ARTICLE

The Early Cretaceous Apple Bay flora of Vancouver Island: a hotspot of fossil bryophyte diversity[1]

Alexandru M.F. Tomescu

Abstract: The pre-Cenozoic bryophyte fossil record is significantly sparser than that of vascular plants or Cenozoic bryophytes. This situation has been traditionally attributed to a hypothesized low preservation potential of the plants. However, instances of excellent pre-Cenozoic bryophyte preservation and the results of experiments simulating fossilization contradict this traditional interpretation, suggesting that bryophytes have good preservation potential. Studies of an anatomically preserved Early Cretaceous (Valanginian) plant fossil assemblage on Vancouver Island (British Columbia), at Apple Bay, focusing on the cryptogamic flora, have revealed an abundant bryophyte component. The Apple Bay flora hosts one of the most diverse bryophyte assemblages worldwide, with at least nine distinct moss types (polytrichaceous, leucobryaceous, tricostate), one complex thalloid liverwort, and two other thalloid plants (representing bryophyte or pteridophyte gametophytes), which contribute a significant fraction of biodiversity to the pre-Cenozoic fossil record of bryophytes. These results (*i*) corroborate previous observations and studies, indicating that the preservation potential of bryophytes is much better than traditionally thought; (*ii*) indicate that the bryophyte fossil record is incompletely explored and many more bryophyte fossils are hidden in the rock record, awaiting discovery; and (*iii*) suggest that the paucity of the pre-Cenozoic bryophyte fossil record is primarily a reflection of inadequate paleobryological capacity.

Key words: fossil, bryophyte, moss, Cretaceous, anatomy, permineralized.

Résumé : Le registre des bryophytes fossiles du pré-Cénozoïque est significativement plus mince que celui de plantes vasculaires ou de bryophytes du Cénozoïque. Cette situation a été traditionnellement attribuée à un hypothétique faible potentiel de préservation de ces plantes. Cependant, des exemples d'une excellente préservation de bryophytes du pré-Cénozoïque et les résultats d'expériences simulant la fossilisation contredisent cette interprétation traditionnelle, suggérant que les bryophytes ont un bon potentiel de préservation. Des études d'un assemblage de plantes fossiles anatomiquement préservées du Crétacé inférieur sur l'Ile de Vancouver (Colombie Britannique), à Apple Bay, se concentrant sur la flore cryptogame, ont révélé une composante importante de bryophytes. La flore d'Apple Bay comporte un des assemblages de bryophytes les plus diversifiés dans le monde, avec au moins neuf types distincts de mousses (Polytrichacées, Leucobryacées, mousses tricostées), une hépatique thalloïde complexe et deux autres plantes thalloïdes (représentant des gamétophytes de bryophyte ou de ptéridophyte), qui contribuent à une fraction significative de la biodiversité du registre des bryophytes fossiles du pré-Cénozoïque. Ces résultats (*i*) corroborent les observations et les études antérieures indiquant que le potentiel de préservation des bryophytes est beaucoup meilleur qu'initialement présumé; (*ii*) indiquent que le registre de bryophytes fossiles est incomplètement exploré et que beaucoup plus de bryophytes fossiles sont cachés dans les couches de roches, dans l'attente d'être découverts et (*iii*) suggèrent que la pauvreté du registre des bryophytes fossiles du pré-Cénozoïque est surtout le reflet d'une capacité paléobryologique inadéquate.

Mots-clés : fossile, bryophyte, mousses, Cretacé, anatomie, permineralisé.

Introduction

Extant mosses count an estimated 13 000 species (Goffinet et al. 2009), yet only about 70 moss species have been described from pre-Cenozoic rocks (older than 66 Ma) (Oostendorp 1987; Ignatov 1990; Taylor et al. 2009). The two other bryophyte lineages, liverworts and hornworts, show similar patterns of marked paucity in the Paleozoic and Mesozoic record (Oostendorp 1987; Taylor et al. 2009). Pre-Cenozoic bryophyte scarcity has been traditionally attributed to a hypothesized low preservation potential of these plants (Stewart and Rothwell 1993; Hemsley 2001; Hübers and Kerp 2012). However, this hypothesis is

A.M.F. Tomescu. Department of Biological Sciences, Humboldt State University, Arcata, CA 95521, USA.

Email for correspondence: mihai@humboldt.edu.

[1]This Article is part of a Special issue entitled "Mesozoic and Cenozoic Plant Evolution and Biotic Change," a collection of research inspired by, and honouring, Ruth A. Stockey.

rejected by the mechanical strength and chemical resilience of bryophytes, as demonstrated by experiments that simulate fossilization conditions (Kroken et al. 1996; Hemsley 2001; Kodner and Graham 2001; Graham et al. 2004), and by instances of exquisite preservation of even seemingly delicate bryophyte structures (Harris 1939; Smoot and Taylor 1986; VanAller et al. 2008). Indeed, when discovered and carefully studied, pre-Cenozoic bryophyte fossils reveal morphology and anatomy in tremendous detail, such as minute and ephemeral reproductive structures (Harris 1939; Konopka et al. 1997; Shelton et al. 2015).

It has been suggested that instead of representing an issue of preservation potential, the sparsity of the bryophyte fossil record may reflect either a real pattern of evolutionary diversification (or, rather, lack thereof) prior to the Cenozoic, or the failure of paleobotanists to detect bryophytic remains (Hemsley 2001). The deep geologic age of bryophytes (Edwards et al. 1995; Wellman et al. 2003), which are widely accepted today as being at least as old as vascular plants (Graham 1993; Kenrick and Crane 1997; Wickett et al. 2014), argues against the former and in support of the latter. This view is corroborated by the discovery of plant fragments attributed to mosses in 330 Ma old Mississippian strata as a result of use of a method uncommon for studies of those rocks (bulk maceration; Hübers and Kerp 2012). These findings have led Hübers and Kerp (2012) to anticipate that future studies will show that mosses were more widespread in the late Paleozoic than previously thought. Taken together, these imply that many more bryophytes await discovery in the pre-Cenozoic rock record.

I argue that an aggravating factor in our inability to thoroughly explore the bryophyte fossil record is inadequate paleobryological research capacity, i.e., the very limited number of botanists trained and interested in the study of both bryophytes and the plant fossil record. This is at least partially due to a disconnect, similar to that pointed out recently in the case of fungi (Taylor et al. 2014), between the scientists who discover the bryophyte fossils (paleobotanists) and those who have the knowledge about extant bryophytes (bryologists) that is needed to understand those fossils. On one hand, because plant fossils abound in the rock record and are crucial to understanding of plant evolution and phylogeny, and of the paleoclimates and paleogeography of different regions and moments in geologic time, the relatively small global paleobotanical community is stretched thin trying to cover as many geologic periods and plant groups as possible. Additionally, bryophytes are less conspicuous than most vascular plants in the fossil record. On the other hand, mastering bryophyte systematics and morphology involves a high degree of specialization, and the number of extant bryophyte systematists is small. Although these factors are not necessarily the root of the disconnect mentioned above, together they may explain why the bryophyte fossil record has been poorly explored to date, albeit not for a lack of fossil material.

The pattern of fossil discoveries corroborates the idea that rather than reflecting low abundance and low diversity of bryophytes in the geologic past, the rarity of bryophyte fossils is due primarily to an incompletely explored fossil record. Indeed, the bryophyte diversity discovered in amber (mostly Cenozoic, but also Cretaceous), demonstrates that under sustained focus of existing bryological capacities, the fossil record turns out to be much richer than expected (e.g., Hentschel et al. 2009; Frahm 2010; Katagiri et al. 2013; Hedenas et al. 2014; Mamontov et al. 2015). Recently, rock units spanning the Cretaceous to Eocene on the West Coast of North America have emerged as repositories of fossil bryophyte diversity, characterized by anatomical preservation, and amenable to in-depth systematic evaluation (Steenbock et al. 2011; Tomescu et al. 2012; Unger and Tomescu 2013; Bippus et al. 2015; Shelton et al. 2015). Among these, the Early Cretaceous Apple Bay flora on Vancouver Island (British Columbia) has received a lot of attention and has been worked extensively by R.A. Stockey, in collaboration with G.W. Rothwell.

Here, I present an overview of bryophyte diversity documented thus far in the Apple Bay flora. Study of the Apple Bay concretions employs the traditional methods of coal ball paleobotany: the concretions are sliced into slabs that are then sectioned using the cellulose acetate peel technique (Joy et al. 1956). That fact that this technique yields serial sections spaced only 20–30 μm apart is both an advantage (high spatial resolution) and a shortcoming (it is time-consuming). Given these constraints, along with the fact that there are thousands of plant-containing concretions collected from Apple Bay, this account necessarily reflects only a subset of the bryophyte diversity preserved in the flora: that uncovered since we started targeted searches for bryophytes, five years ago. Some of the descriptive data compiled here were reported at scientific meetings and come from the corresponding meeting abstracts referenced throughout this article, whereas other data, as well as interpretations and discussions, represent new information. Several pointed publications that detail fossils discussed here will be forthcoming. I dedicate this paper to Dr. Ruth A. Stockey, in honor of her numerous and influential contributions to paleobotany.

