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DIVERSE FOSSIL EPACRIDS (STYPHELIOIDEAE; ERICACEAE) FROM EARLY PLEISTOCENE SEDIMENTS AT STONY CREEK BASIN, VICTORIA, AUSTRALIA

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There is currently intense interest in the radiation of the scleromorphic groups that dominate the Australian flora, but at present, only Proteaceae and Casuarinaceae have fossil records detailed enough to provide useful evidence on the timing of these radiations. This article records a diverse assemblage of fossil leaves of another major scleromorphic group, the epacrids (subfamily Styphelioideae of Ericaceae, formerly known as Epacridaceae). The fossils are from Stony Creek Basin, in the western uplands of Victoria, Australia, and are of earliest Pleistocene age (ca. 1.6 million years old). They include 19 forms sufficiently distinct as to constitute different species. This diversity is considerably greater than the extant diversity of epacrids in the region. Published taphonomic data are used to argue that the actual diversity of the source vegetation of the fossil flora may have been significantly greater and comparable to the current local species richness of the centers of diversity. Ten of the fossil species are assigned to the largest extant tribe (Styphelieae), eight are assigned to Epacrideae or Archerieae, and one is assigned to Cosmelieae. This evidence is used to argue that substantial radiation of the epacrids had occurred by the beginning of the Pleistocene.

Keywords: epacrid, Styphelioideae, evolutionary radiation, Quaternary, fossils, Australia, sclerophylly, scleromorphy.

Introduction

The timing of the radiation of the scleromorphic flora has long been one of the central questions in the history of Australian vegetation (e.g., Crisp et al. 2004). Since scleromorphs (hard-leaved, mostly slow-growing species) can be considered an extreme in a continuum of ecological strategies, it is not possible to make an absolute distinction between scleromorphs and nonscleromorphs. However, Australia's flora has long been recognized as being strongly biased toward the scleromorphic end of this continuum, with many unambiguous scleromorphs in Proteaceae, Ericaceae, Casuarinaceae, Fabaceae, Myrtaceae, and other families. A high proportion of this diversity occurs in seasonally dry areas, especially southwestern Australia. However, scleromorphy is also prominent in some distinctly wet habitats, and most researchers would consider nutrient-poor soils to have played as great a role in the evolution of scleromorphs as dry climates (e.g., Hill 1998).

Scleromorphy is ancient, at least in the families Proteaceae and Casuarinaceae, as shown by scleromorphic fossils of Late Paleocene age (Carpenter et al. 1994; Scriven and Hill 1995). Scleromorphic Fabaceae and Ericaceae subfamily Styphelioideae (Carpenter 1991; Jordan and Hill 1995) and diverse scleromorphic Proteaceae (Jordan et al. 1998) were present

by the Early Oligocene. However, apart from some species of *Banksia* s.l., none of these Paleogene Proteaceae can be assigned to any of the genera (e.g., *Grevillea/Hakea*, *Persoonia*, and any of the diverse genera in Proteoideae) that are diverse in the modern scleromorphic flora. Thus, it is plausible that many of the products of the early radiation of scleromorphs represent extinct lineages. Hill (1994, 1998) argued that although scleromorphy evolved early in Proteaceae and Casuarinaceae, physiological adaptations to dry climates first appear in the fossil record in the Miocene. This conforms well to other evidence suggesting drying of climates in southern Australia (see evidence presented by Frakes [1999, pp. 163–203]).

Therefore, although scleromorphy is an ancient syndrome in Proteaceae, Casuarinaceae, Ericaceae, Fabaceae, and perhaps Myrtaceae, it remains possible that most of the diversification of these taxa is recent. Thus, there is evidence suggesting recent and very rapid radiation of dry-climate taxa in South Africa (Klak et al. 2004). This ambiguity is expressed by Hopper and Gioia (2004), who argued that much of the massive radiation of scleromorphs in southwestern Australia probably occurred in response to the rapid climate cycles of the Pleistocene but that the scleromorphic flora also included much older components. Molecular clock-type approaches show “broomstick” evolution in several groups, suggesting relatively recent radiation (e.g., Crisp et al. 2004), although these approaches are still limited by a scarcity of calibration points.

The Ericaceae form significant components of the scleromorphic floras of southwestern and eastern Australia. Almost

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all species are in the distinctive subfamily Styphelioideae (commonly known as epacrids and formerly recognized as the family Epacridaceae). This monophyletic group (Crayn et al. 1998; Kron et al. 2002) is mainly Australian, although species also occur in the Pacific (most notably New Zealand, New Caledonia, and Hawaii) and Malesia, and one species occurs in temperate South America. Like many other Ericaceae, the Styphelioideae are generally associated with nutrient-poor, often acidic soils. Virtually all species of Styphelioideae are scleromorphic. Most have very small leaves, usually less than 1 cm² in area. The notable exceptions are a few species of *Dracophyllum* and *Richea*, with leaves more than 0.5 m long, although a few species of other genera (e.g., *Leucopogon*, *Cyathodes*, and *Cyathopsis*) can have leaves more than 5 cm long. Although these traits are not formally documented, the leaves of most species are quite hard because of the presence of lignified epidermis and fiber bundles associated with the veins (Stevens et al. 2004), and many are pungent.

The Styphelioideae contain more than 450 species in 37 genera and seven tribes (Stevens et al. 2004; Quinn et al. 2005). This species richness is unevenly distributed phylogenetically and suggests extensive radiation in tribe Styphelieae, especially in at least two clades in the paraphyletic genus *Leucopogon* (Styphelieae) (Taaffe et al. 2001) and lesser radiations (and/or greater extinctions) in Richeeae, Cosmelieae, and Epacrideae (fig. 1).

Three main centers of diversity (southwestern Australia, Tasmania, and central eastern New South Wales; fig. 2) contain more than 75% of the species and all but four (*Agiortia*, *Cyathopsis*, *Decatoca*, and *Lebetanthus*) of the genera. These regions have disparate climates but are characterized by nutrient-poor soils (often extremely so). The greatest species richness is in southwestern Australia, with ca. 190 named

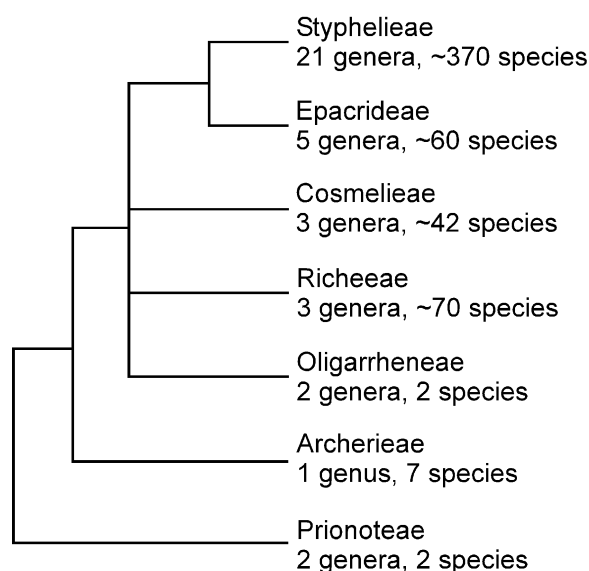


Fig. 1 Species richness and phylogeny of tribes of Styphelioideae. The phylogeny follows Crayn and Quinn (2000). Tribal classification follows Crayn et al. (1998). The species richness in each group follows Stevens et al. (2004) and Quinn et al. (2005).

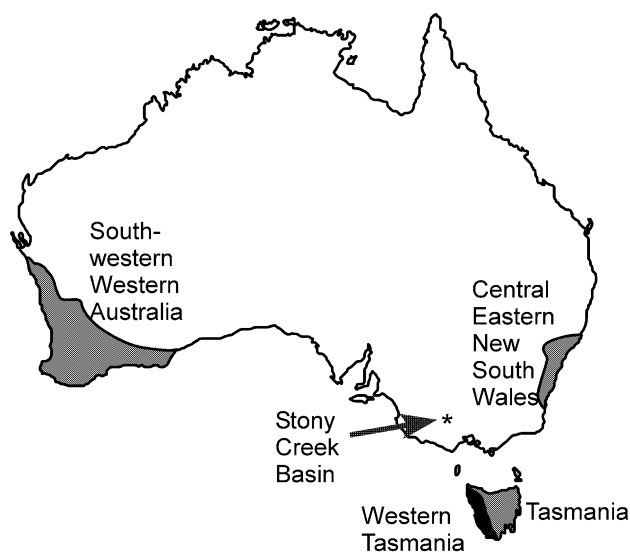


Fig. 2 Map of Australia showing the fossil site and the main centers of diversity of Styphelioideae (which contain over 75% of the species of the subfamily).

species in 17 genera (Keighery 1996, 2002; Cranfield 1998, 2002; Crayn et al. 2003, 2005) and many undescribed taxa (see <http://florabase.calm.wa.gov.au/>). The region is characterized by a Mediterranean-type climate, with warm to hot, dry summers and cool, wetter winters, and a range of soils, often formed on deep sands, laterites, or granites, although almost all are very nutrient poor (Hopper and Gioia 2004). Tasmania is the second center of diversity (92 species, 19 genera; Buchanan 2005; Quinn et al. 2005). Within Tasmania, the wet forest and montane floras of the center and west contain arguably the highest phylogenetic diversity in Styphelioideae, with six of the seven tribes represented in this small region, whereas Western Australia contains five tribes and New South Wales four (Crayn et al. 1998). Western Tasmania is characterized by cool, wet climates and peaty soils overlying quartzite and other highly silica-rich rocks (Jackson 1999). Relatively high diversity (ca. 63 species in 15 genera; Powell 1992; Cherry et al. 2001) also occurs in central eastern New South Wales (near Sydney), particularly on soils derived from Hawkesbury sandstone. This region has moderately high rainfall year-round, and the Hawkesbury sandstone soils are nutrient poor. New Zealand is a minor center of diversity with ca. 48 species, mostly in the genus *Dracophyllum* (de Lange et al. 2006).

Considering the general factors that affect the incidence of plant organs in the fossil record, Styphelioideae would appear to be good candidates for fossilization. These factors include the distance of source plants from a site of fossilization (usually a wet place), the abundance of organs on the source plants, the resistance of these organs to decay, the presence of distinctive features on these organs to allow their identification, and the availability of paleobotanical expertise. Many species of Styphelioideae occur in wet habitats. The toughness of the leaves, and perhaps the small leaf size (resulting in high numbers of leaves being available for fossilization),

should favor fossilization. Hill and Gibson (1986) showed that leaves of a number of species of Styphelioideae were well represented in the superficial sediments of the floor of a subalpine lake in Tasmania. Also, the leaves and fruit have distinctive features that should allow fossils to be readily recognized (Jordan and Hill 1995). Several major groups can be recognized, and closely related species can have quite different leaf forms. However, it can be difficult to differentiate among related genera, and assigning fossil leaves to living species is rarely possible (Jordan and Hill 1995). The endocarps of one tribe, Styphelieae, are distinctive.

In spite of their apparent potential for fossilization, the Styphelioideae have a sparse fossil record (Jordan and Hill 1995, 1996). Fossil pollen shows that the Ericaceae were present in Australia in the Late Cretaceous (Dettmann 1994). However, since this pollen is broadly consistent with a wide range of Ericaceae, there is no unambiguous evidence for the presence of the Styphelioideae before the Early Oligocene (Jordan and Hill 1996). The Oligocene fossils are small, scleromorphic leaves of tribe Richeeae and either tribe Archerieae or tribe Epacrideae (Jordan and Hill 1995, 1996). However, these fossils say little about radiation within Styphelioideae because they represent only a few species, none of which is from derived taxa that would indicate high levels of differentiation within the subfamily (Jordan and Hill 1995, 1996). Much younger (Early Pleistocene) fossils show the presence of a slightly wider range of species in Tasmania but do not demonstrate the presence of high diversity (Jordan and Hill 1996).

The timing and location of diversification of the Styphelioideae therefore remain unclear. The widespread distribution of the family within Australasia with a number of wide disjunctions, combined with high levels of endemism (ca. 98% species endemism in Western Australia [Keighery 1996] and 64% species endemism in Tasmania [Buchanan 2005]) could be used to argue for antiquity of this radiation. However, this argument assumes some uniformity of rates of evolution. It also assumes a low frequency of long-distance dispersals, whereas some distributions of Styphelioideae suggest that this may not be the case. Thus, *Leucopogon parviflorus* (Andrews) Lindley and *Sprengelia incarnata* Smith occur naturally in both Australia and New Zealand, and species of *Leptecophylla* are found on several oceanic islands, including Hawaii (Weiller 1999), distributions that are extremely difficult to explain except as long-distance dispersal events (Jordan 2001). *Cyathodes dealbata* R. Br. (Tasmania) and *Cyathodes pumila* Hook. f. (New Zealand) may be conspecific (Quinn et al. 2005) and therefore fall into the same category. *Leptecophylla* (*Cyathodes*) *juniperina* (Forst. & G. Forst.) C. M. Weiller subsp. *juniperina* and *Pentachondra pumila* (Forst. & G. Forst.) R. Br. also occur in both Australia and New Zealand, although molecular analyses reveal considerable differences between the Australian and New Zealand populations of each species (Quinn et al. 2005; C. J. Quinn, M. M. Heslewood, and D. M. Crayn, unpublished data).

