Cratonia cotyledon* gen. et sp. nov.: a unique Cretaceous seedling related to *Welwitschia

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The fossil history of most extant seed plant groups is relatively well documented. Cycads, conifers and *Ginkgo* all have an extensive fossil record, and the understanding of early angiosperm diversity is increasing. The Gnetales are an exception. Few macrofossils have been described, and character evolution within the group is poorly known. *Cratonia cotyledon* is a new gnetalean fossil from the Early Cretaceous Crato Formation of Brazil. This well-preserved seedling consists of two cotyledons, a feeder and a root. The leaf surface shows polygonal epidermal cells and apparently paracytic or actinocyctic stomata. The cotyledons have a very specific venation pattern, shared only by *Cratonia* and *Welwitschia*, with parallel primary veins and secondary veins fusing to form inverted 'Y's between the main veins. Based on the 'Y'-venation and the presence of a feeder, we assign *Cratonia* to the *Gnetum*–*Welwitschia* clade. Fossil seedlings are unusual and this complete specimen with unambiguously welwitschioid characters is spectacular. *Cratonia* indicates that the evolutionary split between *Gnetum* and *Welwitschia* had occurred in the Early Cretaceous. Further, the close relationship between a West African plant and an east South American Early Cretaceous fossil is consistent with a major geological event: the rifting of the Gondwana continent.

Keywords: Gnetales; fossils; Cretaceous; *Welwitschia*; seedling; Crato Formation

1. INTRODUCTION

The evolutionary history of the Gnetales has mainly been inferred from the rich record of dispersed pollen grains in palynological assemblages. Polyplicate pollen grains of possible gnetalean affinity occur from the Permian (see Osborn *et al.* 1993), onwards. Grains similar to extant *Ephedra* and *Welwitschia* are particularly common in Early and mid-Cretaceous strata, where dispersed forms such as *Ephedripites*, *Equisetoporites* and *Welwitschiapites* have an extensive geographical distribution in low to middle palaeolatitudes (e.g. northern Gondwana; Crane & Lidgard 1989; Osborn *et al.* 1993; Crane 1996). However,

little is known about the plants that produced these pollen grains. Based on the dispersed fossil grains and the pronounced morphological and ecological differences between *Ephedra*, *Gnetum* and *Welwitschia*, it has long been assumed that recent diversity is a small remnant of 'former greatness'. Support for this idea in terms of gnetalean macrofossils is limited, however, and character evolution within the group is poorly understood. Crane (1996) suggested that gnetalean fossils might have been mistaken for conifers or angiosperms, owing to the absence of reliable criteria for characterization of the Gnetales. Several east Asian fossils, described as angiosperms, do in fact possess gnetalean characters and indicate that a considerable diversity of macrofossils from the Early Cretaceous can be assigned to the Gnetales (Crane & Upchurch 1987; Guo & Wu 2000). Among them are taxa with small cone-like reproductive structures, for example *Eragrosites changii* and *Liaoxia chenii* (Cao *et al.* 1998), and fossils with winged seeds, for example *Chaoyangia liangii* (Duan 1998) and *Gurvanella dictyoptera* (Krassilov 1982). *Drewria potomacensis* (Crane & Upchurch 1987), an Early Cretaceous fossil from the Potomac Group of Virginia, is one of the few fossils that has been unambiguously assigned to the Gnetales based, for example, on opposite phyllotaxis and a distinctive venation pattern. *Eoanthus zherikhinii* (Krassilov 1986), from the Early Cretaceous of Lake Baikal, has both ovules with an extended micropylar tube and *in situ* polyplicate pollen grains, characters that strongly associate it with modern Gnetales.

The plant described here is thus unusual in being a gnetalean fossil, but it is also extraordinary in other respects. Fossil seedlings have rarely been described, and this specimen is complete and well preserved. It can be unambiguously assigned to a modern plant group and its geographical and stratigraphical position is consistent with the geological history of the African and South American continents.

2. MATERIAL AND METHODS

The material used is from the Crato Formation of the Araripe Basin, northeastern Brazil, which consists of limestone of late Aptian to early Albian age (Early Cretaceous). The geology and geography of the locality have been described previously (Martill *et al.* 1993; Mohr & Friis 2000). The Crato flora comprise horsetails, schizaeaceous ferns, cycads or bennettitaleans, conifers, angiosperms and an unusually diverse set of plants with gnetalean affinities (Mohr & Friis 2000). A variety of dispersed, polyplicate pollen grains assigned to the Gnetales has been reported from the Crato (Santana) Formation (de Lima 1980; Osborn *et al.* 1993).

