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A Caribbean epiphyte community preserved in Miocene Dominican amber

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Abstract

Fossil tree resins preserve a wide range of animals, plants, fungi and microorganisms 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 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 ~~Parmeliaceae~~, Lecanoromycetes) and described as *P. magna* Kaasalainen, Rikkinen et A. R. Schmidt sp. nov. The moss, *Aptychellites fossilis* Schäf.-Verw., Hedenäs, Ignatov & Heinrichs gen. et sp. nov. closely resembles the extant genus *Aptychella* of the family Pylaisiadelphaceae. The three leafy liverworts comprise the extinct Lejeuneaceae species *Cheilolejeunea antiqua* (Grolle) W.Ye et R.L.Zhu and *Lejeunea miocenica* Heinrichs, Schäf.-Verw., M.A.M. Renner et G.E. Lee sp. nov., as well as the extinct *Radula intecta* M.A.M.Renner, Schäf.-Verw. & Heinrichs sp. nov. of the Radulaceae. The presence of five associated extinct cryptogam species of which four 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, fossil lichens, fossil liverworts, fossil mosses

Epiphytes grow upon other plants and typically derive their moisture and nutrients mainly from the air and rain. 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 food source for various invertebrates, and in some cases, also contributing fixed nitrogen into the ecosystem (Nash 2008; Hietz 2010; Köhler et al. 2010). Vascular plants, like 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 cryptogams 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 increases together 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; Lóriga et al. 2014; and Heinrichs et al. 2015a). This fossil resin derives from extinct species of the extant leguminous tree genus *Hymenaea* L. (Langenheim 1966; Hueber & Langenheim 1986; Poinar 1991; Poinar & Brown 2002), and has an estimated age of 15–20 Ma (Iturralde-Vinent and MacPhee 1996; Penney 2010). 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 characterized as a moist tropical forest, which was not remarkably different from the modern Neotropical 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). Also 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). Some moss fossils from Dominican amber have even been suggested to 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, Villarreal & Renner 2014; Heinrichs et al. 2015b; Váňa et al. 2015).

Here, we present 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*, a moss that is similar but clearly distinguished from the modern genus *Aptychella* and therefore assigned to the new fossil genus *Aptychellites*, as well as three extinct species of the extant leafy liverwort genera *Cheilolejeunea*, *Lejeunea*, and *Radula*. 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 and Poinar (1999) that many of the plants and animals preserved in the Miocene Dominican amber do not have immediate extant descendants.

1. Material & Methods

The fossilized epiphytes are preserved in a ca 3 cm x 2 cm x 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 amber specimen originated from the amber mines in the Cordillera of the Dominican Republic.

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). 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 minimize 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. Results

Amber piece AMNH DR-15-3 contains five cryptogam species: a lichen, a moss and three leafy liverworts. None of the inclusions is assignable to extant species.

2.1 Lichens

Phylum Ascomycota Cavalier-Smith
Class: Lecanoromycetes O.E. Erikss. et Winka
Order: Lecanorales Nannf.
Family: Ramalinaceae C. Agardh
Genus *Phyllopsora* Müll. Arg.

Phyllopsora magna Kaasalainen, Rikkinen et A. R. Schmidt, sp. nov., Fig. 2

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-resembling 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 to 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 organized hyphae (Fig. 2B, D). Isidia elongate, cylindrical to clavate, developing horizontally from the margins of the squamules (Fig. 2C). Ascomata or pycnidia not detected.

Holotype: American Museum of Natural History in New York, USA, AMNH DR-15-3. 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: Magna (Latin): large. The species epithet refers to the exceptionally large size of the thallus lobes of this *Phyllopsora* species.

2.2 Liverworts

Phylum: Marchantiophyta Stotler et Crand.-Stotl.

Class: Jungermanniopsida Stotler et Crand.-Stotl.

Order: Porellales Cavers

Family: Lejeuneaceae Cavers

Genus: *Cheilolejeunea* (Spruce) Steph.

