RELATIONSHIPS AMONG FOSSIL AND LIVING DIPTERIDACEAE: ANATOMICALLY PRESERVED *HAUSMANNIA* FROM THE LOWER CRETACEOUS OF VANCOUVER ISLAND

Ruth A. Stockey,[1,]* Gar W. Rothwell,† and Stefan A. Little*

*Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; and
†Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701, U.S.A.

Anatomically preserved foliage of a dipteridaceous fern has been identified in both calcareous nodules and fine-grained, carbonate-cemented sandstone from the early Cretaceous (Hauterivian-Barremian) Apple Bay locality from Vancouver Island, British Columbia, Canada. Fronds with attached sporangia containing spores are preserved as both compression/impressions and as permineralizations. Fan-shaped laminar segments display paired teeth along the margin. Major veins dichotomize to the lamina edge, and finer veins reticulate, forming square to polygonal areoles, with freely ending veinlets. Veins are enclosed by sclerenchymatous sheaths, and the abaxial epidermis is recessed, producing concave areas between veins. Adaxial cuticle is thick, and the epidermis contains rectangular cells with undulating walls. Anomocytic scattered stomata occur on the abaxial surface. Sporangia and trichomes are scattered across the abaxial epidermis in the areolar concavities. Sporangial stalks are short, two to three cells long and four to six cells wide throughout their length. Sporangia have a vertical annulus that is interrupted by the stalk, and they contain trilete spores that correspond to *Cibotiumspora jurienensis*. Leaf morphology is similar to that of extant *Dipteris novoguineensis* and fossil *Hausmannia* spp. A unique combination of characters demonstrates that *Hausmannia* is a distinct genus of fossil dipterids. An examination of leaves from extant *Dipteris* rhizomes of various ages suggests that the genus *Protorhipis* may represent juvenile *Hausmannia* at some localities. The association of *Hausmannia* with small pieces of delicate moss gametophytes, fern sporelings, and vegetative remains of *Lycopodium* and *Selaginella* at Apple Bay reinforces the interpretation that these fossil dipterids were deposited under storm conditions and that *Hausmannia* may have grown in disturbed habitats.

Keywords: Cheiropleuria, Cibotiumspora, Concavisporites, Cretaceous, Dipteris, ferns, Hausmannia.

Introduction

Dipteridaceae is a small family of Filicales with extant species that are sometimes restricted to the genus *Dipteris* Reinwardt and other times include *Cheiropleuria* C. Presl (Kramer 1990*a*, 1990*b*; Kato et al. 2001). Although *Dipteris* and *Cheiropleuria* have features that are suggestive of highly derived families of the third filicalean radiation (Rothwell 1987; e.g., vertical annulus interrupted by the stalk, mixed soral development, small sporangia with few spores, monolete spores in *Dipteris*), both morphological and molecular phylogenetic analyses infer that they are sister taxa of a systematically isolated, relatively basal clade that may be closely related to Gleicheniaceae, Schizaeaceae, and Matoniaceae as part of the second (Mesozoic) filicalean radiation (Tryon and Lugardon 1991; Cantrill 1995; Kato and Setoguchi 1999). Dipteridaceae have a well-established fossil record consisting of several species assigned to the genera *Goepertella* Ôishi et Yamasita, *Camptopteris* Presl, *Dictyophyllum* Lindley et Hutton, *Clathropteris* Brongniart, *Hausmannia* Dunker, and *Dipteris*, with fossils extending from the Triassic to the Cre-

taceous in Gondwana, Eurasia, and North America (Tidwell and Ash 1994; Cantrill 1995). Of these taxa, the genus *Hausmannia* has the longest stratigraphic range (Cantrill 1995), spanning the Mesozoic (i.e., Triassic through Cretaceous).

The fossil record of *Hausmannia* was reviewed by Cantrill (1995), who included fronds assigned to over 40 species. Cantrill (1995) divided the known fossil species into three groups: those with deeply dissected fronds, those with shallowly dissected fronds, and those with small reniform fronds. In their description of extant *Dipteris* species, Seward and Dale (1901) stated that fronds of some of the fossil species of *Hausmannia* could not be separated from those of extant *Dipteris* and that *Hausmannia* should probably be regarded as a form genus for fossil fronds of *Dipteris*.

All of the previously described species of *Hausmannia* are based on compression/impression fossils. Sporangia are described for only a few species (Raciborski 1894; Halle 1921; Ôishi 1932; Cantrill 1995), and spores are rarely preserved (Antevs 1919; Potonié 1967; Krassilov 1969; Balme 1995). In this article we describe fronds of *Hausmannia* with sporangia and spores that are preserved both as coalified compressions with some anatomical preservation and also as cellular permineralizations. Specimens were all collected at the Apple Bay locality on northern Vancouver Island.

All of the dipteridaceous fossils from Apple Bay are assignable to a single species with a unique set of morphological characters that distinguish it from previously described dipteridaceous ferns. The Apple Bay material provides the first evidence for internal anatomy of *Hausmannia* and is described as *Hausmannia morinii* sp. nov. The large number of newly recognized anatomical characters that *H. morinii* reveals help to clarify the taxonomic status of *Hausmannia* and demonstrate that the genus is distinct from other fossil and living dipteridaceous genera. In addition, an evaluation of ontogenetic variations within living species of *Dipteris* suggests that many structural variations within individual assemblages of dipteridaceous fossils may be developmental as well. If true, then the taxonomic diversity among dipteridaceous fossils may be lower than currently believed.

Material and Methods

Specimens occur both as partially permineralized compressions in a carbonate-cemented silty sandstone and as cellular permineralizations within iron-rich carbonate nodules that are imbedded in the sandstones at the Apple Bay locality on the northern end of Vancouver Island (Smith et al. 2003). In a section of sediments that totals 6.2 m in thickness, there are seven levels that yield the compressed plant fossils and 13 levels that contain the iron-rich nodules (E. H. Gierlowski-Kordesch, personal communication, 2005). The locality is on the beach along Quatsino Sound (50°36′21″N, 127°39′25″W; UTM 9U WG 951068) and is accessible for collecting at low tide. Sediments from which the fossils were collected have been regarded as Lower Cretaceous (Valanginian-Barremian), Longarm Formation equivalents (Jeletzky 1976; Haggart and Tipper 1994), and correspond to Jeletzky's (1976) Barremian, variegated clastic unit (Sweet 2000). However, a recent oxygen isotope analysis has narrowed the age to the Valanginian-Hauterivian boundary (D. R. Gröcke, personal communication, 2005).

Partially permineralized compressions were etched for 30 s in 5% HCl to clarify venation patterns, reveal the presence of sporangia, and increase contrast for photography. Specimens were photographed dry and also immersed in 95% EtOH. Anatomical sections were prepared using the cellulose acetate peel technique (Joy et al. 1956) and mounted on glass slides with Eukitt (O. Kindler, Freiburg, Germany). Images were captured using a Microlumina (Leaf Systems, Bedford, MA) digital scanning camera with a macro lens and a Phase One (Phase One A/S, Frederiksberg, Denmark) digital scanning camera mounted on a Leitz Aristophot bellows camera and a Zeiss WL compound microscope. Spores were examined from inverted peels or were removed from the cellulose acetate peel using a modified Daghlian and Taylor (1979) technique under vacuum on a millipore filter (Millipore, Bedford, MA). Spores were mounted on double-sided tape on SEM stubs, coated with 100 Å Au on a Nanotek Sputter Coater, and examined using a JEOL 6301F scanning electron microscope at 5 kV. All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada.

Because several authors (Seward and Dale 1901; Posthumus 1928; Cantrill 1995) have suggested that the fronds of *Haus-*

mannia are indistinguishable from those of extant *Dipteris* and the Apple Bay material represents the first anatomically preserved species of *Hausmannia*, we have compared morphological and anatomical characters of *Hausmannia morinii* to several living species. Fronds of extant *Cheiropleuria integrifolia* (D.C. Eaton ex Hook.) Kato, Yatabe, Sahashi et Murakami were obtained from Kinsakubaru, Naze City, Kagoshima Prefecture (Amami-Ohshima), 28°20′40″N, 129°26′53″E (1/22/05-Takamiya). Those of *Dipteris conjugata* Reinw. were collected (by R. A. Stockey) 22 km west of Kuching, Sarawak, Malaysia. Spores for SEM were put onto stubs with double-sided tape and viewed as above. Frond material of *D. conjugata* was fixed, embedded in paraffin, and sectioned according to standard techniques (Johansen 1940).

Systematics

Order—Filicales

Family—Dipteridaceae Diels

Genus—Hausmannia *Dunker*

Species—Hausmannia morinii *Stockey, Rothwell et Little sp. nov.*

Diagnosis. Fronds with dichotomizing lamina, fan- to wedge-shaped, at least 9 cm long, 6.5 cm wide, margin crenate; teeth paired, 4–5 mm wide by 2 mm deep. Major veins, thick, dichotomizing at least six to eight times, decreasing in size toward frond margin, entering teeth, accompanied by internal adaxial and abaxial sclerenchyma. Secondary veins arising at angles of 90° forming square to rectangular to polygonal meshes. Tertiary and quaternary veins forming square to polygonal areolae 0.8–1.5 mm in diameter; areolae with freely ending veinlets. Adaxial epidermis of rectangular to polygonal cells with sinuous margins. Mesophyll of loosely packed parenchymatous cells. Abaxial epidermis of sinuous cells, uniseriate trichomes, and randomly arranged anomocytic stomata. Sporangia on abaxial surface in between veins, 8–12 (–13) per areola, scattered; distinct sori lacking; interspersed with uniseriate trichomes. Sporangia small, 110–130 μm × 150–160 μm in diameter, with short sporangial stalk, two to three cells tall, four to six cells in transverse section. Annulus vertical, of eight to 10 cells, interrupted by stalk. Spores trilete, tetrahedral-deltoid, with concave sides; kyrtome on proximal surface, thicker near ends of laesurae; 18–25 μm in diameter; 32 per sporangium.

Etymology. The species is named in honor of Joe Morin (Vancouver Island Paleontological Society), Courtenay, British Columbia, who brought the site to our attention and provided many of the specimens used in this study.

Holotype. P13148 A, B (fig. 2a–2d, 2f; figs. 3, 4; fig. 5a, 5b)

Paratypes. P13667 B; P13317; S59518 A-E; S59519 A-D; S59520 A, B; S59521.

Stratigraphic occurrence. Longarm Formation equivalent.

Age. Valanginian-Hautervian boundary, Early Cretaceous.

Description. *Hausmannia morinii* is represented by 12 incomplete frond laminae preserved as partially permineralized compressions and seven permineralized laminar fragments within the calcareous nodules. Morphological features are most easily recognized from the partially permineralized

compressions, while data about internal anatomy, cuticular features, sporangia, and spores are derived primarily from the permineralized specimens. Characters that are represented by both modes of preservation include venation patterns (cf. fig. 1*d*–1*f* and 2*f*), size and shape of the areoles (cf. figs. 1*f* and 2*f*), blind vein endings within areoles (cf. figs. 1*g* and 2*f*), scattered sporangia within aeroles (cf. figs. 1*g* and 2*f* or 3*b*), and features of the annulus cells (cf. figs. 1*g* and 2*d*).

