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LYCAUGEA EDIEAE GEN. ET SP. NOV., A LATE DEVONIAN LYCOPSID FROM NEW SOUTH WALES, AUSTRALIA

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Premise of research. Resolving the time and patterns of origination of the Isoetales that thrived in the wet habitats of the late Paleozoic and have extant representatives in the genus *Isoetes* requires a better understanding of their early members and precursors. Recent studies conducted for a large part in South China acknowledged the diversification of Middle to Late Devonian taxa that possessed isoetalean traits and either were closely related to the Isoetales or occupied a basal position within this plant order. Recent investigations of Late Devonian floras from Australia show that this area, on the northeastern edge of Gondwana, also yields taxa with combinations of characters unknown elsewhere.

Methodology. The anatomy and external morphology of an anatomically preserved fragment of a lycopsid axis from the Famennian locality of Barraba, in New South Wales, are described. The new specimen is compared to lycopsid taxa on the basis of anatomically preserved specimens ranging from the Middle Devonian to the Late Carboniferous.

Pivotal results. The Barraba specimen shows a new combination of characters consisting of a medullated protosteles, three-zoned cortex with a wide middle cortex, homogeneous primary outer cortex, presumably deciduous leaves, and slightly protuberant widely spaced leaf bases. Leaf bases show a single large parichnos and are covered adaxially by a thick translucent layer. The specimen is interpreted as the distal branch of a new arborescent taxon, *Lycaugea edieae*. Taxa with the closest morphoanatomical characters, such as *Wexfordia hookense*, belong to the Isoetales and are found in deposits of Europe and the eastern United States.

Conclusions. *Lycaugea edieae* is the third lycopsid taxon described from Barraba, which, to date, has yielded a majority of spore-producing plants. It increases the diversity of the early Isoetales around the Devonian-Carboniferous boundary. The Barraba flora is more similar to the contemporaneous flora in southern Laurussia than to that in China.

Keywords: Lycopsida, Isoetales, Famennian, Australia, Gondwana, anatomy.

Online enhancements: appendixes.

Introduction

Numerous studies conducted on anatomically preserved specimens in the 1980s and 1990s provided evidence of the tremendous taxonomic diversity of the Carboniferous lycopsids, especially of the Isoetales sensu DiMichele and Bateman (1996), which thrived in the wet habitats of Laurussia. Ongoing studies of Devonian lycopsids show that the diversification of the Isoetales may have started early, with the origination, in the Middle to Late Devonian, of numerous genera showing some isoetalean traits but for which affinities with this plant order remain uncertain (Chaloner 1967; Fairon-Demaret 1977; Chitaley and McGregor

1988; Senkevitch et al. 1993; Cai and Chen 1996; Chitaley and Pigg 1996; Pigg 2001). Indeed, over the past 20 years, the description of new lycopsids, mainly from China, has shown that characters considered advanced (i.e., unknown in the extinct Drepanophycales and Protolpidodendrales and present in the Isoetales), such as heterospory, ligulate leaves, secondarily derived bipolar growth, stigmatic rootlets, and the production of secondary xylem (see Bateman et al. 1992; Pigg 2001 for a detailed assessment of the characters defining the Isoetales), evolved in the Devonian, some as early as the Middle Devonian (Wang et al. 2003b; Xue 2011; Gerrienne et al. 2018; Xue et al. 2018; Stein et al. 2020). Investigations conducted for Gondwana are much fewer than those for Chinese localities but are not less promising regarding the early evolutionary history of the lycopsids (Prestianni and Gess 2014; Evreinoff et al. 2017).

In Australia, Barraba is a plant locality of Famennian (Late Devonian) age that has yielded specimens preserved both as compressions and as permineralizations. The latter are few, but

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their anatomy is well preserved. Permineralized specimens include stem fragments of fernlike plants (Chambers and Regan 1986; Meyer-Berthaud et al. 2007; Champreux et al. 2020), a large bisporangiate lycopsid cone assigned to the new genus *Cymastrobos* (Evréinoff et al. 2017), and a small lycopsid axis occurring close to *Cymastrobos* in the same layer. Its cone organization, the morphology of its sporophyll-sporangium units, and its spore content suggest that *Cymastrobos* occupied a basal position in the Isoetales. The present article describes the small lycopsid axis found in the vicinity of *Cymastrobos*, provides evidence that it represents a new genus named here *Lycaugea*, and discusses its affinities with the Isoetales. This discovery contributes to a better understanding of the composition of Australian floral assemblages before the Devonian-Carboniferous boundary and to a reevaluation of their diversity.

Material and Methods

The single specimen representing *Lycaugea edieae* was found in the Mandowa Mudstone, a marine formation of the Tamworth Belt in the northeastern part of New South Wales. The Mandowa Mudstone consists of a thick sequence of dark laminated mudstone layers interbedded with thin layers of siltstones and sandstones (Vickery et al. 2010). It records the sedimentation on a distal shelf and continental slope. The Mandowa Mudstone contains abundant plant adpressions of late Famennian age. A single locality at the southeastern edge of the town of Barraba and at the confluence of Connors Creek and the Manilla River has yielded anatomically preserved specimens (Chambers and Regan 1986; Meyer-Berthaud et al. 2007; Evréinoff et al. 2017; Champreux et al. 2020). J. Irving, who collected the *Lycaugea* specimen, mentioned (J. Irving, personal communication) that the axis was found close to the cone assigned to *Cymastrobos*. The axis is referred to as specimen 161.999.0 and is housed in the Museum Victoria in Melbourne. It was preserved by calcium phosphate cellular permineralization. One thin section and 18 serial acetate peels were prepared in transverse section and 17 serial acetate peels in longitudinal section. Acetate peels were mounted on microscope slides.

To evaluate the affinities of *L. edieae*, a comparison that involved 12 morphoanatomical characters was carried out with 59 lycopsid taxa ranging from the Givetian (Middle Devonian) to the Pennsylvanian. The corresponding information, presented in appendixes 1–3 (apps. 1–4 are available online), is substantial, and our discussion focuses only on the taxa most similar to *L. edieae*.

We made a multivariate analysis with the PAST software (Hammer et al. 2001) to show how the phenotypic disparity of the isoetalean lycopsids and allies changed between the Givetian and the Pennsylvanian and to discuss the position of *Lycaugea* in the corresponding morphospace. To avoid biases due to unknown characters, we did not use the full set of taxa and characters recorded in appendixes 1–3. A subset of 28 taxa and nine characters was selected (app. 4). We conducted a principal coordinate analysis based on a dissimilarity matrix, that is, the number of character state differences for each pair of taxa. Characters are binary or have nonordered multistates. Their coding is available in appendix 4.

Description

The specimen consists of an unbranched fragment of axis measuring 30 mm long and 8 mm wide and composed only of primary tissues. It is characterized by a medullated protostele surrounded by a three-parted cortex (figs. 1, 2A). To avoid confusion and because the word “siphonostele” may be associated with the presence of leaf gaps, which are absent in lycopsids, we use the term “medullated protostele” to describe the stele of this specimen and that of all other taxa mentioned in this article showing thin-walled elements in their center. The middle cortex is broad and lacunar. The outer surface of the specimen shows small noncontiguous leaf bases (fig. 3).

