

# 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 19<sup>th</sup> 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 arachnid, 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 Coccozza (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 Coccozza (1967) suggested a late Stephanian age ('Stephanian D' *sensu* Doubringer, 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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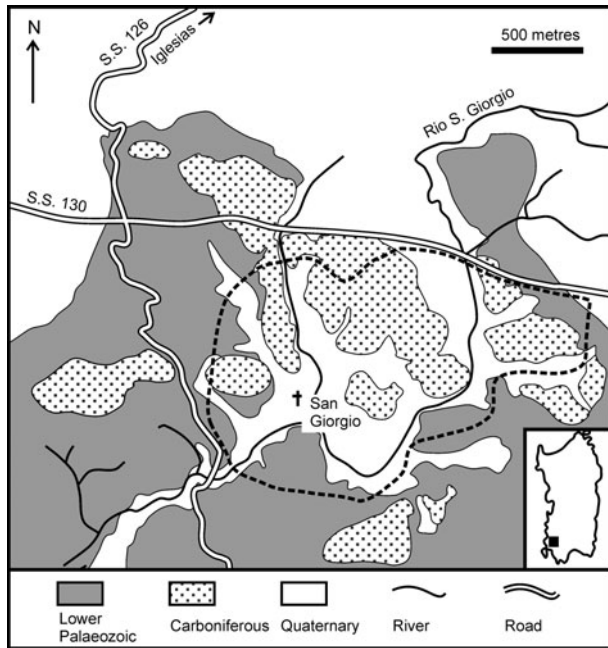


Figure 1. Simplified geological map of the Pennsylvanian-age San Giorgio Basin, SE Sardinia. The dashed line delineates the area now covered by spoil from the nearby Campo Pisano lead and zinc mine. Adapted from Del Rio & Pittau (1999, fig. 7) and Barca & Costamagna (2003, fig. 1).

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<sup>2</sup> 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.

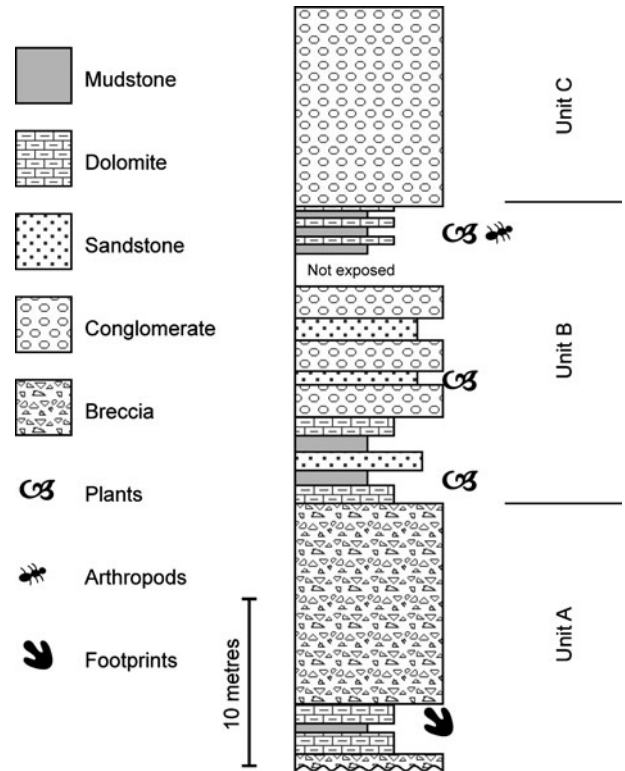


Figure 2. Simplified geological section through the Carboniferous sequence of the San Giorgio Basin, showing main fossiliferous horizons. Re-drawn from Barca & Costamagna (2003, fig. 7).

