

***NODULICHNUS HUNGARICUS* IGEN. ET ISP. NOV. FROM THE EARLY MIOCENE OF NORTH HUNGARY**

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Abstract: The Early Miocene shallow-marine Salgótarján Lignite Formation of northern Hungary is host to a hitherto unknown trace fossil, here named *Nodulichnus hungaricus* igen. et isp. nov. This trace is a vertical, straight, or slightly winding, non-branching, tubular structure, 2–5 mm in diameter, and 50–100 mm long. It is filled with globose pellets, which are 0.5–0.6 mm in diameter. Generally, this trace fossil is isolated, but it may occur in clusters. Ethologically, it is a dwelling structure (domichnion), where the producer organism was living during high tide. Additionally, *Nodulichnus hungaricus* igen. et isp. nov. is accompanied by *Ophiomorpha nodosa* (Lundgren, 1891), *Gyrolithes nodosus* (Mayoral and Muñiz, 1998), *Thalassinoides* isp., *Planolites* isp. and *Tomaculum problematicum* (Groom, 1902), which occur sparsely at this level. The trace fossil assemblage is interpreted as being evolved in a ‘low-energy’, sandy beach setting.

Key words: Ichnotaxa, *Nodulichnus*, subfaecal pellets, Salgótarján Lignite Formation.

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INTRODUCTION

The Miocene siliciclastic sediments of North-Hungary belong to the most investigated Neogene formations in the Carpathian Basin. This is because its Ottnangian-Karpatian deposits contain numerous, paralic coal beds (Papp, 1916; Schréter, 1929; Vadász, 1929; Vitális, 1939; Radnóty, 1948; Csepregy-Meznerics, 1953; Bartkó, 1961; Juhász, 1965, 1966, 1970, 1988; Korecz-Laky, 1985; Hegyi, 1986; Radócz, 1987, 1993; Bohn-Havas *et al.*, 2000). These beds belong to the Salgótarján Lignite Formation (Elek, 1974; Bohn-Havas, 1985). A number of publications mention the bioturbation structures of the formation, but their sedimentological and palaeoenvironmental significance has not been taken into consideration (Bohn-Havas, 1985; Püspöki, 2001).

The Salgótarján Lignite Formation covers large areas of North Hungary. The most recent sedimentological and sequence-stratigraphical study of it was carried out by Püspöki (2002). According to his results, the sediments were formed in a wave-dominated, littoral environment (Püspöki, 2001, 2002; Dávid *et al.*, 2006; Püspöki *et al.*, 2009, 2017). It was shown that the entire Salgótarján Lignite Formation is the transgressive part of a third-order sequence (Püspöki, 2001, 2002).

Though the Neogene sediments of Hungary were investigated for more than a decade, their trace fossils have remained undescribed. Palaeoichnological investigation of the coal-bearing series of the East-Borsod Basin began in 2006 (Dávid *et al.*, 2006). Its goal was to complete the results of the sequence-stratigraphic examinations by giving a detailed and more exact look at the dynamics of the former sedimentary environment. During the course of this research, the authors began to study the formations of an abandoned sand-pit, situated in the northern part of Miskolc-Diósgyőr, where the sediments of the overlying bed of the second coal seam are exposed in an exceptional thickness. The sandy-aleuritic sediments are rich in different bioturbation structures. The revealed ichnoassemblages show great numbers of individuals, but moderate diversity.

Preliminary examinations revealed the predominance of *Macaronichnus segregatis*, *Ophiomorpha nodosa* and *Thalassinoides* isp., which could be distinguished clearly at several levels of the outcrop. The middle section of the exposure contained large quantities of a previously unknown trace fossil. The aim of the paper is twofold: 1) to introduce and analyse the bioturbation structure as a new ichnogenus

and ichnospecies, and 2) to reveal its potential, ethological and palaeoenvironmental significance. The type specimens of the trace fossil are housed in the palaeontological collection of the Mátra Museum of the Hungarian Natural History Museum, in Gyöngyös.

GEOLOGICAL SETTING

The East-Borsod Coal Basin structurally belongs to the Bükk Unit, which is part of the Mid-Hungarian Fault Zone. It is a major tectonic feature of the Intra-Carpathian area, separating two terranes that differ in origin and tectonic structure, the ALCAPA and Tisza Mega-units (Csontos and Nagymarosy, 1998). During the Miocene, the East-Borsod Coal Basin was situated at the northern edge of the Pannonian Basin within the Central Paratethys, together with a series of other small sub-basins (Nógrád Basin, East-Borsod Basin, East Slovakian Basin, Szalay *et al.*, 1976; Király, 1989; Fig. 1A).

In the East-Borsod Coal Basin, the 400–600-m-thick, shallow-marine Miocene series are divided into three parts.

The oldest one is the Karpátian Salgótarján Lignite Formation (0–400 m thick), which contains five paralic coal seams in the east. This is followed by a Badenian marine, sandy-clayey facies of the Badenian Clay Formation (0–200 m thick; Császár, 1997). The youngest member is the Sarmatian Sajó Valley Formation (0–150 m thick), which consists of marine, sandy, and littoral-terrestrial, sandy-gravelly sediments, containing felsic and intermediate volcanic intercalations. These formations follow each other with considerable unconformity (Püspöki, 2002; Fig. 2).

Stratigraphic settings

The Salgótarján Lignite Formation (Fig. 2) is the most extensive Miocene formation in the East-Borsod Coal Basin, North Hungary. Its sediments were deposited in a wave-dominated, microtidal, shallow-marine environment. It was documented in several sedimentological, palaeontological and palaeoichnological publications since the middle of the previous century (Csepreghy-Meznerics, 1953; Bohn-Havas, 1985; Korecz-Laky, 1985; Radócz,

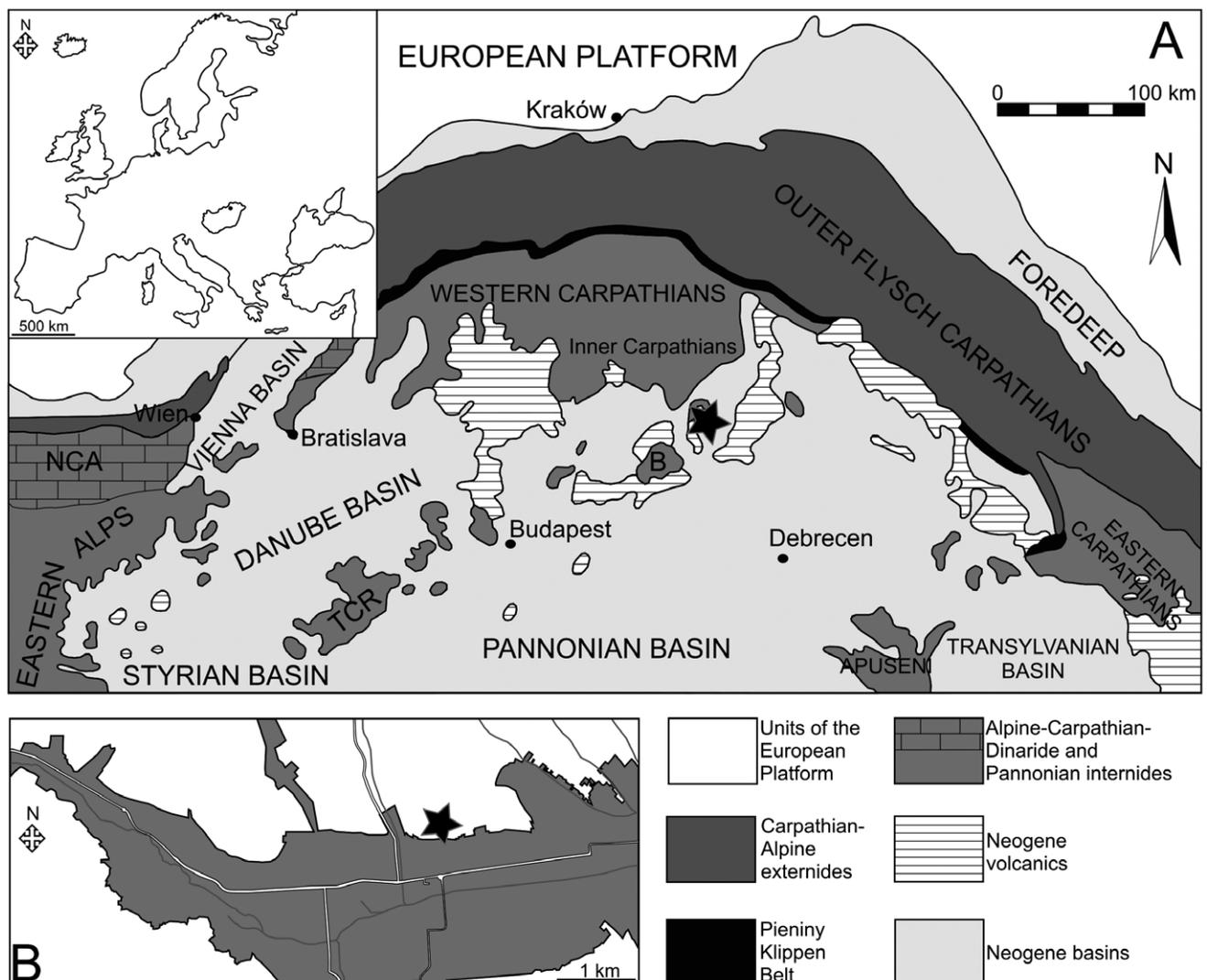


Fig. 1. Geographical position of the locality at Miskolc-Diósgyőr. **A.** Location of the East Borsod Coal Basin in the Carpathian-Pannonian system (B, Bükk; NCA, Northern Calcareous Alps; TCR, Transdanubian Central Range). **B.** Location of the sand pit at Miskolc-Diósgyőr (based on Vršanský *et al.*, 2015). The black star indicates the position of the locality.

