A Caribbean epiphyte community preserved in Miocene Dominican amber

Ulla Kaasalainen[1], Jochen Heinrichs[2], Matthew A. M. Renner[3],
Lars Hedenäs[4], Alfons Schäfer-Verwimp[5], Gaik Ee Lee[2],
Michael S. Ignatov[6,7], Jouko Rikkinen[8,9] and Alexander R. Schmidt[1*]

[1] Department of Geobiology, University of Göttingen, Goldschmidtstraße 3, D-37077 Göttingen, Germany.
   Email: alexander.schmidt@geo.uni-goettingen.de
[2] Department of Biology and Geobio-Center, University of Munich (LMU), Munich, Germany.
[3] Royal Botanical Garden and Domain Trust, Sydney, Australia.
[4] Department of Botany, Swedish Museum of Natural History, Stockholm, Sweden.
[5] Mittlere Letten 11, Herdwangen-Schönach, Germany.
[6] Tsitsin Main Botanical Garden, Russian Academy of Sciences, Moscow, Russia.
[7] Faculty of Biology, Moscow University, Moscow, Russia.
[8] Department of Biosciences, University of Helsinki, Helsinki, Finland.
[9] Finnish Museum of Natural History, Botany Unit, University of Helsinki, Finland.
*Corresponding author

ABSTRACT: Fossil tree resins preserve a wide range of animals, plants, fungi and micro-organisms in microscopic fidelity. Fossil organisms preserved in an individual piece of amber lived at the same time in Earth history and mostly even in the same habitat, but they were not necessarily parts of the same interacting community. Here, we report on an *in situ* preserved corticolous community from a piece of Miocene Dominican amber which is composed of a lichen, a moss and three species of leafy liverworts. The lichen is assigned to the extant genus *Phyllopsora* (Ramalinaceae, Lecanoromycetes) and is described as *P. magna* Kaasalainen, Rikkinen & A. R. Schmidt sp. nov. The moss, *Aptychellites fossilis* Schäf.-Verw., Hedenäs, Ignatov & Heinrichs gen. & sp. nov., closely resembles the extant genus *Aptychella* of the family Pylaisiadelphaceae. The three leafy liverworts comprise the extinct Lejeuneaceae species *Cheilolejeunea antiqua* (Grolle) Ye & Zhu, 2010 and *Lejeunea miocenica* Heinrichs, Schäf.-Verw., M. A. M. Renner & G. E. Lee sp. nov. and the extinct Radulaceae species *Radula intecta* M. A. M. Renner, Schäf.-Verw. & Heinrichs sp. nov. The presence of five associated extinct cryptogam species, four of which belong to extant genera, further substantiates the notion of a stasis in morphotype diversity, but a certain turnover of species, in the Caribbean since the early Miocene.

KEY WORDS: Corticolous communities, fossils, lichens, liverworts, mosses

Epiphytes grow upon other plants and derive their moisture and nutrients from rain, air, leachates and detritus of the host and other epiphytes, material transported by ants and termites, and excreta of animals, which are effectively distributed by stemflow (Johansson 1989). Epiphytic plants and lichens may comprise a remarkable proportion of the forest flora and biomass, and they are ecologically important in intercepting and retaining atmospheric moisture, providing habitat and a food source for various invertebrates and, in some cases, also contributing fixed nitrogen into the ecosystem (Nash 2008; Hietz 2010; Köhler *et al.* 2010; Leuschner 2010). Vascular plants, such as ferns, bromeliads and orchids, form an important proportion of the epiphytic community (Hietz & Hietz-Seifert 1995; Krömer *et al.* 2005; Hietz 2010); however, non-vascular crypto-gams such as mosses and liverworts can make up more of the photosynthetically active epiphytic biomass in these forests than all the other plant groups put together (Hofstede *et al.* 1993). The overall prominence and species richness of non-vascular epiphytes, including bryophytes and lichens, increase with humidity (Gradstein & Pócs 1989; Hietz 2010). Moist

tropical forests harbour the most diverse epiphytic communities, although epiphytic bryophytes and lichens occur in almost all biomes, interacting together as a functional epiphytic community (Cornejo & Scheidegger 2016).

Dominican amber has preserved a plethora of Miocene species such as arthropods, plants and sometimes also fungi and lichens (reviewed in Penney 2010; Heinrichs *et al.* 2013b, 2015a; Lóriga *et al.* 2014). The mines in the northern, eastern and western parts of the Dominican Republic yield ambers with an estimated age of 15–20 million years (Iturralde-Vinent & MacPhee 1996; Penney 2010). This fossil resin derives from extinct species of the extant leguminous tree genus *Hymenaea* Linnaeus, 1753 (Langenheim 1966; Hueber & Langenheim 1986; Poinar 1991; Poinar & Brown 2002). These trees grew in tropical forests with open areas, and were rich in epiphytes (Grimaldi 1996).

Based on its animal and plant inclusions, the Dominican amber forest has been characterised as a moist tropical forest, which was not remarkably different from the modern Neo-tropical lowland rainforest (Grimaldi 1996; Poinar & Poinar 1999). Three species of lichens, 22 species of liverworts and

29 species of mosses have so far been described from Dominican amber, of which the liverworts clearly represent extinct taxa (Poinar *et al*. 2000; Rikkinen & Poinar 2008; Heinrichs *et al*. 2015a). In addition, the fossil lichens have been described as representatives of extinct species; however, the absence of several important chemical and apothecial characters hinders a reliable differentiation between the fossil and morphologically similar extant species (Poinar *et al*. 2000; Rikkinen & Poinar 2008). It has even been suggested that some moss fossils from Dominican amber represent extant species (Frahm & Newton 2005), but recent analyses strongly suggest that assignments of bryophyte fossils from Cenozoic ambers to extant species should only be conducted if a congruent morphology is present, and if the DNA sequence variation of extant species provides certain likelihood for a species age that is in accordance with the age of the amber (Heinrichs *et al*. 2013b, 2015b; Villarreal & Renner 2014; Váňa *et al*. 2015).

Here, we describe a piece of Dominican amber that provides a window on a Miocene Caribbean epiphyte community. The virtually *in situ* preserved cryptogamic community includes a new species of the extant lichen genus *Phyllopsora* Müller, 1894, a moss that is similar to, but clearly distinguished from, the modern genus *Aptychella* (Brotherus) Herzog, 1916 and, therefore, assigned to the new fossil genus *Aptychellites*; as well as three extinct species of the extant leafy liverwort genera *Cheilolejeunea* (Spruce) Stephani, 1890, *Lejeunea* Libert, 1820 and *Radula* Dumortier, 1822.

The members of this community are distinct from extant Caribbean species, further substantiating the notion of a stasis in morphotype diversity, but a certain turnover of species, in the Caribbean since the early Miocene, as recently suggested by Schneider *et al*. (2015). It is also in line with the hypothesis of Poinar & Poinar (1999) that many of the plants and animals preserved in the Miocene Dominican amber do not have immediate extant descendants.

1. Material and methods

The fossilised epiphytes are preserved in a *c*.3 cm × 2 cm × 0.8 cm-sized piece of Dominican amber which is housed in the amber collection of the American Museum of Natural History in New York (AMNH DR-15-3). The specimen originated from the amber mines in the Cordillera of the Dominican Republic. This amber piece contains five cryptogam species: a lichen, a moss and three leafy liverworts (Fig. 1).

The amber surface was ground and polished manually with a series of wet silicon carbide abrasive papers (grit from FEPA P 600–4000; i.e., 25.8 μm to 5 μm particle size, Struers) to minimise light scattering during the investigation. Portions of the lichen thallus reaching the amber surface were further polished to visualise the thallus section (Fig. 2D). The prepared specimen was placed on a glass microscope slide with a drop of water applied to the upper surface of the amber, and covered with a glass coverslip. The inclusions were examined under a Carl Zeiss Stemi 2000 dissection microscope and a Carl Zeiss Axio Scope A1 compound microscope equipped with Canon 5D digital cameras. In most instances, incident and transmitted light were used simultaneously. Oblique incident light was obtained using a goose-neck light guide of a Carl Zeiss CL 1500 Eco cold light source. All presented illustrations are digitally stacked photomicrographic composites of up to 110 individual focal planes, obtained by using the software package HeliconFocus 5.0.

2. Systematic palaeontology

2.1. Lichens

Phylum Ascomycota Cavalier-Smith, 1998
Class Lecanoromycetes Eriksson & Winka, 1997
Order Lecanorales Nannfeldt, 1932
Family Ramalinaceae Agardh, 1821
Genus *Phyllopsora* Müller, 1894

Phyllopsora magna Kaasalainen, Rikkinen &
A. R. Schmidt, sp. nov.
(Fig. 2)

Holotype. American Museum of Natural History, New York, USA, AMNH DR-15-3; MycoBank number MB 818898. The large thallus portion shown in Fig. 2A (middle) represents the holotype.

Type locality. Dominican Republic, Santiago area.

Age and stratigraphic position. Early Miocene, about 15 to 20 million years old.

Etymology. Latin for large. The species epithet refers to the exceptionally large size of the thallus lobes of this *Phyllopsora* species.

Diagnosis. Lobes subfoliose, large, up to 3.1 mm wide; prothallus imperceptible or lacking; upper cortex poorly developed, <5 μm thick; lower side possessing a pseudocortex; isidia marginal, cylindrical to clavate.

