New species of *Picea* A. Dietrich (Pinaceae) from the middle Eocene of Axel Heiberg Island, Arctic Canada

BEN A. LePAGE FLS

Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316, USA

The discovery of several hundred fertile and vegetative remains of three new species of *Picea* A. Dietrich (*P. sverdrupii, P. nansenii, P. palustris*) from the middle Eocene (45 Myr) sediments of the Buchanan Lake Formation on eastern Axel Heiberg Island, Canadian High Arctic provides a basis for re-assessment of the fossil record of the genus and evaluation of the morphological variability in this taxon. The identification and classification of extant *Picea* is based on a whole-tree concept that in turn is based on the importance of one or more of the following features: cross-sectional shape of the leaves; degree of pubescence of the twigs; arrangement of the stomata on the leaves; colour of the leaves and new growth shoots; length and shape of the cones; shape and degree of pubescence of the buds; and cone-scale morphology. However, the degree of intraspecific variability of these characters is poorly understood and has contributed a great deal towards our general inability to interpret reliably the evolutionary history and phylogenetic relationships within the genus. Examination of the bracts of the Axel Heiberg spruces and all extant species of *Picea* indicates that bract morphology is distinctive for each species and useful for species circumscription. These data allow the genus to be divided into two broad morphological groups that are in general agreement with topologies based on molecular data. © 2001 The Linnean Society of London

ADDITIONAL KEY WORDS: Buchanan Lake Formation – Coniferales – Eureka Sound Group – evolution – fossil – phylogeny – systematics.

INTRODUCTION

The genus *Picea* A. Dietrich consists of 34 species of spruce that are restricted to the Northern Hemisphere (Farjon, 1990). The spruces are prominent constituents of the boreal, montane and sub-alpine forests of North America and Eurasia. The North American *P. glauca* (Moench) Voss and *P. mariana* (Miller) Britton, Sterns & Poggenberg, and the Eurasian *P. abies* (L.) Karsten and *P. obovata* Ledebour have extensive transcontinental distributions and typically form the northern limit of trees in North America, Europe and Asia. The remaining 30 species are restricted to the montane regions of North America, Europe and Asia. Although knowledge of some of the economically important species such as *P. glauca* and *P. engelmannii* Parry ex Engelmann is considerable, little is known about character variability, ecological requirements and tolerances, and phylogenetic relationships of most species, especially the geographically restricted species growing in the montane regions of south-west China.

Features that help to distinguish *Picea* from other genera of the Pinaceae include well-developed pulvini on the shoots, a monomorphic branching system, equifacial and dorsiventrally-flattened leaves that are individually attached and helically arranged on shoots, pendulous cones and an evergreen habit. The spruces occur in a variety of ecological habitats, and as a group are adapted to a wide range of climate. In regions such as northern Canada, Alaska and Siberia, where climate is cold and the growing season is short, pure stands of *Picea* are common. Where temperatures are warmer and the growing season is longer, *Picea* commonly occurs mixed with deciduous and evergreen gymnosperms and angiosperms.

The fossil record of *Picea* includes reports of wood,

E-mail: blepage@sas.upenn.edu

Table 1. Fossil record of the genus *Picea* A. Dietrich

Location	Locality	Type of fossils	Name	Age	Author
North America					
Canada					
Axel Heiberg Island	Geodetic Hills 'a'	C	*Picea heibergii* sp. nov.	Eocene	This report
		C, V	*Picea nansenii* sp. nov.	Eocene	This report
		C	*Picea palustris* sp. nov.	Eocene	This report
	Geodetic Hills 'b'	C	*Picea banksii* Hills & Ogilvie	Eocene	Hills & Bustin, 1976; Bustin, 1982
Banks Island	Ballast Brook	C, V	*Picea banksii* Hills & Ogilvie	Miocene	Hills & Ogilvie, 1970
British Columbia	Vancouver Island	C	*Picea sookensis* LaMotte	Oligocene	LaMotte, 1935
	Quilchena	V	*Picea quilchenensis* Penhallow	Eocene/Oligocene	Penhallow, 1906, 1908
	Tranquille River	V	*Picea tranquillensis* Penhallow	Eocene/Oligocene	Penhallow, 1908
	Kettle River	C	*Picea columbiensis* Penhallow	Eocene/Oligocene	Penhallow, 1907, 1908
U.S.A.					
Montana	Red Lodge	P	*Picea grandivescipites* Wodehouse	Paleocene	Wilson & Webster, 1946
Colorado	Green River	P	*Picea grandivescipites* Wodehouse	Eocene	Wodehouse, 1933
Alaska	Kukak Bay	V	*Picea* sp.	Late Eocene	Knowlton, 1904
	Kukak Bay	C	*Picea harrimanii* Knowlton	Late Eocene	Knowlton, 1904; Hollick, 1936
Nevada	Copper Basin	V	*Picea sonomensis* Axelrod	Late Eocene	Axelrod, 1966
	Copper Basin	V	*Picea* sp.	Late Eocene	Axelrod, 1966
	Copper Basin	V	*Picea magna* MacGinitie	Late Eocene	Axelrod, 1966
	Copper Basin	C, V	*Picea lahontense* MacGinitie	Late Eocene	Axelrod, 1966
Montana	Upper Ruby Basin	V	*Picea lahontense* MacGinitie	Oligocene	Becker, 1961
	Upper Ruby Basin	V	*Picea* sp.	Oligocene	Becker, 1961
	Beaverhead Basin	V	*Picea lahontense* MacGinitie	Oligocene	Becker, 1969
	Beaverhead Basin	V	*Picea magna* MacGinitie	Oligocene	Becker, 1969
	Beaverhead Basin	V	*Picea sonomensis* Axelrod	Oligocene	Becker, 1969
	Avon	C	*Picea diettertiana* Miller	Oligocene	Miller, 1970
Colorado	Florissant	V	*Picea lahontense* MacGinitie	Oligocene	MacGinitie, 1953
	Florissant	V	*Picea magna* MacGinitie	Oligocene	MacGinitie, 1953
	Creede Caldera	V	*Picea* sp.	Oligocene	Wolfe & Schorn, 1990
	Creede Caldera	C, V	*Picea coloradensis* Axelrod	Oligocene	Axelrod, 1987
	Creede Caldera	C, V	*Picea lahontense* MacGinitie	Oligocene	Axelrod, 1987
	Creede Caldera	V	*Picea sonomensis* Axelrod	Oligocene	Axelrod, 1987
Idaho	Thunder Mountain	S	*Picea magna* MacGinitie	Eocene	Axelrod, 1998

Table 1. *continued*

Location	Locality	Type of fossils	Name	Age	Author
	Thunder Mountain	C, S, V	*Picea coloradensis* Axelrod	Eocene	Axelrod, 1998
	Thunder Mountain	C	*Picea deweyensis* Axelrod	Eocene	Axelrod, 1998
	Trapper Creek	V	*Picea sonomensis* Axelrod	Miocene	Axelrod, 1964
	Idaho City	V	*Picea* sp.	Miocene	Knowlton, 1898
	Tipton	V	*Pseudotsuga masonii* MacGinitie	Miocene	Smith, 1941
	Thorn Creek	V	Unidentified seed	Miocene	Smith, 1941
	Trapper Creek	V	*Picea magna* MacGinitie	Miocene	Axelrod, 1964
Washington	Republic	S	*Picea* spp.	Eocene	Wehr & Schorn, 1992
	Olympic Peninsula	C	*Picea eichornii* Miller	Oligocene	Miller, 1989
	Vantage	W	*Picea* sp.	Miocene	Beck, 1945a, 1945b
	Vantage	W	*Piceoxylon* sp.	Miocene	Beck, 1945a
	Columbia Plateau	V	*Picea magna* MacGinitie	Miocene	Chaney & Axelrod, 1959
	Columbia Plateau	C, V	*Picea lahontense* MacGinitie	Miocene	MacGinitie, 1933; Chaney & Axelrod, 1959
Oregon	Columbia Plateau	V	*Picea sonomensis* Axelrod	Miocene	Chaney & Axelrod, 1959
	Tipton	V	*Pseudotsuga masonii* MacGinitie	Miocene	Oliver, 1936
	Tipton	C	*Picea* sp.	Miocene	Mason, 1927
Nevada	Virgin Valley	C	*Picea wolfei* Crabtree	Miocene	Crabtree, 1983
	Rainbow Ridge	W	*Piceoxylon* sp.	Miocene	Beck, 1945a
	Fingerrock Wash	V	*Picea breweriana* S. Watson	Miocene	Wolfe, 1964
	Fingerrock Wash	C	*Picea magna* MacGinitie	Miocene	Wolfe, 1964
	Middlegate Basin	V	*Picea lahontense* MacGinitie	Miocene	Axelrod, 1985
	Middlegate Basin	V	*Picea sonomensis* Axelrod	Miocene	Axelrod, 1985
	Buffalo Canyon	C	*Picea lahontense* MacGinitie	Miocene	Axelrod, 1991
	Buffalo Canyon	C	*Picea magna* MacGinitie	Miocene	Axelrod, 1991
	Buffalo Canyon	C	*Picea sonomensis* Axelrod	Miocene	Axelrod, 1991
	Mullen Pass	C	*Picea sonomensis* Axelrod	Miocene	Axelrod, 1992
	Purple Mountain	V	*Picea lahontense* MacGinitie	Miocene	Axelrod, 1995
	Purple Mountain	V	*Picea magna* MacGinitie	Miocene	Axelrod, 1995
	Purple Mountain	V	*Picea sonomensis* Axelrod	Miocene	Axelrod, 1995
Nevada	Aldrich Station	C	*Picea magna* MacGinitie	Miocene/Pliocene	Axelrod, 1956
	Aldrich Station	C	*Picea sonomensis* Axelrod	Miocene/Pliocene	Dorf, 1938; Smith, 1938
Idaho	Hog Creek	C	*Picea lahontense* MacGinitie	Pliocene	Axelrod, 1944b

Table 1. *continued*

Location	Locality	Type of fossils	Name	Age	Author
California	Neer's Hill	C	*Picea sonomensis* Axelrod	Pliocene	Axelrod, 1944b
Oregon	Alvord Creek	C	*Picea lahontense* MacGinitie	Pliocene	Axelrod, 1944a
	Alvord Creek	C	*Picea sonomensis* Axelrod	Pliocene	Axelrod, 1944a
	Tipton	C, V	*Picea* sp.	Pliocene	Brown, 1937
	Tipton	C	*Picea* sp.	Pliocene	Brown, 1937
Greenland	Kap København	C, V	*Picea mariana* (Miller) Britton, Sterns & Poggenberg	Pliocene/ Pleistocene	Bennike, 1990
Asia					
Russia	Kamchatka	C	*Picea snatolensis* Chelebaeva	Late Eocene	Gladenkov *et al.*, 1991
	Kamchatka	C	*Picea fimbriata* Chelebaeva	Late Eocene	Gladenkov *et al.*, 1991
	Kamchatka	V	*Picea magna* MacGinitie	Late Eocene	Gladenkov *et al.*, 1991
	Novy Log	V	*Picea* sp.	Oligocene	Dorofeev, 1970
	Yuzhnogo Mountain	V	*Picea* sp. 1	Oligocene	Rayushkina, 1979
	Yuzhnogo Mountain	V	*Picea* sp. 2	Oligocene	Rayushkina, 1979
	Yuzhnogo Mountain	V	*Picea altaica* Rayushkina	Oligocene	Rayushkina, 1979
	Mugodzhar	C	*Picea mugodzharica* Rayushkina	Oligocene	Rayushkina, 1979
	Ob and Irmish rivers	V	*Picea* sp. 1	Oligocene/Miocene	Dorofeev, 1963
	Ob and Irmish rivers	V	*Picea* sp. 2	Oligocene/Miocene	Dorofeev, 1963
	Sakhalin	V	*Picea kanehari* Tanai & Onoé	Oligocene/Miocene	Fotyanova, 1988
	Botchi River	V	*Picea* sp. 1	Miocene	Akhmetiev, 1973
	Botchi River	V	*Picea* sp. 2	Miocene	Akhmetiev, 1973
	Botchi River	C	*Picea* sp. 3	Miocene	Akhmetiev, 1973
	Botchi River	V	*Picea* sp. 4	Miocene	Akhmetiev, 1973
	Botchi River	V	*Picea* sp. 5	Miocene	Akhmetiev, 1973
	Aldan River	V	*Picea* sp.	Miocene	Dorofeev, 1969
	Tambov	V	*Picea* sp.	Miocene	Dorofeev, 1988
	Omoloi River	C	*Picea wollowsowiczii* Sukaczev	Miocene	Dorofeev, 1972
	Omoloi River	V	*Picea* sp.	Miocene	Dorofeev, 1972
	Kamchatka	V	*Picea jezoensis* (Siebold & Zuccarini) Carrière var. *fossilis* Palibin	Pliocene	Palibin, 1934
Japan	Honshu	S	*Picea* sp.	Eocene	Huzioka & Takahasi, 1970
	Honshu	V	*Picea* sp.	Oligocene/Miocene	Tanai, 1952
	Honshu	V	*Picea kanehari* Tanai & Onoé	Miocene	Tanai and Onoé, 1961

