74-24

RLC

GEOLOGICAL SURVEY OF CANADA

DEPARTMENT OF ENERGY, MINES AND RESOURCES, OTTAWA

PAPER 74-24

CALLIERGON AFTONIANUM STEERE IN LATE TERTIARY AND PLEISTOCENE DEPOSITS OF CANADA

M. KUC

1974

Energy, Mines and Resources Canada
Énergie, Mines et Ressources Canada

GEOLOGICAL SURVEY
PAPER 74-24

CALLIERGON AFTONIANUM STEERE IN LATE TERTIARY AND PLEISTOCENE DEPOSITS OF CANADA

M. KUC

1974

Available by mail from *Information Canada*, Ottawa

from the Geological Survey of Canada
601 Booth St., Ottawa

and

Information Canada bookshops in

HALIFAX — 1683 Barrington Street
MONTREAL — 640 St. Catherine Street W.
OTTAWA — 171 Slater Street
TORONTO — 221 Yonge Street
WINNIPEG — 393 Portage Avenue
VANCOUVER — 800 Granville Street

or through your bookseller

A deposit copy of this publication is also available
for reference in public libraries across Canada

Price: $2.00 Catalogue No. M44-74-24

Price subject to change without notice

Information Canada
Ottawa
1974

CONTENTS

Illustrations

ABSTRACT

The paper critically reviews the North American Late Tertiary and Quaternary mosses which, when described, were considered to have no equivalents in the recent moss flora. They are: *Calliergon aftonianum* Steere, *C. hansenae* Steere, *Camptothecium woldenii* Grout, *Drepanocladus apiculatus* Steere, *Drepanocladus minnesotensis* Williams and *Neocalliergon integrifolium* Williams.

The most distinct taxon is *C. aftonianum*, though its species status is questionable. Its diagnostic features were examined in detail, and critically discussed, on fossil specimens extracted from Late Tertiary and interglacial deposits collected at localities shown in Figure 1 and Table 1.

Calliergon hansenae is not specifically distinct from *C. aftonianum*. *Camptothecium woldenii* is apparently synonymous with *Tomenthypnum nitens* var. *involutum*. *Drepanocladus apiculatus* is within the present-day variability of *D. revolvens*. *D minnesotensis* seems to be an extreme morphological form of *D. exannulatus*. *Neocalliergon integrifolium* is also an extreme form of *Calliergon trifarium*.

RÉSUMÉ

L'auteur passe en revue et analyse les mousses du continent nord-américain de la fin du Tertiaire et du Quaternaire dont la description, lorsqu'elle existe, n'indique aucune équivalence avec les mousses de la flore récente. Ce sont: *Calliergon aftonianum* Steere, *C. hansenae* Steere, *Camptothecium woldenii* Grout, *Drepanocladus apiculatus* Steere, *Drepanocladus minnesotensis* Williams et *Neocalliergon integrifolium* Williams.

C. aftonianum constitue le taxon le plus distinct, quoique l'on ne puisse dire avec certitude s'il s'agit d'une espèce. Ses caractères spécifiques ont fait l'objet de débats critiques et ont été examinés en détail à partir de spécimens fossiles que l'on a extraits de dépôts qui remontent à la fin du Tertiaire et aux stades interglaciaires. Les régions où on les a recueillis sont indiquées à la figure 1 et au tableau 1.

Calliergon hansenae ne se distingue pas specifiquement de *C. aftonianum*. *Camptothecium woldenii* est, selon toute évidence, synonyme de *Tomenthypnum nitens* var. *involutum*. *Drepanocladus apiculatus* ressemble à la variété moderne de *D. revolvens*. *D. minnesotensis* semble être une variété morphologique lointaine de *D. exannulatus*. *Neocalliergon integrifolium* est également une forme lointaine de *Calliergon trifarium*.

CALLIERGON AFTONIANUM STEERE IN LATE TERTIARY AND PLEISTOCENE DEPOSITS OF CANADA

INTRODUCTION

Of several hundred species of mosses hitherto recognized in Pleistocene deposits, about twenty have no equivalents in the recent flora (Jovet-Ast, 1967). Seven such fossil species were described from North America and, until now, are known only from type localities. These are: *Calliergon aftonianum* Steere, *C. hansenae* Steere, *C. kayianum* Steere, *Camptothecium woldenii* Grout, *Drepanocladus apiculatus* Steere, *D. minnesotensis* Williams, and *Neocalliergon integrifolium* Williams. These species raise a number of questions, one of which is the problem of Pleistocene extinctions which, in turn, has major historical implications for the Quaternary biota (Fernald, 1925; Hultén, 1937; Kulczyński, 1923; Leopold, 1967; Steere, 1965; and others). The above-mentioned seven species are important to this discussion only if their taxonomic distinctiveness can be proven; therefore, critical examination of these taxa is necessary before drawing conclusions based on their paleoecological and paleogeographical significance.

