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KEY WORDS

Romania,
Dobrogea,
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Upper Neoproterozoic,
Hiria Formation,
Ediacaran biota,
new records.

ABSTRACT

The Neoproterozoic terranes of Dobrogea (East Romania) yielded imprints formed by chains of arcuate elements on bed surfaces that are identified for the first time as body fossils attributed to the worldwide Ediacaran genus *Palaeopaschichnus* Palič, 1976. These specimens from Romania confirm the Ediacaran age of the Hiria Formation. They also provide new morphological details, as well as insights into paleobiogeographic distribution and paleoenvironmental conditions of *Palaeopaschichnus*.

RÉSUMÉ

Nouvelles occurrences de Palaeopaschichnus Palič, 1976 dans l'Édiacarien de Roumanie.

Les terrains néoproterozoïques de Dobrogea (Est de la Roumanie) ont livré des empreintes formées par des chaînes d'éléments arqués sur les surfaces de bancs, qui sont identifiées pour la première fois comme des corps fossiles attribués au genre édiacarien *Palaeopaschichnus* Palič, 1976, à la répartition mondiale. Ces spécimens de Roumanie confirment l'âge édiacarien de la Formation Hiria. Ils fournissent également de nouveaux détails morphologiques, ainsi que des informations sur la répartition paléobiogéographique et sur les conditions paléoenvironnementales de *Palaeopaschichnus*.

MOTS CLÉS
Roumanie,
Dobrogea,
Palaeopaschichnus,
Néoproterozoïque
supérieur,
Formation Hiria,
Biota édiacarien,
signalements nouveaux.

INTRODUCTION

Palaeopascichnus Palij, 1976 is a worldwide distributed Ediacaran genus and is among the most emblematic fossils of this period before the Cambrian Explosion (see Boag *et al.* 2016; Kolesnikov & Desiatkin 2022). Many studies have been devoted particularly to its description, taxonomy, taphonomy and paleoenvironment (Haines 2000; Dong *et al.* 2008; Antcliffe *et al.* 2011; Lan & Chen 2012; O'Donnell 2013; Hawco *et al.* 2017, 2019; Kenchington *et al.* 2017; Jensen *et al.* 2018; Kolesnikov 2018, 2019; Kolesnikov *et al.* 2018b; Hawco 2020; Liu & Tindal 2020; Desiatkin *et al.* 2021; Kolesnikov & Desiatkin 2022). *Palaeopascichnus* is also considered as an Ediacaran biostratigraphic marker (Kolesnikov 2019), although this opinion is not entirely shared (Liu & Tindal 2020).

Traces of organic activity possibly related to the Ediacaran biota were formerly reported in the Neoproterozoic terranes of Central Dobrogea (Eastern Romania) (Oaie 1992, 1993, 1998, 2010). The distinction between ichnofossils and body fossils and their paleontological affinity, however, remained to be precisely determined considering the more recent data on the Ediacaran biota. In the last 15 years, numerous field investigations led to new discoveries of Ediacaran remains, and allowed the revision of some previous determinations (Saint Martin *et al.* 2012, 2013; Saint Martin & Saint Martin 2018). Among the specimens assigned to Romanian Ediacaran biota, one trace first reported and described by Oaie (1992, 1993) has drawn particular attention. According to this author, it consists of parallel, meandering, segmented “half-moon shaped” imprints, which can be considered as movement trails but their exact ichnological affinity was uncertain. However, a detailed re-examination of this “imprint” leads us to consider it as a body fossil, herein attributed to *Palaeopascichnus*. The recent discovery of another specimen shows a distribution probably wider than what is observable in the field because of fracturing, schistosity and coverage by lichens. Although they are embedded in metamorphosed schistose sediments, these specimens have the advantage of being sufficiently well preserved to provide additional data on this classic Ediacaran fossil. Details of the structure of this fossil are provided and considerations on the stratigraphic and palaeoenvironmental consequences are discussed.

GEOLOGICAL SETTING

The study focuses on imprints observed on bed surfaces of a set of sediments outcropping in Central Dobrogea (Fig. 1). This region is located between the Peceneaga-Camena Fault at the north and the Capidava-Ovidiu Fault at the south (Fig. 1B). It belonged to the Moesian platform with a Precambrian basement represented by Middle and Upper Proterozoic terranes. Neoproterozoic deposits were formerly described as “greenschist formation” in a flyschoid series (Kräutner 1988). However, the sedimentological characteristics indicate weakly metamorphosed mainly fine- and medium-grained sediments

exhibiting numerous original sedimentary structures (Jipa 1967, 1968). These deposits belong to the 5000 m thick Histria Formation (Seghedi & Oaie 1994, 1995) composed of two lower and upper coarse members (Beidaud and Sibioara members) of sandstone separated by the thinner Haidar member with pelites and siltites (Seghedi & Oaie 1995; Oaie 1999). Seghedi & Oaie (1995), Oaie (1999) and Oaie *et al.* (2005) argued that the sedimentological, structural and mineralogical features of the Histria Formation point to foreland basin accumulations, in accordance with results of geochemical and detrital zircon distribution data (Żelaźniewicz *et al.* 2009). The low-grade metamorphic and weakly deformed clastic rocks of the Histria Formation correspond to median to distal turbiditic sequences (Oaie 1998; Oaie *et al.* 2005; Seghedi *et al.* 2005; Balintoni *et al.* 2011; Balintoni & Balica 2016; Melinte-Dobrinescu *et al.* 2020). The basin may have been filled by sediments issued from a continental margin dominated by an active volcanic arc (Oaie *et al.* 2005; Seghedi *et al.* 2005). Nevertheless, the frequent surfaces with various wrinkled structures suggest the occurrence of microbial mats resulting in the formation of Microbially Induced Sedimentary Structures (MISS; Saint Martin *et al.* 2011, 2012, 2013). Thus these microbial mats clearly challenge the distal turbidite paradigm.

A Late Proterozoic-Early Cambrian age was firstly estimated for the Histria Formation, based on geochemical K/Ar datation (about –572 million years; Giușcă *et al.* 1967) and palynological assemblages (Kräutner *et al.* 1988). Detrital zircon U/Pb ages later suggested a maximum Late Ediacaran depositional age (Żelaźniewicz *et al.* 2009; Balintoni *et al.* 2011; Balintoni & Balica 2016). The discovery of various imprints attributable to Ediacaran biota confirms the age of the median Haidar member of the Histria Formation (Oaie 1992, 1993; Saint Martin *et al.* 2011, 2013; Saint Martin & Saint Martin 2018; Melinte-Dobrinescu *et al.* 2020).

STUDIED OUTCROPS

Casimcea

The Neoproterozoic sediments bearing the studied specimens outcrop around the town of Casimcea, north of the Central Dobrogea (Fig. 1B). Field observations were made near a pumping station two kilometers northeast of Casimcea in a small tributary valley of the Casimcea river. In this sector we observe a perianticlinical termination (Fig. 2A), quite tight, a style occasionally recognized in the Casimcea valley (Fig. 2B).

The general direction of the layers is N100, with a dip of 50° towards the SSW. Some surfaces exhibit ripple-trains (Fig. 2B, C), with a 20–25 cm wavelength, a height of crests > 5 cm, and an average direction of the ridges at N150. The ripples are noticeably asymmetrical, weakly dipping to the NE and a steeper side to the SW, illustrating the migration of an oscillating system to the SW. Below the rippled slabs, elementary sequences occur within increasingly thick beds; they are composed of pelitic sediments enriched by detrital flow (Fig. 3A). Among those, two superimposed bedding surfaces, S1 and S2 (Fig. 3B) bear the studied imprints (Fig. 3C, D).

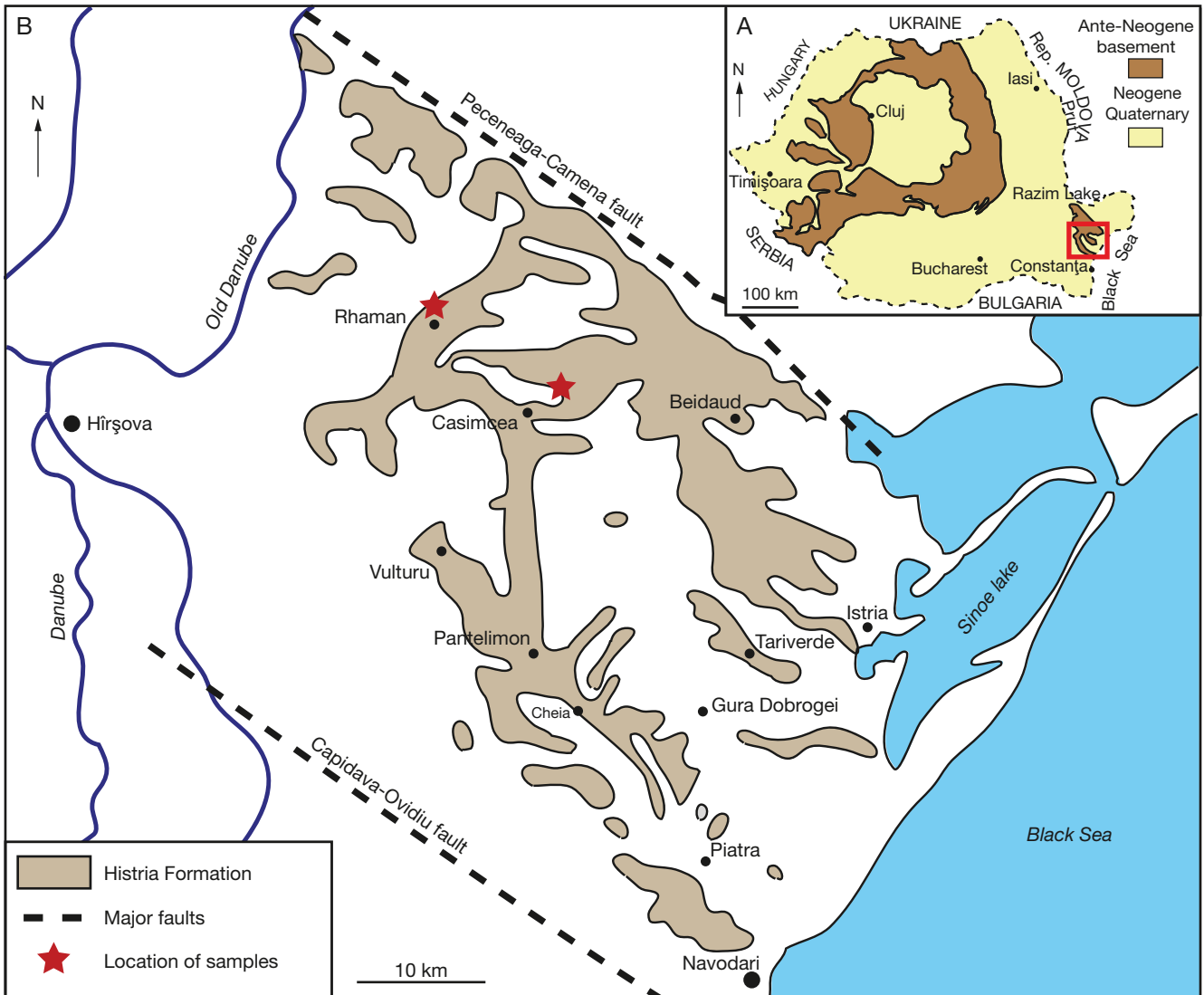


FIG. 1. — **A**, Schematic geological map of Romania and location of the study area (Central Dobrogea); **B**, geologic map of Neoproterozoic terranes in Central Dobrogea and location of the studied outcrops.

