SPEIRSEOPTERIS ORBICULATA GEN. ET SP. NOV. (THELYPTERIDACEAE), A DERIVED FOSSIL FILICALEAN FROM THE PALEOCENE OF WESTERN NORTH AMERICA

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An apparently exindusiate filicalean fern with radial sori, sporangia with a vertical annulus, and monolete spores occurs in Paleocene sediments ca. 57 million years old of central Alberta, Canada. Specimens are preserved as coalified compressions and show features of frond morphology and venation, sporangium morphology and dehiscence mechanism, number of spores per sporangium, and spore fine structure. Fronds have a deltoid blade region and are pinnate + pinnatifid, with fertile pinnules ranging to slightly smaller than vegetative pinnules and with simpler venation. Venation is open, with each lobe of the pinnatifid pinnule having a midvein from which laterals diverge in an alternate pattern. Laterals of vegetative pinnule lobes fork once and terminate at the margin, whereas those of fertile pinnule lobes are unbranched. Sori are round with numerous sporangia and are positioned under a vein. Each sporangium has a vertical annulus that is not interrupted by the stalk and produces ca. 64 spores. Spores are bean shaped and monolete, measuring 26–36 μm long, with exospore that is dense and sculptured by minute scabrae. Perispore is not preserved. This fern, named *Speirseopteris orbiculata* gen. et sp. nov., displays characters that are diagnostic of the highly derived filicalean families and is assigned to the Thelypteridaceae. To a lesser extent, it also resembles the Dryopteridaceae, emphasizing that modern fern genera existed among many extinct genera during the late Cretaceous and Paleogene.

Keywords: Dryopteridaceae, fern, fossil, Paleocene, Thelypteridaceae.

Introduction

Over the past 150 yr, the fossil record has yielded large numbers of Late Cretaceous and Tertiary filicalean fern specimens. The vast majority of such specimens consist of vegetative frond fragments that are preserved as coalified compressions or impressions and are to a large extent described in floristic treatments that focus primarily on descriptions of flowering plants. While some specimens of these types are fertile, easily recognized, and assigned to modern families, most are vegetative and difficult to classify. The latter specimens are often described as morphotaxa of uncertain affinities, but some are attributed to genera and families with living species. Although assignments of specimens to the more basal families with living representatives are often quite convincing, possible representatives of the most highly derived families are frequently far more difficult to identify and classify with confidence (Van Uffelen 1991; Collinson 2001; Kvaček 2001; Skog 2001).

A smaller number of studies emphasize fossil ferns from the Cretaceous and Tertiary or are based on anatomically preserved specimens or compression remains with more complete suites of systematically diagnostic characters. However, up to the present, such studies have been too few to docu-

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ment details of the third radiation of filicaleans (Rothwell 1987) or the patterns of diversification for the most species rich of living fern clades. As a result, fossil data are often routinely excluded from most contemporary analyses of fern systematics and phylogeny. This article is part of a long-term program to describe extinct species of highly derived Cretaceous and Tertiary filicalean fern plants (e.g., Rothwell and Stockey 1991; Stockey et al. 1999; Pigg and Rothwell 2001; Rothwell and Stockey 2006), to provide convincing evidence of their taxonomic relationships, and to eventually develop a record that will allow for the full integration of extinct species into comprehensive analyses of fern phylogeny.

The fern that forms the focus of the current investigation occurs in basal Tertiary deposits and is part of a wetland forest community that had the cupressaceous conifer *Metasequoia foxii* Stockey, Rothwell et Falder (Stockey et al. 2001), the betulaceous dicot *Paleocarpinus joffrensis* Sun et Stockey (Sun and Stockey 1992), an *Aphananthe*-like ulmaceous plant, and *Wardiaphyllum* Hickey (1977) as canopy trees. This fern was part of an understory that also included the dryopterid fern *Onoclea sensibilis* L. (Rothwell and Stockey 1991) and a species of *Equisetum* L. (Vavrek 2004).

The fossil fern displays a diagnostic suite of characters that allows for its recognition as a highly derived filicalean, but assignment to a family with living species is challenging. The material is described as *Speirseopteris orbiculata* gen. et sp. nov., assigned to the Thelypteridaceae and compared with the Dryopteridaceae and other derived families. Difficulties

with confidently classifying compression specimens of fossil ferns are also discussed in relation to the evolution and phylogeny of derived filicaleans.

