

# Gastropods [Trochoidea: Trochidae Rafinesque, 1815 and Calliostomatidae Thiele, 1924 (1847)] from the middle Miocene of Ukraine, Central Paratethys

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## ABSTRACT:

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Over three thousand specimens representing the superfamily Trochoidea Rafinesque, 1815 [Trochidae Rafinesque, 1815 and Calliostomatidae Thiele, 1924 (1847)] from the upper Upper Badenian = Kosovian = lower Serravallian (middle Miocene) marine deposits of Ukraine, housed in the collections of the Polish Academy of Sciences Museum of the Earth in Warsaw (MZ), are studied herein. The abundant material has allowed for investigations of the intraspecific variation and revision of earlier determinations. As a result, 21 species belonging to 5 genera have been identified, described and illustrated, of which one is new [*Clanculus (Clanculopsis) krachi* sp. nov.] and one is left in open nomenclature. *Granulifera* O. Anistratenko, 2000 is considered a junior subjective synonym of *Clanculopsis* Monterosato, 1879; *Granulifera pulla* O. Anistratenko, 2000 is considered a junior subjective synonym of *Monodonta tuberculata* Eichwald, 1830; *Gibbula sytovae* Amitrov, 1961 is considered a junior subjective synonym of *Trochus miocaenicus* Mayer, 1853; *Gibbula volhynica* Friedberg, 1928 is considered a junior subjective synonym of *Trochus novemcinctus* von Buch, 1830; and *Trochus buchii* du Bois de Montpéreux, 1831 is suppressed in favour of the senior subjective synonym *Trochus puschii* Andrzejowski, 1830. The geographic distribution and stratigraphic ranges of the taxa are given. Six species are known only from the Polish-Ukrainian part of the Fore-Carpathian Basin. The protoconch features are systematically studied in the Trochidae and Calliostomatidae from this area for the first time.

**Keywords:** Gastropoda; Taxonomy; Badenian; Middle Miocene; Ukraine; Central Paratethys.

## INTRODUCTION

Upper Badenian (Kosovian; middle Miocene) sandy and carbonate deposits occurring in the north-eastern marginal, relatively shallow part of the Central Paratethys located within the boundaries of today's Ukraine (part of the Volhynian–Podolian area), contain a rich and taxonomically diverse fauna indicating normal marine (euhaline) conditions (Kudrin 1966; Grishkevich 1970; Jasionowski *et al.* 2006). In addition to planktonic foraminifera, corals, echino-

derms, brachiopods, especially richly represented are molluscs – bivalves (Friedberg 1934–1936, 1938; Zelinskaya *et al.* 1968; Studencka *et al.* 1998; Studencka and Jasionowski 2011) and gastropods. The latter have been extensively studied by Eichwald (1829, 1830, 1851a, 1853), Andrzejowski (1830a, 1833), du Bois de Montpéreux (1831), and Friedberg (1911–1928, 1938). All these papers are fundamental for the understanding of Miocene gastropods in western Ukraine and were state of the art in their times. Therefore, a revision of the western Ukrainian

gastropod assemblages is needed to keep pace with important changes in taxonomic systematics and advances in imaging techniques. The mentioned authors, focusing primarily on teleoconch morphology, described many new species. However, the importance of the protoconch characters for taxonomy has become apparent in the last 50 years. Protoconch features are particularly useful at species level, although with Vetigastropoda, for example, they do allow calliostomids to be identified (e.g., Hickman and McLean 1990). Besides, knowledge of the protoconch morphology proved to be particularly important for palaeontologists, as the developmental mode of extinct species can be inferred (e.g., Shuto 1974; Kowalke and Harzhauser 2004; Anistratenko *et al.* 2006; Kowalke 2006), and thus the possibilities of their geographic spread (e.g., Shuto 1974; Jablonski and Lutz 1980). Protoconch type is useful in separating calliostomids from trochids, which often show similar teleoconch characters.

The purpose of the present paper is to provide: (i) an up-to-date taxonomy of the Late Badenian Calliostomatidae and Trochidae from the Ukrainian part of the Fore-Carpathian Basin, taking into account changes in the understanding of the present-day species and their distribution; (ii) a list of the references and synonyms; (iii) detailed descriptions of individual species, including where possible, information on protoconch characters; and (iv) a geographical distribution and stratigraphical range for each species.

## PALAEOGEOGRAPHIC AND GEOLOGICAL CONTEXT

Central Paratethys, including the Fore-Carpathian Basin (as defined by Wysocka *et al.* 2016) and the Pannonian basins complex, was one of the sedimentary basins of the Paratethys that originated in the northern margins of the Tethys Ocean in the late Palaeogene as a result of the Alpine orogeny (Rögl 1998, 1999; Schulz *et al.* 2005). During the Badenian (16.3 to 12.8 Ma after Hohenegger *et al.* 2014), the Central Paratethys stretched in the area of present-day Austria, the Czech Republic, Slovakia, Serbia, Croatia, Slovenia, Bosnia and Herzegovina, Poland, Ukraine, Romania, Bulgaria, Moldova and Hungary (see Kováč *et al.* 2007). The Ukrainian part, placed within the Fore-Carpathian Basin, represented a marginal and relatively shallow fragment of the basin. The lithostratigraphic schemes of Miocene strata in the Ukrainian Precarpathian area were presented

by Petryczenko *et al.* (1994), Andreyeva-Grigorovich *et al.* (1997, 2008), Wysocka and Jasionowski (2006) and Gozhyk *et al.* (2015). Furthermore, Wysocka *et al.* (2016) provided a review and update of the research on the middle Miocene of the region.

Since the Paratethys basins were inland seas, they periodically suffered partial or complete isolation from each other and from open sea waters (e.g., Popov *et al.* 2004; Kováč *et al.* 2017; Sant *et al.* 2017; Palcu *et al.* 2017, 2019). This resulted in the occurrence of sedimentological and biostratigraphic differences between the Mediterranean area and the epicontinental seas of the Paratethys and the establishment of separate chronostratigraphic schemes. A correlation chart of the Miocene regional stages of the Central and Eastern Paratethys and the Mediterranean province were presented, e.g., by Piller *et al.* (2007), Studencka and Jasionowski (2011), Gozhyk *et al.* (2015), Palcu *et al.* (2017) and Kováč *et al.* (2018). Recently, the Badenian has been commonly sub-divided into the Early, Mid and Late (Hohenegger *et al.* 2014). Accordingly, the Wielician and Kosovian substages (formerly regarded as 'middle' and 'upper' Badenian, respectively) correspond to subunits of the Late Badenian (13.82 to 12.829 Ma after Hohenegger *et al.* 2014).

Kováč *et al.* (2007, 2017) presented a scenario of events that took place in the Central Paratethys in the Badenian. In the late Late Badenian (age-equivalent of the Kosovian substage), the Central Paratethys had a narrow connection with the Proto-Mediterranean Sea, as well as being, for a short period of time, linked with the Eastern Paratethys (e.g., Studencka *et al.* 1998; Popov *et al.* 2004; Kováč *et al.* 2007, 2017; Studencka and Jasionowski 2011; Bartol *et al.* 2014; Palcu *et al.* 2015; de Leeuw *et al.* 2018). Therefore, exchange of marine fauna between the basins at that time was possible. It was also the last period with fully marine conditions in the history of the basin. At the end of the Badenian, the extensive seaway connecting the Proto-Mediterranean with the Paratethys became closed (Kováč *et al.* 2007). Significant changes of environmental factors in the whole Paratethys caused dramatic amendments in the marine biota around the Badenian/Sarmatian boundary (e.g., Harzhauser and Piller 2007; Studencka and Jasionowski 2011) dated around 12.8 Ma (Hohenegger *et al.* 2014) or 12.6 Ma (Palcu *et al.* 2015; Mandić *et al.* 2019). At the beginning of the Sarmatian, all Paratethyan basins including the Fore-Carpathian Basin became connected (Palcu *et al.* 2015; Mandić *et al.* 2019) and inhabited by a uniform marine fauna with mainly endemic species (e.g., Popov *et al.* 2004; Harzhauser and Piller 2007; Studencka and Jasionowski 2011).

After the early Late Badenian (age-equivalent of the Wielician substage) isolation of the eastern part of the Central Paratethys, resulting in a salinity crisis which began shortly after  $13.81 \pm 0.08$  Ma (de Leeuw *et al.* 2010) and most likely ended around 13.35 Ma (de Leeuw *et al.* 2018, p. 11; including recalibrated  $40\text{Ar}/39\text{Ar}$  results of Śliwiński *et al.* 2012), a late Late Badenian marine transgression took place from the Proto-Mediterranean (e.g., Kováč *et al.* 2007). As a result, the extent of the Fore-Carpathian Basin was increased considerably compared to earlier Badenian time. The sea entered the far East European Platform, covering its south-western part known as the Volhynian–Podolian Plate, where Upper Badenian (Kosovian) deposits discordantly overlie the pre-Neogene basement. Coralline algal-vermetid reefs developed on elevations of the sea bottom in extremely shallow settings, forming a distinct belt along the northern and eastern margins of the Fore-Carpathian Basin in Poland, Ukraine, Moldova and Romania (Studencka and Jasionowski 2011). These reefs, constituting a narrow 200-km long zone in the Ukraine forming the Medobory Hills (for location see Studencka and Jasionowski 2011, text-fig. 3), separated deeper environments of the Fore-Carpathian Basin with marl and clay sedimentation from coastal facies, dominated by quartzitic sands and sandstones of the shallow basin localised above the Podolian Massif (Maslov and Utrobin 1958). The latter basin gradually became less saline due to increased river input and limited connection with the open sea (Kováč *et al.* 2007), while tectonic processes influenced emerging and shallowing of its marginal areas. The gastropod material described in this study was derived from both sandy and carbonate deposits of the area.