Materials and methods

Locality and flora
The Apple Bay flora is preserved anatomically by calcium carbonate permineralization, in concretions that host an allochthonous fossil assemblage deposited in nearshore marine sediments. The concretions are encased in sandstone (greywacke) beds exposed on the northern shore of Apple Bay, Quatsino Sound, on the west side of Vancouver Island, British Columbia, Canada (50°36′21″N, 127°39′25″ W; UTM 9U WG 951068) (Stockey

and Rothwell 2009). These plant-fossiliferous layers are regarded as Longarm Formation equivalents, and have been dated by oxygen isotope analyses to the Valanginian (Early Cretaceous, ca. 136 Ma) (Rothwell and Stockey 2013).

The flora includes lycophytes, equisetophytes, several fern families (Smith et al. 2003; Hernandez-Castillo et al. 2006; Little et al. 2006a, 2006b; Rothwell and Stockey 2006; Stockey et al. 2006; Vavrek et al. 2006; Rothwell et al. 2014), as well as numerous gymnosperms (Stockey and Wiebe 2008; Stockey and Rothwell 2009; Klymiuk and Stockey 2012; Rothwell and Stockey 2013; Rothwell et al. 2014; Atkinson et al. 2014a, 2014b; Ray et al. 2014), fungi (Smith et al. 2004; Bronson et al. 2013), a lichen (Matsunaga et al. 2013), and numerous bryophytes (Tomescu et al. 2012).

Fossil preparation

Carbonate concretions were sliced into slabs and then sectioned using the cellulose acetate peel technique (Joy et al. 1956). Slides were prepared using Eukitt mounting medium (O. Kindler GmbH, Freiburg, Germany). To obtain a quantitative measure of the abundance of bryophyte fossils, a tally of bryophyte fossils observed in 39 concretions was divided by the total surface area of the sections (produced by cutting into slabs) that exposed plant material in the 39 concretions. Because bryophyte fossils are small, few specimens were exposed in more than one cut; those that were exposed in more than one cut were counted only once for the tally. Micrographs were taken using an Olympus DP73 digital camera mounted on an Olympus SZX16 microscope. Images were processed using Photoshop (Adobe, San José, California, USA). All Apple Bay specimens and preparations are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada; the Budden Canyon Formation material is housed in the Humboldt State University Paleobotanical Herbarium (HPH).

Results

Abundance

A total of 223 distinct bryophyte specimens were exposed in the 39 concretions surveyed, on planes of section totaling 0.162 m² of surface area; therefore, one bryophyte specimen for every 7.25 cm². Of these, 124 are leafy gametophyte stems, 92 are leafless bryophyte axes, and 7 are thalloid gametophytes (Tomescu et al. 2012).

Mosses

The most abundant bryophyte fossils at Apple Bay are the moss gametophytes. Of these, some can be assigned to extant families, while others represent extinct lineages. Among the latter, a prominent feature of the Apple Bay flora is the diversity of tricostate mosses. The tricostate condition is characterized by consistent occurrence of three costae per leaf in a symmetrical arrangement: one central and two lateral costae. This condition,

known exclusively from the fossil record, is approached in the modern flora only by some limbidiate mosses (e.g., *Limbella* Müll. Hal.; see Shelton et al. 2015 for an in-depth discussion). Tricostate mosses were first described by Krassilov (1973), who erected for these forms the genus *Tricostium* Krassilov, which currently includes three species that span the Triassic (or possibly Late Permian) to Late Cretaceous interval (Ignatov and Shcherbakov 2011a, 2011b).

At Apple Bay, another tricostate genus, *Tricosta* Shelton, Stockey, Rothwell et Tomescu, represented by one species (*T. multiplicata* Shelton, Stockey, Rothwell et Tomescu) is characterized by much-branched stems with densely inserted and strongly plicate leaves (Figs. 1A and 1B). The three leaf costae are homogeneous and arise separately in the leaf base. The ovate leaves have small alar regions. The gametophytes bear lateral sessile perigonia and perichaetia with preserved gametangia (Fig. 1B). *Tricosta* represents the oldest unequivocal record of the pleurocarpous superorder Hypnanae and was placed in its own family, Tricostaceae (Shelton et al. 2015). Another member of the Tricostaceae recognized in the Apple Bay flora is *Krassiloviella limbelloides* Shelton, Stockey, Rothwell et Tomescu (Figs. 1C and 1E). Krassiloviella features robust gametophytes with narrow-lanceolate leaves that exhibit small, weakly differentiated alar regions and bear strong homogeneous costae that arise separately in the leaf base and are covered by an epidermal layer (Shelton et al. 2016).

For the time being, it is unclear whether genus *Tricostium* is a member of family Tricostaceae. Because all *Tricostium* species are based on compression material, this genus is defined by a small set of leaf morphological characters. In contrast, Tricostaceae are based on anatomically preserved material that reveals a wealth of characters, most of which cannot be or have not been observed in any of the *Tricostium* species because of their mode of preservation. Thus, the difference in mode of preservation leads to high disparity in the number and type of diagnostically informative characters, and ultimately in how well the Tricostaceae and *Tricostium* are understood. This precludes relevant comparisons and placement of *Tricostium* in the Tricostaceae. In fact, the features recorded in *Tricostium* do not provide enough evidence even for inclusion in the Hypnanae; *Tricostium* should therefore be maintained as a morphogenus (i.e., a taxon defined based only on a subset of characters of the whole plant; Bell and York 2007) for moss compressions with tricostate leaves.

Aside from the two tricostate types already mentioned, the Apple Bay flora hosts at least two other tricostate mosses that await in-depth characterization. One of these is similar to *Tricosta*, with plicate leaves that have a broad lamina, but is much more robust (stems and leaves at least twice as large as those of *Tricosta*) and features more prominent costae (Fig. 1D). Whereas this type prob-

Fig. 1. Early Cretaceous moss gametophytes from Apple Bay (Vancouver Island). (A) *Tricosta plicata* stem, longitudinal section; note lateral branch longitudinal section (arrowhead) and area around asterisk showing conspicuous tricostate plicate leaves in cross section; stem tip points to the right; central tissues of stem and branches not preserved. P15425 Cbot #55a. Scale bar = 500 μm. (B) *Tricosta plicata*, cross-section of stem (s) and two lateral perigonial branches; empty antheridial sacs (two next to each of the asterisks) have sinuous outlines and are surrounded by perigonial leaves; many tricostate plicate leaves are cut in cross section. P15425 Cbot #14a. Scale bar = 300 μm. (C) A second tricostate type; oblique stem section (central tissues not preserved) with leaves diverging toward the top; note robust leaf costae (arrowheads indicate three costae of the same leaf) and lamina with discontinuous preservation. P13131 Dbot #7c. Scale bar = 250 μm. (D) A third tricostate type, stem cross section (central tissues not preserved); note plicate leaves with conspicuous narrow costae (arrowheads indicate three costae of the same leaf). P15800 Cbot #1a. Scale bar = 300 μm. (E) Stem longitudinal section of same moss type as in Fig. 1C; note bases of robust costae diverging along the stem and branch (asterisk); stem tip points to the right. P15800 Cbot #1a. Scale bar = 500 μm.
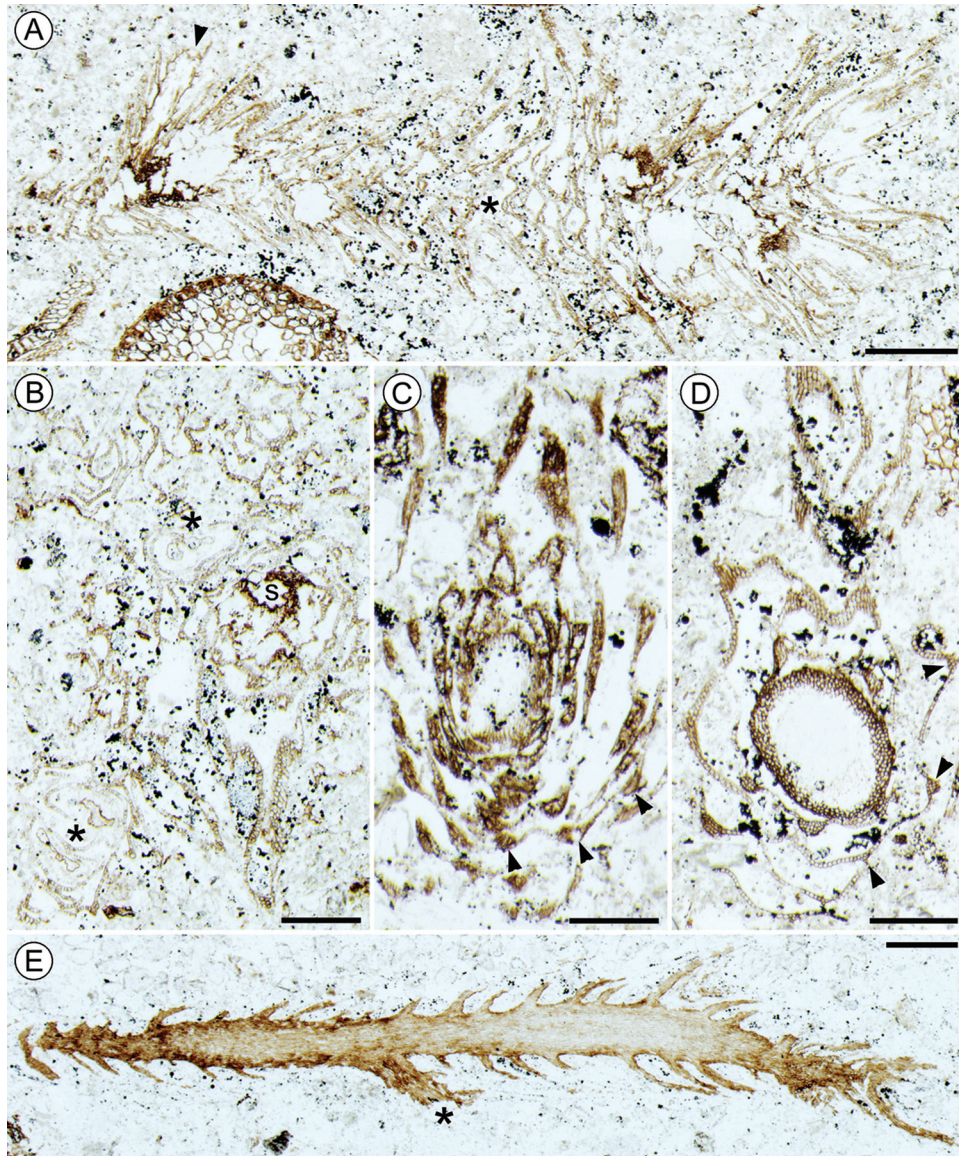

