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In situ spores of lycophytes from the Anisian Kühwiesenkopf/Monte Prà della Vacca flora in northern Italy

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ABSTRACT

Four species of lycophytes have been described from the palaeoflora of the Anisian Dont Formation at the Kühwiesenkopf/Monte Prà della Vacca section in the Dolomites (northern Italy); *Isoetites brandneri*, *Lepacyclotes bechstaedtii* (both Isoëtaceae), *Selaginellites leonardii* (Selaginellaceae), and *Lycopia dezanchei* (order and family indet.). For *I. brandneri* and *S. leonardii*, *in situ* spores have also been reported. We have now restudied *in situ* material from all four species with a focus on the morphological variability of the spores. Microspores and a single megaspore from *L. dezanchei* and possible poorly preserved microspores from *L. bechstaedtii* are described for the first time. The microspores from a paratype of *I. brandneri* proved to be highly variable and unusual, generally with an elliptical (bilobed) cingulum/zona that resembles the sacci of bisaccate pollen. In addition, both micro- and megaspores from a specimen previously assigned to *I. brandneri* showed considerable differences to those from the paratype, suggesting a biologically distinct species.

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Introduction

Lycophytes or lycopsids (club mosses and related plants) are considered a distinct, monophyletic lineage of vascular plants with a long evolutionary history (e.g. Stewart and Rothwell 1993; Kenrick and Crane 1997; Gensel and Berry 2001) assigned to the class Lycopsidea (Kenrick and Crane 1997) or to the subclass Lycopodiidae (Christenhusz et al. 2011). Club mosses are characterized by microphyllous leaves, axillary or adaxially borne reniform sporangia with dehiscence along their distal margin, and mostly exarch xylem maturation. Although today they are a group of mostly inconspicuous, herbaceous plants, they were famously important components of Carboniferous and (early) Permian floras with massive trees (e.g. Taylor et al. 2009). The Early and early Middle Triassic saw the appearance – and temporary dominance – of the last sub-arborescent lycophytes in the order Isoëtiales (family Pleuromeiaceae) but also various small herbaceous forms such as *Tomiostrubus* and *Lepacyclotes*, some of which were geographically widespread and locally abundant (e.g. Kustatscher et al. 2010; Looy et al. 2021; Mendelin et al. 2022). The wide-spread occurrence and abundance of these plants is also evident in the palynological record, where dispersed spores with putative lycophyte affinity are diverse and very abundant, in some cases with distinct spikes in abundance (e.g. Looy

et al. 2001; Hermann et al. 2010; Hochuli et al. 2010; Mendelin et al. 2022). Such spikes have been observed close to the Permian–Triassic boundary and in the Lower Triassic. They have consequently been associated with the re-colonization of terrestrial environments after the major disturbances of the Permo–Triassic terrestrial biosphere crisis (e.g. Looy et al. 2001, 2021). Common microspore types that can be linked to lycophytes due to *in situ* findings include mainly the genera *Aratrisporites* Leschik, 1955 (*in situ* in *Lepacyclotes* Emmons, 1856 and *Cylostrobos* Helby et Martin, 1965), *Densoisporites* Weyland et Krieger, 1953 (*in situ* in *Pleuromeia* Spieker, 1854), *Endosporites* Wilson et Coe, 1940 (isolated internal body of some *Densoisporites* species), *Lundbladispota* Balme, 1963 (found *in situ* in *Isoëtes beestonii* Retallack 1997) and *Uvaesporites* Döring, 1965 (found *in situ* in *Selaginellites leonardii* and *S. coburgensis*; Kustatscher et al. 2010; Van Konijnenburg-van Cittert et al. 2014, 2016; Looy et al. 2021).

The *in situ* spores of *Pleuromeia sternbergii* and *P. rossii* from the Early Triassic (e.g. Sadovnikov 1982; Yaroshenko 1975; Zhelezkova 1985; Lugardon et al. 1999, 2000; Grauvogel-Stamm and Lugardon 2001, 2004), as well as those of *Lepacyclotes zeilleri* (Fliche) (Retallack 1997) from the Middle Triassic (Grauvogel-Stamm and Düringer 1983; Wang and Lou 1990; Balme 1995; Moisan

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and Voigt 2013; Kustatscher et al. 2015; Grauvogel-Stamm and Lugardon 2001; Grauvogel-Stamm et al. 2022; Deng et al. *in press*; Table 1) and *Selaginellites hallei* (Lundblad 1950) from the latest Triassic (Lundblad 1950; Couper 1958; Potonié 1962, 1967, 1970; Chaloner 1967; Balme 1995; Zavialova et al. 2010; Table 2) are particularly well studied. It has been shown that varying states of preservation can cause superficial differences in the spores that have led to dispersed spores from the same species to be assignable to different fossil-genera (Grauvogel-Stamm and Lugardon 2004). On the other hand, different species may produce very similar spores (Yaroshenko 1975). However, little is known on the diversity of the spores within the reproductive organs of most other Triassic lycophytes (for overview on the *Pleuromeia* species and allies see tab. Supplementary Table 2 in Mendelin et al. 2022).

From the Kühwiesenkopf/Monte Prà della Vacca section in the Dolomites (northern Italy), a well-preserved palaeoflora has been described from a horizon in the middle-late Pelsonian (Anisian; early Middle Triassic) Dont Formation (e.g. Broglio Loriga et al. 2002; Kustatscher et al. 2006). This palaeoflora includes four species of lycophytes, representing the Isoëtaceae Reichenbach, 1828 (*Isoetites brandneri* Kustatscher et al. 2010, *Lepacyclotes bechstaedtii*, 2010) and Selaginellaceae Willkomm, 1854 (*Selaginellites leonardii* Kustatscher et al. 2010), as well as a lycophyte incertae sedis (*Lycopia dezanchei* Kustatscher et al. 2010). The original descriptions of *I. brandneri* and *S. leonardii* included both microspores and megaspores that were extracted from the holotypes (Kustatscher et al. 2010). The ultrastructure of the spores from *S. leonardii* has also been studied (Zavialova et al. 2010). The original material from both species was restudied and the descriptions of *in situ* spores were partially emended by Kustatscher et al. (2019), but with several question marks remaining. As part of an ongoing project, the *in situ* sporomorphs of the European Triassic plants are reinvestigated with a focus on morphological variability. Previous studies concerning the *in situ* spores of leptosporangiate and marattialean ferns have already been carried out (Nowak et al. 2022, *submitted*). In this work, we present new findings of *in situ* spores of lycophytes from the late Middle Triassic of the Dolomites and discuss their intra- and interspecific variability. Our aim is to determine the natural range of variation for the spores of individual plants and species and to distinguish characters related to taxonomic boundaries, different stages of maturation, environmental stress, or preservation.

