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THE OCCURRENCE OF THE FERN *ACROSTICHUM* IN OLIGOCENE VOLCANIC STRATA OF THE NORTHWESTERN ETHIOPIAN PLATEAU

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Oligocene (28–27 Ma) leaf fragments displaying morphological affinities with the fern *Acrostichum* are described from volcanic and fluvio-lacustrine strata near Chilga, west-southwest of Gondar on the northwestern Ethiopian Plateau. The fossils consist of elongate pinnae impressions and compressions, with secondary veins that arise from a midvein, anastomose, and create a characteristic reticulate venation without included free veinlets. Modern *Acrostichum* has a pantropical distribution associated with mangrove vegetation, but it occasionally occurs in freshwater settings. The Paleogene fossil record shows that *Acrostichum* usually is preserved in freshwater environments, as it is at Chilga, but elsewhere in Africa it is associated with mangrove taxa. At Chilga, *Acrostichum* occurs in a waterlogged terrain, as indicated by independent environmental assessment based on paleosol analyses. This fern occupied a greater geographic range than it does today in Africa, having occurred in the past on the Ethiopian Plateau in addition to the coastal areas at tropical latitudes.

Keywords: *Acrostichum*, Oligocene, Ethiopia, paleoenvironment, paleoclimate, range.

Introduction

Acrostichum is classified in the Pteridaceae and in the Polypod clade, according to morphological and molecular data (Tryon and Tryon 1982; Pryer et al. 2004; Schneider et al. 2004). This fern is characterized by gregarious growth and pantropical distribution, primarily in association with mangrove habitats (Chapman 1975; Collinson 2002). However, it can sometimes form dense thickets that occur in disturbed areas, freshwater inland settings along rivers, or marshes subjected to the influence of marine tides (Gates 1914; Alston 1959; Macnae 1968; Chapman 1975; Tryon and Tryon 1982; Tomlinson 1986; Thanikaimoni 1987; Spalding et al. 1997; McCarthy 1998).

In Africa today, *Acrostichum aureum* and *Acrostichum speciosum* occur associated with mangrove vegetation in both western and eastern tropical countries, including the island of Madagascar, but in western Africa *A. aureum* is also known from a single inland locality (Tardieu-Blot 1953, 1963; Alston 1959; Schelpe and Anthony 1986; Johns 1991; Saenger 1998; Parris 2001; Verdcourt 2002). The Cenozoic fossil record of *Acrostichum* in Africa consists of poorly dated, primarily coastal occurrences based on dispersed spores from Senegal (Caratini et al. 1991) and the Congo fan (Braccini et al. 1998) and macrofossils from Egypt (Tiffney 1991), Nigeria (Seward 1924), and Ethiopia (Beauchamp et al. 1973). The Ethiopian and Nigerian macrofossils are associated with a published morphological description, although they are not dated radiometrically, and the fossils from Ethiopia could be anywhere from Late Eocene to Miocene age (Hoffman et al. 1997). Furthermore, although Collinson (2002) suggests that *Acrostichum* is associated with freshwater more often during the Paleogene than the Neogene, there is no such assessment for the African continent (table 1). Newly discovered, well-dated, Late Oligocene *Acrostichum* pinnae and associated trilete spores from the Chilga strata in northwestern Ethiopia allow us to describe more thoroughly the fossil species *Acrostichum palaeoaureum* and to explore its ecological role as a pioneer plant in response to disturbance by volcanic ash deposition in a wet climate. Moreover, its occurrence across an area of nearly 100 km^2, in association with particular sedimentary settings, provides information about the important paleoecological role played by *Acrostichum* during the Paleogene in a part of Africa where it is absent today.

Study Area

The fossils studied here come from two localities in a continental basin known as Chilga, 60 km west-southwest of Gondar on the northwestern Ethiopian Plateau (Yemane et al. 1987*a*, 1987*b*; Kappelman et al. 2003; Feseha 2004; Jacobs et al. 2005; fig. 1). Variously thick (up to 150 m) intercalated sedimentary and volcanic rocks are widespread in the basin and are exposed by erosion from small streams or their tributaries (Feseha 2004). Oligocene sediment types consist of siltstones, claystones, sandstones, lignites, and tuff deposits formed in stream channel, overbank, ponded, and airfall

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Table 1

Fossil Record of *Acrostichum* in Africa

Taxon	Type of fossil	Age	Country of origin	Suggested environment	Reference
Acrostichum aureum	Dispersed spores	Paleocene	Walalane, Senegal	Mangrove-like coastal setting	Caratini et al. 1991
Acrostichites cf. *A. lanzaeanus*	Pinnule fragments	Eocene	Near Enugu, Nigeria	Back swamps of an estuarine setting	Seward 1924
Acrostichum palaeoaureum	Pinnule fragments	Oligocene (?)	Debre-Libanos, Ethiopia	Intertrappean fluvio-lacustrine deposits	Beauchamp et al. 1973
Acrostichum	Pinnule fragments	Late Eocene–Early Oligocene	Fayum depression, Egypt	Brackish and mangrove habitat	Tiffney 1991
A. aureum	Dispersed spores	Upper Miocene	Congo fan	Mangrove-like coastal setting	Braccini et al. 1998

