

Extending the diversity of the bryoflora in Kachin amber (Myanmar), with the description of *Radula patrickmuelleri*, sp. nov. and *R. tanaiensis*, sp. nov. (Jungermanniopsida, Porellales, Radulaceae)

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Abstract

The most prolific source of exquisitely preserved bryophyte fossils is amber, which often contains inclusions in a three-dimensional and life-like state of preservation. In recent years, many fossil species have been described from 16 worldwide deposits ranging in age from the Miocene to the Cretaceous. One of the oldest is mid-Cretaceous Kachin amber from Myanmar. It includes the moss genera *Vetiplanaxis* and *Calymperites* as well as the leafy liverwort genera *Frullania*, *Gackstroemia*, *Protofrullania*, and *Radula*. All liverwort fossils belong to the mainly epiphytic Porellales, a group which was probably strongly influenced by the rise of angiosperms and underwent significant lineage turnover in the Cretaceous. Hence, Kachin amber provides important information on the evolution of leafy liverworts during a period characterized by fundamental changes in terrestrial ecosystems. Here, we describe two new species of the mainly epiphytic leafy liverwort genus *Radula* (Radulaceae), *R. patrickmuelleri* sp. nov. and *R. tanaiensis* sp. nov., and emend the description of *Frullania kachinensis* (Frullaniaceae). *Radula* is now represented by four species and one fossil only described to genus level, which indicates a high diversity already in the mid-Cretaceous. Furthermore, we describe additional fossil specimens of Frullaniaceae, including the third fertile specimen of *Frullania baerlocheri*, one sterile fossil of *F. cretacea*, and 12 sterile fossils of *Protofrullania cornigera*. The new fossil evidence necessitates an emendation of a recently published determination key for Cretaceous Jungermanniidae.

Key Words

Amber fossils, Cretaceous, epiphytes, leafy liverworts

Introduction

The description of bryophyte fossils from worldwide amber deposits underwent much progress in recent years with the number of species as well as the number of deposits increasing steadily (e.g., Bouju et al. 2021; Feldberg et al. 2021a, 2021b; Wang et al. 2021). Most of these fossils derive from Cenozoic deposits and have been found in middle Miocene Zhangpu amber from China (Wang et al. 2021), early Miocene Chiapas amber from Mexico (e.g.,

Estrada-Ruiz and Riquelme 2017; Feldberg et al. 2021a), early Miocene Dominican amber (e.g., Frahm and Newton 2005; Feldberg et al. 2021a), early Miocene Shewa amber from Ethiopia (Bouju et al. 2021), Miocene Cape York amber from Australia (Hand et al. 2010), Paleogene Bitterfeld amber from Germany (e.g., Frahm 2010; Feldberg et al. 2021a), late Eocene Baltic amber (e.g., Frahm 2010; Feldberg et al. 2021a), late Eocene Rovno amber from Ukraine (e.g., Ignatov et al. 2019; Feldberg et al. 2021a), late middle Eocene Anglesea amber from

Australia (Stilwell et al. 2020), middle Eocene Sakhalin amber from Russia (Ignatov and Perkovsky 2013), early Eocene Cambay amber from India (e.g., Heinrichs et al. 2016a), and Paleocene-Eocene amber from the Chickaloon Formation in Alaska (Grimaldi et al. 2018). The oldest sources are Late Cretaceous Taimyr amber from Russia (e.g., Ignatov et al. 2016), Late Cretaceous Kuji amber from Japan (e.g., Katagiri et al. 2013; Katagiri and Shinden 2020), mid-Cretaceous Alaskan amber (Heinrichs et al. 2011), and mid-Cretaceous Kachin amber from northern Myanmar (e.g., Hedenäs et al. 2014; Heinrichs et al. 2014; Feldberg et al. 2021a, 2021b; Li et al. 2021b, 2022b). The latter includes the moss genera *Vetiplanaxis* with four species and *Calymperites* with one (Bell and York 2007; Hedenäs et al. 2014; Heinrichs et al. 2014) as well as a very diverse flora of porellalean leafy liverworts which has recently been revised by Feldberg et al. (2021b) and regularly yields new and interesting fossil species (e.g., Li et al. 2020, 2021b, 2022b).

Amber fossils provide important information on the evolution of leafy liverworts (Jungermanniidae) which are otherwise comparatively rare in the fossil record (e.g., Heinrichs et al. 2018; Tomescu et al. 2018). In contrast, thalloid liverworts (Pelliidae, Metzgeriidae, Marchantiopsida) and mosses (Bryophyta) are found more frequently in sedimentary rocks since the Middle Devonian and the Carboniferous, respectively (Tomescu et al. 2018; Ignatov and Maslova 2021). The often excellent and three-dimensional preservation state in amber allows utilization of many amber inclusions as minimum age constraints in divergence time estimates based on molecular phylogenies of extant species (e.g., Feldberg et al. 2014, 2021a; Laenen et al. 2014; Bechteler et al. 2017). Subsequent diversification analyses of Jungermanniidae indicate that the order Porellales, which mainly comprises epiphytes and epiphylls, underwent a lineage turnover beginning in the Cretaceous when flowering plants were on the rise (Feldberg et al. 2014). The Angiosperm Terrestrial Revolution (e.g., Magallón et al. 2019; Benton et al. 2022) caused fundamental changes in terrestrial ecosystems and has likely influenced the evolution of epiphytic lineages. Furthermore, Cretaceous Porellales often show distinct morphological differences to modern taxa which is another indicator of significant changes within this taxon during this period (Feldberg et al. 2021a, 2021b).

The most striking differences can be found in Frullaniaceae, by far the most diverse taxon included in amber. The family includes one extant genus, the mainly epiphytic *Frullania*, which is morphologically well defined but has a very complex subgeneric taxonomy with 576 accepted species in several subgenera whose circumscription is often unclear (e.g., Hentschel et al. 2009b, 2015; Heinrichs et al. 2010; von Konrat et al. 2013; Söderström et al. 2016; Carter et al. 2017). Extant *Frullania* has a subcosmopolitan distribution with a center of diversity in humid tropical regions, but also occurs in temperate as well as arctic and alpine areas (Schuster 1992; Hentschel et al. 2009b). The family also includes the

extinct *Protofrullania cornigera* Heinrichs from Kachin amber (Heinrichs et al. 2017a; Feldberg et al. 2021b) and probably the extinct *Kaolakia borealis* Heinrichs et al. from Alaskan amber (Heinrichs et al. 2011) as well as *Pseudofrullania hamatosetacea* (Grolle) Heinrichs et al. from Bitterfeld amber (Heinrichs et al. 2018).

Despite having an extant center of diversity in the tropics, Cenozoic *Frullania* fossils are rarely reported from tropical regions. To date, only one inclusion of *Frullania* has been found in Dominican amber, which otherwise contains a very diverse leafy liverwort flora (Heinrichs and Schmidt 2010; Feldberg et al. 2021a), and two species have recently been described from Ethiopian Shewa amber, namely *F. shewanensis* Feldberg et al. and *F. palaeo-africana* Feldberg et al. (Bouju et al. 2021). In contrast, the genus is highly diverse in Cenozoic European ambers (Feldberg et al. 2021a). Fifteen species of *Frullania* have been described, with *F. grabenhorstii* Heinrichs et al. and *F. mammilligera* Grolle occurring only in Bitterfeld amber (Grolle 2003; Feldberg et al. 2018), *F. acutata* Casp. only in Baltic amber (Caspary 1887), and *F. ekaterinae* Mamontov et al., *F. riclefgrollei* Mamontov et al., *F. rovnoi* Mamontov et al., *F. schmalhausenii* Mamontov et al., *F. vanae* Mamontov et al., and *F. zerovii* Mamontov et al. only in Rovno amber (Mamontov et al. 2015, 2017, 2018, 2019, 2020). *Frullania baltica* Grolle, *F. casparyi* Grolle, *F. schumannii* (Casp.) Grolle, and *F. truncata* Casp. occur in Bitterfeld as well as Baltic amber (Caspary 1887; Grolle 1981, 1985; Grolle and Meister 2004), *F. pycnoclada* Grolle occurs in Baltic and Rovno amber (Grolle and Meister 2004; Mamontov et al. 2020), and *F. varians* Casp. occurs in Bitterfeld, Baltic, and possibly also Rovno amber (Caspary 1887; Grolle and Meister 2004; Konstantinova et al. 2012; Mamontov et al. 2020). While some of these species show some unique characters, which make an assignment to extant subgenera or sections difficult, many are very similar to the extant diversity and could be employed in divergence times estimates, given extended DNA datasets of extant species which can solve the remaining taxonomic problems (Mamontov et al. 2020; Feldberg et al. 2021a).

The oldest unequivocal Frullaniaceae fossils have been described from Kachin amber and these tend to differ strongly from the extant diversity (Feldberg et al. 2021a, 2021b). The most common leafy liverwort inclusion found in this deposit is *Protofrullania cornigera* (Heinrichs et al. 2017a; Feldberg et al. 2021b), which differs from *Frullania* by its elongated ovate to strap-shaped underleaves which carry rhizoid bundles at their apical regions, a character unknown in *Frullania* where the undivided or bifurcated underleaves carry rhizoid bundles near their base or near the middle. But *Protofrullania* is not the only Frullaniaceae with morphological characters unknown or rare in extant representatives, also the mid-Cretaceous species assignable to *Frullania* show unique or rare characters and character combinations. One example is *F. cretacea* Hentschel et al. (Hentschel et al. 2009a; Heinrichs et al. 2012) with its long ciliate

underleaves, and another is *F. kachinensis* Y.Li et al. (Li et al. 2021b), which has bifurcated underleaves with serrate lobes and rhizoid bundles inserted just below the sinus. The remaining fossil species *F. baerlocheri* Heinrichs et al. and *F. partita* Y.Li et al. might look more similar to the extant diversity, but do not fit any extant lineage within the genus due to the unusual combination of characters (Feldberg et al. 2021b; Li et al. 2021a).

