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RESEARCH PAPER

Did the Czekanowskiales already exist in the late Permian?

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Abstract

Isolated capsule-like reproductive organs from the upper Permian of the Southern Alps, NE Italy, are described as *Brinkia* gen. nov. Two species have been distinguished, i.e. *Brinkia kerpiana* sp. nov. and *B. cortianensis* sp. nov. *Brinkia* capsules resemble in gross morphology single valves of the *Leptostrobus*-type, Mesozoic reproductive organs belonging to the Czekanowskiales. A czekanowskialean affinity is reinforced by the fact that the *Brinkia* remains are found associated with strap-like leaves resembling those of *Czekanowskia*. This would expand the record of the Czekanowskiales to the Wuchiapingian (early Lopingian) and suggests that, during the arid late Permian climate, representatives of the order could occupy the more humid habitats within the deltaic floodplain formed during a sea-level rise.

Keywords Lopingian · Southern Alps · Gymnosperms · Reproductive organs

Introduction

The Permian is a period of important innovations and radiations among the gymnosperms including the peltaspermalean and glossopteridalean seed ferns, cycadophytes, ginkgophytes, Vojnovskiales and conifers. The modern aspect of the flora has been increased lately due to the appearance of 'typical late Permian' taxa such as voltzian conifers in early Permian successions (e.g. DiMichele et al. 2001; Forte et al. 2017, 2018) and of 'typical Mesozoic' plant taxa such as *Dioonitocarpidium* Rühle von Lilienstern 1928, *Swedenborgia* Nathorst 1876 and *Dicroidium* Gothan 1912 in Permian sediments (e.g. DiMichele et al. 2001; Abu Hamad et al. 2008). On the other hand, the botanical affinity of several Permian taxa and even plant groups is under debate. These include, among others, the Vojnovskiales, some putative ginkgophytes or conifers such as *Dicranophyllum* Grand'Eury 1877 and *Trichopitys* de Saporta 1875, Rufloriaceae and a considerable part of the Angaran and Gondwanan putative conifers.

The possibility of discovering such 'abnormal' taxa in the flora is increased by exceptional preservation (e.g. Abu Hamad et al. 2008), high abundance in collected material (e.g. DiMichele et al. 2001; Forte et al. 2017, 2018) and exceptional preservation potential of the sedimentary succession (e.g. Kustatscher et al. 2017a, b). The Bletterbach Gorge (NE Italy) is one of those areas worldwide that has yielded exceptional late Permian floras, including the well-preserved cuticles of the 'cuticle horizon' (Clement-Westerhof 1984, 1986, 1987) and a diverse and articulated flora with plant–animal interactions in the megafossil horizon (Kustatscher et al. 2012, 2014, 2017a, b; Bauer et al. 2014; Labandeira et al. 2016). Thus, it is not surprising that the Bletterbach plant assemblage includes also some scales and

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strap-like leaves that on first view resemble representatives of the order Czekanowskiales.

The Czekanowskiales include plants with persistent leaves borne on deciduous short shoots, subtended by scale-like leaves (Pant 1957; Krassilov 1968, 1972a, b; Taylor et al. 2009). Representatives of this group range from the Late Triassic to the Cretaceous (Ash 1994). The order includes several fossil genera with highly dissected leaves, such as *Czekanowskia* Heer 1876, *Solenites* Lindley and Hutton 1834, *Sphenarion* Harris et Miller in Harris et al. 1974, *Phoenicopsis* Heer 1876 and *Arctobaiera* Florin 1936, distinguished mainly on leaf morphology, arrangement of the leaves on short and/or long shoots and epidermal features. The leaves are hypostomatic or amphistomatic with stomata arranged in short longitudinal lines or bands (e.g. Samylina and Kiritchkova 1993; Kostina 1999). Stomatal distribution and arrangement are used to distinguish three subgenera (Samylina and Kiritchkova 1993), viz. *Czekanowskia* (amphistomatic leaves with stomata arranged in files), *Harrisiella* (amphistomatic leaves with stomata arranged in bands) and *Vachrameevia* (hypostomatic leaves with stomata arranged in files or band).

The reproductive genus *Leptostrobus* Heer 1876 is also assigned to this order. These ovulate cones were found associated, but never in organic connection, with *Czekanowskia*, *Sphenarion*, *Phoenicopsis,* and *Solenites* (Clifford and Camilleri 1998; Liu et al. 2006). The ovuliferous organs are flattened, globose and consist of two valves (together called capsules) with often a crenulate outer margin (Harris 1951; Krassilov 1968). The botanical affinity of the Czekanowskiales is still an open question. The various taxa were assigned to the ginkgophytes based on their highly dissected foliage (Harris 1935, 1951; Schweitzer and Kirchner 1995), distantly related to the seed ferns and conifers, or considered to represent a separate group of poorly defined gymnosperms (Meyen 1987; Taylor et al. 2009).

The aim of this paper is to describe these enigmatic plant remains from the Bletterbach and Cortiana (localities in the Southern Alps, NE Italy), including the capsule-like reproductive organs and the strap-like leaves, both macromorphologically and based on their cuticle. We compare them with possible producing plants in order to understand whether these remains could be the oldest representatives of the order Czekanowskiales, or if these organs belong to another group of gymnosperms. Finally, we discuss the putative ecology of these plants.