Table 1. *continued*

Location	Locality	Type of fossils	Name	Age	Author
	Hokkaido	V	*Picea kanehari* Tanai & Onoé	Miocene	Tanai, 1961; Tanai & Suzuki, 1963, 1965, 1972
	Hokkaido, Honshu	V	*Picea kanoi* Huzioka	Miocene	Tanai, 1961; Tanai & Suzuki, 1963, 1965, 1972
	Hokkaido	V	*Picea ugoana* Huzioka	Miocene	Tanai, 1961; Tanai & Suzuki, 1963, 1965, 1972
	Honshu	V	*Picea sugaii* Tanai & Onoé	Miocene	Tanai, 1955, 1961; Tanai & Onoé, 1959
	Honshu	V	*Picea miocenica* Tanai	Miocene	Tanai, 1961
	Honshu	S	*Picea kanehari* Tanai & Onoé	Miocene	Huzioka, 1963
	Honshu	S	*Picea magna* MacGinitie	Miocene	Huzioka, 1963
	Honshu	S	*Picea kanehari* Tanai & Onoé	Miocene	Matsuo, 1963
	Honshu	S	*Picea kanehari* Tanai & Onoé	Miocene	Ishida, 1970
	Honshu	V	*Picea* sp.	Miocene	Ozaki, 1991
	Hokkaido	C	*Picea garoensis* Tanai & Suzuki	Miocene	Tanai & Suzuki, 1972
	Hokkaido	V	*Picea hiyamensis* Tanai & Suzuki	Miocene	Tanai & Suzuki, 1963
	Hokkaido	V	*Picea magna* MacGinitie	Miocene	Tanai, 1961; Tanai & Suzuki, 1963
	Honshu	C	*Picea cf. maximowiczii* Regel *ex* Masters	Pliocene	Miki, 1941
	Honshu	C, V	*Picea koribai* Miki	Pliocene	Miki, 1948, 1957
	Honshu	V	*Picea polita* (Siebold & Zuccarini) Carrière	Pliocene	Yabe & Endô, 1939
	Honshu	C, V, S	*Picea polita* (Siebold & Zuccarini) Carrière	Pleistocene	Onoé, 1989
Europe					
Belgium	Quenast	P	*Piceapollenites* sp.	Eocene	Pastiels, 1948
Netherlands	Reuver	W	*Picea* sp.	Pliocene	Slijper, 1932
	Reuver	C	*Picea excelsa* (Lamark) Link	Pliocene	Reid & Reid, 1915
Germany	Lausitz	C, V	*Picea beckii* Mai	Late Oligocene	Mai, 1987; Mai & Walther, 1991
	Frankfurt	W	*Piceoxylon* sp.	Pliocene	Mädler, 1939
	Frankfurt	C	*Picea* sp.	Pliocene	Mädler, 1939
	Frankfurt	C	*Picea aff. rubra* (DuRoi) Link var. *fossilis* Kinkelin	Pliocene	Engelhardt & Kinkelin, 1908
	Frankfurt	C	*Picea excelsa* (Lamark) Link var. *fossilis* Geyler & Kinkelin	Pliocene	Engelhardt & Kinkelin, 1908
	Frankfurt	V	*Picea excelsa* (Lamark) Link var. *fossilis* Geyler & Kinkelin	Pliocene	Mädler, 1939

continued

Table 1. *continued*

Location	Locality	Type of fossils	Name	Age	Author
	Frankfurt	C, V	*Picea latisquamosa* Ludwig	Pliocene	Engelhardt & Kinkelin, 1908; Mädler, 1939
	Frankfurt	C	*Picea latisquamosa* Ludwig var. *fusiformis* Kinkelin	Pliocene	Engelhardt & Kinkelin, 1908
	Frankfurt	C	*Picea latisquamosa* Ludwig var. *cylindrica* Kinkelin	Pliocene	Engelhardt & Kinkelin, 1908
	Frankfurt	C	*Abies pectinata* DeCandolle var. *fossilis* Geyler & Kinkelin	Pliocene	Engelhardt & Kinkelin, 1908
	Flörsheim	C	*Picea latisquamosa* Ludwig	Pliocene	Engelhardt, 1911
	Flörsheim	C	*Picea oligocaenica* Engelhardt	Pliocene	Engelhardt, 1911
Poland	Czorsztyna	C	*Picea excelsa* (Lamark) Link var. *fossilis* Geyler & Kinkelin	Pliocene	Szafer, 1954
	Czorsztyna	C	*Picea polita* (Siebold & Zuccarini) Carrière var. *fossilis* Szafer	Pliocene	Szafer, 1954
	Krościenka	C	*Picea excelsa* (Lamark) Link var. *fossilis* Geyler & Kinkelin	Pliocene	Szafer, 1947
	Krościenka	C, V	*Picea polita* (Siebold & Zuccarini) Carrière var. *fossilis* Szafer	Pliocene	Szafer, 1947
	Krościenka	C, V	*Picea rubra* (DuRoi) Link	Pliocene	Szafer, 1947
	Krościenka	C, V	*Picea cf. glehnii* (Fr. Schmidt) Masters	Pliocene	Szafer, 1947
Czechoslovakia	Cheb	V	*Picea omorikoides* Weber	Pliocene	Bůžek, Kvaček & Holý, 1985
Romania	Chiuzbaia	S	*Picea* sp.	Miocene	Givulescu, 1990
	Chiuzbaia	S	*Picea* sp. aff. *P. magna* MacGinitie	Miocene	Givulescu, 1979

C = cones and cone scales; S = seeds; V = leaves and twigs; W = wood; and P = pollen.

seeds, leaves and cones, and indicates that the genus was present in North America and Eurasia during the mid- to late Tertiary (Table 1). Although *Picea* is reasonably well represented in the fossil record, the ambiguous taxonomic status and putative relationships between many of the living species, especially those from south-west China, and the ability of most living species to hybridize have made understanding of living and fossil *Picea* taxonomy and phylogeny difficult to interpret.

Exquisitely preserved fertile and vegetative *Picea* remains recovered from the Buchanan Lake Formation, Eureka Sound Group on Axel Heiberg Island extend the record of this group to the middle Eocene (*c.* 45 Myr). Recognition of three new fossil *Picea* species from the Axel Heiberg Fossil Forests is based on detailed examination of fossil and living representatives. The principal characters used to identify and separate the Axel Heiberg Island spruces into three distinct species are the morphology of the seed cones and bract/scale complexes and facies association. The quality of preservation and large number of *Picea* fossils from this site also permitted assessment of such characters as the seed cones, seeds and leaves and their subsequent utility for taxonomic and systematic interpretation. The results of this examination con-
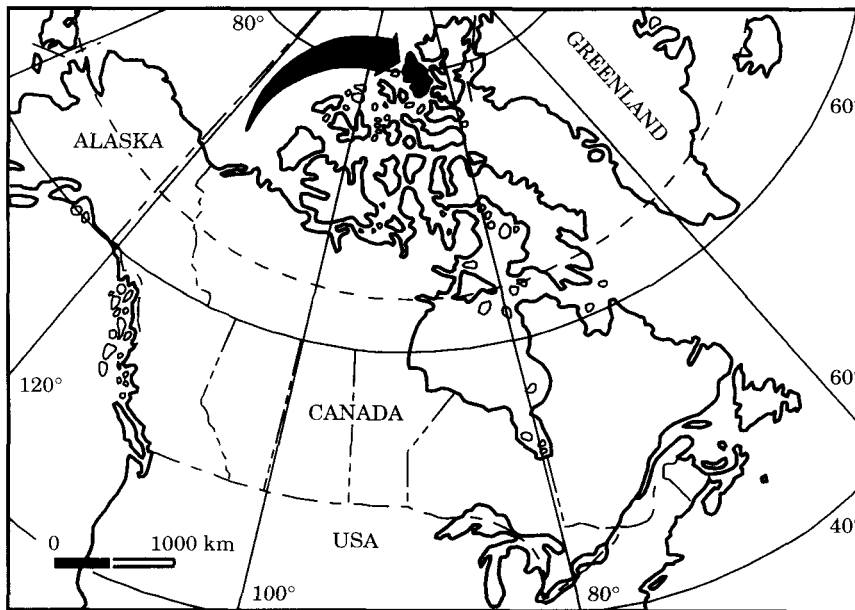
Figure 1. Map of Canada showing the location of Axel Heiberg Island (arrow) in the Canadian High Arctic.

tribute to clarifying the taxonomy and phylogeny of the genus.

MATERIALS

AXEL HEIBERG ISLAND LOCALITY

The fossils were recovered from sediments of the Buchanan Lake Formation, Eureka Sound Group, on Axel Heiberg Island, Canadian Arctic Archipelago (Figs 1, 2; 79°55′N, 89°02′W; Geological Survey of Canada, Map 1301A, Strand Fiord, District of Franklin, 1:250 000). The Buchanan Lake Formation, as described by Ricketts (1986, 1991, 1994), consists of four lithologically distinct and mappable members. The fossils occur in Ricketts's Upper Coal Member, which consists of interbedded sandstone, siltstone and lignite arranged in fining upward sequences.

Based on vertebrate remains, structural, petrographic, stratigraphic and palynological features, the age of these fossiliferous sediments has been determined to be middle Eocene (Ricketts, 1986, 1987, 1994; Ricketts & McIntyre, 1986; McIntyre, 1991; Eberle & Storer, 1999).

The plant fossils occur in two distinct facies associations. Abrasion-resistant allochthonous plant fossils are concentrated in a number of point-bar deposits in the upper part of the formation. More than 500 *Picea* seed cones were recovered from these sands together with unidentifiable woody fragments and rare seed cones of *Larix altoborealis* LePage & Basinger, *Pinus* L. and *Metasequoia* Miki *ex* Hu & Cheng, and

fruits of *Juglans* L. (Basinger, 1991; LePage & Basinger, 1991).

The autochthonous leaf-litter mats occur in the coaly facies in the lower part of the formation and represent the ancient forest floors of poorly-drained meander-plain swamps (Ricketts, 1986, 1991; Basinger, 1991). Plant megafossils recovered from a number of these forest-floor litter mats include the remains of the dominant conifers *Metasequoia* and *Glyptostrobus* Endlicher, and minor occurrences of *Picea*, *Pseudolarix amabilis* (Rehder) Gordon, *Pseudolarix wehrii* Gooch, *Pinus*, *Larix altoborealis*, *Betula* L., *Alnus* Miller, *Carya* Nuttall, *Chamaecyparis* Spach, *Tsuga* (Endlicher) Carrière and *Osmunda* L., as well as a number of unidentified angiosperms and pteridophytes (Ricketts & McIntyre, 1986; Basinger, 1991; LePage & Basinger, 1991, 1995; McIntyre, 1991). The scarcity of *Picea* relative to other taxa in these litters indicates that *Picea* was an uncommon constituent within the Taxodiaceae-dominated swamp-forest communities.

Herbarium, living and fossil specimens of *Picea* used for comparison in this study are listed in Appendices 1 and 2.

METHODS

Mummified *Picea* specimens were demineralized in cold 5% HCl for 24 h to remove all carbonates, rinsed with distilled water and immersed in 48% HF for 3–5 days. The HF was changed at least twice to ensure removal of all silicates. Specimens were then rinsed
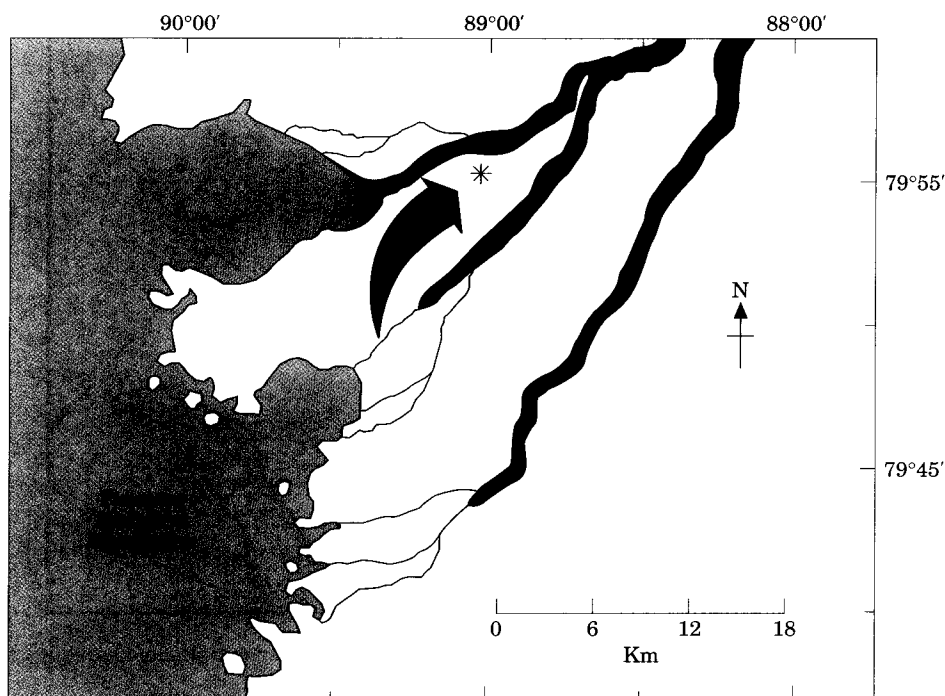
Figure 2. Geodetic Hills area, eastern Axel Heiberg Island, showing location (*) of the Axel Heiberg Fossil Forests (79°55′N, 89°02′W).

with distilled water. Any sediment still adhering to the specimens was removed with a soft-haired artist's brush; more robust specimens were cleaned in an ultrasonic bath for 2–3 min.

Preparation of leaf cuticle was carried out according to the technique of Dilcher (1974), with the following modifications. Leaves that had not been exposed to acids were soaked in Calgon-softened water (30 mL of Calgon to 4.5 L water) for 48 h (J. Skog, pers. comm.). The demineralization process destroys the cuticle of leaves, especially when thin; the cuticle of the Axel Heiberg *Picea* leaves is surprisingly thin, approximately 4 μm, relative to extant *Picea* leaves which are about 10 μm. The leaves were oxidized in full-strength household bleach (6% NaOCl) for 30–60 s. When cleared, cuticular sheaths were rinsed in softened water, opened by micromanipulation, and mounted on stubs with double-sided tape, coated with gold and viewed on a Philips 505 scanning electron microscope at 30 kV.

Leaves of living *Picea* were oxidized in full-strength

bleach for 2–4 h; when clear, they were rinsed with distilled water and then mounted for SEM following the same procedure used for the fossils.

For photography, the surface features of some fossil and living specimens were enhanced by whitening with ammonium chloride (NH₄Cl; Bassler, 1953).

Description of *Picea* morphology follows terminology proposed by Hickey (1973, 1977), Dilcher (1974) and Metcalf & Chalk (1979).

SYSTEMATIC PALAEOBOTANY

ORDER CONIFERALES
FAMILY PINACEAE LINDLEY

Genus *Picea* A. Dietrich
**Picea sverdrupii** LePage **sp. nov.**
(Figs 3, 4, 84, 85)

Specific diagnosis

CONE ovoid to oblong-cylindrical, up to 115 mm long and 28 mm wide. CONE SCALE narrow to wide obovate,

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Figures 3–7. New species of *Picea*. Fig. 3. **Picea sverdrupii sp. nov.** Cones showing variation in size. (A) US237-5613, (B) US237-5614, (C) US237-5615, (D) US237-5616, (E) US237-5617, (F) US237-5618, (G) US237-5619, (H) US237-5620 and (I) US237-5621. Scale bar = 10 mm. Fig. 4. **Picea sverdrupii sp. nov.** SEM of a winged seed. Note its similarity to the *P. brachytyla* seed shown in Figure 19d. US-SEM 153 (US186-5598). Scale bar = 1.0 mm. Fig. 5. **Picea nansenii sp. nov.** Cones showing their range in size. Note how the cones taper basally and apically. (A) US-184-5608,
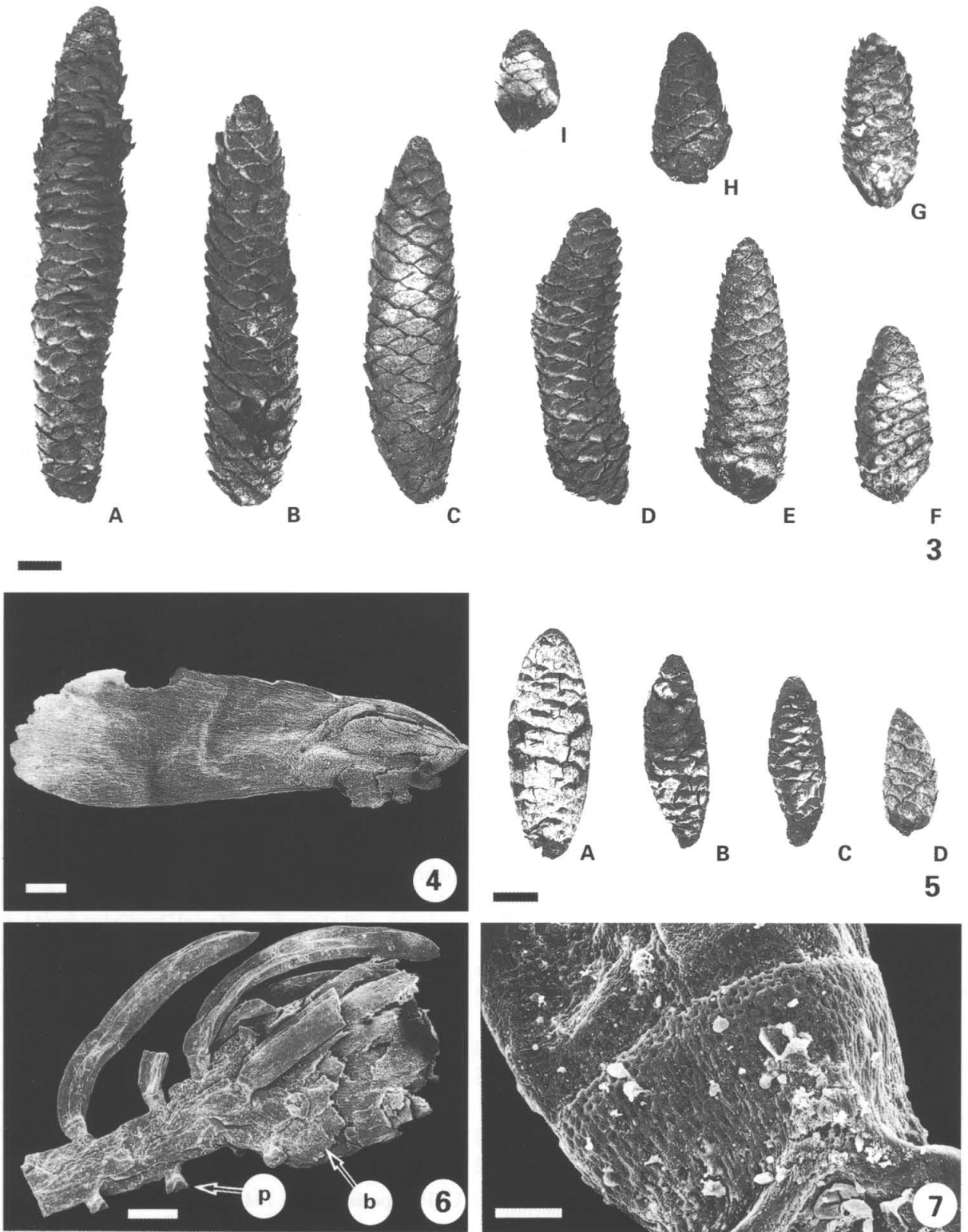
(B) US184-5609, (C) US520-5610 and (D) US220-5611. Scale bar = 10 mm. Fig. 6. **Picea nansenii sp. nov.** SEM of twig showing leaves attached to pulvini (p) and the terminal bud which is protected by bud scales (b) and sub-terminal leaves. US-SEM 138 (US220-5593). Scale bar = 1.0 mm. Fig. 7. **Picea nansenii sp. nov.** SEM close-up of a pulvinus and the attached leaf. US-SEM 138 (US220-5593). Scale bar = 1.0 mm.

