



The trace fossil *Nummipera eocenica* from the Tatra Mountains, Poland: morphology and palaeoenvironmental implications

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The tubular trace fossil *Nummipera eocenica* Hölder 1989 occurs in a single stratigraphical horizon in Eocene nummulitic limestones of the Tatra Mountains, Poland. The wall of *N. eocenica* is built of *Discocyclus* and *Nummulites* (larger foraminifera) tests, very rarely of the *Ditrupa* (Polychaeta) tube fragments, bivalve shell fragments, echinoid spines and coralline algae. Morphotypes are distinguished on the basis of wall composition and structure. Morphotype A is dominated by fusiform *Discocyclus* tests, which were preferentially selected by the trace makers for construction of a well-constructed and resistant wall. Morphotype B contains more robust tests of *Nummulites*, while morphotype C is dominated by saddle-shaped tests of *Discocyclus*. *Nummipera eocenica* was produced during a period of seafloor stabilization caused by a deepening. The succession of the morphotypes B, A reflects diminishing energy and increasing water depth. Probably morphotype C represents even lower energy environment than morphotype A. The trace fossil is interpreted as a domichnion, which wall was constructed for protection. The trace maker can be considered between polychaetes and crustaceans; however, comparisons to the closest recent analogues, the polychaete *Diopatra cuprea* or alpheid shrimps, are not satisfactory. □ Bartonian, burrow, Carpathians, large foraminifera, trace fossils.

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Burrowing animals are an important agent of redistribution of bioclasts (e.g. Bradshaw & Scoffin 2001), not only by disturbance of primary fabric, but also by an active selection, among others by building of bioclast-made burrow walls. Trace fossils distinguished by the bioclast-made burrow wall, known since long as ‘*Terebella*’ (Bather 1911), include the ichnogenera *Lepidenteron* Fritsch, 1878; *Diopatrachus* Kern, 1978; *Crinincaminus* Ettensohn, 1981 (described as a biotaxon, but ichnotaxon in fact), *Nummipera* Hölder, 1989; *Baronichnus* Breton, 2002; and *Ereipichnus* Monaco *et al.*, 2005. They are distinguished on the basis of the main type of bioclasts and their overall orientation.

In this paper, *N. eocenica* Hölder, 1989; a so-far poorly known trace fossil, is re-evaluated. It derives from the Eocene of the Tatra Mountains, West Carpathians, Poland, and was described previously in open nomenclature by Roniewicz (1969, 1970) and Olempska (1973). In this trace fossil, bioclasts, mainly large foraminifera, were actively selected and accumulated in its wall, and this trace fossil is closely related to facies and palaeoenvironment changes.

Geological setting

The Nummulitic Eocene

Eocene deposits in the Tatra Mountains (the so-called Nummulitic Eocene) are a part of the Central Carpathian Palaeogene that overlies discordantly the Variscan basement and its Permian-Mesozoic cover of the alpine Carpathian Orogenic Belt (Fig. 1; Passendorfer 1959; Mahel 1980). Generally, the Eocene deposits form a transgressive sequence, which starts with conglomerates composed of bedrock clasts (Fig. 2; Roniewicz 1969; Kulka 1985; Olszewska & Wieczorek 1998; Bartholdy *et al.* 1999). In the Polish part of the Tatra Mts., their thickness ranges from 0 m to more than 200 m. Their basal parts were probably deposited under freshwater conditions (Gradziński *et al.* 2006), while the upper part in a marine environment. The conglomerates are covered by littoral extraclastic packstones (often called detritic carbonates; 0–300 m thick), which locally contain *Nummulites* rudstone banks (Roniewicz 1969). In the Hruby Regiel Mt. area, the conglomerates and extraclastic packstones fill a

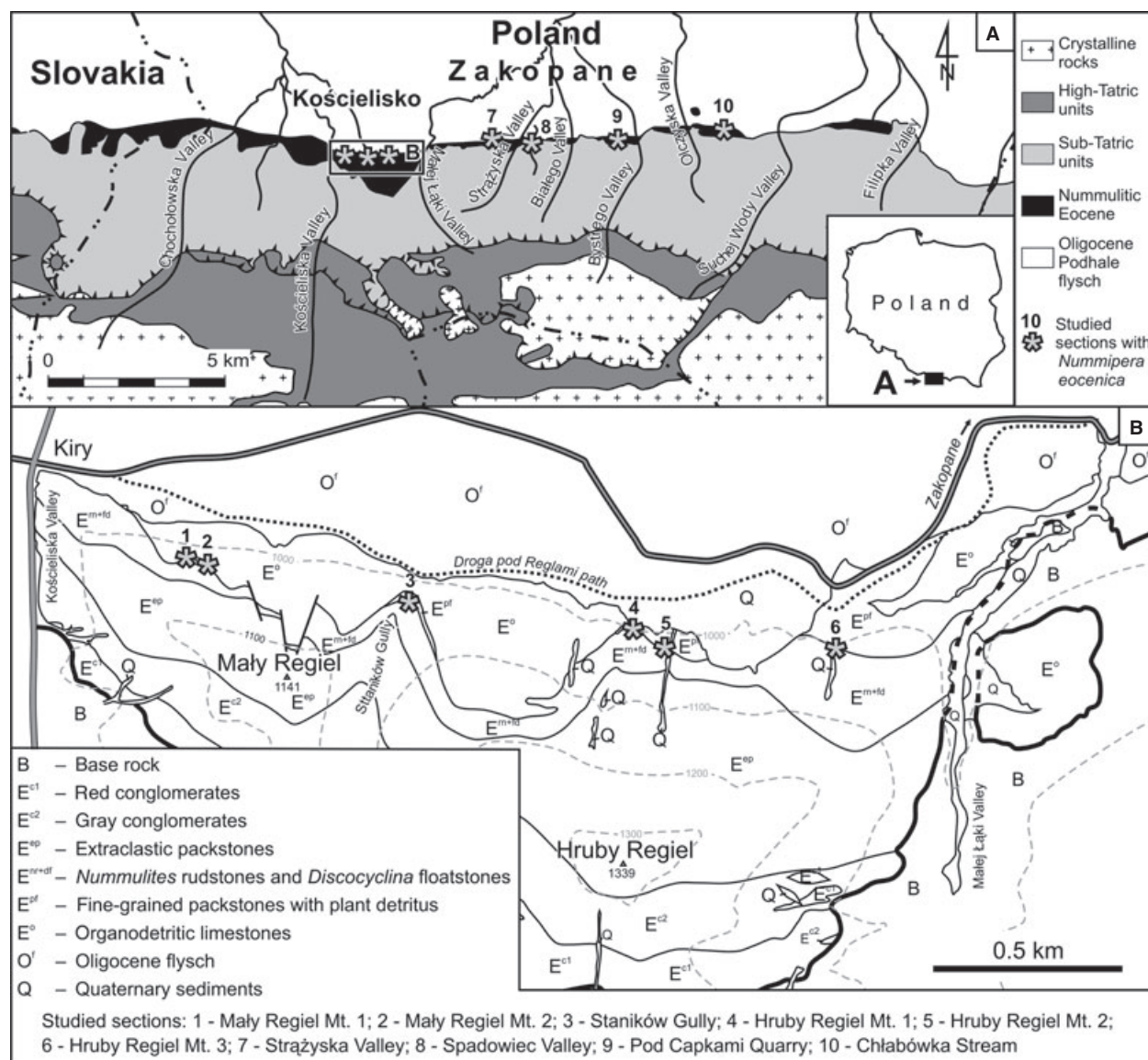


Fig. 1. Location of the study area and the studied sections. A, geological sketch map of the Polish part of the Tatra Mountains (after Bac-Moszaszwili *et al.* 1979; simplified). B, detailed geological map of Hruby Regiel Mt. (after Sokołowski 1959, modified).

local, tectonically controlled depression (Jach *et al.* 2009).

