

Gymnosperms from the Early Cretaceous Crato Formation (Brazil). II. Cheirolepidiaceae

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Abstract

Conifers are common in the Early Cretaceous Crato flora. Sterile foliage shoots of several morphotypes occur. Good preservation of several of these specimens allows detailed morphological and anatomical studies. Based on these characters, two taxa of Cheirolepidiaceae, *Tomaxellia biforme* and *Frenelopsis* sp., are identified. The palaeogeographic distribution of the genus *Tomaxellia* currently extends from southern South America northwards to the palaeoequatorial region. The morphological and anatomical characters of both taxa might be interpreted as adaptations to a warm and temporarily dry palaeoclimate, however their habitat can not be reconstructed yet, due to scarcity of the remains.

Schlüsselwörter: Fossile Koniferen, Cheirolepidiaceae, *Frenelopsis*, *Tomaxellia*, Blattepidermis, Untere Kreide, Apt, Crato-Formation, Brasilien.

Zusammenfassung

Koniferen stellen eine wesentliche Komponente der unterkretazischen Crato-Flora dar. Es kommen sterile beblätterte Zweige verschiedener Morphotypen vor. Die gute Erhaltung einiger dieser Fossilreste lässt detaillierte morphologisch-anatomische Untersuchungen zu. Auf der Basis solcher Merkmale wurden zwei Taxa der Cheirolepidiaceae, *Tomaxellia biforme* und *Frenelopsis* sp., identifiziert. Das Areal der Gattung *Tomaxellia* wird damit vom südlichen Südamerika nordwärts, in die paläoäquatoriale Region erweitert. Morphologische und anatomische Merkmale beider Taxa können als Anpassungserscheinungen an ein warmes und periodisch trockenes Paläoklima interpretiert werden. Auf Grund des seltenen Vorkommens solcher Fossilreste können noch keine Angaben zu ihrem ehemaligen Habitat gemacht werden.

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Introduction

Remains of conifers assigned to the extinct family Cheirolepidiaceae Takhtajan ex Doludenko,

1978 were more or less distributed worldwide during the Mesozoic, except for very high latitudes where macroremains and pollen only rarely occur (e.g. Cantrill & Falcon Lang 2001;

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Falcon Lang & Cantrill 2000; Mohr & Gee 1992). During Jurassic and Cretaceous the maximum diversity and abundance of this conifer family was certainly in southern Laurasia and northern Gondwana. High percentages and large morphological variety of pollen in the respective pollen spectra (Spicer et al. 1994) indicate that these conifers occupied a variety of ecological niches (Watson 1988; Axsmith & Jacobs 2005).

The general morphology of cheirolepidiaceae pollen named *Classopollis* Pflug, 1953 (Traverse 2004) – older synonyms are *Circulina*, *Corollina* and *Gliscopollis* – is the most conspicuous character of this family, while growth habit, morphology and size of leaves and cones as well as cuticle morphology vary substantially. Cheirolepidiaceae have been recognised from the Triassic through to the Late Cretaceous, possibly until the Maastrichtian (Van der Ham et al. 2003). The genera *Brachyphyllum* Lindley & Hutton, 1836 emend. Harris, 1979 (pro parte), *Cupressinocladus* Seward, 1919 (pro parte), *Frenelopsis* Schenk, 1869, *Pseudofrenelopsis* Nathorst, 1893 emend. Srinivasan, 1995, *Pagiophyllum* Heer, 1881 (pro parte), *Tarphyderma* Archangelsky & Taylor, 1986 and *Tomaxellia* Archangelsky, 1963 are Cretaceous members of this family. Additional Cretaceous taxa potentially belonging to the Cheirolepidiaceae are *Androvettia* Hollick & Jeffrey, 1909 and *Glenrosa* Watson & Fisher, 1984 (Watson 1988).

Studies on cheirolepidiaceae conifers focussed first on material from the Northern Hemisphere (e.g. Jung 1968; Harris 1979; Alvin 1982; Francis 1983; Axsmith & Jacobs, 2005). During the 20th Century South and Central American fossil conifers were studied as well (among others Spegazzini 1924; Calder 1953; Archangelsky 1963, 1966, 1968; Archangelsky & Gamarro 1968). Patagonian Mesozoic conifer remains comprise, besides Podocarpaceae Endlicher, 1847, and Araucariaceae Henkel & Hochstätter, 1865, also several taxa of Cheirolepidiaceae. The latter include vegetative parts with preserved cuticles and various strobili (e.g. Archangelsky 1994; Calder 1953), for instance vegetative and fertile parts of *Tomaxellia degiustoi* (Archangelsky 1963) and *T. biforme* (Archangelsky 1966, 1968), and vegetative shoots of *Tarphyderma punctata* (Archangelsky & Taylor 1986, 1991).

Early Cretaceous floras from low latitudes of South America are less well known (see below). Reports exist only from Brazil and Colombia. Conifers have been published from the floras of the Sergipe-Alagoas Basin, Brazil (Linder Dutra

et al. 2002) and from the Araripe Basin, Brazil (Duarte 1985, 1993; Kunzmann et al. 2004; this paper). From the Leiva region, Colombia, several species of *Cupressinocladus*, *Brachyphyllum*, *Pagiophyllum* and *Podozamites* Braun, 1843 have been described and figured (Pons 1988; Van Waveren et al. 2002). However, their botanical affinity is not clear since cuticles are not preserved.

This study is based on specimens of cheirolepidiaceae affinity from the late Aptian Crato Formation of Brazil and thus adds information on the distribution of cheirolepidiaceae conifers of Southern Hemisphere low latitudes. Descriptions of epidermal characters are given, and the respective structures are interpreted palaeoecologically.

