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 fluvo-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 Polypodi 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; Macnab 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 (Carattini et al. 1991) and the Congo Ian (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 palaeoareum* 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 km², 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. 1987a, 1987b; Kappelman et al. 2003; Feseha 2004; Jacobs et al. 2005; fig. 1). Various 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 silts, clays, sandstones, limestones, and tuff deposits formed in stream channel, overbank, ponded, and airfall...
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. 1987a; 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 40Ar/39Ar 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.

### Table 1

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

**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 palaeoaurum* 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 CuKa 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 palaeoareum Beauchamp, Lemoigne & Petrescu 1973 (fig. 2A–2H)

**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. 2A). The stems (1.35–2.42 cm thick) appear erect and are ornamented with several parallel thin (0.1–0.35 cm) grooves (fig. 2B), although this could be the result of diagenesis. Petioles arise in an alternate fashion from the stems (fig. 2B). Fragments of pinnae (12 – 15.9 cm × 6.7 – 7.8 cm) approximate a linear-lanceolate to elliptical shape (fig. 2A, 2C). Also, pinnae have an entire to slightly wavy margin and a cuneate to acute base (fig. 2A). 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. 2D). 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. 2E). As a result, the pinnae have a characteristically reticulate venation pattern (fig. 2E).

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. 2F–2H). The spores are triangular to subtriangular, have straight to slightly concave sides, and have rounded apices (fig. 2F). 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. 2G). The rays of the trilete mark are straight (although slightly undululating in a few specimens), taper toward the end, and extend up to three-quarters of the distance to the equatorial margin (fig. 2G, 2H). The exine appears variously folded in some specimens, while the laesa 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. 2F–2H).

**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. 2A–2E), is consistent with affinities to the extant genus *Acrostichum* (Tryon and Tryon 1982; Tomlinson 1986; Kramer and Green 1990) (fig. 2I, 2J). In addition, numerous triangular to subtriangular trilete granulate spores (fig. 2F–2H) morphologically similar to modern *Acrostichum* (fig. 2K) 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. 2D). 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,
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 1982).
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. 1987a, 1987b; 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. 1987a, 1987b; 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
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

![Map of World Distribution of Extant Acrostichum](image)

**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](http://map.ngdc.noaa.gov/website/timeline/viewer.htm).

**Literature Cited**


Yemane K, C Robert, R Bonefille 1987a Pollen and clay mineral assemblages of a Late Miocene lacustrine sequence from the northwestern Ethiopian highlands. Palaeogeogr Palaeoclimatol Palaeoecol 60:123–141.