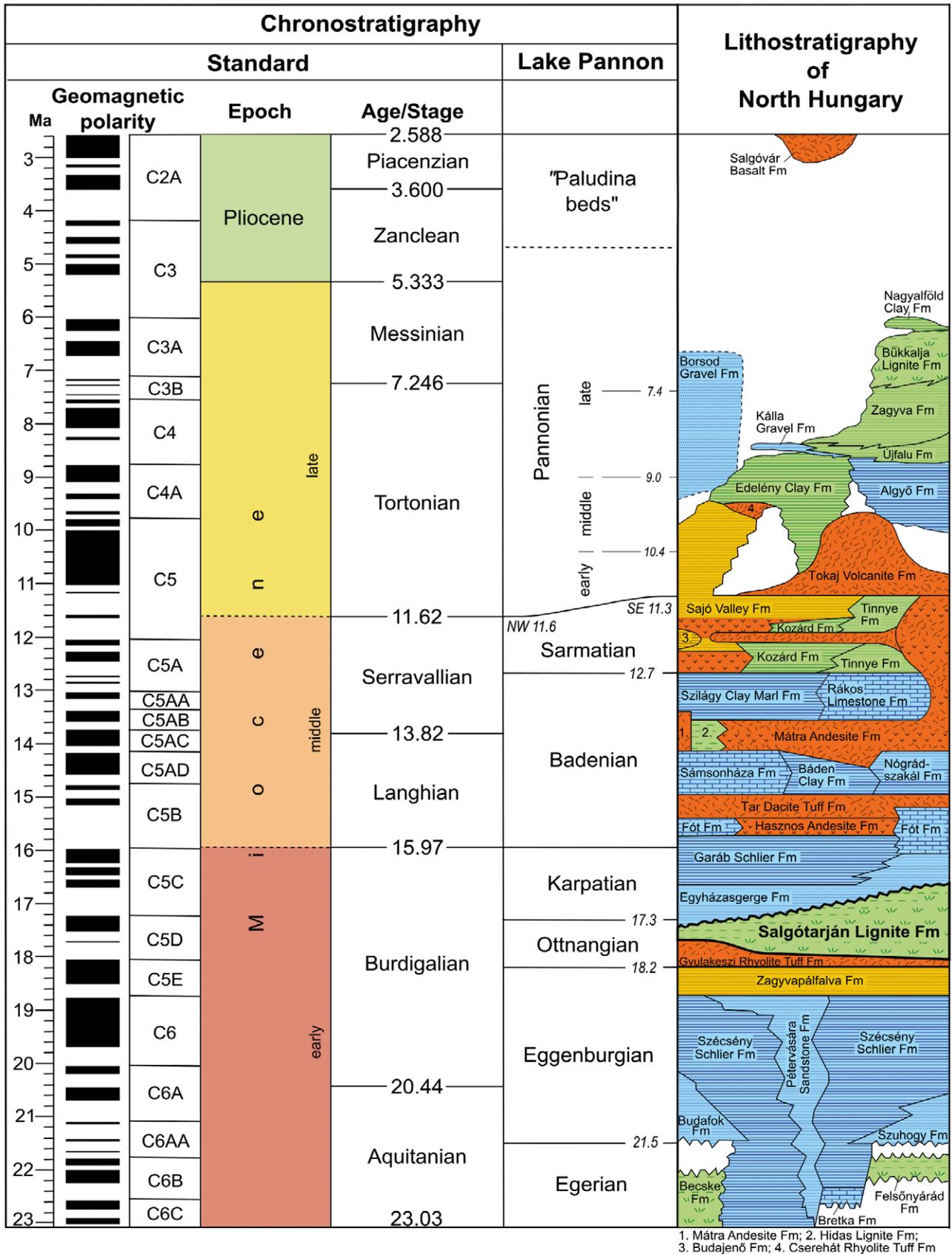


Fig. 2. Chrono- and lithostratigraphy of North Hungary (after Gyalog, 1996)

1993; Bohn-Havas *et al.*, 2000; Püspöki, 2001, 2002; Dávid *et al.*, 2006; Püspöki *et al.*, 2009, 2017). Its thickness varies from 0 to 400 m, with thickening to the east. It is composed of five major, mineable lignite seams, interbedded with shallow-marine sediments, which contain bivalve coquinas (with *Ostrea*, *Crassostrea*, *Congeria*) at discrete, well-defined levels. The oyster coquinas could mark flooding surfaces, referable to transgressive events (Van Wagoner *et al.*, 1990; Püspöki *et al.*, 1995). The coal-bearing series is bioturbated and composed of laminated marl, calcareous marl, cross-bedded and laminated sand, and rarely gravel.

The coal seam and its overlying sequence were divided into 25 parasequences during the course of sequence-stratigraphic studies by Püspöki (2001). However, the whole sequence can be classified as a transgression branch of a third-order cycle and it is equivalent to a half-cycle, showing basin characteristics (deepening) upward (Püspöki, 2001; Fig. 3).

Study area

One of the largest exposures of Salgótarján Lignite Formation is at an abandoned sand pit, which is examined

here, situated in the vicinity of Miskolc-Diósgyőr (geographical coordinates: 48°06'23.25"N, 20°43'51.69"E and 48°06'21.91"N, 20°44'00.77"E; Fig. 1B). The abandoned sand pit is about 14 m high and 210 m long. The same deposits are exposed in two smaller sand pits, located west of the larger one. The sandy-marly formations are rich in bioturbation structures. According to Püspöki (2002), the sedimentary material of the exposure was deposited in the lower, transgressive phase of the 20th parasequence.

The lowermost part of the section is a 1-m-thick limonitic, fine-grained sandstone with planar cross-bedding. Macrofauna is not present, while the microfauna consists of foraminifera and sponge spicules. Trace fossils are rare in this level. Mainly the horizontal components of *Ophiomorpha nodosa* occur here. It is why the bioturbation index does not exceed 2. The lowermost part is overlain by a 5-m-thick, light-grey-coloured, fine-grained sandstone with trough cross-bedding and planar cross-bedding. The lack of macrofauna and the presence of foraminifera and sponge spicules are characteristic features in this layer, too. The sand body can be divided into three parts with regard to trace fossils that are present. The presence of *Ophiomorpha nodosa* and rare *Gyrolithes nodosus* can be detected in

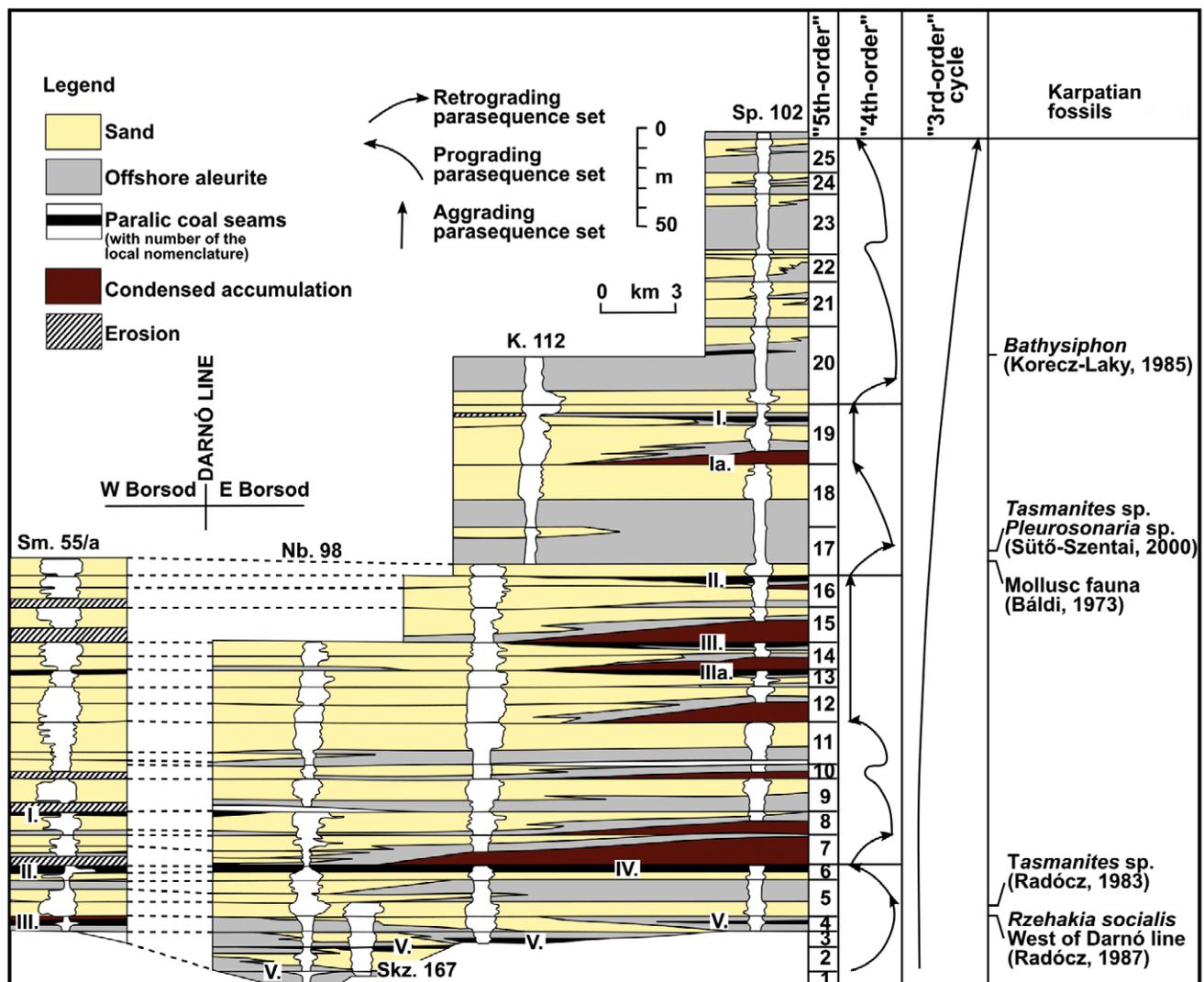


Fig. 3. Sequence-stratigraphic model of the Karpatian coal-bearing series in the Borsod Basin (after Püspöki, 2002; Dávid *et al.*, 2006).

the lower 2 m (BI = 2). The following 1.5-m-thick part shows higher trace fossil diversity. It contains the new ichnotaxon, characterised by small, pelleted burrows. It is dominant in the greyish-coloured, fine-grained sand in this part of the section (Fig. 4A, B). In addition to the horizontal galleries of *Ophiomorpha nodosa*, the trace fossils *Gyrolithes nodosus*, *Planolites* isp., *Thalassinoides* isp. and *Tomaculum problematicum* occur subordinately (BI = 3). The third, uppermost part is 1.5 m thick. *Thalassinoides* isp. is dominant here. Its density is increasing upward permanently. Galleries filled with faecal pellets occur sporadically (BI = 2–4). The upper boundary of the grey-coloured, fine-grained sand is an erosional surface. Above it, a package of a 2.6-m-thick, limonitic, fine-grained sand bed with current ripple cross-lamination is present. As in the previous formations, the lack of a macrofauna is characteristic for the sediment, while the microfauna consists of foraminifera and sponge spicules. The character of the trace fossils changes upward. In the lower 1.5 m, the *Macaronichnus segregatis* is dominant. Some cross-sections and longitudinal sections of *O. nodosa* also occur. But the upper 1.0 m show the dominance of *O. nodosa*. Mostly longitudinal galleries can be seen. Some *G. nodosus* also is present, connected to *Ophiomorpha* boxworks (BI = 2–4; reaching a maximum value at the *Macaronichnus* dominant level). The upper boundary of the limonitic sand is an erosional surface.