Some compressions show the lateral margin of the lamina (fig. 1*a*, 1*b*), while others show either the distal margin (fig. 1*d*) or the central region (fig. 1*c*). Laminar fragments range up to 9.1 cm long (fig. 1*c*) and 5.6 cm wide (fig. 1*d*). Most are wedge- or fan-shaped and asymmetrical with respect to both outline and major venation pattern (fig. 1*a*–1*c*), but one apparently apical fragment is quite symmetrical (fig. 1*d*). Laminar margins are crenate (fig. 1*a*, 1*b*), with teeth that are 4–5 mm wide by 2 mm deep and clearly paired in the distal region (fig. 1*d*). Teeth are rounded and symmetrical with convex margins, becoming increasingly decurrent toward the base of the lamina (fig. 1*a*, 1*b*, 1*d*). One specimen, represented by both part and counterpart, has a crenate margin at one side and a smooth margin that parallels a dichotomizing major vein at the other (fig. 1*a*, 1*b*). There is a narrow zone of ground tissue, possibly only one or two cells wide, adjacent to the major vein (fig. 1*a*, bottom right; fig. 1*f*). A small fragment of tissue that may represent the second half of a bipartite blade is positioned adjacent to the smooth margin near the base of the lamina (fig. 1*a*, 1*b*, arrows).

Major veins dichotomize at least six to eight times in the largest laminar fragments (fig. 1*a*, 1*b*, 1*d*). Such veins are quite thick at the base, decreasing in size toward the frond margin (fig. 1*a*–1*d*). Secondary veins diverge at angles approaching 90°, and form square to rectangular to polygonal meshes (figs. 1*a*–1d, 2*f*). Tertiary and quaternary veins also diverge at nearly right angles, forming square to polygonal areolae (fig. 1*a*, 1*b*; fig. 2*f*). Areolae range from 0.8 to 1.5 mm in diameter and contain freely ending veinlets (figs. 1*g*, 2*f*). Toward the toothed lateral margin of the lamina, branching angles of veins are less regular, and the shape of the secondary vein meshes is increasingly variable (fig. 1*a*, 1*b*). At the laminar margins the veins enter the teeth and branch in a pattern that is consistent with that of the more centrally located minor veins (fig. 1*d*); i.e., areolation is similar in the teeth and the rest of the leaf blade.

Anatomically preserved frond laminae are up to 1.8 cm wide and 1 mm thick (fig. 2*a*), with veins that are prominent in both transverse and paradermal sections (fig. 2). Laminae are thickest at the veins and recessed on abaxial surfaces between veins (fig. 2*a*, 2*b*, 2*d*). Veins are surrounded by adaxial and abaxial sclerenchyma that is I-shaped in cross sections, or more often an inverted T-shape that is broadest toward the abaxial surface (fig. 2*a*–2*c*, 2*e*). Small annulate sporangia are attached and incompletely enclosed within the recessed areolae on the abaxial surface of the frond (fig. 2*a*–2*d*, 2*f*). In paradermal sections the laminae show a reticulate venation pattern with dichotomizing primary veins that give rise to secondary veins at right angles (fig. 2*f*). Closely spaced major veins that are often seen in cross sections (fig. 2*a*) are the result of a recent dichotomy. As in the compressed specimens, tertiary and quaternary veins are produced at nearly

right angles to the secondaries and tertiaries respectively, and quaternary veins produce veinlets that are freely ending within the areolae (fig. 2*f*). Also as with the compressed frond fragments, the aerolae are nearly square to polygonal in outline and 0.8–1.5 mm in diameter (fig. 2*f*).

Several of the frond fragments preserved within nodules have been abraded, but the holotype shows a thick adaxial cuticle and small rectangular epidermal cells in transverse section (fig. 2*d*). In paradermal section, these cells have a sinuous outline and are rectangular to polygonal in shape (fig. 3*f*). Mesophyll of the areole is composed of loosely packed parenchymatous cells, distinct intercellular spaces toward the abaxial surface (fig. 2*b*, 2*d*; fig. 3*a*). In between the veins the abaxial epidermis shows numerous stomata with paired guard cells, sinuous epidermal cells, uniseriate trichomes, and sporangial stalks (fig. 3*a*–3*e*). Stomata are more easily seen on the flanges of the veins and are randomly arranged, anomocytic, and not sunken. Occasional fungal hyphae have also been observed in the areolae on abaxial surfaces (fig. 3*d*, arrow).

Sporangial stalks are short, two to three isodiameteric cells in length (fig. 3*a*), and four to six cells in cross section (fig. 3*a*–3*c*). Larger numbers of cells seen in some transverse sections (fig. 3*a*, 3*c*) represent sections into the base of sporangial capsules. The annulus is vertical, consisting of about eight to 10 cells, and is interrupted by the stalk (figs. 2*d*, 4*a*, 4*b*). Cells of the annulus are 30 μm wide and 33–45 μm tall with prominently thickened inner and radial walls (figs. 2*d*, 4*a*, 4*b*). Sporangial capsules measure up to 170 μm long and 110–130 μm×150–160 μm in transverse section, the larger size occurring in the plane of the annulus.

Small tetrahedral-deltoid trilete spores with concave interradial sides occur within some of the sporangia (fig. 3; fig. 4*a*, 4*b*). Counts of spore numbers from consecutive serial sections suggest that there are about 32 per sporangium. Spores are 18–25 μm in diameter with a relatively smooth exine (fig. 4*a*, 4*b*). At the light microscope level, these spores show a prominent trilete suture on the proximal surface that is flanked by a "kyrtome" (Potonié and Kremp 1955), a fold or band in the interradial areas outside the laesurae (fig. 4*d*–4*f*). This structure is thicker near the ends of the laesurae (fig. 4*a*, 4*e*). Distal surfaces are rounded and relatively smooth (figs. 4*c*, 5*b*). Complete spores were particularly difficult to macerate for SEM because of their small size and numbers. However, they appear to correspond to the sporae dispersae species *Cibotiumspora jurienensis* (Balme) Filatoff (A. Sweet, personal communication, 2005).

Extant Dipterids

Examination of *Dipteris conjugata* in the field near Kuching, Sarawak, Malaysia (by R. A. Stockey) revealed that sporeling frond morphology (fig. 6*a*) differs considerably from that in fronds borne by older rhizomes (fig. 6*c*). In addition to an increasing blade size with successive plant maturity, there is a gradation in the amount of dissection of the frond lamina from those with little dissection (fig. 6*a*) to those with shallow dissection (fig. 6*b*), to blades on the oldest rhizomes showing deeply dissected morphologies (fig. 6*c*). All fronds show a basal dichotomy and have two asymmetrical but equal halves that are mirror images of each other
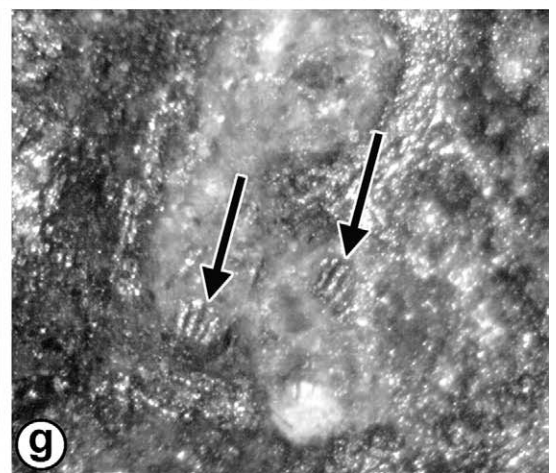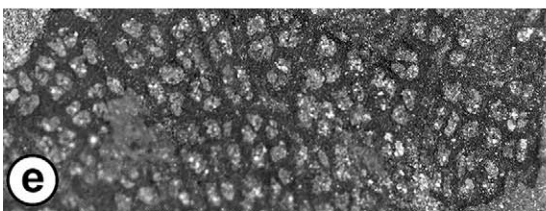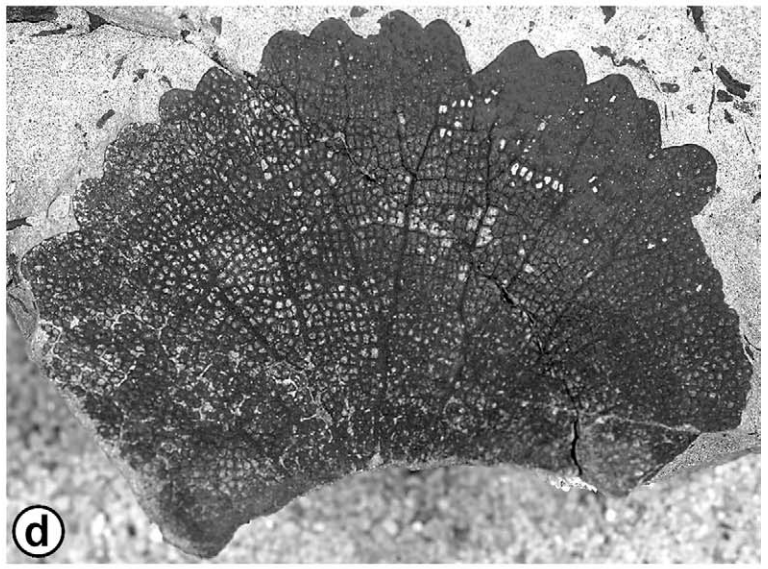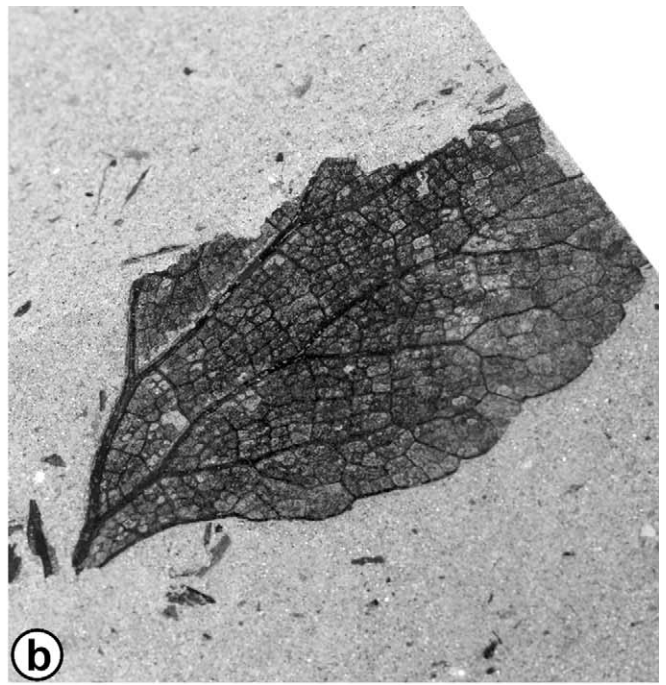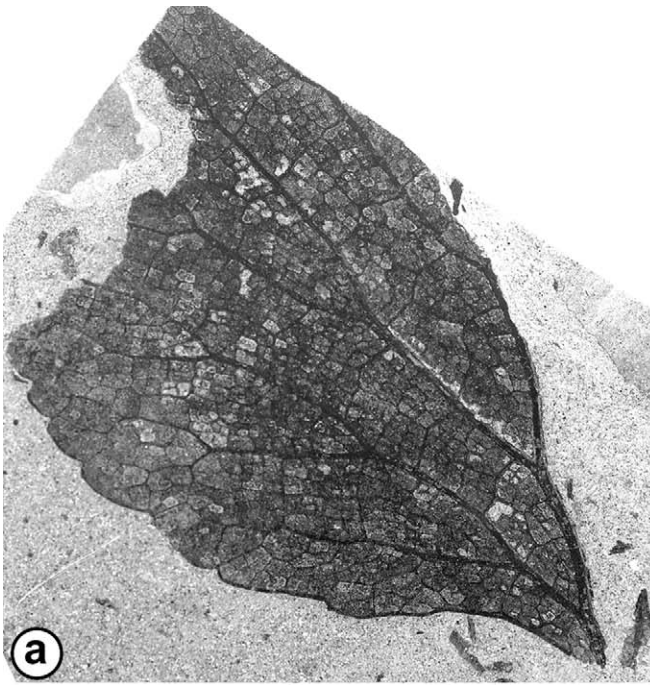
(fig. 6a–6c). However, the most juvenile forms are bilobed with laminar tissue in the center (fig. 6a), whereas larger blades have a central cleft that dissects the frond into two segments (fig. 6b, 6c). While all leaves show a basic dichotomous pattern of major veins, there is a considerable difference in secondary and tertiary vein patterns, with less-regular areolation in the blades of sporeling fronds (fig. 6a). We did not observe sporangia on the surface of small fronds from juvenile rhizomes (fig. 6a or 6b), but as reported by previous authors (Kramer 1990b; Cantrill 1995), immature fronds (croziers) show numerous surficial trichomes that are not present on mature blades. All fronds show marginal teeth or crenations (fig. 6a–6c), but these do not correspond to the major veins as they do in *Hausmannia morinii*. In contrast to *H. morinii*, major veins of the extant *Dipteris* species terminate in the lobes of the blade (fig. 6b, 6c) rather than in the teeth per se. Areolation in fronds from older rhizomes is similar to that seen in the fossils (fig. 6f).