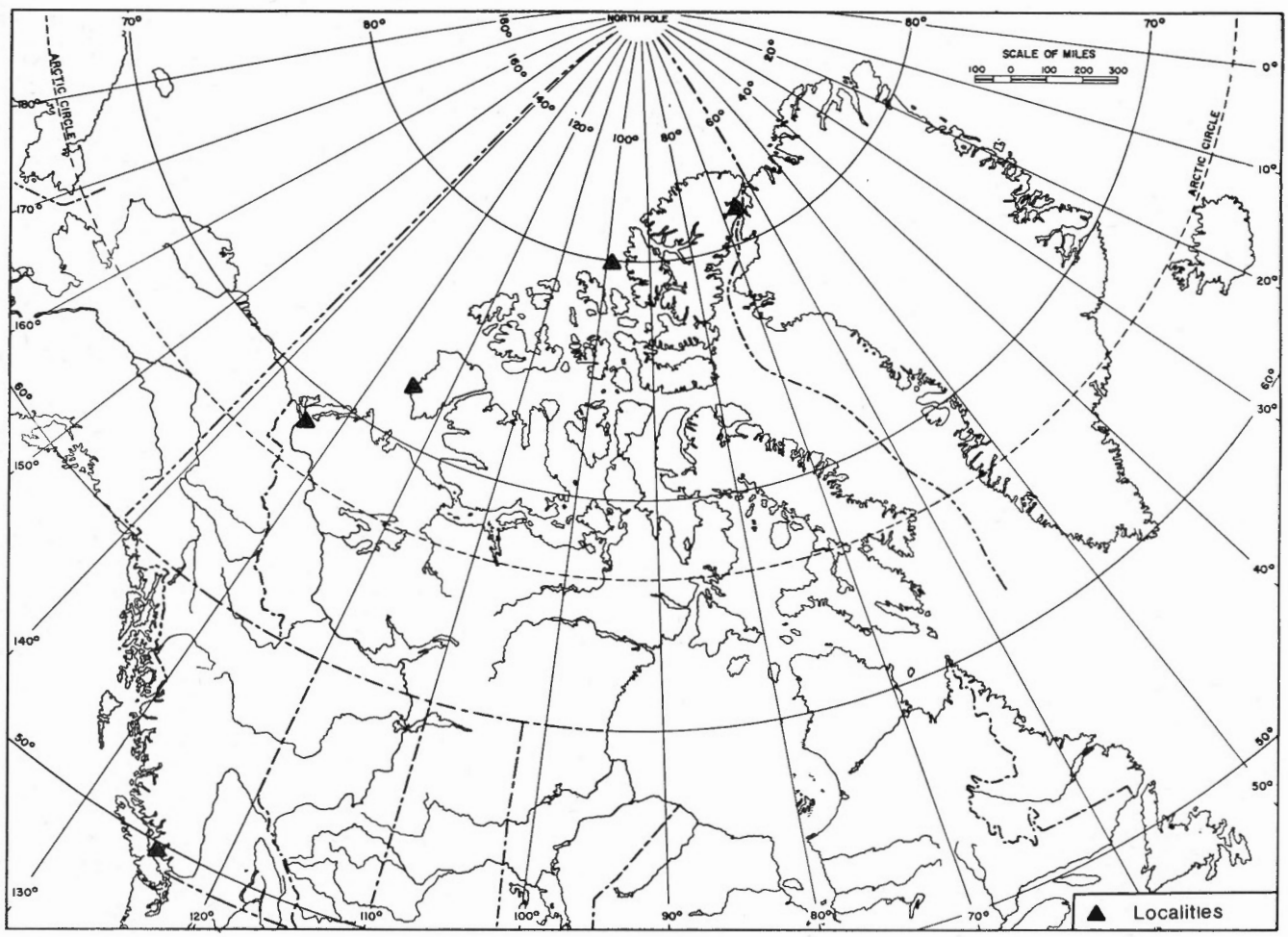


Figure 1. Localities of *Calliergon aftonianum* Steere.

