

New records of *Palaeopaschichnus* Palij, 1976 from the Ediacaran of Romania

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KEY WORDS

Romania,
Dobrogea,
Palaeopaschichnus,
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* Palij, 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 Palij, 1976 dans l'Édiacarien de Roumanie.

Les terrains néoprotérozoïques 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* Palij, 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,
Néoprotérozoïque
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).

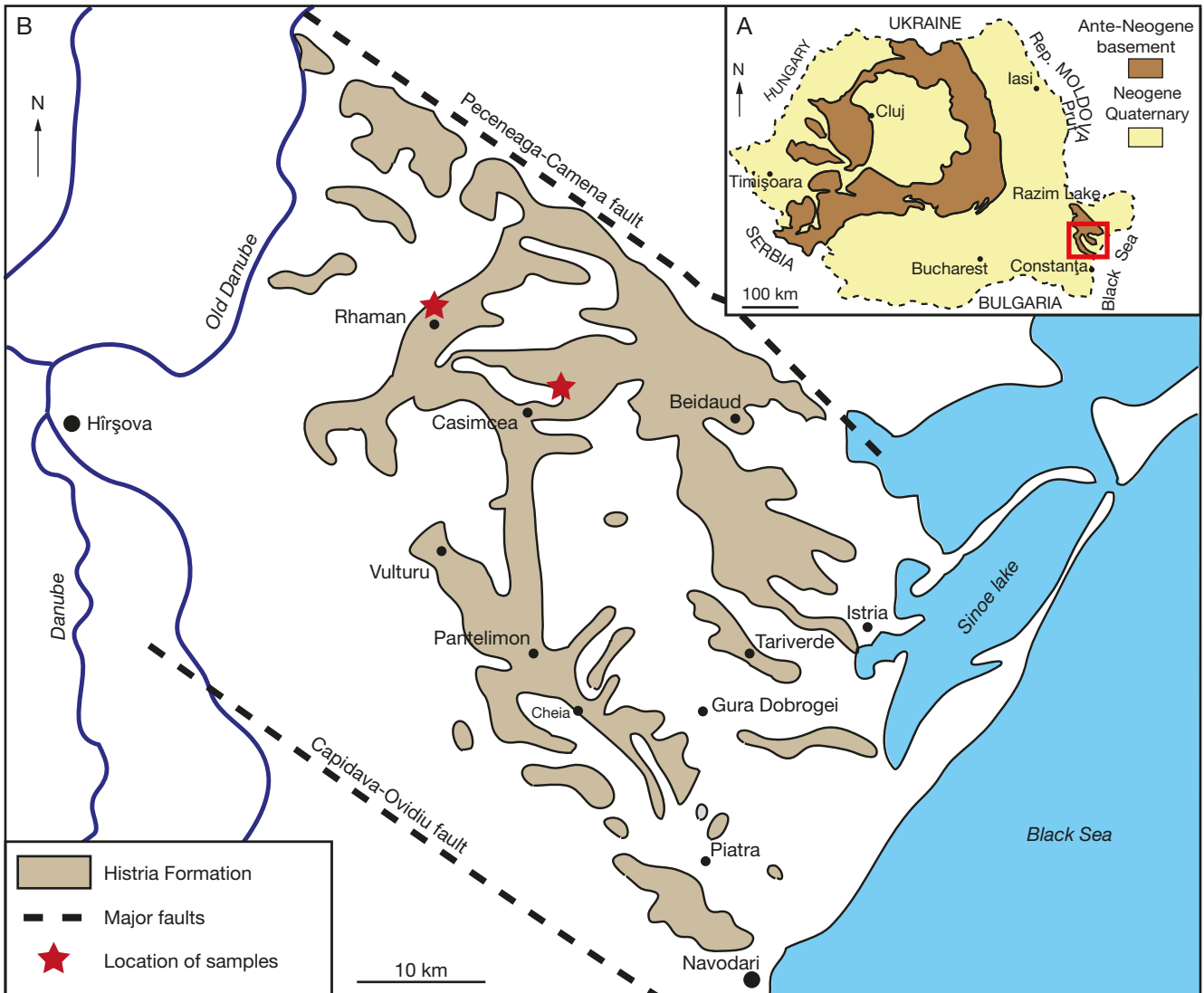


FIG. 1. — **A**, Schematic geological map of Romania and location of the study area (Central Dobrogea); **B**, geologic map of Neoproterozoic terranes in Central Dobrogea and location of the studied outcrops.

