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Source: Acta Palaeontologica Polonica, 61(2) : 327-344

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.00158.2015>

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# Middle Miocene conoidean gastropods from western Ukraine (Paratethys): Integrative taxonomy, palaeoclimatological and palaeobiogeographical implications

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Scarponi, D., Della Bella, G., Dell'Angelo, B., Huntley, J.W., and Sosso, M. 2016. Middle Miocene conoidean gastropods from western Ukraine (Paratethys): Integrative taxonomy, palaeoclimatological and palaeobiogeographical implications. *Acta Palaeontologica Polonica* 61 (2): 327–344.

The late Badenian (early Serravallian) conoideans from the Pidhirtsi Beds of western Ukraine (central Paratethys) have been investigated by means of a comprehensive and easy-to-perform morphometric approach, allowing the characterisation of eleven species, of which seven are new to science: *Mangelia angulicosta* sp. nov., *M. larga* sp. nov., *M. pseudorugulosa* sp. nov., *M. odovychenae* sp. nov., *Bela varovtsiana* sp. nov., *Bela? robusta* sp. nov., *Pyrgocythara turrispiralata* sp. nov. Additionally we also identified *Raphitoma* cf. *R. ringicula*, *Andonia* sp. aff. *A. transsylvanica*, *Teretia* cf. *T. turritelloides*, and *Haedropleura* sp. aff. *H. septangularis*. The relative high number of new species documented, relative to the total previously known from this stratigraphic interval, is interpreted as resulting mainly from combined methodological (dearth of taxonomic studies on Ukrainian conoideans) and environmental (high degree of habitat fragmentation in reef setting) factors. The conoideans documented herein add important information regarding palaeoclimatological and palaeobiogeographical interpretations of the Serravallian Paratethys. The conoideans display strong affinity at the species level and complete overlap at the genus level with Neogene Proto-Mediterranean–Atlantic conoideans, thereby challenging the interpretation of late Badenian Paratethyan macrofaunal assemblage endemism. The lack of typical warm-water indicators (e.g., Conidae, Clavatulidae, or Pseudomelatomidae) within the studied material supports the interpretation that the fauna thrived during the late phase and/or soon after the Middle Miocene Climatic Transition (14.2–13.8 Ma).

**Key words:** Gastropoda, Conoidea, Middle Miocene Climatic Transition, Serravallian, Central Paratethys, Ukraine.

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Received 12 February 2015, accepted 30 September 2015, available online 22 October 2015.

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## Introduction

The road leading to a widely accepted classification framework of the superfamily Conoidea Fleming, 1822 has been winding and paved with contradictions (e.g., Tucker 2004; Puillandre et al. 2008), especially when applied to the fossil record, where only shell characters, which are often subject to strong taphonomic degradation, are available (e.g., Tucker et al. 2011; Mariottini et al. 2012; Landau et al. 2013;

Scarponi et al. 2014a, b). Thanks to the recent large-scale implementation of coupled molecular and morphological studies of the Conoidea, a new family-level framework is now available (Puillandre et al. 2011; Bouchet et al. 2011 and references therein). However, the lower rank (genus to species) conoidean taxonomy, based on integrated phenetic and molecular characters, is still in progress (e.g., Fedosov et al. 2011; Puillandre et al. 2015). Therefore, in order to put in place a conservative usage of the names of fossil taxa and to

promote their stability, especially at lower taxonomic rank, it is important to assess shell characters and define their variation (see also Dayrat 2005; Harzhauser and Kronenberg 2013; Klompmaker et al. 2015). Herein the morphological variability of conoidean representatives of western Ukraine (early Serravallian, Central Paratethys) is examined by means of a comprehensive and easy-to-perform approach to their shell morphology. This approach combines both qualitative and quantitative evaluation of morphological variability within and among taxa in order to allow for a more objective taxonomic identification of specimens. In this respect, the study largely follows the format adopted for the analysis of Neogene representatives of the Proto-Mediterranean and Atlantic as in Scarponi et al. (2011b, 2014b) and Naldi et al. (2013). The conoideans documented herein and their taxonomic subdivision add important information regarding the diversity of Miocene conoideans from Ukraine and support recent palaeoclimatological and palaeobiogeographical interpretations of the Serravallian Paratethys (see Harzhauser and Piller 2007; Bartol et al. 2014).

**Institutional abbreviations.**—IGS-NANU, Institute of Geological Sciences, National Academy of Sciences of Ukraine, Kiev, Ukraine; MGGC, Museo Geologico Giovanni Capellini, Bologna, Italy; MGPT, Museo di Geologia e Paleontologia, Turin, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MSNG, Museo Civico di Storia Naturale Giacomo Doria, Genoa, Italy; MZB, Museo di Zoologia dell'Università di Bologna, Bologna, Italy; NHMW, Natural History Museum, Vienna, Austria; ZISP, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

**Other abbreviations.**—max, maximum; parameter<sub>m</sub>, mean value of targeted parameter; p, probability in support of a null hypothesis; sh(s), shell(s); sd, standard deviation; wh, whorl.

## Geological and geographical setting

The study area is located at the foot of the Medobory Hills, on the south-western margin of the Eastern European Platform in the Khmelnytskyi region of western Ukraine (Fig. 1).

These hills form a distinctive geomorphological element amidst the Ukrainian flatland and represent the remnants of a composite, elongate (almost 300 km in length; Fig. 1A) reef-belt developed on the south-western margin of the European Platform (Central Paratethys), primarily during the Serravallian stage. Along the eastern side of the central sector of the Medobory Hills the sedimentary succession is represented by upper Badenian and lower Sarmatian (i.e., lower Serravallian) deposits. The lowermost part of the succession, constituted of loose sand and sandstone attributed to the Pidhirtsi Beds (Górka et al. 2012 and references therein;

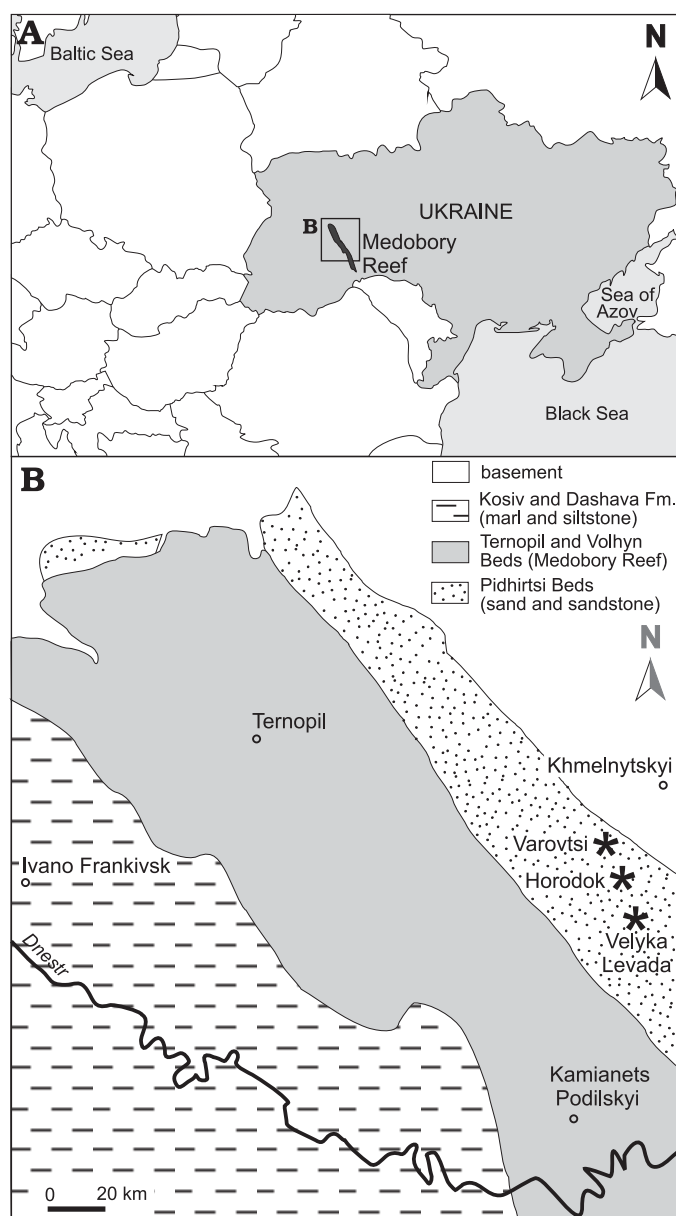


Fig. 1. A. Schematic map of Ukraine and the location of the study area. B. Distribution of the principal lithostratigraphic units in the area of study and location of the three sampled sites (asterisks).

Fig. 1B), discordantly overlies the pre-Miocene basement. The richly-fossiliferous back-reef, shallow marine Pidhirtsi Beds are heteropic, or lateral equivalents, with and partly overlain by biohermal (algal-vermetid reef) and bioclastic grainstone and rudstone that constitute the main structure of the Medobory Hills (i.e., Ternopil Beds; Górka et al. 2012; Fig. 1B). These upper Badenian deposits are representative of the last interval of fully marine conditions in the Central Paratethys (~13.6–12.7 Ma; see Kováč et al. 2007). The age of the Pidhirtsi Beds studied herein was additionally constrained by means of strontium geochronology on bivalve shells from a locality near Olesko (western Ukraine), suggesting an age of  $13.6 \pm 0.4$  Ma (Studencka and Dulai 2010 and references therein).

A geographically widespread and easily identified unconformity at the top of the Ternopil Beds (indicating a phase of emersion of the Medobory reefs), separates the upper Badenian deposits from the overlying Sarmatian deposits. The latter in the study area partially overlay the Badenian reef deposits and are composed of a complex of biogenic and clastic materials indicative of reduced salinity (brackish) palaeoenvironments and collectively assigned to the Volhyn Beds (Andreyeva-Grigorovich et al. 1997; Fig. 1B). The fossil material described in this study is from three back-reef sites: Varovtsi, Horodok, and Velyka Levada, situated along a 30 km long NW-SE oriented transect on the eastern slopes of the Medobory Hills (Khmielnitsky Region, Ukraine; Fig. 1B).

The Varovtsi site (49°20'06" N, 26°34'29" E; see also SOM 1: fig. 1A, Supplementary Online Material available at [http://app.pan.pl/SOM/app61-Scarponi\\_et\\_al\\_SOM.pdf](http://app.pan.pl/SOM/app61-Scarponi_et_al_SOM.pdf)) occurs along the right bank of the River Smotrytch, located within the Podolian Massif in the north-eastern part of the Halicz-Volhynian Depression. All the material studied originates from fossiliferous, homogeneous, weakly-cemented, medium to fine-grained, white quartz sandstone deposits that can reach several metres in thickness. According to Studencka and Dulai (2010), these deposits belong to the Podhortse Beds documented by Muratov and Nevesskaja (1986), but which have also been reported as the Podgirtsi or Pidhirtsi Beds by later authors (see above). The late Badenian (early Serravallian) age of this unit was determined by means of benthic foraminifera and strontium isotope geochronology (Studencka and Dulai 2010).

The Horodok site (49°10'07" N, 26°35'16" E; SOM 1: fig. 1B) is an exposure at the northern periphery of the village of Horodok, located on the roadside opposite a small lake. All the selected material comes from the lowermost part of a > 10 m high cliff of quartzose, weakly-cemented sandstone, herein attributed to the Pidhirtsi Beds.

The Velyka Levada site (49°03'32" N, 26°36'17" E; SOM 1: fig. 1C) is represented by an exposure located ~500 m south of the village of Velyka Levada, along the left flank of the road that leads to Velykyi Karabchiv. All the selected material originates from the quartzose sandstone of the Pidhirtsi Beds, sampled at the base of a cliff 15–20 m in height.

The attribution of the deposits at the Horodok and Velyka Levada sites to the Pidhirtsi Beds is based on a comparison of lithological features with recent surveys and reports investigating fossil fauna and/or the stratigraphic architecture of deposits outcropping in the study area (e.g., Studencka and Dulai 2010).

## Historical background

Despite the richly fossiliferous sedimentary successions of western Ukraine (e.g., Eichwald 1830; Friedberg 1951), the gastropods from the study sites have rarely been the focus of quantitative analyses; this is especially true for

the localities at Horodok and Velyka Levada. Among the localities taken into consideration herein, Varovtsi is by far the most studied. Accounts of the molluscs found here were given by Anistratenko et al. (2006), Anistratenko and Anistratenko (2007) for patellogastropods; Nevesskaja et al. (1993), Studencka et al. (1998), Studencka and Jasionowski (2011) for bivalves and Studencka and Studencki (1988), Studencka and Dulai (2010) for polyplacophorans.

To our knowledge, Laskarew (1914) and Maslov and Utrobin (1958) briefly mentioned the Horodok and Velyka Levada localities, along with Varovtsi. However, the latter paper did not deal with molluscs but focused on stratigraphic aspects, whereas Laskarew (1914) reported a list of 155 molluscan species (72 bivalves, 81 gastropods, and 2 scaphopods) from several localities in the study area. Among the six species of Conoidea reported in Laskarew (1914), only *Pleurotoma anceps* Eichwald, 1830 was recovered from Varovtsi, the other five—*Pleurotoma leufroyi* Michaud, 1827, *P. submarginata* Bellardi, 1847, *P. suessi* Hoernes 1854, *P. helenae* Hoernes and Auinger 1890 and *P. sandleri* Hoernes, 1854—were from localities not included in the present study.

## Material and methods

The bulk material for this study was obtained during three field trips carried out at the selected sites (Fig. 1B) from 2010 to 2012. Each bulk sample was washed using a 1 mm mesh sieve and conoideans were separated from the bulk of residual macrofossils (> 1 mm) for further analysis. In total, 351 specimens were recovered and subsequently grouped into twelve conoidean morphotypes. In order to evaluate intra-taxon variability and to quantitatively compare morphologic variation between allied taxa, a batch of fifteen specimens (or all if  $n < 15$ ) was randomly selected from each morphotype and ten shell parameters were measured for each specimen (see SOM 1: fig. 2, SOM 2). The number of protoconch whorls were counted following the Verduin (1977) method. Morphological descriptive terms are after Arnold (1965) (SOM 1: fig. 2); paucispiral,  $n$  of protoconch  $wh \leq 1.5$ ; multispiral,  $n$  of protoconch  $wh > 1.5$ .

