EARLY JURASSIC OVIPOSITORIES ON BENNETTITALEAN LEAVES FROM ROMANIA

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Abstract. Early Jurassic (Hettangian–Sinemurian) rare insect ovipositories occurring on *Pterophyllum* sp. bennettitalean (cycadeoidalean) leaves are described from Pregheda, a former open cast mine for bituminous coals belonging to the Sirinia Basin, Danubian Units of the South Carpathians, Romania. These ovipositories are represented by groups of 2-3 elliptical bodies, distributed with their longer axis parallel to the leaf venation, and associated in four distinct rows, parallel to the rachis, two rows on each side of it, a peculiar pattern for the ichnospecies *Paleoovoides rectus* (Vasilenko) Sarzetti et al. 2009 to which the material is assigned. The Hettangian–Sinemurian ovipositories recorded in Pregheda belong to fossil representatives of the Order Odonata, such as fossil dragonflies or damselflies. They were generated after the leaf's abscission, in a wetland area associated with a coal-generating marsh.

Keywords: Insect eggs, oviposition, Bennettitales, Early Jurassic, Romania.

INTRODUCTION

Plant-insect interactions were documented in relation to feeding, reproduction, defense and habitation behaviour of insects, spanning in age the Devonian–Recent time interval, reflecting co-evolution of plants and insects and global changes through geological time (Taylor et al., 2009, Labandeira et al. 2002; Wilf, 2008). Endophytic egg deposition (oviposition), beneath leaf or stem surfaces of plants, can be undertaken before or after the plant's organ abscission and it was documented even from Carboniferous formations (Béthoux et al., 2004). Permian, Triassic, Jurassic, Cretaceous and Neozoic examples of oviposition were studied mainly during the last 15 years, such a reproductive behaviour being very rarely documented in the fossil record (Vasilenko and Rasnitsyn, 2007). In Romania, the South Carpathians include continental formations very rich in well-preserved Early Jurassic plants, both in the Getic Nappe and in the Danubian Units (Popa, 2000, 2009, Popa and Van Konijnenburg – Van Cittert, 2006), studied in famous localities such as Anina, formerly known as Steierdorf. Early Jurassic fossil plants and even coals collected from the South Carpathians record various insect-plant interactions, related to insect behaviour such as habitation (Mateescu, 1934), herbivory (Givulescu and Popa, 1994, Popa, 2009) and now reproduction (ovipositories) of insects. Nevertheless, the studies regarding the insect-plant interactions recorded in Early Jurassic plants from Romania are only in their early stages while a large volume of data is assembled.

GEOLOGY

Pregheda is a remote, small-sized, closed quarry for Lower Jurassic bituminous coals, occurring in the northern part of the Almăj Mountains (South Carpathians), close to the Svinecea Mare Peak and the springs of Rudăria and Berzasca rivers (Text-fig. 1). Pregheda is located in the Sirinia Basin (Răileanu, 1953, 1960, Codarcea et al., 1961), within the Danubian Units of the South Carpathians. Sirinia Basin is also known as the Svinița–Svinecea Mare sedimentary zone (Săndulescu, 1984; Mutihac, 1990), including both Paleozoic and Mesozoic coal measures. The Lower Jurassic bituminous coals belong to the Glavcina Formation (Pop et al., 1997), a

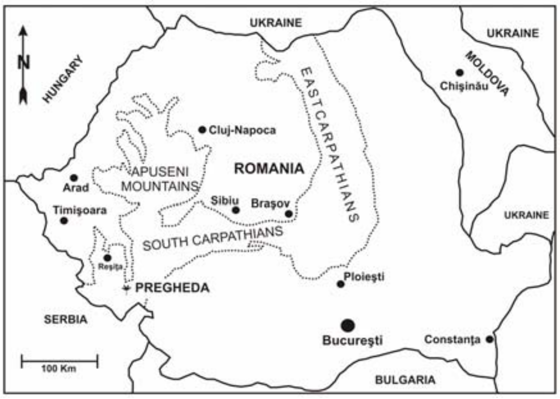

Fig. 1- Location of Pregheda open cast mine in Romania (South Carpathians).