settings (Jacobs et al. 2005). Description and analyses of these sediments, which include qualitative interpretation of paleosols, indicate that the Chilga strata were deposited on a fairly flat-lying plateau in a tropical humid climate (Jacobs et al. 2005). These strata overlie massive plateau flood basalts extruded by Oligocene volcanism (Yemane et al. 1987*a*; Hoffman et al. 1997; Jacobs et al. 2005). A single K-Ar radiometric age of 32.4 ± 1.6 Ma was obtained from basalt directly underlying the Chilga sedimentary strata (Kappelman et al. 2003). The *Acrostichum* fossils discussed here occur in lignitic and volcanic ash sediments within Ash-IV (Feseha 2004). Ash-IV is a 3–7-m-thick, basin-wide unit that occurs stratigraphically above the basalt and is dated by ^{40}Ar/^{39}Ar at 27.36 ± 0.11 Ma (Kappelman et al. 2003). Paleomagnetic reversal stratigraphy of Chilga sediments, which overlie the basalt and include Ash-IV, constrains their age to between 28 and 27 Ma, within the limits of Chron C9n (Kappelman et al. 2003; Jacobs et al. 2005; and see Feseha 2004). Thus, the *Acrostichum* from Chilga is not older than 28 Ma and, because of its occurrence within Ash-IV, is likely to be very close to 27.36 Ma.

Fossil vertebrates and plants are abundant at Chilga (Kappelman et al. 2003; Jacobs et al. 2005). The plant fossils described here outcrop at two localities (fig. 1): along the slopes of the Magargaria River (12°30′31.3″N, 37°6′57.3″E) and along the Guang River (12°30′43.44″N, 37°7′24.18″E). Fossils consist of frond fragments deposited in a dull brown, thin (∼10 cm), semiconsolidated lignitic layer (Magargaria River) within Ash-IV and within the uppermost ∼50 cm of the ash (Guang River). Palynological samples from the lignitic layer, prepared using standard laboratory techniques (Jones and Rowe 1999), produced abundant palynomorphs, including spores with affinities to *Acrostichum*.

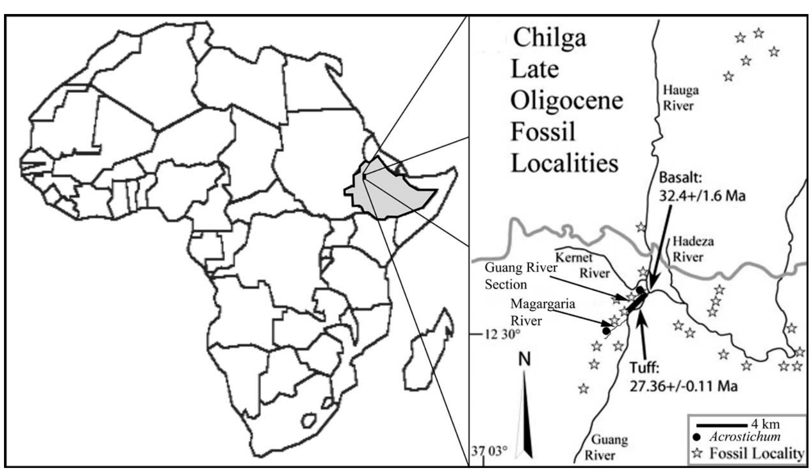


Fig. 1 Map of Ethiopia modified from Kappelman et al. (2003). Enlarged area shows fossil localities in Chilga on the northwestern Ethiopian Plateau, including those along the Guang River and the Magargaria River where *Acrostichum palaeoaureum* has been found. Radioisotopically dated tuff and basalt samples were collected from the areas indicated by the arrows.

Transmitted light microscopy and macrofossil images were obtained using a digital camera mounted on a microscope. The mineralogical composition of the host sediments for *Acrostichum* fossils was determined by x-ray diffraction analysis of powdered samples from the lignitic layer and the ash using a Rigaku Ultima III x-ray diffraction system equipped with CuKα radiation. Data were collected over 2°–70° 2θ in continuous scanning mode at 1° 2θ/min, 30 mA, and 40 kV (app. A). Fossil pinnae are stored under accession numbers CH-79 21 A-B, CH-79 22 A-B, and CH-79 29 for the fossils collected from the Magargaria River slopes and as CH-55 1, CH-55 2, CH-55 3, CH-55 4, CH-55 5, and CH-55 6 for the fossils from the Guang River section. Palynological slides are deposited under accession numbers CH-79 21 A-B #1 and CH-79 22 A-B #1, #2. All specimens will be stored permanently at the National Museum of Ethiopia, Addis Ababa.