up to 17 mm long and 12 mm wide; margin entire; apex rounded; abaxial surface smooth and glabrous. BRACT lanceolate, hidden, up to 8 mm long and 2 mm wide; basally adnate to the cone scale, free medially and apically; apex cuspidate to attenuate, rarely emarginate; margin entire to slightly wavy; glabrous. SEEDS two per scale, winged, up to 9 mm long and 3 mm wide; wing membranous, symmetrical, narrow obovate to oblanceolate, apex rounded; seed-body wide to narrow ovate, up to 3.5 mm long and 2 mm wide.

Holotype

University of Saskatchewan Paleobotanical Collection (USPC), Specimen US 237-5613.

Paratypes

USPC specimens US 186-5598, US 237-5588, US 237-5614-5621.

Collecting localities

US 114, 115, 119, 182, 186, 234, 235, 237, 520, 563, 567, 568, 585, 586, 587.

Etymology

In honour of Otto Sverdrup, Captain of the *Fram* 1893–96.

Detailed description

Seed cones of *P. sverdrupii* vary considerably in size (Fig. 3). The cones comprise 50–250 + imbricate, woody cone scales that are helically arranged around a central cone axis and attached by a short pedicel. Well-preserved specimens possess round cone-scale apices with entire margins and smooth adaxial surfaces (Fig. 84). However, most specimens show some degree of abrasion so that the cones scales have the appearance of being slightly toothed. Moreover, the abaxial surface of the scales are pitted by sand grains due to post-burial compression.

The bract is thin and lanceolate and up to 8 mm long and 2 mm wide. Each bract possesses a small apical tooth which is an extension of the vascular trace and gives the bract a cuspidate to attenuate appearance (Fig. 85).

Winged seeds of *P. sverdrupii* were found in the cone scales of some cones (Fig. 4). The seed-wing margins are entire, and the size and shape of the seeds are typical for the genus (Table 2; Figs 4, 19). Among the living species, the seeds of *P. brachytyla* (Franchet) Pritzel compare favorably to those of *P. sverdrupii* (Fig. 19d).

Remarks

More than 500 seed cones of *P. sverdrupii* were recovered from a number of channel and point-bar deposits that dissected the floodplains and lowland swamps. The establishment of this species is based, in part, on the morphology of the cones and bract-scale complexes and the habitat from which this species is thought to have occupied. Its appearance in predominantly fluvial deposits indicates that *P. sverdrupii* occupied the extrabasinal montane and riparian forest communities growing on the better-drained soils of the rising Princess Margaret Mountains, foothills and possibly in the floodplains on the levees of the streams and rivers that drained the montane watersheds. The small number of *P. sverdrupii* cones found in the autochthonous leafy litter mats indicates that these extrabasinal montane habitats were in close proximity to the swamps. Given the limited abrasion seen on the seed cones, transport was minimal and probably limited to a few kilometres (Spicer & Greer, 1986).

Picea nansenii LePage sp. nov.
(Figs 5–11, 86, 87)

Specific diagnosis

CONE ovoid to oblong-cylindrical, up to 57 mm long and 20 mm wide; composed of 40–100 imbricate, woody cone scales. CONE SCALE round to narrow or wide obovate, up to 13 mm long and 9.5 mm wide; margin entire; apex rounded; abaxial surface smooth and glabrous. BRACT subtending cone scale lanceolate, non-exserted, up to 2.5 mm long and 2 mm wide, resinous; basally adnate to the cone scale, but free medially and apically; apex cuspidate or emarginate; margin entire to crenate; glabrous. LEAVES helically arranged on shoots, basally attached to pulvini, up to 6.5 mm long and 1 mm wide; resinous, awl shaped, equifacial, apex mucronate. Stomata amphistomatic, inconspicuous and sunken. TERMINAL BUD round to ovoid in shape, covered by terminal scales and subterminal leaves. SEEDS two per scale, winged, up to 7 mm long and 3.5 mm wide; wing membranous, symmetrical, narrow obovate to oblanceolate, apex rounded; seed-body wide to narrow ovate, up to 2 mm long and 1.5 mm wide.

Holotype

USPC specimen US 184-5608.

Paratypes

USPC specimens US 184-5573, US 184-5594, US 184-5609, US 220-5572, US 220-5593, US 220-5611, US 520-5610.

Table 2. Comparison of extant members of *Picea* A. Dietrich with fossil representatives of *Picea*

	Cone length[1]	Cone width	L/W ratio	Scale length	Scale width	L/W ratio	Bract length	Bract width	L/W ratio	Leaf length	Leaf width	Seed body length	Seed body width	Wing length	Wing width
Picea abies (L.) Karsten	25–200	15–50	1.7–4.0:1	15–30	10–20	1.5:1	2–7	1.5–2	1.5–3.5:1	8–30	0.8–2	2–5	1–2	6–26	4–6
Picea alcoquiana (Veitch *ex* Lindley) Carrière	50–120	30–55	1.7–2.2:1	15–25	8–21	1.2–1.9–1	2–3.5	1.5–2	1.4–1.6:1	8–20	0.7–1.5	2–5	1.5–3	11–18	6–7.5
Picea asperata Masters	50–160	20–45	2.5–3.6:1	12–24	8–18	1.3–1.5:1	2–7	1.5–3	1.5–2.3:1	10–25	1–2	2–4	1.5–3	8–17	5–7
Picea aurantiaca Masters	95–120	40–45	2.4–2.7:1	20–24	15–18	1.3:1	2–5	1.5–2	1.3–2.5:1	8–20	1–2.5	3–4	2–2.5	12–15	5–6
Picea brachytyla (Franchet) Pritzel	40–120	20–40	2.0–3.0:1	12–20	9–17	1.2–1.3:1	1.5–4.5	1.5–2	1.1–2.3:1	8–25	1–2	2–3	1–2	8–18	3–8
Picea breweriana S. Watson	60–140	20–40	3.0–3.5:1	15–22	13–18	1.2:1	3–6	2–2.5	2.9–3.0:1	15–35	1–2	3–4	2–3	7–9	5–6
Picea chihuahuana Martínez	100–170	30–50	3.3–3.4:1	20–25	15–21	1.2–1.3:1	3–5.5	1–1.5	2.5–4.0:1	12–28	1–2	3–6	1.5–2	10–15	5–8
Picea crassifolia Komarov	50–110	25–35	2.0–3.1:1	15–20	10–17	1.2–1.5:1	2–3	2–2.5	1.0–1.3:1	9–35	1.5–3	3–3.5	0.5–1	10–13	4–5
Picea engelmannii Parry *ex* Engelmann	25–75	20–35	1.3–2.1:1	12–28	9–19	1.3–1.5:1	3–5	2–2.5	1.5–2.3:1	12–30	1–2	1.5–3	1–2	7–12	3.5–5
Picea farreri Page & Rushforth	40–140	25–45	1.6–3.1:1	8–22	8–16	1.0–1.4:1	2–3.5	1.5–2	1.3–1.7:1	15–25	1–1.5	3–4	1.5–2.5	13–16	5–6
Picea glauca (Moench) Voss	30–70	12–25	2.5–2.81	12–15	8–12	1.3:1.5:1	2–4	1.5–2	1.4–2.0:1	8–18	0.8–1.5	2–3	0.3–5	6–10	3–5
Picea glehnii (Fr. Schmidt) Masters	35–85	25–38	1.4–2.2:1	11–18	8–12	1.4:1.5:1	2–3	1–1.5	1.4–2.0:1	6–17	0.7–1.5	2.5–3	1–2	7–10	4–6
Picea jezoensis (Siebold & Zuccarini) Carrière	40–90	20–35	2.0–2.6:1	10–17	6–9	1.7–1.9:1	4–5.5	2–4	1.7–1.9:1	10–24	1.5–2	2.5–3	1–2	5.5–10	3–5
Picea koraiensis Nakai	40–80	25–40	1.5–2.0:1	13–19	9–16	1.2–1.4:1	2–5	1–1.5	1.5–3.6:1	12.0–25.0	1.5–2	3–4	2–2.5	12–16	6–8
Picea koyamae Shirasawa	30–100	25–40	1.2–2.5:1	6–18	6–16	1.1–1.1:1	2–4	1–1.5	2.0–2.7:1	6.0–20.0	1–2	2–4	1.5–2.	5–12	3–5
Picea likiangensis (Franchet) Pritzel	50–150	25–50	2.0–3.0:1	15–26	10–17	1.5:1	2–6	1–4	1.5–2.0:1	6.0–22.0	0.9–1.5	2–4	1–2	7–14	2.5–4
Picea mariana (Miller) B.S.& P.	15–40	15–28	1.0–1.4:1	7–13	6–10	1.2–1.3:1	1–3	1–2	1.0–1.5:1	6.0–18.0	0.7–1	2–2.5	1–2	5–8	3–3.5
Picea maximowiczii Regel *ex* Masters	25–90	25–35	1.0–2.6:1	13–18	10–15	1.2–1.3:1	2–5	1–2	1.7–2.5:1	8.0–18.0	1–1.5	3–4.5	2.5–3	8–10	4–5

Table 2. continued

	Cone length[1]	Cone width	L/W ratio	Scale length	Scale width	L/W ratio	Bract length	Bract width	L/W ratio	Leaf length	Leaf width	Seed body length	Seed body width	Wing length	Wing width
Picea meyeri Rehder & Wilson	60–120	25–40	2.4–3.0:1	10–20	10–16	1.0–1.3:1	4–6	1.5–2	2.3–3.0:1	8.0–30.0	1.5–2	2.5–4	1–2.5	10–15	4–6.5
Picea morrisonicola Hayata	40–70	25–30	1.6–2.3:1	12–18	10–12	1.2–1.5:1	2–5	1–1.5	1.5–3.1:1	8.0–20.0	0.9–2.5	3–3.5	1–2.5	8–10	4–5
Picea neoveitchii Masters	70–140	45–65	1.6–2.2:1	25–32	25–30	1.0–1.1:1	2–10	3.5–4	1.1–2.6:1	15.0–25.0	1.7–2	5–7	2–4.5	15–25	8–11
Picea obovata Ledebour	50–110	20–30	2.5–3.7:1	14–17	9–12	1.4–1.6:1	2.5–4	1–2	2.6–2.4:1	12.0–20.0	0.5–1	1.5–2	1–1.5	10	3–4
Picea omorika (Pančić) Purkyne	30–65	20–30	1.5–2.2:1	10–15	10–13	1.0–1.2:1	2–5	1.5–2	1.2–2.5:1	8.0–23.0	1.5–2.5	2.1–3	1–2.5	6–8	4–6
Picea orientalis (L.) Link	45–100	20–33	2.3–3.0:1	12–17	10–15	1.1–1.2:1	5–6	2–4	1.5–2.3:1	4.0–14.0	0.7–1.5	3–4	2–2.5	6–8	3–5
Picea pungens Engelmann	50–120	25–45	2.0–2.7:1	15–24	10–15	1.5–1.6:1	4–7	1–1.5	3.1–4.7:1	15.0–31.0	1–1.5	2–3	1–2	6–9	5–6
Picea purpurea Masters	25–70	17–30	1.5–2.3:1	10–15	8–12	1.3:1	3–5	1.5–2	1.7–2.5:1	7.0–14.0	0.9–2	2–3	1–2.5	5–8	3–4
Picea retroflexa Masters	80–130	25–50	2.6–3.2:1	15–20	12–17	1.2–1.3:1	1–2	1.5–2	0.6–1.0:1	10.0–25.0	1–2	3–4	0.5–1	8–15	4–7
Picea rubens Sargent	25–60	18–35	1.4–1.7:1	8–15	9–13	0.9–1.2:1	3–6	1.5–2	1.8–3.0:1	10.0–17.0	1	2–3	1–1.5	5–9	3–5
Picea schrenkiana Fisher & Meyer	60–110	25–40	2.4–2.8:1	13–21	12–15	1.1–1.4:1	2–3.5	1.5–2	1.2–1.8:1	15.0–40.0	0.8–1.5	4–5	2.5–3	8–11	5–6
Picea sitchensis (Bongard) Carrière	45–100	15–40	2.5–3.0:1	10–16	5–10	1.6–2.0:1	2–7	1.5–3	1.3–2.7:1	15.0–26.0	1–1.5	2–4	1.5–3	6–10	4–5
Picea smithiana (Wallich) Boissier	85–200	40–60	2.1–3.3:1	18–30	15–24	1.2–1.3:1	4.5–10	1.5–2	2.8–5.0:1	25.0–50.0	0.6–1	4–7	3–4	13–20	7–9
Picea spinulosa (Griffith) Henry	40–120	25–45	1.6–2.7:1	12–20	8–14	1.4–1.5:1	3–5	1.5–2	2.1–2.5:1	15.0–35.0	0.7–2	3–5	1–2	8–14	4–6
Picea torano (Siebold ex K. Koch) Koehne	50–120	30–70	1.7:1	20–28	15–25	1.1–1.3:1	3–5	1.5–2	2.0–2.8:1	10.0–26.0	1.5–2.5	5–7	3–4	15–21	7–10
Picea wilsonii Masters	40–80	25–40	1.6–2.0:1	14–17	9–14	1.2.1.5:1	2–6	1.5–2	1.3–2.9:1	8.0–23.0	0.8–2	3–4.5	2.5–3	8–15	3–7
Picea sverdrupii sp. nov.	27–115	12–28	2.3–4.1:1	4–17	5–12	0.8–1.4:1	5–8	1–2	3.9–5.0:1	–	–	2–3.5	1–2	6.5–9	2.5–3
Picea nansenii sp. nov.	27–57	12–20	2.3–2.8:1	6–13	4–9.5	1.4–1.5:1	1.5–2.5	1–2	1.2–1.5:1	3.5–6.5	0.5–1	1–2	1–1.5	3.5–7	1.5–3.5
Picea palustris sp. nov.	27–112	12–32	2.3–3.5:1	3.5–21	3–19	1.1–1.2:1	2–7	1–2.5	2.3–3.1:1	–	–	1.5–3.5	0.5–3	7–19	2.5–8

Data have been obtained in part from Kent (1900), Lacassagne (1934), Dallimore & Jackson (1948), Gaussen (1966), Hills & Ogilvie (1970); Schmidt-Vogt (1977), Scoggan (1978), Page & Rushforth (1980), Silba (1986), Rushforth (1987), Farjon (1990) and personal observations.
[1] All measurements in mm.

