New ephedroid plant from the Lower Cretaceous Koonwarra Fossil Bed, Victoria, Australia

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A revision of the Lower Cretaceous Koonwarra material first assigned to angiosperms and subsequently to sphenopsids shows morphological and anatomical characters typical of ephedroid (gnetophyte) affinities. Shoots are preserved as clayey-ferruginous films deposited beneath the cuticle reflecting either the interior relief of the epidermal cell pattern or subepidermal sclerenchymous strands (rugulate striations) and vascular tissue of the internodes. The articulate shoots are similar to *Ephedra foliata* and some other extant species with 3-4 decussate, basally connate leaves at each node, sunken stomata in intercostal zones, alternating large and small vascular bundles, paired leaf traces, and the morphology of tracheary elements, but differ in the leaf number per node ranging from two to eight and in the considerably lower ratio of leaves to internode vascular bundles. A new genus and species *Leongathia elegans* is described. The co-occurrence of gnetophytes and early angiosperms in the lower Aptian of Koonwarra is of certain evolutionary and palaeoecological significance. The Koonwarra material increases the known diversity of the Cretaceous gnetaleans by presenting a hitherto unrecorded *Ephedra*-like shoot morphology.

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THE LOWER APTIAN Koonwarra Fossil Bed of Gippsland Basin, Victoria (Fig. 1) is of world significance in providing evidence of an early appearance of angiosperms. In addition to undoubted angiosperm remains (Dettmann 1986; Taylor & Hickey 1990; Dilcher 1989), there are poorly understood angiosperm-like fossils which might represent either ecological associates or even blind alleys of angiosperm phylogeny. Douglas (1969) in his monographic study of Mesozoic floras of Victoria described several such plants, among them the "Angiosperm? sp. b." (GSV, 58667-68669, MUGD 3535A, 3535B, 3539B), stem fragments traversed by four vascular bundles with fine transverse striations between them and bearing decussate sheathing leaves at successive nodes. Although superficially similar to sphenopsid remains they were distinguished by different mode of leaf origin. However, Drinnan & Chambers (1986) included this plant in the synonymy of *Phyllotheca wonthaggiensis* (Chapman), a sphenopsid species based on *Equisetites wonthaggiensis* Chapman from Wonthaggi Borehole (Chapman 1914). *Phyllotheca* is essentially a Palaeozoic genus hitherto not recorded from the Cretaceous.

A few specimens of *"Phyllotheca wonthaggiensis"* were studied from the Museum of Victoria on loan to the Florida Museum of Natural History, University of Florida, Gainesville which revealed anatomical structures incompatible with equisetalean affinities but confirming the initial assignment to seed-plants. This plant has affinities with gnetaleans, a gymnosperm group that approaches angiosperm level of morphological

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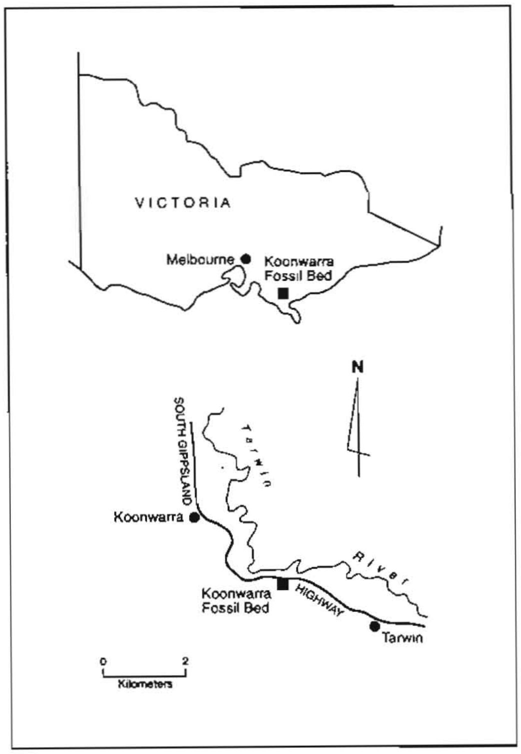


Fig. 1. Simplified maps showing locality of the Koonwarra Fossil Bed, Victoria. Scale refers to lower diagram.