### 3. Materials and methods

The fossil plants of the Pittau – Del Rio Collection stored in the Geological and Palaeontological Museum of Cagliari University (MGPD) 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	<i>Annularia</i> Sternberg, 1821 <i>Palaeostachya</i> Weiss, 1876 <i>Calamites</i> Sternberg, 1820 <i>Pinnularia</i> Lindley & Hutton, 1834
Marattiopsida	Sphenophyllaceae	<i>Sphenophyllum</i> Brongniart, 1828b, nom. cons.
	Psaroniaceae	<i>Cyathocarpus</i> Weiss, 1869 <i>Crenulopteris</i> Wittry et al. 2015 <i>Sydneia</i> Pšenička et al. 2003
Polypodiopsida	Marattiaceae	<i>Renaultia</i> Zeiller, 1883
Noeggerathiopsida	?	<i>Discinites</i> Feistmantel, 1879
Lyginopteridopsida	Lyginopteridaceae	<i>Eusphenopteris</i> Simson-Scharold, 1934, nom. cons.
Cycadopsida	Callistophytaceae	<i>Dicksonites</i> Sterzel, 1881
	Alethopteridaceae	<i>Alethopteris</i> Sternberg, 1825 <i>Trigonocarpus</i> Brongniart, 1828b <i>Neuropteris</i> (Brongniart) Sternberg, 1825
Pinopsida	Potoniaceae	<i>Linopteris</i> Presl in Sternberg, Presl & Corda, 1838
	Cordaianthaceae	<i>Artisia</i> 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.** MGPLD 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 (= *Phyllothea 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 distinct-

ive 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, spatulate 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

