



# How similar are the venation and cuticular characters of *Glossopteris*, *Sagenopteris* and *Anthrophyopsis*?

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## ABSTRACT

Venation architectures and cuticular micromorphology of leaf fossils play important roles in higher-level taxonomic segregation, as these characters are broadly fixed within major plant clades. Three common fossil plant taxa are characterized by similar-shaped leaves or leaflets and anastomosing venation to such an extent that examples have commonly been assigned to the wrong taxon in past studies where fragmentary or ill-preserved material is available. We use standardized descriptions of vein cross-connection types and stomatal features to compare and contrast the venation patterns and stomatal architectures of these genera. Our reanalysis of the macro- and micromorphology of *Glossopteris*, *Sagenopteris* and *Anthrophyopsis* leaves reveals important differences that help segregate these taxa even on the basis of incomplete specimens. *Anthrophyopsis* has distinctive alignments of vein cross-connections in the outer lamina and paracytic stomata consistent with those of Bennettitales. *Glossopteris* has perigenous and monocyclic—normally stephanocytic to actinocytic—stomata commonly protected in pits or by overarching papillae. *Sagenopteris* has more consistently evanescent midribs and surficial anomocytic or stephanocytic stomata with weakly modified subsidiary cells. Considering the putatively close relationship of glossopterids (*Glossopteris*), Caytoniales (*Sagenopteris*) and Bennettitales (here encompassing *Anthrophyopsis*) resolved as members of the ‘glossophyte’ clade in some past phylogenetic studies, cuticular features suggest that these groups are not closely related. In addition, anastomosing venation, superficially similar to that of *Glossopteris*, *Sagenopteris* and *Anthrophyopsis* appears to have arisen independently in numerous other plant groups suggesting that this character has ecological or physiological benefits and is strongly prone to homoplasy.

## 1. Introduction

Reticulate (anastomosing) venation occurs in a broad range of plant groups dating back at least to the Pennsylvanian (Fig. 1). For example, reticulate veins are well documented in various plant groups, such as ferns (Wagner, 1979), Medullosales (Zodrow et al., 2007), Cycadales (Erdei and Manchester, 2015; Coiro et al., 2023), Glossopteridales (Pigg and McLoughlin, 1997), Gigantopteridales (Glasspool et al., 2004), Ginkgoales (Arnott, 1959), Peltaspermales (Krassilov and Shilin, 1995), Bennettitales (Seward, 1903), Petriellales (Bomfleur et al., 2014), Caytoniales (Halle, 1910), Gnetales (Yang, 2015), angiosperms (Sack and Scoffoni, 2013), and various seed plants of uncertain affinities (Harris, 1932a; Trivett and Pigg, 1996; Anderson and Anderson, 2003; Xu et al.,

2021; Fig. 2A–L). Some of these groups clearly are distantly related (McLoughlin, 2021), hence it is assumed that their shared venation style is a convergent character. However, in some cases, anastomosing venation styles are so markedly similar that they might provide evidence of a close phylogenetic relationship.

In the case of glossopterids and caytoniales, striking similarities in leaf/leaflet shape, venation, and associated reproductive organs, have been argued to represent homologous characters that suggest direct evolutionary links (Retallack and Dilcher, 1981; Doyle, 2012), and in several cases, incomplete or poorly preserved examples of *Glossopteris* and *Sagenopteris* have been erroneously assigned to the other genus in early palaeobotanical studies (Feistmantel, 1881; Johnston, 1887). Since the stratigraphic ranges of these taxa do not overlap,

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misidentification of these genera is generally uncommon in modern palaeobotanical studies. However, other taxa with similar leaf forms, such as *Gontriglossa* or *Anthrophyopsis* (Thomas, 1952; Anderson and Anderson, 1989; Xu et al., 2021), might represent intermediate stages in the evolution of a *Glossopteris*–*Sagenopteris* lineage defined by common venation characters. Examples of both *Gontriglossa* and *Anthrophyopsis* have also been mistaken for representatives of either *Glossopteris* or *Sagenopteris* in past studies (Du Toit, 1927; Harris, 1932a). Despite their putative significance in defining a seed-plant lineage that potentially survived both the end-Permian and end-Triassic lineages, and which Melville (1983) suggested was a precursor to angiosperms, the finer details of venation architecture and epidermal patterning have not been seriously compared between these reticulate-veined taxa. Consequently, it is unclear whether the similarities in anastomosing veins are superficial and convergent or are genuinely homologous.

Here we document the patterns of anastomosing venation in three morphologically similar genera, i.e., *Glossopteris*, *Sagenopteris* and *Anthrophyopsis* (Table 1), and make additional comparisons with published examples of several other plant groups to assess commonalities and differences in venation pattern. We also illustrate cuticular details for these genera to assess whether these taxa share distinctive epidermal or stomatal characters (Table 1) that might indicate close affinities.

## 2. Materials and methods

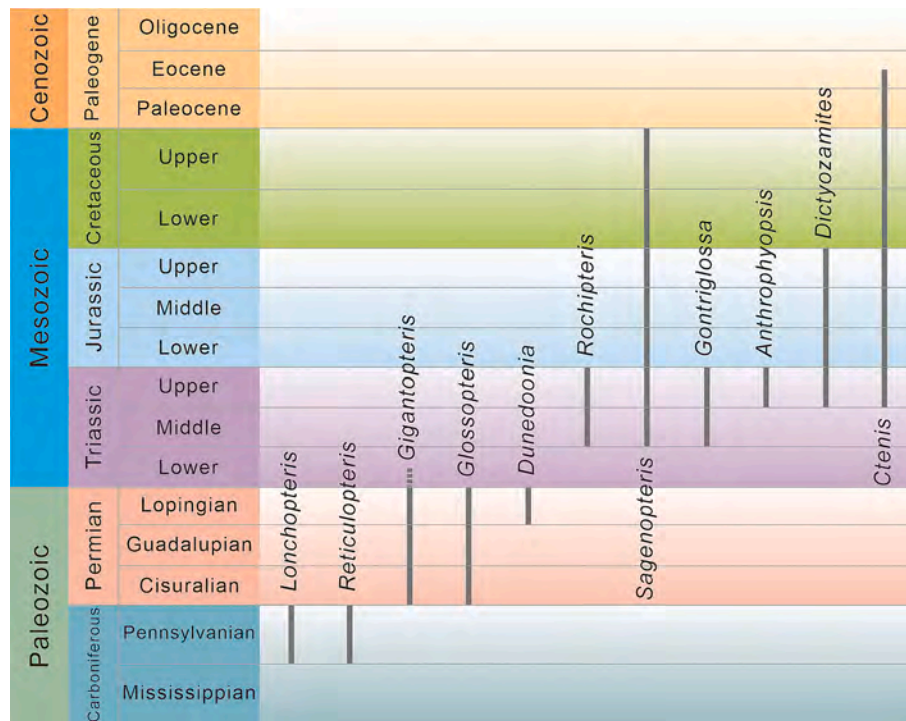
Photographs of 25 macrofossil plant specimens were taken with Canon 40D and 60D cameras equipped with an EF-S 18–135 mm f/3.5–5.6 IS lens, using LED illumination. Of these, PB4726, PB23148 and PB23157 (*Anthrophyopsis*), PB11615 and PB11616 (*Ctenis*) are deposited in the Palaeobotany Collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). Specimens represented by S168921 (*Anthrophyopsis*), S055053, S070622, S075940, S150104, S067564 and S055368 (*Sagenopteris*), S128461 (*Gigantopteris*), S089172 (*Rochipteris*), and S137601 (*Dictyozamites*) are housed in the Swedish Museum of Natural History (Naturhistoriska Riksmuseet:

NRM), Stockholm. Other specimens are held in Australian repositories as follows: UQF79380, UQF79206, UQF79283 (*Glossopteris*) are deposited in the University of Queensland fossil collections now held by the Queensland Museum, Brisbane; AMF57722 (*Sagenopteris*), AMF56472 (*Dunedoonia*), AMF58811 and AMF60031 (*Glossopteris*) are held in the Australian Museum, Sydney; MVP187213 (*Sagenopteris*) is stored in Museums Victoria, Melbourne; and QMF12699 (*Sagenopteris*) is deposited in the Queensland Museum, Brisbane.

Preparation of cuticles from the host rock, involved cautiously choosing the organically preserved remains that could be recovered directly from fossil compressions. A set of dissecting scalpels and needles were used for removing leaves from the rock and later for separating the cuticles from leaf mesophyll. Some further cleaning procedures with Hydrochloric acid (HCl) and Hydrofluoric acid (HF) were undertaken in order to remove all adhering sediment particles, such as carbonates and silicates. After washing with distilled water, the cleaned cuticles were treated with Schultze Reagent (HNO<sub>3</sub> + KClO<sub>3</sub>) until they became brown. Addition of 5% KOH solution was used to remove any remaining opaque organic residue until the cuticle became yellowish and translucent. After washing the samples with distilled water, the material was mounted in glycerine gel on glass slides beneath a cover slip (Kerp, 1990), and studied using an Olympus BX51 light microscope (LM) with an Olympus DP71 digital camera. Some charcoalified leaf fragments were recovered by bulk maceration of sedimentary rocks in 40% HF for two weeks then sieved and cleaned in distilled water.

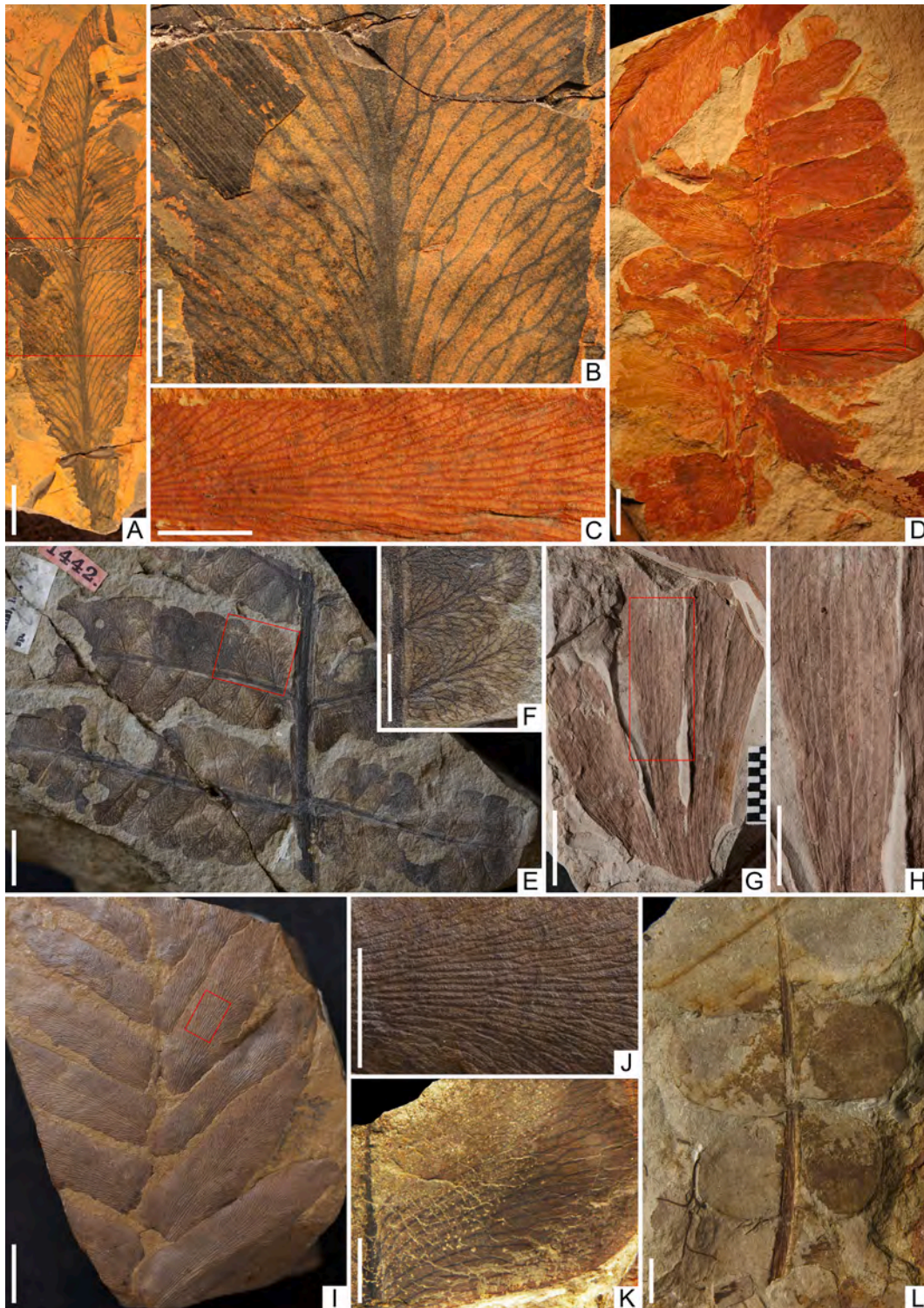
For scanning electron microscopy (SEM), prepared cuticle or charcoalified leaf fragments were placed on aluminum stubs with double-sided adhesive tape, sputter-coated with gold and studied using a LEO 1530 at an acceleration voltage of 20 kV at NIGPAS or a ESEM FEI Quanta FEG 650 SEM at NRM. All slides and SEM stubs are housed and recorded in the Palaeobotany Collection of NRM, with catalog numbers corresponding to their original specimens.