Stele

In transverse section, the 1.8 × 1.9-mm-wide stele comprises a 410–450- μ m-thick ring of primary xylem enclosing a broad pith measuring 1 mm in diameter (fig. 2A, 2B). The contact between the pith and primary xylem is irregular but sharp. The preserved pith cells lining the innermost metaxylem tracheids have thin walls and range from 40 to 75 μ m in diameter (fig. 2D). Metaxylem tracheids have 2–4- μ m-thick walls. Their diameter is 40–90 μ m close to the pith, decreasing to 30–45 μ m for the peripheral ones (fig. 2B, 2E). The protoxylem forms a continuous band of one to four small tracheids encircling the metaxylem (fig. 2B, 2E–2G) and shows a smooth circular outline. With a diameter ranging from 10 to 20 μ m, the protoxylem elements are distinctly smaller than the metaxylem tracheids (fig. 2E–2G), and their walls are thinner (1.5–2.5 μ m). Peripheral to the primary xylem is a 90–100- μ m-wide zone of badly preserved cells that may correspond to the phloem (fig. 2F, 2G).

Cortex

The parenchymatous tissue external to the poorly preserved phloem is interpreted as the inner cortex. It is narrow, represented by a 85–120- μ m-thick band of small tangentially flattened thin-walled cells (figs. 1, 2B, 2E–2G). In transverse section, these cells range from 17 to 50 μ m in tangential dimensions and from 10 to 20 μ m radially.

External to the inner cortex is a wide zone devoid of any cellular elements but containing exogenous remains such as megaspores (figs. 1, 2A, 2B, 2E, 2H). This 0.95–1.15-mm-thick zone, which is nearly as wide as the outer cortex, shows a sharp contact inwardly with the inner cortex and outwardly with the outer cortex. It is connected to the parichnos accompanying the leaf traces in the outer cortex (see “Leaf Traces” below). We interpret it as a middle cortex.

In transverse section, the outer cortex is 1.25–1.35 mm wide (figs. 1, 2A). The cells of the inner part (20–70 μ m in diameter) are larger than those of the outer part (20–42 μ m in diameter; fig. 2C). All have thickened walls. This tissue is bounded externally by a hypodermis with cells that are circular and small (10–25 μ m in diameter), with heavily thickened walls (fig. 2K). The width of the hypodermis is variable, from 200–300 μ m around the leaf bases to 50 μ m between them (fig. 2C, 2K). In longitudinal section, the cells of the outer

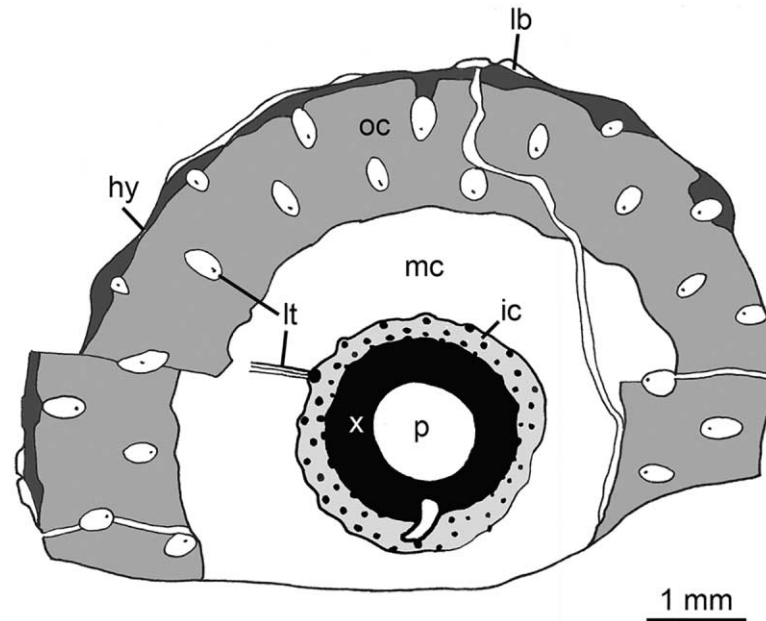


Fig. 1 *Lycaugea edieae*. Schematic view of the stem in transverse section, showing the spatial organization of tissues and leaf traces. The hypodermis is in dark gray. 161.999.0-1 XS 13. hy = hypodermis; ic = inner cortex; lb = leaf base; lt = leaf trace; mc = middle cortex; oc = outer cortex; p = pith; x = xylem.

cortex are light brown in color and elongated and show transverse to oblique end walls (fig. 4A, 4B, 4D, 4E). Their length ranges from 65 to 250 μm . Hypodermal cells in longitudinal section are dark brown (fig. 4B, 4D, 4E).

Leaf Traces

Leaf traces are helically arranged (figs. 1, 3). In transverse section, they depart as small strands of 10–16 narrow tracheids at the surface of the protoxylem ring (fig. 2E–2G). Leaf traces depart at a narrow angle and enlarge in the inner cortex, where they consist of 16–25 tracheids (fig. 2F, 2G). Here, leaf traces acquire an oval outline in cross section, ranging from 70 to 100 μm tangentially and from 40 to 65 μm radially. They cross the middle cortex as a transversely oriented strand of tracheids surrounded by thin-walled cells in continuity with those of the inner cortex (figs. 1, 2I). The course of the leaf traces becomes oblique again in the outer cortex (figs. 1, 2, 4) and is then transversely oriented in the leaf bases (fig. 5C–5E). Leaf traces in the outer cortex consist of a small strand of primary xylem tracheids surrounded by thin-walled cells probably corresponding to phloem elements and cells comparable to those of the inner cortex. Leaf traces are associated with a large abaxial cavity, or parichnos, connected to the middle cortex (figs. 2, 4). Cavities are 220–280 μm broad and radially elongated in transverse section. In longitudinal section, they measure 450–560 μm high in the inner part of the outer cortex and 340–440 μm high in the outer part, where they are cut less obliquely.

Leaf Bases

The leaf bases are slightly raised and separated from each other (figs. 3, 4C–4F, 5). They all have the same length and are all covered by a translucent layer limited by a black line (fig. 5). The black line is not irregular, as would be expected if the leaves had decomposed or broken during transport. Rather, it shows a smooth and consistent shape for all the leaf bases, suggesting that the leaves of this specimen were not torn off but shed naturally and that they were deciduous. The translucent layer, which is thin in the abaxial part of the leaf bases (fig. 5B, 5C), becomes progressively thicker and conspicuous in the adaxial part (fig. 5G–5I).