The overlying bed is a 0.2-m-thick, highly bioturbated sandy marl, which is rich in shell fragments. Locally, it contains *Ostrea* valves. This thin layer, rich in mollusc shells is a lag deposit, which covered the flooding surface during the culmination of a transgression event. The base of the lag is a colonization surface of the underlying sediments, too. Sparsely cross-sections of *Thalassinoides* isp. occur in the sediment (BI = 1). The caprock of the profile is a 5-m-thick, laminated marl, containing several sandy intercalations, which show hummocky cross-stratification with lenticular bedding and current ripples. The marl contains no fossils, except for intercalations of molluscan lumachella that occur at two levels. The poorly preserved, thin-shelled bivalve fragments cannot be determined on higher taxonomic level. This laminated marl contains rare *Thalassinoides* isp. and *Ophiomorpha nodosa*, which originated in the intercalated sand bodies. The bioturbation index is 1 in the sand but is 0 elsewhere (Fig. 4).

METHODS

Trace fossil observations and characterization of the different sedimentary units were carried out in the field in the abandoned sand pit of Miskolc-Diósgyőr. The position of the new ichnotaxon and its relation to other bioturbation structures were documented in order to develop a more detailed and accurate, palaeoenvironmental interpretation. The methods described by Taylor and Goldring (1993) were followed to determine the bioturbation index of the formations. Fifty-one samples were taken for further laboratory examination and selection of the holotype and the paratypes. Each burrow was prepared from the friable, grey-coloured fine-grained sandstone. Eight thin sections were made and the diameters of the burrow-filling pellets

were measured using InkScape 1.0. The following characteristics had been measured for thirty-three trace fossils: 1) diameter and length of the galleries; and 2) diameter of the infilling pellets. At least ten pellets were measured in the case of each trace fossil. Spearman rank correlation was used to reveal the relationship between the diameter of the galleries and the average diameter of the infilling pellets. XRD analysis of two trace fossils and a sand sample was carried out at the Department of Mineralogy, Geochemistry and Petrology, University of Szeged, using Rigaku Ultima IV. X-ray diffractometer.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Nodulichnus* igen. nov.

Type species: *Nodulichnus hungaricus* (see description below).

Etymology: Latin *nodulus*, minute nodes, referring to the small, globose pellets, which fill the tubes and give special morphology to the burrow and Greek *ichnos*, footprint, track, trace.

Diagnosis: Vertical, non-branching, cylindrical trace fossil, filled with spherical pellets. Boundary is sharp and distinct, but no constructional wall is present. Cross-section is circular or elliptical, rarely irregularly oval.

Remarks: There are numerous trace fossils, which are partly or entirely pellet-filled. These pellets are dominantly faecal pellets. On the basis of the literature, the authors found significant differences between the characteristic features of the previously published pellet-filled trace fossils and the ones considered here. These differences are described below. It is also important to point out that there are some taxonomical uncertainties regarding the pellet-filled trace fossils, demonstrated by the numerous synonyms. The morphological characteristics of the ichnotaxa, used in the taxonomical differentiation of *Nodulichnus*, are shown in Tab. 1.

Nodulichnus hungaricus igen. et isp. nov.

Figs 5, 6A–H

Etymology: The ichnospecies is named after Hungary, the country where the trace fossils were found and described. *Hungaricus* is the latinized version of the name of Hungary.

Type specimens: Type specimens are stored in the palaeontological collection of the Mátra Museum (Hungarian Natural History Museum), Gyöngyös, Hungary. Holotype – HNHM-MMPAL Gy/64 (Fig. 5A). Paratypes – HNHM-MMPAL Gy/65, HNHM-MMPAL Gy/66, HNHM-MMPAL Gy/67, HNHM-MMPAL Gy/68 (Figs 5B–D).

Type locality: abandoned sandpit, Miskolc-Diósgyőr, North Hungary.

Stratigraphical occurrence: Salgótarján Lignite Formation (Early Miocene, Karpatian).

Diagnosis: As for the ichnogenus.

Description: *Nodulichnus hungaricus* is a vertical, straight, or slightly winding, non-branching, cylindrical, blind-ending trace fossil. The cross-section of the cylinder is circular, elliptical, or rarely irregularly oval. The length of the galleries

varies between 20–150 mm. The trace fossil is 1.5–5.5 mm in diameter. It is filled with rounded pellets, which are 0.5–0.8 mm in diameter (Tab. 2; Figs 6E–H, 7). On the basis of the measurement of the diameter of 33 burrows and determination of the average diameter of their infilling pellets, it can be concluded that there is no association between the two examined characteristics. This is clearly supported by the results of the Spearman rank correlation analyses (Tab. 2). The pellets are composed mostly of quartz, silt, and clay minerals. Furthermore, XRD examination showed that the mineral composition of the host sediment and burrow fill is largely analogous. A slight increase in clay mineral content (dominantly smectite) was detected in the composition of the “subfaecal” pellets. According to the microscopic observations, the above mentioned, small-grainsized minerals

envelope the surfaces of the pellets. It is assumed that this buildup shows a close connection with the feeding mechanism of the producer organism, like the sorting and selection of nutrients from the inorganic component of the host sediment (Miller, 1961). There is no evidence of a wall, inner tunnel, or other structure within the trace fossil; the pellets are responsible for the verrucose surface of the burrow. The extremely thin, ferruginous coating at the boundary of the trace fossils and the sediment might be of microbial origin. These factors refer to circumstances suitable for iron-oxidizing bacteria. The XRD image at 36–37° 2 θ value refers to the material of this ferruginous coating (Salama *et al.*, 2013; Fig. 8). The distribution of the burrows of *N. hungaricus* do not show any order, and form several levels within the more than 1-m-thick sediment layer. The number

Table 1

Morphological characteristics of the pelletized ichnotaxa, used for comparison and elaboration of *Nodulichnus* igen. nov.

Name	Short description	Shape of pellets	Orientation	References
<i>Nodulichnus hungaricus</i> igen. et isp. nov.	Vertical, non-branching, cylindrical trace fossil, filled with spherical pellets. Boundary is sharp and distinct, but no constructional wall is present. Cross-section is circular or elliptical, rarely irregularly oval.	spherical	vertical	
Pellet lined trace fossils				
<i>Ophiomorpha nodosa</i> Lundgren, 1891	<i>Ophiomorpha</i> with burrow walls consisting predominantly of dense, regularly distributed discoid, ovoid, or irregular, polygonal pellets.	discoid, ovoid, or irregular, polygonal	vertical, horizontal, or inclined	Kennedy and MacDougall, 1969; Frey <i>et al.</i> , 1978; Curran, 1984; Frey and Howard, 1985; Pollard <i>et al.</i> , 1993; Gibert <i>et al.</i> , 1998; Miller and Curran, 2001;
<i>Ophiomorpha puerilis</i> Gibert <i>et al.</i> , 2006	Small, rectilinear, and pellet-lined burrows, occasionally with a somewhat enlarged, terminal chamber. The lining is formed of cylindrical or rod-shaped (capsule-shaped) pellets with rounded ends.	cylindrical or rod-shaped with rounded ends	parallel or inclined with respect to the larger <i>Ophiomorpha</i> or even longitudinally attached to their linings	Gibert <i>et al.</i> , 2006; Netto <i>et al.</i> , 2017
<i>Tubulichnium rectum</i> (Fischer-Ooster, 1858)	Oblique to horizontal, unbranched, straight, or slightly winding, blind ending, filled, or originally almost void but preserved collapsed tube, which may be slightly swollen and stacked in the middle part. It is lined with small, elongate mud pellets.	elongated	oblique or horizontal	Uchman and Wetzel, 2017
Pellet-filled trace fossils				
<i>Alcyonidiopsis</i> Massalongo, 1856	Linear and sinuous, inclined, horizontal burrow, seldom branching and filled with relatively small, ovoid pellets	ovoid, elongated	horizontal	Chamberlain, 1977; Rodríguez-Tovar and Uchman, 2004, 2006; Uchman <i>et al.</i> , 2013
<i>Granularia</i> Rothpletz, 1896	synonym with <i>Alcyonidiopsis</i>			Chamberlain, 1977

Name	Short description	Shape of pellets	Orientation	References
<i>Halymenites</i> Heer, 1865	synonym with <i>Alcyonidiopsis</i>			Chamberlain, 1977
<i>Sacoites</i> Katto, 1974	synonym with <i>Alcyonidiopsis</i>			Katto, 1974
<i>Syncoprulus</i> Richter and Richter, 1939	synonym with <i>Alcyonidiopsis</i>			Chamberlain, 1977
<i>Edaphichnium</i> Bown and Kraus, 1983	Cylindrical, sometime branching structures, filled with carbonate-cemented masses of ovoid or ellipsoidal pellets. Pellet sizes are generally positively correlated with burrow sizes and range from 0.5–11.6 mm long and 0.3–7.5 mm in diameter.	ovoid or ellipsoidal	mostly horizontal	Bown and Kraus, 1983; Hasiotis, 2006
<i>Pennatulites nodosus</i> LoBue, 2006	It is a straight to slightly curved, cylindrical to oval, lined, branched burrows with medial ridge preserved in full relief parallel to bedding. Diameters of burrows range from 10–15 mm. Lining is ~ 1 mm thick and its lining surface is covered with parallel rows of nodes, each ~ 0.1 mm diameter.	mostly ovoid	horizontal	LoBue, 2006
<i>Phymatoderma</i> Brongniart, 1849	Horizontal branching tunnels are usually 3 to 5 mm in diameter. Tunnels are filled with ellipsoidal pellets.	ellipsoidal	horizontal	Uchman and Gaździcki, 2010; Izumi, 2012, 2015; Izumi <i>et al.</i> , 2014
<i>Tomaculum</i> Groom, 1902	Pill-like coprogene pellets, cylindrical with concave terminations, epifaunal originated on bedding planes, arranged as curved or angular strings or bands.	elongated	horizontal	Benton and Hiscock, 1996, Eiserhardt <i>et al.</i> , 2001
<i>Tubotomaculum</i> Garcia-Ramos <i>et al.</i> , 2014	Dominantly horizontal, spindle-shaped simple burrows, displaying spreite and containing ellipsoidal pellets.	ellipsoidal	horizontal	Garcia-Ramos <i>et al.</i> , 2014
Non-pelleted trace fossils				
<i>Saronichnus</i> Pervesler and Zuschin, 2004	A system of vertical to steeply inclined, tubular to blade-shaped, simple, unbranched probes, diverging from broom- or star-like bunches. The bunch structures start from the posterior ventral edge of shell. The probes overlap in the upper part of the bunches and form a spreite structure, visible in cross-section.	–	vertical or steeply inclined	Pervesler and Zuschin, 2004
<i>Skolithos</i> Haldeman, 1840	The burrows are straight, or slightly winding and unbranched. <i>Skolithos linearis</i> could appear isolated or in clusters, but never densely crowded	–	vertical	Alpert, 1974, 1975

Table 2

Morphological characteristics of *Nodulichnus hungaricus* igen. et isp. nov. and the result of the chi-square test of independence (n = 33).

