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ENDRESSINIA BRASILIANA, A MAGNOLIALEAN ANGIOSPERM FROM THE LOWER CRETACEOUS CRATO FORMATION (BRAZIL)

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A fossil angiosperm from the Brazilian Crato Formation, *Endressinia brasiliana* n. gen. n. sp., is described. The fossil consists of a branching axis with attached simple, narrowly ovate leaves and several terminal small flowers. One of these multiparted flowering structures is well preserved and seems close to anthesis. Tepals, staminodes, and apocarpous follicles show cellular details, such as ethereal cells. Broad staminodes bear lateral knobs that are interpreted as glands. The gynoecium consists of ca. 20 free apocarpous carpels. Among recent Magnoliales, several families share with *Endressinia* the floral feature of having staminodes. Only Himantandraceae and Eupomatiaceae share the character of having staminodes with glands, which are broad in *Eupomatia*. Thus, *Endressinia* might be sister to Eupomatiaceae; however, it also might represent an extinct lineage with convergent staminode morphology.

Keywords: fossil angiosperm, Magnoliales, Early Cretaceous, Crato Formation, Brazil.

Introduction

Recent morphological and molecular studies on basal lineages of angiosperms (Nandi et al. 1998; Soltis et al. 2000) group the Eumagnoliids into a stable clade, comprising the Magnoliales plus Laurales and Piperales plus Canellales, the latter with two families, Canellaceae and Winteraceae (Mathews and Donoghue 2000).

The Magnoliales consist of the Myristicaceae (APG II 2003; Chatrou 2003), Magnoliaceae, Degeneriaceae, Himantandraceae, and Eupomatiaceae plus Annonaceae on the basis of morphological and DNA sequence data. The latter two families seem to have a stable sister taxon relationship (Chatrou 2003; Sauquet et al. 2003). Phylogenetic analyses (Doyle and Endress 2000) show that Magnoliales seem to be more derived than Chloranthaceae or the ANITA grade but certainly remain one of the most important lineages in the early radiation of angiosperms. This result, based on characters of living taxa (Endress 2001), appears to be generally in congruence with data from the fossil record. During the Barremian to early Aptian, magnoliid angiosperms, including Chloranthaceae, already had reached a high degree of diversity (Friis et al. 1999, 2000). Unequivocal finds of Magnoliales are present but relatively rare (Crane et al. 1995; Friis et al. 1997).

Magnolialean and winteralean fossils have been described from strata as old as Barremian to early Aptian (Friis et al. 1997). Coarsely reticulate pollen grains with a circular sulcus assignable to Winteraceae have been described as *Walkeripollis gabonensis* from the late Barremian to early Aptian of Gabon (Doyle et al. 1990) and from the late Aptian to early Albian of Israel (Walker et al. 1983). Pollen of Magnoliales *sensu stricto* have been described as *Lethomasites fossulatus* from the Barremian to early Aptian of the Potomac Group of eastern North America (Ward et al. 1989). Dispersed follicles (Barreto et al. 2000) of the same age and stalks with several follicles attached to a receptacle—both from the Crato Formation—might also have affinities to Magnoliales, the latter perhaps to the Annonaceae (Mohr and Friis 2000).

During the mid-Cretaceous, flowers of magnolialean affinity seem to have become more diverse: *Lesqueria*, a fruiting axis from the upper Albian to mid-Cenomanian of the Dakota Formation (Kansas), consists of a head of tightly compacted follicles (Crane and Dilcher 1984). *Archaeanthus linnenbergeri* (also Dakota Formation) has been reconstructed as a multifollicular fruit (Dilcher and Crane 1984) consisting of many carpels. *Protomonimia* (Nishida and Nishida 1988), with more than 50 carpels, and *Hidakanthus*, with more than 170 follicles (Nishida et al. 1996), both from the Late Cretaceous of Hokkaido, Japan, also are considered to be magnolialean flowers. *Prisca reynoldsii* (Retallack and Dilcher 1981) from the early Cenomanian of North America might belong to this order as well. Seeds close in appearance to extant *Liriodendron* are known from the early Late Cretaceous of North America (Frumin and Friis 1996) and Kazakhstan (Frumin and Friis 1999). From the Cenomanian of Central Europe (Bohemia, Czech Republic), a trimerous flower, *Pecinovia annonoides*, has been assigned to the Annonaceae (Kvaček and Eklund 2003).

In this article, a new magnolialean taxon from the Early Cretaceous of northeastern Brazil, most probably of late Aptian age, is described. Characters hitherto not known in fossil Magnoliales are present that add new insights into early angiosperm evolution. Several of these specific features are still

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present in extant Magnolialean families and thus throw light on the ancientness and stability of floral structures.

Geology and Paleoenvironment of the Crato Formation

The Chapada do Araripe, located in the interior of the Brazilian Northeast, occupies an area of 12,200 km^2 and covers parts of the states of Ceará, Pernambuco, and Piaui (fig. 1). The origin and evolution of the Araripe sedimentary basin are related to the opening of the Atlantic Ocean and to the breakup of Western Gondwana. Over a Silurian/Devonian basement (Mauriti Formation), a Late Jurassic to Early Cretaceous sedimentary sequence (Syrio and Rios-Netto 2002) follows that is considered to have been deposited during the rift (Jurassic through Neocomian) and postrift (Aptian and Albian) phases. The latter sequence consists of the Santana Group, which includes the Rio da Batateira, Crato, Ipubi, Romualdo, and Arajara Formations (Neumann and Cabrera 1999) (fig. 2).

The Crato Formation consists of bedded (Plattenkalk) limestone that is considered to have been deposited in a lacustrine environment (Neumann et al. 2002). The large Aptian-Albian paleolake might have covered an area of 7500 km^2 (50 × 150 km). Successions of six different lakes have been discovered in which the limestones were deposited in shallow waters (Neumann et al. 2002). There is also evidence of marine ingressions during this time period. The fish fauna is considered to be marine (G. Arratia, personal communication), and pseudomorphs of salt crystals were observed on many slabs with plant fossils, indicating a (hyper)saline environment.

The age of the Crato Formation originally was considered to be Aptian to Albian (Doyle et al. 1982; Pons et al. 1990) and more recently was refined to the late Aptian (Doyle 1992; Pons et al. 1996). This was confirmed by Arai et al. (2001), who considered a Meso-Alagoas age for the Crato Formation, corresponding to the upper part of the *Sergipea variverrucata* (P-270) Palynozone and a *Cytheridea*(?) Ostracozone (NRT-011), which correlates to the late Aptian (fig. 2).

Material and Methods

The Crato limestone, of light beige to grayish brown color, in which *Endressinia* is embedded, is mined commercially south of Nova Olinda, in the area of Santana do Cariri in northeastern Brazil. These limestones are well known for their rich fauna and flora (Maisey 1991; Martill et al. 1993). The plant fossils, often preserved more or less completely, typically show excellent morphological features, but organic material is rarely preserved. Original tissues are typically replaced by iron oxides, which in most fossils precludes detailed preservation of cell structures, or are dissolved, leaving only imprints of the plant organs.

However, the fossil described here, housed at the paleobotanical collection of the Museum of Natural History's Department of Paleontology in Berlin, has remarkable details preserved. The fossil was studied under a Leica M 420 Microscope with magnifications up to × 80. The photographs were taken with a Nikon 801 camera and a 60-mm Nikkor macro-objective. Agfa PAN APX 25 film was used for the photographs. The SEM pictures were taken at a Hitachi 4300 field emission SEM at 5 kV at the Swedish Museum of Natural History, Stockholm.