Leaf bases are supported abaxially and laterally by a broad sheath of thick-walled hypodermal cells that are embedded relatively deep in the outer cortex (figs. 3B, 4B). In face view, the leaf bases are obovoid and appear almost as wide as high (figs. 3B, 3C, 4D–4F). They measure 700–800 μm wide and 750–820 μm high at the stem surface. They tend to be heart shaped distally in surface view (fig. 4F). Here, however, the upper part is missing. In transverse section, the missing part corresponds to the translucent zone in its thickest part (fig. 5D–5I).

In the leaf base, the vascular strand and the cavity lining it abaxially (i.e., the parichnos) bend and become transversely oriented (fig. 5B–5E). Proceeding in a radial direction, the parichnos becomes filled with parenchyma cells that are contiguous, without any intercellular space, and have progressively thicker walls (figs. 4D, 4E, 4G, 4I, 5A). The parichnos forms a broad scar on the outer surface of the leaf base (fig. 5B). The leaf vascular

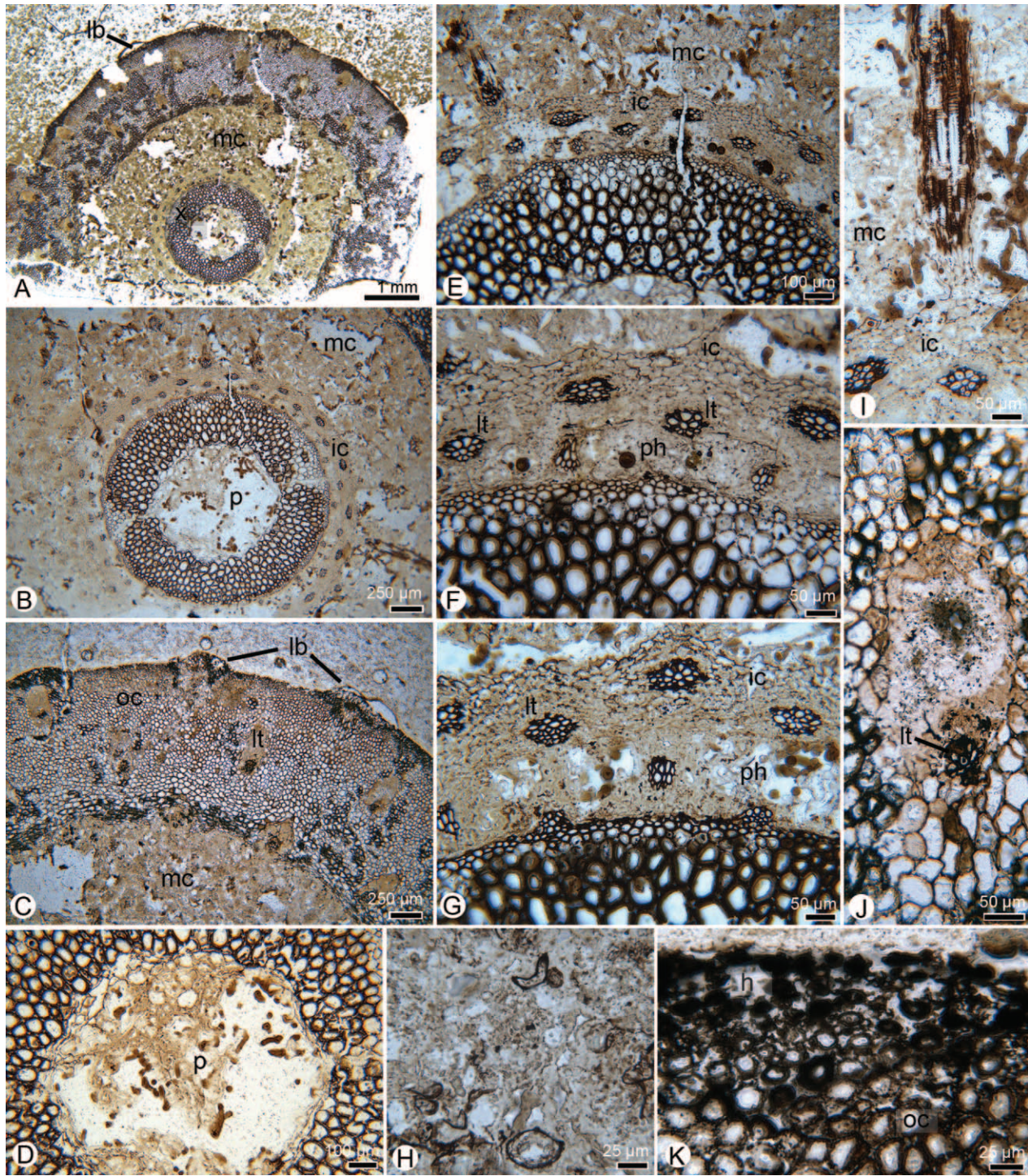


Fig. 2 *Lycaugea edieae* holotype specimen in transverse section. *A*, Stem, general view; 161.999.0-16. Scale bar = 1 mm. *B*, Stele, inner cortex, and part of middle cortex; 161.999.0-10. Scale bar = 250 μ m. *C*, Outer cortex; 161.999.0-5. Scale bar = 250 μ m. *D*, Pith and inner part of the primary xylem; 161.999.0-5. Scale bar = 100 μ m. *E*, Stele and inner cortex; 161.999.0-7. Scale bar = 100 μ m. *F*, Detail of the stele and inner cortex; 161.999.0-9. Scale bar = 50 μ m. *G*, Detail of the stele and inner cortex; 161.999.0-9. Scale bar = 50 μ m. *H*, Detail of the middle cortex; 161.999.0-5. Scale bar = 25 μ m. *I*, Detail of a leaf trace in the middle cortex; 161.999.0-10. Scale bar = 50 μ m. *J*, Detail of a leaf trace in the outer cortex; 161.999.0-7. Scale bar = 50 μ m. *K*, Detail of the outer cortex and hypodermis; 161.999.0-5. Scale bar = 25 μ m. h = hypodermis; ic = inner cortex; lb = leaf base; lt = leaf trace; mc = middle cortex; oc = outer cortex; ph = phloem; p = pith; x = xylem.

