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New late Palaeozoic plant remains in the Ligurian Alps (Italy)

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ABSTRACT - This paper describes palaeobotanical material discovered in new fossiliferous localities from the late Palaeozoic fluvio-lacustrine deposits of the Ollano Formation in the central part of the Ligurian Alps (north western Italy). Despite the tectono-metamorphic history that generally results in poor preservation of plant remains, abundant fossil plant specimens were preserved in less deformed portions of the rock succession. The common presence of Neuralethopteris schlehanii *(Stur, 1877) Laveine, 1967,* Laveinopteris tenuifolia *(Schlotheim ex Sternberg, 1825) Cleal et al., 1990 var.* nordfrancia *Cleal & Shute, 2003,* Neuropteris obliqua *(Brongniart, 1831) Zeiller, 1888, and* Lyginopteris *cf.* L. baeumleri *(Andrae, 1868) Gothan, 1913 provides time constraints for deposition of the Ollano Formation between the latest early Pennsylvanian and early middle Pennsylvanian, most probably within the late Bashkirian (Langsettian-early Duckmantian) with the assemblage corresponding to the* Lyginopteris hoeninghausii/Neuralethopteris schlehanii *fossil plant Zone. Our new findings of plant fossils from this formation confirm an age very close to the late Westphalian, originally proposed by previous palaeobotanical studies. This indicates that further analyses are necessary in order to better constrain the primary relationship between the Ollano Fm. and the adjacent volcanics, whose radiometric dating to the early Permian is problematic.*

RIASSUNTO - [Nuovi resti di piante tardo paleozoici delle Alpi Liguri (Italia)] - *In questo lavoro viene descritto e interpretato materiale paleobotanico proveniente da quattro nuove località fossilifere individuate all'interno dei depositi fluvio-lacustri della Formazione di Ollano, affiorante nel settore centrale delle Alpi Liguri (Italia nord-occidentale). Nonostante la storia tettono-metamorfica di questa formazione possa avere in qualche modo impedito la preservazione diffusa di materiale fossilifero, alcune porzioni di successioni apparentemente meno deformate di quelle adiacenti sono invece caratterizzate da abbondante contenuto paleofloristico. I resti vegetali sono generalmente conservati come impronte e solo alcune parti organiche sono state sostituite da riempimenti minerali. Tra le quattro località studiate solo quella di Riofreddo ha fornito una paleoflora molto diversificata (16 taxa) con* Lycopsida*,* Sphenopsida*,* Pteridopsida *e soprattutto quattro specie di* Pteridospermopsida*. Nella località Case Bertolotti si è rinvenuto soltanto un fusto di* Calamites *sp., mentre le località Pian del Bosco e Rio Farin hanno fornito rispettivamente tre e due specie, tra le quali solo* Lyginopteris *cf.* L. baeumleri *è stata rinvenuta anche a Riofreddo. La presenza di specie con distribuzione stratigrafica limitata nelle tre località più ricche* (Neuralethopteris schlehanii*,* Laveinopteris tenuifolia *var.* nordfrancia*,* Neuropteris obliqua *e* Lyginopteris *cf.* L. baeumleri*) indica che la deposizione della Formazione di Ollano è avvenuta per lo meno nell'intervallo Pennsylvaniano inferiore-medio, molto probabilmente nel Bashkiriano superiore (Langsettiano-Duckmantiano inferiore) per quanto riguarda le località di Pian del Bosco e Riofreddo. Questi dati confermano quindi le interpretazioni di studi precedenti che attribuivano la Formazione di Ollano al Carbonifero superiore (Westfaliano superiore). A questo punto risulta problematica la datazione al Permiano inferiore (Cisuraliano, Artinskiano) delle rocce vulcaniche indicate come eteropiche con la parte inferiore della Formazione di Ollano. Le nuove e più solide indicazioni biostratigrafiche fornite dai resti paleobotanici suggeriscono di riconsiderare i rapporti stratigrafici tra le vulcaniti e i metasedimenti della Formazione di Ollano. In questo senso si rendono necessarie nuove analisi geologiche e paleontologiche che possano dirimere la controversia tra le datazioni radioisotopiche e biostratigrafiche.*

INTRODUCTION

The central part of the Ligurian Alps (north western Italy) hosts several outcrops of late Palaeozoic metasedimentary successions typical of continental environments (Fig. 1; e.g., Cortesogno et al., 1988, 1993). However, in these deposits, classically ascribed to the Ollano Formation (Vanossi, 1971), records of continental floras are scarce and poorly preserved mainly due to the tectono-metamorphic Alpine history. Outcrops of terrestrial sediments, which have yielded more diverse Pennsylvanian floras, are well known in the Western Alps, in Canton Ticino and in other parts of Italy, especially in the Carnic Alps, Tuscany, and Sardinia (e.g., Ronchi et al., 2012 and references therein). The most striking examples were detected in the Briançonnais tectonic unit of the Western Alps, where an up to 2000 m thick continental succession occurs in a narrow belt that starts in Briançon and continues northward in France to the Isère Valley, and proceeds up to the Aosta Valley in NW Italy (Feys, 1963; Havlena, 1963). Another flora of middle Moscovian (Westphalian) age from the Italian southern Alps was recently confirmed in Val Sanagra in western Lombardy (Pšenička et al., 2012). Further east the Namurian-Langsettian (early Westphalian) flora is also documented from the Sava Folds in the northern part of the External Dinarides in central Slovenia (Kolar-Jurkovšek & Jurkovšek, 1985, 1986, 1990, 2002a, b, 2007). Floras of Namurian and/or Westphalian age were also studied in western Serbia (Milovanović, 1995) and eastern Serbia (Pantić, 1955). Continuing to the E and SE, coal-bearing strata of Namurian and/or early Westphalian age are known at Baia Nouă in Romanian Southern Carpathians (Popa & Cleal, 2012) and in the Svoge Basin of NW Bulgaria (Tenchov, 1976, 1977, 2007; Tenchov & Cleal, 2010).

In the Ligurian Alps, the first report on putative Carboniferous macrofloras was published in the second

half of the 19th century (see Vanossi, 1971). Portis (1887) analyzed samples collected a few years before by Domenico Zaccagna in the Viozene area (western part of the Ligurian Alps, Fig. 1) and mentioned the occurrence of *Pecopteris* (*Senftenbergia*) *elegans* Corda, 1845, *Pecopteris nodosa* (Göppert, 1836) Unger, 1845 and *Annularia longifolia* Brongniart, 1828. He attributed this assemblage to the Stephanian. In the same sector, Squinabol (1887) described remains of *Odontopteris obtusa* Brongniart, 1828 and two species of *Cordaites* Unger, 1850, supporting a late Carboniferous age for these deposits. In the same year, remains of *Annularia* Sternberg, 1821 and other plants interpreted as Carboniferous in age were observed by members of the Società Geologica Italiana during a field excursion in the Ollano area (at Pietragliata, between Mallare and Altare in the central Ligurian Alps, as reported in Issel, 1888). Later, again in the Ollano area, Bloch (1966) reported *Pecopteris plumosa-dentata* (Artis, 1825) Brongniart, 1828, *Sphenopteris schatzlarensis* (Stur, 1885) Gothan, 1913, *Neuropteris obliqua*, *Lepidophyllum* sp., and remains of *Calamites* Brongniart, 1828. He assigned this assemblage to the Westphalian, according to the palaeontological interpretation of Bellini (1964).

In this paper, we describe palaeobotanical materials discovered in new fossiliferous localities from the late Palaeozoic deposits of the Ollano Formation in the central part of the Ligurian Alps, which provide relevant information on the age of the hosting sediments (Fig. 1).

GEOLOGICAL SETTING

The Ligurian Alps represent the NW-SE striking segment of the Alpine orogenic system. They consist of different tectono-stratigraphic units derived from the Piedmont-Ligurian oceanic realm or its European marginal sectors, i.e. the Pre-Piedmont and Briançonnais domains (e.g., Vanossi et al., 1986). These units were stacked and juxtaposed during the complex tectono-metamorphic history that was controlled by European and Adriatic relationships that led to the development of the Alpine system. The plant macrofloral assemblages described in this paper belong to the late Palaeozoic deposits of the Mallare unit (Seno et al., 2010), resting in the lower structural level of the Ligurian Briançonnais nappe stack, that is largely exposed in the central part of the Ligurian Alps (Vanossi et al., 1986; Cortesogno et al., 1995).

In this unit, the Variscan continental basement (Barbassiria orthogneiss) is unconformably overlain by laterally discontinuous and < 100 m thick rhyolitic ignimbrites (Case Lisetto metarhyolites). The rhyolites have been dated at 285±1.3 Ma (Dallagiovanna et al., 2009). Often, the orthogneiss is directly overlain by metasediments of the Ollano Formation, up to some hundred meters thick. The Ollano Formation consists of grey to black micaschist and phyllites with metaconglomerate horizons and occurrence of graphite, whose original sedimentological features suggest deposition in fluvio-lacustrine environments (detailed by Vanossi, 1971 and Cortesogno et al., 1995). The Ollano Formation crops out mainly in three sectors (Riofreddo, Osiglia lake and Ollano areas, see Fig. 1b) and other patches are in the Ormea area (Fig. 1a). Although it was affected by blueschist facies metamorphism and intensive deformation (e.g., Dallagiovanna et al., 2009; Seno et al., 2010), a few outcrops of this formation (notably in the Ollano area) preserved plant remains, classically interpreted as late Carboniferous in age.