115-200 m thick Hettangian–Sinemurian terrestrial formation which includes three coal beds in Pregheda, ranging between 0.2 –2.5 m in thickness. Other former localities for small scale mining related to the Glavcina Formation for Hettangian–Sinemurian coals in the Sirinia Basin include Palaşca (Bigăr) galleries, Tâlva cu Rugi, Fântâna lui Dănuț, Chiacovăț, Ostreşu, Pietrele Albe, Stanca, Buschmann, Cozla - among many others (Răileanu, 1963; Petrescu et al., 1987; Preda et al., 1994; Popa and Van Konijnenburg – Van Cittert, 2006).

The continental Glavcina Formation is a particularly rich formation in fossil plants, represented by highly-diverse and well-preserved pteridophytes and gymnosperms. The Hettangian–Sinemurian flora from Pregheda was described by Semaka (1962, 1965, 1970) and Preda et al. (1985), while the coals seams and the associated flora from Rudăria, the closest mine from Pregheda, were studied by Mateescu (1958). Antonescu, in Popa et al. (1976) dated the Glavcina Formation as Hettangian–Lower Sinemurian, based on palynological data, in the absence of any Rhaetian markers. Semaka (1962, 1965, 1970) considered the plant association recorded in Pregheda as Rhaetian–Lower Liassic (Hettangian–Sinemurian), but the Peltaspermalean *Lepidopteris ottonis*, the key marker for the Rhaetian in continental formations, is missing not only from Pregheda, but from all the other localities. However, the flora from Pregheda is very similar to the rest of the

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floras of the Sirinia Basin, as well as to all floras of the Getic Nappe, Hettangian–Sinemurian in age, marked by the associations with *Thaumatopteris brauniana* and *Nilssonia* cf. *orientalis* (Popa and Van Konijnenburg – Van Cittert, 2006).

MATERIAL AND METHODS

The material is represented by well-preserved impressions on fine sandstone, permitting the observation of fine details. The best preserved fragments yielding ovipositories occur on the hand specimens no. PRE52 and PRE53A, belonging to the Ion Preda Collection. This material has been collected by the late Professor Ioan Preda from Pregheda in 1983 (Preda et al., 1985), and it is now curated and revised within the University of Bucharest. The photographs were taken using a Panasonic DMC-L10 camera with Olympus Zuiko Digital 35 mm Macro lens, with lateral illumination for increasing the contrast of fine details, such as veins and insect ovipositories, illustrated in Plate I. The photographs were drawn using Corel Draw ver. 11, in order to detail characters such as venation and distribution patterns of egg deposition, as illustrated in Text-fig. 2. The Early Jurassic flora of Pregheda is currently under revision, based on Semaka and Preda collections, as well as on newly collected material.

SYSTEMATICS

Order Bennettitales Engler 1892
Family Williamsoniaceae (Carruthers, 1870) Nathorst 1913
Genus *Pterophyllum* Brongniart 1825
***Pterophyllum* sp.**
Text-fig. 2, Pl. I, Figs. 1-3

1985 *Otozamites pterophylloides* - Preda, Culda, Bădăluță and Ştreangă, La flore liassique de Pregheda (Banat), p. 74.

Description

The leaf fragments show a thick, transversally wrinkled rachis, well visible along the abaxial surface of the leaf, 3-4 mm wide (Text-fig. 2, Pl. I, Figs. 1-3). The leaflets are inserted oppositely to the rachis, they are elongated, slightly falcate, with an expanded base ranging between 8-10 mm, entire margins, the sinuses between the leaflets being sharp, quickly widening to the sides of the leaf, while the leaflet apices are not preserved (Text-fig. 2, Pl. I, Figs. 2, 3). The venation is parallel, dense, represented by parallel veins inserted directly to the rachis, rarely divided dichotomously (Text-fig. 2, Pl. I, Fig. 3), reaching a maximal density of 16 veins per 1 cm.

Discussion

The leaf fragments occurring on hand specimens PRE52 and PRE53A were identified by Preda et al. (1985) as *Otozamites pterophylloides*, but the material cannot be assigned to this taxon as it shows clear *Pterophyllum* characters, such as the expanded base of the leaflets and the parallel venation. Only impressions were found, no epidermal material was recorded for enabling the cuticle analysis, therefore the lack of cuticles hindered the species identification. The leaf is partially split longitudinally (Text-fig. 2), and the leaflets are slightly contorted, showing short, mild transport and sedimentation in aquatic conditions and fragmenting in soft mud.