Collecting localities

US 116, 184, 220, 234, 235, 236, 237, 520, 563, 567, 568, 587.

Etymology

In honour of Fridtjof Nansen, a 19th century Arctic explorer.

Detailed description

The cones vary in size with each cone comprising 40–100 imbricate, narrow to wide obovate, woody cone scales that are helically arranged around a central cone axis and attached by a short stalk (Fig. 5). The cone-scale margins are entire, the apex is rounded and the abaxial surface smooth and glabrous (Fig. 86). Each cone scale is subtended by a glabrous, non-exserted bract (Fig. 87). The bract margin is erose to crenate and the apex is emarginate to cuspidate. Each bract possesses a small apical tooth which is an extension of the vascular trace. Resin canals may be visible on each side of the vascular trace. The bract is basally adnate to the cone scale, but is free medially and apically.

The leaves are up to 6.5 mm long and 1 mm wide, falcate, and equifacial. Leaves were recovered either as isolated specimens or attached to shoots. Leaves attached to shoots are helically arranged and loosely appressed along the length of the twig. When terminal buds are present on the twig, the subterminal leaves commonly cover the bud (Fig. 6). The leaf is widest near the middle and narrows acropetally to a mucronate apex. Basipetally, the leaves are attached to pulvini (Fig. 7). Prominent abscission zones on the pulvini indicate that the leaves of this species were periodically shed as seen in the living spruces.

The stomata are amphistomatic and arranged in four inconspicuous parallel bands along the length of the leaf, which correspond to the four sides of the leaf. Each band is composed of approximately four rows of stomata. The outer cuticle surface appears slightly granular and is probably a preservational artifact (Fig. 8). The stomata are inconspicuous, sunken, without stomatal plugs and orientated parallel to the long-axis of the leaf.

The cuticle is poorly preserved and details of the inner cuticular micromorphology are limited. The inner cuticle surface appears to be without ornamentation (Fig. 9). The stomatal complexes are about 40 μm long and 30 μm wide and the inner surfaces of the guard cells are plain (Fig. 10).

Winged seeds of *P. nansenii* were found in the cone scales of some cones (Fig. 11). The seed wings are narrow obovate to narrow oblanceolate in shape, symmetrical and membranous. The margins are entire and

the apex is rounded. The shape of the seed body varies from wide ovate to triangular. The size and shape of *P. nansenii* seeds are typical for the genus, with those of *P. smithiana* (Wallich) Boissier showing the closest similarity to the fossils (Table 2; Figs 11, 19aa).

Remarks

Based on the small number of specimens recovered, *P. nansenii* was a rare constituent of the Taxodiaceae-dominated swamp forest communities. The morphology of the *Picea nansenii* cones is consistent among all specimens recovered and cannot be confused with those of *P. sverdrupii*, even when both species occur in the same deposits and they are of the same size. The cones of *P. nansenii* are consistently much smaller than those of *P. sverdrupii* and are prominently tapered basally and apically resembling the cones of *P. torano* (Siebold *ex* K. Koch) Koehne. The unique combination of features and limited occurrence in the basinal forest communities indicates that *P. nansenii* is a distinct species.

Picea palustris LePage **sp. nov.**
(Figs 12, 13, 88, 89)

Specific diagnosis

CONE ovoid to oblong-cylindrical in shape, up to 112 mm long and 32 mm wide; composed of 50–150 + imbricate, resinous, woody cone scales. CONE SCALE deltoid in shape, up to 21 mm long and 19 mm wide; margin entire; apex rounded with some scales possessing a small apical projection; abaxial surface glabrous. BRACT subtending cone scale lanceolate in shape, hidden, up to 7 mm long and 2.5 mm wide; basally adnate to the cone scale, but free above; apex acute to acuminate; margin entire; glabrous. SEEDS two per scale, winged, up to 19 mm long and 8 mm wide; wing membranous, slightly asymmetrical, narrow obovate to oblanceolate, apex slightly falcate; seed-body oval to round, up to 3.5 mm long and 3 mm wide.

Holotype

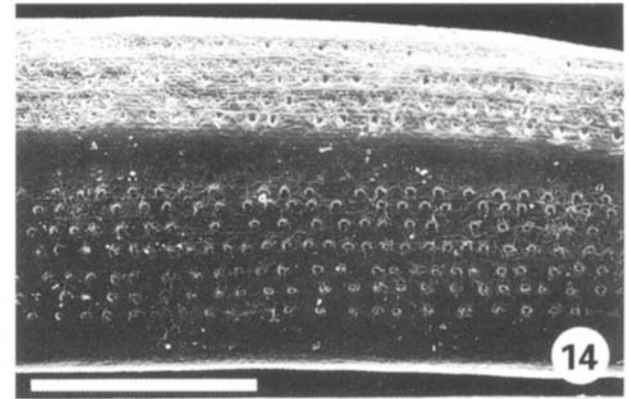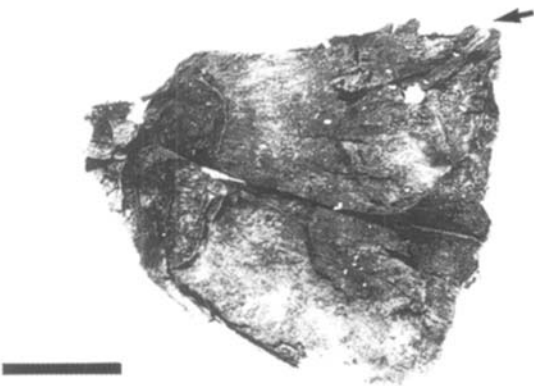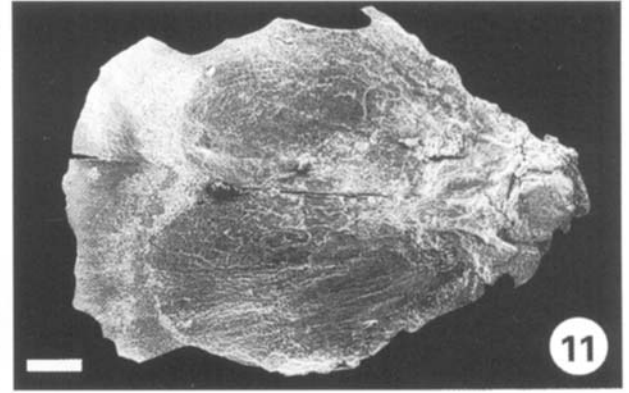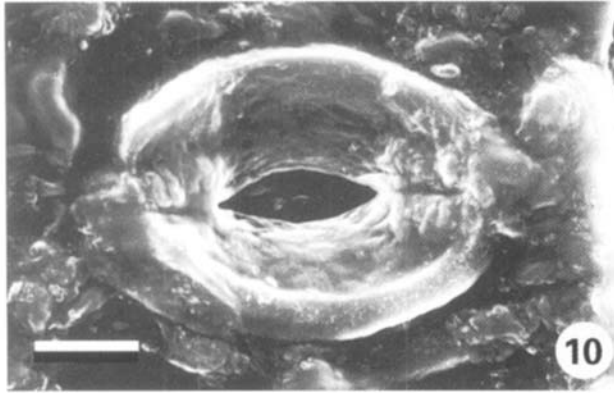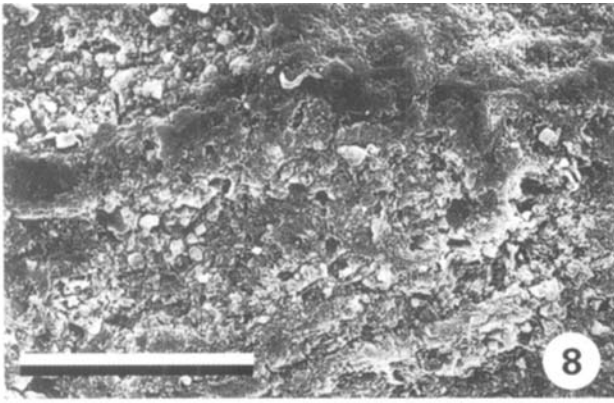USPC specimen US 588-5590.

Collecting locality

US 588.

Etymology

Latin: *palustris* = swamp.

Detailed description

The seed cones of *P. palustris* are as long as those of *P. sverdrupii*, but considerably wider, even after taking

compression into account. The cones are oval to oblong-cylindrical in shape and have broadly-rounded apices and pedunculate bases (Fig. 12). Cones are composed of 50–150 + imbricate, deltoid, woody cone scales that are helically arranged around a central cone axis and attached by a short pedicel. The cone scales are up to 21 mm long and 19 mm wide, resinous and much less woody than those of *P. sverdrupii* and *P. nansenii*. The scales appear to be reflexed, but this attribute may be due to the cleaning process. The margins are entire, the apex broadly rounded and the abaxial surface glabrous (Fig. 88). Some of the cone scales possess a small apical projection and resemble the cone scales of some Chinese spruces such as *P. brachytyla*. Each cone scale is subtended by a non-exserted bract (Fig. 89). The bract is lanceolate in shape, with entire margins and an acute to acuminate apex. The bracts are free from the cone scales medially and apically, but are adnate basally.

Winged seeds of *P. palustris* were found in the cone scales of some cones (Fig. 13). The seed wings are narrow obovate to narrow oblanceolate in shape, slightly asymmetrical and membranous. The margins are entire and the apex is slightly falcate. The shape of the seed body varies from wide oval to round. The size and shape of *P. palustris* seeds are typical for the genus and most closely resemble those of *P. koraiensis* Nakai (Table 2; Figs 13, 19k).

Remarks

The cones of *Picea palustris* are rare and known only from one autochthonous litter horizon. Recognition of a third species of *Picea* is based exclusively on the distinct morphology of the cones and its highly-restricted distribution. However, the preservation of these cones is such that they are nearly flattened and almost unrecognizable in the field. Consequently, the rarity of *P. palustris* cones relative to those of *P. sverdrupii* and *P. nansenii* may be due to the difficulty in recognizing as a cone what initially appears to be a flattened piece of wood.

## DISCUSSION

TAXONOMIC CONSIDERATIONS

Current classification systems of living *Picea* are based on a whole-tree concept, in which one or more of the following features are recognized: cross-sectional shape of the leaves; degree of pubescence of the twigs; arrangement of the stomata on the leaves; colour of the leaves and new growth shoots; length and shape of the cones; shape and degree of pubescence of the buds; and cone-scale morphology (Willkomm, 1887; Mayr, 1890; Lacassagne, 1934; Dallimore & Jackson, 1948; Schmidt-Vogt, 1977; Gaussen, 1966; Liu, 1982; Silba, 1986; Schmidt, 1989).

The genus was originally divided into two sections, *Eupicea* Willkomm and *Omorika* Willkomm, on the basis of leaf shape (Willkomm, 1887). Species assigned to *Eupicea* possessed equifacial and amphistomatic leaves, while those assigned to *Omorika* possessed dorsiventrally flattened and epistomatic leaves. However, it is important to remember that Willkomm's system of classification was based on only eight species.

Mayr (1890) later established a new classification system for the genus that expanded on Willkomm's (1887) scheme. Using the features of the seed cone, the cross-sectional shape of the leaf and the location of the stomata on the leaf, Mayr recognized 17 species of *Picea* and subdivided the genus into three sections, *Morinda* Mayr, *Casicta* Mayr and *Omorika*. Species assigned to *Morinda* possessed equifacial amphistomatic leaves and hard and woody cone scales, those of *Casicta* possessed dorsiventrally-flattened epistomatic leaves and flexible cone scales, while species assigned to *Omorika* possessed broad, rhomboid-shaped epistomatic leaves and hard and woody cone scales.