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.

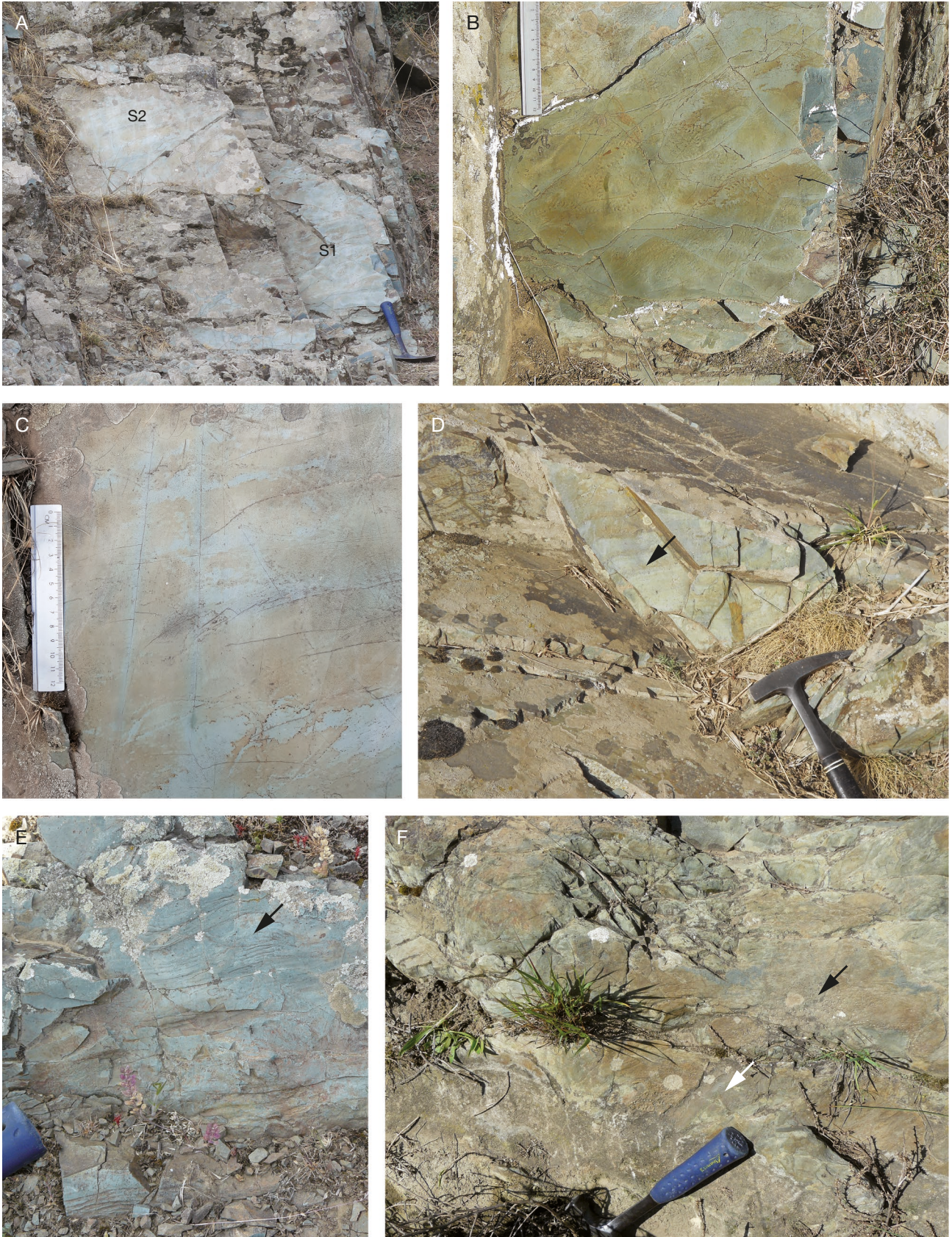


FIG. 3. — Casimcea beds: **A**, view of surfaces **S1** and **S2** exhibiting the *Palaeopascichnus* Palič, 1976 specimens; **C**, detail of surface **S2**; **D**, pluricentimetric bedding in phase with undulations below a surface with large ripples (**arrow**); **E**, natural section showing HCS-type 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* Pali, 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;

