

SPOROPHYTES AND GAMETOPHYTES OF POLYTRICHACEAE FROM THE CAMPANIAN (LATE CRETACEOUS) OF GEORGIA, U.S.A.

ANASTASIA S. KONOPKA,* PATRICK S. HERENDEEN,¹† GARY L. SMITH MERRILL,[‡] AND PETER R. CRANE[†]

*Department of Biological Sciences, University of Illinois, Chicago, 845 West Taylor, Chicago, Illinois 60607; and

†Departments of Geology and ‡Botany, Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605

A new genus and species (*Eopolytrichum antiquum*) of the moss family Polytrichaceae are described for fossil sporophyte capsules and associated gametophytes from the early Campanian (Late Cretaceous) Buffalo Creek Member of the Gaillard Formation in central Georgia, U.S.A. The capsules show diagnostic features of the Polytrichaceae but differ from those of all extant genera. The capsules are terete in cross section, somewhat dorsiventrally flattened, and have a swollen, asymmetrical apophysis and mammillose exothecium. Stomatal complexes, each surrounded by a ring of subsidiary cells, are confined to the apophysis. The operculum is tall and dome shaped, but the calyptra and beak of the operculum are not preserved. The remains of a peristomial membrane are present around the rim of the capsule after the operculum has dehisced, but peristome teeth are absent, and the epiphragm is retained in the operculum. Spores are alete, spherical, and echinulate. Associated sterile and fertile gametophytes have leaves with adaxial, presumed photosynthetic, lamellae on the blade surface in addition to other anatomical structures comparable to extant Polytrichaceae. Inadequacies in the moss fossil record have led to contrasting interpretations as to the age of the origin of mosses and the extent of evolutionary change in the group since the Paleozoic. These fossils, which represent the first unequivocal polytrichaceous sporophytes known from the fossil record, along with other fossil mosses from this early Campanian locality, provide the first definitive evidence of modern families of mosses in the Cretaceous and demonstrate that mosses were already diverse by approximately 80 million years before present.

Introduction

“Bryophytes” are generally treated as comprising three major groups: hornworts (Anthocerotopsida), liverworts (Hepaticopsida), and mosses (Bryopsida), which together form a paraphyletic grade of non-vascular plants at the base of the embryophyte clade (Mishler and Churchill 1984; Mishler et al. 1994; Kenrick and Crane 1997). The hornworts, liverworts, and mosses are thought to have been among the earliest diverging lineages of land plants, and recent phylogenetic analyses using morphological and/or molecular data support this general hypothesis. Precise relationships among the three groups remain equivocal (Mishler and Churchill 1984; Mishler et al. 1994; Kenrick and Crane 1997), but there is a growing consensus that mosses are the likely sister group to the vascular plants (Mishler et al. 1994; Kenrick and Crane 1997).

The pre-Quaternary fossil record of bryophytes (older than 1.6 million years) is very poor. Most pre-Quaternary fossil specimens that have been described are compression fossils of gametophytes that lack systematically informative anatomical and morphological details. Pre-Quaternary bryophyte sporophytes are exceedingly rare. In part, because of the poor fossil record, there is considerable uncertainty as to the origin and evolutionary history of the major bryophyte lineages. Some authors have suggested that extant groups of mosses appeared by the Paleozoic and changed little through the Mesozoic and Cenozoic (Crum 1972; Anderson 1980). Others (Vitt 1984) have noted that such claims are largely unsupported because, with few ex-

ceptions, the pre-Cenozoic fossil record does not include moss material that is clearly referable to extant families or genera.

The fossil record of bryophytes has been reviewed by Lacey (1969), Krassilov and Schuster (1984), Miller (1980, 1984), Edwards (1993), Taylor and Taylor (1993), and Kenrick and Crane (1997). *Pallavicinites* (*Hepaticites*), from the Late Devonian (Frasnian), consisting of a branching thallus with nonseptate rhizoids and lacking reproductive structures, are the earliest unequivocal fossil bryophytes (Hueber 1961; Kenrick and Crane 1997). Recently discovered liverwort thalli from the Early Cretaceous are anatomically preserved and closely resemble extant Aytoniaceae (Crandall-Stotler et al. 1996). *Phaeoceros*-like spores from the Maastrichtian (Late Cretaceous) provide the earliest evidence of probable hornworts (Jarzen 1979; Kenrick and Crane 1997). Material reported from the Upper Carboniferous (*Muscites polytrichaceus*; Renault and Zeiller 1888) is one of the earliest known fossils that may be attributable to mosses. *Muscites plumatus* from the Lower Carboniferous is another early fossil that may be a moss (Thomas 1972; Kenrick and Crane 1997), but conclusive identification of all these fossils remains questionable (Smoot and Taylor 1986). Permineralized moss gametophytes (*Merceria augustica*) are known from the Permian of Antarctica (Smoot and Taylor 1986). Material thought to be related to the Sphagnaceae (*Protosphagnum*; Neuburg 1960) is also known from the Permian, and spores and leaf fragments of *Sphagnum* are known from the Jurassic (Savicz-Ljubitzkaja and Abramov 1959).

In this article, we present well-preserved fossil sporophytes and gametophytes of an extinct genus of moss from Cretaceous sediments that can be assigned

¹Author for correspondence and reprints.

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unequivocally to the extant family Polytrichaceae (known commonly as hair-cap mosses). These fossils are three-dimensionally preserved with fine details of morphology and anatomy that are sufficient for an unambiguous determination of systematic relationships.

Material and methods

The fossils described here were collected from a fossil locality in Crawford County, Georgia, ca. 9.5 km southwest of Roberta. The fossil material was isolated from a carbonaceous clay lens exposed on the south face of the south pit (Allon quarry) of the Atlanta Sand and Supply Company at Gaillard, Georgia (Knoxville Quadrangle, lat. 32°37'47"N, long. 83°59'10"W). The sediments have been assigned to the Buffalo Creek Member of the Gaillard Formation (Huddleston and Hetrick 1991). Based on palynological analyses, the Gaillard Formation is thought to be of earliest Campanian age (Christopher 1979; Huddleston and Hetrick 1991). This site has yielded a rich assemblage of fossils that includes moss sporophytes and gametophytes; fern fragments; conifer shoots and cone scales; and diverse angiosperm flowers, fruits, and seeds (Herendeen et al. 1995; Crane and Herendeen 1996; Keller et al. 1996; Magallon-Puebla et al. 1996).