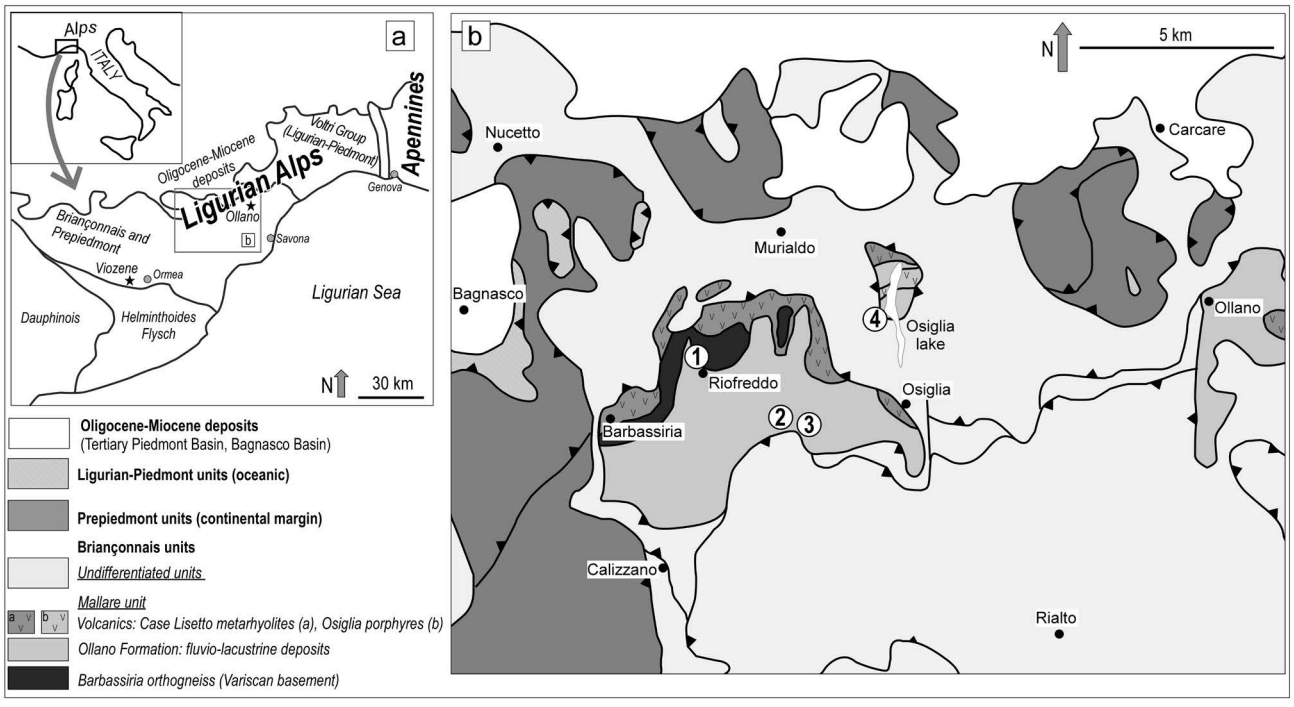


Fig. 1 - a) Regional framework of the Ligurian Alps. Black stars refer to the Viozene and Ollano areas, where possible Carboniferous macrofloras were first reported (explanation in the text). b) Simplified tectonic map of the central Ligurian Alps (after Seno et al., 2010). Numbers refer to the new fossiliferous sites described in this paper 1: Riofreddo, 2: Pian del Bosco, 3: Rio Farin, 4: Case Bertolotti.

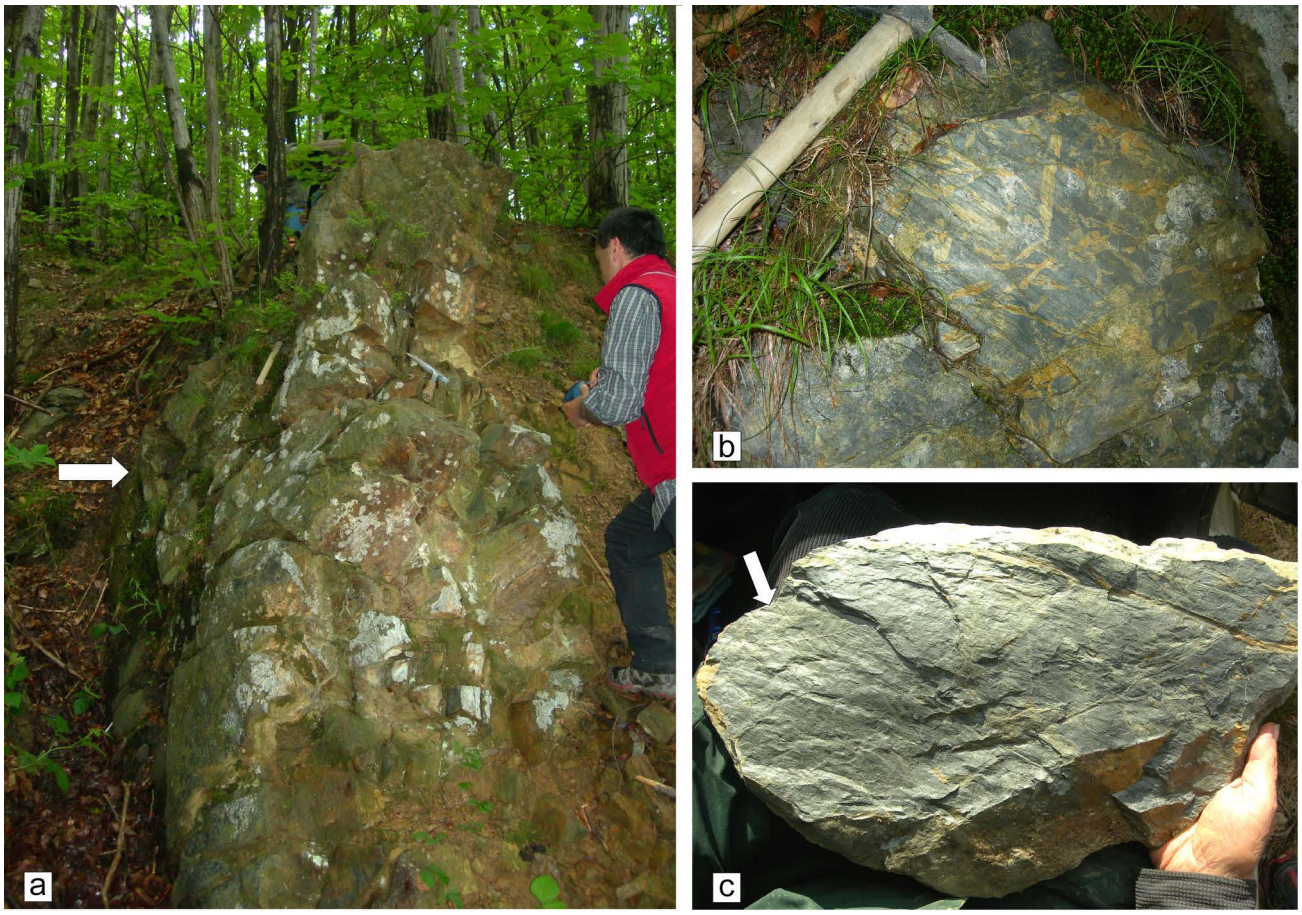


Fig. 2 - (Color online) a) Riofreddo outcrop of the Ollano Formation. White arrow shows the position of metasiltites with plant impressions. b) Details of the bedding plane at the top of the succession with plant impressions. c) Example of a large block of metasiltite containing part of a pinna of *Karinopteris acuta* (shown in Pl. 3, fig. 3).

MATERIALS

Fossil plant remains described in this study were collected from four new fossiliferous localities of the Ollano Formation (Fig. 1). In the localities Pian del Bosco and Rio Farin (sites 2 and 3 in Fig. 1b) plant remains were collected directly from shaly sediments in a short outcropping succession. In the Riofreddo locality (site 1 in Fig. 1b), a short oucropping section (Fig. 2) provided only unidentifiable plant remains preserved in dark grey shale and very fine sandstone, whereas scattered shale blocks in the surrounding woodland provided abundant material. Plant remains have been found also around the Osiglia Lake at Case Bertolotti (site 4 in Fig. 1b).

The plant remains are preserved in all localities as impressions, and only a few organic parts have been replaced by mineral infilling. The embedding rock is usually extensively deformed, and the plant impressions are hardly visible. However, a few small-sized remains preserved an excellent morphological detail, possibly due to early diagenesis.

The plant fossils have been exposed by splitting sediment blocks along the bedding planes; no further preparation was required. The most representative specimens were photographed with a Nikon Coolpix camera and the corresponding rock slabs were registered in the collections of the Museo di Geologia e Paleontologia dell'Università degli Studi di Torino (Tab. 1: coll. nrs MGPT-PU105918-105950).

SYSTEMATIC PALAEONTOLOGY

Class Lycopsida Scott, 1909
Order Lepidocarpales Thomas & Brack-Hane, 1984
Family Uncertain

Genus *Lepidophloios* Sternberg, 1825

Lepidophloios sp.
(Pl. 1, figs 1, 5)

Locality and material - Riofreddo, MGPT-PU105918, 105922.

Description - Lycopsid shoots possess helically arranged rhomboidal leaf cushions, which are wider than long, a feature typical of the genus *Lepidophloios*. The shoot MGPT-PU105918 is about 30 mm long and up to 7 mm wide consisting of a shoot impression without leaves (Pl. 1, fig. 1). Better preserved leaf cushions are visible on MGPT-PU105922 which are 3.8 mm wide and 2.3 mm high, flat with acute lateral angles (Pl. 1, fig. 5). No keel is present. A small, irregular scar situated just

Catalogue nr.	Preliminary sample nr.	Taxa	Locality	Reference to Plates
MGPT_PU105918	/	*Lepidophloios* sp.	Riofreddo	Pl. 1, fig. 1
MGPT_PU105919	2432	*Bergeria* sp.	Riofreddo	Pl. 1, fig. 2
MGPT_PU105920	2415	*Lepidostrobophyllum* sp.	Riofreddo	Pl. 1, fig. 3
MGPT_PU105921	2416	*Lepidostrobophyllum* sp.	Riofreddo	Pl. 1, fig. 4
MGPT_PU105922	2417	*Lepidophloios* sp.	Riofreddo	Pl. 1, fig. 5
MGPT_PU105923	2479	*Cyperites* sp.	Riofreddo	Pl. 1, fig. 6
MGPT_PU105924	2459	*Stigmaria ficoides*	Riofreddo	Pl. 1, fig. 7
MGPT_PU105925	2127	*Calamites* sp.	Case Bertolotti	Pl. 2, fig. 1
MGPT_PU105926	2462	*Asterophyllites equisetiformis*	Riofreddo	Pl. 2, fig. 2
MGPT_PU105927	2472bis	*Asterophyllites charaeformis*	Riofreddo	Pl. 2, fig. 3
MGPT_PU105928	2470	*Sphenophyllum* cf. *S. cuneifolium*	Riofreddo	Pl. 2, fig. 4
MGPT_PU105929	2431	*Zeilleria frenzlii*	Riofreddo	Pl. 2, fig. 5
MGPT_PU105930	2475	*Lyginopteris* cf. *L. baeumleri*	Riofreddo	Pl. 2, fig. 6
MGPT_PU105931	2475	*Lyginopteris* cf. *L. baeumleri*	Riofreddo	Pl. 2, fig. 7
MGPT_PU105932	2410	*Senftenbergia plumosa*	Riofreddo	Pl. 2, fig. 8
MGPT_PU105933	2464	*Karinopteris acuta*	Riofreddo	Pl. 3, fig. 1
MGPT_PU105934	2460	*Karinopteris acuta*	Riofreddo	Pl. 3, fig. 2
MGPT_PU105935	2457	*Karinopteris acuta*	Riofreddo	Pl. 3, fig. 3
MGPT_PU105936	2189	*Eusphenopteris* sp.	Pian del Bosco	Pl. 3, fig. 4
MGPT_PU105937	2408bis	*Laveinopteris tenuifolia*	Riofreddo	Pl. 3, fig. 5
MGPT_PU105938	2396	*Laveinopteris tenuifolia*	Riofreddo	Pl. 3, fig. 6
MGPT_PU105939	2456bis	*Laveinopteris tenuifolia*	Riofreddo	Pl. 3, fig. 7
MGPT_PU105940	2403	*Neuralethopteris schlehanii*	Riofreddo	Pl. 3, fig. 8
MGPT_PU105941	2211	*Linopteris* cf. *L. neuropteroides*	Rio Farin	Pl. 4, fig. 1
MGPT_PU105942	2175	cf. *Neuropteris obliqua*	Pian del Bosco	Pl. 4, fig. 2
MGPT_PU105943	2178bis	cf. *Neuropteris obliqua*	Pian del Bosco	Pl. 4, fig. 3
MGPT_PU105944	2182	cf. *Neuropteris obliqua*	Pian del Bosco	Pl. 4, fig. 4
MGPT_PU105945	2178	cf. *Neuropteris obliqua*	Pian del Bosco	Pl. 4, fig. 5
MGPT_PU105946	2205	*Carpolites* sp.	Rio Farin	Pl. 4, fig. 6
MGPT_PU105947	/	*Samarospis* sp.	Riofreddo	Pl. 4, fig. 7
MGPT_PU105948	2200	enigmatic microfossils on *Linopteris* cf. *L. neuropteroides*	Rio Farin	Pl. 4, fig. 8
MGPT_PU105949	2475	enigmatic microfossils on pteridosperm axis	Riofreddo	Pl. 4, fig. 9
MGPT_PU105950	2398	cf. *Arthropleura* sp.	Riofreddo	Pl. 4, fig. 10