The upper part of the Nummulitic Eocene (Upper Bartonian–Priabonian) is composed of various organodetritic limestones (mostly rudstones, packstones, bindstones) containing numerous nummulites, discocyclines, other large benthic foraminifers and coralline algae (Fig. 2; Bieda 1963). Their thickness attains a maximum of 20 m. In the Pod Capkami Quarry, glauconitic marls with planktonic foraminifers cover *Discocyclina* rudstones (Bartholdy *et al.* 1995; Machaniec *et al.* 2009). In the Hruby Regiel Mountain area, organodetritic limestones are laterally replaced by less energetic fine-grained packstones with plant detritus. Both types of these limestones were deposited

on a middle-distal carbonate ramp. Locally, a higher stratigraphical position (Priabonian) is occupied by conglomerates, which suggest syndimentary tectonic activity (Jach *et al.* 2009). Besides conglomerates, the Priabonian is represented by very locally widespread platform organodetritic limestones. The carbonates are succeeded by about 2.5-km-thick complex of Oligocene turbiditic deposits (Radomski 1959; Soták *et al.* 2001; Ludwiniak 2010).

Nummipera eocenica localities and facies

Nummipera eocenica was found in ten localities: (1) Mały Regiel Mt. 1 (GPS coordinates: N49°16.414'; E19°52.375'); (2) Mały Regiel Mt. 2 (GPS coordinates:

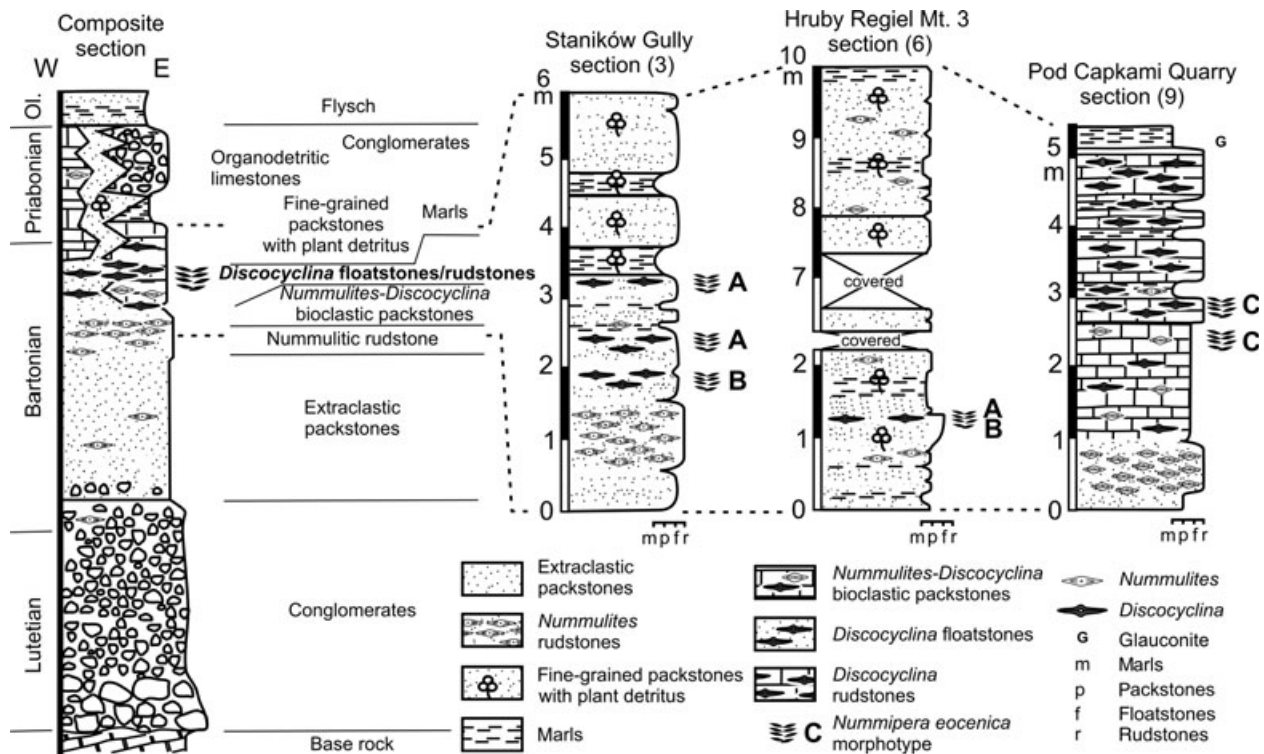


Fig. 2. Left column: composite lithostratigraphic log of Eocene deposits in the Tatra Mountains. Remaining columns: some sections of the Nummulitic Eocene containing *Nummipera eocenica* Hölder 1989.

N49°16.413'; E19°52.393'); (3) Staników Gully (GPS coordinates: N49°16.369'; E19°52.875'), and at three localities on the slopes of Hruby Regiel Mt. i.e. (4) Hruby Regiel Mt. 1 (GPS coordinates: N49°16.383'; E19°53.265'); (5) Hruby Regiel Mt. 2 (GPS coordinates: N49°16.341'; E19°53.356'); (6) Hruby Regiel Mt. 3 (GPS coordinates: N49°16.340'; E19°53.791'); (7) Strážyska Valley (GPS coordinates: N49°16.725'; E19°56.284'); (8) Spadowiec Valley (GPS coordinates: N49°16.741'; E19°57.100'); (9) Pod Capkami Quarry (GPS coordinates: N49°16.746'; E19°58.361'); and (10) Chłabówka Stream (GPS coordinates: N49°16.883'; E20°0.816') (Fig. 1).

The trace fossil *N. eocenica* Hölder occurs only in the *Discocyclus* floatstones, *Nummulites-Discocyclus* bioclastic packstones, and in the *Discocyclus* rudstones (Machaniec et al. 2009). These facies are located in a transition between underlying extraclastic packstones with local *Nummulites* rudstone banks and overlying deposits, which differ in western and eastern part of the study area and include: (1) organodetritic limestones; (2) fine-grained packstones with plant detritus; or (3) glauconitic marls (Fig. 2).

The most abundant *N. eocenica* occur in the *Discocyclus* floatstones, which are up to 1.5 m thick. The highest density of *N. eocenica* is noted in the Staników Gully section (Fig. 1), where about 25 specimens per 1 m² occur. Other localities include: Mały Regiel Mt.

