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A reappraisal of *Neocalamites* and *Schizoneura* (fossil Equisetales) based on material from the Triassic of East Antarctica

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Sphenophytes are a common floral element in the Triassic of Gondwana. Most sphenophyte compression fossils have been conventionally assigned to a few, presumably very widespread species of *Neocalamites* based on vegetative features of the stems (or pith casts) and the foliage. During recent decades, however, new reports on morphological and anatomical details of some of these fossils have cast doubt on the systematic affinities of many Gondwanan Triassic sphenophytes. Here we describe *Neocalamites suberosus* (Artabe & Zamuner) nov. comb. et emend. and *Schizoneura africana* Feistmantel emend. from several Triassic deposits in the central Transantarctic Mountains and Victoria Land, East Antarctica. The material enables a critical reevaluation of morphological and anatomical features that have been historically used to define the two genera, including leaf-base morphology, degree of leaf fusion, stem vasculature and vallecular canals, and features of the nodal diaphragm. The diagnoses of *Neocalamites* and *Schizoneura* are emended so that they more accurately reflect recent advances in our understanding of the anatomy and ontogeny of these plants.

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SPHENOPHYTES are abundant constituents of Triassic plant-fossil assemblages worldwide. In Antarctica, sphenophyte fossils are common in Triassic deposits throughout the Transantarctic Mountains (e.g., Plumstead 1962, Rigby & Schopf 1969, Gabites 1985, Escapa *et al.* 2011). The famous Triassic permineralized peats from Antarctica have yielded *Spaciinodum collinsonii* Osborn & Taylor 1989 emend. Schwendemann *et al.* 2010, an anatomically preserved equisetacean plant that is known in remarkable detail (Osborn & Taylor 1989, Osborn *et al.* 2000, Ryberg *et al.* 2008, Schwendemann *et al.* 2010). In addition, sphenophytes commonly form monotonous mass accumulations of stem compressions and casts in certain marginal-lacustrine sedimentary facies (e.g., Rigby 1969, Retallack & Alonso-Zarza 1998). In contrast to detailed systematic descriptions of Permian sphenophytes from Antarctica (Rigby 1969) and to the anatomically preserved *Spaciinodum*, however, compression remains of Triassic sphenophytes from Antarctica have received little scholarly attention.

Two of the most commonly recognized Mesozoic sphenophyte genera are *Schizoneura* Schimper & Mougeot, 1844 and *Neocalamites* Halle, 1908. Despite their widespread occurrence throughout Gondwana, however, the taxonomic delimitation and systematic classification of these two well-known genera remain problematic. Most Triassic sphenophyte fossils from Gondwana have been assigned to only a few species of *Neocalamites* that were originally described from the Northern Hemisphere (e.g., Walkom 1915, 1924, 1915, Du Toit 1927, Frenguelli 1949). During recent decades, however, new reports on morphological and anatomical details of some of these fossils have cast doubt on the systematic affinities of many Gondwanan Triassic sphenophytes (e.g., Artabe & Zamuner 1991, Brea & Artabe 1999, Holmes 2000, 2001).

Here, we present the first detailed description of Triassic *Neocalamites* and *Schizoneura* fossils from various regions of the Transantarctic Mountains. Based on a critical evaluation of the morphological and anatomical characteristics of the Antarctic fossils and of previously published material, for the problematic genera *Neocalamites* (including *Calamoderma* Sadovnikov, 1986, *Nododendron* Artabe & Zamuner, 1991, and *Zonulamites* Holmes, 2000) and *Schizoneura* (including *Paraschizoneura* Radchenko, 1955); (2) identify a new

Gondwanan representative of *Neocalamites*, i.e., *N. suberosus* (Artabe & Zamuner) nov. comb. et emend.; and (3) re-define the little-known species *Schizoneura africana* Feistmantel, 1899, which appears to be one of the earliest described and most widely distributed Gondwanan sphenophyte fossils.

Material and methods

This study is based on specimens in the Paleobotanical Collections of the Biodiversity Institute at the University of Kansas, Lawrence, Kansas, USA. The material was collected during repeated field trips to the central Transantarctic Mountains and southern Victoria Land over the course of several decades; the sphenophyte fossils presented here were collected from: (1) the Lower to Middle Triassic Fremouw Formation at Gordon Valley and Graphite Peak in the central Transantarctic Mountains, (2) several horizons of uncertain stratigraphic position in Triassic deposits at Mount Wisting and Graphite Peak and (3) the Middle to Upper Triassic Lashly Formation in the Allan Hills, southern Victoria Land (see Escapa *et al*. 2011).

Images were taken with a Nikon D300s digital single-lens reflex camera; polarized or oblique lighting was used to accentuate contrast and surface detail (see Kerp & Bomfleur 2011). Fine details were observed and photographed using a Leica MZ 16 stereo dissecting microscope with an attached Leica DC500 digital camera.

Systematic palaeobotany

Class EQUISETOPSIDA C. Agardh, 1825
Order EQUISETALES Dumortier, 1829
Family unknown

Neocalamites Halle, 1908 emend.

1986 *Calamoderma* Sadovnikov, p. 92. [detached cortices]
1991 *Nododendron* Artabe & Zamuner, p. 288. [leaf whorls, nodal diaphragms and stem cross-sections at node level]
2000 *Zonulamites* Holmes, p. 51.

Type species. *Neocalamites lehmannianus* (Göppert, 1845) Weber, 1968

Emended diagnosis. Stems straight, cylindrical, segmented into internodes and generally swollen nodes; positions of axial vascular bundles of successive internodes varying from opposite to alternate. Leaves borne in whorls at the nodes, numerous, long, linear, narrow, single-veined, broadly attached, free for their entire length; leaf bases straight and free or more-or-less widened, overlapping, to connate. Number of internode bundles generally two to several times greater than number of leaves per whorl.

Remarks. For reasons detailed in the discussion, we propose to emend Halle's (1908) original diagnosis in the following aspects: (1) details of the leaf bases are emended to include separate, close, overlapping and connate bases; (2) information on the surface morphology of the stem, which was originally restricted to a smooth surface, is omitted; (3) in contrast to Sadovnikov's (1986) emendation, the longitudinal ridges on the inner stem surface are (re)interpreted as vascular strands; (4) in contrast to Vladimirovich's (1958) emendation, reproductive features are omitted.

Calamoderma Sadovnikov, 1986 was introduced for detached slabs of *Neocalamites* cortex. *Nododendron* Artabe & Zamuner, 1991 was established for detached nodal diaphragms (and principally stem cross-sections at the node level), which were later confirmed to belong to *Neocalamites* stems (Brea & Artabe 1999, Holmes, 2001) associated with reproductive organs typical of the genus (Brea & Artabe 1999, Holmes 2000). Australian *Neocalamites* specimens with fused leaf bases have recently been reassigned to a new genus, *Zonulamites* (Holmes 2000). As apparent from the relevant discussion sections, we consider these three genera to be junior synonyms of *Neocalamites*, as they represent different aspects or preservational states of plant parts that are attributable to *Neocalamites* Halle emend.

Neocalamites suberosus (Artabe & Zamuner, 1991) nov. comb. et emend. (Figs 1–3)

Basionym. *Nododendron suberosum* Artabe & Zamuner, 1991, p. 288.

Selected synonymy

1925 *Phyllotheca australis* Brongniart; Walkom, p. 216, pl. 24, figs 1–3.
1927 *Neocalamites carreri* (Zeiller) Halle; Du Toit, pp. 315, 396.
1949 *Neocalamites carrerei* (Zeiller) Halle; Frenguelli, p. 150, figs 2, 3, pls 4, 5.
1967 *Neocalamites carreri* (Zeiller) Halle; Jain & Delevoryas, p. 566, pl. 86, figs 4–6.
1991 *Nododendron suberosum* Artabe & Zamuner, p. 288, pls 1–3.
2010 *Nododendron suberosum* Artabe & Zamuner; Morel *et al*., p. 10, fig. 3.5.
2011 *Neocalamites* sp.; Escapa *et al*., fig. 4c, d.

