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Carbon (δ13C) isotope variations indicate climate shifts and reflect plant habitats in the Middle Triassic (Anisian, Pelsonian) succession at Kühwiesenkopf/Monte Prà della Vacca (Dolomites, Northeast Italy)

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ABSTRACT

We report carbon (δ13C) isotope records from the Middle Triassic (Anisian, Pelsonian) Kühwiesenkopf/Monte Prà della Vacca succession in the Dolomites of northeast Italy, to infer palaeoclimate and palaeoenvironmental changes. This interval comprises hemipelagic carbonate-terrigenous facies deposited in a marginal marine setting and includes a well-known allochthonous plant fossil assemblage at one horizon. We obtained two datasets: (1) carbon isotope records of bulk samples (dispersed organic carbon), which comprise a mixture of terrestrial and marine sources, for the whole 200 m thick succession, and (2) taxon-specific records for the plant bed at a single horizon. Analyses of the dispersed organic matter reveal several significant positive excursions through the Kühwiesenkopf/Monte Prà della Vacca section, some of which may be related to local conditions, whereas others match climate shifts recorded elsewhere in the Tethys Realm. For taxon-specific studies of the plant bed, isotopic values show a correspondence with the spectrum of habitats inferred to have been occupied by the plants. Species inferred to have grown in habitats along environmental gradients are characterized by wide isotopic ranges, whereas those restricted to narrow environmental conditions show a low isotopic variability. Our study highlights how organic carbon isotopic analyses on well-preserved plant remains are excellent tools to define the palaeoecology of plants and to improve our palaeoenvironmental reconstructions of the past.

1. Introduction

During the Triassic, most of the land masses were merged together as the supercontinent Pangea and concentrated at mid- to low latitudes (e. g., Ziegler et al., 1983; Fig. 1A). The Triassic greenhouse conditions were now and then interrupted by humid episodes (e.g., Hallam, 1985; Simms and Ruffell, 1989, 1990; Parrish, 1993; Mutti and Weissert, 1995; Simms et al., 1995; Ahlberg et al., 2002, 2003; Galfetti et al., 2007a, 2007b; Berra et al., 2010; Hochuli and Vigran, 2010; Kustatscher et al., 2010a; Preto et al., 2010; Stefani et al., 2010; Dal Corso et al., 2012, 2015, 2018; Fig. 1C) and the paleogeographic configuration (Fig. 1A) favored the establishment of a megamonsoonal regime (e.g., Ziegler et al., 1983; Parrish, 1993; Nordt et al., 2015).

In this study, we focus on the Middle Triassic (Anisian) successions of the Dolomites of northeast Italy, which were located in the north-western margin of the Tethys and composed of several islands surrounded by a tropical sea (e.g., Brack and Kustatscher, 2013; Petti et al., 2013; Fig. 1A). In this region, at least two humid episodes, one in the Bithynian–Pelsonian substage and one in the Illyrian substage (e.g., Preto et al., 2010; Stefani et al., 2010; Li et al., 2018; Fig. 1C), were recorded in several localities (e.g., Brugman, 1986; Breda et al., 2009; Preto et al., 2010; Stefani et al., 2010; Kustatscher et al., 2010a), and caused changes in the terrestrial and marine biota (e.g., Preto et al., 2010; Stefani et al., 2010; Li et al., 2018; Forte et al., 2022).

The Pelsonian (Anisian, Middle Triassic) fossil assemblage of Kühwiesenkopf/Monte Prà della Vacca (Dolomites, NE Italy; Fig. 1B) has been well-known since the 19th century and represents one of the best-known Anisian Fossil-Lagerstätten (e.g., Bechstädt and Brandner, 1970; Senowbari-Daryan et al., 1993; Broglio-Loriga et al., 2002; Kustatscher et al., 2006, 2010a, 2010b; Kustatscher and Roghi, 2006; Van

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Konijnenburg-van Cittert et al., 2006). In addition to several marine fossils, a very rich and well-preserved terrestrial flora is present (e.g., Van Konijnenburg-van Cittert et al., 2006; Kustatscher et al., 2006, 2007, 2010a, 2010b, 2019; Forte et al., 2021, 2022). Here we present a taxon-specific carbon stable isotopic investigation inspired by several integrated studies of palaeobotany, geochemistry and palaeoecology (e. g., Nguyen Tu et al., 1999, 2002; Aucourt et al., 2008).

Stable isotopic analyses of organic carbon from plant fossils are an important tool to investigate the composition of the palaeoatmosphere and, consequently, climate changes (e.g., Faure et al., 1995; Kürschner et al., 1996; Faure and Cole, 1999; Beerling and Royer, 2002; Berner, 2004; Peters-Kottig et al., 2006; Montañez, 2016; Montañez and Poulsen, 2013; Montañez et al., 2007; Tappert et al., 2013; Franks et al., 2014; McElwain et al., 2016). This is because plants, as primary producers, record the isotopic composition and concentration of atmospheric CO_2 in the isotopic composition of their tissues ($\delta^{13}C_{plant}$). The fractionation of carbon from atmospheric CO_2 takes place through several steps during photosynthesis (O'Leary, 1981). The $\delta^{13}C_{plant}$ is influenced by several factors, such as the isotopic composition of the atmospheric CO_2 ($\delta^{13}C_{atm}$; e.g., Farquhar, 1980; Farquhar and Lloyd, 1993; Farquhar et al., 1989; Arens et al., 2000; Tappert et al., 2013), atmospheric pCO_2 (e.g., Schubert and Jahren, 2012, 2015; Cui and Schubert, 2016), photosynthetic pathway (e.g., Farquhar, 1980; Farquhar et al., 1982, 1989; Arens et al., 2000; Bender, 1971; Sternberg et al., 1984), and environmental stresses (e.g., Bocherens et al., 1993; Nguyen Tu et al., 1999, 2002; Dawson et al., 2002; Aucourt et al., 2008; Diefendorf et al., 2010; Lomax et al., 2012). Fractionation takes place during biosynthesis, which results in different isotopic compositions of the different plant tissues (e.g., O'Leary, 1981; Craig, 1953; Leawitt and Long, 1982, 1986; Guehl et al., 1998; Beerling et al., 2002; Gröcke, 2002; Hobbie et al., 2002; Badeck et al., 2005; Cernusak et al., 2009; Dal Corso et al., 2011, 2017; Royer and Hren, 2017). Each of these factors

triggers a decrease or an increase of the $\delta^{13}C_{plant}$ (e.g., Farquhar, 1980; Farquhar et al., 1989; Farquhar and Lloyd, 1993; Cernusak and Marshall, 2001).

Most studies lump together results from different taxa and different parts of fossil plants (e.g., Basu et al., 2015, 2019; Nordt et al., 2016; Dong et al., 2021). However, an increasing number of studies show the importance of taxon-specific carbon stable isotopic analyses also on fossil plants, which may allow to decipher the variability in fractionation of different plant groups (e.g., Leawitt and Newberry, 1992; Ehleringer and Cerling, 1995; Arens et al., 2000; Lo Duca and Pratt, 2002; Peters-Kottig et al., 2006; Aucourt et al., 2008; Cernusak et al., 2009; Dal Corso et al., 2011, 2017).

The aims of this study are (1) to define the intraspecific and intrageneric isotopic variability of organic carbon (e.g., Leawitt and Newberry, 1992) in the taxa from the Kühwiesenkopf/Monte Prà della Vacca flora, in order to define their palaeoecological adaptations, and (2) to identify the humid episodes of the Anisian (e.g., Brugman, 1986; Haas et al., 2012; Kustatscher et al., 2010a; Preto et al., 2010; Stefani et al., 2010; Li et al., 2018) based on carbon isotopic shifts of the organic matter dispersed in the sediment of the Kühwiesenkopf/Monte Prà della Vacca section.

2. Geological setting

The Kühwiesenkopf/Monte Prà della Vacca succession is known since the 19th century for its fossil fauna (e.g., Loretz, 1875; Mojsisovics, 1879, 1882; Bittner, 1890; Pia, 1937). Plant fossils were first published in the 1970s (Bechstädt and Brandner, 1970), and in 1999, a rich fossil plant horizon was discovered (e.g., Broglio-Loriga et al., 2002; Posenato et al., 2004; Kustatscher and Roghi, 2006; Van Konijnenburg-van Cittert et al., 2006; Kustatscher et al., 2006, 2007, 2009, 2010a, 2010b, 2019; Tintori et al., 2001, 2016). The succession includes hemipelagic
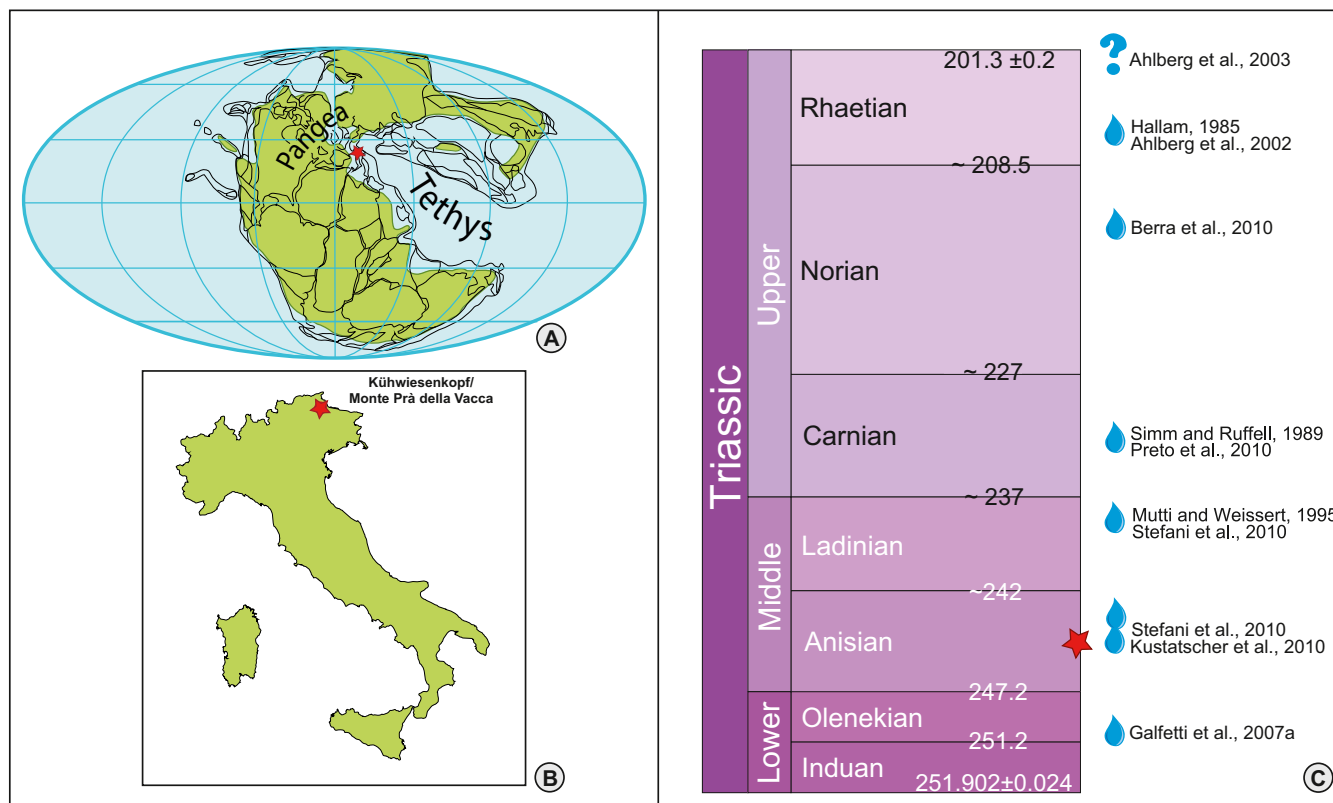