Description. Prothallus not visible. Thallus squamulose; with foliose-like lobes but without the lower cortex (Figs 1, 2A, B). Squamules ascending, large, up to 3.1 mm wide and 3.8 mm long, and approximately 80 μm thick (Fig. 2A, B, D). Shape of the squamules varying from wide flabellate to elongate, with undulating to slightly lobate margins (Fig. 2A–C). Upper surface glabrous and brown, paling towards the margins (Fig. 2A). Cortex very thin (2–4 μm; Fig. 2D). Medulla composed of pale hyphae (Fig. 2D). Lower surface with a pseudocortex, formed by white (occasionally with a hue of rusty-brown), loosely and mainly longitudinally organised hyphae (Fig. 2B, D). Isidia elongate, cylindrical to clavate, developing horizontally from the margins of the squamules (Fig. 2C). Ascomata or pycnidia not detected.

2.2. Liverworts

Phylum Marchantiophyta Stotler & Crandall-Stotler, 2000
Class Jungermanniopsida Stotler & Crandall-Stotler, 1977
Order Porellales Schljakov, 1972
Family Lejeuneaceae Cavers, 1910
Genus *Cheilolejeunea* (Spruce) Stephani, 1890
Cheilolejeunea antiqua (Grolle) Ye & Zhu, 2010
(Fig. 1C)

Description. Sterile, unbranched shoot, *c*.1.6 mm long, 650–700 μm wide. Stem straight, *c*.30–50 μm in diameter, with a *c*.3 cells-wide ventral merophyte; cortical cells rectangular, walls thin- to slightly thick-walled. Rhizoids in bundles at base of underleaves. Leaves remote to weakly imbricate, insertion J-shaped; lobes longer than wide, slightly falcate, orbicular to oblong-ovate, apex broadly rounded, margins entire. Median leaf cells +/– regular, 15–20 μm × 18–27 μm, thin-walled to slightly thick-walled, with weak trigones, occasionally weak intermediate thickenings present; cells towards leaf margins smaller. Cuticle smooth. Lobules well-developed, inflated, ovoid
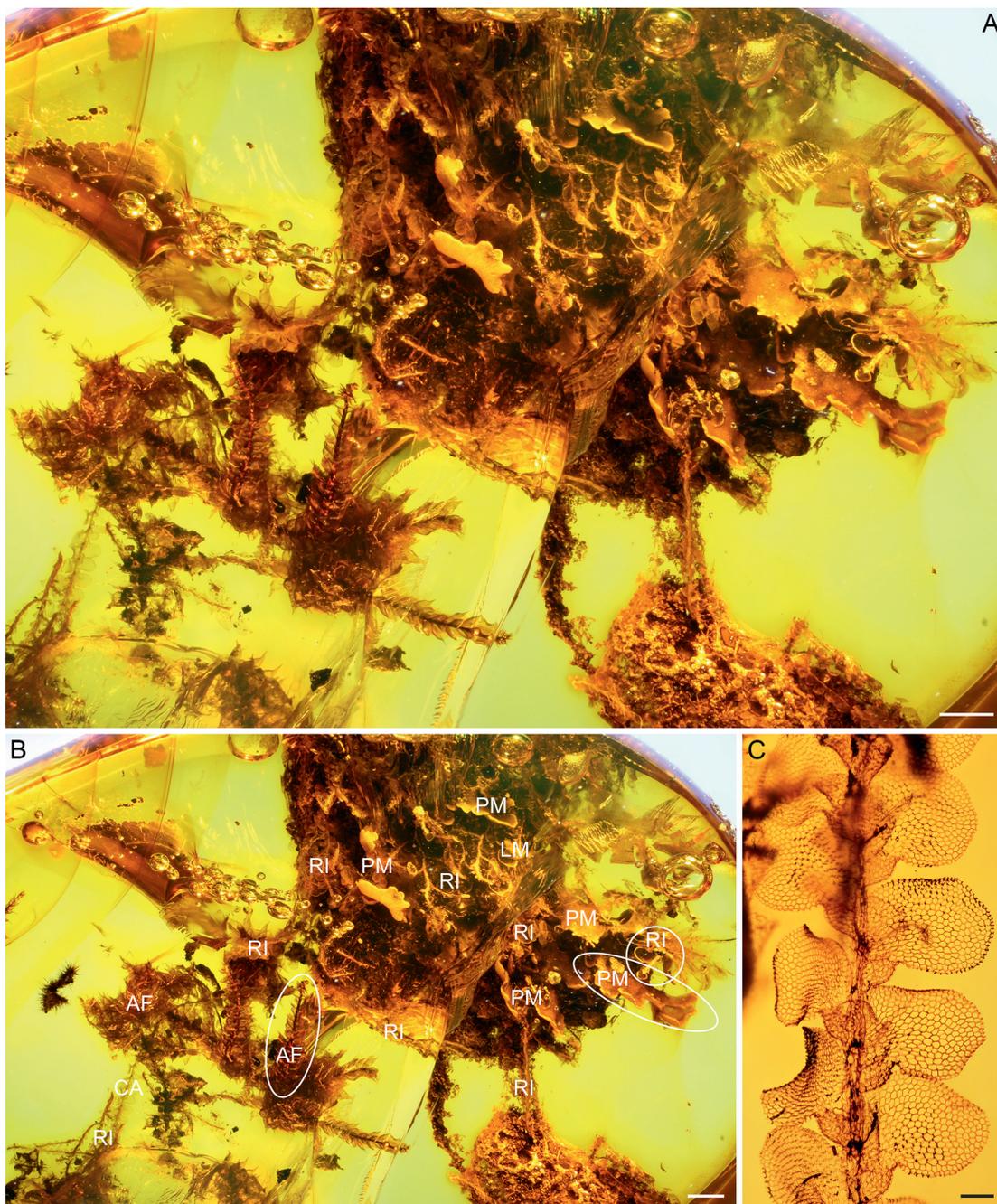
Figure 1 Cryptogamic community preserved in Dominican amber specimen AMNH DR-15-3: (A) overview of the inclusions; (B) overview with inclusions indicated: AF = *Aptychellites fossilis* (holotype circled); CA = *Cheilolejeunea antiqua*; LM = *Lejeunea miocenica* (holotype only visible from the opposite side of the amber piece); PM = *Phyllopsora magna* (holotype circled); RI = *Radula intecta* (holotype circled); (C) *Cheilolejeunea antiqua*. Scale bars = 1 mm (A, B); 100 µm (C).

to ovoid-triangular, *c*.2/5–1/3 of leaf length, free margin often +/− straight, with a short apical tooth. Underleaves [poorly preserved and often somewhat damaged] remote, entire (un-lobed), broadly orbicular to orbicular reniform, *c*.150–200 µm wide, *c*.3.5–4.5 times as wide as shoot.

Genus *Lejeunea* Libert, 1820

Lejeunea miocenica Heinrichs, Schäf.-Verw., M. A. M. Renner & G. E. Lee sp. nov.
(Fig. 3)

Holotype. American Museum of Natural History, New York, USA, AMNH DR-15-3. The gametophyte fragment shown in Figure 3A (left), B and D represents the holotype.

Type locality. Dominican Republic, Santiago area.

Age and stratigraphic position. Early Miocene, about 15 to 20 million years old.

Etymology. The species epithet refers to the Miocene age of the fossil.

Diagnosis. Gametophytes with two cells-wide ventral merophytes, complicate bilobed, incubously inserted leaves with (triangularly) ovate dorsal lobes with obtuse to apiculate apices, a papillose cuticle and well developed ventral lobules, as well as bifid underleaves with often blunt lobes and without lateral appendages.