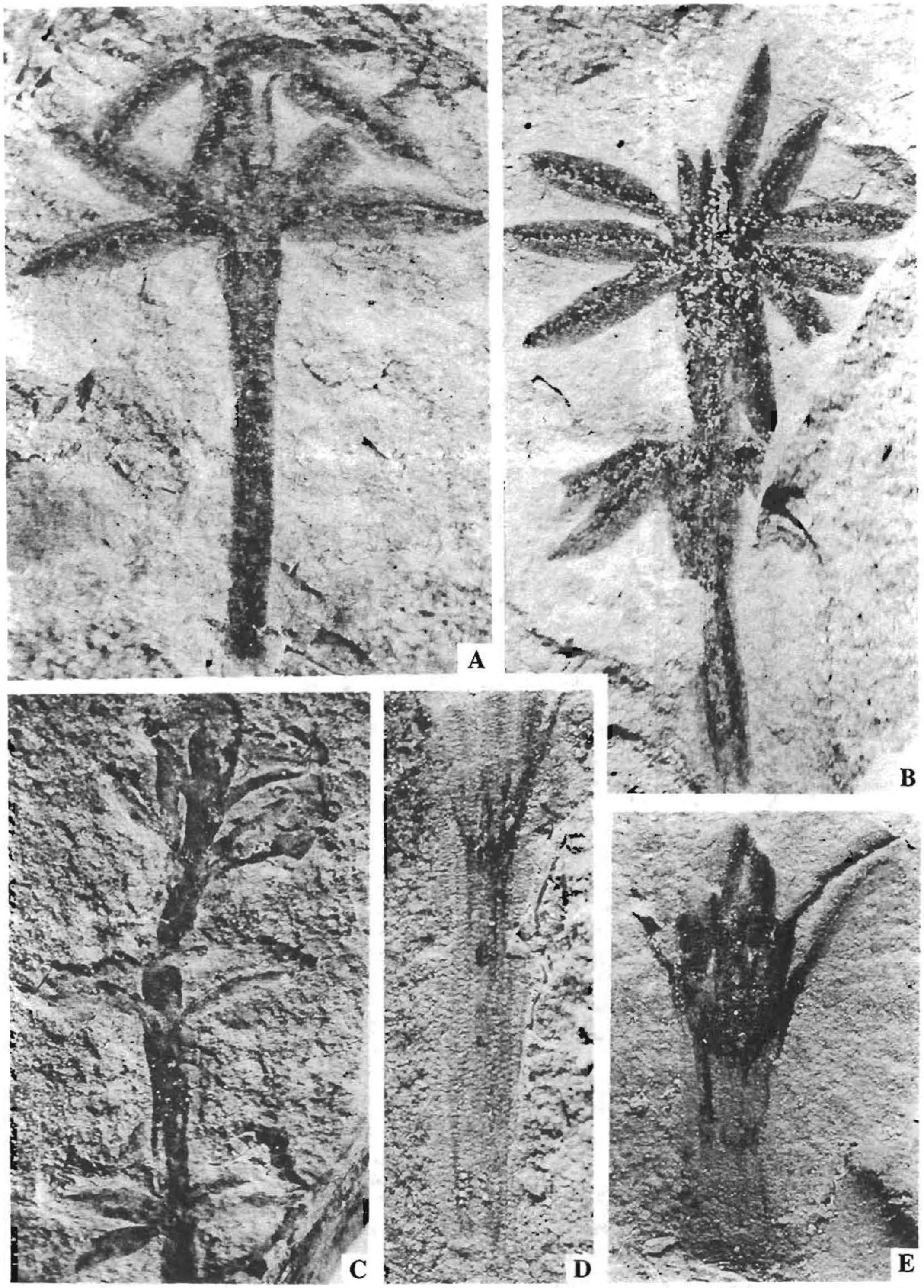
evolution in such features as vessels, leaf venation, cupulate ovules, and archegonia-less embryo sacs (in *Gnetum* and *Welwitschia*), and incipient double fertilization (in *Ephedra*; Khan 1940; Friedman 1990a, b, 1991). Whether angiosperms and gnetaleans are phylogenetically related or their similarities are due to parallel evolution is, as yet, to be learned from the fossil records of both groups.

Until recently the gnetaleans had no fossil record. Commencing with the description of *Eoantha* (Krassilov 1986), their records are rapidly accumulating (see Discussion below) highlighting a considerable diversity of extinct forms, some even more angiosperm-like than the three extant genera. Remarkably, the mid-Cretaceous rise of angiosperms is accompanied by the concomitant rise of gnetaleans, perhaps in response to similar selection pressures. The Koonwarra material contributes to the known diversity of Cretaceous gnetaleans by presenting a hitherto unrecorded *Ephedra*-like shoot morphology. It also provides additional evidence of association of the earliest angiosperm records with those of gnetaleans. Assuming ecological relatedness to the extant species, the ephedroid shoot morphology may suggest a broad range of temperatures at the mean annual precipitation below 250 mm (Pearson 1929).

Material and methods

The shoot fragments are preserved as impressions on light grey or greenish-grey shale. They are the same colour as the shale or differ in a lighter grey or brownish -reddish hue. At magnification the impression surface shows either a finely marked pattern of epidermal cells or a much coarser rugulate pattern of transverse anastomosing striations. Typically only one type of structure prevails along the stem but they occasionally occur in different parts of a single specimen. Several shoot fragments were mounted for SEM, either untreated, washed in distilled water, or after a brief exposure to nitric acid. Observation of the material suggests an impression of a clayey-ferruginous film was deposited beneath the cuticle, the latter then peeled off from the decaying inner tissues in the course of fossilisation. This preservation style whas been described as subcrustation (Krassilov & Makulbekov 1996). Depending on the depth of penetration, the film reflects either the interior relief of the cuticle with epidermal cell pattern or subepidermal sclerenchymous strands (rugulate striation) and occasionally also the vascular tissue of internodes.

