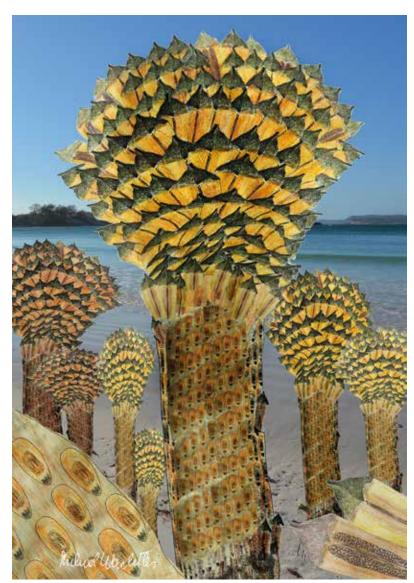
Eocyclotes alexawachtleri. A New Arborescent Lycopod Family from the Early-Middle Triassic

Michael Wachtler
P. P. Rainerstrasse 11, 39038 Innichen, Italy; E-mail: michael@wachtler.com

In the Early-Middle Triassic Dolomites (Northern Italy), the lycopods experienced a strange boom after a decline in the Carboniferous. Beside arborescent *Lycopia dezanchei* exhibiting dichotomous branching and having affinities with the Lepidodendrales, dwarfish double-tufted *Sigillcampeia nana*, probably a descendant from the Sigilariaceae, a new arborescent lycopod was encountered – *Eocyclotes alexawachtleri* nov. gen. sp. n. It can characterised as small monopodial tree with short tongue-shaped, mucronate leaves, heterosporous sporophylls exhibiting a bridge's function between a group of Carboniferous Sigillariaceae, characterised by their single trunk ending in an apical cluster of fertile and sterile leaves and the dwarfish Middle Triassic *Lepacyclotes*-lycopods.

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Keywords: Fossil lycopods, Sigillaria, Alps, Triassic



Eocyclotes alexawachtleri

The Last Survivor of the Paleozoic Giant Clubmosses in the Triassic

It performs a bridge's function between the single tufted Carboniferous Sigillarias and the Middle Triassic *Lepacyclotes*-lycopods. It is rare that the extinction drama of a plant can be followed so well over millions of years as in *Eocyclotes-Lepacyclotes*.

Introduction

From the Carboniferous till the Early Permian, giant lycopods dominated the Earth. Usually they were classified as Lepidodendrales, with their creeping rhizomes and their long-leaved tufts and strobili resembling conifer cones. The other group was the Sigillariaceae, which often were reported having one single or branching in two apical tufts of leaves. Unfortunately, they were so huge that the whole plant could not be preserved. Due to fortunate circumstances in the Early-Middle Triassic of the Alps, dwarf forms of the Sigillariaceae (and also from the Lepidodrenales) were found that explain the enigma of the giant horsetails. With Sigillcampeia nana (Wachtler, 2016), a Sigillariaceae evidencing two apical tufts of leaves was described in which the hermaphroditic fertile organs were inserted. It was widespread in the form of several subspecies (Sigillcampeia blaui) all over the Triassic of the Alps. Another Sigillariaceae was now discovered in the Dolomites that is characterised only by one apical rosette of fertile micro- and macrosporangia. Interestingly, in the same layers, a known dwarfish form can be encountered - Lepacyclotes bechstaedtii.

Systematic Palaeontology

Class: Lycophyta Order: Sigillariaceae

Genus *Eocyclotes* nov. gen. n. sp. WACHTLER 2020

Etymology

It is named after the affinity to the Triassic lycopod *Lepacyclotes*, and the greek word "Eos", meaning dawn, to connect it with its Carboniferous ancestors.

Diagnosis

Medium-growing Lycophyta have spirally disposed leaf scars evidencing a longitudinal ornament remain. The upper part has closely spaced foliage forming a rosette that holds numerous heterosporous sporophylls. They terminate in a triangular to mucronate apex. Mega- and microsporangiate sporophylls are similar. The sporangia are located adaxially and centrally.