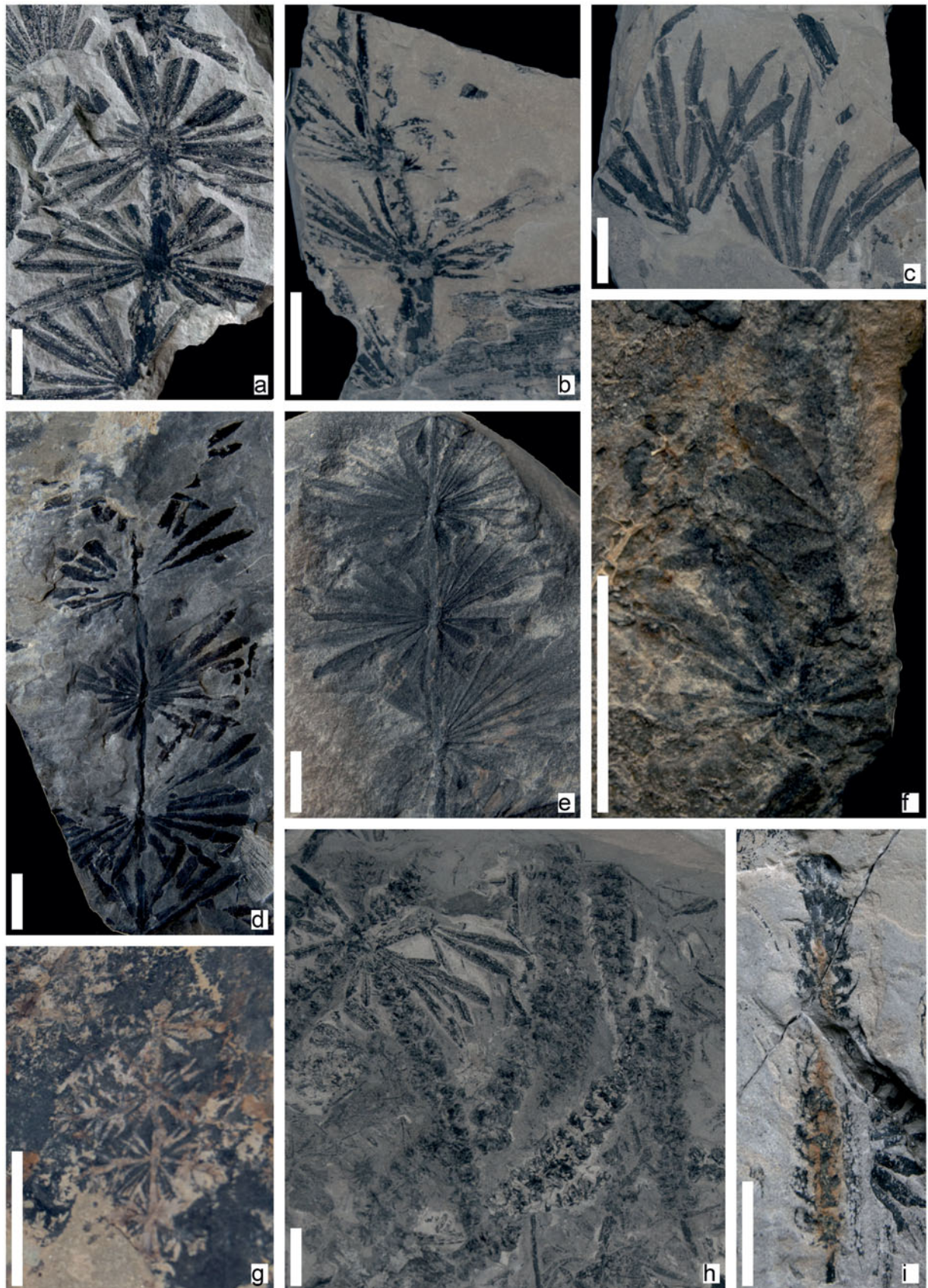


Figure 3. (Colour online) Pennsylvanian plant fossils from the San Giorgio Basin, Sardinia. (a–c) *Annularia sardiniana* sp. nov. (a: MGPDL 17397, holotype; b: MGPDL 17155; c: MGPDL 17111); (d, e) *Annularia spinulosa* Sternberg, 1821 (d: MGPDL 17406; e: MGPDL 17223); (f) *Annularia sphenophylloides*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

