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TAXODIACEOUS POLLEN CONES FROM THE EARLY TERTIARY OF BRITISH COLUMBIA, CANADA

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Two permineralized conifer pollen cones have been identified from the Appian Way locality on the east coast of Vancouver Island, British Columbia. These cones, found in marine calcareous nodules with invertebrates, are Eocene in age and have been studied with the cellulose acetate peel technique. Cones are small, terminal, and globose, with helically arranged subtending leaves, ensheathing leaves, microsporophylls, and pollen sacs with enclosed pollen grains. Peltate microsporophylls have a distal lamina with three abaxial pollen sacs. Pollen grains are small, subspherical, nonsaccate, and papillate, with a distal leptoma and proximal orbicules. Phyllotaxy of subtending leaves and microsporophylls, number of pollen sacs per microsporophyll, and ultrastructure of pollen grains are similar to those of the taxodiaceous Cupressaceae. These cones have closest similarities to *Athrotaxis*, *Cunninghamia*, *Sequoia*, *Sequoiadendron*, *Taiwania*, the extinct *Sewardiodendron laxum* (*sensu* Yao et al.), and *Athrotaxites berryi*. However, they have a combination of characters that make these cones unique among taxodiaceous conifers. Therefore, a new genus and species are described as *Homalcoia littoralis* Hernandez-Castillo, Stockey et Beard. These cones show a novel combination of characters within the Cupressaceae that extends our understanding of the family and shows the presence of another extinct taxodiaceous genus in the North American Eocene.

Keywords: conifer, Cupressaceae, Eocene, pollen cone, Taxodiaceae.

Introduction

Taxodiaceous conifers have an extensive fossil record throughout the Mesozoic and Cenozoic. Although there are many species described, only a few of these include, or are based on, pollen cones. Most taxodiaceous pollen cones have been described from compression/impressions from North American, European, and Asian localities that range in age from Jurassic to Tertiary (Harris 1943; Arnold and Lowther 1955; Christophel 1976; Miller and LaPasha 1983; Srinivasan and Friis 1989; Van Konijnenburg-Van Cittert and Van der Burgh 1989; Aulenback and LePage 1998; Yao et al. 1998; Kvaček 1999, 2002; Stockey et al. 2001). Permineralized pollen cones are extremely rare and have been described from the Middle Eocene Princeton chert of British Columbia (Rothwell and Basinger 1979), the Upper Cretaceous of Drumheller, Alberta (Serbet and Stockey 1991), and the Miocene of Hokkaido, Japan (Matsumoto et al. 1997).

In this article we describe a new species of taxodiaceous Cupressaceae based on pollen cones. These cones are compared with living and fossil taxa of the Cupressaceae s.l. and show affinities to the taxodiaceous group (former Taxodiaceae) based on morphology, anatomy, and pollen ultrastructure.

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Material and Methods

The two pollen cone specimens were recovered from the Appian Way locality on the shore at Oyster Bay. This locality is situated south of Campbell River, British Columbia, at 49°56′00″N 125°11′15″W, UTM 10U CA 433331, on the east coast of Vancouver Island (fig. 1), on the northern periphery of the Tertiary Georgia Basin (Mustard and Rouse 1994). Abundant permineralized plant fossils, gastropods, echinoderms, and bivalves are found in large calcareous nodules embedded in a graywacke matrix representing a shallow marine environment (J. W. Haggart, personal communication, 2003). Pollen from the site indicates both late Paleocene and early Eocene ages (A. R. Sweet, personal communication, 1997). Characteristic invertebrates, decapods, and shark teeth indicate that the calcareous nodules are of Eocene age (Haggart et al. 1997). The stratigraphy of the area is currently being reexamined (A. R. Sweet and J. W. Haggart, personal communication, 2004).

Nodules were slabbed and studied using the cellulose acetate peel technique (Joy et al. 1956). Because of their tendency to crack, individual slabs were reinforced with a mixture of half Poly underlay and half Poly filla (Lepage, Brampton, Ontario), and surfaces were infiltrated with Elmer's Super Fast epoxy (Elmer's Products Canada, Brampton, Ontario), placed under vacuum for 1–2 min, and then dried at room temperature before peeling. Peels were mounted on microscope slides in Eukitt (O. Kindler, Freiburg, Germany) mounting medium.