Original manuscript submitted: June 2, 1972
Final version approved for publication: January 25, 1974

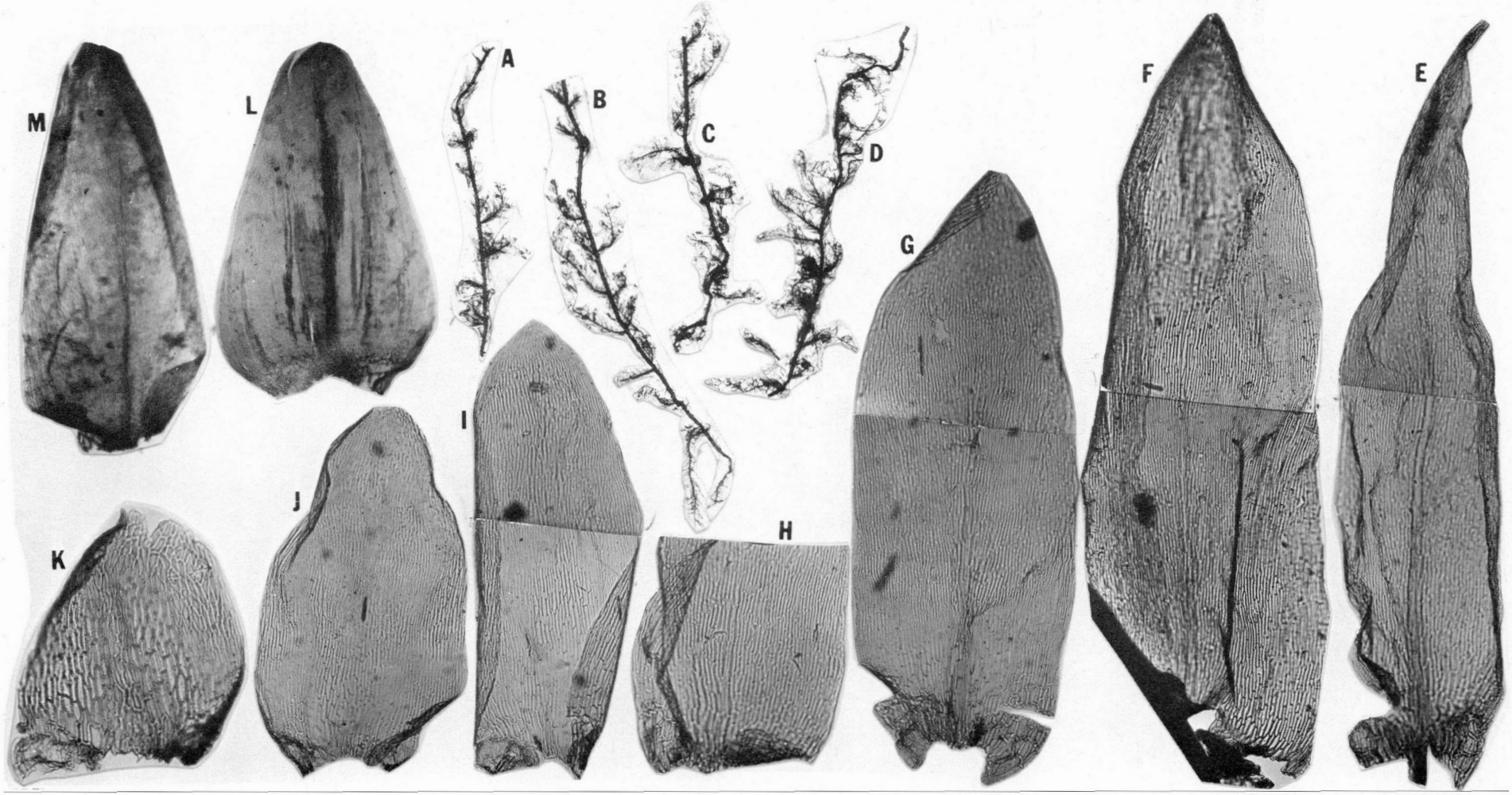


Plate I. A - K *Calliergon aftonianum* Steere.
A - D stems from the Quadra Formation (1:1),
E upper branch leaf (1:55),
F - I middle branch leaves (1:55),
J lower branch leaf (1:55),
K lowermost or primordial branch leaf (1:45);
L upper stem leaf of *C. giganteum* (Schimp.) Kindb. (1:16);
M upper stem leaf of *C. richardsonii* (Mitt.) Kindb. (1:16);
(F - K from the Beaufort Formation (Meighen Island),
L and M from Pleistocene beds).