Additional references that may belong to this species

1899 *Schizoneura gondwanensis* Feistmantel, only pl. 14a, fig. 5.
1915 *Neocalamites hoerensis* (Schimper) Halle; Walkom, p. 33, pl. 2, fig. 1.
1924 *Neocalamites hoerensis* (Schimper) Halle; Walkom, p. 79, pl. 15, fig. 1.
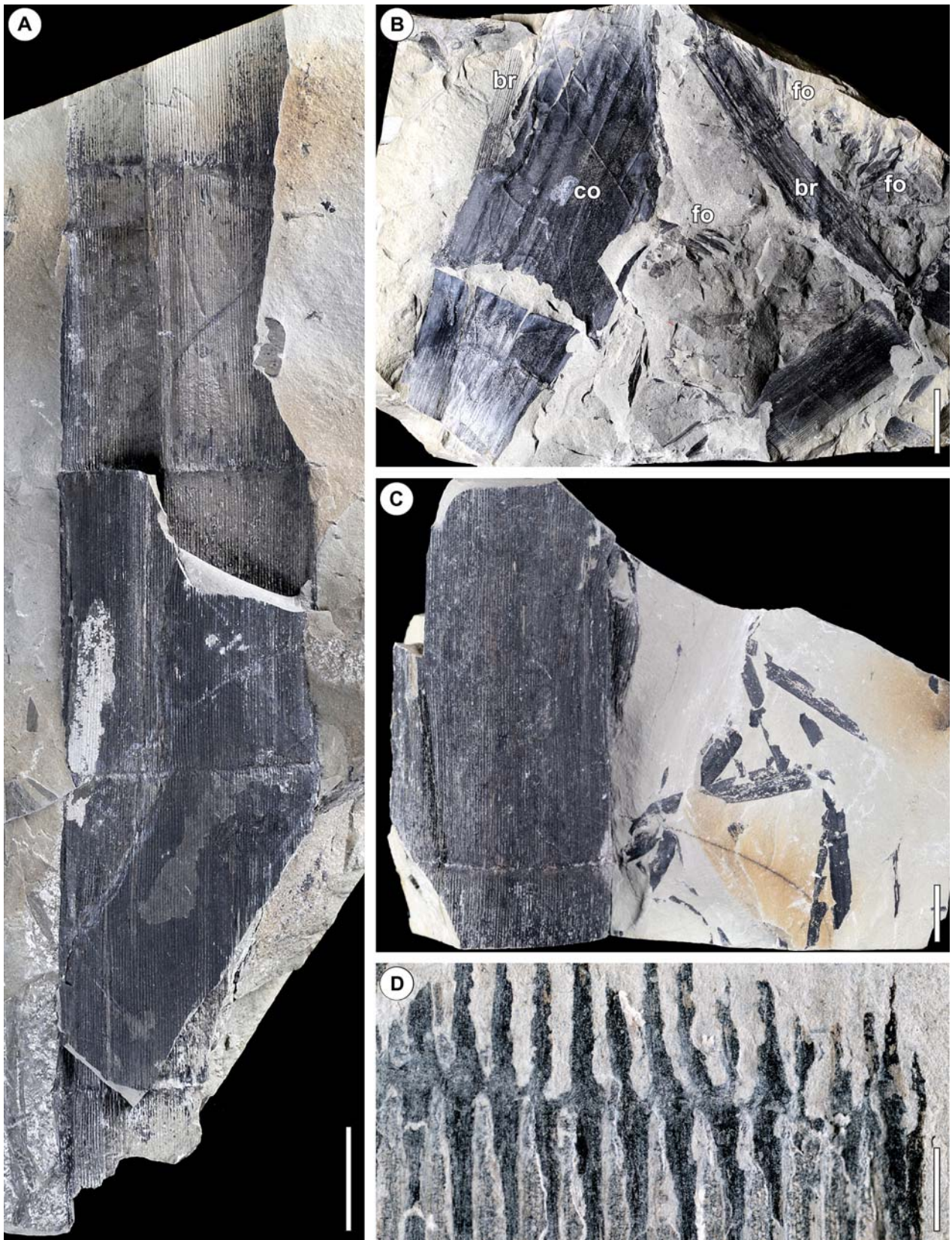
Fig. 1. Neocalamites suberosus (Artabe & Zamuner) nov. comb. et emend. from the Triassic of East Antarctica. **A**, Large stem pith cast and isolated leaves from the Middle Triassic Fremouw Formation at Gordon Valley, Queen Alexandra Range, central Transantarctic Mountains, T-1980; **B**, Detached cortex (co), branches (br) and remains of foliar whorls (fo) on a slab from the Triassic at Graphite Peak, Queen Alexandra Range, central Transantarctic Mountains, T-5411a; **C**, Large stem pith cast and associated, partially attached leaves from the Middle–Upper Triassic Lashly Formation in the Allan Hills, southern Victoria Land, T11-208; **D**, Exposed axial vascular system of a stem from the Triassic at Graphite Peak, Queen Alexandra Range, central Transantarctic Mountains, showing opposite (left), subopposite, and alternate (center right) positions of internode bundles at node level, T-6183. Scale bars for A, B = 2 cm; C = 1 cm; D = 2 mm.
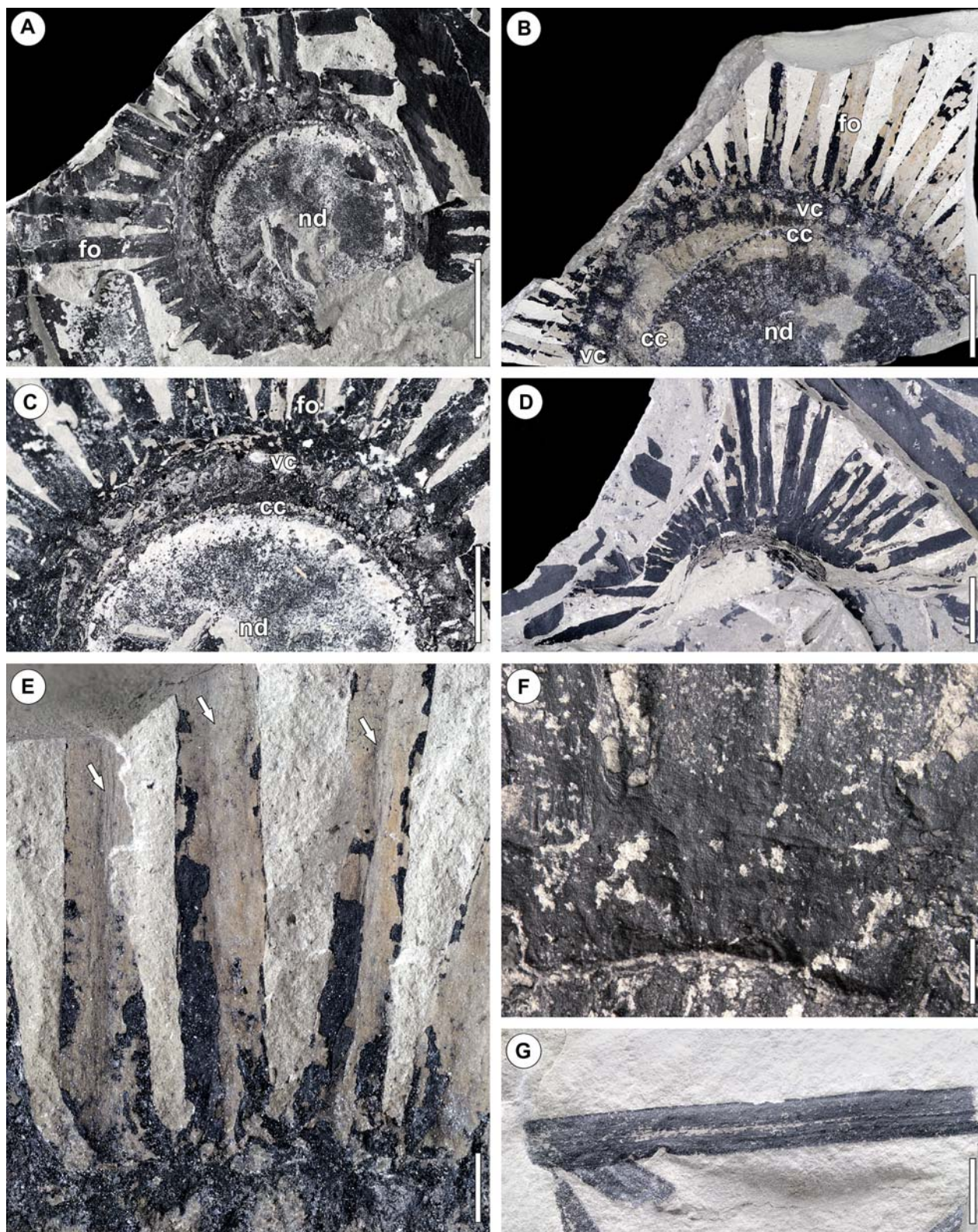
Fig. 2. Neocalamites suberosus (Artabe & Zamuner) nov. comb. et emend. from the Middle–Upper Triassic Lashly Formation, Allan Hills, southern Victoria Land, East Antarctica. **A**, Stem in cross-section at node level, showing the central nodal diaphragm (nd) and attached leaf whorl (fo), T11-657a; **B**, Nodal region showing the central, partly detached diaphragm (nd), vascular cylinder with carinal canals (cc), cortical cylinder with vallecular canals (vc) and attached whorl of radiating leaves (fo), T11-534b; **C**, Detail of the specimen shown in Fig. 2A, showing the nodal diaphragm (nd), vascular cylinder with carinal canals (cc), cortical cylinder with vallecular canals (vc) and attached whorl of radiating leaves (fo); **D**, Oblique view at a node showing a whorl of leaves with connate bases, T11-635a; **E**, Detail of the specimen shown in Fig. 2B, showing attached leaves each with an inconspicuous central vein (arrows); **F**, Detail of Fig. 2E showing fused basal leaf portions; **G**, Detail showing inconspicuous central vein of an isolated leaf fragment, T-213. Scale bars for A, B, D = 1 cm, C, E, G = 5 mm, F = 1 mm.

