Late Gzhelian Pteridosperms with Callipterid Foliage of the Donets Basin, Ukraine

Author: Boyarina, Natalya

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Late Gzhelian pteridosperms with callipterid foliage of the Donets Basin, Ukraine

NATALYA BOYARINA

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Eight species of pteridosperms with callipterid foliage belonging to four genera are described from the upper Gzhelian of Donets Basin. The fossils indicate that the fronds of the callipterids belonging to the genera *Lodevia*, *Dichophyllum*, and *Raminervia* are bipartite in the upper part and are distinguished by the morphology of the penultimate order pinnae. The main diagnostic character of callipterid species with dissected pinnules is the shape of the pinnule segments. The degree of segmentation of pinnules and their size are considered to represent intraspecific variability expressing the heteroblastic development of the foliage. The taphonomical features of the plant remains and facies interpretations of the plant-bearing strata, including floodplain, floodplain-lacustrine and lacustrine deposits, indicate that the callipterids were dominant elements of the floodplain vegetation in the late Gzhelian.

Key words: Pteridospermopsida, Peltaspermales, foliar morphology, frond architecture, palaeoecology, Gzhelian, Donets Basin.

Natalya Boyarina [nboyarina@mail.ru], Institute of Geological Sciences of the Ukrainian NAS, Gonchara 55-b, 01601 Kiev-54, Ukraine.

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Introduction

Pteridosperms with the callipterid foliage are an important group of late Palaeozoic plants. In West and Central Europe, callipterids are known from the upper Stephanian (Němejc 1951; Doubinger 1956; Havlena 1958; Doubinger and Langiaux 1982) and they are regarded as characteristic elements of Autunian flora (Gothan and Gimm 1930; Barthel 1976, 1982; Haubold 1985; Kerp 1988). Callipterids are represented by five form-genera and the natural genus *Autunia* Krasser, 1919 emend. Kerp, 1988 of the family Peltaspermaceae Thomas, 1933 (Kerp and Haubold 1988).

In the Donets Basin, callipterids were found in upper Gzhelian deposits at Luganskoye village (Stschegolev 1960, 1965). Investigation of this site was initiated by Stschegolev (1965, 1975) and continued by the present author (Boyarina and Stschegolev 1989; Boyarina 1994, 2008). Three new taxa have been described, i.e., *Lodevia luganica* (Boyarina and Stschegolev, 1989) Boyarina, 1994, *Raminervia mariopteroides* Boyarina, 1994 and *Dichophyllum cuneatum* Boyarina, 1994. Some other callipterid species have only been named informally, but they have neither been described nor illustrated.

The aim of the present paper is to provide descriptions for eight callipterid species from the locality Luganskoye and to give a review of the main morphological characters of callipterid pteridosperms. Based on a revision of the type material of the previously established genera and species and a careful analysis of a series of the differently shaped pinnule remains illustrating heteroblastic development of these callipterids, revised diagnoses of some taxa are provided. The palaeoecology of callipterids is discussed, based on taphonomic and sedimentological data.

Institutional abbreviation.—SNM PMC, Scientific Natural Museum of National Academy of Sciences of Ukraine, Palaeontological Museum Collection, Kiev, Ukraine.

Geological setting

Callipterids were collected from six plant-bearing strata that are exposed in the gully situated on the west bank of the Lugan River Reservoir opposite Luganskoye village (Fig. 1). The section in the gully reaches a thickness of 50 m and represents the middle part of the Araukaritovaya suite in the interval between the limestones P_5^0 and P_6. This suite represents a part of the Moscovian-Gzhelian paralic succession and consists predominantly of lithological units interpreted as fluvial, lagoonal, bay, marine and peat-swamp deposits (Zhykaljak 1984). The plant-bearing strata (Fig. 2) occuring at Luganskoye are listed below.

Plant-bearing strata no. 1.—The strata with seven plant-bearing beds are exposed in the mouth part of the gully. The lowermost bed, consisting of claystone being up to 24 cm

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Fig. 1. Location of the outcrop at Luganskoye (starlet) in the Donets Basin.

thick, yielded a rich plant assemblage. The following taxa have been identified from this bed: *Autunia conferta* (Sternberg, 1826) Kerp, 1988, *A. naumannii* (Gutbier, 1849) Kerp, 1988, *Lodevia nicklesii* (Zeiller, 1898) Haubold and Kerp, 1988, *L. luganica* (Boyarina and Stschegolev, 1989) Boyarina, 1994. A few small fragments of the *Autunia naumannii* foliage together with the pelecypods were collected in the 7 cm thick siltstones. A single specimen of *Dicranophyllum* sp. was found in a 5 cm thick siltstone bed. The rare plant remains and seeds from four overlying beds belong to *Odontopteris subcrenulata* (Rost, 1839) Zeiller, 1888, *Neuropteris* sp., *Samaropsis bachmutiensis* Boyarina, 2004.

Plant-bearing strata no. 2.—The strata with a thickness of 35 cm are situated in the lower part of the gully and consist of an alternation of claystone and siltstone. The plant assemblages from the siltstone beds include: *Lodevia suberosa* (Sterzel, 1918) Haubold and Kerp, 1988, *Neuropteris* cf. *planchardii* Zeiller, 1888, *Neurodontopteris auriculata* (Brongniart, 1830) Potonié, 1893, *Calamites suckowii* Brongniart, 1888, *Cordaites* sp., *Walchia* sp., *Samarospermum moravicum* (Helmhacker, 1871) Arber, 1914, *Samaropsis bachmutiensis*, and *S. spinifera* Boyarina, 2004.

Plant-bearing strata no. 3.—This claystone bed with a thickness of 45 cm yielded abundant plant fossils. The flora consists almost exclusively of the callipterids *Raminervia mariopteroides* Boyarina, 1994 as well as rare occurrences of *Pecopteris bredovii* Germar, 1845, *Sphenopteris fayolii* Zeiller, 1888 and *Asterophyllites equisetiformis* (Sternberg, 1825) Brongniart, 1828. The common plant remains from the 25 cm thick siltstone interval with thin claystone intercalations are assigned to the following taxa: *Autunia conferta*, *A. naumannii*, *Lodevia nicklesii*, *L. luganica*, *L. suberosa*, *Dichophyllum cuneatum* Boyarina, 1994, *Odontopteris subcrenulata*, *Neuropteris planchardii*, *Sphenophyllum* cf. *angustifolium* (Germar, 1845) Göppert, 1848.

Plant-bearing strata no. 4.—The strata reaching 45 cm in thickness consist of alternating clay-, silt-, and fine-grained sandstones. The plant remains found in the siltstones and the sandstones are frequently fragmented. The recognisable plant fossils were collected in the claystone beds, e.g., *Autunia naumannii* (foliage, small fragments of ovuliferous organs and many ovules), *Lodevia luganica*, *Neurodontopteris* cf. *auriculata*, *Samarospermum moravicum*.

Plant-bearing strata no. 5.—Two plant-bearing beds contain plant material and pelecypods. The bed with a thickness of 25 cm, consisting of an alternation of siltstone and fine-grained sandstone beds, yielded a rich plant assemblage comprising the following elements: *Autunia naumannii* (foliage, ovuliferous organs and ovules), *Alethopteris rubescens* (Sternberg, 1825) Němejc, 1929, *Odontopteris osmundaeformis* (Schlotheim, 1820) Zeiller, 1879, *Walchia* cf. *frondosa* Renault, 1885, *Samaropsis spinifera, Trigonocarpus* sp. Among the rare plant remains from the overlying 20 cm thick siltstones, some taxa were recognised, e.g., *Autunia naumannii* (foliage), *Neurodontopteris* cf. *auriculata, Calamites* sp., *Cordaites* sp., *Samaropsis* sp.

Plant-bearing strata no. 6.—These strata are exposed in the uppermost part of the gully. In this outcrop, rich assemblages of the plant remains were collected from three plant-bearing beds. The 15 cm thick sandstone bed yielded plant material belonging to *Autunia naumannii* (foliage, ovuliferous organs, polliniferous organs), *Lodevia nicklesii*, *L.* cf. *luganica*, *Samaropsis* sp. However, the richest plant assemblage was found in the siltstone bed that is 30 cm thick. The following taxa have been identified from this bed: *Autunia naumannii* (foliage, many fragments of ovuliferous and polliniferous organs, ovules), *Lodevia nicklesii*, *L. luganica*, *L. suberosa*, *Dichophyllum cuneatum*, *D. flabelliferum* (Weiss, 1879) Kerp and Haubold, 1988, *Odontopteris osmundaeformis*, *O. subcrenulata*, *Cordaites* sp., *Walchia* cf. *whitei* Florin, 1939, *Samaropsis spinifera*, *Samarospermum moravicum*. Among the plant fossils from the 15 cm thick claystone bed are *Autunia conferta* and *Lodevia nicklesii*.

Material and methods

The collection of studied callipterids includes more than 340 specimens. The plant remains are mainly preserved as compressions and impressions. The compressions are very thin and difficult to macerate. The specimens have been studied with a binocular dissecting microscope MBS-9.

