

Structure, habitat and seed of *Mariopteris* ZEILLER



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ABSTRACT

The genus *Mariopteris* ZEILLER is distributed from the Namurian A to the early Stephanian in Europe. In the Dobrudzha Basin, numerous specimens are found mainly in flood plain claystones and siltstones. The habitat and reconstruction of the plants suggests a creeping manner of growth. Climatic changes are reflected in the architecture of species. One specimen has an attached seed proving the classification of the genus as a pteridosperm.

Keywords: *Mariopteris*, pteridosperm, creeping plant, attached seed

1. INTRODUCTION

The genus *Mariopteris* has attracted the attention of many palaeobotanists. ZEILLER (1878, 1879) created this genus that is now known to embrace species that were referred to different genera. Many monographs (HUTH, CORSIN, DANZE-CORSIN, BOERSMA), and part-authors of large monographs (ZEILLER, STUR, GOTHAN, KIDSTON dates needed here too), and other articles concern these plants. While the architecture, classification, taxonomy, synonymy and species diversity are frequently discussed, the habitat of this group is rather poorly considered. It is accepted that they are probably creeping, intertwining or climbing, in habit.

2. PLANT ELEMENTS AND TERMINOLOGY

BOERSMA (1972, p. 24) used the term “frond” for the “... spirally arranged leaf-like structures”... DELAVORYAS (1962, p.120) commented that “...at *Medullosa*...leaves in their basal region resemble stems with many steles. Externally, it would be impossible to distinguish between leaf and branch. Here the terms stem, leaf and stalk are used.

2.1. Roots

There is no published information on them, but it is possible that the stem, which is partly covered by wet sediments, also

possesses the function of a root. The trichomes on the stem at the apex of the plant (CORSIN, 1932, Fig. 29) might be root appendices.

2.2. The Stem

It is straight or slightly sinuous and covered by longitudinal striations and regular short transverse bars. A group of plants, regarded by DANZE-CORSIN (1953) as *alinae*, do not have transverse bars and BOERSMA (1972) excludes them from *Mariopteris*.

There are few illustrations of stems. The stem is slightly elliptical with the leaf stalks, or their marks, situated at equal distances on the stem. One pair of leaves is located on the lower external part and another pair is approximately half the distance to the top STUR (1885, pl. 22, fig. 1). STUR (1885, p. 285, pl. 22, fig. 1) regards this arrangement as a spiral of four bases in one cycle. DANZE-CORSIN (1953, figs. 7–9) supposed there to be a helix built of five leaves. ZEILLER (1888) regards the arrangement of the leaves as two generatrice situated at an angle less than 180°. The longitudinal striation of the stem, illustrated in many figures, is straight and does not indicate any spiral growth. The position of each of the four consecutive leaves is repeated along the stem, and can be regarded as helical that is not the result of axial rotation. Therefore, the fourfold alternation characterizes the leaf arrangement – Fig.1.

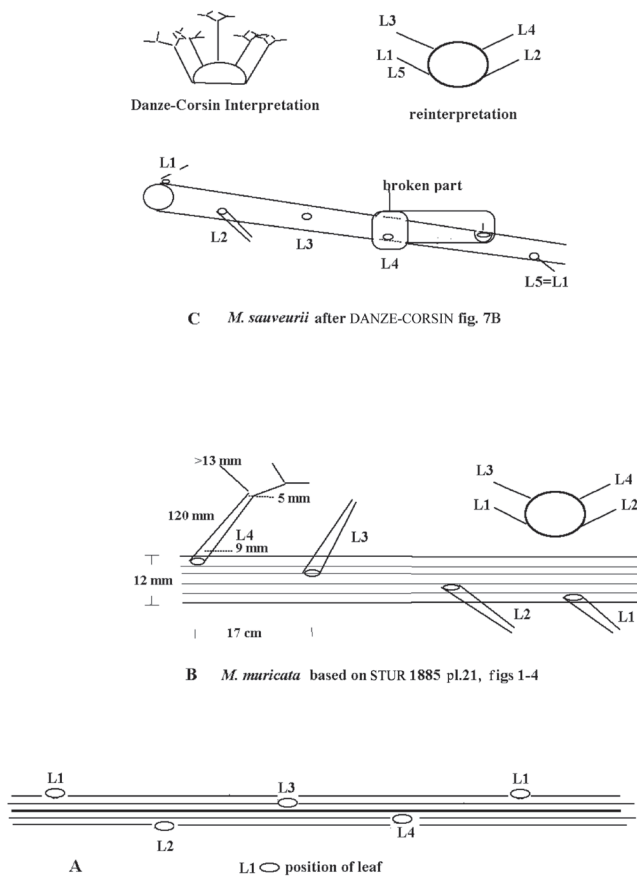


Figure 1: Interpretations of leaf position.