It should be noted that for groups with  $n > 15$  specimens, specimens in which teleoconch was < 2.5 whorls and specimens with excessively-damaged shells (e.g., half or less preserved or with > 4 parameters not measurable) were not considered if sampled during the selection process. Subsequently, for very similar taxa (based on preliminary morphological evaluation), all measured shell characters were compared with one another by estimating confidence intervals (CI) around the mean (Fig. 2) and via several standard statistical tests (parametric and non-parametric see Table 1, SOM 3). In this last respect, a general null hypothesis—the two tested samples are taken from populations showing no difference for the targeted parameter, and the alternative hypothesis—samples differ for the targeted parameter, and a conventional alpha-value ( $\alpha$ ) of 0.05 are assumed for all sta-

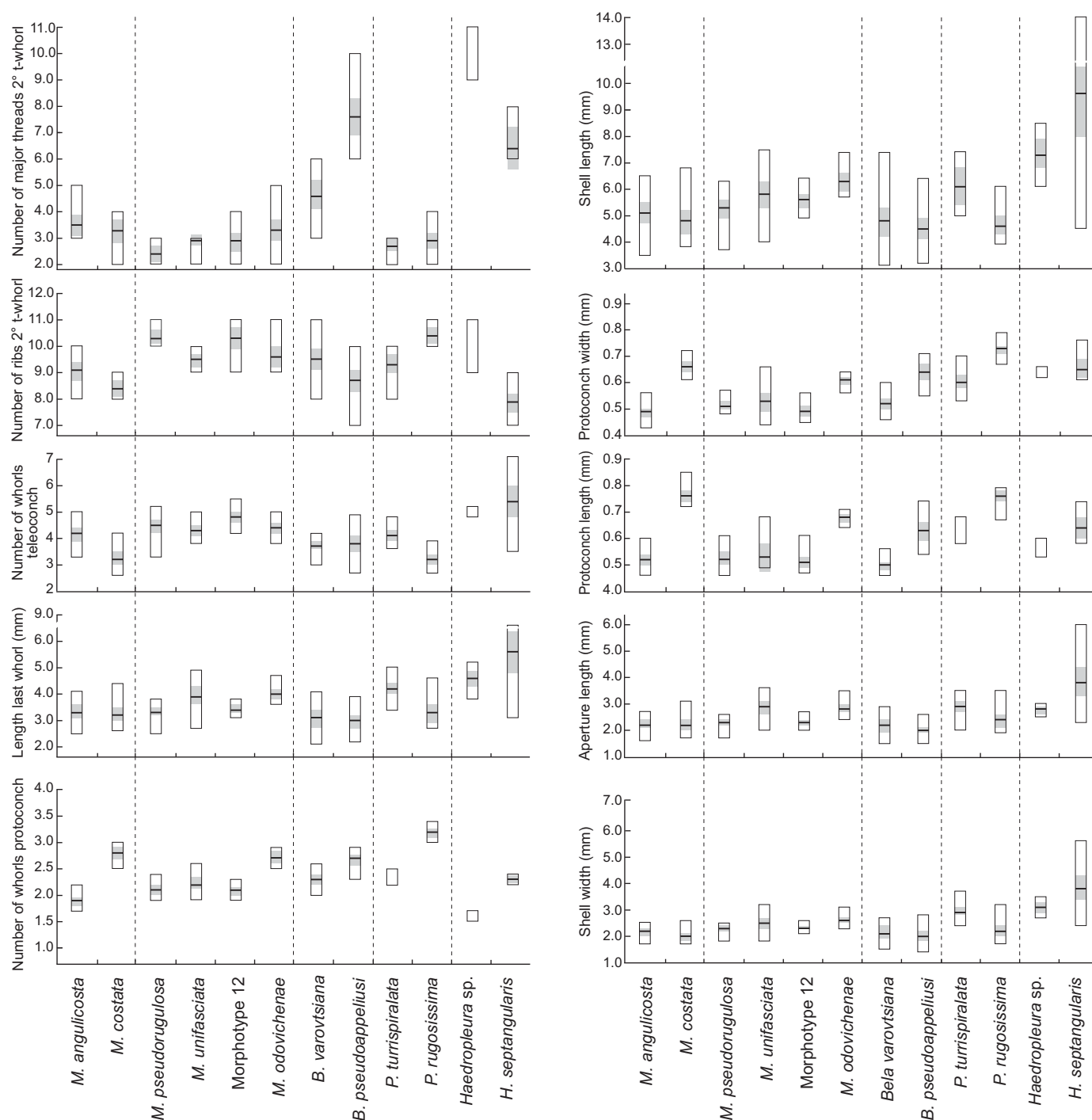


Fig. 2. Comparison of 10 assessed variables between allied taxa: sample mean, horizontal line; 95% confidence intervals (CI), shaded boxes; ranges, open boxes (specimen measurements in SOM 2). The mean sample is a point estimate of the population mean ( $\mu$ ), and the corresponding CI is a range of plausible values for  $\mu$ . If two parameters have non-overlapping CI, they are considered to be significantly different. The 95% confidence interval is based on the standard error for the estimate of the mean and the  $t$  distribution. For extremely small samples ( $n < 5$ ; SOM 2) only ranges are reported (see Beninger et al. 2012). Abbreviations: *M.*, *Mangelia*; *B.*, *Bela*; *P.*, *Pyrgocythara*; *H.*, *Haedroleura*.

tistical analyses, which were carried out in PAST (Hammer et al. 2001). For each new species, the specimen displaying well-preserved examples of all or most of the characters considered the most representative of the newly named species was selected as holotype. The remaining fourteen specimens were consequently designated as paratypes, whereas the residual specimens of the original lot, even though attributed

to the new species, are not considered as belonging to the type series (see provision 72.4.6 of the International Code of Zoological Nomenclature, 2015).

The type material is housed at the Museo Geologico Giovanni Capellini, Bologna, Italy, whereas residual specimens (see above) are housed in the European museums indicated in the institutional abbreviation section.



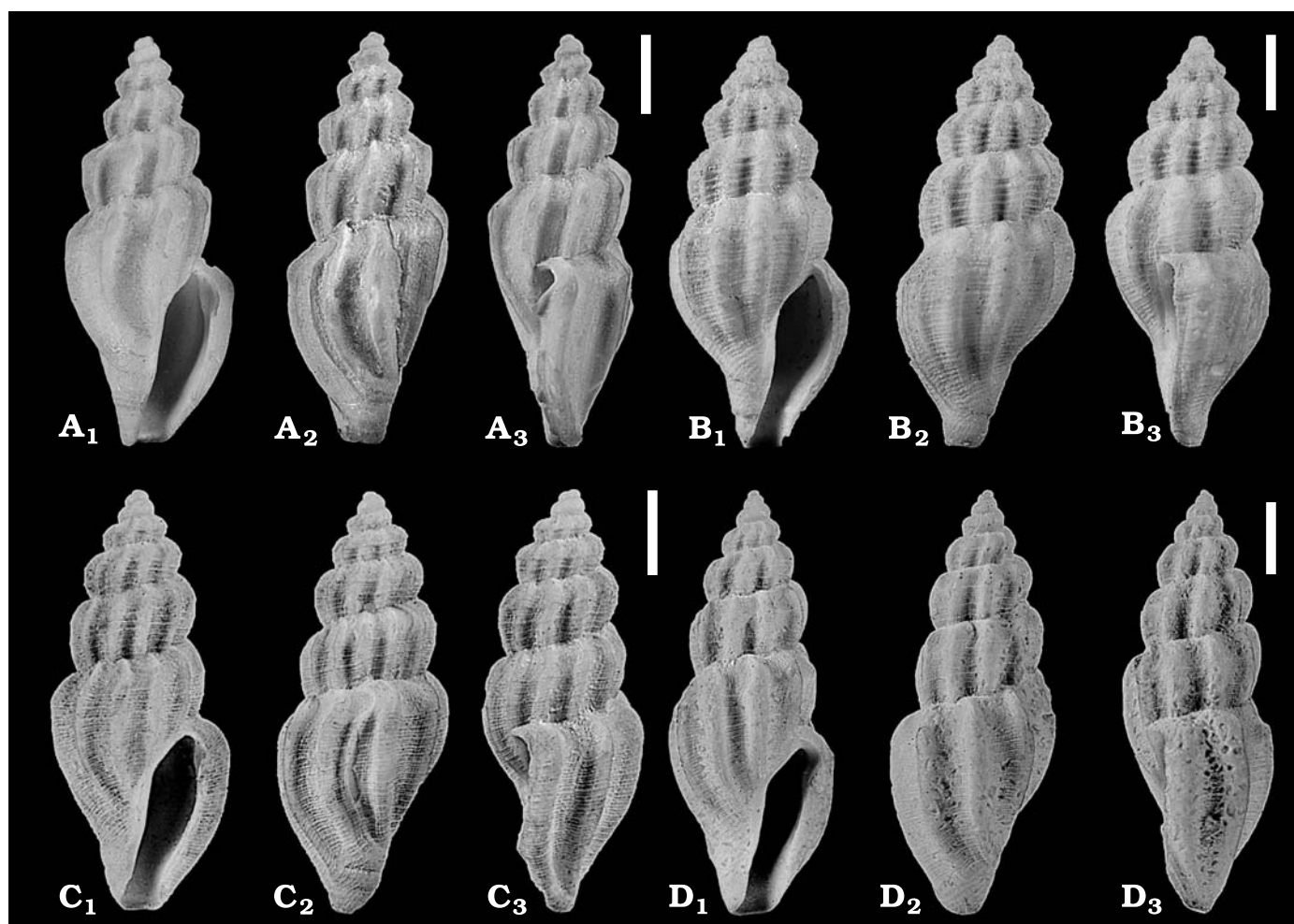


Fig. 3. Photomicrographs of holotype shells of new conoidean gastropods from early Serravallian of western Ukraine, Varovtsi (A–C) and Velyka Levada (D). **A.** *Mangelia angulicosta* sp. nov., MGGC-24505. **B.** *Mangelia larga* sp. nov., MGGC-24507. **C.** *Mangelia pseudorugulosa* sp. nov., MGGC-24509. **D.** *Mangelia odovychenae* sp. nov., MGGC-24511. Views: A<sub>1</sub>–D<sub>1</sub>, apertural; A<sub>2</sub>–D<sub>2</sub>, dorsal; A<sub>3</sub>–D<sub>3</sub>, lateral. Scale bars 1 mm.

## Systematic palaeontology

Order Neogastropoda Wenz, 1938

Superfamily Conoidea Fleming, 1822

Family Mangeliidae Fischer, 1883

Genus *Mangelia* Risso, 1826

*Type species:* *Mangelia striolata* Risso, 1826; San Remo-Ventimiglia (Italy), Recent.

**Remarks.**—The description of the genus *Mangelia* was extremely brief (Risso 1826) and the type species material has been lost (Arnaud 1978). The recent designation of neotype for *Mangelia striolata* (Spada and Della Bella 2010) should bring to a close the long debate concerning the taxonomical validity of the species designation by Risso (1826; see also Scarponi et al. 2011a, 2014b), while stabilising the taxonomic usage of this key species.

*Mangelia angulicosta* sp. nov.

Figs. 3A, 4, 5A; SOM 1: fig. 3A, SOM 2.

**Etymology:** From Latin *angulus*, angle and *costa*, rib; named after the distinctive, sharply angulated profile of its axial ribs.

**Type material:** Holotype, MGGC-24505, adult, well-preserved shell. Paratypes, MGGC-24506/1–14 from the type locality (SOM 2).

**Type locality:** Varovtsi, Ukraine.

**Type horizon:** Massive, white sandstone of the Pidhirtsi Beds, early Serravallian (~14.0–12.7 Ma).

**Material.**—Six topotype specimens from Varovtsi: IGS-NANU-B-I-1/2015 (1 sh), MGPT-PU135044 (1 sh), NHMW-2015/0404/0001 (2 shs), and ZISP-62073 (2 shs).

**Diagnosis.**—A small *Mangelia* species (shell length<sub>m</sub> 5.1 mm, sd 0.7 mm; shell width<sub>m</sub> 2.2 mm, sd 0.2 mm), characterised by a multispiral protoconch (length<sub>m</sub> 0.52 mm, sd 0.04 mm; width<sub>m</sub> 0.49 mm, sd 0.03 mm), a relatively short spire (0.34 shell length<sub>m</sub>, sd 0.02) and a slightly bent columellar lip. Teleoconch sculpture of strongly angulated, narrow and prominent ribs (max 10 on the second whorl) along with dense, thin and, in the last whorl, fairly uniform, flat topped spiral elements.

**Description.**—Shell small-sized, fusiform, spire turreted

(0.34 shell length<sub>m</sub>, sd 0.02); last whorl narrow (2.2 mm, sd 0.2 mm), elongated (3.3 mm, sd 0.4 mm). Protoconch dome-shaped, of 1.9 convex whorls (sd 0.1 wh); nucleus medium-sized, smooth as remaining whorls except the final quarter, where 3–5 weak cordlets override comma-shaped, thin, slightly opisthocline, axial riblets strengthening at the protoconch-teleoconch boundary. Teleoconch<sub>m</sub> of 4.2 whorls (sd 0.4 wh), angulated in profile, with noticeable axials and subdued spiral sculpture; suture undulating. Axials of narrow, well developed, slightly opisthocline, angulated, far apart ribs (typically 9 on second whorl), extending across sutures on spiral whorls, until the base of the last whorl. Spiral sculpture dense, fairly uniform, made of thin, flat-topped threads separated by incised lines; on early whorls, a few (usually 3 on second whorl) thin spiral cords also present. Growth lines occasionally evident. Aperture moderately narrow, sub-rectangular (length<sub>m</sub> 2.2 mm, sd 0.3 mm), siphonal canal short. Outer lip thin-edged, slightly convex in profile, internally thickened; anal sinus C-shaped; columellar lip slightly bent.

**Remarks.**—*Mangelia angulicosta* sp. nov. is similar to *Mangelia atlantica* Pallary, 1920, an extant Atlantic–Mediterranean taxon (SOM 1: fig. 4A, SOM 2), that is currently considered a synonym (or subspecies) of *Mangelia costata* (Pennant, 1777) (Scarponi and Della Bella 2010; WoRMs 2014 and references therein). In particular, the two species share comparable shell dimensions, teleoconch sculpture, and morphology of the aperture and sinuses (e.g., SOM 1: fig. 3A vs. fig. 4A). Quantitative comparison of the previously mentioned teleoconch parameters support a strong overlap between the new species and *M. costata* (e.g., shell length<sub>m</sub> 5.1 vs. 4.8 mm, respectively;  $p = 0.29$ ) as well as comparable coefficients of intraspecific variation (for further details see Fig. 2, Table 1, SOM 3). However, *M. costata*

is characterised (and distinguishable from *M. angulicosta*) by its: (i) smaller number of teleoconch whorls (i.e., 3.2 vs. 4.2) at comparable shell length (see above); (ii) less numerous teleoconch ribs (average on second whorl 8.4 vs. 9.1,  $p < 0.01$ ); (iii) bigger protoconch (length<sub>m</sub> 0.76 vs. 0.52,  $p < 0.01$ ; width<sub>m</sub> 0.66 vs. 0.49 mm,  $p < 0.01$ ) and higher number of protoconch whorls (2.8 vs. 1.9,  $p < 0.01$ ; further details in Fig. 2, Table 1, SOM 3). Furthermore, with respect to *M. costata*, the axial ribs in *M. angulicosta* are sharply angulated at approximately 2/3 of the whorl, then proceed straight toward the adapical suture, giving the spire its characteristic angulated profile (Fig. 3A vs. SOM 1: fig. 4A).

