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Limpet-shaped gastropods of the genus *Diodora* (Vetigastropoda: Fissurellidae) from the Middle Miocene of Western Ukraine

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ABSTRACT:

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The genus *Diodora* Gray, 1821 is widely represented in the Middle Miocene of the Central Paratethys with specimens usually attributed to *D. graeca* (Linnaeus, 1758) or *D. italica* (Defrance, 1820), well-known recent species of the Atlantic / Mediterranean Basin. In samples from the Upper Badenian of Western Ukraine we found two clusters of *Diodora* specimens, showing a similarity with these species, but a review of shell diagnostic characters using a statistical approach has revealed their clear conchological separateness. The first species from Varovtsi and Horodok is attributed herein to *D. nodosa* (Eichwald, 1830), whereas the second species from Maksymivka is described as a new species, *D. stalennuyi* sp. nov. We consider that these molluscs inhabited the Polish-Ukrainian marginal part of the Late Badenian Basin. Detailed descriptions of the protoconch and teleoconch morphology of the taxa involved, including SEM images, are presented.

Key words: Fissurellidae; Diodora; Middle Miocene; Badenian; Western Ukraine.

INTRODUCTION

The cosmopolitan family Fissurellidae Fleming, 1822 (Mollusca: Vetigastropoda), represented by limpet-shaped gastropods commonly possessing a hole, slit or notch in their bilaterally symmetrical shell, shows a long fossil record, from the Triassic onwards (Knight *et al.* 1960; Aktipis *et al.* 2011). Subfamiliar classifications of the Fissurellidae have varied, with studies emphasizing different morphological characters, but classifications based on features of the shell orifice or fissure, and radular structures recognize three subfamilies: Fissurellinae, Emarginulinae and Diodorinae (Knight *et al.* 1960; Hickman 1980, 1981; Aktipis *et al.* 2011). Members of the Diodorinae and Fissurellinae can be differentiated by radular characters and by the presence of a central orifice bounded by a posteriorly truncated callus in the Diodorinae, and the presence of a rounded callus on the underside of the shell surrounding the anal orifice in the Fissurellinae.

The genus *Diodora* Gray, 1821 is well represented in the European Neogene (De Gregorio 1884; Sacco 1897; Cerulli-Irelli 1916; Cossmann and Peyrot 1917;

Text-fig. 1. Location map of the study area. 1 – Varovtsi; 2 – Horodok; 3 – Maksymivka quarry; 4 – Zhukovtse

Glibert 1949, 1952; Malatesta 1960, 1974; Ruggieri and Greco 1965; Cuerda Barceló 1987; da Silva 1990, 2001; Cavallo and Repetto 1992; Borghi and Vecchi 1998; Landau *et al.* 2003) and in the Miocene of the Central Paratethys (Eichwald 1830, 1853; Hörnes 1856; Friedberg 1928; Davidaschvili 1937; Csepreghy-Meznerics 1954; Strausz 1954, 1955, 1966; Korobkov 1955; Kojumdgieva and Strachimirov 1960; Florei 1961; Bielecka 1967; Zelinskaya *et al.* 1968; Rado and Mutiu 1970; Bałuk 1975, 2006; Krach 1981; Il'ina 1993). The specimens of *Diodora* are usually determined as the well known recent Mediterranean and Atlantic *D. graeca* (Linnaeus, 1758) and the Mediterranean *D. italica* (Defrance, 1820), in spite of the restricted water exchange between the Central Paratethys Sea and the Mediterranean Sea in the Middle Miocene (e.g., Harzhauser and Piller 2007) and of the great variability of the fossil material. The wide range of intraspecific shell variability of *D. graeca* and *D. italica* is well-known both in modern and fossil representatives (Bucquoy *et al.* 1882–1886; Cerulli-Irelli 1916).

We have found several specimens of *Diodora* from localities in the Middle Miocene (Badenian) of Central Paratethys (Ukraine) that differ from the widespread recent Mediterranean and Atlantic species *D. graeca* and *D. italica*, and their determination is the aim of the present work.

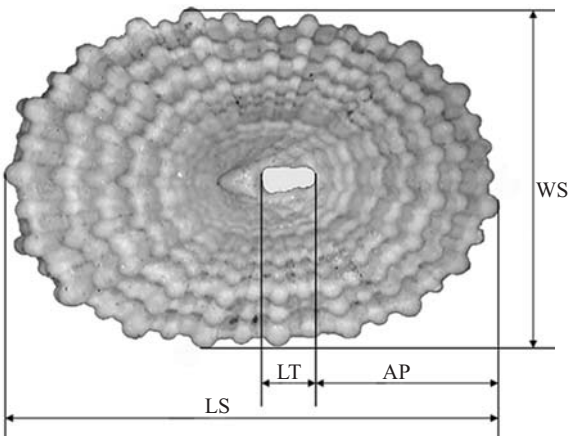
MATERIAL AND METHODS

The material described in this study derives from the Middle Miocene (Badenian) deposits in Western Ukraine (Text-fig. 1).

The site of Varovtsi, along the eastern slopes of the Medobory Hills in Ukraine, Khmielnitsky Region, is represented by an exposure on the right bank of the river Smotrych (49°20'06"N 26°34'29"E), Podil'yan Massif, north-eastern part of the Halicz-Volhynian Depression (Studencka and Dulai 2010). This deposit is Late Badenian in age, representing the last interval with fully marine conditions in the history of the Central Paratethys (~13.6 to 12.7 Ma; see Kováč *et al.* 2007). All the material studied originates from fossiliferous, homogeneous, weakly-cemented, medium to fine-grained, white quartz sandstone deposits that can reach several meters in thickness (Scarponi *et al.* 2016).

The site of Horodok is represented by an exposure at the periphery of the Horodok settlement (49°10'07"N 26°35'16"E), on the opposite side of a road surrounding a small lake. All the studied material comes from the lowermost part of a >10 m high cliff of quartzose, weakly-cemented sandstones. It was reported by Laskarew (1914) and Scarponi *et al.* (2016).