Materials and methods

Bletterbach Gorge is located at the western edge of the Dolomites, between the villages of Aldein/Aldino and Radein/Redagno (Fig. 1). The succession starts with the Auer/Ora Formation, the uppermost formation of the Athesian Volcanic Group (Morelli et al. 2007), whose activity is dated from 284.9 ± 1.6 to 274.1 ± 1.4 million years ago (Bargossi et al. 2007; Avanzini et al. 2007; Marocchi et al. 2008). The Permian volcanites are overlain unconformably by ~ 210 m of the late Permian (Wuchiapingian) Gröden/Val Gardena Sandstone (Cassinis et al. 1999; Morelli et al. 2007). This formation is characterised by red to greyish fluvial siliciclastics, evaporites and mixed carbonate–siliciclastic deposits, deposited in alluvial fans, braided rivers, shallow channels, coastal sabkhas, evaporitic lagoons and shallow marine shelf environments (Italian IGCP 203 1986; Ori 1988; Massari et al. 1988; Kustatscher et al. 2012, 2017a). A warm to hot, semi-arid to dry–subhumid climate with pronounced seasonality has been interpreted for this sedimentary succession (Cassinis et al. 1999). The Gröden/Val Gardena Sandstone is overlain by the Changhsingian Bellerophon Formation, the Early Triassic Werfen Formation, the late Anisian Richthofen Conglomerate and the Contrin Formation (for more details see Kustatscher et al. 2017a).

The Gröden/Val Gardena Sandstone of the Bletterbach is famous for its abundance and high diversity of tetrapod footprints (e.g. Conti et al. 1975, 1977, 1979; Ceoloni et al. 1988; Wopfner 1999; Bernardi et al. 2017), plant megafossils and mudstones rich in dispersed cuticles (e.g. Clement-Westerhof 1984, 1986, 1987; Poort and Kerp 1990; Visscher et al. 2001; Kustatscher et al. 2012, 2017a, b). The fossils discussed here were collected from a thin (~ 1 m thick) horizon at about 70 m from the base of the succession consisting of medium- to coarse-grained greyish sandstones, sometimes with small, intercalated gypsum nodules, termed the 'megafossil horizon' (Kustatscher et al. 2012, 2014, 2017a, b). The age of this plant assemblage is (possibly middle) Wuchiapingian (for more details see Kustatscher et al. 2017a, b).

Additional specimens originate from the transition interval between the Val Gardena Sandstone and the Bellerophon Formation of the Venetian Alps, exposed in a section east of the Village of Cortiana (Municipality of Valli del Pasubio, about 50 km NW of Vicenza; Fig. 1). The interval is characterised by alternating siliciclastic and dolomitic beds. The material did not yield any cuticles, but the carbonaceous impressions in the fine sandstone to siltstone are very well preserved. Other plant fossils from Cortiana mainly include conifer remains (Clement-Westerhof 1984). Comparable to the situation in the Butterloch, the facies transition is usually included in the Bellerophon Formation (Barbieri et al. 1980), and it seems justified to assign a Changhsingian age to these plant fossils.

Cuticles were obtained from most specimens through maceration of small fragments in Schulze's reagent ($KClO_3$ and 30% HNO_3) and neutralised in ammonium hydroxide (NH_4OH, 5%). Cuticles were mounted in glycerin jelly on microscope slides for light microscopic analysis and sealed