Eocyclotes alexawachtleri n. sp. WACHTLER 2020

Type horizon and age

Dolomites, Early-Middle Triassic, Anisian, Pelson-Illyrian (243 - 241 Mya)

Holotype

KÜH 1272; Coll. Wachtler, Dolomythos Museum, Innichen

Paratypes

KÜH 1327 (fertile tuft), KÜH 1319 (stem with leaf-scars; Coll. Wachtler, Dolomythos Museum, Innichen

Material

Eocyclotes alexawachtleri is abundant on Kühwiesenkopf, near the Megachire-lla wachtleri finding place. (KÜH 1277, KÜH 1301, KÜH 1304, KÜH 1305, KÜH 1309, KÜH 1314, KÜH 1315, KÜH 1316, KÜH 1317, KÜH 1320, KÜH 1391.

Etymology

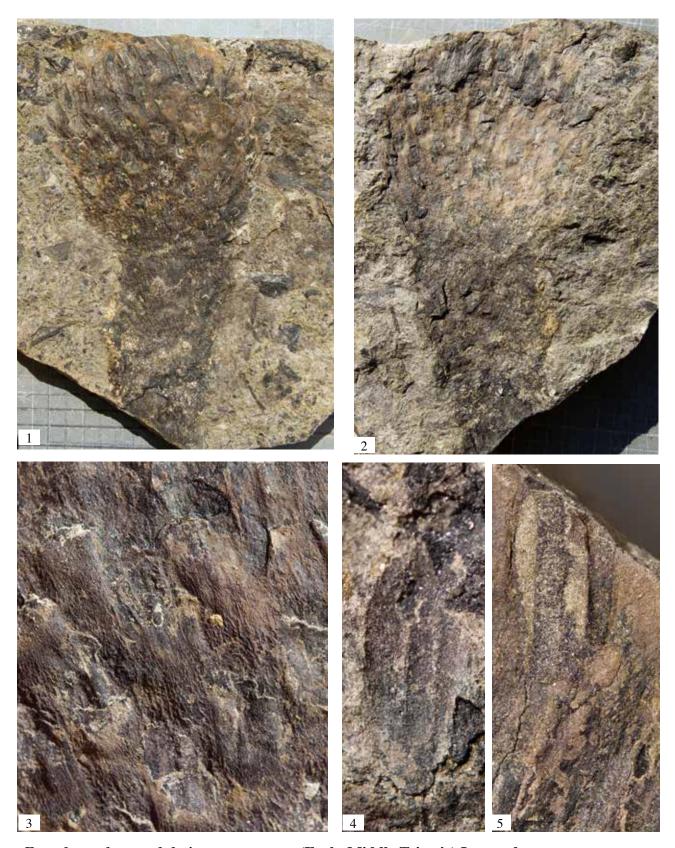
It is in reference to Alexa Wachtler who discovered the holotype and made the conservation.

Description

Stems: They are usually 5–7 cm wide (KÜH 1272, basal 5 cm, apical 7 cm) and probably 30–70 cm long (KÜH 1391=30 cm). The underground rhizomorph system is based mainly on downward-directed subtle vertical roots (KÜH 1314). The lower parts are sometimes covered by leaf cushions in slightly downwards orientated longitudinal rows. Scars elliptic with one abscission point situated over the centre of the leaf scar.

Leaves: The plant holds mainly identical sterile and fertile leaves, which are difficult to separate because they are always densely packed in the apical tuft.

Sporophylls: They are tongue-shaped with wide triangular tips, up to 5 cm long, 2 cm wide and straight to slightly concave with basal break-off points. Sporophylls with a central longitudinal strip. The sporangia are disposed on the adaxial part containing both macro- and micro-spores. The fertile midsection runs lengthwise and is narrower than



Eocyclotes alexawachtleri nov. gen. n. sp. (Early-Middle Triassic) Lycopod

1. Almost complete plant with the apical crowded fertile rosette (KÜH 1272, holotype); 2. Counterplate from the holotype (KÜH 1272); 3. Details of the basal sterile foliage; 4–5. Isolated microsporophyll, adaxial and abaxial part (all KÜH 1272, holotype, Kühwiesenkopf, Anisian, Coll. Wachtler, Dolomythos-Museum Innichen



Eocyclotes alexawachtleri nov. gen. n. sp. (Early-Middle Triassic) lycopod

1. Detail of a fertile tuft (KÜH 1327, paratype); 2. Closed cluster of a rosette (KÜH 1320); 3. Trunk evidencing some leaf-scars (KÜH 1391); All Kühwiesenkopf, Anisian, Coll. Wachtler, Dolomythos-Museum, Innichen)