#### COMMENTS ON EDUARD EICHWALD'S WORKS AND COLLECTIONS

Eduard Eichwald was professor of, among others, the Imperial University of Vilnius (1827–1831); the Medical-Surgical Academy of Vilnius (1832–1838); the Medical-Surgical Academy in St. Petersburg (1838–1851) (now S.M. Kirov Military Medical Academy); and the Institute of the Mining Engineers Corps in St. Petersburg (1838–1854) (now Saint-Petersburg Mining University).

In the period from May to September 1829, Eichwald participated in a physiographic expedition to the region between the Boh and Dniester rivers and the Black Sea (including, among others, Volhynia and

Podolia now located within the Ukraine), organised by the Imperial University of Vilnius. He was the initiator and head of this expedition (Garbowska 1993).

In order to preserve the stability of the use of species names, it is important to determine the precise publication dates of works, especially from the 19<sup>th</sup> century when many new species were established. Coincidences in publication dates have often caused mistakes in determining the priority of a given synonymous species name (see remarks for *Trochus puschi* Andrzejowski, 1830). Article 21.3 of the ICZN (1999) sets out the rules to be applied in the case when the precise date of publication is not specified.

Eichwald's works, commented below, deserve special attention. These works described many new species of Miocene molluscs from the Polish-Ukrainian part of the Fore-Carpathian Basin. The following notes can help researchers to recognise which name of the synonymised species names takes precedence over all other names.

*Zoologia specialis...* 1829. – In this handbook the author included descriptions and illustrations of, among others, his new fossil gastropod species (Eichwald 1829, pl. 5, figs 7, 8, 10, 11, 14–19). The censor's consent to the publication was given on 18<sup>th</sup> January, 1829 – a note on the back of the title page. Moreover, his letter to the readers is dated 30<sup>th</sup> April, 1829 (= “pridie Calend.[as] Maii MDCCCXXIX”) (p. vi).

*Naturhistorische Skizze...* 1830. – In this work, Eichwald included very short descriptions of his new fossil species in footnotes. The censor's consent to the publication was given on 10<sup>th</sup> January, 1830 – a note on the back of the title page. Eichwald dedicated this work to Alexander von Humboldt and promised that he would soon give him numerous plates depicting fossil fauna (which were finally published 20 years later). The date of Eichwald's letter, 23<sup>th</sup> March, 1830, is placed before the main text of his work, on a page without a number. However, in a postscript (pp. 253, 254), Eichwald commented on Andrzejowski's paper (1830b) that was published in May.

*Atlas to Palaeontology of Russia. New period.* 1850, 14 plates. – In this atlas, Eichwald published the figures of, among others, species previously described in *Naturhistorische Skizze...* (Eichwald 1830), but he did not provide plate captions.

*Palaeontology of Russia... New Period.* 1851a. – In this monograph, the plate captions of the atlas (Eichwald 1850, 1851b) are placed on pp. 277–284. Despite the fact that the title page of the work states the year as 1850, the date of publication was adopted on the basis of a note on the back of the title page containing the date 17<sup>th</sup> February, 1851.

*Atlas to Palaeontology of Russia*. 1851b, 14 plates. – In this atlas, Eichwald published the figures of species described in *Palaeontology of Russia... New Period* (Eichwald 1851a), but did not provide plate captions.

*Lethaea Rossica ou Paléontologie de la Russie, dernière période*. 1853. – Eichwald's preface to this work is dated October 1853 (p. vi).

*Lethaea Rossica ou Paléontologie de la Russie. Période modern*. 1859, 14 plates. – In the atlas Eichwald published the figures of species described in *Lethaea Rossica...* (Eichwald 1853) and plate captions (pp. 1–4).

The three editions of the atlas (Eichwald 1850, 1851b, 1859) differ from each other in the title page, the presence or absence of plate captions, and one of the plates. In the atlases of 1850 and 1851b, plate 9 shows a different distribution, numbering and illustrations of some species than in the atlas of 1859 (36 figures, 91 illustrations vs. 34 figures, 89 illustrations). Eichwald (1853, p. vi) noted: “Une des planches a dû être dessinée de nouveau, parce que la pierre s'était cassée pendant l'impression”, which probably explains the differences between these plates.

There is yet another atlas published in 1852 (with plate captions), to which e.g., Landau *et al.* (2013) referred; I did not have, however, access to this edition.

In *Naturhistorische Skizze...*, Eichwald used not only his own palaeontological collections, but also the collections of the Krzemieniec Lyceum (Volhynia) and the teachers who worked in it: Wojciech Zborzewski, Stefan Zienowicz and Antoni Andrzejowski (Andrzejowski 1832a, p. 516; Garbowska 1993, p. 60, 2005, p. 23). After the closure of the Krzemieniec Lyceum and the Imperial University of Vilnius in 1832, the scientific collections of both schools were transferred to the newly established Saint Vladimir Royal University of Kiev (now Taras Shevchenko National University of Kyiv) (Eichwald 1851a, p. 9, footnote, p. 109; Garbowska 1993, p. 56). Unfortunately, during the present study it was not possible to determine whether the palaeontological collection described by Eichwald (1830) is still stored in the Geological Museum of the Geological Department of Kiev University. The questions addressed to the curator remained unanswered. Part of the collection to *Naturhistorische Skizze...* is kept in the S.M. Kirov Military Medical Academy in St. Petersburg (Eichwald 1851a, p. 9, footnote).

The palaeontological collection pertaining to Eichwald's monographs (1851a, 1853) is currently stored in: the Mining Museum of the Saint-Petersburg Mining University, (collection No. 113, contains

only vertebrates, except two valves of *Pecten*; Daria Bezgodova, pers. comm. 2019), Paleontological-Stratigraphic Museum of the Department of Dynamic and Historical Geology of Saint Petersburg State University; and, probably, S.M. Kirov Military Medical Academy (Gataulina and Arcadiev 2010).

Part of Eichwald's collection was dispersed. Harzhauser and Landau (2016) illustrated two Miocene gastropod shells bearing the inventory number of the Zoological Museum of the Zoological Institute of the Russian Academy of Sciences in St. Petersburg.

## MATERIAL AND METHODS

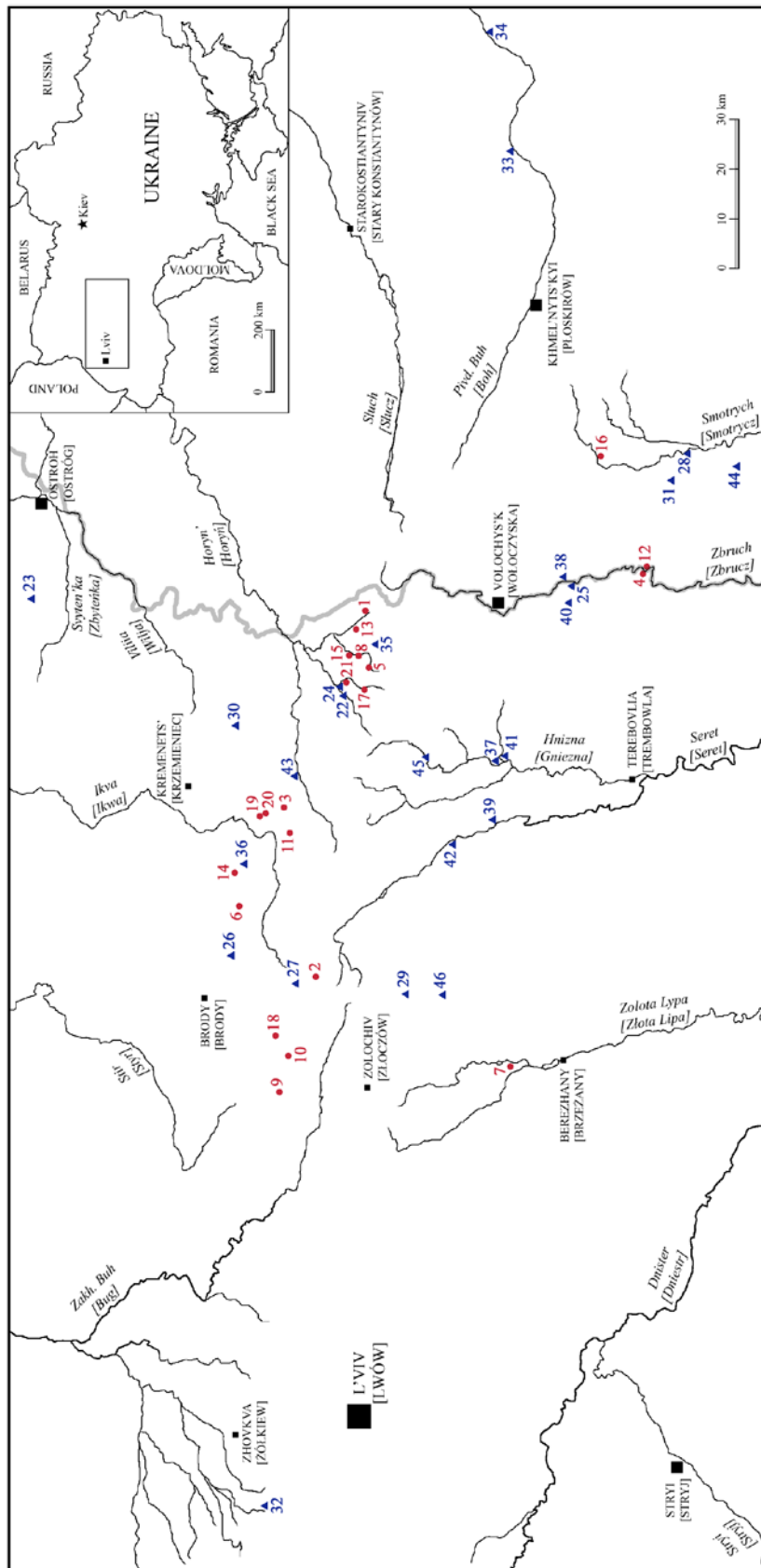
The vast majority of the Trochidae and Calliostomatidae material used in this study is part of the large collection of Neogene molluscs gathered by Kazimierz Kowalewski in the years 1934–1937 and 1939 in the area of the Eastern Borderlands of the Second Polish Republic, now located within Ukraine (see Text-fig. 1). Kowalewski made numerous exploratory field trips on behalf of, and with the funds of the Society of the Museum of the Earth (Kowalewski 1936a, b, 1937; Passendorfer 1938). Fossil lists of only some of the thirty outcrops in the Volhynian–Podolian region have been published (Kowalewski 1936a, b, 1937, 1950). Presently, I am working on a catalogue of gastropods from Kowalewski's collections housed at MZ.