Fig. 1. A) Paleogeographic map of Middle Triassic Pangea (modified after Scotese, 2014); B) Location of Kühwiesenkopf/Monte Prà della Vacca; C) Humid episodes (drops) recorded during the Triassic. Red stars indicate the geographic and chronostratigraphic position of Kühwiesenkopf/Monte Prà della Vacca (modified after Preto et al., 2010). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

carbonate-terrigenous facies of marginal marine environment (e.g., De Zanche et al., 1993; Delfrati et al., 2000; Broglio-Loriga et al., 2002; Tintori et al., 2001; Fig. 2A). The stratigraphic section of Kühwiesenkopf/Monte Prà della Vacca is 200 m thick and crops out at the northeastern margin of the Dolomites (NE Italy; Fig. 1B). The fossil assemblage includes many marine fossils, such as fishes, bivalves, brachiopods and ammonoids (e.g., Broglio-Loriga et al., 2002; Posenato et al., 2004; Tintori et al., 2001, 2016; Fig. 2A), the skeleton of the reptile *Megachirella wachtleri* (Renesto and Posenato, 2002; Renesto and Bernardi, 2014; Simões et al., 2018a, 2018b; Fig. 2A), and very abundant terrestrial plant fossils (e.g., Van Konijnenburg-van Cittert et al., 2006; Kustatscher and Roghi, 2006; Kustatscher et al., 2006, 2007, 2010a, 2010b, 2019; Forte et al., 2021, 2022). The plant level, ca. 1 m thick, crops out at about 75 m from the base of the section and belongs to the Dont Formation, dated middle–late Pelsonian (Anisian; Fig. 2A) based on ammonoids and foraminifera and palynomorphs (Fugagnoli and Posenato, 2004; Kustatscher and Roghi, 2006; Kustatscher et al., 2006, 2010a, 2010b; Gianolla et al., 1998). It represents a rapid burial event produced by submarine flows consequent to heavy storm events (e.g., Tintori et al., 2001; Broglio-Loriga et al., 2002; Van Konijnenburg-van Cittert et al., 2006).

3. Materials and methods

More than 1200 rock slabs with plant remains were collected from the Kühwiesenkopf/Monte Prà della Vacca succession. Impression and compression fossils with preserved organic material include leaves, shoots, roots, stems, dispersed seeds and female and male fructifications belonging to at least 35 taxa of lycophytes, sphenophytes, ferns, seed ferns, cycadophytes and conifers. The excellent preservation allowed to extract cuticles from most of the specimens. Strobili, foliate stems and rhizomes were attributed to at least four lycophyte taxa (e.g., *Lycopia dezanchei*, *Isoetites brandneri*; Fig. 3A–B) of herbaceous and sub-arborescent forms (e.g., Kustatscher, 2004; Kustatscher et al., 2010a, 2010b; Kustatscher and Roghi, 2006). Sphenophytes are the least abundant group of the flora, represented by stem fragments and strobili (e.g., Kustatscher et al., 2007, 2010a). Ferns are instead the most diverse group (Van Konijnenburg-van Cittert et al., 2006), including at least eleven species grouped in eight genera (e.g., *Gordonopteris*, *Neuropteridium*, *Scolopendrites*; Fig. 3C–G). Frond fragments and female reproductive organs are attributed to four species of seed ferns (Kustatscher et al., 2007), among which *Scytophyllum bergeri* had different sun and shade leaves (Fig. 3H, I). The fertile organ *Lugardonia paradoxa* could not be assigned confidently to any botanical group. However, based on spores or prepollen, it may belong to ferns or seed ferns (Van Konijnenburg-van Cittert et al., 2006; Kustatscher et al., 2009; Fig. 3J). Cycadophytes are well represented in the flora and were sub-arboreous plants with big entire (*Bjuvia* cf. *dolomitica*; Fig. 3K) or small entire-leaves (*Taeniopteris* spp.; Broglio-Loriga et al., 2002; Kustatscher et al., 2010a). Conifers are diverse and well represented (e.g., Kustatscher, 2004; Forte et al., 2021). The occurrence of large branches suggests the presence of big trees. So far, five taxa have been identified at species level, based on the macromorphology and epidermal features (Forte et al., 2021), i.e. *Pelourdea vogesiaca*, *Albertia* cf. *latifolia* (Fig. 3M), *Voltzia recubariensis* (Fig. 3O), *V. heterophylla* (Fig. 3L), *V. walchiaeformis* (Fig. 3N), and *V. edithae* (Fig. 3P). Dispersed conifer cones are also present (Fig. 3Q). Amber droplets occur both in association with *Voltzia recubariensis* and dispersed in the sediment (Forte et al., 2022). Six conifer specimens were assigned to *Voltzia* sp., because their degree of preservation did not allow an attribution at species level (Forte et al., 2021).

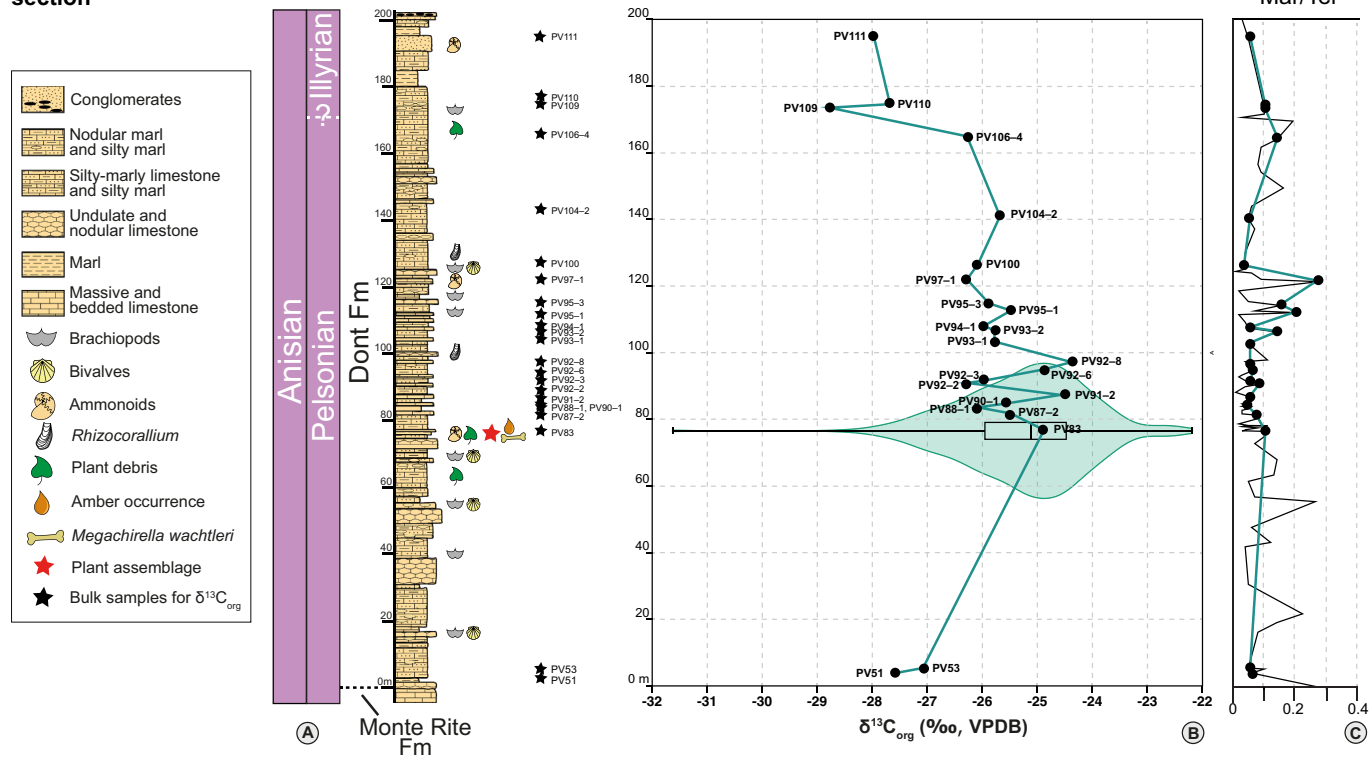The macrofossils are stored at the Museum of Nature South Tyrol in

Fig. 2. A) Stratigraphic section of Kühwiesenkopf/Monte Prà della Vacca (modified after Forte et al., 2021); B) Isotopic composition of the dispersed organic matter along the section, isotopic range of the organic carbon composition of the flora (violin-box plot); C) Marine versus terrestrial dispersed organic matter abundance along the of Kühwiesenkopf/Monte Prà della Vacca section (from Kustatscher et al., 2010a). The grey rectangles highlight the correspondences between the positive shift of the δ13Corg and the increase in terrestrial matter input recorded in the marine sediments.
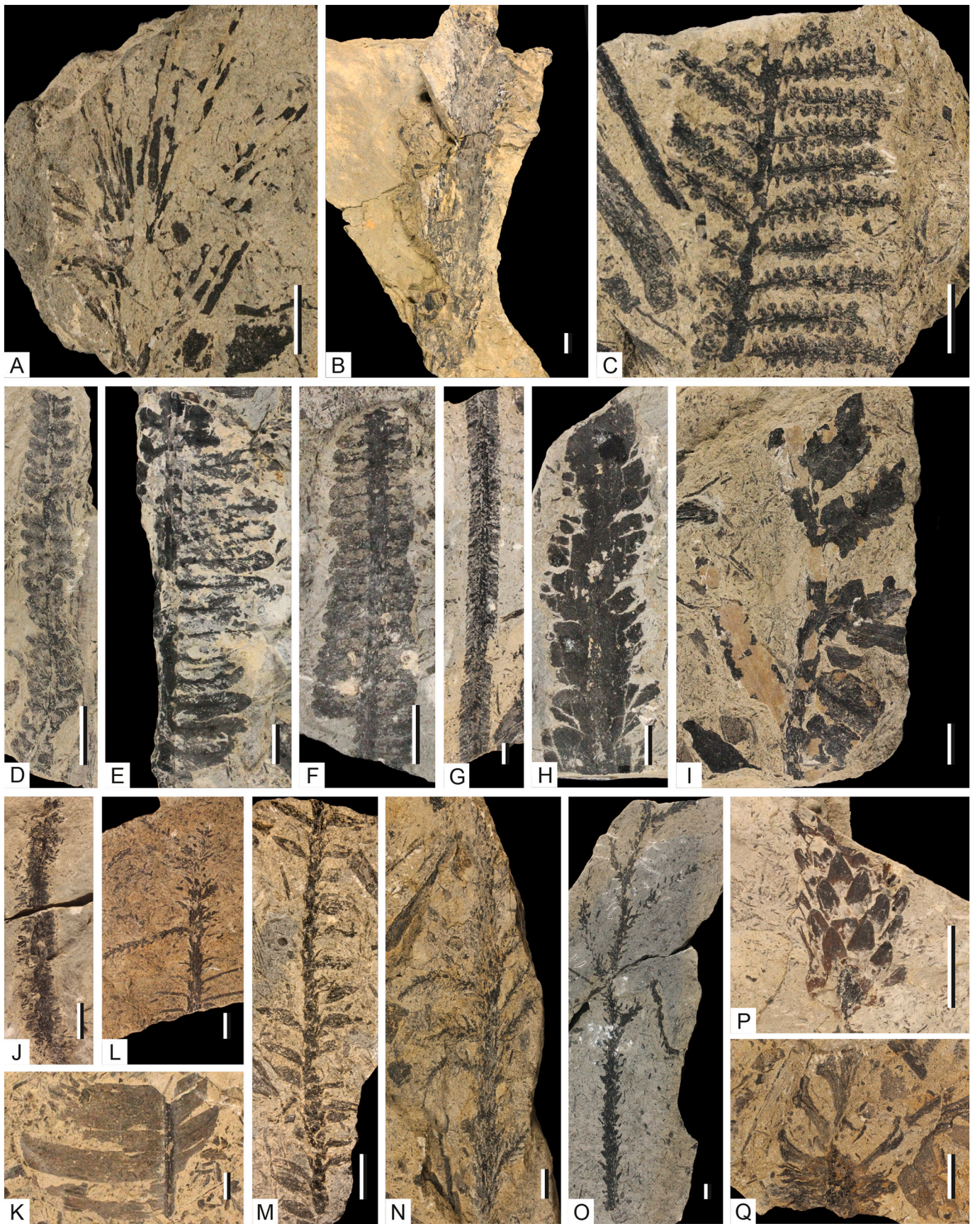
(caption on next page)

