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THE BENNETTITALEAN GENUS *PTEROPHYLLUM* IN THE FOSSIL FLORA OF ROMANIA, AND THE GLOBAL PHYTOSTRATIGRAPHIC–PALEOPHYTOGEOGRAPHIC CONTEXT

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The Bennettitalean foliage *Pterophyllum* is represented in the fossil flora of Romania (eastern Central-Europe) by *P. pectinatum* (Jaeger, 1827) Csaki and Ulrichs, 1985 em. Czier, 2014, *P. semseyanus* Czier n. sp., cf. *Pterophyllum* sp., and aff. *Pterophyllum* sp., all from continental Jurassic deposits. The new species *Pterophyllum semseyanus* is described from the Konservat-Lagerstätte Anina (Banat region). Diagnostic features include narrow lamina, segments ending in a rounded apex, delicate simple veins, elongate trapezoidal cells of the rachis epidermis, smooth adaxial epidermis, zoned and papillate abaxial epidermis, stomata with deep polar spaces, hypodermis with rectangular hypodermal cells, marked intercellular spaces, and large cell wall corner spaces. The fossils occur in the Valea Terezia Sandstone Member (Hettangian *pro parte* – Sinemurian) of the Steierdorf Formation in the Southern Carpathians. *Pterophyllum semseyanus* is element of the *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone for the Early Jurassic of Romania. This is the first case in the history of the genus *Pterophyllum* where the rachis epidermis and hypodermis are described. Studies concerning the hypodermal matrix may have paleoenvironmental and evolutionary significance, and the Hypodermal Matrix Mechanism (HMM) concept is introduced. Based on the hypodermis structure and physiology, the thick Bennettitalean cuticle appears better indicator of a warm paleoenvironment than the thin cuticle. *Pterophyllum semseyanus* is an endemic species in the European Province of the Euro-Sinian Paleofloristic Region. It coexisted with the elements of the allochthon *Clathropteris* Flora, of which the global migration pattern suggests North American origin.

Keywords: *Pterophyllum semseyanus (Bennettitales), taxonomy, stratigraphy, LM–SEM analysis, hypodermal matrix mechanism (HMM), Clathropteris flora, paleophytogeography.*

1. Introduction. *Pterophyllum* (the Bennettitalean genus, not the freshwater fish from the family Cichlidae) is present in the fossil flora of Romania only in Jurassic continental deposits, and this paper is based on the historic Jurassic macroflora collection that is curated in the Hungarian Natural History Museum, Budapest (HNHM-BP). This important collection, dating back to the

19th and 20th centuries, contains specimens from Hungary and Romania. Of particular interest are the Bennettitalean (*Ptilophyllum aninaensis*, *Williamsonia aninaensis*, *Banatozamites chlamydostomus*, *B. remotus*, *B. calvus*, *Pterophyllum pectinatum*) and Ginkgoalean (*Ginkgo marginata banatica*, *G. skottsbergii europeica*) type specimens originating from the famous Early Jurassic locality Anina in South-west Romania (Czier, 1995b, 1996a, 1998a, 2000a, 2008, 2009, 2010, 2011, 2014). The aim of this study initially was to review old determinations and to describe a new species of *Pterophyllum* that is part of the museum's inventory (Sections 5, 6). However, microscopic investigation of the material unexpectedly revealed an interesting internal leaf structure that very likely deserves to be recognized as one of the most important physiological systems of the Bennettitales, namely the manner in which cuticle is produced (Section 7); so a presentation of this topic is another principal scope. In addition, the plant fossils are also important for nomenclature and taxonomy (Section 2), stratigraphy (Section 4), and paleophytogeography (Section 8).

The most important Jurassic paleobotanical locality in Romania nevertheless is the Early Jurassic locality Anina (Banat region), with many sampling points around, and the new *Pterophyllum* material comes even from this locality. Many scientists contributed in various aspects to the geologic, stratigraphic, paleontologic, and paleobotanic research of Anina and of the region. Only few of their so many contributions, especially selecting some of those containing general information about the Romanian Jurassic flora, its bibliography and history of researches are enumerated on this occasion, such as Hantken (1878); Halaváts (1894); Schréter (1912); Papp (1915); Krasser (1921); Thomas (1930); Langer (1947); Răileanu et al. (1957); Semaka (1962a); Oarcea, Semaka (1962); Humml (1969); Antonescu (1973); Biţoianu (1987); Givulescu, Czier (1990); Czier (1995d, 1998c); Givulescu (1998); Wanek (2002); Popa, Van Konijnenburg-Van Cittert (2006); Főzy, Szente (2013); Sotoc (2014); Barbacka et al. (2014, 2016). Siwei Chen (pers. com. 2016) wrote in a comment, “a scientist has to be most complete possible when researching literature and include all valid papers if those are somehow important in the context”. Agreeing this opinion, about a hundred of somehow important papers easily might be added to this enumeration, and scientists nevertheless should proceed in this manner when they elaborate bibliographic catalogues or statistics.

2. Nomenclature and Taxonomy. Many data concerning nomenclatural and taxonomical problems of the genus *Pterophyllum* already were published, a good discussion being that of Pott et al. (2007b). The scope of this section is not to repeat the already known facts, though it must remember some of them to give a coherent discussion of the genus. When someone is going to publish a new species, a new generic discussion is necessary, because supplementary data more often than not may complete the previous discussions. Taxonomists might discuss a new proposal too, concerning the determination of the type specimens and of the common specimens of *Pterophyllum*; this proposal constitutes the second part of the section. To shorten the text, the number of examples is limited to some absolutely necessary, to help avoiding wrong interpretations of the proposal.

Being widespread from the Middle Triassic to Late Cretaceous, *Pterophyllum* is not only one of the most intensively studied foliage genera of the Factor 1 floras (Cleal, Cascales-Miñana, 2014), but is also one of the most problematic Bennettitaleans. As introduced in the literature by Brongniart (1825), this genus has a long controversial history mainly because it lacked a valid type species.

Brongniart (1825) described two species of the genus, *Pterophyllum majus* and *P. minus* from the Rhaetian of Hoer, Sweden without designating type species for either species. Nathorst (1876) later transferred both species to the genus *Anomozamites* Schimper, 1870, leaving *Pterophyllum* with no eligible type (Pott et al., 2007b). Brongniart (1828a) assigned four other species to *Pterophyllum* without adding anything new to the knowledge of the genus. Two of these species, *Pterophyllum meriani* and *P. williamsonis* are *nomina nuda*. The other two species, *Algacites filicoides* Schlotheim, 1822 and *Osmundites pectinatus* Jaeger, 1827 are transfers from other genera. However, these transfers are rather problematic, because Brongniart has renamed the transferred species. Instead of creating a combination based on *Algacites filicoides*, Brongniart has introduced the new name *Pterophyllum longifolium*, and instead of a combination based on *Osmundites pectinatus*, Brongniart created another name, *Pterophyllum jaegeri*. While this may have been acceptable at the time, today such a procedure is unacceptable.

Seward (1917) remarked on *Pterophyllum*’s nomenclatural problem, which arose owing to the transfer of Brongniart's species *P. majus* and *P. minus* to *Anomozamites*. Harris (1932) also has noted this issue. Andrews (1955) designated the illegitimate *Pterophyllum longifolium* as the type species, but later (Andrews, 1970) recognized ‘the problem of citing a type species’. Nevertheless, he maintained his preference for the ineligible *Pterophyllum longifolium* as the type species designate. Other international floral catalogues also continued the usage of this specific name (Jongmans, Dijkstra, 1963; Boersma, Broekmeyer, 1980; Dijkstra, Van Amerom, 1985). Although Zeiller (1906) used the legitimate name for his combination *Pterophyllum filicoides* (Schlotheim) Zeiller, and despite the fact that Thomas (1930) completed the description of *P. filicoides* with new cuticle illustrations, the old illegitimate name continued to be used. Harris (1969) and Watson, Sincock (1992) perpetuated the practice when they emended the diagnosis for *Pterophyllum*.

The scientific community generally accepted the transfer of *Pterophyllum majus* and *P. minus* to *Anomozamites*, and used for the transferred species the names *A. major* and *A. minor*, thus following the illegitimate name change "*A. minor* Brongn." of Nathorst (1881, p. 63). It was only a few years ago that it became clear this transfer was not maintainable. Schweitzer, Kirchner (2003) still maintained *A. major*, based on cuticle-bearing material from the Early Jurassic of Iran. Pott, McLoughlin (2009) hold the generic attribution of *Anomozamites minor*, but they contest *A. major*. By re-evaluating the characters of *Pterophyllum*, *Anomozamites*, and *Nilssoniopteris*, they replace *Anomozamites major* in *Pterophyllum*, under the initial name *P. majus*, and they give an emended specific diagnosis and a detailed discussion on the specific taxonomic history too. However, *Pterophyllum majus* remains irrelevant and improper for type species selection, so long as its epidermal characters are unknown.

Czier (2014) comments that *Pterophyllum longifolium* Brongniart, 1828a is a homotypic synonym of *P. filicoides* (Schlotheim, 1822) Zeiller, 1906. This latter is the name of the type species, which became valid because of the generic name conservation proposed by Pott et al. (2007b), reported by Herendeen (2011), and accepted by the Eighteenth International Botanical Congress (McNeill et al., 2012). Due to the assignment to *Pterophyllum filicoides* of diverse specimens that initially belonged to other species and even to other genera, the type species gradually became a scarcely interpretable artificial cluster. Several morphotypes were included, together with the illegitimate *Pterophyllum jaegeri*. The situation is now clearer because *Pterophyllum jaegeri* Brongniart, 1828a was separated (Czier, 2014) as a homotypic synonym of *Pterophyllum pectinatum* (Jaeger, 1827) Csaki and Ulrichs, 1985 em. Czier, 2014. As a result, the 'cluster' became smaller and easier to understand because it no longer contains '*P. jaegeri*'. Nevertheless, a thorough analysis of the remaining material is still necessary to determine which of the specimens belong to different morphotypes, and which of them are indeed worthy to remain type species. A general revision of the genus *Pterophyllum* could finally resolve this issue.

To be relevant, the type material of any species of *Pterophyllum* must possess a suite of features that separate it from other species of the genus, but also from other genera within the family. The epidermal (and hypodermal if present) characters provide such a set of features. When the generic diagnosis stipulates epidermal characters too, the macromorphologic characters alone are insufficient for generic attribution; at the same time, no specific determination has any sense when the generic attribution is unreliable. Being convinced that it would be advisable using everywhere the same revision method, I propose here a rule (with certain necessary exceptions): to revise the determinations of those specimens of *Pterophyllum* that are lack of one of the two cuticles, as cf. *Pterophyllum* sp., regardless of the initial specific attribute. Of course, the effective and valid publication of its description and figuration proves the presence of a cuticle. The reliability of the generic assignment is even lower when the fossil is only macroscopically described and figured; therefore, in this case before the generic name I propose placing ‘aff’. When the macroscopical description and figuration does not fit into the generic diagnosis, as well as in the so many cases of the not described and/or not figured specimens, the sign ‘?’ should be placed before the generic name. Evidently, in all the cases of unsure generic assignment, no specific determination has sense. Based on my own experience, I note below some exceptions to the proposed rule. Researchers might add from their experience other indispensable exceptions. Paleobotanists working on macrofloras of any ages might consider the proposal, by extending it for specimens of other genera of which the sure taxonomic attribution implies epidermal features, because the methods and rules generally are or should be the same.

First, an exception to the rule must be done when the analyzed specimens belong to the type material of a sustainable species of *Pterophyllum.* For example, the lectotype of a species of this genus may be a specimen lack of cuticle. However, that may be a sustainable species, owing to its cuticle-bearing epitype, which validates the species. Therefore, the specific attribution of such a lectotype, which is part of the type material, is incontestable, and is an exception to the rule. Some species even could be saved from rejection by designating of cuticle-bearing lectotype, neotype, or sustained by conservation procedure. Such actions require exceptions to the rule. The International Code of Nomenclature for algae, fungi, and plants (McNeill et al., 2012) stipulates the typification procedures. If correctly applied, they do not dilute the generic or species concept, because these exceptions to the rule refer only to type specimens, not to the numerous common specimens of which the trustworthy specific or generic assignment is impossible because of their unknown epidermal characters.

Second, when special methods of investigation permit description of epidermal characters even if cuticles are not preserved. Such a useful yet in routine paleobotanical studies rarely used method is the redefined version of the silicone cast technique for SEM examination (Moisan et al., 2011; Moisan, 2012). This method perhaps is not always so efficient as the classical cuticular analysis, because a condition that the examined plant fossil impressions must fulfil is the excellent conservation of their minute details (stomatal apparatus, cell ornamentation, etc.). This happens only in certain cases of very fine granulate rocks as some argillites are, whereas excellently preserved cuticles may be preserved even in sandstones. However, when the investigation of a silicone cast gives results equivalent to the classical cuticular analysis, an exception to the rule must be done. The taxonomical concept surely will remain intact, not only because of the rare usage of this method, but also because of the mentioned equivalence.

Third, when common specimens are better attributable to other genera or their determination is subject of nomenclatural revision. For example, some *Pterophyllum*-like leaves might fit better in the morphogenus *Dioonites* Miquel, 1851. Seward (1895) has given a detailed discussion that could help taxonomists whether they should attribute hand specimens to *Pterophyllum* or *Dioonites*, which may be utile as a starting point for new opinions. The assignment of a plant fossil to another genus is an exception to the rule; it makes stronger both the rule itself and the implied taxa. Of course, such exceptions are not forever definitive. An example is *Pterophyllum longifolium* Brongniart, 1828a, described by Andrae (1855, p. 41, pl. 10, fig. 1) from the Early Jurassic of Anina. Schimper (1871, p. 135) has revised the material, and assigned it to his new species *Pterophyllum andraeanum* Schimper. Krasser (1921, p. 360) considered the material fitting better in *Dioonites* Miquel, and rejected the opinion of Schimper, by assigning the material to his own combination *Dioonites andraeanus* (Schimper) Krasser. However, Givulescu (1989) has not accepted the proceeding of Krasser (1921), and has replaced the material into *Pterophyllum andraeanum* Schimper. Givulescu (1998, p. 31) replaced it even into *Pterophyllum longifolium* Brongniart, but later, Givulescu (1998, p. 33) gave for it again the name *Pterophyllum andraeanum* Schimper. Despite all the assignments and re-assignments, the epidermal features are unknown; therefore, since not attributed to *Dioonites*, the exception to the rule in this particular case is removed, because that material is better assignable to aff. *Pterophyllum* sp.

3. The presence of Pterophyllum in the fossil flora of Romania. A number of species recorded since the beginning of paleobotanical research more than 165 years ago documents the presence of the genus *Pterophyllum* in the fossil flora of Romania. However, apart from the new species described in this paper, only one of the species, *P. pectinatum* (Jaeger, 1827) Csaki and Ulrichs, 1985 em. Czier, 2014 can be attributed with certainty to this genus, because of the transfer of some species to other genera, and because of the unknown or incompletely known epidermal characters of the rest of the species.

Considering the synonyms mentioned by Nathorst (1876, p. 45), the material described by Stur (1860) under the name *Pterophyllum marginatum* Unger (1850) nomenclaturally is transferred herein to *Anomozamites marginatus* (Unger, 1850) Nathorst, 1876. Krasser (1921) had already transferred *Pterophyllum imbricatum* Ettingshausen, 1852, and *Pterophyllum rigidum* Andrae, 1855 to *Ptilophyllum imbricatum* (Ettingshausen) Krasser, and to *Ptilophyllum rigidum* (Andrae) Krasser. However, the presence of the genus *Ptilophyllum* in Romania has been earlier discussed (Czier, 2010) and the determinations of the *Ptilophyllum*-like leaves revised (Czier, 2011). As shown there, with the exceptions of *P. maculatum* Givulescu, 1992, and *P.*

aninaensis Czier, 1995b, the rest of the Romanian species of *Ptilophyllum* are invalid and/or incorrectly assigned to that genus.