Fig. 2. A. Paratype P1202105, shoot showing decussate leaf arrangement, abscissed at the base, x 14. B. Paratype P1202106, shoot with eight leaves in the upper node, x 12. C. Paratype P1202109, shoot with apically crowded leaves, x 8. D, E. Paratypes P1202108 and P1 202107, shoots expanded at nodes and transversely striate, x 14 and x 12.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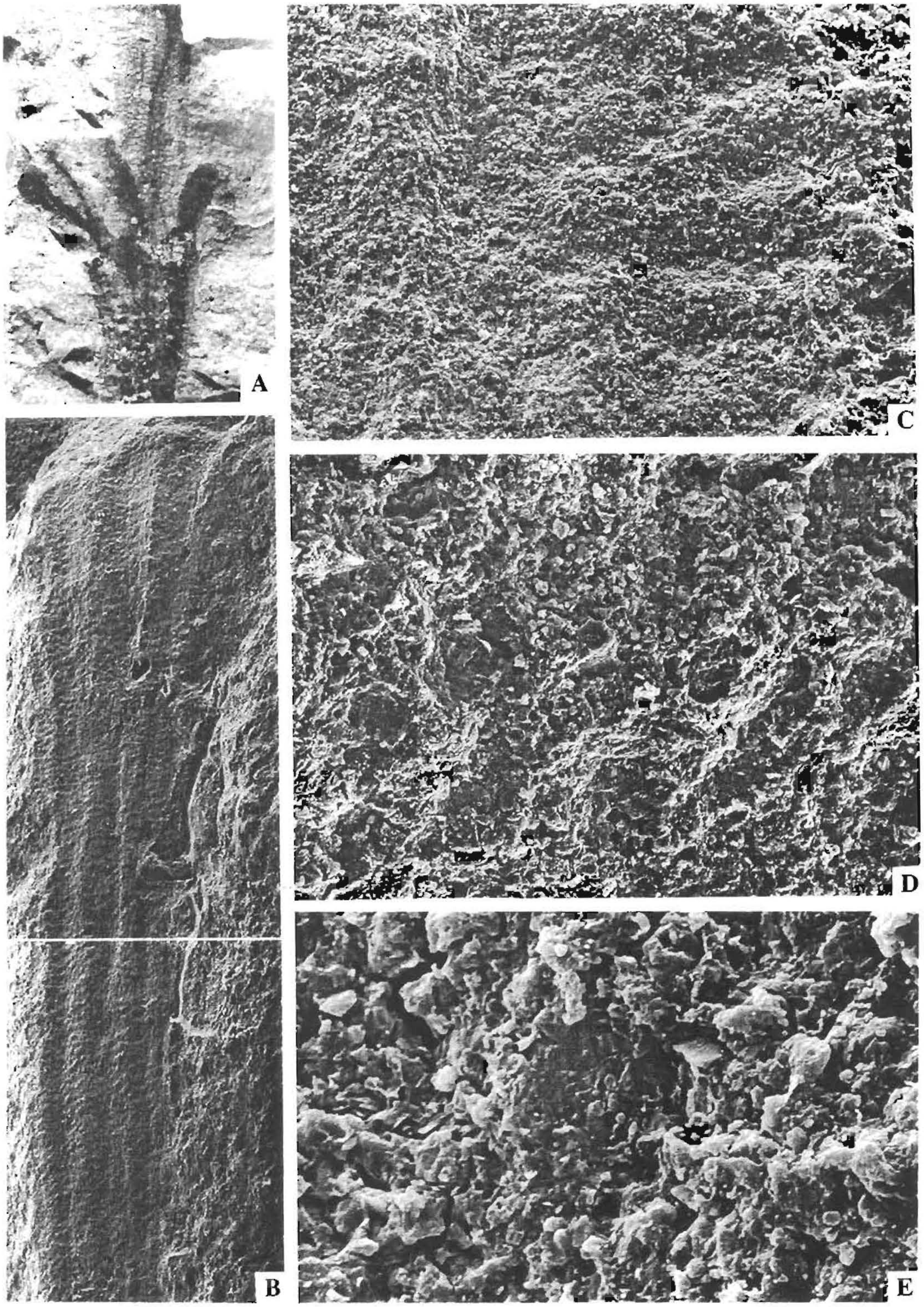
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Systematic palaeobotany

Nomenclature of this plant was left open in the original description (Douglas 1969), whereas the later assignment to *Phyllotheca* (Drinnan & Chambers) is not supported by our revision. *Equisetites wonthaggiensis* Chapman from Wonthaggi Borehole (Chapman 1914) is based on rhizomes and bulbs, with above ground parts poorly preserved, precluding comparison with the Koonwarra material.