Location and stratigraphy

The plant fossils were collected from open cast pits several kilometers south of the town of Nova Olinda, between Nova Olinda and Santana do Cariri exposing the Nova Olinda Member of the Crato Formation of the Araripe Basin, in northeastern Brazil. The Araripe Basin contains Late Jurassic to late Early Cretaceous sediments that were deposited during the early opening of the Atlantic Ocean. The Crato Formation is the lowermost part of the Santana Group, and based on palynological data, is probably late Aptian to earliest Albian in age (Arai et al. 2001; Doyle 1992; Lima 1978; Neumann & Cabrera 1999; Pons et al. 1996). For more detailed geographical and geological information see Regali (1989), Maisey (1991), Martill et al. (1993), Mohr & Bernardes-de-Oliveira (2004).

Material and Methods

The yellowish to light greyish brown bedded limestone (Plattenkalk) delivers a wide array of fossils, including invertebrates and vertebrates, as well as a diverse flora. The plant fossils are variably preserved. Conifer remains constitute a relatively large part of the flora. They are mainly represented by sterile leafy shoots, reproductive material is less frequent.

As it is also true for the other components of the flora, most of the coniferalean remains are preserved as impressions with or without a thin layer of iron oxide which replaced the original organic matter. Rare specimens show a fully and three-dimensional replacement by iron oxide. Nevertheless, some of these specimens show the cellular structure of the leaf epidermis (Fig. 2C).

The fossils were studied under a Leica MZ APO Microscope equipped with a camera lucida and a digital camera DFC 320. Some of the photographs were taken with a Nikon digital camera and a 60 mm Nikkor macro-objective. For SEM studies, small pieces of the iron oxide were removed from the specimen, directly mounted on stubs and sputtered

for 4 minutes with Au/Pd. The SEM-photographs were taken on a LEO 1450VP SEM. Cellular details of the leaf epidermis were partly visible also under the LM. In addition, we tried to obtain leaf cuticles. Small parts of lateral shoots were removed from the specimen and prepared with Schultze solution. However, this method did not prove to be successful.

The material used for this paper is housed in the palaeobotanical collections of the Museum für Naturkunde Berlin, Germany (= MfN PB) and the Palaeobotanical Section of the Forschungsinstitut Senckenberg in Frankfurt/M., Germany (= SM.B).

The Flora of the Araripe Basin

Sporomorphs, as well as macroscopic plant remains are known from the late Aptian Crato and the early Albian Santana Formation. The stratigraphical and biological aspects of the dispersed sporomorphs have been studied intensely (e. g. Arai et al. 2001; Lima 1978; Lima 1979; Osborn et al. 1993; Pons et al. 1996) and show that a variety of gymnosperms, including cycadophytes, gnetophytes and conifers, and angiosperms must have grown relatively close to the site of deposition.

The Crato macroflora consists of a diverse assemblage of pteridophytes, including schizaeaceous ferns (e.g. Bernardes-de-Oliveira et al. 1999) and Isoetaceae (e.g. Bernardes-de-Oliveira et al. 2003) and various gymnosperms such as ephedroid and welwitschioid gnetophytes (Rydin et al. 2003; Mohr et al. 2004; Dilcher et al. 2005), conifers (Duarte 1985, 1993; Kunzmann et al. 2004; this paper), and a variety of angiosperms (Barreto et al. 2000; Mohr & Friis 2000; Mohr & Bernardes-de-Oliveira 2004). In total, about 70–80 taxa have been recognized, of which about 30 are putative angiosperms, mostly magnoliid dicotyledons (Leme et al. 2005; Mohr & Eklund 2003; Mohr & Bernardes-de-Oliveira 2004).

The macroflora of the Santana Formation (Romualdo Member) is less well known, because of relatively rare specimens in nodules that mostly contain vertebrate fossils (fish). However, sometimes such nodules contain various remains of conifers, such as vegetative shoots of frenalopsisid conifers (Bernardes-de-Oliveira et al. 2005), *Brachyphyllum* spp., and cones (Crane, in Mai-sey 1991; Duarte 1985).

The conifers of the Araripe Basin

The conifers of the Crato and Santana Formations were previously known mainly from the pollen record, and secondarily from macrofossils

(Lima, 1979; Duarte 1985, 1993; Bernardes-de-Oliveira et al. 1993; Kunzmann et al. 2004; Martill et al. 2005).

Araucariaceae are represented by pollen of the *Araucariacites*-type (Lima 1979) and by female cones (cf. *Araucaria* sp.; Kunzmann et al. 2004), as well as araucarioid cone scales (Martill et al. 1993) and vegetative shoots of *Brachyphyllum obesum* Heer, 1881 (Kunzmann et al. 2004). Fossil amber in connection with araucarian remains has been described lately (Martill et al. 2005). Leafy shoots of *Lindleycladus* Harris, 1979 (incertae sedis vel Araucariaceae) may perhaps also belong to the Araucariaceae (Kunzmann et al. 2004). Lima (1979) recognised Podocarpaceae by its pollen.

The Cheirolepidiaceae seem to be diverse, but so far only dispersed pollen grains have been described (Lima 1979). *Classopollis alexi* Burger, *C. torosus* (Reissinger) Couper, *C. brasiliensis* (Herngreen), cf. *C. infrareticulatus* Volkheimer, *Circulina parva* Brenner, *C. minima* (Herngreen) Lima, and *C. meyeriana* Klaus certainly represent various biological species. Lima's (1979) *Classopollis* species are very similar in size and shape to those in situ described from *Classostrobus*