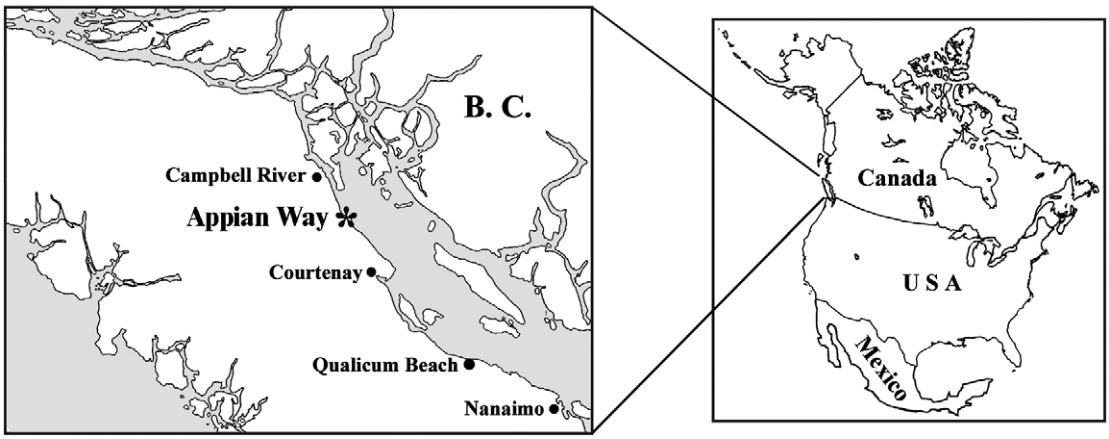

Fig. 1 Appian Way locality, Vancouver Island; locality indicated by an asterisk

Pollen grains were extracted using a modified Daghlian and Taylor (l979) technique from deeply etched peels mounted on filter paper (FSLW 01300) by dissolving the peels in a stainless steel Millipore filter (Millipore, Bedford, MA) with acetone under a vacuum. The filter paper with attached pollen was mounted on specimen stubs with double-sided tape and coated with 100 Å of Au on a Nanotek sputtercoater. Specimens were examined on a JEOL 6301 FXV SEM at 5 kV. Digital images of peels were obtained with a Microlumina (Leaf Systems, Bedford, MA) digital scanning camera and a PowerPhase (Phase One A/S, Frederiksberg, Denmark) digital camera. Files were processed using Adobe Photoshop 6.0. All specimens are housed in the University of Alberta Paleobotanical Collection.

Systematic Description

Order—*Coniferales*

Family—*Cupressaceae*

Genus—Homalcoia *gen. nov.*

Species—Homalcoia littoralis *sp. nov.*
(fig. 2A–2C, 2F, 2G)

Generic diagnosis. Pollen cones small, terminal, globose. Cones simple, with helically arranged subtending and ensheathing leaves and microsporophylls. Subtending leaves with epidermis, hypodermis, spongy mesophyll, and single resin canal adaxial to vascular bundle. Ensheathing leaves thin. Microsporophylls with abaxial heel and inflated apex. Pollen sacs three, abaxial, ellipsoidal. Pollen grains subspherical, nonsaccate, papillate, with distal leptoma and proximal orbicules.

Specific diagnosis. Characters of species those of genus. Cones up to 2 mm in diameter and 2.1 mm long; cone axis with up to seven resin canals. Subtending leaves with thick cuticle, single layered epidermis of rectangular thin-walled cells; hypodermis a single layer of thick-walled cells; spongy mesophyll of polygonal thin-walled cells; large central resin canal adaxial to vascular bundle. Microsporophylls with inflated apex, elongate laminar tip, and prominent keel; stalk with one central resin canal. Pollen sacs abaxial and ellipsoidal. Pollen grains small (11–20 μm), nonsaccate, subspherical with short papilla (2–3 μm), and distal leptoma; distal surface smooth; proximal surface orbiculate, and orbicules with small, echinate projections.

Holotype. AW 292 E top, figure 2*A*–2*C*, 2*F*, 2*G*; figure 3C.

Paratype. AW 394 F top, figure 2*D*, 2*E*; figure 3*A*, 3*B*, 3*D*–3*F*.

Locality. Appian Way locality, south of Campbell River at 49°56′00″N 125°11′15″W; UTM 10U CA 433331.

