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LYCOPHYTES FROM THE MIDDLE TRIASSIC (ANISIAN) LOCALITY KÜHWIESENKOPF (MONTE PRÀ DELLA VACCA) IN THE DOLOMITES (NORTHERN ITALY)

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Abstract: Generally, lycophytes are not well represented in Anisian floras. Nonetheless, four different genera, each with one species, have been distinguished in the Anisian flora from Kühwiesenkopf (Monte Prà della Vacca), Italy. They were well preserved and yielded leaf cuticles in all four taxa and *in situ* spores in two of them. *Lycopia dezanchei* gen. et sp. nov. is the most common form; it is characterized by a dichotomising creeping prostrate rhizome (representing the primary shoot axis) from which arise aerial axes, apically bifurcated and covered with bundles of long leaves. This taxon cannot be attributed to any of the lycophyte orders, but most resembles Lycopodiales. Two representatives of the Isoetales have been found, of which *Isoetites brandneri* sp. nov. is abundant. This species is characterized by a short stem, which is unusual for this genus. *In situ* immature microspores and megaspores were found in some specimens. *Lepacyclotes bechstaedtii* sp. nov. has a quadrilobe corm with fertile scales inserted in whorls or slightly helicoidally. Short sterile leaves arise distally from the corm in some specimens. Selaginellales are very rare in the flora; *Selaginellites leonardii* sp. nov. is represented by a strobilus that yielded both micro- and megaspores. Some sterile fragments have been found associated, but never in organic connection.

Key words: fossil lycophytes, Dolomites, Italy, Middle Triassic, Anisian.

THE Early–Middle Triassic was an important period in the evolution and radiation of several lycophyte groups including the Lycopodiales, Selaginellales, Pleuromeiales and Isoetales. The arborescent Lepidodendrales disappeared worldwide during the Permian (Taylor *et al.* 2009, p. 280). Helby and Martin (1965) suggested that generally arborescent lycopsids did not become extinct at the end of the Palaeozoic, but survived into the Early Jurassic. The discovery of various taxa such as *Skilliostrobus* Ash, 1979 and *Pleuromeia* Corda ex Giebel, 1853 (and its junior synonym *Pleuromoia* Spieker, 1854; see Wang 2008) in the Triassic supported this theory (Ash 1979, p. 87; Pigg 1992, p. 608; Skog and Hill 1992, p. 648). Ash (1979, p. 87), however, considered these taxa 'subarborescent', because they never reached the height of their Pennsylvanian ancestors. A more apt term could be 'pseudoherbaceous' (Taylor *et al.* 2009, pl. 311) or 'pseudoarborescent', because no secondary growth has been observed so far, even if the plants reached a few metres in height.

With the extinction of the arborescent forms, a high variability both of herbaceous (e.g. *Lycopodites* Lindley and Hutton, 1831–3, *Selaginellites* Zeiller, 1906, *Isoetes* Linnaeus, 1753/*Isoetites* Münster, 1842) and 'pseudoarborescent' forms (e.g. *Takhtajanodoxa* Snigirevskaya, 1980, *Chinlea* Daugherty, 1941, *Cyclomeia* White, 1981) are known from the Triassic. Several dispersed reproductive organs (e.g. *Cylostrobus* Helby and Martin, 1965 and its junior synonym *Austrostrobus* Morbelli and Petriella, 1973, *Lycostrobus* Nathorst, 1908, *Bustia* Grauvogel-Stamm, 1991) and isolated sporophylls (e.g. *Lepacyclotes* Emmons, 1856 and its junior synonym *Annalepis* Fliche, 1910) have also been attributed to the lycophytes. The fructification described by Passoni and van Konijnenburg-van Cittert (2003, pp. 339–342) might belong to the lycophytes as well. Most of these taxa are, however, poorly known.

Microspores isolated from Triassic lycophytes belong either to *Aratrisporites* Leschik, 1955, emend. Playford and Dettmann, 1965 (e.g. in *Annalepis zeilleri* Fliche,

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1910 = *Lepacyclotes zeilleri* (Fliche) Retallack, 1997, *Cyclostrobus sydneyensis* (Walkom) Helby and Martin, 1965), or to *Densoisporites* (e.g. *Pleuromeia sternbergii* (Muenster) Spieker, 1854, *Pleuromeia rossica* Neuburg, 1936 = *Lycomeia rossica* (Neuburg) Dobruskina, 1985) or to *Lundbladispora* sp. (cf. *L. springsurensis* De Jersey, 1979, in *Isoëtes beestonii* Retallack, 1997). The number of different genera of megaspores that have been attributed to Triassic lycophytes is even larger, with, for example, *Banksisporites* Dettmann, 1961 emend. Banerji *et al.*, 1978 (in *Cyclostrobus*, Skog and Hill 1992, p. 652), *Dijkstraisporites* Potonié, 1956*b* (in *Annalepis* species from Cina, Skog and Hill 1992, p. 652), *Horstisporites* Potonié, 1956*b* and *Maiturisporites* Maheshwari and Banerji 1975 (in *Skilliostrobus*, Skog and Hill 1992, p. 652; *Maiturisporites rewarensis* Wood and Beeston, 1986), *Minerisporites* Potonié, 1956*b* and *Tenellisporites* Potonié, 1956*b* (e.g. in *Annalepis zeilleri* Fliche, 1910 = *Lepacyclotes zeilleri* (Fliche) Retallack, 1997). This is because both surfaces of megaspores are commonly characterized by different ornamentation; moreover, there seems to be an evident megaspore dimorphism in most of the extant Indian species (Srivastava *et al.* 1993*a*, p. 115).

Recently (see, for example, Broglio Loriga *et al.* 2002; Kustatscher 2004), a rich fossiliferous horizon has been discovered by the second author (MW) in the Anisian succession from Kühwiesenkopf (= Monte Prà della Vacca in Italian; the area is bilingual) in the Pragser-Olanger Dolomites in northern Italy (in the rest of the manuscript we refer simply to Kühwiesenkopf). After a preliminary report on the macroflora in Broglio Loriga *et al.* (2002), a taxonomic revision of different groups from this locality has dealt with ferns (Van Konijnenburg-van Cittert *et al.* 2006), horsetails and seed ferns (Kustatscher *et al.* 2007). This article describes the lycophytes. The most abundant lycophyte species is *Lycopia dezanchei* gen. et sp. nov. followed in order of abundance by *Isoetites brandneri* sp. nov., *Lepacyclotes bechstaedtii* sp. nov. and *Selaginellites leonardii* sp. nov.

GEOLOGY

The Kühwiesenkopf section including the fossiliferous horizon crops out for several hundred metres along the western slope of Kühwiesenkopf, at the northeastern margin of the Dolomites. The section is well known (Bechstädt and Brandner 1970; Senowbari-Daryan *et al.* 1993). It belongs to the Dont Formation (Broglio Loriga *et al.* 2002; Kustatscher 2004; Kustatscher *et al.* 2006), a carbonate-terrigenous sequence more than 200 m thick in this section. The plant-bearing horizon lies *circa* 75 m above a massive carbonate platform attributed to the Gracilis Formation (De Zanche *et al.* 1992; Broglio Loriga *et al.* 2002; Van Konijnenburg-van Cittert *et al.* 2006).

In the fossiliferous horizon, lens-shaped layers of siltstone on a cm-scale and rich in plant remains alternate with silty and marly limestone layers containing a few plant remains, but also marine biota (bivalves, brachiopods, ammonoids and fishes) (Broglio Loriga *et al.* 2002). Studies on brachiopods (Bechstädt and Brandner 1970) and foraminifers (Fugagnoli and Posenato 2004) suggest a Pelsonian (Middle Triassic) age for the section; integrated studies of palynomorphs and ammonoids narrow the time interval for the deposition of the fossiliferous horizon down to the boundary between the middle and upper Pelsonian (Kustatscher and Roghi 2006; Kustatscher *et al.* 2006).

MATERIAL AND METHODS

The specimens described herein have been studied with a dissecting microscope, and, where possible, cuticle and *in situ* spore preparations were made (see also Batten 1999). For this purpose, small leaf pieces were macerated in Schulze's reagent ($KClO_3$ and 30% HNO_3) and neutralized with 5% ammonia. The cuticles were separated with the aid of needles into upper and lower cuticle, sporangia into single or groups of spores (depending on their maturity) and were mounted in glycerine jelly and sealed with paraplast.

The majority of the macrofossil plant collection from Kühwiesenkopf, including all figured specimens, is stored at the Naturmuseum Südtirol in Bozen/Bolzano, Italy, as are the cuticle and spore slides. They all have the specimen code 'KÜH' or 'PAL' followed by a number. The remainder of the collection is in Wachtler's Museum Dolomythos at Innichen (San Candido, Italy).

EK and JvKvC made the descriptions, the cuticular and *in situ* spore analyses and the systematic discussions; EK made the photographs and JvKvC did the literature research; MW collected the majority of the material and partook in discussion.

SYSTEMATIC PALAEONTOLOGY

Division LYCOPHYTA
Subdivision LYCOPHYTINA Kenrick and Crane, 1997
Order SELAGINELLALES Prantl, 1874
Family SELAGINELLACEAE Willkomm, 1854

Genus SELAGINELLITES Zeiller, 1906

Selaginellites leonardii sp. nov.
Plate 1

2004 ?*Selaginellites* sp. Kustatscher, p. 130.

Derivation of name. After Professor Piero Leonardi in recognition of his research on Permian and Triassic plant fossils in the Dolomites.

Holotype. PAL536 (Pl. 1, figs 1–9).

Material. PAL536 only.

Diagnosis. Heterosporous strobilus with helically to sometimes almost decussately arranged sporophylls. Sporophylls ovate with long, acuminate apex and entire margin. Epidermis with isodiametric cells. Sporophylls arranged in rows of microsporophylls and megasporophylls. Microspores in compact tetrads of trilete microspores 55 μm in diameter, proximally punctate (granulate?) or smooth (psilate), distally rugulate. Megaspores oval to circular, around 350 μm diameter, psilate to punctate with thick spore wall.

Description. Only one specimen can be attributed to this new taxon. The holotype (PAL536; Pl. 1, figs 1–3, 5–9) shows two compact strobilus fragments, preserved on slightly different horizons in the block. The two specimens are not in organic connection. Helically to almost decussately arranged sporophylls are aligned in four irregular vertical files. The sporophylls are closely arranged in the larger strobilus fragment (17 × 3 mm) (Pl. 1, figs 2–3). In the upper part of this specimen, the sporophylls themselves are not preserved; however, megaspores are present in their original position within the cone (Pl. 1, fig. 3). The sporophylls are more imbricate in the lower and smaller fragment (8 × 3.5 mm). They are ovate (1.5–2 × 1–1.2 mm) with a long, acuminate apex (about 2 mm long) and an entire margin. Maceration of sporophyll fragments gave small cuticle pieces with isodiametric cells and sporangia containing masses of immature, *in situ* microspores and megaspores (Pl. 1, figs 5–6). Additionally, when the uppermost sporophylls were taken off for maceration, several megaspores were found below them. The microspores are mostly organized in compact tetrads of *c.* 56 (45–62.5) μm in diameter. Well-developed, separated trilete microspores are 46 (42.5–50) μm in diameter, proximally with a punctate (granulate?) or smooth (psilate) spore wall, and distally rugulate (Pl. 1, figs 7–8). Megaspores are psilate to punctate with a 10-μm thick spore wall (Pl. 1, fig. 9). The trilete aperture is delicate or not yet well developed, and only rarely indicated by plicae.

Megaspores, and to a lesser degree microspores, were found both in the lower and upper part of the cone fragments. During maceration, an entire sporophyll with adhering sediment yielded a small cluster of megaspores and an entire immature mass of microspores. This suggests that the sporophylls were probably distributed in rows of microsporophylls and megasporophylls.

Remarks. The genus *Selaginellites* was defined by Zeiller (1906, p. 141, pls 39, 41) for fossil herbaceous lycophytes resembling the living genus *Selaginella*, while *Lycopodites* is used for fossil representatives of the living genera *Lycopodium* (Seward 1910, p. 76). *Selaginellites* is restricted to heterosporous species, whereas *Lycopodites* includes isosporous taxa and other species, which are not known to be heterosporous (Zeiller 1906, p. 141; Halle 1907, pp. 4–5; Seward 1910, p. 76; Andrews 1961, pp. 246–247). Some authors (e.g. Schimper 1869, p. 185; Lee 1951, p. 194; Pal 1984; Schweitzer *et al.* 1997, p. 115) considered dimorphic (anisophyllous) leaves also characteristic for *Selaginellites*; Halle (1907, p. 4) disagreed with this theory. Additionally, Thomas (1992, p. 627) recognized various isophyllous species of fossil *Selaginella* (=*Selaginellites*) and proposed to divide the genus *Selaginella* into two genera or subgenera, i.e., those with anisophyllous and those with isophyllous leaves.

There is some debate as to whether fossil species should be assigned to the recent genus *Selaginella* (comprising about 500 extant species, see Taylor *et al.* 2009, p. 312) or kept apart in the fossil genus *Selaginellites* (e.g. Thomas 1992; Schweitzer *et al.* 1997). One of the main differences between *Selaginella* and *Selaginellites* is the large number of megaspores per sporangium in the fossil material (16–24 against 4 in extant *Selaginella*; Zeiller 1906; Halle 1907), although there are some living species with more than four megaspores per sporangium (Thomas 1992, p. 628 and references therein).

However, the observed characters of our fossil material do not warrant attribution to the living genus, and, thus, we continue using *Selaginellites* herein, as well as because of the features of the sporophylls and heterospory. The associated sterile fragments were not well-enough preserved to observe any trace of more than two rows of leaves.

There is little information on the *in situ* micro- and megaspores of *Selaginellites*. The megaspores of the Mesozoic species were assigned to the genera *Banksisporites* Dettmann, 1961 emend. Banerji *et al.*, 1978 (Collinson 1991, p. 127) or *Trileites* Erdtmann ex Potonié, 1956*a*,*b* (Lundblad 1950*b*, p. 480), and the trilete microspores referred to *Lundbladispora* Balme 1963 emend. Playford 1965 (Collinson 1991, p. 127). Other megaspores with supposed selaginellalean affinity are *Ricinispora* Bergad, 1978, *Horstisporites* Potonié, 1956*b*, and *Rugotriletes* van der Hammen ex Potonié, 1956*b* (Collinson 1991, p. 127).

Comparisons. From the Triassic, only few herbaceous lycophytes are known: *Selaginella anasazia* Ash, 1972, from the Upper Triassic of Arizona; *Selaginellites polaris* Lundblad, 1948, from the Triassic of East Greenland; *Selaginellites hallei* Lundblad, 1950*a* and *Lycopodites scanicus* Nathorst ex Halle, 1907 from the Rhaetic of Sweden; *Lycopodites sahnii* Lele, 1962, from the Triassic of India; and *Selaginellites yunnanensis* Hsü, 1950, from the Rhaetian of China. We have only compared our material with those species that are clearly heterosporous (*Selaginellites hallei* Lundblad 1950*a*, *S. polaris* Lundblad, 1948, *Selaginella anasazia* Ash, 1972, see also Table 1).

The most similar species is *Selaginellites hallei* of Lundblad (1948, 1950*a*; *Selaginella hallei* in Lundblad 1950*b*, p. 480), even if the megaspores of *S. hallei* are slightly bigger (330–425 μm against 270–340 × 300–410 μm) and the microspores are slightly smaller (29–50 μm against 45–62.5 μm) than those from *Selaginellites leonardii*, but fall partly within its variability range. The rugulate sculpture, typical also of *Selaginellites leonardii* was interpreted by Lundblad (1950*b*, p. 483) as because of taphonomic damage or maceration. Both *S. hallei* and *S. leonardii* are very similar, even if the strobili of *S. hallei* are smaller and each of its macrosporophylls contains only four megaspores (Lundblad 1950*b*, p. 478).