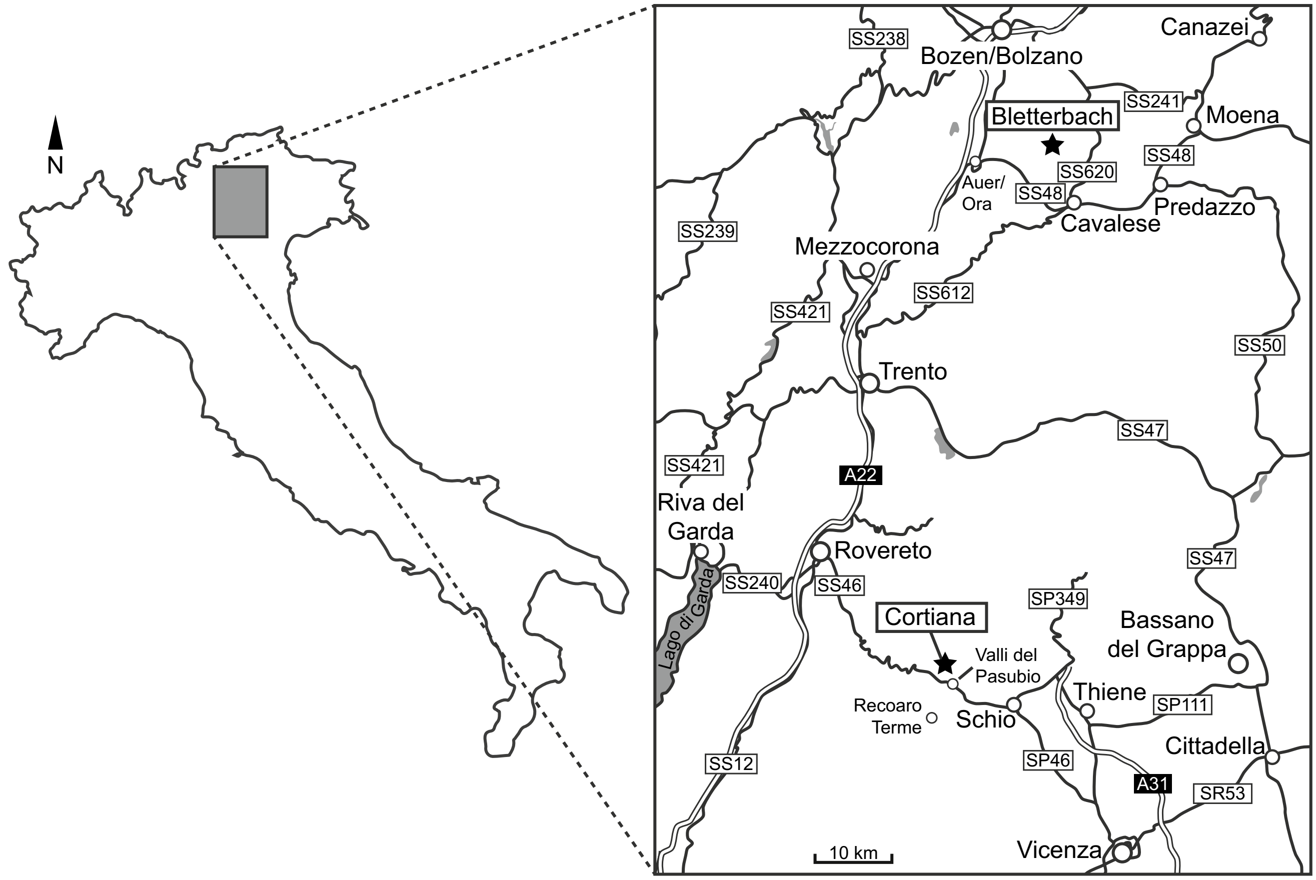


Fig. 1 Map of north-eastern Italy showing the localities of Bletterbach and Cortiana in the Southern Alps

with Paraplast (see Kerp 1990; Kerp and Krings 1999). Hand specimens were photographed with a Canon Eos D550 digital camera according to procedures outlined by Kerp and Bomfleur (2011). Cuticle images were captured with a Leica DMC4500 camera mounted on a Leica DM 2500 LED microscope in transmitted light. Cuticle slides and megafossils from the megafossil horizon at Bletterbach are stored at the Museum of Nature South Tyrol in Bozen/Bolzano (Italy) (specimen numbers preceded by 'PAL'). Specimens from the Bletterbach cuticle horizons and from Cortiana with the prefix 'UU' are from the collections of the Laboratory of Palaeobotany and Palynology, Utrecht University, The Netherlands. One specimen comes from the historical collection of the Museo di Geologia e Palentologia, Dipartimento di Geoscienze—Università di Padova.

Systematic description

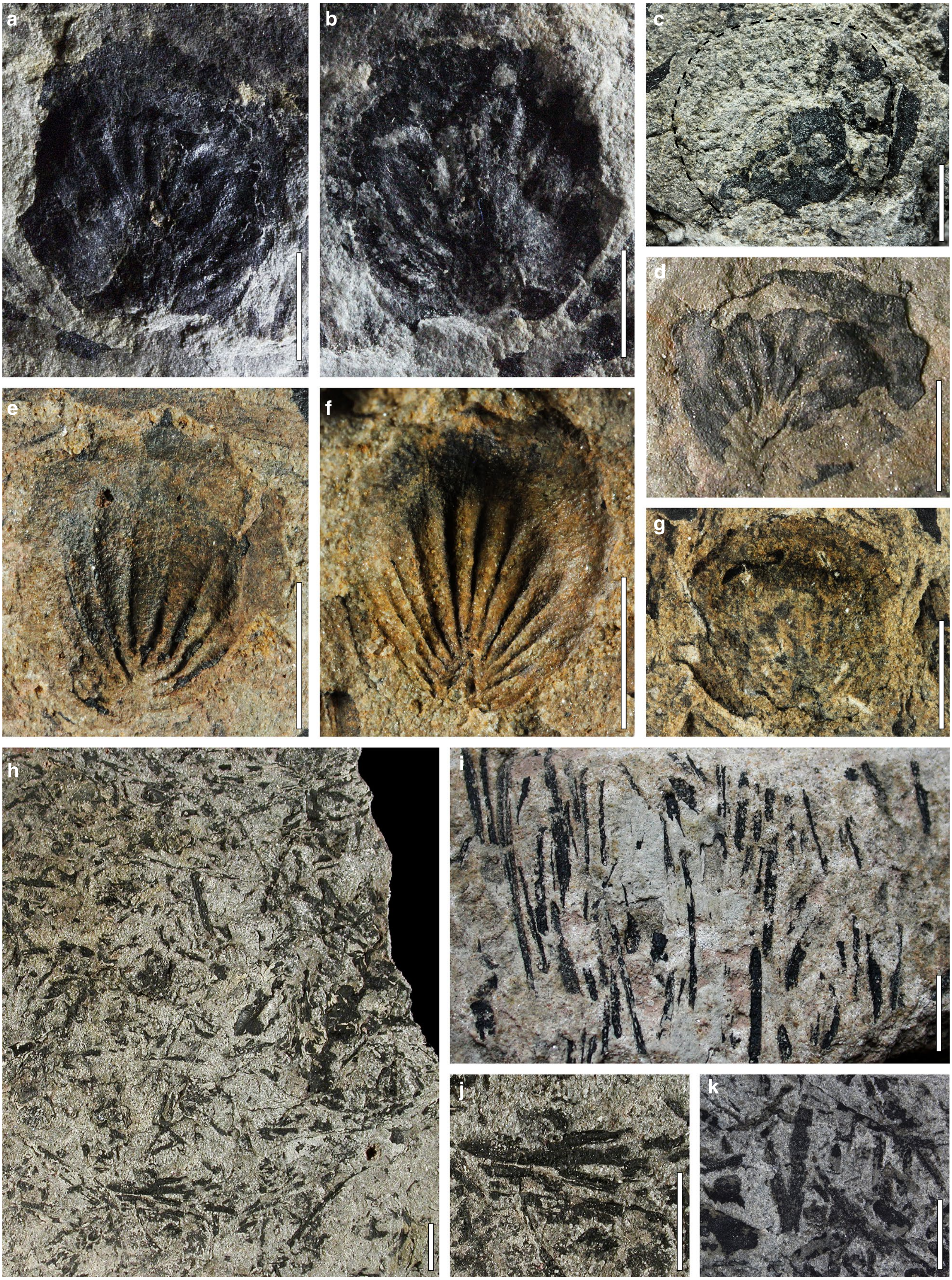
Genus ***Brinkia*** nov.

