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Macrofossil evidence for pleuromeialean lycophytes from the Triassic of Antarctica

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Triassic microfloras from Antarctica contain abundant lycophyte spores. However, macrofossils of this group of plants are missing, and thus the precise affinities of the spore producers remain unknown. Macrofossil remains of a pleuromeialean lycophyte, including an incomplete strobilus, isolated sporophylls and sporangia, as well as abundant megaspores, occur on a single rock sample from the central Transantarctic Mountains. Also occurring on the same surface is *Mesenteriophyllum serratum*, a strap-shaped leaf morphotype of uncertain affinity previously known only from the Kyrgyz Republic and the Taimyr Peninsula. The leaves display alternating transverse ridges and depressions that are similar to structures seen in compressed leaves of various isoetalean lycophytes. Leaf morphology and anatomy, together with the close association of the other lycophyte remains, suggest that *M. serratum* represents a pleuromeialean lycophyte leaf, which was part of the same plant that produced the sporophylls and sporangia. Sedimentological data indicate that this lycophyte inhabited a swampy, probably coal-forming overbank environment, which contrasts with the assumed xero- to halophytic habit of many other pleuromeialean lycophytes.

Key words: Isoetales, *Pleuromeia*, *Mesenteriophyllum*, phytogeography, palaeoecology, air chambers, Transantarctic Mountains, Antarctica.

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Introduction

The continental Triassic of the Transantarctic Mountains has yielded rich, diverse, and in some cases exceptionally well-preserved plant fossils that certainly rank among the most intensely studied and well-known early Mesozoic floras worldwide. Large collections of Triassic impression/compression floras and permineralized peat deposits have been accumulated since the first discoveries of plant fossils from Antarctica in the early 20th century. The Triassic vegetation of Antarctica consisted of a diverse array of plant groups, including horsetails, various fern and seed fern families, cycads, ginkgophytes, and conifers (see, e.g., Taylor and Taylor 1990; Taylor et al. 1993; Axsmith et al. 2000; Phipps et al. 2000; Ryberg et al. 2008; Hermsen et al. 2009; Decombeix et al. 2010; Escapa et al. 2010). In spite of this diversity based on macrofossils, palynofloras document that the high-latitude ecosystems of Antarctica were inhabited by an even wider spectrum of plants, many of which still lack macrofossil evidence. For instance, abundant lycophyte spores have been reported from various regions of East Antarctica, including spores of supposed pleuromeialean, isoetalean, and selaginellalean affinity (Kyle 1977; Kyle and Schopf 1982; Farabee et al. 1990; Taylor et al. 1993; McLoughlin et al. 1997; Askin and Cully 1998). With the exception of a few isolated sporangia (McLoughlin et al. 1997), however, documented evidence of lycophyte macrofossils is lacking. This may be explained by the generally low preservation potential of the small, presumably herbaceous plants, either because the plants themselves had a much lower fossilization potential or because they existed in habitats that were not conducive to fossilization. Alternatively, lycophyte macrofossils may simply have been overlooked or misidentified.

This paper describes the first macrofossil evidence for lycophytes in the Triassic of the Transantarctic Mountains. The material consists of an incomplete strobilus and several isolated sporophylls and sporangia that co-occur with abundant megaspores. Also present on the slab are several specimens of the enigmatic leaf *Mesenteriophyllum serratum* Sixtel, 1961. *Mesenteriophyllum* Sixtel, 1961 has so far been re-

