

SPOROPHYTES AND GAMETOPHYTES OF DICRANACEAE FROM THE SANTONIAN (LATE CRETACEOUS) OF GEORGIA, USA¹

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A new species (*Campylopodium allonense*) of the moss family Dicranaceae is described for fossil sporophyte capsules and associated gametophytes from the late Santonian (Late Cretaceous) Buffalo Creek Member of the Gaillard Formation in central Georgia, USA. The sporophyte capsules are most comparable to those of the living genus *Campylopodium*. Sporangia are curved, cylindrical, and strumose, with an obliquely rostrate operculum, cucullate calyptra, and compound annulus. The peristome is haplolepidous with 16 dicranoid, apically bifid teeth that are vertically striate on the outer surface and asymmetrically trabeculate on the inner surface. Spores are spherical, alete, and finely rugose, and thus differ from the finely papillose spores of extant *Campylopodium*. Associated fossil gametophytes are consistent with the morphology of extant *Campylopodium* and have leaves with a broad sheathing base and a narrow blade. Spores identical to those in the sporangium occur on the leaf surfaces of one of the gametophyte specimens, providing circumstantial evidence that both sporophyte and gametophyte belong to the same species. Inadequacies of the moss fossil record have led to contrasting interpretations of the timing of evolutionary change in this lineage since the Paleozoic. *Campylopodium allonense* unequivocally provides the earliest evidence of Dicranaceae in the fossil record. This material, along with other fossil mosses from this late Santonian locality, indicates the presence of modern families of mosses in the Cretaceous. In a phylogenetic context, these fossils from two different subclasses imply that mosses were already diverse by the Late Cretaceous.

Key words: *Campylopodium*; Cretaceous; Dicranaceae; fossil; moss; Santonian.

Bryophytes consist of three major groups, hornworts (Anthocerotopsida), liverworts (Hepaticopsida), and mosses (Bryopsida), which together form a paraphyletic grade of nonvascular plants at the base of the embryophyte clade (Mishler and Churchill, 1984; Mishler et al., 1994; Kenrick and Crane, 1997). Bryophytes 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 uncertain (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 mosses is poor and generally confined to fragments of gametophyte, rather than the more systematically informative sporophyte.

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Further, most of the available material is preserved as compressions, in which many important anatomical features cannot be observed. Because of the poor fossil record of the group, there is considerable uncertainty as to the origin and evolutionary history of diversity within the major bryophyte lineages. For example, 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), while others (Vitt, 1984) have noted that such claims are largely unsupported because, with few exceptions, 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), Miller (1980, 1984), Krassilov and Schuster (1984), Edwards (1993), Taylor and Taylor (1993), Cantrill (1997), and Kenrick and Crane (1997). The earliest known bryophyte fossils are remains of hepatics, dating back to the lowermost Upper Devonian, *Pallaviciniites devonicus* (Hueber, 1961). The earliest known moss, *Muscites plumatus*, is from the Lower Carboniferous of Gloucester, England (Thomas, 1972). Thomas compared *M. plumatus* with modern *Grimmia* because of the long hairpoints on the leaves and cell wall thickenings. Slightly younger material from the Upper Carboniferous, *M. polytrichaceus*, described by Renault and Zeiller (1888), closely resembles extant Polytrichaceae. Subsequently, there are scattered reports of fossil mosses in the late Paleozoic, Mesozoic, and Cenozoic (e.g., Neuburg, 1956; Savicz-Ljubitzkaja and Abramov, 1959; Krassilov and Schuster, 1984; Smoot and Taylor, 1986). Tertiary mosses from Baltic, Saxonian, Mexican, and Do-

minican amber provide some of the best examples of well-preserved bryophyte material from the pre-Quaternary record (Frahm, 1993, 1994, 1996a, b). Recently discovered sporophytes and gametophytes of Polytrichaceae from the Late Cretaceous demonstrate the potential for recovering well-preserved material from the Mesozoic (Konopka et al., 1997).

In this paper we describe a species of fossil moss collected from Santonian-age sediments (Late Cretaceous) that provide detailed information on both sporophyte and gametophyte structure. These fossils are three-dimensionally preserved with fine details of morphology and anatomy that are sufficient for an unambiguous determination of systematic relationships and assignment to the extant family Dicranaceae.

MATERIALS AND METHODS

The fossil material described here was collected from a Santonian-age (see *Note added in proof*) locality in Crawford County, Georgia, ~9.5 km southwest of Roberta. The fossil material was isolated from a carbonaceous clay lens that is 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 (Huddlestone and Hetrick, 1991). Based on palynological analyses, the Gaillard Formation is thought to be of late Santonian age (Christopher, personal communication; Huddlestone 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, Crane, and Drinnan, 1995; Crane and Herendeen, 1996; Keller, Herendeen, and Crane, 1996; Magallón-Puebla, Herendeen, and Endress, 1996; Magallón-Puebla, Herendeen, and Crane, 1997; Konopka et al., 1997; Sims, Herendeen, and Crane, in press).

Isolation of organic material follows the protocol described in Herendeen, Crane, and Drinnan (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). After initial scanning, some specimens were chosen for further dissection in order to reveal internal characteristics such as peristome structure. Extant species of Dicranaceae were selected from available herbarium specimens and compared with the fossil material. All fossil specimens are deposited in the paleobotanical collection of the Department of Geology, The Field Museum, Chicago (PP).

SYSTEMATICS

Order Dicranales

Family Dicranaceae

Genus *Campylopodium* (C. Müll.) Besch.

Campylopodium allonense Konopka, Herendeen, & Crane, sp. nov.

