Geologia Croatica | 65/3 | 351–360 | 3 Figs. | 1 Tab. | 2 Pls. | Zagreb 2012

Vein reticulation in seed ferns of the Dobrudzha coalfield Bulgaria

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doi: 104154/gc.2012.24

Geologia Croatica

ABSTRACT

Alethopteris, Lonchopteris, Paripteris, Linopteris and *Reticulopteris* are abundant pteridosperm fronds in the Pennsylvanian-age Dobrudzha Coalfield. The transition from fan-shape to reticulate veining in *Lonchopteris, Linopteris* and *Reticulopteris* and in *Laveineopteris* to *Reticulopteris* is documented. The most probable cause for this is the decrease in humidity; in addition to temperature controls on the geographic distribution. The form and positioning of anastomoses are discussed.

Keywords: Carboniferous, pteridosperms, reticulation, palaeoecology, drying, cooling

1. INTRODUCTION

Neuropterids and alethopterids with reticulated veins are known from many coal basins to the north of the Variscan mountains. Their relationship with non-reticulated members of the same groups is widely assumed, although only the transition from *Neuropteris* to *Reticulopteris* has been unequivocally documented (JOSTEN, 1962; TENCHOV & POPOV, 1990). GOTHAN (in POTONIÉ, 1910) suggested that there was a Westphalian intermediate form between the open-veined *Alethopteris* and the anastomosed veined *Lonchopteris*, which he called *Lonchopteridium*. Later, GOTHAN (1953, pl. 13 fig. 2, 2a) figured a specimen of *Alethopteris valida* with clear anastomoses. EGEMEN (1958, pl.6, fig. 1,1a) illustrated a specimen of *Neuropteris gigantea* from the Kozlu Formation, (Langsettian Substage, Turkey), that has several anastomoses to the left of the midvein. Although he did not mention them in the figure explanation, he stated in the text (EGEMEN, 1958, p. 12–13) that the merging of lateral veins indicates "…a gradual change towards drier and more terrestrial conditions of habitat…". POTONIE (in CROOKALL, 1959, p.135) reported *Paripteris* specimens with anastomoses, but did not specify the habitats, geographical positions or stratigraphic horizons.

In Bulgaria (Fig. 1), the Svoge Coalfield lacks any plants with reticulated veins (TENCHOV, 1976; 2011). In the Dobrudzha Coalfield in northeastern Bulgaria, in contrast, reticulate veining is extremely widespread. Some of the earliest examples are of *Cardiopteridium waldenburgense* ZIMMERMANN (samples 5750 and 5775), from the Pendelian Rakovski Formation, in which single anastomoses have been observed. Examples of *Paripteris* with single anastomoses or groups of anastomoses are frequently ob-

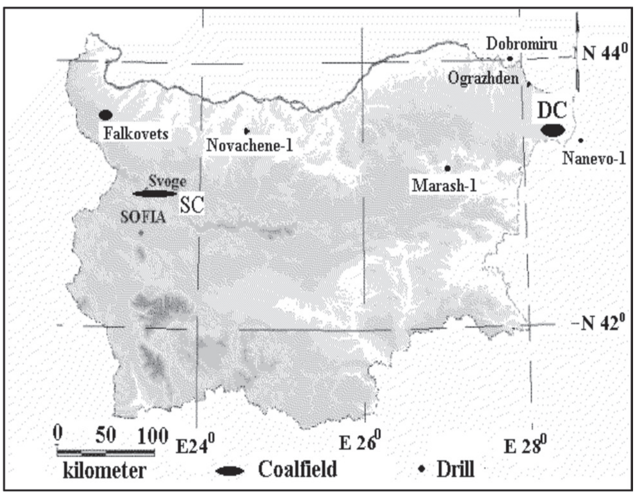


Figure 1: Bulgaria; Location of the Dobrudzha Coalfield – DC.

served (e.g. Pl. 1, Figs. 2–4, 6, 7) (TENCHOV & POPOV, 1987b). There are at least seven *Linopteris* species observed in the Balchik Group, ranging in age from Langsettian to Stephanian A (TENCHOV & POPOV, 1987a), some of which include examples with imperfect reticulation (Pl. 1, Figs 5; Pl. 2, Figs 8, 10). The transition from *Neuropteris* to *Reticulopteris* has been documented between the upper Duckmantian to upper Bolsovian parts of the Balchik Group (TENCHOV & POPOV, 1990), in concordance with what has been reported from the Ruhr Coalfield (JOSTEN, 1962). *Lonchopteris* is represented by six species (TENCHOV, 2004a) ranging from the Langsettian Mogilishte Formation, to the Bolsovian middle Makedonka Formation. No clear evidence has been discovered in the Balchik Group of the transition between *Alethopteris* and *Lonchopteris,* such as documented by GOTHAN (1910, 1953) in the early Langsettian Bochum Formation of the Ruhr and Aachen basins, but deposits of this age are not well-preserved in Dobrudzha.

2. MATERIAL AND STORAGE OF THE SAMPLES

At present, 3600 samples of Carboniferous and Permian fossil plants from Bulgaria are publicly accessible. They are stored in the palaeontology and stratigraphy Museum of the Mining Geological University, “St. Ivan Rilski”, Sofia. Information on their storage is electronically available at the Museum. Another c. 5000 samples are awaiting a place of long-term storage and are not publicly accessible.

Numerous specimens of *Paripteris* that have occasional vein anastomoses are known from the Dobrudzha megaflora, mainly belonging to the *Paripteris gigantea-Paripteris pseudogigantea* complex, and rarely to other species. There are also some *Linopteris* specimens that exhibit imperfect anastomoses (Table 1).