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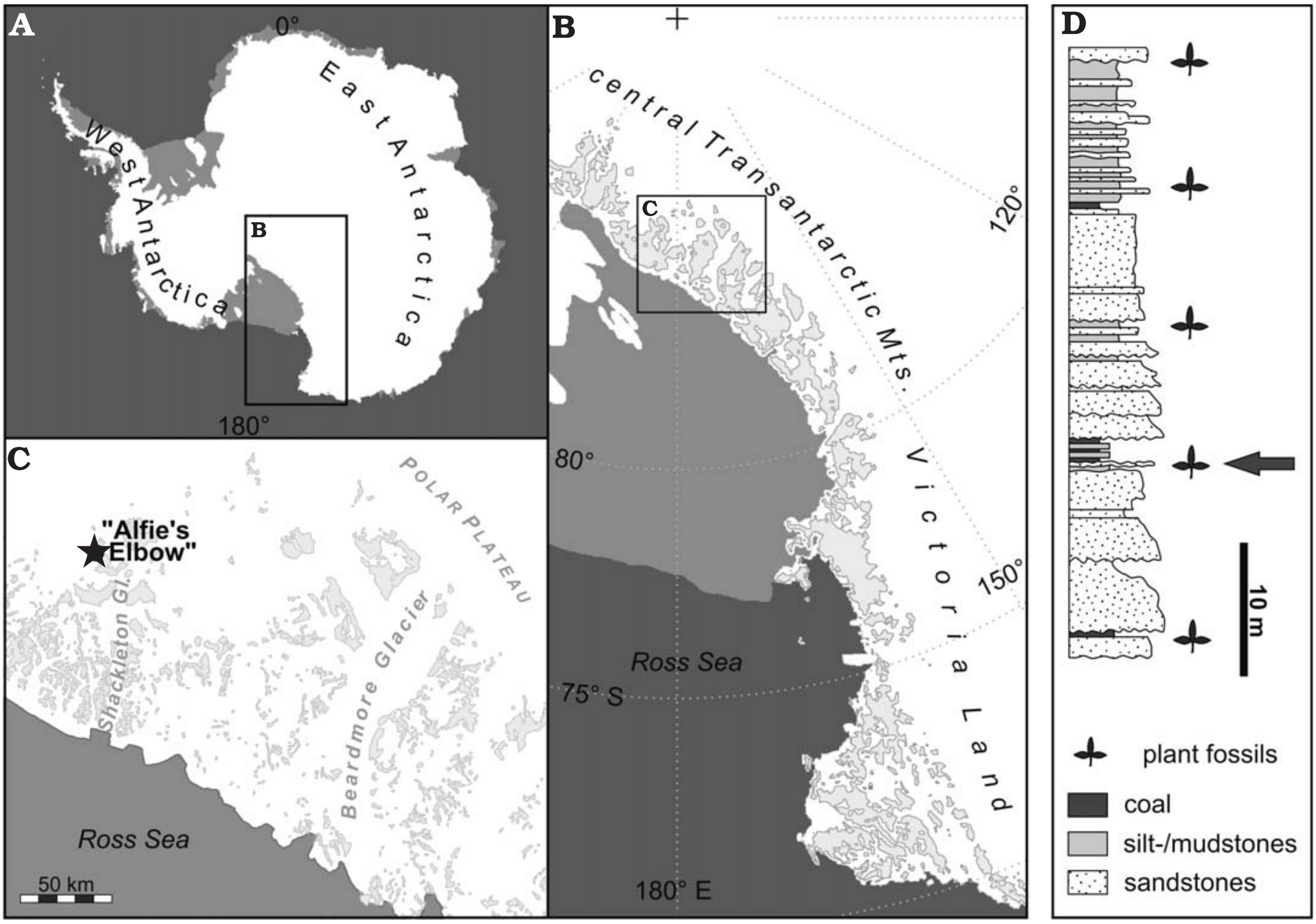

Fig. 1. Geographic location (**A**–**C**) and lithological column (**D**) of the plant-bearing succession at "Alfie's Elbow"; arrow indicates the position of the bed from which the present material was collected. Lithological column after Axsmith et al. (2000).

ported from the Triassic of the Kyrgyz Republic and the Taimyr Peninsula, and is currently regarded as a gymnosperm leaf of unknown affinity. By contrast, the material from the Transantarctic Mountains provides compelling evidence that *M. serratum* in fact represents sterile foliage of a pleuromeialean lycophyte.

Institutional abbreviation.—PCUK, Paleobotanical Collection at the Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence, USA.

Material and methods

The material was collected from an outcrop in the Shackleton Glacier region (central Transantarctic Mountains) that is informally known as "Alfie's Elbow" (Fig. 1A–C) (Axsmith et al. 2000). The section is dated as Late Triassic based on palynomorphs (Askin and Cully 1998). The entire collection of plant fossils from this locality comprises >500 slabs, most of which contain *Dicroidium* Gothan, 1912 and *Heidiphyllum* Retallack, 1981 foliage, as well as associated axes and reproductive organs, including *Umkomasia* Thomas, 1931, *Pteruchus* Thomas, 1933, and *Telemachus* Anderson, 1978.

The plant fossils described in this paper occur on a single block of silty, medium- to dark-grey, carbonaceous mudstone with abundant plant fragments (PCUK T5568). Plant fossils are preserved as impressions and coalified compressions. Cuticles and palynomorphs could not be recovered because the material is too highly altered. The plant fossils show little contrast to the surrounding matrix, which rendered photographic documentation challenging. Macroscopic images were taken under cross-polarization or oblique lighting to enhance contrast and surface details. Specimens were further analysed using a Leica MZ16 stereomicroscope. Microscopic images were taken with a Nikon DS-5M digital camera.