Fig. 3. **A, B**, Isolated nodal portion of an underground stem of *Neocalamites suberosus* (Artabe & Zamuner) nov. comb. et emend., showing nodal diaphragm (nd), lateral roots and rootlets, T11-607 from the Middle–Upper Triassic Lashly Formation of the Allan Hills, southern Victoria Land, East Antarctica. Scale bars = 1 cm.

1947 *Neocalamites hoerensis* (Schimper) Halle; Jones & de Jersey, p. 10.
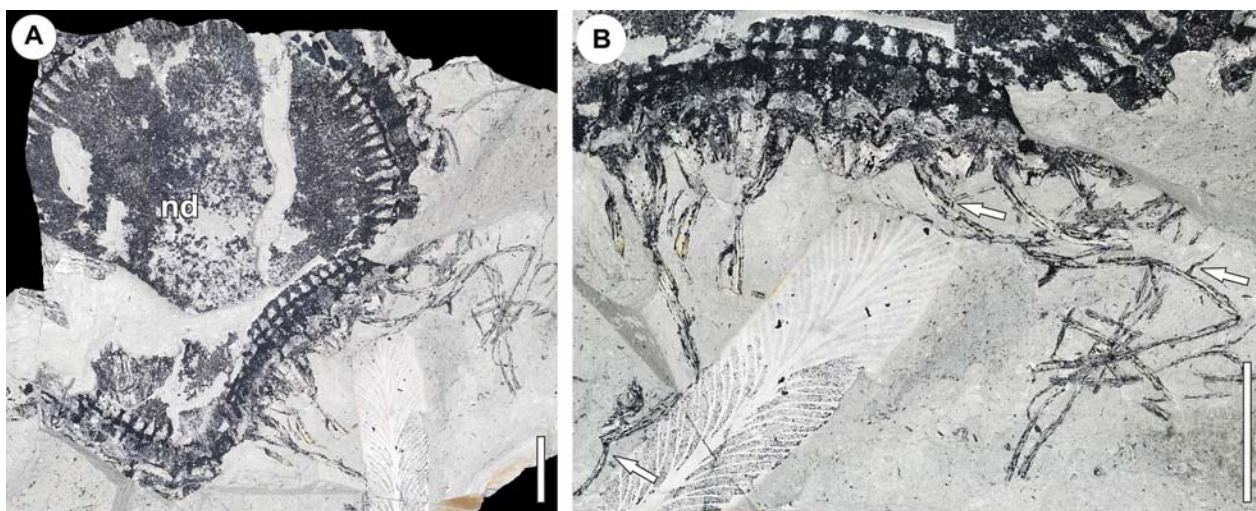
1965 *Neocalamites hoerensis* (Schimper) Halle; Hill *et al.*, pl. 1, fig. 1.

1998 *Neocalamites carrerei* (Zeiller) Halle; Herbst *et al.*, p. 90.

1999 *Neocalamites carrerei* (Zeiller) Halle; Brea & Artabe, p. 391, figs 6a–d, 7c.

1999 aff. *Nododendron suberosum* Artabe & Zamuner; Brea & Artabe, p. 391, fig. 7d.

2000 *Zonulamites nymboidensis* Holmes, p. 51, figs 5, 6.

2009 *Neocalamites carrerei* (Zeiller) Halle; Brea *et al.*, fig. 6d–e.

2009 aff. *Nododendron suberosum* Artabe & Zamuner; Brea *et al.*, fig. 6f.

Holotype. Specimen 20768 in the Palaeobotanical Collection of the Natural Sciences Institute and Museo de La Plata, La Plata, Argentina (single and hence holotype specimen of the basionym *Nododendron suberosum* Artabe & Zamuner, 1991.

Emended diagnosis. Stems straight, cylindrical, hollow, divided into long internodes and swollen nodes; outer surface smooth or with wide and shallow longitudinal grooves; internal surface of internodes with densely distributed, longitudinal, straight vascular bundles; vascular bundles of successive internodes opposite or alternating at node level; cortical cylinder containing prominent vallecular canals. Each branch node with a persistent, membranous, smooth nodal diaphragm and a whorl of up to about 50 linear, straight, single-veined leaves up to 4 mm wide; leaf bases widened, touching or slightly connate being connected by a thin strip of laminar tissue; leaf midvein inconspicuous. Generally about two to four internode vascular bundles per vallecular canal and leaf; positions of leaf bases and vallecular canals alternating at node level.

Material studied. Eight samples (T11-208, 213, 534, 583, 607, 635, 656, 657) from the Middle to Upper Triassic Lashly Formation in the Allan Hills, south Victoria Land, East Antarctica, containing stem cross-sections at node level; four rock samples (T-1980, 5411, 6065, 6183) from Triassic deposits at Graphite Peak containing leafless and leafy stems, leaf fragments and slabs of detached cortex.

Description. Specimens consisting of leafless and leafy stems, foliar whorls, diaphragms, a diaphragm of an underground stem, and isolated rooting structures (Figs 1–3). Stems up to 68+ mm wide in compression, straight, with no evidence of tapering; pith casts with densely disposed (*ca* 16–20 per cm) longitudinal grooves (impressions of vascular bundles; Fig. 1A, C); maximum length of internodes exceeding 70 mm; bundles of two successive internodes generally opposite at node level, in a few cases alternating (Fig. 1D). Pieces of detached cortex of leathery appearance, showing even pattern of alternating longitudinal ridges and shallow-concave furrows about 5–7 mm wide; exterior surface of cortex otherwise smooth (Fig. 1B). At node level, stem cross-sections showing (from inside to outside) a membranous, flat, smooth nodal diaphragm, a surrounding vascular cylinder containing a ring of vascular bundles with enclosed carinal canals, a cortical cylinder containing a ring of vallecular canals, and attached radiating leaves (Fig. 2A–C); carinal canals circular in cross-section, *ca* 0.25–0.75 mm in diameter (Fig. 2A–C, E); vallecular canals rounded-rectangular in cross-section, *ca* 1–2 mm wide (Fig. 2B, C); two to three vascular bundles per vallecular canal; vallecular canals alternating with leaf bases (Fig. 2B, C). Leaves long, linear, straight, entire-margined, 2–4 mm (usually *ca* 2.5 mm) wide, at least 30 mm long, with an indistinct central vein (Fig. 2); leaf bases widened, in some cases fused to form a narrow sheath around the node

(Fig. 2); leaves otherwise entirely separate and radiating evenly from node; each individual whorl consisting of about 40–50 leaves. Nodal diaphragm of underground stem *ca* 6 cm in diameter, smooth (Fig. 3A); outer margin of diaphragm showing radiating spokes equal in number and relative density to the vascular bundles and carinal canals of aerial stems (Fig. 3A); further details of vascular and cortical cylinders poorly visible; exterior surface giving off *ca* 1–2 mm wide, tapering main roots with irregular, delicate lateral rootlets <1 mm wide (Fig. 3B).

Remarks. More than 30 species of *Neocalamites* have been named to date (see Jongmans 1970, Dijkstra & van Amerom 1996, Yang *et al.* 2011). Most *Neocalamites* specimens, however, are either described in open nomenclature or assigned to one of a few very widespread species, i.e., *N. meriani* (Brongniart) Halle, 1908, *N. lehmannianus* (Göppert) Weber, 1968 [including *N. hoerensis* (Schimper) Halle, 1908; see Weber 1968] and *N. carrerei* (Zeiller) Halle, 1908. This practice results from the fact that the few available vegetative characters that could potentially serve as diagnostic criteria in sphenophytes are considered highly variable even within a single population, thus rendering species delimitation especially difficult (see, e.g., Oishi 1932, Kawasaki 1939, Weber 1968). The more generally accepted diagnostic criteria include the leaf width, average ratio of leaf number to number of internode bundles, and branching pattern (Oishi 1932, Frentzen 1933, Kawasaki 1939).

In the Triassic of Gondwana, *Neocalamites* is the most common sphenophyte fossil. The genus has been described from deposits across the entire Gondwanan landmass, including modern South America (Frenguelli 1944a, 1944b, 1949, Artabe *et al.* 2003), South Africa (e.g., Du Toit 1927, Anderson & Anderson 1985), India (Lele 1964), Australia (e.g., Walkom 1915, Jones & de Jersey 1947, Holmes 1982), New Zealand (Retallack 1980) and Antarctica (e.g., Gabites 1985, Barrett *et al.* 1986, Escapa *et al.* 2011). Few species, however, have been recognized. Since the early reports on occurrences of '*N. carrerei*' in the Southern Hemisphere (e.g., Walkom 1915, 1925, Du Toit 1927), the majority of Gondwanan *Neocalamites* fossils have been conventionally assigned to this presumably widespread species (e.g., Frenguelli 1949, Jain & Delevoryas 1967, Retallack 1980, Herbst *et al.* 1998). Most of the figured fossils, however, have little in common with the type material of *N. carrerei* from Vietnam, which is characterized by particularly narrow, only *ca* 1 mm wide leaves that are borne in dense whorls of up to 100 leaves (see Zeiller 1902/1903). Harris (1961) and Retallack (1980) have already pointed out that many of the Gondwanan specimens referred to either *N. hoerensis* or *N. carrerei* likely represent a distinct species, based on the fewer and significantly wider leaves. With descriptions of additional morphological and anatomical details (Artabe

& Zamuner 1991, Brea & Artabe 1999, Holmes 2000, 2001), there is now sufficient information to enable a clearer taxonomic delimitation of these fossils.