Ichnogenus *Paleoovoidus* (Vasilenko) Sarzetti et al. 2009
***Paleoovoidus rectus* (Vasilenko) Sarzetti et al. 2009**
Text-fig. 2, Pl. I, Figs. 1-3

1999 *Odonata eggs* – Van Konijnenburg – Van Cittert, p. 217, Fig. 1;
2007 *Egg scars* – Krassilov, Silantieva, Hellmund and Hellmund, p. 806, Fig. 3D;
2009 *Paleoovoidus rectus* – Sarzetti, Labandeira, Muzon, Wilf, Cuneo, Johnson and Genise, p. 437-438, Figs. 2.3, 2.4.

Description

Impressions preserved as elliptical, grouped marks or bulges on the abaxial (lower) surface of *Pterophyllum* sp. impressions were recorded during the revision of the Preda Collection (Text-fig. 2, Pl. I, Figs. 1-3). Along the leaflets occur elliptic marks, 2-3 mm long and 1-1.5 mm wide, arranged in groups of 2-3 parallel marks (Text-fig. 2, Pl. I, Figs. 1-3). The elliptic marks are always parallel to the leaf venation and they are distributed along four separate rows, two rows of each side of the rachis, parallel to it, two rows closer to the rachis, and two rows more external, occurring towards the leaf outlines. The elliptic marks occur densely in groups, almost in fine contact within each group (Text-fig. 2). Sometimes, only the outline of the groups is preserved, mainly due to the preservation degree of the impression (Text-fig. 2, Pl. I, Fig. 3). The leaf veins run parallel, undisturbed by the elliptical marks (Text-fig. 2, Pl. I, Fig. 3).

Discussion

The elliptic structures grouped on the *Pterophyllum* sp. leaves from Pregheda clearly resemble insect eggs in endophytic ovipositories, as such structures were previously described from Triassic–Jurassic formations by Grauvogel-Stamm and Kelber (1996), Van Konijnenburg – Van Cittert and Schmeissner (1999), Vasilenko and Rasnitsyn (2007), and by Pott et al. (2008) for Triassic–Jurassic fossils.

Grauvogel-Stamm and Kelber (1996) described ovipositions on Middle Triassic *Taeniopteris angustifolia* and on *Equisetites* div. sp. (*E. arenaceus*, *E. foveolatus*, *E. platyodon*) from Germany. These ovipositories show both regular and irregular distribution of elliptical bodies, while these bodies have similar sizes with those from Pregheda. On *Taeniopteris angustifolia* leaves, the elliptical bodies are arranged in linear groups, perpendicular to the leaf venation, thus very differently from the Romanian material.

Pott et al. (2008) described Triassic (Carnian) endophytic insect eggs and ovipositional damage on cycadeoidalean leaves from Lunz (Austria).