Isolation of organic material followed the protocol described in Herendeen et al. (1995). Moss sporophyte and gametophyte specimens were selected for detailed study using a binocular microscope. Specimens were mounted on stubs, coated with gold, and examined with an Amray 1810 scanning electron microscope (SEM) at 5 kV and 10 kV. After initial observations, selected specimens were partially dissected to reveal additional structures and then recoated and examined with the SEM. Capsules and gametophytes of extant Polytrichaceae were selected from herbarium specimens for comparison with the fossil material. All fossil specimens are deposited in the paleobotanical collection of the Department of Geology, Field Museum, Chicago (PP).

Systematics

FAMILY.—POLYTRICHACEAE

GENUS.—*EOPOLYTRICHUM* KONOPKA, HERENDEEN, MERRILL, AND CRANE, GEN. NOV.

TYPE SPECIES.—*EOPOLYTRICHUM ANTIQUUM* KONOPKA, HERENDEEN, MERRILL, AND CRANE, SP. NOV.

GENERIC DIAGNOSIS. Capsules oblong in outline, terete to somewhat dorsiventrally flattened in section, operculum high and dome-shaped (calyptra and beak of operculum not preserved). Exothecium mammillose, stomata restricted to constricted apophysis at the capsule base. Peristomial membrane present at the rim of the capsule, peristome teeth lacking, and epiphragm retained in the operculum. Spores alete, echinulate.

SPECIES.—*EOPOLYTRICHUM ANTIQUUM* KONOPKA, HERENDEEN, MERRILL, CRANE, SP. NOV. (FIGS. 1–16)

SPECIFIC DIAGNOSIS. Sporophyte. Capsules 0.9–1.1 mm long, 0.6–0.8 mm wide. Peristomial membrane at mouth of capsule usually three cells high (0.01–0.03

mm). Apophysis asymmetrical. Spores 7–8 μ m in diameter.

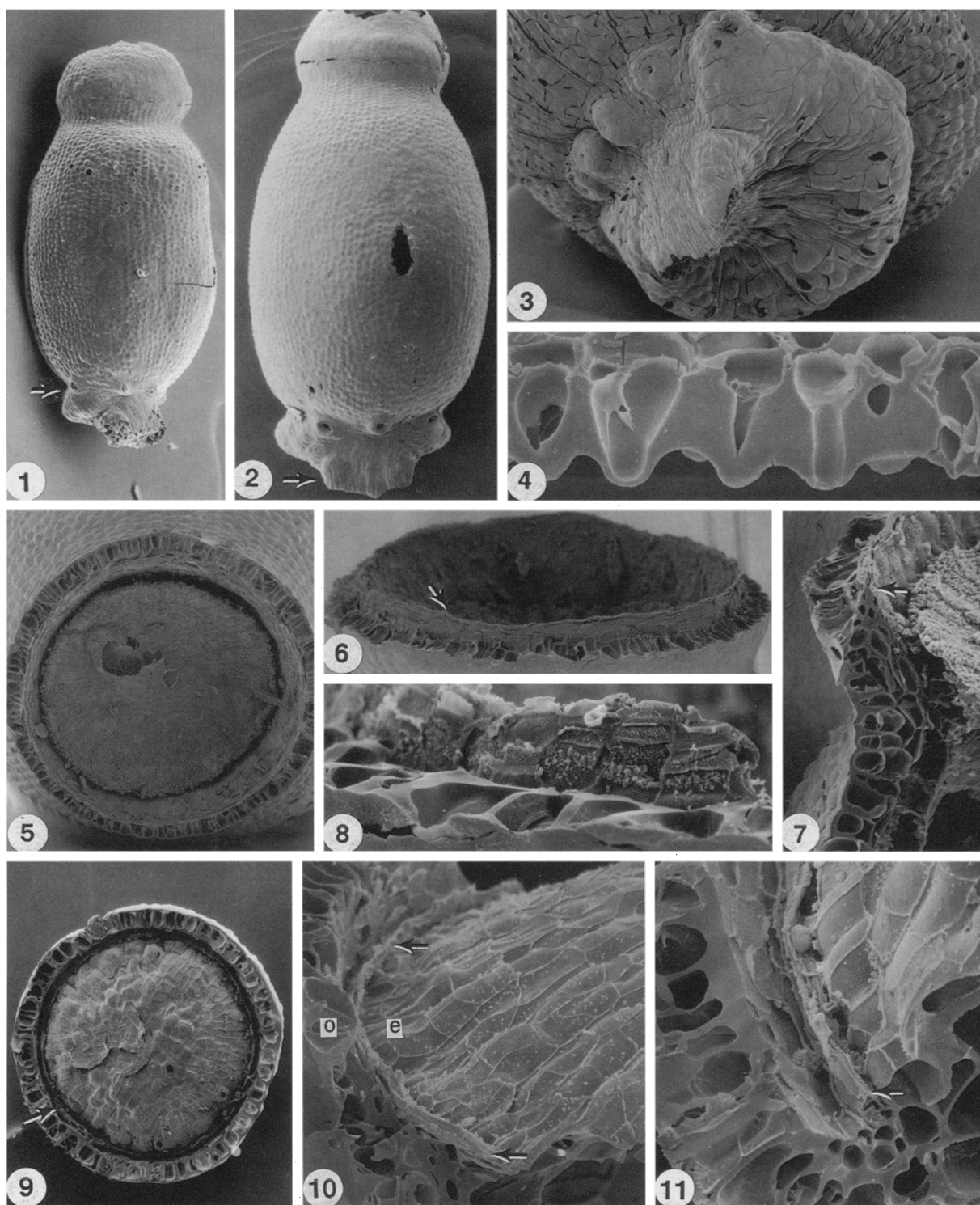
HOLOTYPE. PP44714 (fig. 1).

PARATYPES. PP44715, PP44716, PP44717.

