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LATE PALAEOZOIC PLANTS OF SARDINIA: PALEOGEOGRAPHICAL AND PALAEOECOLOGICAL IMPLICATIONS

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Abstract

The study of the newly collected material and stored material coming from three different localities of Sardinia have been carried out for reaching the goals of this thesis. The oldest one comes from the San Giorgio locality, near Iglesias. The second one comes from Montarbu, and the third one comes from Perdasdefogu, central Sardinia. The last assemblage has been studied to obtain thin section from silicified rocks, unsuccessfully. The systematic study of the Moscovian flora of San Giorgio lets to highlight that the composition of this older flora is different from the younger Montarbu assemblage and reflects a late Moscovian wetland vegetation with a dominant sphenophytes-based flora. The Montarbu flora is composed of 24 taxa belonging to 18 genera with the abundance of mesophytic and xerophytic elements. Here, the conifers and cordaitanthaleans are dominant. The pteridosperms are common, and the most diversified in quantity of taxa, while ferns and rare sphenophytes are present as well. The assemblage reflects probably a very late Ghzelian age, because of the presence of typical taxa of "Stephanian affinity" and the abundance of Acitheca*, peltasperms and conifers, much more meso-xerophytic. After the comparison between the Montarbu flora with those palaeogeographical close, it must be highlighted the strong similarity of the former with that of Igornay, in France. This value mirrors close paleogeographical condition that facilitates the presence of a similar set of vegetation. The similarity is also high with the less close Weissig Basin (Germany). It is assumable that during these times there were no (or weak) geographical barriers between the two floras. The similarity is also high with the floras of the Czech basins. Furthermore, the study of the two floras would also confirm the change of vegetation across the late Palaeozoic, as already seen in the various section of the same palaeolatitude and as evidenced in the regional palynological spectra.*

Riassunto

L'analisi effettuata su reperti risalenti al tardo Paleozoico e provenienti da tre diverse località della Sardegna ha contribuito al raggiungimento degli obiettivi prefissati per la tesi, come lo studio sistematico della vegetazione moscoviana e gzeliana, la comparazione con le località paleogeograficamente vicine e la conferma dell'evoluzione della vegetazione da igrofila a meso-xerofila tra il Moscoviano e lo Gzeliano. Il primo blocco di materiale, facente parte di una collezione custodita presso il Museo di Geologia e Paleontologia "D. Lovisato" dell'Università degli Studi di Cagliari, proviene dalla località di San Giorgio (Iglesias, Sardegna sudoccidentale), mentre il secondo e il terzo blocco provengono rispettivamente dai siti fossiliferi di Montarbu (Sardegna centrale) e Perdasdefogu (Sardegna centro-orientale) e includono esclusivamente materiali di nuova campionatura.

Per quanto riguarda il sito di Perdasdefogu, le rocce raccolte sono state studiate attraverso sezioni sottili con la tecnica dei peels di acetato ma sfortunatamente non ha prodotto risultati. Lo studio sistematico della flora moscoviana di San Giorgio ha permesso di evidenziare che la sua composizione differisce dalla più giovane di Montarbu e rispecchia una vegetazione di zone umide con una flora prevalentemente costituita di sfenofite. Nella flora di Montarbu sono stati riconosciuti 24 taxa appartenenti a 18 con una prevalenza di elementi mesofili e xerofili rappresentati perlopiù da conifere e cordaiti. Le pteridosperme rappresentano le forme più diversificate in numero di taxa, ma sono presenti anche felci e rare sfenofite. La vegetazione di Montarbu riflette probabilmente un'età tardo Gzeliana, per la presenza di taxa tipici di "affinità stefaniana" e l'abbondanza di Acitheca*, peltaspermali e conifere. Il confronto tra la flora di Montarbu e quelle coeve paleogeograficamente vicine attraverso l'ausilio dell'indice di Sørensen-Dice ha messo in evidenza la forte similarità tra la flora sarda con quella di Igornay (Francia). Questo dato rispecchia una condizione paleogeografica che ha favorito lo svilupparsi di una vegetazione abbastanza simile tra le località in esame. La similarità è risultata elevata anche con la flora del bacino del Weissig (Germania). È presumibile che durante la transizione Carbonifero-Permiano non ci fossero barriere geografiche (o fossero lievi) tra le due località. Le flore presenti nei bacini della Repubblica Ceca condividono una buona similarità con la flora di Montarbu. Lo studio incrociato delle flore di Montarbu e San Giorgio poi conferma il cambiamento di vegetazione avvenuto nel tardo Paleozoico, come viene rispecchiato nelle altre località che si trovavano alla stessa paleolatitudine, e come evidenziato negli spettri palinologici a livello regionale.*

1. Introduction

Permo-Carboniferous studies dealing with plants macro-remains of Sardinia started in the second half of the XIX century. Lamarmora (1857), Arcangeli (1901), Comaschi Caria (1959) and Cocozza (1967) described rich macrofloral remains from several localities. The subsequent studies are mainly focused on stratigraphic goals. Detailed systematic studies about plants macro-remains using modern keys are few, and often reporting only floral lists. Moreover, quantitative data carried on different lithologies and numerical comparison with other floras are missing. This fact appears not to be useful for performing analyses that need numerical data.

The best-known outcrops of the Island are located in different sub-regions (Fig. 1), and these are in the Sulcis-Iglesiente area (San Giorgio, Guardia Pisano), Ogliastra (Perdasdefogu), Gerrei (Escalaplano-Mulargia Lake), Barbagia (Seui-Seulo) and Nurra (Lu Caparoni; Cassinis et al. 1999; Pittau et al. 2008; Ronchi et al. 2008; Scanu et al. 2014a). Except the San

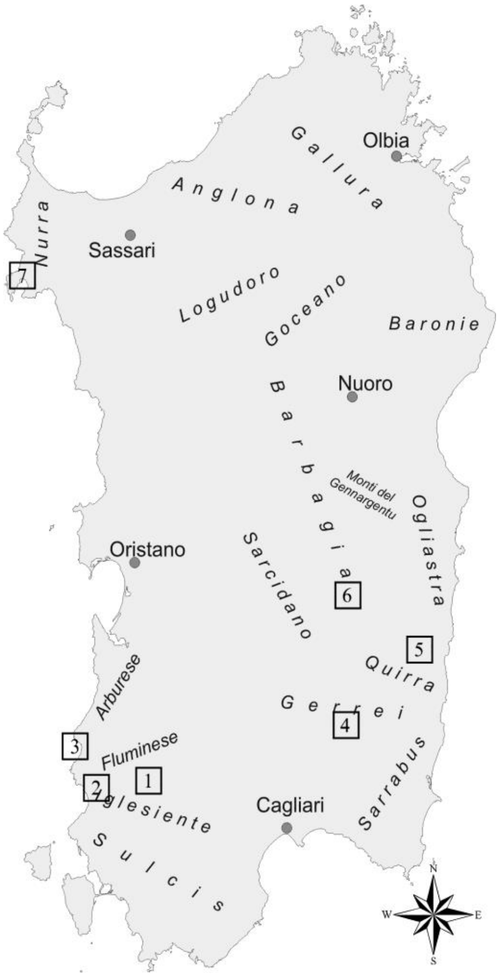

Fig.1.1. Main sub-regions of Sardinia cited in the text. Numbers indicate the late Palaeozoic floras (after Barca 2009, modified). 1) San Giorgio; 2) Guardia Pisano; 3) Tuppa Niedda; 4) Mulargia Lake-Escalaplano; 5) Perdasdefogu; 6) Seui-Seulo; 7) Lu Caparoni.

Giorgio macro- and micro-flora and the Tuppa Niedda microflora (Iglesiente, South-West) which is dated to the Moscovian, all the others are younger (late Carboniferous-early Permian). It is well-known from studied all over the world that a) Carboniferous ecosystems were dominated by spore-producing plants associated with early gymnosperms and b) the global climate changes across the Pennsylvanian forced a vegetational turnover between wet sub-humid and dry sub-humid to possibly semi-arid floral associations.

The study of a newly collected material coming from Montarbu (Seui-Seulo basin, central-East) and fossils already stored in the Geological and Paleontological Museum of the Cagliari University (San Giorgio, Iglesiente, South-West) has been carried out in this work of thesis.

The systematic study of the floras allows to develop quantitative analyses and provide the age of the studied associations. The possibility to include and consider the Montarbu flora as an Autunian flora is discussed after the results of recent studies that propose the Autunian as a West European regional stage (Schneider et al. 2017).

Moreover, the paleoecological interpretation of the floras is based on the different lithofacies recognised; due to the abundance of macro-remains and the diversity in term of taxa, it is possible to carry out statistical analysis to compare this association with the others coeval Europeans floras. Furthermore, the difference between the Moscovian flora of San Giorgio (the complete study is available in Appendix 1) and the late Ghzelian flora of Montarbu is discussed in order to confirm the change of vegetation across the late Palaeozoic also using floral macro-remains and confirming the same trend as already stated in the Island by palynological studies (Pittau et al. 2008).

1.1. Geological background of Sardinia

Sardinian Post Variscan deposits lie on the Palaeozoic basement constituted by a rather continuous Palaeozoic succession made up by metamorphic rocks and a granite batholith. Various degrees of deformations due to the Variscan orogeny are followed by important and widespread post-collisional magmatism, and the age of these events are well defined by stratigraphic and radiometric data. In southern Sardinia, the basement is characterised by a low to very low grade of metamorphism up to the Tournasian (Barca et al. 2000). From South to North three tectonic zones can be distinguished (Fig. 1.2) and these are separated by wide ductile important structural discontinuity (Funedda & Oggiano 2009; Casini et al. 2010):

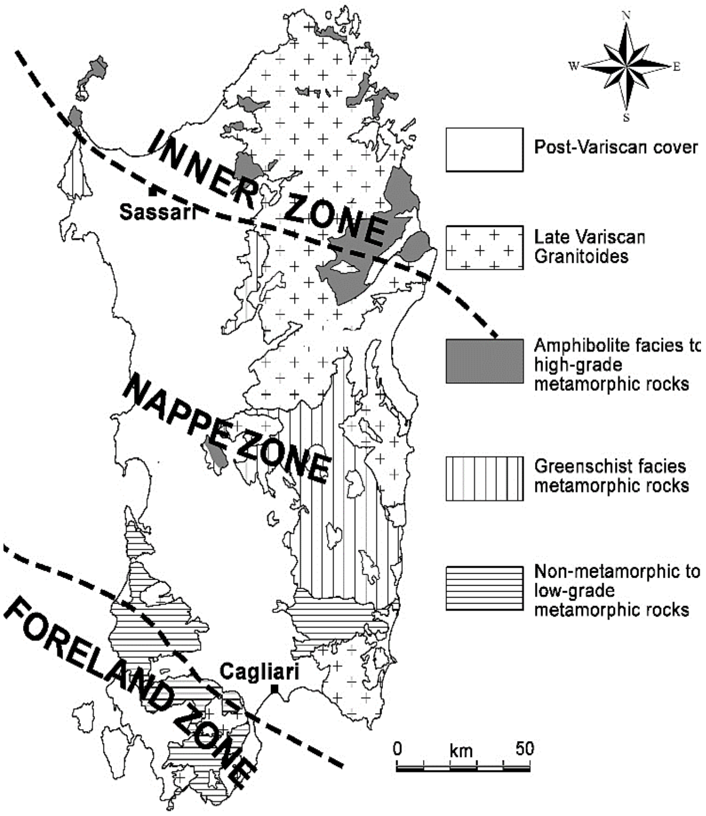

Fig. 1.2. Tectonic and metamorphic partition of the Sardinia (after Funedda & Oggiano 2009, modified).

a) FORELAND zone, in southwestern Sardinia (Iglesiente-Sulcis region), characterized by strong diagenesis to very low metamorphism grade (greenschist facies); the age of these rocks covers a time span comprised of Lower Cambrian to Lower Carboniferous;

b) NAPPE zone: between South and North Sardinia the occurrence of thrusts and folds features enable to distinguish an intermediate “Nappe Zone”, furtherly divided into “Internal Nappes” (Nurra Unit, Baronie Unit, Gennargentu Unit, etc.) and “Outer Nappes” (Sarcidano Unit, Gerrei Unit, Sarrabus Unit, Arburese Unit), whose contact with the High Grade Metamorphic Complex corresponds to the “Posada-Asinara Line” interpreted as a segment of the suture line of the South-Armorican Ocean (Cappelli et al. 1992) or according to some authors interpreted as dextral shear zone (Elter et al. 1990; Rossi et al. 2009). The upper, Arburese unit in greenschist facies, is overthrust on the foreland in southwestern Sardinia;

c) INNER zone, strongly deformed (amphibolitic facies) develops in Northern Sardinia where migmatitic rocks (319/284 Ma; Di Simplicio et al. 1974) define the “High-Grade Metamorphic Complex”.

The youngest pre-Variscan sediments known are early Tournasian in age (Corradini 2008; Mossoni et al. 2015). The stratigraphic sequence encompasses lower Cambrian to the Early Carboniferous, separated by a stratigraphic gap in the middle Ordovician (Barca et al. 1987), evidenced by a strong angular unconformity (Sardic unconformity; Teichmüller 1931) due to the shortening related to the “Sardic phase” in the Iglesiente-Sulcis area (Stille 1939) and in the Sarrabus-Gerrei to the Sarrabese phase (Calvino 1959). However, in the nearest Nappe zone, the strong Variscan deformation have often destroyed and transposed the Caledonian structures (Sarrabese phase). According to various authors (Carmignani et al. 2001; Oggiano et al. 2009; Gaggero et al. 2012), the geodynamic setting of the sardic phase was an Andean-like continental-arc, although recently Cocco & Funedda (2017) demonstrate that the field evidence is not completely consistent with this model.

1.1.1. Post Variscan successions

During the Permo-carboniferous Sardinia was part of the South European Variscan Chain (Carmignani & Pertusati 1977; Carmignani et al. 1978, 2001; Funedda & Oggiano 2009) and this is evidenced by some features such as a) stratigraphical and structural affinities with other Variscan massifs of southern Europe such as Massif Central, Montagne Noire, Maures, etc. (Arthaud & Matte 1966; Westphal et al. 1976); b) palaeomagnetic data indicating the same structural and sedimentary evolution as southern France (Carmignani et al. 2001 and references therein) until the migration of Sardinia–Corse microplate that started in the Palaeogene (south-eastern direction) until it reached its current position in the lower-middle Miocene (Gattacceca et al. 2007; Oggiano et al. 2009).

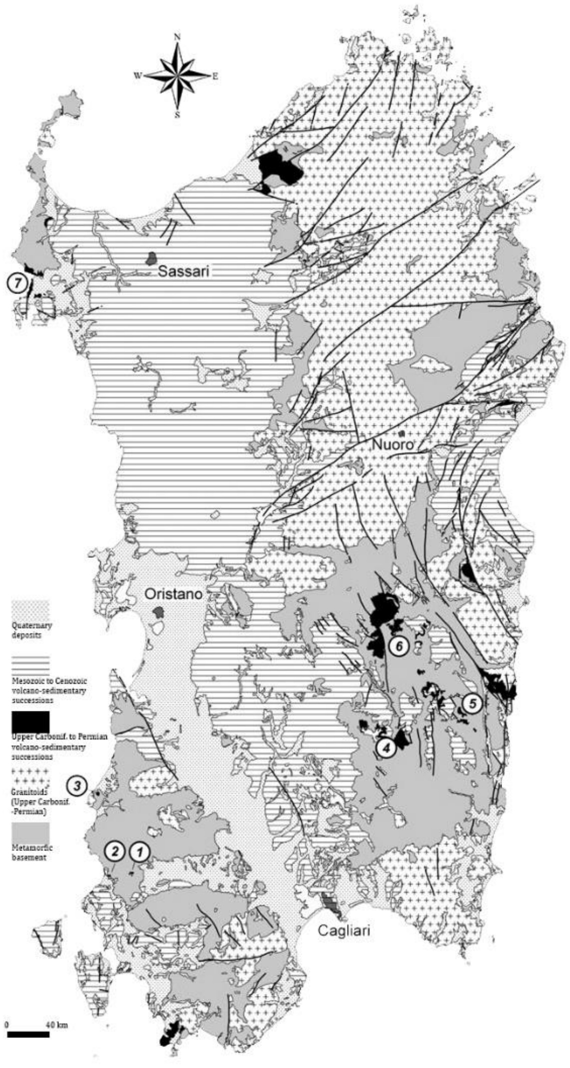

Fig. 1.3. Geological sketch map of Sardinia with the main structural features of the Variscan basement and post-Variscan covers and location of the upper-Carboniferous-Early Permian basins of Sardinia (after Pittau et al. 2008, modified). Basins: 1) San Giorgio; 2) Guardia Pisano; 3) Tuppa Niedda; 4) Mulargia Lake-Escalaplano; 5) Perdasdefogu; 6) Seui-Seulo; 7) Lu Caparoni.

Upper Carboniferous and lower Permian deposits of Sardinia are superposed on the peneplaned Variscan basement. An extensive hiatus encompasses Visean, Namurian and early

Westphalian (Pittau et al. 2008). As in the rest of southern Europe, the Upper Palaeozoic deposits of Sardinia can be subdivided into major tectonic-sedimentary megacycles (Cassinis & Ronchi, 1997, 2002; Cassinis et al. 2003).

The first cycle sequence spans from Moscovian to Asselian and possibly (?)early Sakmarian (Del Rio 1973; Cocozza 1967; Fondi 1979; Pittau et al. 2008; Ronchi et al. 2008; Selden & Pillola 2009; Cleal et al. 2017; Marchetti et al. 2017). The best-known outcrops of this cycle are in several zones of Sardinia (Fig. 1.3.): in the South (San Giorgio; Tuppa Niedda), in Ogliastra (Perdasdefogu), Gerrei (Escalaplano-Mulargia Lake), Barbagia (Seui-Seulo) and Nurra (Lu Caparoni). Sequences are mostly fluvio-lacustrine and reach thicknesses up to 700 m (Pittau et al. 2008). These basins consist of a sequence of terrestrial strata with organic-rich shales and coal seams. On the other hand, the Seui-Seulo basin, in central-eastern Sardinia where peat formed. The San Giorgio deposit is exclusively sedimentary whereas the others occurred during volcanic activity and strata frequently contain these products (Pittau et al. 2008).

The second cycle, cropping out mostly in Nurra, is “post-Autunian” in age (previously known in the historical literature as a non-differentiated “Permo-Triassic” sedimentary unit; Oosterbaan 1936; Pecorini 1962; Vardabasso 1966) and lie unconformably upon the successions of the first cycle. It consists of red alluvial deposits and rhyolitic products (Units 2 and 3 of “Verrucano Sardo” of Gasperi & Gelmini 1979). Some authors also consider the Guardia Pisano outcrop (southern Sardinia) belonging to this cycle (Ronchi 2001; Ronchi et al. 2008) differently from Pittau et al. (2008) that consider this outcrop to belong to the first cycle.

This second cycle, dated middle-late Cisuralian to Roadian, was clearly separated from a third, Early-Middle Triassic one (Cassinis et al. 2003; Cassinis & Ronchi 2002; Ronchi et al. 2008; Ronchi et al. 2011), which is the only one to be attributed to the Germanic Buntsandstein (Lower-Middle Triassic). The 2^nd^ cycle is almost barren of fossils apart from vertebrate remains (Ronchi et al. 2011) or bioturbations (Baucon et al. 2014). Palaeontological records occur in the third cycle and are represented by scarce macroflora (only fragments of *Equisetum mougeoti* found, Pecorini 1962; Scanu et al. 2014b) and rich pollen associations (Pittau Demelia & Flaviani 1982, 1983, Pittau & Del Rio 2002, 2004) which points to a Lower? -Middle Triassic age.

1.1.2. Palaeogeography of western Tethys

The late Paleozoic was a period of reconfiguration of the tectonic plates. During the Carboniferous, convergence between Laurussia and Siberia leads to closure of the intervening ocean (e.g. Mattews et al. 2016) and the Variscan collision of Gondwana and Laurasia was followed by widespread magmatic, intrusive and effusive activity (Cortesogno et al. 1998). The formation of Pangea was, thus, the consequence of the major continental collision between Gondwana and Laurussia (e.g. Golonka 2007). The late Carboniferous Pangea included the nowadays lands of Australia, India, Antarctica, Africa, Arabia, and the Cimmerian plates, South America, Europe, Kazakhstan, and Siberia (e.g. Golonka 2002; Stampfli et al. 2013). Western Tethys was made up of a diverse set of geographical terrains including the western and central Mediterranean (Iberia, Sardinia-Corsica, part of Italy, Greece) and adjacent regions, such as Western Europe, the northeastern maritime coasts of North America, and northernmost in Fig. 4. Here the Late Carboniferous plate reconstruction illustrates the Himalayan- typesetting of the western parts of the Variscan orogen and the Andeantypesetting of its eastern parts (Ziegler & Stampfli 2001). The Variscan terranes have been variously named by several authors, and the different zones close to Sardinia are shown in Fig. 4. Assuming a central position for Sardinia, the Iberian zone (IB-OS-CT) to the West is recognisable. French coeval floras come from a slightly northern position and are recognisable in the map within the abbreviation AQ-AR-CH-LI. The German Saxo-Thuringian zone was located to the North-East (SX) close to the Bohemian and Moravian (actual Czech Republic) terrains (MS) as also shown in the Fig. 1.4 that represents the actual position of these terrains during present times. The tropical belt was restricted to low latitudes, gaining a warm westward-flowing equatorial current which deflected southeastward, upon reaching the continental shelves of the western Tethys Gulf (Angiolini et al. 2007). In the Late Carboniferous, the equator was over the Avalonian microplate crossing actual Scotland. During this period indeed, the Sardinia-Corsica block was situated at a tropical latitude close to France and Spain between of about 10-15 °S (Westphal et al. 1976; Ziegler & Stampfli 2001; Edel 2014). The paleoposition is, therefore, debated (Werneburg et al. 2007). According to these data, Sardinia was

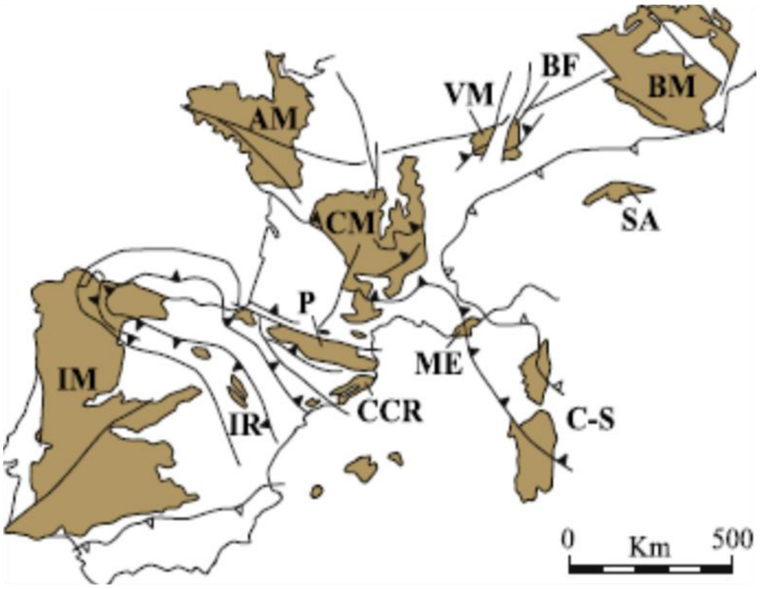

Fig. 1.4. Main southwestern segment of the Variscan chain with the position of emerged lands now. AM: Armorican Massif; BF: Black Forest; BM: Bohemian Massif; VM: Vosges Mountains; CM: Central Massif; CCR: Catalan Coastal Ranges; C-S: Corsica-Sardinia; IM: Iberian Massif; IR: Iberian Ranges; ME: Maurese-Esterel; P: Pyrenees; SA: South Alpine (after Gaggero et al. 2017, modified).

in the Euroamerican Province (also known as Tropical Province), and it was not far from the paleo-equator (Vai & Izart 2000). Obviously, the vegetation reflected also the climate given by the paleo conditions. Later, in Pennsylvanian–Early Permian times, an extensive glaciation affected much of Gondwana (Southern hemisphere; Stephenson et al. 2007; Frank et al. 2008), leaving widespread glacial deposits at high to intermediate southern latitudes and having consequences for the assessments, composition and distribution of palaeofloras. The southern polar ice-cap reached its maximum size (e.g. Francis 1994, Veevers 2004) covering Southern Australia, Antarctica, southern India and Arabia, Madagascar, eastern and southern Africa, and southeastern part of South America.

1.1.3. Brief notes on the Paleokingdoms

During the end of Palaeozoic, the worldwide vegetation was subdivided into four different "palaeokingdoms" (sensu Cleal 1991), also called "phytochoria" (Fig. 1.5). In the southern middle/high palaeolatitudes there were the Gondwanan floras; the Angaran floras in the northern middle/high palaeolatitudes, and the Euramerican and Cathaysian floras in tropical palaeolatitudes. There were also some "mixed floras" which combine elements of high and low latitudinal vegetation and one of the best examples is in Guadalcanal (southern Spain) in which Cathaysian

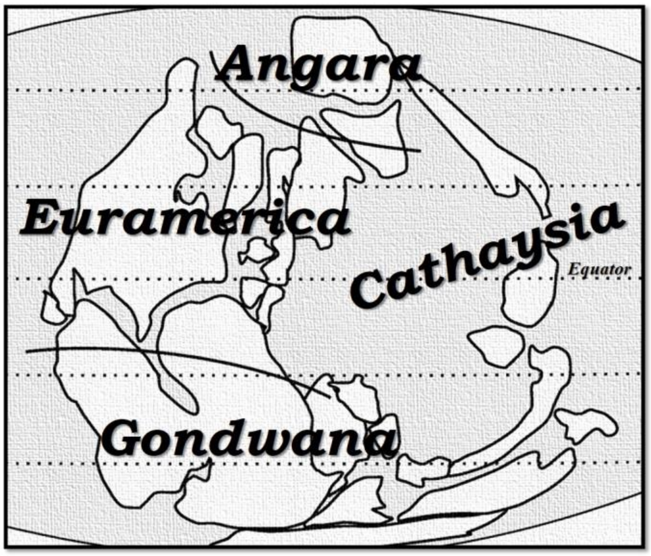

Fig. 1.5. Position of the paleokingdoms in the late Palaeozoic (after Gastaldo et al. 1996, Hilton & Cleal 2007, modified and redrawn).

elements coexist with Euroamerican ones (Broutin 1986). It is noticeable the Gondwanan and Angaran floras are, overall, quite distinct and easily recognised (Hilton & Cleal 2007).

1.2. Correlation of late Palaeozoic western European outcrops

The Carboniferous and Permian periods are characterised by various time scales and intensities climatic changes (Fielding et al. 2008; Montañez et al. 2007) with coeval tectonic processes resulting in mountain belts and basin formation for the assemblage of the supercontinent Pangaea (e.g. Ziegler 1990; McKerrow et al. 2000). The global chronostratigraphical scheme for the Carboniferous Systems is based on fossiliferous marine strata (mainly conodonts) of the Russian platform and Ural foredeep (e.g. Gradstein et al. 2012; Ogg et al. 2016) but in non-marine realms, there are also local stratigraphical schemes based on Pennsylvanian and early Permian terrestrial successions.

In western Europe the scheme has been established mainly on terrestrial macrofloras, palynomorphs, freshwater and terrestrial faunas (e.g.: Wagner 1984; Cleal 1984, 1991; Chateauneuf et al. 1992; Owens et al. 2004; Schneider & Werneburg, 2006, 2012; Wagner & Álvarez-Vázquez 2010; Werneburg & Schneider 2006). The Middle–Late Pennsylvanian to Asselian regional continental stages and substages recognized at European scale have been suggested by various authors according to the state of the art of the discoveries. In the Fig. 1.7 is summarized the correlation of global and regional stages and substages as suggested by Wagner & Alvarez Vasquez (2010) for Spanish outcrops, by Gradstein et al. (2012) and Ogg et al. 2016 for the Geological Time Scale, by Opluštil et al. (2016a) for Czech basins and by Michel et al. (2015) and

Pellenard et al. (2017) for French localities. Thus, the Autunian could be considered also a **defined flora**. As stated before, this flora is now well characterized in a precise interval of time between Ghzelian and the early Sakmarian (Pellenard et al. 2017).

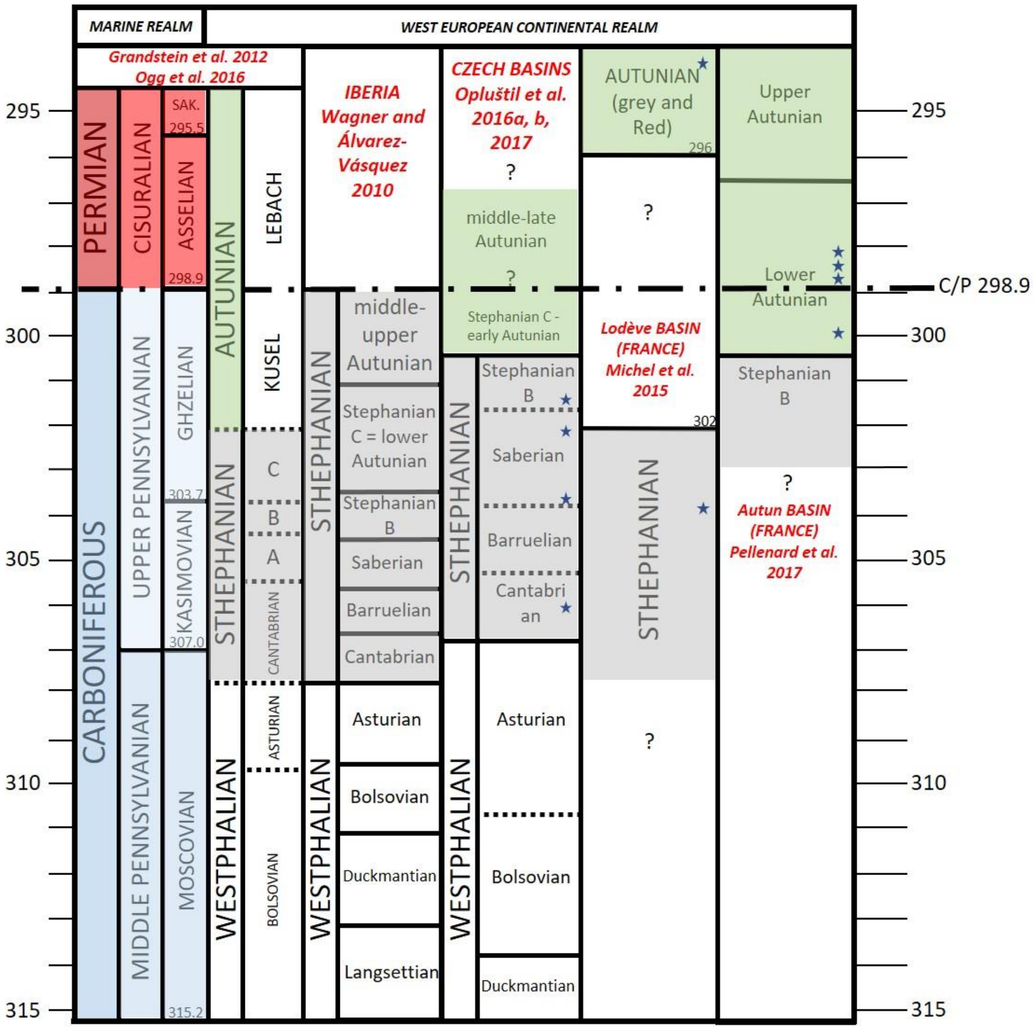

Fig. 1.6. Correlation of global and regional European stages and substages with the standard chronostratigraphy (Grandstein et al. 2012; Ogg et al. 2016). Stars indicate U/Pb CA-ID-TIMS ages (after Michel et al. 2015, Opluštil et al. 2016a, b, 2017, a, b; Pellenard et al. 2017, adapted and redrawn).

1.2.1. Czech basins

Recent studies in the Czech Republic were focused on a re-evaluation of lithostratigraphy of the Late Palaeozoic continental basins of the Bohemian Massif (central European Variscides; Opluštil et al., 2016a, b, 2017, a, b). In the basins, numerous intercalated acid volcanic ash beds were sampled for high-precision radioisotopic analyses and these have been dated using single zircon crystals. Most of the analysed samples come from the Carboniferous part of the succession but several U-Pb ages were obtained from Cisuralian strata (early Permian). The results allowed not the only improvement of the stratigraphy of the central and western Bohemia basins (=central-western Czech Republic) and in the Sudetic area (NE part of the country), but the data have been used for constraining the ages of lithostratigraphic units in different basins and their correlation to global stages. In fact, the radioisotopic ages allowed for calibration of some macrofloral biozones created by Wagner & Álvarez-Vázquez (2010) in the Spanish (Iberian) localities as well as of amphibian and other terrestrial animals (Werneburg & Schneider 2006; Schneider & Werneburg 2006, 2012) for the German area. This study is important because Middle Pennsylvanian to early Asselian floral biozones in the western and central Bohemian basins are improved, based on the newly available radio-isotopic data. These results could be useful for the rest of western Europe. Regarding only to the much recent biozones, in fact, the age of the *Alethopteris zeilleri* Zone coincides with the Saberian Substage (303.7–301.6 Ma). The subsequent *Sphenophyllum angustifolium* Zone (Stephanian B) spans the interval 301.6–300.4 Ma. The upper boundary of the latter biozone coincides with the lower boundary of *Autunia conferta* Zone but unfortunately, the top of which, here, cannot be constrained from the available floral data.

After that, according to Oplustil et al. (2016), the Westphalian/Stephanian (Asturian/Cantabrian in the Spanish nomenclature of stages) boundary falls just above the base of the Kasimovian Stage, whereas the Cantabrian/Barruelian boundary is located approximately in the middle Kasimovian. The Barruelian/Saberian boundary coincides with the upper boundary of Kasimovian while Saberian/Stephanian B boundary falls within the middle of the Gzhelian Stage, and the Stephanian B/Stephanian C–early Autunian boundary corresponds to the late Gzhelian (see Fig. 1.6 for details).

1.2.2. French basins

New data about the correlation of the Carboniferous-Permian boundary in continental basins with the marine stratotype and for the numerical age calibration of non-marine biozones have been recently published by a French-US team (Pellenard et al. 2017). They radio-dated ashfall sediments found in lacustrine to swamp deposits of some French formations of the Autun Basin (French Massif Central). The Autunian regional stratotype was defined in the Autun Basin and used since the end of the XIX century (Gaudry 1883) also in other western European outcrops of Italy (e.g. Cassinis et al. 2007) and Spain (Wagner & Álvarez-Vázquez 2010). Various other authors have correlated this regional stage. For instance, Menning et al. (2006) and McCann (2008) roughly considered it equivalent to the lower part of the Rotliegend Group of the northern European basins (Germany, Austria). Basing on macroflora and palynomorphs the entire regional continental Autunian Stage was attributed by many authors to the late Gzhelian–Artinskian global Stages: the lower Autunian was placed into the Upper Gzhelian global Stage while the upper part into the Asselian to Sakmarian stages (or even Artinskian Stage; e.g. Doubinger 1956; Feys & Greber 1972; Broutin et al. 1999; Gand et al. 2013) and this range attribution is in agreement with the Subcommission on Carboniferous Stratigraphy (SCCS; Heckel & Clayton 2006), the current Geologic Time Scale 2012 (Davydov et al. 2012; Henderson et al.

2012) and Concise Geologic Time Scale 2016 (Ogg et al. 2016). In Spain, according to Wagner & Álvarez-Vázquez (2010), the entire Autunian is placed in the Gzhelian Stage.

In detail, the middle part of the Igornay Formation of the Autun basin is dated at 299.9±0.38 Ma, the upper Lally oil-shale bed is dated at 298.91±0.08 Ma and this corresponds to the C/P boundary. The upper part of the Muse oil-shale bed is dated between 298.05±0.19 and 298.57±0.16 Ma. The isotopic ages of the Muse Formation allow the calibration of biozonations with the marine Standard Global Chronostratigraphic Scale. Indeed, the Muse Formation is the *stratum typicum* of *Apateon dracyi*, a zone-species of the *Apateon dracyi* - *Melanerpeton sembachense* amphibian zone (Schneider & Werneburg 2012).

Another French basin has been studied recently by Michel et al. (2015). The Lodève Basin is situated to the NW of Montpellier, France, on the south-eastern edge of the French Massif Central. This basin consists of ~3000 meters of Carboniferous–Permian siliciclastic rocks ranging from Ghzelian to Cisuralian. Unconformities separate the lower Asselian from upper Asselian strata and the middle Sakmarian from upper Artinskian strata (al. 2006). Only Permian strata outcrop in the Lodève Basin but Carboniferous outcrops occur in the adjacent Graissessac Basin (Bruguier et al. 2003), including Gzhelian (Stephanian C) through lower Asselian strata. The study by Michel et al. (2015) provides new data considering paleosols and high-precision U-Pb zircon ages for tuff beds within the Lodève and adjacent Graissessac basins. The study significantly revises the chronostratigraphy (see Fig. 1.6) of these basins correlating Permian terrestrial ones of eastern Euramerica.

1.2.3. Iberian basins

Wagner and Álvarez-Vázquez (2010) proposed a general review of the Carboniferous floral records in the Iberian Peninsula in the context of the geological history and distribution of the different basins. They considered that the whole Autunian regional stage should belong to the Pennsylvanian. Their supposition, based on megafloral biozones, **is no longer coherent with the new radioisotope ages provided in recent studies**, especially for the French Massif Central (Pellenard et al. 2017) which demonstrate that the Autunian (lower and upper) is mostly Permian, except for the oldest Igornay Fm that encompasses also the final part of the Carboniferous (Ghzelian).

2. Previous Studies

Upper Palaeozoic fossil plant macro-remains of Sardinia have been studied in the past mainly to support stratigraphic and sedimentological works. Most of them do not include pictures or descriptions of the species and are dated back to the ‘900 when the scientific knowledge about plant macro-remains was weak. In fact, detailed systematic papers dealing with this kind of fossils miss and sometimes specimens need to be revised using modern key or approach. It is difficult to find specimens previously mentioned in old works, and this is a big problem when some forms need to be revised, synonymised or studied in detail. The original material collected by various scientists in the first part of the XX century and stored in the Cagliari University misses and/or was lost during the 2nd World War. The plant remains and all the other fossils were kept in boxes and numbered (Comaschi Caria 1979; Scanu et al. 2012). From 1960 onwards, Comaschi Caria created a new inventory list and she rearranged the whole museum collection. This is the reason why in this thesis, only the new collected material from Montarbu and the Carboniferous material of San Giorgio will be discussed. Differently, microflora is well known and several papers have been published to date. Thus, in this chapter I want to summarize all the literature that deals with macrofossils ranging to Carboniferous to Permian in order to understand the history of Sardinian plant macro-remains. I kept the original dating described in the original papers and I put the correspondent for the *International Commission on Stratigraphy* in brackets. Even if the palynology is not subject of this research, a small essay about the Sardinian record will be shown as well.

2.1. Middle Pennsylvanian

The Late Carboniferous fluvio-lacustrine clastic deposits of Rio San Giorgio Fm (Carmignani et al. 2015) are the oldest Late Palaeozoic sediments bearing plant macro-remains in Sardinia (Italy). Plant macrofossils were first recorded by Vittorio Gambera, assistant engineer of the mines of southern Sardinia. He discovered some slabs containing floral macro-remains and sent these to De Stefani (Official of the Geological Survey of Italy) who supposed a Carboniferous age (AA.VV. 1897). The fossil flora was composed by *Annularia longifoglia*, *Asterophyllites*, *Sigillaria*, *Calamites*, *Pecopteris*, *Sphenopteris*, *Neuropteris*, *Cyatheites arborescens*, *Cyatheites dentatus*, *Alethopteris* and *Cordaites* (Capacci 1896; Gambera 1897a, b, c). Sartori (1909) found two fossil fragments in the San Giorgio basin, and one of these is *Cordaites borassifolius*. He postulated the possibility to refer these strata to the Carboniferous or probably to the Permian, because of the analogies with the Seui flora determined by Sterzel and shown by Fraas with a letter to the *Associazione Mineraria Sarda* (AA.VV. 1902a, b). The species reported in this letter are *Callipteris nickesi* (or *C. zeilleri*); *Pecopteris* sp. (or *Callipteridium subelegans*); *Pecopteris hemitelioides*; *Mixoneura obtusa*; *Cordaites* sp.; *Walchia filiciformis*; *Walchia piniformis*. However, Merlo (1911) discredited the presence of Carboniferous layers and said they belong to the Eocene. Testa (1914) recorded numerous sphenophytes, pecopterids and calamites in the upper part of the Rio San Giorgio section. Later, Sartori determined *Annularia stellata*, *Cordaides* cf. *principalis* and *Walchia piniformis* from San Giorgio (AA.VV. 1916; Novarese 1917). If the record of walchian conifers were true, Novarese (1917) would suppose the possibility of dating Autunian (late Ghzelian–Asselian) this deposit. Because of this conviction, the statement of the Autunian age of the outcrop was later confirmed in Novarese & Taricco (1922) and Novarese (1924). After, the Carboniferous age of the San Giorgio outcrop was confirmed by Gambera based on its discoveries (AA.VV. 1932), whereas Cocozza (1965) discussed the locality and the fossils so far found, attributing it to an undetermined Permian or Permo-Carboniferous age. Principi (1938) listed *Calamites*, *Annularia stellata*, *Pecopteris Cordaites* cf. *principalis*, *Walchia piniformis* and *Ernestia* (*Walchia*) *filiciformis* giving a lower Rotilegende age (late Ghzelian–early Asselian) to the San Giorgio outcrop. The earliest attempt at a taxonomic treatment was lately by Cocozza (1967) giving a detailed surveying of sedimentary Pre-Cambric outcrops, outlining the litho-stratigraphy history of the area. According to him the flora is composed by sphenophytes such as *Calamites suckowi* Brongniart, *C. gigas* Brongniart, C. cf. *leioderma* Gutbier, *Annularia stellata* Schlothein, *A. pseudostellata* Potonié, Marattiales like *Pecopteris arborescens* Schlotheim, *P. polymorpha* Brongniart ≡ *Acitheca polymorpha* (Brongniart) Schimper; pteridosperms such as *Callipteridium pteridium* Schlotheim, *Neuropteris planchardi* Zeiller, *Diksonites pluckeneti* f. *sterzeli* Zeiller and cordaitales like *Cordaites* cf. *lingulatus* Grand'Eury. These species underline an Upper Stefanian age (ca. middle Ghzelian).

Only strictly palynological papers have been carried out in the last second part of the XX century (Del Rio 1973; Del Rio & Pittau 1999; Pittau & Del Rio 2002; Del Rio et al. 2002; Del Rio & Pittau in Barca et al. 2004, Pittau et al. 2008). According to these authors, the microflora is dominated by pteridophyte spores. The triletes are the most diversified (*Cristatisporites*, *Densosporites granulosus*, *Savitrisporites camptotus*, *Savitrisporites cingulatus*, *Triquitrites arculatus*, *Triquitrites bransoni*, *Triquitrites sculptilis*, *Triquitrites rugosus*) while monolete spores (*Laevigatosporites*, *Latosporites*, *Puntactosporites*) are poorly represented. *Triquitrites verrucosus* indicate a “Westphalian” affinity even if they are rarely encountered in the sediments. In sandy layers, megaspores of sphenophytes and lycophytes have been recorded (*Calamospora* sp. *Laevigatisporites reinschii*, *Valvisisporites* sp. and *Zonalesporites ovalis*; Pittau & Del Rio 2002). Despite the rare occurrence of cordaitalean leaf compressions as macro-remains, pollen grains originating from these plants such as *Cordaitina* and *Florinites* are well represented in the assemblages. Other gymnospermous pollen is *Limitisporites*, *Pityosporites*, *Vesicaspora* and *Wilsonites*. Although of the restricted lateral extent and vertical thickness, these deposits have yielded not only abundant plant macrofossils and palynofloras, but occasional arachnoid, insect, and a very rich record of vertebrate and invertebrate track remains (Fondi 1979; Del Rio et al. 2002; Benedetti et al. 2002; Pillola et al. 2004; Selden & Pillola 2009; Marchetti et al. 2017).

2.2. Upper Pennsylvanian-Cisuralian

2.2.1. Central-southern Sardinia

Lamarmora (1857, vol. 3, p. 108) was the first who listed and figured plant macro-remains from the late Palaeozoic outcrops of Sardinia, suggesting a Carboniferous age for the Seui-Seulo and Perdasdefogu basins.

According to Meneghini (1857), Brongniart recognised *Pecopteris arborescens*, *Pecopteris dentata*, *Pecopteris unita*, *Pecopteris* aff. *defrancii*, *Neuropteris* sp., *Sphenophyllum dentatum*, *Annularia longifolia*, *Asterophyllites tenuifolia*, *Calamites suckowii* from the same localities combed by Lamarmora (1857). However, Meneghini (1857) did not recognise in the flora (Tab. 2.1) *Sphenophyllum dentatum* and *Neuropteris* sp., *Pecopteris defrancii* previously reported by Brongniart. After new systematic discoveries, Geinitz recommended synonymizing some specimens and Meneghini (1857) put *Coniopteris auriculata* and *Dicrophlebis crenulata* in *Cyatheites miltoni*. He recognized also *Pecopteris polymorpha* and *Pecopteris dentata* and gave an updated list of species (Tab. 2.2) for the "Fossiles de l'Epoque Houillère" of Sardinia (French for "Carboniferous fossils of Sardinia").

Based on the findings of Lamarmora described by Meneghini and Brongniart, Grand'Eury (1877, p. 433) considered the deposits of the Seui-Seulo Basin coeval to those of Saint Etienne, in France (late Carboniferous) and he added the following species: *Asterophyllites hippuroides* Brongniart, *Equisetites infundibuliformis* Sternberg, *Sphenophyllum oblongifolium* Germar et Kaulfuss, *Sphenophyllum fimbriatum* Brongniart, *Calamites suckowi* Brongniart, *Pecopteris arborescens*

Schlotheim, *Pecopteris candoliana* Brongniart, *Pecopteris unita* Brongniart, *Alethopteris ovata* Goeppert v. *major*, *Walchia piniformis* Sternberg.

Taxa	**Affinity**
Lepidodendron sp.	LYCO
Sigillaria (*Syringodendron*) sp.	LYCO
Annularia longifolia Brongniart	SPHENOP
Asterophyllites sp.	SPHENOP
Sphenophyllum sp.	SPHENOP
Calamites suckowii Brongniart	SPHENOP
Calamites cistii Brongniart	SPHENOP
Calamites cannaeformis Brongniart	SPHENOP
Calamodendron sp.	SPHENOP
Aplophlebis cf. *hemitelioides* Brongniart	MARATTIAL
Aplophlebis arguta Brongniart	MARATTIAL
Aplophlebis aequalis Brongniart	MARATTIAL
Aplophlebis arborescens Brongniart	MARATTIAL
Aplophlebis platyrachis Brongniart	MARATTIAL
Aplophlebis aspidioides Brongniart	MARATTIAL
Aplophlebis unita Brongniart	MARATTIAL
Aplophlebis sp.	MARATTIAL
Dicrophlebis gigantea Brongniart	MARATTIAL
Dicrophlebis sillimanii Brongniart	FERN
Dicrophlebis crenulata Brongniart	SEEDF?
Dicrophlebis affinis Brongniart	FERN
Dicrophlebis lepidorachis Brongniart	FERN
Dicrophlebis oropteridius Brongniart	FERN
Pecopteris longifolia Brongniart	MARATTIAL
Sphenopteris patentissima Goeppert	SEEDF?
Coniopteris auriculata Meneghini (nomen nudum)	FERN
Neuropteris sp.	MEDULLOS
Alethopteris lonchitica Brongniart	MEDULLOS
Alethopteris serlii Brongniart	MEDULLOS
Alethopteris sp.	MEDULLOS
Cordaites borassifolia Unger	CORDA
Taeniopteris vittata Brongniart	CYCAD

Tab. 2.1. List of species determinated by Meneghini and included in Lamarmora 1857 (p. 108).

Fossil plants coming from the Seui-Seulo basin (San Sebastiano locality) have also been listed by Pampaloni (1900). These fossils were determined by De Stefani using the approach of French palaeobotanists (e.g. Brongniart) and considering the outcrop of Carboniferous age contrarily to the German palaeobotanists that according to these fossils considered the outcrop belonging to the Permian.

Here the list of taxa recognised: *Sphenopteris* cf. *matheti* Zeiller, *Cyathocarpus arborescens* Goeppert, *Diplazites unitus* Brongniart, *Calamites leioderma* Gutbier, *Annularia stellata* Sternberg, *Buckmannia tubercolata* Sternberg, *Macrostachia carinata* Germar, *Cordaites borassifolius* Unger, *Dorycordaites lingulatus* Grand'Eury, *Aspidiopsis coniferoides* Potonié, *Walchia piniformis* Schlothein.

Taxa	**Affinity**
Sigillaria sp.	LYCO
Lycopodites sp.	LYCO
Calamites cannaeformis Schlothein	SPHENOP
Calamites cisti Brongniart	SPHENOP
Calamites suckowi Brongniart	SPHENOP
Calamites sp.	SPHENOP
Asterophyllites equisetiformis Brongniart	SPHENOP
Annularia longifolia Brongniart	SPHENOP
Sphenophyllum sp.	SPHENOP
Hymenophyllites sp.	FERN
Cyatheites dentatus Goeppert	MARATTIAL
Cyatheites aequalis Goeppert	MARATTIAL
Cyatheites arborescens Goeppert	MARATTIAL
Cyatheites argutus Geinitz	MARATTIAL
Cyatheites candollianus Goeppert	MARATTIAL
Cyatheites miltoni Goeppert	MARATTIAL
Cyatheites oropteroides Goeppert	MARATTIAL
Cyatheites unitus Geinitz	MARATTIAL
Cyatheites sp.	MARATTIAL
Pecopteris gigantea Brongniart	MARATTIAL
Oligocarpia gutbieri Goeppert	GLEICHEN
Alethopteris pluckeneti Geinitz	CALLISTOPH
Alethopteris sp.	MEDULLOS
Odontopteris brardii Brongniart	MEDULLOS
Cordaites borassifolius Unger	CORDA
Carpolites sp.	SEED

Tab. 2.2. List of species by Meneghini (1857) for the Seui-Seulo basin.

De Stefani (1901) discussed the age attributed to the floras of Sardinia collected by Lamarmora, arguing that they should be considered younger than those of Saint Etienne (France; Grand'Eury (1877), and found similarities with the deposits of Jano, in Tuscany (Italy).

Arcangeli (1901) restudied the fossils collected by Lamarmora, De Stefani and Lovisato and gave an updated list of the Late Carboniferous-Early Permian flora of the Seui anthraciferous deposits and only a small number of them is exclusively about Carboniferous or Permian times (Appendix 2).

Later, Fiorentin (1923) considered the black shales of the Seui-Seulo area, containing *Walchia piniformis*, coeval of the French "Autunian" localities.

Maxia (1938) and Vardabasso (1938) described the “Autunian flora” of Perdasdefogu, listing some rare species: *Diksonites pluckenetii*, *Calamites cisti*, *Callipteridium crassinervium*, *Alethopteris serli*.

In his treatise about the Permian floras, Principi (1938) listed *Calamites gigas*, *Callipteris conferta*, *Callipteridium subelegans*, *Odontopteris reichi*, *Pecopteris arborescens*, *Pecopteris dentata*, *Ulmannia brauni*, *Walchia piniformis* for the so called “lower Rotliegende” of Seui. He also noticed the presence of *Samaropsis fluitans* seeds for the Nurra region (northern Sardinia).

Pecorini (1952) found *Walchia* remains in the San Sebastiano mine (Seui), whereas Comaschi Caria (1959) summarised all the palaeobotanic discoveries of Sardinia and added some new findings for some “Autunian” deposits (Miniera Corongiu and San Sebastiano of Seui and Ingurtipani of Seulo; Tab. 2.3).

Vardabasso (1950) summarised both fossiliferous and not fossiliferous Permian outcrops including San Giorgio (southern Sardinia).

Spano (1976) restudied the fossils of some known (San Sebastiano and San Girolamo, Seui; Ingurtipani, Seulo; Riu Su Luda, Perdasdefogu; Mulargia, Orroli) and never explored before localities (Genniaca, Seui; Perda Pera, Ierzu; S’Abba ‘e Ferru, Perdasdefogu). Based on these findings (Appendix 3) the author attributed all the aforementioned localities to the “Autunian”.