For descriptions of the vein reticulation patterns, we use the categories of vein junction types outlined by Melville (1976), mainly represented by “eta junction (H-type)”, expressed by a transverse vein



**Fig. 1.** Geologic ranges of some representative reticulate taxa, including: *Lonchopteris* (Tenchov, 2004); *Reticulopteris* (Tenchov, 2012); *Gigantopteris* (Yu et al., 2015); *Glossopteris* (McLoughlin, 2011); *Dunedoonia* (Srivastava, 1992); *Rochipteris* (Barone-Nugent et al., 2003); *Sagenopteris* (Kustatscher and Van Konijnenburg-van Cittert, 2013); *Anthrophyopsis* (Xu et al., 2021); *Dictyozamites* (Saadatnejad, 2022) and *Ctenis* (Erdei and Manchester, 2015).





**Fig. 2.** Leaves of selected plant groups with anastomosing venation excluding *Glossopteris*, *Sagenopteris* and *Anthrophyopsis*. A, B. Whole spatulate leaf of *Contriglossa verticillata* (Thomas) [Anderson and Anderson, 1989](#) (Gnetales?), and enlargement of mid-lamina showing prominent midrib and anastomosing secondary veins; PRE/F442; Upper Triassic, Molteno Formation, Umkomaas Valley, South Africa. C, D. *Dunedoonia reticulata* [Holmes, 1977](#) (order uncertain), pinnate leaf with reticulate venation, but lacking a midrib in leaflets; AMF56472; Upper Permian, Dunedoo Formation, Dunedoo, Gunnedah Basin, Australia. E, F. *Gigantopteris lagrelii* [Halle, 1927](#) (Gigantopteridales), bipinnate leaf with partially conjoined pinnae with amalgamated reticulate venation; S128461; Lower to Middle Permian, Lower Shihhotse Formation, Taiyuan, Shanxi, China. G, H. *Rochipteris* sp. (Petriellales), digitate leaf with sparsely anastomosing venation; S089172; Upper Triassic, Tivoli Formation, Brassal, Ipswich Basin, Australia. I, J. *Dictyozamites hawelli* [Seward, 1903](#) (Bennettitales), pinnate leaf with anastomosing venation, but lacking a midrib in leaflets; S137601; Jurassic, Marske, Cleveland Basin, UK. K, L. *Ctenis lyrata* [Li and Ye, 1980](#) (Cycadales), pinnate leaf with anastomosing venation in leaflets; PB11615 and PB11616 respectively; Lower Cretaceous, Mo-shi-li-zi Formation, Jiaohe, Jilin, northeastern China. Scale bars for A, D, E, G, I, K, L = 10 mm, for B, C, F, H, J = 5 mm.

**Table 1**Macro- and micromorphological comparisons of *Glossopteris*, *Sagenopteris* and *Anthrophyopsis*.

	<i>Glossopteris</i>	<i>Sagenopteris</i>	<i>Anthrophyopsis</i>
Leaf shape	Predominantly spatulate, rarely elliptical or cordate	Typically tight pinnate (pseudopalmate); individual leaflets mostly elliptical, obovate, lanceolate or oblong in outline	Near-elliptical
Leaf margin	Entire, rarely undulate	Highly variable: almost entire or with slight undulation, to deeply lobed	Generally entire, some are completely lobed or have shallow to deep incisions
Midrib location	At leaf centre	At leaf centre (for apical leaflets) or nearer acroscopic margin (for proximal leaflets)	At leaf centre
Midrib continuity	Formed by tight association of fine veins (equivalent to lateral veins), mostly remaining segregated, and commonly persisting to the apex or evanescent in the distal fifth of the lamina	Gradually evanescent into secondary veins at two-thirds to four-fifths of leaf length in mature leaves; more evanescent or even not developed in juvenile leaves	Straight and stout midrib narrows from base to apex of leaf
Secondary veins	Straight or arched gently across lamina and terminating freely at margin, typically <100 µm in diameter	Inserted on midrib at acute angle, straight or arched gently across lamina, almost 50–80 µm in diameter	Inserted on the midrib from 90° in the middle part to c. 50° in basal and apical parts, thick, c. 0.2–0.3 mm in diameter
Meshes (areolae)	Broader near midrib, narrower and more elongate towards margin	Almost obliquely oriented with irregular shapes	Obviously decreasing in length from midrib to leaf margins
Cross-connection types	H-type generally more common near midrib, X- and Z-types more frequent in the middle and outer lamina	X-type most common, H-, Z-, X- and γ-types locally occur in conjunction to form compound cross-connections	Besides H-, Z-, X- and γ-types junctions, γ-, λ-types are also frequent, Z- series connections are typically common
Stomatal distribution	Variably amphistomatic or hypostomatic	Hypostomatic	Mainly hypostomatic, rarely weakly amphistomatic
Stomatal arrangement	Within mesh areas, vein areas generally without stomata	Within mesh areas, vein areas generally lacking stomata	Within mesh areas, vein areas generally lacking stomata
Stomatal orientation	Without consistent orientation	Without consistent orientation	Without consistent orientation
Stomatal architecture	Normally stephanocytic to actinocytic or cyclocytic; have approximately 4–7 subsidiary cells	Anomocytic or stephanocytic, guard cells generally surrounded by unspecialized epidermal cells by weakly modified subsidiary cells	Syndetocheilic (brachyparacytic), with guard cells (20–25 µm long, 10–12 µm wide) flanked by a pair of semicircular subsidiary cells (26–28 µm long, 16–20 µm wide)
Stomatal protection	Commonly protected in pits or by overarching papillae; in some cases, unprotected and unsunken	Absent	Absent
Interveinal epidermal cells	Vary from rectangular to irregularly polygonal, anticlinal walls can be straight or broadly sinuous	Rectangular, subquadrate, or polygonal shape, anticlinal walls straight or sinuous, c. 50 µm long and c. 35 µm wide	About 50–80 µm long, 16–30 µm wide with highly sinuous anticlinal walls; adaxial cells have more markedly sinuous anticlinal walls and are arranged more irregularly
Epidermal cells over veins	More weakly sinuous walls than interveinal cells	More elongate over the veins, maximum c. 60–70 µm long and c. 20 µm wide	Distinctly narrower and more elongate with less sinuosity, minute but obvious sinuosities along the cell walls
Epidermal ornamentation	Papillae weakly developed in some species, with 1–2 lenticular thickenings per epidermal cell on the adaxial surface	Absent	Absent
References	Pant and Gupta, 1968, 1971; Pant and Singh, 1968, 1971; Pigg, 1990; Pigg and McLoughlin, 1997; This study	Harris, 1932a, 1940, 1964; Kvaček, 1999; Barbacka and Bóka, 2000; Barbacka et al., 2006; This study	Harris, 1926; Sze, 1931; Doludenko and Svanidze, 1970; Xu et al., 2021; This study

between two approximately parallel veins; “chi junction (X-type)”, characterized by the union of veins via convergence then divergence of adjacent veins; “zeta junction (Z-type)” formed by an oblique connecting vein between two approximately parallel veins; and “zeta series (Z-series)” represented by a series of zeta junctions in side-by-side arrangement. In addition to these four most common cross-connection types among *Glossopteris*, *Sagenopteris* and *Anthrophyopsis*, we also applied the terms gamma junctions (γ-type) and lambda junctions (λ-type) as outlined by Melville (1976) for the description of vein dichotomies and connections in some reticulate-veined leaves.