Transverse sections of large fronds show thickenings of the lamina at major veins (fig. 6d); however, these are much less pronounced than in the fossils. Like fronds of *H. morinii*, blades of *D. conjugata* show abaxial and adaxial sclerenchyma bands associated with the vascular bundles (fig. 6d, 6e). While there is a slight abaxial bulge associated with major veins of *D. conjugata* (fig. 6d, 6e), there is no overarching of sclerenchyma (fig. 2b, 2e). As in the fossils, the adaxial epidermis of *D. conjugata* is composed of rectangular epidermal cells in transverse section underlain by a mesophyll that contains more air spaces near the abaxial surface (fig. 6e). In surface view, cells of the adaxial epidermis have a sinuous outline (fig. 6g). Stomata are paracytic and confined to abaxial surfaces between veins (fig. 6h, 6i). Abaxial epidermal cells, like those of the adaxial surface, are sinuous in outline (fig. 6h, 6i). Sporangia in *D. conjugata* are borne in round, exindusiate sori scattered on the abaxial surfaces of the blade in between the veins (fig. 6j, 6l). Sporangial stalks are four-celled in transverse section (fig. 6k, 6l) and are interspersed with small trichomes (fig. 6l, arrow). The annulus is vertical to slightly oblique and interupted by the stalk (fig. 6j). Sori show a gradate development, and there are few spores per sporangium.

Spores of *D. conjugata* are monolete, bean-shaped, or ellipsoidal, 30–40 μm, and have a relatively smooth exine (fig. 7a, 7b). Spores of *Cheiropleuria integrifolia*, however, are trilete, tetrahedral-deltoid, 30–40 μm, and have a slight ridge on the distal surface that parallels the trilete suture (fig. 7c, 7d). The surface of the exine is relatively smooth.

Discussion

Fan-shaped fronds with crenate margins, dichotomizing major veins with reticulate minor veins, freely ending veinlets

in the areolae, and abaxial sporangia identify these ferns from Apple Bay as members of the Dipteridaceae and refer them to the genus *Hausmannia* Dunker (1846). Since its initial description, the genus has undergone considerable revision, and some species have been synonymized, with small reniform fronds formerly described as species of *Protorhipis* Andrae (Richter 1906). Ôishi and Yamasita (1936), in a review of the previously described fossil dipterid taxa, generally agree with Richter's assessment and point out that there is extreme variablity in the degree of dissection of laminae, even within a single species. The genus *Hausmannia* was reviewed by Cantrill (1995), who reevaluated the fossil record and divided the previously described (40 +) species into three categories based on frond shape: deeply dissected fronds, small reniform fronds, and shallowly dissected fronds. He also listed nomina nuda. Species of *Hausmannia* are distinguished from other fossil dipterids such as *Goepertella* Ôishi et Yamasita, *Camptopteris* Presl, *Dictyophyllum* Lindley et Hutton (=*Thaumopteris* Goeppert), and *Clathopteris* Brongniart by their fan-shaped, rather than pinnate, fronds (Cantrill 1995). *Goepertella* species are bipinnate, while the others are once pinnate (Cantrill 1995). *Hausmannia* extends from the Triassic through the Cretaceous and is most common in Upper Jurassic and Lower Cretaceous strata (Corsin and Waterlot 1979; Tidwell and Ash 1994; Skog 2001).

Most species of *Hausmannia* are described from very fragmentary specimens, often lacking margins, and/or from just a few specimens in which details of sporangia and spores are unknown. The specimens described here fit into Cantrill's (1995) "shallow dissected fronds" group of *Hausmannia* species (table 1). This group consists of several Jurassic and Cretaceous species from Europe, Japan, China, South America, India, and Antarctica (Richter 1906; Ôishi 1932; Sze 1933; Ôishi and Yamasita 1936; Feruglio 1937; Gupta 1955; Shah and Singh 1964; Cantrill 1995). All eight species in Cantrill's group have paired and slightly dissected blades (Cantrill 1995). One of the species, *Hausmannia indica* Gupta, is very poorly preserved, fragmentary, and difficult to compare to either the specimens described here or other species of *Hausmannia* (table 1). *Hausmannia crookshankii* Shah et Singh (1964) is also poorly preserved but differs from *Hausmannia morinii* in having an undulating rather than a crenate margin (table 1).

Like *H. morinii*, *Hausmannia leeiana* Sze (1933) has very pronounced veins, but secondary venation appears less regular; margins are slightly undulating but not prominently toothed, and fertile specimens are unknown (table 1). *Hausmannia buchii* (Andrae) Richter also has deeply incised veins, but teeth are not paired (Richter 1906) like those of *H. morinii* (table 1). Major veins in *H. buchii* dichotomize, and one vein ends in the tooth while the second ends in the sinus.

Fig. 1 Compression/impression leaves of *Hausmannia morinii* sp. nov. *a*, One half of leaf showing dichotomous major veins, reticulate higher order veins, and toothed margin. Note piece of leaf in lower right corner. UAPC-ALTA S59519 A, ×12. *b*, Counterpart of leaf in *a*, showing dichotomizing major veins and good areolae. UAPC-ALTA S59518 B, ×12. *c*, Large leaf fragment showing dichotomous major venation and areolae with freely ending veinlets. UAPC-ALTA S59519 A, ×1.1. *d*, Apical portion of leaf with dichotomous major veins, polygonal areolae, and paired teeth at margin. S59520 A, ×1.5. *e*, Rugose leaf surface of fertile specimen showing major veins and areolae. S59521, ×4. *f*, Enlarged segment of leaf in *b* showing strong major vein on inner leaf margin. S59518 B, ×5. *g*, Enlarged leaf segment showing the annulus of two sporangia (arrows) in areola. S59518 C, ×56.
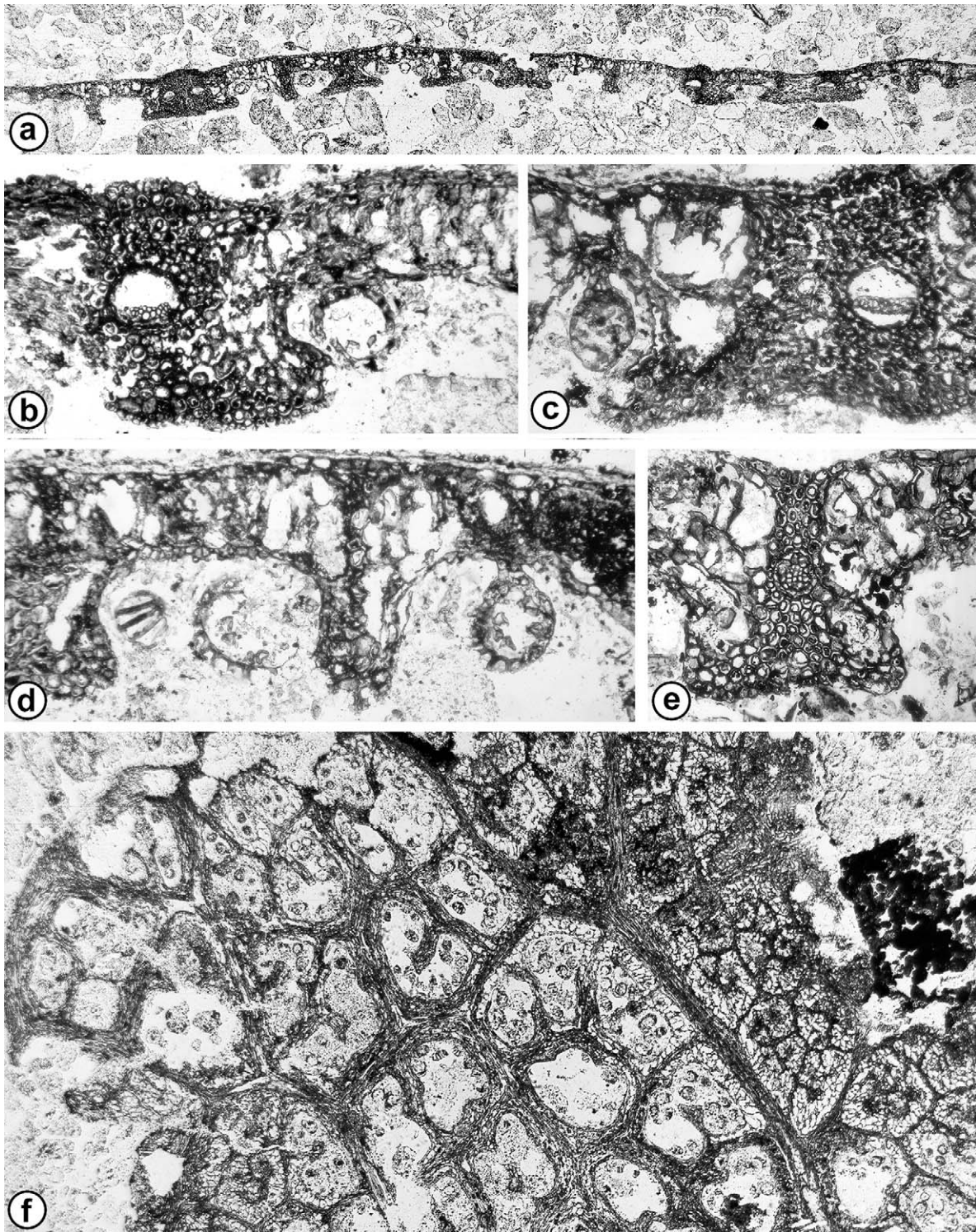
Fig. 2 *Hausmannia morinii* sp. nov., fertile leaves. *a*, Transverse section of leaf showing prominent sclerotic bundle sheath extensions that overarch areas of thinner lamina. Note sporangia in areoles. Holotype UAPC-ALTA P13148 C top #15, ×17. *b*, Transverse section of leaf showing sclerotic bundle sheath extension and terete vascular bundle, with abaxial sporangium (right). Holotype UAPC-ALTA P13148 C top #5, ×106. *c*, Transverse section of leaf showing sclerotic bundle sheath extension, terete vascular bundle, and stalked sporangium (left). Holotype UAPC-ALTA P13148 C top #7, ×99. *d*, Transverse section of leaf showing sporangia attached between veins. Note annulus, at left, and spores in stalked sporangium with vertical annulus, at right. Holotype UAPC-ALTA P13148 B bottom #6, ×117. *e*, Transverse section of leaf showing sclerotic, inverted T-shaped bundle extension. Paratype UAPC-ALTA P13317 G top #9, ×123. *f*, Paradermal section showing reticulate venation and areoles, with numerous sporangia and freely ending veinlets. Holotype UAPC-ALTA P13148 B_2 side #16, ×18.

