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Jean Galtier, Ausonio Ronchi, Jean Broutin. 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*, 2011, 33 (1), pp.43-69. 10.5252/g2011n1a4 . halsde-00675563

**HAL Id: halsde-00675563**

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Submitted on 29 May 2020

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# 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)

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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. DOI: 10.5252/g2011n1a4.

## ABSTRACT

In the Perdasdefogu Basin (Ogliastra, Sardinia) plants occurring in angular cherts are preserved as siliceous permineralizations. The plant assemblage consists of the genera *Sphenophyllum*, *Arthropitys*, *Astromyelon*, *Palaeostachya*, *Pecopteris*, *Scolecopteris*, *Stewartiopteris*, *Psaronius*, *Ankyropteris*, *Anachoropteris*; furthermore, probable medullosan wood and ovules, cordaitan stems, leaves and ovules, and *Dadoxylon* wood have been recorded. Arborescent marattialean ferns are the dominant elements with *Pecopteris* and *Scolecopteris* leaves being the most common; the calamiteans are the second in abundance. Generally the chert blocks contain a large number of plant fragments – roots and leaves are being almost equally represented – suggestive of a coal ball-like plant accumulation. More rarely a chert block may consist of a single plant part, for example a piece of wood. The preservation and accumulation of the plants are closely comparable to the silicified plant assemblages described from the Lower Permian of Autun and the upper Pennsylvanian of Grand-Croix (Massif central, France) and from the Early Permian Döhlen Basin (Germany).

**KEY WORDS**

Silicified floras,  
Autunian,  
Early Permian,  
Sardinia,  
compression macrofloras.

It is certainly significant that the assemblage from the Perdasdefogu Basin is dominated by tree ferns and calamites like the coeval silicified vegetation from Autun. However, like in Autun, the permineralized flora contrasts with the underlying compression floras dominated by conifers and peltasperms. The Perdasdefogu macroflora record suggest a middle-upper Autunian age which corresponds to the Surmoulin and Millery formations of the Autun Basin. This is in agreement with the Asselian-Sakmarian transition as pointed out by the amphibian species found in the same formation, and perfectly correlatable with the same association found in Gottlob-lake (Thuringian Forest Basin). Because of its rich fossil content, the Perdasdefogu Basin represents a reference succession for the Autunian of the entire westernmost palaeo-Tethyan domain and its macrofloral record.

**RÉSUMÉ**

*Flores silicifiées du Permien basal du Bassin de Perdasdefogu (SE de la Sardaigne) : comparaison et corrélation bio-chronostratigraphique avec les flores du Bassin d'Autun (Massif central, France).*

Dans le Bassin de Perdasdefogu (Ogliastra, Sardaigne) des cherts anguleux renferment des plantes préservées sous forme de perminéralisations siliceuses. L'assemblage comprend les genres *Sphenophyllum*, *Arthropitys*, *Palaeostachya*, *Pecopteris*, *Scolecopteris*, *Stewartiopteris*, *Psaronius*, *Ankyropteris*, *Anachoropteris*, du bois et des ovules appartenant probablement à des Médullosales, des tiges, feuilles et ovules de type cordaitales et, rarement, du bois de *Dadoxylon*. Les fougères arborescentes marratiales constituent l'élément dominant avec les feuillages *Pecopteris* et *Scolecopteris* comme fossiles les plus communs ; les sphénopsides calamitales sont deuxième en abondance. Généralement un spécimen de chert contient un grand nombre de fragments végétaux (racines et feuilles presque à égalité) suggestif d'une accumulation végétale de type coal-ball. Plus rarement un spécimen peut correspondre à un seul fragment, par exemple un morceau de bois. La préservation et l'accumulation des végétaux sont très comparables à ceux des assemblages de plantes silicifiées du Permien basal d'Autun et du Pennsylvanien de Grand-Croix (Massif central, France) ainsi que du Bassin Permien basal de Döhlen (Allemagne). Il est certainement significatif que l'assemblage provenant du Bassin de Perdasdefogu soit, comme la végétation silicifiée contemporaine d'Autun, dominé par les fougères arborescentes et les calamitales. Cependant, comme à Autun, la flore perminéralisée contraste avec les flores en compression sous-jacentes qui sont caractérisées par la présence de conifères et de peltaspermes. L'inventaire de la macroflore de Perdasdefogu suggère une datation Autunien moyen-supérieur qui correspond précisément aux formations de Surmoulin/Millery du Bassin d'Autun. Ceci est conforme avec un intervalle de temps à la transition Assélien-Sakmarien, ainsi que le suggère la présence d'amphibiens dans des intervalles stratigraphiques très voisins et parfaitement corrélables avec la même association trouvée au lac Gottlob (Bassin Thuringian Forest). L'analyse comparée des horizons silicifiés fossilifères, bien repérés dans la succession stratigraphique de Perdasdefogu et de ceux provenant des formations de Surmoulin et Millery dans le Bassin d'Autun, suggère qu'ils sont contemporains et d'âge Permien basal. Compte-tenu de son riche contenu fossilifère, le Bassin de Perdasdefogu représente indiscutablement une succession de référence pour l'Autunien dans l'ensemble le plus occidental du domaine paléo-téthysien et pour sa macroflore.

**MOTS CLÉS**

Flores silicifiées,  
Autunien,  
Permien basal,  
Sardaigne,  
macroflores en  
compression.

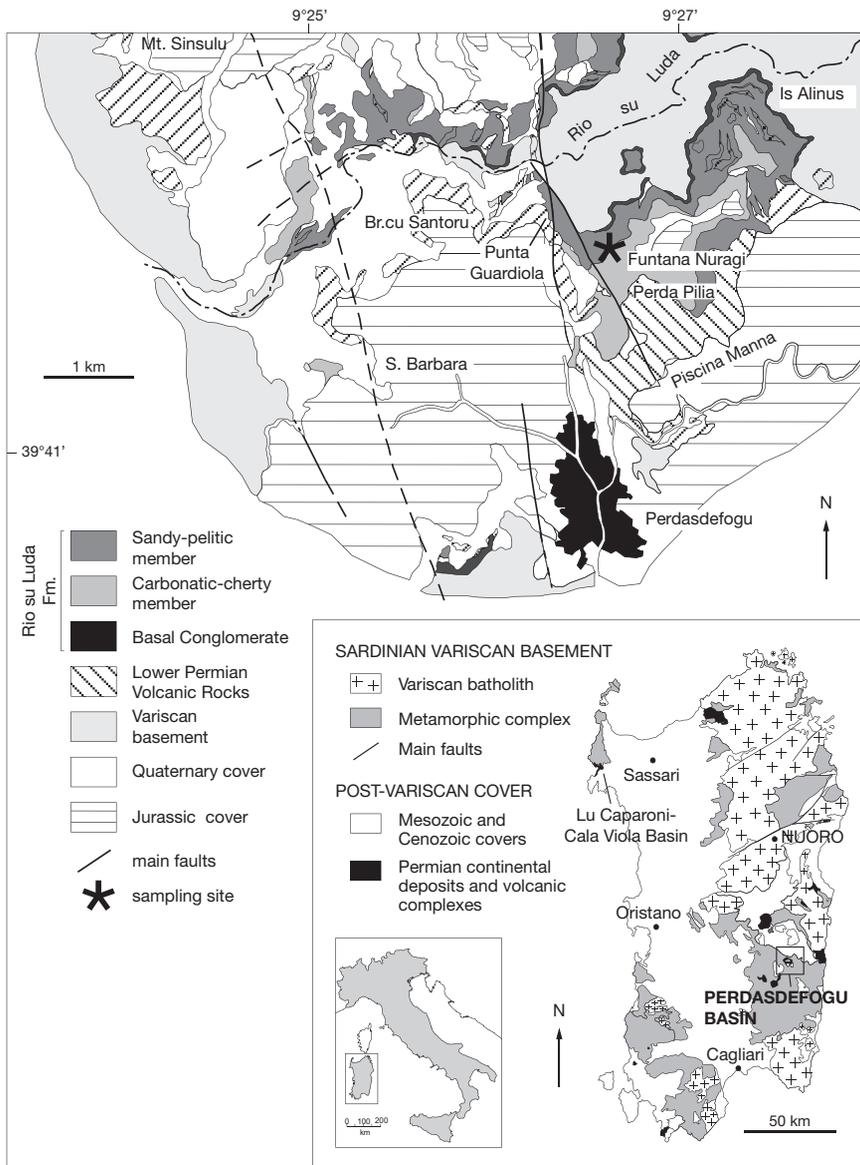


FIG. 1. — Location of silicified floras from the Perdasdefogu Basin (Ogliastra, Sardinia): **A**, Sardinia simplified geological map with position of the major Late Carboniferous-Permian basins; **B**, Southern portion of Perdasdefogu Basin with the site of discovery of permineralized plants.

## INTRODUCTION

Small intramontane basins, formed in Sardinia at the end of the Variscan Orogeny, have been filled up with volcano-sedimentary deposits very rich

in fossils and attributed to a Late Carboniferous-Early Permian age, based mainly on compression macrofloras (Arcangeli 1901; Comaschi Caria 1959). Some of these basins (Perdasdefogu, Escalaplano, Mulargia, Seui-Seulo, Lu Caparoni)

have been recently reinvestigated in great detail (Ronchi 1997; Ronchi *et al.* 1998, 2008; Broutin *et al.* 2000a, b; Cassinis *et al.* 2000; Freytet *et al.* 2002; Werneburg *et al.* 2007). Some of them, such as the Perdasdefogu Basin, yielded new, diverse palaeontological contents (algae, stromatolites, ostracods, bivalves, gastropods, amphibians and fish remains) that allowed dating these sediments as Asselian-Sakmarian (Ronchi *et al.* 1998, 2008; Werneburg *et al.* 2007). A rich and very well preserved silicified flora was also found in the Perdasdefogu Basin during the PhD research of one of us (AR). These plants were found especially in the Funtana Nuragi locality in the upper silicified horizons of the “black limestones” or *lithozone d* of the Rio su Luda Formation (Ronchi & Falorni 2004) and have been first mentioned and briefly described in Ronchi *et al.* (1998) and in Broutin *et al.* (1999; 2000b). The objectives of the present paper are: 1) to describe and illustrate, for the first time in detail, the silicified plant assemblage from Perdasdefogu; 2) to compare it with other contemporaneous European permineralized floras; and 3) to discuss its palaeoecological and palaeogeographical significance with regard to the associated compression macrofloras.

## MATERIAL AND METHODS

### GEOLOGICAL SETTING

The Lower Permian Perdasdefogu Basin extends for about 25 km<sup>2</sup> in the Ogliastra region (central to southeastern Sardinia, Fig. 1A) and is located north of the homonymous village (Fig. 1B). Before a drilling campaign of Pro.Ge.Mi.Sa company (Sarria 1987) and the renewed interest of a multi-disciplinary group of researchers (see e.g., Broutin *et al.* 1996; Ronchi *et al.* 1998, 2008; Cassinis *et al.* 2000; Pertusati *et al.* 2002; Werneburg *et al.* 2007), very few and mostly older studies have dealt with its palaeontologic-stratigraphic content (e.g., Maxia 1938; Fois 1939). In the second half of the 1990s, these studies were coupled with detailed mappings of the area for the 1:50 000 geological maps of the Italian Geological Service (CARG project; Pertusati *et al.* 2002a, b).

Very similarly to other small late Palaeozoic continental troughs in Sardinia (e.g., Escalaplano-Mulargia, Seui-Seulo), the Perdasdefogu Basin is an internally-drained post-Variscan palaeograbben. Drillings have revealed an asymmetrical half-graben structure, controlled by a major normal fault, tilted blocks and by transverse structures. Strike-slip tectonic activity along the fault systems caused the tilting and sinking of basement blocks, giving rise to a pull-apart grabben, presently elongated NW-SE, most of which is now covered by Jurassic carbonate platform sediments. This Lower Permian basin originated in response to post-orogenic transtensive tectonic conditions, broadly similar also to those of many other basins of continental Paleoeurope active from the Late Carboniferous to the Early Permian (e.g., Arthaud & Matte 1977; Cassinis 1996; 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. The best exposures are on both sides of the incised valleys of rivers (Rio Su Luda and (Rio) Flumineddu and to the north of the Jurassic dolostone covers called Tacco (i.e. Plateau) de Giuncus-Monte Perdalonga.