Another diverse genus found in Kachin amber is *Radula*, which comprises ca. 200 extant species in seven subgenera (e.g., Devos et al. 2011; Söderström et al. 2016), most of which are epiphytes or epiphylls. *Radula* has a subcosmopolitan distribution with a center of diversity in tropical to warm temperate regions. In recent years several molecular phylogenetic studies greatly extended the knowledge of this taxonomically challenging genus (Devos et al. 2011; Renner et al. 2013a, 2013b; Renner 2014, 2015; Patiño et al. 2017). However, species delimitation based on morphological characters alone can be difficult because of the high degree of morphological homoplasy and sometimes subtle differences among relatively unrelated taxa (e.g., Renner et al. 2013a, 2014, 2015). This especially applies to fossil material which is often fragmentary and sterile.

Radula has a comparatively extensive fossil record with nine species known from different amber deposits (Grolle 1987; Heinrichs et al. 2016b, 2018; Kaasalainen et al. 2017; Stilwell et al. 2020; Feldberg et al. 2021a, 2021b). Most appear very similar to the extant diversity, though this might be misleading. The youngest fossils are *R. intacta* M.A.M. Renner et al. (Kaasalainen et al. 2017) and *R. steerei* Grolle (Grolle 1987) from Miocene Dominican amber, which are sterile and cannot be assigned to a subgenus with confidence. *Radula intacta* may belong to subg. *Volutoradula* and *R. steerei* has been compared to the extant Japanese endemic *R. fauriana* Steph. (Grolle 1987), which is listed as *incertae sedis* in Söderström et al. (2016) but was included in subgen. *Radula* sect. *Fauriana* by Yamada (1979). Three fossil species have been found in Cenozoic ambers of Europe. *Radula baltica* Heinrichs et al. is known only from the holotype in Eocene Baltic amber, while *R. sphaerocarpoides* Grolle and *R. oblongifolia* Casp. are common fossils in Baltic as well as Bitterfeld amber (Caspary 1887; Grolle 1980; Grolle and Meister 2004; Heinrichs et al. 2016b). The latter species is autoicous and is often preserved with androecia, gynoecia, and sporophyte, while the former two are only known in sterile condition and might represent several biological entities given their morphological heterogeneity (Heinrichs et al. 2016b). Furthermore, two fossil specimens have been reported from late middle Eocene amber of Anglesea, Victoria, Australia (Stilwell et al. 2020) but have not been formally described. The oldest previously described species are *R. cretacea* Bechteler et al., which is preserved with apparently unfertilized gynoecia, and the likely distantly related and sterile *R. heinrichsii* Feldberg et al. from Kachin amber (Bechteler et al. 2017; Feldberg et al. 2021b; Wang et al. in press). *Radula cretacea* is probably a member of subg. *Odontoradula* and may even

represent one of the several crown group lineages, given the shared possession of characters displayed by extant species of *Radula* subg. *Odontoradula* sect. *Acutifoliae* (Bechteler et al. 2017). The relationship of *R. heinrichsii* is more obscure, because its microphyllous (amentulose) branches have no exact equivalent among extant species, though their presence along with the longitudinal lobule stem insertion suggests the species belongs to subg. *Amentuloradula* (Feldberg et al. 2021b).

Here we describe two further fossil species of this diverse genus from Kachin amber as *R. patrickmuelleri* sp. nov. and *R. tanaiensis* sp. nov. and provide an updated determination key for Cretaceous Jungermanniidae. Furthermore, we obtained several new specimens of previously described fossil species which we list and evaluate. These include several sterile specimens of *Protofrullania cornigera*, one sterile specimen each of *Frullania cretacea* and *F. kachinensis*, the third fertile specimen of *F. baerlocheri* with gynoecium, as well as a fossil showing strong similarities to *Radula cretacea*. Furthermore, two additional specimens of the moss *Calymperites burmensis* Heinrichs et al. are illustrated. Most specimens are in good accordance with the type material, others require diagnoses and descriptions to be emended.

Material and methods

All fossils derive from Kachin amber of northern Myanmar which was mined from outcrops about 20 km southwest of the village of Tanai located on the Ledo Road ca. 105 km north of Myitkyina in Kachin State, northern Myanmar (Cruickshank and Ko 2003; Grimaldi and Ross 2017). Several lines of evidence point to a mid-Cretaceous age of Kachin amber (Grimaldi et al. 2002; Grimaldi and Ross 2017). Biostratigraphic studies by Cruickshank and Ko (2003) suggested an age of ca. 100 Ma (late Albian) of the amber-bearing deposit, and Shi et al. (2012) assigned a minimum age of 98 Ma (earliest Cenomanian) based on recent U-Pb dating of zircons. These age estimates have recently been confirmed by the discovery of an ammonite shell of the genus *Puzosia*, a late Albian–late Cenomanian index fossil, enclosed in a piece of Kachin amber (Yu et al. 2019).

The specimens of *Protofrullania cornigera* (BuB 3811, 3812, 4333–4338, 4394, 4408, 4409, 4413), *Frullania cretacea* (BuB4411), and *Calymperites burmensis* (BuB 4339, 4398) are housed in the Patrick Müller Amber Collection (Amber Research Group, c/o Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg). *Frullania baerlocheri* GZG.BST.22039 (BuB4220), *F. kachinensis* GZG.BST.22040 (BuB4431), *Radula patrickmuelleri* GZG.BST.22041 (BuB4395), *R. tanaiensis* GZG.BST.22042 (BuB4329), and *Radula* sp. GZG.BST.22043 (BuB4420) are housed in the Geoscience Centre (GZG) at the University of Göttingen, Germany (all formerly Patrick Müller Amber Collection). *Frullania kachinensis* PB22711a (holotype) is housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Relating to the recent conflicts in Myanmar (e.g., Sokol 2019), we declare that all Kachin amber pieces mentioned in this study have been collected before the year 2017 and that we follow the recommendations by Haug et al. (2020). The specimens from the American Museum of Natural History were provided to the museum prior to 2010 (refer to Hentschel et al. 2009a and Heinrichs et al. 2012). The fossils deposited in the Nanjing Institute of Geology and Palaeontology and the Zhejiang Museum of Natural History were collected in compliance with the laws of Myanmar and China, including Myanmar's import and export regulations of jewelry, and China's fossil law. Specimens deposited in the remaining collections were legally purchased from an authorized trader from Myanmar in 2016.

Frullania kachinensis (PB22711a, holotype) was examined under a ZEISS Axio ZoomV16 microscope equipped with a high-resolution digital camera (Axio-cam 512 colour). All images were digitally stacked photomicrographic composites from ca. 50 individual focal planes using the software package ZEN 2.3 pro. All other specimens were prepared for study according to procedures described by Sadowski et al. (2021). Photographic documentation of the specimens was carried out under Zeiss AxioScope A1 compound microscopes equipped with Cannon Eos 70D and Cannon Eos 5D digital cameras. All images are digitally stacked photomicrographic composites from up to 76 individual focal planes using the software package HeliconFocus version 7.6.1. Pro.

Results

Systematic paleontology

Newly described specimens of new as well as known species are indicated in bold print.

Phylum BRYOPHYTA

Class BRYOPSIDA

Subclass DICRANIDAE

Order DICRANALES

Family *incertae sedis*

Genus *Calymperites*

Calymperites burmensis Heinrichs, Schäf.-Verw., Hedenäs, Ignatov & A.R.Schmidt

Suppl. material 1: Fig. S1

Calymperites burmensis Heinrichs, Schäf.-Verw., Hedenäs, Ignatov & A.R.Schmidt; in Cretaceous Research 51: 261, figs 1, 2. 2014.

Holotype. AMNH Bu ASJH-2, Amber collection of the Division of Invertebrate Zoology of the American Museum of Natural History, New York, USA.

Additional specimens investigated. BuB4339, BuB4398, Patrick Müller Amber Collection.

Locality and horizon. Amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin

State, northern Myanmar, fossil enclosed in upper Albian–lower Cenomanian Kachin amber.

Remarks. To date, this acrocarpous moss was only known from one specimen (Suppl. material 1: Fig. S1A; Heinrichs et al. 2014). As far as the disintegrated state of the new fossils allows to ascertain, they are in good accordance with the type. In both specimens the leaves are erect-spreading and slightly crisped, their bases are oblong-ovate and sheathing the stem before they taper into lanceolate upper regions, and the costa is single and excurrent on intact leaves (Suppl. material 1: Fig. S1B–D). The apices are acute to awned in BuB4398 (Suppl. material 1: Fig. S1B), while they are mostly broken in BuB4339 (Suppl. material 1: Fig. S1C, D). It is not visible if the leaves are serrulate, or if large hyaline cells are present near the apex. Furthermore, the leaf cells are not clearly visible for the largest part, but they appear to be small and quadrate on upper parts of the lamina (Suppl. material 1: Fig. S1D) and more elongated on lower parts (Suppl. material 1: Fig. S1B).

Phylum MARCHANTIOPHYTA

Class JUNGERMANNIOPSIDA

Subclass JUNGERMANNIIDAE

Order PORELLALES

Family FRULLANIACEAE

Genus *Frullania*

Frullania baerlocheri Heinrichs, M.E.Reiner, K.Feldberg, von Konrat, Hentschel, Váňa & A.R.Schmidt

Suppl. material 1: Fig. S2A–E

Frullania baerlocheri Heinrichs, M.E.Reiner, K.Feldberg, von Konrat, Hentschel, Váňa & A.R.Schmidt; in Review of Palaeobotany and Palynology 169: 26, plate IV, figs 2, 3. 2012.