Sample	Trace fossil		Pellet diameter	
	diameter	length	average	standard deviation
	(mm)			
Gy/64	3.00	35.00	0.526	0.040
Gy/65	3.00	34.00	0.682	0.042
Gy/66	5.00	19.00	0.783	0.041
Gy/67	5.00	51.00	0.582	0.048
Gy/68	2.50	48.00	0.532	0.036
3	3.13	26.88	0.506	0.073
3	2.13	28.13	0.531	0.068
5	5.50	35.63	0.600	0.054
6	3.38	24.50	0.599	0.073
11	1.88	19.25	0.587	0.092
11	3.75	23.38	0.556	0.041
15	3.00	34.00	0.682	0.086
17	3.00	29.38	0.581	0.074
18	3.13	14.75	0.559	0.063
19	5.25	20.13	0.565	0.061
21	3.25	18.75	0.614	0.081
21	3.13	23.38	0.617	0.090
22	2.88	29.00	0.567	0.108
23	3.75	22.50	0.641	0.061
30	5.00	27.38	0.641	0.070
31	4.75	9.00	0.604	0.074
36	4.13	13.38	0.597	0.096
39	3.88	24.50	0.647	0.083
43	5.63	16.25	0.607	0.092
45	1.50	12.88	0.520	0.047
45	3.38	33.00	0.659	0.072
46	3.00	53.00	0.543	0.068
49	4.50	18.38	0.513	0.060
49	4.13	22.75	0.559	0.095
SzN2	2.50	20.00	0.617	0.071
SzN3	4.00	35.00	0.517	0.056
SzN4	4.00	31.00	0.521	0.072
SZN5	2.38	14.63	0.585	0.075

Result of Spearman's Rank Correlation calculation

H0 = the trace fossil diameter and the infilling pellet diameter are independent

H1 = the trace fossil diameter and the infilling pellet diameter are dependent

n = 33

p = 0.05

critical value = 0.345

r = 0.190675

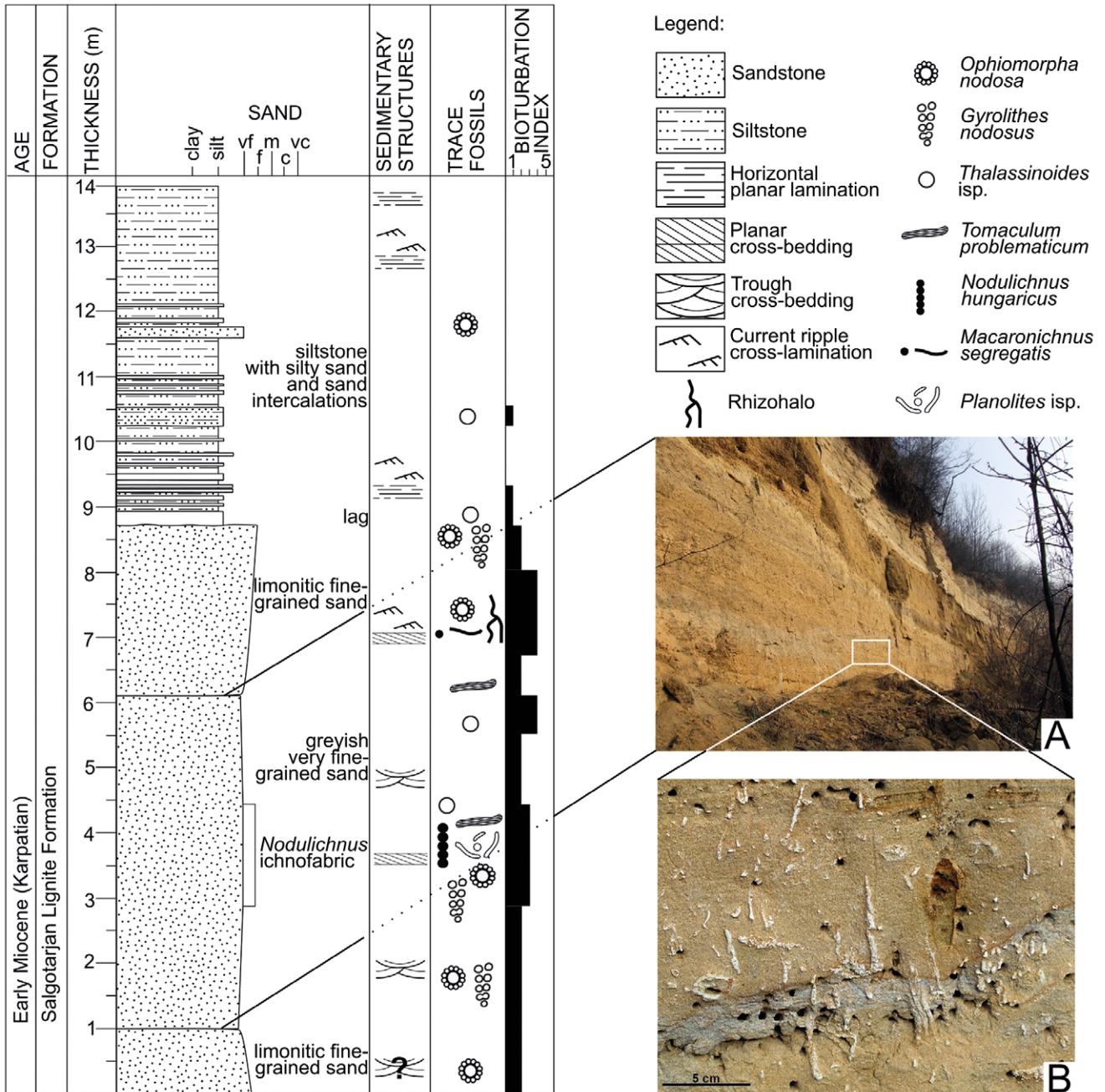
H0 accepted, H1 denied

of trace fossil levels is at least twenty. The exact number of the levels is difficult to determine, owing to the eroded trace fossils and the low degree of preservation of the primary sedimentary structures (Fig. 9). Most specimens of the trace fossil are isolated and scattered in the outcrop (Fig. 10A), but locally they may occur in clusters. The burrows in these clusters are parallel to each other, vertical or inclined at an angle of 85–87° (Fig. 10B, C). The clusters are irregular in cross-section and composed of 2–10 burrows. The morphometrical analyses of the cluster-forming galleries refer to the fact that there is no connection between the diameter of the galleries and the diameter of the pellets within the cluster (Tab. 3). Thus, the morphological characteristics of the trace fossil are not suitable for the determination of sex and age distribution of its tracemaker within the given population. In modern settings, frequently species live sympatrically together, as in the case of *Scopimera philippinensis* Wong *et al.*, 2011 and *Ocypode ceratophthalmus* (Pallas, 1772) at Panay Island, the Philippines (Wong *et al.*, 2011). If the lifestyle of the producer of *N. hungaricus* was similar to that of a member of the Ocypodoidae, it also can be assumed that the producers of the solitary and cluster-forming trace fossils could be sympatric, related species.

Table 3

Morphological characteristics of *Nodulichnus hungaricus* igen. et isp. nov. clusters.

Sample	Trace fossil		Pellet diameter		
	diameter	length	average	standard deviation	
	(mm)				
Cluster 1	Burrow 1	3.418	54.249	0.673	0.098
	Burrow 2	3.332	44.787	0.562	0.044
	Burrow 3	2.960	30.504	0.595	0.054
	Burrow 4	2.215	27.128	0.580	0.058
Cluster 2	Burrow 1	2.728	33.329	0.675	0.052
	Burrow 2	4.404	64.896	0.617	0.055
	Burrow 3	3.061	25.727	0.627	0.056
Cluster 3	Burrow 1	4.186	42.574	0.648	0.060
	Burrow 2	4.341	58.765	0.703	0.051
	Burrow 3	5.303	38.637	0.705	0.074
Cluster 4	Burrow 1	3.359	16.035	0.636	0.048
	Burrow 2	4.736	16.850	0.658	0.076
	Burrow 3	4.329	22.624	0.622	0.086
Cluster 5	Burrow 1	3.346	48.320	0.665	0.053
	Burrow 2	3.844	22.600	0.749	0.054
	Burrow 3	3.071	27.322	0.734	0.053
	Burrow 4	3.415	40.671	0.671	0.036



Ethological analyses

The pellet-filled burrows generally are viewed as feeding traces (fodinichnia), produced by deposit-feeding worms (Katto, 1974; Chamberlain, 1977; Bałuk and Radwański, 1979; Eiserhardt *et al.*, 2001; Rodríguez-Tovar and Uchman, 2004, 2006; Uchman and Gaździcki, 2010; Miller, 2011; Izumi, 2012, 2015; Garcia-Ramos *et al.*, 2014; Izumi *et al.*, 2014; Kulkarni and Panchang, 2015; Giraldo-Villegas *et al.*, 2016; Uchman and Wetzel, 2017), which form a characteristic, morphological group of simple, active-filled (pelletoidal), horizontal burrows (Buatois *et al.*, 2017). Furthermore, these publications describe horizontal more

or less horizontal, generally bifurcated or spindle-shaped burrows, filled with ellipsoidal faecal pellets. These are, because of their characteristic features (at least partly horizontal galleries, elliptical pellets) clearly differentiated from the trace fossils examined and introduced here.

