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Checklist of fossil liverworts suitable for calibrating phylogenetic reconstructions

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Abstract

The number of available liverwort fossils substantially increased within the past decade, which is mainly due to new findings from Cretaceous and Cenozoic amber deposits. Many of them, however, are fragmentary and not predestined for consideration in evolutionary analyses. Here, we list those liverwort fossils that we suggest as suitable for calibrating phylogenetic reconstructions, along with brief descriptions, justification of their use, and age information. Our recommendations are based on thorough microscopic investigation of available fossils from worldwide amber collections including recent findings. We recommend that the following 42 fossil taxa can be used as confident minimum age constraints in phylogenetic reconstructions: *Acrolejeunea ucrainica* (35 Ma), *Anastrophyllum rovnoi* (35 Ma), *Bazzania polyodus* (34 Ma), *Blepharolejeunea obovata* (15 Ma), the genus *Bryopteris* with *B. bispinosa* and *B. succinea* (15 Ma), *Calypogeia stenzeliana* (34 Ma), *Cephaloziella nadezhdae* (35 Ma), the genus *Ceratolejeunea* with *C. antiqua, C. palaeomexicana,* and *C. sublaetefusca* (15 Ma), *Cheilolejeunea latiloba* (34 Ma), *Cheirorhiza brittae* (158 Ma), *Cololejeunea* sp. (15 Ma), *Cyclolejeunea archaica* (15 Ma), *Dibrachiella grollei* (15 Ma), *Diettertia montanensis* (112 Ma), *Drepanolejeunea eogena* (15 Ma), the genus *Frullania* with *F. baerlocheri, F. cretacea,* and *F. partita* (99 Ma), *Frullania* subgen. *Frullania* with *F. casparyi* (34 Ma) and *F. riclefgrollei* (35 Ma), *F.* subgen. *Trachycolea* with *F. rovnoi* (35 Ma) and *F. schumannii* (34 Ma), *Gackstroemia cretacea* (99 Ma), *Geocalyx heinrichsii* (34 Ma), the genus *Lejeunea* with *L. hamatiloba, L. miocenica, L. resinata,* and *L. urbanioides* (15 Ma), *Lopholejeunea subnigricans* (15 Ma), *Marchantites cyathodoides* (228 Ma), *Marchesinia brachiata* (15 Ma), *Metzgeriothallus sharonae* (383 Ma), *Microlejeunea nyiahae* (52 Ma), *Neurolejeunea macrostipula* (15 Ma), *Nipponolejeunea europaea* (34 Ma), *Notoscyphus balticus* (34 Ma), *Odontoschisma* (sect. *Iwatsukia*) *dimorpha* (34 Ma), *Plagiochila groehnii* (34 Ma), *Porella subgrandiloba* (34 Ma), *Protolophozia kutscheri* (34 Ma), *Radula* (subgen. *Odontoradula*) *cretacea* (99 Ma), *R.* (subgen. *Amentuloradula*) *heinrichsii* (99 Ma), *Scapania hoffeinsiana* (34 Ma), *Solenostoma berendtii* (34 Ma), *Spruceanthus polonicus* (34 Ma), *Stictolejeunea squamata* (15 Ma), *Tetralophozia groehnii* (34 Ma), *Thysananthus auriculatus* (15 Ma), *Thysananthus contortus* (34 Ma). Furthermore, we transfer *Lophozia kutscheri* to *Protolophozia*, *Archilejeunea grollei* to *Dibrachiella, Frullania ucrainica* to *Acrolejeunea,* and *Mastigolejeunea extincta* to *Spruceanthus*, based on new fossil evidence and morphological revisions.

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Introduction

Research concerning the evolution and diversification of Marchantiophyta has rapidly progressed in recent years, which coincides with the discovery of new fossils, especially from Cretaceous and Cenozoic amber deposits. The fossil record was reviewed by Heinrichs *et al.* (2018a) for liverworts in amber and by Tomescu *et al.* (2018) for bryophytes from the rock record. Since then, the steady discovery of new fossils led to the description of new taxa and allowed better reconstructions of previously known extinct species which resulted in several taxonomic changes and emended descriptions (Feldberg *et al.* 2018, 2021, Heinrichs *et al.* 2018b, Katagiri 2018, Katagiri & Shinden 2020, Mamontov *et al.* 2018a, 2019, 2020a, Li *et al.* 2020, 2021, Yu *et al.* 2020).

An important tool for the study of liverwort evolution are divergence time estimates based on molecular phylogenies (e.g., Heinrichs *et al.* 2007, 2015b, 2016a, Wilson *et al.* 2007, Cooper *et al.* 2012, Feldberg *et al.* 2013, 2014, 2017, Laenen *et al.* 2014, Sun *et al.* 2014, Villarreal & Renner 2014, Villarreal *et al.* 2016, Bechteler *et al.* 2017a, b, Carter *et al.* 2017, Patiño *et al.* 2017, Silva *et al.* 2017, Lee *et al.* 2020). Especially Bayesian dating methods offer diverse possibilities to define priors and to incorporate information from the fossil record, e.g., BEAST 2 (Bouckaert *et al.* 2014, Drummond & Bouckaert 2015) and MCMCTree (Yang 2007). However, the results of these estimates often vary due to conflicting interpretation of the fossil evidence and the taxonomy of extant groups as well as the use of different DNA marker sets, algorithms, tree priors, and different assumptions on the maximum age of lineages. A thorough evaluation and cross-evaluation of different calibration strategies and prior settings is therefore crucial for this approach (e.g., Parham *et al.* 2012, Warnock *et al.* 2015, 2017, Barba-Montoya *et al.* 2017, Bromham *et al.* 2018, Guindon 2018, Marshall 2019, Beavan *et al.* 2020, Carruthers & Scotland 2020, Didier & Laurin 2020, O'Reilly & Donoghue 2020).

Recent analyses indicate that many liverwort lineages probably predate the Permian-Triassic boundary while most extant genera originated in the Cretaceous or Cenozoic (e.g., Heinrichs *et al.* 2018a). The required age constraints on the molecular phylogenetic trees were obtained by using fossil calibrations of ancestral nodes associated with extant lineages (Heinrichs *et al.* 2007, 2016a, Wilson *et al.* 2007, Cooper *et al.* 2012, Feldberg *et al.* 2013, 2014, Laenen *et al.* 2014, Sun *et al.* 2014, Villarreal *et al.* 2016), by using standard substitution rates (Villarreal & Renner 2014, Heinrichs *et al.* 2015b, Bechteler *et al.* 2017a, Carter *et al.* 2017, Feldberg *et al.* 2017, Patiño *et al.* 2017), or by a combination of both methods (Bechteler *et al.* 2017b, Silva *et al.* 2017, Lee *et al.* 2020).

The classification of fossil material is often challenging, and divergence time estimates which solely rely on fossil constraints might be impeded by incorrect systematic assignment which misleads taxonomic interpretations (e.g., Feldberg *et al.* 2013, 2017, Bechteler *et al.* 2017b, Heinrichs *et al.* 2018a). This is sometimes due to incomplete preservation of fossils but may also result from a high level of morphological homoplasy and cryptic speciation in extant lineages (e.g., Shaw 2001, Renner 2015, 2020, Shaw *et al.* 2015, Renner *et al.* 2017a). However, DNA sequence variation of extant species can be employed to evaluate the morphology-based classification of fossils because, for example, the age of fossils may pre-date divergence times estimated among closely related genera (Heinrichs *et al.* 2015b, 2018a, Villarreal *et al.* 2016, Bechteler *et al.* 2017b, Feldberg *et al.* 2017, Patiño *et al.* 2017). On the other hand, divergence times that rely solely on DNA sequence variation can be problematic in cases of strongly deviating molecular clocks, as seen in the "slowly" evolving complex thalloid liverworts (Villarreal *et al.* 2016). Only a compilation of analyses with different approaches allows a thorough cross-validation of hypotheses concerning the evolution of lineages through time, classification of fossils, and the suitability of the fossils as age constraints. Consequently, fossils should not exclusively be used to calibrate nodes in molecular phylogenies, but independently generated phylogenetic chronograms can be used to evaluate taxonomical assessments of fossils and to balance between different taxonomic solutions (Lóriga *et al.* 2014, Schneider *et al.* 2015, 2016, Sundue & Poinar 2016, Bechteler *et al.* 2017b, Kubilius *et al.* 2017).

Heath *et al.* (2014) proposed a fossilized birth–death approach which is designed to overcome the problem of assigning fossils to certain nodes in divergence time analyses by allowing data-based fossil assignment and the expression of uncertainty in fossil placement. Though this approach requires a dense fossil record and numerous morphological character states of both fossils and extant taxa to be coded (e.g., Arcila *et al.* 2015, Warnock *et al.* 2015, Didier & Laurin 2020, O'Reilly & Donoghue 2020, Pett & Heath 2020) it provides an avenue for overcoming uncertainties in fossil placement, which is crucial for older fossils possessing unique phenotypes not observed in extant lineages. Another useful tool is the phylomorphospace approach as applied by Schneider *et al.* (2015) for ferns. In order to obtain reliable age constraints an extensive fossil record is just as important as the detailed knowledge of extant groups obtained by integrative taxonomy which combines DNA datasets with morphological and ecological data to overcome the species delimitation problems posed by morphological homoplasy and cryptic speciation (e.g., Heinrichs *et al.* 2011a, Dong *et al.* 2012).

Early Paleozoic microfossils give the first hints of the presence of land plants in the fossil record (e.g., Tomescu *et al.* 2018) and were employed as maximum age constraints in several divergence time estimates (e.g., Magallón *et al.* 2013, Feldberg *et al.* 2014, Laenen *et al.* 2014, Morris *et al.* 2017). Some cryptospores that occur from the Ordovician to the Silurian strongly resemble the spores of early diverging liverwort lineages (Renzaglia *et al.* 2015, Taylor *et al.* 2017, Tomescu *et al.* 2018), and also some mesofossils of sporophyte fragments that occur from the Ordovician to the Early Devonian seem related to bryophytes (Edwards *et al.* 2014).

The earliest macrofossils of Marchantiophyta are from the Middle Devonian and represent thalloid forms, e.g., *Metzgeriothallus sharonae* Hernick, Landing & Bartowski (2008: 160), which is considered the oldest liverwort fossil (Hernick *et al.* 2008, Tomescu *et al.* 2018). However, there are older macrofossils dating back to the late Silurian or Early Devonian for which an affinity to thalloid lineages has been discussed (refer to Tomescu *et al.* 2018 for review). Due to the often incomplete preservation, many liverwort-like fossils from sedimentary rock were assigned to fossil genera such as *Hepaticites* Walton (1925: 565), *Thallites* Kidst. ex Walton (1925: 564), *Marchantites* Brongniart (1849: 164) emended Walton (1925: 564), and *Metzgeriites* Steere (1946: 306). To date, only *Metzgeriothallus sharonae* and the Late Triassic *Marchantites cyathodoides* (Townrow 1959: 2) Anderson (1976: 22), which represents the oldest thalloid liverwort fossil with air chambers and shows taxonomic affinities to the crown group Marchantiopsida, have been employed as age constraints (Feldberg *et al.* 2014, Laenen *et al.* 2014, Villarreal *et al.* 2016).

Until the Cretaceous the fossil record is dominated by thalloid forms and mosses. Leafy forms which can be assigned to Jungermanniidae appear sporadically from the early Permian onwards and mostly belong to *Jungermannites* Göppert (1845: 113) emended Steere (1946: 307), which is defined by the presence of two-or three-ranked leaves and a terminal sporophyte with a four-valved capsule. To date 11–12 species have been accepted (e.g., Berry 1919, Poulsen 1974, Scott 1980, Oostendorp 1987). Only a few of the leafy forms preserved in sedimentary rock can be compared with extant families or orders, including the Late Jurassic *Cheirorhiza brittae* Krassilov (1970: 134) and the Early Cretaceous *Diettertia montanensis* Brown & Robison (1974: 170) (Krassilov 1970, 1973, Brown & Robison 1974, Krassilov & Schuster 1984, Schuster & Janssens 1989).

Uncertain classifications become less obstructive from the mid-Cretaceous onwards when the first amber inclusions appear in the fossil record. Contrary to earlier geologic periods the leafy forms are well represented, while only one thalloid form, *Metzgeriites kujiensis* T.Katag. in Katagiri & Shinden (2020: 14), was described from Late Cretaceous Japanese amber. Eight amber deposits yielded leafy liverworts to date, namely 95–100 million-year old (Ma) Alaskan amber (mid-Cretaceous; Heinrichs *et al.* 2011b), ca. 99 Ma Burmese amber (Kachin amber) from northern Myanmar (mid-Cretaceous; Ross *et al.* 2010, Shi *et al.* 2012, Yu *et al.* 2019), 52 Ma Cambay amber from India (Eocene; Rust *et al.* 2010), 34–41 Ma Baltic amber from Europe (Eocene; Sadowski *et al.* 2017, Kasiński *et al.* 2020), 35–37 Ma Rovno amber from the Ukraine (Eocene; Perkovsky *et al.* 2010), presumably 24 Ma Bitterfeld amber (Oligocene; Dunlop 2010), 15–20 Ma Dominican amber (Miocene; Penney 2010, Iturralde-Vinet & MacPhee 2019), and 15–23 Ma Mexican amber (Miocene; Solórzano Kraemer 2010, Serrano-Sánchez *et al.* 2015). Fossils in amber are mostly three-dimensionally preserved in life-like fidelity and often show minute details that are relevant for classification, e.g., cell shape, cell wall ornamentation, gemmae, or leaf teeth. Most specimens are vegetative gametophyte fragments and reveal only a subset of taxonomically relevant characters, but sometimes fertile structures, such as androecia, gynoecia, or sporophytes are preserved and enhance the reliability of the assignment to extant taxa (e.g., Heinrichs *et al.* 2018a). Amber fossils usually allow at least a reliable generic assignment which makes them an invaluable source for reconstructing the morphological evolution of Jungermanniidae (Heinrichs *et al.* 2018a, Renner 2020).

Most amber inclusions belong to the predominantly epiphytic Porellales and especially the families Frullaniaceae and Lejeuneaceae are very diverse. This dominance can be explained by the fact that the resin producing trees grew in humid and warm-temperate to tropical regions (e.g., Penney 2010, Rust *et al.* 2010, Sadowski *et al.* 2017) with microclimates very similar to those prevalent in the main geographic distribution of present-day epiphytic liverworts, but also because the epiphytes might have been closer to resin flows.

The epiphytic liverwort diversity of the Baltic, Bitterfeld, and Rovno amber forests was dominated by species of the genus *Frullania* Raddi (1818: 9), whereas the flora of the Dominican and Mexican amber forests was dominated by representatives of Lejeuneaceae. This is most likely a consequence of the different climates as species of the subcosmopolitan, extant genus *Frullania*, especially subgen. *Trachycolea* Spruce (1884: 31), seem to be better adapted to cool-temperate to warm-temperate climates and much more abundant and diverse in the Holarctic region than the essentially pantropical extant Lejeuneaceae (Schuster 1980, 1992). As compared with Lejeuneaceae, many more species of *Frullania* also grow under rather dry conditions. In North America Lejeuneaceae are largely restricted to southern Florida whereas *Frullania*, especially subgen. *Trachycolea*, is abundant in the temperate part of the continent. In Europe *Frullania* is a common epiphyte throughout the region whereas Lejeuneaceae are rare. The global distribution and strong drought-adaption of *Frullania* not only explains its prevalence in temperate amber, but also its scarcity in tropical Dominican and Mexican ambers, because inside some tropical rainforests *Frullania* is mainly restricted to the canopy and does not grow on the trunks, except in montane cloud forests (e.g., Gradstein *et al.* 2001). In contrast, these trunks are rich in Lejeuneaceae.

During the past decade, we had the opportunity to investigate the majority of fossil liverworts preserved as amber inclusions. In this checklist, we discuss those liverwort fossils that are suitable as age constraints in molecular phylogenetic reconstructions, with a special focus on amber inclusions.

Material and methods

The collections in which the amber fossils are housed are listed in Table 1. When necessary, amber specimens were prepared for study following the procedures described by Kettunen *et al.* (2019). Photographic documentation of the specimens was likewise done as described by Kettunen *et al.* (2019). All images are digitally stacked photomicrographic composites from up to 80 individual focal planes using the software package HeliconFocus version 6.3.3 Pro.

Nomenclature and classification follow Söderström *et al.* (2016), except when more recent taxonomical changes are available. This is indicated in the respective justification sections. These sections also include possible assignments of fossils to molecular phylogenies of extant taxa which are based on morphological comparisons and previous divergence time estimations.

TABLE 1. Institutions housing fossil liverworts and their acronyms.

Acronym	Institution/Collector
AMNH	American Museum of Natural History, New York
FEGI-FEB-RAS (ДВГИ)	Far East Geological Institute, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok
GPIH	Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg (also including several specimens formerly belonging to the Carsten Gröhn Amber Collection)
GRÖHN	Carsten Gröhn Amber Collection (Amber Research Group, c/o Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg)
GZG	Geoscientific Collections of the University of Göttingen (also including the Heinrich Grabenhorst Amber Collection, the botanical part of the Christel and Hans Werner Hoffeins Amber Collection, and several specimens formerly belonging to the Patrick Müller Amber Collection)
HAL-Palaeo	Institut für Geologische Wissenschaften und Geiseltalmuseum, Halle (Saale)
LIEDTKE	Wolfgang Liedtke Amber Collection (Amber Research Group, c/o Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg)
LUDWIG	Walter Ludwig Amber Collection (Amber Research Group, c/o Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg)
MB	Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Berlin
MÜLLER	Patrick Müller Amber Collection (Amber Research Group, c/o Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg)
NICH	Hattori Botanical Laboratory, Nichinan
NMNH	National Museum of Natural History of the Smithsonian Institution, Washington D.C.
NYSM	Paleontology Collection of the New York State Museum, Albany
OSU	Poinar Amber Collection (to be deposited at Oregon State University, Corvallis)
PB	Nanjing Institute of Geology and Palaeontology
SAMC	South African Museum, Cape Town

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TABLE 1. (Continued)

Acronym	Institution/Collector
SIZK	Schmalhausen Institute of Zoology, Kiev
SMNS	Staatliches Museum für Naturkunde, Stuttgart
SNSB-BSPG	Bavarian State Collection for Palaeontology and Geology, Munich
UMPC	University of Montana Paleontological Collection, Missoula
VELTEN	Jürgen Velten Amber Collection (Amber Research Group, c/o Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg)
WAR-MZ	Muzeum Ziemi, Warsaw
WINTER	Gerhard Winter Amber Collection, Karben
WUNDERLICH	Jörg Wunderlich Amber Collection (Amber Research Group, c/o Geological-Palaeontological Institute and Museum (CeNak) of the University of Hamburg)

Results and discussion

In this checklist we provide information on taxonomy, nomenclature, type material, additional specimens (when present), references, age and stratigraphic level of the fossil material, possible calibration points within the phylogeny of related extant taxa, and justification of these assignments. If a genus includes several fossil species from one deposit, age and stratigraphic level as well as justification refer to all of them. Furthermore, if a genus or family includes several species or species which are currently not suitable for calibration, these are discussed within the scope of families and/or genera. Collection numbers of fossils that were investigated for the first time in the course of this study are indicated in bold print in the lists of specimens.

Phylum: Marchantiophyta Stotler & Crand.-Stotl.

Class: Marchantiopsida Cronquist, Takht. & Zimm.

Subclass: Marchantiidae Engl.

Order: Marchantiales Limpr.

Family: incertae sedis

Genus: *Marchantites*

Marchantites cyathodoides

Basionym: *Hepaticites cyathodoides*.—Holotype: SAMC 13929.

≡ *Eomarchantites cyathodoides* (Townrow) R.M.Schust. in Krassilov & Schuster (1984: 1178), *nom. illeg.*

Reference: Townrow (1959), plate 1A, B, figs. 1A–J, 2A.

Age and stratigraphic level: 228–237 Ma, Carnian (Late Triassic), Molteno Formation of South Africa.

Calibration: Minimum age of Marchantiidae.

Justification: This Triassic fossil is the oldest thalloid fossil which can be assigned to Marchantiopsida with high confidence (Townrow 1959, Anderson 1976, Krassilov & Schuster 1984 as *Eomarchantites cyathodoides,* Oostendorp 1987). It is known only in sterile condition and the thallus is characterized by one row of ventral scales along a midrib, reduced air chambers with pores similar to the extant genus *Cyathodium* Kunze ex Lehmann (1834: 17) (Townrow 1959), and smooth, dimorphic rhizoids with thick as well as thin walls similar to the extant *Neohodgsonia* Persson (1954: 40) (Villarreal *et al.* 2016). Except for the simple thalloid Blasiales and the Sphaerocarpales, comparable characters can be found in the majority of complex thalloids. Heinrichs *et al.* (2007) employed this fossil to constrain the stem node of the complex thalloids and Cooper *et al.* (2012), Sun *et al.* (2014), as well as Villarreal *et al.* (2016) used the fossil to constrain the stem node of *Neohodgsonia* and the remaining complex thalloids (Marchantiidae).

Class: Jungermanniopsida Stotler & Crand.-Stotl.

Most fossils resembling the simple thalloid subclasses Metzgeriidae and Pelliidae are found in sedimentary rock and, with the exception of *Metzgeriothallus sharonae*, are difficult to assign to any extant lineage. The fossil genus *Metzgeriites* includes seven species ranging in age from the Early Jurassic to the Early Cretaceous, and *Metzgeriothallus* Schuster (1981: 185) includes two species ranging in age from the Middle Devonian to the late Carboniferous (Katagiri & Shinden 2020). An exception is *Metzgeriites kujiensis,* which represents the only amber fossil of a thalloid liverwort to date and has been found in Late Cretaceous Japanese Kuji amber. The fossil is sterile and cells have not been observed, but it shows close morphological affinities to Metzgeriaceae (Katagiri & Shinden 2020), albeit a classification is difficult and it is therefore not suited as age constraint.

Subclass: incertae sedis

Order: incertae sedis

Family: incertae sedis

Genus: *Metzgeriothallus*

Metzgeriothallus sharonae

Holotype: NYSM 17656.

Additional specimens: Gametophytes NYSM 17657–17660, 17662–17664, sporophyte NYSM 17661, approximately 100 unillustrated gametophytes from Cairo quarry (sample CHD-4.6) and 50 gametophytes from Bates Hollow quarry (sample Bat-7.2).

Reference: Hernick *et al.* (2008), plates I, II.

Age and stratigraphic level: 383–388 Ma, Givetian (late Middle Devonian), Plattekill Formation of the eastern Hamilton Group, New York, USA.

Calibration: Minimum age of Jungermanniopsida/stem Pelliidae.

Justification: *Metzgeriothallus* was established for fossil liverworts which resemble extant *Metzgeria* in having thalli with unistratose, entire-margined wings and a multistratose costa. Besides the typical morphology of the genus, *M. sharonae* has a cylindrical sporophyte capsule with four valves. This character supports the assignment to Metzgeriales (Hernick *et al.* 2008), but similar morphotypes occur not only in Metzgeriales but also in several independent lineages of Jungermanniopsida, namely Metzgeriidae and Pelliidae. Therefore, Feldberg *et al.* (2014) treated it as the most recent common ancestor of Jungermanniopsida with a minimum age of 385.3 Ma, while Laenen *et al.* (2014) assigned an age of 398 Ma to the stem of Pelliidae.

Subclass: Jungermanniidae Engl.

Order: incertae sedis

Family: incertae sedis

Genus: *Cheirorhiza* Krassilov (1970: 132)

Cheirorhiza brittae

Holotype: FEGI-FEB-RAS (ДВГИ) 515-38a.

Additional specimens: Krassilov mentions “about 150” (Krassilov 1970) respective “more than 100” (Krassilov 1973) prepared specimens. In Krassilov (1970) figures for the additional specimens FEGI-FEB-RAS (ДВГИ) 515-8a (XI 8), 515-11 (XI 4, 5), 515-12 (XII 8, 9), 515-15 (XII 5), 515-18 (XI 7), 515-20 (XI 6), 515-23 (XII 2), 515-28 (XII 6), 515-34 (XII 1), 515-37 (XII 3, 4), 515-42 (XII 10), 515-346 (XII 4) are provided.

References: Krassilov (1970), plates XI 4–8, XII 1–10; Krassilov (1973), plates 41–43; Krassilov & Schuster (1984), fig. 1.