**Stratigraphic and geographic range.**—Pidhirtsi Beds, early Serravallian of the Central Paratethys.

### *Mangelia larga* sp. nov.

Figs. 3B, 4B, C, 5B–D; SOM 1: fig. 3B, SOM 2.

**Etymology.** From Latin *larga*, inflated, wide; named after the distinctive, inflated teleoconch whorls.

**Type material.** Holotype, MGGC-24507, adult, fairly preserved shell, outer lip slightly broken. Paratypes, MGGC-24508/1–14 from the type locality (SOM 2).

**Type locality.** Varovtsi, Ukraine.

**Type horizon.** Massive, white sandstone of the Pidhirtsi Beds, early Serravallian (~14.0–12.7 Ma).

**Material.**—Thirteen topotype specimens from Varovtsi: IGS-NANU-B-I-2-3/2015 (2 shs), MNHN.F.A53760 (2 shs), MSNG-58188 (2 shs), MGPT-PU135045 (2 shs), NHMW-2015/0404/0002 (3 shs), ZISP-62074 (2 shs); one from Horodok: IGS-NANU-B-I-2/2015.

**Diagnosis.**—A very small *Mangelia* species (shell length<sub>m</sub> 4.4 mm, sd 0.8 mm; shell width<sub>m</sub> 2.1 mm, sd 0.3 mm), char-

Table 1. Monte Carlo (MC) permutation and t-test results. For each parameter, the sample mean was compared (if  $n \geq 10$ ) between allied species via t-test and MC permutation (10 000 iterations), additional tests are reported in SOM 3. Cells report the probability that the two samples come from populations with equal mean; shaded cells, results where the null hypothesis (given the specified alpha level), can be rejected. NS, not significant results; Bonferroni correction applied (further details in SOM 3). Abbreviations: *M.*, *Mangelia*; *B.*, *Bela*; *P.*, *Pyrgocythara*; *H.*, *Haedrolepura*.

Taxon	Shell		Teleoconch					Protoconch			test
	length	width	aperture length	last-whorl length	# whorls	second whorl		length	width	# whorls	
						ribs	major threads				
<i>M. angulicosta</i> vs. <i>M. costata</i>	NS	0.04	NS	NS	<< 0.01	< 0.01	NS	<< 0.01	<< 0.01	<< 0.01	t-test
	NS	0.04	NS	NS	<< 0.01	0.01	NS	<< 0.01	<< 0.01	<< 0.01	MC permutation
<i>M. pseudorugulosa</i> vs. <i>M. unifasciata</i>	NS	0.01	<< 0.01	< 0.01	NS	<< 0.01	<< 0.01	NS	NS	NS	t-test
	NS	0.01	<< 0.01	< 0.01	NS	<< 0.01	NS	NS	NS	NS	MC permutation
<i>M. pseudorugulosa</i> vs. morphotype 12	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	t-test
	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	MC permutation
<i>M. pseudorugulosa</i> vs. <i>M. odovychenae</i>	<< 0.01	<< 0.01	<< 0.01	<< 0.01	NS	< 0.01	<< 0.01	–	<< 0.01	–	t-test
	<< 0.01	<< 0.01	<< 0.01	<< 0.01	NS	< 0.01	< 0.01	–	<< 0.01	–	MC permutation
<i>B. varovtsiana</i> vs. <i>B. pseudoappeliusi</i>	NS	NS	NS	NS	NS	< 0.01	<< 0.01	<< 0.01	<< 0.01	<< 0.01	t-test
	NS	NS	NS	NS	NS	0.01	<< 0.01	<< 0.01	<< 0.01	<< 0.01	MC permutation
<i>P. turrispiralata</i> vs. <i>P. rugosissima</i>	<< 0.01	<< 0.01	<< 0.01	<< 0.01	<< 0.01	<< 0.01	NS	–	<< 0.01	–	t-test
	<< 0.01	<< 0.01	<< 0.01	<< 0.01	<< 0.01	< 0.01	NS	–	<< 0.01	–	MC permutation
<i>Haedropleura</i> sp. vs. <i>H. septangularis</i>	0.02	0.01	<< 0.01	0.02	–	–	–	–	–	–	t-test
	0.01	0.01	<< 0.01	0.01	–	–	–	–	–	–	MC permutation



acterised by a paucispiral protoconch (length<sub>m</sub> 0.38 mm, sd 0.02 mm; width<sub>m</sub> 0.44 mm, sd 0.03 mm), a very short spire (0.29 the shell length<sub>m</sub>, sd 0.05), inflated teleoconch whorls and a bent columellar lip. Teleoconch sculpture of numerous, rounded, low ribs (max 14 on the second whorl), and a dense pattern of spiral elements of which the two most prominent are in correspondence with, and just below, the periphery.

**Description.**—Shell small-sized, fusiform, spire conical (0.29 the shell length<sub>m</sub>, sd 0.05); last whorl rounded. Protoconch paucispiral, of 1.2 convex whorls (sd 0.1 wh); nucleus large, smooth, remaining portion with numerous, irregularly spaced axial wrinkles overrun by weak cordlets strengthening at the protoconch-teleoconch boundary. The latter sometimes marked by a relatively thick axial scar. Teleoconch<sub>m</sub> of 4.0 (sd 0.6 wh) inflated whorls (first two slightly angulated), with noticeable axial and spiral sculpture; suture slightly undulating. Axial sculpture of rounded, relatively dense, orthocline ribs (usually 11 on second whorl), extending across the sutures, on the last whorl fading towards the base. Growth lines evident, especially near the adapical suture. Spiral sculpture of spaced threads; finer and relatively homogeneous on sutural ramp, varying in strength below periphery; commonly two to four elements thicker than the others. One of the largest marks the edge of the sutural ramp. Aperture moderately wide, lanceolate (length<sub>m</sub> 2.1 mm, sd 0.4 mm); siphonal canal relatively short. Outer lip thin-edged, convex in profile, internally thickened; anal sinus C-shaped; columellar lip bent.

**Remarks.**—*Mangelia larga* sp. nov. shows distinctive features; the combination of its: (i) small size (e.g., length<sub>m</sub> 4.0 mm), (ii) small paucispiral protoconch, (iii) dense axial sculpture (usually 11 ribs on the second whorl), (iv) characteristic spiral sculpture (threads of alternating strength), (v) inflated teleoconch whorls and (vi) fusiform profile, allows *M. larga* sp. nov. to be easily distinguished from species reported herein and from those reported in the literature (e.g., Laskarew 1914; Kautsky 1925; Friedberg 1951; Zelinskaya et al. 1968; Bałuk 2003, 2006; see also SOM 1 for further details). Hence, no further comparative analyses were performed.

**Stratigraphic and geographic range.**—Pidhirtsi Beds, early Serravallian of the Central Paratethys.

### *Mangelia pseudorugulosa* sp. nov.

Figs. 3C, 4D, 5E; SOM 1: fig. 3C, SOM 2.

**Etymology:** From Greek *pseudo*, false, and Latin *ruga*, wrinkle; in reference to affinities with *Mangelia rugulosa* (Philippi, 1844).

**Type material:** Holotype, MGGC-24509, adult, well-preserved shell, outer lip slightly broken. Paratypes, MGGC-24510/1–14, from the type locality (SOM 2).

**Type locality:** Varovtsi, Ukraine.

**Type horizon:** Massive, white sandstone of the Pidhirtsi Beds, early Serravallian (~14.0–12.7 Ma).

**Material.**—Seventy-two specimens, of which sixty-two topotypes from Varovtsi: IGS-NANU-B-I-4-15/2015 (12 shs), MNHN.F.A53761 (10 shs), MSNG-58189 (10 shs),

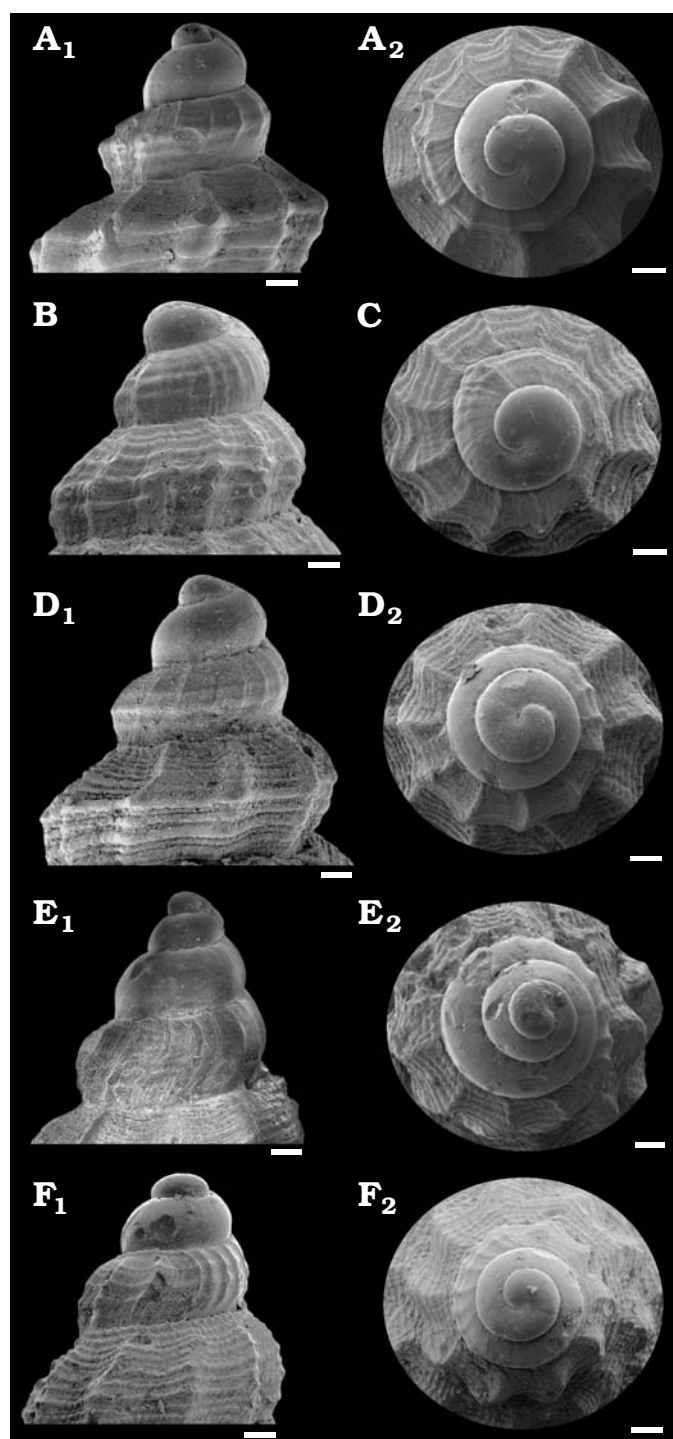


Fig. 4. SEM images of protoconch features of new conoidean gastropods from early Serravallian of western Ukraine, Varovtsi (A–C, F) and Velyka Levada (E). **A.** *Mangelia angulicosta* sp. nov., MGGC 24506/6. **B.** *Mangelia larga* sp. nov., MGGC-24508/1. **C.** *Mangelia larga* sp. nov., MGGC-24508/7. **D.** *Mangelia pseudorugulosa* sp. nov., MGGC-24510/9. **E.** *Mangelia odovychenae* sp. nov., MGGC-24512/1. **F.** *Bela varovtsiana* sp. nov., MGGC-24517/5. Views: A<sub>1</sub>, B, D<sub>1</sub>–F<sub>1</sub>, lateral; A<sub>2</sub>, C, D<sub>2</sub>–F<sub>2</sub>, apical. Scale bars 0.1 mm.

MGPT-PU135046 (10 shs), MZB-32056 (10 shs), NHMW-2015/0404/0003 (10 shs) and three topotypes from Velyka Levada, in batch ZISP-62075 (10 shs).



**Diagnosis.**—A small *Mangelia* species (shell length<sub>m</sub> 5.3 mm, sd 0.6 mm; shell width<sub>m</sub> 2.3 mm, sd 0.2 mm), characterised by a multispiral protoconch (length<sub>m</sub> 0.52 mm, sd 0.04 mm; width<sub>m</sub> 0.51 mm, sd 0.03 mm), a relatively tall spire (0.37 the shell length<sub>m</sub>, sd 0.02), and an almost straight columellar lip. Teleoconch sculpture of apically well rounded and thin ribs (max. 11 on the second whorl) and thin, round-topped threads densely indented by growth lines.

**Description.**—Shell small-sized, fusiform; spire slightly turreted (0.37 the shell length<sub>m</sub>, sd 0.02); last whorl rounded in profile. Protoconch<sub>m</sub> dome-shaped, of 2.1 slightly convex whorls (sd 0.1 wh.); nucleus small, smooth as the remaining whorls except for the final one-third, where 3–4 weak cordlets override low, curved, opisthocline axial riblets; protoconch-teleoconch boundary marked. Teleoconch<sub>m</sub> of 4.5 whorls (sd 0.5 wh), slightly convex in profile (apical ones tumid), with axial and subdued spiral sculpture; suture slightly undulating. Axial sculpture of rounded, well-spaced, slightly opisthocline ribs (usually 10 on second whorl), extending across the sutures on spiral whorls, until the base on the last whorl. Spiral sculpture of dense, thin elements, more homogeneous on sutural ramp, less uniform below periphery. On spiral whorls two to four thicker threads recognizable. Spiral elements densely indented (and/or beaded) by growth lines, the thinner sometimes truncated. Aperture moderately wide, sub-rectangular (length<sub>m</sub> 2.3 mm, sd 0.2 mm); siphonal canal short. Outer lip thin edged, slightly sigmoid in profile, internally thickened. Anal sinus C-shaped; columellar lip almost straight.

**Remarks.**—Friedberg (1951), in his review of molluscs from Poland and neighbouring regions, reported *Mangelia rugulosa* (Philippi, 1844) from the Miocene deposits of Olesko (Ukraine): i.e., the Pidhirtsi Beds of Studencka and Dulai (2010). Bałuk (2003) supported the attribution of the specimens described by Friedberg (1951) to *M. rugulosa* (Philippi 1844) and acknowledged the high degree of morphological variability of this taxon. We cannot confirm if the shells reported by these authors are conspecific with *M. rugulosa* (type locality Palermo, Italy; Philippi 1844), that is currently considered a junior synonym of *M. unifasciata* (Deshayes, 1835), a morphologically variable Atlantic and Mediterranean species (see Tucker 2004; WoRMs 2014). However, it is possible to compare the Varovtsi shells with *M. unifasciata* shells from the Mediterranean (SOM 1: fig. 4B–D, SOM 2).