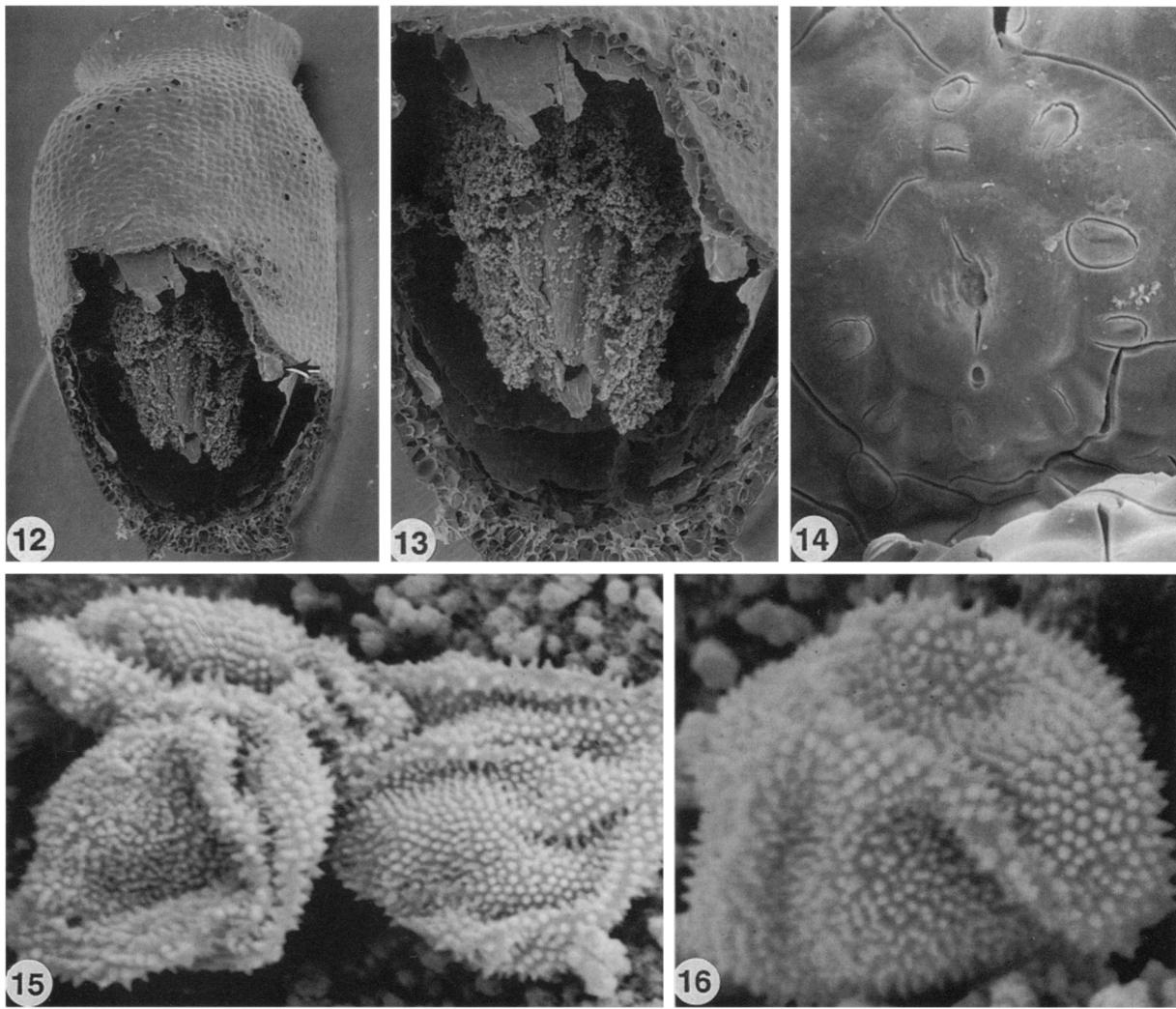
TYPE LOCALITY. Ca. 9.5 km southeast of Roberta, Georgia, at the south pit of the Atlanta Sand and Supply Company at Gaillard, Crawford County, Georgia (USGS Knoxville Quadrangle, lat. 32°37'47"N, long. 83°59'10"W).

AGE AND STRATIGRAPHY. Buffalo Creek Member of the Gaillard Formation (Upper Cretaceous, earliest Campanian).

DESCRIPTION AND REMARKS. The capsules are oblong, terete in cross section, and somewhat dorsiventrally flattened (figs. 1, 2). At maturity the capsules were probably oriented horizontally, based on the seta attachment, which is at a right angle to the long axis of the capsule (fig. 1). The capsule wall consists of bulging-mammillose exothecial cells (figs. 1–3) with abruptly thinned outer cell walls (fig. 4). Based on this structure, the exothecium would probably have appeared pitted in transmitted light, as in extant *Polytrichum*. Stomata (length = 3.8 μ m, width = 3.5 μ m) are restricted to the apophysis on the upper side of the capsule and are elevated and surrounded by a ring of subsidiary cells (figs. 3, 14). The stomata appear to be of the "annular" type, single ring-shaped guard cell, characteristic of many extant Polytrichaceae (Smith 1971, fig. 22). The operculum is rounded, and an annulus is lacking. Dehiscence had begun before preservation (fig. 2), but capsules were still operculate and required the removal of the operculum for study of their internal structure. The beak and calyptra were not preserved in the two specimens in which the operculum was present. The epiphragm is retained within the operculum in both specimens in which the operculum was intact. The proximal portion of the broadened apex of the columella forms a disc (fig. 5; diameter = 0.3–0.4 mm; see discussion of columella-epiphragm structure). The peristome consists of a short peristomial membrane, usually three cells high, which originates just within the rim of the capsule (figs. 6, 8). Peristome teeth are apparently lacking, but there are ca. 64 cells present in the circumference of the peristomial membrane, which indicates that if fully formed teeth had developed in this species, there would have been 32 peristome teeth. The epiphragm is ca. five to seven cells thick at its thickest point, with a convex lower surface (fig. 9). The peristomial membrane attaches distally to the edge of the epiphragm within the operculum (figs. 10, 11). There is a cavity between the upper surface of the epiphragm and the operculum, which indicates that the epiphragm had begun to collapse at the time of preservation (fig. 45). A peristomial chamber is formed by a broad floor beneath the