Systematics

Family—Pteridaceae

*Genus—*Acrostichum *Linn.*

*Species—*Acrostichum palaeoaureum *Beauchamp, Lemoigne & Petrescu 1973 (Fig. 2*A*–2*H*)*

Description. The fossils consist of several impressions of fragments of sterile pinnae, a few of which are still attached to the stem by means of a petiole (fig. 2*A*). The stems (1.35–2.42 cm thick) appear erect and are ornamented with several parallel thin (0.1–.035 cm) grooves (fig. 2*B*), although this could be the result of diagenesis. Petioles arise in an alternate fashion from the stems (fig. 2*B*). Fragments of pinnae (12 – 15.9 cm × 6.7 – 7.8 cm) approximate a linear-lanceolate to elliptical shape (fig. 2*A*, 2*C*). Also, pinnae have an entire to slightly wavy margin and a cuneate to acute base (fig. 2*A*). Each pinna has a thick midvein (0.4–0.65 cm) that appears grooved and from which closely spaced secondary veins arise, first at an acute angle and then immediately curving at a nearly right angle (fig. 2*D*). The secondary veins anastomose repeatedly, forming numerous rectangular to polygonal areoles (four to six sides, 1.15 – 0.72 mm × 0.39 – 0.47 mm) that do not include free veinlets (fig. 2*E*). As a result, the pinnae have a characteristically reticulate venation pattern (fig. 2*E*).

Several trilete spores (26–54 μm) are present in the lignitic matrix surrounding the macrofossils of *Acrostichum* at the locality in the Magargaria River (fig. 2*F*–2*H*). The spores are triangular to subtriangular, have straight to slightly concave sides, and have rounded apices (fig. 2*F*). The exine (1 to ca. 2 μm thick) is granulate (grana ca. 1 μm) on the proximal face in many spores, while the distal one is laevigate (fig. 2*G*). The rays of the trilete mark are straight (although slightly undulating in a few specimens), taper toward the end, and extend up to three-quarters of the distance to the equatorial margin (fig. 2*G*, 2*H*). The exine appears variously folded in some specimens, while the laesura is ruptured, with the borders of the commissure bent outward in an inside-out pattern or just pulled apart from each other in other individuals (fig. 2*F*–2*H*).

Specimen numbers. CH-55 6 (fig. 2*A*), CH-55 4 (fig. 2*B*), CH-55 2 (fig. 2C), CH-79 21 A (fig. 2*D*), CH-79 21 B (fig. 2*E*), and CH-79 21 A-B #1 (fig. 2*F*–2*H*).

Locality. Chilga, ca. 60 km west-southwest of Gondar on the northwestern Ethiopian Plateau, along the slopes of the Magargaria River (12°30′31.3″N, 37°6′57.3″E) and along the Guang River (12°30′43.44″N, 37°7′24.18″E) (fig. 1).

Stratigraphic horizon. Volcanic ash deposits within Ash-IV in the Guang River section and lignitic deposits within Ash-IV in the Magargaria River.

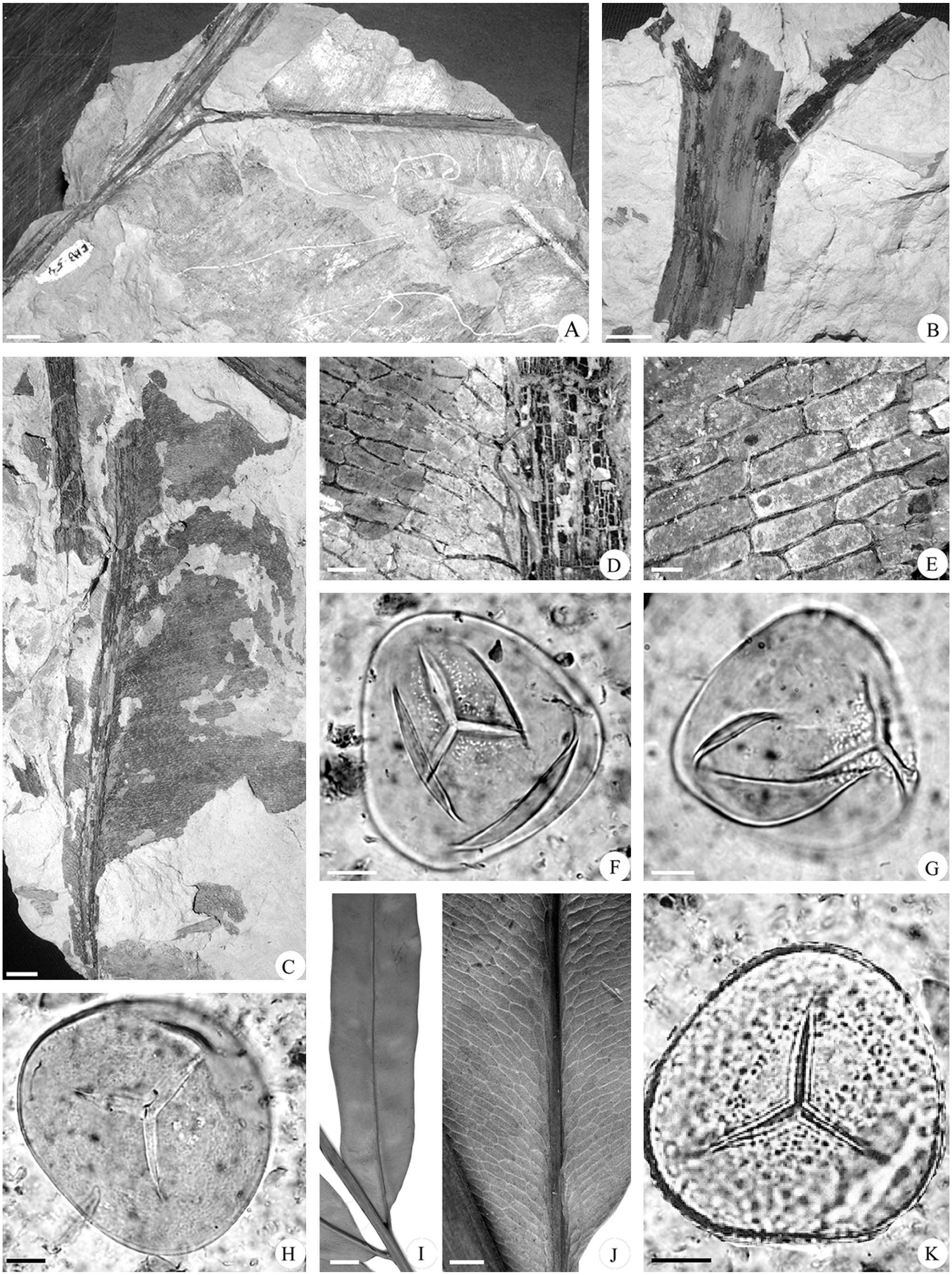
Age. 28–27 Ma (Late Oligocene).