### 3. Results and comparisons

#### 3.1. Leaf morphology and venation

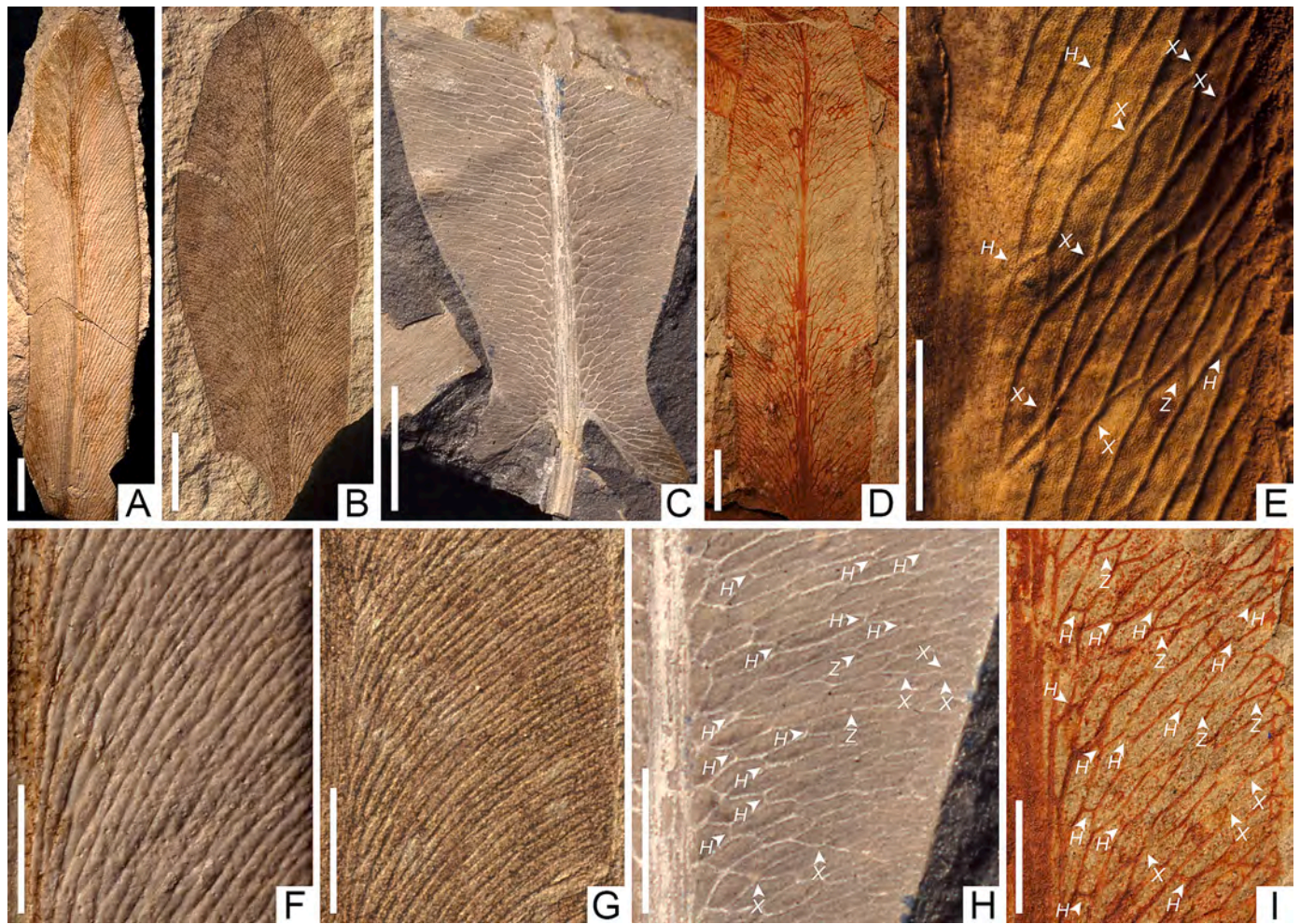
##### 3.1.1. *Glossopteris*

Glossopterid gymnosperms are characterized by predominantly spatulate, generally simple leaves with reticulate venation. *Glossopteris* Brongniart ex Brongniart, 1831, the most characteristic leaf type in this group (Fig. 3A, B, D–G, I), was established by Brongniart (1828), later formalized by Brongniart (1831), and subsequently emended by a series of authors including Schimper (1869), Feistmantel (1876, 1881), Arber (1905), Pant and Gupta (1968) and Banerjee (1978). A few early

Permian representatives of the group (e.g., *Rubidgea* Tate, 1867 and *Euryphyllum* Feistmantel, 1879) lack or have very sparse cross-connections between the veins (Pant, 1987). The median veins are tightly aggregated in *Glossopteris* to form a prominent midrib but are more loosely spaced in *Gangamopteris* McCoy, 1847 and *Palaeovittaria* Feistmantel, 1876. There is a complete continuum in the degree of median vein aggregation between these genera. Impression fossils of *Glossopteris* commonly give the indication that the midrib is represented by a single large vein that gives off secondary veins at various angles, and the venation of many species has been described in that manner. However, anatomical studies of permineralized *Glossopteris* leaves have shown that the median veins typically do not fuse into a single midvein but mostly remain segregated in a tight association (Pigg, 1990; Pigg and McLoughlin, 1997; McLoughlin et al., 2019). There is, essentially, no anatomical difference between the veins of the midrib and the ‘secondary veins’ in glossopterids except that, in some species, the veins forming the midrib are of slightly greater diameter, more closely aggregated and/or develop a modest amount of secondary xylem. The midrib commonly persists to the apex or may evanesce in the distal fifth of the lamina.

Various other genera have been established for glossopterid leaves with additional modifications to the standard leaf architecture, including pinnate forms (*Pteronilsson* Pant et Mehra 1963), cusped





**Fig. 3.** Representative leaf fragments of Glossopterid, showing leaf forms and venation styles. A. *Glossopteris rhombimaculata* McLoughlin, 1994b, spatulate leaf with tapered base and straight secondary veins, and enlargement (F) of mid-lamina venation showing straight course of secondary veins and reduction in areolae width towards margin; UQF79380; Permian, Blackwater Group, central Bowen Basin, Australia (see McLoughlin, 1994a, 1994b). B. *Glossopteris browniana* Brongniart ex Brongniart, 1831, spatulate leaf with gently arched venation, and enlargement (G) of mid-lamina venation showing gently arched secondary veins enclosing falcate areolae; UQF79206; Permian, Blackwater Group, central Bowen Basin, Australia (see McLoughlin, 1994a, 1994b). C. *Glossopteris* [= *Surangeophyllum*] *duocordata* Holmes, 1981, sagittate leaf with broad areolae between secondary veins and major vein running along basiscopic margin of basal lobes, and enlargement (H) of mid-lamina venation showing widely spaced secondary veins enclosing broad areolae; AMF60031; Permian, Illawarra Coal Measures, western Sydney Basin, Australia (see Holmes, 1995). D. *Glossopteris* sp. cf. *G. fitzroyensis*, lorate leaf with gently curved secondary veins enclosing moderate-sized areolae, and enlargement (I) of mid-lamina venation showing elongate polygonal areolae and free-ending secondary veins; AMF58811; Permian, Koogah Formation, Mt. Wingen, Gunnedah Basin, Australia. E. *Glossopteris gladiforma* McLoughlin, 1994a, details of anastomosing venation in mid-lamina showing different types vein connections; UQF79283; Permian, Blackwater Group, central Bowen Basin, Australia (see McLoughlin, 1994a, 1994b). Scale bars for A–E = 10 mm, for F–I = 5 mm. Notes: X = X-type junction; Z = Z-type junction; H = H-type junction.

forms (*Ilexoidephyllum* Rohn and Rösler, 1989), and trilobate forms (*Belemnopteris* Feistmantel, 1876 and *Surangeophyllum* Chandra and Singh, 1986; Fig. 3C, H), but these all share reticulate venation and, in some cases, diagnostic epidermal features (Pant, 1987). *Rhabdotaenia* Pant, 1958 is a glossopterid with taeniopterid venation leaf that may have secondarily lost cross-connections between the veins (Pant, 1982; Blumenkemper et al., 2022).

The reticulate ‘secondary veins’ of classical *Glossopteris* (and *Surangeophyllum*) species enclose chains of areolae that pass either straight to the margin or arch gently across the lamina (Fig. 3A–I). Areolae are typically broader near the midrib and become progressively narrower and more elongate towards the margin, resulting in increased vein density in the outer lamina. Veins form meshes mainly by way of H-, Z- and X-type cross-connections (Fig. 3E, H–I), although these broad categories represent idealized styles within a continuum of junction arrangements. Broad areolae lying adjacent to the midrib are commonly enclosed by H-type connections at their distal limit. In the middle and

outer lamina, X- and Z-type connections become more common. In some cases, X-type connections are represented by barely touching (glancing) veins that show the ‘exchange’ (co-integration) of just a few tracheids (Fig. 4B). In other cases, the connection is robust, forming a very short transverse strut that is as thick or thicker than the adjoining veins (Fig. 4A). Other cross-connection types similarly vary in robustness (Fig. 4B–D). Veins terminate freely at the margin (Fig. 3E–I). No glossopterids are known to have developed a continuous marginal vein. Mid-lamina secondary veins are typically < 100 µm in diameter (Fig. 4A–D).

Over 100 species of *Glossopteris* leaves have been established across the Permian Gondwanan terranes based on a relatively small array of morphological characters. Among these, vein density, degree of vein arching, the marginal angle (angle between the midrib and the vein orientation at the leaf margin), and shapes of the vein-enclosed areolae have been used regularly to distinguish species (Arber, 1905; Archangelsky, 1958; Chandra and Surange, 1979; Kovács-Endrődy, 1981; McLoughlin, 1994a, 1994b). Some glossopterid species and genera



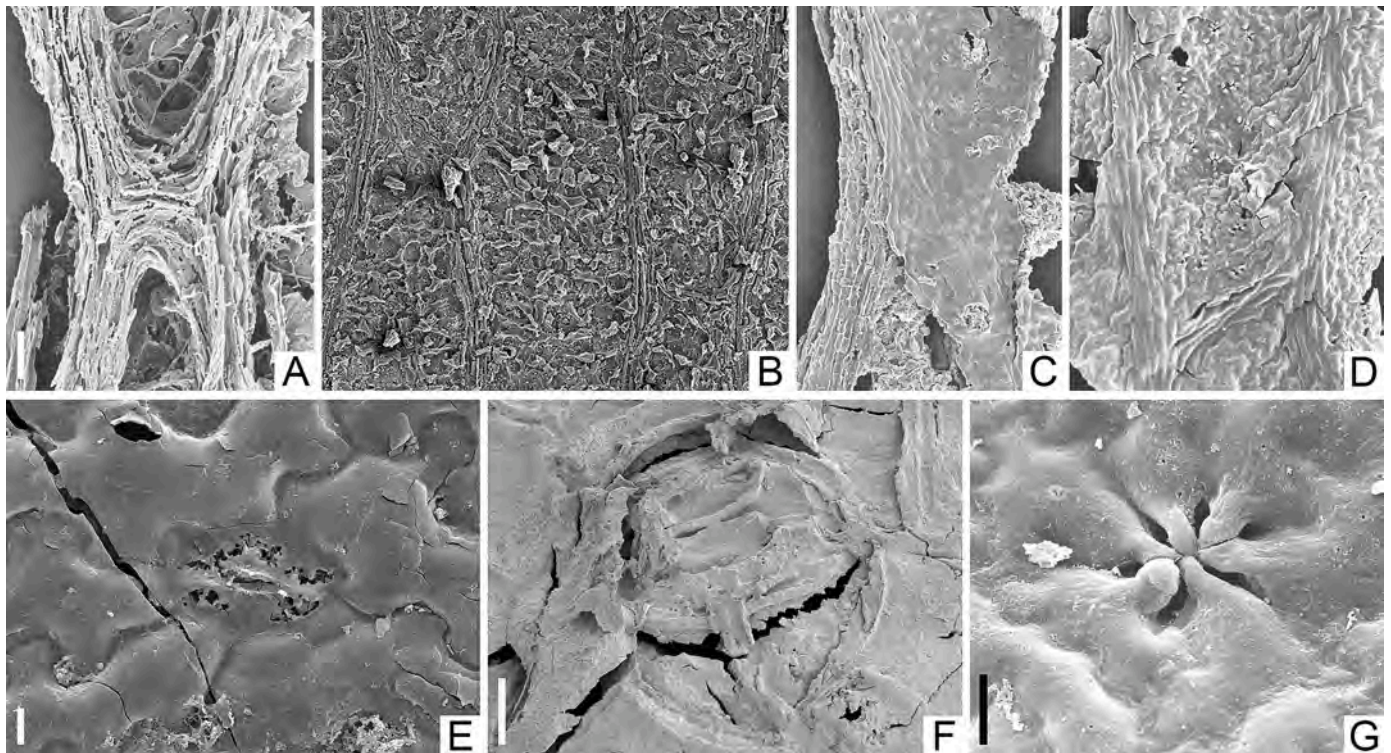
appear to have been established based on early developmental stages of leaves in which the venation has not developed its typical form (Etheridge Jr, 1899; Rigby, 1966; Pant and Nautiyal, 1984). Moreover, few studies have adopted a statistical approach to assess the variation in morphology within leaf populations from any one site that might, for example, detect variations between sun and shade leaves of a single biological species. The difficulties in clearly demarcating species within large assemblages of *Glossopteris* leaves, especially where cuticular details are lacking, remains a major challenge for palaeobotanists, and one that has constrained this prolific fossil group's application to biostratigraphy (McLoughlin, 1993a). *Gontriglossa* Anderson et Anderson, 1989, once considered a Triassic representative of the glossopterid clade, is distinguished by its slightly wavy secondary veins, commonly more longitudinally extended vein segments in X-type cross-connections (Fig. 2A–B), and by having leaves arranged in regular whorls on a slender jointed axis.