= *Frullania pinnata* Heinrichs, K.Feldberg, Schäf.-Verw. & M.Krings; in Cretaceous Research 78: 57, figs 1–3. 2017.—Holotype: GZG.BST.21963, Geoscience Centre (GZG) at the University of Göttingen, Germany; *syn. fide* Li et al., 2021a.

Holotype. AMNH Bu-FB 1 g, Amber collection of the Division of Invertebrate Zoology of the American Museum of Natural History, New York, USA.

Additional specimens investigated. SNSB-BSPG 2021 XII 1 (Müller BuB1874; syninclusion *Protofrullania cornigera*), Bavarian State Collection for Palaeontology and Geology, Munich, Germany; GZG.BST.22015 (Müller BuB3538), **GZG.BST.22039 (Müller BuB4220; with gynoecia)**, Geoscience Centre (GZG) at the University of Göttingen, Germany; PB22712, PB23288 (with gynoecia), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; BuB3681, BuB3682, Patrick Müller Amber Collection; ZMNH155044a (syninclusion *Radula heinrichsii*), ZMNH155047b, c (syninclusion *Frullania kachinensis*), Zhejiang Museum of Natural History, China.

Locality and horizon. Amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar, fossil enclosed in upper Albian–lower Cenomanian Kachin amber.

Remarks. The new fossil specimen is in good accordance with the type as well as subsequently described material and represents the third fertile specimen (Suppl. material 1: Fig. S2A–E; compare descriptions in Heinrichs et al. 2012, 2017b; Feldberg et al. 2021b; Li et al. 2021a). Two unfertilized gynoecia are situated on short side branches similar to specimen PB23288 (Li et al. 2021a), but they are less far developed and most characters are obscured (Suppl. material 1: Fig. S2A, C). A subinvolucral lateral leaf with an explanate lobule is well visible (Suppl. material 1: Fig. S2D, indicated by black arrow), whereas the bracteoles and bracts are concealed for the largest part. The typical acute lobe tip can be seen on one bract (Suppl. material 1: Fig. S2E, indicated by white arrow).

***Frullania cretacea* Hentschel, A.R.Schmidt & Heinrichs**

Suppl. material 1: Fig. S2F, G

Frullania cretacea Hentschel, A.R.Schmidt & Heinrichs; in *Cryptogamie, Bryologie* 30: 326, figs 1–10. 2009.

Holotype. AMNH B-011, Amber collection of the Division of Invertebrate Zoology of the American Museum of Natural History, New York, USA.

Additional specimens investigated. AMNH Bu-FB 1 a–f (AMNH Bu-FB 1 b with gynoecium), AMNH Bu-FB 51, Amber collection of the Division of Invertebrate Zoology of the American Museum of Natural History, New York, USA; GZG.BST.22016, (Müller BuB3533), GZG.BST.22017 (Müller BuB1190), Geoscience Centre (GZG) at the University of Göttingen, Germany; PB23687 Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; BuB1772, BuB3530, **BuB4411**, Patrick Müller Amber Collection; F3157/BU/CJW, Jörg Wunderlich Amber Collection.

Locality and horizon. Amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar, fossil enclosed in upper Albian–lower Cenomanian Kachin amber.

Remarks. This small specimen is in good accordance with the type and previously described material (Suppl. material 1: Fig. S2F, G; compare descriptions in Hentschel et al. 2009a; Heinrichs et al. 2012; Feldberg et al. 2021b). The typical rectangular to ovate underleaves with two long apical cilia (Suppl. material 1: Fig. S2G) and the lobules, which are inserted parallel to the stem to slightly oblique, are well visible.

***Frullania kachinensis* Y.Li, Y.-D.Wang & K.Feldberg**

Figs 1, 2

Frullania kachinensis Y.Li, Y.-D.Wang & K.Feldberg; in *Geological Journal* 56: 5048, figs 1–3. 2021.

Holotype. PB22711a, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Paratypes. PB22711c, d, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; ZMNH155047a, d, e, ZMNH155048c, Zhejiang Museum of Natural History, China.

Additional specimens investigated. **GZG.BST.22040 (Müller BuB4431)**, Geoscience Centre (GZG) at the University of Göttingen, Germany.

Locality and horizon. Amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar, fossil enclosed in upper Albian–lower Cenomanian Kachin amber.

Emended diagnosis. Sterile shoots irregularly branched. Foliation incubous; lateral leaves complicate-trilobed, dorsal lobe ovate to elliptic with rounded apex and mamilllose cells, ventral lobule *Frullania*-type, cylindrical, helmet-shaped to campanulate, with toothed margins, stylus narrow lanceolate to linear. Underleaves distant to contiguous, elliptic to elongate ovate, bilobed 0.3–0.8 × their length; lobes lanceolate, entire-margined to strongly toothed or ciliate, sinus more or less V-shaped. Rhizoids in bundles, inserted just below sinus.

Emended description. Gametophyte fragments 2.89–4.91 mm long, reddish to yellowish brown (Figs 1A, B, 2A), main shoots 0.46–1.00 mm wide, irregularly branched; branches 0.64–1.67 mm long and 0.28–0.92 mm wide. Stem reddish brown to dark brown, 37–65 µm in diameter. Lateral leaves incubous, (sub)horizontally spreading, alternate, imbricate to contiguous, complicate-trilobed. Dorsal lobe slightly concave to nearly flat (Figs 1A–D, 2A–C), ovate to elliptic, on main shoots 290–550 µm long × 200–380 µm wide, length:width ratio 1.2–1.5:1; entire-margined, gradually narrowed towards apex or apex broadly rounded; dorsally extending 0.5–1.2 × the stem width beyond the farther edge of the stem. Lobe cells hexagonal, marginal cells (sub)isodiametric, 15–25 µm in diameter, medial cells slightly elongate, 16–36 µm long × 12–25 µm wide, up to 1.5 × as long as wide (Figs 1C–E, 2B, C); cell walls thin to moderately thickened, with small triangular trigones, no intermediate thickenings seen; one large mamilla per cell, ca. 5 µm high and 7.5–10 µm in diameter (Figs 1E, 2C), or leaf cells smooth. Ocelli not seen, but occasionally dorsal lobes with conspicuous large and elongated cells in the middle. Ventral lobule *Frullania*-type (Figs 1A–D, 2), cylindrical, helmet-shaped to campanulate, inflated, broadest part near opening, 110–220 µm long × 80–210 µm wide, length–width ratio 0.8–2.2:1, inserted in ca. 30–90 µm distance to stem, either nearly parallel to stem or obliquely positioned with upper part oriented towards stem and sometimes overlapping stem; opening not constricted, slightly emarginated, with short, acute tip on outer margin, dorsal and ventral margins angular, with one acute tooth in the middle (Figs 1B–D, 2C, D), tooth up to 10 µm (one cell) long, possibly bearing slime papillae at tip [seen on one tooth in GZG.BST.22040]; lobule cells isodiametric, hexagonal, 11–24 µm in diameter, smooth to mamilllose. Stylus narrow, lanceolate to linear, 30–40 µm long, base 2–3 cells wide with uniseriate apex of 1–3 cells. Underleaves distant to contiguous, 180–310 µm long × 50–150 µm wide,