Comparison

The presence on the fossils of several linear-lanceolate to elliptical petiolate pinnae impressions and compressions with an entire margin and numerous secondary veins arising at an acute angle from a thick midvein, which anastomose to form a characteristic reticulate venation pattern (fig. 2*A*–2*E*), is consistent with affinities to the extant genus *Acrostichum* (Tryon and Tryon 1982; Tomlinson 1986; Kramer and Green 1990) (fig. 2*I*, 2*J*). In addition, numerous triangular to subtriangular trilete granulate spores (fig. 2*F*–2*H*) morphologically similar to modern *Acrostichum* (fig. 2*K*) occur with the frond fragments in the lignitic matrix.

Of those characters that usually are preserved in fossils, reticulate nervation with areoles that do not include free veinlets is the most diagnostic and has been used to make a generic identification even for fragments of leaves with no other features preserved (Chandler 1962; Collinson 2001, 2002). Morphological characters including size, shape, the angle at which secondary veins arise from the midvein, characteristics of the areoles, and aspects of the pinnae margin and base have been used to characterize fossil morphospecies when individuals were found in geographically distant areas in strata of approximately similar age (Chandler 1962; Beauchamp et al. 1973; Awasthi et al. 1996); other morphospecies have been created based on the preservation of a greater number of characters, such as internal anatomy (Arnold and Daugherty 1963; Bonde and Kumaran 2002). However, a different and more complete set of characters not typically preserved among fragmentary fossils (e.g., position and number of fertile and infertile pinnae relative to each other) is used to distinguish among modern *Acrostichum* species (Tryon and Tryon 1982; Tomlinson 1986; Kramer and Green 1990). The Chilga fossils described here generally are larger in size than other fossil *Acrostichum* (Fritel 1910; Reid and Chandler 1926; Beauchamp et al. 1973; Sen and Banerjee 1995) and are variable with respect to characteristics of the margin and base of the pinnae (entire to slightly undulating, cuneate to acute base), the areoles (more or less elongate, four- to six-sided), and the angle at which secondary veins arise from the midvein (acute to right angle) (fig. 2*D*). This variability falls within the range seen among other fossil and modern *Acrostichum*, and some features of the fossils (e.g., grooves in the stem) may become more variable due to diagenetic processes (Collinson 1978).

An extensive fossil record of *Acrostichum* frond impressions and compressions and a few permineralized fronds,


A
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stems, and roots displaying a characteristic reticulate venation and other features similar to those seen in the specimens described here is known from the Cenozoic of the American, European, and African continents and also from the Upper Mesozoic of India (Jongmans 1954; Chandler 1962; Arnold and Daugherty 1963; Tanal 1972; Barthel 1976; Bonde and Kumaran 2002; Collinson 2002). Additionally, fossil spores, paraphyses, and sporangia morphologically comparable to *Acrostichum* are present in Cenozoic strata from the Americas, Europe, Africa, and India (Collinson 1978; Caratini et al. 1991; Kar 1992; Graham 1998; Kar and Singh 2003).

In Africa, *Acrostichum* is known from the Paleocene of Senegal (Caratini et al. 1991), Late Eocene–Early Oligocene of Egypt (Tiffney 1991; Kappelman et al. 1992), Oligocene (?) of Ethiopia (Beauchamp et al. 1973; plateau basalts can be anywhere from Eocene to Miocene age [Hoffman et al. 1997]), Upper Miocene of Congo (Braccini et al. 1998), and Paleogene of Nigeria (Seward 1924) (table 1). Of these, only the specimens from Egypt (Fayum), Nigeria (Enugu), and Ethiopia (Debre Libanos–Ethiopian Plateau) are macrofossils, and only the latter two include a morphological description; however, they both lack radiometric ages. In spite of an apparent resemblance of the fossils from Chilga to those from Nigeria, the very fragmentary nature of the latter hinders a more thorough comparison (Seward 1924). The Chilga specimens share characteristics of pinnae width, entire margin, and size and shape (rectangular) of areoles with those of specimens described from Debre-Libanos, Ethiopia (Beauchamp et al. 1973; pl. 5, figs. 1, 2) (fig. 2*A*, 2*C*, 2*E*). However, the specimens from Chilga are better preserved, and frond fragments are occasionally connected to the main stem by a petiole (fig. 2*A*–2*C*). Nevertheless, it seems reasonable, because of shared characters between the Chilga and Debre-Libanos fossils, to include the Chilga fossils in the species *Acrostichum palaeoaureum* (Beauchamp et al. 1973) rather than to erect a new species based on the available data, which we judge to be insufficient for new species diagnosis.