Pterophyllum cuspidatum Ettingshausen, 1852, *P. longifolium* Brongniart, 1828a, and *P. magoti* Semaka, 1958a were described only macroscopically by Andrae (1855) and by Semaka (1954, 1958a, 1962a); those specimens are aff. *Pterophyllum* sp., because of the unknown epidermal characters. *Pterophyllum oeynhausenianum* Göppert, 1844 described by Thomas (1930, p. 403) also is aff. *Pterophyllum* sp., because in that case only a cuticular description was given, and "unfortunately the identification of the specimen is somewhat doubtful".

Givulescu (1989) had nomenclaturally revised *Pterophyllum dunkerianum* Göppert described by Andrae (1855), as *Pseudocycas dunkeriana* (Göppert, 1844) Florin, 1933. Finally, *Pterophyllum inconforme* Givulescu, 1997 is invalid species, because it is lack of diagnosis; moreover, its adaxial epidermal characters are unknown, therefore the name cf. *Pterophyllum* sp. is acceptable for that material.

4. Geological Setting and Stratigraphy

4.1. Historical background. Anina is a coal-mining town in Caraş-Severin County, Banat region, Romania, eastern Central Europe. The locality, situated in the Southern Carpathians, is also known as Steierdorf, Stájerlak, Steierdorf-Anina, Stájerlakanina, and appears in the geological literature under all of these names (Czier, 1996b, 1998b). The woodsman Miklós Hammer discovered the coal deposits at Steierdorf-Anina in 1790 and the exploitation of the coal seams began in 1803 (Hantken, 1878). The first reference of the fossil plants coming from this locality consists of a note published by Foetterle (1850). However, the prospective significance of this locality in European paleobotany was not recognized until after the publication of Andrae's (1855) monograph. The Anina macroflora, with many pteridophyllaceous and equisetaceous species, dipteridaceous and matoniaceous ferns, pteridosperms, bennettitalean and ginkgoalean gymnosperms, represents a typical Mesophytic flora sensu Gothan (1912) of the European Province of the Euro-Sinian Paleofloristic Region (Czier, 2000a, 2014).

4.2. The Anina coalfield and anticline. The Anina coalfield contains a series of outcrops and mines situated on the flanks of the Anina anticline. The coal beds occur in the Early Jurassic continental deposits of the Reşiţa – Moldova Nouă sedimentary zone, which belongs to the Getic Unit of the Southern Carpathians (Răileanu et al., 1964; Mutihac, 1990; Mutihac et al., 2007). A geological map of the fossil plant locality is provided (Fig. 1).

The deposits along the axis of the Anina anticline are assigned to the Lişava Member, Ciudanoviţa Formation (Bucur, 1991). These deposits belong to the Variscan Molasse and consist of a succession of Early Permian conglomerates, micro-conglomerates, sandstones, and a red-violet clay horizon. This clay horizon contains a macroflora (Telegdi Roth, 1890; Răileanu et al., 1957) of Autunian age as indicated by the associated microfaunal assemblage (Biţoianu, 1987).

4.3. Lithostratigraphy. The Romanian Early Jurassic continental macroflora comes from tectonostratigraphic units of Eastern Carpathians (Leaota Unit), Southern Carpathians (Getic–Supragetic Units and Danubian Units), and Apuseni Mountains (Bihor Unit). Kovács et al. (2011) present ample details concerning all these units; considering the topic of the present paper I would just mention that although several formations contain plant fossils, the most important in this respect is the Steierdorf Formation (Section 4.3.1). Czier (1999a) clarified and discussed the lithostratigraphy of the Early Jurassic macrofloral deposits within all the tectonostratigraphic units in Romania, formally defined lithostratigraphic units and provided new names where was necessary.

The flanks of the Anina anticline consist of Alpine Sedimentary Cycle deposits that unconformably overlay the Permian sequence. Several lithostratigraphic units fit into this cycle. The brief description below refers those units that include the plant fossils at Anina.

4.3.1. The Steierdorf Formation. Three members represent the Steierdorf Formation (Bucur, 1991) at Anina and include the Dealul Budinic Conglomerate Member (Hettangian *pro parte*; Bucur, 1991), the Valea Terezia Sandstone Member (Hettangian *pro parte* – Sinemurian; Bucur, 1991), and the Uteriş Argillitic Member (Pliensbachian; Bucur, 1997).

The first two members show a lithofacies assemblage that closely resembles that at Gresten, Austria; both assemblages are without carbonate (Lachkar et al., 1984; Czier, 1999a, 2008). The Dealul Budinic Conglomerate Member is comprised of a coarse conglomerate and the Valea Terezia Sandstone Member is comprised of conglomerates, micro-conglomerates, sandstones, siltstones, clays, and coal seams. The latter member makes the fossiliferous Anina locality famous. Its macroflora occurs in several finely grained horizons, mainly at the bases and tops of the coal layers and in the sterile intercalations. The Valea Terezia Sandstone Member contains a microfloral assemblage too (Antonescu, 1973).

The Uteriş Argillitic Member consists of black bituminous argillites, with siderite concretions and thin coal intercalations. This member contains sporadic microfloral (Antonescu, 1973; Năstăseanu, 1984) and macrofloral (Andrae, 1855) assemblages.

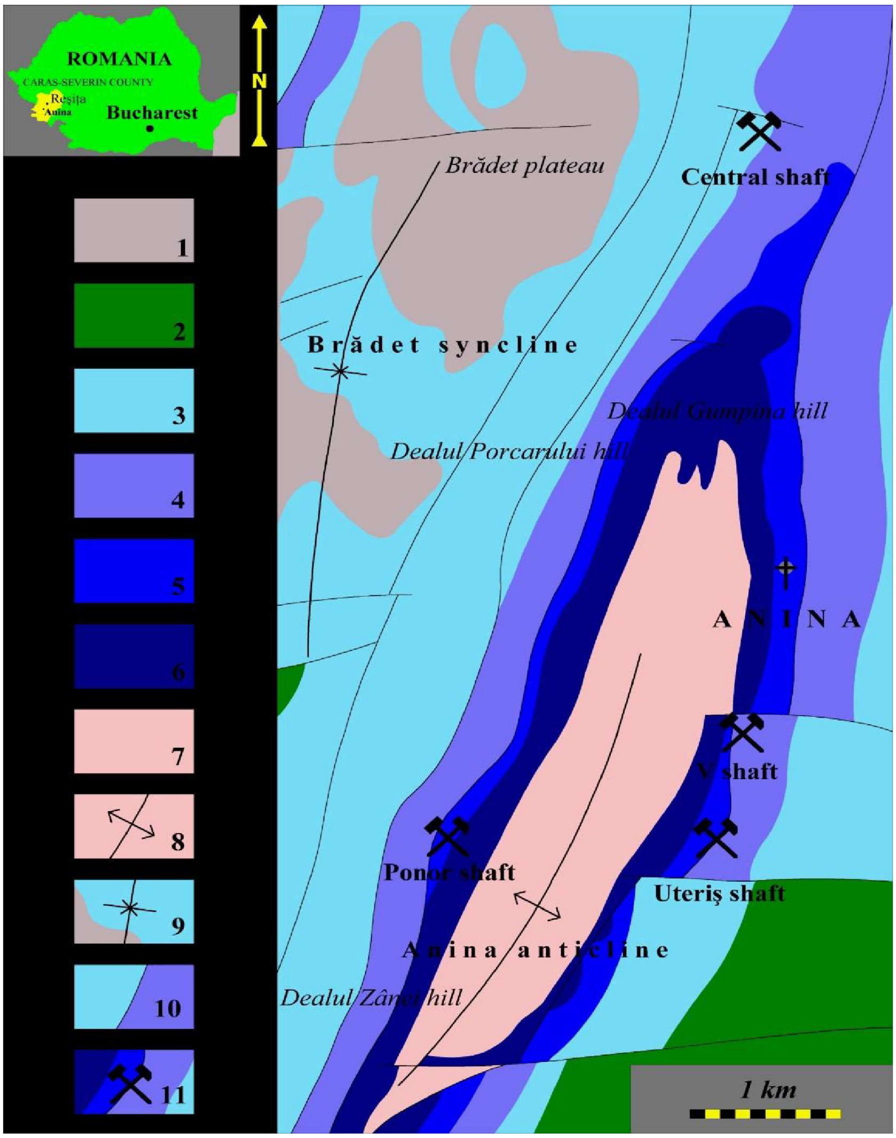

Fig. 1. Geological map of the fossiliferous locality Anina – after Czier (2008), with minor changes. (1) Quaternary; (2) Early Cretaceous; (3) Oxfordian – Tithonian; (4) Aalenian – Callovian; (5) Pliensbachian – Toarcian; (6) Hettangian *pro parte* – Sinemurian; (7) Early Permian; (8) Anticline axise; (9) Syncline axise; (10) Fault; (11) Mine.

Рис. 1. Геологическая карта местонахождения окаменелостей Анина – по Czier (2008) с незначительными изменениями. (1) чертвертичные отложения; (2) раннемеловые отложения; (3) оксфордский – титонский ярусы; (4) аленианский –калловианский ярусы; (5) плинсбахский – торцианский ярусы; (6) хеттангианский частично – синемурианский ярусы; (7) раннепермские отложения; (8) антиклинальная ось; (9) синклинальная ось; (10) разлом; (11) шахта.

4.3.2. The Dealul Zânei Formation (pro parte). The Dealul Zânei Formation (Bucur, 1991) at Anina is divided in two parts. The lower part (Toarcian) is named the Valea Sodol Marl Member (Czier, 1999a), whereas the upper part (Aalenian *pro parte*) conformably overlays the lower part and does not constitute a defined lithostratigraphic member.

Marls and calcareous marls with sandy marlstone intercalations comprise the lithology of the lower part. It contains invertebrate fossils indicating a Toarcian age (Mutihac, 1959; Năstăseanu, 1964; Bucur, 1997) and a macrofloral assemblage (Semaka, 1962b). The macroflora consists of *Anomozamites spectabilis* Semaka, 1962b, and a few other species (in revision). Those occur throughout the Early- to Middle Jurassic in the Getic Unit, which therefore makes it impossible to define a Toarcian biozone using macrofossils.

The upper part consists of marlstones and marly sandstones. It contains invertebrate fossils of Early Aalenian age and a poorly diversified macroflora (Semaka, 1962b).

4.4. Biostratigraphy. A simple scheme showing just the names of the marker fossils concentrates the essence of the Romanian continental Early Jurassic biozonation (Tab. 1).

Czier (1995c) has introduced the first variant of this zonation for the western Romania, because for that region do not exist previously defined phytostratigraphic units. Based on the absolute predominance of a species, that variant defines the *Clathropteris meniscioides* Biozone with its characteristic macrofloral assemblage, valid in Apuseni Mountains for the interval Hettangian *pro parte* – Sinemurian *pro parte*, because as it was shown, no evidence exists to separate in the lithostratigraphic columns of the localities the Hettangian stage from the Sinemurian with stratigraphic limits.

Czier (1999b) elaborated the second variant of the zonation for all Romania, replacing at the same time a local scheme (Semaka, 1970), which became no more applicable. The Romanian fossil flora does not contain the 'Rhaetian index fossil' *Lepidopteris*; nobody has described this genus in the fossil flora of Romania, and the Rhaetian stage is not documented in the Romanian continental stratigraphy. The 'Hettangian global marker' *Thaumatopteris* is absent too, because the thorough and detailed morphological study of Webb (1982) clearly shows that *Thaumatopteris* is a junior synonym of *Dictyophyllum*. However, *Dictyophyllum* is a principal element of the Mesophytic *Dictyophyllum–Clathropteris* Flora (Section 8); therefore, it is not a global biostratigraphic marker for Hettangian. In that second variant, Czier selected the most characteristic macrofloral assemblages for all the regions of Romania, and defined among others the *Banatozamites chlamydostomus* Subzone (Hettangian *pro parte* – Sinemurian) of the *Clathropteris meniscioides* Biozone (Hettangian – Sinemurian).

Table 1

The macro-phytostratigraphic scheme of the Romanian continental Early Jurassic. Based on Czier (1999b, 1999d, 2003), with minor changes and additions.
Макрофитостратиграфическая схема континентальной ранней юры Румынии. Из Czier (1999b, 1999d, 2003) с незначительными изменениями и дополнениями.

<table>
<tr><th colspan="2">AGE</th><th colspan="4">MACRO-PHYTOSTRATIGRAPHY</th></tr>
<tr><th rowspan="2">Standard name</th><th rowspan="2">Old name</th><th>Apuseni Mountains</th><th colspan="2">Southern Carpathians</th><th>Eastern Carpathians</th></tr>
<tr><th>Bihor Unit</th><th>Getic–Supragetic Units</th><th>Danubian Units</th><th>Leaota Unit</th></tr>
<tr><td rowspan="2">Toarcian</td><td>‘Liassic ζ’</td><td rowspan="5">∅</td><td rowspan="2"><i>A.s.</i></td><td rowspan="2">∅</td><td rowspan="4">∅</td></tr>
<tr><td>‘Liassic ε’</td></tr>
<tr><td rowspan="2">Pliensbachian</td><td>‘Liassic δ’</td><td rowspan="2"><i>C.l.</i></td><td><i>C.l.</i></td></tr>
<tr><td>‘Liassic γ’</td><td>∅</td></tr>
<tr><td rowspan="2">Sinemurian</td><td>‘Liassic β2’</td><td rowspan="3"><i>C.m.; B.c.</i></td><td><i>C.m.</i></td><td rowspan="2"><i>A.m.</i></td></tr>
<tr><td>‘Liassic β1’</td><td rowspan="2"><i>C.m.; S.m.</i></td><td rowspan="2"><i>C.m.; N.c.</i></td></tr>
<tr><td rowspan="2">Hettangian</td><td>‘Liassic α2’</td><td rowspan="2">∅</td></tr>
<tr><td>‘Liassic α1’</td><td>∅</td><td><i>C.m.</i></td><td><i>C.m.; L.l.</i></td></tr>
</table>

Notes. A.m. = *Anomozamites marginatus* Biozone; *C.m.* = *Clathropteris meniscioides* Biozone; *L.l.* = *Leptostrobus laxiflora* Subzone; *N.c.* = *Neocalamites carcinoides* Subzone; *B.c.* = *Banatozamites chlamydostomus* Subzone; *S.m.* = *Selenocarpus muensterianus* Subzone; *C.l.* = *Carpolithes liasinus* Biozone; *A.s.* = *Anomozamites spectabilis* assemblage; ∅ = no terrestrial plant macrofossils.

Примечания. A.m. = *Anomozamites marginatus* Biozone; *C.m.* = *Clathropteris meniscioides* Biozone; *L.l.* = *Leptostrobus laxiflora* Subzone; *N.c.* = *Neocalamites carcinoides* Subzone; *B.c.* = *Banatozamites chlamydostomus* Subzone; *S.m.* = *Selenocarpus muensterianus* Subzone; *C.l.* = *Carpolithes liasinus* Biozone; *A.s.* = *Anomozamites spectabilis* группа; ∅ = нет наземных расительных макрофоссилий.

The third variant, rendered on this occasion, contains minor changes. These are the addition to the scheme of the tectonostratigraphic units, the change to *Anomozamites marginatus* of the name *Pterophyllum marginatum* (because of a synonymy already mentioned), and the usage of standard colours.

5. Material and methods. Three specimens consisting of forty-five leaf compressions, preserved on three slabs of fine-grained clastic sedimentary rocks, were studied in details. One of these specimens is appropriate for holotype designation because the cuticle and hypodermal matrix is well preserved (Section 6).

Although the fossil locality is the same, the other two specimens were collected from different sampling points between the last decade of the 19th Century and before the end of the WW II. Additionally, two stem compressions are preserved on two of the slabs, but these are not designated as types, because there is no clear evidence of organic connection with the leaves.