Neocalamites suberosus is characterized by having up to *ca* 50, notably wide leaves with broadened leaf bases that may form a narrow, continuous collar, and by having persistent nodal diaphragms (Fig. 2). This latter feature is of particular importance, as it distinguishes this species from the superficially similar, primarily Northern-Hemisphere species *N. meriani*, whose stems are consistently hollow at maturity (e.g., Kräusel 1959, Kelber 1990, Kelber & Hansch 1995). The few, wide leaves with partially fused bases distinguish *N. suberosus* from *N. carrerei*, which like *N. suberosus* contains persistent diaphragms, but has whorls of up to 100, very narrow leaves (Zeiller 1902/1903, Kon'no 1962, Kimura *et al.* 1982). *Neocalamites lehmannianus* differs from *N. suberosus* in having leaves that are usually entirely free to their bases, and in having presumably ephemeral diaphragms that have not yet been found.

Neocalamites suberosus is a widespread species in the Triassic of Gondwana and is known from South America (e.g., Frenguelli 1949, Jain & Delevoryas 1967, Artabe & Zamuner 1991, Brea & Artabe 1999), South Africa (Du Toit 1927), Australia (e.g., Walkom 1925, Holmes 2000) and Antarctica (Escapa *et al.* 2011, this study). Well-preserved foliated stems that were recently described as *Zonulamites nymboidensis* Holmes, 2000 from the Middle Triassic of Australia are overall very similar to *N. suberosus*, but are smaller (only 12–30 mm wide), have comparably narrow, *ca* 1.5 mm wide leaves, and relatively few leaves per whorl (about 20–30 as opposed to 40–50 in the present material).

Schizoneura Schimper & Mougeot, 1844 emend.

1828 *Convallarites* Brongniart, p. 454.
1844 *Schizoneura* Schimper & Mougeot, p. 48, nom. cons. (Zijlstra *et al.* 2007, Herendeen 2011)
1955 *Paraschizoneura* Radchenko, p. 86.

Type species. *Schizoneura paradoxa* Schimper & Mougeot, 1844, nom. cons. (Zijlstra *et al.* 2007, Herendeen 2011).

Emended diagnosis. Stems divided into long internodes and usually swollen nodes; nodes of main stems bearing whorls of leaves or branches; branch nodes bearing whorls of long, linear, single-veined leaves; immature whorls with leaves entirely fused along the lateral margins, forming a cylindrical sheath; mature whorls with leaves laterally fused into two or more strap-shaped, lanceolate or ovate leaf-sheath segments; in a few specimens, individual whorls with leaves free to their bases.

Remarks. A proposal to conserve the name *Schizoneura* over *Convallarites* (Zijlstra *et al.* 2007) has recently been
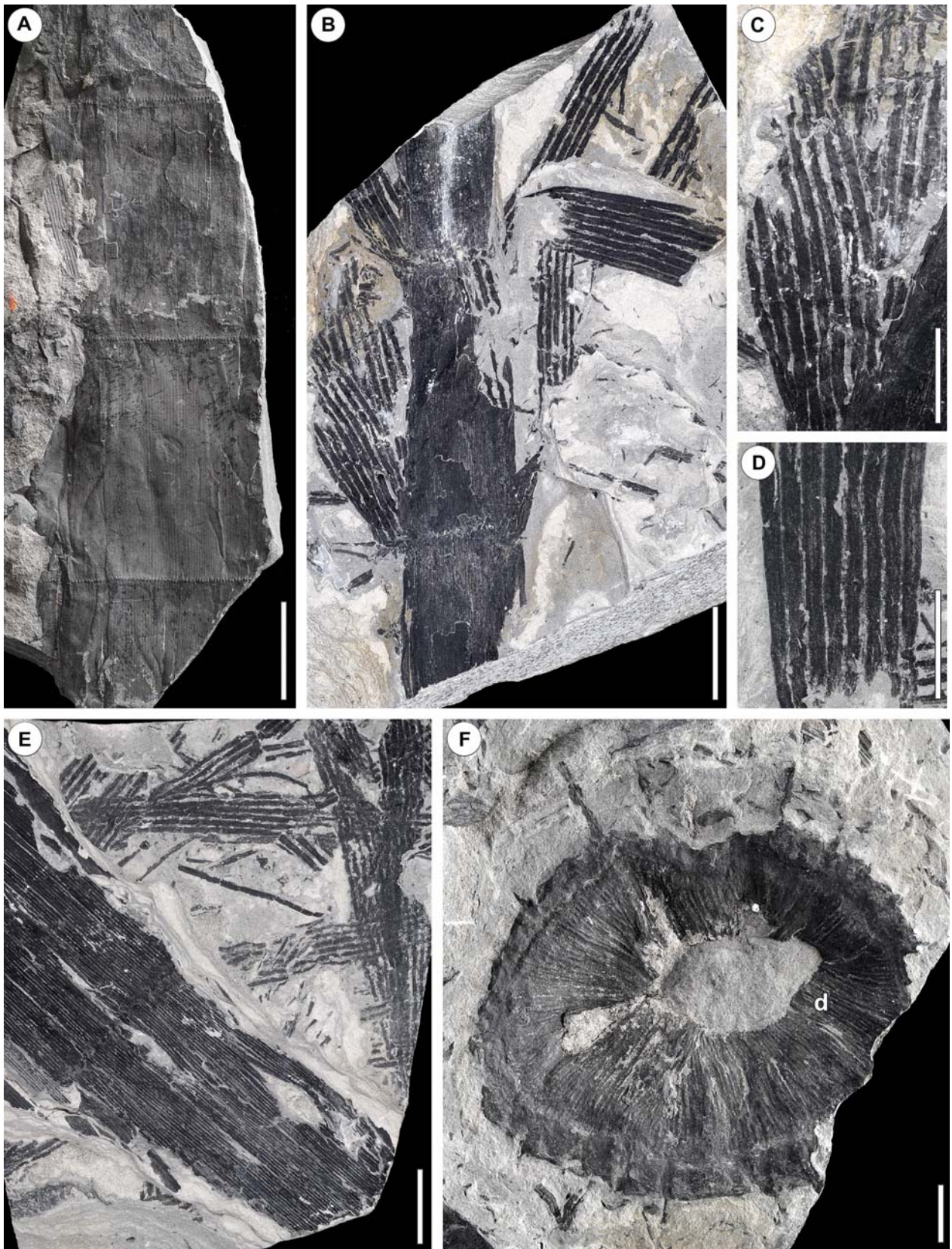
Fig. 4. Schizoneura africana Feistmantel, 1899 emend. from the Triassic of Mount Wisting, central Transantarctic Mountains. **A**, Large leafless stem, T-1893; **B**, Large stem with attached, strap-shaped leaf-sheath segments with five to eight leaves, T-1905; **C, D**, Details of Fig. 4B showing two leaf-sheath segments composed of usually eight, laterally fused leaves; **E**, Bottom surface of the specimen figured on Fig. 4B–D, showing a large stem fragment and abundant fragments of strap-shaped leaf-sheath segments; **F**, Nodal region of a large underground stem with attached remains of radiating lateral roots and a dome-shaped internal structure (d) with radiating spokes, T-6568. Scale bars for A, B, E = 2 cm, C, D, F = 1 cm.
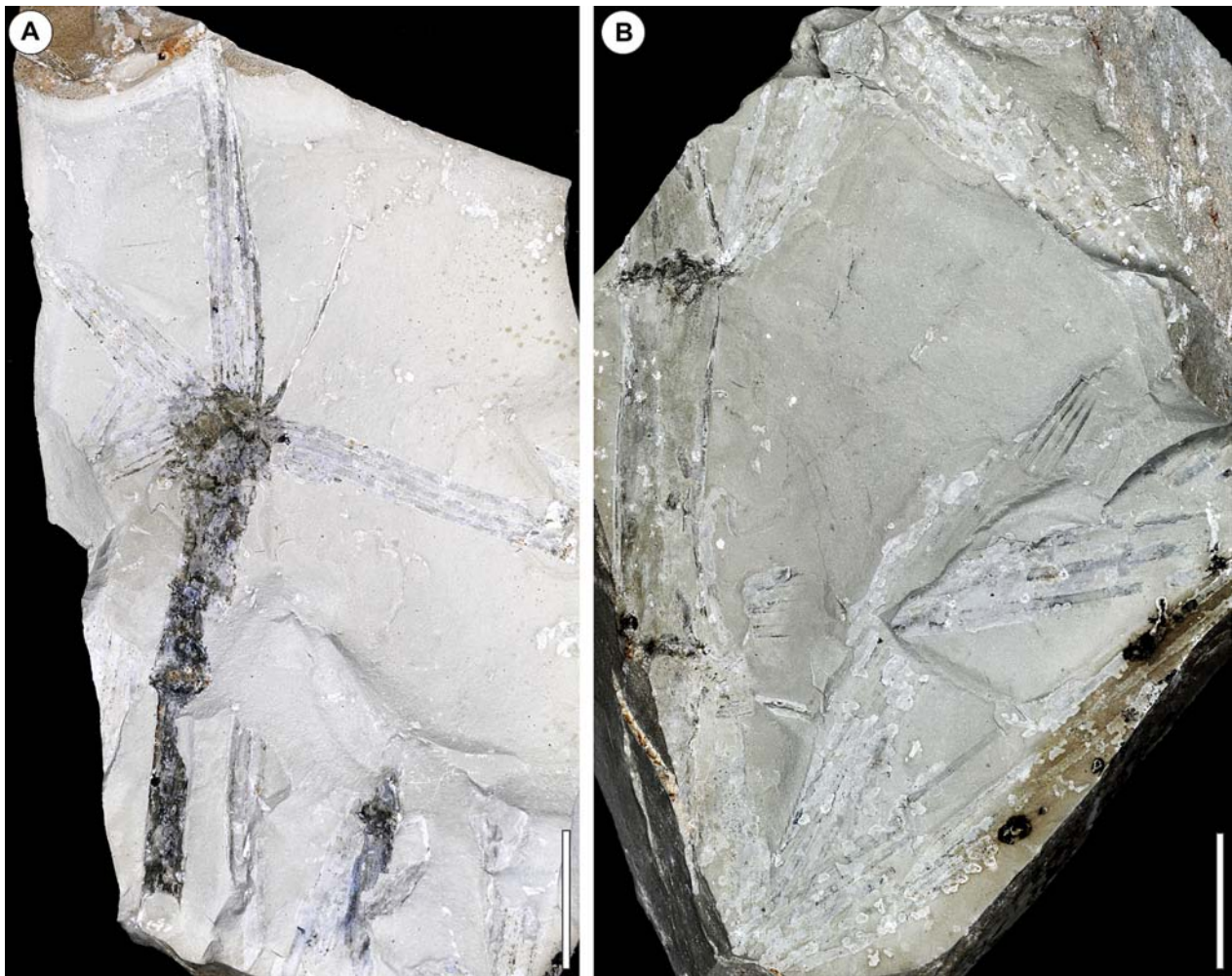
Fig. 5. Schizoneura africana Feistmantel, 1899 emend. from the Lower Triassic of Graphite Peak, central Transantarctic Mountains, East Antarctica. **A**, Small stem with attached remains of at least five narrow leaf-sheath segments, each composed of about four laterally fused, narrow leaves, T-6514a; **B**, Slab showing medium-sized leafy stem and abundant fragments of narrow, strap-shaped leaf-sheath segments composed of three to five laterally fused narrow leaves, T-6515. Scale bars = 2 cm.