Figs. 1–11 Fossil sporophyte capsules of *Eopolytrichum antiquum*. Fig. 1, Capsule lateral view; note mammillose exothecium and asymmetrical apophysis (arrow) and point of seta attachment (bottom right; PP44714, holotype). $\times 50$. Fig. 2, Capsule lateral view. Arrow indicates point of seta attachment (PP44717). $\times 50$. Fig. 3, Swollen asymmetrical apophysis showing raised stomata and seta attachment (PP44716). $\times 100$. Fig. 4, Cross section of mammillose exothecium (PP44716). $\times 750$. Fig. 5, Capsule apical view with operculum removed; note expanded, flattened columella (PP44717). $\times 100$. Fig. 6, Oblique view of mouth of open capsule; note basal membrane present at rim (arrow; PP44717). $\times 150$. Fig. 7, Longitudinal section of capsule wall. Arrow indicates membrane at the capsule rim (PP44714). $\times 300$. Fig. 8, Detail of external surface of basal membrane at the capsule rim; note three cells high and multicellular (PP44714). $\times 700$. Fig. 9, Inner surface of operculum removed from capsule in fig. 1; note epiphragm in center of operculum. Arrow indicates position of basal membrane attachment. (PP44714). $\times 100$. Fig. 10, Oblique view of longitudinally fractured operculum outer wall (*o*) and epiphragm (*e*); arrows indicate insertion of the peristomial membrane at the epiphragm margin (PP44717). $\times 400$. Fig. 11, Enlargement of fractured epiphragm and operculum; note attachment of basal membrane around capsule rim (arrow; PP44717). $\times 750$.



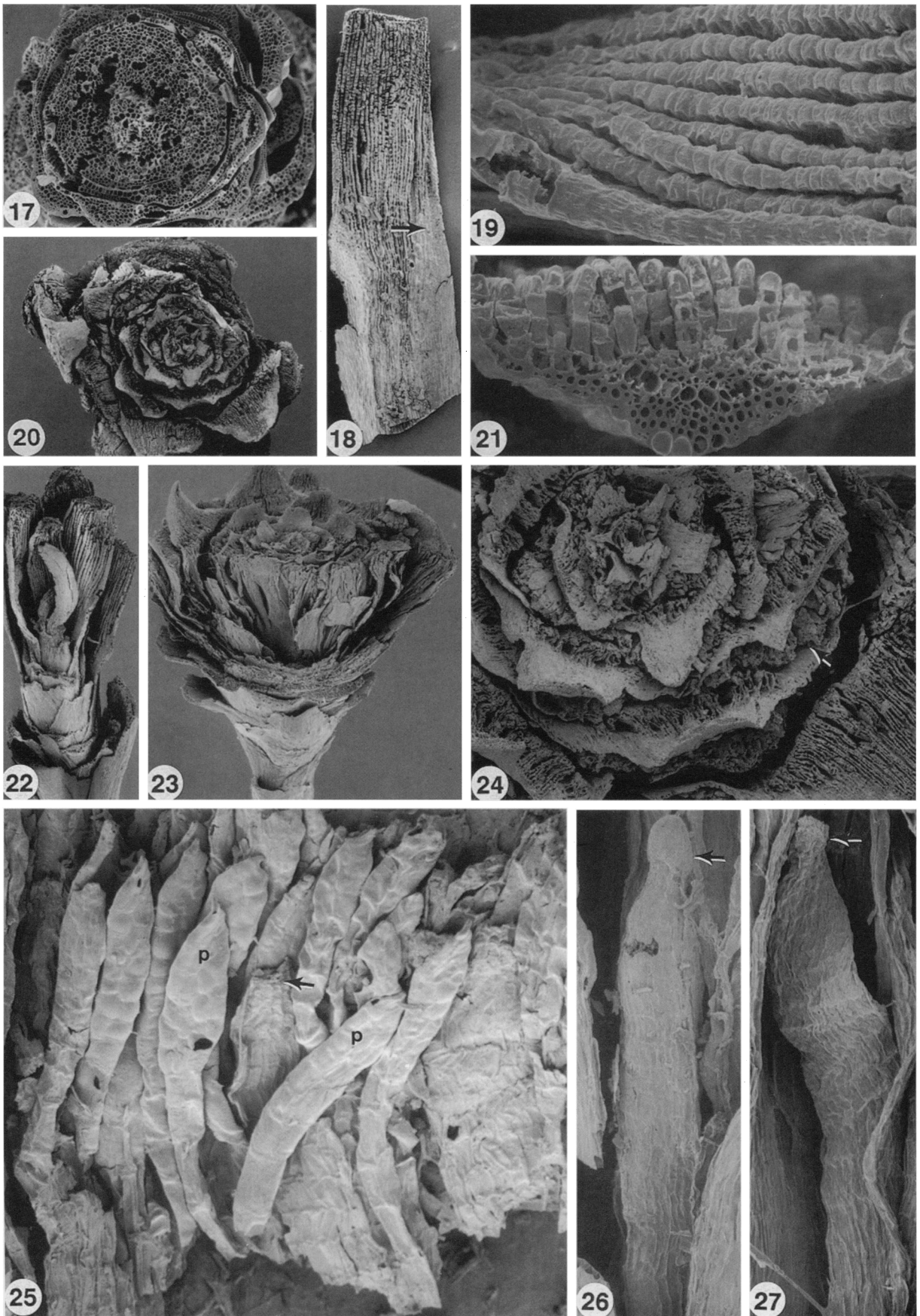
Figs. 12–16 Fossil sporophyte capsule and spores. Fig. 12, Capsule fractured to reveal internal structure; arrow indicates outer wall of spore sac (PP44714). $\times 75$. Fig. 13, Detail of fractured capsule; note central columella outer wall of spore sac adjacent to capsule wall (PP44714). $\times 125$. Fig. 14, Stomatal complex with ring-shaped guard cell on external surface of the apophysis (PP44716). $\times 750$. Fig. 15, Spores with echinulate surface ornamentation (PP44717). $\times 7000$. Fig. 16, Single spore with echinulate surface ornamentation (PP44717). $\times 9000$.