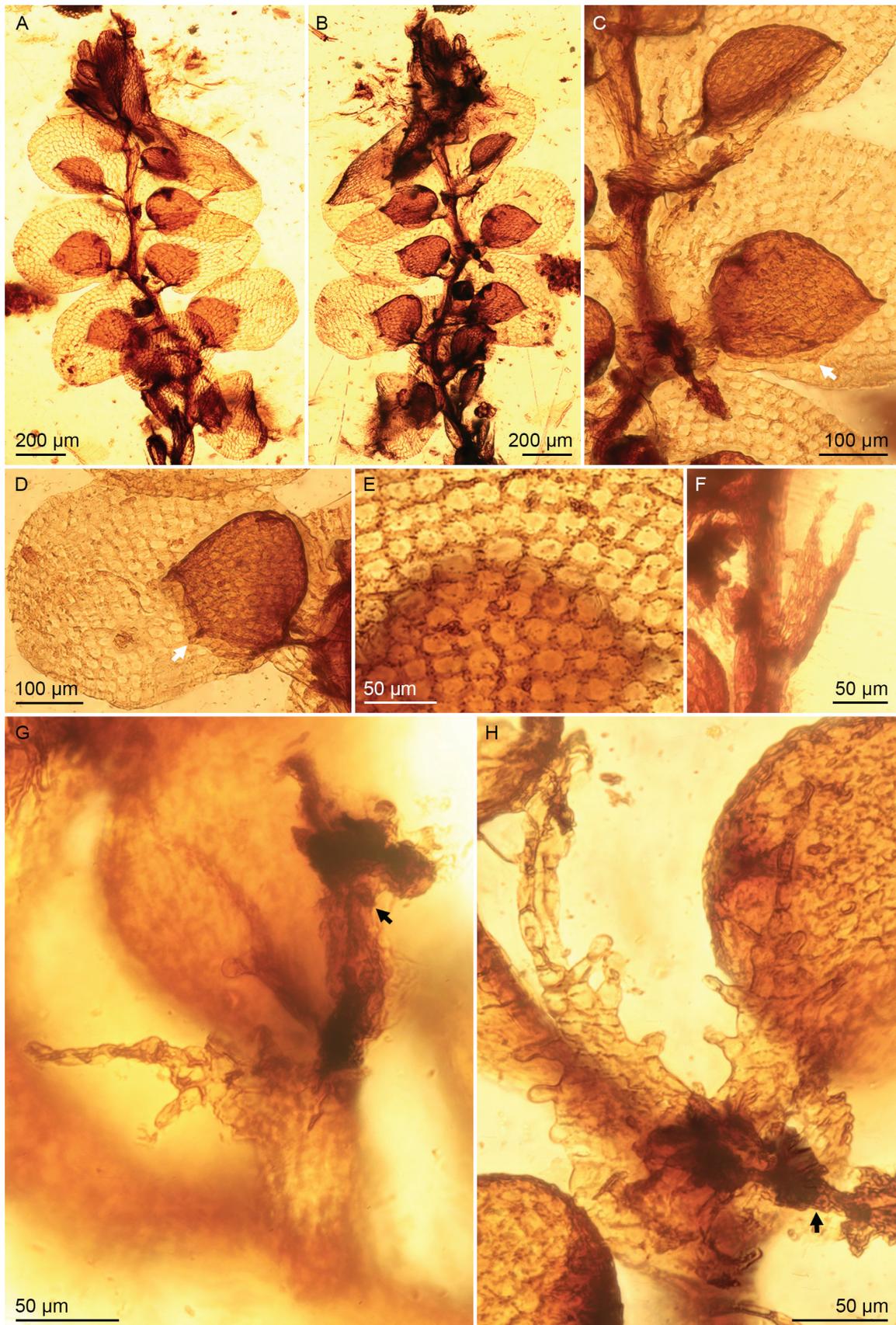


Figure 1. *Frullania kachinensis* Y.Li et al., GZG.BST.22040 (Müller BuB4431). **A.** Gametophyte fragment, dorsal; **B.** Gametophyte fragment, ventral; **C.** *Frullania*-type lobules (marginal tooth indicated by white arrow) and ciliate underleaves, ventral; **D.** Dorsal lobe and ventral lobule (marginal teeth indicated by white arrow); **E.** Lobe cells with large central mamillae, dorsal; **F.** Small underleaf on lower part of stem, lateral; **G, H.** Underleaves with ciliate to toothed lobes and rhizoid bundles (indicated by black arrows) inserted just below the vertexes of the sinus.

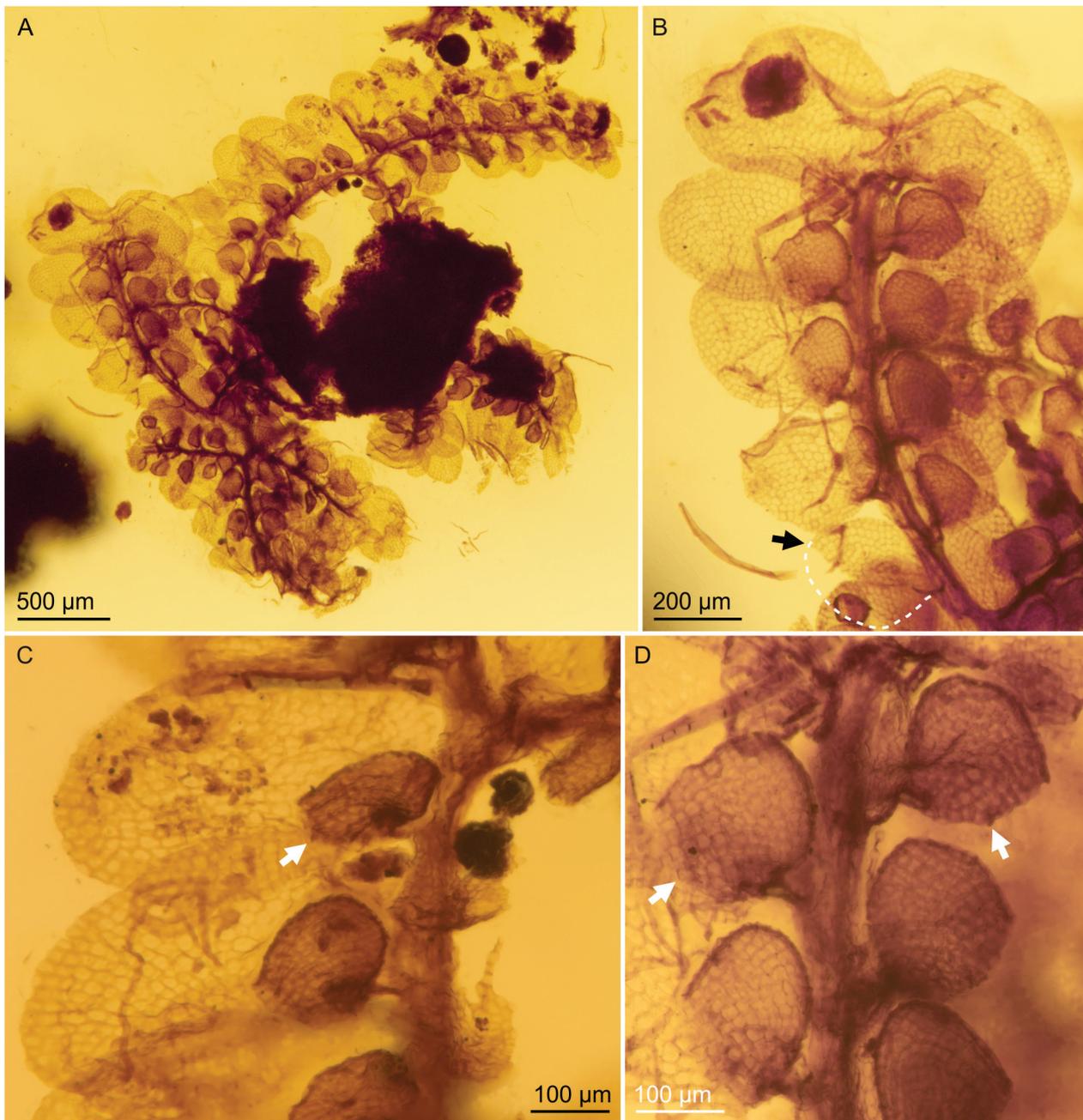


Figure 2. *Frullania kachinensis* Y.Li et al., PB22711a, holotype. **A.** Gametophyte fragment, ventral; **B.** Detail of main shoot, ventral (the black arrow and the dashed line indicate a broken leaf which was described as apiculate in Li et al. 2021a); **C, D.** Leaf lobules with toothed margins (teeth indicated by white arrows) and underleaves, ventral.

length:width ratio 2.1–3.6:1, elliptic to elongate ovate, bilobed $0.3\text{--}0.8 \times$ their length (Figs 1F–H, 2C, D), underleaf lobes lanceolate, (2)4–5(8) cells wide at base [not well visible on GZG.BST.22040], gradually narrowing into a single cell wide filament, apically terminated by a slime papilla; lobes entire or weakly to strongly toothed or ciliate, with up to six 10–55 µm long teeth or cilia consisting of 1–3 uniseriate, quadrate to rectangular cells; teeth and cilia becoming successively smaller towards lobe tip; margins of lower lamina generally entire, occasionally crenulate due to protruding cells or with short teeth (Fig. 2C, D); underleaf sinus more or less V-shaped with an acute to obtuse vertex. Rhizoids in bundles (Fig. 1G, H),

inserted just below sinus of underleaves, bundles up to 160 µm long and 20–30 µm wide at base; rhizoids ca. 10 µm in diameter. Sterile.

Remarks. The new fossil of *F. kachinensis* (Fig. 1) is in rather good accordance with the type (Fig. 2), but some characters are more conspicuous. Most notable are the rhizoid bundles inserted directly below the underleaf sinus as well as the strongly toothed to ciliate underleaf lobes (Fig. 1G, H) and the toothed lobule margins (Fig. 1B–D, indicated by white arrows). A reinvestigation of the holotype also revealed toothed lobule margins (Fig. 2C, D, indicated by white arrows) and the absence of acute lobe apices (Fig. 2B, indicated by black arrow and dashed

line). All lobes are gradually narrowed towards the apex or have a broadly rounded apex. The presence of rhizoids in the type material could not be ascertained.

Genus *Protofrullania*

Protofrullania cornigera Heinrichs

Suppl. material 1: Figs S3–S5

Protofrullania cornigera Heinrichs; in *Cretaceous Research* 74: 225, figs 1, 2, 2017.

Holotype. GZG.BST.21956, Geoscience Centre (GZG) at the University of Göttingen, Germany.

Additional specimens investigated. SNSB-BSPG 2021 XII 1 (Müller BuB1874; syninclusion *Frullania baerlocheri*), SNSB-BSPG 2021 XII 2 (Müller BuB1893; with juvenile gynoecium), SNSB-BSPG 2021 XII 3 (Müller BuB1897), Bavarian State Collection for Palaeontology and Geology, Munich, Germany; GZG.BST.22018 (Müller BuB1999; with perianth), GZG.BST.22019 (Müller BuB3534; with oval underleaves), GZG.BST.22020 (Müller BuB3535; with gynoecium), GZG.BST.22021 (Müller BuB3537; with androecia and oval underleaves), GZG.BST.22022 (Müller BuB3677; with oval underleaves), Geoscience Centre (GZG) at the University of Göttingen, Germany; PB22707, PB22711b (syninclusion *Frullania kachinensis*), PB23289, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; BuB3521, BuB3536, BuB3675, BuB3679 (with oval underleaves), **BuB3811, BuB3812, BuB4333–4338, BuB4394 (with oval underleaves), BUB4408a, b, BUB4409, BUB4413 (with oval underleaves)**, Patrick Müller Amber Collection; F3251/BU/CJW, Jörg Wunderlich Amber Collection.

Locality and horizon. Amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar, fossil enclosed in upper Albian–lower Cenomanian Kachin amber.