This article uses fossil evidence from well-preserved macrofossil material from Stony Creek Basin, Victoria, Australia, to investigate diversity of this group in the earliest Pleistocene and discusses the question of whether the diversity of Styphelioideae is essentially a product of the climatic cycles of the

Pleistocene. The site contains a very diverse array of fossil plant and insect parts, including conifers, ferns, and a wide range of angiosperms. This article describes only the epacrids from this assemblage.

Material and Methods

The Fossil Site

The fossils described here were extracted from Stony Creek Basin, in the western uplands of Victoria, Australia (lat. 144.13°E, long. 37.35°S, 550 m above sea level; fig. 2). The basin is a small paleolake deposit of probable maar origin. The total drainage catchment of the basin at present is ca. 0.5 km² and may have been slightly smaller at the time of deposition of the fossiliferous sediments. The lake sediments comprise ca. 40 m of black, organic-rich, silty clays.

The age of the basin is described in detail by Sniderman et al. (2007). In brief, zircons from a core extracted by hollow-auger drilling in 2000 give ages of 1.93 ± 0.18 million years (Ma) for a thin volcanogenic layer at 29-m depth and 1.99 ± 0.43 Ma for fine sands at the base of the core. These can be used to indicate that the sediments are no older than the latest Pliocene. The sediments in the upper 25 m of the core are of reversed magnetic polarity and therefore predate the Brunhes/Matuyama polarity transition at 0.78 Ma, while the sediments below 25 m are of normal polarity (Sniderman et al. 2007). Considering the zircon dates, this transition can be attributed to end of the Olduvai subchron (1.781 Ma; Lisiecki and Raymo 2005). Correlation of the pollen record with the astronomical timescale based on an age model derived from counting annual sediment laminae indicates that deposition of the pollen sequence occurred between 1.83 and 1.55 Ma (Sniderman et al. 2007), which straddles the Pliocene-Pleistocene boundary at 1.81 Ma (Gradstein et al. 2004).

The fossils described here were extracted from two independent samplings from the site. Some fossils were extracted from two portions of the core described by Sniderman et al. (2007). These parts were between the 2.6- and 4.35-m depths and between the 19.6- and 22.1-m depths, which correspond to ca. 1.6 and 1.7 Ma, respectively. However, most fossils were extracted from a sampling from the wall of a large pit in the basin dug with an excavator in February 2002, ca. 15 m from the core hole. Material was collected from an exposed, undamaged wall of this pit from a depth of 4–6 m. Palynological analyses suggest that the age of this material is equivalent to that of the 2.6–4.35-m core samples (i.e., ca. 1.6 Ma).

Fossil Extraction and Analysis

From the pit, fossils were extracted from blocks of sediment of ca. 500 cm³ sampled at 10-cm intervals. From the core, fossils were extracted from samples of ca. 500 cm³, representing 20-cm intervals down the core. Fossils were extracted by soaking the sediment samples in a concentrated (ca. 5%) aqueous solution of tetrasodium pyrophosphate until the sediment disaggregated (usually taking ca. 3 wk), followed by sieving through nested 850- and 160- μ m sieves. The 850- μ m sievings were sorted under a binocular microscope

at $\times 8$ – $\times 12$ magnification, and all identifiable plant fragments were removed manually. No additional identifiable plant fragments were found in scans of subsamples of the 160- μm sievings.

The macrofossils were found in two states of preservation. Some showed plastic organic preservation, with excellent preservation of cuticles but without recognizable internal anatomy. Other fragments were carbonized. These specimens were brittle but often showed good to exceptional preservation of microscopic surface features and internal anatomy. In particular, the outlines of the epidermal cells were often apparent on the leaf surface or were exposed by erosion of the leaf surface, and cells of the mesophyll and vascular tissue could sometimes be observed after the fossils were broken. It is not clear whether the carbonization was the result of burning or of diagenetic processes in the sediments. However, a few specimens showed intermediate states of preservation, with carbonized inner parts but organically preserved cuticles, implying that at least some of the carbonized specimens had not been burnt. The fossils were often small in comparison to comparable organs of related living species. This could be in part due to diagenetic shrinkage. However, there was little or no indication of distortion of cell shapes by any such process. Also, there was no indication of differences in size between fully carbonized specimens and specimens of the same species showing plastic organic preservation. It therefore appears unlikely that there was a large degree of shrinkage.

Whole fossils were mounted on aluminum stubs, sputter-coated with gold or platinum to a thickness of ca. 20 nm, and observed under high vacuum with either an Electroscan environmental scanning electron microscope (ESEM) or an FEI Quanta 200 ESEM operating at 15 kV. When possible, individual specimens were inverted after observation or broken and set on edge, recoated, and then observed again under the same conditions.

Fossil Identification

Jordan and Hill (1995) described two genera for fossil leaves of Styphelioideae with preservation of cuticular anatomy. These genera were *Richeaphyllum*, used for species of Richeeae, and *Epacriphyllum*, used for other Styphelioideae except Prionoteae and Cosmelieae. Jordan and Hill (1995) also described some key features useful in identifying fossil leaves of Styphelioideae (see fig. 3).

Epacriphyllum is characterized by (1) hypostomatic leaves that possess entire margins or margins with fine serrations that are not associated with veins (fig. 3A–3F); (2) more or less rectangular epidermal cells aligned parallel to the main veins, with sinuous to strongly sinuous anticlinal walls (fig. 3G); (3) stomata aligned parallel to the main veins (fig. 3G); and (4) venation that is parallel or subparallel (except in Prionoteae and some species with very narrow leaves and only one main vein). In addition, many members of Styphelioideae have (5) very short, unicellular conical trichomes that cover the stomatiferous parts of the leaf (fig. 3H, 3I).

Richeaphyllum has features 1–4 (although a few species have a few stomata on the adaxial surface) and two additional features: (6) sessile leaves tapering evenly from sheathing leaf bases and (7) paracytic stomata. Leaves of Cosmelieae (fig.

3C) are similar to those of Richeeae except that they have cyclocytic stomata and are amphistomatic.

The good preservation of many of the Stony Creek Basin fossils allows the observation of significant anatomic features not considered by Jordan and Hill (1995). The location of vascular bundles is perhaps the most significant of these taxonomically. In species of Archerieae, Epacrideae, Oligarrheneae, and Cosmelieae, the vascular bundles are separated from the abaxial epidermal cells by mesophyll cells (Watson 1967; Quinn et al. 2005). In many Richeeae, the vascular bundles are connected to both adaxial and abaxial epidermides by multiple layers of fibers. In most Styphelioideae, the fiber bundle abaxial to each vascular bundle is attached directly to the abaxial epidermis, but in others, the fiber bundles are separated from the abaxial epidermis by a single layer of small lightly lignified cells, by a continuous or discontinuous layer of small unlignified cells, or, in two genera, by one or more layers of mesophyll tissue (Watson 1967; Quinn et al. 2005; C. J. Quinn, personal communication). In addition, the mesophyll of Australian *Archeria* species is detached from the abaxial epidermis. Prionoteae have more typical dicot leaves with secondary veins leading to teeth.

Systematics

Family—Ericaceae

Subfamily—Styphelioideae

Tribe—Epacrideae or Archerieae

Species—*Epacriphyllum* sp. 1 (Fig. 4)

Specimens examined. SCB190_o_epac1, SCB170_o_epac12.

Description. Leaves hypostomatic, broadly cordate, ca. 0.7 mm long, 1 mm wide, slightly concave above, apparently glabrous, margins thick, entire, apex acute but not mucronate. Veins palmate with occasional secondary branches diverging at a very low angle from the main veins, not raised above the lamina. Petiole ca. 0.1 mm long, 0.2 mm wide, flexed toward the abaxial surface by ca. 90°. Epidermal cells rectangular, with sinuous walls, 20–25 μm long, 12–20 μm wide, those of the midrib region aligned with the midrib, those of the upper and mid-lamina diverging at an angle of ca. 30°, those toward the base diverging at higher angles, those in the basal lobes parallel to the leaf margin. Stomata aligned more or less parallel to the epidermal cells. Outline of guard cell pairs circular, 18–21 μm long.

Comments. These tiny leaves are consistent with Epacrideae or Archerieae, with more or less rectangular, sinuous epidermal cells; stomata aligned parallel to these cells; and leaf form similar to that of many Epacrideae (e.g., *Epacris microphylla*; fig. 3E). The leaves are, however, unusual for Styphelioideae in that the epidermal cells and stomata are not parallel to the midrib. However, the arrangement of stomata and epidermal cells of *E. microphylla* is similar to that of the fossils. *Epacris microphylla* differs from the fossils in being narrower and having a pungent apex. Several species of *Epacris* (e.g., *Epacris navicularis* Jarman, *Epacris petrophila* Hook. f., and, occasionally, *E. microphylla*) have leaves of similar size, at least in some populations.

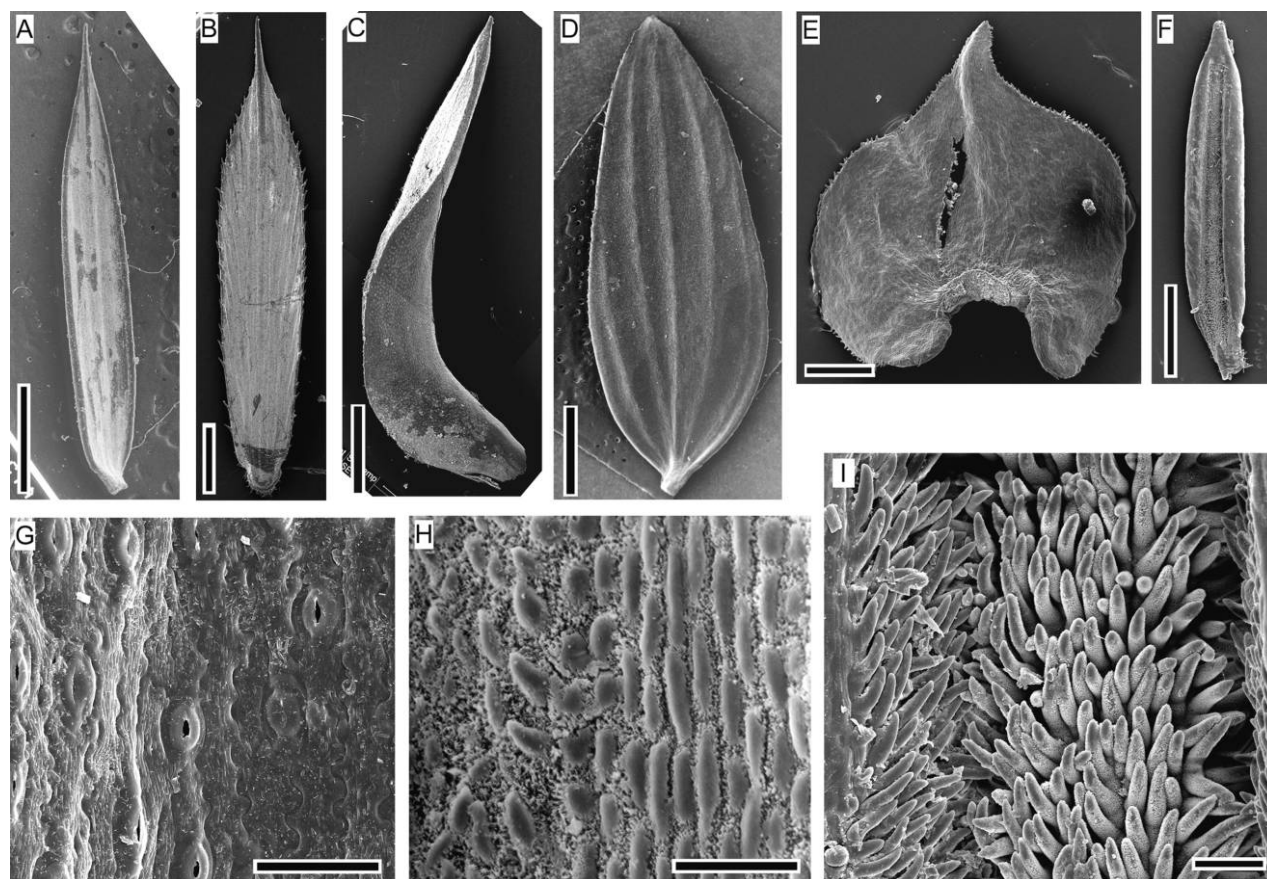


Fig. 3 Scanning electron micrographs of extant species of Styphelioideae. A, Abaxial leaf surface of *Leptecophylla juniperina* (bar = 2 mm). B, Lateral view of a leaf of *Astroloma humifusum* (Benth.) R. Br. (bar = 1 mm). C, Abaxial leaf surface of *Sprengelia incarnata* (bar = 2 mm). D, Abaxial leaf surface of *Trochocarpa cunninghamii* (DC) W. M. Curtis (bar = 2 mm). E, Abaxial leaf surface of *Epacris microphylla* R. Br. (bar = 0.5 mm). F, Abaxial leaf surface of *Androstoma verticillata* (Hook. f.) C. J. Quinn (bar = 0.5 mm). G, Abaxial leaf surface of *Epacris impressa* Labill. showing stomata and epidermal cells aligned with each other and the outlines of the sinuous epidermal cell walls (bar = 50 μ m). H, Abaxial leaf surface of *L. juniperina* showing the short, conical trichomes covering the stomatal regions (left) and elongated cells over the vein (right) (bar = 50 μ m). I, Abaxial leaf surface of *A. verticillata* showing elongated conical trichomes in the groove between a recurved margin and the midrib (bar = 50 μ m).