The Maksymivka Quarry near Ternopil (Ukraine) is well known in the literature for its peculiar Middle Miocene (Badenian) coralgal facies and its fauna (Radwański *et al.* 2006; Studencka and Jasionowski 2011; Górka *et al.* 2012; Forli *et al.* 2015). It embraces an area of several square kilometres (Radwański *et al.* 2006, fig. 3). The reef exposed in this quarry is a member of a unique reef structure (almost 300 km long) formed within the Paratethyan realm, and distributed widely in the north-eastern and eastern borders of the Carpathian Foredeep Basin in Western Ukraine, Moldova and north-east Romania (Górka *et al.* 2012, fig. 1). The coralgal facies at Maksymivka is characterized by coralgal buildups of variable size, molluscs



Text-fig. 2. Morphological terms used for the shell description. LS – length of shell; LT – length of trema; AP – anterior position; WS – width of shell

(bivalves and gastropods), crabs, foraminifera, annelids, bryozoans and echinoderms. Almost all of the originally aragonitic shells were dissolved as a result of postsedimentary diagenesis and the fossils are now preserved in the form of moulds and/or imprints.

The material from Varovtsi and Horodok was collected by one of the authors (BD) from 2010 to 2014, by means of field sampling with the collection of fresh material and large amounts of bulk sediment. Bulk samples were sieved (mesh diameters 0.5, 1.0, 2.0 mm), and the material retained in the 2.0 mm fractions was then examined for small *Diodora* shells or their fragments using a stereomicroscope.

The material from Maksymivka was collected by Alexander Stalennuy (Ternopil, Ukraine) from 2010 to 2014, and by one of the authors (BD) during field work in 2014, by means of field sampling within the reef structure, paying particular attention to prevent crushing of the fossils.

Apart from fossil material, 16 shells of *D. graeca* from the Mediterranean Sea (Genova and Arenzano) and 8 specimens of *D. italica* from the Adriatic Sea have been studied for comparison. Additionally we have examined the photographs of two type specimens of *Patella graeca* Linnaeus, 1758 deposited in the Linnaean Collection, London (Box number: LSL.608 of The Linnaean Collections site: http://linnean-online.org/17191/). The range and limits of the variability of the measured parameters are discussed and reported below. A descriptive statistics was performed using PAST ver. 2.17 c (Hammer *et al*. 2001).

The digital images were obtained using a Motic SMZ-140 Microscope with the software Motic Images Plus. All the specimens are housed in the private collections of the first two authors and in public institutions (see Abbreviations). The SEM images were obtained in the Institute of Geological Sciences, National Academy of Sciences of the Ukraine (Kiev, Ukraine). Shells were mounted on stubs, sputter-coated with gold and then documented using a JSM-6490 Scanning Electron Microscope. All specimens used for SEM investigation are housed in the Institute of Geological Sciences, National Academy of Sciences of the Ukraine (Kiev, Ukraine).

ABBREVIATIONS

BD – Private collection of B. Dell'Angelo, Genova, Italy;

IGS NASU – Institute of Geological Sciences, National Academy of Sciences of the Ukraine, Kiev, Ukraine;

MS – Private collection of M. Sosso, Genova, Italy;

MSNG – Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy;

MZB – Museo di Zoologia dell'Università di Bologna, Bologna, Italy;

TOKM – Ternopil Museum of Regional Studies (Тернопільський обласний краєзнавчий музей), Ternopil, Ukraine;

ZISP – Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

Morphological terms used in text for shell description (see Text-fig. 2):

AA – apical angle;

AP – anterior position, i.e., distance of trema from frontal edge;

DP – maximal diameter of the protoconch;

HS – height of shell;

LS – length of shell;

LT – length of trema;

RR – number of primary radial ribs;

WS – width of shell.

The measurements are in millimetres (mm) and the apical angle is in degrees.

SYSTEMATIC PALAEONTOLOGY

The family Fissurellidae Fleming, 1822 is usually sub-divided into two subfamilies (Fissurellinae and Emarginulinae) based on the anatomy and shell characters. According to this classification, the genus *Diodora* is assigned to the Emarginulinae (e.g., Sasaki 1998). In other classifications, the Diodorinae are sometimes separated from the Emarginulinae (e.g.,

Knight *et al.* 1960); although no prominent difference is found at least in the shell and radular characters, such a distinction has been recently justified by using the DNA analysis approach (Aktipis *et al.* 2011). We follow Bouchet and Rocroi (2005) and accept assignment to the subfamily Diodorinae Odhner, 1932.

Class Gastropoda Cuvier, 1797
Order Vetigastropoda Salvini-Plawen, 1980
Superfamily Fissurelloidea Fleming, 1822
Family Fissurellidae Fleming, 1822
Subfamily Diodorinae Odhner, 1932
Genus *Diodora* Gray, 1821

TYPE SPECIES: *Patella apertura* Montagu, 1803 (= *Patella graeca* Linnaeus, 1758) by monotypy (Rehder 1980). Recent, Eastern Atlantic and Mediterranean Sea.

Diodora nodosa (Eichwald, 1830)
(Text-figs 3 and 4A–C)

1830. *Fissurella nodosa* Eichwald, p. 213.
1853. *Fissurella nodosa* Eichwald, p. 138, pl. 6, fig. 16.
1928. *Fissurella graeca* (non Linnaeus); Friedberg, p. 527, pl. 34, figs 3–5.
1955. *Diodora* (*Diodora*) *graeca* (non Linnaeus) var.; Korobkov, pl. 2, figs 5, 6 (figures from Friedberg 1928, pl. 34, figs 3, 5).
1968. *Diodora graeca* (non Linnaeus); Zelinskaya *et al.*, pl. 27, figs 3, 4 (figures from Friedberg 1928, pl. 34, figs 3, 5).
part 1975. *Diodora* (*Diodora*) *graeca* (non Linnaeus); Bałuk, p. 26, pl. 1, figs 12, 13 (non fig. 14 = *Diodora stalennuyi* sp. nov.).
1981. *Diodora* (*Diodora*) *graeca* (non Linnaeus); Krach, p. 41, pl. 12, figs 5–8 (non vidi, fide Bałuk, 2006).
1993 *Diodora graeca* (non Linnaeus); Il'ina, pl. 1, figs 5, 6.
part 2006. *Diodora graeca* (non Linnaeus); Bałuk, p. 181, pl. 1, fig. 3 (non fig. 4 = *Diodora stalennuyi* sp. nov.).