Since the introduction of Willkomm's (1887) system,

Figures 8–14. Species of *Picea*. Fig. 8. *Picea nansenii* **sp. nov.** SEM of outer surface of the leaf and rows of sunken stomata. US-SEM 139 (US184-5594). Scale bar = 0.1 mm. Fig. 9. *Picea nansenii* **sp. nov.** SEM of non-ornamented inner surface of the leaf cuticle. The stomata are arranged parallel to the long axis of the leaf in four rows. Compare with the inner cuticle surface of the *P. jezoensis* leaf shown in Figure 16 and note the differences. US-SEM 146 (US220-5593). Scale bar = 0.1 mm. Fig. 10. *Picea nansenii*. SEM close-up of a stomatal complex. Compare with the stomatal complex of *P. jezoensis* shown in Figure 17 and note the differences. US-SEM 154 (US184-5594). Scale bar = 10 mm. Fig. 11. *Picea nansenii* **sp. nov.** Winged seeds still adherent to the adaxial surface of the cone scale. Note their similarity to the *P. smithiana* seed shown in Figure 19aa. US-SEM 155 (US220-5572). Scale bar = 1.0 mm. Fig. 12. *Picea palustris* **sp. nov.** Cone after cleaning showing the slightly reflexed cone scales. Note the basal peduncle. US588-5590. Scale bar = 10 mm. Fig. 13. *Picea palustris* **sp. nov.** Winged seeds still adherent to the adaxial surface of the cone scale showing the slightly falcate apex of the seed wing (arrow). Note its similarity to the *P. koraiensis* seed shown in Figure 19k. US588-5590. Scale bar = 5 mm. Fig. 14. *Picea likiangensis*. SEM of parallel arrangement of the stomatal bands on the outer surface of the leaf and the rows of sunken stomata within each band. US-SEM 144 (A 1779). Scale bar = 1.0 mm.
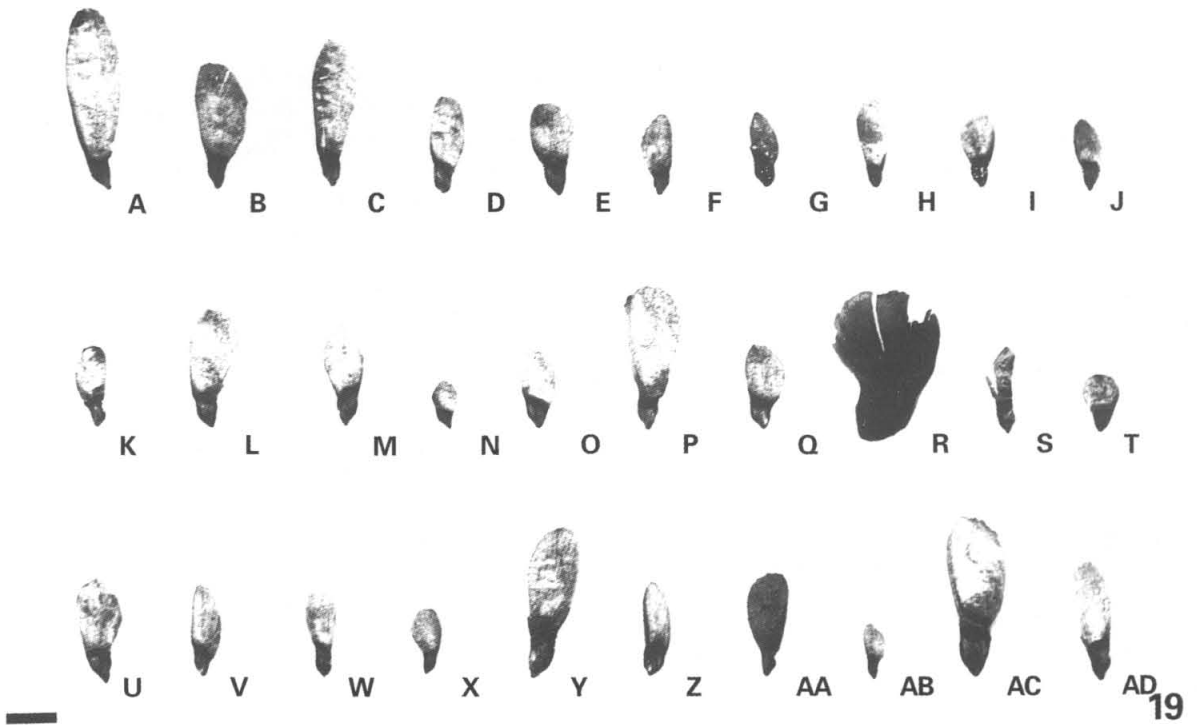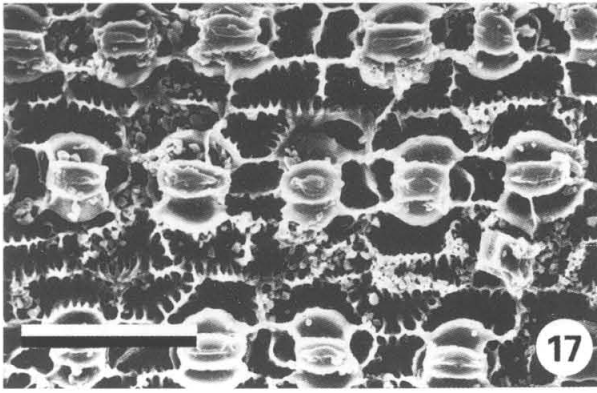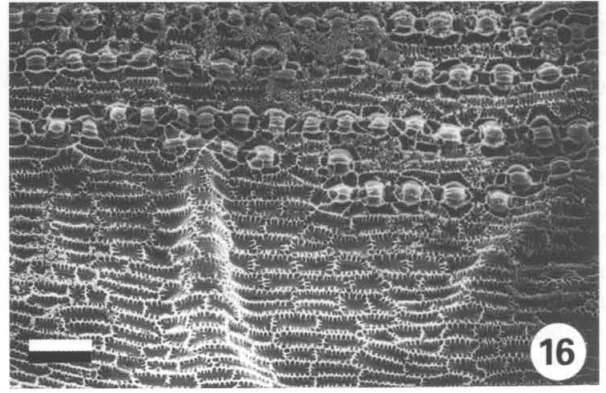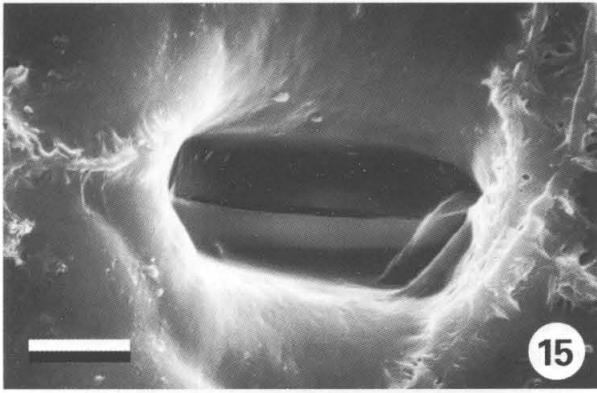
Figures 15–19. Fig. 15. *Picea likiangensis*. SEM close-up of a sunken stomatal complex on the outer surface of the leaf. US-SEM 144 (A 1779). Scale bar = 10 mm. Fig. 16. *Picea jezoensis*. SEM of the inner surface of the leaf cuticle. Note the buttresses arranged perpendicular to the anticlinal walls. Compare with the inner cuticle surface of
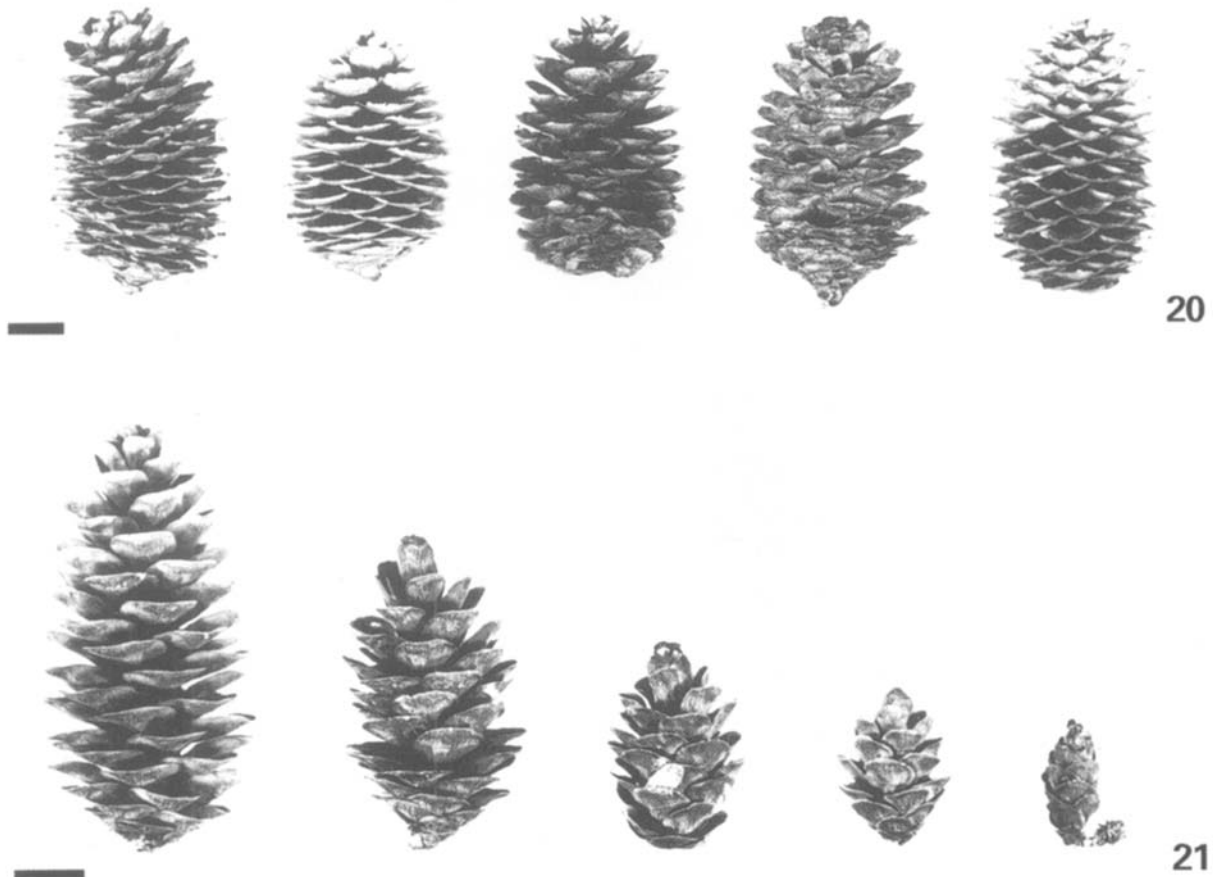
Figures 20 & 21. Fig. 20. Cones representing five species of *Picea* showing the similarity in size and shape. (A) *P. wilsonii* (A 2053), (B) *P. schrenkiana* (A 806), (C) *P. koyamae* (MO 1639472), (D) *P. morrisonicola* (US10901) and (E) *P. glehnii* (SASK 118258). Scale bar = 10 mm. Fig. 21. *Picea glauca*. Cones collected from one tree showing the range in size and shape. SASK 118259. Scale bar = 10 mm.

P. nansenii **sp. nov.** shown in Figure 9. US-SEM 145 (SASK 118257). Scale bar = 0.1 mm. Fig. 17. *Picea jezoensis*. SEM close-up of the stomatal complexes. The inner flanges of the subsidiary cells are plain and conspicuous. Compare with the stomata of *P. nansenii* **sp. nov.** shown in Figures 9 and 10. US-SEM 145 (SASK 118257). Scale bar = 0.1 mm. Fig. 18. *Picea glauca*. Seeds taken from one *P. glauca* cone showing the range in size and shape of the seed wing. SASK 118259. Scale bar = 5 mm. Fig. 19. Seeds from most species of the genus *Picea*. (A) *P. abies* (A Johnsson, unnumbered), (B) *P. alcoquiana* (A Lindquist, unnumbered), (C) *P. asperata* (A 14815), (D) *P. brachytyla* (A 3411), (E) *P. breweriana* (MO 984840), (F) *P. engelmannii* (SASK 94398), (G) *P. farreri* (MO 2060), (H) *P. glauca* (SASK 905), (I) *P. glehnii* (SASK 118258), (J) *P. jezoensis* (SASK 118257), (K) *P. koraiensis* (A 334), (L) *P. koyamae* (MO 807113), (M) *P. likiangensis* (A 1779), (N) *P. mariana* (SASK 909), (O) *P. maximowiczii* (A Tschonoski, unnumbered), (P) *P. meyeri* (A 813), (Q) *P. morrisonicola* (MO 1627050), (R) *P. neoveitchii* (A 2054), (S) *P. obovata* (A 281), (T) *P. omorika* (A Pančić, unnumbered), (U) *P. orientalis* (A 5442), (V) *P. pungens* (SASK 19591), (W) *P. purpurea* (US4059), (X) *P. rubens* (ALTA 25789), (Y) *P. schrenkiana* (A Smirnov, unnumbered), (Z) *P. sitchensis* (SASK 94474), (AA) *P. smithiana* (US2242336), (AB) *P. spinulosa* (A unnumbered), (AC) *P. torano* (A Maximowicz, unnumbered) and (AD) *P. wilsonii* (MO 2929264). Scale bar = 10 mm.
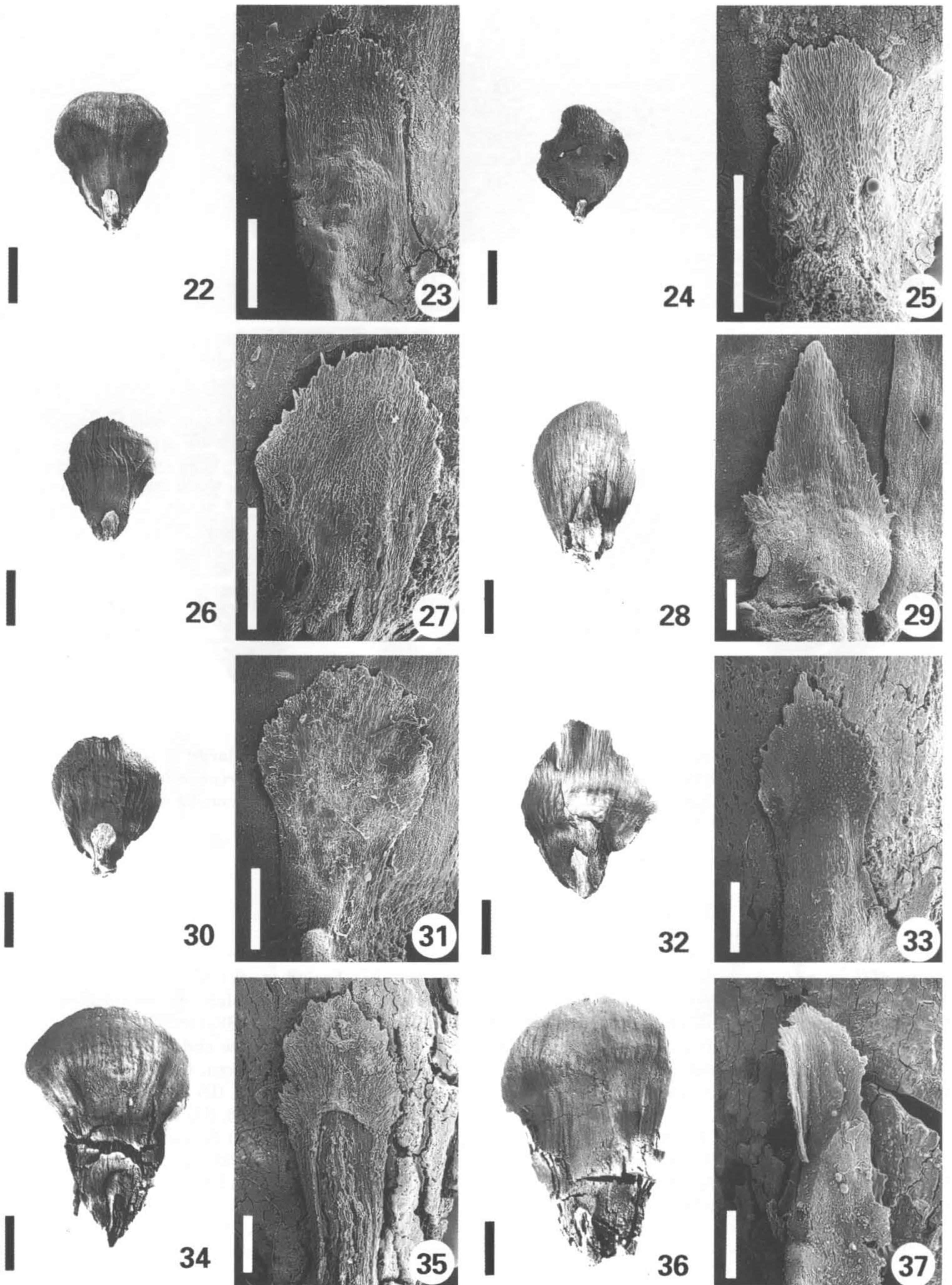
Figures 22–36 (even numbers). Typical cone scales representing species of *Picea* showing the subtending bract. Fig. 22. *P. glauca* (II). SASK 118259. Fig. 24. *P. mariana* (II). SASK 118260. Fig. 26. *P. rubens* (II). ALTA 25789. Fig. 28.

a number of classification schemes proposed follow, in part, either Willkomm's two-section or Mayr's three-section system. Depending on the system of classification used, 20–50 species have been recognized (Pardé, 1911; Dallimore & Jackson, 1948; Bobrov, 1970; Schmidt-Vogt, 1977; Liu, 1982; Silba, 1984, 1986; Krüssmann, 1985; Rushforth, 1987; Schmidt, 1988; Farjon, 1990). Tenets common to these classification schemes include an emphasis of vegetative features rather than the more reliable features of the seed cones and a disregard for recognition of the natural variability of morphological features.