More generally, the sedimentary laminated quartzitic siltstone correspond to a pluricentimetric bedding in phase with undulations announcing a rippled surface (Fig. 3D). The bedding contains coarser material, thus producing mini-sequences. Some natural sections show HCS-type sedimentary structures (Hummocky Cross Stratification; Fig. 3E). Two surfaces show particular textured structures, similar to MISS (Fig. 3F): the first consists of a slightly reddened surface punctuated by numerous holes of about 1–2 cm in diameter, sometimes coalescing. The second shows a very finely reticulate dense network of small wrinkles of millimetric relief.

Rahman

The Histria Formation, mainly formed of quartzitic siltstones, is exposed in a valley located about 1.5 km NE of the village of Rahman (Figs 1B; 4A, B). The sedimentary succession consists of beds with irregular thickness and variable dips. Some massive outcrops, along the edge of a small valley, allow the observation of

bed surfaces (Fig. 4B–D). A smooth surface, intercalated between beds numbered S1 to S3, shows a small imprint corresponding to an isolated element of *Palaeopascichnus* (Fig. 4E). Most of these surfaces display ripple systems, some of complex rhomboid (Fig. 4F) or lingoid appearance (Fig. 5A). HCS-type sedimentary structures are exposed in several natural sections (Fig. 5B, C). Although the bed surfaces are often covered by lichens, several types of reticulate MISS (Fig. 5D, E) are visible in some outcrops.

SAMPLES AND ANALYTICAL TECHNIQUES

The sampling of the surface bearing the studied imprints was impossible because of the outcrop conditions, the nature of the rocks, the schistosity and the fracturing. Thus, a faithful replica of the surfaces was made using silicone molding during fieldwork. Then, a back molding in resin was performed (see Hawco 2020). The technique of photogrammetry finally allowed to highlight details of the reproduced surface. Measurements were performed using ImageJ software (Schneider *et al.* 2012).



FIG. 2. — Casimcea outcrop: **A**, Satellite view (Google Earth) of a periclinal structure within Precambrian terranes (double red arrow) and location of the outcrop (**black arrow**); **B**, view of the fossiliferous site with the Precambrian beds showing large ripples marks (**S3**) and location of bed surfaces **S1** and **S2** bearing *Palaeopascichnus* Palič, 1976; **C**, detail of the surface **S3** exhibiting large ripple marks. Photos : J. P. Saint Martin.

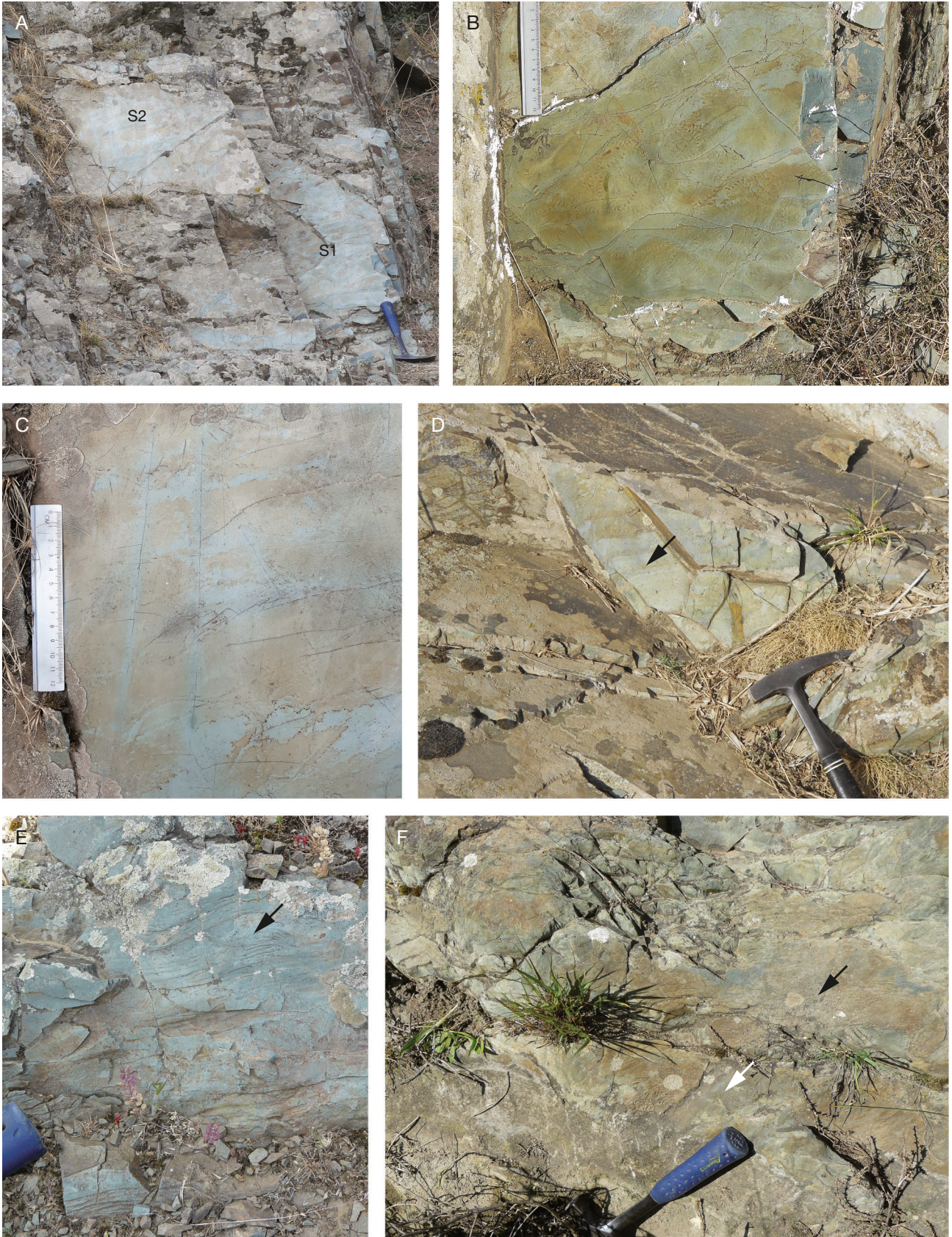


FIG. 3. — Casimcea beds: **A**, view of surfaces **S1** and **S2** exhibiting the *Palaeopascichnus* Palič, 1976 specimens; **C**, detail of surface **S2**; **D**, pluricentimetric bedding in phase with undulations below a surface with large ripples (**arrow**); **E**, natural section showing HCS-type sedimentary structure (**arrow**); **F**, textured surfaces, one punctuated by numerous holes of about 1-2 cm in diameter, sometimes coalescing (**black arrow**), the second showing a very finely reticulated dense network of small wrinkles of millimetric relief (**white arrow**). Photos : J. P. Saint Martin.

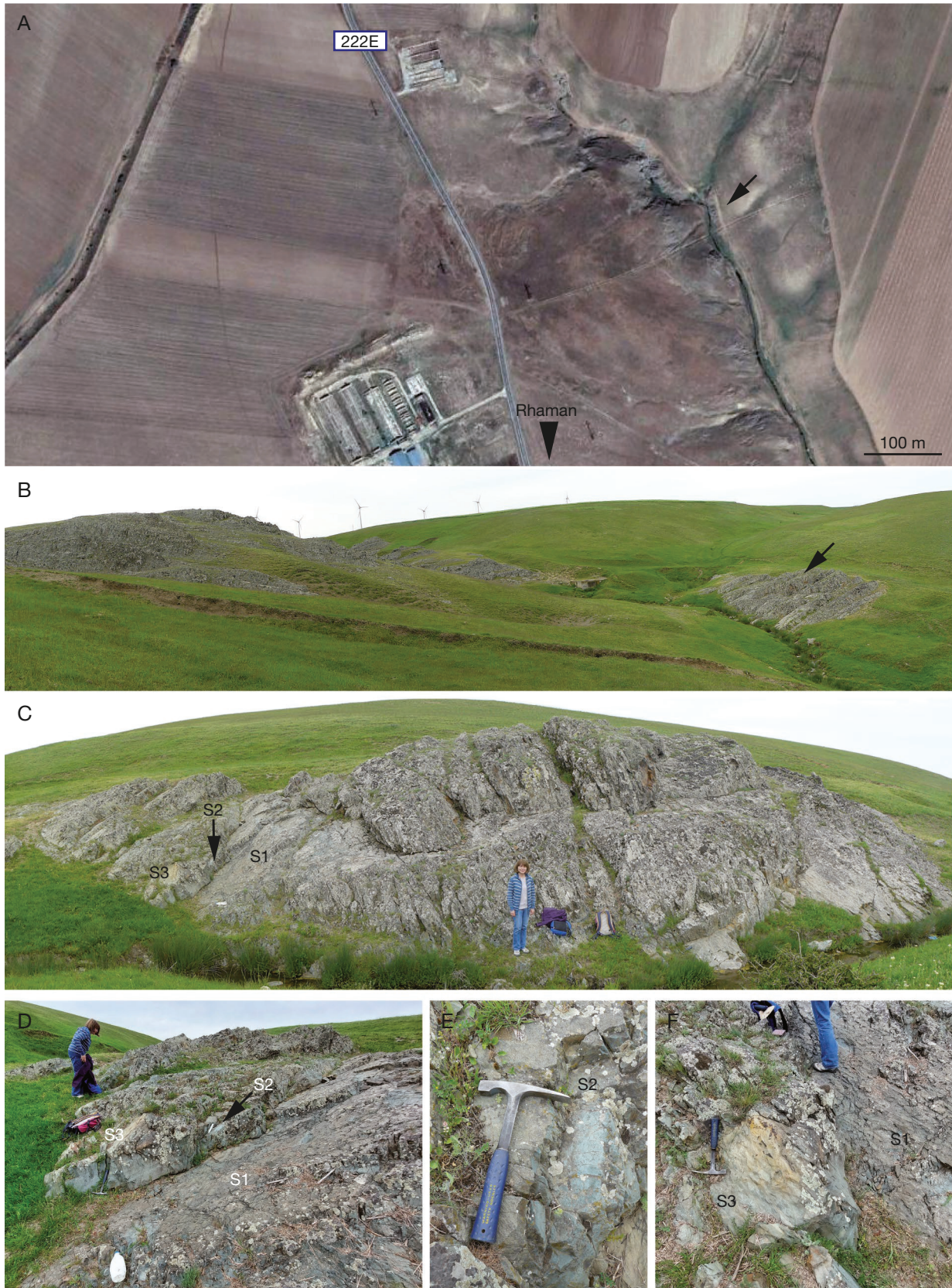


FIG. 4. — Rhaman site: **A**, satellite view (Google Earth) of the Precambrian outcrops around Rahman town and situation of the studied outcrop (white arrow); **B**, natural outcrops along the valley; **C-D**, sedimentary succession showing surfaces **S1-S3**; **E**, **S2** surface bearing the *Palaeopascichnus* Palič, 1976 specimen; **F**, **S3** surface with rhomboid ripples and **S1** surface with large linear ripples. Photos : J. P. Saint Martin.



FIG. 5. — Sedimentary features at Rhaman site: **A**, bed surface with lingoid ripples; **B**, HCS-type sedimentary structures (arrows); **C**, HCS in sedimentary succession (arrow); **D**, bed surface with reticulate MISS; **E**, bed surface with fine reticulate MISS. Photos: J. P. Saint Martin.