Systematic palaeontology

Division Lycophyta Boivin, 1956

Class Isoetopsida Rothmaler, 1951, incertae sedis

?Order Pleuromeiales Zimmermann, 1959

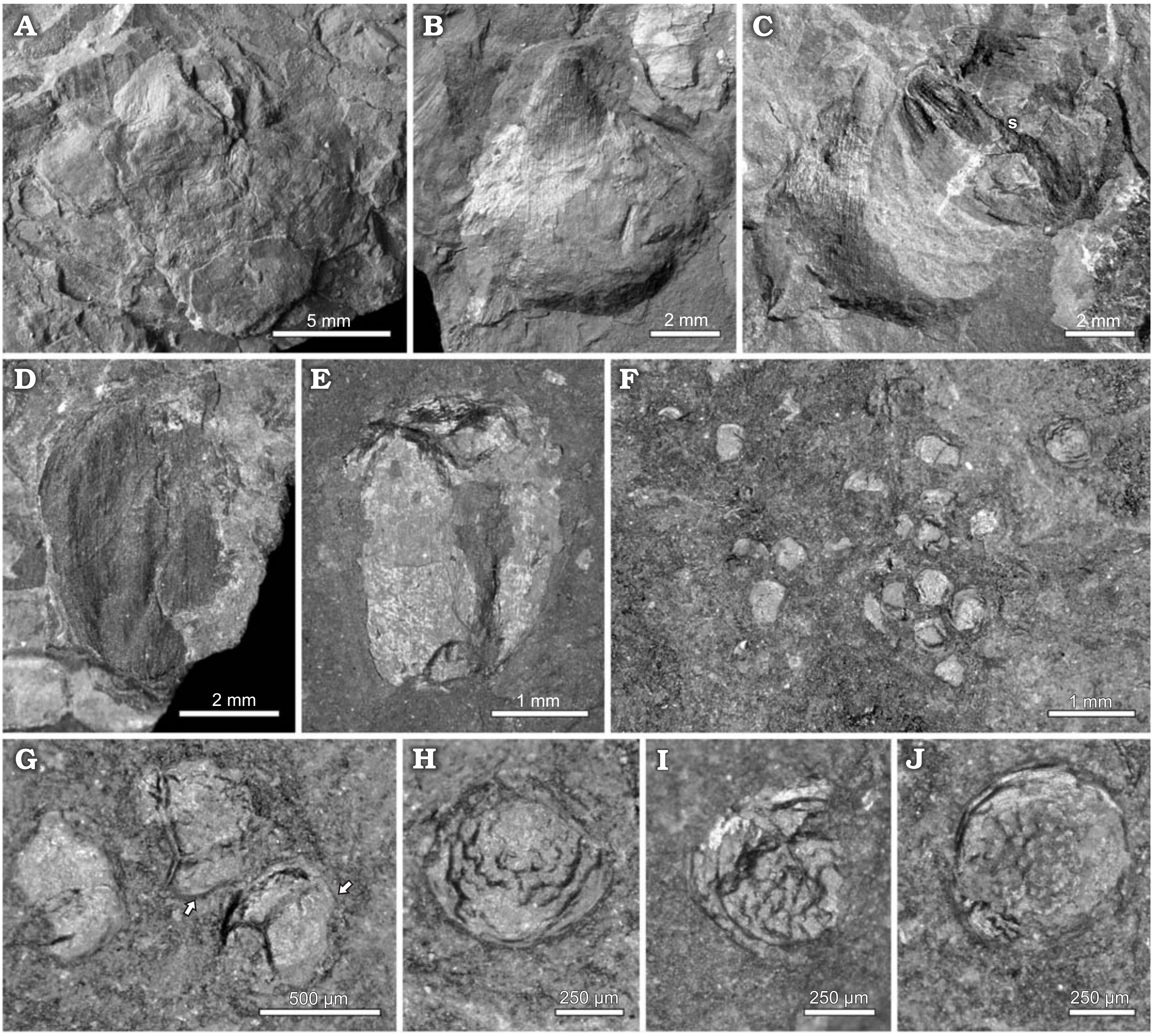

Fig. 2. Pleuromeialean lycophyte reproductive structures from the Upper Triassic of the "Alfie's Elbow" site, central Transantarctic Mountains. **A**. Articulated fragment of a strobilus. Individual sporophylls can be recognized by the longitudinal striations on the abaxial surface (compare Fig. 2B, C; see Fig. 3). **B**. Isolated sporophyll, abaxial surface. **C**. Same sporophyll as Fig. 2B, but after manual preparation, showing globose adaxial sporangium (s) beneath the sporophyll. **D**, **E**. Sporangia. **F**. Cluster of megaspores. **G**. Megaspores showing trilete marks and curvaturae (arrows). **H**–**J**. Distal faces of megaspores showing variation in surface ornamentation or preservation, including verrucate, conate, and echinate patterns.

Family unknown

Isolated reproductive organs

Fig. 2.

Material.—PCUK T5568, one block containing isolated fertile remains, including an incomplete strobilus, four sporophylls, five sporangia, and numerous megaspores.

Description.—Strobilus (Fig. 2A; see also Fig. 3) incomplete, 1.2 cm long and 1.5 cm wide, composed of a central axis bearing helically arranged, imbricate sporophylls, each helix consisting of about five to six sporophylls. Sporophylls symmetrically ovate to subtriangular in outline, about 8 mm long by 7 mm wide, with a broad, in some cases slightly cordate, base; lateral margins of sporophylls up to 2 mm wide; distal margin with a slightly projecting acuminate tip; abaxial surface of sporophyll convex, with distinctive surface pattern composed of narrow longitudinal striae radiating from the base (Fig. 2A, B); sporangia attached in the centre of the sporophyll on the adaxial surface (Fig. 2C). Sporangia circular to ovate in outline, up to 6 mm long by 5 mm wide when compressed, with smooth surface or bearing fine longitudinal striations (Fig. 2C–E). Isolated megaspores trilete, originally subspherical,

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600–800 μm in diameter; haptotypic mark with rays extending to or near to the equator (Fig. 2F, G); in some cases bordered by distinct curvaturae; proximal exine smooth to scabrate, distal exine smooth or with coarse ornamentation composed of conae, rugulae, verrucae, or echinae (Fig. 2H–J).

