A New Species of Pinus Subgenus Pinus Subsection Contortae from Pliocene Sediments of Ch'ijee's Bluff, Yukon Territory, Canada
Author(s): Athena D. McKown, Ruth A. Stockey, Charles E. Schweger
Reviewed work(s):
Source: *International Journal of Plant Sciences*, Vol. 163, No. 4 (July 2002), pp. 687-697
Published by: The University of Chicago Press
Stable URL: http://www.jstor.org/stable/10.1086/340425
Accessed: 15/12/2011 16:09

Int. J. Plant Sci. 163(4):687–697. 2002.

1058-5893/2002/16304-0019$15.00

A NEW SPECIES OF *PINUS* SUBGENUS *PINUS* SUBSECTION *CONTORTAE* FROM PLIOCENE SEDIMENTS OF CH'IJEE'S BLUFF, YUKON TERRITORY, CANADA

Athena D. McKown,* Ruth A. Stockey,[1],* and Charles E. Schweger†

*Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; and
†Department of Anthropology, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Three structurally preserved conifer ovulate cones are described from Pliocene sediments at Ch'ijee's Bluff on the Porcupine River, near Old Crow, Yukon Territory, Canada. Cones are ovoid to conical, symmetrical, 3.4–4.4 cm long and 2.8–3.4 cm wide, with helically arranged cone-scale complexes. Ovuliferous scales are thin at the base, expanded at the apex, 2 cm long and 1 cm wide, with flat, rhomboidal apophyses and minute dorsal umbos. Pith is parenchymatous with scattered sclerenchyma at its outer edge. The parenchymatous inner cortex contains 12–15 small resin canals. Outer cortex is also parenchymatous with a thin outer sclerenchymatous zone. Vascular tissues of the scale and bract originate as a complete cylindrical trace from the axis stele. Resin canals are abaxial to the scale trace as it separates from the bract. The abaxially concave ovuliferous scale trace splits into separate vascular bundles that alternate with resin canals in the most distal sections. Bracts separate from scales medially, lack abaxial lobes, and contain terete traces that are accompanied by two resin canals. The paired seeds are elliptical, 2.7–3.9 mm long and 2.1–2.5 mm wide, with wings up to 16 mm long. Fossils were compared anatomically with extant species of *Pinus* section *Pinus*. The fossil cones most closely resemble those of *Pinus contorta* Dougl. ex Loud. but differ from any previously described fossils of this species or extant subspecies by a combination of cone characters. The symmetrical cone shape, nonreflexed cone base, flattened apophyses, cone serotiny, and seed wing length distinguish these cones from *P. contorta*. These cones are described in a new species of *Pinus* subgenus *Pinus* Subsection *Contortae*, *Pinus matthewsii* sp. nov. Like *P. contorta*, *P. matthewsii* may have been a colonizer of open habitats. The scarcity of these fossil cones, the presence of numerous cones of *Picea* Dietr. and a *Pinus monticola*–like species and abundant *Picea*, *Pinus*, and *Betula* pollen indicate dense forest cover dominated by spruce, soft pines, and birch.

Keywords: Bluefish Basin, Ch'ijee's Bluff, fossil conifers, Pinaceae, *Pinus contorta*, Pliocene, Yukon Territory.

Introduction

The Bluefish Basin of northern Yukon Territory, Canada, is part of the unglaciated Beringian refugium (Duk-Rodkin 1999) and, along with the adjacent Old Crow Basin, is believed to contain one of the most complete Pliocene and early Pleistocene records in northwestern North America (Hughes 1970; Schweger 1989). Ch'ijee's Bluff, a section on the Porcupine River within the Bluefish Basin, exposes fossiliferous sediments from Pliocene to Holocene age. Tertiary pollen assemblages and megafossils from the base of the section have been reported (Lichti-Federovich 1974; Hale 1985; Matthews and Ovenden 1990); however, no detailed anatomical studies have been published on the megafossil remains to date. Ovulate cones from Ch'ijee's Bluff include two *Picea* Dietr., one *Larix* Miller, and two types of cones referable to *Pinus* L. (Stockey 1983). External features of *Larix* cones from Ch'ijee's Bluff were studied by Schorn (1994), but no internal anatomy was described. Internal anatomy of cones from this locality has only just recently been described, including cones similar to extant *Pinus monticola* Douglas ex D. Don (Holden 1998) and *Picea glauca* (Moench.) Voss. (Schwab et al. 2000).

The second type of *Pinus* cone, previously identified as *Pinus* subgenus *Pinus* and classified in some reports as *Pinus contorta* (Schweger 1989; Matthews and Ovenden 1990), is described in this article based on anatomical sections. Of the species in *Pinus* subgenus *Pinus*, only subsections *Sylvestres* Loudon emend. Little & Critchfield, *Ponderosae* Loudon, and *Contortae* Little & Critchfield are thought to have had northern refugia in North America during the Eocene (Millar 1998). From these arose the modern lineages of northern *Pinus* species, supported by their present-day distribution in North America (Critchfield 1985; Millar 1998).