Table 1: Number of standard levels[1] with *Paripteris* and some *Linopteris* species.

Paripteris species	Vein meshes absent	Some vein meshes present
P. gigantea P. Pseudogigante[2]	357	39
P. linguaefolia	37	3
P. schutzeii	90	2
***Linopteris* species**	**Perfect reticulation**	**Imperfect reticulation**
L. neuropteroides	85	2
L. havlenaii	25	03
L. minor	70	1
L. brongniartii, L. subbrongniartii	163	04

[1] A standard level is an interval of strata 1 m thick and so may contain many individual pinnules or fragments of pinna.
[2] The isolated pinnules of *Paripteris gigantea* and *Paripteris pseudogigantea* cannot be separated as different species; this will be the subject for a separate study.
[3] The particular form of reticulation in *Linopteris havlenaii* makes it difficult to identify imperfect reticulation.
[4] In the Polyantsi and Gurkovo formations, *Paripteris* pinnules with reticulate veining and *Linopteris* pinnules with imperfect reticulation have not been observed.

Figure 2 shows the distribution of these species in the Dobrudzha sequence, along with the distribution of other reticulated species or groups of species.

Most examples of reticulated *Paripteris* are isolated pinnules occurring in sandstones, siltstones and claystones, in fining upwards sequences, and only rarely immediately above a coal seam. Coarser grained sediment is more common in the southern part of the Dobrudzha Coal Basin, where there are distal parts of fans that entered the swamp of the basin.

Any 1 metre thickness of core of a borehole in the coalfield is assigned a Standard Level (SL). The concept of Standard Levels was developed by TENCHOV (1993) to facilitate correlation between different borehole sections within the Dobrudzha Coalfield, and was based around a limited number of stratigraphic levels (mainly coal seams), that could be identified across the basin. The base of the sequence is assigned an SL value of 0 m, and the top an SL value of 1600 m.

3. GEOLOGICAL BACKGROUND

3.1. Palaeogeography

The landscape around the Dobrudzha depression (Fig. 3) is part of the Variscides. From south to north it consists of the following.

1. The Variscan Range with an intermontane depression (the Svoge Coalfield) maybe 2000 meters above Sea level. In this depression, the lower temperatures influenced the plant community more strongly than in Dobrudzha basin. The air humidity in the Svoge grabens was less a factor maybe due to the altitude, the river in the depression, and maybe the high mountain ranges around the depression.

2. The Variscan Foreland with a maybe 80 km wide alluvial plane to the south of Seltse Fault. Erosion prevailed close to the depression. The sand substratum drained rainwater away quickly and deeply.

3. A depression to the north of the Seltse fault, the Dobrudzha Coalfield, lay at about 190 meters above sea level (TENCHOV, 1993) and drained waters from the alluvial plane. That depression starts subsiding from Yeadonian times. It remained at a higher elevation than the Russian Plate and lower than the foreland alluvial plane. Swamps, lakes and floodplains covered the depression partly and sometimes completely. River beds occurred mainly near the delimiting faults.

4. Another depression with swamps and maybe lakes with mostly clayey sedimentation was established by the Nanevo-1 Borehole. The water table here was at or near the surface.

5. The Shabla fault, which delimits the Variscan realm from the Russian platform to the north, was formed at about the end of late Viséan times. The Devonian and Tournaisian deposits to the north and south of that fault are shallow-marine and their distribution does not permit any clear differentiation between the tectonic units at that time. The Russian