ably fits the diagnosis of Tricostaceae, the affinities of the fourth tricostate type are less obvious. The latter also features relatively robust gametophytes with very broad leaves, but the costae are elongate-lenticular in cross section and very strong (more than 200 μm wide and 100 μm thick) (Fig. 2A).

Several fossils at Apple Bay exhibit anatomical features (e.g., costal anatomy) suggesting affinities with the extant family Polytrichaceae. A subgroup of these fossils share characters indicating that they represent the same species. This species is characterized by stems with a conducting central strand and densely inserted leaves with typical polytrichaceous morphology and anatomy (Figs. 2B–2D and 3H). The leaves have a broad, unistratose sheathing base and a much narrower, bistratose free lamina (Figs. 2D and 3H). The leaf costa is robust and features complex anatomy (deuters, stereids). Adaxially, the costa is lined with lamellae (Fig. 2D). Additionally,

Fig. 2. Early Cretaceous moss gametophytes from Apple Bay (Vancouver Island). (A) A fourth tricostate type; stem cross section (central tissues not preserved) and leaves with very strong costae (arrowheads indicate three costae of the same leaf); note free margins (asterisks) of leaf sectioned proximally to its divergence from the stem. P13172 G #23a. Scale bar = 250 μm. (B) Polytrichaceous moss; note lenticular gemmae with large cells at center of stem cross section, surrounded by tightly packed leaves forming the gemmae cup. P15393 Bbot #1b. Scale bar = bar = 150 μm. (C) Polytrichaceous moss; leaf cross section with details of costa anatomy including large deuter cells and smaller stereids; note adaxial mammillose cells. P15393 Bbot #10b. Scale bar = 100 μm. (D) Polytrichaceous moss; cross section of distal leaf blade; note bistratose lamina and thick costa with short adaxial lamellae. P15393 Bbot #4b. Scale bar = 100 μm. (E) Leucobryaceous moss; cross section of stem (asterisk; central tissues not preserved) branching in one plane, with one branch on either side; the branch at right has produced its own branch (arrowhead). P13308 Gbot #57a. Scale bar = 200 μm. (F) Leucobryaceous moss, stem cross section; note characteristic leaves with thick wide costa (consisting of two layers of large leucocysts that sandwich a median layer of narrow chlorocysts with triangular cross section) and narrow unistratose lamina (marked with asterisks on three leaves). P13308 Gbot #2a. Scale bar = 150 μm. (G) Stem cross section of moss with tristichous phyllotaxis; note triquetrous stem at center (central tissues not preserved) and leaves tightly packed around it, keeled and with slightly recurved margin (e.g., leaf at bottom right). P13311 Itop #3d. Scale bar = 150 μm. (H) Oblique section of moss with very robust stem (central tissues not preserved) and strong leaf costae diverging toward the right; the leaf lamina is not preserved; note abundant rhizoids sectioned all around the stem. P17345 Ctop #1a. Scale bar = 350 μm.
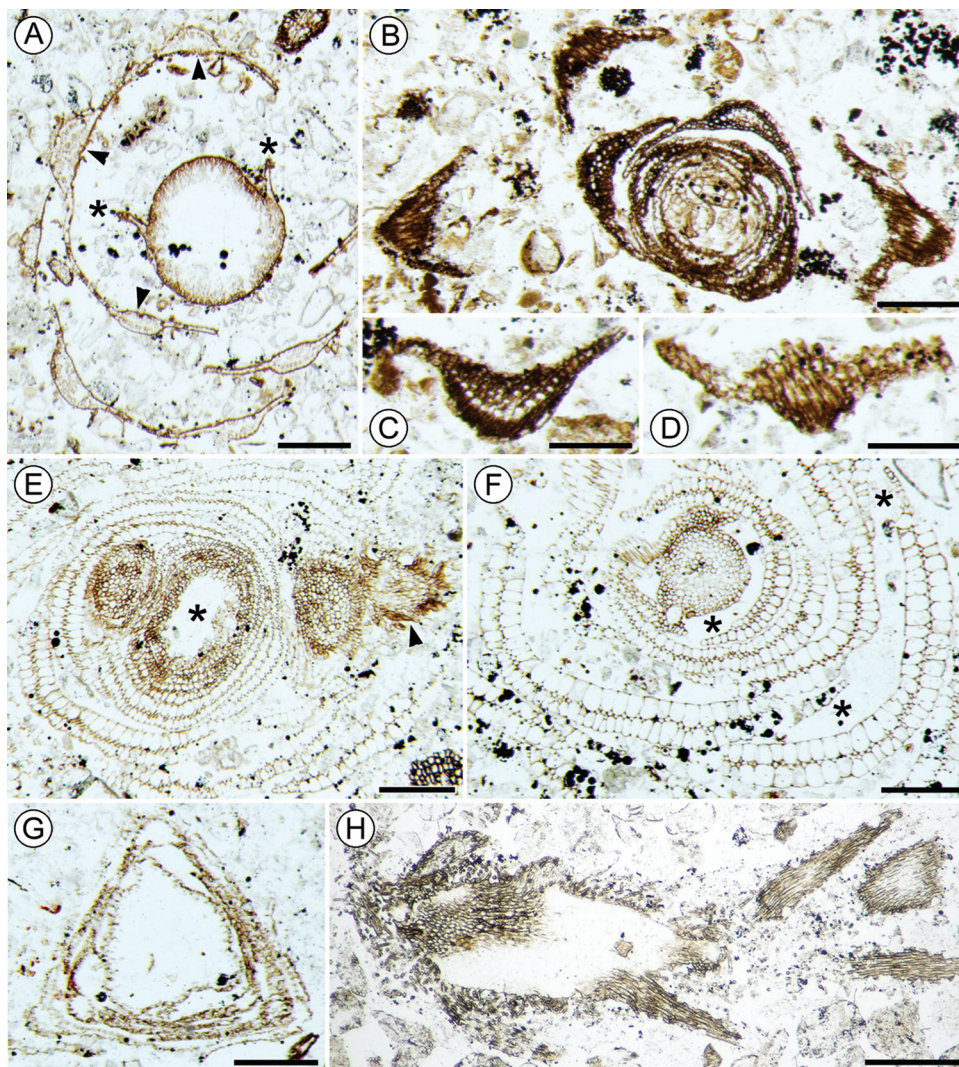
the moss produces gemmae in gemmae cups borne at the tips of gametophyte shoots (Fig. 2B) (Bippus et al. 2013).

This Apple Bay polytrichacean shares the highest number of characters with *Lyellia* R. Br., *Bartramiopsis* Kindb., and *Alophosia* Cardot (Bippus et al. 2015), including a bistratose lamina with an abaxial layer of mammillose cells

and a narrow, abaxially rotund costa with highly similar anatomy. Preliminary results of a morphology-based phylogenetic analysis show the Apple Bay polytrichacean nested in a clade with *Alophosia* and *Lyellia*. However, whereas *Lyellia*, *Bartramiopsis*, and *Alophosia* are thought to form a basal grade in the Polytrichaceae (Bell et al. 2015), in this analysis the clade

including *Alophosia* + Apple Bay polytrichacean + *Lyellia* does not occupy a basal position in the Polytrichaceae, and tree topology is highly sensitive to outgroup selection (Bippus et al. 2015). These indicate a need for further exploration of outgroup options and character coding regimes; further phylogenetic analyses are ongoing. Nevertheless, irrespective of the exact phylogenetic position of this Apple Bay polytrichacean, this moss represents the oldest unequivocal record of the family Polytrichaceae and of moss gemmae.