SYSTEMATIC PALEONTOLOGY

Genus *Palaeopascichnus* Palij, 1976

TYPE SPECIES. — *Palaeopascichnus delicatus* Palij, 1976 by original designation.

INCLUDED FOSSIL SPECIES. — *P. delicatus* Palij, 1976, *P. gracilis* Fedonkin, 1985 and *P. linearis* (Fedonkin, 1976).

REMARKS

The Ediacaran fossils belonging to the palaeopascichnid group and more particularly to *Palaeopascichnus* remain enigmatic. The description and diagnosis of *Palaeopascichnus* and related species were oriented by their morphological characteristics and possible affinity (for example trace fossils *vs.* body fossils). Kolesnikov & Desiatkin (2022) recalled that the initial definition of *Palaeopascichnus* was established for an ichnogenus, a concept subsequently abandoned (see discussion).

Recent taxonomic studies (Kolesnikov *et al.* 2018a, b; Kolesnikov & Desiatkin 2022) proposed to include *Orbisiana* Sokolov, 1976 as well as *P. gracilis* Fedonkin, 1985 and *P. linearis* (Fedonkin, 1976) within the palaeopascichnids. They further

excluded species differing significantly from classic palaeopascichnid fossils such as *Palaeopascichnus minimus* Shen, Xiao, Dong, Zhou & Liu, 2007, *P. meniscatus* Shen, Xiao, Dong, Zhou & Liu, 2007 (Shen *et al.* 2007), *P. wangjiawamensis* (Jigeng, Daqing & Tinggui, 2009), and *P. jiumenensis* (Dong, Xiao, Shen & Zhou, 2008). Consecutively a new approach to *Palaeopascichnus* was proposed by Kolesnikov *et al.* (2018a, b) and Kolesnikov & Desiatkin (2022) as follows:

Recumbent colonial agglutinated chambered organisms. Chambers are globular or elongated; they are organized in series that branch repeatedly. Width and/or length of chambers can be consistent with each specimen, but in most cases it is gradually increasing at various rates.

Palaeopascichnus linearis (Fedonkin, 1976) (Figs 6; 7)

SYNONYMY. — See details in Kolesnikov *et al.* (2018a) and Kolesnikov & Desiatkin (2022). The original name – *Margaritichnus linearis* Fedonkin, 1976 – was first proposed for a supposed trace fossil (chains of faecal pellets). The species was later revised with the diagnosis emended to correspond to a body fossil (see Kolesnikov *et al.* 2018a and Kolesnikov & Desiatkin 2022).

EMENDED DIAGNOSIS. — Test agglutinated, elongated, curved or rectilinear, occasionally branching, consists of a single series of globular or ellipsoidal chambers 1–15 mm in width. The series occasionally diverge dichotomously. Chambers are relatively consistent in size within a series or gradually increase in width before diverging, but the length-to width ratio of the chambers is relatively constant along the series. The wall thickness does not exceed 1 mm. Number of chambers in a series ranges between 3 and 5 and 30–40.

TYPE AGE. — Late Ediacaran.

EXAMINED SPECIMENS. — Romania • 1 specimen (*in situ* specimens and cast); Casimcea; MNHN.F.A92246 • Rahman; 1 specimen (*in situ* specimen).

DESCRIPTION

Casimcea specimens

The specimen from the S1 surface is preserved as positive epirelief visible on a roughly rectangular area (*c.* 30 × 70 cm) exhibiting some slightly marked ripples (Fig. 6A, B). It consists of meandering segments with parallel edges, of fairly constant width (8 mm in average). The segments are composed of a series of generally consecutive apparently incurved-arcuate elements, about 4 mm thick, with low positive epirelief (Fig. 6C). They were considered as chambers by Kolesnikov *et al.* (2018b). Elements are separated by a shallow incurved depression (*c.* 1 mm wide). The parallel edges of the segments are often visible and marked by a fine negative epirelief groove (0.5 mm wide; Fig. 6C). One imprint differs by the lack of the successive elements between the two parallel lines (Fig. 6D).

The photogrammetry of the mold reveals the bumpy appearance of the surface and the arrangement of the fossil (Fig. 6B, C). The lateral delimitation of segments seems to correspond to a tubular structure enclosing the arcuate elements (Fig. 6B). In several cases, a divergence of the segments occurs (Fig. 6C). Just before the branching, the terminal element is wider than the preceding elements and those of the two divergent segments, up to 1 cm. In two cases, a segment can cross another but overlapping (Fig. 6C). This superposition may result from the crushing of two distinct parts of the initial body, not located in the same plane.

The largest surface S2 exhibits discreet meandering imprint with parallel lines and segmented elements (Fig. 7A). Another imprint, perpendicular to the previous one, with two parallel lines without distinguishable constitutive elements (Fig. 7B) is here also present as for the S1 surface (Fig. 6B, D).

Rahman specimen

The specimen is clearly visible only over a length of about 15 cm. It is probably only part of a larger body fossil. It corresponds to a slightly sinuous imprint with parallel edges and constant width (*c.* 1 cm). It is composed of millimeter thick arcuate elements in slightly marked positive relief (Fig. 7C, D). These characteristics are similar to those on Casimcea S2 surface.

DISCUSSION

According to recent studies, the Romanian specimens have palaeopascichnid characteristics: 1) bedding plane-parallel modular fossils consisting of simple or more complex series of

closely spaced millimetric circular, sausage- or kidney-shaped units (Jensen *et al.* 2018); 2) macroscopic modular chain-like fossils (Kolesnikov 2019), serially arranged, millimetre-scale allantoid chambers (Hawco *et al.* 2019); and 3) serially or cluster-like arranged, millimetre- to centimetre-scale globular or allantoid chambers (Kolesnikov & Desiatkin 2022). Morphometric and taxonomic analyses characterized and discriminated different species of *Palaeopascichnus* or morphospecies (Hawco *et al.* 2019; Hawco 2020; Kolesnikov *et al.* 2018b; Kolesnikov 2019; Desiatkin *et al.* 2021; Kolesnikov & Desiatkin 2022). Based on these works, the Romanian specimens are here assigned to *Palaeopascichnus linearis* (Fedonkin, 1976) because of their relative consistency in the size of arcuate elements (considered as chambers) throughout the series, which is not seen in the type species. *Palaeopascichnus linearis* shares common characters with the type species, such as the possible branching of the series, as observed in the Romanian specimens.

GENERAL DISCUSSION

THE PROBLEM OF THE AFFINITY

Although widespread, *Palaeopascichnus* is an enigmatic fossil within the Ediacaran biota. It was originally described as a trace fossil by Palij (1976) and thus referred to an ichnogenus. *Palaeopascichnus* and other similar forms known by numerous Ediacaran occurrences were considered a fossil displacement trace (e.g., Glaessner 1969; Palij *et al.* 1979; Fedonkin 1981; Cope 1982; Palij *et al.* 1983; Glaessner 1984; Fedonkin 1985; Crimes 1987; Hofmann 1987; Narbonne *et al.* 1987; Paczeńska 1989; Fedonkin 1990a; Crimes 1992; Fedonkin 1992; Cope & Bevins 1993; Crimes 1994; Jenkins 1995; Waggoner 1998; Gehling *et al.* 2001; McCall 2006; McIlroy & Horák 2006; Parcha & Pandey 2011; Tiwari *et al.* 2013; Ivantsov *et al.* 2015; Levashova *et al.* 2015; McIlroy & Brasier 2016). The more complete *Palaeopascichnus* specimen from Casimcea, well visible on a bed surface, was also first interpreted as traces of movement on the background, corresponding to an undetermined ichnogenus (Oaie 1992, 1993). Later, Oaie *et al.* (2005) related this meandering trace to the *Nereites* ichnofacies suggesting deep-water environments. Oaie (2010) and Saint Martin *et al.* (2012) only evoked traces of movement or grazing without further details. More recently, Melinte-Dobrinescu *et al.* (2020) discussed the similarity of the Casimcea specimen with the ichnogenus *Scalarituba* Weller, 1899, known only from the Middle Paleozoic to the Recent. Several characters of *Palaeopascichnus* specimens, also observed in the Romanian samples, rule out the hypothesis of a trace of displacement or grazing: the superposition of the prints, the subdivision of the branches, among others. For these reasons, the interpretation of *Palaeopascichnus* as a trace of organic activity was generally abandoned in favor of a body fossil. Several possible similarities or affinities were then proposed: undetermined body fossil (Jensen 2003), algae (Haines 2000; Jensen *et al.* 2006), agglutinated uniseriate foraminifers (Dong *et al.* 2008), agglutinated xenophyophorian rhizopods (Seilacher *et al.* 2003; Seilacher & Mrinjek 2011;

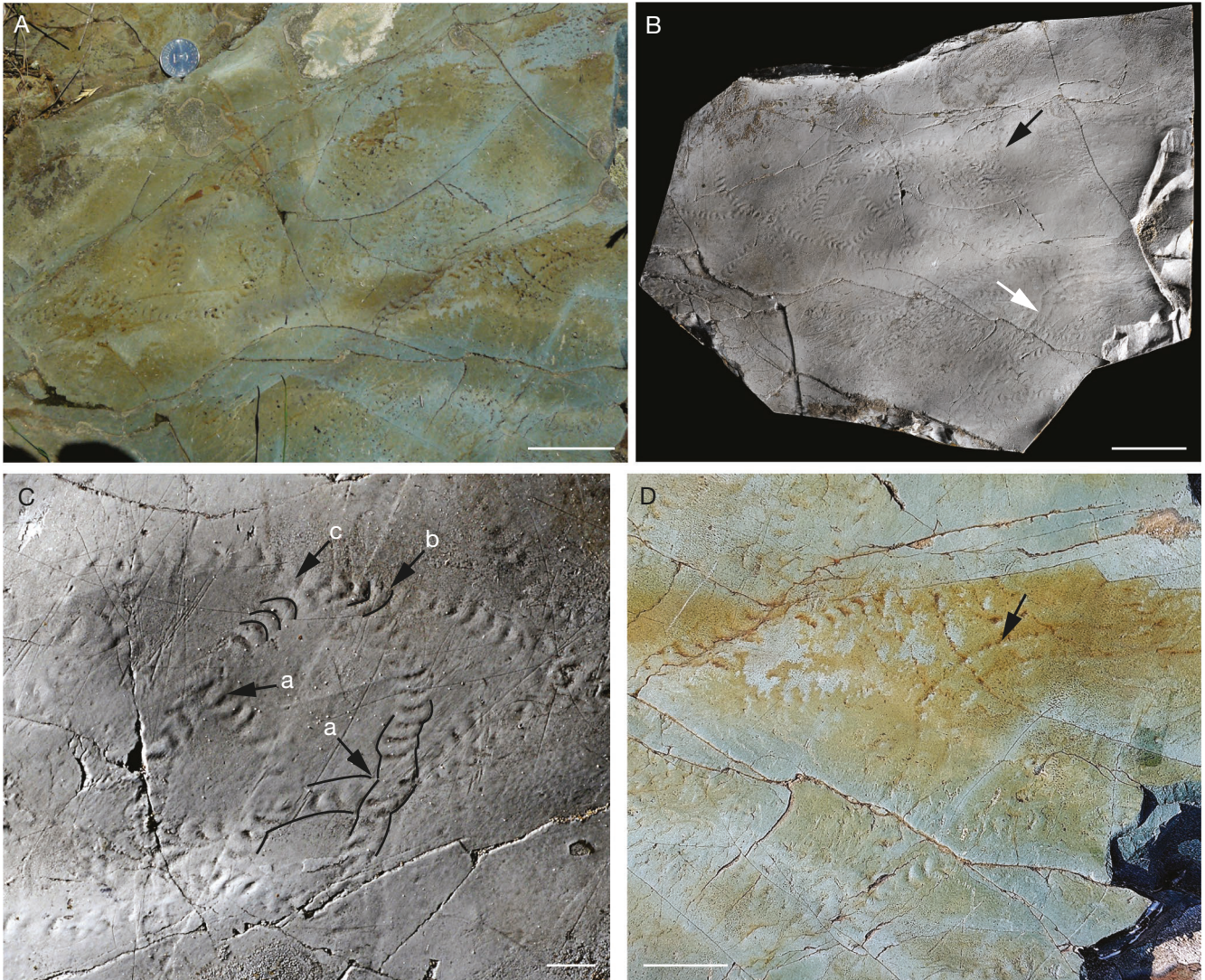


FIG. 6. — Specimens from Casimcea surface S1: **A**, View *in situ* of the *Palaeopascichnus* Palij, 1976 specimen; **B**, photogrammetric representation of the cast showing the poorly marked ridges at the surface (**black arrow**), the network of arcuate meandering elements and the “empty” meandering parallel imprints (**white arrow**); **C**, detailed view showing the well-marked outline of segments, the clear superposition of segments (**a**), the subdivision of segments with elements increasing in size just before the subdivision (**b**); **D**, detail of S1 specimen (close up of **B**, **white arrow**) with arcuate elements and imprint with parallel lines of constant width (c. 1 cm), without internal structures. Photos: J. P. Saint Martin.