Description. Sterile shoots up to *c*.2.5 mm long, 340–490 µm wide. Stems straight, ±25–40 µm wide, with a two cells-wide ventral merophyte; cortical cells rectangular. Leaves distant to
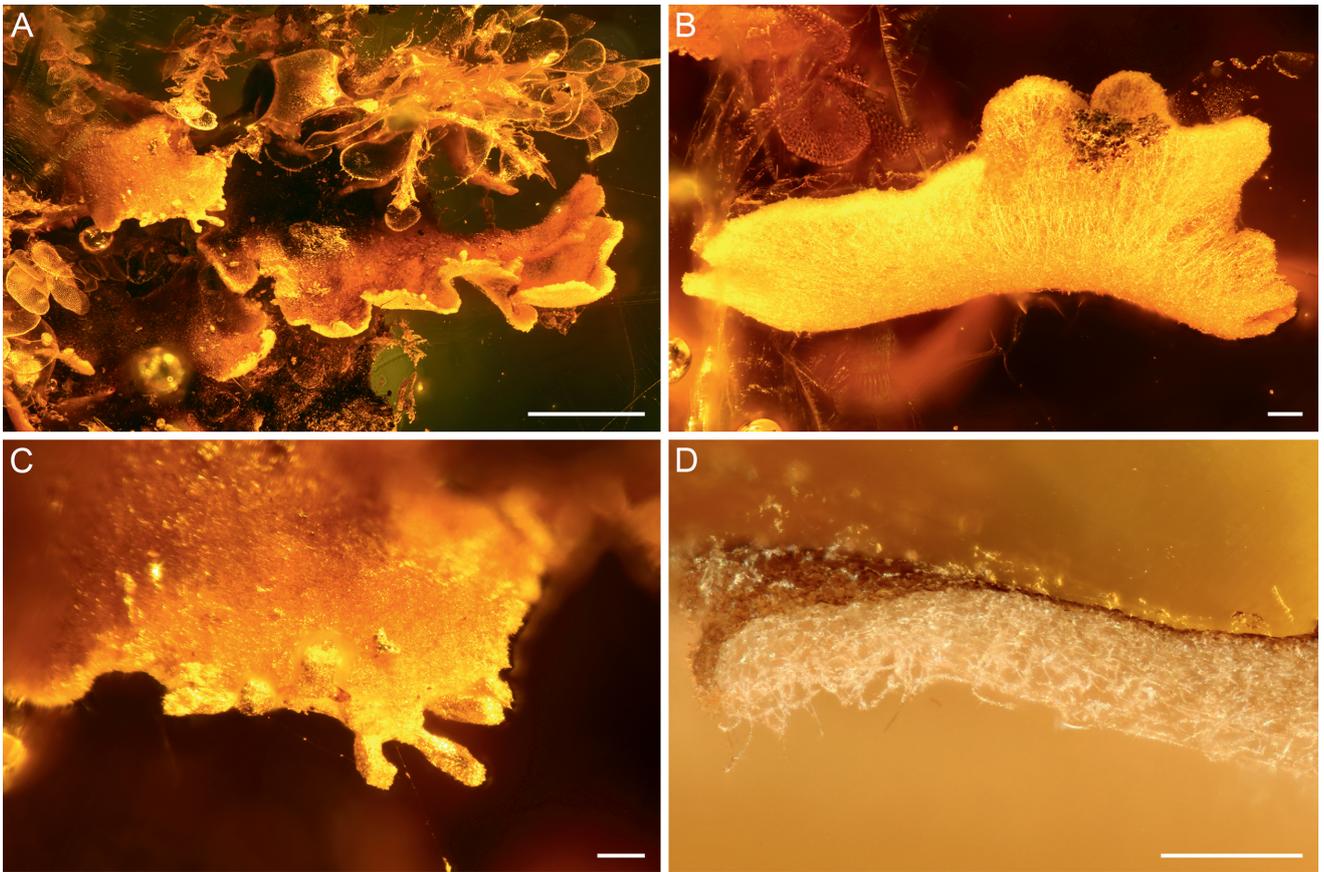
Figure 2 *Phyllopsora magna* sp. nov. in Dominican amber (AMNH DR-15-3): (A) portion of thallus with fabellate to elongate ascending squamules. The large thallus portion represents the holotype (upper half of image shows shoot systems of *Radula intecta*); (B) ascending squamule tip revealing the pseudocortex on the lower side; (C) prominent isidia developing from the tips of the squamules; (D) cross-sections of the thallus showing the thin cortex, medulla and loose pseudocortical hyphae on the lower side. Scale bars = 1 mm (A); 100 μm (B–D).

contiguous, widely to obliquely spreading. Lobes variable in shape, ovate to triangularly ovate, apex obtuse to subacute to apiculate; margin entire to somewhat crenate. Median leaf cells regular, sometimes +/− irregular, *c.*15–25 μm × 20–25 μm, thin-walled, with weak trigones and intermediate thickenings, marginal cells quadrate to rectangular, 10–15 × 10–27 μm. Cuticle finely papillose. Lobules well-developed, *c.*2/5 (−1/2) of leaf length, rounded-rectangular to asymmetrically triangular, somewhat inflated, free margin often +/− straight, involute, apical tooth hidden or sometimes seen *in situ*. Underleaves distant, appressed to stem, *c.*60–100 μm long, 60–95 μm wide, rounded, *c.*1.7–2.5 × the stem width, margins entire, 30–50 % bifid, sinus V-shaped, lobes erect, narrowly obtuse to (sub-)acute, (3–)4–5 cells wide at the base and 1–2 cells wide at the apex, no rhizoids seen. Vegetative distribution possibly by caducous branches. Androecia and gynoecia unknown.

Remarks. Several isolated fragments which are considerably smaller than the main shoots may represent detached branches. These fragments have more remotely inserted leaves, reduced lobules and underleaf lobes that are only 1–2 cells wide at the base.

Family Radulaceae Müller, 1909
Genus *Radula* Dumortier, 1822

Radula intecta M. A. M. Renner, Schäf.-Verw. &
Heinrichs, sp. nov.
(Fig. 4)

Holotype. American Museum of Natural History, New York, USA, AMNH DR-15-3. The gametophyte fragment shown in Figure 4D represents the holotype.

Type locality. Dominican Republic, Santiago area.

Age and stratigraphic position. Early Miocene, about 15 to 20 million years old.

Etymology. Latin for uncovered, exposed, naked. The species epithet refers to the frequently caducous leaf lobes which are often detached in the fossil.

Diagnosis. Gametophytes with incubously inserted, complicate-bilobed, smooth, broadly elliptic leaves with frequently caducous dorsal lobes having ciliate marginal outgrowths, and subquadrate, small ventral lobules; underleaves completely lacking.

Description. Plants sterile, stems 80–120 μm in diameter, indistinctly pinnately branched, branching exclusively of *Radula*-type, secondary shoots of smaller stature than primary shoots. Leaves imbricate, slightly obliquely patent, broadly elliptic with rounded apex, those of primary shoots *c.*650–900 μm long and 340–580 μm wide, margins entire, interior of dorsal margin ampliate but not auriculate, extending over the stem surface in dorsal view and completely obscuring the stem, frequently caducous and older stem sectors frequently denuded of leaf lobes; those that remain attached sometimes producing rhizoids from leaf lobe marginal cells. Keel straight to weakly convex, at an angle of 40–60° to the stem, junction between keel and leaf lobe flush, at that point keel turns to 45° at the keel-lobe-junction. Postical lobe margin straight, otherwise continuously curved. Leaves of secondary shoots possibly rotund, completely caducous, dislocating as a whole along a curved to L-shaped line from top of stem insertion to lobe-lobule junction (two putatively mature lobes from secondary shoots seen). Lobule width 120–160 μm, length 160–180 μm, subquadrate, exterior margin inclined towards stem straight, apex obtuse, antical margin straight to slightly concave, carinal
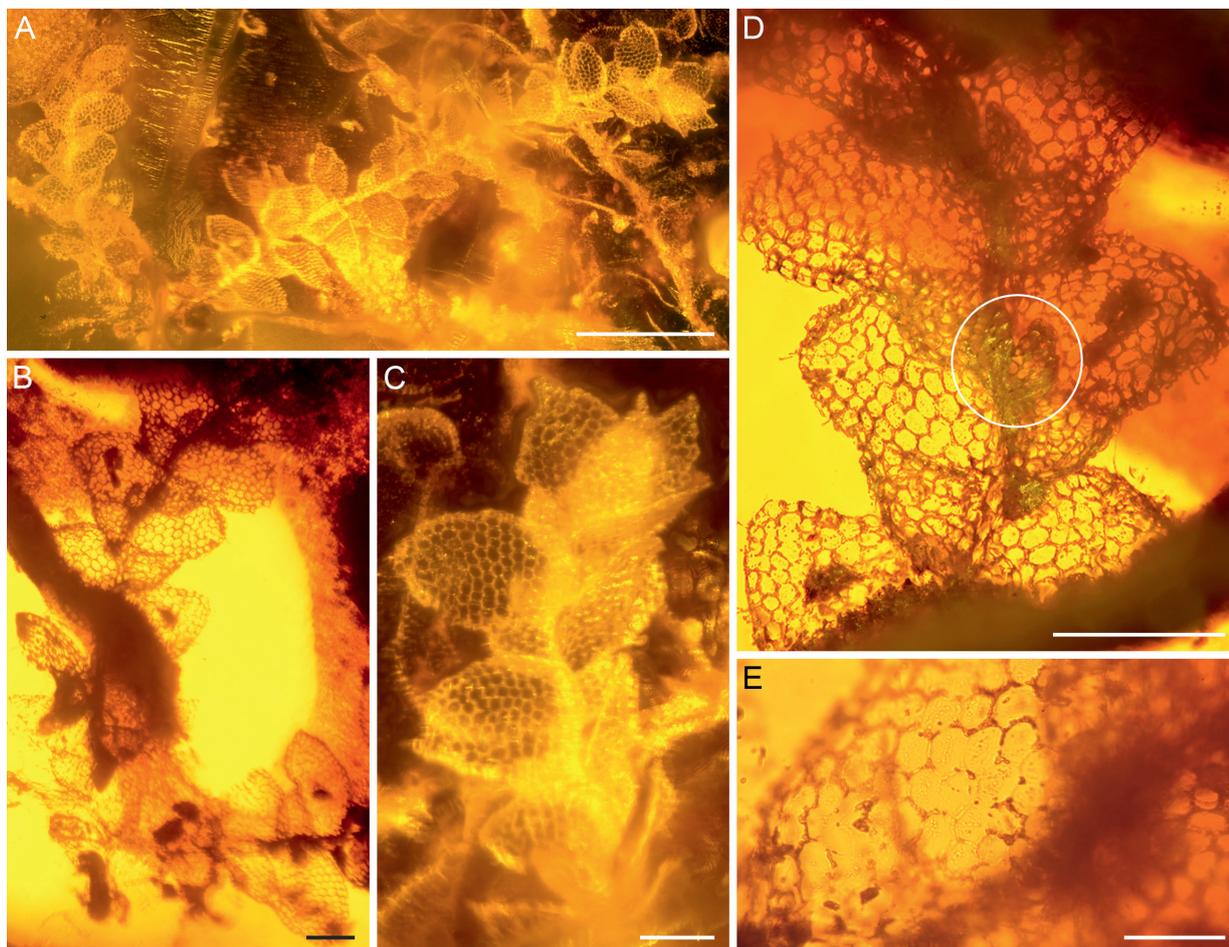
Figure 3 *Lejeunea miocenica* sp. nov. in Dominican amber (AMNH DR-15-3): (A–C) gametophytes in dorsal view. The gametophyte fragment shown in (A) (left), (B) and (D) represents the holotype; (D) holotype in ventral view, one underleaf circled; (E) close-up of the ventral leaf surface of the holotype, showing asperulate cuticle. Scale bars = 500 μm (A); 100 μm (B–D); 50 μm (E).

region indistinctly inflated along keel, insertion longitudinal. Leaf surface smooth, cells isodiametric to slightly elongate, not particularly regular in shape, 15–25 μm in diameter, towards margin quadrate to rectangular, 7–10 μm × 10–30 μm, thin-walled, toward leaf margin continuously thickened except some exterior walls, trigones small, triangular.