There is neither information nor data for the total length of the stem, although the length of one cycle of leaves in a well-developed stem is 280 mm (STUR, 1885, Pl. 22, fig. 1). The known maximum width for a stem is 22 mm with a gradual reduction in each cycle of about 1 mm. If this reduction in width was even, the length would be about $21 \times 280 \text{ mm} = 6.0 \text{ m}$ or more.

2.3. Stalks and leaves

The leaves are pinnate with a massive, longitudinally striate naked stalk (petiole) up to 150 mm long and 7 mm wide at its base. The stalk axes are directed upwards at a 40° angle to the stem axis (DANZE-CORSIN 1953, figs. 7–9). The stalk bifurcates for the first time at an open angle in two parts (rachises in many authors), which in their turn bifurcate up to 5 times. After the third bifurcation they are covered by pinnae (lamina). The leaf blade is parallel to the stem and to the ground. Its axis is either parallel to, or at some angle, to the stem axis. The pinnae in the blade are in one plane that is parallel to the stem axis and the ground. The pinnules length, width and neuropteroid or pectopteroid base depends on the species. BOERSMA (1972, tables VII to XIV) gives data for the size of the leaf elements for 7 species. Table 1 summarizes some of the data. Pinnules near the top of the plant can have spine-like lobes or are totally formed as spines.

In the mariopterids, two architectural types of leaf blades are known and designated as bipartite and quadripartite.

Table 1: Maximum known size of leaves of *Mariopteris* ZEILLER

Species	Length mm	Width mm	Data from:
<i>M. acuta</i>	>500	> 240	Boersma fig. 76 DANZE-CORSIN p. 83
<i>M. beneckeii</i>	750–800	>260	Huth fig 5 DANZE-CORSIN p. 104
<i>M. bourosii</i>	?	?	only P4, P5 known
<i>M. carnosa</i>	>140	> 320	CORSIN pl. 68
<i>M. daviesii</i>	?	?	only P3 known
<i>M. demnoncourtii</i>	600	250	DANZE-CORSIN p. 94
<i>M. grandepinaa</i>	>230	>260	HUTH fig. 1
<i>M. hirsuta</i>	?	?	
<i>M. hirta</i>	350	> 200	DANZE-CORSIN p. 149
<i>M. lobatifolia</i>	>259	160	DANZE-CORSIN pl. 63, fig. 2
<i>M. microsauveurii</i>	>180	>150	DANZE-CORSIN pl. 59, fig. 1
<i>M. muricata</i>	>370	> 180	Huth fig 2 STUR 1877
<i>M. nervosa</i>	>180	>360	BOERSMA text fig. 7
<i>M. odontophylla</i>	160–180	> 120	DANZE-CORSIN p. 137
<i>M. opulenta</i>	750	>440	DANZE-CORSIN p. 175 pl. 68 fig.1
<i>M. pachyphylla</i>	450–600	>200	DANZE-CORSIN p. 202 pl.61, fig.1
<i>M. robusta</i>	?	?	
<i>M. Sauveurii</i>	>180	>160	DANZE-CORSIN figs.
<i>M. Soubeyrianii</i>	>400	300	DANZE-CORSIN p. 213

DANZE-CORSIN (1953, p. 57–58, p. 256) indicated that the fronds of *Mariopteris* have in its base and along its length quadripartite leaves but are bipartite in its sub-terminal part. The transformation to bipartite in quadripartite leaves is documented by DANZE-CORSIN (1953 pl. 40, fig. 1; Pl 10, fig. 1, respectively pl. 11, fig. 2). This can be regarded as acceleration during the growth in the leaf architecture of a species. She (idem p. 58, plate 56) supposed that simple pinna were situated at the terminal part of the stem, but this is not evident in the figures. BOERSMA (1972) does not mention anything about simple pinna, although he accepts that the genus *Mariopteris* consists of two groups of species – one that has bipartite leaves and another that has quadripartite leaves. The bipartite leaf possesses exterior pinna that gradually diminish in length. The quadripartite leaf possesses a long pinna at the base of the tertiary rachis, followed by a pinna of calceolate form. For this reason he divides the mariopterids into two genera: *Karinopteris* BOERSMA for bipartite fronds and *Mariopteris* (ZEILLER, BOERSMA emend.) for quadripartite fronds. BOERSMA (1972) does not comment on the opinion of DANZE-CORSIN that bipartite leaves are situated at the top of plants with quadripartite leaves. However, he indicated as “aberrant forms” those specimens of *Mariopteris* (ZEILLER, BOERSMA emend.) that have bipartite leaves. *M. nervosa* KIDSTON (1925, pl.