Etymology. Generic name honors the nearby Homalco First Nation, part of the Coast Salish People, whose culture relates to the wildlife and the land they share with it. The specific epithet *littoralis* refers to the seashore Appian Way locality.

Description

The two pollen cones from Appian Way are small and globose, up to 2.1 mm long and 2 mm wide (fig. 2*A*–2*D*). Cones are located at the tip of a branch (table 1) with subtending vegetative leaves, but the rest of the vegetative branch is not preserved (fig. 2*A*, 2*B*). Cone axis is 0.6 mm long and 0.3 mm in diameter, with up to seven resin canals at the base and bears helically arranged, basal, subtending leaves (fig. 2*A*, 2*B*). These leaves intergrade with delicate ensheathing leaves that surround the cone (fig. 2*A*, 2*B*). At least three series of subtending and ensheathing leaves can be seen (fig. 2*A*–2*D*).

Subtending leaves are slightly rhomboidal to triangular or ellipsoidal in cross section (fig. 2*A*–2*F*). The epidermis is single layered, composed of rectangular cells 10.3–24.7 μm long and 6.2–17.6 μm wide in cross sections that are covered by a thick cuticle (fig. 2*E*, 2*F*). The hypodermis is a single layer of thick-walled polygonal cells with dark contents 10.3–24.7 × 10.3–29.9 μm in cross section (fig. 2*E*, 2*F*). The mesophyll is composed of thin-walled, polygonal, parenchymatous cells 6.2–47.4 × 8.2–55.6 μm in diameter (fig. 2*A*–2*C*, 2*E*, 2*F*). A large central resin canal is located adaxial to