Leucobryaceous mosses are also recognized in the Apple Bay flora. The group is represented by a type characterized by gametophytes that branch to form flat splays (Fig. 2E). Gametophyte stems have marked epidermis–cortex differentiation and a central conducting strand (Fig. 3K). The leaves have secund tips and typical leucobryaceous anatomy, featuring a very wide costa that consists of one layer of very narrow, elongated chlorocysts sandwiched between an adaxial and an abaxial layer of large leucocysts (Fig. 2F). The leaf lamina, unistratose, is only about 8 cells wide (Unger et al. 2012). This moss shares several characters with a few genera in the family: *Leucobryum* Hampe, *Cladopodanthus* Dozy et Molk., *Holomitriopsis* H. Rob., and *Steyermarkiella* H. Rob. While closely similar to *Leucobryum*, the Apple Bay moss is most similar to *Steyermarkiella*, with which it shares chlorocyst shape and leucocyst arrangement, and from which it differs only in the shape of leucocysts and the distribution of pores in leucocyst and laminal cell walls. This Apple Bay moss is the oldest known record of the leucobryaceous group.

Another moss type present at Apple Bay features a weakly triquetrous stem bearing tristichous, helically arranged, imbricate and evenly keeled leaves (Fig. 2G). The leaves are erect and closely spaced, with slightly recurved margins in the upper half and unistratose lamina, which can be bistratose near the costa. The strong costa is attenuate and exhibits some differentiation between thicker-walled epidermal cells and thinner-walled internal cells (Fig. 2G). In the extant flora, select species of some genera or entire genera exhibiting tristichous helical phyllotaxis are known in several moss families, including the Meesiaceae, Seligeriaceae, Polytrichaceae, Bartramiaceae, Catoscopiaceae, Grimmiaceae, Pottiaceae, Fontinalaceae, Amphidiaceae, and Ditrichaceae. Of these, the Apple Bay tristichous moss compares well with *Seligeria tristicha* (Brid.) Bruch & Schimp. (Seligeriaceae), *Anoectangium* Schwägr. and *Triquetrella* C. Müll. (Pottiaceae), *Tristichum mirabile* (C. Müll.) Herz. (Ditrichaceae), and *Plagiopus oederianus* H. Crum et L.E. Anderson (Bartramiaceae). A complete description of this moss type, currently in progress, will allow for further comparisons leading to more precise taxonomic circumscription.

Two other Apple Bay mosses are clearly distinct from those described above but resolution of their systematic affinities will require in-depth characterization in the future. One of these is a moss with very robust stems (probably the most robust in the assemblage, at >500 μm diameter) exhibiting a well-defined conducting strand and broad leaf bases. Leaf costae are also strong, up to 300 μm or more in width and 100 μm or more in thickness (Fig. 3A). The overall figure and complex costal anatomy of this moss are strongly suggestive of polytrichaceous affinities. The other moss type features relatively thick stems and robust leaf costae consisting predominantly of very narrow and long cells with thick walls; preservation of the leaf lamina is incomplete (Fig. 2H).

Liverworts

One fossil specimen in the Apple Bay flora bears a close resemblance to the thalloid liverworts. Among these, the specimen, although incompletely preserved, exhibits several features characteristic of the complex thalloid liverworts. The specimen is a wide, flat, relatively thick fragment that is devoid of any strands of conducting tissue and consists mostly of large cells, similar to those in the storage layer of complex thalloid liverworts (Fig. 3C). The upper surface of this specimen preserves groups of irregularly arranged small cells with thin walls (Fig. 3G) that could represent remnants of an assimilatory layer that would have been protected by an upper epidermis (which was not preserved). On the lower surface of the specimen, rhizoid bases are recognized, attached to small thin-walled cells representing a lower epidermis (Fig. 3D).

Thalloid fossils

Several specimens in the flora represent thalloid plants whose systematic affinities are difficult to resolve. The absence of vascular tissues in these specimens precludes their interpretation as fragments of tracheophyte leaves. Thus, the only explanation for the nature of these fossils is that they represent thalloid gametophytes belonging to one of three groups: hornworts, liverworts, or seed-free plants (ferns, sphenopsids). Unfortunately, owing to (*i*) the relative simplicity in morphology and anatomy of thalloid plant forms; (*ii*) the broad range of morphological diversity of gametophytes within each group; and (*iii*) the lack of extensive comparative studies covering gametophyte anatomy for the most diverse of the thalloid gametophyte-producing group, the ferns, no operational set of criteria is available for distinguishing between the gametophytes of the different groups. As a result, comparisons and taxonomic decisions are speculative.

One fossil is a very thin thallus that exhibits gaps in the ground tissue between the two epidermal layers. The lower epidermis bears long, smooth rhizoids (Fig. 3F). It is unclear whether the gaps in the ground tissue are due to incomplete preservation or reflect the real anatomy of the plant. If the latter were true, these gaps would be consistent with the mucilage clefts present in hornwort gametophytes or with cavities that host cyanobacterial colonies, as seen in hornworts and some simple thalloid liverworts (e.g., *Blasia* L.).

Fig. 3. Early Cretaceous gametophytes from Apple Bay (Vancouver Island). (A) Cross section of moss gametophyte of probable polytrichaceous affinity; note robust stem with central tissues partially preserved and conducting strand (arrowhead), and leaves with very wide, thick costae, also showing partial tissue preservation (asterisks). P13632 Ftop #1. Scale bar = 200 μm. (B) Thalloid gametophyte cross section; note well-differentiated epidermis, rhizoids attached to or sectioned close to lower epidermis, and intracellular fungal colonization of central region on the lower side of thallus. P13131 Dtop #30d. Scale bar = 400 μm. (C) Cross section of thalloid liverwort gametophyte; note larger cells of storage layer toward upper side of thallus; light-colored remnants of incompletely preserved assimilatory layer are lining the upper surface of the specimen. P15393 Bbot #1b. Scale bar = 250 μm. (D) Detail of same liverwort thallus as in Fig. 3C; note light-colored rhizoid bases on lower thallus side. P15393 Bbot #5b. Scale bar = 100 μm. (E) Putative bryophyte sporangium comparable in size and wall structure with the epidermal layer of some liverwort sporangia (e.g., *Porella*). P13311 Itop #1e. Scale bar = 300 μm. (F) Cross section of thin horizontal thallus with long rhizoids diverging from its lower surface (arrowheads); note rhizoid base (asterisk). P15425 Cbot #2b. Scale bar = 250 μm. (G) Detail of Fig. 3C; note light-colored remnants of incompletely preserved assimilatory layer lining the upper surface. P15393 Bbot #1b. Scale bar = 200 μm. (H) Longitudinal section of bistratose leaf lamina of polytrichaceous moss in Figs. 2B–2D; note mammillose adaxial cells and squat abaxial cells. P15393 Bbot #1b. Scale bar = 50 μm. (I) Cross section of rhizomatous gametophyte stem with two diverging branches seen in longitudinal section; note faint, incompletely preserved leaves around all three stems. P17623 Btop #4. Scale bar = 200 μm. (J) Polytrichaceous moss, stem cross section with conspicuous conducting strand (darker, at center); note large deuter cells in cross-sectioned leaf costae. P13158 Cbot #10. Scale bar = 200 μm. (K) Leucobryaceous moss, stem cross section with central conducting strand (consisting of narrow cells with very thin cell walls). P14330 Bbot #35a. Scale bar = 150 μm.
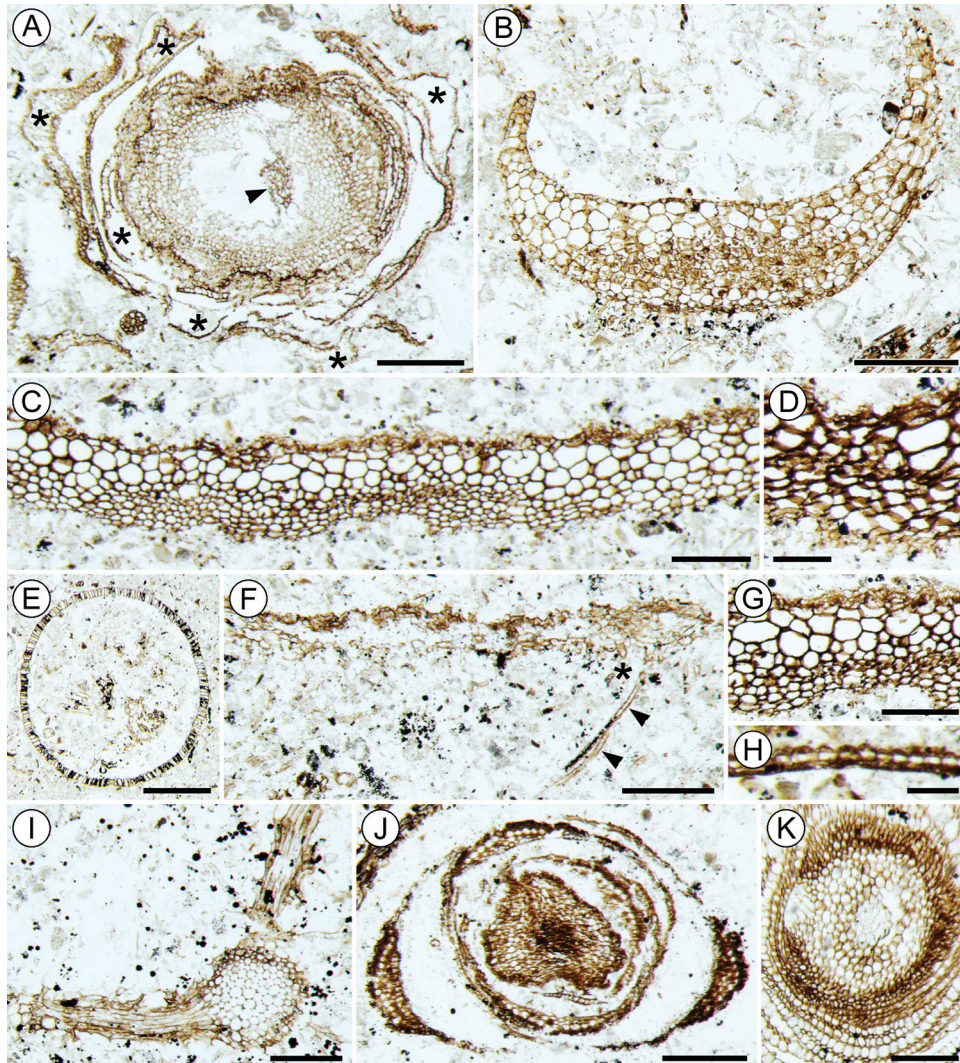
Another fossil is a thallus with upturned sides and crescent-shaped cross section. The thallus exhibits well-differentiated epidermal layers on both upper side and underside (Fig. 3B). The lower epidermis bears rhizoids. A well-circumscribed region located centrally in the lower side of the thallus consistently contains intracellular fungal hyphae (Fig. 3B). This situation is similar to that seen in liverwort and fern gametophytes colonized by