The bivalve collections of Kowalewski were used in the studies of Studencka and Popov (1996), Studencka *et al.* (1998) and Studencka and Jasionowski (2011), while the results of research on chitons were presented by Studencka and Dulai (2010).

The examined material is supplemented by shells: accumulated by Wojsław Zaborski (2 specimens collected in 1910), Antoni Jankowski (6 specimens collected in 1930), employees of the MZ in Warsaw – Gwidon Jakubowski (22 specimens collected in 1978) and Barbara Studencka (185 specimens collected in 1988, 2000, 2006, 2009, 2010), and those donated by Oleg Vladimirovich Amitrov of the Borissiak Paleontological Institute of the Russian Academy of Sciences in Moscow (6 specimens collected in 1960).

The study was based on over 3,000 specimens from 21 localities in western Ukraine, which along with other localities mentioned in the work are indicated with their contemporary Ukrainian names on the map (Text-fig. 1). The Polish names of these localities (along with variant spellings), used in most older references, are given for clarity in the caption to this figure.





Text-fig. 1. Map of Ukraine with localities mentioned in this paper (with former Polish names in square brackets). Red dots – localities where the fauna described in this paper comes from: 1 – Bilozirka [Białozórka, Bialozurka]; 2 – Chepel [Czepiele]; 3 – Dzvyniacha [Zwiniacze]; 4 – Kalaharivka [Kalaharivka]; 5 – Korostova [Korostowa]; 6 – Lidykhiv [Leduchów]; 7 – Nadrichne [Dryszczów]; 8 – Ohryzkyvitsi [Ohryszkowce, Ohryzkowce]; 9 – Oles'ko [Olesko]; 10 – Rydomyl' [Rydomil]; 11 – Rydomyl' [Podhorec]; 12 – Sataniv [Satanów]; 13 – Shushkivitsi [Szuszkowce]; 14 – Staryi Pochaiiv [Poczajów Stary]; 15 – Vanzhuliv [Wanżulów]; 16 – Varyvitsi [Warowce]; 17 – Vyshhorodok [Wyszogródok, Wyżródok]; 18 – Yaseniv [Jasionów]; 19 – Zalizisti [Zalesce]; 20 – Zalizisti – Zhabiak ravine [Zalesce – jar Zabiak]; 21 – Zhukivitsi [Zukowce]; 22 – Bilka [Białka, Biłka]; 23 – Derman' [Derman]; 24 – Domanenka [Domanienka, Domaninka] – former village absorbed by the village of Berezhanka [Bereżanka]; 25 – Faschivka [Faszczówka]; 26 – no Ukrainian name [Holdy] – hummock located 0.5 km from Makitra [Makutra] elevation; 27 – Holubytisia [Holubicia]; 28 – Horodok [Gródek]; 29 – Kabarivitsi [Kabarowce]; 30 – Katerynivka [Katerburg, Katerynburg, Katrynburg]; 31 – Kreminna [Krzenienna]; 32 – no Ukrainian name [Lehurda, Leworda] – hummock located west of the village Mlynky, within Jaworowski National Park; 33 – Medzhybizh [Międzybóż, Międzybórz]; 34 – Novokostiantyniv [Nowy Kostiantynów]; 35 – Plyska [Płiska]; 36 – Pochaiiv [Poczajów]; 37 – Stupky [Stupki, Stupki]; 38 – Tarnorda [Tarnorda]; 39 – Ternopil' [Tarnopol]; 40 – Turivka [Turówka]; 41 – Velyki Birky [Borki Wielkie]; 42 – Velykyi Hlybochok [Hluboczek Wielki, Hluboczek Wielki]; 43 – Vyschnivets' [Wisniowiec]; 44 – Zawadyntsi [Zawadyńce]; 45 – Zbarazh [Zbaraż]; 46 – Zboriv [Zborów]. Grey line – former boundary between the Second Polish Republic and the Ukrainian Soviet Socialist Republic in 1921–1939. The system of transliteration used herein is that adopted in 2002 by the Eighth United Nations Conference on the Standardization of Geographical Names, Berlin.

The new species *Clanculus (Clanculopsis) krachi* sp. nov. was established based on numerous shells (collections of Wilhelm Krach before 1981; collections of Jacek Cibor, Wojciech Macioszczyk and Gwidon Jakubowski from 1982–1989) from the Badenian carbonate deposits of the Roztocze Hills in Poland and only one not fully-grown specimen from western Ukraine.

The analysed material was compared with Miocene gastropods from: the collections of the Natural History Museum of the National Academy of Sciences of Ukraine in Lviv, Ukraine; E. Eichwald's collection housed in the Palaeontological–Stratigraphic Museum of the Department of Dynamic and Historical Geology of Saint Petersburg State University, Russia; Wilhelm Friedberg's and Wilhelm Krach's collections deposited in the Geological Museum of the Institute of Geological Sciences, Polish Academy of Science in Cracow, Poland; and the collection described by Iljina (1993) kept in the Orlov Paleontological Museum of the Borissiak Paleontological Institute of the Russian Academy of Sciences in Moscow, Russia.

The photographs in this work were made by Cyprian Kulicki (SEM photographs, Institute of Paleobiology of the Polish Academy of Sciences in Warsaw), and myself, unless stated otherwise.

Measurements of the studied specimens are given in Table 1 and Appendix 1.

### Repositories

ETHZ – Geological-Palaeontological Collection, Swiss Federal Institute of Technology, Zurich, Switzerland;

KNUSH – Geological Museum of the Geological Department of Taras Shevchenko National University of Kiev, Ukraine;

MfN – Museum of Natural History in Berlin, Germany;

MZ – Polish Academy of Sciences Museum of the Earth in Warsaw, Poland;

PIN – Borissiak Paleontological Institute of the Russian Academy of Sciences in Moscow, Russia;

SMF – Senckenberg Natural History Museum Frankfurt, Germany;

SPbGU – Paleontological–Stratigraphic Museum of the Department of Dynamic and Historical Geology of Saint Petersburg State University, St. Petersburg, Russia;

ZNG PAN – Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Cracow, Poland.

### SYSTEMATIC PART

The following symbol and acronyms are used in the systematic part: • – name cited without description, illustration or synonymy list, and specimens could not be examined; sh – adult and juvenile shells; a – adult shell(s); af – adult fragment(s) of shell(s); sa – subadult shell(s); j – juvenile shell(s); jf – juvenile fragment(s) of shell(s); fp – fragmentarily preserved shell(s).

Class Gastropoda Cuvier, 1795

Subclass Vetigastropoda Salvini-Plawen, 1980

Superfamily Trochoidea Rafinesque, 1815

REMARKS: Trochoidea is a big superfamily of morphologically and ecologically varied marine gastropods. Its taxonomic internal classification is controversial and unstable (see e.g., Hickman and McLean 1990; Bouchet *et al.* 2005; Geiger and Thacker 2005; Williams *et al.* 2008; Williams 2012; Uribe *et al.* 2017b). In the most recent taxonomy (Bouchet *et al.* 2017) the superfamily includes 13 extant and 12 extinct families.

Trochoideans today are virtually pandemic. Many genera are cosmopolitan. Trochoideans can be found on algae and seagrasses, on soft or hard substrates (including coral reefs), and also buried in sediment. “They have developed a variety of feeding habits including both herbivory and carnivory, while others are suspension feeders” (Williams *et al.* 2008, p. 483).

Hickman (1992) summarised the knowledge on the reproduction and development of trochoidean gastropods. In the superfamily, both species with direct development (those hatching as benthic juveniles) and species with planktonic lecithotrophic development are recorded.

Despite the short-living lecithotrophic larvae, some species exhibit surprisingly wide geographic occurrence. This is probably due to rafting of adults, e.g., on macroalgae (Donald *et al.* 2005; Nikula *et al.* 2012; but see also Hadfield and Strathmann 1990).