Pecorini (1974) and Francavilla et al. (1977) reported few species such as *Lebachia* (*Walchia*) *piniformis* and *Autunia* sp. and fragmentary forms for the Mulargia lake outcrops (southeastern Sardinia). The other species found are *Callipteris conferta* Sternberg, *Callipteris naumanni* Gutbier, *Callipteris* cf. *polymorpha* Sternberg, *Lebachia piniformis* (Schlothein) Florin, *Lebachia* cf. *hypnoides*

Taxa	**Affinity**	**Locality**
Sigillaria ichthyolepis (Sternberg) Corda	LYCO	Seui Corongiu
Annularia longifolia Brongniart	SPHENOP	Seui Corongiu
Annularia sphenophylloids Zenker	SPHENOP	Seui San Sebastiano
Asterophyllites equisetiformis Zenker	SPHENOP	Seui San Sebastiano
Calamites sp.	SPHENOP	Seui San Sebastiano
Calamites undulatus Sternberg	SPHENOP	Seulo Ingurtipani
Sphenophyllum oblongifolium (Germar et Kaulfuss) Unger	SPHENOP	Seui San Sebastiano
Asterotheca daubreei Zeiller	MARATTIAL	Seui San Sebastiano
Pecopteris arborescens Brongniart	MARATTIAL	Seui Corongiu
Pecopteris augusta Brongniart	MARATTIAL	Seui Corongiu
Pecopteris cyathea (Schlotheim) Brongniart	MARATTIAL	Seui San Sebastiano
Pecopteris densifolia Goeppert	MARATTIAL	Seui San Sebastiano
Pecopteris lepidorachis Brongniart	MARATTIAL	Seui San Sebastiano
Pecopteris miltoni Artis	MARATTIAL	Seui San Sebastiano
Pecopteris polymorpha Brongniart	MARATTIAL	Seui San Sebastiano
Pecopteris unita Brongniart	MARATTIAL	Seui San Sebastiano
Dactyloteca canavari De Stefani	?	Seui Corongiu
Alethopteris grandini Gutbier	MEDULLOS	Seui San Sebastiano
Linopteris brongniarti Gutbier	MEDULLOS	Seui San Sebastiano
Neuropteris planchardi Zeiller	MEDULLOS	Seui San Sebastiano
Odontopteris obtusa Brongniart	MEDULLOS	Seui San Sebastiano
Callipteris cf. *juteri* Zeiller	PELTASPERM	Seui San Sebastiano
Callipteris conferta Sternberg	PELTASPERM	Seui San Sebastiano
Pseudomariopteris ribeyroni Zeiller	PTERIDOSPERM	Seui San Sebastiano
Sphenopteris sp.	PTERIDOSPERM	Seui Corongiu
Cordaites principalis Germar	CORDA	Seui Corongiu
Lebachia (*Walchia*) *piniformis* Gutbier	CONIF	Seui San Sebastiano
Taeniopteris multinervia Weiss	CYCAD?	Seui San Sebastiano

Tab. 2.3. Species found by Comaschi Caria (1959) for the Seui-Seulo Basin, subdivided in the collecting localities.

Brongniart, *Ernestiodendron* aff. *germanicus* Florin, *Ernestiodendron* cf. *filiciforme* (Schlothein) Florin, *Walchia* sp., *Taeniopteris* sp., *Cordaites borassifolius* Sternberg, *Cordaites* cf. *principalis* Germar, *Cordaites* sp., *Cordaianthus* sp., *Samaropsis* sp.

After decades, Broutin et al. (1996) renewed research on the Permian sedimentary and volcanic deposit of Sardinia (Perdasdefogu Basin, Escalaplano-Mulargia Basin, Lu Caparoni Basin; Appendix 4).

Broutin et al. (in Cassinis et al. 1999) recognised *Culmitzchia* aff. (al. *Lebachia*) *speciosa* in the Escalaplano-Mulargia Basin and identified at Seui *Annularia sphenophylloides*, *Pecopteris* cf. *arborescens*, *Pecopteris cyathea*, *Pecopteris* sp., *Pecopteris* sp. cf. *hemitelioides*, *Pecopteris unita*, *Cordaites* sp., *Sigillaria brardii* and *Artisia* sp.

Taxa	**Affinity**
Annularia mucronata Schenk	SPHENOP
Asterophyllites longifolius (Sternberg) Brongniart	SPHENOP
Acitheca polymorpha (Brongniart) Schimper	MARATTIAL
Pecopteris elaverica Zeill.	MARATTIAL
Gracilopteris strigosa (Zeiller) Kerp	CALLIPT
Autunia conferta (Sternberg) Kerp	PELTASPERM
Lodevia nicklesi (Zeiller) Haubold et Kerp	PELTASPERM
Rhachiphyllum lyratifolia (Goeppert) Kerp	PELTASPERM
Rhachiphyllum schenckii (Heyer) Kerp	PELTASPERM
Odontopteris lingulata (Goeppert) Schimper	MEDULLOS
Alethopteris serlii (Brongniart) Goeppert	MEDULLOS
Callipteridium sp.	MEDULLOS
Neuropteris osmundae (Artis) Kidston	MEDULLOS
Dichophyllum flabelliferum (Weiss) Kerp et Haubold	PTERIDOSP
Cordaites sp.	CORDA
Poacordaites sp.	CORDA
Culmitzschia laxifolia (Florin) Clement-Westernhof	CONIF
Culmitzschia speciosa (Florin) Clement-Westernhof	CONIF
Ernestiodendron filiciforme (Sternberg) Florin	CONIF
Feysia minutifolia Broutin et Kerp	CONIF
Hermitia arnahardti (Florin) Kerp et Clement-Westernhof	CONIF
Lebachia piniformis (Sternberg) Florin 1938	CONIF
Otovicia hypnoides (Florin) Kerp et al.	CONIF
Taeniopteris multinervia Weiss	CYCAD?

Tab. 2.4. List of species reported by Cassinis et al. 1999 for the Perdasdefogu basin

New findings in the Perdasdefogu Basin are described in Cassinis et al. (1999, p. 76; Tab. 2.4). In the Perdasdefogu basin, non-marine algae, amphibian and fish remains have been described as well (Freytet et al. 1999, 2002; Ronchi et al. 1998, 2008; Ronchi & Tintori 1997; Werneburg et al. 2007). Furthermore, In the Perdasdefogu basin, silicified preserved plants occur in angular cherts (Galtier et al. 1998, 2011; Tab. 2.5).

Taxa	**Affinity**
Arthropitys cf. *renaulti* Boureau	SPHENOP
Arthropitys bistriata (Cotta) Goeppert	SPHENOP
Astromyelon sp.	SPHENOP
Palaeostachya sp.	SPHENOP
Sphenophyllum sp.	SPHENOP
Scolecopteris cf. *alta* Millay	MARATTIAL
Scolecopteris cf. *elegans* Zenker	MARATTIAL
Scolecopteris cf. *parvifolia* Millay	MARATTIAL
Anachoropteris pulchra Corda 1845	MARATTIAL
Ankyropteris brongniarti Renault 1869	MARATTIAL
Pecopteris sp.	MARATTIAL
Psaronius sp.	MARATTIAL
Stewartiopteris sp.	MARATTIAL
cf. *Parataxospermum* sp.	CORDA?
Cycadinocarpus augustodunensis (Brongniart) Renault	CORDA?
Cordaites cf. *crassus* Renault	CORDA
Cordaites cf. *lingulatus* Grand'Eury	CORDA
Cordaites sp.	CORDA
Cordaites tenuistriatus Grand'Eury 1877	CORDA
Cordaixylon sp.	CORDA
Dadoxylon cf. *rollei* Unger	CONIF?

Tab. 2.5. List of silicified plants from the Perdasdefogu Basin (Galtier et al. 2011).

In the Guardia Pisano Basin (southern Sardinia) only *Lebachia* and *Pecopteris* (Pittau et al. 2002; Barca & Costamagna 2006) have been found so far. In this outcrop, also freshwater shark remains have been reported (*Lissodus* and *Acanthodes*; Fischer et al. 2010). The upper part of the succession has been radiometrically dated 297±5 Ma (Asselian; Pittau et al. 2002).

2.2.2. Northern Sardinia

Lovisato (1884) was the first to study the Permo-Triassic successions of the Nurra region (northern Sardinia). He did not find Permian fossils but predicted the presence of them in the Lu Caparoni (Alghero, northern Sardinia) siltstones and sandstones. Later, Lotti (1931) recognized the presence of vegetal remains in the anthraciferous levels near to Alghero attributing it to the Carboniferous, but Oosterban (1936) considered Triassic this deposit.

Pecorini (1962) was the first to determine vegetal remains in the Lu Caparoni basin giving an Autunian age to these sediments (Tab. 2.6) that was confirmed by Vardabasso (1966).

Taxa	**Affinity**
Annularia stellata Schlotheim	SPHENOP
Annularia sphenophylloides Zenker	SPHENOP
Pecopteris sp.	MARATTIAL
Odontopteris subcrenulata Rost (≡Mixoneura subcrenulata)	MEDULLOS
Linopteris cf. *brongnarti* Gutbier	MEDULLOS
Callipteris nicklesi Zeiller	PELTASPERM
Callopteris conferta Sternberg	PELTASPERM
Callipteris bergeroni Zeiller	PELTASPERM
Callipteris cf. *flabellifera* Zeiller	PELTASPERM
Callipteris cf. *raymondi* Zeiller	PELTASPERM
*Cordaites*sp.	CORDA
Lebachia (*Walchia*) *piniformis* Florin (Schlotheim)	CONIF
Lebachia (*Walchia*) cf. *gallica* Florin	CONIF
Lebachia (*Walchia*) cf. *laxifolia* Florin	CONIF
Walchia linearifolia Goeppert	CONIF
Ernestiodendron (*Walchia*) *filiciforme* Florin (Schlotheim)	CONIF
Taeniopteris multinervia Weiss	CYCAD

Tab. 2.6. Plants found by Pecorini (1962) for the Permian of northern Sardinia

Francavilla in Gasperi & Gelmini (1979), Broutin et al. (1996), Broutin et al. (in Cassinis et al. 1999) and Ronchi et al. (2008) gave a list of species of northern Sardinia (Tab. 2.7; Tab. 2.8; Appendix 4).

Taxa	**Affinity**
Pecopteris hemitelioides Brongniart	MARATTIAL
Odontopteris sp.	MEDULLOS?
Odontopteris subcrenulata Rost non Zeiller (≡ Mixoneura subcrenulata)	MEDULLOS
Callipteridium sp.	MEDULLOS
Sphenopteris germanica Weiss	PTERIDOSP?
Diplotheca stellata Kidston?	PTERIDOSP
Walchia (*Lebachia*) *piniformis* Schlothein	CONIF
Walchia (*Ernestiodendron*) *filiciformis* Sternberg	CONIF
Walchia sp.	CONIF
Samaropsis fluitans Dawson	SEED
Taeniopteris sp. cf. *T. multinervia* Weiss	CYCAD?

Tab. 2.7. List of plants determined by Francavilla for the Lu Caparoni basin (in Gasperi & Gelmini 1979)

Taxa	**Affinity**
Remia pinnatifida (Gutbier) Knight	FERN?
Pecoperis polymorpha Brongniart	MARATTIAL
Pecopteris sp.	MARATTIAL
Odontopteris cf. *subcrenulata* Rost	MEDULLOS
Autunia (al. *Callipteris*) *conferta* (Brongniart) Haubold et Kerp	PELTASPERM
Rhachiphyllum (al. *Callipteris*) *lyratifolia* (Goeppert) Kerp	PELTASPERM
Dichophyllum (al. *Callipteris*) *flabellifera* (Weiss) Kerp et Haubold	PTERIDOSP
Walchia piniformis Sternberg (sensu Visscher et al. 1986)	CONIF
Otovicia (al. *Walchia*) *hypnoides* (Florin) Kerp et al.	CONIF
Ernestiodendron filiciforme (Sternberg) Florin	CONIF
Taeniopteris sp.	CYCAD

Tab. 2.8. List of plants determined by Broutin (in Ronchi et al. 2008)

2.2.3. Palynological data

Palynological studies of Sardinian late Palaeozoic sediments have been carried out in different localities. In the south, the Guardia Pisano outcrop yielded a very rich microflora (Pittau et al. 2002). In the central Sardinia (Escalaplano-Mulargia basin), the first report of palynomorphs was given by Pittau et al. (2008) that found a high percentage of Cordaites pollen grains. As reported by Pittau et al. (2008), the palynological spectrum for the Perdasdefogu basin is very poorly preserved, and sporomorphs are completely dark. On the contrary, Broutin et al. (in Cassinis et al. 1999) found in the Perdasdefogu basin a rich association found within the macrofloral deposit, dominated by the monosaccate *Potonieisporites* "*novicus-bhardwajii*" complex. The latter authors correlate this basin to that of Lu Caparoni (northern Sardinia) that was lately investigated by Broutin et al. (in Cassinis et al. 1999) In the Seui-Seulo basin, palynological studies from the San Sebastiano and Genn'e Acca sections were carried out by Pittau et al. (2008). The palynological association is very rich and includes several species of *Potonieisporites*, *Hamiapollenites*, *Striatohaploxypinus*, *Costaepollenites*, *Complexisporites* and, seldomly, *Vittatina*. Trilete spores are subordinate. This association is included in the *Potonieisporites* phase (the scheme of the phases is included in Chapter 6) that according to these latter author corresponds to the early Asselian.

3. Methods

Palaeobotanical methods can be quite complex. The sentence by Stewart & Rothwell (1993) shows the main difficulty of palaeobotany because of the fragmentary nature of the fossil plant specimens:

"How much easier the paleobotanist's work would be if plants were preserved in their entirety".

The fossil plants, in fact, are mostly recorded disarticulated, as detached organs, isolated leaves, stems, reproductive structures and so on, and the main goal of palaeobotany is to understand the entire organism, the whole fossil plant concept, and its evolution in time and space.

This specificity of the plant fossil record is recognised in the International Code of Botanical Nomenclature (ICBN or *Saint Louis Code*, adopted since 1999; see McNeill et al. 2012 for details) in existence of fossil-taxon according to Cleal & Thomas (2010a, b). The ICBN defines that the use of separate names is allowed for fossil-taxa that represent different parts, life-history stages, or preservational states of what may have been a single organismal taxon or even a single individual. Thus, the Art. 1.2. (McNeill et al. 2012, p. 24) establishes that “fossil-taxon comprises the remains of one or more parts of the parent organism, or one or more of their life history stages, in one or more preservation states, as indicated in the original or any subsequent description or diagnosis of the taxon”.

3.1. Preparation of fossils

To prepare fossils for identification and study, the surrounding rock had been removed. Thus, the matrix of the specimens was cleaned with a small, rigid-bristled brush or using pneumatic pens driven by compressed air. The plant remains were cleaned with a paintbrush with soft bristles and if necessary, washed with water. Fractured specimens were consolidated using Paraloid B72 (or B-72) that is a thermoplastic resin commonly used as an adhesive by conservator-restorers. One of the major advantages of B-72 is that it is stronger and harder than polyvinyl acetate without being extremely brittle. The choice of B-72 has been made because it is a durable and non-yellowing acrylic resin (ethyl methacrylate copolymer) and it is soluble in acetone, ethanol, toluene, and xylenes and so on.

3.1.1. Acetate peel technique

The attempt to find vegetal remain in the silicified rocks coming from the Perdasdefogu basin (Rio Su Luda Fm) has been made using the acetate peel technique explained by Galtier & Phillips (1999) and in use in the *Laboratoire de Paleobotanique* of CIRAD-AMAP (Montpellier, France). The peel technique was originally developed as a cheap and rapid alternative to the standard thin section method. Thus, it reveals advantages. In fact, this way to study fossils in thin-section lets to obtain very close serial sections. The information obtained from tissues systems allows, among others, the development of ontogenetic and biomechanical approaches in fossil plants. For the preparation, first, specimens must be cut in slices by lapidary saws. Slices need to be deep cleaned and the cut surface smoothed on a lapidary wheel or simply in a thick glass using a paste of abrasive powder with water. After, the smooth surface of the specimen must be put under hydrofluoric acid (HF 25-40%) for

30 seconds to 3 minutes. The specimen is ready when the colouration of the smooth surface reaches the white. After that, the specimen must be washed using water and dried placing it with the etched face up on a surface of the pea-sized gravel. The following step is to place the specimen with the etched surface nearly level and then flood the surface with acetone. From the flooded end, quickly and gently roll the acetate sheet, previously prepared cutting pieces of sufficient size, with flexed tension, across the surface; the excess acetone should be pushed in front of the sheet as it flattens and excludes air bubbles. Let it dry (from 30 minutes to 1 hour) and remove gently pulling from a good edge to obtain the acetate peel. If needed, the specimen is now ready for a repetition of the process after a quick smoothing of its surface and as many as 20 peels may be made from a 1 mm thickness of petrifaction.

3.2. Study of plant fossils

After the preparation of these fossils, the identification of the macro remains has been done following two main steps:

a) to group the macro-remains according to their apparent similarity is the first step. It is not an easy procedure, and sometimes mistakes can occur;

b) for a good identification of plant remains is fundamental a good bibliographic research using updated papers, especially of coeval closest floras to obtain similar species to be compared to those of the studied zone.

It is not obvious to find the same species in two closes floras. A close level of resemblance would be expected at least at the genus level, and discrepancies are due to the presence of local species. In general, plant fossils are preserved in different ways according to a different environment in which they have been buried or different speciation. Specimens are represented by compression/impression. The impressions are often preserved in coarse-grain sandstones mixed with silt and clay. In this case, the rock slab is not well consolidated, and its formation points to low-energy river or floodplain environments. The organic material is not preserved and has been replaced by a clay film that retains a detailed impression of the plant part. Because all specimens are either impressions or poorly preserved compressions (containing high oxidised coal material) and provide any other anatomical evidence, the descriptions are, therefore based merely on the morphology of the plant remains.

The fossils were studied under dissecting microscopes. Photographs were performed using reflex digital system camera (Nikon D60, Canon EOS 1300D, Canon PowerShot G5X) and microscopes (Leica Microsystems DMS1000 digital; Olympus SZX12 binocular). Details of specimens were observed under SEM (JEOL 6380LV property of the Institute of Geology and Palaeontology, Faculty of Sciences, Charles University in Prague). *In situ* spores have been found in the San Giorgio material. They were isolated by taking a small quantity of organic material from the cones with a pointed needle. The organic material was dissolved using HCl (30%) and HF (37%), washed with water and cleaned up with ultrasound to separate the spores from the cone tissue. Any resulting spores were mounted with a synthetic resin in permanent slides for being studied (see Appendix 1 for details of this study).

It is important to identify the flora trying to compare it regarding modern plants, or "nearest living relatives," to obtain a correspondent picture for understanding the palaeoecological and palaeoenvironmental condition of these old plants. The plant remains were subdivided based on their lithology, and for each group, a detailed quantitative analysis was carried out using Microsoft® Excel.

3.3. Analytical methods

With the aim to understand the vegetational composition of the Montarbu flora in the picture of the western Tethys area, a comparison between this flora and the late Palaeozoic and paleogeographically closes floras has been done. Thus, the number of specimens collected permits to do carry on statistical analysis. The relative abundances of the macroflora found in two types of sediments have been studied, and the paleoecological preferences have been evaluated as well.

3.3.1. Abundances in the sediments

For representing the comparing results, the Pareto chart is chosen among others (named after Vilfredo Pareto 1848– †1923). This is a bar chart of frequencies sorted by frequency. It contains both bars and a line graph, in which individual values are represented in descending order by bars. The cumulative total, in percentage, is represented by the line (for details see Wilkinson 2006). It belongs on the Seven Basic Tools of Quality (Ishikawa 1990) which is a designation given to a fixed set of graphical techniques identified as being most helpful in troubleshooting issues. The other graphic representations are given using pie charts divided into slices to illustrate percentage proportions of the floral groups. The ecological preferences are explained in the paragraphs below according to literature data.

3.3.2. Sørensen-Dice (IS) comparison

To analyse the uniformity of the Late Palaeozoic floras palaeogeographically close to that of Montarbu (see below), an attempt to numerical quantify selected fossil plant assemblages is done using the Sørensen-Dice index which is a presence-absence index (IS; Source: Sørensen 1948; Dice 1945); it is mainly useful for ecological community data and is particularly good for comparing the similarity of two samples, and in our case to compare late Ghzelian–early Asselian (C/P) assemblages because of the paucity of these records. Indeed, this index retains sensitivity in more heterogeneous data sets and gives less weight to outliers (McCune et al. 2002). "IS" is given by the following equation "IS= 2G/(2G)+A+B", where "G" represents common genera in both floras samples; "A" is the number of genera in the first sample; "B" represents the number of genera in the second flora. This method has been previously adopted for studying differences in Middle Jurassic Floras (Scanu et al. 2015) The study has been confirmed giving the same results with different methods in Barbacka et al. (2014).

For this analysis, 19 plant assemblages have been chosen among the recently published papers dealing with fossil floras in the western Tethyan area, considering only floras ranging from the boundary Ghzelian–Asselian (Carboniferous–Permian, C/P). The list of references of these plant assemblages is summarised in Tab. 3.1. and the assemblages will be discussed in chapter 6.

For the analyses, some species determined in non-updated papers have been changed according to recent systematic revisions at a global scale: *Callipteris conferta* is considered *Autunia conferta*; *Pecopteris polymorpha* is *Acitheca polymorpha*;

Scolecopteris arborescens is *Pecopteris arborescens*; *Odontopteris subcrenulata* is *Mixoneura subcrenulata*; *Neuropteris planchardii* is *Neurocallipteris planchardii*.

FLORAS	AGE	REFERENCES
Montarbu	late Ghzelian	this paper
E-Pyrenees	early Asselian	Wagner & Álvarez-Vázquez 2010
E-Asturias and Cantabrian mountains	late Ghzelian-early Asselian	Wagner & Martinez Garcia 1982; Gand et al. 1997; Wagner & Álvarez-Vázquez 2010
E-Iberian Range	late Ghzelian-early Asselian	Wagner & Álvarez-Vázquez 2010
E-Andalucía	late Ghzelian-early Asselian	Mingarro-Martin 1962; Broutin 1974, 1986; Wagner & Álvarez-Vázquez 2010
F-Lodève-Graissesac	late Ghzelian-early Asselian	Martín-Closas & Galtier 2005; Michel et al. 2015
F-Igornay	late Ghzelian	Broutin et al. 1999; Pellenard et al. 2017; Galtier pers. comm.
F-Muse	early Asselian	Broutin et al. 1999; Pellenard et al. 2017; Galtier pers. comm.
F-Massif Central (Montceau)	late Ghzelian-early Asselian	Bercovici & Broutin 2008
P-Buçaco basin	late Ghzelian-early Asselian	Teixeira 1944; Wagner & Lemos de Sousa 1983; Wagner & Álvarez-Vázquez 2010
I/A-Carnic Alps	late Ghzelian-early Asselian	Fritz & Krainer 2007
G-Saar	C/P	Trunko & Munk 1980; Kerp & Fichter 1985; Lausberg & Kerp 2000; Uhl & Jasper 2016
G-Döhlen Formation	early Asselian	Barthel 2016
G-Türinger Waldes	late Ghzelian-early Asselian	Barthel 2009; Barthel & Brauner 2015; Schneider et al. 2014
G-Weissig Basin	early Asselian	Barthel et al. 2010
CZ-CWBB	C/P	Opluštil et al. 2013; Martínek et al. 2017
CZ-Krkonose-piedmont Basin	C/P	Opluštil et al. 2013; Opluštil et al. 2016b
CZ-ISB	C/P	Opluštil et al. 2013, 2017b
CZ-Boskovice Basin	C/P	Opluštil et al. 2013, 2017a
CZ-Blanice Basin	C/P	Opluštil et al. 2013

Tab. 3.1. Localities of the floras chosen for the IS comparison, age and references of data.

4. Studied Material

For understanding the differences across the changing of vegetation in different outcrops of Sardinia and compare the flora of Montarbu that is best documented Sardinian C/P flora with those palaeogeographically closes of Europe, material coming from collections and new findings have been studied in this work of thesis. All the specimens are now stored at the “Museo Sardo di Geologia e Paleontologia Domenico Lovisato”, located in the “Dipartimento di Scienze Chimiche e Geologiche”, Università di Cagliari, here designated as repository. New findings and museum material are labelled and sigled MDLCA (Museo Domenico Lovisato CAgliari). In the following paragraphs, the geological framework and the studied material of each studied locality will be discussed.

4.1. The late Pennsylvanian (Moscovian) flora of Sardinia

4.1.1. Geo-Stratigraphic framework

The best documented Moscovian (Pennsylvanian) succession in Sardinia is in the small fault-bounded intramontane San Giorgio Basin, located near Iglesias, in the South West of the Island. The San Giorgio Basin is the stratigraphically oldest of the Sardinian late Variscan basins, belonging to the first cycle (Pittau et al. 2008). The basin, which is of only about 3 km^2 aerial extent (Del Rio & Pittau in Barca et al. 2004), was the result of extensional tectonics (Carmignani et al. 1992; Barca & Costamagna 2003). It contains c. 45 m of mainly coarse clastic deposits with subsidiary finer-grained deposits (together referred to the San Giorgio Formation; Carmignani et al. 2015) lying unconformably on the upper Cambrian/lower Ordovician Cabitza shales Formation (Barca & Costamagna 2003; Barca in Barca et al. 2004). Large parts of the basin have become obscured by spoil tipped from the nearby Campo Pisano lead and zinc mine, and the landscape of this area has been extensively modified by extensive mining activity since the 19th century (Scanu et al. 2016). Cocozza (1967) referred to a fluvial and lacustrine environment these sediments, considering them also of alternatively hot and humid climate. The

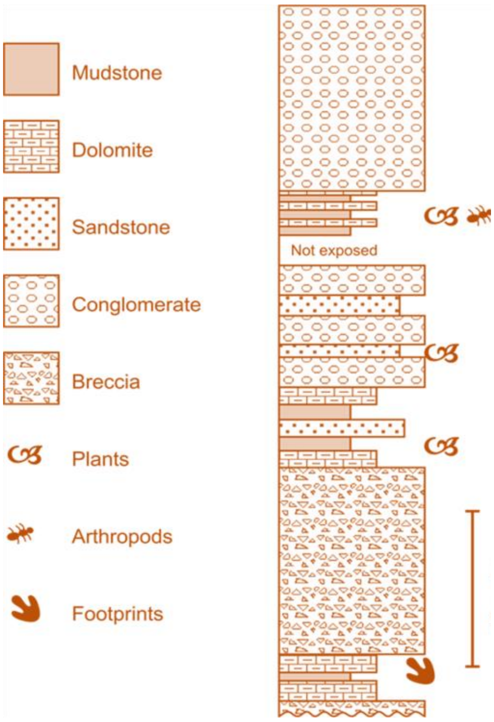

Fig. 4.1. Simplified geological section through the Carboniferous sequence (after Barca & Costamagna 2003, modified, scalebar 10 meters).

sediments, according to this author, by their sedimentological characteristics, are to be referred to Sahelian or Sudanian type. Del Rio et al. (2002) and Del Rio & Pittau (in Barca et al. 2004) described three lithostratigraphic units in the following ascending stratigraphical order (Fig. 4.1):

> Unit A: 0–13 m mainly breccias with dolomitic cement, with subsidiary dolomite and dolomitic siltstone in the lower part.
>
> Unit B: 6–15 m of mainly yellow-grey dolomites with subsidiary well-bedded breccias, siltstones and mudstones, and capped by massive sandstone.
>
> Unit C: 6–11 m of conglomerates, with subsidiary sandstones.

Barca & Costamagna (2003) provided a new detailed lithological and sedimentological analysis of the sequence interpreting it as a series of debris and mass flow deposits resulting from rapid erosion of the adjacent Lower Palaeozoic basement, separated by lacustrine siltstones and mudstones representing intervals of reduced subsidence. The fossils mostly occur in the lacustrine deposits.

4.1.2. Material

The studied material belongs to the Pittau-Del Rio Collection and was collected over the last 20 years during several field trips in the San Giorgio Basin. All studied material comprises 170 slabs containing plant fossils belonging to 23 species (17 genera; Tab. 4.1). Six lithofacies were recognised among the specimens examined:

I) Very pale, grey flaggy but non-laminated mudstone. This was the most commonly found lithology. In the field rocks of this facies appear medium to medium dark grey in colour but became noticeably lighter on drying. The interpretation of these deposits is lacustrine.

II) Flaggy, laminated mudstone with bands of dark mudstone within an otherwise mainly pale mudstone. This was very similar to Lithology I.

III) Laminated, dark grey, hard mudstone. It is interpreted as lacustrine, possibly deposited under lower energy conditions.

IV) Medium to coarse-grained yellow to cream coloured sandstones. These are likely to represent small-scale channel deposits.

V) Blocky, grey mudstone with a distinctive conchoidal fracture. We interpret these as lacustrine deposits.

VI) Medium grey mudstone with distinctive yellow to orange iron staining. In the field, this was found towards the top of the fossiliferous interval, just before the appearance of the overlying conglomeratic unit.

The assemblage is dominated by sphenophytes, but with subsidiary ferns, pteridosperms, (?)noeggerathians and cordaitanthaleans. Sphenophytes are represented by stems with abundant leafy shoots forming whorls of *Annularia* having spatulate-lanceolate shape identified as *A. galioides*, *A. sphenophylloides*, *A. spinulosa*, and *A. sardiniana*. The latter species is often found in association with sphenophyte cones, here determined as *Palaeostachya* sp. The species *Sphenophyllum* cf. *emarginatum* is present as well. *Calamites* pit-casts and roots of *Pinnularia* sp. also compose the equisetalean record. Pteridophytes are represented by fragments belonging to the Marattiales such as *Cyathocarpus sp.*, ?*Crenulopteris* sp., ?*Sydneia* sp. and also small fragments of the herbaceous fern *Renaultia* cf.*villosa*. Pteridosperms are represented by fronds of *Dicksonites plukenetii*, *Eusphenopteris nummularia*, *Alethopteris ambigua*, *Neuropteris ovata*, *Linopteris* cf. *obliqua*, together with *Trigonocarpus* sp. seeds and other fragments impossible to identify to species

(*Alethopteris* sp., *Neuropteris* sp., ?*Neuropteris* sp.). A cone of *Discinites* sp. represents the Noeggeratiopsida. Furthermore, cordaitalean root systems of *Artisia approximata* indicate the presence of gymnosperms.

TAXA	**AFFINITY**
Annularia sphenophylloides (Zenker 1833) Gutbier 1837	SPHENOP
Annularia galioides (Lindley et Hutton 1832) Kidston 1891	SPHENOP
Annularia spinulosa Sternberg 1821	SPHENOP
Annularia sardiniana Cleal et al. 2017	SPHENOP
Sphenophyllum cf. *emarginatum* (Brongniart) Brongniart 1828	SPHENOP
Calamites sp.	SPHENOP
Pinnularia sp.	SPHENOP
Cyathocarpus sp.	FERN
?*Crenulopteris* sp.	FERN
?*Sydneia* sp.	FERN
Renaultia cf.*villosa* (Crépin) Danzé, 1956	FERN
Dicksonites plukenetii (Schlotheim ex Sternberg 1825) Sterzel 1881	SEED-FERN
Eusphenopteris nummularia (Gutbier 1835) van Amerom 1975	SEED-FERN
Alethopteris sp.	SEED-FERN
Alethopteris ambigua Lesquereux 1880	SEED-FERN
Neuropteris sp.	SEED-FERN
?*Neuropteris* sp.	SEED-FERN
Neuropteris ovata Hoffmann 1826	SEED-FERN
*Linopteriscf. Obliqua (*Bunbury) Zeiller emend. Zodrow et al. 2007	SEED-FERN
Trigonocarpus sp.	SEED-FERN
Discinites sp.	NOEGGERAT
Artisia approximata (Brongniart ex Lindley et Hutton 1837) Corda in Sternberg et al. 1838	CORDA

Tab. 4.1 Taxa belonging to the Pittau-Del Rio Collection (San Giorgio Basin, Moscovian)

4.2. The C/P flora of Montarbu

4.2.1. Geo-Stratigraphic framework

The Montarbu sampling locality is about 6 km to the east of Seui-Seulo Basin. The fossiliferous section is located along the SP 198 and the railway tracks. The succession shows strict litho- and biostratigraphical correlation with the closes Seui and Seulo (Ronchi et al. 2008). The Late Palaeozoic succession of Montarbu lies non-conformably over the Basement, composed by metasandstones and metapelites belonging to Cambrian to Devonian Barbagia Low-Grade Metamorphic Complex (Carosi et al. in Carmignani et al. 1992) and below Jurassic shales and dolostones of the Genna Selole Fm and the Dorgali Fm (Dieni et al. 1983; Costamagna et al. 2007, 2018; Costamagna 2016; Scanu et al. 2012, 2015). In the Montarbu area, the succession is overtopped by a decametric volcanic outflow.In the rest of the Seui Basin, the sediments are much more frequently interlayered to rhyolitic and andesitic lavas and intrusive bodies (Cassinis et al. in Cassinis et al. 1999, Cassinis et al. 2003) for a total of about 400 m thick. From a recent geochronological study (Gaggero et al. 2017) the Mt. Tradalei rhyo-dacite dome yielded a weighted mean age of 295.8 +/-4.3 Ma, pointing to an Asselian-early Sakmarian age for the main acidic volcanism in the Seui-Seulo basin (the upper part of the succession). The underlying anthraciferous levels in the Seui basin have been intensively exploited during the 19th century (Novarese 1917; Vardabasso 1966; Accardo et al. 1984). The succession is extensively developed in the subsurface, and the exposed fossiliferous sections are close to the main roads.

The Montarbu succession, about one hundred metres in thickness, could be subdivided in seven different lithozones (Ronchi et al. 2008; Fig.4.2) and in the latest

Geological Map of Sardinia the succession referred to the Rio Su Luda Fm (Carmignani et al. 2008). The succession is also informally assigned to the Seui formation (Pittau et al. 2008). The lithozones are the follow (see also Fig. 4.2):

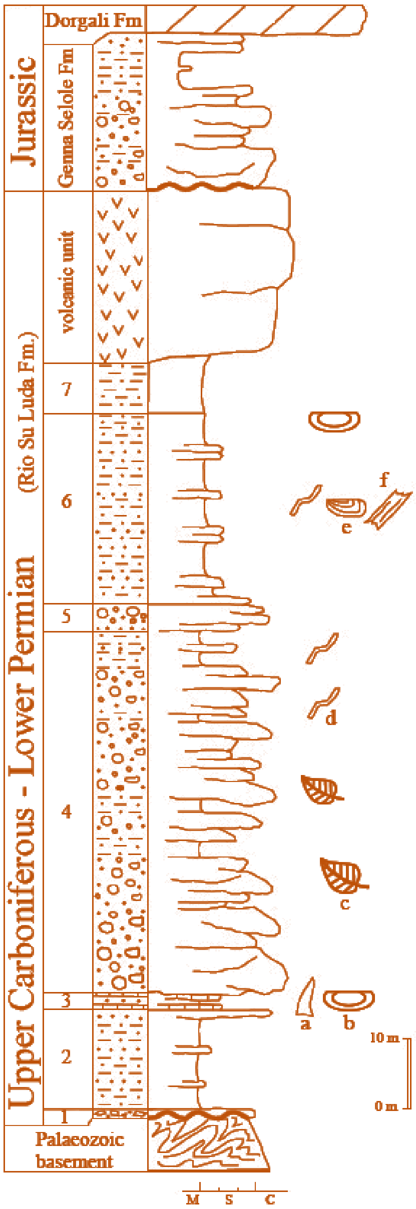

Fig. 4.2. Representative and simplified succession in the Montarbu Basin. Numbers of lithozones are explained in text. Legend: a) fish teeth, b) ostracods, c) macrofloras, d) bioturbations, e) bivalves, f) macroflora fragments (after Ronchi e al. 2008, adapted and modified).

1) thin and irregular basement breccia.

2) black to dark-grey shales and fine sandstones, topped by a heteromeric monogenic conglomerate (0.40 m) made up of well-rounded quartz pebbles (16 m).

3) poorly stratified fine-grained grey sandstones with two thin levels (20 cm and 16 cm respectively) of fossiliferous black limestones (2 m) with locally thin layers of black freshwater fossiliferous limestones yielding articulated ostracods and fish remains.

4) heteromeric monogenic conglomerates made up of well-rounded quartz pebbles, medium-to coarse-grained sandstones in fining and coarsening cycles upwards, and subordinate dark shales with abundant macrofloras (approx. 50 m in thickness). The macroflora collected and figured by Broutin et al. in Cassinis et al. 1999 (p. 90) and listed in Cassinis et al. 2003 should come from the basal part of this lithozone. All the

plant remains of the newly collected material also come from this lithozone (Fig. 4.3), probably in the upper part with respect to the previously cited material.

5) monogenic conglomerates made up of well-rounded quartz pebbles, with fine-grained grey to green sandstones (0.50 m) at the base (5 m thick).

6) fine-grained grey to green sandstones interbedded with grey shales (ca. 25 m thick) sometimes bearing ostracods in light-grey siltstones together with bivalves and macrofloral remains of freshwater, lacustrine to marsh environment.

7) partially covered reddish medium sandstones to siltstones (about 8 m thick). A final volcanic unit of about 30 m tops the Permian sequence.

Fig. 4.3. Sampling locality in the Montarbu area. Fossils come from the lithozone 4.

4.2.2 Material

The late Palaeozoic flora of Montarbu (Seui-Seulo Basin) is included in 290 rock slabs with vegetative shoots and leaves, reproductive organs and seeds (inventory numbers from 17500 to 17791). Macro remains are fragmented but specimen details are in general well preserved and the identification was not problematic; conifers and pteridosperms are found in different level of decomposition. In *Mixoneura* many pinnules show indicia about long stay in water in which they decayed (see Plate 2, 2). The leaves of *Cordaites* are partly destroyed and they seem to be separated along the veins (Plate IV, Fig. 3). This may indicate that the leaves floated in water for a relatively long time. These facts could suggest a transport of these plants at a different distance before deposition.

In this newly collected material, almost all the plant group are represented, and only lycophytes and bryophytes are missing (data from the literature show dispersed spores attributed to *Raistrickia* sp.; Pittau et al. 2008). The flora is preserved as impression. Due to this fact, cuticles and *in situ* spores have not been found. Based on the macroscopical analysis, two different typologies of sediments can be distinguished in the assemblage:

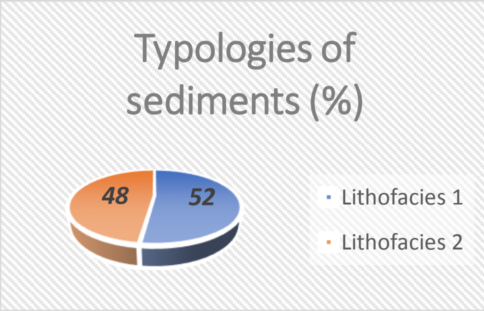

Fig. 4.4. Typologies of sediments.

a) lithofacies 1 corresponds to a mixed medium-fine and fine grey-greenish sandstone mirroring more energy (52% of all samples; Fig. 4.4);

b) lithofacies 2 corresponds to a blackish pelite (48%). These differences between the lithologies have been highlighted during the study of the collection. In the field, these two different lithofacies are interbedded and belong to the lithozone 4.

The study of the plant assemblage shows in total 24 taxa belonging to 18 genera (Tab. 4.2).

Equisetopsida is represented only by a small fragment of shoot belonging to *Annularia* cf. *sphenophylloides*.

Ferns are common with Psaroniaceae as the most diversified family (3 genera of 4 in total). They are represented by following species: *Acitheca polymorpha* which is the most common (4%; Fig. 4.5) of the total assemblage. Unfortunately, only fragments of ultimate pinnae were discovered. The other taxa that belong to the Psaroniaceae are *Pecopteris densifolia* and *Pecopteris* cf. *candolleana*. As *Acitheca polymorpha*, the species *Pecopteris densifolia* is relatively common in the assemblage (2.1%) and it is represented mostly by fragments of ultimate pinnae. The latter occurs occasionally (1.6%). Cf. *Remia pinnatifida* is a small sterile fragment of putative fern found in the locality.

Pteridosperms (seed-ferns) are represented by three families (34.8 % of taxa; Fig. 4.5). The family of Neurodontopteridaceae is represented by three taxa. Several pinnules of different shape are attributed to *Mixoneura subcrenulata*. This taxon is relatively abundant (8% of the total assemblage; see Fig. 4.5). Isolated pinnules or ultimate pinnae of *Neurocallipteris planchardii*, are presented in a percentage of 1.4 of the total assemblage, and many of them show feeding traces. Furthermore, the family of Neurodontopteridaceae includes also the species *Neurocallipteris* cf. *neuropteroides*. The latter is rare, and its percentage is only 0.9 of the total assemblage. It is characterized by pinnule of oblong-triangular shape.

Cyclopteridaceae are constituted by two taxa. The species *Callipteridium pteridium* is present only in one fragment. This taxon indicates a Late Pennsylvanian age.

The casts of *Trigonocarpus* sp. (only two seeds found; 0.5%; see Fig. 4.5) show one or two longitudinal ribs of the three that distinguish the morpho-genus. This morpho-genus also belongs to all pteridosperm taxa.

The Peltaspermaceae are represented by two *Autunia* species and a putative ovuliferous organ. *Autunia conferta* is the most abundant species of this family (5.4% of the total assemblage; see fig. 4.5). Bipinnate fronds bear well-preserved pinnules with clearly recognizable venation pattern. *Autunia naumannii*, on the contrary, is rare and only a few fragments have been identified in the assemblage (0.7%; see fig. 4.5). The ovuliferous organ probably of *Autunia conferta* consists of one specimen with a group of bracts of megasporophylls on the main axes and another ovoid-shaped ovule. Two taxa belong to Cordaitanthaceae. Cordaitalean leaves belonging to *Cordaites* sp. are frequent and one of the most present taxon in the assemblage (16.9 %; see Fig. 4.5). Unfortunately, due to fragmentary character of leaf remains and missing of epidermal characters the precise classification is impossible. *Cardiocarpus* sp. seeds are relatively frequent in the assemblage (4.7 %; see Fig. 4.5).

The conifers are among the most abundant groups in the Montarbu flora. They are represented by shoots of *Ernestiodendron filiciforme* with axes of the last order and falcate leaves. *Culmitzchia speciosa* differs from *E. filiciforme* because the pointed or slightly rounded apex turns close to the end of the leaf. *Walchianthus* sp. is a polliniferous cone that has the microsporophylls spirally arranged on the axis. In the assemblage is present also an ovuliferous cone of walchiacean affinity. The isolated bract of *Gomphostrobus* sp. cf. *Gomphostrobus bifidus* is considered here belonging to the conifers even if it can also be attributed to other plant groups. The platyspermic seed of conifer is putatively attributed to the genus *Samaropsis* sp. In the assemblage, another unidentified oval isolated seed is considered belonging to this plant group as well.

Also, of ambiguous botanical affinity is *Taeniopteris* cf. *multinervia* (1.9%), that

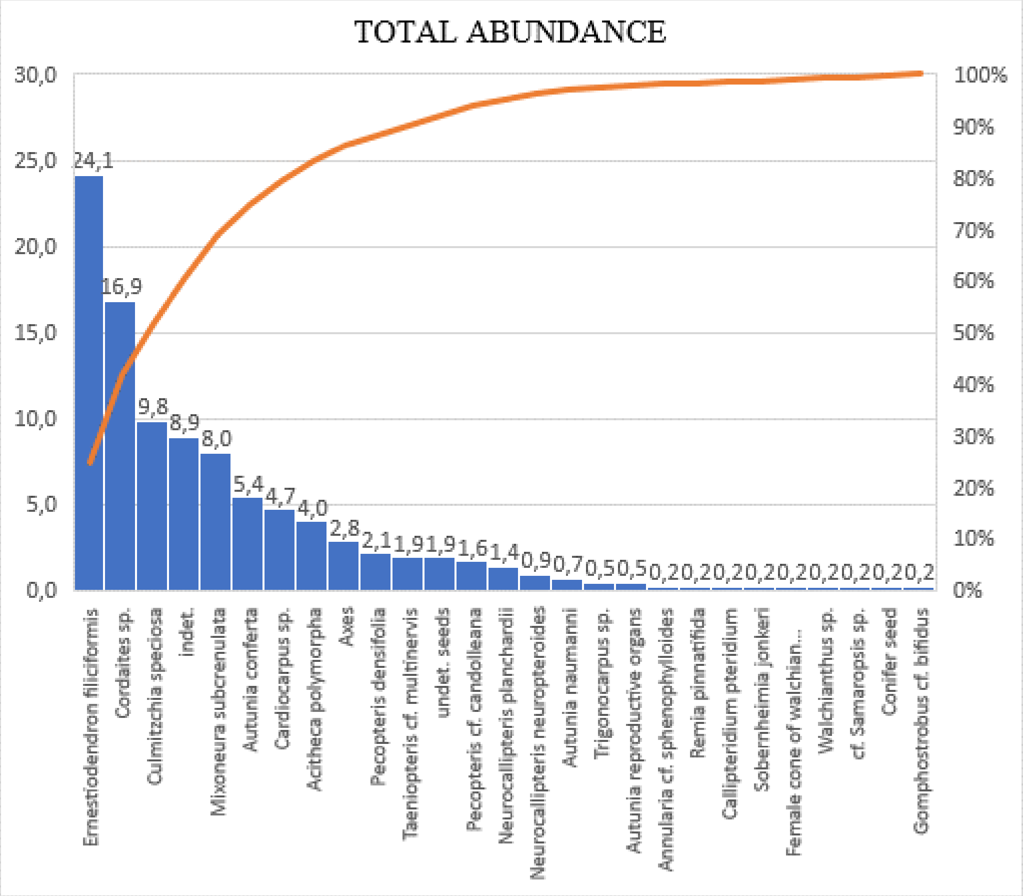

Fig. 4.5. Total abundance of the studied Montarbu flora in Pareto Chart representation (see chapter 3 for details).

probably belongs to the cycadophytes, or pteridosperms or even ferns (Pšenička et al. 2017): leaves are elongated, entire-margined and having perpendicular secondary veins.

Sobernheimia jonkeri is the other unknown affinity remain taxon (0.2%), not included in specific families because the nature of these plants is still unclear (Kerp 1983).

In summing up, in terms of numbers of fossil taxa, the composition of the plant fossils is different (see Fig. 4.6). Fossils are attributed to 23 taxa belonging to equisetopsids (1 taxon, 4.3%), ferns (4 taxa, 17.4%), pteridosperms (8 taxa, 34.8%), cordaitales (2 taxa, 8.7%), conifers (7 taxa, 30.4%) and other remains with an unknown affinity (2 taxa, 8.7%). As said before, plant remains belonging to bryophytes and lycophytes have not been found in this collected material.

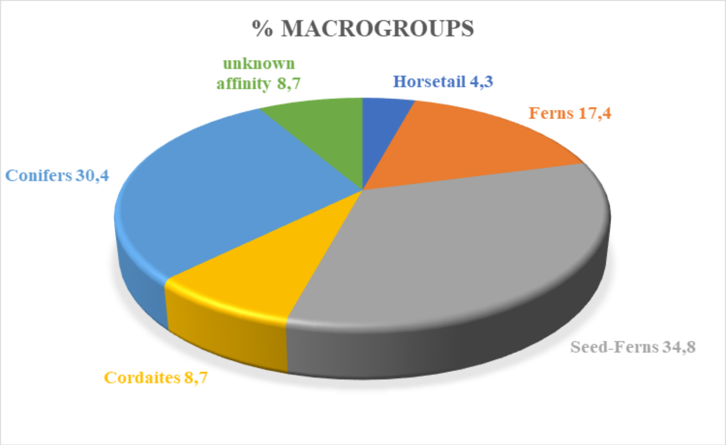

Fig. 4.6. Ecological macrogroups in the Montarbu flora.

The macrofossils are preserved on two similar lithofacies. Samples come from the same stratigraphic horizons and were deposited under the same/similar environmental conditions. The lithofacies are interbedded. A collecting bias can obviously not be excluded, but for avoiding it even small and poorly preserved fragments and well-preserved remains were kept for this study. The more coarse-grained lithofacies 1 is dominated by the conifer *Ernestiodendron filiciforme* (24%), followed by *Cordaites* sp. (14.75%), the seed fern *Mixoneura subcrenulata* (9.22%), *Culmitzchia speciosa* (8.76%) and *Autunia conferta* (6%), representing the 75% of the entire abundance in this first lithofacies (Fig. 4.7). This datum could represent the presence of a luxuriant gymnosperms forest close to the depositional site. Tree ferns as *Acitheca polymorpha* (4.15%), *Pecopteris densifolia* (3.69%) and *P.* cf. *candolleana* (3.23%) are also present in this lithofacies. Rare *Cardiocarpus* sp., *Neurocallipteris* ssp. (<2%) and *Annularia sphenophylloides*, *Remia pinnatifida*, *Taeniopteris* cf. *multinervis*, cf. *Samaropsis* sp., *Gomphostrobus* cf. *bifidus* (<1%) have been reported as well. The presence of undetermined fragments is noticeable in this type of sediment (10.60%), related probably to the poor preservation potential of this coarse sediment and the difficult to determine the fossils inside it. Here, *Callipteridium pteridium*, *Trigonocarpus* sp., *Autunia naumanni*, *Sobernheimia jonkeri*, *Walchianthus* sp. have not been found maybe because all of these taxa prefer growing under calmer environmental conditions or its generic structure does not permit to be preserved in coarse sediments. The conifer *Ernestiodendron filiciforme* (24.4%) and *Cordaites* sp. (19.14%) are also the most abundant taxa in lithofacies 2 (Fig. 4.8), suggesting that they were prominent elements of the Late Palaeozoic floristic assessment of Montarbu. This lithofacies also includes the conifer *Culmitzchia speciosa* (11%) and together these three species represent almost the 70% of the entire

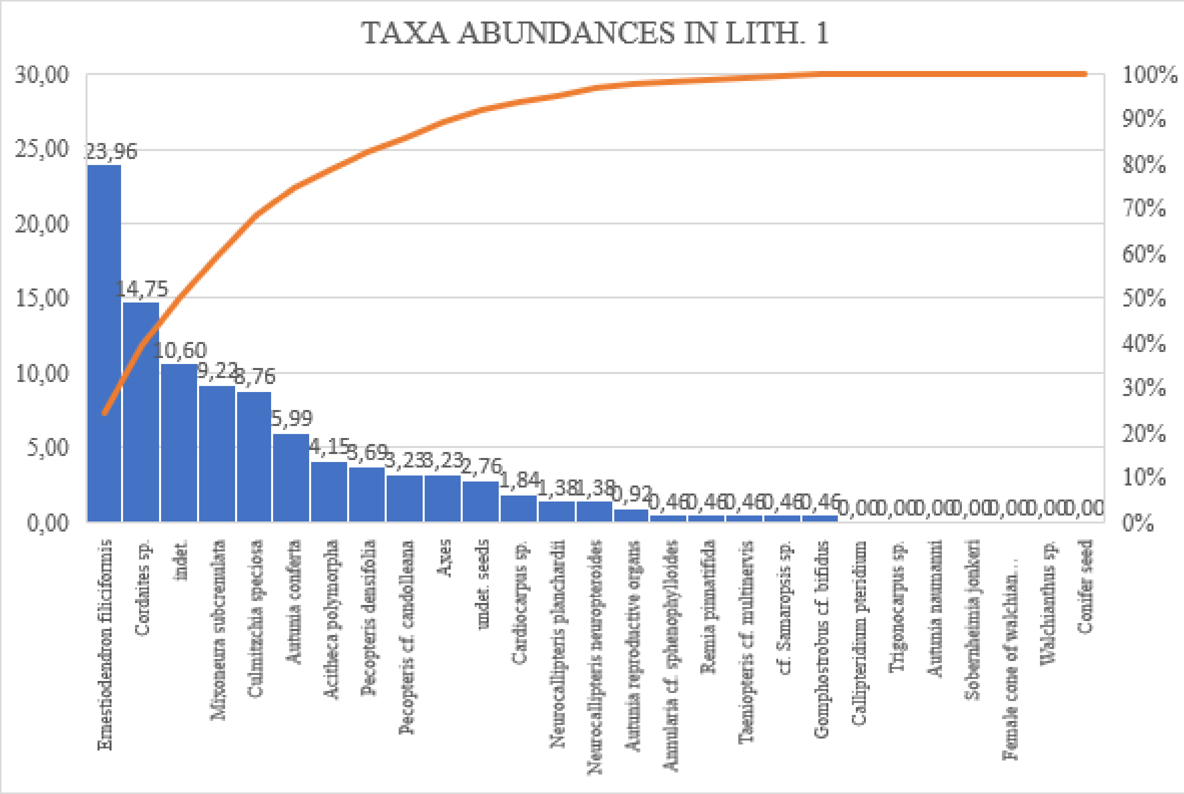

Fig. 4.7. Relative abundances of taxa in Lithofacies 1.

abundance in this lithofacies. Seeds of *Cardiocarpus* sp. (7.66%), the seed-fern *Mixoneura subcrenulata* (6.70%), *Autunia conferta* (4.78%), the fern *Acitheca polymorpha* (3.83%), and *Taeniopteris* cf. *multinervis* (3.35%) are also encountered. The rare pteridosperm *Neurocallipteris planchardii*, *Autunia naumanni* (<2%), and *Trigonocarpus* sp. (<1%) are present as well. The assemblage comprises very rare fragments of the fern *Pecopteris densifolia*, the seed-fern *Neurocallipteris neuropteroides* and *Callipteridium pteridium*, the conifer cone of *Walchianthus* sp., and *Sobernheimia jonkeri* (<0.5%). *Callipteridium* and *Sobernheimia* are exclusively for this silty lithology. Here too undetermined fragments are common (7.18%).