Material and Methods

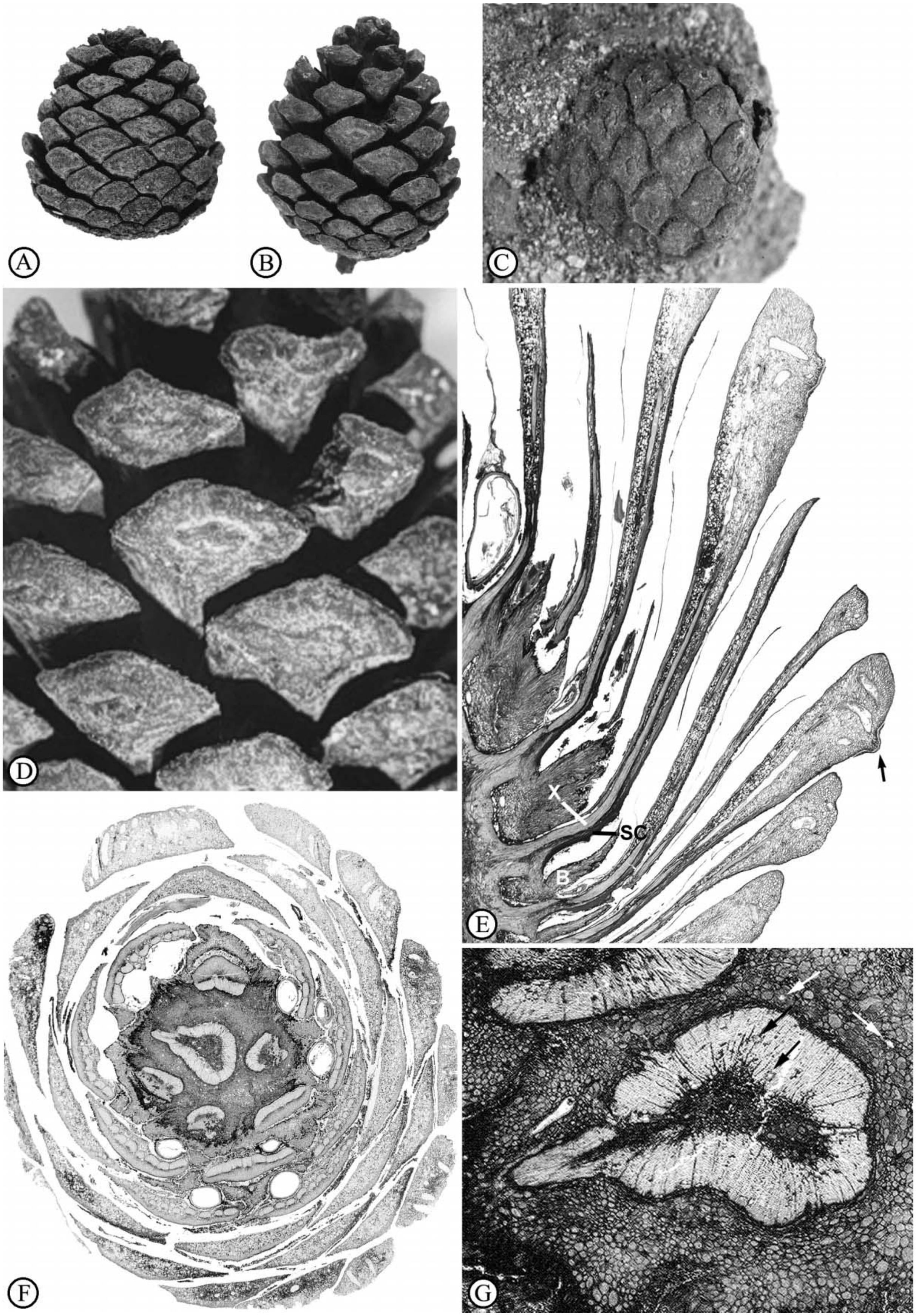
Three structurally preserved ovulate cones were examined from Ch'ijee's Bluff (67°28′N, 139°54′W), located on the Porcupine River near Old Crow in the Bluefish Basin, Yukon Territory, Canada. The cones were found in the basal unit of the section, referred to as "unit 1," described by Hughes (1970) as 3.66 m of coarse sands and gravels with silt lenses, partially cemented, and, in part, oxidized to a red-brown color.

Unit 1 sediments are highly variable, ranging from a silica-

---

[1] Author for correspondence; e-mail ruth.stockey@ualberta.ca.

Manuscript received July 2001; revised manuscript received February 2002.


A
B
C
D
E
X
SC
B
F
G

cemented quartz-rich gravel and coarse sand to a friable well-bedded sand with detrital organic matter that includes cones to a dark-brown clay to clayey gravel. Gravel and coarse sand clasts are angular to subrounded quartz. Clays are mostly massive but appear to have been contorted, perhaps resulting from gravity loading. Some layers include very dark lignitic organic material. Detrital organic material, including conifer cones and wood, are concentrated at the top of the clay, and stumps are rooted in the clay with what are likely trunks lying on the clay surface. Large, 40-cm-across, siliceous concretions with fragmentary plant remains are found along the contact between the clay and overlying fluvial sand. The lower unit 1 may be a forest soil that was rapidly covered by coarse fluvial sands and gravels (C. E. Schweger, personal observation, 1983).

Conifer remains, such as ovulate cones, wood, and *in situ* stumps are present, and pollen-bearing silt lenses allow comparisons with other late Tertiary and Pleistocene assemblages. Wood collected from five unit 1 stumps has been identified as *Pinus* subgenus *Strobus*, *Abies*, two types of *Larix*, and *Picea* (Wheeler and Arnette 1994). Only *Larix* and *Picea* have been identified from wood collected in the overlying unit 2 (Wheeler and Arnette 1994). Unit 1 pollen assemblages do not compare well to the more floristically complex Miocene pollen assemblages from the Bluefish and Old Crow Basins and the Miocene Ballast Brook Formation, Banks Island (Fyles et al. 1994; White and Ager 1994), but are more similar to the Pliocene Beaufort Formation, Banks Island (Fyles et al. 1994). However, only trace amounts of *Pinus* and *Corylus* pollen occur in northern Yukon assemblages dated by fission track to 2.3 Ma (Westgate et al. 1995) and younger. Pleistocene pollen records, including 10 interglacial records, clearly indicate that *Corylus* disappeared from the Yukon flora while *Pinus* was either not present or occurred only as a minor component in the vegetation (C. E. Schweger, unpublished observation). *Pinus* does not reappear as an important component in the vegetation until the last 1500 yr of the Holocene. The cones described here are therefore placed between 2.3 and 5 Ma.

In preparation for anatomical study, two complete cones (specimens P609 and P610) were washed in distilled water and dehydrated in an ethanol series under vacuum. The entire cones were embedded in bioplastic to prevent shattering during thin sectioning. Specimen P609 was cut in transverse section, and P610 was cut in longitudinal section. Faces of the embedded cones were infiltrated with TRA-Bond 2114 Water White Transparent Epoxy Adhesive (TRA-CON, Medford, Mass.) to prevent changes in shape resulting from drying. Thin sections were cut and ground on a Hillquist thin-section machine, and coverslips were mounted with Eukitt (O. Kindler GmbH, Freiburg, Germany) xylene-soluble mounting medium for microscopic examination.

Description of the fossil cones was based on internal and external cone characters, and classification follows Little and Critchfield (1969) and Price et al. (1998). Internal anatomical comparisons were made to extant *Pinus* species from the University of Montana conifer reference collection of C. N. Miller, Jr., now housed at the University of Alberta. External cone morphology was compared to extant *Pinus* specimens from the University of Alberta herbarium, and *Pinus contorta* cones from northern California and southern Oregon were donated by A. Liston, Oregon State University. Cones and slide sections are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Results

