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Palissya : a global review and reassessment of Eastern Gondwanan material

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Abstract

The conifer genus *Palissya* is reviewed giving special attention to assessing the reliability of Gondwanan material referred to this genus. The collection localities of Australasian specimens are mapped on palaeogeographic reconstructions of Eastern Gondwana at relevant times between 179 Ma–119 Ma.

Australasian and other Gondwanan material previously referred to *Palissya* is considered to differ substantially from the generic diagnosis. Specimens from the Toarcian of Australasia are shown to be allied to *Knezourocarpon*; this genus is only known from the Toarcian of eastern Australia. Middle Jurassic–Lower Cretaceous Australasian specimens previously referred to *Palissya* are likely allied to the Knezourocarponaceae fam. nov. The higher taxonomic affinity of this family is unknown but broadly, its structure is suggestive of ginkgoalean or pteridospermous affiliation.

Southern hemisphere specimens were probably catkin-like and megascopically very different from the northern hemisphere *Palissya* and the two groups are unlikely to be closely related. Consequently, genuine *Palissya* cones and foliage appear to be restricted to the Rhaetian–Lower Jurassic of the northern hemisphere.

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1. Introduction

Cones attributed to the Palissyaceae Florin 1958 have been rarely reported from outside of the northern hemisphere. However, in recent decades a considerable amount of material from the Toarcian–Aptian of Australasia has been assigned to *Palissya* Endlicher 1847 emend. Florin 1958. Two separate reviews of *Palissya* differed on major points including the structure and gender of the cone (Parris et al., 1995; Schweitzer and Kirchner, 1996). While each review adopted a global perspective, one focused on the northern hemisphere while the other was largely concerned with Australasian material. These conjectural points have largely been resolved by Wang (2012) prompting a reconsideration of Australasian specimens assigned to this genus. Moreover, the establishment of the genus *Knezourocarpon* Pattemore 2000 based on specimens from the Toarcian of Queensland, Australia, suggests Australasian specimens previously ascribed to *Palissya* should be reassessed.

The compound structure of the *Palissya* cone has been conjectural and has been widely used to support conifer affiliation (or otherwise) of the Palissyaceae; however, this contribution does not attempt to further define the higher taxonomic affinity of this family. Rather, this paper seeks to clarify the geographic and temporal distribution of representatives of the Palissyaceae particularly regarding Gondwana. The palaeogeographic position of Eastern Gondwanan representatives of *Palissya* and *Knezourocarpon* are mapped based on the modelling of Seton et al. (2012).

2. Palissyaceae

Palissyaceae has been regarded historically as a conifer family, but this was doubted by

Parris et al. (1995) because they did not regard the cone, *Palissya*, as compound. This was disputed by Schweitzer and Kirchner (1996). Phylogenetic analysis of conifers by Miller (1999) excluded *Palissya* due to its uncertain affiliation. Meyen (1984) placed the Palissyaceae within rank Pinales and rank Pinopsida while Taylor et al. (2009) assigned *Palissya* to the Coniferales.

2.1. *Palissya*

The genus was established monotypically with *P. braunii* Endlicher 1847 from the Lower Jurassic of Germany. Some authors (eg. Escapa et al., 2008; Bosma et al., 2012) have adopted an alternative orthography; viz. *Palyssia*. The original spelling is accepted here, being patronymic for Bernard Palissy (Endlicher, 1847).

Nathorst (1908) referred *Palissya braunii* to *P. sphenolepis* (Braun 1843) Nathorst 1908 emend. Florin 1958 as a correction of priority and described more material from the Lower Jurassic of Sweden. Endlicher’s (1847) brief diagnosis specified paired sessile leaves and a cone with loosely overlapping scales. Florin’s (1958) emendation of the genus and the type species included a detailed description of ovules, ovule scale complex and foliage cuticle. Reconstructions of *Palissya* bracts were provided by Hirmer (1936) and Florin (1951); Figure 1 (A–B) shows Hirmer’s (1936) bract and ovule scale complex reconstruction. Key references for this genus are listed in Table 1.

[Figure 1]

Over recent decades much new material has been referred to *Palissya* and the genus has been reviewed by Parris et al. (1995) and Schweitzer and Kirchner (1996). The latter authors considered British specimens previously reported in an unpublished manuscript and added new material from Iran. Both reviews differed on major points, notably the likely structure and gender of the cone. However, each account considered only slightly overlapping subsets of all material referred to *Palissya*; one focused on the northern hemisphere, the other on Australasian material. Parris et al. (1995) disputed the assertion that the cone was compound but Schweitzer and Kirchner (1996) disagreed. Wang (2012) described Rhaetian specimens from China which are remarkably similar to the European type species, and reported microscopic examination of the ovuliferous scale complex and ovules. He confirmed Florin's (1958) generic diagnosis regarding the structure of the *Palissya* cone, in particular, stating that the cone is compound and female, thus supporting conifer affiliation.

[Table 1]

Foliage was originally included in the diagnosis of *Palissya* as established by Endlicher (1847), and in at least two subsequent emendations (Florin, 1958; Schweitzer and Kirchner, 1996). Following Seward (1919), Parris et al. (1995) discussed the inclusion of foliage without a clearly associated cone and considered a number of such referrals to have caused considerable confusion. Seward's (1919) viewpoint was based on significant differences in foliage cuticle reported by Schenk (1867) and Nathorst (1908), but Florin (1958) considered Seward's (1919) view as "going too far". Pott and McLoughlin (2011) also considered *Palissya* leaf material and referred new foliage specimens to *Elatocladus* Halle 1913 but within the Palissyaceae.

Stachyotaxus Nathorst 1886 comprises *Elatocladus*-type foliage and male and female cones, and the male cone was considered to be catkin-like (Harris, 1935). *Stachyotaxus* was regarded as a conifer cone similar to *Palissya* but with only a single pair of ovules per bract (Nathorst, 1908; Seward, 1919; Harris, 1935; Stewart and Rothwell, 1993; Arndt, 2002; Taylor et al., 2009; Pott and McLoughlin, 2011); Figure 1 (C–D) shows Hirmer's (1936) bract reconstruction. Stomata of *Stachyotaxus* are in two parallel longitudinal zones on the abaxial surface which is also the case in *Palissya* (Nathorst, 1908). *Stachyotaxus* has been reported by numerous authors (Table 1). Pott and McLoughlin (2011) regarded *Stachyotaxus* as restricted to Rhaetian sediments of Greenland and Scania. Jurassic specimens from Antarctica, referred to the genus by Birkenmajer and Ociepa (2008), are insufficiently preserved for confident identification.

2.2. *Palissya* – northern hemisphere

Northern hemisphere material ascribed to *Palissya* has been reviewed by several authors (Nathorst, 1908; Hirmer, 1936; Florin, 1958; Parris et al., 1995; Schweitzer and Kirchner, 1996). The type species, *P. sphenolepis*, was reported from the Rhaetian–Lower Jurassic of Franconia, Germany and Stabbarp, Sweden (Nathorst, 1908; Florin, 1958; Parris et al., 1995); several uppermost Triassic accounts of the genus from Europe and Asia were summarised by Dobruskina (1994). Other poorly preserved and fragmentary material was described from Sofiero, Sweden as *Palissya* sp. by Nathorst (1908) and *Palissya* sp. 'Sofiero' by Parris et al. (1995).