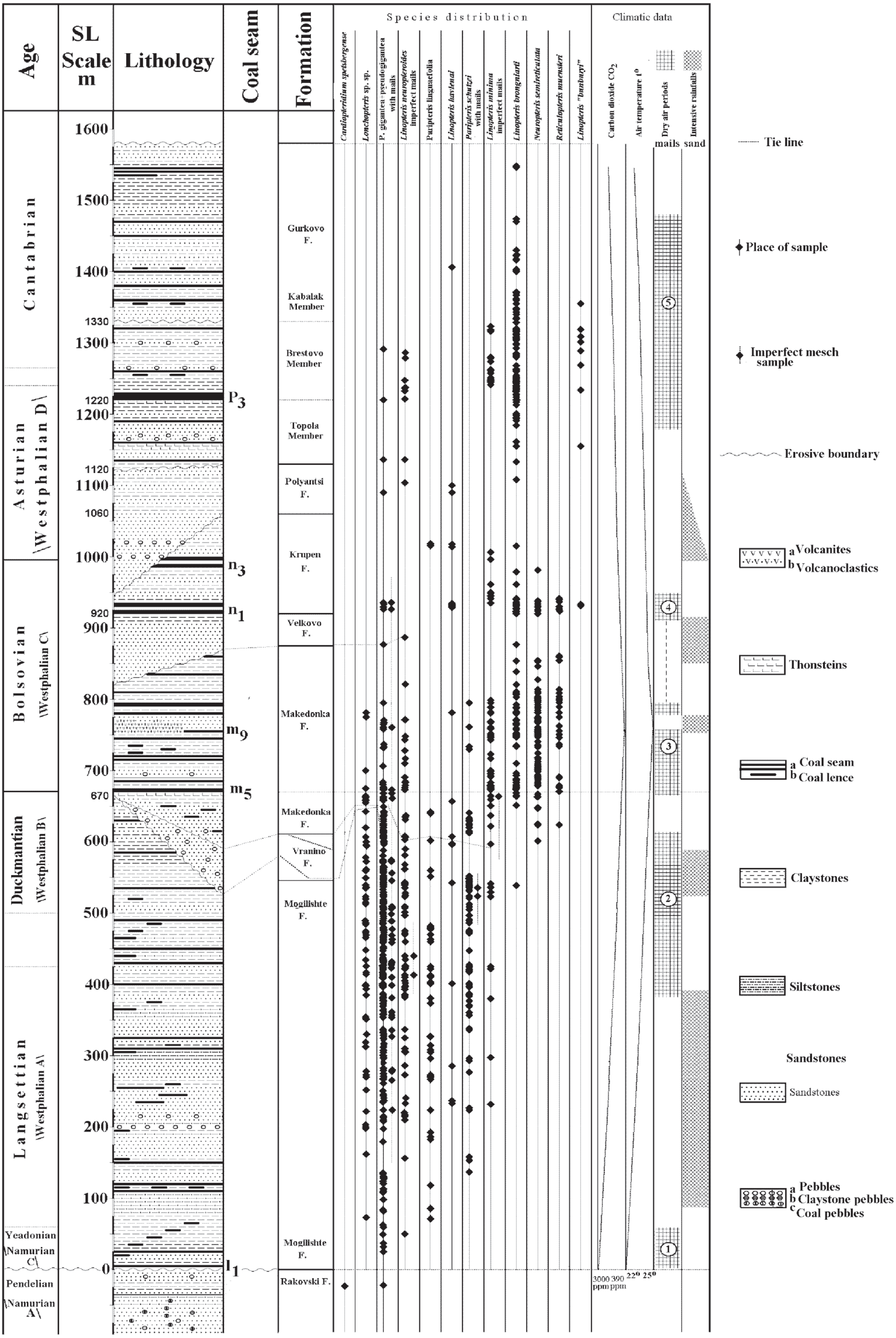


Figure 2: Distribution of reticulated species in the Dobrudzha Coalfield.

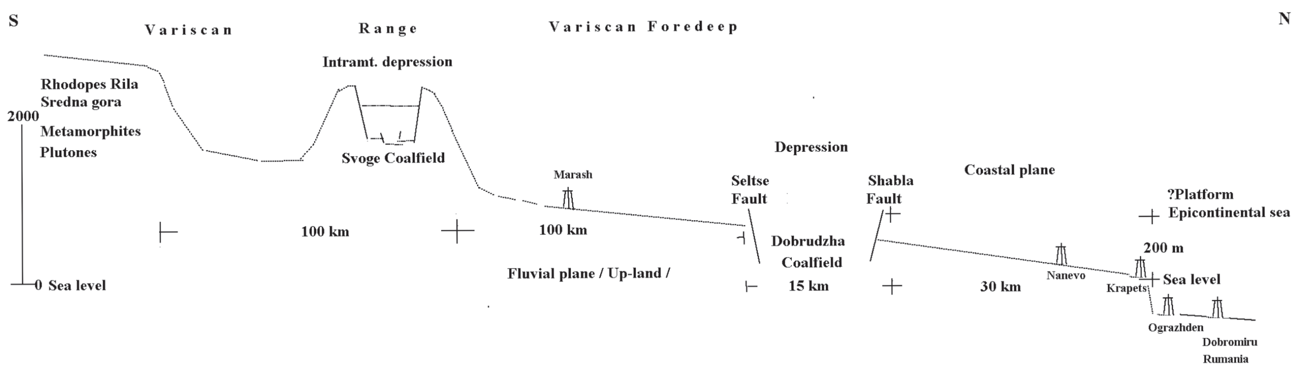


Figure 3: The Variscides in Bulgaria. Explanation in the text.

Epicontinental Sea in the Donets region started to regress and sink intensively at about the end of Viséan times. At about the beginning of Westphalian times, the sea withdrew from both the Bulgarian and Romanian parts of the Dobrudzha territory; the stratigraphically youngest marine deposits that have been recognised are late Viséan to early Namurian in the Ograzhden Borehole in Bulgaria (BONCHEVA et al., 1994) and Namurian to early Westphalian in the Dobromiru Borehole (Fig. 3) in Romania (JORDAN et al., 1987). SPASSOV & YANEV (1966) reported rooted soils in the Ograzhden Borehole and interpreted them as paralic deposits, but they are in fact siltstones with allochtonous plant remains. I have personally examined the entire core of the Ograzhden Borehole and there are no *Stigmaria* rooting structures or root disturbed sediments.

6. A Gulf of the Russian Epicontinental Sea with paralic deposits found in the Dobromiru Borehole (JORDAN et al., 1987) marks a regression.

3.2. Sedimentation processes

During Late Viséan times in the Variscan foredeep of northern Bulgaria, the Trigortsi Formation was established. The lower part of the formation consists mainly of shallow marine claystones, with three thin limestone interbeds yielding foraminifera typical of the Russian Epiplatform Sea (TENCHOV, 2004b). As a result of marine regression the region gradually changed to being a flat coastal plain with subaeral sedimentation and erosion. The lower part of the next, Rakovski Formation (the Konare Member) consists of claystones, siltstones, sandstones and thin coal layers, and has yielded megaflora remains.