arbuscular mycorrhizal fungi (e.g., Duckett et al. 2006; Ogura-Tsujita et al. 2016). Because fern and *Equisetum* gametophytes tend to lack a well-differentiated epidermal layer, which is conspicuous in most complex thalloid liverworts (and some simple thalloid liverworts), the fossil is probably a liverwort.

Sporophytes

Given the abundance of bryophyte material uncovered at Apple Bay, the absence of unequivocal bryophyte sporophytes is intriguing. The many seemingly leafless bryophyte axes observed in the assemblage initially fueled hopes that they would represent sporophytes. However, most of these axes probably represent rhizomatous portions of leafy gametophytes. These are usually characterized by smaller, less robust or already decaying leaves that are more distantly spaced and preserve poorly. Such is the case of an axis that exhibited no attached leaves in the plane of section that exposed it initially, but revealed upon serial sectioning incompletely preserved leaf bases and branching (Fig. 3I).

If some of the leafless bryophyte axes represent fragments of sporophyte setae, none of those that were followed through serial sections to date has substantiated a sporangium or a connection to a gametophyte at either end. Nevertheless, one specimen representing a sporangium with circular cross sectional outline is very similar in size and anatomy (Fig. 3E) to the epidermal layer with I-band thickenings found in sporangia of liverworts such as *Porella* L. (e.g., Crandall-Stotler et al. 2009).

Discussion

Early Cretaceous bryophyte diversity as seen from Apple Bay

Of the ca. 70 moss species known from pre-Cenozoic deposits, only about 10 are known from Early Cretaceous deposits (Krassilov 1973, 1982; Oostendorp 1987; Ignatov and Shcherbakov 2011*a*). With at least nine distinct moss types representing as many new species and possibly genera, the Apple Bay flora doubles the number of Early Cretaceous moss species and increases pre-Cenozoic moss diversity by more than 10%. This represents a significant addition to the known diversity of pre-Cenozoic fossil mosses, especially for the flora of a single locality, and is surpassed in diversity only by the Late Permian Aristovo flora on the Dvina River (Russian Platform; Ignatov 1990), which includes 14 moss species.

The Apple Bay moss flora demonstrates that the Early Cretaceous vegetation hosted representatives of entirely extinct groups, as well as those of extant families. At least four distinct types of tricostate mosses present here add up to the three known species of *Tricostium*. While it is unclear whether all these tricostate types belong in the hypnanaean family Tricostaceae, this diversity of Mesozoic tricostate mosses that have no close living relatives demonstrates once again that the fossil record hosts significant sections of biodiversity (such as entire lineages)

that would remain unknown in the absence of paleobotanical studies (Shelton et al. 2015).

It is noteworthy that the two Apple Bay types that are unequivocally assignable to extant families: the gemmae-producing polytrichaceous type, and the leucobryaceous type; each combine characters of several genera in their respective families. This suggests that at least two lineages of modern mosses were represented by stem-group taxa in the Early Cretaceous. The Apple Bay leucobryaceous moss is most similar to *Steyermarkiella*, a monotypic genus endemic to the Guayana Highlands of Venezuela (Gradstein et al. 2001), whereas the polytrichaceous moss is most similar to *Alophosia*, another monotypic genus endemic to the Azores archipelago (Smith 1971). Both of these cases involve wide, intercontinental distances between the Apple Bay Cretaceous mosses and their putative closest living relatives. Many extant mosses have intercontinental ranges; in a striking example, *Orthotrichum acuminatum* H. Philib., with documented occurrences in the western Nearctic, the western Palearctic, and Paleotropical eastern Africa, demonstrates that in mosses it is not impossible even for single species to have multiple-continent disjunct ranges (Vigalondo et al. 2016). Whereas the phylogenetic position of *Steyermarkiella* is unresolved, *Alophosia* is resolved as the basal-most member of Polytrichaceae in molecular phylogenetic analyses (Bell et al. 2015). Could these imply that *Steyermarkiella* and *Alophosia* are relictual representatives of basal leucobryaceous and polytrichaceous groups that were more widely spread and had originated at least as early as the Early Cretaceous?

Thalloid liverworts are known from rocks as old as the Middle Devonian (Oostendorp 1987; VanAller et al. 2008) and, possibly, the Lower Devonian (Guo et al. 2012). Up to 14 species are recorded in the Cretaceous (Oostendorp 1987) and relatively extensive mats of marchantioid liverworts have been reported in the Lower Cretaceous (Aptian–Albian) of Spain (Diéguez et al. 2007). The presence at Apple Bay of a thalloid liverwort and of thalloid plant gametophytes, in general, adds to the fossil record of thalloid gametophytes and is the first documented occurrence of this type of plants as permineralizations.

Preservation of bryophyte fossils

The bryophytes in the Apple Bay flora provide another confirmation, possibly the strongest to come, thus far, from the fossil record, of the excellent preservation potential of bryophytes. These ideas are reinforced by the fact that the Apple Bay assemblage is undoubtedly allochthonous. The plants are preserved by permineralization within marine sediments, which implies that all the plant material underwent transport over some distance: from land into streams, which then transported it to sea, where it eventually sank to the bottom and was buried in sediment. Although the bryophyte fossils are among the smallest bits in the assemblage, they are preserved just as well as neighboring fragments of wood and conifer

needles, and even exhibit delicate, ephemeral parts such as gametangia.

Given the nature of this allochthonous assemblage, the plant fragments comprising it probably did not enter the taphonomic window all at the same time, as demonstrated by the different degrees of decay we see in the plant tissues across the assemblage. If bryophytes had low preservation potential, then their presence in the Apple Bay assemblage would imply that they are part of the fraction that had the shortest residence time in the taphonomic window. However, the nature of the assemblage makes this very unlikely. Furthermore, the bryophyte material at Apple Bay shows the same range of degrees of decay that we see in the other types of plant material in the assemblage. Thus, if there were any doubts left about the fossil preservation potential of bryophytes, the quantity and quality of the bryophyte material in this allochthonous assemblage thoroughly discount them.

The fact that small and delicate bryophyte structures, such as gametangia, are preserved in some of the specimens indicates that those specimens were among the ones that had the shortest residence time in the taphonomic window. These specimens provide a measure of the timing and intensity of taphonomic processes. The numerous antheridia documented on one *Tricosta* gametophyte (Shelton et al. 2015) could have been preserved only if exposure to taphonomic processes was very short and the intensity of those processes was low. Thus, we can infer that the plant experienced transport over a short distance, resided in the water column for a short time, and became buried in sediment and permineralized rapidly.

Taphonomic inferences of this type have implications for understanding some of the interactions in the local Early Cretaceous ecosystem. For example, the same *Tricosta* plant that preserves gametangia is host to a rich community of fungi (Shelton et al. 2014). In assessing the role of these fungi it is important to take into account the fact that the host moss had a short residence time in the taphonomic window — shorter than it takes ephemeral structures, such as antheridia, to decay. This excludes the possibility that the fungi were saprotrophs. In other words, if the entire taphonomic history of the moss is shorter than the decay time of antheridia, then this interval would not have been long enough to allow for such dense fungal colonization of the moss post-mortem. Therefore, the fungi colonized the moss while it was living and represent either necrotrophs or biotrophs. Some of these fungi show close morphological similarity to bryophilous biotrophic fungi documented in many modern mosses (e.g., Racovitza 1959; Döbbeler 2002; Döbbeler and Hertel 2013).