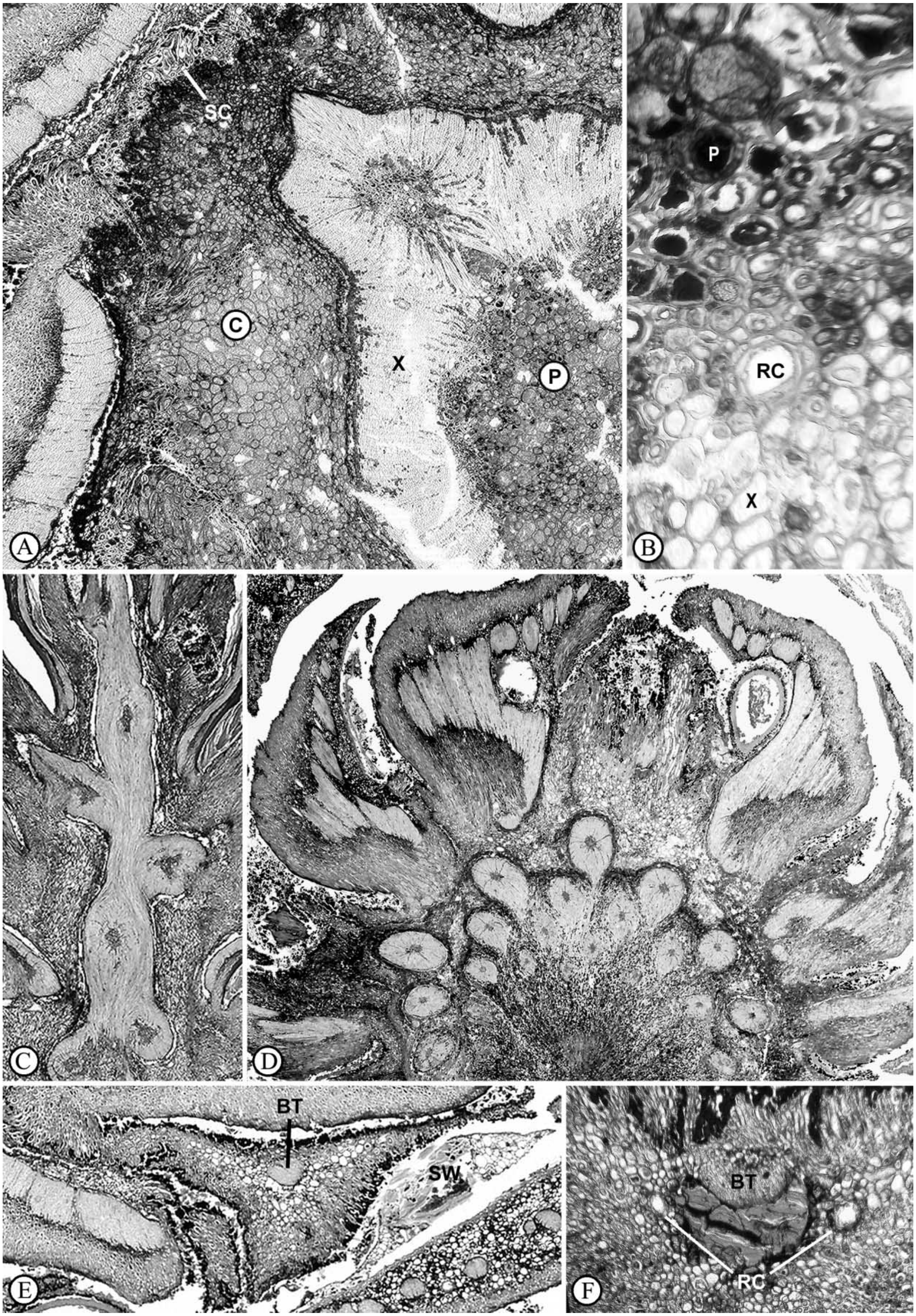
Description

General features. Cones are ovoid to conical in shape, symmetrical with a tapering apex and helically arranged cone-scale complexes (fig. 1*A*, 1*C*, 1*F*). They range from 3.4–4.4 cm long and 2.8–3.4 cm wide. A short, stout peduncle, 3.5 mm long, is preserved on the holotype specimen (fig. 1*B*). Ovuliferous scales are woody, 2 cm long and 1 cm wide (fig. 1*E*, 1*F*). Bracts are smaller than scales, 6 mm long, and lack a keel (fig. 1*E*). The surface of each scale apophysis is flattened and rhomboidal in shape, 10 mm wide and 7.5 mm high (fig. 1*D*). Ovuliferous scales have a minute umbo in the center of the apophysis (fig. 1*D*, 1*E*). Cone tissues and ovules are well preserved in both cones sectioned.

Cone axis. The pith is parenchymatous, with few, scattered sclerenchyma cells near its outer margin (figs. 1*G*, 2*A*). It has a maximum diameter of 6.3 mm and lacks resin canals. Secondary xylem forms a continuous cylinder with a single growth increment, has a maximum thickness of 1.8 mm, and has up to six small resin canals located near the pith (fig. 1*G*; fig. 2*A*, 2*B*). The inner cortex is parenchymatous and contains between 12 and 15 resin canals of uniform diameter (fig. 1*G*). The outer cortex is parenchymatous with a thin layer of sclerenchyma, approximately five cells thick, on its outer edge (fig. 2*A*). The cone axis tapers at both ends and is widest near the middle, with a diameter of ca. 8 mm.

Cone-scale complex. Vascular tissue in the ovuliferous scale and subtending bract originates as a single, continuous cylindrical strand from the axis stele (fig. 2*C*, 2*D*). Bract and scale traces separate in the outer cortex. Near the scale base, the scale trace is thick and concave with abaxial resin canals and a thick layer of sclerenchyma (fig. 1*F*). At the level of the ovules and continuing toward the scale apex, the scale trace splits into 8–12 small, terete bundles with resin canals located abaxially and in between the vascular bundles (fig. 3*A*). Toward the apophysis, the abaxial sclerenchyma layer becomes very thin (fig. 3*B*). At the apophysis, the ovuliferous scale is

Fig. 1 Cones of *Pinus matthewsii* sp. nov. (University of Alberta Paleobotanical Collection). *A*, Lateral view of ovulate cone; P609, × 1. *B*, Lateral view of ovulate cone; holotype P610, × 1. *C*, Ovulate cone in matrix; P611, × 1.5. *D*, Thick rhomboidal scale apices showing minute dorsal umbos; holotype P610, × 3.5. *E*, Longitudinal section of cone showing thin ovuliferous scale that expands at the apophysis, has thin vascular (*X*) and sclerotic tissues (*SC*) and short subtending bracts (*B*). Arrow indicates small dorsal umbo; holotype P610, × 5.7. *F*, Transverse section of cone showing helical arrangement of scales; P609, × 2.9. *G*, Transverse section of cone axis with complete vascular cylinder, parenchymatous cortex, and cortical resin canals. Arrows indicate resin canals in the cortex (white) and secondary xylem (black); P609, × 18.


SC
C
X
P
A
P
RC
X
B
C
D
BT
SW
E
BT
RC
F

enlarged with more parenchymatous tissues and sparse sclerenchyma (fig. 1*E*).

Bracts separate from ovuliferous scales by a medial pouch (fig. 2*E*). The bract trace is terete and accompanied by two lateral resin canals (fig. 2*E*, 2*F*). Vascular tissue extends only a short way into the bract. Bract tissue is parenchymatous, with sclerenchyma at the outer margin.