Figs. 1–12

Specific diagnosis—Capsule urn curved, cylindrical, strumose, and generally smooth, 0.8–1.3 mm long, operculum 0.8–1.1 mm long. Total capsule length (urn and operculum) 1.7–2.4 mm. Compound annulus present. Operculum obliquely rostrate with attached cucullate calyptra. Distinctive basal swelling with superficial stomata, other stomata restricted to the base as well. Peristome haplolepidous with 16 dicranoid, apically bifid teeth, ver-

tically striate abaxially, asymmetrically trabeculate adaxially. Spores 10–12 μm diameter, spherical, and alete with fine rugose sculpture.

Holotype—PP44725 (Fig. 3).

Paratypes—PP44727, PP44728, PP44729, PP44732, PP44733, PP44736, PP44737, PP44740, PP44741.

Additional specimens—PP44726, PP44730, PP44731, PP44734, PP44735, PP44738.

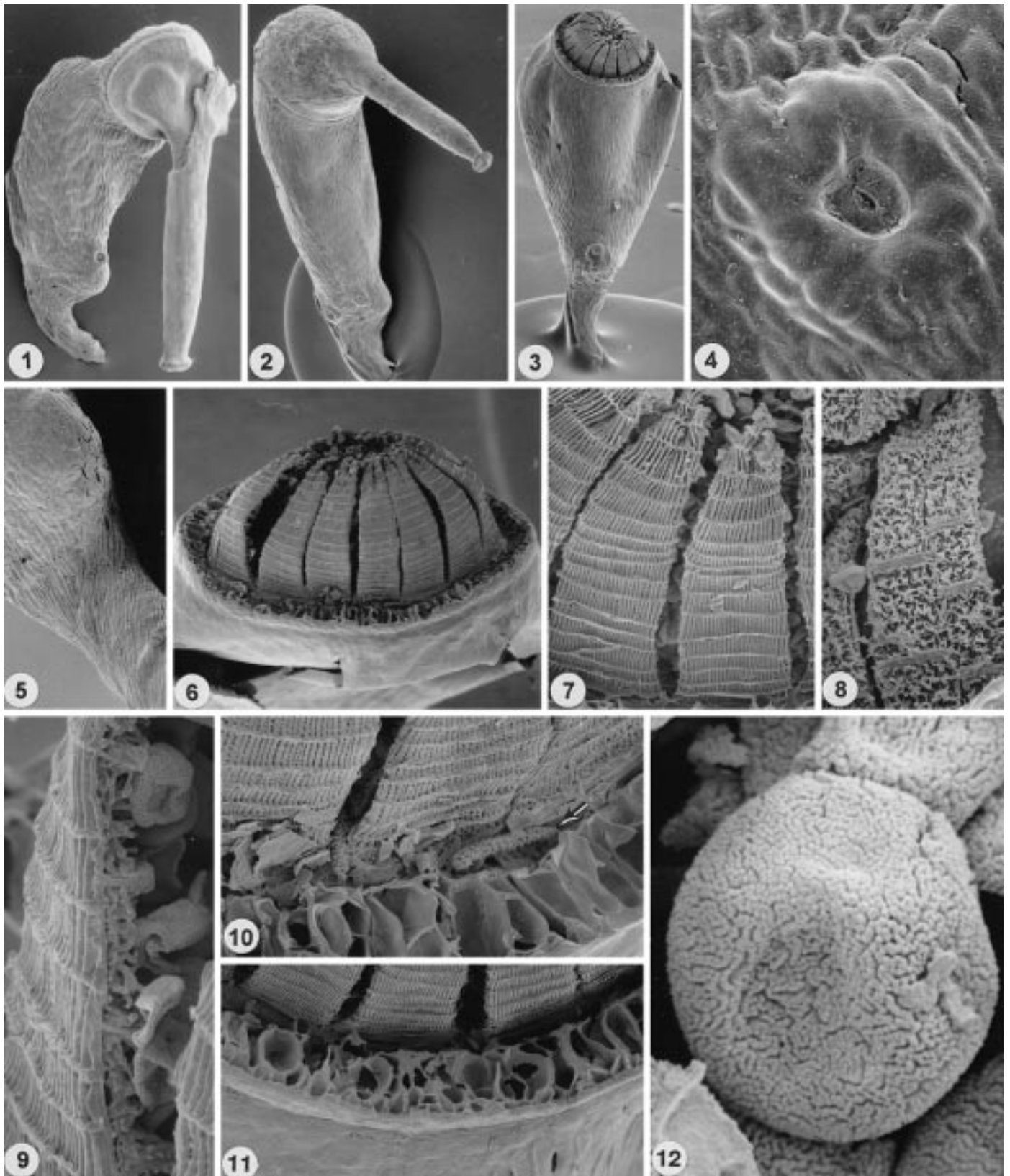
Type locality—Approximately 9.5 km southeast of Roberta, Georgia, at the south pit of the Atlanta Sand and Supply Company at Gaillard, Crawford County, Georgia (USGS Knoxville Quadrangle, lat. 32°37'47" N, long. 83°59'10" W).

Stratigraphic position—Buffalo Creek Member of the Gaillard Formation.

