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Selaginella in Cretaceous amber from Myanmar

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Abstract: *Selaginella* (*Selaginellales*, *Selaginellaceae*) is the most speciose genus of lycophytes and, with approximately 750 recognized present-day species, also one of the largest genera of vascular plants. However, the evolutionary history of this species richness remains largely unresolved. Recent research suggests that *Selaginella* was diverse already in the mid-Cretaceous and shows that *S.* subg. *Stachygynandrum* dates back at least to the incipient Angiosperm Terrestrial Revolution some 100 million years ago. Here, we describe 20 new fossil-species of *Selaginella* based on fertile shoots and spores preserved in mid-Cretaceous Kachin amber from Myanmar and emend the previously described *S. cretacea*. Ten of the species (*S. cilifera*, *S. cretacea*, *S. grimaldii*, *S. heterosporangiata*, *S. longifimbriata*, *S. minutissima*, *S. ohlhoffiorum*, *S. patrickmuelleri*, *S. villosa*, *S. wangxinii*) represent *S.* subg. *Stachygynandrum* because they possess anisophyllous strobili. The other eleven species have isophyllous strobili. Two of them (*S. isophylla*, *S. wunderlichiana*) are tentatively assigned to *S.* subg. *Ericetorum*, whereas the others (*S. amplexicaulis*, *S. aurita*, *S. heinrichsii*, *S. konijnenburgiae*, *S. obscura*, *S. ovoidea*, *S. pellucida*, *S. tomescui*, *S. wangboi*) cannot be placed into any fossil or extant subgenus. The fossils described in this study nearly duplicate the documented record of free-sporing plants from Kachin amber. The abundance and diversity of cryptogams, along with the absence of xerophytes among the taxa, is suggestive of constantly high humidity in the understory of the source forests of this amber.

Keywords: Angiosperm Terrestrial Revolution, bilateral strobilus, Burmese amber, Kachin amber forest, spike mosses, palaeoecology, resupinate strobilus, spike moss palaeodiversity, sporophyll-ptyx, tetrastichous strobilus

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1. Introduction

The lycophytes are the oldest of the present-day lineages of free-sporing vascular plants, dating back to at least the Early Devonian (Wikström & Kenrick 2001; Magallón & al. 2013; Testo & al. 2018). Today, this lineage comprises the homosporous *Lycopodiales* with one family, the *Lycopodiaceae* (clubmosses) with up to 16 recognized gen-

era, and the heterosporous *Isoetales* and *Selaginellales*, which represent sister groups, each with only one extant monotypic family, namely the *Isoetaceae* (quillworts) and *Selaginellaceae* (spike mosses), respectively (Korall & al. 1999; PPG1 2016; Spencer & al. 2020).

The lycophytes initially diversified during the Devonian and Carboniferous (Kenrick & Crane 1997; Morris & al. 2018), which rendered them major elements of the

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late Palaeozoic vegetation (DiMichele & al. 2001). Their present-day diversity, however, is supposed to be a consequence of diversification events in the Late Triassic and Cretaceous (Klaus & al. 2017; Pereira & al. 2017; Testo & al. 2018), such as the Angiosperm Terrestrial Revolution when modern angiosperm lineages became dominant (Schneider & al. 2004; Schuettpelz & Pryer 2009; Barba-Montoya & al. 2018; Morris & al. 2018) and profoundly changed the structure and ecology of terrestrial ecosystems (Benton & al. 2021).

Among the lycophytes, the genus *Selaginella* P. Beauv. is distinct in its own ways. The genus is a perfect example of morphological stasis in plants. Although its fossil record dates back to the Carboniferous or even Devonian, the differences in gross morphology between the earliest unquestionable fossil representatives, such as the Carboniferous *Selaginellites resimus* N. P. Rowe (Rowe 1988) and *Selaginella labutae* Bek & al. (Bek & al. 2009), and present-day taxa are generally small (Korall & al. 1999; Taylor & al. 2009; Klaus & al. 2017). At the same time, *Selaginella* today is by far the largest genus of lycophytes and one of the largest of vascular plant genera in general. Approximately 750 species are currently recognized (Weststrand & Korall 2016a, 2016b). The seemingly paradoxical combination of extreme morphological stability over hundreds of millions of years and present-day hyperdiversity at species level might be linked to comparatively high numbers of new mutations per generation (substitution rates) in *Selaginella*, as well as rate heterogeneity (Korall & Kenrick 2004).

The sporophytes of most present-day *Selaginella* species consist of anisophyllous, flattened shoots with four rows of vegetative leaves (trophophylls) arranged in two dorsal rows of smaller leaves and two ventral rows of larger leaves. However, approximately 50 extant species possess isophyllous instead of anisophyllous vegetative shoots (Jermy 1990; Weststrand & Korall 2016a). Sporophylls are usually arranged in tetrastichous strobili at branch tips, with the exception of *S. selaginoides* (L.) P. Beauv. ex Schrank & Mart. and *S. deflexa* Brack., both of *S. subg. Selaginella*, in which sporophylls are helically arranged. Most extant species are characterized by sporophylls of uniform size and shape arranged in quadrangular strobili, but some 60 species possess dimorphic sporophylls, commonly arranged in bilateral resupinate strobili (Weststrand & Korall 2016a, 2016b). *Selaginella* today is a cosmopolitan genus, with most extant species occurring in moist tropical forests (Korall & Kenrick 2002), but some also growing in warm-temperate, temperate and even boreal ecosystems, including arid areas or places with extreme temperature differences (Jermy 1990; Arigo & al. 2013). Most species are ground dwellers, and the genus comprises some of the few vascular “resurrection plants” (Marks & al. 2021).

Based on analyses of DNA sequence data and morphology, the most recent classification of *Selaginella* recognizes seven subgenera, namely *S. subg. Ericetorum*,

S. subg. Exaltatae, *S. subg. Gymnogynum*, *S. subg. Lepidophyllae*, *S. subg. Rupestrae*, *S. subg. Selaginella* and *S. subg. Stachygynandrum* (Weststrand & Korall 2016b). Time-calibrated molecular phylogenies suggest that all subgenera date back to the Mesozoic (Weststrand 2016), except *S. subg. Selaginella*, which is sister to the rest of the genus and appears to have originated in the Carboniferous, perhaps even in the Devonian (Weststrand 2016; Klaus & al. 2017). However, the incompleteness of the fossil record, along with various preservation constraints, render attempts to assign the vast majority of fossil forms to particular subgenera difficult (e.g. Ash 1972; Thomas 1997; Wierer 1997; Bek & al. 2001, 2009; Thomas 2005; Pšenička & Opluštil 2013; McLoughlin & al. 2014; Van Konijnenburg-van Cittert & al. 2014, 2016). Fossils preserved in pristine conditions and providing complements of structural features that can be used to directly compare them with extant species are, therefore, instrumental to our understanding of the evolutionary history of the *Selaginellaceae* through time. However, such fossils are exceedingly rare.

Amber, fossilized plant resin, is widely known to yield an array of different fossils, from microbes to arthropods to vertebrates, which are typically preserved three-dimensionally and often in cellular fidelity, and therefore today represents one of the most important sources of new information on the biodiversity of late Mesozoic and Cenozoic forest ecosystems (Labandeira 2014). Several major amber deposits, including the Miocene Dominican, Mexican, Ethiopian and Zhangpu ambers, the Palaeogene Baltic and Bitterfeld ambers and the Cretaceous Kachin amber, are important archives of past plant diversity because they contain fossils that are manageable almost in a way like living taxa (Dunlop 2010; Penney 2010; Solórzano Kraemer 2010; Weitschat & Wichard 2010; Grimaldi & Ross 2017; Bouju & al. 2021; Wang & al. 2021). Until very recently, however, no fossils of lycophytes had been reported from any amber deposit worldwide. A possible exception is a structure resembling *Kraeuselisporites* (a genus of palynomorphs with possible affiliation to *Selaginellaceae*) that has been reported in Cretaceous amber from SE Australia (Quinney & al. 2015). However, this structure appears to be a pseudoinclusion sensu Thiel & al. (2016). Schmidt & al. (2020) presented 14 distinct morphologies of Albian-Cenomanian *Selaginella* based on fossils entombed in Kachin amber of Myanmar. Moreover, these authors suggested that the actual diversity of *Selaginella* in the source forests of the Kachin amber must have been even larger because not all *Selaginella* species that were present in these forests also became enclosed in resin outpourings and subsequently fossilized. Moreover, much of the resin produced by the trees probably did not survive processes of erosion, transport and redeposition. Finally, only a small proportion of the amber deposit is excavated and eventually made available for study.

This study details the exceptional diversity of *Selagi-*

nella in Kachin amber at a fine level and compares the fossil morphologies with those seen in extant representatives of this genus. Our survey of publicly accessible Kachin amber collections has yielded 37 amber pieces containing remains of *Selaginella*. Based on sporophyll and other strobilus characters, we define 21 fossil-species, of which ten are characterized by bilateral strobili with dimorphic sporophylls and represent the most speciose *S.* subg. *Stachygynandrum*. The remaining 11 species possess quadrangular strobili with monomorphic sporophylls. Two of them probably belong to *S.* subg. *Ericetorum*, whereas the others cannot be confidently attributed to any fossil or extant subgenus. The fossils described in this study nearly double the documented record of free-sporing plants from Kachin amber and imply that spike mosses were a dominant component of the herbaceous layer of the Kachin amber forest. The documented high diversity of currently 47 species of liverworts, mosses, spike mosses and ferns, along with the absence of evidence of xerophytes among these fossils, is suggestive of constantly humid and likely shaded understory conditions in the source area of the resin that formed Kachin amber.

2. Material and methods

2.1. Provenance and age of the fossils

All material used in this study is present in mid-Cretaceous amber from the Hukawng Valley in Kachin State in N Myanmar. Amber from this area has traditionally been called Burmese amber (or “Burmite”, see Grimaldi & al. 2002). More recently, however, additional fossiliferous amber deposits were discovered in other regions of Myanmar that now necessitate a refined denomination. Amber from the Hukawng Valley is therefore now commonly called Kachin amber (Zheng & al. 2018), while the two other amber deposits of Myanmar are Tilin amber and Hkamti amber. Tilin amber derives from a younger deposit in the Gangaw district of the Magwe region in central Myanmar and is late Campanian in age (c. 72 million years, Zheng & al. 2018). Hkamti amber comes from a new amber-mining area in the Sagaing region of NW Myanmar and has been estimated to be Albian in age (c. 110 million years, Xing & Qiu 2020).

Kachin amber is currently the most important source of three-dimensionally preserved Cretaceous terrestrial biota (Grimaldi & Ross 2017). Approximately 2200 species of organisms (more than 2000 species of which are arthropods) in more than 660 families have been described from this amber deposit (Ross 2022). Moreover, it is the only pre-Cenozoic amber that also contains plant fossils in large numbers, including diverse liverworts, mosses and ferns (Heinrichs & al. 2014; Regalado & al. 2019; Feldberg & al. 2021).

Kachin amber was mined from outcrops at Noiye Bum (“Banyan Mountain”), a hill approximately 20 km SW

of the municipality of Tanai, located on the Ledo road c. 105 km NW of Myitkyina in Kachin State, N Myanmar (Cruickshank & Ko 2003). Several lines of evidence suggest an age of approximately 100 million years (late Albian to early Cenomanian) for Kachin amber (Grimaldi & Ross 2017). Biostratigraphic studies by Cruickshank & Ko (2003) point to a late Albian age of the amber-bearing strata and, based on U–Pb dating of zircons, Shi & al. (2012) suggested a minimum age of 99 million years (early Cenomanian). These age estimates were recently corroborated through the discovery in Kachin amber of an ammonite representing the genus *Puzosia* Bayle, which is a widely recognized late Albian–late Cenomanian index taxon (Yu & al. 2019).

A total of 37 amber pieces containing fertile and sterile inclusions of *Selaginella* were discovered from the following publicly accessible Kachin amber collections: Geoscientific Collection of the University of Göttingen, Germany (GZG), State Museum of Natural History Stuttgart, Germany (SMNS), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (PB), Division of Invertebrate Zoology, American Museum of Natural History, New York (AMNH) and the citizen scientists Carsten Gröhn (Glinde), Max Kobbert (Münster) and Patrick Müller (Zweibrücken, all three in Germany). The fossils housed in the Geoscientific Collection of the University of Göttingen derive from the Patrick Müller, Rainer Ohlhoff and Jörg Wunderlich Amber Collections.

2.2. Specimen preparation and imaging

Amber pieces containing fossils were ground and polished manually using a series of wet silicon carbide papers with grits ranging from FEPA P 600 (25.8 µm grain size) to 4000 (5 µm grain size, Struers company) to produce smooth surfaces. When reaching the proximity of the inclusion, only thin layers of amber (less than 1 mm thick) were ground away from the specimen bit by bit, thereby frequently checking the preparation under a dissection microscope to make sure that a minimal distance between the inclusion and the amber surface was left (Sadowski & al. 2021). Several amber blocks were cut into pieces with a dental drill to separate the *Selaginella* specimens from syninclusions and better access the fossils from all sides without loss of the other contents.

Small amber pieces were embedded in high-grade epoxy (Epo-Tek 301–2, Epoxy Technology) prior to initial grinding and polishing to stabilize them and obtain larger blocks that are easier to handle on the abrasive papers without risk of breakage (for protocols, refer to Sadowski & al. 2021). For optimal documentation of the spores, several tiny amber pieces containing dispersed megaspores and microspores were removed from block GZG.BST.21966, embedded in Epo-Tek 301–2 under vacuum (see Sadowski & al. 2021) and subsequently ground and polished to c. 0.5 mm thickness (Fig. 8E–H).

Prepared amber specimens were adjusted on glass microscope slides with small pieces of modelling tack so that the upper polished surface was orientated horizontally. A drop of water was placed on the upper surface of the amber and covered with a coverslip to reduce light scattering from fine surface scratches and improve optical resolution (Sadowski & al. 2021).

The amber inclusions were examined with a Carl Zeiss Stemi 508 dissecting microscope and a Carl Zeiss AxioScope A1 compound microscope, both of them equipped with a Canon 5D digital camera. Simultaneous use of oblique incident and transmitted light ensured optimal illumination of the inclusions (see Kettunen & al. 2019; Sadowski & al. 2021). To capture the three-dimensionality of the inclusions, all light-microscopic images were digitally stacked to produce photomicrographic composites merged from up to 120 individual focal planes using the software package HeliconFocus version 6.3.3 Pro (Sadowski & al. 2021).

Microcomputed tomography (MicroCT) was used on amber specimen JZC-Bu-1869 to obtain an enhanced illustration of the differently sized sporangia in *Selaginella heterosporangiata*. The specimen was mounted on a stub and scanned with a Phoenix x-ray Nanotom. The scan comprised 1440 projections and was implemented using the following settings: voltage = 90 kV, current = 100 μ A, exposure time = 1000 ms, average = 3, skip = 1 and isotropic resolution = 2.3 μ m. Visualization of the images was achieved with the software Volume Graphics Studio Max 3.4 (Volume Graphics, Heidelberg, Germany).

After examination, all amber pieces were fully embedded in Epo-Tek 301–2 following the protocols described by Sadowski & al. (2021) to prevent deterioration and ensure long-term preservation.

2.3. Analysis of fossils and comparison with extant species

Morphological descriptions from literature were used to assign the fossils to the genus *Selaginella* by comparing the fossil character states with those seen in extant and other fossil lycophytes (Øllgaard 1987; Jermy 1990; Thomas 1997, 2005; Van Konijnenburg-van Cittert & al. 2014, 2016; Field & al. 2016; Weststrand & Korall 2016b). Most of the *Selaginella* species formally described in this study are based on single fertile specimens, which do not reveal the complete range of variability of the fossil-taxa. Nevertheless, we have considered all characters available from the fossils in our comparisons with other taxa, and species delimitations are based on combinations of characters, rather than individual characters. For infrageneric classification of *Selaginella* we followed the recent proposal by Weststrand & Korall (2016b).

As present-day autochthonous *Selaginella* species display a clear pattern of endemism by biogeographic region,

our morphological comparisons with extant species focus on Asian, Australasian and some African-Madagascan representatives of the genus. Data for the comparisons were extracted primarily from comprehensive taxonomic treatments and checklists (Van Alderwerelt van Rosenburgh 1915; Alston 1934, 1935a, 1935b, 1937, 1940, 1945; Quansah 1986; Dixit 1992; Schulz & al. 2013; Zhang & al. 2013; Singh & al. 2014a; Zhou & al. 2015b; Fraser-Jenkins & al. 2015, 2017; Shalimov & al. 2019), but recent taxonomic updates were also considered. Additional data were gathered through the examination of protologues and herbarium specimens (type specimens, if available) housed in B and GOET or online images through the JSTOR Global Plants Initiative portal (<https://plants.jstor.org/>), JACQ consortium (2021), PteridoPortal (2021) and The Herbarium Catalogue, Royal Botanic Gardens, Kew (The Herbarium Catalogue 2021).

2.4. Terminology

The technical terms used in our descriptions of the gross morphology follow the general definitions provided by Lellinger (2002), along with a few other concepts used by Jermy (1990) and Weststrand & Korall (2016a). For the description of spore ornamentation, we followed the terminology proposed by Punt & al. (2007).

Adpressed – tightly pressed against a surface. Here applied to dorsal trophophylls (e.g. *Selaginella heterosporangiata*, Fig. 4I; *S. wangboi*, Fig. 26G; *S. pellucida*, Fig. 30C, D) or ventral sporophylls (e.g. *S. minutissima*, Fig. 3A, C).

Anisophyllous – having leaves of markedly unequal size or shape on the same plant stem. Here applied to vegetative shoots or strobili (e.g. *Selaginella heterosporangiata*, Fig. 4I; *S. grimaldii*, Fig. 7B).

Ascending – obliquely directed away from a surface and toward the apex of the structure on which it is borne (Lellinger 2002).

Axillary trophophyll – leaf borne in a branch dichotomy (e.g. *Selaginella grimaldii*, Fig. 7C).

Carinate – leaf with a sharp, longitudinal ridge (keel), as on the abaxial side of the midrib (Lellinger 2002) (e.g. *Selaginella ohlhoffiorum*, Fig. 8B; *S. patrickmuelleri*, Fig. 13D).

Close – having similar parts closely spaced and so nearly touching; used here for trophophylls and sporophylls.

Dimorphic – having or occurring in two distinct forms. Here applied to leaves (trophophylls or sporophylls) having different forms (e.g. *Selaginella grimaldii*, Fig. 7B; *S. patrickmuelleri*, Fig. 13A).

Distant – having similar parts that are well separated and not overlapping or touching (Lellinger 2002); used here for trophophylls and sporophylls.

Dorsiventral strobilus – strobilus having sporophylls of upper and lower surfaces differing from each other in morphology (e.g. *Selaginella patrickmuelleri*, Fig. 13A).

Imbricate – having similar parts overlapping; used here for trophophylls and sporophylls.

Inequilateral – having both sides of the basal portion of the leaf blade unequal in size and/or shape.

Isophyllous – having leaves of equal size and shape on the same plant stem. Here applied to vegetative shoots or strobili (e.g. *Selaginella wunderlichiana*, Fig. 18F, G; *S. aurita*, Fig. 20B–E).

Ligule – a small, tongue-like, often triangular appendage located near the microphyll base; it is persistent in *Isoetes* L., but caducous in *Selaginella* (Lellinger 2002) (e.g. *S. ciliifera*, Fig. 15G).

Megaspore – a general term for large spores of heterosporous vascular plants, that is, the spores from which the megagametophyte develops (Jackson 1928; Punt & al. 2007) (e.g. *Selaginella ohlhoffiorum*, Fig. 8F–H).

Microphyll – the photosynthetic organ of lycophytes, always lacking a stipe, characterized by its usually minute size and unbranched vascular system (a single vein) (Lellinger 2002).

Microspore – a general term for the smaller spores of heterosporous plants, i.e. the spores from which the microgametophyte develops (Jackson 1928; Punt & al. 2007) (e.g. *Selaginella ohlhoffiorum*, Fig. 8E).

Monomorphic – having or occurring in only one form. Here applied to leaves (trophophylls or sporophylls) having equal form (e.g. *Selaginella wunderlichiana*, Fig. 18F, G; *S. aurita*, Fig. 20B–E).

Psilate – describing a pollen grain or spore with a smooth surface (Wodehouse 1928; Punt & al. 2007) (e.g. *Selaginella amplexicaulis*, Fig. 22E).

Quadrangular strobilus – Strobilus having four angles and four sides (e.g. *Selaginella aurita*, Fig. 20B).

Resupinate – anisophyllous strobilus with the smaller sporophylls on the ventral side, i.e. in the same plane as the larger vegetative leaves (Quansah & Thomas 1985) (e.g. *Selaginella ciliifera*, Fig. 15B).

Rugulate – describing a type of a pollen or spore orna-

mentation composed of elongate sexine elements more than 1 µm long, arranged in an irregular pattern that is intermediate between striate and reticulate (Iversen & Troels-Smith 1950; Punt & al. 2007) (e.g. *Selaginella wangxinii*, Fig. 14J).

Sporophyll – a microphyll subtending a sporangium (Lellinger 2002) (Fig. 1, 2).

Sporophyll-ptyx – a vertical/oblique projection on the adaxial surface of the dorsal sporophyll of a bilateral resupinate strobilus (Quansah & Thomas 1985) (e.g. *Selaginella ohlhoffiorum*, Fig. 9D; *S. patrickmuelleri*, Fig. 13C). The sporophyll-ptyx is complete if it reaches the apex of the sporophyll (*S. wangxinii*, Fig. 1H), and incomplete if it ends below the apex (e.g. *S. ohlhoffiorum*, Fig. 1D).

Strobilus – a compact reproductive structure borne at the tips of branches or axes composed of a central axis bearing sporophylls (Lellinger 2002) (e.g. *Selaginella ohlhoffiorum*, Fig. 9A; *S. amplexicaulis*, Fig. 22A).

Tetrastichous strobilus – sporophylls arranged in four vertical rows (e.g. *Selaginella patrickmuelleri*, Fig. 13A; *S. aurita*, Fig. 20B).

Trophophyll – a vegetative microphyll (Lellinger 2002) (e.g. *Selaginella grimaldii*, Fig. 7B).

3. Results

3.1. Systematic palaeobotany

Class: *Lycopodiopsida*

Order: *Selaginellales*

Family: *Selaginellaceae*

Genus: *Selaginella* P. Beauv. in Mag. Encycl. 9(5): 478, 1804. – Type: *Selaginella selaginoides* (L.) P. Beauv. ex Schrank & Mart. (≡ *Lycopodium selaginoides* L.).

Key to fossil *Selaginella* from Kachin amber

1. Strobili dorsiventrally complanate; sporophylls dimorphic (*Selaginella* subg. *Stachygyndrum*) . . . **2**
 - Strobili quadrangular; sporophylls monomorphic . . . **11**
2. Ventral sporophylls serrulate-denticulate, serrate or dentate at margins **3**
 - Ventral sporophylls short- to long-ciliate at margins . . . **7**
3. Sporophyll-ptyx of dorsal sporophylls nearly entire, with only a few teeth at margins
 - *Selaginella minutissima*
- Sporophyll-ptyx of dorsal sporophylls conspicuously serrulate, with multiple teeth at margins **4**
4. Ventral sporophylls conspicuously serrate or dentate at margins, teeth 25–40 µm long; strobili composed of 2 rows of smaller dorsal sporangia and 2 rows of larger ventral sporangia *Selaginella heterosporangiata*



Fig. 1. Sporophyll morphology of *Selaginella* with bilateral strobili from Kachin amber. Dorsal sporophylls shown on left side of each leaf pair, ventral sporophylls on right. – A: *S. minutissima*; B: *S. heterosporangiata*; C: *S. grimaldii*; D: *S. ohlfforum*; E: *S. cretacea*; F: *S. longifimbriata*; G: *S. patrickmuelleri*; H: *S. wangxinii*; I: *S. ciliifera*; J: *S. villosa*.

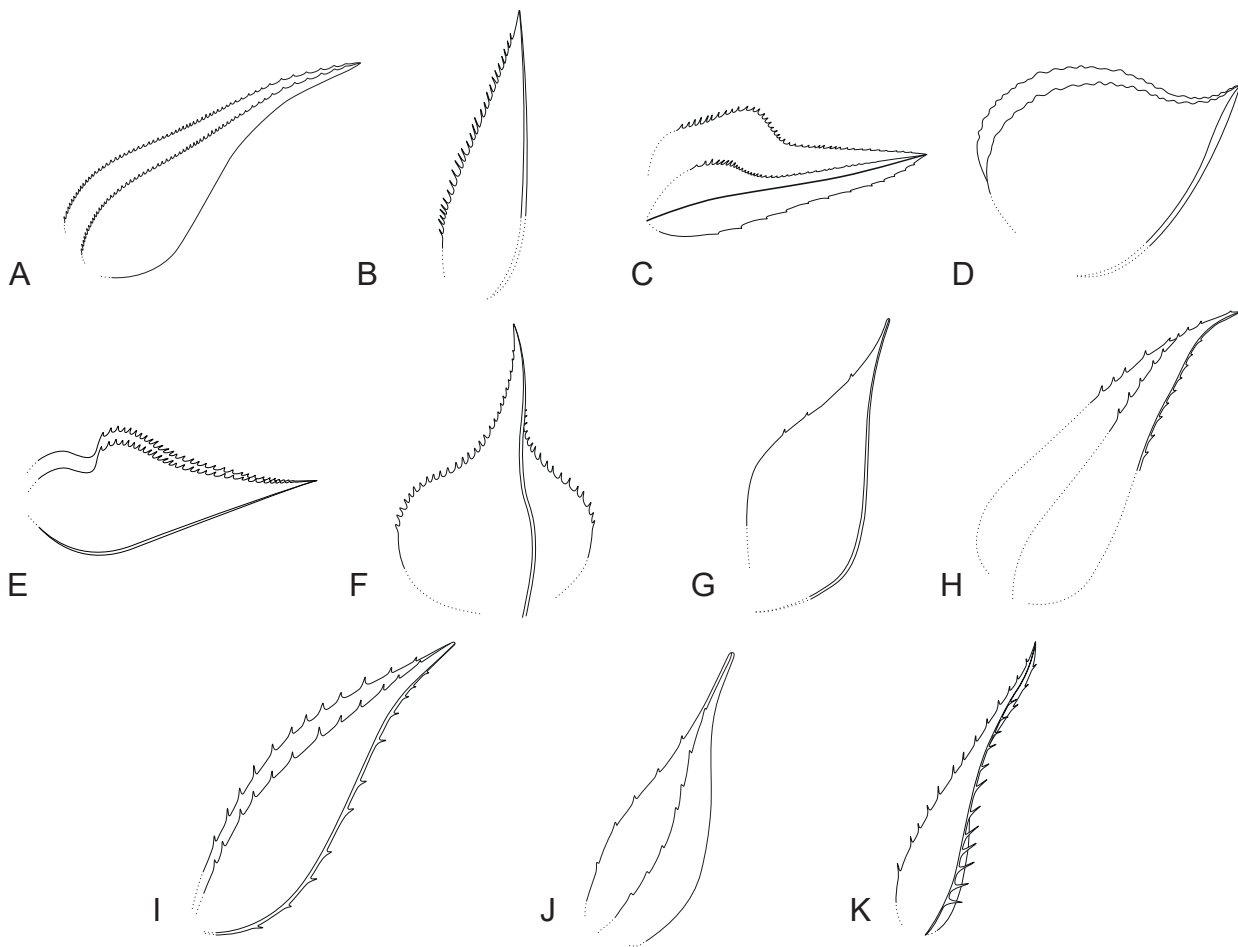


Fig. 2. Sporophyll morphology of *Selaginella* with quadrangular strobili from Kachin amber. – A: *S. wunderlichiana*; B: *S. isophylla*; C: *S. aurita*; D: *S. amplexicaulis*; E: *S. heinrichsii*; F: *S. konijnenburgiae*; G: *S. ovoidea*; H: *S. wangboi*; I: *S. tomescui*; J: *S. pellucida*; K: *S. obscura*.

- Ventral sporophylls denticulate to serrulate at margins, teeth 5–21 µm long; strobili with no particular pattern of sporangial arrangement **5**
- 5. Ventral trophophylls close to imbricate; axillary and ventral trophophylls broadly ovate *Selaginella grimaldii*
- Ventral trophophylls distant from each other; axillary and ventral trophophylls predominantly oblong . . . **6**
- 6. Ventral sporophylls broadly ovate; sporangia orbicular *Selaginella ohlhoffiorum*
- Ventral sporophylls ovate-lanceolate; sporangia ellipsoid *Selaginella cretacea*
- 7. Dorsal sporophylls predominantly dentate or denticulate at margins **8**
- Dorsal sporophylls predominantly ciliate at margins, but also dentate or serrate at basispic margin . . **10**
- 8. Ventral sporophylls nearly orbicular, apex rounded *Selaginella longifimbriata*
- Ventral sporophylls broadly ovate to ovate-lanceolate, apex attenuate **9**
- 9. Strobili up to 3.5 mm long; dorsal sporophylls with incomplete sporophyll-ptyx; megaspores proximally rugulate-reticulate . . *Selaginella patrickmuelleri*
- Strobili up to 6.5 mm long; dorsal sporophylls with nearly complete sporophyll-ptyx; megaspores proximally echinate *Selaginella wangxinii*
- 10. Dorsal sporophylls with sporophyll-ptyx narrow at base; ventral sporophylls acute to obtuse at apex *Selaginella ciliifera*
- Dorsal sporophylls with sporophyll-ptyx broadly enlarged at base forming an auricle; ventral sporophylls acuminate at apex *Selaginella villosa*
- 11. Sporophyll-ptyx present *Selaginella aurita*
- Sporophyll-ptyx absent **12**
- 12. Sporophylls acuminate at apex, entire to erose at margins *Selaginella amplexicaulis*
- Sporophylls attenuate, sometimes aristate at apex, at least denticulate, minutely serrate or dentate at margins **13**
- 13. Trophophylls monomorphic (*Selaginella* subg. *Ericetorum*) **14**
- Trophophylls dimorphic **15**
- 14. Trophophylls lanceolate, attenuate at apex, amplexicaul at base, erose at margins *Selaginella wunderlichiana*
- Trophophylls ovate, short-acuminate at apex, pel-

- tate at base, short-ciliate at basal acroscopic margin, sparsely dentate at medial margins, nearly entire at distal margins *Selaginella isophylla*
15. Basal sporangium (presumably megasporangium) protruding and conspicuously larger than rest of sporangia on strobilus **16**
- Sporangia uniform in size throughout strobilus . . **17**
16. Dorsal trophophylls ovate, obtuse at apex; sporophylls distant, ovate, attenuate at apex, exauriculate at base *Selaginella heinrichsii*
- Dorsal trophophylls oblong-lanceolate, attenuate to aristate at apex; sporophylls imbricate, broadly ovate, attenuate to aristate at apex, rounded at base *Selaginella konijnenburgiae*
17. Sporangia ellipsoid or ovoid . . . *Selaginella ovoidea*
- Sporangia generally suborbicular **18**
18. Axillary trophophylls broadly ovate, nearly entire or with a few sparse teeth or cilia; microspores in monads *Selaginella wangboi*
- Axillary trophophylls elliptic to narrowly elliptic, serrulate-serrate, denticulate-dentate to short-ciliate at margins; microspores in tetrads **19**
19. Axillary trophophylls short-ciliate or denticulate at margins, cilia or teeth 30–60 µm long *Selaginella tomescui*
- Axillary trophophylls mostly serrate or dentate, with teeth 15–50 µm long **20**
20. Strobili 1–2 mm long; sporophylls ovate, attenuate at apex, slightly denticulate to erose at margins, teeth ≤ 10 µm long *Selaginella pellucida*
- Strobili 4.0–5.5 mm long; sporophylls lanceolate, long-attenuate to aristate at apex, sparsely dentate at margins, teeth 30–40 µm long . . *Selaginella obscura*

Selaginella subg. *Stachygynandrum* (P. Beauv. ex Mirb.) Baker in J. Bot. 21: 3. 1883 ≡ *Stachygynandrum* P. Beauv. ex Mirb. in Lam. & Mirb., Hist. Nat. Vég. 3: 477. 1803. – Type: *Selaginella flabellata* (L.) Spring (≡ *Lycopodium flabellatum* L.).

Selaginella minutissima A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.22002 [Fig. 3], Geoscientific Collection of the University of Göttingen. – Fig. 1A; 3 (only specimen available).

Diagnosis — Strobilus terminal, bilateral, dorsiventrally complanate. Dorsal sporophylls imbricate, ovate, carinate, apex acute, margins serrulate; sporophyll-ptyerx incomplete, nearly entire with only a few teeth. Ventral sporophylls imbricate, adpressed, broadly ovate, apex acuminate to aristate, margins dentate.

Description — *Rhizophores*, *branches* and *trophophylls* not preserved. *Strobilus* fragment terminal, compact, bilateral, dorsiventrally complanate, 1.1 × 0.9 mm (Fig. 3A). *Sporophylls* dimorphic. *Dorsal sporophylls* imbricate, ascending, 9 in only available strobilus, 0.4–0.7 × 0.2–0.3 mm, conduplicate, ovate, carinate, base not seen, apex acute, margins serrulate, teeth 5–7 µm long (Fig. 1A; 3B); sporophyll-ptyerx incomplete, nearly entire with only a few teeth similar in size to those of margins (Fig. 1A; 3B). *Ventral sporophylls* imbricate, adpressed, symmetric, 6 in only available strobilus, 0.3–0.6 × 0.3–0.4 mm, broadly ovate, non-carinate, base rounded, apex acuminate to aristate, margins dentate, teeth 20–40 µm long (Fig. 1A; 3C). Epidermis of ventral

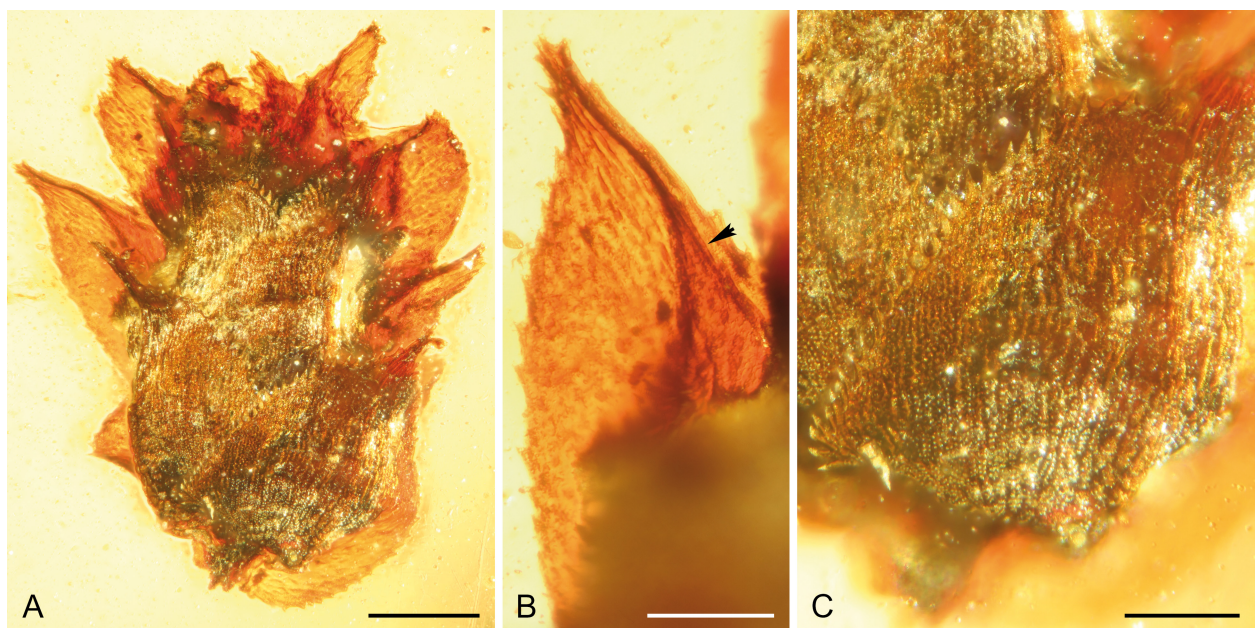


Fig. 3. Holotype of *Selaginella minutissima* from Kachin amber (GZG.BST.22002). – A: ventral view of bilateral strobilus; B: dorsal sporophyll in ventral view showing incomplete sporophyll-ptyerx (arrowhead); C: ventral sporophyll. – Scale bars: A = 200 µm; B, C = 100 µm.

sporophylls composed of elongate cells, with long axes orientated uniformly parallel to long axis of sporophyll (Fig. 3C). *Sporangia* and *spores* not seen.

Remarks — Only a single fragment of a strobilus has been found. Bilateral strobili with a sporophyll-ptyx are known to be produced exclusively by extant species with resupinate strobili, and the seven species from Kachin amber with bilateral strobili and preserved vegetative shoots likewise show this pattern. Although vegetative leaves are not preserved in the *Selaginella minutissima* specimen, it is most probable that the strobili were resupinate and that the sporophylls with a sporophyll-ptyx were positioned dorsally.

Selaginella minutissima is distinguished from all other *Selaginella* inclusions with bilateral strobili by the small size of the strobilus with imbricate, adpressed ventral sporophylls, which are nearly orbicular and aristate at the apex (Fig. 1A; 3A, C), together with the nearly entire-margined sporophyll-ptyx, which possesses only a few teeth in the margins (Fig. 3B). The extant *S. loriae* Hieron., endemic to New Guinea (Van Alderwerelt van Rosenburgh 1915), resembles the fossil in regard to morphology, in particular concerning the small strobili (2–3 mm long), oblong-ovate, minutely dorsal sporophylls and broadly ovate ventral sporophylls (Van Alderwerelt van Rosenburgh 1915). However, *S. minutissima* differs from *S. loriae* by the latter possessing dentate-pellucid-margined dorsal sporophylls with teeth 10–30 µm long and ventral sporophylls denticulate with teeth up to 20 µm long (Hieronymus 1913), whereas the dorsal sporophylls of the fossil are serrulate with teeth up to 7 µm long, not pellucid-margined, and the ventral ones are dentate with teeth 20–40 µm long (Fig. 3A, C).

Etymology — The specific epithet is the superlative of the Latin adjective *minutus*: very small, minute, which refers to the small size of the strobilus.

Selaginella heterosporangiata A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.21999 [Fig. 4A, C, E], Geoscientific Collection of the University of Göttingen. – Fig. 1B; 4–6 (two specimens available).

Diagnosis — Axes compressed. Monostele located in a central canal, connected to cortical tissue by trabeculae. Trophophylls dimorphic. Axillary trophophylls ovate, apex obtuse to acute, base obtuse, margins slightly dentate. Dorsal trophophylls distant, lanceolate, apex acuminate to aristate, base decurrent, margins serrulate. Ventral trophophylls distant, broadly ovate, oblong or obovate, carinate, base obtuse, apex acute to obtuse, sometimes rounded, margins serrulate. Strobili terminal, bilateral, dorsiventrally complanate, resupinate. Sporophylls dimorphic. Dorsal sporophylls distant, oblong-lanceolate,

non-carinate, apex obtuse, rarely acute, margins slightly denticulate; sporophyll-ptyx incomplete, broadly enlarged at base, with serrulate margins. Ventral sporophylls distant, ovate-lanceolate, slightly carinate, apex acuminate, margins sharply serrate-dentate. Sporangia suborbicular, 2 rows of smaller dorsal sporangia and 2 rows of larger ventral sporangia. Microspores proximally rugulate.