All specimens were collected from the Anina coal-bearing sequence of the Valea Terezia Sandstone Member, Steierdorf Formation and the *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone of the Romanian Early Jurassic (Czier, 2014).

5.1. Storage data. Specimen no. 1 consists of a hand specimen (slab HNHM-BP 602041 with 15 leaves), a LM slide (HNHM-BP-LM-ZC-24), and a SEM stub (HNHM-BP-SEM-ZC-1). The hand specimen was sold to the Museum in 1892 by Mr. Ede Thermák.

Specimen no. 2 includes a hand specimen (slab HNHM-BP-602261 with 20 leaves) and LM slide (HNHM-BP-LM-ZC-8). The name of the collector and the exact year the specimen was collected are unknown, but judging from the old keeper box, it appears that the specimen was collected during or prior to the first half or the last century.

Specimen no. 3 includes a hand specimen (slab HNHM-BP-602321 with 10 leaves) and a LM slide (HNHM-BP-LM-ZC-9). The hand specimen was collected from the Frigyes Shaft in the 1940s. It became part of the paleobotanical collection of the Hungarian Natural History Museum when it was transferred from the mineralogical collection of the Hungarian National Museum.

5.2. Microscopy. The material was analysed under light microscopy (LM) with MC1 research microscope and scanning electron microscopy (SEM) with JEOL JSM-35 scanning microscope.

The specimens are exquisitely preserved, which has permitted on this occasion to examine the cuticle of the rachis, the adaxial and abaxial cuticle, and hypodermal matrix of the lamina. This is the first time that *Pterophyllum* rachis cuticle and hypodermal matrix have been examined.

The cuticle was prepared using the preparation methods for LM and

SEM described in Czier (2014). However, cuticle preparation of the second specimen needed special attention, because this specimen had cuticle preserved only on small areas and the attachment of the cuticle to the rock was very strong. A piece of cuticle and rock was successfully detached from the middle of a leaf segment. The fragment was immersed in Hydrofluoric acid (HF 47%) for three days. The HF dissolved the silica component of the rock and freed the leaf cuticle. After this treatment, the cuticle was easily separated from the rest of the rock by the means of a preparation needle.

6. Systematic paleontology

Class Cycadopsida Brongniart, 1843
Order Bennettitales Engler, 1892
Family Williamsoniaceae (Carruthers, 1870) Nathorst, 1913
Genus *Pterophyllum* Brongniart, 1825 emend. Harris, 1969 emend. Watson and Sincock, 1992

Pterophyllum semseyanus n. sp.
(Figs. 2A–D, 3, 4A–D, 5, 6A–D, 7A–D, 8)

Etymology: In honour of Dr. Andor Semsey (22 December 1833, Kassa – 14 August 1923, Budapest), member of the Hungarian Academy of Sciences, who contributed with substantial support to the enrichment of the historic plant fossil collections and of other scientific (paleontologic, mineralogical, petrographic, meteorite) collections of the museums in Budapest and of the Geological Institute of Hungary. Pozsonyi (2002) and Kordos (2009) publish details concerning these collections and the financial support offered by baron Semsey for the development of the geology and paleontology in Hungary.
Holotype: Hand specimen HNHM-BP-602041, slides HNHM-BP-LM-ZC-24 and HNHM-BP-SEM-ZC-1 (Figs. 2A, B, D, 4D, 6B, C, D, 7A, C, D, 8).
Stratum typicum: Steierdorf Formation, Valea Terezia Sandstone Member (Hettangian *pro parte* – Sinemurian).
Type locality: Anina (coordinates 45°05′30″ N.L., 21°51′12″ E.L.), Caraş-Severin County, Banat region, Romania.
Additional material examined: Hand specimens HNHM-BP-602261 and HNHM-BP-60232; Slides: HNHM-BP-LM-ZC-8 and HNHM-BP-LM-ZC-9.
Diagnosis: Lamina narrow, segments ending in rounded apex, veins delicate and simple. Rachis epidermis with elongate trapezoidal cells, adaxial epidermis smooth, abaxial epidermis zoned and papillate, stomata with deep polar spaces. Hypodermis with rectangular hypodermal cells, marked intercellular spaces, and large cell wall corner spaces.

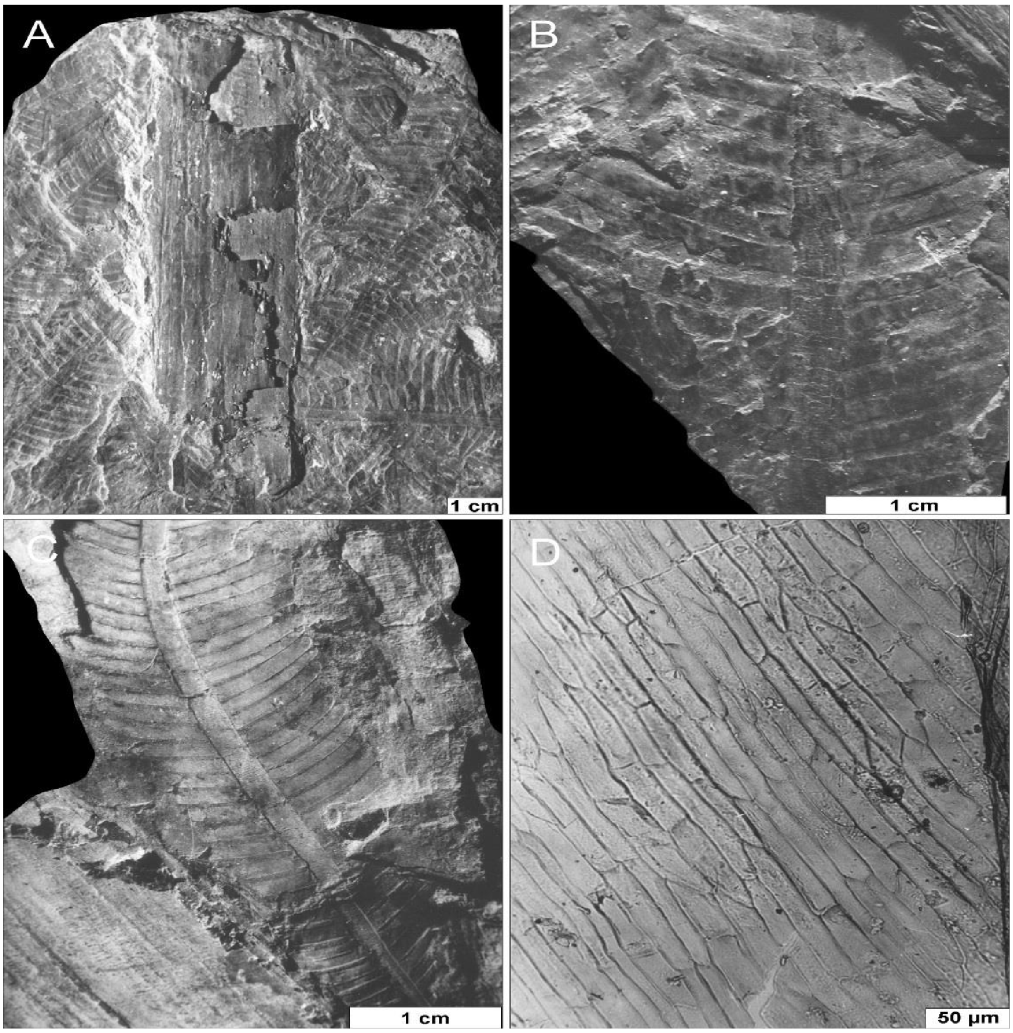

Fig. 2. *Pterophyllum semseyanus* Czier n. sp. From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) Foliage (holotype, HNHM-BP-602041) around a stem; (B) Leaf showing lateral insertion of the segments (holotype, HNHM-BP-602041); (C) Basal-medial portion of a leaf (HNHM-BP-602261), and portion of a stem (bottom and left); (D) Rachis cuticle, showing rows of elongate-trapezoidal cells (holotype, HNHM-BP-LM-ZC-24).

Рис. 2. *Pterophyllum semseyanus* Czier n. sp из Анины, Румыния, часть песчаника формации Valea Terezia, формация Штаердорф, подзона *Banatozamites chlamydostomus* биозоны *Clathropteris meniscioides*, Хеттангий частично – Синемурий. (A) Листья (holotype, HNHM-BP-602041) вокруг стебля; (B) Лист с латеральным прикреплением сегментов (голотип, HNHM-BP-602041); (C) Базально-медиальная часть листа (HNHM-BP-602261) и часть стебля (основание слева); (D) кутикула черешка, демонстрирующая ряды удлиненно-трапециевидных клеток (голотип, HNHM-BP-LM-ZC-24).

Description and measurements: In close association with the holotype, lies a *Bucklandia* stem compression, which belongs likely to *Pterophyllum semseyanus*. It is 110 mm long, 25 mm wide, 1–2 mm thick, and possesses 8–10 longitudinal furrows. There is no clear evidence of organic connection between the stem and leaves and they are arranged and preserved in all directions (Fig. 2A). The disorderly preservation suggests they were deposited under stormy sedimentation or the leaves and stems were not fresh (wilted). The same remark is applicable also to the second specimen, of which the irregularly disposed leaves surround a 220 mm long and 40 mm wide stem (Fig. 2C). The leaves have short and narrow petiole; the petiole of a near complete specimen is 10 mm long and 1 mm wide. The leaves are small and narrow, oblanceolate, having apex obtuse. The length of the 45 leaf fragments is between 40–60 mm, and the estimated maximum length of the largest complete leaves is about 100 mm. The lamina of the leaves have a width of 15–30 mm; the largest mature leaves sometimes are slightly wider, up to 35 mm. The rachis is strong, generally straight in most of the specimens; some leaves are arched in the distal third. The width of the rachis in the basal portion of the leaves ranges from 0.8 to 2 mm, gradually increases to the upper third up to 2 to 4.5 mm, and then decreases distally to 1 to 3 mm. The segments are laterally attached to the rachis at angles of between 70–90° (Fig. 2B). They are slightly expanded basally, inserted oppositely to sub-oppositely. The segments are slightly convex, with margins entire; the distance between the margins of the adjacent segments is of 0.3 to 1.5 mm. They are linear or arch in the acroscopic direction, ending in rounded apex (Fig. 3). Typical segments range from 5 to 25 mm long and 1 to 2.2 mm wide. The venation is delicate; the veins are very fine. The segments possess 3–6 simple veins arising from the base of the segment and running parallel with the margins. The cuticle of the rachis shows an epidermis with parallel rows of elongate-trapezoidal cells (Fig. 2D). The epidermal cells of the rachis have straight anticlinal cell walls, and smooth periclinal walls; no stomata or ornamentation of any type is present. The dimensions of the cells range from 60 to 120 μm long and 10 to 20 μm wide. The lamina is hypostomatic, with distinct costal and intercostal fields (Fig. 4C). All the ordinary epidermal cells possess sinuous anticlinal cell walls. Both the adaxial and the abaxial cuticle have a constant thickness of about 4 μm (range in specimens from 3 to 5 μm), measured in folds. The adaxial cuticle indicates rows of rectangular (Fig. 4A), isodiametric to irregular (Fig. 4B) epidermal cells, mainly oblong elongate to sometimes trapezoidal in the costal fields, mainly squarish, sometimes rounded to polygonal in the intercostal fields (Fig. 5). The cells are disposed with their longer anticlinal walls oriented along the veins. The rows usually are conspicuous, sometimes somewhat less; in the latter case, irregularly shaped cells may be present among the mainly rectangular cells. The anticlinal cell walls are sinuous; the periclinal cell walls are smooth and lack ornamentation. The cells of the costal fields are up to twice longer and narrower than the cells of the intercostal fields. The cell dimension limits in the case of the costal fields that contain 3–5 rows of cells per field are 40–90 / 18–25 µm while the intercostal fields contain 6–8 rows of cells per field and are 20–45 / 36–50 µm. Therefore, the dimensions of the adaxial epidermal cells range between 20–90 / 18–50 µm. The abaxial cuticle shows zoned (i.e. differentiated) epidermis (Fig. 4D). It is differentiated in 150–380 µm wide marginal zones along the edges of the segment and a 700–1400 µm wide central zone between them. The marginal zones consist of epidermal cells ranging from 50 to 120 µm in length and from 15 to 40 µm in width, which resemble the shape of the cells of the adaxial epidermis, but they are up to twice longer and narrower than the latter ones. The cuticle of the holotype shows that the epidermal cells of the marginal zones become more and more elongate nearer to the segment's edges. One or two rows of very elongate cells are present occasionally along the edges even in the adaxial epidermis. The costal and intercostal fields are generally conspicuous and comprise the central zone (Fig. 6A). The costal fields are composed of 2–3 rows of epidermal cells. The rows correspond to the vein courses, and are 60–100 µm wide. The costal fields alternate with 100–280 µm wide intercostal fields that are composed of 3–5 more or less conspicuous rows of stomata and epidermal cells. The epidermal cells of the central zone differ in size, shape, and ornamentation from the cells indicated by the adaxial cuticle. They generally are slightly wider and more isodiametric, between 30–80 / 20–50 µm in the costal fields, and 30–60 / 20–70 µm in the intercostal fields. The costal field epidermal cells are mainly rectangular and, sometimes trapezoidal; intercostal epidermal cells are rectangular, polygonal, rounded, to irregular in shape (Figs. 6A, 6B, 6C). Each ordinary epidermal cell possessed on its outer periclinal wall a central papilla with circular cutinized base of range 12 to 15 µm diameter (Fig. 6B). The cutinized bases of the papillae are clearly visible as some dark round spots in the preparations that show the outer side of the abaxial cuticle surface (Fig. 6D). The subsidiary cells may be papillate or possess a central dorsal cuticle thickening. The stomata usually are perpendicularly oriented to the veins, showing regular transverse orientation, although sometimes they are more or less oblique, with the pore oriented up to 50° from the others (Fig. 6C). Stomata are densely scattered, with a density of 120–160 stomata per square mm and with a stomatal index around of 15%. The abaxial cuticle shows brachyparacytic, sunken stomatal apparatus, with semi-circular to semi-elliptical guard cells, deep polar spaces, rectangular to slightly rounded subsidiary cells possessing straight to slightly sinuous anticlinal walls (Fig. 7A). The guard cells have strongly cutinized crescent shaped dorsal thickenings and weakly cutinized polar ends.