The reviews by Parris et al. (1995) and Schweitzer and Kirchner (1996) differ considerably in their assessments of *Palissya*. Schweitzer and Kirchner (1996) regarded *Palissya* as a compound male cone; by contrast, Parris et al. (1995) considered it as a probable female cone and not compound. Both Parris et al. (1995) and Schweitzer and Kirchner (1996) emended the circumscription of the type species. Whether or not *Palissya* is a compound cone has proved controversial (Seward, 1919; Florin, 1944, 1958; Parris et al., 1995; Schweitzer and Kirchner, 1996; Pott and McLoughlin, 2011). However, *Palissya* material from China has confirmed the compound structure of the cone (Wang, 2012).

In an unpublished thesis, Hill (1974) identified *Palissya* in the Middle Jurassic of Yorkshire and described a "new" species, *P. harrisii*, comprising foliage and female cones. He recorded cuticle of both bract and foliage, also organic attachment in one specimen between foliage and cone (p.167, specimen B1 and plates 24–25). Although Hill (1974) considered the cones to be female, no ovular attachments were identified. The foliage preserved as part of specimen B1 with the attached cone, is poor and cuticle could not be recovered. An “ovuliferous ridge” was identified but the extent to which it is separate from the bract is unclear. Bracts are decurrent on the cone axis and bract arrangement is uncertain.

Parris et al. (1995) doubted evidence for leaf attachment in the Swedish material. These authors did not emend the diagnosis of *Palissya* to exclude foliage, but their emended description of the type species did not allude to foliage remains.

Schweitzer and Kirchner (1996) emended the diagnosis of the type species to include not only *Elatocladus*-type leaves and *Palissya* cones (considered to be male cones by these authors), but also *Compsostrobus*-type female cones based on the discovery of new Iranian material (discussed below). *Metridiostrobus* Delevoryas and Hope 1981 and *Compsostrobus* Delevoryas and Hope 1973 were reported from the Upper Triassic of North Carolina, U.S.A. Schweitzer and Kirchner (1996) considered *Palissya* as a *Metridiostrobus*-type cone. According to Delevoryas and Hope (1981), *Metridiostrobus* is a female cone; however, Schweitzer and Kirchner (1996) re-interpreted the cone as male and as associated with *Compsostrobus*. Delevoryas and Hope (1973, 1981, 1987) did not refer foliage specimens to *Elatocladus*, but did identify unattached conifer foliage co-preserved with *Compsostrobus*. The apparent similarities between the European *Palissya* type species and North American *Metridiostrobus* specimens are remarkable but Delevoryas and Hope (1981) discussed some important differences. This stands in stark contrast to the apparent difference between the European *Palissya* type species and the southern hemisphere *Palissya* specimens described by Parris et al. (1995), as discussed below.

Palissya hunanensis Wang 2012, from the Rhaetian of Hunan Province, China, appears remarkably similar to the type species of *Palissya* and, as discussed above, supports previous interpretations that the cone is female, compound and conifer-like. The cone structure is shown in Figure 2.

Swedish specimens termed *Palissya* sp. by Nathorst (1908) and *Palissya* sp. ‘Sofiero’ by Parris et al. (1995) are too poorly preserved to allow comparative evaluation. Several specimens referred to *Palissya* from the northern hemisphere were judged by Schweitzer and Kirchner (1996) to be dubious representatives of the genus.

[Figure 2]

2.3. ***Palissya*** **– Iran**

Palissya oleschinskii Schweitzer and Kirchner 1996 was described by Schweitzer and Kirchner (1996) from the Rhaetian–Lower Jurassic of Zangerud, Iran. These cones were preserved with *Elatocladus*-type leaves and isolated cones regarded by these authors as female, and referred to *Compsostrobus brevirostratus* Schweitzer and Kirchner 1996. They reported a likely association between the *Elatocladus*-type foliage and *Compsostrobus*-type female cones from another Iranian site, Tazareh, which were found within strata equivalent to those at Zangerud; this forms the basis for their association of all three plant organs. Schweitzer and Kirchner (1996) noted that not all *Elatocladus*-type leaves are referable to *Palissya* as other conifer genera are known to bear similar leaves.

The bract attachment of *Palissya oleschinskii* was considered by Schweitzer and Kirchner (1996) to be helically arranged. However, their figured specimen appears more likely to have been bilateral, opposite and sessile. Further, comparing their figured *P. oleschinskii* specimens and reconstruction, it appears that Schweitzer and Kirchner (1996) considered the end of the cone with the apparently thicker section of axis as the top of the cone. As their reconstruction shows, this places the sporangia on the upper surface of the lamina; thus implying that the cleavage plane must be more-or-less central to the cone axis near the cone’s figured apex and be no longer central to the axis near to cone’s figured base.

Figured lamina attachment does not support this view.

An alternative view is that the apparently thicker axial section constitutes the base of the cone, while the opposing end has poorer preservation with more sediment obscuration; this would be expected if this end were the more delicate apex of the cone. If the stem thickens as Schweitzer and Kirchner (1996) suggested, then it seems more likely that the cone was oriented in a catkin-like manner.

Both these alternatives place the microsporangial surface beneath the lamina, which commonly characterises extant and extinct gymnosperms and pteridophytes by promoting maximum pollen dispersal (Niklas, 1985). The Iranian *Palissya oleschinskii*, although sessile, appears significantly different to other northern hemisphere species of this genus.

2.4. *Palissya* – Gondwana excluding Australasia

Schweitzer and Kirchner (1996) reviewed numerous early descriptions of *Palissya* from India, Antarctica and South America and rejected all except specimens reported by Frenguelli (1949) as *P. conferta* (Oldham and Morris 1862) Feistmantel 1877a and *P. jabalpurensis* Feistmantel 1876b from Chubut, Patagonia. Both these species were originally established from Indian foliage specimens (Feistmantel, 1876a,b, 1877a,b,c, 1879, 1880), while the identifications of them by Frenguelli (1949) comprised foliage and cones. In contrast to Schweitzer and Kirchner's (1996) view, Parris et al. (1995) regarded Frenguelli's (1949) fructifications as unlike the type species. Parris et al. (1995) suggested that Frenguelli's (1949) hand-drawn figures show little resemblance to his figured specimens. These specimens have subsequently been referred elsewhere (Escapa et al., 2008). Additional early descriptions of foliar remains assigned to *Palissya* from the Jurassic–Cretaceous of India were summarised by Lakhanpal et al. (1976); while some of these species are noted as referred elsewhere, the remainder are insufficiently described to confidently be regarded as conforming to the genus.

The fructification *Palissya antarctica* Cantrill 2000, from the Aptian Cerro Negro

Formation of Snow Island, Antarctica (Cantrill, 2000), is relatively small compared to other specimens referred to the genus. The adaxial processes were interpreted as likely pear-shaped ovules; however, it is unclear whether these processes represent ovules or sporangia. The laminae appear to be helically arranged and petiolate, and there is no evidence that the fructification is compound (Cantrill, 2000). The circumscription of this species was based on six incomplete specimens and the arguments presented for referral to *Palissya* were largely informed by the work of Parris et al. (1995) regarding Australasian specimens. It is shown herein that Australasian specimens previously referred to *Palissya* vary significantly from the generic diagnosis. However, it seems possible that *P. antarctica* may be related to Victorian Cretaceous specimens hitherto identified as *Palissya* (see Table 2 and Figure 7).

