Letters

Selaginella was hyperdiverse already in the Cretaceous

The spike mosses (*Selaginella* P.Beauv.; *c.* 750 species) are not only the most speciose extant genus of lycophytes, but also one of the largest land plant genera (Jermy, 1990). In addition to the exceptionally high number of living species it comprises, *Selaginella* is an ancient lineage believed to date back to the Carboniferous or even Devonian, based on fossil evidence (Kenrick & Crane, 1997; Thomas, 1997; Korall *et al.*, 1999; Taylor *et al.*, 2009) and DNA-based divergence time estimates (Klaus *et al.*, 2017; Morris *et al.*, 2018).

Selaginella is notorious for the small morphological differences seen among many species, both extant as well as fossils attributed to this lineage. Most present-day species are characterised by aniso-phyllous, flattened shoots with vegetative leaves (trophophylls) arranged in four rows, that is two dorsal rows of smaller leaves and two ventral rows of larger leaves. Some 50 extant species possess monomorphic vegetative leaves. Sporophylls and sporangia typically occur clustered in the form of tetrastichous (rarely helical) strobili at branch tips. The sporophylls are uniform in size and shape in the majority of extant species; however, there are *c.* 60 extant species in which not only the trophophylls, but also the sporophylls, are dimorphic. Strobili in most of these latter species are resupinate, that is characterised by smaller sporophylls in the same plane as the larger trophophylls.

The relatively undifferentiated gross morphology renders attempts to assess the morphological evolutionary history of the genus difficult. Nevertheless, each subgenus is characterised by a unique combination of morphological characters (Weststrand & Korall, 2016a,b). The vast majority of extant members of the genus belong to the cosmopolitan subgenus *Stachygynandrum* (P.Beauv. ex Mirb.) Baker (Weststrand & Korall, 2016b), of which there is no persuasive fossil record to date.

Based on time-calibrated molecular phylogenies, most of the seven currently recognised extant subgenera within *Selaginella* (Weststrand & Korall, 2016b) are suggested to date back to the late Mesozoic, while the lineage leading to subgenus *Selaginella* (with only two extant species, sister to the rest of the genus) probably originated in the Carboniferous, or even earlier (Weststrand, 2016; Klaus *et al.*, 2017). The record of selaginellalean fossils from the Paleozoic and Mesozoic, however, is heterogeneous and comprised largely of impressions and compressions of sterile leafy shoots, isolated strobili or fertile shoots with strobili (sometimes

Dedication: We dedicate this paper to our late colleague Jochen Heinrichs (1969–2018) with whom we discussed the fossils and who was very excited about the discovery of *Selaginella* in Burmese amber.

containing *in situ* spores), and dispersed spores (e.g. Ash, 1972; Thomas, 1997; Wierer, 1997; Bek *et al.*, 2001, 2009; Pšenička & Opluštil, 2013; McLoughlin *et al.*, 2014; van Konijnenburg-van Cittert *et al.*, 2014, 2016), with few forms so well preserved in all parts that the complete set of structural features necessary for the safe attribution to a subgenus can be obtained (but see Ash, 1972, and Thomas, 2005).

Moreover, as no fossils representing the *Stachygynandrum* clade are known to date, some 80% of the species in *Selaginella* have no calibration point among them, which severely affects the reliability of the dating of this group. It therefore remains unresolved for how long in Earth history *Selaginella* has been a species-rich lineage, and when exactly (and why) the present-day prevalence of subgenus *Stachygynandrum* has evolved.

Selaginella from mid-Cretaceous Burmese amber

It might be expected that the delicate, herbaceous, free-sporing *Selaginella*, which abundantly occurs in humid forests, would have a substantial fossil record in amber (fossil tree resin). However, this was not the case until very recently.

Amber does not occur continuously in Earth history (Seyfullah *et al.*, 2018), and only a few Cretaceous and Cenozoic ambers have preserved plant remains in larger numbers. Kachin amber, the older variety of the more widely known Burmese amber, originates from the Albian-Cenomanian (*c.* 100 million years old (Ma)) of Myanmar (for additional information on provenance and age, refer to Supporting Information Notes S1), and presently represents the most important source of three-dimensionally preserved younger Mesozoic terrestrial organisms (plants, animals and microorganisms). More than 1200 species have been formally described, half of those in the last 3 years (Ross, 2019), including some 20 taxa of free-sporing land plants such as liverworts, mosses and ferns (Hedenäs *et al.*, 2014; Heinrichs *et al.*, 2018; Regalado *et al.*, 2019), which makes Burmese amber the most likely source for Cretaceous lycophyte fossils entombed in amber. Recent screening of several collections of Kachin amber has yielded 14 distinct morphologies of fertile *Selaginella* (Fig. 1) preserved in 29 pieces of amber (for information on handling of the amber, see Methods S1, and for repository information, refer to Table S1).