Selaginellites leonardii differs from all known Triassic species because of the distribution of the sporangia. Additionally, the megaspores are never cingulate and the microspores not cavate, as has been described for *Selaginellites hallei* Lundblad 1950*a* and *Selaginellites polaris* Lundblad, 1948. The presence of a cingulum in the megaspores of *Selaginellites polaris* and *Selaginella hallei* was discussed by Couper (1958) and was considered 'a feature found in (but not confined to) the Selaginellaceae' by Potonié (1962).

Sporophylls are mixed or arranged in rows in our material, while megasporangia were restricted to the lower and microsporangia to the upper part of the strobili in the other three species. No comparison can be made of sterile remains, because our sterile specimens have never been found in organic connection and are badly preserved.

Associated sterile material

A small sterile fragment (Pl. 1, figs 1, 4) had been preserved on the same slab as the strobilus, although not in organic connection (Pl. 1, fig. 1). The two samples were divided during transport of the specimens and bear different numbers (PAL536 for the strobilus and PAL568 for the sterile part). Another sterile plant fragment (30 × 28 mm, PAL1161, Pl. 1, fig. 10) shows axes dichotomizing up to six times without any decrease of the thickness of the lateral branches (1.6–1.2 mm). The angles of the dichotomy are 35–50 degrees. Where leaf remains can be seen (Pl. 1, fig. 10), these leaves seem to be arranged oppositely; no indication of more than two rows of leaves was found. A third sterile specimen (KÜH523) shows up to five times dichotomizing axes, but the preservation is inferior to PAL1161. Some leaf and possible root remains are preserved.

Order ISOETALES Prantl, 1874

Family ISOETACEAE Reichenbach, 1828

Genus ISOETITES Muenster, 1842

Remarks. The genus *Isoetites*, with its type species *Isoetites crociformis*, was created by Münster (1842, pp. 107–108, pl. 4, fig. 4) for a specimen from the Lower Jurassic of Germany (Daiting near Monheim) resembling the living genus *Isoetes*. The entire plant consisted of a corm-like stem with some small rootlets and four long leaves. Most authors today use the generic name *Isoetites* to designate fossil forms with an *Isoetes*-like habit (e.g. Collinson 1991; Skog and Hill 1992); others (e.g. Bock 1962, 1969; Wang 1991) prefer to attribute the fossils to the modern genus. The outermost leaves of *Isoetites* usually bear megasporangia, the next whorl of leaves bears microsporangia and the innermost leaves are sterile (e.g. Brown 1958, p. 358; Bock 1962, p. 53), although the precise shape and structure of their fertile parts are still poorly known (Grauvogel-Stamm and Lugardon 2001, p. 136).

According to Skog *et al.* (1992, p. 151), the name *Isoetes* 'has been assigned to fossil plants that look like *Isoetites* but differ in stem or leaf morphology or in which some plant part is lacking. *Isoetites* has been used for compressions of sporophylls, which may be isolated or attached to cormlike stems'. Pigg (2001, pp. 108–109), however, suggested that lycophyte species should be attributed to the genus *Isoetes* only if characterized by a nonelongated stem such as in modern *Isoetes*. Thus, there

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EXPLANATION OF PLATE 1

Fig. 1. *Selaginellites leonardii* sp. nov. Specimen with the strobilus (holotype) and associated sterile material (PAL568–536); ×1.

Fig. 2. *Selaginellites leonardii* sp. nov. Holotype. Strobilus (PAL536); ×4.

Fig. 3. *Selaginellites leonardii* sp. nov. Holotype. Apical part of the strobilus showing dispersed megaspores (arrow) (PAL536); ×10.

Fig. 4. *Selaginellites leonardii* sp. nov. The sterile fragment originally preserved on the same rock slap as the holotype (PAL568); ×4.

Fig. 5. *Selaginellites leonardii* sp. nov. Holotype. Fragment with megasporangia (PAL536); ×100.

Fig. 6. *Selaginellites leonardii* sp. nov. Holotype. Fragment with microsporangia (PAL536); ×100.

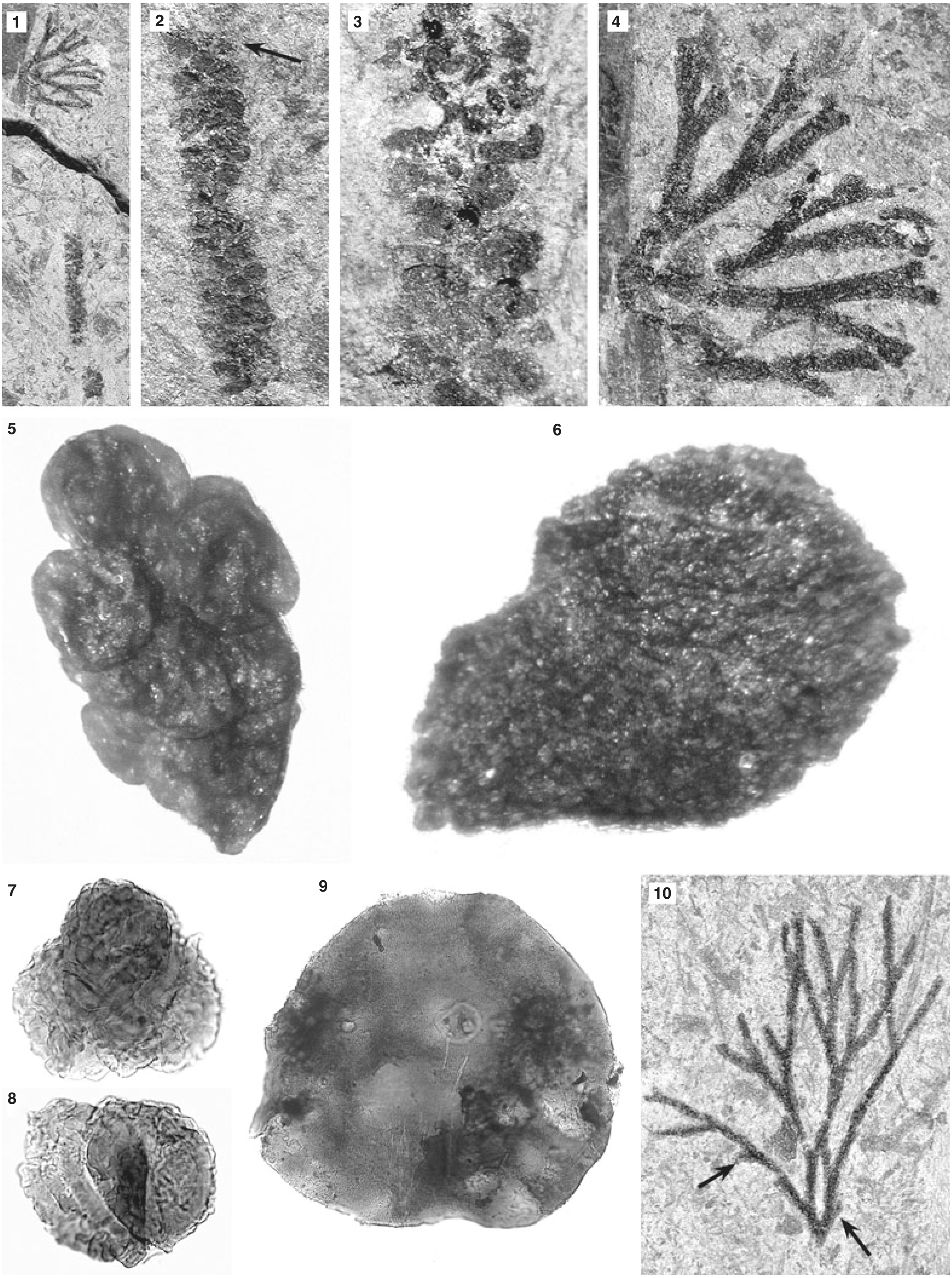
Fig. 7. *Selaginellites leonardii* sp. nov. Holotype. Microspore tetrad (PAL536); ×1000.

Fig. 8. *Selaginellites leonardii* sp. nov. Holotype. Fragment of a microspore tetrad (PAL536); ×100.

Fig. 9. *Selaginellites leonardii* sp. nov. Holotype. Immature megaspore (PAL536); ×1000.

Fig. 10. Sterile leaf fragment that might belong to *Selaginellites leonardii* sp. nov.; arrow indicates small leaf attachment areas (PAL1161); ×100.

PLATE 1



KUSTATSCHER *et al.*, *Selaginellites leonardii*

TABLE 1. Comparison table of the Triassic species of *Selaginella/Selaginellites* (Lundblad 1948, 1950*a*,*b*; *Ash 1972*).

	Selaginellites leonardii sp. nov.	*Selaginellites hallei* Lundblad, 1950*a*	*Selaginellites polaris* Lundblad, 1948	*Selaginella anasazia* Ash, 1972
Strobilus dim.	17 × 3 mm	5 × 1 mm	18 × 7 mm	3 × 1.5 mm
Strobilus	Sporophylls spirally to decussately arranged in four irregular vertical files	Sporophylls imbricate, spirally arranged	–	–
Sporophylls	Ovate with long, acuminate apex (about 2 mm) and entire margin	Monomorph of ovate, deltoid shape	Visible only in the basal part	Megasporophylls ovate, pointed
Cuticle	Isodiametric cells	–	–	–
Sporophyll distribution	Micro- and megasporophylls mixed or organized in vertical files	Megasporophylls restricted to the lower, microsporophylls to the upper part of the strobilus	–	Megasporophylls restricted to the lower, microsporophylls to the upper part of the strobilus
Megasporangia	At least 8 megaspores per megasporangium	Four megaspores per megasporangium	Mass of megaspores	At least three tetrads per megasporangium
Megaspore shape and ornamentation	Psilate to punctuate, trilete mark delicate, rarely plicate	Tetrahedral to spheroidal, psilate to finely granulate, trilete mark with conspicuous costae	Spheroidal, granulate, trilete with three-radiate ridges, wall two-layered (cingulum)	Thick wall, pitted
Megaspore dim.	270–340 × 300–410 μm	330–425 μm	392–431 μm, inner body 274–294 μm	*c.* 200 μm
Microspores	Trilete, proximally punctate (granulate?) to psilate, distally rugulate	Cavate, trilete, faintly to distinctly rugulate (attributed to taphonomic damage)	Cavate, trilete, roundish triangular in polar view, psilate	–
Microspore diameter	46 (42.5–50) μm	29–50 μm	–	–
Sterile parts	–	Dichotomously branched shoots	–	Dichotomously branched, main branch stronger; lateral braches forking, becoming thinner, angle of dichotomy 50–80 degrees
Leaves	–	Dimorphous, ventral leaves spreading, obliquely ovate, slightly falcate, subacute with denticulate apex; dorsal leaves smaller, close to the stem, ovate and acute	–	Leaves in four ranks, two ventral large, ovate and spreading, two dorsal small, lanceolate; apex acute to murornate, midrib containing a vascular bundle
Cuticle	–	–	–	Epidermal cells rectangular; few stomata in rows near midrib; guard cells oval, longitudinal oriented

is no clear distinction recognizable between *Isoetes* and *Isoetites*. Additionally, the type species is based on poorly preserved material, and today a huge variety of species are grouped in the genus, many of them only superficially similar (Chaloner 1967, p. 713).

In our opinion, the extant genus cannot be used as long as we do not have the same information as in the living *Isoetes*. Thus, we prefer to assign our specimens to the fossil genus *Isoetites*.

Emended diagnosis of the genus Isoetites. Herbaceous lycophyte with lanceolate to elongate leaves, expanded basally, bearing mega- and microsporangia. Stem from reduced (almost missing) to short; corm unlobed or slightly lobed. Several to many ligulate sporophylls, erect to spreading. Megasporangia on the outermost whorl of sporophylls, microsporangia on the more inner whorls. Leaves of the innermost whorls generally sterile. Megaspores globose and trilete, microspores elongated to reniforme, monolete, smooth to sculptured.

Isoetites brandneri sp. nov.

Plates 2–4

2002 ?*Isoetites* Broglio Loriga *et al.*, p. 384, pl. 1, fig. 2.
2004 ?*Isoetites* sp. Kustatscher, p. 129, pl. 1, fig. 2.

Derivation of name. After Professor Rainer Brandner, who studied the stratigraphy of the study area and was one of the first to publish on its fossil plants.

Holotype. PAL1263 (KÜH035) (Pl. 2, fig. 1).

Paratypes. PAL1114 (KÜH634, corm, Pl. 2, fig. 2), PAL1136 (KÜH011, microspores, Pl. 2, figs 3–4), PAL1126 (KÜH751, megaspore, Pl. 2, fig. 5).

Material. PAL1112–1114, PAL1115–1126, PAL1128–1137, PAL1140, PAL1143–1145, PAL1149–1156, PAL1158, PAL1162, PAL1163, PAL1164, PAL1203, PAL1224, PAL1258.

Diagnosis. Short stem with helically inserted sporophylls and unlobed corm with simple rootlets. Sporophylls elongate, with pointed apex and enlarged leaf basis, leaving rhomboidal leaf scars on the stem. Epidermis is thick on upper and lower side. Epidermal cells isodiametric in the central part, uncommonly more elongate near the margins. Abaxial epidermal cells protected by papillae. Stomata in irregular rows, sunken and covered partially by papillae of the surrounding 5–7 subsidiary cells. Adaxial epidermis with few or no stomata, epidermal cells without papillae. Variations of the 'normal' epidermis sometimes occur.

Description. About 50 specimens are attributed to this species, most are short stem fragments with attached groups of leaves. One complete (150 mm high and 120 mm wide) specimen was found (PAL1263/KÜH035, Pl. 2, fig. 1). The root system is 37 mm long; various rootlets arise from an unlobed corm, giving origin to a bulb-like structure. Several leaf fragments, up to 80 mm long and 3 mm wide, arise helically from a 40-mm-long stem. The leaf bases enlarge up to 3.5–5.0 mm and show some delicate strap-like structures. Apically, the elongate to lanceolate leaves are narrower, usually with a fold in the middle part. From the base of the leaves, some very immature groups of *in situ* microspores have been extracted (PAL1136/KÜH011, Pl. 2, figs 3–4) and several mature megaspores (PAL1126/KÜH751, Pl. 2, fig. 5).

This taxon shows a range of variability. In older and more mature specimens, the stem is up to 70 mm long and 55 mm wide, covered with helically arranged leaves with enlarged leaf bases containing sporangia (PAL1158/KÜH030, Pl. 3, fig. 1). Apically, the leaf fragments are up to 150 mm long and 3–5 mm wide. The rhomboidal leaf attachment areas reach a width of 4–5 mm. In younger plants, the stem is covered by leaf scars (3.0 × 3.5) mm and leaf fragments (PAL1158/KÜH030, Pl. 3, fig. 1); in older stems, the leaf bases are almost completely gone and only the leaf scars cover the stem (PAL1128/KÜH242, Pl. 3, fig. 2).

Some unlobed corm fragments (*c.* 20 mm in diameter) have been identified (e.g. PAL1114, Pl. 2, fig. 2). Root traces of 1.0–1.5 mm diameter cover the surface.

Particularly interesting is the preservation of two plants (PAL 1133/KÜH1246, Pl. 3, fig. 3) probably growing closely together. The fossil shows the two individuals in a view from below. The stems measure 13.5 and 11.5 mm in diameter, respectively. The elongate leaves are arranged very closely and are up to 46 mm long and 3.0–3.5 mm wide.

Cuticle description: The leaf cuticle is 2.5–3.0 μm thick, both on the upper and lower side. Several different epidermal types can be distinguished.