### STRATIGRAPHIC FRAMEWORK

The Perdasdefogu Basin is characterized by a sequence about 250 m thick in which the strictly sedimentary units are frequently intercalated with and overlain by different magmatic units (Figs 2; 3).

The over 150 m thick siliciclastic/calcareous fluvio-lacustrine sedimentary sequence is represented by the Rio Su Luda Formation (Pertusati *et al.* 2002a, b; Ronchi & Falorni 2004). In the Perdasdefogu Basin, this formation is composed of the stacking of three main lithofacies: it begins with a polygenic basal conglomerate (formally *lithofacies a*, maximum 30 m thick), that bears rock fragments derived from the Variscan metamorphic basement. This first sedimentary unit, locally reddish-violet to grey-greenish, evolves from a lower lithofacies with coarse-to-fine conglomerates to an upper one, composed of microconglomerates to coarse-grained sandstones up to mudstones with even and cross-bedding. The boundary with the basement is marked by a pronounced unconformity.

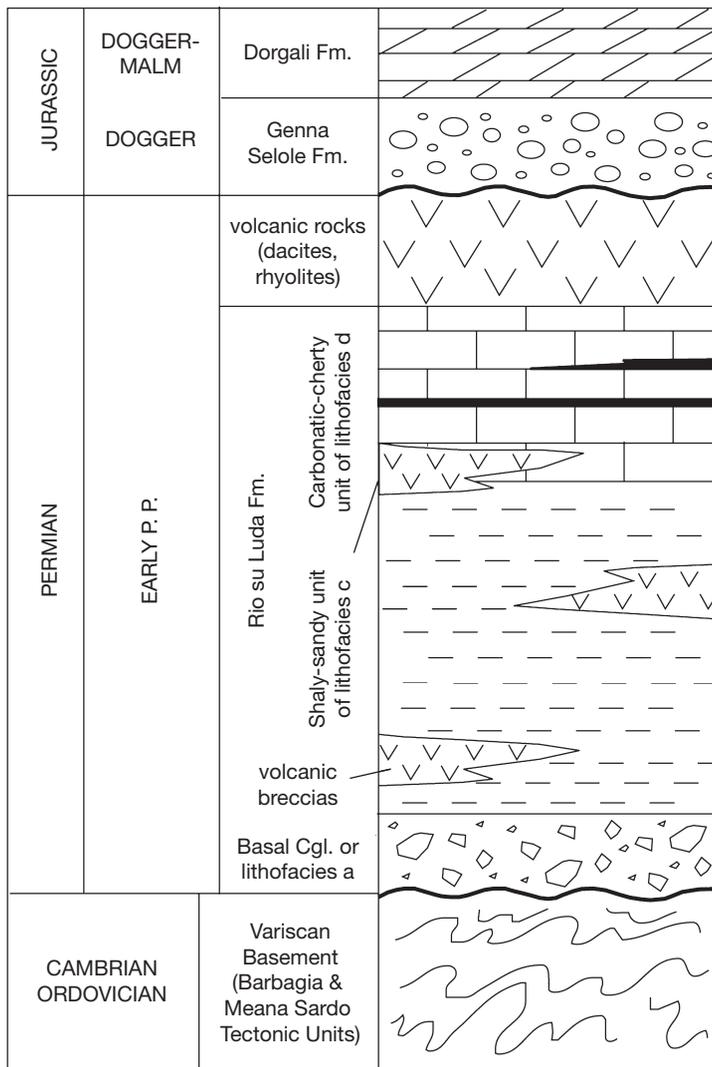


FIG. 2. — Schematic stratigraphic column of the Lower Permian continental deposits in the Perdasdefogu Basin, Sardinia.

Above this first coarse sedimentary unit, a fluvial-lacustrine *lithofacies c*, the “black siltstones” (“unità siltoso-arenacea” of Ronchi [1997] and Ronchi & Sarria *in* Cassinis *et al.* 2000), locally exceeding a thickness of 120 m, crops out. It consists of dark-grey laminated sandstones, siltstones and shales, associated with more or less consistent conglomeratic intervals and calc-alkaline intermediate volcanoclastic breccias and

lava products showing vertical and lateral variations in thickness.

The upper unit (*lithofacies d*, up to 70 m thick), the “black limestone” (“unità calcareo-selciosa” of Ronchi 1997), is composed of lacustrine dark-grey to blackish laminated limestones and dolostones, with frequent fine sandstones to laminated mudstones. Black bedded chert intercalations of volcanic origin occur at different levels and

hyaloclastites-cinerites, representing completely devetrified pomiceous tuff and ash-fall deposits flowed into lacustrine waters appear particularly at its top. In addition, in the lacustrine carbonate beds subordinate anthracitic layers (max. 1.25 m thick) occur medium to fine, as well as thin, conglomerate beds. The presence of cubic pyrite crystals, often inside rounded nodules that are some centimetres in diameter, is consistent with highly reducing environments and by dysoxic conditions at the bottom of the lake. At the top of this lithofacies some tens of meters of coarse-to-fine pyroclastic fall deposits, that are more or less silicified, can occur locally.

The finer laminated sediments and the carbonate layers are referred to a very shallow lacustrine environment.

The early volcanic record in the Perdasdefogu Basin, above the basal conglomerate, is in the SSE area (Perda Pilia) mostly represented by intermediate volcanic breccias that occur in variable thicknesses (0-50 m), interbedded within the pelitic-siltitic lower unit and also laterally occurring in the upper carbonatic unit. These latter sediments are overlain by a widespread dacitic lava flow (Bruncu Santoru high), calc-alkaline in composition, with a thickness that reaches up to a maximum of 180 m. However, in the north-western sector of the basin, these dacitic rocks are associated with or are followed by rhyolitic volcanoclastic sediments, mostly tuffs and ignimbrites, which are also calc-alkaline in composition. Dacitic and rhyolitic dikes linked to this younger volcanic activity, can also sparsely be observed in the basinal area, crossing the Variscan crystalline complex and the overlying units already described (Cassinis *et al.* 1998; Cortesogno & Gaggero *in* Cassinis *et al.* 2000).

Black, silicified decimetric beds of reworked fine-grained vitroclastic materials are widespread in the upper unit; the black colour of these levels is related to the inclusion of abundant plant material. K/Ar (WR) radiometric datings performed on the "quartz-latic lavas" of Bruncu Santoru-Gianni Vuddu were very likely affected by thermal alteration processes, because they yielded ages of  $220 \pm 5$  and  $218 \pm 6$  My, which are not in agree-

ment with the local stratigraphy (Lombardi *et al.* 1974). These deposits are overlain with an angular unconformity by very coarse-grained quartz conglomerates and/or dolostones (respectively "Formazione di Genna Selole" and "Dolomie di Dorgali"); these have been so far ascribed to the Middle Jurassic (Dogger).

The Perdasdefogu permineralized flora was found in the southeastern part of the basin (Funtana Nuragi-Ortu Mannu localities) within stratified limestone layers of the Rio su Luda Formation ("black limestones" member or *lithofacies d*), which also show silicification phenomena. The resulted lithology is represented by black cherts. A complete and detailed stratigraphic section could not be established in this area due to the presence of a large intermediate volcanic to volcanoclastic body (mainly located in Perda Pilia area), which partially disrupts the sedimentary sequence and makes the local geology complicated. For reference, a section (Punta Guardiola) measured a few hundred metres west of the fossil locality is shown in Figure 3.

The Perda Pilia volcanoclastic unit, deposited in a sub-aerial swampy setting, is very likely responsible for the heavy silica input which saturated the waters where the vegetation was accumulating.

## METHODS

The plants occur in angular cherts; they are preserved as siliceous permineralizations showing various degrees of cell wall preservation. When the organic matter is preserved the plant fragments are dark brown and the peel section method, with HF etching (Galtier & Phillips 1999), has been used. However, when the residual carbon has been lost the plants are of light colour, and thin petrographic sections must be prepared. More than 70 chert blocks have been sectioned and cellulose acetate peels were prepared from all the surfaces. For each specimen the taxa and the types of organs, which are present, have been identified. This represents a total of many hundreds plant fragments that provide a preliminary indication of the relative occurrence of plants and organs in the assemblage. The silicified plant material, prefixed by SAR, is kept in the AMAP Research Unit (collections de Paléobotanique, Université Montpellier 2).

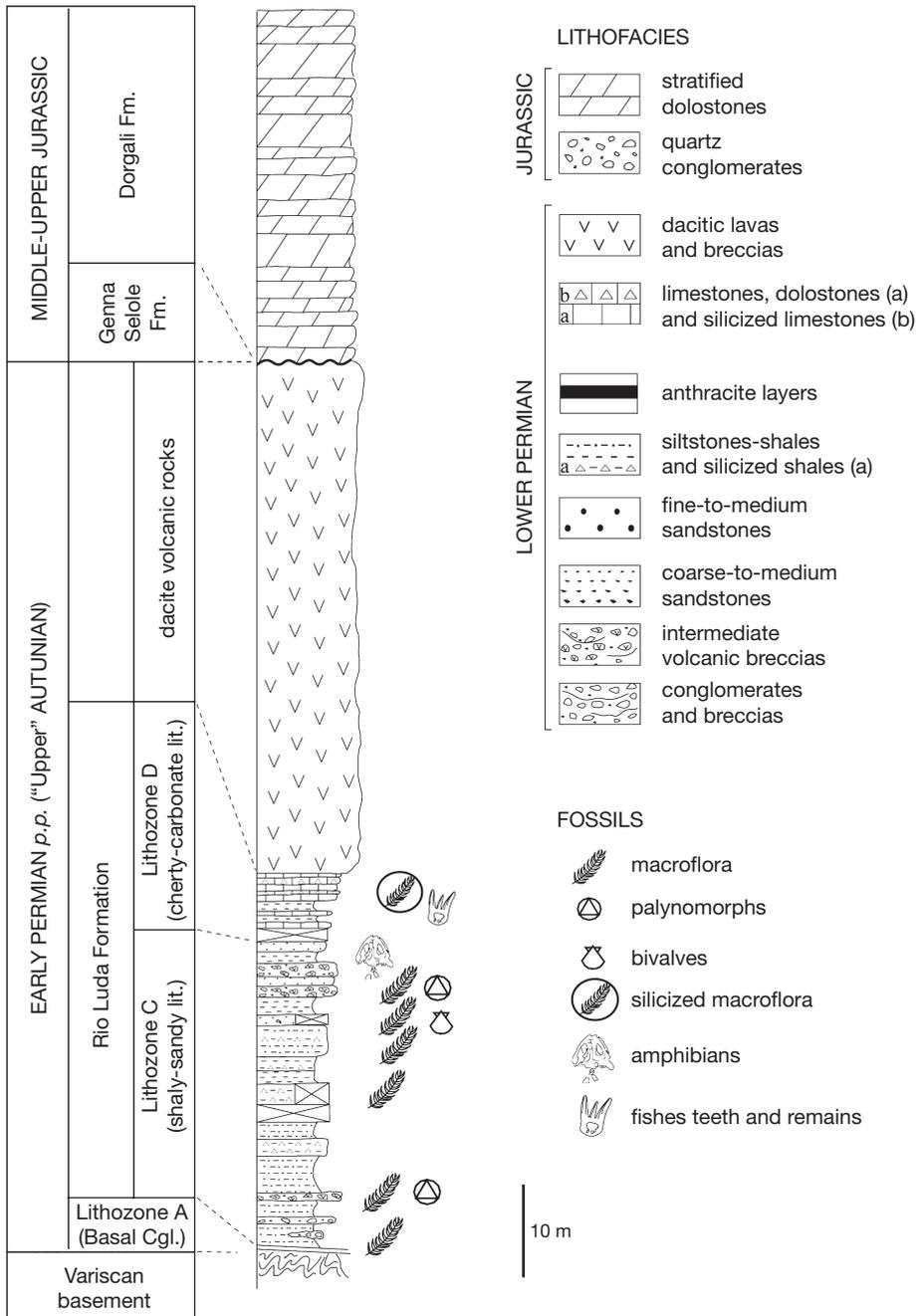


FIG. 3. — The Punta Guardiola reference section, some hundreds of metres west of Funtana Nuragi, Sardinia.