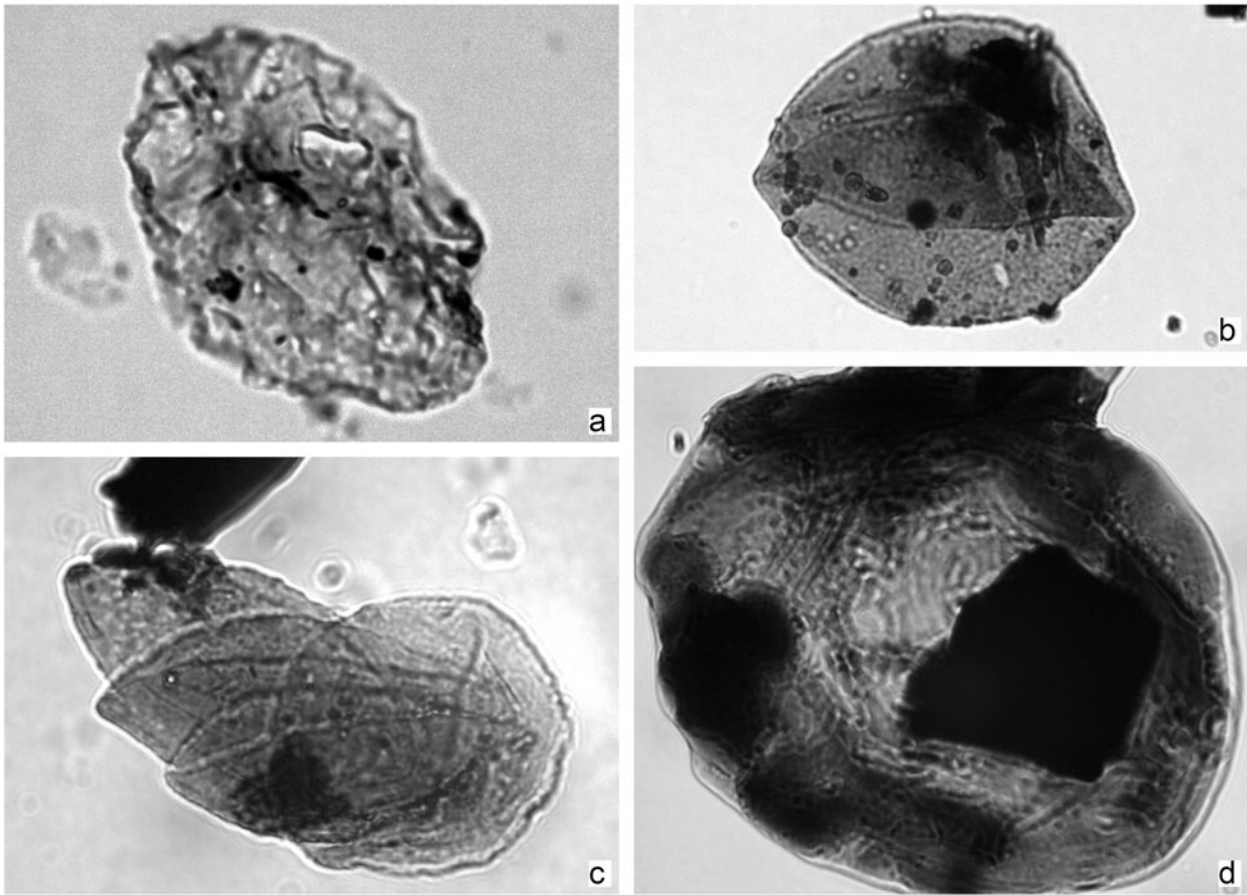


Figure 4. Pennsylvanian *in situ* spores from the San Giorgio Basin, Sardinia. (a) *Calamospora* sp. from *Palaeostachya* sp. cone (MGPD L 17135); (b) *Cyclogranisporites aureus* (Loose) Potonié & Kremp, 1955 from *Sydneia* sp. (MGPD L 17200); (c) *Cyclogranisporites multigranus* Smith & Butterworth, 1967 from *Renaultia* sp. cf. *Renaultia villosa* (Crépin) Danzé, 1956 (MGPD L 17218); (d) *?Latosporites* sp. from *?Discinites* sp. (MGPD L 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, 1828a. However, the preservation especially of the node ends and their tubercles makes it impossible to assign them meaningfully to any fossil-species.