144, fig. 4, 4a); BOERSMA specimens of *M. sauveurii* (his pl. 5, fig.10) and of *M. muricata* (his pl. 21, fig. 55) should all be regarded as “minute fronds of *Mariopteris*”. This suggests that the proposed taxonomy should be re-examined.

Both type of leaves are asymmetric, as is well expressed by the width of their internal and external parts. The asymmetry was the subject of attention by DANZE-CORSIN (1953) in almost all species described by her.

The leaves are large and require strong stalks to support them. The length of the leaves is longer than the length of the distance between the leaf stalks. The plane of the leaf blade most probably is parallel to the ground. In adult plants the lower pair of pinnules is about 7 cm while the next is about 9 cm above the ground.

2.4. Aphlebia

DANZE-CORSIN (1953, fig.7, p. 45) accepts as *Aphlebia* some small excrescences at the base of the leaves. It is not supported here.

2.5. Pinna, pinnules and venation

The pinnae are lanceolate and slightly or more asymmetric elements formed on stalk branches. The width and the length (which can be more than 300 mm), depend on the species and on the position on the leaf. The pinnules are the smallest part of the leaf blade and their morphology depends on the species as detailed by BOERSMA (1972). They are attached by pecopteroid or sphenopteroid bases. The basal basiscopic and acroscopic pinnules in a pinna of ultimate order, have strongly developed outgrowths of their basal basiscopic

lobes. In some cases, the terminal pinnules of a pinna, and part or all of the pinnules in lower situated pinna, are formed in spines, as figured by HUTH (1912, VIII, 143, fig. 1). The pinnules have a midvein that arises obliquely from the stalk, curves and reaches at least halfway up the pinnules and secondary vein branches that emerge alternately from the midvein and dichotomise one or more times, ending at the apex of the pinnules.

Cuticle analysis by BARTHEL (1962) and KERP AND BARTHEL (1993 – but not pl. 5, fig. 1–4!) established that stomata are closely spaced on the lower surface of the pinnules but absent from the upper surface..

2.6. Bud (“Bulbil”)

HUTH (1912) used the term bulbil for round buds, up to 1.5 mm across, occurring on the stems of some species of *Mariopteris*. CORSIN (1932) regarded them as an early stage of unopened pinna. Some of them occur in the axils of normal leaves (HUTH – fig 5) and others on the inter-leaf space of the stem (HUTH fig. 3; CORSIN 1932 pl. 76, fig 1). It seems that they never occur on fully-formed leaves.

The leaf grew by linear development (envelopment, opening) from a spiral. Some phases of this are illustrated by CORSIN (1932, fig. 29 and plate 76, figs 1–5), HUTH (1912, VIII, 141 fig. 2), CORSIN (1932 text-fig 29,) and GOTHAN (1935 pl. 29, fig. 4). They are summarized here in Figure 2. At an early phase the spiral looks like a bud. The leaf spirals are parallel (twin spiral) and visible in fig. 4 of HUTH. After some growth, the two parts separate and turn to left and right as in an open leaf. A phase of this is illustrated by CORSIN (1932 at fig.29 and plate 76).