Ovules. It is notable that numerous seeds are present in the fossil specimens, which indicates that the cones were serotinous or remained closed at maturity. There are two ovules on the adaxial surface of the ovuliferous scale separated by an interseminal ridge that extends up slightly between them (fig. 3*A*). Ovules are ovoid, with a tapered micropylar end and a rounded chalazal end (figs. 1*E*, 3*C*). Seed bodies are 2.7–3.9 mm long and 2.1–2.5 mm wide (fig. 3*C*, 3*D*). The integument is smooth and lacks abaxial ridges, glands, or resin canals (fig. 3*A*, 3*D*). Average integument thickness is 96 μm, composed mostly of sclerotesta (fig. 3*D*, 3*E*). Inside some ovules, megagametophyte tissue is present although no embryos were found. The seed wing is detachable, and several wings detached in the vacuum process used during embedding. There is a prominent parenchymatous pad of tissue at the base of the wing (figs. 1*E*, 3*C*). Wings measure up to 16 mm long and 4–5 mm wide (fig. 3*C*).

Systematics

Genus—Pinus *L.*

Subgenus—Pinus

Section—Pinus

Subsection—Contortae *Little & Critchfield*

Species—Pinus matthewsii *sp. nov. McKown,*
Stockey et Schweger

Diagnosis. Ovulate cones, ovoid to conical, symmetrical with tapering apices; 3.4–4.4 cm long, 2.8–3.4 cm wide; helically arranged cone-scale complexes. Ovuliferous scales thin at base, expanded at apophysis; 2 cm long, 1 cm wide. Bract 6 mm long, lacking keel, separating by medial pouch. Scale apophyses flat, rhomboidal; 10 mm wide, 7.5 mm high with minute dorsal umbo. Cone axis tapering at both ends, 8 mm in diameter. Pith parenchymatous, few sclerenchyma cells near outer margin, lacking resin canals. Secondary xylem cylinder continuous; few resin canals. Inner cortex parenchymatous; 12–15 resin canals. Outer cortex parenchymatous with thin outer sclerenchyma layer. Vascular traces to cone-scale complex united at origin, cylindrical. Resin canals abaxial to scale vasculature at origin. Bract trace terete, entering bract, accompanied by two resin canals; tissue parenchymatous, containing sclerenchyma. Ovules elliptical, 2.7–3.9 mm long, 2.1–2.5 mm wide; wings detachable, 16 mm long.

Holotype. University of Alberta (UAPC-ALTA) specimen P610 and slides P610A1-A7.

Paratypes. UAPC-ALTA specimens P609 and P611 and slides P609A1-A6 and P609B1-B4.

Etymology. The specific epithet is proposed in honor of John V. Matthews, Jr., Geological Survey of Canada, who has contributed significantly to our knowledge of palynology, paleobotany, and paleoenvironmental reconstruction of numerous Tertiary and Quaternary localities in both Alaska and the Yukon Territory.

Locality. Ch'ijee's Bluff (Twelvemile Bluff, HH228) on Porcupine River (67°28′N, 139°54′W), Yukon Territory, Canada.

Horizon. Unit 1 sediments, Pliocene.