Tab. 1 - List of the samples figured in this paper with catalogue numbers (collections of the Museo di Geologia e Paleontologia dell'Università degli Studi di Torino, acronym: MGPT-PU), temporary sample number (marked on the sample during preparation), identification, locality and reference to the Plates.

below the apex probably marks the position of leaf base. Relatively poor preservation, however, allows only for generic determination of the specimen.

Stratigraphical occurrence - Representatives of the genus *Lepidophloios* are typical plants of Bashkirian and Moscovian wetlands (DiMichele & Phillips, 1994), however, their rare remains occur up to late Gzhelian (e.g., Opluštil et al., 2013).

Genus *Bergeria* Presl in Sternberg, 1838

Bergeria sp.
(Pl. 1, fig. 2)

Locality and material - Riofreddo, MGPT-PU105919.

Description - MGPT-PU105919 bears a long, leafy shoot approximately 25 mm long, that dichotomizes at an

acute angle. The shoot is about 2.5 mm wide below the dichotomy. Leaves are narrow, gently S-shaped and at least 6 mm long. Leaf cushions cannot be properly identified.

Remarks - Small narrow leaves are typical for *Paralycopodites* Morey & Morey, 1977, a fossil-genus of anatomically defined arborescent lycopsid, whose corresponding compression (without anatomical detail) is the fossil-genus *Bergeria* that is defined on features of its leaf cushions (Álvarez-Vázquez & Wagner, 2014). The S-shaped leaves of the specimen resemble those of *Lepidodendron simile* Kidston in Jongmans, 1909 from Langsettian and Duckmantian of Belgium and UK and also from the late Duckmantian strata in the basins of central Bohemia, Czech Republic (Němejc, 1947). However, this species differs from the specimen described here in having generally longer leaves and therefore very probably represents a different taxon. The length and partly the shape of leaves of the specimen MGPT-PU105919 can be also compared with the leafy shoots of *Lepidodendron lycopodioides* Sternberg, 1820 from Duckmantian strata of the Czech Republic (e.g., Opluštil et al., 2009). Nevertheless, preservational limitations prevent more reliable comparison, therefore we suggest keeping *Bergeria* sp. as a cautionary determination.

Stratigraphical occurrence - *Bergeria* is a genus that is typical for late Mississippian to middle Pennsylvanian in Europe and North America.

Genus *Lepidostrobophyllum* Hirmer, 1927

Lepidostrobophyllum sp.
(Pl. 1, figs 3-4)

Locality and material - Riofreddo, MGPT-PU105920, 105921.

Description - MGPT-PU105920 preserves a basal lamina fragment with a broken apex. It is 12 mm long and 3.5 mm wide, being widest at the base and tapering to the apex with slightly concave entire margins. The base of the lamina is straight and the midrib is fairly prominent. Another lamina is associated with a sporophyll-bearing sporangium preserved in lateral view. The sporangium is oval, 5 mm long and 3 mm wide. The lamina is incomplete, > 6 mm long. The second specimen MGPT-PU105921 represents a fragment of the apical part of a narrow sporophyll lamina that is 22 mm long and 3 mm wide, with entire margins and gently tapering from base to the apex. The midrib is fairly prominent along the whole preserved length except towards the base. Isolated lycopsid laminae of this size, having entire margins and obviously tapering to the apex, are typical for sporophylls of lepidodendroid cones that after maturation can disarticulate to release individual sporophylls.

Remarks - Relatively small narrow laminae possessing straight or slightly concave margins can be assigned to *Lepidostrobophyllum* when isolated. However, these structures are typical of *Lepidostrobus* (Brongniart, 1828) Brack-Hanes & Thomas, 1983 or *Flemingites* (Carruthers, 1865) Brack-Hanes & Thomas, 1983 type of cones born by some lepidodendroid lycopsids (Bateman et al., 1992). The former is a microsporangiate cone bearing lycospores and the latter is a bisporangiate cone produced by lycopsids of the genus *Paralycopodites*, whose corresponding leaf cushion compression is very probably *Bergeria* (Brack-Hanes & Thomas, 1983; Álvarez-Vázquez & Wagner, 2014). To distinguish between them based on fragmentary evidence is very difficult because isolated sporophylls are often morphologically very similar. Another problem is the variability of sporophylls within the cones as described by various authors (e.g., Boulter, 1968), which further makes a precise identification of the species difficult or impossible. Nevertheless, presence of lepidodendroid sporophylls in the small plant collection from Riofreddo suggests that their parent plants could be fairly common in the palaeovegetation, as typical for early to middle Pennsylvanian tropical wetlands (Phillips, 1981).

Stratigraphical occurrence - *Lepidostrobophyllum* is typical for the middle Pennsylvanian in Europe and North America (Phillips, 1981). However, very rare remains occur up to late Gzhelian (e.g., Opluštil et al., 2013).

Genus *Cyperites* Brongniart, 1828

Cyperites sp.
(Pl. 1, fig. 6)

Locality and material - Riofreddo, MGPT-PU105923.

Description - MGPT-PU105923 shows several parallel grass-like leaves, possibly attached to a shoot. The shoot itself is fully covered by leaves, which excludes more accurate determination based on morphology of leaf cushions. The leaves are incomplete, more than 110 mm long and 3-4 mm wide, with entire margin and clearly recognizable midvein.

Remarks - Such type of leaves are common in association with a wide range of arborescent and subarborescent lycopsid fossil-genera used for woody axes, including *Sigillaria* Brongniart, 1822, *Lepidodendron* Sternberg, 1820, *Lepidophloios* Sternberg, 1820, *Omphalophloios* White, 1898, *Polysporia* Newberry, 1873 and *Spencerites* Scott, 1897. The diameter of the axis to which the leaves are attached excludes most of them, so that the leaf of *Cyperites* sp. was most probably produced by a *Lepidodendron* Sternberg, 1820 or *Lepidophloios* stem.

Stratigraphical occurrence - *Cyperites* is a long-ranging taxon, most common in early to middle Pennsylvanian strata (Phillips, 1981).

Genus *Stigmaria* Brongniart, 1822

Stigmaria ficoides (Sternberg, 1820) Brongniart, 1822
(Pl. 1, fig. 7)

Locality and material - Riofreddo, MGPT-PU105924.

Description - MGPT-PU105924 is a fragment of a stigmarian root that possesses characteristic rounded

appendice scars that are 3 mm in diameter with a smooth surface. Some other specimens, that may also belong to this species, show only dark bands with indistinct small rounded structures which also probably represent stigmarian roots.

Remarks - Remains of arborescent lycopsid "root" system *Stigmaria* have traditionally been interpreted as an indication for in situ plant growth, but fragments may also be transported.

Stratigraphical occurrence - *Stigmaria* co-occurs from Devonian to Permian with such tree form of lycopsids as *Lepidodendron, Lepidophloios,* and other genera (Taylor et al., 2009).

Division Equisetopsida Agardh, 1825
Order Equisetales Dumortier, 1829
Family Calamostachyaceae Meyen, 1978

Genus *Calamites* Brongniart, 1828

Calamites sp.
(Pl. 2, fig. 1)

Locality and material - Case Bertolotti, MGPT-PU105925.

Description - Some very poorly preserved (probably also decayed) specimens probably represent calamitalean main stem fragments. The stem MGPT-PU105925 is ca. 25 mm broad and the distance between successive nodes is 20 mm. Longitudinal canals are straight and 1-2 mm wide. Due to preservational limitations a specific determination is not possible.

Stratigraphical occurrence - *Calamites* occurs from Late Devonian and reached a peak diversity in the Pennsylvanian (Taylor et al., 2009).

Genus *Asterophyllites* Brongniart, 1828

Asterophyllites equisetiformis (Schlotheim, 1820 ex Sternberg, 1825) Brongniart, 1828
(Pl. 2, fig. 2)

Locality and material - Riofreddo, MGPT-PU105926.

Description - MGPT-PU105926 is the best preserved specimen (Pl. 2, fig. 2) which shows shoots attached to a higher order axis. Leaves are typically short, 2.5 mm long, acicular and arranged in whorls. The distance of two adjacent whorls (internode) is 1.1-1.3 mm. The axis with leaves is 0.7 mm wide, whereas the higher order axes is 1.2 mm wide. The distance of two adjacent whorls (internode) on the higher order axis is 5 mm. All axis bear longitudinal canals.

Stratigraphical occurrence - The species is of long stratigraphical range and low importance occurring throughout the entire Pennsylvanian and early Permian.

Asterophyllites charaeformis (Sternberg, 1825) Göppert, 1844
(Pl. 2, fig. 3)

Locality and material - Riofreddo, MGPT-PU105927.

Description - Leaves are very small, 2-3 mm long, curved towards the axis, sometimes as long as the internode and sometimes encroaching on adjacent whorl. The axis is 0.4 mm wide. Number of leaves per whorls is unknown, but based on what is left only few leaves are present per node. *A. charaeformis* is similar to *Asterophyllites grandis* (Sternberg, 1825) Geinitz, 1855. Nevertheless, the latter has longer leaves (5-10 mm) with 16-20 leaves per node, whereas *A. charaeformis* has shorter leaves (1.5-3 mm) and 4-5 leaves per node (Abbott, 1958).