Late Pliocene and Pleistocene deposits studied by the author have yielded numerous specimens of *Calliergon aftonianum* (cf. Kuc, 1974). The purpose of this paper is to discuss the variability of this species and its taxonomic status.

Dr. W.C. Steere, author of *C. aftonianum*, was kind enough to review this manuscript, to examine specimens and to offer valuable remarks. Dr. J.V. Matthews, Jr., also provided comments on the manuscript.

MATERIALS

Some features of examined remains of *C. aftonianum* and the deposits bearing them are briefly summarized in Table 1. Figure 1 shows the location of fossil localities.

Selected specimens are deposited at the Geological Survey of Canada, Ottawa. A considerable number of *C. aftonianum* fragments were contained in the original, unanalyzed parts of the samples. Specimens in the Beaufort Formation, Reindeer Station, Worth Point, and St. Patrick Bay samples were partly disintegrated during maceration.

TAXONOMIC DISTINCTIVENESS OF *CALLIERGON AFTONIANUM* STEERE

The original diagnosis of *C. aftonianum* (Steere, 1942, p. 85) pertains to the most prominent diagnostic features of this plant. It reads: "Plant apparently large, pinnately branched, with the habit of *Calliergon giganteum*; basal leaves oblong, obtuse, 1 mm long and 0.5 mm wide (Pl. III, Figs. 1-2); costa very short or even lacking; apical leaves of branch longer and narrower, lanceolate, up to 2 mm long and 0.3 mm wide, costa extending about one half the length of the leaf, but never percurrent. Known only from isolated branches".

The following descriptions of features of *C. aftonianum* are based on the examination of several hundreds of whole specimens and stem fragments as well as a number of individual leaves.

Habit, size, and type of branching of specimens (Pl. I A-D)

The plant has a distinct main stem and numerous lateral branches. The largest whole specimens extracted from the Quadra Formation are 8 to 9 cms in length, with lateral branches of 2 cm. Short and thin specimens are sometimes bifid. Stems are irregularly pinnate or branch irregularly. Main stems are more flexible than those of *C. giganteum*, probably due to the anatomical structure of the stems (see the description of stem cross-sections). The habit of *C. aftonianum* differs from those of *C. giganteum* and *C. richardsonii* by its smaller stem leaves, which are loosely arranged on stems, making its foliage more or less uniform.

Branch leaves. Uppermost leaves of lateral branches and of uppermost parts of main stems are longly lanceolate, sometimes recurved, with sides gradually converging to a narrow, obtuse apex. Leaf borders are largely recurved and even overlap in the upper part of the leaf, which is often tubulate. There is a rather weak, single nerve that ends before the apical ¼ of the leaf (Pl. I E). The morphology of uppermost branch leaves is the same for *C. aftonianum*, *C. giganteum* and *C. richardsonii*. Leaves of the middle part of later branches are most characteristic for this taxon. They are longly ligulate, flat, commonly cucullate or with recurved borders at the top (Pl. I F-I). Nerve can extend through half of the leaf, but it is usually much shorter or very short and bifid, or multifid or vanishing. These features clearly distinguish *C. aftonianum* from other species of Sec. Eucalliergon. Leaves of the lower part of later branches (Pl. I J) are widely ligulate or elliptic or even orbicular, mostly flat or slightly concave, or with irregularly and narrowly recurved borders. They have a loose cell net with or without a very short nerve. They are smaller in all respects than upper stem leaves. Some leaves are morphologically very similar to *C. cuspidatum*. Lowermost leaves of *C. aftonianum* have a primordial character (Pl. I K).

Stem leaves (Pl. II). They are much more variable than stem leaves of *C. giganteum* and *C. richardsonii*. Upper stem leaves (Pl. II A-E) are longly ovoidal with strongly recurved borders in the upper part of the leaf. Leaves of the upper-middle parts of stems are longly ligulate or narrowly ellipsoidal (Pl. II F-K), usually flat or sometimes with slightly recurved borders. Leaves of lower stem parts are generally smaller than upper ones, ovate (Pl. II L-N) or obovate (Pl. II O) and very similar to *C. giganteum* and *C. richardsonii*. The nerve of most stem leaves does not extend more than half the length of the leaf or is very short and single. In addition to leaves with short nerves, however, larger ones with longer single or forked nerves sometimes occur. In their morphology, these leaves converge with those of *C. richardsonii*.