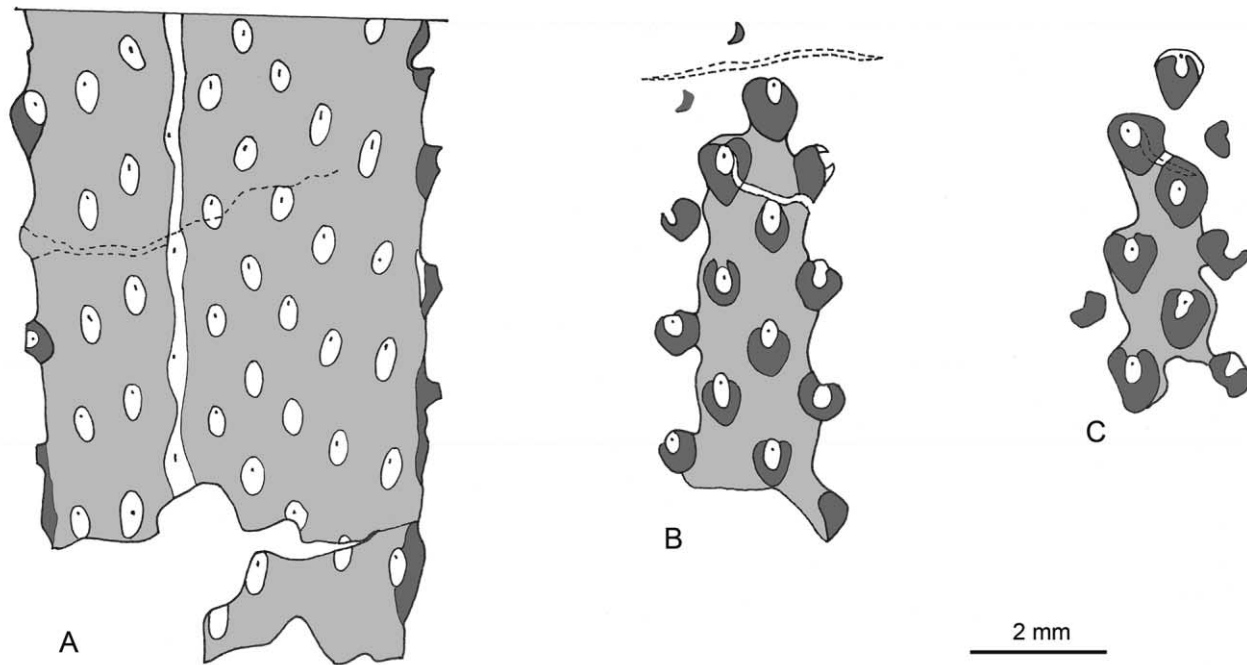


Fig. 3 *Lycaugea edieae*. Longitudinal sections through the stem, showing the helical arrangement of the leaf traces and leaf bases from the inner part (A) to the outermost part (C) of the outer cortex. A, 161.999.0-LS 20. B, 161.999.0-LS 6. C, 161.999.0-LS 2.

trace comes out just above (fig. 5C–5F). Two hypothetical reconstructions of a leaf base in lateral and face views are proposed in figure 6.

Systematic Paleobotany

Class—*Lycopsidea* Kenrick and Crane 1997

Order—*Isoetales* DiMichele and Bateman 1996

Family—*Incertae Sedis*

Genus—*Lycaugea* Meyer-Berthaud,
Decombeix, Blanchard gen. nov.

Type Species—*Lycaugea edieae* Meyer-Berthaud,
Decombeix, Blanchard sp. nov.

Diagnosis. Axis with helically arranged deciduous leaves. Leaf bases showing a parichnos below a small leaf vascular trace. Leaf trace and parichnos located in the upper part of the leaf base. Parichnos in leaf bases large, filled with contiguous parenchyma cells showing thicker walls toward the outer region of the leaf bases. Primary vascular tissues consisting of a medullated stele. Protoxylem continuous, forming a thin ring with a smooth outer border around the metaxylem. Primary cortex three zoned, with a wide middle cortex and a homogeneous outer cortex bounded externally by a hypodermis consisting of narrow cells with heavily thickened walls. Leaf traces in the outer cortex associated with the radially elongated abaxial cavity of the parichnos.

Etymology. *Lycaugea* is a combination of “lyc,” for Lycopsidea, and “augê,” from the Greek ἀυγή, meaning “dawn.” *Lycaugea* is interpreted as an early member of the Isoetales.

Lycaugea edieae Meyer-Berthaud,
Decombeix, Blanchard sp. nov.

Diagnosis. Axes up to 1 cm in diameter or more. Leaf bases obovoid in face view, 1 mm in height and width. Diameter of metaxylem tracheids ranging from 90 μm near pith to 30 μm near protoxylem ring. Diameter of protoxylem tracheids 10–20 μm . Inner cortex narrow, consisting of flattened thin-walled cells. Middle cortex as wide as outer cortex. Outer cortex consisting of 65–250- μm -long thick-walled cells decreasing from 70 to 40 μm in diameter outwardly.

Holotype. Specimen 161.999.0.

Repository. Museum Victoria, Melbourne, Australia.

Age. Upper Devonian, Famennian.

Formation. Mandowa Mudstone.

Locality. Connors crossing, left bank of the Manilla River, Barraba, northeastern New South Wales, Australia.

Etymology. The species name, *edieae*, is given in honor of Professor Edie Taylor for her invaluable contributions to Gondwanan paleobotany.

Discussion

General Features

The single axis representing *Lycaugea edieae* measures less than 1 cm in diameter and is characterized by a distinctive suite