COMPOSITION OF THE FLORA  
AND SYSTEMATICS

Generally, each chert block contains an accumulation of plant fragments (mainly roots and leaves) with frequent occurrences of coprolites of very different sizes. This is suggestive of coal ball-like plant accumulations, therefore, the plant assemblage may be interpreted as a litter. However in some cases a specimen consists of a single woody plant fragment.

## LYCOPSIDS

Stigmarian rootlets occur rarely, associated with calamitean roots; they are the only known representative of lycopsids and certainly belonged to sigillarian plants not yet discovered.

## SPHENOPSIDS

In contrast to lycopsids, the calamiteans are very important elements of the plant assemblage.

*Arthropityx* cf. *renaultii* Boureau, 1964  
(Fig. 4A, E)

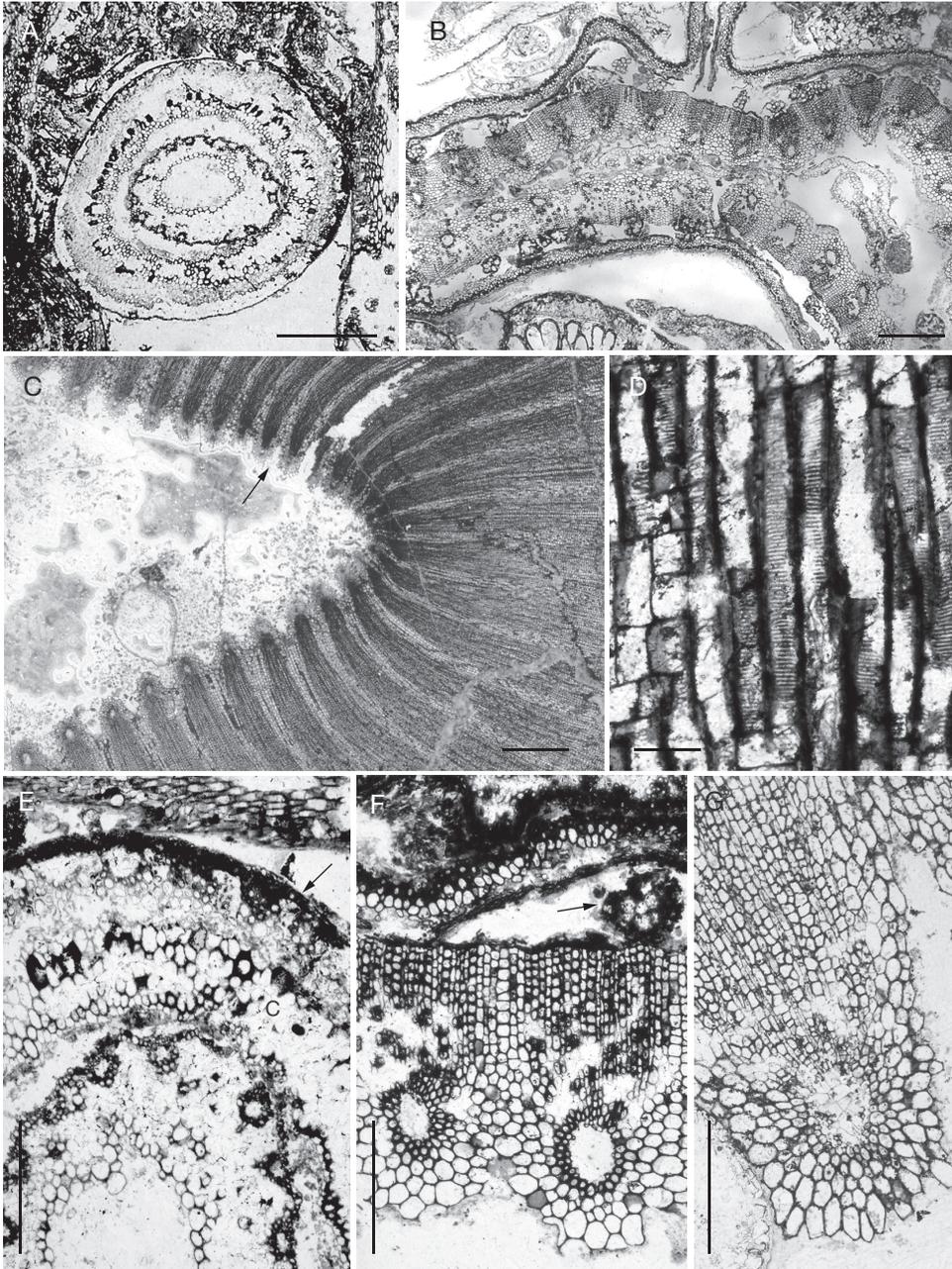
This small stem, about 3 mm in diameter, shows an excellent preservation of the tissues. There are 17 primary xylem strands, with circular carinal canals, surrounding the pith (see detail on Figure 4E). The absence of any secondary xylem supports its interpretation as a very young twig. Other examples of similar small stems have been found with leaves attached. These stems are referred with some reservations, to *A. renaultii* Boureau, 1964 from the Lower Permian of Autun that represents a similar young stem devoid of secondary xylem, but with a larger number (34) of primary xylem strands and with a proportionally narrower cortex. In the present specimen the outer cortex is sclerenchymatous with alternating parenchyma (arrow, Fig. 4E) but the inner cortex shows larger cells (C, Fig. 4E).

*Arthropityx bistriata*  
(Cotta) Goeppert, 1864  
(Fig. 4B-D, F, G)

We attribute a number of stems showing a wide range of sizes and of secondary xylem thickness to this species. The small stem (Fig. 4B) has a diameter of 19 × 5 mm including the cortex; it shows a small development of secondary xylem (0.5 mm thick, i.e. about 15 tracheids); 62 primary xylem strands with carinal canals (80 µm in diameter) are surrounding the pith at 0.7 mm intervals (Fig. 4F). Secondary xylem wedges are separated by interfascicular rays that are 5-6 cells wide. The outer sclerenchymatous cortex is well preserved as well as groups of large cells in the inner cortex (arrow, Fig. 4F). This young stem shows the beginning of development of secondary xylem. In its general organization, small amount of secondary xylem and cortex anatomy, it is very similar to specimens of *A. bistriata* var. *augustodunensis* from Autun illustrated by Renault (1893: pl. 46, fig. 7; pl. 47, figs 1, 2).

Other observed specimens belonged to older parts of plants, with a wood thickness ranging from 1 to 60 mm, but generally the cortex is missing. For example the stem (Fig. 4C) has a wood of 10 mm thick; it represents probably one third of the original woody cylinder. About 30 primary xylem strands are visible; carinal canals are 100 to 250 µm in diameter, their preservation may be excellent (Fig. 4G) and sometimes there is no lacuna (arrow, Fig. 4C). The average distance between carinal canals is 1 mm, it may be up to 2 mm in stems with wood several centimetres thick. In transverse section, interfascicular rays are less than 1 mm wide, made of 5 to 8 parenchymatous cells, and they are generally visible through the whole secondary xylem. The secondary xylem wedges consist of rays and tracheids showing an initial quick increase of their diameter from 30 to 70 µm (Figs 4F, G). Some specimens consist of a single fragment of wood including a portion of the pith and a few primary xylem strands. The observed maximum wood thickness of 60 mm suggests an

FIG. 4. — Silicified plants from the Permian of Sardinia: **A, E**, *Arthropityx* cf. *renaultii* Boureau; **A**, transverse section of a young twig (SAR01B1B01); **E**, detail of the same showing the pith, primary xylem strands with carinal canals and well preserved cortex with large cells (C) in inner cortex and alternating bands of sclerenchyma and parenchyma in outer cortex (arrow); **B-D, F, G**, *Arthropityx bistriata*



(Cotta) Goepfert; **B**, incomplete transverse section of a young stem showing a little development of secondary xylem (SAR40C1T03); **C**, partial transverse section of an older stem with thick secondary xylem and well-marked inter-fascicular rays (SAR58C1B01); **D**, radial longitudinal section in the secondary xylem showing scalariform pitting of tracheids and high ray cells on the left (SAR51BL01); **F**, detail of the stem (**B**) showing two primary xylem strands with circular carinal canals, one inter-fascicular ray, small development of secondary xylem, cluster of large cells (arrow) in inner cortex and sclerenchymatous outer cortex; **G**, detail of one primary xylem strand and secondary xylem wedge of a stem with thick wood (SAR51A01). Scale bars: A-C, 1 mm; E-G, 0.5 mm; D, 100  $\mu$ m.

original stem diameter of at least 15 cm if we include the pith and cortex. This corresponds to some specimens of *A. bistriata* illustrated by Renault (1893: pl. 44, figs 1, 2) as well as original specimens of the species described by Cotta (1832). In all the observed stems the secondary xylem tracheids show scalariform thickening to pitting on their radial walls (Fig. 4D). All the features recognized in these specimens suggest that they belong to *Arthropitys bistriata*. However, the original material of this species was decorticated and Cotta's diagnosis did not include cortical features or information on young stems such as that presented by Renault (1893-1896) for *A. bistriata* var. *augustodunensis*. There is also a strong presumption that the very small stems attributed to *A. renaultii* belong to the same plant. Detailed comparison of this material is out of the scope of the present paper.

*Palaeostachya* sp.  
(Fig. 5A-E)

Small cones 2-4 mm long and up to 10 mm in diameter are relatively common elements of the assemblage. They show whorls of 24 or 28 separate sterile bracts at each node, one half of the bract subtend the 12 or 14 axillary sporangiophores (Fig. 5B). In cross section the cone axis is broadly circular (3-5 mm in diameter) with a pith cavity and 12 or 14 primary xylem bundles with a carinal canal (Fig. 5C). There is a discontinuous narrow zone of secondary xylem and, at the node level, lacunae are present in the cortex of the cone axis, immediately outside the secondary xylem. In most specimens the bracts are broken at their point of attachment to the cone axis (Fig. 5A [B]); they extend perpendicularly outwards for a short distance before ascending vertically for about 10 mm, i.e. a little more than two nodes (Fig. 5A); this is confirmed by transverse sections showing two or three whorls of bracts (Fig. 5A [B]). The measured length of the internodes is 3.7 to 4 mm. Individual bracts show a maximum tangential