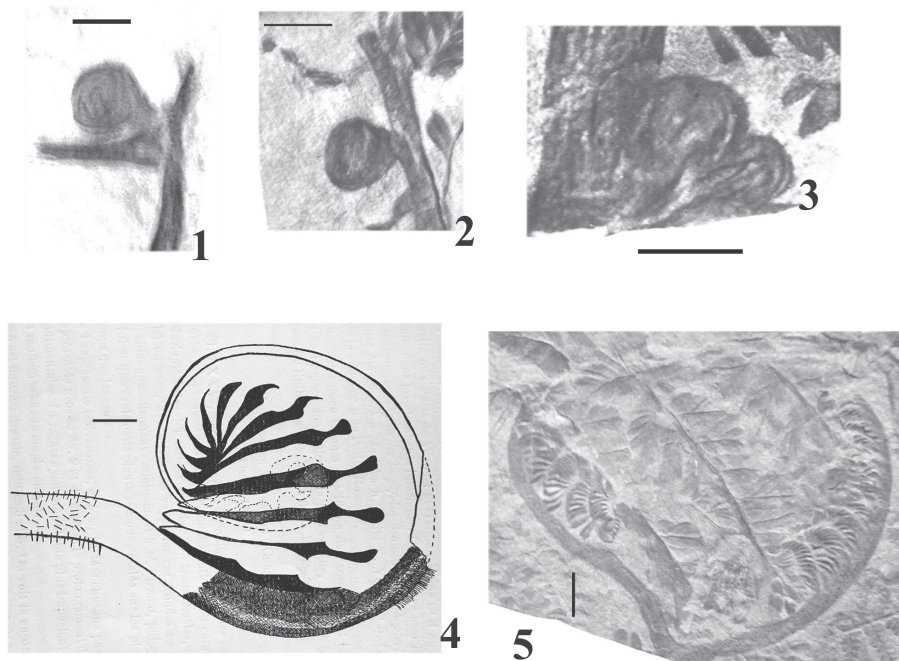


Figure 2: Phases of leaf development. 1/A– a bud in the base of stalk (HUTH, 1912, 141, fig. 5); 2/B– bud in the middle of a stalk (HUTH 141, fig. 3); 3/C– bud developed in a twin spiral (HUTH 141, fig. 4); 4/D– the top of the stem with numerous unopened leaves (CORSIN 1932 fig.29); 5/E– leaf in the opening of the spiral (HUTH 141, fig. 2).

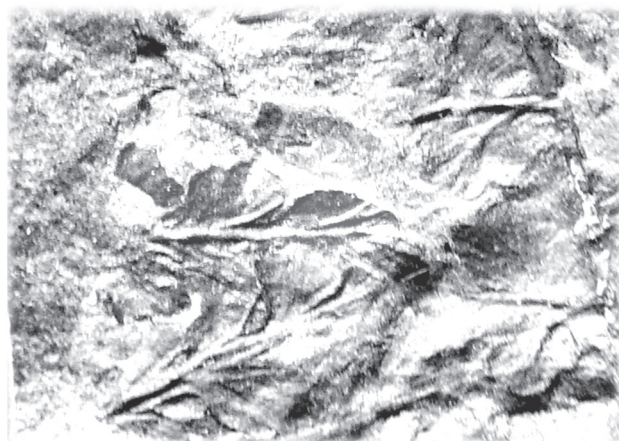
2.7. The spines

The spine-like form of the pinnules seems to be provoked by heliotaxes, when a young specimen is in full shadow below adult plants. In such cases, the leaves of its top part are directed upwards towards the light. They are covered by spine-like pinnules as documented in HUTH (1912, VIII 143, Fig. 1). The spines help the enveloped leaves behind the plant top to intertwine through the leaves of the adult species, (that shade out the light), and then to continue development over the other leaf. This is shown by *M. carnososa* (CORSIN, 1932, Pl. 68). The older specimen has larger pinnules and no spines (left part of the figure). The younger specimen (visible along *x-y* line), has smaller pinnules and numerous spines that are at *y* – the top of the specimen. When the plant reaches the sunny surface, the spine-like pinnules start to transform themselves from their base towards the apex as normal pinnules. Different phases of this transformation are illustrated in numerous figures of CORSIN (1932 – pl. 63, fig. 2, pl. 72, figs. 2, 4), DANZE-CORSIN (1953) and in that of HUTH (1912). Therefore, *Mariopteris* under some conditions can be intertwining with plants at an early phase of growth.

3. REPRODUCTION

Until now, it has generally been accepted that the mariopterids are pteridosperms, but there is a lack of evidence of their method of reproduction. GOTHAN (1935, p.8–14) supposed that vegetative reproduction was possible by means of buds. BOERSMA (1969) established that *Mariopteris latifolia* (BRONGNIART) ZEILLER is really a fern, and referred it to a new genus *Fortopteris* BOERSMA, as *Fortopteris latifolia* (BRONGNIART) BOERSMA. It has quadripartite constructed leaves. This species (and genus) differs from the mariopterids by some denticulation of its pinnules, and by its stem having no transverse bars. The missing transverse bars on the stem stimulated DANZE-CORSIN to create a “group *alineae*” in the mariopterids.