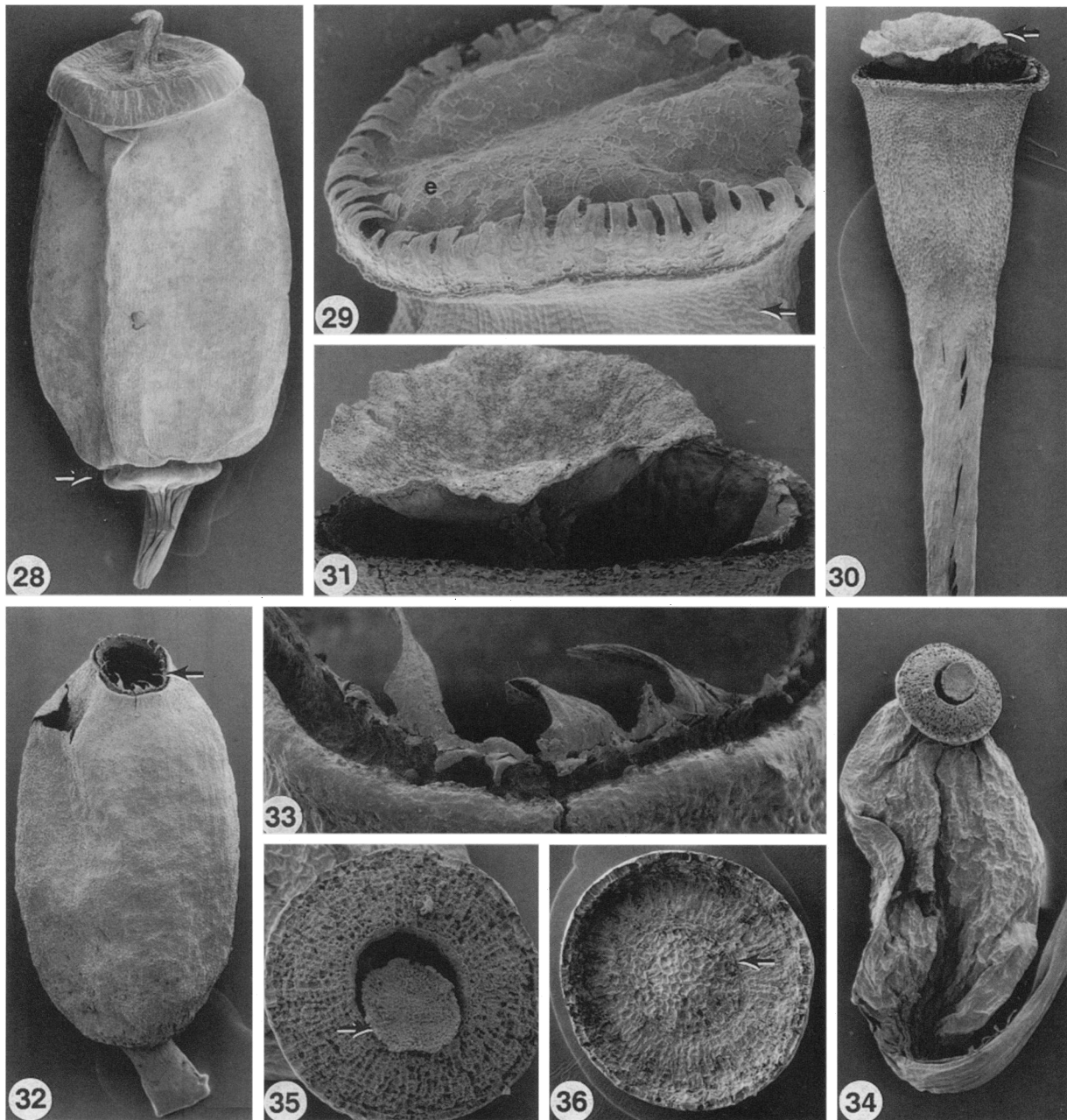
expanded, flattened apex of the columella (figs. 7, 45). The outer wall of the spore sac appears to be directly adjacent to the capsule wall, at least in the upper portion of the capsule (figs. 12, 13). Spores are alete and spherical, 7–8 μm in diameter, with echinulate surface ornamentation (figs. 15, 16).

ASSOCIATED GAMETOPHYTES

Fossil sterile and fertile gametophytes of Polytrichaceae co-occur with the fossil capsules at the Allon quarry site (figs. 17–27). The gametophytes were presumably dioecious, but only male inflorescences have

Figs. 17–27 Sterile and antheridial fossil gametophytes. Fig. 17, Transverse fracture of sterile gametophyte axis (PP44718). $\times 100$. Fig. 18, Single leaf with proximal portion of sheath missing; note differentiated sheath and blade with adaxial lamellae and hinge tissue (arrow; PP44720). $\times 75$. Fig. 19, Detail of lamellae; note bluntly dentate in profile (PP44720). $\times 750$. Fig. 20, Male gametophyte rosette from above (PP44724). $\times 20$. Fig. 21, Transverse section of leaf with adaxial lamellae and detail of conducting strand (PP44720). $\times 500$. Fig. 22, Oblique view of sterile gametophyte (PP44720). $\times 50$. Fig. 23, Oblique view of fertile rosette bearing antheridia (PP44724). $\times 20$. Fig. 24, Detail of male rosette; note lamellae and apices of antheridia and clavate paraphyses (arrow; PP44724). $\times 70$. Fig. 25, Group of sterile paraphyses (*p*) surrounding an antheridium with dehiscent cap, showing truncated apex (arrow). $\times 250$. Figs. 26 and 27, Detail of antheridia; note intact bulbous caps (arrows) that have not yet dehiscent to release sperm. $\times 250$.