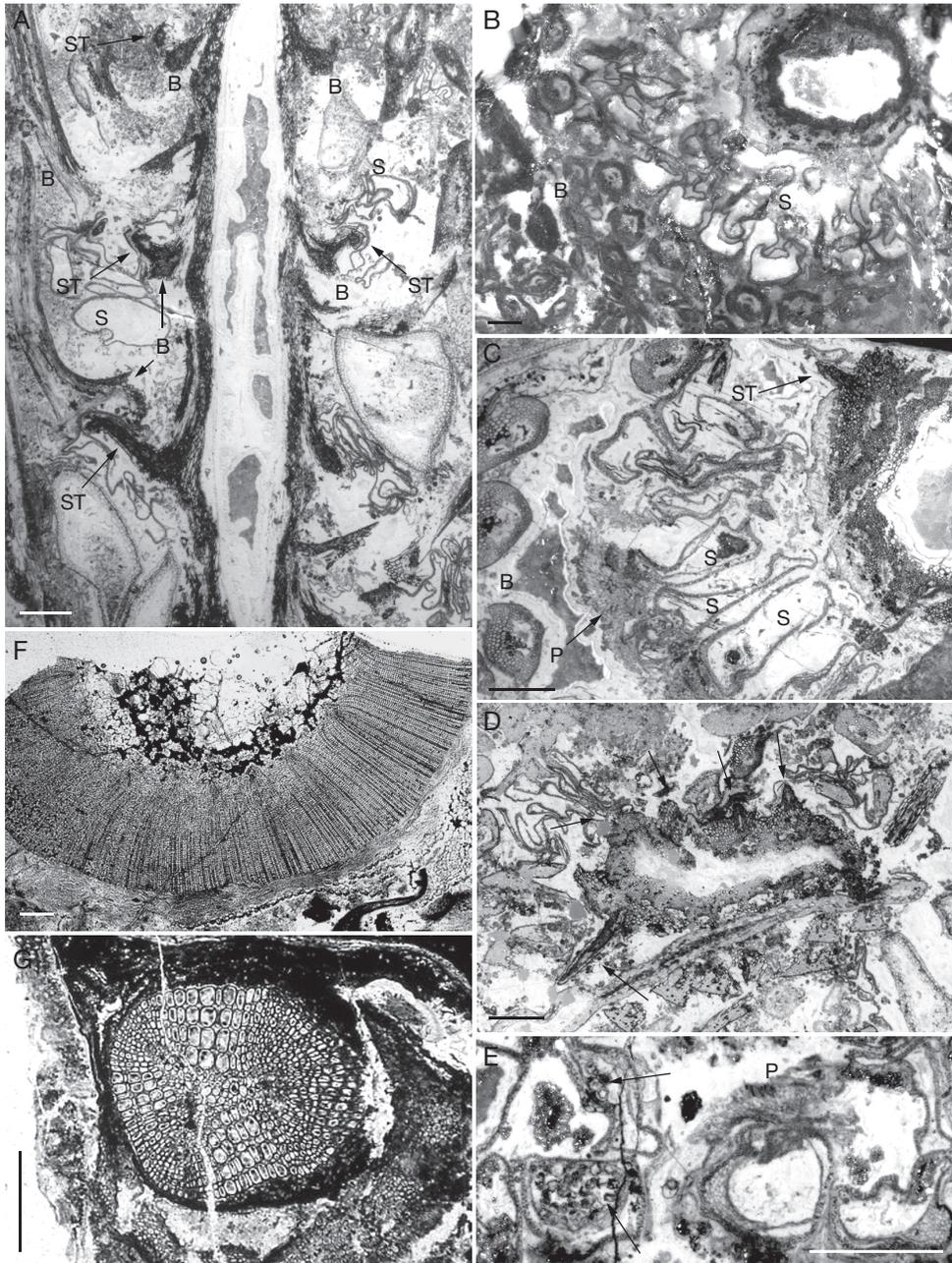
diameter (1 mm) in the ascending lamina. The sporangiophore stalks arise obliquely from the base of the bracts (Fig. 5A [ST]), a characteristic feature of *Palaeostachya* cones. Sporangiophores are borne by two contiguous (fertile) bracts alternating with two sterile ones. The stalks are narrow (0.3 × 0.4 mm in diameter), losangic in transverse section with a sclerenchym with a sclerenchymatous black cortex efficient for mechanical support of the sporangia (arrows on Fig. 5D). The sporangiophores are peltate (Fig. 5C [P]), each bearing 4 sporangia. Nearly all the sporangia (Fig. 5A-C [S]) are dehiscent and distorted, however, we can estimate their length to 2 mm and their diameter to 1 mm. The peltate sporangiophore head (Fig. 5C [P]) is about 2 mm broad and parenchymatous tissue extends at the base of each sporangium. Spores are rarely preserved, spherical, about 100 µm in diameter (arrows, Fig. 5E).

In their general organization these cones are similar to those of *Palaeostachya andrewsii* (Baxter, 1954) from Pennsylvanian coal balls of Iowa based on an exceptionally preserved specimen allowing to recognize features not completely available in our material; in addition, the spores of the American cone are larger. A detailed study is necessary to decide of the taxonomic attribution of the present specimens which can also be compared to *Palaeostachya (Volkmannia) gracilis* cones described by Renault (1876; 1896) from the Lower Permian of Autun. One of us (JG) recently re-investigated Renault's material and recognized strong similarities, but the cones from Autun correspond to several taxa, generally of larger size, with the exception of one specimen described as "*Volkmannia*" sp. (Renault 1896).

*Astromyelon* sp.  
(Fig. 5F)

We will designate under this name the calamitean roots and rootlets which represent one of the most common elements of the plant assemblage, and

Fig. 5. — Silicified plants from the Permian of Sardinia: **A-E**, *Palaeostachya* sp.: **A**, longitudinal section of the cone showing the central axis with pith cavity (**A**) and three nodes with the attachment of bracts (**B**) and sporangiophore stalks (**ST**) arising obliquely. The bracts are often displaced at their base (**B** with two arrows) whilst their distal part is ascending vertically (see on the left) (**S**), de-



hiscent sporangia with folded wall (SAR45A2L08); **B-D**, transverse sections of cones; **B**, part of one section showing the cone axis (upper right) surrounded by whorls of sporangia (**S**) and bracts (**B**) (SAR63A01); **C**, detail of a similar section showing the cone axis, at right, the base of one sporangiophore stalk (**ST**), sporangia in oblique-longitudinal section (**S**), two of them being attached to the sporangiophore peltate head (**P**) and distal lamina of bracts (**B**) at left (SAR01B3L13); **D**, distorted cone axis showing the attachment of several sporangiophore stalks (arrows) (SAR45BB04); **E**, detail of transverse sections of sporangia, one shows attachment to the sporangiophore peltate head (**P**), the two on the left contain spores (arrows) (SAR01B1B03); **F**, *Astromylon* sp., transverse section of a large decorticated root (SAR43CT01); **G**, *Sphenophyllum* sp., transverse section of a stem (SAR33C01). Scale bars: 1 mm.

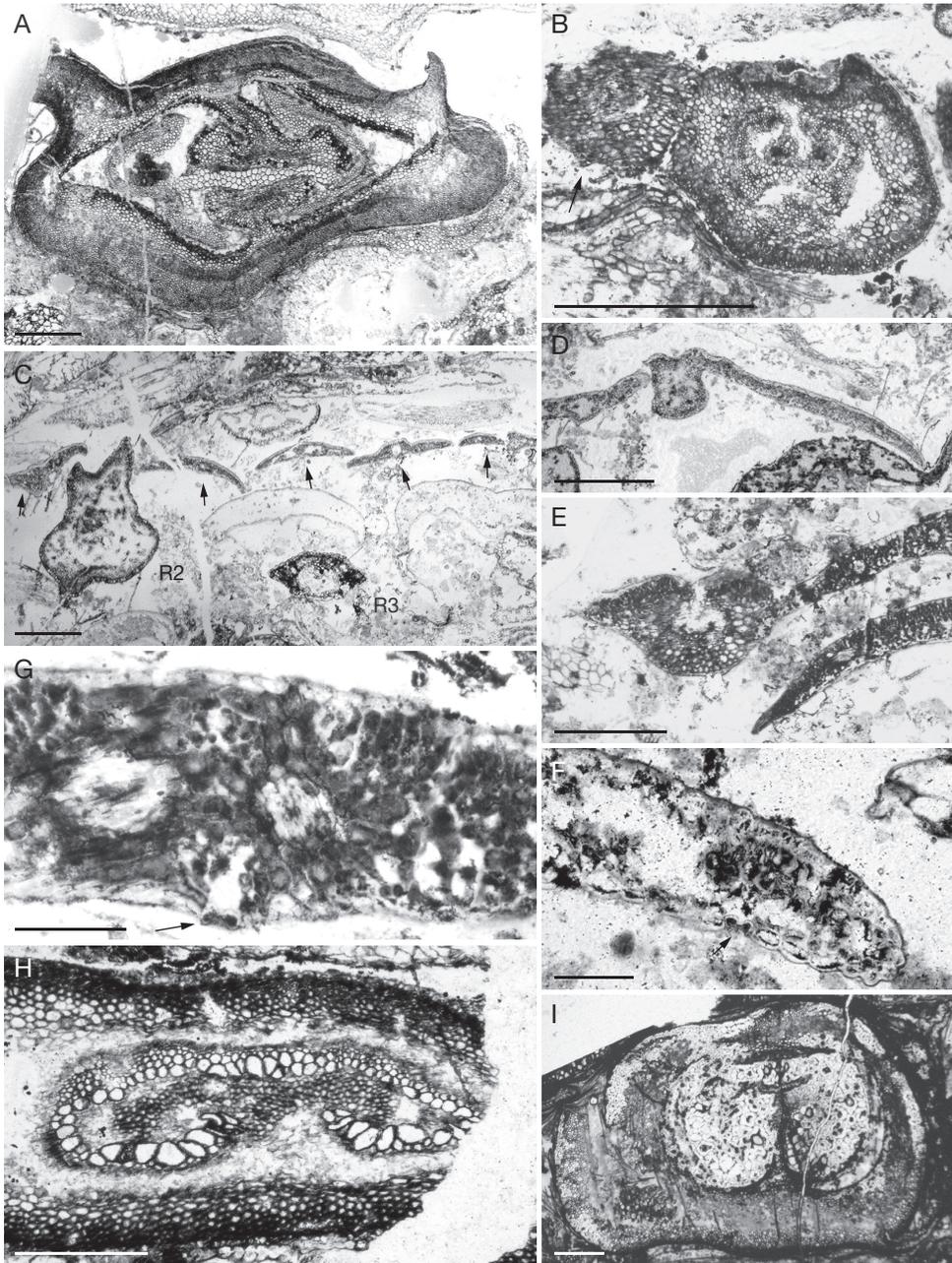


FIG. 6. — Silicified plants from the Permian of Sardinia: **A-G**, *Ankyropteris brongniartii* Renault, transverse sections of rachises and pinnules, all oriented with adaxial surface upwards: **A**, primary rachis (SAR01B1B03); **B**, secondary rachis with the base of a third order one (arrow) (SAR11AS01); **C**, connected rachises of second (**R2**) and third order (**R3**) with pinnules (arrows) (SAR01B1B02); **D**, third order or ultimate rachis with attached pinnules (SAR01A1B02); **E**, another ultimate rachis showing the C-shaped xylem strand and attached pinnules (SAR11AS01); **F, G**, sections of pinnule lamina showing stomata (arrows), thick epidermis on both faces and veinlets in **G** (SAR01B1B01, SAR11AS01); **H-I**, *Anachoropteris pulchra* Corda, transverse sections of probable second order rachis (**H**) and large primary rachis (**I**) showing abaxially enrolled xylem strand (SAR08BB03, SAR24B02). Scale bars: A-D, I, 1 mm; E, H, 0.5 mm; F, G, 100 µm.