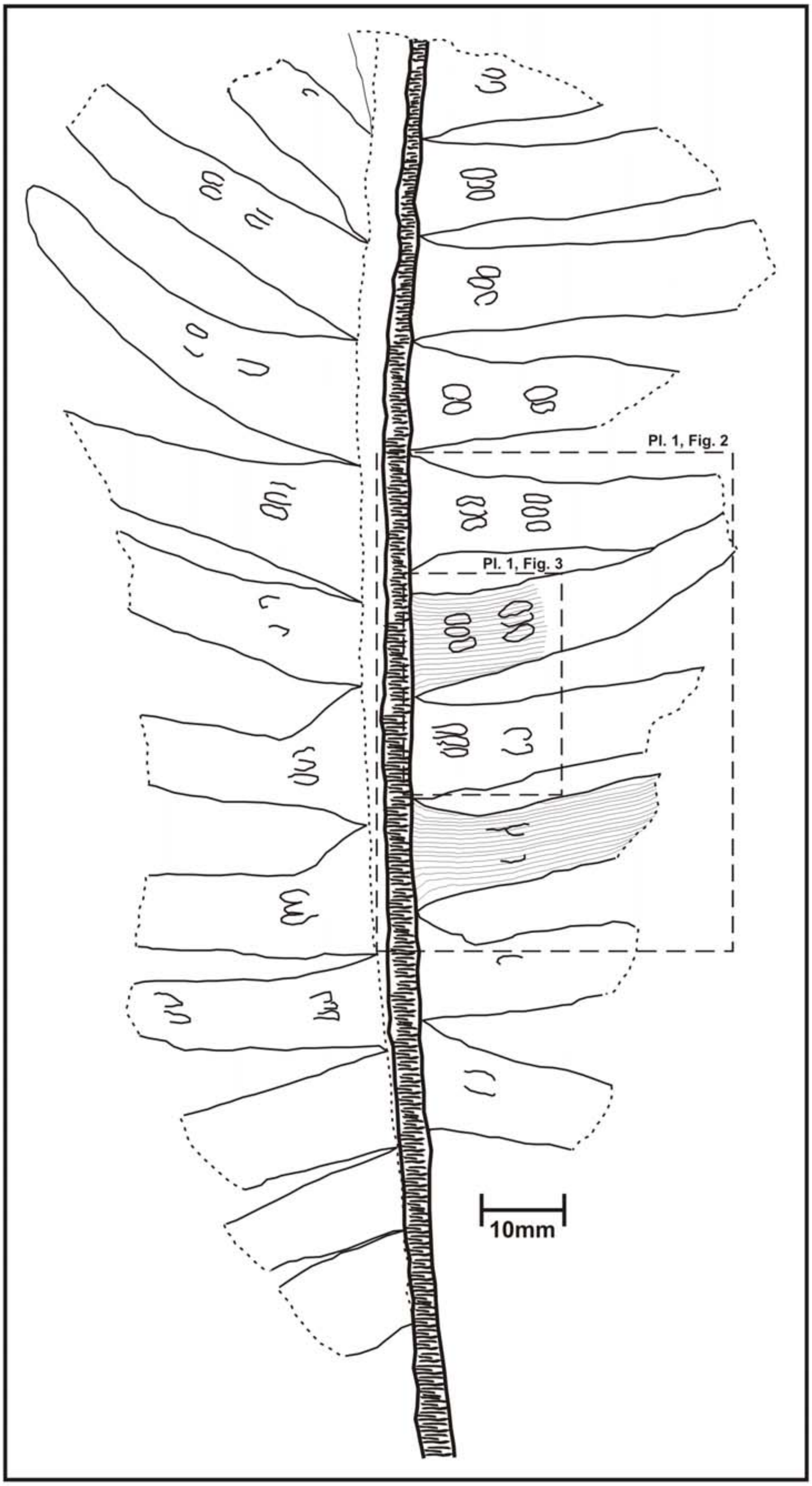

Fig. 2 - *Pterophyllum* sp. split leaf and distribution of ovipositories along the abaxial surface of the leaf, fragment 1 of hand specimen PRE52. The rectangles show the position of Figs. 2 and 3 of Plate I.

These are elliptical eggs and they were found well preserved, together with the cuticles of the bennettite *Nilssoniopteris haidingeri*, their sizes reaching up to 310 μm in length and 180 μm in width.

Van Konijnenburg – Van Cittert and Schmeissner (1999) reported two types of Early Jurassic fossil endophytic eggs, occurring on leaves of *Schmeissneria microstachys* with regular distribution and *Podozamites distans* with rather irregular distribution of eggs, both from Germany (Bavaria). These ovipositories are coeval with the Pregheda ovipositories, being their closest relatives, both in terms of morphology and of age. However, they are still different, as the German Liassic ovipositories include more numerous parallel rows of six elliptical bodies, densely-packed in the case of *Schmeissneria microstachys*; in the case of *Podozamites distans*, the eggs are more irregularly distributed than those from Pregheda. The authors attributed the Liassic Bavarian ovipositories to insects belonging to Order Odonata (dragonflies). The Romanian ovipositories include smaller numbers of eggs per group, and they are arranged in four distinct rows, two on each side of the *Pterophyllum* sp. rachis.