### 3.1.2. *Sagenopteris*

*Sagenopteris* Presl in Sternberg emend. Harris, 1964 is the most common fossil organ (representing leaves) attributed to Caytoniales, and has been known since Nilsson (1820) first illustrated a single leaflet of this taxon at that time ascribed simply to “unknown leaves”. The genus was formally established by Presl (1838 in Sternberg) and subsequently emended by several authors (Harris, 1964; Rees, 1993; Cleal and Rees, 2003). *Sagenopteris* leaves are compound, with several (usually four) lanceolate leaflets attached to the apex of the petiole in a tight pinnate (pseudo-palmate) arrangement (Halle, 1910; Harris, 1964). Beyond this basic architecture, populations of *Sagenopteris* represented by numerous specimens housed at NRM, reveal leaflets with

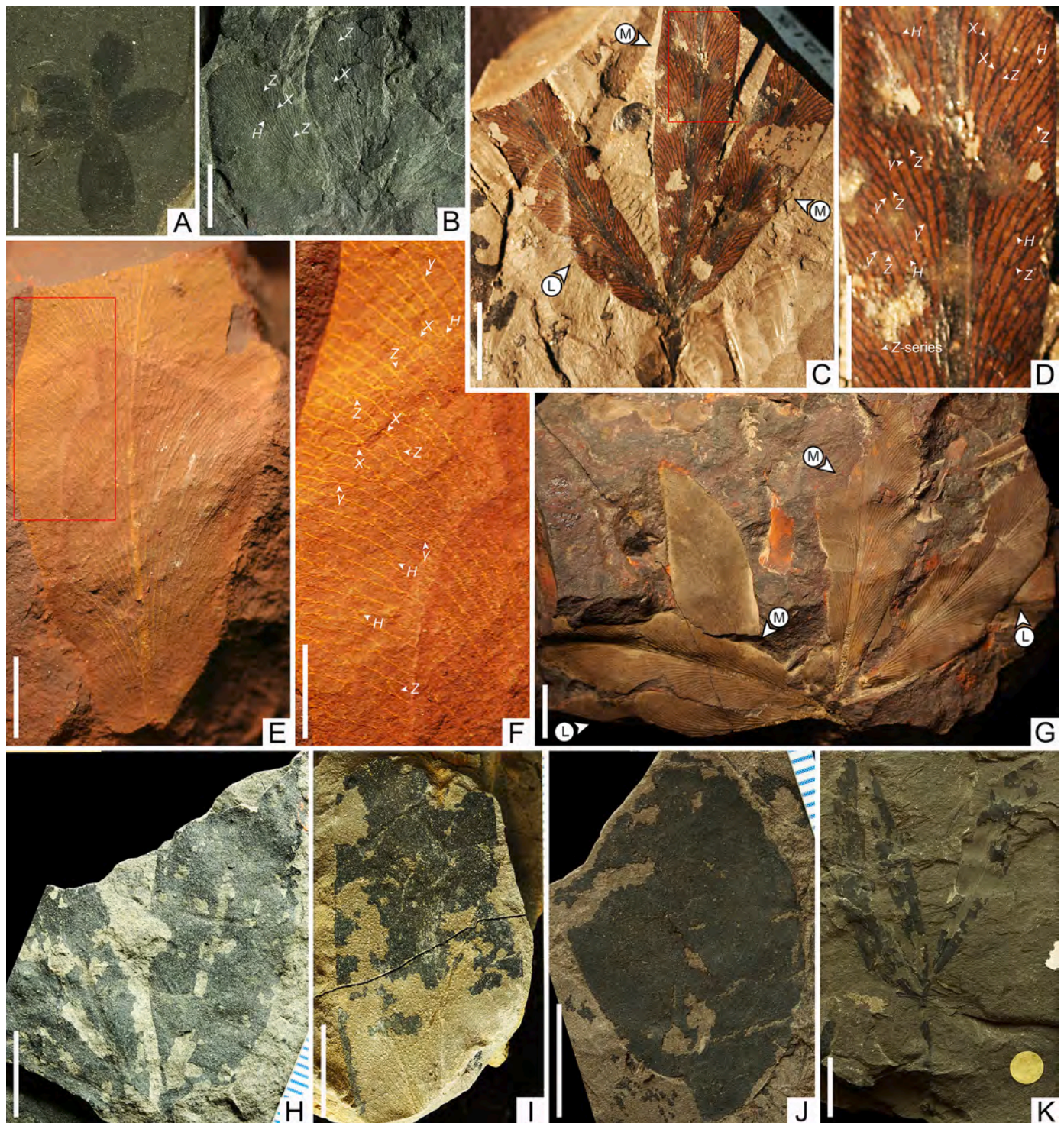
considerable variability in morphological characters. This variability is supported by studies of other collections of *Sagenopteris nilssoniana* (Brongniart) Ward, 1900 from Hope and Botany bays, Antarctica (Rees, 1993; Rees and Cleal, 2004), and rich assemblages of *Sagenopteris trapialensis* Elgorriaga et al., 2019 from the Lonco Trapial Formation in Patagonia (Elgorriaga et al., 2019) that reveal the broad spectrum of intraspecific variation expressed in the foliar developmental series. Consequently, *Sagenopteris* leaves vary in several key features within and between species: the leaf margin can be entire, undulate or even deeply lobed; the midrib can reach 50–95% of the leaflet length before evanescence; and there is a high morphological plasticity evident in petiole width and shape expressed during early development (Fig. 5A).

Typical *Sagenopteris* leaves bear four elliptical, obovate, lanceolate, or oblong leaflets (Fig. 5A–K). Two pairs of apical (central) leaflets generally have a greater length-width ratio and are almost symmetrical, with the midrib located at their centre (Fig. 5C, G). The proximal (lateral) leaflets are proportionately broader, generally asymmetrical, with an eccentric midrib lying nearer the acroscopic margin (Fig. 5C, G). The margins of both pairs of leaflets are highly variable, ranging from almost entire or with slight undulation, to deeply lobed (Rees, 1993; Rees and Cleal, 2004). The prominent midrib runs almost straight from the base of the leaflet, but almost never reaches the leaf apex. No permineralized remains are available to assess the vascular anatomy of *Sagenopteris*. However, the robust appearance of the basal midrib in impression and compression fossils (Fig. 5D, E, G) suggests that it may represent a single amalgamated vein. Along with the successive emergence of lateral veins, the midrib progressively decreases in width as it approaches the leaf apex, and gradually evanescence at two-thirds to four-fifths of the leaf length (Fig. 5G). The prominence of the midrib and its



**Fig. 4.** Micromorphological features of *Glossopteris*. A. SEM of charcoalified *Glossopteris* leaf interior showing H-type vein cross-connection; S090341–07. B. SEM of charcoalified *Glossopteris* leaf from which epidermis has been removed, showing Z- and H-type vein cross-connections; S087802–11. C. SEM of charcoalified *Glossopteris* leaf showing strongly oblique Z-type vein cross-connection and weakly papillate cuticle; S089603–04. D. SEM of charcoalified *Glossopteris* leaf showing weakly oblique Z-type vein cross-connection and papillate subsidiary cells surrounding stomatal pores; S156265. E. SEM of charcoalified leaf surface showing inflated, sinuous-walled epidermal cells and unprotected guard cells of stomate; S088051–05. F. SEM of interior of charcoalified leaf stomatal complex showing paired guard cells surrounded by a ring of about six subsidiary cells; NRM S087838–1. G. SEM of charcoalified leaf surface showing sinuous-walled subsidiary cells bearing well developed beak-like papillae overhanging stomatal pore; S156265. All specimens of Permian age, Toploje Member, Bainmedart Coal Measures, Northern Prince Charles Mountains, East Antarctica (see McLoughlin and Drinnan, 1997). Scale bars for A–D = 100  $\mu$ m; E–G = 10  $\mu$ m.





**Fig. 5.** Representative leaf fragments of *Sagenopteris*, showing leaf forms and venation styles. A. Unexpanded leaves of *Sagenopteris alata* [Nathorst, 1886](#); S055053; Rhaetian, Skåne, Sweden. B. Immature leaves of *Sagenopteris rhoifolia* [Presl, 1838](#); S070622; Hettangian, Helsingborg Member, Påljö, Sweden. C–D. Oxidized leaf of *Sagenopteris phillipsii* (Brongniart) [Presl, 1838](#) showing midrib and anastomosing secondary veins; MVP187213; Jurassic, Scarborough, UK. E–F. *Sagenopteris nilssoniana* (Brongniart) [Ward, 1900](#) showing the range of vein junction styles; QMF12699; Pliensbachian, Marburg Subgroup, Durikai, Australia. G. *S. nilssoniana*; AMF57722; Pliensbachian, Marburg Subgroup, Durikai, Australia. H–K. Leaflet shape variation in *Sagenopteris*: H. *S. nilssoniana*; S075940; Rhaetian, Skåne, Sweden. I. *Sagenopteris colpodes* Harris emend. [Harris, 1964](#); S150104; Rhaetian, Skåne, Sweden. J. *S. nilssoniana*; S067564; Rhaetian, Skåne, Sweden. K. *Sagenopteris undulata* [Nathorst, 1878](#); S055368; Rhaetian, Skåne, Sweden. Notes: M = middle leaflet; L = lateral leaflet; Z-series = Z-series junction;  $\gamma$  =  $\gamma$ -type junction;  $\lambda$  =  $\lambda$ -type junction.

evanescence into secondary veins are variable features within *Sagenopteris*. Midrib definition is better developed in larger, more mature leaves. Juvenile or early-season leaves have more obviously evanescent

midribs, or a midrib may not be developed at all ([Fig. 5B](#)).

Secondary veins are thin (c. 50–80  $\mu\text{m}$  wide), inserted on the midrib at acute angles, and fork and anastomose irregularly ([Fig. 5C–F](#)). H-type



junctions occur almost randomly in the central and marginal parts of the lamina. The *H*-type cross-connections do not, or only slightly disrupt the original routes of the secondary veins such that the two connected secondary veins remain parallel or become only slightly closer to each other at the point of junction (Fig. 5D, F). *X*-type cross-connections are the most common type in the venation of *Sagenopteris*. *H*- and *X*-types locally occur in conjunction to form compound cross-connections (Fig. 5D). The  $\gamma$ -type junctions represent simple dichotomies and commonly occur close to the midrib. *Z*-type cross-connections produce a dichotomy of the secondary veins and are frequently combined with  $\gamma$ -type forks to form compound junctions (Fig. 5D, F). Locally, *Z*-type junctions also occur side by side forming an abutting *Z*-series of cross-connections (Fig. 5D).