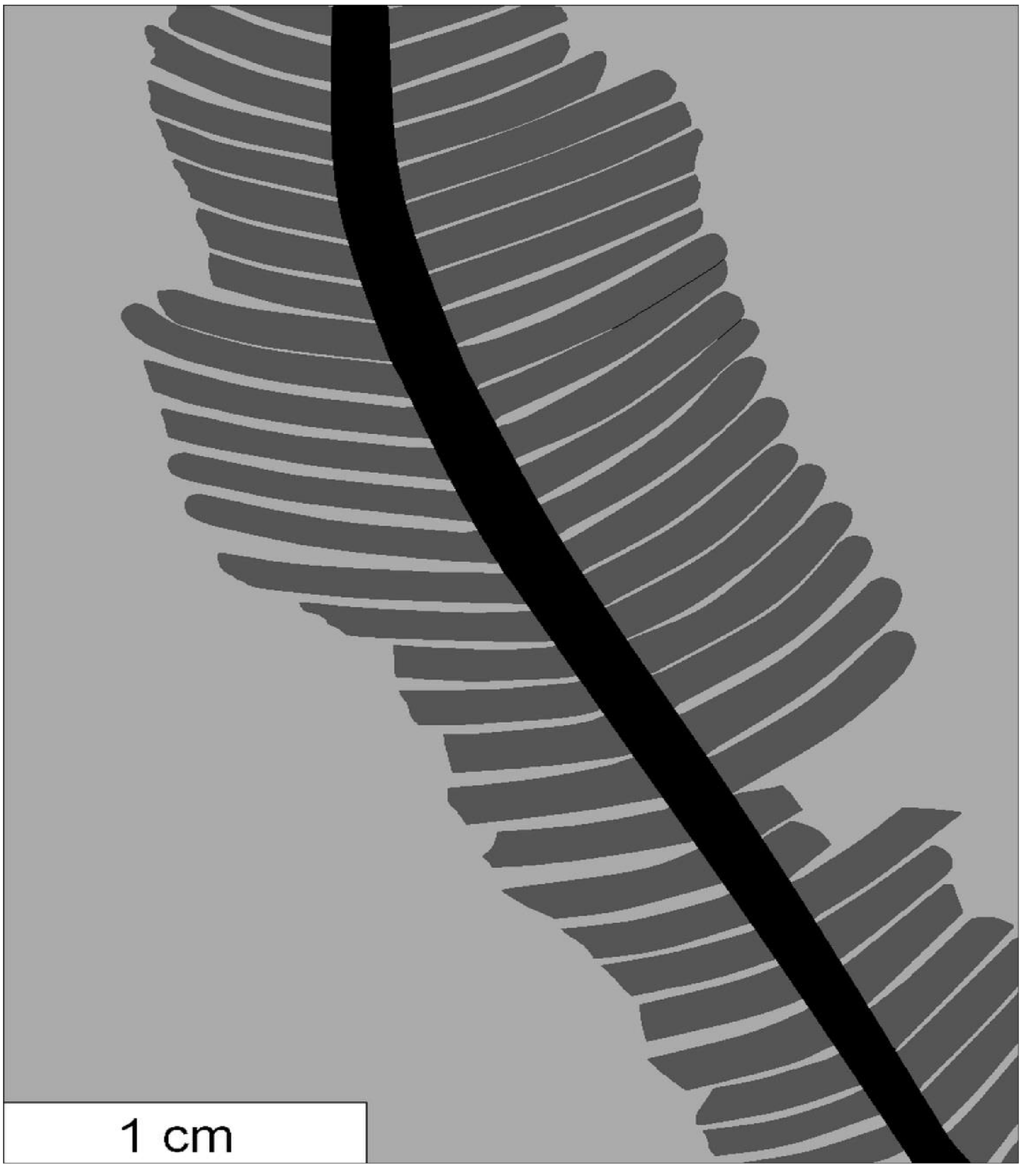

Fig. 3. *Pterophyllum semseyanus* Czier n. sp. From Anina, Romania, the Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. Portion of a leaf showing the rachis and the lateral attached segments with rounded apex (HNHM-BP-602261).

Рис. 3. *Pterophyllum semseyanus* Czier n. sp. из Анины, Румыния, часть песчаника формации Valea Terezia, формация Штаердорф, подзона *Banatozamites chlamydostomus* биозоны *Clathropteris meniscioides*, Хеттангий частично – Синемурий. Часть листа, демонстрирующая черешок и боковое крепление сегментов с округлыми вершинами (HNHM-BP-602261).

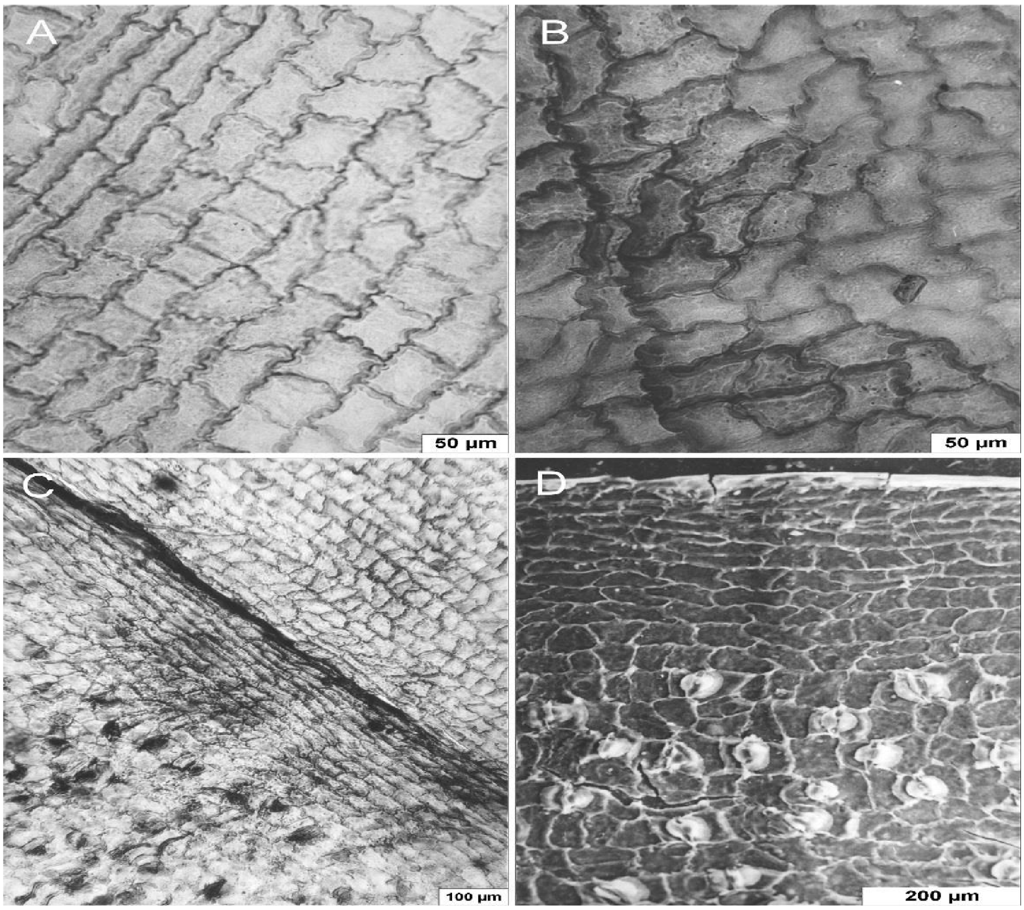

Fig. 4. *Pterophyllum semseyanus* Czier n. sp. From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) Inner adaxial cuticle showing the rectangular epidermal cells (HNHM-BP-LM-ZC-9); (B) Inner adaxial cuticle showing the isodiametric, polygonal, and irregular-shaped epidermal cells (HNHM-BP-LM-ZC-9); (C) Outer edge of the adaxial and abaxial cuticle (HNHM-BP-LM-ZC-8). Note the elongate epidermal cells near the leaf edge, especially on the abaxial surface; (D) Inner abaxial cuticle showing the marginal zone composed of rows of epidermal cells and the central zone composed of stomata and epidermal cells (holotype, HNHM-BP-SEM-ZC-1).

Рис. 4. *Pterophyllum semseyanus* Czier n. sp. из Анины, Румыния, часть песчаника формации Valea Terezia, формация Штаердорф, подзона *Banatozamites chlamydostomus* биозоны *Clathropteris meniscioides*, Хеттангий частично – Синемурий. (A) Внутренняя надосная кутикула, демонстрирующая прямоугольные эпидермальные клетки (HNHM-BP-LM-ZC-9); (B) Внутренняя надосная кутикула, демонстрирующая изодиаметрические, многоугольные и разноформенные эпидермальные клетки (HNHM-BP-LM-ZC-9); (C) Внеший край адаксиальной и абаксиальной кутикулы (HNHM-BP-LM-ZC-8). Обратите внимание на удлиненные эпидермальные клетки вблизи края листа, в особенности на абаксиальной поверхности; (D) Внутренная абаксиальная кутикула, демонстрирующая краевую зону, состоящую из двух рядов эпидермальных клеток и центральную зону, состоящую из устьиц и эпидермальных клеток (голотип, HNHM-BP-SEM-ZC-1).

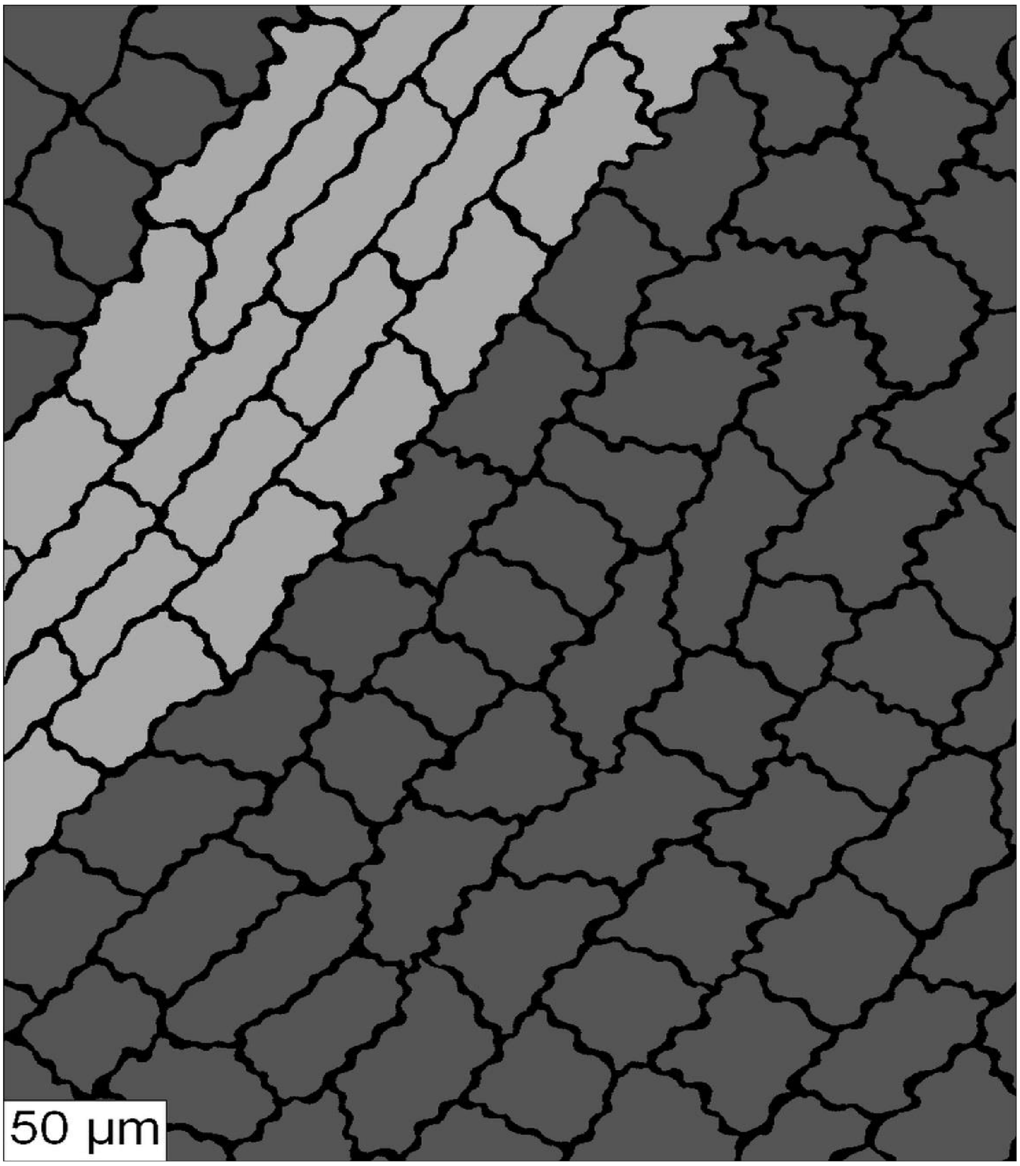

Fig. 5. *Pterophyllum semseyanus* Czier n. sp. From Anina, Romania, the Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. Adaxial cuticle indicating rectangular epidermal cells, costal field with more elongate and narrow cells between two intercostal fields (HNHM-BP-LM-ZC-9).

Рис. 5. *Pterophyllum semseyanus* Czier n. sp. из Анины, Румыния, часть песчаника формации Valea Terezia, формация Штаердорф, подзона *Banatozamites chlamydostomus* биозоны *Clathropteris meniscioides*, Хеттангий частично – Синемурий. Адаксиальная кутикула, демонстрирующая прямоугольные эпидермальные клетки, а также поле жилки с более удлиненными клетками между двумя межжилковыми полями (HNHM-BP-LM-ZC-9).

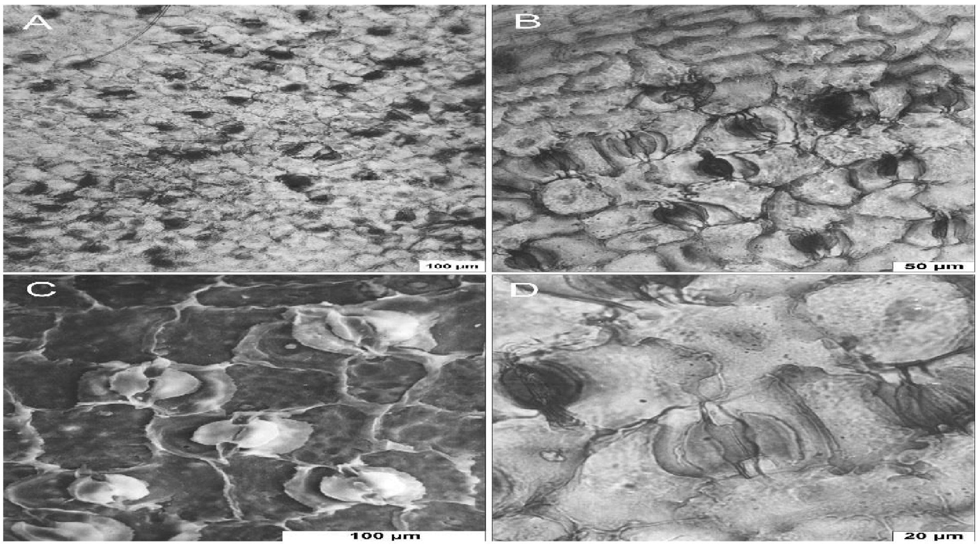

Fig. 6. *Pterophyllum semseyanus* Czier n. sp. From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) Outer abaxial cuticle showing the costal field, which corresponds to a vein and composed of three rows of epidermal cells that are located between two intercostal fields that correspond to the region between the veins (HNHM-BP-LM-ZC-8); (B) Outer abaxial cuticle showing the epidermal cell details (holotype, HNHM-BP-LM-ZC-24). Top and left: non-stomatal band of epidermal cells in rows parallel with the veins. Bottom and right: stomatal region showing stomata with regular transverse orientation, with epidermal cells located between the stomata and with each possessing a circular base of a cutinized papilla; (C) SEM photograph of the central zone of the inner abaxial cuticle, showing typical epidermal cells and stomata with regular transverse to oblique orientation (holotype, HNHM-BP-SEM-ZC-1). Note the pore of each stoma and the polar spaces; (D) Outer abaxial cuticle showing the epidermal cells with cutinized circular papilla bases and transversely oriented stomata (holotype, HNHM-BP-LM-ZC-24).

Рис. 6. *Pterophyllum semseyanus* Czier n. sp. из Анины, Румыния, часть песчаника формации Valea Terezia, формация Штаердорф, подзона *Banatozamites chlamydostomus* биозоны *Clathropteris meniscioides*, Хеттангий частично – Синемурий. (A) Внешняя абаксиальная кутикула, демонстрирующая жилковое поле, которая соотносится с жилкой и состоит из трех рядов эпидермальных клеток, расположенных между двумя межжилковыми полями (HNHM-BP-LM-ZC-8); (B) Внешняя абаксиальная кутикула, демонстрирующая детали строения эпидермальных клеток (голотип, HNHM-BP-LM-ZC-24). Сверху и слева: лишенный устьиц поясок с эпидермальными клетками, расположенными рядами параллельно жилкам. Снизу и справа: устьичный регион с устьицами в правильно поперечной ориентации, с эпидермальными клетками, расположенными между устьицами и несущими основания креплений папилл; (C) фотография электронного сканирующего микроскопа центральной зоны внутренней абаксиальной кутикулы, демонстрирующая типичные эпидермальные клетки и устьица с правильной поперечной и косой ориентацией (голотип, HNHM-BP-SEM-ZC-1). Обратите внимание на поры каждого устьица и полярные пространства; (D) Внешняя абаксиальная кутикула, демонстрирующая эпидермальные клетки с основаниями кутинизированных папилл и поперечно-ориентированными устьицами (голотип, HNHM-BP-LM-ZC-24).