Pre-Triassic endophytic ovipositories were described by Béthoux et al. (2004) from Late Carboniferous *Calamites cistii* stems; they represent the earliest fossils of this type in the geological record. The reported endophytic cavities are very large, probably holding several eggs. Late Permian ovipositories were reported by Vasilenko and Rasnitsyn (2007) on *Pursongia* sp. leaves from northern Russia.

Post-Jurassic ovipositories were reported by Vasilenko and Rasnitsyn (2007) from Lower Cretaceous deposits of Russia, on *Pityophyllum* sp. and *Ginkgoites* sp. leaves. These authors also reported Late Cretaceous ovipositories on *Querexia* sp. leaves from Russia, later detailed by Vasilenko (2008). Krassilov et al (2007) described Zygopteran ovipositories from the Albian of Negev (Israel) on *Acaciaephyllum*-like leaves. Banerji (2004) reported Early Cretaceous ovipositories from the Rajmahal Basin (India), on *Pterophylloides laevis* leaves. Sarzetti et al. (2009) described Odonatan endophytic ovipositories on dicot leaves from the Eocene of Patagonia, assigning them to the ichnogenus *Paleoovoidus* Vasilenko 2005 (*P. rectus*, *P. bifurcatus* and *P. arcuatum*).

Vasilenko (2005) defined the ichnogenus *Paleoovoidus* for structures elliptic in shape, medium-sized elongate, regularly arranged in the leaf lamina. Later, Sarzetti et al. (2009) emended the diagnosis of the genus, as well as that of the ichnospecies *Paleoovoidus rectus*, defined by "lens-shaped scars oriented in a single, linear row, with long axes of scars aligned lengthwise, mostly parallel to the long axis of the leaf and usually occurring along the midrib".

The Pregheda ovipositories (Text-fig. 2) show most of their affinities with *Paleoovoidus rectus* (Vasilenko) Sarzetti et al. 2009, as the elliptical bodies are grouped in a linear manner, with their long axis parallel to the leaf venation; accordingly, they are assigned to this ichnospecies. When compared to the Patagonian, Russian or Israeli material, the Romanian material differs by the fact that the elliptic bodies or scars are first grouped by two or three, with their individual axis perpendicular to the rectilinear axis of the group; thus, they resemble more the ovipositories described by Van Konijnenburg – Van Cittert and Schmeissner (1999) from Germany. Due to the imperfect state of preservation, it is impossible to assess how many eggs per elliptical body were deposited in the case of the Pregheda impressions. Other species of *Paleoovoidus*, such as *P. bifurcatus* Sarzetti et al. 2009, *P. arcuatum* (Krassilov) Sarzetti et al. 2009 show different morphologies.

Vasilenko and Rasnitsyn (2007) indicated the following Odonatan groups as possible producers of ovipositories during the Early Jurassic times: Kennedyina, Libellulina and Heterophlebiina. A representative of any of these groups could have produced them in Pregheda samples during the Hettangian–Sinemurian time interval. More precise assignment to such representatives is unattaignable, considering the age of the studied ovipositories. For Late Cretaceous and Neozoic Odonata eggs, more precise assignment is possible, especially in the case of Calopterygina damselflies.

We assume that the deposition of eggs on the *Pterophyllum* sp. leaves from Pregheda was probably undertaken within a humid area, most probably after the leaf was shed and transported, after it reached a water pool. Bennettites are not swamp dwellers such as sphenophytes or conifers - drier areas were their preferred habitat; however they can be coal generators under certain circumstances (Popa, 2000). As dragonflies and damselflies lay their eggs on plants mostly underwater or on floating leaves, the *Pterophyllum* sp. leaves were probably floating when eggs were deposited. This also suggests that Vasilenko and Rasnitsyn (2007) were right when assessing that the oviposition in living plant tissue is a later, Late Mesozoic or Neozoic behavioural acquisition of these insects.