Qualitative evaluation of some the morphological features of the species described by Philippi such as: (i) sub-rectangular aperture, (ii) short siphonal canal, (iii) thickening of the internal lip and its morphology, and (iv) teleoconch and protoconch shape, suggest a close affinity with *M. pseudorugulosa* sp. nov. (e.g., SOM 1: fig. 4B–D vs. Fig. 5E). Furthermore, statistical analyses performed on a set of *M. unifasciata* specimens from the Mediterranean and the type material of *M. pseudorugulosa* highlight that there is no significant difference between the two species with regard to all measured protoconch features, number of teleoconch

whorls and shell length (Fig. 2, Table 1, SOM 3). On the other hand, quantitative comparison supports a separation of the two taxa; the new species presents: (i) a narrower and shorter last whorl at comparable number of teleoconch whorls (e.g., width<sub>m</sub> 2.3 vs. 2.5,  $p = 0.017$ ); (ii) a greater number of ribs and fewer spiral elements (e.g., ribs<sub>m</sub> on second whorl 10.3 vs. 9.5;  $p < 0.01$ ); and (iii) a shorter aperture (length<sub>m</sub> 2.3 vs. 2.9,  $p < 0.01$ ; for further details see Fig. 2, Table 1, SOM 3). In addition, *M. rugulosa* morphotype (SOM 1: fig. 4C) possesses flatter spiral whorls and finer spiral sculpture. The analyses performed on *M. unifasciata* also suggested a higher coefficient of variation for most of the parameters considered here, supporting the high morphological variability already documented for this species (SOM 3). Lastly, one allied morphotype originally separated (i.e., morphotype 12 in SOM 2) on the basis of: (i) the thinner and more uniform spiral sculpture, (ii) the slender spire, (iii) the wider aperture, and (iv) the thin and smooth inside outer lip; overlapped with *M. pseudorugulosa* in all measured shell parameters (Fig. 2; Table 1, SOM 2, 3). Hence, we now consider it to fit within the intraspecific variability of the species (compare Fig. 5E vs. SOM 1: fig. 4F).

**Stratigraphic and geographic range.**—Pidhirtsi Beds, early Serravallian of the Central Paratethys.

### *Mangelia odovychenae* sp. nov.

Figs. 3D, 4E, 5F–H; SOM 1: fig. 3D, SOM 2.

**Etymology.** Named after Nadiia Odovychena (wife of Bruno Dell'Angelo) for the support provided during fieldwork in Ukraine.

**Type material.** Holotype, MGGC-24411, adult, moderately well preserved shell, outer lip slightly broken. Paratypes, MGGC-24512/1–9 and MGGC-24512/11–14 from the type locality, and MGGC-24512/10 from Horodok (SOM 2).

**Type locality.** Velyka Levada, Ukraine.

**Type horizon.** White sandstone of the Pidhirtsi Beds early Serravallian (~14.0–12.7 Ma).

**Material.**—Three topotypes from Velyka Levada: IGS-NANU-B-I-16-17/2015 (2 shs) and ZISP-62076 (1 sh).

**Diagnosis.**—A small *Mangelia* species (shell length<sub>m</sub> 6.2 mm, sd 0.5 mm; shell width<sub>m</sub> 2.6 mm, sd 0.3 mm), characterised by a relatively large, cone-shaped multispiral protoconch (length<sub>m</sub> 0.68 mm, sd 0.02 mm; width<sub>m</sub> 0.61 mm, sd 0.02 mm), a turreted spire, a straight columellar lip, and a teleoconch sculpture of rounded ribs (max 11 on the second whorl), along with a dense pattern of quite uniform spiral threads. The latter are densely indented and/or beaded at the intersection with growth lines.

**Description.**—Shell small-sized, fusiform; spire slightly turreted (0.36 shell length<sub>m</sub>, sd 0.02); last whorl slightly rounded, elongated (4.0 mm, sd 0.3 mm). Protoconch tall, cone-shaped of 2.7 convex whorls (sd 0.1 wh); nucleus very small, erect, smooth as remaining whorls except the latter half, where spaced, opisthocline, curved riblets are overrun, at the protoconch transition, by faint cordlets. Protoconch-teleoconch boundary abrupt, marked by

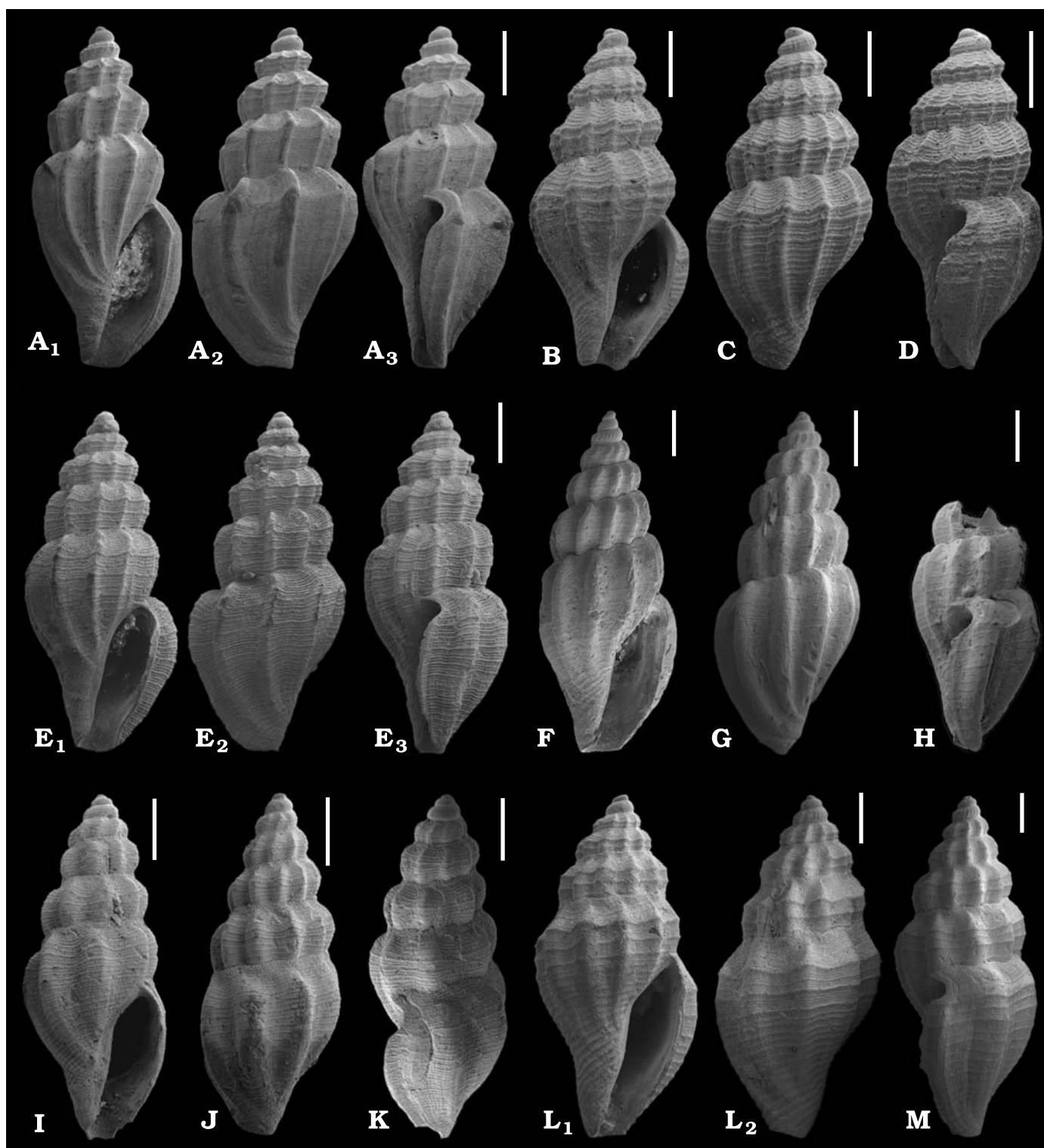


Fig. 5. SEM images of shell features of new conoidean gastropods from early Serravallian of western Ukraine, Varovtsi (A–E, I–M), Horodok (G), and Velyka Levada (F, H). **A.** *Mangelia angulicosta* sp. nov., MGGC-24506/6. **B–D.** *Mangelia larga* sp. nov. **B.** MGGC-24508/11. **C.** MGGC-24508/1. **D.** MGGC-24508/12. **E.** *Mangelia pseudorugulosa* sp. nov., MGGC-24510/9. **F–H.** *Mangelia odovychenae* sp. nov. **F.** MGGC-24512/1. **G.** MGGC-24512/10. **H.** MGGC-24512/topotype. **I–K.** *Bela varovtsiana* sp. nov. **I.** MGGC-24517/8. **J.** MGGC-24517/5. **K.** MGGC-24517/6. **L, M.** *Bela? robusta* sp. nov. **L.** MGGC-24519/8. **M.** MGGC-24519/1. Views: A<sub>1</sub>–L<sub>1</sub>, B, F, I, apertural; A<sub>2</sub>–L<sub>2</sub>, C, G, J, dorsal; A<sub>3</sub>, D, E<sub>3</sub>, H, K, M, lateral. Scale bars 1 mm.

a sinusigera. Teleoconch<sub>m</sub> of 4.4 whorls (sd 0.3 wh), evenly rounded in profile, with axial and subdued spiral sculpture; suture slightly undulating. Axial sculpture of opisthocline,

spaced, rounded ribs (usually 9 on second whorl), extending across the sutures on spiral whorls until the base on the last whorl; growth lines evident. Spiral sculpture of dense,

fairly uniform, thin threads separated by incised lines; however on early whorls and below periphery spiral elements less homogeneous. Spiral elements densely indented (or beaded) by growth lines, the thinner sometimes truncated (as in *M. pseudorugulosa*). Aperture moderately narrow, sub-rectangular (length<sub>m</sub> 2.8 mm, sd 0.2 mm); siphonal canal short but distinct. Outer lip thin-edged, rarely preserved, slightly rounded in profile, internally thickened; anal sinus C-shaped; columellar lip straight.

**Remarks.**—This species shows affinities to *M. pseudorugulosa* with regard to the teleoconch ornamentation pattern and overall outline. However, most of the measured teleoconch features show reduced overlap between the two species (see Fig. 2, SOM 2) and statistical tests allow us to reject the null hypothesis for all the measured features except for the number of teleoconch whorls (e.g., *M. pseudorugulosa* 4.5 vs. 4.4 *M. odovychenae*,  $p = 0.52$ ; for further details see Table 1, SOM 3). In detail, *M. odovychenae* can be reliably and easily separated from *M. pseudorugulosa* on the basis of the bigger teleoconch (e.g., length<sub>m</sub> 6.3 vs. 5.3 mm,  $p < 0.01$ ), the higher last whorl (length<sub>m</sub> 4.0 vs. 3.3 mm,  $p < 0.01$ ) and aperture size (length<sub>m</sub> 2.8 vs. 2.3 mm,  $p < 0.01$ ) at comparable number of teleoconch whorls. In addition, *M. odovychenae* shows a bigger and conical-shaped protoconch with a higher number of whorls (e.g., diameter<sub>m</sub> 0.61 vs. 0.51 mm,  $p < 0.01$ ; for further details see Table 1, SOM 3). Lastly, *M. odovychenae* compared to *M. pseudorugulosa* shows weaker and more reduced protoconch spiral sculpture and a smaller, more erect nucleus (Fig. 4E vs. Fig. 4D, SOM 2).

**Stratigraphic and geographic range.**—Pidhirtsi Beds, early Serravallian of the Central Paratethys.

## Genus *Bela* Leach in Gray, 1847

**Type species:** *Murex nebula* Montagu, 1803, Great Britain seas, Recent.

**Remarks.**—Identification of the type species of this genus was problematic because its type material was thought lost (e.g., Mariottini et al. 2009). Recently, the finding in the Montagu Collection (Exeter, UK) of six specimens of *M. nebula* led to its lectotype designation (Scarponi et al. 2014b). This designation allowed us to shed light on the morphology of this species and preliminarily characterize the great variability within *Bela* as currently conceived (Scarponi et al. 2014b). However, to strengthen the understanding and consistent usage of the genus *Bela*, a detailed quantitative characterisation of the genus is currently underway.

### *Bela varovtsiana* sp. nov.

Figs. 4F, 5I–K, 6A; SOM 1: fig. 3E, SOM 2.

**Etymology:** Named after the type locality (Varovtsi), where it occurs in abundance.

**Type material:** Holotype, MGGC-24516 adult, well-preserved shell. Paratypes, MGGC-24517/1–14 from the type locality (SOM 2).

**Type locality:** Varovtsi, Ukraine.

**Type horizon:** Massive, white sandstone of the Pidhirtsi Beds, early Serravallian (~14.0–12.7 Ma).

**Material.**—One hundred and five topotypes from Varovtsi: IGS-NANU-B-I-18-32/2015 (15 shs), MNHN.F.A53762 (15 shs), MSNG-58190 (15 shs), MGPT-PU135047 (15 shs), MZB-32057 (15 shs), NHMW-2015/0404/0004 (15 shs), and ZISP-62077 (15 shs).

**Diagnosis.**—A small-sized *Bela* (shell length<sub>m</sub> 4.7 mm, sd 1.0 mm; shell width<sub>m</sub> 2.1 mm, sd 0.4 mm), with multispiral protoconch with nodose ribs (length<sub>m</sub> 0.50 mm, sd 0.03 mm; width<sub>m</sub> 0.52 mm, sd 0.03 mm), relatively short spire (0.35 shell length<sub>m</sub>, sd 0.02) made of rounded whorls with a poorly-delimited sutural ramp; last whorl inflated; columellar lip straight and siphonal canal almost indistinct. Teleoconch sculpture of closely spaced, well rounded, relatively strong ribs (max. 11 on the second whorl) and a dense pattern of fine, but uneven and beaded threads.