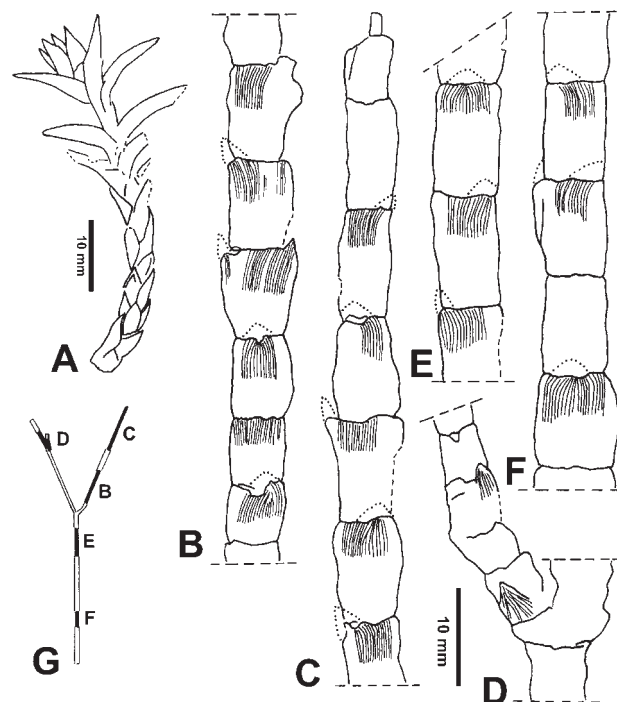


Fig. 1. Camera lucida drawings of selected specimens. **A** – *Tomaxellia biforme* Archangelsky, 1963, leafy shoot with two leaf morphotypes, MfN PB 1998/484; **B–G** – *Frenalopsis* sp., leafy shoot, SM.B 16486; **B–F** – different sections of the shoot, striation on the segment surfaces only figured in the apical parts of the segments to demonstrate curved striae below the free parts of the leaves (leaftips), dotted lines = abraded leaftips; **G** – simplified figure of the shoot, full black parts indicate the position of sections B–F.

comptonensis Alvin et al., 1978 (Axsmith et al. 2004) representing male cones associated with vegetative shoots of *Pseudofrenelopsis*.

Although the pollen record of Cheirolepidiaceae in the Crato flora is known, vegetative remains and male and female cones have not been described so far. It was merely assumed, that the *Brachyphyllum* material (*B. castilhoi* Duarte 1985) partly might belong to the family (e.g. Duarte 1985; Crane in Maisey 1991; Kunzmann et al. 2004).

Systematic descriptions

Class **Coniferopsida** (Endlicher, 1847)

Family **Cheirolepidiaceae** Takhtajan ex Doludenko, 1978

***Tomaxellia* Archangelsky, 1963 emend. Archangelsky, 1966**

***Tomaxellia biforme* Archangelsky, 1966**

Figs 1A, 2

1966 *Tomaxellia biforme* Archangelsky: 291.

1968 *Tomaxellia biforme*. – Archangelsky: 153–165, pl. 1–4, textfigs 1–2; (fertile and sterile organs).

1988 *Tomaxellia biforme*. – Watson: 415, figs 9.1, 9.22.

Material. MfN PB 1998/484 with preparation specimens MfN PB SEM 1998/484–1, 2, 3; MfN PB 2000/1034.

Description. Two ultimate order branchlets are preserved (Fig. 2A, G). Especially the specimen MfN PB 1998/484, a heterophyllous branch of 60 mm length, shows the typical characters of *Tomaxellia biforme*. Leaves are arranged in a simple helix. Short leaves occur basally, longer leaves apically, and at the top an opened bud with longer leaves is visible (Fig. 2B). All leaves appear to have been fleshy.

Short leaves are of the *Brachyphyllum* morphotype sensu Harris (1979) and show the following features: squamiform, leaf base decurrent, free part of the leaf adpressed, with an acute–obtuse apex. The leaf blade is semicircular to triangular in cross section and abaxially keeled. There is a continuous transition from short to long leaves. Leaves are 5–18 mm long and 3–3.5 mm wide.

Long leaves are of the *Pagiophyllum* morphotype sensu Harris (1979). The basal part is decurrent; the free part spreading, arising at 50°–70° from the axis, typically slightly recurved, narrow ovate to narrow elliptical in shape and scarcely narrowing at the base, tapering towards an acu-

minate apex. The leaf blade is semicircular in cross section, with a convex abaxial side, slightly keeled.

Most of the organic matter is replaced by iron oxide, but some of the cellular structure of the leaf epidermis is still visible. There are slightly sunken parallel grooves on the abaxial side of the longer leaves that might represent stomatal rows. Under SEM, several apices of the youngest long leaves show details of the abaxial epidermis (Fig. 2C–E).

Ordinary epidermal cells are elongated and rectangular in shape with straight or slightly curved anticlinal walls, 20–70 µm long and 12–15 µm wide. They are arranged in simple longitudinal files.

There are only a few monocyclic stomata near the apex (Fig. 2C), in the median part of the apex they are arranged in files (Fig. 2F). The orientation of stomatal pori is rarely visible, in these cases it is longitudinal to the leaf axis. The outer epidermal surface shows a ring of 4 to 6 slightly elevated subsidiary cells (Florin ring; Fig. 2D). The ring of subsidiaries is 65–70 µm long and 50–60 µm wide. There are 2 polar, slightly elongated subsidiaries (Fig. 2E). Stomatal pits are rounded to oval, ~25 µm long and 13–15 µm wide, the guard cells are moderately sunken. No papillae have been found. Adaxial side unknown.

Discussion. Among all conifers from the Early Cretaceous of South America, only *Tomaxellia biforme* shows a characteristic heterophylly with two distinct leaf morphotypes (Archangelsky 1966). Although the leaf epidermis of the Crato material is poorly known, it supports the determination as well. SEM photographs of *T. biforme* were published by Watson (1988: figs 9.22C–F). They clearly show a nonpapillate epidermis and nonpapillate stomata with a Florin ring. The features of our material seem to fit the characters described by Watson (1988) and thus justify a specific determination. The Crato material is distinguished from *T. degiustoi* Archangelsky, 1963 by its heterophyllous shoots.

