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Genus *Pronephrium* Presl 1851 (Thelypteridaceae) in Romania

Roxana Pirnea¹ and Mihai Emilian Popa^{2*}

Abstract

Pronephrium stiriicum (Unger) Knobloch et Kvaček 1976 (Filicales, Thelypteridaceae Holttum 1971) is reported from the Oligocene Petroșani Basin and from the Miocene Bozovici Basin in Romania. Morphological variations of this species, such as size of the leaves, venation and marginal teeth, in the Oligocene–Miocene time interval in Romania are described, discussed and illustrated. The distribution of the Thelypteridacean species *Pronephrium stiriicum* is also discussed regarding its European expansion during the Cenozoic. Moreover, the palaeoecology of this species is discussed based on taphonomy and occurrences, as *Pronephrium stiriicum* was a secondary coal generator.

Keywords: Thelypteridaceae, *Pronephrium stiriicum*, Oligocene, Miocene, Romania

1 Introduction

The Family Thelypteridaceae is a large filiclean (fern) family segregated by Holttum (1971) from the Family Dryopteridaceae, having many recent representatives such as *Thelypteris* Schmid, *Cyclosorus* Link, *Cyclogramma* Tagawa, *Coryphopteris* Holttum, and *Pronephrium* Presl, among other genera. The family occurs especially in subtropical and tropical Asia, where they record a higher biodiversity, with a few European representatives. Today, genus *Pronephrium* includes about 70 tropical species. Cenozoic representatives of genus *Pronephrium*, especially *Pronephrium stiriicum*, are recorded widely in Europe and in the world, especially in the Oligocene and Miocene continental formations (Figs. 1 and 2).

For this work, *Pronephrium stiriicum* was collected from two Romanian coal basins, the Petroșani Basin and the Bozovici Basin (Fig. 2). This species was also cited or described by previous authors from the Transylvanian Basin (Givulescu 1968; Petrescu 1968, 1970; Petrescu et al. 1987). Both the Petroșani and Bozovici basins are the Cenozoic molasse, intramontaneous, coal-bearing basins with well preserved, compressive and permineralized floras.

1.1 Geological setting

The Petroșani Basin is mainly the Oligocene in age, with a strong coal-mining industry which enabled fossil

collecting in underground, from extraction galleries as well as sterile dumps (Popa 2011). The fossil flora of the Petroșani Basin occurs mainly in the Chattian Dâlja-Uricani Formation (Fig. 3), which yields 19 bituminous coal seams extracted from several coalfields. Other formations of the Petroșani Basin such as the Rupelian Cimpa-Râscoala Formation and the Aquitanian Lonea Formation are less fossiliferous (Fig. 3). Coals were reported from the Petroșani Basin since 1826, and coal extraction quickly became intensive, for steel and for energy (Răileanu et al. 1963; Petrescu et al. 1987; Preda et al. 1994). The palaeoflora of the basin was reported since the nineteenth Century, as Stur (1863) published the first detailed geological report in which fossil plants were cited for the first time. Heer (1872) described 27 plant taxa, followed by Staub (1887) who described 96 taxa and by Pax (1908) who revised the previous palaeobotanical works, discussing 32 taxa. Răileanu (1955) and Mateescu (1956, 1960) studied the geology and the coal sequences, citing and describing various plant species. Petrescu and Givulescu (1986) and Petrescu et al. (1987) provided palaeoecological reconstructions, and Givulescu (1996) contributed with a modern revision of the Petroșani Basin palaeoflora. Unfortunately, few samples in the historical collections were found by the authors of this paper from the Petroșani Basin, from other areas/formations in Romania (such as Bucharest, Cluj-Napoca, Brașov or Timișoara; Fig. 2), or from abroad (Vienna). Intensive fossil collecting in the basin was undertaken by the authors since 2014, from underground mining horizons and

* Correspondence: mihai@mepopa.com

²Faculty of Geology and Geophysics, Department of Geology, Laboratory of Palaeontology, University of Bucharest, 1, N. Bălcescu Ave, 010041 Bucharest, Romania

Full list of author information is available at the end of the article



from sterile dumps or outcrops in the area. *Pronephrium stiriacum* was previously collected from Aninoasa and Lupeni coalfields, in some cases with a precise stratigraphic position within the Dâlja-Uricani Formation.

The Bozovici Basin is a less studied Romanian coal-bearing basin (Răileanu et al. 1963; Petrescu et al. 1987; Preda et al. 1994), and mainly includes the Miocene Lăpuşnicul Mare Formation with two members (Codrea 2001): the Burdigalian (Eggenburgian) Pârâul Lighidia Member and the Langhian (Badenian) fossiliferous Valea Slătînicului Member. Up to nine lignite seams occur to the top of the Valea Slătînicului Member, with highly fossiliferous roof shales as well as rich, fossiliferous beds in between the seams (Fig. 4). The Miocene flora of Bozovici is both compressive and permineralized, with peculiar cases of petrification of tree trunks (Preda and Nedelcu 1987; Preda et al. 1994). The flora was only

briefly cited by Pop (1959) as a part of one of the first geological works in the area, followed by the contribution of Iliescu (1967). Today, the coal mining activities have almost ceased in the Bozovici Basin, but intensive fossil collecting was still undertaken by the authors in former open cast mines and in outcrops of the area.

2 Materials and methods

The Romanian material is represented by compressions on hand specimens collected from two basins of the South Carpathians: the Petroşani Basin, Oligocene in age, and the Bozovici Basin, Miocene in age.

The studied Oligocene material was collected from several places within the Petroşani Basin: the underground of Aninoasa coal mine, Lupeni, Vulcan and Uricani sterile dumps. The Aninoasa material has the largest and the best-preserved Oligocene fragment, and



Fig. 2 Occurrences of *Pronephrium stiriicum* in Romania

although it is fertile, its sori are missing. This fragment occurs on a sample studied at the Mining Museum in Petroșani, and it has a precisely recorded stratigraphic position: it has been collected from the roof shale of the coal seam no. 17 (Fig. 3). The material curated at the National Geological Museum of the Geological Institute of Romania in Bucharest includes five hand specimens, three belonging to the Emil Pop Collection (P-21224 and P-21225 from Aninoasa, and P-21228 from Vulcan), one belonging to the Ștefan Mateescu Collection (P-20775 from Uricani), and an unknown collector (P-26708) also from Uricani. The supplementary material was collected in 2017 by one of the authors (R. Pirnea) from the Lupeni sterile dump. It includes 17 hand specimens curated at the University of Petroșani (UPLU0010, 0055, 0077, 0075, 0078, 0082, 0084, 0088, 0091, 0092, 0096, 0101, 0104, 0108, 0109, 0110, 0112). Among these samples, UPLU0082 hosts the largest fragment from Lupeni, UPLU0108 has the best-preserved fragment from the area, while UPLU0010 has a fragment which is fertile but poorly preserved.