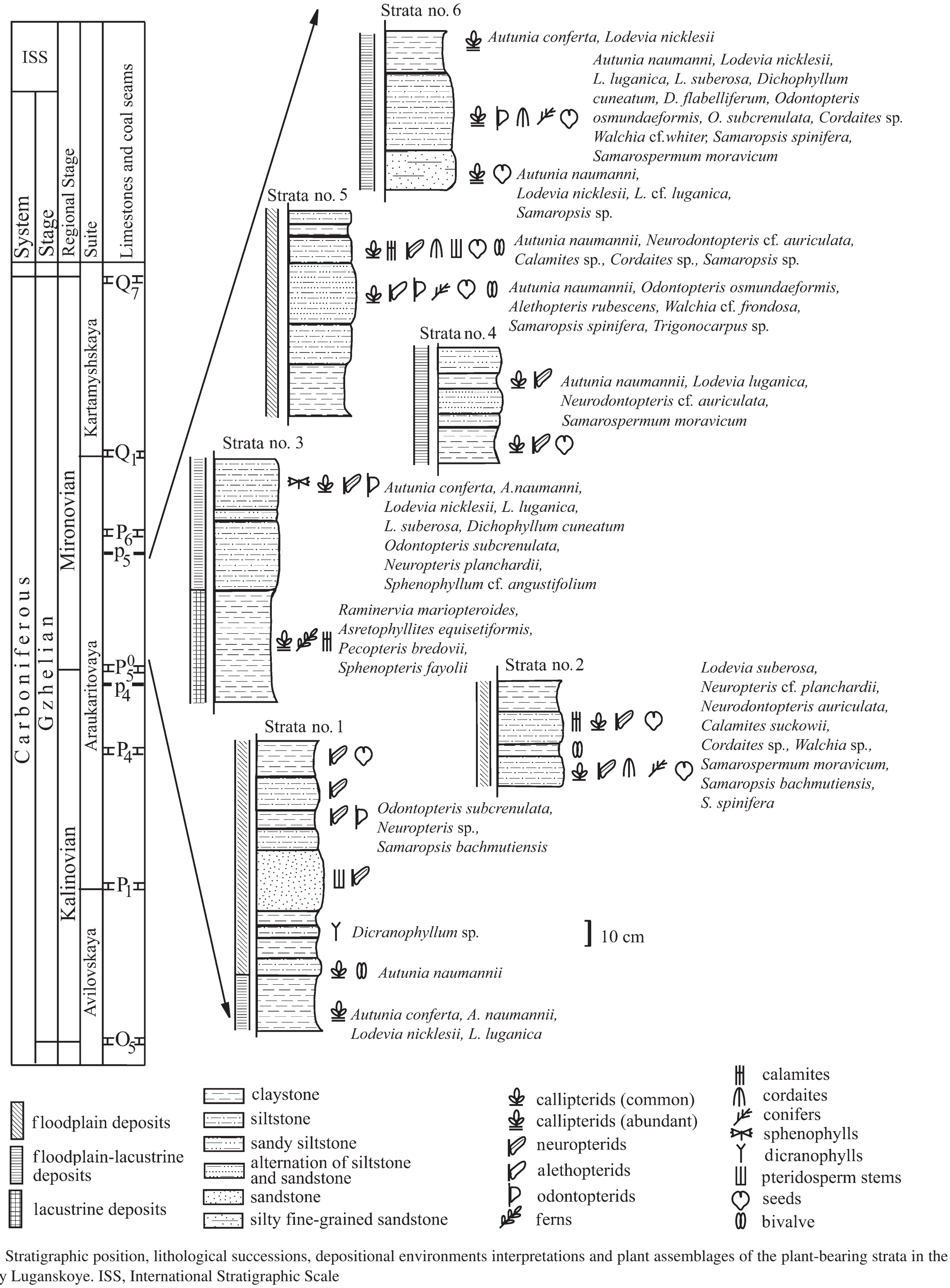

Fig. 2. Stratigraphic position, lithological successions, depositional environments interpretations and plant assemblages of the plant-bearing strata in the locality Luganskoye. ISS, International Stratigraphic Scale

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Systematic palaeontology

Class Pteridospermopsida Oliver and Scott, 1904

Order Peltaspermales Taylor, 1981

Family Peltaspermaceae Thomas, 1933

Genus *Autunia* (Krasser, 1919) Kerp, 1988

Type species: *Autunia conferta* (Sternberg, 1826) Kerp, 1988. Lower Permian, Bohemian Massif, Czech Republic.

Autunia conferta (Sternberg, 1826) Kerp, 1988

Fig. 3A–F, H, J.

1826 *Neuropteris conferta* sp. nov.; Sternberg 1826, I, 4: 17.
1833 *Neuropteris conferta* Sternberg, 1826; Sternberg 1833, II, 5–6: 75, pl. 22: 5.
1849 *Callipteris conferta* (Sternberg, 1826); Brongniart 1849: 73.
1907 *Callipteris conferta* (Sternberg, 1826) Brongniart, 1849; Gothan 1907a: 1–18, text-figs. 1–6.
1988 *Autunia conferta* (Sternberg, 1826); Kerp 1988: 258–305, pl. 1–25.

Material.—Three fragments of the upper parts of the frond—SNM PMC 2216/66, SNM PMC 2216/2, SNM PMC 2216/81; two fragments of the middle frond parts—SNM PMC 2216/23 and SNM PMC 2216/80; one basal portion of a frond—SNM PMC 2216/77; one fragment of an immature frond—SNM PMC 2216/79; one fragment of a pinna—SNM PMC 2216/78.

Description.—The fragments of the fronds are bipinnate (Fig. 3A, C, F). The apical part of the fronds shows the overtopping of the primary rachis (Fig. 3C, F). The pinnules are ovate and decurrent. They vary in a length from 4 to 10 mm. The lateral margins of the pinnules vary from straight to slightly lobed. The small pinna, likely of an immature frond, has very small pinnules folded by halves along the midvein (Fig. 3E). The midvein is strong, decurrent and running to 3/4 of the pinnule length. The lateral veins are slightly pronounced, single or once bifurcated. The intercalary pinnules, up to 4–6 mm long and 2–3 mm wide.

Stratigraphic and geographic range.—Upper Stephanian (Upper Carboniferous) and Autunian (Lower Permian) of Europe.

Autunia naumannii (Gutbier, 1849) Kerp, 1988

Figs. 3G, I, K, 4.

1849 *Sphenopteris naumannii* sp. nov.; Gutbier 1849: 11, pl. 7:1, 4, 6.
1881 *Callipteris naumannii* (Gutbier, 1849); Sterzel 1881: 255–257.
1988 *Autunia naumannii* (Gutbier, 1849); Kerp 1988: 305–308, pl. 26, 27.

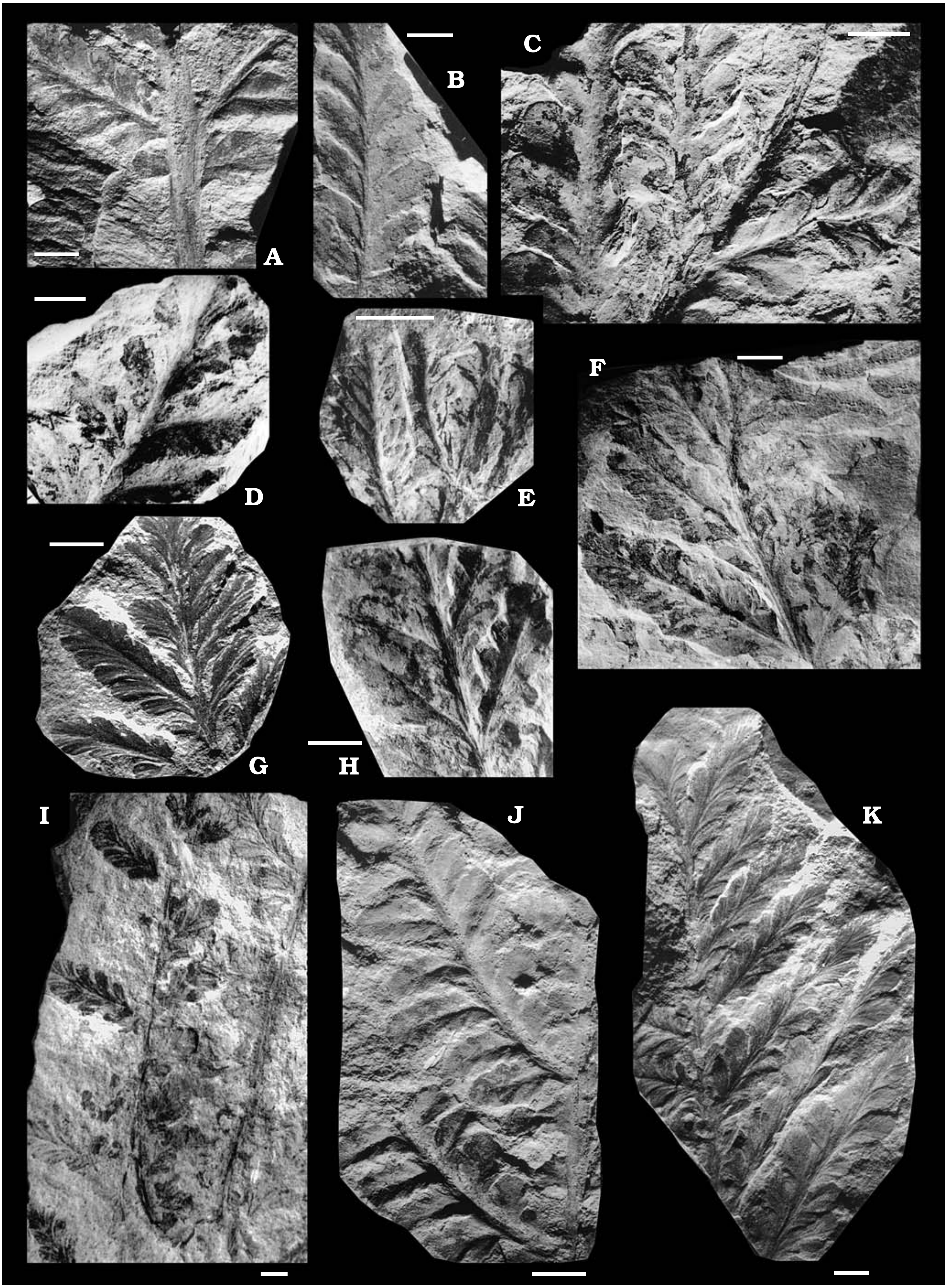
Material.—Four fragments of the upper frond parts—SNM PMC 2216/67, SNM PMC 2216/42, SNM PMC 2216/25, SNM PMC 2216/28; one fragment of the middle frond part—SNM PMC 2216/58; three apical portions of fronds—SNM PMC 2216/24, SNM PMC 2216/43, and SNM PMC 2216/41 in association with the isolated seed; 26 isolated pinnae, including a pinna in association with an isolated megasporophyll—SNM PMC 2216/82. Five fragments of ovuliferous organs and many isolated megasporophylls, polliniferous organs and seeds. The most informative: ovuliferous organs—SNM PMC 2216/68, SNM PMC 2216/69, SNM PMC 2216/71; isolated megasporophylls and seeds—SNM PMC 2216/83, SNM PMC 2216/64; and an isolated polliniferous organ—SNM PMC 2216/72.