Species—*Epacriphyllum* sp. 2 (Fig. 5)

Specimens examined. SCB170_o_epac9.

Description. Leaves hypostomatic, linear, narrow elliptical in cross section, at least 4.5 mm long (apparently at least 8 mm long), ca. 0.75 mm wide, with a short, broad petiole (0.3 mm wide, ca. 0.4 mm long) reflexed at an angle of almost 90°. Epidermis one cell thick, cells linear, ca. 15 μ m wide, up to 45–60 μ m long, ca. 12 μ m tall, with acute ends. Stomata arranged more or less uniformly on each side of the midrib, aligned parallel to the midrib, outline of pair of guard cells elliptical, 20–25 μ m long, 13–17 μ m wide. Vascular bundles 70–100 μ m wide, placed approximately midway between the adaxial and abaxial surfaces. Three vascular bundles of similar size present ca. 1.5 mm above the leaf base. Palisade mesophyll one layer thick, cells ca. 40 μ m tall, 15–20 μ m wide, spongy mesophyll well developed, occupying approximately two-thirds of the thickness of the leaf, attached to the lower epidermis.

Comments. This fossil is consistent in all features with Epacrideae or Archerieae. Although these leaves are very similar in size and shape to those of *Epacriphyllum* sp. 11 (see below), they differ greatly in anatomy. The sinuous epidermal cells are obvious in surface view and less elongate than in *Epacriphyllum* sp. 11, and the cross-sectional anatomy is quite distinct, with the epidermis only one cell thick and the vascular bundles placed midleaf (rather than adjacent to the abaxial epidermis).

Species—*Epacriphyllum* sp. 3 (Fig. 6)

Specimens examined. SCB1985_epac2; SCB90_o_epac3.

Description. Leaves hypostomatic, linear, distinctly thick (elliptical) in cross section, 0.5–0.7 mm wide, 4–5 mm long. Petiole 0.2–0.3 mm wide, ca. 0.4 mm long, straight. Apex obtuse. Abaxial epidermal cells 15–17 μ m wide, 30–35 μ m long, sinuous walled, square ended. Stomata arranged more or less uniformly in one band on each side of the midrib,

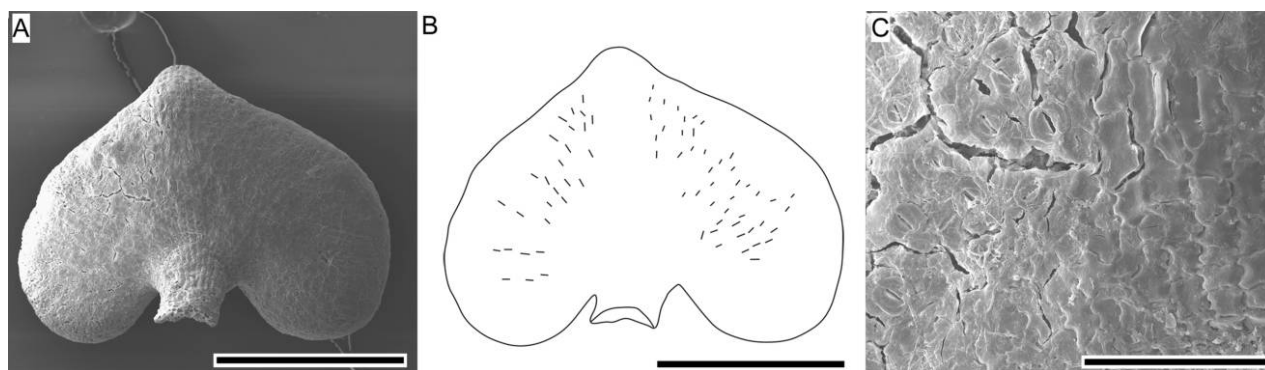


Fig. 4 Scanning electron micrographs and one line drawing of fossil leaves of *Epacriphyllum* sp. 1 (SCB190_o_epac1) from Stony Creek Basin. A, Abaxial leaf surface (bar = 500 μm). B, Line drawing of abaxial leaf surface showing position and alignment of stomata (bar = 500 μm). C, Detail of abaxial leaf surface showing stomata and shape of epidermal cells (bar = 100 μm).

guard cells aligned parallel to the midrib, outline of pair of guard cells circular or wider than long, 15–17 μm long, 16–18 μm wide. Adaxial epidermal cells similar to abaxial epidermal cells.

Comments. This species is similar to *Epacriphyllum* sp. 2 but differs in the size and shape of the petiole; the petiole in this species is much narrower and more elongated and is not bent. Furthermore, the epidermal cells differ in being square ended and shorter than those in *Epacriphyllum* sp. 2. The stomata are not elongated as those in *Epacriphyllum* sp. 2.

Species—*Epacriphyllum* sp. 4 (Fig. 7)

Specimens examined. SCB170_epacris1.

Description. Leaves hypostomatic, broadly ovate/ovate-triangular, widest immediately above the base, ca. 4 mm long, 2.5 mm wide, thick (ca. 400 μm), slightly concave above, apparently glabrous, margins thick, entire, apex acute, mucronate (presumably pungent). Petiole ca. 0.4 mm long, 0.5 mm wide, flexed toward the abaxial surface by ca. 90°. Epidermal cells rectangular, with sinuous walls, ca. 25–30 μm long, ca. 15 μm wide. Stomata aligned more or less parallel to the

epidermal cells. Outline of guard cell pairs circular, 23–25 μm long, ca. 10 μm wide. Palisade mesophyll cells in two layers, ca. 60 μm long, ca. 10 μm wide. Vascular bundles near the abaxial leaf surface but separated by a single layer of parenchyma cells.

Comments. This species is represented by one specimen, which is clearly distinct from the other species described here. It is much larger than *Epacriphyllum* sp. 1, and it has a mucronate/pungent apex and larger stomata. It also has much larger stomata than *Epacriphyllum* sp. 5 (ca. 25 vs. ca. 13 μm long) and narrower palisade mesophyll cells (ca. 10 vs. ca. 18 μm wide). This species is generally consistent with Epacrideae, but the vascular bundles close to the abaxial mesophyll are more typical of Styphelieae.

Species—*Epacriphyllum* sp. 5 (Fig. 8)

Specimens examined. SCB170_o_epac4, SCB_o_epac15, SCB180_o_epac3, SCB180_epac20, SCB190_o_epacris1, SCB190_epac2, SCB200_o_epac1, SCB1985_epac.

Description. Leaves hypostomatic, ovate-elliptical, 2–2.5 mm long, 1–1.5 mm wide, flat to slightly concave above, apparently glabrous, margins thick, entire, apex acute, not mucronate.

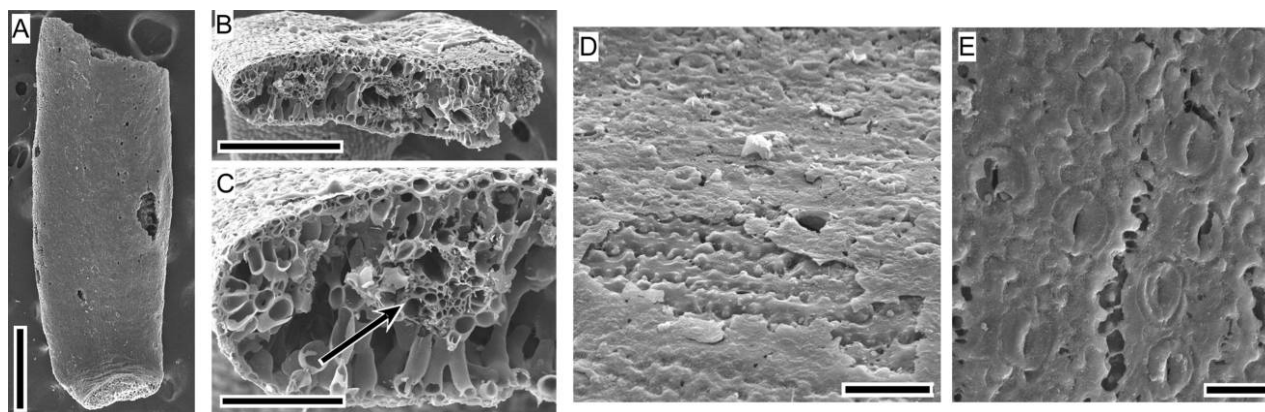


Fig. 5 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 2 (SCB170_o_epac9) from Stony Creek Basin. A, Abaxial surface (bar = 500 μm). B, Cross section (bar = 300 μm). C, Cross section (bar = 100 μm) showing vascular bundle placed approximately midway between adaxial and abaxial surfaces (arrow). D, Abaxial leaf surface showing stomata and elongate epidermal cells with sinuous walls (bar = 50 μm). E, Abaxial leaf surface showing stomata and sinuous cell walls (bar = 20 μm).

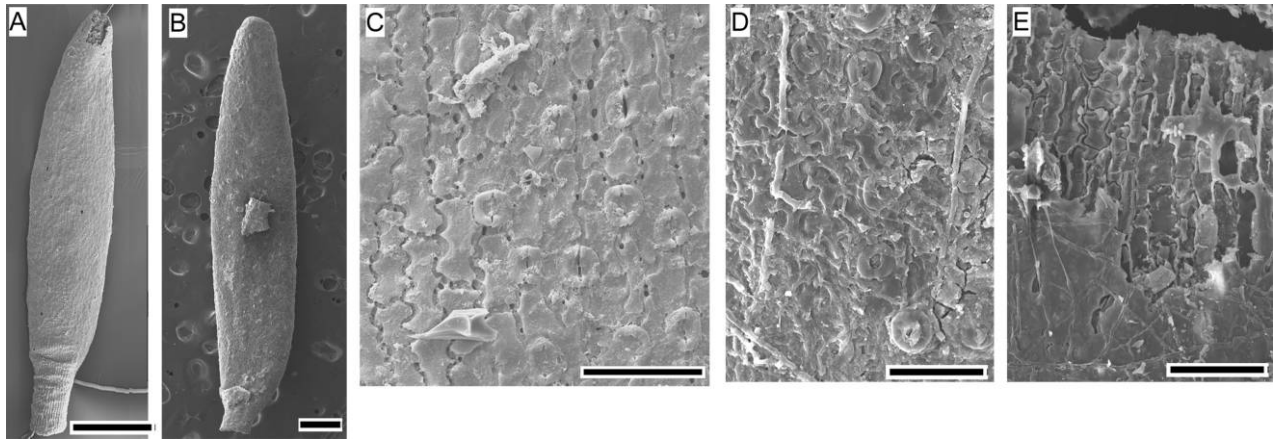


Fig. 6 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 3 from Stony Creek Basin. A, Abaxial leaf surface of SCB90_o_epac3 (bar = 500 μ m). B, Abaxial leaf surface of SCB1985_epac2 (bar = 500 μ m). C, Abaxial leaf surface of SCB90_o_epac3 showing stomata and relatively short epidermal cells with sinuous walls (bar = 50 μ m). D, Abaxial leaf surface of SCB1985_epac2 showing stomata and epidermal cells (bar = 50 μ m). E, Adaxial leaf surface of SCB1985_epac2 showing elongate epidermal cells with sinuous walls (bar = 100 μ m).

Venation palmate/subparallel with approximately seven veins. Petiole ca. 0.2–0.3 mm long, ca. 0.3 mm wide, bent at an angle of ca. 45° toward the abaxial surface. Abaxial epidermal cells sinuous walled, 35–45 μ m long, ca. 18 μ m wide. Stomata aligned more or less parallel to the epidermal cells. Outline of guard cell pairs circular, 15–18 μ m long. Adaxial epidermal cells 25–35 μ m long, 10–13 μ m wide, ca. 10 μ m thick. Palisade mesophyll cells in two layers, ca. 50 μ m long, ca. 18 μ m wide. Vascular bundles placed just less than half-way between the abaxial and adaxial leaf surfaces.

Comments. This is a reasonably common species and is entirely consistent in all features with a number of species of *Epacris*, such as *Epacris heteronema* Labill. Differences from *Epacriphyllum* sp. 4 are noted in the comments on that species. It is much larger than and different in shape from *Epacriphyllum* sp. 1. This species is similar to some previously published fossils of Styphelioideae. The Early Oligocene species from Tasmania *Epacriphyllum macphailii*

G. J. Jord. & R. S. Hill has similar leaf shape and similar-sized stomata but larger leaves (Jordan and Hill 1995). It is also similar to Early Pleistocene species from Tasmania (Jordan and Hill 1996).

Species—*Epacriphyllum* sp. 6 (Fig. 9)

Specimens examined. SCB180_o_epac4, SCB200_o_tiny_epac.

Description. Leaves hypostomatic, ovate-lanceolate, tapering more or less uniformly from approximately one-quarter of the way up the leaf, 2–4 mm long, ca. 0.8 mm wide, slightly concave above, apparently glabrous, margins thick, entire, apex acute, not mucronate. Leaf subsessile, petiole flat, ca. 0.1 mm long, 0.2–0.3 mm wide. Abaxial epidermal cells elongate. Stomata aligned more or less parallel to the midrib. Outline of guard cell pairs elliptical, 9–11 μ m long, 5–6 μ m wide.