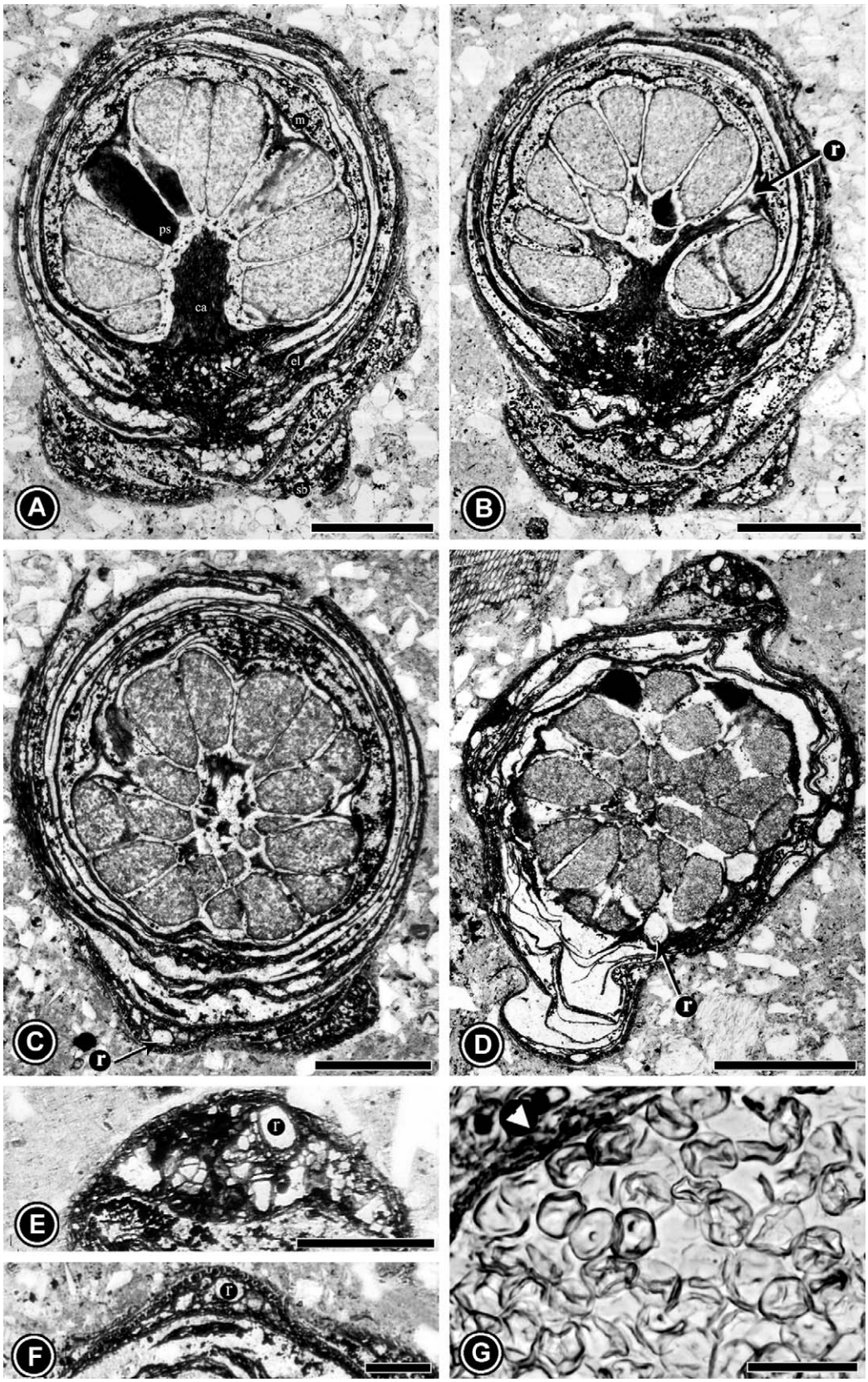

Fig. 2 *Homalcoia littoralis* pollen cones. *A*, Longitudinal section showing subtending leaves (*sb*), ensheathing leaves (*el*), cone axis (*ca*), and microsporophyll (*m*) with central resin canal, upturned distal tip, and adaxial pollen sacs (*ps*). Holotype AW 292 E top #23, scale = 0.5

the vascular bundle in each subtending leaf (fig. 2*D*, 2*E*). Resin canals range from 80 to 146 μm in diameter. These canals have an epithelial lining that is composed of thin-walled parenchymatous cells 8.2–16.5 μm long and 4.1–5.1 μm wide in cross section (fig. 2*E*). The vascular bundles in scale leaves are poorly preserved, with an occasional tracheid visible in some sections (fig. 2*A*–2*F*).

Ensheathing leaves are scalelike, thin, and delicate, 0.8–0.9 mm long (fig. 2*A*–2*D*). Epidermal cells are often found in both longitudinal and cross sections. However, the rest of the tissues are not usually preserved (fig. 2*A*–2*D*).

Microsporophylls are helically arranged and peltate with a stalk that has a large central resin canal (table 1; fig. 2*A*–2*D*). There is a distal lamina with an inflated apex, an adaxial upturned tip, and an abaxial heel (fig. 2*A*, 2*B*). Each microsporophyll bears three pollen sacs (table 1; fig. 2*A*–2*D*). Pollen sacs are ellipsoidal with walls composed of elongate to rectangular thick-walled cells (fig. 2*G*).

Abundant pollen grains are present in all of the pollen sacs (fig. 2*A*–2*D*, 2*G*; fig. 3*A*). Pollen is small, 11–20 μm in equatorial diameter (average 16.5 μm), subspherical, nonsaccate, with a short (2–3 μm long) and sharply bent distal papilla (table 1; figs. 2*G*, 3*B*–3*D*). The distal surface is smoother than the proximal surface, which is covered by a large number of orbicules (fig. 3*B*–3*E*). Orbicules range from 0.2 to 0.5 μm in diameter. Individual orbicules are highly ornamented, showing many small echinate projections (fig. 3*E*, 3*F*).

Discussion

Small terminal globose pollen cones with helically arranged subtending leaves, ensheathing leaves, and peltate microsporophylls bearing three pollen sacs are similar to cones in taxodiaceous Cupressaceae (table 1; Stockey et al. 2004). Small nonsaccate papillate and orbiculate pollen is also similar to the pollen described in these taxa (Erdtman 1957; Kurmann 1992, 1994). The pollen cones from Appian Way have characters that clearly place them within the taxodiaceous Cupressaceae (table 1). However, the combination of characters seen is unique, and they clearly do not belong to any previously described taxon. Therefore, we have described these cones in a new genus and species: *Homalcoia littoralis* Hernandez-Castillo, Stockey et Beard.