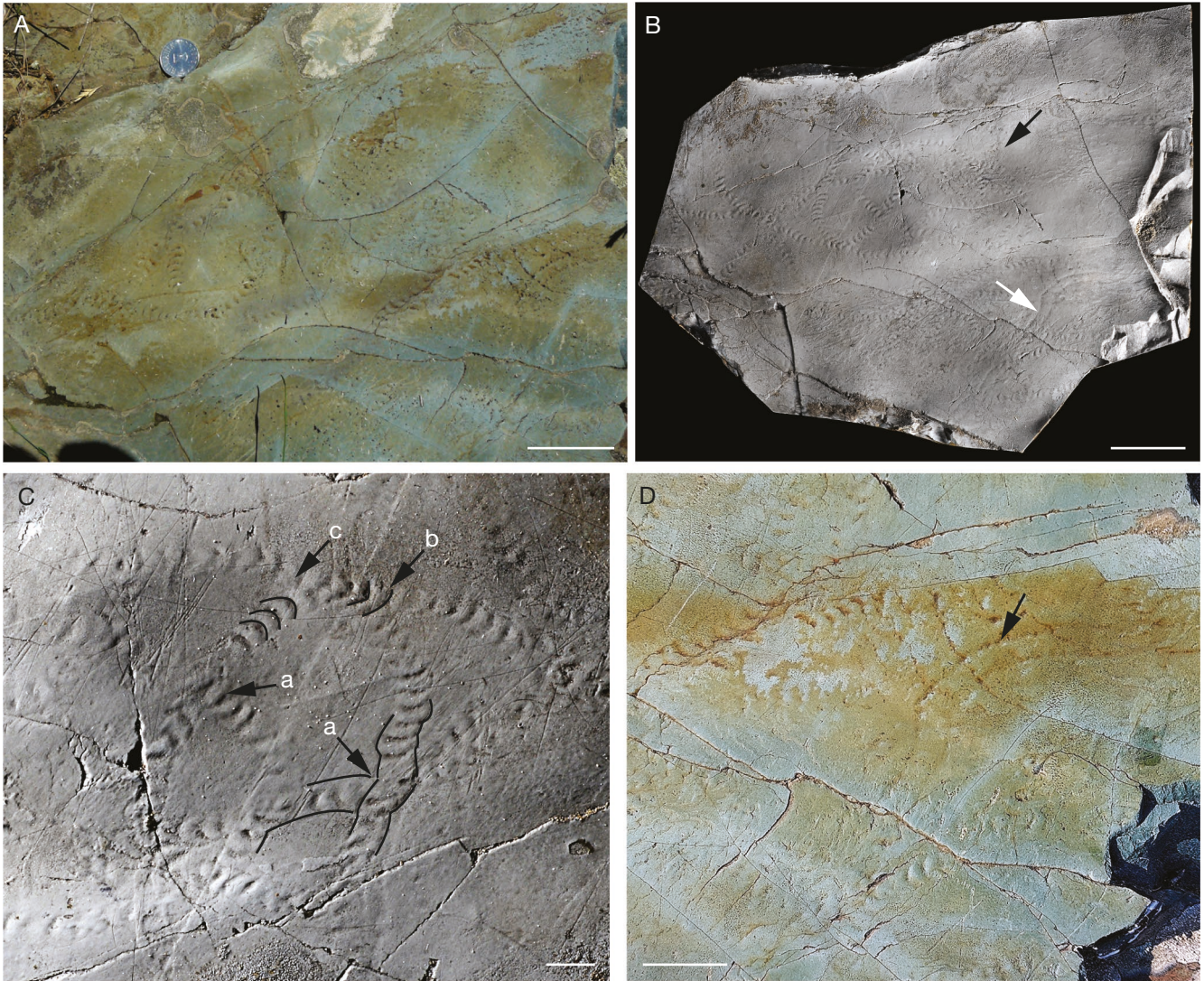


FIG. 6. — Specimens from Casimcea surface S1: **A**, View *in situ* of the *Palaeopascichnus* Palij, 1976 specimen; **B**, photogrammetric representation of the cast showing the poorly marked ridges at the surface (**black arrow**), the network of arcuate meandering elements and the “empty” meandering 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.