**Description.**—Shell small-sized, fusiform; spire conical (0.35 shell length<sub>m</sub>, sd 0.02); last whorl slightly rounded. Protoconch<sub>m</sub> dome-shaped of 2.3 convex whorls (sd 0.2 wh); nucleus small, smooth as the remaining whorls except for the final one-third, where 3–4 faint cordlets override curved axials forming swollen tubercles at the intersections. Protoconch-teleoconch transition with pustules, marked by a sinusigera. Teleoconch<sub>m</sub> of 3.7 whorls (sd 0.3 wh) convex in profile, with strong axials and subdued spiral sculpture; suture marginated, undulating. Axial sculpture of prominent, rounded ribs (usually 10 on second whorl), thicker on their abapical portions, thinner upward, ending in proximity to the adapical suture. Growth lines dense, evident. Spiral sculpture of fine, relatively uniform threads alternating with thicker threads (usually 4 on second whorl), strengthening around periphery, interspaces of variable size. Spiral elements densely beaded by growth lines; the thinner ones often truncated. Aperture moderately wide, lanceolate (length<sub>m</sub> 2.2 mm, sd 0.4 mm); siphonal canal very short (almost indistinct); outer lip thin, smooth within, convex in profile; anal sinus relatively broad, v-shaped on the sutural ramp. Columellar lip slightly bent.

**Remarks.**—The combination of small size, rounded shoulder, shell sculpture, morphology of the aperture and position of the anal sinus suggests assignment to the genus *Bela* and more specifically to the *Bela nebula* group (see remarks in Scarponi et al. 2014b). *Bela varovtsiana* is morphologically similar to the recently described Mediterranean Pliocene *B. pseudoappeliusi* Naldi, Della Bella, and Scarponi, 2013 (SOM 1: fig. 4G, H), particularly in regard to teleoconch features such as: (i) shell dimensions and outline, (ii) number of whorls, (iii) morphology of the aperture and sinuses, and (iv) sculptural pattern of the shell: teleoconch of evident axial ribs overrun by densely beaded threads and protoconch of nodose axials and pustules. Furthermore, a great part of the teleoconch features measured here show a strong overlap between the two species (Fig. 2, SOM 2) with both parametric and non-parametric tests supporting this high morphological homogeneity (Table 1, SOM 3). However, when compared to *B. pseudoappeliusi*, it may be noted that *B. varovtsiana* sp.



nov. shows more numerous teleoconch ribs (mean 9.5 vs. 8.7 on second whorl;  $p < 0.01$ ), and less numerous, more spaced spiral elements (mean 4.6 vs. 7.8 on second whorl,  $p < 0.01$ ; Fig. 2, SOM 2). Furthermore, the protoconch of *B. varovtsiana* is notably smaller with respect to that of *B. pseudo-appeliusi* (e.g., length<sub>m</sub> 0.50 mm vs. 0.63 mm respectively,  $p < 0.01$ ; for further details see Fig. 2, SOM 2); this clear separation is also strongly supported by all relevant tests here employed (Table 1 and SOM 3).

**Stratigraphic and geographic range.**—Pidhirtsi Beds, early Serravallian of the Central Paratethys.

*Bela? robusta* sp. nov.

Figs. 5L, M, 6B, 7A; SOM 1: fig. 3F, SOM 2.

**Etymology:** From Latin *robustus*, hard, firm; named after the solid shape of the teleoconch.

**Type material:** Holotype, MGGC-24518, adult, well-preserved shell. Paratypes, MGGC 24519/1–14 from the type locality (SOM 2).

**Type locality:** Varovtsi, Ukraine.

**Type horizon:** Massive, white sandstone of the Pidhirtsi Beds, early Serravallian (~14.0–12.7 Ma).

**Material.**—Type material only.

**Diagnosis.**—A relatively large, biconical *Bela* (shell length<sub>m</sub> 6.7 mm, sd 2.0 mm; shell width<sub>m</sub> 3.2 mm, sd 0.7 mm), with multispiral protoconch (length<sub>m</sub> 0.57 mm, sd 0.04 mm; width<sub>m</sub> 0.59 mm, sd 0.02 mm), characterised by few and relatively strong riblets. Teleoconch whorls rounded with a sculpture of relatively spaced ribs (max. 11 on the second whorl) and a dense pattern of spiral elements of variable thickness. Outer lip thin, straight in profile, anal sinus on sutural ramp, siphonal canal almost indistinct.

**Description.**—Shell small-sized, biconical, solid; spire slightly turreted (0.32 the shell length; sd 0.03); last whorl elongated (length<sub>m</sub> 4.7 mm, sd 1.2 mm), slightly rounded. Protoconch<sub>m</sub> dome-shaped of 2.2 convex whorls (sd 0.1 wh); nucleus small, smooth as the remaining except for the final-quarter, where 3–4 faint cordlets override curved, relatively thick riblets. Protoconch-teleoconch boundary well-marked by a sinusigera. Teleoconch<sub>m</sub> of 4.5 whorls (sd 0.7 wh), slightly convex in profile, with strong axials and subdued spiral sculpture; suture undulating. Axial sculpture of thick, rounded, narrowly spaced ribs (usually 10 on the second whorl) extending across sutures on spiral whorls, fading out towards the base on last whorl; growth lines dense, evident. Spiral elements densely indented, the thinner ones often truncated, the thicker sometimes beaded by growth lines. Aperture elongate, relatively narrow, sub-rectangular, about half of the shell height (length<sub>m</sub> 3.3 mm, sd 0.8 mm); siphonal canal very short, almost indistinct; outer lip thin, smooth inside, straight in profile; anal sinus relatively broad, commonly L-to-C shaped, on the sutural ramp; columellar lip slightly bent.

**Remarks.**—This species is tentatively assigned herein to the genus *Bela* sensu lato on the basis of comparable teleoconch

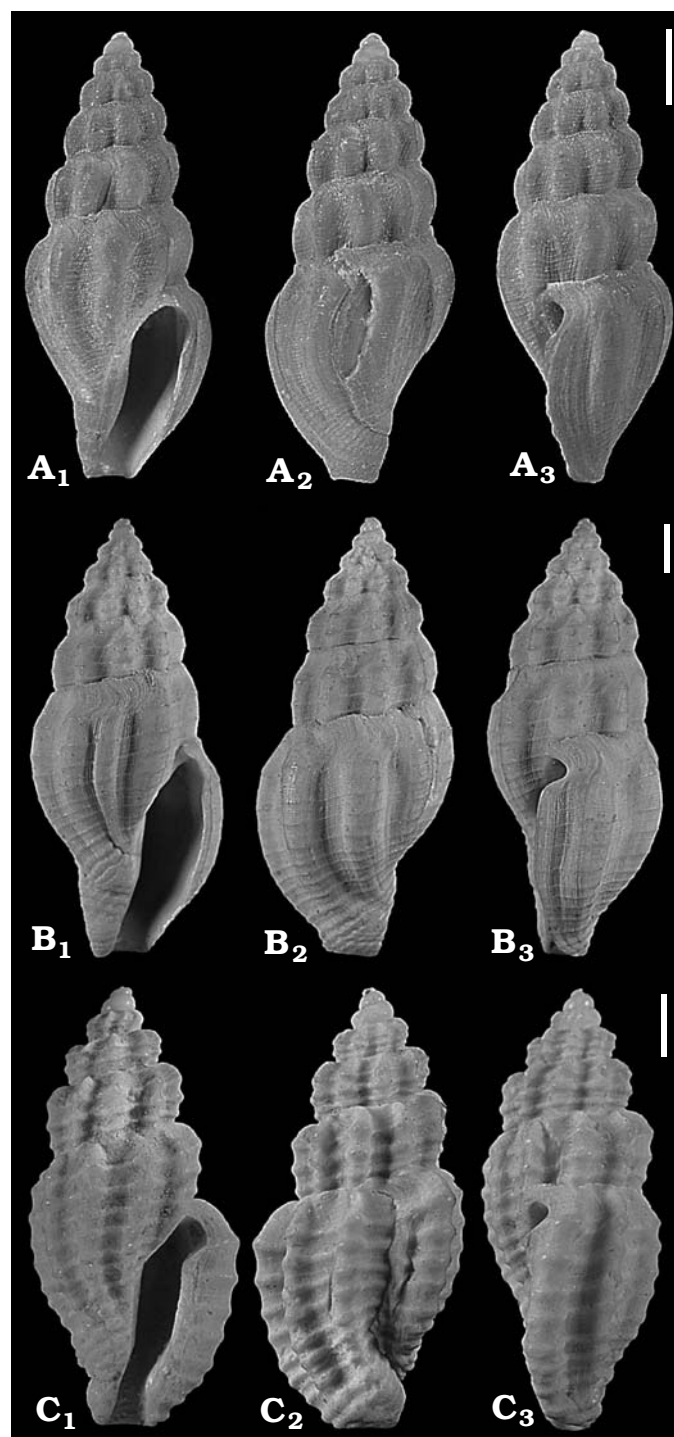


Fig. 6. Photomicrographs of holotype shell of new conoidean gastropods from early Serravallian of western Ukraine, Varovtsi (A, B) and Horodok (C). **A.** *Bela varovtsiana* sp. nov., MGGC-24516. **B.** *Bela? robusta* sp. nov., MGGC-24518. **C.** *Pyrgocythara turrispiralata* sp. nov., MGGC-24514. Views: A<sub>1</sub>–C<sub>1</sub>, apertural; A<sub>2</sub>–C<sub>2</sub>, dorsal; A<sub>3</sub>–C<sub>3</sub>, lateral. Scale bars 1 mm.

and protoconch sculptural pattern and overall shell profile and dimensions. Close affinities are considered also with the genus *Brachycythara* Woodring, 1928. Indeed, the shell differences between the genera *Brachycythara* and *Bela* are minor and mainly refer to the following: *Brachycythara* shells are smaller (length < 9 mm), stouter, with the outer lip



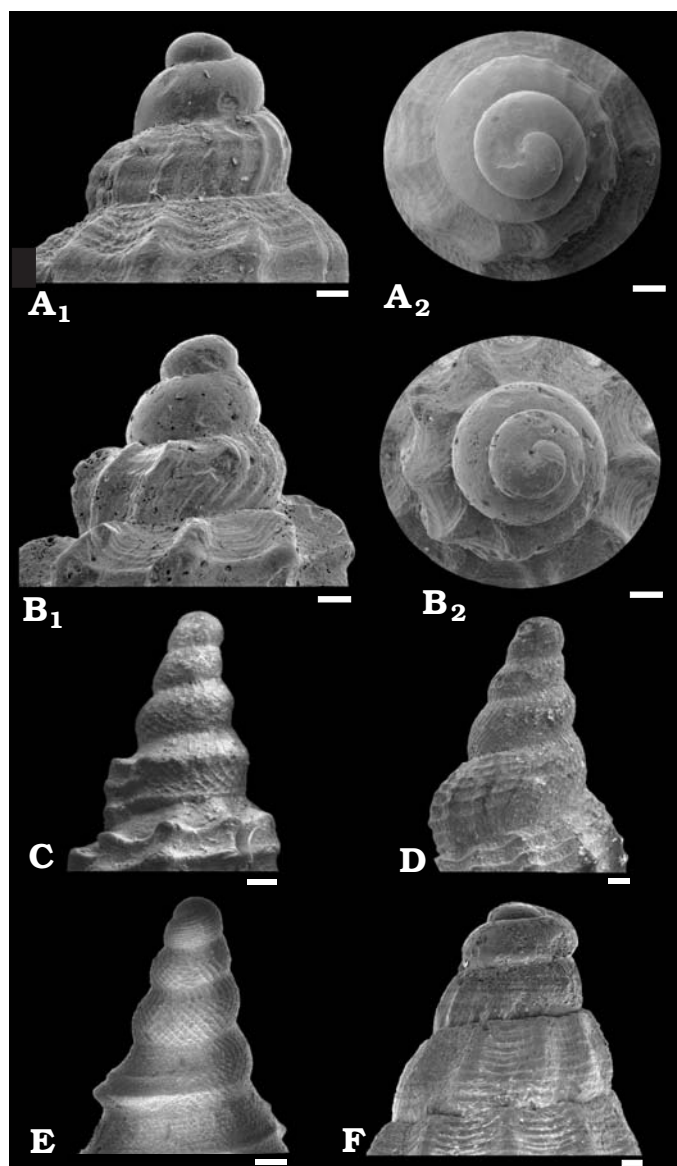


Fig. 7. SEM images of protoconch features of conoidean gastropods from early Serravallian of western Ukraine, Varovtsi (A, C–F) and Horodok (B). **A.** *Bela? robusta* sp. nov., MGGC-24519/8. **B.** *Pyrgocythara turrspirallata* sp. nov., MGGC-24515/11. **C.** *Raphitoma* cf. *R. ringicula* (Boettger, 1902), MGGC-24522/5. **D.** *Andonia* sp. aff. *A. transsylvanica* (Hoernes and Auinger, 1890), MGGC 24523/2. **E.** *Teretia* cf. *T. turritelloides* (Bellardi, 1847), MGGC-24524/5. **F.** *Haedroleura* sp. aff. *H. septangularis* (Montagu, 1803), MGGC-24520/6. Views: A<sub>1</sub>, B<sub>1</sub>, C–F, lateral; A<sub>2</sub>, B<sub>2</sub>, apical. Scale bars 0.1 mm.

slightly thickened and parietal callus moderately developed; protoconch sculpture is of crowded riblets whereas teleoconch sculpture is of stout axial folds overridden by finer (with respect to *Bela*) spiral elements (Powell 1967; Smriglio et al. 2007). Here, the absence of: (i) parietal callus; (ii) lirae inside the outer lip, and (iii) a dense pattern of protoconch riblets suggest caution in the assignment of this new species to the genus *Brachycythara*. However, the current definitions of the genera *Bela* and *Brachycythara* are rather broad and need refining (Smriglio et al. 2007; Scarponi et al. 2014b). For instance, *Brachycythara beatriceae* Mariottini,

2007 and *B. atlantidea* (Knudsen, 1952), two Mediterranean species that show similarities regarding the teleoconch with our material, were recently placed within the genus *Bela* sensu lato (see Mariottini et al. 2012). *Bela? robusta* can be easily distinguished by *B. atlantidea* and *B. beatriceae* by a smaller and less sculptured protoconch, and a less regular teleoconch spiral pattern. Hence, no further comparative analyses were performed.

**Stratigraphic and geographic range.**—Pidhirtsi Beds, early Serravallian of the Central Paratethys.

### Genus *Pyrgocythara* Woodring, 1928

**Type species:** *Pyrgocythara eminula* Woodring, 1928; Bowden (Jamaica); Pliocene.

**Remarks.**—Powell (1967) provided a useful description for this rarely cited but widespread genus (see Tucker 2004; Vera-Pelaez et al. 1999); herein we highlight its main features. The genus is characterised by a protoconch with axial sculpture only, and the teleoconch bears prominent but narrow axial ribs which are overrun by noticeable and widely spaced spiral cords. The interspaces among cords are occupied by dense and thin spiral threads. The aperture is elongate and narrow (rectangular-shaped) with a noticeable anal sinus bearing (inside the outer lip) a tubercle just below its lower edge.

### *Pyrgocythara turrspirallata* sp. nov.

Figs. 6C, 7B, 8A, B; SOM 1: fig. 3G, SOM 2.