Eocyclotes alexawachtleri nov. gen. n. sp. (Early-Middle Triassic) lycopod

1. Trunk with fertile and sterile leaves (KÜH 1301, paratype); 2. Cluster of sporophylls (KÜH 1305); 3–4. Stem evidencing some leaf-scars and detail of them (KÜH 1319, paratype); all Kühwiesenkopf, Anisian, Coll. Wachtler)

the two flanks. Proximal section of the sporophylls is slightly thickened with the umbos curving only slightly outwards. The cluster of sporophylls decomposes after maturing.

Discussion, Remarks and Ecology

The arborescent tree represents one of the most interesting lycopods of the Early-Middle Triassic Anisian sediments of the Dolomites. Eocyclotes alexawachtleri can be found mainly in one layer on the lower part of the Kühwiesenkopf in the Prags-Dolomites, where it is frequently found together with other lycopods like Lycopia dezanchei, Isoetites brandneri, Selaginellites leonardii (Wachtler, 2011), Sigillcampeia nana (Wachtler, 2016) and bechstaedtii Lepacyclotes (Wachtler, 2016). The layers can be interpreted as a lacustrine deposit (also with some molluscs and bivalves), representing the flooding of an area of local vegetation with a high percentage of different lycophytes. Due to its appearance, it can be recognised easily among other clubmosses. Only the low-growing, but trunkless Lepacyclotes bechstaedtii (Emmons, 1856; Fliche, 1910;

Grauvogel-Stamm & Duringer, 1983; Wachtler, 2011; Wachtler, 2016) with closely spaced foliage forming a rosette can sometimes give rise to some doubts.

Why some of the giant clubmosses, commonly thought that they became extinct in the Late Carboniferous (*Lepidodendron*) or the Early Permian (*Sigillaria*) (Taylor et al., 2009), surprisingly survived the Permian-Triassic cataclysm, becoming a heyday as bonsai-forms in the Early-Middle Triassic, especially in the Dolomites is difficult to explain.

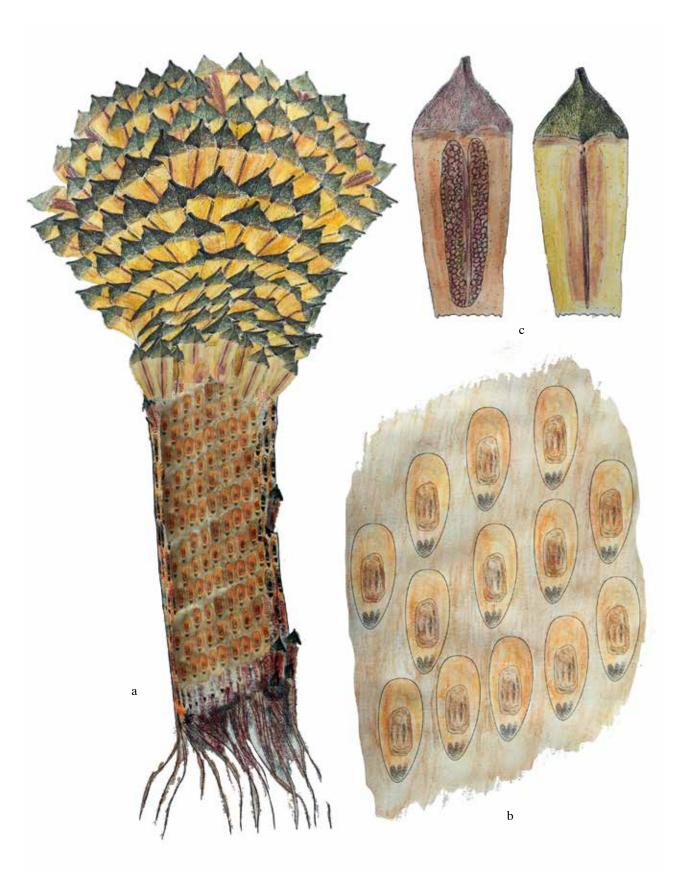
Interestingly, the Lepidodendrales, Sigillarias, *Eocylotes*-lycopods were not so closely related as previously thought. Their common ancestor must have originated in the Devonian. The cones or sporophyll tufts are too different for a close relationship. Isolated stands another character lycopod Early Triassic, *Pleuromeia* from the sternbergii (Kandutsch & Wachtler, 2012). Probably they built a third family, closely related to the Sigillariaceae than the Lepidendrondrales.