654
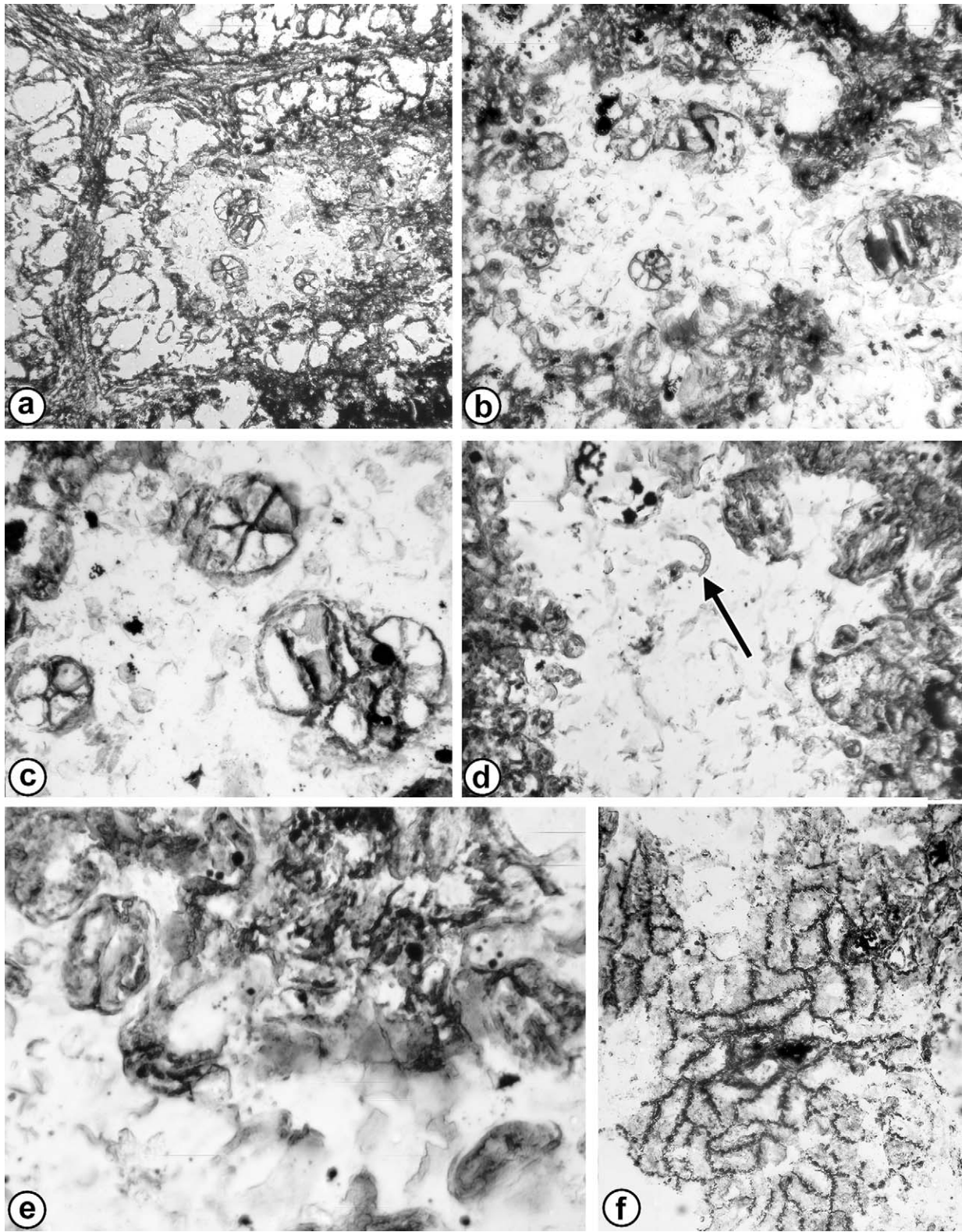
Fig. 3 Paradermal sections of *Hausmannia morinii* sp. nov. UAPC-ALTA Holotype P13148 B$_2$ side. *a*, Abaxial leaf surface showing mesophyll and veins with multiseriate sporangial stalks, at center. Slide #10, ×115. *b*, Abaxial mesophyll and trichomes surrounding multiseriate sporangial stalks. Note annulus cells at right. Slide #9, ×122. *c*, Abaxial view of multiseriate sporangial stalks. Slide #10, ×350. *d*, Abaxial mesophyll and trichomes with guard cells at upper right. Arrow indicates fungal remains. Slide #10, ×320. *e*, Abaxial surface showing guard cells in areola (upper left and bottom right). Slide #9, ×480. *f*, Adaxial epidermal cells with sinuous walls. Slide #10, ×145.
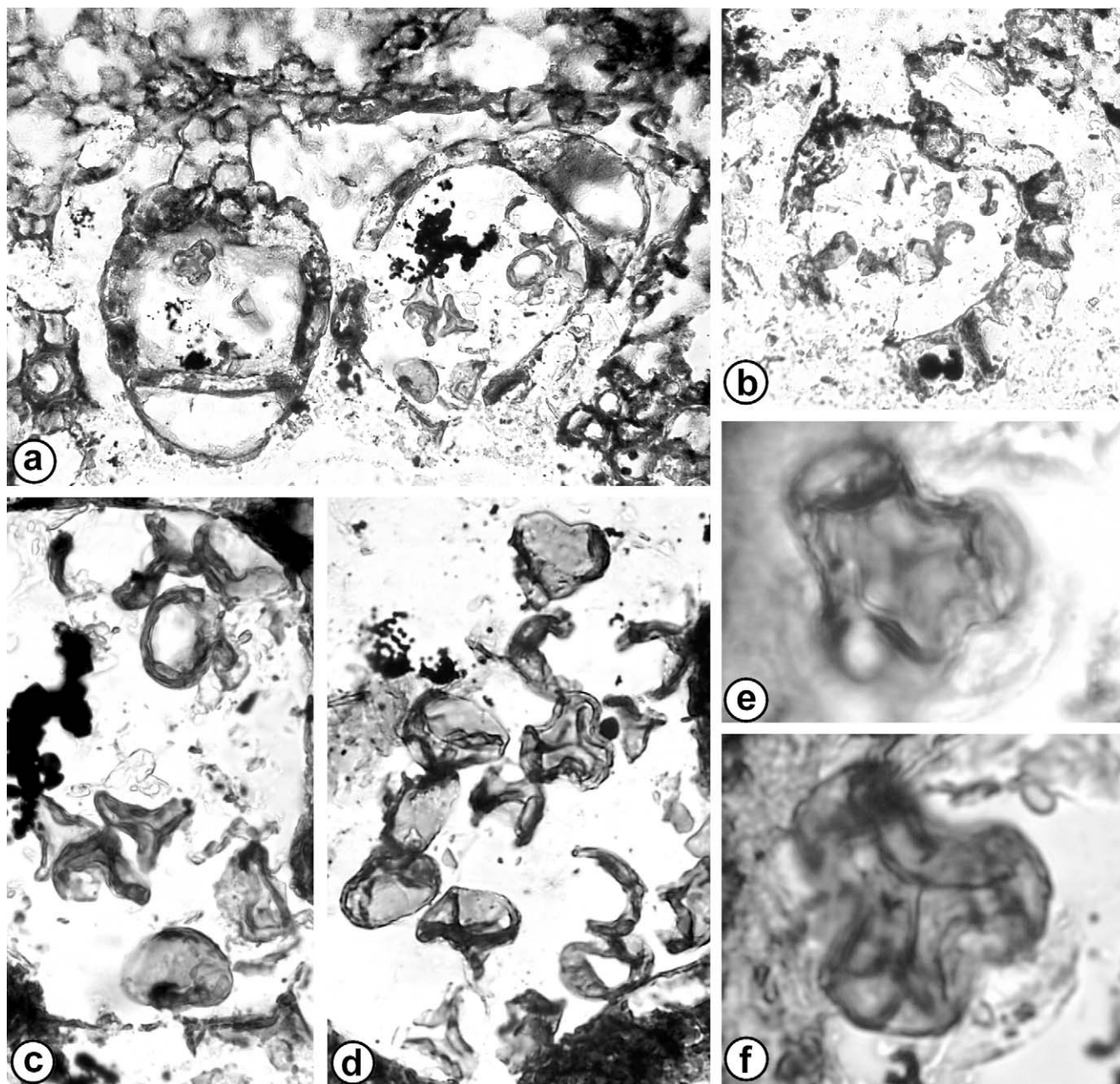
Fig. 4 Sporangia and spores of *Hausmannia morinii* sp. nov. Holotype UAPC-ALTA P13148 B bottom. *a*, Section through two sporangia containing trilete spores. Note wide stalk (left) and enlarged annulus cells. Slide #1, ×297. *b*, Longitudinal section of sporangium containing spores showing stalk and annulus. Note the annulus interrupted by the stalk. Slide #1, ×300. *c*, Spores *in situ* showing triangular shape and dome-like outline in side view (bottom). Slide #1, ×680. *d*, Spores *in situ* showing trilete suture in center. Slide #6, ×760. *e*, *Concavisporites*-type spore showing proximal folds. Slide #1, ×1700. f, *Concavisporites*-type spore showing trilete suture. Slide #1, ×1700.