Description — *Rhizophores* not preserved. Axes compressed. Monostele located in an amber-filled central canal, connected to cortical tissue by trabeculae (Fig. 4J). *Trophophylls* dimorphic (Fig. 4I; 5G). *Axillary trophophylls* somewhat asymmetric, 0.5–1.2 × 0.3–0.5 mm, ovate, apex obtuse to acute, base obtuse, margins slightly dentate, with a few minute teeth. *Dorsal trophophylls* distant, adpressed, ascending, 0.7–1.5 × 0.2–0.4 mm, lanceolate, slightly carinate, base decurrent, apex acuminate to aristate, margins serrulate (Fig. 4I; 5G). *Ventral trophophylls* distant, spreading, slightly asymmetric, 0.6–2.1 × 0.4–0.8 mm, broadly ovate, oblong or obovate, carinate, base obtuse, apex acute to obtuse, sometimes rounded, margins serrulate (Fig. 4I; 5G). *Strobili* terminal, bilateral, dorsiventrally complanate, resupinate, 5.2–5.8 × 2.0–2.7 mm (Fig. 4A–C; 5A, B). *Sporophylls* dimorphic. *Dorsal sporophylls* distant, spreading, asymmetric, 16–18 per strobilus, 1.4–1.9 × 0.4–0.7 mm, oblong-lanceolate, non-carinate, base short-truncate, apex obtuse, rarely acute, margins slightly denticulate, teeth 10–20 µm long; sporophyll-ptyx incomplete, broadly enlarged at base, with serrulate margins, teeth 10–20 µm long (Fig. 1B; 4E; 5F). *Ventral sporophylls* distant, spreading, conduplicate, 10–14 per strobilus, 1.0–1.2 × 0.5–0.8 mm, ovate-lanceolate, slightly carinate, base obtuse to rounded, apex acuminate, margins sharply serrate-dentate, teeth 25–40 µm long (Fig. 1B; 4F; 5D). Epidermis of ventral sporophylls composed of elongate cells, with long axes orientated uniformly parallel to carina (Fig. 4F). *Sporangia* suborbicular, smaller dorsal sporangia 330–460 × 310–480 µm and larger ventral sporangia 750–900 × 780–970 µm, composed of uniform isodiametric cells with thick anticlinal walls (Fig. 4D; 5C, D; 6). *Microspores* numerous, 25–40 µm in diam., proximally rugulate (Fig. 4G, H; 5H, I).

Remarks — Specimen GZG.BST.21999, from which one plant fragment was selected as the holotype of *Selaginella heterosporangiata*, preserves one of the morphological synapomorphies of the *Selaginellaceae*, namely the monostele situated in an air-filled (amber-filled in the fossils) central canal and connected to the cortical tissues by trabeculae (Fig. 4J). Preservation of the anatomical structure of the axis in transverse section is not cellular because the tissue is replaced by pyrite.

Selaginella heterosporangiata differs from the other Kachin fossil *Selaginella* species with bilateral strobili

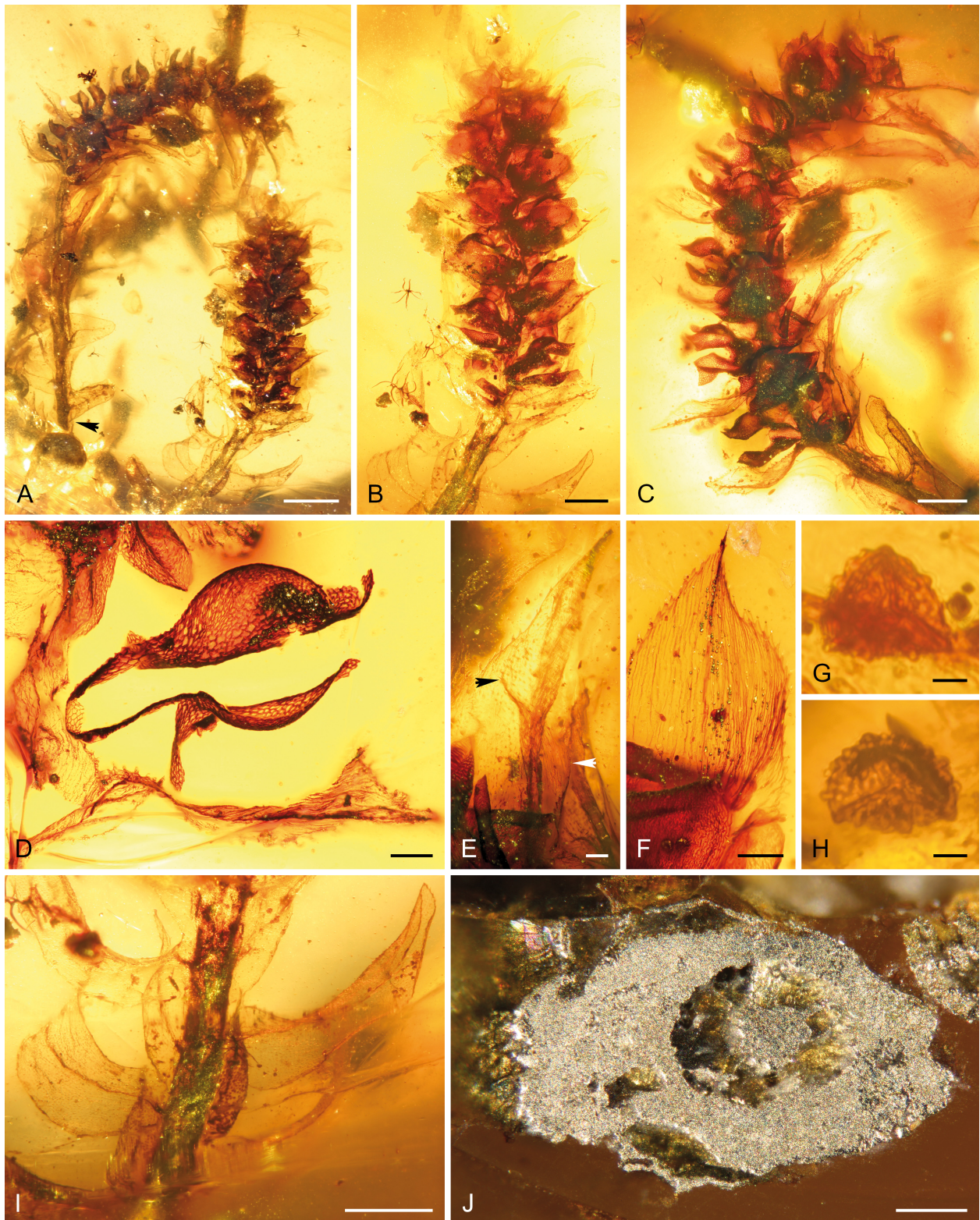


Fig. 4. *Selaginella heterosporangiata* from Kachin amber (GZG.BST.21999). Arrowhead in A indicates shoot portion designated as holotype, also shown in C and E. – A: ventral overview; B: ventral view of bilateral strobilus; C: lateral view of strobilus of holotype; D: ventral sporangium cut laterally at amber surface and adjacent sporophyll below; E: dorsal sporophyll in ventral view showing sporophyll-ptyx (arrowheads); F: ventral sporophyll; G, H: proximal surface of microspores; I: addressed dorsal and spreading ventral trophophylls in ventral view; J: slightly oblique transverse section of branch at amber surface showing organization of monostele and several trabeculae connecting stele and cortical tissue; plant tissue pyritized, void filled by amber. – Scale bars: A = 1 mm; B, C, I = 500 μ m; D–F, J = 100 μ m; G, H = 10 μ m.

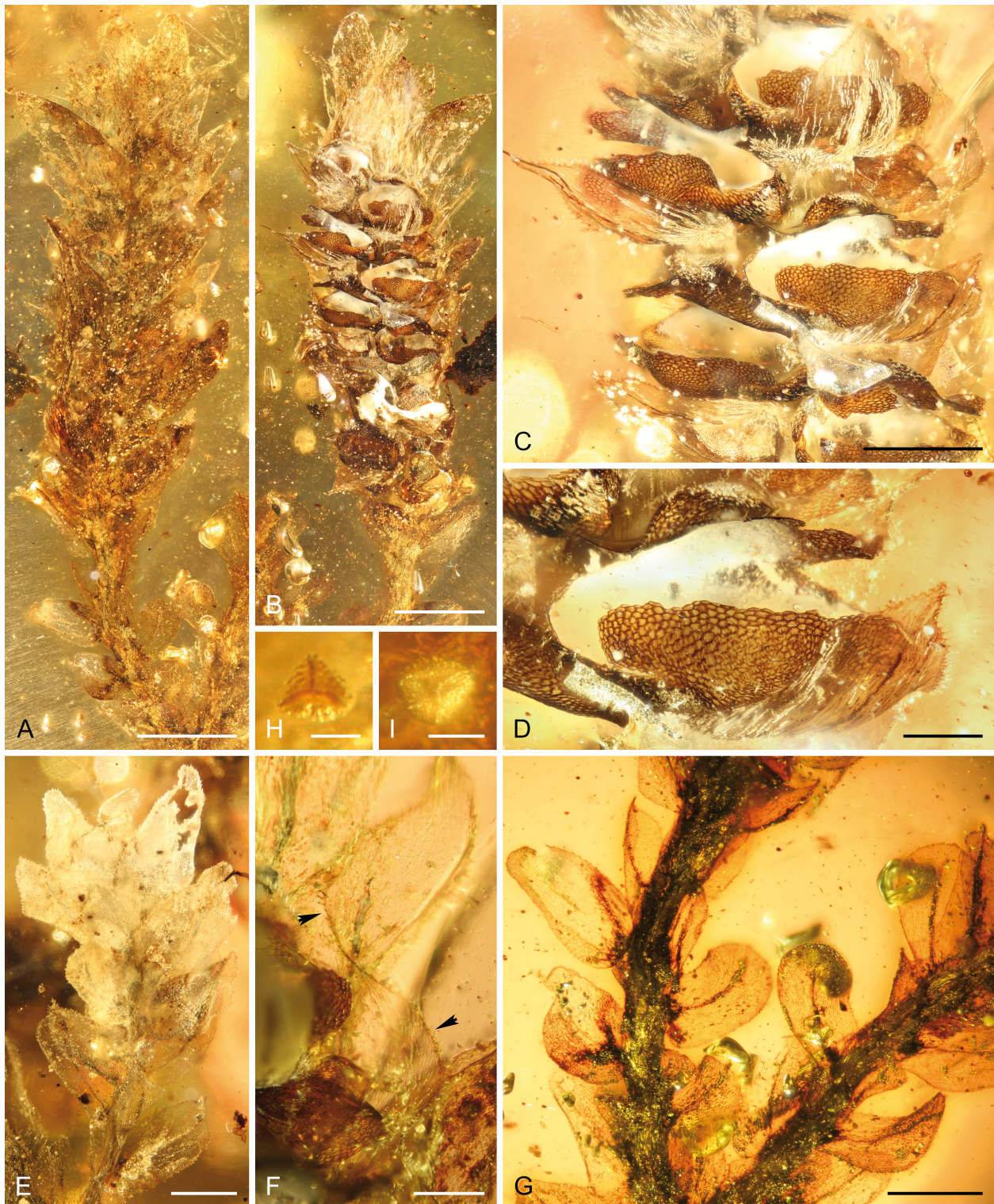


Fig. 5. *Selaginella heterosporangata* from Kachin amber (JZC-Bu-1869). – A, B: large strobilus in dorsal (A) and ventral (B) view; C: central portion of large strobilus in ventral view; D: ventral sporophyll and sporangium; E: smaller strobilus in dorsal view; F: dorsal sporophyll in ventral view showing sporophyll-ptyx (arrowheads); G: addressed dorsal and spreading and ascending ventral trophophylls in dorsal view; H, I: proximal surface of microspores. – Scale bars: A, B = 1 mm; C, E, G = 500 µm; D, F = 200 µm; H, I = 20 µm.

by the conspicuous differences in the size of the dorsal and ventral sporangia (Fig. 4C; 5C; 6), a condition that has not been observed in any other amber inclusion with bilateral strobili. However, it was not possible to verify if

smaller dorsal sporangia correspond to microsporangia and larger ventral sporangia to megasporangia, because all sporangia are empty.

There are several differences between the two exam-

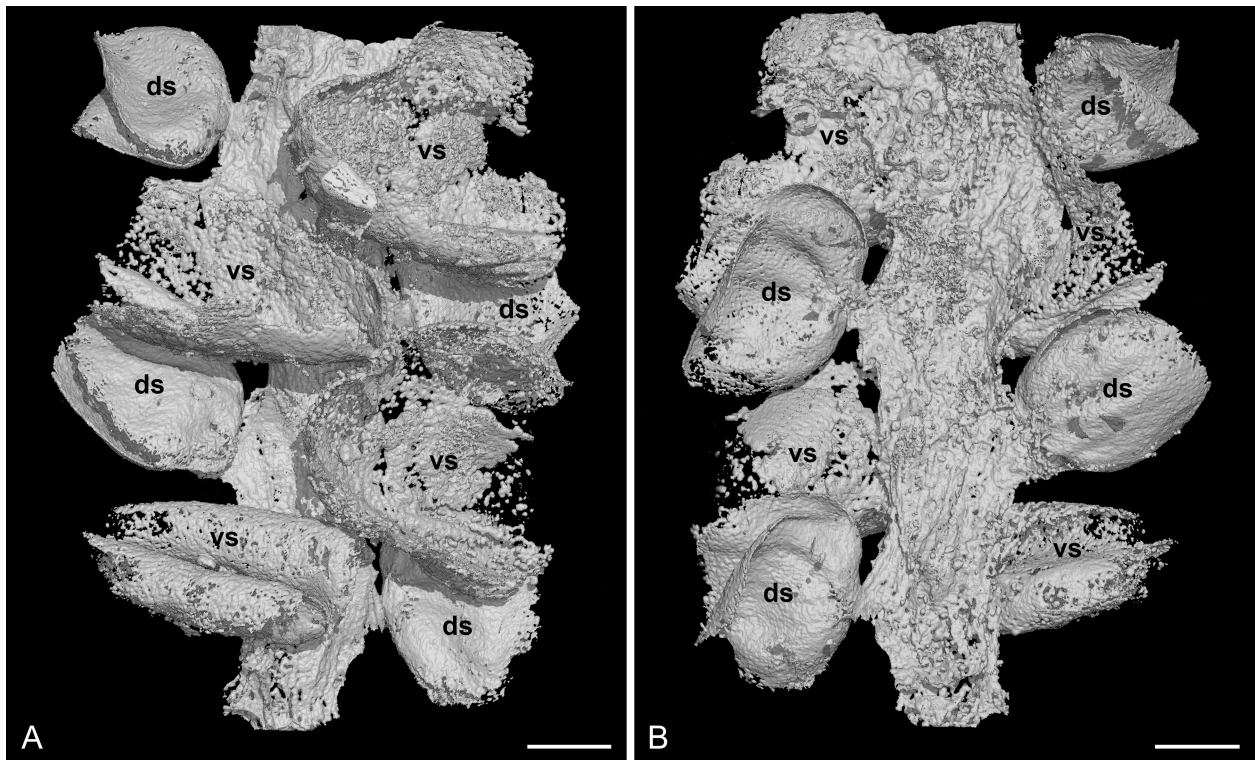


Fig. 6. Microcomputed tomographic reconstructions of central portion of strobilus of *Selaginella heterosporangiata* from Kachin amber (JZC-Bu-1869). – A: ventral view with two rows of larger ventral and two rows of smaller dorsal sporangia; B: dorsal view. – Sporophylls were virtually removed to make size differences in sporangia better visible. – vs = ventral sporangium; ds = dorsal sporangium. – Scale bars: 200 μ m.

ined specimens, specifically with regard to the shape of the dorsal and ventral leaf apices: JZC-Bu-1869 usually has obtuse to rounded ventral trophophylls and aristate dorsal trophophylls, whereas GZG.BST.21999 mostly shows acute ventral trophophylls and short-acuminate dorsal trophophylls. Despite these minor differences, both specimens are congruent and we therefore regard them here as belonging to the same species.

Selaginella kouytcheensis H. Lév. is an extant species endemic to China that resembles the fossil morphology in having bilateral strobili with oblong or lanceolate, denticulate dorsal sporophylls and ovate, acuminate ventral sporophylls, which are dentate at the margins. However, it differs from the fossil in its ovate or elliptic dorsal trophophylls with obtuse apices (Zhang & al. 2013). Additionally, the proximal microspore surface is also different in these two taxa, namely nearly smooth in *S. kouytcheensis* (Zhou & al. 2015a) and rugulate in *S. heterosporangiata* (Fig. 4G, H; 5H, I).

Etymology — The specific epithet is derived from the Greek words *heteros*: different, *spora*: spore and *angeion*: case, capsule or vessel. It emphasizes the conspicuous size difference between the (smaller) dorsal and (larger) ventral sporangia.

Additional specimens studied — JZC-Bu-1869, American Museum of Natural History (Fig. 5, 6).

***Selaginella grimaldii* A. R. Schmidt & L. Regalado, sp. nov.**

Holotype: SMNS Bu-355 [Fig. 7A, C–G], State Museum of Natural History Stuttgart. – Fig. 1C; 7 (only specimen available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Axillary trophophylls symmetric, broadly ovate, non-carinate, base rounded, apex acute to obtuse, margins finely denticulate. Dorsal trophophylls close to imbricate, adpressed, somewhat asymmetric, oblong to slightly obovate, non-carinate, base inequilateral, basicopic portion rounded, acrosopic portion straight, apex acuminate to apiculate, margins denticulate. Ventral trophophylls close to imbricate, ascending, symmetric, broadly ovate, non-carinate, base rounded to slightly truncate, apex acute to slightly acuminate, margins denticulate. Strobili terminal, bilateral, dorsiventrally complanate, resupinate. Sporophylls dimorphic. Dorsal sporophylls close to imbricate, spreading, slightly asymmetric, lanceolate, non-carinate, base inequilateral, apex acute to obtuse, margins serrulate; sporophyll-ptyx incomplete, with serrulate margins similar to those on sporophyll margins. Ventral sporophylls imbricate, slightly conduplicate, symmetric, broadly ovate, slightly carinate, base decurrent, apex acuminate, margins denticulate. Sporangia suborbicular to sometimes ellipsoid. Microspores distally and proximally rugulate.

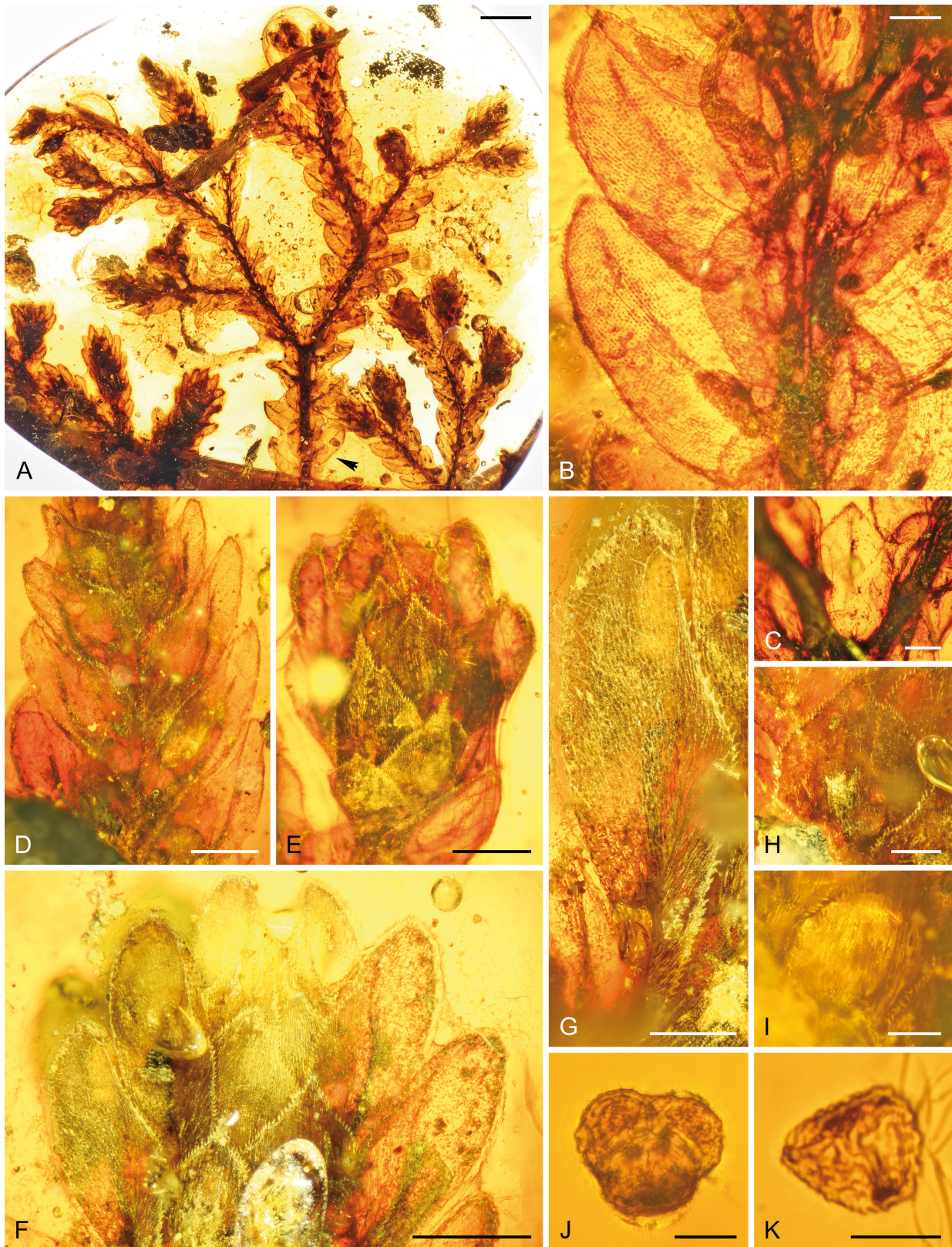


Fig. 7. *Selaginella grimaldii* from Kachin amber (SMNS Bu-355). Arrowhead in A indicates large, central shoot portion designated as holotype, also shown in C–G and I. – A: overview of shoot portions in dorsal view; B: smaller dorsal and larger ventral trophophylls in dorsal view; C: axillary trophophyll in focus; D: strobilus in dorsal view; E: strobilus in ventral view; F: apex of strobilus in ventral view; G: dorsal sporophyll in ventral view; H: ventral sporophyll; I: sporangium beneath ventral sporophyll; J: tetrad of immature microspores; K: proximal surface of mature microspore. – Specimen permanently on display in Amber Cabinet (Bernsteinkabinett) of State Museum of Natural History Stuttgart. – Scale bars: A = 2 mm; B, C, G–I = 200 μ m; D–F = 500 μ m; J, K = 20 μ m.

Description — *Rhizophores* not preserved. *Axes* compressed. *Trophophylls* dimorphic (Fig. 7A, B). *Axillary trophophylls* symmetric, 0.7–0.8 × 0.5–0.6 mm, broadly ovate, non-carinate, base rounded, apex acute to obtuse, margins finely dentate, teeth 10–20 µm long (Fig. 7C). *Dorsal trophophylls* close to imbricate, adpressed, somewhat asymmetric, 0.8–0.9 × 0.4–0.6 mm, oblong to slightly obovate, non-carinate, base inequilateral, basiscopic portion rounded, acroscopic portion straight, apex acuminate to apiculate, margins denticulate, teeth 10–15 µm long. *Ventral trophophylls* close to imbricate, ascending, symmetric, 1.2–1.8 × 0.7–1.1 mm, broadly ovate, non-carinate, base rounded to slightly truncate, apex acute to slightly acuminate, margins denticulate, teeth 10–20 µm long. Epidermis of dorsal and ventral trophophylls not preserved. *Strobili* terminal, bilateral, dorsiventrally complanate, resupinate, 1.4–3.0 × 0.8–2.0 mm (Fig. 7D, E). *Sporophylls* dimorphic. *Dorsal sporophylls* close to imbricate, spreading, slightly asymmetric, 7–10 per strobilus, 0.9–1.2 × 0.3–0.4 mm, lanceolate, non-carinate, base inequilateral, apex acute to obtuse, margins serrulate, teeth 10–20 µm long (Fig. 1C; 7F, G); sporophyll-ptyx incomplete, with serrulate margins similar to those on sporophyll margins (Fig. 1C; 7G). *Ventral sporophylls* imbricate, slightly conduplicate, symmetric, 7–9 per strobilus, 0.8–1.0 × 0.6–0.7 mm, broadly ovate, slightly carinate, base decurrent, apex acuminate, margins denticulate, teeth 10–20 µm long (Fig. 1C; 7E, H). Epidermis of both dorsal and ventral sporophylls not preserved. *Sporangia* suborbicular to sometimes ellipsoid, 260–400 × 180–240 µm (Fig. 7I). *Microspores* sometimes in tetrads when released, 25–30 µm in diam., distally and proximally rugulate (Fig. 7J, K).

Remarks — Among the fossil-taxa with bilateral resupinate strobili, *Selaginella grimaldii* closely resembles *S. ohlhoiffiorum* and *S. cretacea* (Li & al. 2022) in its general morphology. They all share the presence of sporophylls with serrulate-denticulate margins (Fig. 1C–E; 7D–H; 8A–C; 9A–C; 11B, C). They also share the presence of an incomplete sporophyll-ptyx, with serrulate margins in dorsal sporophylls (Fig. 1C–E; 7G; 8C; 9D; 11C). However, some apparent differences were also detected. For example, *S. ohlhoiffiorum* and *S. cretacea* have distant and predominantly oblong ventral trophophylls (Fig. 8A; 11E). This contrasts with the imbricate, broadly ovate ventral trophophylls of *S. grimaldii* (Fig. 7B). Strobili in *S. grimaldii* and *S. cretacea* may be up to 3.2 mm long and sporangia are generally ellipsoidal, whereas *S. ohlhoiffiorum* strobili are longer than 3.5 mm long and contain orbicular sporangia. Furthermore, *S. grimaldii* and *S. cretacea* have strobili of similar sizes although both differ in the number of dorsal and ventral sporophylls: *S. grimaldii* has only 7–10 dorsal sporophylls per strobilus, while *S. cretacea* has c. 14 dorsal sporophylls (Li & al. 2022). Similarly, the number of ventral sporophylls per strobilus differs between both species, i.e. 7–9 ventral

sporophylls in *S. grimaldii* but 12–13 in *S. cretacea* (Li & al. 2022).

Several present-day Asian *Selaginella* species produce strobili that are gross-morphologically similar to the bilateral resupinate strobili of *S. grimaldii* in that they have dentate dorsal and ventral sporophylls, the dorsal ones bearing a sporophyll-ptyx. These species include *S. decipiens* Warb. from India, China and Vietnam (Zhang & al. 2013), *S. monospora* Spring, native to Bhutan, China, India, Myanmar, Nepal, Thailand and Vietnam (Zhang & al. 2013), *S. trichophylla* K. H. Shing from Bhutan, China, India and Vietnam (Zhang & al. 2013) and *S. miniatospora* (Dalzell) Baker and *S. tenera* (Hook. & Grev.) Spring, both endemic to India (Dixit 1992; Fraser-Jenkins & al. 2017). However, the following characters discriminate the extant taxa from *S. grimaldii*: *S. decipiens*, *S. miniatospora* and *S. tenera* all have asymmetric ventral trophophylls, with the acroscopic base strongly enlarged, broader, sometimes overlapping the branches in *S. decipiens* (Zhang & al. 2013), and the acroscopic base is dilated in the other two taxa (Dixit 1992). In contrast, *S. grimaldii* produced symmetric ventral trophophylls with a rounded to truncate base (Fig. 7B). All the other above-mentioned species are distinct from the fossil in that they produce verrucate microspores (Dixit 1992; Zhou & al. 2015a), which differ from the rugulate ornamentation seen in the fossil (Fig. 7K). Additionally, *S. monospora* and *S. trichophylla* are characterized by a complete sporophyll-ptyx in dorsal sporophylls (Zhang & al. 2013), in contrast to the incomplete sporophyll-ptyx in *S. grimaldii* (Fig. 1C; 7G).

Etymology — The specific epithet honours Professor David A. Grimaldi (American Museum of Natural History, New York, U.S.A.), in recognition of his outstanding contributions to our knowledge of amber, amber deposits and amber inclusions.

Selaginella ohlhoiffiorum A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.21966a [Fig. 8A–C], Geoscientific Collection of the University of Göttingen. – Fig. 1D; 8–10 (three specimens available).

Diagnosis — *Axes* compressed. *Trophophylls* dimorphic. *Axillary trophophylls* symmetric, oblong-lanceolate, apex acute to obtuse, base rounded, margins slightly serrate. *Dorsal trophophylls* distant, slightly asymmetric, oblong, non-carinate, aristate at apex, serrulate-denticulate at margins. *Ventral trophophylls* distant, symmetric, oblong to rarely ovate, non-carinate, base truncate, apex obtuse to rounded, margins serrate-serrulate. *Strobili* terminal, bilateral, dorsiventrally complanate, resupinate. *Sporophylls* dimorphic. *Dorsal sporophylls* close to distant, ovate-lanceolate, slightly carinate, apex acute to obtuse, margins serrulate-denticulate; sporophyll-ptyx incomplete, with serrulate margins. *Ventral sporophylls*

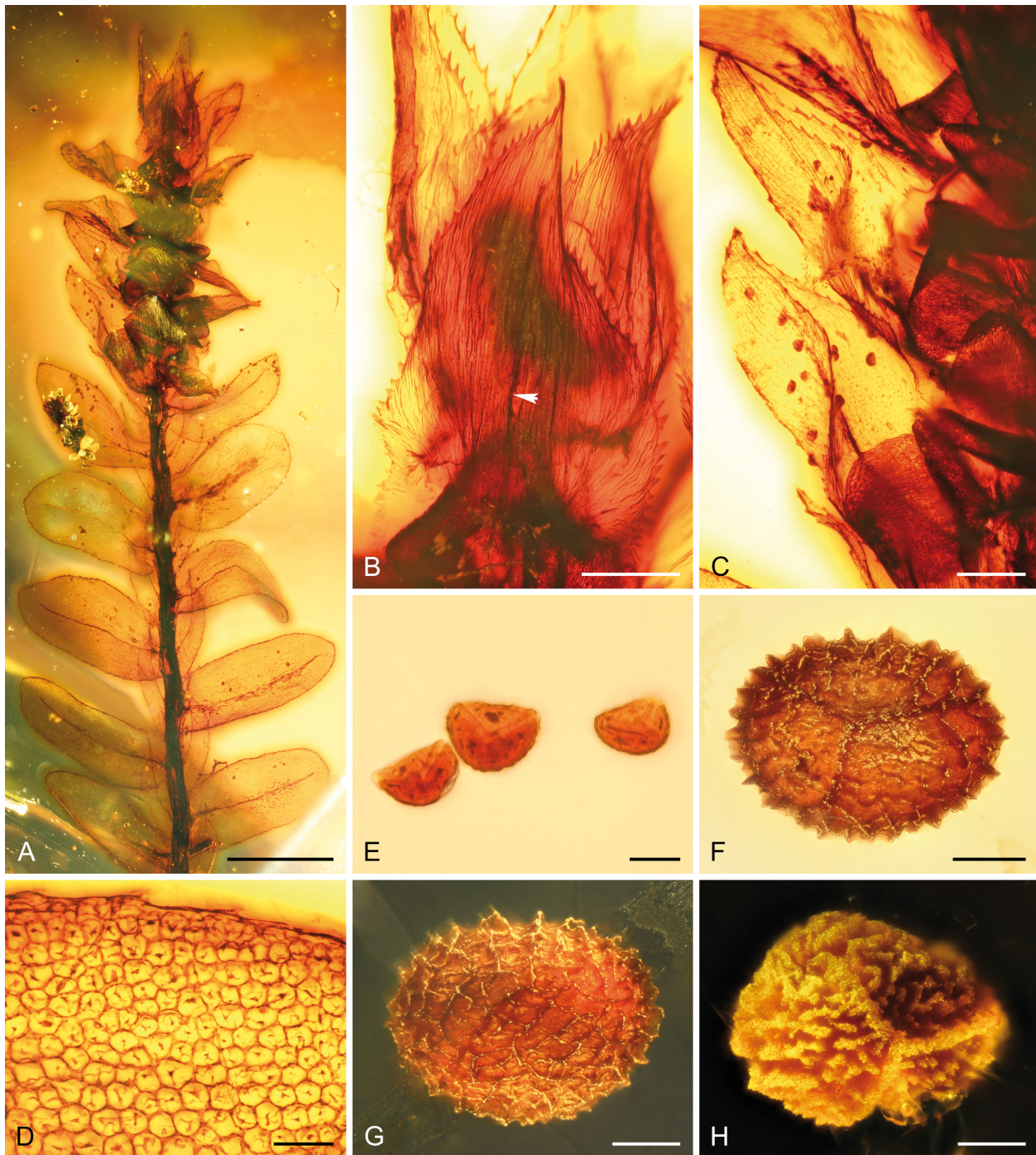


Fig. 8. *Selaginella ohlhoffiorum* from Kachin amber. Shoot portion illustrated in A–C designated as holotype. – A: overview in ventral view (GZG.BST.21966a); B: ventral sporophyll with carina (arrowhead, GZG.BST.21966a); C: two dorsal sporophylls with incomplete sporophyll-ptyeryx (GZG.BST.21966a); D: epidermis of trophophylls (GZG.BST.21966b); E: microspores showing proximal surface (GZG.BST.21966e); F–H: megaspores, F, H: proximal surface, G: distal surface (F, G: GZG.BST.21966c, H: GZG.BST.21966a). – Scale bars: A = 1 mm; B, C = 200 μ m; D = 50 μ m; E = 20 μ m; F–H = 100 μ m.

close to distant, broadly ovate, base decurrent, slightly carinate, apex sharply acuminate, margins denticulate. Sporangia orbicular. Megaspores distally and proximally reticulate. Microspores distally and proximally rugulate.

Description — *Rhizophores* not preserved. *Axes* compressed. *Trophophylls* dimorphic (Fig. 8A; 10A, B). *Axil-*

lary trophophylls symmetric, somewhat conduplicate, 0.9–1.6 \times 0.3–0.4 mm, oblong-lanceolate, non-carinate, base rounded, apex acute to obtuse, margins slightly serrate, teeth 8–20 μ m long. *Dorsal trophophylls* distant, adpressed, somewhat asymmetric, 0.9–1.1 \times 0.3–0.5 mm, oblong, non-carinate, base not seen, apex aristate, margins serrate-dentate, teeth 8–20 μ m long. *Ventral trophophylls*

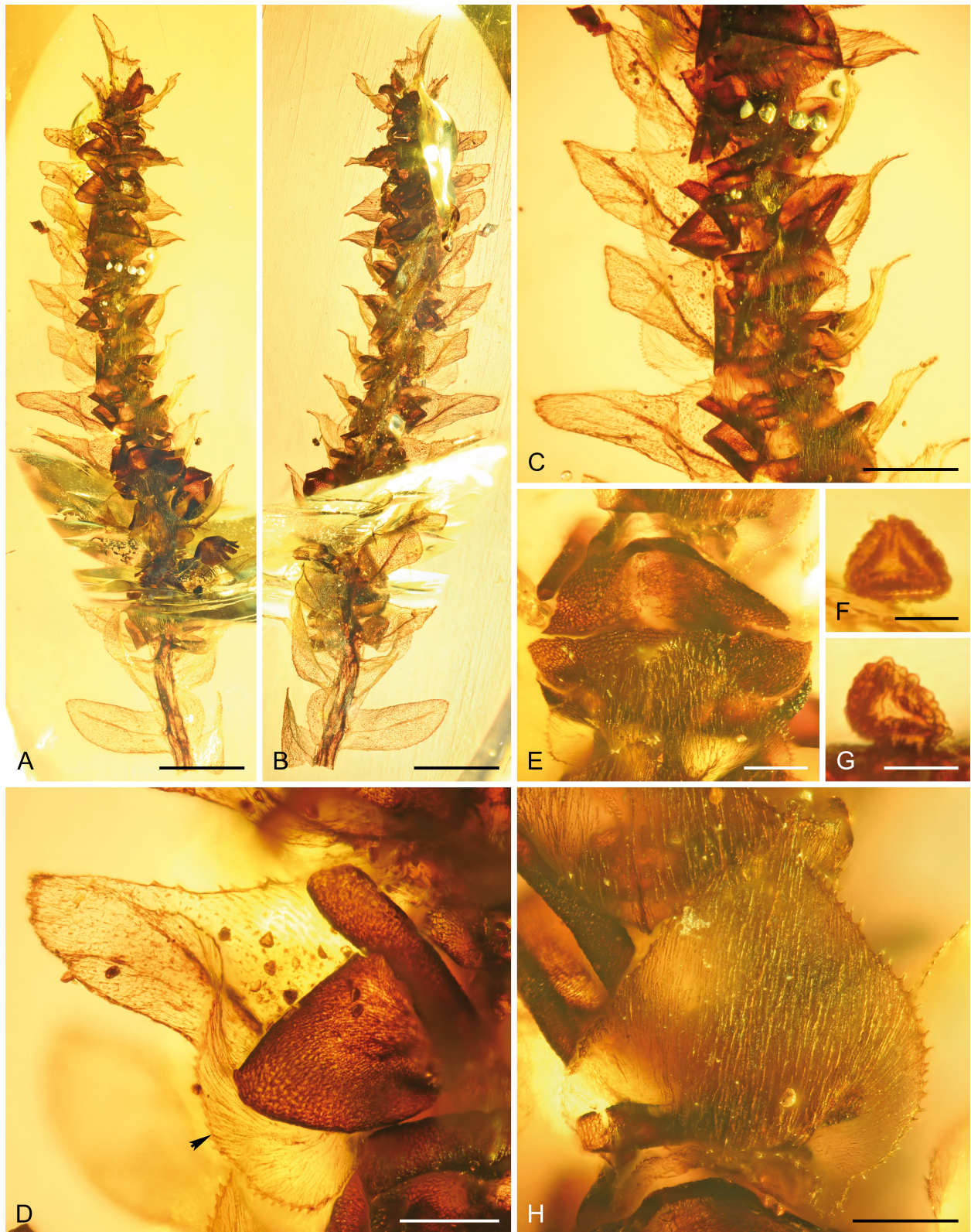


Fig. 9. *Selaginella ohlhoffiorum* from Kachin amber (GZG.BST.22026). – A, B: overview of bilateral strobilus in lateral view; C: central portion of strobilus in ventral view; D: dorsal sporophyll in ventral view showing incomplete sporophyll-ptyx (arrowhead) and corresponding sporangium; E: ventral sporangium; F, G: proximal surface of microspores; H: ventral sporophyll. – Scale bars: A, B = 1 mm; C = 500 μ m; D, E, H = 200 μ m; F, G = 20 μ m.