TYPE MATERIAL: Not traced, repository unknown.

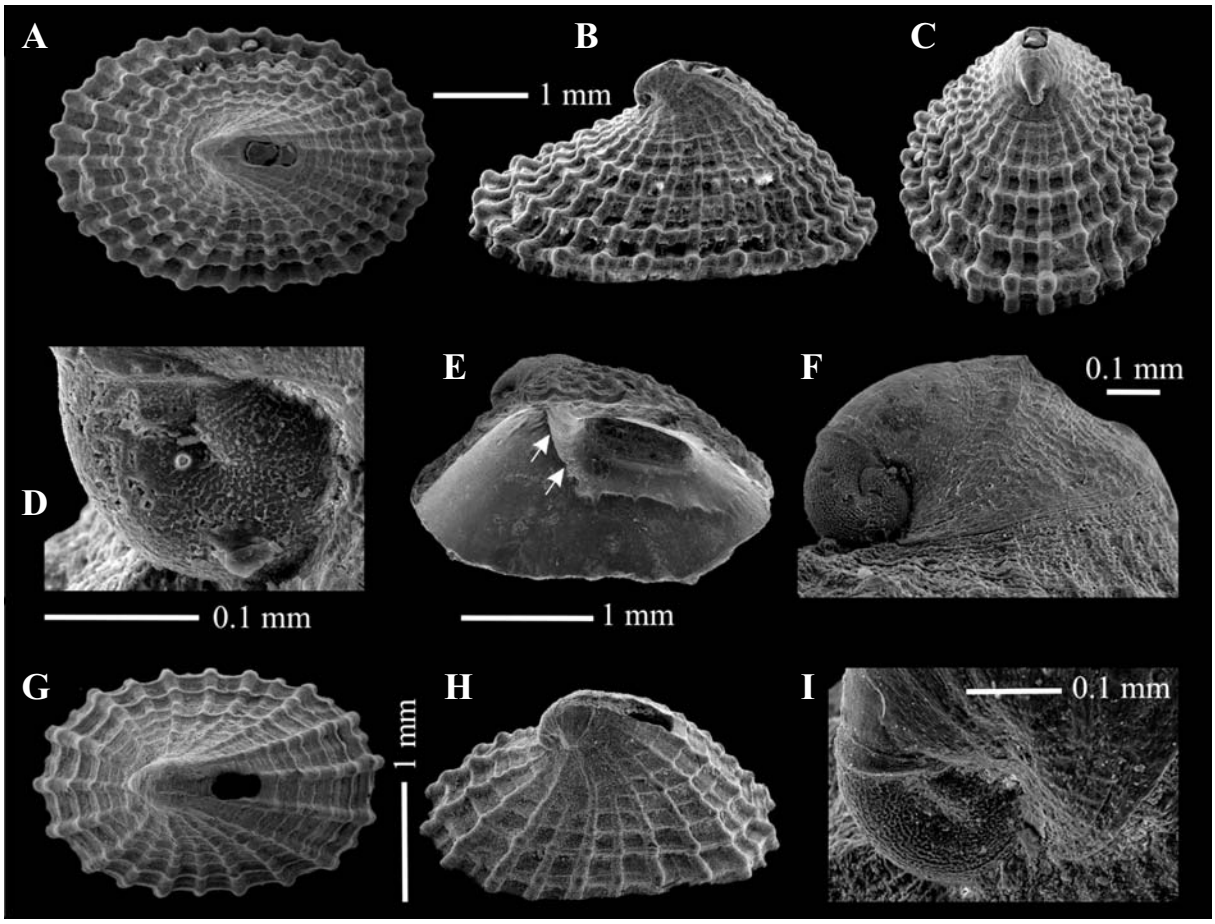
TYPE LOCALITY: Zhukovtse settlement, Western Ukraine.

MATERIAL EXAMINED: Varovtsi: 34 complete shells and 10 fragments (maximum length 8 mm); Horodok: 2 complete shells and 3 fragments (maximum length 8 mm) (see Table 1 for ranges of parameters and comparison with *D. graeca*).

DESCRIPTION: Shell small, solid, conical, oval to elongated, maximum length 19.29 mm, moderately elevated, with a subcentral or slightly anterior apical aperture. Apical aperture subrectangular to bilobate, with evident remains of protoconch, hook-like, consisting of about one smooth whorl facing posteriorly, present in juvenile shells (with lengths up to 8 mm). Anterior and posterior slopes straight. Teleoconch ornamentation prominent, formed by numerous radial ribs, intersected by concentric growth lines. Radial ribs appearing near the apex, their number amounting from 17 to 23. Later on in ontogeny, secondary and, in adult specimens, also a few tertiary ribs. The differ-

Parameter	*Diodora nodosa*			*Diodora graeca*		
	range	mean	st. dev.	range	mean	st. dev.
LS [mm]	2.59–19.29	6.70	3.59	7.77–20.38	12.90	3.37
WS [mm]	1.62–13.50	4.51	2.46	5.02–12.97	8.20	2.12
HS [mm]	1.15–11.59	3.41	2.04	2.76–6.41	4.86	0.92
AP [mm]	1.05–7.96	2.54	1.38	2.54–7.22	4.35	1.28
LT [mm]	0.37–2.58	0.82	0.43	0.68–1.96	1.29	0.32
AA [°]	65–86	74.04	6.62	79–109	94	9.74
RR	17–24	20	1.67	16–22	18.44	1.36
WS / LS	0.61–0.76	0.67	0.03	0.59–0.67	0.64	0.02
HS / LS	0.39–0.60	0.50	0.05	0.28–0.52	0.38	0.06
AP / LS	0.30–0.43	0.38	0.04	0.28–0.36	0.34	0.02
LT / LS	0.10–0.15	0.12	0.01	0.08–0.11	0.10	0.01
HS / WS	0.55–0.94	0.75	0.08	0.43–0.81	0.61	0.10