Interestingly, *Eocyclotes alexawachtleri* acts as a bridge between one group of Upper



Eocyclotes alexawachtleri nov. gen. n. sp.

Stem with roots (KÜH 1314); Kühwiesenkopf, Anisian, Coll. Wachtler, Dolomythos-Museum, Innichen)



Eocyclotes alexawachtleri nov. gen. sp. n. (Early-Middle Triassic) Reconstructions

a. Entire plant (KÜH 1272, holotype); b. Detail of the sterile leaf scars (KÜH 1319); c. Single sporophylls with sporangia, inner and outer view.

Carboniferous-Permian *Sigillaria* clubmosses that usually in literature were described and figured as monopodial stems (sometimes known as *Eurhytidolepis*), in contrast to the distally bifurcating better known *Sigillaria*-lycopods, classified sometimes also as *Favularia* (Hirmer, 1927).

Carboniferous *Sigillaria* as well as Triassic *Sigillcampeia* were characterised by their long, thin, grass-like sterile leaves attached directly to the stem growing in a spiral along the trunk. The leave-abscission holes were smooth and elliptic with one prominent outer rim and usually two abscission points situated just over the centre of the leaf scar. The plant was heterosporous, with one usually huge megaspore and equal microsporophylls filled with many microsporangia that were shed in the same way after fertilisation (Wachtler, 2016).

Eocyclotes-lycopods indeed had tongue-like sterile leaves with a blunt to mucronate apex, whereas the heterosporous sporophylls were mainly identical, forming a cluster on the top of the plant. The leaf cushions were elongated downwards. In that exist so many differences that they can be inserted without hesitation in two distinct families. Therefore, it can be supposed that both lycopod tribes, *Sigillaria* and *Eocyclotes*, have their origin in the Carboniferous, being bigger arborescent lycopods this time.

They gradually reduced their size till they adopted, in the Early Middle Triassic with *Eocyclotes alexawachtleri*, an arborescent, shrubby character. After the Triassic, they disappeared, and today we cannot encounter any living representative. The same can be stated for the Sigillariaceae, which were common with *Sigillcampeia nana* in the Early Middle Triassic Dolomites, rarer in the Late Triassic with *Sigillcampeia blaui*, disappearing shortly after that period.

The Interesting Disappearance of *Eocyclotes* and *Lepacyclotes*

In only a few plants worldwide, the rise and fall of a plant family can be followed so closely as in these lycopods. It seems that the genus Lepacyclotes was a worldwide-ranging Mesozoic Lycophyta, found from the Alps to China [Lepacyclotes (Isoetes) ermayinensis], in Kazakhstan [Lepacyclotes (Tomiostrobus) convexus] and in Australia and America (Grauvo-

gel & Lugardon, 2001) covering a period from the Early Triassic to Early Jurassic (Lepacyclotes kirchneri) (Bauer et al., 2014). Surprisingly, we have on the Anisian Fossillagerstätte Kühwiesenkopf in the Italian Dolomites a coeval appearance of the two parented lycopods Eocyclotes alexawachtleri and Lepacyclotes bechstaedtii. They can also be distinct due to their character: Eocyclotes alexawachtleri was robust and small-arborescent, Lepacyclotes bechstaedtii only small-pineapple sized. Nevertheless, it generated a short stem, mainly an underground root (KÜH 1409), but if it had been fossilised from above (KUH 1400), it would have had all the characteristics of Middle Triassic Lepacyclotes zeilleri.