Cheilolejeunea antiqua (Grolle) W.Ye et R.L.Zhu, Fig. 1C

Sterile, unbranched shoot, ca. 1.6 mm long, 650–700 µm wide. Stem straight, ca. 30–50 µm in diameter, with a ca. 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 x 18–27µm, 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 to ovoid-triangular, ca 2/5–1/3 of leaf length, free margin often +/- straight, with a short apical tooth. Underleaves [poorly preserved and often somewhat damaged] remote, broadly orbicular to orbicular reniform, ca. 150–200 µm wide, ca. 3.5–4.5 times as wide as shoot.

Phylum: Marchantiophyta Stotler et Crand.-Stotl.

Class: Jungermanniopsida Stotler et Crand.-Stotl.

Order: Porellales Cavers

Family: Lejeuneaceae Cavers

Genus: *Lejeunea* Lib.

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

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 ca 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 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, ca. 15–25 x 20–25 µm, thin-walled, with weak trigones and intermediate thickenings, marginal cells quadrate to rectangular, 10–15 x 10–27 µm. Cuticle finely papillose. Lobules well-developed, ca. 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, ca. 60–100 µm long, 60–95 µm wide, rounded, ca. 1.7–2.5 x 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.

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.

Holotype: American Museum of Natural History in New York, USA, AMNH DR-15-3. The gametophyte fragment shown in Fig. 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.

Phylum: Marchantiophyta Stotler et Crand.-Stotl.

Class: Jungermanniopsida Stotler et Crand.-Stotl.

Order: Porellales Cavers

Family: Radulaceae Müll. Frib.

Genus: *Radula* Dumort.

Radula intecta M.A.M.Renner, Schäf.-Verw. et Heinrichs, sp. nov., Fig. 4

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 ca. 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 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 x 10–30 µm, thin-walled, toward leaf margin continuously thickened except some exterior walls, trigones small, triangular.

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

Type locality: Dominican Republic, Santiago area. Age and stratigraphic position: Early Miocene, about 15 to 20 million years old.

Etymology: Intecta (Latin: uncovered, exposed, naked). The species epithet refers to the frequently caducous leaf lobes which are frequently detached in the fossil.

2.3 Mosses

Phylum: Bryophyta Schimp.

Class: Bryopsida (Limpr.) Rothm.

Order: Hookeriales M.Fleisch.

Family: Pylaisiadelphaceae Goffinet & W.R.Buck

Aptychellites fossilis Schäf.-Verw., Hedenäs, Ignatov et Heinrichs gen. et sp. nov., Fig. 5

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, ca. 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 ca. 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 ca. 38–54 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 ca. twice as long as the gemmae cells and that narrows towards its insertion on the stem. Cells of gemmae rectangular, shortly rectangular or (rarely) quadrate, ca. 20–25 µm in diameter, towards apical region sometimes somewhat swollen, then with a diameter of up to ca. 40 µm. Leaves becoming smaller towards gemmae clusters.

Holotype: American Museum of Natural History in New York, USA, AMNH DR-15-3. The plant shown in Fig. 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 emphasizes the presence of an extinct taxon.

3. Discussion

The five epiphyte species preserved in amber piece 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.