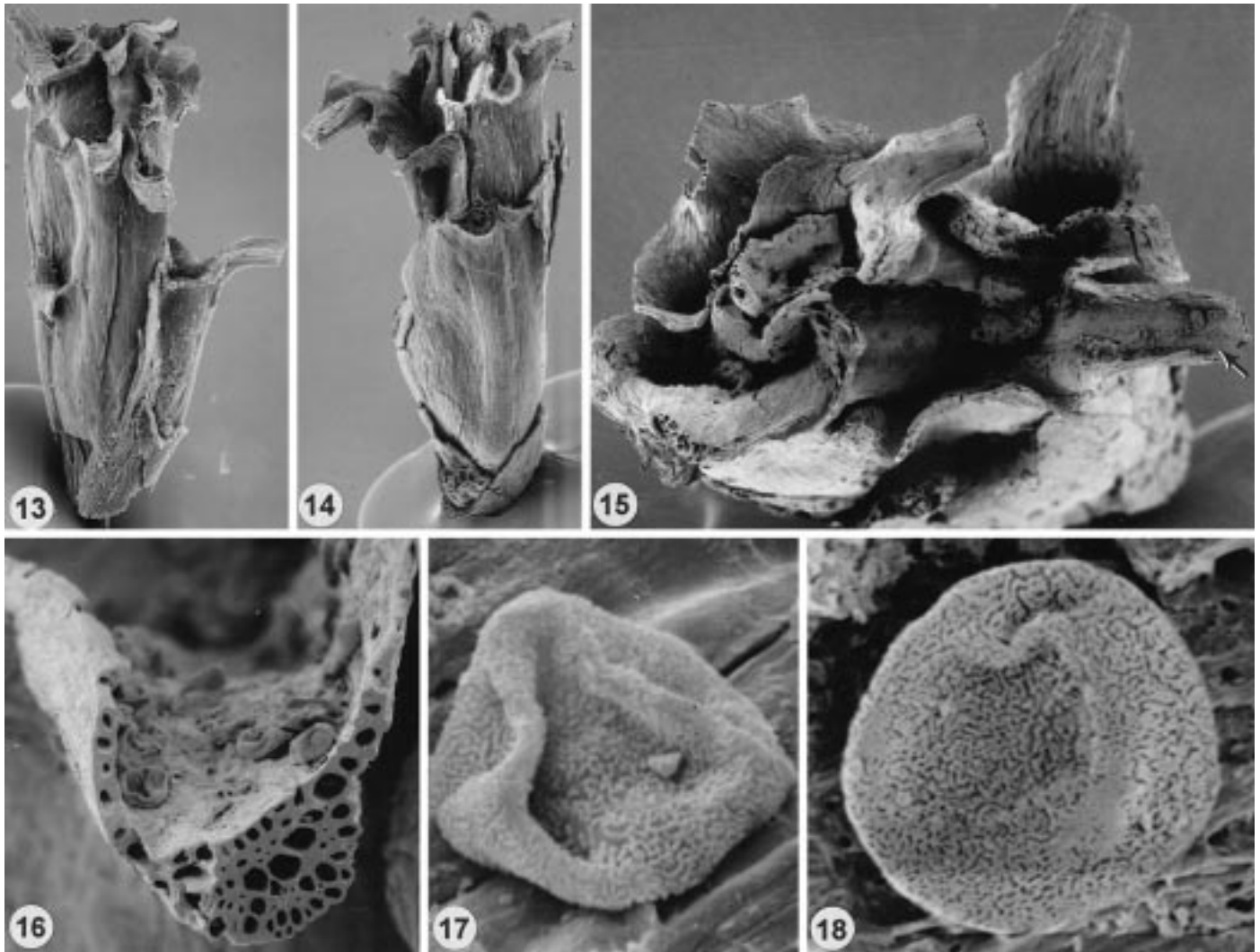
Age—Late Santonian (Upper Cretaceous).

Description and remarks—The capsules are oblong, curved, and nodding, with distinctive basal swelling (struma) (Figs. 1–3). Some capsules are not as strumose as others (Figs. 1–3). The capsule wall is smooth with the superficial stomata (length 17 μm , width 15 μm) that are restricted to the basal swelling and surrounding neck area (Figs. 1–4). Most of the fossil capsules were preserved prior to operculum dehiscence; it is therefore unknown whether capsules would have been furrowed when dry and empty. The operculum is obliquely rostrate (beaked) with a smooth, cucullate, or cone-shaped calyptra, approximately three-quarters as long as the capsule urn (Fig. 1). Apical portions of setae are preserved where they attach to the capsules, and show that the setae were twisted (Fig. 5). It is unknown whether the seta was erect or curved. Capsules appear to have been oriented at 90°–180° to the seta, with the operculum therefore ranging from perpendicular to parallel with the seta (Figs. 1, 2). Capsules that are lacking the operculum show a haplolepidous peristome composed of a single cycle of 16 dicranoid, apically bifid teeth, that are divided one-third of the way down into two forks (Fig. 7). Although the free tips of the teeth are broken, their length can be estimated to be ~70 μm (Fig. 6). Peristome teeth are finely vertically striate on the outer surface (Fig. 7). On the inner surface they are asymmetrically trabeculate with a vermiform sculpture between the trabeculae (Figs. 8, 9). Broken tips of some of the teeth have fallen into the rim area at the base of the peristome (Fig. 10). Enlarged cells present at the rim of the capsule provide evidence that a compound annulus was present (Fig. 11). Spores are spherical (10–12 μm in diameter), with a fine rugose sculpture (Fig. 12).