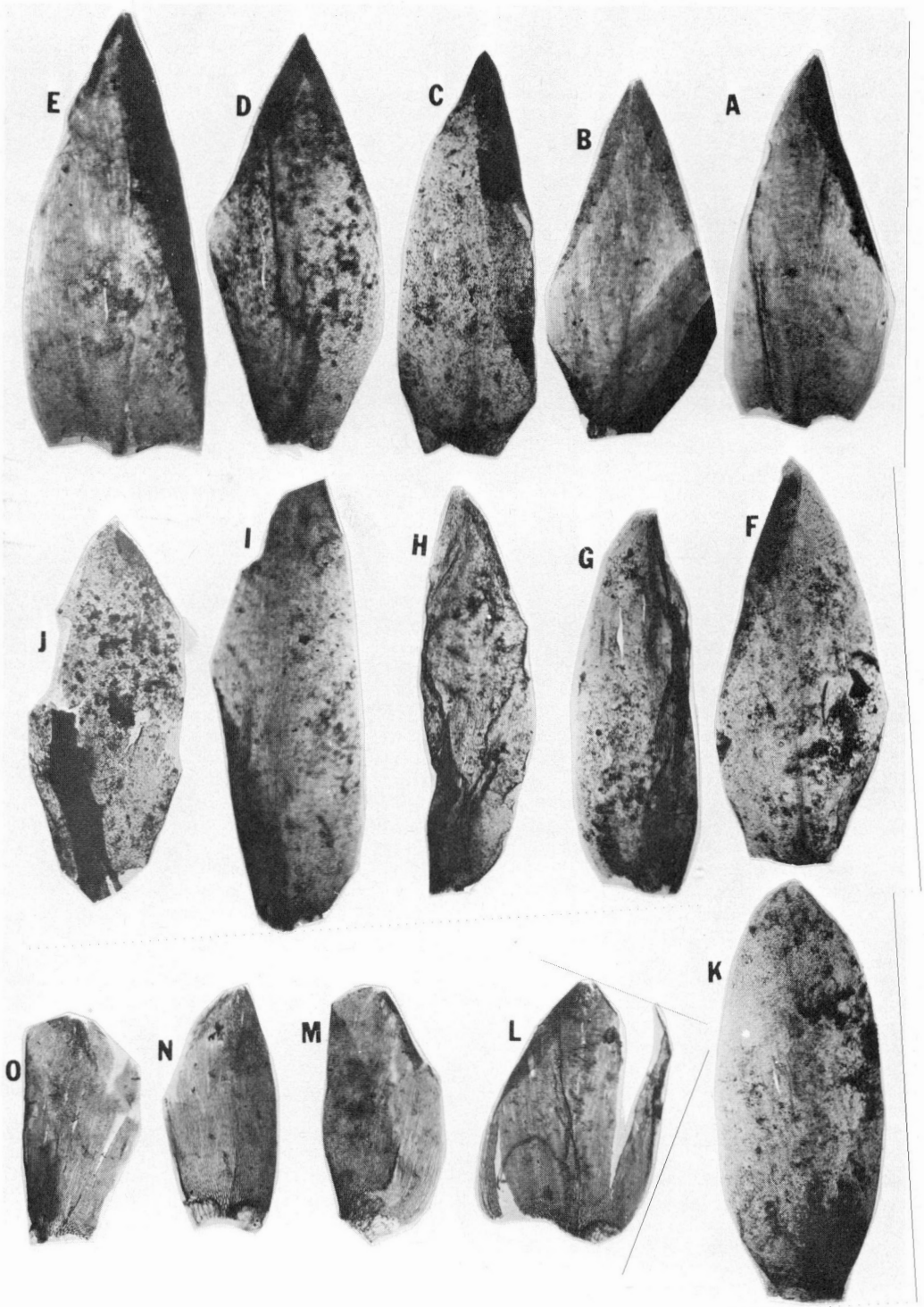
Leaf undulation. Both branch and stem leaves are often longitudinally or transversely undulated in the upper parts of the leaf.

Margin of the apex. It is rarely entire. Usually tops of marginal cells form the crenulation or the irregular, blunt dentition. Teeth closest to the apex are sometimes larger than others and often comprise a bicuspidate dentition (see Steere, 1942, Pl. III, fig. 2).

Primordial leaves. The taxonomic significance of primordial leaves is not well known; therefore, it is difficult to discuss them here as specifically diagnostic features. Comparison of primordial leaves of *C. aftonianum*, *C. giganteum* and *C. richardsonii* indicates that those of the first species are larger, extend higher up the branches, and are usually short, oblong, or ligulate.