Age and stratigraphic level: 158 Ma, Oxfordian (Late Jurassic), Talynjan (Talynzhan) Formation of Bureya Basin, Iravyi bank of the Bureya river near the mouth of the river Umalta, Amur, Russia.

Calibration: Minimum age of Jungermanniidae.

Justification: This species represents one of the few fossils from sedimentary rock which are sufficiently well-preserved to allow a detailed reconstruction of the morphology and to interpret it as a leafy liverwort with confidence. It has terminal as well as intercalary branches, complicate bilobed leaves with the small ventral lobe not attached to the dorsal one, reduced underleaves, scattered, supposedly septate rhizoids, and probably capsules (Krassilov 1973, Krassilov & Schuster 1984). The combination of characters does not allow to assign it to either Porellales or Jungermanniales, therefore it has been employed as a constraint for Jungermanniidae in Heinrichs *et al.* (2007), Sun *et al.* (2014), and Cooper *et al.* (2012).

Order: Jungermanniales H.Klinggr.

Family: incertae sedis

Genus: *Diettertia* Brown & Robison (1974: 170)

Diettertia montanensis

Holotype: UMPC 281.—Paratype: UMPC 297.

References: Brown & Robison (1974), figs. 1–6; Schuster & Janssens (1989), figs. 1, 2, plate I; Krassilov & Schuster (1984).

Age and stratigraphic level: 112 Ma, early Albian (Early Cretaceous), Kootenai Formation, Great Falls, Cascade County, Montana, USA.

Calibration: Minimum age of crown group Jungermanniales.

Justification: *Diettertia montanensis* is the second fossil from sedimentary rock that can be clearly identified as a member of Jungermanniidae. With its complicate bilobed, subtransversely inserted leaves, massive stems, elongated cortical cells, and scattered rhizoids it shows strong morphological affinities to Jungermanniales and resembles the isolated genus *Schistochila* Dumortier (1835: 15) (Krassilov & Schuster 1984, Schuster & Janssens 1989, Heinrichs *et al.* 2007). However, the apparent lack of a ventral merophyte, in combination with the conduplicate bilobed leaves, may also indicate affinities with the Pleuroziales (Schuster & Janssens 1989). The fossil was assigned as age constraint for Jungermanniales in Heinrichs *et al.* (2007), Cooper *et al.* (2012), Sun *et al.* 2014, and Laenen *et al.* (2014).

Family: Anastrophyllaceae L.Söderstr., De Roo & Hedd.

Genus: *Anastrophyllum* (Spruce) Stephani (1893: 139)

Anastrophyllum rovnoi Mamontov, Heinrichs & Váňa in Mamontov *et al.* (2015b: 45)

Holotype: SIZK-K-915-F.

Reference: Mamontov *et al.* (2015b), figs. 1–6.

Age and stratigraphic level: 35–37 Ma, Priabonian (late Eocene), amber quarry "Pugach", Klesov, Ukraine (Rovno amber).

Calibration: Possible minimum age within Anastrophyllaceae (*Anastrophyllum*/*Gymnocolea*).

Justification: This is the first fossil from amber that was identified as a member of the family Anastrophyllaceae and the widely distributed extant genus *Anastrophyllum.* The assignment is based on the similarity between *A. rovnoi* and *A. ellipticum* Inoue (1978: 13) as well as *Gymnocolea inflata* (Hudson 1778: 511) Dumortier (1835: 17), both members of Anastrophyllaceae. *Anastrophyllum rovnoi* shares with both *A. ellipticum* and *G. inflata* the shape of shoots, the shape of the bilobed leaves, and the leaf cells with clear nodulose thickenings. However, the presence of obliquely inserted and thus nearly flat leaves (versus usually transversely inserted and concave-canaliculate in extant *Anastrophyllum* species) means the generic assignment of *A. rovnoi* needs further scrutiny when more completely preserved fossils become available.

Genus: *Tetralophozia* (R.M.Schust.) Schljakov (1976: 227)

Tetralophozia groehnii Heinrichs, Váňa & Schäf.-Verw. in Heinrichs *et al.* (2015b: e0140977 [6])

Holotype: GPIH 4575 (Coll. Gröhn 5827).

References: Heinrichs *et al.* (2015b), figs. 2, 3; Heinrichs *et al.* (2018a), plate II(2).
Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region.
Calibration: Minimum age of *Tetralophozia.*
Justification: This species represents the first fossil evidence of *Tetralophozia,* a small genus of four extant species which are distributed in Asia, Africa, and the Holarctics (e.g., Paton 1999, Schuster 2002). The fossil shows the typical 4-lobed leaves with toothed margins and only differs from extant representatives of the genus by the regular dentation and the presence of teeth with 1–4(–5) celled uniseriate tips (Heinrichs *et al.* 2015b). Divergence time estimates provide evidence of an Eocene origin of *Tetralophozia* and are in good accordance with the age of the fossil (Feldberg *et al.* 2013, 2014). The sterile condition limits the comparison with the extant diversity, but *T. groehnii* is morphologically very similar to extant species and might even belong to the crown group. Hence, it provides a reliable minimum age constraint for the genus.

Family: Calypogeiaceae Arnell

This family is represented by two fossil species of the genera *Calypogeia* Raddi (1818: 31) and *Metacalypogeia* (S.Hatt.) Inoue (1959: 231) in Baltic and Bitterfeld amber. Only the *Calypogeia* fossil provides a reliable age constraint, while the taxonomic assignment of the *Metacalypogeia* fossil is unclear.

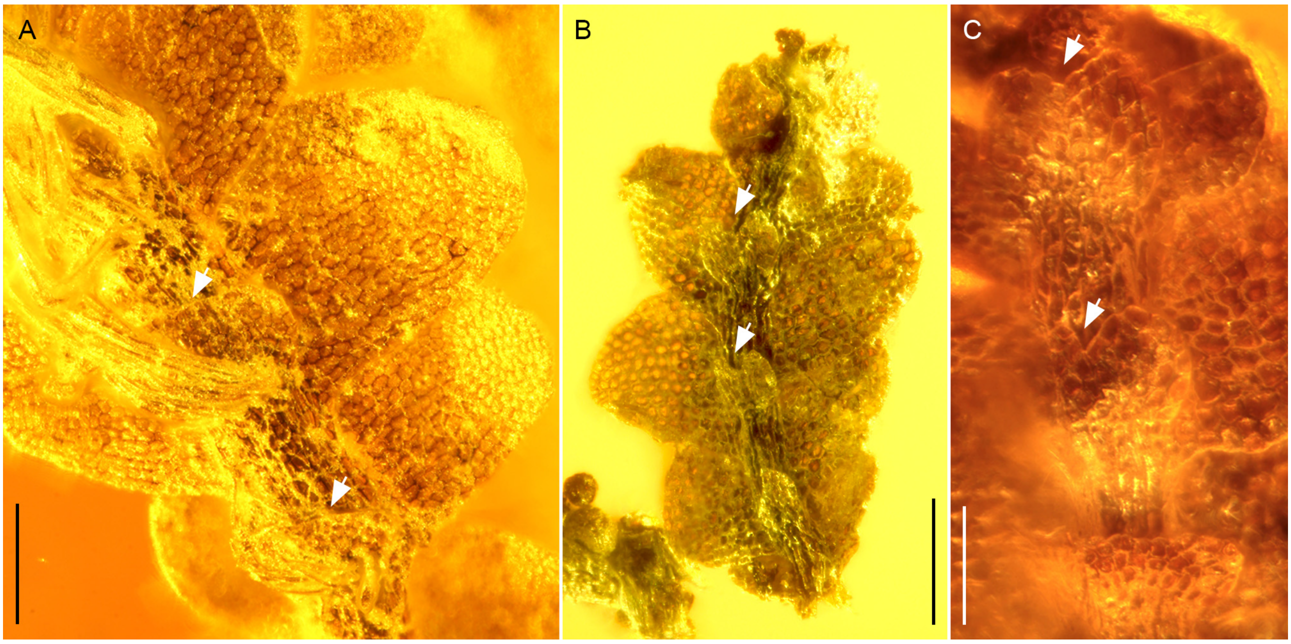

FIGURE 1. Calypogeiaceae. A. *Metacalypogeia baltica,* MB.Pb.1996/1355a (holotype) from Baltic amber, ventral view with underleaves and rhizoid bundles. **B, C.** *Calypogeia stenzeliana.* **B.** MB.Pb.1997/3i (holotype) from Bitterfeld amber, overview ventral. **C.** GRÖHN 2076 from Baltic amber, ventral view with underleaves. White arrows indicate underleaves. Scale bars: A, B=200 µm, C=100 µm.

Metacalypogeia baltica Grolle (1999: 88) has been described from Baltic amber only (Fig. 1A). Extant *Metacalypogeia* is differentiated from *Calypogeia* by cuticular structure (smooth vs. smooth to finely verrucose), gemmae production (lacking vs. present), oil-bodies, and the capsule valves (e.g., Hong 1990), whereas the latter three characters have not been observed in the fossil material. The first character is variable as also some *Calypogeia* species can have a smooth cuticle. Not all fossils of *C. stenzeliana* Grolle (1985a: 41) show a distinctly striolate cuticle and the overall high similarity of *M. baltica* and *C. stenzeliana* might render them conspecific (Fig. 1B, C). The only clear difference between the two fossil species is the furcation of underleaves, but these have proven to be variable in extant species, especially between gemmiparous shoots and the main shoots (Paton 1999). One example is *C. neesiana* (Massalongo & Carestia 1880: 351) Müll.Frib. in Loeske (1905: 320) which is characterized by heterogenous underleaves, which are entire to retuse to emarginate to bilobed. Gemmiparous shoots of this species often have bidentate lateral leaves and more deeply bilobed underleaves than on the main shoot. The underleaves can also vary in having additional lateral teeth. Another example of morphological heterogeneity within one species is *C. sphagnicola*

(Arnell & J.Perss. in Arnell 1902: 26) Warnst. & Loeske in Loeske (1905: 320) which has shoots with subacute to narrowly rounded lateral leaves as well as shoots with retuse lateral leaves.

Genus: *Calypogeia*

Calypogeia stenzeliana; Fig. 1B, C

Holotype: MB.Pb.1997/3i (Coll. Grolle F/1i), Bitterfeld amber.—Paratype: MB.Pb.1997/3k (Coll. Grolle F/1k), Bitterfeld amber.

Additional specimens: Baltic amber: GRÖHN **2076 (det. *Metacalypogeia baltica* in Grolle & Meister 2004b),** 2092; MB.Pb.1996/1356 (Coll. Hoffeins). **Bitterfeld amber:** MB.Pb.1997/3j (Coll. Grolle F/1j).

References: Grolle (1985a), Abb. 1a–d, Tafeln I, II; Grolle & Meister (2004b), plate 2a–d; Heinrichs *et al.* (2018a), plate I(5).

Age and stratigraphic levels: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: Minimum age of *Calypogeia.*

Justification: Apart from the holotype, several well-preserved specimens of *C. stenzeliana* are known from Baltic and Bitterfeld amber and were all investigated for this study. All specimens are known only in sterile condition (Grolle 1985a, Grolle & Meister 2004b), however, the holotype (Fig. 1B) and specimens MB.Pb.1996/1356 as well as GRÖHN 2092 and 2076 are exquisitely preserved and show a wide array of characters, which are sufficient for a reliable generic assignment and in good accordance with the morphology of extant *Calypogeia*, including the incubous, entire to shallowly bilobed lateral leaves, which can be rather variable on one shoot, the mostly bilobed underleaves, and in the latter specimen also the tapering of the shoot with leaves becoming successively smaller and more distant (e.g., Hong 1990, Paton 1999, Schuster 2000). One specimen (GRÖHN 2076) was identified as *Metacalypogeia baltica* in Grolle & Meister (2004b) but is here re-identified as *C. stenzeliana* based on the presence of bifid underleaves (Fig. 1C). It is larger than the holotype with shoots up to 520 µm wide, the stem up to 90 µm wide, a ventral merophyte ca. 6 cells wide, and lateral leaves 250–300 µm long × 230–250 µm wide. The apices of lateral leaves are rounded to truncate to retuse. The leaf cells are quadrate to rectangular and 20–25 µm long × 18–25 µm wide. Underleaves are 0.8–1 × wider than the stem, 100–120 µm long × 130–160 µm wide, ca. 1.3 × wider than long, and bilobed to ca. 0.25–0.3. The sinus is widely V-shaped, and the underleaf lobes are ca. 4 cells wide at base and 2(–3) cells long with an obtuse apex.

The species is resembling *C. suecica* (Arnell & J.Perss. in Arnell 1902: 29) Müller (1904: 224) from temperate-boreal Europe and North America (Grolle & Meister 2004b). However, a more elaborate discussion of its affinities to extant representatives is presently difficult because fertile structures are lacking and the inner taxonomy of *Calypogeia* is still not sufficiently known (Söderström *et al.* 2016). Species are characterized by ecologically induced morphological variation as well as cryptic species complexes (Schuster 1969, Paton 1999, Buczkowska *et al.* 2018).

Calypogeia stenzeliana has already been employed as age constraint in several analyses (Heinrichs *et al.* 2007, Cooper *et al.* 2012, Feldberg *et al.* 2014, Laenen *et al.* 2014, Sun *et al.* 2014). In Feldberg *et al.* (2014) and Laenen *et al.* (2014) it was assigned as most recent common ancestor of the *Calypogeia* crown group. These assignments resulted in an estimated mean age for the genus of 40.03 Ma respective median ages of 44.78–71.23 Ma. The incomplete fossil material does not justify any assignment within the extant crown group of *Calypogeia*, though the morphology of *C. stenzeliana* suggest close affinities.

Family: Cephaloziaceae Mig.

This family is represented by two fossil species of the genera *Odontoschisma* (Dumort.) Dumortier (1835: 19) and *Cephalozia* (Dumort.) Dumortier (1835: 18) in Baltic and Bitterfeld amber. The taxonomic assignment of the latter is currently difficult. *Cephalozia veltenii* Katagiri (2015: 348) is very similar to the stolons or tapering shoots with reduced leaves which are frequently produced by *O. dimorpha* (Caspary 1887: 2) Heinrichs, K.Feldberg, Váňa & Schäf.-Verw. in Feldberg *et al.* (2017: 151)*,* but it can be distinguished from the latter by several characters (Katagiri 2015), e.g., the presence of a stem hyalodermis and the obliquely to transversely inserted leaves which usually do not reach the midline of the dorsal stem surface. The use of *C. veltenii* as age constraint is currently not advisable, not only because of the lack of fossil material, but also because of the taxonomical uncertainties in extant *Cephalozia* (e.g., Feldberg *et al.* 2016).

Genus: *Odontoschisma*

Odontoschisma dimorpha; Fig. 2A–C

Basionym: *Jungermannia dimorpha* Casp.—Holotype: MB.Pb.1979/687a (Coll. Künow 144a), Baltic amber.

≡ *Cephaloziella dimorpha* (Casp.) Grolle (1980a: 184)

≡ *Cylindrocolea dimorpha* (Casp.) Grolle in Grolle & Meister (2004b: 14)

Additional specimens: Baltic amber: GPIH BB1584, 4575 (Coll. Gröhn 5827); GRÖHN 2015, 2038, 2082, **5834, 7622;** GZG.BST.21957 (Coll. Hoffeins 5-43), GZG.BST.21959 (K7.319); MB.Pb.1979/654 (Coll. Künow 95), MB.Pb.1979/688 (Coll. Künow 145), MB.Pb.1979/689 (Coll. Künow 146), MB.Pb.1979/708 (Coll. Künow 165a), MB.Pb.1979/687b (Coll. Künow 144b), **MB.Pb.1996/1357 (Coll. Rasmussen; det. *Lophozia kutscheri* in Grolle & Meister 2004b);** SNSB-BSPG 1958 VIII 44 (Bachofen-Echt amber collection P44), 1958 VIII 95 (Bachofen-Echt amber collection P95). **Bitterfeld amber:** GZG.BST.21958 (Coll. Hoffeins 930-3), **GZG.BST.22049 (Coll. Grabenhorst Le-49),** GZG.BST.22050 (Coll. Grabenhorst Le-51), **GZG.BST.22051 (Coll. Grabenhorst Le-58), GZG.BST.22052 (Coll. Grabenhorst Le-73), GZG.BST.22053 (Coll. Hoffeins 13-2);** MB.Pb.1997/2 (Coll. Kutscher H006), MB.Pb.1997/12 (ser. 8/2a), MB.Pb.1997/16 (Coll. Kutscher M 8/6), MB.Pb.1997/24 (Coll. Grolle M 10/5), MB.Pb.1997/36 (Coll. Grolle M 12/8), MB.Pb.1997/37 (Coll. Grolle M 12/9), MB.Pb.1997/44a (Coll. Grolle M-14/5a).

References: Caspary (1887), Tafel I Bild 3, 4 as *Jungermannia dimorpha;* Caspary & Klebs (1907), Tafel VII Bild 38, 38a–d as *Jungermannia dimorpha;* Grolle (1980a), Abb. 1a–f, Tafeln XIII, XIV, XVIc–e as *Cephaloziella dimorpha;* Grolle (1989), Abb. 1e as *Cephaloziella dimorpha;* Grolle & Meister (2004b), plates 3, 4a–f as *Cylindrocolea dimorpha;* Feldberg *et al.* (2017), figs. 1, 2; Heinrichs *et al.* (2018a), plate I(6).

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: Minimum age of *Odontoschisma* sect. *Iwatsukia* (Kitagawa 1964: 178) Gradstein, Aranda & Vanderpoorten (2014: 232).

Justification: *Odontoschisma dimorpha* is the most abundant representative of Jungermanniales in Baltic as well as Bitterfeld amber, but due to the scarcity of distinct underleaves its true taxonomical affinities were unknown for a long time. The assignment is also complicated by the mostly sterile condition of fossil specimens. Androecia are present in the holotype (Fig. 2A) and one additional specimen (SNSB-BSPG 1958 VIII 44), but gynoecia as well as sporophytes are still unknown. The species is characterized by a very heterogeneous morphology (e.g., Grolle & Meister 2004b, Feldberg *et al.* 2017) which includes vigorous shoots with large, imbricate lateral leaves and well developed bifid underleaves but also stoloniform and tapering shoots with strongly reduced lateral leaves and reduced to lacking underleaves (compare Fig. 2A–C). This combination of characters allows for an assignment to the small tropical genus *Iwatsukia* which has been included in *Odontoschisma* as sect. *Iwatsukia* based on molecular phylogenetic evidence (Vilnet *et al.* 2012, Aranda *et al.* 2014). The fossil is somewhat similar to the extant *Odontoschisma jishibae* (Stephani 1924: 437) L.Söderstr. & Váňa in Váňa *et al.* (2013b: 13) and differs from most other species of *Odontoschisma* in having bifid leaves and evenly thickened cell walls without trigones (compare Gradstein & Ilkiu-Borges 2015, fig. 9).

The taxonomical affinities of *O. dimorpha* have thoroughly been discussed in Feldberg *et al.* (2017) who confirmed the suitability as an age constraint for *Odontoschisma* sect. *Iwatsukia*. Placement of the fossil in Cephaloziaceae profoundly affects divergence time estimates. The reclassification in Feldberg *et al.* (2017) concurs with hypotheses on the divergence times of Cephaloziaceae derived from DNA sequence data that provide evidence of a late Early Cretaceous to early Eocene age of the *Odontoschisma* crown group and an origin of sect. *Iwatsukia* in the Late Cretaceous to Oligocene.

Family: Cephaloziellaceae Douin

This family is represented by two fossil species which could provide minimum age constraints for the genera *Cephaloziella* (Spruce) Schiffner (1893: 98) and *Protolophozia* (R.M.Schust.) Schljakov (1979: 204). However, both genera are taxonomically largely unresolved, and assignments have to be thoroughly evaluated.

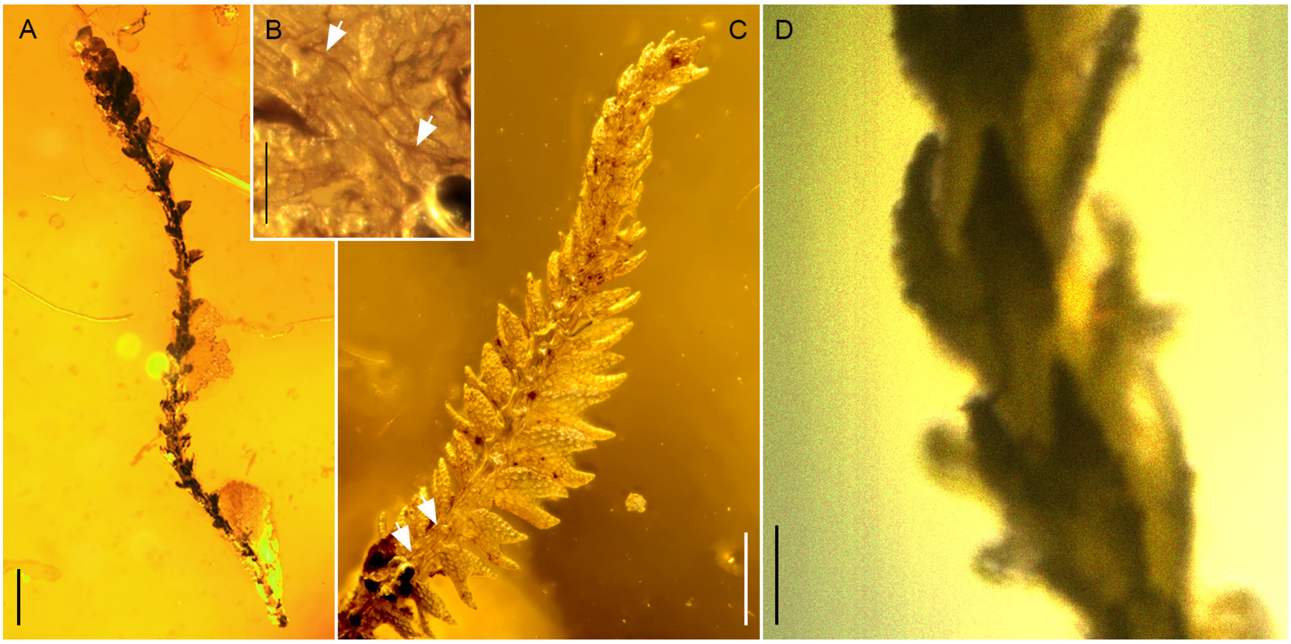

FIGURE 2. Cephaloziaceae and Cephaloziellaceae. A–C. *Odontoschisma* (sect. *Iwatsukia*) *dimorpha.* **A.** MB.Pb.1979/687 (holotype) from Baltic amber, overview in dorso-lateral view with androecium at shoot tip. **B, C.** MB.Pb.1996/1357 from Baltic amber. **B.** Ventral view with reduced underleaves. **C.** Overview ventral with tapering shoot apex. **D.** *Cephaloziella nadezhdae,* SIZK-K-24755-F (holotype) from Baltic amber in lateral view. White arrows indicate underleaves. Scale bars: A=500 µm, B=50 µm, C=200 µm, D=20 µm.

Genus: *Cephaloziella*

Cephaloziella nadezhdae Mamontov, Heinrichs & Váňa in Mamontov *et al.* (2015c: 293); Fig. 2D

Holotype: SIZK-K-24755-F.

Reference: Mamontov *et al.* (2015c), figs. 1–18.

Age and stratigraphic level: 35–37 Ma, Priabonian (late Eocene), amber quarry "Pugach", Klesov, Ukraine (Rovno amber).

Calibration: Minimum age of *Cephaloziella.*

Justification: The sterile shoot fragment is the first representative of this genus in amber. The small size, the basally ciliately toothed leaves, the distinctly mammillose cells, and the presence of gemmae (Fig. 2D) differentiate this specimen clearly from *Cephalozia veltenii* and *Odontoschisma dimorpha* and allow a reliable assignment to *Cephaloziella,* a taxonomically largely unresolved genus characterized by its small size, the bilobed leaves, and often reduced underleaves (e.g., Schuster 1980, 2002, Söderström *et al.* 2016). Species delimitation in extant *Cephaloziella* is very difficult, especially when only sterile material is at hand (Paton 1999). The species is most similar to representatives of the Holarctic and Oceanic subgen. *Schizophyllum* Müller (1912: 110), while the small leaf cells (only 5–8 µm) are reminiscent of *C. microphylla* (Stephani 1908: 513 [343]) Douin (1920: 59) (Mamontov *et al.* 2015c). The sterile condition makes an assignment to extant lineages of *Cephaloziella* difficult, but it provides a minimum age for the genus.