Most of the organic material of the Crato plants has typically been degraded by oxidation. This may have been concomitant with the precipitation of an orange iron oxide, as surface cell details have been cast. Internal cell anatomy may be present in some fossils. Occasionally, original tissue is preserved and several plants contain detailed information on vegetative and reproductive structures, and *in situ* pollen grains. *Cratonia* was investigated using a dissecting microscope and scanning electron microscope (SEM). Before our investigation, sediment had been removed mechanically to expose the fossil fully. Photographs were taken with a high contrast film, Kodak Technical Pan, using a dissecting microscope. Epidermal tissue (dark areas in the central parts of the specimen; figure 1) was removed from the specimen under a dissecting microscope, mounted on aluminium stubs and coated with gold in a sputter coater for examination with a Hitachi 4300 field emission SEM at 5 kV.

3. RESULTS

- (i) Spermatophyta.
- (ii) Order Gnetales.
- (iii) Genus *Cratonia*, gen. nov.

Figure 1. *Cratonia cotyledon* gen. et sp. nov. This Early Cretaceous fossil seedling consists of two partly overlapping cotyledons, a feeder (indicated by an arrow) and a root. Scale bar, 10 mm.

(a) Etymology

The generic name is adopted from the Crato Formation, Brazil.

(b) Generic diagnosis

The cotyledons are ovate and large, rounded at the base and apically convex. The leaf margins are entire. First-order veins are parallel and equidistant throughout the leaves. They fuse apically with a marginal vein. Vein dichotomies are not preserved. Second-order veins diverge at *ca.* 45° to the primary veins, and fuse with the opposite secondary veins in the middle of the area between the corresponding primaries to form a distinct pattern of irregularly fused, inverted 'Y's. The 'Y's are occasionally free ending. Epidermal cells are polygonal. The stomata are slightly sunken and distributed in a scattered pattern. Guard cells are longitudinally arranged, and the subsidiary cells are apparently paracytic or actinocytic. The hypocotyl region is inconspicuous. The root is laterally branched with a major, proximal branching. A thick, lateral feeder is positioned below the cotyledons.

(c) Type

Cratonia cotyledon sp. nov.

(d) Specific diagnosis

As for the genus.

(e) Etymology

From the basic feature and preservation stage of the plant.

(f) Holotype

1999/609, Institut für Paläontologie, Museum für Naturkunde, Berlin (figure 1).

(g) Locality

Araripe Basin, northeastern Brazil (Crato town: 7°10' S, 39°25' W).

(h) Stratigraphical position

Crato Formation (Martill *et al.* 1993), Lower Cretaceous, probably upper Aptian to lower Albian.

4. DISCUSSION

Cratonia cotyledon consists of two partly overlapping cotyledons, a root and a lateral feeder (figure 1). The seedling seems to lack a distinct hypocotyl region at the stage of development at which it is preserved. The cotyledons are ovate and large, 40 mm long and up to 18 mm wide. The oxide layer is rather thick, indicating that the leaves were leathery or fleshy. Guard cells, *ca.* 30 µm long, are preserved in some parts with iron oxide. They are longitudinally arranged, distributed in a scattered pattern and surrounded by weak impressions of subsidiary cells. Detailed epidermal structure is preserved in small areas (dark brown areas in the upper centre; figure 1). These parts show polygonal epidermal cells (figure 2c) and stomata. Stomata with subsidiary cells measure 60–70 µm and appear to be paracytic or actinocytic. However, details of the outer surface do not permit a more precise characterization of the stomata and no internal features have been observed.