1 and 2, Staników Gully and Hruby Regiel Mt. 1, 2 and 3. (Figs 1, 2). The *Discocyclus* floatstones are massive though distinctly bedded locally. *Nummipera eocenica* occurs in a few horizons usually in the uppermost parts of the beds (Fig. 2). The floatstone matrix is composed of dolomite extraclastic grains, less often of limestones and quartz grains, fine-grained bioclasts and micrite. At the localities Staników Gully and Hruby Regiel Mt. 1, 2 and 3 (Fig. 1), the bioclastic matrix is finer. The fusiform in cross-section tests of *Discocyclus pratti*, *Discocyclus fortisi* and less commonly tests of nummulites, mainly *Nummulites perforatus*, constitute more than 10% of grains (Table 1). They are chaotically distributed, with no signs of abrasion. Only some of them are bored. Stylolitic solution contacts between *Discocyclus* tests are common.

In the eastern part of the studied area, single specimens of *N. eocenica* occur in a 0.3-m-thick horizon in the uppermost part of the *Nummulites-Discocyclus* bioclastic packstones and in the lowermost part of the *Discocyclus* rudstones (Fig. 3). The *Nummulites-Discocyclus* bioclastic packstones and the *Discocyclus* rudstones occur at the localities Strážyska Valley, Spadowiec Valley, Pod Capkami Quarry and the Chłabówka Stream (Fig. 1). The *Nummulites-Discocyclus* bioclastic packstones are composed of *Nummulites perforatus*, *Discocyclus* sp., *N. puschi*, rare *N. maximus*, small *Nummulites* sp., very rare coralline

Table 1. *Nummipera eocenica* morphotypes from the Tatra Mts sections.

Locality	No. of sample	Type of the section	Size in mm			Contribution of bioclasts in the wall of <i>Nummipera eocenica</i> in %				Morphotype
			Length	External diameter	Internal diameter	<i>Discocyclina</i> sp.	<i>Nummulites perforatus</i> A	<i>N. perforatus</i> B spp.	<i>Nummulites</i>	
Matý Regiel Mt 1	1a	O	–	28	20	97		3		<i>Discocyclina</i> floatstones
	1b	L	–	32	20	96		3		
	1c (ts)									
Matý Regiel Mt 1	2	L	70	40	20	100				<i>Discocyclina</i> floatstones
	3	P	30	30	15	100				<i>Discocyclina</i> floatstones
	4	P	80	35	20	100				<i>Discocyclina</i> floatstones
Matý Regiel Mt 2	5	O	50	20		95	5			<i>Discocyclina</i> floatstones
	6a	L	45	30		96		2	2	<i>Discocyclina</i> floatstones
	6b (ts)	L								
Matý Regiel Mt 2	7	P	55	40	20	96		4		<i>Discocyclina</i> floatstones
	8	L				100				<i>Discocyclina</i> floatstones
	9	O	–	32	20	100				<i>Discocyclina</i> floatstones
Matý Regiel Mt 2	10a	L	65	40		68				<i>Discocyclina</i> floatstones
	10b	L	80	35	20					<i>Discocyclina</i> floatstones
	10c (ts)	L	60	20		60	40			<i>Discocyclina</i> floatstones
Hrubý Regiel Mt 2	11	L	50	30		100				<i>Discocyclina</i> floatstones
	12a	O	35	35		30				<i>Discocyclina</i> floatstones
	12a-d	P	35	35		20				<i>Discocyclina</i> floatstones
Hrubý Regiel Mt 3	12e (ts)	L	45	30	15	86	12		2	<i>Discocyclina</i> floatstones
	13	L	50	25		75	35			<i>Discocyclina</i> floatstones
	14	L	30	30		55	70			<i>Discocyclina</i> floatstones
Hrubý Regiel Mt 3	15	P	35	35		30				<i>Discocyclina</i> floatstones
	16a	L	35	30	15	94	6			<i>Discocyclina</i> floatstones
	16b (ts)	L				65	11			<i>Discocyclina</i> floatstones
Hrubý Regiel Mt 3	18a,b	L	65	40		89	1			<i>Discocyclina</i> floatstones
	18c (ts)	L	70	45		96				<i>Discocyclina</i> floatstones
	18d (ts)	L								<i>Discocyclina</i> floatstones

Table 1. (Continued)

Locality	No. of sample	Type of the section	Size in mm		Contribution of bioclasts in the wall of <i>Nummipera eocenica</i> in %				Morphotype				
			Length	External diameter	Internal diameter	Contribution of bioclasts in the wall of <i>Nummipera eocenica</i> in %							
						<i>Discocyclina</i> sp.	<i>Nummulites perforatus</i> A	<i>Nummulites perforatus</i> B spp.		<i>Ditrupa</i> sp.	Lithoclasts	Lithology	Contribution of fossils in surrounding deposit in %
Hruby Regiel Mt 3	19	L	100	40		96	4						
Strążyska Valley	20 (ts)	L	30	15		99			1				
Spadowiec Valley	21a 21b (ts)	L	70	30	15	96	1		2				
Pod Capkami Quarry	22a 22b (ts)	L	80	35	15	97	3						
Chłabówka Stream	23a 23b (ts)	L	40	35	15	100							

P, perpendicular; O, oblique; L, longitudinal; N. sp., *Nummulites* sp.; Np, *Nummulites perforatus*; D, *Discocyclina* sp.; d, *Ditrupa*; ts, thin section.

algae, and tubes of *Ditrupa* sp. (Table 1). Large foraminifera tests display mostly robust and ovate shapes. The bioclasts are often fragmented and abraded. The contact with the overlying *Discocyclina* rudstones is sharp. The *Discocyclina* rudstones are built almost exclusively of *Discocyclina*, whose tests are thin, flat. The lower part of the *Discocyclina* rudstones contains numerous saddle-shaped tests of *Discocyclina ephippium*, *Discocyclina sella*, moreover, *Orbitoclypeus varians* and *Asterocyclina stellata*. In the upper part of the rudstone, the *Discocyclina* tests become thinner and flattened, dominated by disc-shaped *Discocyclina sella*, *Discocyclina augustae* and *Discocyclina radians*. The bioclasts are horizontally orientated, densely packed, with rare fragmentation or abrasion. Their matrix is composed of micrite with fragmented tests of *Discocyclina* (Machaniec et al. 2011).

Nummipera eocenica Hölder, 1989 and its morphology

Nummipera eocenica Hölder, 1989 is the only ichnospecies of the ichnogenus *Nummipera* Hölder, 1989. Breton (2002) included the trace fossil left in open nomenclature and described by Roniewicz (1969, 1970) in *Baronichnus* Breton, 2002; being not aware of the paper by Hölder (1989), in which the same trace fossils was included in *N. eocenica* Hölder, 1989. Breton (2004) argued that *N. eocenica* Hölder, 1989 is a *nomen dubium* because of the diagnosis is unclear and that the holotype can be a result of sedimentary processes. These arguments, however, are not convincing and *N. eocenica* Hölder, 1989 is considered in this paper as a valid and useful ichnotaxon.

Nummipera eocenica was described only from Eocene deposits rich in large foraminifers in a few regions of the Alpides in Europe, Asia Minor and North Africa, also in open nomenclature (Table 2).

Nummipera eocenica from the Tatra Mountains was analysed in the field and in 23 samples (institutional abbreviation INGUJ222P), and 11 thin sections, which are housed at the Institute of Geological Sciences of the Jagiellonian University.