In Type 1, the most common type, the normal epidermal cells are isodiametric (around 30–40 × 25–35 μm wide) in the central part; near the margins they become sometimes slightly more elongated (e.g. PAL1126/KÜH751; Pl. 4, fig. 1). The epidermal cells of the abaxial side bear thick papillae (15–25 μm in diameter), but those on the presumed adaxial side bear none (e.g. PAL1126/KÜH751; Pl. 4, fig. 1; PAL1152/KÜH584; Pl. 4, figs 2–3). On the abaxial side, stomata are abundant and arranged in short, irregular rows. The stomata are sunken, often heavily protected by papillae of the 5–7 subsidiary cells (sometimes covering the stomatal pit; e.g. PAL1126/KÜH751; Pl. 4, fig. 4). Uncommonly, especially on the margin of the leaves, more elongated 'hair-like' appendices (up to 20 μm long and 10 μm wide) are visible (e.g. PAL1126/KÜH751; Pl. 4, fig. 5). Stomata are few or absent on the adaxial epidermis, and epidermal cells bear almost no papilla, only rarely slight thickenings.

There are, however, also some additional rarer epidermal types. In Type 2, not all cells are isodiametric, and some rows of more elongated cells (3–5 cells wide) give origin to 'vein-like' epidermal structures (?air channels) (cells 50 × 10–15 μm) (e.g. PAL1140/KÜH004, Pl. 4, fig. 6). Additionally, Type 3 includes cuticle fragments with narrow and elongated cells (50–60 × 15 μm). One leaf side is covered heavily by papillae in type 3, whereas the other one is almost devoid of papillae. The stomata are generally less common on both sides.

The least common structure, Type 4, is a small variation of type 1, where both sides of the leaves are covered by thickenings of the cuticle, but without producing real papillae (e.g. PAL1140/KÜH004, PAL1263/KÜH035; Pl. 4, fig. 7). The stomata are irregularly dispersed and not covered by papillae, just surrounded by sculptured subsidiary cells. In this case, the guard cells are simple and notably bigger than the surrounding isodiametric cells (e.g. PAL1263/KÜH035, Pl. 4, fig. 8).

Masses of immature microspores have been extracted from one specimen (PAL1136/KÜH011, Pl. 2, fig. 4). They are reniform, up to 35–40 μm in longest diameter and are probably monolete. They could belong to the dispersed genus *Aratrisporites*. The surrounding sporoderm (sporangial wall?) is very thin with isodiametric to elongated cells.

Several oval to circular megaspores, 270–300 μm in diameter, have been found in the cuticle slides. Megaspores are convolute to verrucate with a thick spore wall (Pl. 2, fig. 5). Proximally the ornamentation reduces in height. The trilete aperture is delicate, only a few times indicated by plicae. Because the cuticle fragments with the adhering megaspores were taken from the attachment area of the leaves to the stem, there is a high possibility that those megaspores were indeed *in situ* megaspores and the leaves in fact sporophylls.

Remarks. According to Pigg (2001, pp. 108–109), lycophyte species can be attributed to the genus *Isoetites* only if characterized by a nonelongated stem such as in modern *Isoetes*, although she agrees that there exists also a high morphological variation in extant species (branching axes, rhizomorphic structures, etc.). Following Pigg's definition, our specimens should not be attributed to the genus *Isoetites*. However, several Cretaceous *Isoetites* species have already been described with short stems, such as *Isoetites daharensis* Barale, 1991 (although Grauvogel-Stamm and Lugardon 2001, pp. 137–138, considered the morphological distinction between scale-like fertile and elongated sterile leaves not very *Isoetites*-like), *Isoetites phyllophila* Skog *et al.*, 1992 (Skog *et al.* 1992, p. 152; Grauvogel-Stamm and Lugardon 2001, p. 131), and *Isoetites choffatii* (Saporta) Seward, 1910 (Skog and Hill 1992, p. 667). According to Skog *et al.* (1992, p. 152), even the extant species *Isoëtes andina* Spruce ex Hooker, 1861 has a robust corm of 9–60 mm high and 16–50 mm diameter. Taylor *et al.* (2009, p. 320) described *Isoetes* as a plant with 'a short, squat stem (usually less than a few centimetres long) that produces helically arranged, monarch roots from the lower surface and elongated, ligulate leaves in a dense rosette from the upper portion'.

Other Triassic lycophyte genera are not closely related to *Isoetites brandneri*. Species of *Cylostrobus* Helby and Martin, 1965, and *Skilliostrobus* Ash, 1979, from the Lower Triassic of Australia correspond to heterosporous lycophyte cones (Ash 1979, p. 73). The Cretaceous genera *Nathorstiana* Richter, 1909, and *Nathorstianella* Glaessner and Rao, 1955, are related to *Isoetites*. However, *Nathorstiana* shows a very characteristic rooting system (cylindrical with one to four lobes) and organization of the stem (see also Karrfalt 1984, p. 1023), which differs notably from our material, as does the five-lobed, very large corm and elongated stem of *Nathorstianella*. The living genus *Stylites* Amstutz, 1957 with its once forked short stems does not resemble our species; additionally, it has been considered by various authors just a morphological form of *Isoetes* (Taylor *et al.* 2009, p. 320). Thus, the only possible existing genus to which to attribute our new species is *Isoetites*.

Stomata have been so far never recorded from fossil species, thus indicating that they were most probably all growing in aquatic conditions (Srivastava *et al.* 2004, p. 275). Also, in extant species large stomata are found in rows over the air canals on the leaves of some *Isoetes* species (e.g. *I. hystrix*) that are not permanently submerged (Seward 1910, p. 60). They are generally missing in the basal part of the sporophyll. It has been noticed that the presence or absence of stomata is consistent within a species (Masarati and Thomas 1982, p. 156). However, the stomatal distribution varies, both within a species and within a single sporophyll and, thus, is unreliable as a distinctive character between different species (Masarati and Thomas 1982, p. 156). Guard cells are rectangular in terrestrial species and more oval in aquatic species (Masarati and Thomas 1982, p. 157). The well-developed cuticle protected by papillae and its sunken stomata often covered by papillae, as observed in *Isoetites*

EXPLANATION OF PLATE 2

Fig. 1. *Isoetites brandneri* sp. nov. Holotype. Almost complete plant (PAL1263/KÜH035); ×1.

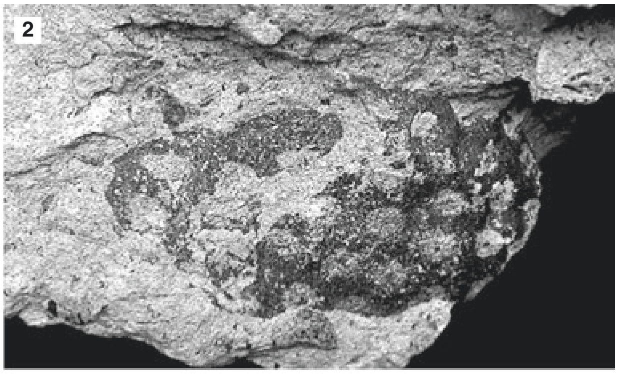
Fig. 2. *Isoetites brandneri* sp. nov. Paratype. Isolated corm fragment (PAL1114/KÜH634); ×3.

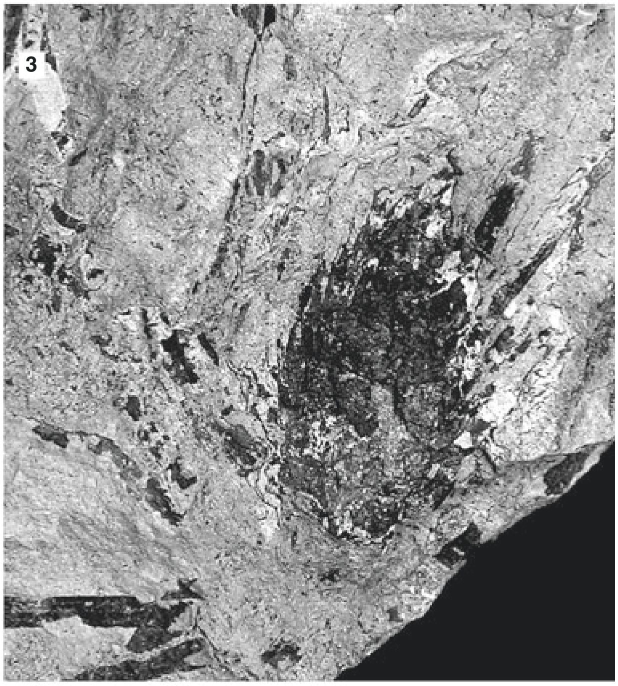
Fig. 3. *Isoetites brandneri* sp. nov. Paratype. The specimen that yielded immature microspores (PAL1136/KÜH011); ×1.5.

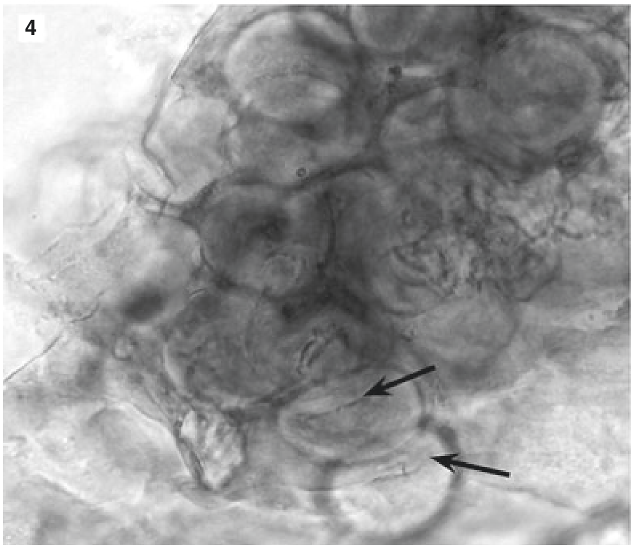
Fig. 4. *Isoetites brandneri* sp. nov. Paratype. Immature microspores; the arrow indicates the monolete aperture (PAL1136/KÜH011); ×800.

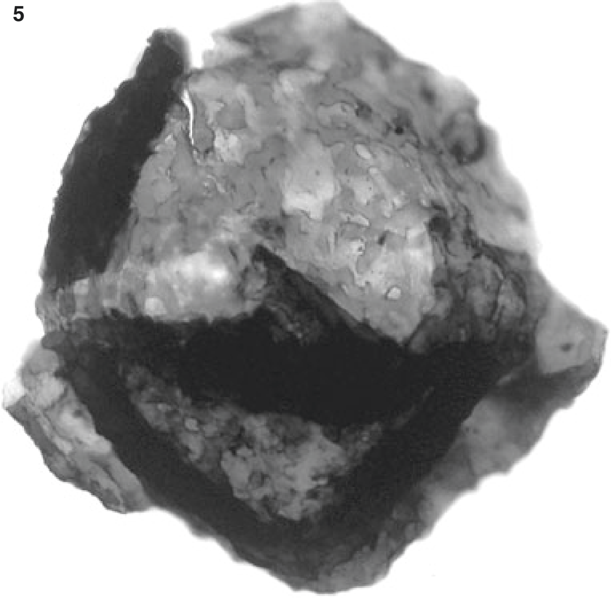
Fig. 5. *Isoetites brandneri* sp. nov. Paratype. Megaspore with convolute, thick spore wall (PAL1126/KÜH751); ×100.

PLATE 2









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brandneri, thus indicate a terrestrial habitat for this plant. Epidermis type 4 seems only a small variation of the 'normal' epidermal type, perhaps corresponding to fragments of the basal part of the sporophyll. Epidermis type 2 might correspond to the area above air channels or veins, if those were present in the extinct species. Type 3 could just belong to a different type of sporophyll, i.e., type 1 corresponds to macrosporophylls and type 3 to the microsporophylls. This suggests that this fossil *Isoetites* species had perhaps a variable cuticle depending on ecological conditions and related to its position on the leaves.

Microspores isolated from *Isoetes/Isoetites* species may belong to *Lundbladispora* spp. (e.g. *L. springsurensis* De Jersey, 1979) as found *in situ* in *Isoëtes beestonii* Retallack, 1997) or *Aratrisporites* Leschik (as in *Isoetes ermayensis* Wang, 1991). The number of different genera to which megaspores have been attributed is much larger, such as, for example, *Horstisporites* Potonié, 1956*b*, *Banksisporites* Dettmann, 1961 emend. Banerji *et al.*, 1978, *Dijkstraisporites* Potonié, 1956*b*, and *Tenellisporites* Potonié, 1956*b*, *Maiturisporites* Maheshwari and Banerji, 1975 and *Minerisporites* Potonié, 1956*a* (Srivastava *et al.* 2004, p. 275). Both surfaces of megaspores are commonly characterized by different ornamentation; moreover, there seems to be an evident megaspore dimorphism in most of the extant Indian species (Srivastava *et al.* 1993*a*, p. 115). Additionally, extant species have a perispore that dissolves when treated with HF (Srivastava *et al.* 2004, p. 275). In our case, the microspores are too immature for close comparison but appear to belong to *Aratrisporites*. The megaspores found might be attributed to the dispersed genus *Verrutriletes* van der Hammen ex Potonié, 1956*b*.

Comparisons. Only a few species of Triassic lycophytes have been assigned to *Isoetes* or *Isoetites* (see also Pigg 1992, p. 589; Skog and Hill 1992). Some of those have subsequently been reattributed to other plant groups and are not compared with our species. For example, *Isoëtes* (*Yorkia*) *gramineoides* (Ward) Bock, 1962 (and 1969), from the Late Triassic of Pennsylvania is now interpreted as an osmundaceous fern stem with attached petiole bases (Skog and Hill 1992, p. 663). Skog and Hill (1992, p. 663) even suggested that the type species, *Isoetites crociformis* Muenster, might be a short shoot of *Czekanowskia*, but this cannot be proven. *Isoetites circularis* (Emmons) Brown, 1958 (and its junior synonyms *I. ellipticus* (Emmons) Brown, 1958 and *Isoetites elegans* Walkom, 1941; see Chaloner, 1967), from the Triassic of North America, do not belong to *Isoetites,* but, as originally described, to *Lepacyclotes* (see below).

The scales of *Isoetites ermayinensis* Wang, 1991 (see also Tables 2, 3) resemble the sporophylls of *Annalepis zeilleri* Fliche, 1910 (see also below). Retallack (1997, p. 507) considered it 'unlikely' that the sporophylls of *Isoetites ermayinensis* Wang 'have borne the wider undulate leaf fragments on their tips as in *Isoetes*' and attributed this species to *Lepacyclotes*. Indeed, the basal *Annalepis*-like remains and the strap-like leaves with spateolate endings and two rows of squarish structures have never been found in association. Similar squarish structures on the leaves, produced by air channels (parichnos, K. Pigg, pers. comm. 2009), were described from the Cretaceous *Isoetites serratus* Brown, 1939, and *Isoetites horridus* (Dawson) Brown, 1939, but have not been identified in our material.

Isoetites serratifolius Bose and Roy, 1964, differs from our species because of its serrated leaf margin (Table 2). *Isoetites indicus* Bose and Roy, 1964 (and its junior synonym *Isoëtes janaianus* Banerji, 1989) differs from *Isoetites brandneri* in the wide, rosette-like arrangement of the sporophylls and the trilete, reticulate megaspores (Table 2) belonging to the dispersed genus *Dijkstraisporites* (Wang, 1991, p. 15).

The lanceolate sporophylls with their basally arranged sporangia of the Middle Triassic *Annalepis brevicystis* Meng 1995 (Meng 1996, pl. 2, figs 11–14; 1998, p. 773; 2000, p. 160; Meng *et al.* 2000, p. 80, pl. 9, figs 8–21, pl. 13, figs 11–18, pl. 19, figs 12–17) suggest an attribution to *Isoetites*. The sporophylls of *Isoetites brandneri* and '*Annalepis brevicystis*' are rather similar in length (up to 80 mm against 45–75 mm), but differ in their width (max. 5 mm against up to 32 mm). Additionally, no information on *in situ* micro- and megaspores sporophylls of '*Annalepis brevicystis*' are available (Table 2).