Trochoidean shells are typically conispiral, with no slit, emargination in outer lip, or tremata (Hickman and McLean 1990), however an exception is a shell in Fossarininae Bandel, 2009, which “can have a slit on its outer lip or not” (Bandel 2009, p. 22). Trochoidean shells may be umbilicate or non-umbilicate, depending on coiling parameters. Male and female specimens are usually not distinguishable by shell features. Nevertheless, sexual dimorphism is documented in the shell of some trochoidean genera, e.g., *Solariella* Wood, 1842 (Marshall 1999) and

*Margarites* Gray, 1847 (in Gray 1847a; for sexual dimorphism see Lindberg 1985; Hickman and McLean 1990).

The larval shells consist of only an organic embryonic shell, which is calcified by the cells of the shell field invagination before, during, or just after the torsion of the larvae (Collin and Voltzow 1998). Originally the bilaterally symmetrical, cup-shaped larval shell is modified into an asymmetrical paucispiral, trochispiral form.

The trochoidean protoconch shows small variability of form and sculpture (see e.g., Bandel 1982; Hickman 1992). Size and shape depend upon egg size and are more closely correlated with water depth than with taxonomic group (Bandel 1982; Hickman 1992). The largest protoconchs with a bulbous, relatively undeformed apex, occur in species with large yolk reserves and in deep-water species. Shallow-water species (0–100 m depth) with little yolk reserves have an angular fold (pointed lateral fold) of the protoconch (Bandel 1982), which is also referred to as pointed tip (Hickman 1992), lateral pouch (Sasaki 1998) or apical beak (Herbert 1993). Protoconchs are smooth or sculptured. Usually, the sculpture is not clear; the most common forms are pits, granules and weak spiral threads. A very distinctive protoconch sculpture – the reticulate, honeycomb pattern was recognised in the family Calliostomatidae Thiele, 1924 (1847) (see Willan 2002). Similar protoconch sculpture, although less regular and less well-defined, occurs in the Umboniinae (family Trochidae). The similarity is probably homoplasious (Herbert 1992). In general, specific differences in protoconch sculpture have minor significance in higher-level systematics, but they are very helpful in distinguishing closely related taxa at lower species and/or genus levels (Sasaki 1998). In the trochoidean protoconch there is no morphological criterion for distinguishing pelagic development from benthic development (Hadfield and Strathmann 1990; Sasaki 1998). Heterostrophy in some species was noted and illustrated by e.g., Hadfield and Strathmann (1990), Sasaki (1998), and herein [see below under *Calliostoma trigonum* (Eichwald, 1830)].

There are numerous shell convergencies among families and subfamilies of Trochoidea (e.g., Williams 2012; Uribe *et al.* 2017b).

The oldest Trochoidea belong to the extinct genera *Dichostasia* Yochelson, 1956 and *Brochidium* Koken, 1889, which appeared in the Permian (Hickman and McLean 1990). Many families of the Trochoidea originated and diversified in the Cretaceous, as suggested by molecular studies (Williams *et al.* 2008) and the fossil record (Hickman and McLean 1990).

## Family Trochidae Rafinesque, 1815

REMARKS: Molecular studies carried out by Williams *et al.* (2008) showed that the family Trochidae *sensu* Hickman and McLean (1990) is not monophyletic, therefore it requires redefinition. Trochidae *sensu* Williams *et al.* (2010) supplemented with an additional subfamily (see Williams 2012) includes ten subfamilies, of which two, Trochinae Rafinesque, 1815 and Cantharidinae Gray, 1857, are represented by the species described herein.

Trochidae is a large family of morphologically highly variable gastropods, including more than 600 species representing over 60 genera, which radiated primarily on tropical intertidal rocky shores in the Indo-West Pacific (Williams *et al.* 2010). Trochidae species are distributed throughout all the world's oceans, predominantly in the tropics or subtropics, but they also occur in temperate regions. Although most species live in shallow water (also in the intertidal zone), some species are found in deeper water and in bathyal depths (Williams *et al.* 2010).

Trochid shells range from tiny (<0.5 cm) to very large (>20 cm) in size (Williams *et al.* 2010), show an oblique aperture without terminal flare or thickening, and usually have a nacreous interior (except Halistylinae Keen, 1958 and Alcyninae Williams, Donald, Spencer and Nakano, 2010). The microstructure of shells of extinct and extant Trochidae was studied by Sladkovskaya (2017); she concluded (p. 1467) that “the microstructural characters are more uniform and conservative in comparison with external shell morphology and independent of it”, and that data on the microstructure of shell can improve diagnosis, and in some cases, substantiate the taxonomic position of extinct trochids. The operculum of Trochidae is multispiral with a short growing edge and never calcified (Hickman and McLean 1990).

## Subfamily Trochinae Rafinesque, 1815

REMARKS: Hickman and McLean (1990) divided this subfamily into three tribes: Trochini, Monodontini (equivalent to Gibbulini) and Cantharidini; however the molecular studies of Williams *et al.* (2008, 2010) showed, that “the three are not collectively monophyletic and should be treated as distinct subfamilies, with some changes to their traditional compositions” (Williams *et al.* 2010, p. 799). In the new definition of the subfamily Trochinae this taxon is “[...] ‘a relatively well-defined entity with comparatively distinct

shell characters', being generally 'larger [than species in Monodontinae and Cantharidinae], having a disjunct columella, four pairs of epipodial tentacles and a strongly papillate foot with hooded epipodial sense organs' (Herbert, 1993, 1998)" (Williams *et al.* 2010, p. 799).

The Trochinae currently includes only fifteen genera (MolluscaBase 2019), among them *Clanculus* Montfort, 1810.

### Genus *Clanculus* Montfort, 1810

TYPE SPECIES: *Trochus pharaonius* Linnæus, 1758, by original designation. Recent, Indo-Pacific.

REMARKS: The genus *Clanculus* appeared in the Late Cretaceous (Hickman and McLean 1990). Today, it has a worldwide distribution; its species occur from the intertidal zone up to depths of 230 m (Poppe and Goto 1991). A review of the Neogene and extant species of European and Eastern Atlantic *Clanculus* was provided by Spadini (2006). Both Herbert (1993) and Spadini (2006) have characterised the shell morphology of this genus.

### Subgenus *Clanculopsis* Monterosato, 1879

TYPE SPECIES: *Trochus cruciatus* Linnæus, 1758, by subsequent designation of Sacco (1896). Recent, Mediterranean.

REMARKS: For diagnosis of the subgenus *Clanculopsis* see Herbert (1993).

### *Clanculus (Clanculopsis) krachi* sp. nov. (Text-fig. 2A–C)

part 1981. *Clanculus araeonis tuberculatus* (Eichwald 1830) [ssp. *trochiformis*]; Krach, p. 43, pl. 12, figs 28–31 [non figs 18, 19, 21, ?24 = *Clanculus (Clanculopsis) robustus* Friedberg, 1928; figs 20, 22, 23, 25–27 = *Clanculus (Clanculopsis) tuberculatus* (Eichwald, 1830)].

TYPE MATERIAL: Holotype (MZ VIII Mg 4703/1) and 13 paratypes (Table 1).

OTHER MATERIAL: Sandy facies: Ukraine–Oles'ko (MZ VIII Mg 4522) 1 sa. Carbonate facies: Poland – Łychów (MZ VIII Mg 5101) 1 a, 2 sa; Węglinek (MZ VIII Mg 5102) 1 a, 3 j, (ZNG PAN A-I-87/76b) 4 a, 2 sa, 4 j (including 4 shells, ZNG PAN A-I-87/76b.1–4, figured by Krach 1981, pl. 12, figs 28–31); Węglin (MZ VIII Mg 4703/15–38) 6 a, 8 sa, 5 j, 5 jf.

TYPE LOCALITY: Węglin, Roztocze Hills, Poland.

TYPE STRATUM: Middle Miocene (Upper Badenian).