The trace fossil comprises a vertically to obliquely oriented, straight to gently curved, tubular, opened upward burrow, up to 140 mm long (field measurement) and 40–45 mm in the external diameter (Figs 4, 5A–E). The morphology of its lower termination is not clear. Roniewicz (1970, fig. 3) suggested that the burrow was closed by tests, which are more or less oriented in the same way like in the wall. However, such impression can result from intersections. Any sure lower termination was not found in the studied material. The burrows are round in the transverse section (Fig. 5D,F). Their lumen is 16–20 mm

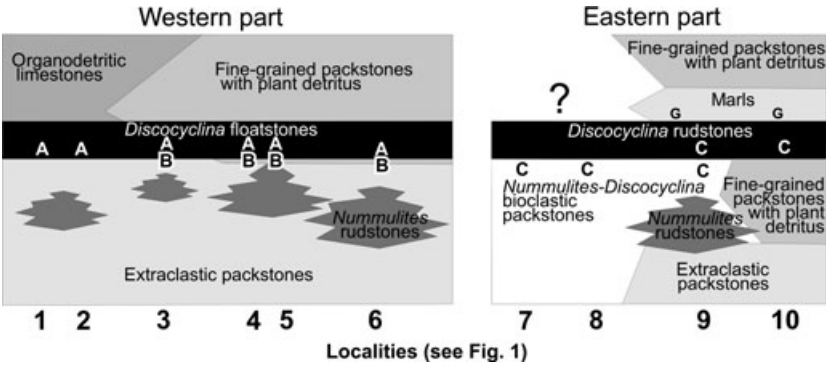


Fig. 3. Location of the *Nummipera eocenica* morphotypes A, B and C against the surrounding facies distribution (after Jach *et al.* 2009).

Table 2. Occurrences of *Nummipera eocenica*.

Region	Original name	References
Tatra Mountains, S Poland	kanaly w wapieniu numulitowym [canals in the nummulitic limestones], concentration of <i>Discocyclus</i> , pocket-like concentration of large foraminifera Tubes lined with foraminiferal Elongate burrows <i>Nummipera eocenica</i>	Roniewicz (1969, p. 573, fig. 20, pl. 9, fig. 2, pl. 11, fig. 1) Roniewicz (1970, p. 443, pl. 2a-c, fig. 3) Olempska (1973, p.76, pl. 18, fig. 1–5) Machaniec <i>et al.</i> (2010, p. 514)
Dalmatian coast, W Croatia	Numuliten-Packung <i>Nummipera eocenica</i> nov. ichnogen. nov. ichnosp. Tubes armoured with nummulite tests <i>Ophiomorpha</i> burrow lined by neatly packed <i>Nummulites</i> <i>Nummipera eocenica</i>	Hölder (1958, p. 378, fig. 1) Hölder (1989, p. 25, fig. 9) Babić & Zupanić (1998, p. 181) Marjanac & Marjanac (2007, p. 499, fig. 4e)
Pyrenees, N Spain	<i>Nummipera eocenica</i>	Serra-Kiel <i>et al.</i> (2003, p. 216)
Gökçeada Island, W Turkey	<i>Nummipera eocenica</i>	Demircan <i>et al.</i> (2010, p. 1)
El Garia Formation, N Tunisia	Biogenically produced fabric; stacked, deflected, tubular tempestites <i>Nummipera eocenica</i>	Beavington-Penney <i>et al.</i> (2005, p. 542, fig. 5)
Seeb Formation, Oman	Biogenically produced fabric; stacked, deflected, tubular tempestites <i>Nummipera eocenica</i>	Beavington-Penney <i>et al.</i> (2006, p. 1142, fig. 4)

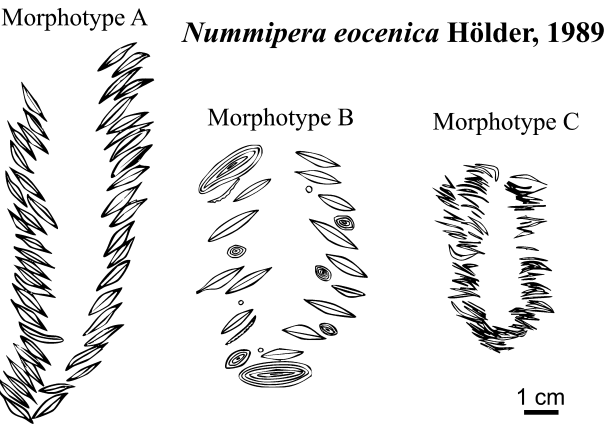


Fig. 4. *Nummipera eocenica* Hölder, 1989, morphotype A, B and C

in diameter (Table 1). The diameter does not change along the burrow; however, some oblique intersections lead to an opposite impression (Fig. 5D). The wall is 10–17 mm thick. The thickness can change in a single specimen. It can be distinctly thicker from one

side (Fig. 5G). The wall is composed of tests of large foraminifers of the family Nummulitidae, mainly *Discocyclus* sp. (Table 1). The tests are often tightly packed, creating a dense wall structure (Fig. 5G). Usually, tests are slightly inclined towards the burrow