[Figure 3]

2.5. *Palissya* – Australasia

2.5.1. Southeast Queensland (Middle Jurassic)

Palissya ovalis Parris, Drinnan and Cantrill 1995 was reported from Reynold’s Creek and Kalbar in southeast Queensland by Parris et al. (1995), and from Mutdapilly (~22 km north of Kalbar) by McLoughlin and Drinnan (1995); see Figure 3 (point R). These authors considered these sites to be within the Walloon Coal Measures, which were regarded as Bathonian in age (Turner et al., 2009; Cook et al., 2013). No exact locality information was provided for the Reynold’s Creek site; however, Queensland Museum specimen records indicate that these were collected from the Parish of Fassifern (3–4 km southwest of Kalbar). Figure 4 (point A) shows these sites juxtaposed with the collection location of similar material from the Callovian of the South Island, New Zealand (discussed below) on a reconstructed map of Eastern Gondwana.

Palissya ovalis fructifications are helically arranged with petiolate, ovate laminae; each lamina bears 5–6 pairs of adaxial processes, although specimens reported by McLoughlin and Drinnan (1995) have 7–8 pairs of such processes. These authors postulated that the larger number of sporangial pairs in their specimens reflected better preservation. Parris et al. (1995) regarded their specimens as representing a range of fructifications from open to closed. Their only figured open fructification (Parris et al., 1995, fig. 9A,B) appears to be oppositely branched, whereas the more closed fructifications appear helically arranged; however, both the open and closed fructifications figured by McLoughlin and Drinnan (1995) appear helically branched.

If the thicker end of the fructification axis shown by Parris et al. (1995, fig. 9A,C) were oriented upward then the sporangia would be pendulous and the fructification catkin-like. This also seems likely for the *P. ovalis* fructifications reported by McLoughlin and Drinnan (1995).

[Figure 4]

2.5.2. South Island, New Zealand (Middle Jurassic)

Edwards (1934) and Parris et al. (1995) reported four specimens from the Waikawa locality, South Island, New Zealand, which were assigned to *Palissya bartrumii* Edwards 1934. The collection site is a seaside rock platform in Curio Bay composed of sediments considered latest Callovian in age (Pole, 2001, 2004). Early palaeobotanical studies from this locality were summarised by Arber (1917), who referred a foliage specimen to *Palissya* that had previously been reported as *Taxites manawao* Hector 1886. The latter, as figured by Hector (1886, fig.30A(2)), is small (albeit with no indication of actual size) and lacks sufficient detail to confirm identification. The Curio Bay site was discussed by Thorn (2001) and fossil wood from there was examined by Thorn (1999).

Parris et al. (1995) ascribed several specimens collected from Slope Point (~7 km west of Curio Bay) to *Palissya bartrumii*. Their material is neither described nor illustrated. The host strata were considered upper Callovian but stratigraphically lower than those at Curio Bay (Pole, 2004).

Two incomplete specimens from Mokoia, near Gore, were referred to *Palissya bartrumii* by Edwards (1934); these were originally identified as *Stachyotaxus* sp. by Arber (1917). Both were substantially larger than other material assigned to *P. bartrumii*; Edwards (1934) considered them to be the only New Zealand specimens to have reflexed laminae, but this may only be a preservational effect. The specimen figured by Parris et al. (1995, fig. 12) shows remarkably different adaxial processes to other Australasian material assigned to this genus. Their figure suggests the fructification has a uniformly dispersed, probable microsporangial array of investments beneath a sporophyll, rather than paired processes as specified in the generic circumscription of *Palissya*. The Mokoia site was dated as Callovian by Parris et al. (1995), but they noted that the actual site may have been obliterated by natural processes.

All these southern New Zealand sites are within the Murihiku Terrane (Pole, 2009); see Figure 3 (points M and C).

Parris et al. (1995) emended the diagnosis of *Palissya bartrumii* to include helical arrangement of sporophylls. Sporophylls are ovate and petiolate, with 3–4 pairs of adaxial processes per sporophyll, apparently assumed from the dendroidal pattern visible in some specimens. The adaxial processes appear to have likely been pendulous sporangia.

The *Palissya bartrumii* material is poorly preserved and only the holotype can be regarded as approaching completeness. These specimens are very similar to those referred to *P. ovalis* from the Middle Jurassic of southeast Queensland (discussed above), except that *P. bartrumii* has fewer reported adaxial processes per sporophyll. Figure 4 (point B) shows the location of these three southern New Zealand sites within a reconstruction of the Eastern Gondwana landmass at approximately the Bathonian–Callovian boundary; this is compared with the palaeogeographic position of the Queensland material (point A).

2.5.3. North Island, New Zealand (Late Jurassic)

A specimen from beds exposed along New Zealand's North Island coastline, at the mouth of the "Huriwai Stream", was reported by Bartrum (1921) as ?*Stachyotaxus* cf. *S. elegans* Nathorst 1908, and was later referred to *Palissya bartrumii* by Edwards (1934). This site is located several kilometres south of Waikato Head (Bartrum, 1921); see Figures 3 (point W), 5 (point A). Parris et al. (1995) considered this specimen to be latest Jurassic–Early Cretaceous in age. While the Huriwai Formation at Waikato Head is now considered Tithonian (Parris et al., 1995; Pole, 2009), it is not clear that the sediments at Bartrum's (1921) collection site can be chronocorrelated as implied by Parris et al. (1995); however, as this site appears to be within the Murihiku Terrane, a Late Jurassic age seems probable.

Bartrum's (1921) specimen was figured by Edwards (1934); this indifferently preserved specimen shows bilateral symmetry of sporophylls, but the adaxial processes are indistinct. Parris et al. (1995) remarked that the fructification is smaller than other New Zealand material assigned to the genus. This specimen is separated geographically and temporally from other material referred to *P. bartrumii* (Table 2).

[Figure 5]

2.5.4. Boola Boola, Victoria (Early Cretaceous)

Palissya elegans Parris, Drinnan and Cantrill 1995 has been reported from several sites within the Boola Boola State Forest, Victoria (Parris et al., 1995); see Figures 3 (point B), 6 (point A). Additional specimens from the same area were assigned to this species by McLoughlin et al. (2002). All were dated as Neocomian by Parris et al. (1995); however, all specimens are from the Locmany Member of the Rintoul Creek Formation, Gippsland Basin (McLoughlin et al., 2002), and this member has been dated as Valanginian (Tosolini et al., 1999).

Palissya elegans was reported to have helically arranged, petiolate, oval to round laminae with three pairs of adaxial processes per lamina (Parris et al., 1995). Laminae have a ~5 mm long narrow apical projection. The only figured specimen to show this projection is the holotype (Parris et al., 1995, fig. 3), which is also the only complete specimen. No cuticle is preserved. Cone fragments were tested for spores but preparations revealed a diverse, presumably part-allochthonous, assemblage (Parris et al., 1995).

The figures by Parris et al. (1995, figs. 3A, 4A-D and 5D) suggest the possibility that laminae are decussate on the axis. The lower laminae in their figure 3A appear decussate; while 4A–D suggest bilateral symmetry. The magnified figure 5D shows two adjacent laminae on the same side of the axis. Given the petiole width and the very close proximity of these two laminae, and moreover that the figure shows no apparent stem twist, it would be difficult to physically fit a helical arrangement of attached laminae over such a short axial section. A poor specimen of *Palissya elegans* figured by McLoughlin et al. (2002, fig. 49A) suggests that this fructification is, in fact, decussate.