Description.—The frond fragments are bipinnate (Figs. 3K, 4A, C, L). The upper parts of the fronds show a single (Figs. 3G, K, 4A, E, H) or double overtopping of the primary rachis (Fig. 4L); as result of the latter, the frond apically has the slightly zigzag-shaped primary rachis. Pinnules are ovate to prolonged and decurrent basiscopically. They are 6 to 12 mm long and 3 to 6 mm wide. The lateral pinnule margins vary from crenulate and lobed to dissected. The midvein is thin, running to the middle of the pinnule. The dissected pinnules have three-seven segments and the pronounced midvein runs to the base of the apical segment. The lateral veins bifurcate in the apical part of each segment. Pinnule segments are wedge-shaped and slightly arcuate. Segments with a pronounced vein show an emarginate apex (Fig. 3I).

Two frond fragments have prolonged pinnules in the apical portion above the overtopping of the primary rachis (Figs. 3G, 4C). These prolonged pinnules with the crenulate margins, a thick midvein and closely spaced, bifurcated lateral veins show the "polymorpha"-aspect, whereas the ultimate order pinnae bear pinnules more typical for *Autunia naumannii* (Fig. 4C).

In association with the *Autunia naumannii* foliage, ovuliferous organs, isolated megasporophylls and seeds were found. The ovuliferous organs are attached to the rachis reaching a width of 10 mm (Fig. 4B). The ovuliferous organs have axes up to 2–4 mm wide and bear the closely spaced megasporophylls (Fig. 4D, H). The megasporophylls are bilaterally symmetrical, broadly flabelliform, 7–9 mm wide, with strong, radiating ribs. The anterior margins of the mega-

Fig. 3. Callipterid pteridosperms *Autunia* (Krasser, 1919) Kerp, 1988 from late Gzhelian (Late Carboniferous) of Luganskoye, Ukraine. **A**–**F**, **H**, **J**. *Autunia conferta* (Sternberg, 1833) Kerp, 1988. **A**–**D**, **F**, **J**. Plant-bearing strata no. 6. **A**. Basal portion of a frond with small closely spaced pinnules, SNM PMC 2216/77. **B**. Fragment of a pinna with entire-margined pinnules, SNM PMC 2216/78. **C**. Fragment of a frond showing the overtopping of the primary rachis, figured by Boyarina and Stschegolev (1989: fig.1a, b), SNM PMC 2216/2. **D**. Apical portion of a frond with lobed and pinnatifid pinnules, SNM PMC 2216/66. **F**. Fragment of a frond with small closely spaced pinnules showing the overtopping of the primary rachis in the apical part, SNM PMC 2216/81. **J**. Fragment of a frond with prolonged pinnules, SNM PMC 2216/23. **E**. Plant-bearing strata no. 1, fragment of an immature frond showing the very small pinnules folded along the midvein, SNM PMC 2216/79. **H**. Plant-bearing strata no. 3, middle portion of a small frond with entire-margined pinnules, SNM PMC 2216/80. **G**, **I**, **K**. *Autunia naumannii* (Gutbier, 1849) Kerp, 1988. **G**. Plant-bearing strata no. 6, apical portion of a frond showing the overtopping of the primary rachis in combination with prolonged and pinnatifid pinnules ("polymorpha"-aspect), SNM PMC 2216/24. **I**. Plant-bearing strata no. 5, pinnae with pinnatifid pinnules, SNM PMC 2216/52. **K**. Plant-bearing strata no. 2, upper portion of a frond with lobed pinnules in combination with the overtopping of the primary rachis, SNM PMC 2216/67. Scale bars 5 mm. →



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sporophylls are crenulate to slightly lobed. One or two ovules are sometimes attached to the megasporophylls (Fig. 4F). The seeds are small, up to 4–5 mm long and 3–3.5 mm wide, ovoid, flattened (Fig. 4G, I).

Isolated polliniferous organs are small and consist of the basally fused and apically free sporangia (Fig. 4J). The sporangia are elongated elliptic, 5–6 mm long.

Stratigraphic and geographic range.—Upper Stephanian (Upper Carboniferous) and Autunian (Lower Permian) of Europe.

Genera supposed to be assigned to Peltaspermales Taylor, 1981

Genus *Dichophyllum* Elias ex Andrews, 1941

Type species: *Dichophyllum moorei* Elias ex Andrews, 1941. Upper Pennsylvanian, Kansas, USA.

Dichophyllum cuneatum Boyarina, 1994

Fig. 5A, D–J.

1960 *Callipteris* aff. *zbyšoviensis* Augusta var. *microphylla*; Stschegolev 1960: 51–52, pl. 2.
1994 *Dichophyllum* "*cuneata*" sp. nov.; Boyarina 1994: 127–130, text-fig. 8, 9.

Material.—Single fragment of the middle frond part—SNM PMC 2216/60; four fragments of penultimate order pinnae—SNM PMC 2216/11, SNM PMC 2216/15, SNM PMC 2216/37, SNM PMC 2216/51; three fragments of ultimate order pinnae—SNM PMC 2216/14, SNM PMC 2216/65, SNM PMC 2216/38.

Brief characterisation.—Frond bipartite in the upper part, and bipinnate. Primary rachis bifurcating and bearing pinnate pinnae below the bifurcation. Primary rachis weakly ribbed, longitudinally striated. Pinnules wedge-shaped to broadly flabelliform with three-five wedge-shaped segments. Midvein bifurcating near the pinnule base. Each segment with a single lateral vein bifurcating 1–2 times. Intercalary pinnules resembling the other pinnules; attached to the rachis between the pinnae.

Description.—The angle of bifurcation is 35° (Fig. 5F). The penultimate order pinnae above the bifurcation have larger and stronger developed ultimate order pinnae on the external than on internal side (Fig. 5A, F). The pinnules show a wide variation in size—being 2–22 mm long and 0.7–20 mm wide and vary from entire-margined (Fig. 5F) to dissected into three-five segments (Fig. 5A, F–J, Table 1). The pinnules have a pronounced midvein bifurcating near the pinnule base and a pronounced lateral vein in each segment.

Stratigraphic and geographic range.—Upper Gzhelian (Upper Carboniferous) of Ukraine.

Dichophyllum flabelliferum (Weiss, 1879) Kerp and Haubold, 1988

Fig. 5B.

1879 *Schizopteris flabellifera* sp. nov.; Weiss 1879: 19, pl. 2: 1.
1879 *Schizopteris hymenophylloïdes* sp. nov.; Weiss 1879: 22, pl. 2: 2, 3.
1988 *Dichophyllum* "*flabellifera*" (Weiss, 1879); Kerp and Haubold, 1988: 147.

Material.—Single small fragment of a pinna—SNM PMC 2216/30.

Description.—The pinna fragment, up to 2 cm long, bear two pinnules. The pinnules reaching 18–25 mm in length are flabelliform and dissected into seven widely spaced segments. The segments are long, lineal, and narrow. The midvein is thin. Each segment has a single lateral vein.

Stratigraphic and geographic range.—Upper Stephanian (Upper Carboniferous) and Autunian (Lower Permian) of Europe and lower Permian of USA.

Genus *Lodevia* Haubold and Kerp, 1988

Type species: *Lodevia nicklesii* (Zeiller, 1898), Haubold and Kerp, 1988. Lower Permian, Lodève, France.

Lodevia luganica (Boyarina and Stschegolev, 1989) Boyarina, 1994

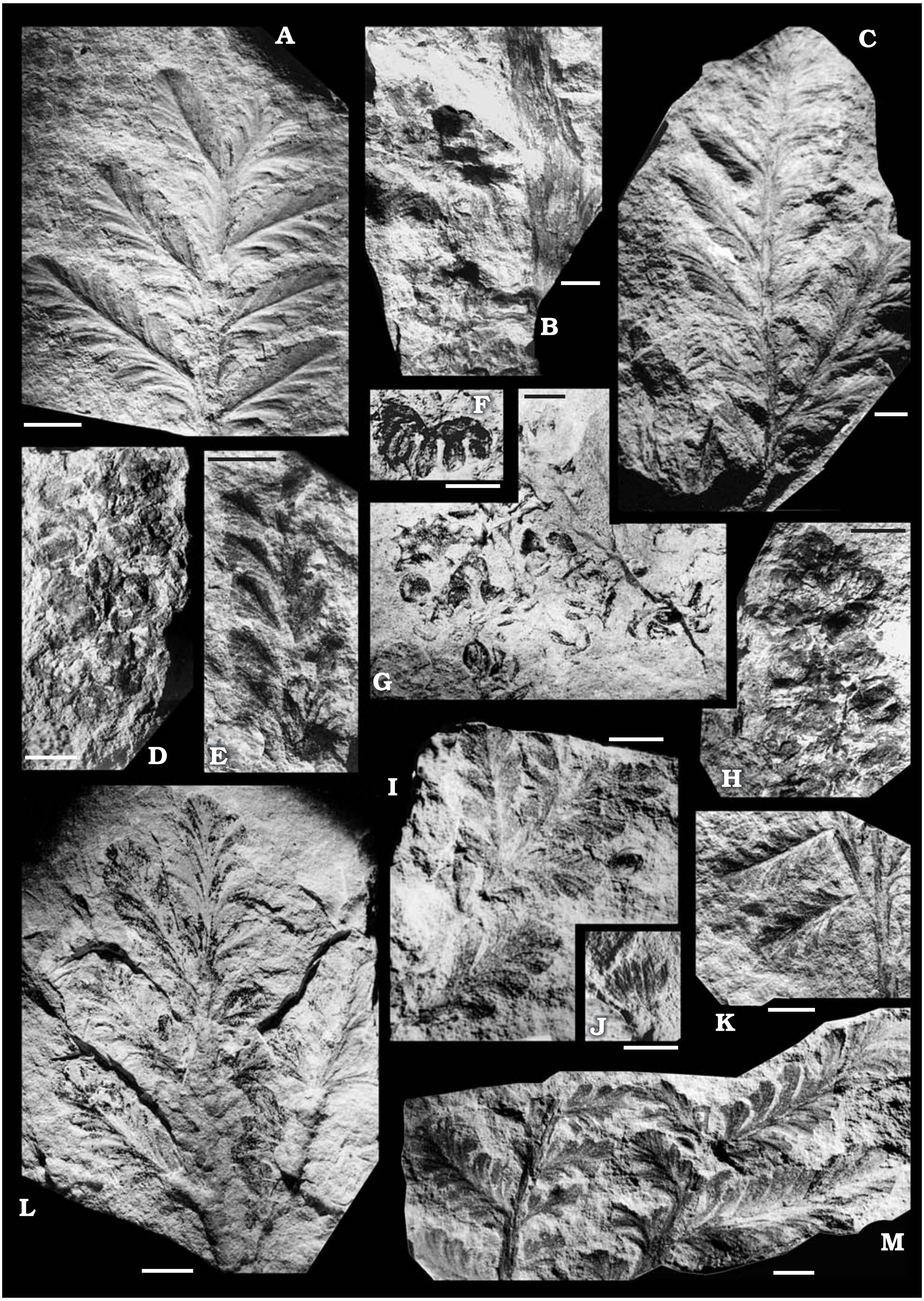
Fig. 5C.