Teeth are large (Hirmer 1927) and tips are acute with concave sides (Richter 1906) rather than convex, as in *H. morinii* (table 1).

Hausmannia deferrariisi Feruglio (1937), like most of the species formerly assigned to *Protorhipis*, has a blade with a cordate base, eight primary veins, and strongly crenate margins (table 1). Feruglio (1937) compared this species with the Japanese *Hausmannia nariwaensis* Ôishi, which has a shallowly dissected blade (table 1). The other Patagonian species, *Hausmannia papilio* Feruglio (1937), has a larger blade with three to four main veins and a crenulate to undulating margin (Herbst 1960, table 1). The latter species was recently reported from Antarctica (Cantrill 1995), where two to four sori per areole are described. Cantrill (1995) expressed the opinion that *H. papilio* and *H. deferrariisi* may represent the same species. Leaves of these species lack the distinct teeth with convex margins seen in *H. morinii* (table 1).
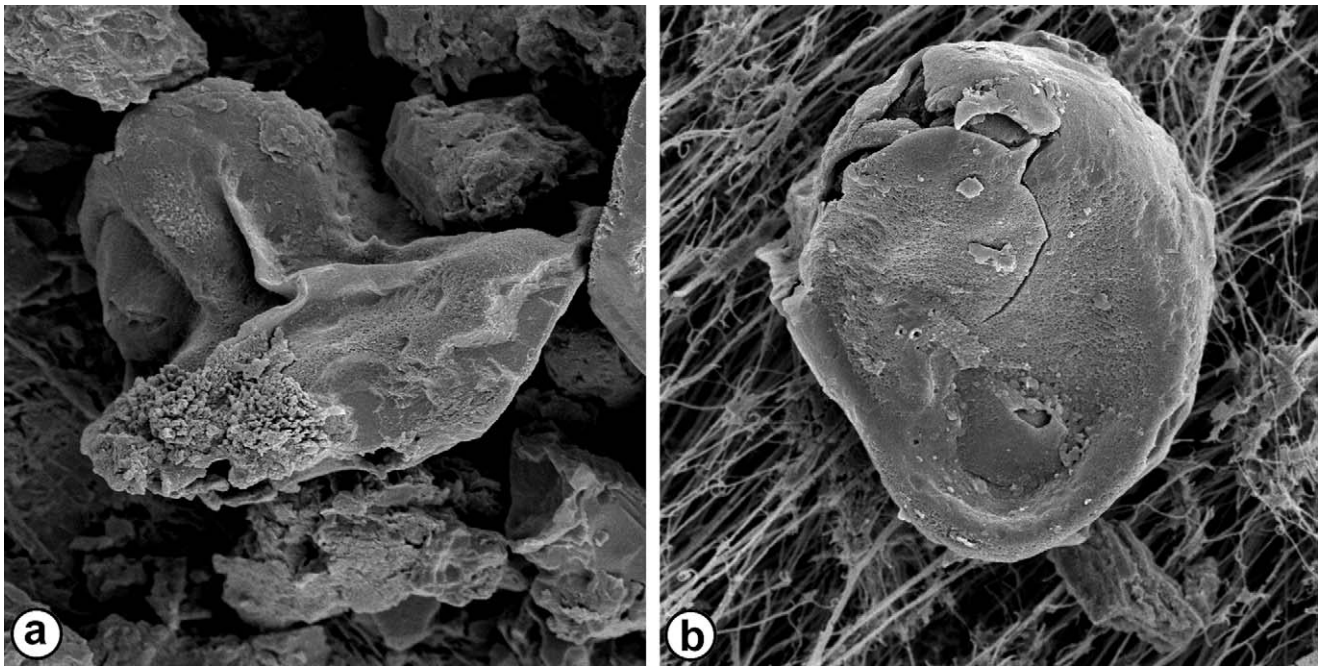
Fig. 5 Spores of *Hausmannia morinii* sp. nov. Holotype UAPC-ALTA P13148 B top #4. *a*, Concave trilete spore. Stub #5, ×3500. *b*, Distal view of spore. Stub #6, ×3500.

Cantrill (1995) placed *Hausmannia forchhammeri* Bartholin (1892) from the Jurassic of Bornholm, Denmark, in his "deeply dissected fronds" category. While the smallest (nonfertile) specimen (Bartholin 1892, Taf. XI, fig. 6) is highly dissected, the other specimens illustrated in figure 4*a* and 4*b* and figure 5*a* and 5*b* of Bartholin (1892) are not. (Note: Harris [1961] synonymized Bartholin's Taf. XI, fig. 6 with the deeply dissected *Hausmannia dichotoma* Dunker). Bartholin's other figures illustrate fronds that are fertile, with teeth that are irregular in shape, elongate, and show tendencies toward pairing (table 1). However, the major veins can end after further dichotomies in a sinus or a tooth, and the meshes formed by secondary veins are not as regular as in most specimens of *H. morinii*. One frond fragment illustrated by Bartholin (1892, Taf. XII, fig. 1) shows a major vein near the inner edge of the blade as in *H. morinii* (our fig. 4*a*, 4*b*), but the Danish frond lacks an outer leaf margin, making further comparisons with that specimen difficult.

Another species in Cantrill's (1995) "deeply dissected fronds" group is *Hausmannia spuria* Richter (1906). While this species, like *H. morinii*, also shows paired teeth, the sinuses between pairs are much deeper than those of *H. morinii* (cf. fig. 1*d* with Taf. V, fig. 12 of Richter 1906).

Specimens described by Raciborski (1894) from the Triassic of Poland, *Hausmannia cracoviensis* (Racib.) Richter (=*Dictyophyllum cracoviense* Racib.), show the closest similarities to the Lower Cretaceous *H. morinii* from Apple Bay (table 1). Makarewiczówna (1928) synonymized the Polish specimens with *H. forchhammeri* Bartholin (1892), but Ôishi and Yamasita (1936) treated them as *H. cracoviensis* (Raciborski) Hirmer. The Polish specimens in question show prominent paired teeth similar to those of *H. morinii*; however, venation is delicate and not deeply incised as in the material from Vancouver Island (table 1). Teeth of the Polish specimens, like those of *H. morinii*, are 4–5 mm wide with convex margins and rounded tips but are much longer (5 mm) than those of *H. morinii* (2 mm). The Polish specimens show four to eight sporangia per areole, within the range of the British Columbia specimens, but spores are unknown.

Hausmannia morinii is the first permineralized species of *Hausmannia* and the first species of the genus that shows the combination of sporangia scattered within each areole, sporangium histology, and *in situ* spore characters. As such, this species provides a rare opportunity to compare the fossil fronds closely to those of extant dipterids. The suggestion that *Hausmannia* species are merely fossil representatives of the genus *Dipteris* goes back to the early literature (Seward and Dale 1901). Cantrill (1995, p. 246) states that, "To date no characters appear to differentiate *Dipteris* and *Hausmannia*, therefore *Hausmannia* is probably best regarded as the form genus for foliage of *Dipteris*." The novel combination of characters in *H. morinii*, however, distinguishes it from living dipterids and other fossil taxa.

Fronds

In the description of the living species *Dipteris novoguineensis*, Posthumus (1928) suggested that he was actually dealing with a "living fossil" because the fronds he described are very similar to those of *Hausmannia crenata* (Nathorst) Möller. Large highly dissected fertile fronds of *D. novoguineensis* have never been reported, but Johns and Bellamy (1979) report that this species can show some intermediates with *Dipteris conjugata*. This suggests that a closer examination may reveal a wider range of variation in frond
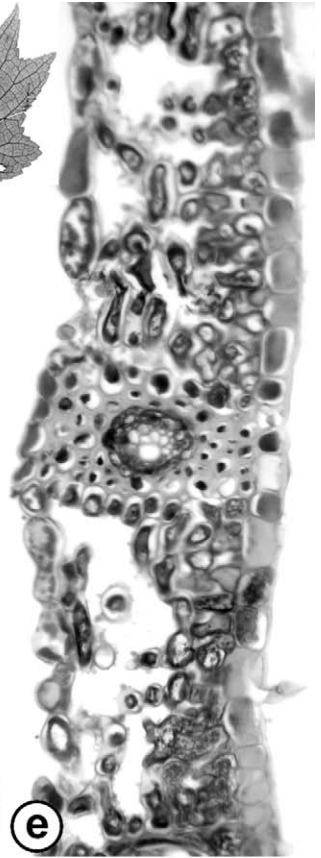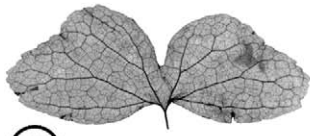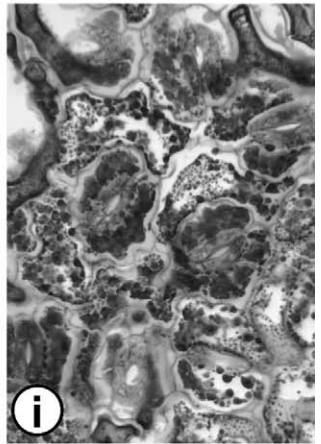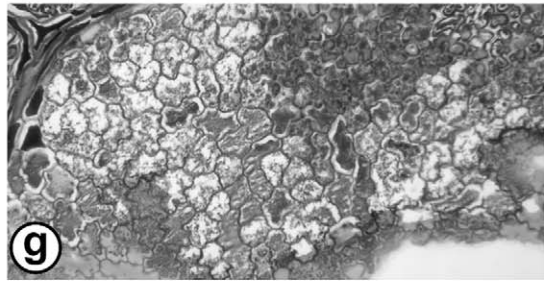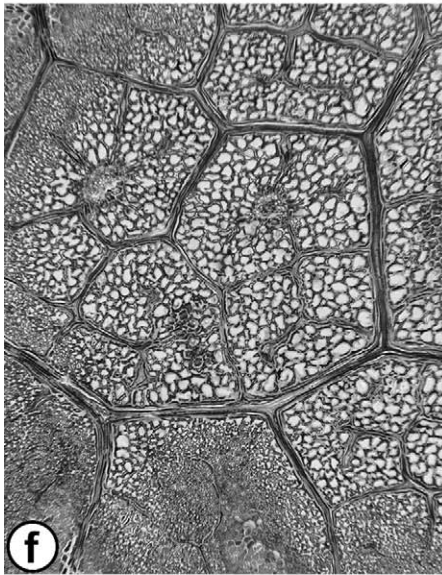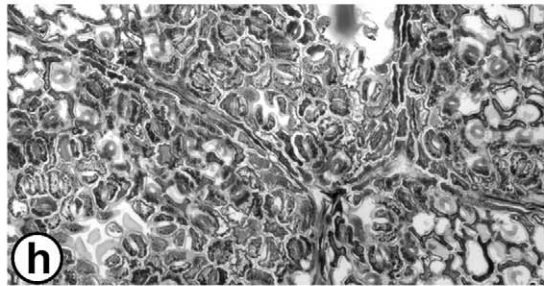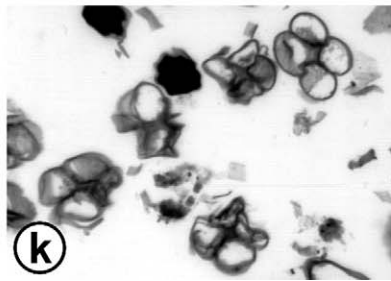
morphology than has been suspected for this species. Field observations (T. Feild, personal communication, 2005) also suggest greater variability than has been published. Perhaps, like species of *Cheiropleuria* (Kato et al. 2001), polyploids and/or hybrids occur among the various *Dipteris* populations that currently are growing in New Guinea. Further comparisons with *H. morinii* await more extensive collecting and field work in New Guinea.