Materials and methods

Samples were taken from fertile structures of lycophyte compression fossils (Figure 1), which stem from the

palaeoflora of the Kühwiesenkopf/Monte Prà della Vacca in the Dolomites, northern Italy. The Kühwiesenkopf/Monte Prà della Vacca flora was found in the Dont Formation and is dated as middle-late Pelsonian (Anisian, early Middle Triassic; Broglio Loriga et al. 2002; Kustatscher et al. 2006; Kustatscher and Roghi 2006). The material is housed at the Museum of Nature South Tyrol in Bozen/Bolzano, Italy.

The sediments of the Dont Formation were deposited in a marginal marine environment and comprise marine carbonates as well as terrigenous siliciclastics. Some particularly fossil-rich layers that yielded well-preserved terrestrial plant material and the skeleton of an early eusquamate together with marine invertebrate (bivalves, brachiopods, ammonoids) and fish remains have been identified as storm beds (Broglio Loriga et al. 2002; Posenato et al. 2004; Tintori et al. 2016; Simões et al. 2018; Kustatscher et al. 2019). The diverse macrofloral assemblage is dominated by conifers (primarily *Voltzia* spp.; Forte et al. 2021, 2022), ferns (e.g. *Neuropteridium elegans* (Brongniart) Schimper, 1879, *Gordonopteris lorigae* (Van Konijnenburg-van Cittert et al. 2006, 2006; Nowak et al. 2022), cycadophytes (e.g. *Nilssonia* sp.; Broglio Loriga et al. 2002; Kustatscher et al. 2019), and pteridosperms (e.g. *Scytosphyllum bergeri* Bornemann, 1856; Kustatscher et al. 2007). Less common elements are lycophytes (Kustatscher et al. 2010; this article), sphenophytes (e.g. *Equisetites mougeotii* (Brongniart) Wills, 1910) (Kustatscher et al. 2007), and plants of uncertain affinity such as *Lugardonia paradoxa* Kustatscher et al., 2009 (Kustatscher et al. 2009). The microflora of the Dont Formation is also diverse with various spore and pollen taxa (Kustatscher and Roghi 2006).

The *in situ* samples were macerated with a variation of the Schulze method, using nitric acid and potassium chlorate, followed by a short treatment with potassium hydroxide (for details, see Nowak et al. 2022). For light microscopy, residues were mounted on glass slides in glycerin jelly and photographed with a Leica DMC4500 camera on Leica DM LED microscope. Fluorescence pictures were made using a TX2 Texas red/green filter cube. Measurements were made with Fiji (Schindelin et al. 2012). A part of the material was studied under an SEM at the University of Vienna.

Results and discussion

In situ spores of *Isoetites brandneri* Kustatscher et al., 2010

Microspores

Masses of microspores (Figures 2 and 3(a–d)) were obtained from specimen PAL 1136 (Figure 1(a)), a paratype for *Isoetites brandneri*

Table 1. Overview of related Triassic Isoëtaceae with reported *in situ* spores.

Species	Type	Amb	Aperture	Size	Wall, ornamentation	Dispersed taxon	References
<i>Annalepis brevicystis</i> Meng, 1996	Megaspores	circular	trilete, thick mark	450–512 µm	verrucate/stick-tumorous	-	Meng (2000), Kustatscher et al. (2010), Deng et al. (in press)
<i>Annalepis latiloba</i> Meng 1998	Megaspores	circular	trilete	450–500 µm	verrucate/rugulate	-	Meng (1998), Meng (2000), Kustatscher et al. (2010)
<i>Isoetes beestonii</i> Retallack 1997	Megaspores	subtriangular to subcircular	trilete, laesurae slightly sinuous, raised lips	280–450 µm	cavate, thin nexine, thick sexine, reticulate	<i>Maiturisporites rewanensis</i> Wood et Beeston, 1986	Retallack (1997)
<i>Isoetes ermayinensis</i> Wang, 1991	Microspores	subtriangular	trilete	34–50 µm	cavate, cingulate, scabrate with spinae	<i>Lundbladispora</i> sp. cf. <i>L. springsurensis</i> de Jersey, 1979	
<i>Isoetes innae</i> Naugolnykh et Mogutcheva 2006	Megaspores	convexotriangular	trilete	137–155 µm	cavate, zonate, endopapillate, granulate to laevigate	<i>Dijkstraesporites</i> , <i>Laevigatisporites</i> , <i>Duosporites</i> , <i>Membranisporites</i> , <i>Horstisporites</i> , <i>Bacutrilletes</i>	Balme (1995), Grauvogel-Stamm and Lugardon (2004), Taylor et al. (2009), Kustatscher et al. (2010)
<i>Isoetes brandneri</i> Kustatscher et al. 2010	Megaspores	oval to circular	monolete trilete	20–30 µm 450–500 µm or ca. 100 µm (abortive?)	cavate, laevigate two-layered, laevigate(?)	<i>Aratrisporites</i> <i>Maiturisporites</i>	Naugolnykh and Mogutcheva (2006; 2013)
<i>Isoetes indicus</i> Bose and Roy, 1964	Megaspores	triangular to subtriangular	trilete, mark membranous, sometimes undulating	270–300 µm	thick, convolute to verrucate, proximally reduced ornamentation	? <i>Verrutrilletes</i>	Kustatscher et al. (2010), (2019)[1], this study [2]
? <i>Isoetes</i> sp.	Megaspores	oval to almost circular	alete/trilete	35–40 µm [1]; 34–(48)–62 µm x 22–(32)–40 µm [2]	cingulate/zonate, central body laevigate, cingulum/zona granulate	~ <i>Triadispora</i> , <i>Alisporites</i>	
<i>Lepacycloles bechistaedtii</i> Kustatscher et al. 2010	Megaspores	circular	trilete	175 µm	cavate, verrucate/gemmate/baculate	? <i>Bacutrilletes</i>	this study
<i>Lepacycloles circularis</i> Emmons, 1856	Megaspores	oval or subcircular	trilete, laesurae thin, long, often indistinct	35–(42)–44 µm	cingulate, rugulate	~ <i>Densosporites</i>	this study
<i>Lepacycloles zelleri</i> (Fliche) Retallack 1997	Megaspores	circular/oval	-	30–35 µm	-	-	this study
<i>Lepacycloles circularis</i> Emmons, 1856	Megaspores	circular	trilete	-	-	-	Brown (1958)
<i>Lepacycloles zelleri</i> (Fliche) Retallack 1997	Megaspores	circular	trilete	600–700 µm [1]; 200–700 µm [3]	distally capillate (capilli up to 200 µm long)	<i>Tenellisporites marcinkiewiczae</i> Reinhardt et Fricke	Grauvogel-Stamm and Düringer (1983)[1], Wang and Lou (1990), Balme (1995), Moisan and Voigt (2013), Kustatscher et al. (2015), Grauvogel-Stamm and Lugardon (2001), Grauvogel-Stamm et al. (2022)
	Microspores	oval	monolete	28–38 µm [1]; 24–(34.9)–41 µm x 18–(25.4)–32 µm [2]; 55–66.7 µm x 43.3–51.7 µm [3]	cavate, granulate/punctate/spongy	<i>Aratrisporites</i>	[2], Deng et al. (in press)[3]

Table 2. Overview of related Triassic Selaginellaceae with reported *in situ* spores and *Lycopia dezanchei*.