Material and Methods

Fossils described in this study were collected from the Munce's Hill (="One-Jaw Gap" of Fox 1990) locality 9 km northeast of Red Deer, Alberta. At Munce's Hill (NW 1/4 sect. S 34, T 38, R 26, W 4), Paleocene sediments (Ti₄) are exposed along a roadcut northeast of the Canyon Ski Quarry ca. 975 m above sea level (Fox 1990; Sun and Stockey 1992). Specimens at this locality are primarily coalified compressions within nonmarine buff to light gray, medium-grained sandstones interbedded with highly fractured, finer-grained sandstones and mudstones of the Paskapoo Formation (Vavrek 2004).

Over the past 20 yr, more than 1800 specimens of the fern described in this article have been collected. Specimens were photographed with reflected light using a Microlumina digital scanning camera (Leaf Systems, Bedford, MA) mounted on a copy stand and a Phase One digital scanning camera (Phase One A/S, Frederiksberg, Denmark) mounted on a Leitz Aristophot bellows camera.

Spores were either examined using SEM directly, without maceration, or recovered from sporangia by standard coal maceration techniques, demineralized in 10% hydrochloric acid, followed by 38% hydrofluoric acid, Schultz's solution, and 10% sodium hydroxide, and rinsed in distilled water. Stubs were coated with 100 Å Au on a Nanotek sputter-coater and examined using a JEOL 6301F scanning electron microscope at 5 kV. For transmission electron microscopy, spores were fixed in OsO_4 for 2 h, dehydrated in an alcohol series, and embedded in Spurr's (1969) resin. Sections 90–100 nm thick were cut using a Reichert Ultracut E microtome. Sections were collected on formvar-coated grids, double stained with uranylacetate and lead citrate, and viewed with a Phillips EM 200 at 60 kV. All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta.

Systematics

Order—Filicales

Family—Thelypteridaceae Pichi Serm.

Genus—Speirseopteris gen. n.

Species—Speirseopteris orbiculata sp. nov.
Stockey, Lantz et Rothwell (Figs. 1–3)

Combined generic and specific diagnosis. Small fern with monomorphic or slightly dimorphic pinnules; blade deltoid, pinnate + pinnatifid, catadromous. Blade up to ca. 16 cm long; pinnules decreasing in size and complexity distally, terminating in confluent, lobed, attenuated apex. Lobed pinnules typically detached from rachis, fertile pinnules ranging to somewhat smaller than vegetative pinnules. Pinnule lobes with straight margins and bluntly pointed to rounded apex. Venation open; pinnules and pinnule lobes with straight midvein; pinnule lobes with pinnate laterals. Laterals forking

once in vegetative pinnules, unbranched in fertile pinnules, terminating at margin; basal veins meeting margin distal to sinus. Sori in two rows on pinnule lobes, orbicular and discrete, apparently exindusiate, on veins; typically with 30–40 sporangia. Sporangia with vertical annulus interrupted by stalk; spore number ca. 64. Spores ellipsoidal to bean shaped, $26–36 \times 15–24$ μm (mean = 31.26×20.83 μm) with monolete extending one-half to two-thirds spore length. Exospore dense, sculptured by minute, rounded scabrae; perispore unknown.

Holotype. Lobed pinnule that is vegetative at base and fertile at tip, UAPC-ALTA S48,028 (figs. 1f, 2c).

Paratypes. Pinnate fronds, UAPC-ALTA S26,917 (fig. 1a) and S26,929 (fig. 1b), and fertile pinnules, UAPC-ALTA S32,692 (fig. 2b) and S44,935 (fig. 2a).

Etymology. The generic name *Speirseopteris* (Speirs + pteris) is proposed in honor of the late Alice Elizabeth (Betty) Speirs, Red Deer, Alberta, whose dedication to fossil plant collecting and selfless contributions of specimens to the University of Alberta have significantly furthered paleobotanical understanding. The specific epithet *orbiculata* refers to the round sori.

Locality. Munce's Hill, a roadcut 3 km northeast of Canyon Ski Quarry (NW 1/4 sect. S 34, T 38, R 26, W 4) in central Alberta, Canada.

Stratigraphic occurrence. Paskapoo Formation.

Age. Late Tiffanian (Ti₄), Paleocene.

Description

Fronds of *Speirseopteris orbiculata* are monomorphic to slightly dimorphic, pinnate + pinnatifid (figs. 1, 2), with open dichotomous venation (fig. 1c, 1e; fig. 2b, 2c) and two rows of round sori on fertile pinnule lobes (figs. 1f, 2). Of the ca. 1800 specimens available for study, 12 consist of a rachis from which pinnatifid pinnules diverge alternately at an angle of ca. 60° (fig. 1a–1c), and the rest are dispersed pinnatifid pinnules (fig. 1d, 1e; fig. 2a, 2b). Both pinnule lobing and venation are catadromous, with a basiscopic lobe and vein consistently diverging below the first acroscopic lobe and vein (fig. 1a–1d).