accepted (Herendeen 2011). For reasons detailed in the Discussion, we regard *Paraschizoneura* as a junior synonym and transfer its two species, *P. sibirica* (Neuburg) Radchenko, 1955 and *P. czekanowskii* (Rasskazowa) Boureau, 1964, back to *Schizoneura*. Features newly included in the emendation, including the leaf origination from a cylindrical sheath of fused leaves on immature axes, are explained in detail in the Discussion.

Schizoneura africana Feistmantel, 1889 emend. (Figs 4 and 5)

1889 *Schizoneura* (?) *africana* Feistmantel, p. 42.
2001 *Paraschizoneura jonesii* Holmes, p. 17.

Selected synonymy

1845 'fossil plant'; Hooker, p. 227, pl. 28, fig. 1.
1845 *Asterophyllites* (?); Bain, p. 225.
1889 *Schizoneura* (?) sp.; Feistmantel, p. 41.
1889 *Schizoneura* (?) *africana* Feistmantel, p. 42

1902 '*Schizoneura*'; Arber, pp. 346, 347.
1905 *Schizoneura* (?) *africana* Feistmantel; Arber, p. 13.
1908 *Schizoneura africana* Feistmantel; Seward, p. 89, fig. 2.
1915 *Schizoneura* cf. *africana* Feistmantel; Walkom, pl. 3, fig. 1.
1921 *Schizoneura gondwanensis* Feistmantel; Seward & Holttum, p. 39, pl. 9, figs a–c, pl. 11, fig. a.
1924 *Schizoneura* cf. *africana* Feistmantel; Walkom, p. 79, text-fig. 1.
1985 *Schizoneura africana* Feistmantel; Anderson & Anderson, p. 103, pl. 42, figs 1–4.

Additional references that may belong to this species

1998 *Phyllotheca brookvalensis* Townrow; Retallack, figs 3a, b.
2010 *Neocalamites carrerei* (Zeiller) Halle; Morel *et al.*, p. 10, fig. 3.4.
2012 *Paraschizoneura* sp. Cariglino, p. 66, pl. 18, figs 1–4.

Holotype. Arber (1905) identified the single specimen figured and described by Hooker (1845) and Feistmantel (1889) as specimen 41,285 in the Geology Department of the British Museum of Natural History, London.

Emended diagnosis. Stems straight, divided into elongate internodes and slightly swollen nodes; large stems up to >75 mm wide in compression, leafless; smaller stems with leaf whorls consisting of several (generally four to seven) strap-shaped leaf-sheath segments, each containing about 3–13 (most commonly 4–8) linear leaves that are laterally fused along the entire leaf length.

Material studied. Four rock samples (T-1900, 1905, 6567 and 6568), containing two large foliated stems together with isolated stems, leaves and a nodal diaphragm, from the Upper Triassic Falla Formation at Mount Wisting, Queen Maud Mountains, central Transantarctic Mountains, East Antarctica; more than 70 fragments of leafy or leafless stems, isolated leaves and rooting structures on 51 rock samples (T6514–6565) from the Lower Triassic lower Fremouw Formation at Graphite Peak, Queen Alexandra Range, central Transantarctic Mountains, East Antarctica.

Description. Material consisting of large leafless and smaller leafy stems, isolated leaf-sheath segments and leaves, an isolated nodal diaphragm and abundant rooting structures (Figs 4, 5). Large stems straight, up to 75 + mm wide when compressed, leafless (Fig. 4A, E); smaller stems generally 5–20 mm, rarely up to 30 mm wide in compression, bearing leaf whorls at the nodes

Fig. 6. Earliest illustration of a plant fossil from South Africa, showing two superimposed whorls of leaf-sheath segments of *Schizoneura africana* Feistmantel emend. from the Permian lower Beaufort Group in the Roggeveld (Fish River). Reproduced from Hooker (in Bain, 1845).

(Figs 4, 5); pith casts of stems with longitudinal grooves (corresponding to positions of vascular bundles), about 14 per cm. Leaf whorls consisting of several (generally four to six) up to 10+ cm long, strap-shaped leaf-sheath segments, each containing about three to 13 (generally four to eight) leaves that are laterally fused over their entire length (Figs 4B–E, 5); individual leaves straight, linear, *ca* 2 mm wide, each with a prominent median vein occupying about one-third or more of the leaf width; lateral leaf margins membranous, with delicate tissue (Fig. 4C, D). Cross-section of underground stem at node level *ca* 70 mm in diameter, originally circular, showing dome-shaped structure with central hole and radiating striae (Fig. 4F); section of surrounding cortical cylinder with a ring of more or less rectangular impressions (vallecular canals?); stem with attached remains of radiating rooting structures (Fig. 4F). Isolated rooting structures compound, with main roots of varying thickness giving off dense, fine lateral roots.

Remarks. The first description of a plant fossil from South Africa (Hooker 1845) shows an illustration of two superimposed leaf sheaths that are split into six (below) and seven (above) radiating, strap-shaped segments (Fig. 6). This fossil was later tentatively referred to as *Schizoneura* (?) *africana* by Feistmantel (1889), who refrained from providing a diagnosis until his interpretation of Hooker's illustration as a *Schizoneura* species would receive further support. Subsequent descriptions of newly collected material (Arber 1902, 1905, Seward 1908) confirmed Feistmantel's observations. In accordance with the provisions of the International Code of Botanical Nomenclature (McNeill *et al.* 2006, Vienna Code, Art. 42.3), we suggest that Feistmantel's (1889) detailed description and reference to Hooker's original publication suffice to validate the name *Schizoneura africana* Feistmantel, 1889.