Type species. *Brinkia kerpiana* sp. nov., from the Wuchiapingian of Bletterbach, Dolomites, Northern Italy.

Diagnosis. Isolated, rounded valves with a lobed rim, and a number of radial ridges and furrows originating from a short basal column.

Etymology. In honour of Wies van den Brink, former palynologist and wife of Hans Kerp, who stimulated and supported him during his career.

Comparisons. So far, all female reproductive organs found in association with *Czekanowskia*, *Sphenarion*, *Phoenicopsis* and *Solenites*, and considered to be czekanowskialean in affinity were assigned to the genus *Leptostrobus*. These ovuliferous organs are flattened, globose and consist of two valves (called together capsules) arranged along a stout axis as slender cones. Although the specimens of *Brinkia* from Bletterbach are never found articulated and/or attached to the axis, the single valves resemble those of *Leptostrobus* in general shape. Both are characterised by globose valves with a distinct margin, a central part divided in ridges and marginal lobes. However, in *Leptostrobus*, each ridge finds its extension in a lobe on the margin and each capsule is much smaller and has much fewer ridges than in *Brinkia*.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◂**Fig. 2** Czekanowskiales megafossil remains from the Lopingian of the Southern Alps. **a** *Brinkia kerpiana* sp. nov., isolated dispersed valve, holotype (PAL 1465, Museum of Nature South Tyrol); **b** *Brinkia kerpiana* sp. nov., isolated dispersed valve, counterpart of the holotype (PAL 1464, Museum of Nature South Tyrol); **c** *Brinkia kerpiana* sp. nov., isolated dispersed valve yielding the cuticle; dotted line indicates the outline of the valve (PAL 865, Museum of Nature South Tyrol); **d** *Brinkia kerpiana* sp. nov., isolated dispersed valve, showing the rim (PAL 1448, Museum of Nature South Tyrol); **e** *Brinkia cortianensis* sp. nov., isolated dispersed valve, holotype (UU 16882A, University of Utrecht); **f** *Brinkia cortianensis* sp. nov., isolated dispersed valve (UU 16881A, University of Utrecht); **g** *Brinkia cortianensis* sp. nov., isolated dispersed valve, holotype (UU 16882C, University of Utrecht); **h** Associated leaves from the Bletterbach (PAL 858, Museum of Nature South Tyrol); **i** Historical sample covered with leaves from the Bletterbach (Museo di Geologia e Palentologia, Dipartimento di Geoscienze—Università di Padova); **j** Forked leaf, detail of **h** (PAL 858, Museum of Nature South Tyrol); **k** Forked leaf (PAL 1394, Museum of Nature South Tyrol). Scale bars 5 mm in the pictures of *Brinkia*, 10 mm in the pictures of the associated leaves

There are a few female conifer remains that superficially look like czekanowskialean fructifications. *Cardiolepis* Neuburg 1965 emend. Meyen 1976 (now called *Angaropeltis* Doweld 2001) from the Permian of western Angara is characterised by large (diameter c. 4 cm) multi-seeded peltate capsules, smooth on the outside, with the ridges and furrows on the inside corresponding to impressions of the seeds (Meyen 1976). In *Brinkia*, on the other hand, the ridges are visible both on the outside and on the inside. Moreover, the capsule of *Cardiolepis* is not composed of two valves like in *Leptostrobus* (and we postulate also for *Brinkia*) but has a distinct stalk, not visible in our specimens.

The conifer *Ullmannia bronnii* Göppert 1850 from the upper Permian of Germany has globose scales differing because of the presence of a distinct stalk, and the completely fused single elements, giving origin to a globose scale without ridges (Florin 1944). *Glyptolepis* Schimper 1872 from the lower–middle Keuper (Ladinian–Carnian) of Germany shows ovuliferous cones with partially fused, stalked scales. The upper part of the scale is expanded and consists of a number of equal-sized lobes with an obtuse apex. *Pachylepis* Kräusel 1952 from the Schilfsandstein (Carnian) of Germany is a conifer cone with scales divided into five lobes, each bearing a single seed. The missing rim and the composite structure with only partially fused elements distinguish *Glyptolepis* and *Pachylepis* from *Brinkia*. The number of seeds and the three-dimensional organisation of these taxa cannot be compared since these are as yet unknown in *Brinkia*.

Remarks. The valves were always found isolated in the sediment. This makes it impossible to interpret whether the valves were organised in capsules like in *Leptostrobus* and how they would be attached and arranged on the axis. This, as well as the differences in dimensions and the presence of the basal column, supports an assignment to a different, new genus.

Brinkia kerpiana sp. nov.
Figures 2a–d, 3a–b

2012 Incertae sedis, valve-like structure—Kustatscher et al.: p. 1, 6, pl. 3, figs. 5, 7.
2017b *Leptostrobus*-like valves—Kustatscher et al.: p. 50, pl. 3, fig. i.

Etymology. In honour of Hans Kerp, who studied the Bletterbach over several decades.

Type material. Holotype PAL 1465 with its counterpart PAL 1464, Fig. 2a–b, here designated.

Additional material. PAL 832, 865, 922 (several isolated specimens), 1149, 1381, 1383, 1448, 2052.

Repository. Palaeobotanical collection, Museum of Nature South Tyrol, Bozen/Bolzano, Italy.

Type locality. Bletterbach, Dolomites, Bozen/Bolzano Province, Northern Italy.