Leongathia gen. nov.

Type species. Leongathia elegans gen. and sp. nov.

Etymology. From Leongatha, aboriginal name for the district around the Koonwarra locality.

Diagnosis. Slender shoots with whorled leaves; internodes of varying length, typically shorter towards the apex. Shoot axis longitudinally ribbed, smooth or showing transverse rugulate striations. Nodes typically four-leaved, occasionally two-three leaved, with up to eight crowded leaves in terminal whorls. Leaves decussate, spreading at acute angles or almost horizontally or pendant, lanceolate, acute, about 2 mm long, connate at the base, sheathing about 1/3 to 1/2 of internode or with the sheaths reduced and then directly inserted upon the node. Stomata densely crowded in grooves between the ribs, sunken, encircled by a thick annular ridge. Cortex with sclerenchymous network. Vascular system of alternating large and small bundles. Leaf traces paired, departing from nodal girdles. Tracheary elements pitted, with reticulate and helical wall thickenings. Pits in two rows or occasionally crowded and some confluent forming porous perforations at the poles.

Leongathia elegans sp. nov. (Figs 2-7)

Etymology. Latin *elegans* chosen, elegant.

Material. Holotype. Museum of Victoria, P167378 (GSV61696 of original description, Douglas 1969, pl. 42, fig. 1). Paratypes P67363, P167364, P167365, P167366, P1202105-P1202110.

Diagnosis. As for genus by monotypy.

Description. The shoot fragments are usually no more than 15 mm long (up to 35 mm as reported by Drinnan & Chambers 1986) showing three - five internodes about 5 mm long decreasing distally, with the middle leaves spreading at an acute angle or almost horizontally or pendant, and the distal leaves crowded around the apex (Figs 2A-E, 3A). Apices are preserved more frequently than the bases. Some smaller specimens show a comparatively long proximal internode neatly abscissed at the base and followed by a strongly reduced apical internode with crowded leaves (Fig. 2A; see also Drinnan & Chambers 1986, figs. 12C, D in which the abscission scar is more conspicuous). They might represent the whole branchlets shed at an early stage of their development. The shoot axes are about 1 mm thick, slightly if at all expanded at the nodes, longitudinally ribbed, some showing rugulate striations. The nodes are typically four-leaved, occasionally two - three leaved, with up to eight leaves in terminal whorls. Decussate leaf arrangement is evident in successive four-leaved internodes (Fig. 2A). Free leaf blades are lanceolate, acute, about 2 mm long, connate at the base, sheathing about 1/3 to 1/2 of the internode or with the sheaths reduced and then appearing directly inserted upon the node (Fig. 2B). It can be seen in SEM that leaves depart at

Fig. 3. A. Paratype P1 202110, shoot with pitted surface in the lower internode and with transverse striation in the upper internode, x 15. B, C. Paratype P1202108, SEM of transverse striation pattern, x 38 and x 250. D. Paratype P1202108, stomatal pit arrangement, SEM, x 500. E. Paratype P1202108, stoma, SEM, x 1800.