Fig. 3. Macroplant remains and amber from the Anisian Kühwiesenkopf/Monte Prà della Vacca flora. A) Plant fragment of *Isoetites brandneri* (NMS PAL 1122). B) Stem fragment of *Lycopia dezanchei* (holotype, NMS PAL 1259). C) Frond fragment of *Gordonopteris lorigae* (NMS PAL 267). D) Frond fragment of *Neuropteridium elegans* (NMS PAL 344). E) Fragment of *Neuropteridium voltzii* frond (NMS PAL 365). F) Frond fragment of *Scolopendrites grauvogelii* (NMS PAL 388). G) Frond fragment of *Scolopendrites scolopendroides* (NMS PAL 409). H) Fragment of *Scytophyllum bergeri* shade leaf (NMS PAL 485). I) Large frond fragment of *Scytophyllum bergeri* with sun leaves (NMS PAL 486). J) Reproductive organ of *Lugardonia paradoxa* (NMS PAL 1105). K) Leaf fragment of *Bjuvia* cf. *dolomitica* (NMS PAL 1171). L) Heterophylly in a shoot fragment of *Voltzia heterophylla* (NMS PAL 751). M) Shoot fragment of *Albertia* cf. *latifolia* (NMS PAL 581). N) Branch fragment of *Voltzia walchiaeformis* (NMS PAL 660). O) Branch fragment of *Voltzia recubariensis* (NMS PAL 2144). P) Stem fragment of *Voltzia edithae* (NMS PAL 658). Q) Dispersed female conifer cone with bilobed bracts (NMS PAL 772). Scale bar = 1 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Bozen/Bolzano and labelled with the prefix "NMS PAL", followed by a number. All specimens were photographed with a Canon EOS D550 digital camera. The calculation of marine/terrestrial sources has been carried out based on the palynomorphs and full methods and data are reported in Kustatscher et al. (2010a). The marine component is given by algal cysts, acritarchs, foraminifera and scolecodont remains whereas the terrestrial component is given by spores, pollen and fungal hyphen among the sporomorphs (see also Kustatscher and Roghi, 2006; Kustatscher et al., 2010a; Fig. 2C).

Stable carbon isotope analyses were carried out on 24 bulk rock samples collected along the Kühwiesenkopf/Monte Prà della Vacca section (Fig. 2A). All the rock samples were crushed and powdered with a mortar grinder at the laboratory of the Museum of Nature of South Tyrol in Bozen/Bolzano. The powders were then treated with HCl 10% in polyethylene Falcon tubes in order to remove carbonates, rinsed with deionized water until neutrality and dried at 60 °C overnight. About 5 mg of each powder were weighted in tin capsules, which were subsequently analyzed.

Carbon stable isotope analyses were also carried out on 424 samples of cuticles, sporangia and coalified fragments of plant fossils. All the taxa present in the palaeobotanical collection were checked and the samples were collected from the best preserved specimens. Each selected plant remain was sampled at least twice or three times from different parts of the plant (i.e., leaves and axis) in order to capture as much of the individual isotopic variability as possible. All the plant specimens are from the same fossiliferous level, cropping out at about 75 m from the base of the section (Fig. 2A). The organic material was extracted from the fossil surface with a preparation needle. Each sample consisted of ~35 μg weighed in silver cups, etched with 60 μl of HCl 10% and dried overnight on a heating plate at 70 °C to remove carbonate minerals. The silver cups were then wrapped, and analyzed. Both the bulk and plant samples picked from plant fossils were analyzed by a Thermo Flash 2000 Elemental Analyzer connected to a Thermo Delta V Advance Isotope Ratio Mass Spectrometer at the Isotopic Ratio Mass Spectrometry Laboratory of the Department of Geoscience of the University of Padova. The results were normalized with two international standards: CH-6 (−10.449‰ Vienna PeeDee Belemnite, VPDB) and CH-7 (−32.151‰ VPDB). A further internal standard (ZER, a C3 plant sucrose) was run along with the samples for quality control and yielded a reproducibility of 0.16‰ during the period of analyses (standard deviation based on >20 repetitions). For selected pairs of plant taxa, i.e., *Lycopia - Isoetites*, and *Albertia – Voltzia*, the statistical significance of the differences between the isotopic ranges was tested by Wilcoxon-Mann-Whitney non-parametric test, whereas for the comparison between all the main plant groups (i.e., lycophytes, ferns, seed ferns, cycadophytes and conifers), and between different plant parts (i.e., shade - sun leaves of *Scytophyllum bergeri*) the Kruskal-Wallis non-parametric test was used instead. The free software R® (version 3.4.1) was used to perform statistical tests (R Core Team, 2017). Violine/box plots were produced with the free software Past® (Hammer et al., 2001). Further results are reported in the supplementary materials.

4. Results

4.1. $\delta^{13}C_{org}$ of the Kühwiesenkopf/Monte Prà della Vacca section

The $\delta^{13}C_{org}$ values obtained from the dispersed organic matter through the Kühwiesenkopf/Monte Prà della Vacca section range from ca. −28.8‰ to −24.4‰, with an average of 26.1 ± 1.1‰ ($n = 24$, 1 σ; Fig. 2B). In the lower part of the section, the isotopic values of the dispersed organic matter range between −27.6‰ and −27.1‰ (Table 1; Fig. 2B). At 76 m above the base of the section, which approximately coincides with the plant assemblage (Fig. 2B), up to c. 100 m, the isotopic values of the organic matter become heavier, with an average of −25.4 ± 0.6‰ ($n = 11$, 1σ; Table 1; Fig. 2B). Within this interval, two positive and two negative peaks can be distinguished, with an amplitude of 1.5–2‰ (Fig. 2B) each. In the upper part of the section, from c. 100 m from the base to the top of the section, the δ ^{13}C of the dispersed organic matter progressively becomes lighter (−28.8‰; Table 1; Fig. 2B).

4.2. Taxon-specific geochemical analyses from the fossil plant bed

The mean isotopic composition of the Kühwiesenkopf/Monte Prà della Vacca flora is −25.4 ± 1.2‰ ($n = 413$, 1σ; Table 2; Fig. 2B). The δ^{13}C values obtained from the different groups analyzed (i.e. lycophytes, ferns, seed ferns cycadophytes and conifers) range between −31.9‰ and −22.2‰ (Table 2; Fig. 4A). The organic carbon isotopic ranges of spore plants (i.e. lycophyte and ferns) and gymnosperms (seed ferns, cycadophytes and conifers) from Kühwiesenkopf/Monte Prà della Vacca largely overlap (Fig. 4A). These two major plant groups are characterized by similar mean isotopic composition, respectively −25.3 ± 1‰ (n

Table 1

Isotopic values of the dispersed organic carbon recorded along the Kühwiesenkopf/Monte Prà della Vacca section, which are reported in the δ^{13}C curve in Fig. 2.

Sample	Height (metres)	δ^{13}C (‰, VPDB)
PV111	193.85	−28.03
PV110	173.3	−27.71
PV109	172.25	−28.84
PV106–4	163.75	−26.26
PV104–2	140	−25.73
PV100	125.75	−26.10
PV97–1	121.2	−26.31
PV95–3	114.08	−25.89
PV95–1	111.95	−25.55
PV94–1	107.32	−25.97
PV93–2	106.14	−25.76
PV93–1	102.72	−25.84
PV92–8	96.6	−24.43
PV92–6	94.47	−24.87
PV92–3	91.08	−26.02
PV92–2	90.45	−26.34
PV91–2	86.88	−24.61
PV90–1	84.29	−25.57
PV88–1	83.18	−26.10
PV87–2	81.35	−25.50
PV83	76.45	−24.90
PV53	5.7	−27.13
PV51	4.2	−27.63

Table 2
Sample size, isotopic ranges (amplitude, minimum and maximum values), mean isotopic composition and standard deviation of the taxa/groups of Kühwiesenkopf/ Monte Prà della Vacca.

Taxon/group	N samples	Min (‰)	Max (‰)	Range (‰)	Average (‰)	St. Dev. (‰)
All the taxa	**413**	**−31.9**	**−22.2**	**−25.4**	**25.4**	**1.2**
Spore plants	**147**	**−27.6**	**−22.6**	**5**	**−25.3**	**1**
Seed plants	**266**	**−31.9**	**−22.2**	**9.7**	**−25.4**	**1.3**
Lycophytes	**76**	**−27.6**	**−22.6**	**5**	**−25.6**	**1.2**
Lycopia dezanchei	53	−27.6	−22.6	5	−25.7	1.2
Isoetites brandneri	24	−26.9	−22.9	3.7	−25.4	1.1
Ferns	**71**	**−26.3**	**−23.7**	**2.6**	**−24.9**	**0.6**
Gordonopteris lorigae	22	−25.7	−23.7	2.0	−24.7	0.5
Neuropteridium	18	−25.9	−24.5	1.4	−25	0.4
N. elegans	10	−25.9	−24.5	1.4	−25.1	0.4
N. voltzii	8	−25.8	−24.6	1.2	−25	0.4
Scolopendrites	31	−26.3	−24.2	2.1	−25	0.6
S. grauvogelii	6	−25.8	−24.2	1.5	−24.7	0.5
S. scolopendroides	17	−26.3	−24.4	1.9	−25.2	0.6
Scolopendrites sp.	8	−25.1	−24.2	0.9	−24.5	0.3
Seed ferns	**46**	**−27.9**	**−23.6**	**4.3**	**−25.8**	**0.9**
Scytophyllum bergeri	46	−27.9	−23.6	4.3	−25.8	0.9
S. bergeri sun leaves	15	−26.5	−24.9	1.6	−25.6	0.5
S. bergeri shade leaves	29	−27.9	−23.6	4.3	−26	1
Uncertain affinity	**10**	**−26.8**	**−22.1**	**4.7**	**−24.8**	**1.7**
Lugardonia paradoxa	10	−26.8	−22.1	4.7	−24.8	1.7
Cycadophytes	**17**	**−27.4**	**−24.6**	**2.8**	**−25.8**	**1**
Bjuvia cf. *dolomitica*	17	−27.4	−24.6	2.8	−25.8	1
Conifers	**156**	**−31.9**	**−22.2**	**9.7**	**−25.2**	**1.3**
Albertia cf. *latifolia*	19	−31.9	−26.5	5.4	−27.7	1.2
Voltzia	137	−28	−22.2	5.8	−24.9	1.1
V. recubariensis	61	−27.2	−22.2	5.1	−24.7	1.2
V. edithae	34	−28	−23.7	4.3	−25.2	1
V. heterophylla	26	−26.8	7	3.1	−25.1	1
V. walchiaeformis	10	−26.1	−24.2	1.9	−25	0.7
Voltzia sp.	6	−25	−23.7	1.3	−24.3	0.6
Female conifer cones	34	−27.3	−24.4	2.9	−25.6	0.7
Male conifer cones	13	−26.3	−23.4	2.9	−25.2	1

= 147, 1σ) and −25.4 ± 1.3‰ (*n* = 266, 1σ; Table 2; Fig. 4A). However, gymnosperms show a wider isotopic variability compared to the spore plants (Table 2; Fig. 4A).

Samples of lycophytes were collected from two species, respectively *Isoetites brandneri* and *Lycopia dezanchei* (Figs. 3B, 5). Lycophytes are characterized by high isotopic variability (ca. 5‰; Table 2), ranging from −27.6‰ to −22.6‰ (Table 2; Fig. 5). Although *Lycopia* has a wider isotopic range and is also more abundant than *Isoetites* (Table 2; Fig. 5) the organic carbon isotopic composition of both species does not differ significantly (*p*-value = 0.261; α = 0.001; Table 2; Fig. 5; supplementary materials).