Type horizon. Megafossil horizon, Gröden/Val Gardena Sandstone, Wuchiapingian, Lopingian, upper Permian.

Diagnosis. Isolated, rounded, globose valves of approximately 11–16 mm, with an up to 2 mm wide marginal lobed rim; central part divided into over 10 radial ridges and furrows originating from a basal short column. Cuticle moderately thick, epidermal cells isodiametric to slightly elongated. Stomata arranged in single, slightly radiating files, often bordering within a file. Stomatal pit surrounded by 6–8 distinctly thickened subsidiary cells bearing a papilla.

Description. The isolated valves are more or less globose, in general a little wider than high. The basal margin is never completely preserved but appears to be straight (PAL 1464; Fig. 2b). The valves are 11 to 16 mm wide and high. They are characterised by an external rim of up to 2 mm width that completely surrounds the central part. The rim shows distinct outer lobes (0.5–1 mm high and 1–2 mm wide) with a rounded apex, both laterally and apically. The central part is well distinguished from the rim, and appears to be raised (or sunken in some specimens) in comparison with the rim (PAL 1448; Fig. 2d). It is divided radially by more than 10 radially arranged ridges and deep furrows that spread from the basal column to the inner margin of the rim. The ridges

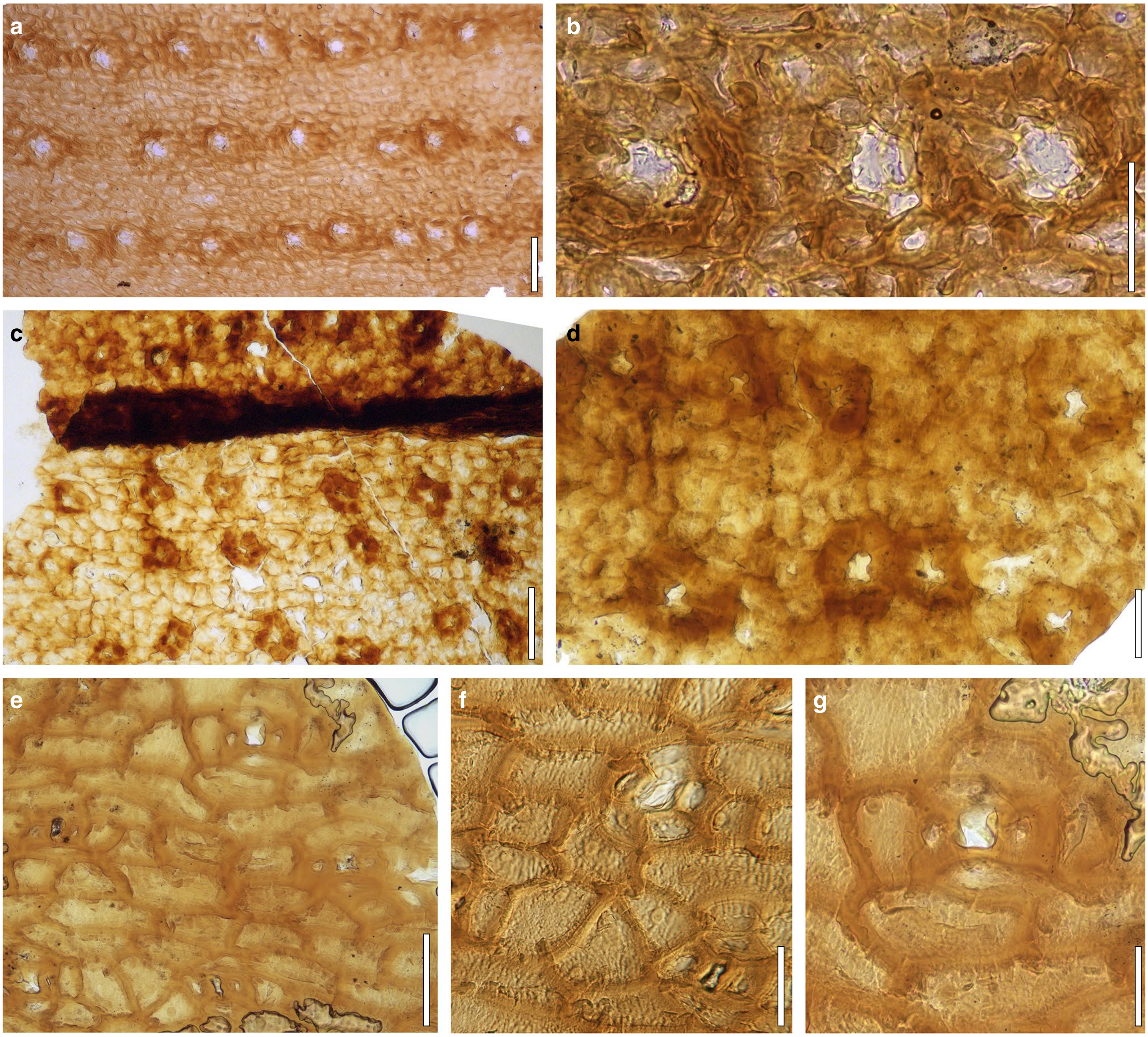

Fig. 3 Czekanowskiales cuticle remains from the Wuchiapingian of the Southern Alps. **a** *Brinkia kerpiana* sp. nov., cuticle of a valve with stomata arranged in rows (PAL 865, Museum of Nature South Tyrol); **b** *Brinkia kerpiana* sp. nov., detail of the cuticle with stomata (PAL 865, Museum of Nature South Tyrol); **c** Attached abaxial and adaxial cuticle of associated leaves (PAL 842, Museum of Nature South Tyrol); **d** Associated leaves, detail of cuticle pattern (PAL 842, Museum of Nature South Tyrol); **e** Associated leaves, detail of the cuticle with more scattered stomata (PAL 858, Museum of Nature South Tyrol); **f** Associated leaves, detail of the cuticle with different stomata (PAL 858, Museum of Nature South Tyrol); **g** Associated leaves, detail of the stomata (PAL 858, Museum of Nature South Tyrol). Scale bars = 100 µm (**a**, **c**, **d**, **e**, **f**) or 50 µm (**b**, **g**)