CONCLUSION

Hettangian–Sinemurian ovipositories belonging to fossil Odonata are reported for the first time in Romania, on *Pterophyllum* sp. bennettitalean leaves from Pregheda, Glavcina coal-bearing Formation, Sirinia Basin of the Danubian Units, South Carpathians. Such ovipositories are very rarely documented in the fossil record and they are represented by linear groups of 2-3 elliptical bodies arranged parallel to the leaf venation, on four parallel rows with the *Pterophyllum* sp. rachis, two along each side of it. Considering the distribution pattern of the elliptical bodies, the ovipositories are assigned to the ichnospecies *Paleoovoidus rectus* (Vasilenko) Sarzetti et al. 2009. The unique peculiar distribution of elliptical bodies along four rows, with their longer axis parallel to the leaf venation is similar only to ovipositories described from the Lower Jurassic of Bavaria (Germany). The eggs were deposited after the leaf reached a water pool, after a short transport from a drier area where the bennettite plant with *Pterophyllum* sp. foliage dwelt.

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REFERENCES

Banerji, J., 2004. Evidence of Insect-plant interactions from the upper Gondwana sequence (Lower Cretaceous) in the Rajmahal basin, India. *Gondwana Research*, V/7/1: 205-210.

Béthoux, O., Galtier, J. and Nel, A., 2004. Earliest evidence of insect endophytic oviposition. *Palaios*, 19: 408-413.

Codarcea, A., Răileanu, G., Pavelescu, L., Gherasi, N., Năstăseanu, S., Bercia, I. and Mercus, D., 1961. Guide des excursions. Carpates Meridionales, Bucureşti, 130 p.

Givulescu, R. & Popa, M.E., 1994. Eine neue *Dictyophyllum* - Art aus dem unteren Lias von Anina (Rumanien). *Documenta Naturae*, 84: 42-46.

Grauvogel-Stamm, L. & Kelber, K.-P., 1996. Plant insect interactions and coevolution during the Triassic in Western Europe. *Paleont. Lombarda*, 5: 5-23.

Krassilov, V., Silantieva, N., Hellmund, M. and Hellmund, W., 2007. Insect egg sets on angiosperm leaves from the Lower Cretaceous of Negev, Israel. *Cretaceous Research*, 28: 803-811.

Labandeira, C.C., Johnson, K.R. and Wilf, P., 2002. Impact of the terminal Cretaceous event on plant-insect associations. PNAS, 99(4): 2061-2066.

Mateescu, I., 1934. Traces d'insectes fossiles dans la houille liasique d'Anina. Annales des Mines de Roumanie, 12: 497-499.

Mateescu, I., 1958. Studiul petrografic al cărbunilor de la Rudăria (Svinecea Mare). *Anuarul Comitetului Geologic*, XXXI: 5-49.

Mutihac, V., 1990. Structura geologică a teritoriului României. Editura Tehnică, Bucharest, 419 p.

Petrescu, I., Nicorici, E., Bițoianu, C., Țicleanu, N., Todros, C., Ionescu, M., Mărgărit, G., Nicorici, M., Duşa, A., Pătruțoiu, I., Munteanu, A. & Buda, A., 1987. Geologia zăcămintelor de cărbuni. 2. Zăcăminte din România, 2. Editura Tehnică, Bucharest, 386 p.

Pop, G., Mărunțiu, M., Iancu, V., Seghedi, A. & Berza, T., 1997. Geology of the South Carpathians in the Danube Gorges. IGR, Bucharest, 28 p.

Popa, E., Năstăseanu, S. & Antonescu, E., 1976. Nouvelles donnees concernant la biostratigraphie du Jurassique inferieur de la zone de Sirinia (Banat). *Dări de seamă ale Şedințelor*, LXIII/4: 7-24.

Popa, M.E., 2000. Early Jurassic land flora of the Getic Nappe, University of Bucharest, Bucharest, PhD thesis, 258 p.

Popa, M.E., 2009. Late Palaeozoic and Early Mesozoic continental formations of the Reşița Basin. Editura Universității din Bucureşti, Bucharest, 197 p.

Popa, M.E. & Van Konijnenburg - Van Cittert, J.H.A., 2006. Aspects of Romanian Early - Middle Jurassic palaeobotany and palynology. Part VII. Successions and floras. *Progress in Natural Sciences*, 16: 203-212.