Samples were collected from three fern genera: *Gordonopteris*, *Neuropteridium* and *Scolopendrites* (Figs. 3C–G, 6A). Since organic material on delicate fern pinnules is often poorly preserved, samples of *Gordonopteris*, *Neuropteridium* and *Scolopendrites* were mainly collected from the frond axes. The *Gordonopteris lorigae* is the most common fern in the flora (Fig. 6B) and has an isotopic composition of −24.7 ± 0.5‰ (*n* = 22,

1σ; Table 2; Fig. 6B). *Neuropteridium* includes two species, *N. voltzii* and *N. elegans*, characterized by similar isotopic ranges, and showing a low interspecific variability (Table 2; Fig. 6B). *Scolopendrites grauvogelii* and *S. scolopendroides* represent respectively the fertile fronds of *Neuropteridium elegans* and *N. voltzii* (Fig. 6B). *Scolopendrites scolopendroides* is the most represented taxon, characterized by lighter organic carbon isotopic composition (Table 2; Fig. 6B). *Scolopendrites grauvogelii* and *Scolopendrites* sp. are characterized by narrow isotopic ranges (< 1‰; Table 2; Fig. 6B) and a mean organic carbon isotopic composition, between −24.7 ± 0.5‰ (*n* = 6, 1σ) and −24.5 ± 0.3‰ (*n* = 8, 1σ; Table 2; Fig. 6B). A statistically significant difference between the isotopic composition of *Lycopia dezanchei* and ferns exists (*p*-value = 0.0001; α = 0.001; supplementary material), while *Isoetites brandneri* and ferns do not differ significantly (*p*-value = 0.008; α = 0.001; supplementary materials).

The fertile organ *Lugardonia paradoxa* is characterized by high isotopic variability (4.7‰; Table 2), with a mean organic carbon isotopic
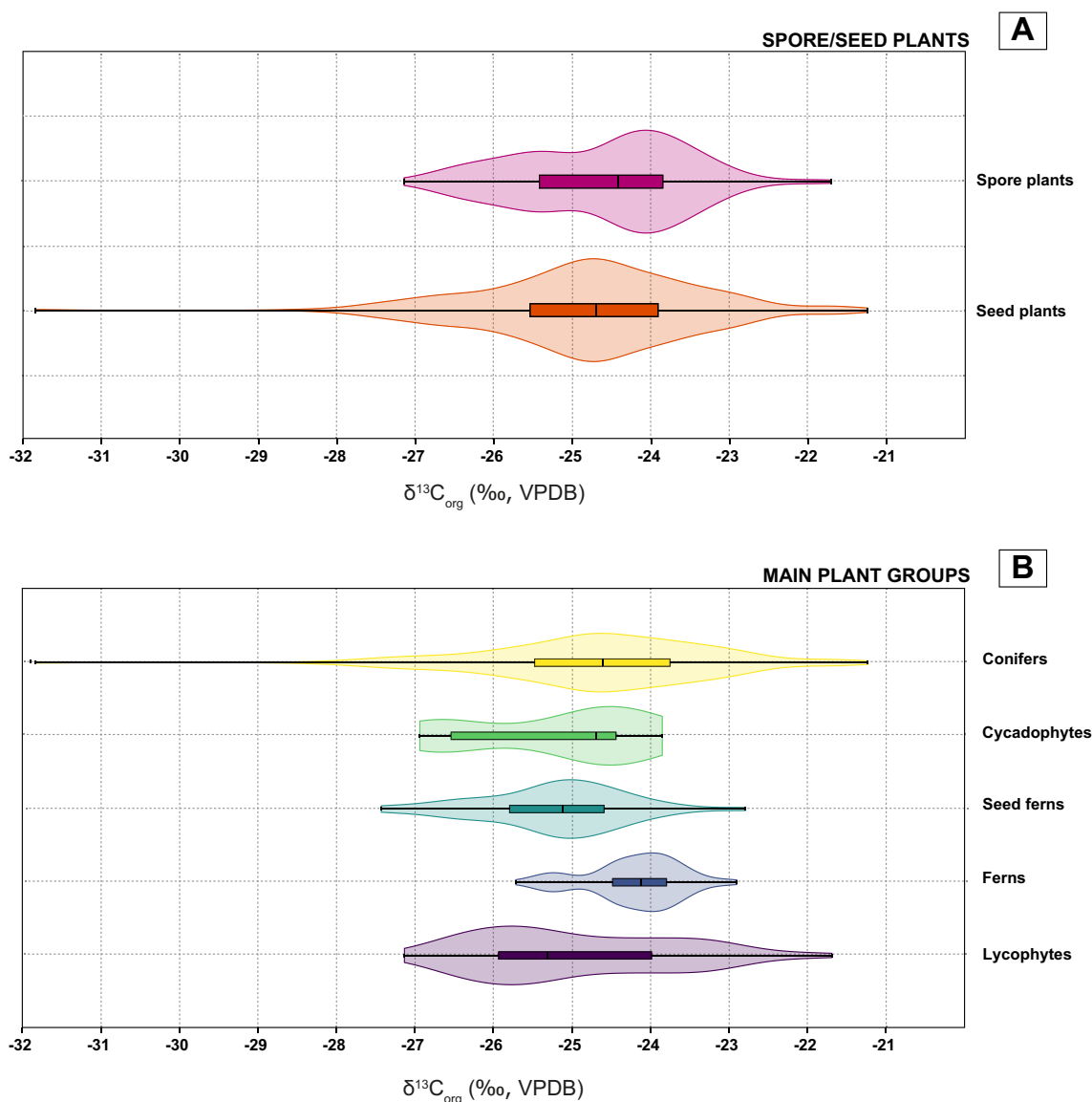
Fig. 4. Geochemical analyses of the plant remains of the Kühwiesenkopf/Monte Prà della Vacca flora. A) Organic carbon isotopic ranges of seed and spore plants and B) of the main plant groups.

composition of $-24.8 \pm 1.7‰$ ($n = 10$, 1σ; Table 2; Figs. 6B, 7B). The organic carbon samples were collected from several parts of the *Lugardonia* specimens, including stalks, microsporangia and palynomorphs.

Samples were collected from only one species of seed fern, *Scytophyllum bergeri* (Fig. 3H, I), which is very well represented in the flora. *Scytophyllum* is characterized by high isotopic variability (4.3‰; Table 2; Fig. 7A) and a mean isotopic composition very similar to that of cycadophytes (Table 2; Fig. 4B). *Scytophyllum bergeri* is also characterized by two leaf morphologies, interpreted as shade and sun leaves (e.g., Kustatscher et al., 2007; Fig. 3H, I). Shade leaves are characterized by a high isotopic variability (4.3‰; Table 2; Fig. 7B), while sun leaves have low isotopic variability (1.6‰; Table 2; Fig. 7B). Although these two leaf types are characterized by different isotopic ranges (Table 2; Fig. 7B) the difference is not statistically significant (*p*-value = 0.119; α = 0.05; supplementary materials).

The cycadophytes are represented by leaves assigned to *Bjuvia* cf. *dolomitica* (e.g., NMS PAL 1171; Fig. 3K). Although well-represented in the flora and characterized by coriaceous appearance, the organic material is often poorly preserved and all the samples were collected from the axes. The mean isotopic composition of *Bjuvia* cf. *dolomitica* is -25.8

$\pm 1‰$ ($n = 17$, 1σ; Table 2; Fig. 7A). In the isotopic composition, no significant differences have been observed between cycadophytes, lycophytes and seed ferns (see also supplementary materials).

The conifers have the highest isotopic variability (9.7‰) and the lightest isotopic composition (Table 2; Fig. 4B). *Albertia* and *Voltzia* are the most common conifer genera, and both are characterized by wide isotopic ranges (Table 2; Fig. 8A) and a significantly different isotopic composition (*p*-value = 1.693e-11; (α): 0.001; supplementary materials). *Albertia* cf. *latifolia* is the species with the lightest $\delta^{13}C$ values in the flora, characterized by a high isotopic variability (5.4‰; Table 2; Fig. 8A) and a mean organic carbon isotopic composition of $-27.7 \pm 1.2‰$ ($n = 19$, 1σ; Table 2), which is significantly different from all the other taxa present in the Kühwiesenkopf/Monte Prà della Vacca flora (i. e. lycophytes, ferns, seed ferns, cycadophytes and *Voltzia*; supplementary materials). The genus *Voltzia*, the most diverse conifer genus of the flora, is also characterized by a wide isotopic variability (5.8‰; Table 2; Fig. 8A). Although *Voltzia* species have a similar mean organic carbon isotopic composition (Table 2), they are characterized by different $\delta^{13}C$ ranges (Table 2; Fig. 8B). *Voltzia recubariensis* has the heavier $\delta^{13}C$ average ($-24.7 \pm 1.1‰$; $n = 61$, 1σ; Table 2) and, in comparison with
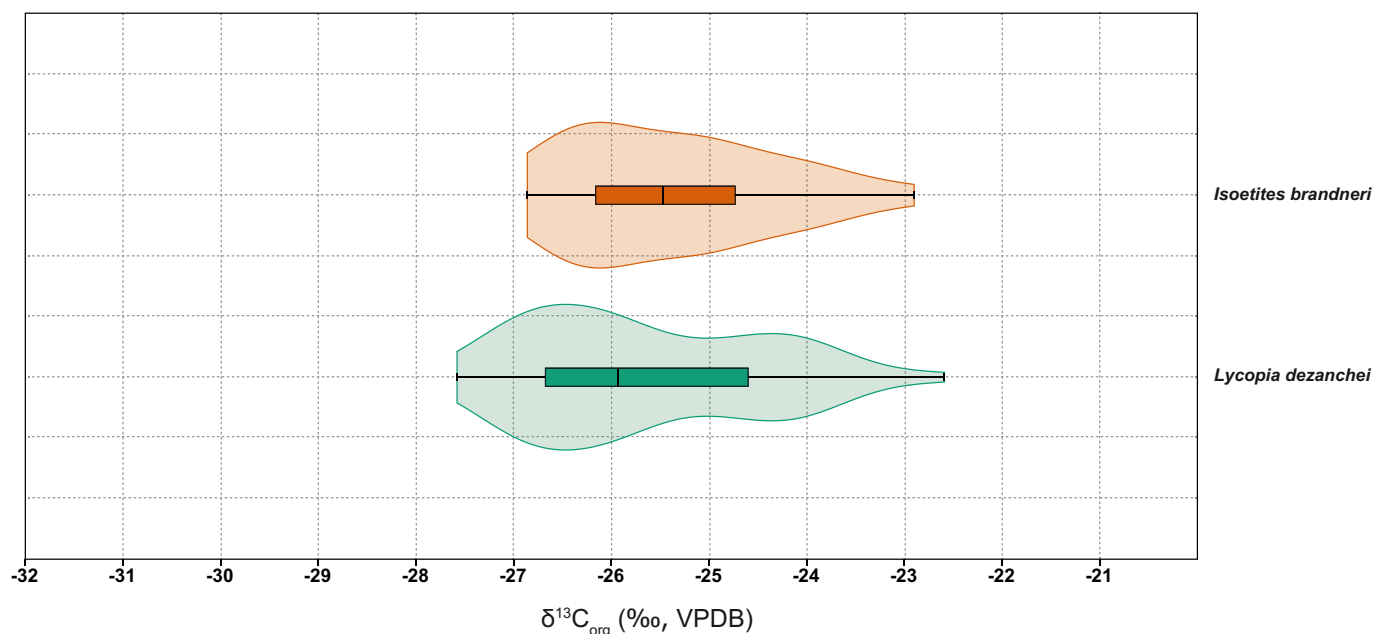
LYCOPHYTES

Fig. 5. Geochemical analyses of the lycophytes samples of *Isoetites brandneri* and *Lycopia dezanchei* from the Kühwiesenkopf/Monte Prà della Vacca flora.

other *Voltzia* species, the highest isotopic variability (5.1‰; Table 2; Fig. 8B). *Voltzia walchiaeformis*, less common than the other conifer species, is characterized by a narrow isotopic range (1.9‰; Table 2; Fig. 8B). *Voltzia heterophylla* and *V. edithae* have comparable mean isotopic compositions, respectively -25.1 ± 1‰ (n = 26, 1σ) and -25.2 ± 1‰ (n = 34, 1σ), although *V. heterophylla* is characterized by a higher isotopic variability (3.1‰; Table 2; Fig. 8B). Dispersed female and male conifer cones are characterized by δ13C ranges that mainly overlap with that of *Voltzia* (Table 2; Fig. 8B). However, female cones are more represented in the flora and, on average, more positive than male cones, with a mean δ13C of -25.6‰ ± 0.7‰ (n = 34, 1σ; Table 2; Fig. 8B).