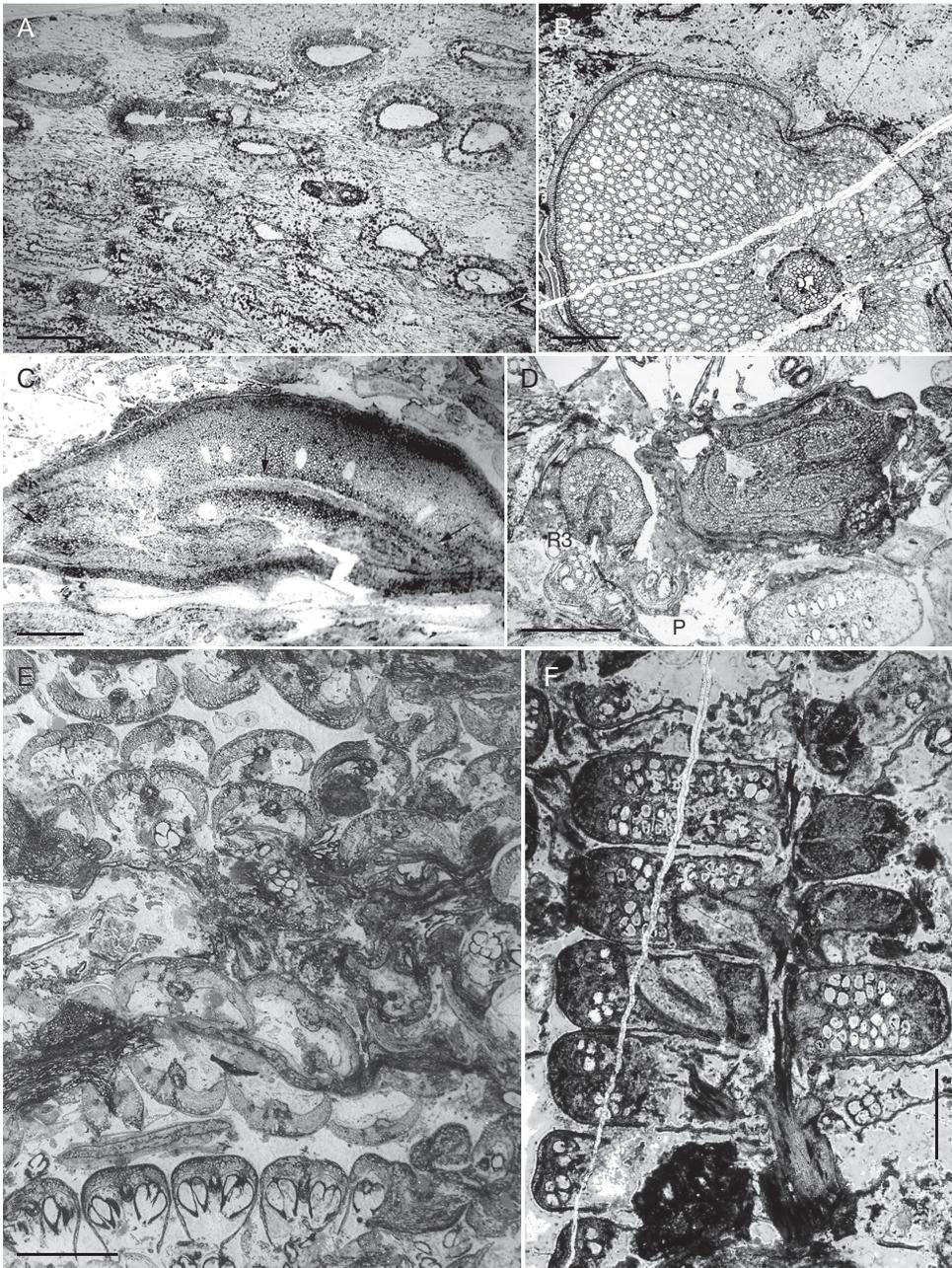


FIG. 7. — Silicified plants from the Permian of Sardinia: **A, B**, *Psaronius* sp.; **A**, part of the inner root mantle of a trunk, transverse section showing the small roots and interstitial tissue (SAR 13BB01); **B**, transverse section of one large free root of the outer zone; note the broad aerenchymatous cortex (SAR10A01); **C, D**, rachises of fronds borne by *Psaronius*; **C**, *Stewartiopteris* sp.1, rachis with a broad C-shaped xylem strand (arrows) and middle cortex with small lacunae (SAR59AT01); **D**, *Stewartiopteris* sp. 2., rachis with a different cortex bearing a probable third order one (**R3**) with fertile pinnule attached (SAR46B01); **E, F**, foliage of fronds borne by *Psaronius*; **E**, accumulation of fronds showing vegetative (above) and fertile pinnules (below) seen in transverse section (SAR40C1T01); **F**, part of a fertile pinna seen in paradermal section (SAR03A1T02). Scale bars: 2 mm.

probably the most important in terms of volume. We illustrate one rather broad but decorticated woody root (Fig. 5F). Smaller roots (less than 1 cm in diameter) with a little or no secondary xylem have generally a lacunose cortex preserved and are assignable to the genus *Myriophylloides*. Similar roots are present in the Autun material, however, *A. augustodunense* Renault, 1896 and *A. reticulatum* Renault 1896 differ in detail of their cortex and correspond to rather large roots like the one illustrated here of which cortical features are missing.

*Sphenophyllum* sp.  
(Fig. 5G)

We only found two specimens of these small stems, partly decorticated but showing well-developed secondary xylem. There is no diagnostic feature allowing a specific identification. This genus extends up to the Early Permian where it has been found preserved as compressions at Autun (Igornay).

FERNS

Ferns, particularly marattialean tree ferns, are the most common element of the flora.

*Ankyropteris brongniartii* Renault, 1869  
(Fig. 6A-G)

This small tedelean fern is one of the best known Palaeozoic ferns (Phillips & Galtier in press); it has a wide stratigraphic range from Early Pennsylvanian to Early Permian where it was first described from Autun by Renault (1869) and from Chemnitz by Stenzel (1889) under the name *Ankyropteris scandens*. This fern is a vine known to have been growing on trunks of the *Psaronius* tree ferns. We found portions of all the different parts of the tripinnate frond in a few specimens. The primary rachis (Fig. 6A) has the characteristic H-shaped xylem strand, and a secondary rachis with the base of third order one is illustrated on Figure 6B. Foliage of this fern was found lying gently within accumulations of leaves of other plants (Fig. 6C). Tertiary rachises (R3, Fig. 6C-E) and pinnules have been observed. Their excellent preservation

reveals unknown details on the anatomy of the rather rigid pinnules (Fig. 6C-G). Their lamina proves to be significantly thicker than in the rare examples previously described from Pennsylvanian material; the histology of the mesophyll is revealed as well as the occurrence of stomata (arrows, Fig. 6F, G). Unfortunately fertile pinnae have not been found.

*Anachoropteris pulchra* Corda, 1845  
(Fig. 6H, I)

A few fragments of rachises of this fern have been found; one (Fig. 6H) shows the characteristic abaxially enrolled xylem strand, a feature more hardly visible in another specimen (Fig. 6I). The latter is a larger rachis with a still more inrolled xylem strand. Both are conform to the species *Anachoropteris pulchra* Corda from Radnice, also recognized at Grand-Croix and Autun (Corsin 1937).

Marattialean tree ferns: fragments of the different parts of the plant are present in nearly 90% of the specimens including *Psaronius* trunks with aerial roots, *Stewartiopteris* petioles and rachises, *Pecopteris* and *Scolecopteris* pinnules

*Psaronius* sp.  
(Fig. 7A, B)

Fragments of root mantle of *Psaronius* trunks are common elements; they occur in about half of the specimens either as portions of the inner root mantle (Fig. 7A) where the roots are cohesive with an interstitial tissue, or as isolated larger roots from the outer zone of the trunk (Fig. 7B) showing a characteristic aerenchymatous cortex and stellate xylem strand. In the absence of information on the stele of the stem a specific attribution is, however, impossible.

*Stewartiopteris* sp. 1 and sp. 2  
(Fig. 7C, D)

The large rachis (Fig. 7C), shows a broad C-shaped xylem strand (arrows, Fig. 7C) and outer sclerenchymatous cortex; it represents the proximal region of

a frond. The smaller rachis shown on Figure 7D is quite distinct in cortical organization. It certainly corresponds to a second order rachis alongside the corresponding third order rachis (R3, Fig. 7D) which is in connection with a fertile pinnule (P, Fig. 7D). These two *Stewartiopteris* rachises certainly belonged to different fronds.

Foliage of these tree ferns occasionally occurs as dense accumulations of vegetative and/or fertile pinnules as shown on Figure 7E. One section of an ultimate pinna, paradermal to the pinnule surfaces (Fig. 7F), reveals their pecopteroid morphology. At least three different taxa occur in the assemblage as is suggested by differences in the fertile pinnae.

*Pecopteris* sp.  
(Fig. 8A)

A transverse section of a vegetative pinnule, similar to those shown on Figure 7E, shows the fleshy texture of the lamina (300–400  $\mu\text{m}$  thick) with palisade and spongy parenchyma; the pinnule margins are flexed downwards and prominent hairs are borne on the lower epidermis. Such pinnules are smaller but very similar in organization to the vegetative pinnules attributed to *Scolecopteris oliveri* from Autun by Scott & Holden (1933); they may belong to the same plant as the associated fertile pinnules described hereafter.

*Scolecopteris* cf. *elegans* Zenker, 1837  
(Fig. 8B)

This oblique transverse section of one pinnule also shows a lamina with palisade and spongy parenchyma but thin, more than 2 mm long, lateral extensions

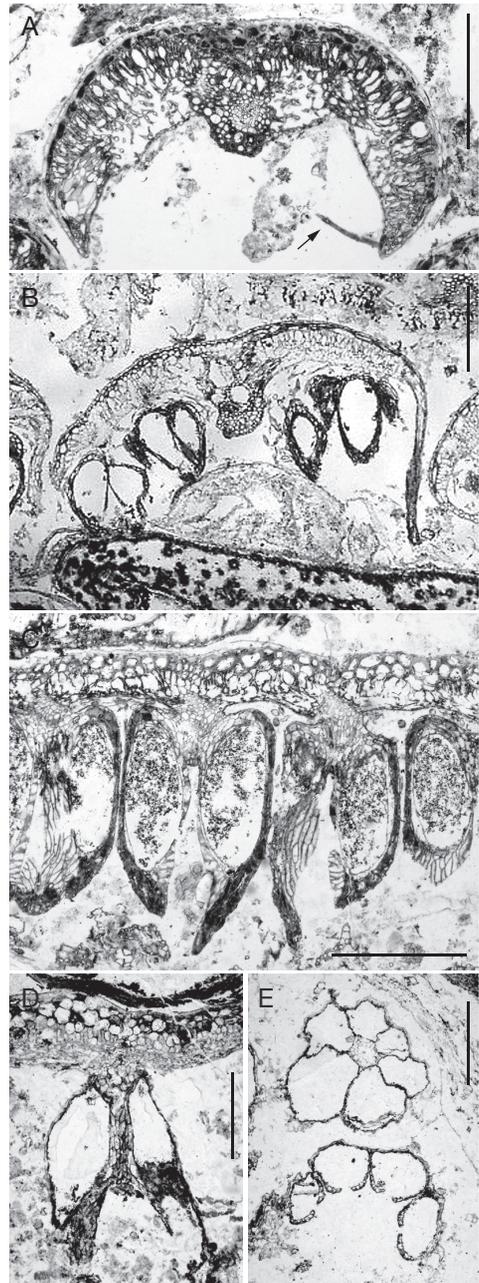


FIG. 8. — Silicified plants from the Permian of Sardinia: **A**, *Pecopteris* sp., transverse section of one vegetative pinnule showing thick lamina with palisade and aerenchyma mesophyll. Note the hair (arrow) attached near the lower extremity (SAR15B1T02); **B**, *Scolecopteris* cf. *elegans* Zenker, oblique transverse section of one pinnule showing two synangia attached on the left side. Note the thick lamina similar to that of *Pecopteris* sp. (**A**) but long thin pinnule extension on the right (SAR40C01); **C**, *Scolecopteris* cf. *parvifolia* Millay, part of a longitudinal section of one pinnule passing through several synangia. Note the relatively thin lamina, synangia borne on a short vascularised pedicel and solid tips of sporangia (SAR56AT02); **D**, **E**, *Scolecopteris* cf. *alta* Millay; **D**, longitudinal section of a synangium showing the characteristic central column; **E**, transverse sections of synangia, the one above is through the basal part of the synangium, the other is through the distal region showing only four dehiscent sporangia (SAR01C2B02). Scale bars: 0.5 mm.

of the lamina enclosing the synangia. These fertile pinnules correspond to those shown in paradermal section on Figure 7F and there is good evidence that they were borne by a rachis of the *Stewartiopteris* sp. 2 type (Fig. 7D). Despite strong similarities in sporangia and synangiate organization with *Scolecopteris oliveri*, the sizes of the pinnules (about 2 mm broad and 4–6 mm long), synangia and sporangia (less than 1 mm long) are smaller than those of *S. oliveri*, according to measurements given by Scott (1932). Moreover, the lateral pinnule extensions are much more pronounced than in *S. oliveri*; in fact, this Sardinian *Scolecopteris* rather resembles the organization and size of fertile pinnules of *S. elegans* Zenker, 1837 from the Lower Permian of Saxony (Barthel & Weiss 1997) or of *S. minor* Hoskins, 1926 from the Upper Pennsylvanian of Illinois which belong to the *Scolecopteris minor* group defined by Millay (1979; 1997).