Palaeobiogeography. The genus *Tomaxellia* is known only from the Early Cretaceous of South America (Archangelsky 1966; Watson 1988). The poorly known type species, *T. degiustoi* Archangelsky, 1963 and the well known species *T. biforme* Archangelsky, 1966 have previously been reported only from the Ticó flora in the Santa Cruz Province in Argentina (Watson 1988). Now, the area of *T. biforme* is extended northwards to significantly lower palaeolatitudes.

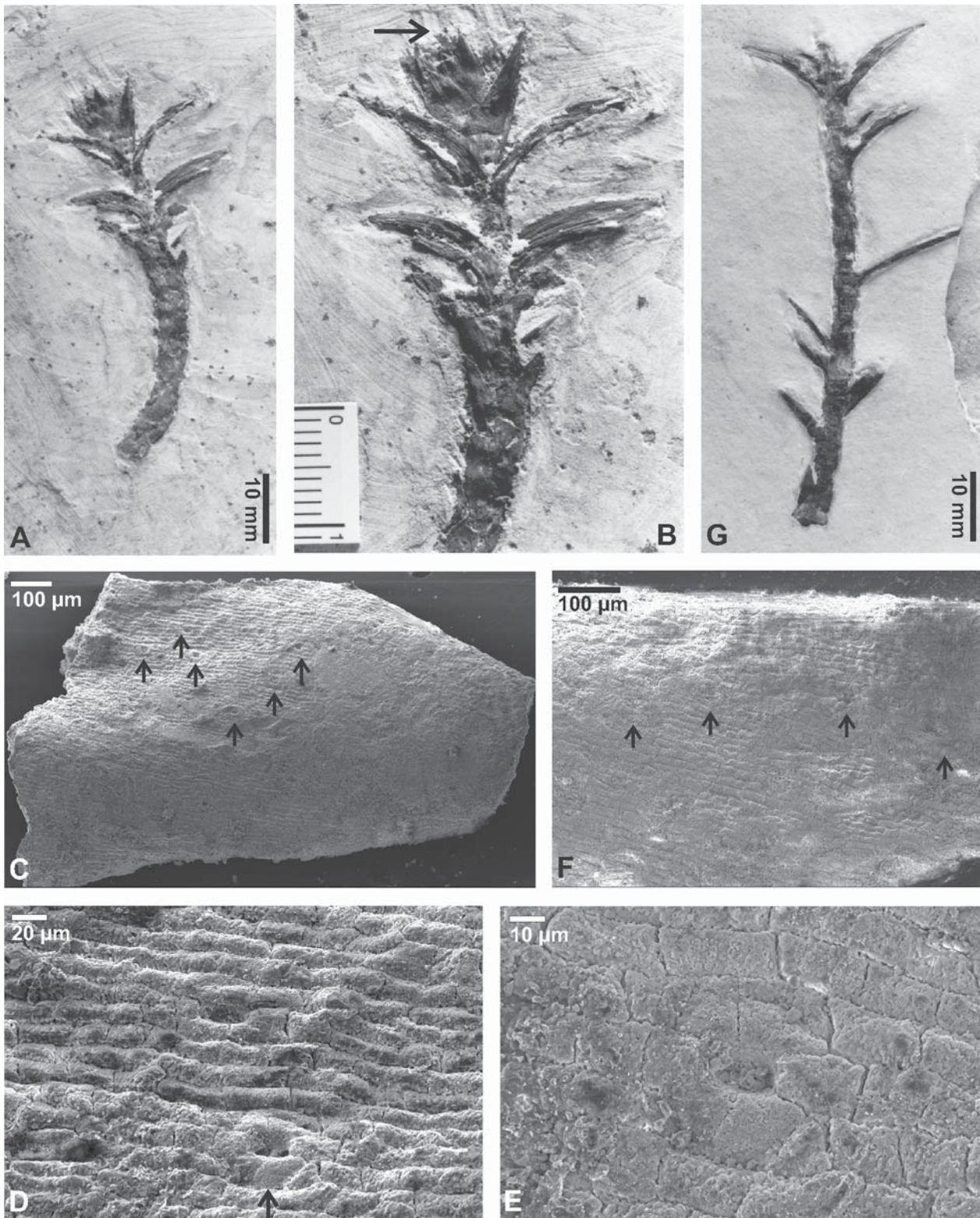


Fig. 2. *Tomaxellia biforme* Archangelsky, 1963. **A–F** – leafy shoot, MfN PB 1998/484; **A** – leafy shoot with two leaf morphotypes; **B** – apical part of the shoot, arrow indicates the position from where material for SEM studies was removed; **C–E** – abaxial epidermis by SEM, MfN PB 1998/484-1; **C** – leaf apex with few stomata (arrows); **D** – detail of C: stomata with Florin rings, arrow indicate stoma figured in E; **E** – detail of D: stoma with 6 subsidiary cells, polar subsidiaries slightly elongated, vertical view; **F** – epidermis by SEM, ordinary epidermis cells and stomata (arrows) partly destroyed, MfN PB 1998/484-3; **G** – leafy shoot, MfN PB 2000/1034.