Remarks. All specimens are in good accordance with the type and previously described material (Suppl. material 1: Figs S3–S5; compare descriptions in Heinrichs et al. 2017a; Feldberg et al. 2021b) and show the characteristic helmet-shaped to campanulate *Frullania*-type lobules which are often large in relation to the lobes (Suppl. material 1: Figs S3D, S4F, S5B, D, F). As in previously investigated material, the form of the underleaves is very heterogenous (Feldberg et al. 2021b). Most are elongate rectangular to strap-shaped and taper progressively towards the apex (Suppl. material 1: Figs S3D, S4B, S5B). Below the apex they are usually somewhat increasing with the uppermost sector being obtriangular or irregularly rounded and often carrying rhizoid bundles and marginal teeth or cilia. Some underleaves on main shoots and occasionally also on primary branches are ovate to obovate to rectangular with the widest part in the middle and often less prominent cilia (Suppl. material 1: Figs S4F, S5F). One specimen (BuB4334) has a very distinct flagelliform branch (Suppl. material 1: Fig. S3E).

Family RADULACEAE

Genus *Radula*

Radula patrickmuelleri K.Feldberg, Schäf.-Verw. & M.A.M.Renner, sp. nov.

<http://zoobank.org/2CC0D59C-44E5-4B9B-B81A-5D40606F24DF>

Figs 3, 4A–E

Holotype. GZG.BST.22041 (Müller BuB4395), Geoscience Centre (GZG) at the University of Göttingen, Germany.

Etymology. The specific epithet honors the amber collector Patrick Müller (Zweibrücken, Germany) who generously supports our research by providing numerous amber fossils for study.

Locality and horizon. Amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar, fossil enclosed in upper Albian–lower Cenomanian Kachin amber.

Diagnosis. Gametophyte with zig-zagged stems and complicate bilobed lateral leaves; dorsal lobe oblong-elliptic with broadly rounded to obtuse apex; ventral lobule small, *Lejeunea*-type, longitudinally inserted, rounded rectangular to ovate with subacute to rounded apex, inner margin not ampliate, not exceeding stem; irregularly shaped gemmae produced on lobe margins.

Description. Unbranched gametophyte fragment ca. 4.84 mm long, yellowish to reddish brown (Fig. 3A–D); main shoot 1.68–2.28 mm wide with leaves. Stem dark reddish brown, distinctly zig-zagged, ca. 60 µm wide [numbers of cell rows not clearly visible, possibly 4–5]; surface cells elongated, 2–3 × as long as wide; ventral and dorsal leaf-free strips ca. 2 cells wide. One rhizoid bundle visible on the lobule of a basal leaf (Fig. 3E), bundle 7.5–10 µm wide, rhizoids up to 130 µm long. Foliation incubous, lateral leaves alternate, complicate bilobed, divided into large dorsal lobe and smaller ventral *Lejeunea*-type lobule enclosing the ventral leaf surface and forming a sharp postical keel (Fig. 3D–F). Dorsal lobes imbricate, oblong-elliptic, longer than wide, nearly flat, spreading to more erect on upper part of shoot, but not obliquely patent (Fig. 3A–D); margin entire to slightly crenulate due to gemmae production; postical margin slightly emarginated at end of keel, then regularly arched towards apex, apex broadly rounded to obtuse, antical margin regularly arched and nearly parallel to postical margin in the lobe middle, abruptly curved near stem and forming an angle of ca. 90° to the inner margin, inner margin not ampliate, extending onto the dorsal stem surface up to 0.5–1 × the stem width; lobe 550–600 µm long × 340–420 µm wide, length:width ratio 1.3–1.7:1, length exterior to keel 410–510 µm, length of stem insertion ca. 170–190 µm [not clearly visible on most leaves]. Cells of lobe margin quadrate to rectangular, 10–20 µm long × 15–25 µm wide, long axis parallel with leaf margin; medial cells hexagonal, mostly isodiametric to occasionally weakly elongated, 20–35 µm long × 20–30 µm wide; basal cells of the same size or slightly larger than medial cells, 20–40 µm long × 20–35 µm wide (Fig. 4A, B); cell walls thin, with small, triangular trigones possibly present at cell

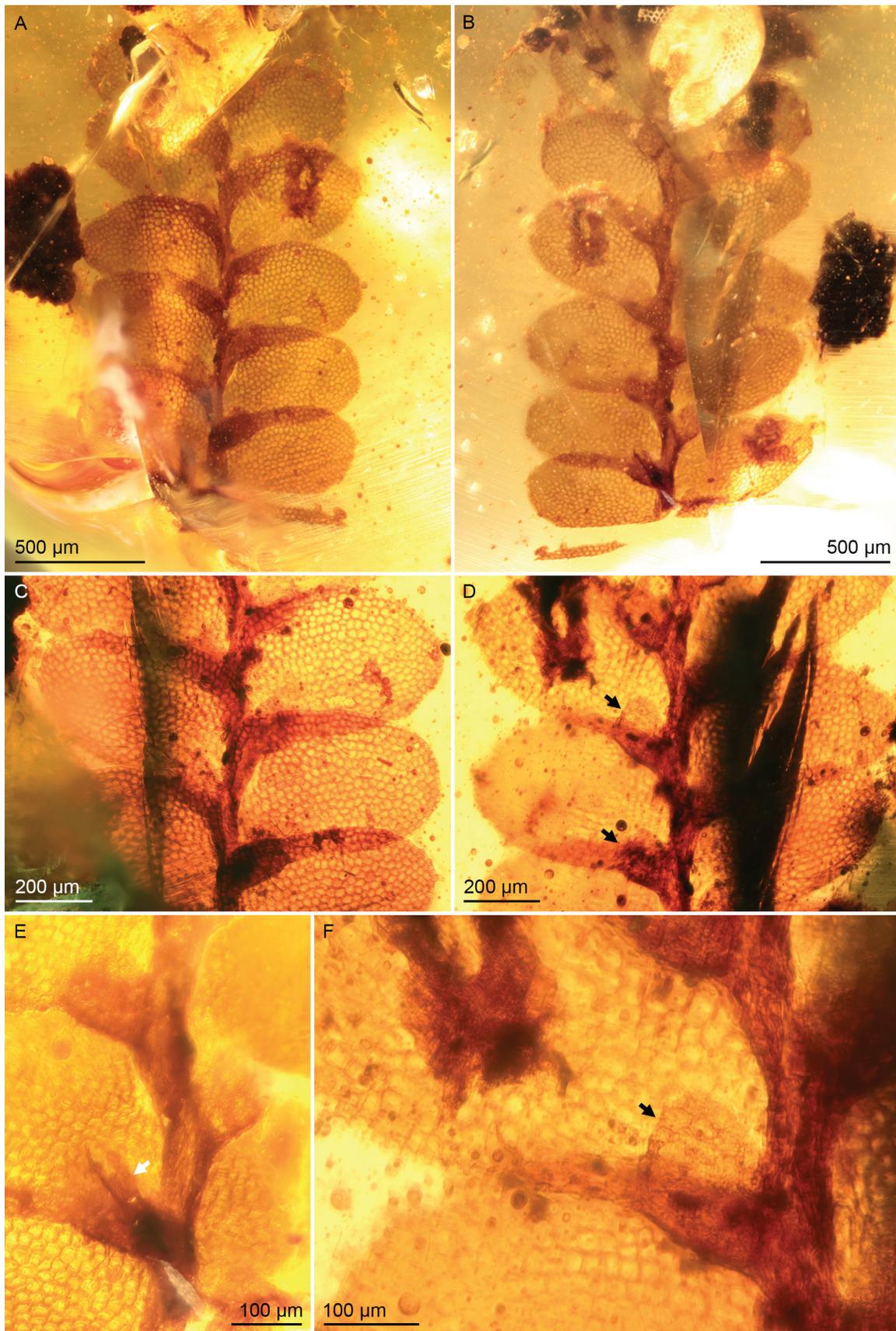


Figure 3. *Radula patrickmuelleri* sp. nov., GZG.BST.22041 (Müller BuB4395), holotype. **A.** Gametophyte fragment, dorsal; **B.** Gametophyte fragment, ventral; **C.** Insertion of leaf lobes, dorsal; **D.** Leaves with large lobes and small lobules (indicated by black arrows), ventral; **E.** Lobules, ventral (rhizoid bundle on the lobule surface indicated by white arrow); **F.** Longitudinally inserted leaf lobule, ventral (lobule indicated by black arrow).