The Miocene material was collected by one of the authors (M. E. Popa) from the Lighidia quarry, Bozovici Basin, in 2015. The Bozovici material is preserved as impressions on red and grey porcelanites, on three samples: LPBUV-0614 (fertile), and LPBUV-0612 and LPBUV-0613 (sterile). The sterile fragments are badly preserved, but the fertile fragments still yield sporangia.

Macrophotographs were undertaken using a Panasonic DMC-L10 digital camera with an Olympus Zuiko

35 mm Macro lens together with a Kaiser copy-stand and Ikea lights, using a lateral illumination for detailing morphological features (Popa 2011). In the field, a Canon Powershot G12 camera was used. More detailed photographs were taken using a Carl Zeiss Stemi 2000C dissecting microscope, with a Carl Zeiss PCL 1500 LCD light source, a Canon A640 camera and with Axiovision Extended Focus software for z-stacking.

3 Systematics

Phylum Pteridophyta

Class Filicopsida

Order Filicales

Family Thelypteridaceae Holttum 1971

Genus *Pronephrium* Presl 1851

Pronephrium stiriicum (Unger) Knobloch et Kvaček 1976

Figs. 5, 6, 7, 8

1847 *Polypodites stiriacus* Unger, pp. 121–122, pl. 36, figs. 1, 2, 3, 4, 5;

1976 *Pronephrium stiriicum* Knobloch et Kvaček, p. 12, pl. 1, fig. 1;

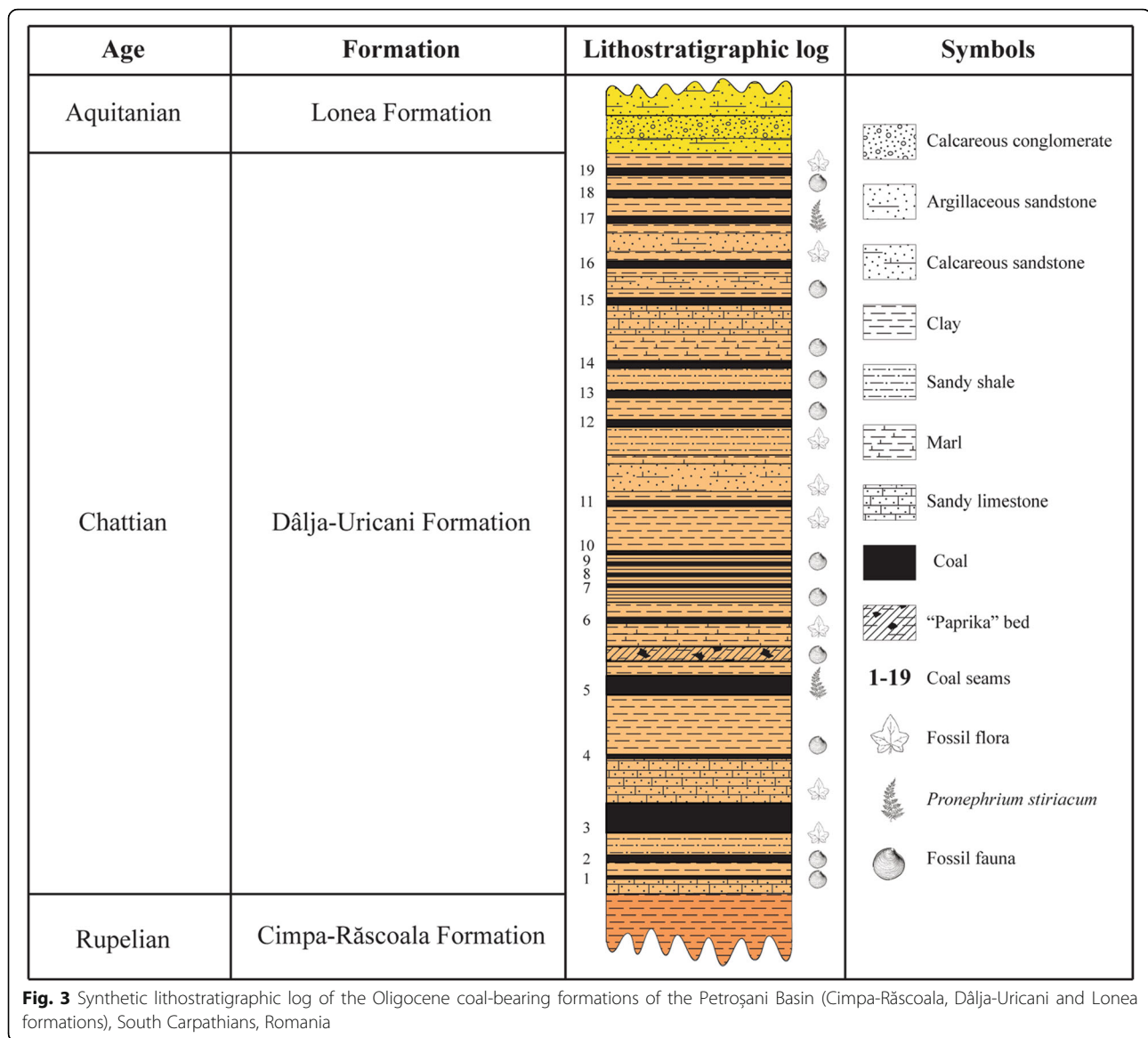
1985 *Pronephrium stiriacus* Hably, pp. 11, 23, 24, 26, 27;

1986 *Pronephrium stiriacus* Givulescu, p. 179;

1986 *Pronephrium stiriicum* Petrescu et Givulescu, p. 110;