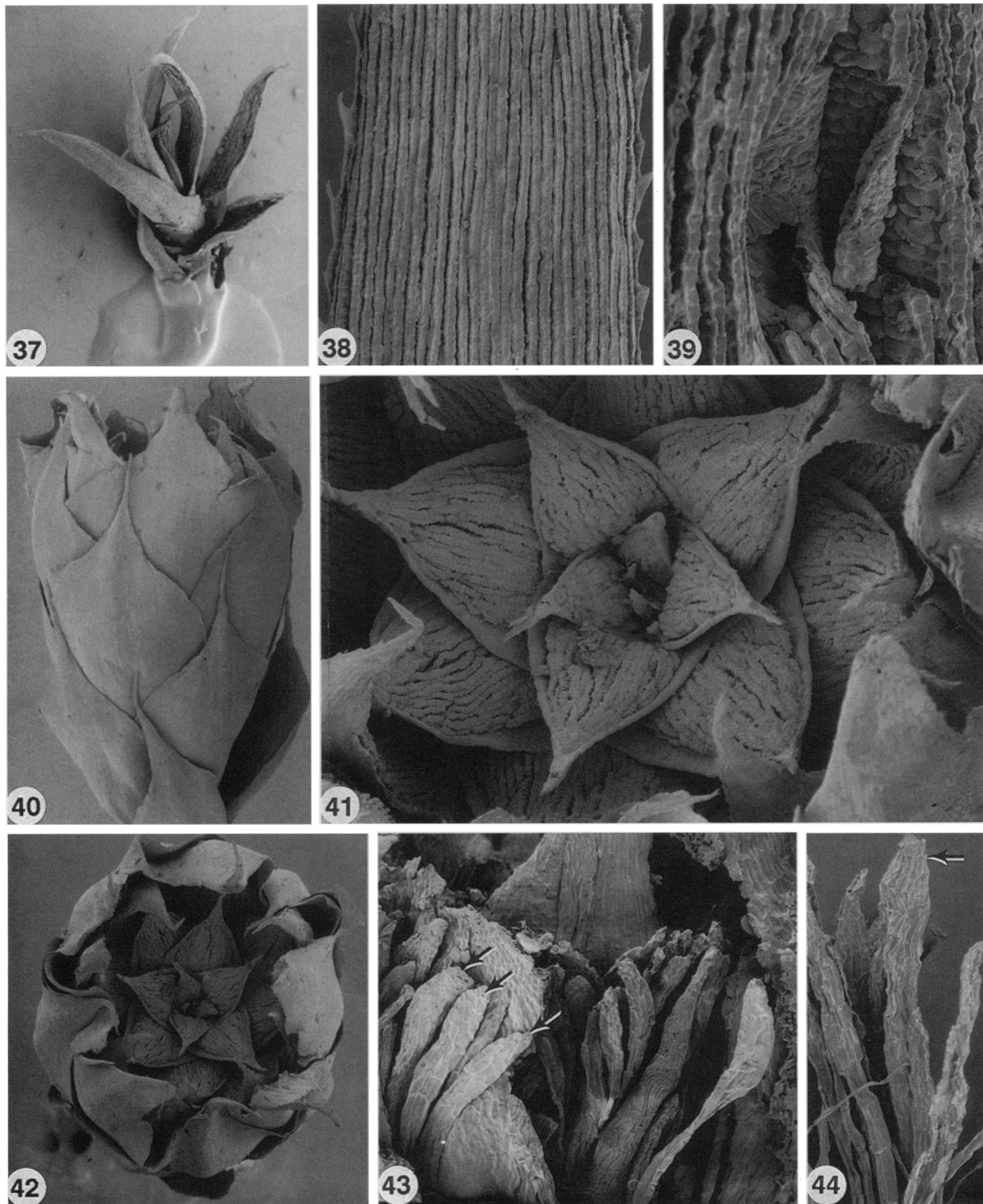




Figs. 28–36 Capsules of extant genera of Polytrichaceae. Fig. 28, Capsule of *Polytrichum commune*; lateral view showing constricted apophysis (arrow). $\times 15$. Fig. 29, Detail of capsule mouth of *Polytrichum piliferum*; note peristome teeth, epiphragm (*e*), and mammillose exothecium (arrow). $\times 70$. Fig. 30, Capsule of *Bartramiopsis lescurii*; note broad flared apex of the columella (arrow) and absence of peristome teeth. $\times 25$. Fig. 31, Detail of columella apex of *B. lescurii*. $\times 70$. Fig. 32, *Notoligotrichum australe* lateral view of capsule; showing irregular peristome teeth at the rim of the capsule (arrow). $\times 15$. Fig. 33, Enlargement of peristome teeth of *N. australe*; note portions of basal membrane lacking teeth. $\times 150$. Fig. 34, Capsule of *Alophosia azorica*; lateral view with operculum removed. $\times 25$. Fig. 35, Detail of capsule mouth of *A. azorica* in apical view; note absence of peristome teeth, flattened columella apex (arrow), and broadened disclike attachment for operculum. $\times 60$. Fig. 36, Lower surface of operculum of *A. azorica*; note epiphragm (upper portion of columella apex; arrow) remaining within the operculum. $\times 60$.

been recovered. Female gametangia have not been seen, and only a short portion of the seta is known attached to the capsule. Male gametophytes are characterized by conspicuous rosettes formed by broadly overlapping perigonal bracts (figs. 20, 23, 24). Interspersed among the bracts are numerous antheridia and clavate paraphyses (figs. 25–27). Several enlarged tips

of antheridia that would have released sperm are still intact on some antheridia (fig. 27). Leaves have a differentiated sheath and blade, but the blade is not squarrose reflexed at the hinge between sheath and blade. Sheath margins are entire, with long tapering shoulders, and there is evidence of a hinge tissue located along the margins of the blade just above the junction



Figs. 37–44 Sterile and antheridial gametophytes of *Polytrichum commune*. Fig. 37, Sterile gametophyte shoot. $\times 25$. Fig. 38, Leaf blade with numerous adaxial lamellae and toothed margins of blade. $\times 100$. Fig. 39, Enlargement of adaxial lamellae. $\times 300$. Fig. 40, Lateral view male rosette. $\times 20$. Fig. 41, Detail of antheridial rosette showing helical arrangement of leaves with adaxial lamellae. $\times 75$. Fig. 42, Overview of antheridial rosette. $\times 25$. Fig. 43, Dissected perigonial rosette showing clavate paraphyses (arrows). $\times 100$. Fig. 44, Same as fig. 43, showing antheridium (arrow). $\times 100$.

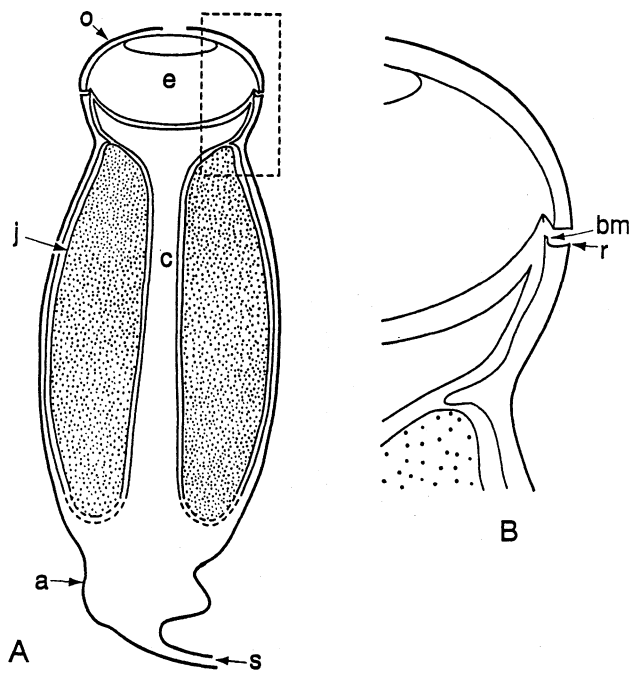


Fig. 45 *Eopolytrichum antiquum* gen. et sp. nov. sporophyte capsule schematic diagram. A, Reconstruction of capsule based on dissection of fossil. The position of the base of the columella and spore sac are conjectural, as indicated by dashed lines; note operculum (*o*), epiphragm (*e*), columella (*c*), spore jacket (*j*), apophysis (*a*), and seta (*s*). B, Enlargement of operculum indicating attachment to capsule rim (*r*) and showing basal membrane (*bm*) insertion into operculum.