When internal anatomical features were considered, Miller (1989) concluded that living species of *Picea* assigned to *Eupicea* (*Picea*), *Omorika* or *Casicta* were no more similar to one another than to members of the other two sections. Miller further noted that assignment of anatomically described fossil *Picea* cones to any one of these three sections did little to resolve or improve our understanding of the phylogeny of the genus. Clearly, the inability of current classification schemes to shed light on phylogenetic aspects within the genus and the lack of consensus regarding the number of species, illustrate the need to reconsider the currently used features and identify more taxonomically-useful features essential for circumscription of the genus.

The use of reproductive characters for phylogenetic interpretation must be chosen carefully. While it is true that detailed study of the anatomical features of seed cones often provide useful data to understand phylogeny, Ohsawa (1994) urges caution when using anatomical features of seed cones such as vasculature for taxonomic circumscription and phylogenetic interpretation. Such features are variable and the extent of variability among taxa has not yet been fully determined.

Examination of fossil and living species of *Picea* revealed that the extent of intra- and inter-specific variability of such characters as size and shape of the leaves, seeds and cones is considerable, and has made identification and classification of fossil and living species difficult (Table 2). Although it is evident that more than one species of *Picea* is represented in the collection of Axel Heiberg spruces, the classification schemes currently in use for living *Picea* provide little useful information for the identification and separation of fossil representatives. Therefore, it was deemed necessary to examine living and fossil *Picea* for characters possessing the morphological stability needed for discrimination among specimens of fossil *Picea*.

LEAVES

Phenotypic differentiation of leaves among living species of *Picea* is slight. Leaves of *Picea* are short, linear, up to 50 mm long and 3 mm wide, equifacial or dorsiventrally flattened, epistomatic or amphistomatic, with inconspicuous sunken stomata (Table 2; Figs 14, 15). Internally, one centrally positioned vascular trace and two marginal resin canals are present. Species within the genus have been traditionally separated into two or three groups based on their cross-sectional shape and arrangement of the stomata (Silba, 1986; Farjon, 1990). Although comparative and detailed micromorphological study of the inner cuticle surfaces of living *Picea* leaves may yield taxonomically useful information, a comprehensive survey of this nature has yet to be done.

The external surface of *P. nansenii* leaves is consistent with that seen on the leaves of living *Picea*. However, the internal cuticle surface of *P. nansenii* differs markedly from that described and illustrated in leaves of *P. jezoensis* (Siebold & Zuccarini) Carrière, *P. aurantiaca* Masters, *P. engelmannii*, *P. sitchensis* (Bongard) Carrière and *P. alcoquiana* (Veitch ex Lindley) Carrière (Florin, 1931). The inner cuticle surface of these species, as exemplified by *P. jezoensis*, reveals a series of anticlinal walls that are basally buttressed and arranged perpendicular to the periclinal walls (Fig. 16) and tetracytic subsidiary cells with conspicuous flanges (Fig. 17). The inner cuticle surface of *P. nansenii* shows smooth, straight, non-ornamented walls (Figs 9, 10). The cuticle is poorly preserved and little else can be reliably said about the internal micromorphology of the leaves. The inner cuticular features of *P. nansenii* are not known to occur in any of the species examined by us or in those reported by Florin (1931). Further analyses of the inner cuticle surface of other living

P. sitchensis (I). MO 1231478. Fig. 30. *P. engelmannii* (I). SASK 94398. Fig. 32. *P. pungens* (I). SASK 19591. Fig. 34. *P. breweriana* (II). MO 1635409. Fig. 36. *P. chihuahuana* (II). MO 1225972. Scale bar = 5 mm. The numerals (I) and (II) in Figures 22–88 (even numbers only) indicate whether the species belongs to the group possessing thin flexible scales (I) or the group possessing thick woody scales (II). Figures 23–37 (odd numbers). SEMs of *Picea* species showing a close-up of the bract. Fig. 23. *P. glauca*. US-SEM 79 (SASK 118259). Fig. 25. *P. mariana*. US-SEM 100 (SASK 118260). Fig. 27. *P. rubens*. US-SEM 98 (ALTA 25789). Fig. 29. *P. sitchensis*. US-SEM 113 (MO 1231478). Fig. 31. *P. engelmannii*. US-SEM 99 (SASK 94398). Fig. 33. *P. pungens*. US-SEM 75 (SASK 19591). Fig. 35. *P. breweriana*. US-SEM 112 (MO 1635409). Fig. 37. *P. chihuahuana*. US-SEM 110 (MO 1225972). Scale bar = 1.0 mm.
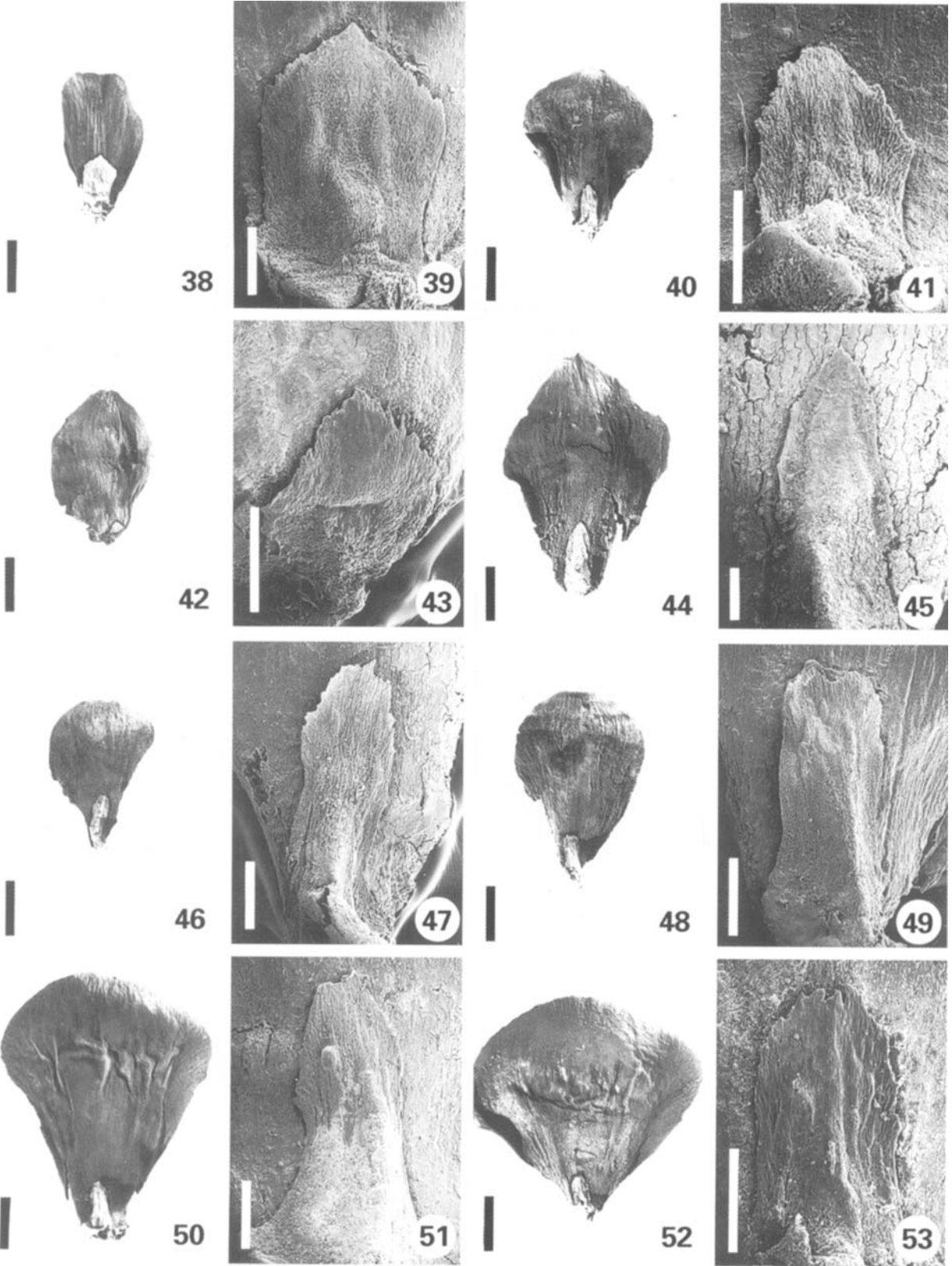
species of *Picea* may, however, reveal features similar to those found in *P. nansenii*.

Picea leaves described and figured from late Eocene deposits in British Columbia (Penhallow, 1908) and Nevada (Axelrod, 1966) and Oligocene/Miocene deposits in Russia (Dorofeev, 1963, 1970, 1972; Akhmetiev, 1973; Rayushkina, 1979) resemble those of *P. nansenii* and living *Picea* in external morphology. However, none of these reports include descriptions of the inner cuticle surfaces, and further comparison between the fossils and living representatives of the genus is not possible. Moreover, until the diagnostic value of cuticle micromorphology within and between species under different environmental conditions can be assessed, the use of cuticular features for species circumscription is deemed inappropriate.

SEEDS

Most species of living *Picea* possess seeds that are remarkably similar to one another in size and in shape and may not be distinguishable at the species level (Fig. 19). Although the natural intraspecific range of size and shape of *Picea* seeds is not well documented, it is considerable in some species and demonstrates the need for detailed morphological and statistical analyses to determine the range of variation and usefulness of such features for phylogeny (Fig. 18). Until such studies are undertaken and given our present understanding of seed morphology it is unlikely that differences or similarities in seed morphology have any meaningful phylogenetic significance. Consequently, assignment of isolated fossil seeds to biologically meaningful taxa is problematic because the seeds of different species may be indistinguishable. Reliable assignment should be limited either to seeds still retained in cone scales possessing bracts or isolated seeds associated with only one type of seed cone. Yet at least ten species of fossil *Picea* have been established using slight differences in the size and shape of the seed (MacGinitie, 1953; Tanai, 1955, 1961; Tanai & Onoé, 1961; Axelrod, 1966; Tanai & Suzuki, 1972; Rayushkina, 1979). It is doubtful whether these species are truly representative

of the actual species diversity, which further complicates interpretation of taxonomic relationships and phylogeny.

SEED CONES

Taxonomists have commonly used such characters as cone scale width to length ratio, length of the seed wing to scale length, taper ratio, cone size and form, cone-scale size and form and bract size and form as a basis for identifying and classifying species of living *Picea* (Horton, 1959; Ogilvie & Rudloff, 1968; Roche, 1969; Hills & Ogilvie, 1970). However, differentiation of cones into discrete, species-specific organs among some of the living species of *Picea* can be a futile exercise (Fig. 20), while in others the intraspecific variability of such features as cone and cone-scale size and shape is considerable (Fig. 21). Clearly, the degree of inter- and intraspecific variability among fossil and living *Picea* limits the taxonomic and systematic usefulness of most features of the cone and demonstrates the need to exercise caution when erecting new species using cone shape and size alone (Table 2).

Nevertheless, within the genus, sub-division of species into two fundamentally different and broad groups using cone-scale morphology is possible. Group I, which includes *P. abies*, *P. obovata*, *P. glehnii* (Fr. Schmidt) Masters, *P. jezoensis*, *P. purpurea* Masters, *P. likiangensis* (Franchet) Pritzel, *P. farreri* Page & Rushforth, *P. brachytyla*, *P. sitchensis*, *P. engelmannii* and *P. pungens* Engelmann, possesses cone scales that are thin, flexible and ovate to very-wide obovate in shape (Figs 28, 30, 32, 38, 40, 42, 44, 64, 68, 70 and 72). Group II includes the remaining twenty-four species, and possesses cone scales that are thicker, woodier, narrow to very-wide obovate in shape and have rounded apices (Figs 22, 24, 26, 34, 36, 46, 48, 50, 52, 54, 56, 58, 60, 62, 66, 74, 76, 78, 80 and 82). It should be noted, however, that segregation of species may not always be precise, for *P. engelmannii*, *P. glauca* and *P. rubens* Sargent possess cone scales exhibiting features common to both groups. The separation here of *Picea* into two groups is by no means meant to imply that

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Figures 38–52 (even numbers). Typical cone scales of species of *Picea* showing the subtending bract. Fig. 38. *P. jezoensis* (I). SASK 118257. Fig. 40. *P. glehnii* (I). SASK 118258. Fig. 42. *P. obovata* (I). A 281. Fig. 44. *P. abies* (I). A Johnsson, unnumbered. Fig. 46. *P. koraiensis* (II). A 334. Fig. 48. *P. morrisonicola* (II). A 10901. Fig. 50. *P. torano* (II). A Maximowicz, unnumbered. Fig. 52. *P. alcoquiana* (II). A Wilson, unnumbered. Scale bar = 5 mm. Figures 39–53 (odd numbers). SEMs of *Picea* species showing a close-up of the bract. Fig. 39. *P. jezoensis*. US-SEM 78 (SASK 118257). Fig. 41. *P. glehnii*. US-SEM 114 (SASK 118258). Fig. 43. *P. obovata*. US-SEM 104 (A 281). Fig. 45. *P. abies*. US-SEM 80 (A Johnsson, unnumbered). Fig. 47. *P. koraiensis*. US-SEM 101 (A 334). Fig. 49. *P. morrisonicola*. US-SEM 102 (A 10901). Fig. 51. *P. torano*. US-SEM 97 (A Maximowicz, unnumbered). Fig. 53. *P. alcoquiana*. US-SEM 96 (A Wilson, unnumbered). Scale bar = 1.0 mm.
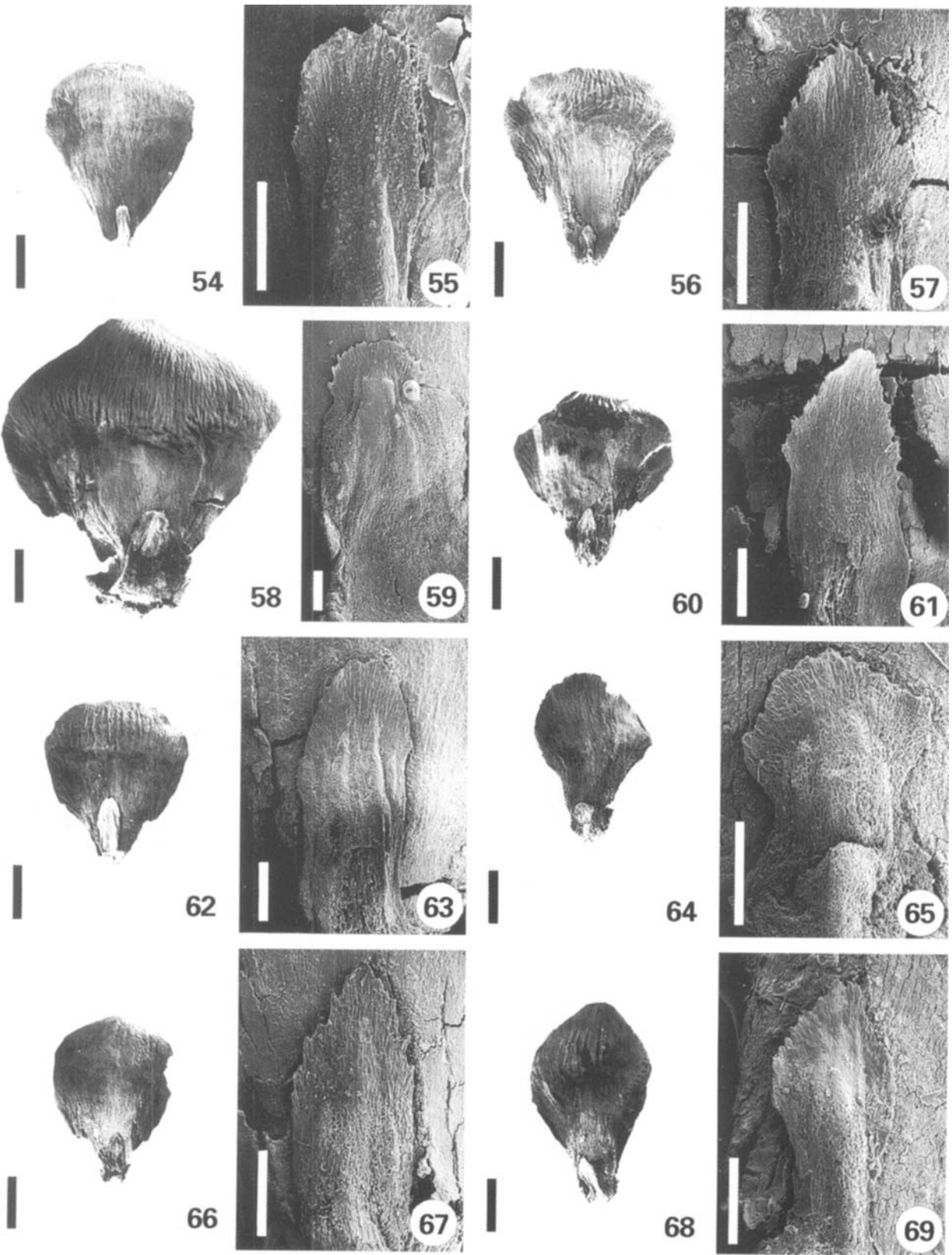
phylogenetic relationships between the taxa of each group exist, but like all other systems of classification currently in use for the genus, it provides an efficient method to quickly discriminate among taxa.