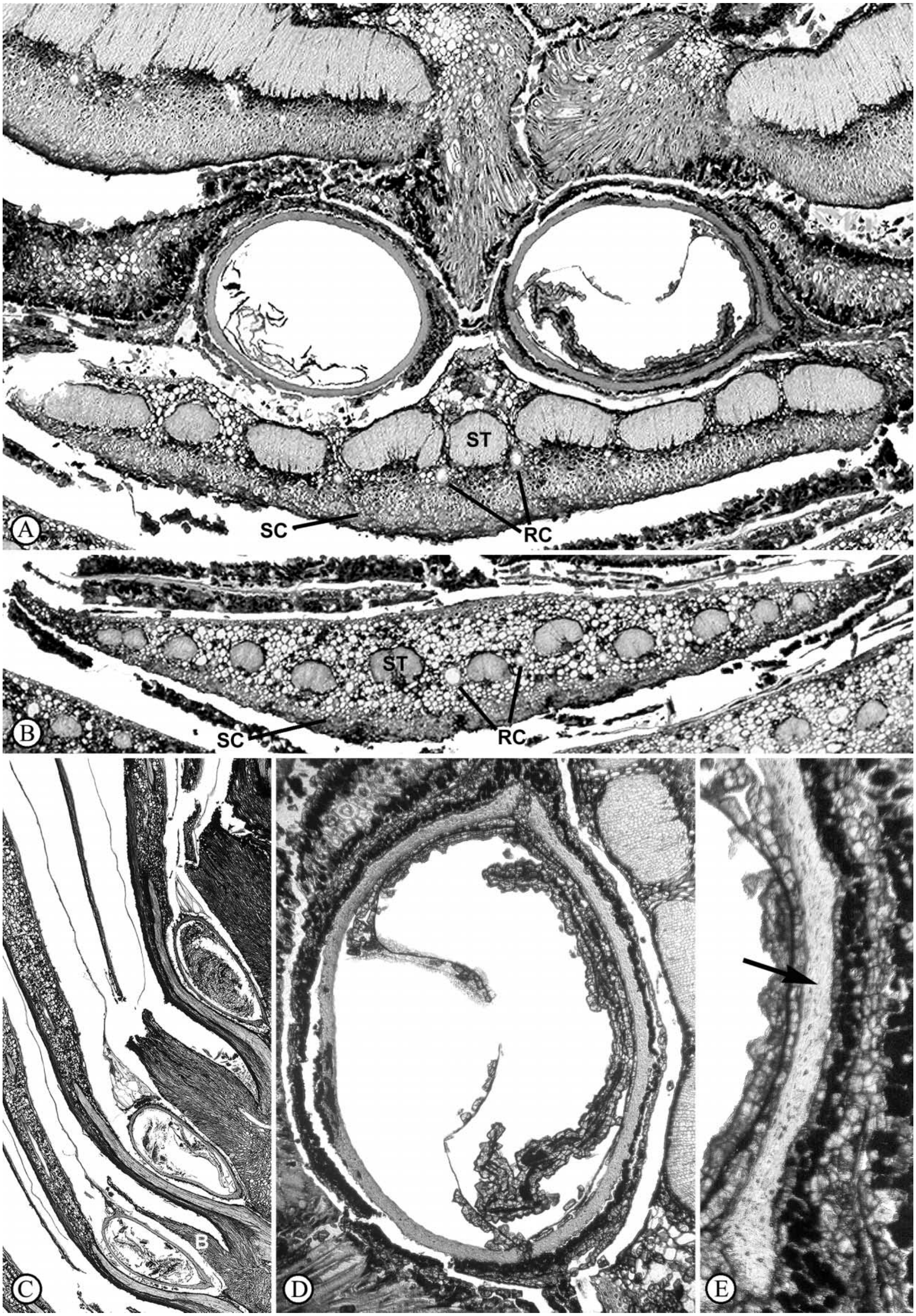
Discussion

The fossil cones from Ch'ijee's Bluff have helically arranged cone-scale complexes, two seeds per scale, traces to the cone-scale complex that are cylindrical at their origin, ovuliferous scales expanded at the apex with an apophysis and umbo, and resin canals abaxial to the scale vascular tissue; they are therefore assignable to the Pinaceae genus *Pinus* L. (Miller 1976). The presence of a dorsal umbo (centrally located prickle in the apophysis) and a detachable seed wing are characters of the subgenus *Pinus* as described by Little and Critchfield (1969). The presence of the sclerotic outer layer in the cortex of the cone axis, a parenchymatous pad of tissue at the base of each seed wing, and triangular-shaped scales in transverse section are distinctive of cones in *Pinus* subsections *Pinus* (= *Sylvestres* Loudon), *Oocarpae* Little & Critchfield, and *Contortae* Little & Critchfield (Miller 1976).

It is unlikely that the fossil cones are in the subsection *Oocarpae* because cones from pines in this subsection have a much greater cone size (Silba 1986) than those reported here. It is generally believed that pines in Subsection *Oocarpae* originated in Mexico and Central America recently and persisted in southern refugia (Millar 1998). Resulting from the Pliocene age of our fossil cones, it seems unlikely that they belong to any species within this group.

Within the subsection *Pinus*, the species *Pinus densiflora* Sieb. & Zucc., *Pinus resinosa* Ait., and *Pinus sylvestris* L. have northern distributions and cones that bear surficial resemblance to the fossil cones from Ch'ijee's Bluff (table 1). These extant species all have small ovoid to conical, symmetrical cones with a short peduncle, and a minute dorsal umbo and,

Fig. 2 Internal anatomy of *Pinus matthewsii* sp. nov. (University of Alberta Paleobotanical Collection). *A*, Transverse section of cone axis showing parenchymatous cortex (*C*) with a thin outer layer of sclerenchyma (*SC*), parenchymatous pith (*P*), and secondary xylem (*X*); P609, × 17. *B*, Transverse section of cone showing secondary xylem (*X*) and resin canal (*RC*) located near pith (*P*); P609, × 257. *C*, Tangential section of cone axis showing origin of cone-scale complexes and bract trace separation; holotype P610, × 6.1. *D*, Cone base transverse section showing diverging cone-scale complexes; P609, × 7.1. *E*, Transverse section of bract showing bract trace (*BT*) and bract sclerenchyma tissues. Parenchymatous pad at base of seed wing (*SW*) wedged between scales; P609, × 15. *F*, Tangential section of bract showing bract trace (*BT*) and resin canals (*RC*); holotype P610, × 41.


ST
SC
RC
A
ST
SC
RC
B
B
C
D
E

therefore, appear to be very similar to our fossil cones. In addition, these species have cone scales that are ca. 2 cm in length, and seed wings between 13 and 19 mm long, similar to the fossils. However, cones of these species in the subsection *Pinus* have secondary xylem that contains more abundant resin canals and a much thicker sclerenchymatous outer zone in the cortex than in the fossils. In addition, these cones have shorter bracts and larger ovules with a thicker integument than those of the fossils. Furthermore, none of these extant species have serotinous cones, whereas the fossil cones were most likely serotinous.

The fossil cones do not share similar morphological or anatomical features with cones of the two southern pines in the subsection *Contortae*, *Pinus clausa* (Chapm.) Vasey ex Sarg. and *Pinus virginiana* Mill. Cones of *P. clausa* are larger and have distinctive protuberant apophyses and larger ovules (Farjon 1984; Silba 1986). The range of cone sizes in *P. virginiana* spans the size of the fossil cones; however, *P. virginiana* cones possess a long peduncle 5 mm in length and seeds with wings that are much shorter (Farjon 1984; Silba 1986). Furthermore, the scales of *P. virginiana* are distinctively different because they exhibit protuberant apophyses adorned with a stout umbo that is 5 mm in length (Farjon 1984; Silba 1986).

The two northern pines in Subsection *Contortae*, *Pinus banksiana* Lamb. and *Pinus contorta* Doug. ex Loud., have internal cone anatomical features that closely resemble the fossil cones (table 1). Length of cones, ovuliferous scales, and bracts are similar to those of the fossil cones. In addition, the pith is tapered at either end, as in the fossils, and ovoid ovule shape and integumentary thickness are very similar to the fossils (table 1).

Although cones of *P. banksiana* share some comparable features with the fossil cones, there are several critical features that differ between the two (table 1). The cone shape of *P. banksiana* is very long and oblique with a cone base reflexed to one side, compared to the symmetrical, ovoid fossil cones. Apophyses are generally dimorphic on either side of the *P. banksiana* cone, with small flat apophyses on the interior of the curve of the cone, and large protuberant apophyses on the exterior edge. The cortex of *P. banksiana* possesses a thicker sclerenchyma band than that of the fossil cones, and resin canals are more abundant in the secondary xylem of *P. banksiana*. Like *P. virginiana*, the seed wing length of *P. banksiana* is distinctly shorter than that found in the fossils (table 1).

The cones of *P. contorta* are more closely comparable to the fossil cones than those of *P. banksiana* (table 1). The fossil cones fall within the cone-size range of *P. contorta*, a species that usually has asymmetrical cones but that can also demonstrate symmetrical cone shapes. The apophyses can be flat in *P. contorta*, like those of the fossil cones, but are usually protuberant. Apophyses are dimorphic in cones that are curved with a reflexed cone base, like the cones of *P. banksiana*. Although cones of *P. contorta* and the fossil cones have a similar number of resin canals in both the secondary xylem and cortex, there is a considerably greater amount of sclerenchyma in the cortex of *P. contorta* cones than in the fossil cones. The ovules of the fossils are in the low range of lengths for seeds in *P. contorta*, but the seed wings in the fossils are longer. Therefore, the fossil ovules are small but possess a long wing, whereas those of *P. contorta* are larger but with shorter wings.