Hausmannia morinii documents a combination of characters that are not present in extant species of *Dipteris*. Major veins extend into the teeth of *H. morinii* rather than ending in the major leaf segments (lobes) as in extant *Dipteris*. There also are larger numbers of teeth in fronds of *Dipteris* of comparable size. Kramer (1990*b*) points to the slightly unequal nature of the dichotomies in the blades of extant *Dipteris* species. Blade shape in *H. morinii* is similar to those described for *D. novoguineensis* (Posthumus 1928; Johns and Bellamy 1979), but teeth are fewer and larger in the fossils, and dichotomies of primary veins are more regular.

Whereas the abaxial surface of the areolae and sporangial attachments are deeply sunken in *H. morinii*, they are not in extant *Dipteris*. In both *H. morinii* and *D. conjugata*, the veins are imbedded in prominent sclerotic ribs. These ribs are more extensive in *H. morinii* and expand outward from the veins on the abaxial surface, giving the veins the "deeply incised" or "pronounced" appearance as seen in compressions of *Hausmannia* species (table 1; see also *H. dichotoma* in Harris 1961). Leaves of both living dipterids and *H. morinii* are characterized by loosely packed mesophyll cells toward the abaxial side of the lamina and display abaxial trichomes.

Epidermal patterns and stomatal distributions are similar for *H. morinii* and *D. conjugata*. Stomata are not sunken lower than the other abaxial epidermal cells, and in *H. morinii* they are most easily seen on the flanks of the vascular bundles in the outer zones of the small areolae. A few *Hausmannia* species also have been described with cuticles that reveal epidermal patterns. *Hausmannia pachyderma* Sukh-Dev (1972) from the Cretaceous of India and *Hausmannia* sp. (probably *H. dichotoma*) from the Wealden of France (Carpentier 1938) both show abaxial stomata with a random orientation in the areolae like those of *H. morinii*. Abaxial epidermal cells also have undulating outlines in all three fossil species (Carpentier 1938; Sukh-Dev 1972). However, epidermal cell shapes in *H. morinii* are most similar to the cells of *H. pachyderma* and *D. conjugata*, which have more sinuous outlines than those reported by Carpentier (1938). Stomata are anomocytic in both *H. pachyderma* and *H. morinii*, while those of *Cheiropleuria* and *Dipteris* are paracytic (Kramer 1990*a*, 1990*b*).

Sporangial Arrangement and Sporangia

Sporangia in *Dipteris* may be tightly clustered into sori that are circular to oval but can become confluent so that their individuality is lost (Seward and Dale 1901). In *Cheiropleuria* there is an "extensive soral area" (Bower 1915). Sporangia of *H. morinii*, however, are scattered within the small areolae, and there are no distinct sori with a common receptacle for the sporangia. Sporangia have been reported in several *Hausmannia* species (Raciborski 1894; Halle 1921; Ôishi 1932; Harris 1961; Cantrill 1995); however, details are often lacking. Fertile fronds in compressions often show bulges on the abaxial surface that are interpreted as sporangia. The actual sporangial structure has been reported for *Hausmannia dentata* (Ôishi 1932), *H. forchammeri* Bartholin var. *dentata* Möller (Halle 1921), and *H. cracoviensis* (Raciborski 1894). The annulus appears to be oblique or vertical in these species, but the sporangia are buried in the matrix so that interpretations of annulus orientation may not be reliable. Similarly, the observed number of sporangia per sorus depends on the preservation of such specimens and is subject to interpretation. Sporangia described for *H. forchammeri* var. *dentata* appear to be numerous and crowded, while those of *H. cracoviensis* are sparse, as in *H. morinii*.

In contrast to extant dipterids, where *Dipteris* species typically have 64 spores per sporangium and *Cheiropleuria* species can have up to 128 (Kramer 1990*a*, 1990*b*), sporangia of *H. morinii* produce only about 32. *Dipteris* and *Cheiropleuria* both show mixed soral development (Seward and Dale 1901; Bower 1915; Kramer 1990*a*, 1990*b*). This is probably true also for *Hausmannia morinii*, because there are differences in the size ranges, apparent wall thicknesses, and other features of the spores preserved in different sporangia. In *H. morinii* sporangia, where spores are smaller (18–20 μm), such spores typically are somewhat collapsed, with apparently thinner walls and with concave radial sides. This, combined with the small number (32) of spores per sporangium in *H. morinii*, contributed to difficulty in obtaining good spore samples for SEM.

Spores

Although many previous species of *Hausmannia* and other genera of extinct Dipteridaceae are described as being fertile, and the number of sporangia per sorus has been noted for several, *in situ* spores have been previously described and illustrated for very few (Watson 1969). Potonié (1967) macerated spores from Bartholin's (1892) type specimens of *H. forchhammeri*, which are housed in the Stockholm Riksmuseet collections. Krassilov (1969) reported spores from a

Fig. 6 Leaves of *Dipteris conjugata*. *a*, Frond from young rhizome. ×0.6. *b*, Frond from rhizome intermediate age between that seen in *a* and *c*. ×0.3. *c*, Whole leaf from mature rhizome showing bifurcating lamina with serrate margin and dichotomous major venation. ×0.27. *d*, Transverse section showing veins with surrounding sclerenchyma. SL13675, ×50. *e*, Transverse section showing leaf histology and vascular bundle; adaxial epidermis at right. SL13676, ×185. *f*, Paradermal section showing mesophyll and net venation pattern of higher order veins. SL13677, ×40. *g*, Paradermal section showing adaxial epidermis and mesophyll; vein at upper left. SL13677, ×140. *h*, Paradermal section showing mesophyll and abaxial epidermis with stomata SL13677, ×75. *i*, Enlarged paradermal section showing stomata SL13677, ×265. *j*, Paradermal section showing cluster of sporangia with spores. Note annulus is interrupted by stalk. SL1367l9, ×110. *k*, Enlarged paradermal section showing sporangial stalks in cross section. SL13678, ×290. *l*, Paradermal section showing sporangia in oblique longitudinal section, sporangial stalks in transverse section, and trichomes (arrow). SL13680, ×130.
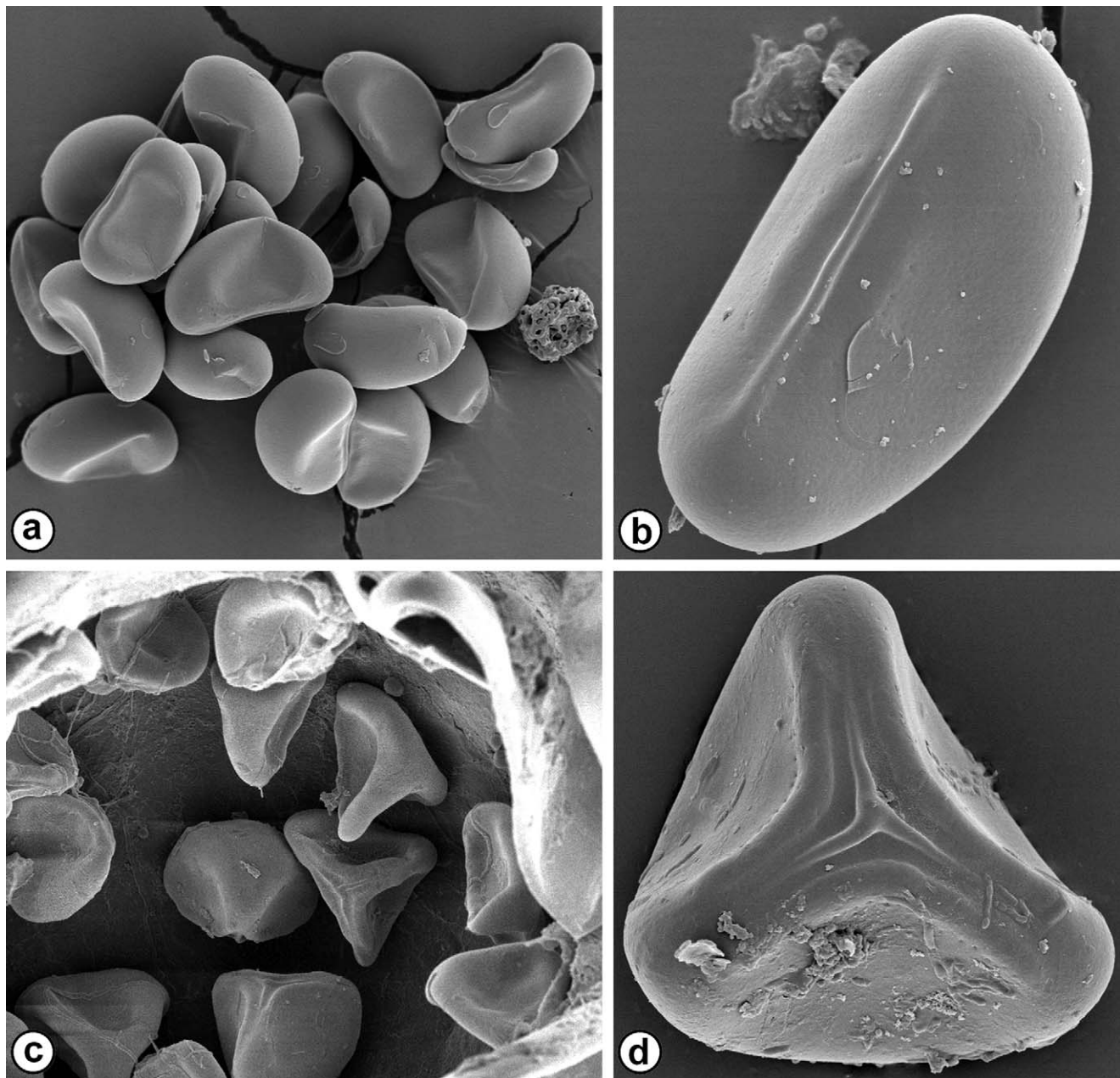
Fig. 7 Spores under SEM. *a*, *Dipteris conjugata* spores. ×675. *b*, Single enlarged monolete spore of *D. conjugata*. ×2500. *c*, *Cheiropleuria integrifolia* spores in sporangium. ×750. *d*, Single enlarged trilete spore of *C. integrifolia*. ×2300.

specimen he identified as *H. leeiana*, but these were not illustrated. In addition, a third specimen described as *Hausmannia* sp. has been macerated for spores (Antevs 1919). In all three the spores were reported as trilete, unlike the monolete spores of *Dipteris*. Potonié (1967, figs. 152, 153) illustrated spores 30 μm in diameter, generally comparable to *Cyathidites/Deltoidospora*, but Balme (1995) states that those spores are of a generally indistinct type referred to *Cyathidites minor* Couper.