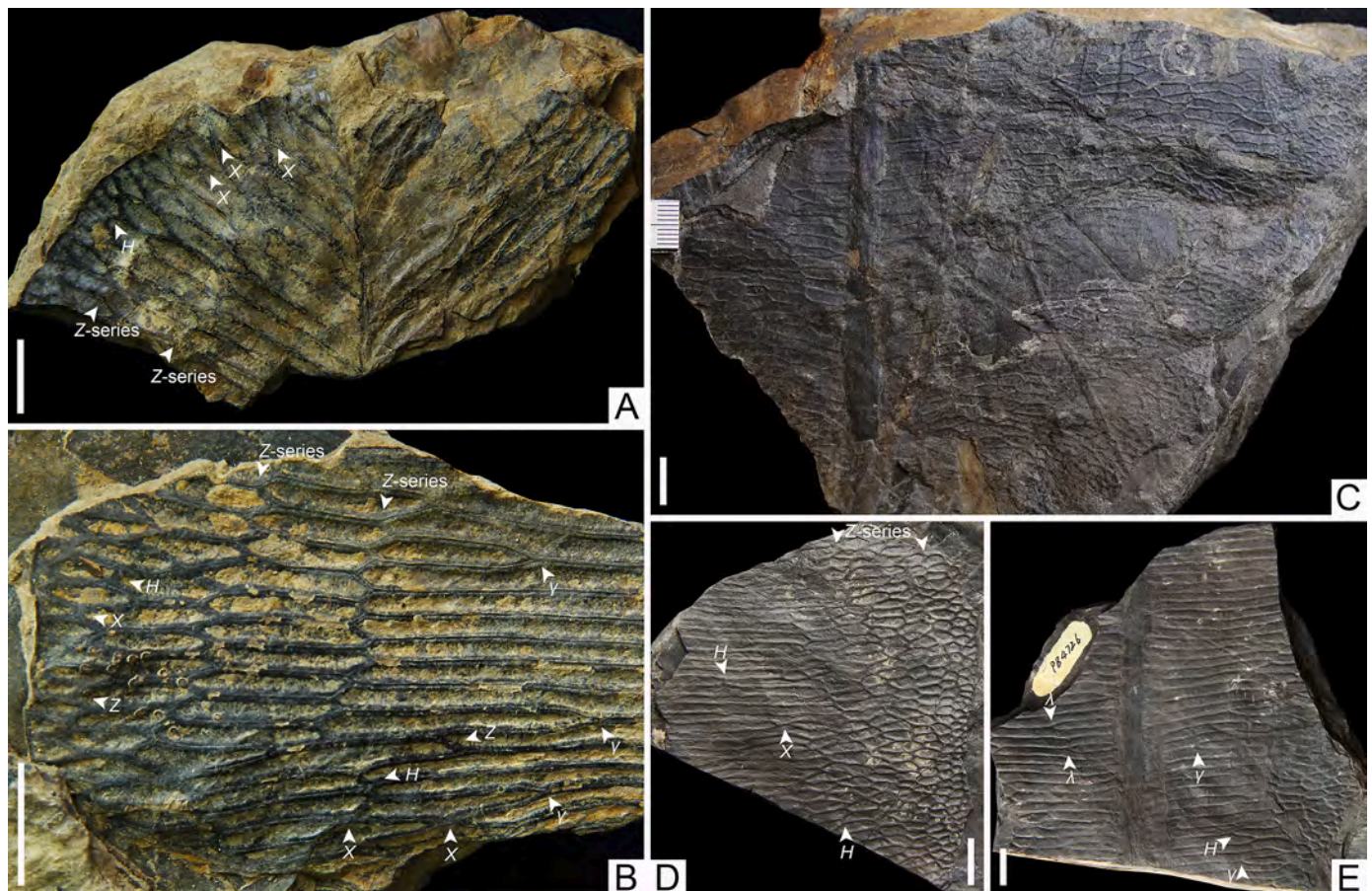
More than 70 species of *Sagenopteris* leaves have been established from Middle Triassic to Upper Cretaceous strata globally. However, most of these species were established on a few isolated leaflets, and a very small percentage of the species have been studied comprehensively or have yielded well-preserved cuticular details. In order to resolve the complex and confusing taxonomic status of *Sagenopteris* species, we are undertaking a separate thorough systematic revision of this genus, which will document the intra- and inter-specific morphological variation of leaves and clarify the criteria for species segregation. Preliminary data indicates that *Sagenopteris* species are best distinguished from each other based on their leaflet margin types, length-width ratios, continuity of the midrib, and especially, cuticular micromorphology.

### 3.1.3. *Anthrophyopsis*

*Anthrophyopsis* Nathorst emend. Xu et al., 2021 is an important but perplexing foliar genus, with highly peculiar morphology marked by a prominent midrib, robust secondary vein meshes and large lamina. Owing to a lack of convincing anatomical details, reproductive structures or other associated organs, the affinity of this taxon has been regarded as uncertain, with postulated links ranging from Cycadopsida and to various ‘seed fern’ groups (Xu et al., 2021).

Morphologically, *Anthrophyopsis* leaves are large, in some cases reaching more than 50 cm long and 20 cm wide (mesophyll-class in the leaf-size categories of Raunkiaer, 1934 and Webb, 1959). The leaves are elliptical, margins are generally entire, but some are completely lobed to the midrib or have shallow to deep incisions (Xu et al., 2021: figs. 5–10). The large leaf is supported by a straight, stout and longitudinally striate persistent midrib that narrows from the base to the apex of the leaf. The midrib reaches a width of about 12 mm at the base in adaxial view (Fig. 6C, E). The thick lamina is inserted adaxially on the midrib and partially covers it (Fig. 6C, E).

The secondary veins are thick, reaching widths of about 0.2–0.3 mm (Fig. 7A–B) and are marked by a median ridge on the lamina surface. The secondary veins are inserted on the midrib at various angles, from 90° in the middle part of the leaf (Fig. 6C, E) to about 50° in both the basal and apical parts of the leaf (Fig. 6A). The venation of *Anthrophyopsis* is characterized by secondary vein meshes that decrease in length substantially from the midrib to the leaf margins (Fig. 6A–E). The reticulate lateral veins of *Anthrophyopsis* retain a roughly constant vein



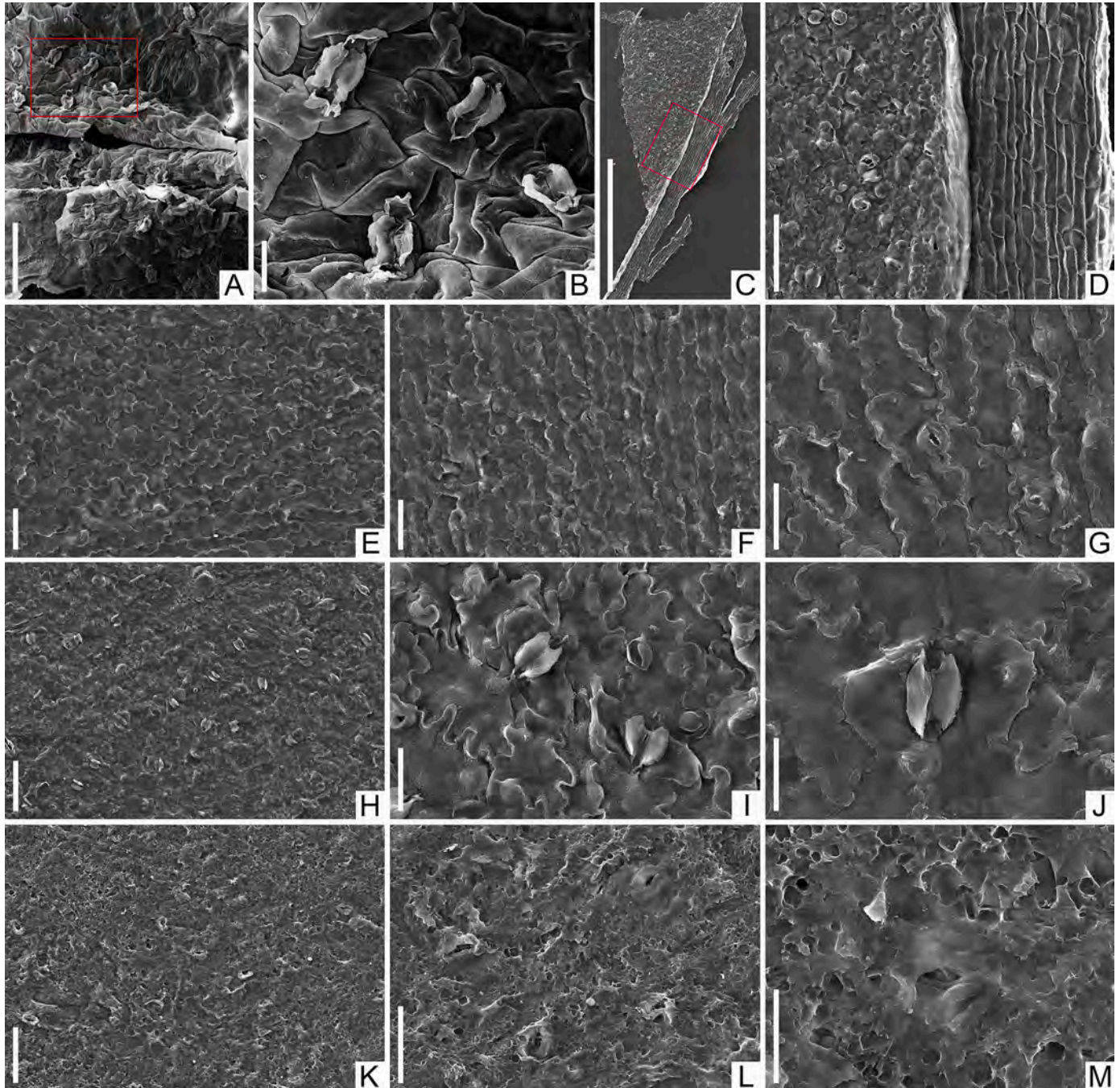
**Fig. 6.** Representative leaf fragments of *Anthrophyopsis crassinervis* Nathorst emend. Xu, Popa et Wang 2021. A. Apical leaf fragment, showing obvious different cross-connection types nearby apical parts; PB23148 (after Xu et al., 2021); Rhaetian, Xujiahe Formation, Sichuan Basin, China. B. Leaf fragment showing various vein connection types, especially typical *Z*-series type junctions; PB23157 (after Xu et al., 2021); Rhaetian, Xujiahe Formation, Sichuan Basin, China. C. Median leaf fragment, showing strong and stout midrib with perpendicularly inserted secondary veins; S168921; Rhaetian, Vardekloft, Sermersooq, Scoresby Sound, East Greenland. D. Marginal leaf fragment, showing obvious different cross-connection types; Reverse surface of PB4726 (after HJCG-NIGPAS, 1968); Upper Triassic, Leping, Jiangxi, China. E. Median leaf fragment; PB4726 (after HJCG-NIGPAS, 1968); Upper Triassic, Leping, Jiangxi, China. Scale bars = 10 mm.



density across the lamina. Veins mainly form meshes by way of *H*-, *X*-, *Z*-types connection, but abutting *Z*-series cross-connections embracing,  $\gamma$ - and  $\lambda$ -types vein branchings also occur frequently. Secondary veins near the midrib are generally parallel to each other, however, bifurcation and fusion locally occur in the form of  $\gamma$ -,  $\lambda$ -types junctions (Fig. 6D–E). Some areolae adjacent to the midrib are enclosed by *H*-type connections or  $\lambda$ -type junctions (Fig. 6D–E), and are notably polygonal and reach 20–30 mm in length. *Z*-series cross-connections are most common in the middle to sub-marginal parts of the lamina, forming regularly side-by-

side polygonal meshes. *X*-type connections emerge randomly and become common near the marginal parts of the lamina. Isolated *Z*-type connections occur randomly. Cross-connecting veins are robust, generally being thicker at the junctions (Fig. 7A). Meshes typically decrease in length near the margins, reducing to 1–4 mm long, and veins terminate freely at the margin (Fig. 6A, D). Areolae are typically sunken in the lamina relative to the encompassing veins (Fig. 6B).