Vegetative frond fragments range up to 15 cm long and consist of the dissected blade region from which the stipe and possibly the basalmost lobed pinnules are missing (e.g., fig. 1a, 1b). The largest attached basal pinnule measures 7.1 cm long. Gauging from the largest dispersed pinnules (i.e., up to 7.8 cm long and 2.6 cm wide), the largest vegetative fronds probably reached slightly more than 16 cm distal to the stipe.

The blade region is deltoid, with the largest pinnatifid pinnules at the base (fig. 1a, 1b, 1d). Progressing distally, the pinnules become successively smaller, with lobes that are decreasingly incised (fig. 1a, 1b). Toward the frond tip, the pinnules have entire margins and then are pinnatifid, grading into an attenuated tip (fig. 1d). Individual pinnules decrease in width toward the tip (fig. 1a, 1b, 1d, 1e; fig. 2b). They are deeply incised toward the base (fig. 1c), becoming less deeply lobed distally and terminating in an attenuated tip (fig. 1e). Pinnule lobes have an entire margin and a tip that ranges from bluntly pointed to rounded (figs. 1, 2).
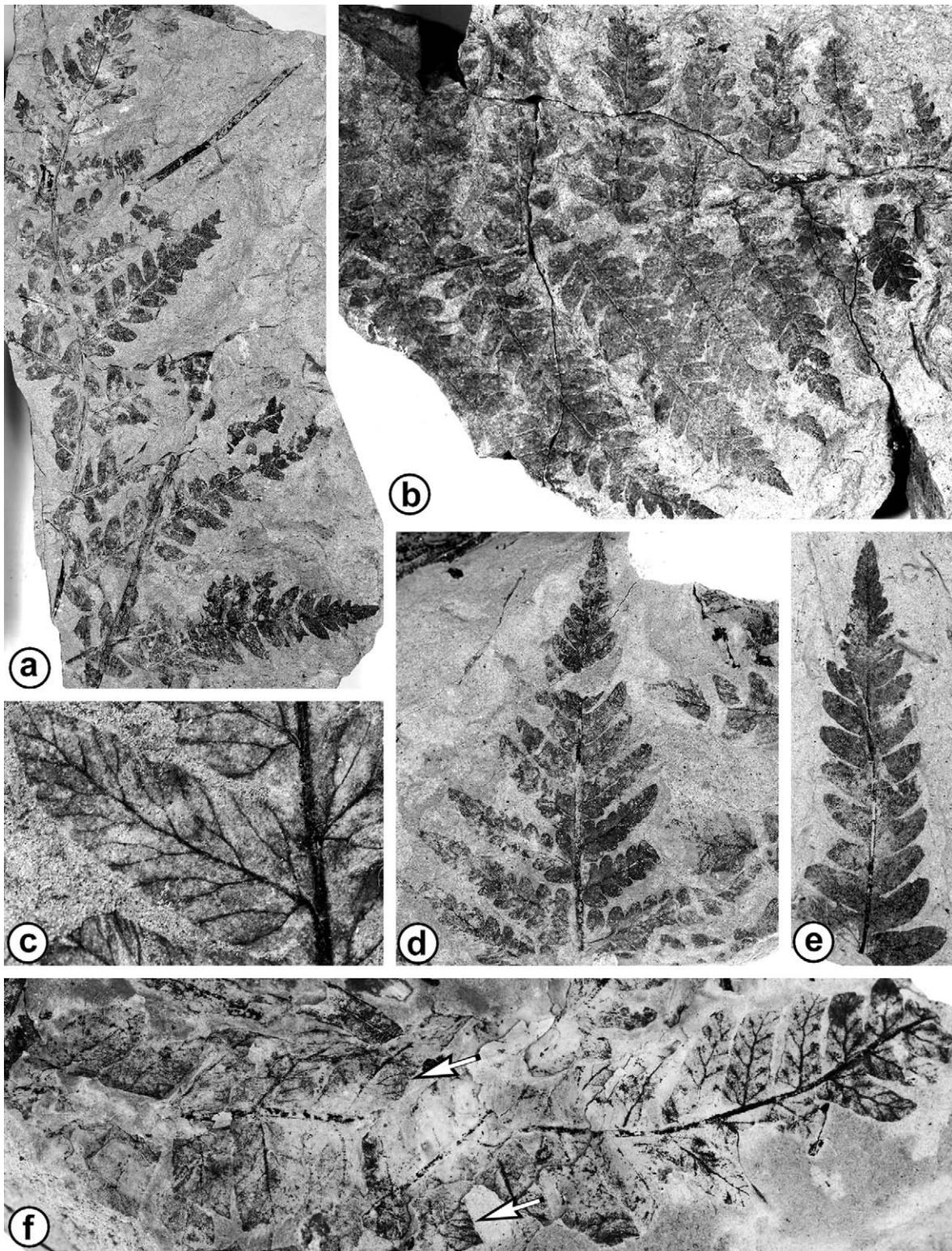
Fig. 1 *Speirseopteris orbiculata* gen. et sp. nov. *a*, Pinnate + pinnatifid vegetative frond (paratype) showing increase in pinnule size and complexity from apex to base of blade. UAPC-ALTA S26,917; ×0.9. *b*, Pinnate + pinnatifid vegetative frond (paratype) showing symmetrical blade and pinnule morphologies. UAPC-ALTA S26,929; ×1.0. *c*, Segment of pinnatifid vegetative pinnule showing shape of lobe and venation. UAPC-ALTA S44,384; ×6.0. *d*, Tip of vegetative frond showing gradation to the attenuated tip. UAPC-ALTA S59,483; ×2.0. *e*, Pinnatifid pinnule showing gradation from lobed base to attenuated tip. UAPC-ALTA S27,446; ×2.3. *f*, Pinnule (holotype) showing morphology and venation (arrows) of vegetative pinnule at base (left) and comparable features of fertile pinnule at apex (right). UAPC-ALTA S48,028; ×3.3.
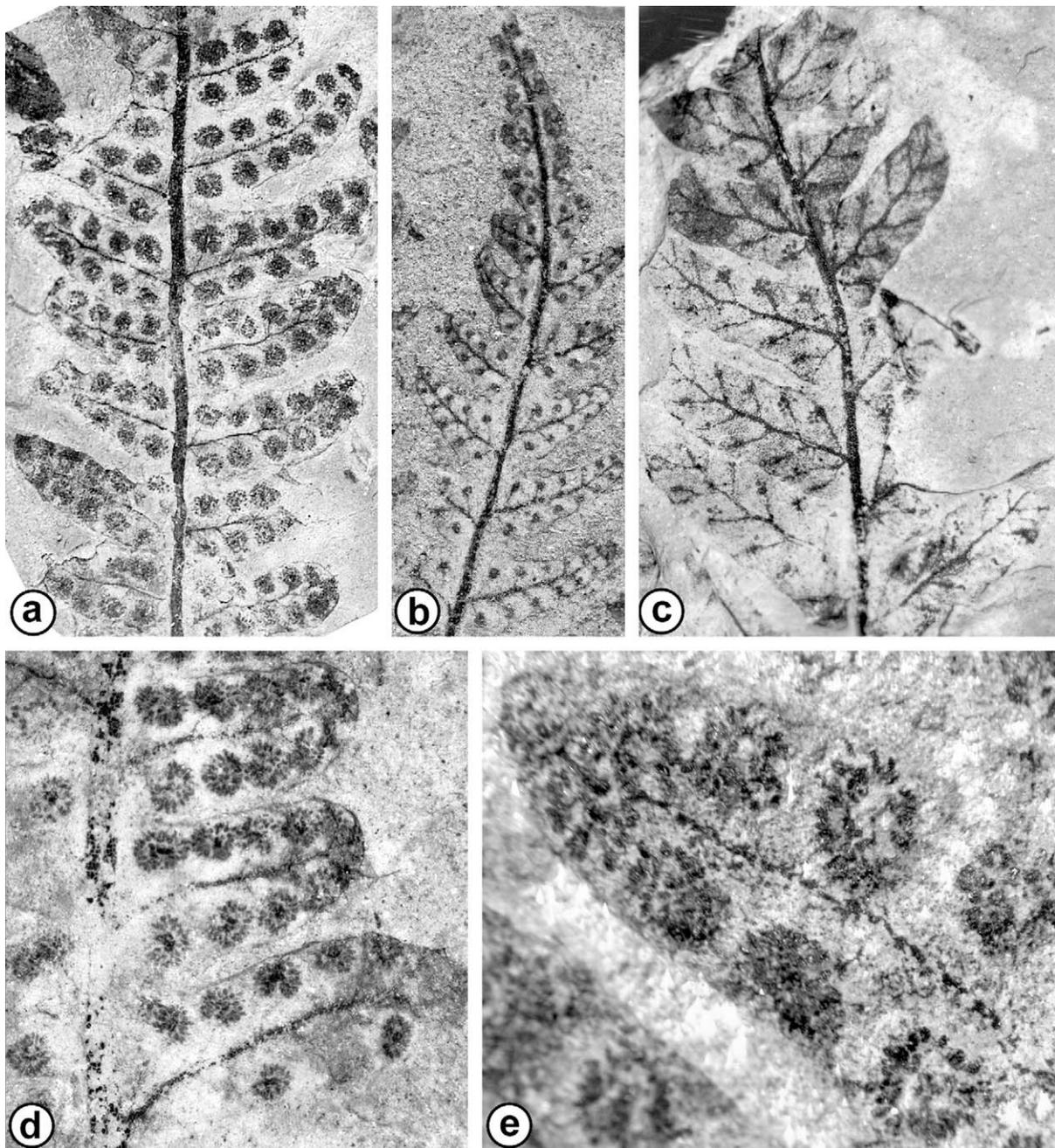
Fig. 2 *Speirseopteris orbiculata* gen. et sp. nov. Fertile pinnules. *a*, Midregion of pinnule (paratype) with two rows of large sori under veins. UAPC-ALTA S44,935; ×4.3. *b*, Fertile pinnule tip (paratype) showing morphology and distribution of small sori. UAPC-ALTA S32,692; ×5.9. *c*, Apical region of holotype pinnule showing small sori, each located under vein. UAPC-ALTA S48,028; ×6.0. *d*, Close-up of fertile lobes showing lobe shapes and sori. UAPC-ALTA S44,935; ×8.6. *e*, Close-up of fertile pinnule lobe showing two rows of discrete sori and large sorus at tip. Note that each sorus consists of numerous sporangia, each of which appears as a black dot. UAPC-ALTA S32,618; ×23.