Species	Type	Amb	Aperture	Size	Wall, ornamentation	Dispersed taxon	References
<i>Selaginella anasazia</i> Ash 1972	Megaspores	-	-	ca. 200 µm	thick, pitted	-	Ash (1972)
<i>Selaginellites coburgensis</i> Van Konijnenburg-van Cittert et al. 2014	Microspores	subcircular	trilete	46–(50)–57 µm [1]; 35.2–(41.0)–45.7 µm [2]	reticulate/verrucate/rugulate, ornamentation distinct distally, reduced or absent proximally	<i>Uvaesporites</i> (immature sometimes resembling <i>Densosporites</i>)	Van Konijnenburg-van Cittert et al. (2014) [1], Van Konijnenburg-van Cittert et al. (2016) [2]
<i>Selaginellites hallei</i> Lundblad 1950	Megaspores	subcircular	trilete, labrate	ca. 425 µm [1]; 330–425 µm [3]; 215–560 µm [4]	cavate, laevigate or finely granulate	<i>Banksisporites</i> (<i>Triletes pinguis</i> Hart, 1935)	Lundblad (1950)[1], Couper (1958)[2], Potonié (1962 [3], 1967, 1970), Chaloner (1967), Balme (1995)[4], Zaviialova et al. (2010)
<i>Selaginellites leonardii</i> Kustatscher et al. 2010	Megaspores	circular, oval, subcircular	trilete	ca. 350 µm [1]; 265–303 µm x 306–336 µm [2]; 270–340 µm x 300–410 µm [3]; 280–(326)–412 µm [4]	cavate?, cingulate, reticulate with irregular ridges	<i>Uvaesporites</i>	Kustatscher et al. (2010) [1], (2019) [3], Zaviialova et al. (2010)[2], this study [4]
	Microspores	rounded triangular to subcircular	trilete, mark often indistinct	45–(56)–62.5 µm [1]; 42.5–50 µm [3]; 48–(53)–60 µm [4]	thick, laevigate or punctate to fossulate	<i>Uvaesporites</i>	
<i>Selaginellites polaris</i> Lundblad 1948	Megaspores	circular	trilete, labrate	392–421 µm	cavate, finely granulate/laevigate	<i>Banksisporites/Bacurifleres</i>	Lundblad (1948), Couper (1958), Potonié (1962, 1967), Chaloner (1967), Balme (1995)
<i>Lycopia dezanchei</i> Kustatscher et al. 2010	Megaspores	subcircular	trilete	ca. 40 µm	cavate, rimulate, endotripapillate, scabrate/laevigate	<i>Densosporites</i>	
	Megaspores	circular	trilete	ca. 220 µm	curvurate, verrucate-rugulate, ornamentation denser and thicker in contact area	-	this study
	Microspores	-	-	31–46 µm	cavate(?)	-	

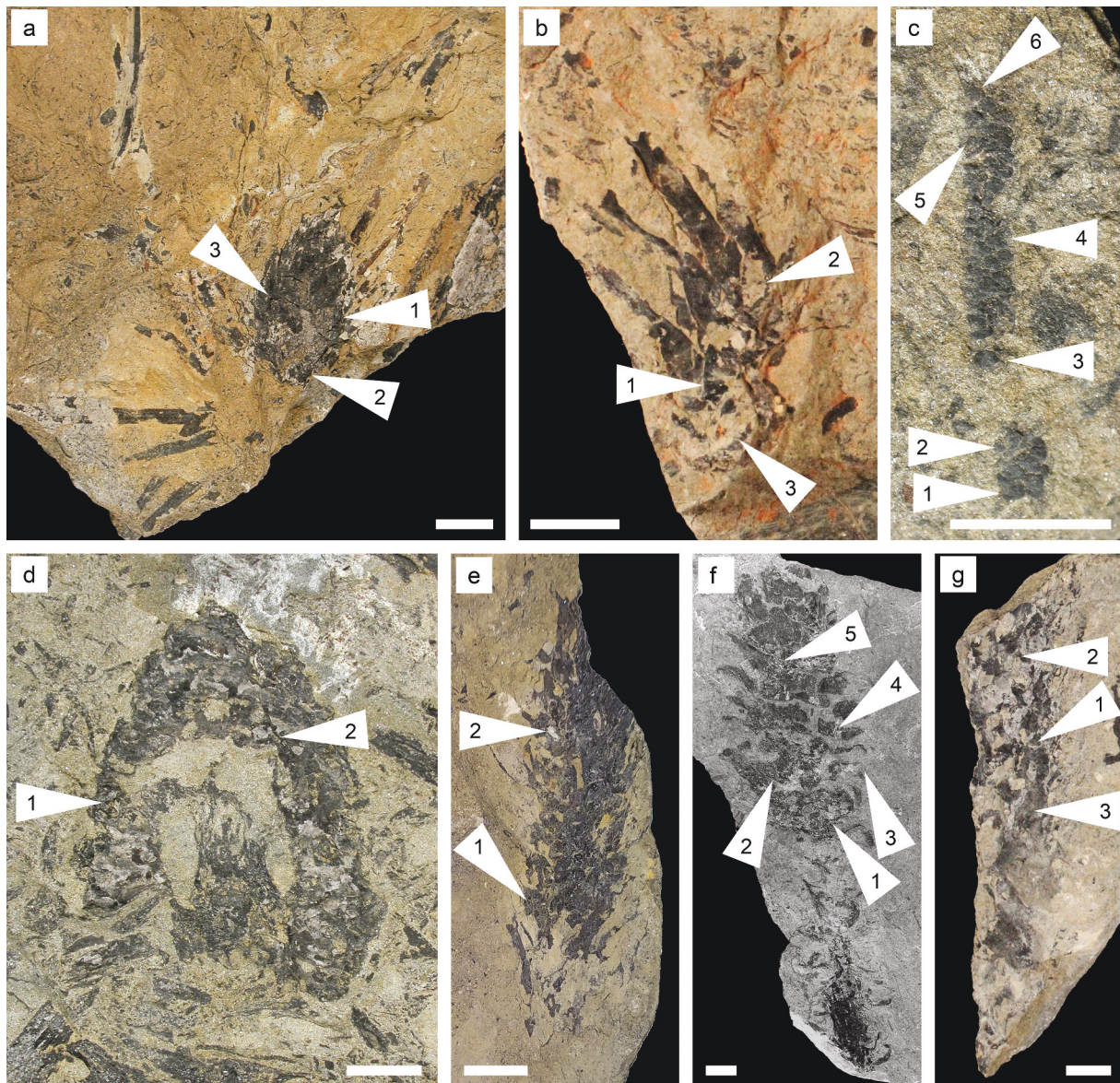


Figure 1. Macrofossils of lycophytes from the Kühwiesenkopf/Monte Prà della Vacca section. White chevrons indicate sampling positions for *in situ* spores. Scale bars = 10 mm. (a) *Isoetites brandneri* paratype, PAL 1136. (b) *?Isoetites* sp., PAL 1145. (c) *Selaginellites leonardii* holotype, PAL 536. (d) *Lepacyclotes bechstaedtii* holotype, PAL 1167. (e) *Lycopia dezanchei*, PAL 1193. (f) *L. dezanchei*, PAL 1211. (g) *L. dezanchei*, PAL 1288.