Associated gametophytes (Figs. 13–16)—Sterile fossil gametophytes of Dicranaceae co-occur with the fossil capsules at the Allon site, but attachment between gametophytes and sporophytes has not been observed. Leaves on the fossil gametophytes are not complete; only broad sheathing leaf bases and partial narrow blades are



Figs. 1–12. Fossil sporophyte capsules of *Campylopodium allonense*. **1.** Capsule lateral view; note strumose base with stomata, and attached cuculate calyptra (PP44727). $\times 75$. **2.** Capsule lateral view; note stomata (PP44736). $\times 50$. **3.** Capsule lacking operculum; note peristome teeth, compound annulus, base slightly strumose with stomata present (PP44725, holotype). $\times 50$. **4.** Stomatal complex at base of capsule (PP44736). $\times 750$. **5.** Base of capsule showing struma and attachment of twisted seta; note twisting of seta (PP44731). $\times 150$. **6.** Lateral view of peristome; note teeth with divided tips and compound annulus (PP44725, holotype). $\times 175$. **7.** Abaxial surface of peristome teeth; note vertical striations, and



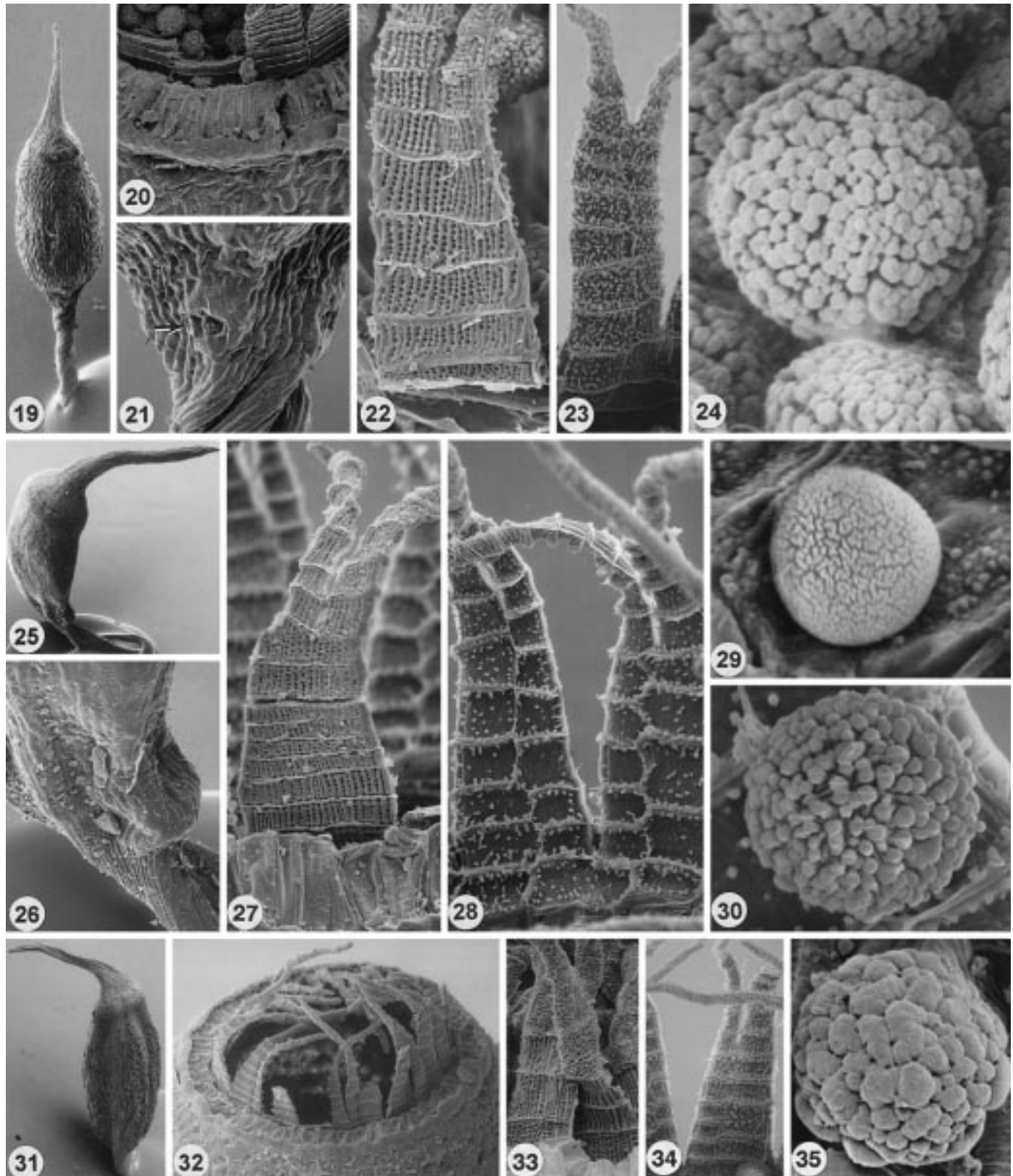
Figs. 13–18. Associated fossil gametophytes and spores. **13.** Lateral view of gametophyte fragment; note broad sheathing base with abruptly narrowed blade (PP44740). $\times 75$. **14.** Lateral view of gametophyte fragment (PP44741). $\times 80$. **15.** Apical view of gametophyte fragment showing spores on the surface of one leaf blade (arrow) (PP44740). $\times 150$. **16.** Transverse section of leaf blade; note spores visible on adaxial surface, guide cells (larger cells internal to costa) visible with adaxial and abaxial stereid bands (smaller cells) (PP44740). $\times 700$. **17, 18.** Detail of spores on adaxial surface of leaf in Fig. 16; note fine rugose sculpture pattern (PP44740). $\times 5000$.

preserved. Whether the costa was excurrent or percurrent is not known. Blades are apparently unistratose, crispate (curled and wavy) with recurvature (bending backwards) on both margins (Fig. 16). Distinct alar cells are not present. In cross section, the costa has 3–5 guide cells with distinct bands of stereid on abaxial and adaxial surfaces that have differentiated outer cells (Fig. 16). Cells on the adaxial surface of the leaf are mostly slightly elongate, while cells on the abaxial surface are rectangular or irregular.