Recognizing bryophyte fossils

If bryophytes have good preservation potential, then their relative scarcity in the pre-Cenozoic fossil record could be explained by (*i*) low abundance in the geologic past; (*ii*) taphonomic biases unrelated to preservation potential (such as growth in environments that hinder entry into taphonomic pathways leading to preservation); or (*iii*) an incompletely explored fossil record. The abundance of bryophytes at Apple Bay demonstrates that they were not rare occurrences in the Early Cretaceous flora, and that at least a fraction of the bryophyte flora was not subject to taphonomic biases. Together, these point to an incompletely explored fossil record as the main cause of fossil bryophyte scarcity. While this is due at least in part to a lack of paleobryological capacity, the latter may be exacerbated by a deficiency in the ability to recognize bryophyte fossils. Indeed, in addition to generally small sizes, owing to which bryophytes can easily go unnoticed, the arcane and rich specifics of bryophyte morphology and anatomy are unfamiliar to most paleobotanists.

To start alleviating this situation, I present below some comments and criteria for recognizing bryophyte fossils in permineralized material. Developed based on observations of the Apple Bay flora and out of the need to address the systematic affinities of bryophytes in this flora, these criteria are not all-encompassing. For example, the general morpho-anatomical criteria discussed below necessarily project into the past characters that differentiate groups of extant plants. Consequently, they bear the shortcomings of such an approach, and risk miss-assigning fossils with combinations of characters unknown in the modern flora. Nevertheless, their application represents a logical first step in the formulation of working hypotheses aimed at addressing the systematic affinities of these fossils.

Most of the bryophyte material at Apple Bay stands out among other plant fossils owing to its coloration, which is different from that of the vascular plant material. Whereas the latter generally exhibits shades of chocolate-brown, dark sepia, and russet (wiki/Category:Shades_of_brown), the bryophytes are usually light yellowish-brown or light ochre to yellow, and a color-based bryophyte search image is easily acquired upon familiarization with the Apple Bay assemblage. The different coloration of bryophyte fossils as compared with that of vascular plants probably reflects differences in cell wall chemistry.

Thalloid bryophytes are most easily identified based on cross sections of gametophyte thalli, which are devoid of vascular strands that include xylem. However, widely-applicable and reliable criteria for distinguishing among these thalloid liverworts (especially simple thalloid liverworts) from hornworts and from pteridophyte thalloid gametophytes based on cross-sectional anatomy are not available. These different groups can be identified only in special cases when diagnostic features, such as pegged rhizoids (complex thalloid liverworts), or characteristic gametangia, are preserved.

Leafy liverworts and mosses are most easily identified based on gametophyte cross sections that expose stem and leaf anatomy. They are all recognized as bryophytes

Fig. 4. Early Cretaceous moss gametophytes. (A) Longitudinal section of stem with conspicuous leaf bases; Apple Bay (Vancouver Island). P13422 D #1. Scale bar = 200 μm. (B) Oblique section of incompletely preserved stem (asterisk) and leaves diverging toward top of image; note leaf costa with polytrichaceous anatomy (large deuter cells; bottom right) and leaf longitudinal section (bottom right to top left); Budden Canyon Formation (California). HPH219 Ctop #4a. Scale bar = 250 μm. (C) Detail of Fig. 1B showing polytrichaceous leaf anatomy in longitudinal section; note wide-lumen deuter cells and lamella 3–4 cells tall on adaxial side. Scale bar = 50 μm.

in this plane of section by the absence of xylem-containing strands in the stems and leaves. Additionally, bryophyte leaves have a unistratose lamina (although in some the lamina can be bistratose; Figs. 2D and 3H). The presence or absence of a leaf costa (midrib) is a relatively straightforward criterion for distinguishing liverworts (characterized by leaves devoid of a costa; ecostate) from mosses, whose leaves have a more or less robust costa (and can have several costae per leaf; Shelton et al. 2015). Additional criteria for distinguishing moss and liverwort gametophytes include (*i*) anisophylly, present in liverworts that have three-ranked leaves (two ranks of lateral leaves and one rank of underleaves); (*ii*) multicellular rhizoids present in mosses; and (*iii*) the presence of a conducting strand in the stem of some mosses (Figs. 3A, 3J, and 3K). Exceptions to all these criteria, such as mosses with ecostate leaves, isophyllous liverworts, and liverworts with a stem conducting strand, exist but do not hinder identification of the two groups once some familiarity with bryophyte morphology and anatomy has been achieved. However, leaf-based criteria are less useful in the case of rhizomatous basal portions of gametophytes, which usually have more widely spaced, smaller, and less well-preserved leaves.

For mosses, the cross-sectional anatomy of gametophyte stems, and particularly leaves, provides diagnostic information allowing for identification of some major lineages. For example, many Polytrichaceae have robust costae with complex anatomy and typically feature photosynthetic lamellae on the adaxial side of leaves; leucobryaceous mosses often have broad costae with a characteristic combination of large leucocysts and small or narrow chlorocysts; sphagnaleans also have leaves with a regular arrangement of leucocysts and chlorocysts. Additionally, stem cross sections reveal phyllotaxis, which can also be a diagnostic character that allows for narrowing down the systematic affinities of the fossils. Conversely, longitudinal sections are more difficult to work with, in terms of documenting leaf anatomy or phyllotaxis (Fig. 4A). Nevertheless, they reveal relatively clearly whether a bryophyte has ecostate leaves or bears costae. Ideally, a combination of cross sections and longitudinal sections through several gametophyte stems will reveal information about a multitude of diagnostic characters, allowing for detailed reconstructions and in-depth understanding of the morphology and anatomy of the plants, as well as high-resolution systematic placement (e.g., Steenbock et al. 2011; Shelton et al. 2015).

Recently, application of the search images and criteria developed during studies of the Apple Bay flora has led to recognition of a large number of anatomically preserved bryophyte fossils in another Early Cretaceous marine unit on the West Coast of North America. The Budden Canyon Formation, in northern California, is only 8–10 million years younger than the Apple Bay assemblage (Unger and Tomescu 2013) and may soon rival the Apple Bay flora in bryophyte diversity; it hosts polytrichaceous (Figs. 4B and 4C), leucobryaceous, tricostate, and other moss types that await detailed studies.

Conclusions

Extensive exploration of a permineralized plant fossil assemblage in the Lower Cretaceous of Vancouver Island, at Apple Bay, has revealed an abundance of bryophyte fossils. The Apple Bay flora hosts at least nine distinct moss types, one complex thalloid liverwort, and two other thalloid plants (that may represent bryophyte or pteridophyte gametophytes), as well as potential for additional discoveries of new bryophytes. All of these contribute a significant fraction of biodiversity to the pre-Cenozoic fossil record of bryophytes. Both the abundance and the diversity of bryophyte fossils in the Apple Bay flora reach levels never before seen in another allochthonous plant fossil assemblage. This fossil bryoflora reveals the presence of extant moss families, represented by new taxa that combine characters of several extant genera (Unger et al. 2012; Bippus et al. 2013, 2015), as well as of extinct but diverse lineages (Shelton et al. 2015). Among these are the oldest unequivocal occurrences for hypnanaean pleurocarps, leucobryaceous mosses, Polytrichaceae, moss gametangia and gemmae, and the only known record of permineralized thalloid liverworts. In-depth characterization of bryophytes in the Apple Bay flora and other similar assemblages, and resolution of their systematic affinities is bound to contribute to understanding of bryophyte evolution and phylogeny.

Although the Apple Bay plant assemblage is allochthonous, the bryophyte material is well preserved, sometimes in surprising detail (gemmae, gametangia). The high quality of preservation, along with the abundance of bryophyte fossils at Apple Bay corroborate previous observations and experimental data, rejecting the traditional hypothesis that bryophytes have low preservation potential and demonstrating, instead, excellent preservation potential of these plants. Seen in this perspective, the scarcity of the pre-Cenozoic bryophyte fossil record appears to be the result of a combination between the small size, and thus, more cryptic nature, of bryophytes and a lack of paleobryological capacity. Fossil floras with a rich bryophyte content, like the Apple Bay flora, are not only encouraging for the preservation potential of these plants, but can also provide excellent opportunities for cross-disciplinary collaboration between extant bryophyte systematists and paleobotanists. In turn these will foster growth in paleobryological capacity and, ultimately, a more densely sampled and better understood bryophyte fossil record.

Acknowledgements

References

Atkinson, B.A., Rothwell, G.W., and Stockey, R.A. 2014*a*. *Hubbardiastrobus cunninghamioides* gen. et sp. nov., evidence for a Lower Cretaceous diversification of cunninghamioid Cupressaceae. Int. J. Plant Sci. **175**: 256–269.

Atkinson, B.A., Rothwell, G.W., and Stockey, R.A. 2014*b*. *Hughmillerites vancouverensis* sp. nov. and the Cretaceous diversification of Cupressaceae. Am. J. Bot. **101**: 2136–2147. PMID: 25480710.