arise along the outer margin of the oval to almost circular basal column that is 2–3 mm long and 1.0–2.5 mm wide (Fig. 2d). The holotype (PAL 1465; Fig. 2a) is 16 mm wide and 15.5 mm high, with a 2 mm wide lobed rim, a central part that is divided into 11 radial ridges and furrows and an up to 3 mm long and 2.5 mm wide column.

Only one specimen (PAL 865; Figs. 2c, 3a, b) yielded a good cuticle of a valve. It is fairly thick, and the stomata are arranged in single files. Near the base of the valve there are only 3 stomatal files, but new files begin more distally either near the margin or in between other files. In the largest, but still incomplete fragment there are 10 files distally. In the basal part of the fragment there is a thicker margin with protrusions. The ordinary epidermal cells are isodiametric to slightly elongate, strongly papillate in the basal part, less heavily papillate distally. Stomata crowded within the files often bordering but never sharing subsidiary cells. The number of the distinctly thickened subsidiary cells is between 4 and 8 (mean 6), each bearing a papilla. In one cuticle fragment, a possible part of the rim was preserved. This small part was less thick than the valve cuticle, showed more elongated, non-papillate epidermal cells and only a few scattered stomata. The subsidiary cells were bearing small papillae.

Comparisons. This is discussed in a special section after the description of both species.

Remarks. The specimens were already mentioned previously as 'valve-like structures' or '*Leptostrobus*-like valves' from the Gröden/Val Gardena Sandstone of the Bletterbach (Kustatscher et al. 2012, 2017b).

Brinkia cortianensis sp. nov.
Figure 2e–g

Etymology. Based on the locality, Cortiana, where the specimens were collected.

Type material. Holotype UU16882A with its counterpart UU16882C, Fig. 2e, g, here designated (Palaeobotanical collection, Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands).

Additional material. UU16881A–D, UU16882B.

Repository. Palaeobotanical collection, Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands.

Type locality. Cortiana, Venetian Alps, Vicenza Province, Northern Italy.

Type horizon. Bellerophon Formation, Changhsingian, Lopingian, upper Permian.

Diagnosis. Isolated, rounded valves, up to 8 mm wide and 10 mm high with an up to 1 mm wide lobed rim with large apical lobes; central part divided into up to 7 radial ridges and furrows originating from a basal short column.

Description. The isolated valves are more or less globose, in general higher than wide. The basal margin is straight and restricted in comparison with the general shape of the valves, being only 4–5 mm wide (UU 16881A; Fig. 2f). The valves are from 7 to 8 mm wide and 7.5–10.0 mm high. They show an external rim of up to almost 2 mm width at the most apical part. The rim decreases in width laterally and disappears for the basal 2 mm of the margin (UU 16881A; Fig. 2f). It is characterised by distinct delicate outer lobes (0.2–0.6 mm high and 1.0–1.5 mm wide) with a slightly smoothed apex, both laterally and apically. At the most apical part there can be a pointed apex (UU 16882A; Fig. 2e). The central part of the valve is well distinguished, and appears to be raised (or sunken in some specimens) in comparison with the rim (UU 16881A; Fig. 2f). It is divided by up to 7 radially arranged ridges and deep furrows that spread from the basal column to the inner margin of the rim. The ridges arise along the outer margin of the subtriangular basal column that is 1–2 mm long and 1.0–1.5 mm wide (UU 16881A; Fig. 2f).

The holotype (UU 16882A; Fig. 2e) is 8 mm wide and 10 mm high, with an up to 2 mm wide rim that extends at the most apical point to 2.5 mm. Basally the scale reduces to 4 mm in width. The central part is divided into 7 radial ridges and furrows and an up to 2 mm long and 1 mm wide triangular column. The base of the triangle corresponds to a roundish area of about 1 mm in diameter.

Comparisons. *Brinkia cortianensis* sp. nov. differs from *Brinkia kerpiana* sp. nov. because of the smaller dimensions, the lower number of ridges and furrows, the non-continuous rim, the triangular shape of the column (against roundish) and the restricted base. As no cuticle has been found to date, we cannot compare the two species for this aspect.

Comparison between *Brinkia* and *Leptostrobus* species

Liu et al. (2006) gave a clear overview of all *Leptostrobus* species known so far (Triassic to Cretaceous in age), and we mainly refer to their work. Here we compare only with the type species *L. laxiflorus* Heer 1876, the best-known species *L. cancer* (both Jurassic in age), and three *Leptostrobus* species known from the Triassic, *L. longus* Harris 1935 from the Rhaetian–Liassic of Jameson Land (Greenland): *L. myeongamensis* Kim et al. 2002 from the Late Triassic of Korea and *L. sphaericus* Wang 1984 from Late Triassic of China (see also Table 1). All of these have axes to which the capsules are attached in a more or less loose spiral, although capsules and/or valves can often be found dispersed. *Leptostrobus laxiflorus* is distinguished from both *Brinkia* species in having oval capsules (versus almost globose ones), and the generally lower number of ribs (3–7). Moreover, the rim is more strongly lobed than in the *Brinkia* species (Heer 1876; Harris et al. 1974; Liu et al. 2006). Its cuticle is unknown, as in most *Leptostrobus* species.