Triangular to subtriangular trilete, proximally granulate spores morphologically similar to those produced by modern *Acrostichum* are found in the lignitic matrix preserving the frond fragments (fig. 2*F*–2*H*, 2*K*). These same characters have frequently been described in fossil taxa and have been used to assign such specimens to modern *Acrostichum* (Collinson 1978; Caratini et al. 1991; Kar 1992; Graham 1998). However, some uncertainty exists as to whether dispersed rather than *in situ* spores with these characteristics should be assigned to *Acrostichum* (Collinson 1978, 2002). Tryon and Tryon (1982) posit that the aforementioned spore features are sufficient to consider them diagnostic for the genus. Nonetheless, both fossil (e.g., *Cyathidites australis*) and modern (e.g., *Pityrogramma trifoliata*) fern taxa other than *Acrostichum* display similar characters (Tryon and Tryon 1982; Schrank 1994). At Chilga, other fern macrofossils occur in the same lignitic layer, adding uncertainty to the affinity of the spores. Typically, *Acrostichum* spores have a size range between 30 and 70 μm, granules that could be widely or closely spaced on the proximal face, a triangular to subtriangular shape, an exine of variable thickness, and extensive trilete mark rays (Macko 1957; Collinson 1978; Tryon and Tryon 1982; Kramer and Green 1990). Some authors faced with this range of variation in a single fossil assemblage have opted to erect morphospecies to include fossil spores assignable to modern *Acrostichum* (e.g., Collinson 1978; Kar 1992), while others assigned similar individuals to modern species (e.g., Macko 1957; Caratini et al. 1991). The spores illustrated here share the range of variation present among living species and some genera. Overall morphology and the distribution of the granules are similar to the fossil *Acrostichum anglicum*, considered to be intermediate in ontogenetic development (Collinson 1978, pl. 2, fig. 2*D*) because of the presence of small grana (ca. 1 μm) concentrated around the trilete mark (fig. 2*G*). While they may be *A. anglicum*, the spores described here are dispersed rather than *in situ*, making their unequivocal assignment to genus or species difficult, and therefore affinities are hypothesized.

Ecological Significance of *Acrostichum*

Acrostichum is known to be a hydrophilic fern that is morphologically and anatomically adapted to grow where soils frequently are inundated by fresh or saline water. Such settings include coastal areas associated with mangrove vegetation, open salt marshes, coastal swamps, areas along estuarine rivers, and, less frequently, inland freshwater swamps and along river margins not subject to the influence of marine tides (Thomas 1905; Gates 1914; Tryon

Fig. 2 *Acrostichum palaeoaureum* Beauchamp, Lemoigne & Petrescu 1973, Oligocene pinna fragments and spores from near Gondar on the northwestern Ethiopian Plateau, Ethiopia. *A*, Pinna fragment with entire margin, cuneate to acute base, attached by means of a petiole to the stem. Sample CH-55 6. Scale bar = 10 mm. *B*, Grooved stem with petioles arranged in an alternation pattern. Sample CH-55 4. Scale bar = 10 mm. *C*, Linear-lanceolate to elliptical fragment of a pinna. Sample CH-55 2. Scale bar = 10 mm. *D*, Detail of a fragment of a pinna showing thick, grooved midvein from which secondary veins arise at angles approaching 90°. Sample CH-79 21 A. Scale bar = 0.5 mm. *E*, Fragment of a pinna showing anastomosed secondary veins forming a reticulum with areoles of a variable size and number of sides and without included free veinlets. Sample CH-79 21 B. Scale bar = 0.25 mm. *F*, Triangular trilete spore in proximal view with slightly convex sides and rounded apices. Slide CH-79 21 A-B #1. Scale bar = 10 μm. *G*, Trilete spore in oblique equatorial view showing a variously folded exine and granulate ornamentation concentrated around the trilete mark on the proximal face. Note slightly undulating rays of the trilete mark. Slide CH-79 21 A-B # 1. Scale bar = 10 μm. *H*, Subtriangular spore in proximal view with rays of the trilete mark extending up to three-quarters of the distance to the equatorial margin. Note separation between rays of the trilete mark. Slide CH-79 21 A-B # 1. Scale bar = 10 μm. *I*, Fragment of a pinna of modern *Acrostichum aureum* (BRIT, R. Randrianaivo et al., 368, Missouri Botanical Garden, MO, Mahajanga, Madagascar, 1999). Scale bar = 10 mm. *J*, Detail of pinna of modern *A. aureum* showing midvein and characteristic reticulate venation. (BRIT, R. Randrianaivo et al., 368, Missouri Botanical Garden, MO, Mahajanga, Madagascar, 1999). Scale bar = 2.5 mm. *K*, Proximal view of a spore of modern *A. aureum* (Roubik and Moreno 1991). Scale bar = 10 μm.