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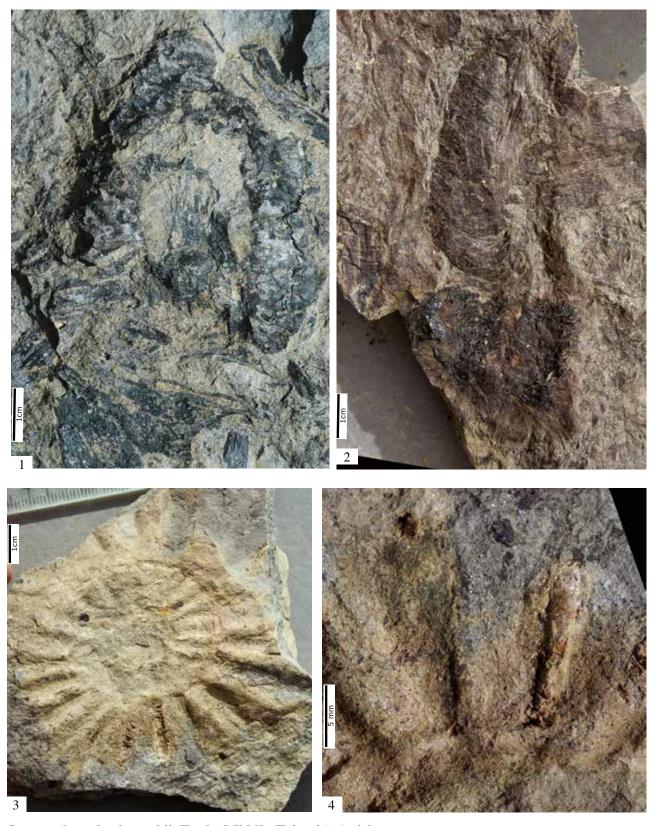
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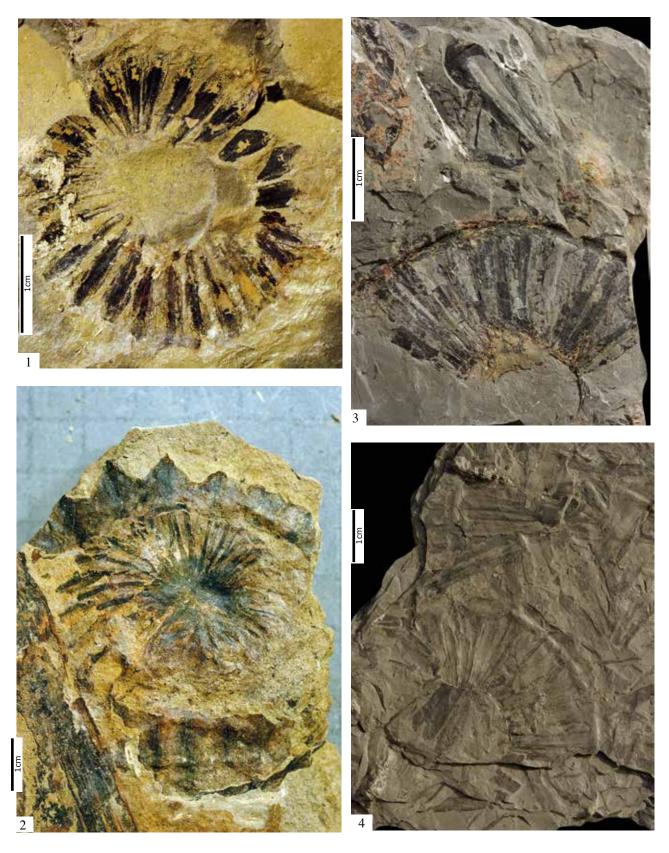
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8 Dolomythos



Lepacyclotes bechstaedtii (Early-Middle Triassic) Anisian

1. Almost complete plant seen from the lateral side (KÜH 1285, holotype); 2. Complete plant's lateral view with the connected root-system (Plant with crowded foliage (KÜH 1409); 3–4. Plant fossilised from above with detail of the sporophylls. It resembles an ammonite, but the charcoaled sporangia prove unambiguously their plant origin (KÜH 1400), All Kühwiesenkopf, Anisian, Coll. Wachtler, Dolomythos-Museum)



Lepacyclotes zeilleri (Middle Triassic) Ladinian

1. Complete juvenile rosette of a plant with sporophylls (ILS 595); 2. Adult plant with two superimposing rosettes (ILS 593 Coll. Nißler); 3–4. Two rossettes (Zwingelhausen, Vaihingen, Coll. Doná), Ladinian



The Upper Triassic Raibl Cataclysm and its impact on the plant world

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