5. Discussion

5.1. Organic carbon isotopic composition and Anisian humid episodes

Several remarkable shifts in the bulk δ13C, over 3‰ in amplitude, are recorded in the Kühwiesenkopf/Monte Prà della Vacca section (Fig. 2B). At present, marine organic carbon is characterized by a mean isotopic composition that is more positive than terrestrial sources (e.g., Arthur et al., 1985). However, before the Cretaceous, terrestrial organic matter could have been more 13C-enriched than marine sources (Arthur et al., 1985). Therefore, during the Triassic a positive isotopic shift of the bulk δ13C values could represent a significant input of terrestrial organic matter in the marine environment.

The marine/terrestrial sporomorphs ratio recorded along the Kühwiesenkopf/Monte Prà della Vacca section was investigated previously, and highlighted several peaks interpreted as transgressive events (Kustatscher and Roghi, 2006; Kustatscher et al., 2010a; Fig. 2C; supplementary materials). No significative correlation between the positive δ13C shifts and the terrestrial spikes in the palynological samples has been observed (Kustatscher et al., 2010a; Fig. 2B, C; supplementary materials).The highest value of the marine/terrestrial sporomorphs ratio is recorded at about 120 m above the base of the section (Fig. 2B), and corresponds with a negative δ13C shift (Fig. 2C; supplementary materials). However, in the corresponding palynological sample (i.e., PV97–1) the marine palynomorphs represent only the 21% of the total

(Fig. 2B, C; supplementary materials).The terrestrial organic component is dominant in the palynological samples over the marine one, exceeding the 90% in most of the cases (Fig. 2C; supplementary materials). This suggests that the δ13C values recorded along the section are mainly representative of the isotopic composition of terrestrial organic matter.

Although high resolution carbonate carbon isotope records (δ13Ccarb) are more common in literature than those based on organic carbon (e.g., Cramer and Jarvis, 2020), the variations in the global isotopic composition of dispersed inorganic carbon (DIC) reservoir (δ13Ccarb) are linked to the redistribution of carbon in the other reservoirs, and thus, also to the variations of δ13Corg (e.g., Cramer and Jarvis, 2020). The burial or oxidation of 13C-depleted organic matter drives increases or decreases in the δ13Ccarb (e.g., Shackleton, 1987; Berner, 1990; Derry et al., 1992; Hayes et al., 1999; Kump and Arthur, 1999; Sundquist and Visser, 2004). Several global δ13Ccarb excursions are documented during the Anisian (e. g., Payne et al., 2004; Galfetti et al., 2007a; Saltzmann and Thomas, 2012; Sun et al., 2012; Burgess et al., 2014; Lyu et al., 2019; Cramer and Jarvis, 2020; Ogg and Chen, 2020). The positive excursion in the δ13Ccarb composition that was documented at the Olenekian–Artinskian boundary was explained by an increase in the burial of isotopically light organic carbon (e.g., Scholle and Arthur, 1980; Holser, 1997). In addition to the main δ13Ccarb positive shift recorded at the Olenekian–Anisian boundary, two minor positive excursions are documented in the Anisian (e.g., Payne et al., 2004; Galfetti et al., 2007a; Saltzmann and Thomas, 2012; Sun et al., 2012; Burgess et al., 2014; Lyu et al., 2019), respectively a δ13Ccarb positive shift of ca. 2‰ recorded in the upper part of Pelsonian (middle–late Anisian, Middle Triassic; Payne et al., 2004) and a ca. 1‰ δ13Ccarb positive shift in the middle Anisian of China (Burgess et al., 2014). The δ13Ccarb positive shifts in the Triassic of Tethys are considered by several authors as events of higher burial rates of organic matter (e.g., Zhang et al., 2015; Lyu et al., 2019) and as major events of terrestrial organic inputs in the marine basins, caused for instance by humid episodes (e.g., Hayes et al., 1999; Schrag et al., 2002; Trotter et al., 2015; Li et al., 2018).

Two such humid episodes are recorded during the Anisian, i.e., during Bithynian–Pelsonian and Illyrian (e.g., Brugman, 1986; Breda et al., 2009; Kustatscher et al., 2010a; Preto et al., 2010; Stefani et al.,
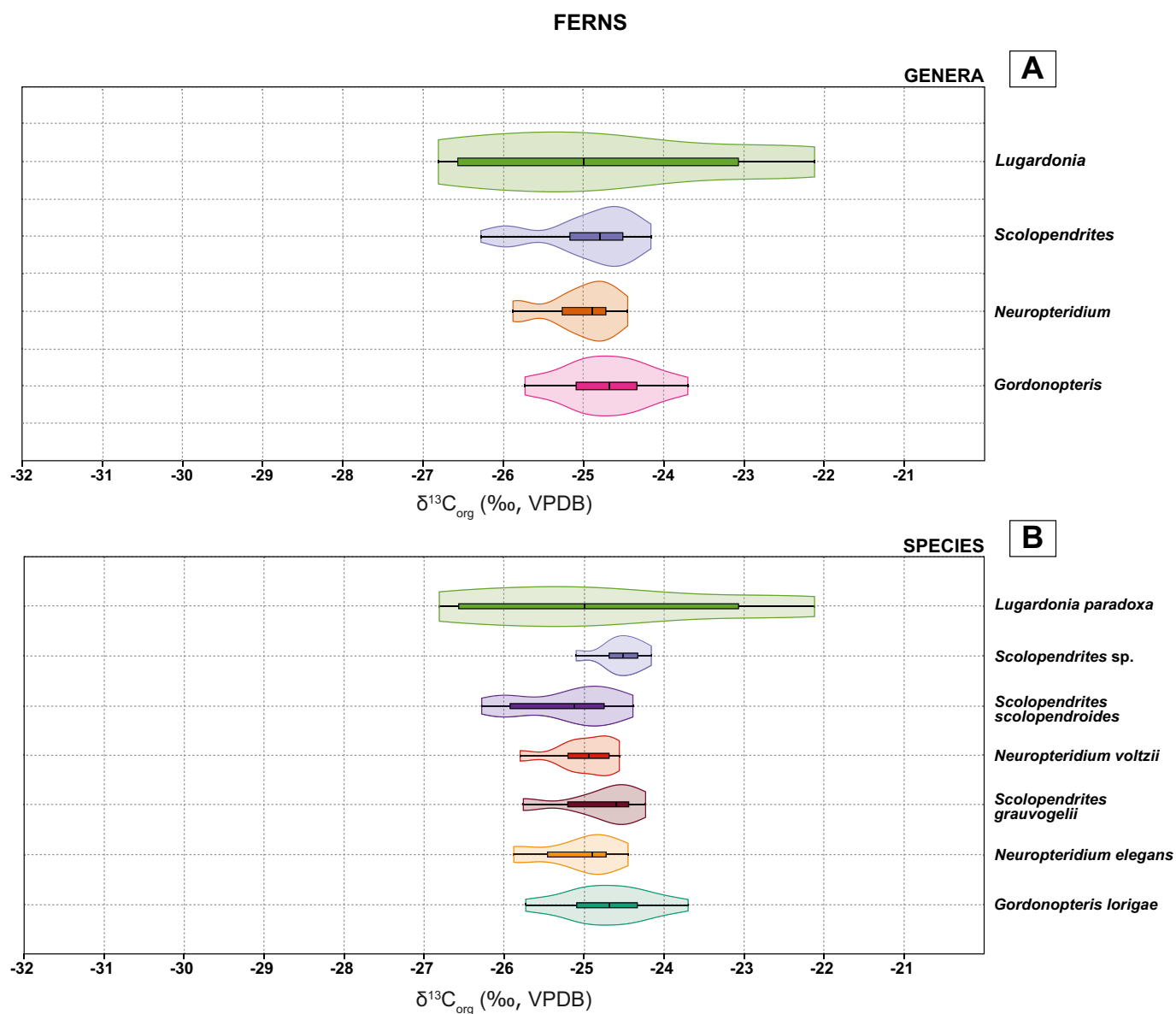
FERNS

Fig. 6. Geochemical analyses of the plant remains of the Kühwiesenkopf/Monte Prà della Vacca flora. A) Organic carbon isotopic ranges of the fern genera *Gordonopteris*, *Scolopendrites*, *Neuropteridium* and of the fertile organ *Lugardonia*. B) $^{13}C_{org}$ ranges of the various fern species and of the fertile organ *Lugardonia paradoxa*.

2010). These episodes could have coincided with peaks of burial of organic matter and, consequently, with positive $\delta^{13}C_{carb}$ shifts (e.g., Hayes et al., 1999; Schrag et al., 2002).

5.2. Isotopic signatures and palaeoecology

Several experiments on modern plants investigated their isotopic composition depending on environmental factors (Balesdent and Mariotti, 1996; Teece and Fogel, 1997; Lallier-Vergès et al., 1997; Huang et al., 1997). It was found that the $\delta^{13}C$ of plants mainly depends on the isotopic composition of the atmospheric CO_2 (e.g., Farquhar, 1980; Farquhar and Lloyd, 1993; Farquhar et al., 1989; Arens et al., 2000) that is adsorbed during the photosynthesis, by the atmospheric pCO_2 (e.g., Schubert and Jahren, 2012, 2015; Cui and Schubert, 2016), and also by the photosynthetic pathway (e.g., Farquhar, 1980; Farquhar et al., 1982, 1989; Bender, 1971; Sternberg et al., 1984; Arens et al., 2000). Post-photosynthetic fractionation mechanisms are also responsible for the different carbon isotopic composition of different tissues (e.g., photosynthetic and non-photosynthetic tissues), components (e.g., cellulose,