Southern Hemisphere Angiosperm Floras

Early Cretaceous Southern Hemisphere floras are rare, compared with those from the Northern Hemisphere (Dilcher 2001). South American angiosperm remains of this age (Romero and Archangelsky 1986; Archangelsky and Taylor 1993) are mostly from high latitudes and are of low diversity (Drinnan and Crane 1990). In Argentina, a leaf of Aptian age, originally interpreted as nymphaeaphyll (Passalia et al. 2003), exhibits imprints of glands and therefore may belong to magnoliids rather than to Nymphaeales. A leaf flora with

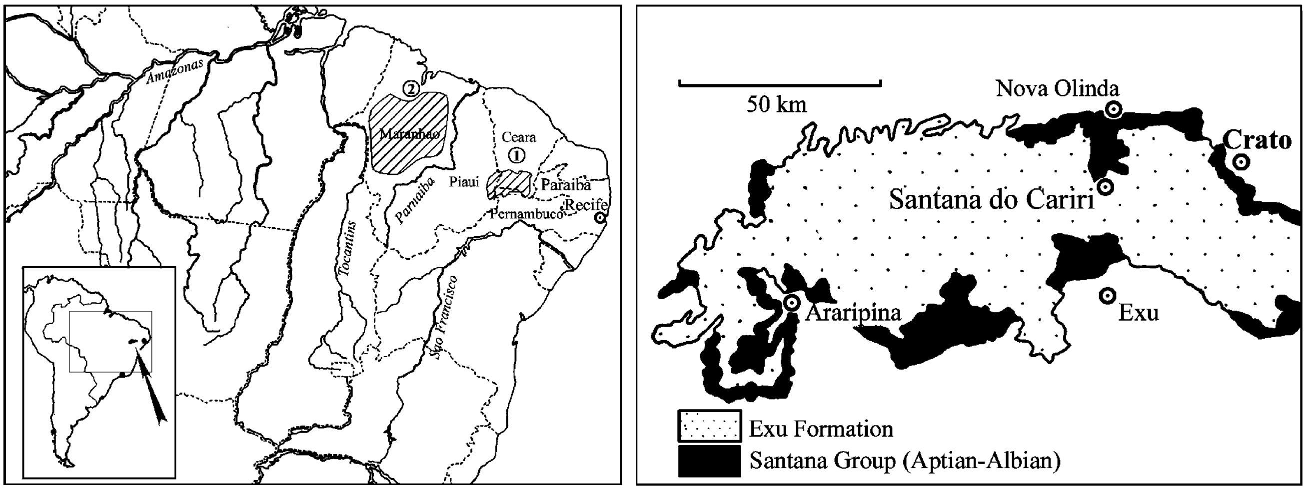
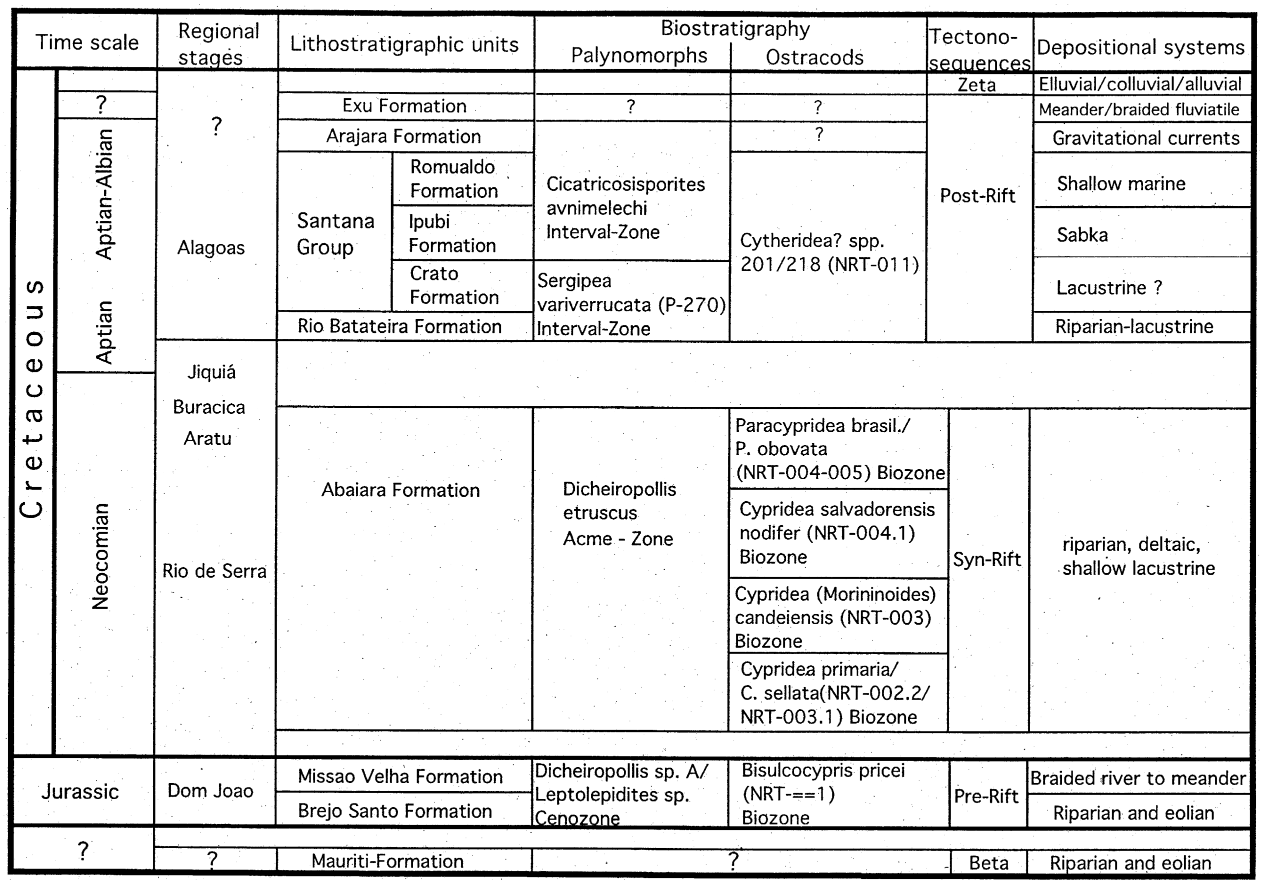


Fig. 1 *Left*, Location of the Araripe and Parnaiba Basins of northeastern Brazil. *Right*, Simplified geological map of the Araripe sedimentary basin.