The large number of well-preserved seed cones from Axel Heiberg provided an opportunity to assess the intraspecific variability of cone features corresponding to that available for living species. The results indicate that the range of morphological variation of the features examined in *P. sverdrupii* were comparable to that seen in living species of *Picea* (Table 2; Figs 3, 19), and that such features as cone and cone-scale size and shape alone are inadequate for interpreting the taxonomy and systematics of fossil spruces. Although the number of cones of *P. nansenii* and *P. palustris* is limited, these species may still be meaningfully compared to living *Picea*.

The cones of *P. sverdrupii, P. nansenii* and *P. palustris* show affinity with the Group II spruces that possess thick, woody cone scales with rounded apices (Figs 84, 86 and 88). Although the dimensions of the cones and cone scales of fossil and living spruces are similar for many species, and alone, may not be reliably used for taxonomic and systematic purposes, the overall morphology of the cone scales combined with features of the bract are useful for identification and assessment of phylogenetic relationships.

BRACTS

Lacassagne (1934) first recognized the significance of the bract for *Picea* taxonomy and indicated that the form of the bract was an important characteristic for species identification. Despite Lacassagne's insight into the problems associated with species identification and classification of living *Picea* and the ability to use the bract to assist in the identification of species, the only bract character he used was whether the bracts were greater than or less than one-half of the length of the cone scale.

Bract morphology has been shown to be consistent within species and useful in segregating species in other genera of conifers, such as *Abies* Miller, *Larix* Miller, *Pseudolarix* Gordon and *Tsuga* (Patschke, 1913; Lacassagne, 1934; Gaussen, 1966; Lui, 1971; LePage, 1991; LePage & Basinger, 1991, 1995). Consequently,

understanding of the range of bract size and form among living and fossil representatives of *Picea* was deemed critical to better understanding the taxonomy and systematics of living and fossil *Picea*.

Bract morphology of each living and fossil species examined was found to be generally consistent among the specimens examined, with each species exhibiting a unique form and providing a basis for identification and separation of species (Figs 23–89, odd numbers only). Among the living species, the bracts of *P. maximowiczii* Regel *ex* Masters, *P. koraiensis* and *P. wilsonii* Masters show the closest morphological similarity to those of *P. sverdrupii* (Figs 47, 55, 63, 85); those of *P. farreri, P. alcoquiana* and *P. smithiana* show the closest similarity to the bracts of *P. nansenii* (Figs 53, 73, 77, 87); and the bracts of *P. omorika* (Pančić) Purkyne, *P. jezoensis* and *P. obovata* are most similar to those of *P. palustris* (Figs 39, 43, 83, 89).

PHYLOGENETIC RELATIONSHIPS AND HYBRIDIZATION

There is evidence that indicates the morphology of the cone scale and bract may be phylogenetically significant (LePage & Basinger, 1991, 1995). Based on comparative morphology of the living and fossil representatives of the genus, the species of *Picea* fall into two groups. The first group possesses cone scales that are thin and flexible, with fimbriate margins, while the second group possesses cone scales that are thick and woody, with entire margins. Although separation of the genus into two groups using features of the cone scales is admittedly artificial, molecular data, in part, support these groupings. In a study where the restriction fragment length polymorphisms (RFLPs) of the cpDNA from 31 species of *Picea* were analysed phenetically and cladistically, Sigurgeisson & Szmidt (1993) generated a number of topologies illustrating the inter-specific relationships within the genus. Their unweighted pair-group method with arithmetic mean (UPGMA) tree showed four groupings. The first group consisted of *Picea breweriana* S. Watson; the second included *P. engelmannii, P. glauca* and *P. mexicana*; the third *P. sitchensis*; and the fourth included the other 26 species that were divided into three nested

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Figures 54–68 (even numbers). Typical cone scales of species of *Picea* showing the subtending bract. Fig. 54. *P. maximowiczii* (II). A 7526. Fig. 56. *P. koyamae* (II). A 7523. Fig. 58. *P. neoveitchii* (II). A 2054. Fig. 60. *P. meyeri* (II). A 813. Fig. 62. *P. wilsonii* (II). A 2114. Fig. 64. *P. purpurea* (I). A 4059. Fig. 66. *P. asperata* (II). A 14444. Fig. 68. *P. brachytyla* (I). A 3411. Scale bar = 5 mm. Figures 55–69 (odd numbers). SEMs of *Picea* species showing a close-up of the bract. Fig. 55. *P. maximowiczii*. US-SEM 84 (A 7526). Fig. 57. *P. koyamae*. US-SEM 85 (A 7523). Fig. 59. *P. neoveitchii*. US-SEM 103 (A 2054). Fig. 61. *P. meyeri*. US-SEM 88 (A 813). Fig. 63. *P. wilsonii*. US-SEM 89 (A 2114). Fig. 65. *P. purpurea*. US-SEM 87 (A 4059). Fig. 67. *P. asperata*. US-SEM 90 (A 14444). Fig. 69. *P. brachytyla*. US-SEM 91 (A 3411). Scale bar = 1.0 mm.
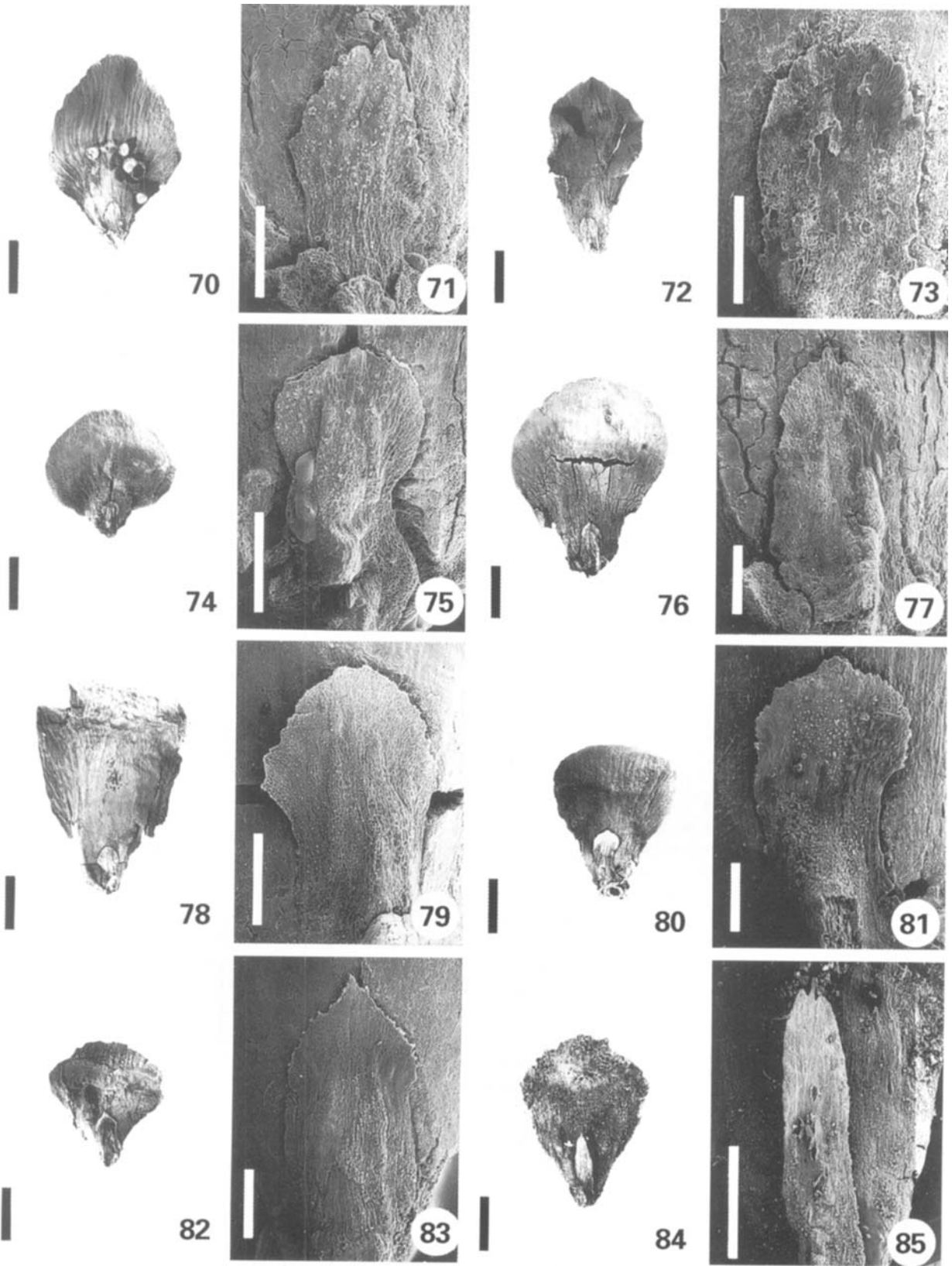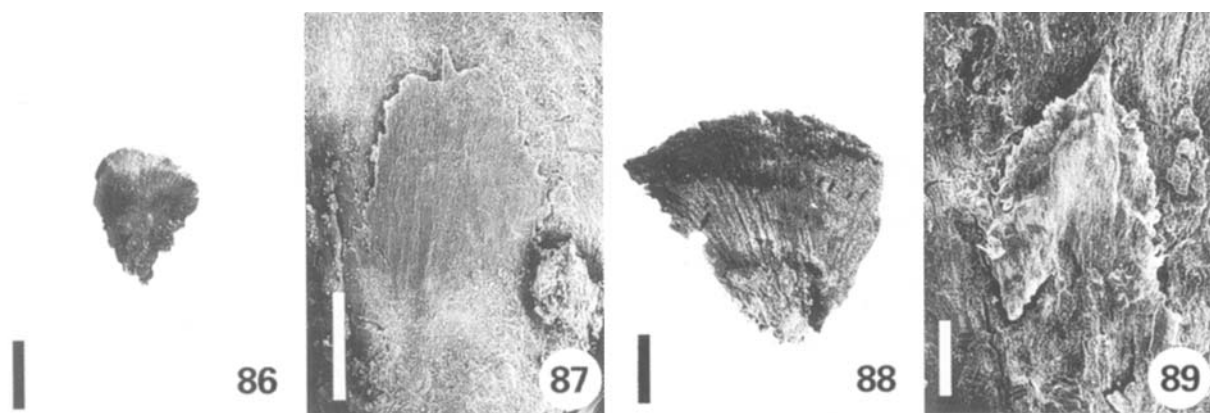
Figures 86–88 (even numbers). Typical cone scales of species of *Picea* showing the subtending bract. Fig. 86. *Picea nansenii* (II). US220-5572. Fig. 88. *Picea palustris* (II). US588-5590. Scale bar = 5 mm. Figures 87–89 (odd numbers). SEMs of *Picea* species showing a close-up of the bract. Fig. 87. *Picea nansenii*. US-SEM 142 (US184-5573). Fig. 89. *Picea palustris*. US-SEM (US588-5590). Scale bar = 1.0 mm.

groupings. The strict and majority-rule consensus trees were more or less similar to one another and differed slightly from the UPGMA tree. The most notable difference between the cladistic and phenetic trees was the grouping of *P. breweriana* and *P. sitchensis* in the bootstrapped majority-rule consensus tree, whereas in the UPGMA tree these taxa represented separate groupings. What is particularly interesting is the manner in which the taxa were related to one another. With few exceptions, the Group I spruces were allied with other Group I spruces and the Groups II spruces clustered with other Group II spruces.

Sigurgeirsson & Szmidt (1993) also indicate low levels of *cp*DNA differentiation when compared to that seen in *Pinus* and suggested that the results either indicate (1) slower evolutionary rates than that seen in *Pinus* or (2) evolutionary radiation events that occurred later than those seen in *Pinus*. When the fossil record of *Picea* is considered (Table 1) a number of important points are noted. First, *Picea* first appears during the middle Eocene. Second, the presence of three species of *Picea* on Axel Heiberg Island indicates that species diversification appears to have occurred more-or-less simultaneously with the appearance of

the genus. Third, compared to *Pinus* which first appears during the Early Cretaceous, *c.* 130 Myr (Alvin, 1960), *Picea* is relatively young and one would not expect to find levels of *cp*DNA differentiation comparable to that seen in *Pinus*. Fourth, although *Picea* first appears during the middle Eocene, the number of species reported during the Eocene and Oligocene is small (Table 1). Large-scale evolutionary diversification of the genus did not occur until the Miocene; a time coincident with massive kilometre-scale uplift of the western Cordillera in North American and Himalayas in Asia and the formation of new montane habitats (LePage, in press).