Remarks.—The presence of megaspores and the helical, imbricate arrangement of sporophylls into a strobilar structure suggest affinities with the Pleuromeiales. Triassic pleuromeialean lycophytes are segregated into two major groups: one is represented by *Pleuromeia* Corda, 1852, whereas the other includes *Annalepis* Fliche, 1910 and a diverse array of related taxa (Pigg 1992, 2001; Grauvogel-Stamm and Lugardon 2001; Taylor et al. 2009). Although terminal cone-like strobili and trilete megaspores occur in both groups, the present fructifications appear more similar to those of *Pleuromeia* than to those of *Annalepis*-type lycophytes. Features typical of *Pleuromeia* include (i) a small number of sporophylls per spiral, resulting in a rather lax appearance to the strobilus, (ii) short, ovate-to-subtriangular outline and abaxially convex morphology of the sporophylls, (iii) circular-to-ovate outline and large size of the sporangium which almost completely covers the adaxial sporophyll surface, and (iv) absence of a longitudinal midline on the sporangium. The Antarctic strobilus fragment and associated sporophylls are remarkably similar to strobili of *Pleuromeia rossica* Neuburg, 1960 (Neuburg 1960: pls. 6, 7) and *Pleuromeia jiaochengensis* Wang and Wang, 1982 (Wang and Wang 1982: pl. 23: 1–9). However, the limited sample size and fragmentary preservation of the fossils do not allow for a more detailed assessment.

The megaspores show varying degrees of exine ornamentation, which likely reflects different modes of preservation (see Wang 1991). Smooth forms are comparable to *Trileites* (Erdtmann 1945, 1947) Potonié, 1956, *Laevigatisporites* Ibrahim, 1933, and *Banksisporites* Dettmann, 1961; depending on the degree of ornamentation; other forms appear similar to *Bacutriletes* (van der Hammen, 1954) Potonié, 1956, *Verrutriletes* (van der Hammen, 1954) Potonié, 1956 emend. Binda and Srivastava, 1968, *Echitriletes* Potonié, 1956, and *Narkisporites* Kannegieser and Kozur, 1972 (e.g., Fuglewicz 1973; Wang 1991). All of these are names used for sporae dispersae grains in stratigraphic studies, but do not refer to biological entities.

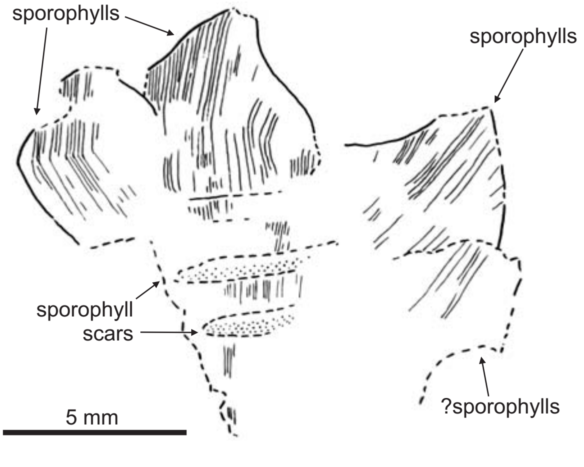

Fig. 3. Interpretative drawing of the strobilus fragment in Fig. 2A, showing the loose, helical arrangement of sporophylls and sporophyll scars.

Our attempts to obtain miospores from the slab containing the macrofossils were unsuccessful. However, Askin and Cully (1998) reported on microfloras from the Alfie's Elbow locality (in their paper referred to as "an unnamed ridge southeast of Shroeder Hill"). These authors stressed the high abundance of lycophyte miospores, i.e., *Uvaesporites verrucosus* (de Jersey, 1964) Helby, 1971 and *Aratrisporites* spp., in some of the samples.

Genus *Mesenteriophyllum* Sixtel, 1961

Type species: *Mesenteriophyllum kotschnevii* Sixtel, 1961; Triassic Madygen Formation, southern Fergana, Kyrgyz Republic.

Mesenteriophyllum serratum Sixtel, 1961

Fig. 4.

Material.—PCUK T5568, one block containing three larger leaf segments and abundant smaller leaf fragments.

Description.—Leaves strap-shaped, apparently sterile, exceeding 10 cm in length, up to 15 mm wide proximally (Fig. 4A), slightly tapering toward the tip, entire-margined, with two longitudinal rows of transversely to slightly obliquely oriented ridges and furrows alternating at regular intervals of about 1 to 2 mm (Fig. 4A–C); in compression fossils the margins having a serrated macroscopic appearance (Fig. 4A, B). Central leaf portion with rectangular elongated cells arranged longitudinally in a brick-like manner (Fig. 4F, G), cuticles with prominent longitudinal striae and dense pattern of small circular depressions (Fig. 4C, E); leaf margins with about fifteen to twenty more or less regular longitudinal rows of transversely elongated, rectangular to rounded cells with smooth cuticle (Fig. 4C, D).