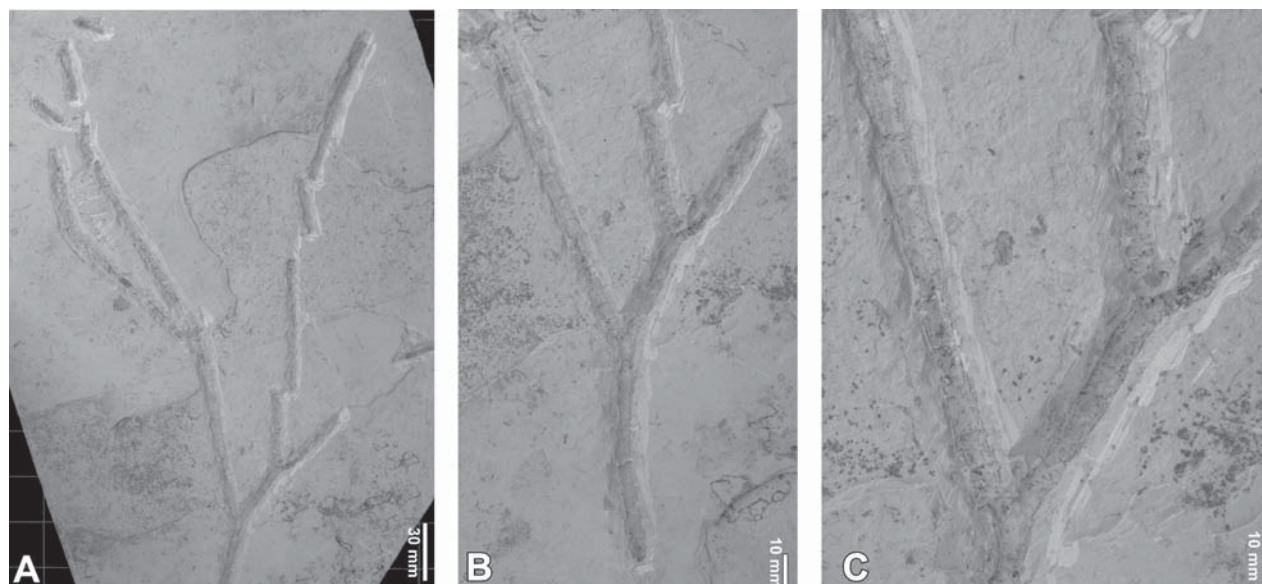


Fig. 3. *Frenelopsis* sp., leafy shoot, SM.B 16447; **A** – complete specimen; **B–C** – details of **A**.

***Frenelopsis* Schenk, 1869 emend. Watson, 1977**

***Frenelopsis* sp.**

Figs 1B–G, 3–5

Material. SM.B 16447, SM.B. 16486, MfN PB 1999/390.

Description. Three specimens are available for this study. One is an impression with partly preserved epidermal characters (SM.B 16447, Fig. 3). In a second specimen the organic matter is replaced by iron oxide, partly with epidermal characters recognisable (SM.B 16486, Fig. 4). The third specimen is a poorly preserved impression (MfN PB.1999/390).

Shoot morphology: The large (340 mm and 410 mm long), probably caduceous shoots are sparsely branched, the branchlets are aligned in one plane. Axes are branching almost dichotomously, but not completely symmetrical, the angle between two branchlets amounts $\sim 25^\circ$. The shoot of specimen SM.B 16447 is branching in three orders; the branchlets between two branching points are 35–150 mm long (Fig. 3A). Segmented shoots bearing whorls of 1 or 2 laterally fused squamiform leaves. The free part of a single leaf is triangular in shape, adpressed and has an acute apex; the free part is 1.5–2.0 mm long and broader than long, (Figs 1D, 5A–B).

In several of the branchlet's segments an opposite arrangement of two free leaf tips is observed (Fig. 5A), while other segments show only one leaf tip, which is not attached at an angle of 90° to those above or below (Fig. 1C). In several cases a decussate arrangement occurs (e.g., Fig. 1B, F). Because the specimen is not diagenetically

flattened this leaf arrangement reflects the original phyllotaxis. If the leaf tips are not preserved or broken, a dense longitudinal striation on the segmental surfaces shows the former position of such leaf tips (Fig. 5C). There is a remarkable curvature of the parallel striae in the apical part of the segment before running into the free leaf tips (Fig. 1B–F). Otherwise the striae are running straight to the upper margin of the segment. Free parts of the leaves continue as a smooth cylindrical segment without sutures (“internodes” sensu Watson 1988: 401). Leaf bases (= segment bases) are slightly contracted. Segment lengths (distance between leaf bases) vary generally from 3 to 12 mm, especially in specimen SM.B 16486 from 7.5–11.5 mm at the main axis, from 5–10.5 mm at branchlets of higher orders. This variation of segment length seems to be randomly distributed. Commonly, shorter segments may be recognized near to the bases of branchlets (Fig. 1D). There is a subtle change in diameter of the segments from 6 mm at the base of the branch to 4 mm at the very top. In cross section, a segment consists of the thick and fleshy cylindrical leafy part and a woody inner part of only 1–3 mm in diameter (Figs 1C, 5D).

In specimen SM.B 16447 parts of the shoot impression show details of the cellular structure of the epidermis of the segments. Numerous longitudinal rows of stomata are observed by LM. Cellular characters of the stomata are not preserved. In specimen SM.B 16486 the surfaces of the segments show densely arranged, parallel grooves that represent rows of stomata (Fig. 5G). In very few cases the surface of the segments is