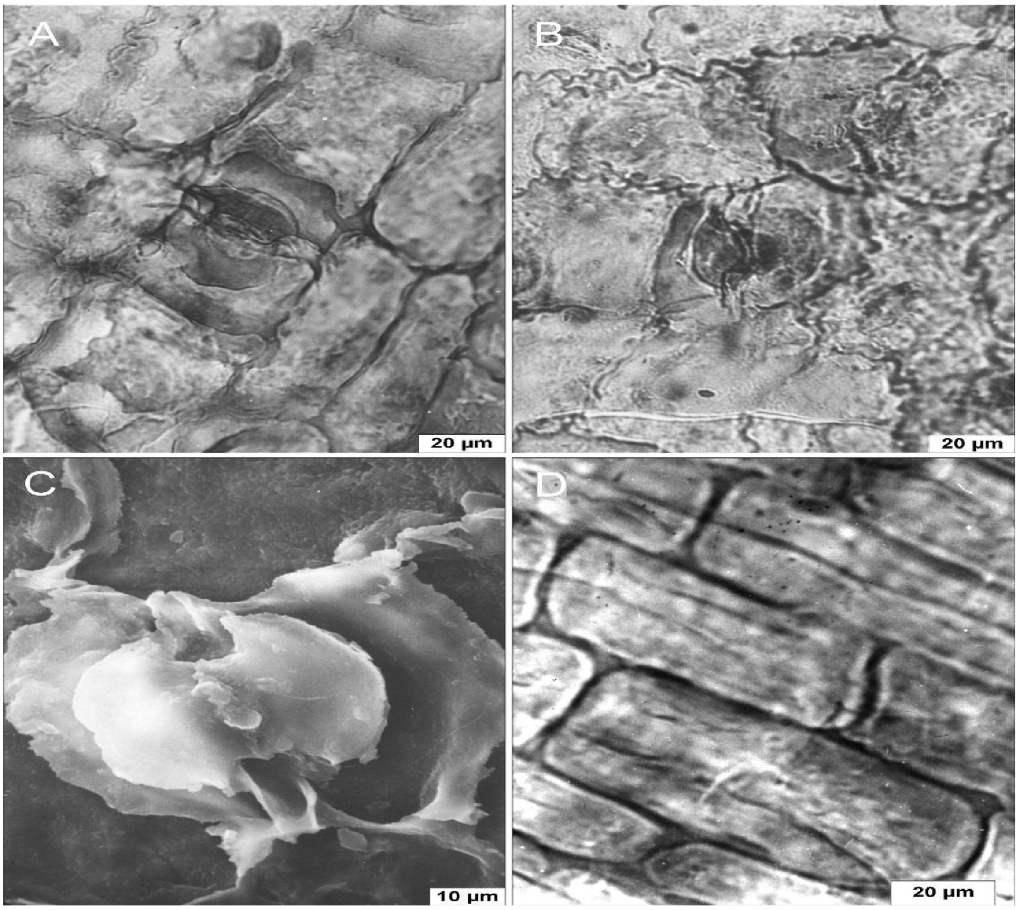

Fig. 7. *Pterophyllum semseyanus* Czier n. sp. From Anina, Romania, Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. (A) Outer abaxial cuticle showing the brachyparacytic stomatal apparatus between the papillate epidermal cells (holotype, HNHM-BP-LM-ZC-24); (B) Outer abaxial cuticle showing the sinuous-walled epidermal cells surrounding a stomatal apparatus (HNHM-BP-LM-ZC-8); (C) High resolution SEM photo showing typical stomatal apparatus (holotype, HNHM-BP-SEM-ZC-1). Note the typical polar spaces; (D) Hypodermal matrix, showing rows of hypodermal cells (holotype, HNHM-BP-LM-ZC-24).

Рис. 7. *Pterophyllum semseyanus* Czier n. sp. из Анины, Румыния, часть песчаника формации Valea Terezia, формация Штаердорф, подзона *Banatozamites chlamydostomus* биозоны *Clathropteris meniscioides*, Хеттангий частично – Синемурий. (A) Внешняя абаксиальная кутикула, демонстрирующая широкий обкладочный аппарат устьица между эпидермальными клетками, несущими папиллы (голотип, HNHM-BP-LM-ZC-24); (B) Внешняя абаксиальная кутикула, демонстрирующая синусостенные эпидермальные клетки, окружающие устьичный аппарат (HNHM-BP-LM-ZC-8); (C) Фото высокого разрешения электронного сканирующего микроскопа, демонстрирующее типичный устьичный аппарат (голотип, HNHM-BP-SEM-ZC-1). Обратите внимание на типичные полярные зоны; (D) Гиподермальный матрикс, демонстрирующий ряды гиподермальных клеток (голотип, HNHM-BP-LM-ZC-24).

Fig. 8. *Pterophyllum semseyanus* Czier n. sp. From Anina, Romania, the Valea Terezia Sandstone Member, Steierdorf Formation, *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone, Hettangian *pro parte* – Sinemurian. Hypodermal matrix, indicating rows of hypodermal cells with marked elongate intercellular spaces and large triangular to quadrilateral cell wall corner spaces (holotype, HNHM-BP-LM-ZC-24).

Рис. 8. *Pterophyllum semseyanus* Czier n. sp. из Анины, Румыния, часть песчаника формации Valea Terezia, формация Штаердорф, подзона *Banatozamites chlamydostomus* биозоны *Clathropteris meniscioides*, Хеттангий частично – Синемурий. Гиподермальный матрикс, демонстрирующий ряды гиподермальных клеток с заметными удлиненными межклеточными пространствами и большими треугольными или четырехугольными пространствами на стыке нескольких клеток (голотип, HNHM-BP-LM-ZC-24).

Guard cells typically are 36 µm long and 18 µm wide when they are semi-circular and up to 40 µm long and 16 µm wide when they are semi-elliptical in shape. Therefore, the stoma length and width range from 36 to 40 µm, and 32 to 36 µm. The width of the subsidiary cells does not differ from the width of the ordinary epidermal cells, but they are usually shorter (Fig. 7B), with their length from 20 to 50 µm. The maximal diameter of the stomatal aperture is between 16–18 µm. The polar spaces at its ends appear clearly, especially in SEM microscopy (Fig. 7C). The preserved hypodermal matrix shows longitudinal rows of more or less elongate, rectangular, cutinized hypodermal cells (Fig. 7D), marked elongate intercellular spaces, and large triangular to sometimes quadrilateral cell wall corner spaces (Fig. 8). The hypodermal cells possessed straight cell walls; the bordering walls of the neighbouring cells are located 2–4 µm from one another. The length of the cells ranges from 70 to 90 µm, their width from 20 to 40 µm.

Discussion: Pterophyllum semseyanus is described as a new species because it possesses a number of diagnostic characters, some of them representing the first evidence for the existence of Hypodermal Matrix Mechanism (HMM) in Bennettitales. The morphological, epidermal, and cuticle specific characters that differentiate *Pterophyllum semseyanus* leaves are: the short petiolate, oblanceolate, small and narrow lamina; the arched segments ending in rounded apex; the delicate venation consisting of a few simple veins; the rachis epidermis consisting of parallel rows of elongate trapezoidal cells; the hypostomatic lamina; the sinuous anticlinal cell walls of all the ordinary epidermal cells; the smooth periclinal cell walls of the adaxial epidermal cells; the typically differentiated abaxial epidermis; the papillate outer periclinal cell walls of the abaxial ordinary epidermal cells; the densely

Table 2

The new species *Pterophyllum semseyanus* compared to relevant species of the genus.
Новый вид *Pterophyllum semseyanus* в сравнении с другими актуальными видами рода.

Species	*Pterophyllum filicoides* (Schlotheim, 1822) Zeiller, 1906	*Pterophyllum aequale* (Brongniart, 1825) Nathorst, 1878 em. Pott and McLoughlin, 2009	*Pterophyllum pectinatum* (Jaeger, 1827) Csaki and Ulrichs, 1985 em. Czier, 2014	*Pterophyllum brevipenne* Kurr ex. Schenk, 1864 em. Pott, Van Konijnenburg-Van Cittert, Kerp and Krings, 2007	*Pterophyllum subaequale* Hartz, 1896 em. Pott and McLoughlin, 2009	*Pterophyllum ptilum* Harris, 1932	*Pterophyllum semseyanus* Czier n. sp.
Character							
Macromorphology							
Outline of the petiole	prominent; up to about 1/5th of the length of the leaf	up to 4 mm wide at the base	long; about 1/4th of the length of the leaf	basally widened; shorter than 1/10th of the length of the leaf	prominent; 10 mm wide at the base	unknown (petiole is not preserved)	short and narrow; about 10 mm long and 1 mm wide
Outline of the leaf lamina	regular, oblong to broadly oval	oblong to lanceolate	thin and flat, oblong to elliptic-elongate	regular oblong to lanceolate or spatulate to inverted-conical	oblong to broadly oval	oblong	narrow, oblanceolate
Shape of the leaf apex	obtuse, rounded	unknown	rounded	obtuse, rounded	unknown	obtuse, rounded	obtuse
Length of incomplete leaves	up to 470 mm	up to 148 mm	up to 214 mm	up to 227 mm	up to 200 mm	up to 50 mm	up to 60 mm

Width of incomplete leaves	up to 203 mm	up to 53 mm	up to 110 mm	up to 60 mm	up to 70 mm	up to 30 mm	up to 35 mm
Length of complete leaves	unknown	200–220 mm	about 270 mm	unknown	300–350 mm	about 200 mm	about 100 mm
Width of complete leaves	unknown	unknown	120 mm	unknown	80 mm	70 mm	15–35 mm
Outline of the rachis	prominent, longitudinally striate	narrow and smooth or transversely wrinkled	not prominent, slender, longitudinally finely striate	prominent, longitudinally striate	prominent, wrinkled, transversely striate	narrow, transversely striate	strong, mostly straight and smooth
Width of the rachis	unknown	up to 2 mm	1.5–2 mm	unknown	unknown	up to 2 mm	0.8–4.5 mm
Attachment of the leaf segments to the rachis and their base	basally more or less constricted, depending of the segment position in the leaf	perpendicularly inserted, not constricted basally	perpendicularly to slightly obliquely inserted, separate to slightly confluent basally, margins may be even decurrent	usually broadly attached, but may occasionally display a profound basal constriction	almost perpendicularly inserted, basally slightly widened, more or less expanded	not constricted basally	perpendicularly to slightly obliquely inserted, basally slightly expanded
Positioning of the leaf segments	oppositely	oppositely to suboppositely	oppositely to suboppositely	oppositely; the proximal one or two leaf segments often lack counterparts on the opposite side of the rachis	oppositely to suboppositely	oppositely to suboppositely	oppositely to suboppositely
Distance between the individual leaf segments	regular within a single leaf, however, intraspecific variations may occur between different leaves	consistent within a single leaf	0.5–3 mm, never exceeding their width; densely to slightly remotely set segments	more or less the same within a single leaf, but may vary slightly between individual leaves; closely spaced segments	consistent within a single leaf, however, variations may occur between different leaves; relatively well separated segments	there is almost no space between them; densely arranged segments	0.3–1.5 mm, does not exceed their width; densely to remotely set segments
Shape of the leaf segments	long and narrow; parallel-sided to spatulate	oblong to linear-lanceolate; narrow, parallel-sided to linear; mostly parallel-sided	elongate, linear or slightly arched in the acroscopic direction, more or less narrowed in their proximal third	narrow and short, spatulate; parallel-sided	long and narrow, linear parallel-sided to curved slightly towards leaf apex, falcate	long and narrow, parallel-sided	linear to more or less arched in the acroscopic direction, having constant width along their entire length
Apex of the leaf segments	obtuse to acutely rounded	mostly truncate; obtusely rounded in some proximal leaflets; commonly with a small central notch	rounded to obtusely rounded	bluntly rounded	obtuse to acutely rounded; large variability	truncate to obtusely rounded	rounded
Length of the leaf segments	up to 110 mm; the proximal leaf segments are short; length slightly increases toward the middle of the leaf, and then gradually decreases toward the leaf tip	15–28 mm; the basal most leaflets are short but of the same width as the leaflets in the distal part of the leaf; length increases slightly toward the middle of the leaf, and then persists with uniform dimensions towards the leaf tip	12–88 mm; usually about 50 mm; segments shorter in the proximal third of the leaf than in the rest of its part	up to 27 mm; proximal segments short, length increases to the apical third of the leaf, gradually decreases towards the leaf apex	up to 38 mm; proximal segments short, length slightly increases towards the middle of the leaf, gradually decreases towards the leaf tip	up to 14 mm; proximal leaflets short	5–25 mm; the proximal leaf segments are short, but the length of the segments gradually increases from the leaf base towards near the apex.
Width of the leaf segments	2–9 mm	3–7 mm	2–4 mm	2.5–5 mm	4–6 mm	1–2 mm	1–2.2 mm
Leaf segment length / width ratio	7–22:1	4–6:1	10–25:1	4–6:1	unknown	10–14:1	5–12:1

Number of veins entering the base of each segment	numerous	up to 17	about 7	numerous	10–12	up to 10	3–6
Bifurcation of veins in the segment	limited to the proximal portion; usually once near the base, occasionally in the proximal portion; veins close to the margins do not fork	basally; usually close to the base, few additionally in the proximal portion; veins close to the margins do not fork	anywhere, but mainly in the proximal half; veins simple, occasionally bifurcated; some veins close to the margins fork	not limited to basal portion; usually near the base, but veins near the margins may fork elsewhere	a few close to the base; sparsely additionally in the proximal portion; veins close to the margins do not fork	unknown (not evident)	veins simple, very fine
General epidermal anatomy							
Stomatic character of the leaf	amphistomatic, with few, occasionally present stomata on the adaxial surface	hypostomatic	hypostomatic	amphistomatic, with few stomata on the adaxial surface, less than on the abaxial surface	hypostomatic	hypostomatic	hypostomatic
Distinctness of the adaxial costal fields	distinguishable	difficult to distinguish	distinguishable	distinguishable	distinguishable	indistinguishable	distinguishable
Zonation of the abaxial epidermis	no	no	no	no	no	no	yes
Distinctness of the abaxial costal fields	distinguishable	readily distinguishable	distinguishable	distinguishable	distinguishable	distinguishable	distinguishable, sometimes rather difficultly
Adaxial epidermal anatomy							
Costal fields							
Number of epidermal cell rows per field	unknown	unknown	2–3	unknown	up to 2–3	unknown	3–5
Shape of the epidermal cells	rectangular; narrow; elongate; isodiametric	rectangular; elongate; isodiametric	rectangular; narrow	rectangular; isodiametric	rectangular	rectangular; narrow	rectangular; isodiametric; irregular; oblong elongate; trapezoidal
Epidermal cell length	45–145 µm	up to 90 µm	20–60 µm; typically about 50 µm	42–85 µm	up to 100 µm	up to 100 µm; mostly 55–70 µm	40–90 µm
Epidermal cell width	22–43 µm	unknown	15–40 µm; typically about 20 µm	27–48 µm	up to 18 µm	20–25 µm	18–25 µm
Outline of the anticlinal cell walls	straight	straight	slightly sinuous to almost straight	straight	unknown	indistinct; tight undulations with 5 arcs per 25 µm	sinuous
Outline of the periclinal cell walls	thickened edges between the anticlinal and periclinal cell walls	smooth; small central cuticular thickening or solid papilla; central cuticular thickening	smooth	thickened edges between the anticlinal and periclinal cell walls	slightly more cutinized than in intercostal fields	smooth	smooth
Intercostal fields							
Number of epidermal cell rows per field	unknown	unknown	10–13	unknown	9–11	unknown	6–8
Shape of the epidermal cells	square; broadly rectangular	square; rectangular; elongate; isodiametric	rectangular; oblong; isodiametric	square; broadly rectangular	rectangular; narrow; elongate	rectangular; narrow	rectangular; isodiametric; irregular; squarish; rounded; polygonal
Epidermal cell length	37–90 µm	40–70 µm; mostly 55–70 µm	20–60 µm; typically about 40 µm	32–58 µm	50–100 µm; mostly 50–70 µm	55–100 µm; mostly 55–70 µm	20–45 µm