1991 *Pronephrium stiriicum* Kvaček et Hably, p. 52, pl. 1, fig. 2;

1995 *Pronephrium stiriicum* Kvaček et Walter, p. 39, text-fig. 4, pl. 1, fig. 1;



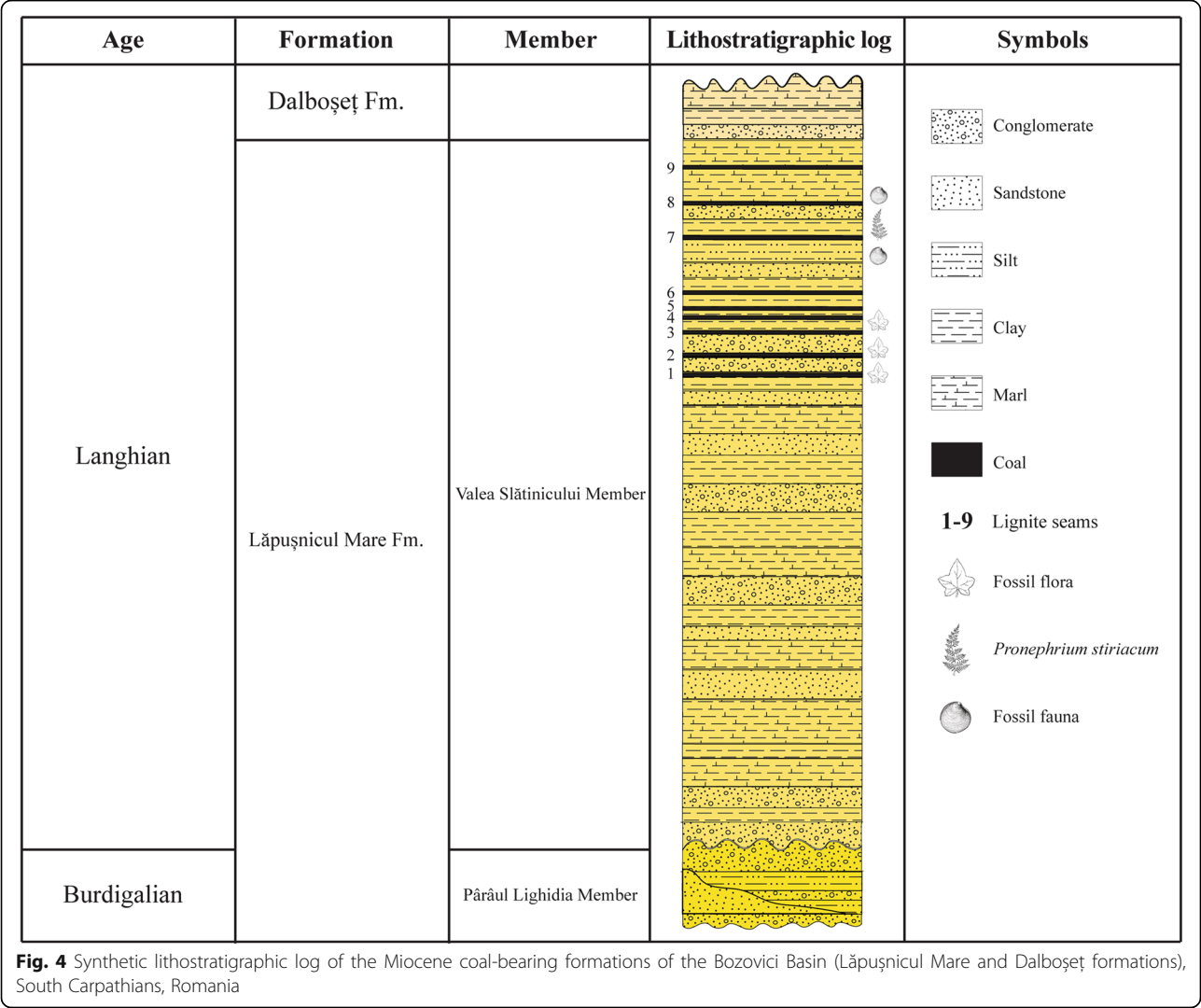
1996 *Pronephrium stiriaceus* Givulescu, pp. 15–17, pl. 30, fig. 1;
 1997 *Pronephrium stiriaceum* Petrescu *et al.*, p. 39, pls. 1, 20, figs. 3, 6;
 1998 *Pronephrium stiriaceum* Kvaček *et al.*, p. 25, pl. 13, fig. 9;
 1999 *Pronephrium stiriaceum* Givulescu, p. 27, pl. 1, fig. 5;
 2000 *Pronephrium stiriaceum* Kvaček *et al.*, p. 4, text-fig. 1.1, pl. 1, figs. 1, 2;
 2004 *Pronephrium stiriaceum* Kovar-Eder *et al.*, p. 52, pl. 1, fig. 3;
 2004 *Pronephrium stiriaceum* Erdei *et al.*, p. 120, text-fig. 7;
 2007 *Pronephrium stiriaceum* Kvaček *et al.*, pp. 391, 395, 400, 402, 403;

2007 *Pronephrium stiriaceum* Teodoridis, p. 416;
 2007 *Pronephrium stiriaceum* Walter *et al.*, p. 91, pl. 1, figs. 1, 2, 3, 4, 5, 6, 7, 8;
 2011 *Pronephrium stiriaceum* Kvaček *et al.*, p. 10, pls. 1, 9, figs. 1, 15;
 2013 *Pronephrium stiriaceum* Hably, pp. 39–40, pls. 1, 35, figs. 2, 3, 4, 5;
 2013 *Pronephrium stiriaceum* Hably *et al.*, p. 17;
 2014 *Pronephrium stiriaceum* Velitzelos *et al.*, pp. 58, 59, pl. I, figs. 1, 2, 3;
 2015 *Pronephrium stiriaceum* Hably *et al.*, p. 287, fig. 3.