Stratigraphical occurrence - Boureau (1964) stated that the stratigraphical range of *A. charaeformis* is from late Bashkirian to Moscovian (Westphalian).

Order Sphenophyllales Dumortier, 1829
Family Sphenophyllaceae Meyen, 1978

Genus *Sphenophyllum* Brongniart, 1828

Sphenophyllum cf. *S. cuneifolium* (Sternberg, 1821) Zeiller, 1879
(Pl. 2, fig. 4)

Locality and material - Riofreddo, MGPT-PU105928.

Description - Only one specimen of the genus *Sphenophyllum* was found in the studied area and

EXPLANATION OF PLATE 1

Plant remains from Riofreddo.

Fig. 1 - *Lepidophloios* sp.; shoot with leave scars; scale bar corresponds to 5 mm.

Fig. 2 - *Bergeria* sp.; dichotomized terminal shoot with leaves; scale bar corresponds to 5 mm.

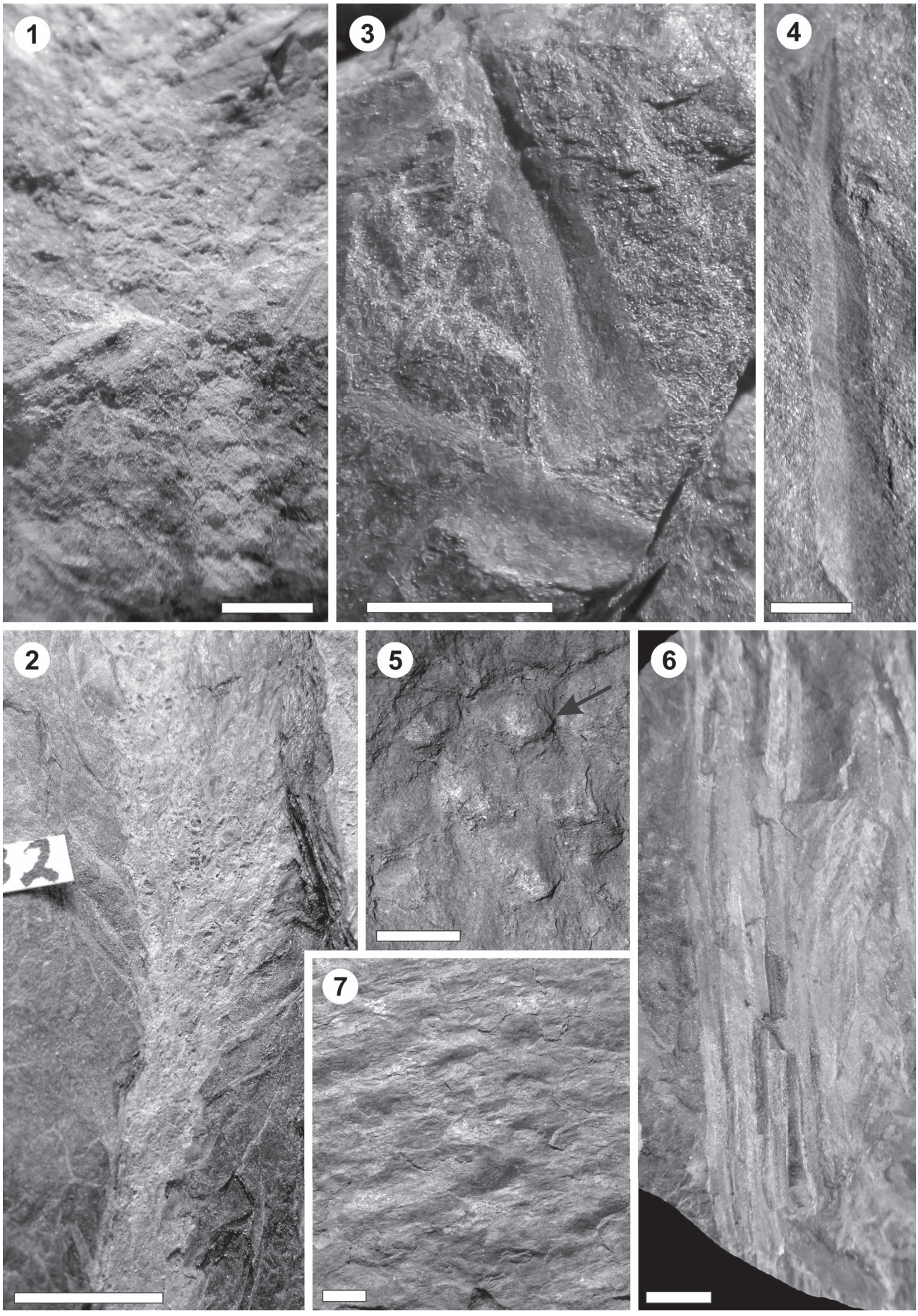
Figs 3-4 - *Lepidostrobophyllum* sp.; scale bars correspond respectively to 5 and 3 mm.

Fig. 5 - *Lepidophloios* sp.; arrow shows leaf scar, SEM photo; scale bar corresponds to 2 mm.

Fig. 6 - *Cyperites* sp.; grass-like leaves which are attached to undefined stem; scale bar corresponds to 10 mm.

Fig. 7 - *Stigmaria ficoides* (Sternberg, 1820) Brongniart, 1822; part of lycopsid "roots"; scale bar corresponds to 10 mm.

Catalogue numbers and localities are reported in Tab. 1.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is assigned to *S. cuneifolium*. MGPT-PU105928 is represented by relatively broad stem and well-organized leaves. Nevertheless, the leaves are not well preserved and some details are impossible to determine. The stem is 1 mm wide and composed of nodes and internodes with longitudinal canals. The interval between nodes is 3 mm. The leaf shape, lamina and venation are unknown.

Stratigraphical occurrence - This species has a long stratigraphical range from the Bashkirian to late Moscovian (e.g., Wagner, 1984) and as a whole indicates an early to middle Pennsylvanian age.

Class Polypodiopsida Cronquist et al., 1966
Order Polypodiales Link, 1833
Family Tedeleaceae Eggert & Taylor, 1966

Genus *Senftenbergia* Corda, 1845

Senftenbergia plumosa (Artis, 1825) Stur, 1885
(Pl. 2, fig. 8)

Locality and material - Riofreddo, MGPT-PU105932.

Description - MGPT-PU105932 is a small, very poorly preserved fragment of this species, represented by part of the distal end of an ultimate pinna that bears several complete pinnules. The ultimate rachis is straight, 0.3 mm wide. Pinnules are lobate, of the pecopterid-type, slightly contracted at the base, and inserted at an angle of 35° to the penultimate rachis. The largest pinnules are 3 mm long and 1 mm wide, showing entire or slightly sinuous margins, bearing probably 2-3 pairs of lobes. The midvein is almost straight and lateral veins are not visible.

Stratigraphical occurrence - *S. plumosa* is a long-ranging taxon reported from early Bashkirian (e.g., Purkyňová, 1962) to Gzhelian (Tásler et al., 1979), i.e. it ranges throughout most of the Pennsylvanian sub-system. Some other species of the genus (e.g., *Senftenbergia saxonica* Barthel, 1975) occur even in early Permian strata (Barthel, 1976).

Order Incerate sedis
Family Incertae sedis

Genus *Zeilleria* Kidston, 1884

Zeilleria frenzlii (Stur, 1883) Kidston, 1884
(Pl. 2, fig. 5)

Locality and material - Riofreddo, MGPT-PU105929.

Description - This species is a common plant from the Riofreddo locality. Specimens often show penultimate pinnae (ca. 18 mm long) which are in some cases attached to penultimate, 0.8 mm broad and straight rachises. Pinnules alternate on a slightly sinusoid, 0.7 mm broad, penultimate rachis (Pl. 2, fig. 5) and they are 4-5 mm long and 3-4 mm wide in the proximal part of ultimate pinna. Pinnules in the distal part of the ultimate pinna are smaller with fewer laminar lobes and pinnules near the apex are bifid (Pl. 2, fig. 5 arrows) or reduced into single linear segments. The largest pinnules are divided into several linear, pointed lobes. Some specimens show fertile pinnules which are represented by small globular organs, longitudinally striated, attached on the lobe apices. The presence of *Zeilleria*-type reproductive organs (Thomas & Crampton, 1971) allows these plant remains to be assigned to the genus *Zeilleria*. Nevertheless, the fertile specimens are very poorly preserved and we cannot provide details of their morphology.

Stratigraphical occurrence - This species was detected from the latest Bashkirian (early Langsettian) (Álvarez-Vázquez, 1999) to the middle part of the Moscovian (Bolsovian) (Němejc, 1953). Mostly it occurs in the lower part of the Moscovian (Duckmantian) (Němejc, 1953).

Class Pteridospermopsida Oliver & Scott, 1904
Order lyginopteridales Corsin, 1960
Family Lyginopteridaceae Potonié, 1900

Genus *Lyginopteris* Potonié, 1897

Lyginopteris cf. *L. baeumleri* (Andrae, 1868) Gothan, 1913
(Pl. 2, figs 6-7)

EXPLANATION OF PLATE 2

Plant remains from Case Bertolotti and Riofreddo.

Fig. 1 - *Calamites* sp.; scale bar corresponds to 10 mm.

Fig. 2 - *Asterophyllites equisetiformis* (Schlotheim, 1820 ex Sternberg, 1825) Brongniart, 1828; shoot with leaves; scale bar corresponds to 5 mm.

Fig. 3 - *Asterophyllites charaeformis* (Sternberg, 1825) Göppert, 1844; shoot with leaves; scale bar corresponds to 5 mm.

Fig. 4 - *Sphenophyllum* cf. *S. cuneifolium* (Sternberg, 1821) Zeiller, 1879; fragment of shoot with leaves; scale bar corresponds to 3 mm.

Fig. 5 - *Zeilleria frenzlii* (Stur, 1883) Kidston, 1884; laminar pinnules attached to ultimate rachis; scale bar corresponds to 5 mm.

