Sigillaria-Lycopods in the Triassic

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It was thought that the giant clubmosses like *Lepidodendron* died out at the end of the Carboniferous or the *Sigillaria* trees at the beginning of the Permian. But strangely enough in the Triassic we have with *Lycopia dezanchei* an enigmatic arising of *Lepidodendron r*esembling lycophyta or with *Sigillcampeia* dwarfish successors of the *Sigillaria*. Whereas *Lycopia dezanchei* exhibiting dichotomous branching and creeping root horizons is till now recorded only until the Early–Middle Triassic (Anisian), representatives of the Sigillarias were present throughout the Triassic with *Sigillcampeia nana* nov. gen. sp. n. covering extensive areas in the Dolomites in Anisian layers and *Sigillcampeia blaui* n. sp. reaching from the Middle to the Upper Triassic. They were characterised by their bonsai-like growth, and give a deep insight into the blueprint, growth and fertilisation of this lycopod family. It is also interesting that beneath microsporangiate sporophylls they also hold macrosporophylls with only one huge sporangia, that in other cases could also be regarded as a seed.

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The last survivors of the Paleozoic giant clubmosses in the Triassic

Left *Sigillcampeia nana*, a descendant of the Sigillarias, and *Lycopia dezanchei,* a suggested successor of the Lepidodendrales

Class Lycopsida
Order Lepidodendrales
Genus Sigillaria BRONGNIART, 1822

Systematic Paleontology

Division Lycophyta
Subdivision Lycophytina Kenrick & Crane, 1997
Order Sigillariaceae

Genus *Sigillcampeia* nov. gen. n. sp. WACHTLER 2016

Etymology

After their affinities to the lycopod *Sigillaria* and Edith Campei, who found the first specimen.

Diagnosis

Small heterosporous lycopsid plants, with similar mega- and micro-sporangiate sporophylls except for their sporangia on the same cone. Leaves slender and elongated, dropped after maturity. Spirally disposed leaf scars evidencing a longitudinal ornament remain. Roots downwards directed.

Sigillcampeia nana n. sp. WACHTLER 2016

Type horizon and age

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

Holotype

PIZ 750 Coll. Wachtler, Dolomythos Museum, Innichen

Paratype

PIZ 742 (Leaves and stem), Coll. Wachtler, Dolomythos Museum, Innichen

Material

Sigillcampeia nana is abundant especially in one layer on Piz da Peres-Miara. Several hundred specimens were obtained.

Etymology

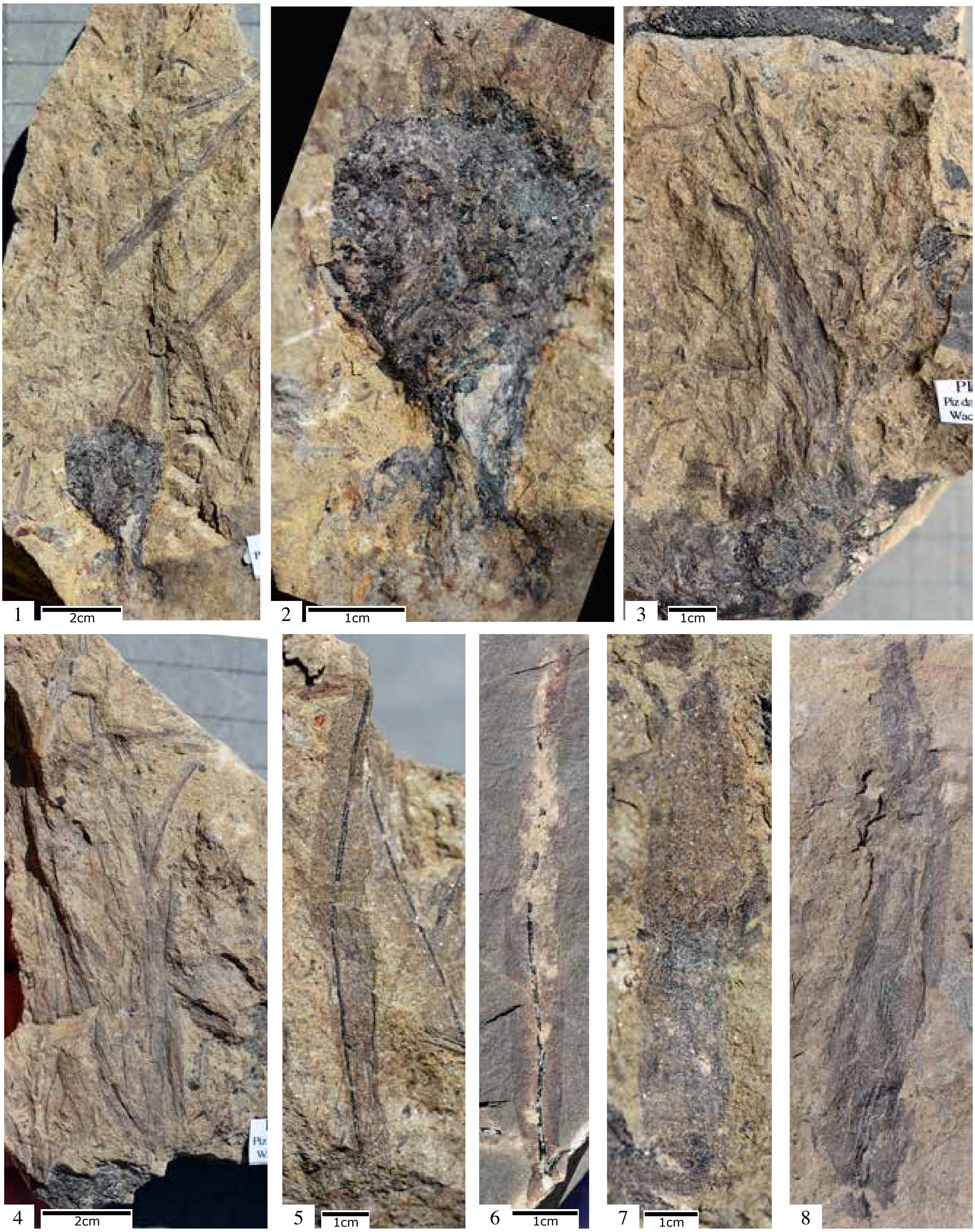
Referring to their dwarfish size in comparison to the Paleozoic Sigillarias.