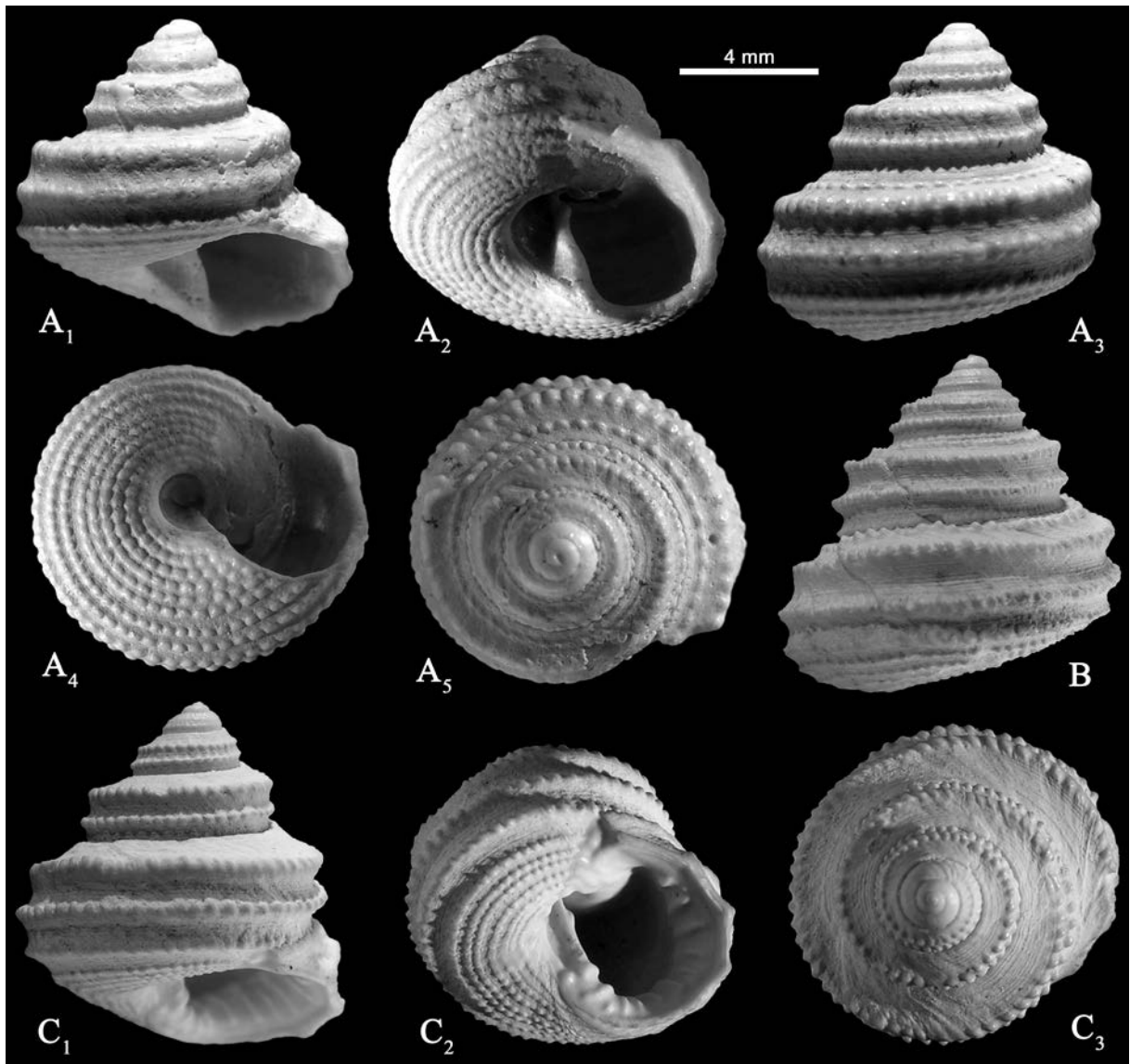
DERIVATION OF NAME: Named in honour of Professor Wilhelm Krach (1907–1985), a Polish researcher of the Miocene stratigraphy and fauna of Poland.

DIAGNOSIS: A *Clanculus (Clanculopsis)* species of medium size with whorls strongly shouldered; three primary beaded cords on last whorl, one at shoulder

Type	Locality	Repository and inventory number	Illustrated herein	Number of shell whorls	Shell height [mm]	Shell width [mm]
Holotype	Węglin, Poland	MZ VIII Mg 4703/1	Text–fig. 2C	7.0	10.0	9.3
Paratype 1	Węglin, Poland	MZ VIII Mg 4703/2	Text–fig. 2B	5.25*	9.8	9.8
Paratype 2	Węglin, Poland	MZ VIII Mg 4703/3	–	5.25*	9.4	9.4
Paratype 3	Węglin, Poland	MZ VIII Mg 4703/4	–	5.0*	8.5	8.5
Paratype 4	Węglin, Poland	MZ VIII Mg 4703/5	–	6.0	8.0	7.7
Paratype 5	Węglin, Poland	MZ VIII Mg 4703/6	–	6.0*	8.0	7.8
Paratype 6	Węglin, Poland	MZ VIII Mg 4703/7	–	5.0*	8.0	8.0
Paratype 7	Węglin, Poland	MZ VIII Mg 4703/8	–	6.25	7.4	8.2
Paratype 8	Węglin, Poland	MZ VIII Mg 4703/9	–	4.75*	7.0	7.8
Paratype 9	Węglin, Poland	MZ VIII Mg 4703/10	–	5.0*	8.0	8.0
Paratype 10	Węglin, Poland	MZ VIII Mg 4703/11	–	5.25*	7.4	7.8
Paratype 11	Węglin, Poland	MZ VIII Mg 4703/12	–	6.0	6.5	6.6
Paratype 12	Węglin, Poland	MZ VIII Mg 4703/13	–	5.0*	6.1	6.4
Paratype 13	Węglin, Poland	MZ VIII Mg 4703/14	–	4.5*	6.4	6.9

Table 1. *Clanculus (Clanculopsis) krachi* sp. nov., type material, inventory numbers and basic parameters. \* – shell without preserved protoconch or shell without preserved protoconch and the first teleoconch whorls.





Text-fig. 2. *Clanculus (Clanculopsis) krachi* sp. nov. from the Badenian of Ukraine and Poland. A – immature specimen without basal columellar tooth and labial ridges from Oles'ko, Ukraine (MZ VIII Mg 4522); B, C – fully grown specimens from Węglin, Poland; B – Paratype 1, MZ VIII Mg 4703/2; C – Holotype, MZ VIII Mg 4703/1. A<sub>1</sub>, C<sub>1</sub> – apertural views; A<sub>2</sub>, C<sub>2</sub> – shell bases in oblique view; A<sub>3</sub>, B – lateral views; A<sub>4</sub> – umbilical view; A<sub>5</sub>, C<sub>3</sub> – apical views.

delimiting wide subsutural platform, one at periphery and one between them; surface covered in spiral threads crossed by extremely fine, close-set prosocline lamellae; weak apertural dentation, basal columellar tooth simple.

**DESCRIPTION:** Shell solid, trochiform, consisting of whorls with angular profile. Protoconch with apical beak, about 0.2 mm in maximum width. Protoconch and first teleoconch whorl surface abraded. Second teleoconch whorl with 4–6 smooth spiral cords of

which two slightly stronger. From beginning of third whorl fine, close-set prosocline ribs cross spiral cords forming beads at intersections, in second half of the whorl ribs weaken and disappear; two beaded cords remain strong. Later spire whorls with horizontal, flat to slightly concave subsutural platform delimited by primary, adapical beaded cord; whorl profile below concave to raised beaded cord, placed just above suture; third most abapical beaded cord completely or partly hidden by subsequent whorl. Last whorl with two strong beaded cords above usually weaker perib-

asal beaded cord, delimiting base. Single secondary spiral beaded cord placed adjacent to adapical suture or at short distance from the suture and in some of the interspaces between primary cords in some specimens. Fine spiral threads in interspaces between primary and secondary spiral sculpture crossed by prosocline lamellae. Shell base somewhat flattened, umbilicate, with five to eight spiral beaded cords of irregular strength and position. Umbilicus narrow and not too deep; spire portion and part of last whorl filled with callus deposit. Periumbilical edge smooth or with weak umbilical denticles (1–4). Mature apertural dentition weakly developed; anal tooth absent; 7–11 labial ridges, single nodules visible occasionally between their ends and others on edge of outer lip; upper columellar fold oblique and almost the same prominent as single basal columellar tooth; one small tubercle placed next to basal columellar tooth. Outer lip with sharp edge. Parietal callus smooth or occasionally bearing four weak parietal ridges. Interior nacreous.

REMARKS: The single specimen (Text-fig. 2A) with strongly angular late teleoconch whorls, from western Ukraine, is not fully-grown, so it does not have all the apertural and columellar armature typical of the genus *Clanculus*. Its protoconch and the sculpture of the earliest teleoconch whorls are not preserved. The specimen is concordant with specimens belonging to one of three morphological groups distinguished within *C. araeonis tuberculatus* (Eichwald, 1830) from the Badenian carbonate deposits of Łychów and Węglinek (Roztocze Hills, Poland) by Krach (1981, p. 43) (see remarks for *C. (C.) robustus* and *C. (C.) tuberculatus* herein). This morphological group “includes specimens having stepped whorls. On the side walls there are three rows of small tubercles. The base and upper part of whorls are flattened. Some of the specimens have a groove-like space between the horizontal rows of tubercles and the single secondary ones between them (pl. 12, figs 28–31). The third group deserves to be recognised as a new subspecies ssp. *trochiformis*” (Krach 1981, p. 43, translated herein). Krach (1981) gave a subspecies rank to his new taxon, but placed it in the subspecies *C. araeonis tuberculatus* [*sic*], therefore the name “*trochiformis*” was proposed as an infrasubspecific rank and thus not available under Article 45.5 of ICZN (1999). Furthermore, this name was preoccupied by the southern African species *Clanculus trochiformis* Turton, 1932, which was later synonymised with *Clanculus (Clanculopsis) miniatus* (Anton, 1838) by Herbert (1993).

I prefer to give the form distinguished by Krach

(1981) a full species rank and name it as *Clanculus (Clanculopsis) krachi* sp. nov. The strongly angular late teleoconch whorls make the species quite distinct from *Clanculus (C.) robustus* (Text-fig. 3A–C), *Clanculus (C.) tuberculatus* (Text-figs 4A–C and 5A–G) and other Miocene European *Clanculus* species.

In designating a holotype an author should give preference to a specimen of which an illustration has been published, however, an infrasubspecific entity is not regulated by the ICZN (1999; Article 1.3.4). Moreover, specimens ZNG PAN A-I-87/76b.1–4 illustrated by Krach (1981, pl. 12, figs 28–31) have turned out to be poorly preserved upon examination in the collection; the protoconch and the first teleoconch whorl(s) are missing (Krach 1981, pl. 12, figs 28–30); the last whorl and umbilicus are completely filled with hard sediment (Krach 1981, pl. 12, fig. 31); and the surface is eroded on upper teleoconch whorls (Krach 1981, pl. 12, fig. 30). Besides, the original Krach’s label indicates the location ‘Węglinek’ for specimens illustrated in Krach (1981, pl. 12, figs 28–31), while the location ‘Łychów’ is given in the plate captions.