Epidermal cell width	30–63 µm	25–30 µm	15–40 µm; typically about 30 µm	30–53 µm	25–35 µm; mostly 25–30 µm	20–25 µm	36–50 µm
Outline of the anticlinal cell walls	straight; smooth	straight	slightly sinuous to almost straight	straight; smooth	weakly undulate with 2 arcs per 25 µm	indistinct; tight undulations with 5 arcs per 25 µm	sinuous
Outline of the periclinal cell walls	smooth; thickened edges between the anticlinal and periclinal cell walls	smooth; central cuticular thickening or solid papilla	smooth	always straight; thickened edges between the anticlinal and periclinal cell walls	unknown	smooth	smooth
Arrangement of the stomata	in open chain within a line of cells	stomata absent	stomata absent	in open chain within a cell line	stomata absent	stomata absent	stomata absent
Orientation of the stomatal pore	perpendicularly to the veins	stomata absent	stomata absent	perpendicularly to the veins	stomata absent	stomata absent	stomata absent
Stomatal pore length	12.5–22.5 µm	stomata absent	stomata absent	15–17.5 µm	stomata absent	stomata absent	stomata absent
Stoma length	37.5–50.5 µm	stomata absent	stomata absent	37.5–50 µm	stomata absent	stomata absent	stomata absent
Stoma width	20–35 µm	stomata absent	stomata absent	20 µm–27.5 µm	stomata absent	stomata absent	stomata absent
Abaxial epidermal anatomy							
Costal fields							
Number of epidermal cell rows per field	3–4	3–4	4–6	3–4	3–4	4–5	2–3
Shape of the epidermal cells	rectangular; narrow; elongate; isodiametric	rectangular narrow	rectangular; more or less elongate; oblong	rectangular; narrow; isodiametric	rectangular; narrow; isodiametric	rectangular; narrow	rectangular; trapezoidal
Epidermal cell length	55–145 µm	55–90 µm	43–80 µm	42–103 µm	30–50 µm	50–70 µm	30–80 µm
Epidermal cell width	22–50 µm	22–25 µm	18–32 µm	22–45 µm	25–30 µm	15–25 µm	20–50 µm
Outline of the anticlinal cell walls	usually straight; occasionally slightly sinuous with faint and irregular undulations	mostly straight; a few with weak and irregular undulations	slightly sinuous	straight	undulate, with up to 3 arcs per 25 µm	densely undulate, with 3–4 arcs per 25 µm	sinuous
Outline of the outer periclinal cell wall	smooth; surface ornamentation difficult to observe clearly	smooth; small central cuticular thickening	smooth	smooth; ornamentation difficult to observe in detail	smooth	smooth	papillate
Occurrence and outline of papilla on the epidermal cells	often; 50–62.5 µm long, hollow papilla in one of the cell corners	often; solid papilla	absent	often; 40–57.5 µm long, hollow, delicate, terminal papilla	unknown	always; short, hollow papilla close to one polar end	always; central papilla with circular base of 12–15 µm diameter
Intercostal fields							
Field width	200–300 µm	unknown	about 300 µm	175–250 µm	unknown	unknown	100–280 µm
Arrangement of the epidermal cells and of the stomata in the field	unknown	7–8 rows; stomata regularly scattered	stomata in 4–5 obvious to sometimes rather irregular rows	stomata arranged in rows	8–9 rows	1–3 rows, almost completely composed of stomata and their subsidiary cells	stomata in 3–5 more or less conspicuous rows; stomata densely scattered
Shape of the epidermal cells	broadly rectangular; isodiametric	rectangular; elongate; isodiametric	rounded; polygonal; isodiametric; irregular	broadly rectangular; isodiametric	broadly rectangular; isodiametric	unknown	rectangular; polygonal; rounded; irregular
Epidermal cell length	30–80 µm	40–60 µm	50–62 µm	25–50 µm	40–60 µm	unknown	30–60 µm
Epidermal cell width	25–63 µm	25–40 µm	33–44 µm	30–50 µm	25–30 µm	unknown	20–70 µm
Outline of the anticlinal cell walls	undulate	mostly straight	sinuous; sinuosities sometimes small, inconspicuous	always straight	unknown	unknown	sinuous

Orientation of the stomatal pore	perpendicularly to the veins	perpendicularly to the veins	mainly perpendicularly to the veins; sometimes slightly obliquely	perpendicularly to the veins	perpendicularly to the veins	perpendicularly to the veins	usually perpendicularly to the veins, sometimes more or less obliquely
Stomatal pore length	15–20 µm	10–12 µm	14–16 µm	12.5–20 µm	18–20 µm	12–15 µm	16–18 µm
Stoma length	37.5–55 µm	25–30 µm	35–43 µm	37.5–50 µm	45–50 µm	25–30 µm	36–40 µm
Stoma width	20–30 µm	25–30 µm	26–34 µm	20–30 µm	45–50 µm	20–25 µm	32–36 µm
Epidermal position of stomata	slightly sunken	slightly sunken	sunken	slightly sunken; sunken	sunken; deeply sunken	slightly sunken	sunken
Shape of the subsidiary cells	rectangular	rectangular	rectangular to nearly semicircular	rectangular	rectangular	rectangular	rectangular to slightly rounded
Subsidiary cell length	unknown	35–40 µm	38–45 µm	unknown	45–50 µm	25–30 µm	20–50 µm
Subsidiary cell width	unknown	unknown	30–42 µm	unknown	20–25 µm	10–13 µm	20–70 µm
Outline of the anticlinal walls of the subsidiary cells	unknown	unknown	slightly sinuous	unknown	undulate	unknown	straight to slightly sinuous
Ornamentation of the outer periclinal cell walls of the ordinary epidermal cells and/or of the subsidiary cells	often small and solid papillae 50–62.5 µm height, or cuticular thickenings	each subsidiary cell with a small papilla that overhangs the pit mouth	typically smooth; very few irregularly distributed, atypical cuticular thickenings of 5–15 µm diameter occasionally may be present	often irregularly distributed solid cuticular applications or thickenings; long, hollow, delicate papillae 40–57.5 µm height	only some regularly but not densely scattered small cells bear in their middle a short hollow papilla, of 30 µm diameter	long, hollow papillae („hairs") may be present	ordinary epidermal cells papillate; subsidiary cells papillate, or just with more or less central dorsal cuticular thickenings

scattered stomata with deep polar spaces and the stomatal aperture oriented perpendicular to oblique relative to the veins; the rows of rectangular hypodermal cells with straight cell walls; the marked elongate intercellular spaces and large triangular to quadrilateral cell wall corner spaces distancing the hypodermal cells; the equal thickness of the adaxial and abaxial cuticle. A series of qualitative and quantitative data concerning the macro-morphologic and epidermal characters allows detailed comparison between the new species and other relevant species of the genus (Tab. 2). The data rendered in the table are based on the works of Schlotheim (1822), Brongniart (1825), Jaeger (1827), Schenk (1864), Nathorst (1878), Hartz (1896), Zeiller (1906), Harris (1932), Lundblad (1950), Csaki, Ulrichs (1985), Pott et al. (2007a), Pott, McLoughlin (2009), Czier (2014), and this study. Considering the cuticle thickness values of diverse genera and species of Bennettitales from one of the most diverse European Jurassic macroflora, the Yorkshire flora (Harris 1969), the following cuticle thickness range may be established: thin cuticle (< 2 µm); moderate thick cuticle (2 to 5 µm); and thick cuticle (> 5 µm). *Pterophyllum filicoides* (Schlotheim, 1822) Zeiller, 1906, *P. aequale* (Brongniart, 1825) Nathorst, 1878 em. Pott and McLoughlin, 2009, *P. brevipenne* Kurr ex. Schenk, 1864 em. Pott, Van Konijnenburg-Van Cittert, Kerp and Krings, 2007a, and *P. subaequale* Hartz, 1896 em. Pott and McLoughlin, 2009 have robust (not defined term, but usually meaning thick and hard, well detachable) cuticles. *Pterophyllum pectinatum* (Jaeger, 1827) Csaki and Ulrichs, 1985 em.

Czier, 2014 has the adaxial cuticle thin, delicate, and the abaxial cuticle thick, robust. Both cuticles of *P. ptilum* Harris, 1932 are thin ('very thin'). The adaxial cuticle is thicker than the abaxial cuticle in *P. filicoides* (Schlotheim, 1822) Zeiller, 1906, *P. brevipenne* Kurr ex. Schenk, 1864 em. Pott, Van Konijnenburg-Van Cittert, Kerp and Krings, 2007a, and *P. ptilum* Harris, 1932. By contrary, the adaxial cuticle is thinner than the abaxial cuticle in *P. pectinatum* (Jaeger, 1827) Csaki and Ulrichs, 1985 em. Czier, 2014, and *P. subaequale* Hartz, 1896 em. Pott and McLoughlin, 2009. *Pterophyllum semseyanus* is characterised by moderately thick cuticles. The adaxial and abaxial cuticles of individual specimens are uniform and of equal thickness. No other species of *Pterophyllum* show this combination regarding the quality of the cuticles. This might reflect particular environmental conditions (Section 7).

Occurrence: Early Jurassic, Euro-Sinian Paleofloristic Region, European Province, Romania.

7. The Hypodermal Matrix Mechanism hypothesis. The epidermis and the hypodermis are tissues that depend on one another, not only regarding the internal structure of the Bennettitalean leaves, but also concerning their internal physiology. This relation may be established based on data provided by investigations on the leaf's cuticle and hypodermal matrix. The entire literature neglects the importance of this statement. The following considerations are intended to fill at least partly this gap in the knowledge of the genus *Pterophyllum*, trying finally to arrive at a preliminary conclusion that has implications for all of the Bennettitales.

Before going to further considerations, a few nomenclatural problems must be clarified, to keep us away from confusions. In relation to the correct nomenclature used in the description of species, expressions like 'hypodermal cuticle' or 'middle cuticle' referring to the presence in the fossil material of a matrix indicating the hypodermis should be avoided. Hypodermal matrix, cutin, or cutan, are the appropriate expressions referring to signs indicating hypodermal tissues of plants from the Jurassic or other geological periods, because "the cuticle is an extracellular matrix composed of cutin polyester and waxes" (Hooker et al., 2007, p. 904). Someone might argue that from a personal experience he or she knows that the hypodermis is often present both in the fossil record as well as in extant plants, but could not have such an experience, because of two facts. First, the hypodermis (real tissue of real cells), like the epidermis (real tissue of real cells), never is present in plant fossils. All what we may see in the preparations is no more than matrix (once secreted by a number of cells, and then fossilized). Second, the hypodermal matrix, at least in the Anina flora, does not at all appears often in preparations, but usually only the cuticles appear, both, or only one. It is important to understand correctly, that the hypodermal matrix (intercellular matrix showing more or less exactly the shape of the once existed hypodermal cells) and the cuticle (extracellular matrix showing more or less exactly the shape of the once existed epidermal cells) may be present in fossils, but not the hypodermis, and not the epidermis. Even if a group of paleobotanist researchers may say ‘but we all know this’, I consider necessary keeping this little paragraph for those who still do not know this, in order to eliminate such confusions concerning the microscopical preparations.

The adaxial and abaxial epidermal cells of the living plant secrete the matrix forming the adaxial and abaxial cuticles. Cuticle has protective role of the vegetative organs and reproductive structures of land plants mainly against the weather conditions and parasites, and may be even paleoclimatological or ecological indicator (Pott, McLoughlin, 2009). The hypodermis is a cell layer situated below the epidermis and consists of hypodermal cells; therefore, the periclinal walls of the epidermal and hypodermal cells stay face to face and the tissues may transfer matrix components one to other. This is rather clear; however, there exist no studies responding to these questions: which tissues and cells, when and why produce the hypodermal matrix? The present study is just an attempt in this respect, and hopefully the beginning in a series. It does not respond to all the questions that may arise, and does not anticipate results of further investigations. Therefore, this section does not go beyond the hypothesis level.

At a first instance, it can be stated that the hypodermal matrix of the *Pterophyllum semseyanus* leaves was produced by the epidermal cells (first possibility), by the hypodermal cells (second possibility), or by both types of cells (third possibility). The first possibility may appear especially when cuticle is thin and delicate. In such cases, few cutin quantities are necessary to form the cuticle, therefore, the hypodermis may have mainly a passive storage role, to deposit that cutin, which for the moment constitutes a surplus, but which the plant might use immediately when needed. The second possibility is probable in cases of thick, robust cuticle, where a large quantity of cutin is needed. Hypodermal cutin production may in such cases frequently supplement the epidermal cutin with the big cutin quantity necessary to produce thick cuticles; therefore, the storage role of the hypodermis must be a much more active role, implying intense fluxes of cutin towards the epidermis and then to the surface of the lamina. The third possibility may appear especially when the cuticle is of moderate thickness. In all of the cases, the presence of the hypodermal matrix denotes hypodermis capable to store this matrix, otherwise the hypodermal matrix were not preserved in the fossil. This was possible if the hypodermis had *adequate structure* for the fulfilment of the *storing physiology*. A *hypodermal matrix storing process* must have existed in all those plants of which the fossils preserve hypodermal matrix, because as it was already mentioned, the hypodermal matrix is preserved in fossil state, not the hypodermis. On the other hand, the existence of the hypodermal matrix in plant fossils denotes a *hypodermal matrix producing process*, because any existence must have a cause. Equally, a *hypodermal matrix using process* must be subsisted, because any existence has a scope. These three processes are conceived as compounding parts of a unique internal structural–physiological mechanism, defined on this occasion *The Hypodermal Matrix Producing–Storing–Using Mechanism*, or shorter, the *Hypodermal Matrix Mechanism (HMM).*

The adaxial and abaxial cuticles of *Pterophyllum semseyanus* are moderately thick; therefore, based on the HMM, the most reliable possibility is that both the epidermal and the hypodermal cells produced the hypodermal matrix of the leaves of this species. To establish the composition and contribution of the hypodermal and epidermal cells to the cuticle forming process, and to investigate deeply the HMM, extensive physical and chemical investigations on the polymer structure of the hypodermal and epidermal matrices are required. HMM seemingly has direct chemical and even mechanical control on the construction of the cuticle that is a veritable defensive weapon of the plant. Hypodermal cells are non-photosynthetic cells, and HMM is not a primary metabolic pathway. However, HMM supposedly might be interacted with metabolic processes through a known non-photorespiratory or even photorespiratory route, or maybe through a still unknown non-photorespiratory route involving serine biosynthesis, because “there is evidence to suggest that serine may be involved in plant responses to various environmental stresses” (Ho, Saito, 2001; Waditee et al., 2007; Ros et al., 2013, p. 708). It seems to be obvious that a detailed research on the HMM of the *P. semseyanus* leaves might give precious information to the knowledge relating to their hypodermal cells and tissues, with consequences on the knowledge of the internal structure and physiology of the plant fossils that are assigned to the order Bennettitales.