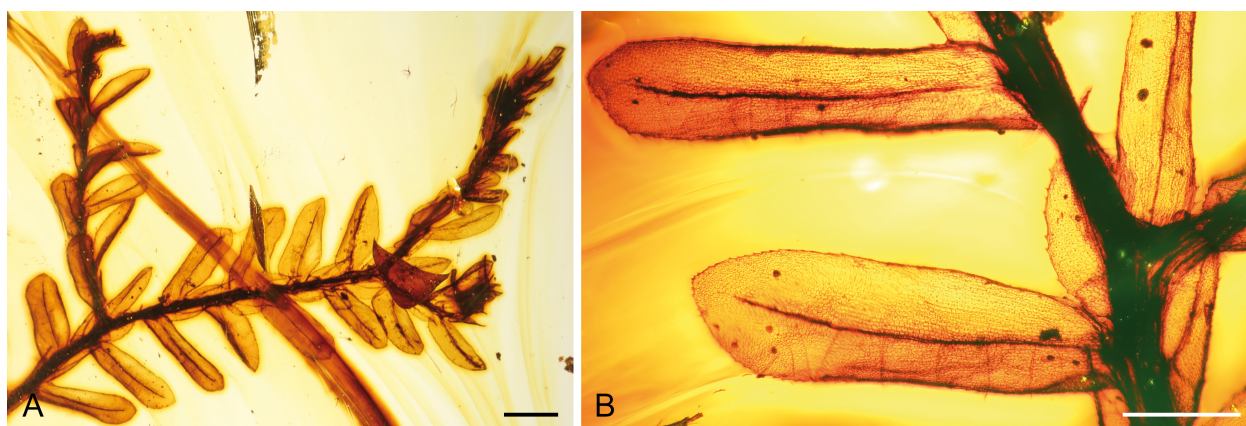


Fig. 10. *Selaginella ohlhoiffiorum* from Kachin amber (GZG.BST.21966b). – A: branched sterile shoot portion with strobili in early stage of development; B: trophophylls. – Scale bars: A = 1 mm; B = 500 µm.

distant, spreading, symmetric, $1.2\text{--}1.7 \times 0.5\text{--}0.8$ mm, oblong to rarely ovate, non-carinate, base truncate, apex obtuse to rounded, margins serrate-serrulate, teeth $8\text{--}35$ µm long. Epidermis of dorsal and ventral trophophylls with uniform polyhedral cells (Fig. 8D). *Strobili* terminal, bilateral, dorsiventrally complanate, resupinate, $3.5\text{--}6.8 \times 1.8\text{--}2.2$ mm (Fig. 8A; 9A–C). *Sporophylls* dimorphic. *Dorsal sporophylls* close to distant, spreading, conduplicate, 10 or 11 per strobilus (–26 in GZG.BST.22026), $0.8\text{--}1.2 \times 0.5\text{--}0.7$ mm, ovate-lanceolate, slightly carinate, base not seen, apex acute to obtuse, margins serrulate-denticulate, teeth $10\text{--}20$ µm long (Fig. 1D; 8C; 9D); sporophyll-ptyx incomplete, with serrulate margins similar to those along sporophyll margins (Fig. 1D; 8C; 9D). Epidermis of dorsal sporophylls composed of uniform polyhedral isodiametric cells. *Ventral sporophylls* close to distant, spreading, slightly conduplicate, symmetric, 10 or 11 per strobilus (–26 in GZG.BST.22026), $1.2\text{--}1.4 \times 0.3\text{--}0.4$ mm, broadly ovate, slightly carinate, base decurrent, apex sharply acuminate, margins denticulate, teeth $5\text{--}12$ µm long (Fig. 1D; 8B; 9H). Epidermis of ventral sporophylls composed of elongate cells, with long axes orientated uniformly parallel to long axis of sporophyll (Fig. 9H). *Sporangia* orbicular, $420\text{--}740 \times 440\text{--}800$ µm, composed of uniform isodiametric cells with thick anticlinal walls (Fig. 9E). *Megaspores* $350\text{--}400$ µm in diam., distally and proximally reticulate (Fig. 8F–H). *Microspores* numerous, $30\text{--}40$ µm in diam., distally and proximally rugulate (Fig. 8E; 9F, G).

Remarks — Among the *Selaginella* amber inclusions with bilateral strobili, *S. ohlhoiffiorum* is very similar morphologically to *S. grimaldii* and *S. cretacea*. However, the latter taxa differ from the former in the shape of the ventral trophophylls, strobilus size and sporangium shape (see description and remarks under *S. grimaldii* for details).

Several extant species, such as *Selaginella decipiens*, *S. miniatospora*, *S. monospora*, *S. tenera* and *S. trichophylla*, share with *S. ohlhoiffiorum* the ovate and denticulate ventral sporophylls and the ovate or lanceolate dorsal

sporophylls possessing denticulate margins and bearing a denticulate sporophyll-ptyx in the adaxial surface (Dixit 1992; Zhang & al. 2013). *Selaginella monospora* and *S. trichophylla* have a complete sporophyll-ptyx in the dorsal sporophylls (Zhang & al. 2013) and verrucate megaspores and microspores (Zhou & al. 2015a), whereas the sporophyll-ptyx is incomplete in *S. ohlhoiffiorum* (Fig. 1D; 8C; 9D), and the taxon produced reticulate megaspores (Fig. 8F, G) and rugulate microspores (Fig. 8E; 9F, G). *Selaginella decipiens* is distinguished from the fossil by its asymmetric ventral trophophylls, with the acroscopic base strongly enlarged, broader, sometimes overlapping the branches (Zhang & al. 2013), and its verrucate megaspores (Zhou & al. 2015a). In contrast, *S. ohlhoiffiorum* has symmetric ventral trophophylls (Fig. 8A; 10B), with a truncate base, and reticulate megaspores (Fig. 9F, G). *Selaginella tenera* and *S. miniatospora* have ventral trophophylls acute to subacute at the apex, asymmetric with a dilated acroscopic base, conspicuously aristate ventral sporophylls and papillate or verrucate megaspores (Dixit 1992). In comparison, the fossil is characterized by distinctly obtuse to rounded ventral trophophylls (Fig. 8A; 10B), acuminate ventral sporophylls (Fig. 8B; 9H) and reticulate megaspores (Fig. 8F, G).

Etymology — The specific epithet honours Astrid, Mara and Rainer Ohlhoff (Saarbrücken, Germany), who discovered the inclusions in amber specimen GZG.BST.21966 and generously made them available for study.

Additional specimens studied — GZG.BST.21966b–e and GZG.BST.22026, Geoscientific Collection of the University of Göttingen (Fig. 9), Patrick Müller Amber Collection BuB2711. Amber specimen GZG.BST.21966 has been cut into five pieces (GZG.BST.21966a to GZG.BST.21966e) to better access the individual plant fragments, megaspores and microspores (Fig. 8; 10).

Selaginella cretacea Ya Li, H. Schneid. & Y. D. Wang in *Cretaceous Res.* 133: 105143, page 3. 2022, **emended**

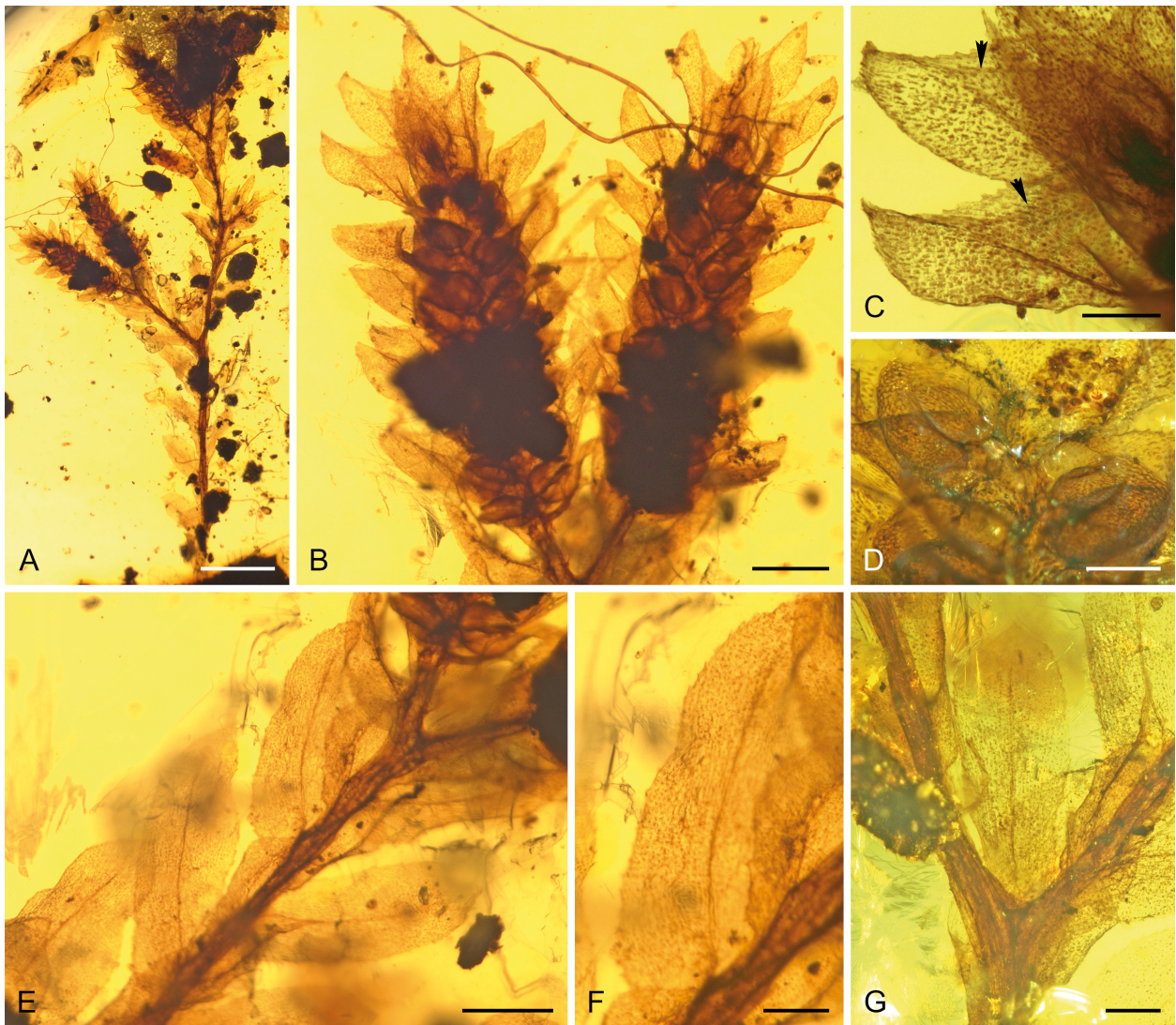


Fig. 11. Holotype of *Selaginella cretacea* from Kachin amber (PB22713). – A: ventral overview; B: ventral view of bilateral strobili; C: dorsal sporophylls in ventral view showing sporophyll-ptyx (arrowheads) D: microsporangia and released microspores (upper right); E: trophophylls in ventral view; F: ventral trophophyll; G: axillary trophophyll. – Images courtesy of Ting Li (Nanjing). – Scale bars: A = 2 mm; B, E = 500 μ m; C, D, F, G = 200 μ m.

here. – Holotype: PB22713, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. – Fig. 1E; 11.

Emended diagnosis — As provided by Li & al. (2022), with following addition: Axillary trophophylls symmetric, oblong, non-carinate, apex apiculate, margins serrulate. Dorsal sporophylls close, ascending, asymmetric, ovate to ovate-falcate; sporophyll-ptyx incomplete, with serrulate margins similar to those on sporophyll margins. Ventral sporophylls imbricate, slightly conduplicate, symmetric, ovate-lanceolate, slightly carinate, apex long-acuminate, margins denticulate to serrulate.

Additional description — *Rhizophores* not preserved. *Axes* compressed. *Trophophylls* dimorphic (Fig. 11E, F). *Axillary trophophylls* symmetric, c. 1.2 \times 0.4 mm, oblong, non-carinate, base not seen, apex apiculate, margins

serrulate, teeth < 20 μ m long (Fig. 11G). *Dorsal trophophylls* distant, addressed, 0.6–1.0 \times 0.2–0.3 mm, lanceolate, non-carinate, base decurrent, apex long-acuminate to aristate, margins denticulate to serrulate, teeth 7–9 μ m long (Fig. 11E). *Ventral trophophylls* distant, ascending, slightly asymmetric, 0.9–1.6 \times 0.3–0.7 mm, oblong to lanceolate, non-carinate, base rounded, non-auriculate, apex acute to apiculate, margins serrulate to serrate, teeth 5–25 μ m long (Fig. 11E, F). Epidermis of dorsal and ventral trophophylls not preserved. *Strobili* terminal, bilateral, dorsiventrally complanate, resupinate, 2.9–3.2 \times 1.4–1.6 mm (Fig. 11B). *Sporophylls* dimorphic. *Dorsal sporophylls* close, ascending, asymmetric, c. 14 per strobilus, 0.8–1.2 \times 0.3–0.5 mm, ovate to ovate-falcate, non-carinate, base not seen, apex acute, margins serrulate, teeth 5–16 μ m long (Fig. 1E; 11C); sporophyll-ptyx incomplete, with serrulate margins similar to those on sporophyll margins (Fig. 1E; 11C). *Ventral sporophylls*

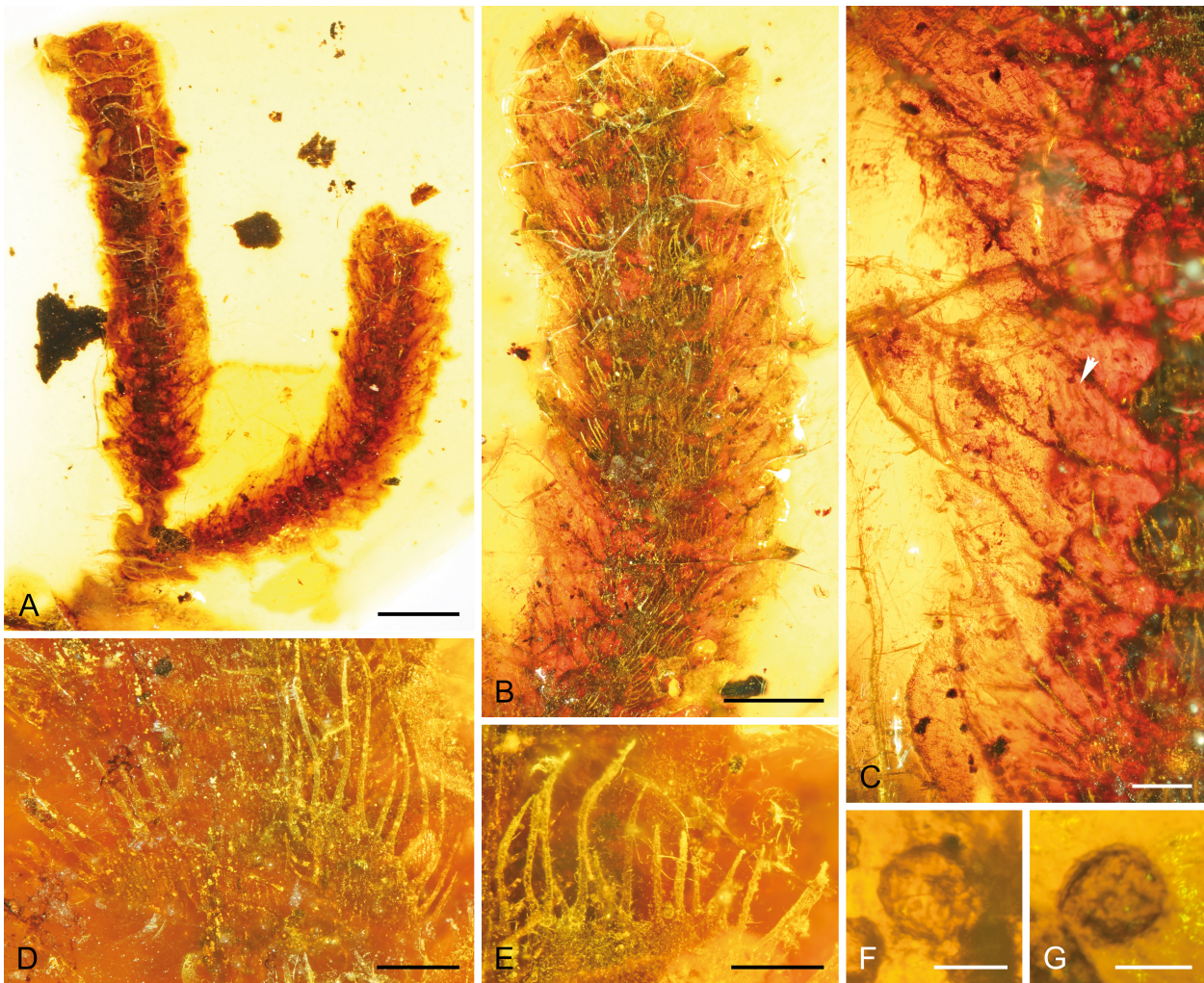


Fig. 12. Holotype of *Selaginella longifimbriata* from Kachin amber (GZG.BST.21998). – A: ventral overview of both strobili; B: ventral view of bilateral strobilus; C: dorsal sporophylls and sporangia in ventral view showing incomplete sporophyll-ptyx (arrowhead); D: ventral sporophyll; E: ciliate margin of ventral sporophyll; F, G: distal surface of microspores. – Scale bars: A = 2 mm; B = 1 mm; C–E = 200 μ m; F, G = 20 μ m.

imbricate, slightly conduplicate, symmetric, 12 or 13 per strobilus, 0.5–0.9 \times 0.3–0.5 mm, ovate-lanceolate, slightly carinate, base not seen, apex long-acuminate, margins denticulate to serrulate, teeth 7–21 μ m long (Fig. 11E). Epidermis of both dorsal and ventral sporophylls not preserved. *Sporangia* ellipsoid, 380–400 \times 190–230 μ m (Fig. 11D). *Microspores* 28–30 μ m in diam., surface not seen (Fig. 11D).

Remarks — Our morphological analysis of images provided by Li & al. (2022), together with new photomicrographs of the type specimen, revealed that there are several discrepancies between the specimen and the original description of the taxon. We have, therefore, emended the diagnosis of *Selaginella cretacea* and provided a new and improved description, which includes also the morphology of the axillary trophophylls and the sporophyll-ptyx of the dorsal sporophylls.

This fossil-taxon is very similar to *Selaginella grimaldii* and *S. ohlhoffiorum* in sharing the presence of

serrulate-denticulate trophophyll and sporophyll margins. However, it differs from *S. grimaldii* in its distant and predominantly oblong ventral trophophylls, (Fig. 11E) and from *S. ohlhoffiorum* in its short strobili (up to 3.2 mm long) and ellipsoid sporangia (see remarks under *S. grimaldii* for further discussion).

The fossil displays morphological similarities to some extant species with bilateral resupinate strobili, including *Selaginella decipiens*, *S. miniatospora*, *S. monospora*, *S. tenera* and *S. trichophylla*. They all share the general shape, type of margins and arrangement of sporophylls and the presence of a sporophyll-ptyx in the dorsal sporophylls (Dixit 1992; Zhang & al. 2013). They can be differentiated by features such as presence of a complete sporophyll-ptyx and details in the shapes of the ventral trophophylls. For example, *S. monospora* and *S. trichophylla* have carinate trophophylls and dorsal sporophylls with a complete sporophyll-ptyx (Zhang & al. 2013). In contrast, *S. cretacea* has non-carinate trophophylls (Fig. 11E, F) and dorsal sporophylls with an incomplete

sporophyll-ptyx (Fig. 1E; 11C). *Selaginella decipiens* differs from *S. cretacea* in having asymmetric ventral trophophylls, with the acroscopic base strongly enlarged, broader and sometimes overlapping the branches (Zhang & al. 2013). *Selaginella miniatospora* and *S. tenera* have ventral trophophylls with an asymmetric base and a dilated basal acroscopic side (Dixit 1992), whereas *S. cretacea* has symmetric ventral trophophylls. Additionally, *S. tenera* has contiguous ventral trophophylls at the branches, which are sometimes imbricate (Dixit 1992) and thus different from the pattern of distant ventral trophophylls seen in the fossil.

Selaginella longifimbriata A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.21998 [Fig. 12], Geoscientific Collection of the University of Göttingen. – Fig. 1F; 12 (only specimen available).

Diagnosis — Strobili terminal, bilateral, dorsiventrally complanate. Dorsal sporophylls imbricate, ovate, apex acute to obtuse, margins slightly denticulate; sporophyll-ptyx incomplete, narrow, margins ciliate. Ventral sporophylls imbricate, adpressed, nearly orbicular, apex rounded, margins long-ciliate. Microspores distally rugulate.

Description — *Rhizophores*, *branches* and *trophophylls* not preserved. *Strobili* terminal, compact, bilateral, dorsiventrally complanate, 11.0–11.8 × 2.4–2.6 mm (Fig. 12A, B). *Sporophylls* dimorphic. *Dorsal sporophylls* imbricate, ascending, c. 40 per strobilus, 1.7–2.1 × 0.4–0.6 mm, ovate, non-carinate, base not seen, apex acute to obtuse, margins slightly denticulate; sporophyll-ptyx incomplete, narrow, ciliate at margins, cilia 80–160 µm long (Fig. 1F; 12C). *Ventral sporophylls* imbricate, adpressed, symmetric, c. 40 per strobilus, 0.7–1.0 × 0.6–0.8 mm, nearly orbicular, non-carinate, base not seen, apex rounded, margins long-ciliate, cilia 100–500 µm long (Fig. 1F; 12D, E). Epidermis of ventral sporophylls composed of elongate cells, with long axes orientated uniformly parallel to long axis of sporophyll. *Sporangia* suborbicular, 380–520 × 480–640 µm. *Microspores* 20–30 µm in diam., distally rugulate (Fig. 12F, G).

Remarks — Although vegetative leaves are not preserved in *Selaginella longifimbriata*, we presume that it possessed resupinate strobili (see remarks under *S. minutissima*).

Selaginella longifimbriata differs from all other Kachin *Selaginella* fossils with bilateral strobili in its large-sized strobili with non-carinate dorsal sporophylls and distally rounded ventral sporophylls with long-ciliate margins (Fig. 1F; 12C–E). Co-occurring with this species in the same amber piece is the holotype specimen of the fern *Cystodium sorbifoloides* L. Regalado & al. described previously by Regalado & al. (2017a).

Selaginella burbidgei Baker, a present-day species endemic to Borneo, resembles *S. longifimbriata* in several structural features, including strobili more than 13 mm long, acute, nearly entire dorsal sporophylls and strongly ciliate ventral sporophylls (Baker 1885; Van Alderwerelt van Rosenburgh 1915). However, *S. longifimbriata* is clearly distinguished from *S. burbidgei* by having nearly orbicular, distally rounded, non-carinate ventral sporophylls (Fig. 1F; 12D, E), in contrast to long-cuspidate and prominently carinate ventral sporophylls in *S. burbidgei*.

Etymology — The specific epithet is derived from the Latin words *longus*: long, and *fimbriatus*: fringed. It refers to the margin of the ventral sporophylls from which long, slender processes extend.

Selaginella patrickmuelleri A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.22000 [Fig. 13], Geoscientific Collection of the University of Göttingen. – Fig. 1G; 13 (only specimen available).

Diagnosis — Strobilus terminal, compact, bilateral, dorsiventrally complanate. Dorsal sporophylls close, ascending, conduplicate, ovate-lanceolate, carinate, apex acute, margins dentate; sporophyll-ptyx incomplete, slightly dentate. Ventral sporophylls imbricate, adpressed, peltate, broadly ovate, strongly carinate, apex attenuate, base rounded, margins sparsely long ciliate. Sporangia suborbicular. Megaspores proximally rugulate-reticulate. Microspores distally and proximally rugulate.

Description — *Rhizophores*, *branches* and *trophophylls* not preserved. *Strobilus* terminal, compact, bilateral, dorsiventrally complanate, 3.5 × 2 mm (Fig. 13A). *Sporophylls* dimorphic. *Dorsal sporophylls* close, ascending, spreading, 13 in only available strobilus, 0.9–1.3 × 0.3–0.6 mm, conduplicate, ovate-lanceolate, carinate, base not seen, apex acute, margins dentate, teeth 25–40 µm long (Fig. 1G; 13B, C); sporophyll-ptyx incomplete, slightly dentate, with teeth similar in size to those of margins (Fig. 1G; 13B, C). *Ventral sporophylls* imbricate, adpressed, peltate, 11 in only available strobilus, 0.8–1.1 × 0.4–0.5 mm, broadly ovate, strongly carinate, base rounded, apex attenuate, margins widely spaced long ciliate, cilia 75–125 µm long (Fig. 1G; 13D). Epidermis of ventral sporophylls with elongate cells, with long axes orientated uniformly parallel to carina (Fig. 13D). *Sporangia* suborbicular, 280–380 × 440–500 µm, composed of uniform isodiametric cells with thick anticlinal walls (Fig. 13E). *Megaspore* (only one preserved) c. 200 µm in diam., proximally rugulate-reticulate (Fig. 13F). *Microspores* 25–30 µm in diam., distally and proximally rugulate (Fig. 13G, H).

Remarks — Vegetative leaves are not preserved in this

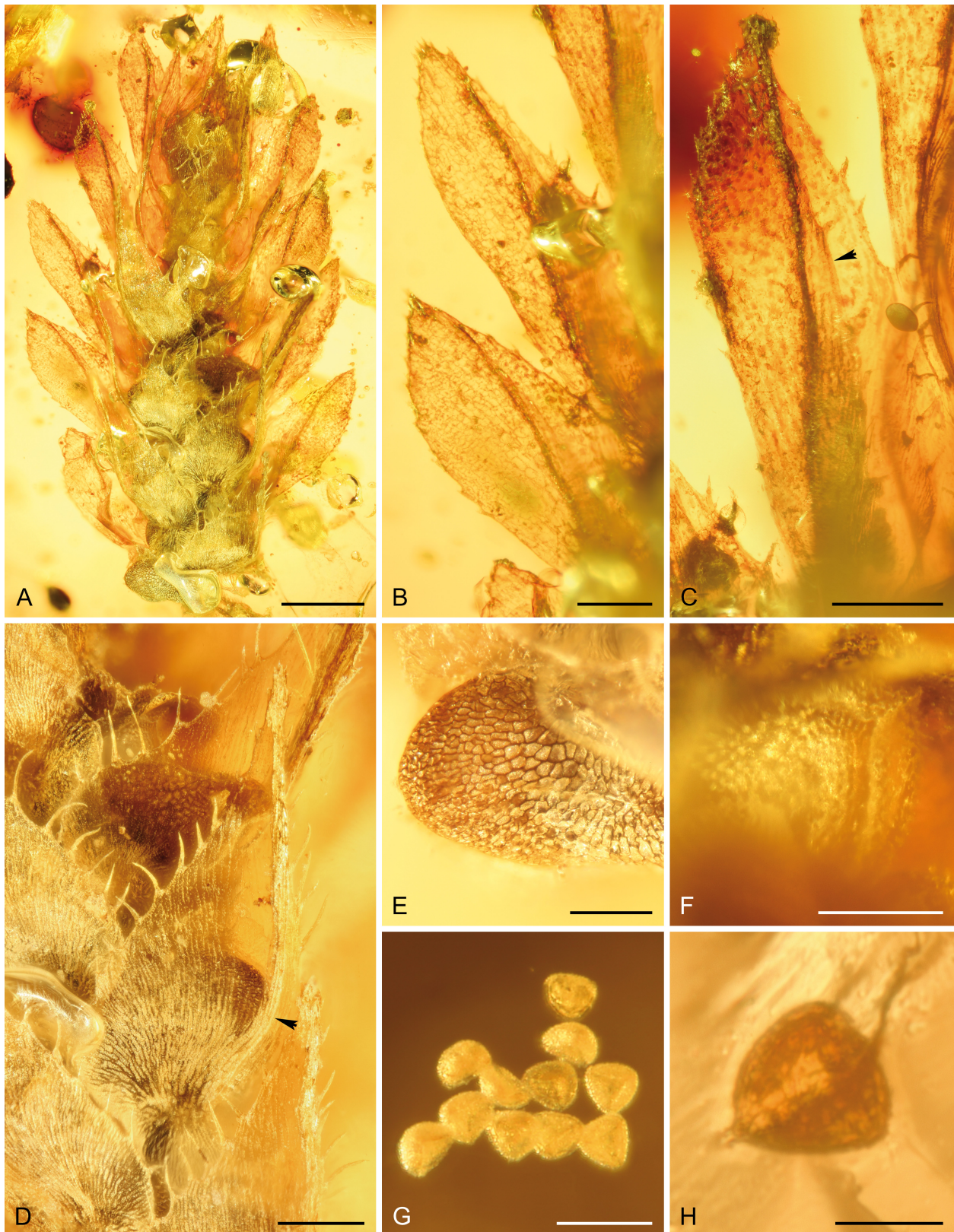


Fig. 13. Holotype of *Selaginella patrickmuelleri* from Kachin amber (GZG.BST.22000). – A: ventral view of bilateral strobilus; B, C: dorsal sporophylls in ventral view showing incomplete sporophyll-ptyx (arrowhead); D: ventral sporophyll with ciliate margins and carina (arrowhead); E: sporangium; F: proximal surface of megaspore; G: microspores; H: proximal surface of microspore. – Scale bars: A = 500 μm ; B–D = 200 μm ; E, F = 100 μm ; G = 50 μm ; H = 20 μm .

fossil, but we presume that *Selaginella patrickmuelleri* possessed resupinate strobili (see remarks under *S. minutissima*).

Among the fossil-taxa with bilateral resupinate strobili that have a sporophyll-ptyx in the dorsal sporophylls and ventral sporophylls with long-ciliate margins, this species closely resembles *Selaginella wangxinii*. They both are characterized by close, ovate-lanceolate dorsal sporophylls, which are acute at the apex and dentate at the margins, and possess a dentate sporophyll-ptyx and broadly ovate ventral sporophylls, which are attenuate at the apex, sparsely ciliate at the margins and strongly carinate. However, the two taxa differ from each other in the size of the strobili, the shape of the sporophyll-ptyx and the ornamentation of the megaspores. *Selaginella patrickmuelleri* has strobili less than 4 mm long, dorsal sporophylls with an incomplete sporophyll-ptyx and megaspores rugulate-reticulate in the proximal surface (Fig. 1G; 13B, C, F), whereas *S. wangxinii* is characterized by strobili 5–6 mm long, dorsal sporophylls with a nearly complete sporophyll-ptyx and megaspores proximally echinate (Fig. 1H; 14D, F, J).

Identification of extant *Selaginella* species is usually based on combinations of characters from both the vegetative and reproductive parts of the plant. As the vegetative part of this fossil remains unknown, we found several extant species with morphological similarities to the fossil. Among the Asian, Australasian and Pacific species of *Selaginella*, 13 taxa closely resemble *S. patrickmuelleri* by having ovate-ciliate ventral sporophylls, including *S. amblyphylla* Alston from China, Myanmar and Thailand (Zhang & al. 2013), *S. bisulcata* Spring from Bhutan, India, Indonesia (Java), Myanmar, Nepal, Thailand and Vietnam (Zhang & al. 2013; Fraser-Jenkins & al. 2017; Shalimov & al. 2019), *S. chaetoloma* Alston, endemic to China (Zhang & al. 2013), *S. chrysocaulos* (Hooker & Greville) Spring, widely distributed in China, India, Pakistan, Nepal and SE Asia (Zhang & al. 2013; Fraser-Jenkins & al. 2017; Shalimov & al. 2019), *S. chrysorrhizos* Spring from Bhutan, India, Nepal and SE Asia (Fraser-Jenkins & al. 2017; Shalimov & al. 2019), *S. ciliaris* (Retz.) Spring, widely distributed in Asia, Australasia and the Pacific islands (Zhang & al. 2013; Fraser-Jenkins & al. 2017; Shalimov & al. 2019), *S. elegantissima* Warb., endemic to Sulawesi (Van Alderwerelt van Rosenburgh 1915), *S. pennata* (D. Don) Spring from China, India, Myanmar, Nepal and Thailand (Zhang & al. 2013; Fraser-Jenkins & al. 2017; Shalimov & al. 2019), *S. proniflora* (Lam.) Baker, endemic to S and peninsular India (Dixit 1992; Fraser-Jenkins & al. 2017), *S. reticulata* (Hook. & Grev.) Spring from Bangladesh, Bhutan, India, Myanmar and Nepal (Dixit 1992; Fraser-Jenkins & al. 2017; Shalimov & al. 2019), *S. subdiaphana* (Wall. ex Hook. & Grev.) Spring, from Bhutan, India, Nepal and Pakistan (Fraser-Jenkins & al. 2017; Shalimov & al. 2019, Irfan & al. 2021) and *S. weinlandii* Hieron. and *S. zahnii* Hieron., both endemic to New Guinea (Van Alderwerelt

van Rosenburgh 1915). However, most of these taxa differ from the fossil in the shape of the sporophyll apex, the margins of the sporophyll-ptyx and sporophylls and the ornamentation of the mega- and microspores. For example, *S. amblyphylla*, *S. bisulcata*, *S. chaetoloma*, *S. chrysocaulos*, *S. proniflora* and *S. reticulata* have ciliate dorsal sporophylls (at least in the acroscopic side) and also a ciliate sporophyll-ptyx (Dixit 1992; Zhang & al. 2013; Shalimov & al. 2019). *Selaginella weinlandii* and *S. zahnii* have dorsal sporophylls with ciliate margins, at least in the basal portions, and a ciliate sporophyll-ptyx (Van Alderwerelt van Rosenburgh 1915). In contrast, *S. patrickmuelleri* has dentate dorsal sporophylls and a dentate sporophyll-ptyx (Fig. 1G; 13B, C). *Selaginella pennata* has non-carinate ventral sporophylls (Zhang & al. 2013) and verrucate megaspores (Zhou & al. 2015a), whereas *S. patrickmuelleri* has strongly carinate ventral sporophylls and rugulate-reticulate megaspores (Fig. 1G; 13D, F). Finally, the arrangement and shape of the sporophylls in *S. chrysorrhizos*, *S. ciliaris*, *S. elegantissima* and *S. subdiaphana* are very similar to those seen in the fossil. However, there are also some differences, in that *S. ciliaris* has a clearly ciliate sporophyll-ptyx (Dixit 1992; Zhang & al. 2013; Johari & Singh 2017) and baculate microspores (Zhou & al. 2015a). The sporophyll-ptyx of *S. elegantissima* is mostly entire or with a few sparse marginal teeth and its microspores are verrucate (Van Alderwerelt van Rosenburgh 1915). *Selaginella chrysorrhizos* and *S. subdiaphana* have verrucate mega- and microspores (Dixit 1992; Shalimov & al. 2019; Irfan & al. 2021). By contrast, the sporophyll-ptyx of the fossil is dentate and the microspores are usually rugulate (Fig. 1G; 13B, C, H).

Etymology — The specific epithet honours Patrick Müller (Zweibrücken, Germany), for his generous support of our work and collaboration on Kachin amber inclusions over many years and for continuously making new amber inclusions available for study.

Selaginella wangxinii A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: PB23101 [Fig. 14], Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. — Fig. 1H; 14 (only specimen available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Dorsal trophophylls distant, adpressed, lanceolate, non-carinate, base decurrent, apex aristate, margins sparsely dentate. Ventral trophophylls distant, spreading, ovate-lanceolate, non-carinate, apex acute to obtuse, margins sparsely denticulate to dentate. Strobili terminal, compact, bilateral, dorsiventrally somewhat complanate, resupinate. Dorsal sporophylls close, ascending, conduplicate, lanceolate, carinate, base slightly decurrent, apex attenuate, margins sparsely dentate to sometimes ciliate at distal basiscope and acroscopic sides; sporophyll-

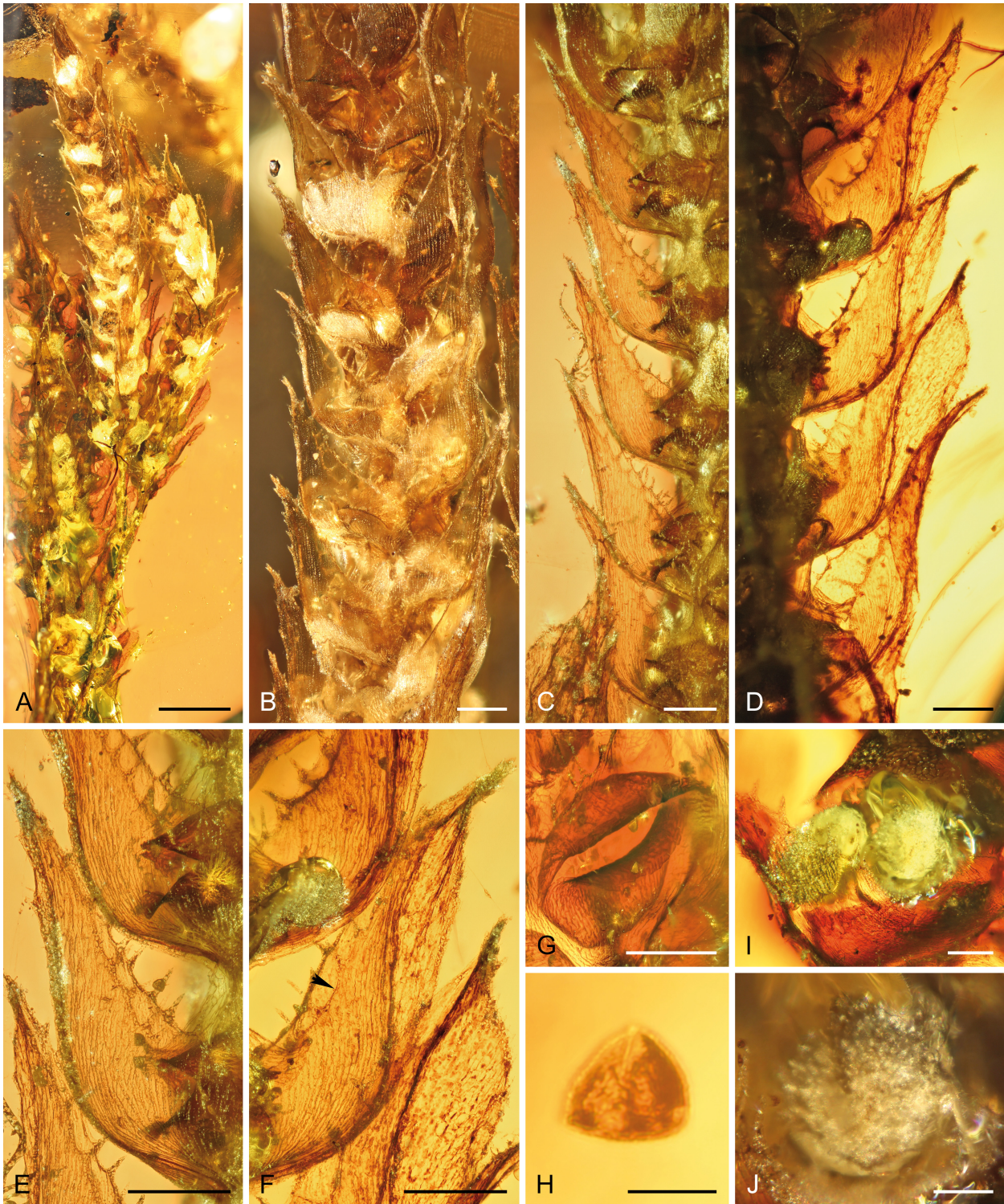


Fig. 14. Holotype of *Selaginella wangxinii* from Kachin amber (PB23101). – A: overview of shoot portion with several strobili; B: central portion of bilateral strobilus showing two rows of ventral sporophylls; C, E: ventral sporophylls in lateral view; D, F: dorsal sporophylls showing sporophyll-ptyx (arrowhead); G: sporangium; H: proximal surface of microspore; I: two megaspores in sporangium; J: proximal surface of megaspore. – Scale bars: A = 1 mm; B–F = 200 µm; G, I = 100 µm; H = 20 µm; J = 50 µm.

ptyx nearly complete, dentate. Ventral sporophylls close, adpressed, broadly ovate-lanceolate, carinate, apex attenuate, margins sparsely dentate-ciliate. Sporangia suborbicular. Megaspores proximally echinate. Microspores proximally rugulate.

Description — *Rhizophores* not preserved. *Axes* compressed. *Trophophylls* dimorphic. *Axillary trophophylls* not preserved. *Dorsal trophophylls* distant, adpressed, 0.7–0.8 × 0.3–0.4 mm, lanceolate, non-carinate, base decurrent apex aristate, margins sparsely dentate, teeth

20–40 µm long. *Ventral trophophylls* distant, spreading, ascending, 0.8–1.2 × 0.4–0.5 mm, ovate-lanceolate, non-carinate, base not seen, apex acute to obtuse, margins sparsely denticulate to dentate, teeth 10–50 µm long. Epidermis of dorsal and ventral trophophylls poorly preserved. *Strobili* terminal, compact, bilateral, dorsiventrally somewhat complanate, resupinate 5.4–6.3 × 0.8–1.2 mm (Fig. 14A, B). *Sporophylls* dimorphic. *Dorsal sporophylls* close, ascending, 24–26 per strobilus, 0.9–1.1 × 0.2–0.3 mm, lanceolate, non-carinate, base slightly decurrent, acute at apex, margins sparsely dentate to sometimes ciliate at distal basiscopic and acroscopic sides, teeth or cilia 40–100 µm long (Fig. 1H; 14D, F); sporophyll-ptyx nearly complete, with margins dentate-ciliate similar to sporophyll margins (Fig. 14D, F). *Ventral sporophylls* close, adpressed, 26–28 per strobilus, 0.9–1.0 × 0.3–0.4 mm, broadly ovate-lanceolate, carinate, base not seen, apex attenuate, margins sparsely dentate or short-ciliate, cilia 20–80 µm long (Fig. 1H; 14C, E). Epidermis cells of ventral sporophylls elongate, with long axes orientated uniformly parallel to carina (Fig. 14E). *Sporangia* suborbicular, 250–350 × 280–320 µm, with uniform isodiametric cells bearing thick anticlinal walls (Fig. 14G). At least 1 megasporangium containing 2 megaspores present proximally in strobilus (Fig. 14I). *Megaspores* 160–190 µm in diam., proximally echinate (Fig. 14J). *Microspores* 25–30 µm in diam., proximally rugulate (Fig. 14H).