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* P. Browne, 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 organized hyphae, and 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). Additionally, 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 (Swinskow & 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 three millimetre 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, also several extant, especially Neotropical, *Phyllopsora* species 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 (Swinskow & Krog 1981). The cortex structures of most taxa can be classified into one of two main types, but also intermediate forms are common. In one type the cortex hyphae are highly gelatinized and their lumina reduced to narrow thread-like channels reminding a network, while in the other type the hyphae are much less gelatinized and the cortex formed by isodiametric cells (Swinskow & 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 (Swinskow & 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* more resembles extant species and cannot be confidently separated from all of them on morphological grounds (Rikkinen & Poinar 2008). Two fossil *Parmelia* species 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 characterized 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 centre of diversity are the humid tropics, and especially in 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 Lib. is one of the largest, including some 300 extant species (Lee 2013). *Lejeunea* is a hyperdiverse genus which differs from the closely related genera *Microlejeunea* (Spruce) Steph. and *Harpalejeunea* (Spruce) Schiffn. by a lack of ocelli (Dong et al. 2013); its morphology-based supraspecific classification is not supported by molecular data (Heinrichs et al. 2013a). The fossil however, resembles members of the polyphyletic *Lejeunea* subg. *Crossotolejeunea* Spruce 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 Carribbean 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* by entire margined lobes with obtuse apices. Since the Mexican amber fossil *Lejeunea palaeomexicana* Grolle has recently been transferred to *Ceratolejeunea* (Spruce) J.B.Jack & Steph. (Lee et al. 2015), only two fossils of *Lejeunea* are currently known. Another sterile inclusion inside amber piece 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, also other Porellales families have 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 the alpine tundra (Devos et al. 2011a). The genus can easily be recognized 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* subg. *Radula* (Devos et al. 2011b) but not necessarily diagnostic of that lineage. In particular, the apparent absence of ornamentation from the leaf-cell surfaces suggest *R. intecta* does not belong to subg. *Radula*, whose crown-group species all have ornamented surfaces (Renner 2014). Species with dimorphic, pinnately branched shoot systems, caducous leaves and smooth cell surfaces also occur in subg. *Odontoradula*. and subg. *Volutoradula*, as such 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 and *Radula oblongifolia* Casp. (Grolle & Meister 2004), and the Miocene Dominican amber species *Radula steerei* Grolle (Grolle 1987). *Radula intecta* differs from these species by 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 (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 exterior margin straight and inclined toward the stem, dislocation of nearly all leaves on both primary and secondary shoots, and 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* Müll. Hal. (Pilotrichaceae), *Jaegerina* Müll. Hal. (Pterobryaceae), *Clastobryopsis* (Pylaisiadelphaceae), *Pylaisiadelpha* Cardot (Pylaisiadelphaceae) (Tixier 1977; Buck 1998; Goffinet & Buck 2004), *Leptotheca* Schwaegr. (Rhizogoniaceae) (Churchill & Buck 1982), and *Gammiella* Broth. (Pylaisiadelphaceae) (Tan & Jia 1999)

Among pleurocarpous mosses, terminal clusters of filamentous gemmae are typical for the Central American species *Brymela crosbyii* (B.H.Allen) B.H.Allen and the Pylaisiadelphaceae genus *Aptychella* (Broth.) Herzog. *Brymela crosbyii* 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* (Broth.) Herzog. The latter species may have Asian ancestors and has possibly colonized 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 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* H.A.Crum (Pylaisiadelphaceae), however, this genus has gemmae on flagellate branches. A single extant species, *Wijkia flagellifera* (Broth.) H.A.Crum 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, 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 amber piece 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 (Swinskow & 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 dryer environment (Cornelissen & Ter Steege 1989; Kürschner et al. 1999; Acebey et al. 2003) and may assist the plants in surviving periods of desiccation. It is thinkable that the preserved cryptogam community once grew on the bark of a *Hymenaea* tree in a rather open environment. On the other hand we cannot exclude an occurrence in a dense forest; however, in this case the cryptogamic community was likely situated in the light-permeated forest canopy.

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Figure captions:

Figure 1. Cryptogamic community preserved in Dominican amber piece AMNH DR-15-3. **(A)** Overview of the inclusions. **(B)** Ibid., biological inclusions indicated: AF: *Aptychellites fossilis* (holotype encircled); CA: *Cheilolejeunea antiqua*; LM: *Lejeunea miocenica* (holotype only visible from the opposite side of the amber piece); PM: *Phyllopsora magna* (holotype encircled); RI: *Radula intecta* (holotype encircled). **(C)** *Cheilolejeunea antiqua*. Scale bars 1 mm (A,B) and 100 µm (C).

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 of the thallus. Scale bars 1 mm (A) and 100 µm (B-D).

Figure 3. *Lejeunea miocenica* sp. nov. in Dominican amber (AMNH DR-15-3). **(A-C)** Gametophytes in dorsal view. The gametophyte fragment shown in Fig. 3A (left), B and D represents the holotype. **(D)** Holotype in ventral view, one underleaf encircled. **(E)** Close-up of the ventral leaf surface of the holotype showing asperulate cuticle. Scale bars 500 µm (A), 100 µm (B-D), and 50 µm (E).

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* or *Lejeunea miocenica* respectively. **(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), and 100 µm (E).

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), and 50 µm (G).