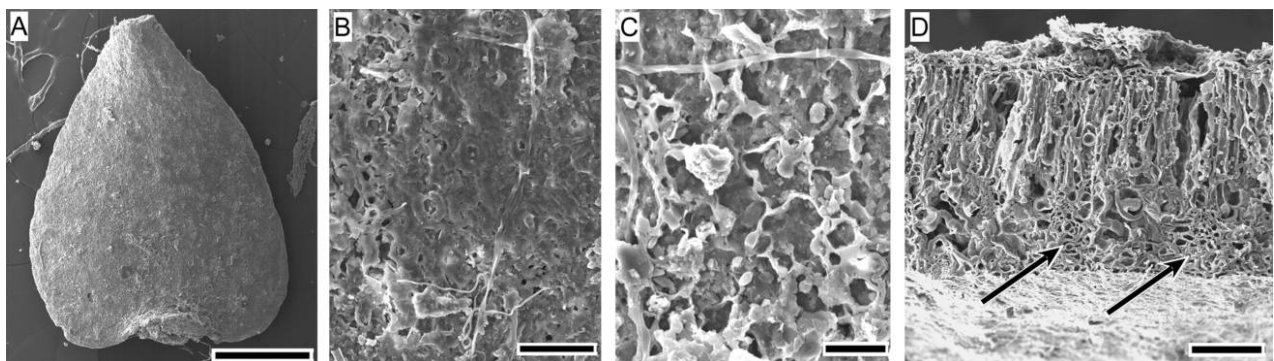


Fig. 7 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 4 (SCB170_epacris1) from Stony Creek Basin. A, Abaxial leaf surface (bar = 1 mm). B, Detail of abaxial leaf surface showing stomata and shape of epidermal cells (bar = 50 μ m). C, Detail of eroded abaxial leaf surface showing the sinuous cell walls of the epidermal cells of veinal region (bar = 20 μ m). D, Cross section of lamina. Note that there has been artifactual thickening of the cell walls of some tissues.

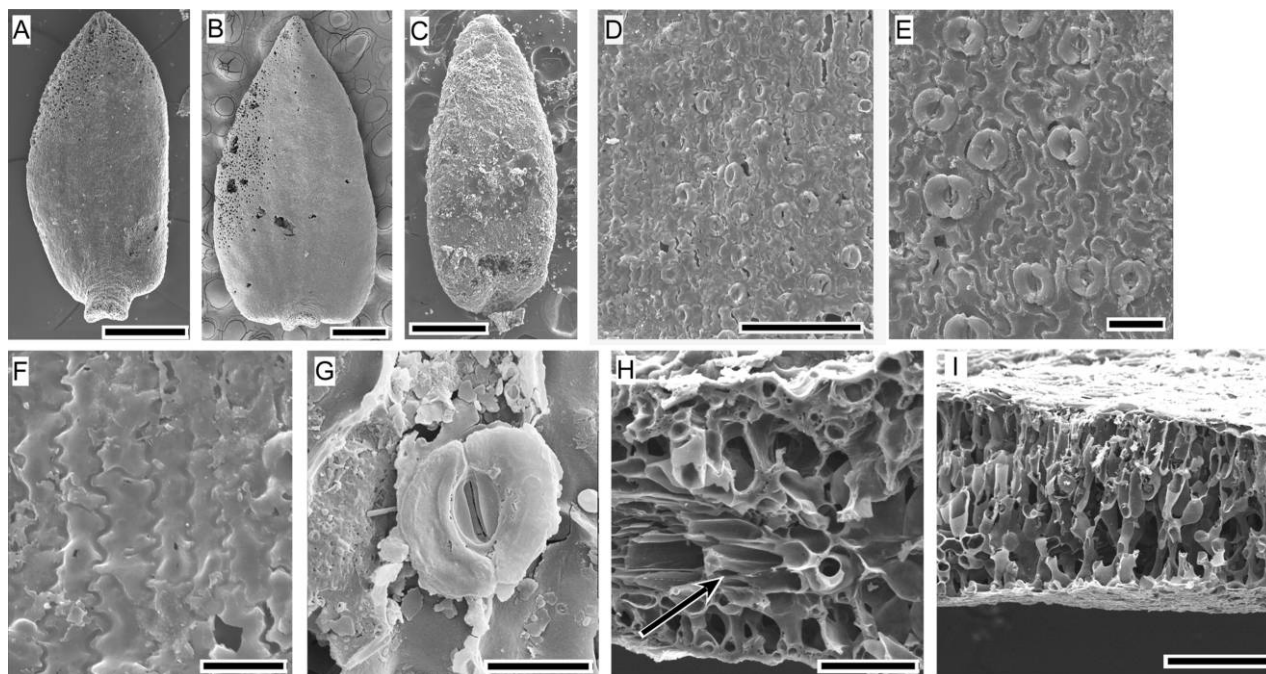


Fig. 8 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 5 from Stony Creek Basin. A, Abaxial leaf surface of SCB190_epac2 (bar = 500 μ m). B, Abaxial leaf surface of SCB180_o_epac3 (bar = 500 μ m). C, Adaxial leaf surface of SCB1985_epac (bar = 500 μ m). D, Partially eroded abaxial leaf surface of SCB190_epac2 showing stomata and epidermal cells (bar = 100). E, Partially eroded abaxial leaf surface of SCB1985_epac showing stomata and short epidermal cells with sinuous walls (bar = 20 μ m). F, Adaxial leaf surface of SCB190_epac2 showing short epidermal cells with sinuous walls (bar = 20 μ m). G, Eroded adaxial leaf surface of SCB190_epac2 showing a stoma (bar = 10 μ m). H, Cross section of SCB190_epac2 showing a vascular bundle (arrow) with mesophyll tissue above and below it. Note also the small epidermal cells (bar = 50 μ m). I, Cross section of SCB190_epac2 showing mesophyll tissue (bar = 100).

Comments. This species is represented by only two specimens, which differ considerably in size and somewhat in shape. Therefore, they could have been derived from different species. They are consistent in leaf shape with several species, including *Epacris impressa*. They are smaller and have much smaller and more elongated stomata (ca. 10×5 vs. ca. 22×20 μ m) than *Epacriphyllum* sp. 7 (below), which

has a somewhat similar shape. It also has subsessile leaves compared to the petiolate leaf of *Epacriphyllum* sp. 7.

Species—*Epacriphyllum* sp. 7 (Fig. 10)

Specimens examined. SCB60_o_epac1.

Description. Leaves hypostomatic, lamina slightly convex above, ovate-lanceolate, tapering more or less uniformly from

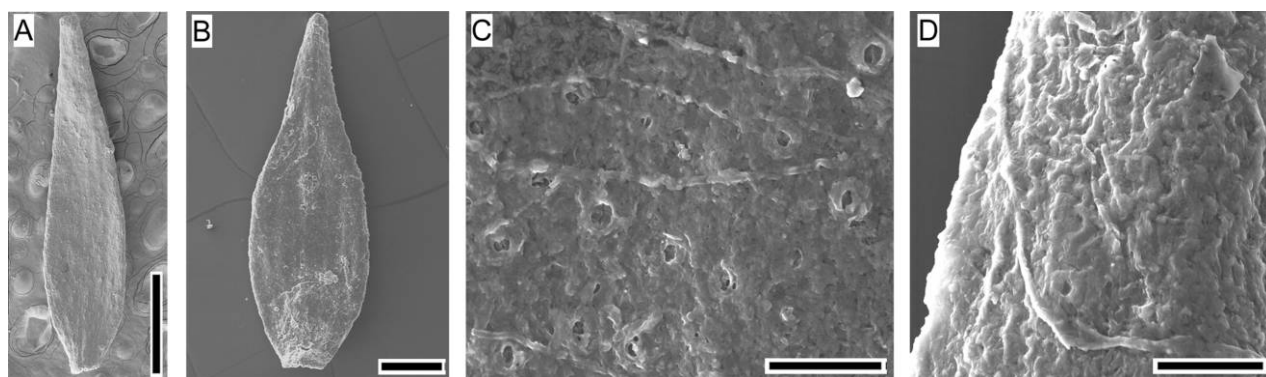


Fig. 9 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 6 from Stony Creek Basin. A, Abaxial leaf surface of SCB180_o_epac4 (bar = 1 mm). B, Abaxial leaf surface of SCB200_o_tiny_epac (bar = 0.5 mm). C, Abaxial leaf surface of SCB200_o_tiny_epac showing stomata (bar = 50 μ m). D, Abaxial leaf surface of SCB200_o_tiny_epac showing collapsed surface indicating the presence of sinuous epidermal cell walls (bar = 50 μ m).

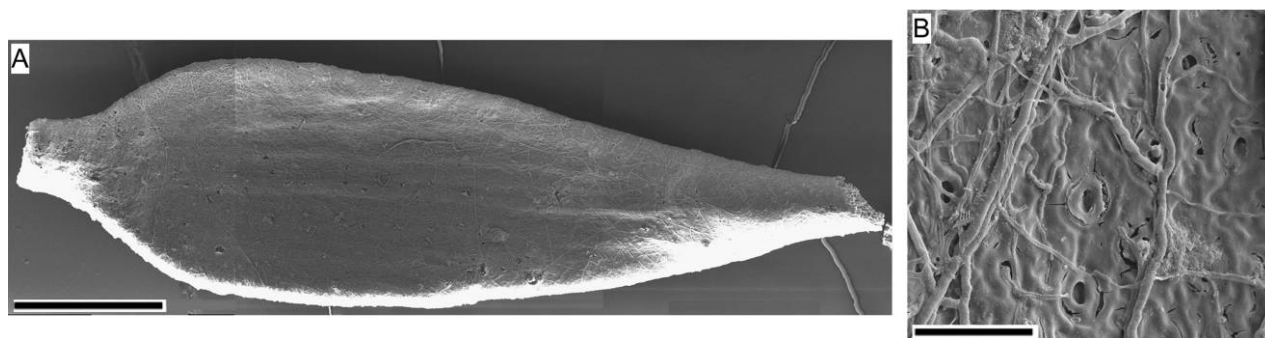


Fig. 10 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 7 (SCB60_o_epac1) from Stony Creek Basin. A, Abaxial leaf surface (bar = 1 mm). B, Abaxial leaf surface showing stomata aligned with the midrib and indications of the presence of sinuous cell walls (bar = 50 μ m).

a point approximately one-quarter of the way up the leaf, ca. 6–7 mm long, ca. 1.5 mm wide, apparently glabrous, margins thick, entire, apex acute. Petiole straight, 0.5 mm long, 0.6 mm wide. Abaxial epidermal cells elongate, with sinuous walls. Stomata aligned more or less parallel to the midrib. Outline of guard cell pairs almost circular, 20–25 μ m long, ca. 20 μ m wide.

Comments. This species is represented by two specimens, which differ considerably in size. It is consistent in leaf shape with several species, including *Epacris impressa*. Comparisons with the only similar fossil species at Stony Creek Basin, *Epacriphyllum* sp. 6, are given above. It also shows some similarity with the Early Oligocene *Epacriphyllum mesibovii* G. J. Jord. & R. S. Hill, although the latter species is widest toward midleaf (Jordan and Hill 1995).

Species—*Epacriphyllum* sp. 8 (Fig. 11)

Specimens examined. SCB200_o_micro2.

Description. Leaves hypostomatic, ovate, widest just below midleaf, ca. 2.3 mm long, ca. 1.1 mm wide, slightly convex above, apparently glabrous, margins thick, entire, apex slightly acuminate. Petiole 0.4 mm long, 0.3 mm wide, reflexed at an angle of ca. 90°. Venation obscure. Abaxial epidermal cells short, 45–70 μ m long, 15–25 μ m wide, with

sinuous walls. Stomata aligned more or less parallel to the midrib. Outline of guard cell pairs elliptical, 22–25 μ m long, 16–18 μ m wide. Vascular bundles separated from the abaxial mesophyll by several layers of cells.

Comments. This species is represented by only one specimen, which shows the sinuous epidermal cell walls and stomata aligned parallel to these cells characteristic of Styphelioideae. The distinctive combination of features is the small, ovate leaves but large epidermal cells and stomata.

Tribe—*Cosmelieae*

Species—*Cosmelieae* sp. (Fig. 12)

Specimens examined. SCB190_spreng; SCB200_spreng; SCB10_spreng.