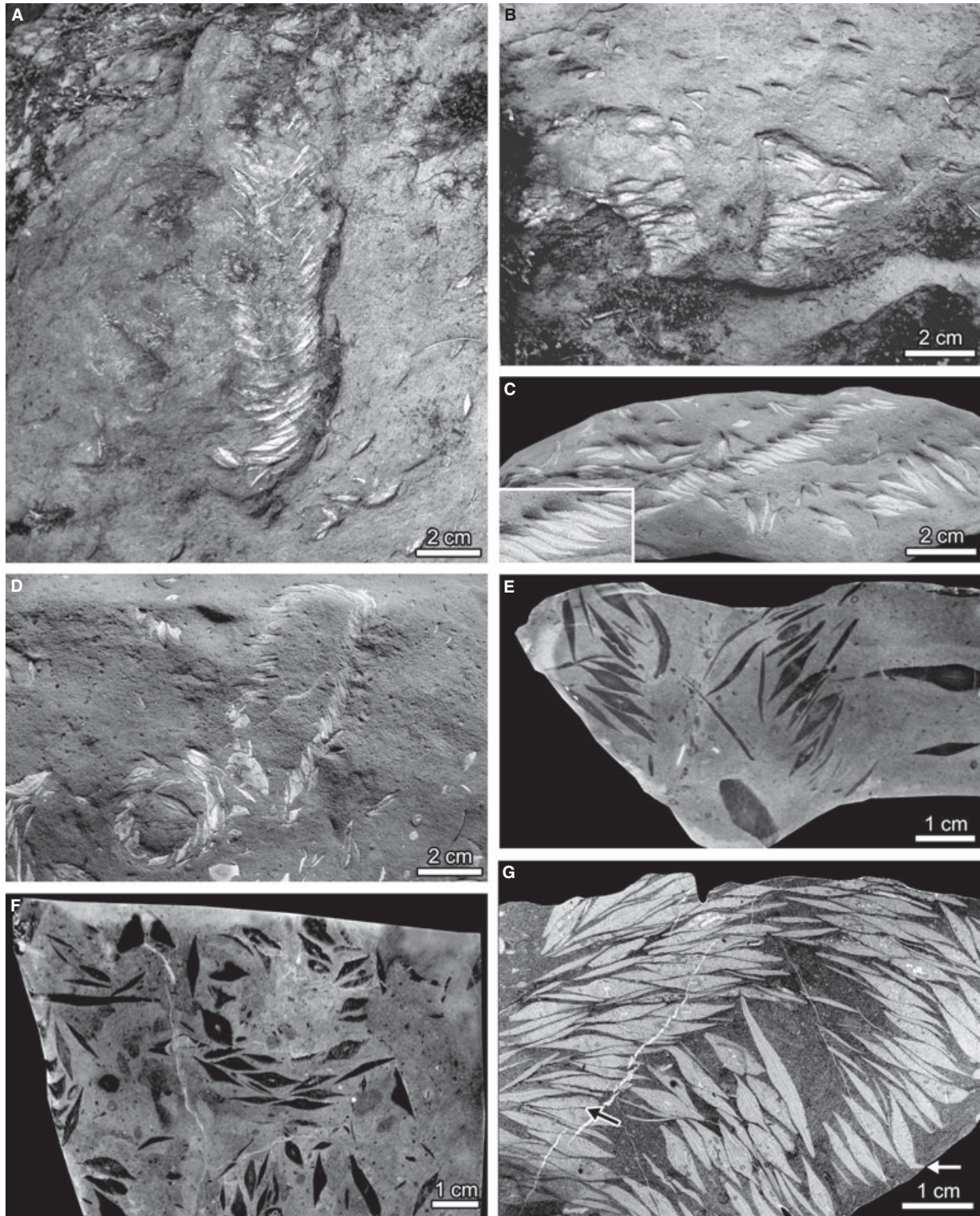


Fig. 5. *Nummipera eocenica* Hölder, 1989, morphotype A. Walls built almost exclusively of well-sorted fusiform tests of *Discocyclus* spp. A-forms. A, longitude section, tests dipping towards the burrow lumen. Hruby Regiel Mt. 2. Field photograph. B, sub-vertical section with well-visible lumen. Hruby Regiel Mt. 2. Field photograph. C, wall built of densely packed tests of *Discocyclus*. Sigmoidal bending of tests in the insert. Maly Regiel Mt. 2. Sample INGJ222P7. D, sub-horizontal and perpendicular sections. Maly Regiel Mt. 2. Sample INGJ222P9. E, vertical section. *Discocyclus* sp. B-form in the lumen Maly Regiel Mt. 1. Sample INGJ222P1b, polished surface. F, perpendicular section. Matrix is bioturbated. Maly Regiel Mt. 2. Sample INGJ222P4, polished surface. G, sub-perpendicular section. Complex and thick wall. The white arrow shows broken edge of a test. The black arrow shows stylolitic contacts between *Discocyclus* tests. Hruby Regiel Mt. 3. Sample INGJ222P18c, thin section.

lumen, less often in the opposite direction, or perpendicular to the burrow axis (Figs 5E, 6A,B). Some of the *Discocyclus* and *Nummulites* tests display microborings (Fig. 6C). Burrow lumen is filled with material identical with surrounding sediment. Locally, fragments of *Ditrupa* (Polychaeta) tubes, bivalve shell fragments, coralline algae echinoid spines and small lithoclasts are incorporated in the wall (Table 1, Fig. 6D). The bioclasts in the wall form a single layer (Fig. 5A,E). Rarely, more complex wall composed of more than one layer can be seen (Fig. 5G). Many apparently double-layered walls resulted from longitudinal intersection close to the wall. At the locality Staników Gully, numerous very short and incomplete specimens of *N. eocenica* can be found. They are the same as the 'nest-type' distinguished by Roniewicz (1970).

In some specimens, edges of *Discocyclus* tests on the external side of the burrow are broken in a characteristic way. The broken out tips of a few adjacent tests are deflected in the same direction (Fig. 5C,G). In one inclined specimen, *Discocyclus* tests show sigmoidal

curvatures, which are consequently oriented up the burrow on the outer side and down the burrow in the inner side (Fig. 5C,G).

The composition and structure of wall is variable, which allows distinguishing three morphotypes of *N. eocenica* Hölder, 1989 in the Tatra Mountains i.e. the morphotypes A, B and C (Fig. 4, Table 1).

Morphotype A

The wall is built of *Discocyclus pratti* and *Discocyclus fortisi*, which have a characteristic fusiform cross-section of the tests with reduced thickness at the margins (Figs 4, 5A–G). Such a shape creates a possibility to build the wall with shingled tests, which closely fit to each other (Fig. 5C,D,G). Stylolitic contacts between *Discocyclus* tests are common (Fig. 5G). Most of the tests dip towards the lumen, forming imbricated pattern in the longitudinal cross-section (Fig. 5A,E). For instance, in the specimen INGUJ222P18c (Fig. 5G), about 150 tests of macrospherical *Discocyclus* of almost the same size, 11–13 mm in diameter,