The helical arrangement of subtending leaves, ensheathing leaves, and microsporophylls of the Appian Way pollen cones resembles that in living *Athrotaxis cupressoides* Don, *Cryptomeria japonica* (Linn. f.) D. Don, *Cunninghamia lanceolata* (Lamb.) Hook, *Glyptostrobus pensilis* (Staunt.) K. Koch, the species of *Taxodium* Rich., *Sequoia sempervirens* (D. Don) Endlicher, *Sequoiadendron giganteum* (Lindl.) Buchholz, and *Taiwania cryptomeroides* Hayata (table 1). The same arrangement is seen in fossil pollen cones of *Athrotaxites berryi* Bell, *Drumhellera kurmanniae* Serbet et Stockey, *Glyptostrobus rubenosawaensis* Matsumoto, Ohsawa, Nishida et Nishida, *Sewardiodendron laxum* Florin (*sensu* Yao et al. 1998), and *Taxodium wallisii* Aulenback et LePage (table 1). In contrast, living and extinct species of *Metasequoia* S. Miki and extinct *Parataxodium wigginsii* Arnold et Lowther display either decussate or decussate/helical arrangement of both subtending leaves and microsporophylls (table 1).

Subtending leaves of the Appian Way cones are characterized by an abaxial hypodermis, spongy mesophyll, and a large central resin canal that is in contact with the vascular bundle. This is similar to that described in *Metasequoia milleri* Rothwell et Basinger, *D. kurmanniae*, and *G. rubenosawaensis* (Rothwell and Basinger 1979; Serbet and Stockey 1991; Matsumoto et al. 1997). However, the hypodermis in *D. kurmanniae* is much thicker than that seen in the Appian Way cones (Serbet and Stockey 1991). In *G. rubenosawaensis* (Matsumoto et al. 1997), preservation of subtending leaves is poor and does not allow a close comparison with our fossil leaves. Therefore, subtending leaves in *M. milleri* are most similar to those found in the cones of Appian Way with a thin zone of abaxial hypodermis (Rothwell and Basinger 1979).

The number of pollen sacs in the Appian Way cones is three. In pollen cones of taxodiaceous Cupressaceae there is variability in the number of pollen sacs per microsporophyll (table 1). Taxa within this group that typically show three pollen sacs per microsporophyll include *A. cupressoides*, *C. lanceolata*, and living and extinct species of *Metasequoia*, *Sequoia*, *Sequoiadendron*, *Sewardiodendron laxum* (*sensu* Yao et al. 1998), and *Taiwania* (table 1). Taxa such as *Sequoia* and *Sequoiadendron* usually have two or three pollen sacs (A. Farjon, personal communication, 2004). However, up to five pollen sacs per microsporophyll have been reported (Pilger 1926; Silba 1986; Watson and Eckenwalder 1993), thus adding variation to the number of pollen sacs in these genera. Many other taxa also have three pollen sacs, but this number is not the most common number for individual species. For example, *Glyptostrobus pensilis* has two to nine pollen sacs, with four to six being the most common number (table 1; A. Farjon, personal communication, 2004). In contrast, living and extinct species of *Metasequoia* always have three pollen sacs per microsporophyll, but their phyllotaxy is quite different from that of the Appian Way cones (table 1). Therefore, *A. cupressoides*, *C. lanceolata*, and *Taiwania* seem to be the closest in this character to *Homalcoia* cones.

Nonsaccate, papillate, and orbiculate pollen grains are commonly found among taxodiaceous conifers (Erdtman 1957, 1965; Ho and Sziklai 1973). Differences among taxa are based mostly on the size of grains, shape and size of the distal papilla, and pollen wall ultrastructure (Erdtman 1957;

Fig. 2 (*Continued*) mm. *B*, Longitudinal section of cone showing subtending leaves with vascular bundle and resin canal and microsporophylls with large central resin canal (*r*). Holotype AW 292 E top #4, scale = 0.5 mm. *C*, Oblique cone section showing helically arranged microsporophylls and pollen sacs. Holotype AW 292 E top #24, scale = 0.5 mm. *D*, Cross section of cone showing four subtending leaves with resin canals (*r*), thin ensheathing leaves, and microsporophylls with attached pollen sacs. Paratype AW 394 F top #3, scale = 0.5 mm. *E*, Cross section of subtending leaf showing epidermis, hypodermis, mesophyll, and central resin canal with epithelial lining. Paratype AW 394 F top #3, scale = 0.2 mm. *F*, Cross section of subtending leaf showing hypodermis, mesophyll, and central resin canal. Holotype AW 292 E top #24, scale = 0.2 mm. *G*, Longitudinal section of pollen sac showing wall (arrowhead) and numerous nonsaccate and papillate pollen grains. Holotype AW 292 E top #24, scale = 100 μm.