(Kustatscher et al. 2010, pl.2, figs. 3 and 4). The spores are embedded in an organic granular matrix (possible remains of a tapetal plasmodium; Figure 2(m–n)) that in most cases prevents the isolation of individual spores. Sample 1 also contained some small clusters and individual spores (Figure 2(b–l)), many of which were stuck to cuticular fragments (Figure 2(b,j–l)). The spores have an oval to almost circular and laevigate central body measuring 25–43 μm by 22–40 μm (mean: 35 μm by 32 μm , $n = 23$), to which a transparent, granular exine layer is attached that can take the form of an elliptic (bilobed) or rarely circular, distally extending zona/cingulum or an incomplete and distally thinning patina. The total length of the spores is 34–62 μm (mean: 48 μm). In zonate

forms, the outer layer is attached on the distal side as a narrow or broad thickening that extends beyond the central body on two opposite sides (Figures 2(c–d) and 3(a–b)), whereas in cingulate cases, the extension encloses two sides or all the distal part of the central body or most of the proximal part as well (Figures 2(h) and 3(c–d)). An aperture is rarely visible, only a few spores show a clear trilete mark with short rays ($\sim 1/4$ – $1/2$ of the diameter of the central body, Figure 2(l)). A few other specimens show a slit that resembles a monolete mark (Figure 2(j)), but this can occur in any position and orientation on the spore rather than in the expected central longitudinal position. Consequently, these cases are considered as secondary cracks.

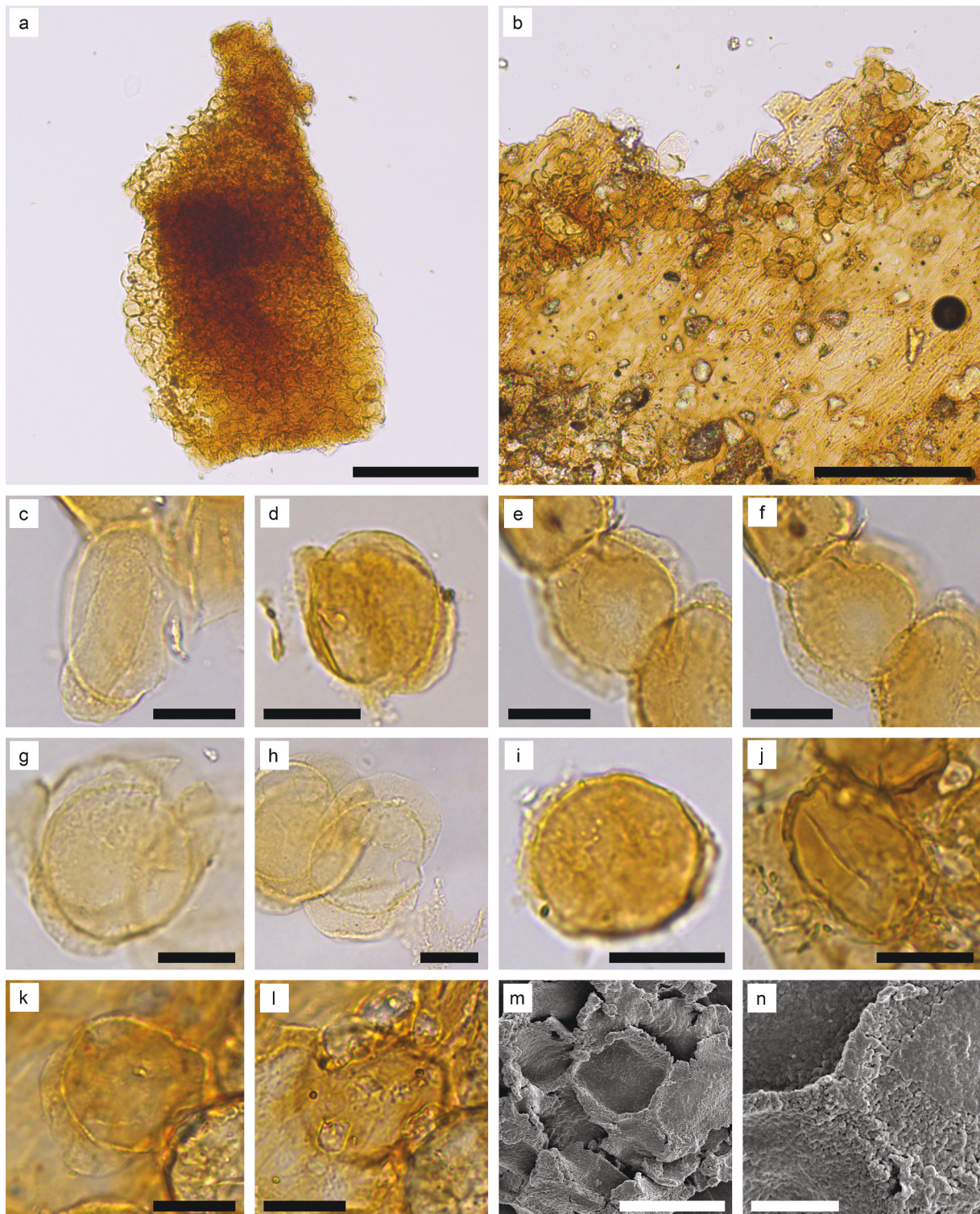


Figure 2. *In situ* spores of *Isoetites brandneri* from specimen PAL 1136 ((a–h, j–n) sample 1; (i) sample 2). Scale bars = 200 μm for (a–b), 5 μm for (n), 20 μm for all others. (a) Mass of microspores. (b) Spores on a cuticular fragment. (c) Spore with a narrow distal thickening extending into a partial zona. (d) Spore with a broad distal thickening extending into a proximally tilted zona. (e–f) Spore with a ring-shaped zona or cingulum. (g) Spore with a broad bilobed zona or cingulum in polar view resembling a bisaccate pollen grain. (h) Spore with a broad bilobed cingulum in lateral view resembling a bisaccate (sulcate) pollen grain. (i) Spore with a short zona/cingulum. (j) Spore with a longitudinal slit resembling a monolete mark. (k–l) Spore with a short trilete mark. (m–n) SEM images of a fragmented spore cluster showing the granular matrix.