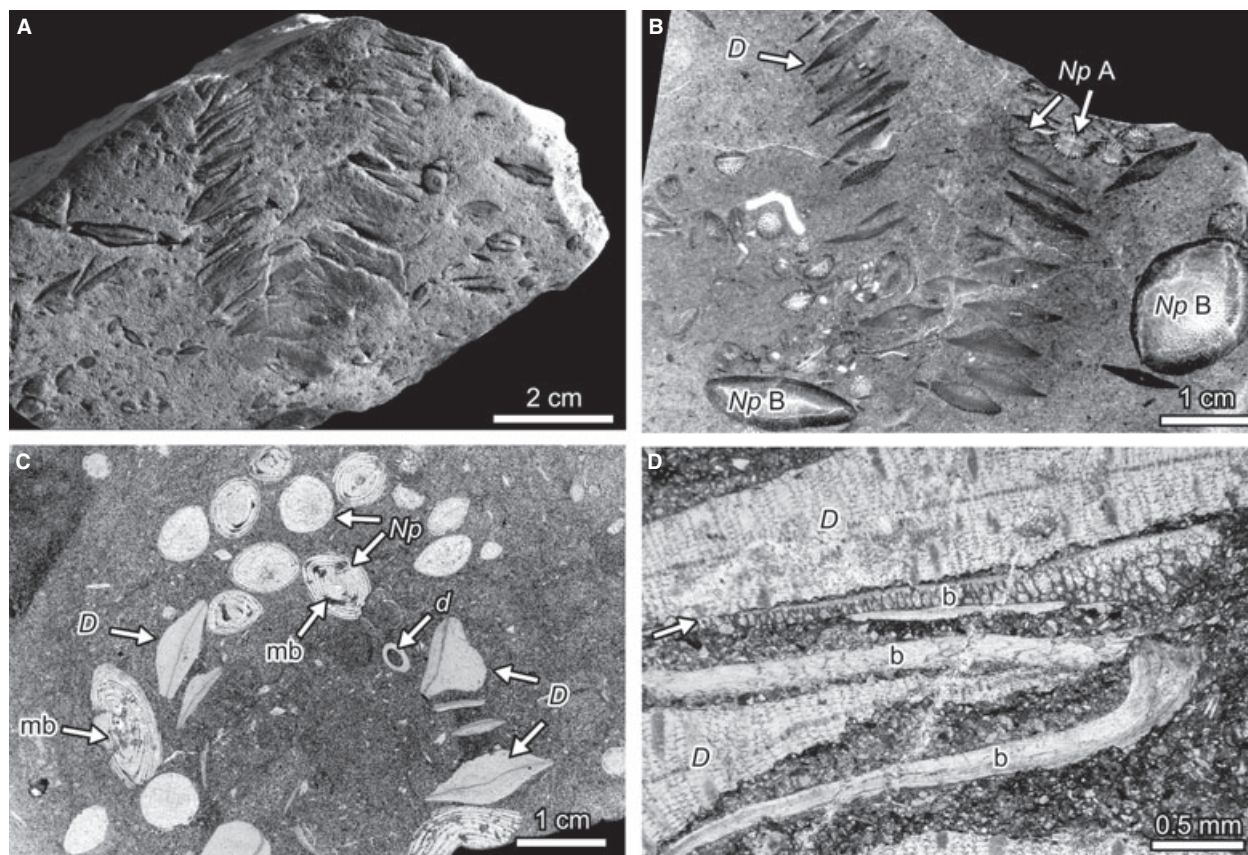


Fig. 6. *Nummipera eocenica* Hölder, 1989, morphotype B. Walls built of the fusiform *Discocyclus* sp. and the robust *Nummulites perforatus* tests. A, sub-longitudinal section. Hruby Regiel Mt. 2. Sample INGUJ222P10a. B, sub-longitudinal section. Walls dominated by *Discocyclus* (D) with single *Nummulites perforatus*, form A (Np A). *Nummulites perforatus*, form B (Np B) in the surrounding. Hruby Regiel Mt. 3. Sample INGUJ222P13. C, perpendicular section. *Discocyclus* (D), *Nummulites perforatus* (Np), fragments of *Ditrupa* (d). See microborings in some tests (mb). Hruby Regiel Mt. 3. Sample INGUJ222P12e, thin section. D, wall fragment. *Discocyclus* tests (D) and fragments of bivalve shells (b). Note the stylolitic contacts of some margins of the *Discocyclus* tests (arrow). Hruby Regiel Mt. 2. Sample INGUJ222P10c, thin section.

2.5–3.2 mm thick, with the T/D ratio 0.2–0.26, form such a pattern. Inside the lumen, the bioclasts are absent or very rare. The morphotype A was found at the localities Mały Regiel Mt. 1 and 2, and the Hruby Regiel Mt. 1, 2 and 3 (Table 1; Figs 1–3).

Morphotype B

The wall is built of the mostly fusiform *Discocyclus* sp. and the ovate *Nummulites perforatus* tests, less frequently of small tests of *Nummulites* sp., and rarely of *Ditrupa* tubes, bivalve shell fragments and lithoclasts (Figs 4, 6A–D). *Nummulites perforatus* is represented mostly by the megalospherical forms with thick, globular tests, which are 5–6 mm in diameter and 2–3 mm thick (Fig. 6A). The average T/D ratio varies between 0.4 and 0.6. The shape of the tests does not permit to build a well-constructed wall as in the morphotype A (Fig. 6B,C). The tests dip towards or outside the lumen (Fig. 6A,B). Inside the lumen, the bioclasts are very rare or absent (Fig. 6B,C). The morphotype B occurs at the localities Staników Gully, Hruby Regiel Mt. 1, 2 and 3 (Table 1; Figs 1–3).

Morphotype C

The wall is built almost exclusively of saddle-shape tests of *Discocyclus ephippium* and less frequent flat and thin *Discocyclus sella* tests, which are 9–11 mm in diameter, 0.8–1.1 mm thick, with the average T/D ratio 0.1–0.1 (Figs 4, 7A–F). In addition, single tests of *Nummulites perforatus* and small *Nummulites* sp. are involved in the wall (Fig. 7E,F). The orientation of the saddle-shape tests of *Discocyclus* within the wall is various (Figs 4, 7B–F). The wall is relatively loosely packed (Fig. 6A,B). The filling of burrow lumen is reach in bioclasts of *Discocyclus sella*, *Nummulites perforatus*, *Nummulites puschi* and other small *Nummulites* sp. (Fig. 7E,F). In the surrounding deposit, very close to *N. eocenica*, *Discocyclus* tests are rare, but at the distance of 2 and more centimetres, the surrounding sediment is rich in *Discocyclus* and *Nummulites* tests (Fig. 7B,C). The morphotype C was found both in the *Nummulites-Discocyclus* bioclastic packstones and *Discocyclus* rudstones at the localities Strążyska Valley, Spadowiec Valley, Pod Capkami Quarry and the Chłabówka Stream (Table 1; Fig. 1).

Discussion

Origin and trace maker

Nummipera is considered as: (1) a shelter burrow crustaceans, probably crabs, which reinforced their

wall with bioclasts (Roniewicz 1970; Olempska 1973); (2) an armoured burrow produced by polychaetes (Hölder 1989); (3) an product of biological bulldozing by a burrowing organism (Beavington-Penney *et al.* 2005, 2006); or (4) storm infilling of a burrow (Beavington-Penney *et al.* 2005, 2006).

Roniewicz (1969) suggested that the arrangement of tests is a by-product of burrowing reworking of sediment, similarly to the bulldozing effect (*sensu* Thayer 1979) invoked by Beavington-Penney *et al.* (2006). However, the evident selection of tests proves the constructional action of the trace maker. The selection and concentration of tests in the wall is also against the interpretation of *Nummipera* as the product of storm infilling of burrows (tubular tempestites *sensu* Wanless *et al.* 1987; Tedesco & Wanless 1991) proposed by Beavington-Penney *et al.* (2006). The comparison of the wall content in the morphotype B to the surrounding sediments shows that the trace maker preferred fusiform tests of *Discocyclus* than the robust *Nummulites* tests, however, did not avoid completely of the latter (Table 1). In the overlying *Discocyclus* floatstones, only the fusiform tests of *Discocyclus* have been used for construction of the wall (morphotype A; Figs 4, 5). Here, the availability of the proper material for construction of well-constructed wall was the best and this promoted the abundance of the burrows.

The determination of trace maker is problematic. The common fossil crustacean burrow produced by decapods, including crabs, such as *Thalassinoides*, or *Psilonichnus* (e.g. Frey *et al.* 1984), are not reinforced by bioclasts. Marjanac & Marjanac (2007) referred a burrows included in *Nummipera* in this study to *Ophiomorpha*. *Ophiomorpha*, produced mainly by decapods, is characterized by a granulated wall, but the granules are composed always of muddy sand (Frey *et al.* 1978).

The only trace maker analogue among crustaceans can be referred to alpheid shrimps, which burrows are commonly cohabitated by gobiid fishes. They can be found in warm seas from the intertidal zone up to the depth of 50 m (Karplus 1987). Their branched burrow system displays apertural segments, mostly 20–30 mm in diameter, mainly oblique which are reinforcement against collapsing only in the roof by shells and coral debris; also completely reinforced part of burrows below vertical openings on a mound or in a funnel are present (Karplus *et al.* 1974; Karplus 1987). The inner margin of such a burrow is rough, like in *Nummipera*. Also the asymmetric reinforcement in oblique burrows is similar, but the material in wall of the alpheid burrows is poorly selected. Moreover, the prolongation of *Nummipera* in an open burrow is not seen.