Spores in the sporangia of *H. morinii* correspond to the sporae dispersae species *Cibotiumspora jurienensis* (Balme) Filatoff (=*Concavisporites jurienensis* Balme; A. Sweet, personal communication, 2005). These spores show a distal "kyrtome" (Potonié and Kremp 1955) or fold that is thicker at the ends of the laesurae (Raine et al. 2005). *Cibotiumspora* (32–44 μm) are found from the Triassic to Jurassic in New Zealand but also occur in China (Zhang and Grant-Mackie 2001; Raine et al. 2005). They are generally believed to belong to the Dicksoniaceae (Zhang and Grant-Mackie 2001), but their occurrence in sporangia of *H. morinii* documents that spores of this type are produced by dipterid ferns.

Among extant ferns, the spores of *H. morinii* are similar to those reported for *Matonia* R. Brown, which are tetrahedral and trilete, with concave interradial sides and a convex distal

Table 1

Comparison of *Hausmannia morinii* to Species of *Hausmannia* Dunker with Mostly Shallowly Dissected Fronds

Species	Leaf margin	Teeth	Tooth margin	Venation
H. morinii sp. nov.	Crenate	Paired	Convex	Pronounced
H. buchii (Andrae) Richter	Dentate	Single, large	Concave acute tips	Pronounced
H. cracoviensis (Raciborski) Richter	Crenate	Paired	Convex	Delicate
H. crenata (Nathorst) Möller	Crenate (deeply incised between pairs of teeth)	Paired	Convex	Pronounced
H. crookshankii Shah et Singh	Undulating	NA	NA	Pronounced
H. dentata Ôishi	Sinuate-dentate	Single, large	Acute	Pronounced
H. deferrariisi Feruglio	Crenate	NA	NA	
H. forchammeri Bartholin (in part)[a]	Crenate, irregular teeth	Nearly paired	Convex	Pronounced
H. indica Gupta	?	?	?	Pronounced
H. leeiana Sze	Undulating	NA	NA	Pronounced
H. nariwaensis Ôishi	Nearly entire-crenulate-undulating	NA	NA	Pronounced primaries
H. papilio Feruglio	Crenulate-undulating	NA	NA	Pronounced primaries

Sources. Modified from Cantrill (1995) with data added from Andrae (1853), Richter (1906), Raciborski (1894), Nathorst (1906), Möller (1902), Shah and Singh (1964), Ôishi (1932), Ôishi and Yamasita (1936), Feruglio (1937), Bartholin (1892), Gupta (1955), Sze (1933), and Herbst (1960).

[a] Bartholin (1982), figures 4 and 5 only; figure 6 was synonymized with *H. dichotoma* Dunker by Harris (1961).

surface (Kato 1993). However, in *Matonia* the exine usually shows granular deposits or a verrucate surface, and spores are generally larger, 50–58 μm (Tryon and Lugardon 1991; Kato 1993). Spores of Gleicheniaceae (*Gleichenia* subgenera *Diplopterygium* and *Gleichenia,* and the genus *Dicranopteris* subgenus *Dicranopteris*) are also similar in shape, but size ranges are slightly larger than in *H. morinii*, and many *Dicranopteris* grains have a foveolate surface (Tryon and Lugardon 1991).

Spores of *H. morinii* are most similar in size and surface ornamentation to diploid species of *Cheiropleuria* (Kato et al. 2001). Spores of *Cheiropleuria bicuspis* (a diploid) range from 22–30 (and up to 38) μm, while those of *Cheiropleuria parva* (diploid) are 20–25.5 μm (Erdtman and Sorsa 1971; Kato et al. 2001). By contrast, spores of the tetraploid species, *Cheiropleuria integrifolia* are larger and can range from 39 to 49 μm (Erdtman and Sorsa 1971; Kato et al. 2001).

Comparison to *Polyphacelus stormensis*

The only other anatomically preserved extinct dipterid consists of frond material described as *Polyphacelus stormensis* Yao, Taylor et Taylor from the Jurassic of Antarctica (Yao et al. 1991). The overall morphology of *P. stormensis* fronds is not known, but there are several orders of reticulate venation that form areolae similar to those of other dipterids. *Polyphacelus stormensis* lacks deeply sunken areolae on the abaxial surface as in *H. morinii*, and there is little or no sclerenchyma associated with individual veins of the lamina. Like extant dipterids and *H. morinii*, *P. stormensis* has loosely spaced mesophyll cells toward the abaxial side of the lamina, and it has abaxial trichomes. Fronds of *P. stormensis* are hypostomatic, like those of extant dipterids and *H. morinii*, but stomata are slightly sunken, with seven or more subsidiary cells. By contrast, the stomata of *H. morinii* and *D. conjugata* are not sunken lower than the other abaxial epidermal cells. Subsidiary cells have not been observed in *H. morinii*, and extant dipterids (including *Cheiropleuria*) are paracytic (Kramer 1990*a*, 1990*b*).

The sporangia of *P. stormensis* are tightly clustered into sori of 10–13 sporangia, whereas those of *H. morinii* are

scattered and appear to be soral only because several occur together within each areole. While the sporangia of *H. morinii* are small (up to 170 μm), with a short stalk and a nearly vertical annulus of eight to 10 cells, those of *P. stormensis* are much larger (up to 375 μm), with an elongated stalk and an oblique annulus consisting of 30–33 cells (Yao et al. 1991). The Antarctic material is silicified, and spores are poorly preserved; but they have been described as monolete, like those of living *Dipteris*. However, some trilete spores may also occur within the sporangia of *P. stormensis* (Yao et al. 1991).

Developmental Considerations

In the fossil record, the genus *Protorhipis* Andrae (1853) was used by various authors to describe *Hausmannia*-like fronds of the reniform type and those that are shallowly dissected. This genus was synonymized by Richter (1906) with *Hausmannia*. Other authors (e.g., Ôishi and Yamasita 1936) retain the name *Protorhipis* as a subgenus of *Hausmannia*. After examining *D. conjugata* in the field, it becomes obvious to us that several of the previously described *Protorhipis* species are probably juvenile forms of their *Hausmannia* counterparts at a given locality. Areolae are less regular in juvenile fronds of *Dipteris* (Bower 1915). The same may be true of some *Hausmannia* species (fig. 1*a*–1*c*). This hypothesis needs to be tested by extensive collecting at good *Hausmannia* sites, such as those in Nariwa, Japan (Ôishi 1932), or Quedlinburg, Germany (Richter 1906), and intermediates or attached fronds should be sought if these localities still exist. At the Quedlinburg site, a number of small fronds have been found lying parallel to one another, suggesting a common attachment to a rhizome (Richter 1906, Taf. III, fig. 2). At the Apple Bay locality, repeated attempts to find the rhizomes of *H. morinii* have proved problematic because of the depositional environment.

The best preserved and most extensively known *Hausmannia* species come from the Late Triassic of the Nariwa District, Okayama (old name, Bitchû) Prefecture, Japan (Ôishi 1932; Ôishi and Yamasita 1936). Two species are common at the same locality (locality no. 1) northwest of Nariwa City: *H. nariwaensis* Ôishi and *H. dentata* Ôishi (Ôishi

1932). *Hausmannia nariwaensis* has a reniform shallowly dissected frond, while *H. dentata* has a larger dissected frond (Ôishi 1932; Cantrill 1995). *Hausmannia nariwaensis* fronds are not fertile, while those of *H. dentata* are covered with sporangia, suggesting that they were from mature plants. A third species, described as *H. crenata* (Nathorst) Möller, is also present at this locality. Fronds of *H. crenata* are reniform and slightly more crenate than *H. nariwaensis* (Ôishi and Yamasita 1936). Further examination of this material and the local geology may help us to understand development in fossil dipterid ferns and their habitat of growth.

Paleoenvironment

The paleoecology of *Hausmannia* was described by Cantrill (1995), who showed that fossils of *H. papilio* Feruglio were buried in floodplain deposits, deposited by braided streams. He also noted that most occurrences of *Hausmannia* worldwide are not *in situ* and that associations of these plants with channel deposits suggest that they were stream-side dwellers. This is true of extant dipterids that may inhabit disturbed sites of forest clearing, roadsides, or stream banks (Johns and Bellamy 1979; Kato 2003). *Dipteris lobbiana* (Hook.) Moore is a rheophyte (Kato 2003) with highly dissected frond blades similar to some of the species of *Hausmannia* (Richter 1906).

Hausmannia morinii may have grown in disturbed habitats near a stream margin. The nodules at Apple Bay contain large numbers of small axes of cryptogams. Small pieces of three types of leafy moss gametophytes; a liverwort; *Lycopodium*, *Selaginella*, and *Equisetum* stems with leaves; fern sporelings; fertile *Osmunda*, *Anemia*, *Cyathea*, and dicksoniaceous and pteridaceous sori are all found in the same nodules with *H. morinii* (Stockey 2004). In addition, large numbers of pinaceous and taxodiaceous conifer needles and cones have been found along with the remains of these small delicate plants (personal observation). Most of the plant remains are abraded, and/or only short segments are preserved. It is believed that the fossils found at this site are the result of sudden floods or storm deposits that contain plants from the forest floor that have been transported by a river to the marine setting. Leaves of *H. morinii* are all fragmentary, which is the case for most *Hausmannia* species thus far described, a fact that contributes to the taxonomic confusion and large numbers of species described for the genus.

Dipteridaceae were most abundant and diverse in the late Triassic and early Jurassic (Herbst 1992; Tidwell and Ash 1994; Cantrill 1995; Collinson 1996, 2001). Corsin and Waterlot (1979) noted the presence of *Hausmannia* in a broad tropical belt during the Jurassic. While fewer genera of the Dipteridaceae were present in the Cretaceous, species of *Hausmannia* were widespread (Skog 2001). These plants grew in areas that were probably subject to monsoonal storms with high but seasonal rainfall, and during the Cretaceous in the Antarctic peninsula under mean annual temperatures that were calculated to range from 13°–27° C (Cantrill 1995).