1989 *Callipteris luganica* sp. nov.; Boyarina and Stschegolev 1989: 101–104, pl. 2: a, b; text-fig. 2.
1994 *Lodevia luganica* (Boyarina and Stschegolev, 1989); Boyarina 1994: 127.

Material.—Single fragment of the upper frond part—SNM PMC 2216/1; three pinnae fragments—SNM PMC 2216/122, SNM PMC 2216/123, and SNM PMC 2216/124.

Emended diagnosis.—Frond bipartite in the upper part, and bipinnate. Primary rachis bifurcating. Penultimate order axes longitudinally striated, finely tuberculate; overtopping. Pinnules palmate, ovate to oblong, decurrent. Pinnule margins crenulated, lobed to dissected into seven-nine seg-

Fig. 4. Callipterid pteridosperm *Autunia naumannii* (Gutbier, 1849) Kerp, 1988 from late Gzhelian (Late Carboniferous) of Luganskoye, Ukraine. → **A**, **L**. Plant-bearing strata no. 1. **B**–**D**, **H**–**K**, **M**. Plant-bearing strata no. 6. **E**–**G**. Plant-bearing strata no. 5. **A**. Apical portion of a frond showing the overtopping of the primary rachis, SNM PMC 2216/43. **B**. Portion of a rachis with two basal parts of the ovuliferous organs, SNM PMC 2216/68. **C**. Upper portion of a frond showing the overtopping of the primary rachis in combination with prolonged and pinnatifid pinnules ("polymorpha"-aspect), SNM PMC 2216/25. **D**. Ovuliferous organ with closely spaced megasporophylls and attached ovules, SNM PMC 2216/71. **E**. Pinna in association with an isolated megasporophyll, SNM PMC 2216/82. **F**. Longitudinal section of a megasporophyll with two attached ovules, SNM PMC 2216/64. **G**. Isolated megasporophylls and seeds, SNM PMC 2216/83. **H**. Ovuliferous organ with closely spaced megasporophylls and attached ovules, SNM PMC 2216/69. **I**. Apical portion of a frond showing the overtopping of the primary rachis in association with an isolated seed, SNM PMC 2216/41. **J**. Isolated polliniferous organ, SNM PMC 2216/72. **K**. Fragment of a small frond with pinnatifid pinnules, SNM PMC 2216/58. **L**. Upper part of a frond showing the repeated overtopping of the primary rachis, SNM PMC 2216/42. **M**. Fragment of a frond most likely above the overtopping of the primary rachis showing stronger developed exterior pinnatifid pinnules than interior one, SNM PMC 2216/28. Scale bars 5 mm.



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ments. Lobes or segments obovate, narrow, more or less arcuate. Venation pronounced. Midvein thick, terminating in the apical lobe or segment. Lateral veins making an acute angle to midvein, single or once bifurcating. Intercalated pinnules resembling the other pinnules; attached to the rachis between the pinnae.

Description.—The angle of the bifurcation is about 40°. The penultimate order axes up to 2 mm wide. One completely preserved pinna of the penultimate order shows the overtopping of the axis and bears the stronger developed ultimate order pinnae on the external than on internal side. Pinnules vary in length from 8 to 24 mm. The pinnules, up to 8–10 mm long and 2–3 mm wide, are entire-margined to crenulated or lobed, strongly decurrent. The midvein is not very pronounced and bifurcates in the middle of the pinnule. The pinnules with a length of 12–24 mm and a width of 6–9 mm are dissected into seven-nine segments.

Stratigraphic and geographic range.—Upper Gzhelian (Upper Carboniferous) of Ukraine.

Lodevia nicklesii (Zeiller, 1898), Haubold and Kerp, 1988

Figs. 6, 7A, B, E.

1898 *Callipteris "nikclesi"* sp. nov.; Zeiller 1898: 46, pl. 4: 2–4.
1988 *Lodevia nicklesii* (Zeiller, 1898); Kerp and Haubold 1988: 146, 147.

Material.—A portion of the upper part of the frond—SNM PMC 2216/46; a portion of the middle part of the frond—SNM PMC 2216/63; four fragments of penultimate order pinnae—SNM PMC 2216/34, SNM PMC 2216/44, SNM PMC 2216/48 and SNM PMC 2216/61 in association with an isolated seed; 32 fragments of ultimate order pinnae, figured are SNM PMC 2216/40, SNM PMC 2216/44, SNM PMC 2216/50, SNM PMC 2216/53 SNM PMC 2216/73.

Description.—The frond fragments show the bifurcation of the primary rachis and the two-parted blade (Fig. 6B, G). The primary rachis is weakly ribbed and longitudinally striated, up to 4 mm wide (Fig. 6G), and bears pinnae with entire-margined to slightly lobed pinnules below the bifurcation and ends in two penultimate order axes being 2.5 mm wide. The penultimate order pinnae bear stronger developed ultimate order pinnae on the external than on internal side (Fig. 6B, C, D) and show the overtopping of the axis (Fig. 6C, E). Pinnules are ovate to oblong, decurrent. They vary in length from 10 mm to 24 mm and display increasing segmentation relatively to increasing of their size, viz., the pinnules, up to 10–13 mm long, are lobed and attached to the axes, up to 1.5 mm wide (Figs. 6A–H, 7B); the pinnules, up to 14–24 mm, are incised into seven to nine segments and attached to the axes with a width of 2.5–3 mm (Figs. 6H, 7A, E). The segments are wedge-shaped, obtuse or with a crenulate apex. The midvein is more or less pronounced, decurrent, usually running to 1/2 pinnule length. The lateral veins are thin, usually bifurcating up to 1–2 times near the midvein. The seed found in association with the foliage is flattened, small, 5 mm long and 3.5 wide, oval (Fig. 6G).

Stratigraphic and geographic range.—Upper Stephanian (Upper Carboniferous) and Autunian (Lower Permian) of Europe.

Lodevia suberosa (Sterzel, 1918) Haubold and Kerp, 1988

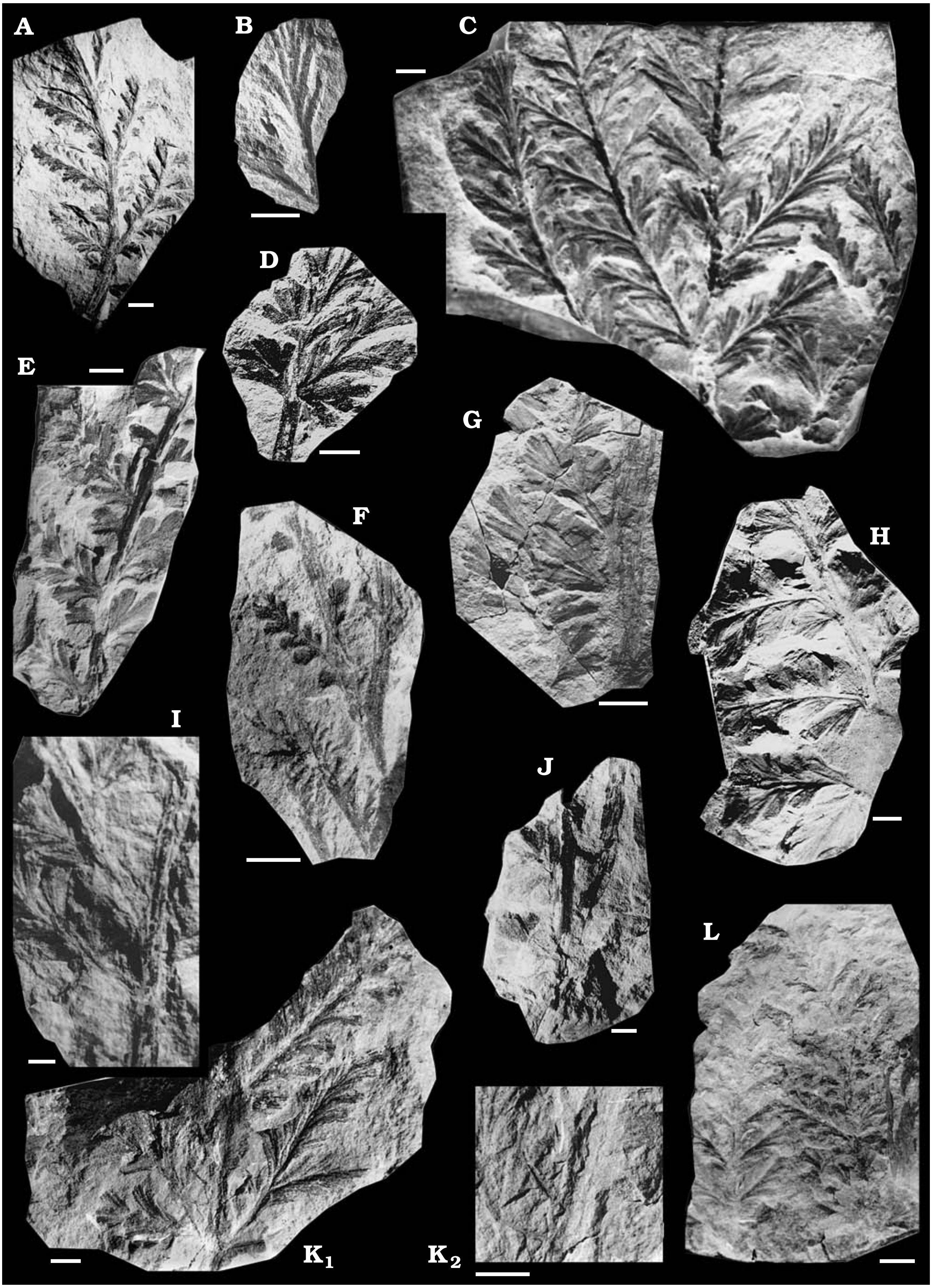
Fig. 5K, L.