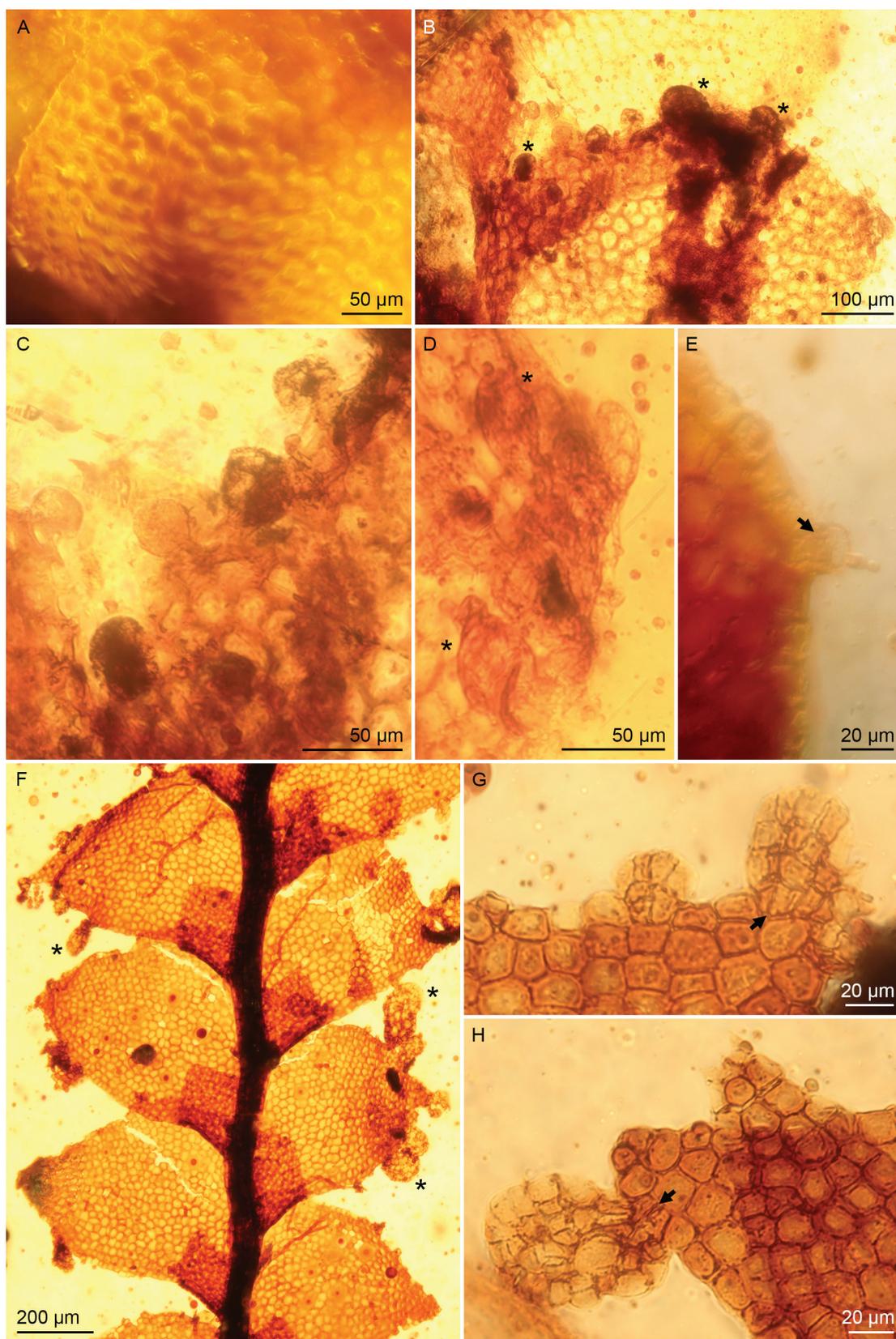


Figure 4. *Radula patrickmuelleri* sp. nov. and *R. cretacea*. **A–E.** *R. patrickmuelleri*, GZG.BST.22041 (Müller BuB4395), holotype; **A.** Lobe cells, dorsal; **B.** Antical leaf margin with gemmae, dorsal; **C.** Detail of gemmae (smaller spherical bodies possibly represent air bubbles and debris); **D.** Lobe apex with large gemmae, dorsal; **E.** Lobe margin with gemmae in the initial stage of development, dorsal (initial periclinal cell division visible and indicated by black arrow); **F–H.** *R. cretacea*, PB22484, holotype; **F.** Gametophyte with large gemmae on the lobe margins, ventral; **G, H.** Gemmae in different stages of development (initial anticlinal cell division visible and indicated by black arrow). The asterisks indicate selected gemmae in different stages of development.

angles; free exterior wall of marginal cells unthickened. Ventral lobules small in relation to lobe ($< 0.2 \times$), rounded rectangular to ovate, insertion longitudinal, exterior margin curved, antical margin slightly curved or nearly straight, interior margin not ampliate, barely extending onto the stem surface (Fig. 3D–F), apex subacute to broadly rounded; keel emerging at an angle of ca. 45° from the stem, slightly convex; lobule ca. $150 \mu\text{m}$ long \times ca. $150 \mu\text{m}$ wide, length:width ratio 0.9–1.1:1, keel length 140–160 μm , length of stem insertion 90–140 μm . Underleaves lacking. Asexual reproduction by gemmae produced from cells of leaf margin (Fig. 4B–E, indicated by asterisks), gemmae possibly unistratose, subdiscooid to obcordate to irregularly thalloid as size increases, 20–110 μm long \times 25–70 μm wide, first cell division seemingly periclinal (Fig. 4C, E); stalk cell of gemmae rectangular. Sterile.

Remarks. This fossil consists of a short, sterile gametophyte fragment but shows all relevant characters to delimitate it from other *Radula* fossils from Kachin amber (Figs 3, 4A–E). The small, rounded rectangular to ovate lobules allow to differentiate it from *R. heinrichsii* as well as *R. tanaiensis* which have much larger lobules (Fig. 5A, B), and the apically rounded lobes with nearly parallel margins distinguish it from *R. cretacea* (Fig. 4F).

***Radula tanaiensis* K.Feldberg, Schäf.-Verw. & M.A.M.Renner, sp. nov.**

<http://zoobank.org/3442B8BB-79AD-44C6-8BCB-A2EAC0259B6F>
Fig. 5A–E

Holotype. GZG.BST.22042 (Müller BuB4329), Geoscience Centre (GZG) at the University of Göttingen, Germany.

Etymology. The specific epithet refers to the village of Tanai, where Kachin amber is mined.

Locality and horizon. Amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar, fossil enclosed in upper Albian–lower Cenomanian Kachin amber.

Diagnosis. Gametophyte irregularly branched, branches similar to main shoot, *Radula*-type. Lateral leaves complicate bilobed; dorsal lobe oval to ovate with rounded apex, deeply emarginated at end of keel; free exterior wall of marginal cells distinctly thickened; ventral lobules *Lejeunea*-type, up to $0.4 \times$ as big as dorsal lobes, ovate to rounded trapezoid, insertion longitudinal, antical free margin often reaching antical margin of lobe.

Description. Branched gametophyte fragment ca. 4 mm long [tip of main shoot broken off], yellowish to reddish brown (Fig. 5A–C); main shoot up to 2.12 mm wide with leaves. Branching irregular, *Radula*-type (Fig. 5A, C); three intact branches with reduced leaves near their base, becoming main shoot-like, 2.6–2.72 mm long and 1.2–2.1 mm wide with leaves. Stem dark reddish brown, straight to slightly zig-zagged, on main shoot ca. 70–90 μm wide [strongly decomposed], on branches ca. 60 μm wide; surface cells not visible; ventral and dorsal leaf-free strips not visible. Rhizoids not seen.

Foliation incubous, lateral leaves alternate, complicate bilobed, divided into large dorsal lobe and smaller ventral *Lejeunea*-type lobule enclosing the ventral leaf surface and forming a sharp postical keel (Fig. 5B). Dorsal lobes imbricate, oval to ovate, insertion longitudinal, flat, spreading, not obliquely patent, riding onto dorsal stem surface; margin entire, postical margin deeply curved along inner half, first nearly straight then evenly curved towards apex along outer half, lobe apex broadly rounded, exterior antical margin evenly curved, interior margin curved and slightly ampliate, overlapping the stem up to $1 \times$ the stem width beyond the father edge of the stem; lobes on main shoot 600–610 μm long \times 440–510 μm wide, length:width ratio 1.2–1.4:1, length exterior to keel 390–400 μm , length of stem insertion not clearly visible; lobes on branches 390–520 μm long \times 300–360 μm wide, length exterior to keel 180–320 μm , length of stem insertion not visible. Marginal lobe cells quadrate to rectangular, 10–20 μm long \times 15–25 μm wide, long axis either perpendicular or parallel with leaf margin (Fig. 5E); medial cells (sub)isodiametric to slightly elongated, 15–30 μm long \times 12.5–25 μm wide (Fig. 5D); basal cells not visible; cell surfaces appearing smooth, but possible ornamentation visible in some parts (Fig. 5D) [cells generally indistinct]; cell walls moderately thickened, with small triangular to subnodulose trigones, free exterior wall of marginal cells distinctly thickened (Fig. 5E). Ventral lobules ovate to rounded trapezoid, up to $0.4 \times$ as big as lobe, free antical margin often reaching antical margin of lobe (Fig. 5B), insertion longitudinal, free exterior and antical margins nearly straight to curved, apex narrowly rounded to rounded, interior margin ampliate, ventrally extending up to $1 \times$ the stem width beyond the farther edge of stem; keel emerging at an angle of ca. 45° from the stem, lobe deeply emarginated at end of keel; lobules on main stem 290–310 μm long \times 340–370 μm wide, length:width ratio ca. 0.9:1, keel length 210–230 μm , length of stem insertion not visible; on branches 270–330 μm long \times 300–340 μm wide, length:width ratio 0.8–1:1. Underleaves lacking. No asexual reproduction. Sterile.

Remarks. The new fossil material consists of a short shoot fragment with the apex broken off and three main shoot-like *Radula*-type branches. It is not very well preserved, and many branches and leaves are broken (Fig. 5A–E). The lobules are generally very large in relation to the lobes (Fig. 5A, B) and differentiate this fossil clearly from *R. patrickmuelleri* as well as the much smaller *R. cretacea* whose lobules are less than $0.2 \times$ the lobe size (Figs 3, 4F). Superficially the new species looks similar to *R. heinrichsii* (Fig. 5F, G; compare descriptions in Feldberg et al. 2021b), but the lobules of *R. tanaiensis* are up to $0.4 \times$ the lobe size and their antical margin often reaches the antical margin of the lobe (Fig. 5B), while the lobules of *R. heinrichsii* remain smaller and are more rounded (Fig. 5F). The lobe cells are somewhat indistinct, but it is clearly visible that the outer walls of the marginal cells are distinctly thickened (Fig. 5E) whereas those of *R. heinrichsii* are thinner (Fig. 5G).