The lower and middle part of the overlying Irechek Member consists mainly of sandstones with specific coal and claystones pebbles. Close to the faults that delimit the basin, sandstones prevail, as shown in R60 and all boreholes in the southern part of the depression (see TENCHOV, 2004b, figs 3–6), but in the north and central boreholes claystones become frequent. The thickness of the Irechek Member is up to 400 m, which indicates the minimum subsidence of the depression. At the top of Irechek Member in the central and northern part of the depression, the sediments are finer and even some thin coals are formed, which suggests relatively calm faulting. The part of the Irechek Member in the depression (Borehole 73) contains *Cardiopteridium waldenburgense*, abundant *Lyginopteris* (*L. stangeri, L. schlehanii, L. larischii, L. divaricata*), *Neuropteris* cf. *antecendens*, *Paripteris gigantea*, *Mariopteris acuta*, and one specimen of *Neuralethopteris* sp. (TENCHOV & CLEAL, 2010). The megaflora indicates a late Visean to Pendelian age. The palynoflora (DIMITROVA, 1993) indicates the same age, though DIMITROVA split the interval into two subzones. The two palynological associations were obtained from two different rock associations – the lower from fluvial deposits, the upper from floodplain sediments with some swamp deposits (including coal); these deposits were laterally adjacent and not in sequence. Quartz sandstones and conglomerates farther to the north in the depression mark the location of a sand bar (TENCHOV, 2004b, figs 7, 8). Some 20 km to the northeast, the borehole R1-Krapets reached Pendleian marine deposits with a marine fauna including *Cravenoceras leion* (SPASSOV in: SPASSOV & YANEV, 1966).

A break in sedimentation with an impressive change in megaflora composition occurs after the Pendleian and before Langsettian times; a similar break occurs in the Silesian Basins. After the break, about 1600 m of Langsettian to Stephanian A, coal bearing sediments were deposited in the depression. During this time, the main source of the clastic sediments that fill the Dobrudzha Coal Basin was south of the Seltse fault. That area seems to have been a subaerial plain, slightly inclined to the north, covered with late Visean sediments of the Konare Member of the Rakovski Formation and the Trigortsi Formation. There is no borehole near the Seltse fault that enters below the Permian strata. About 60 km to the south, the Marash R1 borehole passes through the Konare Member, which consists mainly of sandstones with 50–60 % well rounded quartz grains, and including rare plant remains (Fig. 3). The lack of pebbles indicates that the catchment area was far to the south. Sedimentation occurred in an alluvial plain with migrating rivers that transported the eroded material to the Dobrudzha Coal Basin. Coal grains, fusenized parts of lycophyte, articulate and fern stems, as well as numerous leaves of pteridophylls, mainly of *Paripteris* and *Linopteris*, were imported into the depression.

These all indicate that areas with vegetation cover and also some swamps were very common away from the river beds. The coals are of low ash content and their composition indicates that the water basins in the swamps were of low dynamics (NIKOLOV & STEFANOVA in NIKOLOV, 1988, pp. 121–126).

The Bezvoditsa borehole is about 10 km to the west of the Dobrudzha Coal Basin and passes through a succession with less sandstone and more claystones, and rare thin coal seams. Plant remains were frequently collected, mainly of *Calamites*. The floral composition (*Bothrodendron* sp., *Lyginopteris* sp., and *Diplothmema adiantoides*) in the upper part is similar to that of the topmost layer of the Irechek Member.

Erosion in the alluvial plain and sedimentation within the Dobrudzha Coal Basin was controlled by tectonic activity at the delimiting faults and in the Variscan Range, as well as by more intensive rainfall. In two, possibly three episodes, erosion and then fluvial conditions invaded the Dobrudzha depression (TENCHOV 1993). This first occurred about the end of Duckmantian times when the Seltse fault was activated. Drainage in the depression at the time was halted, and a 76 metre deep erosion channel is recorded (borehole 105), followed by sedimentation of the Vranino Formation. The lowermost 3-4 metres of the formation consist of sandstones, mainly grains of massive metamorphic rocks (POPOVA, in: NIKOLOV, 1988), indicating active uplift of the Variscan range to the south. These are followed by mainly volcaniclastic sediments, as well as red-coloured quartz. Drainage in the depression was restored by some unknown means. To the south of the Seltse Fault, erosion became less active and sedimentation of the lower part of Makedonka Formation began. The riverbeds were filled first. Frequent landslides here and there dammed the valleys and created temporary swamps. The collected megaflora from the cover of the coal layers and close to the swamps indicates similar conditions to the south of the Seltse Fault. Autochtonous plant remains are present, among them numerous *Lyginopteris*, *Lonchopteris*, *Mariopteris*, *Eusphenopteris* and *Sphenopteris*, pinnules of *Paripteris* with normal veining or with some anastomoses, and *Linopteris* with occasionally imperfect reticulation. The vein meshes indicate that the plants suffered from a lack of water due to dry air and deep drainage caused by the sandstones.

Evidence that swamp-lake conditions were discontinued for a second time is found in the upper part of Makedonka Formation, with erosional down-cutting of up to 115 m being recorded (borehole 147). The infill there is with oligomictic quartz, to quartz sandstones and there are no clay particles to filling the porosity of the sands. This composition indicates long-term weathering to the south, which seems to have taken place at the same time as the formation of the $m_5 – m_{12}$ coal-bearing interval in the upper part of the Makedonka Formation, and can be correlated with the Duckmantian – middle Bolsovian interval in the paralic coal basins in Western Europe. Coal grains and plant fragments are rare in the Velkovo Formation with vegetation cover probably temporarily restricted to the south.

Swamp-lake conditions were discontinued for a third time after deposition of the Polyantsi Formation, which is overlain by the lowermost part of the Gurkovo Formation. In this case, however, the analogy is less obvious.

4. THE RELATIONSHIP BETWEEN *PARIPTERIS* AND *LINOPTERIS*

At present around the European Variscan range the following *Paripteris – Linopteris* couplets have been recognised:

- *Paripteris gigantea* and *Linopteris neuropteroides*;
- *Paripteris pseudogigantea* and *Linopteris subbrongniartii*;
- *Paripteris linguaefolia* and *Linopteris havlenaii*;

Data from the Dobrudzha Coalfield also point to a connection between *Paripteris schutzeii* and *Linopteris minor*. The rare *Linopteris regniezii* Laveine also has similar shaped pinnules to *Linopteris minor* and may indicate a separate trend in vein reticulation in another area.