Table 1. Ranges and mean values of measured parameters for *Diodora nodosa* (Eichwald, 1830) (34 from Varovtsi and 2 from Horodok) and *Diodora graeca* (Linnaeus, 1758) (16 specimens from the Mediterranean Sea). St. dev. – stands for standard deviation



Text-fig. 3. *Diodora nodosa* (Eichwald, 1830) from the Late Badenian of Varovtsi, Ukraine. A-D – Specimen IGS NASU, B-II-1/2016, apical (A), lateral (right side) (B), posterior (C) views of the same specimen, and the view of the protoconch (D). E, F – Specimen IGS NASU, A-II-2/2016, lateral (right side) view (E), arrows show the callus posteriorly truncated; close-up of the protoconch of the same specimen (F), fine reticulated sculpture on the surface of the embryonic shell and clear demarcation between the protoconch and teleoconch is visible. G-I – Specimen IGS NASU, B-II-5/2016, apical (G), lateral (right side) (H) views of the same specimen, and the view of the protoconch (I)

ence in rib thickness gradually diminishing (from the primary to the tertiary ribs), but the thickness of the secondary ribs practically the same as of the primary ribs in mature specimens. Concentric growth lines, at first fairly thin, gradually becoming thicker. Evident roundish nodes formed at the intersections of both ribbing systems. Shell periphery internally crenulated. Opening internally rimmed by a callus, rounded anteriorly and truncate posteriorly. Protoconch planispiral, paucispiral, consisting of about 0.75–0.80 whorls and having a maximum diameter around 0.20 mm. Lateral pouch weakly constricted, producing a deep sutural line. Outer surface ornamented by reticulated sculpture consisting of numerous irregular axial threads crossed by several more or less regular spiral ribs on the periphery. Boundary between protoconch and teleoconch clearly demarcated by apertural lip of protoconch. Occasionally elements of a reticulate ornamentation having a more or less regular distribution (Text-fig. 3F and I), although usually producing a net with no clear regularity (Text-fig. 3D).

ONTOGENY: Most of the specimens are small (LS < 8 mm), and present evident remains of the protoconch. In the process of shell growth, the number of radial ribs (costae) gradually increases (specimen in Text-fig. 3A is larger than specimen in Text-fig. 3G and accordingly bears considerably more costae). On the other hand, the character of sculpture in all studied specimens remains the same and does not depend on the individual age of the shell. We illustrate the largest specimen found (Text-fig. 4A–C).

REMARKS: Eichwald (1830) described and illustrated the new species *Fissurella nodosa* from Zhukovtse (Ukraine). This species, included by

Bałuk (1975) and Landau *et al*. (2003) in the synonymy of "*Diodora graeca*", has the apical aperture internally rimmed by a callus that is truncate posteriorly (Eichwald 1853, fig. 16d) and therefore can be attributed to the genus *Diodora* (the genus *Fissurella* has a rounded callus, see Knight *et al*. 1960, p. *I*230). For this reason, the taxon *Diodora nodosa* can be considered as valid, whereas "*Fissurella nodosa*" should not be used, because the name is preoccupied by *Fissurella nodosa* (Born, 1778) from the Caribbean. The characters of the material studied from Varovtsi and Horodok agree with the attribution to *Diodora nodosa*.

The Mediterranean / Atlantic recent species *Diodora graeca* (Linnaeus, 1758) (= *Patella apertura* Montagu, 1803) has been reported from the Neogene of many parts of Europe (Sacco 1897; Cerulli-Irelli 1916; Malatesta 1960, 1974; Borghi and Vecchi 1998; Landau *et al*. 2003), and also from the Middle Miocene (Badenian) units of Central Paratethys (Hörnes 1856; Friedberg 1928; Csepreghy-Meznerics 1954; Strausz 1954, 1955, 1966; Korobkov 1955; Kojumdgieva and Strachimirov 1960; Florei 1961; Bielecka 1967; Zelinskaya *et al*. 1968; Rado and Mutiu 1970; Bałuk 1975, 2006; Krach 1981; Il'ina 1993). The shells of *D. graeca* exhibit a wide range of variability, which has resulted in the recognition of a great number of varieties and synonyms (e.g., Sabelli *et al*. 1990, p. 123). However, comparison of shells of extant *D. graeca* from the Mediterranean Sea (Genova and Arenzano) reveals a set of constant differences between the measured parameters of modern individuals and the specimens collected from the Badenian of the Ukraine (Table 2). The studied fossil specimens conform well with the original description, measurements and illustrations provided by Eichwald (1830, 1853). Both the teleoconch and protoconch of modern *Diodora* sp. from the Sea of Japan (e.g., Sasaki 1998) bear the same kind of ornamentation and have similar dimensions as specimens from the Upper Badenian of Western Ukraine.

Diodora nodosa differs from *D. graeca* mainly in the following features:

- the values of the measured parameters and their ratios are quite different, as reported in Table 1, and this justifies the different shapes of the two species. The maximum length of recent *Diodora graeca* is reported as 35 mm by Cossignani and Ardovini (2011), compared to the maximum length of just above 19 mm for *D. nodosa*. The shell of *D. nodosa* is more elevated (maximum height 11.59 mm *vs*. 6.41 mm in *D. graeca*), and the apical angle shows a smaller range (65–86° *vs*. 79–109° in *D. graeca*). The comparison of HS to LS and HS/WS to LS is shown in Text-figs 5 and 6. Multivariate analysis also proves the differences (MANOVA, Wilks' lambda is 0.28, df1 is 4, df2 is 50; $F = 31.63$; $p < 0.0001$);
- the ornamentation of the shell is different, with evident roundish nodes formed at the intersections of both ribbing systems (radial ribs and concentric growth lines) in *D. nodosa*, whereas the intersections are imbricated in *D. graeca*;
- the thickness of the secondary (and tertiary in adult specimens) ribs tends to reach the same size of the primary ones, therefore they are practically indistinguishable near the periphery of the shell in *D. nodosa*, whereas in *D. graeca* the ribs are always well discernible.