Venation is pinnate, with a straight midvein in each pinnule and pinnule lobe. Laterals diverge from the midvein of the pinnule lobes in a subopposite to alternate arrangement. In vegetative pinnule lobes, the lateral veins fork once and extend to the margin (fig. 1*c*; fig. 1*f*, arrows). In fertile pinnules, the veins also extend to the margin of the lobes, but they are unbranched (fig. 1*f*, right; fig. 2*b*, 2*c*). The catadro-

mous basal vein of each lobe meets the margin above the sinus in both vegetative and fertile pinnules (figs. 1*c*, 2*c*).

Fertile pinnules range to slightly smaller than vegetative pinnules, measuring up to 5.3 cm long and 1.3 cm wide. All have been found as isolated specimens. They have slightly simpler venation and more rounded tips than the vegetative pinnules but otherwise are of similar morphology. Almost all

fertile pinnules have two rows of round sori on all pinnule lobes (fig. 2a, 2b, 2d, 2e). However, the holotype specimen (fig. 1f) has vegetative pinnule lobes with forked lateral veins (fig. 1f, arrows) in the basal region (fig. 1f, left) and fertile lobes with unbranched lateral veins at the tip (fig. 1f, right; fig. 2c). This specimen demonstrates that the fertile pinnules were produced by the same species of ferns as the vegetative frond segments.

Sori are round and most often large, consisting of 30–40 sporangia (fig. 2a, 2d, 2e). They can be crowded (fig. 2d) and may be united at the tip of a pinnule lobe (fig. 2e) but otherwise are not fused to each other (fig. 2). In a few specimens, the sori are smaller with only a few sporangia (fig. 2b, 2c). The latter specimens reveal that the sori are positioned under but not at the tip of a lateral vein (fig. 2b, 2c).

Sporangia appear as black dots under light microscopy (figs. 1f, 2a–2e). Macerated sporangia (fig. 3a, 3b) and those viewed with SEM on the rock surface show remnants of cells that make up a vertical annulus. Otherwise cells are not preserved, and sporangium size and shape are preserved by the mass of spores (fig. 3a–3d). The annulus cells extend vertically as a single row from near the base of the capsule, over the top, and down the other side (fig. 3a–3d). Although the stalk is not preserved, orientation of the annulus and the shape of the spore mass indicate that the annulus was interrupted by the stalk (fig. 3a, 3c). Individual sporangial capsules are 130–160 μm long × 90–110 μm wide and contain ca. 64 spores (fig. 3a–3c).

Spores are ellipsoidal to bean shaped, with a monolete suture that extends one-half to two-thirds the length of the spore (fig. 3e, 3f). They measure 26–36 μm × 15–24 μm (mean = 31.26×20.83 μm; $n = 20$) and are assignable to the *sporae dispersae* genus *Laevigatosporites* (*Laevigatosporites ovatus* Miner s.l.). Under light microscopy they appear to be psilate, but SEM images reveal that they are sculptured by minute, rounded scabrae (fig. 3f, 3g). Transmission electron microscopy shows the sporoderm to be dense and solid and that it makes up the scabrae (fig. 3h, 3i). There is no evidence of perispore.