About 16 species of *Anthrophyopsis* have been reported from Triassic strata of China, East Greenland, Georgia, Iran, Mozambique, Russia,



**Fig. 7.** Micromorphological features of *Anthrophyopsis crassinervis*. A–B. Inner view of the abaxial cuticle, recovered from lectoparatype specimen of *Anthrophyopsis crassinervis*, showing scattered stomata (A), and details of stomatal complex (B), the strong tortuosity of the epidermis is probably due to its thin cuticular texture and the excessive oxidation; PB23150 (see Xu et al., 2021: fig. 6a); Rhaetian, Xujiache Formation, Sichuan Basin, China. C–M. Cuticular structures of *Anthrophyopsis crassinervis*, recovered from specimen in Fig. 5C; S168924. E–G. Inner view of the adaxial cuticle, showing elongated epidermal cells with obviously sinuous anticlinal walls, and the infrequent stoma (F–G); H–J. Inner view of the abaxial cuticle, showing irregularly distributed stomata (H), more sinuous anticlinal walls than the upper epidermis (I), and details of stomatal complex (J); K–M. Outer view of the lower cuticle, showing scattered stomatal pits (K–L) and their details (M). Scale bars for A, D, H, K = 100  $\mu$ m; for B = 20  $\mu$ m; for C = 1 mm; for E–F, L = 50  $\mu$ m; for G, I = 30  $\mu$ m; for J, M = 20  $\mu$ m.



Sweden and Tajikistan, but, following a comprehensive systematic appraisal of the genus, only three species are regarded as valid (Xu et al., 2021). Vein density, cross-connection types, margin types and surface ornamentation between the secondary veins are regarded as the most important characters for distinguishing species in this genus (Xu et al., 2021). Some *Anthrophyopsis* species established in early palaeobotanical studies are now regarded as synonyms, since they had been established based on small leaf fragments, or they represent other genera, such as *Ctenis*, *Glossopteris*, or *Gontriglossa* (Nathorst, 1886; Anderson and Anderson, 1989). Some of these early-collected fragments of *Anthrophyopsis* led to an inaccurate understanding of the plant's true appearance and distribution (Nathorst, 1878; Harris, 1926). Although complete *Anthrophyopsis* plants have never been discovered, reconstructions by Sze (1931) and Doludenko and Svanidze (1970) inspired a better understanding of its lamina appearance, and the recent discoveries of well-preserved *Anthrophyopsis* fragments from South China have contributed to reconstructing the intraspecific variation and morphology of these plants (Xu et al., 2021).

### 3.2. Epidermal micromorphology

#### 3.2.1. *Glossopteris*

*Glossopteris* cuticle is typically thin, brittle, and difficult to prepare. Consequently, relatively few of the large number of established *Glossopteris* species have known epidermal and stomatal characters. Most data on glossopterid cuticular structure has come from the Raniganj Formation in the Damodar Valley, India (Pant and Verma, 1964; Pant and Singh, 1968, 1971; Pant and Gupta, 1968, 1971), in which coal is typically of low thermal maturity (vitrinite reflectance values of 0.53–0.72%), i.e., high-volatile bituminous rank (Panwar et al., 2017; Chattaraj et al., 2019). Some additional epidermal details have been recovered from paradermal sections of silicified (permineralized) leaves (Pigg, 1990; Pigg and McLoughlin, 1997). We also highlight opportunities to gather additional epidermal details from charcoallified leaves recovered from bulk macerations of carbonaceous shales and silicified peats (Fig. 4A–G).

Glossopterid leaves are variably amphistomatic or hypostomatic (Pant and Gupta, 1968); the adaxial surface is substantially more cutinized (c. 1.5–3 µm thick) than the abaxial surface (normally c. 1 µm thick; Pant and Gupta, 1968; Degani-Schmidt et al., 2011). Epidermal cells over veins are elongate rectangular with inflated periclinal walls (Fig. 4B, C) that are smooth or bear longitudinal striae. Papillae are absent or weakly developed as 1–2 lenticular thickenings per epidermal cell on the adaxial surface (Fig. 4B). In rare cases, numerous small wart-like papillae occur on the periclinal walls (Pant and Gupta, 1971). Abaxial epidermal cells vary from rectangular to irregularly polygonal to isodiametric with periclinal walls that are smooth, slightly inflated (Fig. 4C), or bear papillae (Pant and Gupta, 1968), and in some cases, prominent trichomes (Pant and Gupta, 1971; Degani-Schmidt et al., 2011). Epidermal cell anticlinal walls can be straight (Fig. 4F), but, more commonly, are broadly sinuous (Fig. 4E, G). Cells over veins tend to have more weakly sinuous walls than those in interveinal areas. Cells in interveinal areas generally lack common orientation and are normally c. 30–80 µm in maximum dimensions.

Stomata may be surficial, unspecialized and unprotected (Fig. 4E) or considerably sunken beneath the lamina surface forming a stomatal pit (Pigg and McLoughlin, 1997) and protected by overhanging beak-like papillae or lappets (Fig. 4G) (Pigg, 1990). Stomata are haplocheilic perigenous (haplocheilic of Florin, 1931) and monocyclic—normally stephanocytic to actinocytic (sensu Carpenter, 2005) or cyclocytic (sensu Dilcher, 1974). They are rarely amphicyclic (Pant and Gupta, 1968)—incorporating a double ring of 4–8 subsidiary cells. Stomatal pits are typically 6–50 µm long and 4–25 µm wide with apertures having variable orientations. Guard cells are reniform, typically 30–50 µm long and 10–15 µm wide. Stomatal densities are typically c. 30–150 per mm<sup>2</sup> but may reach extreme densities of up to 480 per mm<sup>2</sup> (Degani-Schmidt

et al., 2011).

Convincing resin bodies and oil glands have not been detected in glossopterid leaves. However, rings of heavily cutinized papillae fused to a trichome base or hollow pedestal occur on the abaxial cuticle of *Glossopteris pubescens* (Guerra-Sommer) Degani-Schmidt et Guerra-Sommer 2016 (Degani-Schmidt and Guerra-Sommer, 2016), and these may represent glandular features used for defense against herbivores. Where papillae are arranged along the veins, e.g., in *Glossopteris papillosa* Guerra-Sommer, 1992 (Guerra-Sommer, 1992) they might have aided protection of the vascular supply from fluid-sucking insects (McLoughlin et al., 2021).

#### 3.2.2. *Sagenopteris*

The cuticle of *Sagenopteris* is also very thin and difficult to prepare for optical microscopy. Consequently, of the greater than 70 species of *Sagenopteris* established worldwide, only a few have yielded cuticular details, and these have come from a small range of fossil localities (Harris, 1932a, 1940, 1964; Kvaček, 1999; Barbacka and Bóka, 2000; Barbacka et al., 2006). Here we re-examined cuticle preparations housed in NRM, and we prepared additional specimens for epidermal analysis via scanning electron microscopy (Fig. 8A–F).

*Sagenopteris* leaves are hypostomatic. The upper cuticle generally reveals epidermal cell outlines of rectangular, subquadrate, or polygonal shape with straight anticlinal walls. Epidermal cells with sinuous walls also exist in some species (e.g., *Sagenopteris colpodes* Harris emend. Harris, 1964). Cells are notably more elongate over the veins (Fig. 8A, D). The costal cells reach maximum lengths of c. 60–70 µm and widths of c. 20 µm (Fig. 8A, D). The intercostal cells are c. 50 µm long and 35 µm wide (Fig. 8A, D). The epidermal cells on the abaxial surface resemble the adaxial examples, but have more variable shapes as numerous stomata are distributed irregularly among the pavement epidermal cells. Stomata are anomocytic or stephanocytic. Guard cells are 20–60 µm long, 10–15 µm wide, and are generally surrounded by unspecialized, irregular epidermal cells without typical subsidiary cells, representing an anomocytic arrangement (Harris, 1932a, 1940, 1964; Barbacka and Bóka, 2000). In some cases, the guard cells are surrounded by weakly modified subsidiary cells representing the stephanocytic type (Kvaček, 1999; Barbacka et al., 2006). In a few cases, the subsidiary cells bulge over the guard cells, and a ring of encircling cells may be present or absent; the edges of subsidiary cells commonly form distinct ridges underneath the guard cells (Fig. 8B–C, E–F; Harris, 1964).

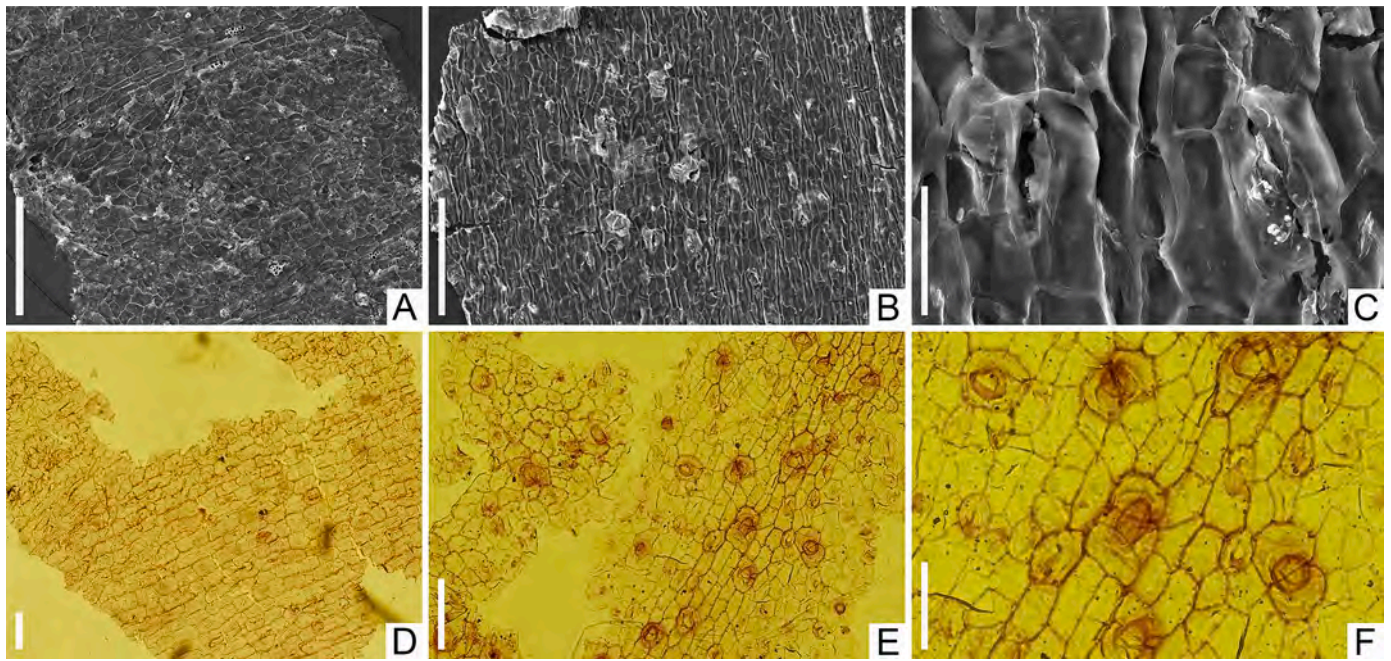
The ontogenetic series of stomatal development in *Sagenopteris* was deduced based on numerous immature and early-season leaves collected from the Lower Jurassic (Hettangian) deposits at Komló, southern Hungary (Barbacka and Bóka, 2000). According to studies of cuticle from different growth stages, the stomatal development in *Sagenopteris* is typically of perigenous type (Barbacka and Bóka, 2000).