The possibility that *Mariopteris* is a seed fern is based on an analogy with *Dicksonites pluckenetyii* which has small seeds situated on the lower surface of its pinna. In *Mariopteris* the majority of fossils show the upper surface. This suggested re-examination of slabs with *Mariopteris* in the Dobrudzha collection. A seed-bearing *Mariopteris beneckeii* (sample N 16344) was found on a sample from borehole number 218 at 1406 m depth, corresponding to a level about 218 m above the base of the Mogilishte Formation in the middle part of the Langsetian. The specimen shown on Fig. 3 is from a young leaf in which a part is reversed, exposing its lower surface possessing at least one small seed. This suggests that *Mariopteris* as many other ancient plants e.g. some lepidodendrons, after some time in a vegetative phase entered a reproductive phase that then led to the death of the plant. Two advantages of this strategy are that the seed is dispersed far from the mother plant root (6 m. or more) and may be out of the *Mariopteris* carpet thereby enlarging its range, and secondly in opening up places in the habitat for a new generation of plants.



/-----/ 1 cm

Figure 3. The seed-bearing specimen 16344 Dobrudzha Coalfield borehole 214, 1508 m in the Mogilishte Formation in the mid part of the Langsetian. I think this image would benefit from annotation eg an arrow pointing to the seed?

In the one metre interval at 1406 m depth in borehole 218, there are seven samples of *Mariopteris* and another two with *Eusphenopteris*. Individual pieces of shale are about 1 cm thick and the unexposed parts of them also contain plant remains. The plants were preserved with their upper surface upwards, either by being flattened by an inrush of turbid flood water, or death after a reproduction phase. Leaves reversed with their lower surface upwards are rarely found and illustrated. This seems to indicate that mariopterids lived in places with a low water dynamic.

4. MARIOPTERIS CONSTRUCTION

Parts of the published accounts of several species are used for the construction of the *Mariopteris* plant. Those stems possessing the marks of leaf bases show them to be equally spaced with the distances between them being no more than 170 mm. The leaves are flat and directed at angle to the stem direction. The construction of the fronds is regarded as phases in architecture building with the steps as: appearance – acceleration – retardation – disappearance – Figure 4.

5. HABITAT

The habitat of the mariopterids has been rather poorly discussed in the past, although the opinion by GOTHAN (1913 p.88) that *Mariopteris* lived on the forest floor as a creeping, climbing and intertwining plant is generally accepted. Unfortunately, there is no real evidence to support this view. KERP & BARTHEL (1993 plate 5, figures 1–4) accept that the documented hooks are of a climbing *Karinopteris*, but the plant seems to be *Eusphenopteris* So, a climbing habit of *Mariopteris* is not supported by the facts.

In the Dobrudzha Coalfield, *Mariopteris* specimens occur in all coal bearing lithostratigraphic units. They are rare in the Rakovski Formation (Namurian A), frequent in the Mogilishte, Makedonka and Krupen Formations (Namurian

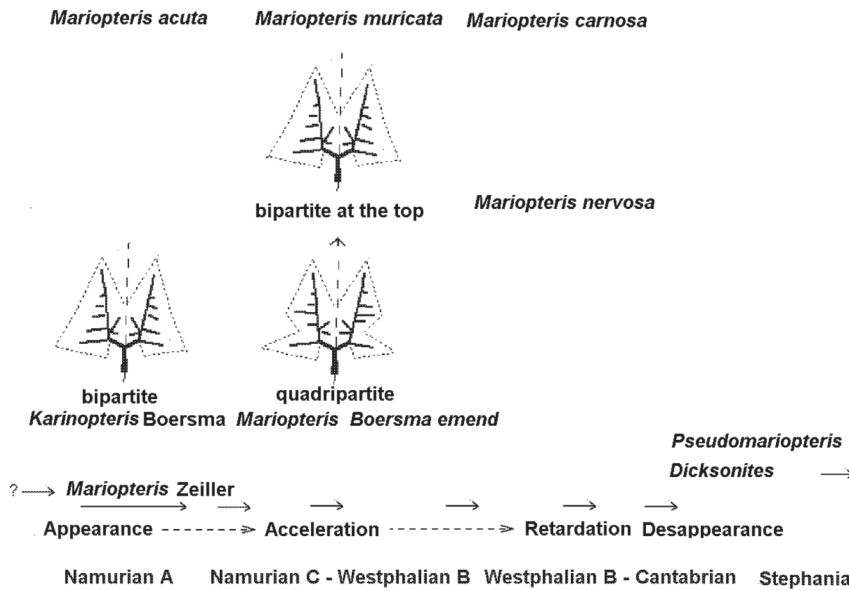


Figure 4. Phases in architecture building.