hemicellulose, lignin and lipids) and organs of the plant (e.g., Craig, 1953; Leawitt and Long, 1986; Badeck et al., 2005; Marshall et al., 2007; Cernusak et al., 2009). Other parameters like salinity, nutrients availability, temperature, irradiance and altitude can influence the mean $\delta^{13}C$ of plants (e.g., Farquhar, 1980; Farquhar et al., 1989; Farquhar and Lloyd, 1993; Cernusak and Marshall, 2001; Fig. 9), which adapt to different environmental conditions and environmental stress through physiological mechanisms (e.g., Guy et al., 1986; Tieszen, 1991; Bocherens et al., 1993; Lockheart et al., 1997; Gröcke, 1998, 2002; Arens et al., 2000; Beerling et al., 2002; McCarroll and Loader, 2004; Diefendorf et al., 2010; Kohn, 2010; Lomax et al., 2012). Plants characterized by wide ranges of $\delta^{13}C$ values may reflect a higher diversity of growth environments and indicate the presence of local gradients in environmental parameters, whereas taxa with narrow isotopic ranges are generally restricted to a precise niche and are less tolerant to changes in environmental parameters (e.g., Leawitt and Newberry, 1992; Ehleringer and Cerling, 1995; Benner et al., 1987; Rundgren et al., 2003; Badeck et al., 2005; Dal Corso et al., 2011, 2017; Fig. 9). Therefore, the isotopic composition of plants indirectly tells us about their ecology and
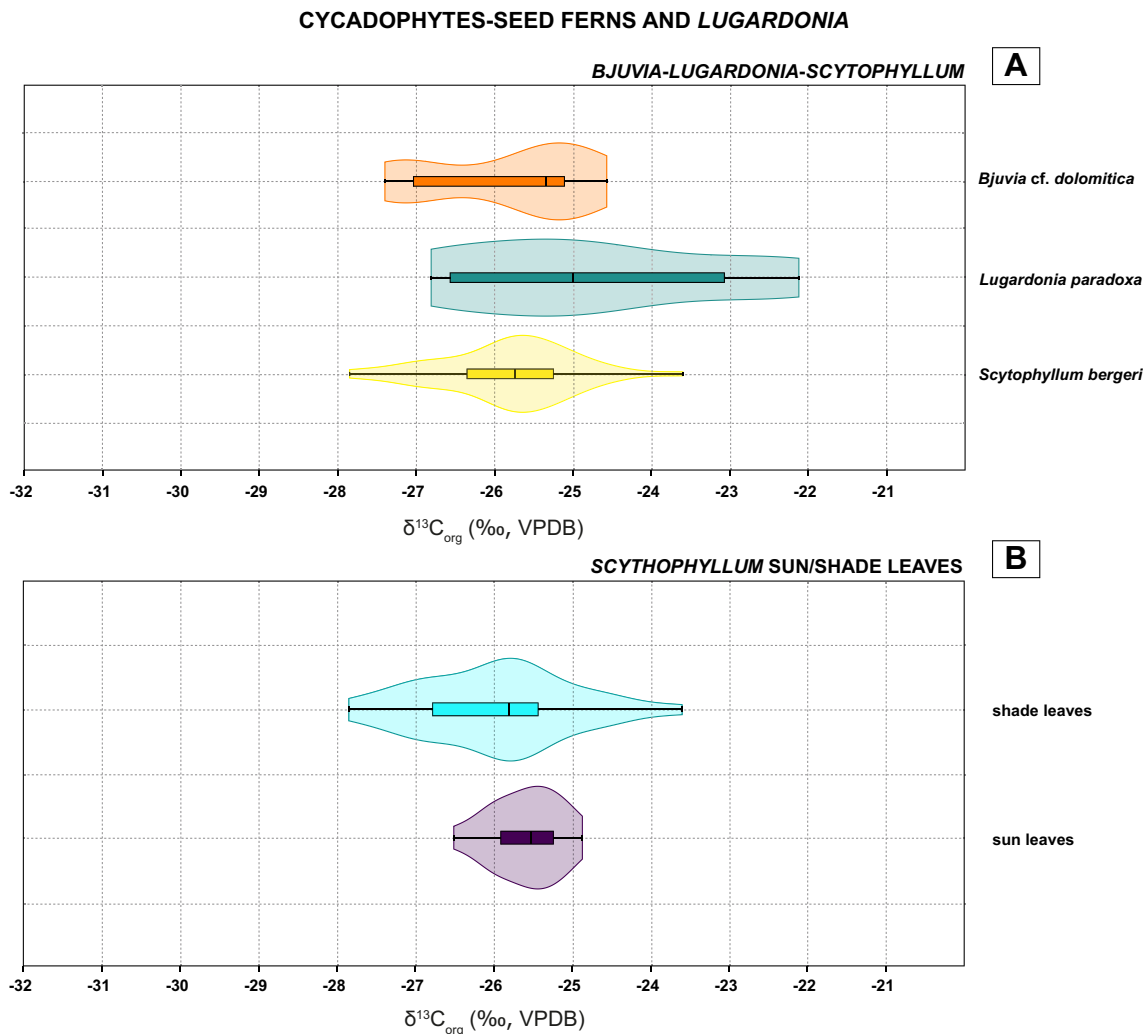
CYCADOPHYTES-SEED FERNS AND *LUGARDONIA*

Fig. 7. Geochemical analyses of the plant remains of the Kühwiesenkopf/Monte Prà della Vacca flora. A) $\delta^{13}C_{org}$ ranges of the cycad *Bjuvia* cf. *dolomitica*, the fertile organ *Lugardonia paradoxa* and the seed fern *Scytophyllum bergeri*. B) $\delta^{13}C_{org}$ ranges of shade and sun leaves of *Scytophyllum bergeri*.

the degree of environmental stress to which the plants were subjected (e. g., Bocherens et al., 1993; Nguyen Tu et al., 1999, 2002; Dawson et al., 2002; Aucourt et al., 2008; Diefendorf et al., 2010).

Geochemical investigations on plant fossils showed that they overall retain the original isotopic composition, and that the diagenetic events do not influence significantly the original $\delta^{13}C$ (e.g., Degens, 1969; Nambudiri et al., 1978; Rigby et al., 1981; Wilson et al., 1987; Aucourt and Hillaire-Marcel, 1993; Bocherens et al., 1993; Meyers et al., 1995; Cody, 1997; Nguyen Tu et al., 1999). The organic carbon isotopic composition of fossil plants can thus provide information about their photosynthetic pathway, palaeoecology and the environment they lived in (e.g., Arens et al., 2000; Nguyen Tu et al., 1999, 2002; Aucourt et al., 2008; Nordt et al., 2016; Basu et al., 2019; Dong et al., 2021). However, it is often not possible to measure the isotopic composition of the different fossil plant tissues. Therefore, it is important to refer to the mean $\delta^{13}C$ of the whole plant by a multiple sampling of the specimens, including as much of the plant as possible, in order to better represent the isotopic variability within each individual plant taxon.

5.3. Geochemistry of the Kühwiesenkopf/Monte Prà della Vacca flora

The exceptional preservation of plant remains form Kühwiesenkopf/ Monte Prà della Vacca allowed us to carry out taxon-specific geochemical analyses of a rich plant community, and to compare

several plant groups.

The high organic carbon isotopic variability of seed plants at Kühwiesenkopf/Monte Prà della Vacca (i.e., seed ferns, cycadophytes and conifers; Table 2; Figs. 7, 8) and their common occurrence in the flora are interpreted to represent a higher adaptability of these plants to different environments. On the contrary, the dependence of spore plants (e.g., ferns) from wet environments such as lakes, ponds and rivers necessary for germination of spores, and thus, for their reproduction, should have resulted in narrow ranges of carbon isotopic compositions.

The more positive $\delta^{13}C$ values recorded from lycophytes (e.g., *Isoetites*, *Lycopia*; Table 2; Fig. 5) are consistent with their adaptation to coastal environments, where they were subjected to marine influence (e. g., Bocherens et al., 1993; Aucourt et al., 2008; Fig. 9). The physiological response of plants to water- and/or salinity-stress consists of several mechanisms (e.g., Farquhar et al., 1982; Evans et al., 1986) that overall lead to the decrease of the fractionation rate (Fig. 9). In the organic remains of both extant and fossil plants subjected to salt-stress, ^{13}C-enrichment has been observed (e.g., Guy et al., 1980, 1986; Lipp et al., 1996; Nguyen Tu et al., 1999, 2002; Arens et al., 2000; Aucourt et al., 2008). However, among lycophytes, *Lycopia dezanchei* is characterized by a wider $\delta^{13}C$ range than *Isoetites brandneri* (Table 2; Fig. 5) and significantly differs from ferns (see supplementary materials), possibly indicating a wider environmental adaptation, likely occupying also part of the inland or other wet areas, less subjected to marine influence. This
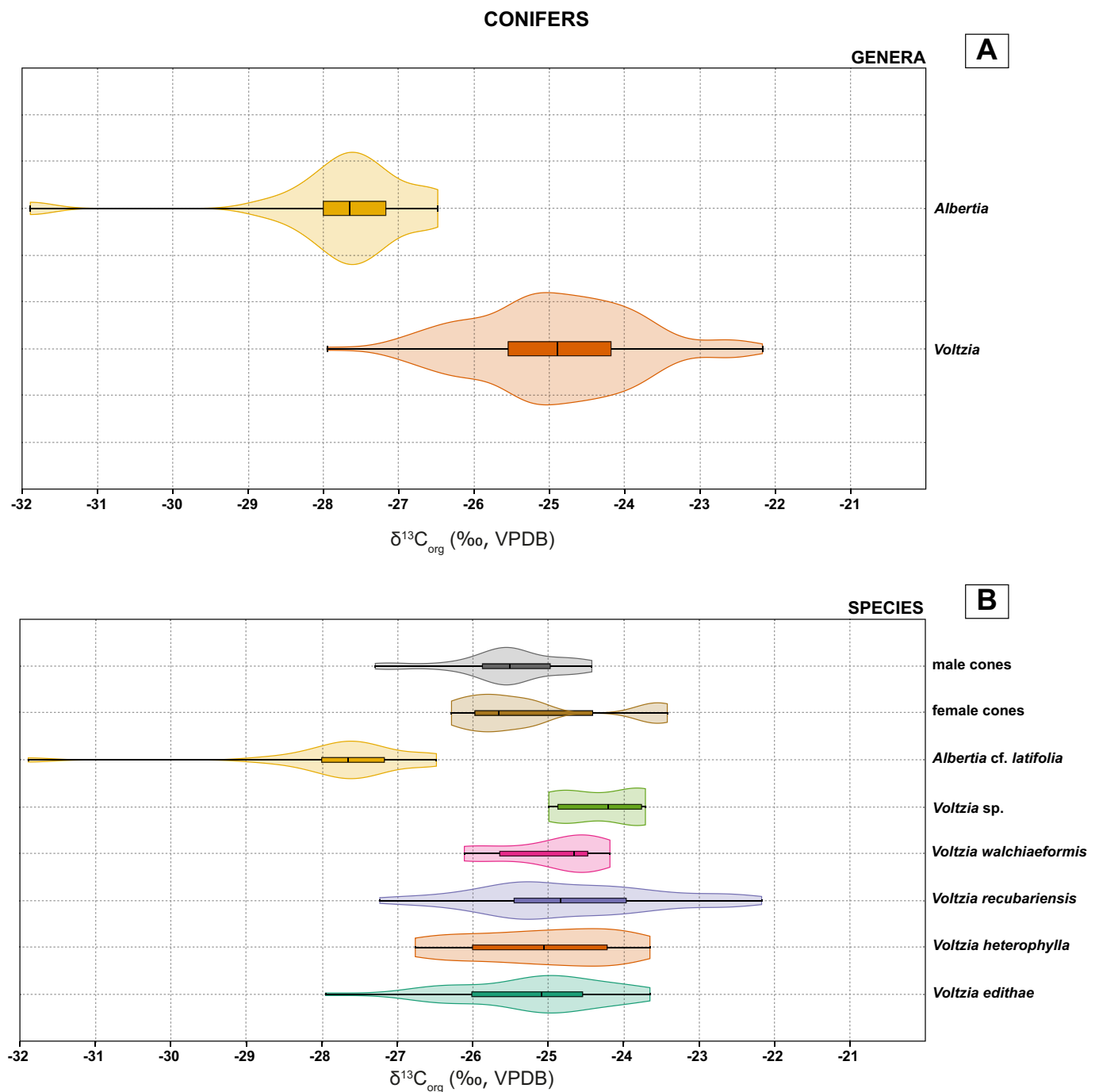
CONIFERS

Fig. 8. Geochemical analyses of the plant remains of the Kühwiesenkopf/Monte Prà della Vacca flora. A) Organic carbon isotopic ranges of the conifer genera *Albertia* and *Voltzia*. B) $\delta^{13}C_{org}$ ranges of the vegetative remains of the various conifer species and not better distinguished reproductive organs.

is typical also in the halophytic angiosperms (e.g., *Salicornia, Pucci-nellia*), and other extinct gymnosperms (e.g., *Frenelopsis*), often charac-terized by wide $\delta^{13}C$ ranges when living along an environmental salinity gradient (Guy et al., 1980, 1986; Sternberg et al., 1984; Nguyen Tu et al., 1999; Aucourt et al., 2008).