Time scale		Regional stages	Lithostratigraphic units		Biostratigraphy		Tectono-sequences	Depositional systems
					Palynomorphs	Ostracods		
Cretaceous		?					Zeta	Elluvial/colluvial/alluvial
	?		Exu Formation		?	?	Post-Rift	Meander/braided fluviatile
	Aptian-Albian		Arajara Formation		Cicatricosisporites avnimelechi Interval-Zone	?		Gravitational currents
		Alagoas	Santana Group	Romualdo Formation		Cytheridea? spp. 201/218 (NRT-011)		Shallow marine
				Ipubi Formation				Sabka
	Aptian			Crato Formation	Sergipea variverrucata (P-270) Interval-Zone			Lacustrine ?
			Rio Batateira Formation					Riparian-lacustrine
	Neocomian	Jiquiá Buracica Aratu						
		Rio de Serra	Abaiara Formation		Dicheiropollis etruscus Acme - Zone	Paracypridea brasil./ P. obovata (NRT-004-005) Biozone	Syn-Rift	riparian, deltaic, shallow lacustrine
						Cypridea salvadorensis nodifer (NRT-004.1) Biozone		
						Cypridea (Morininoides) candeiensis (NRT-003) Biozone		
						Cypridea primaria/ C. sellata(NRT-002.2/ NRT-003.1) Biozone		
Jurassic		Dom Joao	Missao Velha Formation		Dicheiropollis sp. A/ Leptolepidites sp. Cenozone	Bisulcocypris pricei (NRT-==1) Biozone	Pre-Rift	Braided river to meander
			Brejo Santo Formation					Riparian and eolian
?		?	Mauriti-Formation		?		Beta	Riparian and eolian

Fig. 2 Sedimentary sequences of the Araripe Basin and stratigraphic correlations (data mainly from Neumann and Cabrera 1999; Arai et al. 2001).

myrtoid leaves from Patagonia might be of late Early Cretaceous age (Passalia et al. 2001). Other Southern Hemisphere floras of Aptian to early Albian age from Australia, such as the Koonwarra flora (Taylor and Hickey 1990), seem to contain angiosperms in minor quantities and at low diversity (Douglas 1994). Diversity increases to seven leaf species only during the late Albian in high latitudes, such as Antarctica (Cantrill and Nichols 1996). In southern high latitudes, the taxonomic, as well as the quantitative, increase from the late Albian to the early Cenomanian is also reflected in the pollen record, e.g., at the Kerguelen Plateau, where during this time interval angiosperm pollen reach 3%–5% of the palynomorph spectra (Mohr 1995).

By the late Early Cretaceous, low-latitude floras, in contrast, exhibit relatively high species diversity of angiosperms. On the basis of the pollen record, angiosperms reach 20%–40% of the general diversity (Crane and Lidgard 1989).

Megafloras are known from the Early Cretaceous of Colombia (Pons 1988; van Waveren et al. 2002). These floras seem to be dominated by ferns or gymnosperms. One seed genus, *Sterculiocarpus*, might be assignable to angiosperms. Early Cretaceous Brazilian floras are known from the Crato Formation (Araripe Basin) and from the Codó Formation (Parnaiba Basin), both of northeastern Brazil (fig. 1). From the Codó Formation, only one taxon is known, considered by the authors to represent a nymphaealean plant (Duarte and Silva Santos 1993). Thus, the Crato plant fossils reveal for the first time the significance and evolutionary status of angiosperms in the low-latitude paleoequatorial vegetation.

The Crato Flora

The Crato flora is diverse, comprising ca. 70 taxa. Palynological studies by de Lima (1978, 1980, 1989), Pons et al. (1990, 1996), Arai et al. (2001), and Arai and Machado-Coelho (2001), as well as studies of the macroflora, revealed a wide array of spore-bearing and seed plants. Horsetails, lycopods, including *Isoetes*, and filicophytes are present. Schizaeaceae is the most abundant fern family (Crane 1991), partly identified as *Anemia* (de Oliveira-Babinsky and de Lima 1991).

The gymnosperm component consists of conifers, cycads, and gnetophytes. Among the conifers, cones and shoots of Araucariaceae (Duarte 1985; Bernardes-de-Oliveira et al. 1993), *Lindleycladus* (Kunzmann et al. 2004), and Cheirolepidiaceae (*Pseudofrenelopsis* and *Tomaxellia*) were observed. Among the gnetophytes, representatives of Ephedraceae (Pons et al. 1992; Osborn et al. 1993; Mohr et al. 2004) and a plant related to *Welwitschia* were described (Rydin et al.

2003). In addition, there are several gnetophyte taxa that do not resemble any living genus.

The angiosperm component of the Crato flora is unique in that flowering structures connected to vegetative parts are preserved. Almost all of these plant fossils belong to the dicots, except for one putative monocot taxon, *Trifurcatia flabellata* (Mohr and Rydin 2002). Water plants, partly closely related to the Nymphaeales, are relatively common (Mohr and Friis 2000). A magnoliid taxon, *Araripia florifera*, shows similarities to the Calycanthaceae but also shares features with Magnoliales (Mohr and Eklund 2003). Several stalks with free carpels attached to a receptacle might be of magnolialean origin (Mohr and Friis 2000), as might an unpublished pluricarpellate flowering structure that resembles a young inflorescence of *Magnolia*. Eudicots may have been present as well, perhaps belonging to early platanoids.

Systematic Descriptions

Order—Magnoliales

Family—Unknown

*Genus—*Endressinia *Mohr and Bernardes-de-Oliveira*

Diagnosis. Angiosperm, axis with leaves and multiparted flowers. Leaves small, narrowly ovate, pinnate, second-order venation brochidodromous, margin entire. Higher-order veins very irregular. Flowers solitary, axillary, consisting of tepals and spirally arranged inner organs, borne on a flattened receptacle. Toward the center, several rows of staminodes with marginal glands. In the center, several apocarpous follicles.

Etymology. In honor of Peter K. Endress (Zürich), who has published on various aspects of basal angiosperm flowers.

Type species. *Endressinia brasiliana* Mohr and Bernardes-de-Oliveira.

*Species—*Endressinia brasiliana *Mohr and Bernardes-de-Oliveira*

Holotype. Specimen MB. PB. 2001/1455 (figs. 3–7).

Repository. Museum of Natural History, Institute of Paleontology, Berlin, Germany.

Type locality. Open-air pit south of Nova Olinda.

Type stratum. Crato Formation, Araripe Basin.

Etymology. Named after the provenance of the fossil, Brazil.

Diagnosis. Characters as for the genus. Small (less than or ca. 10 mm in diameter), multiparted flowers, consisting of tepals and spirally arranged inner organs, borne on a more or less flattened receptacle. Toward the center, several spirally arranged rows of flat, elongated staminodes with marginal glands. In the center, ca. 20 narrowly apocarpous follicles with small, distinct, glabrous stigmatic area.

General Description

Axis

The branching twig/axis is ca. 8 cm in length. The width of this twig at the base is ca. 0.3 cm. At least three branchings can be observed. The flowers are terminal on branches of at least fourth order (fig. 3*A*).

The last-order axes are thin, less than 1 mm in width. Axes are probably woody; however, it cannot be excluded that *Endressinia* was herbaceous. Internal structures are not well preserved, but scalariform pitting seems to have been present (fig. 4*C*–4*F*).

Leaves

Leaves are alternately arranged, simple, narrowly ovate to obovate, with an entire margin (fig. 3*A*, 3*B*). Petioles are short or absent. No complete leaves are preserved, but the estimated length of mature leaves is ca. 4 cm or more. Margins are also not completely preserved, but we deduce from the remains that the width would have been at least 1.0–1.5 cm in the largest leaf. Venation is pinnate, brochidodromous, and poorly organized (fig. 3*B*). Primary and secondary veins are clearly visible; third-order veins are only partly visible. Leaves show long epidermis cells on the surface (fig. 3*C*) and are densely covered on both sides with small spherical cells that are considered to represent ethereal oil cells (fig. 3*D*). Irregularly distributed stomata seem to have been present on one leaf surface (fig. 3*E*, 3*F*). The iron oxide layer that replaced the organic matter of the leaf is rather thick, indicating that the leaf was originally tough and coriaceous.