We have reported all the bibliographical references of *Diodora* species regarding the areas of Ukraine and Poland (considering that many old reports are related to the "Volhynia-Podil'ya" area, which now is partly included in the Ukraine), and almost all the specimens identified as *Diodora graeca*, based mainly on the available descriptions and illustrations where the features of the new species are well evident, can be attributed to *Diodora nodosa*. It is not the aim of this work to check the records of *D. graeca* for the remaining part of the Central Paratethys and for the Neogene of Europe, to verify the true distribution of this species or a possible interaction with *D. nodosa*.

Another species reported from the Miocene of the Paratethys is *Diodora ornata* (Reuss, 1860), which differs from *D. nodosa* in the presence of a selenizone, the apex being more deflected posteriorly and a more convex posterior slope. This species was originally described within the genus *Cemoria* Leach, 1852 (= *Puncturella* Lowe, 1827), and attributed to the genus *Diodora* by Bałuk (1975) based on the lack of a shelly plate on the inner side and the occurrence of a typical callus near the trema.

DISTRIBUTION: Middle Miocene: Central Paratethys (Upper Badenian): Poland and Ukraine (this paper); Eastern Parathethys (Il'ina 1993).

Diodora stalennuyi sp. nov.
(Text-fig. 4G–O)

part 1928. *Fissurella italica* (non Defrance); Friedberg, p. 527, pl. 34, fig. 7 (non fig. 6).
1937. *Diodora* (*Fissurella*) *italica* (non Defrance); Davidaschvili, p. 540, pl. 1, fig. 1.

1955. *Fissurella* (*Fissurella*) *italica* (non Defrance); Korobkov, pl. 2, fig. 4 (figures from Friedberg 1928, pl. 34, fig. 7).
1967. *Fissurella graeca* (non Linnaeus); Bielecka, p. 140, pl. 5, fig. 4.
1968. *Fissurella italica* (non Defrance); Zelinskaya *et al*., pl. 27, fig. 2 (figures from Friedberg 1928, pl. 34, fig. 7).
part 1975. *Diodora* (*Diodora*) *graeca* (non Linnaeus); Bałuk, p. 26, pl. 1, fig. 14 (non figs 12, 13 = *Diodora nodosa*).
part 2006. *Diodora graeca* (non Linnaeus); Bałuk, p. 181, pl. 1, fig 4 (non fig. 3 = *Diodora nodosa*).

TYPE MATERIAL: Holotype and 10 paratypes (Table 2).

OTHER MATERIAL: Maksymivka: 3 complete shells (see Table 3 for ranges of measured parameters for the type material and additional material of *Diodora stalennuyi* sp. nov., compared with *D. italica*).

TYPE LOCALITY: Maksymivka, Western Ukraine.

TYPE STAGE: Middle Miocene (Upper Badenian).

DERIVATION OF NAME: Named after Alexander Stalennuy (Ternopil, Ukraine) for his support provided during field work in the Ukraine.

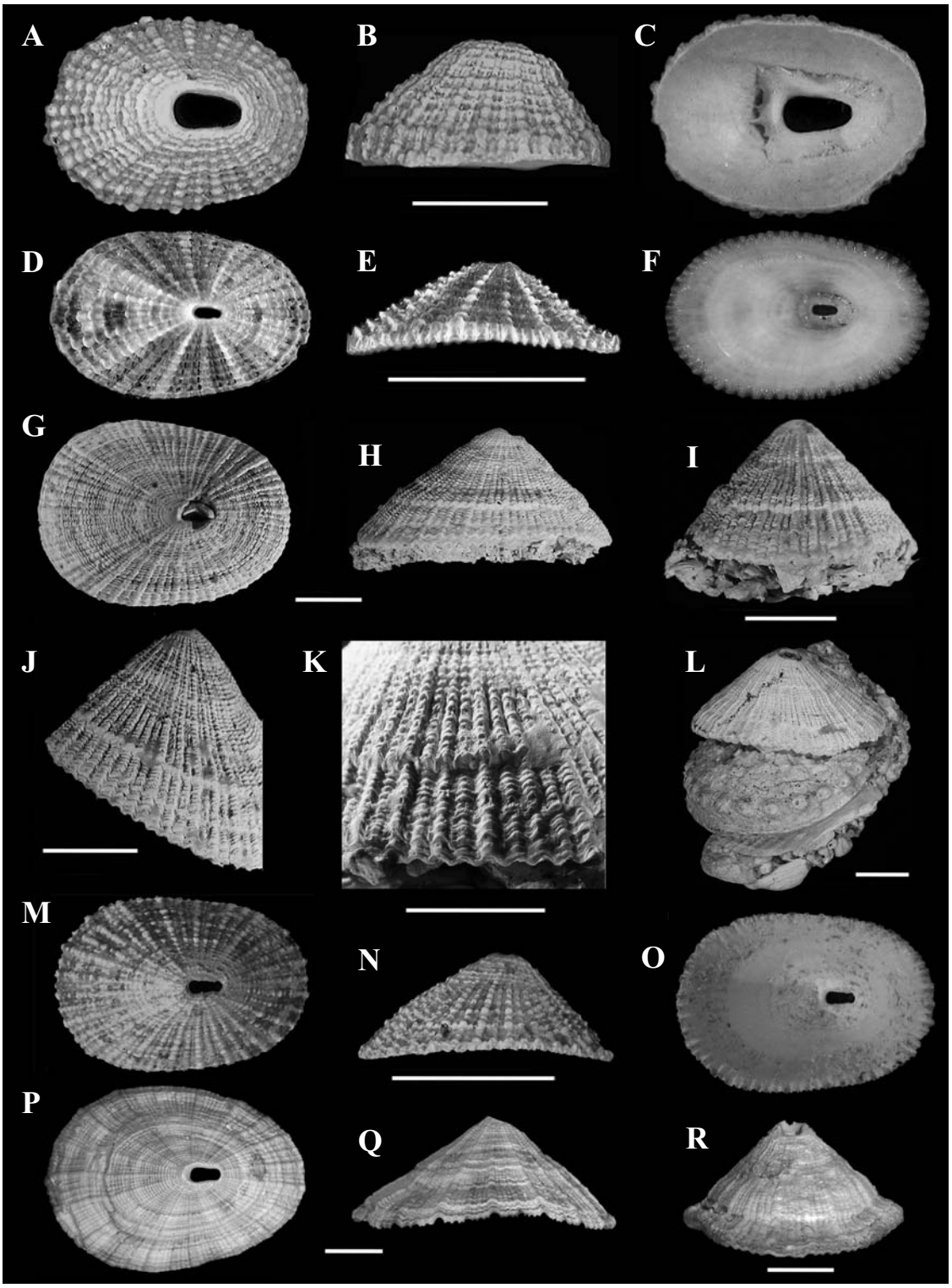
DESCRIPTION: Shell large, solid, conical, oval-elongated, maximum length 44.4 mm, moderately elevated, with a subcentral or slightly anterior apical aperture. The apical aperture oval, not bilobate. Anterior and posterior slopes straight. Shell ornamentation prominent, formed by numerous radial ribs, intersected by concentric growth lines. Radial ribs appearing near the apex, primary ribs thicker and secondary ones less thick, ca. 40 ribs (20 primary and 20 secondary, all starting from the apex). Just below the apex, another rib (tertiary) appearing between each couple of primary and secondary ribs, c. halfway from the apex to the periphery, less thick than primary and secondary ribs, sometimes obsolete. Concentric growth lines, at first fairly thin, gradually becoming thicker. Imbricate intersections formed at the intersections of both ribbing systems. Shell pe-