Description

Stems: Usually 5–12 cm wide (PIZ 907, 885 =11 cm wide) and up to 15 cm long (PIZ 747=13 cm long), divided on the apical part into two separated trunks. The apical part of the stem was topped on each side with a plume of long, grass-like leaves. The underground rhizomorph system is based mainly on downward-directed vertical roots, reaching deep into the ground and adapting the plant well as a coloniser in swamps or nearshore areas. Fertile parts on each upper side, revealing two separate tufts of sporophylls. Lower parts covered by leaf cushions in slightly downwards orientated longitudinal rows. Scars smooth and elliptic with one prominent outer rim. Two abscission points situated just over the centre of the leaf scar. Sporophylls cushions sharply delimited at the apex, larger and narrower, undulate.
Leaves: Long, thin, grass-like leaves attached directly to the stem growing in a spiral along the trunk. Foliage papery, lanceolate, up to 25 cm long by a maximum width of 1.5–2 cm and divided by a single mid-vein, but also other accompanying subtle veins can be noted in some specimens. Scattered individual leaves are found in consistent amounts, but often fractured and broken. Leaf margins are parallel through most of the length and only on the apical part are they restricted to form a pointed to slightly rounded apex. Usually one mid-vein longitudinally in the middle can be observed running the full length of the leaves.
Sporophylls: Megasporophylls with megasporangia are situated on the lower part of the fertile cluster, while microsporophylls with microsporangia are present on the upper part. Megasporophylls are elliptical to rounded, from 3 to 5 cm long and 2.5 to 4 cm wide (PIZ 963 = 4 cm length x 3.8 cm width), microsporophylls more elongated and lacerated on the apical side. Both closely pressed and attached compactly in tight spirals to the stem apex. On the basal side they are slightly concave, the fracture pathway across about two-thirds of the sporophyll. When, as in most cases, the sporophylls were dropped off, waved cushions or scars typically remained on the upper part of the stem bulbs (PIZ 909 = waves 2 cm x 0.1 cm). Megasporophylls holding only one huge megaspore are completely enveloped by an integument-

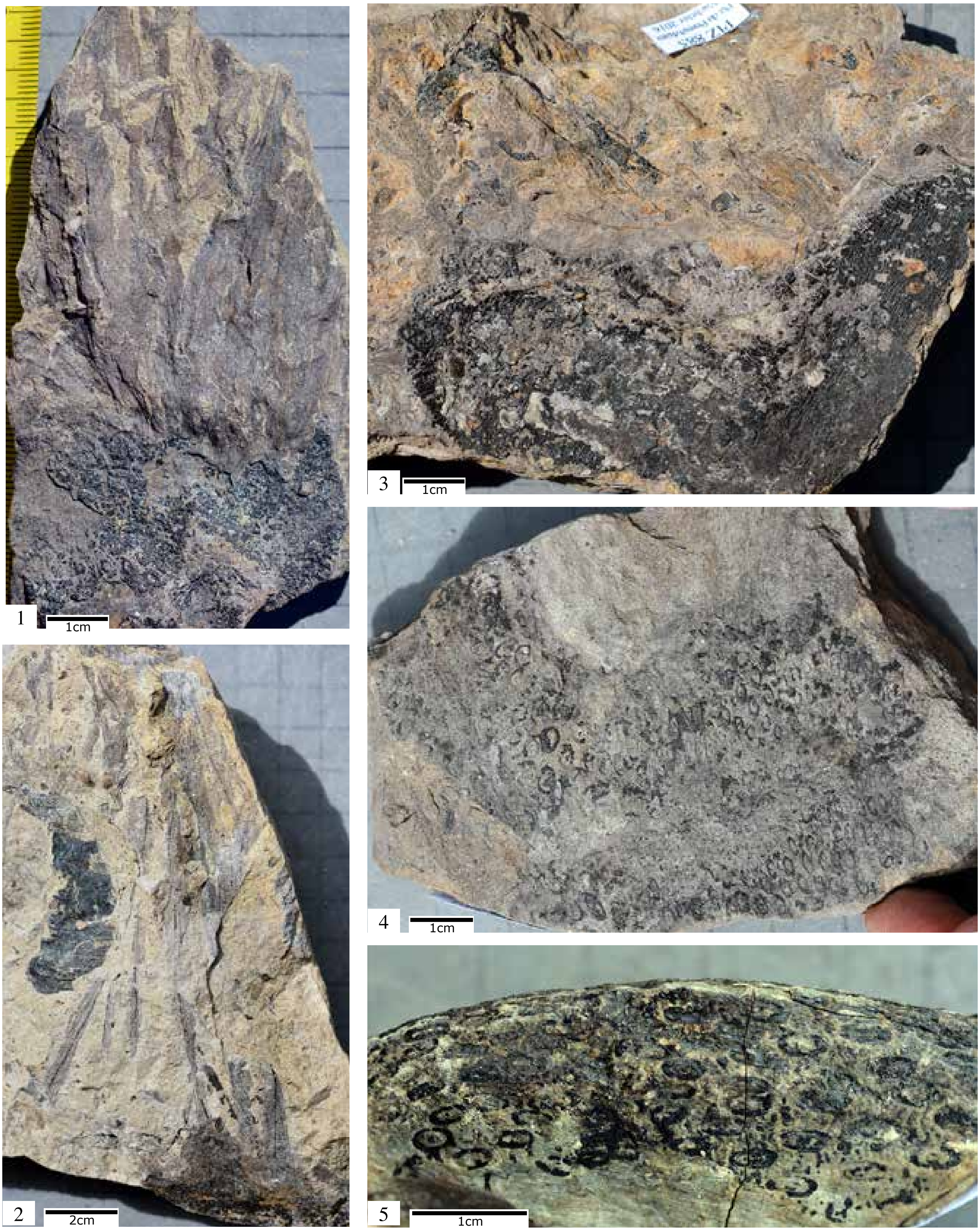
Sigillcampeia nana **nov. gen. n. sp. (Early-Middle Triassic) reconstructions**

a. Juvenile plant (PIZ 750); b. Adult plant; c. Single leaf (PIZ 838); d. Leaves and abscission scars; e. Detail of the sterile leaf scars (PIZ 933, 957); f. Single abscission scar with typical leave attachment points; g. Scars from dropped sporophylls (PIZ 902, 909); h. Entire sporophyll tuft with basal megasporophylls and apical microsporophylls (PIZ 741); i. Megasporophyll holding one megasporangia (PIZ 892, 888); j. Microsporophyll with microsporangia (PIZ 862) Piz da Peres, Dolomites