Seilacher & Gishlick 2015; Kolesnikov 2019; Kolesnikov & Desiatkin 2022), undetermined protozoan (Antcliffe *et al.* 2011), agglutinated foraminifera (Kenchington *et al.* 2017), possible protistan (Hawco *et al.* 2019). The putative affinities of *Palaeopascichnus* as body fossils are actually closely dependent on how the interpretation of the elements of the chains, often described as chambers. The recent studies were naturally oriented towards an affinity with organisms possessing chambers. The protist hypothesis is then logical and seems legitimate. Thus, morphometry analyses (Kenchington *et al.* 2017; Hawco *et al.* 2019; Kolesnikov & Desiatkin 2022) indicated compatibility with a protist nature with an agglutinated body or test. The agglutinated contour of the chambers may point to organisms close to tested protozoa whose phylogeny with fossil or current groups remains to be established (Kolesnikov & Desiatkin 2022). The Romanian

specimens lack evidence for agglutination of chamber walls and thus cannot provide definitive arguments in favor of a well-argued affinity. The S1 Casimcea specimen clearly shows a tubular outline containing the succession of segments. On the other hand, surfaces S1 and S2 in Casimcea also display parallel meandering traces of the same width without visible segments, which could correspond to “empty” chains of *Palaeopascichnus*. Buatois & Mangano (2016) described similar specimens from the Ediacaran of Newfoundland (Canada) and interpreted them as poorly preserved structure mimicking a fossil trace. This fact raises the possibility of hypothetical tube-dwelling segmented organism. Considering the segments structuring the *Palaeopascichnus* body fossils as chambers does however not resolve the question of communications between chambers and the growth of the supposedly unicellular individual from one chamber to the other.

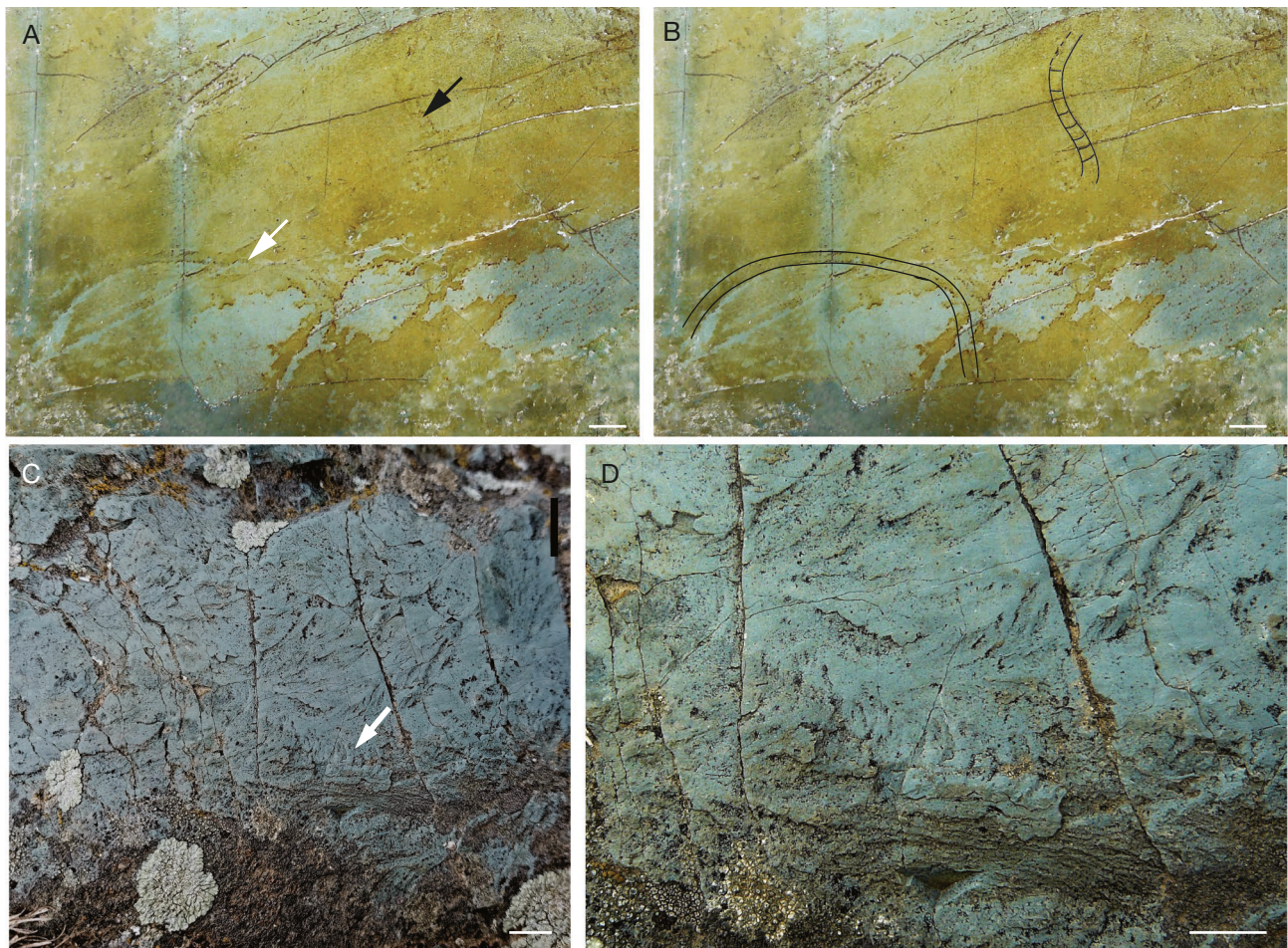


FIG. 7. — **A**, Specimens from Casimcea surface S2 with a meandering succession of slightly arcuate element (black arrow) poorly expressed and imprint with parallel lines of constant width (c. 1 cm), without internal structures (white arrow) similar to Fig. 6D; **B**, same picture as **A** with specimens highlighted; **C**, **D**, specimens from Rhaman; **C**, meandering succession of arcuate elements (arrow) on S2 surface; **D**, detail of **C**. Photos: J. P. Saint Martin.

PALAEOGEOGRAPHIC AND STRATIGRAPHIC CONSEQUENCES

According to recent studies (Kolesnikov *et al.* 2018b; Kolesnikov 2019; Kolesnikov & Desiatkin 2022), only *P. delicatus*, *P. linearis* and *P. gracilis* should be retained within the corpus of *Palaeopascichnus*. Their paleogeographic distribution is worldwide with occurrences for instance in Europe, Asia, Australia, North America. The distribution of *P. linearis* detailed by Kolesnikov *et al.* (2018b) and Kolesnikov & Desiatkin (2022) is large: China, India, Newfoundland (Canada), Australia, Norway, Wales (U.K.), Ukraine, Russia (White Sea, Urals, Siberia...). The discovery of *P. linearis* in Romania enlarges its paleogeographic distribution (westward domain) in line with the previous occurrences reported in Ukraine (Grytsenko 2016; Golubkova *et al.* 2017; Nesterovsky *et al.* 2018; Soldatenko 2018).

The age range of all Neoproterozoic terranes of Dobrogea is not clearly established. The Haidar member of the Histria Formation containing the *Palaeopascichnus* specimens yields other members of the Ediacaran biota (Saint Martin *et al.* 2013; Melinte-Dobrinescu *et al.* 2020), such as *Beltanelliformis brunsa* Menner, 1974 (Saint Martin & Saint Martin 2018). Although the Ediacaran-Cambrian

boundary cannot be formally identified on the field, the presence of *Palaeopascichnus* confirms the Ediacaran age of the Haidar member (Fedonkin 1990b; Fedonkin *et al.* 2007; Gehling & Droser 2009; Grytsenko 2016; Högström *et al.* 2013; Brasier *et al.* 1994; Carbone & Narbonne 2014; Liu & Conliffe 2015; Ebbestad *et al.* 2016; Ivantsov 2017; Golubkova *et al.* 2017; Høyberget *et al.* 2017; Ivantsov 2018; Ivantsov *et al.* 2018; Jensen *et al.* 2018; Nesterovsky *et al.* 2018; Bobrovskiy *et al.* 2019; Hawco *et al.* 2019; Kolesnikov 2019; Soldatenko *et al.* 2019; Liu & Tindal 2020; Desiatkin *et al.* 2021; Moczyłowska *et al.* 2021; Kolesnikov & Desiatkin 2022; Bowyer *et al.* 2023; Clarke *et al.* 2023; Kolesnikov *et al.* 2023a, b). It should be noted that the Neoproterozoic sediments of Podolia (Ukraine) dated around -557 Ma (Soldatenko *et al.* 2019) contain an Ediacaran biota close to that observed in Romania in the Haidar member of the Histria Formation (Saint Martin *et al.* 2013; Melinte-Dobrinescu *et al.* 2020; unpublished personal data), which is compatible with the youngest occurrence of *Palaeopascichnus linearis* according to Kolesnikov & Desiatkin (2022) and Kolesnikov *et al.* (2023a).

PALAEOENVIRONMENTAL INDICATIONS

Since all the Histria Formation has been attributed to deposits of turbidite system, the levels containing *Palaeopascichnus* in Casimcea have been naturally described as belonging to a system of distal fine-grained turbidites (Oaie 1992; Melinte-Dobrinescu *et al.* 2020). In this case, the comparison with the shallow water ichnogenus *Scalarituba* suggested by Melinte-Dobrinescu *et al.* (2020) is irrelevant (Conkin & Conkin 1968; Archer 1984).