Remarks.—The genus *Mesenteriophyllum* has been characterized in the original description as long, linear leaves with a single, thick, centrally positioned vein and a transversely wrinkled or folded lamina (Sixtel 1961, 1962). The present specimens are assigned to *Mesenteriophyllum serratum* (Fig. 5), which differs from the type species *M. kotschnevii* in its smaller size (100–150 mm length by 10–15 mm width), tapering outline, and by the characteristic small "teeth" along the lateral margins (Sixtel 1961, 1962). The Antarctic specimens indicate that the margins are in fact entire, and that the serrate macroscopic appearance represents an alternating pattern of transverse ridges and depressions close to the leaf margins.

Discussion

The present material constitutes the first unequivocal macrofossil evidence of lycophytes in the Triassic of the Transantarctic Mountains. The remains of reproductive organs closely resemble those of *Pleuromeia*, in particular *Pleuromeia rossica* and *Pleuromeia jiaochengensis* (Neuburg

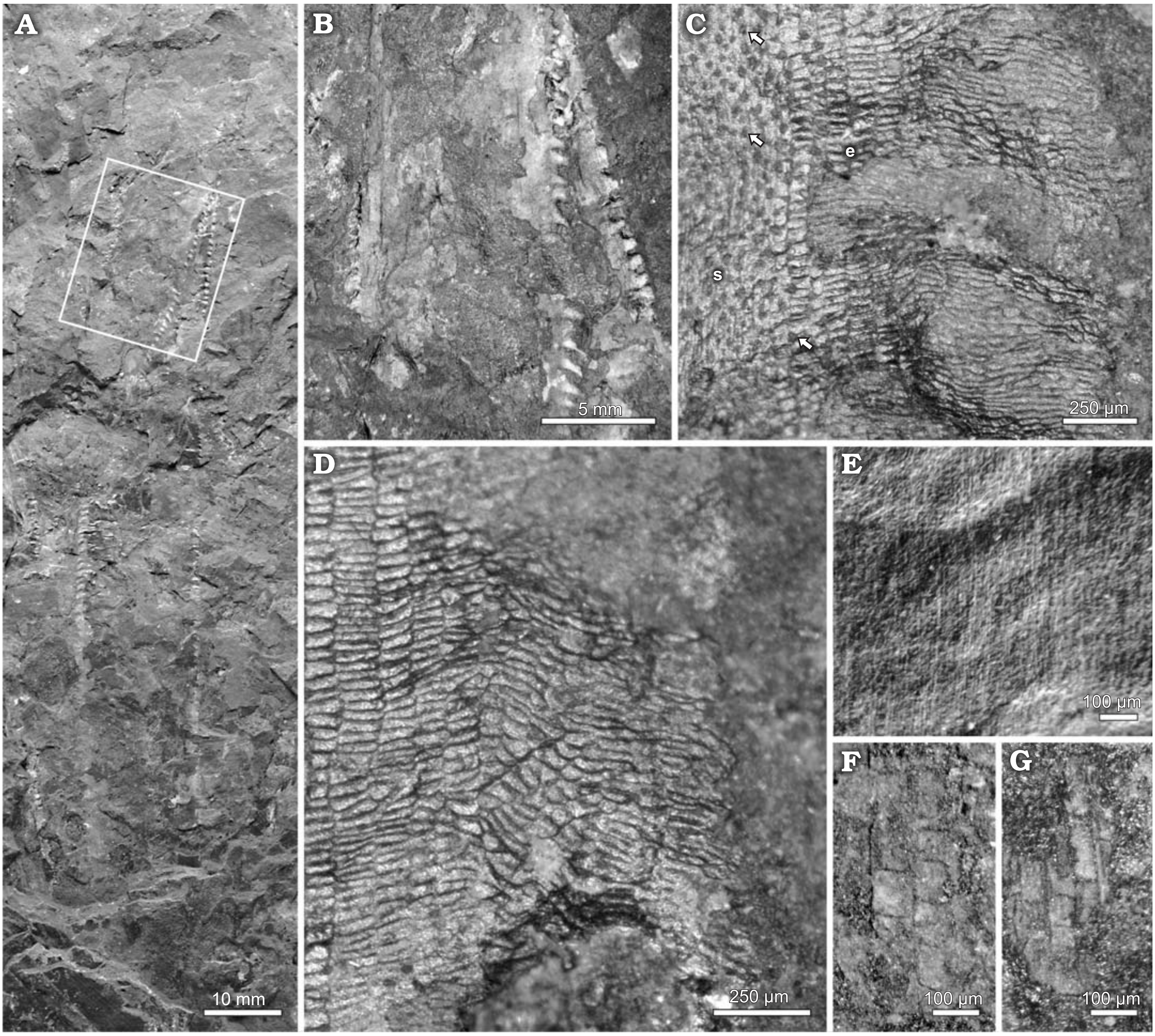

Fig. 4. Pleuromeialean lycophyte leaf *Mesenteriophyllum serratum* Sixtel, 1961 from the Upper Triassic of the "Alfie's Elbow" site, central Transantarctic Mountains. **A**. Two overlying leaf fragments recognizable primarily by the distinct serrate appearance of the leaf margins. **B**. Detail of A showing serrate appearance of margins. **C**. Detail of leaf margin with alternating transverse ridges and furrows, and preserved cell pattern. Note longitudinal striae (s), circular holes on central leaf portion (some marked with arrows), and vertical alignment of transversely elongated epidermal cells (e) on leaf margin. **D**. Detail of leaf margin with cellular preservation, showing transversely elongated cells aligned in vertical rows. **E**. Detail of longitudinal striae on central leaf portion. **F**, **G**. Orthogonal pattern of epidermal cells in central leaf portion, visible only in places where carbonized cuticle layer is lifted off.

1960; Wang and Wang 1982). This is remarkable, because *Pleuromeia* has previously not been reported from strata younger than early Middle Triassic (Retallack 1975, 1997; Mader 1990). Moreover, pleuromeialean lycophytes are regarded by many authors as xero- and halophytic plants inhabiting either coastal lagoonal or ephemeral (semi)desert environments (e.g., Mägdefrau 1931; Retallack 1975, 1980, 1997; Wang and Wang 1982; Mader 1990; Fuchs et al. 1991; Meng 1996). Co-occurring leaf remains are assigned to *Mesenteriophyllum serratum* and represent the first record of *Mesenteriophyllum* from the Southern Hemisphere, and only the third report of this genus. *Mesenteriophyllum* has long been considered endemic to the Triassic Madygen Biota of the Kyrgyz Republic (Sixtel 1961; Dobruskina 1995), but has recently also been reported from the Lower Triassic of the eastern Taimyr Peninsula (Sadovnikov 2008). Including the fossils from East Antarctica described here, *Mesenteriophyllum* is now known from northern temperate regions and northern and southern high latitudes (Fig. 6).