It is important to compare the fossil cones to combinations of characters seen in *P. contorta* cones because these vary over geography (table 2). Four taxonomically distinct subspecies of *P. contorta* are recognized from different regions of North America: *P. contorta* ssp. *bolanderi* (Parl.) Critchfield, *P. contorta* ssp. *contorta*, *P. contorta* ssp. *latifolia* (Engelm.) Critchfield, and *P. contorta* ssp. *murrayana* (Balf.) Critchfield (Critchfield 1957; Price et al. 1998). These subspecies are thought to have arisen as a result of repeated periods of glaciation, subsequent population fragmentation, and the subsequent dissimilar environments (Critchfield 1985). Samples of cones from three of the four subspecies were collected from northern California, southern Oregon, and Alberta. These include *P. contorta* ssp. *contorta*, *P. contorta* ssp. *latifolia*, and *P. contorta* ssp. *murrayana*. Information on the fourth subspecies, *P. contorta* ssp. *bolanderi*, was obtained from Critchfield (1957), Farjon (1984), Silba (1986), and Krüssman (1985). All cone specimens exhibit the characteristic reflexed cone bases and dimorphic apophyses at the cone base, at least to some degree, unlike the fossil cones. Furthermore, *P. contorta* ssp. *contorta* has nonserotinous, asymmetrical cones that possess moderately thick cone scales, unlike those of the symmetrical fossil cones (Critchfield 1957). *Pinus contorta* ssp. *murrayana* has cones that are more symmetrical like the fossil cones but are nonserotinous and have very fragile scales (Critchfield 1957). *Pinus contorta* ssp. *latifolia* has serotinous cones, like the fossils; however, the cone shape is mostly asymmetrical, the scales are thick, and the apophyses are protuberant (Critchfield 1957). Although the cones of *P. contorta* ssp. *bolanderi*, the fourth subspecies, are serotinous like the fossil cones, they are also asymmetrical and have thick scales (Critchfield 1957). Therefore, it is evident that despite the variety of character combinations that occur in cones of the subspecies of *P. contorta*, there is no extant subspecies that has an exact combination of characters that match those seen in the fossil cones.

Several Tertiary fossils have been identified as belonging to Subsection *Contortae*, but most are based on conifer remains other than ovulate cones or ovules. *Pinus weasmae* Miller is known from one ovulate cone from the Pliocene of Idaho. This species was described as similar to *P. contorta* and *P. banksiana* (Miller 1992). *Pinus weasmae* differs from the Ch'ijee's Bluff fossils in having a larger cone size, a more asymmetrical shape,

---

Fig. 3 Internal anatomy of *Pinus matthewsii* sp. nov. (University of Alberta Paleobotanical Collection). *A*, Transverse section of ovuliferous scale showing presence of two adaxial ovules per scale, scale trace (*ST*), abaxial sclerenchyma (*SC*), and resin canals (*RC*) abaxial to scale trace; P609, ×21. *B*, Transverse section of ovuliferous scale distal to seed attachment showing vascular bundles (*ST*), thin band of abaxial sclerenchyma (*SC*), and resin canals (*RC*) between bundles; P609, ×18. *C*, Longitudinal section of cone showing bract (*B*), inverted ovules, and seed wings with parenchymatous pad at seed wing base; holotype P610, ×6.7. *D*, Transverse section of ovule; P609, ×35. *E*, Transverse section of ovule showing integument. Arrow indicates sclerotesta; P609, ×88.

Table 1

Cone Character Data of *Pinus matthewsii* sp. nov. from Ch'ijee's Bluff and Extant *Pinus densiflora*, *Pinus resinosa*, and *Pinus sylvestris* (Subsection *Pinus*) and *Pinus banksiana* and *Pinus contorta* (Subsection *Contortae*)

Character	*P. matthewsii*	*P. densiflora*	*P. resinosa*	*P. sylvestris*	*P. banksiana*	*P. contorta*
Geographic location	Northern Yukon	Japan, Korea	Eastern North America	Northern Europe, Asia	Western NWT to eastern North America	Central Yukon to southern Colorado
Cone shape	Ovoid to conical	Ovoid to conical	Ovoid to conical	Ovoid to conical	Conical, curved	Ovoid to conical, often curved
Cone base	Symmetrical	Symmetrical	Symmetrical	Symmetrical	Reflexed, asymmetrical	Reflexed, asymmetrical
Cone length (cm)	3.4–4.4	3.0–5.0	4.0–6.4	2.5–7.9	3.0–6.0	1.9–6.4
Cone width (cm)	2.8–3.4	3.0	3.0–3.5	2.0–3.5	1.3–2.5	2.0–3.0
Peduncle present	Yes	Yes	No (or nearly absent)	Yes	No (or nearly absent)	No (or nearly absent)
Cone axis shape	Tapered at either end, widest in middle	Tapered at either end, widest near base	Tapered at either end, widest near base	Tapered at upper end, widest at base	Tapered at either end, axis narrow	Tapered at either end, axis narrow, widest in middle
Maximum 2°× thickness (mm)	1.8	1.8	2.0	2.5	2.9	1.2
Cortex par/scl	4 : 1	1 : 1	1 : 1	1 : 1	1 : 4	1 : 3
Resin canals in 2°×	Few	Abundant	Very abundant	Abundant	Abundant	Few
Cortical resin canals	12–15	15	13–16	6–7	8	15–20
Bract length (mm)	5.0–6.0	4.5	4.5	3.0–3.5	5.6	5.0
Scale length (cm)	1.8–2.0	2.0–2.7	1.9	2.0	1.7	1.3–1.9
Ovule shape	Ovoid	Ovoid	Ovoid	Conical	Ovoid	Ovoid
Ovule length (mm)	2.7–3.9	4.2–6.4	2.4–5.0	3.0–5.1	2.5–4.8	3.2–5.0
Ovule width (mm)	2.1–2.5	2.6–3.0	2.0–2.8	2.0–2.5	1.9	1.7–2.0
Integument thickness (μm)	96	130	200	100	94	92
Seed wing length (mm)	13.5–16.0	13.0–19.0	18.0–19.0	15.0	12.0–12.7	12.0–14.0
Cone serotiny	Yes	No	No	No	Yes	Yes

Note. NWT = North West Territories; par = parenchyma; scl = sclerenchyma; x = xylem. Data from University of Montana Conifer Reference Collection; University of Alberta Herbarium; Critchfield and Little 1966; Farjon 1984; Krüssmann 1985; Silba 1986.