The occurrences of *Palaeopascichnus* are generally related to relatively shallow variable marine settings, from very shallow littoral, to upper slope shelf or deltaic front environments (Narbonne *et al.* 1987; Haines 1987, 1990; Cope & Bevins 1993; Gehling *et al.* 2000; Haines 2000; Martin *et al.* 2000; Grazhdankin 2004; Fedonkin & Vickers-Rich 2007a, b, c, d; Gehling & Droser 2009; Grazhdankin *et al.* 2009; Corrick 2012; Fedonkin *et al.* 2012; Gehling & Droser 2013; Menon *et al.* 2013; Grazhdankin 2014; Paczeńska 2014; Dong *et al.* 2015; Liu *et al.* 2015; Liu & McIlroy 2015; Buatois & Mangano 2016; Grytsenko 2016; McIlroy & Brasier 2016; Ivantsov *et al.* 2018; Nesterovsky *et al.* 2018; Reid *et al.* 2018; Hawco *et al.* 2019; Becker-Kerber *et al.* 2020, 2021, 2024; Bobrovskiy *et al.* 2020; Xiao *et al.* 2021; Bowyer *et al.* 2023; Clarke *et al.* 2023; Kolesnikov *et al.* 2023a). The spatial distribution of fossil body assemblages from different Ediacaran deposits led Boag *et al.* (2016) to integrate *Palaeopascichnus* into White Sea-type assemblages, in an inner shelf position. The occurrences of *Palaeopascichnus linearis* point to the following possible deposit environments: shallow inner shelf (Kolesnikov *et al.* 2015, 2019), internal ramp affected by wave and current activity (Kolesnikov *et al.* 2018b), extremely shallow and intertidal setting (Desiatkin *et al.* 2021; Kolesnikov *et al.* 2023a, b), prodelta system (Bobkov *et al.* 2019) or nearshore marine setting (Liu & Tindal 2020). A probable link with subaqueous shrinkage cracks and MISS has also been reported (Gehling & Droser 2009; Hawco *et al.* 2019; Liu & Tindal, 2020). Moreover, the nearest known occurrences of *Palaeopascichnus* are issued from the Mogilev Formation cropping out Podolia (Ukraine), which points to shallow water conditions with the frequent implication of microbial mats (Fedonkin & Vickers-Rich 2007b; Ivantsov *et al.* 2015; Grytsenko 2016; Nesterovsky *et al.* 2018; Soldatenko 2018; Martyshyn & Uchman 2021). The depositional environment of the specimens studied here thus likely corresponds to depth much shallower than that of deep turbidites, in line with our sedimentological observations. The HCS-type structures observed locally at Casimcea (Fig. 3E) and widely distributed at Rahman (Fig. 5B, C) indeed illustrate the influence of storm waves. The co-occurrence of palaeopascichnid remains and HCS-like structures has also been reported in numerous other Ediacaran sedimentary series (e.g., Narbonne *et al.* 1987; Haines 1987, 1990; Jenkins *et al.* 1993; Gehling 2000; Gehling *et al.* 2000; Grazhdankin 2004; McIlroy & Horák 2006; Grazhdankin *et al.* 2009; Corrick 2012; Kolesnikov *et al.* 2015; Nagovitsin *et al.* 2015; McIlroy & Brasier 2016; Bobkov *et al.* 2019; Becker-Kerber *et al.* 2020; Shahkarami *et al.* 2020; Xiao *et al.* 2021; Bowyer *et al.*

2023). The Romanian specimens of *Palaeopascichnus* occur in sediments with oscillating ridges (Casimcea, Fig. 2C) or lingoid ridges (Rahman; Figs 4F, 5A) resulting from currents and/or oscillating waves. The Casimcea and Rahman surfaces with MISS-type textured structures also testify the presence of microbial mats (Figs 3F, 5D-E). According to several studies (Hawco *et al.* 2019; Becker-Kerber *et al.* 2020, 2021), microbial mats promoted the preservation of *Palaeopascichnus*, as also demonstrated by actualistic experiments (Bobrovskiy *et al.* 2019). More generally, the widespread presence of MISS in other Ediacaran deposits of Central Dobrogea led to the same conclusions (Saint Martin *et al.* 2011, 2013; Oaie *et al.* 2012).

CONCLUSION

Fossils of *Palaeopascichnus* from Neoproterozoic terranes of Dobrogea confirm the widespread palaeogeographic distribution of this genus as well as its occurrence in shallow marine environments. Because these fossils are not easy to distinguish on the field, like other Ediacaran fossil bodies in the region, we can assume that new field prospecting could lead to the discovery of additional specimens. The Ediacaran outcrops of Romania should be carefully resampled and reinterpreted in terms of palaeoenvironments, owing that the present observations are not compatible with distal turbidite system. The Ediacaran outcrops of Romania thus constitute a potential for understanding a new bioprovince of the Ediacaran biota.

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REFERENCES

- ANTCLIFFE J. B., GOODAY A. J. & BRASIER M. D. 2011. — Testing the protozoan hypothesis for Ediacaran fossils: a developmental analysis of *Palaeopascichnus*. *Palaeontology* 54: 1157-1175. <https://doi.org/10.1111/j.1475-4983.2011.01058.x>.
- ARCHER A. W. 1984. — Preservational control of trace-fossil assemblages: Middle Mississippian carbonates of South-Central Indiana. *Journal of Paleontology* 58 (2): 285-297. <https://www.jstor.org/stable/1304784>

- BALINTONI I., BALICA C., SEGHEDI A. & DUCEA M. N. 2011. — Peri-Amazonian provenance of the Central Dobrogea terrane (Romania) attested by U/Pb detrital zircon age patterns. *Geologica Carpathica* 62: 299-307. <https://doi.org/10.2478/v10096-011-0023-x>
- BALINTONI I. & BALICA C. 2016. — Peri-Amazonian provenance of the Euxinic craton components (Romania): a detrital zircon study. *Precambrian Research* 278: 34-51. <https://doi.org/10.1016/j.precamres.2016.03.008>
- BECKER-KERBER B., PAIM P. S. G., JUNIOR F. C., GIRELLI T. J., DA ROSA A. L. Z., EL ALBANI A., OSES G. L., PRADO G. M. E. M., FIGUEIREDO M., SIMOES L. S. A. & PACHECO M. L. A. F. 2020. — The oldest record of Ediacaran macrofossils in Gondwana (~563 Ma, Itajaí Basin, Brazil). *Gondwana Research* 84: 211-228. <https://doi.org/10.1016/j.gr.2020.03.007>
- BECKER-KERBER B., EL ALBANI A., KONHAUSER K., ELMOLA A. A., FONTAINE C., PAIM P. S. G., MAZURIER A., PRADO G. M. E. M., GALANTE D., KERBER P. B., DA ROSA A. L. Z., FAIRCHILD T. R., MEUNIER A. & PACHECO M. L. A. F. 2021. — The role of volcanic-derived clays in the preservation of Ediacaran biota from the Itajaí Basin (ca.563 Ma, Brazil). *Nature, Scientific Reports* 11, 5013: 1-10. <https://doi.org/10.1038/s41598-021-84433-0>
- BECKER-KERBER B., PRADO G. M. E. M., ARCHILHA N. L., WARREN L. V., SIMÕES M. G., LINO L. M., QUIROZ-VALLE F. R., MOURO L. D., EL ALBANI A., MAZURIER A., PAIM P. S. G., CHEMALE F., ZUCATTI DA ROSA A. L., DE BARROS G. E. B., EL KABOURI J. & BASEI M. A. S. 2024. — Ediacaran tectographs from the Itajaí Basin: A cautionary tale from the Precambrian, *Precambrian Research* 403, 107307. <https://doi.org/10.1016/j.precamres.2024.107307>
- BOAG T. H., DARROCH S. A. F. & LAFLAMME M. 2016. — Ediacaran distributions in space and time: testing assemblage concepts of earliest macroscopic body fossils. *Paleobiology* 42: 574-594. <https://doi.org/10.1017/pab.2016.20>
- BOBKOV N. I., KOLESNIKOV A. V., MASLOV A. V. & GRAZHDANKIN D. V. 2019. — The occurrence of *Dickinsonia* in non-marine facies. *Estudios Geológicos* 75 (2), e096: 1-5. <https://doi.org/10.3989/egol.43587.551>
- BOBROVSKIY I., KRASNOVA A., IVANTSOV A., LUZHNYAYA (SEREZHNIKOVA) E. & BROCKS J. J. 2019. — Simple sediment rheology explains the Ediacara biota preservation. *Nature Ecology and Evolution* 3: 582-589. <https://doi.org/10.1038/s41559-019-0820-7>
- BOBROVSKIY I., HOPE J. M., GOLUBKOVA E. & BROCKS J. J. 2020. — Food sources for the Ediacara biota communities. *Nature Communications* 11: 1261. <https://doi.org/10.1038/s41467-020-15063-9>
- BOWYER F. T., ZHURAVLEV A. Y., WOOD R., ZHAO F., SUKHOV S. S., ALEXANDER R. D., POULTON S. W. & ZHU M. 2023. — Implications of an integrated late Ediacaran to early Cambrian stratigraphy of the Siberian Platform, Russia. *Geological Society of America Bulletin* 135 (9-10): 2428-2450. <https://doi.org/10.1130/B36534.1>
- BRASIER M., COWIE J. & TAYLOR M. 1994. — Decision on the Precambrian-Cambrian boundary stratotype. *Episodes* 17 (1-2): 3-7. <https://doi.org/10.18814/epiugs/1994/v17i1.2/002>
- BUATOIS L. A. & MANGANO M. G. 2016. — Ediacaran Ecosystems and the Dawn of Animals, in MANGANO M. G. & BUATOIS L. A. (eds), *The Trace-Fossil Record of Major Evolutionary Events*. Springer Science, Business Media Dordrecht: 27-72 (Topics in Geobiology; 39). https://doi.org/10.1007/978-94-017-9600-2_2
- CARBONE C. A. & NARBONNE G. M. 2014. — When life got smart: the evolution of behavioral complexity through the Ediacaran and early Cambrian of Nw Canada. *Journal of Paleontology* 88 (2): 309-330. <https://doi.org/10.1666/13-066>
- CLARKE A. J. I., KIRKLAND C. L., MENON L. R., CONDON D. J., COPE, JOHN C. W., BEVINS R. E. & GLORIE S. 2023. — U-Pb zircon-rutile dating of the Llangynog Inlier, Wales: constraints on an Ediacaran shallow-marine fossil assemblage from East Avalonia. *Journal of the Geological Society* 181 (1): 1-12. <https://doi.org/10.1144/jgs2023-081>
- CONKIN J. E. & CONKIN B. M. 1968. — *Scalarituba missouriensis* and its stratigraphic distribution. *University of Kansas Paleontological Contributions* paper 31: 1-7. <http://hdl.handle.net/1808/3699>
- COPE J. C. W. 1982. — Precambrian fossils of the Carmarthen area. Dyfed. *Nature in Wales (New Series)* 1 (2): 11-16.
- COPE J. C. W. & BEVINS R. E. 1993. — The stratigraphy and setting of the Precambrian rocks of the Llangynog Inlier, Dyfed, South Wales. *Geological Magazine* 130: 101-111. <https://doi.org/10.1017/S0016756800023761>
- CORRICK A. J. 2012. — *Resolving the Diagenetic and Marine Influences on the Carbon Isotopic Composition of the Ediacaran Wonoka Formation, South Australia*. Unpublished Thesis, University of Adelaide, 54 p. <https://hdl.handle.net/2440/92057>
- CRIMES T. P. 1987. — Trace fossils and correlation of late Precambrian and early Cambrian strata. *Geological Magazine* 124: 97-119. <https://doi.org/10.1017/S0016756800015922>
- CRIMES T. P. 1992. — The Record of Trace Fossils across the Proterozoic-Cambrian Boundary, in LIPPS J. H. & SIGNOR P. W. (eds), *Origin and the Early Evolution of Metazoa*. Plenum Press, New York: 87-129.
- CRIMES T. P. 1994. — The period of early evolutionary failure and the dawn of evolutionary success: The record of biotic changes across the Precambrian-Cambrian boundary, in DONOVAN S. K. (ed.), *The Palaeobiology of Trace Fossils*. Johns Hopkins University Press, Baltimore, Md.: 105-133.
- DESIATKIN V. D., KOLESNIKOV A. V., RIMSKY A. A., SYSOEVA A. O., TEREKHOVA V. A., KUZNETSOV N. B., SHAZILLO A. V., LATYSHEVA I. V., ROMANYUK T. V. & FEDONKIN M. A. 2021. — Palaeopascichnids from the Upper Vendian Chernyi Kamen Formation of the Middle Urals (Perm Region). *Doklady Earth Sciences* 499 (2): 643-647. <https://doi.org/10.1134/S1028334X21080043>
- DONG L., XIAO S., SHEN S. & ZHOU C. 2008. — Silicified *Hordyskia* and *Palaeopascichnus* from Upper Ediacaran cherts in South China: tentative phylogenetic interpretation and implications for evolutionary stasis. *Journal of the Geological Society* 165: 367-378. <https://doi.org/10.1144/0016-76492007-074>
- DONG L., SHEN B., LEE C. T. A., SHU X., PENG Y., SUN Y., TANG Z., RONG H., LANG X., MA H., YANG F. & GUO W. 2015. — Germanium/silicon of the Ediacaran-Cambrian Laobao cherts: Implications for the bedded chert formation and paleoenvironment interpretations. *Geochemistry, Geophysics, Geosystems* 16: 1-13. <https://doi.org/10.1002/2014gc005595>
- EBBESTAD J. O., HÖGSTRÖM A. E. S., JENSEN S., MEINHOLD G., TAYLOR W. L., PALACIOS T., HOYBERGET M., NOVIS L. K. & OU Z. 2016. — The Ediacaran succession and fauna of the Digermulen Peninsula, northern Norway. Abstracts of the 32nd Nordic Geological Winter Meeting, 13th-15th January 2016, Helsinki, Finland, *Bulletin of the Geological Society of Finland*, Special Volume: 196-197.
- FEDONKIN M. A. 1976. — Sledy mnogokletotchnykh iz valdaiskoi serii. *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya* 4: 129-32 (in Russian).
- FEDONKIN M. A. 1981. — Belomorskaja biota venda. *Trudy Akademii Nauk SSSR* 342: 1-100 p.
- FEDONKIN M. A. 1985. — Paleoikhnologiya vendskikh metazoa, in SOKOLOV B. S. & IVANOVSKY A. B. (eds), *Vendkaya Sistema*. 1. Nauka, Moscow: 112-117.
- FEDONKIN M. A. 1990a. — Paleoichnology of Vendian Metazoa, in SOKOLOV B. S. & IWANOWSKI A. B. (eds), *The Vendian System*. 1. *Paleontology*. Springer-Verlag, Berlin: 132-137.
- FEDONKIN M. A. 1990b. — Systematic description of Vendian metazoa, in SOKOLOV B. S. & IWANOWSKI A. B. (eds), *The Vendian System*. 1. *Paleontology*. Springer-Verlag, Berlin: 71-120.
- FEDONKIN M. A. 1992. — Vendian faunas and the early evolution of Metazoa, in LIPPS J. H. & SIGNOR P. W. (eds), *Origin and the Early Evolution of Metazoa*. Plenum Press, New York: 87-129.
- FEDONKIN M. A. & VICKERS-RICH P. 2007a. — The White Sea's Windswept Coasts, in FEDONKIN *et al.* (eds), *The Rise of Animals*. The Johns Hopkins University Press, Baltimore: 115-146.