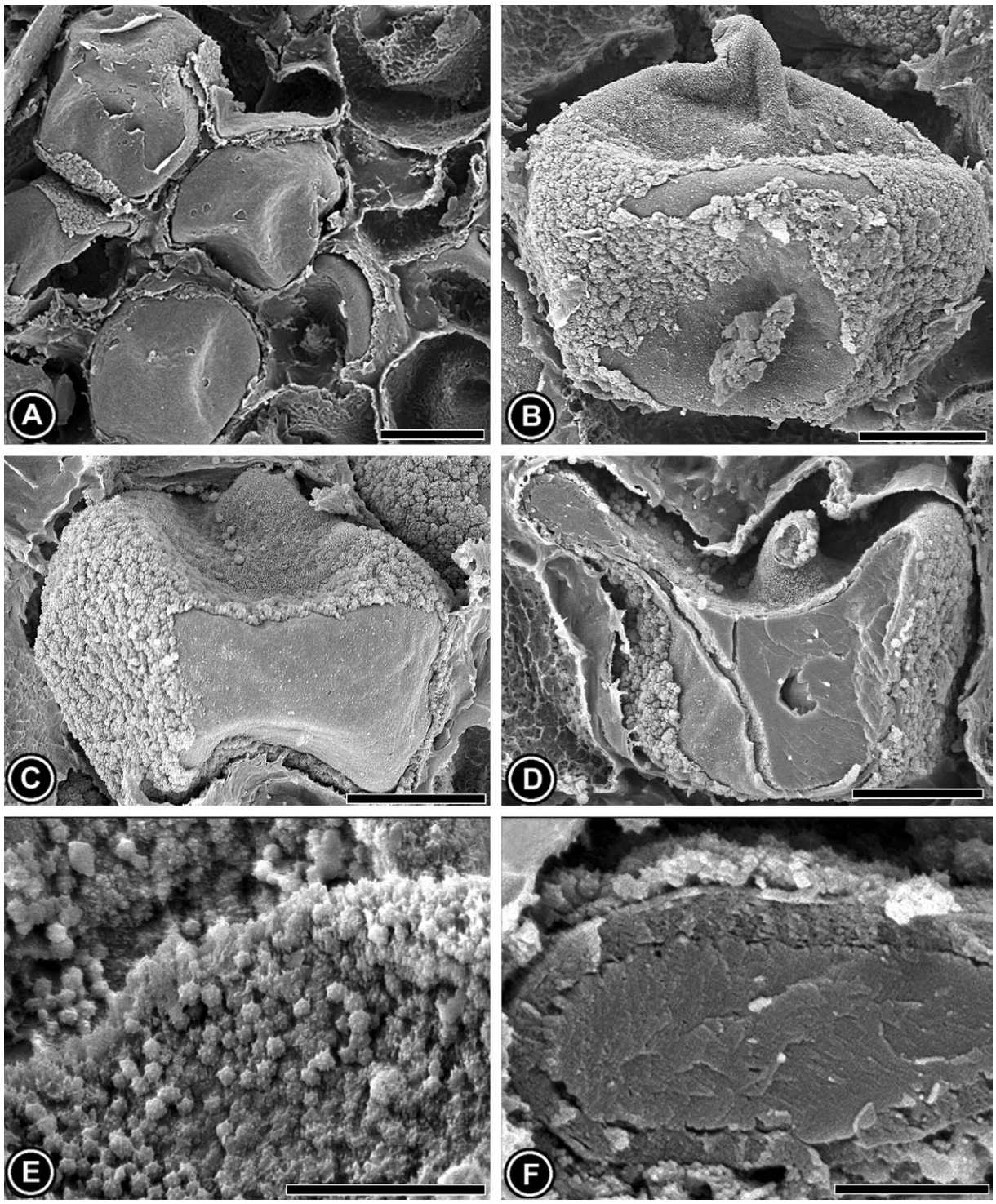

Fig. 3 *Homalcoia littoralis* SEM pollen grains. *A*, General view. Paratype AW 394 F top #6, scale = 10 μm. *B*, One pollen grain showing distal papilla and orbicules. Paratype AW 394 F top #33, scale = 5 μm. *C*, Pollen grain with distal papilla, orbicules on proximal end. Holotype AW 292 F top #28, scale = 5 μm. *D*, Longitudinal section of grain showing proximal orbicules and smooth distal surface with papilla. Paratype AW 394 F top #33, scale = 5 μm. *E*, Orbicules on proximal surface. Paratype AW 394 F top #6, scale = 2 μm. *F*, Section of grain showing exine with overlying orbicules. Paratype AW 394 F top #33, scale = 1 μm.

Table 1

Comparison of *Homalcoia littoralis* Hernandez-Castillo, Stockey et Beard to Extinct and Extant Taxodiaceous Pollen Cones

Taxa	Cone attachment	Arrangement		Number of pollen sacs	Pollen grains		
		Subtending leaves	Microsporophylls		Distal papilla[a]	Range (μm)	Mean (μm)
Homalcoia littoralis	Terminal on regular shoots	Helical	Helical	3	Short, sharply bent	11–20	15.8
Athrotaxites berryi[b]	Terminal on regular shoots		Helical	2–3	...	...	...
Athrotaxis cupressoides	Terminal on regular shoots	Helical	Helical	(2–) 3 (–4)	Very short	27–30	...
Cryptomeria japonica	Terminal and lateral on regular shoots	Helical	Helical	(3–) 4–5 (–6)	Long, slightly bent or straight	23.9–39	...
Cunninghamia lanceolata	Terminal and lateral on regular shoots	Helical	Helical	3–4	Very short	31–54	...
Drumhellera kurmanniae[b]	Terminal and lateral on specialized shoots	Helical	Helical	2	Very short	12–16	14
Glyptostrobus pensilis	Terminal on regular shoots	Helical	Helical	(2–) 4–6 (–9)	Short, slightly or sharply bent	25.4–31.8	30.8