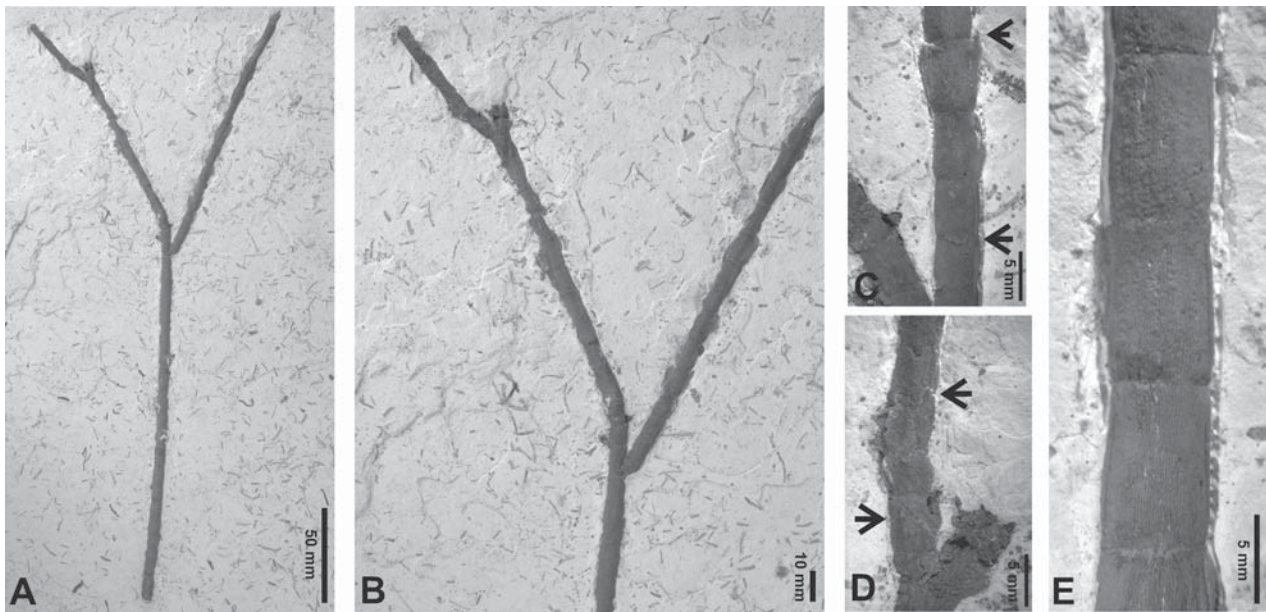


Fig. 4. *Frenelopsis* sp., leafy shoot, SM.B 16486; **A** – complete specimen; **B** – details of **A**; **C–E** – few segments of the shoot with dense parallel striation on the surface and with free leaf tips (arrows).

not abraded, thus the cellular structure of the epidermis is visible by LM (Fig. 5E–G). Stomata are arranged in parallel continuous uniseriate rows that densely cover the whole epidermis of the segments. One or two rows of ordinary epidermal cells separate rows of stomata. The stomata are monocyclic or incompletely dicyclic. The orientation of stomatal pori is transverse or oblique to the axis of the segment. The ring of

subsidiary cells is oval, with an outer periclinal wall (Florin ring; Fig. 5F), the guard cells are sunken into the epidermis. Ordinary epidermal cells show papillae on the periclinal surfaces (Fig. 5F).

Discussion. The leaf morphology with more than one leaf in a sutureless whorl characterizes the morphogenus *Frenelopsis* (Watson 1977,

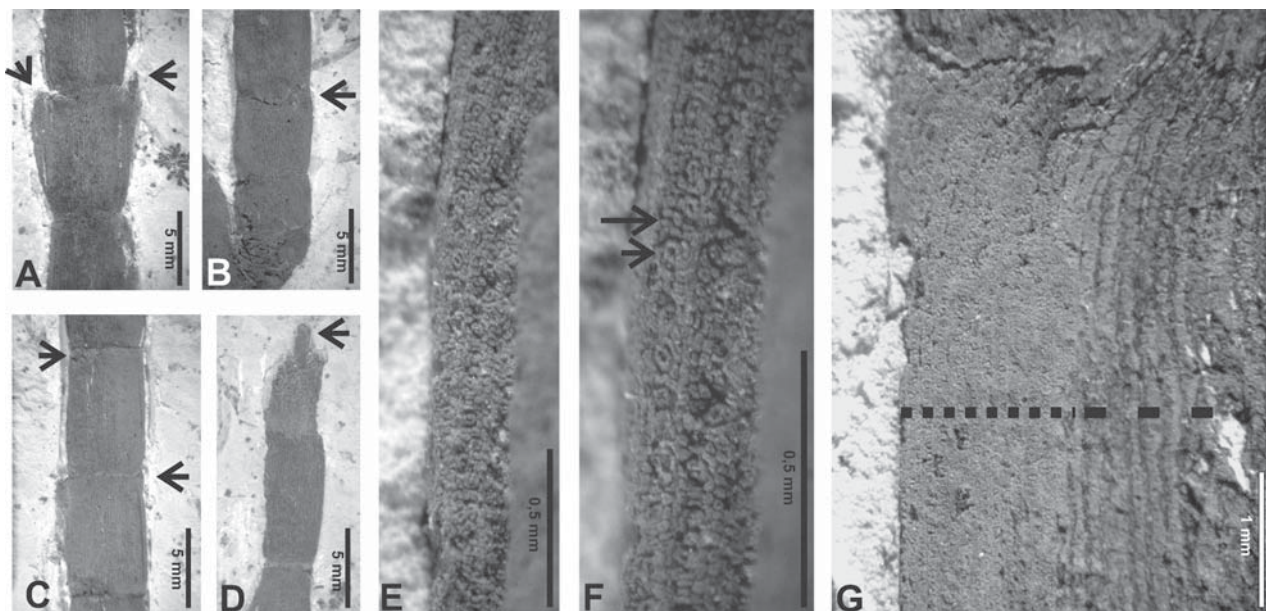


Fig. 5. *Frenelopsis* sp., leafy shoot, SM.B 16486; **A–C** – segments of the shoot with dense parallel striation on the surface and with free leaf tips (arrows), **A** – detail of Fig. 4C, segment with opposite free leaf tips; **B** – detail of Fig. 4C; **C** – leaf tips abraded; **D** – ultimate branchlet with abraded leaves showing a wide zone of parenchymatous tissue between the wood (arrow) and the epidermis in the segments (= fleshy leaves); **E** – part of the epidermis of a cylindrical segment, three longitudinal stomata rows; **F** – detail of **E**, stomata with Florin ring (short arrow), ordinary epidermal cells with papillae (long arrow), oblique orientation of stomata; **G** – surface of a segment, preservation of epidermis cells in the left part (dotted line) with dense longitudinal stomata rows, right part with abraded epidermis (broken line).