Table 2

Cone Character Data of *Pinus matthewsii* sp. nov. from Ch'ijee's Bluff and Extant *Pinus contorta* ssp. *bolanderi, Pinus contorta* ssp. *contorta, Pinus contorta* ssp. *latifolia,* and *Pinus contorta* ssp. *murryana* (Subsection *Contortae*)

Character	*P. matthewsii*	*P. contorta* ssp. *bolanderi*	*P. contorta* ssp. *contorta*	*P. contorta* ssp. *latifolia*	*P. contorta* ssp. *murrayana*
Geographic location	Northern Yukon	Northern California coast	Coastal mountains from British Columbia to Oregon	Northern Canada through Rocky Mountains to Colorado	Southwestern Washington to northern Baja California, Mexico
Cone shape	Ovoid to conical	Conical, curved	Conical, curved	Conical, curved	Ovoid to conical
Cone base	Symmetrical	Reflexed, asymmetrical	Reflexed, asymmetrical	Reflexed, asymmetrical	Reflexed, asymmetrical
Apophyses	Flattened	Protuberant to nearly flattened	Protuberant to flattened	Protuberant	Protuberant to flattened
Relative scale thickness	Thin, lightweight	Thick, heavy	Thick, moderately heavy	Thick, heavy	Thin, lightweight
Peduncle present	Yes	No	No	No	No or nearly absent
Cone serotiny	Yes	Yes	No	Yes	No

Note. Data from samples donated by A. Liston, Oregon State University; University of Alberta Herbarium; Critchfield 1957; Farjon 1984; Farjon and Styles 1997; Krüssmann 1985; Silba 1986.

and a thicker band of sclerenchyma in the cortex, similar to *P. banksiana* and *P. contorta*.

Another Tertiary species of *Pinus* described as similar to *P. contorta* is *Pinus alvordensis* Axelrod, which was described based on one winged seed (Axelrod 1944). The ovule is 2–3 mm long, elliptical in shape, and similar to the ovules of our fossil cones. However, the wing is only 10 mm long and therefore is similar to *P. contorta* but shorter than seed wings in the fossil cones from Ch'ijee's Bluff.

It is clear that the fossil cones described here have their closest affinities to *Pinus* Subsection *Contortae*, and although they most closely resemble those of extant *P. contorta*, based on internal features, the fossil cones are not similar enough, in our opinion, to be placed directly in this species despite the large variation within *P. contorta*. We have, therefore, described these cones as a new species, *Pinus matthewsii* McKown, Stockey et Schweger.

The range of *P. matthewsii* extended farther north than the present range of *P. contorta* (Critchfield and Little 1966), an indication that the late Tertiary climate was warmer in the northern Yukon than today. This idea is supported by the presence of megafossils and pollen from warm temperate species in many Tertiary deposits of similar age in the Yukon (Matthews and Ovenden 1990). The relative abundance of fossil cones similar to those discussed here is low in arctic and subarctic regions because few cones have been found and collected in any of the northern localities. In addition, only small amounts of *P. contorta*–like pollen exist in the Tertiary sediment samples from the entire basin area (Matthews and Ovenden 1990). *Pinus monticola*–like and *Picea glauca*–like pollen and cones are far more abundant at the Ch'ijee's Bluff locality, and other northern Yukon and Alaska sites, which indicates a greater occurrence of these two taxa in comparison with *P. matthewsii* (Matthews and Ovenden 1990; Ager et al. 1994; White and Ager 1994; N. Holden, personal communication, 1998; H. Schwab, personal communication, 1999).

Like *P. contorta* (Critchfield 1985), *P. matthewsii* may have been a shade-intolerant species adapted to a colonizing lifestyle. The small size of the fossil seeds with their long wings indicates a colonizing lifestyle, allowing the seed to be dispersed further by wind (Lanner 1998). The low abundance of this cone type could be a result of competition and vegetation domination by *P. glauca*–like and *P. monticola*–like Pliocene conifers and Betulaceae at the Ch'ijee's Bluff/Bluefish Basin locality. Pollen records at Ch'ijee's Bluff indicate that *Betula* pollen dominates the assemblage, with smaller amounts of *Corylus*, *Pinus*, and *Picea* (C. E. Schweger, unpublished observation).

Shaw (1914) considered oblique cone shape, short peduncle length, cone serotiny, and apophysis dimorphism to be highly advanced characteristics of *Pinus* species in the subgenus *Pinus*. He theorized that the evolutionary sequence was linear and proceeded from a dehiscent, symmetrical cone with fragile scales to one that was asymmetrical, with a reflexed base and harder tissues, and that preserved the seed internally for years before shedding. The outer scales of this curved cone also became swollen and protuberant for seed protection and resistance to weathering. Critchfield (1957) demonstrated that the subspecies of *P. contorta* may illustrate the likelihood of this sequence of cone evolution because *P. contorta* is thought to have migrated northward during the Quaternary (Critchfield 1985). Using Shaw's (1914) criteria, the southern subspecies, *P. contorta* ssp. *murrayana*, is the least evolved of the four subspecies with a northward progression of evolution because the cones become more asymmetrical and serotinous moving northward, as illustrated by the other subspecies.

Our fossil cones partially support the evolutionary ideas of Shaw (1914) because they are Tertiary and possess characters, such as a symmetrical shape, flat apophyses, long peduncle, thin scales, and little sclerenchyma in their tissues. Cones of *P. weasmae* (also from the Pliocene) demonstrate more of Shaw's derived characters (Miller 1992). The combined information provided by these two fossil species is an indication that *P. contorta*–like species were not static during the Tertiary, as previously believed, and were evolving prior to glaciation. Because both *P. weasmae* and *P. matthewsii* possess serotinous cones, it is unlikely that cone serotiny is a highly evolved characteristic of the Quaternary period, but it was present prior to Pleistocene glaciation. Critchfield (1957) also suggests that cone serotiny is not an evolutionary advancement but rather a response to environmental factors, as appears to be the case with the most northern subspecies, *P. contorta* ssp. *latifolia*, in response to fire. The presence of large amounts of sclerenchyma in pines of Subsection *Contortae* (Shaw 1914), however, may make them resistant to colder temperatures. *Pinus matthewsii* cones from the Yukon are not as sclerified as those of other pines in Subsection *Contortae*. *Pinus weasmae* from Idaho, however, shows abundant cortical sclerenchyma. Miller (1992) also notes that the abraded cone surface of *P. weasmae* shows that this cone was transported a long distance before preservation and suggests that this species grew in the mountains near the basin of deposition.

Critchfield (1985) proposed that the curvature observed in *P. contorta* cones is from genetic mixing with *P. banksiana* during interglacial periods, rather than evolution from symmetry to asymmetry, as Shaw (1914) suggested. *Pinus banksiana* and *P. contorta* are thought to have diverged sometime during the Pleistocene or, perhaps, in the late Tertiary (Critchfield 1984). The fossil cones from Ch'ijee's Bluff indicate that this divergence probably occurred much earlier than the Pleistocene because they are not as similar to those of *P. banksiana*. Because of the presence of some symmetrical cones of *P. banksiana* in eastern North America, however, it is possible that *P. matthewsii* also represents an ancestor to both *P. banksiana* and *P. contorta*, and the Quaternary produced very large changes in the cone morphology of *P. banksiana*. Without further fossil evidence, however, the Tertiary history of *P. banksiana* and *P. contorta* and the time of divergence between the two species is merely speculative.