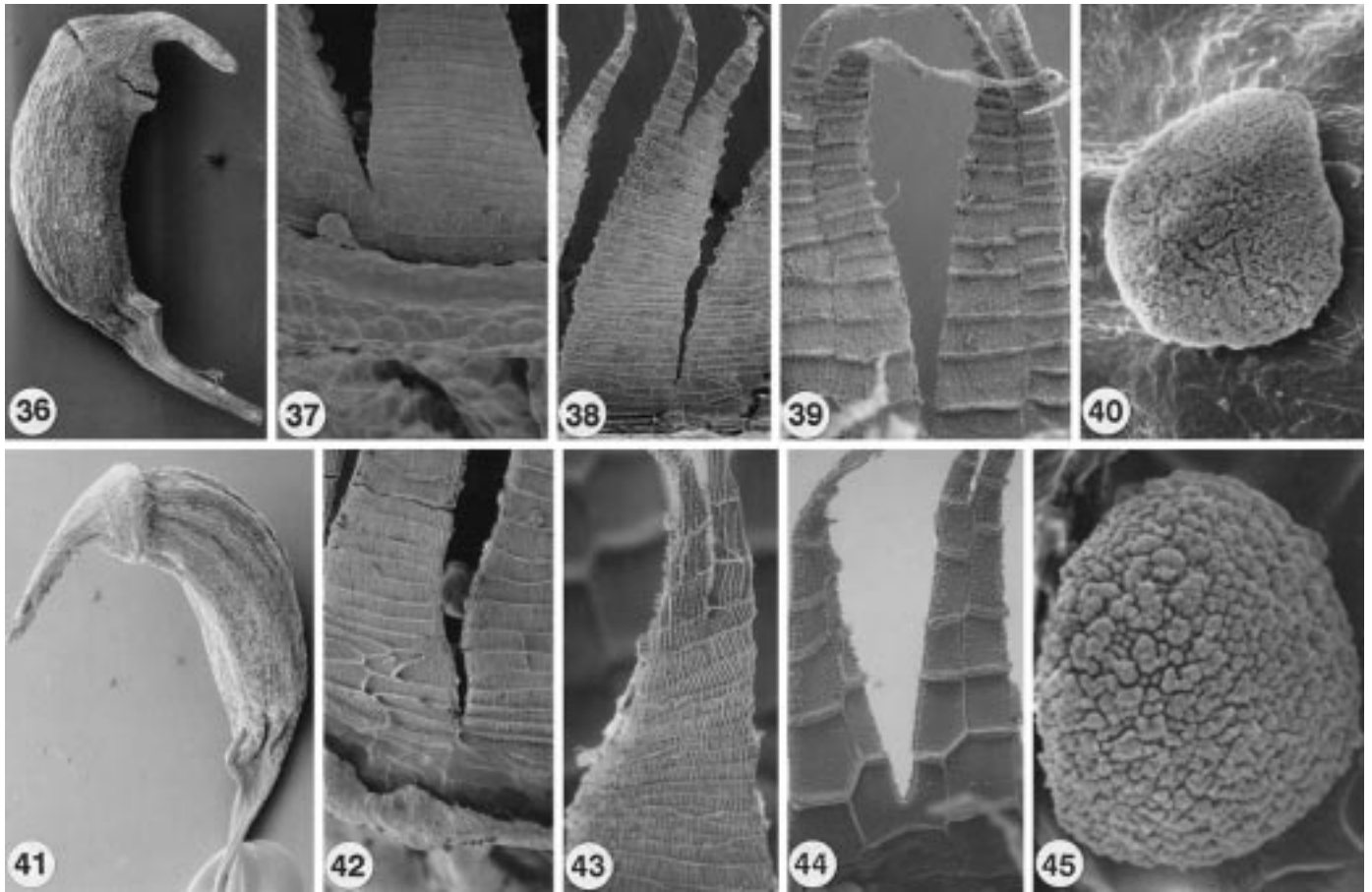
Association of sporophytes and gametophytes—Although the fossil capsules and gametophytes described here are not attached to each other, we believe they belong to the same species. The capsules and gametophytes were found at the same locality and are independently attributable to the Dicranaceae, based on morphological and anatomical features. In addition, spores (9–11 μm in diameter) identical to those recovered from the capsules were found covering the leaf surfaces of one of the gametophyte specimens (Figs. 12, 15, 17, 18). Other moss

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divided tips (PP44728). $\times 500$. **8.** Adaxial surface of peristome teeth; note asymmetrical trabeculae and vermiform sculpture (PP44727). $\times 700$. **9.** Oblique view of peristome tooth; note adaxial vermiform sculpture and spores (PP44725, holotype). $\times 500$. **10.** Enlarged view of annulus at base of peristome teeth; broken tips of some teeth are present in the capsule rim area (PP44725, holotype). $\times 750$. **11.** Enlarged view of compound annulus; note smaller cells toward the outer rim and larger cells directed inward (PP44725, holotype). $\times 400$. **12.** Single spore with fine rugose sculpture (PP44725, holotype). $\times 6000$.



Figs. 19–35. Sporophytes of extant Dicranaceae. Figs. 19–24. *Campylopodium medium*. 19. Lateral view of capsule. $\times 35$. 20. Detail of compound annulus. $\times 250$. 21. Detail of capsule base; note stomata (arrow) and twisted seta. $\times 200$. 22. Abaxial surface of peristome teeth; note vertical striations. $\times 800$. 23. Adaxial surface of peristome tooth; note asymmetrical trabeculae and vermiform sculpture. $\times 450$. 24. Single spore; note fine papillose sculpture. $\times 2500$. Figs. 25–30. *Dicranella*. 25. Lateral view of capsule of *D. cerviculata*; note slightly strumose. $\times 35$. 26. Enlarged view of strumose base of *D. cerviculata*. $\times 200$. 27. Abaxial surface of peristome teeth of *D. beyrichiana*; note vertical striations. $\times 600$. 28. Adaxial surface of peristome tooth of *D. beyrichiana*; note asymmetrical trabeculae and slightly vermiform sculpture. $\times 600$. 29. Single spore