The figured “ovule” (Parris et al., 1995, figs. 5D,E) appears to be of a size, shape and orientation that is inconsistent with their reconstruction (Parris et al., 1995, figs. 6B,C) and with the argument that cup-like investments held an ovule. Parris et al. (1995, figs. 4E and 5A,B) showed circular features which were apparently on the lamina and surrounded by adaxial processes somewhat like the type species as described by Nathorst (1908), and this feature was interpreted as a “cup”. It was suggested that this circular area encompassed an indentation; however, this indentation appears to have been assumed based upon the exposure of sediment within this feature. The indentation is only visible at one point on one figured specimen. The adaxial processes have striations which radiate from the circular feature, thus enhancing the optical effect of the “cup”. The characteristic dendroidal pattern with a “central stalk”, often observed in Australasian specimens referred to *Palissya*, was considered by Parris et al. (1995) to be the broken edges of overlapping processes, with the “central stalk” inferred to represent adpressed inner margins of the adaxial processes. In considering this explanation, if a specimen cleaved through the adaxial processes, it would be expected instead to produce a series of touching, or nearly touching, circles; ie. in section, similar to that figured by Arndt (2002, pl. 2, fig. 6). The adaxial processes with striations radiating from the circular features are only visible arising from approximately half of each circular feature. It seems likely that these so called cup-shaped processes are illusory (suggested by the striated radiating pattern), and were probably small convex microsporangial leaf-like blades.

The apical projections appear more likely to have been a drip-tip (accuminate); if so, the fructification was probably catkin-like. Further, the fine and slender disposition of the fructification strongly suggests that it was catkin-like rather than a rigid upright cone.

[Figure 6]

2.5.5. Koonwarra Fossil Bed, Victoria (Lower Cretaceous)

A few indifferently preserved specimens were referred to *Palissya* sp. ‘Koonwarra’ by Parris et al. (1995) from the Koonwarra Fossil Bed, Gippsland Basin, Victoria; see Figures 3 (point K), 7 (point A) . The host sediments were considered of Aptian age (McLoughlin et al., 2002) and thus ~17 million years younger than the Boola Boola specimens which were assigned to *Palissya elegans* (as discussed above). Dettmann (1986) identified a diverse spore-pollen assemblage from this site dated as possibly Aptian. The collection site of *Palissya* specimens from the Aptian of Antarctica (discussed above) is juxtaposed on Figure 7 (point B).

The only complete specimen, described by Drinnan and Chambers (1986, p.70, figs. 37-

38A), lacks clearly visible adaxial processes. Additional material provided by Parris et al. (1995) is very fragmentary but appears to show adaxial processes. The specimen reported by Seward (1904, pl. 19, figs. 39, 40) as ?Ginkgoalean female flower, and partially figured by Parris et al. (1995, fig. 8C), is a very poor, almost unidentifiable specimen.

Palissya sp. 'Koonwarra' was interpreted by Parris et al. (1995) as possessing helically arranged petiolate sporophylls, each bearing four pairs of adaxial processes. Sporophyll arrangement on the axis is presumably based on the specimen of Drinnan and Chambers (1986) as that is the only specimen which clearly shows the axis. The detail of sporophylls is presumably determined from the fragmentary new material of Parris et al. (1995). Axis detail in the complete specimen is insufficient for attachment to be regarded as convincingly helical and the bilateral symmetry of preserved sporophylls suggests otherwise.

[Figure 7]

2.5.6. Discussion

Parris et al. (1995) noted that the type species of *Palissya* "appears very different" from Australasian species. These authors accounted for this difference on the grounds of preservation and shape and placement of processes on the lamina. They reinterpreted the fructification as neither compound nor conifer-like, but possibly ovuliferous, largely from their examination of a European specimen which has been significantly damaged (Parris et al., 1995) since its study by Florin (1958). Given the recent work of Wang (2012), the reinterpretation of *Palissya* by Parris et al. (1995) cannot be supported. Key features of the *Palissya* fructification, as listed below, are based upon the descriptions of Nathorst (1908), Florin (1958), Hill (1974), Schweitzer and Kirchner (1996) and Wang (2012).

- A woody compound cone structure;
- bracts helically arranged and lanceolate with an acute or obtuse apex;

- bracts strongly decurrent on the axis and sessile (not petiolate laminae);
- cup-like investments containing ovules, and attached to an axillary structure closely subtended by a bract.

[Table 2]

Australasian *Palissya* specimens (summarised in Table 2) diverge considerably from those from the northern hemisphere and probably represent members of more than one genus. In particular:

- sporophylls are petiolate laminae in contradistinction to the sessile conifer-like bracts of northern hemisphere species;
- lamina are distinctly branched helically, bilaterally or possibly even decussate from the main axis and show no indication of being decurrent on the axis;
- they show no indication of possessing cup-like investments mounted on an ovule scale complex;
- they are long slender fructifications, apparently delicate, not woody, and likely oriented catkin-like with pendulous sporangia mounted beneath the lamina;
- general form is not suggestive of conifer affiliation, but rather ginkgoalean, or perhaps pteridospermous.

Accordingly, the inclusion of the Australasian material in *Palissya* and the Palissyaceae cannot be substantiated. Further, *Palissya* specimens from elsewhere in Gondwana are also unlikely to belong to *Palissya*. Consequently, *Palissya* can only be confidently regarded as a conifer from the Rhaetian–Lower Jurassic of the northern hemisphere.

3. Systematic palaeobotany

Incertae ordinus

Knezourocarponaceae Pattemore fam. nov.

Diagnosis: Catkin-like fructifications with leaf-like lamina borne on a central axis. Lamina constituting an upper surface beneath which are positioned pendulous sporangia or ovules.

Knezourocarpon Pattemore 2000

Type species: *Knezourocarpon narangbaensis* Pattemore 2000; Toarcian, Landsborough Sandstone, Nambour Basin, Queensland, Australia; by monotypy.

Knezourocarpon narangbaensis Pattemore 2000

Figure 8A–F.

Synonymy:

2000 *Knezourocarpon narangbaensis* Pattemore, p.189–192, figs. 3–6.

2008 *Caytonia cucullata* McLoughlin in Jansson, McLoughlin, Vajda and Pole, p.16, figs. 8A–F.

Diagnosis: see Pattemore (2000).

Discussion: *Knezourocarpon* was based on numerous specimens and comprises female and male fructifications. Circumscription and comparisons with other genera were provided by Pattemore (2000); the collection location is shown on Figures 3 (point N), 9 (point A) herein.

Six fragmentary remains of *Caytonia cucullata* were described by Jansson et al. (2008b) from siltstone of Inverleigh Quarry, in the Clarence-Moreton Basin; see Figures 3 (point I), 9 (point B). The host deposits were considered to be within the Marburg Subgroup and probably upper Gatton Sandstone (Jansson et al., 2008a,b) and are located stratigraphically below an oolitic marker horizon which is present in a number of southern Queensland basins

(McKellar, 1993; Cranfield et al., 1994; Cook et al., 2013); the description of the local geology by Jansson et al. (2008b) suggests a likely age range of latest Pliensbachian–middle Toarcian (Cook et al., 2013). Specimens referred to *Knezourocarpon narangbaensis* by Pattemore (2000) from Toarcian sediments of the Narangba Quarry in the Nambour Basin, were reported to be just above this oolitic marker horizon. The Narangba Quarry sediments were considered to be within the uppermost section of the Landsborough Sandstone (Pattemore, 2000) within the Marburg Subgroup (Cook et al., 2013).