In all these cases the non-reticulated specimens of *Paripteris* continue to exist in parallel with their reticulated equivalent *Linopteris* species. However, several other *Linopteris* species including *Linopteris brongniartii* and *Linopteris bunburii* appeared later, and they have no clear analogues among the *Paripteris* species. Most probably these later linopterids did not arise through reticulation of paripterids, as many of them appear after the disappearance of *Paripteris*. Other post-Bolsovian linopterids have vein meshes resembling those of *L. neuropteroides*. These species are similar to *L. brongniartii* and *Linopteris obliqua* (ZODROW et al., 2007), but the latter have shorter mainly hexagonal meshes.

Reticulation in *Paripteris* is observed only in large pinnules. It seems that in young pinnules near the top of the frond, the water supply is regular. Vein meshes are never observed in the smaller, orbicular pinnules. The distribution of meshes in different parts of the pinnules may be related to greater solar exposure. The size of the meshes decreases from the mid rib towards the pinnules border.

The form of the meshes (areolas), which affected the space between the veins of a leaf, resulted from several factors:

1. Coalescence of undulating lateral veins with two forms: pseudoanastomosis (the laterals touch only), and anastomosis (accretion of adjacent veins). Such vein meshes develop between veins of equal rank and is seen in *Lonchopteridium* and *Reticulopteris*.

2. Connection (junction) of two neighbouring lateral veins realised through the lower order splitting of a lateral vein and another split one level higher; giving a wedge appearance. The vein meshes can be rhomboidal (four-sided), pentagonal, or hexagonal. This is best seen in *L. neuropteroides*.

3. Mutual delta-formed crossing of laterals that produces rhombic meshes (*Lonchopteris eschweilleri, Linopteris regnietzii*).

Towards the end of the pinnule, the meshes become isometric, usually hexagonal. This leads to homeomorphism of the meshes in *Linopteris brongniartii, Barthelopteris germarii, Lonchopteris silesiaca, L. rugosa and L. elegans*. The isometric hexagonal form permits the density and regularity of veining to be maximised, and was important for equalising water distribution to all cells because it ensured the shortest distance between the water supply lines in the pinnules and the individual cells. Therefore, reticulation of pinnules is an organisation for dealing with water supply and water deficit compensation.

Linopteris and *Reticulopteris* survived many climatic changes and, in contrast to *Lonchopteris*, disappeared in the Permian Period. Maybe the shedding of pinnules and the formation of hairs helped them survive.

5. PALAEOECOLOGY

There may be many reasons why a single genus or species evolves, but the transformation of numerous taxa in one habitat indicates that a common factor may have been at work. KRASSILOV (1972) reviewed the palaeoecology of plants, including the effects of changes in temperature and air humidity.

5.1. Cooling

According to data cited by FRAKES (1979), the drop in levels of atmospheric CO_2 during Namurian and mid-Westphalian times caused a 25 °C drop in temperature. This had several consequences. Some plants became extinct, but others migrated to lowland regions with temperatures similar to those of their previous habitats. It was somewhat easier for true ferns, and to a degree for seed-ferns. Migration from the cooling northern areas towards the warmer southern areas, across the Variscan range through dry-land areas, is possible. In the European Variscan range however, there were areas that were not high. Some were even below sea level, such as the Danube Iron Gate in central and west Serbia, where marine fauna from the Russian Epiplatform Sea penetrated the Tethys; and the Straits or Sea of Marmora, where a marine northern fauna penetrated the Palaeotethys during Viséan-Namurian times. Such migrations may have been accomplished via some intermountain depressions with high altitude, such as Svoge (TENCHOV, 1976); Lower Silesia, and the Caucasus basins. In the latter area, paripterids but no linopterids existed; there were few or no *Alethopteris*, *Lonchopteris* and *Mariopteris*, and many *Eusphenopteris* (ANISIMOVA, 1979). Some of the depressions at lower elevations such as the Saar-Lorraine and the southern part of the Briannçonaise Alps, and the Turah Mountains in Austria and Switzerland frequently host *Linopteris*, while *Linopteris* is not known or is extremely rare in the northern territory of the Variscan foredeep (Upper Silesia, Donets, Lvov-Volinsk), even in northern parts of the West-European Variscan Foredeep.

5.2. Water supply regime

The periodic drying that started in Pendeleian times to the north of the Variscan Range is most probably related to the growing area of dry land, which led to the continentalisation of the climate, combined probably with a rain shadow effect caused by the rising Variscides. It is unlikely that the narrow Palaeotethys provided enough moisture for the atmosphere. This is directly comparable to the contemporary low influence of the Mediterranean on rain fall regimes in the inner parts of Eastern Europe.

The gradual drying of Pennsylvanian climates is reflected in the seed ferns. Their fronds were richly covered in hairs, had more linear, narrower and smaller pinnules, dense lateral veins, and a tendency for the pinnules to be shed. There was a history of increasing retardation in frond development. It is also reflected in their branches and reproductive organs. Reticulation in seed ferns also reflects a scarcity of water.

5.3. CO_2 deficit

An example of this is the extinction of *Sigillaria* and *Lepidodendron* during Bolsovian times and their replacement by species with a smaller habit. Newcomers from the high mountains may have had some advantage in this respect, because of the lower atmospheric content of CO_2 at higher altitudes, due to that gas being heavier than other components of the atmosphere. Evolution also acted here, driving adaptation to changing conditions.