3.1 Description

3.1.1 The Petroșani Oligocene material

The hand specimen from Aninoasa yields three exceptional fragments, a large fragment exposing the abaxial



surface of the leaf (F1), an apical fragment exposing the adaxial surface (F2) and a small, detached pinnule (F3; Fig. 5, with fragments marked with F1–F3). The leaf is unipinnate and imparipinnate, with pinnules having a thin lamina substance. The apical part of the frond has an elongated apical pinnule prolonging the rachis (Figs. 5, 6). The primary rachis is 3–4 mm wide, 4 mm wide at the base of the fragment, 3 mm wide to the apical end of the fragment, while the length of the fragmented rachis is 170 mm. The rachis is straight, smooth, with a longitudinal, short and slightly rounded median ridge (Figs. 5, 6). In cross section, the rachis is triangular or V-shaped. No clear hair bases or scales occur along the primary rachis. The pinnules are strongly elongated in shape, lanceolate, short petiolate, with an asymmetrical base, dentate margins and acute apex (Figs. 5, 6, 9a). The petiole is less than 1 mm long and 1 mm wide. The pinnules are inserted suboppositely to alternately to the rachis, with angles between 45°–50° (Fig. 5). The basiscopic part of the

pinnule's base is rounded, and the acroscopic part of the base is straight, parallel to the rachis (Figs. 5, 6). The pinnules are 100–170 mm long and 10–15 mm wide at the base, where they are the widest. The usual width of the pinnules varies between 14–15 mm. The pinnule margins are dentate, with falcate and wide teeth, sometimes even slightly mucronate, separated by narrow and shallow sinuses. The teeth are usually 0.5–0.7 mm long, while the smallest pinnules are weakly dentate (Figs. 5, 6, 9a). The venation is prominent abaxially and weakly expressed adaxially. The midrib is 0.9–1 mm wide, rounded or slightly ridged abaxially, slightly depressed adaxially, straight, reaching the pinnule's apex. No hair bases occur along the midrib (Figs. 6a, c, 9a). The secondary veins are straight, inserted oppositely to suboppositely to the midrib. Each secondary vein reaches the apex of a marginal tooth. The secondary veins are very narrow, about 0.2 mm wide. The tertiary veins are straight, inserted oppositely to the secondary veins, interconnected to the neighboring



Fig. 5 *Pronephrium stiriaceum* from Aninoasa, roof shale of coal seam no. 17, Oligocene, Petroșani Basin, general view. F1, F2, F3: *Pronephrium stiriaceum* leaf fragments. Hand specimen no. 1, Mining Museum in Petroșani. Scale bar: 10 mm

tertiary veins along a straight, interconnecting vein reaching each sinus between two neighboring marginal teeth (Fig. 6b, c). The sori occur in the middle of each tertiary

vein and the interconnecting vein (Figs. 6b, 7a, 9a). Each sorus is circular, about 0.6–0.8 mm in diameter. Unfortunately, all sori are missing along the tertiary veins, leaving

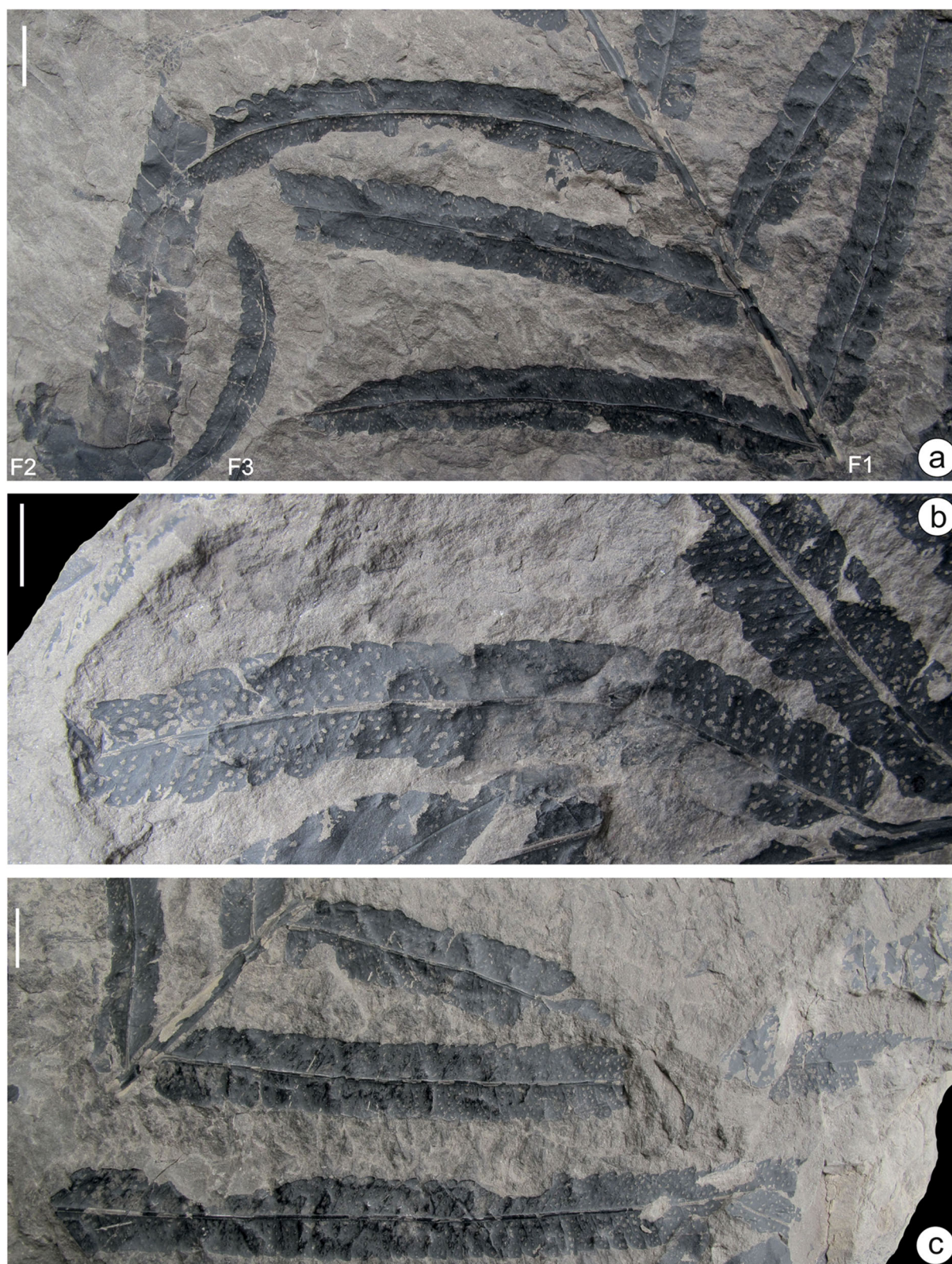


Fig. 6 *Pronephrium stiriicum* from Aninoasa, roof shale of coal seam no. 17, Oligocene, Petroșani Basin. **a** Details of leaf fragments F1 (abaxial view), F2 (abaxial view) and F3 (apical fragment, adaxial view); **b–c** Details of pinnules of leaf fragment F1 in abaxial view, showing the primary rachis, petioles, asymmetric bases, venation, dentate margins and missing sori. Hand specimen no. 1, Mining Museum in Petroșani. Scale bar: 10 mm