Figs. 36–45. Sporophytes of extant genera of Dicranaceae. Figs. 36–40. *Oncophorus*. **36.** Lateral view of capsule of *O. virens*; note struma. $\times 25$. **37.** Lateral view of capsule rim area of *O. wahlenbergii*. $\times 200$. **38.** Abaxial surface of peristome teeth of *O. wahlenbergii* showing vertical striations. $\times 200$. **39.** Adaxial surface of peristome tooth of *O. wahlenbergii*; note asymmetrical trabeculae, and poorly developed sculpture. $\times 175$. **40.** Single spore of *O. virens*; note fine rugose sculpture. $\times 1500$. Figs. 41–45. *Cynodontium strumiferum*. **41.** Lateral view of capsule; note struma. $\times 25$. **42.** Lateral view of annulus area; note that the annulus is deciduous and no longer present. $\times 250$. **43.** Abaxial surface of peristome teeth showing vertical striations. $\times 400$. **44.** Adaxial surface of peristome teeth showing asymmetrical trabeculae and poorly developed sculpture. $\times 250$. **45.** Single spore; note rough sculpture. $\times 2800$.

taxa have been recovered from this site (Konopka et al., 1997), but only one sporophyte and one gametophyte type are referable to the Dicranaceae. However, in the absence of attachment between the sporophyte and gametophyte, the gametophyte specimens are not included in the formal taxonomic description of *Campylopodium allonense*.

DISCUSSION

Comparison of *Campylopodium allonense* with extant Dicranaceae—The fossil exhibits several characters that indicate a relationship to the Dicranaceae and especially the genus *Campylopodium* (Table 1; Figs. 19–45). The single most definitive feature that unequivocally attri-

butes the fossil to the Dicranaceae is the structure of the peristome (Figs. 6–8, 22, 23, 27, 28, 38, 39, 43, 44). In the dicranoid peristome, the outer face of each tooth is composed of the adaxial walls of a single column of cells (hence the term haplolepidous), while the inner face is composed of the abaxial walls of one and a half columns of cells (see Edwards [1979], for a discussion of peristome structure). This accounts for the characteristically asymmetric adaxial trabeculae. Generally, haplolepidous peristomes consist of a single cycle of peristome teeth and the diplolepidous peristomes (with two columns of cells to the outside and a single column to the inside) have two cycles of teeth. The peristome of Dicranaceae is composed of a single cycle of 16 teeth, each of which is divided apically at least one-third of the distance to the

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of *D. usambaria* showing fine rugose sculpture. $\times 2500$. **30.** Single spore of *D. beyrichiana* showing fine papillose sculpture. $\times 2500$. Figs. 31–35. *Microcampylopus*. **31.** Lateral view of *M. laevigatum*. $\times 35$. **32.** Oblique view of capsule of *M. leucogaster* showing peristome teeth and simple annulus with small square cells of uniform size and shape. $\times 175$. **33.** Abaxial surface of peristome teeth of *M. laevigatum*; note vertical striations. $\times 480$. **34.** Adaxial surface of peristome tooth of *M. subnanus* showing asymmetrical trabeculae and vermiform sculpture. $\times 300$. **35.** Single spore of *M. leucogaster* showing verrucate sculpture. $\times 2000$.

base to form two prongs (Figs. 23, 27, 28, 34, 38, 39, 43). The outer surface of the teeth is vertically striate (Figs. 7, 22, 27, 33, 38, 43); the inner face has prominent cross walls (Figs. 8, 23, 28, 34, 39, 44). The diversity within the Dicranaceae is illustrated by the recognition of six subfamilies (Trematodontoideae, Anisotheciodeae, Campyloporiadeae, Paraleucobryoideae, Rhabdoweisiodeae, and Dicranoideae) that range in size from two genera (Paraleucobryoideae) to 24 genera (Dicranoideae) (Brotherus, 1924).

The fossil shares characters with several genera of Dicranaceae, but the specific combination of features is most comparable to that of extant *Campyloporium* (Table 1). Similarities with *Campyloporium* include: presence of stomata (Figs. 1–4, 21); compound annulus (Figs. 11, 20), sculpture on the inner sides of the peristome teeth (Figs. 8, 23), and struma (Figs. 1–3; variably present in *Campyloporium*; Giese and Frahm, 1985b). However, spore size and sculpture in the fossil are different from those in *Campyloporium* (Figs. 12, 17, 18, 24). *Campyloporium* has finely papillose spores nearly twice the size of the fossil (15–24 μm compared with 10–12 μm in the fossil). Further, the closely related genus *Dicranella*, which contains many more species than *Campyloporium*, includes species with spores that are identical in sculpture and size to that of the fossil (Fig. 29) and species with spores that are similar to those of *Campyloporium* (Fig. 30). *Dicranella*, *Campyloporium*, and the fossil also all share a compound annulus that consists of two kinds of cells (Figs. 11, 20, 27). This differs from the simple annulus exhibited in *Microcampylopus*, which consists of small square cells of uniform size and shape (Fig. 32; H. Crum, personal communication).

Gametophytes of *Dicranella*, *Campyloporium*, *Microcampylopus*, and *Oncophorus* are indistinguishable and all have leaves with a broad sheathing base and a narrow blade (Figs. 46–49; Giese and Frahm, 1985a, b). In *Oncophorus* spore sculpture is smooth to rugose like the fossil, but the capsules lack an annulus, and inner tooth sculpture is not well developed (Figs. 37, 39). Several species once included in *Oncophorus* (currently placed in *Cynodontium*; Williams, 1913; Crum and Anderson, 1981) do contain a compound annulus, but setae are erect, inner tooth sculpture is nearly smooth, spore sculpture is rough, and gametophyte morphology is different from that seen in the fossils (Figs. 50, 51). An earlier comparison of this fossil material to *Oncophorus* was based on literature that included species of *Cynodontium* among *Oncophorus* species (Konopka et al., 1996).