*Scolecopteris* cf. *parvifolia* Millay, 1979  
(Fig. 8C)

This may represent a second type of fertile parts with large pinnules (6 to 8 mm long and 2–2.5 mm wide), bearing two rows of up to 14 synangia, each consisting of 4 to 5 sporangia. The lamina is thin (200 µm) without a well-marked palisade or spongy tissue; sporangia (up to 0.9 mm long) are borne on a short vascularised pedicel (250 µm broad) and they are united around this pedicel in their proximal region. The sporangia tips are solid and bluntly pointed. This fertile structure is similar to that of *S. parvifolia* as defined by Millay (1979: pl. 10, fig. 66) from the Pennsylvanian American coal balls.

*Scolecopteris* cf. *alta* Millay, 1982  
(Fig. 8D, E)

This third type of *Scolecopteris* is the less common but the most distinctive, with synangia circular in cross section, 0.8 mm in diameter and more than

1 mm long, generally consisting of 6 sporangia fused in their basal half (along about 600 µm) around a central column of parenchyma and fibers. Sporangia are less than 1 mm long and 200–400 µm in diameter with thin outer walls, even in their free distal region (Fig. 8E). The synangium pedicels are very short, broad (600 µm), parenchymatous and attached to relatively thick (400 µm) pinnules showing large mesophyll cells (Fig. 8D) but there is no well-differentiated palisade tissue. These fertile pinnules clearly belong to the “Altus group” of Millay (1979) and they appear more similar to the Pennsylvanian *Scolecopteris alta* (Watson) Millay, 1982. The present material may also be compared to *Scolecopteris globiforma* from Grand-Croix and *S. unita* from the Lower Permian of Autun (Millay & Galtier 1990), however, these two species differ from the Sardinian pinnules by their thick outer sporangial walls bearing hairs.

These fertile fronds of marattialeans represent one of the most important elements of the flora but the taxonomic elucidation needs additional investigation, which is out of the scope of this paper – it will be the object of a separate, detailed study.

However, we wish to emphasize that the three distinct types of *Scolecopteris* show differences in pinnule morphology and sporangial organization suggesting an important diversity of marattialeans at Perdasdefogu. In a palaeoecological perspective it is significant that most show rather thick pinnules (? xeromorph) which may have been efficient for water conservation in drier environments (see Barthel & Weiss 1997).

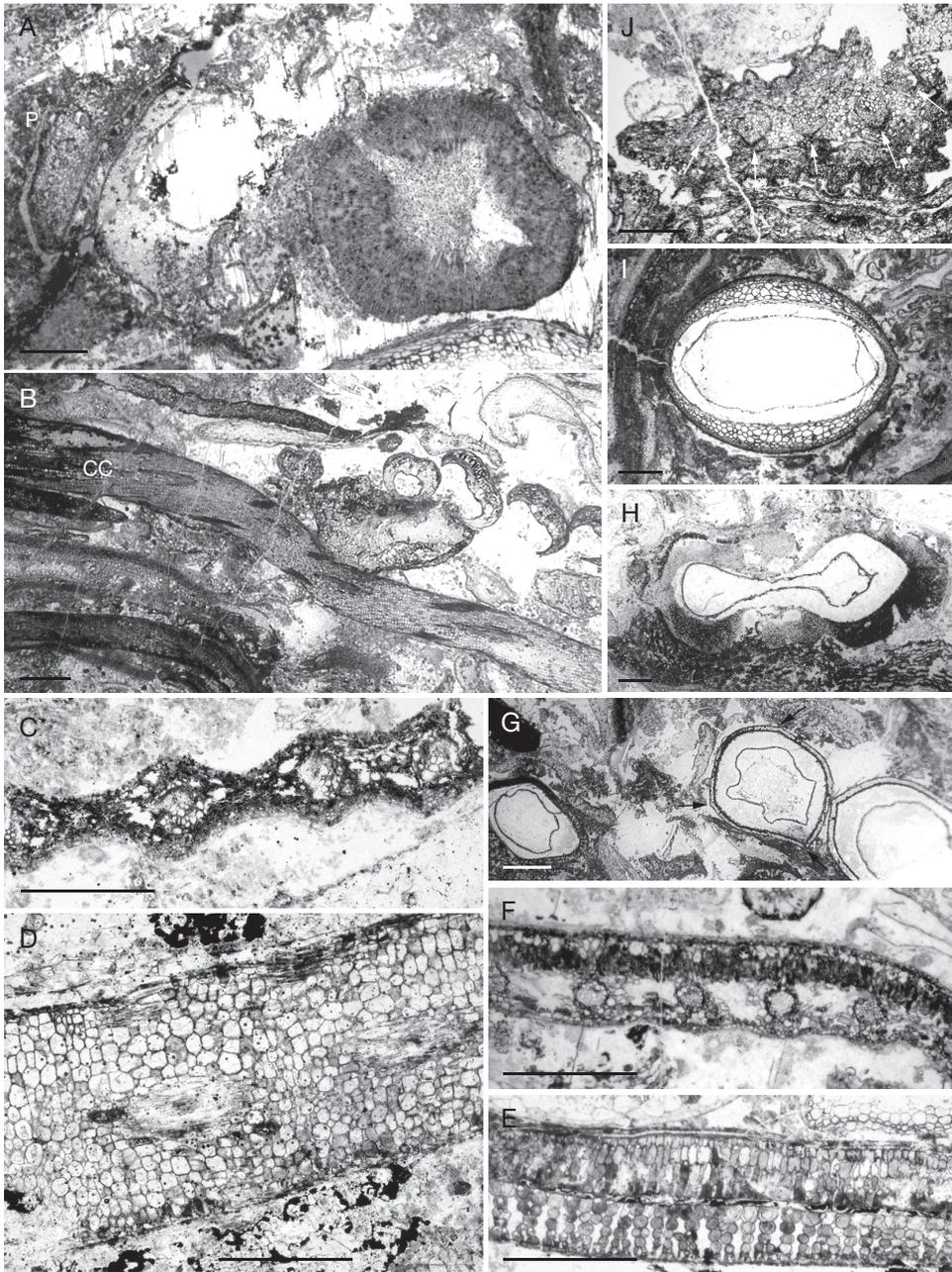
#### SEED PLANTS

Fragments of seed plants occur in less than 1 of 4 specimens; they correspond to stems, leaves, rachises, seeds and pieces of cortex and wood of periderms or cordaites.

#### *Petiole or rachis of Heterangium type (Fig. 9J)*

Such isolated rachises with up to 6 mesarch bundles (arrows, Fig. 9J) resemble petioles of some

Fig. 9. — Silicified plants from the Permian of Sardinia: **A**, *Cordaixylon* sp., transverse section of a partly decorticated small stem with a solid parenchymatous pith; on the left the closely associated rachis (**P**) with several xylem bundles may represent a petiole of the same plant (SAR24B4L13); **B**, *Cordaites* leaves associated with *Pecopteris* pinnules; the broadest leaf (**CC**) with interfascicular scleren-



chyma strands conforms to the species *C. crassus* Renault (SAR01AS03); **C-E**, SAR01B1aB01; **C**, *Cordaites tenuistriatus* Grand'Eury, detail of transverse section of the lamina; **D**, *Cordaites* cf. *crassus*, detail of transverse section of the thick lamina; **E**, *Cordaites* sp., detail of a longitudinal section of the lamina showing excellent preservation of the mesophyll; **F**, *Cordaites* cf. *lingulatus* Grand'Eury, transverse section of lamina (SAR24B4L07); **G**, transverse section of three small radially symmetrical ovules showing three sutures (arrows) of the sclerotesta (SAR47A1B01); **H**, *Cycadinocarpus augustodunensis* (Brongniart) Renault, transverse section of the ovule (SAR15BT01); **I**, cf. *Parataxospermum*, transverse section of the ovule (SAR40C2T09); **J**, rachis of possible lyginopterid affinities showing five mesarch xylem bundles (arrows). Scale bars: A, B, G-J, 1 mm; C-F, 0.5 mm.

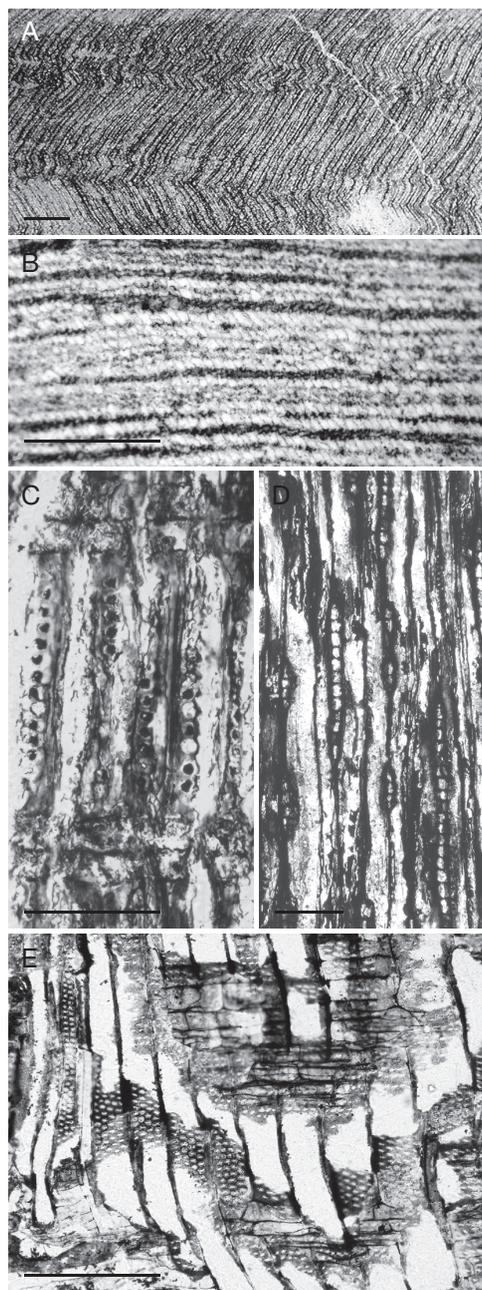


FIG. 10. — Silicified plants from the Permian of Sardinia: **A-D**, *Daadoxylon* cf. *rollei* Unger, isolated wood fragment; **A**, transverse section showing the distorted files of tracheids (SAR07BB03); **B**, detail of the same showing rows of tracheids separated by narrow rays; **C**, radial longitudinal section showing poorly preserved uni- to biseriate circular pits of tracheids between two rays (SAR07BLR01); **D**, tangential longitudinal section showing the narrow (uni-seriate) rays of variable height (SAR07AL07); **E**, isolated wood of pteridosperm affinities, radial longitudinal section showing the broad tracheids with multi (4 to 5)-seriate pitting (SARBB02). Scale bars: A, 1 mm; B, 0.5 mm; C-E, 100  $\mu$ m.

Pennsylvanian *Heterangium* illustrated by Pigg et al. (1987). *Heterangium* stems are known from the Lower Permian of Autun but they have not yet been found at Perdasdefogu.

#### *Radially symmetrical ovules* (Fig. 9G)

These rare, very small ovules (2.5 to 3 mm in diameter) show a well-marked radial symmetry with evidence of three sutures of the sclerotesta (arrows, Fig. 9J). Despite their small size, this is suggestive of affinities with medullosan pteridosperms.

#### *Probable medullosan wood* (Fig. 10E)

A few fragments of wood, sometimes fusinized, show very broad tracheids (60-100  $\mu$ m in diameter) with multiseriate (3 to 5-seriate) pitting on their radial walls and high multiseriate rays; they have characteristics of pteridosperm secondary xylem and may be attributed with some reservation to medullosans. This is supported by the occurrence of fragments of outer cortex, with parenchyma and sclerenchyma strands, of the *sparganium*-type which are characteristic of the stem and rachises of this group of seed ferns.