Previously, the spores of *Isoetites brandneri*, also based on material from specimen PAL 1136, were described as probably monolete and having a single layered wall (Kustatscher et al. 2010, 2019). At the time only tight spore masses had been extracted, in

which observations of the state of the aperture and the presence of a zona or cingulum are difficult. Moreover, both features are not evident in all spores, probably at least in part due to their immaturity. The *in situ* spores have been tentatively compared to *Aratrisporites*

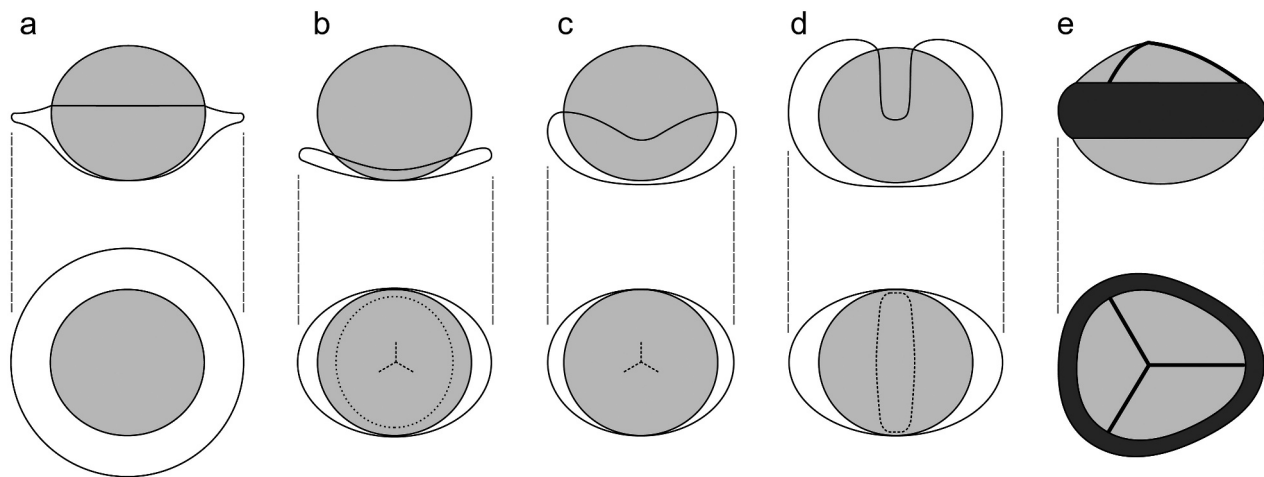


Figure 3. Schematic drawings of spore types in (a–d) *Isoetites brandneri* and (e) *?Isoetites* sp.

Leschik in Kräusel et Leschik, 1955 (Kustatscher et al. 2010) and later *Laevigatosporites* Ibrahim, 1933 (Kustatscher et al. 2019). Both are monolete forms and not suitable comparisons if the spores are alete or trilete. It should be noted that both monolete and trilete microspores are known from Isoëtales (Table 1; Mendelin et al. 2022).

The bilobed cingulate spores are deceptively similar to bisaccate (Figures 2(g–h) and 3(d)) or in some cases monosaccate (Figures 2(e–f) and 3(a)) pollen grains. What distinguishes them – apart from being extracted from an unambiguously spore-producing plant – is the lack of a saccus reticulum and the fact that they form a spectrum with less pollen-like spores. However, most of the forms in this assemblage are highly unusual (to our knowledge even unprecedented, see Table 1) for lycophyte spores. In dispersed assemblages, especially those that are less well preserved so that the lack of a reticulum is not obvious, similar spores could easily be misidentified, e.g. as *Alisporites* Daugherty, 1941 when alete, or as *Triadispora* Klaus, 1964 when a trilete mark is visible. All of these have been reported from dispersed sporomorph assemblages of the Dont Formation at the Kühwiesenkopf/Monte Prà della Vacca section (Kustatscher and Roghi 2006; Kustatscher et al. 2010).

Megaspores

Our samples did not contain megaspores, but several were extracted from the same specimen by Kustatscher et al. (2010), indicating that *Isoetites brandneri* is bisporangiate. The megaspores are described as oval to circular, with a diameter of 270–300 µm, a thick spore wall, a convolute to verrucate, proximally reduced ornamentation, and a delicate, rarely plicate trilete aperture. They have been tentatively compared to the dispersed genus *Verrutrilletes* Van der Hammen ex Potonié, 1956 (Kustatscher et al. 2010, 2019).

In situ spores of ? *Isoetites* sp.

Description

A fragmentary specimen (PAL 1145, Figure 1(b)) that was assigned to *Isoetites brandneri* by Kustatscher et al. (2010) yielded spores (Figures 3(e) and 4) that are clearly very different from those of specimen PAL 1136. In the light of this observation and considering the incomplete state of the specimen, it seems prudent to reconsider its identification. The plant fragment is about 40 mm long. The leaves are arranged spirally around an only partly preserved axis. Individual leaves are 27–31 mm long and 3–3.2 mm wide. The basis of the leaves (about 12 mm long) is enlarged reaching about 4.6 mm in width.

Microspores

Specimen PAL 1145 yielded several microspores (Figure 4(c–j)) that are generally not well-preserved, but a few better examples show that they are trilete with long rays (almost reaching the equator), having an oval or subcircular amb with a diameter of 35–44 µm (mean: 42 µm, n = 14) and a relatively thick (up to 5 µm) exine, often with a cingulum, and sometimes showing a low-relief rugulate ornamentation. In one case, they are preserved as a tetragonal tetrad (Figure 4(h)). The trilete mark is marked by thin crests and not always visible.

Compared to the microspores of *Isoetites brandneri*, those from specimen PAL 1145 show a morphology that is more common for lycophyte spores. Although monolete microspores of the *Aratrisporites*-type are more common among the Triassic Isoëtaceae, trilete microspores are also known, such as from *Isoetes beestonii* Retallack, 1997 (Retallack 1997; Table 1). When it is conspicuous, the ornamentation of the spores of ? *Isoetites* sp., is similar to what is seen in the microspores from *Selaginellites leonardii* (see below), and in this regard resembles *Uvaesporites* Döring, 1965. However,