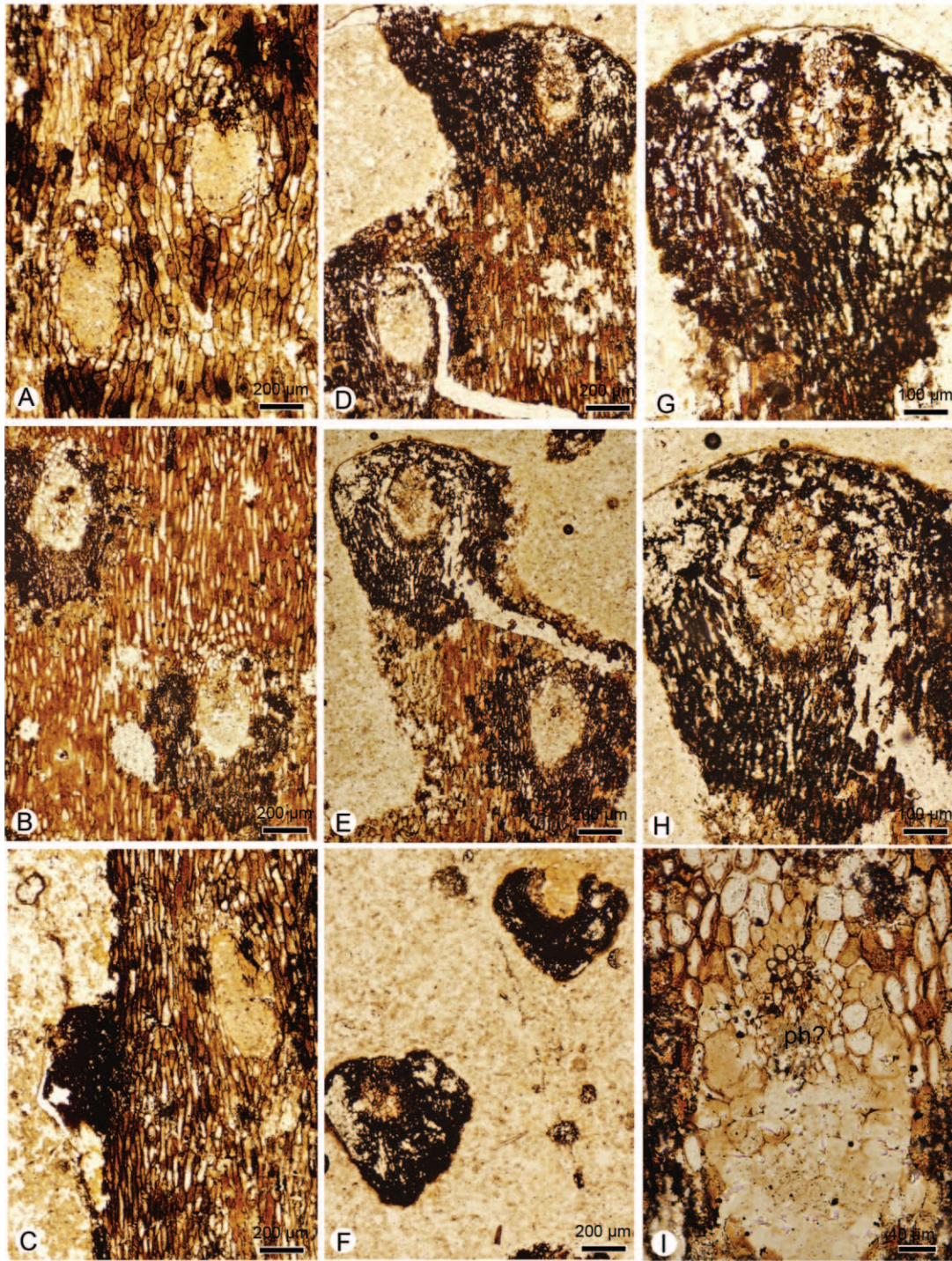


Fig. 4 *Lycaugea edieae* holotype specimen: outer cortex and leaf bases in longitudinal section. *A*, Inner part of the outer cortex, showing two leaf traces and their empty abaxial cavity; 161.999.0-CL20. Scale bar = 200 μm . *B*, Outer part of the outer cortex, showing two leaf traces and their abaxial cavity surrounded by thick-walled hypodermal elements; the uppermost cavity is filled with parenchyma cells; 161.999.0-CL6. Scale bar = 200 μm . *C*, Outer part of the outer cortex, showing a leaf trace, its empty cavity, and a partially preserved leaf base attached on the left side; 161.999.0-CL20. Scale bar = 200 μm . *D*, Outermost part of the outer cortex, showing two leaf bases, the upper one almost detached, and abaxial cavities filled with parenchyma; 161.999.0-CL7. Scale bar = 200 μm . *E*, Next section. The uppermost leaf base is the lowermost one in *D*; the abaxial cavities are filled with parenchyma; 161.999.0-CL2. Scale bar = 200 μm . *F*, Outer part of two partially preserved leaf bases; 161.999.0-CL3. Scale bar = 200 μm . *G*, Detail of a partially preserved leaf base; 161.999.0-CL6. Scale bar = 100 μm . *H*, Detail of the uppermost leaf base in *E*; 161.999.0-CL2. Scale bar = 100 μm . *I*, Detail of a leaf trace and its abaxial cavity becoming filled with parenchyma cells in the outer cortex; 161.999.0-CL6. Scale bar = 40 μm . ph = phloem.

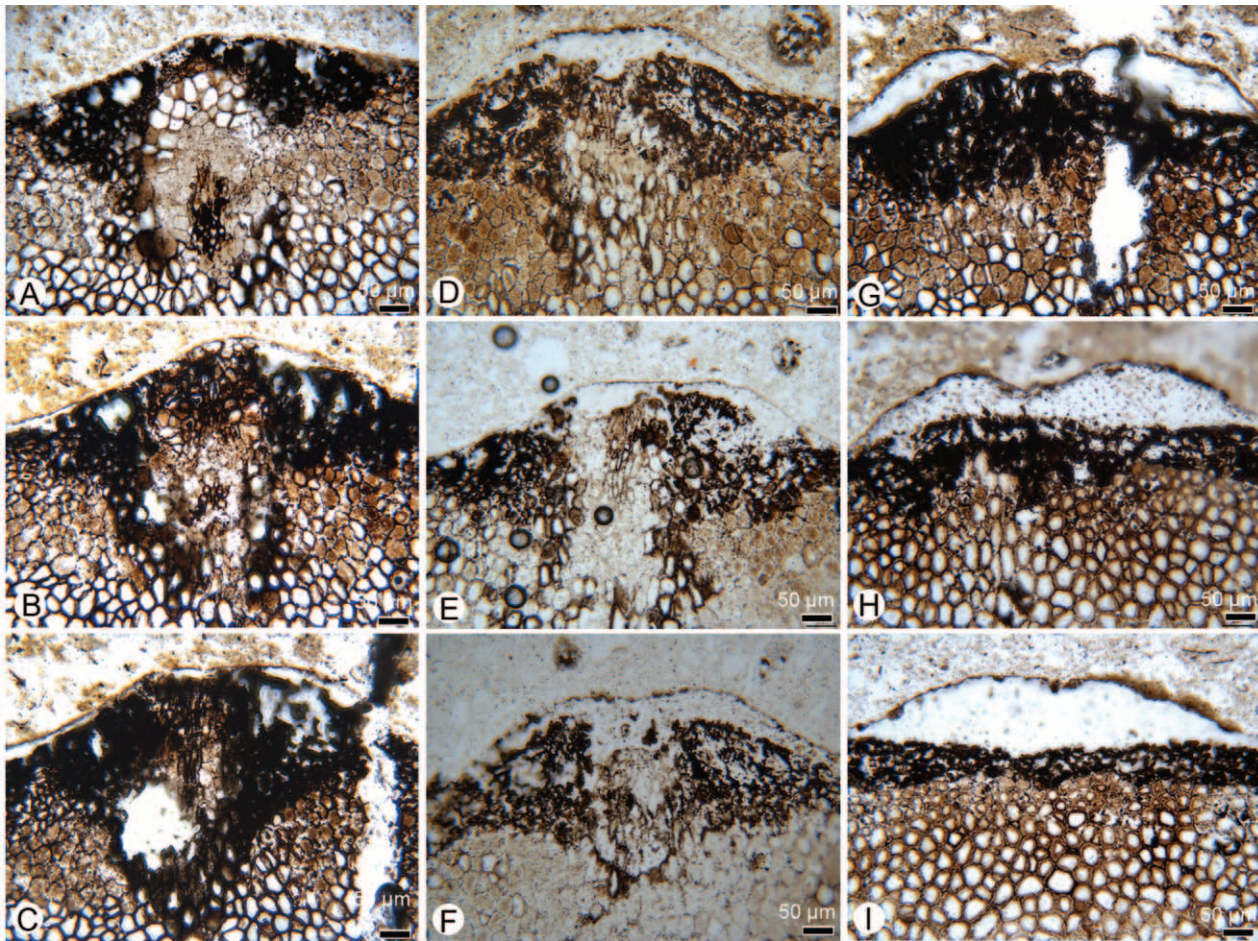


Fig. 5 *Lycaugea edieae* holotype specimen: series of transverse sections showing upward anatomical changes in the leaf bases, from the base (A) to the top (I). A, B, Levels with an abaxial cavity filled with tightly appressed parenchyma cells forming a parichnos that opens to the outside in B. C–F, Levels with a horizontal leaf trace (xylem and surrounding tissues) reaching the presumed surface of a leaf scar. G–I, Upper part of the leaf bases; the depressed zone in G and H corresponds to a putative leaf scar. A, 161.999.0-17. B, 161.999.0-16. C, 161.999.0-15. D, 161.999.0-5. E, 161.999.0-2. F, 161.999.0-3. G, 161.999.0-13. H, 161.999.0-9. I, 161.999.0-7. Note the increasing thickness of the hypodermis around the leaf bases from A to C. Scale bars = 50 μm .