- FEDONKIN M. A. & VICKERS-RICH P. 2007b. — Podolia's Green Valleys, in FEDONKIN *et al.* (eds), *The Rise of Animals*. The Johns Hopkins University Press, Baltimore: 149-156.
- FEDONKIN M. A. & VICKERS-RICH P. 2007c. — The Siberian Tundra, in FEDONKIN *et al.* (eds), *The Rise of Animals*. The Johns Hopkins University Press, Baltimore: 157-167.
- FEDONKIN M. A. & VICKERS-RICH P. 2007d. — The Urals, in FEDONKIN *et al.* (eds), *The Rise of Animals*. The Johns Hopkins University Press, Baltimore: 169-173.
- FEDONKIN M. A., GEHLING J. G., GREY K., NARBONNE G. M. & VICKERS-RICH P. 2007. — *The Rise of Animals*. The Johns Hopkins University Press, Baltimore, 326 p.
- FEDONKIN M. A., VICKERS-RICH P., SWALLA B. J., TRUSLER P. & HALL M. 2012. — A new metazoan from the Vendian of the White Sea, Russia, with possible affinities to the ascidians. *Paleontological Journal* 46: 1-11. <https://doi.org/10.1134/S0031030112010042>
- GEHLING J. G. 2000. — Environmental interpretation and a sequence stratigraphic framework for the terminal Proterozoic Ediacara Member within the Rawnsley Quartzite, South Australia. *Precambrian Research* 100: 65-95. [https://doi.org/10.1016/S0301-9268\(99\)00069-8](https://doi.org/10.1016/S0301-9268(99)00069-8)
- GEHLING J. G., JENSEN S., DROSER M., MYROW P. M. & NARBONNE G. 2001. — Burrowing below the basal Cambrian Gssp, Fortune Head, Newfoundland. *Geological Magazine* 138 (2): 213-218. <https://doi.org/10.1017/S001675680100509X>
- GEHLING J. G., NARBONNE G. M. & ANDERSON M. M. 2000. — The first named Ediacaran body fossil, *Aspidella terranovica*. *Palaeontology* 43: 427-456. <https://doi.org/10.1111/j.0031-0239.2000.00134.x>
- GEHLING J. G. & DROSER M. L. 2009. — Textured organic surfaces associated with the Ediacara biota in South Australia. *Earth Science Reviews* 96: 196-206. <https://doi.org/10.1016/j.earscirev.2009.06.004>
- GEHLING J. G. & DROSER M. L. 2013. — How well do fossil assemblages of the Ediacara Biota tell time? *Geology* 41: 447-450. <https://doi.org/10.1130/G33881.1>
- GIUȘCĂ D., IANOVICI V., MĂNZATU S., SOROIU E., LEMNE M., TĂNĂȘESCU A. & IONCĂ M. 1967. — Asupra vârstei absolute a formațiunilor cristalofiliene din forlandul orogenului carpatic. *Studii și cercetări de geologie, geofizică, geografie, seria Geologie* 12: 287-297.
- GLAESSNER M. F. 1969. — Trace fossils from the Precambrian and basal Cambrian. *Lethaia* 2: 369-393. <https://doi.org/10.1111/j.1502-3931.1969.tb01258.x>
- GLAESSNER M. F. 1984. — *The Dawn of Animal Life. A Biohistorical Study*. Cambridge University Press, 182 p.
- GOLUBKOVA E. YU., PLOTKINA YU. V., KULIKOV A. M., KUSHIM E. A. 2017. — Koltsevidnye organizmy *Orbisiana* sp. iz verkhevendskikh otlozhenij vostochnoevropejskoj platformy, in *Integrativnaya paleontologiya: perspektivy razvitiya dlya geologicheskikh tselej*. Material LXIII sessii Paleontologicheskogo obshchestva pri Ran: 56-58.
- GRAZHDANKIN D. V. 2004. — Late Neoproterozoic sedimentation in the Timan foreland, in GEE D. G. & PEASE V. (eds), *The Neoproterozoic Timanide Orogen of Eastern Baltica*. Geological Society of London, London, Memoir 30: 37-46.
- GRAZHDANKIN D. V. 2014. — Patterns of evolution of the Ediacaran soft-bodied biota. *Journal of Paleontology* 88: 269-283. <https://doi.org/10.1666/13-072>
- GRAZHDANKIN D. V., MASLOV A. V. & KRUPENIN M. T. 2009. — Structure and Depositional History of the Vendian Sylvitsa Group in the Western Flank of the Central Urals. *Stratigraphy and Geological Correlation* 17 (5): 475-492. <https://doi.org/10.1134/S0869593809050025>
- GRYTSENKO V. 2016. — A new discovery of Metazoa imprints and ichnofossils in the Vendian Mohyliv Suite from the Bernashivka Quarry. *Proceedings of the National Museum of Natural History of Ukraine* 14: 23-34. http://nbuv.gov.ua/UJrn/Vnnpm_2016_14_4
- HAINES P. W. 1987. — *Carbonate Shelf and Basin Sedimentation, Late Proterozoic Wonoka Formation, South Australia*. Unpublished PhD Thesis, University of Adelaide, Adelaide, South Australia, 152 p.
- HAINES P. W. 1990. — A late Proterozoic storm-dominated carbonate shelf sequence: the Wonoka Formation in central and southern Flinders Ranges, South Australia. *Special Publication of the Geological Society of South Australia* 16: 177-198.
- HAINES P. W. 2000. — Problematic fossils in the late Neoproterozoic Wonoka Formation, South Australia. *Precambrian Research* 100: 97-108. [https://doi.org/10.1016/S0301-9268\(99\)00070-4](https://doi.org/10.1016/S0301-9268(99)00070-4)
- HAWCO J. B., KENCHINGTON, C. G. & MC ILROY D. 2019. — A quantitative and statistical discrimination of morphotaxa within the Ediacaran genus *Palaeopascichnus*. *Papers in Palaeontology* 7 (2): 657-673. <https://doi.org/10.1002/spp2.1290>
- HAWCO J. B., KENCHINGTON C. G., MATTHEWS J., MACBEATH D. A. & MC ILROY D. 2017. — The palaeobiology of Ediacaran *Palaeopascichnus*: new insights from morphometric and geochemical analysis. The Paleontological Association, 61st Annual Meeting, London, Abstracts, 1 p.
- HAWCO J. B. 2020. — *The Palaeontology of Ediacaran Avalonia: new Insights using Morphometrics and Multivariate Statistical Analyses*. Unpublished thesis, Memorial University of Newfoundland, Canada, 165 p. <https://research.library.mun.ca/14326/1/thesis.pdf>
- HOFMANN H. J. 1987. — Precambrian biostratigraphy. *Geoscience Canada* 14 (3): 135-154. https://id.erudit.org/iderudit/geocan14_3art01
- HÖGSTRÖM A. E. S., JENSEN, S., PALACIOS, T. & EBBESTAD, J. O. R. 2013. — New information on the Ediacaran-Cambrian transition in the Vestertana Group, Finnmark, northern Norway, from trace fossils and organic-walled microfossils. *Norwegian Journal of Geology* 93: 95-106. <https://hdl.handle.net/10037/18954>
- HÖYBERGET M., HÖGSTRÖM A. E. S., EBBESTAD, J. O. R. & JENSEN S. 2017. — Fantastiske fossilfunn i Finnmark. *Natureen* 3: 94-100. <https://doi.org/10.18261/issn.1504-3118-2017-03-02>
- IVANTSOV A. Y. 2017. — Finds of Ediacaran-Type Fossils in Vendian Deposits of the Yudoma Group, Eastern Siberia. *Doklady Earth Sciences* 472 (2): 143-146. <https://doi.org/10.1134/S1028334X17020131>
- IVANTSOV A. Y. 2018. — Vendian Macrofossils of the Yudoma Group, Southeast of the Siberian Platform. *Paleontological Journal* 52 (12): 1335-1346. <https://doi.org/10.1134/S0031030118120092>
- IVANTSOV A. Y., GRITSENKO V. P., KONSTANTINENKO L. I., MENASOVA A. S., FEDONKIN M. A., ZAKREVSAYA M. A. & SEREZHNIKOVA E. A. 2015. — *Makrofossilii verkhnego vendia Vostochnoy Yevropy. Sredneye Pridnestrovy'e i Volyn'* [Macrofossils of the Upper Vendian of Eastern Europe. Middle Transdnistria and Volyn]. Russian Academy of Sciences, Moscow, 144 (in Russian).
- IVANTSOV A. Y., RAZUMOVSKIY A. A., ZAKREVSAYA M. A. 2018. — *Upper Vendian Macrofossils of Eastern Europe. Middle and Southern Urals*. Pin Ras, Moscow; 190 p.
- JENKINS R. J. F. 1995. — The problems and potential of using animal and trace fossils in terminal Proterozoic biostratigraphy. *Precambrian Research* 73: 51-69. [https://doi.org/10.1016/S0301-9268\(94\)00071-X](https://doi.org/10.1016/S0301-9268(94)00071-X)
- JENKINS R. J. F., LINDSAY J. F. & WALTER M. R. 1993. — *Field Guide to the Adelaide Geosyncline and Amadeus Basin, Australia*. Australian Geological Survey Organisation, 133 p.
- JENSEN S. 2003. — The Proterozoic and earliest Cambrian trace fossil record; patterns, problems and perspectives. *Integrative and Comparative Biology* 43: 219-228. <https://doi.org/10.1093/icb/43.1.219>
- JENSEN S., DROSER M. D. & GEHLING J. G. 2006. — A critical look at the ediacaran trace fossil record, in XIAO S. & KAUFMAN A. J. (eds), *Neoproterozoic Geobiology and Paleobiology*. Topics in Geobiology 27. Springer, Dordrecht: 115-157. https://doi.org/10.1007/1-4020-5202-2_5
- JENSEN S., HÖGSTRÖM A. E. S., HÖYBERGET M., MEINHOLD G., MCILROY D., EBBESTAD J. O. R., TAYLOR W. L., AGIĆ H. & PALACIOS T. 2018. — New occurrences of *Palaeopascichnus* from the Ståhpogieddi Formation, Arctic Norway, and their bearing on the age of Varanger Ice Age. *Canadian Journal of Earth Sciences* 55: 1253-1261. <https://doi.org/10.1139/cjes-2018-0035>