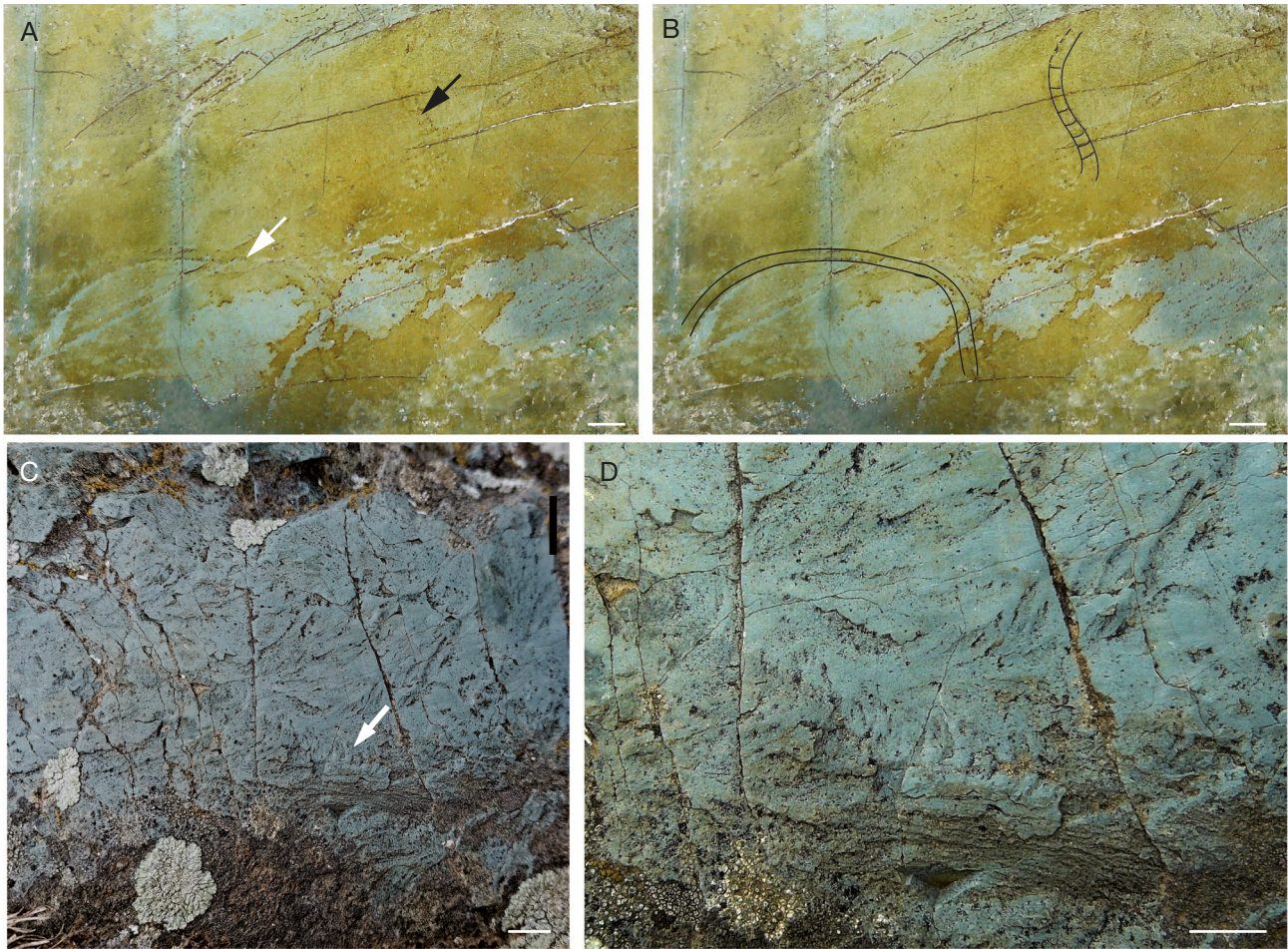


FIG. 7. — **A**, Specimens from Casimcea surface S2 with a meandering succession of slightly arcuate element (black arrow) poorly expressed and imprint with parallel lines of constant width (c. 1 cm), without internal structures (white arrow) similar to Fig. 6D; **B**, same picture as **A** with specimens 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; Moczydlowska *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 *Scalartituba* 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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