Bell, N.E., and York, P.V. 2007. *Vetiplanaxis pyrrhobryoides*, a new fossil moss genus and species from Middle Cretaceous Burmese amber. Bryologist, **110**: 514–520. doi:10.1639/0007-2745(2007)110[514:VPANFM]2.0.CO;2.

Bell, N.E., Kariyawasam, I.U., Hedderson, T.A.J., and Hyvönen, J. 2015. *Delongia* gen. nov., a new genus of Polytrichaceae (Bryophyta) with two disjunct species in East Africa and the Himalaya. Taxon, **64**(5): 893–910. doi:10.12705/645.2.

Bippus, A.C., Shelton, G.W.K., Stockey, R.A., Rothwell, G.W., and Tomescu, A.M.F. 2013. A polytrichaceous moss with gemmae from the Early Cretaceous of Vancouver Island (Canada). Botanical Society of America meeting abstract. Available from http://2013.botanyconference.org/engine/search/index.php?func=detail&aid=800 [accessed 17 February 2016].

Bippus, A.C., Stockey, R.A., Rothwell, G.W., and Tomescu, A.M.F. 2015. Phylogenetic relationships in the Polytrichaceae (Bryophyta): a morphology-based approach. Botanical Society of America meeting abstract. Available from http://2015.botanyconference.org/engine/search/index.php?func=detail&aid=589 [accessed 17 February 2016].

Bronson, A.W., Klymiuk, A.A., Stockey, R.A., and Tomescu, A.M.F. 2013. A perithecial sordariomycete (Ascomycota, Diaporthales) from the Lower Cretaceous of Vancouver Island, British Columbia, Canada. Int. J. Plant Sci. **174**: 278–292. doi:10.1086/668227.

Crandall-Stotler, B., Stotler, R.E., and Long, D.G. 2009. Morphology and classification of the Marchantiophyta. *In* Bryophyte biology. 2nd ed. *Edited by* B. Goffinet and A.J. Shaw. Cambridge University Press, Cambridge, UK. pp. 55–138.

Diéguez, C., Rodríguez-López, J.P., and Meléndez, N. 2007. Marchantiopsid colonization mats from the Upper Aptian – Lower Albian of the Escucha Formation (Oliete sub-basin, Iberian Ranges, eastern Spain). C. R. Palevol. **6**: 413–422. doi:10.1016/j.crpv.2007.09.022.

Döbbeler, P. 2002. Microniches occupied by bryophilous ascomycetes. Nova Hedwig. **75**, 275–306. doi:10.1127/0029-5035/2002/0075-0275.

Döbbeler, P., and Hertel, H. 2013. Bryophilous ascomycetes everywhere: distribution maps of selected species on liverworts, mosses and Polytrichaceae. Herzogia, **26**(2): 361–404. doi:10.13158/heia.26.2.2013.361.

Duckett, J.G., Carafa, A., and Ligrone, R. 2006. A highly differentiated glomeromycotean association with the mucilage-secreting, primitive antipodean liverwort *Treubia* (Treubiaceae):

clues to the origins of mycorrhizas. Am. J. Bot. **93**(6): 797–813. doi:10.3732/ajb.93.6.797. PMID:21642142.

Edwards, D., Duckett, J.G., and Richardson, J.B. 1995. Hepatic characters in the earliest land plants. Nature, **374**: 635–636. doi:10.1038/374635a0.

Frahm, J.-P. 2010. Die Laubmoosflora des Baltischen Bernstein-waldes. Weissdorn-Verlag, Jena, Germany.

Goffinet, B., Buck, W.R., and Shaw, A.J. 2009. Morphology, anatomy, and classification of the Bryophyta. *In* Bryophyte biology. 2nd ed. *Edited by* B. Goffinet and A.J. Shaw. Cambridge University Press, Cambridge, UK. pp. 55–138.

Gradstein, S.R., Churchill, S.P., and Salazar-Allen, N. 2001. Guide to the bryophytes of tropical America. New York Botanical Garden Press, New York.

Graham, L.E. 1993. Origin of land plants. J. Wiley & Sons, New York.

Graham, L.E., Wilcox, L.W., Cook, M.E., and Gensel, P.G. 2004. Resistant tissues of modern marchantioid liverworts resemble enigmatic Early Paleozoic microfossils. Proc. Natl. Acad. Sci. U.S.A. **101**: 11025–11029. doi:10.1073/pnas.0400484101. PMID:15263095.

Guo, C.-Q., Edwards, D., Wu, P.-C., Duckett, J.G., Hueber, F.M., and Li, C.-S. 2012. *Riccardiothallus devonicus* gen. et sp. nov., the earliest simple thalloid liverwort from the Lower Devonian of Yunnan, China. Rev. Palaeobot. Palynol. **176–177**: 35–40. doi:10.1016/j.revpalbo.2012.03.012.

Harris, T. 1939. *Naiadita*, a fossil bryophyte with reproductive organs. Ann. Bryol. **12**: 57–70.

Hedenas, L., Heinrichs, J., and Schmidt, A.R. 2014. Bryophytes of the Burmese amber forest: amending and expanding the circumscription of the Cretaceous moss genus *Vetiplanaxis*. Rev. Palaeobot. Palynol. **209**: 1–10. doi:10.1016/j.revpalbo.2014.05.008.

Hemsley, A. 2001. Comparison of *in vitro* decomposition of bryophytic and tracheophytic plant material. Bot. J. Linn. Soc. **137**: 375–384. doi:10.1111/j.1095-8339.2001.tb02332.x.

Hentschel, J., Schmidt, A.R., and Heinrichs, J. 2009. *Frullania cretacea* sp. nov. (Porellales, Jungermanniopsida), a leafy liverwort preserved in Cretaceous amber from Myanmar. Crypt. Bryol. **30**: 323–328.

Hernandez-Castillo, G.R., Stockey, R.A., and Rothwell, G.W. 2006. *Anemia quatsinoensis* sp. nov. (Schizaeaceae), a permineralized fern from the Lower Cretaceous of Vancouver Island. Int. J. Plant Sci. **167**: 665–674.

Hübers, M., and Kerp, H. 2012. Oldest known mosses discovered in Mississippian (late Visean) strata of Germany. Geology, **40**: 755–758. doi:10.1130/G33122.1.

Ignatov, M.S. 1990. Upper Permian mosses from the Russian platform. Palaeontographica B, **217**: 147–189.

Ignatov, M.S., and Shcherbakov, D.E. 2011*a*. Lower Cretaceous mosses from Khasurty (Transbaikalia). Arctoa, **20**: 19–42. doi:10.15298/arctoa.20.02.

Ignatov, M.S., and Shcherbakov, D.E. 2011*b*. Lower Triassic mosses from Yamanus (Mongolia). Arctoa, **20**: 65–80. doi:10.15298/arctoa.20.04.

Joy, K.W., Willis, A.J., and Lacey, W.S. 1956. A rapid cellulose peel technique in palaeobotany. Ann. Bot. **20**: 635–637.

Katagiri, T., Mukai, M., and Yamaguchi, T. 2013. A new fossil moss *Muscites kujiensis* (Bryopsida) preserved in the Late Cretaceous amber from Japan. Bryologist, **116**: 296–301. doi:10.1639/0007-2745-116.3.296.

Kenrick, P., and Crane, P.R. 1997. The origin and early diversification of land plants. Smithsonian Institution Press, Washington.

Klymiuk, A.A., and Stockey, R.A. 2012. A Lower Cretaceous (Valanginian) seed cone provides the earliest fossil record for *Picea* (Pinaceae). Am. J. Bot. **99**: 1069–1082. doi:10.3732/ajb.1100568. PMID:22623610.

Kodner, R.B., and Graham, L.E. 2001. High-temperature, acid-hydrolyzed remains of *Polytrichum* (Musci, Polytrichaceae) resemble enigmatic Silurian–Devonian tubular microfossils. Am. J. Bot. **88**:462–466. doi:10.2307/2657111. PMID:11250824.

Konopka, A.S., Herendeen, P.S., Smith Merrill, G.L., and Crane, P.R. 1997. Sporophytes and gametophytes of Polytrichaceae from the Campanian (Late Cretaceous) of Georgia, USA. Int. J. Plant Sci. **158**: 489–499. doi:10.1086/297459.

Krassilov, V.A. 1973. Mesozoic bryophytes from the Bureja Basin, Far East of the USSR. Palaeontographica B, **143**: 95–105.

Krassilov, V.A. 1982. Early Cretaceous flora of Mongolia. Palaeontogr. B, **181**(1–3): 1–43.

Kroken, S.B., Graham, L.E., and Cook, M.E. 1996. Occurrence and evolutionary significance of resistant cell walls in charophytes and bryophytes. Am. J. Bot. **83**: 1241–1254. doi:10.2307/2446108.

Little, S.A., Stockey, R.A., and Rothwell, G.W. 2006*a*. *Solenostelopteris skogiae* sp. nov. from the Lower Cretaceous of Vancouver Island. J. Plant Res. **119**: 525–532. PMID:16941064.