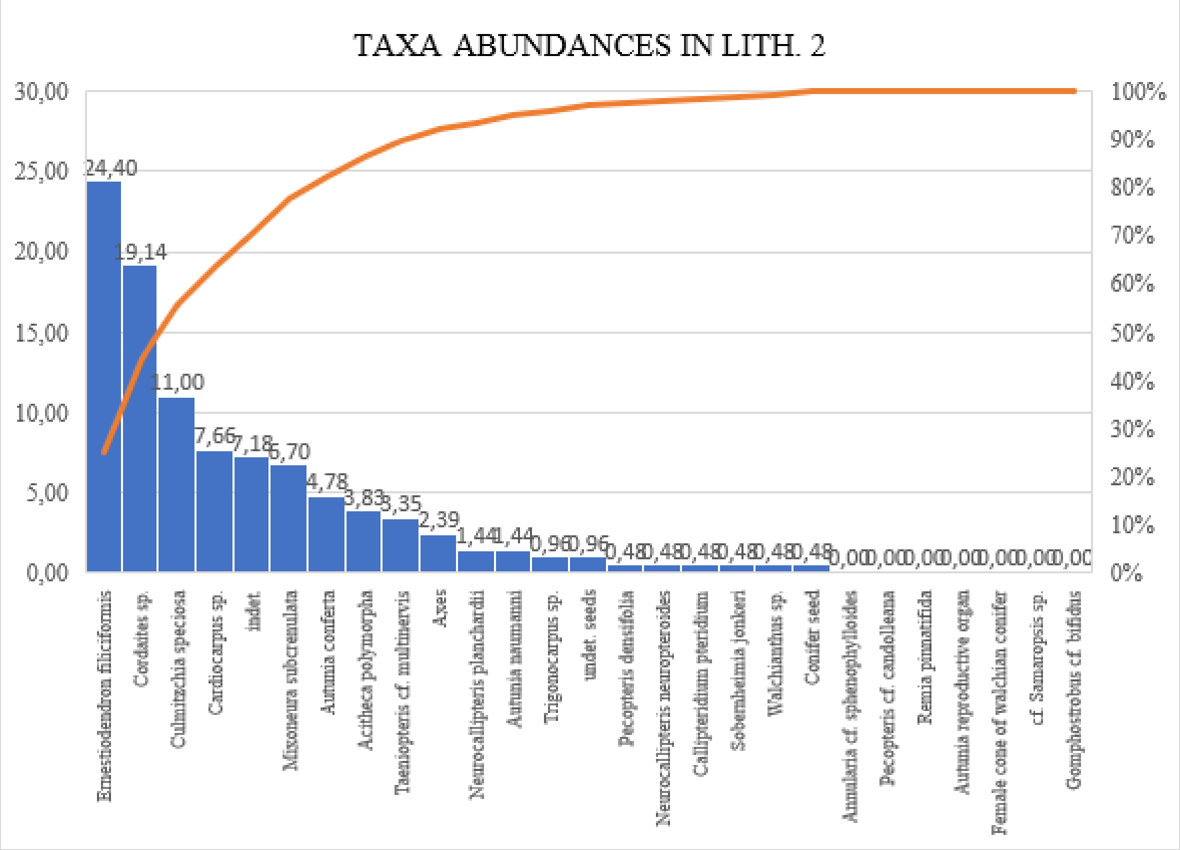

Fig. 4.8. Relative abundances of taxa in Lithofacies 2.

Fig. 4.9. Some collected specimens from the Montarbu outcrop.

4.3. Perdasdefogu (central Sardinia)

4.3.1. Geo-Stratigraphic framework

The Lower Permian Perdasdefogu Basin extends for about 25 km^2 in central to southeastern Sardinia (Ogliastra region; Pertusati et al. 2002) and is located north of the homonymous village. It belongs to the Rio Su Luda Formation (Ronchi & Falorni 2004). This basin originated in response to post-orogenic transtensile tectonic conditions, and it is similar also to those of many other basins of continental Paleo-Europe (e.g. France, Spain) active from the Late Carboniferous to the Early Permian (for details see Arthaud & Matte 1977; Ziegler & Stampfli 2001; Virgili et al. 2006). The Permian sedimentary and volcanic units are exposed with variable lateral extension and thickness related to the palaeomorphology of the basin and tectonic movements and the best exposed and studied sections are close to the Rio Su Luda river (Galtier et al. 2011).

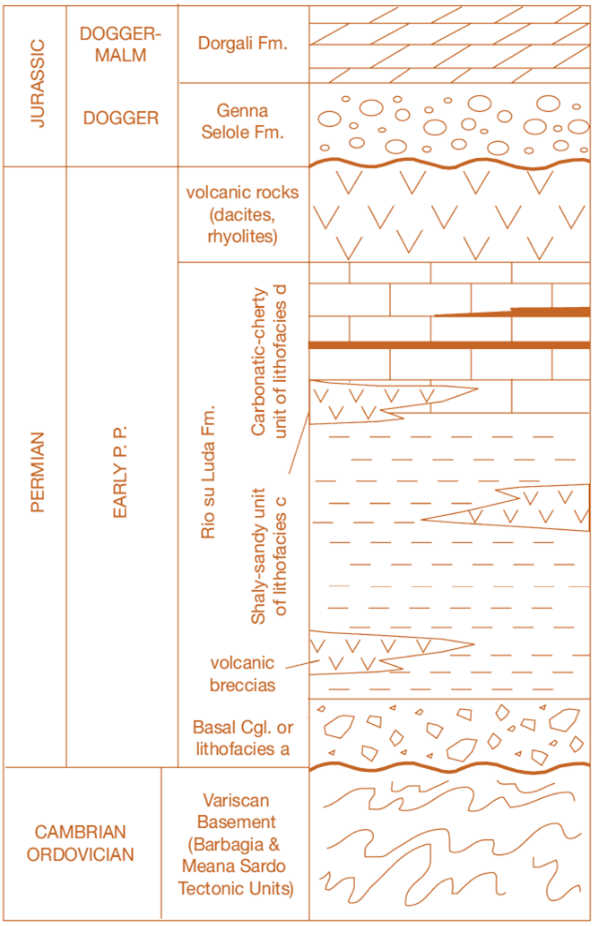

Fig. 4.10. Simplifed geological section through the Perdasdefogu basin (after Galtier et al. 2011, modified).

According to Galtier et al. (2011), the Perdasdefogu basin is about 250 m thick. It is characterised by a sequence in which the sedimentary units are frequently intercalated with and overlain by different magmatic units. It could also be subdivided into four lithofacies as follows (Fig. 4.10):

a) polygenic basal conglomerate (formally lithofacies a, maximum 30 m thick) composed of rock fragments derived from the Variscan metamorphic basement.

b) Fluvial to- lacustrine lithofacies (locally exceeding a thickness of 120 m), already known as *unità siltoso-arenacea* (black siltstones; Ronchi 1997; Ronchi & Sarria in Cassinis et al. 1999) consisting of dark-grey laminated sandstones, siltstones and shales with volcanites associated.

c) *unità calcareo-selciosa* (black limestone; Ronchi 1997) composed of lacustrine dark-grey to blackish laminated limestone and dolostone (with fine sandstones to laminated mudstones). Inside, black bedded chert intercalations of volcanic origin occur at different levels. Locally, at the top, some tens of meters of coarse to- fine pyroclastic fall deposits more or less silicified, can also occur.

4.3.2. Material

In the attempt to find fossil plant remains in silicified sediments a sampling has been done from two different sections belonging to the Perdasdefogu basin: the *Ortumannu* and *Bruncu su Fenugu* sections. As already stated by Galtier et al. (2011), in the Perdasdefogu Basin plants occur in angular cherts in which are preserved as siliceous permineralization. Ten blocks of silicified limestone have been processed according to the methodology. After many tries to extract peels in the “Laboratoire de Paléobotanique” of the CIRAD-AMAP of Montpellier (France) under the guidance of Prof. J. Galtier and Meyer-Berthaud B., the cherts were barren of vegetal macro-remains.

5. Systematic Palaeobotany

In the following analysis, the plant fossils have been named using fossil-taxa as defined by McNeill et al. 2012, with each taxon referring to a particular plant part, life history stage and preservation state. In this chapter, only the species from the late Ghzelian Montarbu locality will be discussed. The description of the taxa encountered, the remarks on the similarities, the history of each taxon and the distribution is given as well. The systematic palaeobotany of the Moscovian species of San Giorgio is included in Appendix 1.

Class Equisetopsida Agardh 1825

Order Equisetales Dumortier 1829

Family Calamostachyaceae Meyen 1978

Genus ***Annularia*** Sternberg 1821

Annularia cf. ***sphenophylloides*** (Zenker 1833) Gutbier 1837

Plate I, Figure 1

1833 *Galium sphenopylloides* - Zenker, p. 398, pl. 5, fig. 6-9.

1837 *Annularia sphenophylloides* (Zenker) - Gutbier, p. 436

1958 *Annularia sphenophylloides* (Zenker) Gutbier - Abbott, p. 319, pl. 35, fig. 6, pl. 41, fig. 55

1976 *Annularia sphenophylloides* (Zenker) Gutbier - Spano, p. 394, pl. 1, fig. 1.

2004 *Annularia sphenophylloides* (Zenker) Gutbier - Barthel, p. 24, text fig. 23.

2008 *Annularia sphenophylloides* (Zenker) Gutbier - van Waveren et al., p. 342, text-fig. 3.

2010 *Annularia sphenophylloides* (Zenker) Gutbier - Wagner & Álvarez-Vázquez, p. 269, pl. 14, fig. 2.

2016 *Annularia sphenophylloides* (Zenker) Gutbier - Barthel, p. 148, text fig. 79.

2017 *Annularia sphenophylloides* (Zenker) Gutbier - Cleal et al., p. 1157, text fig. 3f.

Description

Only one small fragment has been discovered in the studied locality. This is a half-preserved whorl of 6 leaves. Each leaf is 0.5 mm wide and 5 mm long, and its shape is linear to spathulate.

Remarks

This species is quite similar in the general aspect and shape to *Annularia stellata* (Schlotheim 1804) Wood 1860 but differs from it by the form of the leaf. The latter is widest at or near the middle, while *A. sphenophylloides* is widest at the tip. There are differences also in the lateral margins of the leaf; indeed, those of *A. sphenophylloides* are straight while those of *A. stellata* is convex. Also, the number of leaves per verticil in *A. stellata* is usually greater.

Distribution

This species is a typical element of the uppermost Moscovian to lowermost Permian floras of Europe and North America (e.g. Abbott 1958; Crookall 1969; Laveine 1989). According to Josten (2005) in North West Germany, it has a chronostratigraphical range that spans from "Westphalian A" to "Autunian". It occurs in late Palaeozoic of Spain and Portugal (Wagner & Álvarez-Vázquez 2010), in the Ghzelian (Late Carboniferous) of France (Broutin et al. 1999; Martín-Closas & Galtier 2005; Charbonnier et al. 2008; Pellenard et al. 2017; Galtier pers. comm.), in the lower Permian of Germany (Barthel 2004, 2016). In the Stephanian of the Netherlands (van Waveren et al. 2008), in the C/P of the Czech basins (Opluštil et al. 2013). Spano (1976) listed this species for the Ingurtipani locality of the Seui-Seulo basin.

Class Marattiopsida Doweld 2001

Order Marattiales Link 1833

Family Psaroniaceae Unger in Endlicher 1842

Genus ***Acitheca*** Schimper 1879

Acitheca polymorpha (Brongniart 1834) Schimper 1879

Plate I, Figure 2

1828 *Pecopteris polymorpha* Brongniart, p. 56 (*nomen nudum*).

1834 *Pecopteris polymorpha* Brongniart - Brongniart, p. 331, pl. 113, figs 2–5.

1879 *Acitheca polymorpha* (Brongniart) - Schimper, p. 91, fig. 66.

2006 *Acitheca polymorpha* (Brongniart) Schimper - Zodrow et al., p. 271, pls 1–9, 11–14.

Description

This species is relatively common in the Montarbu flora. Ultimate rachides appear straights. They are 4 mm wide. Ultimate pinnae are asymmetrical about the rachis with basiscopic pinnules being more elongate and more oblique than the rachis with acroscopic pinnules. Pinnules are inserted on the upper side of ultimate rachis, and they are up to 7–8 mm long and 3-4 mm wide, linguaeform with rounded, obtuse sub-triangular apex. Pinnules are closely spaced. A clear venation pattern is visible only in few specimens. The midvein is straight and lies in a shallow furrow. Lateral veins show polymorphopterid-veining pattern (*sensu* Wagner 1958), arch relatively sharply to meet the pinnule margin at 80–90° and fork twice, where the first dichotomy is close to the midvein.

Remarks

Only fragments of ultimate pinnae were discovered which indicates long transport from the original growing site. Unfortunately, no reproductive organs were found in the locality, and this genus must be regarded as morpho-genus. The taxonomy of this species, including its generic position, has most recently been analysed in detail by Zodrow et al. (2006). *A. polymorpha* is similar to *Pecopteris densifolia* (Goeppert 1864) Weiss 1869 and could be distinguished based on venation because *P. densifolia* has lateral veins firstly dichotomised further of midvein; midvein and shape of pinnule apex are oblong in ascoscopic as well as in the basiscopic side of the ultimate pinna. Based on these facts we distinguished both species on the locality.

Distribution

Acitheca polymorpha is interpreted as an important element of tropical vegetation through the upper Moscovian/Kasimovian–lower Gzhelian Stages, becoming rarer and eventually extinct in the Asselian (Kerp & Fichter 1985; Zodrow et al. 2006). In Sardinia, this species has been listed as *P. polymorpha* in the early Permian Perdasdefogu basin (Cassinis et al. 1999) and also in the close Ingurtipani locality (Seulo, Spano 1976).

Genus ***Pecopteris*** Brongniart 1822

Pecopteris densifolia (Goeppert 1864) Weiss 1869

Plate I, Figures 3–4

1864 *Cyatheites densifolius* - Goeppert, p. 120, pl. 17, figs 1–2.

1869 *Pecopteris densifolia* (Goeppert) - Schimper, p. 503.

1869 *Pecopteris densifolia* (Goeppert) - Weiss, p. 65.

1888 *Pecopteris densifolia* (Goeppert) - Zeiller, 152, pl. 16, figs. 1–4.

2016 *Scolecopteris densifolia* (Goeppert) Barthel - Barthel, p. 182, fig. 145.

Description

This species is mostly represented by fragments of ultimate pinnae. One specimen shows part of penultimate pinnae with three incomplete ultimate pinnae (Plate I, fig. 3). The ultimate rachis is straight, punctate and 0.8 mm wide. Ultimate pinnae are linear, and it ends with a small rounded or subtriangular pinnule (Plate I, 4). Pinnules are alternate, attached to ultimate rachis with the entire basis with an angle of 70°. The basis is very slightly constricted (Plate I, fig. 4). Pinnules are tongue-shaped with the obtuse apex, 3–3.5 mm long and 1.4–2 mm wide. Pinnules on acroscopic and basiscopic sides have more or less the same shape. Adjacent pinnules are slightly overlapped. Midvein is 1/2–2/3 of pinnule size. Lateral veins are often once divided, and the division is in the further part of the midvein. Sometimes lateral veins fork twice.

Remarks

As *Acitheca polymorpha* the species *Pecopteris densifolia* is relatively common in the studied locality. According to Barthel (2016), taxonomically, *Pecopteris densifolia* is rather controversial. The same author alerted that the Goeppert type shows very deep forked lateral veins, which can be scarcely distinguished from *Pecopteris oreopteridia* (Schlotheim 1820) Sternberg 1826. To understand better the species *Acitheca polymorpha*, *Pecopteris densifolia* and *Pecopteris oreopteridia* that are very similar each other, a revision of all species based on the types will be necessary. In the Montarbu flora, the species *Acitheca polymorpha* and *Pecopteris densifolia* have been distinguished considering characters of pinnules and venation pattern. A specimen of *P. densifolia* has less dense venation and lateral veins are often once divided further of midvein. The pinnules of *P. densifolia* have rather an obtuse apex than subtriangular which is typical for *A. polymorpha*. Adjacent pinnules of *P. densifolia* are partly overlapped.

<u>*Distribution*</u>

P. cf. *densifolia* was also identified by Galtier et al. (2011, p. 61, fig. 11 k) in charts from the Perdasdefogu locality (central Sardinia). Spano (1976) listed this species in the Autunian schists of Seulo (central Sardinia). It occurs in the Carboniferous and Permian strata of South-Central Pyrenees (Talens & Wagner 1995). This species occurs also in Germany (Barthel 2016).

Pecopteris cf. ***candolleana*** Brongniart 1834

Plate I, Figures 5–6

1828 *Pecopteris candolliana* - Brongniart, p. 56 (*nomen nudum*)

1834 *Pecopteris candolleana* - Brongniart, p. 305, pl. C, fig. 1.

1857 *Cyatheites candollianus* - Meneghini, p 187, pl. D, fig. 5/1

Description

This species occurs on the locality occasionally. Only small parts of ultimate pinnae with several pinnules are known from here. Both sterile and fertile pinnules were discovered, but fertile part is represented by one fertile pinnule only. Ultimate rachis of the sterile pinna is 0.5 mm wide. Pinnules are alternate, slightly oblique to the rachis, sides parallel, contracted at the base on both sides. Pinnules are free, of unequal length, 5–6 mm long and 2.5–3 mm wide. Pinnule apex is obtuse. Midvein is thick, straight, curved on base, extending almost pinnule apex. Lateral veins are not visible.

The fertile pinnule has the same dimensions. Synangia are placed between the midvein and the margin of the pinnule, in two rows (Plate I, Fig. 6). Synangia are 0.6 mm in diameter and also has four sporangia 0.5 mm long and 0.3 mm wide.

Remarks

Like in many others pecopterids, the clear taxonomical concept of *Pecopteris candolleana* still does not exist. This species was established by Brongniart in the “Prodrome” (1828, p. 56) under the name *P. candolliana* and subsequently re-described and figured in the “Histoire des Végétaux Fossiles” (1928–1934 p. 305; pl. C, 1). The original diagnosis given by this author fits with the Montarbu specimens because of the general shape of the pinnules and how they are distanced each other. Later, Corsin (1951) published the latest official diagnose of *P. candollei* (≡ *P. candolleana*) including the Brongniart and the Kidston’s (1924, pl. 116, figs 1, 2) specimens in the synonymy list. Corsin (1951) indicated pinnule length 8–10 mm which is a little bit larger than specimens in hand. Differences in dimensions could be anyway explained because of the position of the pinnules in the frond or, from an ecological point of view, different habitat.

On the other hand, Corsin stated that the specimen described and figured by Kidston is attributable to the species *Pecopteris saraefolia* Bertrand 1928 because of the margin of the pinnules that turn to itself. After the check of the figured specimens in Kidston (1924 pl. CXVI, f. 1–2) it has been stated that the interpretation of Corsin could be wrong because the pinnules have a straight and long shape as in the original Brongniart's (1834) description. The similarity of *P. candolleana* can be found in the size of the pinnules of *P. lepidorachis* Brongniart 1834 which differs mainly for the close arrangement of these and the straight base of midvein coming from the ultimate rachis. *Cyatheites candollianus* (≡ *P. candolleana*) Goeppert is mentioned and figured in the first paleontological treatise of Sardinian palaeontology by Meneghini (in Lamarmora 1857). The exact collecting locality of each sample is not present, but we can assume, according to the text (Lamarmora 1857, vol. III, I, p.95), that could come from a close basin respect of Montarbu. Unluckily, the original specimens are now unavailable for detailed studies. Sometimes, when there are old published works, to find originally described specimens is always problematic. They also could not correspond to the original one (for example see Pšenička & Bek 2001).

Distribution

Pecopteris candoleana is typical for Kasimovian and Gzhelian strata (France, Corsin 1951), but it is also known for the Permian (Germany, Kerp & Fichter 1985). *Pecopteris candollei* has also been recorded by Spano (1976) for the close Ingurtipani outcrop (Seulo).

Class Unknown

Order Unknown

Family Unknown

Genus ***Remia*** Knight 1985

cf. ***Remia pinnatifida*** (Gutbier 1835) Knight 1985 emend. Cleal 2015

Plate I, Figure 7

1835 *Neuropteris pennatifida* - Gutbier, p. 61, pl. 8, figs. 1–3.

1985 *Remia pinnatifida* (Gutbier) - Knight, p. 7, pl. 1, figs. 2, 3a, 3b.

1991 *Remia pinnatifida* (Gutbier) Knight - Kerp et al., p. 200, pl. I-II.

2015 *Remia pinnatifida* (Gutbier) Knight - Cleal, p. 12, text-fig. 2.

Refer to Kerp et al. 1991 for further synonymy.

Description

Only one small sterile fragment of this plant was discovered in the locality. The specimen shows isolated profoundly lobed pinnule with rounded apex, 11 mm long and 5 mm wide. The midvein is well developed. Lateral veins are poorly visible but they seem to fork three times.

Remarks

Due to the small dimensions of this fragment, the identification is uncertain. *Remia pinnatifida* was established based on fertile pinnules (Knight 1985) but Kerp et al. (1991) emended the original diagnosis including details of the sterile foliage. Cleal (2015) also emended the species describing the distinctive veining pattern. The species is often placed to the marattialean ferns (Remy 1954; Taylor et al. 2009) but many authors (e.g. Knight 1985; Meyer-Berthaud 1989; Kerp et al. 1991) put doubts on this affinity highlighting a possible pteridosperm or a progymnospermous affinity.

Distribution

In Sardinia, this species has been described for the "Autunian" of Lu Caparoni (northern Sardinia, Broutin et al. in Cassinis et al. 1999). This species has also been recorded in Spain (Knight 1985; Wagner & Mayoral 2007). In general, it is rather common in Europe and the range has been extended to the Carboniferous (Kerp et al. 1991).

Class Pteridospermopsida Oliver et Scott 1904

Order Medullosales Corsin 1960

Family Neurodontopteridaceae (Neurodontospermae) Laveine 1967 ex Cleal et Shute 2003

Genus ***Mixoneura*** Weiss 1869

Mixoneura subcrenulata (Rost 1839) Zeiller 1888

Plate II, Figures 1–2

1839 *Neuropteris subcrenulata* - Rost, p. 22.

2009 *Odontopteris subcrenulata* Rost - Barthel, p. 56, fig. 137.

Refer to Krings et al. 2000 for further synonymy.

Description

A larger number of specimens having different shapes of the pinnules have been attributed to this species. Some specimens from this locality consist of pinnae bearing individualised pinnules. In this case, the pinnules are elongated (26 mm long and 12 mm wide), linguaeform, irregularly triangular, with blunt apex and significant midrib. Pinnules from the distal part of the pinnae show broad basal attachment, and multiple veins together with distinctive midrib that goes into the lamina. The basiscopic side of pinnules is elongated along the axis and in some pinnules, it turns into an elongated lobe). The acroscopic side of pinnules is significantly constricted. This phenomenon is visible also in other pinnules. These consist of pinnae segments which comprise small pinnules at the base (4–7 mm long), fusing into elongate linguaeform laminar elements, which are in the final part of the ultimate pinnae. These small pinnules often occur isolated. Terminal pinnules of probably penultimate pinnae are large, irregularly triangular in shape with blunt apex and lobes on their base.

Remarks

Krings et al. (2000) and DiMichele et al. (2013a) mentioned that mixoneuroids have high pinnules variability depending on the position in the frond or the development of the plant. Due to this fact, isolated pinnules in the fossil record could be placed into several species or even different genera (DiMichele et al. 2013a). Therefore, it is not surprising that some isolated leaves from the Montarbu locality are very similar to *M. lingulata* (Goeppert) Wagner et Castro 1998 or even *Neuropteris ovata* Hoffmann 1826. Nevertheless, *M. lingulata* is different to *N. ovata*. The latter has a cordate base, while *M. subcrenulata* has an elongated basiscopic side of pinnules along the axis and the acroscopic one turns into an elongated lobe. Many pinnules show indicia about long stay in water where they decayed.

Distribution

As a typical component of the Autunian vegetation (DiMichele et al. 2013a), *Mixoneura subcrenulata* occurs in several localities all over the world. For example, it has been found in the U.S.A. (DiMichele et al. 2013a), Portugal (Correia et al. 2010), in Germany and France (Doubinger & Remy 1958).

Genus ***Neurocallipteris*** Sterzel 1895

Neurocallipteris planchardii (Zeiller 1888) Cleal, Shute et Zodrow 1990

Plate II, Figure 3

1888 *Neuropteris planchardi* - Zeiller, p. 246, pl. 28, figs 8– 9.

1990 *Neurocallipteris planchardii* (Zeiller) - Cleal et al., p. 489.

Description

This species is common in the studied locality. Isolated pinnules and pinnules attached to ultimate rachis were found. The specimen figured in Plate III, 3 shows the distal part of incomplete pinnae of 65 mm of length and the rachis of 2 mm wide. Alternate pinnules are attached at a straight angle to the main rachis with the middle part of the basis (Plate III, Fig. 3). Pinnules are always distanced and never touch each other. Pinnules have a strictly contracted basis, and the general shape is oblong with an obtuse apex. At the bottom of the pinnae, pinnules are 20x7 mm while in the upper part they reduce to 7x5 mm. Midvein is clear and visible for almost 2/3 of the whole pinnule. Secondary veins are dense, they arise from the rachis forking three/four times, and there are at least 40 veins per 10 mm of pinnule margins. Isolated pinnules (Plate III, Fig. 2) are identical in shape with the pinnules figured in Plate III, Fig. 3. In general, isolated pinnules are found larger, and this is also the trend of this paleontological record. Many of them show feeding traces by insects (Plate III, Fig. 2 arrows).

Remarks

In 1967 Laveine described the family of Neurodontopteridaceae. Cleal & Shute (2003) split this into two families. The Neurodontopteridaceae, *sensu stricto*, includes the genera *Neuropteris*, *Reticulopteris*, *Odontopteris*, *Macroneuropteris*, and possibly *Neurocallipteris*, *Neurodontopteris*, and *Barthelopteris*, and the Cyclopteridaceae includes *Laveineopteris*, *Margaritopteris*, and *Callipteridium*. According to the general description of Zeiller (1888), this species resembles *Neuricallipteris gallica* (Zeiller) Cleal et al. 1990 but latter has longer pinnules, and the general shape is much more oblong. According to Castro Martínez (2005) indeed, *N. gallica* has in general similar shape and size differences could be considered as interspecific features. Another remarkable feature is the absence of hair in *N. planchardii*, but this could be observed only in specimens in a good state of preservation. In 1990 Cleal et al. moved this species from *Neuropteris* into the form-genus *Neurocallipteris*. *Neurocallipteris* have been shown to have more complex stomatal apparatuses than typical neuropterids (Cleal & Shute 1995).

Distribution

This species has a cosmopolitan distribution in the northern hemisphere. It has also been found in the Pennsylvanian of North America (DiMichele et al. 2010), in the C/P boundary of Czech Republic (Opluštil et al. 2013, 2016) and the Lower Permian of

Germany (Barthel 2016). It has also been reported from the upper Cantabrian (lower Stephanian) of Spain in the context of an allochthonous assemblage in marine strata (Wagner & Winkler Prins 1970). It also occurs in the "late Stephanian" of Central France (Pellenard et al. 2017).

Neurocallipteris cf. ***neuropteroides*** (Goeppert 1836) Cleal, Shute et Zodrow 1990

Plate II, Figure 4

1836 *Gleichenites neuropteroides* - Goeppert, p. 186, pl. 4–5.

1990 *Neurocallipteris neuropteroides* (Goeppert) - Cleal et al., p. 489.

Description

Isolated and incomplete pinnae have been found in the Montarbu assemblage. Isolated pinnules have oblong-triangular shape; they are 14 mm long and 6 mm wide. A clear midvein is not present, and sometimes it is slightly visible in the middle of the pinnule. Secondary veins are dense, almost 20 veins per 10 mm of pinnule margin. They usually fork at 2/3 of the pinnula, close to the entire margin. Unfortunately, the basal part of these isolated pinnules is not well preserved. The specimen figured in Plate III, 4 shows pinnules attached to the main grooved rachis (1.5 mm) with the entire basis. Their margins are close each other, but they never touch. Pinnules of this pinnae fragment are slightly smaller due probably to the different position in the plant.

Remarks

Neurocallipteris neuropteroides (Goeppert) Cleal et al. 1990 (≡ *Gleichenites neuropteroides* Goeppert 1836), is rather a species from the Gzhelian Stage. The isolated, large subtriangular pinnule is also compatible *Neuropteris ovata* Hoffmann 1826. These two species are difficult to separate without cuticles (Cleal & Shute 1995). Despite that, it is very difficult to identify correctly if some information misses.

Distribution

This species has a cosmopolitan distribution in the northern hemisphere. It has been found in the Czech Republic (Šimůnek & Martínek 2009; Opluštil et al. 2017a), in the Lower Permian (Rotliegend) flora of the Döhlen Formation (Germany, Barthel 2016), in the early Permian of Texas (Glasspool et al. 2013), in the Carboniferous and Permian strata of South-Central Pyrenees (Talens & Wagner 1995) and even in Indonesia (Sumatra, Van Waveren I.M. et al. 2007).

Family Cyclopteridaceae Corsin 1960

Genus ***Callipteridium*** (Weiss) Zeiller in Renault et Zeiller 1888

Callipteridium pteridium (Schlotheim 1804) Zeiller in Renault et Zeiller 1888

Plate II, Figure 5

The complete list of synonymies is included in Cleal et al. 2015.

Description

Only one specimen has been found and this is a distal part of the pinna with pinnules inserted at right angles to the main rachis. It also evidenced a well-marked bilateral symmetry. Pinnules are parallel-sided for most of the length, ca. 12 mm long and 5 mm wide and terminated by a subtriangular obtuse apex. The midvein is typically straight, it extends for almost two-thirds of the pinnule length, and it is perpendicular to the rachis. Lateral veins are poorly preserved but appear to arise at a nearly right angle to the midvein.

Remarks

The specimen is similar to *Callipteridium gigas* (Gutbier) Weiss 1870. Cleal et al. (2015) stated that taxonomy and nomenclature of the relationship of both species are in confusion.

Distribution

Callipteridium pteridium could indicate Gzhelian age (uppermost Pennsylvanian; Doubinger & Germer 1972; Cleal et al. 2015). This species has been found in others late Pennsylvanian localities of Europe, such as Croatia (Cleal et al. 2015), Austria (Boersma & Fritz 1986). This species has been reported in Sardinia by Spano (1976) for the “Autunian” of Seui-Seulo. According to new data, it is also present in French Massif Central localities of early Asselian age (Pellenard et al. 2017).

Order Unknown

Family Unknown

Genus ***Trigonocarpus*** Brongniart 1828

Trigonocarpus sp.

Plate II, Figure 6

Description

The casts found in this locality show one or two of the three longitudinal ribs that distinguish the morpho-genus. The dimensions of these ovules are up to 18 mm length and 10 mm width. No more features are visible in this casts, and the determination is at the genus level.

Remarks

The morpho-genus *Trigonocarpus* was originally instituted by Brongniart in 1828 for casts, but Krick (1932) applied it to compression forms. It represents preserved medullosalean ovules with three longitudinal ribs. If they are preserved as petrifactions, they are assigned to other fossil genera.

Order Peltaspermales Delevoryas 1979

Family Peltaspermaceae Thomas 1933 ex Harris 1937

Genus ***Autunia*** Krasser 1919 emend. Kerp 1982

Autunia was established by Krasser (1919) as a form-genus for a certain type of ovuliferous organ previously assigned to *Cycadospadix* Schimper 1870. In his work Kerp (1982) described new specimens attributed to *Autunia milleryensis* (Renault) Krasser 1919 (≡ *Autunia conferta* (Sternberg) Kerp et Haubold 1988) emending the generic diagnosis in the sense of a form-genus for ovuliferous organs of peltaspermaceous affinity and correlating it with the sterile pinnules of the species *Callipteris conferta* (Sternberg) Brongniart 1849.

Nowadays the genus *Autunia* gains a natural status for both vegetative and reproductive organs and can be assigned to the family Peltaspermaceae (Kerp & Haubold 1988).

Autunia conferta (Sternberg 1826) Kerp in Kerp et Haubold 1988

Plate II, Figures 7–8

1826 *Nevropteris conferta* - Sternberg, pl. 22 fig. 5.

1988 *Autunia conferta* (Sternberg) – Kerp in Kerp & Haubold, p. 143.

Description

Several fragments in a good state of preservation are attributed to this species. They are preserved as impression and with venation pattern recognisable. Fronds are bipinnate and oval in the general outline (Plate II, Fig. 7). The robust striated primary rachis is 3–4 mm thick. Pinnae attached alternately to the main rachis arising at an angle of 50°. Pinnules (5x3 mm) are attached with the entire basis to the rachis. They are subalternate and never overlap. Midveins are marked and sunken, they unequally divide the pinnules and go straight just to the apex. Lateral veins arise from the midvein forming an angle of 45° and go parallel straight or arcuate till the edge, forking once, apparently close to the midvein (Plate II, Fig. 8).

Remarks

In this assemblage, both sterile leaves and a putative ovuliferous organ were found and, according to Kerp & Haubold 1988 could be related to this natural species. Callipterid foliage appears to be very variable, and in some cases, the intraspecific variation can be demonstrated by material originating from the same population (Kerp 1988). As a result of the correlation between reproductive organs and foliage, the name *Autunia* appears to be the oldest usable synonym of the old *Callipteris,* and it has been selected available for the inclusion of *C. conferta*.

Distribution

This species occurs in the Euroamerican floristic province (Kerp & Haubold 1988). It is a key species for the attribution to the relative macro floristic zone (Autunian). It is considered radiate from the Euramerican province until the Cathaysian floristic domine (China, Sze 1935; Wang et al. 2014).

Putative ovuliferous organs of ***Autunia conferta***

Plate III, Figures 1–3

Description

Some specimens have been identified as putative ovuliferous organs of *Autunia conferta*. In the Plate IV, fig. 3 (and the magnificence in fig. 4) a group of megasporophylls seems to be helically arranged in the main axes. These are broadly flabelliform with ribs radiating from the petiole. Unfortunately, ovules are not well recognised in this specimen. The potential ovule is shown in Plate IV, fig. 4 and it is covered by megasporophylls. The ovule has 8 mm in diameter. In the Plate IV, fig 5 an isolated putative ovule is shown. It has ovoid shape and seems to differentiate into an inner body and an outer layer.

Remarks

The poor preservation of specimen figured in Plate III, does not permit to obtain more details. Nevertheless, our specimens more or less correspond with ovuliferous organ figured by Kerp (1988, Plate XXV, fig. 4) in his treatise about Peltaspermaceae plants. Isolated ovules which presented in this paper correspond in size and character with ovules figured by Kerp (1988, Plate XXV, figs 5, 6). Association of sterile and fertile remains strengthen the fact that both taxa belong to the same species. These organs have been found for the first time in Sardinia.

Autunia naumannii (Gutbier 1849) Kerp in Kerp et Haubold 1988

Plate III, Figure 4

1849 *Sphenopteris naumannii* - Gutbier, p. 11, p. 8, fig. 4

1988 *Autunia naumannii* (Gutbier) - Kerp in Kerp et Haubold, p. 143.

Description

This species has been identified over few small fragments. The main one is composed by two left pinnules of 8x3 mm. The ultimate rachis (1 mm) is grooved and straight. Pinnules are attached with a small part of the basis; they should be alternate (there is a small piece of the right pinnula preserved). Pinnule margins crenulate and incised. Midvein is distinguished. It goes through the pinnula and terminates in a cleft on the last two lobes. Secondary veins unforked, reaching the edge of the lobe; they are slightly strong or sometimes arcuate depending on the general shape of the organ.

Remarks

Autunia naumanni was first established by Gutbier (1849) and placed into the genus *Sphenopteris* Brongniart 1822 and later moved to *Callipteris* Brongniart 1849 by Sterzel (1881). Kerp (1988) and Kerp & Haubold (1988) recognise in the same ex *Callipteris naumanni* two specific groups, one informally called *C. naumannii sensu stricto* and the other called *C. naumannii* forma *suberosa* Sterzel 1918. The first one appears to belong to the group of callipterids with alethopteroid to pinnately lobed pinnules, but the second one shows more affinities with the callipterids with palmate, (prolonged) flabelliform to biserially segmentated pinnules. In fact, the *suberosa* form has been moved in the species *Lodevia suberosa* (Sterzel) Kerp et Haubold 1988. Furthermore, based on the comparison of the reproductive organ (*Sphenopteris* *naumanni*), Kerp in Kerp & Haubold (1988) moved the species into the genus *Autunia* Krasser 1919.

Distribution

This species is rather known from the Saxonian and Thuringian basin and is a rare element in the other basin (Kerp 1988). Recently this species has been found in the Central Appalachian Basin of controversial age (USA, DiMichele et al. 2013a) and the Cathaysian continent (China, Wang et al. 2014). In France, this species is present only in the Muse Formation (Early Asselian of Autun; Pellenard et al. (2017).

Order unknown

Family unknown

Genus ***Sobernheimia*** Kerp 1983

Sobernheimia jonkeri Kerp 1983

Plate IV, Figure 1

1983 *Sobernheimia jonkeri* - Kerp, pl. 1.

Description

One specimen from the studied locality represents an enigmatic *Sobernheimia jonkeri* which belongs probably to a special evolution line of Pteridosperms (Kerp 1983; Pšenička et al. 2017). This specimen is represented by a phylloid organ bearing two rows of seed-like bodies in the lateral margins. The middle part is named “axe” by Kerp (1983, p. 177) and it is 7 mm wide, it seems to have a flattened lamina with longitudinal striations. In the lateral margins, the lamina is divided into several lobes, nearly perpendicular to the "axis". The elongate lobes are 13 mm long and 1.2 mm wide, terminated by the rounded apex. The ovoid bodies are alternating with the lobes. These bodies are ~5 mm in diameter. The bodies are poorly preserved but appear to be rounded (Plate V, fig. 2). Unfortunately, the exact mode of attachment of these bodies is not clear.

Remarks

This mono-typified genus has been listed only in the lower Permian of the Nahe area (Germany). Since the description given by Kerp (1983) this genus has been considered a form intermediate between pteridosperms and cycads. Recently, Pšenička et al. (2017) revised some pteridosperm-like organ genera considering *Sobernheimia* to be probably of this evolution line. These authors compared *Soberheimia* with the new established genus *Ovulepteris* Pšenička et al. 2017 that differs in the style of placement of ovules. In *Ovulepteris* indeed, ovules are situated at the end of lateral veins in protruding segments, while their attachment in *Soberheimia* is unclear, appearing to be close to the midrib. Pšenička et al. (2017) supposed that this type of plant represents some particular group of pteridosperms.

Class unknown

Order unknown

Family unknown

Genus ***Taeniopteris*** Brongniart 1828

Taeniopteris cf. ***multinervia*** Weiss 1869

Plate IV, Figure 2

1869 *Taeniopteris multinervia* - Weiss, pl. 6, fig. 13.

Description

Taeniopterid leaves represent another element of the plant assemblage on the studied locality. Leaves are preserved incompletely but taper gradually toward the base. Leave margin is straight and slightly lobed in proximal part. Leaves were more than 60 mm long and 30 mm wide. The midrib appears rigid, 2.5 mm broad, longitudinally striated. Lateral veins are thin, arise at an acute angle (ca. 17°), thereafter arching strongly before extending to the margin of the leaf, and branch once or twice in close succession near the midrib. The first bifurcation is close to the midrib. Lateral veins reach the lateral margin at 80-90°. The venation density is c. 34 veins per 10 mm of leaf margin.

Remarks

Taeniopteris is a widespread genus, and its range extends from Carboniferous to Cretaceous. This genus is characterised by strap-shaped leaves with marked midrib and secondary veins which bifurcate once or several times before reaching the margin (entire). Because of it is a heterogeneous fossil genus, *Taeniopteris* has been associated with several plant groups such as Filicopsida (Harris 1961), pteridosperms (Barthel et al. 1975), Cycadales (Harris 1932; Haworth et al. 2011; Mickle et al. 2011), Bennettitales (Pott et al. 2007) and Pentoxylales (Sahni 1948). The species we found in the Montarbu basin misses of important characters (cuticle, reproductive organs associated) to better understand the botanical affinity.

Distribution

This species has been listed for the lower Permian of the Nurra region (NW Sardinia, Broutin et al. in Cassinis et al. 1999). It also occurs in the late Palaeozoic of China (Yan et al. 2017), Spain (Broutin & Gisbert 1985; Talens & Wagner 1995; Wagner & Martinez Garcia 1982), in the Upper Triassic of Middle Asia (Dobruskina 1995).

Class Pinopsida Burnett 1835

Order Cordaitanthales Meyen 1984

Family Cordaitanthaceae Meyen 1984

Genus ***Cordaites*** Unger 1850

Cordaites sp.

Plate IV, Figures 3–4

Description

Cordaitanthalean leaves are frequent in the studied locality. Large leaves are often more than 100 mm long and ca. 25 mm wide (Plate III, Fig. 4). Unfortunately, the entire leaf was not discovered. Thus the shape and terminal part are unknown. Coal material is not preserved so that cuticular structure information is unknown.

Remarks

This genus is common for the Late Palaeozoic of Sardinia (Cassinis et al. 1999). We opted for a generic identification because important features are missing. Indeed, this group of plants is recognisable at species level if the epidermal structure is preserved. Many leaves show a high level of decay. Indeed, these leaves are partly destroyed and they seem to be separated along the veins (Plate IV, Fig. 3). This may indicate that the leaves floated in water for a relatively long time.

Genus ***Cardiocarpus*** Brongniart 1881

Cardiocarpus sp.

Plate IV, Figures 5–7

Description

This three-dimensional preservation of *Cardiocarpus* seeds is the only discovered in the studied locality. Seeds are wingless, platyspermic, round-oval, 12 mm long and 13 mm wide, and in their terminal parts a slightly tapered.

Remarks

The state of preservation and the absence of anatomically preserved structures do not permit an identification at a specific level.

Order Voltziales Andreanszky 1954

Family Utrechtiaceae Mapes et Rothwell 1991

Genus *Ernestiodendron* Florin 1934

Ernestiodendron filiciforme (Schlotheim 1820) Florin 1934

Plate V, Figures 1–3

The complete list of synonymies is included in Kerp et al. 1990.

Description

Several specimens are attributed to this taxon and the intraspecific diversity in axes and leaves is very high. Axes of the last order with short, broad, rigid, and wide branches are present, and leaves are falcate (Plate V, Fig. 1): they arise from the axis with an angle of about 70–80° and are attached with a large base. They are about 3–4 mm long and 1.2 mm wide. The apex is pointed and bends to the front.

In Plate V, Fig. 3 a putative polliniferous cone that could belong to this species has been found attached to other sterile branches.

Remarks

Notes on the nomenclature of *Ernestiodendron filiciforme* are explained in Kerp et al. 1990. These authors discussed the holotype and the synonymy since the establishment of this species. *Ernestiodendron* differs from *Otovicia* because the latter has more than a single ovule per dwarf-shoot (Kerp et al. 1990).*Distribution*

This conifer is among others the most widespread species in the Euroamerican province, and it is rather frequent in upper Pennsylvanian and lower Permian horizons. For example, it has been listed in the Czech Republic (Šimůnek & Martínek 2009, Opluštil et al. 2013), Romania (Popa 1999), France (e.g., Lodève, Galtier & Broutin 1995, 2008); Portugal (Wagner & Álvarez-Vázquez 2010); USA (Glasspool et al. 2013).

Female cone

Plate V, Figure 4

The ovuliferous cone with walchian affinity measures 16x3 mm. The bracts have a broad base but, unfortunately, apexes are not preserved. Every bract seems to bear two ovules, and this is a characteristic seen for the species *Otovicia hypnoides* (Brongniart) Kerp et al. 1990, described for the late Carboniferous-upper Permian of SW Germany.

Thus, the bad state of preservation does not permit to identify this organ better.

Genus ***Walchianthus*** Florin 1940 emend. Clement-Westerhof et Kerp in Visscher et al. 1986

Walchianthus sp.

Plate V, Figure 5

Description

These compact polliniferous cones are up to 30 mm long and 4-5 mm wide. In these fossils, the microsporophylls are spirally arranged on the axis and have an upturned distal portion that overlaps the base of the one above slightly.. The apex is acute and in general parallel to the cone-axis.

Remarks

The cones are assumed to be polleniferous because they do not appear to contain ovules, and the apices of the sporophylls are not bifid as in typical walchian female cones.

Genus ***Culmitzchia*** Ullrich 1964 emend. Clement-Westernhof 1984

Culmitzschia speciosa (Florin 1939) Clement-Westernhof 1984

Plate V, Figures 6–-7

1939 *Lebachia speciosa* - Florin, p. 113, pl. LXV, LXVI, figs. 6–7.

1984 *Culmitzschia speciosa* (Florin) - Clement-Westernhof, p. 115.

Description

Various specimens are attributed to this taxon. The shoot fragments are up to 27 mm long and 40 mm wide (Plate VI, 6) with axes of 2–3 mm wide. Lateral shoots (up to 25×1.5 mm) arise oppositely (Plate VI, 7) or alternately with an angle of 80°. Leaves are arranged in a spiral (70–90°) and inserted with the entire basis. The leaves are falcate with only one visible vein and a pointed or slightly rounded apex that turns close to the end of the leaf (Plate VI, 6). They are up to 4 mm long and 1–1.5 mm wide.

Remarks

Culmitzschia has been emended by Clement-Westerhof (1984) to include sterile walchiaceous remains with preserved epidermal structure. Mapes & Rotwell (1991) consider *Culmitzschia* as a form-genus. The lack of cuticles and epidermal characters does not allow us to include these specimens in a right order and family and unfortunately, this does not permit to have a certain determination on the species level.

Distribution

This species has been identified by Broutin for the early Permian of Escalaplano (central Sardinia; Pertusati et al. 2002), but specimens and pictures are not available anymore. *Culmitzchia* (al. *Lebachia*) speciose has also been described in northern Italy (Clement-Westerhof 1984); Germany (Florin 1939); Czech Republic (Šimůnek & Martínek 2009); Urals (Naugolnykh 2007); Maroc (Doubinger & Roy-Dias C. 1986). In the western equatorial Pangea, it has also been listed in the USA (DiMichele et al. 2013a).

Genus ***Samaropsis*** Goeppert 1864 emend. Seward 1917

cf. ***Samaropsis*** sp.

Plate V, Figure 8

Description

The only seed attributed to this genus has broadly elliptical shape, platyspermic. Close to the upper part of the organ, a fracture is present, and this could be because in general, this seed has a mid-ridge in the median part. The micropyle is evident and emarginate. It is 6 mm long and 5 mm wide. The central body is indistinct.

Remarks

The bad state of preservation does not permit an attribution at the species level. Seward (1917) established differences between *Samaropsis* and the similar *Cordaicarpus* Seward 1917. In fact, as stated in this specimen, *Samaropsis* has the testa composed by one inner narrower border. In *Cordaicarpus* the border is outer and much delicate.

Conifer seed

Plate V, Figure 9

Description

This small isolated seed has an oval shape and measures 2.5 x 1.2 mm. The bad state of preservation does not permit to identify this organ.

Form-Genus **Gomphostrobus** Marion 1892

Gomphostrobus sp. cf. **Gomphostrobus bifidus** (Geinitz 1873) Zeiller in Florin 1938

Plate V, Figure 10

The complete list of synonymies is included in Barthel et al. 2010.

Description

Only one specimen is recognisable as isolated bract of a walchiaceous ovuliferous cone. Its base is 5 mm wide, and the bract is 12 mm long, assuming a triangular shape. The apex is not well preserved in this specimen but is slightly recognisable and it appears biforked (bifidus).

Remarks

Gomphostrobus is here considered a form-genus of uncertain affinity because the material cannot be definitely correlated with taxa established on foliage or cones. Moreover, Thomas & Seyfullah (2016) considered some species of this genus to be lycophytes. This form is rather typical in the Permian of Europe and North America (DiMichele et al. 2017; Kerp et al. 1990; Šimůnek & Martínek 2009).

6. Discussions

The main subject of this study is the Late Palaeozoic flora of Montarbu. The systematic study of this late Palaeozoic plant assemblage aims to track different considerations. Montarbu reflects a typical Autunian assemblage. The Autunian falls into a still debated period of time, with different schools of thinking. Nonetheless, the Autunian regional stratotype has been recently radiometrically dated (Pellenard et al. 2017) and it spans from the very late Ghzelian to the early Asselian (see fig. 1.6). Extrabasinal species such as callipterids and conifers were considered markers for the C/P boundary (Pellenard et al. 2017). Unfortunately, their appearance changes from one place to another. For example, *Autunia conferta* has been found also in early Stephanian strata (middle Pennsylvanian, Souss Basin, Hmich et al. 2006). This was considered, for the most, a key species for the attribution to the Autunian regional stage and this fact is clearly reflected in Thuringia: *Autunia conferta* appears in the Ilmenau Fm which has a late Ghzelian–early Asselian age. The differences of the apparition of the species are due probably to the gradual turnover of vegetation type at worldwide scale during the end of Palaeozoic and this change has been correlated with aridification, northwards plate motion, Variscan orogeny and forefront destroying large areas of formerly lowland basinal settings (Hilton & Cleal 2007).

The study of the San Giorgio flora is done to support another goal of this thesis and it is completely available in Appendix 1. The compositional difference between the oldest Moscovian San Giorgio assemblage and the Montarbu flora shows the change of vegetation occurred across the late Palaeozoic also in Sardinia. This has been reflected also in several previous studies at worldwide scale (e.g. DiMichele et al. 2001a; Rees 2002; Roscher & Schneider 2006; Opluštil et al. 2013; Cleal & Cascales-Miñana 2014).

6.1. Relative abundances in the Montarbu flora and ecological preferences

The most representative taxa found in the assemblage are the conifer *Ernestiodendron filiciforme*, the cordaitanthalean remains attributed to *Cordaites* sp. and the seed-fern *Mixoneura subcrenulata*. These are in common in both of the two lithofacies recognized. The abundance of gymnosperms is a typical characteristic in the composition of the floras in the late Carboniferous/Early Permian, that differs from the older assemblages mainly composed of equisetopsids and ferns.

Specimens of equisetopsids miss in the lithofacies 2, and this is explainable because of the paucity of fossils in this locality. The sphenophytes are considered restricted to humid environments, due to their need for water during the reproductive

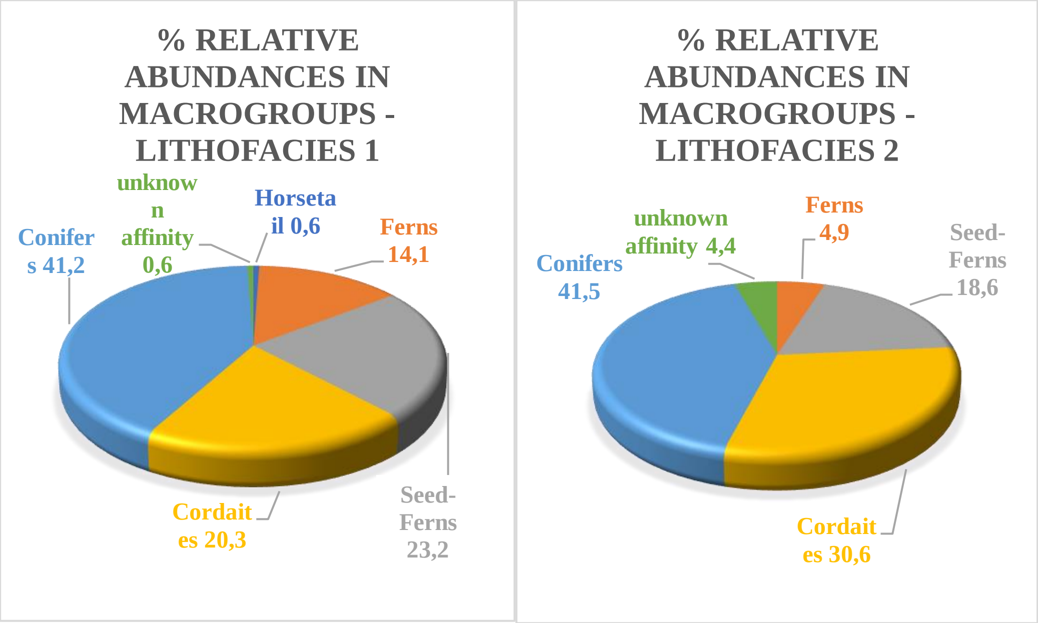

Fig. 6.1. Relative abundances of ecological macrogroups in lithofacies 1 & 2.

cycle. According to some authors, these plants grew in areas characterised by the aggrading or unstable substrate, such as stream and lake margins, and clastic flood basins (Scott 1978; Gastaldo 1987) except for some rare taxa indicated for dryer environments (Barthel & Rössler 1996).