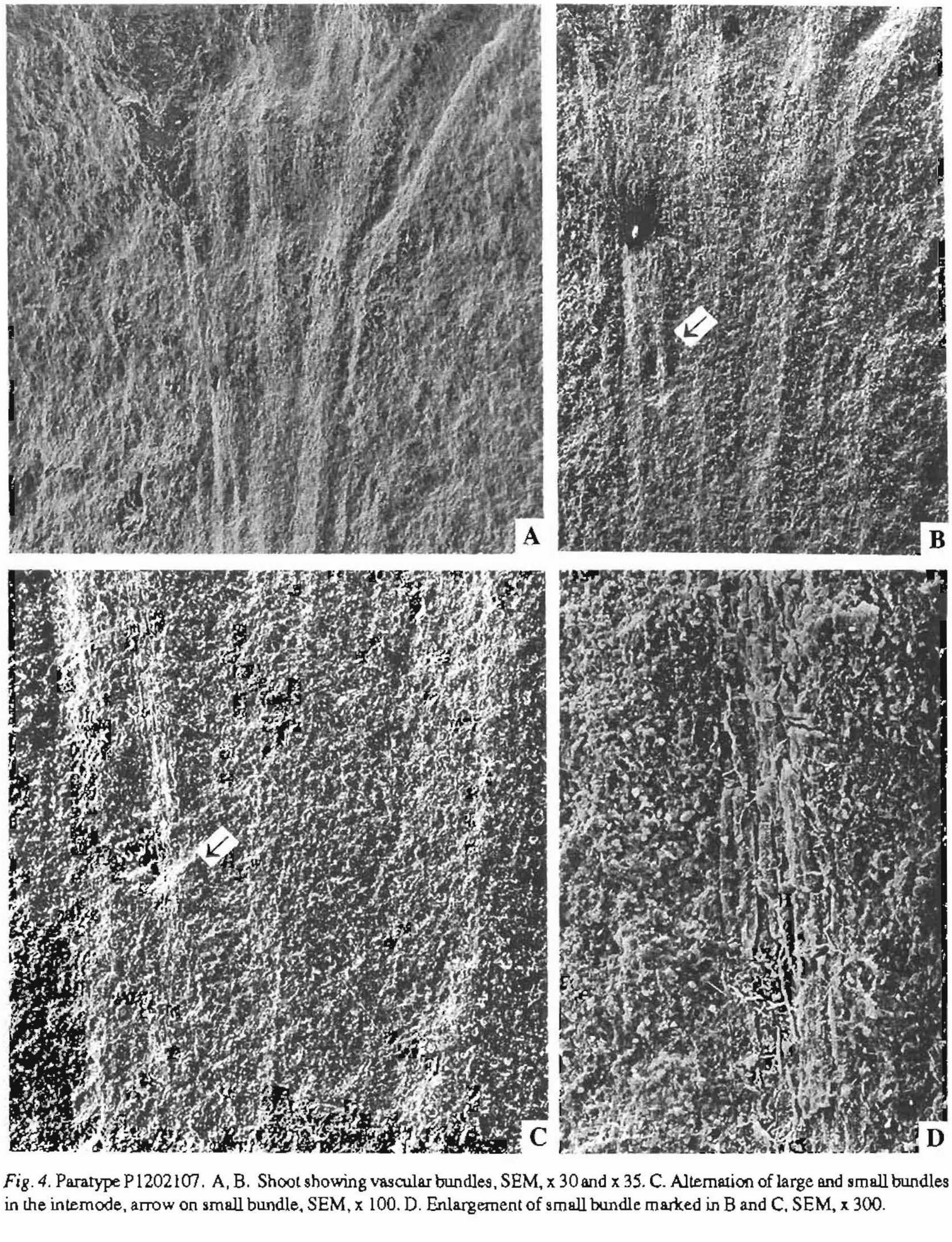


Fig. 4. Paratype P1202107. A, B. Shoot showing vascular bundles, SEM, x 30 and x 35. C. Alternation of large and small bundles in the internode, arrow on small bundle, SEM, x 100. D. Enlargement of small bundle marked in B and C, SEM, x 300.

slightly different levels within the nodal zone (Fig. 4A).

SEM micrographs show, depending on preservation, cuticular and/or subepidermal structures. Stomata occur in grooves between the ribs as elliptical pits 22-26 mm long, surrounded