**Etymology.** From Latin *turris*, tower, and Greek *speira*, spire; named after the characteristic turreted spire.

**Type material:** Holotype, MGGC-24514, adult, well-preserved shell. Paratypes, MGGC-24515/1–14 from the type locality (SOM 2).

**Type locality:** Horodok, Ukraine.

**Type horizon:** Weakly-cemented sandstone, attributed to the Pidhirtsi Beds, early Serravallian (~14.0–12.7 Ma).

**Material.**—Twenty-two topotype specimens from Horodok: IGS-NANU-B-I-33-35/2015 (3 shs), MNHN.F.A53763 (3 shs); MSNG-58191 (3 shs), MGPT-PU135048 (3 shs), MZB-32058 (4 shs), NHMW-2015/0404/0005 (3 shs), ZISP-62078 (3 shs) and one (not well preserved) from Varovtsi: IGS-NANU-B-I-33/2015.

**Diagnosis.**—A medium-sized *Pyrgocythara* (shell length<sub>m</sub> 6.3 mm, sd 0.6 mm; shell width<sub>m</sub> 2.9 mm, sd 0.3 mm), with a multispiral, conical-shaped protoconch (width<sub>m</sub> 0.60 mm, sd 0.04 mm) and characterised by a few, strongly curved riblets. The teleoconch shows a turreted spire (0.33 the shell length<sub>m</sub>, sd 0.03) and a noticeable spiral pattern of strong cords on spiral whorls (commonly 3 on the second whorl); the last whorl is elongated and varicose, bearing a sub-rectangular and narrow aperture.

**Description.**—Shell small-sized, fusiform; spire strongly turreted (0.33 the shell length<sub>m</sub>, sd 0.03); last whorl slightly rounded, elongated (length<sub>m</sub> 4.2 mm, sd 0.4 mm), varicose. Protoconch conical, of 2.5–2.2 whorls, nucleus very small, smooth as the remaining whorls except for few opisthocline,

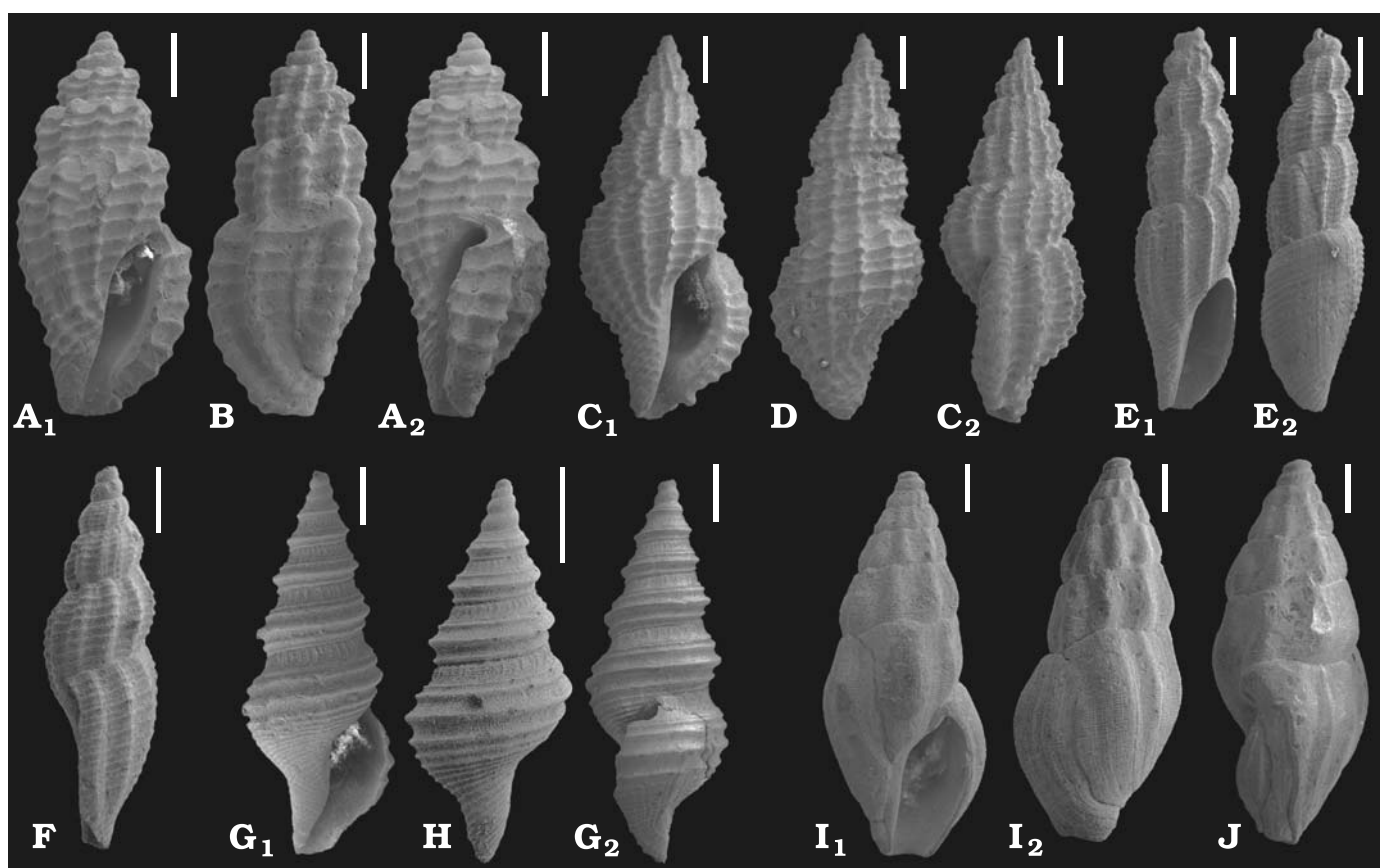


Fig. 8. SEM images of shell features of conoidean gastropods from early Serravallian of western Ukraine, Horodok (A, B) and Varovtsi (C–J). **A, B.** *Pyr-gocythara turrispiralata* sp. nov. **A.** MGGC-24515/11. **B.** MGGC-24515/9. **C, D.** *Raphitoma* cf. *R. ringicula* (Boettger, 1902). **C.** MGGC-24522/1. **D.** MGGC-24522/3. **E, F.** *Andonia* sp. aff. *A. transsilvanica* (Hoernes and Auinger, 1890). **E.** MGGC-24523/1. **F.** MGGC-24523/3. **G, H.** *Teretia* cf. *T. turritelloides* (Bellardi, 1847). **G.** MGGC-24524/3. **H.** MGGC-24524/5. **I, J.** *Haedropleura* sp. aff. *H. septangularis* (Montagu, 1803). **I.** MGGC-24520/6. **J.** MGGC-24520/11. Views: A<sub>1</sub>, C<sub>1</sub>, E<sub>1</sub>, G<sub>1</sub>, I<sub>1</sub>, apertural; B, D, E<sub>2</sub>, H, I<sub>2</sub>, dorsal; A<sub>2</sub>, C<sub>2</sub>, F, G<sub>2</sub>, J, lateral. Scale bars 1 mm.

curved axial riblets in the final-quarter; protoconch-teleoconch boundary abrupt, marked by a sinusigera. Teleoconch<sub>m</sub> of 4.1 whorls (sd 0.3 wh), flattened in profile, with both strong axial and spiral sculpture; suture almost straight. Axial sculpture of prominent, slightly opisthoclinal, rounded and spaced ribs (usually 9 on second whorl), extending across the sutures on spiral whorls, until the base on last whorl; growth lines occasionally evident. Spiral pattern of relatively thick, widely spaced cords (usually 3 on second whorl) separating small groups of very thin threads indented by growth lines; on sutural ramp threads less homogeneous than below periphery. Aperture elongated (mean 2.9 mm, sd 0.3 mm), narrow, sub-rectangular; outer lip almost straight in profile, internally thickened. Anal sinus relatively wide, C-shaped, bearing (inside the outer lip) a swollen tubercle; siphonal canal very short, clearly distinct; columellar lip almost straight.

**Remarks.**—Various authors have already documented few species that show morphological similarities to *P. turrispiralata* sp. nov. for the Central Paratethys and Mediterranean areas. Among others, Friedberg (1951) and Bałuk (2003) report: (i) *Clathromangelia clathrata* (Serres, 1829) from the Miocene of Ukraine and Poland; (ii) *Mangelia monterosati* Bellardi, 1877 from the Ukraine (Friedberg 1951); (iii) *Man-*

*gelia contracta* Bellardi, 1877 from Poland (Bałuk 2003). *Clathromangelia clathrata* shows a somewhat comparable shell outline and teleoconch ornamental pattern; however, it can be easily differentiated from *P. turrispiralata* by its (*Raphitoma*-like) protoconch sculpture and the teleoconch spiral ornamentation, consisting of two prominent cords on spiral whorls (for further details see Glibert 1954; Bałuk 2003).

In reference to *Mangelia monterosati*, the type material is missing (Ferrero Mortara et al. 1981). Regrettably, the original description and accompanying iconography do not provide sufficient detail to characterise the species. Consequently, it should be considered a nomen dubium.

The type material of *M. contracta* is housed at the Museo Regionale di Scienze Naturali in Turin (Italy). Ferrero Mortara et al. (1981) illustrated the two syntypes; both show more flattened and tall teleoconch whorls, with less numerous ribs (max. 9) and more numerous spiral elements than *P. turrispiralata* (see also Bellardi 1877). Unfortunately, both specimens are lacking the apex and thus the highly diagnostic protoconch features cannot be evaluated. At the present time *M. contracta* cannot be precisely characterised until new material from the type locality is found.

Lastly, *Pyrgocythara rugosissima* (Seguenza, 1875), an extinct Mediterranean Pliocene mangeliid (Tucker 2004; Scarponi and Della Bella 2010; SOM 1: fig. 4I), is morphologically comparable to *P. turrispiralata*, in particular with regard to the aperture and sinus morphology and the teleoconch sculpture. However, detailed quantitative comparison of shell characters between batches of specimens allowed a clear separation of the two allied species (Fig. 2, SOM 2). *P. rugosissima* shows a notably larger protoconch (e.g., width<sub>m</sub> 0.73 mm, sd 0.03) and the final one and half whorls bear ornamentation, whereas *P. turrispiralata* is smaller (e.g., width<sub>m</sub> 0.60, sd 0.04) bearing ornamentation only on its final quarter (for further details see Fig. 2, SOM 2). In addition, all the measured teleoconch features (except for spiral sculpture) show reduced or no overlap between the two taxa, with *P. rugosissima* showing smaller values than those of *P. turrispiralata* (see Fig. 2, SOM 2) and relevant statistical tests allow us to reject the null hypothesis (i.e., no difference between the two samples) for all features (Table 1) except for the major threads on the second whorl (i.e., 2.7 vs. 2.9,  $p = 0.42$ ; SOM 3).

**Stratigraphic and geographic range.**—Pidhirtsi Beds, early Serravallian of the Central Paratethys.

## Family Raphitomidae Bellardi, 1875

### Genus *Raphitoma* Bellardi, 1847

**Type species:** *Raphitoma hystrix* Jan in Bellardi, 1847; Asti and surroundings (Northern Italy); Pliocene.

#### *Raphitoma* cf. *R. ringicula* (Boettger, 1902)

Figs. 7C, 8C, D; SOM 1: fig. 3H, SOM 2.

**Material.**—Five specimens from Varovtsi, Pidhirtsi Beds, early Serravallian; MGGC-24522/1–5, one nearly complete, four with broken protoconch and outer lip (SOM 2).

**Remarks.**—The type material of this small raphitomid, along with many other conoideans from the Middle Miocene (Badenian) of Kostež (Transylvania, Romania), were destroyed during the second world war (Ronald Janssen 2014 personal communication). No type material is currently available; hence our attribution is tentative and mainly based on the original documented description (Boettger 1902) and illustrations by Zilch (1934) and Bałuk (2006).

### Genus *Andonia* Harris and Burrows, 1890

**Type species:** *Fusus bonellii* Gené in Bellardi and Michelotti, 1840; Colli Astesi (Northern Italy); Pliocene.

#### *Andonia* sp. aff. *A. transsylvanica* (Hoernes and Auinger, 1890)

Figs. 7D, 8E, F; SOM 1: fig. 3I, SOM 2.

**Material.**—Four specimens from Varovtsi, Pidhirtsi Beds, early Serravallian; MGGC-24523/1–4, one juvenile specimen is complete (SOM 2).

**Remarks.**—*A. transsylvanica* is a rare species with affinity to *A. bonelli* (Bellardi and Michelotti, 1840). Our specimens

fall within the morphological variability of the original type material illustrated in Hoernes and Auinger (1890: pl. 32: 9, 11) and housed at NHMW (two syntypes, inventory number 1867/0019/0172; Mathias Harzhauser, personal communication 2014). The two syntypes, however, show quite different morphological features, and recently were considered to belong to different species (Landau et al. 2013). The latter authors designated as lectotype of *A. transsylvanica* the shell illustrated as fig. 9 in Hoernes and Auinger (1890; SOM 1: fig. 4J), and considered the shell illustrated as fig. 11 as an open nomenclature species. The material from Ukraine is perhaps conspecific with the latter unnamed specimen (i.e., Hoernes and Auinger 1980: fig. 11; SOM 1: fig. 4K, SOM 2). Unfortunately, our material (and the material housed at NHMW) is scanty and not well preserved. Given these premises, it is preferable at the moment to leave this taxon in open nomenclature: more material is needed to study in detail its variability and its taxonomic relation to allied material from the Miocene of the North Sea Basin (see Janssen 1984).

### Genus *Teretia* Norman, 1888

**Type species:** *Pleurotoma anceps* Eichwald, 1830; Żukowce (Ukraine); Miocene.

#### *Teretia* cf. *T. turritelloides* (Bellardi, 1847)

Figs. 7E, 8G, H, SOM 1: fig. 3J, SOM 2.

**Material.**—Five specimens from Varovtsi Pidhirtsi Beds, early Serravallian; MGGC-24524/1–5, three in good conditions (SOM 2).

**Remarks.**—This morphotype resembles *Teretia fusianiceps* Nordsieck, 1972, however, the carinated spiral whorls along with a shorter protoconch allow for an immediate separation from *T. fusianiceps* (see Janssen and Wienrich 2007). Our specimens fully correspond to the description and iconography of *T. turritelloides* type material as reported in Bellardi (1847), Ferrero Mortara et al. (1981) and Brunetti and Vecchi (2003). Unfortunately no complete protoconch was available from the type material that ranges in age from the Serravallian to Pliocene (Ferrero Mortara et al. 1981). As the protoconch characters are of fundamental importance in the identification of the majority of the conoideans, we herein recommend the conservative *Teretia* cf. *T. turritelloides* usage pending future revision of protoconch characters on new material from the type area.