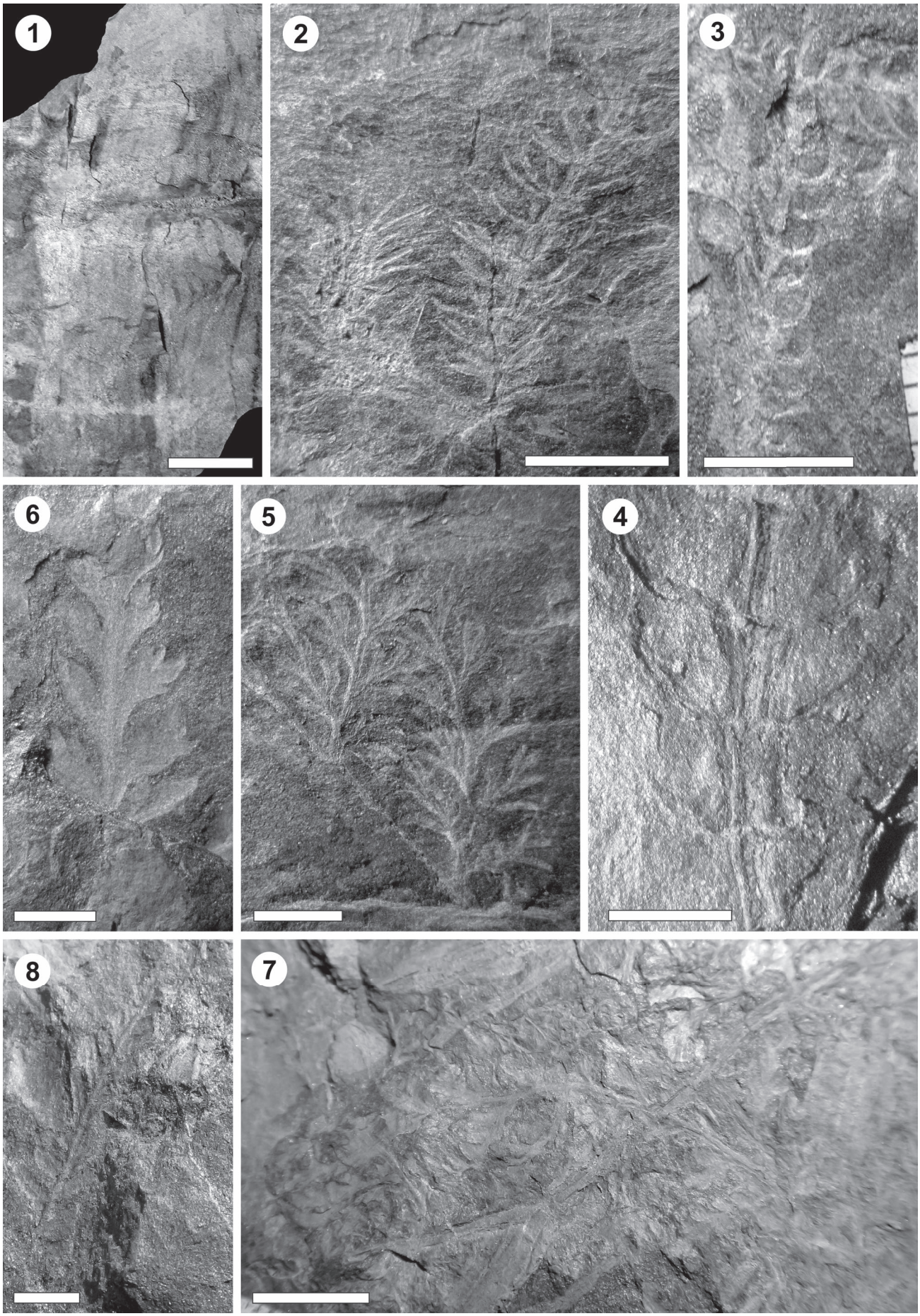
Figs 6-7 - *Lyginopteris* cf. *L. baeumleri* (Andrae, 1868) Gothan, 1913.

6 - terminal part of penultimate pinna; scale bar corresponds to 3 mm;

7 - distal parts of penultimate pinnae; scale bar corresponds to 10 mm.

Fig. 8 - *Senftenbergia plumosa* (Artis, 1825) Stur, 1885; terminal part of ultimate pinna with small pinnules; scale bar corresponds to 5 mm.

Catalogue numbers and localities are reported in Tab. 1.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Localities and material - Riofreddo, MGPT-PU105930, MGPT-PU105931; Pian del Bosco.

Description - This species is relatively frequent at the Riofreddo locality and is represented by several small fragments of the plant. The distal end of a penultimate pinna with several deformed and incomplete ultimate pinnae is preserved in MGPT-PU105931. The isolated fragments of the penultimate rachis are hairy. The penultimate rachis is 0.8 mm wide, partly winged, especially in the apical part (Pl. 2, fig. 6). Pinnules are very small, 2.0-3.5 mm long and 1.2-2.0 mm wide, attached to the supporting rachis by their entire base, but sometimes pinnule bases may be slightly constricted. According to Potonié (1900), typical pinnules of this species are widely elliptic, ovate to ovate-elliptic with rounded small lobes, as observed (Pl. 2, fig. 7) in MGPT-PU105931. Venation is not visible.

Remarks - The morphology of the studied pinnules corresponds with the type specimens of the species, but venation in the new materials is not preserved, hence the tentative assignment to *L.* cf. *L. baeumleri*.

Stratigraphical occurrence - This species is typically found in the latest Bashkirian (Langsettian) (Patteisky, 1957; Purkyňová, 1962; Cleal & Thomas, 1996).

Genus *Eusphenopteris* Simon-Scharold, 1934

Eusphenopteris sp.
(Pl. 3, fig. 4)

Locality and material - Pian del Bosco, MGPT-PU105936.

Description - MGPT-PU105936 shows a complete lobate sphenopterid pinnule which indicates an eusphenopterid pteridosperm plant. The pinnule is 17 mm long and 12 mm wide, with lobate/sub-lobate margins and a very constricted base. Lobes are obtuse and venation is not visible.

Remarks - Pinnule morphology is very similar to *Eusphenopteris sauveurii* (sensu Crépin, 1880) Simons-Scharold, 1934 f. [forma] *sauverurii* Van Amerom, 1975, but the pinnule of the present specimen is too large for that species. Our specimen more closely resembles *E. sauverurii* f. *grandipungens* Van Amerom, 1975, which is characterized by larger pinnules than *E. sauveurii* f. *sauverurii.* Nevertheless, due to the fact that only one complete pinnule without venation is preserved, the specimen cannot be identified at species level.

Stratigraphical occurrence - *E. sauveurii* f. *sauverurii* is late Bashkirian (Langsetian) to middle Moscovian (Bolsovian) in age and it is very abundant in late Bashkirian (Langsetian) (Van Amerom, 1975). Occurrence of *E. sauveurii* f. *grandipungens* approximately corresponds to that of the foregoing form.

Family Incertae sedis

Genus *Carpolites* Sternberg, 1820

Carpolites sp.
(Pl. 4, fig. 6)

Locality and material - Rio Farin, MGPT-PU105946.

Description - MGPT-PU105946 shows a very small object (1.6 x 1.2 mm) with some morphological traits of the seeds of lyginopterid plants (Gensel & Skog, 1977). Nevertheless, the seed is longitudinally compressed, so that the length is unknown. The dark area which surrounds the seed probably represents the vegetative envelope with a protective function (e.g., a uniovular cupule or integument).

Remarks - Some similarities with the seeds *Rhabdocarpus* Göppert & Berger in Berger, 1848 can be observed, especially the small species *Rhabdocarpus*

EXPLANATION OF PLATE 3

Plant remains from Pian del Bosco and Riofreddo.

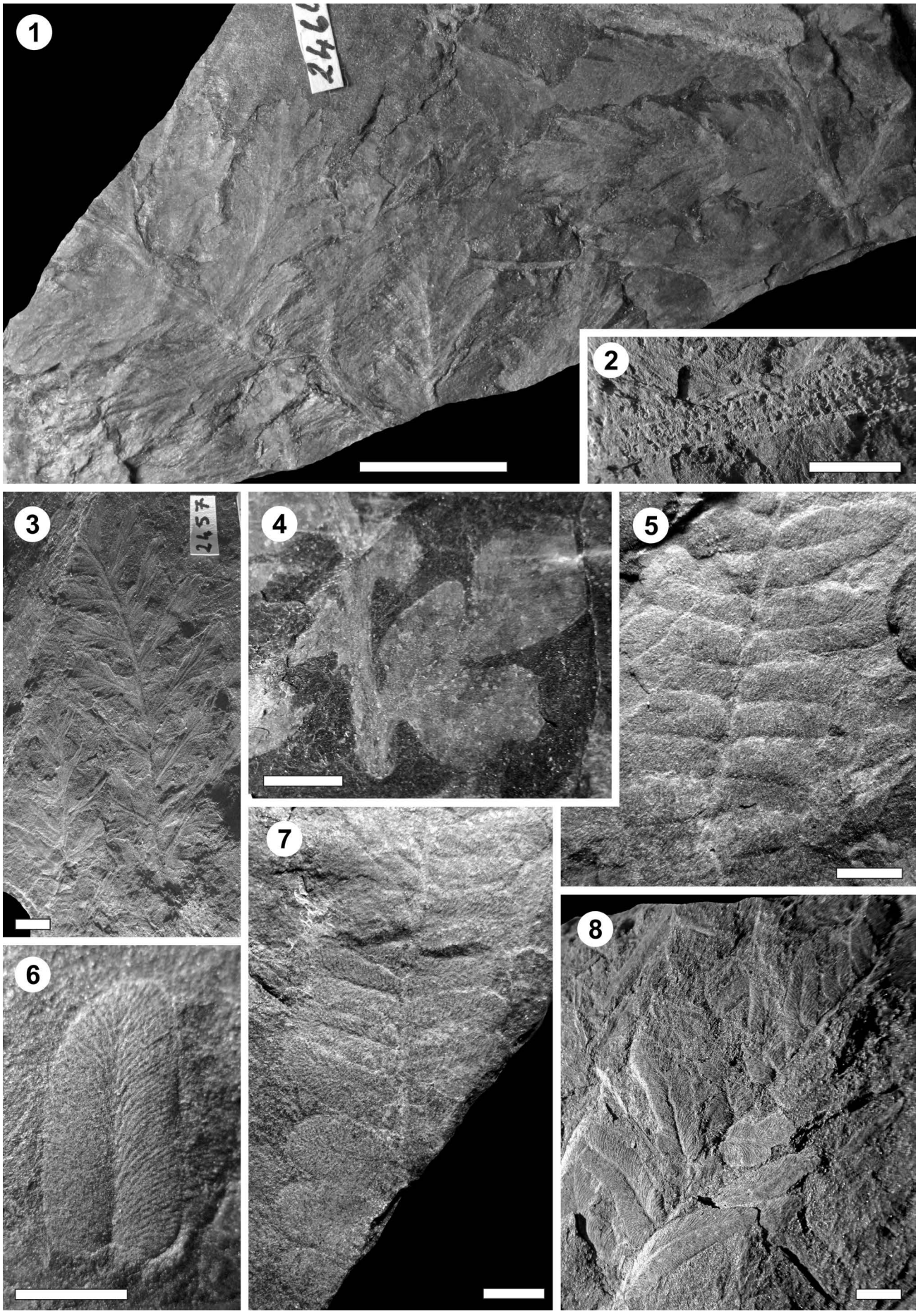
Figs 1-3 - *Karinopteris acuta* (Brongniart, 1828) Boersma, 1972.
1 - pinnules attached to rachis; scale bar corresponds to 10 mm;
2 - detail of rachis with transversal marks; scale bar corresponds to 10 mm;
3 - upper part of pinna; scale bar corresponds to 5 mm.