Isoëtes beestonii Retallack, 1997 resembles *Isoetites brandneri* in the dimensions of the elongated leaves (90 × 5 mm against up to 80 × 3 mm). However, the stomatal furrows and traverse undulations between the furrows, as well as the traverse trabeculae, are missing in *Isoetites brandneri* (Table 2). Our species is characterized by a somewhat elongated stem; in *Isoëtes beestonii*, the stem seems to be very short or completely missing. The reticulate sexine of the megaspores (*Maiturisporites rewarensis* Wood and Beeston, 1986) is not observed in our megaspores nor are our microspores cingulate and trilete as in *Isoetes beestonii* (*Lundbladispora* sp. cf. *L. springsurensis* De Jersey, 1979).

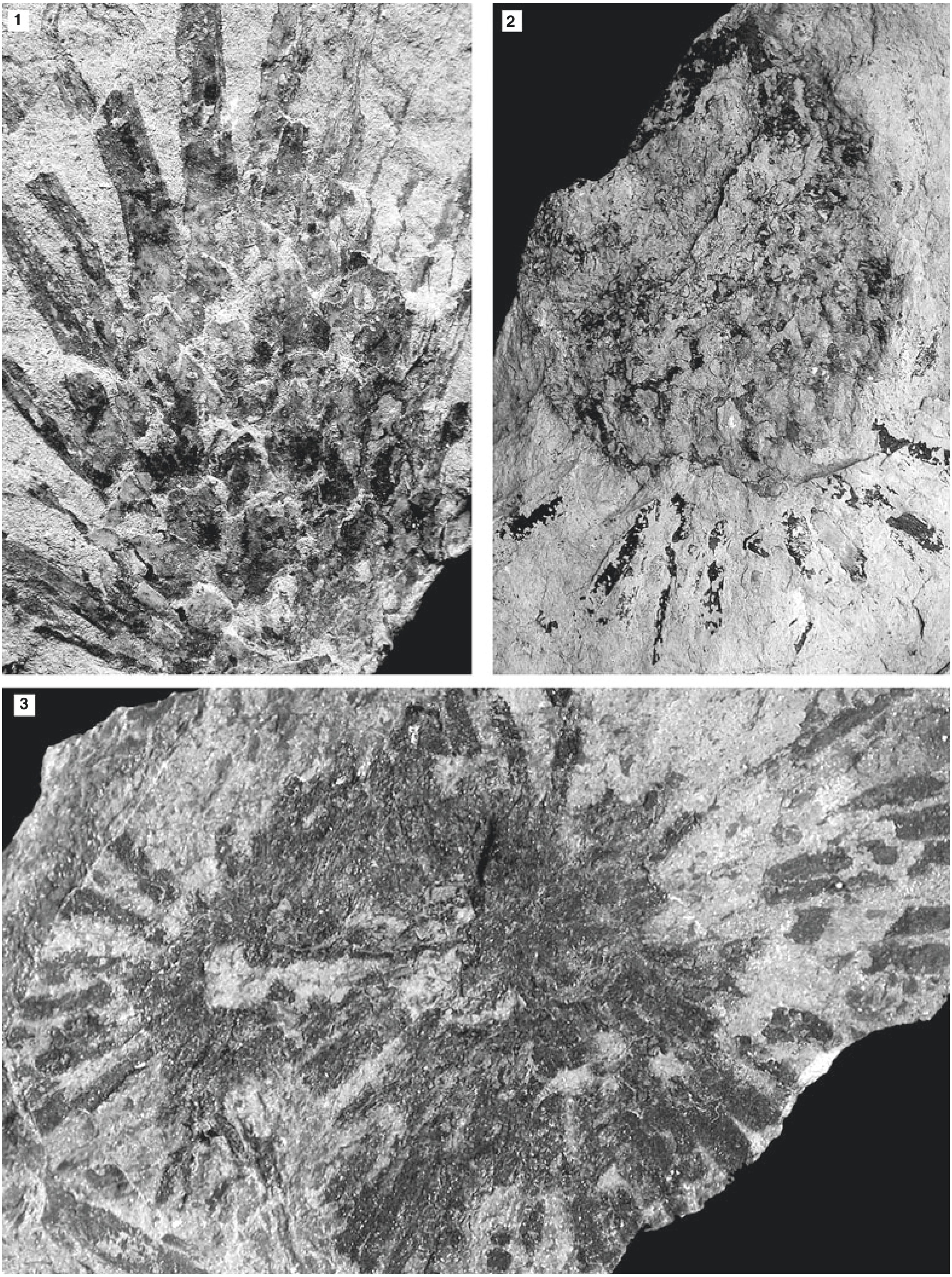
Isoetites sagittatus Wang and Wang, 1990, differs from *Isoetites brandneri* because of the arrow-like form of their sporophylls. *Isoetites* sp. (Kelber and Hansch 1995, pp. 50, 54, fig. 109) is rather similar to our specimens. It shows the elongated leaves and an enlarged leaf basis just as in our material. Unfortunately, data regarding the epidermis structure, and the presence of *in situ* micro- and megaspores, are not available. Thus, the speci-

EXPLANATION OF PLATE 3

Fig. 1. *Isoetites brandneri* sp. nov. Detail of the enlarged leaf bases containing sporangia (PAL1158/KÜH030); ×2.

Fig. 2. *Isoetites brandneri* sp. nov. Old stem fragment covered by leaf scars (PAL1128/KÜH242), ×1.

Fig. 3. *Isoetites brandneri* sp. nov. Two plants growing very closely together (PAL 1133/KÜH1246), ×1.5.



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men cannot be compared in detail with *Isoetites brandneri*, although the two taxa are comparable in gross morphology.

The megaspores *Triletes isoetodendron* Bock from the Late Triassic of Virginia (USA) are similar to those of recent *Isoëtes* species (Bock 1969, p. 52) and were found attached to the stem of *Isoetodendron strata* Bock, 1969. This stem was about 70 mm thick (Bock 1969, p. 51), the plant thus being bigger than *Isoetites brandneri*. Additionally, the plant lacks information on its leaf features and had different megaspores. Also, the stem of *Takhtajanodoxa mirabilis* Snigirevskaya, 1980 (transferred later to *Tomiostrobus* by Retallack 1997, p. 505), was much bigger (400 mm high and 30–200 mm diameter) than that of *Isoetites brandneri*; the bifurcating rhizomorphic base (see also Pigg, 1992, p. 598) is not present in our specimens nor does the large trilete, spinate megaspores resemble our specimens. *Tomiostrobus* Neuburg, 1936 *sensu* Retallack, 1997 is characterized by a short stem with helically inserted sporophylls. The frayed apices of the sporophylls as well as the very dilatated bases with twin abaxial stomatal furrows and a central vascular strand distinguish the species from *Isoetites brandneri*. *Pleuromeia jiaochengensis* Wang and Wang, 1982 resembles *Isoetites brandneri* superficially because of its small shrub-like size (up to 30 cm high). However, it is generally considered one of the smallest *Pleuromeia* species (e.g. Grauvogel-Stamm and Lugardon 2001) with the typical terminal strobilus of a *Pleuromeia*. Because of the lack of sterile leaves and the presence of the distinctive terminal strobilus, it cannot be compared with our species in more detail.

Species of *Lepacyclotes (Annalepis)* differ from *Isoetites brandneri* because of their short, spateolate sporophylls. *Lepacyclotes bechstaedtii* (see below) has a central part with sterile, elongated leaves such as *Isoetites brandneri*, but the fertile sporophylls are still scale-like as in other *Lepacyclotes* species and not elongated with sporangia at the enlarged base such as in *Isoetites*.

Genus LEPACYCLOTES Emmons, 1856

Remarks. The genus *Lepacyclotes*, with its type species *Lepacyclotes circularis* from the Triassic of the USA, was created by Emmons (1856, p. 332) for circular to elliptical discs of unknown affinity composed of numerous scales terminating outwardly in triangular points that form a border outside of a circular ridge.

Fontaine (1883) considered *Lepacyclotes* to be an araucarian cone and fused the two species created by Emmons (*Lepacyclotes ellipticus* and *L. circularis*), creating the new species *Araucarites carolinensis*. Afterwards, Ward (1900, p. 313) considered it a node with leaf sheath of *Equisetum rogersii*. Fliche (1910, pp. 267–273) created the new genus *Annalepis* for fertile material of uncertain affinities. He discussed (p. 269) its similarity to *Lepacyclotes*, but, because of the discussion by Fontaine (1883) of the araucariaceous affinity of *Lepacyclotes*, Ward's (1900) idea of it belonging to *Equisetum*, and his own comparisons with *Albertia* and bracts of *Welwitschia mirabilis,* he wanted to create the new genus *Annalepis* for this type of material and give it a name that did not show any taxonomic affinity. Daugherty (1941, p. 82) interpreted *Lepacyclotes circularis* as a 'basal portion of the flower of a *Williamsonia*', while Brown (1958, p. 359) considered it a quillwort and moved it to the genus *Isoetites*. Grauvogel-Stamm and Duringer (1983) finally confirmed that the scales of *Annalepis* belong to the lycophytes and contained microspores attributable to the dispersed genus *Aratrisporites* (see also Grauvogel-Stamm and Lugardon 2001, p. 127). Retallack (1997, p. 507) synonymized *Annalepis* with the earlier described, but not much used, genus *Lepacyclotes*. He based his synonymy also on the fact that the *in situ* spores of both genera belong to *Aratrisporites* (Retallack 1997, p. 507 and references therein).

Because the genus *Annalepis* (and its type species *Annalepis zeilleri*) is, however, the better known genus, and precise information on the structure and the *in situ* spores of *Lepacyclotes* are missing, Grauvogel-Stamm and Lugardon (2001, p. 132) proposed the former as the type

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EXPLANATION OF PLATE 4

Fig. 1. *Isoetites brandneri* sp. nov. Paratype. Leaf cuticle with isodiametric epidermal cells bearing papillae and more elongated, less cutinized epidermal cells near the margin (PAL1126/KÜH751); ×100.

Fig. 2. *Isoetites brandneri* sp. nov. Abaxial side of cuticle with isodiametric epidermal cells bearing thick papillae (PAL1152/KÜH584); ×100.

Fig. 3. *Isoetites brandneri* sp. nov. Adaxial side of cuticle with isodiametric epidermal cells without papillae (PAL1152/KÜH584); ×100.

Fig. 4. *Isoetites brandneri* sp. nov. Paratype. Stomata protected by papillae (PAL1126/KÜH751); ×200.

Fig. 5. *Isoetites brandneri* sp. nov. Paratype. Cuticle with elongated 'hair-like' appendices (PAL1126/KÜH751); ×200.

Fig. 6. *Isoetites brandneri* sp. nov. Cuticle type 2 with irregularly dispersed stomata and rows of more elongated cells (arrow) (PAL1140/KÜH004); ×100.

Fig. 7. *Isoetites brandneri* sp. nov. Holotype. Cuticle type 4 with irregularly dispersed stomata and epidermal cells with thickenings (PAL1263/KÜH035); ×100.

Fig. 8. *Isoetites brandneri* sp. nov. Holotype. Detail of stomata with surrounding subsidiary cells, inner view (PAL1263/KÜH035); ×200.

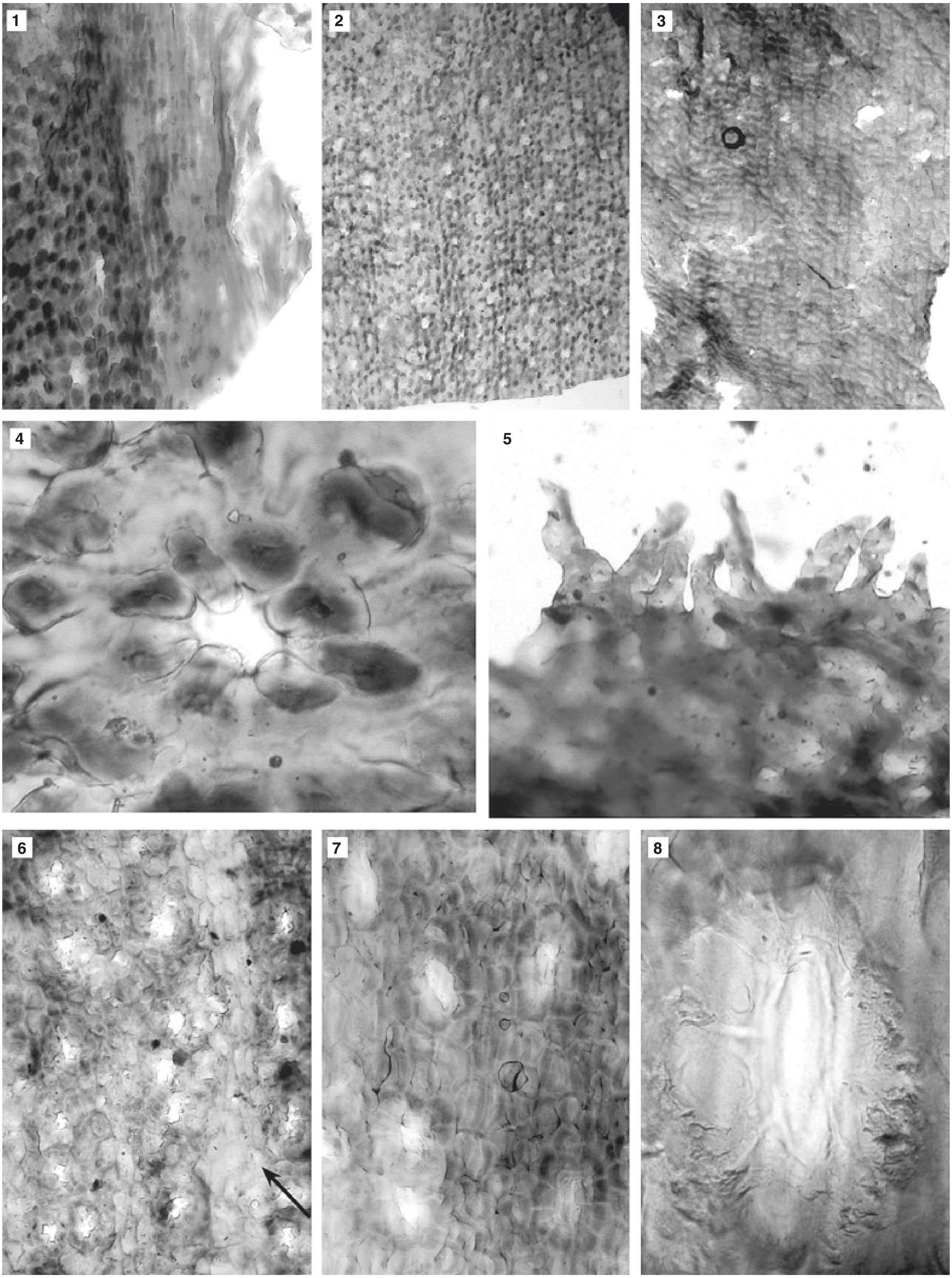

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TABLE 2. Comparison table of the Triassic species of *Isoetites/Isoetes* (Bose and Roy 1964; Wang 1991; Meng 1996; Retallack 1997; Srivastava *et al.* 2004).