Description. Leaves triangular, tapering from a sheathing leaf base, 1.5–2.5 mm wide, approximately three times as long as broad, venation parallel with five to 10 veins, very unevenly amphistomatic. Stomata widespread and common on the abaxial surface, sparse on adaxial surface, restricted to the area immediately above the sheathing section. Veins adjacent to the abaxial surface but with parenchyma or mesophyll cells between the vascular bundles and the adaxial surface. Stomata cyclocytic, outline of guard cell pairs almost

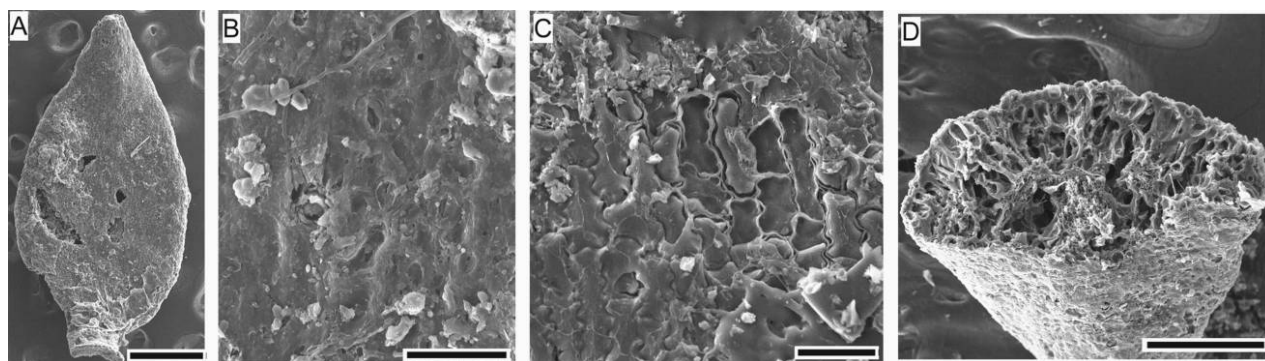


Fig. 11 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 8 from Stony Creek Basin. A, Abaxial surface of SCB200_o_micro2 (bar = 500 μ m). B, Abaxial surface of SCB200_o_micro2 showing stomata (bar = 50 μ m). C, Partially eroded adaxial surface of SCB200_o_micro2 showing short, sinuous-walled epidermal cells (bar = 50 μ m). D, Cross section of SCB200_o_micro2 showing distribution of mesophyll cells and vascular bundles (bar = 200 μ m).

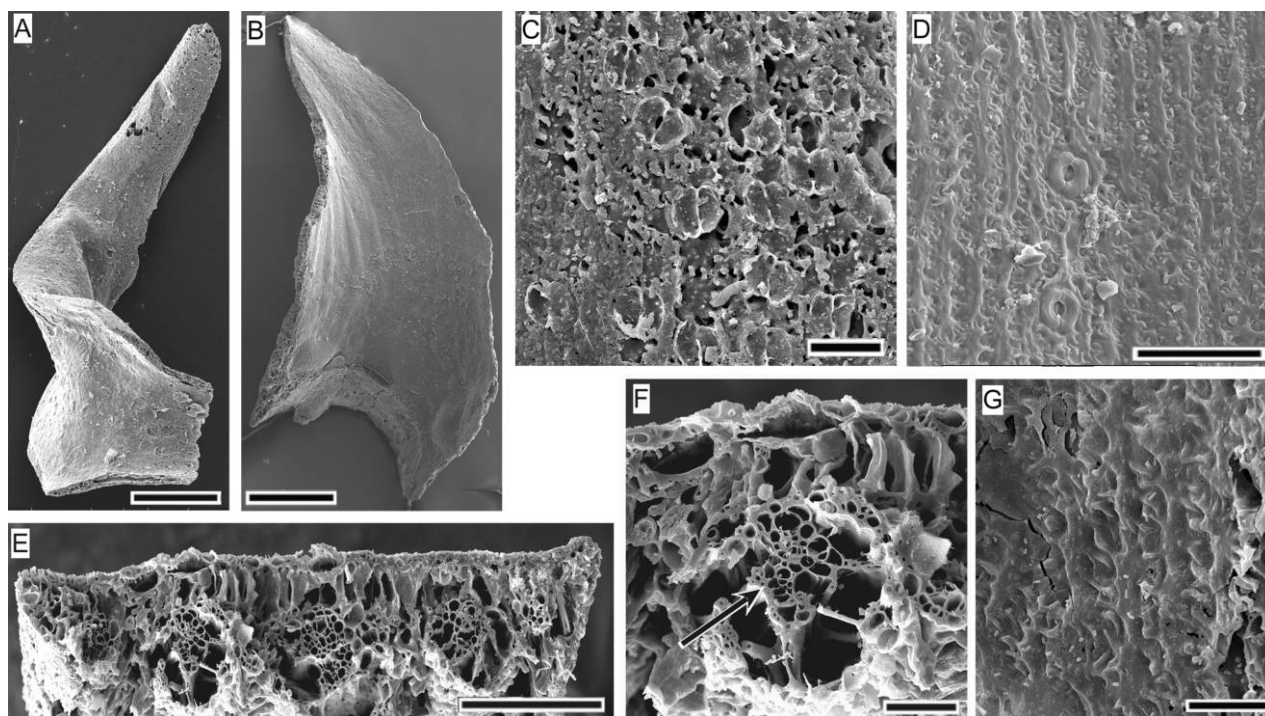


Fig. 12 Scanning electron micrographs of fossil leaves of *Cosmelieae* sp. from Stony Creek Basin. *A*, Abaxial surface of SCB200_spreng (bar = 500 μm). The lateral parts of the leaf base have been broken off. *B*, Composite micrograph of abaxial surface of SCB190_spreng (bar = 500 μm). *C*, Partially eroded abaxial surface of SCB190_spreng showing stomata and sinuous cell walls (bar = 50 μm). *D*, Abaxial surface of SCB200_spreng showing cyclocytic stomata and sinuous-walled epidermal cells (bar = 50 μm). *E*, Cross section of SCB200_spreng showing several vascular bundles adjacent to the adaxial surface (bar = 100). *F*, Cross section of SCB200_spreng showing a vascular bundle adjacent to the abaxial surface and separated from the abaxial surface by mesophyll cells (arrow) (bar = 20 μm). *G*, Adaxial surface of SCB10_spreng showing depressions indicating sinuous-walled epidermal cells (bar = 20 μm).

circular, 13–15 μm long. Epidermal cells aligned parallel with the veins, with very sinuous walls, abaxial cells along veins 40–60 μm long, 10–12 μm wide, those among the stomata shorter, adaxial cells 30–50 μm long, ca. 10–12 μm wide.

Comments. These fossils clearly show the distinctive sheathing leaf bases characteristic of tribes Richeeae and *Cosmelieae*. They are also amphistomatic, which is almost unknown in *Styphelioideae* except in these tribes. The stomata and extremely sinuous cell walls are also typical of these tribes. The presence of cyclocytic stomata places this species into *Cosmelieae* and excludes the *Richeeae*, which have paracytic stomata (Watson 1967). Also, the vascular bundles are connected by sclerenchyma to both the upper and lower epidermides in almost all species of *Richeeae* (Watson 1967; G. J. Jordan, unpublished data). However, there is one significant difference between this species and extant *Cosmelieae*. In all species in which the leaf anatomy has been documented (Watson 1967; G. J. Jordan, unpublished data), the vascular bundles are in the middle of the mesophyll or adjacent to the adaxial surface. However, in these fossils, the bundles are adjacent to the abaxial leaf surface. *Cosmelieae* includes *Sprengelia*, which is extant in eastern mainland Australia, and *Cosmelia* and *Andersonia*, which are endemic to Western Australia. The fossil leaves are consistent in size and shape with several species of *Sprengelia*, e.g., *Sprengelia*

montana R. Br., *Sprengelia monticola* (DC.) Druce, and small *Sprengelia incarnata*. However, given the anomalous placement of the vascular bundles, it is plausible that this represents an extinct genus or species of *Cosmelieae*.

Tribe—*Styphelioideae*

Species—*Epacriphyllum* sp. 9 (Fig. 13)

Specimens examined. SCB150_o_epac1.

Description. Leaves hypostomatic, ovate/oblong, widest just below midleaf, ca. 3.5 mm long, ca. 1.8 mm wide, base cordate, flat apart from a downcurved apex, apparently glabrous, margins thick, with scattered trichome bases, apex obtuse. Petiole 0.2 mm long, 0.3 mm wide, flat, reflexed at an angle of ca. 45°. Leaf with five main veins running from the petiole, with the central vein straight and the outer veins curved. Abaxial epidermal cells short, 30–40 μm long, ca. 20 μm wide, with sinuous walls. Stomata aligned more or less parallel to the midrib. Outline of guard cell pairs broadly elliptical, 18–20 μm long, ca. 16 μm wide.

Comments. This species is represented by only one specimen. Features that distinguish it from the other taxa described here are the presence of a blunt, downcurved apex, trichome bases along the margins, a cordate base, and a very short petiole. The presence of only weakly sinuous epidermal cell walls is consistent with *Styphelioideae*, except *Trochocarpa*

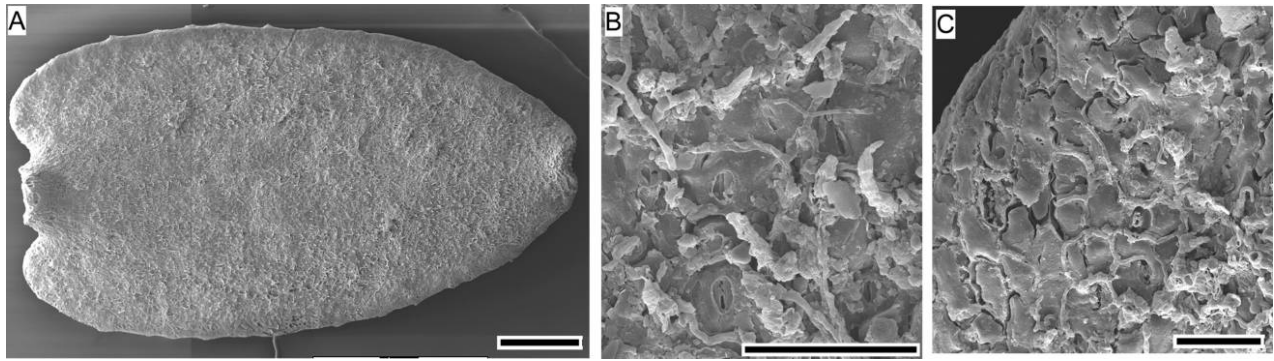


Fig. 13 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 9 (SCB150_o_epac1) from Stony Creek Basin. A, Abaxial surface (bar = 500 μm). B, Abaxial surface showing stomata (bar = 50 μm). The specimen shows some fungal overgrowth (the wavy hairlike structures). C, Partially eroded abaxial surface showing sinuous-walled epidermal cells (bar = 50 μm).

(Jordan and Hill 1995). The shape and venation of the leaf is consistent with *Trochocarpa* and *Pentachondra*, although species of *Trochocarpa* lack trichomes along their margins and have strongly sinuous epidermal cell walls (Jordan and Hill 1995). The fossil probably shows most similarity to *Pentachondra* species, which often have ciliate leaf margins and similar venation, epidermal cells, and glabrous leaf surfaces to the fossil (see Jordan and Hill 1995). However, the fossil cannot be confidently assigned to *Pentachondra* because of the absence of particular diagnostic characters.

Species—*Epacriphyllum* sp. 10 (Fig. 14)

Specimens examined. SCB170_o_epac8 (with anatomy), SCB170_o_epac11, SCB170_o_epac12.

Description. Leaves hypostomatic, linear, slightly convex above/narrow-elliptical in cross section, at least 5 mm long, 1 mm wide, apex acute with a protruding, presumably pungent point, margins thick, entire. Epidermis two cells thick, cells very elongate, 20–25 μm wide, up to 150 μm long, ca. 15 μm tall, with acute ends. Stomata arranged more or less

uniformly on each side of the midrib, aligned parallel to the midrib, outline of pair of guard cells elliptical, 24–33 μm long, 15–19 μm wide. Vascular bundles 50–70 μm wide, attached to the abaxial epidermis. Palisade mesophyll two layers thick, cells 80 μm tall, 25–30 μm wide. Spongy mesophyll thin, attached to the abaxial epidermis.

Comments. The sinuous epidermal cell walls typical of Styphelioideae cannot be observed unambiguously in these fossils, but this may be an artifact of preservation. However, the stomatal form and arrangement is typical of the subfamily. Furthermore, the cross-sectional anatomy of these leaves, particularly the location of the small vascular bundle adjacent to the lower epidermis, is characteristic of Styphelioideae. The arrangement of these bundles also suggests parallel or subparallel venation.

Species—*Epacriphyllum* sp. 11 (Fig. 15)

Specimens examined. SCB170_epac10.

Description. Leaves hypostomatic, ovate elliptical, ca. 5 mm long, 1.2 mm wide, concave above, apparently glabrous,

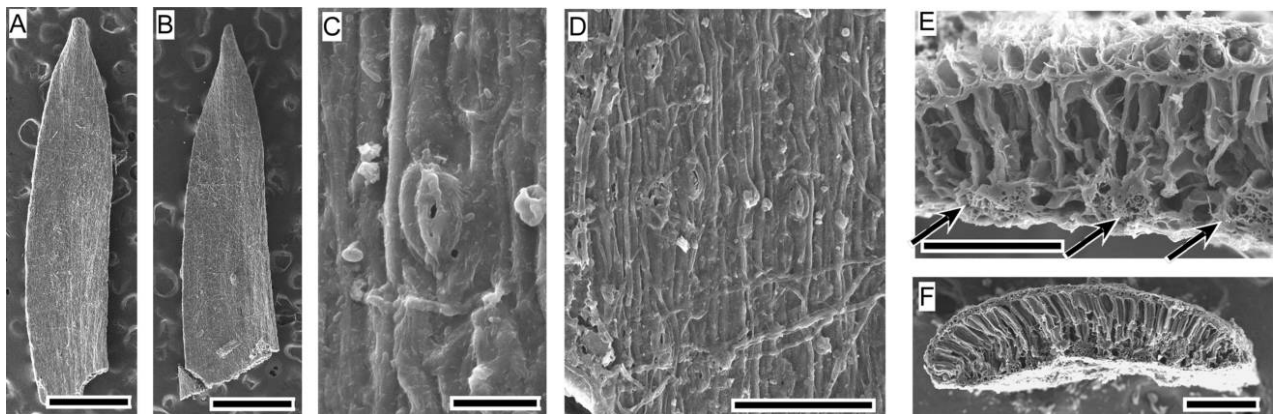


Fig. 14 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 10 from Stony Creek Basin. A, Abaxial surface of SCB170_o_epac12 (bar = 1 mm). B, Abaxial surface of SCB170_o_epac11 (bar = 1 mm). C, Detail of abaxial surface of SCB170_o_epac8 showing a stoma (bar = 20 μm). D, Detail of abaxial surface of SCB170_o_epac8 showing stomatal distribution (bar = 100). E, Cross section of SCB170_o_epac12 showing vascular bundles attached to the lower epidermis (bar = 100). F, Cross section of SCB170_o_epac8 (bar = 200 μm).