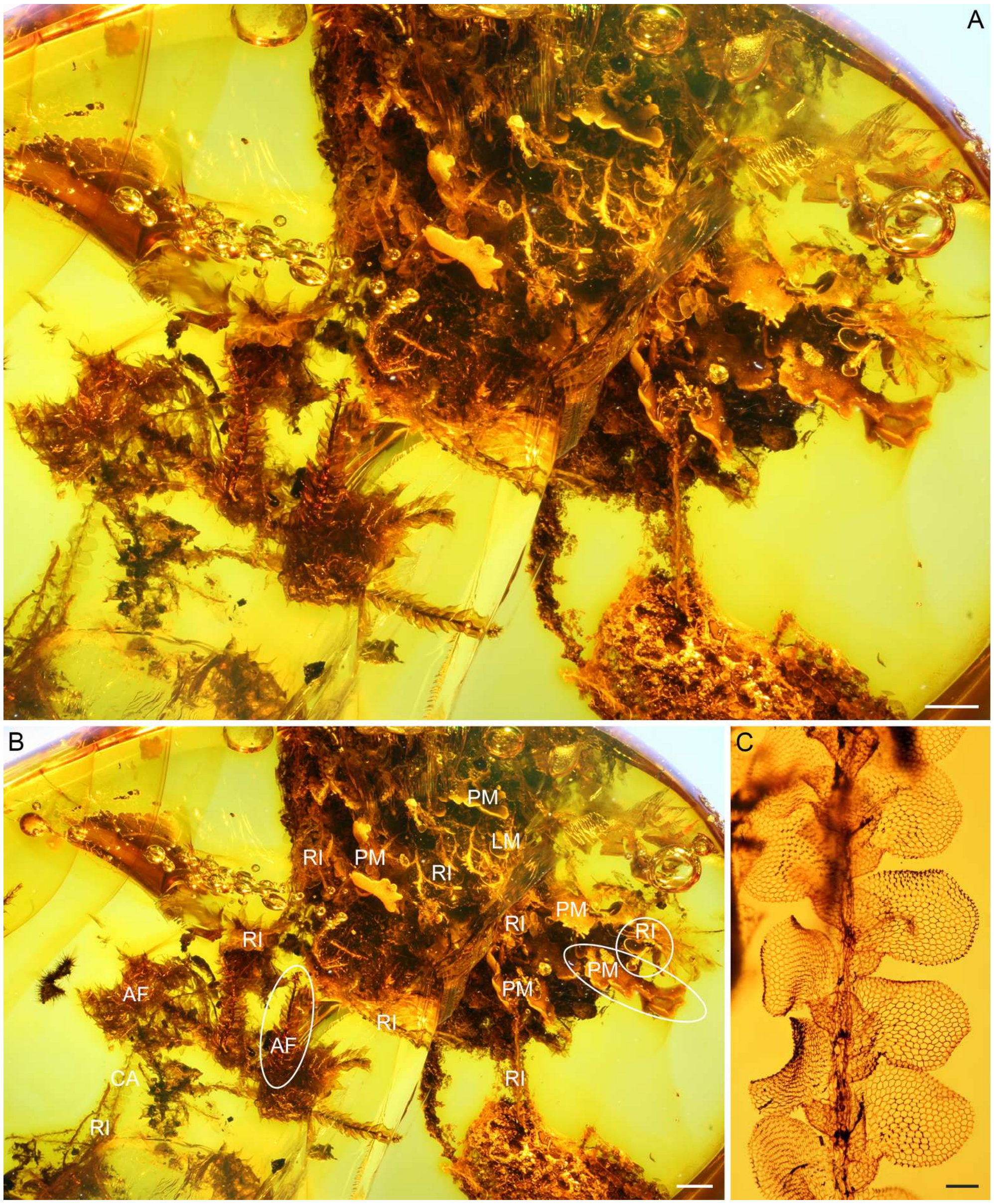

Figure 1 Overview and Cheilolejeunea antiqua
199x241mm (300 x 300 DPI)