All the other ecological macro groups are present in both the recognised lithofacies.

The number of fern taxa is high in the lithofacies 1 (14.1%; Fig. 6.1) becoming less in the lithofacies 2 (4.9%; see Fig. 6.1). The pteridophytes prefer humid environments. Marattialean ferns such as *Acitheca* and *Pecopteris* are relatively common in the Montarbu flora. In Europe, marattialean ferns remained an important element of tropical vegetation (Zodrow et al. 2006) through the upper Moscovian-Kasimovian–lower Gzhelian Stages (~300Ma), until getting extinct during the Asselian (Kerp & Fichter 1985). Both genera found in this assemblage (*Acitheca* and *Pecopteris*) are referred to arborescent marattialean fern with large, tripinnate or quadripinnate fronds that could represent, according to the relative abundance of these findings, an important puzzle of the Montarbu vegetation during the C/P.

The relative abundance of the pteridosperms has more or less the same trend in the two lithofacies (23.2% in lithofacies 1 and 18.6% in lithofacies 2; see Fig. 6.1). In the assemblage both Medullosalean and Peltaspermalean taxa are present, and the abundance regarding fossil remains for each slab is high (18.8%; Fig. 6.2). Seed-ferns are much more represented in the Lithofacies 2 (41.2%; Fig. 6.3) because in general fine-grained sediments permit relative better preservation also of small macro remains while they are much abundant in the coarser lithofacies 1. *Autunia conferta* grew under relatively dry conditions on elevated sandy lake margins and river banks (Kerp &

Fichter 1985; Kerp 1988; Barthel & Rössler 1996). In general, the presence of large frond parts in claystone and minute pinnae fragments in more coarsely grained rocks may correspond to a variation in energy of depositional environment and distance from the growing site. In the Montarbu flora, the second option is well reflected. According to Kerp (1988), the other *Autunia naumannii* preferred relatively dry habitats and this is explainable because of its thick lamina (cuticle). The latter species is rare in the assemblage and found only in the fine-grained lithofacies 2. In the Montarbu assemblage, the abundance of *Mixoneura subcrenulata* is high compared to the other plant remains (8%). Species of mixoneurid-type indicate seasonally dry climatic setting, perhaps dry sub-humid (Cecil 2003). *Mixoneura subcrenulata* is considered a mesophile element (DiMichele et al. 2013b). Seed-ferns are a paraphyletic group of plants (Rothwell & Serbet 1994; Nixon et al. 1994; Doyle 1996; Hilton & Bateman 2006; DiMichele et al. 2006). Thus, different pteridosperm orders represent plants having different ecological needs, and it is not exactly known what the particular ecological demands of individual species were. Furthermore, several authors have speculated on ecological adaptations of various taxa (DiMichele et al. 2006).

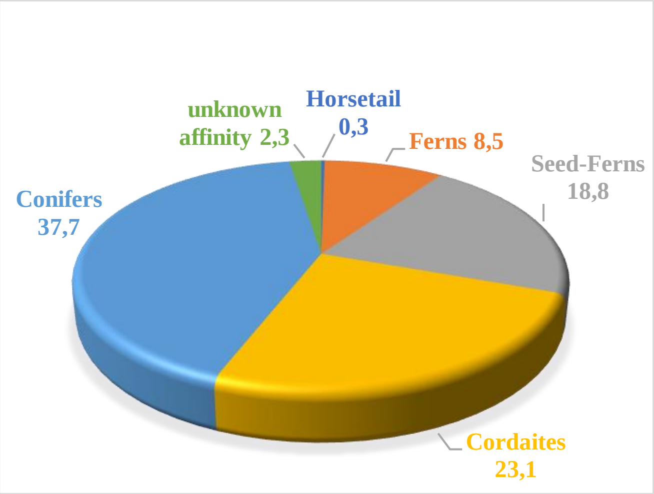

Fig. 6.2. Abundance of taxa in the ecological macrogroups.

Taeniopteris cf. *multinervia* may belong to pteridosperms, cycads or true ferns. The characteristics of these leaves demonstrate that this plant was well-adapted to humid environments. According to DiMichele et al. (2013b), the large-leaved *Taeniopteris* were typical of non-wetland (especially peat-forming) environments.

The abundance of cordaithaleans fragments (lithofacies 1: 20.3%; lithofacies 2: 30.6%) may indicate that these plants grew luxuriantly; on the other hand, the leaves show signs of fragmentation due to the transport which could mean a distance from the growing site to the depositional one. According to Zodrow et al. (2000), this group of plants may come from a drier, well-drained floodplain or extra basinal lowlands.

Conifers are the most abundant group in Montarbu, and the percentage is almost 41% for each lithofacies. They are also well represented in terms of diversity of taxa (see Fig. 6.2). *Ernestiodendron filiciforme* it's a species that generally grew in mesophilic biotope (Remy & Remy 1977). As stated in the Montarbu assemblage, the species *E. filiciforme* and *Culmitzschia* cf. *speciosa* have also been found in association in meso- to xerophilous environments (e.g. Czech Republic; Šimůnek & Martínek 2009). Furthermore, *Gomphostrobus* is related to seasonally dry habitats (Mamay & Mapes 1992).

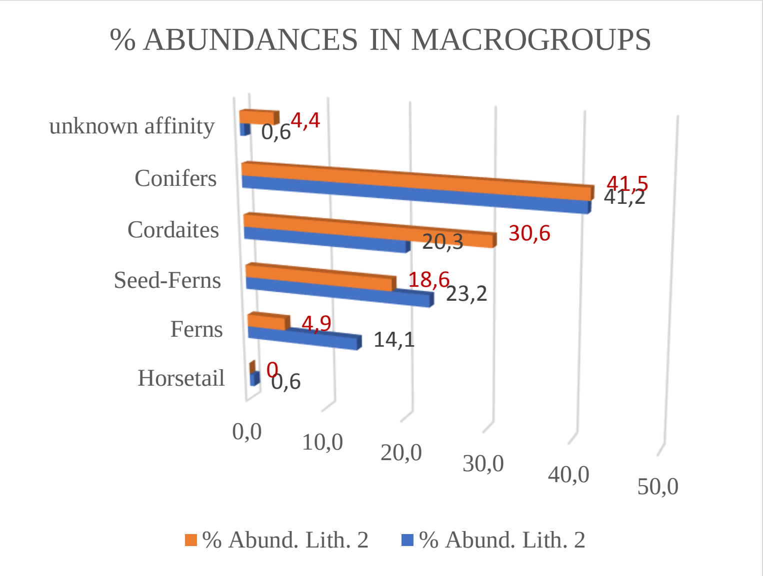

Fig. 6.3. Comparison between abundances of ecological macrogroups in lithofacies 1 & 2.

The hypothetical reconstruction of the Montarbu vegetation, based on macro floristic records, shows a prevalence of dryland elements (conifers, cordainthaleans and peltasperms) and some wetland elements (rare sphenopsid, ferns, some pteridosperms):

a) a forest mainly composed of walchian-type conifers (*Ernestiodendron*) probably covered the surrounding reliefs or slopes;

b) the piedmont zone was occupied by cordaithaleans and mixoneurid pteridosperms, in which the soil was slightly humid;

c) ferns and other plants needing more water were present in the surrounding areas. The analysis of the macro remains shows that these plants are mostly fragmented and in a different level of decomposition, especially conifers and pteridosperms. This suggests that the material was subjected to transport at a different distance before deposition.

The different composition of the two lithofacies may be much more related to taphonomic selection and preservation biases than to differences in the general composition of the flora.

6.2. The Montarbu flora in the western Tethyan context

The paleogeographic position of emerged land in Europe was different from the actual configuration during the Carboniferous-Permian (C/P) interval (see Fig. 1.5). This different setting lets to find similarities in paleofloras that nowadays are geographically distant. Data from the literature show a huge diversity at genus level for the analysed assemblages. To develop the statistical comparison for understanding similarity and dissimilarity in the western Tethyan area, the choice of the assemblages has been done including those from a precise late-Ghzelian–early Asselian interval of time. In the Tab. 6.1 is reported the number of genera of these floras, the "exclusive

FLORAS	GENERA	"EXCLUSIVE TAXA"	REFERENCES (LOCALITIES)
Montarbu	18	0	This work
E-Pirenei (UA)	20	1 (*Feysia*)	Wagner & Álvarez-Vázquez 2010 (Coll de Jou/Baró; Arcalis)
E-Asturias and Cantabrian mountains	6	1 (*Supaia*)	Wagner & Martinez Garcia 1982; Gand et al. 1997; Wagner & Álvarez-Vázquez 2010 (Cueli)
E-Iberian Range	24	0	Wagner & Álvarez-Vázquez 2010 (Valdesotos/Retiendas; Fombuena)
E-Andalucía	60	16 (*Arthropitys*, *Danaeites*, *Dorycordaites*, *Entsovia*, *Ginkgoites*, *Ginkgophytopsis*, *Koretrophyllites*, *Lobatannularia*, *Pelourdea*, *Phyllotheca*, *Protoblechnum*, *Prynadaeopteris*, *Psygmophyllum*, *Rhipidopsis*, *Schizostachys*, *Ullmannia*)	Mingarro-Martin 1962; Broutin 1974, 1986; Wagner & Álvarez-Vázquez 2010 (Guadalcanal; Valdeviar)
P-Buçaco basin	33	2 (*Blanzyopteris*, *Lescuropteris)*	Teixeira 1944; Wagner & Lemos de Sousa 1983; Wagner & Álvarez-Vázquez 2010
F-Graissesac-Lodève	36	4 *(Codonospermum*, *Hexagonocarpus*, *Pachycordaites*, *Sphenophyllostachys*)	Martín-Closas & Galtier 2005, Michel et al. 2015
F-Igornay	26	1 (*Lesleya*)	Broutin et al. 1999; Pellenard et al. 2017; Galtier pers. comm.
F-Muse	26	1 (*Eusigillaria*)	Broutin et al. 1999; Pellenard et al. 2017; Galtier pers. comm.
F-Montceau-les-Mines	15	1 (*Trichophitys*)	Bercovici & Broutin 2008
			continue...

Tab. 6.1. Number of genera of the floras included in the IS analysis, exclusive taxa and source of data.

taxa" and the source of these data. According to this research, 135 genera have been reported for the western Tethyan area (Appendix 5).

FLORAS	GENERA	"EXCLUSIVE TAXA"	REFERENCES (LOCALITIES)
I/A-Carnic	33	3 (*Carpolithes, Diplocalamites, Sphenobaiera*)	Fritz & Krainer 2007
G-Saar	44	4 (*Cordaicarpus, Eucalamites, Peltaspermum, Schizopteris*)	Trunko & Munk 1980; Kerp & Fichter 1985; Kerp 1986; Lausberg & Kerp 2000; Uhl & Jasper 2016
G-Döhlen Formation	36	3 (*Botryopteris, Bowmanites, Dactylotheca*)	Barthel 2016
G-Türinger Waldes	22	2 (*Dadoxylon, Pterispermostrobus*)	Barthel 2009
G-Weissig Basin	25	2 (*Carpentieria, Pterophyllum*)	Barthel 2010
CZ-CWBB	21	0	Opluštil et al. 2013
CZ-Krkonose-piedmont Basin	39	1 (*Lepidostrobus*)	Opluštil et al. 2013
CZ-ISB	11	0	Opluštil et al. 2013
CZ-Boskovice Basin	39	1 (*Zamites*)	Opluštil et al. 2013
CZ-Blanice Basin	23	0	Opluštil et al. 2013

Tab. 6.1. (continued). Number of genera of the floras included in the IS analysis, exclusive taxa and source of data.

As stated in the Introduction chapter of this thesis, Wagner & Álvarez-Vásquez (2010) considered all the Autunian belonging to the Ghzelian, and to compare Spanish basins I opted for considering only the middle-upper Autunian outcrops of Wagner & Álvarez-Vásquez (2010), that roughly corresponds to the new radio-datation of the Autunian Stratotype (late Ghzelian-Asselian) of Pellenard et al. (2017) and leave all the others out. Recently, Juncal et al. (2016) reveal a Kungurian age for the Sotres Formation (Asturian and Cantabrian Mountains) instead of a lower Autunian age previously reported by Wagner & Álvarez-Vásquez (2010). These data will be skipped for the IS comparison. The subdivision of Iberian (Spain, Portugal) basins has been done according to Arche & López-Gómez (2006) and Wagner & Álvarez-Vásquez (2010) and five of these have been included in this study: Pyrenees (Coll de Jou-

Baró/Arcalis localities), Asturian and Cantabrian mountains (Cueli), Iberian Range (Valdesotos/Retiendas, Fombuena), and Andalucía (Guadalcanal, Valdeviar). The only Portuguese basin included for the IS comparison is the Buçaco basin (NW of the country).

The French basins included for IS comparison have been recently dated (Michel et al. 2015; Pellenard et al. 2017). The floras from the Graissesac-Lodève Basin are stored in different formations and I consider only those ranging from the Gzhelian-Asselian interval (Graissesac). The C/P floras from the Autun basin come from the sections of Igornay and Muse. The flora of Montceau-les-Mines (Massif Central) described by Charbonnier et al. (2008) is a freshwater flora of late Carboniferous and according to Pellenard et al (2017) of Stephanian age (older than the Montarbu one). Because of the not detailed age of this flora and the impossibility to compensate for it, this will be skipped from IS comparison. From a few kilometres far from Montceau, another flora has been recently re-described. Bercovici & Broutin (2008) restudied the collection stored at the Paris 6 University. This flora has been studied in the past by Zeiller (1906) and Doubinger (1956). Bercovici & Broutin (2008) gives information about macro-remains, taphonomy and palynology. These authors consider the flora an Autunian Flora of basal Permian age. For the analyses, I consider all the genera indicated in the paper except for the doubtful ones.

In the Italian-Austrian border, the Carnic flora has been included as well. This flora has been described in several papers published in the review Carinthia II (e.g.: Fritz & Krainer 2004, 2006, 2007). Recently Pšenička et al. (2014) argued about the determination of species of the Carnic flora. According to these authors, there are many misinterpretations especially among the pecopterid group of plants. For developing the IS comparison, I included only genera. The systematic revision at species level of these fossils is not the goal of this research. Papers are in German language and sometimes the age of sediments is not clearly reported, so I consider only plants from a certain late Carboniferous-early Permian age, described in Fritz & Krainer (2007). The floras belong to the Grenzland Fm of early Asselian age and from Drauzuges and Gurktaler Decke areas, *unterperm* (probably ?early Asselian). Other Austrian localities are described in an old paper by Tenchov (1980). Data are referred to very old published works dated back the nineteen century. Taxa identified need a strong systematic revision and they will be skipped from the IS comparison

The German floras included in the IS comparison are located in the Saar-Nahe area, the Döhlen Formation, Türinger Waldes and the Weissig basin. Kerp & Fichter (1985) summarized the history of paleobotanical investigation on the Rotliegends of the Saar-Nahe area. Lausberg & Kerp (2000) described a conifer-dominated flora from this area. Within the basin, the Rotliegend group is subdivided into two subgroups (Menning et al. 2006, Boy et al. 2012): the Glan subgroup (~Lower Rotliegend: Gzhelian–Asselian) and the Nahe subgroup (~Upper Rotliegend: Asselian–Kungurian). Uhl & Jasper (2016) studied the macroflora of the Remigiusberg Fm (first formation of the Glan subgroup) and they dated the upper part of this formation not older than late Ghzelian. For the IS comparison, I consider fossil assemblages from the Remigiusberg Fm and the overlaid formations of the Glan subgroup. Barthel (2016) considers the Döhlen Formation flora to be early Permian (Asselian). I opted to include the flora in the IS comparison for the similar composition with the Montarbu one. The Türinger Waldes basin comprises many formations ranging from the middle Carboniferous to the middle Permian. For the IS comparison, I included the flora from the Ilmenau Fm that according to recent stratigraphical schemes (see Schneider et al. 2014 for details) is late Ghzelian–early Asselian.

The Weissig Basin flora comes from strata determined Asselian by means of insect remains (Schneider & Werneburg 1993) and more precisely as upper Lower Rotliegend by means of plant fossils, that roughly corresponds to the first part of the Asselian.

For the Czech area, five main basins have been included in the IS comparison (Opluštil et al. 2013): The Central and Western Bohemian Basins (CWBB in the text), the Krkonoše-piedmont, the Intra Sudetic (ISB in the text), the Boskovice and the Blanice Basin.

The Klobuky member in the Líně Fm (CWBB) is referred to late Ghzelian-early Autunian (Martínek et al. 2017) and the flora yielded have been included in the IS analysis. Data of the Krkonoše-piedmont Basin come from the Semily Fm (late Ghzelian; Opluštil et al. 2016b). The flora of the subsequent Vrchlabí Fm (early Asselian, Opluštil et al. 2016b) is also included in the IS comparison. The flora of the ISB included in the IS comparison comes from the lower part of the Chvaleč Fm that according to Opluštil et al. (2016b) is Stephanian C, corresponding to the lower Autunian of Pellenard et al. (2017) and close to the C/P boundary for the International Commission of Stratigraphy. The Boskovice basin has been recently radio dated (Opluštil et al. 2017a). The top of the Rosice-Oslavany Fm (in the lower part) nearly corresponds to the C/P boundary (298.88±0.9 Ma). Flora from the overlaid early "Autunian" Padochov Fm is also considered for the IS comparison. The sedimentary fill of the Blanice Basin spans the interval from the late Ghzelian (Stephanian C) to the “Autunian” (early Asselian) and the flora coming from the Černý Kostelec Fm is included in the IS comparison.

6.3. Comparison with the localities

The flora of Montarbu is one of the southernmost floras of this period, and the paleogeographic position would suggest that this area should have mixt floras with western and eastern elements. Paleogeographycally close to that of Montarbu and disposed slightly to East is the flora of the Carnic Area (IA-Carnic; between Austria and Italy). The Andalucía basin (in Spain), to the West, is the most abundant (60 genera) together with that of the Saar basin (44 genera) in Germany, located to East and close to the palaeoequator (see Tab 6.1 for details). Many floras are composed of about forty to thirty genera, and they are Krkonose-piedmont and Boskovice basin floras in the Czech Republic; Mont-Pelé, Graissesac-Lodève in France; Döhlen Formation in Germany; the Portuguese Buçaco flora. The others floras are composed of thirty to ten genera, and only one has less than ten genera (Asturias and Cantabrian mountains). The analysis also evidences the presence of “exclusive taxa” in the floras. These are not only in the most numerous assemblages but also in the small ones (see Tab. 6.1 for details).

In E-Andalucía (southern Spain), taxa not in common with other western Tethyan selected localities are sixteen. Here Broutin (1986) showed the presence of several ginkgoaleans, remarking predominantly humid climatic conditions and producing a record of coal measure type floras typical of the everwet Cathaysian realm. In fact, the paleogeographical position of Andalucía during this period was different and much close to the East.

In the Carnic area between Italy and Austria, the flora has three elements not shared with other localities. According to Pšenička et al. (2014), there are many misinterpretations of species in the papers by Fritz & Krainer (2004, 2006, 2007), especially among the pecopterid group of plants. Thus, this fact could have influenced the final list of taxa. Two German basins (Saar and Döhlen Formation) have a good number of exclusive taxa probably because of the variety of original environment and the relative sediment in which fossils are buried. A reason could also be the number of genera recorded in the assemblages (they are two of the most diversified selected floras) or the eastern paleogeographic position respect of the other much western floras. The other floras have few exclusive taxa or, in the majority of cases, such as Montarbu, nothing (see Tab. 6.1). It is noticeable the presence of widespread taxa for the selected assemblages: for example, *Annularia* is recorded in 17 of 20 floras, *Autunia*, *Pecopteris* and *Taeniopteris* 18/20 remarking a general similarity of the assemblages.

6.3.1. Comparison with western localities

The Iberian floras (except Andalucía) lie more to the West respect of that of Montarbu. The Portuguese locality (Buçaco basin) lie much to the West and shares ten genera. The other Spanish localities have fewer genera in common. With the closer Iberian Range flora the shared genera are eight, here sphenophytes (*Annularia*), ferns (*Pecopteris*), seed-ferns (*Autunia*, *Callipteridium*, *Mixoneura*, *Neurocallipteris*), conifers (*Ernestiodendron*) and *Taeniopteris* are in common, remarking very similar environmental conditions. With Asturias and Cantabrian, the shared genera are only 4 and comprise some typical taxa of this period (*Autunia*, *Culmitzschia*, *Neurocallipteris*, *Taeniopteris*). These similarities show the uniformity of the vegetation in this area of the western Tethys and discrepancies could be due to local environmental factors. Finally, the comparison between Andalucía and Montarbu floras remarks 14 genera in common. This comprises all the paleoecogroups reported in Sardinia. This astonishing similarity could be due to the abundance of taxa in the Andalusian basin and similar environment.

6.3.2. Comparison with northern localities

The France localities lie more to the North. The closer flora is that of Graissesac-Lodève. This assemblage shares six genera with the Montarbu flora and the most important taxa of this period are in common (*Annularia*, *Pecopteris*, *Callipteridium*), representing almost all the paleoecological groups.

The floras from Igornay and Muse (Autun basin) shares exactly the same genera with Montarbu and all the paleoecological groups are represented. The other French flora comes from the Massif Central that lie more the North (Montceau). Here the genera in common are 8. In summing up, the Montarbu flora shares almost half genera with the French studied floras, and this highlights the paleoposition of these localities during the Permo-Carboniferous interval and the similar paleoenvironmental conditions.

6.3.3. Comparison with south-eastern localities

Are included in this comparison the floras lie to the south-east in respect of that of Montarbu. The Carnic flora (Italy and Austrian Alpes) comprises 33 genera and 9 in common with the Sardinian one. As said above, the systematic attribution of these assemblages needs revision. Neglecting that, for the analysis at genus level the similarity is high and all the paleo eco-groups are shared: sphenophytes (*Annularia*), ferns (*Acitheca*, *Pecopteris*), seed-ferns (*Autunia*, *Callipteridium*), Cordaitales (*Cordaites*), conifers (*Ernestiodendron*) and *Taeniopteris*. Given that the Montarbu flora is composed of 18 genera only, the degree of similarity appears to be high and the close paleogeographic position could be the reason.

6.3.4. Comparison with north-eastern localities

More to North-east, several floras can be compared to that of Montarbu. The German and Czech basins show a high degree of similarity with the Montarbu flora. Here the source of data is updated and this lets to interpret well these similarities. One of the most numerous floras of this interval of time is that recorded in the G-Saar basin: 12 genera out of 44 are in common with Montarbu. This similarity is also reflected in the others basin such as the Weissig (13/25 genera in common), the Boskovice (12/39), the Krkonose-piedmont (13/39) and in the Döhlen Formation (10/36). All the paleo eco-groups are in common probably because of the strong similarities of the paleoecological conditions. Probably there were not strong geographical barriers between these zones that paleogeographically were not so close in respect to the others (e.g. France, Spain).

6.4. Index of Similarity

Using the Index of Similarity (IS, see Chapter 3 for details) a squared matrix of 190×2 values was drafted (Tab. 6.2), wherein the IS values for each couple of flora assemblages are reported.

Floras	**Montarbu**	**E- Pyrenees**	**E-Asturias and Cantabrian mts**	**E-Iberian Range**	**E-Andalucía**	**P-Buçaco basin**	**F-Graissesac-Lodève**	**F-Igornay**	**F-Muse**	**F-Montceau (Massif Central)**	**I/A-Carnic**	**G-Saar**	**G-Döhlen Formation**	**G-Türinger Waldes**	**G-Weissig Basin**	**CZ-CWBB**	**CZ-Krkonoše-piedmont Basin**	**CZ-ISB**	**CZ-Boskovice Basin**	**CZ-Blanice Basin**
Montarbu	-	0,32	0,25	0,28	0,26	0,28	0,21	0,41	0,31	0,33	0,26	0,26	0,27	0,29	0,36	0,26	0,31	0,22	0,30	0,31
E- Pyrenees	0,32	-	0,24	0,37	0,26	0,31	0,18	0,28	0,26	0,48	0,21	0,26	0,40	0,22	0,26	0,20	0,34	0,24	0,32	0,27
E-Asturias and Cantabrian mts	0,25	0,24	-	0,17	0,11	0,17	0,00	0,20	0,20	0,28	0,13	0,11	0,13	0,13	0,19	0,07	0,15	0,19	0,15	0,17
E-Iberian Range	0,28	0,37	0,17	-	0,33	0,39	0,23	0,32	0,24	0,24	0,28	0,26	0,38	0,23	0,27	0,35	0,38	0,29	0,35	0,36
E-Andalucía	0,26	0,26	0,11	0,33	-	0,36	0,28	0,28	0,26	0,19	0,30	0,31	0,32	0,23	0,26	0,31	0,35	0,22	0,35	0,31
P-Buçaco basin	0,28	0,31	0,17	0,39	0,36	-	0,29	0,37	0,34	0,25	0,35	0,31	0,38	0,27	0,26	0,40	0,40	0,29	0,39	0,39
F-Graissesac-Lodève	0,21	0,18	0,00	0,23	0,28	0,29	-	0,33	0,26	0,07	0,37	0,29	0,31	0,26	0,19	0,31	0,29	0,20	0,29	0,31
F-Igornay	0,41	0,28	0,20	0,32	0,28	0,37	0,33	-	0,38	0,25	0,31	0,29	0,33	0,20	0,22	0,32	0,33	0,30	0,33	0,36
F-Muse	0,31	0,26	0,20	0,24	0,26	0,34	0,26	0,38	-	0,25	0,29	0,27	0,30	0,25	0,26	0,30	0,36	0,24	0,34	0,33
F-Montceau (Massif Central)	0,33	0,48	0,28	0,24	0,19	0,25	0,07	0,25	0,25	-	0,23	0,27	0,14	0,18	0,23	0,25	0,27	0,24	0,27	0,27
I/A-Carnic	0,26	0,21	0,13	0,28	0,30	0,35	0,37	0,31	0,29	0,23	-	0,34	0,32	0,29	0,28	0,39	0,35	0,29	0,35	0,38
G-Saar	0,26	0,26	0,11	0,26	0,31	0,31	0,29	0,29	0,27	0,27	0,34	-	0,31	0,30	0,29	0,32	0,37	0,25	0,37	0,31
G-Döhlen Formation	0,27	0,40	0,13	0,38	0,32	0,38	0,31	0,33	0,30	0,14	0,32	0,31	-	0,29	0,28	0,31	0,36	0,23	0,35	0,34
G-Türinger Waldes	0,29	0,22	0,13	0,23	0,23	0,27	0,26	0,20	0,25	0,18	0,29	0,30	0,29	-	0,36	0,27	0,30	0,27	0,30	0,29
G-Weissig Basin	0,36	0,26	0,19	0,27	0,26	0,26	0,19	0,22	0,26	0,23	0,28	0,29	0,28	0,36	-	0,26	0,32	0,31	0,33	0,29
CZ-CWBB	0,26	0,20	0,07	0,35	0,31	0,40	0,31	0,32	0,30	0,25	0,39	0,32	0,31	0,27	0,26	-	0,40	0,33	0,38	0,45
CZ-Krkonoše-piedmont Basin	0,31	0,34	0,15	0,38	0,35	0,40	0,29	0,33	0,36	0,27	0,35	0,37	0,36	0,30	0,32	0,40	-	0,31	0,47	0,42
CZ-ISB	0,22	0,24	0,19	0,29	0,22	0,29	0,20	0,30	0,24	0,24	0,29	0,25	0,23	0,27	0,31	0,33	0,31	-	0,29	0,35
CZ-Boskovice Basin	0,30	0,32	0,15	0,35	0,35	0,39	0,29	0,33	0,34	0,27	0,35	0,37	0,35	0,30	0,33	0,38	0,47	0,29	-	0,40
CZ-Blanice Basin	0,31	0,27	0,17	0,36	0,31	0,39	0,31	0,36	0,33	0,27	0,38	0,31	0,34	0,29	0,29	0,45	0,42	0,35	0,40	-

LEGEND:

🟥 IS values 0-0,20

🟩 IS values 0,21-0,34

IS values 0,35-0,48

Tab. 6.2. Matrix of similarity (IS) for the selected localities in the western Thetyan area.

It is important to remember when comparing assemblages for palaeoecological aspects (see Tab 6.3) the numbers of taxa for the couples of floras can vary noticeably. It is only in E-Andalucía that the number of taxa is very high, reaching 60 taxa. Several floras having about 40-25 taxa (e.g. Carnic, Saar, etc.) are present. The number of genera in the floras is often less than 25 (e.g. Türinger Waldes, I-Montarbu) or less than 15 (e.g. Asturias and Cantabrian mnt, ISB). Nevertheless, through this analysis, indications regarding the taxa distribution and the similarity at genus level for the selected assemblages studied is done. Their growing environment was obtained as well (Tab. 6.3). The cross comparison of the IS allows considering three value ranges (low-good-high) between 0 (null) and 0.48, from totally dissimilar to similar for almost half flora (48%; no higher similarity has been observed).

FLORAS	Notes on environment and typology of vegetation	REFERENCES
I-Montarbu	fluvio-lacustrine	Ronchi et al. 2008
E-Pyrenees	savannah	Broutin & Gisbert 1985
E-Asturias and Cantabrian mnt.	xerophilous–mesophilous	Wagner & Martínez-García 1982; Wagner & Álvarez-Vázquez 2010
E-Iberian Range	lacustrine, hygrophile elements	van Amerom et al. 1993; Sopeña & Sánchez Moya 1999
E-Andalucía	fluvio-lacustrine	Broutin 1986; Wagner & Mayoral 2007
P-Buçaco basin	lacustrine	Wagner & Álvarez-Vázquez 2010
F-Graissesac-Lodève	freshwater	Martín-Closas & Galtier 2005
F-Igornay	transititonal	Gand et al. (eds) 2015
F-Muse	swamp/lacustrine	Pellenard et al. 2017
F-Montceau (Massif Central)	fluvio-lacustrine?	Bercovici & Broutin 2008
I/A-Carnic	alluvial to lacustrine	Fritz & Krainer 2004
G-Saar	fluvio-lacustrine	Uhl & Jasper 2016
G-Döhlen Formation	mostly swamp	Barthel 2016
G-Türinger Waldes	alluvial to lacustrine	Eberth et al. 2000
G-Weissig Basin	xerophilous–mesophilous	Barthel 2010
CZ-CWBB	lacustrine	S. Opluštil et al. 2013
CZ-Krkonoše-piedmont Basin	fluvial to lacustrine	S. Opluštil et al. 2013
CZ-ISB	fluvial, deltaic and lacustrine	S. Opluštil et al. 2013
CZ-Boskovice Basin	lacustrine	S. Opluštil et al. 2013
CZ-Blanice Basin	fluvial, deltaic and lacustrine	S. Opluštil et al. 2013

Tab. 6.3. Notes on environment and typology of vegetation of the selected assemblages for the IS analysis.

6.4.1. Interval IS 0-0.20 (low)

In this interval, only 27 IS values are included. This datum could mean that the similarity between the floras of all the selected localities is high. However, the most diverse plant assemblage from all the other is the Asturias and Cantabrian mountains one and almost all the couples of values of this flora fall into this range. This result could be explainable for the paucity of taxa in this locality with a xerophilous–mesophilous vegetation. No genera in common have been noticed between E-Asturias and Cantabrian mountains and Graissesac-Lodève. This latter shares few taxa also with the paleogeographically close Montceau (Massif Central) and this datum could be explainable for the difference of environment between these. Montceau (Massif Central) has low values with Döhlen Formation (IS=0.14) and Andalucía (IS=0.19). Low data are noticed between localities paleogeographycally distant such as Andalucía vs Montceau (Massif Central). Here the cathaysian affinity of the Andalusian flora is the key to this difference, also considering the paleodistance between the two localities. Pyrenees and CWBB have also a low IS (0.20). Only one value between the Montarbu flora and the other localities falls in this range nonetheless the Graissesac-Lodève lies paleogeographycally close but has different paleoenvironment.

In coeval floras these strong differences are due to various factors: a) distance between floras, b) different environment, c) taphonomic biases, d) some geographical barrier between them.

6.4.2. Interval IS 0.21-0.34 (good)

In this interval 127 IS values are included and this is the most numerous one. The high quantity of values in this range shows the good similarity between floras and this reflects the general trend at a local scale for the studied interval of time. It is noticeable that almost all the comparison values of the Montarbu flora with the other selected localities fall into this interval (except three). The matrix shows a good similarity of the Sardinian assemblage with the coeval in the Paleoeurope. Montarbu has good IS values with the Czech localities because they share similar environments and the IS values become higher with the decrease of the paleo-distance (e.g.: Montceau, Pyrenees, Muse). Considering the close paleoposition of these floras, the IS should, therefore, be higher. Probably small limitation intercurred between the Montarbu flora and the others floras. For instance, some French localities were in the middle of the Variscan range while Sardinia was much to the South and this geographic barrier could justify these data. Even if Andalucía flora is considered a mixt flora with Catahysian affinity, comparison with this assemblage and the others of the area gave 14 (of 20) values in this interval, and this could be because of the abundance of record and the same palaeoecological conditions between the compared assemblages. Analysing the other IS values the floras, it is noticeable the good similarity of floras that share same ecological features nonetheless the paleo distance was big, for example, Iberian Range vs Carnic (IS=0.28), Buçaco basin vs ISB (IS=0.29), Igornay vs Krkonoše-piedmont Basin (IS=0.33), Iberian Range vs CWBB (IS=0.35). The similarity also increases when there is a drop in the paleo distance (ISB vs Blanice Basin IS=0.35).

6.4.3. Interval IS 0.35-0.48 (high)

In this interval 36 IS values are included. In this interval there are couples of palaeofloras paleogeographycally closes that belong to a variety of environments ranging from continental freshwater to coastal with a marine influence. The Czech basins floras have many IS values that fall into this interval and they are in general well similar to the others. The Spanish localities, except for Andalucía, follow the same trend of the Czech ones and many values are in this range. On the contrary, French localities have few values in this range.

The highest value of this comparison is between two closes floras Pyrenees vs Montceau (IS=0.48), two small assemblages with apparent different paleoenvironment. In fact, the Spanish assemblage is considered drier in respect of the French one, but in this case, almost half of the genera are in common. Not to exclude the presence of microenvironment in which the same plants could live.

After the analysis must be highlighted the strong similarity of the Montarbu flora with the Igornay, in France (IS=0.41). This value mirrors close paleogeographical condition that facilitates the presence of a similar set of vegetation. Another IS value of Montarbu falls into this interval, with the less close Weissig Basin (IS=0.36). It is assumable that during these times there were not strong geographical barriers between the two floras and the palaeoenvironmental conditions were similar.

6.5. Biostratigraphic notes of Montarbu

As stated in some eastern localities of the Czech basins (Boskovice basin, C/P) and in Thuringia (basal Rotliegend≡C/P) the great diversification of callipterids and conifers is also reflected in the Montarbu flora. In the Montarbu basin, both the dominant and the rarer taxa are biostratigraphically informative. The occurrence of *Autunia conferta* and its relative good abundance lets to consider the possibility to include the Montarbu strata bearing macroflora in the *Autunia conferta* zone (*sensu* Opluštil et al. 2016). According to Opluštil et al. (2016). the basis of this zone is located in the late Ghzelian stage. Also, the species *Neurocallipteris planchardii* and *Pecopteris candolleana* are included in this zone. The occurrence *Callipteridium pteridium* could indicate a late Gzhelian age as well (Doubinger & Germer 1972; Cleal et al. 2015) or according to Pellenard et al. (2017) also the lower Asselian. In the Autun basin (France), the first occurrence of *Autunia naumannii* is placed at the end of the Ghzelian (Pellenard et al. 2017). *Acitheca polymorpha* is rather typical in the Pennsylvanian but becomes rare in the Asselian. In the Montarbu assemblage is one of the most abundant ferns. *Remia pinnatifida* is rather common in Europe in Early Permian of Spain and its range has been extended to the Carboniferous. In summing up the Montarbu assemblage reflects a C/P flora and probably a late Ghzelian age for this assemblage is assumed. The presence of typical taxa of “Stephanian affinity” and the abundance of *Achiteca*, peltasperms and conifers justify this attribution.

6.6. Other plants from Montarbu and Seui: brief notes

Sardinian vegetal macro-remains were studied in the past mainly to support stratigraphy and sedimentology. Most of this works do not include pictures or descriptions of the species. Sometimes the lists of taxa need to be updated because the knowledge was weak. Detailed systematic papers dealing with these fossils miss. In this small paragraph, I discuss briefly the closes records, even if the specimens included in the old papers are not available for detailed studies. Close to Montarbu, some other localities have been studied and fossils come from the same Seui-Seulo Basin. In San Sebastiano locality (Comaschi Caria 1959) taxa are indicatives of the more humid environment but meso-xerofilous species were present as well. Here the sphenophytes and ferns were present with many species (see Tab. 2.3) while conifers were rare with only *Lebachia* (*Walchia*) *piniformis* reported. According to these few data, the age of these fossils could be from slightly older to coeval to Mortarbu. Spano (1976) studied some fossils of this area attributing a general "Autunian" age to the outcrops. On the other hand, the macroflora collected and figured by Broutin et al. in Cassinis et al. 1999 (p. 90) and listed in Cassinis et al. 2003 should indicate an older Stephanian-like assemblage. In fact, according to the mere composition distinguishable from the published pictures (unfortunately specimens are not available), these plant remains are indicatives of oldest age in respect of the newly collected material of Montarbu and this material should come from the basal part of the same lithozone.

6.7. The Moscovian flora of San Giorgio

The systematic description of the species is included in the peer-reviewed paper by Cleal et al. (2017; see Appendix 1 for details). In this paragraph, a discussion concerning the composition of the flora and its palaeoecological features will only be done. For details see Appendix 1.

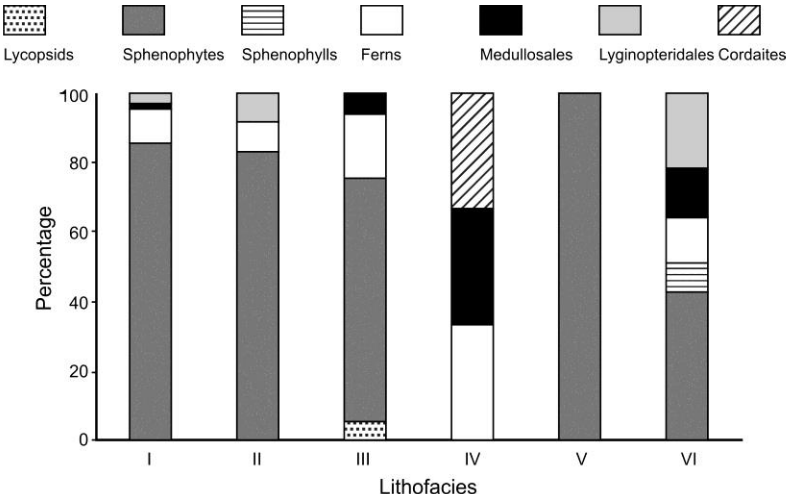

Fig. 6.4. Distribution of the major plant groups in the six recognized lithologies (after Cleal et al. 2017).

As explained in Chapter 4, six lithofacies were recognised among the studied material. The interpretation of these deposits is as the last phases of the lacustrine fill, as the basin became better drained. Data are also explored using the Shannon t-test (see Appendix 1 for details) and all of the results confirm the essential homogeneity of the fossil floras found in lithologies I, III and III, both regarding overall representation of plant groups and of fossil-species. They are dominated by the sphenophyte species *Annularia sardiniana* with minor contributions (usually < 20 %) of ferns, medullosaleans and lyginopteridaleans. These facies were all sampling the dominant vegetation in the basin, which consisted largely of sphenophytes that produced the *Annularia sardiniana* foliage. It is generally acknowledged that this group of plants usually favoured muddy substrates on the margins of areas of standing water or possibly fluvial channels (Gastaldo 1992; Bashforth et al. 2011; Thomas 2014). Except for *Renaultia* and *Eusphenopteris,* nearly all of the other fossil-species in lithologies I, II and III were represented by isolated and usually poorly preserved fragments. It is possible that these are the remains of plants that were rare in the vegetation growing here. However, since the small fragments are generally poorly preserved compared with the sphenophyte remains, we suggest they were probably allochthonous remains of vegetation that had drifted into the basin from surrounding areas. Lithology V compares lithologically with Lithology I except in colour and the tendency to develop a conchoidal fracture. Although also probably lacustrine, the presence of a different species of calamostachyalean sphenophyte suggests that the adjacent shore had different substrate conditions. The channel sandstone (Lithology IV) contained very few plant remains, other than a single piece of cordaitanthalean pith cast and a pteridosperm fragment. In contrast, Lithology VI yielded a high diversity of plant remains, including a significantly higher proportion of ferns, medullosaleans and lyginopteridaleans, as well as rare sphenophylls not seen in the other facies. Lithology VI is located at the top of the fossiliferous part of the basin fill, and it seems likely that the plant remains represent vegetation that occupied the basin as it started to fill in with sediment and the water table fell. Some of the species that occur in this facies also occur as rare drifted fragments in lithologies I, II and III. The palaeoecological picture of the San Giorgio Basin in southwestern Sardinia shows a domination of parautochthonous sphenophyte remains representing the vegetation growing around the margins of a freshwater lake. However, there are also allochthonous remains of a more diverse fern-pteridosperm dominated vegetation, broadly similar in both species composition and relative representation of major plant groups to late Asturian (late

Moscovian) wetland vegetation preserved north of the Variscan Mountains (e.g. South Wales). The basin was relatively short-lived and after a time started to drain so that the sphenophyte vegetation became replaced by the fern-pteridosperm dominated the vegetation. Furthermore, thanks to this study (see Appendix 1 for details) a late Asturian age for the San Giorgio Basin suggests that the extensional tectonics responsible for its formation were related to the Leonian Phase of Variscan tectonics, whose effects can be seen across Europe. The basin should, therefore, be regarded as late Variscan rather than post-Variscan.

6.7.1. The change across the Pennsylvanian

During Carboniferous, the landscape was dominated by spore-producing plants and early-gymnospermous seed-plants (DiMichele et al. 2001a). The climate became step by step more dryer passing in Permian times with a consequent change of the vegetational pattern. According to many studies, it is noticed the similarity of climate in Late Carboniferous and Early Permian (Gastaldo et al. 1996; DiMichele et al. 2001a; Greb et al. 2006). So that, it is noticeable a similarity also in the floral/vegetation composition (DiMichele & Aronson 1992). In these times, three broad paleogeographic realms divided the emerged and not-emerged lands: the Euramerican, Angaran, and Gondwanan Province (Chaloner & Lacey 1973; Meyen 1982; Archangelsky 1990; Wagner 1993; Gastaldo et al. 1996). Every province had distinct floras with biomes that reflected climatic and edaphic local or regional differences. The end of the Carboniferous was the period in which arborescent lycophytes became extinct in Europe and North America and replaced by arborescent tree ferns (e.g. *Psaronius*; Gradstein & Kerp 2012) while the former persisted in northern China (e.g. Wang & Chen 2001). The arborescent sphenophytes also started to decline at the end of the Carboniferous while new groups of seed plants arose, becoming important biostratigraphic markers during the Permian (e.g. peltasmermales, glossopterids, conifers). Thus, the dynamic of vegetation history can be interpreted regarding a series of turnovers (Cleal & Cascales-Miñana 2014). In fact, the upcoming Cisuralian carried on the increasing of aridification in the palaeoequatorial zones, going to the detriment of the deglaciation of the southern Hemisphere pole. These results are reflected in a progressive change from sub-humid to semi-arid and arid climates reaching the late Cisuralian (Tabor & Poulsen 2008; Michel et al. 2015) with a consequent modification of the vegetation (Schneider et al. 2006; Montañez et al. 2007; Tabor & Poulsen 2008; Michel et al. 2015; Gulbranson et al. 2015). This setting is also reflected in Italian Kungurian localities such as Tregiovo with abundant conifers constituting the flora (NW Italy, Forte et al. 2017). Especially in the Euramerican context, the transition from Palaeophytic to Mesophytic vegetation reflects a general global change of climate (Gastaldo et al. 1996; Di Michele et al. 2006) or tectonically induced modification of landscapes (Cleal & Thomas 1999, 2005; Cleal et al. 2010, 2011). The diminution of fern traces in Permian sediments and the increase of seed plants probably justify an increase of global warming and aridification of the planet Earth (e.g. DiMichele et al. 2001b, 2004, 2006; Chaney & Di Michele 2007 Chaney et al. 2009). This general picture in a global context is more complex (Rees 2002): for example, in China, there was the persistence of tropical wetlands habitats in the Permian that had disappeared in Euramerica (Hilton & Cleal 2007; Wang et al. 2012).

In palaeoequatorial position, this change is given by a stepwise substitution from pteridophyte-dominated lowland floras to drought-tolerant seed plants (DiMichele et al. 2006). Data from the literature show that the change is well reflected in Sardinia analysing the palynological spectra. With the aim to improve and reinforce this concept, the systematic study carried out on the palaeoflora of the San Giorgio Basin (southern Sardinia) confirm the previous statement based on the palynological record. In fact, the dominant sphenophytes-based flora of San Giorgio (data from the literature show another small coeval outcrop which yielded a rich palynoflora in the Tuppa Niedda locality; see Appendix 1 for details) was step by step replaced by mesophytic and xerophytic elements remarking this climate change. According to Pittau et al. 2008, three palynological phases at regional scale have been distinguished for the Lower Permian (Fig. 6.5). Each of these represents an evolutionary stage of the Sardinian post–collisional Variscan tectonic, each of which having its ecological significance: the *Florinites* phase (Stephanian–Autunian interval), the *Potonieisporites* phase (lower Asselian interval) and the *Vittatina*-Striatiti phase (Asselian-Sakmarian interval). Pollen analysis of the Seui-Seulo Basin have been carried out in San Sebastiano (Seui) and Genn’e Acca (close to Montarbu) sections yielded a rich microflora (Pittau et al. 2008). Monosaccate pollen grains include *Potonieisporites novicus, P. grandis, P.*

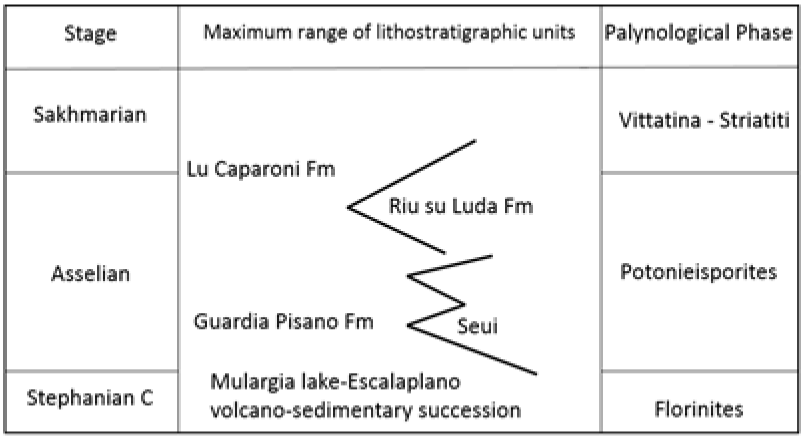

Fig. 6.5. Correlation hypothesis for lithostratigrapic units and palynological phases in the Carboniferous-Permian of Sardinia. (after Pittau et al. 2008, modified).

bharadwaji, *Florinites pellucidus*, *F. florinii*, *F. similis*, *Plicatipollenites malabarensis*, *Mosulipollenites* sp. Taeniatae disaccate pollen grains include *Hamiapollenites* sp., *Striatohaploxypinus* sp., *Costaepollenites ellipticus*, *Complexisporites polymorphus*. Polyplicatepollen grains such as *Vittatina* sp. are not frequent and the spore content is subordinate (*Apiculatisporis*, *Raistrickia*, *Verrucosisporites*, *Convolutispora*). According to Pittau et al. (2008), the association found in the San Sebastiano (Seui) and Genn'e Acca (Montarbu) sites is referred to the *Potonieisporites phase* and would indicate an early Asselian age for the studied layers. In this phase, differently from the others recognised at a regional scale (see Pittau et al. 2008 for details), the coniferous community and the total assemblages were dominated by *Potonieisporites* produced by Voltziales or Walchian conifers. The age attributed with palynomorphs appear slightly young compared to the macrofloral results of this study, and this could be explained because the samples come from the top of the Permo-Carboniferous succession. In the Montarbu basin, indeed, both Carboniferous and Permian strata could be present.

7. Conclusions

The study of the three assemblages coming from central-East (Montarbu), East (Perdasdefogu) and South-West (San Giorgio) Sardinia allows exposing different conclusions.

- The flora of Montarbu (Seui-Seulo basin) is a well-preserved flora of the C/P transition with 24 taxa belonging to 18 genera. The conifers and cordaitanthaleans are dominant. The pteridosperms are common, while ferns and rare sphenophytes are also present. Pteridosperms are among others the most diversified (8 taxa), followed by conifers (7), ferns (4), cordaitanthaleans (2) and sphenophytes (1).
- The Montarbu assemblage reflects a C/P flora and probably a late Ghzelian age is assumed. The presence of typical taxa of "Stephanian affinity" and the abundance of *Acitheca*, peltasperms and conifers justify this attribution. In the assemblage is also present the taxa *Autunia naumanni* and *Callipteridium pteridium* considered exclusive for the Ghzelian but extended also to the first part of the Asselian thanks to recent studies. Since *Autunia conferta* is considered one of the key species for the attribution to the Autunian (recently dated late Gzhelian/early Asselian), it should be necessary to consider this change also in the others Sardinian outcrops that, probably, could be slightly olders.
- The quantitative analysis of the two different lithofacies recognised shows few differencies in the composition. This should reflect very slight habitat

differences but may be much more related to taphonomic selection and preservation biases than to differences in the general composition of the flora.

- The analysis of the macro remains shows that these plants are mostly fragmented and in a different level of decomposition, especially conifers and pteridosperms. This fact suggests a transport of these plants at a different distance before deposition.
- The hypothetical reconstruction of the Montarbu vegetation shows a prevalence of dryland elements (conifers, cordaitanthaleans and peltasperms) and some wetland elements (sphenopsid, ferns, some pteridosperms). It can be summarised as a) a forest mainly composed of walchian-type conifers (*Ernestiodendron*) probably covered the surrounding reliefs or slopes; b) the piedmont zone occupied by cordaitanthaleans and mixoneurid pteridosperms, in which the soil was slightly humid; c) ferns and other plants needing more water were present in the surrounding areas.
- After the IS comparison between the Montarbu flora with those palaeogeographical close, it must be highlighted the strong similarity of the former with that of Igornay, in France. This value mirrors close paleogeographical condition that facilitates the presence of a similar set of vegetation. The similarity is also high with the less close Weissig Basin (Germany). It is assumable that during these times there were no (or weak) geographical barriers between the two floras. The similarity is also high with the floras of the Czech basins. Moreover, the comparison between the Montarbu flora with the others paleogeographical closes (France, Spain) gave

good IS values and probably limitation intercurred between them. For example, the French floras were in the middle of the Variscan range while Sardinia was located more to the South.

- The systematic study of the Moscovian flora of San Giorgio lets to highlight that the composition of this older flora is different from the younger Montarbu assemblage. The palaeoecological picture of the San Giorgio Basin in southwestern Sardinia shows a domination of parautochthonous sphenophyte remains that represents the vegetation growing around the margins of a freshwater lake. However, there are also allochthonous remains of a more diverse fern-pteridosperm dominated vegetation, broadly similar in both species composition and relative representation of major plant groups to late Moscovian wetland vegetation.
- The study of the San Giorgio (Moscovian) and Montarbu (late Ghzelian) floras confirms the change of vegetation across the late Palaeozoic. In fact, the dominant sphenophytes-based flora of San Giorgio was replaced by mesophytic and xerophytic elements remarking the climate change, as also saw in the various localities of the same palaeolatitude. A gradual transition between the two floras in Sardinia is, therefore, evidenced by the palynological spectra.
- The attempt to find fossil plant remains in silicified rocks of the Perdasdefogu basin (eastern Sardinia) was unsuccessful.