between sheath and blade (fig. 18). The blade is rather narrow (the total length of leaf is not known; only the lower portion is seen) and broadly lamellate on the upper surface. The marginal lamina is narrow, erect, and entire in the lower portion, but has unicellular teeth toward the extreme tip (seen in immature leaves at the shoot apex). The lamellae of the sheathing base are low and confined to the conducting portion of the costa (fig. 21). They are flanked by a bistratose portion of the leaf lamina, but most of the sheath is unistratose. Lamellae of the blade are numerous, closely spaced, smooth, and crenulate to bluntly dentate in profile (fig. 19). Marginal cells are undifferentiated proximally (fig. 21) but broadly pyriform distally. The costa in cross section has a typical polytrichoid anatomy of deuters, socii, and central cells (fig. 21), but the socii in the blade portion of the leaf are often obliterated by cells of the abaxial stereid band (for terminology, see Lorentz 1864; Smith 1971, fig. 4). The abaxial epidermal cell layer of the costa in the sheathing portion of the leaf has isolated groups of two to four enlarged, thick-walled cells (their common walls thin) forming rounded protuberances on the back of the sheath.

ASSOCIATION OF SPOROPHYTES AND GAMETOPHYTES

Although the fossil capsules and sterile and fertile gametophytes were not found in attachment, we believe that they belong to the same species. The spo-

rophytes and the gametophytes were recovered from the same sediment sample and are independently attributed to the Polytrichaceae based on external morphology and anatomical characteristics. Although fossil sporophytes and gametophytes of other moss taxa have been recovered from the Allon site, only one type of sporophyte and one type of gametophyte type are referable to the Polytrichaceae. However, because definitive evidence linking the sporophyte and gametophytes is lacking, we have not included the gametophyte in the taxonomic diagnosis of *E. antiquum*, which is based only on capsules.

Discussion

SYSTEMATIC RELATIONSHIPS OF *EOPOLYTRICHUM*

Anatomical details seen in SEM photographs clearly indicate that the fossil sporophytes described here belong to the family Polytrichaceae, but the combination of features exhibited does not occur in any extant genus (table 1). Features of the fossil sporophyte characteristic of Polytrichaceae include (i) epiphragm, (ii) presence of broadened columella apex, (iii) peristomial membrane structure, and (iv) echinulate spore sculpture. The associated fossil gametophytes exhibit the distinctive lamellae and leaf anatomy of the Polytrichaceae, and the male gametophyte contains characteristic clavate paraphyses and antheridia. Toothed leaf margins and pyriform marginal cells of lamellae occur in several extant genera of Polytrichaceae, but the rounded abaxial protuberances of the sheath are unique to the fossil.

Extant genera of Polytrichaceae are distinguished primarily on sporophyte characters. The capsule and spore morphology of *Eopolytrichum antiquum* are most specifically comparable to the extant genus *Polytrichum* (*sensu stricto*, Smith 1971; Merrill 1992) in the following characteristics: dorsiventral symmetry of the capsule (figs. 1, 2, 28; table 1), mammillose exothelial cells (figs. 1–4, 28, 29), the distinctly constricted apophysis (figs. 1, 28), and echinulate spores (Smith 1974, figs. 3, 4). However, *Eopolytrichum* differs from *Polytrichum* in other characteristics, such as capsule cross section (terete in fossil, sharply angled in *Polytrichum*), extreme broadening of the columella apex, epiphragm position (retained in operculum in the fossil, attached to teeth in *Polytrichum*), and absence of peristome teeth (teeth present in most genera of Polytrichaceae, absent in the fossil and a few extant genera; table 1).

Eopolytrichum antiquum shares features with the genera *Bartramiopsis*, *Lyellia*, and *Alophosia* that include absence of peristome teeth, presence of a broad flattened disc at the apex of the columella (figs. 5, 30, 31), and retention of the epiphragm (the distal portion of the columella apex) within the operculum (figs. 9, 36; see discussion of columella-epiphragm structure). *Dawsonia* also lacks peristome teeth, but its brushlike peristome makes it unique among all other Polytrichaceae. Sporophytes of *Bartramiopsis*, *Lyellia*, and *Al-*

Table 1
COMPARISON OF SPOROPHYTE CHARACTERS OF SELECTED GENERA OF POLYTRICHACEAE

Taxa ^a	Capsule section	Capsule symmetry	Exothecium	Stomata type	Constricted apophysis	Epiphragm position	Basal membrane	Peristome type	Columnella apex	Interface of operculum with capsule wall	Floor of peristomial chamber	Spore sculpture
<i>Eopolytrichum</i>	Terete	Dorsiventral	Mammillose	Superficial	Present	Retained in operculum	Present	Membrane	Expanded, flattened	Narrow	Broad	Echinulate
<i>Polytrichastrum</i>	Obusely 4-6-angled or terete	Dorsiventral	Smooth	Superficial	Present	Attached to teeth	Present	Teeth	Blunt	Narrow	Broad	Papillose
<i>Polytrichum</i>	4 sharp angles	Dorsiventral	Mammillose	Superficial	Present	Attached to teeth	Present	Teeth	Blunt	Narrow	Broad	Echinulate
<i>Dawsonia</i>	2 sharp angles	Dorsiventral	Smooth	Superficial	Absent	Cylindrical, retained in operculum	Absent	Bristles	Blunt	Broad	Absent	Echinulate
<i>Notoligotrichum</i>	2-angled	Bilateral	Smooth	Cryptopore	Absent	Attached to teeth	Present	Teeth	Blunt	Narrow	Narrow	Papillose
<i>Itatiella</i>	Terete	Radial	Smooth	Absent	Absent	Retained in operculum?	Absent	Absent	Blunt	Narrow	Narrow	Papillose
<i>Lyellia</i>	2-angled	Dorsiventral	Smooth	Superficial	Absent	Retained in operculum	Absent	Absent	Expanded, flattened	Broad	Absent	Echinulate
<i>Aliphosia</i>	2-angled	Dorsiventral	Smooth	Superficial	Absent	Retained in operculum	Absent	Absent	Expanded, flattened	Broad	Absent	Echinulate
<i>Bartramioopsis</i>	Terete	Radial	Smooth	Superficial	Absent	Retained in operculum	Absent	Absent	Expanded, flattened	Narrow	Absent	Rugose

Note. This table illustrates character conditions that predominate in listed genera but may not reflect all character states found in all species within any given genus. A more detailed examination of all genera and all species within genera is required to complete the character analysis.