[Figure 8]

Caytonia cucullata was diagnosed as a suboppositely–alternately branched, dorsiventral, pinnate megasporophyll with up to 23 ovuliferous lamina. The female fructification, *Caytonia* Thomas 1925, is known in considerable detail (Thomas, 1925; Harris, 1932, 1933, 1940; Reymanówna, 1973, 1974; Krassilov, 1977), but ovules were not described in the diagnosis or description of *C. cucullata* by Jansson et al. (2008b) and ovule insertion proved unclear. No likely associated microsporophyll was reported.

Re-examination of the Inverleigh Quarry material assigned to *Caytonia*. *cucullata* indicates that lamina attachment was incorrectly reported by Jansson et al. (2008b) and should be regarded as opposite to sub-opposite. The adaxial processes appear in most cases to have been overlapping lamina, probably pendulous leaf-like sporangia. One specimen reported by these authors is re-figured herein (Figure 8A).

Jansson et al. (2008b) suggested that their specimens of *Caytonia* were unlike others of Jurassic age in that they lacked the characteristically club shaped cupules and pedicels. They compared their specimens to those which they considered to have kidney-shaped cupules. *Caytonia orientale* Krassilov 1964, from the Lower Cretaceous of Russia, is a poor and indistinct specimen; comparision with this specimen is most unconvincing. While some aborted cupules of *C. indica* Bose and Banerji 1984 are reniform, mature cupules are not, and this cannot be regarded as characterising the species. Bose and Banerji's (1984) specimens comprise a very fragmentary collection of cupules; apparently none are attached to an axis and very few were considered to be ovulate. Both *C. orientale* and *C. indica* in no way resemble the Inverleigh Quarry specimens.

The specimens referred to *Caytonia cucullata* by Jansson et al. (2008b) clearly conform to *Knezourocarpon narangbaensis* in every available megascopic detail. Further, as suggested above, the sediments from the Inverleigh and Narangba quarries are approximately coeval; the Inverleigh Quarry specimens are likely latest Pliensbachian to middle Toarcian in age, while the Narangba specimens are middle Toarcian.

This new family is proposed with uncertain higher taxonomic position. Although there are some similarities with the Caytoniaceae Thomas 1925, there are some very significant differences as follows.

• The *Caytonia* female fructification was formed from a modified leaf lamina which has curled and deformed sufficiently to form a cupule containing ovules; whereas *Knezourocarpon* has a separate, apparently unprotected, ovule beneath an otherwise unmodified lamina.

• *Caytonia* and *Caytonanthus* Harris 1937 do not appear to have been catkin-like; whereas both male and female *Knezourocarpon* fructifications were most likely catkin-like.

[Figure 9]

The catkin-like arrangement of *Knezourocarpon* suggests possible ginkgoalean affiliation. While poorly preserved specimens reported as Conifer cone sp. A by Pattemore and Rigby (2005) from the *Knezourocarpon* type locality may be interpreted as short shoots, it seems most unlikely that these were associated with this genus; the abscission marks are too small to suggest attachment to a *Knezourocarpon* axis. Further, no ginkgoalean foliage was reported from the Inverleigh or Narangba quarry sites by Pattemore (2000), Pattemore and Rigby (2005) or Jansson et al. (2008b).

Knezourocarpon sp. cf. ***K. narangbaensis*** Pattemore 2000

Synonymy:

1883 *Walchia milneana* Tenison-Woods, single specimen, identified as “male amentum”, p. 163–164, pl. 6 (fig. 8).

1986 “Cone of Seed-fern” of White (1986), p. 163, fig. 244.

1986 “Cone of Pteridosperm” of White (1986), p. 251.

1995 *Palissya* sp. ‘Talbragar’ of Parris et al. (1995), p. 98–99, fig. 10A–C.

Discussion: Parris et al. (1995) referred a complete specimen and fragments to *Palissya* sp. ‘Talbragar’, which they described as “faint and indistinct”. This indifferently preserved specimen from the Talbragar River, New South Wales, was originally figured by White (1986); see Figures 3 (point T1), 9 (point C). The Purlawaugh Formation, as exposed along the Talbragar River in the vicinity of the collection locality, was regarded as Toarcian (Parris et al., 1995; Beattie and Avery, 2012). Parris et al. (1995) suggested a stratigraphic correlation with the nearby Talbragar Fish Beds; however, a recent study dates those beds as Late Jurassic (Beattie and Avery, 2012). The fructification’s branching arrangement is unclear but the four sporophylls at the apparently thicker end of the fructification axis appear petiolate and bilaterally opposed. The remainder of the fructification is less well preserved. If the branching arrangement is confirmed then this fructification is likely attributable to *Knezourocarpon narangbaensis*.

Tenison-Woods (1883) assigned conifer-like foliage and co-preserved fructifications, identified as “male amentum”, to his species *Walchia milneana* from the Ballimore Hill coal mine, east of Dubbo near the Talbragar River (Feistmantel, 1890); see Figures 3 (point T2), 9 (point C). The Ballimore Coal Measures (now Ballimore Formation) are dated as Early Jurassic; its extent is limited to the Ballimore area where it underlies the Purlawaugh Formation (Dulhunty, 1973; Pogson et al., 1999). Tenison-Woods's (1883) diagnosis of *W. milneana* was based exclusively on foliage. The fructifications were considered associated with the foliage due to their co-preservation; they were described as distichous with scales bearing comb-like projections. His specimen (pl. 6, fig. 8), is very similar to *Knezourocarpon narangbaensis* in that: (1) laminae are oppositely arranged; (2) laminae bear adaxial processes which were probably pendulous sporangia. The structure of the fructification suggests that it is not coniferous and therefore unlikely to be associated with the co-preserved foliage. However, the figured fructification shows insufficient detail to confidently refer it to *K. narangbaensis*.

4. Conclusion

Australasian specimens previously referred to *Palissya* are shown to diverge considerably from the type species and from other northern hemisphere material referred to this genus; none are demonstrably allied with the Palissyaceae. Toarcian specimens are considered attributable or akin to *Knezourocarpon narangbaensis*, while others probably represent new genera and are likely affiliated with the Knezourocarponaceae Pattemore fam. nov.

Palissya specimens from elsewhere in Gondwana are likewise considered doubtful attributions to the genus. Consequently, genuine *Palissya* specimens are likely restricted to the Rhaetian–Lower Jurassic of the northern hemisphere.

Knezourocarpon is restricted to the Toarcian and possibly the upper Pliensbachian of eastern Australia. Representatives of the Knezourocarponaceae likely range in age from the Toarcian to the Aptian in Eastern Gondwana. This family is unknown elsewhere. It likely has ginkgoalean or pteridospermous affinity.