Discussion

Speirseopteris orbiculata is represented by vegetative and fertile frond material that displays a distinctive suite of characters not previously known from the fossil record. Vegetative fronds are pinnate + pinnatifid and catadromous, with alternate to subopposite pinnules that form a deltoid blade up to ca. 16 cm long and wide. Venation is open, with a pinnule midvein, a straight pinna midvein, and catadromous pinnately arranged laterals that fork once and extend to the margin. The basalmost laterals meet the margin distal to the sinus. Fertile pinnules are quite similar, except that they range to slightly smaller than the vegetative pinnules and have lateral veins that are unbranched. Sori are orbicular, appear to be exindusiate, and are borne in two rows on the pinnule lobes. They consist of up to 40 sporangia that have a vertical annulus and that contain ca. 64 monolete spores. Spores appear to be psilate in light microscopy, but electron microscopy reveals that they are sculptured by minute scabrae (i.e., only up to ca. 100 nm) that are part of the dense sporoderm. Perispore is not preserved.

Among living Filicales, this combination of characters is found in the eupolypods *sensu* Schneider et al. (2004), including ferns of the Aspleniaceae Frank in Leunis, Blechnaceae C. Presl., Dryopteridaceae Ching, Nephrolepidaceae Pichi Serm., Polypodiaceae Berchtold et J.C. Presl., and Thelypteridaceae Pichi Serm. (*sensu* Kramer and Green 1990). Superficial sori of sporangia that have a vertical annulus interrupted by the stalk and that produce 64 monolete spores clearly place *S. orbiculata* among these clades, but assignment to a family is more difficult.

Speirseopteris orbiculata and many other fossils preserved by coalified compression lack some or all of the scales and trichomes, cuticular detail, cellular preservation of sporangial and epidermal cells, surface features of the stipe, rachis and pinnae, stelar and frond anatomy, and perispore that are used in the classification of living ferns. This leaves many of the systematically informative characters for living ferns (Tryon and Tryon 1982; Kramer and Green 1990; Tryon and Lugardon 1991) in question. For example, the orbicular sori of *S. orbiculata* appear to be exindusiate. However, epidermal cells and cuticles are not preserved, so that even if an indusium had been present in life, it might not be represented in the fossil. Likewise, small bits of dark material that remain attached to the pinna rachis of some specimens (e.g., fig. 2d) could possibly represent trichomes. However, careful examination reveals that they are angular fragments of coal and that surfaces to which the sediments are attached are too coarse to preserve these fine details.

Whereas *S. orbiculata* is represented by a large number of specimens from which numerous characters of vegetative and fertile frond morphology, venation, sorus structure, sporangial structure, and spores are available, the majority of compressed fern fossils from Cretaceous and Paleogene deposits are described from a much smaller number of frond fragments that show far fewer characters (Collinson 2001). Among the better known species, *S. orbiculata* shares a vertical annulus and monolete spores with several Lower Cretaceous species from northern China (reviewed by Deng 2002) and numerous fossils from Tertiary deposits wordwide (reviewed by Collinson 2001).

The Lower Cretaceous Chinese ferns include several species with a vertical annulus interrupted by the sporangial stalk and that appear to represent the oldest evidence for some of the most highly derived filicaleans (Deng 2002). These include *Adiantopteris elegans* Deng and several less completely known species of *Adiantopteris* that are assigned to the Adiantaceae (Deng 2002), a family characterized by trilete spores. Other Lower Cretaceous Chinese ferns are similar to *S. orbiculata* in the production of monolete spores, including species assigned to the Dryopteridaceae, Athyriaceae, and Pteridaceae (Deng 2002). The best known of these are several species of the genus *Dryopterites* Deng that are tentatively assigned to the Dryopteridaceae, *Eogymnocarpium sinensis* (Lee et Yhe) Li, Ye et Zhou, and species of *Athyrium* (Athyriaceae; Deng 2002). All of these Chinese species are easily distinguished from *Speirseopteris* by the occurrence of sori that are crescent shaped (Deng 2002) rather than round, and most have fronds that are more highly dissected and/or more elongated than the blade of *S. orbiculata*.