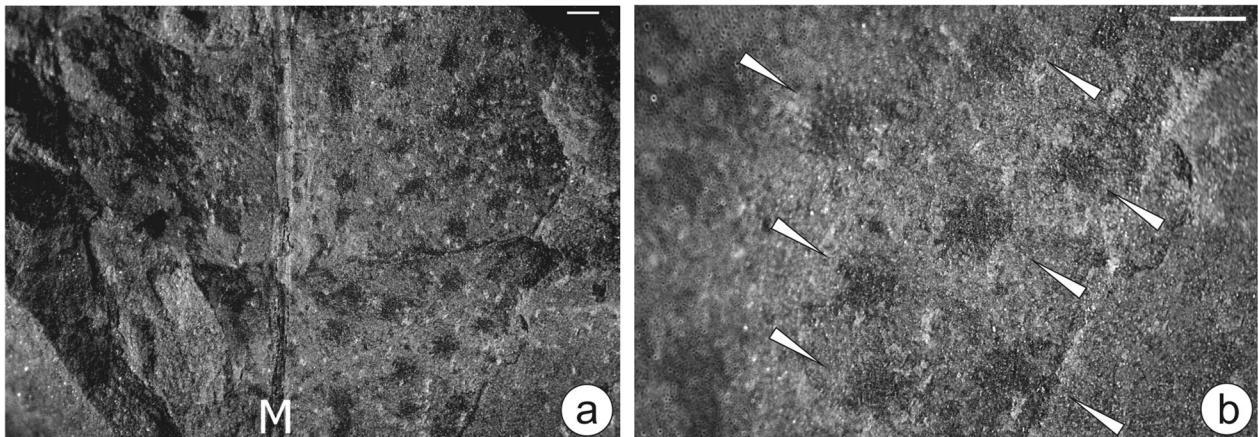


Fig. 7 *Pronephrium stiriacum*, fertile fragment, from Lupeni sterile dump, Oligocene, Petroșani Basin. **a** Fragment of a fertile pinnule, showing the midrib (M), secondary veins, tertiary veins, connecting veins and sori; **b** Detail of the same fertile fragment, with arrows indicating the poorly preserved sori. Hand specimen UPLU0010, University of Petroșani. Scale bars: 1 mm

a circular piercing in the thin lamina. The only exception is a poorly preserved fertile fragment occurring on the hand specimen UPLU0010 from the Lupeni sterile dump, with sori reaching 0.6–0.8 mm in diameter (Fig. 7). These sori are irregular clusters of sporangia, very difficult to separate due to the poor preservation (Fig. 7). They usually occur to the middle part of the tertiary veins, uniformly distributed between the midrib and pinnule margins.

3.1.2 The Bozovici Miocene material

The collected material includes only dispersed pinnules, both sterile and fertile. The pinnules are short petiolate, elongated in shape, linear, with a slightly asymmetric base, with strongly dentated margins and acute apices (Fig. 8a, b). The marginal teeth are symmetrical, with a slightly attenuated apex, and they are separated by a symmetrical, wide sinus. The pinnules' length varies between 40–60 mm, and their width varies between 10–15 mm, with the widest part toward the pinnule base. The petiole is 4–5 mm long and 0.5 mm wide, ornamented with fine longitudinal striae (Fig. 8b). The midrib is 0.5–0.7 mm wide, finely striated longitudinally, with a short ridge along the abaxial surface. The rachis is marked along its abaxial surface by rare dots representing large trichomial bases (Fig. 8b, c). The secondary veins are more prominent abaxially, they are inserted oppositely to the midrib at angles between 70°–80°, and they are straight, smooth, reaching each apex of the marginal tooth (Figs. 8c, d, 9b). The tertiary veins are also straight, inserted oppositely to the secondary veins, and about five tertiary veins along each secondary one. Their tertiaries interconnect with their neighboring counterparts, thus a supplementary vein is generated,

reaching each marginal sinus (Figs. 8c, d, 9b). In fertile pinnules, the sori occur along the tertiary veins in the middle region between the secondary veins and the supplementary veins (Figs. 8c, d, 9b). They are usually circular, 0.7–1.0 mm in diameter and few reniform (Fig. 8d, middle one), with numerous small, spherical sporangia distributed irregularly but clustered. Nearly 12–17 sporangia occur in each sorus, but their precise number is difficult to assess. No indusium and no in-situ spores were observed (Fig. 8c, d). Their distribution is uniform, occurring in the middle, between connecting veins and secondary veins, always on the tertiary veins.

3.2 Remarks

We consider pinnules as the large, petiolate, laminate and dentate structures attached to the primary rachis. Indeed, in morphology, these large structures seem very similar to structures generated by fusing into large pinnae of smaller, neighboring pinnules with simple, undivided, secondary veins. But the studied material shows no separation between smaller pinnules within the larger structures, therefore these large, pinnae-like structures cannot be named pinnae here. Givulescu (1999) admitted that the large laminar lobes can be in fact fused pinnules into larger pinnae. However, the pinnae term is widely used in recent and in fossil material; and, in the recent, involving in living species, the term pinna is exclusively used (Mirza 2007; Salino et al. 2014). The recent *Pronephrium parishii* from Bangladesh has reduced, rounded teeth (Mirza 2007), like those of *Pronephrium gymnopteridifrons* and *P. megacuspe* from China (Zhang 2012), strongly different from those of *P. articulatum*, *P. lakhimpurensis* and *P. nudatum* developed in Bangladesh (Mirza 2007) and in China (Zhang 2012).