2.3. Mosses

Phylum Bryophyta Schimper, 1879
Class Bryopsida Pax, 1900
Order Hypnales W. R. Buck & Vitt, 1986
Family Pylaisiadelphaceae Goffinet & Buck, 2004

Aptychellites fossilis Schäf.-Verw., Hedenäs, Ignatov & Heinrichs gen. & sp. nov.
(Fig. 5)

Holotype. American Museum of Natural History, New York, USA, AMNH DR-15-3. The plant shown in Figure 5C represents the holotype.

Type locality. Dominican Republic, Santiago area.

Age and stratigraphic position. Early Miocene, about 15 to 20 million years old.

Etymology. The genus name points to the similarities of the fossil to the extant genus *Aptychella*. The species epithet emphasises the presence of an extinct taxon.

Diagnosis. Gametophytes with denticulate, spirally inserted, acute, concave leaves without or with a very short costa, prosenchymatous leaf cells and groups of alar cells, and apiculate clusters of filamentous, uniseriate gemmae.

Description. At least eight branches or secondary stems with branches present. Stems ca 50–80 μm in diameter, contrastingly darker than leaves, glossy, well visible between leaves, robust, without hyalodermis, fasciculately branched and without pinnate branching in the subapical 5 mm parts of stems. Leaves spirally arranged, *c*.20 per 1 mm of stem, erect to spreading on the larger gametophyte portions, patent on the weaker branch portions and towards the attenuate branch ends. Leaves mostly ovate, sometimes obovate-oblong and widest shortly below the constriction to acumen, gradually tapered to the base, above suddenly narrowed to distinct set-off acumen, strongly concave. Largest leaves *c*.1 mm long (acumen 0.2 mm) and 0.4 mm wide. Alar region not auriculate. At least branch leaves not decurrent. Costa not visible; i.e., very short or absent. Leaf margin serrate in acumen and above the widest level of the leaf, serrulate to subentire below, plane. Median leaf lamina cells narrowly linear, incrassate or at least slightly so and smooth, cells in acumen shorter and wider, alar cells (few seen in one leaf) rectangular or shortly rectangular, inflated and incrassate. Leaf lamina cells in central portions of largest leaves *c*.38–54 μm x 4–5 μm or longer, towards leaf apex becoming shorter and often only 15–25 μm long. Apical clusters of filamentous, up to at least 16 cells-long uniseriate gemmae frequently present. Gemmae originating from a 'basal' cell that is *c*. twice as long as the gemmae
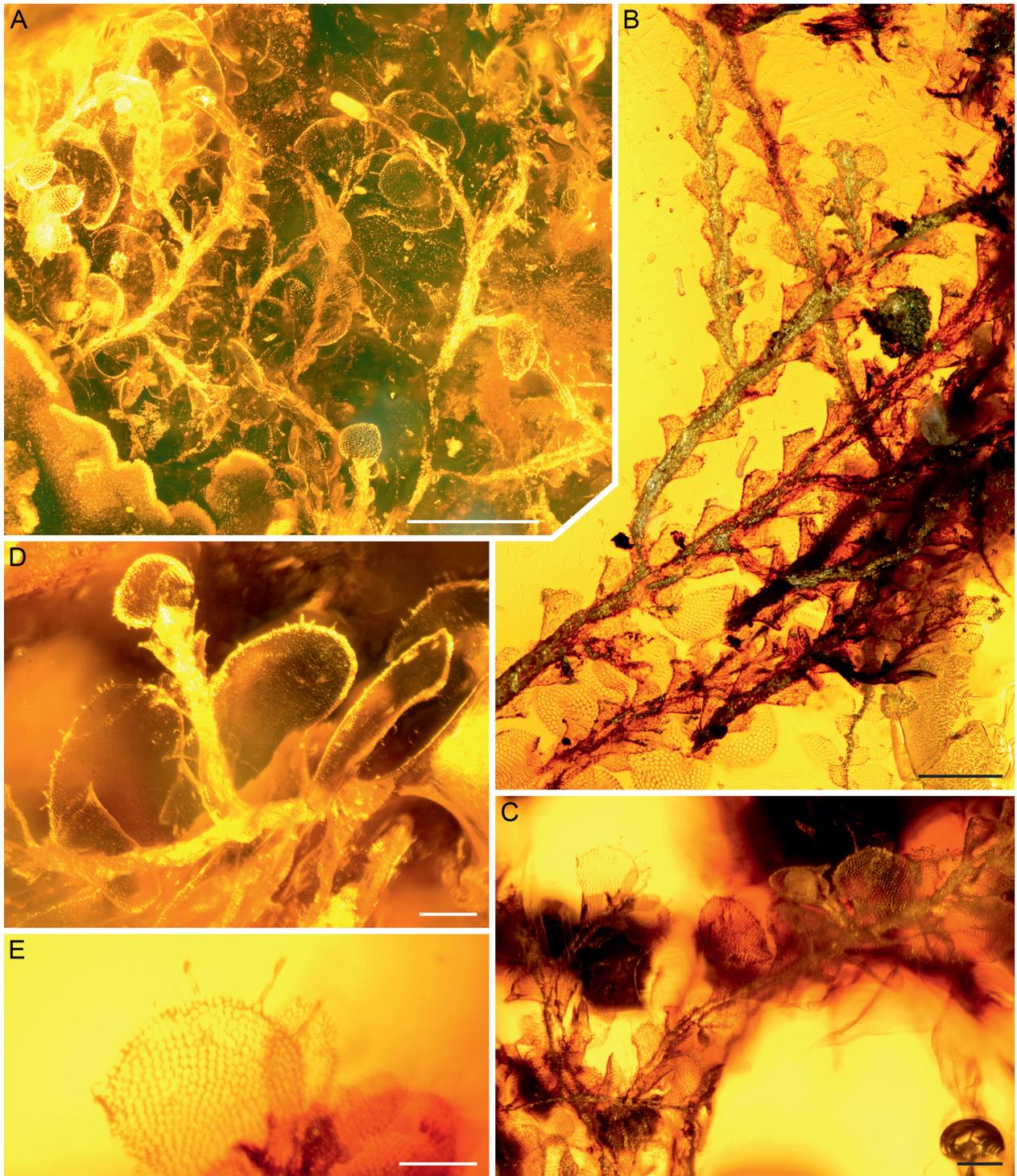
Figure 4 *Radula intecta* sp. nov. in Dominican amber (AMNH DR-15-3): (A) shoot system in ventral view. The bright shoot fragment at the left margin of the image belongs to *Lejeunea miocenica*; (B) shoot system with detached lobes. The plant fragments with complete leaves in the lowermost portion of the image belong to *Cheilolejeunea antiqua* and *Lejeunea miocenica*; (C–E) portions of shoots with partly detached leaf lobes. Some lobe margins with ciliate outgrowths. The gametophyte fragment shown in (D) represents the holotype. Scale bars = 500 µm (A); 200 µm (B–D); 100 µm (E).

cells and narrows towards its insertion on the stem. Cells of gemmae rectangular, shortly rectangular or (rarely) quadrate, *c*.20–25 µm in diameter, towards apical region sometimes somewhat swollen, then with a diameter of up to *c*.40 µm. Leaves becoming smaller towards gemmae clusters.