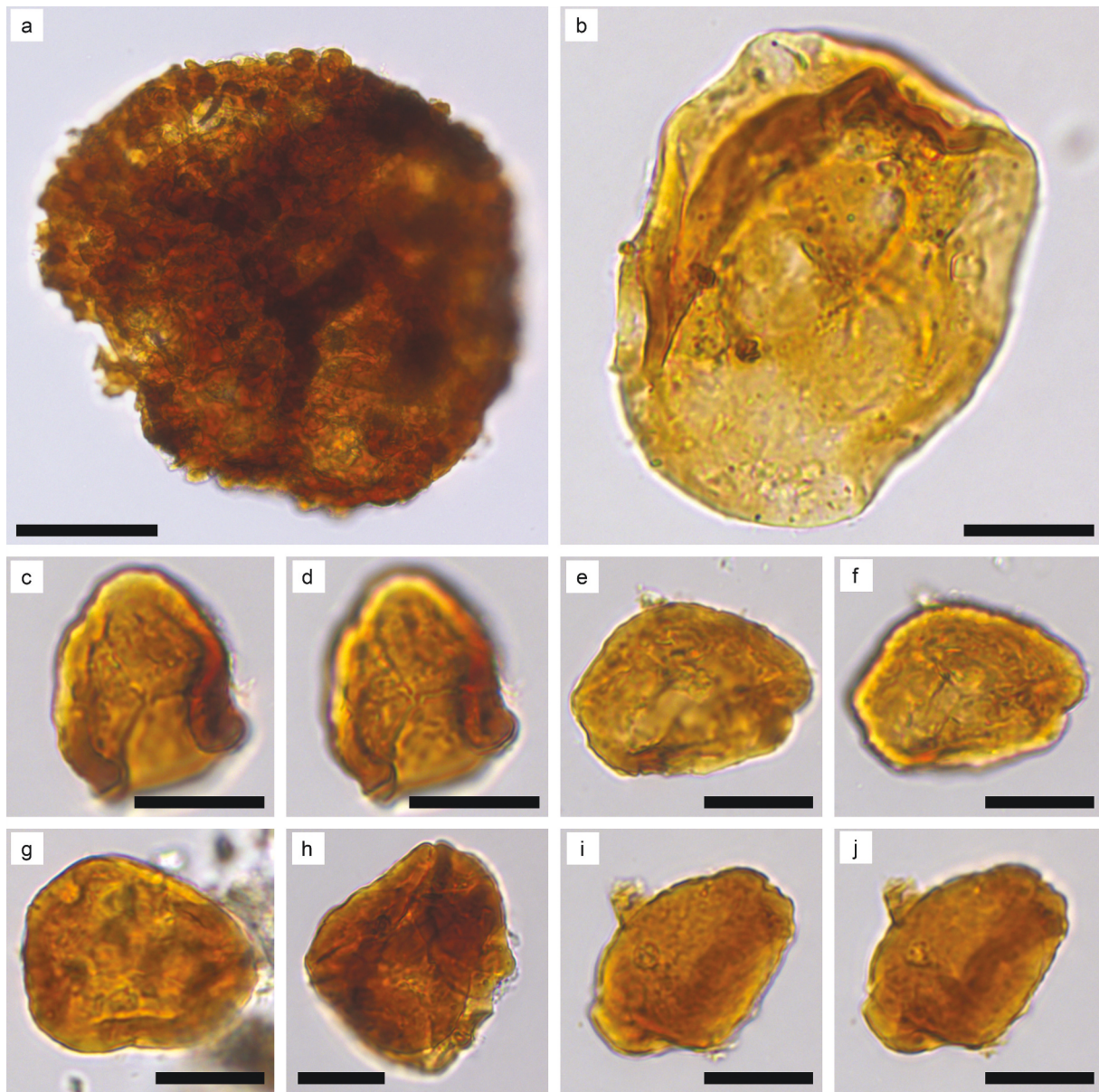


Figure 4. *In situ* spores of *?**Isoetites* sp. from specimen PAL 1145 ((a) sample 2, (b–j) sample 1) Scale bars = 50 μm for (a), 20 μm for all others. (a) Megaspore, sample 2. (b) Possible undeveloped megaspore or endospore, sample 1. (c–f) Spores with visible trilete marks. (g) Subcircular spore with a faint trilete mark. (h) Tetrad. (i–j) Spore with cingulum in lateral view.

the latter does not have a proper cingulum. Two cingulate genera that can be broadly compared to the spores of *?**Isoetites* sp. have been reported from the dispersed sporomorph assemblages of the K uhwiesenkopf/Monte Pr a della Vacca section (Kustatscher and Roghi 2006): *Gordonispora* Van der Eem, 1983 and *Densosporites* Berry emend. Butterworth et al., 1964. *Gordonispora* is characterized by a distal thickening, which is not seen in our material, whereas *Densosporites* is supposed to have only small sculptural elements but should fit at least the less ornamented specimens.

Megaspores

A single megaspore was obtained from PAL 1145, sample 2 (Figures 4(a) and 5(a)). It is cavate, has a more or less circular amb, an equatorial diameter of 175 μm , triradiate ridges that probably

signify a trilete mark but are not straight, and a dense ornamentation with verrucae, gemmae, and baculae on the outer exospore, while the central body appears to be laevigate and has a diameter of ca. 125 μm . This megaspore differs from previously described megaspores of *Isoetites brandneri* that were derived from specimen PAL 1136 (see Kustatscher et al. 2010, 2019) in its smaller size (175 μm in PAL 1145 versus 270–300 μm in PAL 1136) and in having more protruding sculptural elements (previously described as convolute to verrucate), as well as a cavum. The previously described megaspores of *I. brandneri* were compared tentatively to *Verrutriteles* Van der Hammen ex Potoni e, 1956, whereas the new specimen is better compared to *Bacutriteles* Potoni e, 1956.