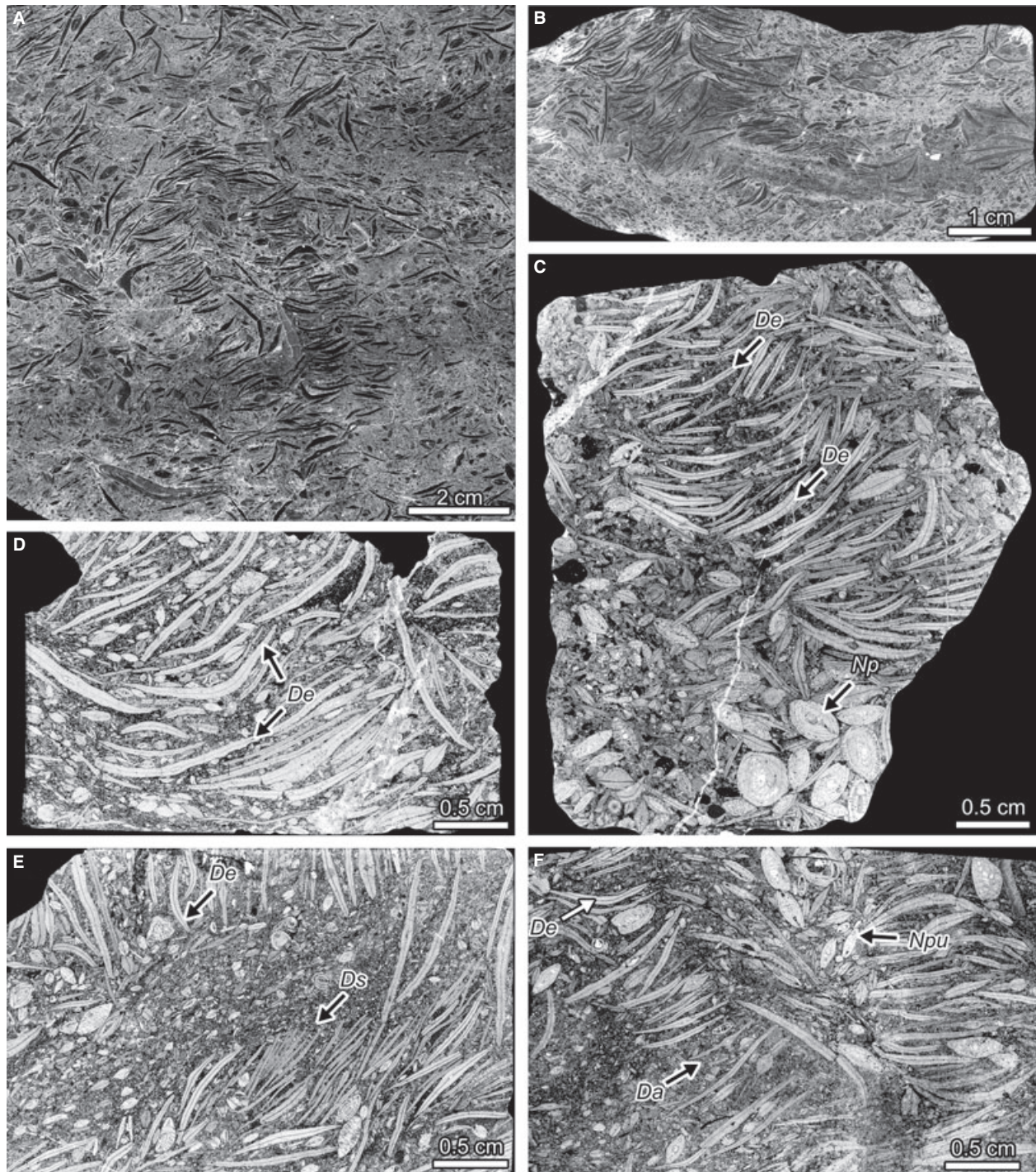


Fig. 7. *Nummipera eocenica* Hölder, 1989; morphotype C. Walls built almost exclusively of the saddle-shape tests of *Discocyclina ephippium* and flat and thin *Discocyclina sella* tests. A, oblique section. Spadowiec Valley. Sample INGUJ222P1a. B, longitudinal section. The lumen filling is rich in bioclasts of *Discocyclina sella*, *Discocyclina augustae*, *Discocyclina* sp., *Nummulites perforatus*, *Nummulites puschi* juvenile forms and other small *Nummulites* sp. Pod Capkami Quarry. Sample INGUJ222P22a. C, longitudinal section. Wall of *Nummipera eocenica* Hölder, 1989 built of *Discocyclina ephippium* tests (De). In the surrounding, numerous tests of *Nummulites perforatus* (Np) and *Nummulites* sp. Strążyska Valley. Sample INGUJ222P20, thin section. D, longitudinal section. Wall of *Nummipera eocenica* Hölder, 1989 composed of *Discocyclina ephippium* tests (De). Pod Capkami Quarry. Sample INGUJ222P22c, thin section. E, Longitudinal section. Wall of *Nummipera eocenica* Hölder, 1989 composed of tests of *Discocyclina ephippium* (De) and *Discocyclina sella* (Ds), Pod Capkami Quarry. Sample INGUJ222P22b, thin section. F, Longitudinal section. In the wall of *Nummipera eocenica* Hölder, 1989, *Discocyclina ephippium* (De), *Discocyclina augustae* (Da), and *Nummulites puschi* (Npu) tests. Spadowiec Valley. Sample INGUJ222P21b, thin section.

Hölder (1989) and Demircan *et al.* (2010) considered polychaetes as the trace makers by the analogy to *Diopatra cuprea* (family Onuphidae), known from warm and temperate shelf seas, which reinforces a part of its vertical, tubular burrow standing above sediment surface (tube caps) by variable bioclasts glued by mucus. The tube caps serve as food traps, camouflage, barrier for sediment inflow into the burrow, and a tool in water exchange (see Skoog *et al.* 1994 for review). The reinforced part of the burrow can be buried by sediment and a new segment of burrow above the surface can be reinforced (Myers 1972). This polychaete is considered as an analogue of the trace maker of the trace fossil *Diopatrachus* Kern, 1978 (see also Gibert 1996). Extrapolation of such interpretation to *Nummipera* is problematic. *Nummipera* does not display any prolongation into a thin-lined tube, which is characteristic of the *Diopatra* burrows. Similar doubts have been raised by Gibert (1996), who compared some *Nummipera* from the Ebro Basin (Spain) to *Diopatrachus oldingi*, described by him from the Middle Jurassic of England. Moreover, the inner burrow margin in *Diopatra* is smooth and lined with finer material (e.g. Myers 1972), while it is rough, without such a lining in *Nummipera*. The coarser material in the *Diopatra* tube caps is poorly sorted, while *Nummipera* displays the sorting. Size is not a crucial parameter in ichnology (Bertling *et al.* 2006), but it is worthy to note that the reinforced part of the burrow in *Diopatra*, is shorter (mostly 20–30 mm; Myers 1972) and its lumen more than two times narrower (5–8 mm; Barwis 1985; Bromley 1996) than the lumen of *Nummipera* (16–20 mm). Other onuphiid polychaetes, such as *Diopatra obliqua*, also line their burrows with bioclasts mainly mollusc shells, displaying differences in size, density and shell arrangements (Kern 1978). However, data derived from the literature are insufficient for assessment of these *Diopatra* species as the potential trace maker of *Nummipera*. The same concerns polychaetes of the Oweniidae family, which some species can build tubes incorporating shells (Gibert 1996; for review). Polychaetes of the Terebellidae tubes can be referred rather to the ichnogenus *Lepidenteron* Fritsch, 1878; which is lined with remains of fishes, plants and other bioclasts, which are generally arranged parallel to the burrow course (Sühr 1988).