References

AA.VV. 1897. Extract to: Resoconti delle riunioni dell'Associazione mineraria Sarda, 2(2): 5–8.

AA.VV. 1902a. II. Resoconti delle riunioni dell'Associazione mineraria Sarda, 7(2): 3.

AA.VV. 1902b. Allegato B. Resoconti delle riunioni dell'Associazione mineraria Sarda, 7(2): 8.

AA.VV. 1916. Seconda Adunanza Ordinaria tenuta in Roma il 20 dicembre 1916. Bollettino della Società Geologica Italiana, 35(3): 78–88.

AA.VV. 1932. Extract to: Resoconti delle riunioni dell'Associazione mineraria Sarda, 37(2): 9–10.

Abbott M.L. 1958. The American species of Asterophyllites, Annularia and Sphenophyllum. Bulletin of American Paleontology, 38: 289–390.

Accardo P., Marini C. & Sarria E. 1984. I giacimenti antracitiferi sardi. L'industria mineraria, 1: 23–29.

Agardh C.H. 1825. Aphorismi botanici. Classes plantarum, pars 1. Berling, Lund.

Amerom H.W.J. van, Broutin J., Ferrer J., Gámez-Vintaned J.A., Gisbert J. & Liñán E. 1993. Les flores du Permien basal et la paléoichnologie de la fosse de Fombuena (province de Zaragoza, Espagne). Mededelingen Rijks Geologische Dienst, 48: 1–63.

Andreanszky G. 1954. Ősnövénytan. Akadémia Kiado, Budapest.

Angiolini L., Gaetani M., Muttoni G. Stephenson M.H. & Zanchi A. 2007. Tethyan oceanic currents and climate gradients 300 m.y. ago. Geology, 35: 1071–1074.

Arcangeli G. 1901. Contribuzione allo studio dei vegetali permo-carboniferi della Sardegna. Paleontographia Italica, 7: 91–120.

Archangelsky S. 1990. Plant distribution in Gondwana during the Late Paleozoic. In Antarctic paleobiology, Springer, New York, NY: 102–117.

Arche A. & López-Gómez J. (2006). Late Permian to Early Triassic transition in central and NE Spain: biotic and sedimentary characteristics. Geological Society, London, Special Publications, 265(1): 261–280.

Arthaud F. & Matte P. 1966. Contribution à l'étude de tectoniques superposées dans la chaine hercynienne: étude microtectonique des séries metamorphiques du Massif des Maures (Var.). Comptes Rendus de l'Académie des Sciences de Paris, 262: 436–439.

Arthaud F. & Matte P.H. 1977. Late Palaeozoic strike-slip faulting in Southern Europe and Northern Africa: results of a right-lateral shear zone between the Appalachians and Urals. Bulletin of the Geological Society of America, 88: 1305–1320.

Barbacka M., Bodor E., Jarzynka A., Kustatscher E., Pacyna G., Popa M.E., Scanu G.G., Thévenard F. & Ziaja J. (2014). European Jurassic floras: Statistics and palaeoenvironmental proxies. Acta Palaeobotanica, 54: 173–195.

Barca S. & Costamagna L.G. 2003. The Upper Carboniferous S. Giorgio succession (Iglesiente, SW Sardinia): stratigraphy, depositional setting and evolution of a late to post-Variscan molassic basin. Bolletino della Società Geologica Italiana, Special Volume, 2: 89–98.

Barca S. & Costamagna L.G. 2006. Stratigrafia, analisi di facies ed architettura deposizionale della successione permiana di Guardia Pisano (Sulcis, Sardegna SW). Bollettino della Società Geologica Italiana, 125: 3–19.

Barca S. 2009. The Silurian of Sardinia (Italy): more than one and half century of researches.

In Corradini C., Ferretti A. & Storch P. (eds). Rendiconti della Società Paleontologica Italiana, 3 (1): 11–22.

Barca S., Carannante G., Cassinis G., Cherchi A., Corrandini C., Cortesogno L., Del Rio M., Durand M., Ferretti A., Fontana D., Funedda A., Gaggero L., Garau A.M., Leone M., Macciotta G., Marchi M., Matteucci R., Murru M., Neri C. Loi A., Pillola G.L., Pittau P., Ronchi A., Salvadori I., Sarria E., Schroeder R., Serpagli E., Simone L. & Stefani C. (eds). 2004. Sardinian Palaeozoic basement and its Meso-Cainozoic covers (Italy). 32nd International Geological Congress, Field Guide Book, P39.

Barca S., Cocozza T., Del Rio M., Pillola G.L. & Pittau Demelia P. 1987. Datation de l'Ordovicien inférieur par Dictyonema flabelliforme et Acritarches dans la partie supérieure de la formation "Cambrienne" de Cabitza (SW de la Sardaigne, Italie): conséquences géodynamiques. Comptes Rendus de l'Académie de Sciences de Paris, 305 (2): 1109–1113.

Barca S., Corradini C. & Spalletta C. 2000. Nuovi dati sui "Calcari a Clymenie" della Sardegna. In Cherchi A. & Corradini C. (eds). Crisi biologiche, radiazioni adattative e dinamica delle piattaforme carbonatiche. Accademia Nazionale di Scienze, Lettere e Arti di Modena, Collana di Studi, 21: 25–28.

Barthel M. & Brauner S. 2015. Die Rotfliegendflora des Thüringer Waldes Supplementum. Semana, 30: 3–37.

Barthel M. & Rossler R. 1996. Palaeontologische Fundschichten in Rotliegend von Manebach (Thuringer Wald) mit Calamites gigas (Sphenophyta). Veroffentlichungen Naturhistorische Museum Schleusingen, 11: 3–21.

Barthel M. 2004. Paläobotanische Aspekte des Döhlen-Beckens. (Veränderte Fassung eines Vortrages). Veröff. Museum für Naturkunde Chemnitz, 27: 17–28.

Barthel M. 2009. Die Rotfliegendflora des Thüringer Waldes. Naturhistorisches Museum Schloss Bertholdsburg.

Barthel M. 2016. Die Rotliegendflora der Döhlen-Formation. Geologica Saxonica, 61: 105–238.

Barthel M. Eichler B. & Reichel W. 2010. The Lower Permian (Rotliegend) flora of the Weissig Basin. Geologica Saxonica, 56: 159–192.

Barthel M., Mütze M. & Simon R. 1975. Neue Funde fossiler Pflanzen ausdem Saale-Trog. Wissenschaftliche Zeitschrift der Humboldt-Universität, Mathematisch-Naturwissenschaftliche 24, 475–483.

Bashforth A.R., Drábková J., Opluštil S., Gibling M.R. & Falcon-Lang H.J. 2011. Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nýřany Member, Central and Western Bohemian Basin, Czech Republic). Review of Palaeobotany and Palynology, 163(3): 153–189.

Baucon A., Ronchi A., Felletti F. & Neto de Carvalho C. 2014. Evolution of Crustaceans at the edge of the end-Permian crisis: ichnonetwork analysis of the fluvial succession of Nurra (Permian-Triassic, Sardinia, Italy). Palaeogeography Palaeoclimatology Palaeoecology, 410, 74–103.

Benedetti E., Dessì R., Muntoni F. & Pillola G.L. 2002. Il Bacino Carbonifero di San Giorgio (Iglesias-Sardegna Sud- Occidentale). Proposta di Tutela e Valorizzazione In Convegno Nazionale, Genova, 27–29 Giugno 2002 "La Geologia Ambientale: strategie per il nuovo millennio", Sigea e Lab. Geomorfologia Applicata, Dip. Polis, Univ. Genova.

Bercovici A. & Broutin J. 2008. La flore autunienne du site de l'étang de Martenet (Blanzy–Montceau-les-Mines, Bourgogne, France): description, étude taphonomique et implications paléoenvironnementales. Comptes Rendus Palevol, 7(1): 1–16.

Bertrand P. 1928. L'échelle stratigraphique du terrain houiller de la Sarre et de la Lorraine Ier Congr. Stratigraph. Carbonifère, Heerlen: 83–90.

Boersma N. & Fritz A. Makropaläobotanische Ergebnisse zur Stratigraphie jungpaläozoischer Ablagerungen in den Karnischen Alpen, Österreich. Carinthia II, 176: 19–37.

Boy J.A., Haneke J., Kowalczyk G., Lorenz V. Schindler T. & Thum H. 2012. Rotliegend im Saar-Nahe-Becken, am Taunus-Südrand und im nördlichen Oberrheingraben. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, 61: 254–377.

Brongniart A. 1822. Sur la classification et la distribution des végétaux fossiles en général, et sur ceux des terrains de sediment supérieur en particulier. Mémoires du Museum d'Histoire Naturelle, Paris.

Brongniart A. 1828. Prodrome d'une Histoire des végétaux fossiles. F.G. Levrault, Paris & Strasbourg.

Brongniart A. 1828–37. Histoire des végétaux fossiles 1(8–9), 289–336. G. Dufour & E. d'Ocagne, Paris.

Brongniart A. 1849. Tableau des genres végétaux fossiles considérés sous le point de vue de leur classification botanique et géologique. In D'Orbigny C. (ed). Dictionnaire Universel d'Histoire Naturelle, 13: 52–176.

Brongniart A.T. 1881. Recherches sur les Graines Fossiles Silicifieés. Masson, Paris.

Broutin J. & Gisbert J. 1985. Entorno paleoclimático y ambiental de la flora stephano-autuniense del Pirineo catalán. In. Dixième Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid 1983, 3: 53–66.

Broutin J. 1974. Sur quelques plantes fossiles du bassin Autuno-stéphanien de Guadalcanal (province de Seville, Espagne). Lagascalia, 4(2): 221–237.

Broutin J. 1986. Étude paléobotanique et palynologique du passage Carbonifère Permien dans le sud-ouest de la Péninsule Ibérique. Cahiers de Paléontologie, Éditions du CNRS, France.

Broutin J., Cassinis G., Cortesogno L., Gaggero L., Ronchi A. & Sarria E. 1996. Research in progress on the Permian deposits of Sardinia (Italy). Permophiles, 28: 45–48.

Broutin J., Châteauneuf J.J., Galtier J. & Ronchi A. 1999. L'Autunien d'Autun reste-t-il une référence pour les dépôts continentaux du Permien inférieur d'Europe? Apport des données paléobotaniques. Géologie de la France, 2: 17–31.

Bruguier O., Becq-Giraudon J.-F., Champenois M., Deloule E., Ludden J. & Mangin D. 2003. Application of in situ zircon geochronology and accessory phase chemistry toconstraining basin development during post-collisional extension: a case study from the French Massif Central. Chem. Geol., 201: 319–336.

Burnett G.T. 1835. Outlines of Botany, including a general history of the Vegetable Kingdom, in which plants are arranged according to the system of natural affinities H. Renshaw, London.

Calvino F. 1959. Lineamenti strutturali del Sarrabus-Gerrei (Sardegna sud-orientale). Bollettino del Servizio Geologico d'Italia, 81 (4–5): 489–556.

Capacci C. 1896. Studio sulle miniere di Monteponi, Montevecchio e Malfidano in Sardegna. Bollettino della Societò Geologica Italiana, 15: 1–205.

Cappelli B., Carmignani L., Castorina F., Di Pisa A., Oggiano G. & Petrini R. 1992. A Hercynian suture zone in Sardinia: geological and geochemical evidence. Geodinamica Acta, 5: 101–118.

Carmignani L. & Pertusati P.C. 1977. Analisi strutturale di un segmento della catena ercinica: il Gerrei (Sardegna sud-orientale). Bollettino della Società Geologica Italiana, 96: 339–364.

Carmignani L., Coltorti M., Corradini C., Cruciani G., Franceschelli M., Loi A. & Pillola G.L. 2015. Foglio 555 Iglesias. Carta Geologica 1:50.000 dell'Istituto Geografico Militare. Roma.

Carmignani L., Cortecci G., Dessau G., Duchi G., Oggiano G., Pertusati P. & Saitta M. 1978. The antimony and tungsten deposit of Villasalto in south-eastern Sardinia and its relationship with Hercynian tectonics.

Schweizerische Mineralogische und Petrographische Mitteilungen, 58: 163–188.

Carmignani L., Oggiano G., Barca S., Conti P., Salvadori I., Eltrudis A., Funedda A. & Pasci S. 2001. Geologia della Sardegna. Note illustrative della Carta Geologica della Sardegna a scala 1:200.000. Istituto Poligrafico e Zecca dello Stato, Roma. 283 pp.

Carmignani L., Oggiano G., Funedda A., Conti P., Pasci S. & Barca S. 2008. Carta geologica della Sardegna (Geological map of Sardinia), scale 1: 250000. Litografia Artistica Cartografica, Firenze.

Carmignani L., Pertusati P.C., Barca S., Carosi R., Di Pisa A., Gattiglio M., Musumeci G. & Oggiano G. 1992. Struttura della Catena Ercinica in Sardegna. Gruppo Informale di Geologia Strutturale, Escursione in Sardegna, 24-29 Maggio 1992, Siena.

Casini L., Funedda A. & Oggiano G. 2010. A balanced foreland–hinterland deformation model for the Southern Variscan belt of Sardinia, Italy. Geological Journal, 45(5–6): 634–649.

Cassinis G. & Ronchi A. 1997. Upper Carboniferous to Lower Permian continental deposits in Sardinia (Italy). Geodiversitas, 19(2): 17–20.

Cassinis G. & Ronchi A. 2002. The (late-) Post-Variscan continental succession of Sardinia. Rendiconti della Società Paleontologica Italiana, 1: 77–92.

Cassinis G., Cortesogno L., Gaggero L., Pittau P., Ronchi A. & Sarria E. (eds). 1999. Late Palaeozoic Continental Basins of Sardinia. The Continental Permian - International Congress - Brescia 15–25 September 1999. Earth Science Department, Pavia University.

Cassinis G., Cortesogno L., Gaggero L., Ronchi A., Sarria E., Serri R. & Calzia P. 2003. Reconstruction of igneous, tectonic and sedimentary events in the latest Carboniferous-Early Permian Seui Basin (Sardinia, Italy), and evolutionary model. Bollettino della Società Geologica Italiana, Volume speciale 2: 99–117.

Cassinis G., Perotti C. & Ronchi A. 2007. The "Autunian": its Stratigraphic and Tectonic Significance in Italian Geology. In Early Permian continental environments-International Symposium-Autun (Burgundy, France) 2-4 July 2007: 13–15.

Castro Martínez M.P. 2005. La flora estefaniense B de La Magdalena (León, España): un referente europeo. Antecedentes y analísis florístico. Instituto Geológico y Minero de España.

Cecil C.B. 2003. The Concept of Autocyclic and Allocyclic Controls on Sedimentation and Stratigraphy, Emphasizing the Climatic Variable. SEPM Special Publication, 77: 13–20.

Chaloner W.G. & Lacey W.S. 1973. The distribution of Late Palaeozoic floras. In Organisms and continents through time. (ed. N. F. Hughes), Special Papers in Palaeontontology, 12: 271–789.

Chaney D.S. & Di Michele W.A. 2007. Paleobotany of the classic redbeds (Clear Fork Group-Early Permian) of north-central Texas. In T.E. Wong (ed), Proceedings of the XV International Congress on Carboniferous and Permian Stratigraphy. Utrecht, the Netherlands, August 10–16, 2003. Royal Netherlands Academy of Arts and Sciences Edita-KNAW Amsterdam, the Netherlands: 357–366.

Chaney D.S., Mamay S.H., Di Michele W.A. & Kerp H. 2009. Auritifolia gen. nov., probable seed plant foliage with comioid affinities from the Early Permian of Texas, USA. International Journal of Plant Sciences, 170(2): 247–266.

Charbonnier S., Vannier J., Galtier J., Perrier V., Chabard D. & Sotty D. 2008. Diversity and paleoenvironment of the flora from the nodules of the Montceau-les-Mines biota (Late Carboniferous, France). Palaios, 23(4): 210–222.

Châteauneuf J.J., Farjanel G., Pacaud G., Broutin J. 1992. The Autun Permian Basin, the Autunian stratotype. In: Permian basins in the French Massif Central. 8th International Palynological Congress, Aix-en-Provence, Excursion E: Cahiers de Micropaléontologie, 7 (1/2): 123–139.

Cleal C.J. & Cascales-Miñana B. 2014. Composition and dynamics of the great Phanerozoic Evolutionary Floras. Lethaia, 47: 469–484.

Cleal C.J. & Shute C.H. 1995. A synopsis of neuropteroid foliage from the Carboniferous and Lower Permian of Europe. Bulletin of the Natural History Museum, 51: 1–52.

Cleal C.J. & Shute C.H. 2003. Systematics of the Late Carboniferous medullosalean pteridosperm Laveinopteris and its associated Cyclopteris leaves. Palaeontology 46: 353–411.

Cleal C.J. & Thomas B.A. 1999. Tectonics, tropical forest destruction and global warming in the Late Palaeozoic. Acta Palaeobotanica, Supplement 2: 17–19.

Cleal C.J. & Thomas B.A. 2005. Palaeozoic tropical rainforests and their effect on global climates: is the past the key to the present? Geobiology, 3: 13–31.

Cleal C.J. & Thomas B.A. 2010a. Botanical nomenclature and plant fossils. Taxon, 59(1): 261–268.

Cleal C.J. & Thomas B.A. 2010b. (101–103) Proposals to modify the provisions in the Code for naming plant fossils. Taxon, 59(1), 312–313.

Cleal C.J. (ed). 1991. Plant fossils in geological investigation: the Palaeozoic. Ellis Horwood, Chichester. pp. 233.

Cleal C.J. 1984. The Westphalian D floral biostratigraphy of Saarland (Fed. Rep. Germany) and a comparison with that of South Wales. Geological Journal, 19: 327–351.

Cleal C.J. 2015. The generic taxonomy of Pennsylvanian age marattialean fern frond adpressions. Palaeontographica Abteilung B, 1–21.

Cleal C.J., Oplustil S., Thomas B.A. & Tenchov Y. 2010. Late Moscovian terrestrial biotas and palaeoenvironments of Variscan Euramerica. Netherlands Journal of Geosciences, 88: 181–278.

Cleal C.J., Oplustil S., Thomas B.A. & Tenchov Y. 2011. Pennsylvanian vegetation and climate in tropical Variscan Euramerica. Episodes, 34: 3–12.

Cleal C.J., Scanu G.G., Buosi C., Pittau P. & Kustatscher E. 2017. Middle Pennsylvanian vegetation of the San Giorgio Basin, southern Sardinia (Italy). Geological Magazine, 154: 1155–1170.

Cleal C.J., Shute C.H. & Zodrow E.L. 1990. A revised taxonomy for Palaeozoic neuropterid foliage. Taxon, 39: 486–492.

Cleal C.J., Tenchov Y.G., Sremac J., Đerek T. & Japundžić. J. 2015. Pennsylvanian fossil flora from the Velebit Mountains and Lika region (SW Croatia). Bulletin of Geosciences 90: 721–742.

Clement-Westerhof J.A. 1984. Aspects of Permian palaeobotany and palynology. IV. The conifer Ortiseia Florin from the Val Gardena Formation of the Dolomites and the Vicentinian Alps (Italy) with special reference to a revised concept of the Walchiaceae (Goeppert) Schimper. Review of Palaeobotany and Palynology, 41: 51–166.

Cocco F. & Funedda A. 2017. The Sardic Phase: field evidence of Ordovician tectonics in SE Sardinia, Italy. Geological Magazine: in press.

Cocozza T. 1965. Contributo alla stratigrafia del Paleozoico sardo: nuove ricerche sull'affioramento permiano di San Giorgio (Iglesias) Nota preliminare. Prestampe per il Symposium "Problemi Minerari della Sardegna"., Associazione Mineraria Sarda - Cagliari-Iglesias: 3–4.

Cocozza T. 1967. Il Permo-carbonifero del bacino di San Giorgio (Iglesiente, Sardegna sud-occidentale). Memorie della Società Geologica Italiana, 6: 607–642.

Cohen K.M., Finney S.C., Gibbard P.L. & Fan J.-X. (2013; updated). The ICS International Chronostratigraphic Chart. Episodes 36: 199–204.

Comaschi Caria I. 1959. Le piante fossili della Sardegna. Memorie VII. Rivista Italiana di Paleontologia e Stratigrafia, 7: 1–176.

Comaschi Caria I. 1979. Storia e vicende del Museo geo-paleontologico Domenico Lovisato dell'Università di Cagliari. Litotiporafia Il Torchio, Cagliari.

Corradini C. 2008. Revision of Famennian-Tournaisian (Late Devonian-Early Carboniferous) conodont biostratigraphy of Sardinia, Italy. Revue de micropaléontologie, 51: 123–132.

Correia P., Loureiro J.P. & de Jesus A.P. 2010. Ocorrência de novos elementos megaflorísticos na Bacia Carbonífera do Douro (Estefaniano C inferior) [Gzheliano inferior], NW de Portugal. Proceedings of theVIII Congresso Nacional de Geologia. Revista Electrónica de Ciências da Terra - Geosciences On-line Journal, 17(10): 1–4.

Corsin P. 1951. Bassin houiller de la Sarre et de la Lorraine: Flore fossile. Les Petits-fils de L. Danel.

Corsin P. 1960. Classification des Ptéridophytes et des Ptéridospermophytes du Carbonifère. Bulletin de la Société Géologique de France, Série 7, 2: 566–572.

Cortesogno L., Cassinis G., Dallagiovanna G., Gaggero L., Oggiano G., Ronchi A. Senob A. & Vanossi M. 1998. The Variscan post-collisional volcanism in late Carboniferous–Permian sequences of Ligurian Alps, southern Alps and Sardinia (Italy): A synthesis. Lithos, 45(1), 305–328.

Costamagna L.G. 2016. The Middle Jurassic Alpine Tethyan Unconformity and the Eastern Sardinia – Corsica Jurassic High: A sedimentary and regional analysis. Journal of Iberian Geology, 42(3): 311–334.

Costamagna L.G., Barca S. & Lecca L. 2007. The Bajocian–Kimmeridgian Jurassic sedimentary cycle of eastern Sardinia: Stratigraphic, depositional and sequence interpretation of the new ‘Baunei Group’. Comptes Rendus Geoscience, 339(9): 601–612.

Costamagna L.G., Kustatscher E., Scanu G.G., Del Rio M., Pittau P. & van Konijnenburg-van Cittert J.H.A. 2018. A palaeoenvironmental reconstruction of the Middle Jurassic of Sardinia (Italy) based on integrated palaeobotanical, palynological and lithofacies data assessment. Palaeobiodiversity and Palaeoenvironments, 98(1): 111–138.

Crookall R. 1969. Fossil plants of the Carboniferous rocks of Great Britain [Second Section]. Part 5. Memoirs of the Geological Survey of Great Britain, Palaeontology, 4: 573–792.

Davydov V.I., Korn D. & Schmitz M.D. 2012. The Carboniferous Period. In Gradstein F.M., Ogg J.G. & Schmitz M. & Ogg G. (eds). The Geologic Time Scale 2012: 603–651.

De Stefani C. 1901. Flore carbonifere e permiane della Toscana. Pubblicazioni del Regio Istituto di Studi Superiori Pratici e Perfezionamento in Firenze, Sezione di scienze fisiche e naturali. Carnesecchi, Firenze.

Del Rio M. & Pittau P. 1999. The Upper Carboniferous of the San Giorgio Basin. In Cassinis G., Cortesogno L., Gaggero L., Pittau P., Ronchi A. & Sarria E. (eds), Late Palaeozoic continental basins of Sardinia. Field trip guidebook 15 - 18 September 1999. Earth Science Department, University of Pavia, Pavia: 37–39.

Del Rio M. 1973. Palinologia di un livello “permocarbonifero” di San Giorgio (Iglesiente, Sardegna sud-occidentale). Bollettino della Società Geologica Italiana, 93: 113–124.

Del Rio M., Pillola G.L. & Muntoni F. 2002. The Upper Carboniferous of the San Giorgio basin. Rendiconti della Società Paleontologica Italiana, 1: 223–229.

Delevoryas T. 1979. Cycadales: a brief note on their history. Cycad. Newsletter,3: 2–6.

Di Simplicio P., Ferrara G., Ghezzo C., Guasparri G., Pellizzer R., Ricci C.A., Rita F. & Sabatini G. 1974. Il metamorfismo e il magmatismo paleozoico della Sardegna. Rendiconti della Società Italiana di Mineralogia e Petrografia, 30: 979–1068.

Dice L.R. 1945. Measures of the amount of ecologic association between species. Ecology, 26: 297–302.

Dieni I., Fisher J.C., Massari F., Salard-Cheboldaeff M. & Vozenin-Serra C. 1983. La succession de Genna Selole (Baunei) dans le cadre de la paléogéographie mésojurassique de la Sardaigne orientale. Memorie di Scienze Geologiche, Padova, 36: 117–148.

DiMichele W.A. & Aronson R.B. 1992. The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. Evolution, 46(3): 807–824.

DiMichele W.A., Chaney D.S., Kerp H. & Spencer G.L. 2010. Late Pennsylvanian floras in Western Equatorial Pangea, Cañon Delcobre, New Mexico. In Lucas S.G., Schneider J.W. & Spielmann J.A. (eds). Carboniferous-Permian Transition in Cañon del Cobre, northern New Mexico. New Mexico Museum of Natural History and Science Bulletin, 49: 75–114.

DiMichele W.A., Hook R.W., Nelson W.J. & Chaney D.S. 2004. An unusual Middle Permian flora from the Blaine Formation (Pease River Group: Leonardian–Guadalupian Series) of King County, west Texas. Journal of Paleontology, 78: 765–782.

DiMichele W.A., Kerp H., Sirmons R., Fedorko N., Skema V., Blake B.M. & Cecil C.B. 2013a. Callipterid peltasperms of the Dunkard Group, Central Appalachian Basin. International Journal of Coal Geology, 119: 56–78.

DiMichele W.A., Lucas S.G., Looy C.V, Kerp H. & Chaney D.S. 2017. Plant fossils from the Pennsylvanian-Permian Transition in western Pangea, Abo Pass, New Mexico. Smithsonian contributions to paleobiology, 99.

DiMichele W.A., Mamay S.H., Chaney D.S., Hook R.W. & Nelson W.J. 2001b. An Early Permian flora with Late Permian and Mesozoic affinities from north–central Texas. Journal of Paleontology, 75: 449–460.

DiMichele W.A., Pfefferkorn H.W. & Gastaldo R.A. 2001a. Response of Late Carboniferous and Early Permian plant communities to climate change. Annual Review of Earth and Planetary Sciences, 29(1): 461–487.

DiMichele W.A., Tabor N.J., Chaney D.S. & Nelson W.J. 2006. From wetland to wet spots: environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. In S.F. Greb & W.A. Di Michele (eds). Wetlands through Time, Geological Society of America, Special Papers, 399: 223–248.

DiMichele W.A., Wagner R.H., Bashforth A.R. & Álvarez–Vázquez C. 2013b. An update on the flora of the Kinney Quarry of central New Mexico (Upper Pennsylvanian), its preservational and environmental significance. New Mexico Museum of Natural History and Science Bulltin, 59: 289–325.

Dobruskina I.A. 1995. Keuper (Triassic) Flora from Middle Asia (Madygen, Southern Fergana): Bulletin 5 (Vol. 5). New Mexico Museum of Natural History and Science, Albuquerque.

Doubinger J. & Germer R. 1972. Die Gattung Callipteridium im Saarkarbon. Geologica er Palaeontologica, 6: 93–109.

Doubinger J. & Remy W. 1958. Bemerkungen über Odontopteris subcrenulata Rost und Odontopteris lingulata Göppert. Abhandlungen der deutschen Akademie der Wissenschaften zu Berlin, 5: 7–14.

Doubinger J. & Roy-Dias C. 1986. La paléoflore autuno-stéphanienne de la région de Demnate (Est de Marrakech-Maroc). Geobios, 19: 549–571.

Doubinger J. 1956. Contribution à l'étude des flores autuno-stéphaniennes. Mémoires de la Société géologique de France 35.

Doweld A. 2001. Prosyllabus Tracheophytorum. Tentamen systematis plantarum vascularium (Tracheophyta). Geos, Moscow.

Doyle J.A. 2006. Seed ferns and the origin of angiosperms. Journal of the Torrey Botanical Society 133: 169–209.

Dumortier B.C. 1829. Analyse des familles des plantes, avec l'indication des principaux genres qui s'y rattachent. J. Casterman, Tournay.

Eberth D.A. Berman D.S. Sumida S.S. & Hopf H. 2000. Lower Permian terrestrial paleoenvironments and vertebrate paleoecology of the Tambach Basin (Thuringia, central Germany): the upland holy grail. Palaios, 15(4), 293–313.

Edel J.B., Casini L., Oggiano G., Rossi P. & Schulmann K. 2014. Early Permian 90 clockwise rotation of the Maures–Esterel–Corsica–Sardinia block confirmed by new palaeomagnetic data and followed by a Triassic 60 clockwise rotation. Geological Society, London, Special Publications, 405: 333–361.

Elter F.M., Musumeci G. & Pertusati P.C. 1990. Late Hercynian shear zones in Sardinia. Tectonophysics, 176(3-4): 387–404.

Endlicher S.L. 1842. Genera plantarum secundum ordines naturales deposita, suppl. 2. F. Beck, Vienna.

Feys R. & Greber C. 1972. L'Autunien et le Saxonien en France. In: Falke H. (ed). Rotliegend. Essays on European Lower Permian, Leiden: 114–136.

Fielding C.R., Frank T.D. & Isbell J.L. 2008. The late Paleozoic ice age—A review of current understanding and synthesis of global climate patterns. Geological Society of America Special Papers, 441: 343–354.

Fiorentini L. 1923. Rilevamento geologico della regione antracitifera della Barbagia compresa tra Seùi e Seulo. Bollettino del Regio Ufficio Geologico d'Italia, 49: 1–21.

Fischer J., Schneider J.W. & Ronchi A. 2010. New hybondontoid shark from the Permocarboniferous (Gzhelian–Asselian) of Guardia Pisano (Sardinia, Italy). Acta Palaeontologica Polonica, 55(2): 241–264.

Florin R. 1934. Note on the nomenclature of Palaeozoic conifers. Svensk Botanisk Tidskrift, 28: 468–469.

Florin R. 1938–1945. Die Koniferen des Oberkarbons und des unteren Perms. Palaeontographica, 85B.

Fondi R. 1979. Orme di microsauri nel Carbonifero superiore della Sardegna. Memorie della Società Geologica Italiana, 20: 347–356.

Forte G., Kustatscher E., van Konijnenburg-van Cittert J.H., Looy C.V. & Kerp H. 2017. Conifer diversity in the Kungurian of Europe—Evidence from dwarf-shoot morphology. Review of Palaeobotany and Palynology, 244: 308–315.

Francavilla F., Cassinis G., Cocozza T., Gandin A., Gasperi G., Gelmini R., Rau A., Tongiorgi M. & Vai G.B. 1977. Macroflora e datazione di alcuni affioramenti (tardo)-postercinici presso il lago del Mulargia Sardegna sud-orientale. Gruppo di Lavoro sul Paleozoico 2 supplement: 31–33.

Francis J.E. 1994. Palaeoclimates of Pangea – Geological Evidence. Global Environments and Resources Memoir, 17: 265–274.

Frank T.D., Birgenheier L.P., Montañez I.P., Fielding C.R. & Rygel M.C. 2008. Late Paleozoic climate dynamics revealed by comparison of ice-proximal stratigraphic and ice-distal isotopic records. In C. R. Fielding, T.D. Frank & J.L. Isbell (eds), Resolving the late Paleozoic Ice Age in time and space: GSA Special Paper, 441: 331–342.

Freytet P., Galtier J., Ronchi A., Schneider J.W., Tintori A. & Werneburg R. 2002. Early Permian continental biota from Southeastern Sardinia (Ogliastra and Gerrei). In A. Cherchi, C. Corradini & M.T. Putzu (eds), Sardinia field trip - palaeontology and stratigraphy. Rendiconti della Società Paleontologica Italiana, 1: 169–176.

Freytet P., Toutin-Morin N., Broutin J., Debriette P., Durand M., El Wartiti M., Gand G., Kerp H., Orszag F., Paquette Y., Ronchi A. & Sarfati J. 1999. Palaeoecology of non marine algae and stromatolites: Permian of France and adjacent countries. Annales de paléontologie, 85(2): 99–153.

Fritz A. & Krainer K. 2004. Pflanzenfossilien aus den Grenzlandbanken der Rattendorfer Alm (Karnten, Karnische Alpen). Carinthia II, 194/114: 445–454.

Fritz A. & Krainer K. 2006. Vegetationsgeschichtliche und florenstratigraphische Untersuchungen im Oberkarbon und Unterperm der Ost- und Sudalpen (Teil 1). Carinthia II, 196/116: 93–120.

Fritz A. & Krainer K. 2007. Vegetationsgeschichtliche und florenstratigraphische Untersuchungen im Oberkarbon und Unterperm der Ost- und Sudalpen (Teil 2). Carinthia II, 197/117: 91–148.

Funedda A. & Oggiano G. 2009. Outline of the Variscan basement of Sardinia. In C. Corradini, A. Ferretti & P. Storch (eds). The Silurian of Sardinia. Rendiconti della Società Paleontologica Italiana, 3 (1): 23–35.

Gaggero L. Oggiano G., Funedda A. & Buzzi L. 2012. Rifting and arc-related early Paleozoic volcanism along the North Gondwana margin: geochemical and geological evidence from Sardinia (Italy). Journal of Geology, 120(3): 273–292.

Gaggero L., Gretter N., Langone A. & Ronchi A. 2017. U–Pb geochronology and geochemistry of late Palaeozoic volcanism in Sardinia (southern Variscides). Geoscience Frontiers. In press.

Galtier J. & Broutin J. 1995. La flore de la zone de transition de l'Autunien supérieur de Lodève. Sciences Géologiques Bulletin, Strasbourg 48: 83–93.

Galtier J. & Broutin J. 2008. Floras from red beds of the Permian Basin of Lodève (Southern France)/Floras en las capas rojas de la cuenca pérmica de Lodève (Sur de Francia). Journal of Iberian Geology, 34: 57–72.

Galtier J. & Phillips T.L. 1999. The acetate peel technique. In T.P. Jones & N.P. Rowe (eds), Fossil Plants and Spores: modern techniques. Geological Society, London: 67–70.

Galtier J. Decombeix A.L., Meyer-Berthaud B. & Scanu G.G. (eds). 2017. 5th International Meeting of Agora Paleobotanica. Field trip in the Lodève basin: Permian Floras. 10-12/07/2017, Montpellier (France).

Galtier J., Broutin J. & Ronchi A. 1998. A new permineralized flora from the Permian of Sardinia. V European Paleobotany and Palynology conference, Cracow, June 1998, Abstract volume: 58.

Galtier J., Ronchi A. & Broutin J. 2011. Early Permian silicified floras from the Perdasdefogu Basin (SE Sardinia): comparison and bio-chronostratigraphic correlation with the floras of the Autun Basin (Massif central, France). Geodiversitas, 33(1): 43–69.

Gambera V. 1897a. Relazione sulla scoperta di Fauna e Flora fossile nell'lglesiente, presentata all'Associazione mineraria Sarda per la seduta del 17 Gennaio 1897. Fascicolo I. 13 pp. Tipografia Iglesiense, Iglesias.

Gambera V. 1897b. Sulla scoperta di Fossili nell'Iglesiente (Sardegna). Fascicolo II. Tavole annesse alla relazione presentata all'Associazione mineraria Sarda. 10 pp. Tipo Litografia Commerciale, Cagliari.

Gambera V. 1897c. Tettonica dei terreni dell'Iglesiente. 12 pp. Tipo Litografia Commerciale, Cagliari.

Gand G. Kerp H. Parsons C. & Martínez-García E. 1997. Palaeoenvironmental andstratigraphic aspects of animal traces and plant remains in Spanish Permian red beds (Peña Sagra, Cantabrian Mountains, Spain). Geobios, 30(2): 295–318.

Gand G., Galtier J., Broutin J., Van Waveren I. (eds). 2015. Field-trip in the Autun basin, July 9, 2015. Two stops in the Muse Formation. AGORA PALEOBOTANICA 2015 Meeting, Autun, France.

Gand G., Galtier J., Garric J., Teboul P.A. & Pellenard P. 2013. Discovery of an Autunian macroflora and lithostratigraphic re-investigation on the western border of the Lodève Permian basin (Mont Sénégra, Hérault, France). Paleoenvironmental implications. Comptes Rendus Palevol, 12: 69–79.

Gasperi G. & Gelmini R. 1979. Ricerche sul Verrucano. 4. Il Verrucano della Nurra (Sardegna nord-occidentale). Memorie della Società Geologica Italiana, 20: 215–231.

Gastaldo R.A. 1987. Confirmation of Carboniferous clastic swamp communities. Nature, 326: 871–896.

Gastaldo R.A. 1992. Regenerative growth in fossil horsetails following burial by alluvium. Historical Biology, 6: 203–19.

Gastaldo R.A. Di Michele W.A. & Pfefferkorn H.W. 1996. Out of the Icehouse into the Greenhouse: a Late Paleozoic analog for modern global vegetational change. GSA Today. 6: 1–7.

Gattacceca J., Deino A., Rizzo R., Jones D.S., Henry B., Beaudoin B. & Vadeboin F. 2007. Miocene rotation of Sardinia: New paleomagnetic and geochronological constraints and geodynamic implications. Earth and Planetary Science Letters, 258 (3–4): 359–377.

Gaudry A. 1883. Les enchaînements du monde animal dans les temps géologiques. Fossiles Primaires. Masson, Paris.

Geinitz E. 1873. Versteinerungen aus dem Brandschiefer der unteren Dyas von Weissig bei Pillnitz. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie: 691–704.

Glasspool L.J., Wittry J., Quick K., Kerp H. & Hilton J. 2013. A preliminary report on a Wolfcampian age floral assemblage from the type section for the Neal Ranch Formation in the Glass Mountains, Texas. In Lucas S.G., DiMichele W.A., Barrick J.E., Schneider J.W. & Spielmann J.A. (eds). The Carboniferous-Permian Transition, New Mexico Museum of Natural History and Science, Bulletin, 60: 98–102.

Goeppert H.R. 1836. Die fossilen Farrenkräuter (Systema filicum fossilium) Nova Acta Leopoldina, 17: 1–486.

Goeppert H.R. 1864–1865. Die fossile Flora der permischen Formation. Palaeontographica: 1–316.

Golonka J. 2002. Plate-tectonic Maps of the Phanerozoic. In W. Kiessling, E. Flügel, J. Golonka (eds), Phanerozoic Reef Patterns. SEPM (Society for Sedimentary Geology) Special Publication, 72: 21–75.

Golonka J. 2007. Phanerozoic paleoenvironment and paleolithofacies maps. Late Paleozoic. Geologia 33(2): 145–209.

Gradstein F.M., Ogg J.G. Schmitz M. & Ogg G. (Eds.). 2012. The Geologic Time Scale 2012. Elsevier, Amsterdam.

Gradstein S.R. & Kerp H. 2012. A brief history of plants on Earth. The Geologic Time Scale 2012: 233–237.

Grand'Eury M.F.C. 1877. Mémoire sur la flore carbonifère du département de la Loire et du centre de la France: étudiée aux trois points de vue botanique, stratigraphique et géognostique. Imprimerie nationale, Paris.

Greb S.F., DiMichele W.A. & Gastaldo R.A. 2006. Evolution and importance of wetlands in earth history. Geological Society of America Special Papers, 399: 1–40.

Gulbranson E.L., Montanez I.P., Tabor N.J., Limarino C.O. 2015. Late Pennsylvanian aridification on the southwestern margin of Gondwana (Paganzo Basin, NWArgentina): a regional expression of a global climate perturbation. Palaeogeography, Palaeoclimatology Palaeoecology, 417: 220–235.

Gutbier A. 1835–36. Abdrücke und Versteinerungen des Zwickauer Schwarzkohlengebirges und seiner Umgebungen. Zwickau, Verlag der G. Richat'schen Buchhandlung.

Gutbier A. 1837. Über die gegenseitige sehr gesonderte Lagerung und die gänzlich von einander abweichenden Pflanzenabdrücke des Rothliegenden und der Kohlen-Formation in der Gegend von Zwickau. Sitzungsberichte der Naturwissenschaftlichen Gesellschaft Isis zu Jena. Oldenbourg.

Gutbier A. 1849. Die Versteinerungen des Rothliegenden in Sachsen. Arnold, Dresden, Leipzig.

Harris T. 1932. The fossil flora of Scoresby Sound, East Greenland. 2. Description of seed plants incertae sedis together with a discussion of certain cycadophyte cuticles. Meddelelser Om Grønland, 85.

Harris T.M. 1937. The fossil flora of Scoresby Sound, East Greenland. Part 5: Stratigraphic relations of the plant beds. Meddelelser om Grønland, 112.

Harris T.M. 1961. The Yorkshire Jurassic Flora I. Tallophyta–Pteridophyta. British Museum (Natural History), London.

Haworth M., Fitzgerald A. & McElwain J.C. 2011. Cycads show no stomatal-density and index response to elevated carbon dioxide and subambientoxygen. Australian Journal of Botany 59, 630–639.

Heckel P.H. & Clayton G. 2006. The Carboniferous System. Use of the new official names for the subsystems, series, and stages. Geologica Acta, 4: 403–407.

Henderson C.M., Davydov V.I., Wardlaw B.R. & Gradstein F.M. 2012. The Permian Period. In Gradstein F.M., Ogg J.G. & Schmitz M. & Ogg G. (eds). The Geologic Time Scale 2012: 653–659.

Hilton J. & Bateman R.M. 2006. Pteridosperms are the backbone of seed-plant phylogeny. Journal of the Torrey Botanical Society 133: 119–168.

Hilton J. & Cleal C.J. 2007. The relationship between Euramerican and Cathaysian tropical floras in the Late Palaeozoic: palaeobiogeographical and palaeogeographical implications. Earth-Science Reviews, 85: 85–116.

Hmich D., Schneider J.W., Saber H., Voigt S. & El Wartiti M. 2006. New continental Carboniferous and Permian faunas of Morocco - implications for biostratigraphy, palaeobiogeography and palaeoclimate. In: Lucas S.G., Cassinis G. & Schneider J.W. (eds). Non-marine Permian biostratigraphy and biochronology. Geological Society, London, Special Publications, 265: 297–324.

Hoffmann F. 1826. Ober die Pflanzenreste des Kohlengebirges von Ibbenbüren und vom Piesberge bei Osnabrück. In Keferstein C. Deutschland geognostisch-geologisch dargestellt 4", Weimar: 150–160.

Ishikawa K. 1990. Introduction to Quality Control. 3A Corp, Tokyo.

Josten K.-H. 2005. Florenstratigraphie des Oberkarbons in Nordwestdeutschland Courier Forschungs-Institut Senckenberg, 254: 119–132.

Juncal M., Ferrer J.B.D., Broutin J., & García E.M. 2016. Palynoflora from the Permian Sotres Formation (Picos de Europa, Asturias, Northern Spain). Spanish journal of palaeontology, 31(1): 85–94.

Kerp H. & Fichter J. 1985. Die Makrofloren des saarpfälzischen Rotliegenden (? Ober-Karbon-Unter-Perm; SW-Deutschland). Mainzer Geowissenschaftliche Mitteilungen, 14: 159–286.

Kerp J.H.F. & Haubold H. 1988. Aspects of Permian palaeobotany and palynology. VIII. On the reclassification of the West- and Central European species of the form-genus Callipteris Brongniart 1849. Review of Palaeobotany and Palynolology, 54: 135–150.

Kerp J.H.F. 1982. Aspects of Permian palaeobotany and palynology. II. On the presence of the ovuliferous organ Autunia milleryensis (Renault) Krasser (Peltaspermaceae) in the Lower Permian of the Nahe area (FGR) and its relationship to Callipteris conferta (Sternberg) Brongniart. Acta Botanica Neerlandica, 31: 417–427.

Kerp J.H.F. 1983. Aspects of Permian palaeobotany and palynology. I. Sobernheimia jonkeri nov. gen., nov. sp., a new fossil plant of cycadalean affinity from the Waderner Gruppe of Sobernheim. Review of Palaeobotany and Palynology, 38: 173–183.

Kerp J.H.F. 1988. Aspects of Permian palaeobotany and palynology. X. The West- and Central European species of the genus Autunia Krasser emend. Kerp (Peltaspermaceae) and the form-genus Rhachiphyllum Kerp (callipterid foliage). Review of Palaeobotany and Palynology, 54: 249–360.

Kerp J.H.F., Poort R.J., Swinkels H.A.J.M. & Verwer R. 1990. Aspects of Permian palaeobotany and palynology. IX. Conifer-dominated Rotliegend floras from the Saar-Nahe Basin (?Late Carboniferous-Early Permian; SW-Germany) with special reference to the reproductive biology of early conifers. Review of Palaeobotany and Palynology, 62: 205–248.

Kerp J.H.F., Poort R.J., Swinkels H.A.J.M. & Verwer R. 1991. An emendation of the genus Remia Knight - A case of a realistic classification of Late Palaeozoic plant megafossils. Review of Palaeobotany and Palynology, 67: 199–203.

Kidston R. 1925. Fossil Plants of the Carboniferous Rocks of Great Britain. First Section [With Plates]. HM Stationery Office.

Knight J. 1985. The Stratigraphy of the Stephanian Rocks of the Sabero Coalfield, Léon (NW. Spain) and an investigation of the fossil flora. Part III: Systematic palaeobotany; pecopterids. Palaeontographica Abteilung B,187: 1–80.

Krasser F. 1919. Studien über die fertile region der cycadophyten aus den Lunzer schichten: makrosporophylle. Denkschriften der Akademie der Wissenschaften. Math. Natw. Klasse 97: 1–32.

Krick H.V. 1932. Structure of seedlike fructifications found in coal balls from Harrisburg, Illinois. Botanical Gazette, 93: 151–172.

Krings M., Kerp H. & Uhl D. 2000. Epidermale Anatomie von Odontopteris subcrenulata (Rost) Zeiller aus dem Stefan (Oberkarbon) von Blanzy-Montceau (Zentralfrankreich). Feddes Repertorium, 111: 385–398.

Lamarmora A. 1857. Voyage en Sardaigne, ou description statistique, physique e politique de cette île. 4 volumes. Imprimerie Royal, Turin.

Lausberg S. & Kerp H. 2000. Eine Coniferen-dominierte Flora aus dem Unterrotliegend von Alsenz, Saar-Nahe-Becken, Deutschland. Feddes Repertorium, 111(7-8): 399–426.

Laveine J.P. 1967. Contribution à l’étude de la Flore du Terrain Houiller. Les Neuroptéridées du Nord de la France. Études Géologiques pour l’Atlas de Topographie Souterraine, Volume 5. Le Service Géologique des Houilléres du Bassins du Nord et du Pas-de-Calais: Lille.

Laveine J.-P. 1989. Guide Palèobotanique dans le Terrain Houiller Sarro-Lorrain. Merlebach: Houilleres du Bassin de Lorraine.

Link J.H.F. 1833. Hortus regius botanicus berolinensis 2. G. Reimer, Berlin.

Lotti B. 1931. Relazione generale riassuntiva dei tre sondaggi per la ricerca del carbone paleozoico nei piani di Alghero. Bollettino del Regio Ufficio Geologico, 56(6): 5–15.

Lovisato D. 1884. Nota sopra il Permiano ed il Triassico della Nurra in Sardegna. Bollettino Comitato Geologico Italiano, 15: 305–325.

Mamay S.H. & Mapes G. 1992. Early Virgilian plant megafossils from the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico. New Mexico Bureau of Mines and Mineral Resources Bulletin, 138, 61–85.

Mapes G. & Rothwell G.W. 1991. Structure and relationships of primitive conifers. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 183: 269–287.

Marchetti L., Petti F. M., Zoboli D., & Pillola G. L. 2017. Vertebrate and Invertebrate Trace Fossils in the Late Pennsylvanian (Carboniferous) Fluvio-Lacustrine San Giorgio Basin (South-West Sardinia): Remarks on the Oldest Continental Ichnoassociation of Italy. Ichnos, 1-12.

Marion A.F. 1890. Sur le Gomphostrobus heterophylla, conifère prototypique du Permien de Lodève. Academie du Science Paris, Comptes Rendus, 110 : 892–894.

Martín-Closas C. & Galtier J. 2005. Plant taphonomy and paleoecology of Late Pennsylvanian intramontane wetlands in the Graissessac-Lodève basin (Languedoc, France). Palaios, 20(3): 249–265.

Martínek K., Pešek J. & Opluštil S. 2017. Significant hiatuses in the terrestrial Late Variscan Central and Western Bohemian basins (Late Pennsylvanian–Early Cisuralian) and their possible tectonic and climatic links. Geologica Carpathica, 68(3): 269–281.

Matthews K.J., Maloney K.T., Zahirovic S., Williams S.E., Seton M. & Müller R.D. 2016. Global plate boundary evolution and kinematics since the late Paleozoic. Global and Planetary Change, 146: 226–250.

Maxia C. 1938. Alcune osservazioni sulla flora autuniana di Perdasdefogu e sul Paleozoico recete della Sardegna. Rivista Italiana di Paleontologia e Stratigrafia, 44: 107–126.

McCann T. 2008. The geology of Central Europe: volume 1: Precambrian and Palaeozoic. Geological Society of London.

McCune B., Grace J.B. & Urban D.L. 2002. Analysis of ecological communities. MjM software design, Gleneden Beach, Oregon.

McKerrow W.S., Mac Niocaill C. & Dewey J.F. 2000. The Caledonian orogeny redefined. Journal of the Geological Society, 157(6): 1149–1154.

McNeill, J., Barrie F.R., Buck W.R., Demoulin V. Greuter W., Hawksworth D.L., Herendeen P.S., Knapp S., Marhold K., Prado J. & Prud'Homme Van Reine W.F. 2012. International Code of Nomenclature for Algae, Fungi, and Plants (Melbourne Code). Koeltz Scientific Books, Oberreifenberg (Regnum Veg, 154).

Meneghini G. (1857). Paléontologie de l'île de Sardaigne ou déscription des fossiles recueillis dans cette contrée par le général A. Lamarmora pour faire suite à la troisieme partie du Voyage en Sardaigne. Imprimerie Royal, Turin.

Menning M., Alekseev A.S., Chuvashov B.I., Davydov V.I., Devuyst F.X., Forke H.C., Grunt T.A., Hance L., Heckel P.H., Izokh N.G., Jin Y.G., Jones P.J., Kotlyar G.V., Kozur H.W., Nemyrovska T.I., Schneider J.W., Wang X.D., Weddige K., Weyer D. & Jin Y.G. 2006. Global time scale and regional stratigraphic reference scales of central and west Europe, east Europe, Tethys, south China, and North America as used in the Devonian–Carboniferous–Permian Correlation Chart 2003 (DCP 2003). Palaeogeography, Palaeoclimatology, Palaeoecology, 240: 318–372.

Merlo G. 1911. Dell'esistenza di un lembo carbonifero fra Monteponi e Iglesias. Resoconti delle Riunioni della Associazione Mineraria Sarda, Allegato D, 16: 25–27.

Meyen S.V. 1978. An attempt at a radical improvement of suprageneric taxonomy of fossil plants. Phyta, 1: 76–86.

Meyen S.V. 1982. Carboniferous and Permian floras of Angaraland (a synthesis). Biological Memoirs, 7.

Meyen S.V. 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. The Botanical Review, 50(1), 1-111.

Meyer-Berthaud B. 1989. First gymnosperm fructifications with trilete prepollen. Palaeontographica Abteilung B, 211: 87–112.

Michel L.A., Tabor N.J., Montañez I.P., Schmitz M.D. & Davydov V.I. 2015. Chronostratigraphy and paleoclimatology of the Lodève Basin, France: evidence for a pan-tropical aridification event across the Carboniferous–Permian boundary. Palaeogeography, Palaeoclimatology, Palaeoecology, 430: 118–131.

Mickle J., Lumaga M.R.B., Moretti A. & De Luca P. 2011. Scanning electron microscopy studies of cuticle micromorphology in Cycas L. (Cycadaceae). Plant Biosystems, 145: 191–201.

Mingarro Martín F. 1962. Estudio del Carbonífero del norte de la provincia de Sevilla. Boletín Instituto Geológico y Minero de España, 73: 469–624.