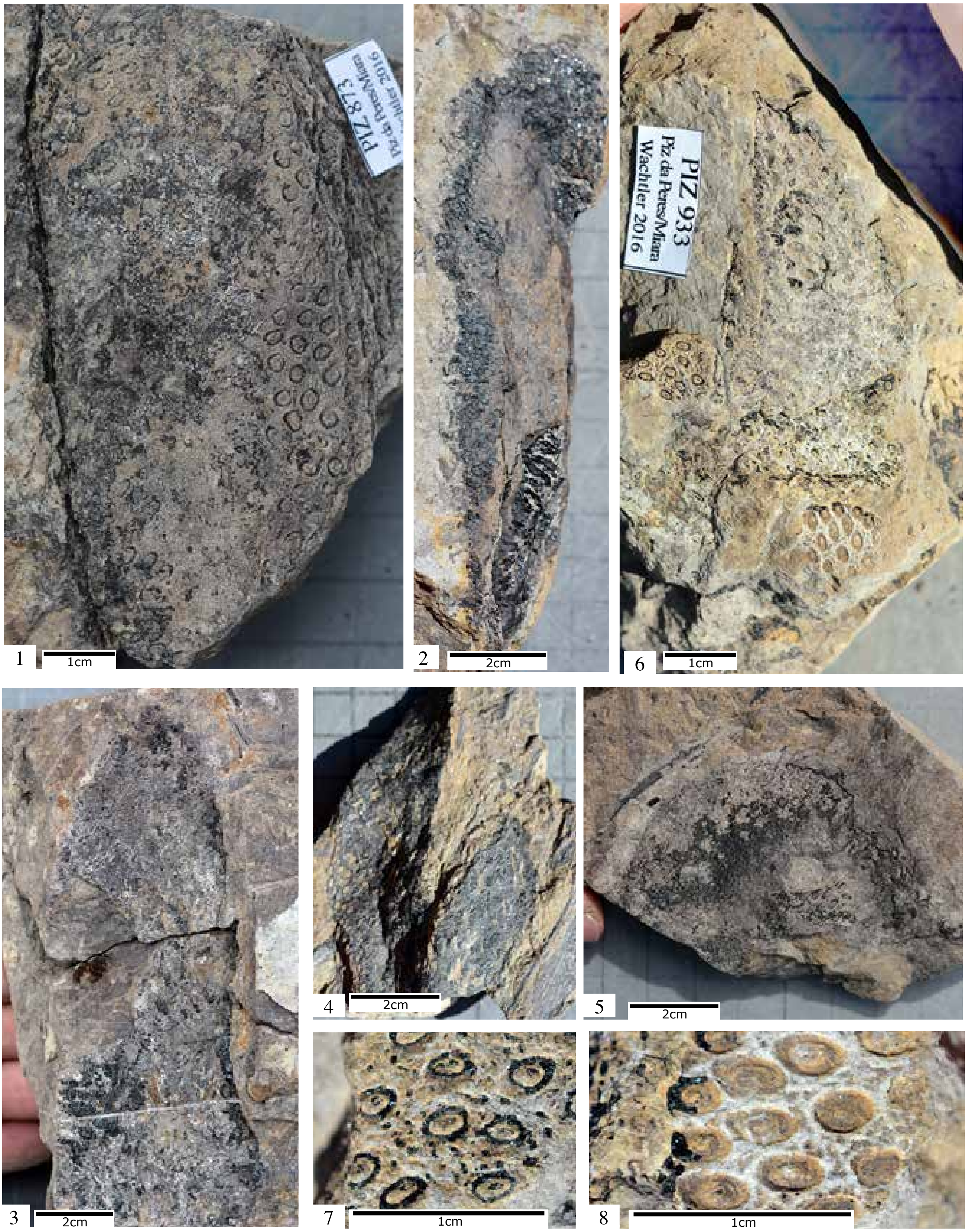
***Sigillcampeia nana* nov. gen. n. sp. (Early-Middle Triassic) Juvenile plants and leaves**

1. Juvenile plant with leaves and roots (PIZ 750); 2. Detail of the bulb and the roots (PIZ 750 designated holotype); 3. Juvenile plant. Observe the doubled bulbs and leaf tufts (PIZ 809); 4. Detail of the juvenile leaves (PIZ 740); 5–8. Papery leaves with a prominent midrib (PIZ 750, 922, 748, 838). All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler



***Sigillcampeia nana* nov. gen. n. sp. (Early-Middle Triassic) Plants and bulbs**

1. Adult plant evidencing the bifurcating leaf tufts (PIZ 742 Paratype); 2. Juvenile plant with two tufts (PIZ 886); 3. Doubled bulbs with leaf tufts (PIZ 885); 4. Furcating bulb (PIZ 882); 5. Border of a leafless bulb (PIZ 904). All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler



***Sigillcampeia nana* nov. gen. n. sp. (Early-Middle Triassic) Plant and bulbs**

1. Unusually elongated stem (PIZ 873); 2. Slender stem (PIZ 747); 3. Apical part of a stem (PIZ 910); 4. Bifurcating stem (ALP 02, Hochalpenkopf upper part); 5. Broad apical part of a stem (PIZ 889); 6–8. Several stems with characteristic leave-abscission holes (PIZ 933). All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler

Sigillcampeia nana nov. gen. n. sp. (Early-Middle Triassic) Bulbs and leaves

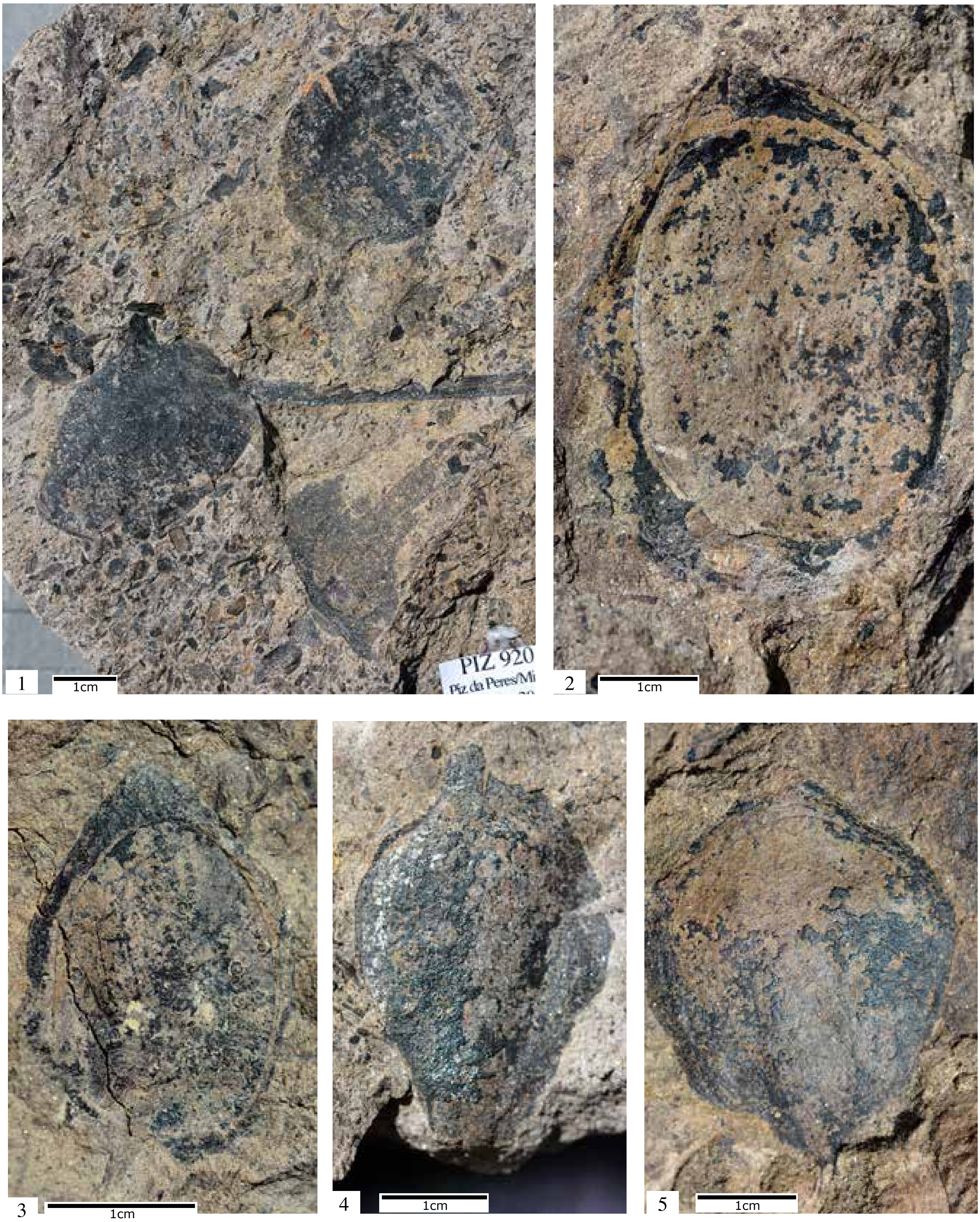
1–2. Apical part of a stem with elongated longitudinal rib-scars from the sporophylls and rounded leaf scars from (PIZ 957, 861); 3–4. Scars remaining after dropping the sporophylls (PIZ 902, 909); 5. Leave tuft connected with the trunk (PIZ 876); All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler

Sigillcampeia nana nov. gen. n. sp. (Early-Middle Triassic) Plant and fertile parts

1. Trunk stump with attached leaf tufts (PIZ 796); 2. Detail of a trunk with abscission ridges of the leaves (PIZ 929); 3–5. Trunk with two connected fertile cones, evidencing (4) lower megasporophylls and (5) upper microsporophylls (PIZ 741); All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler

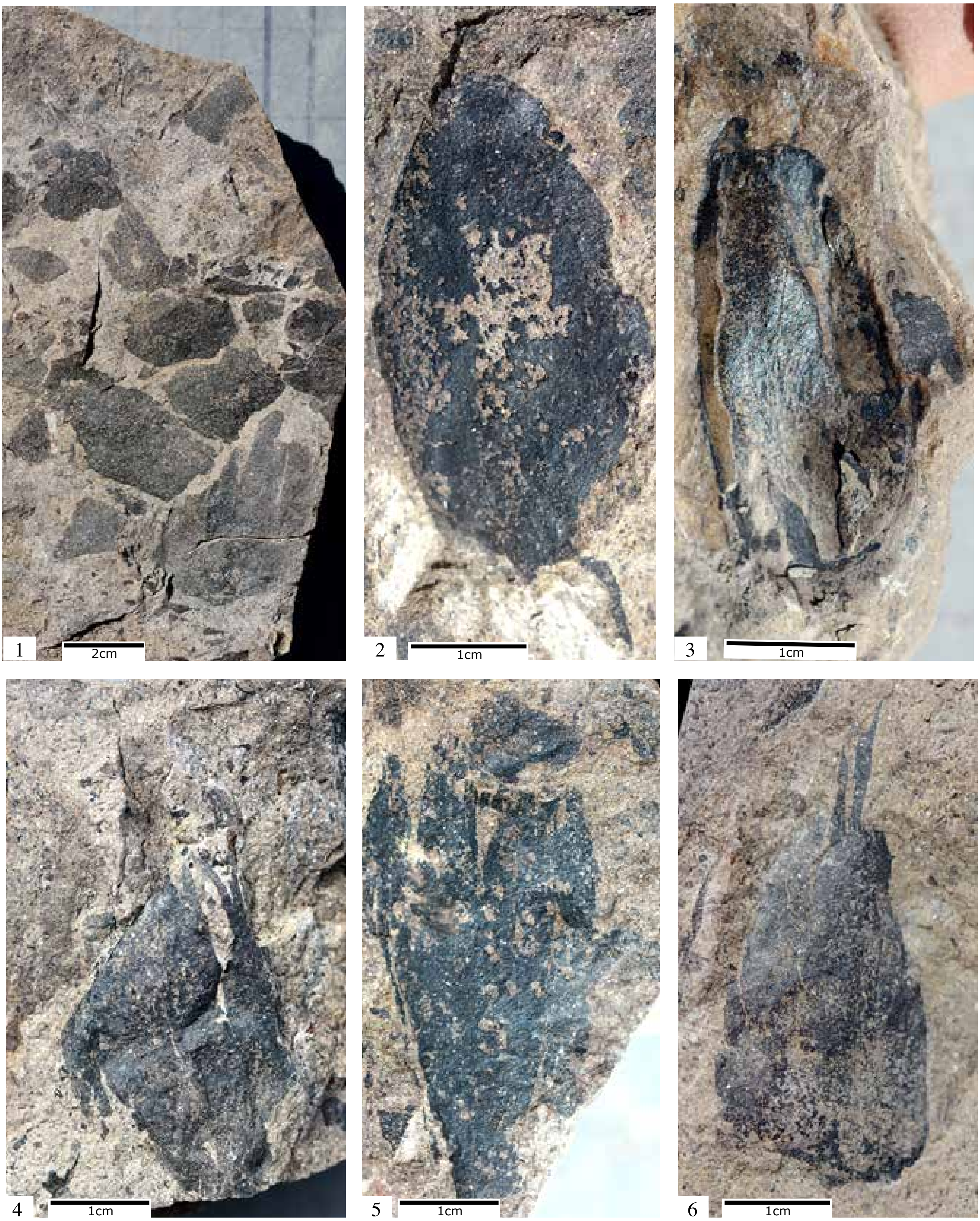
Sigillcampeia nana **nov. gen. n. sp. (Early-Middle Triassic) Plant and fertile parts**