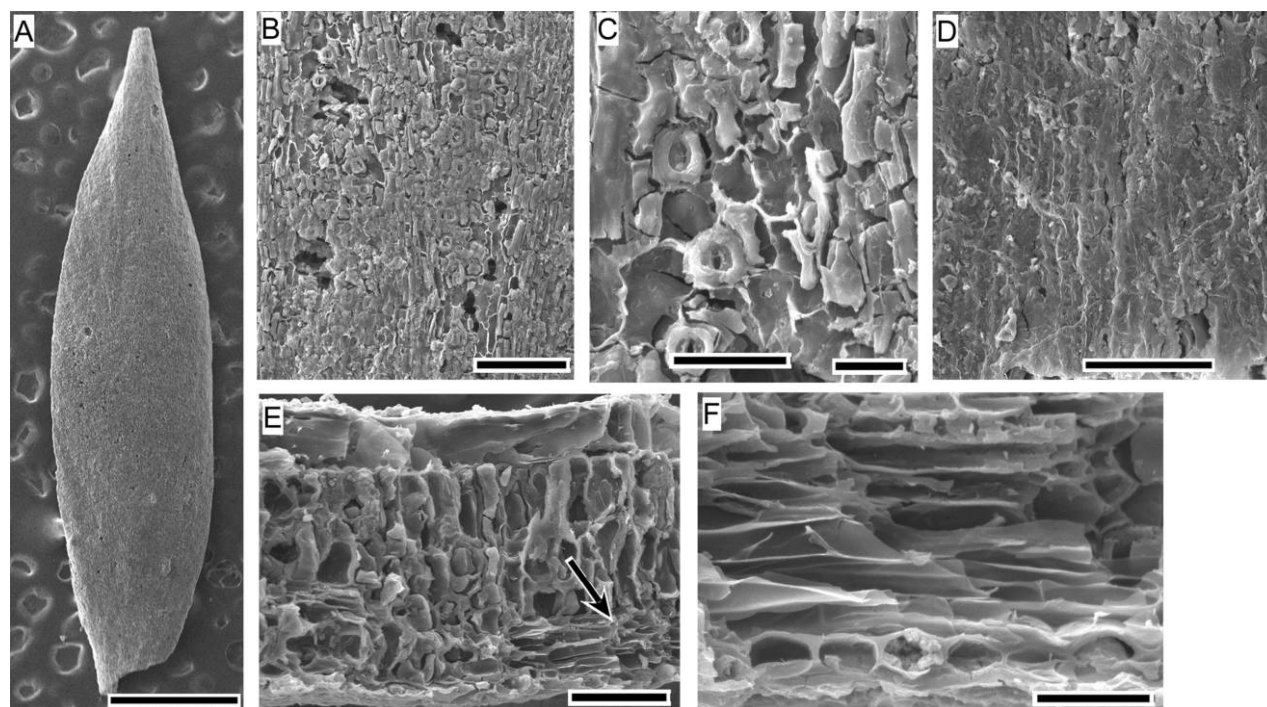


Fig. 15 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 11 (SCB170_o_epac10) from Stony Creek Basin. *A*, Abaxial surface (bar = 1 mm). *B*, Partially eroded abaxial surface showing stomatal distribution (bar = 100). *C*, Partially eroded abaxial surface showing stomata and weakly sinuous-walled epidermal cells (bar = 20 μm). *D*, Adaxial surface showing sinuous-walled epidermal cells (bar = 100). *E*, Cross section showing tall adaxial epidermal cells. Note also vascular bundle adjacent to the abaxial epidermis (arrow) (bar = 50 μm). *F*, Cross section showing vascular bundle adjacent to the abaxial epidermis (bar = 20 μm).

margins thick, entire, apex acute, somewhat attenuated into a thick, presumably pungent tip. Abaxial epidermal cells sinuous walled, 15–18 μm long, ca. 10 μm wide. Stomata aligned more or less parallel to the epidermal cells. Outline of guard cell pairs elliptical, 15–17 μm long, 13–15 μm wide. Adaxial epidermal cells very large, ca. 30 μm thick. Palisade mesophyll cells in two layers, ca. 35 μm long, ca. 15 μm wide. Vascular bundles adjacent to the abaxial leaf surface.

Comments. This species has all the features of Styphelioideae and in particular has the vascular bundles adjacent to the abaxial epidermis, which would suggest that this species belongs to the Styphelieae. It lacks the characteristic trichomes of many Styphelieae, such as *Monotoca* and the *Cyathodes* group of taxa (fig. 3H, 3I; see also Quinn et al. 2005). The walls of the epidermal cells between the stomata are only weakly sinuous, which is also typical of Styphelieae (Jordan and Hill 1995).

Species—*Epacriphyllum* sp. 12 (Fig. 16)

Specimens examined. SCB200_o_serrate.

Description. Leaves hypostomatic, ovate, at least 2.5 mm long (probably ca. 4 mm long), ca. 1 mm wide, flat to very slightly convex above, margins flat, finely serrate with acuminate, forward-pointing teeth ca. 30 μm long. Venation palmate but nearly parallel, with ca. 10 main veins. Petiole flat, straight, ca. 0.3 mm long, ca. 0.3 mm wide. Abaxial surface glabrous, stomata restricted to interveinal areas, overall out-

line of stomata elliptical (14–17 μm long, 8–10 μm wide), raised to form two banana-shaped ledges. Epidermal cells above the veins square ended, sinuous walled, ca. 50 μm long, ca. 8 μm wide, epidermal cells between veins weakly sinuous walled, square ended, ca. 20 μm long, ca. 15 μm wide.

Comments. This species is represented by only one specimen but is distinctive. The serrate margins and venation are very similar to those of *Astroloma humifusum* (fig. 3B), which differs in having larger leaves and the “teeth” elongated into trichomes. It is possible that such trichomes were present in the living plant that produced the fossils but were lost in the process of fossilization.

Species—*Epacriphyllum* sp. 13 (Fig. 17)

Specimens examined. SCB170styph, SCB170_styph1, SCB170_o_mono1, SCB170_o_mono2, SCB170_o_mono3, SCB170_o_mono4, SCB170_o_mono5, SCB170_o_mono9, SCB170_o_mono15, SCB180_o_mono, SCB180_o_mono2, SCB180_o_mono3, SCB180_o_mono4, SCB200_o_mono, SCB200_o_mono1.

Description. Leaves hypostomatic, linear-oblong, sometimes slightly falcate, 4–7 mm long, 0.8–0.9 mm wide, flat, margins flat or slightly recurved, finely serrate, apex acute, apex mucronate or pungent. Petiole 0.6–0.7 mm long, 0.2–0.3 mm wide, straight or slightly reflexed. Leaf with three parallel main veins plus two minor veins leading from the base. One to three minor veins leading to the margin at an

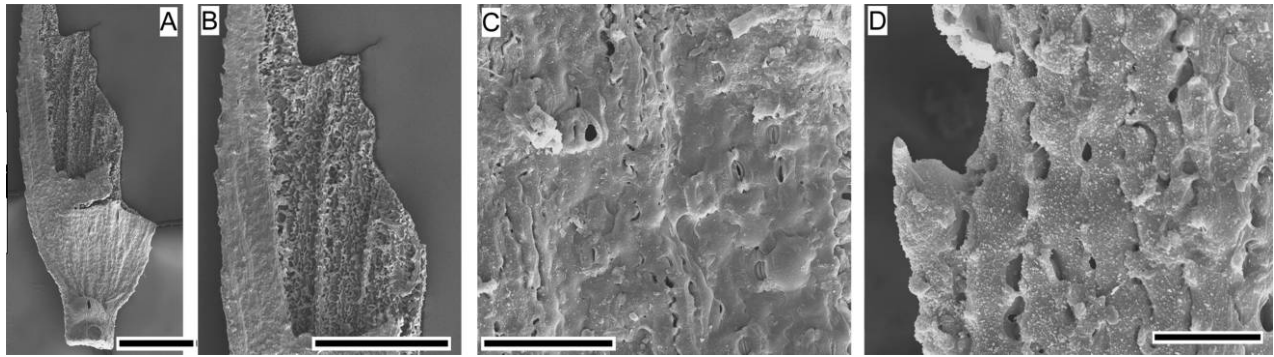


Fig. 16 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 12 (SCB200_o_serrate) from Stony Creek Basin. A, Abaxial surface (bar = 0.5 mm). B, Abaxial surface showing teeth, veins, and stomatal distribution (bar = 0.5 mm). C, Abaxial surface showing stomata and sinuous cell walls (bar = 50 μ m). D, Margin of abaxial surface showing a tooth/trichome base (bar = 20 μ m).

acute angle from the upper part of the outer main veins. Stomata restricted to interveinal areas, which are slightly depressed and covered with abundant, short conical trichomes. Stomata aligned with veins, elliptical in outline, ca. 25 μ m long by ca. 18 μ m wide. Abaxial epidermal cells rectangular, 40–120 μ m long, 10–15 μ m wide, walls sinuous, ca. 8 μ m tall. Adaxial leaf surface glabrous, epidermal cells elongate,

ca. 10–15 μ m wide, ca. 15 μ m tall, with strongly sinuous walls. Vascular bundles adjacent to the abaxial leaf surface.

Comments. This is one of the most abundant of the species and is consistent with a number of genera, especially *Monotoca*. The characteristic feature is short, conical trichomes covering the area of the shallow depressions between the veins and obscuring the stomata. The presence of minor veins

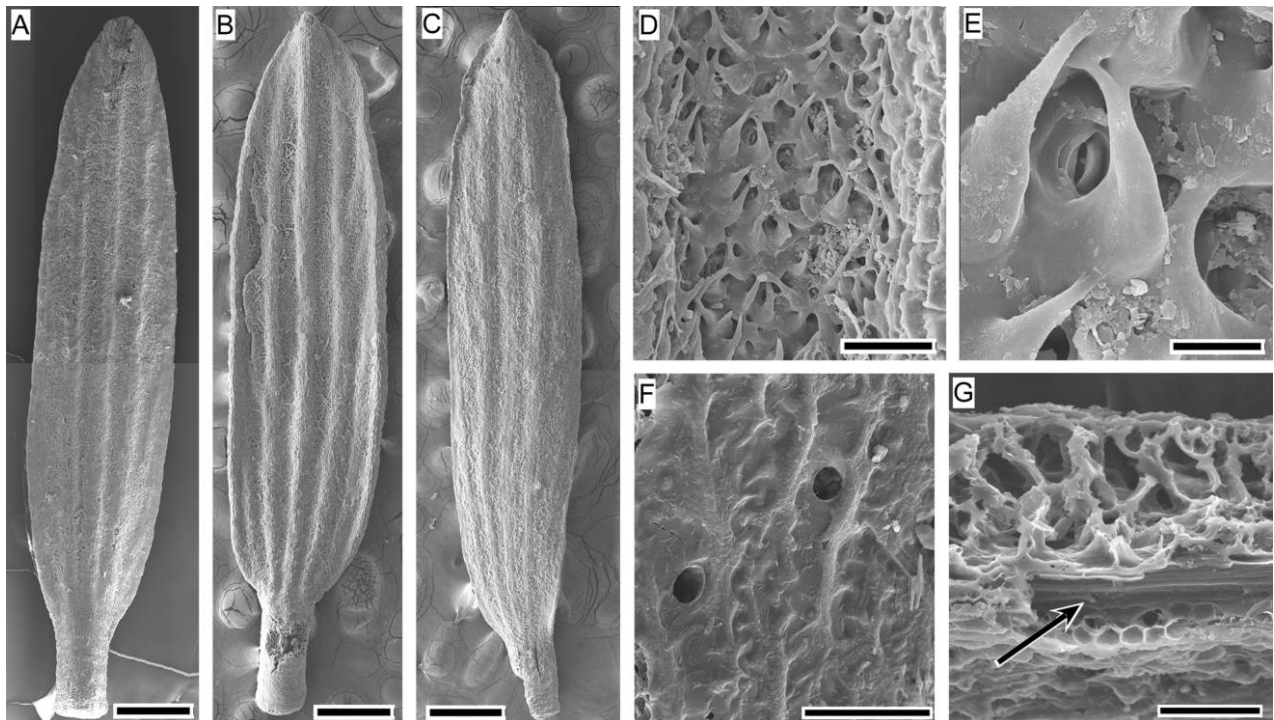


Fig. 17 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 13 from Stony Creek Basin. A, Abaxial surface of SCB200_o_mono1 (bar = 0.5 mm). B, Abaxial surface of SCB180_Monotoca_like (bar = 0.5 mm). C, Abaxial surface of SCB180_o_mono_4 (bar = 0.5 mm). D, Abaxial surface of SCB180_o_mono_3 showing stomata and trichomes restricted to interveinal regions as well as sinuous epidermal cell walls of veinal regions (bar = 50 μ m). E, Abaxial surface of SCB180_o_mono_3 showing a stoma and trichomes (bar = 10 μ m). F, Adaxial surface of SCB200_o_mono_1 showing sinuous epidermal cell walls (bar = 20 μ m). G, Cross section of SCB170_o_mono_4 showing a vascular bundle adjacent to the small epidermal cells of the abaxial surface (bar = 50 μ m).

leading to the margins from the outer main veins is typical of this genus. Some of the leaves are slightly curved to one side, but this is not taken to be sufficient evidence to represent a different species.