Well-known, modern analogues are, for example, the vertical, 2–3-mm-diameter burrows of *Heteromastus* and *Hediste* (former *Nereis*), containing characteristic Y-shaped or U-shaped bifurcations (Schlirf and Uchman, 2005; Kulkarni and Panchang, 2015). These are connected to the surface by one or two openings. Occurrences of active fill have been observed in the case of *Hediste diversicolor* only in muddy, tidal-flat environment. The animal

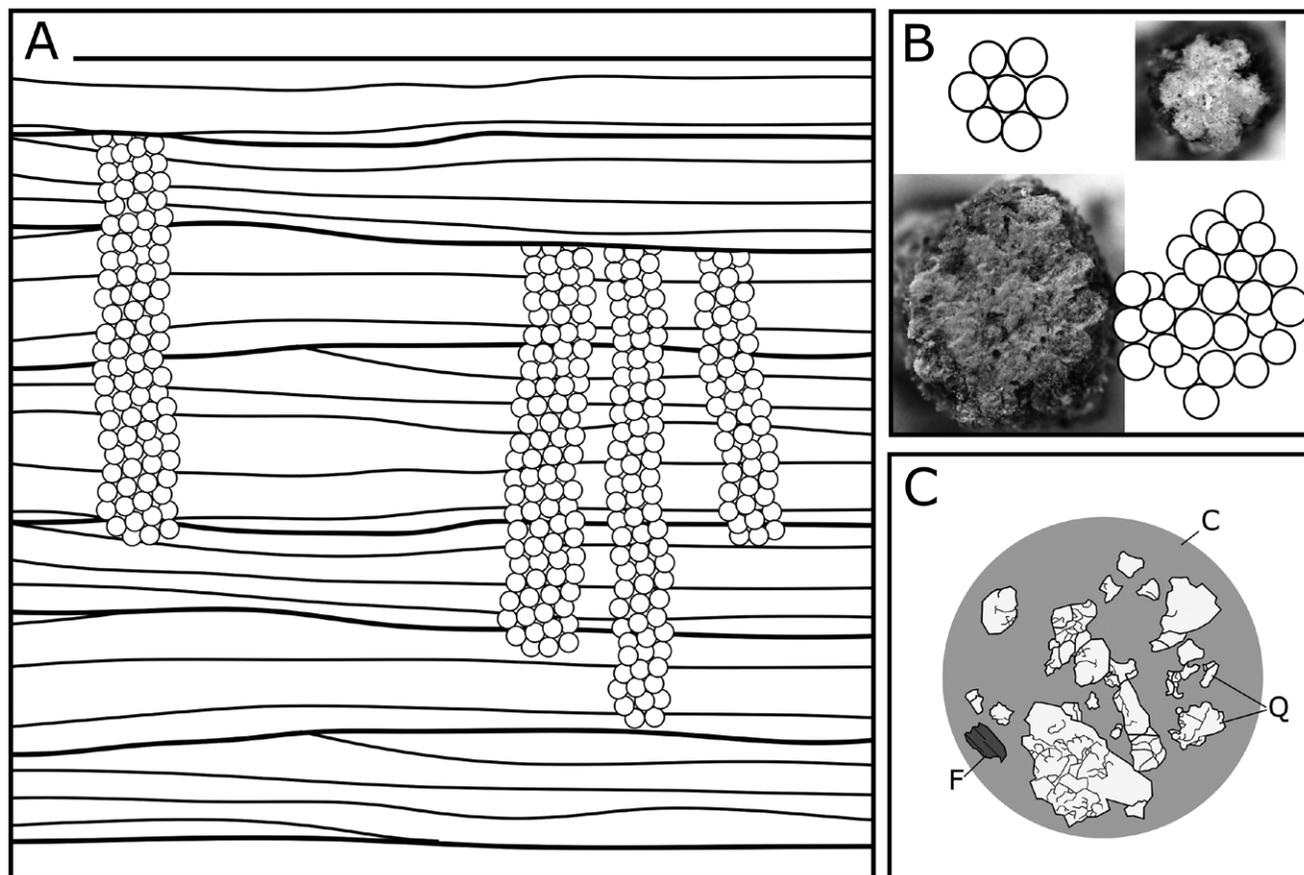


Fig. 5. Schematic drawing of *Nodulichnus hungaricus* igen. nov. et isp. nov. **A.** Longitudinal section of the solitary and clustered burrows. There is a sharp boundary between the sediment and the burrow. The primary sediment structure has not been modified by the producer organisms since the lamination is undisturbed. Certain hydrochemical alterations are shown by the presence of a micron-scale, ferruginous coating at the boundary of the trace fossil. **B.** Pellet positions in the case of regular, cross-sectioned (above) and irregular, cross-sectioned (below) burrows. The burrows are totally filled with pellets in both cases. **C.** Thin section of a pellet. The “aggregate” of the pellet-forming minerals is enveloped by small grains of clay-minerals, increasing the fossilization potential (Q – quartz, F – feldspar, C – clay-mineral).

filled its bifurcating burrows randomly with elliptical pellets (Kulkarni and Panchang, 2015).

There are some recent genera of sand-bubbler crabs, belonging to the superfamily Ocypodoidea, which produce burrows and pellets, similar to those of *Nodulichnus hungaricus*. These animals live in a tropical or subtropical climate in littoral conditions. They leave their burrows during low tide to consume the organic material of the surface sediments. The inorganic particles are left behind as small, globular, “subfaecal” pellets (sensu Ansell, 1988) at the entrances to their burrows. The crabs are minute and their carapaces are between 2–7 mm in diameter. According to Fishelson (1983), the diameters of their burrows are almost the same as the size of the carapace of the producer organism. Their burrows are straight, cylindrical, or slightly club-shaped. They are oriented vertically or at an angle within the sediment (Hayasaka, 1935; Wong *et al.*, 2011). Some of them show a slightly spiral shape (Silas and Sankarankutty, 1967; Ansell, 1988).

The burrow structure and pellet morphology of *Nodulichnus hungaricus* igen. et isp. nov. show considerable similarity with the same characteristics of the sand-bubbler crabs. Accordingly, it can be assumed that the pellets

filling *Nodulichnus hungaricus* igen. et isp. nov. are subfaecal pellets, which were produced by a deposit-feeding animal during the course of foraging. On the basis of the lack of phosphate content minerals in the pellets, one might assume that the material did not pass through the alimentary canal of the producer organism. The organic content of the sediment could have been filtered previously, then the unexploitable parts as small balls have been returned back to the bottom. According to the literature, these balls are called subfaecal pellets (Ansell, 1988). The members of the Ocypodoidea superfamily are well-known in the fossil record since the Late Cretaceous (Collins and Morris, 1975). On the basis of the morphological similarity of the trace fossils and the infilling pellets as well as the environmental conditions, it can be assumed that the producer organisms of *Nodulichnus hungaricus* could have been such deposit-feeders, depending on tides and light. This presumed, rhythmic activity means that the animals fed on the organic matter, covering the surface during low tide. If the Ocypodoidea are modern analogues, there are two hypotheses for the origin of the pellets filling the burrows: 1) The producer organism spent the night and the high-tide periods inside its burrow, covering the opening with a sediment nodule. Before going upward to the surface,