Pott, C., Labandeira, C.C., Krings, M. & Kerp, J.H.F., 2008. Fossil insect eggs and ovipositional damage on bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria. *Journal of Paleontology*, 82/4: 778-789.

Preda, I., Culda, V., Bădăluță, A. & Streangă, V., 1985. La flore liassique de Pregheda (Banat). *Analele Universității Bucureşti*, XXXV: 71-75.

Preda, I., Turculeț, I., Bădăluță, A., Barus, T. & Androhovici, A., 1994. Geologia zăcămintelor de cărbuni. Partea a II-a. Răspândirea zăcămintelor de cărbuni, 2. Editura Universității din Bucureşti, Bucureşti, 392 p.

Răileanu, G., 1953. Cercetări geologice în regiunea Svinița-Fața Mare. *Bul. Şt.*, 5/2: 307-409.

Răileanu, G., 1960. Recherches géologiques dans la région Svinița-Fața Mare. *Ann. Com. Geol.*, XXVI-XXVIII: 347-383.

Răileanu, G., Grigoraş, N., Onescu, N. & Plişcă, T., 1963. Geologia zăcămintelor de cărbuni, cu privire specială asupra teritoriului RPR, Bucureşti, 344 p.

Sarzetti, L.C., Labandeira, C.C., Muzon, J., Wilf, P., Cuneo, N.R., Johnson, K.R. & Genise, J., 2009. Odonatan endophytic oviposition from the Eocene of Patagonia: the ichnogenus *Paleoovoidus* and implications for behavioral stasis. *Journal of Paleontology*, 83/3: 431-447.

Săndulescu, M., 1984. Geotectonica României. Editura Tehnică, Bucureşti, 336 p.

Semaka, A., 1962. Asupra Rheticului de la Bigăr. *Dări de Seamă ale Şedințelor Comitetului Geologic*, XLV: 173-176.

Semaka, A., 1965. Zur Kenntnis der *Nilssonia orientalis*-Flora in den Sudkarpaten. *Acta Palaeobotanica Polonica*, VI/2: 27-39.

Semaka, A., 1970. Geologisch-Paleobotanische Untersuchungen in S.O. *Banaten Danubikum. Memorii*, XI: 1-79.

Taylor, T.N., Taylor, E.L. & Krings, M., 2009. Paleobotany: the biology and evolution of fossil plants. Elsevier, Amsterdam, 1230 p.

Van Konijnenburg - Van Cittert, J.H.A. & Schmeissner, S., 1999. Fossil insect eggs on Lower Jurassic plant remains from Bavaria (Germany). *Palaeogeography, Palaeoclimatology, Palaeoecology,* 152: 215-223.

Vasilenko, D.V., 2005. Damages on Mesozoic plants from the Transbaikalian locality Chernovskie Kopi. *Paleontological Journal,* 39: 54-59.

Vasilenko, D.V., 2008. Insect on aquatic leaves *Querexia* from the upper Cretaceous of the Amur Region. *Paleontological Journal,* 42: 514-521.

Vasilenko, D.V. and Rasnitsyn, A.P., 2007. Fossil ovipositions of dragonflies: review and interpretation. *Paleontological Journal,* 41/11: 1156-1161.

Wilf, P., 2008. Insect-damaged fossil leaves record food web response to ancient climate change and extinction. *New Phytologist*, 178: 468-502.

PLATE CAPTIONS

PLATE I

Fig. 1. *Pterophyllum* sp., fragment 1 of hand specimen PRE52. General view of the abaxial surface of the leaf, showing the transversally-wrinkled rachis, leaflets, venation and ovipositories. Scale bar: 10 mm.

Fig. 2. Detail of *Pterophyllum* sp., fragment 1 of hand specimen PRE52, showing the abaxial surface of several leaflets, rachis and ovipositories. Text-fig. 2 indicates the occurrence of the photo within the leaf fragment. Scale bar: 10 mm.

Fig. 3. Detail of *Pterophyllum* sp., fragment 1 of hand specimen PRE52, showing the abaxial surface of two leaflets, parallel venation, striated rachis and elliptical bodies in linear groups of 2 and 3. Text-fig. 2 indicates the occurrence of the photo within the leaf fragment. Scale bar: 10 mm.

PLATE I