	Isoetites brandneri sp. nov.	*Isoetes ermayensis* Wang, 1991	*Isoetites serratifolius* Bose and Roy, 1964	*Isoetites indicus* Bose and Roy, 1964	*Annalepis brevicystis* Meng 1995	*Isoetes beestonii* Retallack, 1997
Max. plant dimensions	150 × 120 mm	–	–	–	–	–
Stem	40–70 × <55 mm	–	–	–	–	Rounded to crudely tetragonal
Corm	Unlobed, bulb-like	–	–	2.4 cm in diameter	–	Rounded to crudely tetragonal
Roots	Root traces 1.0–1.5 mm diameter in corm; rootlet <1 m mm long	Adventitious roots delicate, dichotomously branched	–	–	–	Rootlets fine (1–2 mm), occasionally bifurcating
Leaves	Elongated, folded in middle part	Narrow, lanceolate with blunt apex, thick vascular bundles and lateral lacunae	–	Numerous, forming rosettes of 2.5–4.5 mm diameter	–	90 mm long, 5 mm broad with transverse undulations, base cordate
Sporophylls	Elongated to lanceolate, folded in middle part, bases enlarged with sporangia	?sagitate or spatulate, 11 × 5 mm, base tapering	Base spoon-shaped, obovate, with prominent vascular trace, margin serrated	Sporophylls oval with entire margin	Large, lanceolate, spatulate with acuminate apex	Sporangia on unmodified leaves with traverse trabeculae
Sporangia	–	Oval to wedge-shaped, 7 × 2 mm – 22 × 5 mm	Obovoid, 12 × 3 mm	More than 1500 megaspores	Attached closely to the basal part, elliptic or stick-shaped	Apex covered partially with velum, megasporangia near base, microsporangia near apex
Ligula	–	Narrowly lanceolate lamina fitting on round base (labium)	–	–	Round, 2 mm diameter with labellum	Base flaring into a sunken ‘glossopodium’
Leaf dimensions	<150 × 3–5 mm	22 × 2.5–3 mm	–	–	–	–

TABLE 2. (*Continued*).

	Isoetites brandneri sp. nov.	*Isoetes ermayensis* Wang, 1991	*Isoetites serratifolius* Bose and Roy, 1964	*Isoetites indicus* Bose and Roy, 1964	*Annalepis brevicystis* Meng 1995	*Isoetes beestonii* Retallack, 1997
Cuticle	Variable along the leaf, epidermal cells isodiametric (some times elongated), abaxially with papillae, near margin ‘hair-like’ appendices	–	–	–	–	Stomatal furrows
Stomatal distribution	Abundant and in irregular rows on abaxial side, few or absent on the adaxial epidermis	–	–	–	–	–
Stomata	Sunken, protected by 5–7 subsidiary cells	–	–	–	–	–
Microspores	Immature, reniform, monolete, *Aratrisporites* type	Smooth, delicate, monolete, *Aratrisporites* type	–	–	–	Trilete, subtriangular, cavate, scabrate with spinae, *Lundbladispora* type
Microspore diameter	35–40 μm	20–30 μm	–	–	–	34–50 μm
Megaspore	Oval to circular, convolute to verrucate, trilete mark delicate, sometimes with plicae, *Verrutriletes* type	Various types, mostly *Dijkstraisporites* and *Laevigatisporites* type	–	Trilete, (sub) triangular, reticulate, infragranulate, zone or flange, *Dijkstraisporites* type	Rounded, trilete mark thick, with stick-tumours sculptures	Trilete, cavate, subtriangular to subcircular, reticulate, trilete mark sinuous with conspicuous lips, *Maiturisporites* type
Megaspore dim.	270–300 μm	500 μm or 288–600 μm	–	284–430 μm	–	280–450 μm

of this kind of sporophyll. This is, however, not in agreement with article 11.3 of the IBCN (McNeill *et al.* 2007).

Meng (2000, p. 160) added *Tomiostrobus* to this synonymy, because of a 'comparative morphology of sporophyll, corm structure, micro- and megaspores'. As already pointed out by Retallack (1997, p. 507), 'unlike *Tomiostrobus*, *Lepacyclotes* lacks a long distal limb to the sporophyll and has bluntly pointed to mucrornate sporophylls'.

According to the emended diagnosis by Retallack (1997), *Lepacyclotes* is characterized by a short lobed to rounded stem with roots and ligulate, elongate leaves inserted helically on the corm. Most of the apex is covered by sporophylls, the sporangia are sunken at the basal part of the sporophylls and covered by the velum. The apex of the sporophylls is acuminate to pointed. The plant is heterosporous with megasporophylls in the outermost part and microsporophylls near the apex. The megaspores are trilete, roundish to subtriangulate and cavate, the microspores monolete, spherical to oval, cavate.

Because we consider the two genera *Annalepis* and *Lepacyclotes* to be identical, and *Annalepis* is thus only a junior synonym, we use the genus *Lepacyclotes* herein as proposed by Retallack (1997). We do not, however, include *Tomiostrobus* into this synonymy because of the long distal limb, not present in any species of *Annalepis*.

Lepacyclotes bechstaedtii sp. nov.
Plate 5, Plate 6, figure 1

2004 *Annalepis* sp. Kustatscher, p. 130, pl. 1, fig. 2.

Derivation of name. After Professor Thilo Bechstädt, who studied the stratigraphy of the north-eastern part of the Dolomites.

Holotype. PAL1167 (KÜH1285) (Pl. 5, fig. 1).

Paratype. PAL1141/1142 (KÜH638A/B, structure of scales, Pl. 5, fig. 2).

Other material. PAL512, PAL1127, PAL1138, PAL1139, PAL1146, PAL1147, PAL1157, PAL1159, PAL1160.

Diagnosis. Sporophylls inserted in whorls or helically, closely spaced. Sporophylls spateolate, *circa* 16–17 mm long and 7–10 mm wide; central fertile area oval. Sterile leaves at the innermost circles, 5–6 mm wide and up to 20 mm long, with a central costae. Corm quadrilobate.

Description. Several plant fragments and one isolated sporophyll have been attributed to this species. From the stem (11–15 mm in diameter and at least 20 mm height) arise several closely spaced sporophylls. The sporophylls are inserted in various whorls or helices creating an up to 45 mm high plant with a total diameter of 40–70 mm (e.g. PAL1167, Pl. 5, fig. 1). In most specimens, the detailed morphology of the sporophylls is difficult to identify because they are very densely inserted on the stem. The sporophylls are spateolate, 16–17 mm long and 7–10 mm wide. In some cases, the apical part does not seem just simply triangular in shape, but almost trilobate (e.g. PAL1141/KÜH638A; PAL1142/KÜH638B, Pl. 5, fig. 2). The isolated sporophyll is 15 mm long and maximum 8 mm wide and shows a central elongated fertile area, 9 mm long and 5 mm wide (PAL512/KÜH655, Pl. 5, fig. 3). Unfortunately, preservation was too poor to obtain *in situ* spores. Only small cuticle fragments (KÜH2122; PAL1160/KÜH007, Pl. 5, figs 4–5) have been extracted so far. The normal epidermal cells are elongate (40–50 × 10 μm), on one side with and on the other without papillae. A few stomata are irregularly distributed on both epidermal sides. The stomata are simple, and the guard cells large and elongate (PAL1160/KÜH007, Pl. 5, fig. 5).

In two specimens, some elongate leaf fragments have been identified in the centre, inside the whorls of sporophylls. The basal leaf fragments are 5–6 mm wide and up to 20 mm long, with a central costa (e.g. PAL1160/KÜH007, Pl. 5, fig. 6). One of these fragments (PAL1157, Pl. 6, fig. 1) shows also a putative quadrilobate corm. The lobes are up to 14–17 mm in diameter, the basal root fragments are 23 mm long and 2 mm wide.

Remarks. Lepacyclotes Emmons, 1856, and *Annalepis* Fliche, 1910, were described originally as sporophylls arranged in whorls. In both cases, no sterile leaves were described in either the original diagnosis or in the emended diagnosis of Retallack for *Lepacyclotes*. Retallack (1997, p. 507) indicated that 'most of the apex' is 'covered by sporophylls'. The existence of elongate leaves in our specimens points at a close resemblance between *Isoetites/Isoetes* and *Lepacyclotes/Annalepis*. This has often been remarked on (e.g. Meng 2000, p. 160) and also cre-

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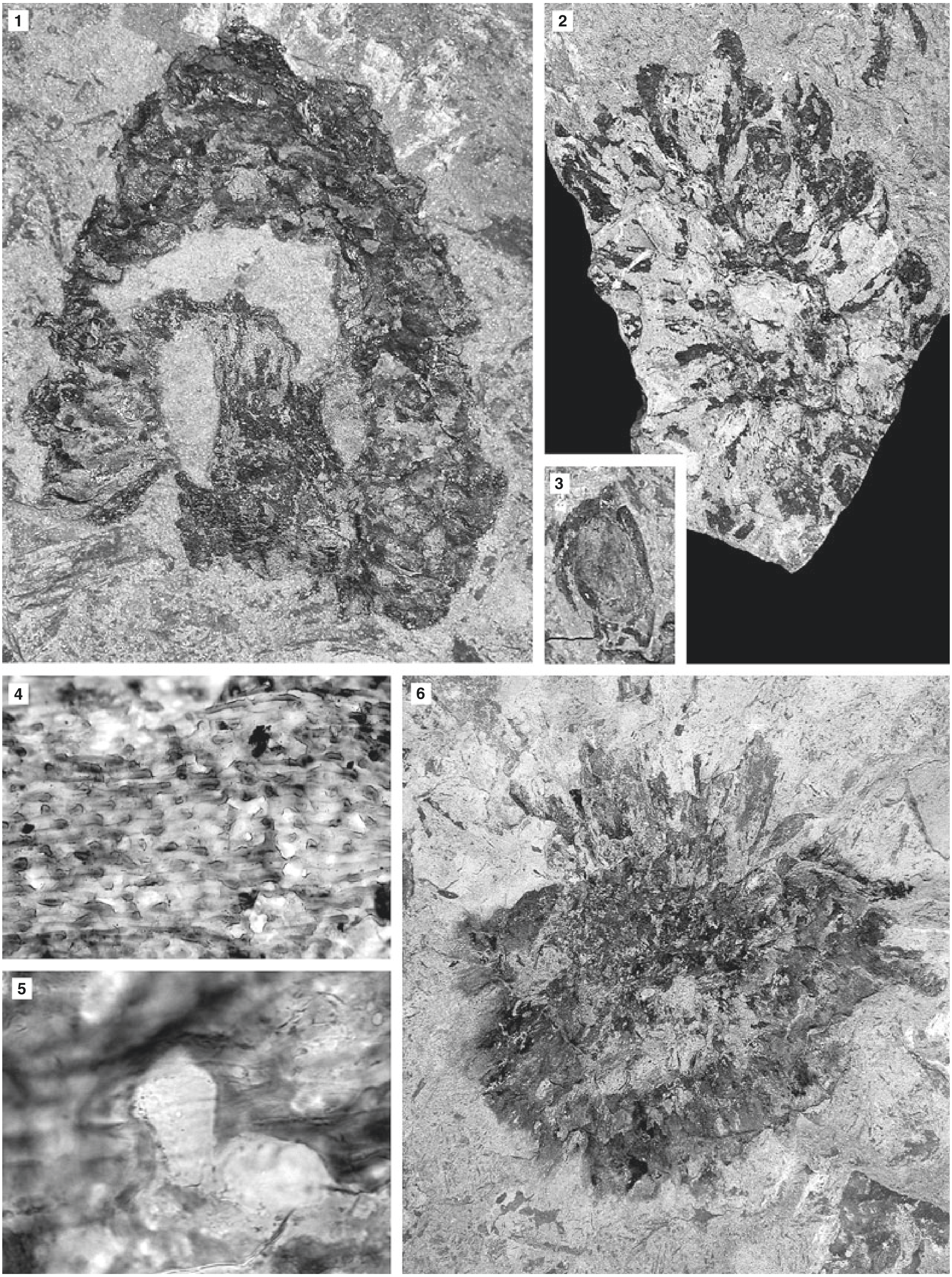
EXPLANATION OF PLATE 5

Fig. 1. *Lepacyclotes bechstaedtii* sp. nov. Holotype. (PAL1167/KÜH1285); ×2.
Fig. 2. *Lepacyclotes bechstaedtii* sp. nov. Paratype. (PAL1142/KÜH638B); ×2.
Fig. 3. *Lepacyclotes bechstaedtii* sp. nov. Isolated sporophyll fragment (PAL512/KÜH655); ×200.
Fig. 4. *Lepacyclotes bechstaedtii* sp. nov. Cuticle fragments with epidermal cells bearing papillae. (PAL1160/KÜH007); ×100.
Fig. 5. *Lepacyclotes bechstaedtii* sp. nov. Simple stoma. (PAL1160/KÜH007); ×200.
Fig. 6. *Lepacyclotes bechstaedtii* sp. nov. Specimen with an inner circle of elongated leaf fragments. (PAL1160/KÜH007); ×1.

PLATE 5



KUSTATSCHER *et al.*, *Lepacyclotes bechstaedtii* ated some confusion on the attribution of several species. Wang (1991, pp. 5–9) described *Annalepis*-like scales and sterile tuberculate leaves together in *Isoetites ermayinensis* Wang, 1991, but they were never found in organic connection. Grauvogel-Stamm and Lugardon (2001, p. 136) indicated that 'sterile partitioned leaves have never been found associated with *A. zeilleri* from the Triassic of eastern France' but described long, sterile leaves attached to an axis found associated with sporophylls of *Annalepis* sp. in the Triassic of Germany. Those were assigned to *Isoetites* sp. by Kelber and Hansch (1995).

Microspores isolated from *Lepacyclotes/Annalepis* belong typically to the dispersed genus *Aratrisporites* (Retallack 1997, pp. 504–505). However, *Aratrisporites* spores have also been extracted from other taxa such as *Tomiostrobus radiatus* Neuburg, 1936, *Tomiostrobus australis* (Ash) Sadovnikov, 1982, *Lycostrobus scottii* (Nathorst) Nathorst, 1908, and *Cyclostrobus sydneyensis* (Walkom) Helby and Martin, 1965. The megaspores were attributed to a number of different genera (e.g. *Baculitriletes* van der Hammen, 1955 ex Potonié, 1956*b*, *Singhisporites* Potonié, 1956*b*, *Dijkstraisporites* Potonié, 1956*b*, *Tennellisporites* Potonié, 1956*b*). Some of them were even found together in the same spore-bearing organ and interpreted as different stages of spore development (Wang and Lou 1990, p. 397). Unfortunately, so far no *in situ* micro- and megaspores have been found in the Anisian specimens of the Dolomites.

Comparisons. Lepacyclotes bechstaedtii differs from all other Triassic species of *Lepacyclotes/Annalepis* because of the presence of sterile leaves. Additionally, *Lepacyclotes bechstaedtii* differs from *Annalepis zeilleri* because of the larger dimensions of the sporophylls of the latter (15–46 × 20 mm), the pointed apex of *Annalepis zeilleri* (not clearly visible in our specimens), and the dimensions and shape of the fertile part (elongated and narrow) (Table 3). Additionally, our material lacks *in situ* micro- and megaspores, while the German and French material yielded *Aratrisporites* microspores and *Tenellisporites* megaspores (Fliche 1910; Grauvogel-Stamm and Duringer 1983). The specimens described by Kelber and Hansch (1995, pp. 54, 96, figs 112–115, 199–200) as *Annalepis zeilleri*, and discussed afterwards by Grauvogel-Stamm and Lugardon (2001, p. 132) as a putative new species temporarily named *Annalepis* sp., differ from *Lepacyclotes bechstaedtii* because of the dimensions and shape of the fertile parts of the German specimens (not visible in our material).