Entombment of the plants in amber has preserved all essential characteristics of these *Selaginella* fossils, including: (1) an axial stele situated in an air-filled (amber-infilled in the fossils) central canal and connected to the cortical tissue by so-called trabeculae (Fig. 2a) is a synapomorphy for Selaginellaceae; (2) a ligule (i.e. a minute, scale-like flap of tissue) located proximally on the adaxial leaf surface (Fig. 2b) is a characteristic of all extant heterosporous lycophytes (Isoetaceae Rchb. and Selaginellaceae Willk.); (3) rhizophores (root-like structures that typically are borne in the branch dichotomies of aerial shoots, Fig. 2c); and (4) megaspores
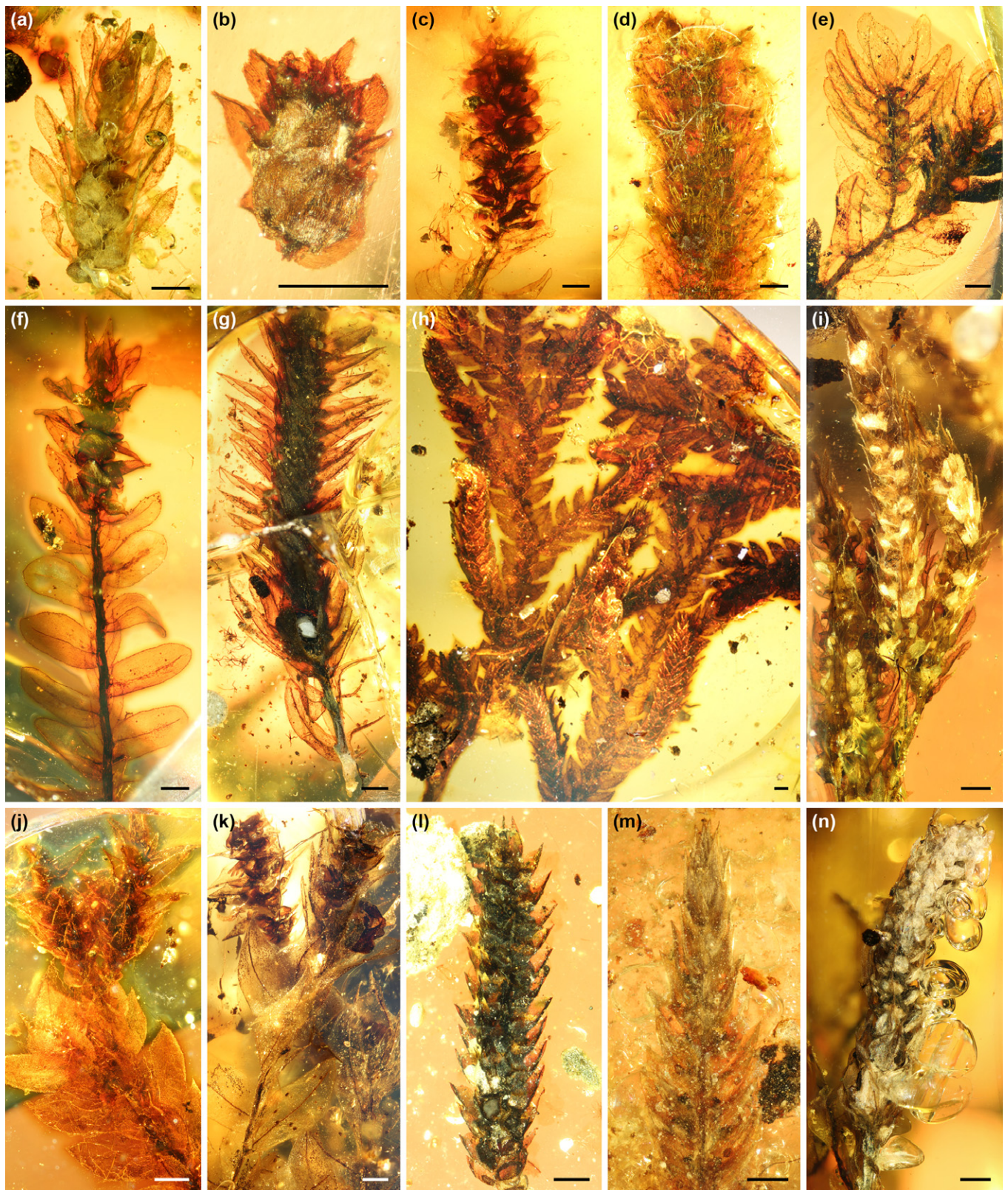
Fig. 1 Diversity of *Selaginella* from Albian-Cenomanian Burmese amber (Kachin amber) of Myanmar. Gross morphology of the 14 currently available fertile taxa. Specimens housed in the collections of the Geoscience Centre at the University of Göttingen (GZG) and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (PB). (a) GZG.BST.22000, (b) GZG.BST.22002, (c) GZG.BST.21999, (d) GZG.BST.21998, (e) GZG.BST.21997, (f) GZG.BST.21966, (g) GZG.BST.22001, (h) GZG.BST.22006, (i) PB23101, (j) PB23159, (k) GZG.BST.22004, (l) PB23160, (m) GZG.BST.22005, (n) GZG.BST.22003. Bars, 500 μm.
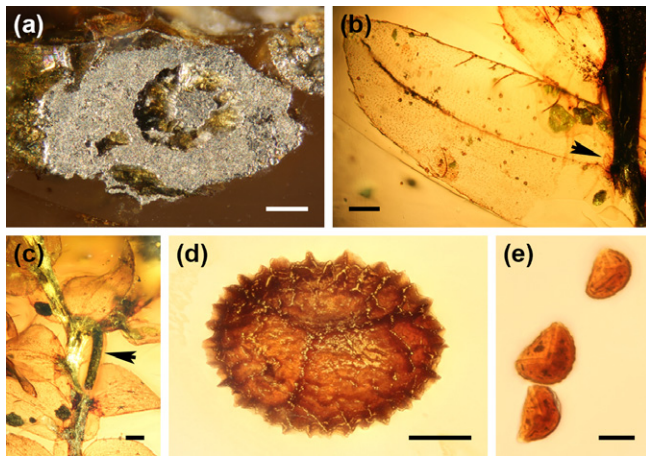
Fig. 2 Characteristics justifying assignment of the Burmese amber inclusions to *Selaginella*. (a) Slightly oblique section exposed at the amber surface, showing central stele and several trabeculae connecting stele and outer tissue. The void is filled by amber (GZG.BST.21999). (b) Ventral trophophyll with ligule (arrowhead, GZG.BST.21997). (c) Rhizophore (arrowhead, PB23161). (d) Megaspore (GZG.BST.21966). (e) Microspores of the same specimen (GZG.BST.21966). Bars: (b, c), 200 μm; (a, d), 100 μm; (e), 20 μm.