Other leaf features. Margin, alar cells, and areolation do not differ from analogous features of *C. giganteum* and *C. richardsonii*.

Transverse cross-section of stem. Same as the stem cross-section of *C. richardsonii*. The scleroderm is bistratose and composed of substereoidal cells. Cross-sections of *C. aftonianum* stems have less scleroidal elements than those of *C. giganteum*.



A - F upper stem leaves (1:40-45) from Mackenzie Delta beds,
G - K upper-middle stem leaves (1:40-45) from Mackenzie Delta beds,
L - O middle and lower stem leaves (1:50-55) from interglacial Worth Point deposits.

Plate II. Variability of stem leaves of *Calliergon aftonianum* Steere.

TABLE 1

Data on collection sites, deposits, and remains

Locality (Fig. 1)	Age	Type of material	Remains	Associates	Collector/year Nos. of microscop. preparations
1) Meighen Island, N.W.T.; 49°50'45"N, 99°09'W	Late Pliocene-early Pleistocene, Beaufort Formation (Kuc, 1974)	woody moss peat	branches and stems, individual leaves	*Calliergon giganteum, C. richardsonii, Campylium polygamum, Drepanocladus exannulatus*	M. Kuc, 1968 MI-87, 110, 114
2) 15 miles north of Reindeer Station, East Channel, Mackenzie River, N.W.T.; 68°53'N, 134°30'W	Pleistocene, higher in section than peat sample dated >44,000 C^{14} years (L-522A); Olson and Broecker, 1961; Mackay, 1963	reworked woody, freshwater sediment with mosses	short stem fragments	*Drepanocladus exannulatus, Scorpidium scorpioides, Tomenthypnum nitens; Picea* sp., *Potamogeton* sp.	V.N. Rampton, 1969 66-ROV-46
3) Worth Point, western Banks Island, N.W.T.; 72°15'N, 125°37'W	Interglacial, >38,000 [I (GSC)-26] Walton *et al.*, 1961, and >49,000 (GSC-367) C^{14} years, Dyck *et al.*, 1966	woody and mossy sapropel	stem fragments	*Calliergon* sp., *Drepanocladus exannulatus; Carex* sp., *Potamogeton* sp., *Ranunculus aquatilis*, plankton; Bryozoa (*Cristatella mucedo* statoblasts); Mollusca, etc.	J.G. Fyles, 1959 FG-59-50
4) Eastern Denman Island, British Columbia; 49°N, 124°W	Quadra Formation about 20,000 to >52,000 C^{14} years, the equivalent of Sangamon and mid-Wisconsin intervals (*see* Fyles, 1963, p. 36-39; Prest, 1970, p. 703-705, and references cited). The age of this sample was not determined by C^{14} dating	*Calliergon-Drepanocladus* peat	whole plants	*Drepanocladus exannulatus*, plankton	J.G. Fyles, 1957 FG-57-36
5) Delta, 3 mi. N.W. of mouth of St. Patrick Bay, N.E. Ellesmere Island, N.W.T.; 81°50'N, 64°25'W	in mixed material of unknown age	woody and mossy detritus, probably not in situ	short, small stem fragments	small, rounded wood fragments and numerous arctic mosses, e.g., *Aulacomnium turgidum, Desmatodon heimii* var. *arcticus, Orthothecium* sp. (*O. chryseum* or *O. rufescens*)	J.H. England, 1971 FG-10-1971 (JHE)

Plate III. Variability of remains of *Calliergon aftonianum* Steere.

Of the features described above, the most characteristic one for *C. aftonianum* is the longly oblong leaves with a short nerve or without one altogether (Pl. III).

The specific status of *C. aftonianum* is dependent on one's point of view of the definition of a species. In the author's opinion, *C. aftonianum* is a clearly recognizable taxon but its species status is questionable. It is most closely related to *C. richardsonii* and connected to it by intermediate forms.