Round sori like those of *S. orbiculata* are more common in the Dryopteridaceae, Polypodiaceae, and Thelypteridaceae
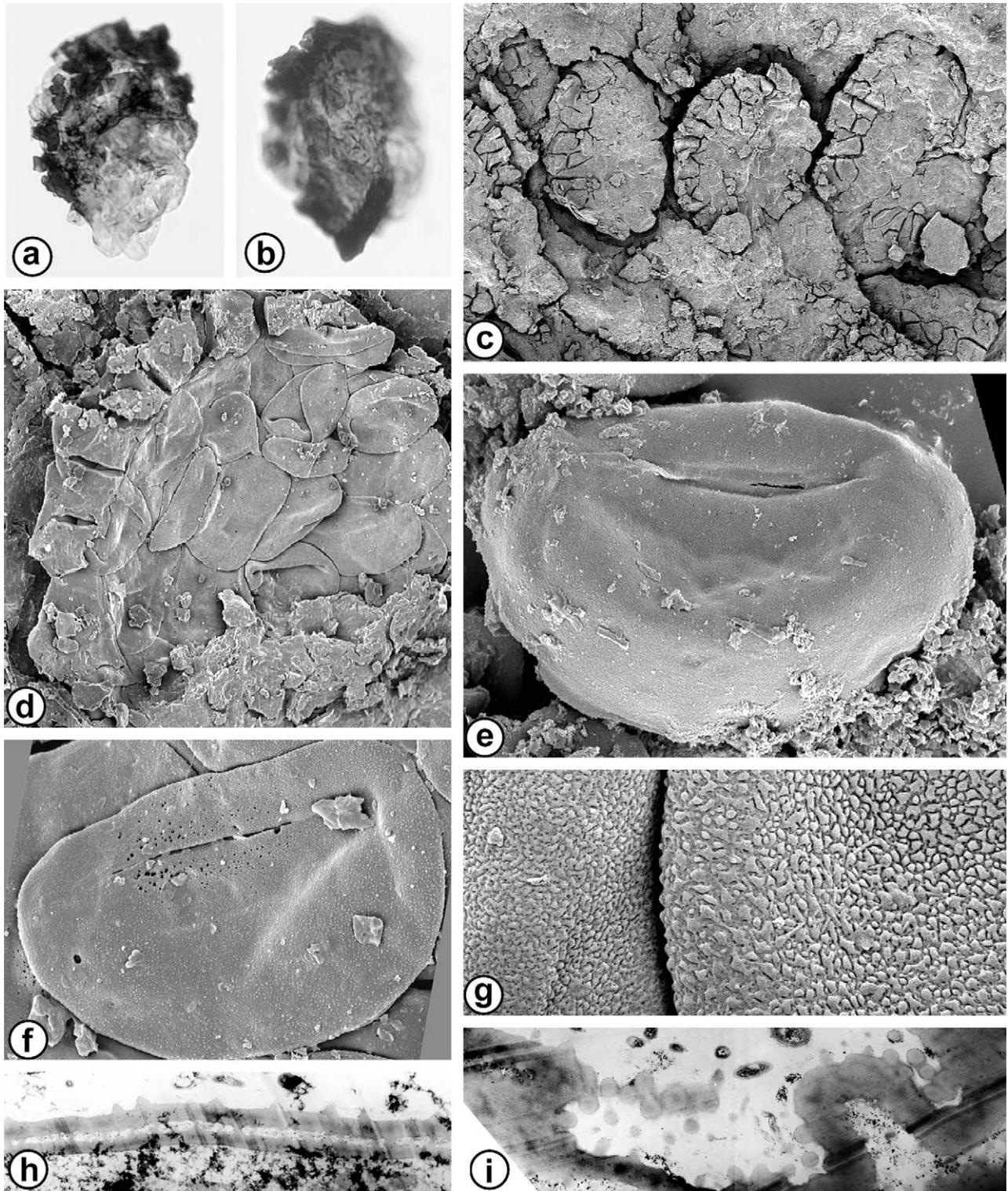
Fig. 3 *Speirseopteris orbiculata* gen. et sp. nov. Sporangia and spores. *a*, *b*, Sporangia macerated from matrix showing overall shape of capsule and vertical annulus that extends from near stalk region, over capsule, and down to midregion of other side. UAPC-ALTA S32,658; ×120. *c*, SEM of several sporangia in sorus. UAPC-ALTA S32,737; ×100. *d*, SEM of sporangial capsule on rock surface showing shape, annulus, and spores. UAPC-ALTA S32,737; ×300. *e*, SEM of spore showing proximal suture and surface sculpturing. UAPC-ALTA S32,737; ×2000. *f*, SEM of spore showing features of proximal surface UAPC-ALTA S32,737; ×1100. *g*, Close-up of spore wall showing fine scabrae on exterior of exospore. UAPC-ALTA S32.716; ×6000. *h*, *i*, TEM of exospore showing dense construction, smooth inner surface, and scabrae of outer surface in section view. UAPC-ALTA S33,578; ×7000.