1–2. Plant with connected sterile leaves and on the (2) upper part fertile sporophylls (PIZ 745); 3. Detail of semi-mature sporangia attached on a trunk (PIZ 796); 4. Detail of attached sporophylls connected with the stem (PIZ 744); 5. Sporophyll in lateral view (PIZ 801); All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler



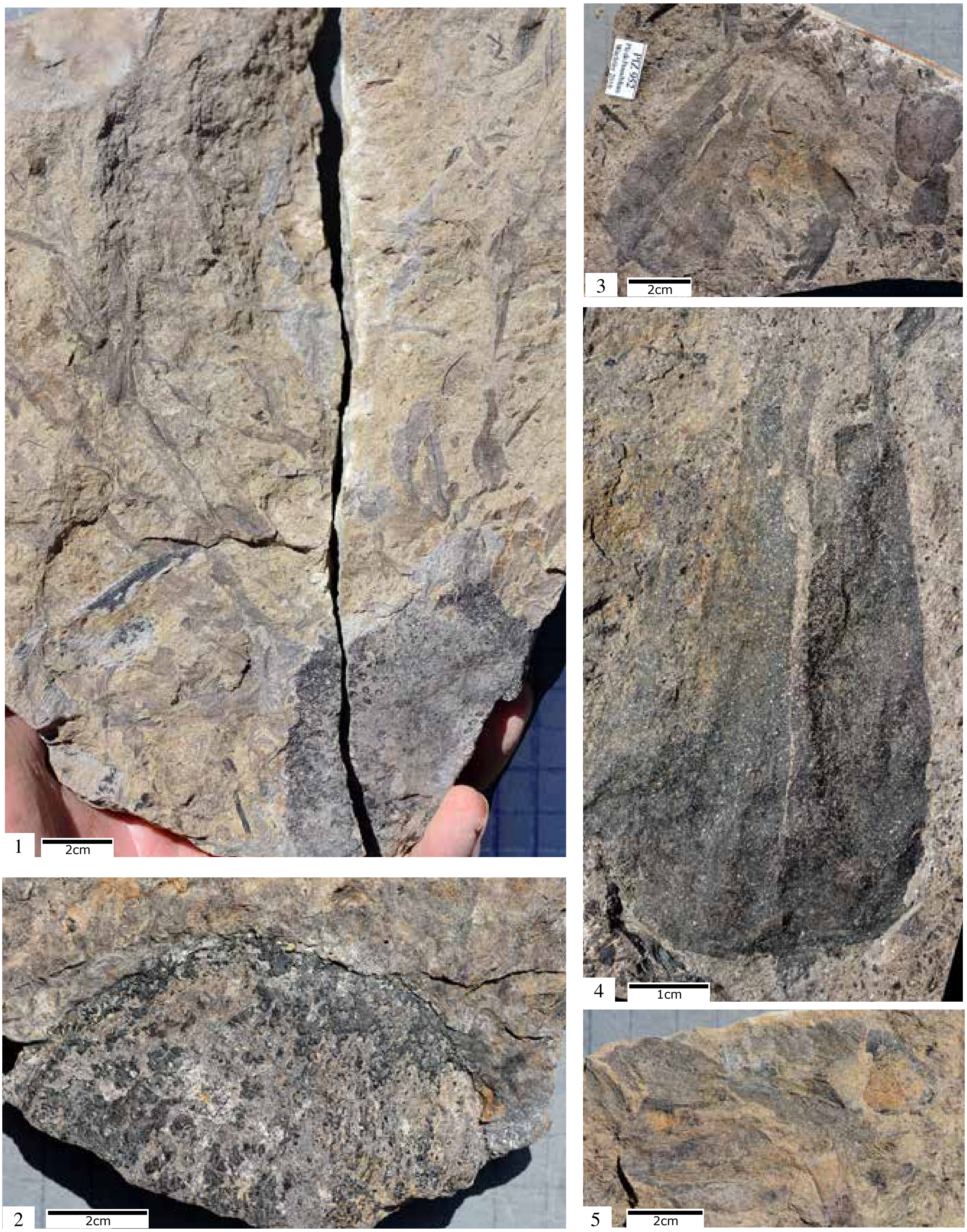
Sigillcampeia nana nov. gen. n. sp. (Early-Middle Triassic) Sporophylls

1. Two sporophylls, the lower one shedding microsporangia (PIZ 920); 2. Megasporangia enclosed inside a megasporophyll that functioned like the integument having one single megaspore (PIZ 892); 3–5. Detail of several sporangia. Note the apical extension (PIZ 743, 914, 888); All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler



Sigillcampeia nana **nov. gen. n. sp. (Early-Middle Triassic) Sporophylls**

1. Typical sporophyll carpet on a slab (PIZ 918); 2–3. Closed microsporophyll (PIZ 895, 812); 4–6. Microsporangia characterised by their elongated torn form (PIZ 862, 856, 900). All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler



Sigillcampeia nana **nov. gen. n. sp. (Early-Middle Triassic) Interesting facts**

1. Trunk with abscissions scars (7 x 7 cm) an 16-cm-long leaves (PIZ 839); 2. Large (10 cm) apical part of a stump (PIZ 907); 3–4. Extraordinary long microsporophyll (8 x 4.5 cm) with normal sized (3 x 2.5 cm) megasporophyll (PIZ 952); 5. Slab with long microsporangia (PIZ 825); All Piz da Peres, Wachtler gorge, Anisian, Coll. Wachtler

like lateral lamina. The megaspore is almost entirely enclosed in one or two sterile sporophytic coats or integuments except for a slit-like opening on the top functioning as a micropyle. Microsporophylls filled with microsporangia were shed in the same way after fertilisation, releasing their spores.