1849 *Sphenopteris erosa* sp. nov.; Gutbier 1849: pl. 8: 8.
1918 *Callipteris naumannii* (Gutbier, 1849) forma *suberosa*; Sterzel 1918: 288.
1988 *Lodevia suberosa* (Sterzel, 1918); Kerp and Haubold 1988:146.

Material.—One fragment of a penultimate order pinna—SNM PMC 2216/54, and two fragments of ultimate order pinnae—SNM PMC 2216/55, SNM PMC 2216/125.

Description.—The axis of the penultimate order is 3 mm wide and longitudinally striated, bears the ultimate order pinnae, up to 4 cm long on one side and to 2–3 cm in other side (Fig. $5K_1$). The axes bear spines. One spine is attached to the axis of penultimate order, between the ultimate order pinnae. The other spine is inserted on the axis of the ultimate order, between the pinnules. The spines with the thickened base reach 7–8 mm in length (Fig. $5R_2$). The pinnules having a length of 9–12 mm and a width of 3–5 mm are ovate, slightly or not deccurent, incised or dissected into five to seven segments. The segments are lineal, narrow and straight. The midvein is pronounced and runs to the middle of the pinnule. Each segment has a pronounced straight lateral vein.

Fig. 5. Callipterid pteridosperms of morphogenera *Dichophyllum* Elias ex Andrews, 1941 and *Lodevia* Haubold and Kerp, 1988 from late Gzhelian (Late Carboniferous) of Luganskoye, Ukraine. **A**, **D**, **F**, **H**–**J**. Plant-bearing strata no. 6. **A**, **D**–**J**. *Dichophyllum cuneatum* Boyarina, 1994. **A**. Asymmetrically developed pinna of the penultimate order with lobed to incised pinnules, figured by Boyarina (1994: fig. 8A), holotype SNM PMC 2216/11, natural size. **B**. *Dichophyllum flabelliferum* (Weiss, 1879) Kerp and Haubold, 1988. Plant-bearing strata no. 6, small fragment a pinna, SNM PMC 2216/30. **C**. *Lodevia luganica* (Boyarina and Stschegolev, 1989) Boyarina, 1994. Plant-bearing strata no. 6, fragment of a frond above a bifurcation of the primary rachis showing the overtopping of the penultimate order axis in combination with lobed to dissected pinnules, figured by Boyarina and Stschegolev (1989: fig. 2a, b), holotype SNM PMC 2216/1. **D**. Fragment of a pinna with dissected pinnules, figured by Boyarina (1994: fig. 9B), SNM PMC 2216/14. **E**. Plant-bearing strata no. 3. , fragment of a penultimate order pinna with lobed to incised pinnules, SNM PMC 2216/51. **F**. Middle portion of a frond with a bifurcation of the primary rachis showing the pinnate pinna below the bifurcation, SNM PMC 2216/60. **G**. Plant-bearing strata no. 3., fragment of a pinna with dissected pinnules, SNM PMC 2216/38. **H**. Fragment of a penultimate order pinna with incised pinnules, SNM PMC 2216/37. **I**. Fragment of a penultimate order pinna with dissected pinnules, figured by Boyarina (1994: fig. 9C), SNM PMC 2216/15. **J**. Fragment of a penultimate order pinna with dissected pinnules, SNM PMC 2216/65. **K**, **L**. *Lodevia suberosa* (Sterzel, 1918) Haubold and Kerp, 1988. **K**. Plant-bearing strata no. 6, SNM PMC 2216/54. K_1. Fragment of penultimate order pinna with dissected pinnules and spines on the axes. K_2. Detail, showing a spine on the primary rachis. **L**. Plant-bearing strata no. 3, pinnae with dissected pinnules, SNM PMC 2216/55. Scale bars 5 mm. →



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Stratigraphic and geographic range.—Rotliegend (Upper Carboniferous–Lower Permian) of Germany and upper Gzhelian (Upper Carboniferous) of Ukraine.

Genus *Raminervia* Boyarina, 1994 emend. nov.

Type species: *Raminervia mariopteroides* Boyarina, 1994. Upper Gzhelian, Donets Basin, Ukraine.

Emended diagnosis.—Frond bipartite with bifurcated primary rachis in the upper part, bipinnate, with intercalary laminate elements between pinnae. Penultimate order axes in the apical part terminating in a pseudodichotomy. Pinnules wedge-shaped, round-lobed with a contracted base. Midvein pronounced to the middle of the pinnule.

Remarks.—The genus *Raminervia* Boyarina, 1994 with a single species *Raminervia mariopteroides*, was originally established as the natural genus to include the callipterid foliage and the fertile pinnules with the seed scars (Boyarina 1994). Previously the rings on the pinnules (Fig. $8G_2$) were interpreted as the seed scars on the fertile pinnules, but now they are considered to be traces of insect activity as suggested by Hans Kerp (written communication 2009). Therefore, the genus *Raminervia* is now reinterpreted as a morphogenus.

Raminervia mariopteroides Boyarina, 1994

Figs. 7C, D, F–H, 8.

1994 *Raminervia mariopteroides* sp. nov.; Boyarina, 1994: 120–127, text-figs. 2–5.

Material.—Five fragments of fronds with a bifurcation of the primary rachis, figured are SNM PMC 2216/6, SNM PMC 2216/118 and SNM PMC 2216/27; 24 fragments of penultimate order pinnae, the most informative are SNM PMC 2216/4, SNM PMC 2216/32, SNM PMC 2216/35, SNM PMC 2216/36, SNM PMC 2216/39, SNM PMC 2216/47, SNM PMC 2216/49, SNM PMC 2216/74, SNM PMC 2216/76; 27 fragments of ultimate order pinnae, figured are SNM PMC 2216/5, SNM PMC 2216/10 and SNM PMC 2216/119.

Emended diagnosis.—Frond bipartite in the upper part, and bipinnate. Primary rachis bifurcating. Axes of penultimate order pinnae longitudinally striated, terminating in a pseudodichotomy. Pinnules obovate or wedge-shaped to prolonged, decurrent. Lateral pinnule margins vary from entire-margined and lobed to dissected into five to seven segments. Segments obovate to wedge-shaped, relatively broad, with obtuse or rounded apex and convex lateral margins. Midvein thin, bifurcating in the basal or middle part of the pinnule. Lateral veins thin, bifurcating 1–2 times near the midvein. Intercalary pinnules resembling the other pinnules.

Description.—The primary rachis bifurcates with an angle of 35° (Fig. 8A). The pinnae of penultimate order bear larger and stronger developed ultimate order pinnae on the external than on the internal side (Figs. 7C, G, H; 8A, D, F). The apical part of the axis of penultimate order shows the pseudodichotomy (Fig. 7F). Pinnules vary in the size, being 8–30 mm long and 5–12 mm wide. The pinnules, up to 8–12 mm long and 5 mm wide, are obovate or wedge-shaped, with crenulate lateral margins to slightly lobed (Figs. 7C, D, G, H; 8B, F). The pinnules with a length of 13–30 mm and a width of 6–15 mm are lobed to dissected into five to seven segments (Fig. $8G_1$). One of the fragments of the penultimate order pinnae shows the basal basiscopic pinnule on the ultimate order pinna being stronger developed than other pinnules as in mariopterids (Fig. 8C).

Remarks.—The foliage of *Raminervia mariopteroides* is different from other callipterids. Nevertheless, some morphological similarity is observed between the small pinnules of the *Raminervia mariopteroides* fronds and the small pinnules of *Rhachiphyllum schenkii* (Heyer, 1884) Kerp, 1988. However, because the genus *Rhachiphyllum* Kerp, 1988 has been established for forms with a monopodial frond (Kerp and Haubold 1988), the asymmetrically developed pinnae of the penultimate order of *R. mariopteroides* are easily distinguished from the symmetrical frond of *R. schenkii*. However, isolated pinnae or small fragments of the fronds with small pinnules are difficult to identify. After the revision, some specimens originally attributed to *R. schenkii* deserved re-interpretation. One specimen (Fig. 3J) has been identified as *Autunia naumannii*, the rest has been attributed to *R. mariopteroides*. Two specimens are figured in the present paper (Figs. 7G, 8D).