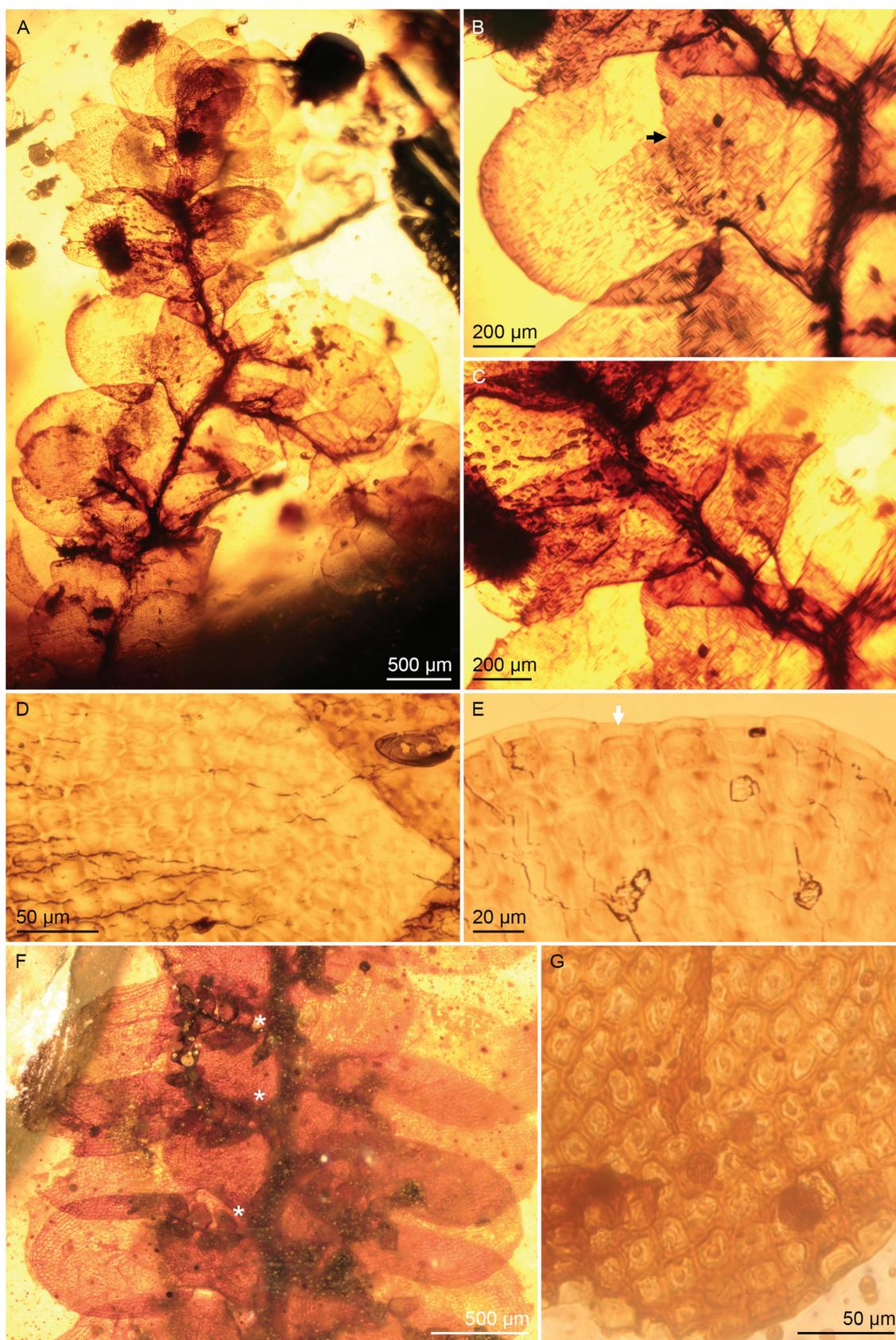


Figure 5. *Radula tanaiensis* sp. nov. and *R. heinrichsii* Feldberg et al. **A–E.** *R. tanaiensis*, GZG.BST.22042 (Müller BuB4329), holotype; **A.** Gametophyte, ventral; **B.** Lobe and lobule, ventral (lobule indicated by black arrow); **C.** Lower part of *Radula*-type branch; **D.** Medial lobe cells; **E.** Marginal lobe cells with thickened free exterior walls (indicated by white arrow); **F, G.** *R. heinrichsii*, GZG.BST.22023 (Müller BuB3683), holotype; **F.** Gametophyte with microphyllous (amentulose) branches (indicated by asterisks), ventral; **G.** Lobe cells with central mamillae.

Radula sp.

Suppl. material 1: Fig. S6

Locality and horizon. Amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar, fossil enclosed in upper Albian–lower Cenomanian Kachin amber.

Specimen investigated. GZG.BST.22043 (Müller BuB4420), Geoscience Centre (GZG) at the University of Göttingen, Germany.

Remarks. The new fossil GZG.BST.22043 is not very well preserved, and the identification is difficult. It strongly

resembles *R. cretacea* (Fig. 4F–H) in having smooth lobe cells (Suppl. material 1: Fig. S6E, F), quadrate to trapeziform lobules (Suppl. material 1: Fig. S6C, D, indicated by arrows), which are very small in relation to the lobes, and globose gemmae on the lobe margins (Suppl. material 1: Fig. S6F). However, the new fossil has obliquely patent leaves on the upper part of the shoot, whereas the posture of the lower leaves is not as dorsoventrally erect and more similar to *R. cretacea* (Figs 5F, Suppl. material 1: S6A–D). It also differs in having slightly narrower leaf lobes with a longer acuminate apex (Suppl. material 1: Fig. S6), though the obliqueness of the lobes makes this difficult to assess.

Key to leafy liverworts from Cretaceous ambers

- 1 Leaves with *Frullania*-type lobule, enclosing the dorsal leaf surface and having a postical opening (Figs 1, 2) 2
- Leaves with *Lejeunea*-type lobule, enclosing the ventral leaf surface and having an antical opening (Figs 3–5) 8 (*Radula*)
- 2 Lobules with a long cilium on the outer margin *Gackstroemia cretacea* Heinrichs et al.
- Lobules occasionally toothed, but never with cilium on outer margin 3
- 3 Two lobules per leaf, underleaves apparently lacking *Kaolokia borealis*
- One lobule per leaf, underleaves usually present 4
- 4 Underleaves generally longer than the lobules, strap-shaped to long ovate, with two apical and 0–4 lateral teeth or cilia; rhizoids inserted on apical part of underleaf (Suppl. material 1: Figs S3–S5) *Protofrullania cornigera*
- Underleaves of a different shape, shorter than lobules and rectangular to ovate with apical cilia and lateral teeth, elliptic to ovate and bifurcated, or undivided with entire margins ('holostipous') 5 (*Frullania*)
- 5 Underleaves undivided and entire ('holostipous'), ovate to suborbicular to reniform (Suppl. material 1: Fig. S2A–E) *F. baerlocheri*
- Underleaves with apical cilia and lateral teeth, or bifurcated with entire or serrate margins 6
- 6 Lobe apex acute to acuminate; lobules small in relation to lobes; underleaves bifurcated, entire *F. partita*
- Lobe apex rounded; underleaves with two apical cilia and few lateral teeth, or underleaf lobes toothed to strongly serrate 7
- 7 Underleaves elliptic, bifurcated up to 0.5–0.8 × their length, lobes weakly to strongly serrate (Figs 1, 2) *F. kachinensis*
- Underleaves rectangular to elongate triangular or ovate, with two slender apical cilia and often few additional lateral teeth (Suppl. material 1: Fig. S2F, G) *F. cretacea*
- 8 Plants small, ≤ 1.2 mm wide; lobe apex acute; small lobules quadrate to trapeziform (Fig. 4F–H) *R. cretacea*
- Plants larger, ≥ 1.3 mm wide; lobe apex rounded 9
- 9 Leaf lobules small in relation to the lobes (< 0.2 ×), inner margins not ampliate, not overlapping the stem (Figs 3, 4A–E) *R. patrickmuelleri* sp. nov.
- Leaf lobules larger in relation to the lobes (> 0.2 ×), inner margins ampliate, overlapping stem 10
- 10 Leaf lobules ovate to rounded trapezoid, very large in relation to lobes (0.3–0.4 ×), apices rounded to narrowly rounded, free margins curved to nearly straight; microphyllous branches unknown (Fig. 5A–E) *R. tanaiensis* sp. nov.
- Leaf lobules orbicular to obovate, ca. 0.2–0.3 × as big as lobes, apices broadly rounded, free margins strongly curved; microphyllous (amentulose) branches present (Fig. 5F, G) *R. heinrichsii*

Discussion

The new fossil material described in this publication includes some well-preserved sterile specimens of *Frullania cretacea* (Suppl. material 1: Fig. S2F, G), which is represented by 15 fossils in total, and *Protofrullania cornigera* (Suppl. material 1: Figs S3–S5), which is now represented by altogether 30 fossils. The latter is by far the most common species found in Kachin amber and the only species for which androecia as well as gynoecia are known (Feldberg et al. 2021b). *Frullania baerlocheri* (Suppl. material 1: Fig. S2A–E) is now represented by 12 fossils, including

three fertile specimens with gynoecia, while *F. kachinensis* (Figs 1, 2) is known from eight sterile fossils, and *F. partita* from only two specimens (Li et al. 2020, 2022a). Several of these species occur together in individual amber pieces, namely *F. baerlocheri* and *P. cornigera* (SNSB-BSPG 2021 XII 1; described in Feldberg et al. 2021b), *F. kachinensis* and *P. cornigera* (PB22711; described in Li et al. 2021b), *F. kachinensis* and *F. baerlocheri* (ZMNH155047; described in Li et al. 2021a), and *F. baerlocheri* and *Radula heinrichsii* (ZMNH155044; described in Wang et al. in press). This indicates that these species grew very close to each other, obviously even on the same tree.