The species was later reported from several additional localities in Australia (Walkom 1915, 1924) and southern Africa (Seward & Holttum 1921, Anderson & Anderson 1985). Similar plant fossils from the Lower Triassic of Australia were described as a new species *Paraschizoneura jonesii* Holmes, 2001 based on the supposedly wide temporal and geographic separation from the South African material (Holmes 2001). We contend that a Late Permian versus an Early Triassic age and occurrence in Australia versus South Africa should not serve as systematic criteria, and regard *P. jonesii* as a junior synonym of *Schizoneura africana*.

The present material was collected from two localities in the Transantarctic Mountains. The fossils from the two sites differ in their average dimensions; foliated stems from Mount Wisting are considerably larger (*ca* 2.5 cm wide; Fig. 4B) than most specimens from Graphite Peak, which are usually 1–2 cm wide (Fig. 5). In addition, the leaf-sheath segments in the Mount Wisting fossils are more uniformly developed and generally
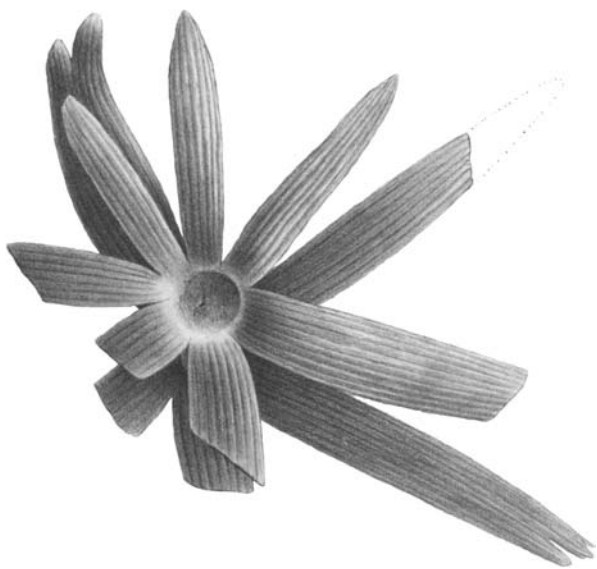
contain eight leaves (Fig. 4B–D), whereas those from Graphite Peak are narrower, more numerous and composed of fewer individual leaves (Fig. 5), similar to the previously described specimens from South Africa (Hooker 1845, Seward 1908, Anderson & Anderson 1985; Fig. 6) and Australia (Holmes 2001). In both respects, however, there are a few specimens at the two sites that demonstrate a significant morphological overlap; the largest foliated stem at Graphite Peak measures 2.8 cm in width, and there are also a few dispersed leaf-sheath segments at Mount Wisting that contain only four leaves (Fig. 4E). Given that many foliar characters in *Schizoneura* plants, e.g., leaf number, width and number of sheath segments, are to some degree controlled by the thickness and ontogenetic stage of the leaf-bearing stem (Feistmantel 1880, Surange 1966, Rohn & Rösler 1986, this study), we see no meaningful criteria to distinguish between these specimens, and include all in a rather broadly defined species.

The nature of the dome-shaped internal structure with radiating striae that occurs at the node level of an underground stem (Fig. 4F) remains elusive. Holmes (2001) interpreted a similar structure arising from the node of a small leafy *Schizoneura* stem as an attached stem internode fragment. The almost tubular morphology of this structure in the present specimen may lend further support for this interpretation, as it might represent a collapsed vascular cylinder of an attached internodal stem fragment.

As in the case of *Neocalamites* described above, *Schizoneura africana* in the present collection (and elsewhere) occurs in either apparently monospecific mass accumulations or in plant-fossil assemblages that lack any identifiable types of different sphenophyte taxa. Therefore, we are confident in assigning also the large, leafless stems co-occurring with the foliar remains at the two sites to the same species.

Schizoneura africana differs from the somewhat similar *S. gondwanensis* Feistmantel, 1876 in having considerably larger foliated axes with leaf sheaths being split into usually more than four, in few cases up to seven strap-shaped or narrow wedge-shaped segments. *Schizoneura africana* is now known from the Permian Beaufort Group of South Africa (Hooker 1845, Feistmantel 1889, Arber 1902, 1905, Seward 1908, Anderson & Anderson 1985), from the Upper Permian of the Sydney Basin (S. McLoughlin, pers. comm. 2012), from the Lower Triassic of Australia and Antarctica (Holmes 2001, this study) and from Middle to possibly Upper Triassic strata of Australia (Walkom 1915, 1924), Zimbabwe (Seward & Holttum 1921) and Antarctica (this study). Of particular importance is the little-known material from the Triassic Somabula Karoo deposits near Gweru, Zimbabwe; it includes probably the most complete specimen known to date, which consists of a more than 20 cm long, slender, laterally compressed stem with ten nodes bearing attached leaf remains (Seward & Holttum 1921). Morel *et al.* (2010)

figured a specimen from the Middle Triassic Potrerillos Formation, Argentina, identified as *Neocalamites carrerei*; the figured specimen bears leaves apparently fused into at least five strap-shaped sheath segments vaguely similar to the present material. Cariglino (2012) further reported an occurrence of '*Paraschizoneura* sp.', from the Permian La Golondrina Formation in Santa Cruz Province, Argentina, described as being closely similar to *Schizoneura africana* as figured by Anderson & Anderson (1985).

Discussion

Rationale for a new emendation of Neocalamites

Neocalamites was established by Halle (1908) to accommodate several Mesozoic sphenophyte species that had previously been assigned to *Schizoneura*. The essential distinguishing features of *Neocalamites* were suggested to be that the leaves are single-veined and entirely separate down to their base (as opposed to being fused into sheath segments as in *Schizoneura*), and that the number of leaves is considerably lower ('at least half') than that of the internode vascular bundles (Halle 1908). The original diagnosis and taxonomic concept of *Neocalamites* have since been emended by various authors (Vladimirovich 1958, Sadovnikov 1986). In addition, several new generic names have been introduced for different preservational states of plant parts that are clearly attributable to *Neocalamites*. Finally, descriptions of new *Neocalamites* species that in a strict sense do not conform to the original diagnosis or its emended versions (e.g., Yang *et al.* 2011, Zan *et al.* 2012) make it necessary to propose a new emendation. Here we provide a detailed explanation of our rationale to modify certain features of the generic diagnosis.

Leaf-base morphology and the case of Zonulamites. The leaves in *Neocalamites* were diagnosed to be entirely free and separate from one another even at the point of origin. Halle (1908) placed particular emphasis on this feature, stating that leaf separation is evident even in cases where the leaves are crowded. As a result, Holmes (2000) established the genus *Zonulamites* for sphenophyte remains that had previously been assigned to *Neocalamites* (Holmes 1982), but which supposedly differed in that the leaves are basally fused to form a narrow collar at the node (Holmes 2000). We suggest, however, that this approach is perhaps too narrow an interpretation, as there is a high degree of overlap in the leaf-base morphologies.

The exact leaf-base morphology is extremely difficult to discern in typical compression specimens, and interpretation remains somewhat subjective in almost every case. For example, in well-preserved specimens of the common and well-known European species *Neocalamites meriani* and *N. lehmannianus*, leaf bases

may appear to be clearly separate (Kelber 1990, figs 44 and 46; Kelber & Hansch 1995, fig. 105) or to be fused to form a distinct, narrow collar at the node (e.g., Kräusel 1959, pl. 1, fig. 1; Weber 1968, figs 21–23; Kelber & Hansch, 1995, text-figs 96, 195). Even in the present material, in which cellular details are well preserved, it is difficult to determine the transition from cortical epidermis to leaf tissue (Fig. 2C–F). In addition, recent descriptions of otherwise typical *Neocalamites* species explicitly state that the leaves in some whorls may be basally fused (Yang *et al.* 2011, Zan *et al.* 2012). Finally, it should be noted that the primary reason that Halle (1908) established *Neocalamites* was to separate these fossils from typical *Schizoneura* specimens; hence, it may be argued that the feature of leaf separation received particular emphasis only to facilitate distinction from the fused leaf-sheath segments in the latter genus. Collectively, this information shows that there is strong evidence to deviate from the strict practice of assigning only those specimens to *Neocalamites* in which the leaf bases are (or appear to be) entirely separate from one another.

In this respect, *Neocalamites* Halle emend. may become superficially somewhat similar to the genus *Townroviamites* Holmes, 2001 and to those representatives of the morphogenus *Phyllotheca* Brongniart, 1828 that are relatively large and have strongly reduced leaf sheaths, e.g., *P. equisetitoides* Schmalhausen, 1879 or *P. griesbachi* Zeiller, 1902 emend. Surange, 1956 (see, e.g., Surange 1956, 1966, Boureau 1964). The genera can, however, be easily distinguished from *Neocalamites*, as both *Phyllotheca* and *Townroviamites* are characterized by a quite different stem vasculature, in which the number of leaves is equal to the number of internode vascular bundles (e.g., Townrow 1955, Holmes 2001). In *Neocalamites*, by contrast, an individual bundle in the axial vascular cylinder passes through at least two internodes before entering a leaf base, which results in the number of vascular bundles of a given internode being considerably greater than the number of leaves in the whorl of the corresponding node (Halle 1908). This distinction, which is based on vegetative criteria, likely reflects a more natural organism-based classification, as the affiliated reproductive organs in the two groups are distinct (e.g., Townrow 1955, Boureau 1964, Escapa & Cúneo 2006).