Flowering Structures

Flowers are solitary, apparently axillary, and borne on long pedicels that are ca. 1.2 mm in diameter. One or two flowers (flowers *a* and *b*; fig. 3*A*) appear to be preserved at a stage close to anthesis, while two flowers seem to have been buds (flowers *c* and *d*; fig. 3*A*) when the twig was imbedded. The flowers are hypogynous, apparently bisexual, multiparted, 4–5 mm long, and 6–7 mm in diameter. There are numerous floral parts borne on a flattened to slightly concave receptacle (fig. 4*A*). The cores of the flowers are three-dimensionally preserved, while the outer parts are preserved as impressions.

The flowers appear to have a few large broad tepals (visible at flowers *a* and *b*; fig. 3*A*; fig. 4*A*, 4*B*). They are seen as impressions, but their original number and shape are not clear. They are characterized by the presence of densely spaced, spherical cells, ca. 35–40 μm in diameter, interpreted as ethereal oil cells (fig. 4*A*, 4*B*).

In one flower (flower *a*; fig. 3*A*), the core floral organs are still present, while in the other flowers, these parts have fallen out or were destroyed by oxidation. The following description is exclusively based on this one flower. The tepals surround numerous flattened, narrow, and densely packed structures (fig. 5*A*). The nature of these structures is not clear. The outermost might belong partly to the perianth or the androecium. This is not clear, because stamens and/or pollen grains have not been observed in any of the flowers of *Endressinia* because of the poor preservation of the outer flower organs, which are more densely packed and altered. Along the margins of the innermost narrow structures,

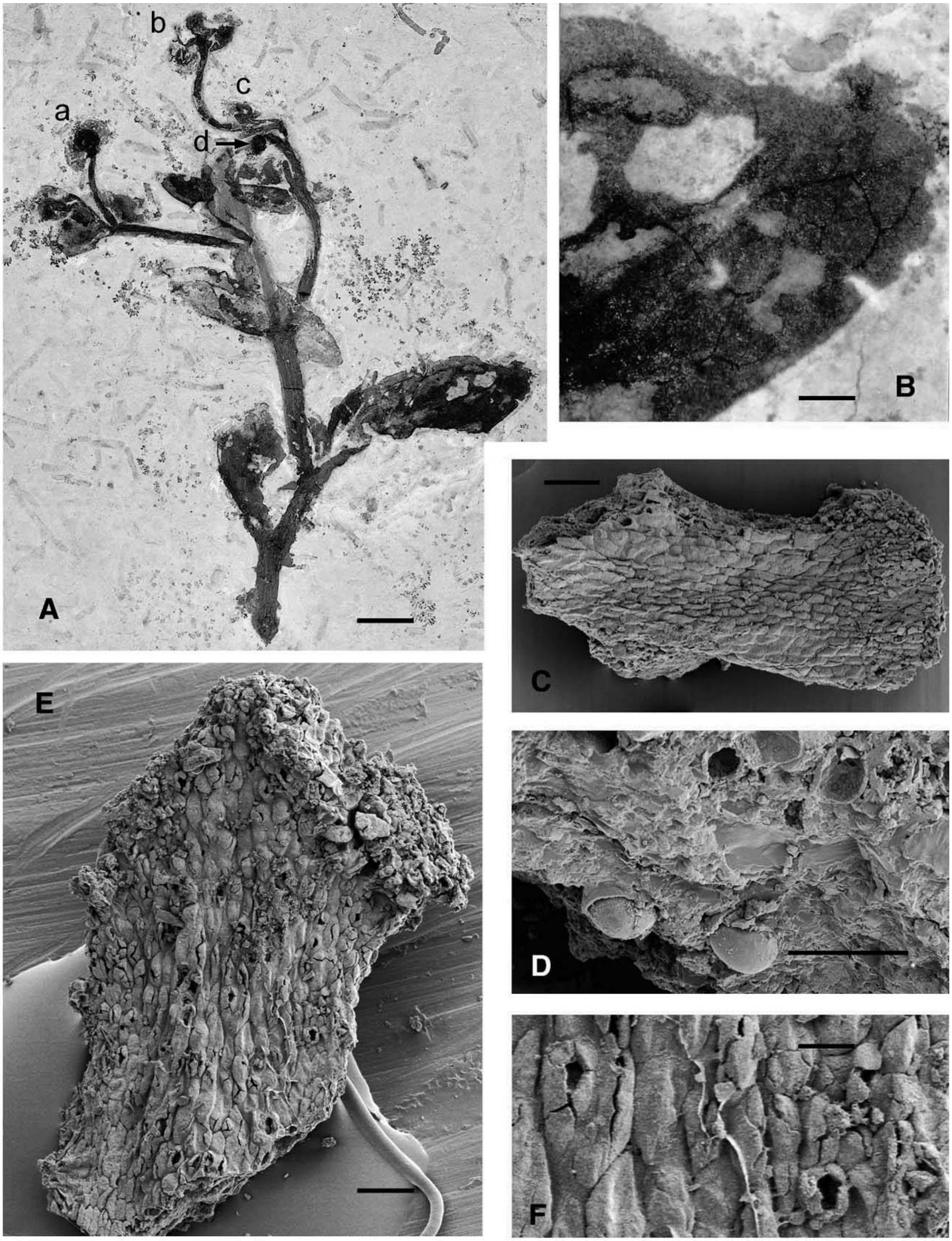


Fig. 3 *Endressinia brasiliana* n. gen. n. sp. *A*, Complete specimen of *E. brasiliana* n. gen. n. sp. (bar = 0.7 cm) with four floral structures (*a*, *b*, *c*, and *d*); *c* and *d* are most likely buds. *B*, Detail of leaf with veins (bar = 1.0 mm). *C*, Leaf fragment with epidermis (bar = 90 μm). *D*, Cross section through a leaf with ethereal oil cells (bar = 60 μm). *E*, Leaf fragment with stomata (bar = 50 μm). *F*, Leaf fragment with stomata, detail (bar = 30 μm).