While most of the fossils of *Hausmannia* are fragmentary remains, specimens such as those of *H. morinii* are providing more details of frond structure than have previously been described. The Apple Bay fossils are the first permineralized *Hausmannia* specimens. They allow us to describe, for the first time, details of frond anatomy, sporangial structure, and *in situ* spores for the genus. While *Hausmannia* shows closest anatomical similarities to species of *Dipteris*, spore morphology of the fossil genus is closer to that in the sister taxon *Cheiropleuria*. The unique set of characters, including venation patterns and sclerenchyma distribution, anomocytic stomata, scattered sporangia, trilete spores, and small number of spores per sporangium (i.e., 32), reveal that *Hausmannia* is a distinct genus of extinct Dipteridaceae, not merely a morphogenus for fossilized *Dipteris* fronds. It is hoped that further excavation at the Apple Bay locality will reveal rhizome and stipe anatomy of these ferns that, like many of their extant counterparts, probably grew in disturbed habitats at the edges of rivers.

Acknowledgments

Literature Cited

Andrae KT 1853 Beiträge zur Kentniss der fossilen Flora Sienbenbürgens und des Banates. Hof- und Staatsdruckerei, Wien. 48 pp.

Antevs E 1919 Die liassische Flora des Hörsandsteins. K Sven Vetenskapsakad Handl 59:3–71.

Balme BE 1995 Fossil in situ spores and pollen grains: an annotated catalogue. Rev Palaeobot Palynol 87:83–323.

Bartholin CT 1892 Nogle i den bornholmske Juraformation forekommende Planteforsteninger. Bot Tidsskr 18:12–28.

Bower FO 1915 Studies in the phylogeny of the Filicales. V. *Cheiropleuria bicuspis* (Bl.), Presl, and certain other related ferns. Ann Bot 29:495–429.

Cantrill D 1995 The occurrence of the fern *Hausmannia* Dunker (Dipteridaceae) in the Cretaceous of Alexander Island, Antarctica. Alcheringa 19:243–254.

Carpentier MA 1938 Utilisation de l'étude des cuticules pour la détermination des végétaux Wealdiens. Ann Soc Sci Brux 58:72–74.

Collinson ME 1996 "What use are fossil ferns?" 20 years on: with a review of the fossil history of extant pteridophyte families and genera. Pages 349–394 *in* JM Camus, M Gibby, RJ Johns, eds. Pteridology in perspective. Royal Botanic Gardens, Kew.

——— 2001 Cainozoic ferns and their distribution. Brittonia 53: 173–235.

Corsin P, M Waterlot 1979 Palaeobiogeography of the Dipteridaceae and Matoniaceae of the Mesozoic. Pages 51–70 *in* B Laskar, CSR Rao, eds. Fourth International Gondwana Symposium: papers, January 1977, Geological Survey of India, Calcutta. Hindustan, Delhi.

Daghlian CP, TN Taylor 1979 A new method for isolating pollen and spores from acetate peels for scanning electron microscopy. Rev Palaeobot Palynol 27:85–89.

Dunker W 1846 Monographie der norddeutschen Wealdenbildung. Ein Beitrag zur Geognosie und Naturgeschichte der Vorwelt. Oehme & Müller, Braunschweig. 83 pp.

Erdtman G, P Sorsa 1971 Pollen and spore morphology/plant taxonomy, Pteridophyta. Almqvist & Wiksell, Stockholm. 302 pp.

Feruglio E 1937 Dos nuevas de especies de "*Hausmannia*" de la Patagonia. Notas Mus La Plata 2:125–136.

Gupta KM 1955 *Hausmannia indica* sp. nov. Gupta, a dipteridaceous leaf from the Jurassic of Rajmahal Hills, Bihar (India). Proc Natl Acad Sci India Sect B 21:147–148.

Haggart JW, HW Tipper 1994 New results in Jura-Cretaceous stratigraphy, northern Vancouver Island, British Columbia. Geol Surv Can Curr Res 1994E:59–66.

Halle TG 1921 On the sporangia of some Mesozoic ferns. Ark Bot 17:1–28.

Harris TM 1961 The Yorkshire Jurassic flora. I. Thallophyta-Pteridophyta. British Museum of Natural History, London. 212 pp.

Herbst RE 1960 Descripcion de ejemplares fertiles de *Hausmannia* (*Protorhipis*) *papilio* Feruglio. Procedentes de los Estratos de Baqueró. Acta Geol Lilloana 3:227–232.

——— 1992 Propuesta de classification de las Dipteridaceae (Filicales) con un atlas de las especies de Argentina. D'Orbignyana 6: 1–71.

Hirmer M 1927 Handbuch der Paläobotanik. Vol 1. Thallophyta-Bryophyta-Pteridophyta. Oldenbourg, Munich. 708 pp.

Jeletzky JA 1976 Mesozoic and Tertiary rocks of Quatsino Sound, Vancouver Island, British Columbia. Geol Surv Can Bull 242:1–243.

Johansen DA 1940 Plant microtechnique. McGraw-Hill, New York. 523 pp.

Johns RJ, A Bellamy 1979 The Dipteridaceae. The ferns and fern allies of Papua New Guinea, pt. 5. Papua New Guinea Forestry College and Papua New Guinea University of Technology, Bulolo.

Joy KW, AJ Willis, WS Lacey 1956 A rapid cellulose peel technique in paleobotany. Ann Bot, NS, 20:635–637.

Kato M 1993 A taxonomic study of the genus *Matonia* (Matoniaceae). Blumea 38:167–172.

——— 2003 Evolution and adaptation in the rheophytes. Bunrui 3: 107–122. (In Japanese.)

Kato M, H Setoguchi 1999 An *rbc*L-based phylogeny and heteroblastic leaf morphology of Matoniaceae. Syst Bot 23:391–400.

Kato M, Y Yatabe, N Sahashi, N Murakami 2001 Taxonomic studies of *Cheiropleuria* (Dipteridaceae). Blumea 46:513–525.

Kramer KU 1990*a* Cheiropleuriaceae. Pages 68–69 *in* Kramer KU and PS Green, eds. The families and genera of vascular plants: pteridophytes and gymnosperms. Vol 1. Springer, Berlin.

——— 1990*b* Dipteridaceae. Pages 99–101 *in* KU Kramer and PS Green, eds. The families and genera of vascular plants: pteridophytes and gymnosperms. Vol 1. Springer, Berlin.

Krassilov VA 1969 A critical review of the taxonomy of fossil ferns of the U.S.S.R. with spores *in situ*. Iskopaemaya fauna I flora Dal'nego Vostoka, Akademia Nauk SSSR, Vladivostok 1:117–128. (In Russian with English summary.)

Makarewiczówna A 1928 Flora dolno-liasowa okolic Ostrowca (Étude sur la flore fossile du lias inferieur des environs d'Ostrowiec, Pologne) Prace Towarzystwa Przyjaciól Nauk w Wilnie. Wydziat nauk matamatycznych i przyrodniczych. Tome 3:1–49.

Möller H 1902 Bidrag teil Bornholms fossila Flora: Pteridofyter. Acta Reg Soc Physiogr Lund 13:1–63.

Nathorst AG 1906 Über *Dictyophyllum* und *Camptopteris spiralis*. K Sven Vetenskapsakad Handl 41:1–24.

Ôishi S 1932 The Rhaetic plants from the Nariwa District, Province Bitchû (Okayama Prefecture), Japan. J Fac Sci Hokkaido Univ Ser IV Geol Mineral 1:257–380.

Ôishi S, Yamasita 1936 On the fossil Dipteridaceae. J Fac Sci Hokkaido Univ Ser IV Geol Mineral 3:135–184.

Posthumus O 1928 *Dipteris novo-guineensis*, ein "lebendes Fossil." Recl Trav Bot Neerl 25:244–249.

Potonié R 1967 Versuch der Einordnung der fossilen Sporae dispersae in das phylogenetische System der Pflanzenfamilien. Pt 1. Thallophyta bis Gnetales. Forschungsberichte des Landes Nordrhein-Westfalen, no. 1761. Westdeutscher, Köln.

Potonié R, GOW Kremp 1955 Die sporae dispersae des Ruhrkarbons, ihre Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte. Palaeontogr Abt B Palaeophytol 98:1–136.

Raciborski M 1894 Flora kopalna ogniotrwalych glinek Krakowskich. Część. 1. Rodniowce (Archaegoniatae). Nakladem Akademii Umiejetnosci, Krakowie.

Raine JI, DC Mildenhall, EM Kennedy 2005 New Zealand fossil spores and pollen: an illustrated catalogue. Institute of Geological and Nuclear Sciences information series 68, version l. http://www. gns.cri.nz/what/earthhist/fossils/spore_pollen/catalog/index.htm.

Richter PB 1906 Beiträge zur Flora der unteren Kreide Quedlinburgs. Pt 1. Die Gattung *Hausmannia* Dunker und einige seltenere Pflanzenreste. Engelmann, Leipzig. 22 pp.

Rothwell GW 1987 Complex Paleozoic Filicales in the evolutionary radiation of ferns. Am J Bot 74:458–461.

Seward AC, E Dale 1901 On the structure and affinities of *Dipteris*, with notes on the geological history of the Dipteridinae. Philos Trans R Soc Lond B 194:487–513.

Shah SC, G Singh 1964 *Hausmannia crookshanki* sp. nov. from Jabalpur Series of India. Curr Sci 33:751–752.

Skog JE 2001 Biogeography of Mesozoic leptosporangiate ferns related to extant ferns. Brittonia 53:236–269.

Smith SY, GW Rothwell, RA Stockey 2003 *Cyathea cranhamii* sp. nov., anatomically preserved tree fern sori from the Lower Cretaceous of Vancouver Island, British Columbia. Am J Bot 90:755–760.

Stockey RA 2004 Anatomically preserved pteridophytes: unexpected diversity for the early Cretaceous. Abstracts of Ferns for the 21st Century: An International Symposium on Pteridophytes. Symposium 4: Fossils, pp. 25–26. Royal Botanic Garden, Edinburgh.

Sukh-Dev 1972 Ferns from the Cretaceous of Madhya Pradesh. 3. Dipteridaceae-*Hausmannia pachyderma* n. sp. Palaeobotanist 19: 281–283.

Sweet AR 2000 Applied research report on two samples of Cretaceous age from Vancouver Island, British Columbia as requested by J. Haggart (GSC Pacific, Vancouver). Geological Survey of Canada Paleontological Report ARS-2002-02.

Sze HC 1933 Beiträge zur mesozoichen Flora von China. Paleontologia Sinica, ser A, no. 4. Geological Survey of China, Peiping.

Tidwell WD, SR Ash 1994 A review of selected Triassic to early Cretaceous ferns. J Plant Res 107:417–442.

Tryon AF, B Lugardon 1991 Spores of the Pteridophyta. Springer, New York. 648 pp.

Watson J 1969 A revision of the English Wealden flora. I. Charales-Ginkgoales. Bull Brit Mus (Nat Hist) Geol 17:207–254.

Yao X, TN Taylor, EL Taylor 1991 Silicified dipterid ferns from the Jurassic of Antarctica. Rev Palaeobot Palynol 67:353–362.

Zhang W, A Grant-Mackie 2001 Late Triassic-Early Jurassic palynofloral assemblages from Murihiku strata of New Zealand, and comparisons with China. J R Soc NZ 31:575–683.