With the revision of *Campyloporium* by Giese and Frahm (1985b), only two of 12 species remain included in the genus. *Campyloporium* is very closely related to *Dicranella* and *Microcampylopus* (Giese and Frahm, 1985a, b). *Dicranella* sporophytes, with erect setae, differ from *Campyloporium* and *Microcampylopus*, which have curved setae. *Campyloporium* is also distinguished from *Microcampylopus* by the presence of stomata on the capsule neck (Giese and Frahm, 1985a, b). Although capsules of some species of *Dicranella* do bear stomata, they do not possess an annulus (Noguchi, 1987). Other species of *Dicranella* possess an annulus, but they lack stomata (Noguchi, 1987). Thus, the combination of the presence of stomata and an annulus in the fossil is a primary dis-

TABLE 1. Comparison of sporophyte and gametophyte characters of selected genera of Dicranaceae.^a

Taxa	Extant species	Peristome tooth split	Inner tooth sculpture	Operc. length ^b	Stomata	Annulus	Struma	Setae	Spore structure	Spore size (μm)	Sheathing leaf base	Narrow blade	Alar cells
<i>Campyloporium</i>													
<i>allonense</i>	N/A	~1/3	vermiform	1/2	yes	compound	yes	??	finely rugose	10–12	yes	yes	no
<i>Campyloporium</i> ^d	2	~1/2	vermiform	2/3	yes	compound	yes or no	curved	finely papillose	15–24	yes	yes	no
<i>Dicranella</i> ^e	~60 ^c	~1/2	vermiform– ± smooth	2/3	yes or no	none or compound	yes or no	erect	finely papillose, rugose, smooth	11–22	yes	yes	no
<i>Microcampylopus</i> ^f	3	2/3 or totally	vermiform	1/2–2/3	no	simple	no	curved	verrucate	16–24	yes	yes	no
<i>Oncophorus</i> ^g	12	1/2 or more	± smooth	1/3–1/2	yes	none	yes or no	erect	rugose or smooth	14–24	yes	yes	not distinct
<i>Cynodontium</i> ^h	10	none–2/3	± smooth	1/3–2/3	yes	none or compound	yes or no	erect	slightly rough	13–23	no	no	not distinct

^a Of the nearly 50 genera in Dicranaceae, only these five exhibited sufficient similar characteristics to compare with the fossil.

^b Operculum length/entire capsule length.

^c According to Walther (1983) the number of species contained in *Dicranella* is 180, but this estimate is prior to revision, and J. P. Frahm (personal communication) estimates more conservatively that there are ~60 species within *Dicranella*. Species that contain stomata do not have an annulus; those that have an annulus do not have stomata.

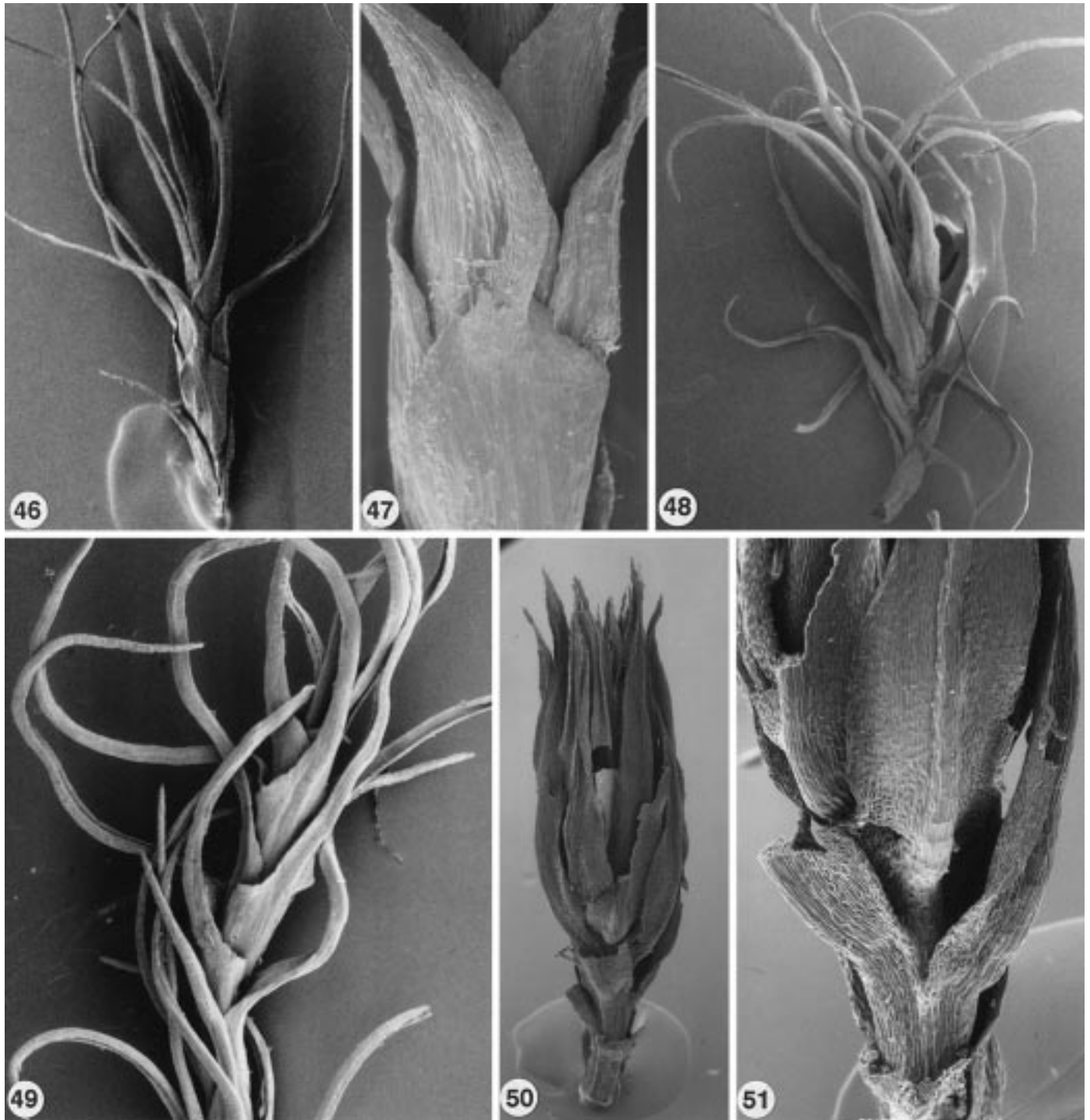
^d *C. lineare* endemic to New Zealand; *C. medium* throughout Indonesia, Java, Sumatra, Celebes, Malaysia, Philippines, New Guinea, New Zealand, Samoa, Fiji, Hawaii, New Caledonia, Taiwan, Japan, Chile, and Puerto Rico.