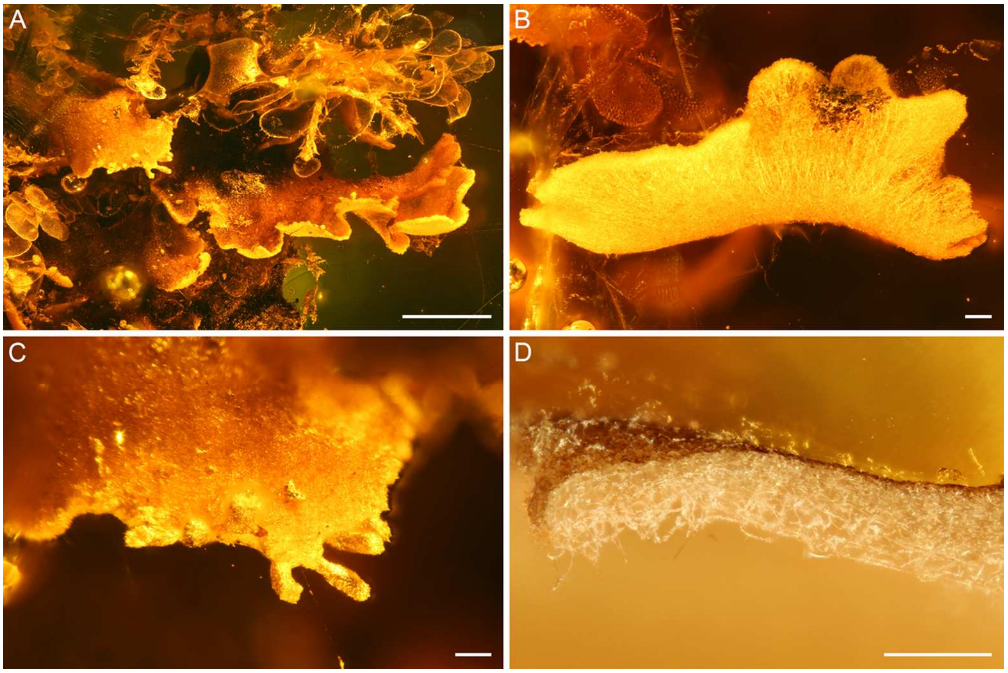

Figure 2 Phyllopsora magna
109x72mm (300 x 300 DPI)

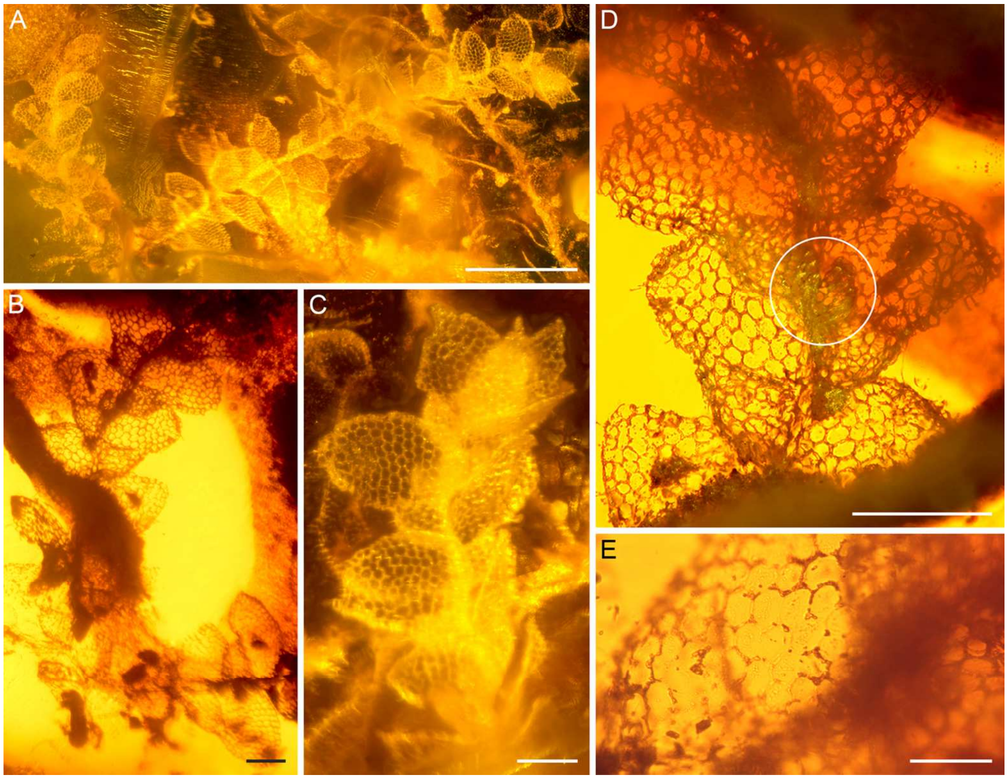

Figure 3 Lejeunea miocenica
127x98mm (300 x 300 DPI)