Brinkia kerpiana sp. nov. and *B. cortianensis* sp. nov. differ from *Leptostrobus cancer* Harris 1951 because, in the latter, each ridge corresponds to a lobe on the margin and the ridges are slightly increasing in width towards the margin. Moreover, in *L. cancer*, the ridges run only slightly radially but mostly parallel to each other from the base towards the margin. Each capsule of *L. cancer* is much smaller (3–5 mm

Table 1 Comparison between the two *Brinkia* species and five selected *Leptostrobus* spp.

	Brinkia kerpiana	*Brinkia cortianensis*	*Leptostrobus laxiflora*	*Leptostrobus cancer*	*Leptostrobus longus*	*Leptostrobus sphaericus*	*Leptostrobus myeongamensis*
Capsules arranged on axis	Unknown	Unknown	Helically	Helically	Helically	Helically	Helically with subtending bract
Capsule shape	Globose	Rounded, slightly oval	Oval	Obovate	Cup-shaped	Globose	Globose
Capsule size	11–16 mm	7–10 mm	6–9 mm	3–7 mm	2–3 mm	ca. 5 mm	Unknown
Number of ribs (ridges/furrows)	Over 10	Up to 7	3–7 (commonly 5)	5	5–6	5	Unknown
Rim	Almost continuous to base, crenulate	Lower 1/3 of capsules without rim; rim crenulate with a pointed apical lobe	Continuous, crenulate	Continuous, slightly crenulate	Continuous, strongly crenulate	Almost continuous, slightly crenulate	Crenulate
Cuticle thickness	Moderately thick	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Epidermal cells	Papillate	Unknown	Papillate	Non-papillate	Non-papillate	Unknown	Unknown
Stomatal arrangement	In a large number of single, crowded files	Unknown	Unknown	Scattered	Scattered	Unknown	Unknown
Number and shape of subsidiary cells	6–8, distinctly thickened cell walls, papillate	Unknown	Unknown	4–7, non-thickened, non-papillate	4–7, slightly thickened, non-papillate	Unknown	Unknown

versus 11–16 or 7–10 mm) and has many fewer ridges (3–5) than *B. kerpiana* (at least 10) or *B. cortianensis* (up to 7). In *L. cancer*, each lobe corresponds to a 2 mm long and up to 1 mm wide seed. If the depressions close to the margin of the central part of the valves of *B. kerpiana* were indeed attachment areas of seeds or depressions of seeds (PAL 1465; Fig. 2a), these would be up to 2.5 mm long and 1.5 mm wide. However, there would not be enough space for each of the ridges to contain a single seed as described in *L. cancer*.

There are also a few cuticular differences between *Leptostrobus cancer* and *Brinkia kerpiana*; the most obvious one is that the stomata in *L. cancer* are scattered while they are arranged in a number of single, crowded files in *B. kerpiana*. Moreover, the epidermal cells in *B. kerpiana* are papillate, versus non-papillate in *L. cancer*. The number of subsidiary cells is slightly larger in *B. kerpiana* (6–8), versus 4–7 in *L. cancer*. And finally, the subsidiary cells in *B. kerpiana* are thickened and papillate, versus non-thickened and non-papillate in *L. cancer*. *Brinkia cortianensis* did not yield a cuticle, just as most *Leptostrobus* species (see Liu et al. 2006).

Leptostrobus longus from Greenland is the only other *Leptostrobus* species for which cuticular details are known (Harris 1935, 1951). It is quite close to *L. laxiflorus* in gross morphology but smaller in capsule size. Its cuticle is similar to that of *L. cancer* in having polygonal epidermal cells and scattered stomata. It is different in being thinner and having more thickly cutinised subsidiary cells in an irregular ring. Oishi and Takahashi (1996) described one *Leptostrobus* cone fragment from the Rhaetian of Japan as cfr. *Leptostrobus laxiflorus*, but noted in the paper that, after seeing Harris's *L. longus* from Greenland, they thought their material more closely related to the latter. Too few details of the specimen are known to include in Table 1.

Leptostrobus myeongamensis from the Late Triassic of Korea (Kim et al. 2002; Kim 2010) differs considerably from all other species in showing a scale leaf below each capsule along the axis. Other species often show a few scale leaves below the whole fructification but never below a capsule (Kim 2010). For a close comparison between these species, see Table 1.

Associated leaves

Both in the Bletterbach and at Cortiana, strap-like, elongated leaf fragments (up to 30 mm long and 2 mm wide) were found (Fig. 2h–k). Sometimes they show a bifurcation (e.g. PAL 858, 1394; Fig. 2h, j, k). In some cases, they may even cover entire bedding planes (e.g. Leonardi specimen, PAL 1394, 2014, Fig. 2h, i, k).

The cuticle is fairly thick and amphistomatic with stomata arranged in short, irregular files (Fig. 3e–g). The epidermal cells are isodiametric to elongate (Fig. 3c, d), sometimes papillate (Fig. 3d). Stomata within the files never share subsidiary cells, and the distance between 2 stomata is generally at least 2–3 epidermal cells. The distal and anticlinal walls of the subsidiary cells are thickened; the ends of the anticlinal walls may be interrupted by small pits or extensions into the lumina of the cells. The stomatal pit is roundish to square, sometimes covered by overarching papillae of the subsidiary cells. The stomata are typically haplocheilic with (4) 5 to 6 (8) monocyclic subsidiary cells with the anticlinal and distal walls thickened (Fig. 3e–g). In some stomata with only 4 subsidiary cells, these are arranged in 2 polar and 2 lateral cells; the two polar cells small and square to rectangular, the two lateral subsidiary cells half-moon shaped (Fig. 3e, g).