Based on the above presented data and theory, it is supposable, the hypodermis of *P. semseyanus* was able to store a hypodermal matrix regardless of the provenance of this matrix, and possibly was able to synthesize at least some chemical components in order to supply the epidermis with the necessary stock for cutin and wax production. In a larger context, the presence of marked hypodermal intercellular spaces and of large cell wall corner spaces in a species of *Pterophyllum* supports the new supposition that the hypodermis has had storage function for the cuticle and could had worked as capable HMM to synthesize matrix components used by at least some Bennettitaleans for the construction of their cuticle. However, the stored hypodermal matrix possibly had other roles too; for example, it supposedly was a thermo-mechanical regulator of the plant’s thermal regime, thus contributing to the maintenance of thermically stabile bennettitalean-dominated paleoecosystems. It cannot be excluded the possibility that intensively working HMM produced thick cuticles in bennettitalean leaves to protect the plant against desiccation, but considering the generally wet climate along the northern border of the Tethys (Section 8) from where the described material originates, it is more probable that the thick cuticle protected the plant against the excessive temperature oscillations. Cuticle of extant plants may have a role to reduce the desiccation of the plant (Edwards et al., 1982), however, the thickness of the cuticle does not show correlation with its water permeability (Schreiber, Riederer, 1996; Kerstiens, 1996); therefore, a supposition in this sense regarding the extinct order of the Bennettitales would be hazardous.

If the HMM is present solely within the Bennettitales, this has evolutionary, paleoenvironmental, and implicitly paleoclimatological significance. Considering the Cenomanian–Oligocene Bennettitalean ghost lineage (McLoughlin et al., 2011), this order ranges from the Middle Triassic near the end of the Oligocene. This is a major argument that let suppose, the HMM appeared after the Early Triassic ‘hothouse conditions’ of the Earth (Retallack, 2013; McLoughlin, Kear, 2015), and it has persisted a very long time in the Earth's history. The Paleocene–Eocene thermal maximum (Aubry et al., 1999; Khozyem et al., 2015) probably was not difficulty for the HMM persistence. The Eocene still was the world’s last global greenhouse period, but the late Eocene is supposed to be a period of gradual decline of global mean annual temperatures, and the prominent climatic transition from greenhouse to icehouse world was during the Late Paleogene (Moraweck et al., 2015; Li et al., 2016). Therefore, the HMM supposedly still existed in Rupelian (Early Oligocene), but has disappeared before the end of the Chattian (Late Oligocene) together with the extinction of the Bennettitales, in a moment that approximatively corresponds to the global Oligocene thermal minimum. Eventually, HMM perhaps was present in some plants before the Early Triassic and maybe will be reported. Considering that the Miocene was the last warm episode on the Earth (Kayseri Özer et al., 2014), maybe HMM still was locally present for a while in some land plants of which the ancestors were bennettitaleans, but in this moment, there is no evidence in this respect. However, it is admitted here that no extant species possess the HMM, because this mechanism has been not described in extant plants, and it is known that only the epidermal cells synthesize cuticle in the living plants (Kolattukudy, 1996). Therefore, even if the hypodermis of the extant plants does not produce a cuticle-forming matrix, the Bennettitalean hypodermis most probably produced such a matrix. To avoid a misunderstanding, this does not mean that hypodermis may be not present in extant plants; it is absent in angiosperms, but still may be present in some gymnosperms, like the ‘living fossil’ maidenhair tree *Ginkgo biloba*. However, since the hypodermis of the extant plants does not contribute to the cuticle forming process, there is good reason to announce that the HMM has disappeared in geological times.

It appears that the evolution finally has eliminated the HMM that was enough important to be maintained in the Mesophytic and possibly even in a rather long time interval of the Cenophytic, but which seemingly became superfluous in the post Oligocene period. The gradually cooling of the Earth's climate, culminating with the Pleistocene ice ages, may be a cause of this involution, and perhaps even of the extinction of the Bennettitales. Consequently, it appears that the HMM was present only in the ‘warm’ paleoenvironmental–paleoclimatic conditions of the past times, and does not exist in the ‘cool’ present time. On the other hand, the known examples suggest that the mechanism worked intensely, thus probably the most efficiently, in cases of moderately thick and thick cuticles. *Pterophyllum semseyanus* represents the second description of a hypodermis in the Romanian fossil flora. The first description of this feature is based on leaves of *Ptilophyllum aninaensis* Czier, 1995b. That species, assigned to a sister genus, possesses thin cuticles, and relatively thin hypodermal matrix that does not show the marked hypodermal intercellular spaces and the large cell wall corner spaces specific to *Pterophyllum semseyanus*. However, the hypodermal matrix of *P. aninaensis* shows rather hard distinguishable rows of uniform sized, in many cases polygonal cells, and narrow intercellular spaces. Therefore, the presence of the HMM points to warm paleoenvironment, and the thicker a bennettitalean cuticle is, the HMM worked more intensely. Such paleoenvironment might have been caused by warm oceanic paleoclimate like in the case of the fossil locality Anina, or by other warm-generating factors even in regions with temperate Mesophytic climate, for example by post-volcanic activities with geysers, hot springs, warm rivers, and thermal lakes. The presence in floristic associations of ferns like *Clathropteris meniscioides* (Brongniart, 1825) Brongniart, 1828b, which needed warm and wet environment, may serve as supplementary argument sustaining the warm paleoenvironment suggested by the presence of the HMM in Bennettitalean leaves. Therefore, apart from the biostratigraphy, the paleophytogeography of this species is worth to a discussion in this context too (Section 8).

According to Ben LePage (pers. com. 2015) “one could argue that cuticle thickness is a function of moisture in the environment; wet environments produce thin cuticle, while plants growing in much drier environments produce thicker cuticle”. My opinion in the case of the Bennettitaleans possessing the HMM mechanism, is that further cuticular and hypodermal matrix investigations are necessary to establish a correlation between the cuticle, hypodermal matrix, and the paleoenvironmental–paleoclimatological aspects. A much more sure statement that may be done is that the fossil locality Anina is a Konservat-Lagerstätte. Two things sustain this opinion. One of them is the exceptional preservation of its fossilized flora, and the other, that it connects to a seemingly important moment in the evolution of the life, the apparition in the Early Jurassic of the Hypodermal Matrix Mechanism.

8. Global phytostratigraphic–paleophytogeographic context. The biggest part of the Romanian continental Jurassic macroflora comes from the Hettangian–Sinemurian interval, and the principal biostratigraphic key fossil in Romania for this interval is the Dipteridaceous fern *Clathropteris meniscioides* (Section 4.4). The new species *Pterophyllum semseyanus* is a local element of the *C. meniscioides* Biozone, and this is the case of many other genera and species described from the Romanian Early Jurassic (Czier 1995b, 1995c, 1996a, 1998a, 1999a, 1999b, 1999c, 2000a, 2003, 2008, 2009, 2010, 2011; Barbacka et al. 2014, 2016). The Hettangian stage does not possess a global macro-phytostratigraphic marker, because the plant fossils known under the name *Thaumatopteris*, in fact are specimens of *Dictyophyllum*, if some of them not something else. This latter is the case of the Romanian material. Popa et al. (2004) correctly recognize that the specimens they described and figured from Şuncuiuş (Apuseni Mountains) are not specimens of *Dictyophyllum*; therefore, they should redetermine their material. Barbacka et al. (2016, p. 46, fig. 2) should proceed alike concerning the still not published Anina specimen(s) that serves as base for the putative Hettangian/Sinemurian limit of their scheme. However, new or at least modified phytostratigraphic schemes should replace worldwide the old schemes based on *Thaumatopteris*, because this genus is mentioned also from regions outside Romania, otherwise not only from Hettangian deposits. It also is present in the Middle Triassic, for example in the late Ladinian of Monte Agnello, Dolomites, in Italy (Wappler et al. 2015). The genus *Thaumatopteris* (a junior synonym of *Dictyophyllum*) cannot be recognized as globally valid Hettangian biostratigraphic marker, and this does not need any further discussion. The Romanian scheme presented in this paper is just the first in the series of the new regional schemes that researchers should elaborate. Apart from a few citations (Mészáros et al., 2000; Wanek, 2002; Popa et al., 2004; Sotoc, 2014), it is unknown in literature; this is why it is reminded here. Researchers, who are going to elaborate their schemes for the countries or regions where they work, surely will thoroughly analyze the local stratigraphic conditions. However, before they select markers for the stratigraphic units they define, I would recommend giving more attention to the sometimes-ignored paleophytogeography. This especially could be utile later, when a general review of the Jurassic macrofloral biozones and subzones will be a main subject of a research, and the correlations of diverse regional stratigraphic units with the geological time scale will be another. Attaining of such goals is possible by knowing the territorial spreading of the floristic elements and the ages of their occurrences, therefore, it should be a good idea to accomplish an extensive paleophytogeographic study too. The *Clathropteris* flora and its Romanian biozone probably do not are the most important for the global Jurassic paleobotany and stratigraphy. However, owing to the pointed circumstances including the paleoenvironmental importance (Section 7), they are worth of presentation in global paleophytogeographic context.

The Romanian Jurassic continental macroflora is a heterogeneous flora, of mixed origin, in which the autochthon European elements predominate (near 3/4 of the taxa) and the allochthon elements are subordinate (slightly more than 1/4 of the taxa) (Czier, 1999c, 2000a, 2001a, 2003). Some years ago, Czier (1998a, p. 371) published a global map showing the main migration routes of the taxa present in the Early Jurassic Romanian macroflora, particularly of the Eastern floristic elements of warm and wet paleoclimate, and of the Western floristic elements of temperate and seasonally wet paleoclimate. The routes continue to be valid, and they may constitute a general base at the determination of the Mesophytic migration patterns of diverse macroflora genera and species. However, to elaborate new maps of the main migration routes of particular taxa, such as the genus *Clathropteris* in this case, new data and occurrences reported in the literature published in the past two decades must used too.

An important set of additions to the suggested migration routes of the Eastern elements, which must be done on the new paleophytogeographic map (Fig. 9) showing the suggested *Clathropteris* distribution pattern, are in connection with the new and old, yet not cited data concerning the Northern Hemisphere, namely with the European and North American Late Triassic – Early Jurassic floras.

Regarding the Northern Hemisphere, the oldest *Clathropteris* occurrence might be in the European Ladinian, but it appears that this stage cannot have this significance, despite the massive European presence of the genus. This is because unlike the rest of the material, the age of the *Clathropteris* specimens unfortunately is unsure, as “we cannot completely be sure that the specimens were collected at the same stratigraphic level” (Kustatscher, Van Konijnenburg-Van Cittert, 2011, p. 240).

Dzik et al. (2008, p. 733) note concerning the presence of the Rhaetian in Poland: “The dipteridacean fern *Clathropteris*, a member of a generally Jurassic flora of SE Asian origin, which entered Europe and Greenland in the Rhaetian (Harris, 1937; Lundblad, 1950; Mader, 1995; Czier, 1998a), was reported from a carbonate facies which overlies the clastic strata in this region (Roemer, 1867), although Ash (2005) claimed presence of *Clathropteris* in the early Norian of western North America.” The Early Norian presence of *Clathropteris* is in concordance with the general migration of the *Clathropteris* Flora from East to West, however, this flora should be considered originating even beyond the Far East, from the western North America. According to Taugourdeau-Lantz, Vozenin-Serra (1987), the paleoecology of the *Clathropteris* Flora along the northern border of the Tethys links to warm and wet oceanic climate, and referring to that region, they mention even a *Dictyophyllum*–*Clathropteris* Flora.

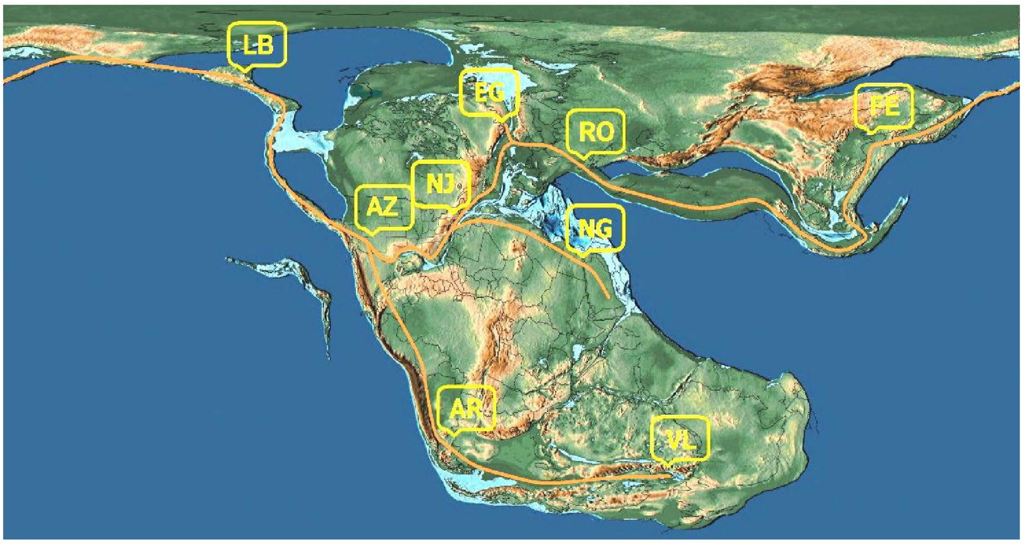

Fig. 9. Suggested region of origin and migration pattern of the Late Triassic – Early Jurassic *Clathropteris* Flora. Based on the data provided in this study and the maps published by Czier (1998a, p. 371, text-fig. 8), Bomfleur, Kerp (2010, p. 151, fig. 3), and Scotese (2013, p. 20, map A). AZ = Arizona, North America. NJ = New Jersey, North America. LB = West–East land bridge between North America and East Asia. FE = Far East, Asia. RO = Romania, Europe. EG = East Greenland, Europe. NG = North Gondwana, Africa and Near East. AR = Argentina, South America. VL = Victoria Land, Antarctica.

Рис. 9. Предложенный регион происхождения и пути миграции позднетриасовой – раннеюрской флоры *Clathropteris*. Основаны на данных, полученных в ходе настоящего исследования, и картах, опубликованных в Czier (1998a, с. 371, текст-рис. 8), Bomfleur, Kerp (2010, с. 151, рис. 3) и Scotese (2013, p. 20, map A). AZ = Аризона, Северная Америка. NJ = Нью Джерси, Северная Америка. LB = мост между между Северной Америкой и Восточной Азией. FE = Дальний Восток, Азия. RO = Румыния, Европа. EG = Восточная Гренландия, Европа. NG = Северная Гондвана, Африка и Ближний Восток. AR = Аргентина, Южная Америка. VL = Земля Королевы Виктории, Антарктика.

In other regions of the Earth, *Dictyophyllum* and *Clathropteris* do not always appear together in the floristic associations, and their stratigraphic distributions may differ. The oldest described and figured record of the genus *Dictyophyllum* is known from the Middle Triassic (Anisian–Ladinian) of East Australia (Webb, 1982), but no one specimen of *Clathropteris* is surely documented from there. Therefore, the Australian record does not allow to state that East Australia is the origin region of *Clathropteris*. This implicitly means, at least based on the actual knowledge, that East Australia is not the origin area of the entire Dipteridaceae family. In a larger context, it seems to be unsure whether all the Dipteridaceae ferns originate from the same region of the Earth or not. The origin of this family is a still unsolved problem, and this section deals only with the migration pattern of one of its genera. The most frequent species of this genus globally is *Clathropteris meniscioides*. Furthermore, this is the most abundant fossil in the Romanian continental Early Jurassic, and even gives here the name of the biozone from where the herein described material originates.