and microspores that are comparable in size and shape with the spores seen in extant *Selaginella* (Fig. 2d,e).

Trophophylls, where preserved, are dimorphic and arranged in four rows; two rows of smaller dorsal leaves and two rows of larger ventral leaves (e.g. Fig. 1f). Strobili are tetrastichous (i.e. sporophylls arranged in four rows) and isophyllous (i.e. with monomorphic sporophylls) in eight of the fossil morphologies (Fig. 1g–n), but anisophyllous (i.e. bilateral strobili with dimorphic sporophylls) in the others (Fig. 1a–f). Whenever trophophylls are preserved, the bilateral strobili are evidently resupinate. Based on the presence of bilateral strobili, six of the fossils (Fig. 1a–f) can be assigned confidently to the extant subgenus *Stachygynandrum* (Weststrand & Korall, 2016b; see high magnification annotated images of specimens confidently assigned to subgenus *Stachygynandrum* in Figs S1, S2).

The fossil morphologies are distinguished in characteristics that are also used in the discrimination of extant species, including: (1) strobilus size; (2) size and shape of sporophylls and trophophylls (including axillary leaves); (3) either monomorphic or dimorphic sporophylls; (4) presence or absence and size of marginal teeth in sporophylls and trophophylls; (5) presence or absence and length of cilia at sporophyll and trophophyll margins; (6) presence or absence on sporophylls of a keel and its dentation; and (7) the ornamentation of the megaspores (for description and quantification of these key characters in each of the specimens see Tables S2, S3). As there is little variation of extant species in the combination of these characters, we regard the fossil morphologies to represent extinct species. Individual species descriptions will be presented in a separate paper.