## Family Horaiclavidae Bouchet, Kantor, Sysoev, and Puillandre, 2011

### Genus *Haedropleura* Bucquoy, Dautzenberg, and Dollfus, 1883

**Type species:** *Murex septangularis* Montagu, 1803; Falmouth, Salcomb Bay and Weymouth; Recent.

**Remarks.**—The genus has recently been placed within the family Horaiclavidae (Bouchet et al. 2011), mainly on the basis of its morphological affinity to *Horaiclavus* Oyama,



1954 (type genus of Horaiclavidae). Further details regarding the taxonomic placement of *Haedropleura* are given in Bouchet et al. 2011; Scarponi et al. 2011b).

*Haedropleura* sp. aff. *H. septangularis* (Montagu, 1803)

Figs. 7F, 8I, J; SOM 1: fig. 3K, SOM 2.

**Material.**—Eleven specimens from Varovtsi, Pidhirtsi Beds, early Serravallian; MGGC-23525/1–11, of which only three are in fair/good conditions (SOM 2).

**Remarks.**—Our specimens show affinity with *Haedropleura septangularis*, a Recent Mediterranean and East Atlantic species also cited in the “Helvetian” of the Loire Basin (Glibert 1954; this material needs further investigation), Pliocene of England (Harmer 1915) and Plio–Pleistocene of the Mediterranean (Scarponi et al. 2011b). The two taxa present comparable juvenile development and similar teleoconch morphology (see Scarponi et al. 2011b; SOM 1: fig. 4L, M, SOM 2). However, Ukrainian specimens relative to *H. septangularis* show a smaller teleoconch (and shorter last whorl and aperture; Fig. 2, SOM 2). Also statistical tests do not support equality of the targeted teleoconch parameters between the two taxa (Table 1, SOM 3). However, the extremely small sample size for all protoconch and sculpture features of *Haedropleura* sp. (i.e., only 2–4 observations; Table 1, SOM 3), suggest caution and additional, well preserved, material is needed to reach more reliable conclusions. Also, *Haedropleura pseudoseptangularis* Gürs, 2001, seems to be another related (but distinct) species. Unfortunately, *H. pseudoseptangularis* is rarely found (Tucker 2004), and its intra-specific variability, at the moment, cannot be assessed. Indeed, only one specimen has been described from the upper Miocene (~14.5 Ma) of the North Sea Basin. We refer to Gürs (2001) for illustration and description of the only known specimen. In conclusion, our morphotype presents certain protoconch and teleoconch features akin to *H. septangularis* whereas the teleoconch sculpture (especially rib morphology), and final whorl resemble *H. pseudoseptangularis* (Gürs 2001). Unfortunately the small number of well-preserved specimens from Varovtsi (SOM 2) is considered insufficient to assess the variability of this taxon; therefore its taxonomic position is left open.

## Concluding remarks

**Methodologic and taxonomic inferences.**—Herein, a comprehensive approach was adopted in order to incorporate interspecific and intraspecific variation in shell morphology when describing taxa. Basic measurements of shell characters coupled with descriptive terminology have allowed morphologically very similar taxa to be distinguished (e.g., *Pyrgochytara rugosissima* vs. *P. turrispiralata* or *Mangelia rugulosa* vs. *M. pseudorugulosa*). The implication is that,

when numerous specimens are available, taxonomic investigations are greatly aided by employing quantitative methods, as the results can be used to validate qualitative interpretations.

The analyses conducted here allowed for the identification of eleven species, belonging to seven genera and representing three families within the Conoidea. The recovered taxa constitute just a small fraction of the Serravallian conoideans known from the Central Paratethys and surrounding areas (e.g., Bałuk 2003; Landau et al. 2013 and references therein). In comparison to previous papers (see references above), this research highlights a significant increase in alpha-diversity of conoideans within the studied deposits as well as a minimum in geographic overlap with previously reported conoideans at the species level. However, the implications of this study for biotic trends at the regional scale are limited given its reduced area and taxonomic range (only conoideans). Interestingly, seven (out of eleven) species are new to science, while the remaining are attributed (with different levels of confidence) to previously documented taxa. This high degree of new species with respect to the total recognized should not be overemphasised, as a combination of methodological factors may have conspired to enhance this trend (e.g., previous taxonomic homogenization coupled with a dearth of taxonomic conoidean studies for the studied area; see previous sections). Lastly, none of the species studied were recovered in all three sites and six out of eleven species occur in only one site. This elevated patchiness at the species level suggests a high degree of habitat-fragmentation within a relatively restricted area. This interpretation agrees well with the environmental setting (back-reef to shallow marine) of the study area during the interval of deposition of the Pirdhirs Beds (Studencka and Dulai 2010).

**Palaeoclimatological and palaeobiogeographical inferences.**—At family- and genus-level, the low richness of conoideans in western Ukraine needs to be explained. Indeed, of the documented fifteen families of Conoidea (Bouchet et al. 2011), only three have been collected in the lower Serravallian deposits of western Ukraine: Mangeliidae, Raphitomidae, and Horaiclavidae. These families, here represented by three, three, and one genera respectively (SOM 2), are represented cumulatively by at least 100 genera in the Paratethys. The limited area of study coupled with the lithological constraint (i.e., only coarse-sand deposits sampled), may have played a role in limiting recovered richness. However, the lack of entire groups of warm-water, shallow-marine taxa (e.g., Conidae, Clavatulidae or Pseudomelatomidae) cannot be accounted for by study-area limitations and/or lithofacies constraints alone. Representatives of these warm water taxa have commonly been found in back barrier/shallow marine sandy facies of many modern environments (e.g., Tunnell et al. 2010) and comparable shallow water settings of the Paratethys (e.g., Friedberg 1951; Bałuk 2003). The “impoverished” conoidean fauna from the western region of Ukraine during



the early Serravallian (13–14 Ma, see Geological setting section) is interpreted as mainly resulting from the middle Miocene climatic transition (MMCT 14.2–13.8 Ma), a major global cooling (Shevenell et al. 2004). According to Harzhauser and Piller (2007), the Paratethys experienced a drop of the minimum sea-surface temperature from at least 16–18°C during the early Badenian optimum to 14–15°C during the MMCT in the late Badenian. Hence, climate deterioration is considered the main driver of the lack of warm-water indicators among conoideans of western Ukraine. Indeed, the most abundant family represented here is the Mangeliidae; specifically *Mangelia* (SOM 2), a genus well-represented among conoideans in modern Mediterranean–Eastern Atlantic shallow marine environments (e.g., Tucker 2004; Spada and Della Bella 2010).

The palaeobiogeographical aspects of the genera included herein suggest a clear proto-Mediterranean–Atlantic affinity. At the species level, *Raphitoma* cf. *R. ringicula* and *Andonia* sp. aff. *A. transsylvanica* have a Paratethyan origin, whereas *Teretia* cf. *T. turritelloides* belongs to the proto-Mediterranean realm. Additionally, *Haedroleura* sp. aff. *H. septangularis*, *Mangelia pseudorugulosa* sp. nov., and *Pyrgochythara turrispiralata* sp. nov. show close morphological affinities to Neogene proto-Mediterranean–Atlantic taxa. These findings support the recent challenge to the supposed high endemism of the late Badenian Central Paratethys in favour of a more complex and intermingled pattern of communication between the Paratethys and neighbouring regions (Landau et al. 2013; Bartol et al. 2014, among others). Unfortunately, our sampling scheme, focusing on a relatively small geographic area coupled with a lack of species level systematization of the Conoidea in classical literature (which primarily focused on teleoconch shell characters and gave little information regarding protoconch features), hampers detailed paleogeographic reconstructions of the primary connections between the Paratethys and the Proto-Mediterranean through late Badenian (e.g., via the Slovenian Corridor and/or Axios Trench; see Bartol et al. 2014 for a detailed discussion on this topic). In order to move forward, we suggest a re-evaluation of historical samples of conoideans from central-eastern Europe utilising a more quantitatively-based approach in order to accurately reconstruct the palaeogeographic pattern of dispersal between Proto-Mediterranean and Paratethys thorough the Miocene.

## Acknowledgements

We wish to thank Nadiia Odovychena (wife of one of the authors, BD) and her children (Roman and Liudmyla) for the support provided during the field research in Ukraine. Olga and Vitalij Anistratenko (IGS-NANU) for the support given during fieldwork in 2009. We are also indebted to Mathias Harzhauser (NHMW), Ronald Janssen (Senckenberg Research Institute and Natural History Museum Frankfurt a. Main, Germany); Daniele Ormezzano (MSNT), and Boris Sirenko (ZISP) for help with type material under their care. Sergio Raffi (Bologna University, Italy) for helpful discussions on this topic. We thank also

Didier Merle (Muséum National d'Histoire Naturelle, Paris, France), Bernard Landau (Naturalis Biodiversity Center, Leiden, Netherlands) and an anonymous reviewer for their comments that improved this manuscript. This work was supported by Bologna University as part of Ricerca Fondamentale Orientata 2013 (coordinator: DS).

## References

- Andreyeva-Grigorovich, A.S., Kulchytsky, Y.O., Gruzman, A.D., Lozynyak, P.Y., Petrashkevich, M.I., Portnyagina, L.O., Ivanina, A.V., Smirnov, S.E., Trofimovich, N.A., Savitskaya, N.A., and Shvareva, N.J. 1997. Regional stratigraphic scheme on Neogene formations of the Central Paratethys in the Ukraine. *Geologica Carpathica* 48: 123–136.
- Anistratenko, O.Yu. and Anistratenko, V.V. 2007. Minute patellogastropods (Mollusca, Lottiidae) from the Middle Miocene of Paratethys. *Acta Geologica Polonica* 57: 343–376.
- Anistratenko, O.Yu., Bandel, K., and Anistratenko, V.V. 2006. A new genus of patellogastropod with unusual protoconch from Miocene of Paratethys. *Acta Palaeontologica Polonica* 51: 155–164.
- Arnaud, P.M. 1978. Revision des taxa malacologiques méditerranéens introduit par Antoine Risso. *Annales du Muséum d'Histoire Naturelle de Nice* 5: 101–150.
- Arnold, W.H. 1965. A glossary of a thousand-and-one used in conchology. *Veliger* 7 (Supplement): 1–50.
- Baluk, W. 2003. Middle Miocene (Badenian) gastropods from Korytnica, Poland; part IV–Turridae. *Acta Geologica Polonica* 53: 29–78.
- Baluk, W. 2006. Middle Miocene (Badenian) gastropods from Korytnica, Poland; Part V. Addenda et Corrigenda ad Prosobranchia. *Acta Geologica Polonica* 56: 177–220.
- Bartol, M., Mikuž, V., and Horvat, A. 2014. Palaeontological evidence of communication between the Central Paratethys and the Mediterranean in the late Badenian/early Serravalian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 394: 144–157.
- Bellardi, L. 1847. Monografia delle Pleurotome fossili del Piemonte. *Memorie della Reale Accademia delle Scienze di Torino, Serie 2* 9: 531–650.
- Bellardi, L. 1875. Novae pleurotomidarum Pedimonti et Liguriaie fossilium: dispositionis prodromus. *Bullettino della Società Malacologica Italiana* 1: 16–24.
- Bellardi, L. 1877. I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte II. *Memorie della Reale Accademia delle Scienze di Torino, Serie 2* 29: 1–373.
- Bellardi, L. and Michelotti, G. 1840. Saggio oritographico sulla classe dei gasteropodi fossili dei terreni terziarii del Piemonte. *Memorie della Reale Accademia delle Scienze di Torino, Serie 2* 3: 93–174.
- Beninger, P.G., Boldina, I., and Katsanekakis, S. 2012. Strengthening statistical usage in marine ecology. *Journal of Experimental Marine Biology and Ecology* 426–427: 97–108.
- Boettger, O. 1902. Zur Kenntnis der Fauna der Mittelmiozänen Schichten von Kostež im Krassó-Szörénver Komitat. *Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt* 51: 1–200.
- Bouchet, P., Kantor, Y.I., Sysoev, A., and Puillandre, N. 2011. A new operational classification of the Conoidea. *Journal of Molluscan Studies* 77: 273–308.
- Brunetti, M. and Vecchi G. 2003. Sul ritrovamento di *Teretia elegantissima* (Foresti, 1868) in terreni pliocenici dell'Emilia e della Toscana. *Bollettino della Società Paleontologica Italiana* 42: 49–57.
- Bucquoy, E., Dautzenberg, P., and Dollfus, G. 1883. *Les Mollusques Marins de Roussillon. Tome Premier: Gastropodes avec Atlas de 66 Planches*. 196 pp. J.-B. Baillière & Fils, Paris.
- Dayrat, B. 2005. Toward integrative taxonomy. *Biological Journal of the Linnean Society* 85: 407–415.
- Deshayes, G.P. 1835. *Expédition Scientifique de Morée. Vol. 3 (Mollusques)*. 203 pp. Bertrand, Paris.