Genus: *Protolophozia*

Protolophozia kutscheri (Grolle) Heinrichs, Feldberg, Mamontov, Schäfer-Verwimp & Schmidt, *comb. nov.;* Fig. 3

Basionym: *Lophozia kutscheri* Grolle in Grolle & Meister (2004a: 79).—Holotype: MB.Pb.1996/1338, Bitterfeld amber.

Additional specimens: Baltic amber: GRÖHN 5803, **5843. Bitterfeld amber:** MB.Pb.sn (Coll. Kutscher Ku-98H03/a); **GZG.BST.22054 (Coll. Grabenhorst Le-22),** GZG.BST.22055 (Coll. Grabenhorst Le-42), **GZG.BST.22056 (Coll. Hoffeins 945).**

References: Grolle & Meister (2004a), figs. 1, 2 as *Lophozia kutscheri;* Grolle & Meister (2004b), plate 13 as *Lophozia kutscheri;* Heinrichs *et al.* (2018a), plate II(1) as *Lophozia kutscheri*.

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: Possible minimum age of *Protolophozia.*

Emended description: *Shoots* red brown, about 5 mm in length and 0.7–1.0(–1.1) mm wide [GRÖHN 5843 only visible in lateral view; Fig. 3D, E], holotype unbranched and accompanied by a few much smaller and simplified shoot fragments (three ± parallel to its base and a single across apex; Fig. 3A, B), one with bifid leaves near the base and trifid leaves near the apex; specimen GRÖHN 5843 with flagelliform branch much thinner than main shoot (Fig. 3E), 0.15–0.35 mm wide with leaves; shoot apex distinctly turned upwards. *Stem* dark red brown, round to dorsoventrally flattened, 170–180 µm in diameter, cortical cells short to long rectangular, walls pale, equally moderately thickened, lumen dark red brown; on flagelliform branch 30–50 µm in diameter. *Rhizoids* colorless, numerous, irregularly scattered or forming a continuous row along ventral side of stem up to apex. *Ventral leaf free zone* ca. 2 cells broad. *Lateral leaves* imbricate to loosely contiguous, widely patent, in dorsal half ± transversely inserted, in ventral half with ± oblique, succubous, and straight insertion line (Fig. 3A, D, E), slime papillae probably present on coarse teeth near leaf base; leaves obtrapeziform, 400–600 µm long × 330–400 µm wide, widest part below bases of lobes, slightly canaliculate-concave (in dorsal view), often subkeeled near sinus base, on lower parts of shoots often equally bifid, on upper parts mostly unequally 3(–4)-lobed, divided up to 0.3 × the leaf length, the median leaf lobe large, the other two equal in size or one of them distinctly smaller, sometimes even reduced to a spine; lobes triangular to broadly lanceolate, somewhat diverging, almost flat, at base 6–8 cells wide, apex acute to ± acuminate with a short to long triangular tip cell, or if apex gemmiferous then somewhat obtuse; dorsal leaf margin slightly and regularly curved, distinctly upturned, base somewhat turned inwards, slightly but distinctly ampliate, but not overlapping, not decurrent; ventral leaf margin slightly and regularly curved, flat, base slightly ampliate, not overlapping, not decurrent; sinus variable, wide to narrow, with rounded base, mostly gibbous. *Leaf cells* somewhat irregular, pentagonal or hexagonal, mostly isodiametric, some ± elongated, 17–21 × 17–34 µm (sometimes elongated to 45 µm near ventral base), walls pale, moderately equally thickened, almost without trigones, lumen red brown; cuticle faintly punctate-papillose. Lateral leaves on flagelliform branch contiguous to distant, transversely to slightly obliquely inserted, ovate to rectangular, 70–110 µm long × 50–60 µm wide, bifid to ca. 0.5 × their length, lobes lanceolate, acute, 2–3 cells wide at base and 3–4 cells long, incl. single short tip cell. *Underleaves* absent in greater part of type specimen, only in its most vigorous middle three rather large underleaves visible (Fig. 3 C), 0.5 × the lateral leaf length, variably shaped, lanceolate-ovate to bifid, irregularly laciniate-spinose, spines forward directed [seemingly missing or obscured by rhizoids in GRÖHN 5843]. *Asexual reproduction* by gemmae arising in clusters at tips of leaf lobes, ± intact clusters present at shoot apex of type. Otherwise gemmae apparently dispersed and hence merely remnants of clusters on older leaves; gemmae angular, colorless or similar in color to leaf lobes, number of cells not clearly visible. *Sterile.*

Justification: The fossil species does not conform to the current circumscription of *Lophoziaceae* nor the genus *Lophozia* (Dumort.) Dumortier (1835: 17) (Söderström *et al.* 2016), therefore, the taxonomy is re-evaluated here. Based on molecular phylogenies and morphological studies, the taxonomy of Lophoziaceae underwent fundamental changes in recent years (De Roo *et al.* 2007, Vilnet *et al.* 2008, 2010, Váňa *et al.* 2013a, Bakalin & Vilnet 2019). Species included in *Lophozia* lack flagelliform branches and stolons, are characterized by transversely to subhorizontally inserted, 2(–3–4)-lobed leaves, and underleaves are mostly lacking or simple and lanceolate (Schuster 1969, 2002). Especially the latter character distinguishes the type of *L. kutscheri* from extant representatives; it has irregularly shaped lanceolate-ovate to bifid, laciniate-spinose underleaves which can also be lacking (Fig. 3C; also compare Grolle & Meister 2004a, b). The new specimen from Baltic amber (GRÖHN 5843) is in good accordance with the type and provides additional characters which facilitate the taxonomic assignment. It has a flagelliform branch, a character not occurring in *Lophozia*. The branch insertion seems to be lateral but an affiliation to the lateral leaves is not clearly visible. It might be lateral-intercalary and is much thinner than main shoot.

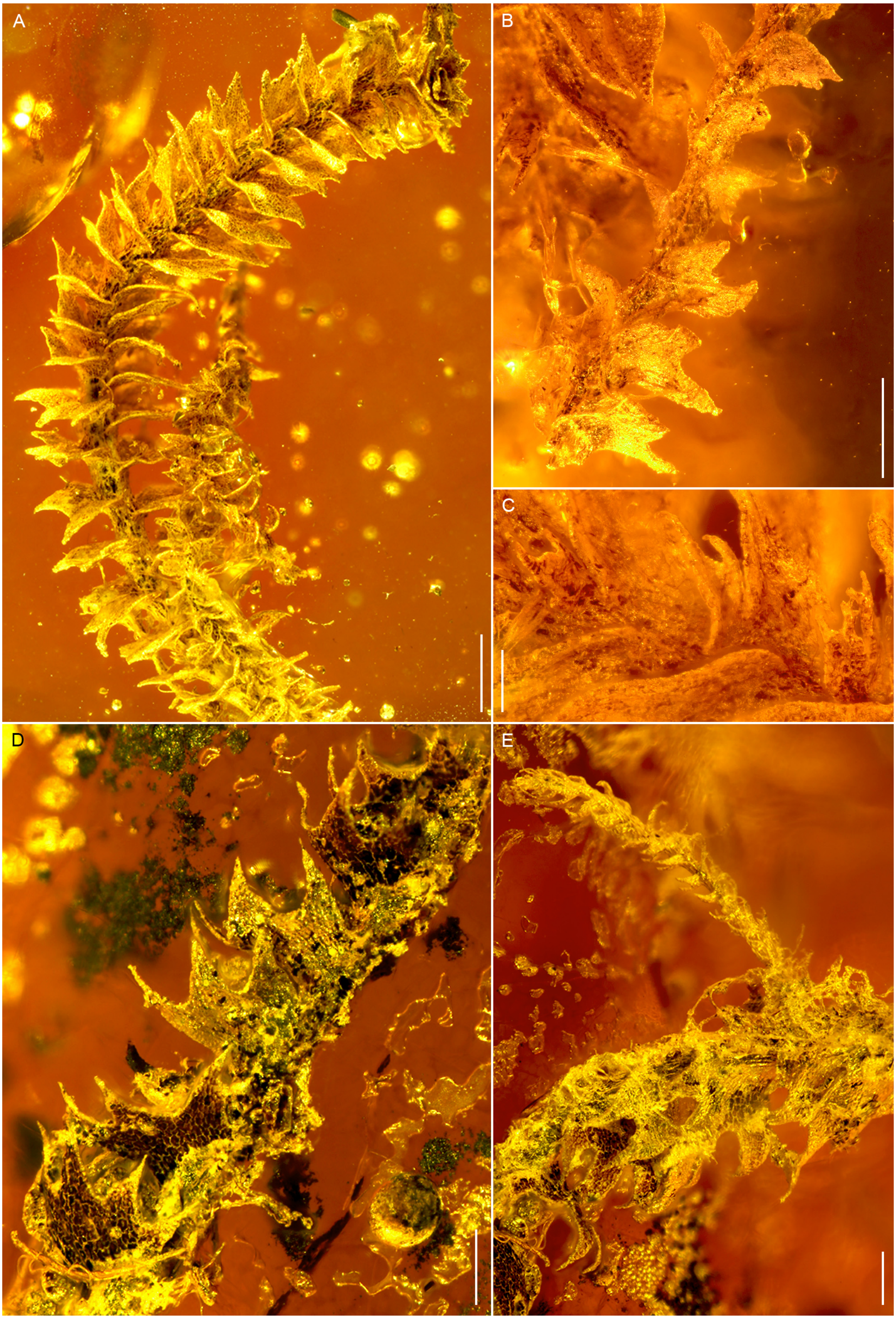

FIGURE 3. Cephaloziellaceae. A–E. *Protolophozia kutscheri, comb. nov.* **A–C.** MB.Pb.1996/1338 (holotype) from Bitterfeld amber. **A.** Dorsal view of large shoot (holotype) with trifid leaves accompanied by smaller shoots with bifid leaves. **B.** Detail of smaller shoot in ventro-lateral view. **C.** Underleaves from holotype. **D, E.** GRÖHN 5843 from Baltic amber in lateral view. **D.** Middle part of shoot with scattered rhizoids. **E.** Flagelliform branch. Scale bars: A=500 µm, B, D, E=200 µm, C=100 µm.

Species with trifid leaves are rare in extant *Lophozia*. They can occur in *L. ciliata* Damsh., L.Söderstr. & H.Weibull in Söderström *et al.* (2000: 3) which also has relatively large lanceolate to 3-lobed, dentate to laciniate underleaves. The plant differs from the fossil species in the form of the ovate-rectangular to obovate lateral leaves, which can be bifid up to 0.5 × their length and are generally longer than wide with more or less straight margins which are gradually narrowed toward the leaf base. The 3-lobed leaves of the fossil are wider than long, and their margins are curved and ampliate. Furthermore, *L. ciliata* has specialized flagelliform shoots with reduced leaves which produce gemmae at their apices. Other genera of Lophoziaceae with occasionally to frequently 3-lobed leaves are *Heterogemma* (Jørg.) Konstantinova & Vilnet (2009: 67), *Trilophozia* (R.M.Schust.) Bakalin (2005: 34), and *Tritomaria* Schiffn. ex Loeske (1909: 13), all of which lack underleaves.

3(–4)-lobed leaves are a highly homoplastic character and occur in several families of Jungermanniales: in Anastrophyllaceae [e.g., *Barbilophozia* Loeske (1908: 37), *Neoorthocaulis* Söderström, De Roo & Hedderson (2010: 49), *Orthocaulis* Buch (1932: 293), *Schljakovianthus* Konstantinova & Vilnet (2009: 66)], in Scapaniaceae [e.g., *Pseudotritomaria* Konstantinova & Vilnet (2009: 66), *Schistochilopsis* (N.Kitag.) Konstant. in Konstantinova & Vasiljev (1994: 125)], and in Cephaloziellaceae [*Protolophozia*].

Though the form of the lateral leaves is superficially similar, *Barbilophozia* differs from *L. kutscheri* in several characters: the leaf insertion is generally oblique, the lateral leaves are basally armed with postical teeth or cilia, and the underleaves are larger, more deeply bifid, and ciliate. More similar is *Neoorthocaulis,* which is characterized by (2–)3(–4)-lobed leaves (divided up to 0.4 × their length) with a revolute sinus and few or no cilia on the postical margin. The underleaves are lacking to large and bifid, have few lateral teeth or cilia (Söderström *et al.* 2010), and clearly differ from the fossil with its variably shaped, lanceolate-ovate to bifid, and irregularly laciniate-spinose underleaves. Furthermore, *Neoorthocaulis* has only few rhizoids while at least the fossil specimen GRÖHN 5843 has dense, scattered rhizoids. *Orthocaulis* clearly differs in having small and unlobed underleaves while *Schljakovianthus* has more deeply and mostly 4-lobed (up to 0.6 × their length) lateral leaves with basal teeth, no gemmae, and bilobed underleaves which are more deeply bifid and have distinct cilia only near their base. *Pseudotritomaria* and *Schistochilopsis* can also have 2–3-lobed leaves, but both genera differ from the fossil by lacking underleaves entirely.

Protolophozia is a small, mainly Austral genus which is still insufficiently known (Váňa *et al.* 2013a). It was treated either as genus or as a subgenus of *Lophozia* (Schuster 2002). Based on molecular phylogenetic evidence the generic status is currently accepted and it was tentatively transferred to Cephaloziellaceae (Vilnet *et al.* 2010, Söderström *et al.* 2016). The genus lacks terminal branching, leaves are 2–3(–4)-lobed, underleaves and gemmae are present. The extant *Protolophozia lancistipa* (Grolle 1971: 230) Váňa & L.Söderstr. in Váňa *et al.* (2013a: 51), *P. crispata* (Schuster 1968: 474) Váňa & L.Söderstr. in Váňa *et al.* (2013a: 51)*,* and *P. verruculosa* (Schuster 1978: 242) Váňa & L.Söderstr. in Váňa *et al.* (2013a: 52) have lateral intercalary branches from the leaf axils, intermingled 2-and 3-lobed leaves, cells with weak trigones, and conspicuous, irregularly shaped, often bifid underleaves. The circumscription of *Protolophozia* is in good accordance with the morphology of the fossil. The form of the 2–3-lobed lateral leaves, the rather irregularly shaped underleaves with only few teeth or cilia and the presence of a flagelliform branch fit the description of this genus, therefore, we transfer *Lophozia kutscheri* to *Protolophozia*.

Lophozia kutscheri has been employed as age constraint in several studies (Feldberg *et al.* 2013, 2014, Laenen *et al.* 2014). Feldberg *et al.* (2014) assigned it to a broadly circumscribed genus *Lophozia* (including *Barbilophozia*) which resulted in an estimated mean age of 43.32 Ma. Laenen *et al.* (2014) assigned it to *Lophozia* and estimated median ages of 34.22–45.92 Ma. A re-assignment that reflects the taxonomical changes of extant genera is currently difficult because only one species of *Protolophozia, P. elongata* (Stephani 1902: 41) Schljakov (1979: 204), has been included in a molecular phylogeny.

Family: Geocalycaceae H.Klinggr.

Genus: *Geocalyx* Nees (1833b: 97)

Geocalyx heinrichsii Katagiri (2018: 113)

Holotype: NICH-492966.
Reference: Katagiri (2018), fig. 1.
Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region.
Calibration: Minimum age of *Geocalyx.*
Justification: This species is the only representative of this monogeneric family in amber. The obliquely inserted,

succubous lateral leaves, the large bifid underleaves, and the presence of gemmiferous, microphyllous shoots are in good accordance with extant representatives (Katagiri 2018). It is similar to the extant Asian species *G. lancistipulus* (Stephani 1922: 281) Hattori (1953: 234), but the sterile condition prevents a more specific comparison.

To date, this species has not been employed as an age constraint. It could provide a minimum age for the crown group of *Geocalyx* which is molecularly and morphologically well defined (e.g., Shaw *et al.* 2015). The stem node of *Geocalyx* has a mean age of 169.31 Ma in Feldberg *et al.* (2014), while the median ages for the genus in Laenen *et al.* (2014) are 74.23–96.93 Ma. Considering the confidence intervals, the latter estimate is in good accordance with the fossil material.

Family: Lepidoziaceae Limpr.

Genus: *Bazzania* Gray (1821: 704)

Bazzania has a largely tropical and subtropical distribution range with expansions into the Arctic and sub-Antarctic regions. The genus includes ca. 100 extant as well as two fossil species and the taxonomy has been intensively studied in recent years (e.g., Zhou *et al.* 2012, Bakalin 2016, Cheah & Yong 2016, Gradstein 2017, Khotimperwati *et al.* 2018, Meagher 2019). Based on new fossil material we emend the description of *B. polyodus* (Caspary 1887: 4) Grolle (1980a: 188) from Baltic and Bitterfeld amber, which is well suited as age constraint.

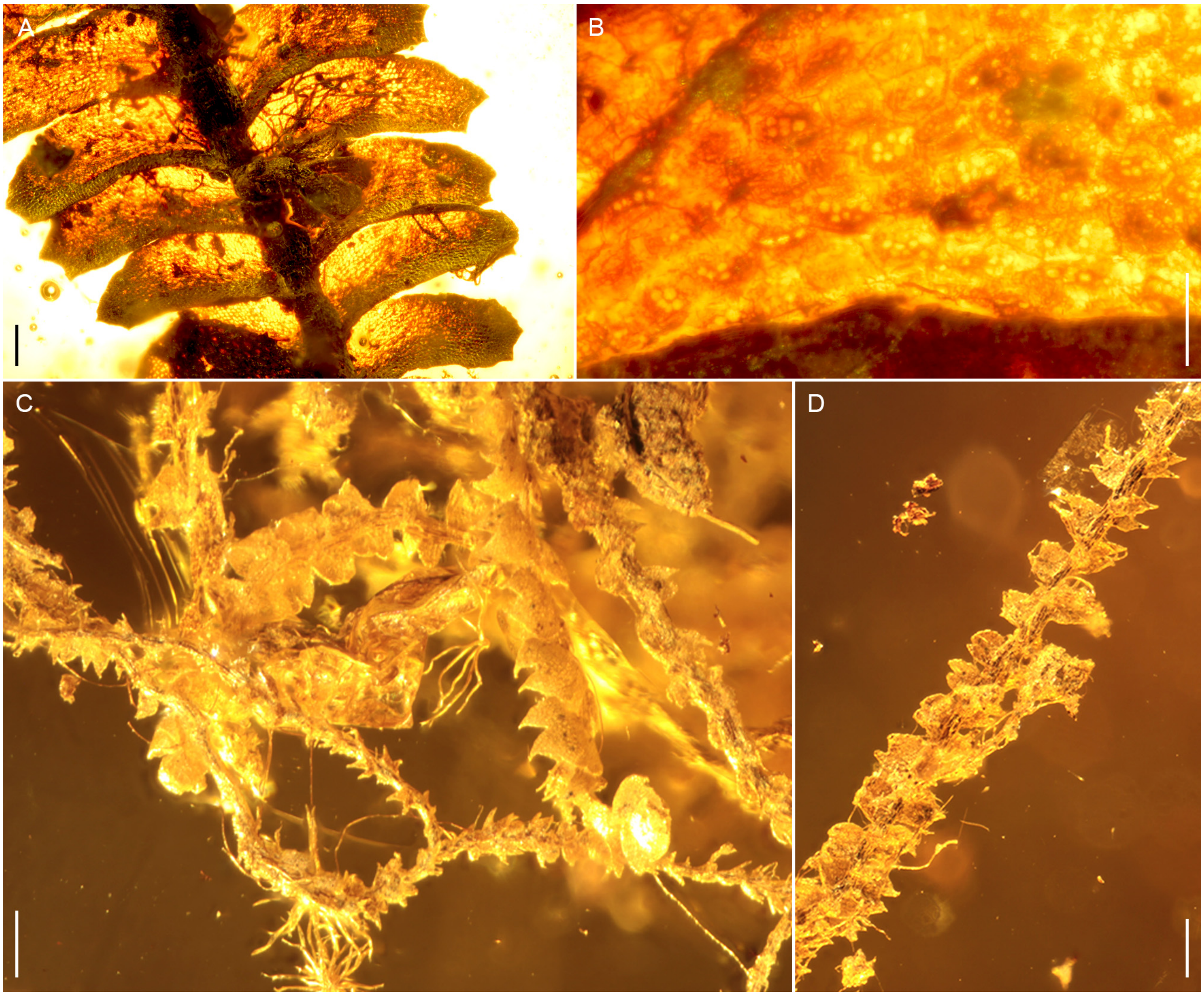

FIGURE 4. Lepidoziaceae. A, B. *Bazzania oleosa,* SMNS do-4100-M-1 (holotype) from Dominican amber. **A.** Ventral view with broken *Bazzania*-type branch (middle). **B.** Leaf cells with oil-bodies. **C, D.** *Bazzania polyodus,* GRÖHN 5844 from Baltic amber. **C.** Shoot system of large, typical shoots and stoloniform shoots. **D.** Stoloniform shoot in ventral view. Scale bars: A, C, D=200 µm, B=50 µm.

Bazzania oleosa Grolle in Grolle & Braune (1988: 102) from Dominican amber is only known from the sterile holotype. Though the fossil is exquisitely preserved and allows a detailed study of many diagnostically important characters, e.g., the ventral *Bazzania*-type branches (Fig. 4A) and the leaf cells with suspected oil-bodies preserved (Fig. 4B), it is currently not possible to assign it to any lineage within the crown group. It shows similarities to *B. hookeri* (Lindenb. in Gottsche *et al.* 1845a: 226) Trevisan (1877: 414) and the common Neotropical *B. longistipula* (Lindenb. in Gottsche *et al.* 1845a: 228) Trevisan (1877: 415) but also differs in several important characters and might not be closely related (Grolle & Braune 1988, Gradstein 2017).

Many of the vegetative characters in extant *Bazzania* are variable and may be affected by environmental factors (e.g., Gradstein 2017), but given extensive molecular datasets combined with morphological analyses, it might yet be possible to assign both fossil species to a lineage within the crown group.

Bazzania polyodus; Fig. 4C, D

Basionym: *Lophocolea polyodus* Casp.—Holotype: MB.Pb.1979/690 (Coll. Künow 147), Baltic amber.

Additional specimens: Baltic amber: GPIH 4327; GRÖHN 443, 2077, **5844;** VELTEN 0017c. **Bitterfeld amber:** LUDWIG Bi2005; MB.Pb.1996/1339 (Coll. Teuber).

References: Caspary (1887), Tafel I Bild 12, 13 as *Lophocolea polyodus;* Caspary & Klebs (1907), Tafel VI Bild 36, 36a–c as *Lophocolea polyodus;* Grolle (1980a), Abb. 1g–k, Tafel XV, XVIa, b; Grolle & Meister (2004b), plate 1; Heinrichs *et al.* (2018a), plate I(1).

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: Minimum age of *Bazzania*.