^e Species distributed throughout North America, northern South America, northern and central Europe, the Caucasus, Japan, Asia Minor, China, and the Himalaya Mountains.

^f *M. curvisetus* throughout Central and South America; *M. laevigatus* eastern Africa, Madagascar, India, southeast Asia, Philippines; *M. khasianus* India, southeast Asia, Philippines.

^g Number of species according to van der Wijk, Margadant, and Florschütz (1959). Species throughout north and central Europe, Morocco, Crete, the Caucasus, Siberia, Tibet, Japan, Greenland, Newfoundland south to Great Lakes region and Nova Scotia, Yukon to California, Arizona, Colorado, New England, Pennsylvania, and the southern Appalachians.

^h Number of species according to van der Wijk, Margadant, and Florschütz (1959). Species throughout north and central Europe, Siberia, Japan, Greenland, Alaska, Yukon, Ontario, Quebec, British Columbia to Saskatchewan, and south to Colorado, New England, and Great Lakes region.



Figs. 46–51. Gametophytes of extant Dicranaceae. **46.** *Campylopodium medium*; note sheathing leaf bases with narrowed blades. $\times 35$. **47.** Detail of gametophyte of *C. medium*; note broad sheathing leaf base with abruptly constricted blade. $\times 150$. **48.** *Dicranella heteromalla*; note sheathing leaf bases with narrowed blades. $\times 35$. **49.** *Oncophorus rauii*; note sheathing leaf bases with narrowed blades. $\times 35$. **50.** Shoot of *Cynodontium strumiferum*. $\times 30$. **51.** Detail of *Cynodontium strumiferum*; note sheathing leaf base with narrow blade not present. $\times 75$.

tinguishing feature of *Campylopodium* (Giese and Frahm, 1985a, b), which allows for unequivocal assignment of the fossil material to *Campylopodium* despite dissimilarities in spore structure. Although spore sculpture is uniform in *Campylopodium* (Fig. 24), it is variable within

Dicranella (Figs. 29, 30) and some species of this genus exhibit spore sculpture similar to the fossil.

There is some question as to the merits of distinguishing *Campylopodium* (two extant species) and *Microcampylopus* (contains only three extant species)

from each other (Giese and Frahm, 1985a, b) and perhaps also from *Dicranella*. In cladistic terms these genera may be nested within a more inclusive *Dicranella* clade. However, phylogenetic relationships are currently poorly understood and it is unknown whether *Dicranella*, *Campylopodium*, and *Microcampylopus* together form a monophyletic group. Ongoing monographic and phylogenetic studies of Dicranaceae (J. P. Frahm, personal communication) should clarify relationships among *Dicranella*, *Microcampylopus*, and *Campylopodium* including *C. allonense*.

Evolutionary significance—The presence of mosses has been documented from the late Paleozoic onward, but fossil evidence has been insufficient to determine the timing of diversification within the group at the family and generic levels. The fossil material presented here, along with material of Polytrichaceae (*Eopolytrichum antiquum*; Konopka et al., 1997) from the same locality, provides clear evidence that extant families, and in some cases extant genera, of mosses were already diverse by the Late Cretaceous. *Campylopodium allonense* provides the first evidence of the extant family Dicranaceae in the fossil record and together with *Eopolytrichum antiquum* shows that some groups of mosses have persisted with little morphological change for at least 80 million years.

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NOTE ADDED IN PROOF

The age of the Allon deposit was recently reinterpreted as late Santonian based on palynological evidence (Dr. R. A. Christopher, Clemson University, written communication, 1998). Although a palynologic zonation for the Upper Cretaceous of the southeastern Coastal Plain Prov-

ince has yet to be published, R. A. Christopher examined terrestrial palynomorphs from the Allon locality and considers the sediments to be biostratigraphically equivalent with marine units that have been assigned a late Santonian age on the basis of calcareous nannofossils (i.e., equivalent to the lower part of calcareous nannofossil zone CC17 of Burnett [1996]). The age of the Allon locality was previously cited as early Campanian based on a less precise understanding of the biostratigraphy (Herendeen, Crane, and Drinnan, 1995; Crane and Herendeen, 1996; Keller, Herendeen, and Crane 1996; Magallón-Puebla, Herendeen, and Crane, 1996; Konopka et al., 1997).

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