PALEOECOLOGY OF *CALLIERGON AFTONIANUM* AND ITS BIOSTRATIGRAPHIC SIGNIFICANCE

Slender, soft, long, pinnate branching specimens of *C. aftonianum*, as well as the aquatic plants and animals associated with them (e.g., *Calliergon giganteum, C. richardsonii, Drepanocladus exannulatus, Potamogeton* sp., *Ranunculus aquatilis, Scorpidium scorpioides*, and Bryozoa, Mollusca and abundant plankton) and kinds of deposits in which they are found (moss-peat, sapropel, water detritus), indicate the hydrophilous character of the plant. Most probably it grew in stagnant, shallow water bodies. Specimens extracted from the Quadra Formation are coated with a white substance, rich in plankton covers, which reacts with HCl. This suggests the calciphilous nature of the moss. Until now its remains have not been found in tundra deposits but occur only in interglacial or preglacial beds associated with tree fossils and other boreal forest plants. Certainly, it was the plant of open water areas and, therefore, in addition to being a calciphile it is also a photophile. *C. aftonianum* is a typical peatformer and the component of detrital sapropel. In the bryocenological sense it belongs to Helophytia, inhabiting shallow, stagnant, eutrophic, warmer water bodies and deep swampy bogs.

C. aftonianum has existed in fully developed morphological forms since at least the late Tertiary and is well represented in interstadial or interglacial deposits. So far its remains have not been discovered in postglacial in situ deposits and, therefore, it is considered to be an extinct species.

REMARKS ON OTHER NORTH AMERICAN PLEISTOCENE MOSSES, WHICH ALSO LACK REPRESENTATION IN THE RECENT FLORA

Calliergon hansenae Steere: In the critical examination of its status Steere (1942, p. 85-86) wrote, "This species is probably most closely allied to *C. aftonianum* or to *C. giganteum*". The relationship with *C. giganteum* is rather unlikely because *C. hansenae* has "leaves narrowly lanceolate, 1-1.7 mm long (average length about 1.5 mm); costa short, to one half the length of the leaf; apex obtuse to obtusely acute" (Steere, op. cit.) which are features of branch leaves of *C. aftonianum*. He also pointed out the elongated alar cells of *C. hansenae*, which also occur on some of the branch leaves of *C. richardsonii*, as its diagnostic feature.

C. kayianum Steere: The author fully agrees with Steere (op. cit., p. 86-87) that it greatly resembles *Scorpidium scorpioides*. "Symmetrical and not at all secund" leaves separate it from typical leaves of *S. scorpioides*. Leaves of the *C. kayianum* type commonly are found on the thin lateral stems and the uppermost parts of some main stems, in apical, budlike tops of lateral branches of fossil *S. scorpioides* specimens (cf. Kuc and Hills, 1971, Pls. 28 A, E and 29 D), and also on some recent specimens collected in the Canadian Arctic. On the other hand, leaves of the type *C. kayianum* were not found among the many collections of *S. scorpioides* from southern Holarctic regions of Europe and North America. If future study confirms this observation, the *C. kayianum* leaf forms will have the paleoecological significance of indices of colder habitats.

Camptothecium woldenii Grout: Jovet-Ast (1967, p. 141) suggested that it is "très proche du *C. aureum* actuel". Grout (1917) stated that *C. woldenii* is "most closely allied" with *C. pinnatifolium* but differs from *C. aureum* and *C. pinnatifolium* "in entire leaves and very few isodiametric alar cells". Both these features are taxonomically very important and preclude confusion of *C. woldenii* with either of these two species. Other features of *C. woldenii* shown in the original diagnosis and figures (Grout, 1917, p. 9; Pl. 1, Figs. 1-3) can be summarized as follows: robust specimens at least five inches long, pinnate, branching, and densely leaved. Leaves more or less uniform, large (2.0 - 2.5 x 0.75 mm), appressed or patent, strict, elongate-lanceolate (triangular with ovoidal base), gradually narrowing from the base or a little above, acuminated, very strong and deeply plicated along the whole leaf, margin entire. Nerve straight, ending above 3/4 the length of the leaf, prominent. Cells long-linear. Alar cells rounded or quadrate (isodiametric), rarely extending above widest point of the leaf base. The plant with such features is most probably *Tomenthypnum nitens* (syn. *Camptothecium nitens*). Grout (op. cit.) did not point out the very characteristic, dense tomentum of rhizoids coating stems of *Tomenthypnum*. Judging from photographs of *C. woldenii*, its specimens are very similar to *Tomenthypnum nitens* var. *involutum* (a common component of tundra deposits) which is characterized by the lack of the tomentum.

C. woldenii was found in strata of Kansan Glacial age. *C. aureum* and *C. pinnatifolium* are southern species in Canada and their occurrence in glacial deposits is rather doubtful.

Drepanocladus apiculatus Steere: This taxon is characterized by very concave leaves, with distinct, often recurved apiculus and very short costa (Steere, 1942). The author has observed submerged stems of arctic specimens of *D. revolvens* (most closely allied with *D. apiculatus*) possessing leaves with a recurved, thin point, similar to an apiculus and with a short nerve (extending to half the length of the leaf), but the leaves were not concave. It seems possible that *D. apiculatus* has a taxonomic status similar to that of *Calliergon aftonianum*.