Evolutionary implications

Lycophytes originated in the Silurian (Morris *et al.*, 2018) and evolved to become the dominant floral elements of the later Paleozoic (DiMichele *et al.*, 2001). While the initial diversification of the lycophytes occurred during the Devonian and Carboniferous (Kenrick & Crane, 1997; Morris *et al.*, 2018), much of their extant diversity has been suggested to have originated considerably later. Apart from the early divergences in the Lycopodiopsida in the Late Triassic, most extant lineages are supposed to have diversified during the Cretaceous (Klaus *et al.*, 2017; Pereira *et al.*, 2017; Testo *et al.*, 2018), coinciding with the rise of modern fern and angiosperm lineages (Schneider *et al.*, 2004; Schuettpelz & Pryer, 2009; Barba-Montoya *et al.*, 2018; Morris *et al.*, 2018).

Our newly discovered fossils support the notion of a Cretaceous diversification also for *Selaginella*, and suggest that the genus has been hyperdiverse since at least this period of geological time. The Burmese amber inclusions provide evidence of at least 14 species of *Selaginella* that occurred in the source area of the amber. Moreover, six of these taxa represent the first compelling fossils of members of the extant subgenus *Stachygynandrum*. However, the diversity of *Selaginella* in the amber source forests probably was still higher, taking into account that not all species of an ecosystem with resinous trees become enclosed in resin outpourings. Furthermore, much of the resin may not have survived processes of erosion, transport and re-deposition and not all amber pieces are eventually found and made available for study. Reports of marine isopods, ostracods, and even a juvenile ammonite in this amber (Xing *et al.*, 2018; Yu *et al.*, 2019) suggest a near-coastal lowland area as a source of Kachin amber, and a rich fossil flora of ferns, liverworts and mosses indicates that high humidity prevailed in the tropical Burmese amber forest (Hedenäs *et al.*, 2014; Heinrichs *et al.*, 2018; Regalado *et al.*, 2019).

Likewise, most extant species of *Selaginella* occur in primary tropical moist forests (Korall & Kenrick, 2002). For instance, more than 75% of the nearly 300 species inhabiting the Neotropics thrive in humid forests (Alston, 1952; Mickel & Smith, 2004; Hirai, 2015; Smith & Kessler, 2018). Similarly, the majority of the *c.* 200 South-East Asian *Selaginella* species grows in lowland to midmontane primary and secondary forests (Camus, 1997; de Winter & Jansen, 2003). About half of the African species are also inhabitants of humid forests (Quansah, 1986; Roux, 2009). These available numbers are for larger areas, rather than particular forest types in narrower regions. Extant autochthonous *Selaginella* species are characterised by a clear pattern of endemism by biogeographic region. There is virtually no example of a pantropical or cosmopolitan species in extant tropical *Selaginella*. In contrast to the rather continental fern flora of the West Indies, for example, only five of the 37 *Selaginella* species from these islands also occur in mainland tropical America, thus reflecting more than 80% endemism. One likely cause for this notable level of endemism is the limited dispersal capacity of megaspores. The megaspores (as well as possibly fragments of leafy shoots) are large and relatively heavy, and hence not likely to be transported far by wind.

Confirmed species numbers for narrower regions, if available, are much lower. For example, local diversity in South-East Asia ranges between seven and 14 species. Ten species of *Selaginella* have been counted in the lowland rainforest of Khao Nan National Park that is said to harbour the highest diversity of free-sporing vascular plants in Thailand (Boonkerd *et al.*, 2008); 11 species have been

documented in two gradients in northern and northwestern Myanmar (Khine *et al.*, 2017); 12 species have been recorded along a transect in Java (Setyawan *et al.*, 2016); 12 species in Seram and Ambon, Moluccas (Kato, 1988); seven species in a karst forest of Bohol Island, the Philippines (Barcelona *et al.*, 2006); and Bautista *et al.* (2018) collected 22 species in the mountains of Mindanao Island, the Philippines, but no more than 14 species were found in any individual mountain area. These extant species numbers from different tropical regions show that, in a world with hundreds of *Selaginella* species, the local number of species in an ecosystem type or biome compares well with the number of taxa recorded for Burmese amber.