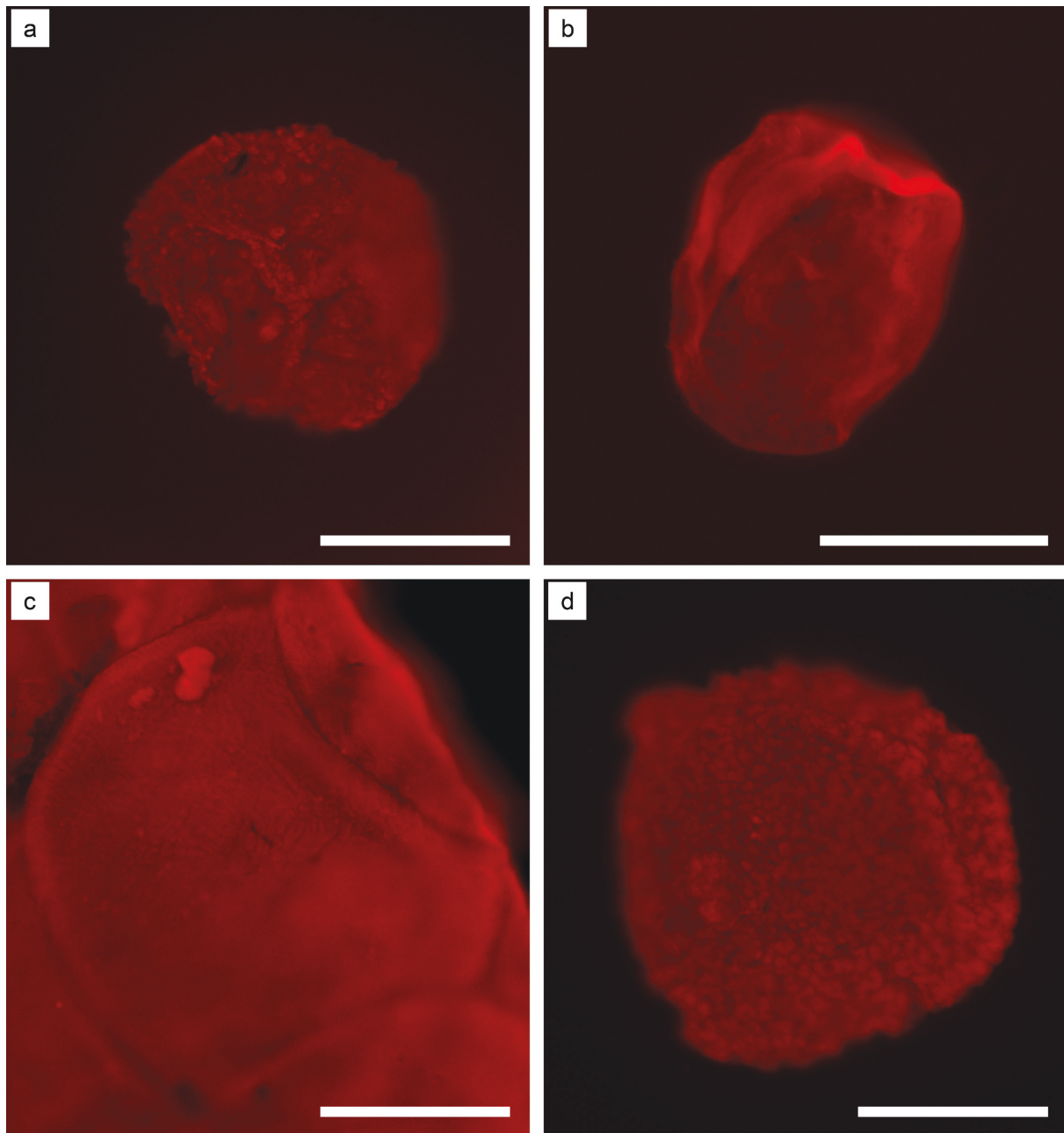


Figure 5. *In situ* megaspores of *?**Isoetites* sp., *Selaginellites leonardii*, and *Lycopodia dezanchei* under fluorescent light. Scale bars = 100 μ m for (a, c–d), 50 μ m for (b), (a) Megaspore of *?**Isoetites* sp. from specimen PAL 1145, sample 2. (b) Possible undeveloped megaspore or endospore, sample 1. (c) Megaspores of *S. leonardii*, PAL 536, sample 4. (d) Megaspore of *L. dezanchei*, PAL 1288, sample 1.

Another sample (1) from specimen PAL 1145 yielded an even smaller macrospore-like object (Figures 4(b) and 5(b)) that probably represents an isolated endospore or an underdeveloped megaspore; it measures 75 μ m in diameter and does not show a clear aperture, contact area, or ornamentation.

In situ spores of *Selaginellites leonardii* *Kustatscher et al., 2010*

Microspores

Masses of microspores were extracted from several points on the holotype of *Selaginellites leonardii*

(PAL 536; Figure 1(c)). These masses are mostly opaque and solid, with only relatively few spores having been isolated successfully (Figure 6(e–f)). More commonly, they retain a tetrad formation (Figure 6(c–d)). The microspores are trilete, with a rounded triangular/subcircular amb and an equatorial diameter of 48–60 μ m (mean: 53 μ m, n = 9), proximally laevigate or granulate, distally and equatorially rugulate. The trilete mark is represented by usually thin crests and often indistinct. The equatorial ornamentation can be somewhat thickened and thereby appear as a cingulum. Spores in lateral view show the polar diameter to be less than the equatorial diameter.

The diameter of the *in situ* microspores of *S. leonardii* has originally been reported as 45–62.5 μm (Kustatscher et al. 2010), and our measurements also fall into this range. By contrast, Kustatscher et al. (2019) reported smaller diameters of 42.5–50 μm based on the original material, which may have been caused by a calibration

mismatch. Otherwise, our findings do not significantly diverge from previous ones (Kustatscher et al. 2010, 2019; Zavalova et al. 2010). As has been noted in those earlier studies, the *in situ* microspores of *S. leonardii* correspond to the dispersed genus *Uvaesporites* Döring, 1965. Similar *in situ* microspores comparable to *Uvaesporites* are