Remarks — The overall appearance and morphology of strobili and sporophylls of *Selaginella wangxinii* are very similar to those seen in *S. patrickmuelleri*. Both taxa share the general shape of the dorsal and ventral sporophylls, the shape of the sporophyll apices, bases and margins and the presence of carinae. However, they differ from each other in the size of the strobili, the shape of the sporophyll-ptyx and ornamentation of the megaspores (see remarks under *S. patrickmuelleri* for details).

The morphology of *Selaginella wangxinii* resembles three extant species, namely *S. chrysocaulos*, *S. ciliaris* and *S. elegantissima*, all of which are characterized by dorsal sporophylls with an incomplete sporophyll-ptyx (ending midway to apex) (Dixit 1992; Zhang & al. 2013; Johari & Singh 2017), which is mostly entire-margined in *S. elegantissima* (Van Alderwerelt van Rosenburgh 1915), whereas the fossil has a nearly complete sporophyll-ptyx with dentate-ciliate margins (Fig. 1H; 14D, F). Additionally, *S. chrysocaulos* and *S. elegantissima* have verrucate microspore ornamentations (Van Alderwerelt van Rosenburgh 1915; Zhou & al. 2015a) and *S. ciliaris* has baculate microspores, which differ from the rugulate pattern observed in the fossil (Fig. 14H).

Etymology — The specific epithet honours Professor Xin Wang (Nanjing), who discovered the fossil in the collection of the Nanjing Institute of Geology and Palaeontology.

Selaginella ciliifera A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.21997 [Fig. 15], Geoscientific Collection of the University of Göttingen. – Fig. 1I; 15, 16 (two specimens available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Axillary trophophylls symmetric, ovate, non-carinate, base short-truncate, apex acute to obtuse, margins ciliate to long-ciliate. Dorsal trophophylls distant, adpressed, symmetric to somewhat asymmetric, ovate, non-carinate, base decurrent, apex acute to obtuse, margins sparsely ciliate. Ventral trophophylls distant, ascending, symmetric, oblong to ovate, non-carinate, ligulate, base truncate, apex obtuse to acute, sometimes rounded, margins dentate on basiscopic and distal acroscopic sides, sparsely long-ciliate on medial and proximal acroscopic side. Ligule situated on proximal acroscopic side, close to leaf insertion to branch, ovate. Strobili terminal, compact, bilateral, dorsiventrally complanate, resupinate. Sporophylls dimorphic. Dorsal sporophylls close to distant, spreading, ascending, asymmetric, lanceolate, slightly carinate, base inequilateral, basiscopic side straight, acroscopic side rounded, apex obtuse to acute, sometimes rounded, margins mostly ciliate, occasionally dentate; sporophyll-ptyx incomplete, narrow at base, with ciliate margins. Ventral sporophylls close, adpressed, ovate to broadly ovate, carinate, apex acute to obtuse, margins long-ciliate. Sporangia nearly orbicular. Microspores distally and proximally rugulate.

Description — *Rhizophores* not preserved. Axes compressed. *Trophophylls* dimorphic (Fig. 15A, B; 16A). *Axillary trophophylls* symmetric, 0.9–1.3 × 0.4–0.5 mm, ovate, non-carinate, base short-truncate, apex acute to obtuse, margins ciliate to long-ciliate, cilia 60–220 µm long. *Dorsal trophophylls* distant, adpressed, symmetric to somewhat asymmetric, 0.9–1.3 × 0.4–0.6 mm, ovate, non-carinate, base decurrent, apex acute to obtuse, margins sparsely ciliate, cilia 40–140 µm long. *Ventral trophophylls* distant, spreading, ascending, symmetric, 1.2–2.7 × 0.7–1.0 mm, oblong to ovate, non-carinate, ligulate, base truncate, apex obtuse to acute, sometimes rounded, margins dentate on basiscopic and distal acroscopic sides, sparsely long-ciliate on medial and proximal acroscopic side, teeth 20–50 µm long, cilia 70–150 µm long (Fig. 15A, B, F). *Ligule* situated on proximal acroscopic side, close to leaf insertion to branch, 120 × 60 µm, ovate (Fig. 15G). *Strobili* terminal, compact, bilateral, dorsiventrally complanate, resupinate, 3.4–5.4 × 2.6–3.2 mm (Fig. 15A, B; 16A). *Sporophylls* dimorphic. *Dorsal sporophylls* close to distant, spreading, ascending, asymmetric, conduplicate, 10 or 11 per strobilus (–14 in JZC-Bu-004), 1.5–2.4 × 0.4–0.8 mm, lanceolate, slightly carinate, base inequilateral, basiscopic side straight, acroscopic side rounded, apex obtuse to acute, sometimes rounded, margins mostly ciliate, occasion-

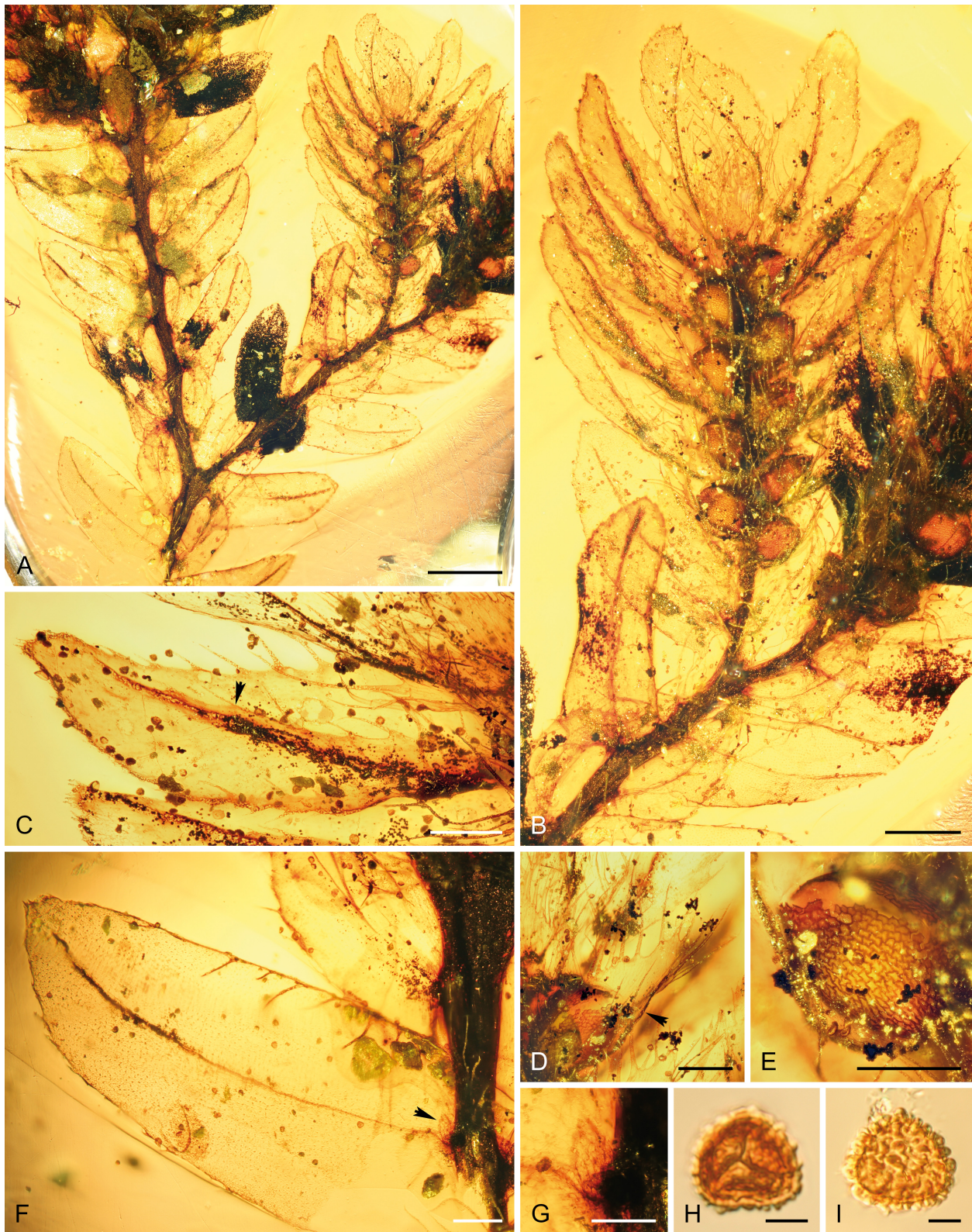


Fig. 15. Holotype of *Selaginella ciliifera* from Kachin amber (GZG.BST.21997). – A: ventral overview; B: ventral view of bilateral strobilus and adjacent branch with adpressed dorsal and ascending ventral trophophylls; C: dorsal sporophyll in ventral view showing incomplete sporophyll-ptyx (arrowhead); D: ventral sporophyll with carina (arrowhead); E: sporangium; F: ventral trophophyll with ligule (arrowhead) near leaf base; G: ligule; H, I: microspores, H: proximal surface, I: distal surface. – Scale bars: A = 1 mm; B = 500 μ m; C–F = 200 μ m; G = 100 μ m; H, I = 10 μ m.

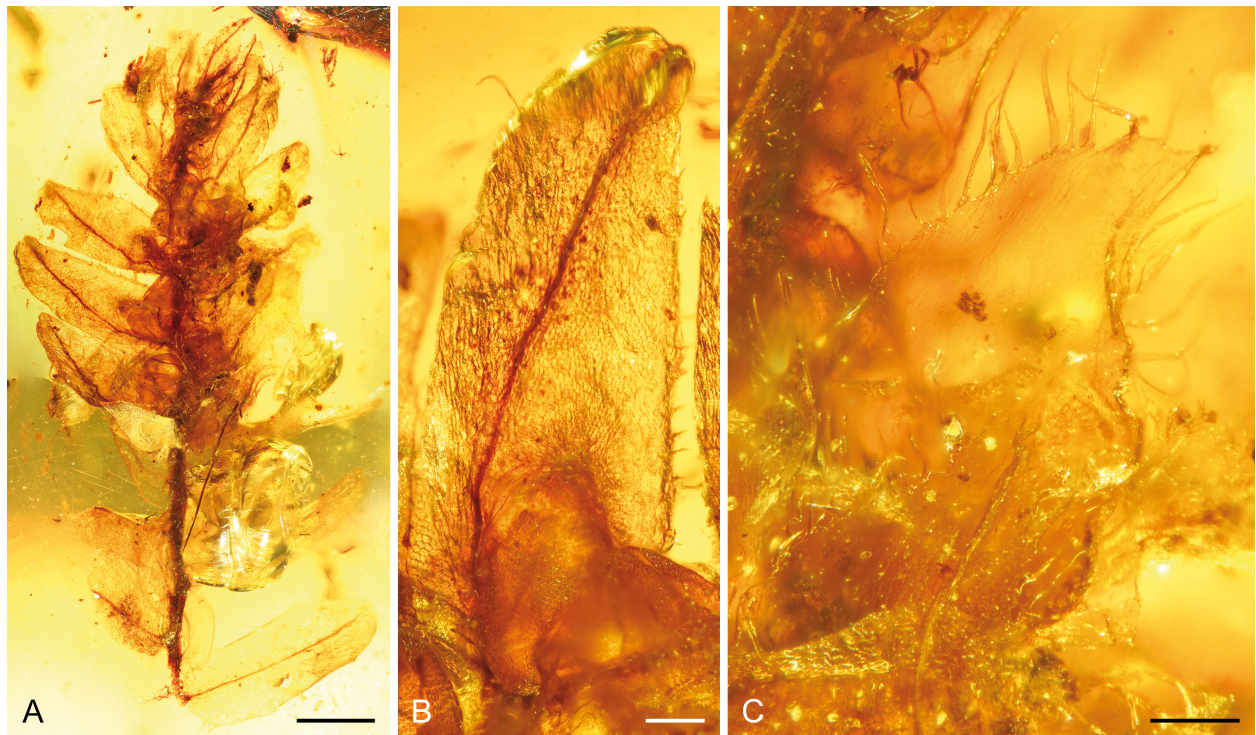


Fig. 16. *Selaginella ciliifera* from Kachin amber (JZC-Bu-004). – A: ventral view of bilateral strobilus and adjacent, adpressed dorsal and ascending ventral trophophylls; B: dorsal sporophyll in ventral view; C: ventral sporophyll. – Scale bars: A = 1 mm; B, C = 200 μ m.

ally dentate, teeth or cilia 40–340 μ m long (Fig. 11; 15C; 16B); sporophyll-ptyx incomplete, narrow at base, with ciliate margins, cilia similar in size to those on sporophyll margins (Fig. 11; 15C). Epidermis of dorsal sporophylls composed of uniform isodiametric cells. *Ventral sporophylls* close, adpressed, conduplicate, 9 or 10 per strobilus, 0.7–1.7 \times 0.4–0.8 mm, ovate to broadly ovate, carinate, base not seen, apex acute to obtuse, margins long-ciliate, cilia 90–520 μ m long (Fig. 11; 15D; 16C). Epidermis of ventral sporophylls composed of elongate cells, with long axes orientated at angles of 15–30° to carina. *Sporangia* nearly orbicular, 300–480 \times 340–500 μ m, composed of uniform isodiametric cells with thick anticlinal walls (Fig. 15E). *Microspores* 25–35 μ m in diam., distally and proximally rugulate (Fig. 15H, I).

Remarks — The specimen selected here as the holotype (GZG.BST.21997) shows the presence of a basal ligule on the adaxial leaf surface (Fig. 15F, G) that is considered a synapomorphy of the heterosporous lycophytes (i.e. *Selaginellaceae* and *Isoetaceae* and extinct relatives).

This fossil-taxon closely resembles the general morphology of *Selaginella villosa* in possessing conspicuously ciliate trophophylls and sporophylls. Despite these similarities, the two taxa differ in the shape of the sporophyll-ptyx of the dorsal sporophylls and the apex of the ventral sporophylls. *Selaginella ciliifera* has dorsal sporophylls with a sporophyll-ptyx that is narrow at the base and ventral sporophylls that are acute to obtuse at the apex (Fig. 11; 15C, D), whereas *S. villosa* possesses

dorsal sporophylls with a sporophyll-ptyx that is broadly enlarged at the base, forming an auricle, and ventral sporophylls that are acuminate at the apex (Fig. 11; Fig. 17C–E).

Four present-day taxa share with *Selaginella ciliifera* the strobili with ciliate dorsal and ventral sporophylls, including *S. albociliata* P. S. Wang, endemic to China (Zhang & al. 2013), *S. apoensis* Hieron. from the Philippines (Mindanao), Sulawesi and Maluku (Seram) (Van Alderwerelt van Rosenburgh 1915), *S. longiciliata* Hieron., from New Guinea to Australia (N Queensland) (Van Alderwerelt van Rosenburgh 1915; Jermy & Holmes 1998) and *S. macroblepharis* Warb., endemic to New Guinea (Van Alderwerelt van Rosenburgh 1915). *Selaginella apoensis*, *S. longiciliata* and *S. macroblepharis* differ from *S. ciliifera* by having ventral sporophylls that are acuminate to aristate at the apex and microspores with smooth surfaces (Van Alderwerelt van Rosenburgh 1915). The fossil has ventral sporophylls that are acute to obtuse at the apex and rugulate microspores (Fig. 11; 15H, I). *Selaginella apoensis* differs from the fossil in several other structural aspects, namely dorsal and ventral sporophylls that are similar in size and shape (distinctly different in *S. ciliifera*) and longer strobili (c. 20 mm long). Strobili of the fossil-taxon are hardly more than 5.5 mm long. *Selaginella albociliata* differs from the fossil by having longer strobili (6–10 mm long), dorsal sporophylls that are acuminate at the apex and verrucate microspores (Wang 1990). In contrast, *S. ciliifera* has shorter strobili, dorsal sporophylls that are obtuse to

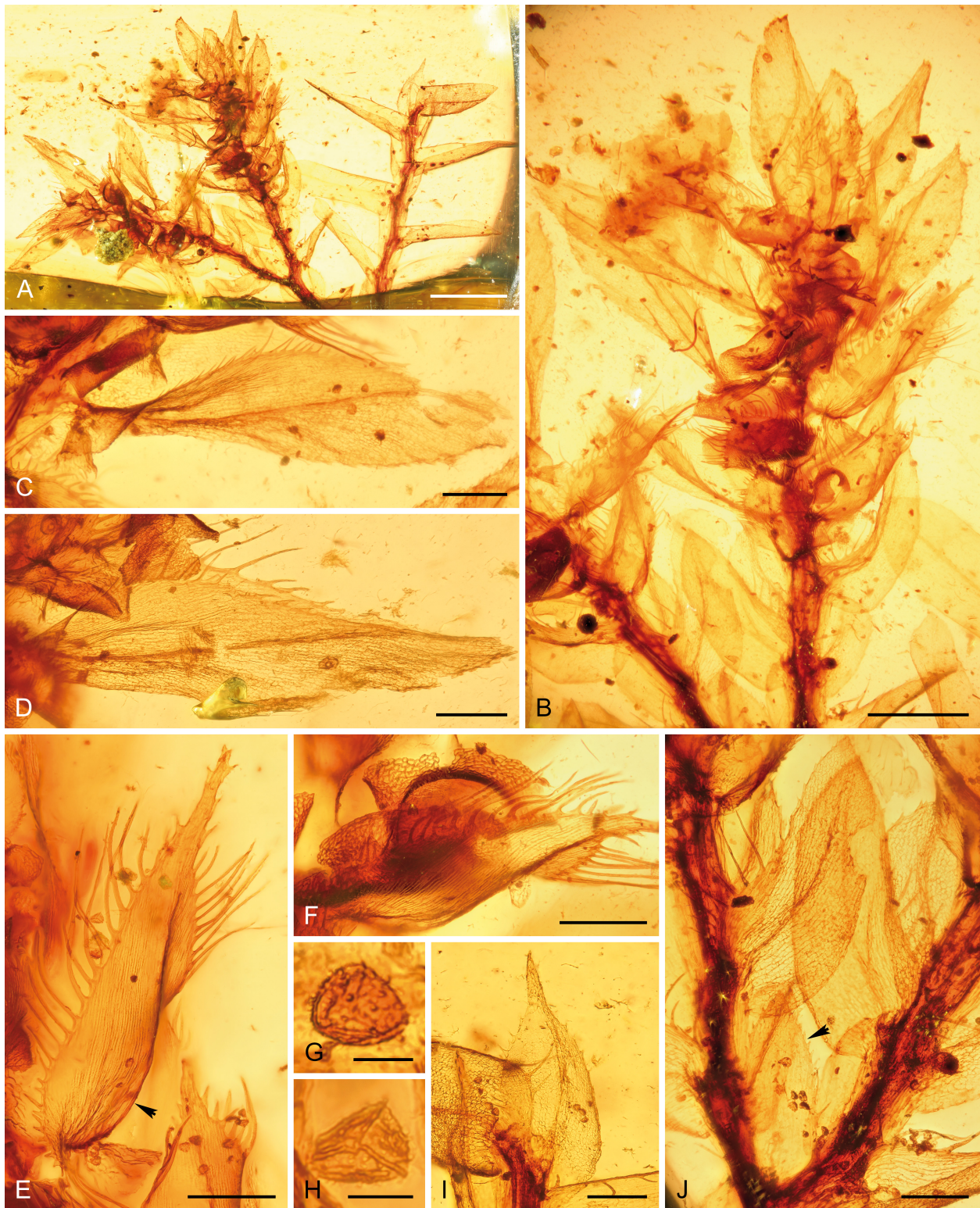


Fig. 17. *Selaginella villosa* from Kachin amber (GZG.BST.22028). Fertile shoot portion designated as holotype. – A: ventral overview; B: ventral view of bilateral strobilus and adjacent adpressed dorsal and ascending ventral trophophylls; C, D: dorsal sporophylls in ventral view showing incomplete sporophyll-ptyx; E: ventral sporophyll with carina (arrowhead); F: ventral sporophyll and sporangium; G, H: microspores, G: distal surface, H: proximal surface; I: dorsal trophophyll; J: ventral view of axillary (arrowhead) and ventral trophophylls. – Scale bars: A = 1 mm; B = 500 μ m; C–F, I, J = 200 μ m; G, H = 20 μ m.

acute at the apex and rugulate microspores (Fig. 15B, C, H, I; 16B).

Etymology — The specific epithet is derived from the Latin words *cilium*: hair-like process, and *ferre*: to bear, carry. It refers to the numerous and long ciliae which occur especially at the margins of the sporophylls.

Additional specimens studied — JZC-Bu-004, American Museum of Natural History (Fig. 16), PB25339, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Selaginella villosa A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.22028 [Fig. 17], Geoscientific Collection of the University of Göttingen. — Fig. 1J; 17 (only specimen available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Axillary trophophylls symmetric, oblong, non-carinate, base rounded, apex acute, distal and medial margins denticulate, proximal margins ciliate. Dorsal trophophylls close to distant, adpressed, symmetric, oblong-ovate or elliptic, slightly carinate, base decurrent, apex, margins mostly denticulate, ciliate only on proximal acroscopic side. Ventral trophophylls close to distant, spreading, symmetric, oblong, non-carinate, base rounded to truncate, apex acute or less frequently obtuse, margins mostly dentate-denticulate, proximal acroscopic margin ciliate. Strobili terminal, compact, bilateral, dorsiventrally complanate, resupinate. Sporophylls dimorphic. Dorsal sporophylls close, ascending, asymmetric, ovate-lanceolate, non-carinate, base inequilateral, basispic side straight, acroscopic side rounded, apex acute to attenuate, basispic margin serrulate, acroscopic margin ciliate; sporophyll-ptyx incomplete, broadly enlarged at base forming an auricle, ciliate on distal margins and dentate-denticulate in auricle. Ventral sporophylls close, conduplicate, ovate, carinate, base decurrent, apex acuminate, margins long-ciliate, dentate in apical portion. Sporangia suborbicular. Microspores distally and proximally rugulate.

Description — *Rhizophores* not preserved. Axes compressed. *Trophophylls* dimorphic (Fig. 17A, B, J). *Axillary trophophylls* symmetric, c. 0.6×0.2 mm, oblong, non-carinate, base rounded, apex acute, distal and medial margins denticulate, proximal margins ciliate, teeth $10\text{--}20$ μm long, cilia $50\text{--}80$ μm long (Fig. 17J). *Dorsal trophophylls* close to distant, adpressed, symmetric, $0.5\text{--}0.9 \times 0.2\text{--}0.4$ mm, oblong-ovate or elliptic, slightly carinate, base decurrent, apex acuminate, margins mostly denticulate, ciliate only on proximal acroscopic margin, teeth $15\text{--}20$ μm long, cilia $50\text{--}70$ μm long (Fig. 17I). *Ventral trophophylls* close to distant, spreading, symmetric, $1.2\text{--}1.7 \times 0.4\text{--}0.5$ mm, oblong, non-carinate,

base rounded to truncate, apex acute or less frequently obtuse, margins mostly dentate-denticulate, proximal acroscopic margin ciliate, teeth $10\text{--}30$ μm long, cilia $50\text{--}150$ μm long (Fig. 17J). *Strobili* terminal, compact, bilateral, dorsiventrally complanate, resupinate, $2.6\text{--}3.0 \times 1.9\text{--}2.3$ mm (Fig. 17A, B). *Sporophylls* dimorphic. *Dorsal sporophylls* close, ascending, asymmetric, 7 or 8 per strobilus, $1.4\text{--}1.6 \times 0.3\text{--}0.4$ mm, ovate-lanceolate, non-carinate, base inequilateral, basispic side straight, acroscopic side rounded, apex acute to attenuate, basispic margin serrulate, acroscopic margin ciliate, teeth $10\text{--}20$ μm long, cilia $150\text{--}320$ μm long (Fig. 1J; 17C, D); sporophyll-ptyx incomplete, broadly enlarged at base forming an auricle, ciliate on distal margins and dentate-denticulate in auricle, teeth $10\text{--}30$ μm long, cilia < 100 μm long (Fig. 1J; 17C). Epidermis of dorsal sporophylls formed by uniform isodiametric cells. *Ventral sporophylls* close, conduplicate, 7–9 per strobilus, $0.7\text{--}1.1 \times 0.4\text{--}0.5$ mm, ovate, carinate, base decurrent, apex acuminate, margins long-ciliate, dentate in apical portion, teeth $20\text{--}50$ μm long, cilia $70\text{--}450$ μm long (Fig. 1J; 17E). Epidermis of ventral sporophylls with elongate cells, with long axes orientated uniformly parallel to carina. *Sporangia* suborbicular, $300\text{--}450 \times 450\text{--}480$ μm , composed of uniform isodiametric cells with thick anticlinal walls (Fig. 13F). *Microspores* $30\text{--}35$ μm in diam., distally and proximally rugulate (Fig. 17G, H).

Remarks — Among the Kachin *Selaginella* inclusions detailed in this study, *S. villosa* most closely resembles *S. ciliifera* because both taxa have ciliate trophophylls and sporophylls. However, differences in the shape of sporophyll-ptyx of the dorsal sporophylls and in the apex of ventral sporophylls discriminate these two taxa (see remarks under *S. ciliifera* for details).

The extant *Selaginella albociliata*, *S. apoensis*, *S. longiciliata* and *S. macroblepharis* share with the fossil the general morphology of the dorsal and ventral sporophylls that are conspicuously ciliate, particularly the ventral sporophylls with acuminate apices (Van Alderwerelt van Rosenburgh 1915; Wang 1990). However, the fossil differs from these taxa in that it has rugulate microspores (Fig. 17G, H), rather than verrucate or smooth microspores as in the extant species (Van Alderwerelt van Rosenburgh 1915; Jermy & Holmes 1998; Wang 1990). Furthermore, *S. albociliata* and *S. apoensis* have longer strobili ($6\text{--}20$ mm long) (Van Alderwerelt van Rosenburgh 1915; Wang 1990), whereas *S. villosa* produces strobili only up to 3 mm long.

Etymology — The specific epithet is derived from the Latin word *villosus*: having many long, weak hairs. It refers to the numerous long ciliae, especially those seen on the ventral sporophylls.

Selaginella subg. *Ericetorum* Jermy in Fern Gaz. 13: 117. 1986. — Type: *Selaginella uliginosa* (Labill.) Spring.

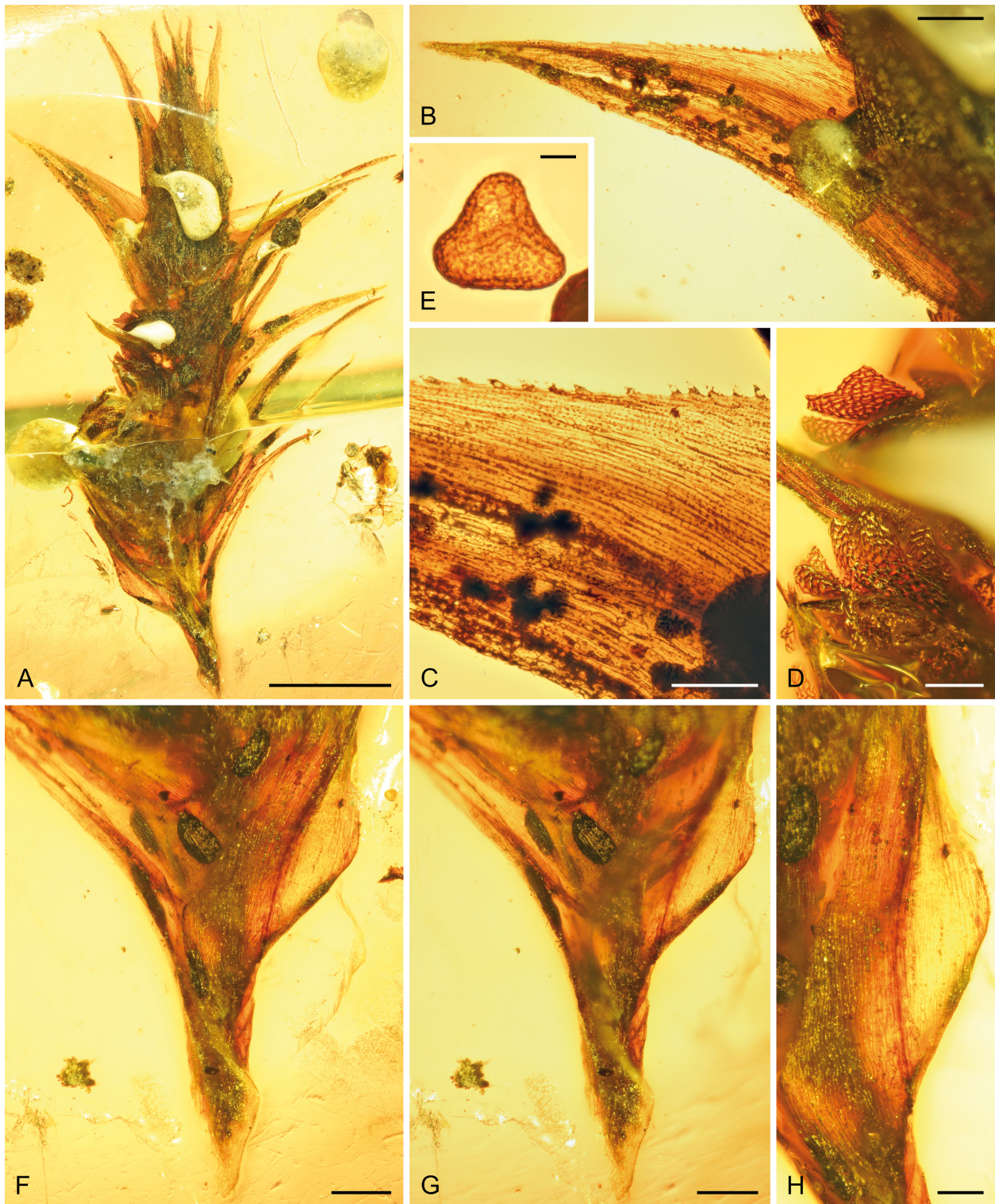


Fig. 18. Holotype of *Selaginella wunderlichiana* from Kachin amber (GZG.BST.22029). – A: overview; B: sporophyll; C: sporophyll epidermis; D: sporangia; E: proximal surface of microspore; F, G: decussately arranged monomorphic trophophylls; H: central portion of trophophyll. – Scale bars: A = 1 mm; B, F, G = 200 µm; C, D, H = 100 µm; E = 10 µm.

Selaginella wunderlichiana A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.22029 [Fig. 18], Geoscientific Collection of the University of Göttingen. – Fig. 2A; 18 (only specimen available).

Diagnosis — Axes compressed. Trophophylls monomorphic, decussately arranged, adpressed, close to imbricate, lanceolate, apex long-attenuate, base amplexicaul, margins erose. Strobilus terminal, compact, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate,

conduplicate, lanceolate, carinate, carina sparsely denticulate as in the sporophyll margins, base rounded, apex attenuate, margins sparsely denticulate. Sporangia suborbicular, with uniform isodiametric cells with thick anticlinal walls. Microspores proximally verrucate.

Description — Axes compressed. *Trophophylls* monomorphic, 2.5–2.6 × 0.3–0.4 mm, decussately arranged (Fig. 18F, G), adpressed, close to imbricate, lanceolate, slightly carinate, base amplexicaul apex long-attenuate, (Fig. 18A, F, G), margins erose or slightly denticulate, teeth < 10 µm long. Epidermis of elongate cells, with long axes orientated uniformly parallel to long axis of trophophyll (Fig. 18H). *Strobilus* terminal, compact, tetrastichous, quadrangular, 4.8 × 3.2 mm (Fig. 18A). *Sporophylls* monomorphic, imbricate, conduplicate, c. 32 in only available strobilus, 1.8–2.0 × 0.4–0.5 mm, lanceolate, carinate, carina sparsely denticulate as in the sporophyll margins, apex attenuate, base rounded, margins sparsely denticulate, teeth 10–20 µm long, sporophyll-ptyx absent (Fig. 2A; 18B, C). Epidermis of sporophylls composed of elongate cells, with long axes orientated uniformly parallel to carina (Fig. 18C). *Sporangia* suborbicular, 350 × 250 µm, with uniform isodiametric cells with thick anticlinal walls (Fig. 18D). Microspores 25–35 µm in diam., proximally verrucate (Fig. 18E).

Remarks — Among the Kachin *Selaginella* inclusions, only *S. wunderlichiana* and *S. isophylla* possess monomorphic trophophylls. Both species differ from one another in the overall shape of trophophylls and in the shape of the leaf apices, bases and margins. *Selaginella wunderlichiana* has lanceolate trophophylls that are attenuate at the apex, amplexicaul at the base and erose at the margins (Fig. 18A, F–H), whereas *S. isophylla* has ovate trophophylls that are short-acuminate at the apex, peltate at the base and short-ciliate at the basal acroscopic margin, sparsely dentate at the medial margins and nearly entire at the distal margins (Fig. 19E–G).

This fossil-taxon is assigned here to *Selaginella* subg. *Ericetorum* because it shares the decussately arranged, monomorphic trophophylls with extant species belonging to this subgenus (Jermy 1986a; Schulz & al. 2013). *Selaginella* subg. *Ericetorum* presently comprises eight extant species, namely *S. aboriginalis* C. Schulz & Homberg, *S. gracillima* (Kuntze) Spring ex Salomon and *S. uliginosa* (Labill.) Spring, all from Australia and Tasmania (Jermy & Holmes 1998; Schulz & al. 2013), *S. lyallii* (Hook. & Grev.) Spring, *S. moratii* W. Hagemann & Rauh and *S. pectinata* Spring, all endemic to Madagascar (Stefanović & al. 1997; Smith & al. 2016), *S. pygmaea* (Kaulf.) Alston, from South Africa (Schulz & al. 2013) and *S. royenii* Alston, endemic to New Guinea (Schulz & al. 2013).

The fossil has decussately arranged monomorphic trophophylls (Fig. 18A, F–H) and thus is clearly different from *Selaginella lyallii*, *S. moratii* and *S. pectinata*,

which all have dimorphic trophophylls arranged in two rows of smaller dorsal trophophylls and two rows of larger ventral trophophylls (Stefanović & al. 1997). The extant *S. aboriginalis*, *S. gracillima*, *S. pygmaea*, *S. royenii* and *S. uliginosa* differ from *S. wunderlichiana* by having nearly entire-margined vegetative leaves (Jermy & Holmes 1998) and microspores with mostly smooth or echinate (in *S. pygmaea*), rarely gemmate or verrucate, proximal surfaces (Schulz & al. 2013). In contrast, *S. wunderlichiana* has trophophylls with erose or slightly denticulate margins (teeth < 10 µm long) and microspores with a verrucate proximal surface (Fig. 18E).

Etymology — The specific epithet honours Jörg Wunderlich (Hirschberg an der Bergstraße, Germany), who generously supported our research by making amber inclusions available for study.

Selaginella isophylla A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.22005 [Fig. 19], Geoscientific Collection of the University of Göttingen. – Fig. 2B; 19 (only specimen available).

Diagnosis — Axes compressed. Trophophylls monomorphic, close to imbricate, arranged in 4 rows, symmetric, ovate, non-carinate, base peltate, rounded or truncate, apex short-acuminate, basal acroscopic margin short-ciliate, medial margins sparsely dentate, distal margins close to apex nearly entire. Strobilus terminal, compact, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate, conduplicate, lanceolate, carinate, carina smooth, apex long-attenuate, medial and proximal margins denticulate, distal margins close to apex nearly entire, sporophyll-ptyx absent.

Description — *Rhizophores* not preserved. Axes compressed. *Trophophylls* monomorphic, close to imbricate, arranged in four rows, symmetric, ascending, 0.8–1.2 × 0.4–0.5 mm, ovate, non-carinate, base peltate, rounded or truncate, apex short-acuminate, basal acroscopic margin short-ciliate, medial margins sparsely dentate, distal margins close to apex nearly entire, teeth or cilia 25–50 µm long (Fig. 19A, E–G). Epidermis cells polygonal, sometimes elongate, with long axes orientated uniformly parallel to long axis of trophophyll. *Strobilus* terminal, compact, tetrastichous, quadrangular, 2.6 × 1.2 mm (Fig. 19A, B). *Sporophylls* monomorphic, imbricate, conduplicate, 20 in only available strobilus, 1.0–1.2 × 0.4–0.6 mm, lanceolate, carinate, carina smooth, base not seen, apex long-attenuate, medial and proximal margins denticulate, distal margins close to apex nearly entire, teeth 10–20 µm long, sporophyll-ptyx absent (Fig. 2B; 19C, D). Epidermis of sporophylls similar to trophophyll epidermis. *Sporangia* immature, obscure, not seen.

Remarks — The monomorphic trophophylls arranged

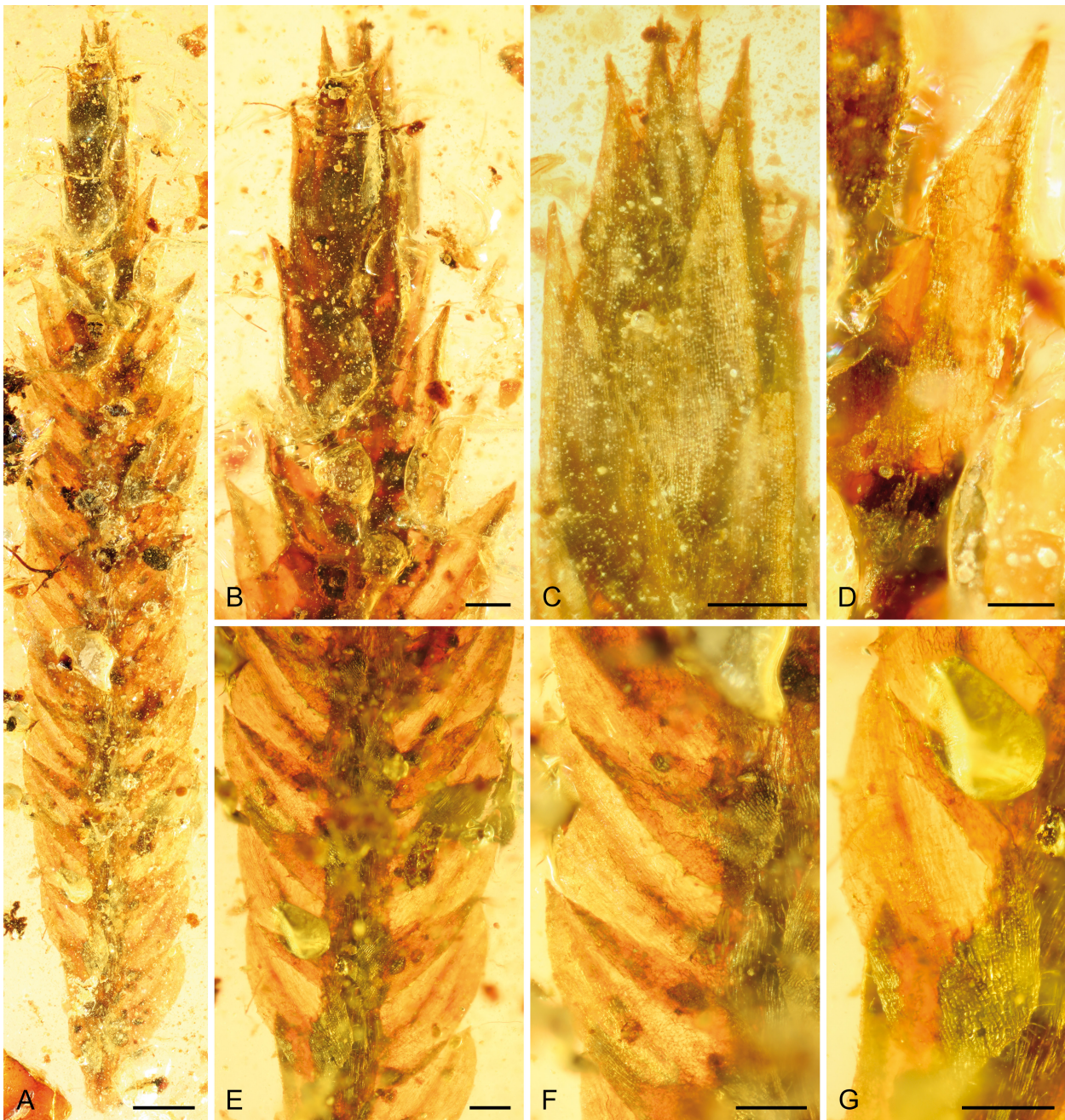


Fig. 19. Holotype of *Selaginella isophylla* from Kachin amber (GZG.BST.22005). – A: overview; B: strobilus; C, D: sporophylls; E: branch with four rows of monomorphic trophophylls; F, G: monomorphic trophophylls. – Scale bars: A = 500 µm; B, C, E–G = 200 µm; D = 100 µm.

in rows and monomorphic sporophylls arranged in tetra-stichous quadrangular strobili are suggestive of affinities of this fossil to *Selaginella* subg. *Ericetorum*. The trophophylls are typically decussately arranged (at least in the proximal portions of the plant) in all members of this subgenus (Jermy 1986a; Schulz & al. 2013). However, because the attachment sites of the leaves are not clearly visible in the amber fossil it is impossible to assess whether the vegetative leaves are truly decussately arranged in the fossil. Other diagnostic characters of *S.* subg. *Ericetorum*, such as megaspores with wing-like laesurae and that are highly porose at the proximal pole

(Schulz & al. 2013; Weststrand & Korall 2016b), could also not be positively identified in the fossil due to the immature stage of the preserved strobilus.