C –Westphalian D), and rare upwards to the Stephanian (Gurkovo Formation). They are also rare in the fluvial sediments where allochthonous fragments are rarely observed. As autochthonous specimens they are frequent in the sediments overlying the coal seams, especially in the upper part of the Mogilishte Formation.

In the flood plains, the *Mariopteris* formed a thick carpet of creeping and intertwining *Mariopteris* plants. Here and there, some bush-like plants of *Sphenophyllum* and some seed ferns such as *Neuralethopteris*, *Alethopteris*, *Lonchopteris* and *Eusphenopteris* – Table 2 occurred. Parnopterids are allochthonous. The detached seeds are autochthonous and did not germinate in the full shadow and cold milieu below the *Mariopteris* carpet.

Table 2: *Mariopteris* and associated plants in flood plain of the Svoge and Dobrudzha Coalfields

	Svoge Coalfield		Dobrudzha Coalfield	
	<i>Mariopteris</i>	Associated	<i>Mariopteris</i>	Associated
Westphalian D-Cantabrian	absent		<i>robusta</i> , <i>sarana</i>	<i>Sphenophyllum</i> , <i>Alethopteris</i> , <i>Callipteridium</i>
Westphalian C	absent		<i>sarana</i>	<i>Sphenophyllum</i> , <i>Alethopteris</i>
Westphalian B	<i>nervosa</i>	<i>Sphenophyllum</i>	<i>muricata</i> , <i>nervosa</i>	<i>Sphenophyllum</i> , <i>Alethopteris</i> , <i>Lonchopteris</i>
Westphalian A	<i>acuta</i> , <i>muricata</i>	<i>Sphenophyllum</i> , <i>Neuralethopteris</i>	<i>muricata</i> , <i>nervosa</i>	<i>Sphenophyllum</i> , <i>Alethopteris</i> , <i>Lonchopteris</i> , <i>Neuralethopteris</i>
Namurian C	<i>acuta</i> , <i>muricata</i>	<i>Sphenophyllum</i> , <i>Neuralethopteris</i>	<i>acuta</i> , <i>muricata</i> , <i>beneckei</i>	<i>Sphenophyllum</i> , <i>Alethopteris</i> , <i>Lonchopteris</i> , <i>Neuralethopteris</i>
Namurian A	absent		<i>acuta</i>	<i>Sphenophyllum</i> , <i>Alethopteris</i> , <i>Neuralethopteris</i>

During flooding, the creeping plants were submerged in muddy water and fine sediment may have been deposited on them. This could explain why *Mariopteris* has no stomata on the upper surface, as they would have been filled by the fine sediment. The stalk was massive enough to support the large leaf and the fine sediment covering it after the retreat of the flood water. Sediment could be washed away by rainfall, but if it dried the plant might die. In cases when the floods covered the plain to significant depth, the amount of the fine sedimentary deposit could be so thick and heavy, that the *Mariopteris* plants were crushed below it. This is the most probable reason why the leaves are mainly preserved with their smooth upper surface uppermost.

The reproduction problem could also be bound up with floods. The area of a flood plain that is covered by deep water loses all its *Mariopteris* carpet, but the carpet seems to be restored very rapidly, post flooding. Ferns, of course, can quickly re-establish from dispersed spores. For *Mariopteris* there are two possibilities that are at present hypothetical. The plants may quickly spread from areas beyond the reach of the flood waters or be re-established by seeds.

6. STRATIGRAPHIC DISTRIBUTION IN EUROPE

The genus is known from the Namurian A to the Cantabrian and the stratigraphic distribution in Europe is considered by HUTH (1912). *M. acuta*, *M. beneckei*, *M. muricata* and *M. carnosa* are found in the Donets Basin (NOVIK, 1952) and the North Caucasus (ANISIMOVA, 1979; NOVIK, 1978). The species diversity in the Dobrudzha Coalfield is comparable with that of other basins around the Variscan ranges in Europe.