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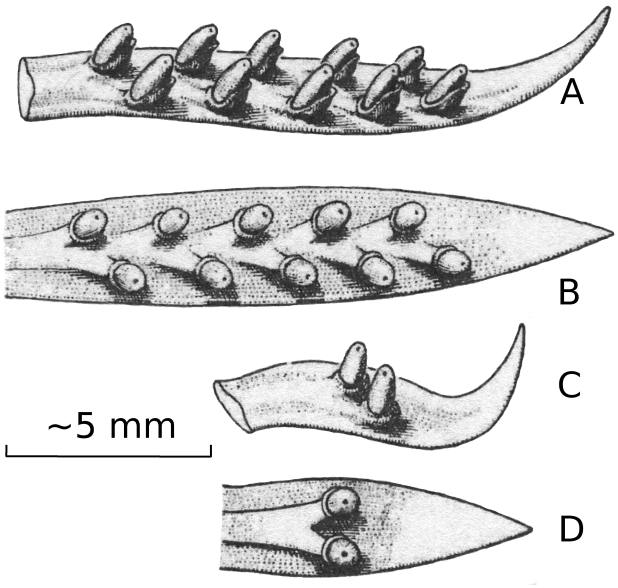

Figure 1

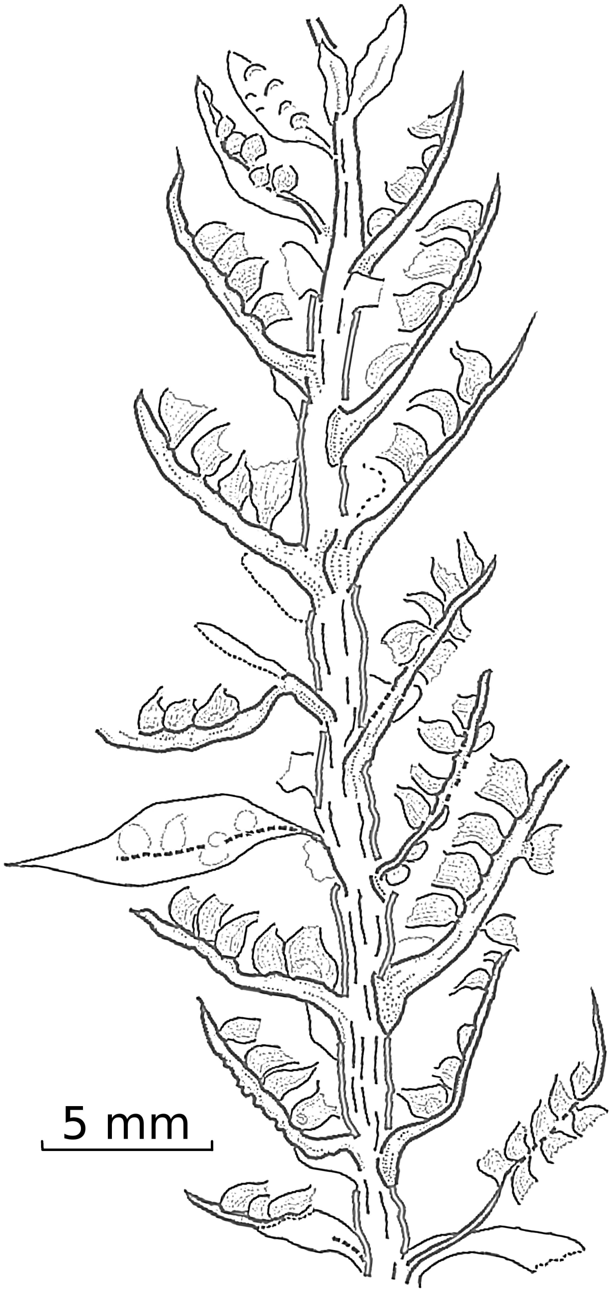

Figure 2

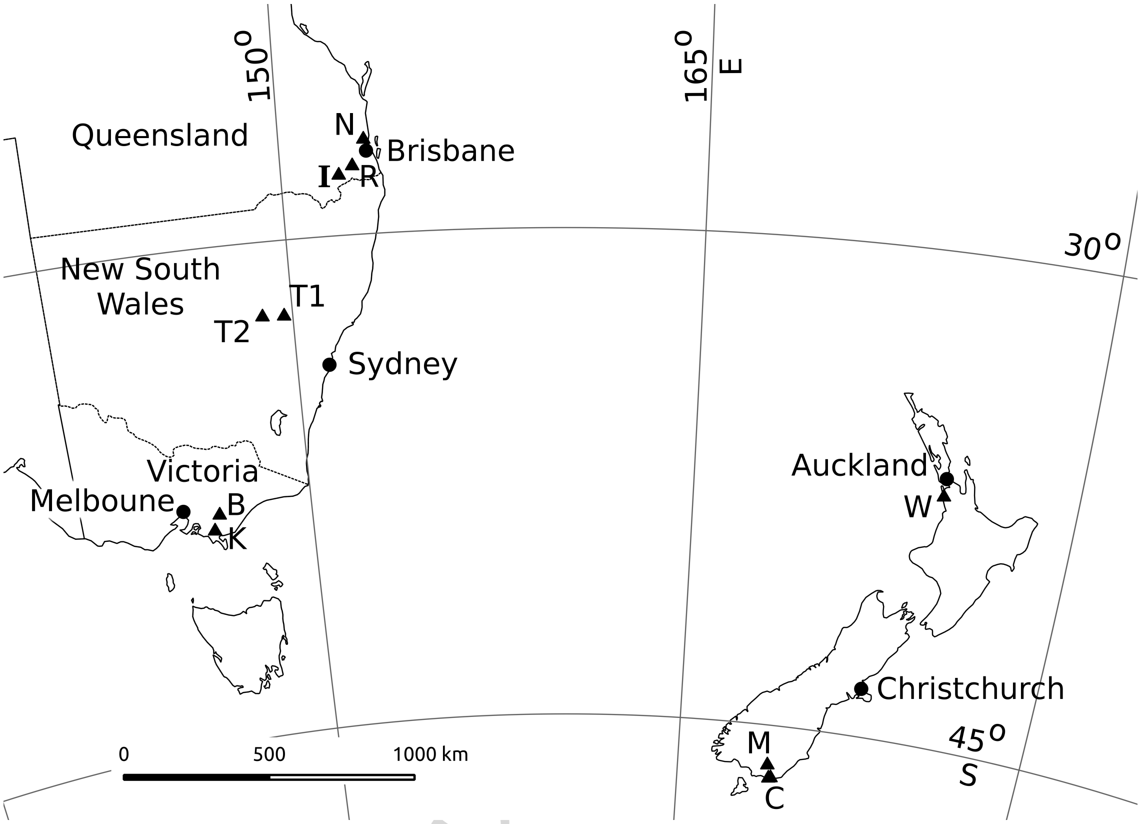
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Figure 3