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

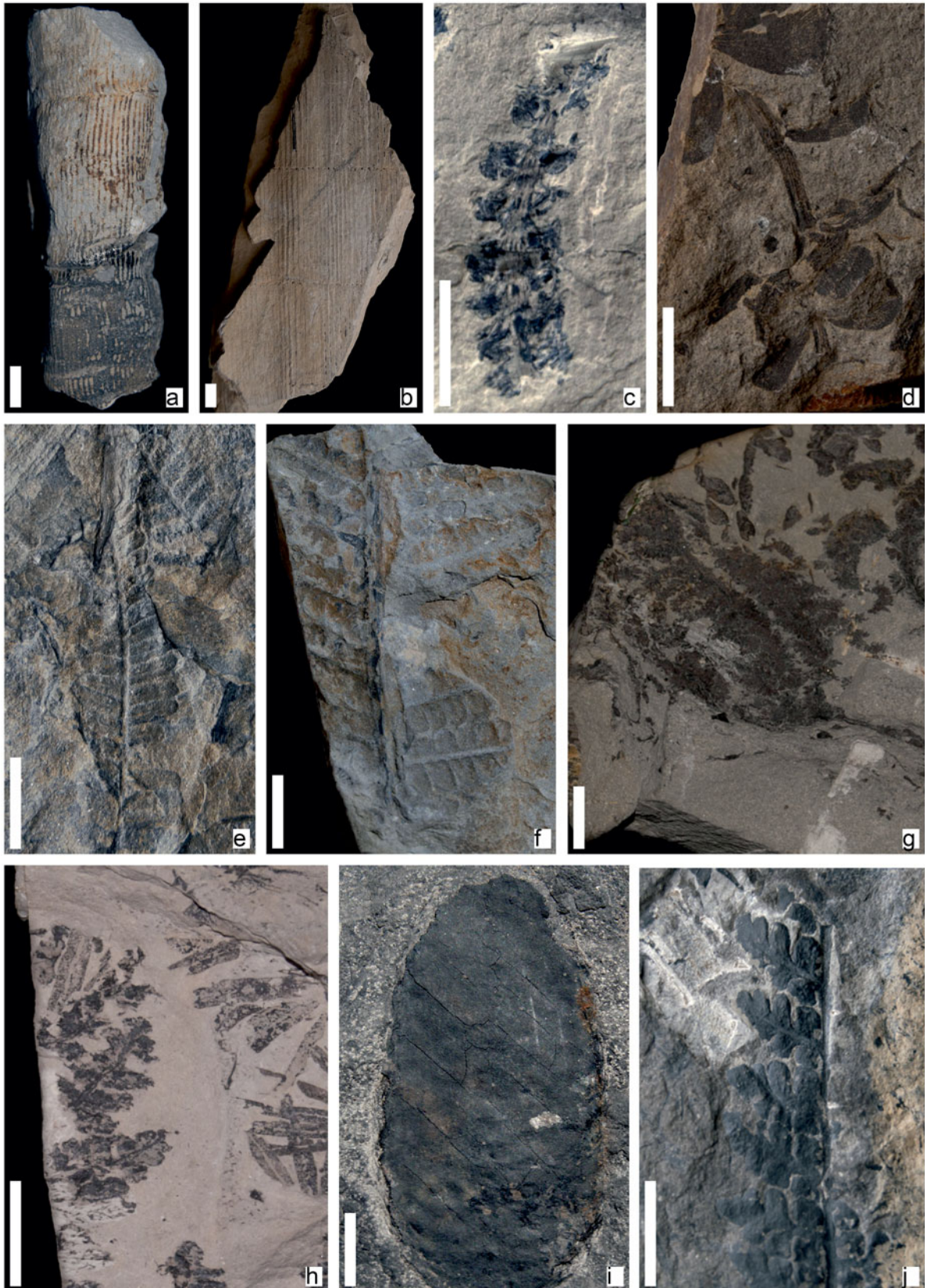


Figure 5. (Colour online) Pennsylvanian plant fossils from the San Giorgio Basin, Sardinia. (a, b) *Calamites* sp. (a: MGPDL 17162; b: MGPDL 17400); (c) *Palaeostachya* sp. (MGPDL 17135); (d) *Sphenophyllum* sp. cf. *Sphenophyllum emarginatum* (Brongniart) Brongniart, 1828b (MGPDL 17408); (e) *Cyathocarpus* 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, 1828b  
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 & Drábková, 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 Coccozza (1967) are not very clear but appear to be of a *Dicksonites* and so are assumed to be probably of the same species. Coccozza 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 Zодrow & Cleal (1998), in particular 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 (MGPD 17117); (c) *Alethopteris* sp. (MGPD 17409); (d) *Trigonocarpus* sp. (MGPD 17409); (e) *Neuropteris ovata* Hoffmann, 1826 (MGPD 17409); (f) *Neuropteris* sp. (MGPD 17221); (g) (?)*Neuropteris* sp. (MGPD 17170); (h) *Linopteris* sp. cf. *Linopteris obliqua* (Bunbury) Zeiller emend. Zödrög, Tenchov & Cleal, 2007 (MGPD 17409); (i) *Annularia sardiniana* sp. nov. (MGPD 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, 2010a).

*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. Coccozza (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. Coccozza (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 Coccozza (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
<i>Annularia sardiniana</i>	67.75	17	18	0	0	5.6
<i>Annularia spinulosa</i>	0	0	0	0	11	0
<i>Annularia galioides</i>	1.25	0	0	0	0	0
<i>Annularia sphenophylloides</i>	0	0	0	0	0	1.4
<i>Sphenophyllum</i> cf. <i>emarginatum</i>	0	0	0	0	0	1
<i>Cyathocarpus</i> sp.	0	0	3	1	0	0
<i>Crenulopteris</i> sp.	1	0	0	0	0	2
<i>Sydneia</i> sp.	1	0	0	0	0	0
<i>Renaultia</i> cf. <i>villosa</i>	7	1	0	0	0	0
? <i>Discinites</i> sp.	0	0	1	0	0	0
<i>Eusphenopteris nummularia</i>	2	1	0	0	0	3
<i>Alethopteris ambigua</i>	1	0	0	0	0	1
<i>Alethopteris</i> sp.	0	0	0	0	0	1
<i>Neuropteris ovata</i>	0	0	0	0	0	1
<i>Neuropteris</i> sp.	0	0	1	0	0	0
(?) <i>Neuropteris</i> sp.	0	0	0	1	0	0
<i>Linopteris</i> cf. <i>obliqua</i>	0	0	0	0	0	1
<i>Artisia approximata</i>	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 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 conchoidal fracture. Although also probably lacustrine, the presence of a different species of calamostachyalean sphenophyte suggests that the adjacent shore had different substrate conditions.