6. DISCUSSION

Linopteris neuropteroides and its predecessor *Paripteris gigantea* both inhabited alluvial plains and intramontane depressions. *P. gigantea* became extinct during Cantabrian times, probably due to aridisation, but *L. neuropteroides* survived until the Early Permian. The reticulate veining of *L. neuropteroides* may have given this species some sort of advantage for survival. During Stephanian times, the paralic and paralimnic coal building realms to the north of the Variscan range were replaced by fluvial plain conditions with rare, small swamps, where *L. neuropteroides*, *Reticulopteris muensteri* and *Barthelopteris germarii* were well represented. The effect of a cooling climate from Pendeleian to Asturian times on reticulation is unclear. Still, the cold-resistant *Paripteris gigantea*, *Neuropteris obliqua* and *Alethopteris* spp, occurred in the colder, higher elevation Svoge basin, which in the lower elevation basins developed reticulate veining.

A shortage of water can arise from low levels of water in the soil or subsoil, and also as a result of seasonal or periodic low air humidity. The study of recent and fossilized plants has established that they have many tools to compensate for insufficient water supply, including the retardation of plant architecture (KRASSILOV, 1972), but vein reticulation has not been discussed. The large size of leaves in *Glossopteris* is regarded as proof of a genuinely tropical (equatorial) climate. The Euramerican Carboniferous megaflora inhabited warm and temperate zones, but this does not necessarily mean tropical; some use the alternative term pseudotropical. The application of contemporary classifications of floral climatic zones for the geological past is rather arbitrary and lacks clear reasoning.