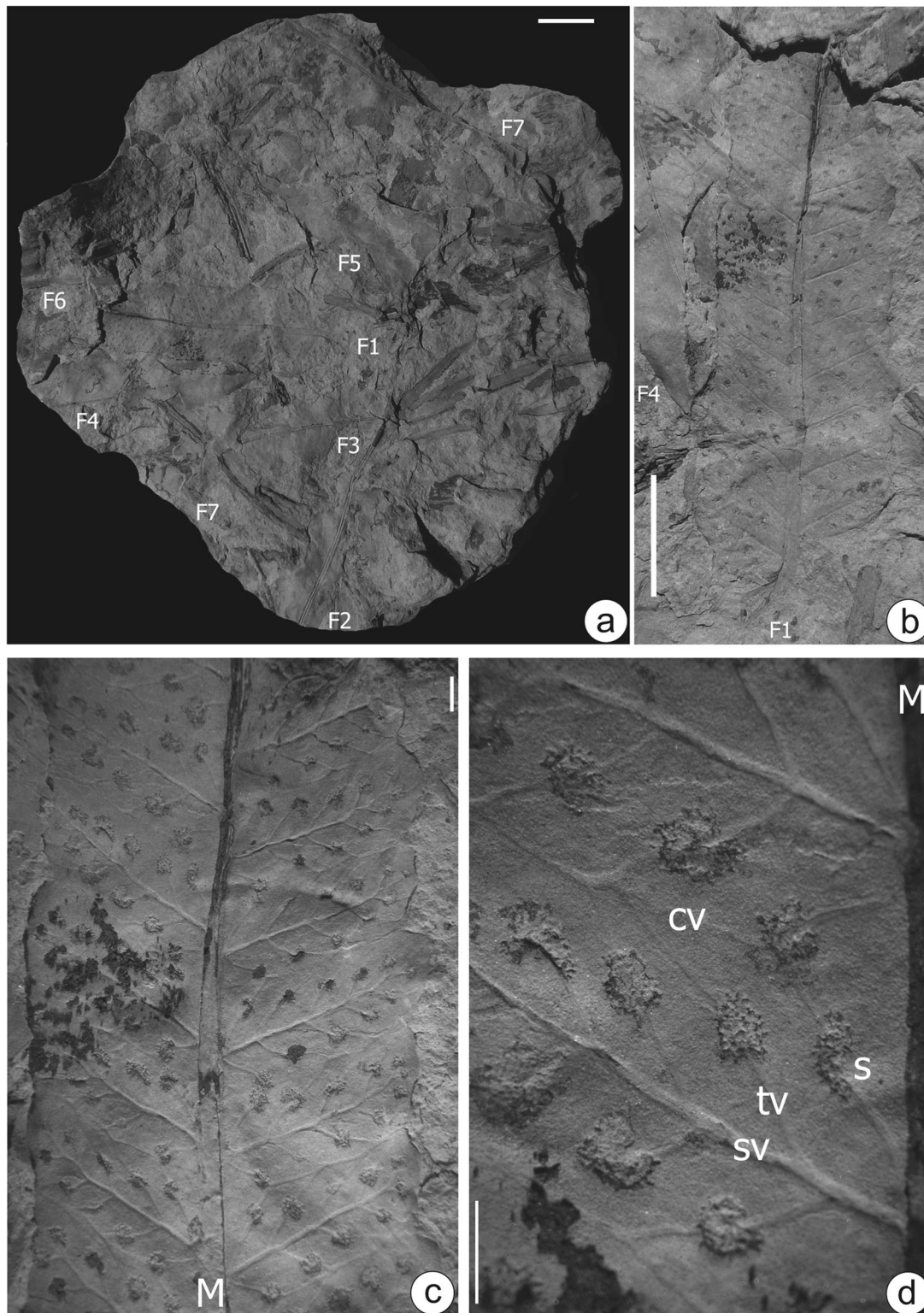


Fig. 8 *Pronephrium stiriacum*, fertile and sterile fragments, from Lighidia quarry, Miocene, Bozovici Basin. All from hand specimen LPBUIV-0614, University of Bucharest, Department of Geology, Laboratory of Palaeontology. **a** General view of the hand specimen LPBUIV-0614. F1: Fertile fragment, F2-F7: Sterile fragments. Scale bar: 10 mm; **b** Fertile fragment (F1) and sterile fragment (F4). Scale bar: 1 mm; **c** Detail of fertile fragment (F1), showing the midrib (M), secondary, tertiary and connecting veins and sori. Scale bar: 1 mm; **d** Detail of fertile fragment (F1), showing the midrib (M), secondary (sv), tertiary (tv) and connecting veins (cv) and sori (s). Scale bar: 1 mm

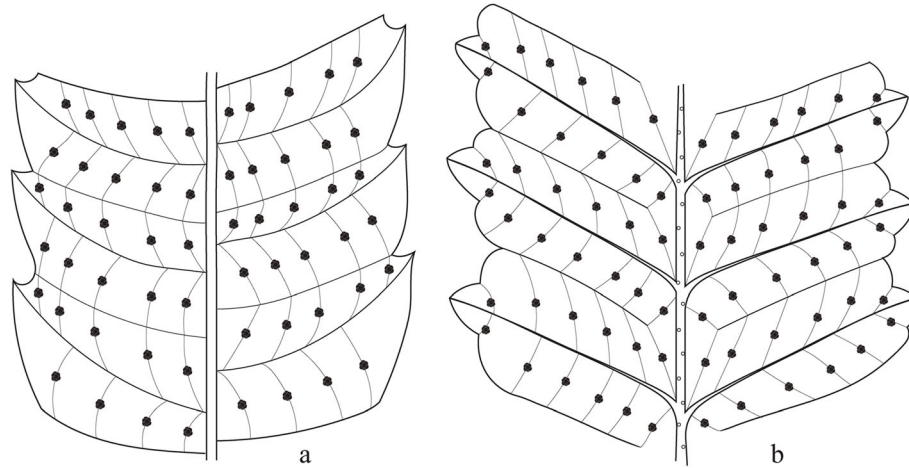


Fig. 9 Diagrams of the pinnules of *Pronephrium stiriicum* in Romania. **a** The Oligocene material from the Petroșani Basin; **b** The Miocene material from the Bozovici Basin