#### *Cordaixylon* sp. (Fig. 9A)

We illustrate a small, partly decorticated stem, about 6 mm in diameter. The cylinder of secondary xylem averages 4 mm and the pith 1.5 mm in diameter. The wood tracheids are small, ranging from 12-15  $\mu$ m in diameter for the innermost ones to 20-30  $\mu$ m in diameter at the periphery. The endarch maturation of the primary xylem conforms to the genus *Cordaixylon* Grand'Eury. On the surfaces studied the pith is solid and consists of a parenchyma of small cells (around 30  $\mu$ m in diameter). One incomplete rachis, crescent-shaped in cross section (P, Fig. 9A), is closely associated with the stem; it certainly represents one petiole of this plant, as suggested by its vascular anatomy consisting of more than six bundles as it should be expected in the petiole of such a young cordaitean stem. Associ-

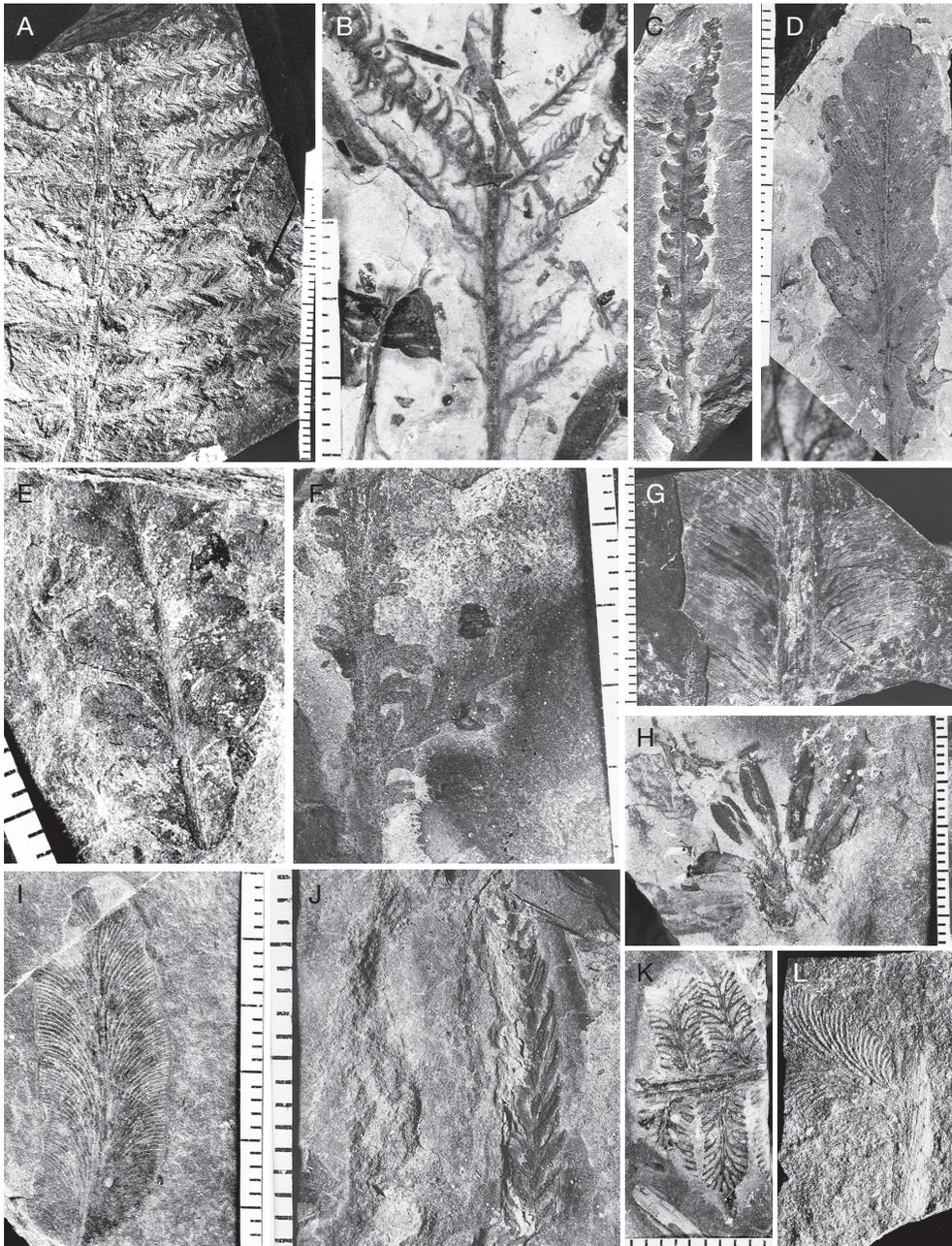


FIG. 11. — Representative elements of the compression macroflora from Sardinia; **A**, *Walchia piniformis* Sternberg; **B, C**, *Ernestiodendron filiciforme* (Sternberg) Florin; **D**, *Rhachiphyllum schenkii* (Heyer) Kerp; **E**, *Autunia conferta* (Brongniart) Haubold & Kerp; **F**, *Rhachiphyllum lyratifolia* (Goepfert) Kerp; **G**, *Taeniopteris abnormis* Gutbier; **H**, *Annularia mucronata* Schenk; **I**, *Odontopteris lingulata*; **J**, *Otovicia hypnoides* (Brongniart) Kerp et al.; **K**, *Pecopteris* cf. *densifolia* (Goepfert) Weiss; **L**, *Neuropteris osmundae* (Artis) Kidston. Scale bar graduations: 1 mm; B and C are at the same scale; L and K are at the same scale.

ated in the same chert block we found fragments of leaves with a thin lamina (Fig. 9E, see below).

#### *Cordaites leaves*

Some rock specimens contain diverse cordaitan leaves interspersed among leaves of other plants (Fig. 9B). These leaves, of different thickness and anatomy, are illustrated at the same magnification on Figure 9C-F.

#### *Cordaites tenuistriatus* Grand'Eury, 1877 (Fig. 9C)

In this leaf the lamina is thin and of variable thickness: 0.2 mm between veins to 0.4 mm at the level of veins due to the presence of triangular hypodermal sclerotic strands above and below the bundle sheath. This results in a typical superficial ribbing characteristic of the species *C. tenuistriatus* as illustrated by Renault (1879) from the Pennsylvanian of Grand-Croix. The interval between veins is less than 0.6 mm, i.e. about 17 veins per cm.

#### *Cordaites cf. crassus* Renault, 1879 (Fig. 9B [CC]; 9D)

In contrast, this leaf found associated with the previous one, shows a very thick (up to 1 mm) lamina and a superficial surface smooth. Sclerotic strands do not extend to the bundle sheath and intermediate strands occur between veins as illustrated by Renault (1879) for specimens from Grand-Croix and by Harms & Leisman (1961) from American Pennsylvanian coal balls. The interval between veins is about 0.7 mm, i.e. about 14 veins per cm.

#### *Cordaites cf. lingulatus* Grand'Eury, 1877 (Fig. 9F)

This leaf, found associated with the stem of Figure 9A, has a thin lamina (0.4 mm), a smooth surface and very closely spaced veins (less than 0.4 mm interval, i.e. about 25 per cm). Rectangular sclerotic strands extend above and below veins; the mesophyll is differentiated into palisade and more

or less spongy tissues. Despite similarities with the species *C. lingulatus* Grand'Eury as illustrated by Renault (1879) this leaf may represent variability of other species like *Cordaites principalis* Germar, as illustrated by Harms & Leisman (1961).

#### *Cordaites* sp. (Fig. 9E)

This radial section shows the excellent preservation of the lamina with vertical mesophyll plates separated by lacunae and palisade-like tissue in a leaf similar to the previous one.

#### *Cycadinocarpus augustodunensis* (Brongniart) Renault, 1896 (Fig. 9H)

Groups of dispersed ovules of this type are found in a few specimens. They are up to 9 mm long, 6-8 mm wide in the major plane and 3-5 mm wide in the minor plane of symmetry. They conform to the description of the species *Cycadinocarpus augustodunensis* (Brongniart) Renault (1896) from Autun. This ovule was previously described as *Cordaicarpus augustodunensis* by Brongniart (1881). The generic change, from *Cordaicarpus* to *Cycadinocarpus*, proposed by Renault (1896) was supported by Bertrand (1908). This ovule is mostly characterized by the irregular sclerotesta varying greatly in thickness and appearing trabeculate in tangential sections (Brongniart 1881: pl. III, fig. 14). Original type material of this species, kept in the Muséum national d'Histoire naturelle, Paris (MNHN), has been re-investigated by one of the authors (JG) and the non-artefactual nature of this irregular sclerotesta was confirmed as well as the specific identification of the Sardinian ovules to the species of Autun.

#### *cf. Parataxospermum* (Fig. 9I)

Dispersed cardiocarpalean ovules of this type are the most common, occurring in about 1/10 of specimens.

They are up to 1 mm long and 6 × 5 mm wide. They are characterized by a prominent sclerotesta up to 1 mm thick composed of large thick-walled cells 50 to 200 µm in diameter gradually decreasing in size in the outermost sclerotesta and near the base of the ovule. Detailed description of these ovules will be presented in another paper but it is worth mentioning that they are most similar with ovules from Carboniferous-Permian coal balls from Shanxi Province in China described by Li (1993).

*Dadoxylon* cf. *rollei* Unger, 1859  
(Fig. 10A-D)

A rather large specimen consists of a single fragment of distorted wood (Fig. 9A); however characteristic features are preserved: the files of secondary xylem tracheids (30-50 µm in diameter) are separated by narrow (uniseriate) rays of variable height (2 to 20 cells) (Fig. 9B, D); pitting, restricted to radial walls, shows uni- to biseriate rows of crowded circular bordered pits (Fig. 9C). This anatomy is similar to that of woody trunks of *Dadoxylon rolei* Unger from the Lower Permian of Germany and from Autun. Marguerier (1971), who investigated trunks from Autun, consider that characteristics of tracheid pittings of such woods suggest affinities with walchian conifers rather than with cordaites.

## DISCUSSION

### COMPOSITION OF THE PLANT ASSEMBLAGE AND COMPARISON WITH THE AUTUN AND OTHER PERMINERALIZED FLORAS

Even if some sectioned chert blocks contained several tens of identifiable plant remains, our analysis of the occurrence of organs and taxa concerns less than one hundred chert specimens and may not be considered as a significant quantitative analysis. However, this preliminary inventory of the permineralized flora provides some indication on the relative occurrence of plants and organs. As shown on Figure 12A, the most common plants are calamiteans and tree ferns before cordaites, small filicalean ferns, seed ferns and *Sphenophyllum*. Roots – of calamiteans

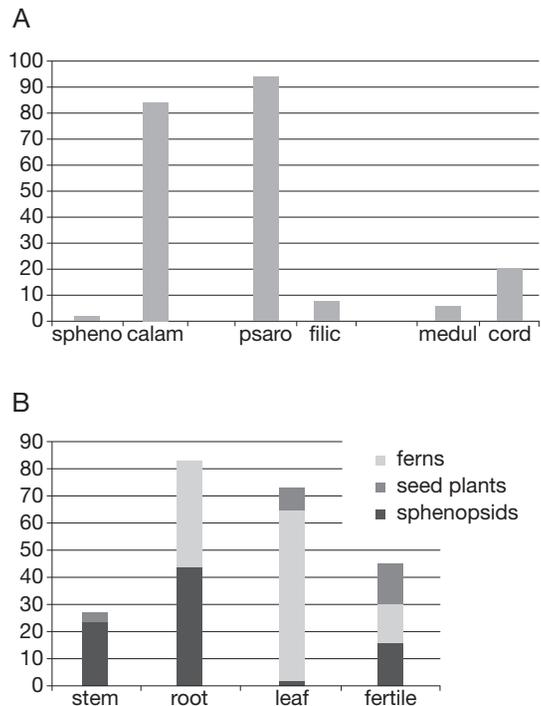


FIG. 12. — Composition of the permineralized plant assemblage: **A**, abundance of taxa expressed by the number of chert specimens containing sphenophyllean (**spheno**) and calamitean (**calam**) sphenopsids, marattialean/psaroniacean (**psaro**) and filicalean ferns (**filic**), medullosan (**medul**) and cordaitan (**cord**) seed plants; **B**, abundance of organs by taxa expressed by the number of chert specimens containing stem, root, leaf and fertile parts, respectively of sphenopsids, ferns and seed plants.

often co-occurring with detached *Psaronius* aerial roots – are the most common organs before leaves mainly belonging to ferns (Fig. 12B). In contrast, the stems, mainly represented by calamiteans, are less common whilst fertile parts belonging to ferns, calamitean cones and cordaitan ovules are about equally represented.