Montañez I.P., Tabor N.J., Niemeier D., Di Michele W.A., Frank T.D., Fielding C.R., Isbell J., Birgenheier L.P. & Rygel M.C. 2007. CO2-forced climate and vegetation instability during Late Paleozoic deglaciation. Science, 315: 87–91.

Mossoni A., Carta N., Corradini C., & Spalletta C. 2015. Conodonts across the Devonian/Carboniferous boundary in SE Sardinia (Italy). Bulletin of Geosciences, 90(2): 371–388.

Naugolnykh S.V.2007. Permskie flory Urala (Permian Floras of the Urals). GEOS, Moscow.

Nixon K.C., Crepet W.L., Stevenson D.W. & Friis E.M. 1994. A reevaluation of seed plant phylogeny. Annals of the Missouri Botanical Garden 81: 484–533.

Novarese V. & Taricco M. 1922. Cenni sommari sul Paleozoico dell'Iglesiente. Bollettino della Società Geologica Italiana, 41: 316–325.

Novarese V. 1917. L'Autuniano in Sardegna. Bollettino della Società Geologica Italiana, 36: 58–91.

Novarese V. 1924. Autuniano. Contributo alla geologia dell'Iglesiente: la Serie Paleozoica. Bollettino del Regio Ufficio Geologico d'Italia, 49 (10): 55.

Ogg J.G., Ogg G. & Gradstein F.M. 2016. A Concise Geologic Time Scale 2016. Elsevier, Amsterdam.

Oggiano G., Funedda A., Carmignani L. & Pasci S. 2009. The Sardinia–Corsica microplate and its role in the Northern Apennine Geodynamics: new insights from the Tertiary intraplate strike-slip tectonics of Sardinia. Bollettino della Società Geologica Italiana, 128 (2): 527–541.

Oliver F.W. & Scott D.H. 1904. On the structure of the Palaeozoic seed Lagenostoma lomaxi, with a statement of the evidence upon which it is referred to Lyginodendron. Philosophical Transactions of the Royal Society of London, 197B: 193–247.

Oosterbaan A.M. 1936. Étude géologique et paléontologique de la Nurra avec quelques notes sur le Permien et le Trias de la Sardaigne méridionale. PhD Thesis, University of Utrecht.

Opluštil S., Jirásek J., Schmitz M. & Matýsek D. 2017a. Biotic changes around the radiosotopically constained Carboniferous-Permian boundary in the Boskovice Basin (Czech Republic). Bulletin of Geosciences, 92: 95–122.

Opluštil S., Schmitz M., Cleal C.J. & Martínek K. 2016a. A review of the Middle-Late Pennsylvanian west European regional substages and floral biozones, and their correlation to the Geological Time Scale based on new U–Pb ages. Earth-Science Reviews, 154: 301–335.

Opluštil S., Schmitz M., Kachlík V. & Štamberg S. 2016b. Re-assessment of lithostratigraphy, biostratigraphy, and volcanic activity of the Late Paleozoic Intra-Sudetic Krkonoše-Piedmont and Mnichovo Hradiště Basins (Czech Republic) based on new U-Pb CA-ID-TIMS ages. Bulletin of Geosciences, 91: 399–432.

Opluštil S., Šimunek Z., Pšenicka J., Bek J. & Libertín M. 2017b. A 25 million year macrofloral record (Carboniferous-Permian) in the Czech part of the Intra-Sudetic Basin; biostratigraphy, plant diversity and vegetation patterns. Review of Palaeobotany and Palynology, 244: 241–273.

Opluštil S., Šimůnek Z., Zajíc J. & Mencl V. 2013. Climatic and biotic changes around the Carboniferous/Permian boundary recorded in the continental basins of the Czech Republic. International Journal of Coal Geology, 119: 114–151.

Owens B., McLean D. & Bodman D. 2004. A revised palynozonation of British Namurian deposits and comparisons with eastern Europe. Micropaleontology, 50(1): 89–103.

Pampaloni L. 1900. I terreni carboniferi di Seui e oolitici della Pedaliana. Rendiconti dell'Accademia Nazionale dei Lincei, 9: 345–349.

Pecorini G. 1952. Relazione delle escursioni della LVI Riunione Estiva. Bollettino della Società Geologica Italiana, 71 (1): 159–179.

Pecorini G. 1962. Nuove osservazioni sul Permico della Nurra (Sardegna nord-occidentale). Accademia Nazionale dei Lincei - Rendiconti della Classe di Scienze fisiche, matematiche e naturali, 32: 377–380.

Pecorini G. 1974. Nuove osservazioni sul Permo-Trias di Escalaplano (Sardegna sud-orientale). Bollettino della Societa Geologica Italiana, 93: 991–999.

Pellenard P., Gand G., Schmitz M., Galtier J., Broutin J. & Stéyer J. S. 2017. High-precision U-Pb zircon ages for explosive volcanism calibrating the NW European continental Autunian stratotype. Gondwana Research, 51: 118–136.

Pertusati P.C., Sarria E., Cherchi G.P., Carmignani L., Barca S., Benedetti M., Chighine G., Cincotti F., Oggiano G., Ulzega A. Orru P. & Pintus C. 2002. Note Illustrative della Carta Geologica d'Italia alla scala 1: 50.000, Foglio 541 Jerzu. Servizio Geologico d'Italia, Roma.

Pillola G.L., Petti F.M., Sacchi E., Piras S., Zoboli D. & Nicosia U. 2004. Tetrapod footprints and associated biota: new evidences from the Upper Carboniferous of SW Sardinia (Italy). Geological Society of America, Abstract book, 36(4): 82.

Pittau Demelia P. & Flaviani A. 1982. Aspects of the palynostratigraphy of the Triassic Sardinian sequences (preliminary report). Review of Palaeobotany and Palynology, 37: 329–343.

Pittau Demelia P. & Flaviani A. 1983. Palinostratigrafia della serie triassica di Punta del Lavatoio (Sardegna nord-occidentale). Rivista Italiana di Paleontologia e Stratigrafia, 88: 401–416.

Pittau P. & Del Rio M. 2002. Palynofloral biostratigraphy of the Permian and Triassic sequences of Sardinia. In A. Cherchi, C. Corradini & M.T. Putzu (eds), Sardinia field trip - palaeontology and stratigraphy. Rendiconti della Società Paleontologica Italiana, 1: 93–109.

Pittau P. & Del Rio M. 2004. Upper Carboniferous to Triassic terrestrial palynofloras of Sardinia: biostratigraphic, palaeoclimatologic and paleophytogeographic implications. Geological Society of America (Annual Meeting, Boise-Idaho), Abstracts with Programs 36-7: 83.

Pittau P., Barca S., Cocherie A., Del Rio M., Fanning M. & Rossi P. 2002. Le bassin permien de Guardia Pisano (Sud-Ouest de la Sardaigne, Italie): palynostratigraphie, paléophytogéographie, corrélations et âge radiométrique des produits volcaniques associés. Geobios, 35: 561–580.

Pittau P., Del Rio M. & Funedda A. 2008. Relationships between plant communities characterization and basin formation in the Carboniferous-Permian of Sardinia. Bollettino della Società Geologica Italiana, 127: 637–653.

Popa M.E. 1999. The Early Permian Megaflora from the Resita Basin, South Carpathians, Romania. Proceedings of the 5th EPPC. Acta Palaeobotanica, 47–59.

Pott C., Krings M. & Kerp H. 2007. First record of Nilssoniopteris (Gymnospermophyta, Bennettitales) from the Carnian (Upper Triassic) of Lunz, LowerAustria. Palaeontology, 50: 1299–1318.

Principi P. 1938. Le flore del Permiano. Atti della Società di scienze e lettere di Genova, 3(3): 187–246.

Pšenička J. & Bek J. 2001. Oligocarpia lindsaeoides (Ettingshausen) Stur and its spores from the Westphalian of Central Bohemia (Czech Republic). Acta Musei nationalis Pragae, Series B - historia naturalis 57: 57–68.

Pšenička J., Correia P., Šimůnek Z., Sá A.A., Murphy J. B. & Flores D. 2017. Revision of Ilfeldia and establishment of Ovulepteris gen. nov. from the Pennsylvanian of Europe, with a discussion on their concepts. Review of Palaeobotany and Palynology, 236: 59–73.

Pšenička J., Kolar-Jurkovšek T., Opluštil S. & Novak M. 2014. Stephanian Fossil Flora from Paralic Carboniferous Deposits of the Jesenice Area (Slovenia) and Its Comparison with Czech Localities. Folia, 48(1-2): 21–64.

Rees P.M. 2002. Land-plant diversity and the end-Permian mass extinction. Geology, 30: 827–830.

Remy W. & Remy R. 1977. Die Floren des Erdaltertums. Einfürung in Morphologie, Anatomie, Geobotanik und Biostratigraphie der Pflanzen des Paläophytikums Verlag Glückauf GMBH, Essen.

Remy W. 1954. Beitrage zur Kenntnis der Rotliegendflora Thiiringens: Teil II: Fruktifikationen: Sitzungsberichte der Deutschen Akademie der Wissenschaften zu Berlin. Klasse für Mathematik und allgemeine Naturwissenschaften, 1953(3), 1–20.

Renault B. & Zeiller R. 1888–1890. Études sur le terrain houiller de Commentry. Livre deuxiéme. Flore fossile. Société de l'Industrie Minérale, St-Étienne.

Ronchi A. & Falorni P. 2004. Formazione di Rio su Luda. Carta Geologica d'Italia scala 1:50.000. Catalogo delle Formazioni, Unità validate (a cura della Comm. Ital. Stratigr.). Quaderni serie III, 7 (5): 155–159.

Ronchi A. & Tintori A. 1997. First Amphibian Find in Early Permian from Sardinia (Italy). Rivista Italiana di Paleontologia e Stratigrafia, 103(1): 29–38.

Ronchi A. 1997. I prodotti sedimentari e vulcanici dei bacini permiani di Escalaplano e Perdasdefogu nella Sardegna sudorientale: stratigrafia e loro inquadramento nell'evoluzione tardo-paleozoica del settore sudeuropeo. Unpublished Thesis, University of Parma.

Ronchi A. 2001. Upper Paleozoic and Triassic continental deposits of Sardinia: a stratigraphic synthesis. In Permian continental deposits of Europe and other areas. Regional reports and correlations. Museo Civico di Science Naturali di Brescia, 139–148.

Ronchi A., Broutin J., Diez J.-B., Freytet P., Galtier J. & Lethiers F. 1998. New paleontological discoveries in some Early Permian sequences of Sardinia. Biostratigraphic and paleogeographic implications. Comptes Rendus de l'Académie de Sciences de Paris, 327: 713–719.

Ronchi A., Sacchi E., Romano M. & Nicosia U. 2011. A huge caseid pelycosaur from north western Sardinia and its bearing on European Permian stratigraphy and palaeobiogeography. Acta Palaeontologica Polonica, 56(4), 723–738.

Ronchi A., Sarria E. & Broutin J. 2008. The «Autuniano Sardo»: basic features for a correlation through the Western Mediterranean and Paleoeurope. Bollettino della Società Geologica Italiana, 127: 655–681.

Roscher M. & Schneider J.W. 2006. Permo-Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context. Geological Society, London, Special Publications, 265(1), 95–136.

Rossi P., Oggiano G. & Cocherie A. 2009. A restored section of the “southern Variscan realm” across the Corsica–Sardinia microcontinent. Comptes Rendus Geoscience, 341(2): 224–238.

Rost W. 1839. De filicum ectypis obviis in lithanthracum vettinensium lobeiunnensiumque fodinis Halle.

Rothwell G.W. & Serbet R. 1994. Lignophyte phylogeny and the evolution of the spermatophytes: A numerical cladistic analysis. Systematic Botany 19: 443–482.

Sahni B. 1948. The Pentoxylae: A new group of Jurassic gymnosperms from the Rajmahal Hills of India. Botanical Gazette, 110: 47–80.

Sartori F. 1909. Dell'esistenza di un lembo carbonifero fra Monteponi e San Giorgio. Resoconti delle riunioni dell'Associazione mineraria Sarda 14(5), 13–14.

Scanu G.G., Buosi C., Del Rio M. & Pittau P. 2014a. La flora del Permiano della Sardegna – The Permian flora of Sardinia. In Kustatscher E., Roghi G., Bertini A. & Miola A. (eds). La storia delle piante fossili in Italia – The palaeobotany of Italy. Volume speciale del Museo di Scienze Naturali dell'Alto Adige, 9: 104–113.

Scanu G.G., Buosi C., Del Rio M. & Pittau P. 2014b. La flora del Triassico della Sardegna – The Triassic flora of Sardinia. In Kustatscher E., Roghi G., Bertini A. & Miola A. (eds). La storia delle piante fossili in Italia – The palaeobotany of Italy. Volume speciale del Museo di Scienze Naturali dell'Alto Adige, 9: 146–151.

Scanu G.G., Corriga M.G., Pillola G.L. & Corradini C. 2016. The mining area near Iglesias in southwestern Sardinia (Pennsylvanian). In Suttner T.J., Kido E., Königshof P., Waters J.A., Davis L. & Messner F. (eds). Planet Earth in Deep Time – Palaeozoic Series, Devonian & Carboniferous. Schweizerbart Science Publishers, Stuttgard: 124–125.

Scanu G.G., Kustatscher E. & Pittau P. 2012. The Jurassic plant fossils of the Lovisato Collection: preliminary notes. Bollettino della Società Paleontologica Italiana, 51(2): 71–84.

Scanu G.G., Kustatscher E. & Pittau P. 2015. The Jurassic Flora of Sardinia–a new piece in the palaeobiogeography puzzle of the Middle Jurassic. Review of Palaeonotany and Palynology, 218: 80–105.

Schimper W.P. 1869-1874. Traité de paléontologie végétale ou La flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel. JB Baillière et fils, Paris. 3 volumes.

Schimper W.P. 1879. Handbuch der Palæontologie II Band. I. Lieferung, Oldenbourg, Munich.

Schlotheim von E.F. 1804. Beschreibung merkwürdiger Kräuter-Abdrücke und Pflanzen-Versteinerungen: ein Beitrag zur Flora der Vorwelt (Vol. 1). In der Becker'schen Buchandlung, Gotha.

Schlotheim von E.F. 1820. Die Petrefaktenkunde auf ihremjetzigen Standpunkte, durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert. In der Becker'schen Buchandlung.

Schneider J.W. & Werneburg R. 1993. Neue Spiloblattinidae (Insecta, Blattodea) aus dem Oberkarbon und Unterperm von Mitteleuropa sowie die Biostratigraphie des Rotliegend. Naturhistorisches Museum Schloss Bertholdsberg, Schleusingen, Veröffentlichungen, 718: 31–52.

Schneider J.W. & Werneburg R. 2006. Insect biostratigraphy of the Euamerican continental Late Pennsylvanian and Early Permian. In: Lucas S.G., Schneider J.W. & Cassinis G. (Eds.), Non-marine Permian Biostratigraphy and Biochronology. Geological Society Special Publication: 325–336.

Schneider J.W. & Werneburg R. 2012. Biostratigraphie des Rotliegend mit Insekten und Amphibien. Deutsche Stratigraphische Kommission: Stratigraphie von Deutschland X. Rotliegend. Teil I: Innervariscische Becken. - Schriftenr. Dt. Ges. Geowiss, Heft, 61: 110–142.

Schneider J.W., Körner F., Roscher M. & Kroner U. 2006. Permian climate development in the northern peri-Tethys area - the Lodève basin, French Massif Central, compared in a European and global context. Palaeogeography, Palaeoclimatology, Palaeoecology, 240: 161–183.

Schneider J.W., Opluštil S. & Scholtze F. 2014. CPC-2014 Field Meeting on Carboniferous and Permian Nonmarine – Marine Correlation - Excursion Guide. Wissenschaftliche Mitteilungen, 46: 1–121.

Schneider J.W., Scholze F., Voigt S., Götz A., Opluštil S., Ronchi A., Bordy E., Silantiev V., Zahrinova V., Marchetti L., Spencer G.L., Shen S.-Z., Barrick J., Werneburg R., Rößler R., & Kerp H., Golubev V., Saber H. & López-Gómez J. 2017. Report on the activities of the Late Carboniferous – Permian – Early Triassic Nonmarine-Marine Correlation Working Group for 2016 and 2017. Permophiles, 65: 16–24.

Scott A.C 1978. Sedimentological and ecological control of Westphalian B plant assemblages from west Yorkshire. Proceedings of the Yorkshire Geological Society, 41: 461–508.

Selden P.A. & Pillola G.L. 2009. A trigonocarpid arachnid from the Upper Carboniferous of the San Giorgio Basin, Sardinia. Rivista Italiana di Paleontologia e Stratigrafia, 115: 269–274.

Seward A. 1917. Fossil Plants III. Hafner Publishing, New York.

Šimůnek Z. & Martínek K. 2009. A study of Late Carboniferous and Early Permian plant assemblages from the Boskovice Basin, Czech Republic. Review of Palaeobotany and Palynology, 155: 275–307.

Sopeña A. & Sánchez-Moya Y. 1999. El bosque petrificado de la Sierra de Aragoncillo. In Aguirre, E. & Rábano I. (coord.). La huella del pasado. Fósiles de Castilla-La Mancha. Patrimonio histórico. Arqueología Castilla-La

Mancha, Junta de Comunidades de Castilla-La Mancha, 127–130.

Sørensen T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. Videnski Selskab Biologiske Skrifter, 5: 1–34.

Spano C. 1976. Nuovo contributo alla conoscenza delle piante del paleozoico della Sardegna. Rendiconti del Seminario della Facoltà di Scienze dell'Università di Cagliari, 46(3–4): 383–433.

Stampfli G.M., Hochard C., Vérard C. & Wilhem C. 2013. The formation of Pangea. Tectonophysics, 593: 1–19.

Stephenson M.H., Angiolini L. & Leng M.J. 2007. The Early Permian fossil record of Gondwana and its relationship to deglaciation: A review. In M. Williams, A. Haywood, J. Gregory & D. Schmidt (eds), Deep time perspectives on climate change: Marrying the signal from computer models and biological proxies. Publication of The Micropalaeontological Society London, Special Publications. GSL: 103–122.

Sternberg K. 1820-1838. Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Leipzig, Prague.

Sterzel J.T. 1881. Paläontologischer Charakter der oberen Steinkohlenformation und des Rothliegenden im Erzge birgischen Becken. Bericht Der Naturwissenschaftlichen Gesellschaft Zu Chemnitz, 7: 155–270.

Sterzel J.T. 1895. Die Flora des Rotliegenden von Oppenau im badischen Schwarzwald (Blatt Petersthal-Reichenbach). Mitteilungen der Badischen Geologischen Landesanstalt, 3: 261–352.

Sterzel J.T. 1918. Die organischen Reste des Kulms und Rotliegenden der Gegend von Chemnitz. Abhandlungen der Mathematisch-Physischen Klasse der Königlich-Sächsischen Gesellschaft der Wissenschaften. Leipzig, 5: 205–315.

Stewart W.N. & Rothwell G.W. 1993. Paleobotany and the evolution of plants. Cambridge University Press, Cambridge.

Stille H. 1939: Bemerkungen betreffend die "Sardische" Faultung und den Ausdruck "Ophiolitisch". E. Zeitschrift der Deutschen Geologischen Gesellschaft, 91: 771–773.

Sze H.-C. 1935. Ueber das Vorkommen von Callipteris conferta STERNB. in der Unteren Shihhotze Serie in Central-Shansi. Bulletin of the Geological Society of China, 14: 569–580.

Tabor N.J. & Poulsen C.J. 2008. Palaeoclimate across the Late Pennsylvanian–Early Permian tropical palaeolatitudes: a review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. Palaeogeography, Palaeoclimatology, Palaeoecology, 268: 293–310.

Talens J. & Wagner R. H. 1995.Stratigraphic implications of late Carboniferous and early Permian megafloras in Lérida, south-central trences; Comparison with the Cantabrian Mountains. Coloquios de Paleontología,47: 177–92.

Taylor T.N., Taylor E.L. & Krings M. 2009. Paleobotany: the biology and evolution of fossil plants. Academic Press, Elsevier: Amsterdam.

Teichmüller R. 1931. Zur Geologie des Tyrrhenisgebietes. Teil 1: Alte und junge Krustenbewegungen im südlichen Sardinien. Abhandlungen der Gesellschaft der Wissenschaft zu Göttingen, Klasse mathematische-physische, 3: 857–950.

Teixeira C. 1944. O Antracolítico continental português. (Estratigrafia e Tectónica). Unpublished Thesis, Universidade do Porto.

Tenchov Y. 1980. Die paläozoische Megaflora von Österreich. Eine Übersicht. verhandlungen der geologischen bundesanstalt, 2: 161–174.

Testa L. 1914. Il terreno carbonifero a sud di Monteponi. Resoconti delle Riunioni della Associazione Mineraria Sarda, Allegato D, 19: 31–34.

Thomas B.A. & Seyfullah L.J. 2016. Two new species of megasporangiate Sigillariostrobus

Schimper (Sigillariostrobaceae) fructifications from the British Coal Measures. Mitteilungen aus dem Museum für Naturkunde in Berlin. Fossil Record, 19: 1–9.

Thomas B.A. 2014. In situ stems: preservation states and growth habits of the Pennsylvanian (Carboniferous) calamitaleans based upon new studies of Calamites Sternberg, 1820 in the Duckmantian at Brymbo, North Wales, UK. Palaeontology, 57(1): 21–36.

Thomas H.H. 1933. On some pteridospermous plants from the Mesozoic rocks of South Africa. Philosophical Transactions of the Royal Society of London. Series B, 222: 193–265.

Trunkó L. & Munk W. 1990. Makrofloren aus dem Unterrotliegenden (Unterperm) von Alsenz bei Bad Kreuznach. Rheinland-Pfalz, Carolinea, 48: 21–30.

Uhl D. & Jasper A. 2016. New data on the macroflora of the basal Rotliegend group (Remigiusberg Formation; Gzhelian) in the Saar-Nahe Basin (SW-Germany). Fossil Imprint, 72(3-4): 239–250.

Ullrich H. 1964. Zur stratigraphie und Paläontologie der marin-beeinflussten Randfazies des Zechsteinbeckens in Ostthiiringen und Sechsen. Verlag für Grundstoffindustrie, Freiburg Forschungsh., C 169: 1–163.

Unger F. 1850. Genera et Species Plantarum Fossilium, APUD Wilhelmum Braumueller, Wien.

Vai G.B. & Izart A. 2000. Moscovian. Atlas Peri-Tethys, Palaeogeographical Maps-Explanatory Notes. CCGM/CGMW, Paris: 1–9.

Van Waveren I.M. Abbink O.A. Van Hoof T.B. & Van Konijnenburg-van Cittert J.H.A. 2008. Revision of the late Carboniferous megaflora from the De Lutte-06 well (Twente, the Netherlands), and its stratigraphical implications. Netherlands Journal of Geosciences, 87(4), 339–352.

Van Waveren I.M., Iskandar E.A.P., Booi M. & Van Konijnenburg-van Cittert J.H.A. 2007. Composition and palaeogeographic position of the Early Permian Jambi flora from Sumatra Scripta Geologica, 135: 1–28.

Vardabasso S. 1938. Il Permico dell’Ogliastra (Sardegna Orientale) (nota preliminare). Rendiconti del Seminario della Facoltà di Scienze, 8 (1): 2–3.

Vardabasso S. 1950. Il Permico in Sardegna. Rendiconti dell’Accademia Nazionale dei Lincei (Classe di Scienze fisiche, matematiche e naturali) serie VIII, 8 (6): 540–545.

Vardabasso S. 1966. Il Verrucano sardo. Atti del Symposium sul Verrucano, Pisa settembre 1965. Società Toscana di Scienze Naturali: 293–310.

Veevers J.J. 2004. Gondwanaland from 650-500 Ma assembly through 320 Ma merger in Pangea to 185-100 Ma breakup: Supercontinental tectonics via stratigraphy and radiometric dating. Earth-Science Reviews, 68: 1–132.

Virgili C., Cassinis G. & Broutin J. 2006. Permian to Triassic sequences from selected continental areas of soutwestern Europe. In Lucas S.G., Cassinis G. & Schenider J.W. (eds). Non-Marine Permian Biostratigraphy an Biochronology. Geological Society of London, Special Publications, 265: 231–259.

Visscher H., Kerp J.H.F. & Clement-Westerhof J.A. 1986. Aspects of Permian palaeobotany and palynology. VI. Towards a flexible system of naming Palaeozoic conifers. Acta botanica neerlandica, 35: 87–100.

Wagner R.H. & Álvarez-Vázquez C. 2010. The Carboniferous floras of the Iberian Peninsula: a synthesis with geological connotations. Review of Palaeobotany and Palynology, 162: 239–324.

Wagner R.H. & Castro M.P. 1998. Neuropteris obtusa, a rare but widespread Late Carboniferous pteridosperm. Palaeontology, 41: 1–22.

Wagner R.H. & Lemos de Sousa M.J. 1983. The Carboniferous megafloras of Portugal - a revision of identifications and discussion of stratigraphic ages. In Lemos de Sousa M.J. & Oliveira J.T. (eds). The Carboniferous of

Portugal: Memórias dos Serviços Geológicos de Portugal (Lisboa), 29: 127–152.

Wagner R.H. & Martínez García E. 1982. Description of an early Permian flora from Asturias and comments on similar occurrences in the Iberian Peninsula. Trabajos de Geología, Universidad de Oviedo, 12: 273–287.

Wagner R.H. & Mayoral E.J. 2007. The Early Permian of Valdeviar in Sevilla province, SW Spain: basin history and climatic/palaeogeographic implications-El Pérmico Inferior de Valdeviar (Sevilla), SW de España: geología histórica de la cuenca e implicaciones climáticas y paleogeográficas. Journal of Iberian Geology, 33: 93–124.

Wagner R.H. & Winkler Prins C.F. 1970. The stratigraphic succession, flora and fauna of Cantabrian and Stephanian A rocks at Barruelo (prov. Palencia), NW Spain: Congrès et Colloques Université de Liège, 55: 487–551.

Wagner R.H. 1958. Pecopteris pseudo-bucklandi Andrae and it generical affinities. Mededelingen van de Geologische Stichting, New Series, 12, 25-30.

Wagner R.H. 1984. Megafloral zones of the Carboniferous. Compte Rendu 9ème Congrès International du Carbonifère, Washington and Champaign-Urbana 1979 : 109–134.

Wagner R.H. 1993. Climatic significance of the major chronostratigraphic units of the Upper Palaeozoic. In Proceedings of the 12th International Congress on Carboniferous/Permian Stratigraphy and Geology (Buenos Aires, 1991). Nanjing University Press, Nanjing, 1: 83–108.

Wang J., Kerp H., & Pfefferkorn H. W. 2014. The earliest occurrence of peltasperms in the basal Permian strata of the North China Block and the radiation of this group. Geological Journal, 49, 129–142.

Wang J., Pfefferkorn, H.W., Zhang Y. & Feng Z. 2012. Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. Proceedings of the National Academy of Sciences, 109: 4927–4932.

Wang Z.-Q. & Chen A.-S. 2001. Traces of arborescent lycopsids and dieback of the forest vegetation in relation to the terminal Permian mass extinction in North China. Review of Palaeobotany and Palynology, 117(4): 217–243.

Weiss C.E. 1869–72. Fossile Flora der jüngsten Steinkohlenformation und des Rothliegenden im Saar-Rhein-Gebiete. A. Henry, Bonn.

Weiss C.E. 1870. Studien uber Odontopteriden. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften, 22: 853–888.

Werneburg R., Ronchi A. & Schneider J.W. 2007. The Early Permian branchiosaurids (Amphibia) of Sardinia (Italy): systematic palaeontology, palaeoecology, biostratigraphy and palaeobiogeographic problems. Palaeogeography, Palaeoclimatology, Palaeoecology, 252: 383–404.

Werneburg, R., Schneider, J.W., 2006. Amphibian biostratigraphy of the European Permo-Carboniferous. In: Lucas, S.G., Schneider, J.W., Cassinis, G. (Eds.), Non-Marine Permian Biostratigraphy and Biochronology. Geological Society Special Publication: 201–215.

Westphal M. & Orsini J.B. & Vellutini P. 1976. Le micro-continent corso-sarde, sa position initiale: données paléomagnétiques et raccords géologiques. Tectonophysics, 30: 141–157.

Wilkinson L. 2006. Revising the Pareto Chart. The American Statistician, 60(4): 332–334.

Wood H.C. 1860. Contributions to the Carboniferous flora of the United States. Academy National Philadelphia, Proceedings, 12.

Yan M.-X., Liu, L. & Wang J. 2017. Taeniopteris cf. multinervis Weiss with cuticle anatomy from the lower Permian of Baode, North China. Palaeoworld, 26, 83–94.

Zeiller R. 1888. Etudes sur le terrain houiller de Commentry. II. Flore fossile (B. Renault & Zeiller R.). Atlas Société Industrie minérale, II: 1–366.

Zeiller R. 1906. Bassin houiller et Permien de Blanzy et du Creusot. II. Flore fossile, Études «

Gîtes minéraux de la France », ministère des Travaux Publics, Paris, France.

Zenker F. C. 1833. Beschreibung von Galium sphenophylloides. Neues Jahrbuch für Mineralogie Geognosie, Geologie und Petrefaktenkunde, 4: 398–400.

Ziegler A.M. 1990. Phytogeographic patterns and continental configurations during the Permian Period. Geological Society, London, Memoirs, 12(1): 363–379.

Ziegler P. A. & Stampfli G. M. 2001. Late Palaeozoic-Early Mesozoic plate boundary reorganization: collapse of the Variscan orogen and opening of Neotethys. In G. Cassinis (ed), Permian continental deposits of Europe and other areas. Regional reports and correlations. Natura Bresciana, Museo Civico di Scienze Naturali, 25: 17–34.

Zodrow E.L., Mastalerz M., Orem W.H., Šimůnek Z. & Bashforth A.R. 2000. Functional groups and elemental analyses of cuticular morphotypes of Cordaites principalis (Germar) Geinitz, Carboniferous Maritimes Basin, Canada. International Journal of Coal Geology, 45: 1–19.

Zodrow E.L., Šimůnek Z., Cleal C.J., Bek J. & Pšenička J. 2006. Taxonomic revision of the Palaeozoic marattialean fern Acitheca. Review of Palaeobotany and Palynology, 138: 239–280.

Appendix 1

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Middle Pennsylvanian vegetation of the San Giorgio Basin, southern Sardinia (Italy)

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Abstract – The small, intramontane San Giorgio Basin in southwestern Sardinia has yielded plant macrofossils dominated by sphenophytes, but with subsidiary pteridosperms, ferns, (?)noeggerathians and cordaitanthaleans. They belong to the upper part of the *Crenulopteris acadica* Zone or possibly the *Odontopteris cantabrica* Zone, indicating a late Asturian or Cantabrian (≡ late Moscovian) age. They therefore correlate with the post-Leonian deposits in northern Spain, the Nýřany Member in Western and Central Bohemia, and the Llantwit Beds in South Wales. The presence of post-tectonic deposits of this age is further evidence of the widespread influence of the Leonian Phase of tectonic activity in middle Asturian times, whose effect can be observed across Europe. The San Giorgio Basin is therefore a late Variscan rather than post-Variscan basin.

Keywords: palaeobotany, biostratigraphy, Moscovian, Sardinia.

1. Introduction

The best documented Pennsylvanian (upper Carboniferous) succession in Sardinia is in the small, intramontane San Giorgio Basin near Iglesias, in the southwest of the island (Fig. 1), in an area where the landscape has been extensively modified by extensive mining activity since the 19th century (Scanu *et al.* 2016). Although of restricted lateral extent and vertical thickness, these deposits have yielded abundant plant macrofossils and palynofloras, as well as occasional arachnoid, insect and tetrapod remains (Fondi, 1979; Del Rio, Pillola & Muntoni, 2002; Pillola *et al.* 2004; Selden & Pillola, 2009). Plant macrofossils were first recorded by Gambera (1897), Testa (1914), Novarese (1917) and Novarese & Taricco (1923), and the earliest attempt at a taxonomic treatment was by Cocozza (1967). Despite large parts of the basin having become obscured by spoil tipped from the nearby Campo Pisano lead and zinc mine, there has been continued interest in the geology (e.g. Barca & Costamagna, 2003), and palaeobotany (Pittau & Del Rio, 2002; Del Rio, Pillola & Muntoni, 2002; Del Rio & Pittau *in* Barca *et al.* 2004, p. 16; Ronchi *et al.* 2012), including the relationship between floral changes, basin evolution and Variscan chain elevation (Pittau, Del Rio & Funedda, 2008).

There have been disagreements about the age of these deposits. Novarese (1917) and Novarese & Taricco (1923) argued for an Autunian age based partly on the reported presence of walchian conifer remains. Merlo (1911) and Testa (1914) proposed a general Carboniferous age, while Cocozza (1967) suggested a late Stephanian age ('Stephanian D' *sensu* Doubinger, 1956), based on the presence of species such as *Neuropteris planchardii* and *Callipteridium pteridium*, as well as rare walchian conifers. A slightly older, Stephanian B age was suggested by Del Rio (1973), Del Rio & Pittau (1999) and Pittau & Del Rio (2002) based mainly on palynology. Most recently, Fondi (1979) used evidence of tetrapod footprints to argue for a late Westphalian age.

With the aim of resolving this issue, this paper gives a revised taxonomic synopsis of the San Giorgio Basin macroflora and will attempt to place it in the most recent biostratigraphical scheme developed by Wagner (1984, 1998), Cleal (1991) and Cleal & Thomas (1994). An attempt will also be made to provide a palaeoenvironmental interpretation of the basin during Pennsylvanian times.

2. Geological background

As in the rest of southern Europe, the upper Palaeozoic deposits of Sardinia represent two major tectono-sedimentary megacycles (Cassinis & Ronchi, 1997, 2002; Cassinis, Perotti & Ronchi, 2013): (1) upper Carboniferous to early Guadalupian volcanic to fluvio-lacustrine deposits formed in relatively small

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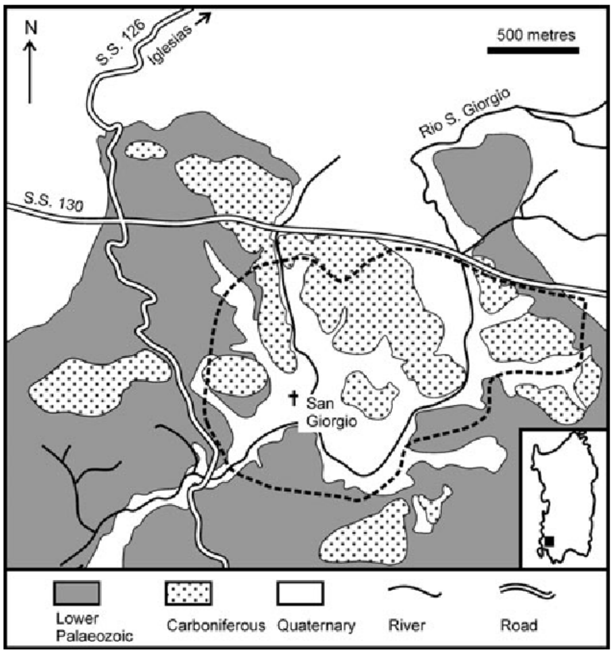

Figure 1. Simplified geological map of the Pennsylvanian-age San Giorgio Basin, SE Sardinia. The dashed line delineates the area now covered by spoil from the nearby Campo Pisano lead and zinc mine. Adapted from Del Rio & Pittau (1999, fig. 7) and Barca & Costamagna (2003, fig. 1).

extensional basins, and (2) arid upper Guadalupian and Lopingian deposits. The small fault-bounded intramontane San Giorgio Basin is the stratigraphically oldest of the basins in Sardinia representing the earlier megacycle (Pittau, Del Rio & Funedda, 2008).

The basin, which is of only about 3 km^2 aerial extent (Del Rio & Pittau *in* Barca *et al.* 2004, p. 16), was the result of extensional tectonics (Barca & Costamagna, 2003; Cassinis, Perotti & Ronchi, 2013). It contains *c.* 45 m of mainly coarse clastic deposits with subsidiary finer-grained deposits (together referred to the San Giorgio Formation) lying unconformably on the upper Cambrian – lower Ordovician Cabitza Shales Formation (Barca & Costamagna, 2003; Barca *in* Barca *et al.* 2004, p. 15). Three lithostratigraphical units are now recognized (Del Rio, Pillola & Muntoni, 2002; Del Rio & Pittau *in* Barca *et al.* 2004, p. 16), in the following ascending stratigraphical order (Fig. 2).

Unit A: 0–13 m of mainly breccias with dolomitic cement, with subsidiary dolomite and dolomitic siltstone in the lower part.

Unit B: 6–15 m of mainly yellow-grey dolomites with subsidiary well-bedded breccias, siltstones and mudstones, and capped by massive sandstone.

Unit C: 6–11 m of mainly conglomerates, with subsidiary sandstones.

The sequence has been interpreted as a series of debris and mass flow deposits resulting from rapid erosion of the immediately adjacent lower Palaeozoic basement, separated by lacustrine siltstones and mudstones representing intervals of reduced subsidence (Barca & Costamagna, 2003). The fossils mostly occur in the lacustrine deposits.

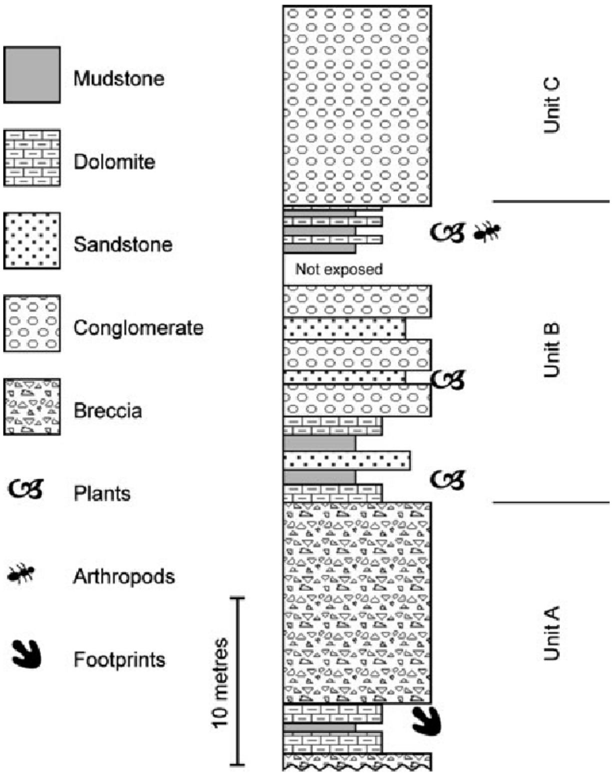

Figure 2. Simplified geological section through the Carboniferous sequence of the San Giorgio Basin, showing main fossiliferous horizons. Re-drawn from Barca & Costamagna (2003, fig. 7).

3. Materials and methods

The fossil plants of the Pittau – Del Rio Collection stored in the Geological and Palaeontological Museum of Cagliari University (MGPDL) were collected over the last 20 years during several field trips to the San Giorgio Basin. The matrix of the specimens was cleaned with a small, rigid-bristled brush, and the plant remains were cleaned with a paintbrush with soft bristles. Fractured specimens were consolidated using Paraloid B72.

In situ spores were isolated by taking a small quantity of organic material from the cones with a pointed needle. The organic material was dissolved using HCl (30 %) and HF (37 %), washed with water and cleaned up with ultrasound to separate the spores from the cone tissue. Any resulting spores were mounted with synthetic resin in permanent slides for study.

4. Palaeobotany

In the following analysis, the plant fossils have been named using fossil-taxa as defined by McNeill *et al.* (2012), with each taxon referring to a particular plant part, life history stage and preservation state as defined in its diagnosis. More detailed descriptions of the fossils are provided in the online Supplementary Material (available at http://journals.cambridge.org/geo). The systematic positions of the species discussed are shown in Table 1.

Table 1. Summary of systematic position of the fossil-genera reported in this paper from the San Giorgio Basin.

Class	Family	Fossil-genus
Equisetopsida	Calamostachyaceae	*Annularia* Sternberg, 1821
		Palaeostachya Weiss, 1876
		Calamites Sternberg, 1820
		Pinnularia Lindley & Hutton, 1834
	Sphenophyllaceae	*Sphenophyllum* Brongniart, 1828*b*, nom. cons.
Marattiopsida	Psaroniaceae	*Cyathocarpus* Weiss, 1869
		Crenulopteris Wittry *et al.* 2015
	Marattiaceae	*Sydneia* Pšenička *et al.* 2003
Polypodiopsida	?	*Renaultia* Zeiller, 1883
Noeggerathiopsida		*Discinites* Feistmantel, 1879
Lyginopteridopsida	Lyginopteridaceae	*Eusphenopteris* Simson-Scharold, 1934, nom. cons.
	Callistophytaceae	*Dicksonites* Sterzel, 1881
Cycadopsida	Alethopteridaceae	*Alethopteris* Sternberg, 1825
		Trigonocarpus Brongniart, 1828*b*
		Neuropteris (Brongniart) Sternberg, 1825
	Potonieaceae	*Linopteris* Presl *in* Sternberg, Presl & Corda, 1838
Pinopsida	Cordaianthaceae	*Artisia* Sternberg *in* Sternberg, Presl & Corda, 1838

Annularia sardiniana sp. nov.
Figures 3 a–c, 6i

Diagnosis. Leafy shoots with circular leaf whorls of typically 36 mm (sometimes up to 70 mm) diameter; each whorl with 11–30 (typically 20) linear-lanceolate, 2.0–2.5 mm wide, rather lax leaves with acute to bluntly acute apex, basally fused to 1.0–1.5 m wide collar.

Holotype. MGPDL 17397 (Fig. 3a), San Giorgio, near Iglesias (Sardinia, Italy), San Giorgio Fm, Carboniferous (Middle Pennsylvanian).

Etymology. Named for Sardinia, the region where this species has been described for the first time.

Remarks. This is by far the most abundant fossil-species in the San Giorgio flora and was evidently the foliage of the plant that dominated the vegetation within the main, wetland part of the basin. It is readily distinguished from all other previously described *Annularia* species in the size of the leaf whorls, and the wide basal collar to which the leaves of each whorl are fused. *Annularia spinulosa* Sternberg, 1821 has similar sized leaf whorls, but in the latter the whorls often have an oval outline, the leaves tend to have a more rigid appearance and are often terminated by a mucronate tip, and the basal collar of the whorls is far narrower. *Annularia pseudostellata* Potonié, 1899 also has similar sized leaves which can also have a rather lax appearance, but differ from *A. sardiniana* in the leaves being much more slender and lacking a basal collar. The only other species reported from a Pennsylvanian flora of Euramerica with a well-developed basal collar to each leaf whorl is *Annularia rallii* (Zeiller) Jongmans, 1955 (= *Phyllotheca rallii* Zeiller, 1899) from northern Turkey. However, the leaf whorls are much smaller.

Annularia spinulosa Sternberg, 1821
Figure 3d, e

Remarks. This is the species that has traditionally been referred to as *Annularia stellata* (Schlotheim) Wood, 1869, but which Barthel (2000) showed to be more correctly named *Annularia spinulosa*. It is a very distinctive species with large whorls of leaves that has been widely reported from upper Westphalian, Stephanian and Autunian floras of Europe and North America (e.g. Abbott, 1958; Crookall, 1969; Laveine, 1989). It differs from *Annularia sardiniana* sp. nov. in that the leaf whorls often have a distinctly oval outline, and the individual leaves tend to have a more rigid outline, be widest in the distal part, and often terminated in a small, mucronate tip. Although the two species occur at the same locality in Sardinia, they are found in distinctly different rock layers. A specimen from San Giorgio was figured by Del Rio, Pillola & Muntoni (2002, Fig. 3) as *Annularia stellata*.

Annularia sphenophylloides (Zenker) Gutbier, 1837
(= *Galium sphenophylloides* Zenker, 1833)
Figure 3f

Remarks. This distinctive species was represented by a single fossil preserving two leafy shoots. The small, spathulate leaves are quite different from the other species found in this flora. Like *A. spinulosa*, this species has been widely reported from upper Westphalian, Stephanian and Autunian floras of Europe and North America (e.g. Abbott, 1958; Crookall, 1969; Laveine, 1989).

Annularia galioides (Lindley & Hutton) Kidston, 1891 (= *Asterophyllites galioides* Lindley & Hutton, 1832)
Figure 3g

Remarks. Details are difficult to see because the specimen is preserved among mineral growth. Nevertheless, the small, lanceolate leaves resemble closely this species. There is also some comparison with *Annularia spicata* Gutbier (as figured by Barthel, 2012) but the latter tends to have smaller and more slender leaves, and more leaves per whorl.

Palaeostachya sp.
Figures 3h, i, 4a, 5c

Remarks. These cones were found in close association with the *Annularia sardiniana* sp. nov. foliage and they

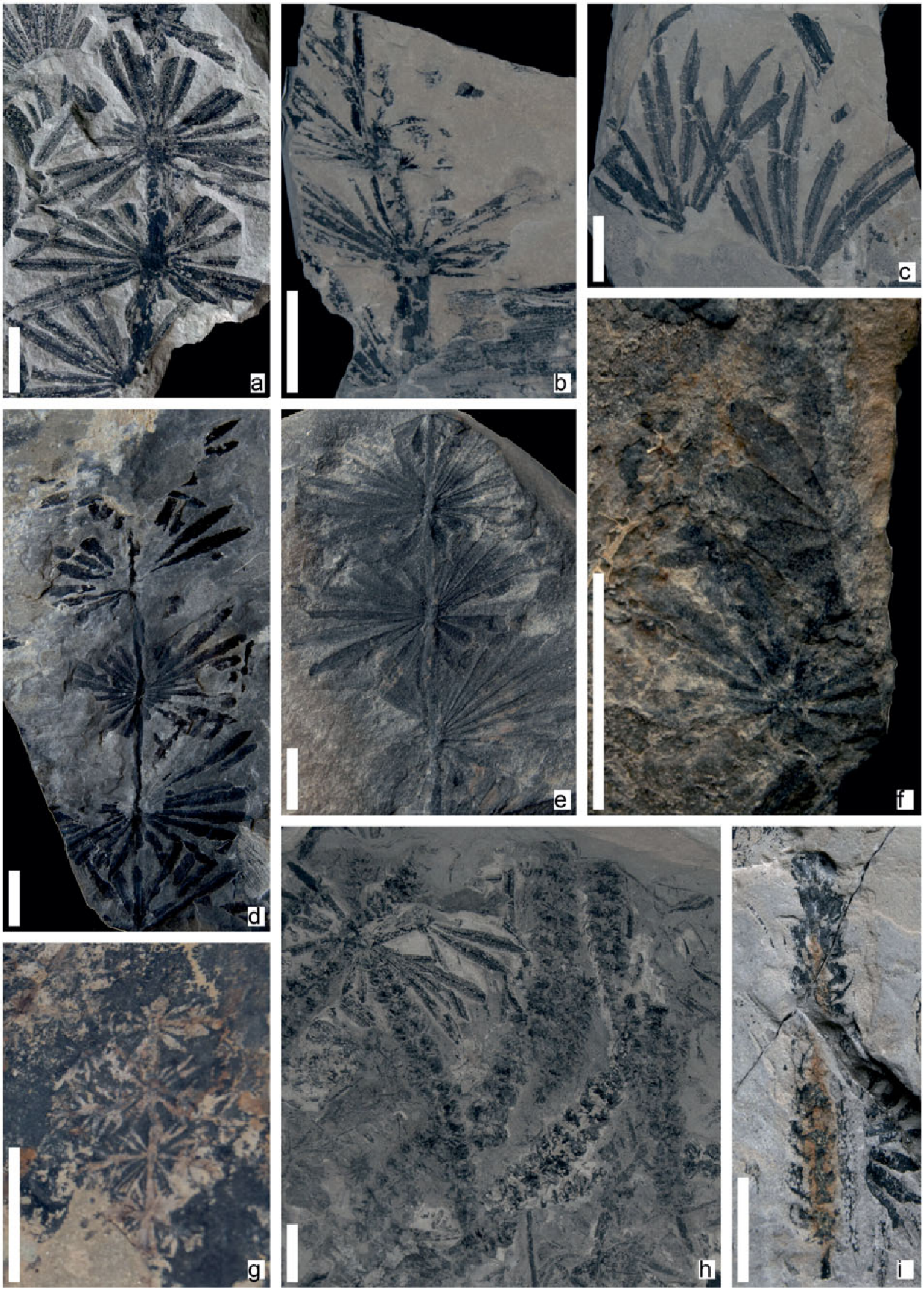

Figure 3. (Colour online) Pennsylvanian plant fossils from the San Giorgio Basin, Sardinia. (a–c) *Annularia sardiniana* sp. nov. (a: MGPDL 17397, holotype; b: MGPDL 17155; c: MGPDL 17111); (d, e) *Annularia spinulosa* Sternberg, 1821 (d: MGPDL 17406; e: MGPDL 17223); (f) *Annularia sphenophylloides* (Zenker) Gutbier, 1837 (MGPDL 17193); (g) *Annularia galioides* (Lindley & Hutton) Kidston, 1891 (MGPDL 17201); (h, i) *Palaeostachya* sp. (h: MGPDL 17399; i: MGPDL 17134).

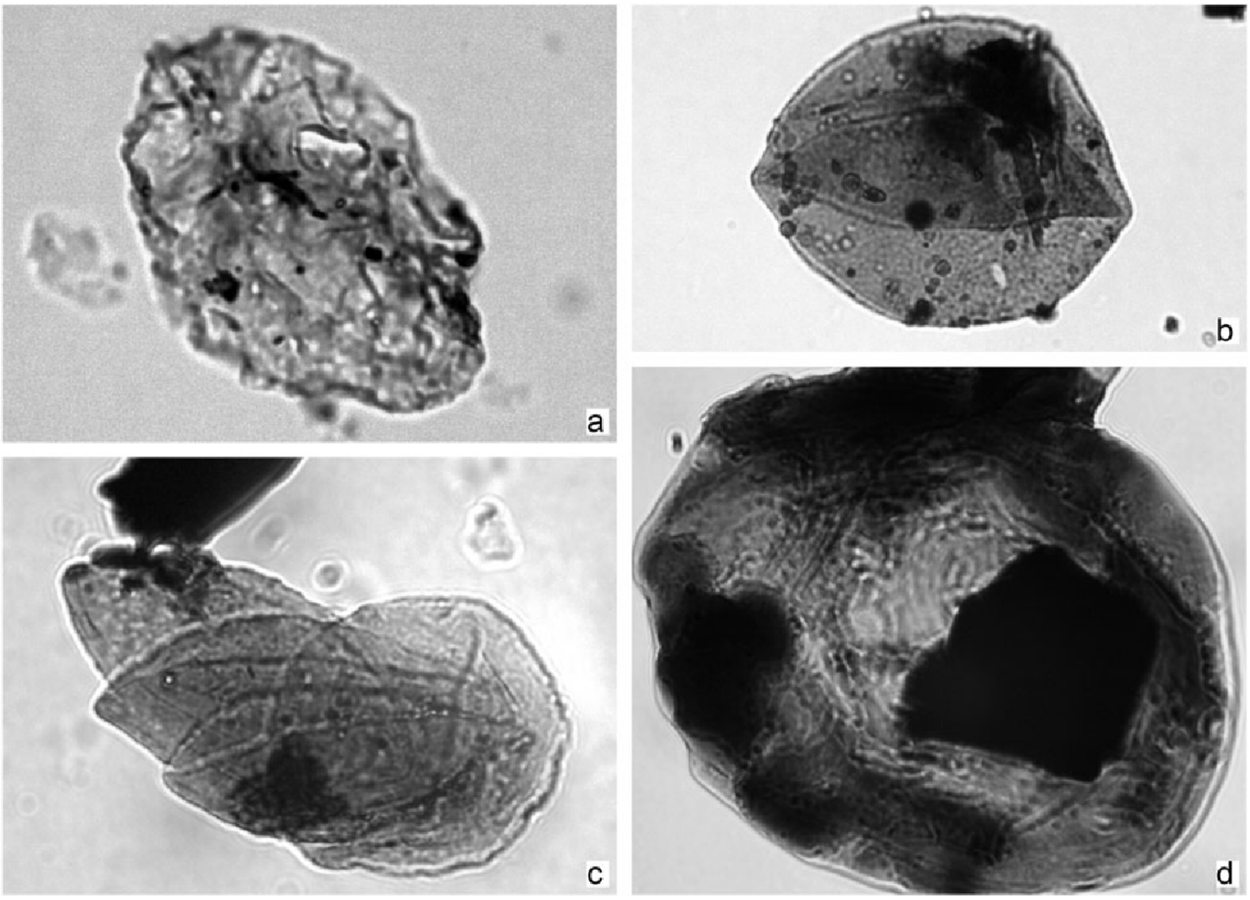

Figure 4. Pennsylvanian *in situ* spores from the San Giorgio Basin, Sardinia. (a) *Calamospora* sp. from *Palaeostachya* sp. cone (MGPDL 17135); (b) *Cyclogranisporites aureus* (Loose) Potonié & Kremp, 1955 from *Sydneia* sp. (MGPDL 17200); (c) *Cyclogranisporites multigranus* Smith & Butterworth, 1967 from *Renaultia* sp. cf. *Renaultia villosa* (Crépin) Danzé, 1956 (MGPDL 17218); (d) ?*Latosporites* sp. from ?*Discinites* sp. (MGPDL 17172).

probably belonged to the same plants. They occur at different stages of maturity, in some cases with the bracts strongly curved (e.g. Fig. 3i) so their distal ends are parallel to the cone axis (assumed to be immature) and in others with the bracts extending directly out from the cone (assumed to be mature). They are also in different stages of decay such that in some cases the cones are starting to fall apart and thereby reveal aspects of their internal structure. Some such cones, for instance, clearly show the sporangiophores being attached to the axil of the bract and cone axis, indicating they belong to the fossil-genus *Palaeostachya* (Cleal & Thomas, 1994).