- Eichwald, E. 1830. *Naturhistorische Skizze von Lithauen, Volhynien und Podolien in Geognostisch-Mineralogischer, Botanischer und Zoologischer Hinsicht*. 256 pp. J. Zawadzki, Vilnius.
- Fedosov, A., Watkins, M., Heralde III, F.M., Corneli, P.S., Concepcion G.P., and Olivera, B.M. 2011. Phylogeny of the genus *Turris*: Correlating molecular data with radular anatomy and shell morphology. *Molecular Phylogenetics and Evolution* 59: 263–270.
- Ferrero Mortara, E., Montefameglio, L., Pavia, G., and Tampieri, R. 1981. Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco, parte I. *Museo Regionale di Scienze Naturali Cataloghi* 6: 1–327.
- Fischer, P. 1883. Diagnoses d'espèces nouvelles de mollusques recueillis dans le cours des expéditions scientifiques de l'avis le Travailleur (1882).-Pars II. *Journal de Conchyliologie* 30: 273–277.
- Fleming, J. 1822. *The Philosophy of Zoology, a General View of the Structure, Functions and Classification of Animals*. 618 pp. Constable and Co., Edinburgh.
- Friedberg, W. 1951. *Mięczaki miocenne ziem Polskich i Krajów Przyległych (Mollusca miocenica Poloniae et regionum Vicinarum)*, 1. *Ślimaki (Pars 1. Gasteropoda)*. Second edition. 234 pp. Polskie Towarzystwo Geologiczne, Kraków.
- Glibert, M. 1954. Pleurotomes du Miocène de la Belgique et du bassin de la Loire. *Institut Royal des Sciences Naturelles de Belgique Mémoire* 129: 1–75.
- Górka, M., Studencka, B., Jasionowski, M., Hara, U., Wysocka, A., and Poberezhskyy, A. 2012. The Medobory Hills (Ukraine): Middle Miocene reef systems in the Paratethys, their biological diversity and lithofacies. *Biuletyn Państwowego Instytutu Geologicznego* 449: 147–174.
- Gray, J.E. 1847. The classification of the British Mollusca, by W.E. Leach, M.D. *Annals and Magazine of Natural History* 20: 267–273.
- Gürs, K. 2001. Neues zur Fauna und Entwicklung des Nordseebeckens im Mittel- und Obermiozän. *Meyniana* 53: 51–74.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 43: 1–9. [http://palaeoelectronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeoelectronica.org/2001_1/past/issue1_01.htm)
- Harmer, F.W. 1915. The Pliocene Mollusca of Great Britain being supplementary to S. V. Wood's Monograph of the Crag Mollusca. Part II. *Monograph of the Palaeontological Society* 68: 201–302.
- Harris, G.F., and Burrows, H.W. 1890 *The Eocene and Oligocene Beds of the Paris Basin*. 129 pp. Geological Association of London, London.
- Harzhauser, M. and Kronenberg, G. 2013. The Neogene strombid gastropod *Persististrombus* in the Paratethys Sea. *Acta Palaeontologica Polonica* 58: 785–802.
- Harzhauser, M., and Piller, W.E. 2007. Benchmark data of a changing sea —palaeogeography, palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253: 8–31.
- Hoernes, M. 1854. Die fossilen Mollusken des Tertiär-beckens von Wien. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 3: 297–384
- Hoernes, R. and Auinger, M. 1890. Die Gastropoden der Meeresablagerungen der ersten und zweiten Miocenen Mediterran-Stufe in der Oesterreichisch-Ungarischen Monarchie. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 12: 283–382.
- International Commission on Zoological Nomenclature 2015. *International Code for Zoological Nomenclature, IV edition*. 90 pp. International Trust for Zoological Nomenclature, London (accessed 07 July 2015).
- Janssen, A.W. 1984. Mollusken uit het Mioceen van Winterswijk-Miste. Een inventarisatie, met beschrijvingen en afbeeldingen van alle aangetroffen soorten. *Bibliotheek van de Koninklijke Nederlandse Natuurhistorische Vereniging* 36: 1–451.
- Janssen, R. and Wienrich, G. 2007. Turridae. In: G. Wienrich (ed.), *Die Fauna des marinen Miozäns von Kavelaer (Niederrhein)*. Vol. 4, *Gastropoda*. 71 pp. Backhuys Publishers BV, Leiden.
- Kautsky, F. 1925. Das Mioceen von Hemmoor und Basbeck-Osten. *Abhandlungen der Preussischen Geologischen Landesanstalt* 97: 1–225.
- Klompmaier, A.A., Hyžný, M., Portella, R.W., and Kowalewski, M. 2015. Growth, inter- and intraspecific variation, palaeobiogeography, taphonomy and systematics of the Cenozoic ghost shrimp *Glypturus*. *Journal of Systematic Palaeontology* 13 (published online).
- Knudsen, J. 1952. Marine prosobranchs of tropical West Africa collected by the Alantide Expedition, 1945–46. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn* 114: 129–185.
- Kováč, M., Andreyeva-Grigorovich, A., Bajraktarević, Z., Brzobohatý, R., Filipescu, S., Fodor, L., Harzhauser, M., Oszczykpo, N., Nagymarosy, A., Pavelić, D., Rögl, F., Saftić, B., Sliva, L., and Studencka, B. 2007. Badenian evolution of the Central Paratethys Sea: paleogeography, climate and eustatic sea level changes. *Geologica Carpathica* 58: 479–606.
- Landau, B.M., Harzhauser, M., İslamoğlu, Y., and da Silva, C.M. 2013. Gastropods of the Miocene Karaman Basin, Turkey. *Cainozoic Research* 11–13: 3–584.
- Laskarew, W. 1914. Carte géologique générale de la Russie d'Europe. Feuille 17 [in Russian]. *Transaction of the Geological Committee, New Series* 77: 1–669.
- Mariottini, P. 2007 *Brachycythara beatriceae*, a new species from the Alboran Sea and the eastern Atlantic Ocean (Gastropoda: Neogastropoda: Conidae). *Nautilus* 121: 159–167.
- Mariottini, P., Smriglio, C., Calascibetta, S., and Di Giulio, A. 2012. Taxonomic remarks on *Bela alantidea* (Mollusca: Gastropoda: Mangeliidae) and updated distribution in the Mediterranean basin. *Marine Biodiversity Records* 5: 1–6.
- Mariottini, P., Smriglio, C., Di Giulio, A., and Oliverio, M. 2009. A new fossil conoidean from the Pliocene of Italy with comments on the *Bela menkhorsti* complex (Gastropoda: Conidae). *Journal of Conchology* 40: 5–14.
- Maslov, V.P. and Utrobin, V.N. 1958. Distribution of the Tertiary Rhodophyceae of the Ukrainian Soviet Socialist Republic and their connection with sea transgression [in Russian]. *Bulletin of the Academy of Sciences of the USSR, Series Geology* 1958: 73–93.
- Michaud, A.L.G. 1828 Description de plusieurs espèces nouvelles de coquilles vivantes de le Méditerranée. *Bulletin d'Histoire Naturelle de la Société Linnéenne de Bordeaux*, 2: 119–122.
- Montagu, G. 1803. *Testacea Britannica or Natural History of British Shells, Marine, Land, and Fresh-water; Including the Most Minute: Systematically Arranged and Embellished with Figures*. 606 pp. J. White, London.
- Muratov, M.V. and Nevesskaja, L.A. (eds.) 1986. *Neogenovaya sistema. Stratigraphiya SSSR. Vol. 1*. 419 pp. Nedra, Moskva.
- Naldi, F., Della Bella, G., and Scarponi, D. 2013. Descrizione di *Bela pseudoappeliusi* n. sp. (Neogastropoda, Mangeliidae) dal Plio-Pleistocene dell'Italia. *Bollettino della Società Paleontologica Italiana* 52: 71–79.
- Nevesskaja, L.A., Gontsharova, I.A., Paramonova, N.P., Popov, S.V., Babak, E.V., Bagdasarjan, K.G., and Voronina, A.A. 1993. Identification book of Miocene bivalve molluscs of south-western Eurasia [in Russian]. *Transactions of the Paleontological Institute, Russian Academy of Sciences* 247: 1–412.
- Nordsieck, F. 1972 *Die Miozäne Molluskenfauna von Miste-Winterswijk NL (Hemmoor)*. 187 pp. Fischer Verlag, Stuttgart.
- Norman, A.M. 1888. *Museum Normanianum, or a Catalogue of the Invertebrata of Europe, and the Arctic North Atlantic Oceans. IV Mollusca Marina. V. Brachiopoda*. 30 pp. Privately printed, Durham.
- Oyama, K. 1954. Review of the known species of Japanese Turridae (2). *Venus* 18: 17–20.
- Pallary, P. 1920 *Exploration Scientifique du Maroc Organisée par la Société de Géographie de Paris et Continué par la Société des Sciences Naturelles du Maroc. Deuxième Fascicule. Malacologie*. 108 pp. Institut Chérifien, Rabat.
- Pennant, T. 1777 *The British Zoology. Vol. 4 Crustacea, Mollusca, Testacea*. 156 pp. Benjamin White, London.
- Philippi, R.A. 1844. *Enumeratio Molluscorum Siciliae cum Viventium tum in Tellure Tertiaria Fossilium quae in Itinere suo Observavit Auctor. Volumen Secundum Continens Addenda et Emendanda, nec non Comparationem Faunae Recentis Siciliae cum Faunis Aliarum Terrarum et cum Fauna Periodi Tertiariae*. 303 pp. E. Anton, Halis Saxonum.

- Powell, A.W.B. 1967. The family Turridae in the Indo-Pacific. Part 1a. The subfamily Turrinae concluded. *Indo-Pacific Mollusca* 1: 409–444.
- Puillandre, N., Duda, T.F., Meyer, C., Olivera, B.M., and Bouchet, P. 2015. One, four or 100 genera? A new classification of the cone snails. *Journal of Molluscan Studies* 81: 1–23.
- Puillandre, N., Kantor, Y.I., Sysoev, A., Couloux, A., Meyer, C., Rawlings, T., Todd, J.A., and Bouchet, P. 2011. The dragon tamed? A molecular phylogeny of the Conoidea (Gastropoda). *Journal of Molluscan Studies* 77: 259–272.
- Puillandre, N., Samadi, S., Boisselier, C., Sysoev, A.V., Kantor, Y.I., Cruaud, C., Couloux, A., and Bouchet, P. 2008. Starting to unravel the toxoglossan knot: Molecular phylogeny of the “turrids” (Neogastropoda: Conoidea). *Molecular Phylogenetics and Evolution* 47: 1122–1134.
- Risso, A. 1826. *Histoire Naturelle des Principales Productions de l'Europe Méridionale et Particulièrement de Celle des Environs de Nice et des Alps Maritimes*. Vol. 4. 439 pp. F.-G. Levrault, Paris.
- Scarponi, D. and Della Bella, G. 2010. *Molluschi marini del Plio-Pleistocene dell'Emilia-Romagna e della Toscana. Superfamiglia Conoidea. Vol. 3. Conidae II*. 127 pp. L'Informatore Piceno, Ancona.
- Scarponi, D., Ceregato, A., Della Bella, G., and Tucker, J.K. 2011a. *Pleurotoma scabriuscula* Brugnone, 1862 (currently *Mangelia scabriuscula*; Mollusca, Gastropoda, Conoidea): proposed conservation. *Bulletin of Zoological Nomenclature* 68: 180–183.
- Scarponi, D., Della Bella, G., and Ceregato, A. 2011b. The genus *Haedrop-leura* (Neogastropoda, Toxoglossa-Conoidea) in the Plio-Quaternary of the Mediterranean basin. *Zootaxa* 2796: 37–55.
- Scarponi, D., Huntley, J.W., Capraro, L., and Raffi, S. 2014a. Stratigraphic paleoecology of the S. Mauro Marchesato Section (Crotone Basin, Italy): a candidate GSSP of the Middle Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 402: 30–43.
- Scarponi, D., Landau, B., Janssen, R., Mongerntoth, H., and Della Bella, G. 2014b. Lectotype designation for *Murex nebula* Montagu 1803 (Mangeliidae) and its implications for *Bela* Leach in Gray 1847. *Zootaxa* 3884: 45–54.
- Seguenza, G. 1875 Studi stratigrafici sulla Formazione pliocenica dell'Italia Meridionale. *Bollettino del Regio Comitato Geologico d'Italia* 6: 203–211.
- Serres, M. de 1829 *Géognosie des Terrains Tertiaires, ou Tableau des Principaux Animaux Invertébrés des Terrains Marins Tertiaires du Midi de la France*. 276 pp. Pomathio-Durville, Paris.
- Shevenell, A.E., Kennett, J.P., and Lea, D.W. 2004. Middle Miocene Southern Ocean cooling and Antarctic cryosphere expansion. *Science* 305: 1766–1770.
- Smriglio, C., Di Giulio, A., Gubbioli, F., and Mariottini, P. 2007. *Brachy-cythara atlantidea* (Knudsen, 1952) (Gastropoda, Neogastropoda, Conidae), first report from the western Mediterranean Sea. *Basteria* 71: 29–32.
- Spada, G. and Della Bella, G. 2010. Identification of *Mangelia striolata*, type species of the genus *Mangelia* Risso, 1826. *Bollettino Malacologico* 46: 76–83.
- Studencka, B. and Dulai, A. 2010. Chitons (Mollusca: Polyplacophora) from the Middle Miocene sandy facies of Ukraine, Central Paratethys. *Acta Geologica Polonica* 60: 257–274.
- Studencka, B. and Jasionowski, M. 2011. Bivalves from the Middle Miocene reefs of Poland and Ukraine: A new approach to Badenian/Sarmatian boundary in the Paratethys. *Acta Geologica Polonica* 61: 79–114.
- Studencka, B. and Studencki, W. 1988. Polyplacophora from the Badenian (Middle Miocene) marine sandy facies of the Holy Cross Mts. (Central Poland). *Prace Muzeum Ziemi* 40: 37–46.
- Studencka, B., Gontsharova, I.A., and Popov, S.V. 1998. The bivalve fauna as a basis for reconstruction of the Middle Miocene history of the Paratethys. *Acta Geologica Polonica* 48: 285–342.
- Tucker, J.K. 2004. Catalogue of Recent and fossil turrids (Mollusca: Gastropoda). *Zootaxa* 682: 1–1295.
- Tucker, J.K., Tenorio, M.J., and Stahl Schmidt, P. 2011. The genus *Benthofascis* (Gastropoda: Conoidea): A revision with descriptions of new species. *Zootaxa* 2796: 1–14.
- Tunnell, J.W., Jr., Andrews, J., Barrera, N.C., and Moretzsohn, F. 2010. *Encyclopedia of Texas Seashells. Identification, Ecology, Distribution and History*. 512 pp. Everbest Printing Co., Louisville.
- Vera-Peláez, J.L., Martinell, J., and Lozano-Francisco, M.C. 1999. Turridae (Gastropoda, Prosobranchia) del Plioceno inferior de Málaga (España). *Iberus* 17: 1–19.
- Verduin, A. 1977. On a remarkable dimorphism of the apices of sympatric closely-related marine gastropod species. *Basteria* 41: 91–95.
- Wenz, W. 1938. *Handbuch der Paläozoologie. Band 6: Gastropoda*. 240 pp. Borntraeger, Berlin.
- Winter, J.C.F. de 2013. Using the student's *t*-test with extremely small sample sizes. *Practical Assessment, Research & Evaluation* 18: 1–12.
- Woodring, W.P. 1928. Miocene mollusks from Bowden, Jamaica. Part II. Gastropods and discussion of results. Contributions to the geology and paleontology of the West Indies. *Carnegie Institution of Washington Publication* 385: 1–564.
- WoRMS Editorial Board 2014 *World Register of Marine Species*. At VLIZ. Available from: <http://www.marinespecies.org> (accessed 18 December 2014).
- Zelinskaya, V.A. [Zelinskaâ, V.A.], Kulichenko, V.G. [Kuličenko, V.G.], Makarenko, D.E., and Sorochan, E.A. 1968. *Paleontologičeskij Spravočnik. Tom 2 Brushonogie i Lopatonogie Molluski Paleogena i Miocena Ukrainy*. 281 pp. Akademiâ Nauk Ukrainskoj SSR, Institut Geologičeskij Nauk, Kiev.
- Zilch, A. 1934. Zur Fauna des Mittel-Miocäns von Kostež (Banat). Typus-Bestimmung und Tafeln zu O. Boettger's Bearbeitungen. *Senckenbergiana* 16: 193–302.