1988). *Pseudofrenelopsis* Nathorst, 1893 emend. Srinivasan, 1995 differs in bearing almost one leaf per whorl and mainly “open” segments with sutures or gaps. The Crato material shows sutureless segments with one or two leaves. If only small sections of the branchlets with only one leaf per segment are available, the determination of the morphogenus is very problematic.

Srinivasan (1995) discussed this problem for material from the early to middle Albian Puddledock locality, USA (Potomac Group). She described shoots with partly opposite-decussate phyllotaxis and partly sections with single-leaved “internodes” with and without sutures, while the stomatal characters are typical for the *Pseudofrenelopsis* type. *Pseudofrenelopsis nathorstiana* Srinivasan, 1995 clearly shows that differences in

phyllotaxis may no longer provide sufficient grounds for the separation of *Frenelopsis* and *Pseudofrenelopsis* (Srinivasan 1995). However, the segments of *Frenelopsis* are only of the sutureless type. Without any formal consequences, Srinivasan (1995) suggested to consider a merger of the morphogenera *Frenelopsis* and *Pseudofrenelopsis*.

Frenelopsis consists of several morphospecies typically bearing three leaves per whorl (Kvaček 2000; Watson 1988), but two species have been assigned to *Frenelopsis*, that show two opposite leaves per whorl and a decussate phyllotaxis. These species are *F. teixeirae* Alvin & País, 1978 from the Hauterivian to Barremian of Portugal and *F. choshiensis* Kimura et al., 1985 from the Barremian of Japan (Table 1).

Table 1. Cretaceous species of *Frenelopsis* Schenk, 1869 and their numbers and arrangements of free leaf tips in comparison with *Pseudofrenelopsis* Nathorst, 1893.

Species	Occurrence	Stratigraphy	Reference	Leaves per segment	Phyllotaxis of free leaf tips
<i>F. alata</i> (K. Feistmantel, 1881) Knobloch, 1971	Czech Republik, France, Portugal	Albian- Cenomanian (Turonian)	Kvaček 2000	3	whorls of 3 in cyclic arrangement
<i>F. harrisii</i> Doludenko & Reymanówna, 1978	Tadzikistan	Cenomanian	Doludenko & Reymanowna 1978	3	whorls of 3 in cyclic arrangement
<i>F. hoheneggeri</i> (Ettingshausen, 1852) Schenk, 1869	Czech Republic, Poland	Hauterivian	Watson 1988	3	whorls of 3 in cyclic arrangement
<i>F. kaneviensis</i> Barale & Doludenko, 1985	Ukraine	Late Albian	Barale & Doludenko 1985	3	whorls of 3 in cyclic arrangement
<i>F. occidentalis</i> Heer, 1881	Portugal	Aptian/Albian	Alvin 1977	3	whorls of 3 in cyclic arrangement
	NW Germany	Berriasian	Watson & Alvin 1999	3	whorls of 3 in cyclic arrangement
<i>F. oligostomata</i> Romariz, 1946	Portugal	Cenomanian	Kvaček 2000	3	whorls of 3 in cyclic arrangement
<i>F. ramosissima</i> Fontaine, 1889	Potomac Group localities, USA	Barremian – Albian	Axsmith & Jacobs 2005	3	whorls of 3 in cyclic arrangement
<i>F. rubiesensis</i> Barale, 1981	Spain	Berriasian	Barale 1981	3	whorls of 3 in cyclic arrangement
<i>F. silfloana</i> Watson, 1983	Nubian Sandstone, Sudan	Early Cretaceous	Watson 1988	3	whorls of 3 in cyclic arrangement
<i>F. teixeirae</i> Alvin & País, 1978	Portugal	Hauterive- Barremian	Alvin & País 1978	2	opposite pairs in decussate arrangement
<i>F. choshiensis</i> Kimura et al., 1985	Japan	Barremian	Kimura et al. 1985	2	opposite pairs in decussate arrangement
<i>F. sp.</i>	Araripe Basin, NE Brazil	Late Aptian	this paper	1 or 2	partly opposite pairs
<i>Pseudofrenelopsis</i> Nathorst, 1893	Europe, Asia, Africa, North America	Cretaceous	Watson 1988	1	simple helix
<i>Pseudofrenelopsis</i> <i>nathorstiana</i> Srinivasan, 1995	Puddledock, USA	Early/Middle Albian	Srinivasan 1995	1 or 2	mostly simple spiral, partly cyclic arrangement

Except for *Frenelopsis ramosissima* Fontaine, 1889 the morphogenera *Frenelopsis* and *Pseudofrenelopsis* are distinguished from each other also by stomatal characters. *Pseudofrenelopsis* shows a papillate Florin ring, the papillae are overhanging the stomatal pits, and *Frenelopsis* shows nonpapillate Florin rings, but papillae on the subsidiary cells are developed completely down inside the large outer stomatal pit (e.g. Srinivasan 1995; Watson 1988). *F. ramosissima* bears stomata with papillate Florin rings and no papillae inside the stomatal pit (Watson 1977).

Independent from the ongoing discussion on the concept of the genus *Frenelopsis* (e.g., Axsmith & Jacobs 2005; Kvaček 2000), an assignment of the Crato material to this genus on the base on shoot morphology alone appears appropriate. In addition, stomata with nonpapillate Florin rings are mainly characteristic for the genus *Frenelopsis*. However, any assignment of our material to a distinct species is impossible due to the lack of distinctive epidermal characters, although phyllotaxis shows similarities to *F. teixeirae* and *F. choshiensis*. From *Pseudofrenelopsis nathorstiana* the Crato material differs in bearing only cylindrical sutureless segments.

Palaeobiogeography. *Frenelopsis* was distributed more or less worldwide during the Early Cretaceous. Species with 3 leaves per whorl are reported from the Early Cretaceous of North America, Europe, Africa and Asia (Table 1).