Unger (1847) defined *Polypodites stiriicum* under the following diagnosis: “*Fronde pinnata, pinnis lienaribus elongatis serratis, nervis secundariis e nervo primario angulo subacuto egredientibus pinnatis, ramulis alternatis obliquis parallelis trans medium soriferis*”. The type material was collected from Parschlug in Styria, Austria, and it is Miocene (Karpatian–early Badenian) in age (Kovar-Eder et al. 2004). The holotype showed in Unger (1847) in his Fig. 1 and plate 36 is a large fragment of an unipinnate frond with elongated–dentate pinnules, with marginal teeth of short–rounded apex, and with more acute apex which is rather symmetric (Figs. 2, 5) or slightly asymmetric (Fig. 4). Its connecting veins are strong and conspicuous, extremely alike with the Romanian Miocene material from Bozovici. Knobloch and Kvaček (1976) assigned their Bohemian Miocene material to *Pronephrium stiriicum* (Unger) Knobloch et Kvaček, making a new nomenclatorial combination. They also stressed the synonymy between *Pronephrium* Presl 1851 and *Abacopteris* Fee 1852, with *Pronephrium* having priority. Their material has elongated, large pinnules with symmetrical marginal teeth, similar to our Bozovici material. Givulescu (1996) described similar *Pronephrium* material under the name *P. stiriacus*, with falcate teeth along large pinnules and later (Givulescu 1999) under the name *P. stiriicum*. Pinnules were named pinnae by Givulescu (1996, 1999), and considered as a result from the fusion between regular pinnules. His material, which includes sori, was collected from Aninoasa and Vulcan (Petroșani Basin), and was studied in the collections of the Geological Institute of Romania in Bucharest (nos. P. 21224, P. 21225 from Aninoasa and P. 21228 from Vulcan). Givulescu (1986) only cited this species. Petrescu and Givulescu (1986) and Petrescu et al. (1997) cited and described *Pronephrium stiriicum* from the Petroșani Basin and from the Transylvanian Basin (Jac and Coruș). They

considered the material as having dentate pinnules, not pinnae. Kvaček and Hurník (2000) described *Pronephrium stiriicum* from the Miocene of the Czech Republic (Dobruč locality), where it formed large leaf accumulations related to several swamp levels. The Czech material is also preserved in porcelanite, the leaves are fertile, with oppositely inserted pinnules, symmetrical marginal teeth and rather deep sinuses in between, very similar with our Bozovici Miocene material, although the connecting veins of the Czech material are not so prominent. Kvaček and Walther (1995, 1998) described *Pronephrium stiriicum* from the Oligocene tuffs of Sulečice and Kundratice. Kvaček and Teodoridis (2007) only cited this species from the Czech Republic. Kovar-Eder et al. (2004) described the Miocene *Pronephrium stiriicum* from Austria, while Erdei and Wilde (2004) described a badly preserved fragment from Hungary, Oligocene in age. Kvaček et al. (2011) described *Pronephrium stiriicum* from the Miocene of France, with large pinnules and goniopterid venation. Hably (1985, 2013) considered the Miocene material as fused pinnules generating dentate pinnae, while Hably and Magyar (2013) only cited this species. Hably et al. (2015) described both fertile and sterile materials. Velitzelos et al. (2014) illustrated *Pronephrium stiriicum* with teeth apices very attenuated and rounded, almost entirely margined.

4 Discussion

Several morphological differences occur between the Petroșani (Aninoasa and Lupeni) Oligocene material and the Bozovici Miocene material. In Aninoasa, the pinnules are very elongated (Figs. 5, 6), while in Bozovici they tend to be shorter (Fig. 8). In Aninoasa, no hair bases occur along the midrib (Fig. 6b, c), while in Bozovici they are visible (Fig. 8b, c), a typical character of Thelypteridaceae. In Aninoasa, the marginal teeth are falcate and sharp (Fig. 6),

but in Bozovici the marginal teeth are usually symmetrical and slightly rounded, with a median inflexion of the margin, between the apex and the sinus (Fig. 8a-c). In Aninoasa material, the interconnecting veins are very weak (Figs. 6, 7, 9a), while in Bozovici material they are much more prominent (Figs. 8, 9b). The sori are difficult to compare, considering the poor preservation of the Petroşani material. They are approximately of the same size, clustered irregularly with spherical sporangia. The distribution of the sori within the surface of the pinnules is approximately the same in both the Oligocene and the Miocene materials. Such differences point to ecological adaptations rather than to species differences, although recent, living species are separated on even finer morphological variations.

Pronephrium stiriaceum has been recorded in the Oligocene and Miocene terrestrial formations of Europe (Fig. 1), but usually its descriptions and illustrations are brief, without considering its variations. The earliest occurrence of *Pronephrium stiriaceum* is recorded in Czechia, in the Upper Eocene deposits of North Bohemia at Kučlín (Kvaček and Teodoridis 2011). Some Oligocene fragments of *Pronephrium stiriaceum* were described from North Bohemia, in Sulečice and in Kunderatice (Kvaček and Walther 1998). In the Dobruška area, *Pronephrium stiriaceum* was described from the Lower Miocene porcelanite beds (Kvaček and Hurník 2000). In northwestern Bohemia it was described from the Lom Formation of the Most Basin (Teodoridis and Kvaček 2006; Teodoridis 2007) as rare fragments, Miocene in age. In the westernmost part of Bohemia, *Pronephrium stiriaceum* was cited from the Cypris Formation of both Cheb and Sokolov basins, Early Miocene in age, and also from the Nové Sedlo Formation, but Oligocene in age (Kvaček and Teodoridis 2007). From Doupovské hory Mountains, between the Sokolov and the Most basins, a few sites with the Oligocene floristic assemblages yield *Pronephrium stiriaceum* remains. From the Bohemian part of the Zittau Basin, close to the state boundary of Germany, *Pronephrium stiriaceum* was described from the Upper Coal Seam of the Hrádek Formation (Kvaček and Teodoridis 2007), Middle Miocene in age. In Germany, *Pronephrium stiriaceum* was only described from the Oligocene diatomite deposits of Seifhennersdorf, Saxony Region (Walther and Kvaček 2007). In Hungary, *Pronephrium stiriaceum* has a high frequency in both the Oligocene and the Miocene deposits. From Oligocene deposits abundant remains were described from the Mátyás Formation (Hably et al. 2015), outcropping in Környe. Discussing its ecology, Hably et al. (2015) considered this species as indicating wet environments. It also has been described from an Upper Oligocene sequence of Central Paratethys at Eger-Wind brickyard (Kvaček and Hably 1991) and from the Dorog Basin at Csolnok (Erdei and Wilde 2004). *Pronephrium*