3. Discussion

The five epiphyte species preserved in specimen AMNH-DR-15-3 were part of a corticolous community of lichens, mosses and liverworts in a Miocene Caribbean forest ecosystem. Previous records of cryptogams from Dominican amber included an exceptional finding of seven species of bryophytes in a single piece of amber (Frahm & Newton 2005), providing evidence that the bark of the resinous *Hymenaea* trees was covered by diverse cryptogamic communities. However, it is still unclear if the *Hymenaea* bark was generally covered by cryptogamic communities or if only some parts of the tree, or single individuals, hosted cryptogams.
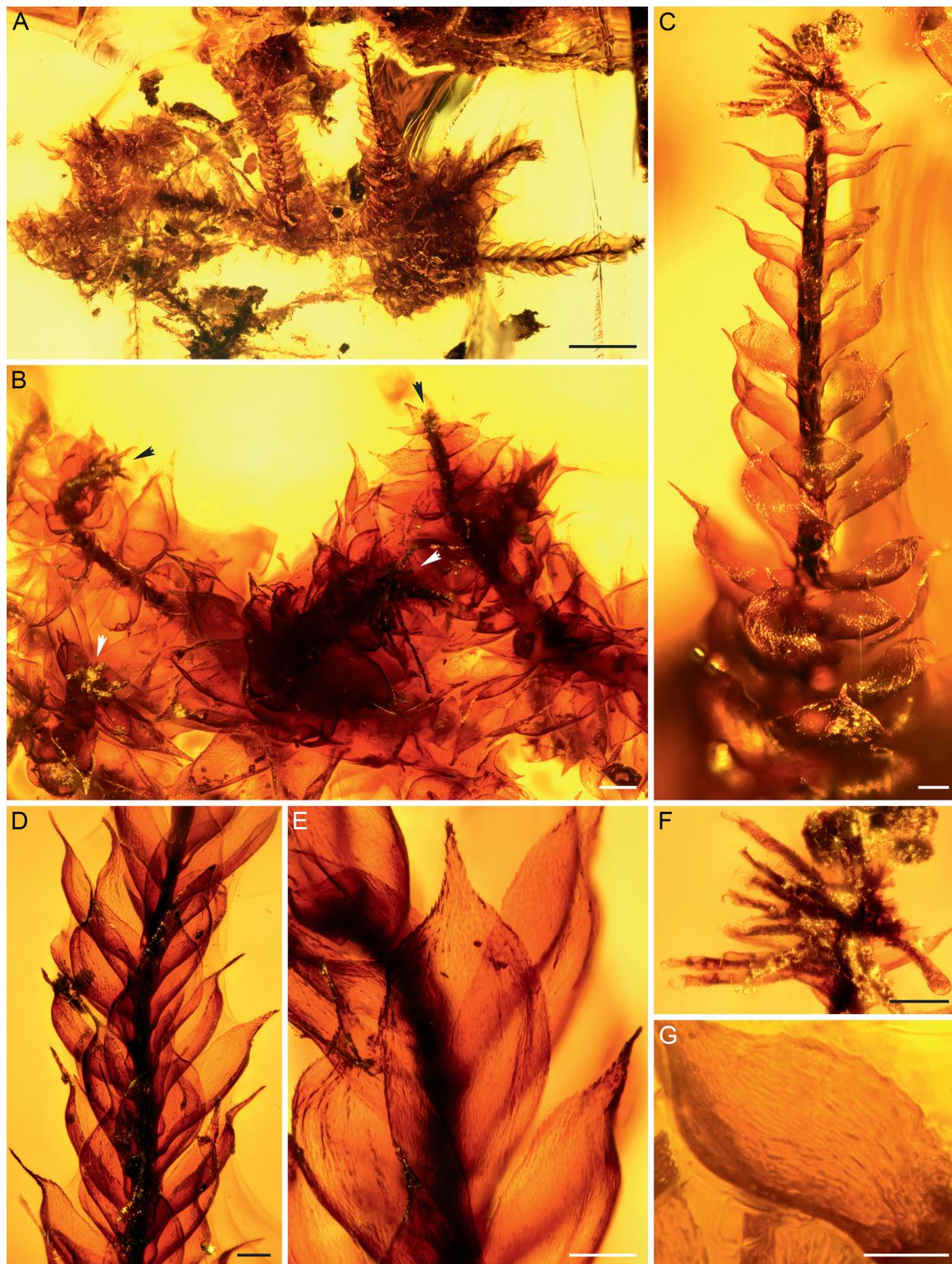
Figure 5 *Aptychellites fossilis* gen. et sp. nov. in Dominican amber (AMNH DR-15-3): (A) overview; (B) portion of a shoot system showing apical gemmae clusters (arrows); (C) holotype with apical gemmae cluster. The inclusions above the gemmae clusters are detritus and do not belong to the moss; (D, E) portions of leafy shoots; (F) apical gemmae cluster; (G) leaf in lateral view with group of alar cells. Scale bars = 1 mm (A); 100 μm (B–F); 50 μm (G).

3.1. Systematic assignment of the cryptogamic inclusions

3.1.1. Lichens. The fossil lichen has a squamulose thallus consisting of relatively wide lobes without a lower cortex. Similar structures are produced by many lichen genera, including *Phyllopsora* and *Cladonia* Browne, 1756, which are both likely candidates for preservation in amber. The fragile habit and very thin upper cortex of the thallus lobes more resemble those in some extant *Phyllopsora* species (e.g., Timdal 2008, 2011) than in the primary squamules of *Cladonia* species, which tend to be more robust and have a thick upper cortex (Osyczka & Rola 2013). Additionally, the ventral pseudocortex formed by longitudinally organised hyphae, together with clearly corticated, clavate marginal isidia, indicate that the fossil lichen belongs to *Phyllopsora*. The genus includes more than 100 extant, crustose to squamulose species, of which 34 are present in the West Indies (Timdal 2011). In addition, one fossil species, *Phyllopsora dominicanus* Rikkinen (Rikkinen & Poinar 2008), has been previously described from Dominican amber (Rikkinen & Poinar 2008).

The most distinctive feature of *Phyllopsora magna* are the large squamules, which give it an almost foliose appearance. Most extant *Phyllopsora* species and the fossil *P. dominicanus*, have squamules less than one millimetre wide (Swinscow & Krog 1981; Brako 1991; Timdal & Krog 2001; Upreti *et al.* 2003; Elix 2006; Rikkinen & Poinar 2008; Mishra *et al.* 2011; Timdal 2008, 2011; McCarthy 2016). Some of the larger species may have lobes up to two millimetres wide (Brako 1991; Timdal 2008, 2011), which are still notably smaller than the over 3 mm-wide lobes observed in *Phyllopsora magna*.

The fossil lichen does not seem to have had a prothallus, a characteristic structure of many extant *Phyllopsora* species. However, the base of the thallus is covered by bryophytes and thus not clearly visible. Some rusty hued hyphae occur among the otherwise white pseudocortex hyphae, possibly indicating the presence of a poorly developed prothallus, which is reddish brown in the extant taxa. However, several extant, especially Neotropical, *Phyllopsora* species also do not seem to produce prothalli (Timdal 2008, 2011). The structure of the upper cortex is an important feature used to discriminate between extant *Phyllopsora* species (Swinscow & Krog 1981). The cortex structures of most taxa can be classified into one of two main types, but intermediate forms are also common. In one type, the cortex hyphae are highly gelatinised and their lumina are reduced to narrow thread-like channels resembling a network; whilst in the other type the hyphae are much less gelatinised and the cortex is formed by isodiametric cells (Swinscow & Krog 1981). The thickness of the cortex may vary from five to 60 micrometres and seems to be related to the size of the squamules (Swinscow & Krog 1981; Brako 1991). The cortex of *Phyllopsora magna* is very thin and not assignable to the main structure types. Similar, poorly-developed upper cortices are known from some extant Neotropical *Phyllopsora* species (Timdal 2008, 2011).

The combination of characters observed in *Phyllopsora magna* is unique and the species thus seems to represent an extinct, fossil taxon. The previously known *Phyllopsora dominicanus* better resembles extant species and cannot be confidently separated from all of them on morphological grounds (Rikkinen & Poinar 2008). Two fossil species of *Parmelia* Acharius, 1803, previously described from Dominican amber, were only tentatively placed in that genus, and may well represent other parmelioid genera (Poinar *et al.* 2000).

3.1.2. Liverworts. All observed liverworts belong to Porellales, a largely epiphytic lineage of leafy liverworts characterised by exclusively lateral branching, incubous foliation, rhizoids in bundles, frequent occurrence of complicate bi- or trilobed leaves, endosporous protonemata and a complete lack of mycorrhiza-like mutualisms (Heinrichs *et al.* 2005; Feldberg *et al.* 2014). With more than 1000 species, Lejeuneaceae is the most speciose family of the Porellales (He & Zhu 2011). Their centres of diversity are the humid tropics, and especially tropical lowland forests, where Lejeuneaceae can account for 70 % of the species diversity of liverworts (Cornelissen & Ter Steege 1989; Gradstein 2006). Some 70 genera of Lejeuneaceae are currently accepted (Bechteler *et al.* 2016; Wang *et al.* 2016) of which *Lejeunea* is one of the largest, including some 300 extant species (Lee 2013). *Lejeunea* is a hyper-diverse genus which differs from the closely related genera *Microlejeunea* (Spruce) Stephani, 1898 and *Harpalejeunea* (Spruce) Schiffner, 1893 by a lack of ocelli (Dong *et al.* 2013); its morphology-based supra-specific classification is not supported by molecular data (Heinrichs *et al.* 2013a). The fossil, however, resembles members of the polyphyletic *Lejeunea* subgenus *Crossotolejeunea* Spruce, 1884 in the circumscription of Reiner-Drehwald & Goda (2000), in having bifid underleaves with blunt lobes and variably shaped leaf lobes with obtuse to acute apices, an asperulate cuticle and sometimes crenate margins. *Lejeunea* is a Cenozoic genus with several species lineages dating back to the early Miocene (Heinrichs *et al.* 2016). Several *Crossotolejeunea* species occur in modern Caribbean rainforests; however, taxonomically relevant characters of extant species, such as perianth shape, oil body type and branching pattern, are not preserved in the fossil. We therefore abstain from assigning the fossil to an extant species and describe it as a fossil taxon.

Another sterile *Lejeunea* fossil from Dominican amber was identified to genus level only (Reiner-Drehwald *et al.* 2012). It differs from *Lejeunea miocenica* in having entire lobe margins with rounded apices. Since the Mexican amber fossil *Lejeunea palaeomexicana* Grolle, 1984 has recently been transferred to *Ceratolejeunea* (Spruce) Jack & Stephani, 1892 (Lee *et al.* 2015), only two fossils of *Lejeunea* are currently known.

Another sterile inclusion inside specimen AMNH DR-15-3 matches the morphology of the Dominican amber species *Cheilolejeunea antiqua,* although the leaf lobules are somewhat smaller than in the original description (Grolle 1983). This species has already been observed several times and seems to be a rather common element of the liverwort flora of the Dominican amber forest.