Emended description: Plants light olive to yellowish brown to reddish brown, shoots up to 5.5 mm long and up to 0.75 mm wide; apices occasionally tapering. Irregularly branched, branches ventral-intercalary, similar to main axis or stoloniform (Fig. 4C); stolons 0.1–0.17 mm wide. *Stem* somewhat translucent to brown, without hyalodermis, distinctly dorsiventrally applanate, 85–120 µm in diameter; cortex of ventral merophyte 4–6 cells wide, cells rectangular, with equally thickened colorless walls. *Rhizoids* arising only at the base of underleaves, mostly in ± loose bundles. *Leaves* incubous, insertion strongly oblique, straight, length of insertion half the leaf width, imbricate to sometimes remote, planodistichous, often with ± decurved apex; semiovate to ovate, 100–420 µm long × 90–310 µm wide in the middle, longer than wide, length:width ratio 1.1–1.3:1, leaves on stolons and tapering shoots becoming more distant and smaller (Fig. 4C, D); entire margined; bilobed to ca. 0.2 × the length at apex, on very slender shoots bilobed to 0.3 (Fig. 4D), sinus ca. 45° or less wide, U-to V-shaped, lobes equal in size, triangular, sometimes ± claw-like decurved, with very sharp spinous tip, whose terminal cell is longer than wide and often broken off; ventral margin slightly arcuate to almost straight, dorsal one strongly arcuate, especially in basal half, on slender shoots and stoloniform branches more symmetric; with rounded ampliate basal margin extending slightly beyond middle of stem without overlapping leaves of the other side. *Cells* with colorless, equally thickened walls, without trigones, ± isodiametric throughout, hexagonal to quadrate to short rectangular, partly seriate, subapically 10–14 × 10–16 µm, in basal middle somewhat elongated (20 µm). *Underleaves* free, with transverse, almost straight insertion; reniform, 50–230 µm long × 50–230 µm wide, wider than long or about as long as wide, length:width ratio 0.8–1:1, 2–3 × wider than stem; on very slender shoots broad elliptic to obovate, about as wide as stem, on stoloniform branches scale-like; base shallowly ampliate and occasionally shortly spurred to cuneate-arcuate, tightly adjacent to stem or obliquely spreading, irregularly quadrilaciniate for 0.3–0.5 × the length, laciniae almost equal in size or the outer somewhat smaller, directed straightly forward, long triangular to lanceolate with very sharp spinous tip; on slender shoots and stolons underleaves irregularly dentate; lateral margin on both sides of underleaves with (1–)2–3(–5) additional spines and teeth of various sizes; terminal cell of laciniae and spines twice or more longer than wide, other cells as those of leaves. *Sterile.*

Justification: *Bazzania polyodus* is known from several well-preserved fossils in Baltic as well as Bitterfeld amber. All specimens are sterile, but the vegetative characters allow a reliable assignment to the genus (Grolle & Meister 2004b). Due to the rareness of fertile specimens in extant *Bazzania,* the identification relies on gametophytic characters of the lateral leaves and underleaves, like shape, size, number of apical lobes, and presence of marginal teeth, as well as the connateness of the underleaves to the lateral leaves. Another important character is the branching pattern, including the characteristic *Bazzania*-type branches. The fossil species is characterized by squat, shortly bilobed lateral leaves and irregularly quadrilaciniate underleaves and does not seem to be related to any of the extant species in Europe but rather to representatives of tropical East Asia and Melanesia (Grolle & Meister 2004b). Grolle & Meister (2004b) noted that fossils of *B. polyodus* lack the diagnostically important stoloniform *Bazzania*-type branches, but a newly discovered specimen from Baltic amber (GRÖHN 5844) represents a rather extensive shoot system with stolons and allows for an emended description. The specimen (Fig. 4C, D) includes several yellowish to dark red brown gametophyte fragments with the larger fragments in good accordance with type specimen but also with many slender, stoloniform shoots with distant leaves and small, scale-like underleaves. This specimen emends the description of *B. polyodus* in a particularly important character that might facilitate an assignment to extant taxa.

Bazzania polyodus is well suited as a minimum age constraint for the crown group of *Bazzania* and was already applied in Heinrichs *et al.* (2007), Cooper *et al.* (2012), Feldberg *et al.* (2014), Laenen *et al.* (2014), and Sun *et al.* (2014). In Feldberg *et al.* (2014) the crown group of *Bazzania* has an estimated mean age of 60.14 Ma, in Laenen *et al.* (2014) median ages of 34.21–45.99 Ma.

Family: Notoscyphaceae Crand.-Stotl., Váňa & Stotler

Genus: *Notoscyphus* Mitten (1871: 407)

Extant *Notoscyphus* currently contains only the paleotropical *Notoscyphus lutescens* (Lehm. & Lindenb. in Lehmann 1832: 16) Mitten (1871: 407). The species is characterized by a rather heterogenous morphology and might represent a cryptic species complex (e.g., Wigginton 2004, Váňa & Long 2009, Braggins *et al.* 2014, Shaw *et al.* 2015, Söderström *et al.* 2016). Two fossil species have been described from Baltic and Bitterfeld amber respectively, namely *N. balticus* Heinrichs, Schmidt, Schäfer-Verwimp, Gröhn & Renner (2015c: 40) which provides an age constraint for the genus, and *Notoscyphus grollei* Váňa, Schäf.-Verw. & Heinrichs in Váňa *et al.* (2015a: 153) which is currently not suitable as age constraint because it is known only from Bitterfeld amber whose age is still a matter of discussion.

Notoscyphus grollei is morphologically so similar to *N. lutescens* that it was first described as the extant species by Grolle (1988). It only differs in having distinctly mammillose leaf cells (Váňa *et al.* 2015a). This species also closely resembles *N. balticus* from Baltic amber but can be distinguished by its larger and mammillose leaf cells and very narrow, colorless rhizoids (Váňa *et al.* 2015a).

Notoscyphus balticus

Holotype: GPIH 4565 (Gröhn 5800).

Reference: Heinrichs *et al.* (2015c), plates I, II.

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region.

Calibration: Minimum age of *Notoscyphus*.

Justification: Though the assignment is somewhat hampered by the lack of generative structures and branches, *N. balticus* is in good accordance with the description of the genus (Heinrichs *et al.* 2015c). The most apparent differences between the fossil and extant *Notoscyphus* are the brown color of the gametophyte, the larger diameter of the rhizoids, and the slightly smaller leaf cells (Heinrichs *et al.* 2015c). Morphological differences of the underleaves are somewhat ambiguous due to potential damage of the fossil material and the morphological heterogeneity of the extant species.

Currently, the lack of comprehensive molecular data of *Notoscyphus* hampers a reconstruction of its crown group age and the assignment of the fossil *Notoscyphus* species. However, the interpretation of the Eocene fossil as a representative of the extant genus *Notoscyphus* is not conflicting with divergence time estimates. According to Feldberg *et al.* (2014), who did not use the fossil as a constraint, *Notoscyphus* originated in the Mesozoic, well before the formation of the Paleogene fossil. It was applied as an age constraint for the genus in Laenen *et al.* (2014) which resulted in estimated median ages of 35.15–69.04 Ma.

Family: Plagiochilaceae Müll.Frib.

Genus: *Plagiochila* (Dumort.) Dumortier (1835: 14)

Plagiochila groehnii Grolle & Heinrichs (2003: 289)

Holotype: GPIH 4309 (Coll. Gröhn 2088b).

References: Grolle & Heinrichs (2003), figs. 1, 2; Grolle & Meister (2004b), plate 19e–i.

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region.

Calibration: Minimum age of *Plagiochila.*

Justification: *Plagiochila groehnii* is the only fossil representative of this large subcosmopolitan genus from amber and known only from two shoot fragments. A comparison of *P. groehnii* with extant species is currently hampered by the sterile and very fragmentary state of the fossil and by the taxonomic uncertainties in extant *Plagiochila* (e.g., Patzak *et al.* 2016, Renner *et al.* 2017b, Renner 2018), particularly as the full spectrum of morphological diversity expressed by *Plagiochila* has not yet been incorporated into the revised framework for infrageneric classification. *Plagiochila groehnii* closely resembles the flagelliform tapering shoots of the extant *P. sciophila* Nees ex Lindenberg (1840: 100) from Southeast Asia and southeastern North America, a widely distributed and morphologically heterogenous taxon. The fossil differs from the extant species in having coarser teeth on the leaf margins (Grolle & Heinrichs 2003). Also, the Neotropical *P. subplana* Lindenberg (1840: 73) and the African *P. integerrima* Stephani (1886a: 83) show similarities to the fossil. Long ciliate teeth are characteristic of, but not unique to, many species of *Plagiochila* sect. *Cucullatae* Schiffner (1900: 107) to which *P. sciophila* belongs (Renner 2018).

Plagiochila groehnii shows all relevant characters to be assigned to *Plagiochila* with high confidence. Therefore, it has already been employed as an age constraint for the genus in several divergence time estimates, e.g., Heinrichs *et al.* (2007), Cooper *et al.* (2012), Feldberg *et al.* (2014), and Laenen *et al.* (2014). As with *Bazzania*, capturing data on morphological character expression and distribution across the genus may facilitate more nuanced assignment of the fossil within the *Plagiochila* crown group.

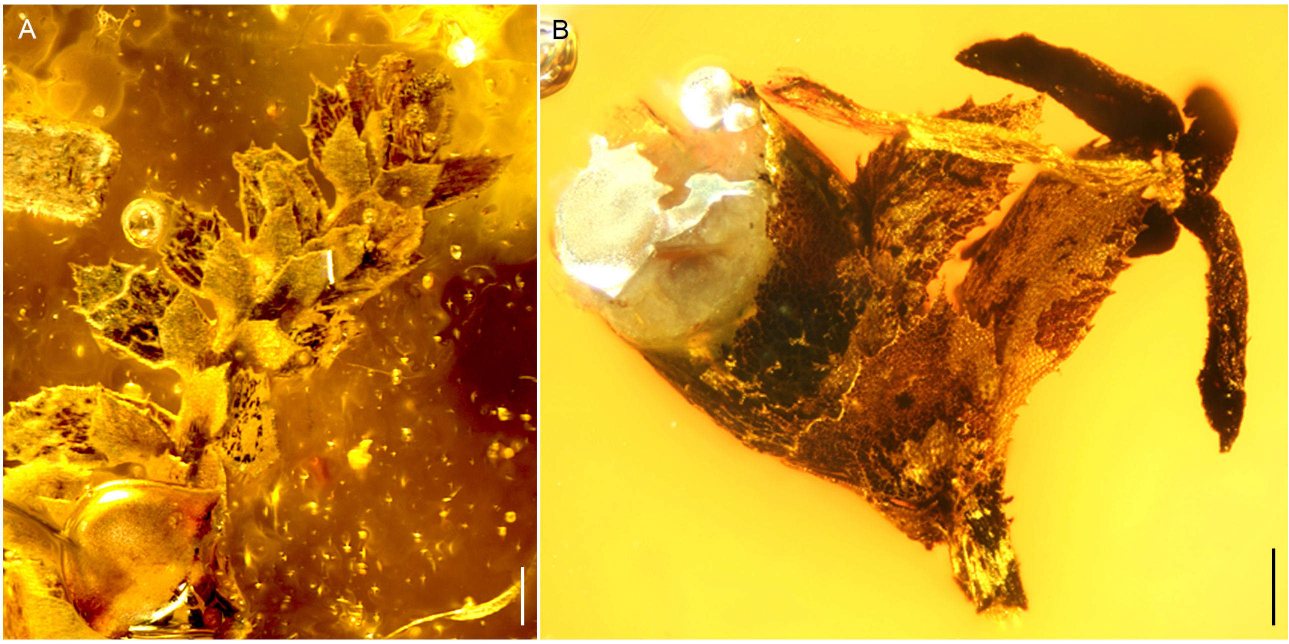

FIGURE 5. Scapaniaceae. A, B. *Scapania hoffeinsiana.* **A.** GRÖHN 5824 from Baltic amber in dorsal view. **B.** MB.Pb.1996/1358a (holotype) from Bitterfeld amber with broken perianth and capsule. Scale bars: A, B=200 µm.

Family: Scapaniaceae Mig.

Genus: *Scapania* (Dumort.) Dumortier (1835: 14)

Scapania hoffeinsiana Grolle in Grolle & Schmidt (2001: 362); Fig. 5

Holotype: MB.Pb.1996/1358a (Coll. Kutscher), Bitterfeld amber.—Paratypes: MB.Pb.1996/1358b (Coll. Kutscher), Bitterfeld amber; GZG.BST.22057 (Coll. Hoffeins 952a), GZG.BST.22058 (Coll. Hoffeins 952b), Bitterfeld amber.

? = *Scapanites acutifolius* Gottsche (1886: 122), *nom. nud.*—Original material: destroyed (“Danziger Museum”, coll. Menge 25).—Cf. Grolle & Meister 2004b.

Additional specimens: Baltic amber: GRÖHN 5824. **Bitterfeld amber:** GZG.BST.22059 (Coll. Hoffeins 1512-2).

References: Grolle & Schmidt (2001), figs. 1–10; Grolle & Meister (2004b), plate 23a–e; Frahm & Gröhn (2013), figs. 7, 8; Heinrichs *et al.* (2018a), plate II(3, 4).

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: Minimum age of *Scapania*.

Justification: *Scapania* has a mainly Laurasian distribution and includes 102 accepted extant species (e.g., Söderström & Séneca 2006, Söderström *et al.* 2016, Heinrichs *et al.* 2012a, Potemkin & Müller 2020). *Scapania hoffeinsiana* is the only fossil species known from this genus and one of the rarer cases preserved with perianth and capsule (Grolle & Schmidt 2001, Grolle & Meister 2004b). The complicate bilobed leaves (Fig. 6A) with a smaller dorsal lobe which is folded against the ventral one forming a keel and the lack of a vitta are in good accordance with the morphological description of the genus (e.g., Paton 1999, Schuster 2002, Potemkin & Müller 2020). Though the perianth has been damaged and only the lower part is preserved, the remains of the gynoecium and the sporophyte support the generic assignment of the holotype (Fig. 6B). The paratypes and the additional specimens are sterile but allow a detailed study of vegetative characters (Grolle & Meister 2004b, Frahm & Gröhn 2013). A comparison with extant species is currently difficult. Despite molecular phylogenetic analyses (Heinrichs *et al.* 2012a, Mamontov *et al.* 2018b) and morphological revisions (e.g., Choi *et al.* 2012, Potemkin & Müller 2020) the taxonomy of extant *Scapania* is still subject to controversy and many species remain insufficiently known.

Grolle & Schmidt (2001) have compared the fossil to *Douinia ovata* (Dickson 1793: 11) Buch (1928: 14) which differs by its subentire leaf lobes and strongly plicate perianth, and with *S. stephanii* Müller (1905: 273) [(now *S. ligulata* Stephani (1904: 14) subsp. *stephanii* (Müll.Frib.) Potemkin, Piippo & Koponen (2004: 423)] from Japan which differs by its broader lobes of stem and involucral leaves and slightly winged keel. The fossil shows strong morphological affinities to extant subgen. *Scapania* (Feldberg *et al.* 2014) and might belong to sect. *Apiculatae* Buch (1928: 53). It resembles the European-North American *S. umbrosa* (Schrader 1797: 5) Dumortier (1835: 14) which differs by the broader lobes of stem and involucral leaves with less coarse dentation and by a somewhat winged, longer keel. Because of the reliable generic placement, *S. hoffeinsiana* has been employed as age constraint in Feldberg *et al.* (2013, 2014) and Laenen *et al.* (2014).

Family: Solenostomataceae Stotler & Crand.-Stotl.

Genus: *Solenostoma* Mitten (1864b: 51)

Solenostoma berendtii (Grolle) Váňa, Schäf.-Verw. & Heinrichs in Váňa *et al.* (2015b: 287)

Basionym: *Jungermannia berendtii* Grolle (1980b: 401).—Holotype: MB.Pb.1979/477 (Coll. Berendt).

References: Grolle (1980b), Abb. 1a–c, Tafeln XXX, XXXI as *Jungermannia berendtii;* Grolle & Meister (2004b), plate 12h–i as *Jungermannia berendtii;* Váňa *et al.* (2015b), figs. 1–3; Heinrichs *et al.* (2018a), plate I(4).

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region.

Calibration: Minimum age of *Solenostoma*.

Justification: This fossil is only known from the sterile type specimen and has been placed in *Jungermannia* Linnaeus (1753: 1131) subgen. *Solenostoma* (Mitt.) Amakawa (1960: 53) by Grolle (1980b). Recently, the genus *Solenostoma* was reinstated based on molecular phylogenetic evidence (Hentschel *et al.* 2007, Shaw *et al.* 2015) and the fossil was therefore transferred to *Solenostoma* (Váňa *et al.* 2015b).

The fossil resembles the Asiatic *S. truncatum* (Nees 1830: 29) R.M.Schust. ex Váňa & Long (2009: 509) of subgen. *Plectocolea* Mitten (1864a: 156) in having numerous long rhizoids, distinct trigones, and subquadrate-rotund to elongate-elliptical leaves, but the lack of fertile structures and the scarce fossil material make a detailed assessment of the relationships currently impossible. The relatively reliable generic assignment provides a minimum age for the genus *Solenostoma.* It has been employed as age constraint by Laenen *et al.* (2014) for *Jungermannia* s.l.

Order: Porellales Schljakov

Family: Frullaniaceae Lorch

Frullaniaceae represent a lineage of mainly epiphytic leafy liverworts within the Porellales and one of the most species rich taxa found as amber inclusions (Grolle & Meister 2004b, Hentschel *et al.* 2009a, Heinrichs & Schmidt 2010, Heinrichs *et al.* 2011b, 2012b, c, 2017a, b, 2018a, Konstantinova *et al.* 2012, Mamontov *et al.* 2015a, 2017, 2018a, 2019, 2020a, Feldberg *et al*. 2018, 2021, Li *et al.* 2020, 2021). Approximately 15 species from different amber deposits have already been described, dating from the mid-Cretaceous to the Miocene. The family includes two to four genera: the extant *Frullania,* the extinct *Protofrullania* Heinrichs (2017a: 225), and probably also the extinct genera *Kaolakia* Heinrichs, M.E.Reiner, K.Feldberg, von Konrat & A.R.Schmidt in Heinrichs *et al.* (2011b: 236) as well as

Pseudofrullania Heinrichs, K.Feldberg, M.A.M.Renner & Schäf.-Verw. in Heinrichs *et al.* (2018a: 225), though the familial assignment of the latter two is not entirely certain (Heinrichs *et al.* 2011b, 2018a, Feldberg *et al.* 2021) and they can consequently not be employed as age constraints.

Fossil Frullaniaceae represent two major groups, namely the Cretaceous representatives which often differ significantly from extant taxa, and the Cenozoic ones which are generally more similar to the extant diversity. The number of Cretaceous Frullaniaceae fossils is relatively low. However, their peculiar morphologies indicate a turnover within the family during this period (e.g., Heinrichs *et al.* 2018a).

This group contains several interesting morphotypes which might not be closely related to one another or to Cenozoic species. One of these types is *Kaolakia borealis* Heinrichs, M.E.Reiner, K.Feldberg, von Konrat & A.R.Schmidt in Heinrichs *et al.* (2011b: 236) from mid-Cretaceous Alaskan amber. The most notable character of this taxon is the presence of two saccate ventral segments per leaf, a character which is rarely expressed in extant Frullaniaceae (von Konrat & Braggins 2001, Heinrichs *et al.* 2011b, Feldberg *et al.* 2021). The majority of extant and fossil Frullaniaceae possess leaves with strongly unequal lobes, of which the dorsal lobe is always explanate (laminar) and reniform or cordate, the ventral, smaller lobule is mostly saccate with a posterior opening (*Frullania*-type lobule) or occasionally explanate, and the third is represented by a more or less small, filiform to triangular stylus situated between the lobule and the stem (e.g., Schuster 1992). Two saccate structures per leaf are occasionally formed on the first leaf of a branch (von Konrat & Braggins 2001), and the two saccate structures on every leaf of *Kaolakia* might represent an extreme version of this tendency. In general, the leaf characters in *Kaolakia* as well as the shape of beaked perianth are characteristic of *Frullaniaceae*, therefore this genus might represent a separate, specialized lineage of the family.

Another type of Cretaceous Frullaniaceae is represented by *Protofrullania cornigera* Heinrichs (2017a: 225) described from mid-Cretaceous Kachin amber (Myanmar). In the description of *Protofrullania*, Heinrichs *et al.* (2017a) noted that the fossil resembles *Frullania* in its general habit, color, and leaf shape, and also recently described male and female fossils (Feldberg *et al.* 2021) support the assignment to Frullaniaceae. The differentiating features of *Protofrullania* are the strap-shaped, ciliate underleaves and the development of rhizoids in the upper portion of these underleaves.

Genus: ***Frullania***

The only extant genus of Frullaniaceae is *Frullania* which is morphologically well circumscribed, yet has a very complex subgeneric taxonomy (e.g., Hentschel *et al.* 2009b, 2015, Heinrichs *et al.* 2010, Ramaiya *et al.* 2010, von Konrat *et al.* 2010, 2012, 2013, Carter *et al.* 2017, Mamontov *et al.* 2020b). The genus has a subcosmopolitan distribution with most species occurring in humid tropical regions but also as xerophytes and in temperate as well as arctic and alpine areas (Schuster 1992, Hentschel *et al.* 2009b).

Three fossil species of *Frullania* occur in mid-Cretaceous Kachin amber from Myanmar and provide a minimum age for the genus (Fig. 6 A–C). Most Cenozoic fossils of *Frullania* are found in Paleogene Baltic, Bitterfeld, and Rovno ambers, while only one fossil from Miocene Dominican amber was described to date. The morphological features of all these species, including the shape and reciprocal proportions of leaf lobes and lobules, underleaves, bracts and bracteoles, and also perianths, are characteristic of extant *Frullania*, so all these fossils can be considered part of the crown group. However, the assignment to subgenera and sections is not easy. Research concerning the taxonomy of *Frullania* has rapidly progressed in recent years, but definite morphological distinctions between lineages can be difficult (von Konrat *et al.* 2006, 2010, 2011, 2013, Hentschel *et al.* 2015, Carter *et al.* 2017).

Recently some important nomenclatural changes were made for the genus *Frullania* which necessitated changes of the subgeneric classification (Lima *et al.* 2020). *Frullania tamarisci* (Linnaeus 1753: 1134) Dumortier (1835: 13) is again considered the lectotype of the genus (Stotler & Crandall-Stotler 2017). Since *F. tamarisci* belongs to subgen. *Thyopsiella* Spruce (1884: 41) this subgenus becomes subgen. *Frullania* whereas subgen. *Frullania* fide Hentschel *et al.* (2015) and Söderström *et al.* (2016) becomes subgen. *Trachycolea*.

Many taxa found in European Baltic, Bitterfeld, and Rovno amber show close morphological affinities to representatives from the Southern Hemisphere or belong to genera which are restricted to this area today (Grolle 1988, Mamontov *et al.* 2015b, Heinrichs *et al.* 2015c). Therefore, it is interesting that representatives resembling extant lineages of *Frullania* with a main distribution in the Southern Hemisphere, especially subgen. *Chonanthelia* Spruce (1884: 8), subgen. *Homotropantha* Spruce (1884: 35), and subgen. *Meteoriopsis* Spruce (1884: 37), have not yet been found among the Cenozoic species. Moreover, there are no species that would undoubtedly be considered to belong to subgen. *Microfrullania* (Schuster 1970: 280) Schuster (1992: 34) in the present sense (Carter *et al.* 2017). Grolle & Meister (2004b) assigned *F. varians* Caspary (1887: 5), which occurs in Baltic, Bitterfeld, and Rovno amber, to this subgenus. The autoecious species is by far the most frequent inclusion with far over 60 fossils (Konstantinova *et al.* 2012) and is known with androecia, gynoecia with perianth (Fig. 6D), and sporophyte (Fig. 6E). The complete preservation might render it suitable as age constraint, but due to its heterogeneous morphology it needs a thorough revision before the affinities to the extant diversity can be assessed with confidence. *Frullania varians* might represent a complex of closely related species as in extant *Frullania,* where species complexes and semi-cryptic to cryptic species are common (e.g., Heinrichs *et al.* 2010, Mamontov *et al.* 2015a, Carter *et al.* 2017).

Most fossil *Frullania* species resemble the extant subgenera *Diastaloba* Spruce (1884: 55) s.l., *Frullania,* and *Trachycolea*, which are the groups with a mostly northern (Laurasian) or worldwide distribution. However, the combinations of character states are unusual in several Eocene and Oligocene representatives, so an affiliation of these species to any extant subgenera is challenging and few species can be assigned with confidence.

Currently the assignment of species with morphological affinities to *Diastaloba* s.l. is very problematic even if copious and well-preserved material is at hand. Extant representatives occur in tropical America, Asia, and Oceania and have been resolved as polyphyletic in molecular phylogenetic and morphological studies (Hentschel *et al.* 2009b, 2015, Söderström *et al.* 2016, Silva *et al.* 2017, Winter & Schäfer-Verwimp 2020). Typical characters, e.g., lobules inserted remotely from the stem, also occur in subgenera *Microfrullania* and *Mammillosae* Hattori (1986: 226), whereas the latter has not been investigated by molecular methods yet. *Frullania baltica* Grolle (1985b: 89), which is preserved with androecia, gynoecia, and sporophyte (Grolle 1998; Fig. 6F), and *F. schmalhausenii* Mamontov, Ignatov & Perkovsky (2019: 1100), which is only known from the sterile holotype, are both very similar to the extant Neotropical *F. obcordata* (Lehm. & Lindenb. in Lehmann 1834: 51) Lehm. & Lindenb. in Gottsche *et al.* (1845b: 447) (Mamontov *et al.* 2019), a species belonging to the lineage Diastaloba IV in the molecular phylogenetic analyses by Hentschel *et al.* (2009b), respectively to the recently established subgenus *Caulisequa* Winter & Schäfer-Verwimp (2020: 14). An additional fossil with a *Diastaloba*-like morphology has been described from Miocene Dominican amber, but due to the incomplete preservation only to subgenus level (Heinrichs & Schmidt 2010). A thorough revision based on extended datasets and thorough morphological studies is needed to obtain a sufficient characterization of the lineages and a reliable assignment of the *Diastaloba*-like fossils, but preliminary studies indicate that morphological definitions are possible (Hentschel *et al.* 2015).