Fig. 4 - *Eusphenopteris* sp.; isolated pinnule; scale bar corresponds to 5 mm.

Figs 5-7 - *Laveinopteris tenuifolia* (Schlotheim, 1820 ex Sternberg, 1825) Cleal et al., 1990 var. nordfrancia Cleal & Shute, 2003.
5 - several pinnules attached to ultimate rachis; scale bar corresponds to 5 mm;
6 - isolated pinnule with very dense venation; scale bar corresponds to 5 mm;
7 - several pinnules attached to ultimate rachis; scale bar corresponds to 5 mm.

Fig. 8 - *Neuralethopteris schlehanii* (Stur, 1877) Laveine, 1967; several pinnules attached to ultimate rachis in distal part of pinna; scale bar corresponds to 5 mm.

Catalogue numbers and localities are reported in Tab. 1.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fasciculatus Lesquereux, 1879. Seeds of *Rhabdocarpus* are ovate or oblong, striate, with acute or acuminate tip, surrounded by a vegetative envelope (Lesquereux, 1879). However, as in the other specimens from the studied area, the bad state of preservation does not provide sufficient details for a precise comparison, and we just notice that this is a "seed". The assignment to lyginopterids is only based on size, therefore classification is very uncertain and the fossil is assigned to *Carpolites*, a repository for carpological remains from almost all geological horizons (Martinetto, 2015).

Stratigraphical occurrence - The artificial genus *Carpolites* was described from Devonian to Cenozoic strata (Taylor et al., 2009; Martinetto, 2015).

Order Callistophytales Rothwell, 1981
Family Callistophytaceae Stidd & Hall, 1970

Genus *Karinopteris* Boersma, 1972

Karinopteris acuta (Brongniart, 1828) Boersma, 1972
(Pl. 3, figs 1-3)

Locality and material - Riofreddo, MGPT-PU105933, 105934, 105935.

Description - Fossil remains of this species are very common at Riofreddo, including large frond fragments (e.g., Pl. 3, fig. 1). According to the terminology of Boersma (1972, p. 19), R3 (1 mm broad) and R4 (0.5 mm) rachises are shown on Pl. 3, figs 1 and 3. P4 pinnae are 16-22 mm long and 7 mm wide. Basiscopic and acroscopic pinnules on ultimate pinnae (P4) do not show a particularly abnormal development. Pinnules are elongated, 5 mm long and 2-3 mm wide, partly coalescent in the lowermost part, attached to R4 rachis with the broad, slightly constricted base. The pinnule margin is dentate (Pl. 3, fig. 1). Venation is not clearly visible, but in some parts it appears that pinnules have a distinct midvein from which lateral veins, branching several times, depart at acute angles.

Remarks - *K. acuta* is very similar to *Mariopteris sarana* Potonié ex Huth, 1912, but the last one differs in having a distinctly dentate pinnule margin. This type of margin (or laciniate) is present in *Mariopteris laciniata* Potonié ex Huth, 1912, but pinnules of this species are different from the Italian specimens in having constricted pinnule bases.

Stratigraphical occurrence - *K. acuta* is typical for Bashkirian (Opluštil et al., 2016).

Order Medullosales Corsin, 1960
Family Alethopteridaceae Corsin, 1960

Genus *Neuralethopteris* Cremer, 1893 emend. Laveine, 1967

Neuralethopteris schlehanii (Stur, 1877) Laveine, 1967
(Pl. 3, fig. 8)

Locality and material - Riofreddo, MGPT-PU105940.

Description - *N. schlehanii* is represented by numerous isolated pinnules or pinna fragments. MGPT-PU105940 (Pl. 3, fig. 8) shows the terminal part of an ultimate pinna where pinnules are reduced in size. The terminal pinnule is not preserved and lateral pinnules are tongue-shaped, elongated, sometimes tending to be subtriangular, and ca. 16 mm long and 5 mm wide. The pinnule apex is mostly rounded, very occasionally bluntly acuminate, and the pinnule base, except in the distal part of the pinna, is weakly cordate. The pinnules alternate with the space between margin. The midvein is distinct, extends for 4/5 of the pinnule length. Lateral veins are produced from the midvein at angles varying from 32-40°, and then proceed in a somewhat angular manner towards the pinnule margin, with a slight kink at each fork of the veins. The veins usually meet the pinnule margin at ca. 80°. The veins

EXPLANATION OF PLATE 4

Plant remains and enigmatic fossils from Pian del Bosco, Rio Farin and Riofreddo.

Fig. 1 - *Linopteris* cf. *L. neuropteroides* (Gutbier in Geinitz, 1855) Potonié, 1897; isolated pinnule with venation; scale bar corresponds to 5 mm.

Figs 2-5 - cf. *Neuropteris obliqua* (Brongniart, 1831) Zeiller, 1888.

2 - tip of ultimate pinna with apical pinnules; scale bar corresponds to 5 mm;

3 - distal end of pinna; scale bar corresponds to 5 mm;

4 - distal end of pinna; scale bar corresponds to 5 mm;

5 - oblique pinnules attached to support rachis; scale bar corresponds to 5 mm.

Fig. 6 - *Carpolites* sp.; small seed; scale bar corresponds to 1 mm.

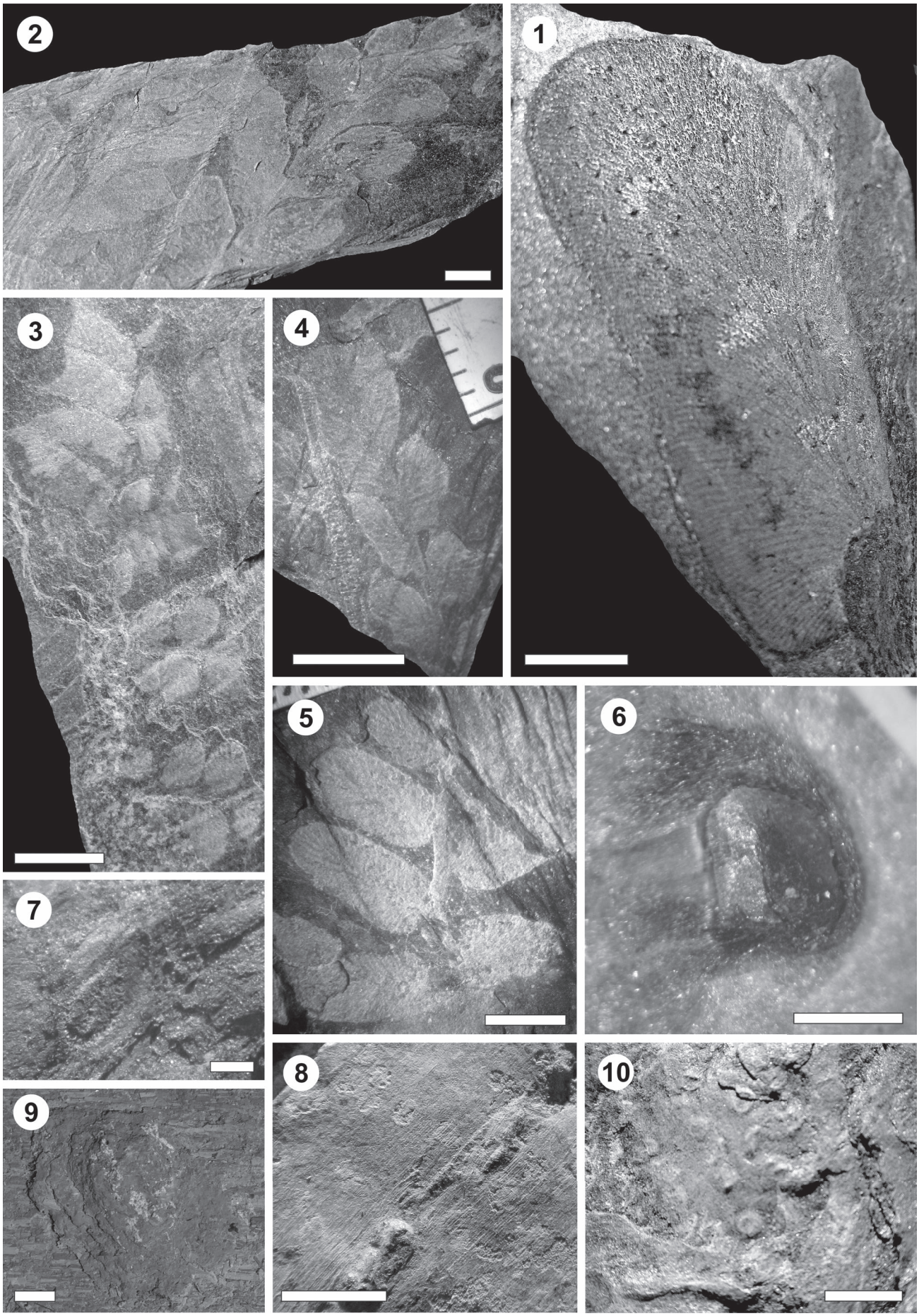
Fig. 7 - *Samarospis* sp.; small seed; scale bar corresponds to 2 mm.

Fig. 8 - Enigmatic microfossils on *Linopteris neuropteroides* pinnules, SEM photo; scale bar corresponds to 200 µm.

Fig. 9 - Enigmatic microfossils on pteridosperm axis; scale bar corresponds to 5 µm.

Fig. 10 - cf. *Arthropleura* sp.; putative exoskeleton fragment; scale bar corresponds to 5 mm.

Catalogue numbers and localities are reported in Tab. 1.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usually fork twice, to produce a vein density that varies between 36 and 45 per 10 mm of the pinnule margin.

Remarks - The species *N. schlehanii* is characterized by typical venation pattern with angular course of the lateral veins. Laveine (1967) established a new species *Neuralethopteris jongmansii* Laveine, 1967 which is similar to *N. schlehanii.* Both forms are distinguished based on the shape of pinnules and venation, which is more apparent with very regular venation in *N. jongmansii*.

Stratigraphical occurrence - *N. schlehanii* occurs from Serpukhovian (Namurian) to late Bashkirian (Langsetian) (Goubert et al., 2000).