Lejeuneaceae are the most diverse family in Dominican amber; however, other Porellales families have also been reported, namely representatives of the monogeneric families Frullaniaceae and Radulaceae (Heinrichs *et al.* 2015a). The genus *Radula* includes at least 200 extant species (Yamada 2003) and has an almost world-wide distribution, with the majority of species occurring in humid, tropical or warm-temperate regions (Devos *et al.* 2011a). Most species are obligate or facultative epiphytes on bark or leaves, and they exist in a variety of habitats varying from rainforests to alpine tundra (Devos *et al.* 2011a). The genus can easily be recognised by the total lack of underleaves and the presence of rhizoid bundles on the lobule surface rather than on the stem. The caducous leaves which produce marginal rhizoids, the distinct trigones of the leaf cell walls and the pinnately branched dimorphic shoot systems of *Radula intecta* are consistent with the extant *Radula* subgenus *Radula* (Devos *et al.* 2011b), but not necessarily diagnostic of that lineage. In particular, the apparent absence of ornamentation from the leaf-cell surfaces suggests that *R. intecta* may not belong to the subgenus *Radula*, whose crown-group species mostly have ornamented surfaces (Renner 2014). Species with dimorphic, pinnately branched shoot systems, caducous leaves and smooth cell surfaces also occur in the subgenera *Odontoradula* Yamada, 1979 and *Volutoradula*

Devos et al., 2011b; thus it is not possible to assign the fossil to a subgenus with confidence.

Three fossil Radula species are currently accepted, the Paleogene Baltic and Bitterfeld amber taxa Radula sphaerocarpoides Grolle, 1980 and Radula oblongifolia Caspary, 1887 (Grolle & Meister 2004), and the Miocene Dominican amber species Radula steerei Grolle (Grolle 1987). Radula intecta differs from these species in the frequent presence of caducous leaf lobes.

Among extant Radula species, Radula intecta resembles the Neotropical Radula cubensis Yamada (Yamada 1983) and Radula schaefer-verwimpii Yamada (Yamada 1990) in having caducous leaves; however, the leaf margins of both extant species lack the ciliate outgrowths of R. intecta. Such cilia are present in some forms of the polyphyletic Radula javanica Gottsche in Gottsche et al., 1845 (Renner 2014); however, this extant species has a puncticulate leaf lobe cuticle and is more robust than R. intecta. The combination of subquadrate lobules whose lamina is plane (not reflexed) and its exterior margin straight and inclined toward the stem, the dislocation of nearly all leaves on both primary and secondary shoots, and the production of rhizoids from leaf lobe marginal cells, is distinctive for the new fossil.

3.1.3. Mosses. Several pleurocarpous families of mosses include species with filamentous, uniseriate gemmae. These gemmae usually cluster in leaf axils and/or on specialised brood branches; e.g., in Crossomitrium Müller, 1874 (Pilotrichaceae); Jaegerina Müller, 1876 (Pterobryaceae); Clastobryopsis Fleischer, 1923 (Pylaisiadelphaceae); Pylaisiadelpha Cardot, 1912 (Pylaisiadelphaceae) (Buck 1998; Goffinet & Buck 2004; Tixier 1977); Leptotheca Schwaegrichen, 1823–1827 (Rhizogoniaceae) (Churchill & Buck 1982); and Gammiella Brotherus, 1908 (Pylaisiadelphaceae) (Tan & Jia 1999).

Amongst pleurocarpous mosses, terminal clusters of filamentous gemmae are typical for the Central American species Brymela crosbyi (Allen) Allen, 2010 and the Pylaisiadelphaceae genus Aptychella. Brymela crosbyi, however, has lanceolate to elongate-triangular, long acuminate, strongly plicate leaves and faint costae that extend more or less two-thirds the leaf length (Allen 2010) and is thus not closely related to the moss fossil. Aptychella occurs with some nine extant species in Asia and includes a single extant Neotropical species, Aptychella proligera (Brotherus) Herzog, 1916. The latter species may have Asian ancestors and has possibly colonised the Neotropics in rather recent times (Akiyama et al. 2015). It is a montane rather than a lowland species and occurs from Mexico southwards to Bolivia, in Brazil and in the Caribbean (Buck 1998). Although the numerous gemmae clusters of the Dominican amber fossil suggest a relationship with Aptychella, the strongly concave and rather densely denticulate, spreading leaves are untypical for this genus (Tixier 1969). The concave, denticulate leaves are more indicative of Wijkia Crum, 1971 (Pylaisiadelphaceae); however, this genus has gemmae on flagellate branches. A single extant species (Wijkia flagellifera (Brotherus) Crum, 1971) occurs in montane forests of the Dominican Republic.

As a consequence of the somewhat deviant morphology of the fossil and extant taxa, we prefer to place the fossil in a new genus, Aptychellites, and name it A. fossilis. This taxon may have also been observed by Frahm (1993) in the Dominican amber collection of the Naturkundemuseum Stuttgart; however, Frahm identified it as "Clastobryum spec." Beside the terminal clusters of gemmae, we observed a single gemma in the axil of a leaf; however, we felt unable to decide if this gemma originated at the leaf base or, in fact, represents a detached gemma from a terminal cluster. We were also not able to decide on the number of individuals preserved in the piece of amber, since it is difficult to see if some of those that appear connected are, in fact, separate pieces.

3.2. Palaeoecology

The taxonomic diversity of organisms and the habit of the bryophytes preserved in specimen AMNH DR-15-3 closely resemble extant epiphytic communities living on trunks and branches in lowland to submontane and relatively humid Caribbean tropical forests. Extant Phyllopsora species grow primarily on bark in humid forests of the tropics and subtropics, but sometimes also on bryophytes (Swinscow & Krog 1981; Brako 1991; Timdal & Krog 2001; Mishra et al. 2011; Timdal 2011). The poorly developed upper cortex and the relatively large, ascending lobes without proper lower cortex enable efficient water evaporation and suggest a moist and shaded environmental preference. Coexistence with the moisture-binding bryophytes might have facilitated the maintenance of the favourable microclimatic conditions. Pleurocarpous mosses and Porellalean liverworts are known to include numerous epiphytes and are common elements of the Dominican amber forest (Frahm & Newton 2005; Heinrichs et al. 2013b, 2015a). Many of these species are exposed to direct sunlight and thus need to cope with periodical dehydration. The water lobules and sacs in Frullaniaceae, Lejeuneaceae and Radulaceae have been interpreted as adaptations to a drier environment (Cornelissen & Ter Steege 1989; Kürschner et al. 1999; Acebey et al. 2003) and may assist the plants in surviving daily periods of desiccation. It is considered that the preserved cryptogam community once grew on the bark of a Hymenaea tree in a rather open environment. However, we cannot exclude an occurrence in a dense forest; though in this case the cryptogamic community was likely situated in the light-permeated forest canopy.

Acknowledgements

5. References

Acebey, A., Gradstein, S. R. & Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. Journal of Tropical Ecology 19, 9–18.

Acharius, E. 1803. Methodus qua Omnes Detectos Lichenes Secundum Organa Carpomorpha ad Genera, Species et Varietates Redigere atque Observationibus Illustrare Tentavit Erik Acharius. Stockholmiae: F.D.D. Ulrich. 394 pp.

Agardh, C. 1821. Aphorismi botanici, p. 93. Lundae: Literis Berlingianis.

Akiyama, H., Schäfer-Verwimp, A., Printarakul, N., Suleiman, M., Tan, B. C., Goffinet, B., Yong, K. T. & Müller, F. 2015. Phylogenetic study of the genus Aptychella (Pylaisiadelphaceae, Musci). The Bryologist 118, 273–83.

Allen, B. H. 2010. Moss Flora of Central America, Part 3. Anomodontaceae-Symphyodontaceae. Monographs in Systematic Botany from the Missouri Botanical Garden 117, i–x, 1–731.

Bechteler, J., Lee, G. E., Schäfer-Verwimp, A., Pócs, T., Peralta, D. F., Renner, M. A. M., Schneider, H. & Heinrichs J. 2016. Towards a monophyletic classification of Lejeuneaceae IV: reinstatement of Allorgella, transfer of Microlejeunea aphanella to Vitalianthus and refinements of the subtribal classification. Plant Systematics and Evolution 302, 187–201.

Brako, L. 1991. Phyllopsora (Bacidiaceae). Flora Neotropica 55, 1–66.

Brotherus V. F. 1908. Gammiella. In Engler, H. G. A. & Prantl, K. (eds) Die natürlichen Pflanzenfamilien 1(3). Leipzig: W. Engelmann. 1067 pp.

Browne, P. 1756. *Civil and natural history of Jamaic.* London: Osborn & Shipton. 503 pp.

Buck, W. R. 1998. Pleurocarpous mosses of the West Indies. *Memoirs of the New York Botanical Garden* **82**, 1–400.

Buck, W. R. & Vitt, D. H. 1986. Suggestions for a new familial classification of pleurocarpous mosses. *Taxon* **35**, 21–60.

Cardot, J. 1912. *Pylaisiadelpha*, genre noveau de la famille des Entodontacées. *Revue Bryologique* **39**, 57–58.

Caspary, R. 1887. Einige neue Pflanzenreste aus dem samländischen Bernstein. *Schriften der Königlichen Physikalisch-Ökonomischen Gesellschaft zu Königsberg (Abhandlungen)* **27**, 1–8.

Cavalier-Smith, T. 1998. A revised six-kingdom system of life. *Biological Reviews* **73**, 203–66.

Cavers, F. 1910. The interrelationships of the Bryophyta. *New Phytologist* **9**, 269–304.

Churchill, S. P. & Buck, W. R. 1982. A taxonomic revision of *Leptotheca* (Rhizogoniaceae). *Brittonia* **34**, 1–11.

Cornejo, C. & Scheidegger, C. 2016. Cyanobacterial gardens: the liverwort *Frullania asagrayana* acts as a reservoir of lichen photobionts. *Environmental Microbiology Reports* **8**, 352–57.