Millar (1998) suggested that during the Eocene, *Pinus* subgenus *Pinus* Subsection *Contortae* was divided into northern and southern refugia, with the extant lineages of *P. banksiana* and *P. contorta* originating in the northern refugium. At the onset of glaciation during the Pleistocene, pines and other taxa were displaced by ice, and the pine habitat became fragmented, isolating populations of pines geographically and genetically in ice-free refugia (Critchfield 1985). The Quaternary is considered to be a stressful period for pines resulting in the acquisition of many of the characters seen in extant species of *Pinus*, and it is during this time period that *P. contorta* is thought to have evolved some of its distinctive geographic variations (Critchfield 1985). Further study of late Tertiary pinaceous conifers is needed to determine whether a species such as *P. matthewsii* extended further south prior to Pleistocene glaciation, where it may have survived in a refugium.

The study of the fossil history of Pinaceae is constrained by a number of factors, including availability of suitable outcrops with fossil material, the proximity of paleobotanists to the material, and the quality of fossil preservation. Comparisons of extinct taxa to extant species and speculation on their migration patterns are equivocal until more careful work is done. Only by close morphological and anatomical studies of fossil pines with comparative data from living species can we identify taxa with some degree of certainty and begin to assess their biogeography.

Acknowledgments

We would like to thank Aaron Liston, Oregon State University, for providing cone collections of *Pinus contorta*; Charles N. Miller, Jr., University of Montana, for helpful discussion and use of the conifer reference collection; John N. Owens, University of Victoria, for helpful discussion; and John V. Matthews, Jr., Geological Survey of Canada, for field assistance, encouragement, and helpful discussion. This work was supported in part by Natural Sciences and Engineering Research Council of Canada grants A-6908 to R. A. Stockey and 823-98 to C. E. Schweger.

Literature Cited

Ager TA, JV Matthews, W Yeend 1994 Pliocene terrace gravels of the ancestral Yukon River near Circle, Alaska: palynology, palaeobotany, palaeoenvironmental reconstruction and regional correlation. Quat Int 22/23:185–206.

Axelrod DI 1944 The Alvord Creek flora. Pages 225–262 *in* RW Chaney, ed. Pliocene floras of California and Oregon. Byrd, Richmond, Va. 407 pp.

Critchfield WB 1957 Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation Publication 3. Harvard University, Cambridge, Mass. 118 pp.

——— 1984 Impact of the Pleistocene on the genetic structure of North American conifers. Proceedings of the Eighth North American Forest Biology Workshop (Logan, Utah, July 30–August 1, 1984). Utah State University, Logan. 196 pp.

——— 1985 The late Quaternary history of lodgepole and jack pines. Can J For Res 15:745–772.

Critchfield WB, EL Little 1966 Geographic distribution of pines of the world. US Dep Agric For Serv Misc Publ 1991. 97 pp.

Duk-Rodkin A 1999 Glacial limits of Yukon Territory. Indian and northern affairs Canada geoscience map 1999-2. Geol Surv Can Open File 3694, scale 1 : 1,000,000.

Farjon A 1984 Pines: drawing and descriptions of the genus *Pinus*. Brill & Backhuys, Leiden.

Farjon A, BT Styles 1997 *Pinus* (Pinaceae). New York Botanical Garden, Bronx, N.Y. 291 pp.

Fyles JG, LV Hills, JV Matthews, R Barendregt, J Baker, E Irving, H Jette 1994 Ballast Brook and Beaufort Formations (late Tertiary) on northern Banks Island, Arctic Canada. Quat Res 22/23:141–171.

Hale RM 1985 A Pleistocene/Pliocene pollen record, Porcupine River, northern Yukon. Honors thesis. University of Alberta. 30 pp.

Holden NA 1998 Description of a fossil *Pinus* from the Pliocene of Ch'ijee's Bluff, Yukon Territory, Canada. Undergraduate thesis. University of Alberta.

Hughes OL 1970 Surficial geology of northern Yukon Territory and northwestern district of MacKenzie, Northwest Territories. Geol Surv Can Pap 69-36:1–11.

Krüssmann G 1985 Manual of cultivated conifers. Timber, Portland, Oreg. 361 pp.

Lanner RM 1998 Seed dispersal in *Pinus*. Pages 281–295 *in* DM Richardson, ed. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge. 527 pp.

Lichti-Federovich S 1974 Palynology of two sections of Late Quaternary sediments from the Porcupine River, Yukon Territory. Geol Surv Can Pap 74-23:1–6.

Little EL, WB Critchfield 1969 Subdivisions of the genus *Pinus* (pines). US Dep Agric For Serv Misc Publ 1144. 51 pp.

Matthews JV, LE Ovenden 1990 Late Tertiary macrofossils from localities in Arctic/Subarctic North America: a review of the data. Arctic 43:364–392.

Millar CI 1998 Early evolution of pines. Pages 69–91 *in* DM Richardson, ed. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge. 527 pp.

Miller CN 1976 Early evolution in the Pinaceae. Rev Palaeobot Palynol 21:101–117.

——— 1992 Structurally preserved cones of *Pinus* from the Neogene of Idaho and Oregon. Int J Plant Sci 153:147–154.

Price RA, A Liston, SH Strauss 1998 Phylogeny and systematics of *Pinus*. Pages 49–68 *in* DM Richardson, ed. Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge. 527 pp.

Schorn HE 1994 A preliminary discussion of fossil latches (*Larix*, Pinaceae) from the Arctic. Quat Int 22/23:173–184.

Schwab HC, RA Stockey, CE Schweger 2000 Ovulate cones of *Picea* from the lower Pliocene Ch'ijee's Bluff, Yukon Territory, Canada. Am J Bot 87(suppl):77.

Schweger CE 1989 The Old Crow and Bluefish Basins, northern Yukon: development of the Quaternary history. Pages 30–33 *in* LD Carter, TD Hamilton, JP Galloway, eds. Late Cenozoic history of the interior of Alaska and the Yukon. US Geol Surv Circ 1026.

Shaw GR 1914 The genus *Pinus*. Publications of Arnold Arboretum, no. 5. Riverside, Cambridge, Mass. 96 pp.

Silba J 1986 Encyclopaedia Coniferae. Phytologia memoirs, no. 8. H. N. Moldenke and A. L. Moldenke, Corvallis, Oreg. 217 pp.

Westgate J, CE Schweger, A Sandu, R Morlan, J Matthews 1995 Tephrochronological, paleomagnetic and paleoenvironmental studies of late Cenozoic deposits in northern Yukon, Canada. Geol Soc Am Abstr Program.

Wheeler EA, CG Arnette Jr 1994 Identification of Neogene woods from Alaska-Yukon. Quat Int 22/23:91–112.

White JM, TA Ager 1994 Palynology, paleoclimatology and correlation of middle Miocene beds from Porcupine River (locality 90-1), Alaska. Quat Int 22/23:43–77.