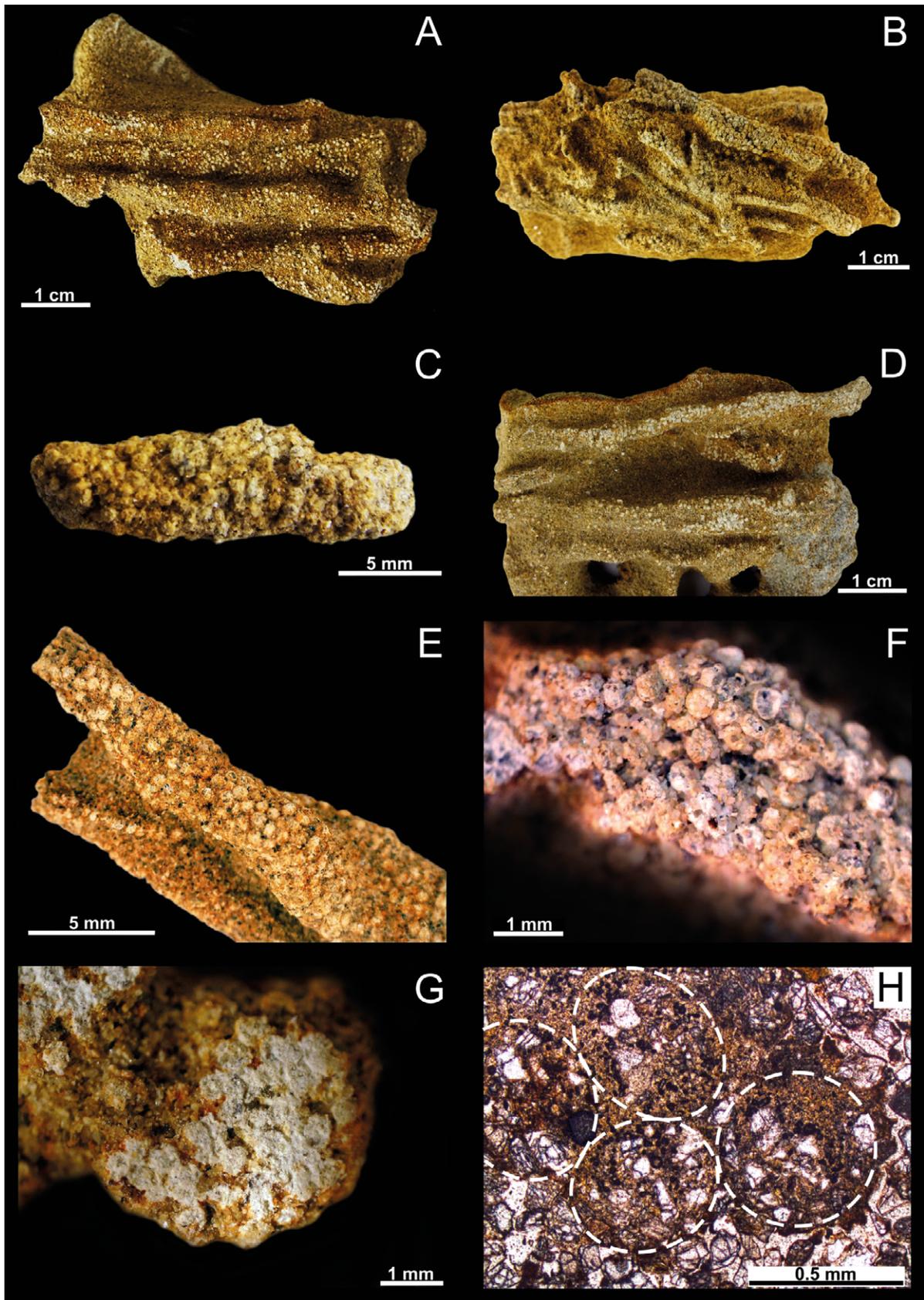


Fig. 6. Type specimens and morphological characteristics of *Nodulichnus hungaricus* igen. nov. et isp. nov. **A.** Holotype – HNHM-MMPAL Gy/64. **B.** Paratype – HNHM-MMPAL Gy/65. **C.** Paratype – HNHM-MMPAL Gy/66. **D.** Paratype – HNHM-MMPAL Gy/67. **E.** Longitudinal section of specimen No. 29. Verrucose surface of burrow, resulting from pellets. **F.** Close-up view of specimen No. 21. The spherical pellets closely fill the burrow. **G.** Irregularly oval cross-section of specimen No. 10. The tunnel is filled with globose pellets. The presence of the small amount of sand among the pellets indicates passive fill. **H.** Thin section of specimen No. 2. Rounded pellets are composed of clay minerals and quartz.

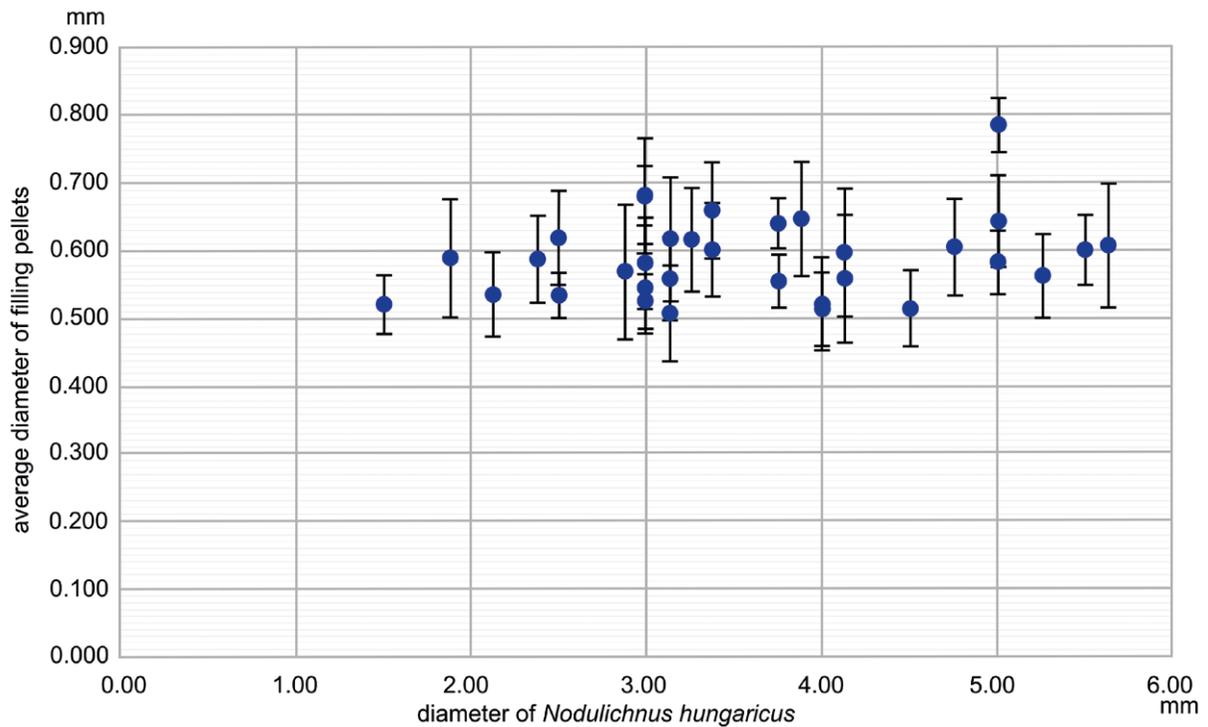


Fig. 7. Relation of the diameter of *Nodulichnus hungaricus* and the average diameter of the infilling pellets. The standard deviation of the diameter of the pellets also is indicated.

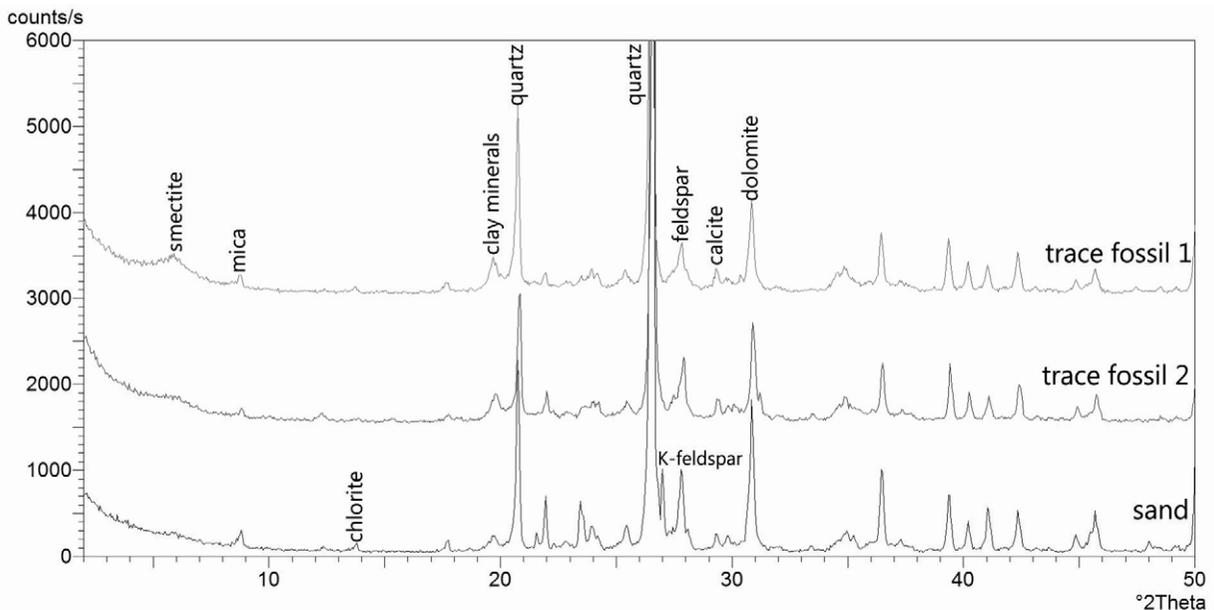


Fig. 8. Comparison of XRD analysis diagram of *Nodulichnus* samples and the fine-grained, greyish sand. The curves of *Nodulichnus* samples have a characteristic peak for smectite. This clay mineral builds up the external parts of the pellets.

the burrow had to be opened. During this process, the animal formed sandballs and returned those back into the burrow (Ansell, 1988). 2) It can be assumed that the producer breathed atmospheric oxygen. In this case, the bottom of the burrow always had to be above the water table in pore space. This means that the burrows were not flooded entirely. The trough cross-stratified sand above the level of the

sediment containing *Nodulichnus* marked an increase in water depth. The animal was forced to keep up with the increase in level of the sea water and to fill entirely its burrow to store enough oxygen for its survival during high tide. Taking this into consideration, the presence of *Nodulichnus hungaricus* could be viewed as an indicator of slow rise in sea level.