Type	Repository	Type locality	LS [mm]	Illustrated herein
Holotype	MZB 32132	Maksymivka	38.3	Text-fig. 4G–K
Paratype 01	TOKM 1731	Maksymivka	33.4	
Paratype 02	MSNG 58542	Maksymivka	21.6	
Paratype 03	MZB 32133	Maksymivka	23.0	
Paratype 04	MSNG 58543	Maksymivka	27.4	
Paratype 05	ZISP 62121	Maksymivka	13.5	
Paratype 06	IGS NASU B-II-13/2016	Maksymivka	32.0	
Paratype 07	BD 127	Maksymivka	38.0	Text-fig. 4L
Paratype 08	ZISP 62122	Maksymivka	39.0	
Paratype 09	MS 101	Maksymivka	29.6	
Paratype 10	IGS NASU B-II-12/2016	Maksymivka	15.4	Text-fig. 4M–O

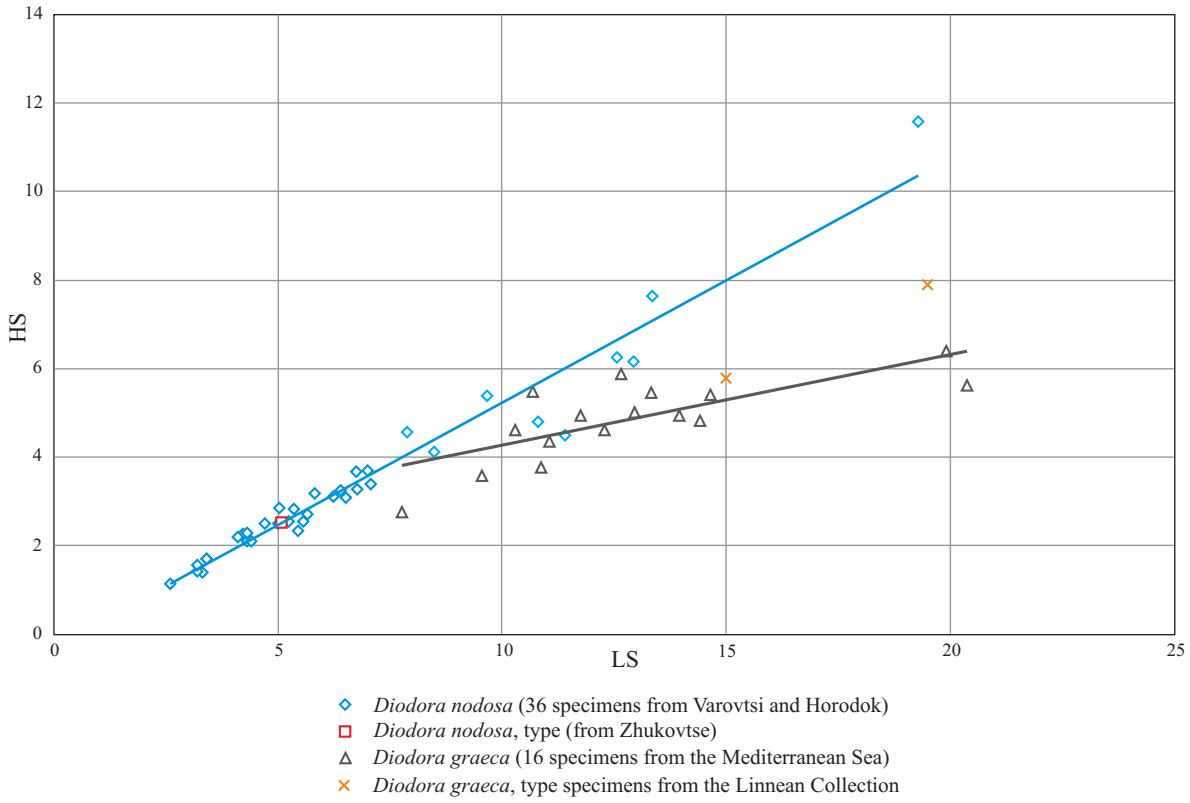
Table 2. *Diodora stalennuyi* sp. nov., type material and its repositories. LS – stands for length of shell