Several other fossils are difficult to assign because they display characters not seen in extant *Frullania.* One group is represented by *F. acutata* Caspary (1887: 5) emended Grolle (1981a: 144) from Baltic amber, *F. ekaterinae* Mamontov, Ignatov & Perkovsky (2019: 1096) from Rovno amber, *F. pycnoclada* Grolle (2004b: 25) from Baltic as well as Rovno amber, and *F. vanae* Mamontov, Atwood, Perkovsky & Ignatov (2020a: 424) from Rovno amber. The isolated characters, including acute to obtuse leaf lobe apices in *F. acutata* and *F. ekaterinae*, dimorphic underleaves (different stem and branch ones) in *F. acutata* and *F. pycnoclada*, as well as the shape of leaf lobules are typical for subgen. *Frullania*. However, the front surface of lobules in these species (in *F. vanae* only the ones on branches) bears two rows of opposite mammillae, a morphological character unknown of extant subgen. *Frullania*. These species might be related to one another and represent an extinct subgenus or section (Mamontov *et al.* 2020a).

***Frullania* subgenus: incertae sedis**

***Frullania baerlocheri* Heinrichs, M.E.Reiner, K.Feldberg, von Konrat, Hentschel, Váňa & A.R.Schmidt in Heinrichs *et al.* (2012b: 26); Fig. 6A**

Holotype: AMNH Bu-FB 1 g.

= *Frullania pinnata* Heinrichs, K.Feldberg, Schäf.-Verw. & Krings in Heinrichs *et al.* (2017b: 57).—Holotype: GZG.BST.21963.—Syn. fide Li *et al.* (2021).

Additional specimens: PB23288; GZG.BST.22015 (Coll. Müller BuB3538); MÜLLER BuB3681, BuB3682; SNSB-BSPG 2021 XII 1 (Coll. Müller BuB1874; syninclusion *Protofrullania cornigera*).

References: Heinrichs *et al.* (2012b), plate IV, fig. 2; Heinrichs *et al.* (2017b), figs. 1–3; Heinrichs *et al.* (2018a), plate IV(7); Li *et al.* (2021), figs. 1–3; Feldberg *et al.* (2021), figs. 1D, E, 2A, B, 3.

***Frullania cretacea* Hentschel, Schmidt & Heinrichs (2009a: 326); Fig. 6B**

Holotype: AMNH B-011.

Additional specimens: AMNH Bu-FB 1 a–f, Bu-FB 51; GZG.BST.22016 (Coll. Müller BuB3533), GZG.BST.22017 (Coll. Müller BuB1190); MÜLLER BuB1772, BuB3530; WUNDERLICH F3157/BU/CJW.

References: Hentschel *et al.* (2009a), figs. 1–10; Heinrichs *et al.* (2012b), plates I, II, fig. 1; Heinrichs *et al.* (2018a), plate IV(4); Feldberg *et al.* (2021), figs. 1F, 2C, 4A, B.

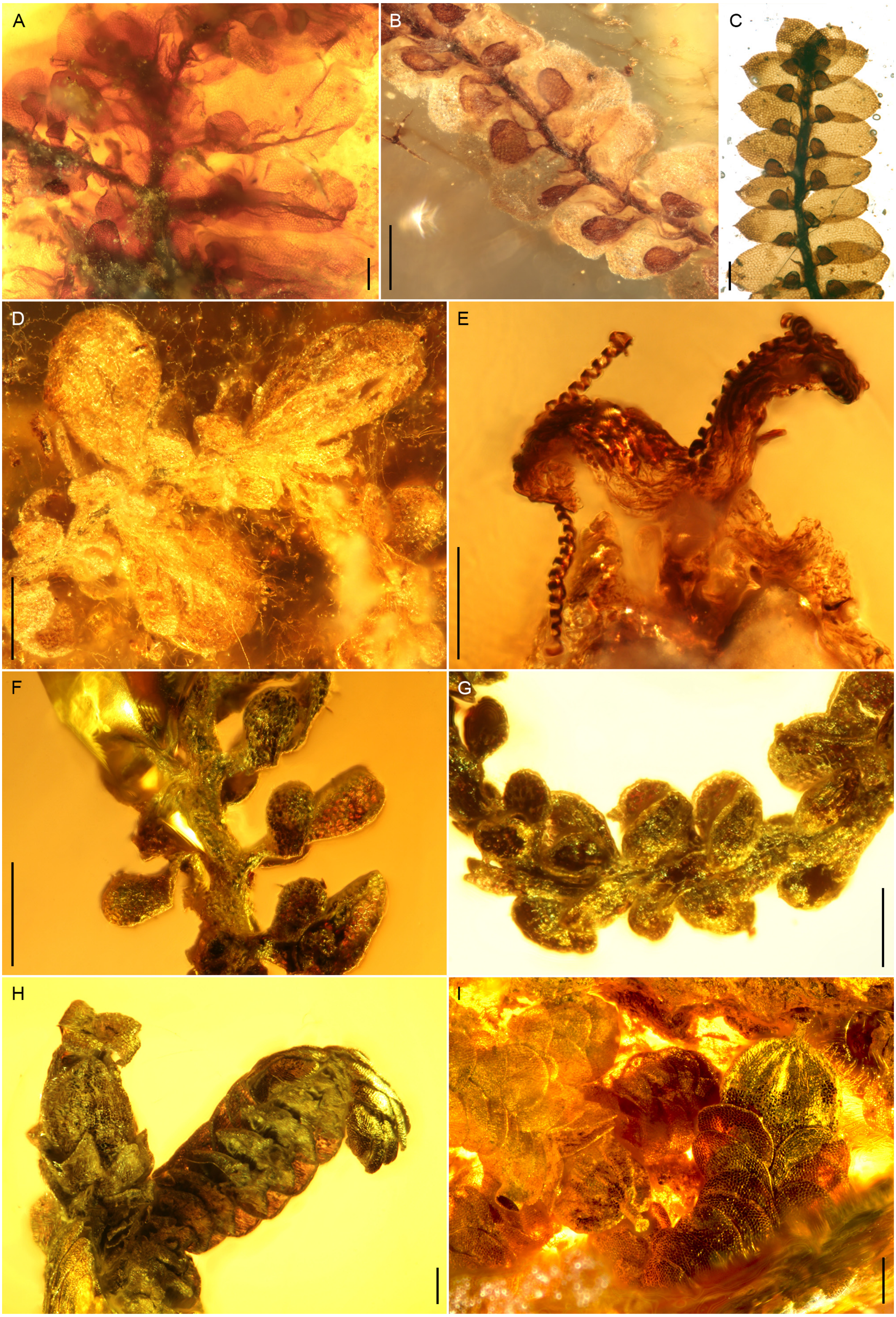
A
B
C
D
E
F
G
H
I

FIGURE 6. *Frullania*. A. *Frullania baerlocheri,* GZG.BST.22015 from Burmese amber in ventral view with rounded (holostipous) underleaves. **B.** *Frullania cretacea,* GZG.BST.22016 from Burmese amber in ventral view with ciliate underleaves. **C.** *Frullania partita,* PB23146 (holotype) in ventral view with bifid underleaves. **D, E.** Examples of fertile structures in fossil *Frullania.* **D.** *Frullania varians,* GZG.BST.22045 from Bitterfeld amber in ventral view with two androecia and one terminal gynoecium with perianth. **E.** *Frullania varians*, GZG.BST.22046 from Bitterfeld amber with capsule and elaters. **F.** *Frullania baltica,* GZG.BST.22047 from Bitterfeld amber in ventral view. **G.** *Frullania casparyi,* GZG.BST.22060 from Bitterfeld amber in ventral view. **H, I.** *Frullania schumannii.* **H.** GRÖHN 2058 from Baltic amber in ventral view with perianth and capsule. **I.** GZG.BST.22063 from Bitterfeld amber with two beaked perianths. Scale bars: A–D, F, H=200 µm, E, G=100 µm, I=500 µm.

Frullania partita Li, Wang, Schneider & Wu (2020: 104341 [2]); Fig. 6C

Holotype: PB23146.

References: Li *et al.* (2020), figs. 1, 2; Feldberg *et al.* (2021), figs. 1G, 2D, 4C, D.

Age and stratigraphic level: *Frullania baerlocheri*, *F. cretacea,* and *F. partita* derive from 99 Ma, late Albian–early Cenomanian (Late Cretaceous) amber mined southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar (Burmese amber).

Calibration: *Frullania baerlocheri*, *F. cretacea,* and *F. partita* provide the minimum age of *Frullania.*

Justification: *Frullania baerlocheri* (Fig. 6A)*, F. cretacea* (Fig. 6B)*,* and *F. partita* (Fig. 6C) can confidently be assigned to the extant genus *Frullania* (Heinrichs *et al.* 2018a, Feldberg *et al.* 2021, Li *et al.* 2020, 2021). However, the combinations of morphological characters these species display are unknown in extant crown group lineages and they might thus represent stem or extinct crown group lineages. Of the three species, *F. partita* is most similar to extant crown group representatives of the genus. The remotely inserted lobules are reminiscent of the polyphyletic and largely unrevised extant subgen. *Diastaloba* s.l. (Hentschel *et al.* 2009b, 2015). A somewhat similar extant species is *F. apiculata* (Reinwardt, Blume & Nees 1824: 222) Nees in Gottsche *et al.* (1845b: 452) from tropical Asia, albeit the lobules are more elongated and the underleaves broader.

The reliable generic assignment of Cretaceous *Frullania* already provided age constraints for the *Frullania* crown group. Based on this constraint Feldberg *et al.* (2014) estimated a mean age of 107.9 Ma, Laenen *et al.* (2014) median ages of 123.67–174.7 Ma, and Silva *et al.* (2017) a mean age of 166.75 Ma for *Frullania.*

Frullania subgenus: *Frullania* (fide Lima *et al.* 2020)

Fossils resembling this subgenus are rather common, but except for *F. casparyi* Grolle (1985b: 92) and *F. riclefgrollei* Mamontov, Heinrichs, Schäfer-Verwimp, Ignatov & Perkovsky (2015a: 32), which might provide a minimum age for this subgenus, not many can be assigned with high confidence. Another species which has been assigned to this subgenus but shows unusual characters is *F. mammilligera* Grolle (2003: 155) from Bitterfeld amber (Grolle & Meister, 2004b). This species is known only from the fertile holotype and has ocelli, but the strongly mammillose lobule surface is unique within the subgenus. The unclear assignment to the extant diversity as well as the restriction to Bitterfeld amber, whose age is still debated, render it currently unsuitable as age constraint.

Also *F. truncata* Caspary (1887: 4) and *F. zerovii* Mamontov, Ignatov & Perkovsky (2018a: 104) might belong to subgen. *Frullania*. These species resemble one another in having rounded leaf lobes, leaf lobules with a smooth surface, equal semicircular mouth margins, a constriction above the lobule mouth, and the widest part in the upper half. The species differ mainly by the shape of underleaves. The leaves and underleaves are most similar to those in extant *F. chilcootiensis* Stephani (1886b: 98) [sin. *F. hattoriana* Godfrey & Godfrey (1980: 321)] of subgen. *Frullania* (Mamontov *et al.* 2020b, Atwood & Mamontov 2020). These fossils can potentially be considered to belong to sect. *Frullania* though none of them has ocelli. However, as follows from Hentschel *et al.* (2009b) and Mamontov *et al.* (2020b), an absence of ocelli could not exclude an affiliation of any species to subgen. *Frullania*, although its presence remains an important feature in the case of fossils, until an independent origin of ocelli in different lineages of *Frullania* is found.

Frullania casparyi; Fig. 6G

Holotype: WAR-MZ 17449 (Coll. Giecewicz), Baltic amber.

? = *Frullania tenella* Caspary (1887: 5), *nom. illeg.* [*non* Sande Lac. 1855].—Type: destroyed.—Cf. Grolle (1985b: 92).

Additional specimens: Baltic amber: GRÖHN **5841;** MB.Pb.1979/481 (Coll. Thomas); WAR-MZ 469/16 (Coll. Rieband); VELTEN H0001b. **Bitterfeld amber: GZG.BST.22060 (Coll. Grabenhorst Le-44), GZG.BST.22061 (Coll. Hoffeins 5-22), GZG.BST.22062 (Coll. Hoffeins 5-41);** MB.Pb.1992/19 (Coll. Kutscher H003), MB.Pb.1992/20 (Coll. Kutscher H019), MB.Pb.1992/21 (Coll. Kutscher H016), MB.Pb.1997/31 (Coll. Grolle M-12/2), MB.Pb.1997/43 (Coll. Grolle M-14/4), MB.Pb.1997/7 (Coll. Grolle 87/F4a + b).

References: Grolle (1985b), plate III, fig. 2e–i; Kosmowska-Ceranowicz (2001), phot. 2; Grolle & Meister (2004b), plate 6a–e.

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Frullania riclefgrollei

Holotype: SIZK-K-2012.

Reference: Mamontov *et al.* (2015a), plates I, II.

Age and stratigraphic level: 35–37 Ma, Priabonian (late Eocene), amber quarry "Pugach", Klesov, Ukraine (Rovno amber).

Calibration: *Frullania casparyi* and *F. riclefgrollei* provide a minimum age for *Frullania* subgen. *Frullania;* possibly sect. *Microphyllae* (Schuster 1985: 370) Gradst., Ilk.-Borg. & E.Lima in Lima *et al.* (2020: 122).

Justification: *Frullania casparyi* and *F. riclefgrollei* are morphologically quite similar but differ in some important characters (Mamontov *et al.* 2015a). *Frullania casparyi* (Fig. 6G) is much smaller than *F. riclefgrollei*, its underleaves are less deeply bifid and have lobes with a 1–3 cells rather than 1 cell long uniseriate apex, and the ocelli form a moniliate row consisting of 2–5 cells rather than a 1–2 cells wide row of 12–18 ocelli. The rows of ocelli of both species are larger and more refractive than the surrounding cells, as is typical for subgen. *Frullania* (Grolle 1985b, Grolle & Meister 2004b, Hentschel *et al.* 2009b, Mamontov *et al.* 2015a, Lima *et al.* 2020). While *F. casparyi* is a dioecious species preserved with androecia as well as gynoecia, *F. riclefgrollei* is known only in sterile condition. Both species seem to be closely related to the European species *F. microphylla* (Gottsche in Rabenhorst 1862: 109 [209]) Pearson (1894: 328) of subgen. *Frullania* sect. *Microphyllae* which also has caducous leaves, rounded leaf apices, an oblique lobule insertion, deeply bifid underleaves, and 1–2(3) cells wide rows of ocelli (Paton 1999, Grolle & Meister 2004b, Mamontov 2015a, Lima *et al.* 2020). However, this species is much smaller and has leaf cell walls without distinct trigones. Subgen. *Frullania* is further characterized by spreading, semi-cordate leaves with one auricle at the leaf base, narrow clavate to cylindrical lobules, and a smooth, keeled perianth (Hentschel *et al.* 2009b, Lima *et al.* 2020). Morphologically also rather similar is the largely tropical subgen. *Meteoriopsis* which is differentiated by absence of ocelli (Hentschel *et al.* 2009b, Mamontov *et al.* 2017). The fossils can provide a minimum age constraint for subgen. *Frullania* and possibly even sect. *Microphyllae*.

Frullania subgenus: *Trachycolea* (fide Lima *et al.* 2020)

Frullania subgen. *Trachycolea* is morphologically diverse and forms a robust lineage which is well separated from the remainder of the genus (Hentschel *et al.* 2009b). Two fossils are known from European ambers. *Frullania rovnoi* Mamontov, Hentschel, Konstantinova, Perkovsky & Ignatov (2017: 337) and *F. schumannii* (Caspary 1887: 3) Grolle (1981b: 102) can be assigned with some confidence and might provide a minimum age for the subgenus or even the Southern Hemispheric sect. *Australes* Verdoorn (1930: 58) as is discussed below.

Another species with close morphological affinities to this section is *F. grabenhorstii* Heinrichs, K.Feldberg, Alina S.Müll., Schäf.-Verw., von Konrat & A.R.Schmidt in Feldberg *et al.* (2018: 94), but it is known only from Bitterfeld amber and therefore currently not suitable as age constraint. Also, *F. zerovii* shows strong affinities to this section through some characters of the leaf lobes and lobules (Mamontov *et al.* 2018a).

Frullania rovnoi

Holotype: SIZK-K-10049F.

Reference: Mamontov *et al.* (2017), figs. 1, 2.

Age and stratigraphic level: 35–37 Ma, Priabonian (late Eocene), amber quarry "Pugach", Klesov, Ukraine (Rovno amber).

***Frullania schumannii;* Fig. 6H, I**

Basionym: *Lejeunea schumannii* Casp.—Neotype: MB.Pb.1979/692 (Coll. Künow 149), Baltic amber; designated by Grolle (1985b).—Holotype: destroyed ("Altstädtisches Gymnasium of the former Königsberg", 1868, coll. V. Duisburg).—Cf. Grolle 1981b, 1985b, Grolle & Meister 2004b.

= *Frullania scyphoides* Mägdefrau (1957: 434).—Holotype: SNSB-BSPG 1967 XX 2 (Coll. Scheele), Baltic amber.—Syn. fide Grolle (1981b).

Additional specimens: Baltic amber: GRÖHN 2013, 2026, 2057, 2058, 2059, 2090; LIEDTKE B650 P4; WAR-MZ 2172/1, 20102); VELTEN H1001. **Bitterfeld amber:** GRÖHN **379; GZG.BST.22063 (Coll. Grabenhorst Le-68), GZG.BST.22064 (Coll. Hoffeins 622-1);** MB.Pb.1996/1350a (Coll. Striebich), MB.Pb.1996/1350b (Coll. Striebich), MB.Pb.1996/1353 (Coll. Kutscher), MB.Pb.1997/10, MB.Pb.sn (Coll. Kutscher Ku-98H02b).

References: Caspary (1887), Tafel I Bild 10 as *Lejeunea schumannii;* Caspary & Klebs (1907), Tafel III Bilder 20, 20a, b, 21 as *Lejeunea schumannii;* Mägdefrau (1957), Tafel XII Figs. 2–4 as *Frullania scyphoides;* Grolle (1981b), figs. 1–5; Grolle (1985b), plate IV, fig. 3; Weitschat & Wichard (2002), plate 2a, c; Grolle & Meister (2004b), plates 10d–g, 11; Feldberg *et al.* (2018), fig. 3D–F; Heinrichs *et al.* (2018a), plate IV(2).

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: *Frullania rovnoi* and *F. schumannii* provide a minimum age for *Frullania* subgen. *Trachycolea;* possibly sect. *Australes*.

Justification: *Frullania* subgen. *Trachycolea* sect. *Australes* is mainly distributed in Eastern Asia and Australasia and is well characterized by leaf cells with distinct trigones, large campanulate leaf lobules with a constricted mouth inserted close to the stem, nearly flat underleaves, and 4-plicate smooth perianths (Grolle 1981b, Hentschel *et al.* 2015, Mamontov *et al.* 2017). In molecular phylogenies, the section forms a robust subclade within a largely polytomous subgen. *Trachycolea* (Hentschel *et al.* 2009b as subgen. *Frullania*). Both fossils are in good accordance with the morphological definition of sect. *Australes* and can be differentiated by underleaf characters. The underleaves of *F. rovnoi* are widest in the middle and bear several lateral teeth or angular projections, whereas those of *F. schumannii* are widest above the middle and ornamented with only 1–2 rounded, rarely tooth-like lateral projections (Mamontov *et al.* 2017). Only a couple of the extant species, e.g., *F. dentata* Hattori (1974: 231) from Papua New Guinea, have roughly and irregularly dentate-angulate underleaf margins like those of *F. rovnoi*. While in *F. rovnoi* there has been found only one juvenile perianth, the autoecious *F. schumannii* is known to have androecia on short side branches as well as terminal gynoecia with smooth 4-plicate perianths (Fig. 6H, I). In combination with a thorough morphological investigation of extant species and molecular phylogenetic datasets the species could provide a minimum age for the section.

Silva *et al.* (2017) estimated a mean age of 24.40 Ma for the crown group of subgen. *Trachycolea* (as subgen. *Frullania*), but the appearance of fossils with the typical morphology of this subgenus as well as sect. *Australes* already in the Eocene indicates that the radiation of subgen. *Trachycolea* might have started much earlier. A thorough cross-validation comparing age estimates obtained by different age constraints could elucidate the diversification of this large subgenus (e.g., Feldberg *et al.* 2013, Bechteler *et al.* 2017b).

Family: Jubulaceae H.Klinggr.

Genus: *Nipponolejeunea* Hattori (1944: 124)

***Nipponolejeunea europaea* Grolle (1981a: 146)**

Holotype: MB.Pb.1979/471-E (Coll. Künow), Baltic amber (syninclusions *Cheilolejeunea latiloba* (Caspary 1887: 3) Grolle (1984c: 230) 471-B, G, H; *Frullania acutata* 471-C; *Radula sphaerocarpoides* Grolle (1980b: 404) 471-A).

Additional specimens: Baltic amber: GRÖHN 2014, 2035, 2052b, 2053; GZG.BST.22065 (Coll. Hoffeins 1151),

GZG.BST.22066 (Coll. Hoffeins 1499/7); MB.Pb.1979/471-D (Coll. Künow), MB.Pb.1979/471-F (Coll. Künow), MB.Pb.1979/480 (Coll. Thomas). **Bitterfeld amber: GZG.BST.22067 (Coll. Grabenhorst Le-3);** LUDWIG Bi2014; MB.Pb.1996/1352 (Coll. Gröhn 0366a), MB.Pb.sn (Coll. Kutscher Ku-98H16a).

References: Caspary (1887), Tafel I Bild 24 as *Frullania acutata;* Grolle (1981a), Abb. 3, Tafeln 3–6; Grolle & Meister (2004b), plates 17, 18 as the extant *Nipponolejeunea subalpina* (Horikawa 1939: 360) Hattori (1944: 125); Heinrichs *et al.* (2018a), plate III(1, 2).

Age and stratigraphic levels: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: Minimum age of *Nipponolejeunea.*

Justification: *Nipponolejeunea* is a morphologically and molecularly strongly isolated genus of Jubulaceae with two extant species in Northeastern Asia (Grolle 1981a, Ahonen 2006, Söderström *et al.* 2016). *Nipponolejeunea europaea* is so similar to *N. subalpina* that the fossil has been transferred to the extant species by Grolle & Meister (2004b). However, molecular phylogenetic analyses showed that DNA-sequences of the extant species are very similar and that the split between them occurred in the Miocene (Heinrichs *et al.* 2007). Therefore, the fossil probably represents an extinct species. *Nipponolejeunea europaea* is a suitable constraint for the genus and it has already been employed in Heinrichs *et al.* (2007), Wilson *et al.* (2007), and Cooper *et al.* (2012) for Jubulaceae. Feldberg *et al.* (2014) and Sun *et al.* (2014) assigned it to the stem of *Nipponolejeunea*, which resulted in mean ages of 74.3 Ma respective 84.82 Ma. Laenen *et al.* (2014) assigned it to *Nipponolejeunea* with resulting median ages of 34.22–46.8 Ma.

Family: Lepidolaenaceae Nakai

Genus: *Gackstroemia* Trevisan (1877: 397)

Gackstroemia cretacea Heinrichs, Schäfer-Verwimp, Feldberg & Schmidt (2014b: 49)

Holotype: AMNH BU ASJH-1.

References: Heinrichs *et al.* (2014b), plate I, fig. 1; Heinrichs *et al.* (2018a), plate III(4); Feldberg *et al.* (2021), fig. 1A.

Age and stratigraphic level: 99 Ma, late Albian–early Cenomanian (Late Cretaceous), amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar (Burmese amber).

Calibration: Minimum age of *Gackstroemia.*

Justification: The family is characterized by incubous foliation and complicate bilobed lateral leaves with a large dorsal lobe and saccate, helmet-shaped, *Frullania*-type lobules (e.g., Crandall-Stotler *et al.* 2009, Heinrichs *et al.* 2014b). Contrary to Frullaniaceae, these saccate lobules are formed on the lateral leaves and also on the underleaves.