As with other Pennsylvanian-age *Palaeostachya* cones (Balme, 1995) those from the San Giorgio Basin yielded *Calamospora in situ* spores (Fig. 4a); *Calamospora microrugosa* (Ibrahim) Schopf, Wilson & Bentall, 1944 is well represented in the dispersed palynological assemblages from the basin (Pittau, Del Rio & Funedda, 2008). However, spores are not important taxonomic characters in calamostachyacean cones (Bek & Opluštil, 1998). A more important obstacle to providing a species identification for the cones is that they are all more or less fragmentary and their mode of attachment to the rest of the plant is not preserved. For this reason, we have opted to record these cones merely as *Palaeostachya* sp. (contrast with a newly described species based on more complete material: Cleal & Shute, 2016).

Calamites sp.
Figure 5a, b

Remarks. From the prominence of the longitudinal ribs and the absence of branch scars, these appear to be pith casts rather than stem compressions. The distinctive feature was the very long internode distances, much larger than is typical in the most common fossil-species such as *Calamites cistii* Brongniart, 1828*a*. However, the preservation especially of the node ends and their tubercles makes it impossible to assign them meaningfully to any fossil-species.

Cocozza (1967, figs 17, 18) figured similar *Calamites* specimens from San Giorgio as *Calamites suckowii* Brongniart, 1828*a*, *Calamites* sp. cf. *Calamites suckowii*, *Calamites gigas* Brongniart, 1828*a* and *Calamites* cf. *leioderma* Gutbier.

?*Pinnularia* sp.

Remarks. This fragment can be compared with the specimen figured by Crookall (1969, pl. 109, fig. 8) as

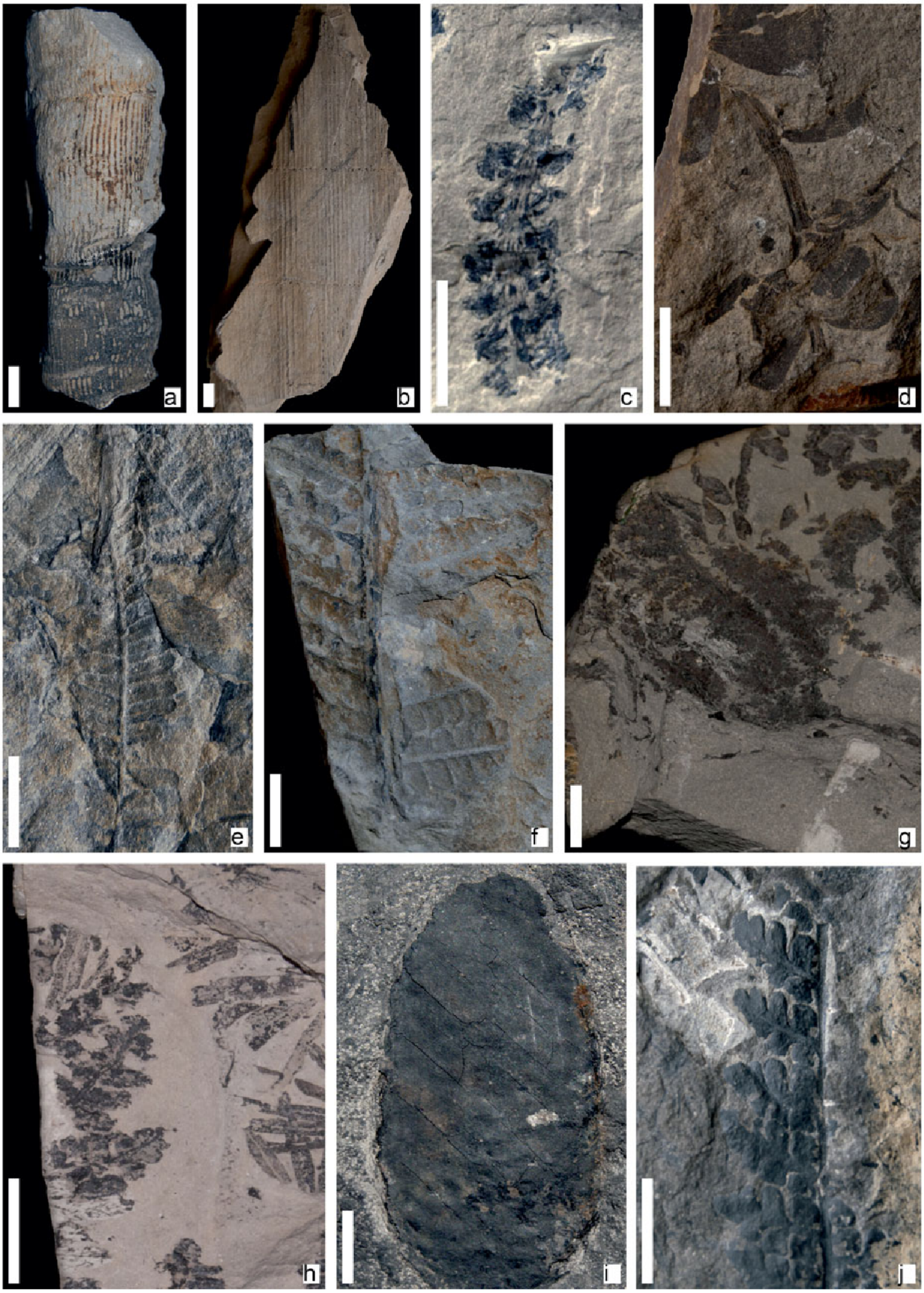

Figure 5. (Colour online) Pennsylvanian plant fossils from the San Giorgio Basin, Sardinia. (a, b) *Calamites* sp. (a: MGPDL 17162; b: MGPDL 17400); (c) *Palaeostachya* sp. (MGPDL 17135); (d) *Sphenophyllum* sp. cf. *Sphenophyllum emarginatum* (Brongniart) Brongniart, 1828*b* (MGPDL 17408); (e) *Cyathocarpus* sp. (MGPDL 17390); (f) ?*Crenulopteris* sp. (MGPDL 17212); (g) ?*Sydneia* sp. (MGPDL 17200); (h) *Renaultia* sp. cf. *Renaultia villosa* (Crépin) Danzé, 1956 (MGPDL 17187); (i) ? *Discinites* sp. (MGPDL 17172); (j) *Eusphenopteris nummularia* (Gutbier) van Amerom, 1975 (MGPDL 17400).

Pinnularia capillaceae Lindley & Hutton, 1834. However, it is so small that the identification must be regarded as tentative.

Sphenophyllum cf. *emarginatum* (Brongniart)
Brongniart, 1828*b*
Figure 5d

Remarks. Although this tiny fragment is undoubtedly a *Sphenophyllum* and the leaf shape appears to indicate *S. emarginatum*, it is far too incomplete for definite identification at species level.

Cyathocarpus sp.
Figure 5e

Remarks. These small fragments of fern frond with small, linguaeform, somewhat elongate pinnules clearly resemble *Cyathocarpus* but are too fragmentary for a species identification.

?*Crenulopteris* sp.
Figure 5f

Remarks. We are using this fossil-genus in the sense of Wittry *et al.* (2015) for the species that had previously been incorrectly assigned to *Lobatopteris* Wagner, 1959. This type of marattialean fern is represented here by just two frond fragments. Neither is well enough preserved to allow a species identification, or even to be certain that they belong to the same species. The specimen with pinnatifid pinnae bears some resemblance to '*Pecopteris*' *camertonensis* (Kidston) Wagner, 1959 as figured by Kidston (1924, pl. 122, fig. 1), but is too small to confirm the identity.

?*Sydneia* sp.
Figures 4b, 5g

Remarks. The affinities of this specimen are uncertain. The shape and arrangement of the sporangia has some resemblance to the putative marattiacean fern *Sydneia* Pšenička *et al.* 2003, but yielded trilete spores (resembling the dispersed species *Cyclogranisporites aureus* (Loose) Potonié & Kremp, 1955) rather than monolete spores (Fig. 4b).

Renaultia cf. *villosa* (Crépin) Danzé, 1956
Figures 4c, 5h

Remarks. When fertile, these small, lobed pinnules are covered by small, globular sporangia, clearly resembling *Renaultia* as documented by Brousmiche (1983). The small, oblique, somewhat pecopteroid pinnules resemble *Renaultia villosa* as figured by Brousmiche (1983, pl. 47; see also Danzé, 1956, pl. 27). However, the San Giorgio specimens are too fragmentary for a definite species identification.

The spores obtained from the San Giorgio specimens (Fig. 4c) have a cingulum similar to *Lycospora*, but they do not always develop an equatorial crassitude. They compare with the dispersed species *Cyclogranisporites multigranus* Smith & Butterworth, 1967 and are rather larger than those reported by Brousmiche (1983) from *Renaultia villosa*, which have a diameter of *c.* 25 µm).

?*Discinites* sp.
Figures 4d, 5i

Remarks. There is little structure visible on the surface of this cone, other than lozenge-shaped markings, which may be at least partly taphonomic in origin. The miospores found in the cone (Fig. 4d) were similar to *Latosporites* Potonié & Kremp, 1954 and *Punctatosporites* (Ibrahim) Potoné & Kremp, 1954, and are similar to the dispersed *Latosporites* found in the microflora assemblages of the same section (Pittau, Del Rio & Funedda, 2008). It is likely that the *in situ* spores were at different stages of ontogenetic development, with the glossy specimens being immature, and those with intra-structured exine being more mature or even possibly somewhat degraded; in dispersed palynomorph assemblages, these stages would be attributed to different pollen species and genera. Spores of *Latosporites*–*Laevigatosporites* have been reported from glossopteridalean cones (Surange & Chandra, 1974) and *Sphenophyllalean strobili* (Libertin, Bek & Dràbkovà, 2014).

Eusphenopteris nummularia (Gutbier) van Amerom,
1975 (= *Sphenopteris nummularia* Gutbier, 1835)
Figure 5j

Remarks. Although only small specimens, they show the distinctive subtriangular pinnules with a vaulted limb that is a very characteristic feature of this species. Van Amerom (1975) has given the best photographic documentation and a detailed account of the taxonomy of this species. A previous record of this species from Sardinia (Del Rio, 2002, fig. 4) has been under the name *Sphenopteris rotundiloba* Němejc, 1937, which is very similar to *E. nummularia* except that the pinnules and pinnae are significantly larger.

Dicksonites plukenetii (Schlotheim ex Sternberg)
Sterzel, 1881 (= *Pecopteris plukenetii* Schlotheim ex
Sternberg, 1825
Figure 6a

Remarks. The short, squat, parallel-sided pinnules with a vaulted limb and angular lobes are highly characteristic for this species, and compare closely with the specimens figured by Galtier & Béthoux (2002). The figures of specimens from San Giorgio in Cocozza (1967) are not very clear but appear to be of a *Dicksonites* and so are assumed to be probably of the same species. Cocozza assigned the specimens to forma *sterzelii*, presumably based on *Dicksonites sterzelii* (Zeiller) Danzé, 1956, but the latter species tends to have significantly smaller and more subtriangular pinnules than *D. plukenetii*.

Alethopteris ambigua Lesquereux, 1880
Figure 6b

Remarks. We are interpreting this species in the same sense as Zodrow & Cleal (1998), in particular in including the type of *Alethopteris lesquereuxii* Wagner, 1968 within the circumscription of *A. ambigua*. The slender, linguaeform pinnules, strong midvein and once-forked lateral veins clearly indicate this species. It

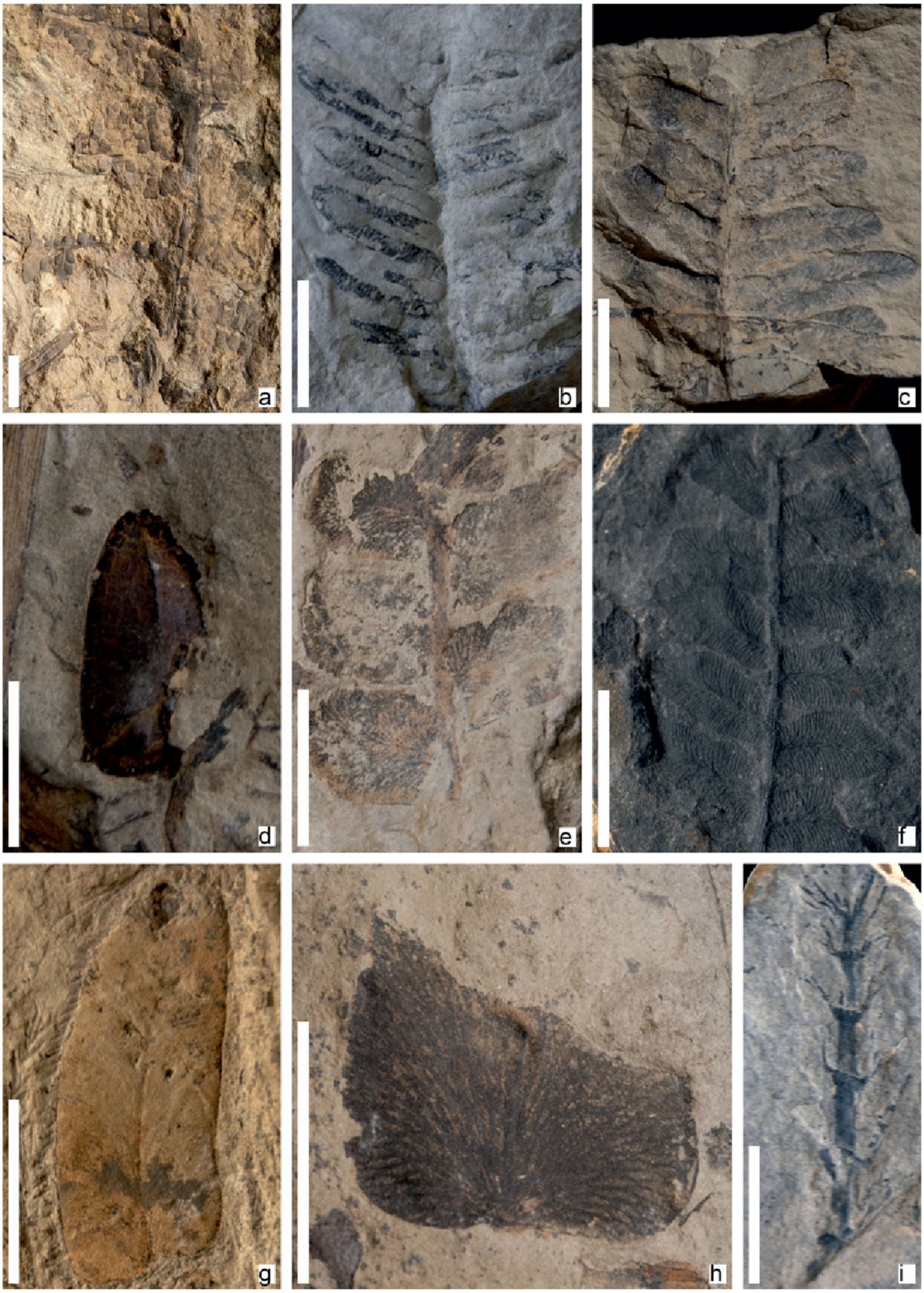

Figure 6. (Colour online) Pennsylvanian plant fossils from the San Giorgio Basin, Sardinia. (a) *Dicksonites plukenetii* (Schlotheim ex Sternberg) Sterzel, 1881 (MGPD 2764); (b) *Alethopteris ambigua* Lesquereux, 1880 (MGPDL 17117); (c) *Alethopteris* sp. (MGPDL 17409); (d) *Trigonocarpus* sp. (MGPDL 17409); (e) *Neuropteris ovata* Hoffmann, 1826 (MGPDL 17409); (f) *Neuropteris* sp. (MGPDL 17221); (g) (?)*Neuropteris* sp. (MGPDL 17170); (h) *Linopteris* sp. cf. *Linopteris obliqua* (Bunbury) Zeiller emend. Zodrow, Tenchov & Cleal, 2007 (MGPDL 17409); (i) *Annularia sardiniana* sp. nov. (MGPDL 17133).

can be distinguished from *Alethopteris pennsylvanica* Wagner, 1968 in that the latter has more widely spaced pinnules that tend to be basally fused, and the veins lie at nearer to right-angles to the pinnule margin. Also similar is *Alethopteris leonensis* Wagner, 1964, but this has more tapered, decurrent pinnules with a less rounded apex, a less prominent midvein and less dense lateral veins (Wagner & Álvarez-Vázquez, 2010*a*).

Alethopteris sp.
Figure 6c

Remarks. Although clearly alethopterid and having a rather denser venation than the *A. ambigua* specimens, these pinnules are too small to identify to species.

Trigonocarpus sp.
Figure 6d

Remarks. The species taxonomy of these ovules when preserved as casts or adpressions remains highly confused (e.g. see comments by Gastaldo & Matten, 1978), with few published species being adequately circumscribed.

Neuropteris ovata Hoffmann, 1826
Figure 6e

Remarks. Although small, this specimen appears to have the characteristic venation of *N. ovata*. The density of veining and squat form of pinnules make it close to the characteristically Stephanian *N. ovata* var. *grandeuryi* Wagner, 1963.

Neuropteris sp.
Figure 6f

Remarks. This specimen differs from that assigned to *N. ovata* in the pinnules being less squat, the midvein being longer and the veining generally being more thickly marked.

(?)*Neuropteris* sp.
Figure 6g

Remarks. These isolated pinnules are impossible to identify to species or even definitely to genus. Cocozza (1967) identified one specimen as *Neuropteris planchardii* Zeiller, 1888 (= *Neurocallipteris planchardii* (Zeiller) Cleal, Shute & Zodrow, 1990) but that species does not have the subfalcate pinnules with a markedly cordate base as seen in the San Giorgio specimens. There is a superficial similarity with some *Paripteris* species, but they also do not have a cordate base and the midvein is generally not as thick. Some comparison can also be made with the larger pinnule forms of *Laveineopteris* such as *Laveineopteris jongmansii* (Crookall) Cleal & Shute, 1995 but the veins in the San Giorgio specimens are much denser and finer.

Linopteris cf. *obliqua* (Bunbury) Zeiller emend.
Zodrow, Tenchov & Cleal, 2007
Figure 6h

Remarks. This small basal fragment of a pinnule undoubtedly belongs to *Linopteris* and bears some similarities to the larger pinnules of *Linopteris obliqua*, notably in the shape and number of vein meshes. However, it is impossible to identify these species without evidence of the overall pinnule shape, which we cannot determine.

Artisia approximata (Brongniart ex Lindley & Hutton) Corda *in* Sternberg, Presl & Corda, 1838 (= *Sternbergia approximata* Brongniart ex Lindley & Hutton, 1837).

Remarks. This pith cast was the only cordaitanthalean remains in our collection. Cocozza (1967, fig. 20) illustrated specimens that were interpreted as *Cordaites* cf. *lingulatus* Grand'Eury, 1877. However, the vein density appears to be only about ten per centimetre across the leaf, which is rather low for *Cordaites* (compare with vein density values given in Šimůnek, 2007); these specimens could perhaps represent fine-ribbed *Calamites* similar to the specimen figured by Cocozza (1967, fig. 18a).

5. Discussion

5.a. Palaeoecology

Six lithologies were recognized among the specimens examined during this study (Fig. 7).

(I) Very pale, grey flaggy but non-laminated mudstone. This was the most commonly found lithology. In the field rocks of this facies appear medium to medium-dark grey in colour but became noticeably lighter on drying. We interpret these deposits as lacustrine.

(II) Flaggy, laminated mudstone with bands of dark mudstone within an otherwise mainly pale mudstone. This was clearly similar to Lithology I.

(III) Laminated, dark grey, hard mudstone. We also interpret these as lacustrine, possibly deposited under lower energy conditions.

(IV) Medium to coarse-grained yellow to cream coloured sandstones. These are likely to represent small-scale channel deposits.

(V) Blocky, grey mudstone with a distinctive conchoidal fracture. We interpret these as lacustrine deposits.

(VI) Medium grey mudstone with distinctive yellow to orange iron staining. In the field this was found towards the top of the fossiliferous interval, just before appearance of the overlying conglomeratic unit. We interpret these deposits as the last phases of the lacustrine fill, as the basin became better drained.

The relative abundance of the different species in these lithologies is shown in Table 2 and the general balance of major plant groups in Figure 7. We also explored the data using the Shannon t-test (Table 3) described by Magurran (1988), which compares both the species richness and species evenness of pairs of assemblages (analysis using the PAST statistical package; Hammer, Harper & Ryan, 2001). In order to get more meaningful results from the latter test, the fossil-species were rationalized into biologically more meaningful units. The sphenophyte cone records were combined with *Annularia sardiniana* sp. nov. as they were

Table 2. Distribution of taxa in the six lithologies identified in the fossiliferous sequence of the San Giorgio Basin. The numbers of specimens for each species have been adjusted using an approach summarized in the text.

	Lithofacies					
	I	II	III	IV	V	VI
Annularia sardiniana	67.75	17	18	0	0	5.6
Annularia spinulosa	0	0	0	0	11	0
Annularia galioides	1.25	0	0	0	0	0
Annularia sphenophylloides	0	0	0	0	0	1.4
Sphenophyllum cf. *emarginatum*	0	0	0	0	0	1
Cyathocarpus sp.	0	0	3	1	0	0
Crenulopteris sp.	1	0	0	0	0	2
Sydneia sp.	1	0	0	0	0	0
Renaultia cf. *villosa*	7	1	0	0	0	0
?*Discinites* sp.	0	0	1	0	0	0
Eusphenopteris nummularia	2	1	0	0	0	3
Alethopteris ambigua	1	0	0	0	0	1
Alethopteris sp.	0	0	0	0	0	1
Neuropteris ovata	0	0	0	0	0	1
Neuropteris sp.	0	0	1	0	0	0
(?)*Neuropteris* sp.	0	0	0	1	0	0
Linopteris cf. *obliqua*	0	0	0	0	0	1
Artisia approximata	0	0	0	1	0	0

all of consistent morphology and were consistently in close association with that fossil-species of foliage. The *Calamites* stems, in contrast, were allocated pro-rata to the *Annularia* species present in that facies as there was less certainty as to their affinities. The *Trigonocarpus* records were omitted from the analysis because of the uncertainty as to which medullosalean they should be assigned and, as the number of specimens was very small, the effect on the results would be expected to be negligible.

All of the results confirm the essential homogeneity of the fossil floras found in lithologies I, II and III, both in terms of overall representation of plant groups and of fossil-species. They are dominated by the sphenophyte species *Annularia sardiniana* sp. nov. with minor contributions (usually < 20 %) of ferns, medullosaleans and lyginopteridaleans. We conclude that these facies were all sampling the dominant vegetation in the basin, which consisted largely of sphenophytes that produced the *Annularia sardiniana* foliage. It is generally acknowledged that this group of plants usually favoured muddy substrates on the margins of areas of standing water or possibly fluvial channels (Gastaldo, 1992; Bashforth *et al.* 2011; Thomas, 2014).

With the exception of *Renaultia* and *Eusphenopteris*, nearly all of the other fossil-species in lithologies I, II and II were represented by isolated and usually poorly preserved fragments. It is possible that these are the remains of plants that were rare in the vegetation growing here. However, since the small fragments are generally poorly preserved compared with the sphenophyte remains, we suggest they were probably allochthonous remains of vegetation that had drifted into the basin from surrounding areas.

Lithology V compares lithologically with Lithology I except in colour and the tendency to develop conchoidal fracture. Although also probably lacustrine, the presence of a different species of calamostachyalean sphenophyte suggests that the adjacent shore had different substrate conditions.

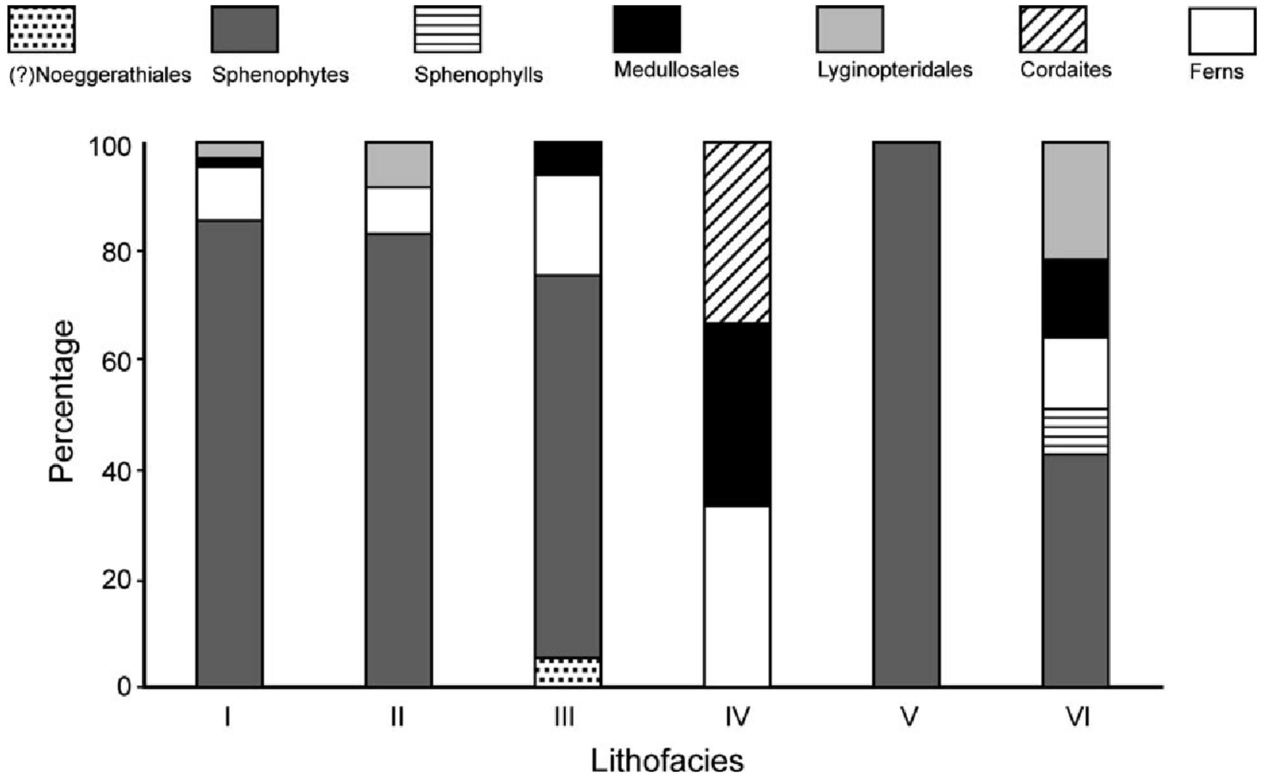

Figure 7. Distribution of the major plant groups in the six lithologies recognized in this study (see text for details).

Table 3. Comparison of fossil floras derived from the six lithologies defined in the text, using the Shannon t-test.

	II	III	IV	V	VI
I	**0.58 (d.f. = 33, p = 0.56)**	**0.86 (d.f. = 44, p = 0.40)**	**0.20 (d.f. = 4, p = 0.85)**	4.93 (d.f. = 80, $p < 0.01$)	5.15 (d.f. = 37, $p < 0.01$)
II		**1.19 (d.f. = 40, p = 0.24)**	**0.57 (d.f. = 7, p = 0.50)**	2.21 (d.f. = 19, p = 0.04)	4.54 (d.f. = 35, $p < 0.01$)
III			**0.38 (d.f. = 6, p = 0.72)**	4.22 (d.f. = 23, $p < 0.01$)	3.49 (d.f. = 40, $p < 0.01$)
IV				**2.30 (d.f. = 3, p = 0.11)**	3.03 (d.f. = 5, p = 0.03)
V					9.88 (d.f. = 17, $p < 0.01$)

Values that have a $p_{(\text{same})} > 0.05$ are shown in bold. d.f. = degrees of freedom.

The channel sandstone (Lithology IV) contained very few plant remains, other than a single piece of cordaitanthalean pith cast and a pteridosperm fragment. In contrast, Lithology VI yielded a high diversity of plant remains, including a significantly higher proportion of ferns, medullosaleans and lyginopteridaleans, as well as rare sphenophylls not seen in the other facies. Lithology VI is located at the top of the fossiliferous part of the basin fill and it seems likely that the plant remains represent vegetation that occupied the basin as it started to fill in with sediment and the water table fell. Some of the species that occur in this facies also occur as rare drifted fragments in lithologies I, II and III.

Our palaeoecological interpretation of the San Giorgio Basin is, therefore, that it was a small pull-apart basin that was partly filled with a lake whose muddy waterlogged shores supported mainly calamostachyalean sphenophytes. On the margins of the basin, rather better drained substrates supported vegetation with predominantly ferns and pteridosperms, whose remains occasionally drifted into the lake, transported either by water or wind. Even more distal vegetation away from the centre of the basin supported pteridosperms and cordaitanthaleans, and occasional fragments of these plants also found their way into the basin sediments transported along with coarser grained arenaceous deposits, perhaps representing flooding events. As the basin eventually drained and water tables fell, the fern and pteridosperm-dominated vegetation from the better drained substrates spread over the basin, replacing the calamostachyalean sphenophyte vegetation (a similar succession was noted in the Middle Pennsylvanian Nýřany Member in the Czech Republic; Bashforth *et al.* 2011).

These results are largely compatible with the palynological spectra obtained from the San Giorgio Basin by Del Rio, Pillola & Muntoni, (2002), Pittau & Del Rio (2002) and Pittau, Del Rio & Funedda (2008). These were essentially equally divided between sphenophytes, ferns and gymnosperms (mainly cordaites and conifers), reflecting the more regional vegetation.

5.b. Biostratigraphy

Although the dominant taxa in the San Giorgio macroflora are not biostratigraphically informative, the rarer, allochthonous taxa are. The presence of *Eusphenopteris nummularia*, *Dicksonites plukenetii*, *Alethopteris ambigua*, *Neuropteris ovata* and *Linopteris obliqua* together indicate either the upper *Crenulopteris acadica* Zone (*Dicksonites plukenetii* Subzone) or the *Odontopteris cantabrica* Zone in the scheme of Wagner (1984, 1998), Cleal (1991) and Cleal & Thomas (1994). The absence of evidence specifically indicating the *O. cantabrica* Zone (e.g. *Odontopteris minor* Brongniart, *Nemejcopteris feminaeformis* (Schlotheim ex Sterzel) Barthel) tends to swing the argument in favour of the *D. plukenetii* Subzone, albeit on negative criteria (Fig. 8). This in turn indicates a late Asturian (or possibly Cantabrian) age for the San Giorgio macroflora, which is compatible with the age determination based on tetrapod footprint evidence (Fondi, 1979).

Previous authors (e.g. Cocozza, 1967) have placed emphasis on the presence of conifer remains to support the idea of a younger age. We have seen no macrofloral evidence of conifers from this basin, either in our collection or in the published literature. Even if we had, however, this would not have been of any significance for the age of these deposits. It is well documented that conifers were growing in extra-basinal habitats at least as early as middle Westphalian (early Moscovian) times and occasionally find their way into the macrofossil record (e.g. Lyons & Darrah, 1989; Galtier *et al.* 1992); and there is palynological evidence of even earlier occurrences (Zhou, 1994). Given that the San Giorgio Basin was so small it would not be surprising to find the occasional conifer fragment from extra-basinal vegetation that had found its way into the depositional system here; this would have neither stratigraphical nor palaeoclimatic significance.

5.c. Comparisons with other floras

The only other deposits in Sardinia of comparable age are at Tuppa Niedda, *c.* 20 km northwest of San Giorgio. Like the San Giorgio sequence, that at Tuppa Niedda is dominated by conglomerates and sandstones (Costamagna & Barca, 2008; Costamagna, Cruciani & Franceschelli, 2012) probably representing alluvial conditions (Pittau, Del Rio & Funedda, 2008). Although no macrofloras have been reported, Pittau, Del Rio & Funedda (2008) have listed a palynoflora from Tuppa Niedda indicating a similar age to the San Giorgio sequence.

A late Asturian age for the San Giorgio Basin suggests that the extensional tectonics responsible for its formation were related to the Leonian Phase of

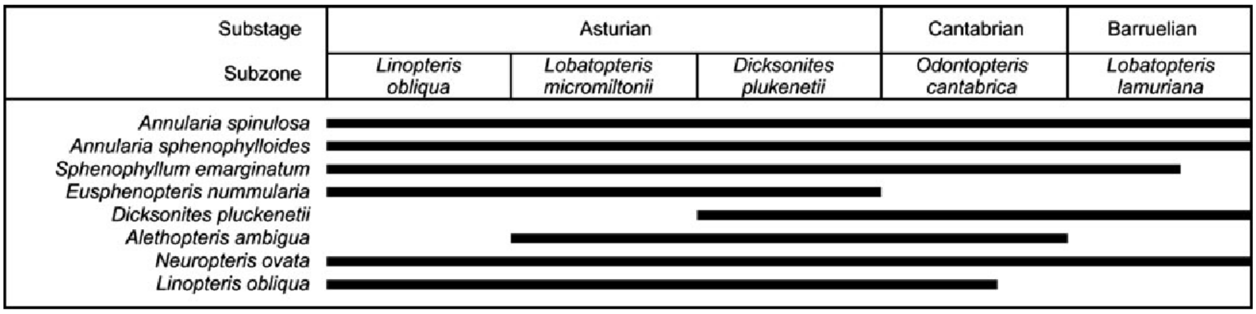

Figure 8. Stratigraphical ranges of key taxa in the San Giorgio Basin, based on data from Wagner (1984, 1998), Cleal (1991) and Cleal & Thomas (1994).

the Variscan Orogeny, whose effects were widespread across Europe (Dvořak *et al.* 1977; Opluštil & Cleal, 2007; Cleal *et al.* 2010). Post-Leonian depositional basins are best documented in northern Spain, notably in the Cantabrian Mountains of Palencia and León (Wagner, 1966; Wagner, Fernandez-Garcia & Eagar, 1983; Wagner & Álvarez-Vázquez, 2010*b*) the main difference being that deposition there was mostly paralic and continued through into Barruelian times. It also coincided with changes in depositional patterns in the Central and Western Bohemia (Opluštil & Pešek, 1998), Intra Sudetic (Opluštil & Kędzior *in* Cleal *et al.* 2010) and Upper Silesia basins (Kędzior *et al.* 2007), in southwestern Britain (Cleal, 1997), northeastern Bulgaria (Tenchov, 2007) and northern Turkey (Cleal & van Waveren, 2012). The onset of late Carboniferous basin formation in Sardinia was therefore part of a continent-wide late Variscan tectonic event.

The Leonian Phase also coincided with a significant change in coal swamp vegetation north of the Variscan Mountains, notably with an increase in the abundance and diversity of marattialean ferns and medullosalean pteridosperms, recognizable in both the macrofloral and palynological record (Cleal *et al.* 2007, 2010). The San Giorgio macroflora is overwhelmingly dominated by parautochthonous sphenophytes, reflecting the local lacustrine conditions. However, the macroflora probably derived from the late phases of the basin fill (preserved in Lithology VI) consists of marattialean and medullosalean remains and is broadly compatible in the broad balance of the major plant groups with that seen in similar age strata in South Wales (Davies, 1929). However, in Sardinia this wetland vegetation was short-lived, and based on palynological data there was a progressive change to drier conditions during Stephanian and early Permian times, linked with changing landscapes and climate resulting from late Variscan tectonic uplift (Pittau, Del Rio & Funedda, 2008).

6. Conclusions

The macrofloras from the San Giorgio Basin in southwestern Sardinia are overwhelmingly dominated by parautochthonous sphenophyte remains representing the vegetation growing around the margins of a freshwater lake. However, there are also allochthonous remains of a more diverse fern–pteridosperm-dominated vegetation, broadly similar in both species composition and relative representation of major plant groups to late Asturian (late Moscovian) wetland vegetation preserved north of the Variscan Mountains (e.g. South Wales). The basin was relatively short-lived and after a time started to drain, so that the sphenophyte vegetation became replaced by the fern–pteridosperm-dominated vegetation.

The palynological assemblages of the San Giorgio Basin and the nearby Tuppa Niedda area reflect a continental environment with a lake surrounded by a widespread alluvial plain vegetation in a tropical zone.

A late Asturian age for the San Giorgio Basin suggests that the extensional tectonics responsible for its formation were related to the Leonian Phase of Variscan tectonics, whose effects can be seen across Europe. The basin should therefore be regarded as late Variscan rather than post-Variscan.

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Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0016756816000765.

References

ABBOTT, M. L. 1958. The American species of *Asterophyllites*, *Annularia*, and *Sphenophyllum*. *Bulletin of American Paleontology* **38**, 289–390.

AMEROM, H. W. J. VAN. 1975. Die eusphenopteridischen Pteridophyllen aus der Sammlung des Geologischen Bureaus in Heerlen, unter besonderer Berücksichtigung ihrer Stratigraphie bezüglich des südlimburger Kohlenreviers. *Mededelingen Rijks Geologische Dienst, Serie C-III-1* **7**, 1–202.

Balme, B. E. 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology* **87**, 81–323.

Barca, S., Carannante, G., Cassinis, G., Cherchi, A., Corrandini, C., Cortesogno, L., Del Rio, M., Durand, M., Ferretti, A., Fontana, D., Funedda, A., Gaggero, L., Garau, A. M., Leone, M., Macciotta, G., Marchi, M., Matteucci, R., Murru, M., Neri, C., Loi, A., Pillola, G. L., Pittau, P., Ronchi, A., Salvadori, I., Sarria, E., Schroeder, R., Serpagli, E., Simone, L. & Stefani, C. 2004. *Sardinian Palaeozoic Basement and its Meso – Cainozoic Covers (Italy)*. 32nd International Geological Congress, Field Guide Book, P39, 64 pp.

Barca, S. & Costamagna, L. G. 2003. The Upper Carboniferous S. Giorgio succession (Iglesiente, SW Sardinia): stratigraphy, depositional setting and evolution of a late to post-Variscan molassic basin. *Bolletino della Società Geologica Italiana, Special Volume* **2**, 89–98.

Barthel, M. 2000. *Annularia stellata* oder *Annularia spinulosa*? *Veröffentlichungen Naturkundemuseum Erfurt* **19**, 37–42.

Barthel, M. 2012. *Annularia spicata* (Gutbier) Schimper – Calamitenzweige des Rotliegend. *Veröffentlichungen Museum für Naturkunde Chemnitz* **35**, 17–28.

Bashforth, A. R., Drábková, J., Opluštil, S., Gibling, M. R. & Falcon-Lang, H. J. 2011. Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nýřany Member, Central and Western Bohemian Basin, Czech Republic). *Review of Palaeobotany and Palynology* **163**, 153–89.

Bek, J. & Opluštil, S. 1998. Some lycopsid, sphenopsid and pteropsid fructifications and their miospores from the Upper Carboniferous basins of the Bohemian Massif. *Palaeontographica, Abteilung B* **248**, 127–61.

Brongniart, A. 1828a. *Histoire des Végétaux Fossiles, 1(1–2)*. Paris: G. Dufour & E. d'Ocagne, pp. 1–136, pls 1–27.

Brongniart, A. 1828b. *Prodrome d'une Histoire des Végétaux Fossiles*. Paris & Strasbourg: F.G. Levrault, 223 pp.

Brousmiche, C. 1983. Les fougères Sphénoptéridiennes du bassin houiller Sarro-Lorrain. *Publication Société Géologique du Nord* **10**, 1–480.

Cassinis, G., Perotti, C. & Ronchi, A. 2013. Geological remarks on the Carboniferous–Permian continental successions of southwestern Europe. In *The Carboniferous–Permian Transition* (eds S. G. Lucas, K. Krainer & J. W. Schneider), pp. 57–63. New Mexico Museum of Natural History, Albuquerque (Bulletin, 60).

Cassinis, G. & Ronchi, A. 1997. Upper Carboniferous to Lower Permian continental deposits in Sardinia (Italy). *Geodiversitas* **19**, 217–20.

Cassinis, G. & Ronchi, A. 2002. The (late-) post-Variscan continental succession of Sardinia. *Rendiconti della Società Paleontologica Italiana* **1**, 77–92.

Cleal, C. J. (ed.) 1991. *Plant Fossils in Geological Investigation: The Palaeozoic*. Chichester: Ellis Horwood, 233 pp.

Cleal, C. J. 1997. The palaeobotany of the upper Westphalian and Stephanian of southern Britain and its geological significance. *Review of Palaeobotany and Palynology* **95**, 227–53.

Cleal, C. J., Opluštil, S., Thomas, B. A. & Tenchov, Y. 2010. Late Moscovian terrestrial biotas and palaeoenvironments of Variscan Euramerica. *Netherlands Journal of Geosciences* **88**, 181–278.

Cleal, C. J. & Shute, C. H. 1995. A synopsis of neuropteroid foliage from the Carboniferous and Lower Permian of Europe. *Bulletin of the British Museum (Natural History), Geology Series* **51**, 1–52.

Cleal, C. J. & Shute, C. H. 2016. A new late Carboniferous calamitacean sphenophyte from South Wales, United Kingdom. *Spanish Journal of Palaeontology* **31**, 25–40.

Cleal, C. J., Shute, C. H. & Zodrow, E. L. 1990. A revised taxonomy for Palaeozoic neuropterid foliage. *Taxon* **39**, 486–92.

Cleal, C. J., Tenchov, Y. G., Dimitrova, T. Kh., Thomas, B. A. & Zodrow, E. L. 2007. Late Westphalian–Early Stephanian vegetational changes across the Variscan Foreland. In *Proceedings of the XVth International Congress on Carboniferous and Permian Stratigraphy. Utrecht, the Netherlands, 10–16 August 2003* (ed. Th. E. Wong), pp. 367–77. Amsterdam: Royal Netherlands Academy of Arts and Sciences.

Cleal, C. J. & Thomas, B. A. 1994. *Plant Fossils of the British Coal Measures*. London: Palaeontological Association, 222 pp.

Cleal, C. J. & van Waveren, I. M. 2012. A reappraisal of the Carboniferous macrofloras of the Zonguldak Amasra Coal Basin, north-western Turkey. *Geologia Croatica* **65**, 283–97.

Cocozza, T. 1967. Il Permo-Carbonifero del bacino di San Giorgio (Iglesiente, Sardegna sud-occidentale). *Memorie della Società Geologica Italiana* **6**, 607–42.

Costamagna, L. G. & Barca, S. 2008. Depositional architecture and sedimentology of the Tuppa Niedda conglomerates (Late Carboniferous, Arburese, SW Sardinia, Italy). *Bolletino della Società Geologica Italiana* **128**, 625–36.

Costamagna, L. G., Cruciani, G. & Franceschelli, M. 2012. Late Carboniferous to Permian volcano-sedimentary successions in SW Sardinia: a sedimentological, mineralogical and petrographical review. *Rendiconti Società Geologica Italiana* **21**, 1038–40.

Crookall, R. 1969. Fossil plants of the Carboniferous rocks of Great Britain [Second Section]. Part 5. *Memoirs of the Geological Survey of Great Britain, Palaeontology* **4**, 573–792.

Danzé, J. 1956. Contribution à l'étude des *Sphenopteris*. Les fougères Sphénoptéridiennes du bassin houiller du Nord de la France. *Études Géologiques pour l'Atlas Topographie Souterraine* **1** (2), 1–568.

Davies, D. 1929. Correlation and palæontology of the Coal Measures in east Glamorganshire. *Philosophical Transactions of the Royal Society of London, Series B* **217**, 91–153.

Del Rio, M. 1973. Palinologia di un livello "permo-carbonifero" do San Giorgio (Iglesiente, Sardegna sud-occidentale). *Bolletino della Società Geologica Italiana* **93**, 113–24.

Del Rio, M., Pillola, G. L. & Muntoni, F. 2002. The Upper Carboniferous of the San Giorgio basin. *Rendiconti della Società Paleontologica Italiana* **1**, 223–29.

Del Rio, M. & Pittau, P. 1999. The Upper Carboniferous of the San Giorgio Basin. In *Late Palaeozoic Continental Basins of Sardinia. Field Trip Guidebook 15–18 September 1999* (eds G. Cassinis, L. Cortesogno, L. Gaggero, P. Pittau, A. Ronchi & E. Sarria), pp. 37–9. Pavia: Earth Science Department, University of Pavia.

Doubinger, J. 1956. Contribution à l'étude des flores Autuno-Stéphaniennes. *Mémoires de la Société géologique de France, N. S.* **75**, 1–180.

Dvořak, J., Mirouse, R., Paproth, E., Pelhate, A., Ramsbottom, W. H. C. & Wagner, R. H. 1977. Relations entre la sedimentation Eodévonien-Carbonifère et la tectonique Varisque en Europe centrale et occidentale. *Colloque International du Centre National de la Recherche Scientifique, Rennes* **243**, 241–73.

Feistmantel, K. 1879. Eine neue Pflanzengattung aus Böhmischen Steinkohlenschichten. *Sitzungsberichte der König Böhmischen Gesellschaft der Wissenschaften in Prag* **3**, 298–303.

Fondi, R. 1979. Orme di microsauri nei Carbonifero superiore della Sardegna. *Memorie della Società Geologica Italiana* **20**, 347–56.

Galtier, J. & Béthoux, O. 2002. Morphology and growth habit of *Dicksonites pluckenetii* from the Upper Carboniferous of Graissessac (France). *Geobios* **35**, 525–35.

Galtier, J., Scott, A. C., Powell, J. H., Glover, B. W. & Waters, C. N. 1992. Anatomically preserved conifer-like stems from the Upper Carboniferous of England. *Proceedings of the Royal Society of London, Series B* **247**, 211–4.

Gambera, V. 1897. *Sulla Scoperta di Nuove Zone di Carbonifero e Sulla Stratigrafia dell'Iglesiente.* Tip. Commerciale, Cagliari, 5 pp.

Gastaldo, R. A. 1992. Regenerative growth in fossil horsetails following burial by alluvium. *Historical Biology* **6**, 203–19.

Gastaldo, R. A. & Matten, L. C. 1978. *Trigonocarpus leanus*, a new species from the Middle Pennsylvanian of southern Illinois. *American Journal of Botany* **65**, 882–90.

Grand'Eury, F. C. 1877. La flore Carbonifère du Département de la Loire et du Centre de la France: étudiée aux trois points de vue, botanique, stratigraphique et géognostique. *Mémoires de L'Académie des Sciences Naturelles, Paris* **24**, 1–624.

Gutbier, A. V. 1835. *Abdrücke und Versteinerungen des Zwickauer Schwarzkohlengebirges.* Zwickau: G. Richter, 80 pp., 11 pls.

Gutbier, A. V. 1837. Über die gegenseitige sehr gesonderte Lagerung und die gänzlich von einander abweichenden Pflanzenabdrücke des Rothliegenden und der Kohlen-Formation in der Gegend von Zwickau. *Sitzungsberichte der Naturwissenschaftlichen Gesellschaft Isis zu Jena* **1837**, 435–36.

Hammer, Ø., Harper, D. A. T. & Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* **4**(1), 9 pp.

Hoffmann, F. 1826. Untersuchungen über die Pflanzen-Rest des Kohlengebirges von Ibbenbühren und vom Piesberg bei Osnabrück. *Karsten's Archiv für Bergbau und Hüttenwesen* **13**, 266–82.

Jongmans, W. J. 1955. Notes paléobotaniques sur les Bassins houillers de l'Anatolie. *Mededelingen van de Geologische Stichting, Serie C* **9**, 55–89.

Kędzior, A., Gradziński, R., Doktor, M. & Gmur, D. 2007. Sedimentary history of a Mississippian to Pennsylvanian coal-bearing succession – an example from the Upper Silesia Coal Basin. *Geological Magazine* **144**, 487–96.

Kidston, R. 1891. Notes on the Palæozoic species mentioned in Lindley and Hutton's "Fossil Flora." *Proceedings of the Royal Physical Society of Edinburgh* **10**, 345–91.

Kidston, R. 1924. Fossil plants of the Carboniferous rocks of Great Britain. Part 5. *Memoirs of the Geological Survey of Great Britain, Palaeontology* **2**, 377–522.

Laveine, J.-P. 1989. *Guide Palèobotanique dans le Terrain Houiller Sarro-Lorrain.* Merlebach: Houilleres du Bassin de Lorraine, 154 pp.

Lesquereux, L. 1880. *The Coal Flora of Pennsylvania, and the Carboniferous Formation throughout the United States, 1–2. Second Geological Survey of Pennsylvania, Report of Progress.* Harrisburg PA: Board of Commissioners for the Second Geological Survey, 694 pp.

Libertin, M., Bek, J. & Dràbkovà, J. 2014. New sphenophyllaleans from the Pennsylvanian of the Czech Republic. *Review of Palaeobotany and Palynology* **200**, 196–210.

Lindley, J. & Hutton, W. 1832. *The Fossil Flora of Great Britain. Volume 1, Part 2.* London: W. J. Ridgeway and Sons, pp. 49–166, pls 15–49.

Lindley, J. & Hutton, W. 1834. *The Fossil Flora of Great Britain, Volume 2, Part 2.* London: W. J. Ridgeway and Sons, pp. 57–156, pls 100–37.

Lindley, J. & Hutton, W. 1837. *The Fossil Flora of Great Britain. Volume 3, Part 3.* London: W. J. Ridgeway and Sons, pp 123–208, pls 195–230.

Lyons, P. C. & Darrah, W. C. 1989. Earliest conifers of North America: upland and/or paleoclimatic indicators? *Palaios* **4**, 480–6.

Magurran, A. 1988. *Ecological Diversity and its Measurement.* Princeton: Princeton University Press, 192 pp.

McNeill, J., Barrie, F. R., Buck, W. R., Demoulin, V., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Marhold, K., Prado, J. & Prud'homme Van Reine, W. F. 2012. *International Code of Nomenclature for Algae, Fungi, and Plants (Melbourne Code).* Oberreifenberg: Koeltz Scientific Books (Regnum Veg, 154), 240 pp.

Merlo, G. 1911. Dell'esistenza di un lembo carbonifero fra Monteponi e Iglesias. *Resoconti delle Riunioni della Associazione Mineraria Sarda* **16**, 25–7.

Němejc, F. 1937. The sphenopterides stated in the Permocarboniferous of Central Bohemia (a preliminary report. II. part). *Vestník Královské Èeské Spoleènosti Nauk* **2**, 1–14.

Novarese, V. 1917. L'Autuniano in Sardegna. *Bollettino della Società Geologica Italiana* **36**, 58–91.

Novarese, V. & Taricco, M. 1923. Cenni sommari sul Paleozoico dell'Iglesiente. *Bollettino della Società Geologica Italiana* **41**, 316–25.

Opluštil, S. & Cleal, C. J. 2007. A comparative analysis of some Late Carboniferous basins of Variscan Europe. *Geological Magazine* **144**, 417–48.

Opluštil, S. & Pešek, J. 1998. Stratigraphy, palaeoclimatology and palaeogeography of the Late Palaeozoic continental deposits in the Czech Republic. *Geodiversitas* **20**, 597–619.

Pillola, G. L., Petti, F. M., Sacchi, E., Piras, S., Zoboli, D. & Nicosia, U. 2004. Tetrapod footprints and associated biota: new evidences from the Upper Carboniferous of SW Sardinia (Italy). *Geological Society of America, Abstracts with Programs* **36** (4), 82.

Pittau, P. & Del Rio, M. 2002. Palynofloral biostratigraphy of the Permian and Triassic sequences of Sardinia. In *Sardinia Field Trip – Palaeontology and Stratigraphy* (eds A. Cherchi, C. Corradini & M. T. Putzu). *Rendiconti della Società Paleontologica Italiana* **1**, 93–109.