Evidence for lycophyte affinities of *Mesenteriophyllum serratum*.—*Mesenteriophyllum* has been regarded as a gym-

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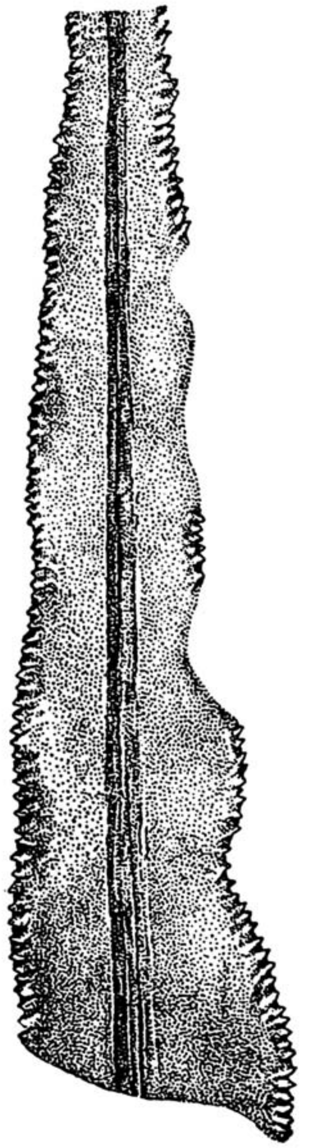

Fig. 5. Pleuromeialean lycophyte leaf *Mesenteriophyllum serratum* Sixtel, 1961 from the Triassic Madygen Formation, Kyrgyz Republic. Modified from Sixtel (1961). Leaf width up to ~12 mm.

nosperm leaf of uncertain affinities (Sixtel 1961, 1962; Dobruskina 1995). Leaf morphology and anatomy of the present material provide evidence that *Mesenteriophyllum* represents sterile foliage of an early Mesozoic lycophyte. The most striking evidence is the wrinkled or toothed appearance of the leaf margins which is due to a regular pattern of alternating transverse ridges and depressions (Fig. 3A–C). This feature has been previously interpreted as resulting from desiccation of a fleshy, probably succulent leaf lamina (Sixtel 1962). However, we suggest that this peculiar morphology is the result of the collapse of internal air chambers after burial, with the ridges reflecting the transverse septa of the leaf. This is a feature that has so far only been reported from fossil lycophyte leaves (see Brown 1939). For comparison, virtually identical structures are seen in the lacunate sporophylls of *Isoetes choffatii* Saporta, 1894 (Saporta 1894; see Teixeira 1948: pl. 26: 4), *Isoetites serratus* Brown, 1939 and *Isoetites horridus* (Dawson, 1883) Brown, 1939 (Brown 1939: figs. 5, 6, 1958: figs. 10, 12), *Isoetites phyllophila* Skog, Dilcher, and Potter, 1992 (Skog et al. 1992: figs. 1–8, 10), *Isoetes ermayiensis* Wang, 1991 (Wang 1991: pl. 2: 3–7) and cf. *Isoetites* (Pigg 2001: figs. 2, 3). All of these fossils are presumably closely related to extant *Isoetes* or even considered congeneric. Air chambers in the leaves of Triassic Pleuromeiales have not yet been demonstrated, but this may be due to taphonomic conditions. The genus *Pleuromeia* was established for casts of stems and rhizophores that are usually preserved in sandstones (e.g., Grauvogel-Stamm 1999). This rather coarse-grained clastic depositional setting is unlikely to preserve features of the internal anatomy of co-occurring foliage in detail. Nevertheless, Mägdefrau (1931) noted the presence of transverse wrinkles in some well-preserved leaves of *Peuromeia sternbergii* (Münster, 1839) Corda, 1852, which were later tentatively interpreted as collapsed air chambers (Grauvogel-Stamm 1999).