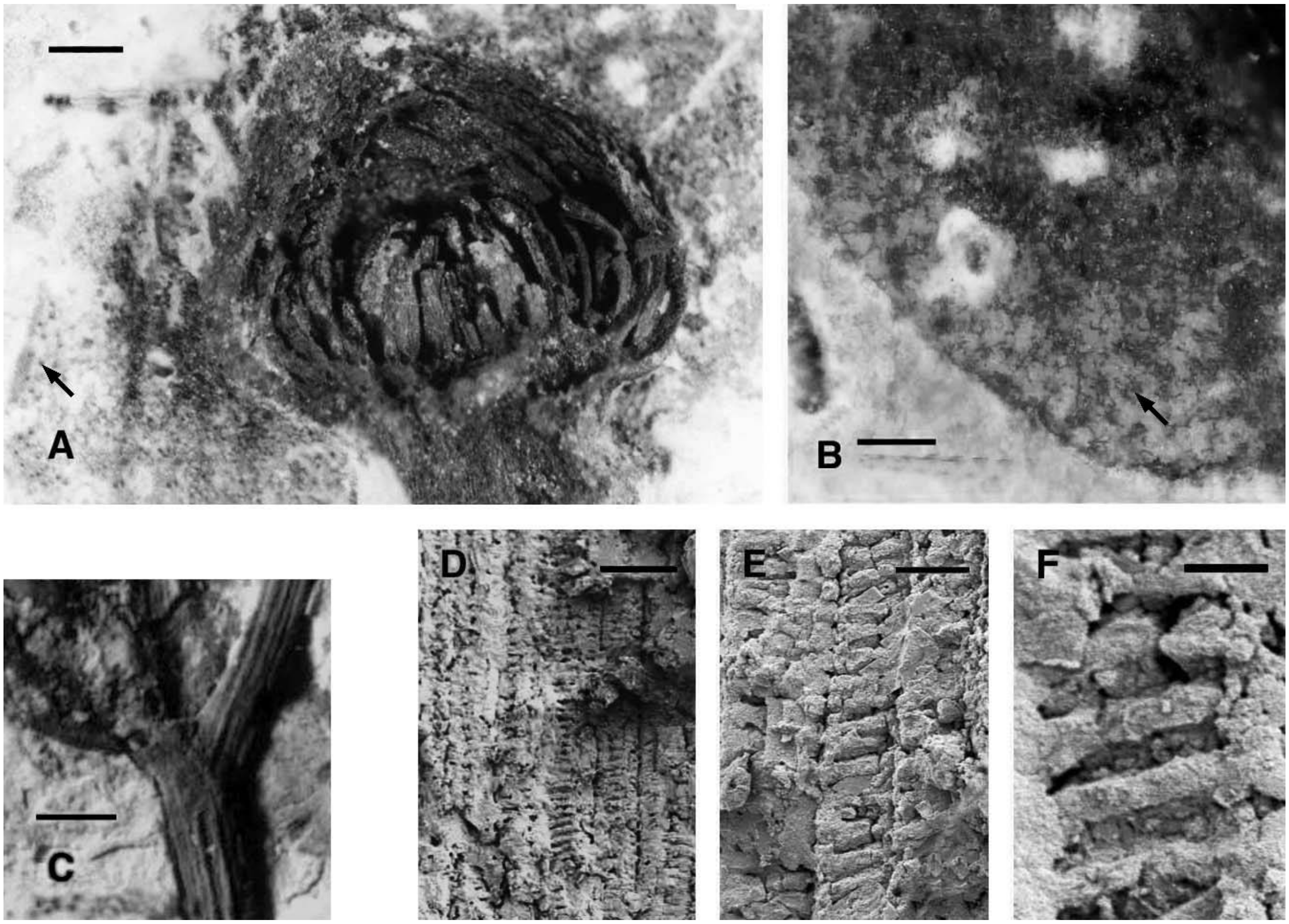


Fig. 4 Details of *Endressinia brasiliana* n. gen. n. sp. *A*, Flower *a* (see fig. 3*A*), three-dimensionally preserved (bar = 0.7 mm). *B*, Tepal with ethereal oil cells (arrows in *A* and *B*) (bar = 0.2 mm). *C*, Stem, LM (bar = 2.5 mm). *D*, Stem, SEM (bar = 100 μm). *E*, Stem, SEM (bar = 50 μm). *F*, Stem, SEM (bar = 10 μm).

distinct stalked glandular knobs are attached (fig. 5*B*–5*G*). The organs are therefore interpreted as staminodes. The staminodes are covered with rows of relatively large elongated cells. The glandular structures seem to be multicellular organs with secretory canals (fig. 5*D*). The staminodes seem to have had two or most likely three vascular strands (fig. 5*F*).

The gynoecium in the center of the flower is apocarpous, consisting of many (estimated number ca. 20?) most likely spirally arranged carpels (fig. 5*A*). Carpels are narrowly ovate, ca. 0.5–1.0 mm long, at most 0.3 mm wide, plicate, and with a distinct ventral split that is open in all carpels studied (fig. 6*A*, 6*B*; fig. 7*A*, 7*B*, 7*D*, 7*E*). Less-developed younger carpels are in the inner center of the flower (figs. 4*A*, 7*A*). The stigmatic area is distinct but small and not raised from the carpel (fig. 6). Epidermal features of the carpel walls are well preserved. The cells that cover the stigmatic area are distinctly larger than those of the epidermis, which covers the remaining parts of the carpel and are glabrous (fig. 7*C*). The epidermal cells are arranged in longitudinal rows; along the ventral opening, they are clearly smaller (fig. 7*B*). Even in more mature carpels no ovules have been observed.

Discussion

Comparison with Fossil Magnoliales

Several fossil taxa belonging to the Magnoliales have been described from the mid-to-Late Cretaceous of the Northern Hemisphere. *Archaeanthus linnenbergeri* is a multifollicular fruit sitting on an elongate axis (Dilcher and Crane 1984). Stamens and perianth parts are not preserved; however, scars of these organs seem to be present below the crested carpels. Leaves, known as *Liriophyllum*, represent most likely the foliage of *Archaeanthus*. *Archaeanthus* shares with *Endressinia* the character of having many spirally arranged carpels. However, the carpels in *Endressinia* are not attached to an elongate axis but sit in a slightly concave receptacle. The leaves of *Archaeanthus* also differ from those of *Endressinia*. While *Liriophyllum* is deeply lobed and large, with a camptodromous second-order venation, the leaves of *Endressinia* are small and oval in shape and brochidodromous.

Lesqueria elocata is a fruit, consisting of a receptacle, bearing a tight, ovoid cluster of helically arranged follicles at the apex (Crane and Dilcher 1984). Below these fruits are helically arranged laminar flaps that leave scars after abscission.