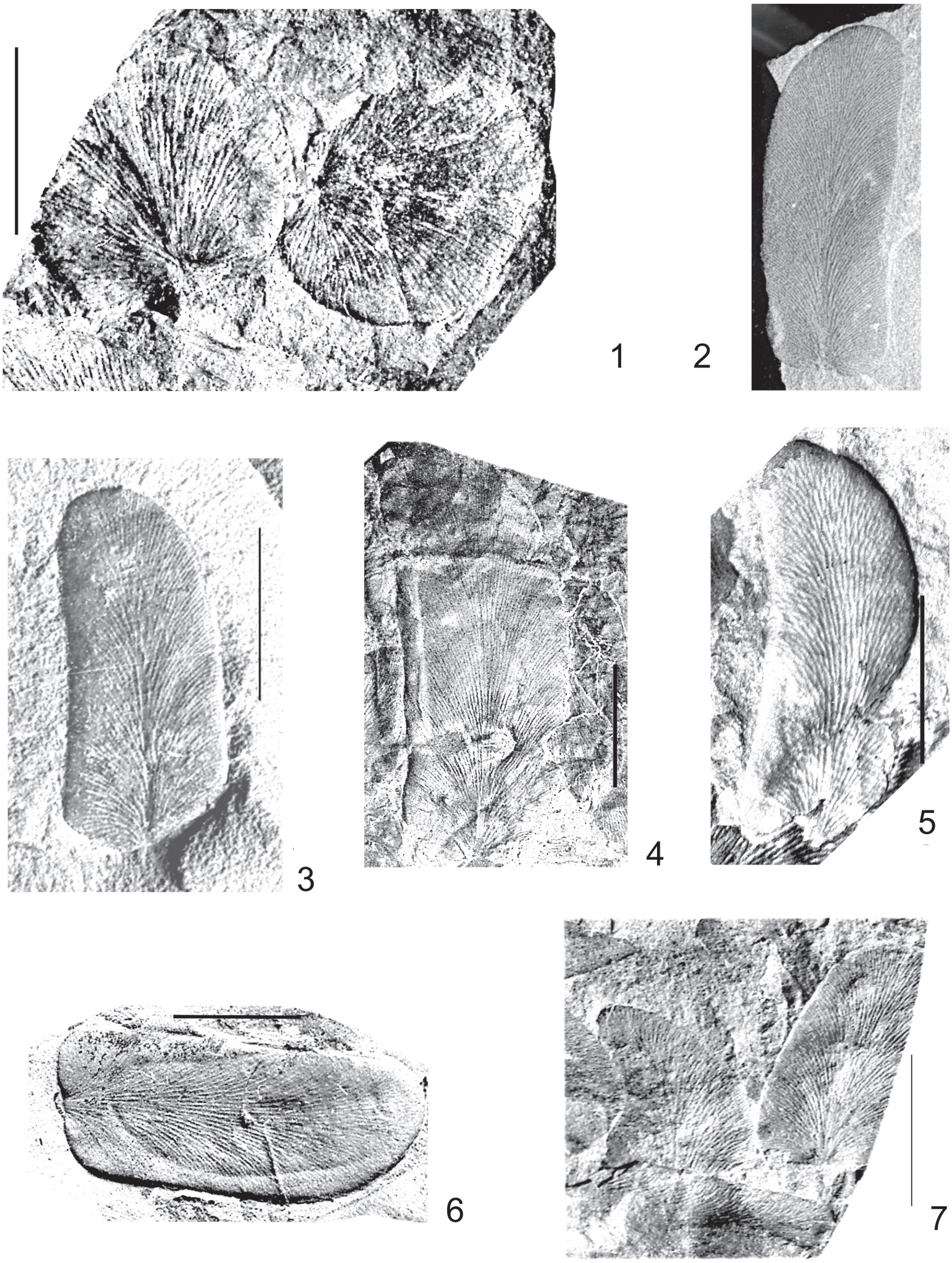


PLATE 1

1 *Cardiopteridium waldenburgense* Sample 05750, Drill 56, 1640 m SL -321, Rakovski F, Pendelian. Single connection between veins.
2 *Paripteris gigantea* upper side. Sample 06541 lower surface of the sample. Drill 73, 1651 m, SL 141, Mogilishte F, Langsetian. Meshes near to midvein.
3 *Paripteris gigantea* upper side. Sample 06529 Drill 73, 1582 m, SL 210, Mogilishte F, Langsetian. Meshes at left part and near to the midrib. TENCHOV & POPOV 1987b, Pl. 2, fig. 3.
4 *Paripteris linguaefolia* upper side. Sample 15252. Drill 179, 1442 m, SL 261, Mogilishte F, Langsetian. Rarer meshes.
5 *Linopteris neuropteroides* upper side. Sample 08542. Drill 90, 1727 m, SL 381, Mogilishte F, Langsetian. Imperfect reticulation in lower half around midvein.
6 *Paripteris gigantea* upper side. Sample 09418 Drill 95, 1896 m, SL 386, Mogilishte F, Langsetian. Imperfect reticulation in lower half around midvein. TENCHOV & POPOV 1987a, Pl. 2, fig. 5.
7 *Paripteris pseudogigantea* upper side. Sample 08305 Drill 81, 1866 m, SL 668, Makedonka F, Duckmantian top. Partly anastomosed.

The scale bars are 1 cm.

The diminishing size of the pinnules is usually viewed as a sign of water shortage, but it is noticeable that many late Westphalian pectopterids have relatively large pinnules. Also, in swamp conditions, air humidity is not low, especially close to the surface. Cooling has a similar effect on pinnule size, as demonstrated in the Svoge basin (TENCHOV, 1976). A decisive dry spell would lead to thicker cuticles, and stomata with a negative relief and neighbouring trichomes. Stomatal densities have never been studied in the Dobrudzha Coalfield. Trichomes could sometimes act as water reservoirs. Trichomes within the same species, in the same area and level, are dense in some pinnules and not dense in others. The vaulted form of the pinnules probably diminished water consumption.

Linear pinnule borders are more widespread in the upper levels of the Westphalian Stage. Pinnules with a denticulate or undulating border are much more common in the lower levels of the Westphalian, such as seen in *Pecopteris plumosa*, *Mariopteris acuta*, *M. muricata*, and some *Eusphenopteris* species; these are replaced at a later date by species with more straight-edged pinnules including *Mariopteris nervosa* and *Pecopteris huchetii*. Changes in vein density should be evaluated for one and the same species at different stratigraphic levels or in a lineage of species such as *Alethopteris urophylla – A. densinervosa – A. serlii*.

The flexuosity of veins can lead to partial or complete reticulation as is the case with *Neuropteris obliqua – N. semireticulata – Reticulopteris munsteri*. Touching of laterals is realised in some *Alethopteris* species with dense and flexuous lateral veins (Pl. 2, Fig. 12), but this does not lead to the type of reticulation seen in *Lonchopteris*.

The fact that *Paripteris*/*Linopteris* and *Alethopteris*/*Lonchopteris* reticulated simultaneously during early Westphalian times points to a common cause – drier conditions. In the Dobrudzha Coal Basin reticulation is even observed in seeds (Pl. 2. Fig. 12).

Pinnule shedding is a characteristic only for some neuropteridians.

7. CONCLUSIONS

The composition of Bulgarian Carboniferous megafloras supports the idea that cooling took place during late Carboniferous times (TENCHOV, 1976, 2011). The cooling is related to a considerable drop in atmospheric CO_2 (FRAKES, 1979).

After analysing the deposits from the European Upper Carboniferous, STRACHOV (1960) defined a region of aridity, which extended from Britain to Lvov-Volinsk and lay within the Variscan foredeep. Many characteristics of the Westphalian plants indicate adaptation to drier air. Such adaptations can be observed in the Pendeleian Substage, but are more strongly expressed in several episodes preserved within the Westphalian Stage.