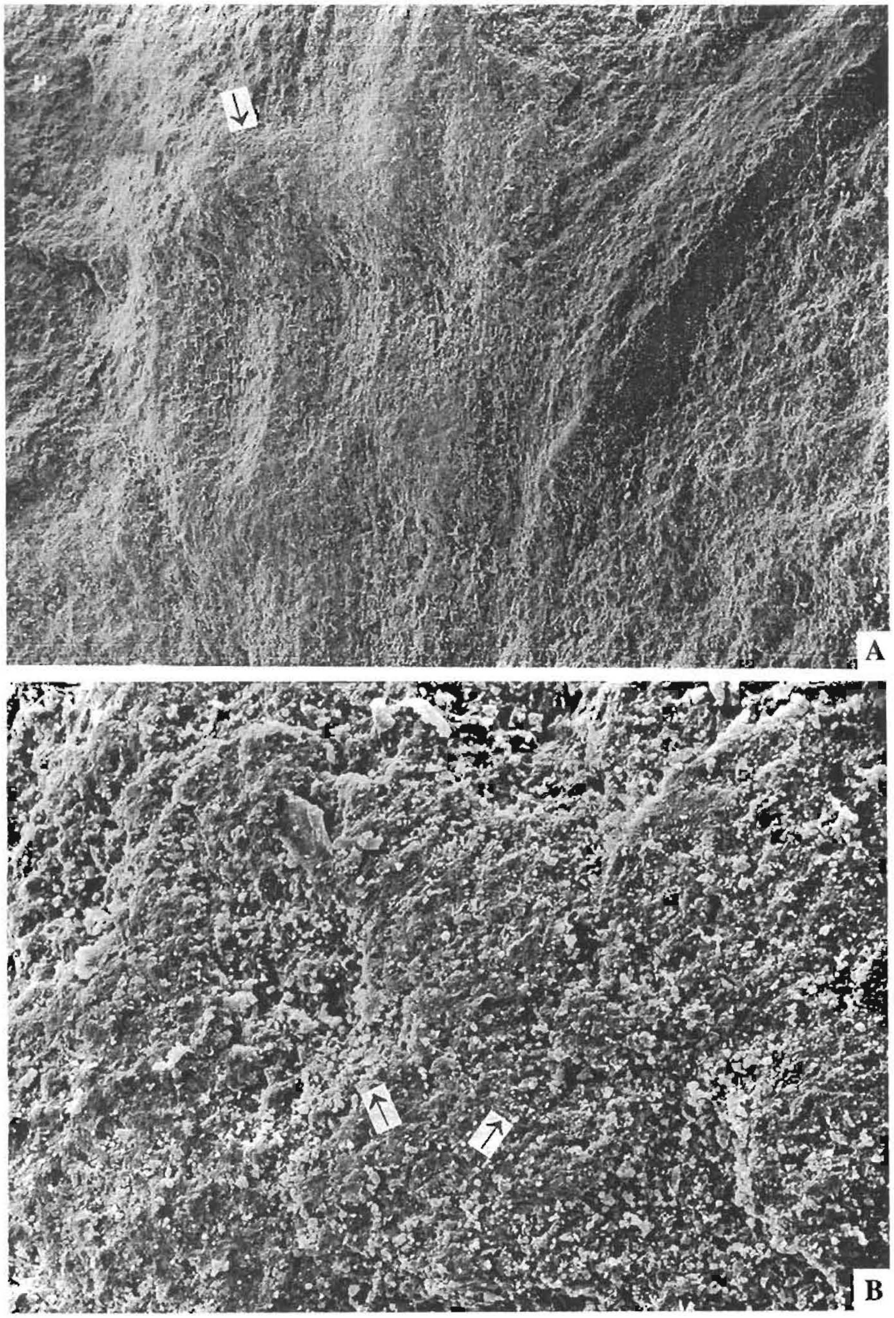
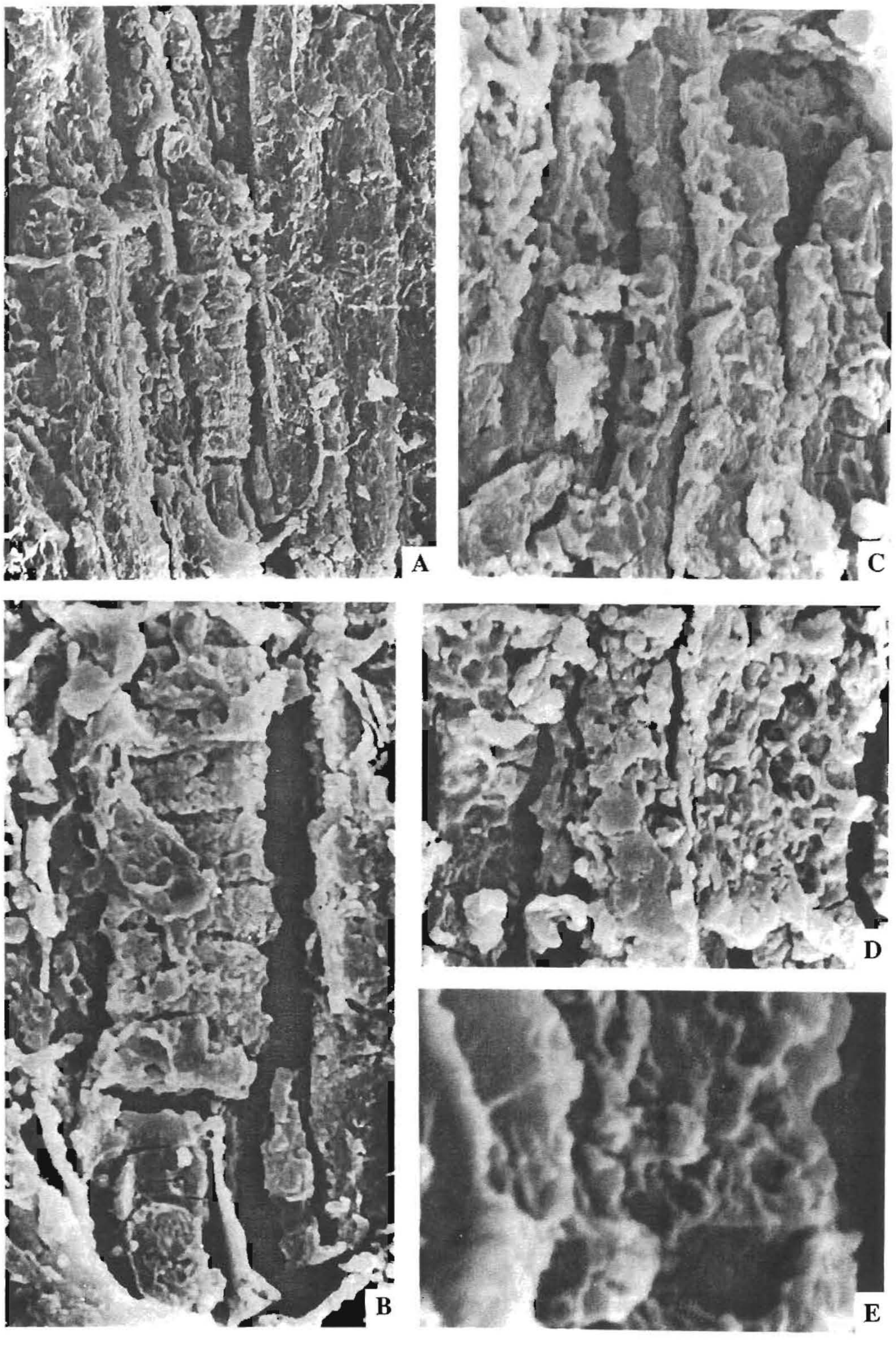