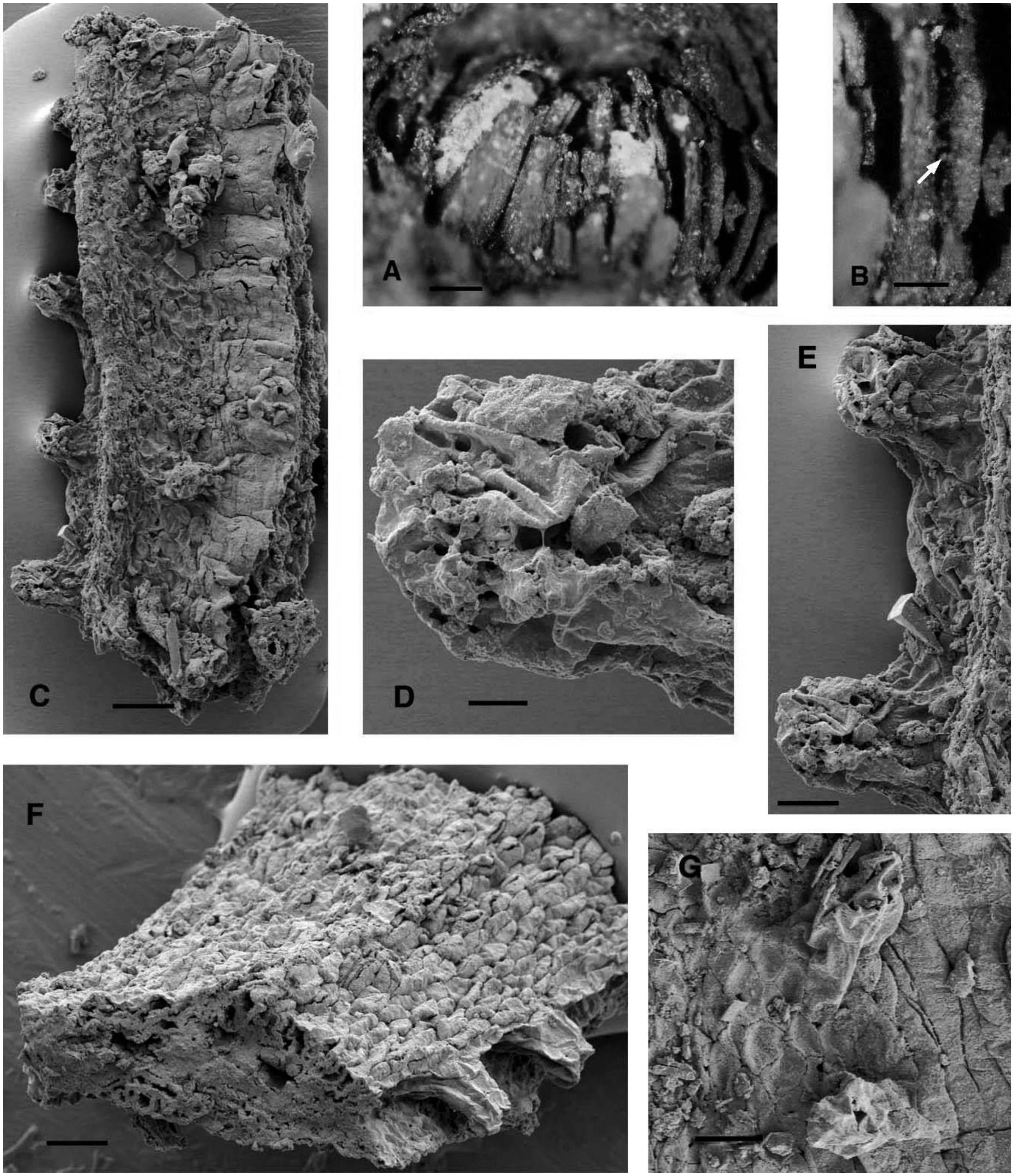


Fig. 5 Details of *Endressinia brasiliana* n. gen. n. sp. *A*, Interior of flower *a* (see fig. 3*A*), with carpels and staminodes (bar = 0.5 mm). *B*, Staminodes, LM (bar = 0.2 μm); arrow indicates glands. *C*, Staminode with glands (bar = 30 μm). *D*, Gland with secretory canals (bar = 6 μm). *E*, Glands in detail (bar = 15 μm). *F*, Cross section through a staminode with glands (bar = 30 μm). *G*, Staminodes in detail (bar = 30 μm).

In contrast to *Endressinia*, *Lesqueria* seems to lack staminodes, while *Endressinia* lacks abscission scars on the flowering axes. Both taxa share, however, the relatively high numbers of free carpels.

Protomonimia, a permineralized magnolialean reproductive structure from Japan (Nishida and Nishida 1988), consists of a receptacle bearing more than 55 helically arranged apocarpous carpels. Another taxon from northern Japan

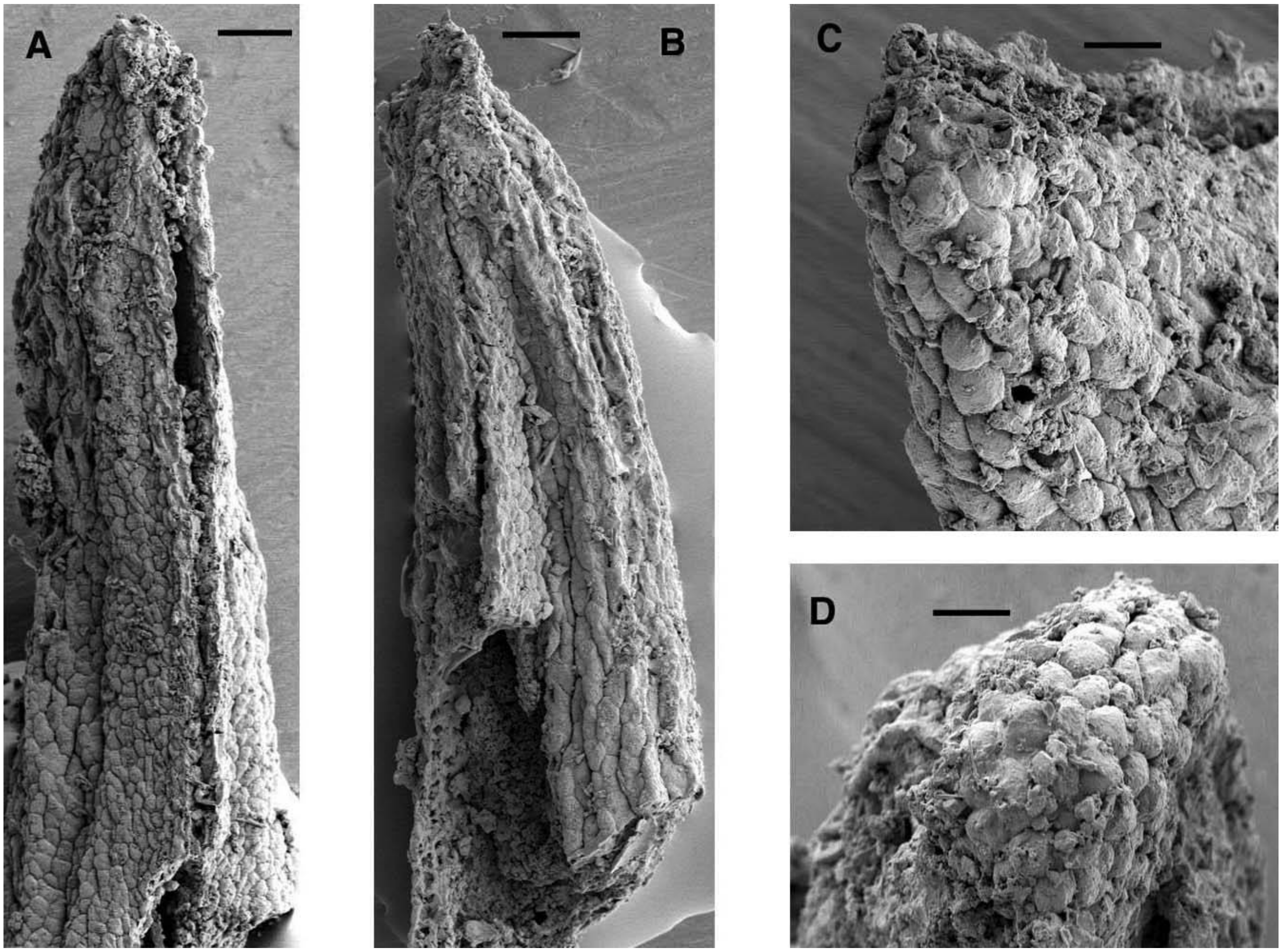


Fig. 6 Details of carpels of *Endressinia* n. gen. n. sp. *A*, Complete carpel (bar = 90 μm). *B*, Complete carpel, partly broken (bar = 90 μm). *C*, Stigmatic area of carpel (bar = 35 μm). *D*, Stigmatic area of carpel (bar = 35 μm).

with similar preservation, *Hidakanthus*, bears more than 170 stalked follicles on a slightly convex discoid receptacle (Nishida et al. 1996). In the two Japanese taxa, the number of follicles per flower exceeds by far that of *Endressinia*. Furthermore, both flowering structures seem to lack staminodes, which are present in *Endressinia*.