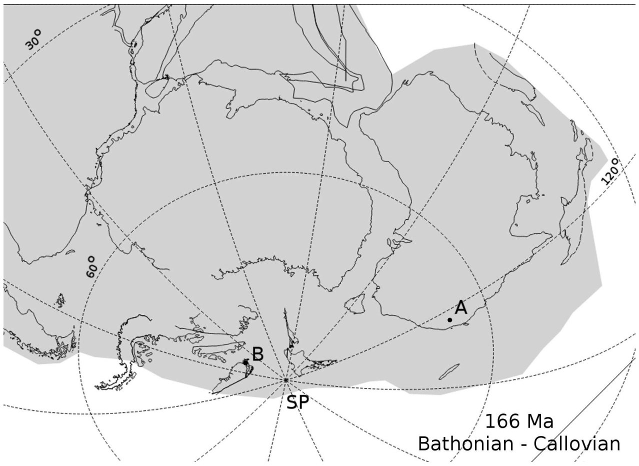

Figure 4

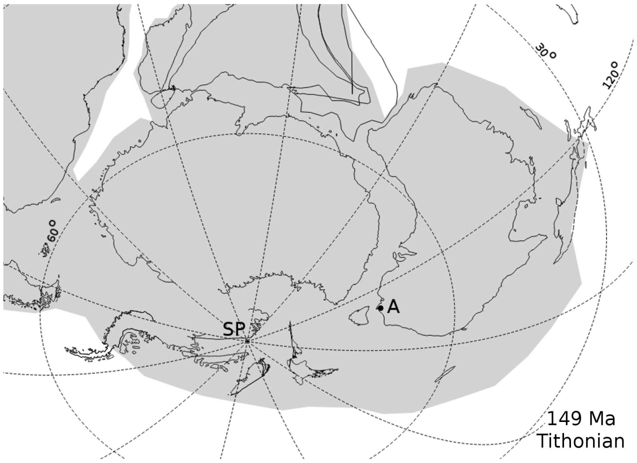

Figure 5

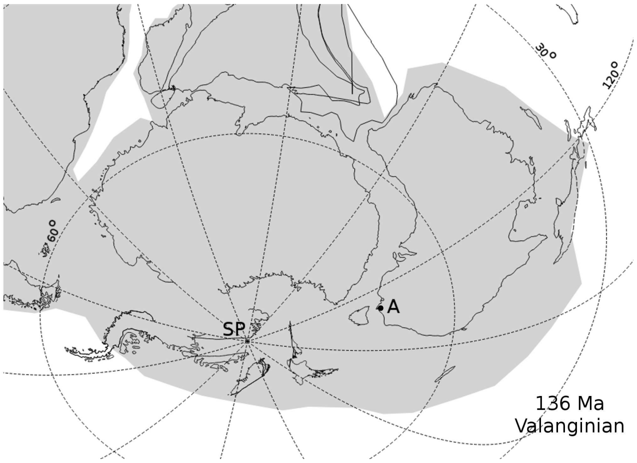

Figure 6

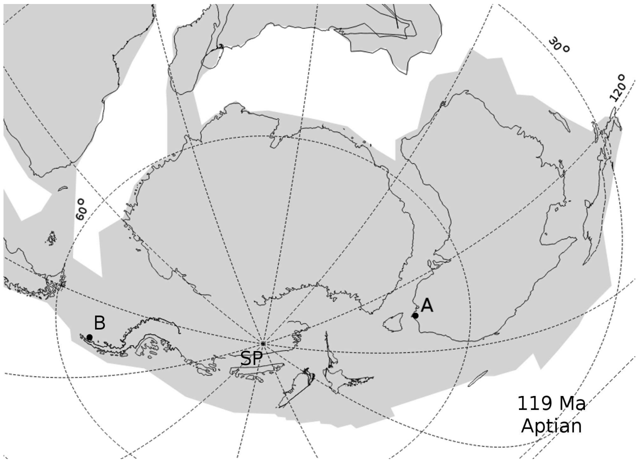

Figure 7

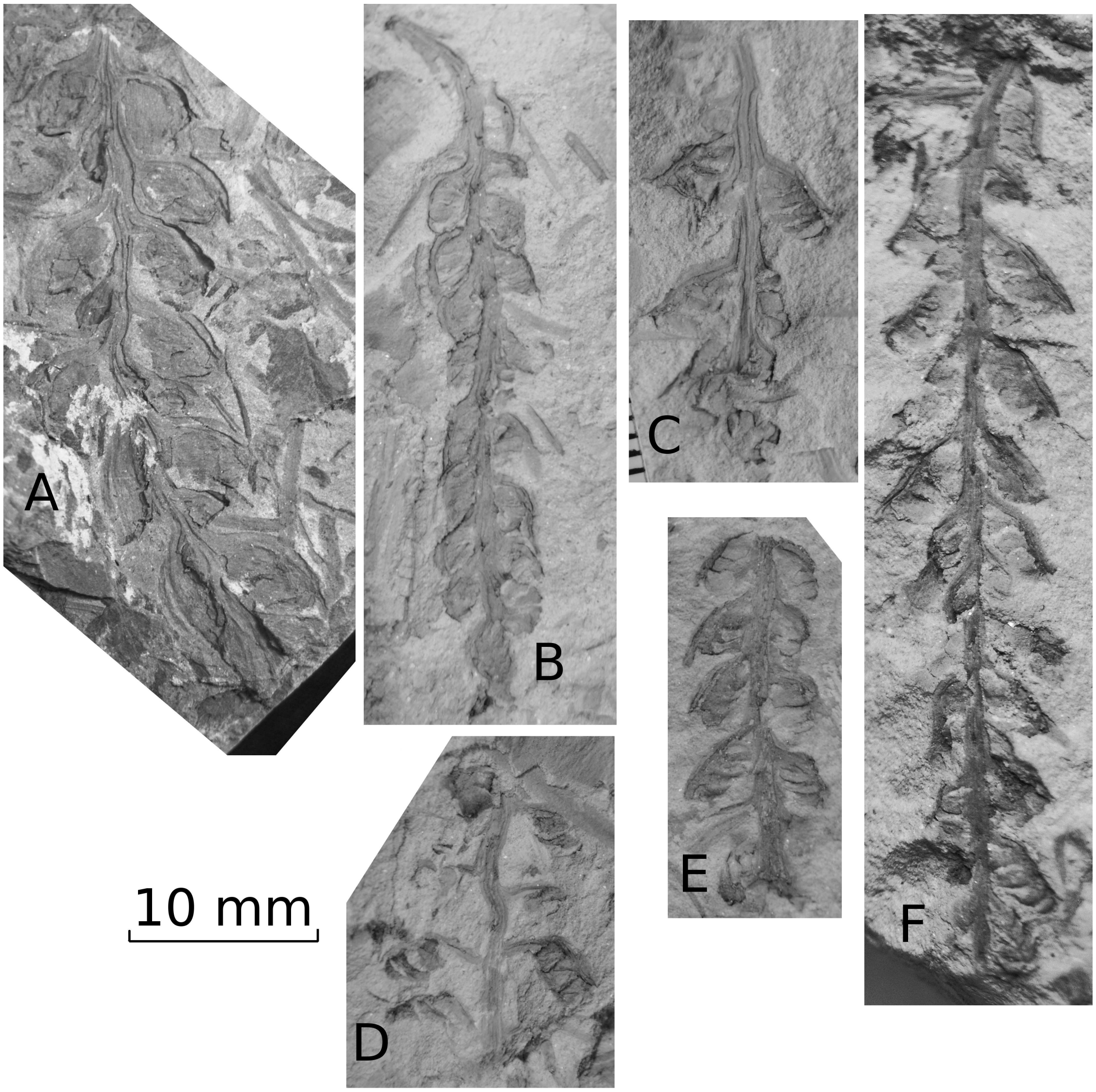

Figure 8

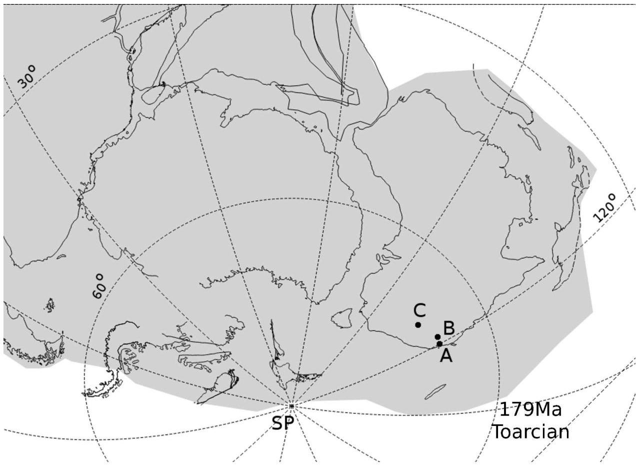

Figure 9

Figure captions

[Figure 1]

Reconstructed bracts and ovule scale complex of: **A--B**, *Palissya sphenolepis* (type species); **C--D**, *Stachyotaxus elegans*. **A--D** modified from Hirmer (1936).