Cornelissen, J. H. C. & Ter Steege, H. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *Journal of Tropical Ecology* **5**, 131–50.

Crum, H. A. 1971. Nomenclatural changes in the Musci. *The Bryologist* **74**, 165–74.

Devos, N., Renner, M. A. M., Gradstein, R., Shaw, A. J., Laenen, B. & Vanderpoorten, A. 2011a. Evolution of sexual systems, dispersal strategies and habitat selection in the liverwort genus *Radula*. *New Phytologist* **192**, 225–36.

Devos, N., Renner, M. A. M., Gradstein, S. R., Shaw, A. J. & Vanderpoorten, A. 2011b. Molecular data challenge traditional subgeneric divisions in the leafy liverwort genus *Radula*. *Taxon* **60**, 1623–32.

Dong, S., Schäfer-Verwimp, A., Pócs, T., Feldberg, K., Czumaj, A., Schmidt, A. R., Schneider, H. & Heinrichs, J. 2013. Size doesn̦t matter – recircumscription of *Microlejeunea* based on molecular and morphological evidence. *Phytotaxa* **85**, 41–55.

Dumortier, B. C. J. 1822. *Commentationes botanicae*. Tournay: Ch. Casterman-Dien. 118 pp.

Elix, J. A. 2006. Five new species of *Phyllopsora* (lichenized Ascomycota) from Australia. *Australasian Lichenology* **59**, 23–29.

Eriksson, O. E. & Winka, W. 1997. Supraordinal taxa of Ascomycota. *Myconet* **1**, 1–16.

Feldberg, K., Schneider, H., Stadler, T., Schäfer-Verwimp, A., Schmidt, A. R. & Heinrichs, J. 2014. Epiphytic leafy liverworts diversified in angiosperm-dominated forests. *Scientific Reports* **4**, 5974.

Fleischer, M. 1923. *Die Musci der Flora von Buitenzorg* **4**, i–xxxi, 1104–729. Leiden: E. J. Brill.

Frahm, J. -P. 1993. Mosses in Dominican amber. *Journal of the Hattori Botanical Laboratory* **74**, 249–59.

Frahm, J. -P. & Newton, A. E. 2005. A new contribution to the moss Flora of Dominican amber. *The Bryologist* **108**, 526–36.

Goffinet, B. & Buck, W. R. 2004. Systematics of the Bryophyta (mosses): from molecules to a revised classification. *Monographs in Systematic Botany from the Missouri Botanical Garden* **98**, 205–39.

Gottsche, C. M., Lindenberg, J. B. W. &, Nees, C. G. 1845. *Synopsis hepaticarum*, fasc. 2, 145–304. Hamburg: Meissner.

Gradstein, S. R. 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. *Cryptogamie Bryologie* **27**, 141–52.

Gradstein, S.R. & Pócs, T. 1989. Bryophytes. *In* Lieth, H. & Werger, M. J. A. (eds) *Tropical Rain Forest Ecosystems*, 311–25. Amsterdam: Elsevier Science Publishers.

Grimaldi, D. A. 1996. *Amber: Window to the past*. New York: Harry N. Abrahams Inc. & American Museum of Natural History. 216 pp.

Grolle, R. 1980. Lebermoose im Bernstein 2. *Feddes Repertorium* **91**, 401–07.

Grolle, R. 1983. *Leucolejeunea antiqua* n. sp., das erste Lebermoos aus Dominikanischem Bernstein. *Stuttgarter Beiträge zur Naturkunde, Serie B* **96**, 1–9.

Grolle, R. 1984. *Lejeunea palaeomexicana* n. sp., das erste Moos aus Mexikanischem Bernstein. *Stuttgarter Beiträge zur Naturkunde, Serie B* **108**, 1–7.

Grolle, R. 1987. *Radula steerei* sp. nov. A further hepatic in Dominican amber. *Memoirs of the New York Botanical Garden* **45**, 259–63.

Grolle, R. & Meister, K. 2004. *The Liverworts in Baltic and Bitterfeld Amber*. Jena: Weissdorn. 91 pp.

He, Q. & Zhu, R. -L. 2011. Spore output in selected species of Lejeuneaceae. *Cryptogamie Bryologie* **32**, 107–12.

Heinrichs, J., Gradstein, S. R., Wilson, R. & Schneider, H. 2005. Towards a natural classification of liverworts (Marchantiophyta) based on the chloroplast gene *rbc*L. *Cryptogamie Bryologie* **26**, 131–50.

Heinrichs, J., Dong, S., Schäfer-Verwimp, A., Pócs, T., Feldberg, K., Czumaj, A., Schmidt, A. R., Reitner J, Renner, M. A. M., Hentschel, J., Stech, M. & Schneider, H. 2013a. Molecular phylogeny of the leafy liverwort *Lejeunea* (Porellales): evidence for a Neotropical origin, uneven distribution of sexual systems and insufficient taxonomy. *PLoS ONE* **8**, e82547.

Heinrichs, J., Vitt, D. H., Schäfer-Verwimp, A., Ragazzi, E., Marzaro, G., Grimaldi, D. A., Nascimbene, P. C., Feldberg, K. & Schmidt, A. R. 2013b. The moss *Macromitrium richardii* (Orthotrichaceae) with sporophyte and calyptra enclosed in *Hymenaea* resin from the Dominican Republic. *Polish Botanical Journal* **58**, 221–30.

Heinrichs, J., Kettunen, E., Lee, G. E., Marzaro G., Pócs, T., Ragazzi, E., Renner, M. A. M., Rikkinen, J., Sass-Gyarmati, A., Schäfer-Verwimp, A., Scheben, A., Solórzano Kraemer, M. M., Svojtka, M. & Schmidt, A. R. 2015a. Lejeuneaceae (Marchantiophyta) from a species-rich taphocoenosis in Miocene Mexican amber, with a review of liverworts fossilised in amber. *Review of Paleobotany and Palynology* **221**, 59–70.

Heinrichs, J., Scheben, A., Lee, G. E., Váňa, J., Schäfer-Verwimp, A., Krings, M. & Schmidt, A. R. 2015b. Molecular and morphological evidence challenges the records of the extant liverwort *Ptilidium pulcherrimum* in Eocene Baltic amber. *PLoS ONE* **10**, e0140977.

Heinrichs, J., Scheben, A., Bechteler, J., Lee, G. E., Schäfer-Verwimp, A., Hedenäs, L., Singh, H., Pócs, T., Nascimbene, P. C., Peralta, D. F., Renner, M. & Schmidt, A. R. 2016. Crown group Lejeuneaceae and pleurocarpous mosses in early Eocene (Ypresian) Indian amber. *PLoS ONE* **11**, e0156301.

Herzog, T. 1916. Die Bryophyten meiner zweiten Reise durch Bolivia. *Bibliotheca Botanica* **87**, 1–347.

Hietz, P. 2010. Ecology and ecophysiology of epiphytes in tropical montane cloud forests. *In* Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds) *Tropical Montane Cloud Forests*, 67–76. Cambridge, UK: Cambridge University Press.

Hietz, P. & Hietz-Seifert, U. 1995. Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Science* **6**, 487–98.

Hofstede, R. G. M., Wolf, J. H. D. & Benzing, D. H. 1993. Epiphytic biomass and nutrient status of a Colombian upper montane rain forest. *Selbyana* **14**, 37–45.

Hueber, F. M. & Langenheim, J. 1986. Dominican amber tree had African ancestors. *Geotimes*, **31**, 8–10.

Iturralde-Vinent, M. & MacPhee, R. D. E. 1996. Age and paleogeographical origin of Dominican amber. *Science* **273**, 1850–52.

Jack, J. B. & Stephani, F. 1892. Hepaticae Wallisianae. *Hedwigia* **31**, 11–27.

Johansson, D. R. 1989. Vascular epiphytism in Afric. *In* Lieth, H. & Werger M. J. A. (eds) *Tropical Rain Forest Ecosystems: Biogeographical and Ecological Studies*, 183–94. Amsterdam: Elsevier Science Publishers. xvii + 713 pp.

Köhler, L., Hölscher, D., Bruijnzeel, L. A. & Leuschner, C. 2010. Epiphyte biomass in Costa Rican old-growth and secondary montane rain forests and its hydrological significance. *In* Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds) *Tropical Montane Cloud Forests*, 67–76. Cambridge, UK: Cambridge University Press. 768 pp.

Krömer, T., Kessler, M., Gradstein, S. R. & Acebey, A. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography* **32**, 1799–809.

Kürschner, H., Frey, W. & Parolly, G. 1999. Patterns and adaptive trends of life forms, life strategies and ecomorphological structures in tropical epiphytic bryophytes – a pantropical synopsis. *Nova Hedwigia* **69**, 73–99.

Langenheim, J. H. 1966. Botanical source of amber from Chiapas, Mexico. *Ciencia* **24**, 201–10.

Lee, G. E. 2013. A systematic revision of the genus *Lejeunea* Lib. (Marchantiophyta: Lejeuneaceae) in Malaysia. *Cryptogamie Bryologie* **34**, 381–484.

Lee, G. E., Schäfer-Verwimp, A., Schmidt, A. R. & Heinrichs, J. 2015. Transfer of the Miocene *Lejeunea palaeomexicana* to *Ceratolejeunea*. *Cryptogamie Bryologie* **36**, 335–41.

Leuschner, C. 2010. Epiphyte biomass in Costa Rican old-growth and secondary montane rain forests and its hydrological significance. *In* Bruijnzeel, L. A., Scatena, F. N. & Hamilton, L. S. (eds) *Tropical Montane Cloud Forests*, 268–74. Cambridge, UK: Cambridge University Press. 768 pp.