Referring to the plant fossils from the Petrified Forest National Park from northeastern Arizona, Ash (2005, p. 61) concludes: "using both their morphology and the climatic preferences of their nearest living relatives of the fossil plants in the Chinle flora, it is evident that the majority of them at least lived under a humid subtropical to tropical climate". Based on the evident paleoclimatological similarity, and the resembling paleofloristic composition conferred by the *Clathropteris* Flora, it is supposable that East Asia and North America were in contact in the Late Triassic. This contact was by the means of a land bridge or an archipelago bridge with flourishing vegetation containing Dipteridaceae ferns that were able to spreading from an island to another, by floating their spores and transport them by water and wind. *Clathropteris* already was present in the Asian Late Triassic, and maintained several of its species, like *C. meniscioides*, *C. elegans*, in the Early Jurassic of China (Zhou, 1984, 1989).

Interesting and important information concerning the presence of *Clathropteris* in the Late Triassic and Early Jurassic members of the Newark Supergroup in eastern North America arrived to me recently. According to Sidney Ash (pers. com., 2015), many of the known specimens of *C. meniscioides* collected from these lithostratigraphical units are kept in the US National Museum of Natural History in Washington, DC, and these shall involved in the global migration of the genus. The significant flora that outcrops along the East Coast of the US nevertheless needs revision, but Professor Ash saw the *C. meniscioides* specimens and he sustains their correct identification. Surprisingly or not, the flora generally is not among those cited in the modern paleobotanical literature. Most of what little is known about the presence of *Clathropteris* in the mentioned strata is found in old, long out-of-print papers, the most recent and comprehensive treatment of the genus in eastern North America being contained in the 'obscure book of the long deceased amateur paleobotanist Wilhelm Bock (1969)'. Anyway, the book is a publication that researchers must take into consideration. The *Clathropteris* Flora of the East Coast fits in the proposed map, by considering a migration route from the western North America towards the East. This route follows the continental sequences of sedimentary strata in the rift basins of the Central Atlantic Margins of North America, which "are the result of the incipient rifting of Pangea" (Olsen, 1997, p. 387).

Another important set of additions is in connection with the Southern Hemisphere. It is the presence of a few years ago discovered *Clathropteris meniscioides* in the Early Jurassic deposits of Antarctica, which "grew under very unstable environmental conditions with high volcanic activity", in association with other dipteridaceous ferns (Bomfleur, Kerp, 2010, p. 143). The most possible origin of this population also seems to be the Early Norian of western North America, because no earlier *Clathropteris*-containing flora certificates the floral spreading. Apart from the Antarctic material, the unequivocal record of *Clathropteris* from the Early Jurassic of Piedra Pintada, central Argentina (Frenguelli, 1941; Herbst, 1966), sustains the migration route in this part of the Southern Hemisphere.

Based on the data above, western North America is the most probably origin region of the *Clathropteris* Flora. Several localities with plant fossils, all assigned to the Chinle Formation, belong to this region, near the common borders of states Arizona, New Mexico, Colorado, and Utah (Ash 2014, p. 280, Fig. 1).

If the presented data do not indicate very clear migration routes, there is still place for suppositions. The new paleophytogeographic map suggests three spreading directions of the *Clathropteris* Flora originating from the Early Norian of northwestern North America. The first is from West to East, along the Pangean rift basins of the Central Atlantic Margins of North America, reaching the US East Coast. The second direction is towards the West: the flora migrated in Asia via a land–archipelago bridge. From the Far East, the flora spread along the northern border of the Tethys Ocean. It entered Europe in the Rhaetian, expanding from Central Europe in all directions, to the North even reaching East Greenland. *Clathropteris meniscioides* was present in Europe near the end of the Sinemurian, the Romanian occurrences, especially Şuncuiuş and Anina, being among the most relevant regarding the presence of this species (Czier 2000a, 2001a, 2003). The migration route of the flora, from the Early Jurassic of Europe to the Middle Jurassic of Central America and northern Gondwana, is the same as represented on the old map (Czier, 1998a), though these regions still need many intensive researches. The third route of the flora begins in the Early Norian of northwestern North America and ends in East Antarctica. The flora expanded along the western coast of South America, was present in Argentina during the Early Jurassic, and after a direction change from North–South to West–East, reached Antarctica. The entire warm seaway that represented a moisture source in the circum-Tethyan part of Late Triassic to Early Jurassic Pangea (Parrish, 1993; Demko et al., 2005) generally is characterized by the *Clathropteris* Flora, as shown by the paleogeographic positions of the occurrences.

Contrary to the allochthon migration tendency remarked in Pteridophyta, the Romanian Bennettitales predominantly represent a European autochthon group. This group encloses among others two species of

Ptilophyllum (Czier, 2011) and two species of *Banatozamites* (Czier, 2008, 2009); only some representatives of a third *Banatozamites* (Czier, 1996a) appear in other regions, particularly in the Middle Jurassic of Israel (Krassilov et al., 2013). *Pterophyllum pectinatum* is an exclusive attribute of the Euro-Sinian realm, showing migration tendency towards the East. This species appeared in the Ladinian of the European province, where it persisted in the Hettangian–Sinemurian; it expanded into the Middle Asia province and the East Asia province during the Carnian, and existed in Asia until the beginning of the Jurassic period, as a coexistent element of the *Dictyophyllum–Clathropteris* flora (Czier, 2014). *Pterophyllum semseyanus* is an endemic element of the European Early Jurassic autochthon flora, but also is a European coexistent element of the here allochthon *Clathropteris* flora that originated in North America and globally expanded during the Mesophytic.

9. Results and Discussion. The genus *Pterophyllum* is present in the fossil flora of Romania with the taxa *P. pectinatum* (Jaeger, 1827) Csaki and Ulrichs, 1985 em. Czier, 2014, *P. semseyanus* Czier n. sp., cf. *Pterophyllum* sp., and aff. *Pterophyllum* sp., all coming from Early Jurassic deposits.

A new species named *Pterophyllum semseyanus* Czier has been defined from the Early Jurassic deposits of Anina, Romania. The short petiolate, oblanceolate, small and narrow lamina, the arched segments ending in rounded apex, the delicate venation consisting of a few simple veins, the rachis epidermis consisting of parallel rows of elongate trapezoidal cells, the hypostomatic lamina, the sinuous anticlinal cell walls of all the ordinary epidermal cells, the smooth periclinal cell walls of the adaxial epidermal cells, the typically differentiated abaxial epidermis, the papillate outer periclinal cell walls of the abaxial ordinary epidermal cells, the densely scattered stomata with deep polar spaces and the stomatal aperture oriented perpendicular to oblique relative to the veins, the rows of rectangular hypodermal cells with straight cell walls, the marked elongate intercellular spaces and large triangular to quadrilateral cell wall corner spaces distancing the hypodermal cells, and the equal thickness of the adaxial and abaxial cuticle, are its distinguishing characters. The exquisitely preserved specimens permitted examination of the rachis cuticle, of the adaxial and abaxial cuticle of the leaf segments, and of the hypodermal matrix of the lamina. This is the first case in the history of the genus *Pterophyllum* when a rachis epidermis and a hypodermis are described, and the second time this latter has been done for all the Romanian plant fossils. As about the hypodermal features used in diagnose, these are at the same rank with the epidermal features. Both seem to be climatically influenced, but this possibility has nothing to do with any concept of the species. The epidermal and hypodermal features equally can be used for species description. However, as hypodermal features never were described before in *Pterophyllum*, this structure in the new species is something unusual if not exceptional. Since suggested by several scientists, the diagnosis of the new species must be the shortest possible, and it nevertheless must contain the hypodermal characters. Therefore, I have shortened the diagnosis so much as possible, agreeing that it must contain the most important diagnostic characters, while the other characters shall be in a table, for comparison to relevant species of the genus.

The presence of the marked hypodermal intercellular spaces and large cell wall corner spaces supports the idea that the hypodermis had storage and synthesizing function for the cuticle matrix components. At least some Bennettitaleans used the Hypodermal Matrix Mechanism (HMM) for the construction of their cuticle. Based on the HMM, of which the structural-physiological concept is introduced, the thick bennettitalean cuticle appears the best indicator of the warm paleoenvironment. The Konservat-Lagerstätte locality Anina connects to an important moment in the evolution of the life, represented by the apparition in the Early Jurassic of the Hypodermal Matrix Mechanism.

Concerning the biostratigraphy, it is important to retain, that no one zone or subzone of the scheme is an automatic global replacement. Their protologue clearly define these phytostratigraphic units, both ‘horizontally’ and ‘vertically’. Actually, they have validity only for the Romanian Jurassic. Stratigraphers know well that biozones and subzones are spatial-temporal units possessing both extensions. However, not all the readers are stratigraphers and not everybody realize the significance of these extensions. Even reviewers may think to a biozone just in ‘vertical’ sense when they reject manuscripts. They should know that the ages of the biostratigraphic units of a region for which these units are defined, are not necessarily the ages of diverse lithostratigraphic units of other regions. Nobody should confound lithostratigraphy with biostratigraphy, and nobody should wonder why *Clathropteris meniscioides* is not automatically Hettangian–Sinemurian marker outside Romania. A fossil may be present in a region only in strata of certain ages, but it may appear in other regions in strata of earlier or later ages. Biological entities and entire populations of plants and animals may migrate from a place to other; a species may change its spreading area for example when the climatic conditions change, so it may flourish in a new area, while it disappears from the old place and habitat. Nobody should automatically use any scheme's fossils as markers for other countries or regions, because the geochronology and local stratigraphy in some cases might allow the usage of a certain fossil as marker, but in other cases definitely not. The *Clathropteris meniscioides* Biozone might be extended well for example to Hungary, because *C. meniscioides* is an easily determinable common species found in the Hettangian–Sinemurian deposits from there. *Clathropteris meniscioides* is the most frequent element of the Vasas flora (Czier, 2004), and is well represented in the rest of the Mecsek, therefore good premises exist for the usage of this fossil as marker for the continental Hettangian–Sinemurian deposits of Hungary. Then, of course, local subzones might be defined there (e.g. a subzone with *Pachypteris*). This also may be the case of some other countries or regions, or may be not, but as mentioned, this depends of the local conditions. In any case, the Romanian scheme should present much more interest, and it should be not considered as something just of local importance, because it has a worldwide message: other macrofloral biozonation schemes might be renewed too. Some zonation schemes need just minor changes. For example, in the East Greenland scheme probably only the name *Thaumatopteris* should be replaced with something else, while all the stratigraphic limits and floral zones may remain as they are, because relevant stratigraphic and paleontologic arguments sustain them in that region of the globe (Steinthorsdottir et al., 2015). However, can be used in diverse other regions even far from Europe, the old zones of Nathorst (1910), otherwise defined just for the Rhaetian–Jurassic deposits of Greenland and Western Europe (partially), when the most important markers *Lepidopteris* and *Thaumatopteris* are absent, like in Romania? How can be used *Thaumatopteris* for the determination of the Rhaetian/Hettangian and Hettangian/Sinemurian limits, when this genus is a junior synonym of *Dictyophyllum* that has large distribution in almost the entire Mesophytic? Obviously, all these are impossible by using these genera.

Pterophyllum semseyanus is a phytostratigraphic element of the *Banatozamites chlamydostomus* Subzone of the *Clathropteris meniscioides* Biozone of the Early Jurassic in Romania, and is an autochthon element in the European Province of the Euro-Sinian Paleofloristic Region. It coexisted in the Romanian Early Jurassic with the allochthon elements of the *Clathropteris* Flora. The origin region of the *Clathropteris* Flora supposedly is in northwestern North America. A new paleophytogeographic map presents the suggested migration routes of this typically Late Triassic – Early Jurassic flora. It migrated from northwestern North America towards East, West, and South. To the East the flora reached eastern North America. To the West it expanded through a land bridge in East Asia; from the Far East migrated towards the West along the northern border of the Tethys Ocean; from Central Europe reached East Greenland, Central America, and North Gondwana. To the South, the flora reached East Antarctica, spreading along the western coast of South America. An interesting question is this: if *Clathropteris* appears first in the western North America, why it migrated by the three routes to eastern North America, to Asia than to Europe, to South America then to Antarctica. The paleogeography of the Mesophytic (the opening of the Tethys Ocean from East to the West, the ‘bridge’ between North America and East Asia, etc.), the positions and the ages of the occurrences based on the data from the cited literature and from this paper (including personal communications), suggest this distribution and migration. Paleoclimatological data also are in concordance with this pattern, for example, it is better understood why the Asian massive presence of *Clathropteris* in the Early Jurassic was followed there by a very strong regress of this genus, if we consider, that „the Chinese region progressively dried through the Middle Jurassic” (Pole et al., 2016). Of course, new data filling old gaps in the fossil record might modify the map, and then someone probably will be able indicating clearer migration routes.

10. Conclusions. *1.* Although the Romanian *Pterophyllum* flora is rich in specimens, actually it contains only two species. *2.* Cuticular study is decisive for sure determination of any *Pterophyllum* specimen. *3.* Studies concerning the HMM have at least paleobotanical, evolutionary and paleoenvironmental–paleoclimatological significance. *4.* The hypodermis structure and physiology of the new species *Pterophyllum semseyanus* and of the previously described *Ptilophyllum aninaensis* suggests that the thick bennettitalean cuticle is better indicator of a warm paleoenvironment than the thin cuticle. *5.* The Early Jurassic paleobotanical locality Anina (Banat region, Romania) is Konservat-Lagerstätte. *6.* The European autochthon species *Pterophyllum semseyanus* coexisted with the allochthon elements of the *Clathropteris* Flora.

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РОД БЕННЕТИТОВ *PTEROPHYLLUM* В ИСКОПАЕМОЙ ФЛОРЕ РУМЫНИИ И ГЛОБАЛЬНЫЙ ФИТОСТРАТИГРАФИКО-ПАЛЕОФИТОГЕОГРАФИЧЕСКИЙ КОНТЕКСТ

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Листья беннетита рода *Pterophyllum* представлены во флоре Румынии (восток Центральной Европы) *P. pectinatum* (Jaeger, 1827) Csaki and Ulrichs, 1985 em. Czier, 2014, *P. semseyanus* Czier n. sp., cf. Pterophyllum sp., и aff. *Pterophyllum sp.*, происходящими из континентальных юрских отложений. Новый вид *Pterophyllum semseyanus* описан из отложений Анина (регион Банат). Диагностические черты включают узкую ламину, сегменты с закругленными вершинами, тонкие простые жилки, удлиненные трапециевидные клетки эпидермиса черешка, гладкий адаксиальный эпидермис, зонированный и несущий папиллы абаксиальный эпидермис, устьица с глубокими полярными участками, гиподермис из прямоугольных гиподермальных клеток, хорошо выраженные межклетники и большие межклеточные пространства в месте контакта нескольких клеток. Окаменелости описываемого вида встречаются в песчаниках из группы Валея Терезия (Хеттанний частично – Сеймурий) формации Штайердорф в Южных Карпатах. *Pterophyllum semseyanus* является элементом подзоны *Banatozamites chlamydostomus* биозоны *Clathropteris meniscioides*, характерных для ранней юры Румынии. Это первый случай в истории рода *Pterophyllum*, когда приводятся описания эпидермиса жилки и гиподермиса. Исследования, касающиеся гиподермального матрикса могут быть важны для реконструкции окружающей среды прошлого и эволюционых процессов. Вводится концепция гиподермального механизма матрикса (ГММ). Исходя из структуры и физиологии гиподермиса, можно предположить, что толстая кутикула беннетитовых служит лучшим индикатором теплых условий окружающей среды, чем тонкая кутикула. *Pterophyllum semseyanus* является эндемичным видом Европейской провинции Евро-Синианского палеофлористического региона. Он сосуществовал с элементами аллохтонной флоры *Clathropteris*, глобальные пути миграции которой говорят о ее североамериканском происхождении.

Ключевые слова: *Pterophyllum semseyanus (Bennettitales), таксономия, стратиграфия, световая и сканирующая электронная микроскопия, гиподермальный механизм матрикса (ГММ), флора Clathropteris, палеофитогеография.*

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