Little, S.A., Stockey, R.A., and Rothwell, G.W. 2006*b*. *Stramineopteris aureopilosus* gen. et sp. nov.: reevaluating the role of vegetative anatomy in the resolution of leptosporangiate fern phylogeny. Int. J. Plant Sci. **167**: 683–694. doi:10.1086/501156.

Mamontov, Y.S., Heinrichs, J., Schafer-Verwimp, A., Ignatov, M.S., and Perkovsky, E.E. 2015. Hepatics from Rovno amber (Ukraine), 4. *Frullania riclefgrollei*, sp. nov. Rev. Palaeobot. Palynol. **223**: 31–36. doi:10.1016/j.revpalbo.2015.08.007.

Matsunaga, K.K.S., Stockey, R.A., and Tomescu, A.M.F. 2013. *Honeggeriella complexa* gen. et sp. nov., a heteromerous lichen from the Lower Cretaceous of Vancouver Island (British Columbia, Canada). Am. J. Bot. **100**: 450–459. doi:10.3732/ajb.1200470.

Ogura-Tsujita, Y., Hirayama, Y., Sakoda, A., Suzuki, A., Ebihara, A., Morita, N., and Imaichi, R. 2016. Arbuscular mycorrhizal colonization in field-collected terrestrial cordate gametophytes of pre-polypod leptosporangiate ferns (Osmundaceae, Gleicheniaceae, Plagiogyriaceae, Cyatheaceae). Mycorrhiza, **26**: 87–97. doi:10.1007/s00572-015-0648-1. PMID:26047572.

Oostendorp, C. 1987. The bryophytes of the Palaeozoic and the Mesozoic. Bryophytorum Bibliotheca, **34**: 1–112.

Racovitza, A. 1959. Étude systématique et biologique des champignons bryophiles. Mém. Mus. Nat. Hist. Nat. Bot. **10**.

Ray, M.M., Rothwell, G.W., and Stockey, R.A. 2014. Anatomically preserved Early Cretaceous bennettitalean leaves: *Nilssoniopteris corrugata* n. sp. from Vancouver Island, Canada. J. Paleontol. **88**: 1085–1093.

Rothwell, G.W., and Stockey, R.A. 2006. Combining characters of Pteridaceae and tree ferns: *Pterisorus radiata* gen. et sp. nov., a permineralized Lower Cretaceous filicalean with radial sori. Int. J. Plant Sci. **167**: 695–701.

Rothwell, G.W., and Stockey, R.A. 2013. Evolution and phylogeny of gnetophytes: evidence from the anatomically preserved seed cone *Protoephedrites eamesii* gen. et sp. nov. and the seeds of several bennettitalean species. Int. J. Plant Sci. **174**: 511–529.

Rothwell, G.W., Stockey, R.A., and Millay, M.A. 2014. Evolution of modern Marattiales; superficially *Christensenia*-like synangia in the Early Cretaceous. Botanical Society of America meeting abstract. Available from http://2014.botanyconference.org/engine/search/index.php?func=detail&aid=283 [accessed 17 February 2016].

Shelton, G.W.K., Stockey, R.A., Rothwell, G.W., and Tomescu, A.M.F. 2014. Bryosymbiotic fungi from the Early Cretaceous (Valanginian) of Vancouver Island, British Columbia, Canada. Botanical Society of America meeting abstract. Available from http://2014.botanyconference.org/engine/search/index.php?func=detail&aid=751 [accessed 17 February 2016].

Shelton, G.W.K., Stockey, R.A., Rothwell, G.W., and Tomescu, A.M.F.

2015. Exploring the fossil history of pleurocarpous mosses: Tricostaceae fam. nov. from the Cretaceous of Vancouver Island, Canada. Am. J. Bot. **102**: 1883–1900. PMID:26542845.

Shelton, G.W.K., Stockey, R.A., Rothwell, G.W., and Tomescu, A.M.F. 2016. *Krassiloviella limbelloides* gen. et sp. nov.: additional diversity in the pleurocarpous moss family Tricostaceae (Valanginian, Vancouver Island, British Columbia). Int. J. Plant Sci. **177**: (In press)

Smith, G.L. 1971. Conspectus of the genera of Polytrichaceae. Mem. N.Y. Bot. Gard. Vol. 21, issue 3.

Smith, S.Y., Rothwell, G.W., and Stockey, R.A. 2003. *Cyathea cranhamii* sp. nov. (Cyatheaceae), anatomically preserved tree fern sori from the Lower Cretaceous of Vancouver Island, British Columbia. Am. J. Bot. **90**: 755–760. PMID:21659172.

Smith, S.Y., Currah, R.S., and Stockey, R.A. 2004. Cretaceous and Eocene poroid hymenophores from Vancouver Island, British Columbia. Mycologia, **96**: 180–186. doi:10.2307/3762001. PMID:21148842.

Smoot, E.L., and Taylor, T.N. 1986. Structurally preserved fossil plants from Antarctica: II. A Permian moss from the Transantarctic Mountains. Am. J. Bot. **73**: 1683–1691.

Steenbock, C.M., Stockey, R.A., Beard, G., and Tomescu, A.M.F. 2011. A new family of leafy liverworts from the middle Eocene of Vancouver Island, British Columbia, Canada. Am. J. Bot. **98**: 998–1006. doi:10.3732/ajb.1000396. PMID:21613072.

Stewart, W.N., and Rothwell, G.W. 1993. Paleobotany and the evolution of plants. 2nd ed. Cambridge University Press, Cambridge.

Stockey, R.A., and Rothwell, G.W. 2009. Distinguishing angiophytes from the earliest angiosperms: a Lower Cretaceous (Valanginian–Hauterivian) fruitlike reproductive structure. Am. J. Bot. **96**: 323–335. doi:10.3732/ajb.0800295. PMID:21628191.

Stockey, R.A., and Wiebe, N.J.P. 2008. Lower Cretaceous conifers from Apple Bay, Vancouver Island: *Picea*-like leaves, *Midoriphyllum piceoides* gen. et sp. nov. (Pinaceae). Botany, **86**(7): 649–657. doi:10.1139/B08-061.

Stockey, R.A., Rothwell, G.W., and Little, S.A. 2006. Relationships among fossil and living Dipteridaceae: anatomically preserved *Hausmannia* from the Lower Cretaceous of Vancouver Island. Int. J. Plant Sci. **167**: 649–663. doi:10.1086/503268.

Taylor, T.N., Taylor, E.L., and Krings, M. 2009. Paleobotany. The biology and evolution of fossil plants. 2nd ed. Academic Press, Burlington, Mass.

Taylor, T.N., Krings, M., and Taylor, E.L. 2014. Fossil fungi. Academic Press, London, UK.

Tomescu, A.M.F., Steenbock, C.M., Friedman, M., and Stockey, R.A. 2012. The Early Cretaceous Apple Bay flora of Vancouver Island: a hotspot of fossil bryophyte diversity. Botanical Society of America meeting abstract. Available from http://2012.botanyconference.org/engine/search/index.php?func=detail&aid=962 [accessed 17 February 2016].

Unger, C.R., and Tomescu, A.M.F. 2013. Reappraising the Early Cretaceous permineralized flora of the Chickabally Mudstone (Budden Canyon Formation, Baremian–Aptian, California). Botanical Society of America meeting abstract. Available from http://2013.botanyconference.org/engine/search/index.php?func=detail&aid=813 [accessed 17 February 2016].

Unger, C.R., Ortiz, A., Stockey, R.A., and Tomescu, A.M.F. 2012. An anatomically preserved leucobryaceous moss from the Early Cretaceous (Valanginian–Hauterivian) of Vancouver Island, British Columbia, Canada. Botanical Society of America meeting abstract. Available from http://2012.botanyconference.org/engine/search/index.php?func=detail&aid=646 [accessed 17 February 2016].

VanAller Hernick, L., Landing, E., and Bartowski, K. 2008. Earth's oldest liverworts: Metzgeriothallus *sharonae* sp. nov. from the Middle Devonian (Givetian) of eastern New York, USA. Rev. Palaeobot. Palynol. **148**: 154–162. doi:10.1016/j.revpalbo.2007.09.002.

Vavrek, M.J., Stockey, R.A., and Rothwell, G.W. 2006. *Osmunda vancouverensis* sp. nov. (Osmundaceae), permineralized fertile frond segments from the Lower Cretaceous of British Columbia, Canada. Int. J. Plant Sci. **167**: 631–637. doi:10.1086/500994.

Vigalondo, B., Lara, F., Draper, I., Valcarcel, V., Garilleti, R., and Mazimpaka, V. 2016. Is it really you, *Orthotrichum acuminatum*? Ascertaining a new case of intercontinental disjunction in mosses. Bot. J. Linn. Soc. **180**: 30–49. doi:10.1111/boj.12360.

Wellman, C.H., Osterloff, P.L., and Mohiuddin, U. 2003. Fragments of the earliest land plants. Nature, **425**: 282–285. doi:10.1038/nature01884. PMID:13679913.

Wickett, N.J., Mirarab, S., Nguyen, N., Warnow, T., Carpenter, E., Matasci, N., et al. 2014. Phylotranscriptomic analysis of the origin and early diversification of land plants. Proc. Natl. Acad. Sci. U.S.A. doi:10.1073/pnas.1323926111.