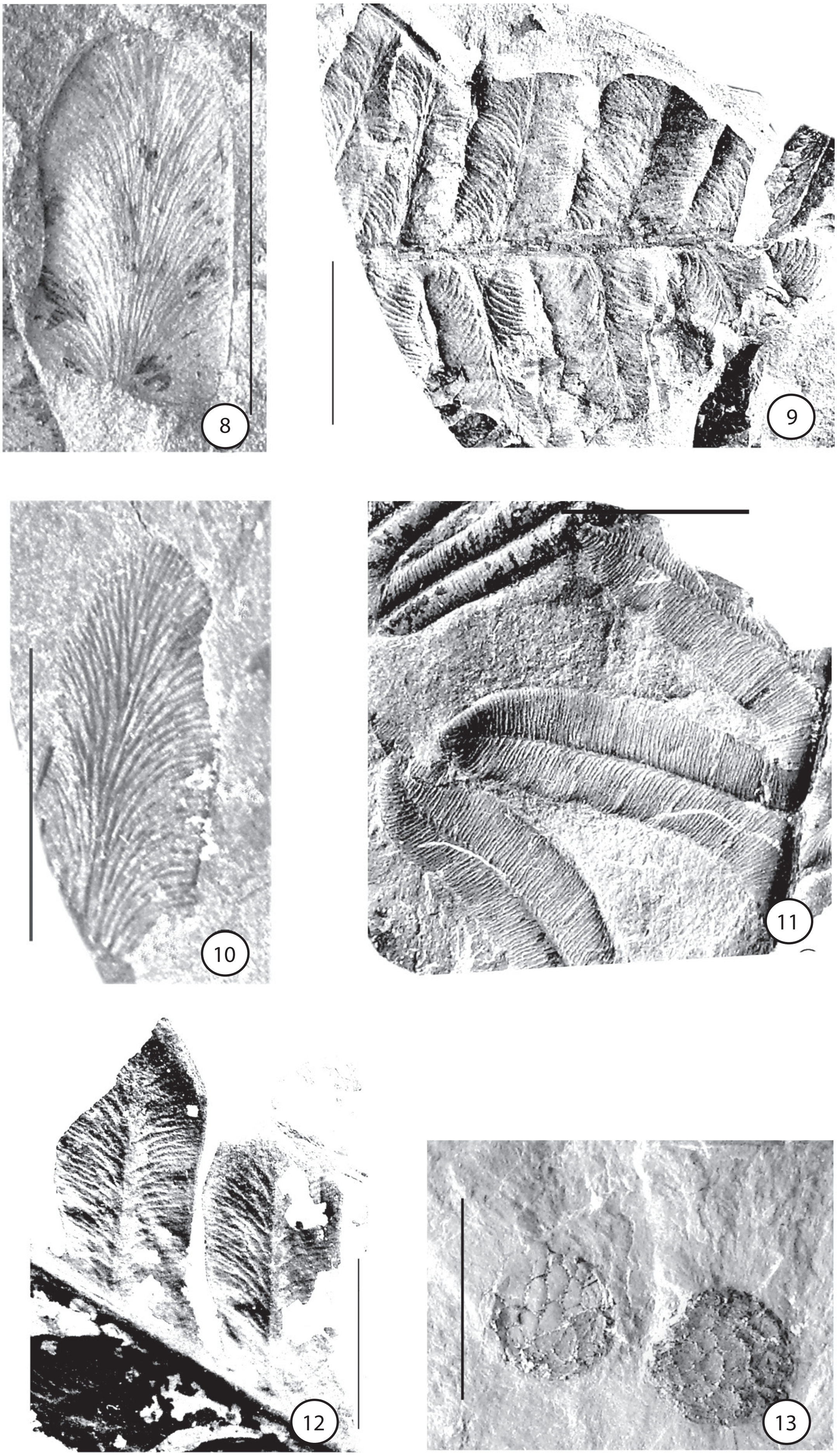
During the Namurian, alethopterids started the process of reticulation of veining, resulting in the appearance of *Lonchopteridium* and *Lonchopteris* (Fig. 2 – anastomosis – step1). Later, towards the end of Namurian times and the beginning of the Westphalian Age, vein reticulation started in *Paripteris* (Fig. 2 – anastomosis – step 2), resulting in *Linopteris*. The same happened with *Neuropteris obliqua* about the end of Duckmantian times and its transformation into *Reticulopteris* (Fig. 2 – anastomosis – step 3-4). This is when the real *Linopteris* first appeared, which were not merely reticulated *Paripteris*. The next step is the appearance of *L. bunburii* (Fig. 2 – anastomosis – step 5) with perfect isometric small vein meshes – about 1 mm in size. In the Dobrudzha Coalfield, the transition to *Linopteris* and *Reticulopteris* is well-represented by intermediate forms of partial reticulation in *Paripteris* and *N. obliqua*. The transformation of *Alethopteris* into *Lonchopteris* at about the end of Yeadonian times, or the beginning of Langsettian times, is poorly represented in the Dobrudzha Coalfield, but the early appearance of *Lonchopteris baurii* (TENCHOV, 2004a) demonstrates that this happened in this region too. The occasional vein reticulation around the end of the Westphalian Age did not lead to new reticulated species or genera. It seems that local *Linopteris*, such as *L. subbrongiartii* and *L. regniezii*, appear in other Variscan regions. *Linopteris neuropteroides* and *Reticulopteris* outlive many other pteridosperms and become an important element of Stephanian and lowermost Permian megafloras, when climate aridification became strongly expressed once again.

The periodic reduction in rainfall affected large regions. In the Dobrudzha Coal Basin it is reflected in the reduced amount of imported eroded material in the Mogilishte Formation (SL 0-50, 450-660), with a short intensive break during deposition of the Vranino Formation (SL 670-870), and a long break at about the end of Bolsovian times (SL 1200-1300). The reduction in rainfall at SL 670-870 also produced strong weathering of sediments to the south of the Seltse Fault, which is reflected in the quartz sandstones of the Velkovo Formation.

PLATE 2

8 *Linopteris* sp. Sample 13426 Drill 160, 1470 m, SL 685, Makedonka F, Bolsovian. Partly anastomosed. TENCHOV & POPOV, 1987a, pl. 3, fig. 3
9 *Alethopteris grandinioides* early form. Sample 12109 Drill 131, 1691 m, SL 731, Makedonka F, Bolsovian. Single touching lateral veins.
10 *Linopteris* sp. Sample 14979 Drill 173, 1691 m, SL 1149, Gurkovo F, Asturian. Imperfect reticulation.
11 *Alethopteris densinervosa*. Sample 11420 Drill 107, 1357 m, SL 1242, Gurkovo F, Cantabrian. Single meshes.
12 *Alethopteris pseudograndinioides* var *zeilleri*. Sample 12278 Drill 134, 1452 m, 1538 SL Gurkovo F, Cantabrian. Touching lateral veins.
13 Reticulated seed most probably of *Reticulopteris muensteri* Sample5995, Drill 64, 1640 m, SL721, Bolsovian.

The scale bars are 1 cm.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The Dobrudzha region is a place in which new taxa at the rank of species and genus developed during Namurian-Westphalian times. The reticulation in the veining discussed here was a result of climate changes. I am far from the opinion that this is a unique area, but it is one where these changes have been clearly recognised.

ACKNOWLEDGEMENT

This paper is a contribution to IGCP 575 “Pennsylvanian terrestrial habitats and biotas of southeastern Euramerica”. Thanks go to Chris CLEAL and Erwin ZODROW for discussion on the problem and to the former also for linguistic assistance.

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Manuscript received January 11, 2012
Revised manuscript accepted October 03, 2012
Available online October 30, 2012