The best fully grown specimen MZ VIII Mg 4703/1 is selected here as the holotype from among numerous specimens from Węglin better preserved than the specimens figured by Krach (1981, pl. 12, figs 28–31). Węglin is located about 1 km south of Węglinek.

*Clanculus (C.) krachi* sp. nov. is variable in both shape and sculpture. Some shells are more depressed, whilst others have a elevated spire. The subsutural platform is variable in width, almost flat to strongly concave. The shape of the beads is also variable: primary beads may range from spherical to axially elongated; secondary beads, if any, are occasionally horizontally elongated. The strength of the beaded cords and width of their interspaces on both the lateral flank and on the shell base also vary.

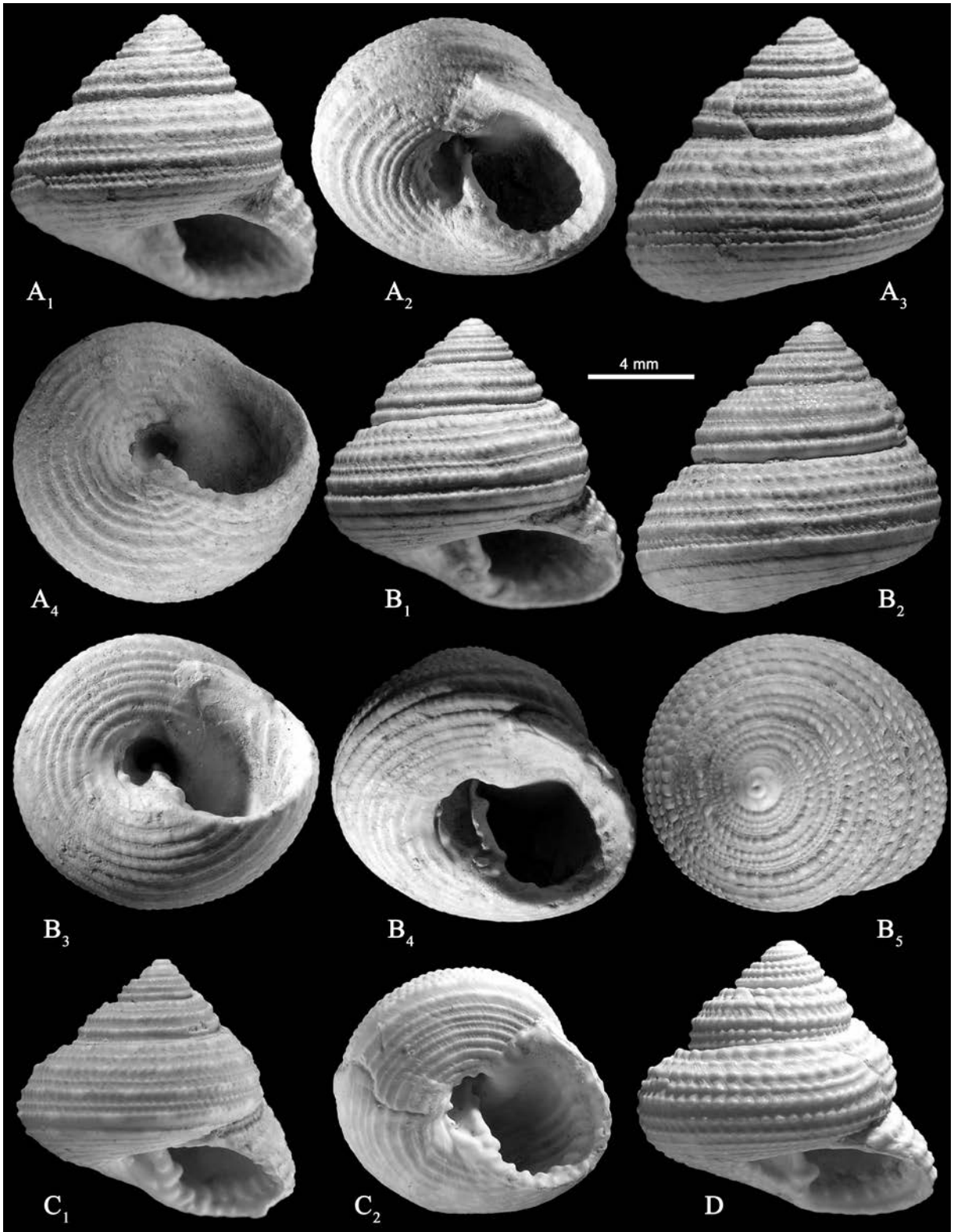
OCCURRENCE: Middle Miocene of the Central Paratethys: Badenian of Poland (Krach 1981 and this study) and western Ukraine (this study); for details see Appendix 2.

*Clanculus (Clanculopsis) robustus* Friedberg, 1928  
(Text-fig. 3A–C)

1928. *Clanculus Araonis* Bast. var. *robusta* Friedb.;  
Friedberg, p. 480, pl. 30, fig. 7.

1938. [*Clanculus Araonis* Bast.] var. *robusta* Friedb.;  
Friedberg, p. 51.

part 1950. *Clanculus araeonis* Bast.; Kowalewski, p. 42.



Text-fig. 3. Species of *Clanculus* Montfort, 1810 from the middle Miocene of Ukraine and France. A–C – *Clanculus (Clanculopsis) robustus* Friedberg, 1928. A, B – Saryi Pochaiv, Ukraine; A – MZ VIII Mg 4521/1; B – MZ VIII Mg 4521/2; C – Lidykhiv, Ukraine; MZ VIII Mg 4520/1. A<sub>1</sub>, B<sub>1</sub> C<sub>1</sub> – apertural views; A<sub>2</sub>, B<sub>4</sub>, C<sub>2</sub> – shell bases in oblique view; A<sub>4</sub>, B<sub>3</sub> – umbilical views; A<sub>3</sub>, B<sub>2</sub> – lateral views; B<sub>5</sub> – apical view. D – *Clanculus (Clanculopsis) baccatus* (Defrance, 1824) from Pontlevoy, France; MZ VIII Mg 451/1 in apertural view.



1955. *C.[lanculus] robusta* Friedb.; Korobkov; p. 97, pl. 4, fig. 8 [figures from Friedberg 1928, pl. 30, fig. 7].
1968. *Clanculus robusta* Friedberg, 1928; Kulichenko and Sorochan, p. 103, pl. 28, figs 9, 10 [figures from Friedberg 1928, pl. 30, fig. 7a–b].
- part 1981. *Clanculus araoonis tuberculatus* (Eichwald 1830); Krach, p. 43, pl. 12, figs 18, 19, 21, ?24 [non figs 20, 22, 23, 25–27 = *Clanculus (Clanculopsis) tuberculatus* (Eichwald, 1830); figs 28–31 = *Clanculus (Clanculopsis) krachi* sp. nov.].
2001. *C.[lanculus] robusta* Friedberg, 1928; Anistratenko and Anistratenko, p. 185.

**MATERIAL:** Sandy facies: Yaseniv (MZ VIII Mg 4515) 1 j, 3 jf; Oles'ko (MZ VIII Mg 4516, 4517) 1 a, 1 af; Pidhirtsi (MZ VIII Mg 4518) 2 jf; Shushkivtsi (MZ VIII Mg 4519) 1 jf. Carbonate deposits: Lidykhiv (MZ VIII Mg 4520) 4 a; Staryi Pochaiv (MZ VIII Mg 4521) 9 a, 2 sa. All specimens are from western Ukraine.

**DESCRIPTION:** Shell solid, trochiform, with a moderately elevated conical spire. Protoconch eroded. First teleoconch whorl bearing two spiral cords of roughly equal strength and prosocline axial ribs, slightly weaker than cords. Second whorl, a third weaker cord develops below adapical suture, rapidly gaining in strength; axial ribs disappear. Third whorl, a fourth cord often developed just above abapical suture or between cords 1 and 2; cords become beaded and remain so thereafter. Fourth whorl bearing 3–4 primary beaded cords, with single secondary beaded cord developed in some of the interspaces; secondary beads usually horizontally elongated. Prosocline lamellar growth lines visible in interspaces between cords. Last whorl bearing 7–8 beaded cords of irregular strength; fine spiral threads in interspaces between primary and secondary spiral sculpture crossed by closely-set growth lines. Closer-set two cords bearing rounded to slightly quadrangular beads, placed adjacent to adapical suture in some specimens. Teleoconch whorls flat-sided to convex. Suture impressed. Last whorl rounded at periphery, its last part in mature shells descending noticeably near aperture; outer lip joining penultimate whorl below periphery. Base somewhat flattened, umbilicate, bearing 8–10 beaded to almost smooth spiral cords of irregular strength and position; spiral threads crossed by growth lines in interspaces between cords. Umbilicus open, spire portion filled with callus. Simple basal columellar tooth small, with tubercle below, usually more weakly protruding than

upper oblique columellar fold; 2–3 nodules situated between them on side of umbilicus. Umbilical denticles (4–5) more or less prominent. Inner side of outer lip bearing 9–11 long labial ridges, sometimes extending far inside aperture. Single nodules visible occasionally between ends of long labial ridges. Additional nodules visible on edge of outer lip (see Text-fig. 3C<sub>2</sub>). Parietal ridges very weak. Some specimens with slightly stepped profile. Colour pattern of spiral rows of white spots arranged on dark background, preserved in some specimens.