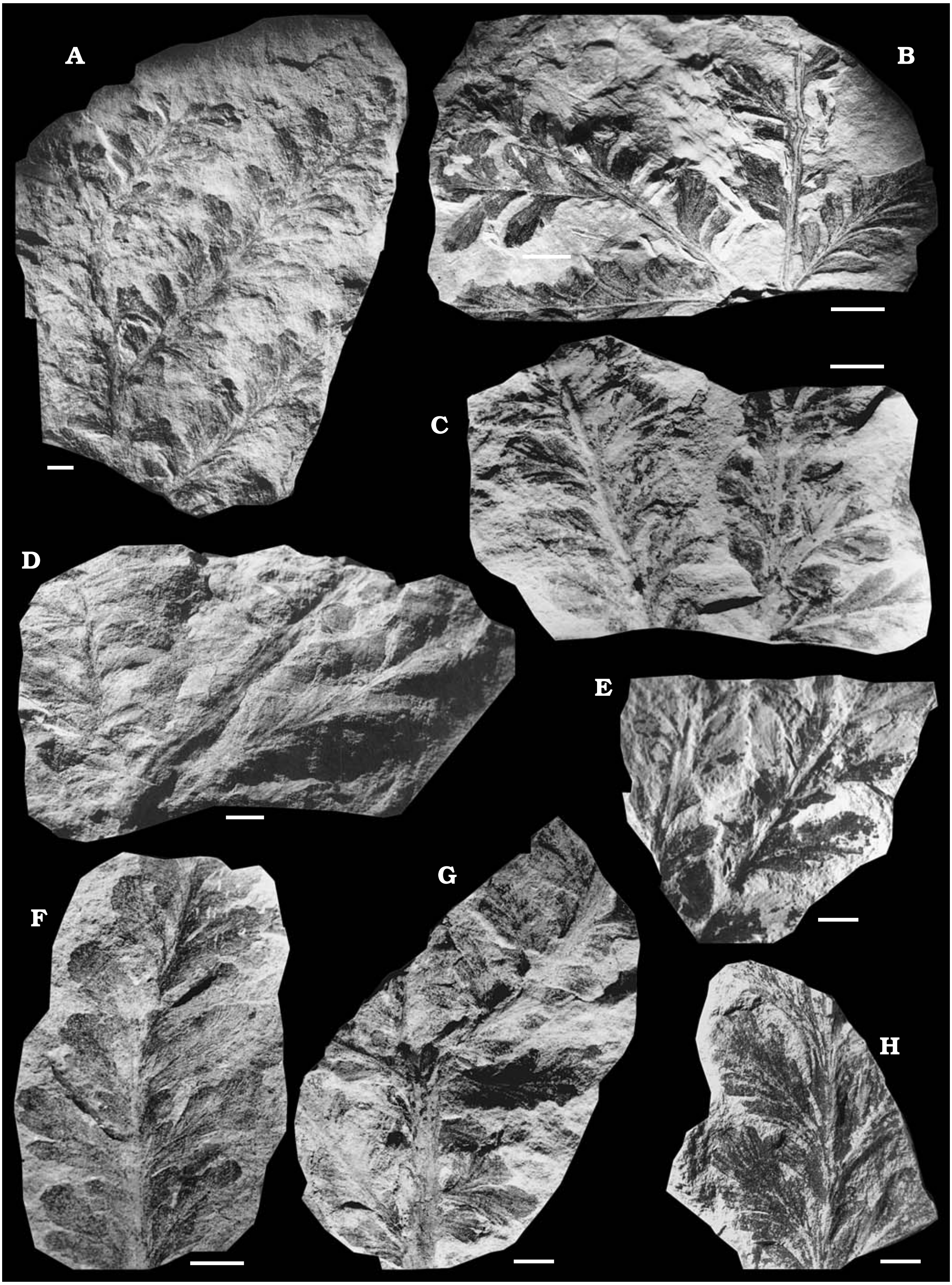
Stratigraphic and geographic range.—Upper Gzhelian (Upper Carboniferous) of Ukraine.

Morphological analysis of the frond architecture and the foliage

The results of the study of the morphology of callipterids are summarised in the Table 1. The reconstructions of the callipterid fronds presented here are based on the specimens representing the middle or upper parts of fronds.

In *Autunia conferta* fronds, the overtopping in the apical part and the terminal pseudodichotomy have been noticed by Gothan (1907a), Barthel and Haubold (1980) and indicated as diagnostic species characters by Kerp (1988). In our col-

Fig. 6. Callipterid pteridosperm *Lodevia nicklesii* (Zeiller, 1898), Haubold and Kerp, 1988 from late Gzhelian (Late Carboniferous) of Luganskoye, Ukraine. → **A**, **C**–**H**. Plant-bearing strata no. 6. **A**. Fragment of a penultimate order pinna with lobed pinnules, SNM PMC 2216/44. **B**. Plant-bearing strata no. 1, fragment of a frond showing the bifurcation of the primary rachis and lobed pinnules, SNM PMC 2216/46. **C**. Fragment of a penultimate order pinna showing the overtopping of the penultimate order axis in combination with lobed pinnules, SNM PMC 2216/48. **D**. Fragment of a penultimate order pinna in association with a seed, SNM PMC 2216/61. **E**. Fragment of a penultimate order pinna showing the overtopping of the penultimate order axis in combination with lobed pinnules, SNM PMC 2216/34. **F**. Pinna with incised pinnules, SNM PMC 2216/40. **G**. Fragment of a frond with the bifurcation of the primary rachis and pinnate pinnae below the bifurcation, SNM PMC 2216/63. **H**. Portion of a pinna with incised pinnules, SNM PMC 2216/53. Scale bars 5 mm.



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lection there are some fragments of *A. conferta* fronds with an apical overtopping of the primary rachis (Fig. 3C, F). The *Autunia naumannii* fronds show the overtopping of the primary rachis either once (Figs. 3G, 4A) or twice (Fig. 4L). It should be noticed, that fronds with small and frequently fused pinnules exhibit the overtopping of the primary rachis in combination with a terminal pseudodichotomy (Fig. 4A). The fronds with larger and loosely spaced pinnules interpreted to be of more mature fronds have the repeated overtopping (Fig. 4L).

The callipterid fronds belonging to the form-genera *Lodevia*, *Dichophyllum*, and *Raminervia* display a bipartite blade in the upper part (Figs. 5C, F, 6B, G, 7H, 8A). Their bifurcated primary rachis results in two equal parts being the penultimate order axes. The penultimate order pinnae are asymmetrically developed. They bear interior pinnae of ultimate order being reduced and less well developed in order to avoid overlapping. This general appearance of the fronds is typical for pteridosperms with a bifurcation of the primary rachis (Laveine 1997). The studied callipterids show some differences in the architecture in the upper parts of the frond above the bifurcation.

The penultimate order pinnae of *Dichophyllum cuneatum* show the gradual steps of progressive decrease in a differentiation of the ultimate order pinnae toward the frond apex, viz., the penultimate order pinnae have the normal shape of a pinnate pinna (Fig. 5A). Below the bifurcation, the primary rachis bears the pinnate pinnae (Fig. 5F; Boyarina 1994: fig. 9a). The same type of frond architecture is seen in *Dichophyllum flabelliferum* frond in Gothan (1907b: fig. 1). Therefore, the frond of callipterids of the genus *Dichophyllum* may be designated as bipartite in the upper part, and bipinnate with the pinnate pinnae below the bifurcation.

Three fragments of *Lodevia nicklessii* fronds (Fig. 6B–D) and one fragment of a *L. luganica* frond (Fig. 5C) show the overtopping of the penultimate order axes. Information about the proximal part of the frond is based on the frond fragment of *L. nicklessii* that shows the pinnate pinnae below the bifurcation (Fig. 6G). This fossil material suggests that fronds in two species of the genus *Lodevia* were bipartite in the upper part and bipinnate, with an overtopping of the penultimate order axes. The species of the genus *Lodevia* are also distinguished by the surface structure of the rachis (Table 1).

The frond and pinnae fragments of *Raminervia mariopteroides* (Figs. 7G, F, 8F) show the gradual steps of progressive decrease in a differentiation of the ultimate order pinnae toward the frond apex and the penultimate order axis terminating in a pseudodichotomy. Therefore, the *R. mariopteroides* frond is designated as bipartite in the upper part, and bipinnate with an apical pseudodichotomy of the penultimate order axes.