Among extant members of *Selaginella* subg. *Ericetorum*, *S. isophylla* can be easily distinguished from *S. lyallii*, *S. moratii* and *S. pectinata* by its monomorphic trophophylls, which are dimorphic in the three extant species (Stefanović & al. 1997). Additionally, the presence of trophophylls that are short-ciliate on their basal acroscopic margin and sparsely dentate in both basispic and acroscopic margins of the middle portion (Fig. 19F, G) discriminate the fossil from several extant spe-

cies such as *S. aboriginalis*, *S. gracillima*, *S. pygmaea*, *S. royenii* and *S. uliginosa*, which all have nearly entire-margined vegetative leaves (Jermy & Holmes 1998).

Etymology — The specific epithet is derived from the Greek words *isos*: equal and *phyllon*: leaf. It emphasizes that the species is isophyllous in its vegetative part, i.e. possessing monomorphic trophophylls.

Fossils with unresolved infrageneric affinities

Subgenus not determined

Selaginella aurita A. R. Schmidt & L. Regalado, **sp. nov.**
Holotype: GZG.BST.22001 [Fig. 20], Geoscientific Collection of the University of Göttingen. — Fig. 2C; 20, 21 (two specimens available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Dorsal trophophylls distant, adpressed, lanceolate, non-carinate, apex long-aristate, margins entire. Ventral trophophylls distant, ascending, symmetric, oblong-lanceolate, apex acute, base short-truncate, margins nearly entire or sparsely denticulate, non-carinate. Strobilus terminal, compact, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate, somewhat conduplicate, lanceolate, carinate, base auriculate on acroscopic side, apex acute, margins sharply dentate; sporophyll-ptyx nearly complete, auriculate at base, with dentate margins similar to sporophyll margins. Sporangia suborbicular. Microspores proximally rugulate.

Description — *Rhizophores* not preserved. Axes compressed. *Trophophylls* dimorphic (Fig. 20A, F; 21). *Axillary trophophylls* not preserved. *Dorsal trophophylls* distant, adpressed, 1.0–1.6 × 0.2–0.6 mm, lanceolate, non-carinate, base not seen, apex long-aristate, margins entire (Fig. 21C, D). *Ventral trophophylls* distant, ascending, symmetric, 1.5–1.8 × 0.4–0.7 mm, oblong-lanceolate, non-carinate, base short-truncate, apex acute, margins nearly entire or sparsely denticulate (Fig. 20F; 21B). Epidermis of dorsal and ventral trophophylls poorly preserved. *Strobilus* terminal, compact, tetrastichous, quadrangular, 7.5 × 3.5 mm (Fig. 20A, B). *Sporophylls* monomorphic, imbricate, somewhat conduplicate, c. 72 in only available strobilus, 1.5–1.9 × 0.5–0.9 mm, lanceolate, carinate, base auriculate on acroscopic side, apex acute, margins sharply dentate, teeth 5–35 µm long (Fig. 2C; 20C–E); sporophyll-ptyx nearly complete, auriculate at base, with dentate margins similar to sporophyll margins (Fig. 2C; 20C–E). Sporophyll epidermis poorly preserved. *Sporangia* suborbicular, 500–740 × 400–560 µm, composed of uniform isodiametric cells with very thick anticlinal walls (Fig. 20G). *Microspores* 20–30 µm in diam., proximally rugulate (Fig. 20H, I).

Remarks — *Selaginella aurita* differs from all other

Kachin *Selaginella* fossils by its monomorphic sporophylls, which are acroscopically auriculate (Fig. 2C; 20C–E). Furthermore, *S. aurita* is the only form with quadrangular strobili bearing a sporophyll-ptyx on monomorphic sporophylls (Fig. 2C; 20C–E). This structure is present in all four rows of sporophylls. In our comparisons to extant species from Asia, Australasia and Africa, we could not find any morphology that is particularly close to that seen in this fossil-species.

Etymology — The specific epithet is derived from the Latin word *auritus*: eared, auriculate, and refers to the acroscopic base of the sporophyll and to the sporophyll-ptyx.

Additional specimens studied — PB25336, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Fig. 21).

Selaginella amplexicaulis A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: PB23160 [Fig. 22], Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. — Fig. 2D; 22 (only specimen available).

Diagnosis — Strobilus compact, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate, conduplicate, broadly ovate, strongly carinate, carina smooth, base biauriculate, apex acuminate, margins entire to erose, sporophyll-ptyx absent. Sporangia suborbicular.

Description — *Rhizophores*, *branches* and *trophophylls* not preserved. *Strobilus* compact, tetrastichous, quadrangular, 5.3 × 1.4 mm (Fig. 22A). *Sporophylls* monomorphic, imbricate, conduplicate, 60 in only available strobilus, 0.7–0.9 × 0.4–0.6 mm, broadly ovate, strongly carinate, carina smooth, apex acuminate, base biauriculate, margins entire to erose, sporophyll-ptyx absent (Fig. 2D; 22B, C). Epidermis of sporophylls composed of elongate cells, with long axes orientated uniformly parallel to carina. *Sporangia* suborbicular, 320–370 × 350–600 µm, with uniform isodiametric cells with thick anticlinal walls (Fig. 22D). *Microspores* 20–25 µm in diam., probably immature, proximally psilate (Fig. 22E).

Remarks — The sporophylls, which are acuminate at apex and entire to erose at the margins (Fig. 2D; 22B, C), discriminate *Selaginella amplexicaulis* from all other Kachin *Selaginella* taxa with quadrangular strobili.

The morphology of the sporophylls and strobili of *Selaginella amplexicaulis* is very similar to that of four modern species, namely *S. inaequalifolia* (Hook. & Grev.) Spring, native to India, Myanmar and Thailand (Dixit 1992; Fraser-Jenkins & al. 2017), *S. ornithopodioides* (L.) Spring, endemic to Sri Lanka (Dixit 1992; Fraser-Jenkins & al. 2017), *S. trichoclada* Alston, endemic

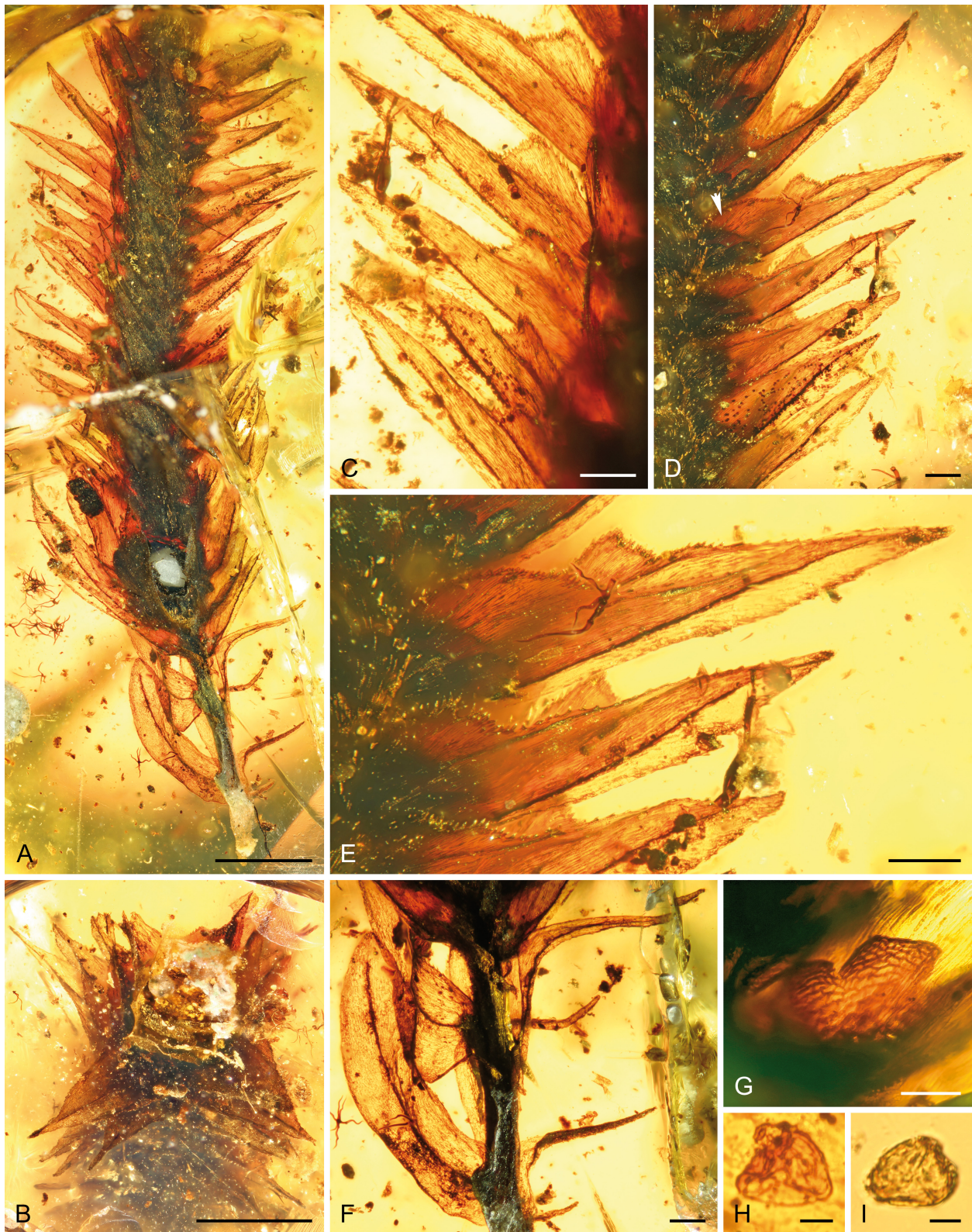


Fig. 20. Holotype of *Selaginella aurita* from Kachin amber (GZG.BST.22001). – A: overview of strobilus and adjacent trophophylls; B: strobilus in slightly oblique top view; C–E: sporophylls showing sporophyll-ptyx (arrowhead); F: dorsal (right) and ventral (left) trophophylls in lateral view; G: sporangium; H, I: proximal surface of microspores. – Scale bars: A, B = 1 mm; C–F = 200 µm; G = 100 µm; H, I = 10 µm.

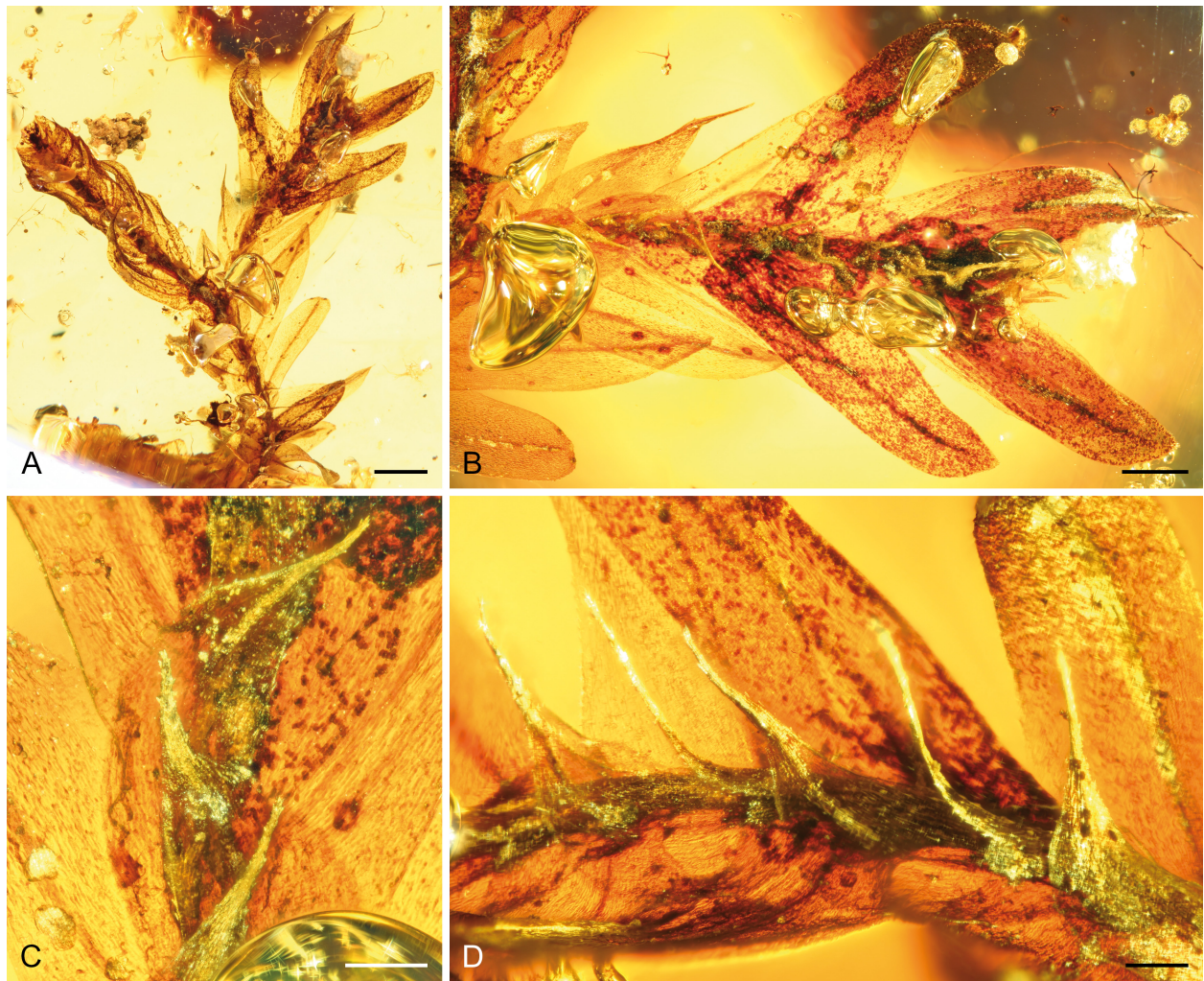


Fig. 21. Sterile *Selaginella aurita* shoot portion from Kachin amber (PB25336). – A: overview of branched specimen; B: trophophylls in dorsal view; C, D: detail of dorsal trophophylls with long-aristate apices. – Scale bars: A = 1 mm; B = 500 µm; C, D = 200 µm.

to China (Zhang & al. 2013) and *S. willdenowii* (Desv.) Baker, from China, India and SE Asia (Dixit 1992; Fraser-Jenkins & al. 2017; Zhang & al. 2013). As the vegetative portion of *S. amplexicaulis* is not preserved, it is difficult to separate it from these extant species. However, there are subtle differences that can be used to distinguish the fossil-taxon. For instance, the extant species all have sporophylls that are obtuse, truncate or rounded at the base (Alston 1932; Dixit 1992; Zhang & al. 2013), in contrast to the auriculate sporophylls of *S. amplexicaulis* (Fig. 2D; 22B, C).

Etymology — The specific epithet is derived from the Latin words *amplexus*: clasping, and *caulis*: stem. It refers to the sporophyll bases clasping the strobilus stem.

Selaginella heinrichsii A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.22004 [Fig. 23], Geoscientific Collection of the University of Göttingen. – Fig. 2E; 23 (only specimen available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Axillary trophophylls symmetric, broadly ovate, non-carinate, base rounded to obtuse, apex acute, margins nearly entire or serrulate. Dorsal trophophylls distant, adpressed, ovate, non-carinate, base slightly decurrent, apex obtuse, margins serrate-serrulate. Ventral trophophylls mostly symmetric, occasionally asymmetric, distant, spreading, ascending, oblong-ovate, non-carinate, base with basiscopic side rounded and acroscopic side truncate, apex obtuse to acute, margins serrate-serrulate. Strobili terminal, tetrastichous, quadrangular. Sporophylls monomorphic, distant, spreading, ascending, conduplicate, ovate, carinate, base exauriculate, apex attenuate, margins profusely denticulate, sporophyll-ptyx absent. Sporangia suborbicular, a single considerably larger sporangium situated at base of strobilus. Microspores proximally psilate.

Description — *Rhizophores* not preserved. *Axes* compressed. *Trophophylls* dimorphic (Fig. 23A, H). *Axillary trophophylls* symmetric, c. 1.4 × 0.8 mm, broadly ovate, non-carinate, base rounded to obtuse, apex acute, mar-

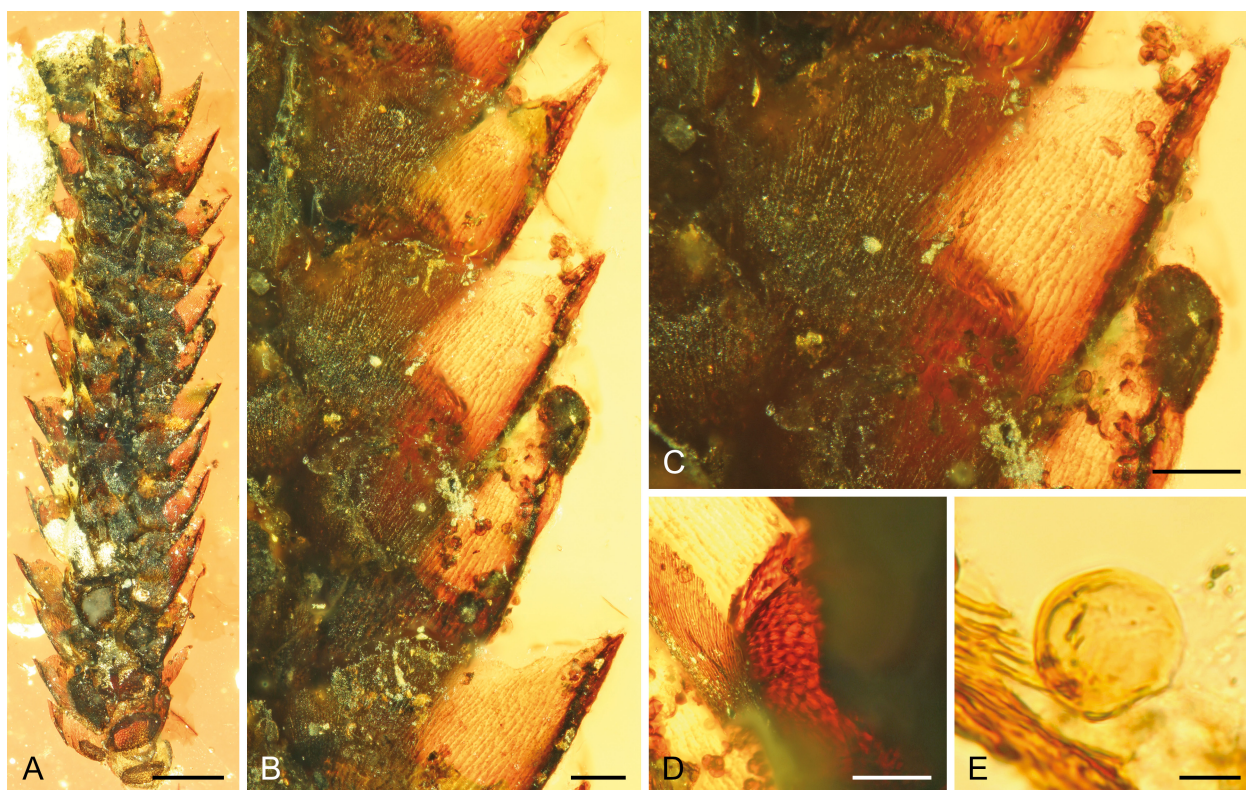


Fig. 22. Holotype of *Selaginella amplexicaulis* from Kachin amber (PB23160). – A: overview of strobilus; B: central portion of strobilus showing sporophylls in lateral view; C: sporophyll; D: portion of sporangium wall; E: proximal surface of microspore. – Scale bars: A = 500 μ m; B–D = 100 μ m; E = 10 μ m.

gins nearly entire or serrulate, teeth ≤ 10 μ m long (Fig. 23H). *Dorsal trophophylls* distant, adpressed, 1.2–1.7 \times 0.5–0.9 mm, ovate, non-carinate, base slightly decurrent, apex obtuse, margins serrate-serrulate, teeth 8–30 μ m long (Fig. 23H). *Ventral trophophylls* mostly symmetric, occasionally asymmetric, distant, spreading, ascending, 1.2–2.3 \times 0.9–1.2 mm, oblong-ovate, non-carinate, base with basispic side rounded and acroscopic side truncate, apex obtuse to acute, margins serrate-serrulate, teeth 10–30 μ m long. Epidermis of dorsal and ventral trophophylls composed of rectangular cells (Fig. 23I). *Strobili* terminal, tetrastichous, quadrangular, c. 6.0 \times 1.8–2.3 mm (Fig. 23A, C). *Sporophylls* monomorphic, distant, spreading, ascending, conduplicate, c. 56 per strobilus, 0.7–1.2 \times 0.5–0.7 mm, largest basal one 1.7–2 \times 1.4–1.5 mm, ovate, carinate, base exauriculate, apex attenuate, margins profusely denticulate, teeth 10–25 μ m long, sporophyll-ptyx absent (Fig. 2E; 23C–E, G). Epidermis of sporophylls composed of elongate cells, with long axes orientated uniformly parallel to carina. *Sporangia* suborbicular, 280–400 \times 450–550 μ m (Fig. 23F), a single considerably larger sporangium situated at base of strobilus 0.8–1.1 \times c. 1.5 mm (Fig. 23G), with uniform isodiametric cells with thick anticlinal walls. *Microspores* 25–30 μ m in diam., proximally psilate (Fig. 23B).

Remarks — *Selaginella heinrichsii* clearly differs from the other fossil *Selaginella* with dimorphic trophophylls,

quadrangular strobili and monomorphic sporophylls in possessing dorsal trophophylls that are apically obtuse and distant sporophylls that are exauriculate at the base (Fig. 2E; 23C–E, G, H).

Two extant species from SE Asia share the gross morphology with *Selaginella heinrichsii* by having oblong, apically obtuse ventral trophophylls, which are denticulate or serrulate at the margins, and quadrangular strobili with monomorphic, ovate sporophylls, the latter acute, apically attenuate or acuminate, abaxially carinate and denticulate at the margins. These species include *S. brooksii* Hieron. from Borneo and *S. lonkobatu* Hieron. & Alderw. from Maluku and Sulawesi (Van Alderwerelt van Rosenburgh 1915). However, both differ from the fossil by having strobili with imbricate sporophylls that are rounded at the base (Van Alderwerelt van Rosenburgh 1915), whereas *S. heinrichsii* has lax strobili with distant sporophylls that are exauriculate at the base (Fig. 2E; 23C–E, G). Additionally, *S. lonkobatu* has dorsal trophophylls that are gradually cuspidate at the apex (Van Alderwerelt van Rosenburgh 1915) in contrast to the obtuse dorsal trophophylls seen in the fossil (Fig. 23H).

Etymology — The specific epithet honours the late Professor Jochen Heinrichs (1969–2018) of Munich, Germany, with whom we discussed the fossils and who expressed excitement when we discovered the first *Selaginella* in Kachin amber.

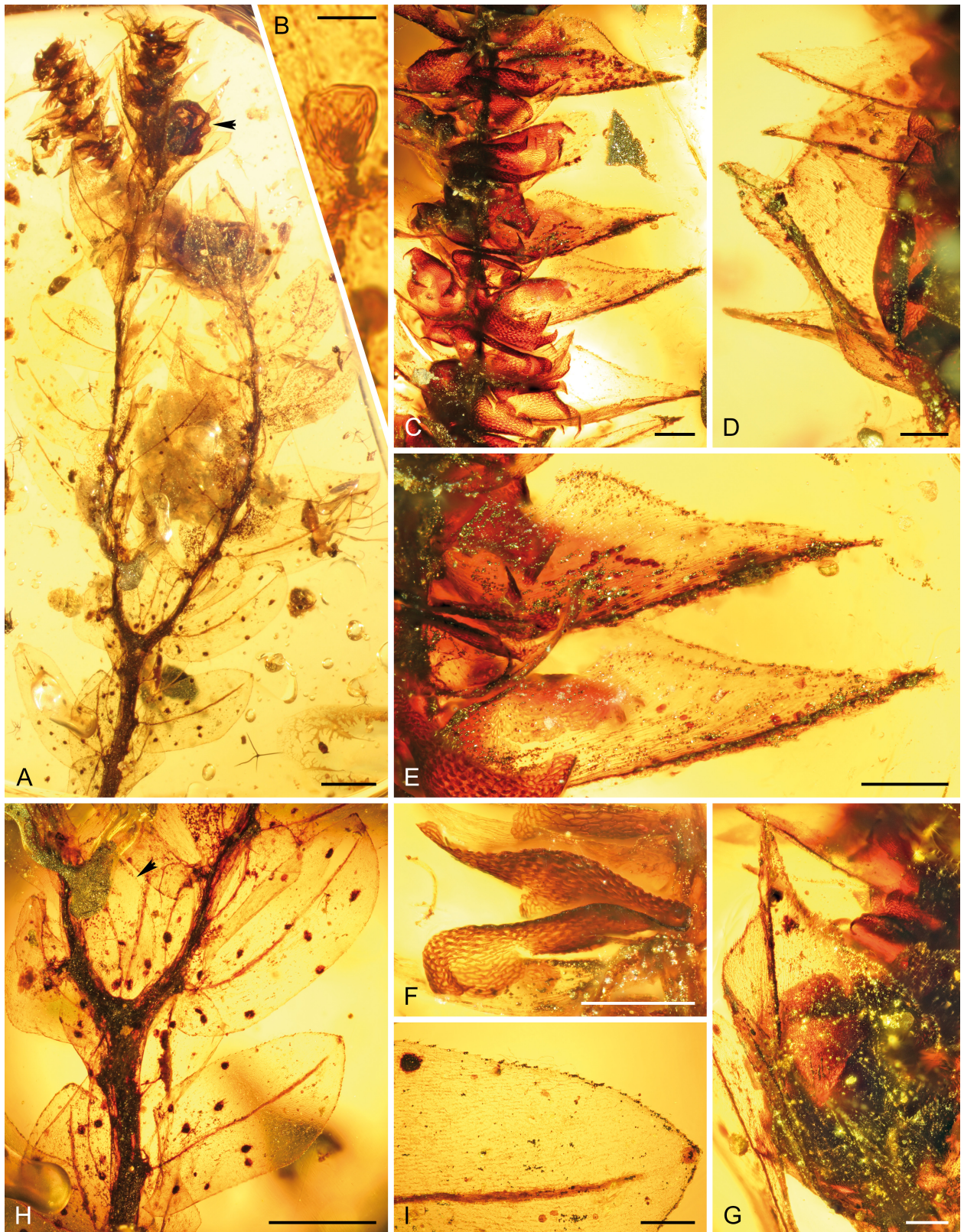


Fig. 23. Holotype of *Selaginella heinrichsii* from Kachin amber (GZG.BST.22004). – A: overview of branched specimen possessing two strobili, arrowhead indicates single large sporangium at base of strobilus; B: proximal surface of microspore; C: central portion of strobilus; D: exceptionally large basal sporophyll (middle) and two additional adjacent sporophylls (above); E: two sporophylls; F: sporangium; G: larger sporophyll and corresponding larger sporangium at base of strobilus; H: trophophylls, arrowhead indicates axillary trophophyll; I: epidermis of ventral trophophyll. – Scale bars: A, H = 1 mm; B = 20 µm; C–G, I = 200 µm.

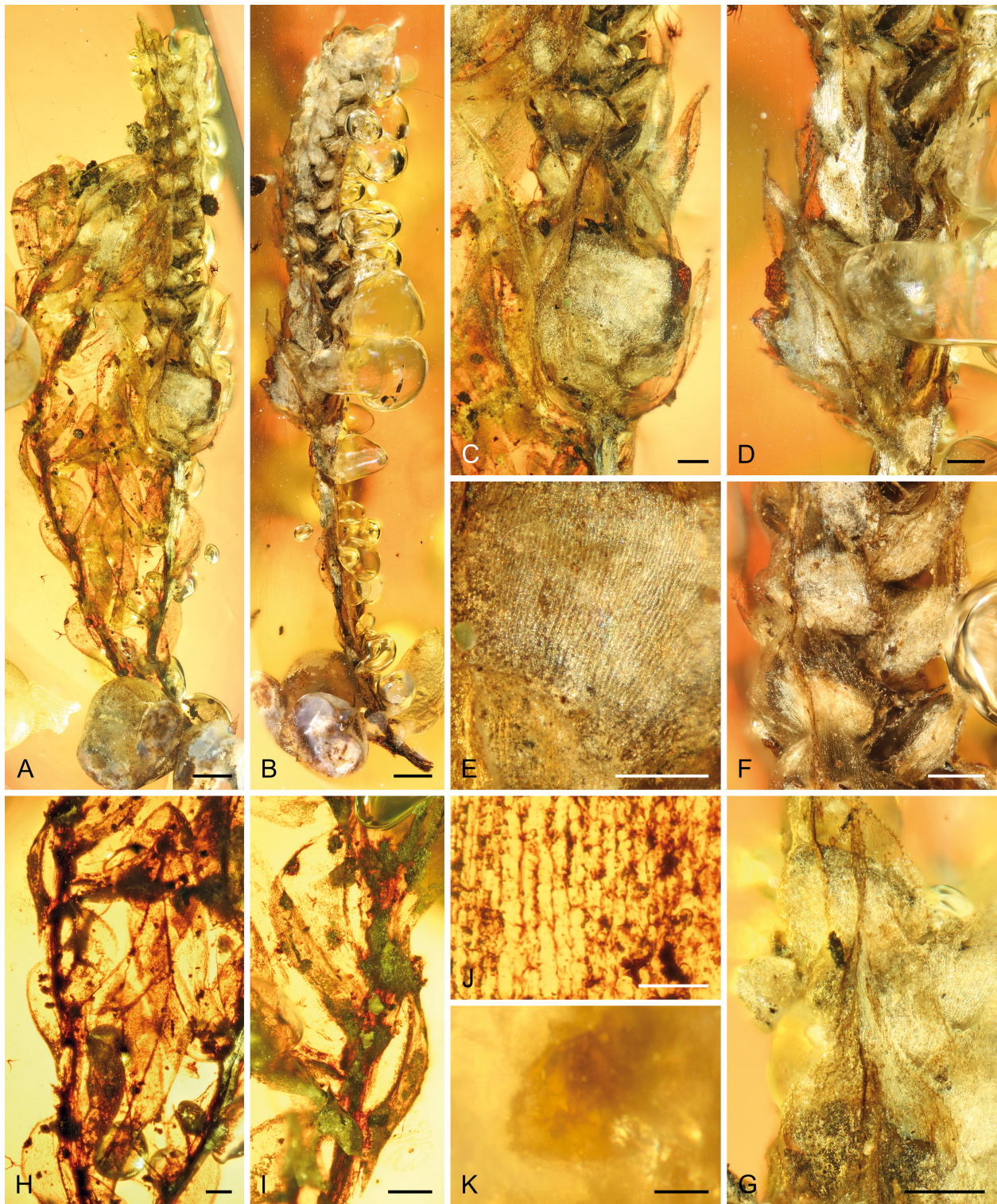


Fig. 24. Holotype of *Selaginella konijnenburgiae* from Kachin amber (GZG.BST.22003). – A, B: overview in dorsal (A) and lateral (B) view; C, D: base of strobilus showing larger sporangium; E: sporophyll epidermis; F, G: sporophylls and sporangia; H, I: dorsal and ventral trophophylls; J: trophophyll epidermis; K: proximal surface of microspore. – Scale bars: A, B = 500 µm; C–I = 200 µm; J = 50 µm; K = 10 µm.

Selaginella konijnenburgiae A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: GZG.BST.22003 [Fig. 24], Geoscientific Collection of the University of Göttingen. – Fig. 2F; 24 (only specimen available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Dorsal trophophylls distant, adpressed, somewhat conduplicate, oblong-lanceolate, slightly carinate, base truncate, apex attenuate to aristate, margins entire to serrulate-denticulate. Ventral trophophylls mostly symmetric, some-

times asymmetric, distant, spreading, ascending, oblong-ovate, non-carinate, base with basiscopic side rounded, acroscopic side truncate, apex obtuse, margins serrulate. Strobilus terminal, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate, broadly ovate, slightly carinate, base rounded, apex attenuate to aristate, margins serrulate-denticulate, sporophyll-ptyx absent. Sporangia suborbicular, a single considerably larger sporangium situated at base of strobilus. Microspores proximally rugulate.

Description — *Rhizophores* not preserved. *Axes* compressed. *Trophophylls* dimorphic (Fig. 24H, I). *Axillary trophophylls* not preserved. *Dorsal trophophylls* distant, adpressed, somewhat conduplicate, 0.5–0.9 × 0.1–0.3 mm, oblong-lanceolate, slightly carinate, base truncate, apex attenuate to aristate, margins entire to serrulate-denticulate, teeth ≤ 10 µm long. *Ventral trophophylls* mostly symmetric, sometimes asymmetric, distant, spreading, ascending, 1.5–2.7 × 0.4–0.9 mm, oblong-ovate, non-carinate, base with basiscopic side rounded, acroscopic side truncate, apex obtuse, margins serrulate, teeth ≤ 10 µm long (Fig. 24H, I). Epidermis of dorsal and ventral trophophylls composed of elongate cells, with long axes orientated uniformly parallel to long axis of trophophyll (Fig. 24J). *Strobilus* terminal, tetrastichous, quadrangular, 5.6 × 1.1 mm (Fig. 24A, B). *Sporophylls* monomorphic, imbricate, 48 in only available strobilus, 0.9–1.1 × 0.4–0.6 mm, broadly ovate, slightly carinate, base rounded, apex attenuate to aristate, margins serrulate-denticulate, teeth 10–25 µm long, sporophyll-ptyx absent (Fig. 2F; 24C, D, F, G). Epidermis of sporophylls is composed of elongate cells, with long axes orientated uniformly parallel to long axis of sporophyll (Fig. 24E). *Sporangia* suborbicular, (300–)460–500 × (260–)280–340 µm, a single considerably larger sporangium situated at base of strobilus 900 × 800 µm, with uniform isodiametric cells with thick anticlinal walls. *Microspores* 25–30 µm in diam., proximally rugulate (Fig. 24K).

Remarks — The presence of a basal sporangium (presumably a megasporangium), protruding and conspicuously larger than all other sporangia, separates *Selaginella konijnenburgiae* from all other *Selaginella* inclusions with quadrangular strobili, with the exception of *S. heinrichsii*. The latter species differs from *S. konijnenburgiae* in its distant sporophylls, which are exauriculate (Fig. 2E). In contrast, *S. konijnenburgiae* has imbricate sporophylls with a rounded base (Fig. 2F).

Three extant species are somewhat similar to the fossil morphology, namely *Selaginella davidii* Franchet, endemic to China (Zhang & al. 2013), *S. kraussiana* (Kunze) A. Braun, from Macaronesia and tropical and S Africa (Quansah 1986; Zhang & al. 2013) and *S. remotifolia* Spring, native to India, China, Indonesia, Japan, Nepal and the Philippines (Van Alderwerelt van Rosenburgh 1915; Dixit 1992; Zhang & al. 2013; Fraser-Jenkins & al. 2017; Shalimov & al. 2019). These species share with *S.*

konijnenburgiae the presence of ovate-lanceolate, long-acuminate or aristate, denticulate dorsal trophophylls, combined with the presence of quadrangular strobili, with ovate, monomorphic sporophylls that are attenuate, apically aristate or acuminate and serrulate or denticulate (Van Alderwerelt van Rosenburgh 1915; Dixit 1992; Zhang & al. 2013; Shalimov & al. 2019). However, the three extant species differ from the fossil in having mostly acute ventral trophophyll margins (Van Alderwerelt van Rosenburgh 1915; Dixit 1992; Zhang & al. 2013; Shalimov & al. 2019), in contrast to the obtuse ventral trophophylls of the fossil. *Selaginella kraussiana* has a densely denticulate carina, whereas *S. konijnenburgiae* has a smooth carina on the abaxial surface of the sporophylls. Additionally, *S. davidii*, *S. kraussiana* and *S. remotifolia* have microspores with an echinate proximal surface (Quansah 1986; Zhou & al. 2015a), whereas *S. konijnenburgiae* has microspores with a rugulate proximal surface (Fig. 24K).

Etymology — The specific epithet honours Professor Johanna H. A. van Konijnenburg-van Cittert (Leiden and Utrecht), for her contributions to the knowledge of fossil free-sporing vascular plants, including *Selaginella*.

***Selaginella ovoidea* A. R. Schmidt & L. Regalado, sp. nov.**

Holotype: AMNH-Bu-KL-8-7 [Fig. 25], American Museum of Natural History. – Fig. 2G; 25 (only specimen available).

Diagnosis — *Axes* compressed. *Trophophylls* dimorphic. *Dorsal trophophylls* close, adpressed, symmetric, ovate, non-carinate, base decurrent, apex aristate, sparsely dentate at margins. *Ventral trophophylls* close, slightly imbricate, spreading, ascending, somewhat asymmetric, ovate, non-carinate, base decurrent, acute at apex, sparsely denticulate to dentate at margins. *Strobilus* terminal, compact, tetrastichous, quadrangular. *Sporophylls* monomorphic, imbricate, adpressed, conduplicate, lanceolate, carinate, base rounded, apex long-attenuate, serrulate at margins, sporophyll-ptyx absent. *Sporangia* ellipsoid or ovoid. *Microspores* in tetrads, distally rugulate.