Glyptostrobus rubenosawaensis[b]	Terminal?	Helical	Helical	4–8	...	...	...
Metasequoia foxii[b]	Lateral on specialized shoots	Decussate	Decussate	3	...	17.5–24	...
Metasequoia glyptostroboides	Terminal and lateral on specialized shoots	Decussate	Helical	3	Very short to short, slightly or sharply bent	17.2–26.5	24.3
Metasequoia milleri[b]	Terminal and lateral on specialized shoots	Decussate	Helical	3	Short, erect	19–27	23
Metasequoia occidentalis[b]	Terminal and lateral on specialized shoots	Decussate	Decussate?	3	...	...	...
Parataxodium wigginsii[b]	Terminal and lateral on specialized shoots	Decussate	...	...	...	...	...
Sequoia sempervirens	Terminal on regular shoots	Helical	Helical	(2–) 3 (–5)	Long, slightly or sharply bent	30.5–40.6	34.7
Sequoiadendron giganteum	Terminal on regular shoots	Helical	Helical	(2–) 3 (–5)	Very long, slightly or sharply bent	25.4–30.5	28.4
Sewardiodendron laxum[b]	Terminal on regular shoots	Helical ?	Helical	3	Very short	37.5–56	...
Taiwania cryptomeroides	Terminal on regular shoots	Helical	Helical	(2–) 3 (–4)	Very short	20–31	...
Taxodium distichum, *Taxodium mucronatum*	Terminal and lateral on specialized shoots	Helical	Helical	(2–) 4–6 (–10)	Very short to short, bent sharply	22.9–27.9	25.6
Taxodium wallisii[b]	Terminal and lateral on regular shoots	...	Helical	5–9	Very short	14–22.5	20

Note. Table modified from Serbet and Stockey (1991). Additional data from Veitch and Kent (1900), Pilger (1926), Dallimore and Jackson (1931), Harris (1943), Erdtman (1957, 1965), Ho and Sziklai (1973), Liu and Su (1983), Miller and LaPasha (1983), Silba (1986), Srinivasan and Friis (1989), Aulenback and LePage (1998), Yao et al. (1998), Fu et al. (1999), Kunzmann (1999), and A. Farjon (personal communication, 2003, 2004).