of characters related to its outer surface and anatomy. The holotype of *L. edieae* is devoid of any secondary tissues. The protostele is characterized by a large empty central zone whose only preserved elements are parenchyma cells immediately adjacent to the primary xylem. Given the good preservation of all thick-walled cells in this specimen, we believe that if the central zone contained such cells, they would have been preserved. We therefore hypothesize that the central zone originally contained only thin-walled cells. However, we agree that this point remains uncertain. The metaxylem is bordered by a smooth ring of protoxylem that does not form any prominent teeth in transverse section. The cortex is three parted, with a wide middle cortex. Cells in this latter part have not been preserved. The outer cortex is homogeneous. A hypodermis of heavily thickened cells supports the leaf bases abaxially and laterally. Leaf traces are associated with an abaxial parichnos connected to the middle cortex.

The smooth clear-cut distal surface of the leaf bases suggests that the leaves were deciduous. The leaf bases are helically arranged and separated from each other. Their outer surface is ob-

ovoid and small, less than 1 mm in height and width. The leaf bases are covered by a translucent layer that corresponds to a tissue that is no longer preserved. This layer is thick in the adaxial part of the leaf bases (figs. 5D–5I, 6). It may have been involved in the abscission of the leaves. The actual surface of attachment of the leaf is conjectural. Whether the parichnos was infrafoliar (fig. 6A, 6B) or continued its course within the leaf lamina (fig. 6C, 6D) is uncertain. In both cases, the tissue without intercellular spaces filling the parichnos when leaves were no longer functional and after leaf abscission could have prevented the entry of pathogens into the axis (Patharkar and Walker 2018). No ligule was observed in the leaf bases, but a ligule may have been produced either in the upper field of the leaf bases, that is, in the area now represented by the thick part of the translucent layer, or distally, on the detached part of the leaves.

The Barraba specimen has a relatively small diameter, and all its tissues are primary. It may represent the stem of a small herbaceous plant such as *Oxroadia gracilis* (Alvin 1965; Bateman

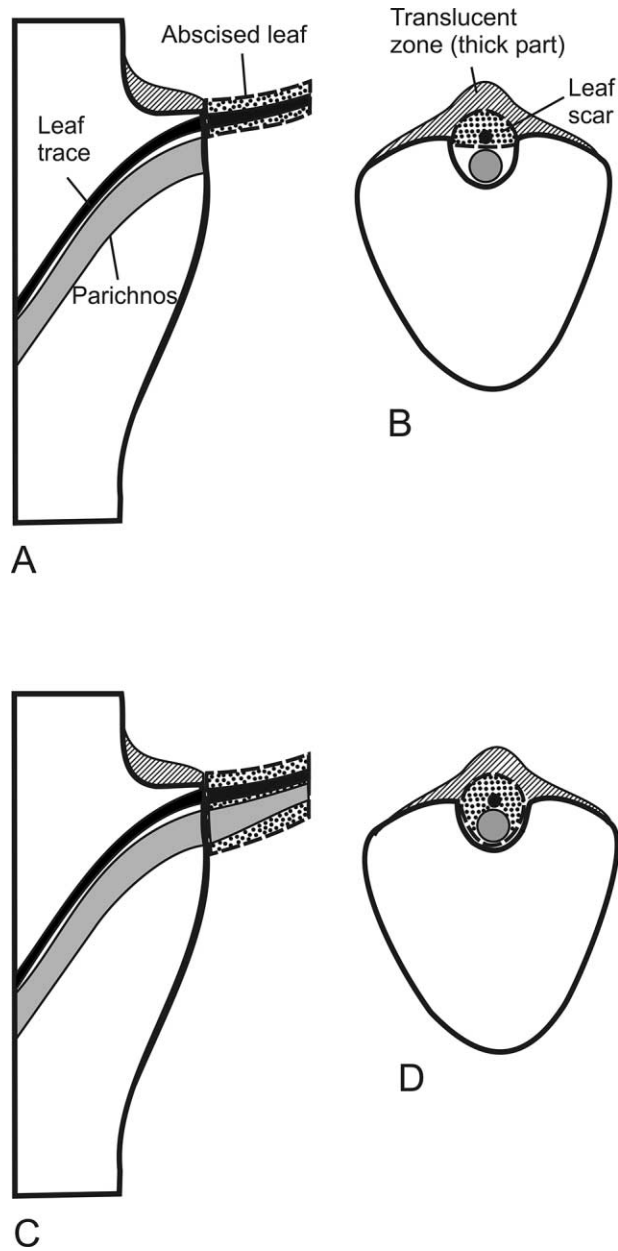


Fig. 6 *Lycaugea edieae*: reconstructed leaf base and basal part of a hypothetical deciduous leaf in lateral (A, C) and face (B, D) views. A and B correspond to a leaf containing the leaf trace and inserted above the parichnos scar. C and D correspond to a larger leaf containing the leaf trace and an intrafoliar parichnos.

1992), the stem of a juvenile tree, or the distal part of a large-sized plant (Eggert 1961). The Barraba specimen has a medullated rather than solid protosteles, and its leaves were probably deciduous. These features are common in the distal parts of the arborescent Isoetales and rare in the herbaceous representatives of the order. Young trunks keep their leaves attached for a long period of time (Chaloner and Meyer-Berthaud 1983). We hypothesize, therefore, that the Barraba specimen represents a distal portion of branch in an arborescent individual that may have produced secondary tissues in more proximal parts.

Comparison with the Barraba Lycopsids

A single anatomically preserved lycopsid cone was collected at Barraba and was recently referred to the new genus *Cymastrobos* (Evréinoff et al. 2017). The cone axis is about the same diameter as the *L. edieae* type specimen, and both have a medullated protosteles. However, the cone axis of *Cymastrobos* shows an undulated rather than a smooth outline of the primary xylem, and its sporophyll traces are produced between the lobes, not according to the superficial mode of *L. edieae*. The cone, therefore, does not belong to the same plant.

Leptophloeum rhombicum, on the other hand, is abundantly represented by adpressions at Barraba. The arrangement, the shape, and the structure of the *Leptophloeum* leaf bases, which are rhomboidal and contiguous and lack any parichnos scar, are clearly different from those of *L. edieae* (Dawson 1862; Lemoigne 1982). Moreover, the primary xylem outline of *Leptophloeum* is not smooth but shows prominent teeth on its outer surface (Wang et al. 2005). *Lycaugea*, therefore, represents a third lycopsid genus at Barraba.