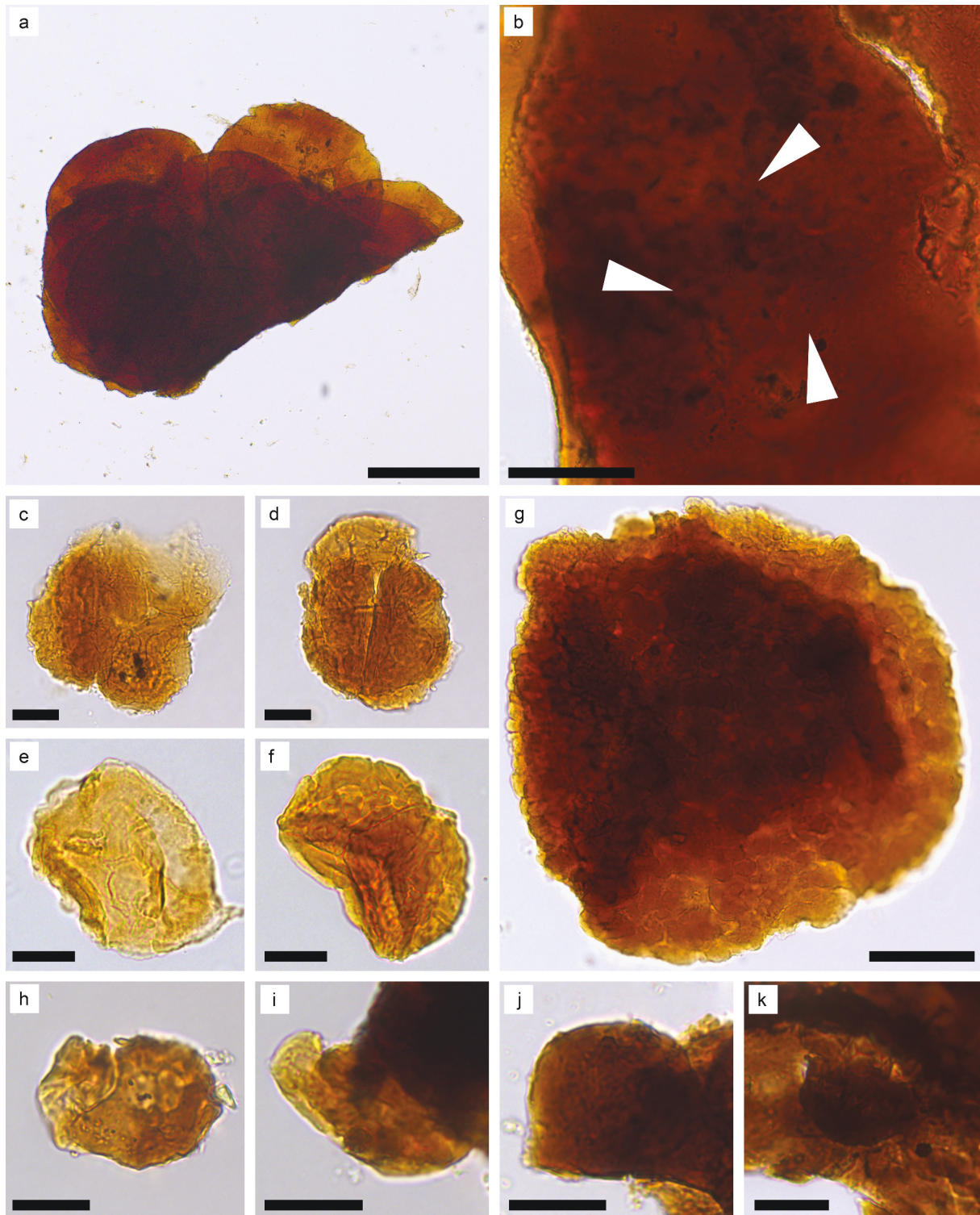


Figure 6. *In situ* spores of *Selaginellites leonardii*, *Lepacyclotes bechstaedtii*, and *Lycopia dezanchei*. Scale bars = 200 μm for (a), 50 μm for (b, g), 20 μm for all others. (a) Megaspores of *S. leonardii*, PAL 536, sample 4. (b) Fragmented megaspore of *S. leonardii* with faint trilete mark (indicated by white chevrons), PAL 536, sample 5. (c–d) Microspore tetrads of *S. leonardii*, PAL 536, sample 6. (e–f) Microspores of *S. leonardii*, PAL 536, original material of Kustatscher et al. (2010). (g) Megaspore of *L. dezanchei*, PAL 1288, sample 1. (h–i) Microspores of *L. dezanchei*, PAL 1193, sample 1. (j–k) Possible microspores of *L. bechstaedtii*, PAL 1167, sample 1.

known from *S. hallei* Lundblad, 1950 (Lundblad 1950; Couper 1958; Potonié 1962, 1967, 1970; Chaloner 1967; Balme 1995; Zavalova et al. 2010) and *S. coburgensis* van Konijnenburg-van Cittert et al., 2014 (Van Konijnenburg-van Cittert et al. 2014, 2016) (Table 2). Some of the spores with a reduced/corroded ornamentation also bear a similarity to the microspores of *Isoetites* sp.

Megaspores

Several megaspores were present in three of the new samples (4–6) from specimen PAL 536 (Figures 5(c) and 6(a–b)). Most of them are clustered in megasporangial fragments (Figure 6(a)). In samples 4 and 6, they co-occur with microspores, while sample 5 yielded only megaspores. They are approximately circular, oval, or subcircular in outline, with a diameter of 280–412 µm (mean: 326, n = 16, including sample material from Kustatscher et al. 2010), having a thick wall with a more or less (corroded) laevigate or punctate, in some cases fossulate, ornamentation and an internally granular appearance. A thin trilete mark is rarely visible (Figure 6(b)), measuring ca. 1/2 of the radius.

The megaspores of *S. leonardii* were described by Kustatscher et al. (2010) as having a diameter of around 350 µm, whereas Zavalova et al. (2010), based on material from the same macrofossil, gave a size range of 265–303 µm by 306–336 µm and finally Kustatscher et al. (2019) listed a size range of 270–340 µm by 300–410 µm. In our measurements, only four megaspores in the original slides of Kustatscher et al. (2010) exceeded 320 µm, with up to 412 µm along the longest axis, whereas the rest had relatively consistent longest diameters of 280–326 µm across samples. Evidently, the maximum sizes are affected by a few outliers. Zavalova et al. (2010) determined that the wall of the megaspores was altered, but also that it was two-layered, with some uncertainty about the presence of a cavum.

In situ spores of *Lycopodia dezanchei* Kustatscher et al., 2010

Microspores

Two specimens assigned to *Lycopodia dezanchei* (PAL 1193, 1211; (Figure 1(e, f)) delivered clusters of microspores (Figure 6(h–i)). These are distorted and mostly not well preserved. Consequently, they do not show many details such as the original form or the aperture, but they appear to be cavate (Figure 6(i)). They measure up to 31–46 µm (n = 5).

In situ spores of *Lycopodia dezanchei* have not previously been described (Kustatscher et al. 2010). In fact, it was uncertain if the sampled specimens represent the strobili of this species since none of them was found in anatomical connection. Ideally, these spores could help to determine the exact affinity of *L. dezanchei*, which is of unknown family and order (Kustatscher et al. 2010). Unfortunately, due to the lack of details, comparisons with the *in situ* spores of other lycophytes are impossible based on the visible characteristics alone, although they may provide more information in the future with a planned ultrastructural analysis.

Megaspore

A single, but well-preserved megaspore (Figure 5(d) & 6(g)) was extracted from specimen PAL 1288 (Figure 1(g)). It is approximately circular in outline, being compressed slightly off from the polar position, with an equatorial diameter of ca. 220 µm. It has a pronounced verrucate-rugulate ornamentation, which is denser and thicker in the contact area, which is bordered by a curvatura. A faint trilete mark with long rays can be seen.

In situ spores of *Lepacyclotes bechstaedtii* Kustatscher et al., 2010

Possible microspores

One of two samples from the holotype of *Lepacyclotes bechstaedtii* (PAL 1167; Figure 1(d)) contained very few oval structures with a length of 30–35 µm (n = 3), which may be poorly preserved spores (Figure 6(j–k)). However, details are not visible and given the low number, it is possible that they are not originally from the same plant. It should also be noted that Kustatscher et al. (2010) failed to extract *in situ* spores. Still, the size and form resemble spores of *Lepacyclotes* (Table 1).

Conclusions

Compared to the first description of *in situ* spores from the lycophytes of the Kühwiesenkopf/Monte Prà della Vacca flora, we can add many new details. The finding of both microspores and a megaspore in three different strobili of *Lycopodia dezanchei*, as well as some possible microspores of *Lepacyclotes bechstaedtii* proves the worth of thorough sampling. Meanwhile, the study of isolated microspores of *Isoetites brandneri* revealed unexpected characters that were not obvious from observations on spore masses. They show morphologies that are not known from related taxa. Moreover, their often deceptive similarity to bisaccate pollen grains warrants

a reconsideration of the identifications of some dispersed sporomorphs. In addition, the discovery of markedly different spores in a specimen that was presumed to belong to *I. brandneri* provides evidence for a macromorphologically indistinguishable, but biologically distinct species. Given the small sample size, since not many specimens are suitable for the extraction of *in situ* spores, this may be a rare coincidence, but it can also be seen as a hint at a hidden biodiversity. It is not certain if the differences here observed in the spores of *I. brandneri* and *?Isoetites* sp. are indeed taxonomically relevant or if they could be caused by pathologies or even differences in preservation.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Author contributions

HN and EK conceived the study and took samples. EK and JHAVKvC reviewed the macrofossils. HN, EK, and GR reviewed the spores. HN performed analyses, prepared figures, and wrote the paper. All authors read and commented on drafts.

Data availability

The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.6426441>.

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