[a] Very short protuberance <2μm; short protuberance 2–3 μm; long protuberance 3–4 μm; very long protuberance >4 μm.

[b] Extinct taxa.

Liu and Su 1983; Kurmann 1992, 1994). The pollen of *Homalcoia* is most likely mature, as the grains are not borne in tetrads, they are fully formed, and they have large numbers of orbicules on the proximal surface (fig. 3*A*–3*F*). *Homalcoia* grains contrast with immature pollen grains observed in other taxa (e.g., *Taiwania*), where tetrads of pollen grains with concave distal faces have been described (Liu and Su 1983).

Although *Homalcoia* pollen grains are clearly like those of Cupressaceae s.l., the size of grains and size and shape of the distal papilla are different from other known taxa (table 1). The Appian Way cones have some of the smallest pollen grains known (average = 15.8 μm) in living or fossil taxodiaceous conifers (table 1). Most pollen grains in taxodiaceous conifers range from 17 to 39 μm (table 1). Only the extinct *D. kurmanniae* have similar size pollen grains (average = 14 μm) to those of the Appian Way (table 1, Serbet and Stockey 1991). The distal papilla in *Homalcoia* pollen grains is short (2–3 μm), sharply bent, and most similar to those seen in living *Glyptostrobus*, *Metasequoia*, and *Taxodiun* species (table 1). However, the overall size of pollen grains and papillae differ from those of *Homalcoia* (Erdtman 1957, 1965; Ho and Sziklai 1973; Liu and Su 1983; Kurmann 1992, 1994).

Homalcoia littoralis has a unique combination of characters within the taxodiaceous Cupressaceae (table 1). This new species is most similar to taxa with helically arranged subtending leaves and microsporophylls with three pollen sacs per microsporophyll, such as *Athrotaxis cupressoides*, *Cunninghamia lanceolata*, *Sequoia*, *Sequoiadendron*, *Taiwania*, and the fossils *Sewardiodendron laxum* (*sensu* Yao et al. 1998) and *Athrotaxites berryi* (table 1). However, all these taxa have larger pollen grains and a smaller (*Athrotaxis*, *Cunninghamia*, *Sewardiodendrum*, and *Taiwania*) or larger (*Sequoia* and *Sequoiadendron*) bent distal papilla than that in pollen of *H. littoralis* (table 1). It is clear that *Homalcoia* belongs to this group, but its systematic relationships are uncertain, and its affinities will be known only when a whole plant reconstruction of this taxon is completed.

Homalcoia littoralis is only the fourth permineralized pollen cone of taxodiaceous Cupressaceae so far described in the fossil record. While *Homalcoia* shares a number of characters with *Drumhellera kurmanniae* from the Cretaceous of Alberta, *Metasequoia milleri* from the Eocene of Princeton, British Columbia, and *Glyptostrobus rubenosawaensis* from the Miocene of Hokkaido, it differs in its combination of characters. These three taxa have been described as whole plants based on isolated and attached organs as well as internal anatomy (Rothwell and Basinger 1979; Matsumoto et al. 1997; Serbet 1997). In addition to *Homalcoia*, seed cones of taxodiaceous Cupressaceae have also been identified at Appian Way, and since conifer vegetative remains are common, it is hoped that we will be able to reconstruct this and other conifers from this site in the near future.

Our knowledge of permineralized fossil plants from marine nodules on the west coast of North America has been increasing in the past several years. Large numbers of well-preserved plant organs have been recovered from these nodules that range in age from Lower Cretaceous to Eocene (Beard 1999; Hernandez-Castillo and Stockey 2001; Little et al. 2002; Smith and Stockey 2002; Smith et al. 2003, 2004; Stockey and Rothwell 2003). In addition to conifers, cycadeoids, ferns, and fungi, numerous angiosperms have also been identified (Beard 1999; Little et al. 2002; Rothwell and Stockey 2003; Smith et al. 2003, 2004; Stockey and Rothwell 2003). Shelf fungi represented by poroid hymenophores, described as *Appianoporites vancouverensis* Smith, Currah et Stockey, were the first fossil remains to be described from the Eocene Appian Way locality (Smith et al. 2004). *Homalcoia littoralis* is now the first vascular plant and the first of the conifers described from Appian Way. Further work at this locality is needed to reconstruct complete conifers and the paleoenvironment in which they lived.

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