Fig. 5. Paratype P1202107. A. Nodal zone, arrow on leaf traces, SEM, x 50. B. Pair of leaf traces marked in A, SEM, x 400.

by a thick annular ridge (Fig. 3D, E). They are about 7-8 per groove width, densely crowded, hardly more than one cell apart, irregularly orientated, not forming distinct files. The guard cells are sunken, with apertures faintly marked but lacking distinct ledges. Outlines of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individual subsidiary cells are not discernible within the annular ridge.

The surface pattern of anastomosing ridges corresponds to a subepidermal network of thick sclerenchymous strands (Figs 3C, 6D). The internode of a shoot with four-membered nodes shows four large vascular bundles along the ribs (Fig. 4A, B). Their complete number should be eight. Small bundles between them are surfacing sporadically from a deeper level within the vascular system (Fig. 4B-D). The bundles coalesce at the nodes. The leaf traces depart in pairs from the larger bundles at their joining the nodal girdle (Fig. 4A, B and 5A, B).

The large bundles are four times thicker than the small bundles and apparently contain more thick-walled fibers that are minutely pitted (Fig. 6A). The tracheary elements are 7-10 mm wide showing reticulate wall pattern and indistinctly bordered pits that are arranged in two rows or, less commonly, in irregular groups on the radial walls (Figs 6B, C). Vessels differ from tracheids in that the pits at their poles are transformed into dense perforations (Fig. 6D) that are irregularly confluent sometimes forming larger pores (Fig. 6E). The secondary and tertiary wall thickenings are preserved as casts of the infillings of the tracheary elements (Figs 6A, B, 7A). They are helical or occasionally annular with fine longitudinal striation.

Discussion

In leaf arrangement this plant resembles *Ephedra* rather than *Phyllotheca* or other sphenopsids. The cuticular and vascular characters also indicate ephedroid affinities. The extant *Ephedra* growing in arid and semiarid environments produce abundant deciduous branchlets that are shed by an abscission layer at the base of an internode with the onset of the dry season. The Koonwarra material might represent such branchlets abscissed at various growth stages and, therefore, show a variable number of leafy nodes and likewise variable internode lengths. In the majority of extant *Ephedra* species there are 2 leaves that arise from each node, but in *E. foliata, E. torreyana, E. trifurcata* and some other species there are 3-4 leaves per node (Pearson 1920). The leaves of successive nodes are typically decussate, basally connate, with the sheaths variable, sometimes much reduced. Characteristic of *Ephedra* are sunken stomata in the interrib zones, their guard cells lacking cuticular ledges. The number of vascular bundles in the axis loosely correlates with the number of leaves, so that in the 2-leaved shoots there are typically eight bundles while the 4-leaved shoots may have up to sixteen or occasionally twenty bundles (Deshpande & Keswani 1963). The alternation of large and small bundles, the latter situated deeper in the axis, appears more constant within the genus. According to Pearson (1920) the leaf traces depart separately from the nodal girdle, appearing as a continuation of the smaller bundles, but Deshpande and Keswani (1963) describe them as departing alternatively from the larger and smaller bundles before the nodal girdle is formed. The tracheids and vessels show circular bordered pits and helical thickenings, whereas perforations of the end walls are formed of enlarged or confluent bordered pits.

All these characters agree well with the fossil material. However, in the latter, the leaf number ranges from two to eight, far exceeding the range of extant species. Moreover, the ratio of leaf to internode bundle numbers is considerably less than in *Ephedra*. The Koonwarra plant can thus be described as having an ephedroid shoot morphology, but with a considerably less reduced foliar component than in the extant species of the genus. Because

Fig. 6. Paratype P1202107. A. Small vascular bundle showing tracheary elements and fibers, SEM, x 1200. B, Enlargement of a tracheary element with annular thickenings and a finely pitted perforation plate at one end. C. Tracheary elements with remains of pits and helical thickenings, SEM, x 2500. D, E. Tracheary elements with small terminal perforations and, in E, a large porous perforation, SEM, x 2800 and x 7000.