Examination of the fossil record of *Picea* indicates that the Group I and II spruces have existed since the Eocene. Reports of fossil *Picea* seed cones are limited to about 40 reports worldwide (Table 1). In North America, imprints of *P. sookensis* LaMotte cones from the late Oligocene Sooke Formation on Vancouver Island, Canada indicate an affinity to the group of living species of *Picea* possessing thin flexible cone scales and fimbriate margins. LaMotte (1935) suggested that *P. sookensis* was most closely related to *P. sitchensis*, but this comparison is based exclusively on

Figures 70–84 (even numbers). Typical cone scales of species of *Picea* showing the subtending bract. Fig. 70. *P. likiangensis* (I). A 13876. Fig. 72. *P. farreri* (I). A 19572. Fig. 74. *P. spinulosa* (II). A Wilson, unnumbered. Fig. 76. *P. smithiana* (II). A 10202. Fig. 78. *P. schrenkiana* (II). A Smirnov, unnumbered. Fig. 80. *P. orientalis* (II). A 5442. Fig. 82. *P. omorika* (II). A Zahlbmakner, unnumbered. Fig. 84. *Picea sverdrupii* (II). US237-5588. Scale bar = 5 mm. Figures 71–85 (odd numbers). SEMs of *Picea* species showing a close-up of the bract. Fig. 71. *P. likiangensis*. US-SEM 93 (A 13876). Fig. 73. *P. farreri*. US-SEM 94 (A 19572). Fig. 75. *P. spinulosa*. US-SEM 82 (A Wilson, unnumbered). Fig. 77. *P. smithiana*. US-SEM 83 (A 10202). Fig. 79. *P. schrenkiana*. US-SEM 95 (A Smirnov, unnumbered). Fig. 81. *P. orientalis*. US-SEM 86 (A 5442). Fig. 83. *P. omorika*. US-SEM 108 (A Zahlbmakner, unnumbered). Fig. 85. *Picea sverdrupii*. US-SEM 141 (US237-5588). Scale bar = 1.0 mm.

the external form of the cone and cone scales. Axelrod (1966, 1987) suggested that *P. lahontense* MacGinitie cones from the late Eocene Copper River Basin in Nevada are similar to cones of *P. engelmannii, P. likiangensis* and *P. jezoensis*, all of which are Group I spruces, while those of *P. coloradensis* Axelrod from the Oligocene Creede Flora in south-west Colorado resemble the cones of *P. pungens*. Anatomically preserved cones of *P. eichhornii* Miller from the early Oligocene Makah Formation, Olympic Peninsula, Washington also possess cone scales with thin flexible margins (Miller, 1989).

Picea fossils showing affinity to living species of *Picea* having thick woody cone scales and entire margins include *P. harrimanii* Knowlton, *P. breweriana, P. lahontense* MacGinitie, *P. wolfei* Crabtree, *P. diettertiana* Miller, *P. banksii* Hills & Ogilvie, *P. sonomensis* Axelrod and *P. mariana* (MacGinitie, 1933; Wolfe, 1964; Hills & Ogilvie, 1970; Miller, 1970; Crabtree, 1983; Axelrod, 1944a, 1987; Bennike, 1990). Many of these cones are reported to be similar to the those of *P. breweriana* (MacGinitie, 1933; Axelrod, 1944a; Wolfe, 1964; Crabtree, 1983).

In Eurasia, the cones of *P. koribai* Miki, *P. garoensis* Tanai & Suzuki, *P. snatolensis* Chelebaeva, *Picea* sp. 3, *P. mugodzharica* Rayushkina and *P. polita* (Siebold & Zuccarini) Carrière possess cones with woody cone scales, rounded apices and entire margins (Szafer, 1947, 1954; Miki, 1957; Tanai & Suzuki, 1972; Akhmetiev, 1973; Rayushkina, 1979; Gladenkov, Sinelnikova & Shantser, 1991). Cones of *P. fimbriata* Chelebaeva, *P. wollosowiczii* Sukaczev, *P. excelsa* (Lamarck) Link and *P. latisquamosa* Ludwig possess cone scales that are thin and flexible and have fimbriate margins and resemble the Group I *Picea* (Engelhardt & Kinkelin, 1908; Engelhardt, 1911; Reid & Reid, 1915; Mädler, 1939; Szafer, 1947, 1954; Rayushkina, 1979; Gladenkov *et al.*, 1991).

Most of these cones are based on incomplete descriptions or occur as compression fossils and comparison with living species is based entirely on the size and shape of the cones and cone scales. While it is possible to suggest relationships between fossil and living representatives of *Picea*, the use of cone and cone-scale morphology alone provide a less than complete assessment of the characters necessary for reliable species circumscription. Sigurgeirsson & Szmidt's (1993) RFLP analysis is the only study in which the phylogeny of the genus using molecular data was examined. While their study has provided valuable insight into the relationships that appear to exist within the genus, further studies in which all species are examined and the sequencing of different regions (e.g. *rbcL* (*cp*DNA) and *ITS* (*nr*DNA)) of the genome are needed.

In addition to the lack of suitable data, understanding of the systematic relationships within the genus is further complicated because of hybridization and introgression. It is well known that where range overlaps most species of *Picea* will hybridize where opportunity arises (Dallimore & Jackson, 1948; Wright, 1955; Horton, 1959; Daubenmire, 1968; Ogilvie & Rudloff, 1968; Roche, 1969; Krüssmann, 1985; Farjon, 1990). Wright (1955) suggested that introgressive hybridization may have played an important role in the evolution of many modern species. Consequently, such problems as determining the exact number of species in south-east Asia and interpretation of systematic relationships within the genus may be related to hybridization and introgression.

It is also interesting to note that Gaussen (1966) considered small cones with hidden bracts as being ancestral and large cones with exserted bracts as being derived. However, *P. sverdrupii* and *P. palustris* possess large cones and all of the Axel Heiberg spruces possess hidden bracts which contradict Gaussen's hypothesis. In fact, exserted bracts are unknown among fossil and living species of *Picea*.

GENERIC-LEVEL RELATIONSHIPS

Based on the morphology of reproductive and vegetative structures, Frankis (1989) concluded that *Picea*, like *Pinus*, has no close relatives. Hart's (1987) cladistic analysis of anatomical and morphological features shows *Picea* as being the sister group to the *Cathaya* Chun & Kuang-*Pinus* clade, whereas Price, Olsen-Stojkovich & Lowenstein's (1987) immunological analysis of the family shows *Pinus* as being the sister group to *Picea*. Although their data set contained members of only eight of the eleven recognized genera of the Pinaceae (*sensu* Farjon, 1984, 1990), Xiao-Quan *et al.* (1997) provide two phylogenetic topologies for the Pinaceae using RFLP analysis of *cp*DNA. One (Wagner tree generated by the Branch and Bound option of PAUP 3.1.1) presents *Picea* as being the sister group to a clade containing *Cedrus* Trew, *Pinus*, *Cathaya, Larix*, and *Pseudotsuga* Carrière, with *Keteleeria* Carrière being the sister group to the previous clade (including *Picea*) and *Abies* being the sister group to the other seven genera used in the analysis. The second (neighbour joining), indicates that *Picea* is the sister group to *Cedrus, Abies*, and *Keteleeria*, with *Pinus, Cathaya, Pseudotsuga*, and *Larix* forming a separate clade. The RFLP analysis of the *cp*DNA of Tsumura *et al.* (1995) places *Cedrus* as the sister group to *Picea* within its own clade. Clearly the ancestry of *Picea* remains unresolved and illustrates the need for further detailed anatomical, morphological and molecular analyses. Although the ancestry of *Picea* remains unknown, Miller (1988, 1989) has suggested

that the genus probably had its roots in the late Cretaceous/early Tertiary and is most likely related to taxa included in the extinct *Pityostrobus* Nathorst *ex* Dutt and *Pseudoaraucaria* Fliche complexes.

The fossil spruces from Axel Heiberg Island reliably extend the fossil record of *Picea* to the middle Eocene and provide the earliest evidence for the lineage possessing thick and woody cone scales with entire margins. The presence of three species on Axel Heiberg Island also indicates that diversification of the genus occurred early in the evolution of the group and that it was well underway, at least in the Canadian High Arctic during the early Tertiary.

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APPENDIX 1

Extant herbarium specimens used for comparison during this study were provided by the Arnold Arboretum, Harvard University Herbarium, Cambridge, Massachusetts, U.S.A. (A); British Museum (Natural History), London, England (BM); Missouri Botanical Garden, St. Louis, Missouri, U.S.A. (MO); Fraser Herbarium, University of Saskatchewan, Saskatoon, Saskatchewan, Canada (SASK); University of Alberta Herbarium, Edmonton, Alberta, Canada (ALTA); United States National Herbarium, Smithsonian Institution, Washington, D.C., U.S.A. (US).

Living specimens of *Picea* were collected from Heritage Lake (53°56′N, 105°09′W), Saskatchewan, Canada (*P. mariana* and *P. glauca*); Elbow Summit (49°42′N, 114°59′W), Alberta, Canada (*P. engelmannii*); Powder Face Trail (50°55′N, 114°55′W), Alberta, Canada (*P. engelmannii*); Bedgebury Pinetum, Bedgebury, Kent, England (*P. abies*); The Royal Botanic Gardens, Kew, England (*P. abies*); near Cerin, France (*P. abies*); Kiyozumi-cho, Misaka (43°15′N, 141°54′E), Hokkaido, Japan (*P. jezoensis*); Nayoro Forest Tree Breeding Station, Hokkaido University, Nayoro (44°39′N, 142°25′E), Hokkaido, Japan (*P. glehnii*); Forestry and Forest Product Research Institute, Hokkaido Research Center, Sapporo, Hokkaido, Japan (*P. jezoensis, P. jezoensis* var. *hondoensis, P. glehnii* and *P. koyamae*). These specimens have been deposited in the Fraser Herbarium (SASK).

Specimens examined
Picea abies (L.) Karsten: US: 481520, 272364; A: Ronniger, Stefanoff & Georgioff, Lindquist, Johnsson;

MO: 875923, 875924, 875925, 1635470, 1635469; BM: 38305, 38296.

Picea alcoquiana (Veitch *ex* Lindley) Carrière: US: 2498207, 764406; A: 7861, 6064, 1959, 7777, unnumbered.

Picea asperata Masters: US: 776060, 1331967, 1245488, 1332066, 776014, 1331996, 775988, 775987, 320, 4066; A: 14815, 14444, 13666, 8050, 4066; BM: 38311.

Picea brachytyla (Franchet) Pritzel: US: 776069, 775996, 1345665, 1330232, 2052, 775997, 1330155, 2072, 1330192, 2076; A: 3411, 9549, 4470, 2052, 2052, 11705, 9108, 2075, 2076, 22902.

Picea breweriana S. Watson: MO: 1243441, 1178204, 984840, 1635409.

Picea chihuahuana Martínez: MO: 1225972.

Picea engelmannii Parry *ex* Engelmann: MO: 2505160 (Type specimen), 1505159, 3539164, 2505868, 2505844, 2505850, 1216982, 2505833, 922704, 2505161, 2505155, 2505158, 3574111; SASK: 94398.

Picea farreri Page & Rushforth: A: 19572.

Picea glauca (Moench) Voss: SASK: 879, 880, 882, 884, 886, 887, 888, 890, 891, 893, 894, 895, 899, 900, 901, 904, 905, 906, 907, 21017, 21083, 27720, 28838, 28840, 28841, 28842, 38283, 40301, 40562, 40564, 57876, 61069, 61070, 65195, 67421, 70182, 70183, 76637, 78400, 78405, 79057, 80220, 90367, 94462, 95556, 95557, 95570, 95623, 95628, 95634, 96057, 118259.

Picea glehnii (Fr. Schmidt) Masters: US: 764405, 764404; A: 7404, Abo 1884, 6652; BM: 38313; SASK: 118258.

Picea jezoensis (Siebold & Zuccarini) Carrière: US: 764188, 778297, 1274386, 7520, 9245; A: 9148, 725, 7772, Tokubuchi 1889, 7317, 6062; MO: 1639467, 865739, 865725, 2782001; BM: 38294, 38295, 38304, 38299, 38315; SASK: 118257.

Picea koraiensis Nakai: A: 334; MO: 1639472.

Picea koyamae Shirisawa: US: 74385, 1274457, 764403, 8963; A: 8963, 7523, 7523; MO: 807113; BM: 38314.

Picea likiangensis (Franchet) Pritzel: US: 1510899, 1510201, 1330157, 1334811, 1334139, 1674231, 776070, 1674237, 776054, 599459, 775986, 775990, 775985, 1674234, 2060, 2056, 2059; A: 17444, 4420, 1779, 13876, 2064, 2066, 7710; MO: 1030376, 1619805, 1619706; BM: 38292, 38301, 38302, 38312, 38310, 38309.

Picea mariana (Miller) Britton, Sterns & Poggenberg: SASK: 909, 910, 911, 912, 913, 917, 918, 920, 921, 925, 926, 927, 928, 27646, 27703, 29072, 29074, 29997, 32429, 40323, 40559, 44367, 44368, 44369, 45374, 45375, 45968, 47787, 51555, 51562, 52088, 52090, 52091, 52092, 52093, 52095, 52096, 55891, 57360, 60644, 60645, 60647, 62126, 62131, 62274, 62275, 62279, 62483, 66118, 67648, 70701, 76631,

76632, 78137, 78154, 78407, 78408, 78411, 78412, 79059, 79728, 80261, 80423, 81282, 81346, 81450, 90528, 93844, 93859, 95700, 118260.

Picea maximowiczii Regel *ex* Masters: US: 2501381; A: Fudgiyama 1864, 7526, Azusayama 3/10 1959; MO: 1635499.

Picea meyeri Rehder & Wilson: A: 813.

Picea morrisonicola Hayata: US: 1372613, 1274489, 10901; A: 1978, 20676, unnumbered; MO: 1627050; BM: 38317, 38316.

Picea neoveitchii Masters: US: 2054; A: 2054, 61554.

Picea obovata Ledebour: A: 281; BM: 38298.

Picea omorika (Pančić) Purkyne: US: 3029029, 1576572; A: Pančić, Zahlbmohner.

Picea orientalis (L.) Link: A: Gay 1884, Schneider, 5542; BM: 38290, 38291, 38306.

Picea pungens Engelmann: MO: 1635434, 2505866; SASK: 17570, 19591.

Picea purpurea Masters: US: 1245988, 776011, 1331827, 1703092, 1245818, 1245817, 1331843, 4059, 4062; A: 4059, 804, 13427, 13344, 7955; BM: 38318.

Picea retroflexa Masters: BM: 38307.

Picea rubens Sargent: ALTA: 25789.

Picea schrenkiana Fisher & Meyer: US: 790, 813, 806; A: 81828, Litnow, unnumbered, Transchel, 19728.

Picea sitchensis (Bongard) Carrière: MO: 2818, 2489, unnumbered, 5015, 1231478, 1635404, 1635402; SASK: 37436, 88050, 94474.

Picea smithiana (Wallich) Boissier: US: 2242336; A: 10202.

Picea spinulosa (Griffith) Henry: US: 2394904; A: 16675, 5349, Wilson, 3890; BM: 38297, 38303.

Picea torano (Siebold *ex* K. Koch) Koehne: US: 1311907, 2496758; A: Wilson 1914, 1862, 2580.

Picea wilsonii Masters: US: 2053, 1529366, 1345667, 1332064, 1332007, 2053; A: 14975, 2114, 8051, 1823, 2053; MO: 3754892, 2929264; BM: 38308.

APPENDIX 2

Fossil specimens used for comparison during this study were provided by the Smithsonian Institution, Department of Paleobiology, Washington, D.C., U.S.A. (USNM) and the Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada (TMP).

Specimens examined
Picea banksii Hills & Ogilvie: TMP: 84-57-2–84-57-17.
Picea harrimanii Knowlton: USNM: 30070, 30071, 30096, 30097.
Pinus sp.: USNM: 30073, 30074.
Picea sp.: USNM: 30075, 30079A, 30079B.
Picea? sp.: USNM: 30090.
Piceites cretaceus Brown: USNM: 39280, 222835, 222836.