Gackstroemia cretacea can be clearly identified has a member of the genus by the incubous leaves with large, dorsal lobes that bear one apical cilium and ventral saccate *Frullania*-type lobules with apical cilia. Also, the underleaves are converted into pairs of saccate, *Frullania*-type lobules on the upper part of the shoot and only the underleaf at the base of the shoot is a laminar and bifid. It is possible that the amber inclusion represents a terminal branch fragment, what is indicated by the development of the underleaves and the complete lack of branches (Heinrichs *et al.* 2014b). The interpretation of the fossil as a member of *Gackstroemia* is also supported by divergence times estimates. Cooper *et al.* (2012) reconstructed the split between *Gackstroemia* and *Lepidolaena* Dumortier (1835: 13) in the Cretaceous, Feldberg *et al.* (2014) and Laenen *et al.* (2014) who did not employ this fossil as age constraint estimated a mean age of 126.76 Ma respective a median age of 135.73 Ma for Lepidolaenaceae and a mean age of 99.71 Ma respective median ages of 46.79–57.91 Ma for the stem of *Gackstroemia*.

Family: Lejeuneaceae Cavers

Lejeuneaceae represent the most species-rich family of liverworts and include ca. 1000 species in 72 currently accepted genera (e.g., Gradstein 2013, 2020, Bechteler *et al.* 2016, Wang *et al.* 2016). They are predominantly epiphytes and most diverse in humid tropical forests (Gradstein *et al.* 2001). The oldest putative fossil is the poorly preserved Middle Jurassic compression fossil *Sinolejeunea yimaensis* Yang & Wu (2011: 229). Although its position in Lejeuneaceae is weakly supported by morphology, it is in accordance with the Late Triassic origin of Lejeuneaceae estimated by Feldberg *et al.* (2014), who did not use this fossil as an age constraint. The fossil record of Lejeuneaceae becomes more diverse in Cenozoic ambers, especially in Miocene Dominican and Mexican ambers. So far 17 extant genera are recognized (Grolle 1984a, b, c, d, 1993a, b, Gradstein 1993, Grolle *et al.* 2001, Ye & Zhu 2010, Reiner-Drehwald *et al.* 2012, Heinrichs *et al.* 2014a, 2015a, 2016a, 2018b, Lee *et al.* 2015a, b, 2017, Kaasalainen *et al.* 2017, Sukkharak & Gradstein 2017, Yu *et al.* 2020). The genera from Miocene Dominican and Mexican ambers represent all main lineages of modern Lejeuneaceae (Wilson *et al.* 2007, Yu *et al.* 2020) and provide some evidence that the cryptogamic communities of the Caribbean Miocene already resembled the extant ones (Heinrichs *et al.* 2014a, Kaasalainen *et al.* 2017).

Despite much progress in recent years, the classification of Lejeuneaceae is still a challenging task (Gradstein 2013). A particularly important feature are female involucres, which provide valuable information for recognizing genera and species, while sterile plants can sometimes only be classified to genus level (e.g., Heinrichs *et al.* 2015a). This offers some difficulties with the assignment of fossils as age constraints.

Subfamily: Lejeuneoideae C.Massal.

Tribe: Brachiolejeuneeae van Slageren & Berendsen

Subtribe: Brachiolejeuneinae Gradst.

Genus: *Blepharolejeunea* Arnell (1962: 335)

Blepharolejeunea obovata Gradstein (1993: 357)

Holotype: MB.Pb.1984-805.

Reference: Gradstein (1993), fig. 2.

Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.

Calibration: Minimum age of *Blepharolejeunea.*

Justification: The truncate, bidentate lobule and the small cordate trigones are suggestive of the small montane Neotropical genus *Blepharolejeunea,* though the fossil does not match the morphology of any of the five extant species (Gradstein 1993). Main differences are the obovate outline of the lobule and the similar shape of the lobule teeth which are usually of a different size in extant species. The truncate lobule apex shows affinities to the closely related genus *Brachiolejeunea* (Spruce) Schiffner (1893: 128), though extant representatives of this genus are more robust, have squarrose leaves, and larger, imbricate underleaves with an arched insertion (Gradstein *et al.* 2001). This fossil has provided age constraints for the stem of the *Brachiolejeunea/Blepharolejeunea*-clade in Wilson *et al.* (2007) and for *Blepharolejeunea* in Laenen *et al.* (2014) who estimated median ages of 17.3–31.78 Ma.

Subtribe: Stictolejeuneinae Gradst.

Genus: *Neurolejeunea* (Spruce) Schiffner (1893: 131)

Neurolejeunea macrostipula Gradstein (1993: 368)

Holotype: MB.Pb.1984-812.

Reference: Gradstein (1993), fig. 9.

Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.

Calibration: Minimum age of *Neurolejeunea.*

Justification: Extant *Neurolejeunea* includes only four species and is mainly distributed in the Neotropics (Gradstein 1993, Gradstein *et al.* 2001, Pócs *et al.* 2015). *Neurolejeunea macrostipula* lacks ocelli, a character shared by the extant *N. breutelii* (Gottsche in Gottsche *et al.* 1845b: 324) Evans (1907: 13) which it resembles most (Gradstein 1993). It was employed as age constraint for the stem of *Neurolejeunea* in Wilson *et al.* 2007 and in Laenen *et al.* (2014) who estimated median ages of 5.48–10.9 Ma.

Genus: *Stictolejeunea* (Spruce) Schiffner (1893: 131)

Stictolejeunea squamata **(Willd. ex F.Weber) Schiffner (1893: 131)**

Basionym: *Jungermannia squamata* Willd. ex Weber (1815: 33).—Type: West Indies, „In corticibus Myrti caryophyllatae", sterile, unknown collector (S, STR, W hb. Lindenberg 6171 & 6172); extant species.

Additional fossil specimen: MB.Pb.1984-1076.
Reference: Gradstein (1993), fig. 10.
Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.
Calibration: Minimum age of the extant species *Stictolejeunea squamata.*
Justification: *Stictolejeunea squamata* is an extant species also known as fossil from Dominican amber. The inclusion possibly represents a branch (Gradstein 1993) but can confidently be assigned because of its four cells wide ventral merophyte, the scattered ocelli in leaves and underleaves, the curved lobules with their opening turned towards the base of the stem, and the reniform, undivided underleaves with deeply arched insertion. The fossil has not yet been used as age constraint, but the age is mostly consistent with several divergence time estimates. Feldberg *et al.* (2014) estimated a mean stem age of 48.54 Ma which is consistent with Wilson *et al.* (2007) who also estimated a middle Eocene origin. Laenen *et al.* (2014) estimated median ages of 5.48–10.9 Ma for *Stictolejeunea*.

Tribe: Lejeuneeae Dumort.

Subtribe: Ceratolejeuneinae Gradst.

Genus: *Ceratolejeunea* (Spruce) Jack & Stephani (1892: 16)

Ceratolejeunea is a large pantropical genus with ca. 40 species and a center of diversity in the Neotropics (Dauphin 2003, Gradstein 2013, 2020, Heinrichs *et al.* 2014a). It is known from Miocene Dominican amber with one species identified only to genus level (Gradstein 1993, Feldberg *et al.* 2014) and three species from contemporaneous Mexican amber (Heinrichs *et al.* 2014a, 2015a, Lee *et al.* 2015b), which provide a minimum age for the genus.

Ceratolejeunea antiqua **Heinrichs & Schäf.-Verw. in Heinrichs *et al.* (2014a: 11); Fig. 7A**

Holotype: SMNS Mx 284.
Reference: Heinrichs *et al.* (2014a), figs. 1, 2.

Ceratolejeunea palaeomexicana **(Grolle) Lee, Schäfer-Verwimp, Schmidt & Heinrichs (2015b: 339)**

Basionym: *Lejeunea palaeomexicana* Grolle (1984d: 2).—Holotype: SMNS Mx-119-D-1.
References: Grolle (1984d), Abb. 1–10; Lee *et al.* (2015b), figs. 1–7; Heinrichs *et al.* (2018a), plate VII(6).

Ceratolejeunea sublaetefusca **Heinrichs, Pócs & Schäf.-Verw. in Heinrichs *et al.* (2015a: 62)**

Holotype: SMNS Mx-443 (syninclusion *Spruceanthus extinctus* (Heinrichs, Gyarmati & Schäf.-Verw. in Heinrichs *et al.* 2015a: 62) Gradstein & Sukkharak, *comb. nov.*).
Reference: Heinrichs *et al.* (2015a), plate III.

Age and stratigraphic level: *Ceratolejeunea antiqua, C. palaeomexicana,* and *C. sublaetefusca* derive from 15–23 Ma, Langhian–Aquitanian (early to middle Miocene) amber mined in Simojovel, Chiapas, Mexico.
Calibration: *Ceratolejeunea antiqua, C. palaeomexicana,* and *C. sublaetefusca* provide a minimum age for *Ceratolejeunea.*
Justification: The presence of three species of *Ceratolejeunea* in Mexican amber and one only identified to genus level in contemporaneous Dominican amber as well as molecular phylogenetic studies indicate that this epiphytic genus was already diverse in the Miocene (Gradstein 1993, Feldberg *et al.* 2014, Scheben *et al.* 2016). Today, the genus shows a disjunct distribution and comprises pantropical species and regional endemics, whereas the center of diversity is South America (Scheben *et al.* 2016). *Ceratolejeunea antiqua* (Fig. 7A) shows morphological similarities to subgen. *Ceratolejeunea* and especially the species *C. laetefusca* (Austin 1876: 36) Schuster (1956: 306), *C. cubensis*

(Montagne 1842: 481) Schiffner (1893: 125), and *C. cornuta* (Lindenberg 1829: 23) Stephani (1895: 65) (Dauphin 2003, Heinrichs *et al.* 2014a, Söderström *et al.* 2016). However, the fossil is sterile which hinders a comparison with the extant diversity. Another fossil with strong affinities to this subgenus is *C. sublaetefusca* which can only be separated from *C. laetefusca* and *C. cubensis* by the more bifid underleaves and more acute lobes. It might belong to the stem lineage of either species. Heinrichs *et al.* (2015a) could not entirely rule out that *C. sublaetefusca* is another fossil of an extant species, but again, the sterile condition of the fossil impedes the comparison with the extant diversity. The same problem occurs once more in the third species from Mexican amber, *C. palaeomexicana*. An assignment of these species within the crown group is therefore difficult. Some characteristic features like utriculi and perianths might be lacking, but the generic assignment is reliable, and the occurrence of *Ceratolejeunea* in Miocene ambers provides a minimum age for the genus. In Wilson *et al.* (2007) the presence of *Ceratolejeunea* sp. in Dominican amber (Gradstein 1993) was employed as constraint for the stem and in Feldberg *et al.* (2014) for the crown group resulting in a mean age of 36.53 Ma.

Subtribe: Cheilolejeuneinae Gradst.

Genus: *Cheilolejeunea* (Spruce) Stephani (1890: 284)

Cheilolejeunea is a large pantropical and mainly epiphytic genus with ca. 130 species (Ye *et al.* 2015, Bastos & Gradstein 2020, Gradstein 2020). The fossil record of this genus is rather diverse, with one species described from Eocene Baltic amber (Grolle 1984c, Grolle & Meister 2004b) and three from Miocene Dominican amber (Ye & Zhu 2010, Heinrichs *et al.* 2018b, Grolle *et al.* 2001).

While the species from Baltic amber provides a minimum age for the genus, the three species from Miocene Dominican amber, namely *C. antiqua* (Grolle 1983: 2) Ye & Zhu (2010: 280), *C. lamyi* Heinrichs, Schäfer-Verwimp, Renner & Feldberg (2018b: 156), and *C. suzannensis* (Grolle 1984b: 27) Grolle & R.L.Zhu in Grolle *et al.* (2001: 1073) cannot be assigned easily. A utilization of these fossils as age constraints would require assignments within the crown group what is currently difficult due to the complex taxonomy of *Cheilolejeunea*. *Cheilolejeunea antiqua* and *C. suzannensis* are known only in sterile condition what makes their assignment even more difficult, whereas *C. lamyi* has been described with a gynoecium lacking the perianth. The latter species has been identified by Grolle as the extant *C. rigidula* (Nees ex Montagne 1840: 336) Schuster (1971: 102) of subgen. *Euosmolejeunea* (Spruce 1884: 241) Kachroo (1968: 6) but differs in having partly subacute, slightly elongate leaf lobes, often apiculate underleaf lobes, and more acute lobes of the bracteole (Heinrichs *et al.* 2018b). Given an extensive sampling and thorough morphological studies it might be assigned to an extant subgenus.

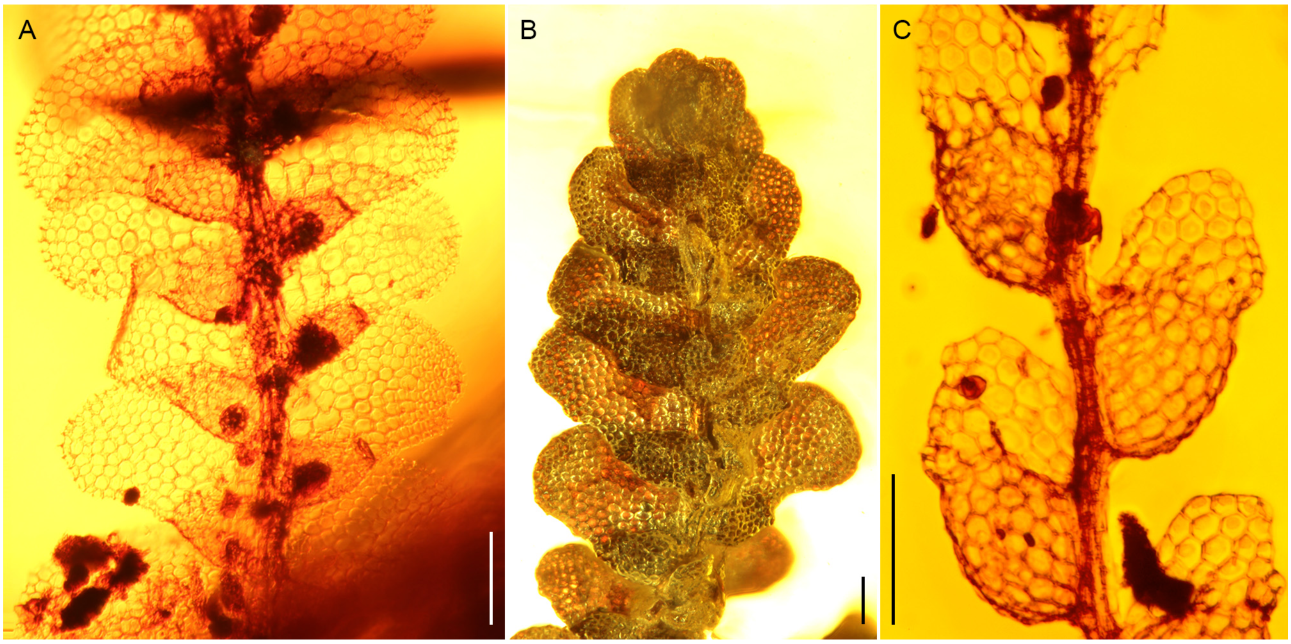

FIGURE 7. Lejeuneeae. A. *Ceratolejeunea antiqua,* SMNS Mx 284 (holotype) from Dominican amber in ventral view. **B.** *Cheilolejeunea latiloba,* GRÖHN 2065 from Baltic amber in ventral view. **C.** *Microlejeunea nyiahae,* AMNH-Tad-441-A (holotype) from Indian Cambay amber in ventral view. Scale bars: A, C=100 µm, B=200 µm.

Cheilolejeunea latiloba (Casp.) Grolle (1984c: 230); Fig. 7B

Basionym: *Lejeunea latiloba* Caspary (1887: 3).—Holotype: MB.Pb.1979/637 (Coll. Künow 69), Baltic amber.

= *Lejeunea pinnata* Caspary (1887: 3).—Holotype: MB.Pb.1979/471-G (Coll. Künow), Baltic amber (syninclusions *Frullania acutata* 471-C; *Nipponolejeunea europaea* 471-D–F; *Radula sphaerocarpoides* 471-A).—Syn. fide Grolle (1984c).

Additional specimens: Baltic amber: GRÖHN 2027, 2037, 2065, 2066, 2073, 2079, **2080, 2085;** MB.Pb.1979/471-B (Coll. Künow), MB.Pb.1979/471-H (Coll. Künow). **Bitterfeld amber:** MB.Pb.1997/3a–d, h (Coll. Grolle F/1a–d, h), MB.Pb.1997/19 (ser. 9/2a), MB.Pb.1997/41 (Coll. Grolle M-14/2), MB.Pb.1996/1349 (Coll. Striebich); **GZG. BST.22068 (Coll. Grabenhorst Le-61).**

References: Caspary (1887), Tafel I Bild 9 as *Lejeunea latiloba,* Tafel I Bild 26 as *Lejeunea pinnata;* Caspary & Klebs (1907), Tafel III Bild 23, 23a, b as *Lejeunea latiloba;* Barthel & Hetzer (1982), Tafel 1, Fig. 2a as *Lejeunea latiloba;* Grolle (1984c), Abb.1, Tafeln XXXI–XXXVI; Grolle & Meister (2004b), plate 2e–g.

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: Minimum age of *Cheilolejeunea*.

Justification: Well-preserved fossils of *C. latiloba* are frequently found in Baltic and Bitterfeld amber. The ventral merophyte of the thin stem is ca. 2 cells wide, the cells of the lateral leaves have slightly thickened walls, the lobules have a large tooth on the outer margin and show a probable insertion point of a hyaline papilla, the underleaves are bifurcated, and one specimen has unfertilized gynoecia with gynoecial innovations of the *Pycnolejeunea*-type but without perianth (Grolle 1984c, Grolle & Meister 2004b). Morphologically it resembles the extant Azorean endemic *C. cedercreutzii* (Buch & Persson 1941: 9) Grolle (1976: 188) of subg. *Euosmolejeunea* (Grolle 1984c, Grolle & Meister 2004b, Söderström *et al.* 2016). The holotype is preserved in a taphocoenosis with *Radula sphaerocarpoides, Nipponolejeunea europaea,* and *Frullania acutata* as well as several insects and provides an excerpt of an Eocene bark community (Grolle 1984c). The rather complete preservation substantiates the generic assignment, and the species has been employed as age constraint in several divergence time estimates (Heinrichs *et al.* 2007, Wilson *et al.* 2007, Cooper *et al.* 2012, Feldberg *et al.* 2014, Laenen *et al.* 2014). Feldberg *et al.* (2014) assigned the fossil to the crown group and estimated a mean age of 43.89 Ma. Laenen *et al.* (2014) estimated median ages for *Cheilolejeunea* of 19.85–25.14 Ma.

Subtribe: Cololejeuneinae Gradst.

Genus: *Cololejeunea* (Spruce) Stephani (1891: 208)

Cololejeunea sp.

Specimen: OSU Poinar B 1-23, holotype of *Phyllopsora dominicanus* Rikkinen in Rikkinen & Poinar (2008: 1008).

Reference: Rikkinen & Poinar (2008).

Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.

Calibration: Minimum age of *Cololejeunea.*

Justification: The liverwort inclusion in this amber specimen has not yet been described, but the complicate-bilobed, incubously inserted leaves and the lack of underleaves are indicative of *Cololejeunea.* However, for a final assignment to this genus and the description of a new species it would be necessary to determine the lateral to ventral merophyte ratio. The presence of this mainly epiphyllous genus in Dominican amber provided an age constraint for Feldberg *et al.* (2014) who assigned it to the crown group of the genus and estimated a mean age of 63.31 Ma.

Subtribe: Cyclolejeuneinae Gradst.

Genus: *Cyclolejeunea* Evans (1904: 193)

Cyclolejeunea archaica Grolle (1984a: 274)

Holotype: SMNS Do-3868-B-1.

Reference: Grolle (1984a), Abb. 1E–G, Taf. 3, 4.

Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.

Calibration: Minimum age of *Cyclolejeunea.*
Justification: The lateral leaves of the fossil have cells with one central mammilla and thin cell walls without trigones. These characters can only be found in the extant *Lejeunea* sect. *Echinocolea* (Schuster 1963: 125) Gradstein (2018: 7) and in *C. accedens* (Gottsche in Gottsche *et al.* 1845b: 339) Evans (1904: 201). Gynoecia or vegetative propagules might be lacking but the overall similarity to the latter species provides a reliable classification (Grolle 1984a). This fossil has been used as age constraint in Laenen *et al.* (2014) who estimated median ages of 31.7–42.54 Ma.

Subtribe: Drepanolejeuneinae Gradst.

Genus: *Drepanolejeunea* (Spruce) Stephani (1891: 209)

Drepanolejeunea eogena Grolle (1993b: 376)

Holotype: SMNS Do-3927-M-11.
Reference: Grolle (1993b), figs. 1, 2.
Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.
Calibration: Minimum age of *Drepanolejeunea.*
Justification: The presence of ocelli is not clear, but the fertile fossil can be assigned to *Drepanolejeunea* with high confidence because of the bifid underleaves with lanceolate lobes, a perianth with irregularly toothed folds, and the pycnolejeuneoid gynoecial innovation (Grolle 1993b). There is no extant species closely related to the fossil; therefore, it might provide a minimum constraint for the genus. It has already been used in Wilson *et al.* (2007) for a clade comprising Drepanolejeuneinae and Cololejeuneinae, a group which includes many mainly epiphyllous genera.

Subtribe: Lejeuneinae Gradst.

Genus: *Lejeunea* Libert (1820: 373)

In recent years, molecular phylogenetic studies have greatly refined the classification of this large pantropical genus which comprises ca. 300 extant species, but to date it remains taxonomically difficult (e.g., Wilson *et al.* 2007, Gradstein 2013, Heinrichs *et al.* 2013, Lee 2013, Renner *et al.* 2013c, Lee *et al.* 2020). Four fossil species described from Dominican amber suggest a high diversity of *Lejeunea* in the Miocene Caribbean forest (Kaasalainen *et al.* 2017, Lee *et al.* 2017) what is in good accordance with the Miocene origin estimated for this genus (Heinrichs *et al.* 2016a). However, all fossils are sterile, which makes comparisons with extant taxa problematic.

Lejeunea hamatiloba G.E.Lee, Schäf.-Verw., M.A.M.Renner & Heinrichs in Lee *et al.* (2017: 147)

Holotype: MB.Pb.2016/1865.
Reference: Lee *et al.* (2017), plates I.1, II.1, 2, fig. 1.

Lejeunea miocenica Heinrichs, Schäf.-Verw., M.A.M.Renner & G.E.Lee in Kaasalainen *et al.* (2017: 323)

Holotype: AMNH DR-15-3.
Reference: Kaasalainen *et al.* (2017), figs. 1B, 3.

Lejeunea resinata G.E.Lee, Schäf.-Verw., M.A.M.Renner & Heinrichs in Lee *et al.* (2017: 147)

Holotype: MB.Pb.2016/1866.
Reference: Lee *et al.* (2017), plates I.2, II.3, 4, fig. 2.

Lejeunea urbanioides G.E.Lee, Schäf.-Verw., M.A.M.Renner, Heinrichs in Lee *et al.* (2017: 148)

Holotype: NMNH 372452.
References: Reiner-Drehwald *et al.* (2012) as *Lejeunea* sp.; Lee *et al.* (2017), plates I.3, II.5, 6, fig. 3.

Age and stratigraphic level: *Lejeunea hamatiloba, L. miocenica, L. resinata,* and *L. urbanioides* derive from 15–20 Ma, Langhian–Burdigalian (early to middle Miocene) amber mined in the La Toca Formation, Dominican Republic.
Calibration: *Lejeunea hamatiloba, L. miocenica, L. resinata,* and *L. urbanioides* provide a minimum age for *Lejeunea*.
Justification: Though all fossils are sterile, the generic assignment is reliable (Lee *et al.* 2017). The plants are characterized by two cells wide merophytes, long-inserted leaf lobes, small, toothed lobules, the lack of differentiated ocelli, and bifid underleaves (Kaasalainen *et al.* 2017, Lee *et al.* 2017). *Lejeunea miocenica* shows characters typical of the polyphyletic subgen. *Crossotolejeunea* Spruce (1884: 161) (Kaasalainen *et al.* 2017, Reiner-Drehwald & Goda 2000) which is a common element of the Caribbean rainforests today. The presence of a typical *Lejeunea* in Dominican amber provided a minimum age constraint for the crown group in Feldberg *et al.* (2014) who estimated a mean age of 51.59 Ma. Heinrichs *et al.* (2007) and Laenen *et al.* (2014) assigned *L. palaeomexicana* from Mexican amber to the genus, a species which has been transferred to *Ceratolejeunea*. However, since Mexican and Dominican amber are contemporaneous this assignment resulted in the same constraint with median ages of 25.19–34.15 Ma estimated in Laenen *et al.* (2014) for the genus. Lee *et al.* (2020) did not employ any *Lejeunea* fossil due to the difficulties in assigning them to any extant subclade of the genus but used *Microlejeunea nyiahae* Heinrichs, G.E.Lee, Schäf.-Verw. & A.R.Schmidt in Heinrichs *et al.* (2016a: e0156301 [5]) from 52 Ma Indian amber as minimum age constrain for the stem, what resulted in estimates of 42.2–52 Ma for the *Lejeunea* crown group.