and Tryon 1982; Tomlinson 1986; Tryon 1989; Spalding et al. 1997). Members of this genus are widespread over tropical and subtropical American, Asian, Australian, and African continents, in areas where precipitation is ca. 1200 mm/yr and mean annual temperatures average 22°C (Gates 1914; Tardieu-Blot 1953, 1963; Rao et al. 1973; Tryon and Tryon 1982; Johns 1991; McCarthy 1998; Saenger 1998) (fig. 3; app. B). In Africa, these requisites are met between ca. 14°N and 6°S in the west and 0.5°S and 31°S to the east. However, *Acrostichum* is primarily a coastal plant in Africa (Tardieu-Blot 1953, 1963; Schelpe and Anthony 1986; Johns 1991; Saenger 1998; Verdcourt 2002); only a single occurrence is documented for inland territory in the west (Agona-Mankrong, Ghana; Alston 1959). The fossil record demonstrates that *Acrostichum* had a greater geographical distribution during the Paleogene within the interior of northeastern Africa, where it is absent today. Perhaps the combined influence of Cenozoic global climate change, the northward movement of Africa, and the elevation of the northwestern Ethiopian Plateau created more arid and cool conditions or an increase in seasonality, triggering the retreat of *Acrostichum* to wetter regions along the southeastern African coast (Chapman 1975; Bown et al. 1982; Yemane et al. 1987*a*, 1987*b*; Tryon 1989; Plaziat and Cavagnetto 1996; Saenger 1998; Jacobs 2004).

Acrostichum was widespread during the Paleogene in the American, European, and Asian continents in lacustrine to fluvio-lacustrine environments (Collinson 2001, 2002). From lithology, sedimentology, and qualitative paleosol analyses, the fossils at Chilga are known to have been deposited in a fluvio-lacustrine environment in a basin exhibiting relatively little topographic relief, and they were subject to repeated episodes of volcanic ashfall associated with the initial stages of East African Rift development (Kappelman et al. 2003; Jacobs et al. 2005). *Acrostichum* occurs at Chilga in stratigraphic layers composed of two different types of sediments, semiconsolidated lignite and tuff, which represent a rapid change in environment from poorly drained, swampy conditions to airfall or fluvially reworked ash. Modern *Acrostichum* has been found to occur in organic and clay-rich soils with acid to neutral pH and high salinity (Rao et al. 1973; Tomlinson 1986). Moreover, its occurrence is promoted by increasing acidification of the soil from the release of organic acids and/or natural or human disturbance of preexisting local vegetation (Rao et al. 1973; Tomlinson 1986; Thanikaimoni 1987; Saenger 1998).

Petrographic and x-ray diffraction analyses of lignites from Chilga (including the matrix in which *Acrostichum* occurs) document the presence of the clay mineral kaolinite, a weathering product associated with acid soils (app. A, fig. A1, *A*). In addition, the preservation of shallow *in situ* tree roots with primarily horizontal orientation in the lignitic matrix indicates poor drainage conditions that likely characterized a shallow, anoxic, or dysoxic groundwater table (Yemane et al. 1987*a*, 1987*b*; Feseha 2004; Jacobs et al. 2005). Petrographic and x-ray diffraction analyses of the *Acrostichum*-bearing ash overlying the lignite indicate the presence of short-range-order, poorly crystalline material that is likely to represent unweathered volcanic glass along with the clay mineral smectite (app. A, fig. A1, *B*). The ecological distinctiveness that allows *Acrostichum* to inhabit this type of environment derives at least partially from its dispersal ability as a pioneer plant (Tomlinson 1986; Saenger 1998) adapted to rapidly colonize disturbed habitats devoid of local vegetation (Page 2002). Open habitats provide the proper setting for the arrival of spores of colonizing taxa transported by wind currents (Parris 2001).

We suggest that the Chilga basin experienced recurrent disturbance due to episodic ashfall that dammed local streams and created shallow and closed bodies of water. These