Description — *Rhizophores* not preserved. *Axes* compressed. *Trophophylls* dimorphic (Fig. 25A, H–J). *Axillary trophophylls* not preserved. *Dorsal trophophylls* close, adpressed, symmetric, 0.6–0.8 × 0.3–0.4 mm, ovate, non-carinate, base decurrent, apex aristate, margins sparsely dentate, teeth 12–35 µm long (Fig. 25I). *Ventral trophophylls* close, slightly imbricate, spreading, ascending, somewhat asymmetric, 1.3–1.5 × 0.5–0.6 mm, ovate, non-carinate, base decurrent, apex acute, margins sparsely denticulate to dentate, teeth 8–40 µm long (Fig. 25H, J). Epidermis of dorsal and ventral trophophylls composed of uniform isodiametric cells (Fig. 25J). *Strobilus* terminal, compact, tetrastichous, quadrangular,

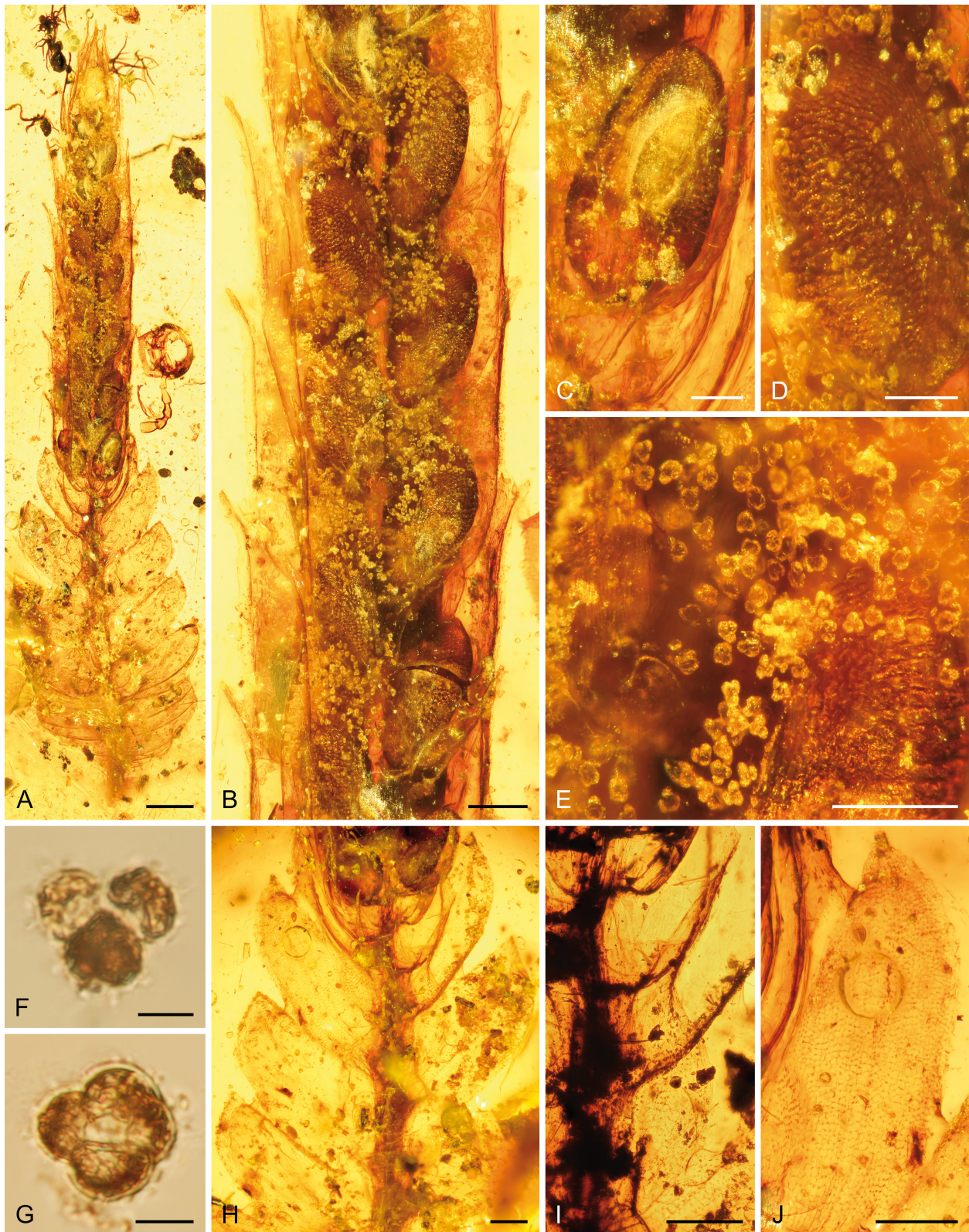


Fig. 25. Holotype of *Selaginella ovoidea* from Kachin amber (AMNH-Bu-KL-8-7). – A: overview; B: central portion of strobilus; C: sporangium; D: sporangium wall; E–G: microspore tetrads; H: ventral trophophylls; I: dorsal trophophyll; J: trophophyll epidermis. – Scale bars: A = 500 μ m; B, H–J = 200 μ m; C–E = 100 μ m; F, G = 10 μ m.

4.6 × 0.9 mm (Fig. 25A, B). *Sporophylls* monomorphic, imbricate, adpressed, conduplicate, 28 in only available strobilus, 1.0–1.5 × 0.2–0.3 mm, lanceolate, carinate, base rounded, apex long-attenuate, margins serrulate, teeth < 10 µm long, sporophyll-ptyx absent (Fig. 2G; 25B). Epidermis of sporophylls poorly preserved. *Sporangia* ellipsoid or ovoid, 480–600 × 220–280 µm, formed by uniform isodiametric cells bearing thick anticlinal walls (Fig. 25C, D). *Microspores* in tetrads, distally rugulate (Fig. 25E–G).

Remarks — *Selaginella ovoidea* is the only Kachin *Selaginella* that is characterized by quadrangular strobili with very distinctive ellipsoid or ovoid sporangia (Fig. 25C, D).

Among extant *Selaginella*, two species closely resemble the fossil, namely *S. rolandi-principis* Alston from China and Vietnam (Zhang & al. 2013) and *S. roxburghii* (Hook. & Grev.) Spring, native to the Malay Peninsula, Vietnam (Alston 1937) and presumably also China according to Zhang & al. (2013), who referred to this taxon using the synonym *S. commutata* Alderw. These species share with the fossil the presence of ovate, aristate or cuspidate dorsal trophophylls, oblong-ovate ventral trophophylls that are sparsely denticulate at the margins, quadrangular strobili with lanceolate to ovate sporophylls with an acute to attenuate apex and serrulate margins, and ellipsoid sporangia. Additionally, both *S. rolandi-principis* and *S. ovoidea* produce microspores in tetrads, although it is not possible to be sure that this is a permanent condition in either of them. Both *S. rolandi-principis* and *S. roxburghii* differ from *S. ovoidea* in that the microspores have a baculate ornamentation on the distal surface (Zhou & al. 2015a), which differs from the rugulate pattern seen on the distal surface of the fossil microspores (Fig. 25F).

Etymology — The specific epithet is derived from the Latin word *ovoideus* and refers to the egg-shaped sporangia.

Selaginella wangboi A. R. Schmidt & L. Regalado, **sp. nov.**

Holotype: PB23159 [Fig. 26], Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. – Fig. 2H; 26–28 (four specimens available).

Diagnosis — Rhizophores arising from branch dichotomies, ventrally orientated, base covered by axillary trophophyll. Axes compressed. Trophophylls dimorphic. Axillary trophophylls somewhat asymmetric, broadly ovate, non-carinate, base obtuse, apex acute to slightly acuminate, margins nearly entire or with a few teeth on proximal acroscopic margin. Dorsal trophophylls close to distant, adpressed, ovate, non-carinate, base obtuse, apex aristate, slightly decurrent, margins serrate-denticulate. Ventral trophophylls mostly symmetric, occasion-

ally asymmetric, close to distant, spreading, ascending, broadly ovate, non-carinate, base rounded to obtuse, apex acute to slightly acuminate, basisopic margin serrulate, acroscopic margin short-ciliate-denticulate. Strobili terminal, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate, ascending, conduplicate, ovate, carinate, carina slightly serrate, base rounded, apex attenuate, margins dentate-serrate, sporophyll-ptyx absent. Sporangia suborbicular. Megaspores distally and proximally reticulate. Microspores proximally rugulate.

Description — *Rhizophores* arising from dichotomy of branch, ventrally orientated, base covered by axillary trophophyll (Fig. 27E, F). *Axes* compressed. *Trophophylls* dimorphic (Fig. 26G; 27C–F; 28B). *Axillary trophophylls* somewhat asymmetric, 1.2–1.3 × 0.6–0.8 mm, broadly ovate, non-carinate, base obtuse, apex acute to slightly acuminate, margins nearly entire or with a few teeth on proximal acroscopic margin, teeth 10–25 µm long (Fig. 27F). *Dorsal trophophylls* close to distant, adpressed, 0.6–1.2 × 0.2–0.5 mm, ovate, non-carinate, base obtuse, apex aristate, slightly decurrent, margins serrate-denticulate, teeth 10–20 µm long. *Ventral trophophylls* mostly symmetric, occasionally asymmetric, close to distant, spreading, ascending, 1.1–1.7 × 0.5–0.9 mm, broadly ovate, non-carinate, base rounded to obtuse, apex acute to slightly acuminate, basisopic margin serrulate, teeth 10–20 µm long, acroscopic margin short-ciliate-denticulate, cilia 50–70 µm long, teeth 20–30 µm long (Fig. 26H; 27C). Epidermis of dorsal and ventral trophophylls composed of uniform isodiametric cells. *Strobili* terminal, tetrastichous, quadrangular, 2.3–3.0 × 1.4–1.9 mm (Fig. 26C, D; 27B; 28A). *Sporophylls* monomorphic, imbricate, ascending, conduplicate, 12–32 per strobilus, 0.8–1.2 × 0.3–0.5 mm, ovate, carinate, carina slightly serrate, teeth of carina ≤ 10 µm long, base rounded, apex attenuate, margins dentate-serrate, teeth 20–30 µm long, sporophyll-ptyx absent (Fig. 2H; 26E, F). Epidermis of sporophylls composed of elongate cells, with long axes orientated uniformly parallel to carina (Fig. 26E, F). *Sporangia* suborbicular, (200–)290–350 × 210–290 µm, composed of uniform isodiametric cells with thick anticlinal walls. *Megaspores* 170–200 µm in diam., distally and proximally reticulate (Fig. 26I–K). *Microspores* 20–30 µm in diam., proximally rugulate (Fig. 26L).

Remarks — Among the Kachin *Selaginella* species with quadrangular strobili, *S. wangboi* (Fig. 2H; 26–28), *S. tomescui* (Fig. 2I; 29), *S. pellucida* (Fig. 2J; 30) and *S. obscura* (Fig. 2K; 31, 32) are very similar in regard to overall morphology. They all show the following coincident characters: trophophylls dimorphic with dorsal trophophylls aristate, sporophylls dentate, serrate or at least erose, carinate with the carina serrate or erose, without sporophyll-ptyx, sporangia mostly suborbicular, relatively uniform in size throughout the strobilus, and rugulate microspores. However, minor differences between

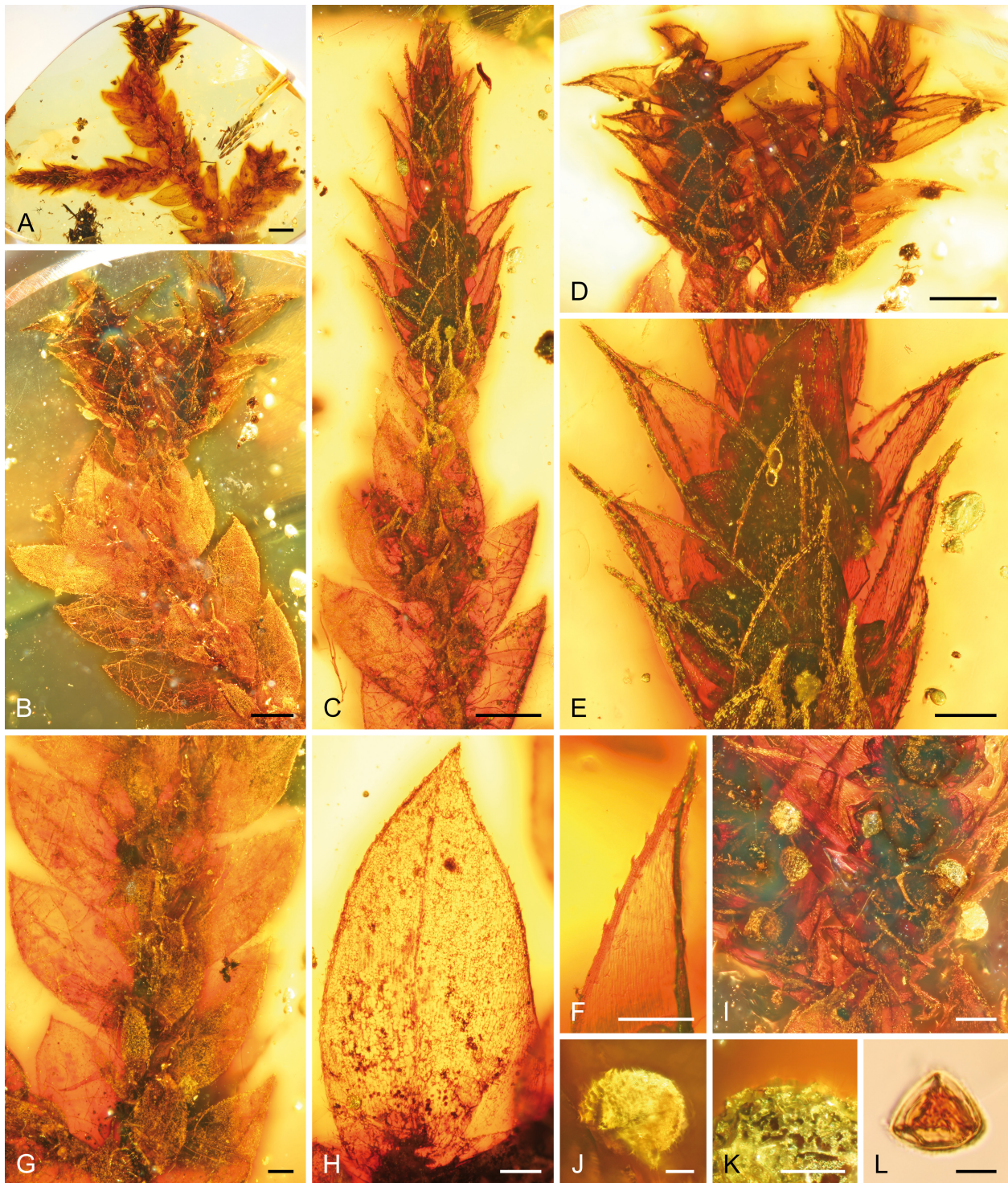


Fig. 26. Holotype of *Selaginella wangboi* from Kachin amber (PB23159). – A: overview; B, C: branches with strobili; D: two strobili; E: sporophylls and sporangia; F: sporophyll margin; G: trophophylls in dorsal view; H: ventral trophophyll; I: several released megaspores close to strobili shown in D; J: proximal surface of megaspore; K: megaspore surface; L: proximal surface of microspore. – Scale bars: A = 1 mm; B–D = 500 μ m; E–I = 200 μ m; J, K = 50 μ m; L = 10 μ m.

them also exist. For example, *S. wangboi* differs from the other three taxa in that it has nearly entire axillary trophophylls, with only a few sparse teeth on the proximal acroscopic margin, these teeth 10–25 μ m long (Fig. 27F). Additionally, the fertile specimens of *S. wangboi* released microspores in monads (Fig. 26L). In contrast,

S. tomescui (Fig. 2I; 29), *S. pellucida* (Fig. 2J; 30) and *S. obscura* (Fig. 2K; 31, 32) have axillary trophophylls, which are short-ciliate, serrate or conspicuously dentate at the margins, and released the microspores in tetrads.

Among the extant species of *Selaginella*, the common pattern is that microspores are disseminated indi-

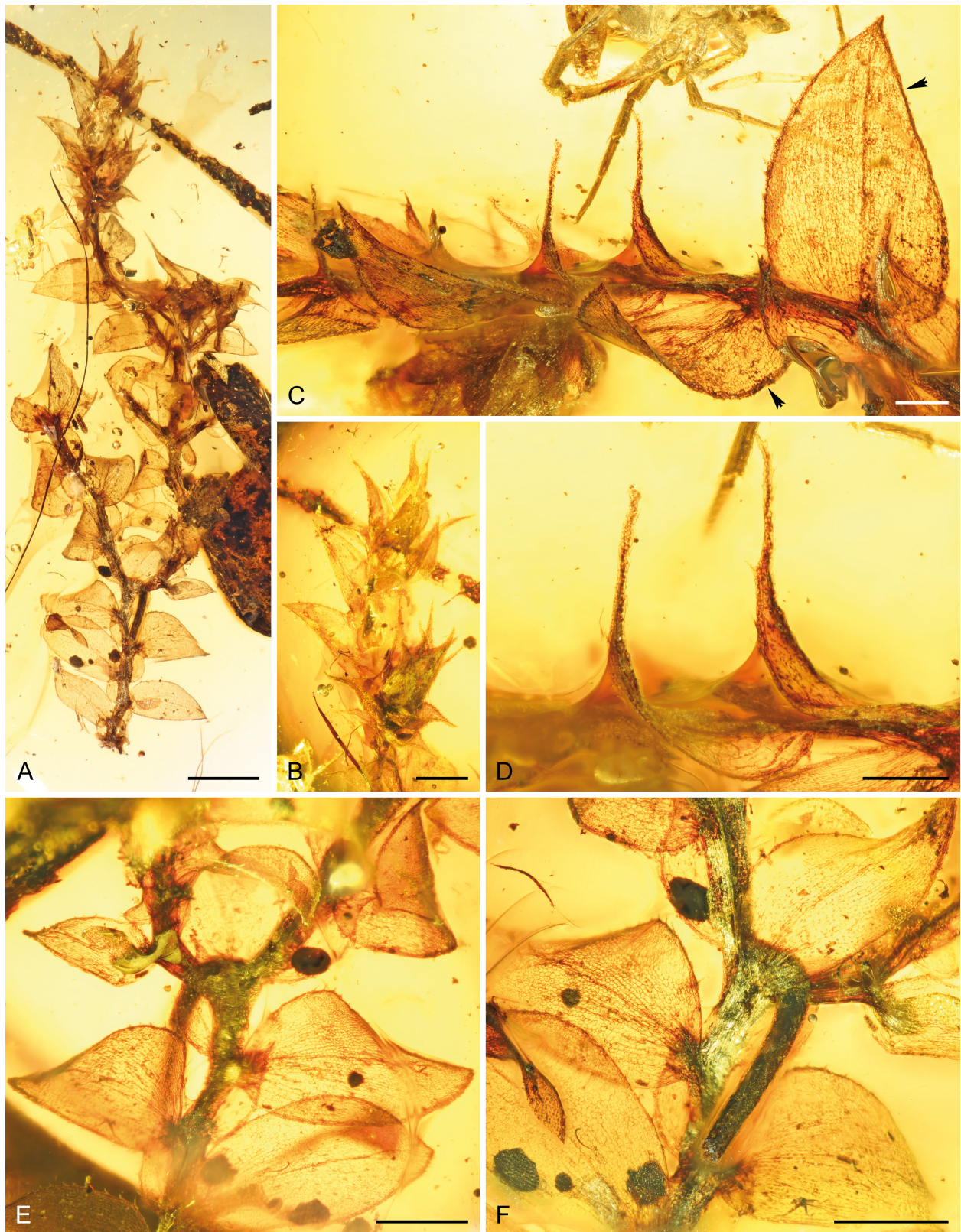


Fig. 27. *Selaginella wangboi* from Kachin amber (PB23161). – A: overview; B: strobili; C: trophophylls, arrowheads indicate ventral trophophylls; D: apices of dorsal trophophylls; E, F: rhizophore arising in dichotomy of branch in dorsal position seen from dorsal (E) and ventral (F) views. – Scale bars: A = 1 mm; B, E, F = 500 μ m; C, D = 200 μ m.

vidually (as monads), but they may also remain in tetrads after their release due to different connections or fusions of the spore wall (Morbelli & al. 2001; Tryon & Lugardon 2001; Morbelli & Lugardon 2012; Zhou & al. 2015a; Singh & al. 2016). Preservation of the fossil inclusions renders it impossible to examine if there were any connections among the individual microspores forming a tetrad in *S. tomescui* (Fig. 29H, J), *S. pellucida* (Fig. 30E) and *S. obscura* (Fig. 31E; 32G, H), but this condition was taken into account when establishing boundaries between taxa, especially in order to separate *S. wangboi* from all other taxa with similar overall morphology. However, a much larger sample set would be necessary to verify whether these differences are truly constant and discrete.

We believe that there are four specimens (i.e. PB23159, PB23161, P288–12 and the sterile specimen JZC-Bu-1868) of *Selaginella wangboi* currently available. They all are very similar in regard to vegetative morphology, so they are attributed to the same species. However, preservation of tissues in specimen PB23159 made it sometimes difficult to recognize the details of the trophophyll margins.

Among modern species, four species display morphological similarities with this fossil, including *Selaginella involvens* (Sw.) Spring, from Bhutan, China, India, Japan, Korea, Nepal and SE Asia (Dixit 1992; Zhang & al. 2013; Fraser-Jenkins & al. 2017; Shalimov & al. 2019), *S. moellendorffii* Hieron., native to China, Japan, the Philippines and Vietnam (Zhang & al. 2013), *S. radicata* (Hook. & Grev.) Spring, endemic to India and *S. brachyblepharis* Alderw., endemic to Borneo (Van Alderwerelt van Rosenburgh 1915). They have in common with the fossil the presence of quadrangular strobili with ovate-lanceolate sporophylls that are acute to acuminate at the apex, denticulate at the margins and carinate (Van Alderwerelt van Rosenburgh 1915; Dixit 1992; Zhang & al. 2013; Shalimov & al. 2019). However, all extant species differ from *S. wangboi* by having strobili longer than 5 mm (up to 15 mm) and baculate or verrucate microspores (Van Alderwerelt van Rosenburgh 1915; Dixit 1992; Zhou & al. 2015a), whereas the fossil has strobili 2–3 mm long and rugulate microspores (Fig. 26L). *Selaginella radicata* differs from the fossil by having verrucate microspores (Dixit 1992). Furthermore, *S. involvens* and *S. moellendorffii* appear to release microspores in tetrads (Zhou & al. 2015a), whereas they are discharged singly in *S. wangboi* (Fig. 26L).

Etymology — The specific epithet honours Professor Bo Wang (Nanjing), who has supported research collaborations on E Asian ambers for many years and has shared new discoveries with us.

Additional specimens studied — PB23161, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Fig. 27), JZC-Bu-1868, American Muse-

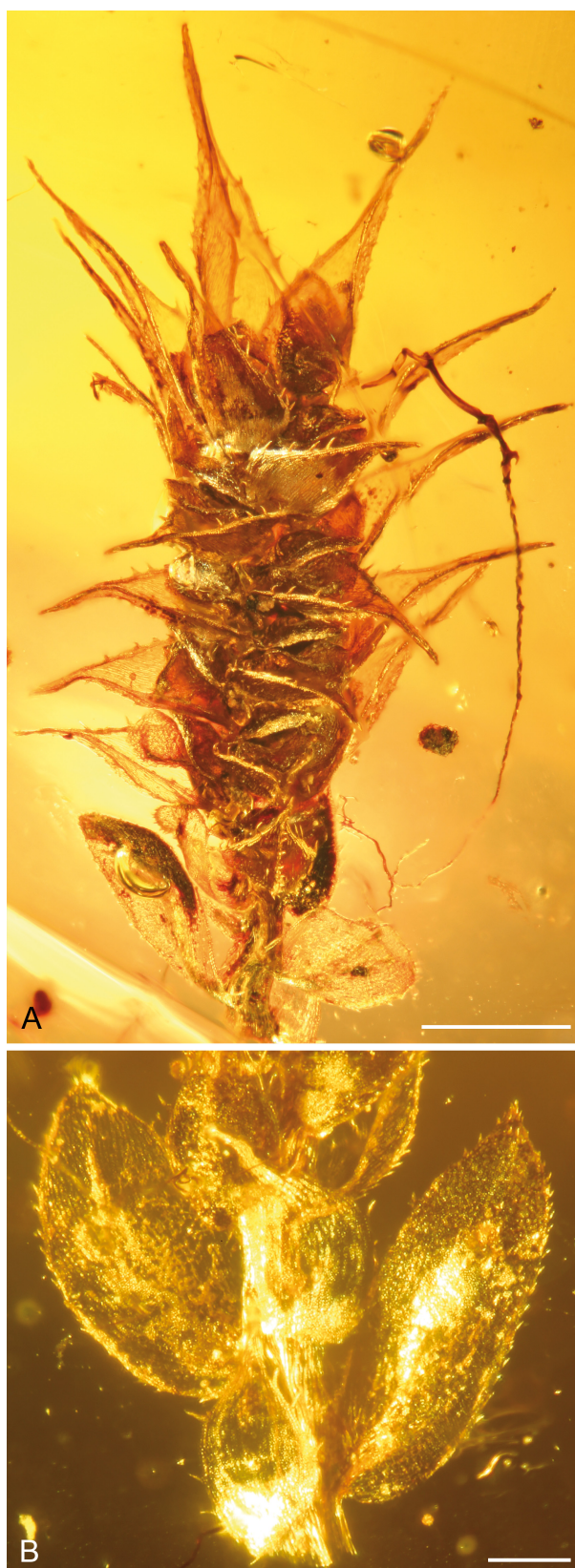


Fig. 28. *Selaginella wangboi* from Kachin amber (Max Kobbert Amber Collection P288–12). – A: overview of strobilus; B: trophophylls. – Scale bars: A = 500 μ m; B = 200 μ m.

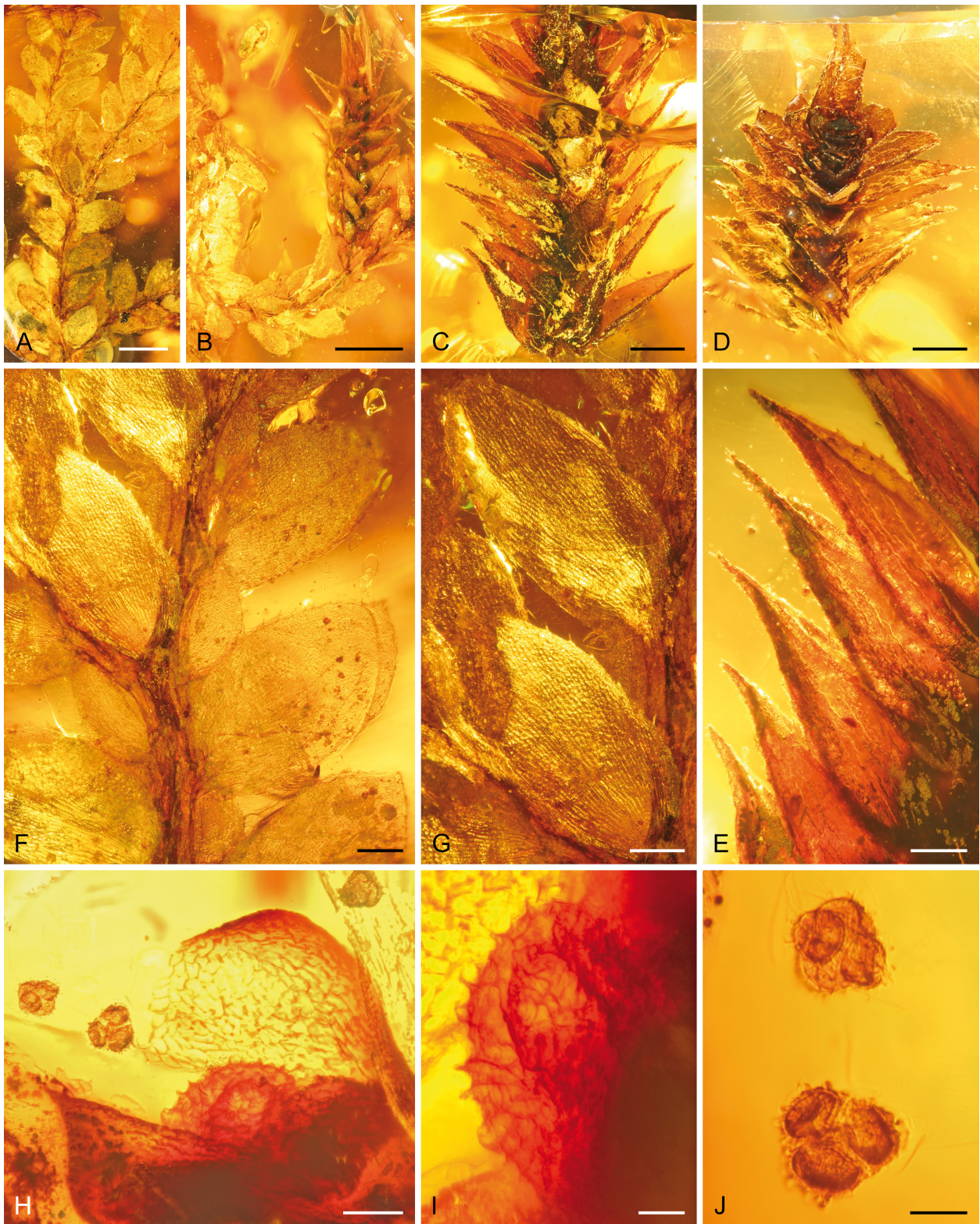


Fig. 29. *Selaginella tomescui* from Kachin amber (JZC-Bu-1692). Shoot portion illustrated in A, B, F and G designated as holotype. – A: branched specimen with trophophylls; B: curved branch with strobilus; C: lateral view of strobilus; D: strobilus in slightly oblique top view; E: sporophylls; F, G: trophophylls in dorsal view; H: open megasporangium containing megaspores and nearby microspore tetrads; I: megaspore; J: microspore tetrads. – Scale bars: A, B = 1 mm; C, D = 500 μ m; E–G = 200 μ m; H = 50 μ m; I, J = 20 μ m.

um of Natural History, Max Kobbert Amber Collection Münster, Germany, P288–12 (Fig. 28).

***Selaginella tomescui* A. R. Schmidt & L. Regalado, sp. nov.**

Holotype: JZC-Bu-1692 [Fig. 29A, B, F, G], American Museum of Natural History. – Fig. 2I; 29 (only specimen available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Axillary trophophylls symmetric, elliptic, non-carinate, base obtuse to rounded, apex acute to obtuse, margins short-ciliate or denticulate. Dorsal trophophylls close, adpressed, symmetric, ovate to elliptic, non-carinate, base decurrent, apex aristate, margins sparsely denticulate. Ventral trophophylls close, spreading, ascending, somewhat asymmetric, ovate to oblong-ovate, non-carinate, base rounded to short-truncate, apex obtuse to acute, margins sparsely denticulate. Strobili terminal, compact, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate, conduplicate, lanceolate carinate, carina sparsely dentate-denticulate similar to sporophyll margins, base rounded, apex attenuate, margins sparsely denticulate, sporophyll-ptyx absent. Sporangia suborbicular. Megaspores reticulate-rugulate. Microspores in tetrads, distally rugulate.

Description — *Rhizophores* not preserved. Axes compressed. *Trophophylls* dimorphic (Fig. 29A, F). *Axillary trophophylls* symmetric, 0.7–1.0 × 0.5–0.6 mm, elliptic, non-carinate, base obtuse to rounded, apex acute to obtuse, margins sparsely short-ciliate or denticulate, cilia or teeth 30–60 µm long (Fig. 29F). *Dorsal trophophylls* close, adpressed, symmetric, 0.6–0.8 × 0.2–0.3 mm, ovate to elliptic, non-carinate, base decurrent, apex aristate, margins sparsely denticulate, teeth 20–30 µm long (Fig. 29F). *Ventral trophophylls* close, spreading, ascending, somewhat asymmetric, 0.8–1.2 × 0.4–0.6 mm, ovate to oblong-ovate, non-carinate, base rounded to short-truncate, apex obtuse to acute, margins sparsely denticulate, teeth 20–40 µm long (Fig. 29G). Epidermis of dorsal and ventral trophophylls mostly composed of uniform isodiametric cells (Fig. 29G). *Strobili* terminal, compact, tetrastichous, quadrangular, 2.0–3.4 × 1.6–2.2 mm (Fig. 29B–D). *Sporophylls* monomorphic, imbricate, conduplicate, 28–36 per strobilus, 0.9–1.1 × 0.3–0.4 mm, lanceolate, carinate, carina sparsely dentate-denticulate similar to sporophyll margins, base rounded, apex attenuate, margins sparsely denticulate, teeth 10–40 µm long, sporophyll-ptyx absent (Fig. 2I; 29E). Epidermis of sporophylls composed of elongate cells, with long axes orientated uniformly parallel to carina. *Sporangia* suborbicular, 280–300 × 300–340 µm, with uniform isodiametric cells bearing thick anticlinal walls (Fig. 29H). *Megaspores* 130–150 µm in diam., reticulate-rugulate (Fig. 29I). *Microspores* in tetrads, distally rugulate (Fig. 29J).

Remarks — Of all the Kachin *Selaginella* inclusions, *S. tomescui* has the highest level of morphological correspondence to *S. wangboi*, *S. pellucida* and *S. obscura*. They all have in common the general outline and apex shape of the dorsal trophophylls and sporophylls, the type of sporophyll margins, the shape of the sporangia and the type of microspore ornamentation, among other features. However, *S. tomescui* differs from the other three taxa by its axillary trophophylls, which are short-ciliate or denticulate at the margins, with teeth or cilia 30–60 µm long (Fig. 29F). In comparison, the margins of the axillary trophophylls of *S. wangboi*, *S. pellucida* and *S. obscura* are mostly serrate or dentate, with teeth 15–50 µm long.

There are four extant species (*Selaginella brachyblepharis*, *S. involvens*, *S. moellendorffii* and *S. radicata*) that are somewhat similar morphologically to *S. tomescui*. However, the fossil differs from them in having distally rugulate microspores (Fig. 29J) (see remarks under *S. wangboi* for further details). The strobili being less than 5 mm long is also a feature that separates *S. tomescui* from *S. brachyblepharis*, *S. involvens* and *S. moellendorffii*, all of which have strobili longer than 5 mm, usually between 10 and 20 mm long.

Etymology — The specific epithet honours Professor Alexandru Mihail Florian Tomescu (Humboldt State University, Arcata, California, U.S.A.), for his contributions to the knowledge of fossil cryptogams.

***Selaginella pellucida* A. R. Schmidt & L. Regalado, sp. nov.**

Holotype: GZG.BST.22027 [Fig. 30], Geoscientific Collection of the University of Göttingen. – Fig. 2J; 30 (only specimen available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Axillary trophophylls asymmetric, narrowly elliptic, non-carinate, base obtuse to rounded, apex acute to slightly acuminate, margins serrate-dentate. Dorsal trophophylls distant, adpressed, conduplicate, ovate, carinate, base obtuse and decurrent, apex aristate, dentate at margins. Ventral trophophylls slightly asymmetric, distant, spreading, ascending, elliptic, non-carinate, base rounded to obtuse, somewhat decurrent, apex acute to slightly acuminate, basispic margin denticulate, acroscopic margin dentate. Strobili terminal, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate, ascending, conduplicate, ovate, carinate, carina slightly erose, base rounded, apex attenuate, margins somewhat denticulate to erose, sporophyll-ptyx absent. Sporangia mostly suborbicular, sometimes ellipsoid. Microspores in tetrads, distally rugulate.

Description — Axes compressed. *Trophophylls* dimorphic (Fig. 30B–D). *Axillary trophophylls* asymmetric, 0.8–1.4 × 0.3–0.7 mm, narrowly elliptic, non-carinate,

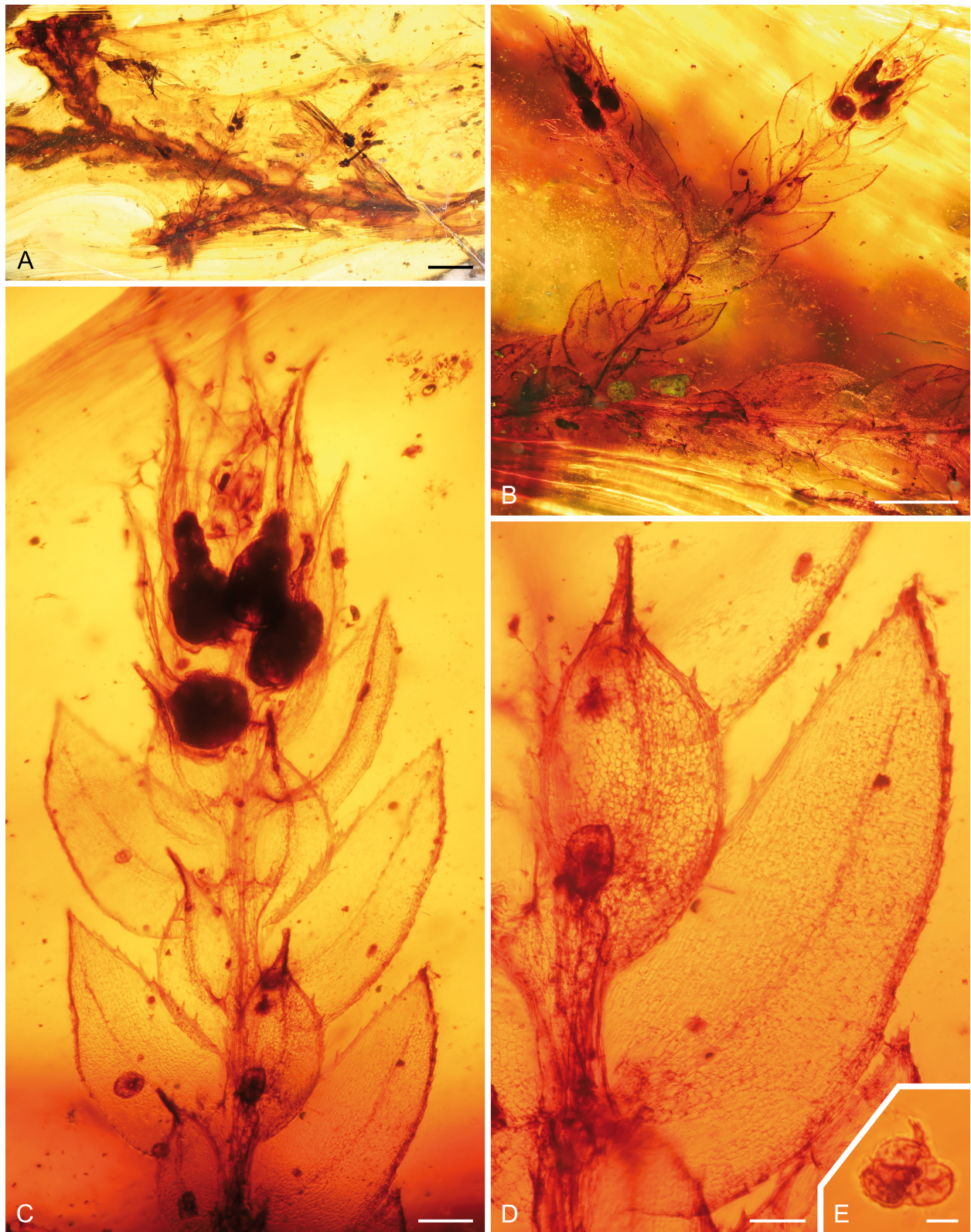


Fig. 30. Holotype of *Selaginella pellucida* from Kachin amber (GZG.BST.22027). – A: overview; B: branches with two strobili; C: dorsal view of branch showing trophophylls and strobilus; D: dorsal and ventral trophophyll in dorsal view; E: microspore tetrad. – Scale bars: A = 2 mm; B = 1 mm; C = 200 μ m; D = 100 μ m; E = 10 μ m.

base obtuse to rounded, apex acute to slightly acuminate, margins serrate-dentate, teeth 20–40 μm long. *Dorsal trophophylls* distant, adpressed, conduplicate, 0.8–1.0 \times 0.3–0.4 mm, ovate, carinate, base obtuse and decurrent, apex aristate, margins dentate, teeth 30–60 μm long (Fig. 30D). *Ventral trophophylls* slightly asymmetric, distant, spreading, ascending, 1.1–2.7 \times 0.5–0.8 mm, elliptic, non-carinate, base rounded to obtuse, somewhat decurrent, apex acute to slightly acuminate, basisopic margin denticulate, teeth \leq 10 μm long, acroscopic margin dentate, teeth 15–60 μm long (Fig. 30D). Epidermis of dorsal and ventral trophophylls composed of uniform isodiametric cells (Fig. 30D). *Strobili* terminal, tetrastichous, quadrangular, 1.2–1.6 \times 0.7–0.8 mm (Fig. 30C). *Sporophylls* monomorphic, imbricate, ascending, conduplicate, c. 12 per strobilus, 0.9–1.0 \times 0.3–0.4 mm, ovate, carinate, carina slightly erose, base rounded, apex attenuate, margins slightly denticulate to erose, teeth \leq 10 μm long, sporophyll-ptyx absent (Fig. 2J). Epidermis of sporophylls poorly preserved. *Sporangia* mostly suborbicular (Fig. 30C), sometimes ellipsoid, 300–350 \times 220–300 μm , with uniform isodiametric cells with thick anticlinal walls. *Microspores* in tetrads, distally rugulate (Fig. 30E).