Several angiosperm taxa with multiparted flowers are known from the Brazilian Crato Formation. One solitary flowering structure, considered to be possibly related to the Annonaceae (Mohr and Friis 2000; fig. 3*D*, 3*E*, and possibly also 3*F*), bears approximately a dozen free apocarpous carpels on an almost spherical receptacle. This flowering structure has a diameter of ca. 3.5–4.0 cm and is therefore much larger than the flowering structure of *Endressinia*. In addition, the unnamed fossil lacks tepals, stamens, and staminodes, so that a comparison is restricted to the gynoecium.

A putative annonaceaen flower, *Pecinovia annonoides*, comes from the Cenomanian of Bohemia (Kvaček and Eklund 2003). It is apparently trimerous and therefore dissimilar to *Endressinia*. Liriodendroid fossils, such as seeds of the genus *Liriodendroidea* that are common from the Cenomanian to Maastrichtian in the Northern Hemisphere, cannot be compared with *Endressinia* because seeds of *Endressinia* were not observed.

To summarize, the Cretaceous fossils with magnolialean affinities published during the last decades share characters with *Endressinia*, mainly the feature of having many spirally arranged floral organs, but also differ in several characters present in *Endressinia*.

Systematic Affinities

The characters of the fossil described strongly indicate a relationship to modern members of the Magnoliales. Critical characters supporting this assignment include the presence of scalariform pitting (Herendeen et al. 1999); the presence of resin bodies, interpreted as ethereal oil cells, in leaves and floral parts that are common in woody ranales (West 1969); alternate phyllotaxis; brochidodromous and poorly organized leaf venation; solitary flowers; broad tepals; multiparted androecium with inner staminodes; and an apocarpous gynoecium consisting of many plicate carpels.

In *Endressinia*, the arrangement of the flower is solitary. This is also the case in most magnolialean families, except

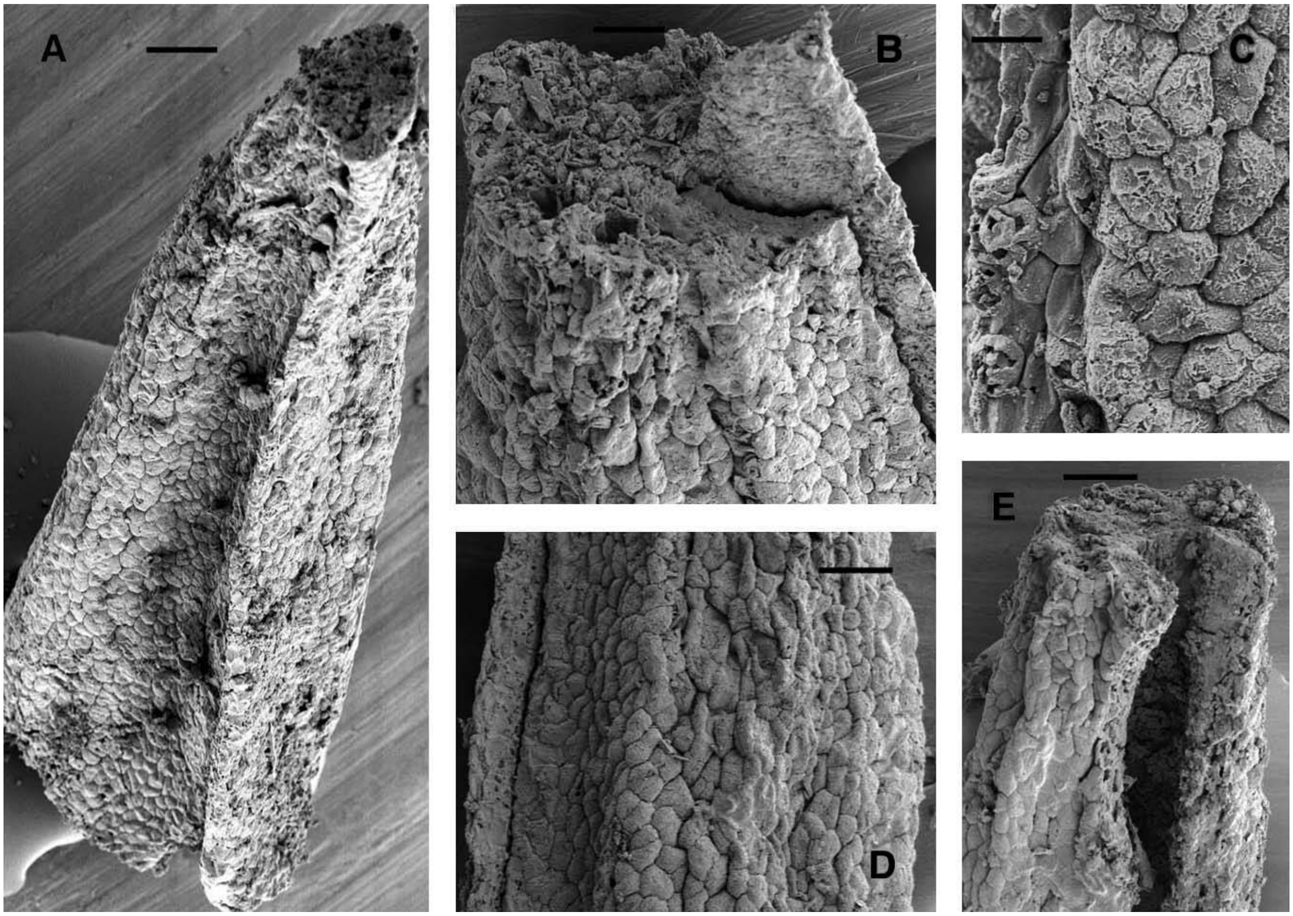


Fig. 7 Details of the carpels of *Endressinia* n. gen. n. sp. *A*, Young carpel (bar = 100 μm). *B*, Broken carpel (bar = 50 μm). *C*, Carpel wall with glands? (bar = 30 μm). *D*, Ventral slit of mature carpel (bar = 50 μm). E, Broken carpel and interior of carpel (bar = 70 μm).

for several genera of Annonaceae and Myristicaceae. Ethereal oil cells are found in all magnoliids, including in their carpels, except in the Amborellaceae, Nymphaeales, and Austrobaileyales (Endress and Igersheim 2000). Oil cells are usually scattered in the tissues, but they are commonly missing at the morphological surface. Among the basalmost angiosperms, surface oil cells are present in the carpels of the Austrobaileyales and partly in Chloranthaceae (Endress and Igersheim 2000). In Annonaceae (Magnoliales), ethereal oil cells are generally found scattered in the lower and upper palisade parenchymas and in the spongy parenchyma of the leaves (Kessler 1993). *Endressinia* seems to show a similar pattern. Ethereal oil cells are scattered in the inner tissues (fig. 3*D*) but also on or close to the leaf and tepal surface (figs. 3*C*, 4*B*). On some of the carpels, oil cells were observed as well (fig. 7*C*).

Broad tepals similar to those found in the fossil flower are known in the Magnoliaceae, Annonaceae, and Degeneriaceae (table 1). All of these families have reasonably large flowers, while the fossil flower is small.

The particular state of possessing a multiparted flower with many staminodes is present in two extant basal angiosperm groups, the Austrobaileyales and four families of Magnoliales: Annonaceae, Eupomatiaceae, Degeneriaceae, and Himantandraceae. The number of stamens is usually high in these families but is not known in the fossil flower (table 1).