Comparison with Devonian and Carboniferous Lycopsids

Three orders of lycopsids, the Drepanophycales, the Protolepidodendrales, and the Isoetales sensu DiMichele and Bateman (1996), have Devonian representatives (Bateman 1992; Taylor et al. 2009; Xue 2011; Gerrienne et al. 2018). The two former ones comprise homosporous plants with a unipolar, herbaceous, erect, or creeping habit. They have persistent leaves that are eligulate in the Drepanophycales and ligulate in some Protolepidodendrales. Their unmodified sporophylls are arranged in fertile zones. Anatomically, they lack secondary growth, and their primary vascular tissues form solid protosteles, the primary xylem being deeply lobed or dentate on its outer border. The combination of features characterizing *Lycaugea* (see “General Features”) is found in the Isoetales, a heterosporous group of ligulate lycopsids that possess bipolar rhizomorphs bearing stigmarian rootlets and producing secondary tissues (DiMichele and Bateman 1996; Pigg 2001). The Isoetales show a wide range of habits, from herbaceous to arborescent (Long 1986; DiMichele and Bateman 1992, 1996; Wang et al. 2003a; Wang and Xu 2005). Their leaves are deciduous in arborescent forms, and their modified sporophylls may form strobili (DiMichele and Phillips 1985). Their vascular and cortical tissues show a large variety of configurations (Bateman et al. 1992; Taylor et al. 2009).

On the basis of the information recorded in appendixes 1–3, the taxa that share the most characters with *L. edieae* are dated to the Famennian–Tournaisian time interval. *Phytokneme rhodona*, from a Late Devonian locality in Kentucky, is one of them (Andrews et al. 1971). It shows a smooth outline of the primary xylem and a three-zoned cortex with a wide middle cortex, but, unlike *L. edieae*, *P. rhodona* has a solid protosteles and an outer cortex characterized by irregularly thickened cells. Information regarding its leaves is missing. In the same time range, numerous taxa possess a medullated protosteles like that of *L. edieae*. Some, such as *Smeadialia clevelandensis* (Chitale and Li 2004) and *Trabicaulis boylensis* (Roy and Matten 1989) from the United States or the species of *Trabicaulis* and *Landeyrodendron* from Southern France (Meyer-Berthaud 1984), also share a three-zoned cortex with *L. edieae*. However, they differ in the narrowness of their

middle cortex, the possession of special cells in the outer cortex (i.e., cells with inner threads in *Smeadia* and papillate cells in the other taxa), and the persistent character of their leaves. *Sublepidodendron songziense* from China (Wang et al. 2002, 2003a) has a medullated protosteles, and its primary xylem cylinder has a smooth outline, as in *L. edieae*. However, the external features of this species, which has persistent leaves, clearly differ from those of *L. edieae*. Close to the Devonian–Carboniferous boundary, the taxa with a medullated protosteles that have more characters in common with *L. edieae* are *Wexfordia hookense* from Ireland (Matten 1989; Klavins 2004), the lycopsid from the New Albany Shale in Kentucky described by Cichan and Beck (1987), and the one from Donetz referred to as “*incertae sedis*” and reported by Lemoigne and Itschenko (1980). The Donetz specimen, which lacks secondary tissues and is in the same range of diameter as the *L. edieae* holotype, differs from the latter in its persistent leaves and dentate border of the primary xylem. Like *L. edieae*, *Wexfordia* and the New Albany Shale specimen show a smooth outline of their primary xylem cylinder. They also share a three-zoned primary cortex comprising a wide middle part and a lack of any specific type of cells in the outer cortex. The New Albany Shale specimen, which is much larger than the *L. edieae* holotype, shows abundant secondary tissues, a feature probably related to its position in the whole plant. Its leaf characters are unknown. For these reasons, the systematic proximity of this specimen to *L. edieae* is difficult to assess. Within the Late Devonian to earliest Mississippian time interval, it is with the isoetalean genus *Wexfordia* that *L. edieae* shares the highest number of morphoanatomical characters (app. 1). Indeed, the Barraba specimen is thought to have had deciduous leaves, like *Wexfordia*, and the possibility that it was ligulate has not been dismissed. The only difference is that the parichnos in *L. edieae* is not divided in the leaf bases.

A slightly younger taxon sharing many characters with *L. edieae* is the Tournaisian species “*Lepidodendron calamopsoides*” from Scotland (Long 1964). In addition to a medullated protosteles in some parts of the plant, it has a three-zoned cortex including a wide middle cortex and an outer cortex devoid of any special cells (app. 2). Interestingly, all specimens of “*L.*” *calamopsoides*, including the largest ones, are devoid of secondary tissues. “*Lepidodendron calamopsoides*” differs from *L. edieae* in the dentate outline of its primary xylem border.

The Visean species “*Lepidodendron brownii*” from Scotland (Calder 1933) and *Paralycopodites brevifolius* from Visean to mid-Pennsylvanian localities of Europe and the United States (Morey and Morey 1977; DiMichele 1980; Pearson 1986; DiMichele and Bateman 2020) have a medullated protosteles and a three-zoned cortex. “*Lepidodendron brownii*” differs from *L. edieae* in its dentate primary xylem outline and papillate cells in the outer cortex. Its outermost tissues and leaves/leaf bases are unknown. Features of *Paralycopodites* that differ most from those of *L. edieae* are related to its leaves, which are persistent and show two parichnos strands (app. 3).

Most Pennsylvanian lycopsids are affiliated with the four best-circumscribed isoetalean families of the Carboniferous, the Chaloneriaceae, Sigillariaceae, Diaphorodendraceae, and Lepidodendraceae (DiMichele and Bateman 1996; Dunn et al. 2012). The Chaloneriaceae, represented by *Chaloneria* (Pigg 1992) and *Winslowia* (Dunn et al. 2012), have few characters in common with *L. edieae* (app. 3). The stele of *Winslowia* is

a solid protosteles, that of *Chaloneria* is dissected by parenchyma plates, and both show a dentate outline of the primary xylem. Leaf traces of *Chaloneria* and *Winslowia* are bilobed in the outer cortex. Leaves are persistent in *Chaloneria*. On the other hand, with its medullated protosteles, wide middle cortex, and deciduous leaves, *L. edieae* shares the basic anatomical organization of the Sigillariaceae, Diaphorodendraceae, and Lepidodendraceae (app. 3). These isoetalean families, however, are characterized by the higher complexity of their cortex, leaf bases, and, within the Sigillariaceae and Lepidodendraceae, leaf trace emission patterns.