Species—*Epacriphyllum* sp. 14 (Fig. 18)

Specimens examined. SCB170_o_leuc1, SCB140_revolute.

Description. Leaves hypostomatic, narrow-oblong, ca. 3 mm long, ca. 0.4 mm wide, margins strongly revolute, obscuring most of the lamina. Leaf with one main vein apparent. Petiole ca. 0.3 mm long, ca. 0.2 mm wide, straight. Abaxial lamina with long simple trichomes in the stomatal region. Stomata mostly aligned parallel with the midrib, pair of guard cells elliptical in outline, ca. 30 μm long, ca. 20 μm wide. Adaxial epidermal cells with sinuous walls, 50–70 μm long, ca. 10 μm wide, 15–20 μm tall. Epidermal cells of the abaxial midrib with sinuous walls very elongated, ca. 6 μm wide.

Comments. This species is clearly consistent with *Styphelioideae*, with sinuous epidermal cell walls. The overall leaf size, leaf form, presence of long trichomes covering the stomatal area, and cell sizes (including the unusually tall adaxial epidermal cells) are consistent with *Androstoma verticillata*.

Species—*Epacriphyllum* sp. 15 (Fig. 19)

Specimens examined. SCB170_o_mono6, SCB170_o_mono7, SCB170_o_mono13, SCB170_o_mono14.

Description. Leaves hypostomatic, obovate, 4–5 mm long, 1.1–1.3 mm wide, flat, margins flat in the lower two-thirds of the leaf, narrowly revolute in the upper third of the leaf, apex obtuse, shortly mucronate. Leaf with five to seven subparallel main veins. A few minor veins diverging from the upper part of some of the main veins at an acute angle. Leaf subsessile, petiole straight, ca. 0.3 mm long, ca. 0.5 mm wide. Stomata restricted to interveinal areas, which are slightly depressed and covered with abundant short, conical trichomes. Stomata aligned with veins, elliptical in outline, ca. 18 μm long by ca. 14 μm wide. Abaxial epidermal cells rectangular, 40–100 μm long, 8–10(–15) μm wide, walls weakly sinuous. Adaxial leaf surface

glabrous, epidermal cells 50–100 μm long, 13–15 μm wide, with strongly sinuous walls.

Comments. The leaf shape, short, conical trichomes, and venation make this species consistent with *Monotoca*. It is distinguished from *Epacriphyllum* sp. 13 by the leaf shape (broader and widest above the middle), the short, broad petiole, the venation (which may be related to the leaf shape), and larger stomata.

Species—*Epacriphyllum* sp. 16 (Fig. 20)

Specimens examined. SCB170_o_mono8 (probably), SCB190_o_epacrid, SCB_360_epacrid.

Description. Leaves hypostomatic, elliptical-obovate, 6–7 mm long, 1.6–1.8 mm wide, flat, margins flat, apex acute, mucronate. Leaf with five to seven subparallel main veins plus two minor veins leading from the base. Several minor veins leading to the margin at an acute angle from the upper part of the outer main veins. Petiole 0.5 mm long, 0.3 mm wide, straight. Stomata exposed, restricted to interveinal areas, which are slightly depressed. Stomata aligned with veins, elliptical in outline, 16–18 μm long by ca. 12 μm wide. Abaxial epidermal cells rectangular, ca. 60 μm long, 8–12 μm wide, walls sinuous but not visibly so on the surface, epidermal cells with a single line of papillae. Adaxial leaf surface glabrous, epidermal cells elongate, ca. 9–15 μm wide, with sinuous walls.

Comments. The lack of conical trichomes clearly distinguishes this from *Epacriphyllum* spp. 13 and 14. This is unlikely to be an artifact; the preservation of anatomy and surface features is so good that it is unlikely that the trichomes have been lost. This species also differs from *Epacriphyllum* sp. 12, which has toothed/ciliate margins and is smaller (ca. 4 vs. 6–7 mm).

Species—*Epacriphyllum* sp. 17 (Fig. 21A–21C)

Specimens examined. SCB200_o_styph1.

Description. Leaves hypostomatic, narrow-oblong, 4 mm long, ca. 0.4 mm wide, margins recurved. Apex acuminate (presumably pungent). Leaf with three to five parallel veins.

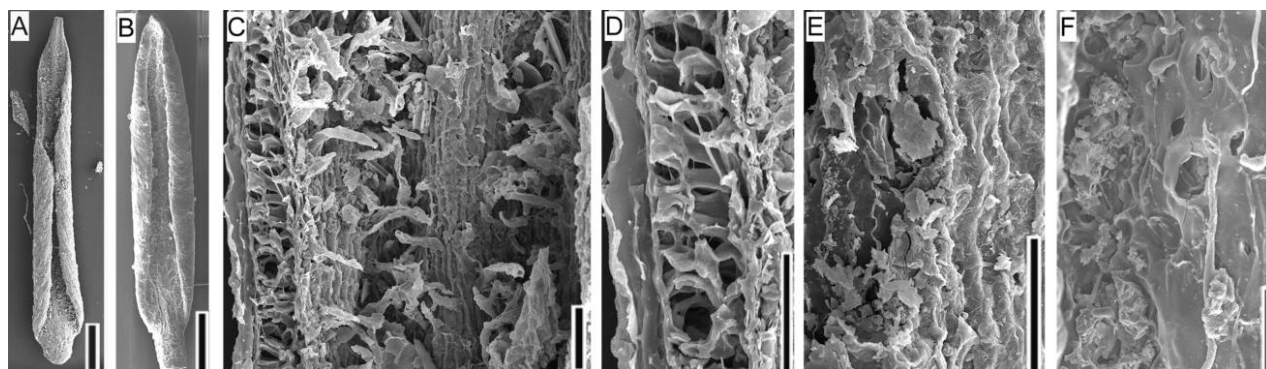


Fig. 18 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 14 from Stony Creek Basin. A, Abaxial surface of SCB140_o_revolute (bar = 0.5 mm). B, Abaxial surface of SCB170_o_leuc1 (bar = 0.5 mm). C, Upper part of abaxial surface of SCB140_o_revolute showing the revolute margin, midrib, and long trichomes (bar = 50 μm). D, Longitudinal section of SCB140_o_revolute showing the tall epidermal cells and tall mesophyll (bar = 50 μm). E, Partially eroded region of adaxial surface of SCB140_o_revolute showing the elongate epidermal cells with sinuous walls (bar = 50 μm). F, Upper part of abaxial surface of SCB170_o_leuc1 showing stomata (bar = 50 μm).

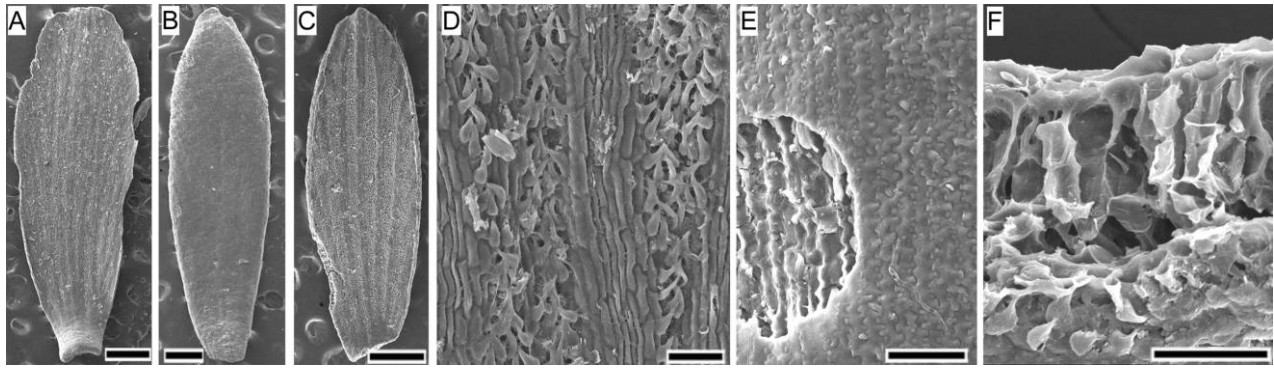


Fig. 19 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 15 from Stony Creek Basin. *A*, Abaxial surface of SCB170_o_mono7 (bar = 0.5 mm). *B*, Adaxial surface of SCB170_o_mono14 (bar = 0.5 mm). *C*, Abaxial surface of SCB170_o_mono6 (bar = 0.5 mm). *D*, Abaxial surface of SCB170_o_mono6 showing stomata and trichomes restricted to interveinal regions and sinuous epidermal cell walls of veinal regions (bar = 50 μ m). *E*, Adaxial surface of SCB170_o_mono14 showing sinuous epidermal cell walls. Part of the surface has been eroded (bar = 50 μ m). *F*, Cross section of SCB170_o_mono14 showing epidermal and mesophyll cells (bar = 50 μ m).

Petiole ca. 0.2 mm long, ca. 0.3 mm wide, flattened, reflexed ca. 45°. Stomata restricted to interveinal regions, abaxial lamina without conical trichomes in the stomatal region. Stomata aligned parallel with the midrib, pair of guard cells elliptical in outline, ca. 15 μ m long, ca. 10 μ m wide. Epidermal cells papillose, with strongly revolute walls, ca. 30 μ m long, ca. 7 μ m wide.

Comments. This species is based on a single specimen. However, the overall leaf form is completely consistent with that of recurved/revolute-margined *Leucopogon* species (e.g., *Leucopogon collinus* [Labill.] R. Br.). It differs from *Epacriphyllum* sp. 14 in having a pungent apex, multiple veins, recurved rather than closely revolute margins, a flattened petiole, and much smaller stomata.

Species—*Epacriphyllum* sp. 18 (Fig. 21D, 21E)

Specimens examined. SCB170_o_mono12.

Description. Leaves hypostomatic, narrow elliptical, 2 mm long, ca. 0.7 mm wide, margins thin, flat. Apex acuminate (presumably pungent). Leaf with three parallel veins. Petiole

cylindrical, ca. 0.3 mm long, ca. 0.2 mm wide, reflexed to ca. 45°. Stomata restricted to interveinal regions, abaxial lamina with conical trichomes in the stomatal region. Stomata aligned parallel with the midrib, pair of guard cells elliptical in outline, ca. 26 μ m long, ca. 18 μ m wide. Epidermal cells with weakly revolute walls, very elongated, 40–ca. 100 μ m long, ca. 7 μ m wide.

Comments. This species is based on a single specimen. It has the extremely distinctive conical trichomes typical of the *Cyathodes* group of genera (and some other Styphelioideae). It is a tiny, distinctive leaf, broadly consistent with a species such as *Cyathodes dealbata*.

Discussion

The fossils from Stony Creek Basin demonstrate that this place contained high species richness of Styphelioideae at the beginning of the Pleistocene. The diversity included 19 fossil leaf types distinctive enough to suggest that they represented

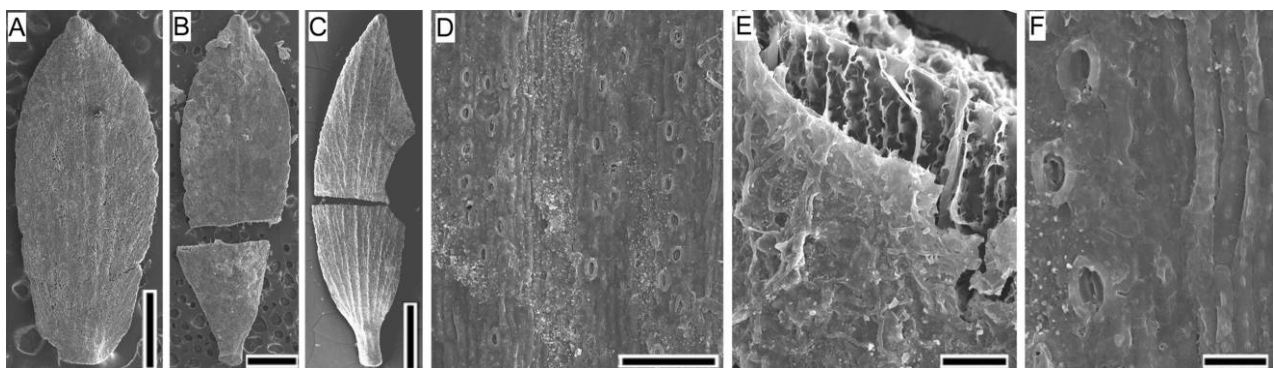


Fig. 20 Scanning electron micrographs of fossil leaves of *Epacriphyllum* sp. 16 from Stony Creek Basin. *A*, Abaxial surface of SCB170_o_mono8 (bar = 1 mm). *B*, Abaxial surface of SCB360_epacrid (bar = 1 mm). *C*, Abaxial surface of SCB190_o_epacrid (bar = 1 mm). *D*, Abaxial surface of SCB360_epacrid showing stomata restricted to interveinal regions and sinuous epidermal cell walls of veinal regions (bar = 100). *E*, Partially eroded adaxial surface of SCB360_epacrid showing sinuous epidermal cell walls (bar = 50 μ m). *F*, Abaxial surface of SCB360_epacrid showing small papillae on interveinal region (bar = 20 μ m).