Family Neurodontopteridaceae (Neurodontospermae) Laveine, 1967 ex Cleal & Shute, 2003

Genus *Laveinopteris* Cleal et al., 1990 emend. Cleal & Shute, 2003

Laveinopteris tenuifolia (Schlotheim, 1820 ex Sternberg, 1825) Cleal et al., 1990 var. *nordfrancia* Cleal & Shute, 2003
(Pl. 3, figs 5-8)

Locality and material - Riofreddo, MGPT-PU105937, 105938, 105939.

Description - *L. tenuifolia* is common at the Riofreddo locality. This species is often represented by fragments of ultimate pinnae and isolated pinnules. Ultimate pinnae appear to be parallel-sided (Pl. 3, fig. 7). Pinnules are tongue shaped, elongated, having a cordate base (Pl. 3, figs 5-6) and a round or bluntly acuminate apex (Pl. 3, figs 5-7). Larger pinnules are 11-14 mm long and 4-5 mm wide, subtriangular (Pl. 3, fig. 5) to subfalcate (Pl. 3, fig. 8), with anterior margin shallowly concave. Smaller pinnules are oval (Pl. 3, figs 6-7), with an obtuse apex (Pl. 3, fig. 7). The midvein is well marked at the base, distinct for three-quarters of pinnule length. Lateral veins are fine, emerging from midvein at acute angle, arched and forking usually two or three times, and meeting the margin at rather open angles. Lateral veins are moderately crowded with a vein density commonly around 35-39 veins per 10 mm of pinnule margin.

Remarks - *L. tenuifolia* could readily be confused with *Laveinopteris loshii* (Brongniart, 1828) Cleal et al., 1990, however, the latter can be distinguished by the generally shorter pinnules and lower vein density (Laveine, 1967). Both species are well distinguishable based on cuticles (Šimůnek & Cleal, 2011), but due to the absence of organic remains it is impossible to obtain any fragment of cuticle from the Riofreddo specimens.

Stratigraphical occurrence - *L. tenuifolia* occurs from late Bashkirian (Langsettian) to Moscovian with common occurrence in middle Moscovian (Bolsovian) (Cleal & Shute, 2003). Cleal & Shute (2003) distinguished two following variants, namely, *L. tenuifolia* var. *tenuifolia* Cleal & Shute, 2003 which occurs from middle Moscovian (Bolsovian) to late Moscovian (earliest Asturian) and *L. tenuifolia* var. *nordfrancia*, which occurs mainly in late Bashkirian (Langsettian) to early Moscovian (Duckmantian). The morphology of the present specimens suggests that they belong to the var. *nordfrancia*, because pinnules have a high vein density along the pinnule margins (> 35 per 10 mm of pinnule margin).

Genus *Neuropteris* Brongniart, 1828

cf. *Neuropteris obliqua* (Brongniart, 1831) Zeiller, 1888
(Pl. 4, figs 2-5)

Locality and material - Pian del Bosco, MGPT-PU105942, 105943, 105944, 105945.

Description - Many pinnae fragments of cf. *N. obliqua* occur at Pian del Bosco. MGPT-PU105942 (Pl. 4, fig. 2) shows the distal parts of the pinna with incomplete apical pinnules. MGPT-PU105943 (Pl. 4, fig. 3) shows the distal part of the penultimate pinna with fragments of the basal parts of larger pinnules attached to the penultimate rachis and smaller basal pinnules attached to the ultimate rachis in the distal part of the penultimate pinna. The main rachis is not visible. Pinnules are linguaeform (Pl. 4, fig. 5), sometimes subtriangular in the apical part of the pinnae (Pl. 4, fig. 2), with cordate bases and rounded apices (Pl. 4, fig. 5). Typical lateral pinnules are 6-8 mm long and 3-3.5 mm wide and alternate on the support rachis. Smaller pinnules of the ultimate pinna, situated near the distal part of the penultimate pinna, are 3-4 mm long and 2-2.5 mm wide, oval (Pl. 4, fig. 3), with an obtuse apex. The large pinnules from the distal part of the penultimate pinna are 13-15 mm long and 6-7 mm wide with decurrent pinnule bases. Midvein is not distinct and almost straight. Lateral veins are fine, emerging from the midvein and arching broadly to meet the pinnule margin, widely forking usually two or three times. Vein density varies commonly from 21 to 25 veins per 10 mm of pinnule margin.

Remarks - The available remains are poorly preserved. The venation tends to be widely forked, which suggests affinity with *N. obliqua* based on specimens figured by Laveine (1967, pl. 50, figs 2-3). Typical for this species is the decurrent pinnule base in the terminal parts of the pinnae (Pl. 4, fig. 2). Similarities can be found also with *Neuropteris parvifolia* Stockamns, 1933, but *N. parvifolia* has generally smaller typical pinnules and flexuous lateral veins. Nevertheless, since we have only fragmentary material where several important features are missing or poorly preserved, we use the open nomenclature cf. *Neuropteris obliqua*.

Stratigraphical occurrence - *N. obliqua* is typical for Bashkirian (Langsettian and Duckmantian) strata of European and American localities (Laveine, 1967; Lyons et al., 1976).

Family Potonieaceae Halle, 1933

Genus *Linopteris* Presl in Sternberg, 1838

Linopteris cf. *L. neuropteroides* (Gutbier in Geinitz, 1855) Potonié, 1897
(Pl. 4, fig. 1)

Locality and material - Rio Farin, MGPT-PU105941.

Description - Many isolated pinnules of *L.* cf. *L. neuropteriodes* come from the Rio Farin locality. Pinnules are elongate linguaeform or linear subfalcate, 30-48 mm long and 9-16 mm wide with asymmetric cordate bases and straight parallel margins which gradually converge towards an obtuse apex. The midvein occupies 1/2 of the pinnule length, except in the shorter pinnules where it is relatively shorter. The venation is probably anastomosing with lines-of-areolae (Zodrow et al., 2007). Subhexagonal elongate areolae are 2-5 mm long and 0.2-0.3 mm wide. Toward the pinnule margin, areolae gradually decrease in size. At the margin they are consistently elongate, open-ended. A typical feature for this species is the basal areolate, rosette-like structure (in combination with the pinnule size), but this is not developed in the studied fossils.

Remarks - The difference among linopterid species lies in the meshes forming the pinnule veins. However, this morphological feature is not always diagnostic; many transitional forms of venation patterns are known (Caride et al., 1973; Zodrow et al., 2007) which complicate classification of poorly preserved materials. The Italian specimens do not allow to separate the pinnule's lamina from the rock and therefore we cannot answer these questions: 1) Is there true anastomosing with lateral veins forming a closed area (areola), bounded by the straight veins in the shape of an elongate hexagon? 2) Are lateral veins tangential to each other, so that we percieve areolae as hexagons (sensu Zodrow & Vasey, 1986)? Furthermore, some isolated pinnules (where venation is not visible) of the Rio Farin locality are relatively wider than the typical slender and long pinnules of *L. neuropteroides*.

Stratigraphical occurrence - Gothan & Remy (1957) stated that *L. neuropteriodes* occurs from late Bashkirian (Langsetian) to late Moscovian (Asturian), but the peak of the occurrence is at the Bashkirian/Moscovian boundary (Duckmantian).

Class Inceratae sedis
Order Incertae Sedis
Family Incertae sedis

Genus *Samaropsis* Göppert, 1864

Samaropsis sp.
(Pl. 4, fig. 7)

Locality and material - Riofreddo, MGPT-PU105947.

Description - MGPT-PU105947 shows an object that we interpret as an ovate nucule completely surrounded by a membranous wing, which is the most important feature for the genus (eventually endowed of minute apical horns).

Remarks - The genus *Samaropsis* was erected by Göppert (1864), in a revision of the heterogeneous genus *Cardiocarpon* Brongniart, 1828. The seeds *Samaropsis* belong to different gymnospermous groups, including cordaitaleans, some walchian conifers and also some pteridosperms. The seeds are generally rather small, but can exceptionally be relatively large, flat, usually circular to oval, but very occasionally reniform or vertically elongated. The base may be rounded, pointed or cordate, and the apex rounded, pointed or notched. The micropyle is usually fairly long.

Stratigraphical occurrence - The genus *Samaropsis* occurs in Pennsylavanian to Permian strata (Šimůnek & Libertín, 2006; Taylor et al., 2009).

Enigmatic fossils from the studied area

Many plant remains from all studied localities bear irregularly scattered ellipsoid structures with a diameter smaller than 0.1 mm (Pl. 4, figs 8-9). These structures are especially concentrated on *Linopteris* pinnules (Pl. 4, fig. 9) or large pteridosperm axes (Pl. 4, fig. 8). They are from 0.8 to 1.2 mm in diameter. Some of these structures are granulate along the periphery (Pl. 4, fig. 8) and may represent fungi. Some round structures, which appear to be spirally organized, may be classified as cf. *Microconchus* sp. Nevertheless, the strong deformation (Pl. 4, fig. 9) makes this classification very uncertain.

The last enigmatic fossil (Pl. 4, fig. 10) consists in a fragment of ca. 15 x 10 mm with 12 traces of small tubercles on the surface, whose diameter varies from 0.5 to 2 mm. Large tubercles are distributed in rows and small tubercles are irregularly distributed. Some tubercles have broken-off tips and appear truncated because of this. This remain may represent a fragment of the exoskeleton of the arthropod *Arthropleura* sp.

PLANT ASSEMBLAGES FROM INDIVIDUAL LOCALITIES

Individual localities differ in species composition (Tab. 2); nevertheless, pteridosperms are abundant in all of the studied localities, apart Case Bertolotti. The Pian del Bosco locality is characterized by the occurrence of cf. *Neuropteris obliqua*, *Lyginopteris* cf. *L. baeumleri* and rare *Eusphenopteris* sp. The Riofreddo locality is the richest in terms of diversity, since 16 plant fossil taxa occur, including lycopsids, sphenopsids, pteridopsids and pteridospermopsids. Lycopsids are represented by vegetative organs (bark, leafy shoots) of the arborescent genera *Lepidodophloios* and *Bergeria*, isolated leaves of *Cyperites* sp. and a root-like system of *Stigmaria ficoides*, as well as by reproductive organs (remains of cones *Lepidostrobophyllum* sp.). Sphenopsids are represented by two types of foliage (*Asterophyllites equisetiformis* and *A. charaeformis*), stems of *Calamites* sp. and herbaceous member *Sphenophyllum* cf. *S. cuneifollium*. True ferns are represented by abundant *Zeilleria frenzlii* and rare *Senftenbergia plumosa*. The most abundant fossil plants are pteridosperms with *Laveinopteris*

tenuifolia var. *nordfrancia, Karinopteris acuta* and *Lyginopteris* cf. *L. baeumleri.* These pteridosperms are accompanied by the small seed *Samaropsis* sp., which belonged either to the pteridosperms or to other gymnosperms. The Rio Farin locality contains only two species; nevertheless, isolated pinnules of *Linopteris* cf. *L. neuropteroides* are very abundant at this locality. The second kind of plant fossil remain occurring at this site is a single, small seed, probably belonging to the lyginopterids (*Carpolites* sp.).