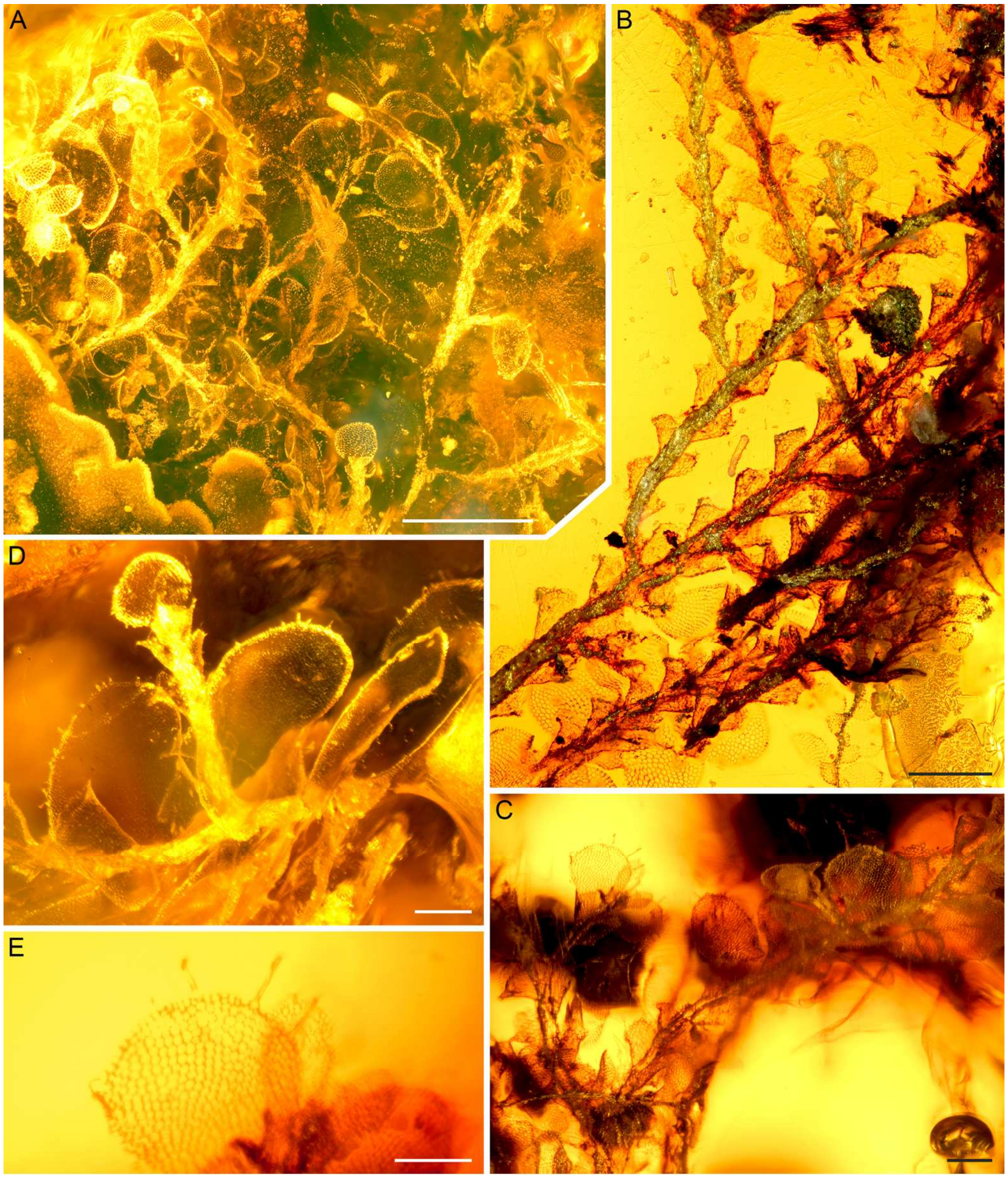

Figure 4 Radula intecta
193x226mm (300 x 300 DPI)