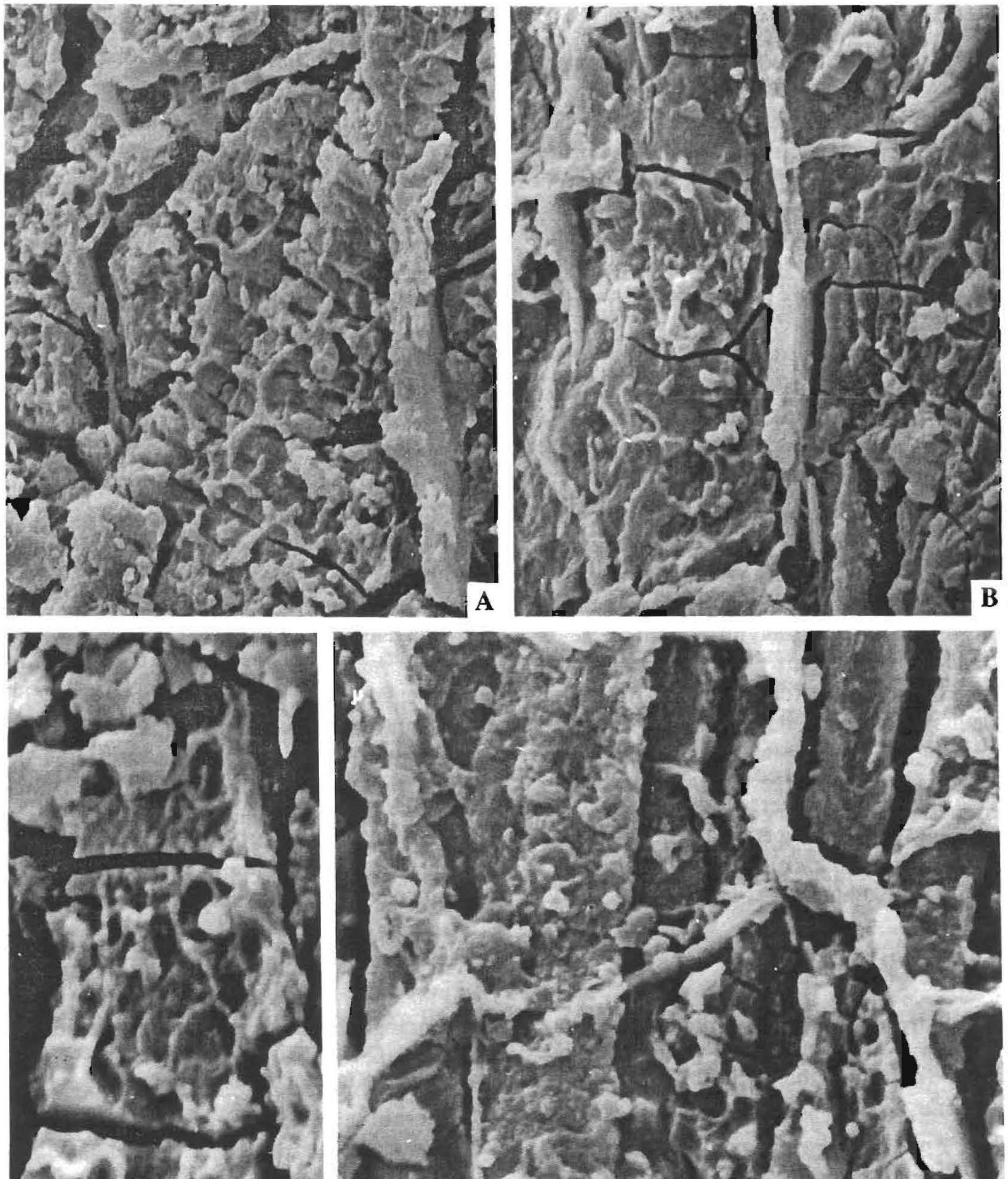

Fig.7. Paratype P1202107. A. Tracheary elements of large bundle showing spiral thickenings, x 2000. B, C. Tracheary elements with remains of bordered pits, x 3000 and x 5000, D. Sclerenchymous network over the vascular tissue, x2700.

of these differences and incomplete anatomical data the fossil plant can not be assigned to *Ephedra*. Among other known fossil forms, *Ephedrites* Goeppert & Berendt in Berendt (1845) includes featureless shoot impressions with no anatomical information. *Eoantha*, a proangiospermous plant of gnetalean affinities roughly contemporaneous to the Koonwarra fossil (Krassilov 1986) has linear graminoid leaves. In *Drewria potomacensis* the leaves are elongate, with goniopteroid venation (Crane & Upchurch 1987). *Ephedrites sinensis* (Wu, *et al.* 1986) is superficially similar, but differs in having three scaly leaves per node while in Jurassic *Heerala* (Krassilov & Bugdaeva 1988) the vegetative morphology is insufficiently known, precluding a comparison with the Koonwarra material.

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