#### 3.2.3. *Anthrophyopsis*

Previous studies reporting micromorphological features of *Anthrophyopsis* were based on material obtained from leaf fragments or bulk maceration (Harris, 1926, 1932b; Li, 1964; Zhou, 1989). On this basis, there is uncertainty whether these cuticles genuinely related to *Anthrophyopsis*. Notably, Florin (1933) doubted the cuticular characters reported by Harris (1926) for *Anthrophyopsis*. The cuticles of this genus are very thin and can be easily degraded during the oxidation process, leading to complete loss or recovery of only uninformative cuticular details (Xu et al., 2021).

During the course of our study, one of the historical specimens of *Anthrophyopsis crassinervis* Nathorst emend. Xu et al., 2021 (NRM S168921) collected from the Upper Triassic (Rhaetian) strata at Vardekloft, Sermersooq, Scoresby Sound, Greenland, by K.R. Pedersen in 1970 was found to yield well-resolved epidermal micromorphology. Cuticles of the studied specimen can be readily separated from the compression with a dissecting scalpel and needles, which ensures the provenance of the epidermal characters (Fig. 7C–M). Moreover, we also





**Fig. 8.** Micromorphological features of *Sagenopteris*. A. Inner view of adaxial epidermis corresponding to specimen in Fig. 4H, showing notably more elongate epidermal cells over the veins; S075940. B–C. Inner view of abaxial epidermis and details of stomatal complex corresponding to specimen in Fig. 4I; S150104. D. Inner view of adaxial epidermis derived from specimen in Fig. 4K, showing rectangular epidermal cells; S055368. E–F. Cuticle details from specimens in Fig. 4J, showing scattered stomata and details of stomatal complex; S067564. Scale bars for A = 200 µm; for B = 300 µm; for C, F = 50 µm; D, E = 100 µm.

studied the cuticle of the lectoparatype (fig. 6a in Xu et al., 2021) of *Anthrophyopsis crassinervis* to confirm the consistency of our results (Fig. 7A–B).

The leaves are mainly hypostomatic or rarely weakly amphistomatic (having just a few stomata on the adaxial surface: Fig. 7E–J). The cuticles are very thin and delicate; epidermal cells over the veins are distinctively narrower and more elongate than pavement epidermal cells (Fig. 7C–D). The adaxial epidermis has cells irregularly disposed but more elongate over the veins (Fig. 7E). The epidermal cells are about 50–80 µm long and 16–30 µm wide, with highly sinuous anticlinal walls (Fig. 7E–G). The sinuosities have a (wavelength) density of about 6–10 per 100 µm (Fig. 7E–G). Stomata are sparse and consist of two guard cells that form an isodiametric ring around the pore (Fig. 7F–G).

The abaxial epidermal cells are similar in size and outline to those of the adaxial surface, but are arranged more irregularly and have more markedly sinuous anticlinal walls (Fig. 7H). The sinuosities have a (wavelength) density of about 10–15 per 100 µm (Fig. 7I). Stomata are apparently syndetocheilic, confined to intercostal areas, and distributed among the epidermal cells without consistent orientation (Fig. 7C–D, H–I). The stomatal apparatus consists of guard cells flanked by a pair of prominent semicircular subsidiary cells (brachyparacytic arrangement: Fig. 7I–J). The guard cells are sunken and overlapped by the subsidiary cell with the exposed part of the guard cells forming the bottom of a shallow stomatal pit as viewed from the exterior (Fig. 7M). Guard cells are about 20–25 µm long and 10–12 µm wide (Fig. 7A–B, I–J). The subsidiary cells are obviously smaller than ordinary pavement epidermal cells, about 26–28 µm long and 16–20 µm wide, and have less sinuous anticlinal walls (Fig. 7I–J). Epidermal cells located over veins are less sinuous, almost rectangular, 50–65 µm long and 15–18 µm wide, with minute but obvious sinuosities along the cell walls (Fig. 7C–D).

*Anthrophyopsis* was once interpreted to be generically inseparable from *Ctenis* on the basis of micromorphological details of their cuticles (Harris, 1926, 1932b; Zhou, 1989). On the basis of leaf and cuticle morphology, particularly its similarities to *Ctenis fallax* Nathorst, 1886, *Anthrophyopsis* was considered to have systematic affinities with Cycadales (Harris, 1926, 1937; Florin, 1933; Sze et al., 1963). Alternatively,

resemblances in its venation pattern to *Glossopteris* led others to infer affiliation with the polyphyletic group ‘seed ferns’ (Sze, 1931, 1933; Schweitzer and Kirchner, 1998; Kustatscher and Van Konijnenburg-van Cittert, 2013). However, the uncertainty in provenance of the fragmentary cuticles illustrated in earlier studies has left these interpretations unconvincing.

Our observations of the epidermal micromorphology of *Anthrophyopsis* reveals strong similarities to Bennettitales. The brachyparacytic stomata (characterized by a single pair of lateral subsidiary cells), distinctive guard-cell cuticular thickenings, irregular stomatal orientations, markedly undulating anticlinal epidermal cell walls, and perpendicular orientation of the secondary veins to the midvein, are all features that favor alliance with Bennettitales (Sincock and Watson, 1988; Rudall and Bateman, 2019). Although most Bennettitales do not possess reticulate venation, representatives of *Dictyozamites* have well-developed anastomoses (Fig. 2I, J), and Cretaceous specimens of *Dictyozamites falcatus* (Morris) Medlicott and Blanford, 1879 have remarkably similar epidermal features and stomatal apparatuses (Bose and Zeba-Bano, 1976; pl. 2, figs. 9–14). We contend, on the basis of both macro- and micromorphological characters, that there is a high probability that *Anthrophyopsis* is affiliated with Bennettitales.

## 4. Discussion

### 4.1. Infrageneric diversity

As noted by Pant and co-workers, several *Glossopteris* species defined on epidermal characters are more or less indistinguishable in gross morphology from other species established for specimens lacking organic remains (Pant and Gupta, 1968; Pant and Singh, 1968, 1971). Moreover, Pant and Singh (1971) failed to find epidermal characters enabling consistent differentiation of *Glossopteris* from *Gangamopteris*. Further cuticular studies revealed that the epidermal features of *Pteronilssonina* (Pant and Mehra, 1963), *Palaeovittaria* (Pant and Verma, 1964), *Belemnopteris* (Chauhan et al., 2012) and *Rhabdotaenia* (Blenkemper et al., 2022) lack any major differences from the collective



micromorphological features of *Glossopteris*. Whereas, Pant and his colleagues argued that the variation in cuticular characters indicated that the diversity of *Glossopteris* leaves was far greater than previously recognized, it is also possible that the subtle differences they recognized in cuticular micromorphology were to some extent influenced by microenvironment on an individual tree or within a plant community. Where large numbers of leaves have been found attached to reproductive organs (Anderson and Anderson, 1985; Prevec, 2011), these show considerable variation in lamina size, shape and venation details that might reflect differences in positioning on the parent tree or stage of seasonal development. Consequently, the number of biologically discrete glossopterid species may be significantly less than that established in the historical literature, and apparent diversity may have been inflated by establishment of separate species for leaves with and without epidermal details. In the absence of clear boundaries between biological species, some authors have resorted to simply assigning dispersed glossopterid leaves to informal morphotypes (Prevec et al., 2009, 2010). As noted by McLoughlin and Prevec (2019, 2021), the reproductive organs of glossopterids have more diverse morphologies than the leaves and are more readily referable to discrete taxa. Hence, a better understanding of the true diversity of Permian glossopterids will likely derive from studies of their ovuliferous fertilizers, which incorporate leaves and adnate polysperms (McLoughlin, 2011).

*Sagenopteris* leaf populations show a high degree of morphological plasticity, especially in their lamina size, shape, margin form and venation orientation (Rees, 1993; Rees and Cleal, 2004). Most *Sagenopteris* species have been described based on a single leaflet or several broken fragments lacking cuticular details. Where large masses of specimens are available, e.g., from Hope and Botany bays, Antarctica (Rees, 1993; Rees and Cleal, 2004) and the Lonco Trapial Formation, Patagonia (Elgorriaga et al., 2019), the morphological variation within a leaf population is pronounced, especially in terms of differences in petiole and lamina shape through developmental series. The lamina is small and bud- or scale-like, extending from particularly short and broad petioles in unexpanded or early-season leaves, but leaflets become lanceolate, petiolulate, palmately arranged and borne on a long slender petiole in mature forms (Elgorriaga et al., 2019). Even among mature leaves, infraspecific and infrageneric diversity is also apparent, with leaflets varying between entire-, undulate- and lobe- margined forms (Rees, 1993). A more detailed analysis of the infrageneric diversity of *Sagenopteris* will be presented in a forthcoming paper systematically revising the genus.

As noted by Xu et al. (2021), among 16 species of *Anthrophyopsis* that were globally reported, only three are now regarded as valid, all of which are segregated on macromorphological criteria, especially venation pattern and inter-veinal ornamentation. Incised margins and distinctly lobed margins have been reported only in *Anthrophyopsis crassinervis*. The prominent tubercles between the lateral veins represent a special character of *Anthrophyopsis tuberculata* Chow et Yao emend. Xu et al., 2021. A markedly higher vein density and more slender secondary veins distinguish *Anthrophyopsis venulosa* Chow et Yao emend. Xu et al., 2021. A better understanding of the infrageneric diversity of epidermal features of *Anthrophyopsis* requires further investigation, as only the type species (*Anthrophyopsis crassinervis*) has been studied in this respect (Xu et al., 2021).

#### 4.2. Does reticulate venation reflect a close relationship?

Leaf vein networks show great variations in their form. Variation in venation patterns is useful for species differentiation and has been confirmed to be closely related to leaf conductance, photosynthetic rates, and has been widely applied as an important proxy for palaeoclimatic reconstruction (Sack and Scoffoni, 2013). Results from the fossil record indicate that the earliest simple reticulate venation networks appeared during the late Carboniferous in taxa such as *Lonchopteris* Brongniart, 1828 and *Reticulopteris* Gothan, 1941 (Trivett and

Pigg, 1996; Fig. 1). Veins provide several important functions in the life of a plant, especially transport of water, nutrients and food solutes, and mechanical stabilization of the lamina. Closed/reticulate venation systems have certain obvious advantages over open vein networks (Roth-Nebelsick et al., 2001; Sack and Scoffoni, 2013). Consequently, it appears that reticulate venation systems developed rapidly in a range of plant groups, including ferns, Medullosales, Gigantopteridales, Glossopteridales, Cycadales, Gnetales, various other enigmatic seed plants (e.g., *Furcula* Harris, 1932b; *Gontriglossa* Anderson and Anderson, 1989; *Dunedoonia* Holmes, 1977; Figs. 1–2) and, especially, angiosperms.