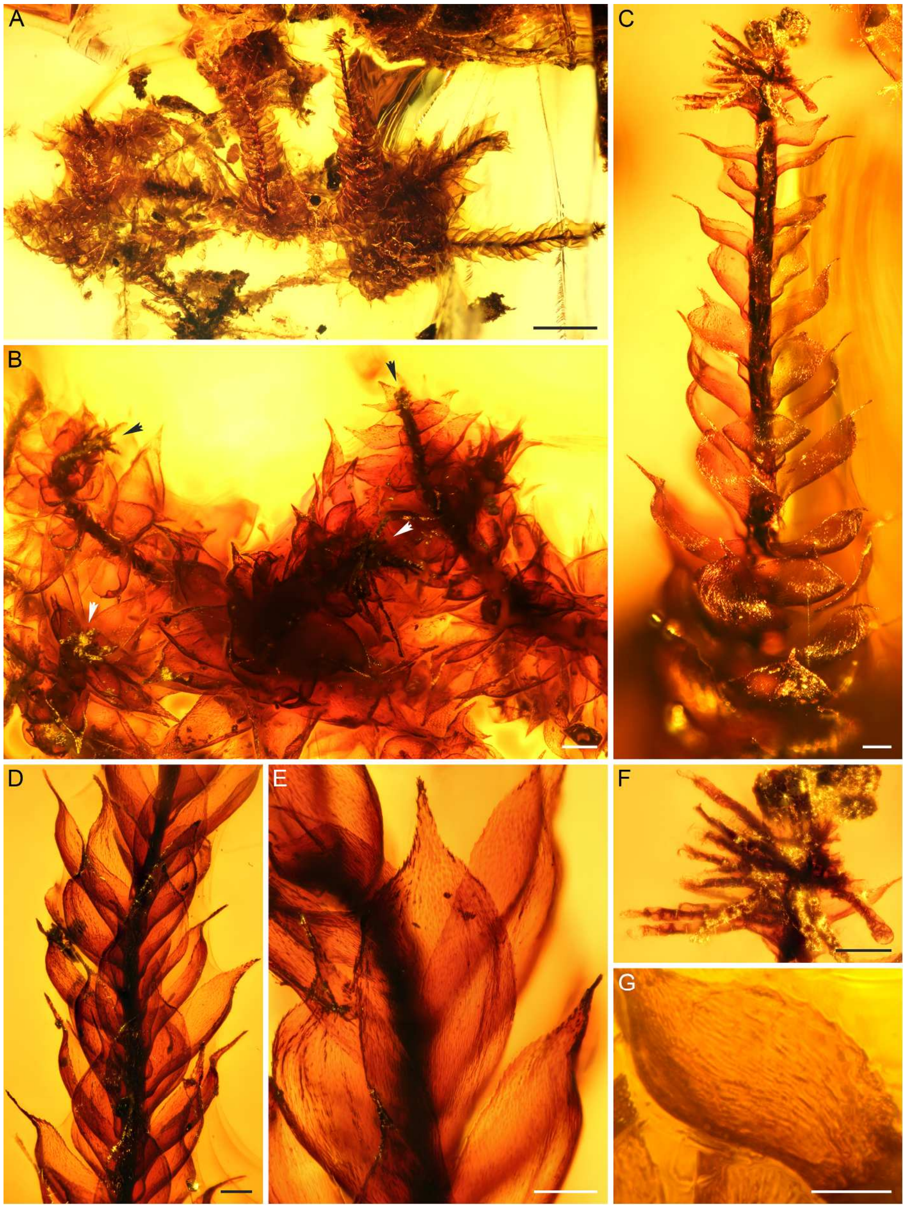

Figure 5 Aptychellites fossilis
219x293mm (300 x 300 DPI)