The new material allowed us to emend the diagnosis and description of *F. kachinensis*. Like many fossil species from Cretaceous ambers, *F. kachinensis* shows some characters that are unusual or even unknown in extant Frullaniaceae, e.g., rhizoid bundles inserted directly below the underleaf sinus (Fig. 1G, H). Extant *Frullania* has rhizoid bundles inserted at the base of underleaves or towards the middle (e.g., Hattori 1975, 1983; Schuster 1992), and the unusual insertion point aligns *F. kachinensis* with *Protofrullania cornigera*. The form of the underleaves, however, is completely different. While *P. cornigera* mostly has strap-shaped underleaves with a wider apical area armed with two to four cilia and carrying the rhizoid bundle (Suppl. material 1: Figs S3–S5), *F. kachinensis* has elliptic to elongate ovate underleaves which are bifid to ca. 0.3–0.8 × their length into two lanceolate lobes and are more consistent with typical underleaves of extant *Frullania* in this aspect (Figs 1F–H, 2C, D). However, another difference to extant species is the strong armature of the underleaf lobes which can be weakly to strongly toothed or ciliate and resemble the bracteoles of extant species more than vegetative underleaves (Figs 1G, H, 2C). Some extant *Frullania* species from different subgenera, e.g., *F. monocera* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees of subgen. *Acutilobae*, *F. blepharozia* Spruce of subgen. *Chonantheia*, *F. curvistipula* Steph. of subgen. *Diastaloba* I, and *F. amamiensis* Kamim. of subgen. *Frullania*, also have toothed vegetative underleaf lobes, but these teeth are mostly shorter and situated on the outer side of the triangular lobes (Yuzawa 1991, 2001). Another example would be *F. papulosa* Steph., which has lanceolate, pilose underleaf lobes with two spinose teeth at the lower margins.

Radula tanaiensis, *R. patrickmuelleri*, and the additional fossil GZG.BST.22043 can be confidently assigned to the genus. The presence of complicate bilobed lateral leaves with a large dorsal lobe and a small *Lejeunea*-type lobule, the absence of underleaves, as well as the presence of rhizoids on the lobules in the case of *R. patrickmuelleri* allow a definite assignment to *Radula*. The new species are morphologically well differentiated from the other two fossil species from Kachin amber, while the classification of *R. sp.* is ambiguous.

Radula tanaiensis can be clearly differentiated from *R. cretacea*, *R. heinrichsii*, and *R. patrickmuelleri* by the very large lobules on what are probably primary shoots. Lobules are up to 0.4 × as big as the lobes and their free antical margin often reaches the antical margin of the lobe (Fig. 5A, B). Lobules in *R. cretacea* are less than 0.2 × as big as the lobes and also the acute triangular-ovate lobes separate it from the new species (Fig. 4F). *Radula patrickmuelleri* has similarly small lobules and the lobes are less wide and have nearly parallel postical and antical margins in their middle parts (Fig. 3). *Radula heinrichsii* is the most similar species, but the lobules are only 0.2–0.3 × as big as the lobes, obovate to nearly orbicular instead of ovate to rounded trapezoid, and have more broadly rounded apices (Fig. 5A, B, F). The lobes of *R. heinrichsii* are more elongated, and the free exterior cell walls of the marginal lobe cells are not as distinctly thickened as

in *R. tanaiensis* (Fig. 5E, G). Contrary to *R. heinrichsii*, the cell walls of *R. tanaiensis* also appear smooth for the largest part (Fig. 5D, E), but the cells are often indistinct, and some might have rounded mamillae in their center. Furthermore, microphyllous axes (Fig. 5F) have not been seen in the new species. It has three intact branches with a few small and somewhat reduced basal leaves which soon become main shoot-like and some broken remnants of branches whose character is not discernible (Fig. 5A, C).

Radula patrickmuelleri has roughly the same shoot size as *R. heinrichsii* and *R. tanaiensis* but can be clearly separated by the size and shape of the small lobules which are less than 0.2 × as big as the lobes, the absence of microphyllous branches, and the gemmae formation (Figs 3, 4). *Radula cretacea* resembles *R. patrickmuelleri* at first glance, because it also has small lobules as well as irregular gemmae on the lobe margins (Fig. 4F–H). The form of the lobules and the longitudinal insertion might be similar, but those of *R. cretacea* are quadrate to trapeziform, have slightly curved exterior and antical margins which are somewhat irregular due to bulging marginal cells, and an obtuse to slightly attenuate apex with a papilla in a shallow notch (Fig. 4F). In contrast, the lobules of *R. patrickmuelleri* are rounded rectangular to ovate, have more strongly curved exterior and antical margins which do not show any bulging marginal cells, and subacute to broadly rounded apices (Fig. 3D–F). Notches with papillae have not been seen. The most conspicuous differences are the size of the plants and the form of the dorsal lobes. *Radula cretacea* is much smaller and has triangular-ovate leaf lobes (Fig. 4F) while *R. patrickmuelleri* is larger and has oblong-elliptic lobes (Fig. 3A–D). The antical and postical margins of the lobes also show a different curvature. The antical lobe margin of *R. cretacea* is more strongly arched than the postical margin, whereas *R. patrickmuelleri* has nearly parallel medial postical and antical margins. Furthermore, *R. cretacea* has acute to slightly acuminate lobe apices, whereas *R. patrickmuelleri* has broadly rounded lobe apices. Another differentiating character are the gemmae. While the first cell division in the gemmae of *R. cretacea* seems to be mainly anticlinal (Fig. 4G, H), all clearly visible first divisions in *R. patrickmuelleri* are periclinal (Fig. 4B–E).

The presence of four species in Kachin amber and recent divergence time estimates indicate a high diversity of *Radula* already in the Cretaceous (Bechteler et al. 2017; Patiño et al. 2017; Feldberg et al. 2021a, 2021b). *Radula cretacea* and *R. heinrichsii* show close morphological affinities to the extant subgenera *Odontoradula* and *Amentuloradula*, respectively (Bechteler et al. 2017; Feldberg et al. 2021b). The assignment of the two new species, however, is more difficult due to the scarcity of the fossil material. Based on the available evidence, it is not possible to assign *R. patrickmuelleri* and *R. tanaiensis* to any subgenus with confidence, and because of the high degree of morphological homoplasy in extant *Radula*, a comparison with extant lineages is premature. The gemmae formation in *R. patrickmuelleri* is perhaps consistent with an epiphyllous lineage in extant subg.

Metaradula, where the first cell division is always periclinal. However, the species also shares some similarities with the extant *R. pugioniformis* M.A.M. Renner of subgenus *Odontoradula* but differs in having larger leaf lobe cells with thin walls and distinct trigones, as well as gemmae (Renner et al. 2013b). A more accurate assignment of the new species might be possible when more fossil material is discovered. Both the age of each *Radula* subgenus, and the relatively long stem lineages leave open the possibility that fossils belong to extinct lineages that diverged from the various stem lineages. Bechteler et al. (2017) evaluated how misleading an assignment solely based on morphological similarity may be, and assigned *R. cretacea* to different nodes in the molecular phylogeny of *Radula*. An assignment of *R. cretacea* to the stem of subgenus *Odontoradula* proved to be most likely and resulted in an estimated mean age of 176.3 Ma for the genus.

Conclusions

DNA-based divergence time estimates provide evidence for a species turnover within Jungermanniidae during the Angiosperm Terrestrial Revolution, and fossils in Kachin amber offer unique insights into the evolution and diversification of leafy liverworts during this time span (Feldberg et al. 2014; Laenen et al. 2014; Benton et al. 2022). They are essential as age constraints in divergence time estimations, because only very few Mesozoic fossils from the rock record show enough details to allow a reliable assignment to extant lineages (Heinrichs et al. 2018; Tomescu et al. 2018; Feldberg et al. 2021a, 2021b).

Unfortunately, neither *Radula patrickmuelleri* nor *R. tanaiensis* can contribute to age constraints beyond what is already gleaned from other fossils, which is an absolute minimum age for the lineage stem node of *Radula*, though they provide more evidence of a high species diversity of *Radula* already in the mid-Cretaceous. The newly detected fossil of *Frullania kachinensis* allowed emendation of the species diagnosis and description for some important characters but can likewise not provide new age constraints, because some unusual characters make it impossible to assign it to any group within the crown group of *Frullania*. The rhizoid insertion resembles *Protofrullania cornigera* more than any extant *Frullania* and it might thus be more closely related to this genus.

Our results suggest that new fossil liverwort material should preferably be described based on as many specimens as possible, as every specimen is incomplete. Not only does fossil material often consist of sparse and damaged fragments which do not show all relevant characters, leafy liverworts often show significant morphological homoplasy between lineages as well as some morphological plasticity within a species, with characters varying in expression between individuals or even between different parts on the same plant, e.g., the main shoot and branches. This high variability may obscure species boundaries in extant leafy liverworts and is even more obstructive in the description of extinct species.

Author contribution (CRediT)

K.F. designed research. K.F. and Y.L. prepared and documented the specimens. K.F., A.S.-V., Y. L., and M.A.M.R. analyzed the data and wrote the paper. All authors commented on the manuscript.

Competing interests

The authors have no competing interests to declare.

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Supplementary material 1

Figures S1–S6

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Data type: Images (PDF file).

Explanation note: Extending the diversity of the bryoflora in Kachin amber.

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