BIOSTRATIGRAPHY

The stratigraphical ranges of biostratigraphically important species of the Ollano Formation documented in this paper, when plotted against the standard macrofloral biozones for the Pennsylvanian Series (Wagner, 1984; Wagner & Alvarez-Vázquez, 2010), show that the assemblage from the Riofreddo locality most closely corresponds to the *Lyginopteris hoeninghausii/ Neuralethopteris schlehanii* Zone (Fig. 3). This is suggested by the common presence of *Neuralethopteris schlehanii* and *Lyginopteris* cf. *L. baeumleri*, both typical for Bashkirian (Kinderscoutian and Langsettian) floras (Purkyňová, 1962; Wagner, 1984; Cleal & Thomas, 1996; Wagner & Alvarez-Vázquez, 2010). A Langsettian to Duckmantian age is further suggested by the presence of *Laveineopteris tenuifolia* and *Karinopteris acuta.* A Langsettian age is also suggested for the Pian del Bosco locality based on the presence of *Neuropteris obliqua* and *Lyginopteris* cf. *L. baeumleri*, whereas only a Westphalian (Bashkirian to Moscovian) age can be inferred for the Rio Farin locality from the presence of *Linopteris* cf. *L. neuropteroides*.

In conclusion, by following the widely used macrofloral zones of Wagner (1984) and Wagner & Alvarez-Vázquez (2010), the new palaeobotanical assemblages described in this study constrain the deposition of the Ollano Formation at least to the late early Pennsylvanian or the early middle Pennsylvanian, most probably within the late Bashkirian (Langsettian-early Duckmantian).

CONCLUDING REMARKS AND OPEN QUESTIONS

The occurrence of Pennsylvanian floras in Southern Europe within units with an Alpine tectonic overprint is not exceptional (see Introduction), but the material studied in this paper provides interesting new evidence

	Lycopsida					Sphenopsida				Pteridopsida		Pteridospermopsida							Inc. sedis
	stem		cones	leaves	"roots"	Calamitaceae			Sphenophyllales	Tedeleaceae	Incertae sedis	Medullosales			Callistophytales	Lyginopteridales			Trigonocarpales	Incertae sedis
Localities	***Lepidophloios* sp.**	***Bergeria* sp.**	***Lepidosptrobophyllum* sp.**	***Cyperites* sp.**	***Stigmaria ficoides***	***Asterophyllites equisetiformis***	***Asterophyllites charaeformis***	***Calamites* sp.**	***Sphenophyllum* cf. *cuneifolium***	***Senftenbergia plumosa***	***Zeilleria frenzlii***	***Neuropteris obliqua***	***Linopteris* cf. *neuropteroides***	***Laveinopteris tenuifolia* var. *nordfrancia***	***Mariopteris sarana***	***Lyginopteris* cf. *baeumleri***	**seed**	***Eusphenopteris* sp.**	***Neuralethopteris schlehanii***	***Samaropsis* sp.**
PIAN DEL BOSCO												3				2		1		
RIO FARIN													3				1			
RIOFREDDO	2	2	2	1	2	2	2	2	1	1	3			3	3	2			3	1
CASE BERTOLOTTI								1												

Tab. 2 - (Color online) Distribution of plant taxa in the four studied localities. Numbers indicate relative frequency of species at each locality: 1) rare - 3) abundant.

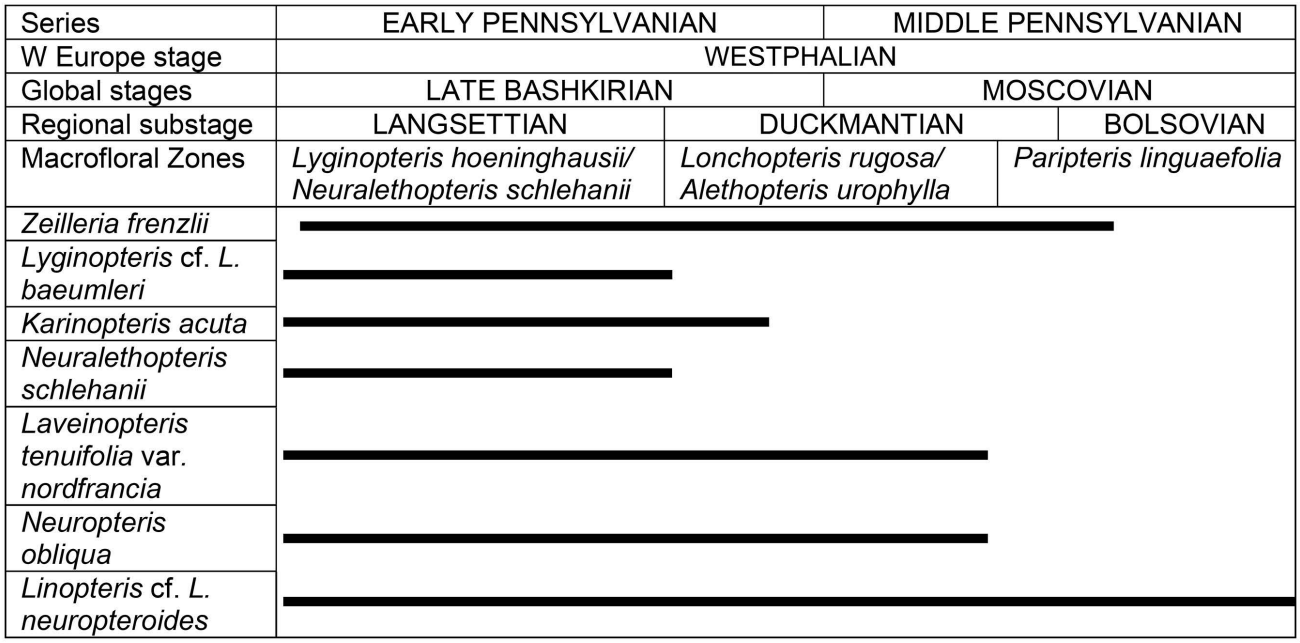

Fig. 3 - Stratigraphical ranges of selected plant species from the studied localities. The ranges are plotted against the biozones proposed by Wagner (1984) and modified by Wagner & Alvarez-Vázquez (2010). The correlation of the zones with the regional substages and global stages is based on Wagner (1998) and Wagner & Alvarez-Vázquez (2010).

for the Ligurian Alps and, together with the palaeofloral assemblages found in southwestern Europe (e.g., Ronchi et al., 2012; Cassinis et al., 2013 with references) and eastwards till to NW Bulgaria (Pantić, 1955; Tenchov, 1976, 1977, 2007; Kolar-Jurkovšek & Jurkovšek, 1985, 1986, 1990, 2002a, b, 2007; Milovanović, 1995; Tenchov & Cleal, 2010), suggests an early phase of intra-montane basin development on the southern side of the Variscan Mountains.

Our new report of plant fossils from the Ollano Formation provides a further clue for its early to middle Pennsylvanian (late Westphalian) age, originally suggested by Portis (1887) and Bloch (1966) on the basis of similar plant assemblages. However, an important mismatch exists between this biostratigraphically defined latest early Pennsylvanian age and the Cisuralian (Artinskian) age recently inferred for the Ollano Formation on the basis of radioisotopic dating of volcanic rocks (Case Lisetto metarhyolites, dated at 285.6 ± 1.3 Ma in Dallagiovanna et al., 2009). The last ones were described as geometrically below and laterally adjacent (both rest on the Palaeozoic basement) to the lower part of the Ollano Formation itself (Dallagiovanna et al., 2009; Seno et al., 2010). Although this is beyond the scope of this paper, it is currently very problematic for us to provide an univocal explanation of this incongruity from available data. In any case, the presence of lepidodendroid lycopsids, on one hand, and the absence of marattialean ferns and conifers, on the other hand, do not permit to doubt the early to middle Pennsylvanian age of the fossil plant assemblages described in this study. Lepidodendroid and other arborescent lycopsids dominated late Palaeozoic wetlands till the end of middle Pennsylvanian time, but later their species diversity and populations drastically decreased (Phillips et al., 1985; DiMichele et al., 2010; DiMichele, 2014). Although they can occur rarely up to the late Gzhelian, they seem to disappear completely after this age (Opluštil et al., 2013). The decline in dominance of arborescent lycopsids at the middle/late Pennsylvanian transition allowed marattialean ferns to dominate the European wetlands for the entire duration of the late Pennsylvanian. Conifers were fairly common during this time interval, however their fossil remains are often found in discrete beds separated from those containing wetland assemblages (DiMichele, 2014; DiMichele et al., 2016).

Early Permian (Cisuralian) floras in Europe are typically lacking lepidodendroid lycopsids (e.g., genus *Lepidophloios* or *Bergeria*) and show the dominance of conifers and callipterid pteridosperms in the fossil record. Also the marattialean ferns can still be common. Floras from the Southern Alps of proven Permian age are dominated by conifers (e.g., Kustatscher et al., 2016), but these are absent in the Ollano flora. Instead, we have identified remains of lepidodendroid lycopsids and some key taxa of late early Pennsylvanian floral zones. An hypothetic revision of the biostratigraphic schemes would create a strong contrast with the well-constrained ones previously documented in adjoining Variscan sectors (presently identifiable in the Alps and Apennines). The survival of typical early-middle Pennsylvanian wetland flora for further 25-30 Ma is unrealistic. Although differences in first occurrence of stratigraphically important taxa among various European coalfields were documented, they implied an age shift of one or few million years (Opluštil et al., 2016), which is insufficient to explain the apparent inconsistency of biostratigraphic and radioisotopic data in the Ligurian Alps. Therefore, assuming that the identification of the fossil flora and radioisotopic data are both correct, the effective relationship between the sediments of the Ollano Formation and its underlying/adjacent volcanic rocks must be revised. From one hand, the radioisotopic age determination of the volcanic rocks seems to indicate a

magmatic activity subsequent to the onset of the Ollano Formation deposition. Alternatively, the Ollano Formation itself could be a composite formation of a number of stratigraphic units (sub-basins?) of different ages, and the fossil flora localities may be included in tectonic slices over the Case Lisetto metarhyolites.

At present, obviously, we cannot lean clearly towards any of the presented hypotheses. Therefore, it is recommended to continue the analysis of the fossil plant assemblages and of the relationships between fossil-bearing lithostratigraphic units and volcanic rocks, in order to clear up the inconsistency of their ages and to interpret correctly the palaeogeography, the palaeoenvironments, and the tectonic relationships.

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