- JICHENG Y., DAQING L. & TINGGUI H. 1993. — Discovery of trace fossils from the Sinian-Cambrian boundary beds in Eastern Yunnan and their significance for global correlation. *Acta Geologica Sinica* 6 (4): 429-445. <https://doi.org/10.1111/j.1755-6724.1993.mp6004005.x>
- JIPA D. 1967. — Cross-stratification as a criterion of palaeocurrent direction in flysch deposits. *Scottish Journal of Geology* 3 (2): 227-234. <https://doi.org/10.1144/sjg03020227>
- JIPA D. 1968. — Azimuthal relationships between cross-Stratification and current markings of central Dobrogea, Romania. *Journal of Sedimentary Petrology* 38 (1): 192-199. <https://doi.org/10.1306/74D71915-2B21-11D7-8648000102C1865D>
- KENCHINGTON C., MACBEATH A., MATTHEWS J. & MCILROY D. 2017. — Constraining the nature of Ediacaran *Palaeopascichnus* using morphology and geochemistry. *Geophysical Research Abstracts* 19, Egu2017-12542.
- KOLESNIKOV A. V. 2018. — *Paleobiology of the Ediacaran Biota during and after the Kotlinian Crisis Event: Insights from Palaeopascichnids and Microbially Induced Morphostructures*. Unpublished thesis, Univ. Lille, 310 p. <https://pepite-depot.univ-lille.fr/Libre/Edsmre/2018/50376-2018-Kolesnikov.pdf>
- KOLESNIKOV A. V. 2019. — Stratigraphic correlation potential of the Ediacaran palaeopascichnids. *Estudios Geológicos* 75 (2), e102: 1-5. <https://doi.org/10.3989/egool.43588.557>
- KOLESNIKOV A. V. & DESIATKIN V. 2022. — Taxonomy and palaeoenvironmental distribution of palaeopascichnids. *Geological Magazine* 159: 1175-1191. <https://doi.org/10.1017/S0016756822000437>
- KOLESNIKOV A. V., MARUSIN V. V., NAGOVITSIN K. E., MASLOV A. V. & GRAZHDANKIN D. V. 2015. — Ediacaran biota in the aftermath of the Kotlinian Crisis: Asha Group of the South Urals. *Precambrian Research* 263: 59-78. <https://doi.org/10.1016/j.precamres.2015.03.011>
- KOLESNIKOV A. V., LIU A. G., DANELIAN T. & GRAZHDANKIN D. V. 2018a. — A reassessment of the problematic Ediacaran genus *Orbisiana* Sokolov 1976. *Precambrian Research* 316: 197-205. <https://doi.org/10.1016/j.precamres.2018.08.011>
- KOLESNIKOV A. V., ROGOV V. I., BYKOVA N. V., DANELIAN T., CLAUSEN S., MASLOV A. V. & GRAZHDANKIN D. V. 2018b. — The oldest skeletal macroscopic organism *Palaeopascichnuslinearis*. *Precambrian Research* 316: 24-37. <https://doi.org/10.1016/j.precamres.2018.07.017>
- KOLESNIKOV A. V., LATYSHEVA I. V., SHATSILO A. V., KOLESNIKOV A. S., DESIATKIN V. & ROMANYUK T. V. 2023a. — Ediacara-Type Biota in the Upper Precambrian of the Timan Range (Dzhezhim-Parma Hill, Komi Republic). *Doklady Earth Sciences* 510: 289-292. <https://doi.org/10.1134/S1028334X23600032>
- KOLESNIKOV A. V., MARUSIN V. V., RUD'KO S. V. & POKROVSKY B. G. 2023b. — Shadows of the past: An Ediacara-style taphonomic window in advent of Cambrian bioturbators. *Precambrian Research* 399 (2023): 107238. <https://doi.org/10.1016/j.precamres.2023.107238>
- KRÄUTNER H. G., MUREŞAN M. & SEGHEDI A. 1988. — Precambrian of Dobrogea, in ZOUBEK V. (ed.), *Precambrian in Younger Fold Belts*. John Wiley, New York: 361-379.
- LAN Z. W. & CHEN Z. Q. 2012. — Possible animal body fossils from the Late Neoproterozoic interglacial successions in the Kimberley region, northwestern Australia. *Gondwana Research* 21: 293-301. <https://doi.org/10.1016/j.gr.2011.05.014>
- LEVASHOVA N. M., BAZHENOV M. L., MEERT J. G., DANUKALOV K. N., GOLOVANOVA I. V., KUZNETSOV N. B. & FEDOROVA N. M. 2015. — Paleomagnetism of upper Ediacaran clastics from the South Urals: Implications to paleogeography of Baltica and the opening of the Iapetus Ocean. *Gondwana Research* 28: 191-208. <https://doi.org/10.1016/j.gr.2014.04.012>
- LIU A. G. & CONLIFFE J. 2015. — The Ediacaran fossils of the Avalon Peninsula., Geological Association of Canada, Newfoundland and Labrador section-Fall field trip 2015, 62 p. [<https://www.gov.nl.ca/iet/files/mines-geoscience-publications-openfiles-gac-seg-mac-ft-guides-of-nfld-3320-ft-2015.pdf>]
- LIU A. G. & MCILROY D. 2015. — Horizontal surface traces from the Fermeuse Formation, Ferryland (Newfoundland, Canada), and their place within the late Ediacaran ichnological revolution, in MCILROY D. (ed.), *Ichnology: papers from Ichnia III. Geological Association of Canada Miscellaneous Papers* 9: 141-146.
- LIU A. G. & TINDAL B. H. 2020. — Ediacaran macrofossils prior to the ~580 Ma Gaskiers glaciation in Newfoundland, Canada. *Lethaia* 54: 259-270. <https://doi.org/10.1111/let.12401>
- LIU A. G., MATTHEWS J. J., HERRINGSHAW L. G. & MCILROY D. 2015. — Mistaken point ecological reserve field trip guide, in MCILROY D. (ed.), *Ichnology: papers from Ichnia III. Geological Association of Canada Miscellaneous Papers* 9: 231-272.
- MARTIN M. W., GRAZHDANKIN D. V., BOWRING S. A., EVANS D. A. D., FEDONKIN M. A. & KIRSCHVINK J. L. 2000. — Age of Neoproterozoic bilaterian body and trace Fossils, White Sea, Russia: implications for Metazoan evolution. *Science* 288: 841-845. <https://doi.org/10.1126/science.288.5467.841>
- MARTYSHYN A. & UCHMAN A. 2021. — New Ediacaran fossils from the Ukraine, some with a putative tunicate relationship. *Paläontologische Zeitschrift* 95: 623-639. <https://doi.org/10.1007/s12542-021-00596-1>
- MCCALL G. 2006. — The Vendian (Ediacaran) in the geological record: Enigmas in geology's prelude to the Cambrian explosion. *Earth-Science Reviews* 77: 1-229. <https://doi.org/10.1016/j.earscirev.2005.08.004>
- MCILROY D. & HORÁK J. M. 2006. — Neoproterozoic: the late Precambrian terranes that formed Eastern Avalonia, in BRENCHLEY P. J. & RAWSON P. F. (eds), *The Geology of England and Wales*. The Geological Society, London: 9-23.
- MCILROY D. & BRASIER M. D. 2016. — Ichnological evidence for the Cambrian explosion in the Ediacaran to Cambrian succession of Tanafjord, Finnmark, northern Norway, in BRASIER A. T. MCILROY D. & MCLOUGHLIN N. (eds), *Earth system evolution and early life: a celebration of the work of Martin Brasier. Geological Society Special Publications* 448: 351-368. <https://doi.org/10.1144/Sp448.7>
- MELINTE-DOBRINESCU M., SEGHEDI A. & ROBAN R. D. 2020. — *Dobrogea and Danube Delta: geology and geomorphology. Field Trip Guidebook*. GeoEcoMar edition: 1-50.
- MENON L. R., MCILROY D. & BRASIER M. D. 2013. — Evidence for Cnidaria-like behavior in ca. 560 Ma Ediacaran *Aspidella*. *Geology* 41: 895-898. <https://doi.org/10.1130/G34424.1>
- MOCZYDŁOWSKA M., KEAR B. P., SNITTING D., LIU L., LAZOR P. & MAJKA J. 2021. — Ediacaran metazoan fossils with siliceous skeletons from the Digermulen Peninsula of Arctic Norway. *Journal of Paleontology* 95 (3): 440-475. <https://doi.org/10.1017/jpa.2020.105>
- NARBONNE G. M., MYROW P., LANDING E. & ANDERSON M. M. 1987. — A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. *Canadian Journal of Earth Sciences* 24: 1277-1293. <https://doi.org/10.1139/e87-124>
- NAGOVITSIN K. E., ROGOV V. I., MARUSIN V. V., KARLOVA G. A., KOLESNIKOV A. V., BYKOVA N. V. & GRAZHDANKIN D. V. 2015. — Revised Neoproterozoic and Terreneuvian stratigraphy of the Lena-Anabar Basin and north-western slope of the Olenek Uplift, Siberian Platform. *Precambrian Research* 270: 226-245. <https://doi.org/10.1016/j.precamres.2015.09.012>
- NESTEROVSKY V. A., MARTYSHYN A. I. & CHUPRYNA A. M. 2018. — New biocenosis model of Vendian (Ediacaran) sedimentation basin of Podilia (Ukraine). *Journal of Geology, Geography and Geoecology* 27 (1): 95-107. <https://doi.org/10.15421/111835>
- OAIE G. 1992. — Traces of organic activity in the greenschist series of Central Dobrogea (Romania). *Studii și Cercetări de Geologie* 37: 77-81.
- OAIE G. 1993. — Necesitatea protejării urmelor de activitate organică de vârstă precambrian superior din cadrul seriei șisturilor