The low organic carbon isotopic variability of ferns (0.9‰–2.0‰; Table 2; Fig. 6A, B) suggests that these plants were instead restricted to wet areas (e.g., Nguyen Tu et al., 1999, 2002). Although ferns represent the most diverse group in the flora (at least eleven species; Kustatscher et al., 2010a, 2019; Van Konijnenburg-van Cittert et al., 2006), the species analyzed are characterized by different but narrow isotopic ranges $\delta^{13}C$ (Table 2; Fig. 6A), indicating an adaptation to restricted and

particular ecological niches and a low tolerance to changes of environ-mental parameters (e.g., Leawitt and Newberry, 1992; Ehleringer and Cerling, 1995; Benner et al., 1987; Rundgren et al., 2003; Badeck et al., 2005; Dal Corso et al., 2011, 2017). Nonetheless, among the diverse Kühwiesenkopf/Monte Prà della Vacca fern species, *Gordonopteris lor-igae* is the most common and it is also the one characterized by the highest isotopic variability (Table 2; Fig. 6A, B). Its abundance in the flora and the wider $\delta^{13}C$ range (Table 2; Fig. 6B) might suggest a better adaptation to diverse humid environments. *Neuropteridium elegans* and *N. voltzii* have very similar $\delta^{13}C$ ranges (Table 2; Fig. 6B), suggesting a low interspecific isotopic variability, but also that both species occupied the same or similar environments. The comparison between the sterile
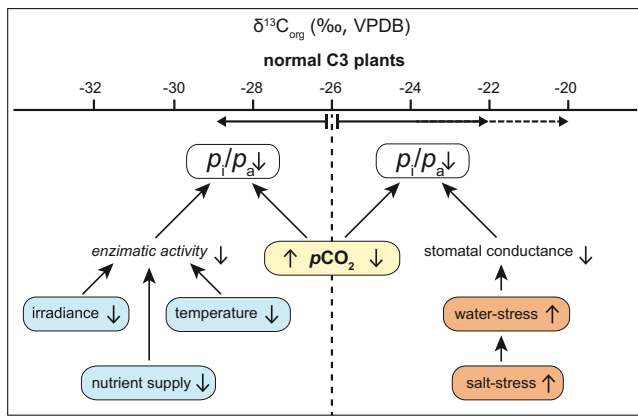
Fig. 9. Variations of $\delta^{13}C_{org}$ in extant C3 plants with environmental parameters (modified from Bocherens et al., 1993).

and fertile fronds of *Neuropteridium elegans - Scolopendrites grauvogelii* and *N. voltzii - S. scolopendroides* show different isotopic compositions. Fertile fronds of *Scolopendrites* are in both cases (i.e., *S. grauvogelii* and *S. scolopendroides*) characterized by a higher isotopic variability and are, on average, more positive than the sterile ones (Table 2; Fig. 6A, B). This difference may be due to a different isotopic composition of the reproductive organs/tissues than the sterile ones. Samples of *Scolopendrites* might include a more heterogeneous mixture of plant tissues, such as part of the fertile fronds with spore-producing structures and spores. Different tissues of the plant have a different isotopic signature because of the post-photosynthetic fractionation that characterizes the biosynthetic processes (e.g., Badeck et al., 2005; Cernusak et al., 2009) and can be discriminated through more specific analyses (e.g., Compound Specific Isotopic Analysis; Hayes et al., 1990; Freeman et al., 1990; Rieley et al., 1991). In modern gymnosperms and angiosperms the $\delta^{13}C$ of pollen and of the stem are different, with $\delta^{13}C$ pollen being $< \delta^{13}C$ stem, or $\delta^{13}C$ pollen $> \delta^{13}C$ stem, depending on the taxon and the environmental conditions (Jahren, 2004). Similar studies are unfortunately not available for spores and spore plants. The putative presence of reproductive structures (e.g., sporangia, spores) could explain the higher isotopic variability in *Scolopendrites*, however, more investigations are needed to confirm it.

Lugardonia paradoxa, a fertile organ of unresolved botanical affinity, is composed of helically arranged short stalks, each bearing a cluster of 3 or 4 elongate microsporangia, interpreted by some authors as spores or prepollen (Kustatscher et al., 2009, 2019). The isotopic range of *Lugardonia* is one of the widest in the flora (4.7‰; Table 2; Fig. 6A, B), being remarkably higher than those of ferns (*Neuropteridium, Scolopendrites, Gordonopteris*; Table 2; Fig. 6A) and partly overlapping with those of gymnosperms (e.g., *Scytophyllum bergeri* and *Bjuvia* cf. *dolomitica*; Table 2; Fig. 7). This highly variable isotopic composition may have two possible explanations: i) presence of different kinds of tissues (e.g., axes, prepollen/spores), characterized by different isotopic compositions; ii) adaptation to different conditions and environments of the plant that produced the fertile organ *Lugardonia*. Further investigations (e.g., Compound Specific Isotopic Analyses; Hayes et al., 1990; Freeman et al., 1990; Rieley et al., 1991) are needed to test these two hypotheses. So far, a fern or seed fern affinity of *Lugardonia paradoxa* remains unclear.

The seed fern *Scytophyllum bergeri,* characterized by high organic carbon isotopic variability (4.2‰; Table 2; Fig. 7A), was adapted to a wider range of environments and produced sun and shade leaves (Kustatscher et al., 2007). The differences between these two types are both macro- and micromorphological. Leaves directly exposed to the sun light are characterized by rare sunken stomata in the upper side of the leaf and abundant papillae, to protect the stomatal aperture and reduce the loss of water by evapotranspiration. Stomata are more abundant on the upper side of the shade leaves, papillae on epidermal cells are rare.

Moreover, the two leaf types have different isotopic ranges and isotopic variability (Table 2; Fig. 7B). Studies on extant plants show that the morpho-anatomical and physiological adaptations/responses of sun leaves include a higher photosynthetic rate than in shade leaves, and are comparable to the leaf features of drought tolerant plants, whereas shade leaves resemble drought intolerant plants (e.g., Ashton and Berlyn, 1992; Dörken and Lepetit, 2018). This influences the isotopic composition, which is more negative in shade leaves than in sun leaves (e.g., Li et al., 2007), however, sun leaves of *Scytophyllum bergeri* have a mean $\delta^{13}C$ comparable to that of shaded ones (Table 2; Fig. 7B; supplementary material).

Cycadophytes (i.e. *Bjuvia* cf. *dolomitica*) have the lower organic carbon isotopic variability when compared to the other seed plants, i.e., seed ferns and conifers (Table 2; Fig. 7A). The isotopic ranges of *Bjuvia* and of the seed fern *Scytophyllum bergeri* are similar (supplementary materials), and wider than those of ferns (Table 2; Figs. 6, 7A), suggesting that these taxa not only occurred in the wetland areas, but also in other environments, thanks to their better adaptation to drier conditions.

The conifers likely occupied different environments, including coastal settings, uplands, river margins or arid areas. This adaptation to different environments can be one of the causes behind the high isotopic variability of the conifers from Kühwiesenkopf/Monte Prà della Vacca (Table 2; Fig. 8A, B). *Voltzia* includes different species that likely occupied different environments. *Voltzia recubariensis*, the most abundant conifer species of the flora (Forte et al., 2021) is characterized by a wide $\delta^{13}C$ range and more positive isotopic values, up to – 22.2‰, compared to the other conifer species (Table 2; Fig. 8A, B). The wide isotopic range of *V. recubariensis*, the more positive $\delta^{13}C$ values that partly overlap with that of lycophytes (*Isoetites* and *Lycopia*) and the presence of epidermal structures to prevent and reduce the water loss, such as thick cuticles, almost hypostomatic, with heavily papillate epidermal cells, and well developed papillae on subsidiary cells (Forte et al., 2021), would suggest not only an adaptation to dryer conditions but also to salt-stress environments (Fig. 9). More positive $\delta^{13}C$ values, ranging ca. from $-25‰$ to $-22‰$, have indeed also been recorded from different species of the Cretaceous conifer genus *Frenelopsis*, known for its resistance to the salt stress and adaptation to coastal and lagoonal environments (e.g., Daghlian and Person, 1977; Louail, 1984; Bocherens et al., 1993; Nguyen Tu et al., 1999), as for other members of the Cheirolepidiaceae family (Hughes and Moody-Stuart, 1967; Batten and McLennan, 1984; Watson, 1977, 1988). The wide adaptation of *Voltzia recubariensis* and its abundance in the flora support the presence of this species in several environments, from the coast to the uplands (Table 2; Figs. 8B, 10). Compared to *Voltzia recubariensis*, the other species of *Voltzia*, such as *V. heterophylla*, *V. edithae* and *V. walchiaeformis*, are characterized by narrower isotopic range and lighter isotopic composition (Table 2; Fig. 8B). The organic carbon isotopic composition suggests that *V. heterophylla*, *V. edithae* and *V. walchiaeformis* and the other seed plants occupied the lowland up to the upland, tolerating both humid to dry conditions (Fig. 10). The isotopic composition of *Albertia* cf. *latifolia* differs remarkably from those of the other conifer species (supplementary materials). The $\delta^{13}C$ lighter on average, which can be due to the higher fractionation rate of this plant and/or to the occupation of a different niche. One of the causes linked to the higher fractionation rate is the decrease of light availability (Fig. 9). The decreasing $\delta^{13}C$ of leaves along a gradient of light, from the canopy top to the understory, is known from several studies (e.g., Francey et al., 1985; Ehleringer et al., 1986, 1987; Hanba et al., 1997). The shrub-like habitus of *Albertia* cf. *latifolia* suggest that it may have had to compete with other plants for light, and its broad-leaf morphology and its lax and open phyllotaxy (Fig. 3M) could represent an adaptation of this taxon to low irradiance conditions (e.g., Nordhausen, 1909; Lichtenthaler, 1971, 1981; Björkman et al., 1972; Lichtenthaler et al., 1981; Ashton and Berlyn, 1992.; Pandey and Nagar, 2002; Xu et al., 2009).
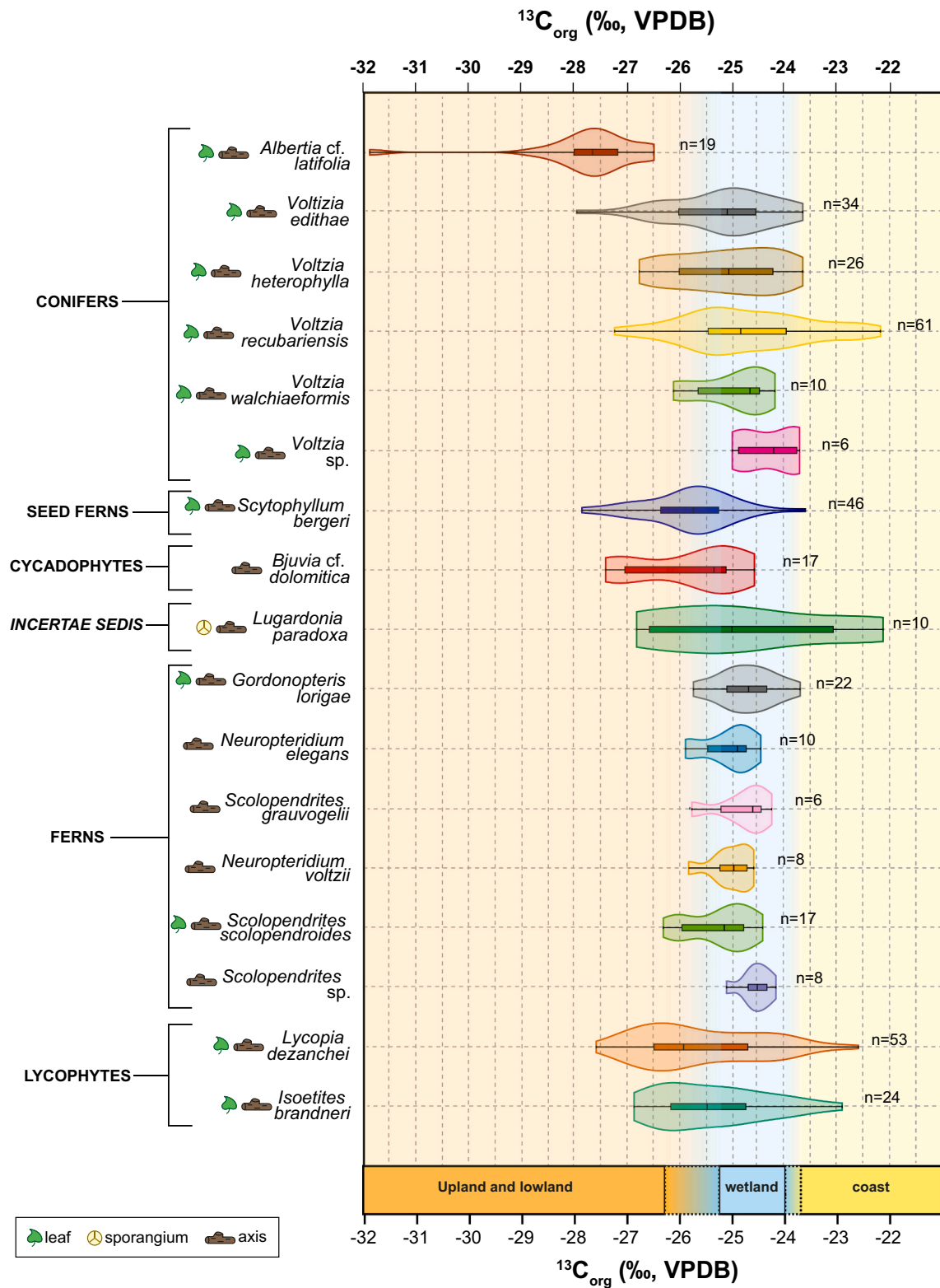
Fig. 10. Isotopic ranges of the taxa the different environments of Kühwiesenkopf/Monte Prà della Vacca. For each species, symbols indicate the different parts of the plants that were sampled.