Parameter	*Diodora stalennuyi* sp. nov.			*Diodora italica*		
	range [mm]	mean [mm]	st. dev.	range [mm]	mean [mm]	st. dev.
LS	13.40–44.40	28.41	9.96	14.70–49.60	32.51	14.60
WS	8.61–30.00	20.56	7.27	8.50–33.00	21.68	10.38
HS	5.00–20.00	12.84	4.84	5.50–18.00	12.19	5.45
AP	4.20–19.40	11.60	4.85	4.81–19.30	11.83	5.86
LT	1.60–3.61	2.75	0.78	1.95–6.92	3.91	1.92
WS / LS	0.64–0.79	0.72	0.04	0.58–0.70	0.66	0.04
HS / LS	0.37–0.51	0.45	0.05	0.33–0.45	0.37	0.03
AP / LS	0.31–0.49	0.40	0.05	0.33–0.41	0.36	0.03
LT / LS	0.09–0.14	0.10	0.02	0.12–0.15	0.13	0.01
HS / WS	0.50–0.69	0.62	0.06	0.52–0.67	0.57	0.05

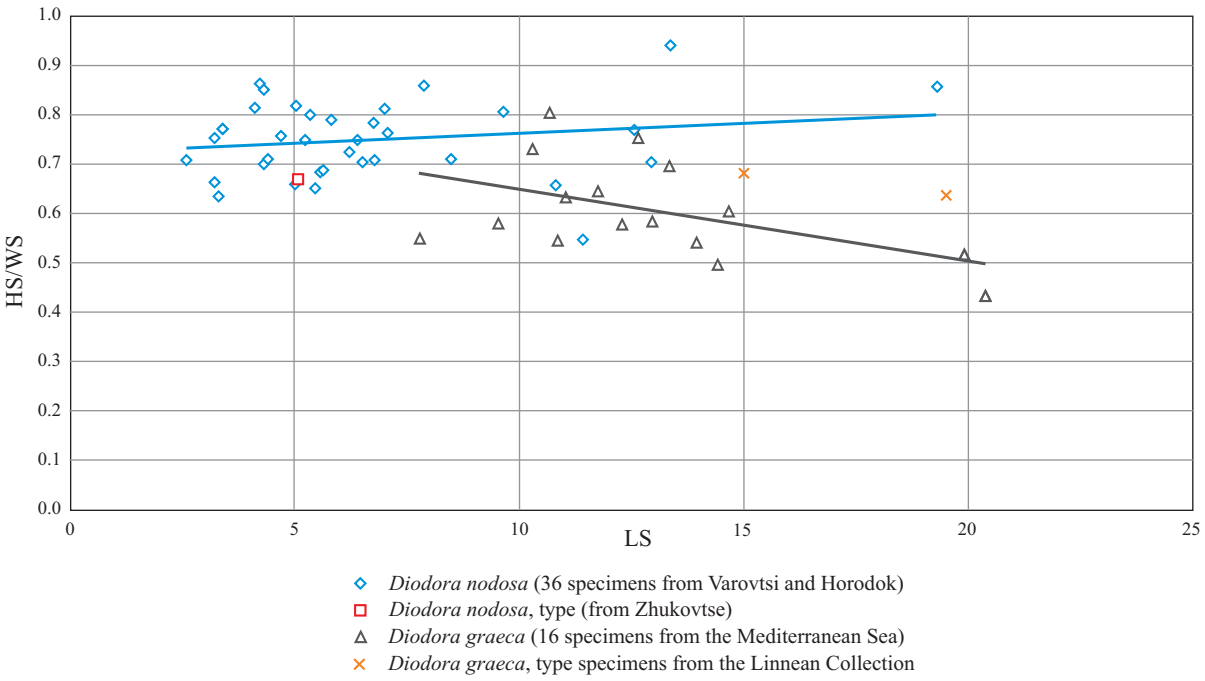
Table 3. Ranges and mean values of measured parameters for *Diodora stalennuyi* sp. nov. (14 specimens from Maksymivka) and *Diodora italica* Defrance, 1820 (8 specimens from the Mediterranean Sea). St. dev. stands for standard deviation



Text-fig. 4. **A-C** – *Diodora nodosa* (Eichwald, 1830), larger specimen from Varovtsi, apical (A), lateral (B) and ventral (C) views. D-F – *Diodora graeca* (Linnaeus, 1758), specimen from Arenzano (Genova), apical (D), lateral (E) and ventral (F) views. **G-O** – *Diodora stalennuyi* sp. nov., specimen from Maksymivka: G-K – Holotype, MZB 3132, apical (G), lateral (H), posterior (I) views and detail of ornamentation (J-K); L – Paratype 7, BD 127, block with specimen of *Diodora stalennuyi* sp. nov., *Haliotis volhynica* Eichwald, 1829 and other shells; M-O – Paratype 10, IGS NASU, B-II-12/2016, apical (M), lateral (N) and ventral (O) views. **P-R** – *Diodora italica* (Defrance, 1820), specimen from Croatia, apical (P), lateral (Q) and posterior (R) views. Scale bars 10 mm



Text-fig. 5. Relationship between shell height (HS) and shell length (LS) and regression lines for *Diodora graeca* (Linnaeus, 1758) and *Diodora nodosa* (Eichwald, 1830)



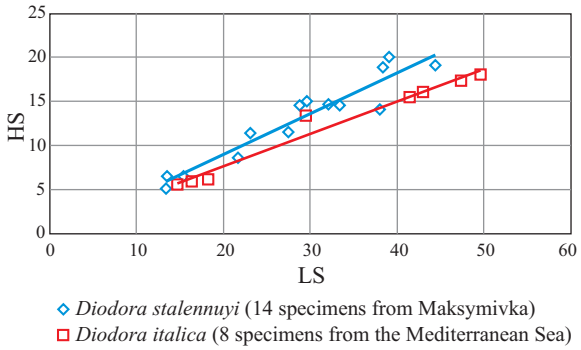
Text-fig. 6. Relationship between shell height/shell width ratio (HS/WS) and shell length (LS) and regression lines for *Diodora graeca* (Linnaeus, 1758) and *Diodora nodosa* (Eichwald, 1830)

riphery slightly crenulated internally. Opening internally rimmed by a callus, rounded anteriorly and truncate posteriorly.