[Figure 2]

Structure of *Palissya hunanensis* from the Rhaetian of Hunan Province, China; from Wang (2012).

[Figure 3]

Locality map showing reports of *Knezourocarpon* and *Palissya* in Australia and New Zealand. **N**, *K. narangbaensis* from Narangba (Toarcian, Landsborough Sandstone, Marburg Subgroup, Nambour Basin); **R**, *Palissya ovalis* from Reynold’s Creek, Kalbar and Mutdapilly (Bathonian, Walloon Coal Measures, Clarence-Moreton Basin); **I**, *K. narangbaensis* from Inverleigh Quarry (Toarcian, Gatton Sandstone, Marburg Subgroup, Clarence-Moreton Basin); **T1**, *Knezourocarpon* sp. cf. *K. narangbaensis* from the Ballimore Hill coal mine (Lower Jurassic, Ballimore Formation, Gunnedah Basin); **T2**, *Knezourocarpon* sp. cf. *K. narangbaensis* from the Talbragar River (Toarcian, Purlawaugh Formation, Gunnedah Basin); **B**, *Palissya elegans* from the Boola Boola State Forest (Valanginian, Locmany Member of the Rintoul Creek Formation, Gippsland Basin); **K**, *Palissya* sp. ‘Koonwarra’ from near Koonwarra (Aptian, Koonwarra Fossil Bed, Gippsland Basin). **W**, *Palissya bartrumii* from near Waikato Head (Upper Jurassic, Murihiku Terrane); **M**, *Palissya bartrumii* from Mokoia, near Gore (Callovian, Murihiku Terrane); **C**, *Palissya bartrumii* from Curio Bay and Slope

Point (Callovian, Murihiku Terrane). See text for published references.

[Figure 4]

Eastern Gondwana, shown in grey, at approximately the Bathonian--Callovian boundary; **SP**, South Pole. Collection sites: **A**, Bathonian, Queensland, *Palissya ovalis*; **B**, Callovian, South Island, New Zealand, *Palissya bartrumii*. Palaeogeographic reconstruction based on Seton et al. (2012).

[Figure 5]

Eastern Gondwana, shown in grey, during the Tithonian; **SP**, South Pole. Collection site: **A**, mouth of the "Huriwai Stream", near Waikato Head, North Island, New Zealand, *Palissya bartrumii*. Palaeogeographic reconstruction based on Seton et al. (2012).

[Figure 6]

Eastern Gondwana, shown in grey, during the Valanginian; **SP**, South Pole. Collection site: **A**, Boola Boola State Forest, Victoria, Australia, *Palissya elegans*. Palaeogeographic reconstruction using data from Seton et al. (2012).

[Figure 7]

Eastern Gondwana, shown in grey, during the Aptian; **SP**, South Pole. Collection sites: **A**, Koonwarra fossil bed, Victoria, Australia, *Palissya* sp. 'Koonwarra'; **B**, Snow Island, Antarctica, *Palissya antarctica*. Palaeogeographic reconstruction based on Seton et al. (2012).

[Figure 8]

A, *Knezourocarpon narangbaensis* (QMF50949), specimen previously reported as *Caytonia cucullata* by Jansson et al. (2008); **B**, *K. narangbaensis* (QMF39240); **C**, *K. narangbaensis* (QMF42599); **D**, *K. narangbaensis* (QMF39277); **E**, *K. narangbaensis* (QMF39315); **F**, *K. narangbaensis* (QMF39236) with enhanced contrast. QMF label refers to the Queensland Museum specimen number. Scale as shown applies to A–F.

[Figure 9]

Eastern Gondwana, shown in grey, during the Toarcian; **SP**, South Pole. Collection sites: **A**, Narangba Quarry, Queensland, *Knezourocarpon narangbaensis*; **B**, Inverleigh Quarry, Queensland, *K. narangbaensis*; **C**, Talbragar River area, east of Dubbo, New South Wales, *Knezourocarpon* sp. cf. *K. narangbaensis*. Palaeogeographic reconstruction based on Seton et al. (2012).

Table 1
Palissya and *Stachyotaxus*: key references.

Genus	**References**
Palissya	Braun (1843); Endlicher (1847); Nathorst (1908); Hirmer (1936); Florin (1951, 1958); Dobruskina (1994); Parris et al. (1995); Schweitzer and Kirchner (1996); Wang (2012).
Stachyotaxus	Nathorst (1886, 1908); Schenk (1887); Harris (1935, 1937); Florin (1944, 1951, 1954, 1963, 1966); Dobruskina (1994); Arndt (2002); Pott and McLoughlin (2011).

Table 2
Summary of Australasian material referred to *Palissya* as identified by Parris et al. (1995).

Epoch	Age	Designation	References	Location	Summary of assessment herein
Early Cretaceous	Aptian	*P*. sp. 'Koonwarra'	Drinnan and Chambers (1986); Parris et al. (1995).	Victoria	Unclear sporophyll arrangement; no clear relationship to the Palissyaceae but likely related to other Victorian specimens previously described as *P. elegans*.
	Valanginian	*P. elegans*	Parris et al. (1995); McLoughlin et al. (2002).	Victoria	Unclear sporophyll arrangement but possibly decussate; probably a new genus but with no clear relationship to the Palissyaceae. It may belong to Knezourocarponaceae Pattemore fam. nov.
Late Jurassic	Tithonian?	*P. bartrumii* ("Huriwai Stream" specimen)	Bartrum (1921); Edwards (1934); Parris et al. (1995).	New Zealand, North Island	One poor specimen; no clear relationship to the Palissyaceae.
Middle Jurassic	Callovian	*P. bartrumii*	Edwards (1934); Parris et al.(1995).	New Zealand, South Island	Helical sporophyll arrangement; no convincing relationship to the Palissyaceae but probably related to specimens previously described as *P. ovalis*.
	Bathonian	*P. ovalis*	McLoughlin and Drinnan (1995); Parris et al. (1995).	Queensland	Helical sporophyll arrangement; probably a new genus but with no convincing relationship to the Palissyaceae. It may belong to Knezourocarponaceae Pattemore fam. nov.
Early Jurassic	Toarcian	*P*. sp. 'Talbragar'	White (1986); Parris et al. (1995)	New South Wales	Single very poor specimen; no clear relationship to the Palissyaceae. Most likely assignable to *Knezourocarpon narangbaensis* described from the Toarcian of Queensland.

Highlights

- The genus *Palissya* is reviewed globally.
- *Palissya* is likely restricted to the Rhaetian–Lower Jurassic of the northern hemisphere.
- Material previously assigned to *Palissya* from Australasia is likely allied to the Knezourocarponaceae fam. nov.
- Toarcian material from Australia previously assigned to *Palissya* and *Caytonia* is referred to *Knezourocarpon*.