5.4. The palaeoenvironments of the Kühwiesenkopf/Monte Prà della Vacca flora

The storm events and the rapid burial event that allowed preservation of the Kühwiesenkopf/Monte Prà della Vacca flora (Tintori et al., 2001; Broglio-Loriga et al., 2002), caused the transportation and accumulation of plants from terrestrial environments to the sea. The various plants occupied different terrestrial environments and had different ecological adaptations. Some taxa were tolerant to a wide range of environmental conditions, living likely along environmental gradients.

This is true for conifers and, more in generally, for seed plants, which are more tolerant to environmental change than spore plants. The isotopic ranges of these plants represent the mean isotopic composition of plants that occupied different areas in the landscape and that lived under different conditions. In this case, it is difficult to discriminate, within the same taxon, the isotopic composition of plants that occupied different environments. This would instead be possible with an in situ palaeoflora and detailed sedimentological data (e.g., Nguyen Tu et al., 1999). However, for other groups of plants adapted to narrower ranges of environmental conditions or to specific environments, a different degree of interpretation is possible. This can be the case of spore plants (e.g., lycophytes, ferns), which are linked to wetland (Fig. 11), since they depend on water to spread their spores and reproduce. Moreover, unlike seed plants, spore plants are missing many physiological adaptations to desiccation. Although ferns represent one of the most diverse plant groups of the Kühwiesenkopf/Monte Prà della Vacca flora (e.g., Van Konijnenburg-van Cittert et al., 2006; Kustatscher et al., 2010a), they are characterized by the lowest isotopic diversity, which never exceed 2‰ (Table 2; Figs. 6, 10). This can be due to their ecology, tightly linked to the wetland, understory and generally the fresh water environments (Fig. 11). The isotopic range of ferns can be considered characteristic of wetlands and can be used as element of comparison with the other taxa.

The coastal environment was occupied by plants adapted to high salinity to brackish conditions, with cuticle features optimized to reduce the water loss caused by salt-stress. The isotopic values of the lycophytes confirm they occurred both in humid environments and in coastal areas (Fig. 11). The thick cuticles and well-protected stomata of *Lycopia* support the hypothesis of an adaptation to coastal-halophytic conditions (Wang and Wang, 1982; Meng, 1996; Kustatscher et al., 2010b) similarly to other Triassic lycophytes which grew by costal lakes, lagoons or

interdistributary bays environments, forming extensive, sometimes monospecific thickets (e.g., Mägdefrau, 1931; Hirmer, 1933; Neuburg, 1960; Kon'on Kon'on, 1973; Krassilov and Zakharov, 1975; Retallack, 1975, 1980, 1997; Sun et al., 1990; Meng, 1996). The heavy isotopic values of *Voltzia recubariensis*, comparable with those of the lycophytes, positions this species also in the coastal environments (Fig. 11). This is also supported by its epidermal features, such as thick cuticles, increased guard cells cutinization, heavily papillate epidermal cells and presence of trichomes (Forte et al., 2021), which represent adaptations to salt/water stressed environments, where the high salinity conditions could cause dehydration. This explains the abundance of this taxon and the presence of large branches in all Anisian marine to proximal marine assemblages of the Southern Alps (e.g., Recoaro, Agordo, Bagolino, Piz da Peres; e.g., Brack and Kustatscher, 2013; Kustatscher et al., 2011, 2012; Roghi et al., 2017; Forte et al., 2021, 2022).

Humid environments were dominant in Kühwiesenkopf/Monte Prà della Vacca and were occupied by rich and diverse plant communities (Fig. 11). They were mainly colonized by ferns (e.g., *Gordonopteris*, *Scolopendrites*, *Neuropteridium*), which represent an abundant group in the Kühwiesenkopf/Monte Prà della Vacca flora (Kustatscher et al., 2010a) and are strictly linked to water-rich conditions, as suggested by their low organic carbon isotopic variability which never exceeds 2‰ (Table 2). Some lycophytes (*Isoetites*, *Lycopia*), seed ferns (*Scytophyllum*) and cycadophytes (*Bjuvia* cf. *dolomitica*) also thrived in wetlands, as well as some conifers belonging to the genus *Voltzia* (Fig. 11).

More arid lowlands and uplands were occupied by gymnosperms, such as seed ferns (*Scytophyllum*), cycadophytes (*Bjuvia* cf. *dolomitica*) and conifers, better adapted than spore plants (i.e. lycophytes and ferns) to dry conditions such those of well-drained soils of the uplands and/or lowland areas far from water bodies (Fig. 11). Arboreal and shrub plants
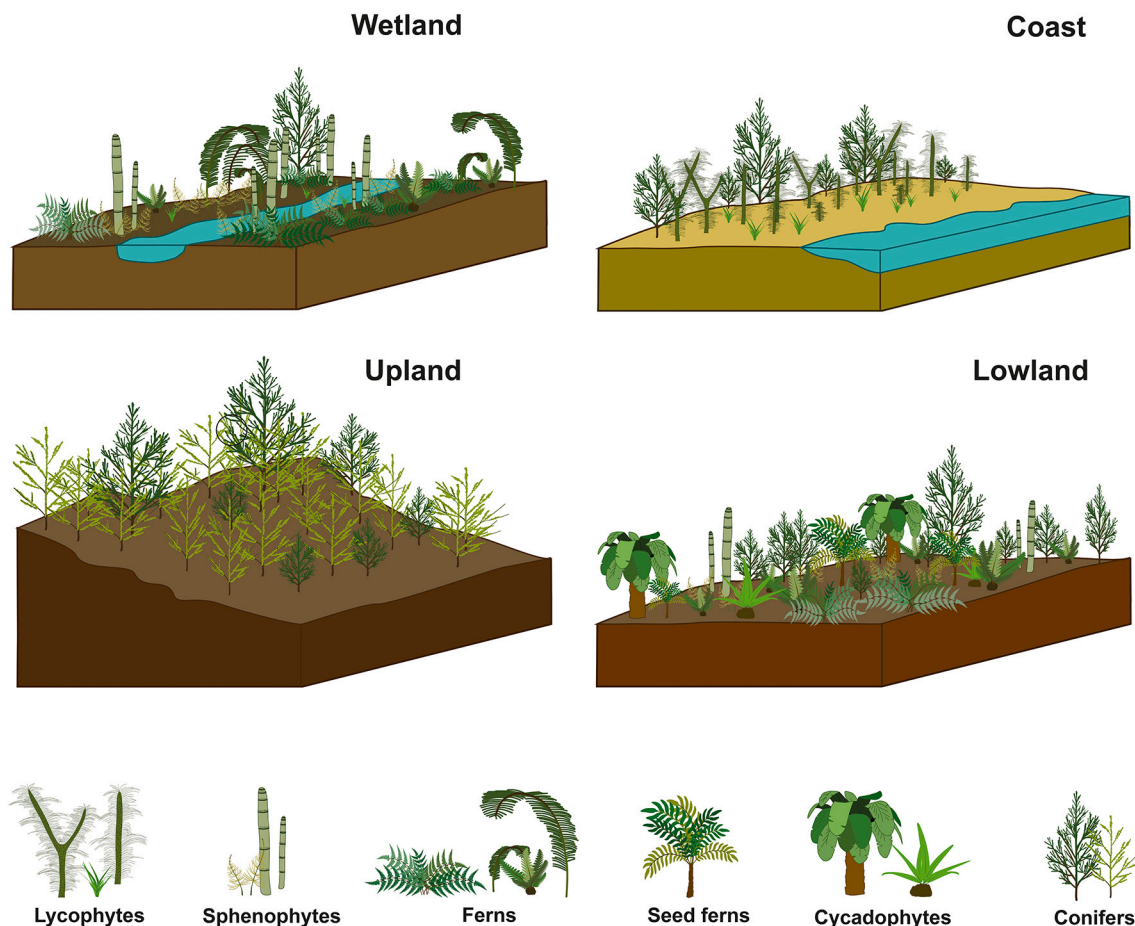

Fig. 11. Sketch of the palaeoenvironment reconstruction of Kühwiesenkopf/Monte Prà della Vacca, from coastal to wetland, lowland and upland environments.

in these areas might have formed a conspicuous vegetation cover, created shaded areas and led some plants to compete for light. This might have been the case of *Albertia* cf. *latifolia*, which was a shrub-like conifer and was remarkably different from other *Voltzia* species for its open phyllotaxy, the broad leaf-shape, and lighter isotopic composition, which could be due to the occupation by this taxon of a low irradiance niche (Fig. 11).

6. Conclusion

The isotopic composition of the dispersed organic matter in the Kühwiesenkopf/Monte Prà della Vacca section encompasses a wide positive excursion of the δ^{13}C, which may be correlated to similar shifts recorded in the Tethys realm (e.g., Southern China). There is a strong evidence that the provenance of the organic matter is mainly terrestrial. Further investigations should be carried out in order to disentangle a global isotopic signal from local effects.

Taxon-specific organic carbon isotopic analyses on various parts of well-preserved plant fossils reveal a complex pattern of intra-specific and inter-specific variability. Most notably, taxa expected to have strong environmental limitations, such as ferns, show minimal isotopic variability, whereas taxa belonging to plant groups that are adapted to a larger spectrum of habitats (e.g., conifers) show the maximum ranges of carbon isotopic compositions.

The palaeoenvironmental reconstruction of Kühwiesenkopf/Monte Prà della Vacca inferred by the organic carbon isotopic composition is fully consistent with the ecology of the different taxa previously provided based on macroremains and palynological data. Thus, plants that lived in coastal or humid habitats have ^{13}C enriched carbon isotopic compositions, whereas plant fossils attributed to lowland and upland environments have, on average, the most ^{13}C depleted isotopic compositions. However, the geochemical analysis highlights differences in the same plant groups, particular adaptations of single species and the occupation of different niches. We suggest that stable organic carbon isotope analysis of fossil plants offers a valuable contribution to paleoenvironmental interpretations of deep past plant biocenoses, especially where palaeobotanical affinity and/or functional ecology provide only partial information.

Organic carbon geochemical analyses are, thus, a very useful tool in palaeoenvironmental/palaeoecological studies, which can be combined with other investigation methods, in order to refine paleoenvironmental and paleoecological reconstructions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2022.111098.

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