Leaves of *Pleuromeia* are strap-shaped to elongate-lanceolate and may be over 1 cm wide and 10 cm long (e.g., Mägdefrau 1931; Kon'no 1973; Grauvogel-Stamm 1999). This is well within the dimensions reported for *Mesenteriophyllum serratum* (Sixtel 1961, 1962). Moreover, *Mesenteriophyllum* was originally described as without lateral veins, which corresponds to a microphyllous organization (Sixtel 1961, 1962). The cuticle of the Antarctic specimens has a distinctive surface ornamentation composed of continuous, fine longitudinal striae (Fig. 3C, E). A similar surface pattern is an important diagnostic character for many extant species of *Isoetes* (Rolleri and Prada 2007), as is the rectangular arrangement of the epidermal cells (Skog and Hill 1992; Skog et al. 1992; Rolleri and Prada 2007). Even though cuticle and epidermal patterns are preserved over large portions of the leaf, stomata are apparently absent, which is a typical feature for certain extant and fossil Isoetales (Pfeiffer 1922; Skog and Hill 1992; Rolleri and Prada 2007). The densely spaced, small circular holes on the central portion of the leaf are interpreted as hair bases or remnants of broken papillae. It is interesting to note that densely papillate leaf surfaces are known to occur in sterile sporophyll portions of fossil Isoetales as well (e.g., Brown 1958: fig. 9).

Further evidence for a lycophyte affinity of *Mesenteriophyllum serratum* is the close association with pleuromeialean remains at all known localities. In the Triassic Madygen Formation, *Mesenteriophyllum* occurs together in greater abundance only in strata that also yield *Annalepis*-type sporophylls and partially articulated strobili (Sebastian Voigt and Jörg Schneider, Freiberg, and Philippe Moisan, Münster, personal communications 2009). In the Fadyu-Kuda Formation, eastern Taimyr Peninsula, *Mesenteriophyllum* is found in a single horizon associated with abundant *Pleuromeia* remains (Sadovnikov 2008). In the present assemblage from Alfie's Elbow, *Mesenteriophyllum* and isolated pleuromeialean sporophylls and sporangia co-occur on a single slab, but are otherwise absent.