With regard to taxa, the most common elements are *Pecopteris-Scolecoperis* which correspond to vegetative and fertile leaves of at least three different species of marattialean ferns also represented by *Stewartiopteris* rachises and *Psaronius* fragments of stems and root mantle. *Astromyelon-Myriophylloides* roots are also common whilst *Arthropitys* occurs as fragments ranging from young twigs to large woody stems. Together with *Palaeastachya* cones, these ca-

lamitean remains may correspond to different parts of the same whole plant. *Cordaitea* leaves, ovules and stems are rare while representatives of other groups (sphenophylls, tedelean and anachoropterid ferns, and seed ferns) are still less frequent. One must note the occurrence of rootlets as the only indication of the presence of (?sigillarian) lycopsids and of a *Dadoxylon* wood of possible conifer affinity.

Like in coal balls, the present plant assemblage consists of an accumulation of roots and aerial organs (mainly of tree ferns and calamitean) which is suggestive of little or no transport and may be interpreted as a litter with autochthonous to parautochthonous elements.

It is interesting to compare these results to quantitative analysis carried out previously on silicified material from the Late Pennsylvanian of Grand-Croix and the Lower Permian of Autun (France) following procedures of Phillips *et al.* (1977) using a transparent overlay grid system (1 cm<sup>2</sup>). This study (Galtier & Phillips 1985) revealed a difference between the two French assemblages with cordaiteans dominating the Grand-Croix vegetation, as confirmed by a recent study of Galtier (2008), whilst tree ferns and calamiteans dominated in Autun. This difference was interpreted in terms of environment and ecology. It is certainly very significant that the new assemblage from Sardinia is dominated by tree ferns and calamiteans like the contemporaneous silicified vegetation of Autun. However, the long studied flora from Autun is very rich (35 genera and 73 species) and can hardly be compared to the Perdasdefogu flora that is limited to about 16 genera and a little more than twenty taxa according to this preliminary study. However, it is significant that all the genera found at Perdasdefogu, except *Parataxospermum*, are present in Autun as well as several species including the ovule *Cycadinocarpus augustodunensis* which is, up to now, only known from these two assemblages. It must be noted also that a number of taxa (e.g., *Arthropitys bistriata*, *Ankyropteris brongniartii*, *Scolecopteris elegans*) are in common with the Early Permian floras from the Döhlen Basin of Germany (Barthel *et al.* 1995; Rössler 2006). The similarity between permineralized floras of Perdasdefogu and Autun is further supported by the comparison of the associated compression floras of the two basins.

#### COMPRESSION MACROFLORAS OF THE PERDASDEFOGU BASIN AND SPOROMORPH ASSEMBLAGES

Among a large number of macroflora specimens collected from the underlying *lithofacies c* (black siltstones) (Broutin *et al.* 1996; Ronchi *et al.* 1998; Broutin *et al.* 2000a; Cassinis & Ronchi 2002) one must point out the presence of the following plants: *Asterophyllites longifolius* (Sternberg) Brongniart, *Annularia mucronata* Schenk (Fig. 11H), *Pecopteris elaverica* Zeiller, *Odontopteris lingulata* (Goepfert) Schimper (Fig. 11I), *Neuropteris osmundae* (Artis) Kidston (= *Odontopteris dufresnoyi*) (Fig. 11L), *Taeniopteris abnormis* Gutbier (Fig. 11G), *Autunia* (*al. Callipteris*) *conferta* (Brongniart) Haubold & Kerp (Fig. 11E), *Rhachiphyllum* (*al. Callipteris*) *schenkii* (Heyer) Kerp (Fig. 11D), *Rhachiphyllum* (*al. Callipteris*) *lyratifolia* (Goepfert) Kerp (Fig. 11F), *Dichophyllum* (*al. Callipteris*) *flabellifera* (Weiss) Kerp & Haubold, *Lodevia* (*al. Callipteris*) *niclesii* (Zeiller) Haubold & Kerp, *Ernestiodendron filiciforme* (Sternberg) Florin (Fig. 11B, C), *Otoviccia* (*al. Walchia*) *hypnoides* (Brongniart) Kerp *et al.* (Fig. 11J), *Walchia piniformis* Sternberg (*sensu* Visscher *et al.* 1986) (Fig. 11A), *Culmitzchia* (*al. Lebachia*) *laxifolia* (Florin) Clement-Westerhof.

According to Broutin (*in* Ronchi *et al.* 1998; Broutin *et al.* 1999, 2000a) the Perdasdefogu macrofloras permit to relate these strata to the middle-upper Autunian of the French Massif central and more precisely to the Surmoulin and Millery formations (“Upper Autunian” A3 association; Doubinger 1974) of the Autun Basin (Chateaufort *et al.* 1992) and to the Catalan Pyrénées basins (Gerri de la Sal succession, Sierra del Cadi; Dalloni 1930; Gisbert 1983, 1984; Broutin unpublished revision). This is in agreement with the upper Asselian to Asselian-Sakmarian transition time-interval pointed out by the amphibian species found in strata immediately below, and perfectly correlatable with the same association found in Gottlob-lake (Thuringian Forest Basin: Werneburg *et al.* 2007).

Within the same deposits yielding macrofloras a rich sporomorph association has been found. The palynological assemblage of the Perdasdefogu Basin, except for the local characteristics, displays

the same qualitative and quantitative composition, both at generic and specific levels, as that recorded from the Punta Lu Caparoni Formation (Broutin *et al.* 2000b) in Nurra (NW Sardinia). These two very similar associations can be compared with that defined by J. Doubringer (1974), for the biozone “A3”, in her revision of the Autunian of Europe.

Both are dominated by monosaccate pollen grains, the *Potonieisporites* “*novicus-bhardwajii*” complex being especially diversified and constituting some 50% of the total assemblage. Bisaccate grains (20%) are associated with typical “Autunian” genera such as *Vittatina* or *Costapollenites*. The following groups and species have been identified:

– spores: *Convolutispora* sp. 2 (Peppers 1964), *Verrucosisorites* spp., *Laevigatosporites* spp., *Lundbladispota* sp.;

– pollen: monosaccates: *Potonieisporites novicus-bhardwajii*, *Florinites diversiformis*, *F. mediapudens*, *Florinites* spp., *Nuskosporites* cf. *klausii*; non-striate bisaccates: *Vesicaspora ovata*, *Gardenasporites leonardii*, *Illinites tectus*, *Illinites* spp., *Limitisporites* spp.; striate bisaccates: *Protohaploxyipinus samoilovichii*, *Protohaploxyipinus* sp., *Hamiapollenites* sp., *Straitoabieites* sp.; plicates: *Vittatina ovalis*, *Vittatina* sp., *Costapollenites* sp.

The Perdasdefogu sporomorph association was also discussed in a review on the Permo-Carboniferous to Triassic palynofloral association by Pittau & Del Rio (2002). For these authors, the proposed correlation of the Perdasdefogu palynoflora to biozone “A3” of the Autunian of Europe leaves some doubts with regard to the age of these assemblages, in the light of the controversy that still surrounds the status of the Autunian stage and its correlations with the standard scale that have still to be ascertained. According to a more recent paper by Pittau *et al.* (2008) the preservation of Perdasdefogu sporomorphs is poor and therefore a qualitative and quantitative assessment of the palynoflora is difficult; it would even be difficult to determine whether *Florinites* or *Potonieisporites* is the dominant pollen genus. Therefore, for these authors, the sporomorph assemblages of this basin might be compared with the younger Lu Caparoni assemblages, or even with the older Seui-Seulo assemblage.

#### *Palaeogeographic and palaeoclimatic interpretation*

From a palaeogeographical point of view, it is significant that a very similar compression flora has been recorded from Lodève (southern France) and from the Catalan Spanish Pyrenees: this is in agreement with the palaeoposition proposed by Broutin *et al.* (1994), based on structural and magmatic data, and later confirmed by Cassinis & Ronchi (2002) and Cassinis *et al.* (2003): the Sardinian block is aligned in an East-West direction linking northwestern Sardinia with the Provençal area and, at least the central part of the island, with the southern Pyrenean domain.

The dominance of black shaley siliciclastics (*lithofacies c*) and the repeated occurrence of millimetre-to-pluricentimetre thick anthracite horizons in *lithofacies d* (boghead coal?) could suggest a frequent cyclic alternation of marsh and lacustrine environments. The Rio su Luda Formation environments thus indicate a humid to semi-humid climate. Very few indicators for dry conditions, such as mud-cracks or clay chips, occur in the siliciclastic part of the sequence (*lithozone c*), whereas tepee-like structures appear in the uppermost part of the freshwater limestones of *lithofacies d*, indicating a major lake emersion event.

On the basis of facies analysis of the Autunian Sardinian sequences, Ronchi *et al.* (2008) infer climatic conditions of high precipitation dominated by monsoonal and seasonal to subseasonal cycles of prolonged rainfall and shorter dry periods. Lithofacies and palaeontological records confirm such wet climatic phases, which interrupted the overall Permo-Carboniferous aridisation trend as indicated by Schneider *et al.* (2006) and Roscher & Schneider (2006). According to Ronchi *et al.* (2008), the Perdasdefogu Basin sequence seems to fall into the “topmost Lower Rotliegend wetness phase” of Schneider *et al.* (2006) (Asselian/Sakmarian transition). This humid to semihumid phase, recognized by Ronchi *et al.* (2008) also in other basins of Sardinia (Escalaplano, Lu Caparoni), is characterized by a complex intercalation of alluvial fan and fluvial conglomerates, wet alluvial plain and perennial lacustrine fine clastics, lacustrine black-shales and limestones, sometimes decimetre-thick coal seams and frequent pyroclastic horizons. A slight

change towards warmer climatic conditions was envisaged in the microfloristic associations of the Lu Caparoni and Perdasdefogu basins by Pittau et al. (2002). The sporomorph assemblages of such basins lack numerous taxa with respect to Guardia Pisano (Sulcis) and, according to these authors, this could reflect even dryer conditions during the late Asselian. The similarity between the Lu Caparoni and Perdasdefogu megaflores, indicated by Broutin et al. (1999), suggests that the two basins developed under similar climatic conditions and were likely coeval. In contrast, according to Pittau et al. (2008), the Lu Caparoni palynological assemblage differs sufficiently (relative abundance of taeniate pollen is considerably higher than in those of southwestern and central-eastern basins) to allow the recognition of a different ecostratigraphic unit, which they called the *Vittatina*-Striatiti pollen Phase. This phase corresponds to a notable increase of the genera *Vittatina*, *Hamiapollenites*, *Protohaploxylinus* with a consistent reduction of *Potonieisporites* and *Florinites* prepollen. The high percentage of pteridosperms producing striate pre-pollen and pollen grains is indicative of an increase of arid or less humid habitats. These new palynological data lead to postulate that the Lu Caparoni basin was not “coeval” with the Perdasdefogu one, as suggested on the base of their megaflores, but slightly younger. Therefore, the intercalibration between the micro- and megaflores zonation for the Asselian-Sakmarian time span in this area remains to be established using the other data sets available.

### Acknowledgements

We are indebted to G. Gand and an anonymous reviewer for their helpful remarks and constructive criticism. This research was partially funded by PRIN 2008 grants (G. Oggiano resp.).

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*Submitted on 5 March 2010;  
accepted on 10 November 2010.*