Diagnosis, remarks and ecology

Early–Middle Triassic *Sigillcampeia nana* will be found especially in one sediment on Piz da Peres Miara (Wachtler gorge). There it is abundant and covers extended areas in monocultures. It can be noted that on one side of this layer can be encountered juvenile plants, on the other adult plants and isolated mega- or microsporangia. The layers can be interpreted as a lacustrine deposit (also with some molluscs and bivalves), representing the flooding of an area of local vegetation. Apart from the fragile calcareous slabs many juvenile plants were deposited entirely with stumps and leaves, whereas isolated sporophyll carpets suggest that they were shed just before the inundation. It can therefore be interpreted as a restricted lycophyte swamp, partially covered by saline water. This suggests that *Sigillcampeia* was the plant best adapted to sea-water at this time, filling the niche of today's mangrove swamps.

Sigillcampeia blaui n. sp. WACHTLER 2016

Type horizon and age

Dolomites, Late Triassic, Carnian, (235- 228 Mya)

Holotype

SEE 14 (Coll. Wachtler, Dolomythos Museum, Innichen)

Paratype

SEE 02 (leaves) (Coll. Wachtler, Dolomythos Museum, Innichen)

Etymology

Honouring Joachim Blau, Institute for Geo-Sciences, Frankfurt am Main for his researches in the Lienz Dolomites.

Description

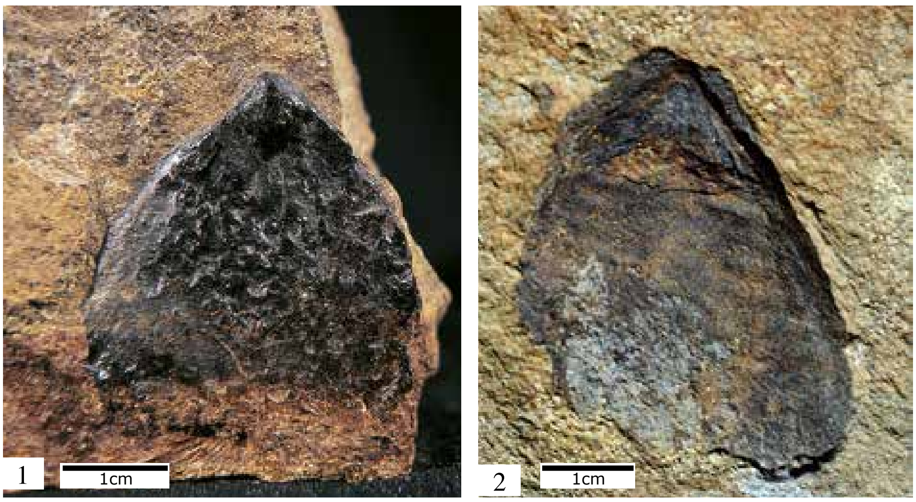
Stems: Bulbous, covered with leaf scars (SEE 05).
Leaves: From 10 to 20 cm long, 1 to 1.5 cm wide (SEE 05 = 15 cm x 1.5 cm), lanceolote, attached on the whole basal part on the stem. Base slightly concave, crossed vertically entirely from longitudinal veins (about 15 for each centimetre). Apex strongly tapered. Leaves released after maturity and therefore found in high numbers in the layers together with the sporophylls (SEE 11, 14).
Sporophylls: Megasporophylls rounded and smooth, holding only one megaspore. All coated by sterile integuments, only apically opened by a small slit. About 3 cm in size, length and width (SEE 14, 35, 17). Microsporophylls elongated, 5 cm in length, 3 cm wide (SEE 25), holding microspores.

Discussion

Lycophytes can be defined as vascular cryptogamic plants characterised by monopodial growth or dichotomical branching, densely covered by helically arranged microphylls which are vascularized by a vein without interruption from the caulinar stele (Gensel & Berry, 2001). It was thought that the giant clubmosses became extinct in the Late Carboniferous (*Lepidodendron*) or the Early Permian (*Sigillaria*) but surprisingly they lived on even in the Triassic, maybe the Jurassic. A first step was the discovery of L*ycopia dezanchei* (Wachtler, 2011), an arborescent lycophyta with affinities to the Lepidodendrales, and after that, mainly in the same layers, clubmosses with amazing resemblances to the Sigillarias appeared. Their obvious similarities, their dwarfish habit and their bonsai-like nature also allow us to understand the Carboniferous–Permian ancestors better. Due to their small size, all their structures, the stems, attachment of the leaves or their sporangiate cones could be studied more easily.
Therefore, it can now be stated that the Lepidodendrales as well as the Sigillarias 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. Connections with other extant