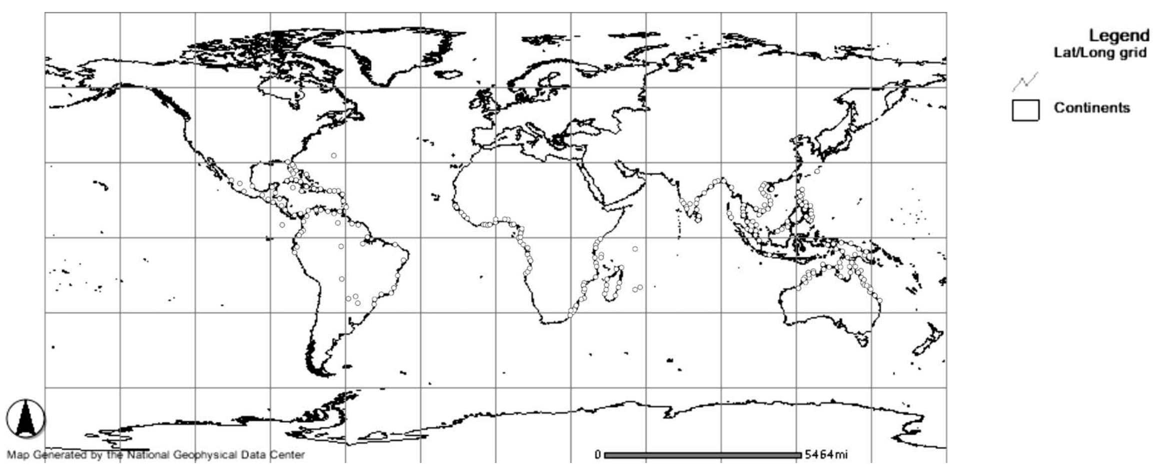

Fig. 3 World distribution of extant *Acrostichum* (from Tardieu-Blot 1953, 1963; Alston 1959; Johnson 1960; Rao et al. 1973; Chapman 1975; Tryon and Tryon 1982; Schelpe and Anthony 1986; Tomlinson 1986; Kramer and Green 1990; Johns 1991; Zuloaga and Morrone 1996; Spalding et al. 1997; McCarthy 1998; Saenger 1998; Verdcourt 2002; National Institute of Oceanography, Council of Scientific and Industrial Research, Goa, India, Gateway to the Indian Ocean [http://www.indian-ocean.org/bioinformatics/mangrove/MANGCD/geog/geog.htm]; University of South Florida, Institute for Systematic Botany, Atlas of Florida Vascular Plants [http://131.247.163.11/website/plantatlas/maps.asp?plantID=3611 and http://131.247.163.11/website/plantatlas/maps.asp?plantID=2191]; United Nations Environment Programme, World Conservation Monitoring Centre [http://sea.unep-wcmc.org/isdb/Taxonomy/tax-species-result.cfm?source=plants&genus=Acrostichum&species=aureum&tabname=distribution]; and Tropicos Vast specimen database, Missouri Botanical Garden Specimen Database.

ponded areas apparently evolved to become poorly drained swamps that were dominated by the accumulation of *in situ* organic matter during periods of volcanic quiescence. There, this accumulation of decaying plant debris from taxa that inhabited the margins of the swamp would have resulted in increasing acidification of the soil, which would have enhanced the occurrence of *Acrostichum*. Abrupt cessation of organic matter sedimentation from extensive, periodic, and rapid airfall accumulation would have formed an unstable land surface that would have been recurrently colonized by *Acrostichum* because of its high dispersal ability as well as its tolerance to disturbed habitat. This is made evident by its persistent *in situ* occurrence in the uppermost 50 cm of Ash-IV.

Conclusions

(1) This record from inland Ethiopia shows that fossil *Acrostichum* had a more extensive geographical range in interior Africa than does its modern counterpart. (2) The modern distribution of *Acrostichum* relative to temperature and precipitation indicates a moist tropical to subtropical paleoclimate for Chilga, and this is consistent with previous conclusions (Jacobs et al. 2005). (3) Successional environments in response to varying degrees of disturbance, including swamps and ash-covered landscapes, are indicated by sedimentology and paleosol types. *Acrostichum* is uniquely associated with these environments. (4) *Acrostichum* played a primary ecological role as a pioneer taxon at Chilga; we base this conclusion on the recurrent vertical stratigraphic occurrence of *Acrostichum* in readily disturbed sites at Chilga.