**REMARKS:** Friedberg (1928, 1938) recognised only one species, *Clanculus araoonis* (Basterot, 1825), of the genus *Clanculus* from the middle Miocene of the Fore-Carpathian Basin. Within the species, he distinguished a new variety *C. araoonis* var. *robusta* for two specimens from the Upper Badenian sands of Rybnica, Poland and *C. araoonis* mut. *tuberculata* (Eichwald, 1830) (Friedberg 1928). Two specimens of *C. araoonis* var. *robusta* (ZNG PAN A-I-50/1557), including the specimen illustrated in Friedberg (1928, pl. 30, fig. 7; ZNG PAN A-I-50/1557a), are present in the ZNG PAN collection. Friedberg (1928, p. 480) said that his *robusta* is similar, if not identical to *Clanculus praecruciatius* Mikhailovsky, 1903 from the Tarkhanian (middle Miocene after Golovina *et al.* 2019 and Palcu *et al.* 2019) of southern Ukraine, however, the description and illustrations (Mikhailovsky 1903, pp. 70–72, 228–230, pl. 3, figs 26–33) of the species are not clear. Therefore, it is unreasonable to consider whether these two taxa are synonyms, because the apertural and umbilical characters of the shells of Mikhailovsky's species are unknown.

Later, Krach (1981) distinguished three morphological groups within *C. araoonis tuberculatus* based on the variability of the specimens from Badenian carbonate deposits of Łychów and Węglinek (Roztocze Hills, Poland). In the first group, divided into subgroups, Krach (1981, p. 43, pl. 12, figs 18, 19, 21, 24) included specimens that he considered “conspecific with the mutation *robusta* in Friedberg (1928, p. 480, pl. 30, fig. 7), and also specimens assigned by Glibert to *C. baccatus* from the Miocene of Belgium (Defr. Glibert 1949, p. 65, pl. 4, fig. 1)” (Krach 1981, p. 43, translated herein). In fact, the description and illustrations of the species *Clanculus baccatus* (Defrance, 1824) given by Glibert (1949a) refer to specimens from the Loire Basin, France. The original Krach's label in ZNG PAN indicates the location ‘Węglinek’ for some specimens illustrated in Krach (1981, pl. 12, figs 19, 21, 24), whereas the location ‘Łychów’ is given in the plate captions.



*Clanculus (Clanculopsis) baccatus* and *Clanculus (Clanculopsis) araoonis* were originally described from the middle and lower Miocene of France, respectively. Both Peyrot (1938) and Glibert (1949a) noted that the differences between specimens described under these names are not very clear and inconstant. Consequently, Dollfus and Dautzenberg (1886, p. 142), and also Peyrot (1938, pp. 20, 21) considered *C. araoonis* to be a junior synonym of *C. baccatus*. This opinion is not shared by Lozouet *et al.* (2001), who illustrated a French shell from the lower Miocene under the name *Clanculus (Clanculopsis) araoonis*, without further comment. Glibert (1962, pp. 60, 61), Ceulemans *et al.* (2016, p. 58) and Landau *et al.* (2017, p. 93) also distinguished *C. (C.) araoonis* from *C. (C.) baccatus*; moreover, they did not include references to *C. (C.) araoonis* in their synonymy of *C. (C.) baccatus*.

The middle Miocene shells of *Clanculus (Clanculopsis)* from the Fore-Carpathian Basin should not to be united with the French species (see synonymy), at the same time the differences between the apertural and columellar features, and also the sculpture of *C. (C.) robustus* and *C. (C.) tuberculatus* (compare Text-fig. 3A–C with Text-figs 4A–C and 5A–G) are sufficient to treat them as distinct species. However, it must be noted that some shells are difficult to assign to either of these species, particularly when juvenile.

On the other hand, there is a similarity in shell shape and sculpture of the late teleoconch whorls of *C. (C.) robustus* to those of *C. (C.) baccatus* illustrated by Glibert (1949a, pl. 4, fig. 1) from the Langhian (middle Miocene) of Pontlevoy, Loire Basin. The six specimens of *C. (C.) baccatus* in the MZ collection (MZ VIII Mg 451) from Pontlevoy have the protoconch poorly preserved but, as in *C. (C.) robustus*, two spiral cords are visible on the first teleoconch whorl, and a little further the third spiral cord occurs near the adapical suture. *Clanculus (C.) baccatus* differs from *C. (C.) robustus* in having: prominent, slightly prosocline axial ribs between the spiral cords on the second, third and fourth whorl; almost twice as wide interspaces between prosocline ribs; coarser sculpture; and stronger developed basal columellar tooth (see Text-fig. 3D; specimen MZ VIII Mg 451/1). These differences are sufficient to retain them as distinct species.

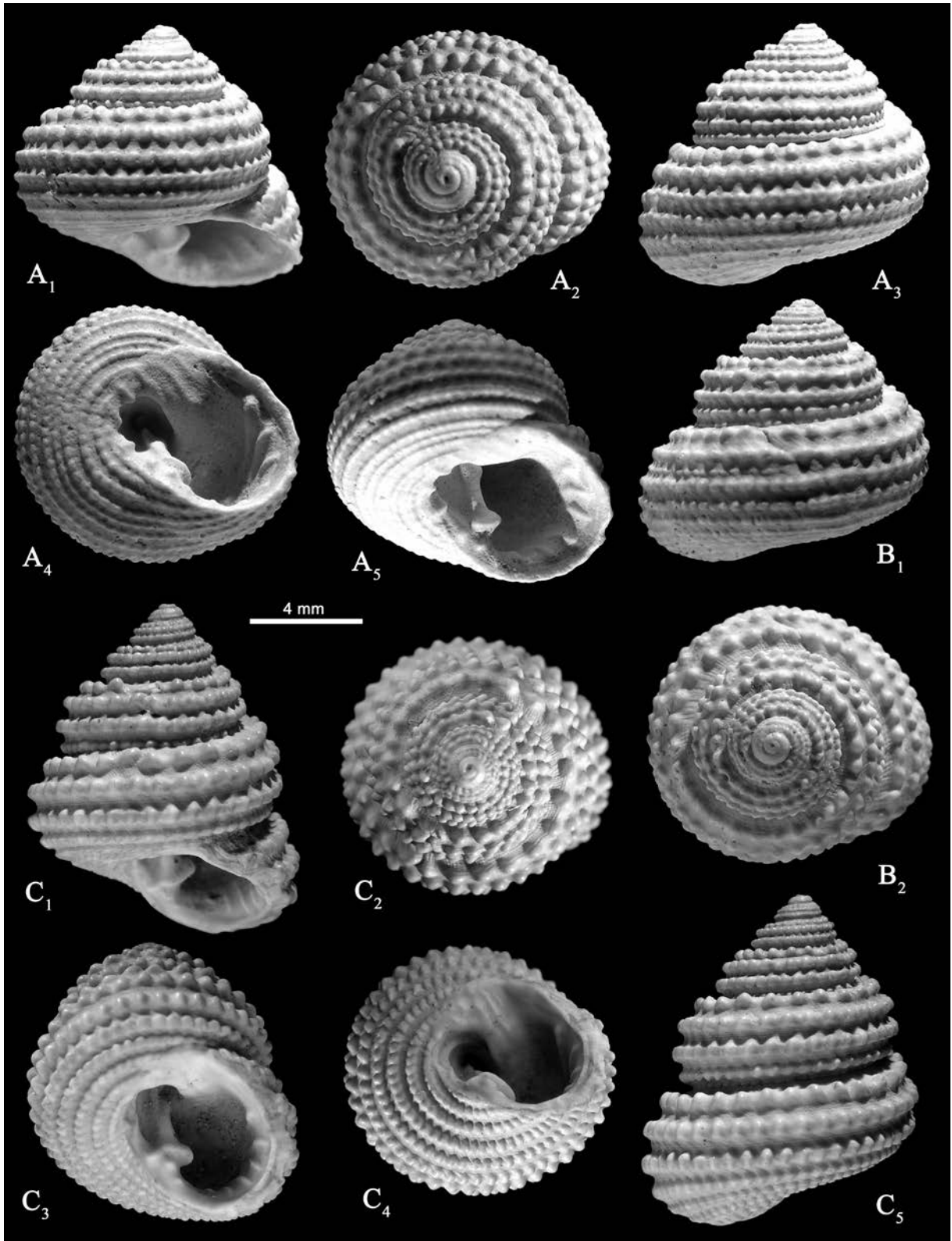
Another middle Miocene *Clanculopsis* species, *C. (C.) cruciatus* (Linnæus, 1758), was recently illustrated by Landau *et al.* (2013, pl. 1, fig. 3) from the late Serravallian of the Karaman Basin, Turkey. Images of two other specimens of *C. (C.) cruciatus* from the same locality (Seyithasan) kindly sent by

Bernard Landau (Department of Geology Naturalis Biodiversity Center) show some variability of this species, which differs from *C. (C.) robustus* in details of the surface sculpture.