7. CONCLUSION

Mariopteris plants formed a cover in the coastal and alluvial plains and around the swamps. This, combined with their creeping growth form, explains why they are so widely dis-

tributed in the Variscan foreland of Europe. Their creeping habit helped them to cover the plains and to migrate along river beds and the flood terraces. Even if they advanced yearly by only 1 metre, in the 2–3 Million years (life span of *M. acute* and of *M. medicate*) they could migrate 2–3.000 kilometres along river banks, the coastal margin of the sea, the outer fringes of large lakes and through the swamps from the British isles to the Turkish Black sea coast and the Caucasus. The climatic changes towards drier conditions and longer periods without rainfall would have reduced their habitat until they disappeared around the beginning of the Stephanian.

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REFERENCES

- ANISIMOVA, O.I. (1979): Flora i fitostratigrafia srednego karbona Severnogo Kavkasa, Naukova dumka, Kiev (in Russian). 47 pls., 107 p.
- BARTHEL, M. (1962): Epidermisuntersuchungen in einigen inkohlten Pteridospermenblättern des Oberkarbons und Perms.– Geologie, Beih, 33, 1–140.
- BOERSMA, M. (1969): A fertile leaf of “*Mariopteris latifolia*”. Meded. Rijks Geol. Dienst, N. Ser, 20, 65–77.
- BOERSMA, M. (1972): The heterogeneity of the form genus *Mariopteris* Zeiller, Atlas 43 plates, 172 p.
- CORSIN, P. (1932): *Mariopteridees*. Et. git. miner. France Bassin houiller de la Sarre et de la Lorraine. I. Flore fossile 3me fasc, 111–173.
- DANZE-CORSIN, P. (1953): Contribution a l’etude des Mariopteridees. Les *Mariopteris* du Nord de la France. Etud. Geol. Atlas Topogr. Souterr. Serv. Geol. H.B.N.P.C., 1/1, Atlas, 78 plates, 269 p.
- DELAVORYAS, T. (1962): Morphology and Evolution of Fossil Plants. Holt, Rinehart & Winston, N.Y. Chicago, San Francisco, Toronto, London, 189 p.
- HUTH, W. (1912): *Mariopteris*. – In: H. POTONIE (ed): Abbildungen und Beschreibungen fossiler Pflanzen-Reste.– Koenigl. Preuss. Geol. Landes-Anstalt, 8, 140–160.
- GOTHAN, W. (1913): Die oberschlesische Steinkohlenflora. I Farne und faranliche Gewachse. Abhhandl. Konigl. Preuss. Landesanstalt. N. Folge, 278 p.
- GOTHAN, W. (1935): Die Steinkohlen Flora der westlichen parasilischen Steinkohlenreviere Deutschlands. Lief. 3.–Abh. Preuss. Geol. Landesanstalt; pls. 32–47, 82 p.
- KERP, H. & BARTHEL, M. (1993): Problems of cuticular analysis of pteridosperms.– Rev. Palaeobotany and Palynology, 78, 1–18.
- KIDSTON, R. (1925): Fossil plants of the Carboniferous rocks of Great Britain.– Mem. Geol. Surv. Gt. Brit., Palaeontol., 2/6.
- NOVIK, E.O. (1952): Kamenougolnaya flora evropeiskoi chasti SSSR. (in Russian) – Ac. Sc. SSSR, 468 p.
- NOVIK, E.O. (1978): Flora I fitostratigrafia vhnego karbona Severnogo Kavkasa (in Russian) Kiev, Naukova dumka, 31 pls., 164 p.
- STUR, D. (1885): Die Carbonflora der Schatzlarer Schichten. Abt. I: Die Farne der Carbonflora der Schatzlarer Schichten.– Beitr. Kennt. Flora Vorwelt, Keiser. Koenigl. Geol. Reichsanstalt, 11/1, 418 p.
- ZEILLER, R. (1878): Vegetaux fossiles du terrain Houiller de la France. Atlas.
- ZEILLER, R. (1879): Vegetaux fossiles du terrain Houiller de la France. – Explic. Carte geol. France, 4/2, 185 p.
- ZEILLER, R. (1888): Vegetaux fossiles du bassin houiller de Valenciennes.– Etude des gites minereaux de la France, 731 p.

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