Drepanocladus minnesotensis Williams: This plant is very similar to water forms of *Drepanocladus exannulatus*, which are characterized by entire leaves, strong but shorter nerves, and alar cells forming the large group extending to the nerve.

Fossils of *D. minnesotensis* (together with molluscs and *Calliergon giganteum*) were found in a layer of late Pleistocene age "formed some thirty thousand years ago" (Williams, 1930).

Neocalliergon integrifolium Williams: Fossils of this name are probably fragments of *Calliergon trifarium* instead. Apart from having leaves with a distinct nerve, *N. integrifolium* also has ovoid, concave leaves with a short, bifid nerve (or without one). Other features of *N. integrifolium* (Williams, op. cit.) such as (1) slightly divided julaceous stems, (2) oval, concave leaves, (3) the character of alar and blade cells, and (4) porous cell walls, confirm its very close relationship with *C. trifarium*.

N. integrifolium has been found together with *Drepanocladus minnesotensis* (Williams, op. cit.).

REFERENCES

Dyck, W., Lowdon, J.A., Fyles, J.G., and Blake, W. Jr.
1966: Geological Survey of Canada radiocarbon dates V; Radiocarbon 8, p. 96-127.

Fernald, M.L.
1925: Persistence of plants in unglaciated areas of boreal America; Mem. Amer. Acad. Arts Sci., v. 15, p. 241-342.

Fyles, J.G.
1963: Surficial geology of Horne Lake and Parksville map-areas, Vancouver Island, British Columbia; Geol. Surv. Can., Mem. 318, 142 p.

Grout, A.J.
1917: A fossil Camptothecium; The Bryologist, v. 20, p. 9.

Hultén, E.
1937: Outline of the history of arctic and boreal biota during the Quaternary period; Bokforlags Aktiebolaget Thule, Stockholm, 168 p., 43 pl.

Jovet-Ast, S.
1967: Bryophyta; in "Traité de paléobotanique", E. Boureau (ed.), Paris, v. 2, pt. 1, p. 17-186.

Kuc, M.
1974: Fossil flora of the Beaufort Formation, Meighen Island, Northwest Territories; in Report of Activities, Pt. A, April to October, 1973, Geol. Surv. Can., Paper 74-1, Pt. A, p. 193-195.

Kuc, M., and Hills, L.V.
1971: Fossil mosses, Beaufort Formation (Tertiary), Northwestern Banks Island, Western Canada Arctic; Can. J. Bot., v. 49, no. 7, p. 1089-1094.

Kulczynski, S.
1923: Das boreale und arktisch-alpine Element in der Mittel-Europäischen Flora; Bull. Intern. de l'Acad. Polonaise des Sci., nos. 1-10, p. 127-214.

Leopold, E.B.
1967: Late-Cenozoic patterns of plant extinction; in "Pleistocene extinctions", P.S. Martin and H.E. Wright, Jr. (eds.), New Haven and London, Yale University Press, p. 203-246.

Mackay, J.R.
1963: The Mackenzie Delta area, N.W.T.; Canada Dept. Mines Tech. Surveys, Geograph. Br., Mem. 8, 202 p.

Olson, E.A., and Broecker, W.S.
1961: Lamont natural radiocarbon measurements VII; Radiocarbon 3, p. 141-175.

Prest, V.K.
1970: Quaternary geology of Canada; Chap. XII in Geology and Economic Minerals of Canada, R.J.W. Douglas (ed.), Econ. Geol. Rept. 1, 5th ed., Geol. Surv. Can., p. 676-764.

Steere, W.C.
1942: Pleistocene mosses from the Aftonian Interglacial deposits of Iowa; Papers Mich. Acad. Sci. Arts Lett., v. 27 (1941), p. 75-104, pls. I-IV.

1965: The boreal bryophyte flora as affected by Quaternary glaciation; in "The Quaternary of the United States", H.E. Wright (ed.), Princeton Univ. Press, Princeton, N.J., p. 485-495.

Walton, A., Trautman, M.A., and Friend, J.P.
1961: Isotopes, Inc. radiocarbon measurements I; Radiocarbon 3, p. 47-59.

Williams, R.S.
1930: Pleistocene mosses from Minneapolis, Minnesota; The Bryologist, v. 33, p. 33-36.