Genus: *Microlejeunea* (Spruce) Stephani (1888a: 61)

Recent molecular phylogenetic studies clearly separate this pantropical genus from *Lejeunea* (e.g., Dong *et al.* 2013, Heinrichs *et al.* 2013, Lee *et al.* 2020). Fossil material has been described from Eocene Indian amber and Miocene Dominican amber. *Microlejeunea nyiahae* represents the oldest crown group member of Lejeuneaceae (Heinrichs *et al.* 2016a, Lee *et al.* 2020). A much younger fossil also assigned to this genus is *M. miocenica* Lee, Bechteler, Schäfer-Verwimp & Heinrichs (2015a: 17) which is preserved with juvenile gynoecia characterized by winged bracts which substantiate an assignment to this genus. It does not closely match the morphology of any extant Neotropical species but somewhat resembles the extant *M. subulistipa* Stephani (1896b: 115) in its vegetative characters, and *M. epiphylla* Bischler (1963: 378) as well as *M. aligera* (Mitten 1860a: 113) Stephani (1915: 827) in having toothed female bracts. Currently, it cannot be assigned to any taxon within the crown group.

Microlejeunea nyiahae; Fig. 7C

Holotype: AMNH-Tad-441-A.
Reference: Heinrichs *et al.* (2016a), figs. 1A, 2, 3.
Age and stratigraphic level: 52 Ma, Ypresian (early Eocene), Tadkeshwar Lignite Mine of Gujarat State, India (Cambay amber).
Calibration: Minimum age of tribe Lejeuneeae.
Justification: The sterile specimens (Fig. 7C) are in good accordance with the circumscription of *Microlejeunea*, except that the presence of ocelli can neither be confirmed nor rejected because they do not differ in size from the surrounding cells in this genus, and because oil bodies are mostly not preserved in fossils (Heinrichs *et al.* 2016a). It is also possible that this fossil belongs to *Lejeunea*, though paleotropical representatives are only present in early diverging lineages of *Microlejeunea* but not of *Lejeunea.* In their divergence time estimation, Heinrichs *et al.* (2016a) conducted a thorough cross evaluation of different assignments of this fossil and the assumption of an early crown or stem group member of *Microlejeunea* or *Lejeunea* led to the most likely age estimates. The genera of Lejeuneinae might have been established Late Cretaceous or Paleogene, while the crown group of Lejeuneaceae genera diversified in Cenozoic, angiosperm-dominated forests. The fossil was also employed by Lee *et al.* (2020) to constrain the *Microlejeunea*-*Lejeunea* clade.

Subfamily: Ptychanthoideae Mizut.

Genus: *Acrolejeunea* (Spruce) Schiffner (1893: 128)

Acrolejeunea ucrainica Mamontov, Heinrichs & Schäf.-Verw. in Mamontov *et al.* (2013: 95); Fig. 8

Holotype: SIZK-K-10052F.

= *Frullania ucrainica* Konstant. & Ignatov in Konstantinova *et al.* (2012: 269).—Holotype: SIZK-K-6581.—***Syn. nov.***
References: Mamontov *et al.* (2013), figs. 1–10; Konstantinova *et al.* (2012), figs. 11–14.
Age and stratigraphic level: 35–37 Ma, Priabonian (late Eocene), amber quarry "Pugach", Klesov, Ukraine (Rovno amber).
Calibration: Minimum age of *Acrolejeunea*.
Justification: *Acrolejeunea* is a pantropical genus of ca. 20 extant species which occur as epiphytes in rather dry environments (Gradstein 1975, Wang *et al.* 2014). The holotype is sterile but vegetative characters like the suberect upper shoot sector with small leaves, the subvertically positioned, squarrose leaves with revolute dorsal margins, the arrangement of the lobe cells in curved rows which parallel the dorsal margin, and the presence of cordate trigones as well as intermediate thickenings distinguish it from other fossil representatives of Ptychanthoideae and are typical for *Acrolejeunea* (Mamontov *et al.* 2013).

Another fossil from the same locality, which has initially been described as *Frullania ucrainica*, also belongs to *A. ucrainica* and is fertile (female, Fig. 8A). It is characterized by densely imbricate leaves, undivided reniform underleaves, elongate cells, as well as inflated *Lejeunea*-type lobules with a long, arched keel (Fig. 8B). While species of *Frullania,* including those with wide and entire underleaves, have shallowly to deeply bilobed, more or less elongated female bracteoles (Hattori 1973, Schuster 1992), the fossil has a very wide and undivided innermost female bracteole which is rather similar to underleaves of vegetative parts, a character typical for Ptychanthoideae. Also, the presence of a pluriplicate perianth (Fig. 8A) is indicative of Ptychanthoideae.

The presence of two innovations below the gynoecium indicates that *A. ucrainica* might be a member of sect. *Trocholejeunea* (Schiffn. in Dixon *et al.* 1932: 160) Jian Wang bis & Gradst. in Wang *et al.* (2014: 38). It is very similar to the extant *A. sandvicensis* (Gottsche 1857: 344) Stephani (1896a: 312) as suggested by Sun *et al.* (2018). *Acrolejeunea* sect. *Trocholejeunea* is a small group of species with an extant distribution in subtropical and warm-temperate regions of East Asia (Wang *et al.* 2014). Its occurrence in Rovno amber indicates that the section was more widespread in the Holarctics during the late Eocene. The crown group of *Acrolejeunea* diversified in the Paleogene (e.g., Laenen *et al.* 2014). Hence, the Eocene amber inclusion could represent either a member of the stem or the crown group.

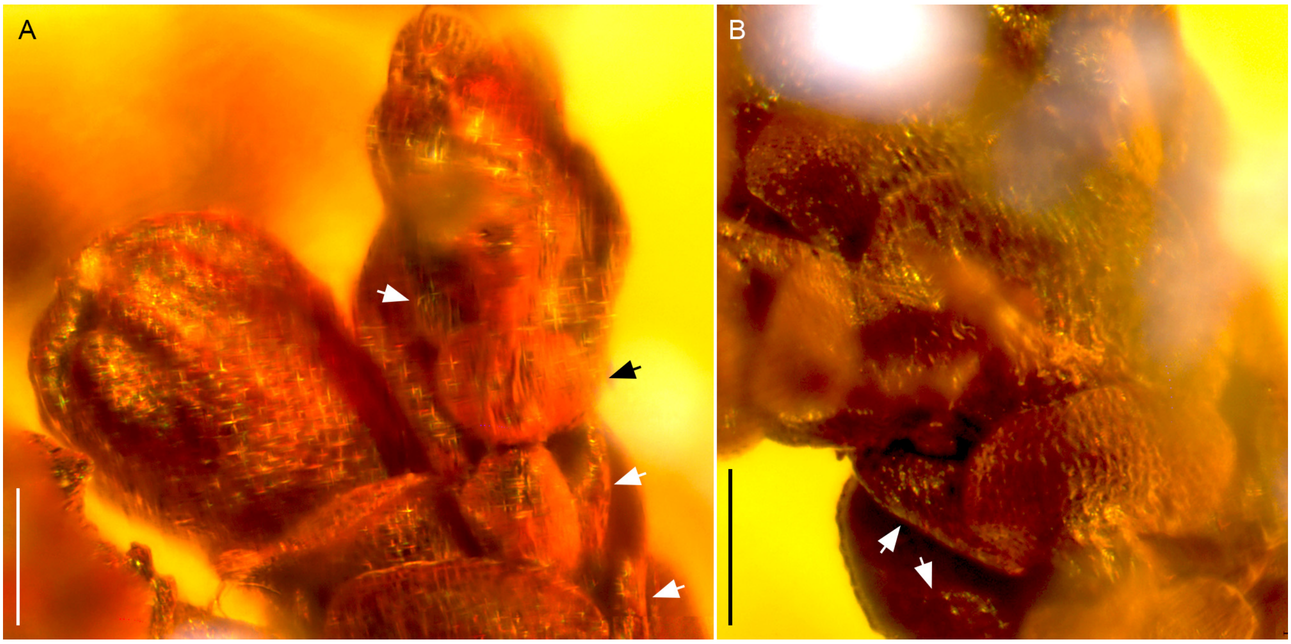

FIGURE 8. Lejeuneaceae subfam. Ptychanthoideae. A, B. *Acrolejeunea ucrainica,* SIZK-K-6581 (holotype of the synonymous species *Frullania ucrainica*) from Rovno amber. **A.** Perianth and subgynoecial innovation with *Lejeunea*-type lobules of lateral leaves and undivided underleaves. **B.** Detail of shoot in ventral view showing *Lejeunea*-type lobules of lateral leaves and large undivided underleaves. Black and white arrows indicate lobules of lateral leaves. Scale bars: A, B=200 µm.

Genus: *Bryopteris* (Nees) Lindenb. in Gottsche *et al.* (1845a: 284)

Bryopteris, with two species in tropical America and one in Madagascar, is a common element of the montane and submontane rainforests of the Neotropics (Grolle 1993a, Gradstein 2020, Gradstein *et al.* 2001) and morphologically well differentiated. Two species have been described from Dominican amber and provide a minimum age for the genus.

***Bryopteris bispinosa* Grolle (1993a: 73)**

Holotype: SMNS Do-3924-M-2.

References: Grolle (1993a), Abb. 1, 2; Heinrichs *et al.* (2018a), plate VI(1, 2).

***Bryopteris succinea* Grolle (1984a: 271)**

Holotype: SMNS Do-4128-M-1.

References: Grolle (1984a), Abb. 1A–D, Taf. 1, 2; Heinrichs *et al.* (2018a) Plate VI(3).

Age and stratigraphic level: *Bryopteris bispinosa* and *B. succinea* derive from 15–20 Ma, Langhian–Burdigalian (early to middle Miocene) amber mined in the La Toca Formation, Dominican Republic.

Calibration: *Bryopteris bispinosa* and *B. succinea* provide a minimum age for *Bryopteris.*

Justification: The species from Dominican amber can be assigned to the genus with high confidence. *Bryopteris bispinosa* closely resembles the extant Neotropical *B. diffusa* (Swartz 1788: 144) Nees in Gottsche *et al.* (1845a: 286) which is the only extant species with long teeth similar to the fossil on the lobules (Grolle 1993a). An assignment to the stem or crown of this species might therefore be justified. The fossil only differs in having coarsely toothed lobes while *B. diffusa* generally has entire lobes, rarely with a few small teeth near the apex (Gradstein 1994). *Bryopteris succinea* has entire leaf lobules and resembles *B. filicina* (Swartz 1788: 145) Nees in Gottsche *et al.* (1845a: 284). It might provide an age constraint for this taxonomically complicated species (e.g., Hartmann *et al.* 2006) though a clear morphological differentiation from the sister clade *B. gaudichaudii* Gottsche (1857: 340) would be necessary.

The presence of *Bryopteris* in Dominican amber has provided an age constraint for the genus in Wilson *et al.* (2007) and also in Laenen *et al.* (2014) who estimated median ages of 10–20.28 Ma. However, assignments within the crown group might also be possible, given enhanced molecular datasets combined with morphological studies.

Genus: *Dibrachiella* (Spruce) Shi, Zhu & Gradstein (2015: 888)

Dibrachiella grollei* (Gradst.) Gradstein, *comb. nov.

Basionym: *Archilejeunea grollei* Gradstein (1993: 354).—Holotype: MB.Pb.1984-1074.

Reference: Gradstein (1993), fig. 1.

Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.

Calibration: Minimum age of *Dibrachiella*.

Justification: *Dibrachiella* is a genus of nine species that is distributed in tropical America and Africa (Gradstein 2020). Previously the genus was treated as a subgenus of *Archilejeunea* (Spruce) Stephani (1888b: 113) but molecular analysis showed that *Archilejeunea* is polyphyletic and that *Dibrachiella* merits generic status (Shi *et al.* 2015).

The fertile fossil can be assigned to the genus with high confidence but has not yet been employed in divergence time estimates. It is morphologically similar to the extant *D. parviflora* (Nees 1833a: 353) Shi, Zhu & Gradstein (2015: 889) though there are differences in the female involucre (Gradstein 1993). It is a possible constraint of the *Dibrachiella-Spruceanthus*-clade (Shi *et al.* 2015) and has been employed as age constraint in Wilson *et al.* (2007) for the stem of *Archilejeunea.*

Genus: *Lopholejeunea* (Spruce) Stephani (1890: 285)

***Lopholejeunea subnigricans* Gradstein (1993: 359)**

Holotype: MB.Pb.1985-2.

Reference: Gradstein (1993), fig. 4.

Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.

Calibration: Minimum age of *Lopholejeunea.*

Justification: *Lopholejeunea* is one of the larger pantropical genera with ca. 35 species (Gradstein 2020). Neotropical species occur in lowland and lower montane rainforests where they grow as bark epiphytes or on rock. The fossil matches typical extant representatives of *Lopholejeunea* in having undivided underleaves, isodiametric leaf cells, blackish cell walls, and large epidermis cells on the stem (Gradstein 1993). It is very similar to *L. nigricans* (Lindenb. in Gottsche *et al.* 1845b: 316) Schiffner (1898: 293), a species widely distributed throughout the tropics, whereas the fossil has smaller and more flattened lobules instead of swollen ones, a more conspicuous tooth, smaller leaf cells, and strongly squarrose underleaves. This fossil has been employed as a minimum age constraint for the crown group in Feldberg *et al.* (2014) resulting in a mean age of 22.15 Ma. Laenen *et al.* (2014) did not employ this fossil as a constraint but estimated similar median ages of 18.99–29.94 Ma.

Genus: *Marchesinia* Gray (1821: 689)

The Afro-American genus is represented by two fossil species in Miocene Dominican amber, one extinct and one extant. Contrary to the extant *M. brachiata* (Swartz 1788: 144) Schiffner (1893: 128), the extinct *M. pusilla* Gradstein (1993: 362) cannot be as easily assigned within the crown group of the genus. The lobule is suggestive of *M. brachiata,* but the ovate-concave leaves and small size are more similar to the African *M. excavata* (Mitten 1860b: 58) Schiffner (1893: 128) (Gradstein 1993). The fossil seems to deviate from both taxa by its large, contiguous trigones which are never radiate and by the lack of intermediate thickenings.

Marchesinia brachiata

Basionym: *Jungermannia brachiata*.—Type: Jamaica, *Swartz s.n.* (Holotype, S; Isotypes, BM, E, S); extant species.
Additional fossil specimen: MB.Pb.1985-1262.
References: Heinrichs *et al.* (2009); Gradstein (1993), fig. 5; Gradstein (2012).
Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.
Calibration: Minimum age of the extant species *Marchesinia brachiata.*
Justification: The fossil specimen is sterile but shows the characteristic features of the extant species complex (Gradstein 1993, 2012): a robust stem with a ventral merophyte eight cells wide, large, flattened lobules which probably bear more than one tooth along the free margin, isodiametric cells with small radiate trigones as well as intermediate thickenings, and large underleaves with deeply arched insertion. The fossil cannot be distinguished from the extant species and provides a reliable minimum age.

Marchesinia has been employed as age constraint in Wilson *et al.* (2007), in Laenen *et al.* (2014) who estimated median ages of 45.5–63.4 Ma for this genus, and in Feldberg *et al.* (2014) who estimated a mean age of 47.29 Ma.

Genus: *Spruceanthus* Verdoorn (1934: 151)

Extant *Spruceanthus* comprises 16 species and is distributed in tropical Asia and Australia with only one species occurring in the Neotropics and one in West Africa (Wang *et al.* 2015, Sukkharak & Gradstein 2017, Gradstein 2020). The plants are mainly epiphytes in humid environments. Two fossils of this genus are known from Eocene Baltic and Miocene Mexican amber (Grolle 1985c, Heinrichs *et al.* 2015a). The Eocene fossil provides a reliable minimum age for the genus, while the Miocene fossil cannot be easily assigned within the crown group. It has been described as *Mastigolejeunea extincta* Heinrichs, Gyarmati & Schäf.-Verw. in Heinrichs *et al.* (2015a: 62) but its morphology does not fit the description of *Thysananthus* Lindenb. in Lehmann (1844: 24) subgen. *Mastigolejeunea* (Spruce 1884: 100) Sukkharak & Gradstein (2017: 101); therefore, we transfer it to *Spruceanthus* and provide an emended description based on new fossil material.

Spruceanthus extinctus (Heinrichs, Gyarmati & Schäf.-Verw.) Gradstein & Sukkharak, *comb. nov.*; Fig. 9

Basionym: *Mastigolejeunea extincta*.—Holotype: SMNS Mx-443.
Additional specimens: GRÖHN **10410, 10411.**
Reference: Heinrichs *et al.* (2015a), plate II.
Age and stratigraphic level: 15–23 Ma, Langhian–Aquitanian (early to middle Miocene), Simojovel, Chiapas, Mexico.

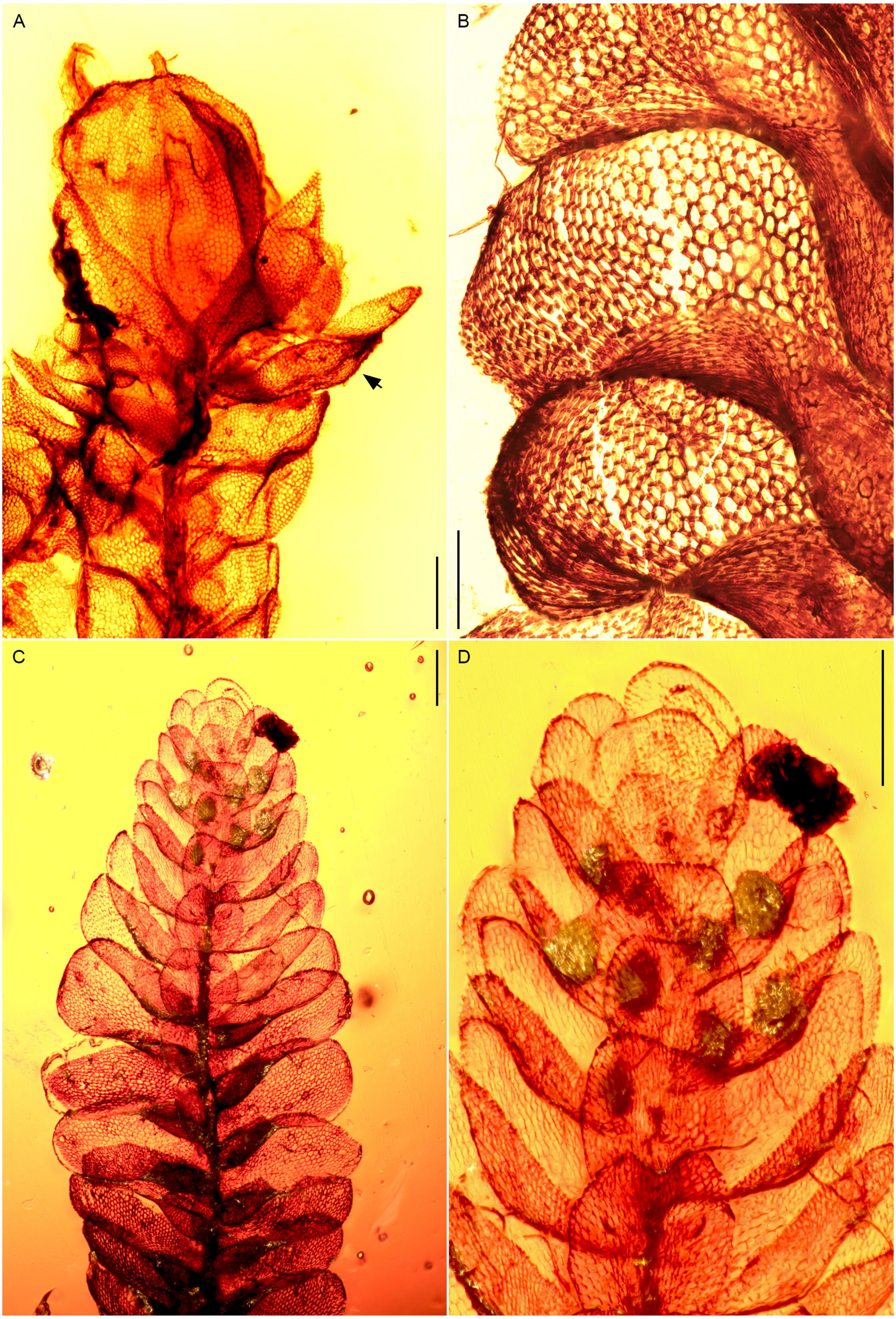

FIGURE 9. Lejeuneaceae subfam. Ptychanthoideae. A–D. *Spruceanthus extinctus* from Mexican amber. **A.** SMNS Mx-443 (holotype) in dorsal view with smooth, plicate perianth and subgynoecial innovation (indicated by arrow). **B.** GRÖHN 10411 in ventral view showing the isodiametric cells of lateral leaves. **C, D.** Male plant GRÖHN 10410 in ventral view. **C.** Overview of the vegetative lower part and fertile upper part. **D.** Androecium with bracts and several antheridia. Scale bars: A, C, D=200 µm, B=100 µm.

Emended diagnosis: Incubously foliated liverwort with a ventral merophyte ca. 4–6 cells wide, complicate bilobed leaves consisting of a 0–1 toothed inflated lobule folded against the lobe and an oblong-ovate dorsal lobe with rounded to obtuse apex, mostly isodiametric leaf cells with small triangular trigones, and obdeltoid underleaves; androecia terminal, consisting of ca. 6 pairs of bracts with hypostatic ventral lobules almost as long as the dorsal lobe and 1–2 antheridia per bract; gynoecium terminal, with 1 subfloral innovation, erect-spreading bracts with acute lobes, and a large, beaked, smooth perianth with 5–6 smooth and irregularly developed folds.

Emended description: Upper portion of female holotype 4 mm long, 0.6–0.7 mm wide, brown. Stem 50–60 µm in diameter, cortical cells thick-walled and elongate; ventral merophyte ca. 4–6 cells wide. Leaves convex, lobes oblong-ovate (Fig. 9A–C), ca. 0.4–0.45 × 0.25–0.3 mm, apex rounded or obtuse, median leaf lobe cells 14–25(–30) × 12–18 µm (Fig. 9B), trigones small, triangular; lobules about 0.30–0.45 the length of the lobe (Fig. 9C), inflated, with apex often merging into ventral lobe margin, without or with a single tooth on free margin. Underleaves (remote to) moderately imbricate (Fig. 9C, D), concave and somewhat squarrose, obdeltoid, symmetrical, the margins contracted at the base, ca. 0.2 mm long × 0.22–0.30 mm wide, apex plane or recurved, emarginate. Androecia [specimen GRÖHN 10410; Fig. 9C, D] terminal, consisting of ca. 6 pairs of bracts with hypostatic ventral lobules almost as long as the dorsal lobe, apices broadly rounded; bracteoles present throughout androecium, similar to underleaves of vegetative shoot part, antheridia visible in the axils of five bracts (Fig. 9D), 1–2 per bract, globose. Gynoecium with 1 subfloral innovation (Fig. 9A), bracts erect-spreading, lobes ca. 0.6 mm long, triangularly-ovate, acute, ending in a 1 cell long, blunt, uniseriate tip, bracteole ± as long as bracts, ca. 0.6 mm long × 0.45 mm wide, obovate, apex emarginate. Perianth emergent, 0.75 mm long × 0.57 mm wide, obovate, flattened, with 5–6 smooth and irregularly developed folds; beak 75 µm long. Sporophyte unknown.

Calibration: Possible future calibration point within the genus, once the precise assignment will be possible.