Pittau, P., Del Rio, M. & Funedda, A. 2008. Relationships between plant communities characterization and basin formation in the Carboniferous–Permian of Sardinia. *Bolletino della Società Geologica Italiana* **127**, 637–53.

Potonié, H. 1899. *Lehrbuch der Pflanzenpalaeontologie.* Berlin: Dümmler, 402 pp.

Potonié, R. & Kremp, G. 1954. Die Gattungen der paläozoischen Sporae dispersae und ihre Stratigraphie. *Geologisches Jahrbuch* **69**, 111–94.

Potonié, R. & Kremp, G. 1955. Die Sporae dispersae des Ruhrkarbons, ihre Morphographie und Stratigraphie mit Ausblicken auf Arten andere Gebiete und Zeitabschnitte: Teil I. *Palaeontographica, Abteilung B* **98**, 1–136.

Pšenička, J., Bek, J., Zodrow, E. L., Cleal, C. J. & Hemsley, A. 2003. A new late Westphalian fossil marattialean fern from Nova Scotia. *Botanical Journal of the Linnean Society* **142**, 199–212.

Ronchi, A., Kustatscher, E., Pittau, P. & Santi, G. 2012. Pennsylvanian floras from Italy: an overview of the main sites and historical collections. *Geologia Croatica* **65**, 299–322.

Scanu, G. G., Corriga, M. G., Pillola, G. L. & Corradini, C. 2016. The mining area near Iglesias in southwestern Sardinia (Pennsylvanian). In *Planet Earth in Deep Time – Palaeozoic Series, Devonian & Carboniferous* (eds T. J. Suttner, E. Kido, P. Königshof, J. A. Waters, I. Davis & F. Messner), pp. 124–5. Stuttgart: Schweizerbart Science.

Schopf, J. M., Wilson, R. L. & Bentall, R. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. *Illinois Geological Survey, Reports of Investigations* **91**, 1–66.

Selden, P. A. & Pillola, G. L. 2009. A trigonocarpid arachnid from the Upper Carboniferous of the San Giorgio Basin, Sardinia. *Rivista Italiana di Paleontologia e Stratigrafia* **115**, 269–74.

Simson-Scharold, E. 1934. Zur Kenntnis der Carbonflora des Saargebietes. *Palaeontographica, Abteilung B* **79**, 1–66.

Šimůnek, Z. 2007. New classification of the genus *Cordaites* from the Carboniferous and Permian of the Bohemian Massif, based on cuticle micromorphology. *Sborník Národního Muzea v Praze, Serie B, Přírodní Vědy* **62**, 97–210.

Smith, A. H. V. & Butterworth, M. A. 1967. Miospores in the coal seams of the Carboniferous of Great Britain. *Special Papers in Palaeontology* **1**, 1–324.

Sternberg, K. M. von. 1820. *Versuch einer Geognostisch-Botanischen Darstellung der Flora der Vorwelt, 1(2).* Leipzig: F. Fleischer, 24 pp., pls 1–13.

Sternberg, K. M. von. 1821. *Versuch einer Geognostisch-Botanischen Darstellung der Flora der Vorwelt, 1(2).* Leipzig: F. Fleischer, 33 pp., pls 14–26.

Sternberg, K. M. von. 1825. *Versuch einer Geognostisch-Botanischen Darstellung der Flora der Vorwelt, 1(4), Tentamen.* Regensburg: Brenck's Wittwe, 48 + xlii pp., pls 40–59, A–E.

Sternberg, K. M. von, Presl, K. B. & Corda, A. C. J. 1838. *Versuch einer Geognostisch-Botanischen Darstellung der Flora der Vorwelt, 2(7–8).* Prague: G. Hässe & Söhne, pp. 81–220, pls 27–68, A–B.

Sterzel, J. T. 1881. Paläontologischer Charakter der oberen Steinkohlenformation und des Rotliegenden im erzgebirgischen Becken. *Bericht der Naturwissenschaftlichen Gesellschaft zu Chemnitz* **7**, 155–270.

Surange, K. R. & Chandra, S. 1974. Some male fructification of Glossopteridales. *The Palaeobotanist* **21**, 255–66.

Tenchov, Y. G. 2007. Late Westphalian and Stephanian sediments of the Dobrudzha Coalfield. *Geological Magazine* **144**, 497–511.

Testa, L. 1914. Il terreno carbonifero a sud di Monteponi. *Resoconti delle Riunioni della Associazione Mineraria Sarda* **19**, 31–4.

Thomas, B. A. 2014. *In situ* stems: preservation states and growth habits of the Pennsylvanian (Carboniferous) calamitaleans based upon new studies of *Calamites* Sternberg, 1820 in the Duckmantian at Brymbo, north Wales, UK. *Palaeontology* **57**, 21–36.

Wagner, R. H. 1959. Some Stephanian pecopterids from NW. Spain. *Mededelingen van de Geologische Stichting, New Series* **12**, 5–23.

Wagner, R. H. 1963. Stephanian B flora from the Ciñera-Matallana Coalfield (León) and neighbouring outliers. I: Introduction, *Neuropteris. Notas y Communicaciones del Instituto Geológico y Minero de España* **72**, 5–69.

Wagner, R. H. 1964. Stephanian floras in NW. Spain, with special reference to the Westphalian D – Stephanian A boundary. *Compte rendu 5e Congrès International de Stratigraphie et de Géologie du Carbonifère (Paris, 1963)* **1**, 835–51.

Wagner, R. H. 1966. Palaeobotanical dating of Upper Carboniferous folding phases in NW. Spain. *Memorias del Instituto Geologico y Minero de España* **66**, 1–169.

Wagner, R. H. 1968. Upper Westphalian and Stephanian species of *Alethopteris* from Europe, Asia Minor and North America. *Mededelingen van de Rijks Geologische Dienst, Serie C, III-1* **6**, 1–388, pls 1–64.

Wagner, R. H. 1984. Megafloral zones of the Carboniferous. *Compte rendu 9e Congrès International de Stratigraphie et de Géologie du Carbonifère (Washington, 1979)* **2**, 109–34.

Wagner, R. H. 1998. Consideraciones sobre los pisos de la Serie Estefaniense. *Monografías Academia de Ciencias de Zaragoza* **13**, 9–19.

Wagner, R. H. & Álvarez-Vázquez, C. 2010a. A redescription of the Stephanian species *Callipteridium virginianum* (Fontaine & White, 1880) comb. nov. and *Alethopteris leonensis* Wagner, 1964. *Scripta Geologica, Special Issue* **7**, 93–139.

Wagner, R. H. & Álvarez-Vázquez, C. 2010*b*. The Carboniferous floras of the Iberian Peninsula: a synthesis with geological connotations. *Review of Palaeobotany and Palynology* **162**, 239–324.

Wagner, R. H., Fernandez-Garcia, L. & Eagar, R. M. C. 1983. *Geology and Palaeontology of the Guardo Coalfield (NE León – NW Palencia), Cantabrian Mts.* Madrid: Instituto Geologico y Minero de España, 109 pp.

Weiss, C. E. 1869. *Fossile Flora der jüngsten Steinkohlenformation und des Rothliegenden im Saar-Rhein-Gebiete. Band I.* Bonn: A. Henry, 100 pp.

Weiss, C. E. 1876. Steinkohlen-Calamarien, I., mit besonderer Berucksichtigung ihrer Fructifikationen. *Atlas zu den Abhandlungen der geologischen Spezialkarte von Preussen und den Thüringischen Staaten* **2**(1), 1–149, 19 pls.

Wittry, J., Glasspool, I. J., Béthoux, O., Koll, R. & Cleal, C. J. 2015. A revision of the Pennsylvanian marattialean fern *Lobatopteris vestita* auct. and related species. *Journal of Systematic Palaeontology* **13**, 615–43.

Wood, H. C. 1869. Contributions to the Carboniferous flora of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* **1869**, 236–40.

Zeiller, R. 1883. Fructifications de fougères du terrain houiller. *Annales des Sciences Naturelles, 6e Série, Botanique* **16**, 177–209.

ZEILLER, R. 1888. *Études sur le terrain houiller de Commentry. Livre 2, Flore Fossile*. St-Étienne: Théolier, 366 pp, 42 pls.

ZEILLER, R. 1899. Étude sur la flore fossile du basin houiller d'Héraclée (Asie Mineure). *Mémoires de la Société Géologique de France, Paléontologie* **21**, 1–91.

ZENKER, F. C. 1833. Beschreibung von *Galium sphenophylloides*, Zenk. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* **1833**, 398–400.

ZHOU, Y.-X. 1994. Earliest pollen-dominated microfloras from the early Late Carboniferous of the Tian Shan Mountains, NW China: their significance for the origins of conifers and palaeophytogeography. *Review of Palaeobotany and Palynology* **81**, 193–211.

ZODROW, E. L. & CLEAL, C. J. 1998. Revision of the pteridosperm foliage *Alethopteris* and *Lonchopteridium*(Upper Carboniferous), Sydney Coalfield, Nova Scotia, Canada. *Palaeontographica, Abteilung B* **247**, 65–122.

ZODROW, E. L., TENCHOV, Y. & CLEAL, C. J. 2007. The arborescent *Linopteris obliqua* plant (Medullosales, Pennsylvanian). *Bulletin of Geosciences* **82**, 51–84.

Appendix 2

Appendix 2 List of species recognised by Arcangeli (1901) for the permo-carboniferous of Sardinia and temporal occurrence according to the author.

Taxa	**Affinity**	**Occurence**
Alethopteris serlii Brongniart	MEDULLOS	"Middle" Carboniferous
Asterotheca abbreviata (Brongniart) Presl	MARATTIAL	"Middle" Carboniferous
Neuropteris cf. *flexuosa* Sternberg	MEDULLOS	"Middle" Carboniferous
Sigillaria cf. *camptotaenia* Wood	LYCO	"Middle" Carboniferous
Oligocarpia gutbieri Goeppert	GLEICHEN	Upper Carboniferous
Alethopteris grandinii Brongniart	MEDULLOS	Undet. C/T
Asterotheca arborescens (Schlotheim) Presl	MARATTIAL	Undet. C/T
Asterotheca crenulata (Brongniart) Presl	MARATTIAL	Undet. C/T
Asterotheca candolleana (Brongniart) Presl	MARATTIAL	Undet. C/T
Asterotheca cyathea (Schlotheim) Presl	MARATTIAL	Undet. C/T
Asterotheca euneura (Brongniart) Presl	MARATTIAL	Undet. C/T
Asterotheca hemithelioides (Brongniart) Presl	MARATTIAL	Undet. C/T
Asterotheca paleacea Zeiller	MARATTIAL	Undet. C/T
Callipteridium pteridium (Schlotheim) Zeiller	MEDULLOS	Undet. C/T
Crossoteca pinnatifida Gutbier	FERN	Undet. C/T
Dactylotheca dentata (Brongniart) Zeiller	MARATTIAL	Undet. C/T
Dicksonites pluckenetii (Schlotheim) Sterzel	CALLISTOPH	Undet. C/T
Goniopteris feminaeformis Schlotheim	MARATTIAL	Undet. C/T
Odontopteris reichiana Gutbier	MEDULLOS	Undet. C/T
Pecopteris oreopteridia Schloteim	MARATTIAL	Undet. C/T
Pecopteris pennaeformis Brongniart	MARATTIAL	Undet. C/T
Pecopteris cf. *subaspera* Potonié	MARATTIAL	Undet. C/T
Ptychocarpus unitus (Brongniart) Weiss	MARATTIAL	Undet. C/T

Scolecopteris polymorpha (Brongniart) Zenker	MARATTIAL	Undet. C/T
Annularia sphenophylloides Zenker	SPHENOP	Undet. C/T
Annularia stellata (Schlotheim) Wood	SPHENOP	Undet. C/T
Asterophyllites equisetiformis Sternberg	SPHENOP	Undet. C/T
Astherophyllites hippuritoides Brongniart	SPHENOP	Undet. C/T
Buckmannia tubercolata Sternberg	SPHENOP	Undet. C/T
Buckmannia subcalathifera Arcangeli	SPHENOP	Undet. C/T
Calamites cistii Brongniart	SPHENOP	Undet. C/T
Calamites lejoderma Gutbier	SPHENOP	Undet. C/T
Calamites suckowi Brongniart	SPHENOP	Undet. C/T
Macrostachya infundibuliformis Schimper	SPHENOP	Undet. C/T
Sphenophyllum oblongifolium Germar et Kaulfus	SPHENOP	Undet. C/T
cf. *Lepidodendron* sp.	LYCO	Undet. C/T
Stigmaria ficoides Brongniart	LYCO	Undet. C/T
Stigmaria eveni Lesquereux	LYCO	Undet. C/T
Cordaites acutus Grand'Eury	CORDA	Undet. C/T
Cordaites borassifolius Sternberg	CORDA	Undet. C/T
Cordaites intermedius Grand'Eury	CORDA	Undet. C/T
Cordaites principalis Germar	CORDA	Undet. C/T
Dorycordaites lingulatus Grand'Eury	CORDA	Undet. C/T
Dorycordaites palmaeformis Grand'Eury	CORDA	Undet. C/T
Asterotheca daubrei Zeiller	MARATTIAL	Permian
Callipteris conferta (Sternberg) Brongniart	PELTASPERM	Permian
Callipteridium crassinervium Potonié	MEDULLOS	Permian
Callipteridium subelegans Potonié	MEDULLOS	Permian
Calamites gigas Brongniart	SPHENOP	Permian
Sphenopteris minutisecta Fontaine et White	SEEDF	Permian
Ulmannia bronnii Goeppert	CONIF	Permian
Walchia piniformis Sternberg	CONIF	Permian
Sphaerites craterigenus Arcangeli	FUNGI	Undefinited
Hysterites cordatis Grand'Eury	FUNGI	Undefinited

Callipteridium sp.	MEDULLOS	Undefinited
Neuropteris meneghiana Arcangeli	MEDULLOS	Undefinited
Neuropteris de-stefaniana Arcangeli	MEDULLOS	Undefinited
Schizopteris sp.	FERN	Undefinited
Schizopteris subdichotoma Arcangeli	FERN	Undefinited
Asterophyllites longifolius (Sternberg) Brongniart	SPHENOP	Undefinited
cf. *Lepidodendron* sp.	LYCO	Undefinited
Sigillariophyllum meneghinii Arcangeli	LYCO	Undefinited
Calamites sp.	SPHENOP	Undefinited
Equisetites sp.	SPHENOP	Undefinited
Equisetites rugosus Schimper	SPHENOP	Undefinited
Sporangites sp.	ALGAE?	Undefinited
Sigillariophyllum seuense Arcangeli	LYCO	Undefinited
Sigillariophyllum canavarii Arcangeli	LYCO	Undefinited
Cardiocarpus sp.	CORDA?	Undefinited
Cardiocarpus sardous Arcangeli	CORDA?	Undefinited
Rhabdocarpus ovoideus Goeppert et Berger	CORDA?	Undefinited
Trigonocarpus sp.	MEDULLOS	Undefinited
Aspidiopsis coniferoides Potonié	INC SEDIS	Undefinited
Noeggerathia cf. *platynervia* Goeppert	PROGYMNOSP	Undefinited

Appendix 3

Appendix 3 List of species recognized by Spano (1976) for the Permian of Sardinia, with the collecting localities

Taxa	**Affinity**	**Locality**
Stigmaria ficoides (Sternberg) Brongniart	LYCO	Seulo Ingurtipani
Annularia sphenophylloides (Zenker) Gutbier	SPHENOP	Seulo Ingurtipani
Annularia stellata (Schlotheim) Wood	SPHENOP	Seulo Ingurtipani
Asterophyllites equisetiformis (Sternberg) Brongniart	SPHENOP	Seulo Ingurtipani, Seui San Sebastiano, Seui San Gerolamo, Seui Genniaca
Calamites cisti Brongniart	SPHENOP	Seui San Sebastiano
Calamites gigas Brongniart	SPHENOP	Seui San Sebastiano, Seui San Gerolamo
Calamites leioderma Gutbier	SPHENOP	Seulo Ingurtipani
Calamites suckowii Brongniart	SPHENOP	Seulo Ingurtipani, Seui San Sebastiano
Calamostachys tuberculata (Sternberg) Weiss	SPHENOP	Seulo Ingurtipani, Seui San Sebastiano
Macrostachya infundibuliformis (Brongniart) Schimper	SPHENOP	Seulo Ingurtipani, Seui San Sebastiano
Sphenophyllum longifolium (Germar) Geinitz	SPHENOP	Seulo Ingurtipani
Sphenophyllum oblongifolium (Germar et Kaulfuss) Unger	SPHENOP	Seulo Ingurtipani, Seui San Sebastiano
Sphenophyllum thonii Mahr var. *minor* Sterzel	SPHENOP	Seulo Ingurtipani
Sphenophyllum verticillatum (Schlotheim) Zeiller	SPHENOP	Seulo Ingurtipani
Acitheca polymorpha (Brongniart) Schimper	MARATTIAL	Seulo Ingurtipani, Seui San Sebastiano, Jerzu Perda Pera
Lobatopteris viannae (Teixeira) Wagner	MARATTIAL	Seulo Ingurtipani
Nemejcopteris feminaeformis (Schlotheim) Barthel	MARATTIAL	Seulo Ingurtipani, Seui San Sebastiano
Pecopteris arborescens (Schlotheim) Sternberg	MARATTIAL	Seulo Ingurtipani, Seui Corongiu
Pecopteris candolleana Brongniart	MARATTIAL	Seulo Ingurtipani
Pecopteris cyathea (Schlotheim) Brongniart	MARATTIAL	Seulo Ingurtipani, Seui San Sebastiano
Pecopteris densifolia (Goeppert) Weiss	MARATTIAL	Seulo Ingurtipani, Seui San Sebastiano
Pecopteris hemitelioides Brongniart	MARATTIAL	Seulo Ingurtipani, Seui San Sebastiano
Pecopteris unita Brongniart	MARATTIAL	Seulo Ingurtipani, Seui San Sebastiano
Pecopteris plumosa-dentata Brongniart (≡Senftenbergia plur	FILICAL	Seulo Ingurtipani, Seui San Sebastiano
Sphenopteris matheti Zeiller	PTERIDOSP	Seulo Ingurtipani
Alethopteris grand'euryi Zeiller	MEDULLOS	Seulo Ingurtipani
Alethopteris grandini Brongniart	MEDULLOS	Seulo Ingurtipani, Seui San Sebastiano
Alethopteris serlii (Brongniart) Goeppert	MEDULLOS	Seulo Ingurtipani, Seui San Sebastiano
Alethopteris subelegans (Potonié) Doubinger	MEDULLOS	Seulo Ingurtipani, Seui San Sebastiano
Callipteridium gigas (Gutbier) Weiss	MEDULLOS	Seulo Ingurtipani, Seui San Gerolamo
Callipteridium pteridium (Schlotheim) Zeiller	MEDULLOS	Seulo Ingurtipani
Callipteridium rochei Zeiller	MEDULLOS	Seulo Ingurtipani
Callipteridium subelegans Potonié	MEDULLOS	Seulo Ingurtipani
Neurocallipteris planchardii (Zeiller) Cleal et al.	MEDULLOS	Seulo Ingurtipani, Perdasdefogu S'Abba e Ferru

Odontopteris brardi (Brongniart) Brongniart	MEDULLOS	Seulo Ingurtipani
Odontopteris minor Brongniart	MEDULLOS	Seulo Ingurtipani
Pecopteridium costei (Zeiller) Bertrand	MEDULLOS	Seulo Ingurtipani
Autunia conferta (Sternberg) Kerp	PELTASPERM	Seulo Ingurtipani, Seui San Sebastiano
Dicksonites plukenetii (Schlotheim ex Sternberg) Sterzel	CALLISTOPH	Seulo Ingurtipani
Cordaites principalis (Germar) Geinitz	CORDA	Seui San Sebastiano, Seui Corongiu
Lebachia piniformis (Sternberg) Florin	CONIF	Seulo Ingurtipani, Seui San Sebastiano, Orroli Mulargia, Perdasdefogu S'Abba e Ferru
Taeniopteris multinervia Weiss	CYCAD	Seulo Ingurtipani, Seui San Sebastiano
Taeniopteris jejunata Grand'Eury	CYCAD?	Seulo Ingurtipani

Appendix 4

Appendix 4 List of species by Broutin et al. 1996

Taxa	Affinity	Locality
Asterophyllites longifolius (Sternberg) Brongniart	SPHENOP	Perdasdefogu basin
Annularia mucronata Schenk	SPHENOP	Perdasdefogu basin
Pecopteris elaverica Zeiller	MARATTIAL	Perdasdefogu basin
Odontopteris lingulata (Goeppert) Schimper	MEDULLOS	Perdasdefogu basin
Neuropteris osmundae (Artis) Kidston (≡ *Odontopteris dupesnoyi*)	MEDULLOS	Perdasdefogu basin
Autunia (al. *Callipteris*) *conferta* (Brongniart) Haubold et Kerp	PELTASPERM	Perdasdefogu basin
Rhachiphyllum (al. *Callipteris*) *schenkii* (Heyer) Kerp	PELTASPERM	Perdasdefogu basin
Rhachiphyllum (al. *Callipteris*) *lyratifolia* (Goeppert) Kerp	PELTASPERM	Perdasdefogu basin
Lodevia (al. *Callipteris*) *nicklesii* (Zeiller) Haubold et Kerp	PELTASPERM	Perdasdefogu basin
Dichophyllum (al. *Callipteris*) *flabellifera* (Weiss) Kerp et Haubold	PTERIDOSP	Perdasdefogu basin
Ernestiodendron filiciforme (Sternberg) Florin	CONIF	Perdasdefogu basin
Otovicia (al. *Walchia*) *hypnoides* (Florin) Kerp et al.	CONIF	Perdasdefogu basin
Walchia piniformis Sternberg (sensu Visscher et al. 1986)	CONIF	Perdasdefogu basin
Culmitzchia (al. *Lebachi* a) *laxifolia* (Florin) Clement-Westerhof	CONIF	Perdasdefogu basin
Taeniopteris abnormis Gutbier	CYCAD	Perdasdefogu basin
Pecopteris cf. *densifolia* (Goeppert) Weiss	MARATTIAL	Mulargia basin
Ernestiodendron filiciforme (Sternberg) Florin	CONIF	Mulargia basin
Otovicia (al. *Walchia*) *hypnoides* (Florin) Kerp et al.	CONIF	Mulargia basin
Walchia piniformis Sternberg (sensu Visscher et al., 1986)	CONIF	Mulargia basin
Hermitia (al. Walchia) sp.	CONIF	Mulargia basin
Culmitzchia (al. *Lebachia*) *laxifolia* (Florin) Clement-Westerhof	CONIF	Mulargia basin
Pecoperis polymorpha Brongniart (≡ Achiteca polymorpha)	MARATTIAL	Lu Caparoni basin
Pecopteris sp.	MARATTIAL	Lu Caparoni basin
Remia pinnatifida (Gutbier) Knight	FERN?	Lu Caparoni basin
Autunia (al. *Callipteris*) *conferta* (Brongniart) Haubold et Kerp	PELTASPERM	Lu Caparoni basin
Rachiphyllum (al. *Callipteris*) *lyratifolia* (Goeppert) Kerp	PELTASPERM	Lu Caparoni basin
Odontopteris cf. *subcrenulata* Rost (≡ *Mixoneura subcrenulata*)	MEDULLOS	Lu Caparoni basin
Dichophyllum (al. *Callipteris*) *flabellifera* (Weiss) Kerp et Haubold	PTERIDOSP	Lu Caparoni basin
Walchia piniformis Sternberg (sensu Visscher et al. 1986)	CONIF	Lu Caparoni basin
Otovicia (al.*Walchia*) *hypnoides* (Florin) Kerp et al.	CONIF	Lu Caparoni basin
Ernestiodendron filiciforme (Sternberg) Florin	CONIF	Lu Caparoni basin
Taeniopteris sp.	CYCAD	Lu Caparoni basin

Appendix 5

Appendix 5. Genera recorded in the western Tethyan area for the interval late Ghzelian-early Asselian.

TAXA	AFFINITY	TAXA	AFFINITY	TAXA	AFFINITY
Acitheca	FERN	*Eusigillaria*	LYCO	*Pelourdea*	CONIF
Alethopteris	SEEDF	*Eusphenopteris*	SEEDF	*Peltaspermum*	SEEDF
Annularia	SPHENOP	*Feysia*	CONIF	*Phyllotheca*	SPHENOP
Aphlebia	SEEDF	*Ginkgoites*	GINKGO	*Poacordaites*	CORDA
Arnhardtia	SEEDF	*Ginkgophyllum*	GINKGO	*Potoniea*	SEEDF
Arthropitys	SPHENOP	*Ginkgophytopsis*	GINKGO	*Protoblechnum*	SEEDF
Artisia	CORDA	*Gomphostrobus*	CONIF	*Prynadaeopteris*	FERN
Asolanus	LYCO	*Gondomaria*	SEEDF?	*Psaronius*	FERN
Asterophyllites	SPHENOP	*Gracilopteris*	SEEDF	*Pseudomariopteris*	SEEDF
Asterotheca	FERN	*Helenopteris*	SEEDF	*Psygmophyllum*	GINKGO
Autunia	SEEDF	*Hepaticites*	LIVERW	*Pterispermostrobus*	SEEDF
Baiera	GINKGO	*Hermitia*	CONIF	*Pterophyllum*	CYCAD
Barthelopteris	SEEDF	*Hexagonocarpus*	SEEDF	*Rachiphyllum*	SEEDF
Blanzyopteris	SEEDF	*Holcospermum*	SEEDF	*Remia*	FERN?
Botryopteris	FERN	*Huttonia*	SPHENOP	*Renaultia*	FERN
Bowmanites	SPHENOP	*Knorria*	LYCO	*Reticulopteris*	CYCAD
Calamites	SPHENOP	*Koretrophyllites*	EQUIS	*Rhabdocarpus*	CORDA
Calamostachys	SPHENOP	*Lebachia*	CONIF	*Rhachiphyllum*	SEEDF
Callipteridium	SEEDF	*Lepidodendron*	LYCO	*Rhipidopsis*	GINKGO
Callipteris	SEEDF	*Lepidophloyos*	LYCO	*Samaropsis*	SEED
Cardiocarpus	CORDA	*Lepidostrobophyllum*	LYCO	*Schizopteris*	FERN
Carpentieria	CONIF	*Lepidostrobus*	LYCO	*Schizostachys*	FERN
Carpolithes	SEED	*Lescuropteris*	SEEDF	*Schutzia*	CORDA
Codonospermum	SEEDF	*Lesleya*	SEEDF	*Scolecopteris*	FERN
Cordaicarpus	CORDA	*Lilpopia*	EQUIS	*Senftenbergia*	FERN
Cordaicladus	CORDA	*Linopteris*	SEEDF	*Sigillaria*	LYCO
Cordaitanthus	CORDA	*Lobatannularia*	EQUIS	*Sigillariostrobus*	LYCO
Cordaites	CORDA	*Lobatopteris*	FERN	*Sobernheimia*	SEEDF?
Corynepteris	FERN	*Lodevia*	SEEDF	*Sphenobaiera*	GINKGO
Culmitzschia	CONIF	*Macrostachya*	EQUIS	*Sphenophyllostachys*	SPHENOP
Cyclocarpus	SEED	*Metacalamostachya*	EQUIS	*Sphenophyllum*	SPHENOP
Cyclopteris	SEEDF	*Mixoneura*	SEEDF	*Sphenopteris*	SEEDF
Cyperites	LYCO	*Nemejcopteris*	FERN	*Sphenozamites*	SEEDF
Dactylotheca	FERN	*Neurocallipteris*	SEEDF	*Spiropteris*	FERN, CYCAD
Dadoxylon	CONIF	*Neurodontopteris*	SEEDF	*Stigmaria*	LYCO
Danaeites	FERN	*Neuropteris*	SEEDF	*Supaia*	SEEDF
Dichophyllum	SEEDF	*Noeggerathia*	NOEGG	*Syringodendron*	LYCO
Dicksonites	SEEDF	*Odontopteris*	SEEDF	*Taeniopteris*	CYCAD
Dicranophyllum	SEEDF	*Oligocarpia*	FERN	*Trichophitys*	GINKGO
Diplazites	FERN	*Omphalophloios*	LYCO	*Trigonocarpus*	SEEDF
Diplocalamites	SPHENOP	*Otovicia*	CONIF	*Ullmannia*	CONIF
Dorycordaites	CORDA	*Pachycordaites*	CORDA	*Walchia*	CONIF
Entsovia	CONIF	*Pachytesta*	SEEDF	*Walchianthus*	CONIF
Ernestiodendron	CONIF	*Palaeostachya*	SPHENOP	*Walchiostrobus*	CONIF
Eucalamites	SPHENOP	*Pecopteris*	FERN	*Zamites*	CYCAD

PLATES

Plate I

scalebar 10 mm

1) Small fragment of ***Annularia*** cf. ***sphenophylloides*** (Zenker 1833) Gutbier 1837 with 6 leaves preserved in the whorl (MDLCA 17791).

2) Fragments of ultimate pinnae of ***Acitheca polymorpha*** (Brongniart 1834) Schimper 1879 discovered in the Montarbu locality, indicates long transport from the original growing site (MDLCA 17556).

3) Part of penultimate pinnae with three incomplete ultimate pinnae of ***Pecopteris densifolia*** (Goeppert 1864) Weiss 1869 (MDLCA 17774).

4) Linear ultimate pinnae of ***Pecopteris densifolia*** (Goeppert 1864) Weiss 1869 ending with a small rounded or subtriangular pinnule (MDLCA 17517).

5) Alternate pinnules of ***Pecopteris*** cf. ***candolleana*** Brongniart 1834 (MDLCA 17528).

6) Fertile pinnule of ***Pecopteris*** cf. ***candolleana*** Brongniart 1834 bearing synangia between the midvein (MDLCA 17773).

7) Profoundly lobed pinnule with rounded apex of ***Remia pinnatifida*** (Gutbier 1835) Knight 1985 emend. Cleal 2015 (MDLCA 17513).


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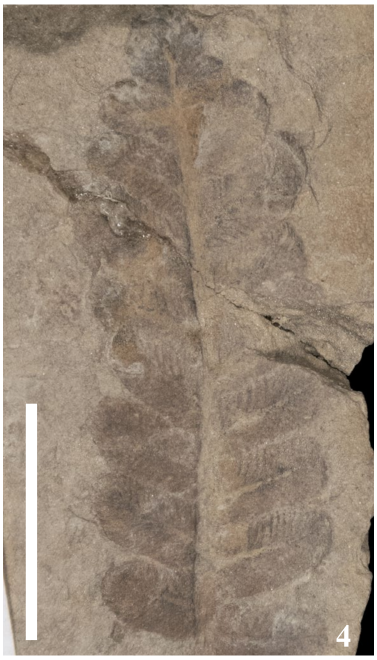
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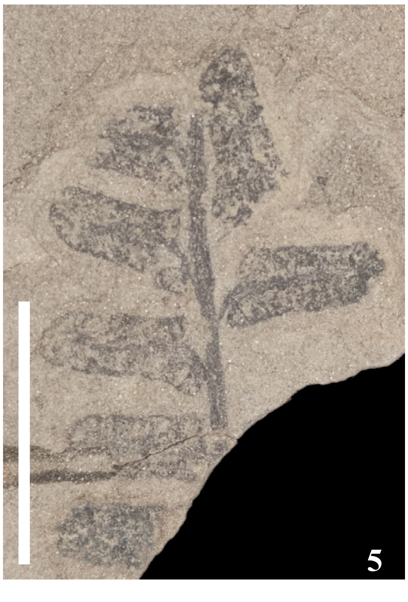
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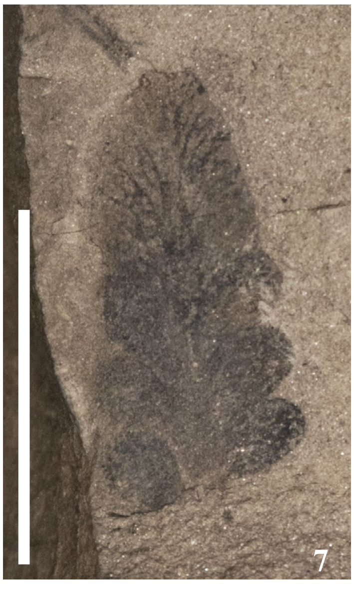
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Plate II

scalebar 10 mm

1) Fragment of pinnae bearing individualised pinnules of ***Mixoneura subcrenulata*** (Rost 1839) Zeiller 1888 (MDLCA 17780).

2) Isolated These small pinnules of ***Mixoneura subcrenulata*** (Rost 1839) Zeiller 1888 (MDLCA 17782a).

3) Distal part of incomplete pinnae of ***Neurocallipteris planchardii*** (Zeiller 1888) Cleal, Shute et Zodrow 1990 (MDLCA 17763).

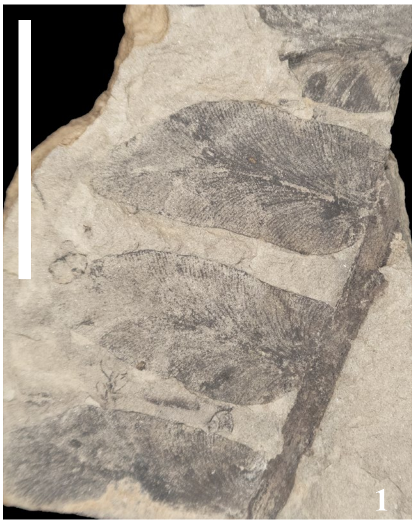
4) Pinnules with oblong-triangular shape of ***Neurocallipteris*** cf. ***neuropteroides*** (Goeppert 1836) Cleal, Shute et Zodrow 1990 (MDLCA 17565).

5) ***Callipteridium pteridium*** (Schlotheim 1804) Zeiller in Renault et Zeiller 1888 preserved as distal part of the pinna with pinnules inserted at right angles to the main rachis (MDLCA 17767).

6) ***Trigonocarpus*** sp. casts showing one of the three typical longitudinal ribs (MDLCA 17545a)

7) Bipinnate and oval frond of ***Autunia conferta*** (Sternberg 1826) Kerp in Kerp et Haubold 1988 (MDLCA 17568).

8) ***Autunia conferta*** (Sternberg 1826) Kerp in Kerp et Haubold 1988 showing the venation pattern (MDLCA 17765).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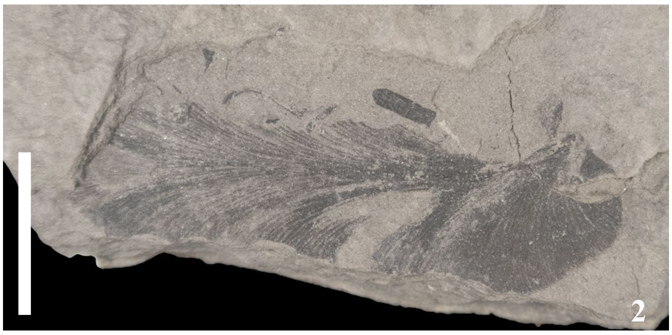
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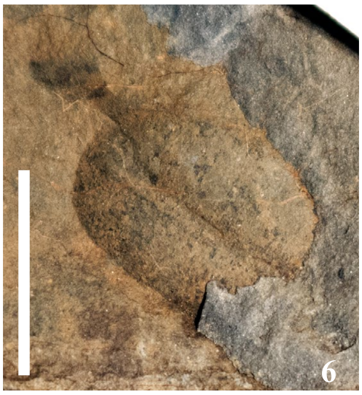
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Plate III

scalebar 5 mm

1) Putative ovuliferous organs of ***Autunia conferta*** showing a group of megasporophylls helically arranged in the main axes. (MDLCA 17587b).

2) Magnificence of the putative ovuliferous organs of ***Autunia conferta*** (MDLCA 17587b).

3) Isolated putative ovule of ***Autunia conferta*** (MDLCA 17521)

4) Pinnules are attached with a small part of the basis in ***Autunia naumannii*** (Gutbier 1849) Kerp in Kerp et Haubold 1988 (MDLCA 17567).


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Plate IV

scalebar 5 mm

1) ***Sobernheimia jonkeri*** Kerp 1983 phylloid organ bearing two rows of seed-like bodies (MDLCA 17790).

2) Long leaf of ***Taeniopteris*** cf. ***multinervia*** Weiss 1869 with rigid midrib (MDLCA 17761);

3) Partly destroyed leaves of ***Cordaites*** sp. meaning floating in water for long time (MDLCA 17757)

4) Long leaf of ***Cordaites*** sp. (MDLCA 17581a).

5 Three-dimensional preservation of ***Cardiocarpus*** sp. in lateral view (MDLCA 17629)

6) Three-dimensional preservation of ***Cardiocarpus*** sp. in frontal view (MDLCA 17629)

7) Round-oval seed of ***Cardiocarpus*** sp. (MDLCA 17777)


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Plate IV

scalebar 5 mm

1) Axis of *Ernestiodendron filiciforme* (Schlotheim 1820) Florin 1934 with falcate leaves (MDLCA 17724).

2) *Ernestiodendron filiciforme* (Schlotheim 1820) Florin 1934 (MDLCA 17655).

3) Putative polliniferous cone attached to other sterile branches of *Ernestiodendron filiciforme* (Schlotheim 1820) Florin 1934 (MDLCA 17722).

4) Undetermined Female cone (MDLCA 17679) with walchian affinity.

5) Compact polliniferous cone of *Walchianthus* sp. (MDLCA 17593)

6) Axes of *Culmitzschia speciosa* (Florin 1939) Clement-Westernhof 1984 (MDLCA 17785a).

7) Pointed or slightly rounded apex that turns close to the end of the leaf in *Culmitzschia speciosa* (Florin 1939) Clement-Westernhof 1984 (MDLCA 17754).

8) Broadly elliptical and platyspermic seed of cf. *Samaropsis* sp. (MDLCA 17671).

9) Conifer seed (MDLCA 17582a) with oval shape.

10) Isolated bract of a walchiaceous ovuliferous cone identified as *Gomphostrobus* sp. cf. *Gomphostrobus bifidus* (Geinitz 1873) Zeiller in Florin 1938 (MDLCA 17696).


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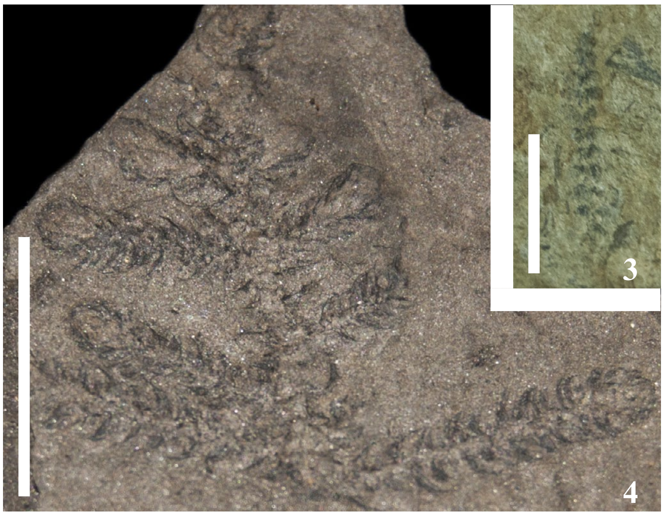
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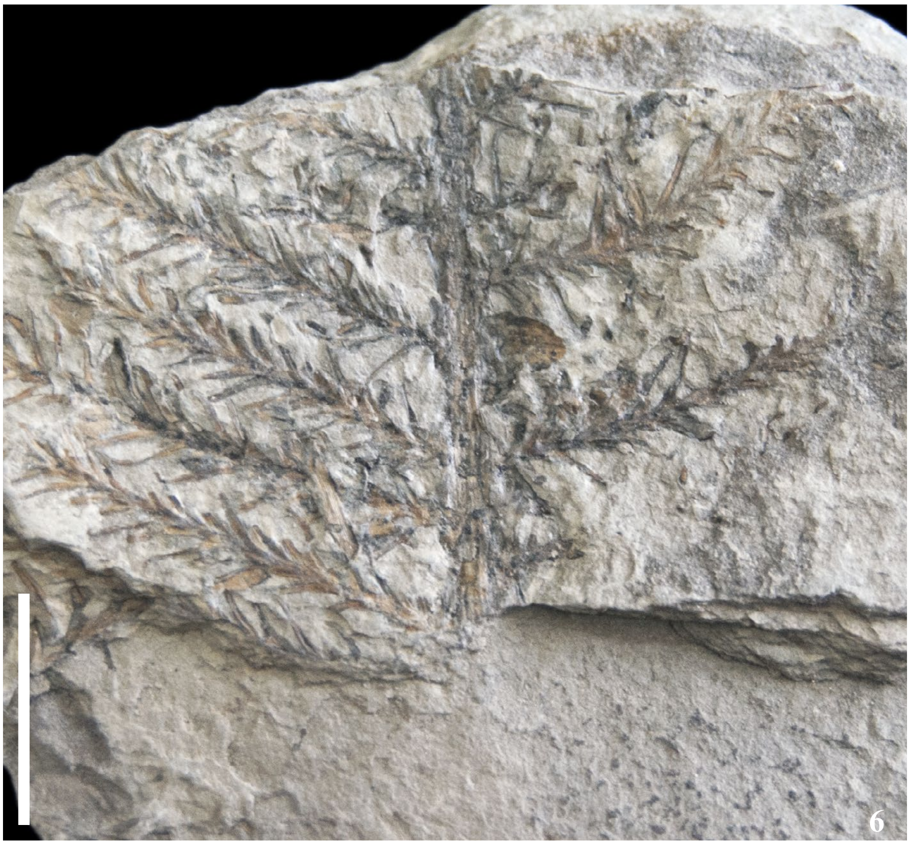
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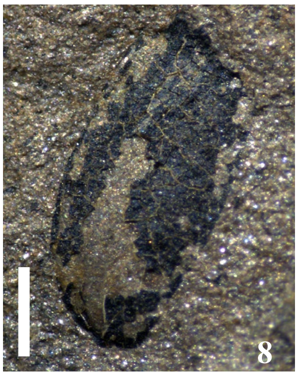
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10

International Chronostratigraphic Chart (Cohen et al. 2013)

INTERNATIONAL CHRONOSTRATIGRAPHIC CHART

www.stratigraphy.org

International Commission on Stratigraphy

v 2017/02

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	GSSP	numerical age (Ma)
						present
Phanerozoic	Cenozoic	Quaternary	Holocene		✓	0.0117
			Pleistocene	*Upper*		0.126
				Middle		0.781
				Calabrian	✓	1.80
				Gelasian	✓	2.58
		Neogene	Pliocene	Piacenzian	✓	3.600
				Zanclean	✓	5.333
			Miocene	Messinian	✓	7.246
				Tortonian	✓	11.63
				Serravallian	✓	13.82
				Langhian		15.97
				Burdigalian		20.44
				Aquitanian	✓	23.03
		Paleogene	Oligocene	Chattian	✓	27.82
				Rupelian	✓	33.9
			Eocene	Priabonian		37.8
				Bartonian		41.2
				Lutetian	✓	47.8
				Ypresian	✓	56.0
			Paleocene	Thanetian	✓	59.2
				Selandian	✓	61.6
				Danian	✓	66.0
	Mesozoic	Cretaceous	Upper	Maastrichtian	✓	72.1 ±0.2
				Campanian		83.6 ±0.2
				Santonian	✓	86.3 ±0.5
				Coniacian		89.8 ±0.3
				Turonian	✓	93.9
				Cenomanian	✓	100.5
			Lower	Albian	✓	~ 113.0
				Aptian		~ 125.0
				Barremian		~ 129.4
				Hauterivian		~ 132.9
				Valanginian		~ 139.8
				Berriasian		~ 145.0

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	GSSP	numerical age (Ma)
						~ 145.0
Phanerozoic	Mesozoic	Jurassic	Upper	Tithonian		152.1 ±0.9
				Kimmeridgian		157.3 ±1.0
				Oxfordian		163.5 ±1.0
			Middle	Callovian		166.1 ±1.2
				Bathonian	✓	168.3 ±1.3
				Bajocian	✓	170.3 ±1.4
				Aalenian	✓	174.1 ±1.0
			Lower	Toarcian	✓	182.7 ±0.7
				Pliensbachian	✓	190.8 ±1.0
				Sinemurian	✓	199.3 ±0.3
				Hettangian	✓	201.3 ±0.2
		Triassic	Upper	Rhaetian		~ 208.5
				Norian		~ 227
				Carnian	✓	~ 237
			Middle	Ladinian	✓	~ 242
				Anisian		247.2
			Lower	Olenekian		251.2
				Induan	✓	251.902 ±0.024
	Paleozoic	Permian	Lopingian	Changhsingian	✓	254.14 ±0.07
				Wuchiapingian	✓	259.1 ±0.5
			Guadalupian	Capitanian	✓	265.1 ±0.4
				Wordian	✓	268.8 ±0.5
				Roadian	✓	272.95 ±0.11
			Cisuralian	Kungurian		283.5 ±0.6
				Artinskian		290.1 ±0.26
				Sakmarian		295.0 ±0.18
				Asselian	✓	298.9 ±0.15
		Carboniferous: Pennsylvanian	Upper	Gzhelian		303.7 ±0.1
				Kasimovian		307.0 ±0.1
			Middle	Moscovian		315.2 ±0.2
			Lower	Bashkirian	✓	323.2 ±0.4
		Carboniferous: Mississippian	Upper	Serpukhovian		330.9 ±0.2
			Middle	Visean	✓	346.7 ±0.4
			Lower	Tournaisian	✓	358.9 ±0.4

Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	GSSP	numerical age (Ma)
						358.9 ± 0.4
Phanerozoic	Paleozoic	Devonian	Upper	Famennian	✓	372.2 ±1.6
				Frasnian	✓	382.7 ±1.6
			Middle	Givetian	✓	387.7 ±0.8
				Eifelian	✓	393.3 ±1.2
			Lower	Emsian	✓	407.6 ±2.6
				Pragian	✓	410.8 ±2.8
				Lochkovian	✓	419.2 ±3.2
		Silurian	Pridoli		✓	423.0 ±2.3
			Ludlow	Ludfordian	✓	425.6 ±0.9
				Gorstian	✓	427.4 ±0.5
			Wenlock	Homerian	✓	430.5 ±0.7
				Sheinwoodian	✓	433.4 ±0.8
			Llandovery	Telychian	✓	438.5 ±1.1
				Aeronian	✓	440.8 ±1.2
				Rhuddanian	✓	443.8 ±1.5
		Ordovician	Upper	Hirnantian	✓	445.2 ±1.4
				Katian	✓	453.0 ±0.7
				Sandbian	✓	458.4 ±0.9
			Middle	Darriwilian	✓	467.3 ±1.1
				Dapingian	✓	470.0 ±1.4
			Lower	Floian	✓	477.7 ±1.4
				Tremadocian	✓	485.4 ±1.9
		Cambrian	Furongian	*Stage 10*		~ 489.5
				Jiangshanian	✓	~ 494
				Paibian	✓	~ 497
			Series 3	Guzhangian	✓	~ 500.5
				Drumian	✓	~ 504.5
				Stage 5		~ 509
			Series 2	*Stage 4*		~ 514
				Stage 3		~ 521
			Terreneuvian	*Stage 2*		~ 529
				Fortunian	✓	541.0 ±1.0

Eonothem / Eon		Erathem / Era	System / Period	GSSP / GSSA	numerical age (Ma)
					541.0 ±1.0
Precambrian	Proterozoic	Neoproterozoic	Ediacaran	✓	~ 635
			Cryogenian		~ 720
			Tonian	◷	1000
		Mesoproterozoic	Stenian	◷	1200
			Ectasian	◷	1400
			Calymmian	◷	1600
		Paleoproterozoic	Statherian	◷	1800
			Orosirian	◷	2050
			Rhyacian	◷	2300
			Siderian	◷	2500
	Archean	Neoarchean		◷	2800
		Mesoarchean		◷	3200
		Paleoarchean		◷	3600
		Eoarchean		◷	4000
	Hadean				~ 4600

Units of all ranks are in the process of being defined by Global Boundary Stratotype Section and Points (GSSP) for their lower boundaries, including those of the Archean and Proterozoic, long defined by Global Standard Stratigraphic Ages (GSSA). Charts and detailed information on ratified GSSPs are available at the website http://www.stratigraphy.org. The URL to this chart is found below.

Numerical ages are subject to revision and do not define units in the Phanerozoic and the Ediacaran; only GSSPs do. For boundaries in the Phanerozoic without ratified GSSPs or without constrained numerical ages, an approximate numerical age (~) is provided.

Numerical ages for all systems except Lower Pleistocene, Upper Paleogene, Cretaceous, Triassic, Permian and Precambrian are taken from 'A Geologic Time Scale 2012' by Gradstein et al. (2012); those for the Lower Pleistocene, Upper Paleogene, Cretaceous, Triassic, Permian and Precambrian were provided by the relevant ICS subcommissions.

Colouring follows the Commission for the Geological Map of the World (http://www.ccgm.org)

Chart drafted by K.M. Cohen, D.A.T. Harper, P.L. Gibbard

To cite: Cohen, K.M., Finney, S.C., Gibbard, P.L. & Fan, J.-X. (2013; updated) The ICS International Chronostratigraphic Chart. Episodes 36: 199-204.

URL: http://www.stratigraphy.org/ICSchart/ChronostratChart2017-02.pdf

Aknowledgements/Remerciements/Ringraziamenti

Durante il mio percorso ho vissuto in prima persona parecchie difficoltà date da un sistema che probabilmente necessita di qualche aggiustatina. Non mi sento di elogiare nessuno in particolare, all’interno del mondo accademico. Elogio la tenacia e la forza di volontà che mi è spuntata nel momento del bisogno, quando, per salvare tutto mi sono messo in discussione e ho deciso di andare ad imparare cose nuove all’estero, da luminari del settore, che mi hanno accolto stupendamente e mi hanno fatto sentire come se fossi a casa. Spendo particolari parole per le persone che più mi sono state vicino e mi hanno incoraggiato: avendo sempre avuto fiducia nei miei mezzi, dimostrandomi attenzioni e attaccamento alla mia causa. Cito il prof. Aldo Muntoni, coordinatore del corso di Dottorato. È stato, in primis, la persona che mi ha fatto capire che mollare non sarebbe stata la soluzione giusta, per tutto ciò che avevo prodotto in questi anni. Lui rappresenta un gruppo di persone che hanno sempre creduto nelle mie capacità. L’elenco di sostenitori comprende docenti, tecnici e pensionati che hanno mostrato un lato umano eccezionale, e loro lo sanno! È doveroso ringraziare Carla, collega di mille avventure, che con la sua disponibilità mi ha sostenuto e aiutato ogni qualvolta ne avessi avuto bisogno. Indispensabile ringraziare Maria Franca. Assieme a lei è stato semplice reperire qualsiasi tipo di referenza bibliografica, sia quando stavo in Italia, sia nei miei periodi all’estero: James Bond! Sono inoltre grato a Salvatore, Fabio, Fabrizio, Daniel, Laura e gli altri colleghi del dipartimento per le centinaia di pause caffè/birra/ecc., utili a staccare gli occhi dallo schermo e recuperare un po’. Un grazie anche a due colleghi storici che ormai sono più che amici, per i loro consigli e supporto: Walter e Giovanni.

Je pense avec plaisir au moment dont j'ai décidé de demander de l'aide pour étudier des échantillons permiens de la Sardaigne. J'adresse mes remerciements à l'équipe paléobotanique du CIRAD Montpellier pour l'accueil dans les laboratoires et les conditions de travail privilégiées qui m'ont été offertes, et tout particulièrement Brigitte Meyer-Berthaud, Jean Galtier, Anne-Laure Decombeix et les autres personnes du "labo". Je sais tout particulièrement gré à Giorgio, Mélanie, Haythem et Lorenzo. J'ai vécu d'incroyables moments avec eux. Je tiens à remercier profondément Françoise : je ne t'oublierai jamais parce que tu as été vraiment importante pour moi.

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Non posso escludere di ringraziare la mia famiglia e i miei amici, perché ci sono sempre stati, e le persone che non ho citato direttamente, ma che leggendo queste righe sapranno di essere incluse!

In ultimo, ma non per importanza, desidero dire grazie di cuore alla persona che è arrivata in un momento molto difficile del mio percorso, proprio quando stavo decidendo di mollare. Ci siamo aiutati reciprocamente e grazie a lei ho capito di dover assolutamente concludere un qualcosa che pensavo non mi appartenesse più. Sei arrivata col sorriso, e me l'hai trasmesso. Ti devo molto. Scrivo queste righe nonostante le cose si siano messe diversamente dalle aspettative. Qualcosa di forte però è sempre qua Chiara, e sai benissimo che queste non sono solo parole di routine.