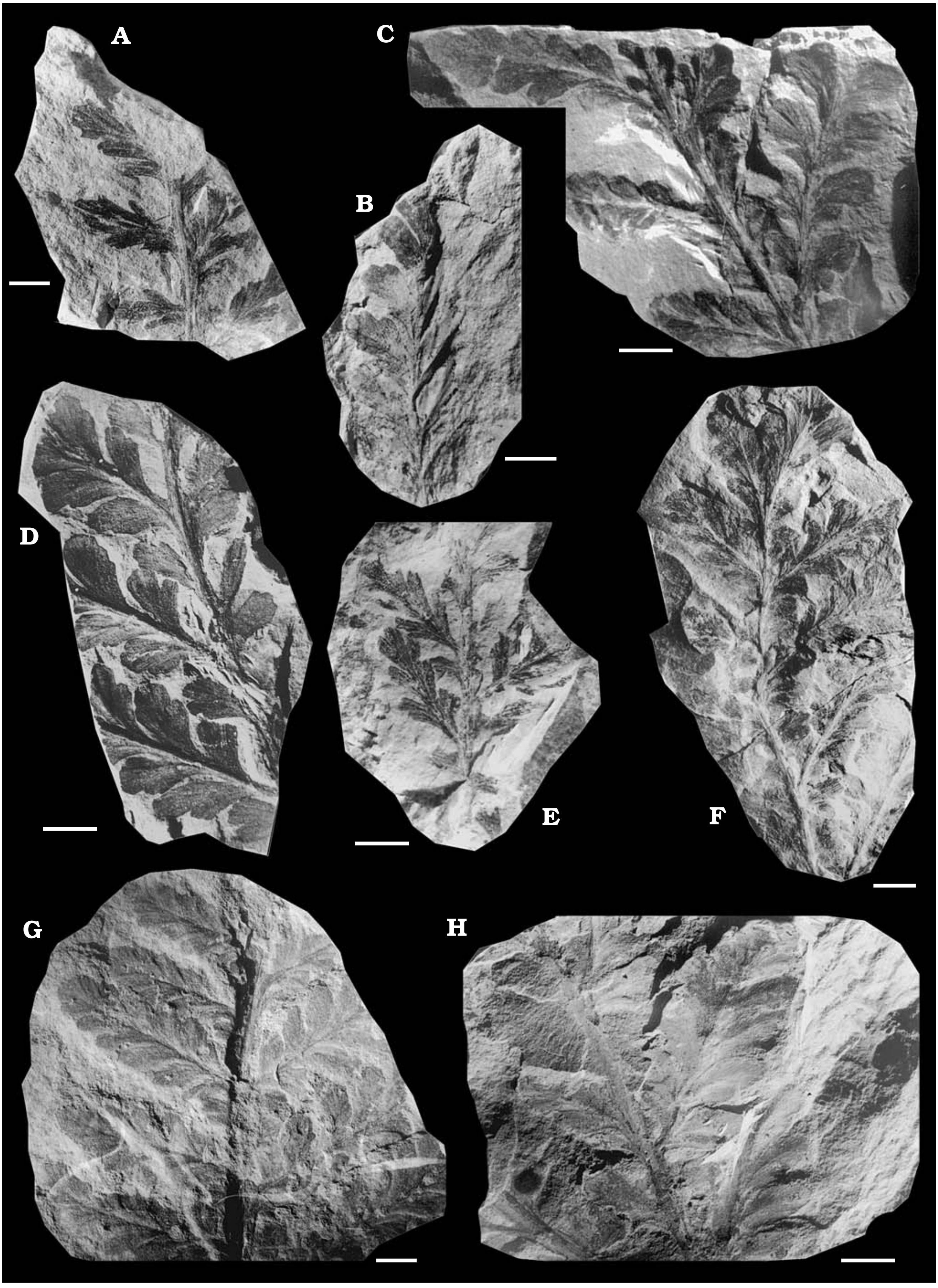
The foliage of the described callipterids demonstrates also considerable heterophylly that is an expression of the heteroblastic development already documented for some callipterids (Kerp 1988; Boyarina 1994). Heterophylly in the callipterids with the segmented lamina of the ultimate order elements is expressed in the progressively increasing segmentation of the pinnules correspondently to increasing its sizes (Table 1). The fact that the appearance of the pinnule segments, dissected in a different degree, is identical, the shape of lobes or segments is accepted as a diagnostic species character, whereas, the degree of segmentation of the pinnules and their sizes are considered to be intraspecific variability of the pinnules reflecting successive growth stages of the foliage.

Palaeoecological implications

The callipterids are, on the whole, considered as elements of the non-peat-forming mesophilous vegetation grown on sandy river banks and natural levees above the ground water level (Gothan and Gimm 1930; Barthel 1976, 1982; Remy and Remy 1977), although there are a few but extremely rich occurrences of *Autunia conferta* from peat-forming environments (Haubold 1985; Kerp 1988). Only the ecology of *Autunia conferta* has been interpreted in detail (Roselt 1980; Haubold 1985; Kerp 1988).

The fossil plants from the locality Luganskoye give additional information about the ecology of callipterids. At Luganskoye callipterid remains are found in fluvial deposits that are represented by greenish-grey clay-, silt-, and sandstone beds, occurring a few meters above the alluvial, grey fine-, and middle-grained sandstones with the cross and sinuous lamination (Zhykaljak 1984). The fluvial deposits alternate with the lagoonal strata. The latter are represented by barren siltstone and fine-grained sandstone beds. The continuous succession, consisting of alternating the fluvial and lagoonal sediments is interpreted as a sequence of a delta plain setting. Three types of depositional environments have been recognised based on the facies of these deposits and the taphonomical analysis of the plant remains reconstructing their transport history. It includes: lacustrine, floodplain-lacustrine, and floodplain settings (Fig. 2).

Fig. 7. Callipterid pteridosperms of morphogenera *Lodevia* Haubold and Kerp, 1988 and *Raminervia* Boyarina, 1994 emend. nov. from late Gzhelian (Late Carboniferous) of Luganskoye, Ukraine. **A**, **B**, **E**. *Lodevia nicklesii* (Zeiller, 1898), Haubold and Kerp, 1988. **A**, **E**. Plant-bearing strata no. 6. **C**, **D**, **F–H**. Plant-bearing strata no. 3. **A**. Portion of a pinna with incised pinnules, SNM PMC 2216/45. **B**. Plant-bearing strata no. 3, pinna with lobed pinnules, SNM PMC 2216/50. **C**, **D**, **F–H**. *Raminervia mariopteroides* Boyarina, 1994. **C**. Fragment of a pinna showing its asymmetrical development in combination with slightly lobed pinnules, SNM PMC 2216/76. **D**. Fragment of a penultimate order pinna with lobed to slightly incised pinnules, figured by Boyarina (1994: fig. 2C), holotype SNM PMC 2216/4. **E**. Pinna with dissected pinnules, SNM PMC 2216/73. **F**. Fragment of a penultimate order pinna terminating in a pseudodichotomy, SNM PMC 2216/49. **G**. Fragment of a pinna showing its asymmetrical development in combination with slightly lobed pinnules, SNM PMC 2216/35. **H**. Fragment of a frond above the bifurcation of the primary rachis showing the asymmetrical penultimate order pinna and slightly lobed pinnules, SNM PMC 2216/118. Scale bars 5 mm. →



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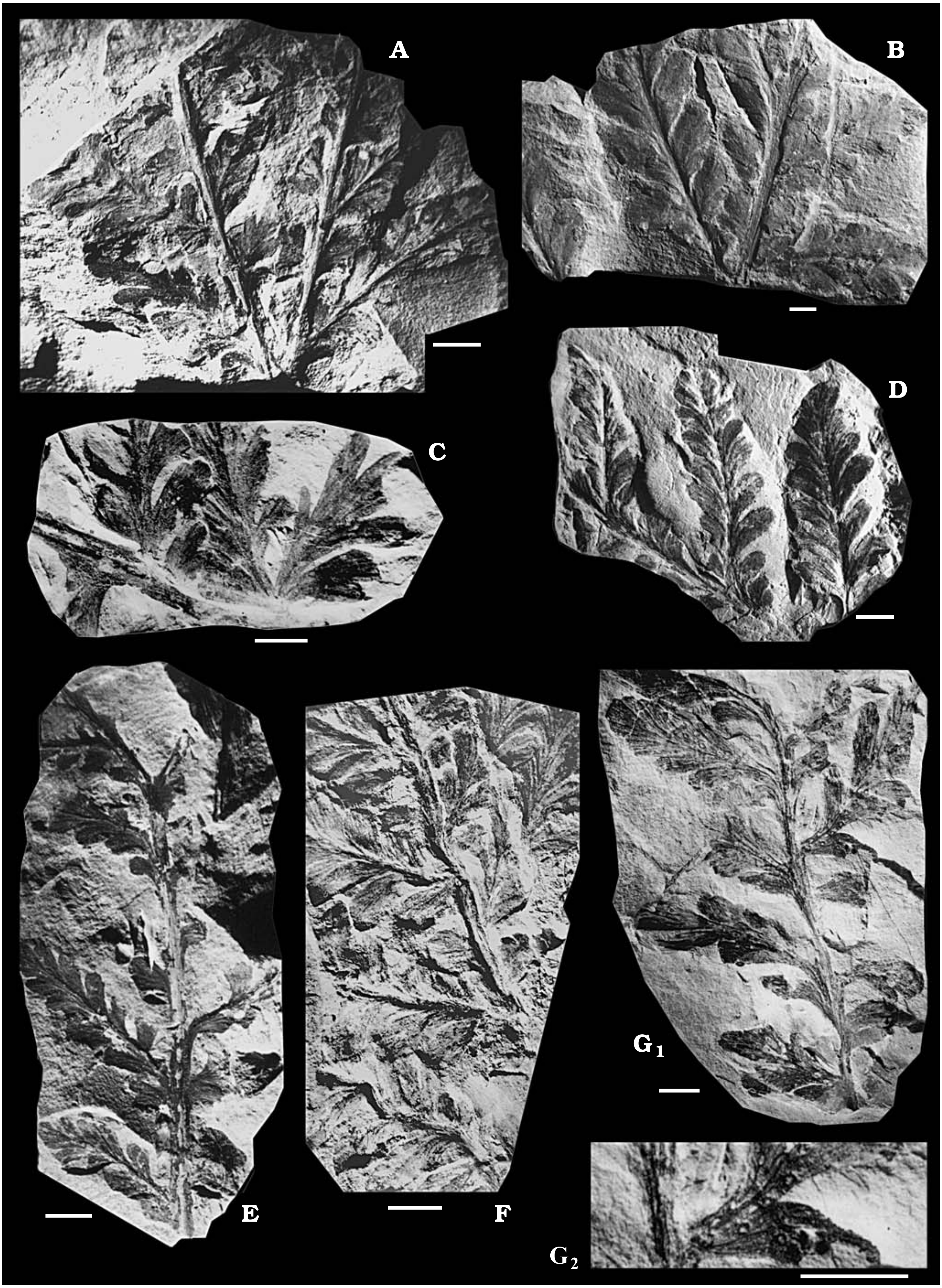
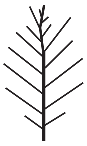
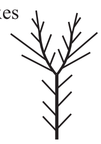
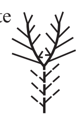

A
B
C
D
E
F
G1
G2

Table 1. Main characters of the sterile foliage of the described callipterids.