Justification: The generic placement of *Mastigolejeunea extincta* was discussed by Sukkharak & Gradstein (2017), who suggested that the species might be a member of *Lopholejeunea* because of the mostly isodiametric leaf cells (Fig. 9B), narrow underleaf base, absence of true innovations, and lack of a high median keel on the ventral perianth surface. Nevertheless, the 5–6 smooth and irregularly developed folds on the perianth of *M. extincta* (Fig. 9A) are abnormal for *Lopholejeunea*, which normally produces 4 or 5 toothed keels (very rarely keels almost entire) and are more suggestive of *Spruceanthus* (Wang *et al*. 2016). Moreover, the short branch in the gynoecium of *M. extincta* (Fig. 9A), interpreted by Sukkharak & Gradstein (2017) as a “pseudo-innovation”, is in fact probably a true innovation because of its position at the base of the inner bract (Heinrichs *et al.* 2015a). Presence of true innovations also separates *Spruceanthus* from *Lopholejeunea*. Because of this evidence, *M. extincta* is transferred to the genus *Spruceanthus*. Two further fossils of *S. extinctus* have been found in Mexican amber (GRÖHN 10410, 10411), including one shoot with mature androecia (GRÖHN 10410). The androecia (Fig. 9C, D) are terminal on the shoot and consist of six pairs of bracts. The bract lobules are hypostatic and almost as long as the lobe, with a broadly rounded apex of lobules, and the bracteoles are similar to the underleaves and are present throughout the male spike (Fig. 9C). The antheridia are globose and 1–2 per bract (Fig. 9D). *Spruceanthus extinctus* is the second fossil species of this genus described from amber and the first one from tropical America. The utilization of *S. extinctus* as age constraint requires an assignment within the crown group of the genus and hence a thorough comparison with extant species.

Spruceanthus polonicus Grolle (1985c: 79)

Holotype: WAR-MZ Coll. Rieband 469-2.

Additional specimen: Baltic amber: cf. GRÖHN 5808.

References: Grolle (1985c), plates I, II, fig. 1; Grolle & Meister (2004b), plate 23f, g; Frahm & Gröhn (2013), figs. 9, 10.

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region.

Calibration: Minimum age of *Spruceanthus.*

Justification: *Spruceanthus polonicus* is known with gynoecium and is morphologically very similar to the extant *S. semirepandus* (Nees 1830: 39) Verdoorn (1934: 153) in having entire margined vegetative lateral leaves and underleaves, an irregularly dentate subinvolucral underleaf, and a bract and bracteole with coarse thorny teeth (Grolle 1985c). It differs in having lobules 0.3–0.4 × the size of the lobe instead of 0.25 × and entire instead of 1–3 dentate lobule apices. *Spruceanthus polonicus* has been employed as age constraint in Heinrichs *et al.* (2007), Wilson *et al.* (2007), Feldberg *et al.* (2014), and Laenen *et al.* (2014) for the stem of *Spruceanthus*.

Genus: *Thysananthus*

Thysananthus is a largely paleotropic genus with ca. 30 species (e.g., Sukkharak & Gradstein 2017). One fossil species has been described from Baltic as well as Bitterfeld amber and three species are known from Dominican amber, one of them representing an extant species. One extinct species from Dominican amber, *T. bidentulus* (Gradstein 1993: 365) Sukkharak & Gradstein (2017: 103), is preserved only in sterile condition and difficult to assign to an extant lineage within the crown group. The second extinct species, *T. weiweianus* N.-N.Yu & Gradst. in Yu *et al.* (2020: 59), is preserved with androecia, gynoecia, and perianth. The species closely resembles the extant *T. plicatiflorus* (Spruce 1884: 104) Sukkharak & Gradstein (2017: 102) but differs in the larger lobules, autoicous sexuality, and the somewhat expanded keels and plicae of the perianth (Yu *et al.* 2020). The fertile condition might allow an assignment within the crown group.

Except for the newly described *T. weiweianus*, all species have previously been assigned to *Mastigolejeunea* which has been lowered to a subgenus of *Thysananthus* (Sukkharak & Gradstein 2017). The subgenera *Mastigolejeunea* and *Thysananthus* are not easily distinguished even when fertile material is at hand, therefore the assignment of the extinct species is difficult.

Thysananthus auriculatus (Wilson & Hook.) Sukkharak & Gradstein (2017: 102)

Basionym: *Jungermannia auriculata* Wilson & Hook. in Wilson (1841: no. 170).—Type: USA, Louisiana, New Orleans, Drummond s.n., Musci Americani (Southern States) 170 (Holotype, BM; Isotypes, MANCH, PC); extant species.

≡ *Mastigolejeunea auriculata* (Wilson & Hook.) Stephani (1892: 171).

Additional fossil specimen: MB.Pb.1984-1075.

Reference: Gradstein (1993), fig. 7 as *Mastigolejeunea auriculata.*

Age and stratigraphic level: 15–20 Ma, Langhian–Burdigalian (early to middle Miocene), La Toca Formation, Dominican Republic.

Calibration: Minimum age of the extant species *Thysananthus auriculatus.*

Justification: The fossil specimen is preserved with androecia as well as gynoecia and mature perianth on separate shoots, therefore it might be dioicous (Gradstein 1993). This allows a detailed comparison with extant representatives of the species which belongs to subgen. *Mastigolejeunea* sect. *Mastigolejeunea*. The specimen is characterized by elongated, distinctly convex-concave leaves with rounded apices, large, 1-toothed lobules with very oblique distal ends, elongated leaf cells with cordate trigones, obdeltoid underleaves with truncate apices, male bracts (4–6 pairs) with large, hypostatic lobules, gynoecia with single, repeatedly fertile innovations with lejeuneoid leaf sequences, densely imbricate, broadly oblong female bracts and bracteoles with rounded apices and entire margins, and immersed, sharply and smoothly trigonous perianths with a short beak and a very narrow ventral perianth keel which is as wide as the lateral keels.

Thysananthus contortus (Göpp. & Berendt) Sukkharak & Gradstein (2017: 103)

Basionym: *Jungermannites contortus* Göpp. & Berendt in Göppert (1845: 114).—Holotype: MB.Pb.1979/479 (Coll. Berendt), Baltic amber.

≡ *Phragmicoma contorta* (Göpp. & Berendt) Caspary (1887: 2).

≡ *Trocholejeunea contorta* (Göpp. & Berendt) Gradst. & Grolle in Grolle (1982: 178).

≡ *Mastigolejeunea contorta* (Göpp. & Berendt) Gradst. & Grolle in Grolle *et al.* (2004: 119).

= *Phragmicoma magnistipulata* Caspary (1887: 2).—Holotype: MB.Pb.1979/714 (Coll. Künow 171), Baltic amber.—Syn. fide Grolle (1982).

= *Phragmicoma suborbiculata* Caspary (1887: 2).—Holotype: MB.Pb.1979/470 (Coll. Berendt), Baltic amber.—Syn. fide Grolle (1982).

= *Phragmicoma suborbiculata* var. *sinuata* Caspary (1887: 2).—Holotype: MB.Pb.1979/713 (Coll. Künow 170), Baltic amber.—Syn. fide Grolle (1982).

= *Lejeunea alifera* Casp. in Caspary & Klebs (1907: 29).—Holotype: destroyed ("Amber collection of the Physikalisch-Ökonomische Gesellschaft at the former Königsberg" 134).—Syn. fide Grolle *et al.* (2004).

= *Lejeunea serpyllifolia* sensu Göppert [non Libert] (1853: 456).—Syn. fide Caspary (1887).

= *Radula complanata* sensu Göppert [non (L.) Dumort.] (1853: 456).—Syn. fide Caspary (1887).

= *Trocholejeunea sandvicensis* sensu Weis [non (Gottsche) Mizutani] (2001: 114).—Syn. fide Grolle *et al.* (2004).

Additional specimens: Baltic amber: GPIH 701, 2541a; GRÖHN 0154, 0908, 1557, 1540b, 2011, 2052a, 2061,

2074, 2078 (det. *Cheilolejeunea latiloba* in Grolle & Meister 2004b), 2084, **2086,** 2098, **5838;** WAR-MZ s.n. (Coll. Deptula 1807); VELTEN H0001a; WINTER 2897 (Coll. Gröhn). **Bitterfeld amber: GZG.BST.22069 (Coll. Hoffeins 5-22),** GZG.BST.22070 (Coll. Hoffeins 622-1), GZG.BST.22071 (Coll. Hoffeins 930-1), GZG.BST.22072 (Coll. Grabenhorst Le-29), GZG.BST.22073 (Coll. Grabenhorst Le-31), **GZG.BST.22074 (Coll. Grabenhorst Le-56),** GZG.BST.22075 (Coll. Grabenhorst Le-60), GZG.BST.22076 (Coll. Grabenhorst Le-65), **GZG.BST.22077 (Coll. Grabenhorst Le-67), GZG.BST.22078 (Coll. Grabenhorst Le-85), GZG.BST.22044 (Coll. Grabenhorst Le-117);** MB.Pb.sn (Coll. Kutscher Ku-98H01), MB.Pb.sn (Coll. Kutscher Ku-98H02a), MB.Pb.sn (Coll. Kutscher Ku-98H08), MB.Pb.sn (Coll. Kutscher Ku-98H11a), MB.Pb.1996/1342a (Coll. Kutscher), MB.Pb.1997/15 (ser. 8/5a), MB.Pb.1997/26 (Coll. Grolle M-11/2).

References: Göppert (1845), Tafel VI Figs. 40, 41 as *Jungermannites contortus;* Caspary (1887), Tafel I Bild 6 as *Phragmicoma contorta,* Tafel I Bild 5 as *P. magnistipulata,* Tafel I Bild 7 as *P. suborbiculata,* Tafel I Bild 8 as *P. suborbiculata* var. *sinuata;* Caspary & Klebs (1907), Tafel II Bild 16, 16a–c as *P. contorta,* Tafel II Bild 15, 15a–c as *P. magnistipulata,* Tafel II Bild 17, 17a–c as *P. suborbiculata,* Tafel II Bild 18, 18a–c as *P. suborbiculata* var. *sinuata,* Tafel III Bild 24, 24a–c as *Lejeunea alifera;* Grolle (1982), fig. 1a, b, tables 1–7 as *Trocholejeunea contorta;* Grolle (1985c), fig. 2a, b as *Lejeunea alifera*, fig. 2c as *Trocholejeunea contorta;* Grolle (1989), Abb. 1c, d as *Trocholejeunea contorta;* Grolle *et al.* (2004), figs. 1, 2 as *Mastigolejeunea contorta;* Grolle & Meister (2004b), plates 14, 15 as *Mastigolejeunea contorta;* Heinrichs *et al.* (2018a), plate VI(4, 5) as *Mastigolejeunea contorta*.

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region; and 24 Ma, Chattian (late Oligocene), Bernsteinschluff Horizon in the upper part of the Cottbus Formation of the Goitzsche mine, Bitterfeld, Germany.

Calibration: Minimum age of *Thysananthus.*

Justification: *Thysananthus contortus* is known with gynoecia and perianth. The entire margined female involucre and the underleaves, which are not adnate to the lateral leaves, suggest affinities to subgen. *Mastigolejeunea,* but there are exceptions concerning both characters (Sukkharak & Gradstein 2014, 2017). The fossil has been employed as age constraint for *Mastigolejeunea* in several divergence time estimates (Heinrichs *et al.* 2007, Wilson *et al.* 2007, Cooper *et al.* 2012, Feldberg *et al.* 2014, Laenen *et al.* 2014, Sun *et al.* 2014) but due to the current taxonomy, it should better be assigned to *Thysananthus* s.l.

Family: Porellaceae Cavers

Genus: *Porella* Linnaeus (1753: 1106)

Porella subgrandiloba Grolle & So (2004: 485)

Holotype: GPIH 4328 (Coll. Gröhn 2096).

References: Grolle & So (2004), figs. 1–4; Grolle & Meister (2004b), plate 20 a–d.

Age and stratigraphic level: 34–41 Ma, Priabonian–Bartonian (Eocene), Baltic region.

Calibration: Minimum age of *Porella.*

Justification: The generic assignment of the sterile fossil is reliable but the affinity to extant species is uncertain (Grolle & So 2004). *Porella subgrandiloba* lacks mature perianths and basal appendages. It is small in relation to extant species and might represent a detached branch. The morphologically most similar extant species are the much larger *P. grandiloba* Lindberg (1872: 234) and *P. obtusata* (Taylor 1846: 380) Trevisan (1877: 407) var. *macroloba* (Stephani 1910: 292) Hattori & Zhang (1985: 325). It has been employed as an age constraint in Laenen *et al.* (2014) who estimated median ages of 34.27–47.33 Ma for *Porella,* and in Feldberg *et al.* (2014) who estimated a mean age of 39.65 Ma.

Family: Radulaceae Müll.Frib.

Genus: *Radula* Dumortier (1822: 112)

This subcosmopolitan genus includes ca. 200 extant species (in seven subgenera), two extinct species from Cretaceous Burmese amber, and five extinct species from Cenozoic ambers (e.g., Heinrichs *et al.* 2016b, 2018a, Söderström *et al.* 2016, Kaasalainen *et al.* 2017). The center of diversity is in humid, tropical to warm temperate regions, and the majority of species are epiphytes or epiphylls. Integrative taxonomy based on extensive molecular phylogenetic datasets and morphological studies has extended the knowledge on species delimitations (e.g., Devos *et al.* 2011, Renner *et al.* 2013a, b, Renner 2014, 2015, Patiño *et al.* 2017), but *Radula* remains taxonomically challenging. Species exhibit complex patterns of variation which tend to obscure species boundaries, and morphological homoplasy in critical taxonomic characters, including lobule shape, appears to be common (Renner *et al.* 2013a, Renner 2015). Morphologically similar plants may belong to different main lineages (Devos *et al.* 2011, Renner 2015), a feature that makes confident placement of fossils difficult.

The Cretaceous species provide the oldest ages for subgenera of *Radula*, and *R. cretacea* Bechteler, M.A.M.Renner, Schäf.-Verw. & Heinrichs in Bechteler *et al.* (2017b: 206) has already been employed as constraint (Fig. 10A).

The additional use of the much younger Cenozoic species as constraints would therefore require thorough morphological studies to assign them to corresponding lineages, though this might not be possible with the sterile material. Species from Baltic amber are *R. baltica* Heinrichs, Schäf.-Verw. & M.A.M.Renner in Heinrichs *et al.* (2016b: 158) which is only known from the sterile holotype, the autoecious *R. oblongifolia* Caspary (1887: 4) which also occurs in Bitterfeld amber and is preserved with androecia, gynoecia, and sporophyte (Fig. 10B), as well as *R. sphaerocarpoides* which is also know from several inclusions but only in sterile condition (Fig. 10C). What complicates the assignment of the latter two species is the morphologically heterogenous fossil material. It is possible that these species represent more than two biological entities (Heinrichs *et al.* 2016b). The youngest fossil is *R. intecta* M.A.M.Renner, Schäf.-Verw. & Heinrichs in Kaasalainen *et al.* (2017: 324) from Miocene Dominican amber which is sterile and cannot be assigned to a subgenus with confidence.

The presence of *Radula* in Baltic amber has provided age constraints for Heinrichs *et al.* (2007), Feldberg *et al.* (2014), and Laenen *et al.* (2014). Feldberg *et al.* (2014) estimated a mean age of 119.53 Ma for the crown group and Laenen *et al.* (2014) median ages of 97.34–122.44 Ma. These ages are significantly younger than those of Bechteler *et al.* (2017b) who estimated a mean age of 183.8 Ma with standard substitution rates as calibration and 176.3 Ma by assigning *R. cretacea* to the stem of subgen. *Odontoradula* Yamada (1979: 209).

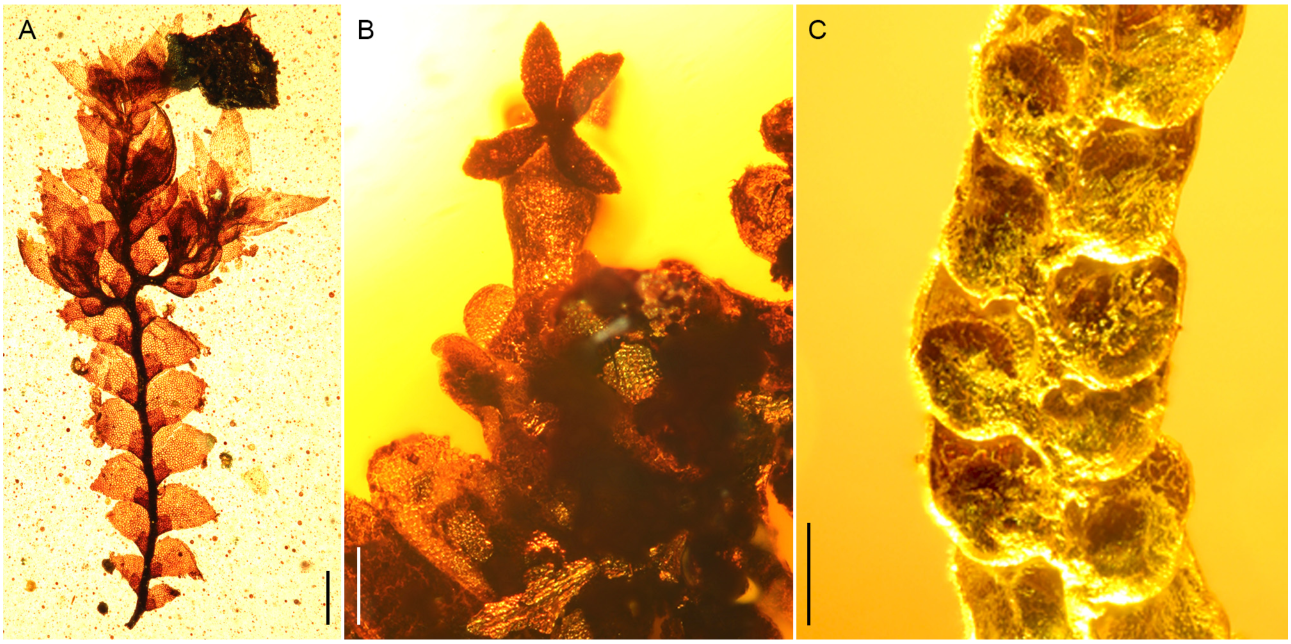

FIGURE 10. Radulaceae. A. *Radula cretacea,* PB22484 (holotype) in ventral view with gynoecia. **B.** *Radula oblongifolia,* MB.Pb.1997/1 from Bitterfeld amber with perianth and capsule. **C.** *Radula sphaerocarpoides,* GRÖHN 5815 from Baltic amber in ventral view. Scale bars: A=500 µm, B, C=200 µm.

Radula subgenus: *Odontoradula*

Radula cretacea; Fig. 10A

Holotype: PB22484.

References: Bechteler *et al.* (2017b), fig. 1; Heinrichs *et al.* (2018a), plate V(1, 2); Feldberg *et al.* (2021), fig. 1H.

Age and stratigraphic level: 99 Ma, late Albian–early Cenomanian (Late Cretaceous), amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar (Burmese amber).

Calibration: Stem of *Radula* subgen. *Odontoradula.*

Justification: The fossil is characterized by spreading lateral leaves with acute to acuminate dorsal lobes and small quadrate to trapeziform lobules as well as gynoecia with two bract pairs terminal on the leading axis and on short branches (Fig. 10A; Bechteler *et al.* 2017b). These characters are in good accordance with the extant representatives of subgen. *Odontoradula* sect. *Acutifoliae* Castle ex Grolle (1970: 666) ser. *Acutifoliae* Yamada (1979: 214). Bechteler *et al.* (2017b) thoroughly evaluated the assignment of the fossil by comparing divergence time estimates obtained by calibrating different nodes of the phylogeny. An assignment within the crown group to sect. *Acutifoliae* ser. *Acutifoliae* led to unrealistically old estimates that exceeded most estimates for land plants (e.g., Magallón *et al.* 2013), whereas an assignment of the fossil to the stem of subgen. *Odontoradula* led to age estimates in good accordance with analyses based on standard substitution rates (Patiño *et al.* 2017) as well as other age estimates for liverworts (Heinrichs *et al.* 2007, Cooper *et al.* 2012, Feldberg *et al.* 2014, Laenen *et al.* 2014) and provides evidence for a late Cretaceous origin of most subgenera and a Paleogene diversification of crown groups.

Radula subgenus: *Amentuloradula* Devos, Renner, Gradstein, Shaw & Vanderpoorten (2011: 1630)

Radula heinrichsii K.Feldberg, Schäf.-Verw., M.A.M.Renner, von Konrat & A.R.Schmidt in Feldberg *et al.* (2021)

Holotype: GZG.BST.22023 (Coll. Müller BuB3683).

Reference: Feldberg *et al.* (2021), figs. 1.I, 7.

Age and stratigraphic level: 99 Ma, late Albian–early Cenomanian (Late Cretaceous), amber mines southwest of the village of Tanai ca. 105 km north of Myitkyina in Kachin State, northern Myanmar (Burmese amber).

Calibration: Possible minimum age for stem of *Radula* subgen. *Amentuloradula.*

Justification: The sterile fossil is characterized by longitudinally inserted ventral lobules and the presence of *Radula*-type microphyllous branches. Among extant species this combination of characters only occurs in the Asian and Australasian subgen. *Amentuloradula*. However, there are also some differences to extant representatives of the subgenus. The microphyllous leaf lobes and lobules are more inflated and widely spaced than is typical of amentulose branches, and their stature relative to the primary shoot is generally smaller than typical microphyllous axes found in extant species (Feldberg *et al.* 2021). In these characteristics they bear some resemblance to the microphyllous/amentulose axes borne by *R. brunnea* Stephani (1910: 232) of subgen *Dactyloradula* Devos, Renner, Gradstein, Shaw & Vanderpoorten (2011: 1630) which represents an ancient lineage sister to all *Radula* species bar the isolated subgen. *Cladoradula* Spruce (1885: 315) (Devos *et al.* 2011). Unlike *R. brunnea* though, *R. heinrichsii* has a longitudinal lobule insertion. The species probably has mammillae on its dorsal leaf surface which would be unusual for subgen. *Amentuloradula*. Mammillose leaf cells on the main shoot are not very common in this subgenus and only occur in *R. ornata* Brown & Pócs (2001: 436) while they are restricted to the amentulose branches in other species. Furthermore, the shape of the leaf lobes is rectangular-reniform instead of rounded and the trigones are small instead of large. These characters are somewhat inconsistent with the circumscription of subgen. *Amentuloradula* (leaves rounded, cells smooth, with large trigones) as given by Devos *et al.* (2011), but this circumscription has been pending revision since Patiño *et al.* (2017) demonstrated that morphologically disparate species such as *R. marginata* Gottsche, Lindenberg & Nees (1845a: 261) and *R. patens* Yamada (1984: 197) also belonged to the subg. *Amentuloradula* lineage. That this somewhat unusual combination of characters occurred in stem-lineage *Radula* species now extinct can therefore not be discounted on present knowledge. This is supported by Patiño *et al.* (2017) who estimated an Eocene age for the crown group of subgen. *Amentuloradula*. The use as age constraint should include a thorough cross evaluation of the fossil assignment as has been done for *R. cretacea* (Bechteler *et al.* 2017b).

Order: Ptilidiales Schljakov

Family: Ptilidiaceae H.Klinggr

Genus: *Ptilidium* Nees (1833b: 95)

A fossil of this genus from Baltic amber was described as the extant *Ptilidium pulcherrimum* (Weber 1778: 150) Vainio (1878: 88) in Grolle & Meister (2004b), but a recent divergence time estimation calibrated with standard substitution rates conflicts with the status of the fossil as an extant species, because the results indicate a Miocene origin of *P.*

pulcherrimum (Heinrichs *et al.* 2015b). Furthermore, the fossil shows significant morphological differences to extant *P. pulcherrimum*, which also supports the assumption that it is an extinct rather than an extant species. Unfortunately, the specimen SMNS-BB2379 seems to be lost and morphological comparisons had to depend on the photos published in Grolle & Meister (2014b, plate 21), therefore Heinrichs *et al.* (2015b) did not describe a new species. The fossil was employed as minimum age constraint in Feldberg *et al.* (2014) who estimated a mean age of 93.75 Ma for the stem of the genus and by Laenen *et al.* (2014) who estimated median ages of 34.5–55.87 Ma for *Ptilidium.* Based on substitution rates Heinrichs *et al.* (2015b) estimated mean ages of 114.15 Ma for the stem and 33.71 Ma for the crown.

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