than the other eupolypod families (Kramer and Green 1990). Upon initial examination, the fertile specimens of *S. orbiculata* appear to resemble fronds of the Polypodiaceae, but closer scrutiny reveals that such specimens are the pinnules of a pinnate + pinnatifid frond. Also, the veins of *S. orbiculata* extend to the margin instead of having an inflated tip located behind the margin, as in the Polypodiaceae (Kvaček 2001). In agreement with *S. orbiculata*, many species of the Thelypteridaceae and Dryopteridaceae have open venation with veins that do extend to the margin of the pinnules.

The known features of *S. orbiculata* are generally comparable to those of many Dryopteridaceae. Frond shape, degree of pinnule dissection, catadromy, pinnule shape, venation, sorus position, and shape are particularly reminiscent of the dryopterid genus *Ctenitis* C. Chr. (Tryon and Tryon 1982; Kramer and Green 1990). Spores of *S. orbiculata* and many species of Dryopteridaceae display sculpturing patterns that are generally comparable (Tryon and Lugardon 1991). However, the pattern of living Dryopteridaceae is markedly coarse as compared with the minute scabrae of *S. orbiculata*. Moreover, the exospore of most dryopterid species is smooth (Tryon and Lugardon 1991), and the sculpturing pattern of living dryopterid fern spores is produced by the perispore. By contrast, perispore is not preserved in *S. orbiculata*, and the minute scabrae are produced by the outer surface of the exospore. Therefore, the sculpturing of *S. orbiculata* spores is actually more comparable to the irregular outer surface of the exospore in Thelypteridaceae (e.g., figs. 149.27–149.34 of Tryon and Lugardon 1991) than to the much coarser contours of Dryopteridaceae spores, which are produced by perispore material deposited over the smooth outer surface of the exospore (e.g., figs. 159.47–159.50 of Tryon and Lugardon 1991).

The difficulties of confidently assigning compression fossils to Thelypteridaceae and distinguishing them from species of Dryopteridaceae in the absence of trichomes, scales, and internal anatomy have been emphasized previously (Collinson 2001). Nevertheless, all of the characters known for *S. orbiculata* are found within the Thelypteridaceae (Smith 1990). On the other hand, many characters of *S. orbiculata* are relatively uncommon among living thelypterid species (A. R. Smith, pers. comm., 2005), and the entire suite is not present in any modern genus. For example, deltoid pinnate + pinnatifid fronds with catadromous venation like those of *S. orbiculata* occur among species of *Phegopteris* (C. Presl) Fée,

but lateral veins in that genus are usually unforked. In contrast, lamina shape is usually not deltoid in *Thelypteris* Schmidel, but forked lateral veins nearly identical to those in *S. orbiculata* occur in *T. palustris* Schott (cf. fig. 1*c* and fig. 124*A* of Smith 1990). The distinctive suite of characters displayed by *S. orbiculata* renders our assignment of *S. orbiculata* to the Thelypteridaceae somewhat tentative. However, this situation may also reflect the relatively recent evolution of many living thelypterid genera (Schneider et al. 2004) and species.

Several extinct species of probable Thelypteridaceae have been described previously. These are reviewed by Collinson (2001). Fossils similar to *Cyclosorus* Link and segregate genera are widely distributed throughout Europe and North America in deposits that range from the Eocene onward (Collinson 2001). Among other characters, such fossils can be distinguished by the presence of various vein anastomoses that are absent in *S. orbiculata*. Confirmation of our assignment of *Speirseopteris* to the Thelypteridaceae would make *S. orbiculata* the oldest species of the family, extending the fossil record back to the base of the Tertiary.

If most of the species richness among filicalean ferns has evolved in conjunction with diversification of flowering plants in the Upper Cretaceous and Tertiary (Lovis 1977) as is currently believed (Rothwell 1987; Schneider et al. 2004), then the generic distinctiveness of *Speirseopteris* and many other Cretaceous and Paleogene fossil ferns is to be expected. Such genera are best regarded as extinct sister groups to the living genera. This reasoning supports our tentative assignment of *S. orbiculata* to the Thelypteridaceae and prompts the prediction that the ongoing characterization of extinct Filicales will eventually reveal a pattern of evolutionary diversification that includes both living species with extreme longevity (e.g., Rothwell and Stockey 1991; Serbet and Rothwell 1999; Pigg and Rothwell 2001) and their extinct sister groups.

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