Genus	Frond architecture	Pinnule morpho-logy	Species	Primary rachis and axes	Shape of lobes or segments	Heteroblastic development of pinnules
Autunia	Frond bipinnate with repeated overtopping of the primary rachis 	Alethopteroid	*Autunia conferta*	Longitudinally striated		Ovate; 4-6 mm long - entire-margined; 7-10 × 2-5 mm - crenulate to slighty lobed 
			Autunia naumannii	Longitudinally striated	Wedge-shaped, slightly arcuate	Ovate, obovate to prolonged; 6-8 mm long - crenulate to lobed, 10-12 mm long - dissected 
Dichophyllum	Frond bipartite bipinnate 	Flabelliform	*Dichophyllum cuneatum*	Finely ribbed and longitudinally striated	Wedge-shaped	2-3 × 0.7-1 mm - entire-margined to crenulate; 4-22 × 2-20 mm - incised to dissected 
			Dichophyllum flabelliferum		Lineal	Up to 25 mm long - dissected 
Lodevia	Frond bipartite bipinnate with overtopping of the penultimate order axes 	Palmate, prolonged flabelliform	*Lodevia luganica*	Finely tuberculate	Narrow-obovate, often arcuate	Ovate to oblong; 8-10 × 2-5 mm - entire-margined to lobed, 12-24 × 6-9 mm - dissected 
			Lodevia nicklesii	Longitudinally striated	Wedge-shaped, narrow	Ovate to oblong; 10-13 × 5-5 mm - lobed, 14-24 × 6-8 mm - dissected 
			Lodevia suberosa	Longitudinally striated with short longitudinal marks and spines	Lineal, narrow, straight	Ovate to oblong; 9-12 × 3-5 mm - lobed to dissected 
Raminervia	Frond bipartite bipinnate with penultimate order axes terminating in a pseudodichotomy 	Wedge-shaped, round-loded	*Raminervia mariopte-roides*	Longitudinally striated	Obovate to wedge-shaped, broad	Obovate,wedge-shaped to prolonged; 8-12 × 4-5 mm - entire-margined to slightly lobed, 13-30 × 6-15 mm - lobed to dissected 

The lacustrine deposits are represented by massive greenish-grey claystone with a thickness of 45 cm (lower part of the strata no. 3), which yielded a rich plant assemblage consisting of the dominant callipterid *Raminervia mariopteroides* and rare pecopterids. The claystone facies indicates a very low-energy environment like an oxbow lake. The association of callipterids and ferns indicates that the plants grew on lowland shores with humid ecological niches.

The floodplain-lacustrine deposits consist of an alternation of clay-, silt-, and fine-grained sandstone beds (lower part of the strata no. 1, upper part of the strata no. 3, strata nos. 4 and 6), which contain the abundant callipterids, rare neuropterids and odontopterids. The fine-grained deposits with well-preserved large and small fragments of callipterid fronds indicate that the depositional environments ranged from low-energy to moderately high-energy settings and that the plant remains have been transported over a minimal distance. These strata are interpreted as delta lake levee deposits, and the fossils occurring in them may have derived from the plants that spread on delta levees. The sandy silt- and sandstone beds within this sequence yielded the fragmented pteridosperm remains. These deposits may have formed by minor sheetfloods during brief flooding episodes.

The floodplain deposits are composed of the horizontally or vaguely laminated siltstones and the fine-grained sandstones (upper part of the strata no. 1 and strata nos. 2 and 5), that contain rare callipterids, neuropterids, odontopterids, cordaites, conifers, seeds as well as plant detritus and bivalves. All plant material consists of fragmented pinnae and isolated pinnules, which were likely to have been transported to the site of deposition during floods from delta levees and valley-side slopes.

← Fig. 8. Callipterid pteridosperm *Raminervia mariopteroides* Boyarina, 1994. Plant-bearing strata no. 3. from late Gzhelian (Late Carboniferous) of Luganskoye, Ukraine. **A**. Middle portion of a frond showing the bifurcation of the primary rachis, figured by Boyarina (1994: fig. 3A), paratype SNM PMC 2216/6. **B**. Fragment of an asymmetrical penultimate order pinna with lobed pinnules, SNM PMC 2216/36. **C**. Fragment of a penultimate order pinna showing the strongly developed basal basiscopic pinnule as in mariopterids, SNM PMC 2216/39. **D**. Fragment of a penultimate order pinna with entire-margined and slightly lobed pinnules, SNM PMC 2216/32. **E**. Fragment of a frond with small entire-margined and slightly lobed pinnules, possibly a basal part of an immature frond under the bifurcation, SNM PMC 2216/27. **F**. Fragment of an asymmetrical penultimate order pinna with entire-margined pinnules, SNM PMC 2216/47. **G**. SNM PMC 2216/10, figured by Boyarina (1994: fig. 2A). Fragment of a pinna with dissected pinnules (G_1), detail, showing insect damage of the pinnule (G_2). Scale bars 5 mm.

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It is necessary to note that the co-occurrence of pteridosperms and cordaites, both in the floodplain-lacustrine and floodplain deposits, suggests that these fossils may have originated from plants, which could grow both within a floodplain and on valley-side slopes. Conifers are only rarely concentrated in floodplain deposits related to high-energy environments, therefore they are interpreted as plants exclusively occurring on slopes.

Taphonomical features of the plant remains from the different facies indicate some ecological differentiation among individual callipterid populations within the delta plain.

Autunia conferta.—*A. conferta* foliage is only known from floodplain-lacustrine deposits represented by claystone beds (strata nos. 1 and 6) and thin claystone interlayers within the siltstone bed (strata no. 3). The occurrence of relatively well-preserved fragments of apical and middle portions of fronds in lacustrine deposits of low-energy settings indicates that *A. conferta* may have principally spread on shores of delta levee lakes.

Autunia naumannii.—This is one of the dominant elements of the plant assemblages in this locality. Frond fragments of *A. naumannii* are abundant in the floodplain-lacustrine siltstone (strata no. 6) and common in the clay- and sandstone beds (strata nos. 1, 3, and 4). The well-preserved fragments of the fronds in the clay- and siltstone beds, which represent rather low-energy facies, indicate that the fossil material was transported over a minimal distance. In addition, *A. naumannii* rarely occurs together with other pteridosperms and conifers in the silt- and sandstone beds interpreted as the floodplain deposits (strata no. 5). The small portions of fronds and pinnae from the sandstone beds represent plant material drifted during floods. Thus, *A. naumannii* may be considered as a widespread element of the delta plain vegetation growing both on shores of delta levee lakes and on delta levees.

Lodevia nicklesii.—Frond and pinnae fragments of *L. nicklesii* are abundant in the floodplain-lacustrine silt- and sandstones (strata no. 6), and common in the claystone (strata nos. 1 and 6) and the siltstone beds (strata no. 3). Consequently, *L. nicklesii* may be regarded as a dominant element of the floodplain vegetation like *A. naumannii* that grew within delta levees and near delta levee lakes.

Lodevia luganica.—*Lodevia luganica* foliage was found in the floodplain-lacustrine deposits, viz., in the claystone (strata nos. 1 and 4) and the siltstone beds (strata nos. 3 and 6). The occurrence of a few frond and pinnae fragments in the deposits of not very high-energy depositional environments indicates that *L. luganica* was a rare element of the floodplain vegetation and could spread within delta levees together with dominant the forms *Autunia naumannii* and *Lodevia nicklesii*.

Lodevia suberosa.—A few small fragments of *L. suberosa* were found in the floodplain-lacustrine siltstone (strata nos. 3 and 6) and the floodplain siltstone (strata no. 2). The division of the pinnules into the narrow segments and the presence of the spines on the axes may suggest a mesophytic nature. Rare small remains of *L. suberosa* in the rich plant-bearing beds (strata nos. 3 and 6) indicate that this species was a rare element of the plant communities and that these callipterids grew at some distance from lakes within the floodplain. It is possible, that *L. suberosa*, regarding its mesophytic nature, could grow on delta levees as well as on valley-side slopes.

Dichophyllum cuneatum.—The common well-preserved remains of the *D. cuneatum* foliage from the floodplain-lacustrine siltstone (strata nos. 3 and 6) point at a short distance of transportation. Therefore, *D. cuneatum* may be considered to have been a widely distributed element of the floodplain vegetation growing mainly on delta levees.

Dichophyllum flabelliferum.—A single specimen of *D. flabelliferum* was found in the siltstone interpreted as the floodplain-lacustrine deposit (strata no. 6) together with other callipterids that occur abundantly. These data are not sufficient for ecological interpretations. By analogy with the associated callipterids, *D. flabelliferum* was possibly a rare element of the floodplain or valley-side slopes vegetation.

Raminervia mariopteroides.—The abundant frond fragments of *R. mariopteroides* were found in lacustrine claystone (strata no. 3). *Raminervia mariopteroides* is accompanied by rare remains of the hydrophilous and hygrophilous plants, i.e., *Pecopteris bredovii* Germar, 1845*, Sphenopteris fayolii* Zeiller, 1888 and *Asterophyllites equisetiformis* (Sternberg, 1825) Brongniart, 1828. Consequently, *R. mariopteroides* can be considered to be the dominant element of the plant community that occupied lowland shores of oxbow lakes.

Conclusions

Late Gzhelian pteridosperms with callipterid foliage in the Donets Basin are represented by eight species including three endemic taxa and belong to four genera. The callipterids of the morphogenera *Lodevia*, *Dichophyllum*, and *Raminervia* are characterised by a bifurcation of the primary rachis in the upper part of the bipinnate fronds and can be distinguished by the morphology of the penultimate order pinnae. The penultimate order pinnae of *Dichophyllum cuneatum* have the normal shape of pinnate pinnae. *Lodevia nicklessii* and *L. luganica* are characterised by the overtopping of the penultimate order axes. The penultimate order axes of *Raminervia mariopteroides* terminate in the pseudodichotomy.

The form of segments and a degree of segmentation of pinnules are used for the specific delimitation of the callipterids with dissected pinnules. The shape of the lobes or segments of the pinnules is considered as the main diagnostic species character. The degree of segmentation of the pinnules and their size represent the intraspecific variability related to the heteroblastic development of the foliage.

In the upper Gzhelian, the callipterids occur in the floodplain, floodplain-lacustrine and lacustrine deposits and they are interpreted as elements of the floodplain vegetation within a delta plain. They were spread within delta levees and on the shores of delta levee lakes. *Raminervia mariopteroides* a species that was associated by ferns grew on oxbow lake shores. The floodplain vegetation was dominated by *Autunia naumannii* and *Lodevia nicklesii*.

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