lycopsids such as *Selaginella, Lycopodium* or *Isoetes* are just as difficult to find.
The clubmoss *Lepidodendron* can be defined as an arborescent lycopsid evidencing an extensive apical crown formed by near-isotomous apical branching, with leaf cushions higher than broad, and fertile parts much more resembling gymnosperm cones. Carboniferous and also Early Permian *Sigillaria* were tree-like plants reaching in best cases a height up to 30 m, normally about 20 m, with a tall, single or only once-forked stem. The elongated leaves were attached directly to the stem, but shed easily so that characteristic leaf scars, often in vertical rows, covered the stems for almost the whole trunk. Early Permian *Sigillaria brardii*, known due to their longitudinal and spiral rows of leaf cushions from many fossil sites in the northern hemisphere, was till now regarded as a last representative. The leaves of *Sigillaria brardii* may bear one or two mid-veins. In comparison to coeval *Lycopia dezanchei* with its creeping roots *Sigillcampeia* reach deeper underground, being able to survive not only in drier environments but also to cling better against storms or inundations.
Apart from all these properties the most characteristic distinction features have to be searched for in their strobili. But here also arose the biggest problems. Usually Paleozoic Sigillarias (Schopf, 1941; Taylor et al., 2009) were described as having pedunculate strobili arising from the trunk in a circular ring pattern. Such a pattern of strobilus attachment was described as typically of *Sigillaria*, and unknown in other groups of lycopsids. The strobili of other groups of Late Paleozoic lycopsids may be borne among the crown of distal branches or on the deciduous lateral branches (DiMichele, 1980). Both formerly described cones as well as *Mazocarpon* or *Sigillariostrobus* cones were often characterised as pedunculate and hanging downwards from the stems and are not terminally attached to ordinary leafy twigs like *Lepidostrobus* belonging to *Lepidodendron* or also today's *Selaginella* and more advanced species of *Lycopodium*. In that sense Paleozoic *Sigillaria* cones were completely different from the strobili of *Sigillcampeia,* which were not pedunculate and not hanging. But another Paleozoic fertile organ resembles the Triassic *Sigillaria*-sporophylls: *Lepidocarpon*.
The presence of an integument and micropyle, the single functional megaspore,

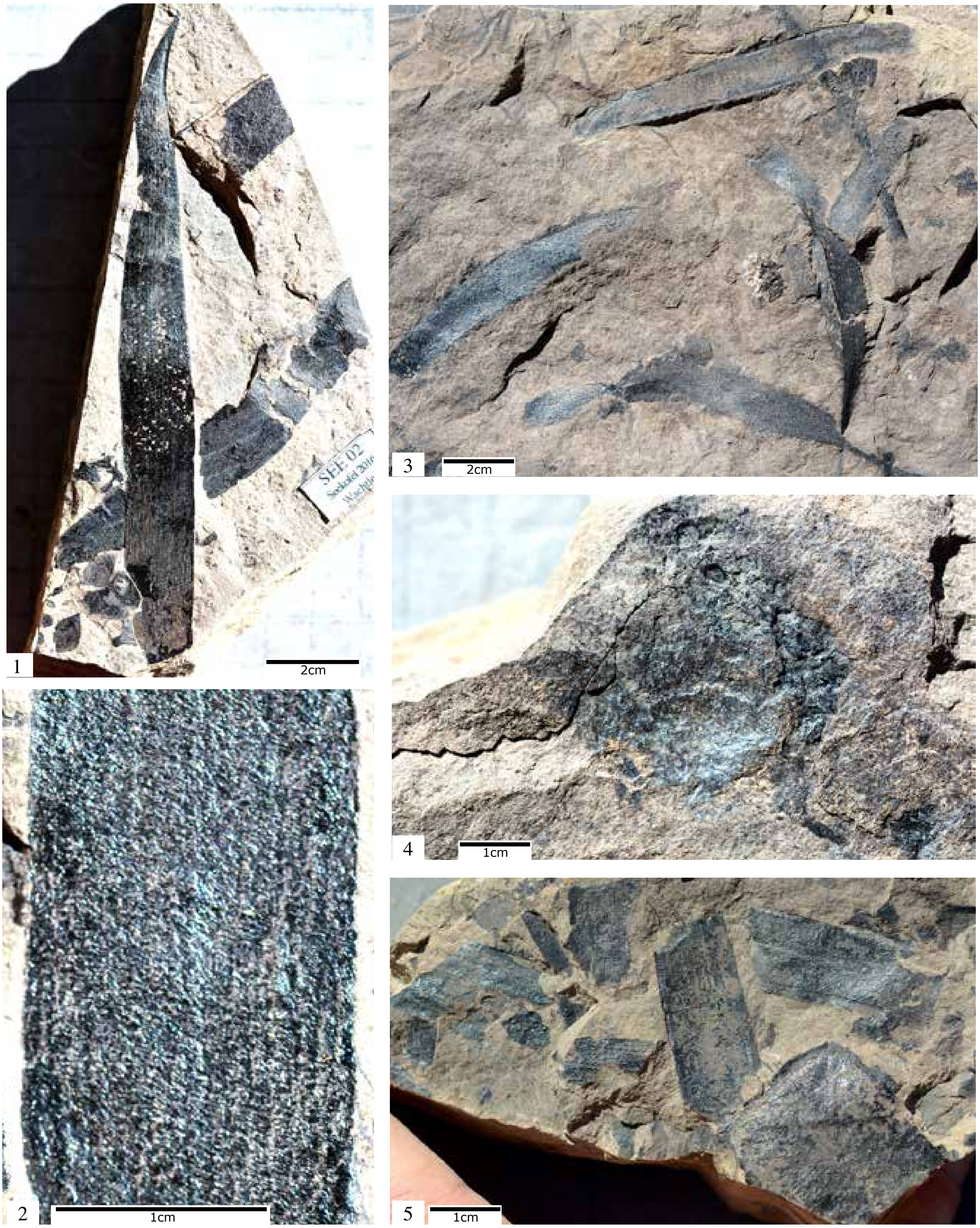
Extraordinary big-sized sporophyll (12 x 8 cm) of Sigillcampeia (Ladinian), Jadersdorf, Coll. Weiss



Sigillcampeia sp. Two samples of Ladinian sporophylls. Many isolated leaves classified as *Pelourdea vogesiaca* must be reviewed (1. Ritberg, Wengen, 2. Preseglie, Coll. Wachtler)