Lycaugea in the Isoetales’ and Allies’ Morphospaces

The results of the principal coordinate analysis investigating the morphoanatomical disparity of the Isoetales and allies during the Givetian–Pennsylvanian time interval are presented in figure 7. The first three axes represent 81.76% of the total variation, with the first one standing for 56.4%, the second one for 15.5%, and the third one for 9.9%. This analysis does not take into account the diversity of characters and character states related to the primary vascular architecture, the cortex, and the morphology of the leaf bases observed in the lycopsids of Carboniferous age. The result is a probable underestimation of the morphospace occupied by the Mississippian and Pennsylvanian taxa. Caution should also be exercised when interpreting the morphological proximity of overlapping points in figure 7 when they represent Carboniferous taxa. These points may correspond to taxa having the same broad stelar and cortical organizations but differing in details of leaf trace emission, cortical cell composition, or leaf base shape and morphology. However, we think that it is reasonable to consider that the Givetian and the Pennsylvanian morphospaces did not overlap. Equally probable are the large portions of the morphospace (i.e., important morphoanatomical disparity) occupied by the Late Devonian and Mississippian taxa and their intermediate position between that of the Givetian and the more derived Pennsylvanian taxa. *Lycaugea* is well included in the group encompassing the Late Devonian and Mississippian lycopsids. Its position close to the center of this group when the first two axes of the analysis are considered is remarkable.

Plant Diversity at Barraba

Lycaugea edieae adds a new genus to the plant assemblage deposited at Barraba, which now counts three genera (*Keraphyton*, *Cymastrobis*, *Lycaugea*; Evreinoff et al. 2017; Champreux et al. 2020) and one species (*Polyxylon australe*; Chambers and Regan 1986; Meyer-Berthaud et al. 2007) unknown elsewhere. Although different, these plants have more characters in common with taxa described from Late Devonian–early Mississippian deposits from southern Laurussia (southern Europe, eastern United States) than with those from South China, a result consistent with that obtained for fishes (Young 1990; Torsvik and Cocks 2013). This might be the result of the presence of a marine barrier between South China and Gondwana, while a contact between northwestern Gondwana and southern Laurussia during the Late Devonian–early Carboniferous has been hypothesized by some authors (Klootwijk 2010). Interestingly, from a time

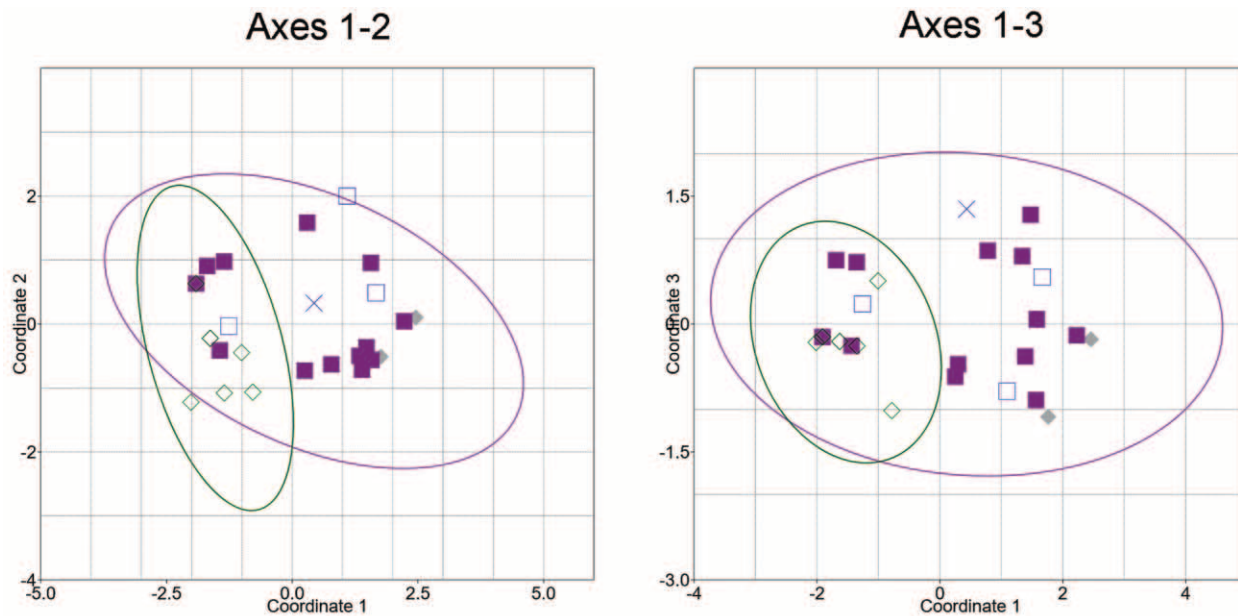


Fig. 7 Results of a principal coordinate analysis based on 28 taxa and nine characters showing the morphoanatomical disparity of the vegetative body of Middle Devonian to Upper Carboniferous Isoetales and allied taxa. Ninety-five percent confidence ellipses. Axis 1 stands for 56% of the total variation, axis 2 for 15.5%, and axis 3 for 10%. X = *Lycaugea edieae*; filled diamonds = Givetian taxa; open squares = Upper Devonian to lowermost Mississippian taxa; filled squares = Mississippian taxa; open diamonds = Pennsylvanian taxa.

when early seed plants also diversified markedly, all the taxa recorded to date at Barraba correspond to spore-producing plants, suggesting that they were the dominant components of the floras of Barraba's nearby coastal habitats.

Conclusions

1. *Lycaugea* is unique within the lycopsids in possessing the following combination of characters: a medullated protostele with a smooth outer border of the primary xylem, a wide middle cortex, deciduous leaves, and leaf bases with a single large parichnos scar below the leaf trace.

2. Except for the lack of division of the parichnos in the leaf bases, these features characterize the Isoetales. Within that order, the late Famennian genus from Ireland *Wexfordia* is the closest genus to *Lycaugea*. *Lycaugea* is also close to the Tournaisian taxon "*Lepidodendron*" *calamopsoides* from Scotland. With its direct mode of leaf trace emission, homogeneous cortex, and leaf bases lacking the complexity of those of the Sigillariaceae, Diaphorodendraceae, and Lepidodendraceae, *Lycaugea* is interpreted as a basal member of the Isoetales.

3. The discovery of *Lycaugea* in the late Famennian of Australia is one more piece of evidence of the marked taxonomic diversity and morphological disparity of the anatomically preserved lycopsids from the Late Devonian–Mississippian time interval.

4. At Barraba, the permineralized fossils are few compared with the adpression remains, but they show surprising taxonomic diversity. Five genera represented by anatomically preserved specimens are reported from this locality, two corresponding to early-

diverging fernlike plants (*Polyxylon*, *Keraphyton*), two to early isoetales (*Cymastrobos*, *Lycaugea*), and one to an archeopteridalean lignophyte (*Callixylon*).

5. Four of the five taxa from Barraba represented by permineralized specimens (*Polyxylon australe*, *Keraphyton*, *Cymastrobos*, *Lycaugea*) are specific to this locality, indicating that Australian floras of late Famennian age may have included endemic elements.

6. All the plants reported to date in this late Famennian locality produced spores. Taphonomical biases cannot be discarded, but this suggests that seed plants were not dominant components in the floras of the nearby coastal habitats.

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