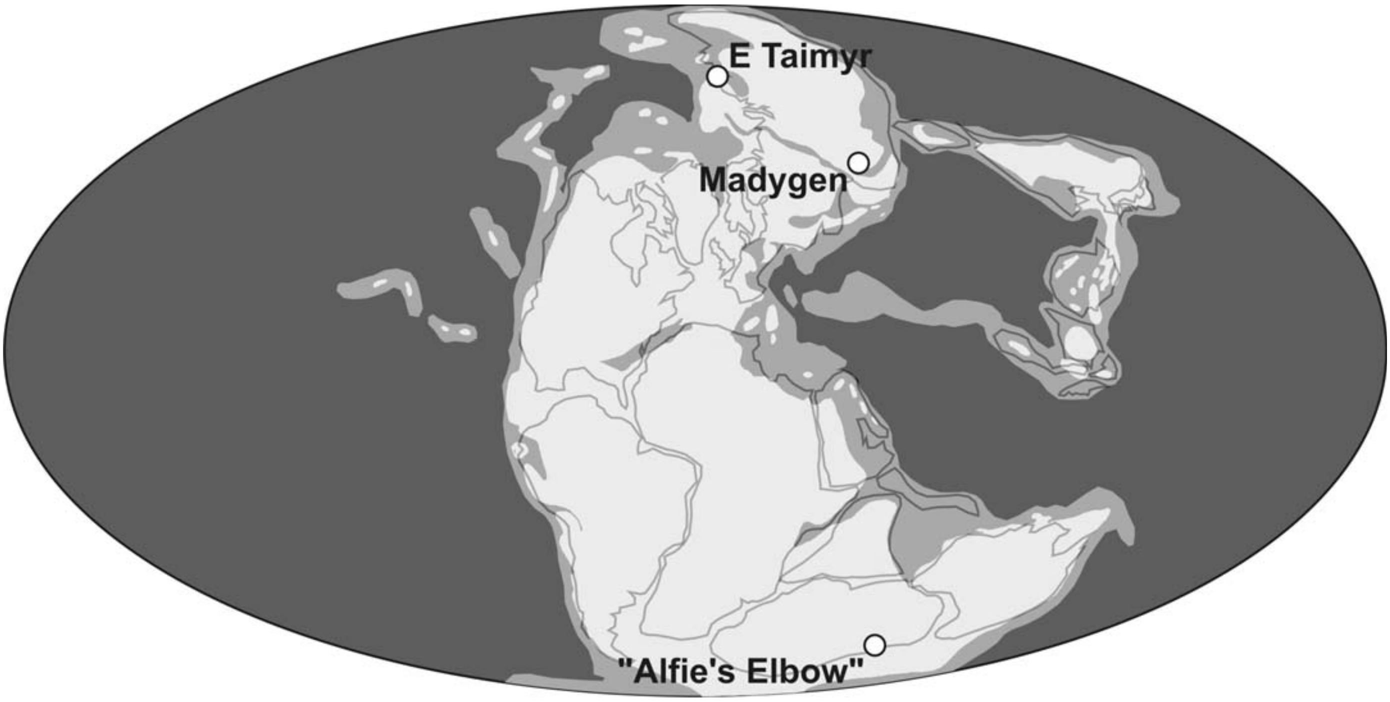

Fig. 6. Known palaeogeographic distribution of *Mesenteriophyllum* Sixtel, 1961 in the northern and southern hemisphere Triassic. Palaeogeography after Golonka (2007).

Palaeoecology.—The plant-bearing beds at Alfie's Elbow are interpreted as overbank deposits of a low-energy braided-stream system (Axsmith et al. 2000). The majority of specimens from Alfie's Elbow are articulated *Dicroidium* fronds that occur in medium-grey, fine-grained siltstones and shales (Fig. 1D) representing crevasse splay deposits (Axsmith et al. 2000). *Dicroidium* plants commonly formed riparian vegetation on well-drained levees fringing major channel margins (e.g., Cairncross et al. 1995; Cúneo et al. 2003). It appears that the lycophytes described here may have occupied a different habitat within the river system. Although the entire collection at the University of Kansas Natural History Museum was investigated during this study, lycophyte remains and *Mesenteriophyllum* occur only on a single slab (~25 × 20 cm in size). The lithofacies of the lycophyte-bearing bed differs from that of the rest of the collection. The rock matrix is crumbly and comparatively dark, indicating higher content of organic material with abundant plant fragments. We interpret this facies as representing a deposit of a stagnant water body, perhaps in a swampy overbank environment, with relatively high accumulation of organic remains and less frequent clastic input. The close association of the various lycophyte organs on a single slab may indicate parautochthonous deposition within this particular facies. We therefore assume that the *Mesenteriophyllum*-producing lycophyte inhabited a backswamp environment. There may be some support for this hypothesis in the fact that stomata are absent. In extant *Isoetes* non-stomatiferous leaves typically occur in aquatic or semiaquatic species (Rolleri and Prada 2007). For instance, *Isoetes andicola* (Amstutz, 1957) Gómez, 1980 is a peat-forming species that lacks stomata, even though it has a very thick cuticle that is impermeable to CO_2 and H_2O vapour (Keeley et al. 1984). Carbon dioxide uptake in *Isoetes andicola* is entirely via the root system that is embedded into a substrate of highly decomposed, CO_2-rich peat (Keeley et al. 1984).

Conclusions

The present study identifies the first macrofossil candidates that can be related to the diverse array of lycophyte spores in the Upper Triassic of Antarctica. In the present instance, lycophyte reproductive organs and associated foliage occur in a particular, carbonaceous sedimentary facies that otherwise contains only fragmented and rather poorly preserved gymnosperm remains. In order to obtain a more complete understanding of the Late Triassic high-latitude vegetation of Antarctica, we suggest that future collecting should also focus on those sedimentary facies that have up to now only yielded sparse or fragmentary plant fossils.

On the basis of this material we suggest that *Mesenteriophyllum serratum* represents foliage of a pleuromeialean lycophyte. The Antarctic fossils demonstrate that pleuromeialean leaves possessed several characteristics that are similar to those of fossil *Isoetes* and *Isoetites*, including air chambers, rectangular-shaped epidermal cell patterns, and the absence of stomata. These morphological and anatomical characters also offer another argument for close affinities between early Mesozoic and typically Cenozoic-extant rhizomorphic lycophytes.

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Details of the co-occurring fertile organs indicate affinities to *Pleuromeia* rather than *Annalepis* or related taxa. If future studies confirm this tentative interpretation, this would greatly expand the stratigraphic and palaeoecological ranges of *Pleuromeia*. The Late Triassic Antarctic lycophytes apparently existed in swampy overbank environments of the humid high-latitude ecosystems of southern Gondwana, and may have contributed to peat accumulation and coal formation. Although the picture is far from complete, we hypothesize that during the Middle Triassic *Pleuromeia* may have radiated into high-latitude ecosystems adapting to peat-forming environments, where it persisted as a relictual element well into the Late Triassic, having long disappeared from its typical lower-latitude habitats.

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