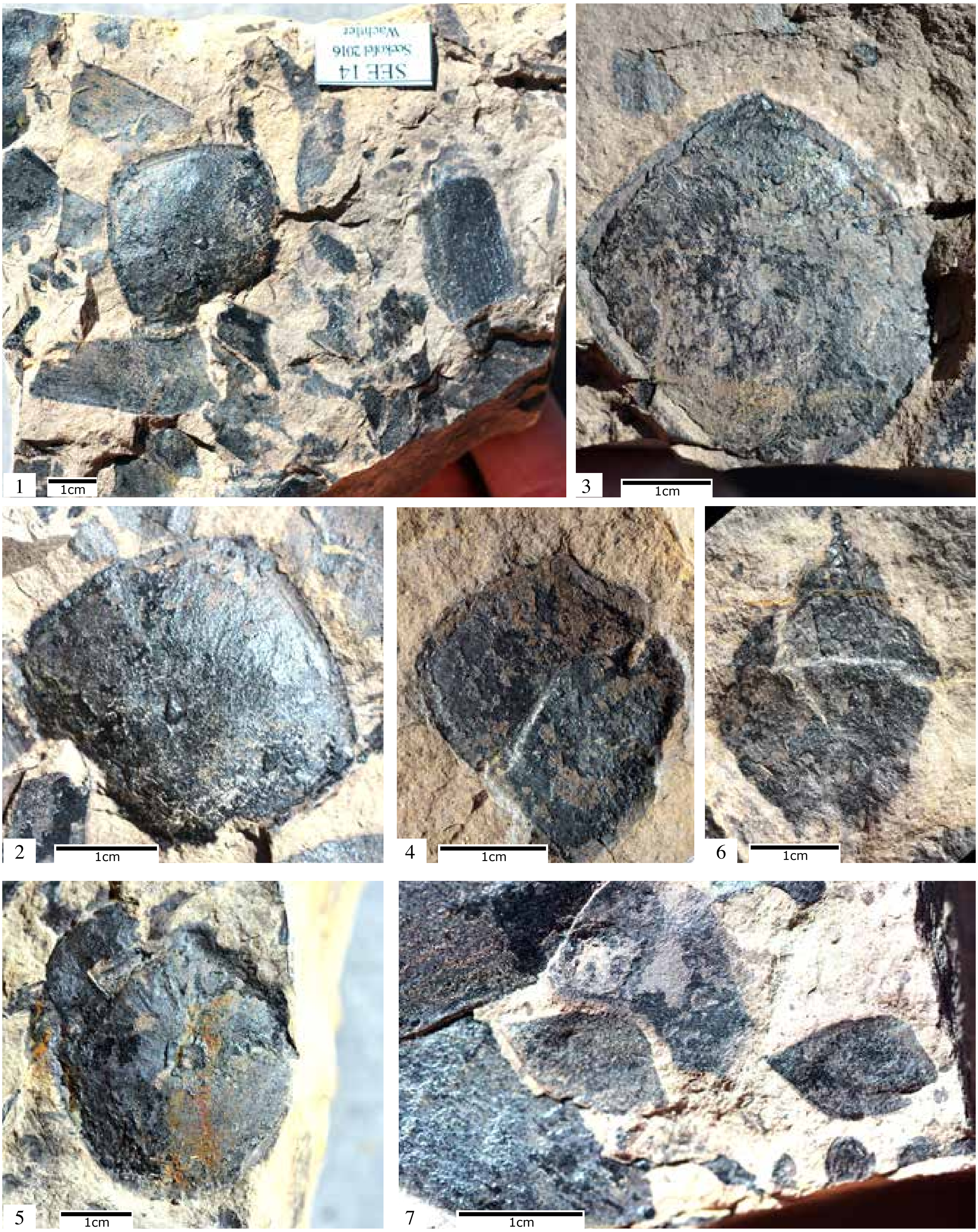
***Sigillcampeia blaui* n. sp. (Late Triassic) Reconstructions**

a. Inner structure of a plant; b. Single leaf (SEE 02); c. Detail of the veins (SEE 02); d. Megasporophyll with megasporangia (SEE 14, 35, 17); e. Microsporophyll with microsporangia (SEE 25), Seekofel-Lienz-Dolomites



Sigillcampeia blaui n. sp. (Late Triassic) Female and male cones

1. Leaves with tapered apex and basal sporophylls (SEE 02 paratype); 2. Detail of the venation (SEE 02); 3. Several leaves on a slab (SEE 05); 4. Part of a stem (SEE 05); 5. Leaves and sporophylls (SEE 11); All Coll. Wachtler, Seekofel, Lienz-Dolomites, Carinthian part, Carnian



Sigillcampeia blaui **n. sp. (Late Triassic) Female and male cones**

1. Megasporophylls and leaves on a slab (SEE 14, designated holotype); 2. Detail of the megasporophyll (SEE 14); 3. Other megasporophyll on the same slab (SEE 14); 4. Megasporophyll with typical tapered apex (SEE 35); 5. Megasporophyll (SEE 17); 6–7. Microsporophyll (SEE 25, 02); All Coll. Wachtler, Seekofel, Lienz-Dolomites, Carinthian part, Carnian

Piz da Peres, Wachtler gorge. The Anisian *Sigillcampeia nana h*orizon. Photo M. Dammann

Seekofel, Tuffbad. The Carnian *Sigillcampeia blaui* horizon is located on the upper part. Photo M. Wachtler

and the detachment of the indehiscent, seed-like organ as a whole correspond not only to *Sigillcampeia* but are also an important analogy with true seeds. Although differing in some detail from the seeds of gymnosperms it is worth taking this into account in further studies. It is difficult to establish if all prerequisites of seed evolution typical for gymnosperms and angiosperms were reached completely by *Lepidocarpon* or *Sigillcampeia.* These prerequisites concern the protection of the gametophytes and the young developing sporophytes from drying and injury, provision of nourishment for their proper development and freedom from external water required during fertilisation for transference of gametes (Gensel et al., 2001). *Lepidocarpon* as well as *Sigillcampeia* had megasporangia enclosed inside a megasporophyll that functioned like the integument and were equipped by one single functional megaspore indicating in that way one possibility in which the seed habit was attained.

The most complex question is the Gordian knot to bridge the *Lepidodendron* and *Sigillaria* border. And here only a pragmatic answer can be given: "Despite the advances in recent years there is still much to be learned about the biology of sigillarian plants" (Taylor et al., 2009). This can be confirmed totally. Probably not all *Sigillaria* bore pedunculate hanging cones but one family was equipped with clustered mega- and microsporangiate cones. Many of the so-called *Lepidodendron–Lepidocarpon i*solated megasporophylls belonged in reality to some *Sigillaria* tribe. Too many well-preserved pieces of the Triassic bonsai-like Sigillarias have been recovered for there to be doubts about their growth and habit. In particular the small-sized structures help more with understanding the whole *Sigillaria* story than all other huge but fragmented trees. And in this lies the importance of the *Sigillcampeia* discoveries all over the Triassic.

Whether they became extinct at the end of the Triassic or whether they survived also in the Jurassic is difficult to establish. The only sure observation is that today we do not have any living representative of the Sigillarias -that for so long ruled this planet-, whereas other lycopods, like *Selaginella* or *Isoetes*, can still be encountered.

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