The selection of bioclasts and their constructional arrangement prove that *N. eocenica* is a burrow; however, the trace maker is not satisfactorily determined. The discussion above shows that neither the oweniid polychaetes nor alpheid shrimps can be considered as the definite trace makers. The trace maker paid a lot of effort in construction of resistant, well-constructed wall. This suggests that the wall was a protection

(Roniewicz 1970) for a domicinal organism, rather against predators, for instance fishes, or burrowing animals. The latter could damage the domiciles. Their activity is seen as bioturbational structures in some specimens (Fig. 5F). The wall was probably also a protection against collapsing of the burrow. It is not clear how the wall was constructed: by adding bioclasts around the burrow on the surface or by pushing of them into the sediment from inside. The broken edges of tests on the outer side of the wall suggest compression. Also the sigmoidal bending can be explained by compression by the trace maker from the inside of the burrow (Fig. 5C,G). Even if the trace maker pushed the tests in sediment, this took place rather in the upper part of burrow. In such a case, it is expected that the burrow is open from the lower side.

Palaeoenvironmental implications

The occurrences of *N. eocenica* in the eastern part of the study area (localities 7–10 in Fig. 1) is restricted to the abrupt transition from the *Nummulites-Discocyclus* bioclastic packstones of proximal middle ramp setting to the *Discocyclus* rudstones of middle to distal middle ramp. Thus, this trace fossil is clearly associated with a quick facies change during general progressive deepening. The boundary between the changing facies is sharp and marked by a change in the content of the benthic foraminifera assemblage, foremost *Discocyclus*, along with textural features of the sediment (Fig. 2).

Discocyclus is considered as a good indicator of energy regime, light intensity and trophic conditions. Usually, it occurs in the deeper, distal middle ramp (Vennin *et al.* 2003) or in the outer ramp (Papazzoni 1994; Racey 1994; Beavington-Penney *et al.* 2006 and references therein). It is generally accepted that *Discocyclus* test morphology is environmentally dependant, mainly because of adaptation to hosted symbiont algae (Hottinger 1983, 1997; Hallock & Glenn 1986; Ferrandez-Cañadell 1998; Hallock 1999; Hohenegger 2006). The saddle tests shape is interpreted as an adaptation to algal symbiosis, which allows absorption of sunlight illuminating the surface of the test at the different angle in deeper settings. These settings were inhabited by very flat *Discocyclus*, which were perfectly adapted to dim waters. In contrast, the shallow photic zones were inhabited by large foraminifers, whose tests were predominantly ovate (Hallock & Glenn 1986; Hallock 1999; Beavington-Penney *et al.* 2006; Zamagni *et al.* 2008). Low-diverse foraminifera assemblage of *Discocyclus* facies, dominated by K-strategic forms, indicates extremely oligotrophic conditions (Hottinger 1983; Racey 2001; Čosović *et al.* 2004; Bassi 2005). In the eastern part of the study area,

the *Nummulites-Discocyclus* bioclastic packstones and *Discocyclus* rudstones, *Discocyclus* display a trend of flattening of the tests and increase in abundance. The *Nummulites-Discocyclus* bioclastic packstones contain mainly ovate tests typical of the middle ramp setting. The numerous saddle-shaped tests in the lower part of the overlying *Discocyclus* rudstones point to a deeper settings. Further deepening is marked by the predominance of the very thin and flat *Discocyclus* tests in the uppermost part of the *Discocyclus* rudstones. The vertical trend points to a gradual deepening and lowering of energy, which is consistent with the generally transgressive trend in the Nummulitic Eocene.

The foraminifera assemblage of the *Discocyclus* rudstones is paraautochthonous in the outer ramp setting (Papazzoni 1994; Racey 1994, 2001). The low degree of tests abrasion and the scarce occurrence of micrite is an effect of intense winnowing below the storm wave base (Aigner 1982), which leads to concentrations of *Discocyclus* tests. Thus, the test-supported fabric seems to be an effect of winnowing, slower sedimentation rate and sediment starvation (Aigner 1982; Bassi 2005). The starvation is marked by a 20- to 30-cm-thick glauconite marl layer at the top of the *Discocyclus* rudstones (Figs 2, 3). This layer is regarded as a maximum flooding surface (Bartholdy *et al.* 1999).

In the western part of the study area, the *Discocyclus* floatstones contain mainly fusiform tests indicating a photic zone which was shallower and higher energetic than that interpreted for the discussed above *Discocyclus* rudstones. The foraminifera assemblage of the *Discocyclus* floatstones seems to be autochthonous. This is proven by the ratio of A to B forms and the floatstone texture (cf. Aigner 1985; Racey 2001).

Taking into account the above considerations, it can be concluded that in the eastern part of the study area the facies suite the *Nummulites-Discocyclus* bioclastic packstones-*Discocyclus* rudstones indicates lowering energy and deepening. The morphotype C of *N. eocenica* occurs in the transition between these facies (Fig. 3). *Nummipera eocenica* is less frequent than in the western part, where shallow-water facies dominate and *N. eocenica* is represented by the morphotypes A and B (Fig. 3). In the section Hruby Regiel Mt. 2, the morphotype B occurs rarely in the lowermost part of the *Discocyclus* floatstones. It is replaced by abundant morphotype A up the section.

Judging from the distribution of *N. eocenica*, it is possible to conclude that the morphotypes can be ordered according to the diminishing in energy and increasing in depth in succession of the morphotype B and A. The morphotype C, which occurs in the eastern part of the study area, represents even lower

energy (deeper) environment than morphotype A. Their occurrence at the time of general deepening and close to the maximum flooding surface can be related to the stabilization of the substrate. During marine flooding the seafloor is stabilized due to significant drop of sedimentation rate and drop of energy. In such conditions, the wall can be constructed and maintained. The maximum of abundance in the *Discocyclus* floatstones shows that this was an optimal facies for *Nummipera* trace maker, most probably because of availability of the proper building material.

Conclusions

1. *Nummipera eocenica* Hölder, 1989 is a fossil simple burrow in Eocene nummulitic limestones, which wall is built of large foraminifera tests, mainly *Discocyclus* and *Nummulites*. The only recent analogues can be related to the tube caps of the Oweniid polychaete *Diopatra cuprea* and to the upper part of some alpheid shrimp burrows, which, however, differ in many important aspects from *N. eocenica*.
2. Three morphotypes of *N. eocenica*, A, B and C are distinguished on the basis of the wall. Well-packed fusiform *Discocyclus* tests dominate in the morphotype A, more loosely packed *Discocyclus* and robust *Nummulites* are typical in the morphotype B, while the saddle and flat *Discocyclus* tests characterize the morphotype C.
3. In the Tatra Mountains, *N. eocenica* occurs in a single stratigraphical horizon on a transition of facies related to the maximum flooding surface during a general deepening. The morphotypes are facies specific. The succession of the morphotypes B and A expresses decrease in energy and deepening. The morphotype C represents even lower energy and deeper environment than the morphotype A. The trace fossils originated during stabilization of bottom, which enabled construction of burrows with walls for protection, probably against predators, burrowing organisms and from collapse. The trace fossils are most abundant in *Discocyclus* floatstones, which supplied the best tests for construction of well-constructed wall.

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