Lepacyclotes circularis Emmons, 1856 (and, according to Retallack 1997, p. 507, its junior synonyms *L. ellipticus* Emmons, 1857, and *Lepacyclotes americana* Bock, 1969) were attributed subsequently by Brown (1958, p. 360) to *Isoetites*. As already discussed by Chaloner (1967) and Bock (1969, p. 46), the sporophylls have a short, triangular apex, but there are no long, sterile leaves similar to those of *Isoëtes* (Grauvogel-Stamm and Lugardon, 2001, p. 136). *Lepacyclotes circularis* is bigger than our specimen (diameter of *c.* 100 mm) and bears 20–24 leaves in each 'rosette' (up to 120 in *Lepacyclotes americana*); in *Lepacyclotes bechstaedtii*, preservation does not permit the number of sporophylls in each whorl to be counted (Table 3). The innermost "rosette" is noticeably smaller than the outer ones in *Lepacyclotes circularis*, with a serrate margin of the apical part; neither of these features has been observed in *Lepacyclotes bechstaedtii*. *Lepacyclotes convexus* (Brik, 1952) Retallack, 1997, differs from *L. bechstaedtii* because of the mucronate apex of the sporophylls (Retallack 1997, p. 507).

Some species described originally in the genera *Isoetes/Isoetites* are also close to *Lepacyclotes/Annalepis*. As mentioned above, Wang (1991, pp. 5–9) combined *Annalepis*-like scales with sterile tuberculate leaves together in *Isoetites ermayinensis* Wang, 1991, although sterile and fertile leaves have never been found in organic connection. Grauvogel-Stamm and Lugardon (2001, p. 135) pointed at the 'very close similarities with the sporophylls of *Annalepis zeilleri*' ('The sporophylls of *Isoetites ermayinensis* are so similar to *A. zeilleri* that the inclusion of that taxon in *Isoetites* is surprising'). Retallack (1997, p. 507) attributed this species to *Lepacyclotes*; Meng (*in* Li *et al.* 1995, p. 309) moved the species to *Annalepis* ('*Annalepis* (=*Isoetes*) *ermayingensis*'). It differs from our species because our specimens lack the apical mucronate sporophyll apex and the distinct longitudinal keel (Table 3). *Annalepis latiloba* Meng, 1998, *A. angusta* Meng, 1995, *A. furongqiaoensis* Meng *et al.,* 2000, *A. sangzhiensis* Meng, 1995, *A. zeilleri* Fliche, 1910, and *A. brevicystis* Meng, 1996, are known from the Middle Triassic of China. *Annalepis latiloba* is much broader and generally much bigger than *Lepacyclotes bechstaedtii*; furthermore, the 2–3 longitudinal ridges of *A. latiloba* are not observed in our material (Table 3). *Annalepis angusta* and *A. sangzhiensis* have a long narrow leaf tip emerging abruptly from a rounded apex (Grauvogel-Stamm and Lugardon 2001, p. 131), a feature absent in our specimens. *Annalepis furongqiaoensis* sporophylls are smaller and wider than our species (Table 3). *Annalepis brevicystis*, with its lanceolate leaves and basally arranged sporangia (Table 3), more closely resembles *Isoetites brandneri* than *Lepacyclotes bechstaedtii* (see above). The specimens described as *Annalepis zeilleri* by Meng *et al.* (2000, p. 79) have lateral wings just as in the French sporophylls (Grauvogel-Stamm and Lugardon 2001 did not consider the Chinese material to belong to the same species as the French specimens); lateral wings are not visible in *Lepacyclotes bechstaedtii*.

The sporophylls of *Tomiostrobus*, *Skilliostrobus*, *Lepacyclotes* and some *Isoetites* species have a similar narrow base, which widens distally and extends into a more or less long pointed, triangular apical part (Grauvogel-Stamm and Lugardon 2001, p. 138). The adaxial sporangium is long and oval, the ligule positioned immediately distally to it. However, *Tomiostrobus* (and its junior synonym *Skilliostrobus*) differ from *Lepacyclotes* in possessing sporophylls with a distal elongated limb. Additionally, it is still not clear if *Tomiostrobus/Skilliostrobus* is an isolated lycophyte strobilus (e.g. Ash 1979) or an entire plant (Retallack 1997). *Cyclostrobus/Austrostrobus* strobili differ from *Lepacyclotes bechstaedtii* in the high number of straplike sporophylls in each whorl, and the presence of *Banksisporites* megaspores and *Aratrisporites* microspores, which were never found in our specimens.

TABLE 3. Comparison table of the most similar Triassic species of *Lepacyclotes/Annalepis* and some related species assigned to Isoetites (Fliche 1910; Bock 1969; Grauvogel-Stamm and Duringer 1983; Kelber and Hensch 1995; Meng 1995; Retallack 1997; Meng 1998, Meng *et al.* 2000; Grauvogel-Stamm and Lugardon 2001).

	Lepacyclotes bechstaedtii sp. nov.	*Annalepis zeilleri* Fliche, 1910	*Lepacyclotes circularis* Emmons, 1856	*Isoetites ermayinensis* Wang, 1991	*Annalepis brevicystis* Meng, 1996	*Annalepis latiloba* Meng, 1998	*Annalepis furongqiaoensis* Meng *et al.*, 2000
Max. plant dimensions	45 mm high	–	–	–	–	–	–
Stem diameter	11–15 mm	–	–	–	–	–	–
Stem height	20 mm	100 mm	–	–	–	–	–
Corm	Putative quadrilobate corm, lobes to 14–17 mm in diameter	Rounded, furrowed rhizomorphs, 4-lobed	About 20 mm in diameter	–	–	–	–
Roots	Root fragments, 23 mm long and 2 mm wide	>300 × 3–7 mm	–	Adventitious roots delicate, dichotomously branched	–	–	–
Leaves	Elongated leaf with a central costa	–	–	? narrow, lanceolate with blunt apex, thick vascular bundles and lateral lacunae	–	–	–
Leaf dim.	5–6 × <20 mm	–	–	22 × 2.5–3 mm	–	–	–
Cuticle	Epidermal cells elongated, one side with, the other without papillae	–	Lengthwise striated, squarish to rectangular cells, organized in rows	–	–	–	–
Stomata distribution	Few, irregularly distributed on both epidermal sides	–	–	–	–	–	–
Stomata	Simple, guard cells large and elongated	–	–	–	–	–	–

TABLE 3. (*Continued*).

	Lepacyclotes bechstaedtii sp. nov.	*Annalepis zeilleri* Fliche, 1910	*Lepacyclotes circularis* Emmons, 1856	*Isoetites ermayinensis* Wang, 1991	*Annalepis brevicystis* Meng, 1996	*Annalepis latiloba* Meng, 1998	*Annalepis furongqiaoensis* Meng *et al*., 2000
Sporophyll arrangement	Various rosettes or spirals (total diam. 40–70 mm)	Cones (total diam. of the plant 14 cm)	4–5 concentric rosettes, 20–100 sporoph. in each rosette (total diam. *c*. 100 mm)	–	Rosette		
Sporophylls	Spateolate, apical part triangular to almost trilobite, central fertile area	Trapezoid with transverse ridge, triangular apex with pointed tip	Short, spear-like to high trapezoid form, strong midrib, undulated margin triangular apex with serrate margin	?sagitate or spatulate, 11 × 5 mm, base tapering	Lanceolate, spatulate with acuminate apex, longitudinal creases on lateral margins	Sagittate top part and cuneate body, slightly curved transverse ridge at broadest part and two longitudinal ridges	Spatulate to subsectorial, curved transverse ridge and longitudinal crease
Sporophyll dim.	15–17 × 7–10 mm	15–46 × <20 mm	30 × 10 mm	7–22 × 2–5 mm	45–75 × 18–32 mm	Max 33 × 27 mm	6–10 × 5–13 mm
Fertile area	9 × 5 mm	Elongated and narrow	12 × 8–9 mm	Oval to wedge-shaped	Basally, elliptic or stick-shaped, 12–20 × 5–8 mm	Stick-shaped, 23 × 25 mm with longitudinal groove	Oblong or subtriangular, 5–8 × 2–5 mm with longitudinal groove
Ligula	–	–	–	Narrowly lanceolate lamina fitting on round base (labium)	Round, 2 mm diameter with labellum	Rotund, 0.5 mm diameter	Small
Microspores	–	*Aratrisporites*	–	*Aratrisporites*	–	–	–
Megaspores	–	*Tenellisporites*	Tetrahedral, trilete	Various: e.g. *Dijkstraisporites*, *Duosporites*, *Membranisporites*, *Horstisporites*, *Baculitriletes*	Rounded, trilete mark thick, with sculptures	Circular, trilete, verrucate	–

Order UNKNOWN
Family UNKNOWN

Genus LYCOPIA gen. nov.

Diagnosis. Subarborescent lycophyte. Dichotomising rhizome covered with small rootlets. Stems bifurcating apically, covered by leaves inserted in close helices. Leaves lanceolate to elongate with central midrib/costa. Cuticle thick, epidermal cells isodiametric to rectangular. Stomata sunken and protected by the papillae.

Derivation of name. The first part of the name is because of the lycopsid affinity of the material. The second part is after Julius Pia, stratigrapher of Austria.

Type species. Lycopia dezanchei sp. nov.

Remarks. A number of subarborescent lycophytes have been described from the Mesozoic (Pigg 1992; Skog and Hill 1992; Retallack 1997; Grauvogel-Stamm and Lugardon 2001). They are generally small, with an elongate and unbranched stem, and unlobed or lobed corms such as *Pleuromeia* Corda ex Giebel, 1853, *Takhtajanodoxa* Snigirevskaya, 1980, *Chinlea* Daugherty, 1941, *Cyclomeia* White, 1981, and *Ferganodendron* Dobruskina, 1974. Cones probably belonging to these sterile genera were described separately as *Cylostrobus* Helby and Martin, 1965 (and its junior synonym *Austrostrobus* Morbelli and Petriella, 1973), *Lycostrobus* Nathorst, 1908, and *Skilliostrobus* Ash, 1979, the latter considered by Retallack (1997) a junior synonym of *Tomiostrobus*.

Recently, a taxon of a subarborescent lycophyte has been found in the Dolomites with different characteristics, such as a dichotomising creeping rhizome and an apically bifurcated stem. This lycophyte resembles no taxon published hitherto and is described below as *Lycopia dezanchei* gen. et sp. nov.

Some strobili were found associated with this material, although never in organic connection. They may have been the fertile structures of *Lycopia*.

Lycopia dezanchei sp. nov.
Plate 6, figures 2–3; Plates 7–8; Text-figure 1

2004 *Lycophyta* gen indet. sp. indet. Kustatscher, p. 131, pl. 1, fig. 4.

Derivation of name. After Vittorio De Zanche, professor at the University of Padova, Italy.

Holotype. PAL1264 (Pl. 7, fig. 1).

Paratype. PAL1262 (Rhizome, Pl. 6, figs 2–3).

Other material. PAL542, PAL62, PAL652, PAL744, PAL1106–1107, PAL1165–1166, PAL1168–1170, PAL1172, PAL1174–1192, PAL1194–96, PAL1198–1202, PAL1204–1209, PAL1212–1214, PAL1215–1223, PAL1225–1245, PAL1248–57, PAL 1259–62, KÜH192, KÜH529, KÜH0641, KÜH1115, KÜH1322.

Diagnosis. Subarborescent lycophyte. Dichotomising rhizome with stem fragments arising alternately, first parallel to the rhizome, then curving upwards perpendicular to the rhizome. Rhizome covered by small rootlets. Proximally, stems with rhomboidal leaf scars; apically, stems with leaves inserted in dense helices; stems sometimes once bifurcate apically. Leaves long, lanceolate to elongate with central midrib/costae. Cuticle thick, amphistomatic; normal epidermal cells isodiametric to rectangular; stomata on one side (upper?) few and scattered, common on the other (lower?) side and there arranged in rows. Stomata sunken and protected by papillae.

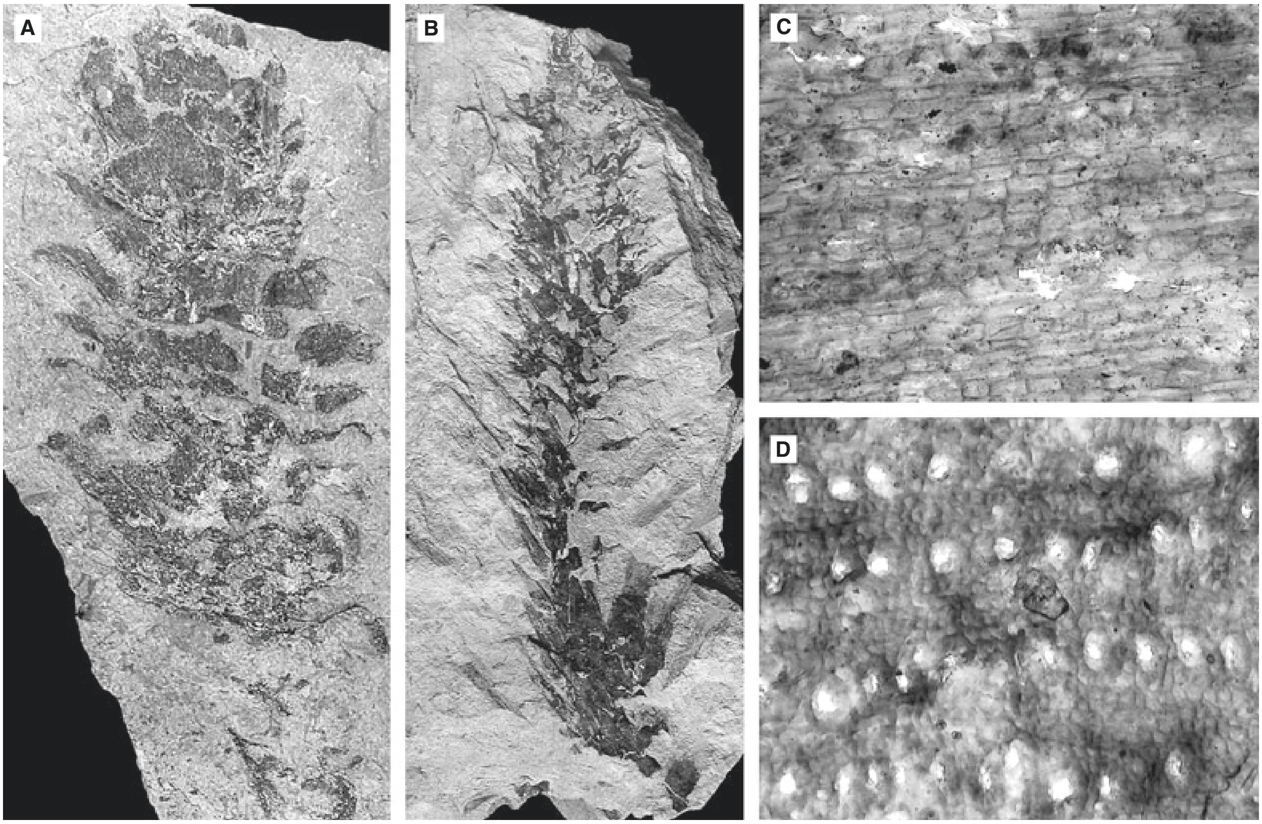
Description. Many stem fragments and a number of rhizome fragments have been assigned to this species. The stem fragments are up to 500 mm long and up to 40–60 mm wide (e.g. PAL1264, Pl. 7, fig. 1). The leaves are inserted in close helices around the stem. The elongated leaves are at least 125–150 mm long and 4.5 mm wide (e.g. PAL1192/KÜH1268, Pl. 8, fig. 1). Uncommonly, a central midrib or costa can be seen on the leaves.

The leaf scars are rhomboidal, 7–10 mm high and 9–11.5 mm wide (e.g. PAL1255/KÜH1229, Pl. 8, fig. 2). In the older and bigger stem fragments, these leaf scars can even get as high as wide, seeming almost circular (e.g. PAL1190, Pl. 8, fig. 3). A side branch commonly departs apically (holotype, Pl. 7, fig. 1). This is also visible in some juveniles (e.g. PAL1226, Pl. 8, fig. 4).