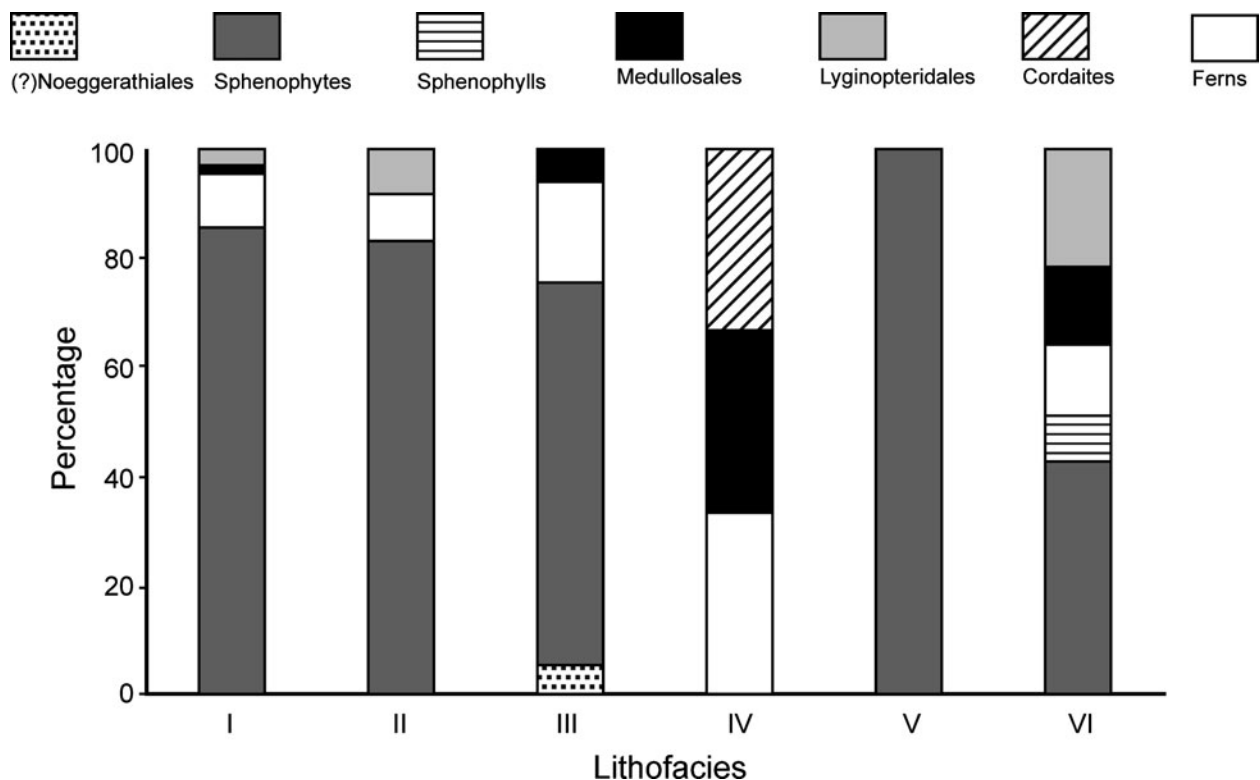


Figure 7. Distribution of the major plant groups in the six lithologies recognized in this study (see text for details).

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	<b>0.58</b> (d.f. = 33, p = 0.56)	<b>0.86</b> (d.f. = 44, p = 0.40)	<b>0.20</b> (d.f. = 4, p = 0.85)	4.93 (d.f. = 80, p < 0.01)	5.15 (d.f. = 37, p < 0.01)
II		<b>1.19</b> (d.f. = 40, p = 0.24)	<b>0.57</b> (d.f. = 7, p = 0.50)	2.21 (d.f. = 19, p = 0.04)	4.54 (d.f. = 35, p < 0.01)
III			<b>0.38</b> (d.f. = 6, p = 0.72)	4.22 (d.f. = 23, p < 0.01)	3.49 (d.f. = 40, p < 0.01)
IV				<b>2.30</b> (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 *Crenopteris 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 Toppa Niedda, c. 20 km northwest of San Giorgio. Like the San Giorgio sequence, that at Toppa 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 Toppa 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



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