arrangement of seeds, and they are not known to have seeds occurring in paired rows.

CONCLUSION

1. Permineralised specimens attributed to *Palissya tillackiorum* sp. nov. have provided the opportunity to review this poorly understood genus. *Palissya* represents ovulate fructifications having helically arranged bract/scale complexes, each comprising a bract with an adaxial ovule/scale complex formed from several ovule/scale units that are positioned in two parallel rows on either side of the midline of the bract/scale complex.

2. Each ovule/scale unit has an ovule mounted terminally on a vascular trace and is subtended by a pair of scales that surround the ovule, forming a cup-like shape. The scales

are not fused to the ovule and probably served a protective function. The seeds were shed separately and were likely anemochorus. The cones were catkin-like and were shed as a complete unit some time after seed dispersal.

3. The ovule/scale units in the ovule/scale complex of *Palissya* are highly synorganised, demonstrating that Mesozoic pinopsids were capable of a degree of synorganisation analogous to that seen in angiosperms. Our morphological model for *Palissya* augments and further develops those previously advanced by Nathorst (1908) and Florin (1958), and clarifies the organographic relationships within the ovule/scale units that were interpreted previously as cups or arils.

4. *Palissya* shares morphological features with taxa belonging to Pinopsida, and in particular, ovule/scale units on the adaxial surface of a bract/scale complex and orthotropous ovules subtended by scales. The ovule/scale units in Taxaceae, Podocarpaceae and Ephedrales have been interpreted as highly reduced (Stützel & Röwekamp 1999, Farjon 2010, Rydin et al. 2010), and the cones of *Palissya* may represent an appropriate organographic model for a precursor to one of these extant groups. However, the phylogenetic affinities remain unclear – Palissyales may represent an extinct lineage within Pinopsida that shares generalised features with several taxa within this class.

5. *Palissya* cones are known from the uppermost Triassic–Middle Jurassic of Eurasia and the Middle Jurassic–Lower Cretaceous (Aptian) of Eastern Gondwana, apparently terminating coincidentally with early angiosperm species radiation.

6. The synonymy of *Palissya* and *Knezourocarpon* cannot be supported: the latter lacks paired scales that form a cup-like adaxial structure, ovules or ovule attachment points. *Knezourocarpon* has adaxial processes (probable sporangiophores) mounted in two parallel rows that attach directly to the lamina's midrib. Accordingly, *Palissya ovalis* Parris et al. 1995 is transferred to *Knezourocarpon*.

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