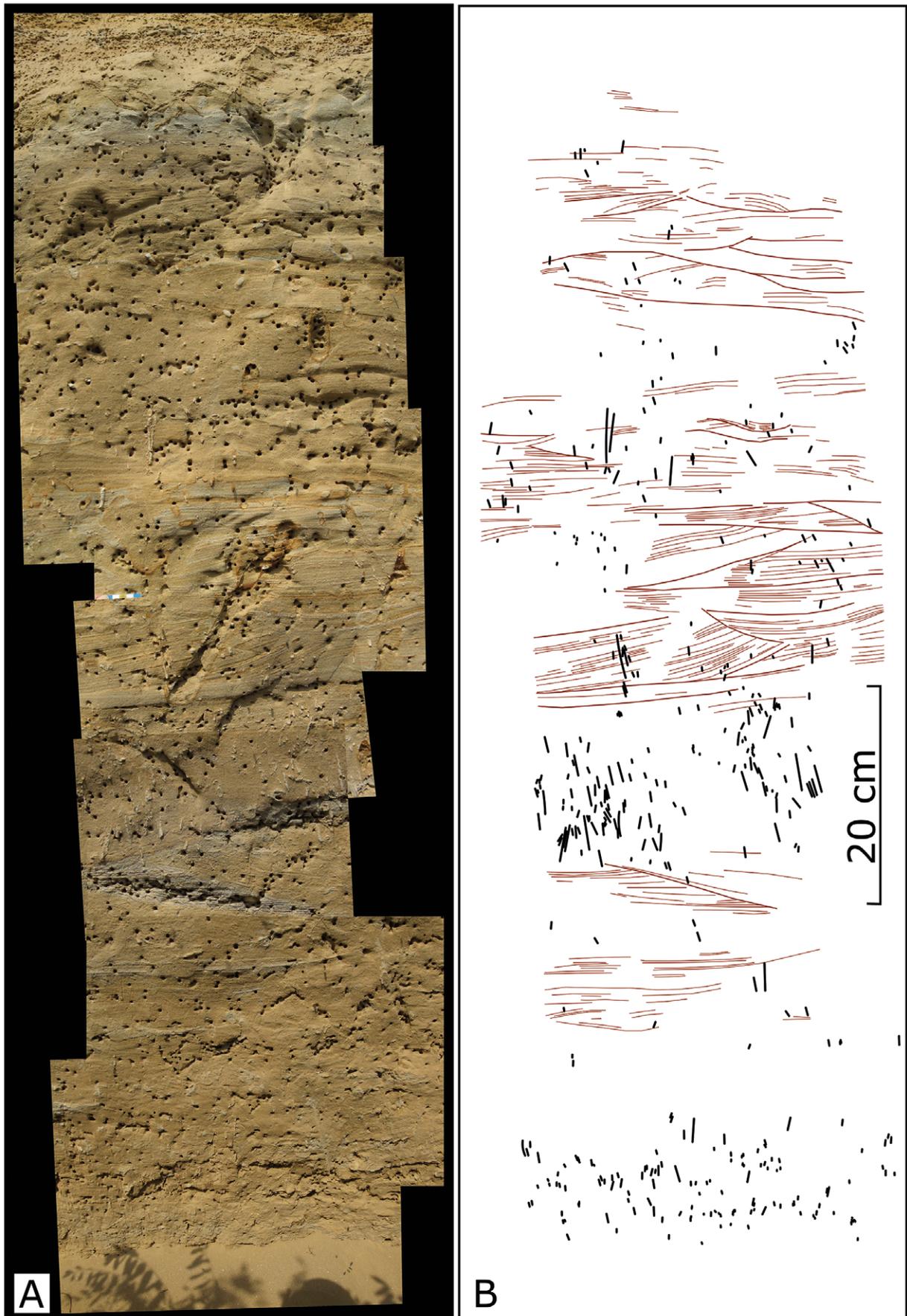


Fig. 9. Distribution of *Nodulichnus hungaricus* in the light-grey-coloured sand body. **A.** Detail of the outcrop containing *Nodulichnus hungaricus*. The holes are the recent burrows of hymenopterans. **B.** The position of *Nodulichnus hungaricus* marked by vertical lines and dots. The straight or slightly arcuate lines show the laminated, cross-bedded stratification of the sediment.

Environmental analysis

Those sediments, where the *Nodulichnus hungaricus* is dominant, were deposited on a low-energy, sandy shore between low and high tides. The shore was flooded during high tide. This is evidenced by the well-sorted, fine-grained sand and the laminar cross-bedding of the sediment. The sand

body is bounded by trough cross-bedded sand, referable to the upper shoreface, where there was periodic shallowing. This could be explained by local tectonic movements or sudden increases in the supply of transported sediments (Fodor *et al.*, 1999; Püspöki, 2002). As proved by pollen analyses, the climate was tropical or subtropical during the Karpatian stage (Nagy, 1992).

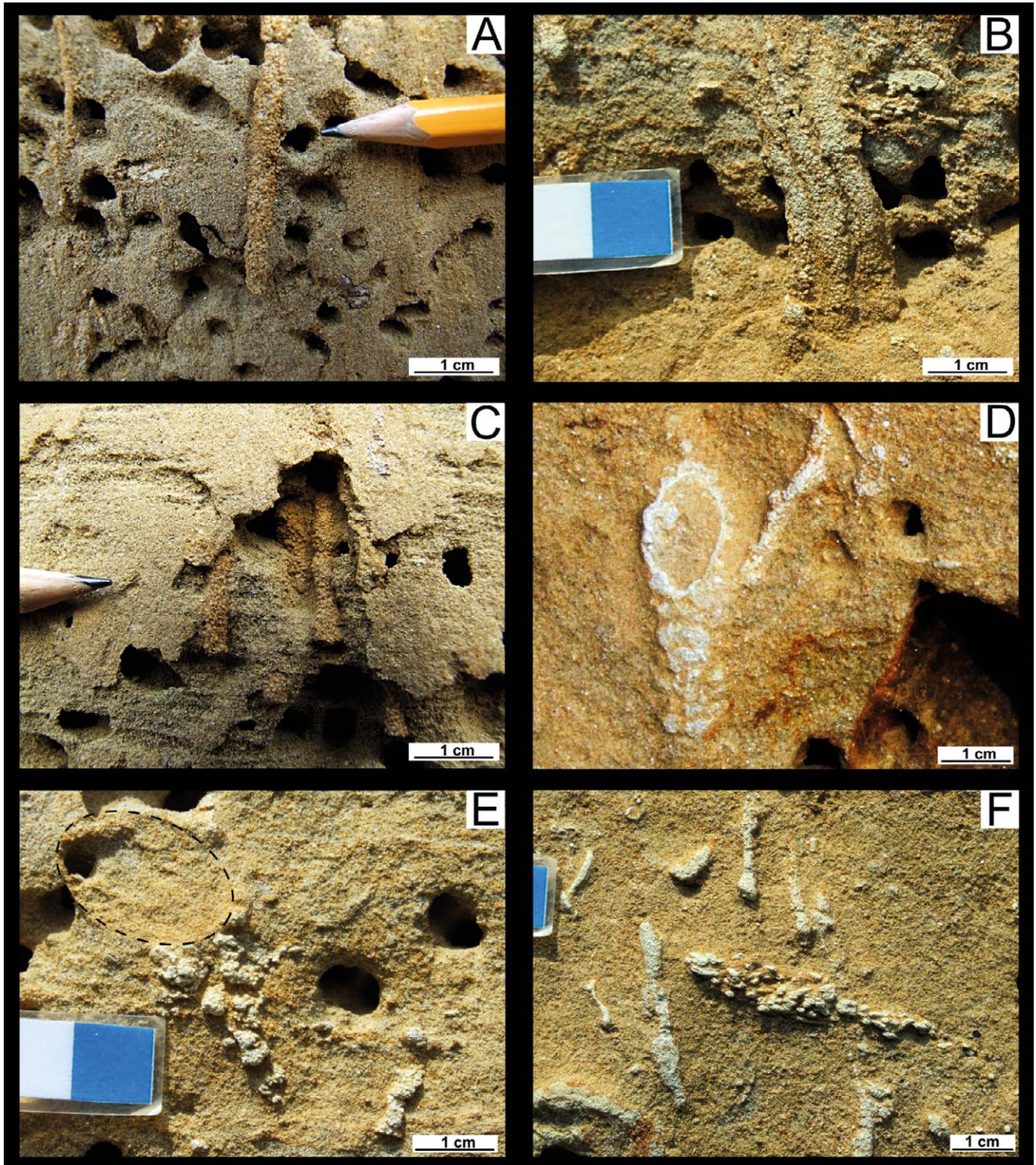


Fig. 10. Morphological characteristics of *Nodulichnus hungaricus* igen. nov. et isp. nov. **A.** Isolated and scattered specimens in the sand. **B.** Group of parallel and curved specimens. **C.** Group of *Nodulichnus hungaricus* inclined at 85–87°. **D.** *Nodulichnus hungaricus* crosscut by *Ophiomorpha nodosa*. **E.** *Nodulichnus hungaricus* crosscut by *Thalassinoides* isp. **F.** *Nodulichnus hungaricus* crosscut by a pellet-filled burrow.

Nodulichnus hungaricus occurs in at least twenty levels and their distribution do not show any order in the sand body. It frequently happens that burrows differing in length occur close together. According to modern analogues this can be attributed to climatic features. In subtropical circumstances, the formation of the shore is greatly affected by the annual variation of dry and wet seasons. During the dry season, the shore is populated by infaunal organisms. During the wet period, when erosion is increased on the shore, the above mentioned infaunal community could disappear partly or totally (Ono, 1965; Fishelson, 1983; Clayton and Al-Kindi, 1998). The emptied or partially pellet-filled burrows could have been eroded to different degrees as a result of this process. This explains the lack of shallow-tier trace fossils in the sediments examined. After the return of the dry season, the shore again was colonized by invertebrate organisms. Frequent repetition of the process caused the formation of the above mentioned distribution of trace fossils.

ICHTNOFABRIC DESCRIPTION

Nodulichnus hungaricus and the accompanying other bioturbation structures form a well-defined ichnofabric, which occurs only at a certain level in the whole exposure. This ichnofabric is characteristic for the middle level of the grey-coloured, very fine-grained sand. The sediment shows planar cross-bedding, which can be studied only in patches because of the burrows of modern insects, which cover the surface in high density.

Nodulichnus hungaricus makes up 41.5% of the ichnofabric. *Ophiomorpha nodosa*, *Gyrolithes nodosus*, *Thalassinoides* isp., *Planolites* isp. and *Tomaculum problematicum* occur subordinately (BI = 3).

Three different ichnoguilds can be differentiated: 1) *Nodulichnus-Tomaculum-Planolites* ichnoguild. It consists

of the traces of vagile, deposit-feeder organisms and represents the middle tier in this case, since the producers burrow at least some ten centimetres depth into the sediment. The formation of *Nodulichnus* took place during low tide, while *Tomaculum* formed during high-tide conditions; 2) *Ophiomorpha-Gyrolithes* ichnoguild. It contains mainly deep-tier burrows of semi-vagile sediment feeder organisms. These traces can reach a depth of 1–2 m; 3) *Thalassinoides* ichnoguild. It is composed of a 3D boxwork of *Thalassinoides* isp. built by numerous generations. These are the deep-tier traces of semi-vagile deposit feeders (Fig. 11). *Nodulichnus* is often crosscut by the traces of callianassid crabs and *Planolites* isp. (Fig. 10D–F). This fact refers to certain trace fossils being formed at different times.