The biggest dichotomising rhizome fragment (paratype, PAL1262, Pl. 6, figs 2–3) is 480 mm long and 135 mm wide. Five stem fragments arise alternating, at first parallel to the rhizome. Afterwards they curve upwards and proceed perpendicularly to the rhizome. The biggest stem fragment attached to the rhizome reaches 125 mm in length and 40 mm in width. The entire rhizome is covered by rootlet scars of 1.0–0.5 mm diameter (Pl. 6, fig. 2). Attached rootlets reach 2–5 mm length.

Cuticle. The thick leaf cuticle is amphistomatic. The normal epidermal cells are isodiametric to rectangular (25–30 × 40–50 μm). On one side (presumably the upper side), stomata are few and irregularly scattered; on the other side, the stomata are more common and organized in rows (e.g. PAL652/KÜH008, Text-fig. 1C; PAL1187/KÜH014, Text-fig. 1D). All stomata are protected by papillae on the 4–6 subsidiary cells.

Remarks. Lycopia dezanchei differs from all the other Triassic subarborescent (or subarborescent) genera, including *Pleuromeia* Corda ex Giebel, 1853, *Lycomeia* Dobruskina 1985, *Chinlea* Daugherty, 1941, *Ferganadendron* Dobrusk-



TEXT-FIG. 1. A, Broad strobilus with spatiolate sporophylls associated with *Lycopia dezanchei* gen. et sp. nov. (PAL1171/KÜH1276), ×0.5. B, Strobilus with long, spatiolate sporophylls associated with *Lycopia dezanchei* gen. et sp. nov (PAL1211), ×1. C, *Lycopia dezanchei* gen. et sp. nov. Upper leaf cuticle with rectangular epidermal cells (PAL652/KÜH008); ×200. D, *Lycopia dezanchei* gen. et sp. nov. Lower leaf cuticle with rectangular epidermal cells and stomata in rows (PAL1187/KÜH014); ×150.

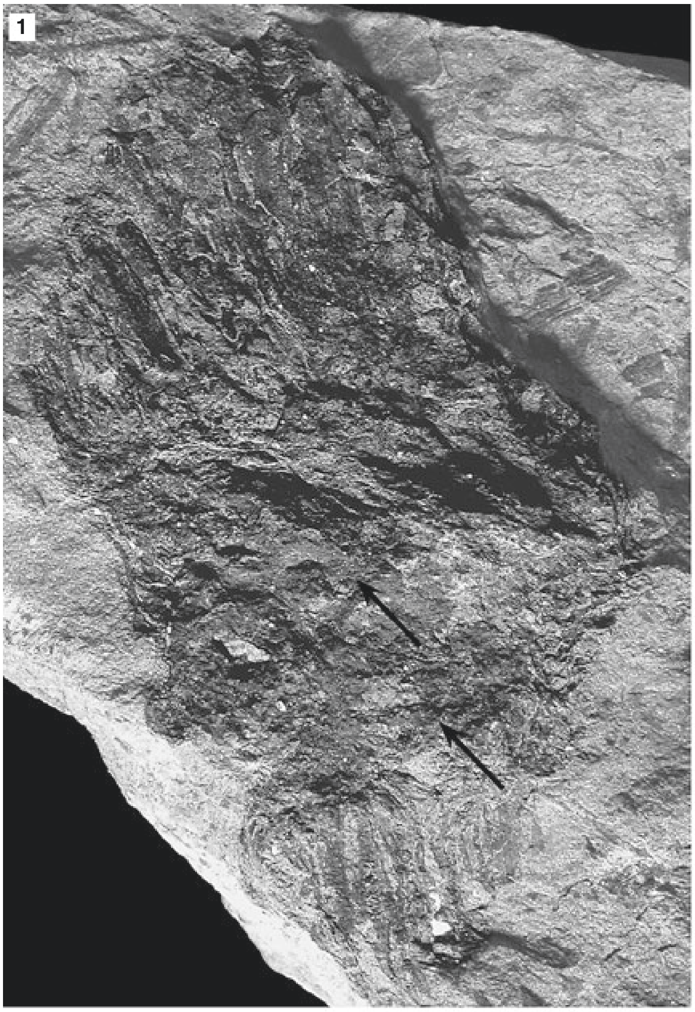
ina, 1974, *Cyclomeia* White, 1981, *Pleurocaulis* Cantrill and Webb, 1998, *Isoetodendron strata* Bock, 1969, *Taktajanodoxa mirabilis* Snigirevskaya, 1980 and *Cyclostrobus indicus sensu* Retallack, 1997, because of the absence of a corm-like rooting structure and the presence of a forking stem. Additionally, in species of *Pleuromeia* the corm is lobed several times (usually twice) (e.g. Grauvogel-Stamm 1993) and the stem shows widely separated leaf scars while the leaves are closely inserted on the stem in *Lycopia dezanchei*. *Lycomeia* Dobruskina, 1985 differs from *Lycopia* because of its limited plant size and the absence of sterile leaves. *Chinlea* Daugherty, 1941 is preserved as a petrified trunk. The genus is characterized by about 165 leaf scars in one transverse section, much more than *Lycopia dezanchei* can ever have. The difference in preservation between *Chinlea* and *Lycopia* makes a detailed comparison impossible. *Ferganodendron* Dobruskina is a subarborescent plant with a thick stem (200–300 mm) and small leaf scars. The leaves are more widely spaced, but more common than in *Pleuromeia*, and found only on the more distal part of the plant; in *Lycopia dezanchei* they are up to 150 mm long and cover the entire stem. *Cyclomeia* White, 1981 differs from *Lycopia dezanchei* because of an only slightly lobed rhizophore and monoecious strobili with elongated cone scales (Cantrill and Webb 1998, p. 190, considered that *Cyclomeia* was a *nomen nudum* because it lacks a species assignment). *Pleurocaulis* Cantrill and Webb, 1998 differs from *Lycopia*

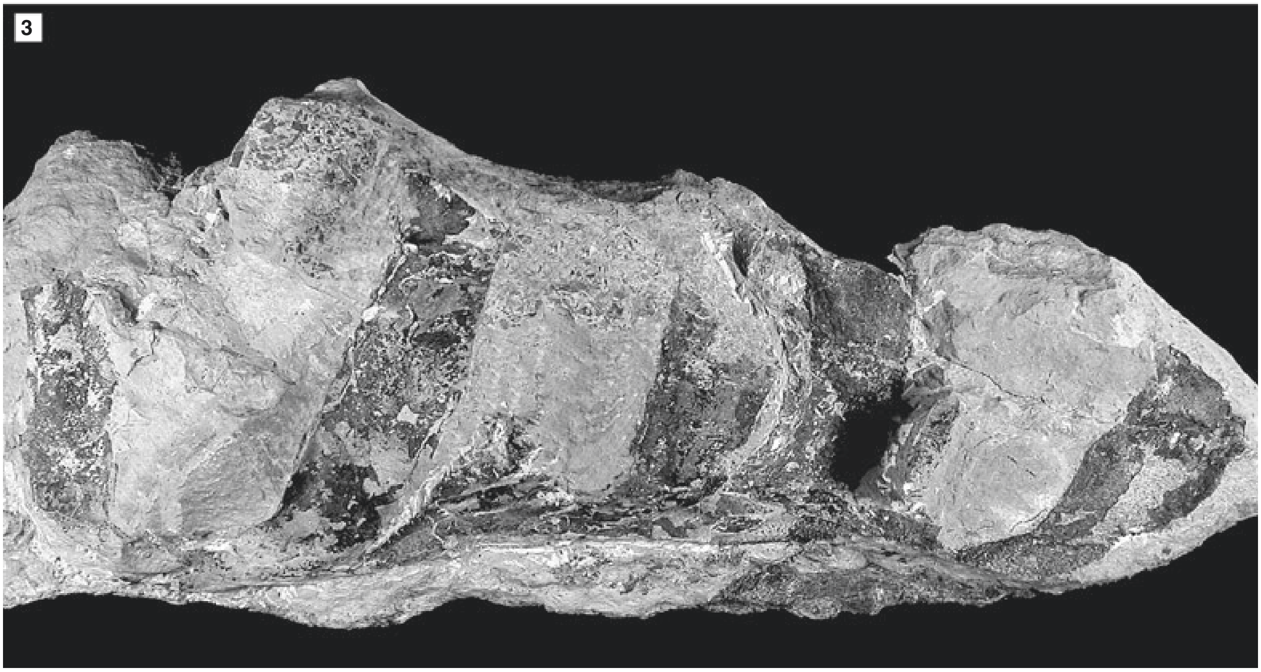
EXPLANATION OF PLATE 6

Fig. 1. *Lepacyclotes bechstaedtii* sp. nov. Quadrilobate corm. (PAL1157); ×1.

Fig. 2. *Lycopia dezanchei* gen. et sp. nov. Paratype. Detail of stem fragment arising from the rhizome (PAL1262), ×1.

Fig. 3. *Lycopia dezanchei* gen. et sp. nov. Paratype. Rhizome (PAL1262), ×0.4.





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dezanchei because of the circular to oval leaf scars. The different preservation mode (petrified or internal casts against compressions) makes more comparison difficult. *Isoetodendron strata* Bock, 1969 differs from *Lycopia dezanchei* because of the groups of megaspores attributed to *Triletes isoetodendron* Bock, 1969, which were found on the stem surface (Bock 1969, pp. 51–52). *Takhtajanodoxa mirabilis* Snigirevskaya, 1980 differs from *Lycopia dezanchei* in its limited height (up to 400 mm against at least 1.5 m). Both species differ from *Lycopia dezanchei* because of the lack of information regarding the leaves and the megaspores found attached to the stem.

Seward (1931, p. 302) mentioned some Triassic Lycopodiales interpreted as survivals from the Palaeozoic lycophytes, namely *Caulopteris tessellata* Schimper and Mougeot, 1844 (p. 64, pl. 29), *Lesangeana* Mougeot, 1849 and *Lepidostrobus palaeotriassicus* Frentzen, 1914. The latter is in all probability a coniferous male cone (Grauvogel-Stamm 1978, p. 125). Seward also mentioned *Poecilitostachys* Fliche, 1910, a large cone, 'probably lycopodiaceous and allied to the cones (*Lepidostrobus*) of the older arborescent lycopods' (Seward 1931, p. 303). Blanckenhorn (1886, p. 132) figured '?*Thamnopteris vogesiaca* Schimper' and '*Sigillaria oculina* n. sp.' (the latter moved by Potonié (1904, p. 15) to *Pleuromeia*, with which Grauvogel-Stamm (1978, p. 23) agreed), two stem fragments with leaf scars that are much further apart than in *Lycopia dezanchei*; and no other information about reproductive organs and root system is available for comparison. Blanckenhorn (1886, p. 146) also discussed the genus *Lesangeana* Mougeot, 1849, considering it positioned between lycophytes, ferns and cycads. According to him, the stem (100 mm in diameter and 40 mm high) is covered by helically arranged leaf scars with a ring of vascular bundles (Blanckenhorn 1886, p. 146). Whorls of leaves which are fused at their base arise from the leaf scars (Mougeot 1849). *Lesangeana hasselotii* Mougeot, 1849 differs from *Lycopia dezanchei* because of the arrangement of the leaf scars (separated against closely inserted in our material) and the whorls of the '*Yuccites vogesiacus*'-type (today *Pelourdea vogesiaca* (Schimper and Mougeot, 1844) Seward, 1917) not present in *Lycopia dezanchei*. The Carboniferous genus *Oxroadia* Alvin (1965) is also characterized by dichotomously branched stems without distinct leaf cushions; this genus was, however, much smaller than our species (stems only 2.5–6.5 mm in diameter).

Comparison with extant Lycophyta. When comparing *Lycopia dezanchei* with the three extant orders in the Lycophyta, it is clear that both the Selaginellales and Isoetales appear to be distinct, especially in the structure of their root system (rhizophores in the Selaginellales and a corm in the Isoetales) and the presence of ligulate leaves. The Lycopodiales is the only extant order that shows comparable features in the root system, and does not have ligulate leaves. Living Lycopodiales have a creeping stem with rootlets, giving off upright branches exactly in the same way as in *Lycopia dezanchei*. The main difference with the extant Lycopodiales is that these plants are small herbaceous plants without any secondary growth in root and branch systems. We have not been able to observe anatomical stem and root details in *Lycopia dezanchei,* but the size of these fossils implies the presence of some sort of secondary growth. As we have not yet been able to extract spores from the strobili associated with *L. dezanchei* (see below), we cannot prove that these are homosporous as the extant Lycopodiales and, therefore, we cannot attribute *Lycopia* to this extant order.

Distribution. Lycopia dezanchei has been found in the Upper Anisian (middle–upper Pelsonian Regional Stage) of Kühwiesenkopf/Monte Prà della Vacca.

Associated strobili

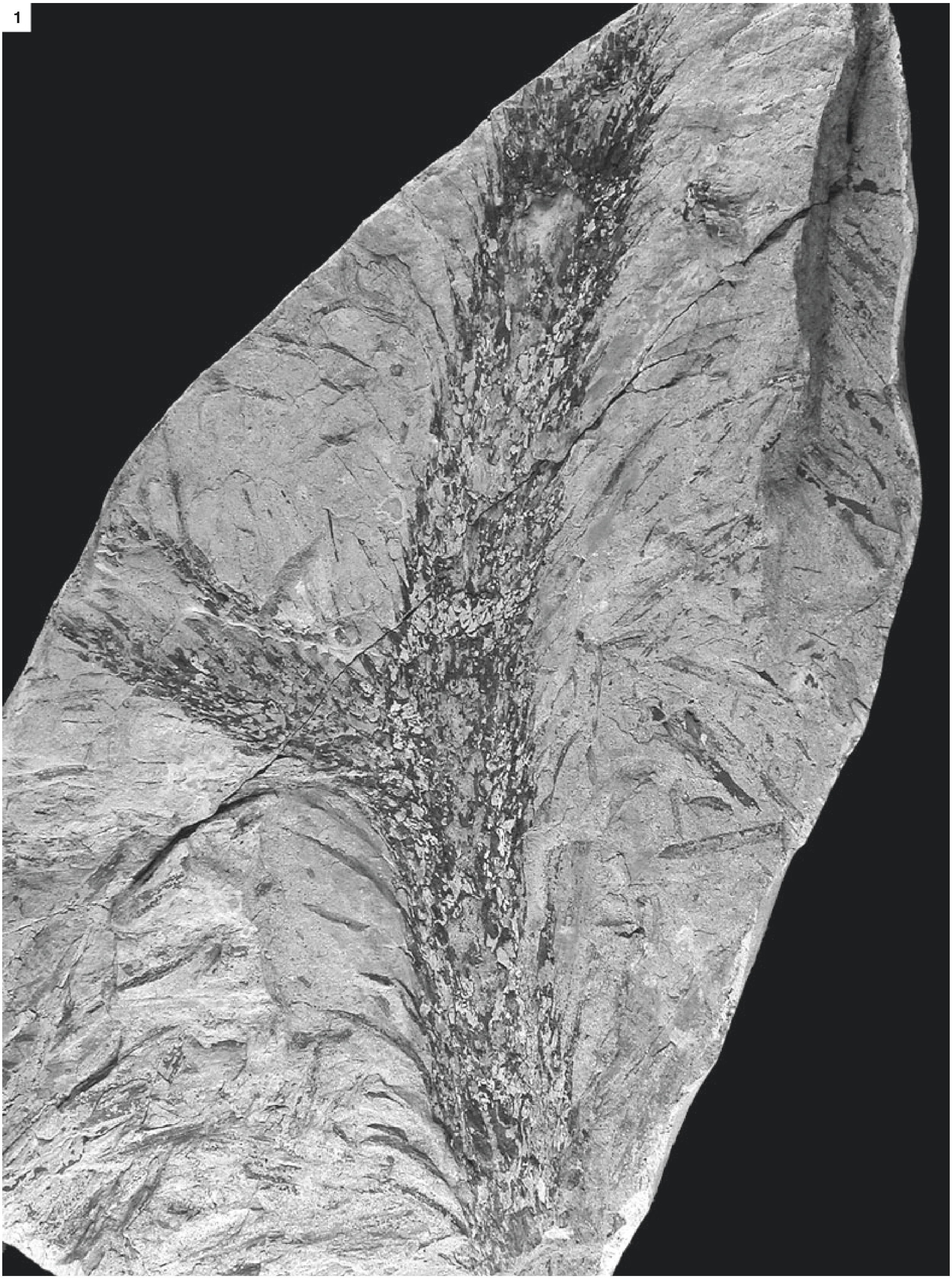
Several strobili have been found in association with the material, although never in organic connection (e.g. PAL1171, PAL1193, PAL 1197, PAL1211, Text-fig. 1B). They are up to 155 mm long and 55 mm wide (e.g. PAL1171, Text-fig. 1A). Spatiolate sporophylls arise helically from an axis (8–16 mm wide). The basis of the sporophylls is up to 9 mm wide, with a long middle part (3.0–4.5 mm wide) and terminates in a pointed apex. Unfortunately, no micro- or megaspores have been extracted. These strobili might represent the fertile material of *Lycopia dezanchei* but this is not certain and they are consequently not included in the species.