Libert, M. -A. 1820. Sur un genre nouveau d'hépatiques, *Lejeunia*. *Annales générales des sciences physiques* **6**, 372–74.

Linnaeus, C. 1753. *Species Plantarum*. Stockholm: Salvius.

Lóriga, J., Schmidt, A. R., Moran, R. C., Feldberg, K., Schneider, H. & Heinrichs, J. 2014. The first fossil of a bolbitidoid fern belongs to the early-divergent lineages of *Elaphoglossum* (Dryopteridaceae). *American Journal of Botany* **101**, 1466–75.

McCarthy, P. M. 2016. *Checklist of the Lichens of Australia and its Island Territories*. Australian Biological Resources Study, Canberra. Version 22 January 2016.

Mishra, K. M., Upreti, D. K., Nayaka, S. & Haridas, B. 2011. New taxa and new reports of *Phyllopsora* (lichenized Ascomycotina) from India. *Mycotaxon* **115**, 29–44.

Müller, C. 1874. Novitates bryothecae Muellerianae. 2. Musci Novo-Granatenses Wallisiani adjecis nonnullis aliis muscis novis andinis vel tropico-americanis vel australasiacis. *Linnaea* **38**, 572–620.

Müller, C. 1876. Musci Hildebrandtiani in Archipelago Comorense et in Somalia littoris Africani anno 1875 ab I. M. Hildebrandt lecti. *Linnaea* **40**, 225–300.

Müller, J. 1894. Conspectus systematicus lichenum Novae Zelandiae. *Bulletin de [Herbier Boissier*. **2** (App. 1), 1–114.

Müller, K. 1909. *Die Lebermoose Deutschlands, Oesterreichs und der Schweiz*, 2nd ed. (Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz, Band 6 Lieferung 7), 385–448. Leipzig: Eduard Kummer.

Nannfeldt, J. A. 1932. Studien über die Morphologie und Systematik der nichtlichenisierten inoperculaten Discomyceten. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* **8**, 1–368.

Nash, T. H. III. 2008. Nitrogen, its metabolism and potential contribution to ecosystems. *In* Nash, T. H. III (ed.) *Lichen biology*, 2nd edition, 216–33. Cambridge, UK: Cambridge University Press. 502 pp.

Osyczka, P. & Rola, K. 2013. Phenotypic plasticity of primary thallus in selected *Cladonia* species (lichenized Ascomycota: Cladoniaceae). *Biologia* **68**, 365–72.

Pax, F. 1900. *Prantl's Lehrbuch der Botanik* (11th ed.), 1–200. Leipzig: W. Engelmann.

Penney, D. 2010. Dominican Amber. *In* Penney, D. (ed.) *Biodiversity of fossils in amber from the major world deposits*, 22–41. Manchester: Siri Scientific Press.

Poinar, G. O. Jr. 1991. *Hymenaea protera* sp. n. (Leguminosae, Caesalpinioideae) from Dominican amber has African affinities. *Experientia* **47**, 1075–82.

Poinar, G. O. Jr., Peterson, E. B. & Platts, J. L. 2000. Fossil *Parmelia* in New World amber. *Lichenologist* **32**, 263–69.

Poinar, G. O. Jr. & Brown, A. E. 2002. *Hymenaea mexicana* sp. nov. (Leguminosae: Caesalpinioideae) from Mexican amber indicates Old World connections. *Botanical Journal of the Linnean Society* **139**, 125–32.

Poinar, G. O. Jr. & Poinar, R. 1999. *The amber forest: A reconstruction of the vanished world*. Princeton: Princeton University Press. 292 pp.

Reiner-Drehwald, M. E., Schmidt, A. R. & Heinrichs, J. 2012. The genus *Lejeunea* in Miocene amber from the Dominican Republic. *Cryptogamie, Bryologie* **33**, 33–38.

Reiner-Drehwald, M. E. & Goda, A. 2000. Revision of the genus *Crossotolejeunea* (Lejeuneaceae, Hepaticae). *Journal of the Hattori Botanical Laboratory* **89**, 1–54.

Renner, M. A. M. 2014. *Radula* subg. *Radula* in Australasia and the Pacific (Jungermanniopsida). *Telopea* **17**, 107–67.

Rikkinen, J. & Poinar, G. O. Jr. 2008. A new species of *Phyllopsora* (Lecanorales, lichen-forming Ascomycota) from Dominican amber, with remarks on the fossil history of lichens. *Journal of Experimental Botany* **59**, 1007–11.

Schiffner, V. 1893. Hepaticae. *In* Engler, A. & Prantl, K. (eds) *Die Natürlichen Pflanzenfamilien* **Teil. I, Abt. 3**, 1–144. Leipzig: Engelmann.

Schimper, W. P. 1879. Palaeophytologie. *In* von Zittel, K. A. (ed.) *Handbuch der Palaeontologie*, 1–958. München: Oldenbourg.

Schljakov, R. N. 1972. [On the higher taxa of liverworts – class Hepaticae s.str.] *Botanicheskii Zhurnal* **57**, 496–508. [In Russian.]

Schneider, H., Schmidt, A. R., Nascimbene, P. C. & Heinrichs, J. 2015. A new Dominican amber fossil of the derived fern genus *Pleopeltis* confirms generic stasis in the epiphytic fern diversity of the West Indies. *Organisms Diversity & Evolution* **15**, 277–83.

Schwägrichen, C. F. 1823–1827. *Species Muscorum Frondosorum, Supplementum Secundum*. Leipzig: Lipsiae.

Spruce, R. 1884. Hepaticae amazonicae et andinae. I. *Transactions and Proceedings of the Botanical Society of Edinburgh* **15**, 1–308.

Stephani, F. 1890. Hepaticae africanae novae in insulis Bourbon, Maurice et Madagascar lectae. *Botanical Gazette* **15**, 281–92.

Stephani, F. 1898. Species hepaticarum 1. *Bulletin de l'Herbier Boissier* **6**, 309–43.

Stotler, R. E. & Crandall-Stotler, B. J. 1977. A checklist of the liverworts and hornworts of North Americ. *Bryologist* **80**, 405–28.

Stotler, R. E. & Crandall-Stotler, B. J. 2000. Morphology and classification of the Marchantiophyta. *In* Shaw, A. J. & Goffinet, B. (eds) *Bryophyte Biology*, 21–70. Cambridge: Cambridge University Press.

Swinscow, T. D. V. & Krog, H. 1981. The genus *Phyllopsora*, with a report on East African species. *Lichenologist* **13**, 203–47.

Tan, B. C. & Jia, Y. 1999. A preliminary revision of Chinese Semato-phyllaceae. *Journal of the Hattori Botanical Laboratory* **86**, 1–70.

Timdal, E. 2008. Studies on *Phyllopsora* (Ramalinaceae) in Peru. *Lichenologist* **40**, 337–62.

Timdal, E. 2011. The lichen genus *Phyllopsora* (Ramalinaceae) in the West Indies. *Bibliotheca Lichenologica* **106**, 319–51.

Timdal, E. & Krog, H. 2001. Further studies on African species of the lichen genus *Phyllopsora* (Lecanorales). *Mycotaxon* **77**, 57–89.

Tixier, P. 1969. De Sematophyllaceis. I. Essay de revision des Clasto-bryaceae de Luzon. *Journal of the Hattori Botanical Laboratory* **32**, 21–34.

Tixier, P. 1977. Clastobryoidées et taxa apparentés. *Revue Bryologique et Lichénologique* **43**, 397–464.

Upreti, D. K., Divakar, P. K. & Nayaka, S. 2003. Notes on species of the lichen genus *Phyllopsora* in India. *Bibliotheca Lichenologica* **86**, 185–91.

Váňa, J., Schäfer-Verwimp, A., Bechteler, J., Schmidt, A. R. & Heinrichs, J. 2015. *Notoscyphus grollei* sp. nov. in Bitterfeld amber rather than the extant *Notoscyphus lutescens* (Lehm. & Lindenb.) Mitt. *Phytotaxa* **222**, 151–54.

Villarreal, J. C. & Renner, S. S. 2014. A review of molecular-clock calibrations and substitution rates in liverworts, mosses and hornworts, and a timeframe for a taxonomically cleaned-up genus *Nothoceros*. *Molecular Phylogenetics and Evolution* **78**, 25–35.

Wang, J., Zhu, R. -L. & Gradstein, S. R. 2016. Taxonomic revision of Lejeuneaceae subfamily Ptychanthoideae (Marchantiophyta) in China. *Bryophytorum Bibliotheca* **65**, 1–141.

Yamada, K. 1979. A revision of Asian taxa of *Radula*, Hepaticae. *Journal of the Hattori Botanical Laboratory* **45**, 201–322.

Yamada, K. 1983. Four new species of *Radula* from Cuba. *Journal of the Hattori Botanical Laboratory* **54**, 241–49.

Yamada, K. 1990. Two new species of *Radula* (Hepaticae) from Australia and Brazil. *Journal of Japanese Botany* **65**, 1–6.

Yamada, K. 2003. Radulaceae. *In* Gradstein, S. R. & Costa, D. P. (eds) *The Hepaticae and Anthocerotae of Brazil*. *Memoirs of the New York Botanical Garden* **87**, 1–318.

Ye, W. & Zhu, R. -L. 2010. *Leucolejeunea*, a new synonym of *Cheilolejeunea* (Lejeuneaceae), with special reference to new combinations and nomenclature. *Journal of Bryology* **32**, 279–82.