Palaeoenvironmental interpretation

The ichnoguilds introduced above are genetically in close association with each other. These collectively indicate sea-level fluctuations in the area and also the responses of infaunal organisms to these changes. On the basis of the above descriptions, three colonisation events can be differentiated within the grey-coloured, fine-grained sand. The middle-tier trace fossils, such as *N. hungaricus* and *Planolites* isp., were produced by mud-feeding, vagile organisms on the upper shoreface, during low tide (Fig. 12A). On the basis of the dominance of *N. hungaricus*, one might interpret where infaunal organisms came up to the surface to feed during low tide, then spent the times of high tide in their burrows. This could be a variation of the *Skolithos* ichnofacies, where organisms of similar life habit, such as the sand-bubbled crab, *Scopimera*, were the main producers. The sequence of sedimentary features at the locality was generated during a transgression. The water depth and the rate of sedimentation increased the parts dominated by *Nodulichnus* because of the slow rise in sea level. The sediments were colonised by

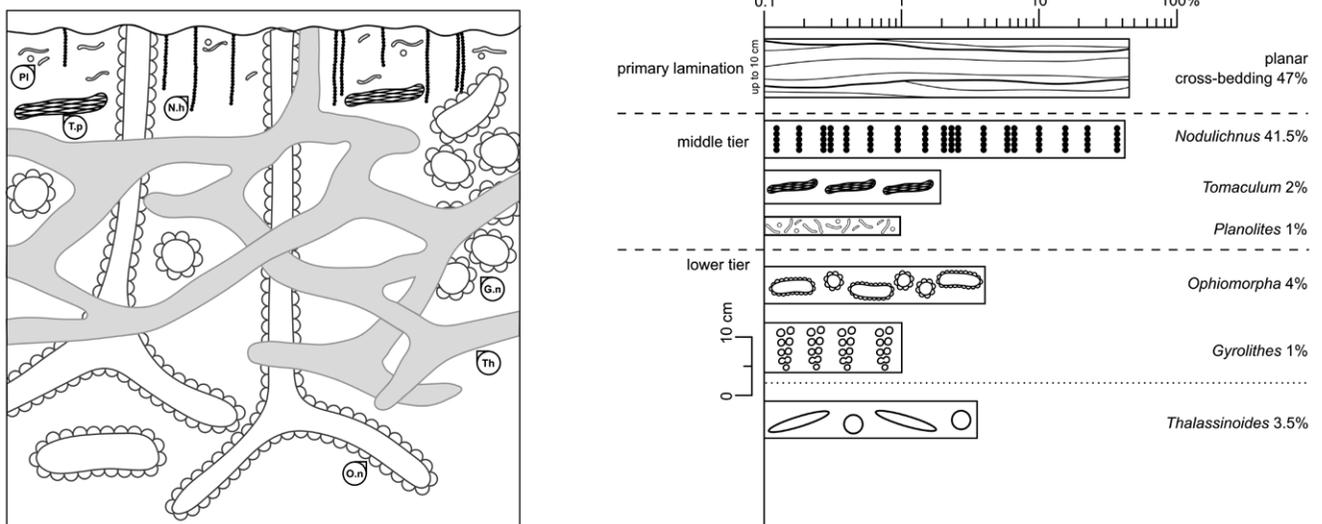


Fig. 11. 2D idealised sketch and ichnofabric constituent diagram (see Taylor and Goldring, 1993; Gibert and Goldring, 2007) for the *Nodulichnus* ichnofabric. The three ichnoguilds represent different colonization events within this ichnofabric. The first one is the *Nodulichnus-Tomaculum-Planolites* ichnoguild. It consists mainly of middle-tier traces of deposit-feeder organisms. The second one is the *Ophiomorpha-Gyrolithes* ichnoguild. It represents deep-tier traces of semi-vagile deposit-feeder organisms. But middle-tier traces of vagile deposit-feeder organisms are also present here. The third one is the *Thalassinoides* ichnoguild. It was built by a well-developed, multi-generation 3D boxwork of callianassids. The lack of shallow-tier traces refers to frequent, erosional events.

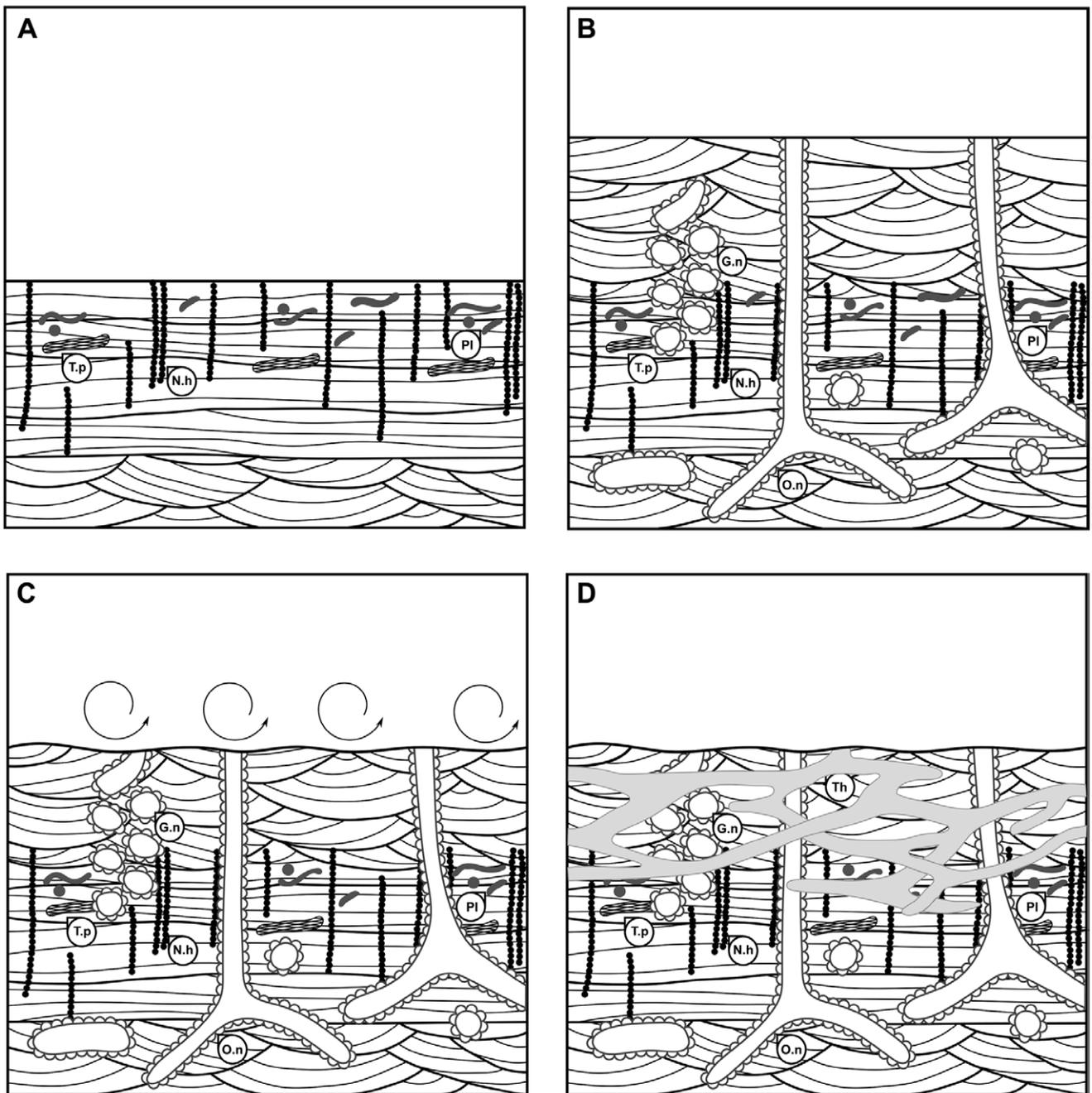


Fig. 12. Colonization model of the grey-coloured, fine-grained sand. **A.** Colonization of infaunal organisms, producing middle-tier life traces in the splash zone. **B.** Settlement of callianassids at the upper shoreface. Formation of upper-shoreface environment due to the rising sea-level. As a consequence of the altered, environmental conditions, the surface of the sediment was colonized by callianassid crabs, producing *Ophiomorpha nodosa* and *Gyrolithes nodosus*. **C.** Erosional event. Owing to a further sea-level rise the bottom was eroded and this led to the exposure of the deeper, semi-consolidated sand. **D.** Formation of *Glossifungites* ichnofacies at the semi-consolidated bottom, exposed by erosion. The freshly formed surface was colonized again. The callianassids, as pioneer organisms, developed their 3D boxwork traces. Three generations of traces can be distinguished. This reflects at least three erosional events prior to the latest phase of sediment accumulation.

callianassid crabs. The formation of the *Ophiomorpha nodosa*-*Gyrolithes nodosus* boxwork took place. These trace fossils form the low-energy, wave-dominated, littoral variation of the *Skolithos* ichnofacies (Fig. 12B). These burrows crosscut the *N. hungaricus* burrows in some places and reach down to the underlying sediment. As the transgression increased, erosion could become dominant. Therefore,

wave and littoral currents could wash and transport the upper, unconsolidated part of the bottom sediment (Fig. 12C). The firmground developed was colonised by callianassids, forming the *Thalassinoides* boxwork and also crossing some of the *N. hungaricus* (Fig. 8E, F). This led to the formation of the *Glossifungites* ichnofacies (Fig. 12D).

CONCLUSIONS

The East-Borsod Coal Basin formed at the northern edge of the Central Paratethys. It was filled with shallow-marine, siliciclastic sediments during the Early Miocene (Karpatian).

The mainly sandy-marly beds belong to the Salgótarján Lignite Formation, which contains five lignite seams, interbedded with highly bioturbated, laminated marl, calcareous marl, and cross-bedded and laminated sand. A characteristic exposure of the Salgótarján Lignite Formation is a large sand pit, situated in the vicinity of Miskolc-Diósgyőr. There is a 5-m-thick, light-grey-coloured, trough-cross-bedded, fine-grained sandstone, which contains the trace fossil, described in the present account and named as *Nodulichnus hungaricus* igen. et isp. nov. It is a vertical, straight, or slightly winding, non-branching, cylindrical, blind-ending trace fossil. The cross-section of the cylinder is circular, elliptical, and more rarely, irregularly oval. The length of the galleries varies between 20 and 150 mm. The trace fossil is 1.5–5.5 mm in diameter. It was actively filled with globose pellets, which are 0.5–0.8 mm in diameter. The high proportion of clay fraction in the composition of the pellets reflects biological reworking of the sediment. It can be assumed that the pellets infilling the trace fossil *Nodulichnus hungaricus* igen. et isp. nov. are subfaecal pellets, which were produced by a deposit-feeding animal during the course of feeding activity. The burrow structure and pellet morphology of *N. hungaricus* show considerable similarity to the analogous features of the sand-bubbler crabs, *Scopimera* and *Dotilla*, which belong to the Dotillidae family. The presence of *N. hungaricus* and co-occurring trace fossils indicate fluctuations in sea-level. Infaunal organisms responded to these fluctuations and their traces record three colonisation events. These refer to changes in palaeoenvironmental conditions from a low-energy, wave-dominated, littoral setting (*Skolithos* ichnofacies), to upper shoreface conditions (*Cruziana* and *Glossifungites* ichnofacies), as the transgression progressed.

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