Stem surface features. The outer cortical surface of most *Neocalamites* species is smooth or shows relatively broad and shallow furrows. New finds of typical *Neocalamites*-type fossils with associated strobili from China, however, indicate that the cortex in some species produced characteristic surface ornamentations (Zan *et al.* 2012). Therefore, the character of a smooth outer stem surface, as included in Halle's (1908) original diagnosis, should be omitted. It remains unclear whether the shallow-concave longitudinal grooves on some *Neocalamites* stems (Fig. 1B) are in fact features of the

outer cortical surface, or whether they formed as a result of collapse of internal vallecular canals or from simple mechanical effects during the compaction of the cylindrical stem.

Nodal preservation and the case of Nododendron. *Nododendron* was established based on an isolated node and associated stem in lateral compression that had both been assigned previously to *Neocalamites carrerei* (Frenguelli 1949, Artabe & Zamuner 1991). The node was interpreted as bearing a whorl of lateral branches, one of which bore an attached whorl of minute, *ca* 100 μm wide *Asterophyllites*-type leaves. Re-examination of the type material by Holmes (2001) and one of us (BB, 2012), however, showed that the supposed leaf whorl represents an unknown leaf fragment overlying the stem, and the supposed branches are leaves with fused bases. This reinterpretation is further supported by some *Nododendron*-type stem cross-sections described herein, which clearly demonstrate that the radiating appendages are actual leaves (Fig. 2).

Holmes (2000, 2001) was the first author to draw attention to the peculiar phenomenon that nodal diaphragms are commonly preserved even in small collections of Gondwanan *Neocalamites* assemblages, whereas they are absent from typical European *Neocalamites* species, i.e., *N. lehmannianus* and *N. meriani*. Indeed, there is comprehensive evidence to indicate that this phenomenon is of biological origin, and can not be explained, for example, to be a result of taphonomic bias. Previous authors have commented on the conspicuous absence of *Neocalamites* diaphragms in European assemblages, even in large collections that contain abundant diaphragms of other equisetalean taxa (e.g., Harris 1931, 1961, Roselt 1954, Kräusel 1959, Weber 1968, Kelber 1990, Kelber & Hansch 1995). Moreover, in rare cases where leaf whorls of European *Neocalamites* species are described, they have never been demonstrated to contain the actual diaphragm (e.g., Kelber 1990, fig. 46; Kustatscher *et al.* 2007, pl. 2, fig. 3; Pott & McLoughlin 2011, text-fig. 3d). As a result, it has been proposed that mature stems of these plants were in fact hollow even at the nodes (Harris 1961, Weber 1968). Consequently, Holmes (2000, 2001) interpreted the presence of persistent nodal diaphragms together with the fused leaf bases as evidence that *Nododendron* Artabe & Zamuner, 1991 emend. Holmes, 2001 and *Zonulamites* were representatives of a separate, supposedly endemic Gondwanan sphenophyte lineage that was different from the Northern Hemisphere *Neocalamites*.

We agree with Holmes (2000, 2001) that the preservation of nodal diaphragms in the Gondwanan forms reflects a systematically relevant anatomical feature. Two important observations, however, suggest that this feature should be used only for delimitation at the species level. First, there is some evidence that the development of diaphragms among *Neocalamites* species is variable. Although it is true that nodal diaphragms are

not known in the typically European species, there are several descriptions of such structures occurring in other well-established members of the genus from East Asia, including the widespread *N. carrerei* (e.g., Kon'no 1962, 1973, Kimura *et al.* 1982, Kim & Roh 2008). In addition, the few reproductive structures that have been found associated with the vegetative remains of these Gondwanan sphenophytes are similar to the typical Northern Hemisphere 'Neocalamostachys' strobili (Retallack 1987, Brea & Artabe 1999, Holmes 2000), indicating that the plants were probably closely related. Based on this evaluation we contend that the presence of persistent nodal diaphragms is an appropriate character only at the species level.

Vascular cylinder and the case of Neocalamites *Halle, 1908 emend. Sadovnikov, 1986.* Sadovnikov (1986) described various sphenophyte organs from the Triassic of Iran that show exquisite preservation of cellular detail. The author reinterpreted the characteristic longitudinal striations on the inner surfaces of *Neocalamites* stems as representing sclerenchymatous strands that functioned in support, and emended the diagnosis of *Neocalamites* accordingly (Sadovnikov 1986). This interpretation, however, is at odds with many detailed investigations on the anatomy of *Neocalamites* stems (e.g., Halle 1908, Weber 1968, Artabe & Zamuner 1991), and has consequently gained little acceptance. The sections of stems at the level of the node illustrated here (Fig. 2A–C, E) show a thin cylinder with canals that correspond exactly in number, position and arrangement with the striations seen on casts of the interior internodal surface. Our interpretation is that these structures correspond to the carinal canals within the vascular cylinder, similar to the stem anatomy of extant and other fossil sphenophytes.

Reproductive features and the problematic genera 'Neocalamostachys' *and* 'Equisetostachys'. The morphology of reproductive organs associated with *Neocalamites* appears to be distinct from that of other co-occurring equisetalean fossils. They consist of more-or-less elongate strobili that lack intercalated sterile bracts, and are borne terminally on a narrow lateral branch that represents a single, elongated internode (Vladimirovich 1958, Kon'no 1962, 1972).

Fertile *Neocalamites* remains have been described sporadically from the Triassic of Europe and Asia (Compter 1911, 1922, Takahashi 1949, Kuhn 1957), but these reports have received little attention (but see Kon'no 1962, Grauvogel-Stamm 1978, Kelber 1990). The earliest, more widely recognized description of fertile *Neocalamites* is that of Vladimirovich (1958), who described stems with attached strobili, and emended the genus to include reproductive features. Similar strobili from the Triassic of Japan were assigned to *Equisetostachys* (*Neocalamites?*) *pedunculatus* (Kon'no 1962). This latter author stressed the affiliation of the organs with

Neocalamites vegetative parts, and suggested that the strobili should probably be assigned to a new genus informally named 'Neocalamostachys' if further studies should provide more direct evidence for affiliation (Kon'no 1962). The name *Neocalamostachys* was later adopted by Boureau (1964) and has been widely used since (e.g., Kon'no 1972, Dobruskina 1995, Brea & Artabe 1999, Holmes, 2000), regardless of the fact that it was never formally diagnosed or properly typified (see Escapa & Cúneo 2006, Weber 2008). Further complicating this issue is the fact that the alternative name *Equisetostachys* is a *nomen nudum* that was created invalidly at least twice (Halle 1908, Jongmans 1927); Boureau (1964) and other authors cite Nathorst (1878) as the authority for *Equisetostachys* although the name was first introduced by Halle (1908; see Nathorst 1878).

We propose that the most reasonable solution to this problematic nomenclatural situation is an approach similar to that used with the well-known equisetalean genus *Equisetites*. In our view the generic diagnosis of *Neocalamites* should be restricted to vegetative characters, and information on reproductive organs might be included in the relevant species diagnosis when an affiliation is firmly established (compare, e.g., *Equisetites arenaceus*: Kelber & van Konijnenburg-van Cittert 1998). Isolated *Neocalamites*-type reproductive structures should be referred to in open nomenclature until an appropriate generic name, most likely the less committal name *Equisetostachys*, has been validated.