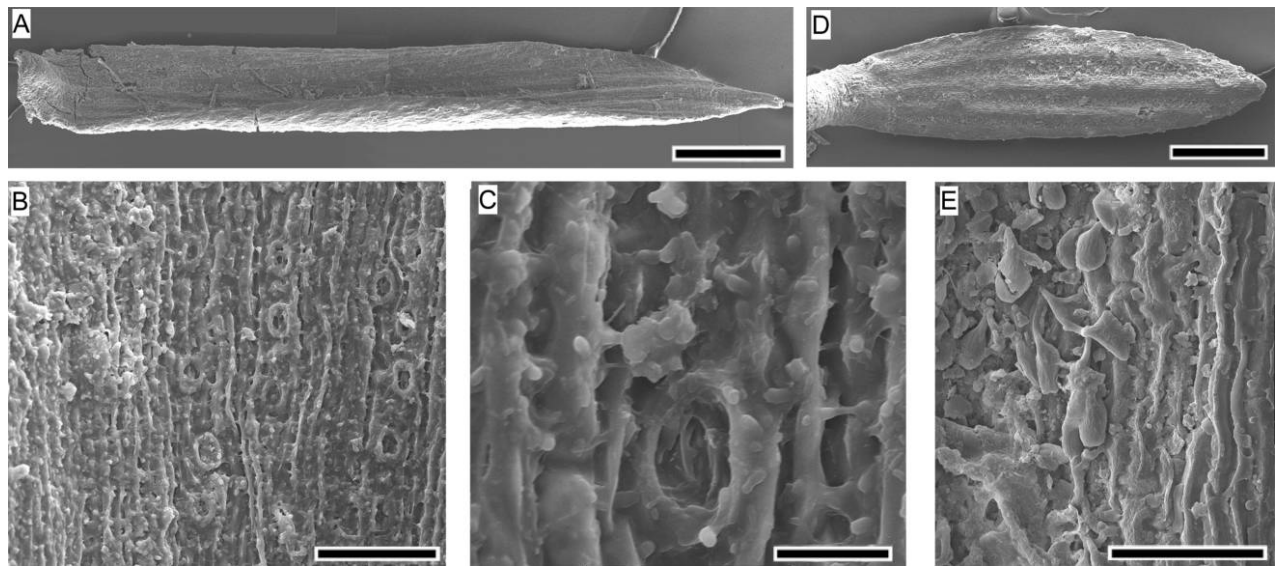


Fig. 21 Scanning electron micrographs of fossil leaves of spp. 17 (SCB200_o_styph1) and 18 (SCB170_o_mono12) from Stony Creek Basin. A, Abaxial surface of SCB200_o_styph1 (bar = 0.5 mm). B, Abaxial surface of SCB200_o_styph1 showing aligned stomata restricted to interveinal regions and sinuous epidermal cell walls of veinal regions (bar = 50 μ m). C, Abaxial surface of SCB200_o_styph1 showing a stoma and degraded waxes (bar = 10 μ m). D, Abaxial surface of SCB170_o_mono12 (bar = 0.5 mm). E, Abaxial surface of SCB170_o_mono12 showing outlines of sinuous-walled epidermal cells and stomata aligned parallel to the midrib and obscured by conical trichomes (bar = 50 μ m).

different species (table 1). These were mostly of the Epacri-
deae/Archerieae and Styphelieae types, but Cosmelieae were
also present. The 170–180-cm sample alone contains 13 species.
Given the rarity of most species in all the samples, it is
plausible that other species of Styphelieae occurred in the

source vegetation of this time but are not represented purely
through random sampling effects. In particular, an additional
six species were present in the other samples from the pit,
five of which occurred in the 30 cm below or above the 170–
180-cm sample.

Table 1

Summary of Fossil Styphelioideae in Different Samples from Stony Creek Basin

Species	Comparable taxa	Samples
Tribe Epacriadeae or Archerieae:		
<i>Epacriphyllum</i> sp. 1	Tiny <i>Epacris</i> (e.g., <i>Epacris microphylla</i>)	170, 190
<i>Epacriphyllum</i> sp. 2	<i>Epacris</i> spp. (e.g., <i>Epacris obtusifolia</i> Smith)	170
<i>Epacriphyllum</i> sp. 3	<i>Epacris</i> spp. (e.g., <i>Epacris obtusifolia</i>)	90, 1985
<i>Epacriphyllum</i> sp. 4	<i>Epacris</i> spp. (e.g., <i>Epacris heteronema</i>)	170
<i>Epacriphyllum</i> sp. 5	<i>Epacris</i> spp.	150, 170, 180, 190, 200, 1985
<i>Epacriphyllum</i> sp. 6	<i>Epacris</i> spp.	180, 200
<i>Epacriphyllum</i> sp. 7	<i>Epacris</i> spp. (e.g., <i>Epacris impressa</i>)	60
<i>Epacriphyllum</i> sp. 8	<i>Epacris</i> spp.	170, 200, 150
Tribe Cosmelieae:		
Cosmelieae sp.	<i>Sprengelia</i> spp.	10, 170, 190
Tribe Styphelieae:		
<i>Epacriphyllum</i> sp. 9	<i>Pentachondra</i> spp.	150
<i>Epacriphyllum</i> sp. 10	<i>Leucopogon</i> spp.	170
<i>Epacriphyllum</i> sp. 11	<i>Leucopogon</i> spp.	170
<i>Epacriphyllum</i> sp. 12	<i>Astroloma humifusum</i>	200
<i>Epacriphyllum</i> sp. 13	<i>Monotoca</i> spp.	170, 180, 200
<i>Epacriphyllum</i> sp. 14	<i>Androstoma verticillata</i>	140, 170
<i>Epacriphyllum</i> sp. 15	<i>Monotoca</i> spp.	170
<i>Epacriphyllum</i> sp. 16	<i>Leucopogon</i> spp.	170, 190, 360
<i>Epacriphyllum</i> sp. 17	<i>Leucopogon</i> spp. (e.g., <i>Leucopogon collinus</i>)	200
<i>Epacriphyllum</i> sp. 18	<i>Cyathodes dealbata</i>	170

Note. Comparable extant species are also listed. These are species similar to but not necessarily closely related to the fossils.

This species richness is higher than that currently present in the Victorian western uplands. According to Albrecht (1996), only 12 members of Ericaceae (*Acrothamnus hookeri* [Sond.] C. J. Quinn, *Acrotriche prostrata* F. Muell., *Acrotriche serrulata* R. Br., *Astroloma humifusum*, *Brachyloma daphnoides* [Sm.] Benth., *Epacris impressa*, *Leucopogon virgatus* [Labill.] R. Br., *Leucopogon microphyllus* [Cav.] R. Br., *Leucopogon glacialis* Lindl. in T. L. Mitchell, *Leucopogon ericoides* [Smith] R. Br., *Lissanthe strigosa* [Smith] R. Br., and *Monotoca scoparia* [Smith] R. Br.) are recorded as now occurring within 10' of latitude or longitude of Stony Creek Basin (an area of more than 1000 km²). Furthermore, it is exceedingly unlikely that any catchment of size comparable to that of Stony Creek Basin (0.5 km²) would contain all of these species. Also, the segregation of fossil morphological forms into species in this article was relatively conservative—where the variation among forms was small, they were lumped into one taxon. Many closely related modern species differ little in leaf form, and some may be indistinguishable (e.g., *Leucopogon exolasius* [F. Muell.] Benth. and *L. ericoides* [Sm.] R. Br.). Thus, it is possible that some of the taxa described here are equivalent to several modern species. Many of the fossil species are represented by only a few specimens. This suggests that the flora included a large number of uncommon species; as a result, other rare species may not have been captured in the fossil assemblage.

Furthermore, the observed diversity at Stony Creek Basin may have underestimated the total diversity in the catchment. In support of this, the taphonomic analysis of Lake Dobson in central Tasmania by Hill and Gibson (1986) showed a significant underrepresentation of local diversity. That study sampled leaves in superficial sediments. The leaves therefore represented the contribution from modern vegetation to sediments and were comparable to fossil assemblages. Lake Dobson represents a catchment of size (ca. 0.8 km²) similar to that of Stony Creek Basin, but it is within one of the centers

of diversity of Styphelioideae. In spite of intensive sampling, (156 sediment samples containing more than 27,000 identified leaves), Hill and Gibson (1986) could recognize only six distinct leaf types of Styphelioideae from the sediments. Thus, the true species richness of Styphelioideae of the Lake Dobson catchment (20 species; table 2) was more than three times that indicated from the sediment samples.

It is therefore plausible that the local species richness in and around Stony Creek Basin was similar to, or even greater than, that found in modern floras in the centers of diversity of the group. However, neither the tribal nor the generic diversity was very high. The fossil assemblage contains three of the tribes of Styphelioideae (Epacrideae, Cosmelieae, and Styphelieae), whereas the generic diversity is difficult to determine; the minimum value is three (the subfamilies), but six or seven is probably a more realistic estimate (assuming that the fossil species resembling *Monotoca*, *Leucopogon*, *Androstoma*, *Pentachondra*, and *Astroloma* were derived from taxa equivalent to separate modern genera).

Members of Styphelieae and *Epacris*-like species (most, if not all, probably members of Epacrideae) dominate the fossil flora. The Epacrideae are best represented in New South Wales and Tasmania, with ca. 25 species in each region (Powell 1992; Buchanan 2005). The high diversity of *Epacris*-like species is consistent with a relatively wet climate (as found in much of Tasmania and central eastern New South Wales). The Styphelieae are diverse in each of the centers of diversity of the subfamily, particularly in Western Australia. There is no indication of the presence of the highly phylogenetically isolated groups found in western Tasmania (*Archeria*, *Prionotes*, and *Richeae*), although it remains possible that some of the *Epacris*-like taxa could be *Archeria* or some other near-basal lineage that is now extinct. Thus, the diversity of Styphelioideae found in the Stony Creek Basin flora appears to be mainly in the groups that now make up large parts of the radiation of this subfamily, especially in eastern Australia.

The presence of such high diversity outside the current centers of diversity of the subfamily can be explained in two ways. The diversity in the modern centers of diversity may have immigrated from elsewhere (e.g., Victoria's western uplands). However, this appears unlikely, given the very high levels of endemism of the centers of diversity, including endemic genera (e.g., Powell 1992; Hill and Orchard 1999) and the strong association of these centers of diversity with extremely low-nutrient soils (which are much less well represented in Victoria's western uplands). Alternatively, the geographic range of diverse epacrid floras may have been much wider than it now is, but local extinction reduced the diversity of some regions (e.g., the Victorian western uplands). Since there is now clear evidence for extensive Pleistocene extinctions in southern Australia (e.g., Jordan 1997; Sniderman et al. 2007), the latter is the more plausible explanation for the Stony Creek Basin data. This would then imply that the modern radiation of Styphelioideae in eastern Australia was well advanced by the beginning of the Pleistocene, at a time when warm temperate rain forest still occurred in the Victorian western uplands (Sniderman et al. 2007), a region now dominated by cool temperate sclerophyllous vegetation and entirely lacking rain forest.

Table 2

Species of Styphelioideae Currently Present in the Lake Dobson Catchment

<i>Acrothamnus montanus</i> (R. Br.) C. J. Quinn
<i>Archeria serpyllifolia</i> Hook. f.
<i>Cyathodes dealbata</i>
<i>Cyathodes glauca</i> Labill.
<i>Cyathodes straminea</i> R. Br.
<i>Dracophyllum minimum</i> F. Muell.
<i>Epacris serpyllifolia</i> R. Br.
<i>Leptecophylla juniperina</i>
<i>Monotoca empetrifolia</i> R. Br.
<i>Pentachondra pumila</i> (Forst. & G. Forst.) R. Br.
<i>Planocarpa petiolaris</i> (DC) Weiller
<i>Richea gunnii</i> Hook. f.
<i>Richea pandanifolia</i> Hook. f.
<i>Richea scoparia</i> Hook. f.
<i>Richea sprengelioides</i> (R. Br.) F. Muell.
<i>Richea Xcurtisiae</i> A. M. Gray
<i>Sprengelia incarnata</i>
<i>Sprengelia montana</i>
<i>Trochocarpa cunninghamii</i>
<i>Trochocarpa thymifolia</i> (R. Br.) Sprengel

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