In Himantandraceae and Degeneriaceae, staminodes are intrastaminal. The flowers of, e.g., *Galbulimima baccata* (Himantandraceae) exhibit a circle of outer staminodes, stamens, and 10–20 inner staminodes that take part in the optical attractiveness (Endress 1984). In *Endressinia*, the staminodes do not seem to be intrastaminal, because the staminodes are present in several inner circles. These staminodes seem to have two or three vascular strands in *Endressinia* (see "Flowering Structures"). In many Magnoliales, such as the Magnoliaceae and Eupomatiaceae, the stamens often have three vascular strands (Hiepko 1965; Endress 1994).

Staminodes with papillae and glands are found in Austrobaileyales, as well as in several magnolialean families, such as Eupomatiaceae, Degeneriaceae, and Himantandraceae (table 1). Staminodes of the Austrobaileyales develop secretory tissue with papillae (Endress 1984), but Magnoliales, such as Himantandraceae, Degeneriaceae, and Eupomatiaceae, share glandular structures (Endress 1977) similar to *Endressinia*. Although Himantandraceae have narrow staminodes, they are introrsely cucullate in Degeneriaceae (Kubitzki 1993). Only taxa within Eupomatiaceae share a broad shape with the fossil. Himantandraceae have, in addition, a gynoecial

Table 1

Flower Morphology of Eupomatiaceae (*Eupomatia*), Himantandraceae (*Galbulimima*), and Degeneriaceae (*Degeneria*) Compared with *Endressinia* n. gen. n. sp. (Family Unknown)

Genus	Size of flower	Phyllotaxis	Perianth	Stamens	Staminodes	Staminode characters	Carpels
Eupomatia	3–4 cm	Spiral	Perianthless, cap (one or two bracts)	20–100	40–80 petal-like inner staminodes	Marginal and laminar glands	13–70, partly fused
Galbulimima	2–4 cm	Spiral	Perianthless, two caps	13–130	3–23 outer, 13–20 inner	Ribbon-like acute, marginal and laminar glands	7–28
Degeneria	Large	Whorled and spiral	3 sepals, 12–25 petals	Numerous	Fewer than stamens, intrastaminal	Laminar, two pairs of microsporangia	Monocarpellate
Endressinia	8 mm	Spiral?	Several tepals?	Unknown	Numerous	Marginal glands	Ca. 20

Note. Data are from Endress (1990) and Kubitzki et al. (1993).

cone that is not developed in *Endressinia*, and in Degeneriaceae, the pistil is monocarpellate. In *Eupomatia*, the carpels are congenitally fused for more than half of their length (Endress 1993, 2003), while in *Endressinia*, all carpels seem to be free. Both Himantandraceae and Eupomatiaceae possess a hemispherical cap that is not observed in *Endressinia*.

In summary, *Endressinia* shares features with nearly all families of the Magnoliales. Special characters, which include the loss of the perianth and development of a cap (calyptras) (Endress 2003), both missing in *Endressinia*, are interpreted as derived character states, developed after the Early Cretaceous. Thus, *Endressinia* is seen as a sister taxon to Eupomatiaceae. There is, however, also the possibility that *Endressinia* might represent an extinct magnolialean lineage with convergent staminode morphology.

Flower Biology, Biogeography, and Ecology

In living members of relic Magnoliales, the staminodes take over various functions during the pollination process. Staminodal glands are partly colored and produce odors that attract pollinators, mostly flies and beetles (Endress 1990). To avoid self-pollination, the staminodes of *Eupomatia* bend over the already pollinated gynoecium. We assume that *Endressinia* had developed these features already, because the morphology of the staminodes and staminodal glands is more or less identical with some of the recent Magnoliales, especially Eupomatiaceae.

The pollen of *Eupomatia* is subglobose, with a thick, bandlike, encircling aperture at the equator and an atectate exine (Endress 1986; Sampson 2000). In the fossil record, only one pollen, possibly belonging to *Eupomatia*, has been described by Chmura (1973) as pollen type E from the Campanian-Maastrichtian of California (Muller 1981). If this pollen is indeed from Eupomatiaceae, this would imply that during the Cretaceous plants related to extant Eupomatiaceae were present in the Americas, while recent *Eupomatia* grows exclusively in Australia and New Guinea (table 2). It is also interesting to note that Annonaceae (such as the genus *Anaxagorea*), considered to be the sister taxon of Eupomatiaceae (Mathews and Donoghue 2000), are present in South America (Kessler 1993).

Table 2

Ecology of Selected Magnolialean Families

Family/genus/species	Distribution	Adaptations to climate	Habit
Annonaceae:			
Many	Pantropical	Rain forest	Trees
Eupomatiaceae:			
Eupomatia laurina	East coast Australia, New Guinea, relatively wide range	Rain forest, high altitude	Shrub, up to 5 m high
Eupomatia bennettii	New South Wales and southern Queensland	Adapted to temporal drought	Low shrubs, 50 cm high
Himantandraceae:			
Galbulimima baccata	Queensland, New Guinea, New Britain, and Moluccas	Rain forests, up to 2700 m	Large trees, part of canopy
Galbulimima belgraveana	Malaysia	Rain forests	Large trees, part of canopy
Degeneriaceae:			
Degeneria vitiensis	Fiji Islands	Forest	Trees
Degeneria roseiflora	Fiji Islands	Forest	Trees
Unknown:			
Endressinia brasiliana	South America	Adapted to temporal drought	Unknown, shrub?

Note. Data are from Endress (1983) and Kubitzki et al. (1993).

Among recent relic Magnoliales with an Australasian distribution, most seem to be adapted to the rain forest (table 2). *Eupomatia* has the widest ecological range, is adjusted to longer dry periods, and lives not only in the rain forest but also close to sclerophyll forest (Endress 1983). *Endressinia* also shows characters that are typical for plants adapted to a seasonally dry environment, e.g., small and coriaceous leaves.

The assumption that *Endressinia* lived in a relatively (seasonally) dry habitat fits observations on other plants from the Crato Formation. Some of the fern fronds are covered with spiny hairs; putative monocots developed a xeromorphic vegetative morphology and (salt?) glands (Mohr and Rydin 2002); and dicot leaves are usually small and often coriaceous.

These observations fit very well some of the climate models of the Early Cretaceous that have been developed during the past years. According to these models, during the Berrasian and Aptian the humidity in tropical areas was not high enough to support tropical rain forests. However, streams and (ephemeral) lakes were present that might have had their source on mountainous flanks of rift valleys (Skelton 2003). The Crato taphoflora might have originally grown in a similar environment and under a comparable climate regime.

For the deposition of the Crato flora, a model can be hypothesized where rivers might have risen dramatically after a periodic rainfall. The torrential waters ripped out complete plants with roots, partly from backwater environments (aquatic elements, such as Nymphaeales), partly from the vegetation of the riverbanks, and transported the plants to the deposition site, where they were buried together with insects and vertebrate fossils, such as fishes, frogs, turtles, and crocodiles.

Conclusions

Endressinia brasiliana gen. nov. sp. nov. is an unusually well-preserved early angiosperm. The flowers are three-dimensional, in contrast to the vegetative parts, and allow detailed study of the flower structure. The vegetative and floral parts of *Endressinia* share characters with the Magnoliales.

The bisexual flowers contain broad staminodes with specific features, such as glands, and imply that *Endressinia* is possibly related to Eupomatiaceae. *Endressinia* is the oldest fossil magnolialean flower described and confirms the ancientness of Magnoliales earlier inferred by dispersed pollen. *Endressinia* seems to be adapted to a seasonally dry climate.

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