stiriaceum was cited from the Miocene of Ipolytarnóc (Hably 1985), close to the northern rim of the Pannonian Basin, and from the Miocene sedimentary deposits of the Pannonian Basin at Balatonszentgyörgy, Felsőtárkány, Sé and Visonta (Hably 2013). From the Miocene of Austria, *Pronephrium stiriaceum* was only described from the Parschlug Basin (Kovar-Eder et al. 2004) as a single, poorly preserved fragment. In Romania, *Pronephrium stiriaceum* occurs in the Oligocene deposits of the Transylvanian Basin at Coruş (Givulescu 1968), Jac (Petrescu 1968, 1970), and Corneşti (Petrescu et al. 1997); and in the Oligocene deposits of the Petroşani Basin (Givulescu 1986). Its occurrence in the Bozovici Basin is here reported for the first time for the Miocene deposits of Romania. In the Cenozoic floras of Greece, *Pronephrium stiriaceum* was cited from the Oligocene beds at Lagina and Fylakton, Evros Region (Velitzelos et al. 2002); from the Lower Miocene sequences at Grevena and Mudros, Lemnos Region (Berger 1953; Süß and Velitzelos 1993); and from the Upper Miocene deposits in Strymon Basin (Velitzelos 1993) and of the Platana Formation (Kleinholter 1994; Velitzelos et al. 2014). In southwestern France, Kvaček et al. (2011) described *Pronephrium stiriaceum* from the Miocene of Arjuzanx.

The first attempt for reconstructing the Oligocene flora of the Petroşani Basin was undertaken by Givulescu (1996) based on the very first, general reconstructions of Teichmüller (1958) and Knobloch (1977). In this reconstruction, Givulescu (1996) placed *Pronephrium stiriaceum* in the shrub peat bog zone. It was described as a flooding-prone zone and it was dominated by *Myrica*, *Cyrtilla*, *Osmunda*, *Blechnum*, *Calamus* and numerous lauraceous taxa such as *Daphnogene*.

A vegetation reconstruction from Seifhennersdorf, Germany (Walther 1977; Walther and Kvaček 2007) was placing *Pronephrium stiriaceum* in the monocot-fern swamp undergrowth, along with *Osmunda lignitum* and monocots such as *Spiromatospermum wetzleri*, pointing out that the undergrowth vegetation breed as well along the water courses, under the canopy. The remains of frogs and salamanders in the same bed with *Pronephrium stiriaceum* and its associated taxa, strengthen the idea of a humid palaeoenvironment.

In the flora of Környe, Hungary, *Pronephrium stiriaceum* represented the dominant fern according to Hably et al. (2015). All the associated taxa with *Pronephrium* have affinities for water bodies: *Glyptostrobus*, *Nyssa* and *Alnus*. Also, the high frequency of the lauraceous taxa such as *Daphnogene* fits best a hygrophite plant palaeocommunity.

The well-preserved fronds of *Pronephrium stiriaceum* in both Petroşani and Bozovici basins suggest the short distance transportation of the material and underline its autochthonous character. Considering our taphonomical data and the former palaeoecological reports, we can also assess that *Pronephrium stiriaceum* was thriving

near to the water bodies, in a warm environment, during the Oligocene–Miocene timespan in the Petroșani and Bozovici basins.

Moreover, this palaeoecological context of *Pronephrium stiriaceum* also emphasizes the coal generating character of this species. This species is frequently found in the roof shales of various coal seams, therefore it is a coal generator. Although it was not a swamp dweller, such as reeds were, it contributed to genesis of coal as it could quickly cover the mire areas in their closing phases, as an opportunistic species. Popa (1998, 2014) defined these species as secondary coal generators, in contrast with the primary coal generators which are represented by swamp dwellers. The secondary coal generators were not swamp dwellers, but they were opportunistic species which jumped in the closing mire, therefore contributing to the coal genesis and therefore were deposited also in the roof shales of the coal seams (Popa 1998, 2014). Such a coal genesis mechanism was described by Popa (1998, 2014) for European and Greenlandic Triassic and Jurassic coals, with primary coal generators such as sphenopsids and conifers, and secondary coal generators represented by a ternary association between a fern, a Bennettitalean and a ginkgoalean representative, also called by Popa (2014) as a ternary rule. This ternary rule was later demonstrated statistically by Barbacka et al. (2016). Now it can be demonstrated that during the Cenozoic times, *Ponephrium stiriaceum* played the same role as a secondary coal generator, the same way a fern representative played during the Jurassic within its ternary association.

5 Conclusions

Pronephrium stiriaceum (Filicales, Thelypteridaceae) material was collected from the Oligocene sediments of the Petroșani Basin (Aninoasa, an underground coal mine) and from the Miocene sediments of the Bozovici Basin (Lighidia open cast mine), showing a series of morphological variations during the Oligocene–Miocene time interval. Such variations include venation, pinnule margins and sorus size, and they indicate local ecological variations in the habitat of this fern. Although intensively occurring in the fossil material with this stratigraphic range, these variations are not strong enough for segregating *Pronephrium stiriaceum* into separate Oligocene and Miocene species. From a palaeoecological point of view, this species was not a swamp dweller, although it generated coal as a successful secondary coal generator in the Cenozoic phytocoenoses.

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Authors' contributions

Both authors read and approved the final manuscript.

Competing interests

The authors declare they have no competing interests.

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Author details

¹Faculty of Geology and Geophysics, Doctoral School of Geology, University of Bucharest, 1, N. Bălcescu Ave, 010041 Bucharest, Romania. ²Faculty of Geology and Geophysics, Department of Geology, Laboratory of Palaeontology, University of Bucharest, 1, N. Bălcescu Ave, 010041 Bucharest, Romania.

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