Remarks — *Selaginella pellucida* differs from the morphologically similar *S. wangboi*, *S. tomescui* and *S. obscura* by having sporophylls with somewhat denticulate to erose margins, with teeth \leq 10 μm long and a slightly erose carina (Fig. 2J). Conversely, the aforementioned species possess sporophylls with dentate or serrate margins, with teeth 10–40 μm long and a serrate or denticulate carina.

This fossil-taxon is morphologically similar to several extant species, including *Selaginella brachyblepharis*, *S. involvens*, *S. moellendorffii* and *S. radicata*. However, it differs from all of them by its shorter strobili (up to 1.6 mm long) and in having microspores with a rugulate distal surface (see remarks under *S. wangboi* for further discussion).

Etymology — The specific epithet is derived from the Latin word *pellucidus*, which refers to the semi-transparent, delicate preservation of the tissue in this fossil.

***Selaginella obscura* A. R. Schmidt & L. Regalado, sp. nov.**

Holotype: PB25334 [Fig. 31A, B], Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. – Fig. 2K; 31, 32 (three specimens available).

Diagnosis — Axes compressed. Trophophylls dimorphic. Axillary trophophylls symmetric, narrowly elliptic, non-carinate, base obtuse, apex acute, margins somewhat to conspicuously dentate. Dorsal trophophylls close, adpressed, lanceolate or elliptic, non-carinate, apex aristate, margins nearly entire to sparsely serrate. Ventral tropho-

phylls distant, mostly symmetric, spreading, ascending, elliptic or ovate, non-carinate, base rounded, apex acute to acuminate, margins serrate to denticulate. Strobili terminal, compact, tetrastichous, quadrangular. Sporophylls monomorphic, imbricate, conduplicate, lanceolate, carinate, carina sparsely dentate as in sporophyll margins, base rounded, apex long-attenuate to aristate, margins sparsely dentate, sporophyll-ptyx absent. Sporangia suborbicular. Megaspores distally reticulate-rugulate. Microspores in tetrads, distally rugulate.

Description — *Rhizophores* not preserved. *Axes* compressed. *Trophophylls* dimorphic (Fig. 31A, B; 32A, E). *Axillary trophophylls* symmetric, 0.8–1.3 \times 0.4–0.6 mm, narrowly elliptic, non-carinate, base obtuse, apex acute, margins somewhat to conspicuously dentate, teeth 40–50 μm long (15–20 μm long in GZG.BST.22006). *Dorsal trophophylls* close, adpressed, 0.7–1.3 \times 0.3–0.4 mm, lanceolate or elliptic, non-carinate, base not seen, apex aristate, margins nearly entire to sparsely serrate, teeth 40–50 μm long. *Ventral trophophylls* distant, mostly symmetric, spreading, ascending, 1.1–1.7 \times 0.5–0.8 mm, elliptic or ovate, non-carinate, base rounded, apex acute to acuminate, margins serrate to denticulate, teeth 30–45 μm long (10–25 μm long in GZG.BST.22006) (Fig. 31D; 32F). Epidermis of dorsal and ventral trophophylls poorly preserved. *Strobili* terminal, compact, tetrastichous, quadrangular, 4.0–5.4 \times 1.3–1.6 mm (Fig. 32B, C). *Sporophylls* monomorphic, imbricate, conduplicate, (12–)28–56 per strobilus, 0.8–1.4 \times 0.3–0.4 mm, lanceolate, carinate, carina sparsely dentate as in sporophyll margins, base rounded, apex long-attenuate to aristate, margins sparsely dentate, teeth 30–40 μm long, sporophyll-ptyx absent (Fig. 2K; 31C; 32D). Sporophyll epidermis poorly preserved. *Sporangia* suborbicular, 300–340 \times 220–260 μm , composed of uniform isodiametric cells with thick anticlinal walls. *Megaspores* 160–240 μm in diam., distally reticulate-rugulate (Fig. 31F, G). *Microspores* in tetrads, distally rugulate (Fig. 31E; 32G, H).

Remarks — *Selaginella obscura* shares the gross-morphology with *S. wangboi*, *S. tomescui* and *S. pellucida*. However, it differs from those species in having 4.0–5.4 mm long strobili and sporophylls with a long-attenuate to aristate apex (Fig. 2K; 31C; 32D). Conversely, the strobili of *S. wangboi*, *S. tomescui* and *S. pellucida* are less than 3.4 mm long and the sporophyll apex is attenuate. Although there are minor differences in the size of the axillary and ventral trophophyll indentations between the two examined specimens (PB25334 and GZG.BST.22006), they are both regarded as belonging to the same species because they correspond in all other characters.

Like *Selaginella wangboi*, *S. tomescui* and *S. pellucida*, *S. obscura* resembles several extant species from Asia and the Pacific, including *Selaginella brachy-*

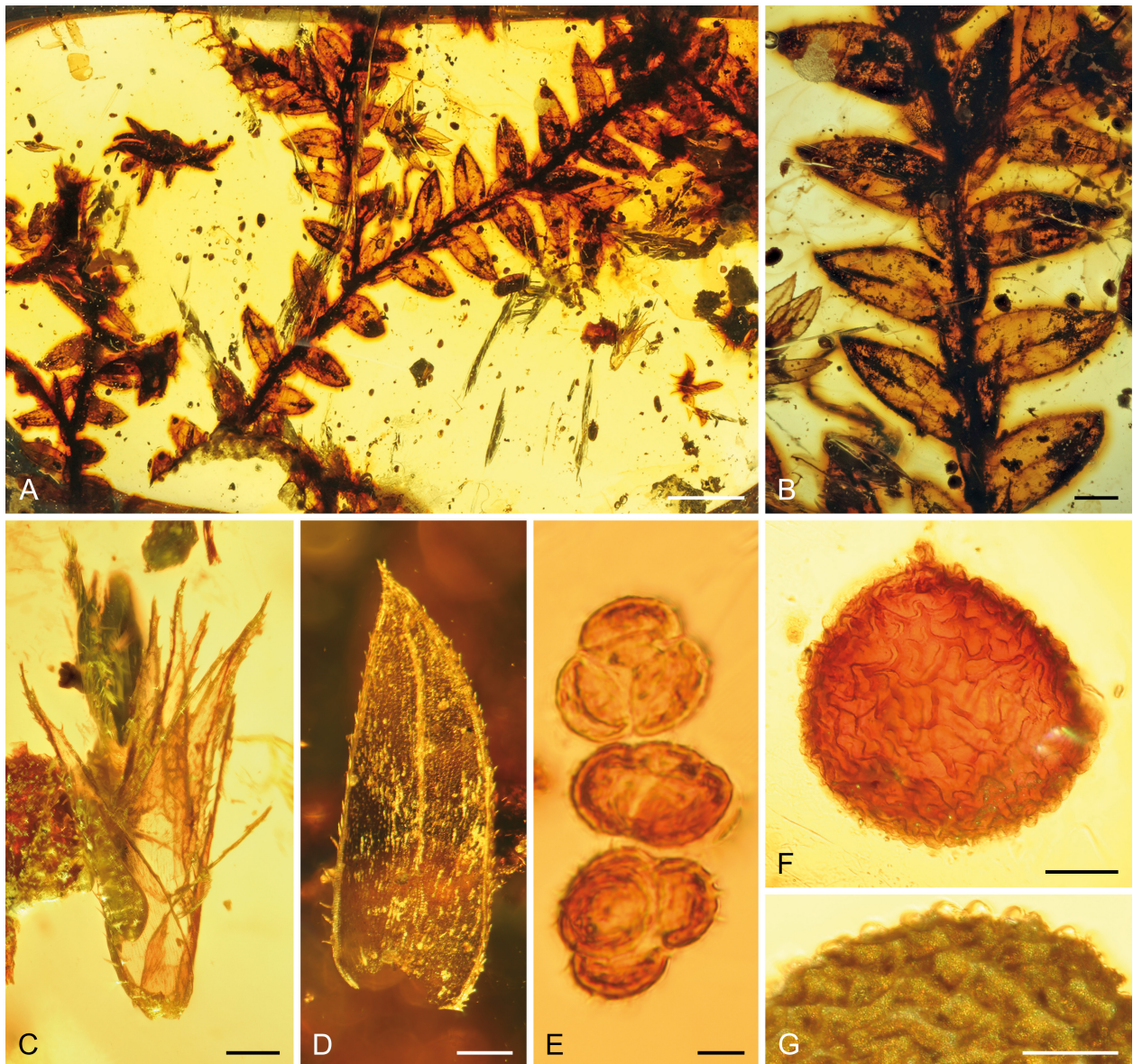


Fig. 31. *Selaginella obscura* from Kachin amber (PB25334). Large shoot portion shown in A and B designated as holotype. – A: overview of shoot portions interspersed with scattered megaspores; B: branch with trophophylls; C: apical fragment of strobilus; D: ventral trophophyll; E: microspore tetrads; F: distal surface of megaspore; G: megaspore surface. – Scale bars: A = 2 mm; B = 500 μ m; C, D = 200 μ m; E = 10 μ m; F, G = 50 μ m.

blepharis, *S. involvens*, *S. moellendorffii* and *S. radicata*. However, these extant species all have baculate or verrucate microspores (Van Alderwerelt van Rosenburgh 1915; Dixit 1992; Zhou & al. 2015a), while they are rugulate in *S. obscura* (Fig. 31E; 32G, H).

Etymology — The specific epithet is derived from the Latin word *obscurus*: dark, indistinct or obscure, and refers to the dark and poorly preserved tissue.

Additional specimens investigated — GZG.BST.22006, Geoscientific Collection of the University of Göttingen, PB25335, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Additional sterile morphologies

A few additional specimens have been discovered that represent vegetative branches with trophophylls, but without any connection to strobili. These fossils further substantiate the local abundance and diversity of *Selaginella* in the mid-Cretaceous Kachin amber forest, but cannot presently be assigned to any of the above-described species with confidence. They are here briefly described informally as *Selaginella* species 1, 2 and 3.

***Selaginella* sp. 1** – Fig. 33–35.

Specimens studied — PB25337 (Fig. 33), PB25338

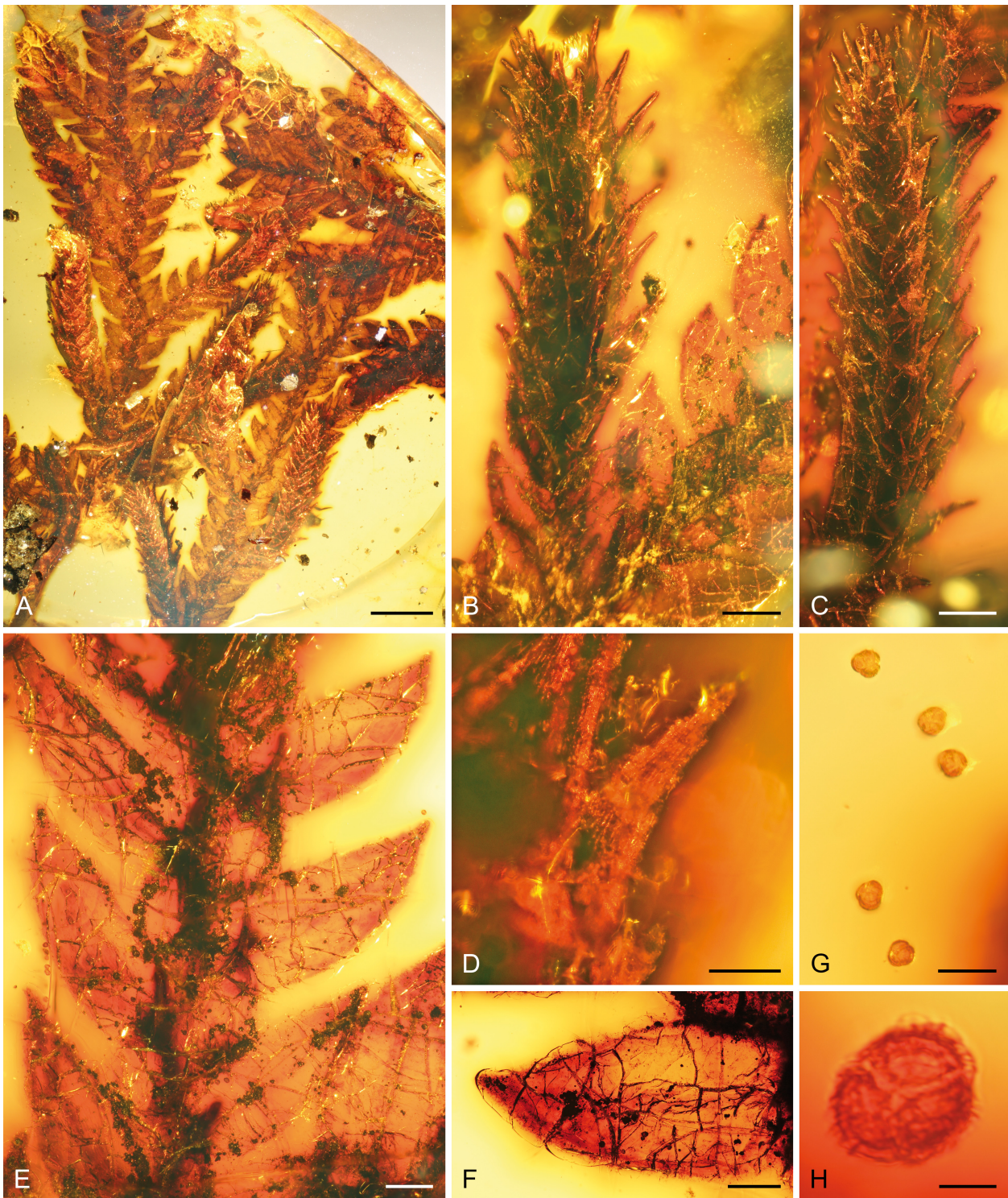


Fig. 32. *Selaginella obscura* from Kachin amber (GZG.BST.22006). – A: overview of branched shoot portions; B: strobilus at branch; C: strobilus; D: apex of sporophyll; E: dorsal and ventral trophophylls; F: ventral trophophyll; G, H: microspore tetrads. – Scale bars: A = 2 mm; B, C = 500 μ m; D = 100 μ m; E, F = 200 μ m; G = 50 μ m; H = 10 μ m.

(Fig. 34), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, GZG.BST.22030 (Fig. 35), Geoscientific Collection of the University of Göttingen, Patrick Müller Amber Collection BuB173, BuB3532, BuB2713.

Description — Axes compressed. *Trophophylls* dimorphic (Fig. 33A; 34A, B; 35A, B). *Axillary trophophylls* symmetric, 0.4–0.6 \times 0.2–0.3 mm, ovate, acute, apex slightly acuminate, base rounded, margins nearly entire (Fig. 34A). *Dorsal trophophylls* close, base slightly

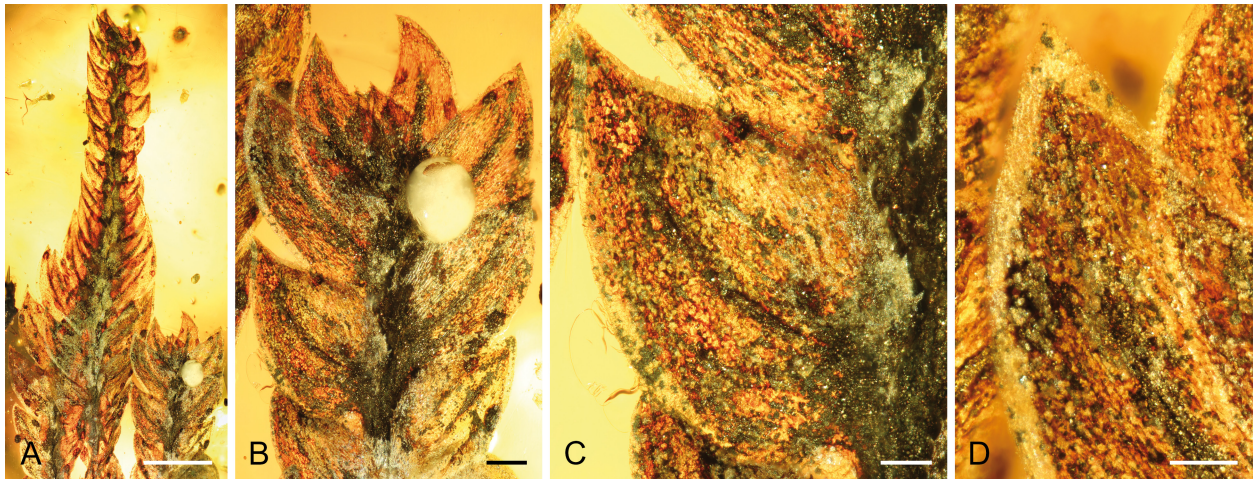


Fig. 33. Sterile *Selaginella* sp. 1 shoot portion from Kachin amber (PB25337). – A: overview; B: branch tip; C: ventral trophophyll with hyaline fringe; D: trophophyll margin with hyaline fringe. – Scale bars: A = 1 mm; B = 200 μ m; C, D = 100 μ m.

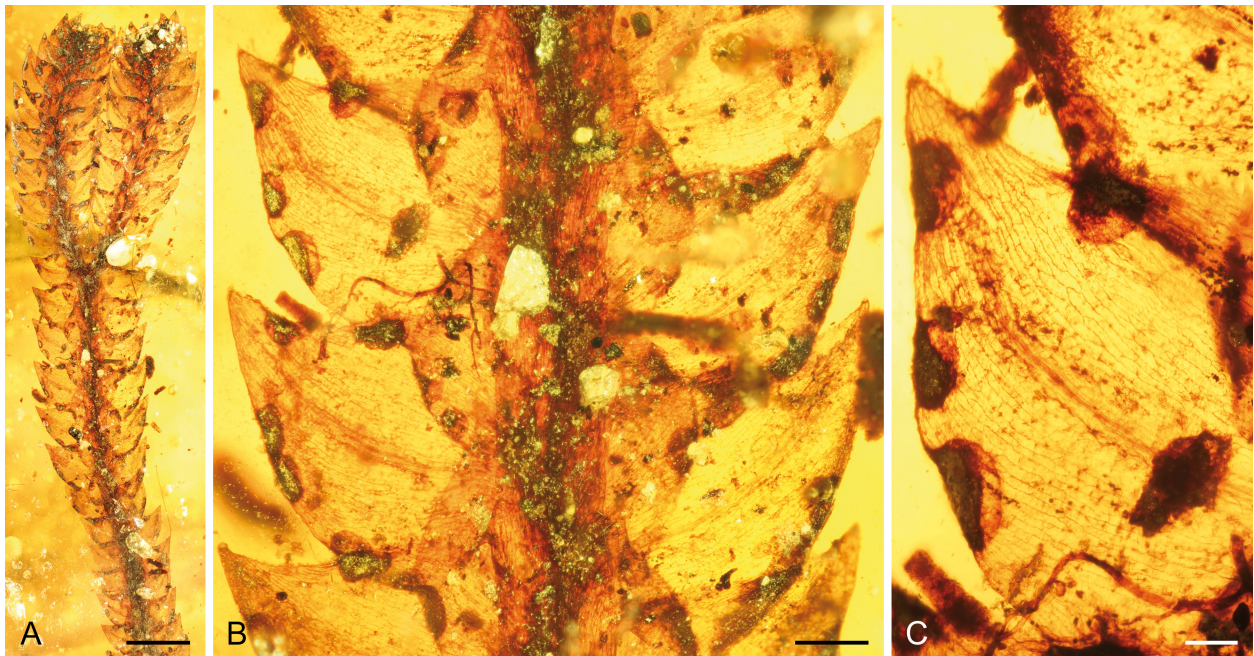


Fig. 34. Sterile *Selaginella* sp. 1 shoot portion from Kachin amber (PB25338) with conspicuous fungal colonization of leaf margins. – A: overview; B: trophophylls in dorsal view; C: ventral trophophyll. – Scale bars: A = 1 mm; B = 200 μ m; C = 50 μ m.

asymmetric, 0.3–0.9 \times 0.2–0.4 mm, ovate to broadly ovate, base decurrent, apex short acuminate to aristate, margins nearly entire, sometimes slightly denticulate, teeth < 10 μ m long. *Ventral trophophylls* close, almost imbricate, falcate, base slightly asymmetric, 0.5–1.5 \times 0.5–0.7 mm, ovate, broadly ovate or triangular, base obtusely decurrent, apex acute or slightly acuminate, margins entire, but may also be sparsely denticulate in proximal acroscopic portion, teeth 10–30 μ m long (Fig. 33C, 34C).

Remarks — Specimen PB25337 possesses a particular hyaline fringe 20–30 μ m wide that occurs along all margins of the ventral trophophylls and represents a charac-

ter not seen in any other specimen (Fig. 33D).

Selaginella sp. 2 – Fig. 36.

Specimen studied — Collection Carsten Gröhn, Glinde, CCGG 20005.

Description — *Axes* compressed. *Trophophylls* dimorphic (Fig. 36A). *Dorsal trophophylls* imbricate, adpressed, 0.8–1.1 \times 0.5–0.6 mm, broadly ovate, base decurrent, apex apiculate to short-aristate, margins denticulate, teeth 10–15 μ m long, slightly carinate (Fig. 36B). *Ventral trophophylls* close, slightly imbricate, mostly symmetric, 1.5–1.9 \times 0.8–0.9 mm, oblong, acute, base truncate, apex

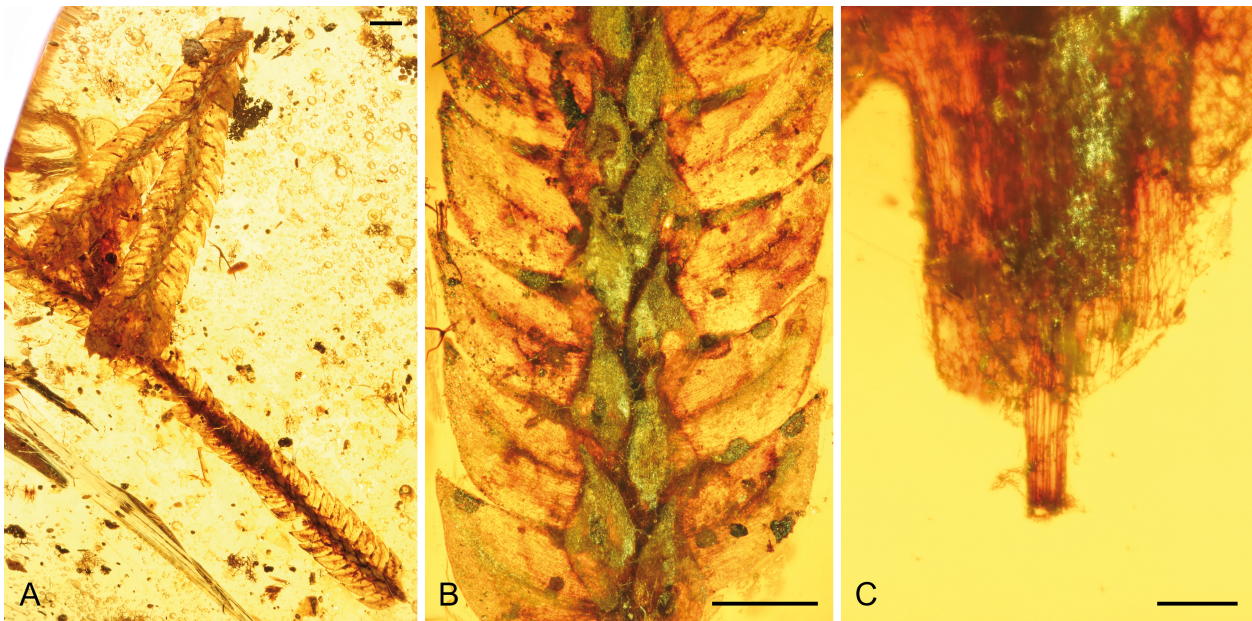


Fig. 35. Sterile *Selaginella* sp. 1 shoot portion from Kachin amber (GZG.BST.22030). – A: overview of two branched specimens; B: dorsal and ventral trophophylls in dorsal view; C: stele protruding at base of branch. – Scale bars: A = 1 mm; B = 500 μ m; C = 50 μ m.

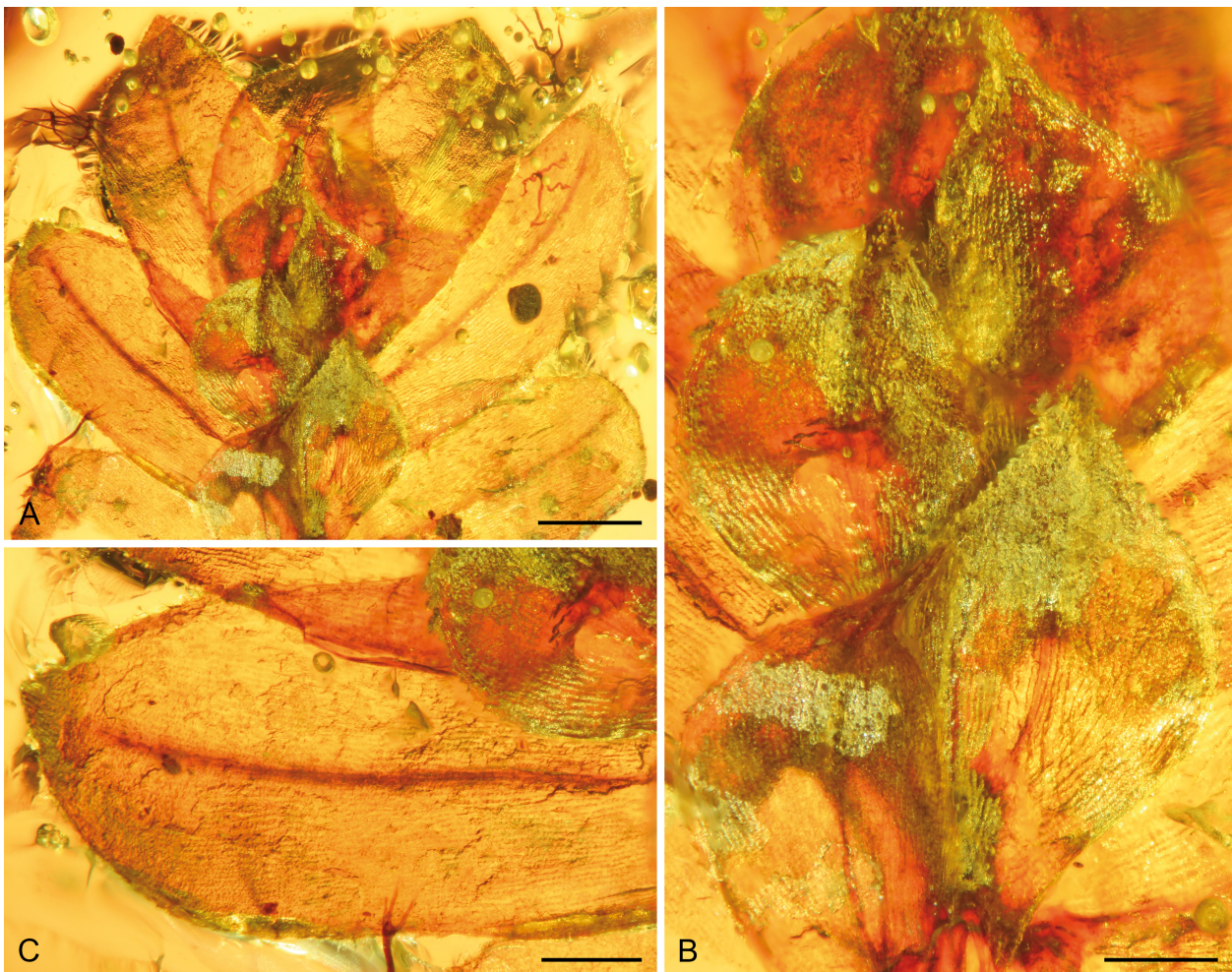


Fig. 36. Sterile *Selaginella* sp. 2 shoot portion from Kachin amber (Collection Carsten Gröhn, Glinde, CCGG 20005). – A: overview of branch tip; B: dorsal trophophylls; C: ventral trophophyll. – Scale bars: A = 500 μ m; B, C = 200 μ m.

obtuse or rounded, margins denticulate, teeth < 10 µm long, non-carinate (Fig. 36C).

Selaginella sp. 3 – Fig. 37.

Specimen studied — GZG.BST. 22031, Geoscientific Collection of the University of Göttingen.

Description — *Axes* compressed. *Trophophylls* dimorphic (Fig. 37A, B). *Dorsal trophophylls* close, slightly imbricate, adpressed, 0.9–1.1 × 0.2–0.3 mm, ovate, base decurrent, apex long-aristate, margins dentate, teeth 10–25 µm long (Fig. 37D). *Ventral trophophylls* close, slightly imbricate, base asymmetric, 1.1–1.8 × 0.4–0.5 mm, oblong-ovate, base inequilateral, with basal acroscopic side wider, apex acuminate, dentate mainly at distal and acroscopic margins, teeth 10–50 µm long, non-carinate (Fig. 37C).

4. Discussion

4.1. Assignment of the fossils to the genus *Selaginella*

The present-day heterosporous lycophytes include two orders, the *Isoetales* and *Selaginellales*. Members of both taxa possess a basal ligule on the adaxial leaf surface (the ligulate lycophytes). The *Selaginellales*, with its sole family *Selaginellaceae*, is characterized by two morphological synapomorphies, namely a central cauline stele that is surrounded by an air-filled cavity and connected to the peripheral tissues by trabeculae, and megasporangia that usually contain up to four megaspores (Jermy 1990; Kenrick & Crane 1997; Weststrand & Korall 2016a). However, these characters are not always preserved or readily discernible in fossils, and therefore we had to use other structural features that are diagnostic for certain groups within *Selaginella* and usually more frequently preserved in recognizable form, such as (1) dimorphic trophophylls arranged in four rows, two rows of smaller dorsal leaves and two rows of larger ventral leaves; and (2) tetrastichous strobili (sporophylls arranged in four rows) with either monomorphic sporophylls (forming isophyllous strobili) or dimorphic dorsiventrally arranged sporophylls (forming anisophyllous strobili) (Jermy 1990; Weststrand & Korall 2016a, 2016b). If these characters were also not preserved or remained doubtful, our approach was to discard possible affinities to other lineages of lycophytes.

Three genera of non-ligulate *Lycopodiaceae* (i.e. *Diphasiastrum* Holub, *Diphasium* C. Presl ex Rothm. and *Pseudodiphasium* Holub) are characterized by anisophyllous trophophylls arranged in rows (Øllgaard 1987; Field & al. 2016), precisely as in most *Selaginella* species. However, the spatial arrangement of the leaves clearly differs from the patterns seen in *Selaginella*. *Diphasiastrum* is characterized by trimorphic vegetative leaves with one dorsal and one distinct ventral row of narrow leaves and

two lateral rows of equally shaped, broad leaves. *Diphasiastrum* has dimorphic vegetative leaves with broad dorsal leaves organized in two rows and narrow ventral leaves in two to three rows (Field & al. 2016). *Pseudodiphasium* is distinguished by having trimorphic vegetative leaves in one or two dorsal rows and one ventral row of narrow leaves and two lateral rows of broad, compressed, subopposite leaves (Field & al. 2016). As a result, whenever there are trophophylls that are dimorphic and arranged in four rows (i.e. two rows of smaller dorsal and two rows of larger ventral leaves), the fossil can be attributed to *Selaginella* with some degree of confidence.

The vast majority of extant *Selaginella* species produce tetrastichous strobili, in which the sporophylls are arranged in four rows (Jermy 1990; Weststrand & Korall 2016a). The only two species producing strobili with helically arranged sporophylls are the circumboreal *S. selaginoides* and the Hawaiian *S. deflexa* (Weststrand & Korall 2016a, 2016b). Most Asian and Australasian *Selaginella* species have strobili that range in size from 0.2 to 2 cm long, in rare cases up to 6 cm long (Van Alderwerelt van Rosenburgh 1915; Dixit 1992; Zhang & al. 2013; Shalimov & al. 2019). There are, however, several notable exceptions with strobili up to 8 cm long (*S. sanguinolenta* (L.) Spring) and 9 cm (*S. magnifica* Warb.) long. Other examples of long strobili are found in some African, Madagascan and Mascarene species, with up to 2 cm in *S. distachya* Cordem., 2.5 cm in *S. obtusa* (P. Beauv.) Spring and *S. fruticulosa* (Bory ex Willd.) Spring, 3 cm in *S. versicolor* Spring and *S. concinna* (Sw.) Spring, 4 cm in *S. myosurus* (Sw.) Alston and 6 cm in *S. pectinata* Spring (Quansah 1986; Stefanović & al. 1997; Badré 2008). In contrast, strobili in *Lycopodiaceae* usually show helical or spiral sporophyll arrangement (Øllgaard 1987, 1990), although there are also a few exceptions in Australasian species of *Phlegmariurus* Holub (e.g. *P. marsupiiiformis* (D. L. Jones & B. Gray) A. R. Field & Bostock, *P. phlegmarioides* (Gaudich.) A. R. Field & Bostock, *P. proliferus* (Blume) A. R. Field & Bostock and *P. tetrastichoides* (A. R. Field & Bostock) A. R. Field & Bostock), with sporophylls arranged in four rows either decussately or not (Chinnock 1998; Field & Bostock, 2008, 2013; Field & al. 2016). In most of these species, strobili range from 4 to 25 cm long; however, they are only up to 2 cm long in *P. phlegmarioides* (Chinnock 1998).

The fossil *Selaginella isophylla* has monomorphic vegetative leaves arranged in four rows and monomorphic sporophylls occurring in tetrastichous, quadrangular strobili. It therefore represents one of those cases in which the affinities at first remained unclear because there are also several extant species of *Phlegmariurus* from Australasia (mentioned above) that are characterized by monomorphic microphylls and sporophylls arranged in four rows (Chinnock 1998; Field & Bostock 2008). However, both the vegetative leaves (5–14 mm long) and strobili (2–25 cm long) in *Phlegmariurus* species are considerably larger than in extant *Selaginella* (Chinnock 1998;

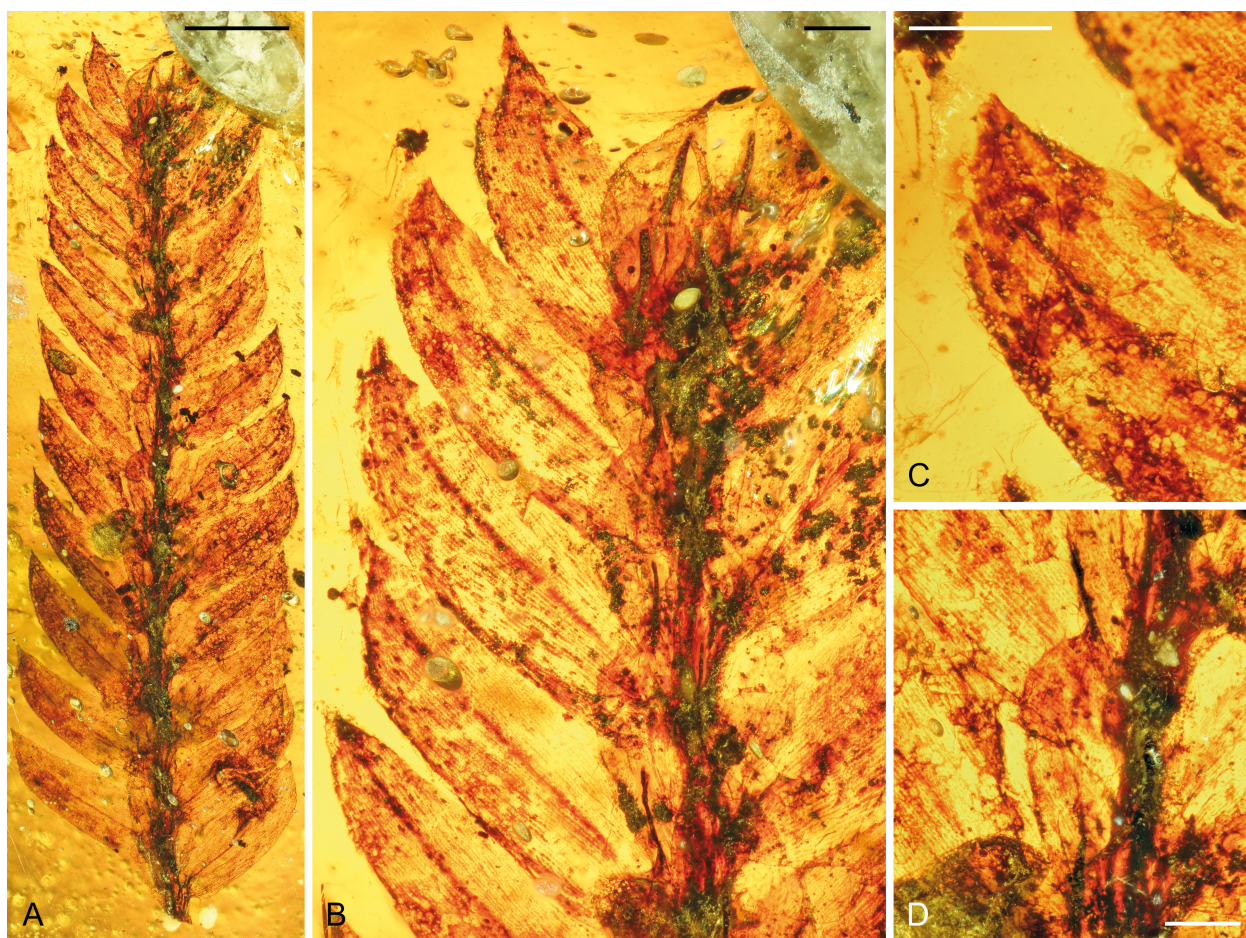


Fig. 37. Sterile *Selaginella* sp. 3 shoot portion from Kachin amber (GZG.BST. 22031). – A: dorsal overview of branch tip; B: dorsal and ventral trophophylls; C: distal portion of ventral trophophyll; D: dorsal trophophyll. – Scale bars: A = 1 mm; B–D = 200 μ m.

Field & Bostock 2008) and even larger than in all Kachin *Selaginella* fossils. The fossil was therefore assigned to *S.* subg. *Ericetorum* because of its general morphological affinities to this group, which likewise has monomorphic vegetative leaves arranged in four rows and monomorphic sporophylls organized in tetrastichous, quadrangular strobili. Additionally, the dimensions of the trophophylls (up to 1.2 mm long) and strobilus (up to 2.6 mm long) are comparable with the dimensions in extant species of this subgenus (Jermy & Holmes 1998) (see next section for further discussion).

The genus *Selaginellites* was described by Zeiller (1906) and has been used for fossils that are macro-morphologically indistinguishable from extant *Selaginella* (Banks 2009; Van Konijnenburg-van Cittert & al. 2014), but have a larger number of megaspores per sporangium, i.e. 16–24 in *Selaginellites* vs 1–4 in *Selaginella*. The larger number of megaspores per sporangium has long been regarded as the main difference between the two taxa (Zeiller 1906; Thomas & Quansah 1991). However, it was dismissed by Thomas (1992) based on reports of modern *Selaginella* producing more than four megaspores per sporangium (Mitchell 1910; Duerden 1929; Quansah 1986). On the other hand, Quansah

(1986) questioned reports of variations in the number of megaspores per sporangium in *Selaginella involvens*, *S. vogelii* and *S. willdenowii* because they were not consistent and unique for any of these modern species. All amber fossils that contained *in situ* megaspores have four or fewer megaspores per sporangium. For that reason, we assigned all fossils from Cretaceous Kachin amber to genus *Selaginella*.