- verzi din Dobrogea centrală. *Ocotirea Naturii și a Mediului în conjurător* 37 (2): 133-137.
- OAIÉ G. 1998. — Sedimentological Significance Of Mudstone Microclast Intervals In Upper Proterozoic Turbidites, Central Dobrogea, Romania. *Sedimentary Geology* 115: 289-300.
- OAIÉ G. 1999. — *Sedimentologia și tectonica seriei Șisturilor Verzi din Dobrogea Centrală și prelungireaei în acvatoriul Mării Negre*. Teza de doctorat, Universitatea din București, 105 p.
- OAIÉ G. 2010. — Le patrimoine paléochronologique de la vie primitive en Dobrogea (Roumanie), in SAINT MARTIN J. P., SAINT MARTIN S., OAIÉ G., SEGHEDI A. & GRIGORESCU D. (eds), Le patrimoine paléontologique. Des trésors du fond des temps. *GeoEcoMarina suppl.* 18: 39-46.
- OAIÉ G., SEGHEDI A., RĂDAN S. & VAIDA M. 2005. — Sedimentology and source area composition for the Neoproterozoic-Eocambrian turbidites from East Moesia. *Geologica Belgica* 8 (4): 78-105. <https://popups.uliege.be/1374-8505/index.php?id=784>
- OAIÉ G., SEGHEDI A., SAINT MARTIN J. P. & SAINT MARTIN S. 2012. — Signification sédimentologique des traces mécaniques et biogènes des dépôts précambriens et paléozoïques de Dobrogea centrale et du nord. *GeoEcoMarina suppl.* 18, 18: 38-39.
- O'DONNELL K. H. 2013. — *Constraining the Ediacaran-Cambrian Boundary in South China using Acanthomorphic Acritarchs and Palaeopascichnus Fossils*. Unpublished Master of Science in Geosciences, faculty of Virginia Polytechnic Institute and State University, 56 p.
- PACZEŚNA J. 1989. — Polski i globalny zapis biozarzenia na granicy Prekambr-Kambr. *Przegląd Geologiczny* 37 (11): 542-546.
- PACZEŚNA J. 2014. — Lithostratigraphy of the Ediacaran deposits in the Lublin-Podlasie sedimentary basin (eastern and south-eastern Poland). *Biuletyn Państwowego Instytutu Geologicznego* 460: 1-24. <https://geojournals.pgi.gov.pl/bp/article/view/28834>
- PALIJ V. M. 1976. — Remains of soft-bodied animals and trace fossils from the Upper Precambrian and Lower Cambrian of Podolia, in KELLER B.M. & ROZANOV A. YU. (eds), *Palaeontology and Stratigraphy of Upper Precambrian and Lower Cambrian of South-western East European Platform*. Naukova Dumka, Kiev: 63-76.
- PALIJ V. M., POSTI E. & FEDONKIN M. A. 1979. — Soft-bodied Metazoa and trace fossils in Vendian and Lower Cambrian, in KELLER B. M. & ROZANOV A. YU. (eds), *Paleontologiya Verkhnedokembrijskikh i Kembrijskikh Otlozhenij Vostochno-Evropskoj Platformy*. Nauka, Moscow [title translated from Russian]: 49-82.
- PALIJ V. M., POSTI E. & FEDONKIN M. A. 1983. — Soft-bodied Metazoa and animal trace fossils in the Vendian and early Cambrian, in KELLER B. M., ROZANOV A. YU. (eds), *Upper Precambrian and Cambrian Palaeontology of the East-European Platform*. Edited by A. Urbanek and A.Yu. Rozanov. Wydawnictwa Geologiczne, Warszawa: 56-94.
- PARCHA S. K. & PANDEY S. 2011. — Ichnofossils and their significance in the Cambrian successions of the Parahio Valley in the Spiti Basin, Tethys Himalaya, India. *Journal of Asian Earth Sciences* 42, 1097-1116. <https://doi.org/10.1016/j.jseas.2011.04.028>
- REID L. M., HOLMES J. D., PAYNE J. L., GARCÍA-BELLIDO D. C. & JAGO J. B. 2018. — Taxa, turnover and taphofacies: a preliminary analysis of facies-assembly relationships in the Ediacara Member (Flinders Ranges, South Australia). *Australian Journal of Earth Sciences* 67 (6): 905-914. <https://doi.org/10.1080/08120099.2018.1488767>
- SAINT MARTIN J. P. & SAINT MARTIN S. 2018. — *Beltanelliformis brunsa* Menger in Keller, Menger, Stepanov & Chumakov, 1974: an Ediacaran fossil from Neoproterozoic of Dobrogea (Romania). *Geodiversitas* 40 (23): 537-548. <https://doi.org/10.5252/geodiversitas2018v40a23>. <http://geodiversitas.com/40/23>
- SAINT MARTIN J. P., CHARBONNIER S., SAINT MARTIN S., OAIÉ G., SEGHEDI A. & RICHIR P. 2011. — Evidence of microbial mats in the Ediacaran deposits of Dobrogea (Romania). *GeoEcoMarina Suppl.* 17: 151-153.
- SAINT MARTIN J. P., SAINT MARTIN S., OAIÉ G. & SEGHEDI A. 2012. — Traces of organic activity and microbial mats in the Ediacaran basement of the Moesian Platform, Romania, in 34th International Geological Congress, Brisbane, Australia, Abstracts, 1 p.
- SAINT MARTIN J. P., FERNANDEZ S., OAIÉ G., SEGHEDI A., SAINT MARTIN S., CHARBONNIER S. & ANDRÉ J. P. 2013. — Le monde édiacarien de Dobrogea, in SAINT MARTIN J. P. (ed.), *Recherches croisées en Dobrogea*. Editura Amanda Edit, Bucarest: 29-39.
- SCHNEIDER C. A., RASBAND W. S. & ELICEIRI K. W. 2012. — Nih Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671-675. <https://doi.org/10.1038/nmeth.2089>
- SEGHEDI A. & OAIÉ G. 1994. — Tectonic setting of two contrasting types of pre-Alpine basement: North versus Central Dobrogea. *Romanian Journal of Tectonics and Regional Geology* 75, suppl. 1: 56-57.
- SEGHEDI A. & OAIÉ G. 1995. — Palaeozoic evolution of North Dobrogea, in SÂNDULESCU M., SEGHEDI A., OAIÉ G., GRĂDINARU E. & RĂDAN S. (eds), *Field Guidebook, Central and North Dobrogea*. IGCP project No. 369 "Comparative evolution of Peri-Tethyan Rift Basins", Mamaia 1995: 1-75.
- SEGHEDI A., BERZA T., IANCU V., MĂRUNȚIU M. & OAIÉ G. 2005. — Neoproterozoic terranes in the Moesian basement and in the Alpine Danubian nappes of the South Carpathians. *Geologica Belgica* 8 (4): 4-19. <https://popups.uliege.be/1374-8505/index.php?id=746>
- SEILACHER A. & GISHLICK A. D. 2015. — *Morphodynamics*. CRC Press, Boca Raton, London, New York, 551 p. <https://doi.org/10.1201/b17557>
- SEILACHER A. & MRINJEK E. 2011. — Benkovac Stone (Eocene, Croatia): a deep-sea Plattenkalk? *Swiss Journal of Geosciences* 104 (suppl. 1): 159-166. <https://doi.org/10.1007/s00015-011-0051-7>
- SEILACHER A., GRAZHDANKIN D. & LEGOUTA A. 2003. — Ediacaran biota: the dawn of animal life in the shadow of giant protists. *Paleontological Research* 7: 43-54. <https://doi.org/10.2517/prpsj.7.43>
- SHAHKARAMI S., BUATOIS L. A., MÁNGANO M. G., HAGADORN J. W. & ALMOND J. 2020. — The Ediacaran-Cambrian boundary: Evaluating stratigraphic completeness. *Precambrian Research* 345, 105721: 26 p. <https://doi.org/10.1016/j.precamres.2020.105721>
- SHEN B., XIAO S., DONG L., ZHOU C. & LIU J. 2007. — Problematic macrofossils from Ediacaran successions in the North China and Chaidam blocks: implications for their evolutionary root and biostratigraphic significance. *Journal of Paleontology* 81: 1396-411. <https://doi.org/10.1666/06-016R.1>
- SHEN B., XIAO S., ZHOU C., DONG L., CHANG J. & CHEN Z. 2017. — A new modular palaeopascichnid fossil *Curviacus ediacaranus* new genus and species from the Ediacaran Dengying Formation in the Yangtze Gorges area of South China. *Geological Magazine* 154: 1257-1268. <https://doi.org/10.1017/S001675681700036X>
- SOKOLOV B. S. 1976. — Organicheskiy mir zemli na puti k fanerozoiskoj differentsiatsii. *Vestnik Akademii Nauk Ssr* 1976 (1): 126-143.
- SOLDATENKO Y. 2018. — *Évolution des environnements sédimentaires du bassin de Podolya (Ukraine) à l'avènement des premiers métazoaires édiacariens*. *Géologie appliquée*. Université de Poitiers; Université nationale des mines (Dnipropetrovsk, Ukraine), 323 p. <https://theses.hal.science/tel-02064630>
- SOLDATENKO Y., EL ALBANI A., RUZINA M., FONTAINE C., NESTEROVSKY V., PAQUETTE J. L., MEUNIER A. & OVTCHAROVA M. 2019. — Precise U-Pb age constrains on the Ediacaran biota in Podolia, East European Platform, Ukraine. *Scientific Reports* 9, 1675. <https://doi.org/10.1038/s41598-018-38448-9>
- TIWARI M., PARCHA S. K., SHUKLA R. & HARSHITA J. 2013. — Ichnology of the Early Cambrian Tal Group, Mussoorie Syncline, Lesser Himalaya, India. *Journal of Earth System Science* 122: 1467-147. <https://doi.org/10.1007/s12040-013-0360-5>

- WAGGONER B. 1998. — Interpreting the Earliest Metazoan Fossils: What Can We Learn? *American Zoologist* 38 (6): 975-982. <https://doi.org/10.1093/icb/38.6.975>
- XIAO S., CHEN Z., PANG K., ZHOU C. & YUAN X. 2021. — The Shibantan Lagerstätte: insights into the Proterozoic-Phanerozoic transition. *Journal of the Geological Society* 178: 1-12. <https://doi.org/10.1144/jgs2020-135>
- ŻEŁAŻNIEWICZ A., BUŁA Z., FANNING M., SEGHEDI A. & ZABA J., 2009. — More evidence on Neoproterozoic terranes in southern Poland and southeast Romania. *Geological Quarterly* 53: 93-123.

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