One of the key advantages of reticulate vein systems is a more efficient irrigation system to the leaf mesophyll cells (Roth-Nebelsick et al., 2001; Price and Weitz, 2014). Generally, the flow velocity of substances inside the vein system decreases with increasing distance from the midrib (Jeje, 1985). Reticulate vein systems obviously increase the vein length per leaf area (VLA), which leads to higher flow rates across the lamina, and improves the efficiency of substance movement from the midrib to the secondary veins and throughout the lamina (Sack et al., 2008; Sack and Scoffoni, 2013). Therefore, higher VLA permits greater stomatal density and conductance, ensures photosynthetic efficiency, and also enables higher rates of gas exchange (Roth-Nebelsick et al., 2001; Sack and Scoffoni, 2013). Although the increased VLA of reticulate networks requires higher resource allocation to vein construction, it is a trivial cost compared to the greater benefits from improved water/solute distribution (Price and Weitz, 2014). The increases of VLA from the basal part of the midrib to the marginal part of the lamina in some reticulate-veined plant taxa with especially large leaves (e.g., *Anthrophyopsis*, *Ctenis*) are likely to reflect trade-offs between enhanced fluid supply, material consumption, and lamina stability. Enhanced concentration and reticulation of veins at the margin is a strategy that achieves the same results as vein tapering, which has been confirmed to provide cost-efficiency to the venation network and economic distribution of fluids (Sack and Scoffoni, 2013).

Anastomosing venation also enhances tolerance of fine-scale damage or vein blockage by improving the capacity to divert resources around the damaged area (Raimondo et al., 2003; Harayama et al., 2019), enabling maintenance of lamina productivity. This can be particularly important for plants subject to high levels of herbivory (Vincent, 1990; Roth-Nebelsick et al., 2001; Read and Stokes, 2006). Compared with open vein systems, reticulate networks are able to compensate for the truncated vein transport paths resulting from arthropod and other herbivore damage (Roth-Nebelsick et al., 2001), and can even confer more resistance to insects with specialized feeding habits (e.g., leaf miners, mucivores and margin-feeders) by limiting easy access to zones of vein-free mesophyll and forcing some leaf feeders to spend more energy to penetrate or cut through dense vein networks (Vincent, 1990; Read and Stokes, 2006).

Besides more efficient substance transport, more effective mechanical stability is achieved by reticulate venation and it may confer benefits for plasticity in leaf form. Veins provide strength for leaves against gravity, tearing by wind, and other mechanical processes and ensure that the leaves are firm enough to optimize interception of solar radiation (Niklas, 1999; Blonder et al., 2010). Reticulate venation can minimize the leaf mass per area ratio (LMA), and enable the leaf to effectively maximize the functional surface area without resorting to folds, sinuses or other modes of deformation (Niklas, 1999).

Architecturally, there appears to be a limited range of styles in which veins can interconnect. Although some groups, e.g., Gigantopteridales (Fig. 2E, F), Petriellales (Fig. 2G, H), Gnetales and angiosperms, have very distinctive reticulation patterns, most other groups appear to have adopted very similar patterns of anastomoses. The striking similarities in reticulate venation patterns between *Glossopteris*, *Sagenopteris* and *Anthrophyopsis* (along with several other groups) have been noted by many researchers, and lamina fragments of these taxa are difficult to distinguish in the absence of complete leaves (Feistmantel, 1876; Harris, 1932a, 1932b; Ash, 1981; Kustatscher and Van Konijnenburg-van



Cittert, 2013). However, these taxa resolve in disparate positions on the major seed-plant phylogenies that incorporate fossil groups (Crane, 1985; Doyle and Donoghue, 1992; Rothwell and Serbet, 1994; Nixon et al., 1994; Doyle, 2006; Hilton and Bateman, 2006). Hence, such similarities in venation appear to be primarily convergent. Moreover, fine-scale analysis of the venation of such plants reveals subtle differences. For example, the meshes of *Anthrophyopsis* are obviously enclosed by thicker secondary veins, and are composed of more frequent Z-series cross-connections than *Glossopteris* or *Sagenopteris*, which might be due to its greater demand for irrigation of the mesophyll and mechanical support owing to its larger leaf size (Sack and Scoffoni, 2013). *Sagenopteris* tends to have more evanescent midribs and more longitudinally extended X-type cross-connections than *Glossopteris*. Moreover, the differences we identify in the stomatal architecture between these groups suggest that they are not closely related. In general, the superficial structural similarities of meshed venation in *Glossopteris*, *Sagenopteris* and *Anthrophyopsis* are likely to be convergent traits adopted for similar functional benefits (Table 1).

#### 4.3. Do cuticular characters link these plant groups?

Cuticular characters, especially the stomatal complexes are arguable among the most consistent micromorphological features in fossil plants (Rudall et al., 2013). They represent features of great significance for phylogenetic reconstructions, but also have strong ecological significance (Bateman et al., 1998; Raven, 2002; McAdam and Brodribb, 2012).

All three target genera have relatively thin cuticles that are difficult to prepare. This might be a consequence of a shared deciduous habit (McLoughlin, 1993b; Elgorriaga et al., 2019) that required less investment in lamina protection. Deciduousness is also inferred from matted leaf occurrences and by the basally expanded long petioles of leaves in these genera and their sharp lines of abscission (McLoughlin, 2011; Elgorriaga et al., 2019; Xu et al., 2021) similar to the features of extant *Ginkgo biloba*.

Our revised cuticular analysis of *Anthrophyopsis* reveals epidermal and brachyparacytic stomatal architectures consistent with Bennettitales (Table 1). Considering that transverse orientation of stomata is probably related to parallel venation in this group (Watson and Sincrook, 1992), the irregular distribution and orientation of stomatal complexes in *Anthrophyopsis* may be due to epidermal cell developmental space constraints between their remarkable network of reticulate veins, as appears to be the case in *Dictyozamites* (Bose and Zeba-Bano, 1976).

Based on their respective cuticular features, *Glossopteris* and *Sagenopteris* have somewhat greater similarities in stomatal architecture. Both *Glossopteris* and *Sagenopteris* have anomocytic/stephanocytic stomata, which lack typical subsidiary cells or possess a weakly defined encircling ring of subsidiary cells. *Sagenopteris* differs by having prominently cutinized and large guard cells that are not sunken but lie flush with the surface of encircling epidermal cells (see descriptions above, and Barbacka and Bóka, 2000). *Glossopteris* has a greater array of stomatal features, including some forms with strongly sunken stomata protected by overhanging papillae, but others with relatively unspecialized surficial stomata. *Glossopteris* also has more consistently sinuous epidermal cell outlines compared to the normally straight anticlinal walls of *Sagenopteris*. We find no cuticular features that suggest a very close relationship between *Glossopteris* and *Caytoniales* (Table 1).

Several traditional comparative studies and later phylogenetic analyses incorporating fossil seed plants have generally found *Glossopteris*, *Caytoniales* and *Bennettitales* to be close relatives of angiosperms based on characters of their leaves, reproductive organs and epidermal structures (Thomas, 1925; Harris, 1951; Retallack and Dilcher, 1981; Crane, 1985; Doyle, 2012). Although reproductive organs contribute more important structural evidence for phylogenetic relationships between these seed plants and angiosperms, epidermal features still

provide important indications of their ancestral condition (Rudall and Bateman, 2019). The shared possession of paracytic stomata is generally accepted as an important homologous character associating bennettites and angiosperms (Doyle and Donoghue, 1986). Barbacka and Bóka (2000) tentatively proposed that perigenous anomocytic stomata, based on ontogenetic stomatal development series of *Sagenopteris*, indicates a derived position of *Caytoniales* and a close relationship to the ancestors of angiosperms, but similarities acquired through ecophysiological constraints need to be more clearly distinguished from shared ancestral characters. For example, the brachyparacytic stomata of *Anthrophyopsis* indicate affiliation with *Bennettitales*, but similarities with stomatal arrangements shared by that group, *Gnetales*, and some angiosperms might be characters acquired through convergence (Rudall and Bateman, 2019). As the overall details and development of *Glossopteris* stomata are still limited, more data are needed for further comparison, but in general architecture they are not dissimilar to the stomatal organization of many conifers and related gymnosperms (Pole, 2000; Jansson et al., 2008; Rudall et al., 2013).

Of the three studied genera, *Glossopteris* is confined to the Permian of Gondwana and was a primary casualty of the end-Permian mass extinction event (Vajda and McLoughlin, 2007; Fielding et al., 2019; McLoughlin et al., 2021). The range of *Glossopteris* is separated from that of *Sagenopteris* by a stratigraphic gap spanning 10 million years. *Sagenopteris* first appears in the Middle Triassic, reached its acme in abundance and broadest geographic (global) distribution in the Early to Middle Jurassic, then declines to extinction in the Late Cretaceous. Confidently identifiable representatives of *Anthrophyopsis* are confined to the Late Triassic (Xu et al., 2021). This genus may have been an important casualty of the end-Triassic mass-extinction event in northern low to middle palaeolatitudes. The ranges of various other reticulate-veined plant groups precede, overlap, and succeed those of the studied genera (Fig. 1), but there appear to be no taxa with intermediate suites of characters that would indicate close evolutionary linkages between *Glossopteris*, *Sagenopteris* and *Anthrophyopsis*.

## 5. Conclusions

Our study reveals for the first time that *Anthrophyopsis* has cuticular features consistent with *Bennettitales*. Although past phylogenetic and morphological analyses have commonly placed *Glossopteris*, *Caytoniales* and *Bennettitales* in close association (in some cases within a 'glossophyte' clade together with some other seed fern groups and angiosperms: Thomas, 1925; Harris, 1951; Retallack and Dilcher, 1981; Crane, 1985; Doyle and Donoghue, 1992; Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 2006, 2012; Hilton and Bateman, 2006), we find that the foliar characters shared between *Glossopteris*, *Sagenopteris* and *Anthrophyopsis* are primarily convergent. Moreover, we note that our analyses recover subtle differences in both vein architecture and cuticular micromorphology that suggest the similarities between these groups are largely superficial. We conclude that convergence in lamina characters was likely driven by ecological and physiological factors, such as deciduousness, optimization of fluid distribution, enhancement of lamina rigidity, and response to herbivory.

Reproductive organs have not yet been found linked to *Anthrophyopsis*. We argue that the contrasting characters between the leaves of *Glossopteris* and *Sagenopteris* are consistent with the significant differences evident between the reproductive organs of these plants. Indeed, reproductive architectures provide a greater range of characters that are less likely to be influenced by ecological convergence than foliar features, and we urge a greater research emphasis on resolving the architectures and associations of the diverse array of late Paleozoic and Mesozoic gymnosperms.

## Declaration of Competing Interest

The authors declare the following financial interests/personal



relationships which may be considered as potential competing interests:

The authors declared that they do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

## Data availability

No data was used for the research described in the article.

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