^a Extant diversity and distributions: *Polytrichastrum*, 12 spp., primarily northern temperate, higher elevations in the tropics; *Polytrichum*, 75 spp., cosmopolitan; *Dawsonia*, nine spp., Australasia, Malasia; *Notoligotrichum*, 10 spp., southern and Andean South America, Mexico, Australasia; *Itatiella*, one species, Brazil; *Lyellia*, four spp., Nepal into Bhutan and Yunnan, Arctic; *Aliphosia*, one species, Azores and Madeira islands; *Bartramioopsis*, one species, northwest Canada, Alaska, north Pacific Oceanic, and Japan.

ophosia differ from *Eopolytrichum* in other features, namely, the exothecium is not mammillose, the apophysis is not constricted (*Bartramiopsis*), the peristomial membrane is absent, and a broad peristomial chamber floor is absent. Whereas the contact (abscission zone) between the operculum and the capsule wall is narrow in the fossil and in most extant genera of Polytrichaceae, it is broad in *Lyellia* and *Alophosia*, forming a conspicuous disc surrounding the capsule mouth (figs. 34, 35; Smith 1971, figs. 25, 26). The echinulate spore sculpture in *Polytrichum* and *Eopolytrichum* is also present in *Lyellia*, *Alophosia*, and *Dawsonia*, but not in *Bartramiopsis* (Smith 1974, figs. 6, 7, 15, 16).

The presence of typical Polytrichaceae lamellae allows for the unequivocal assignment of the fossil gametophytes associated with *E. antiquum* capsules to this family (figs. 37–39). The leaves of the associated fossil gametophytes have a unistratose marginal lamina, as in *Polytrichum* and many other extant genera of Polytrichaceae, whereas in *Lyellia*, *Alophosia*, and *Bartramiopsis*, the elamellate portion of the leaf is broad and bistratose (lamellae absent in *Alophosia*). The fossil male gametophytes exhibit clavate paraphyses and antheridia very similar to those of extant *Polytrichum* (figs. 40–44). Details of antheridia and paraphyses have not been broadly surveyed within the Polytrichaceae, and it is therefore unclear how systematically informative these characters may be within the family.

A more precise understanding of the relationships of *Eopolytrichum* within the Polytrichaceae will require cladistic analysis that includes the fossil and relevant extant taxa of mosses. More detailed information is needed about epiphragm, columella, peristomial membrane, and tooth structure among extant taxa to determine structural homologies within and among Polytrichales, Bryales, Tetraphidales, and other major lineages of mosses.

DIVERSITY OF THE PERISTOME AND COLUMELLA-EPIPHRAGM APPARATUS

Much of the variation in peristome, columella, and epiphragm structure among extant Polytrichaceae is a function of the presence or absence of peristome teeth and the precise position of the abscission between the columella and epiphragm. In some genera that lack peristome teeth (*Lyellia*, *Alophosia*, *Bartramiopsis*, and *Eopolytrichum*), there appears to be a transverse plane of abscission that divides the broadened columella apex at maturity into proximal and distal portions. The proximal portion remains as the flared apex of the columella (*Eopolytrichum*, fig. 5; *Bartramiopsis*, figs. 30, 31; *Alophosia*, fig. 35), and the distal portion (epiphragm) is retained in the operculum after dehiscence. In contrast, when peristome teeth are present, there does not appear to be a differentiation of the proximal and distal portions of the epiphragm, and the broadened columella apex (epiphragm) is attached to the tips of the peristome teeth (*Polytrichum*, fig. 29) and is completely detached from both the columella

and the operculum at the time of dehiscence. Peristome teeth function in the regulation of spore release; and in genera lacking peristome teeth, a restricted opening, bristles at the capsule mouth (*Dawsonia*), or an expanded columella apex may also contribute to a gradual dispersal of spores.

A peristomial membrane that is three cells high and three cells thick at the base is present around the rim of the capsule in *Eopolytrichum*. The shape of the cells that comprise the basal membrane in the fossil indicates this structure is homologous to the polytrichaceous peristome membrane even though teeth are not formed (fig. 7; compare Edwards 1984, fig. 13*d*). In *Polytrichum*, the peristome teeth are formed through the elongation of whole cells into teeth rather than the addition of new cells. Whether the absence of peristome teeth in the fossil indicates the original absence of teeth or a secondary loss cannot be determined. Among extant Polytrichaceae, species of *Oligotrichum* and *Notoligotrichum* (Smith 1971, p. 32) have been suggested to have secondarily lost teeth. Peristomes with poorly formed teeth are found in some species of *Notoligotrichum* (*Notoligotrichum australe*, figs. 32, 33), which possess a basal membrane similar to that of *Eopolytrichum* (figs. 6–8).

EVOLUTIONARY IMPLICATIONS

Sufficient fossil data are available to demonstrate the presence of mosses by the Mesozoic, but the data are inconclusive regarding the timing of family and generic level differentiation. As a result, interpretations drawn from the fossil record have differed widely. The material presented here, which is the first unequivocal polytrichaceous sporophyte material known from the fossil record, and fossils referable to the modern family Dicranaceae from the same fossil locality (Konopka et al. 1996) clearly demonstrate that extant families of mosses were already present by the Late Cretaceous and provide unequivocal evidence of substantial family level diversification among mosses by 80 million years ago.

The discovery of *Eopolytrichum* and associated gametophyte axes, along with the dicranalean fossils, provides a valuable new insight into the Mesozoic diversity of mosses. As suggested by Lacey (1969), the nature of the preservation described here also indicates that additional assemblages of fossil mosses from the Paleozoic and the Mesozoic will be forthcoming with careful sorting of plant mesofossils sieved from fine-grained freshwater sediments. In particular, these fossils highlight the importance of charcoalfied material, which provides the three-dimensional preservation necessary for detailed comparisons with extant taxa.

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