Frenelopsis species with less than 3 leaves per whorl also appear to be distributed worldwide in the Early Cretaceous: they are known from the Hauterivian to Barremian of Portugal (*F. teixeirae* Alvin & Pais, 1978), from the Barremian of Japan (*F. choshiensis* Kimura et al., 1985) and now also from the Aptian of Brazil. The occurrence of *Frenelopsis* in South America at the time when the Gondwana continents had just started to drift apart in the Early Cretaceous is not unexpected.

A worldwide distribution in the Early Cretaceous is also recorded for *Pseudofrenelopsis* (North America, Srinivasan 1995; Africa, Watson 1983; Europe, Central America, Watson 1977; Asia, Mussa et al. 1991 and Zhou Zhiyan 1995).

Taphonomy, palaeoecology and palaeogeobotany

Many of the conifer specimens from the Crato Formation are relatively fragmentary and partly abraded. This seems also to be the case with

Tomaxellia biforme of which only two relatively small pieces have been observed in various collections among several hundred fossils. Therefore, we assume that the majority of the *Tomaxellia biforme* plants did not grow close to the area of deposition and the plant fragments were transported by rivers.

Due to their fragility (SM.B 16448; Fig. 3A), large, almost completely preserved shoots of *Frenelopsis* sp., most likely were not transported over long distances. This genus might have grown near the place of deposition and thus its habitat was probably under a brackish influence of a hypothesized lagoon (Martill et al. 1993).

There is no indication that these frenelopsid plants were shrubs or large trees. An occurrence of frenelopsids in a monospecific or low diversity assemblage, as known from other localities (e.g., Axsmith & Jacobs 2005), can be excluded for the Crato flora because of its rarity in the respective taphocoenoses.

All conifer taxa encountered at the Crato locality, including *Tomaxellia biforme*, bear rather thick, coriaceous leaves. In *Frenelopsis* sp. the wide zone of parenchymatous tissue between the wood and the epidermis in the segments of ultimate vegetative shoots ("fleshy leaf"; Fig. 5D) possibly indicates succulence (e.g., Axsmith & Jacobs 2005). However, the common interpretation of frenelopsids as arid coastal forest-inhabiting xerophytes (Vakhrameev 1970) was modified by Gomez et al. (2002). They asserted that the frenelopsids were adapted to a wider ecological range and thus habitats of different species might have varied substantially. Axsmith & Jacobs (2005) conclude for *F. ramosissima* found at sites in the Texas and the Potomac Group (USA) that some species may have had also exhibited large ecological amplitudes. However, due to the lack of a palaeosociological concept for the Crato flora and the sparse record of *Frenelopsis* sp. within the flora the palaeoecological interpretation of the Crato frenelopsids remains vague.

A warm to hot, temporarily dry (possibly seasonally dry) climate during the late Early Cretaceous in the palaeoequatorial region has been hypothesized by various authors (e.g. Skelton 2003). For the Crato region this assumption is validated by various plant groups. Ferns, several gymno- and angiosperms show adaptations to drought, such as spines and coriaceous and/or reduced leaves (Mohr & Rydin 2002; Mohr & Bernardes-de-Oliveira 2004). Some of the characters of the Crato conifers, such as coriaceous leaves and thick cuticles as well as succulent

twigs in *Frenelopsis* sp., also support this assumption.

It is worth mentioning that a flora of the same age from Tunisia shares several taxa with the Crato flora, among them *Podozamites* and various angiosperms, such as *Trifurcatia* Mohr & Rydin, 2002 and nymphaealean waterplants (Barale & Ouaja 2001; Mohr et al. in press). The flora of the Early Cretaceous of Portugal also shares several taxa with the Crato flora, among them the conifers *Brachyphyllum obesum*, *Podozamites* sp. and *Frenelopsis teixeirae*, a *Frenelopsis*-type with less than 3 leaves per whorl (Teixeira 1948). The flora of the Leiva region in Colombia (Aptian, Early Cretaceous) contains also conifers of the *Brachyphyllum*- and the *Podozamites*-morphotype and female cones of Araucariaceae (Van Waveren et al. 2002).

Most of the conifer families of early to mid-Cretaceous floras such as Araucariaceae and Cheirolepidiaceae seem to have been relatively widely distributed. This is due to the fact that palaeofloristic exchange between Gondwana (South America, Africa, Australia) and the Northern Hemisphere (North America, Europe, Asia) was possible during the Jurassic, perhaps until the Early Cretaceous. However, endemic taxa and/or typical groups of conifers, characteristic for a region or a continent, seem to have existed as well. *Tomaxellia*, most likely endemic to South America, did not reach Africa or Europe during the Early Cretaceous. This might imply a relatively late evolution of the genus during the latest Jurassic/earliest Cretaceous, when the successive opening of the Atlantic made migrations much more difficult.

Conclusions

Cheirolepidiaceae conifers from the Crato Formation (late Aptian, Early Cretaceous) of north-eastern Brazil were studied. The material consists of sterile leafy shoots that are partly well preserved. Two genera were recognized based on morphological and anatomical characters, *Frenelopsis* and *Tomaxellia*, the latter known previously only from Patagonia, Argentina. Detailed investigations of the leaf epidermis of *Tomaxellia biforme* were carried out by using the scanning electron microscope (SEM). The leaf epidermis of *Frenelopsis* sp. was studied by light microscope (LM). *Frenelopsis* sp. might have grown near the Crato-lagoon/lake under brackish influence. The palaeoecology of *Tomaxellia biforme* remains

unresolved. Its habitat might have been relatively far from the locality of deposition due to its rare occurrence and fragmentary preservation. The morphological and anatomical characters of both conifers are interpreted as adaptations to a warm and temporarily dry climate.

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