Reinterpretation of Schizoneura (including Paraschizoneura*)*

The name *Schizoneura* was introduced by Schimper & Mougeot (1844) for several sphenophyte fossils from the Triassic of France that had previously been described as monocot leaves under the name *Convallarites* Brongniart (see Zijlstra *et al.* 2007). *Schizoneura* is characterized by leaf sheaths that are split into usually two strap-shaped leaf-sheath segments. Earlier authors who primarily studied the common European species *S. paradoxa* noted that the leaf sheaths in *Schizoneura* sporadically split into more than two segments (e.g., Schimper & Mougeot 1844, Feistmantel 1880, 1889, Wills 1910a, 1910b, Vernon 1910, Seward 1908, Hirmer 1927). This observation, however, later received little attention, especially with the increasing number of descriptions of the smaller Gondwanan species *S. gondwanensis*, whose leaf sheaths are typically divided into only two segments. As a consequence, the misconception that *Schizoneura* leaf sheaths were essentially split into two symmetrical, opposite, sheathing segments has become more-or-less established in the literature (see, e.g., Boureau 1964, Stewart & Rothwell 1993). *Paraschizoneura* was erected for foliage in which each leaf sheath is split into presumably four uneven foliar segments with free bases (Radchenko 1955; see Boureau 1964).
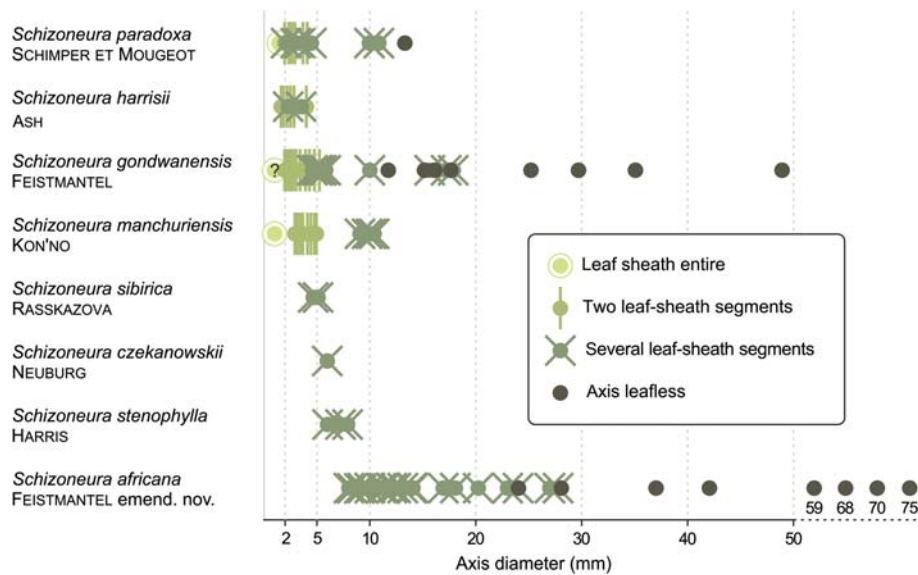
Fig. 7. Schematic diagram showing a comparison of leaf-sheath morphology *versus* stem thickness in selected species of *Schizoneura* Schimper & Mougeot emend. Data were compiled from measurements provided or taken from illustrations by Hooker (1845), Feistmantel (1880, 1889), Seward (1908), Harris (1931, 1961), Boureau (1964), Grauvogel-Stamm (1978), Pant *et al*. (1982), Ash (1985), Rohn & Rösler (1986), Kelber (1990), Kelber & Hansch (1995), Holmes (2001), Cariglino (2012), and from the present material. The question mark relates to a comment of Feistmantel (1880), who noted that immature sheaths in *S. gondwanensis* were most likely entirely fused, as individual segments in some further-developed sheaths were observed to be only incompletely separated. For the purpose of clarity, individual and consistent data points in crowded portions may have been omitted or show an uncertainty interval of about ±0.5 mm.

There is strong evidence that these various foliar morphologies belong to a similar group of plants, and to regard *Paraschizoneura* as a junior synonym of *Schizoneura*. A comparison of foliar morphology versus stem thickness in selected well-known species of *Schizoneura* (including forms formerly assigned to *Paraschizoneura*) illustrates this concept (Fig. 7): (1) across different species, leaf sheaths on presumably immature stems with a diameter smaller than 2 mm are entirely fused (Feistmantel 1880, Kon'no 1960, Grauvogel-Stamm 1978; see also *Schizoneura megaphylla* Wang & Wang 1990, pl. 2., figs 8, 10); (2) 'typical' *Schizoneura* foliage with two opposite leaf-sheath segments, e.g., those of *S. gondwanensis* and *S. manchuriensis* Kon'no, 1960, are borne on stems that are *ca* 2–5 mm wide (see, e.g., Feistmantel 1880, Kon'no 1960); (3) at stem diameters greater than *ca* 5 mm, leaf sheaths of all species considered are split into more than two segments (see, e.g., Feistmantel 1880, Kon'no 1960, Rohn & Rösler 1986); (4) the largest stems (main stems?) of a species are usually leafless.

These observations lead us to suggest that the number of leaf-sheath segments in *Schizoneura* is primarily determined by the original leaf number and the diameter and ontogenetic stage of the leaf-bearing stem (see also Rohn & Rösler 1986). A complete developmental series of a *Schizoneura* leaf sheath would, therefore, begin with the formation of an entirely fused, cylindrical sheath that initially splits into two opposite segments (Feistmantel 1880, Surange 1966, Rohn & Rösler 1986). These segments may become further separated during subsequent thickening of the stem until they disintegrate into individual leaves that are ultimately shed

(see, e.g., Kon'no 1960, Rohn & Rösler 1986). Thus, the *Paraschizoneura*-like morphology can be regarded simply as the larger form of a typical *Schizoneura* plant, in which the leaf sheaths split into more than two segments as a result of the increased stem diameter. *Schizoneura africana* is by far the largest known species of the group, with stems up to 75 mm wide in compression (Fig. 4).

A further distinguishing feature noted by Boureau (1964) is the interpretation that the basal parts of the leaf-sheath segments in *Schizoneura* are sheathing, whereas those in *Paraschizoneura* are entirely free. We suggest, however, that the degree of sheathing is directly related to the leaf number, stem diameter, attachment angle and number of segments. Leaf sheaths on narrow stems that split into two segments are likely to remain attached at more or less acute angles and, consequently, with more-or-less sheathing basal parts. As the stem continues to thicken, the leaf sheath will continue to split as a result of strain, which then allows the individual segments to bend down from the stem at wider angles.

Morphological and systematic diversity of Schizoneura plants

The comparison of leaf morphology *versus* stem thickness (Fig. 7) also provides evidence for different growth habits in this plant group. *Schizoneura gondwanensis*, *S. manchuriensis* and *S. africana* all show stem size classes and a distinct correlation of leaf morphology and stem diameter. We suggest that this may be a result of a monopodial, (sub)arborescent habit with an upright, naked main stem and leafy lat-

eral branches. Size-class distinction and correlation with leaf morphology, by contrast, is less clear in the type species, *S. paradoxa*, and the similar species *S. harrisii* from North America (Fig. 7). This situation may be due to more profuse branching in these species. For example, large and well-preserved specimens of *S. paradoxa* from the type area in the Vosges Mountains indicate that this plant may have been highly branched and shrub-like (Grauvogel-Stamm 1978). Interestingly, this possible growth-habit difference also coincides with what is known about the reproductive features in this group. *Schizoneura paradoxa* and *S. harrisii* are known to have produced strobili of the *Echinostachys* type (Grauvogel-Stamm 1978, Ash 1985), whereas the reproductive structure of *S. manchuriensis* has been assigned to *Manchuriostachys* (Kon'no 1960). Based on these different types of reproductive organs, Grauvogel-Stamm (1978) instituted two distinct families, Echinostachyaceae and Manchurostachyaceae, within the Equisetales. The apparently different growth habits in the two groups may provide further evidence for morphological disparity in the *Schizoneura*-like Equisetales.

Summary and conclusions

In contrast to the Palaeozoic Calamitaceae, most Mesozoic sphenophytes still remain poorly understood. This is in part because of the seemingly uniform vegetative morphology and the overall scarcity of detailed anatomical information and reproductive structures. The discovery of well-preserved compressions of *Neocalamites* and *Schizoneura* from the Triassic of Antarctica has necessitated a review of these genera and a detailed reevaluation of the morphological and anatomical features that have been used in their taxonomy. These fossils contribute to a better understanding of certain surface, nodal and internal features that can now be used to more accurately describe and interpret the internal organization of the plants. For example, the various types of longitudinal ribs and striations on stem compressions can now be interpreted as vallecular and carinal canals similar to those seen in stems of modern *Equisetum*. Another important outcome of this study of vegetative sphenophyte remains is that the re-classification of *Neocalamites* based on vegetative characters matches favorably with the co-occurrences of certain types of stalked and bractless reproductive structures of the *Neocalamostachys*-type. This independent line of evidence provides compelling proof that it is possible to develop a more natural classification for these widespread Mesozoic sphenophytes.

In addition to understanding the natural affinities of the detached organs, it is important to view plant-fossil specimens within the context of ontogenetic stages and growth dynamics. By some authors, *Schizoneura* has

been principally defined on the number and attachment of leaf segments. Using the material from Antarctica and other specimens, however, it has been possible to demonstrate a direct correlation of certain vegetative characters (leaf segmentation *versus* stem diameter) that reflect growth. When plotted together with other members of the genus, one can distinguish two major sub-groups of *Schizoneura* based on growth morphology. It is interesting, as in the case of *Neocalamites*, that these two sub-groups of *Schizoneura* also appear to have distinct types of reproductive structures; one group contains profusely branched, shrub-like plants with highly dissected leaf sheaths and cones of the *Echinostachys*-type, whereas the other includes large monopodial, probably sub-arborescent plants with leafy lateral branches and, presumably, *Manchuriostachys*-type cones.

We hope that this contribution stimulates additional research on compressed fossil plants in order to obtain biological information that leads to a more natural classification, and to build a more robust basis for understanding the distribution of sphenophytes in time and space.

Acknowledgements

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