These strap-like, elongated leaves of *incertae sedis* (Kustatscher et al. 2012: p. 1, 5, pl. 2, figs. 4, 6) were considered to resemble leaf fragments of *Dicranophyllum* Grand'Eury 1877 (Bauer et al. 2014: p. 276, fig. 3G; Bernardi et al. 2017: p. 23, fig. 4K; Kustatscher et al. 2017b: p. 45, pl. 2, fig. f), or even leaves of the Czekanowskiales group, although some fragments were in the past interpreted as leaves of '*Lepidodendron* cfr. *sternbergi* Lind. et Hutt. vel *Schizolepis permensis* Heer' (Leonardi 1948: p. 6–7, pl. 1, fig. 6).

Discussion on leaves

Strap-like leaves were produced by several Permian and Mesozoic plant genera. These include *Dicranophyllum*, *Trichopitys* de Saporta 1875, *Polyspermophyllum* Archangelsky and Cúneo 1990 and all the leaf genera of the order Czekanowskiales. They are mostly distinguished by their width, the presence or absence of bifurcations of the leaves and their organisation in fascicles and/or attachment to short or long shoots. The fragmentary preservation of our leaves impedes any information regarding the way of attachment or three-dimensional organisation on short or long shoots. Thus, a good comparison can only be made with taxa that both bifurcate and for which the cuticle is known.

Bifurcated strap-like leaves of late and middle Permian age are relatively rare. One specimen from the Estérel, SE France, called 'late Permian plant species A' has been figured by Boersma and Visscher (1969: p. 58, pl. 2, fig. 3). The age of the fragment should now be regarded as middle Permian (probably Wordian; Durand 2006). It shows a stem with perpendicularly arising fascicles of elongated leaves that might be characterised by bifurcations. Unfortunately, no cuticles are preserved from this specimen, but our dispersed leaves could well represent parts of this plant. More strap-like, bifurcated leaves are known from the early Permian. The leaves of *Trichopitys*, *Polyspermophyllum* and

Dicranophyllum are also dissected several times (Zalessky 1932; Florin 1949, 1951; Barthel 1977; Archangelsky and Cúneo 1990; Barthel et al. 1998). However, the fact that these forms have not yet yielded any cuticles makes a comparison with these genera impossible.

Krassilov and Karasev (2009) mentioned and figured a fragment of a bifurcated leaf fragment from the upper Permian of Russia as 'comparable with the Mesozoic Czekanowskiales, also on account of their stomatal structures'. Although not identical (epidermal and subsidiary cells less papillate), this fossil and its cuticle resemble the leaves associated in the Bletterbach with *Brinkia kerpiana* and may indeed have belonged to the Czekanowskiales.

The genera among the Czekanowskiales that include bifurcated or dissected leaves are *Czekanowskia* and *Sphenarion*, although occasionally leaves of *Arctobaiera* bifurcate near their apex. *Czekanowskia* includes elongated, highly dissected leaves with a single vein that enter the base and dichotomise below each bifurcation. Within the genus, the subgenus *Czekanowskia* is the most similar to our material because we are dealing with amphistomatic leaves and stomata organised in files, which is the main character for that subgenus (Samylina and Kiritchkova 1993). The stomata of the genus *Czekanowskia* are very variable, but in most cases two subsidiary cells are polar and 2–4 subsidiary cells lateral, whereas in our specimens most stomata are surrounded by a circle of subsidiary cells. Individual leaves of *Sphenarion* are narrowly wedge shaped, bifurcate at least once and show no distinction between petiole and lamina (Harris et al. 1974; Huang et al. 2017). In our fragments, bifurcations are only rarely observed. The monocyclic stomata resemble those from our material, but in *Sphenarion* the stomata are scattered within bands.

Concluding remarks

The shape and epidermal features of both the female reproductive organs and the associated leaves strongly support their assignment to the order Czekanowskiales. This notably expands the geographic distribution, since this is the first record for this order from the Southern Alps. More importantly, the temporal distribution of the order is extended from the Late Triassic (Liu et al. 2006) into at least the Wuchiapingian (early Lopingian), although a 'progenitorial czekanowskialean leaf' was figured previously from the Changhsingian of European Russia (Krassilov and Karasev 2009). This much earlier appearance in the fossil record of czekanowskialean plant remains is in line with a series of 'typically Mesozoic' groups in late Palaeozoic sediments, especially at low latitudes (DiMichele et al. 2001; Abu Hamad et al. 2008).

On the other hand, this opens a discussion on the palaeoenvironmental adaptation of the early representatives of the order, since Mesozoic members of the Czekanowskiales are considered to comprise seasonally deciduous trees or shrubs and be one of the dominant elements of the Mesozoic temperate or warm–temperate floras (e.g. Vakharameev 1991; Sun 1992; Zhou and Wu 2006; Li et al. 2015a, b). By contrast, the late Permian successions of Bletterbach and Cortiana were deposited under hot and arid climatic conditions, although sea-level rise may have given origin to a riparian environment, covered by an intrazonal hygrophytic vegetation. This is why the megafossil horizon (Flora A in Kustatscher et al. 2017a) is composed not only of conifers and peltaspermalean seed ferns with thick cuticles, but also of hygrophytic elements such as taeniopterids, sphenopterids and sphenophytes. The latter are characterised by thinner cuticles, although still protected by papillae (for more details see Kustatscher et al. 2017a). The cuticles of *Brinkia kerpiana* and of the associated leaves are of moderate thickness and demonstrate a papillate nature, similar to other hygrophytic elements found in the Bletterbach flora. This suggests that the plants may have occupied the more humid habitats within the deltaic floodplain that originated during sea-level rise.

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