4.2. Assignment of amber fossils to *Selaginella* subgenera

Morphological stability and conservatism within the genus render any attempt to reconstruct the long evolutionary history of *Selaginella* based on fossils a challenging, if not impossible task. Divergence time estimates based on molecular evidence suggest that at least six of the seven extant subgenera of *Selaginella* diversified during or before the Cretaceous (Weststrand 2016; Klaus & al. 2017). It has been shown by Weststrand & Korall (2016a) that each of the seven currently recognized subgenera in *Selaginella* is characterized by a unique combination of morphological traits. However, not all of these traits,

such as rhizophores, stelar arrangement and megaspore surface ornamentation, are always preserved and readily accessible in fossils, not even in amber fossils that are three-dimensionally preserved in cellular fidelity. This is primarily due to amber inclusions not normally yielding all parts and stages of the life cycle of a plant, but rather representing more or less small fragments of plants that were embedded in the resin in one particular phase of their life cycle. Moreover, fine anatomical details, if at all preserved in recognizable form, are hard to access due to the nature of the amber matrix.

Based on the presence of bilateral strobili with dimorphic sporophylls, ten of the fossil-species described in this study, namely *Selaginella ciliifera*, *S. cretacea*, *S. grimaldii*, *S. heterosporangiata*, *S. longifimbriata*, *S. minutissima*, *S. ohlhoiffiorum*, *S. patrickmuelleri*, *S. villosa* and *S. wangxinii* (Fig. 3–17), are safely assigned to *S.* subg. *Stachygynandrum* as circumscribed by Weststrand & Korall (2016b). Moreover, seven of these species (i.e. *S. ciliifera*, *S. cretacea*, *S. grimaldii*, *S. heterosporangiata*, *S. ohlhoiffiorum*, *S. villosa* and *S. wangxinii*) evidently produced resupinate strobili. As to whether the strobili of *S. longifimbriata* (Fig. 12), *S. minutissima* (Fig. 3) and *S. patrickmuelleri* (Fig. 13) were also resupinate cannot be determined because trophophylls are not preserved in the specimens. Whether the strobilus is resupinate or non-resupinate does not affect the assignment to the subgenus. Although they likely had evolved independently in several remotely related species groups within the subgenus, strobili with dimorphic sporophylls (both non-resupinate and resupinate ones) are only seen in *S.* subg. *Stachygynandrum* (Weststrand & Korall 2016a).

Selaginella subg. *Ericetorum* is characterized by monomorphic trophophylls that are decussately arranged (Jermy 1986a; Schulz & al. 2013), at least in the proximal parts of the plant (Weststrand & Korall 2016b). The monomorphic sporophylls are arranged in tetrastichous strobili. Megaspores are characterized by wing-like laesurae and are highly porous at the proximal pole, forming a “complex mass” in some species (Korall & Taylor 2006; Schulz & al. 2013; Weststrand & Korall 2016b). We have assigned the amber fossil *S. wunderlichiana* to *S.* subg. *Ericetorum* with some degree of confidence because it shares with the present-day representatives of this taxon the monomorphic and decussately arranged trophophylls (Fig. 18). *Selaginella isophylla* is also reminiscent of certain extant species in *S.* subg. *Ericetorum* based on the monomorphic trophophylls arranged in rows and monomorphic sporophylls arranged in tetrastichous quadrangular strobili (Fig. 19). However, the pattern of trophophyll arrangement cannot be determined in the fossil because the attachment sites of the leaves are not clearly visible. Moreover, the single strobilus that is known of this species is immature and does not, therefore, provide insights into the morphology of mature sporangia. We have nonetheless placed *S. isophylla* in *S.* subg. *Ericetorum* because we hold the opinion that this is

the most plausible systematic position, but we still regard the assignment as provisional until further fossils of this morphology become available for study.

The remaining amber fossils of *Selaginella* with monomorphic sporophylls arranged in tetrastichous strobili (i.e. *S. amplexicaulis*, *S. aurita*, *S. heinrichsii*, *S. konijnenburgiae*, *S. obscura*, *S. ovoidea*, *S. pellucida*, *S. tomescui* and *S. wangboi*) cannot presently be assigned to any of the extant subgenera with confidence because the diagnostic characters required to support such assignments (e.g. the presence/absence of rosetted habit, stem articulation, rhizophore position, stelar arrangement and megaspore ornamentation) are not preserved. Only *S.* subg. *Selaginella* can be ruled out because the sporophylls are not helically arranged.

4.3. Sporophyll-ptyeryx

As defined by Quansah & Thomas (1985), the sporophyll-ptyeryx is a vertical/oblique projection of the adaxial surface of the dorsal sporophyll of a bilateral resupinate strobilus (see left-side drawings in Fig. 1A–J). Jermy (1986b) stated that this feature occurs in the larger sporophylls of all *Selaginella* species with resupinate strobili and suggested that it is presumably the result of an ontogenetic “twist” in the development of a bilateral strobilus. Because the margin of the ptyeryx shows features of the opposite sporophyll margin (e.g. in regard to dentation), Jermy (1986b) furthermore suggested that the basiscopic margin has folded over and then become fused, rendering the sporophyll-ptyeryx a structure that protects the sporangium like the indusium in ferns and the integument indusium in Carboniferous *Lepidocarpon*.

We are not aware of any documented evidence of the sporophyll-ptyeryx in modern *Selaginella* species with quadrangular strobili. Our analysis of the Kachin amber fossils, however, has yielded evidence of this structure not only in the ten species with bilateral strobili (i.e. *S. ciliifera*, *S. cretacea*, *S. grimaldii*, *S. heterosporangiata*, *S. longifimbriata*, *S. minutissima*, *S. ohlhoiffiorum*, *S. patrickmuelleri*, *S. villosa* and *S. wangxinii*), but also in one form with quadrangular strobili composed of monomorphic sporophylls (i.e. *S. aurita*; Fig. 2C, 20A–E). It is noteworthy that, in this species, the sporophylls in all four rows possess a sporophyll-ptyeryx. All sporophylls are clearly twisted (arranged in an “upright” position), precisely as the larger sporophylls in species with bilateral strobili. This suggests that the function of the sporophyll-ptyeryx is the same in the different strobilus architectures. The margin of the sporophyll-ptyeryx in *S. aurita* likewise “mirrors” characters of the acroscopic sporophyll margin, not only in regard to the dentation, but also in the formation of a basal auricle.

This interesting discovery indicates that the sporophyll-ptyeryx is not an exclusive character of *Selaginella* species with bilateral resupinate strobili, but rather that,

during the Cretaceous, there were several lineages within the genus that were characterized by this trait. Based on an evaluation of the sporophyll heteromorphism in a phylogenetic context, Weststrand & Korall (2016a) suggested that monomorphic sporophylls are the plesiomorphic state for the genus, with several origins of dimorphic sporophylls in the *Stachygynandrum* clade. Because both types of sporophyll arrangement co-occur exclusively in the extant *S.* subg. *Stachygynandrum*, and all extant species with a sporophyll-ptyx belong to this clade, it is possible that *S. aurita* also represents a member of this subgenus. Therefore, we refrain from placing *S. aurita* into a new fossil-subgenus accommodating species with monomorphic sporophylls and a sporophyll-ptyx.

4.4. Spore morphology

Spore morphology of modern *Selaginella* species has been extensively used in taxonomy, with particular consideration of the surface ornamentation of both megaspores and microspores (Tryon & Lugardon 1991; Morbelli & al. 2001; Schulz & al. 2013; Singh & al. 2014b; Zhou & al. 2015a; Singh & al. 2016; Yan & al. 2016; Wang & al. 2018). Attempts to standardize the terminology used to describe the ornamentation of both megaspore and microspore surfaces have been challenging (Wang & al. 2018). However, at least six distinct surface ornamentation patterns (reticulate, verrucate, granulate, rugulate, scabrate and baculate) of megaspores and 12 patterns of microspores (foveolate, reticulate, verrucate, granulate, verrucate, rugulate, tuberculate, baculate, echinate, cristate, striate and papillate) have been described for extant *Selaginella* (Tryon & Lugardon 1991; Morbelli & al. 2001; Korall & Taylor 2006; Schulz & al. 2013; Singh & al. 2014b; Zhou & al. 2015a; Singh & al. 2016).

The numbers of different ornamentation patterns of megaspore and microspore surfaces is comparatively low in the fossil Kachin *Selaginella* species. There are three different megaspore ornamentation patterns, i.e. reticulate (Fig. 8F–H), echinate (Fig. 14J) and a combination of reticulate and rugulate (Fig. 13F) that is the most common type as it occurs in three of the six fossils containing megaspores. Microspores are rugulate in 14 species (e.g. Fig. 4G, H; 5H, I; 7J, K; 8E; 9F, G; 12F, G; 13G, H; 14H; 15H, I; 17G, H), psilate in two (Fig. 22E; 23B) and verrucate in one (Fig. 18E).

The microspores of modern *Selaginella* are usually released individually (Tryon & Lugardon 1991; Morbelli & al. 2001; Morbelli & Lugardon 2012). However, sometimes the tetrad condition is retained due to the fusion of exospore in the equatorial area, because of links in the area of the apertural folds, or due to the presence of a common envelope that connects the equatorial and distal regions of the spores (Morbelli & Lugardon 2012). Microspores discharged in tetrads have been reported in at least 26 extant species (Morbelli & al. 2001; Morbelli &

Lugardon 2012; Zhou & al. 2015a; Singh & al. 2016), although it is not always clear if it is the norm in these plants or occurs only from time to time. Among the fossil *Selaginella* species from Kachin, spore tetrads have been observed in four species, namely *S. obscura* (Fig. 31E; 32G, H), *S. ovoidea* (Fig. 25E–G), *S. pellucida* (Fig. 30E) and *S. tomescui* (Fig. 29H, J). Unfortunately, it is impossible to determine if connections of the exospore existed between the spores of a tetrad because of limitations of microscopic analysis of amber-preserved microfossils at high magnifications, caused by light-scattering effects of the amber matrix.

4.5. Extant *Selaginella* biodiversity

Within their biogeographic regions, extant autochthonous *Selaginella* species are characterized by a clear pattern of endemism (Schmidt & al. 2020). Most extant *Selaginella* species occur in moist tropical forests (Korall & Kenrick 2002), and there are generally no pantropical or cosmopolitan species. The endemism in the Neotropics is eminently continental, with 86% of the endemic species confined to the mainland, while more than 85% of the Australasian endemic *Selaginella* species occur exclusively on islands. The Afrotropical and Indo-Malayan endemic diversity is more equally distributed among mainland and islands, with only 48% and 38%, respectively, of the endemic species occurring on islands. High patterns of endemism have been recorded in continental islands like the Greater Antilles (80%), Madagascar (70%) and New Guinea (70%).

The extant endemism pattern is likely caused by the rather limited dispersal capacity of the megaspores. These large and relatively heavy dispersal units generally are not well-suited for wind dispersal, although there are a few species that display active horizontal and vertical spore ejection (Schneller & Kessler 2020). The two spore types in heterosporous ferns and lycophytes generally differ profoundly in their respective primary dispersal distances: while microspores can be transported over long distances by wind or water, megaspores are predominantly dispersed locally (Filippini-DeGiorgi & al. 1997), although active spore ejection into wind currents may considerably increase the dispersal distance (Schneller & Kessler 2020). Active or passive release of spores from sporangia also affects the dispersal capacity in heterosporous ferns and lycophytes (Koller & Scheckler 1986). For instance, active spore release by the megasporangium could enhance cross-fertilization, especially in calm conditions where the majority of microspores would normally also be deposited in close proximity to the source plant (Filippini-DeGiorgi & al. 1997). In contrast, synaptospory, i.e. the electrostatic adherence of microspores to the megaspores, which has been observed in several *Selaginella* species, could favour joint dispersal and therefore facilitate self-fertilization (Schneller & Kessler

2020). As a likely result of the limited dispersal capacity of the megaspores, the total number of *Selaginella* species in certain areas, such as protected primary forests of lowlands or mountain ranges, is relatively low, even in tropical regions. Schmidt & al. (2020) provided available local species numbers from the mainland and islands of SE Asia, including Myanmar, Thailand, Java, the Moluccas and the Philippines, that vary between seven and 14 species. These relatively small areas might be somewhat similar to the source area of Kachin amber. Schmidt & al. (2020) concluded that the number of *Selaginella* species in Kachin amber concurs with modern local species numbers and that, despite the total global diversity of c. 750 extant species, the local number of *Selaginella* species in an ecosystem compares well with the number of taxa recorded for Kachin amber. The Kachin amber species described in this study support the conclusion reached by Schmidt & al. (2020) that the mid-Cretaceous world already contained hundreds of *Selaginella* species.

Selaginella subg. *Stachygynandrum* comprises c. 600 extant species and therefore represents approximately 80% of the modern species diversity of *Selaginella* (Weststrand & Korall 2016a, 2016b). Prior to the discovery of the Kachin *Selaginella* fossils (Schmidt & al. 2020), this subgenus lacked any *bona fide* fossil representatives. It is therefore noteworthy that representatives of this subgenus are not rare as inclusions in Kachin amber and that nearly half of the species described to date are assignable with confidence to *S.* subg. *Stachygynandrum*. Furthermore, we cannot exclude that some of the other fossil-species from Kachin amber with monomorphic sporophylls also belong to this subgenus because most of its extant members have monomorphic sporophylls.

The large number of different *Selaginella* species preserved in Kachin amber strongly suggests that 100 million years ago *Selaginella* was already a species-rich, likely hyperdiverse genus. Although most modern species of *S.* subg. *Stachygynandrum* appear to be phylogenetically young, predominantly Cenozoic in age (Weststrand 2016), the fossils from Kachin show that representatives of this subgenus were prevalent at least since the early Late Cretaceous.

The organisms preserved in Kachin amber existed during the onset of the Angiosperm Terrestrial Revolution, a process that lasted from the first appearance of high angiosperm diversity in the beginning of the Late Cretaceous approximately 100 million years ago to their overwhelming dominance in biodiverse terrestrial ecosystems in the early Palaeogene c. 50 million years ago (Benton & al. 2021). The tremendously increasing diversity on land during this interval is seen in light of a sustained increase in humidity in angiosperm-dominated forest, as a consequence of significant evaporation from angiosperm leaves (Boyce & al. 2010). The prevalence of angiosperms has altered climate and water cycles, as the much higher transpiration rates of angiosperms increased local humidity, which likely triggered further diversifi-

cation of the angiosperms themselves, but also of other plants, animals and fungi that all depended or benefited from flowering plants or at least from constant atmospheric humidity, in a positive feedback loop (Benton & al. 2021). In the absence of frost, extant regional biodiversity is likewise correlated with precipitation (Kreft & Jetz 2007).

Although the producers of the Kachin tree resin are gymnosperms (Grimaldi & Ross 2017), inclusions of angiosperm flowers and leaves are abundant and taxonomically diverse in Kachin amber (Liu & al. 2018b). This fits well into a picture of a tropical Cretaceous forest during the early phase of the Angiosperm Terrestrial Revolution. Persisting humid conditions in the herbaceous layer probably favoured the growth of abundant *Selaginella*. The Kachin fossils of *Selaginella* are strongly suggestive of a remarkable palaeobiodiversity of *S.* subg. *Stachygynandrum* already c. 100 million years ago and a radiation of this most speciose extant subgenus that predated the early Late Cretaceous.

4.6. Palaeoecological implications for the reconstruction of the Kachin amber forest

The *Selaginella* fossils from Kachin are the only lycophytes reported to date from any amber deposit worldwide. Conversely, other free-sporing plants that are similar to *Selaginella* in body size and fragility, such as leafy liverworts and mosses, are frequently encountered as fossils in Miocene Mexican, Dominican, Ethiopian and Zhangpu ambers, as well as in Palaeogene Baltic, Bitterfeld and Rovno ambers (Gradstein 1993; Frahm & Newton 2005; Frahm 2009; Heinrichs & al. 2015; Lee & al. 2017; Bouju & al. 2021; Wang & al. 2021). A total of 16 bryophyte species are today known from Kachin amber (Hedenäs & al. 2014; Heinrichs & al. 2014; Feldberg & al. 2021, 2022). Many amber bryophytes likely were epiphytes, while extant *Selaginella* species are predominantly ground-dwellers. It is, therefore, relevant that a large amount of the resin exuded by trees in modern forests oozes down and eventually solidifies on the forest floor (Seyfullah & al. 2018). Evidence of tree resin that had solidified on the forest floor primarily occurs in the form of amber specimens of certain arthropods known to be ground-dwelling organisms (e.g. Perrichot 2004; Perrichot & Girard 2009). Therefore, small herbaceous plants growing on the forest floor likely were also readily entombed in oozing tree resin. Plant inclusions are, however, generally rare in most amber deposits. Only the eight amber deposits mentioned above have to date yielded plant fossils in larger numbers; Dominican, Baltic and Kachin ambers are particularly rich in plant fossils (Penney 2010; Bouju & al. 2021; Wang & al. 2021).

Contrary to bryophytes and the remains of seed plants, free-sporing vascular plants occur infrequently and are species-poor in Cenozoic ambers, with only two

confirmed ferns from Baltic amber, one from Bitterfeld amber (Sadowski & al. 2019) and three from Dominican amber (Gómez 1982; Lóriga & al. 2014; Schneider & al. 2015). With ten hitherto described fern species representing at least eight different families, Kachin amber is likewise outstanding in this regard, confirming a high diversity of free-sporing vascular plants in its source area (Poinar & Buckley 2008; Schneider & al. 2016; Regalado & al. 2017a, 2017b, 2018, 2019; Li & al. 2020a, 2020b; Poinar 2021; Wang & al. 2021; Zhang & al. 2022). This suggests that the Kachin amber forest was quite different from the warm-temperate source forests of Baltic amber and the tropical Dominican amber forest, especially with regard to the presence of various microhabitats within the groundcover or herbaceous layer. For instance, the low diversity of ferns in Baltic amber is believed to be related to the drier and cooler climate of the source forest and the presence of well-lit open habitat patches (Sadowski & al. 2019). In contrast, the Kachin amber forest shows strong affinities to extant tropical forests in which ferns and *Selaginellaceae* are more diverse. This could be an indication for humid tropical conditions in the Kachin amber forest.

With more than 2000 described taxa, the Kachin amber is currently the most relevant source of three-dimensionally preserved Cretaceous terrestrial organisms, including microorganisms, plants and animals. The high number of arthropods preserved in this amber and the number of different higher-ranked taxa to which these fossils have been assigned (i.e. eight classes, 66 orders, 596 families, 1357 genera and 2059 species; see Ross 2022 for details), suggests that the source area of this resin provided numerous ecologically distinct niches and microenvironments (Schmidt & al. 2020). A reconstruction of the “Kachin amber forest” has not been presented, as was done for Baltic amber based on plant fossils and other taxa that serve as proxy indicators of habitat structure and climate (Kaasalainen & al. 2017; Sadowski & al. 2017a, 2017b, 2020, 2022; Rikkinen & Schmidt 2018). This renders understanding the palaeoecology of the resin source area difficult. Nevertheless, along with the diverse fern fossils, the *Selaginella* fossils now provide relevant new insights into the Kachin amber forest, because they facilitate a partial reconstruction of the groundcover or herbaceous layer as one that was rich in free-sporing plants. This is also significant for the interpretation of the large number of arthropod taxa that must have inhabited the same microhabitats.

The number of free-sporing plants preserved in Kachin amber is high and balanced between diverse lineages, with 26 previously described species, including ten liverwort species of the families *Frullaniaceae*, *Lepidolaenaceae* and *Radulaceae*, six mosses of the *Dicranales* and *Hypnodendrales* and ten fern species in at least five families, such as *Cystodiaceae*, *Dennstaedtiaceae*, *Lindsaeaceae*, *Pteridaceae* and *Thyrsopteridaceae* (Hedenäs & al. 2014; Heinrichs & al. 2014; Schneider & al. 2016;

Regalado & al. 2017a, 2019; Li & al. 2020a, 2020b; Feldberg & al. 2021, 2022). *Selaginella* exceeds the diversity of bryophytes and accounts for nearly half of the documented free-sporing plant diversity in Kachin amber. This suggests that *Selaginella* was an important if not dominant component of the herbaceous layer. The abundance and ecological significance of *Selaginella* and leafy liverworts of similar dimensions is also expressed by the existence in these forests of insects mimicking these plants (Fig. 38). Xu & al. (2021) summarized the evidence of mimicry and camouflage in mid-Cretaceous insects and showed that mimics of spike mosses and leafy liverworts existed among neuropterans and orthopterans. *Phyllochrysa huangi* Liu & al., a Chrysopidae (green lacewing family) larva (Fig. 38A), possessed several lateral, broadly foliate thoracic and abdominal plates resembling both the dorsal sporophylls of bilateral strobili and trophophylls of *Selaginella* and the leaves of leafy liverworts (Liu & al. 2018a; Xu & al. 2021; Li & al. 2022). Whereas debris-carrying camouflage (carrying exogenous materials) is common among past and present Chrysopidae larvae (Wang & al. 2016), mimesis of plant parts is known only in *Phyllochrysa huangi*. Larvae of this neuropteran family prey on small arthropods, and the plant mimicry was likely advantageous while acting as stealthy hunters or ambush predators and at the same time lowered predation risk (Liu & al. 2018a). Moreover, Xu & al. (2021) reported on *Phyllotridactylus wangi* Xu & al., a new fossil genus and species within the orthopteran family Tridactylidae (pygmy mole crickets), which mimics spike mosses or leafy liverworts (Fig. 38B). This fossil insect is characterized by inflated leg parts, such as metafemur, mesofemur and mesotibia. The greatly enlarged metafemur possibly imitates sporophylls and ventral trophophylls of *Selaginella* and leaves of leafy liverworts, whereas the planar expansions of mesofemur and mesotibia resemble the smaller dorsal trophophylls of *Selaginella* (Xu & al. 2021). These modifications likely protected these algivorous or herbivorous insects from predators. Arthropods specifically mimicking *Selaginella* have hitherto not been reported in modern ecosystems.

None of the 21 Kachin *Selaginella* species shows adaptations to arid conditions, such as clustered leaves to reduce surface exposure to direct sunlight (Arrigo & al. 2013) or tightly curled branches (Weststrand & Korall 2016b), stomata mostly distributed on the adaxial surface of the microphylls that are tightly attached to stems, or particularly small and thick microphylls (Yu & al. 2022). Rather, several characters of the Kachin *Selaginella* plants are suggestive of constantly humid conditions. For example, the epidermal cells of both the adaxial and abaxial leaf surfaces are often well visible, even from one side, and the vascular bundles of the trophophylls are sometimes clearly discernible (e.g. Fig. 18H; 34C). This suggests that the leaves *in vivo* were not overly thick and did not contain any specialized elements effective in water-loss protection (e.g. Fig. 8D; 10B; 17C, D, J).

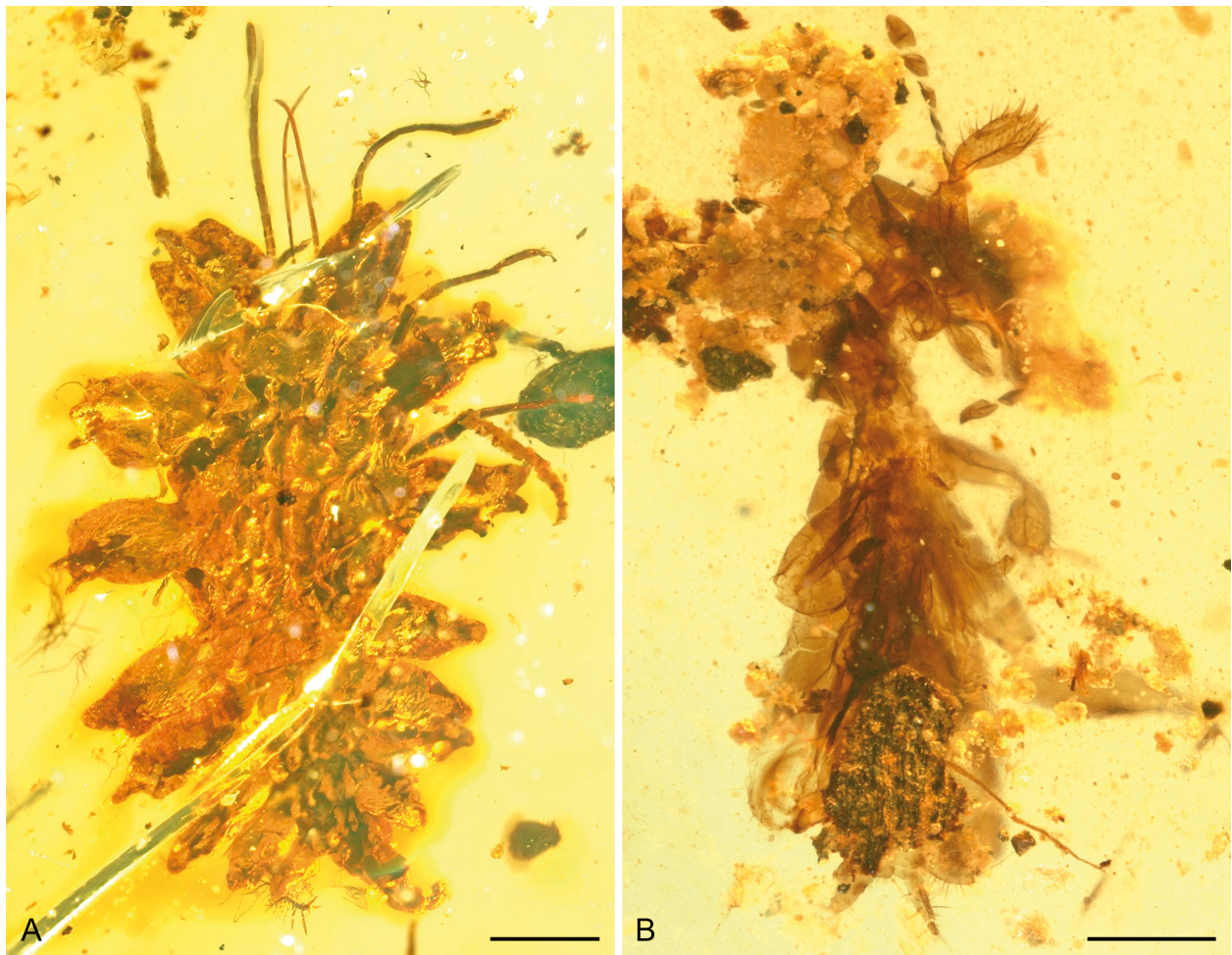


Fig. 38. Amber fossils of insects from Kachin mimicking leaves of spike mosses and leafy liverworts. – A: green lacewing larva *Phyllochrysa huangi* (Neuroptera, Chrysopidae) possessing lateral, broadly foliate thoracic and abdominal plates; B: pygmy mole cricket *Phyllotridactylus wangi* (Orthoptera, Tridactylidae) with femoral and tibial inflations. – Images courtesy of Bo Wang (Nanjing). – Scale bars: A = 1 mm; B = 500 μ m.

Although the epidermal cells are well preserved in most of the fossils, no evidence of stomata was found. This is reminiscent of the leaves in the extant fern *Leptopteris* C. Presl (*Osmundaceae*). The leaf lamina is reduced to a single cell layer (except for the areas along the veins) and lacks stomata, which renders the plants highly susceptible to low air humidity (Kramer 1990; Hietz 2010).

Approximately one third of the *Selaginella* inclusions from Kachin show signs of fungal colonization (e.g. Fig. 23H; 34; 39E–H). For example, dark spots, 30–110 μ m in diam. and sometimes co-occurring with hyphae, are frequently preserved on trophophylls and sporophylls. They resemble modern fly-speck fungi, which predominantly comprise ascomycetes of the order *Capnodiales*. The abundance of these fungi is suggestive of free water on the plant surface and high humidity (Gleason & al. 2019). We detected similar fungal remains also on numerous herbarium specimens of present-day *Selaginella* species from SE Asian tropical rainforests, including specimens of *S. longiaristata* Hieron. (B 20 0147148), *S. ornithopodioides* (B 20 0180398), *S. pickringii* Hieron.

(B 20 0129238) and *S. tenera* (B 20 0120775) kept in the Berlin herbarium.

The amber piece containing the type specimen of *Selaginella heterosporangiata* also contains another plant fossil, likely a seed-plant leaf, which is partly overgrown by sooty moulds (Fig. 39D). Branching and sometimes anastomosing moniliform aerial hyphae emerge from a dark superficial subiculum. These hyphae branch in wide angles and taper distally, characters seen today in some members of the ascomycete order *Capnodiales*. The term sooty moulds is used in an ecological sense for distantly related epiphytic ascomycetes with dark-coloured hyphae that often produce conspicuous black growth on leaves and other surfaces of living plants. These saprotrophic fungi grow predominantly on plant exudates and honeydew (Hughes 1976). Sooty moulds are today most abundant and speciose in humid tropical and warm-temperate forests and are likewise considered ancient components of humid forest ecosystems (Chomnunti & al. 2014; Schmidt & al. 2014).

Amber specimen GZG.BST.21998 demonstrates the

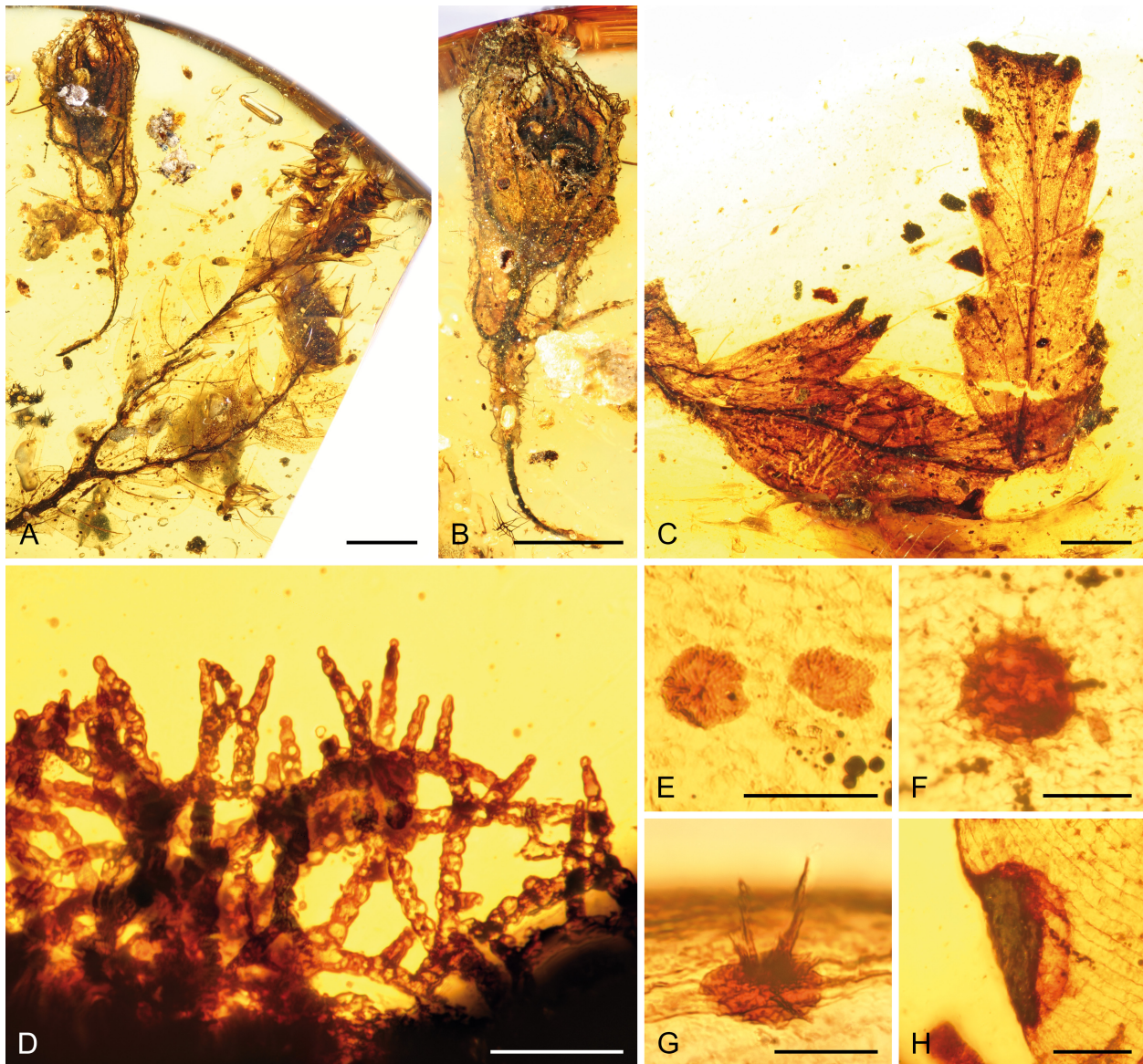


Fig. 39. Vascular plants and fungi associated with *Selaginella* from Kachin amber. – A, B: angiosperm flower *Antiquifloris latifibris* preserved close to *S. heinrichsii* (GZG.BST.22004); C: leaf fragment of fern *Cystodium sorbifolioides* (GZG.BST.21964a); fossil originally present in same amber block that also contained *S. longifimbriata* (GZG.BST.21998), but later cut away to better access different inclusions; D: branching and anastomosing moniliform aerial hyphae of sooty moulds on a plant fragment preserved close to holotype of *S. heterosporangiata* (GZG.BST.21999); E–H: structures resembling fly-speck fungi (*Ascomycota*, *Capnodiales*) on ventral trophophylls of *S. heinrichsii* (E, F: GZG.BST.22004), *S. villosa* (G: GZG.BST.22028) and sterile *Selaginella* preserved in PB25338 (H). – Scale bars: A–C = 2 mm; D–H = 50 μ m.

syntopic occurrence of spike mosses and ferns in the Kachin amber forest, because it contains *Selaginella longifimbriata* and *Cystodium sorbifolioides* (Fig. 39C) as syninclusions. The family *Cystodiaceae* presently comprises only one fossil and one extant species. The extant *C. sorbifolium* thrives exclusively in the tropical forests of the SE Asian archipelago (Regalado & al. 2017). *Selaginella heinrichsii* is preserved along with a specimen of *Antiquifloris latifibris* Poinar & R. Buckley (Poinar & al. 2016, Fig. 39A, B), an enigmatic angiosperm flower, for which no ecological data are yet available.

Regardless of the pending reconstruction of the canopy structure of the Kachin amber forest, we consider the

high number of free-sporing plants and associated fungi, in absence of evidence of adaptations to arid conditions, as indicative of constant high humidity in the herbaceous layer. The Kachin amber cryptogamic diversity would best fit in year-round constantly humid conditions where it formed a shaded groundcover under a more or less closed canopy rather than in an open forest. This contrasts with the semi-open conditions suggested for the Palaeogene Baltic amber forest (Kaasalainen & al. 2017; Sadowski & al. 2017a, 2017b, 2020, 2022; Rikkinen & Schmidt 2018).

Permanent humidity on the forest floor is furthermore substantiated by the discovery of several specimens of

peripatid velvet worms in Kachin amber (Grimaldi & al. 2002; Oliveira & al. 2016). Although these members of the Onychophora possess a dry skin and uricotelic metabolism, they are unable to sufficiently control their respirative water loss via cuticle and tracheae (Manton & Ramsay 1937). They are therefore generally confined to microhabitats with year-round high moisture levels and atmospheric humidity close to saturation (Bursell & Ewer 1950). If shelter in moist, rotten logs or deeper soil layers is unavailable, even a short phase of desiccation is usually not survived (Ruhberg 1985). Although onychophorans have efficient adaptations for a terrestrial life, the type of tracheal system may have been responsible for the group not becoming more widespread and abundant (Manton & Ramsay 1937). The restriction to permanently damp microhabitats, which lowers dispersal ability, is even considered one reason for the high endemism of onychophoran species (Oliveira & al. 2011). This ecological trait is intrinsic in all known extant onychophorans, whether tropical or temperate, because it is based on their body plan, so that it is plausible that Cretaceous representatives were likewise confined to environments with constantly humid conditions.

Amber containing marine isopods, ostracods and a juvenile ammonite (Xing & al. 2018; Yu & al. 2019) attest that the Kachin amber forest grew close to the coast. Marine organisms may become preserved in amber along with terrestrial taxa if the resinous trees grew in coastal settings (Girard & al. 2008; Schmidt & al. 2018). This renders lowland forests that received moisture through frequent precipitation the most likely source areas for the Kachin amber.

5. Summary

The diversity of *Selaginella* in Kachin amber currently comprises 21 species, which renders *Selaginella* the most diverse plant genus recorded to date for any amber deposit worldwide. Ten species can safely be assigned to the extant *S.* subg. *Stachygynandrum*, which accounts for approximately 80% of the present-day *Selaginella* diversity (Weststrand & Korall 2016a, 2016b). However, prior to the discovery of the Kachin amber inclusions, this subgenus was without a *bona fide* fossil record. The occurrence of bilateral strobili is restricted to a minority of about 60 modern species within *S.* subg. *Stachygynandrum*. Finding ten species with bilateral strobili in Kachin amber, therefore, suggests that *S.* subg. *Stachygynandrum* dominated the diversity within the genus already in the mid-Cretaceous. Furthermore, Kachin amber has yielded the first macrofossils attributable to *S.* subg. *Ericetorum*. As a result, the Kachin amber fossils substantially contribute to our understanding of the last 100 million years of evolutionary history of the genus *Selaginella* and confirm the divergence time estimates by Weststrand (2016) and Klaus & al. (2017),

suggesting that these subgenera date back to the late Mesozoic.

The number of *Selaginella* species in the source area of the Kachin amber was probably considerably higher than presently documented and exceeds any local species number in modern ecosystems (see Schmidt & al. 2020, for discussion). As the limited dispersal capacity of megaspores is a likely cause of endemism and relatively low local species numbers, the high number of species in Kachin amber argues for a mid-Cretaceous world with hundreds of *Selaginella* species (Schmidt & al. 2020). Notably, this past diversity comprised character combinations that are unknown in *Selaginella* today, such as the occurrence of a sporophyll-pterix in sporophylls of isophyllous strobili.

The high diversity and abundance of *Selaginella* strongly suggest that this taxon was a major component of the groundcover or herbaceous layer in the Kachin amber forest. This is underpinned by the identification of otherwise unknown insects mimicking spike mosses from this amber deposit. We consider the high number of *Selaginella* fossils and species, along with abundance of associated fungi and high diversity of free-sporing plants in general, and the absence of xerophytes, as being indicative of year-round high atmospheric humidity in the herbaceous layer of the source area of Kachin amber. The highly diverse arthropod fauna from Kachin amber (Ross 2022) suggests that numerous distinct microenvironments and niches existed in the source forests. Each of these niches and microenvironments could well have been the habitat of one or several *Selaginella* species that were well-adapted to the conditions prevailing in their respective places of growth. The diversity of *S.* subg. *Stachygynandrum* in Kachin amber suggests that the evolutionary origins of the present-day *Selaginella* diversity predate the early phase of the Angiosperm Terrestrial Revolution.

Author contributions

ARS and LR designed the study, examined the fossils, performed the primary morphological analyses and wrote the taxonomic treatment. ARS, PK, MK, SW and LR evaluated the validity of the new fossil-species and the characters used to define them. ARS prepared and photographed the fossils. EMS segmented the microCT data. LB crafted the line drawings. ARS, PK, MK, SW, EMS, JB, JR and LR analysed the ecological data. All authors reviewed the results, commented on the manuscript and approved the final version.

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The current complex political situation and armed conflict in Kachin State of Myanmar severely affects and aggravates the living conditions of the local population (e.g. Sokol 2019). We would like to point out that the research presented in this study is based exclusively on fossils purchased before the outbreak of the hostilities in 2017 and that we support all recommendations given by Haug & al. (2020) and Peretti (2021). The ongoing conflict in Myanmar is in desperate need of increased international awareness. We hope that publication of the results of our research on *Selaginella* fossils from Kachin State will contribute to bringing Myanmar and its unique natural heritage to the attention of a diverse audience and that this, in turn, will raise awareness also for the political situation.

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