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Appendix A

X-ray Diffractograms of Powdered Samples

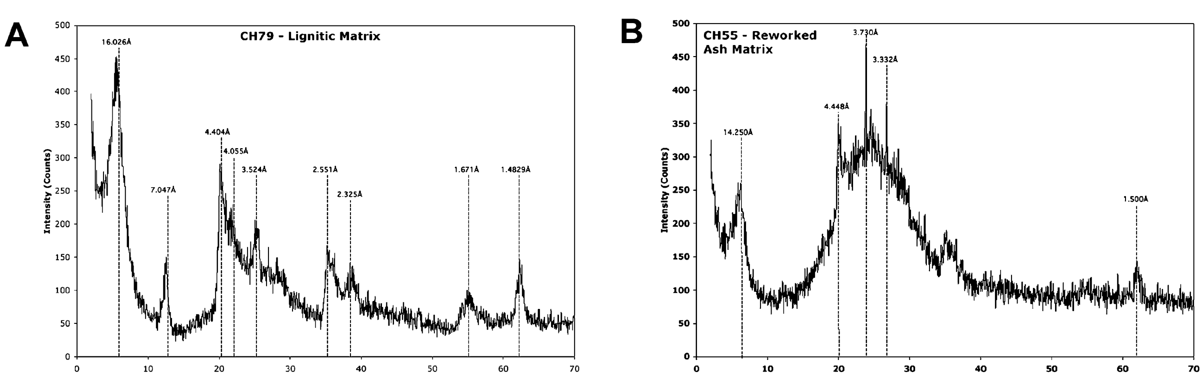

Fig. A1 X-ray diffractograms of powdered samples from (*A*) lignite-rich matrix associated with sample CH-79 and (*B*) reworked ash matrix associated with sample CH-55. Peak positions that were used for mineralogical identification are marked by dashed lines. Spacing (for CuKα, given in angstroms) is given above the dashed lines. *A*, Sharp peaks near ~16 and 7 Å probably reflect the d (001) of 2 : 1 phyllosilicate (smectite) and 1 : 1 phyllosilicate (kaolinite), respectively, in the sample. Other peaks that occur at larger 2θ (smaller Å) values correspond to other d (hkl) indices for smectite and kaolinite. *B*, The broad and low peak near ~14.2 Å probably reflects the d (001) of poorly ordered 2 : 1 phyllosilicate (smectite). The broad hump, beginning near 12° and ending near 40° 2θ is characteristic of the presence of short-range-order materials that do not have a crystalline structure (i.e., it is not a mineral).

Appendix B

World Distribution of Extant *Acrostichum*

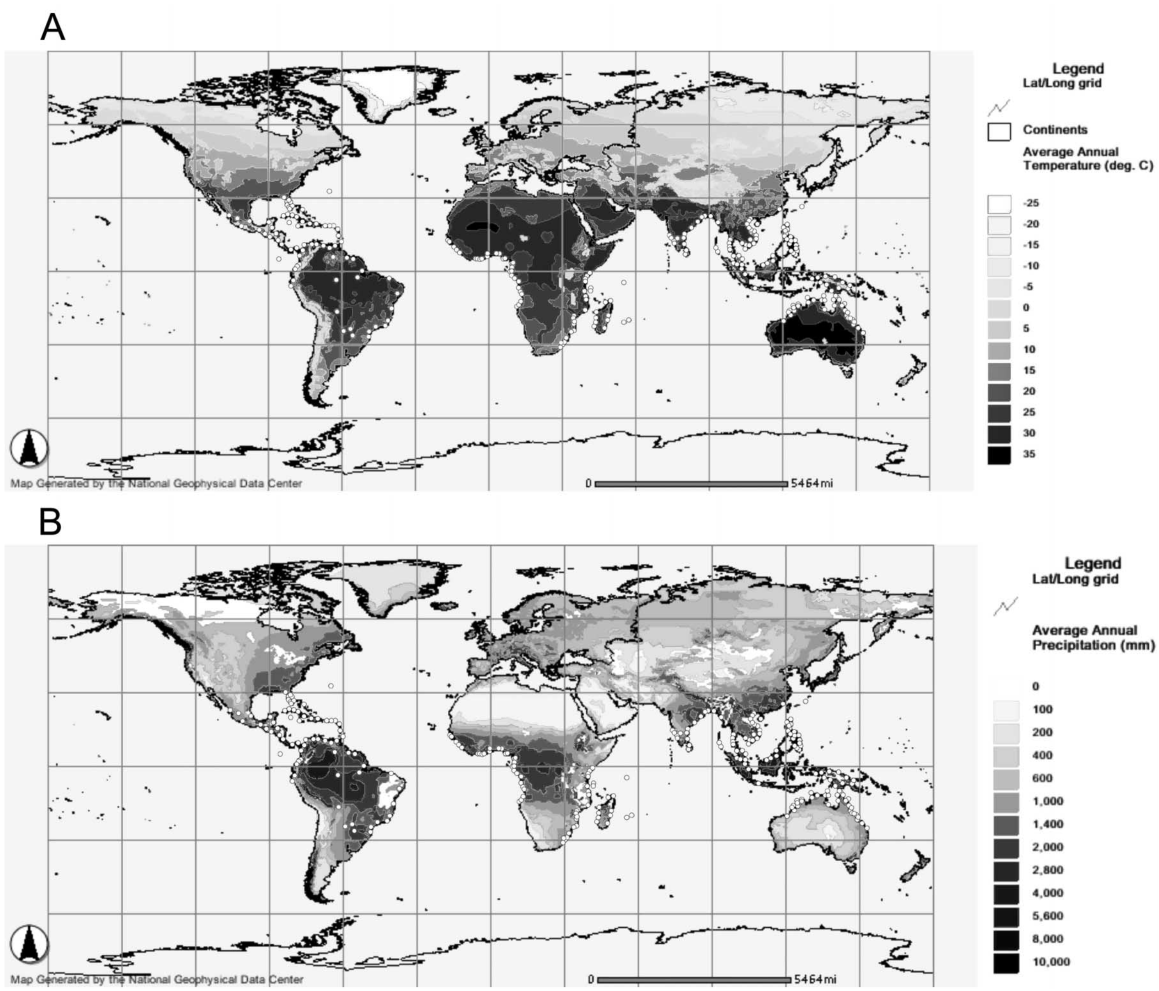

Fig. B1 World distribution of extant *Acrostichum* relative to mean annual temperature (*A*) and mean annual precipitation (*B*). Data from the National Oceanic and Atmospheric Administration interactive Geographical Information System (GIS) climate maps, National Geophysical Data Center (http://map.ngdc.noaa.gov/website/timeline/viewer.htm).

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