Approximately 20 main longitudinal veins constitute the first order venation (figure 2a). The veins are evenly distributed, 1.0–1.6 mm (0.6–1.0 mm in the basal-most parts) from each other in a parallelodromous-like pattern. In contrast to the primary veins of monocotyledons, they seem to fuse successively with a marginal vein. The distance between the main veins is thus equal throughout the leaf, but the number of veins decreases. Dichotomies are absent in preserved regions (figure 2a). Higher-order veins arise from the main veins, *ca.* 1 mm from each other. These secondary veins fuse in pairs and form arches, shaped like inverted 'Y's (figure 2b). The single resulting vein can often be traced until it ultimately fuses with the next arch, but sometimes it seems to end freely. This distinct and unique venation pattern is, to our knowledge, known only from the leaves of *Welwitschia* (Rodin 1953, 1958), a monotypic genus now restricted to Namibia, western Africa. Similar arches, but less regular and distinct, are also present in the Early Cretaceous fossil *Drewria* (chevrons; Crane & Upchurch 1987), and perhaps in the 'sporophylls' (bracts?) of *Dechellyia gormani* (Ash 1972). The apparent differences in venation patterns between these two fossils and *Welwitschia* and *Cratonia* may reflect different stages of preservation. In *Welwitschia* seedlings, two vascular bundles enter each cotyledon and divide by simple dichotomies at the leaf base, into about six longitudinal main veins that produce the higher-order 'Y's (Rodin 1953). The primary vein branching of *Cratonia* is unknown because the basal parts of the cotyledons are poorly preserved.

Figure 2. *Cratonia cotyledon* gen. et sp. nov. (a–b) Photographs taken with Kodak Technical Pan Film, using a stereo dissecting microscope. (c) SEM micrograph. (a) Overlapping cotyledons. Note the distinct venation pattern, especially prominent in the upper parts. (b) Close-up of the ‘Y’-venation. (c) Polygonal epidermal cells. Scale bars: (a) 5 mm; (b) 1 mm; (c) 50 µm.

An elongated structure, *ca.* 5 mm long and 1.5 mm wide, occurs immediately below the cotyledons, perpendicular to the axis of the plant. It has a similar position and shape to the feeder, uniquely present in the seedlings of *Welwitschia* and its living sister taxon *Gnetum*. In living plants, the feeder arises from the hypocotyl region and functions as an absorptive structure. It stays in contact with the seed and can persist until the second or third pairs of leaves have been formed in a *Gnetum* seedling (Maheshwari & Vasil 1961). *Ephedra* lacks a well-developed feeder (but see Pearson 1929, p. 14). The root of *Cratonia* is *ca.* 60 mm long, approximately 1.5 times as long as the shoot. As in *Welwitschia*, the root seems to possess a major branch in its proximal part. The distal-most parts branch intensively and form tiny rootlets. These are partly detached, and the full length and morphology of the root are unknown.

When all characters of *Cratonia* are considered, there can be no doubt that this is a gnetalean plant. Higher-order venation, embryo feeder and stomata with distinct subsidiary cells distinguish *Welwitschia* and *Gnetum* from *Ephedra* and have been suggested as synapomorphies of the former two, in morphological analyses (Crane 1985; Doyle 1996). The presence of these characters in *Cratonia*

Figure 3. Character optimization on the hypothesized topology. Characters: 1, decussate phyllotaxis; 2, embryo feeder; 3, higher-order venation; 4, stomata with distinct subsidiary cells; 5, stomata distribution scattered; 6, Y-venation; 7, guard cells longitudinally arranged; 8, epidermal cells polygonal; 9, cotyledons broadly ovate.

excludes a relationship to any other group but the *Welwitschia*–*Gnetum* clade. Further, well-developed cotyledons with the distinct ‘Y’-venation and longitudinally arranged guard cells distributed in a scattered pattern are

present only in *Welwitschia*. All currently available data imply that *Cratonia* is closely related to *Welwitschia* (figure 3). *Cratonia* dates the evolutionary split between *Welwitschia* and its living sister group *Gnetum* to the Aptian–Albian or earlier. The discovery of a South American fossil, closely related to *Welwitschia*, also demonstrates that the *Welwitschia*-lineage was present in the equatorial Gondwana region prior to the final separation of Africa and South America during the Albian–Cenomanian.

The knowledge and understanding of historic Gnetales will probably expand rapidly in the immediate future through reinterpretations of previously described fossils and new discoveries in Brazil, Portugal and China. Information from fossils has been shown to enhance reconstruction of ancestral states in phylogenetic analyses (Gauthier *et al.* 1988) and additional information on character evolution and diversity within the Gnetales may contribute to resolve an intensely debated subject—the phylogeny of modern seed plants.

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