REMARKS: The Mediterranean extant species *Diodora italica* (Defrance, 1820) has been reported from the Neogene of many parts of Europe (Cerulli-Irelli 1916; Cossmann and Peyrot 1917; Glibert 1949; Malatesta 1960, 1974; da Silva 1990, 2001; Borghi and Vecchi 1998; Landau *et al*. 2003) and from the Middle Miocene (Badenian) units of Central Paratethys (Hörnes 1856; Friedberg 1928; Davidaschvili 1937; Strausz 1954, 1966; Korobkov 1955; Bielecka 1967; Zelinskaya *et al*. 1968; Bałuk 1975, 2006; Schultz 1998; Harzhauser 2002). Notwithstanding the great variability of recent *D. italica*, which has resulted in the recognition of a large number of varieties and synonyms (e.g., Sabelli *et al*. 1990, p. 124), the study of the relevant material from Maksymivka has revealed enough constant differences compared with *D. italica* from the Mediterranean Sea to describe the specimens from the Badenian of the Ukraine as a new species.

Diodora stalennuyi sp. nov. differs from *D. italica* mainly in:

- a higher shell, more flattened in *D. italica* (see Text-fig. 7). The maximum length of recent *D. italica* is reported as 45 mm by Cossignani and Ardovini (2011), compared to the maximum length of slightly above 44 mm for *D. stalennuyi*. Multivariate analysis shows a hiatus between the species discussed (MANOVA, Wilks' lambda is 0.40; df1 is 4, df2 is 17; F = 6.25; p = 0.0028);
- the ornamentation of the shell, characterized by the structure of primary, secondary and tertiary ribs described above for *Diodora stalennuyi*, *vs*. many unequal radial ribs, generally a strong primary rib followed by several (3–4 or more, up to 6–7) thicker and weak ribs in *D. italica s. str*., not divisible into primary and secondary ones;
- the shape, tending to become significantly closer to the front, less accentuated and more oval in *D. stalennuyi*.



Text-fig. 7. Relationship between shell height (HS) and shell length (LS) and regression lines for *Diodora stalennuyi* sp. nov. and *Diodora italica* Defrance, 1820

We have reported all the bibliographical references of *Diodora* species regarding the areas of Ukraine and Poland (considering that many old reports are related

		D. nodosa	*D. graeca*	*D. stalennuyi* sp. nov.	*D. italica*
Shape	range of LS [mm]	2.59–19.29	7.77–20.38	13.40–44.40	14.70–49.60
	range of WS [mm]	1.62–13.50	5.02–12.97	8.61–30.00	8.50–33.00
	range of HS [mm]	1.15–11.59	2.76–6.41	5.00–20.00	5.50–18.00
	range of AP [mm]	1.05–7.96	2.54–7.22	4.20–19.40	4.81–19.30
	range of LT [mm]	0.37–2.58	0.68–1.96	1.60–3.61	1.95–6.92
	range of AA	65–86°	79–109°		
Apical aperture	position of apical aperture	subcentral or slightly anterior	anterior	subcentral or slightly anterior	anterior
	shape of apical aperture	subrectangular to bilobate	oval	oval, not bilobate	oval
	LT / LS (mean)	12%	10%	10%	13%
Ornamentation	sculpture	17–24 primary ribs starting near the apex, secondary ribs tending to reach the same size as the primary ribs, tertiary ribs rare in adult specimens	16–22 ribs starting near the apex, secondary ribs always well discernible	c. 20 thicker primary ribs and 20 less thick secondary ribs, starting near the apex, not from the apex, sometimes obsolete	numerous (c. 80) rounded unequal radial ribs
	intersection of radial ribs and concentric growth lines	roundish nodes	imbricated	imbricated	imbricated

Table 4. Main characters of the *Diodora* species considered herein

to the "Volhynia-Podil'ya" area, which now is partly included in the Ukraine), and almost all the specimens identified as *D. italica*, based mainly on the available descriptions and illustrations where the features of the new species are well evident, can be attributed to *Diodora stalennuyi* sp. nov. It is not the aim of the present work to check the several records of *D. italica* for the remaining part of the Central Paratethys and for the Neogene of Europe, to verify the true distribution of this species or a possible interaction with the new subspecies described herein.

DISTRIBUTION: Middle Miocene: Central Paratethys (Upper Badenian): Poland and Ukraine (this report).

CONCLUSIONS

The specimens of *Diodora* from the Upper Badenian of the Central Paratethys have been usually attributed mainly to *D. graeca* or *D. italica*, which are extant species of the Atlantic / Mediterranean Basin. Specimens from our material show a similarity with these species but a review of the main diagnostic characters using a statistical approach has revealed their clear conchological separateness. We consider these specimens inhabited the Polish-Ukrainian marginal part of the Late Badenian Basin as two distinct species, *D. nodosa* (Eichwald, 1830) and *D. stalennuyi* sp. nov. The main characters of the species considered herein are given in Table 4.

Another recent species of *Diodora* from the Mediterranean / Atlantic is *D. gibberula* (Lamarck, 1822), noted as a fossil species from the Plio-Pleistocene (Landau *et al.* 2003), the Miocene of Northern Italy (Sacco 1897) and the Karaman Basin, Turkey (Landau *et al.* 2013), but never recorded from the Middle Miocene of Paratethys. It is characterized by its rather small shell, more regular sculpture than most of its congeners, the apical aperture placed more posteriorly than in most Recent European *Diodora* species, and by a more concave base.

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71–318 (1924); 77, 51–256 (1925); 78, 199–256 (1926); 79, 5–263 (1928); 82, 73–126 (1931); 83, 5–116 (1931); 84, 5–288 (1933); 85, 5–71 (1933); 86, 257–353 (1935).

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