Burmese amber opens a window into the Cretaceous Terrestrial Revolution (KTR) 125 to 80 Ma (Lloyd *et al.*, 2008; Benton, 2010; Liu *et al.*, 2018), when angiosperms rose to ecological dominance, and terrestrial biodiversity of macroscopic species exceeded that in the sea (Vermeij & Grosberg, 2010). The explosive radiation of angiosperms during this period of time probably interacted with the diversification of key elements of the modern biosphere (Dilcher, 2000; Meredith *et al.*, 2011; Barba-Montoya *et al.*, 2018). New ecological niches emerged and, in turn, triggered further diversification of other plant groups such as the core of polypod ferns (Schneider *et al.*, 2004) and epiphytic liverworts (Feldberg *et al.*, 2014), as well as insects such as bees, lepidopterans and beetles (Grimaldi, 1999; Misof *et al.*, 2014; Zhang *et al.*, 2018). Apart from the co-evolution of angiosperms and insects, much of the increasing diversity in the KTR is seen in the light of a sustained increase in humidity in angiosperm-dominated forests, as a consequence of significantly increasing evaporation from angiosperm leaves (Boyce *et al.*, 2010). The highly diverse arthropod fauna preserved in Burmese amber (Ross, 2019) is another proxy indicator of the presence of numerous different niches and micro-environments in the Burmese amber source area. Spatial heterogeneity (e.g. micro-topographical gradients) in extant tropical forests is a major reason for high species numbers (Wright, 2002), and was perhaps also a driving force in the diversification of *Selaginella* within the Burmese amber forest.

High substitution rates and rate heterogeneity were reported to occur in *Selaginella* (Korall & Kenrick, 2004). It has been argued that land plant clades with higher background substitution rates may undergo successful diversification under new conditions. These clades are therefore more likely to survive in rapidly changing or novel environments, in spite of the fact that they otherwise are more susceptible to the various pressures that cause extinction because of their relatively higher levels of mutational genetic load (Lancaster, 2010). Increase in speciation and a decrease in extinction, as well as robustness and adaptability were discussed as reasons for higher 'node density' (diversity) in *Selaginella* (Klaus *et al.*, 2017). The high Cretaceous species diversity is suggestive of a steadily high speciation rate for *Selaginella* species, rather than a lower extinction rate and, consequently, a steady turnover of species (Banks *et al.*, 2011; Baniaga *et al.*, 2016).

The presence of at least 14 distinct morphologies demonstrates that species diversity in *Selaginella* was high in the mid-Cretaceous. We therefore suggest that *Selaginella* was hyperdiverse already 100

Ma, possibly even comprising hundreds of species. Discovery of the first fossils of representatives of the subgenus *Stachygynandrum* confirms that this lineage dates back to at least the Albian-Cenomanian, and six distinct amber-preserved morphologies of this subgenus indicate that *Stachygynandrum* had already then risen to dominate *Selaginella* diversity. The combination of diverse niches and favourable humid tropical climate, together with the adaptability and high substitution rates of *Selaginella*, may have triggered the high species number recorded here for the first time for the mid-Cretaceous.

Author contributions

ARS designed the research. PM, BW and XW provided fossil specimens. ARS and EJ prepared and documented the specimens. ARS, LR, SW, PK, E-MS, HS, EJ, JB, MK, XW, JR and LJS analysed the fossils and wrote the manuscript. All authors commented on the manuscript.

Data availability

The fossils reported in this study are part of the publicly accessible collections of the Geoscience Centre at the University of Göttingen (GZG) and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (PB). See figure captions and Table S1 for collection numbers.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Shoot with resupinate strobili of a fossil representative of subgenus *Stachygynandrum* from Kachin amber.

Fig. S2 Anisophyllous (bilateral) strobilus of a fossil representative of subgenus *Stachygynandrum* from Kachin amber.

Methods S1 Preparation and microscopy.

Notes S1 Provenance and age of the amber.

Table S1 Repository information for the specimens of Kachin amber that form the basis of this study.

Table S2 Synopsis of important characters of fossil *Selaginella* species from Kachin amber 1; forms with anisophyllous (bilateral) strobili.

Table S3 Synopsis of important characters of fossil *Selaginella* species from Kachin amber 2; forms with isophyllous strobili.

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