Comparison with some other Triassic lycopsid strobili. The cones found attributed to *Pleuromeia* differ from the cones assigned to *Lycopia dezanchei* because of the ovate form of their sporophylls, while the cones assigned to *Tomiostrobus* Neuburg (*Skilliostrobus* Ash) are distinguished because of the distal lobe of the sporophylls and the peduculate structure of the cone. Retallack (1997, p. 503) emended the diagnosis of *Tomiostrobus* in order to extend it to entire plants. He transferred *Skilliostrobus australis* Ash, 1979 to *Tomiostrobus* as well as *Takhtajanodoxa mirabilis* Snigirevskaya, 1980, *Selaginellites polaris* Lundblad, 1948 and *Pleuromeia taimyrica* Sadovnikov, 1982. However, according to Article 11.7 in the International Code of Botanical Nomenclature (ICBN) (McNeill *et al.* 2007), this cannot be carried out. A morphogenus remains a morphogenus and cannot become a natural genus (see example 28 in the ICBN, directly after Art. 11.7). We still consider the genus *Tomiostrobus* a morphogenus for lycophyte cones.

EXPLANATION OF PLATE 7

Fig. 1. *Lycopia dezanchei* gen. et sp. nov. Holotype. Bifurcating apical stem fragment. (PAL1264), ×0.5.

1



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Cyclostrobus Helby and Martin, 1965, is characterized by cuneate sporophylls with *in situ Banksisporites* Dettmann megaspores and *Aratrisporites* Leschik microspores. Unfortunately, the lack of *in situ* spores in the strobili attributed to *Lycopia dezanchei* makes a detailed comparison between the two strobili impossible. Our strobili are, however, much higher than broad and the sporophylls are lanceolate in shape. In *Lycostrobus* Nathorst, 1908, the sporophylls show keeled, upturned apices (against the spateolate sporophylls in *Lycopia dezanchei*) with *Nathorstisporites* Jung, 1958 megaspores and *Aratrisporites* microspores.

ECOLOGICAL CONSIDERATIONS

The plant fossils from Kühwiesenkopf are probably an accumulation of remains originally growing in different environments, in the near basinal successions in front of a continent or island (see also Broglio Loriga *et al.* 2002; Kustatscher *et al.* 2010). The lycophyte taxa in the Kühwiesenkopf flora probably occupied different habitats as well.

Selaginellites leonardii sp. nov. was a small, moss-like, herbaceous lycophyte with a thin cuticle, similar to most extant forms. This indicates a protected environment without humidity stress, such as the understorey of woodland or near water.

The habitat of extant species of *Isoetes* in North America varies from ephemeral terrestrial to evergreen aquatic (Taylor and Hickey 1992, p. 616); perhaps they are indicative of wetland environments or fine tidal flats (Tryon and Tryon 1982; Skog *et al.* 1992, p. 159). The Cretaceous and Tertiary dispersed megaspore genera such as *Minerisporites* were often found ‘in facies, which imply a wetland habitat for the parent plants’ (Collinson 1991, p. 126 and references therein). Fossil *Isoetes* or *Isoetites* species seem to have grown in ephemeral ponds during humid seasons and became dormant by disarticulation during periods of stress because of moisture limitation (Wang 1991, 1996, p. 134). The presence of a thick cuticle with stomata protected by papillae suggests that *Isoetites brandneri* grew either during an arid climate phase, the papillae thus being a climatic adaptation, or was living in environmental stressed conditions. Quantitative palynomorph analyses exclude the first hypothesis (Kustatscher 2004; Kustatscher *et al.* 2010). Thus, the heavy protection of the stomata was probably related to the environment the plant grew in, for example, environments influenced by saline winds as in coast areas. Sometimes these plants could also grow more inland, such as near ponds, but they were probably never aquatic plants.

Lepacyclotes (=*Annalepis*) has been considered a ‘small type of aquatic herb’ growing in land swamps near the coast, in shallow water or in wet soil (Meng 1996, p. 342) or the ‘marginal area of the nearshore together with *Pleuromeia* shrubs’ (Meng *et al.* 2000, p. 73). The boat-like shape of the sporophylls was interpreted as a ‘drift ecological character in water’ (Meng *et al.* 2000, p. 73). The midrib of the leaves was considered a result of the collapsed inner spaces, the leaves thus being flat and spatulate, adapted to float on the water surface (Brown 1958, p. 361). Just like *Isoetites brandneri*, *Lepacyclotes bechstaedtii* was probably never submerged in water. Its thick cuticle, protected by papillae, indicates an adaptation to a restrictive environment such as the coast. The reduced midrib of the sporophylls as well as the root system and the general growing pattern (the surface for drifting would be too reduced, in comparison with the general dimension of the plant) indicate that the plant was not growing within the tidal flat and, thus, drifted occasionally on the water.

Ecological considerations of *Lycopia dezanchei* are more difficult. The most similar pseudoarborescent (subarborescent) Triassic lycophyte is *Pleuromeia*. *Pleuromeia* is considered an opportunistic pioneer plant living often in monospecific associations (Pigg 1992, p. 608; Grauvogel-Stamm and Lugardon 2004, p. 631), especially in coastal regions (Mägdefrau 1931, p. 132) or in brackish or mangrove-type coastal environments, or marginally on deltas (e.g. Krassilov and Zakharov 1975, p. 231; Retallack 1975, p. 4; Sun *et al.* 1990, p. 317). Because of its fleshy stem and leaves (Mägdefrau 1931; Sun *et al.* 1990, p. 317), it has also been considered a ‘typical xerophyte’. The similarities in the ‘stem’ morphology, the thick cuticle and well-protected stomata may suggest a close environmental affinity between these two genera. Thus, *Lycopia* might have grown in a coastal environment.

EXPLANATION OF PLATE 8

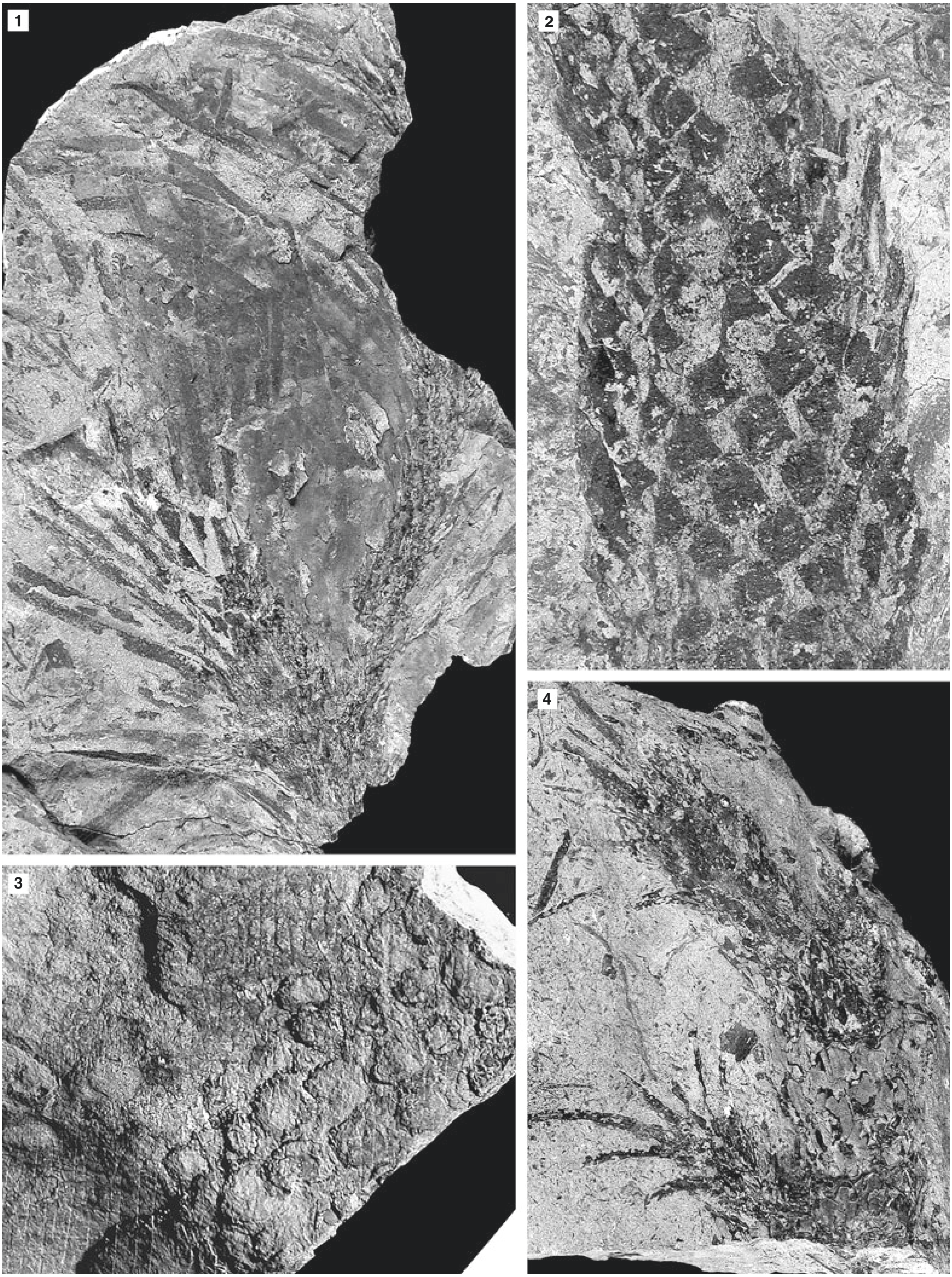
Fig. 1. *Lycopia dezanchei* gen. et sp. nov. Bifurcate stem fragment with long leaves (PAL1192/KÜH1268), ×0.5.

Fig. 2. *Lycopia dezanchei* gen. et sp. nov. Bases of leaf attachment with rhomboidal leaf scars on stem fragment (PAL1255/KÜH1229), ×1.

Fig. 3. *Lycopia dezanchei* gen. et sp. nov. Almost circular leaf scars on an older stem fragment (PAL1190), ×1.

Fig. 4. *Lycopia dezanchei* gen. et sp. nov. Young bifurcate apical stem fragment. (PAL1226), ×1.

PLATE 8



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EVOLUTIONARY CONSIDERATIONS

The discovery of several new species and one new genus of lycophytes in the lower Middle Triassic of the Southern Alps shed some interesting light on the evolution of this group. The Triassic was a time of important radiation and change in several key morphological characters of the Lycophytes.

It seems clear that the lycopod reductional series (*Sigillaria* => *Pleuromeia* => *Nathorstiana* => *Isoetes*) suggested by Potonié (1902) is not valid. This is supported by the discovery of new data on the lycopods, such as developmental stages of the embryos (Taylor *et al.* 2009, p. 326). Additionally, *Isoetes*-like plants have been discovered in the Triassic, well before the appearance of the Cretaceous genus *Nathorstiana*, and almost coeval with (or just slightly before) *Pleuromeia* in several upper Buntsandstein floras (Anisian, lower Middle Triassic) in Europe and in Australia during the Early Triassic (Retallack 1997). Thus, Retallack (1997, pp. 515–516) suggested that it 'seems more likely that subarborescent Triassic lycopsids evolved from herbaceous *Isoetes*, and these from subarborescent Palaeozoic lycopsids such as *Chaloneria* (Pigg and Rothwell 1983*a*, *b*), rather than from arborescent Palaeozoic lycopsids such as *Sigillaria* (Mägdefrau 1931, p. 133)'. Although *Isoetes beestonii* appears very early after the Permian/Triassic boundary, this does not necessarily mean that it is the linking group between the Palaeozoic and Mesozoic arborescent to subarborescent lycophytes.

Meng (1998, p. 768; 2000, p. 160; discussed also by Grauvogel-Stamm and Lugardon 2001, p. 143) proposed *Lepacyclotes* (=*Annalepis*) to be ancestral to *Isoetes*, based on the similarities between *Annalepis* (e.g. *A. brevicystis*) and *Isoetes*. The discovery of both genera in the Anisian flora of Kühwiesenkopf and the presence of *Isoetes beestonii* in the lowermost Lower Triassic (Retallack 1997) makes this proposal highly improbable. Grauvogel-Stamm and Lugardon (2001, p. 142) considered *Pleuromeia* a plant with an elongate stem covered by sterile leaves and a terminal cone. According to these authors, the fact that many or all of the leaves are fertile in *Isoetes* might be because of the loss of sterile leaves (Pigg 2001) or because of an 'evolutionary reduction and transfer of the reproductive function of the vegetative leaves, as in the gymnosperms and the angiosperms' (Grauvogel-Stamm and Lugardon 2001, p. 142). In our case, the stem of *Lepacyclotes* is reduced and sterile leaves have been observed at the centre of the circle of sporophylls, similarly to *Isoetites*. This further emphasizes the close relationship between *Isoetites* and *Lepacyclotes*, but is not in accordance with the reduction series of Meng (1998).

Pigg (1992, p. 608) and Rothwell and Erwin (1985) demonstrated that the isoetaleans cannot be considered as a distinct lineage; probably they are a more complex group of heterosporous lycopsids, possibly a rhizomorphic clade. Meng (2000, p. 160; Meng *et al.* 2000, p. 76) proposed to unify *Pleuromeia* and *Nathorstiana* into the family Pleuromeiaceae, while *Lepacyclotes/Annalepis*, *Skilliostrobus*, *Isoetites* and perhaps *Tomiostrobus*, as junior synonym of *Annalepis*, belonged to the family Isoetaceae. The close resemblance in growing pattern, leaf morphology, and *in situ* micro- and megaspores between *Lepacyclotes* and *Isoetites* suggests in any case a close relationship between the two fossil lycopsid genera *Lepacyclotes (Annalepis)* and *Isoetites*. The systematic position of *Lycopia*, on the other hand, is still not completely clear. The growing pattern would suggest it to be some sort of giant *Lycopodium* possibly with secondary growth. Unfortunately, its systematic attribution cannot yet be solved, as no strobilus with *in situ* spores can be assigned to the vegetative structure.

Thus, it would seem that subarborescent lycophyte genera attributed to different orders crossed the Permian/Triassic boundary or evolved shortly after that. Even other herbaceous lycophyte genera, such as *Isoetites* and *Lepacyclotes*, seem to be characterized by a short stem in some cases. The complete reduction of this stem giving origin to the recent genus *Isoetes* probably took place later on. This evolutionary picture will, however, not be completed without more lycophyte remains from the Triassic.

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