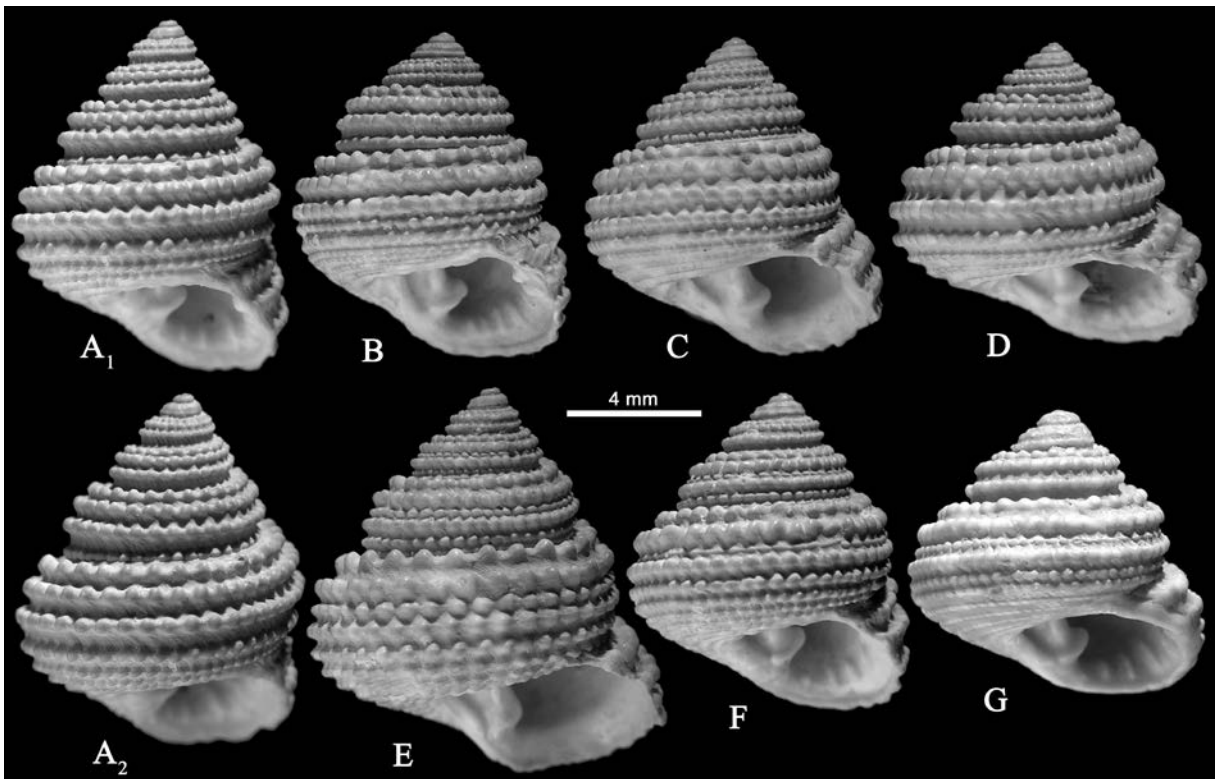
OCCURRENCE: Middle Miocene of the Central Paratethys: Badenian of Poland (Friedberg 1928, 1938; Kowalewski 1950; Bałuk and Radwański 1968; Krach 1981; MZ collection) and western Ukraine (Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001, and this study; for details see Appendix 2); Paratethys: Sarmatian (= upper Serravallian) of Poland (Friedberg 1938).

*Clanculus (Clanculopsis) tuberculatus*  
(Eichwald, 1830)  
(Text-figs 4A–C and 5A–G)

- 1830. *Monodonta tuberculata*, m.; Eichwald, p. 220.
- 1837. *Monodonta Araonis* Bast.; Pusch, p. 105, pl. 10, fig. 4.
- 1850. [*Monodonta tuberculata* m.]; Eichwald, pl. 10, fig. 36 (atlas).
- 1851a. *Monod.[onta] tuberculata* m.; Eichwald, pp. 118, 119, 283.
- 1851b. *Monodonta tuberculata* m.; Eichwald, pl. 10, fig. 36 (atlas).
- 1853. *Monod.[onta] tuberculata* m.; Eichwald, pp. 242, 243.
- 1859. *Monodonta tuberculata*; Eichwald, p. 3, pl. 10, fig. 36 (atlas).
- part 1928. *Clanculus Araonis* Bast. mut. *tuberculata* Eichw.; Friedberg, pp. 478, 479, pl. 30, figs 5, 6.
- 1937. *Clanculus Araonis* Bast. mut. *tuberculata* Eichw.; Kowalewski, p. 7.
- part 1938. *Clanculus Araonis* Bast. var. *tuberculata* Eichw.; Friedberg, p. 51.
- 1955. *Clanculus tuberculatus* Eichw.; Korobkov, p. 97, pl. 4, figs 9, 10 [figures from Friedberg 1928, pl. 30, figs 5, 6].
- 1960. *Clanculus (Clanculopsis) araoonis* var. *tuberculata* (Eichwald 1853); Kojumdgieva, pp. 85, 86, pl. 28, figs 12, 13.
- 1968. *Clanculus tuberculatus* (Eichwald, 1830); Kulichenko and Sorochan, p. 104, pl. 28, figs 11, 12 [figures from Friedberg 1928, pl. 30, figs 5a, 6].
- part 1981. *Clanculus araoonis tuberculatus* (Eichwald 1830); Krach, p. 43, pl. 12, figs 20, 22, 23, 25–27 [non figs 18, 19, 21, ?24 = *Clanculus (Clanculopsis) robustus* Friedberg, 1928; figs 28–31 = *Clanculus (Clanculopsis) krachi* sp. nov.].
- 2000. *Granulifera pulla* O. Anistratenko sp. n.; Anistratenko, pp. 4–6, text-fig. 1.



Text-fig. 4. *Clanculus (Clanculopsis) tuberculatus* (Eichwald, 1830) from the Badenian of Ukraine. A, B – Zalistsi; A – MZ VIII Mg 4531/1, B – MZ VIII Mg 4530/1; C – Staryi Poचाiv; MZ VIII Mg 4534/1. A<sub>1</sub>, C<sub>1</sub> – apertural views; A<sub>2</sub>, B<sub>2</sub>, C<sub>2</sub> – apical views; A<sub>3</sub>, B<sub>1</sub>, C<sub>5</sub> – lateral views; A<sub>4</sub>, C<sub>4</sub> – umbilical views; A<sub>5</sub>, C<sub>3</sub> – shell bases in oblique view.



Text-fig. 5. *Clanculus (Clanculopsis) tuberculatus* (Eichwald, 1830). Apertural views of specimens from the Badenian of Węglin, Poland, showing variability of the shape and ornamentation of the shells. A – MZ VIII Mg 4704/1; B – MZ VIII Mg 4704/2; C – MZ VIII Mg 4704/3; D – MZ VIII Mg 4704/4; E – MZ VIII Mg 4704/5; F – MZ VIII Mg 4704/6; G – MZ VIII Mg 4704/7.

2001. *C.[lanculus] tuberculatus* (Eichwald, 1830); Anistratenko and Anistratenko, p. 185.  
 2003. *Granulifera pulla* O. Anistratenko, 2000; Anistratenko *et al.*, pp. 111, 112, figs 18–32.

**MATERIAL:** Sandy facies: Yaseniv (MZ VIII Mg 4523) 1 j, 5 jf; Oles'ko (MZ VIII Mg 4524–4526) 2 a, 1 sa, 8 fp; Pidhirtsi (MZ VIII Mg 4527, 4528) 12 jf; Shushkivtsi (MZ VIII Mg 4529) 3 fp; Zalisti (MZ VIII Mg 4530, 4531) 5 a, 1 j; Vanzhuliv (MZ VIII Mg 4678) 1 a, 3 j; Varivtsi (MZ VIII Mg 4679) 1 j; Vyshhorodok (MZ VIII Mg 4532) 1 j. Carbonate deposits: Lidykhiv (MZ VIII Mg 4533) 1 sa; Staryi Pochaiv (MZ VIII Mg 4534) 2 a; Zhukivtsi (MZ VIII Mg 4716) 1 a, 1 sa. All specimens are from western Ukraine.

**DESCRIPTON:** Shell solid, trochiform, with depressed to strongly elevated conical spire. Paucispiral protoconch, about 0.2 mm in width, with apical back. Teleoconch starts without sculpture. Two smooth spiral cords appearing in latter part of first teleoconch whorl. On second or third teleoconch whorl single spiral cord appears below adapical suture and occa-

sionally between spiral cords; cord quickly disappearing in interspace. On third whorl cords transform into rows of tubercles and remain so thereafter. One or two secondary tuberculate cords emerging out of abapical suture and another tuberculate cord appears between second and third primary rows of tubercles on later whorls in some specimens. The result are 4–6 spiral rows of tubercles of irregular strength and position on the penultimate whorl. Fine spiral threads in interspaces between primary and secondary spiral sculpture crossed by closely-set prosocline axial growth lines. Teleoconch whorls flat-sided to convex. Suture impressed. Last whorl rounded at periphery. Last part of last whorl in mature shells descending noticeably near aperture; outer lip joining penultimate whorl below periphery. Base somewhat flattened, umbilicate, bearing 5–7 spiral beaded cords. Umbilicus narrow and deep, spire portion filled with callus. Basal columellar tooth simple, large with 1–2 small tubercles below and much more protruding than upper oblique columellar fold. Umbilical denticles (3–4) more or less prominent. Inner side of outer lip bearing 5–7 (typically 6) long labial ridges; sometimes weak labral



denticles at ends of external spiral cords. Parietal ridges very weak. Sculpture of slender specimens coarser, especially on shell base, than in depressed specimens. Interior nacreous. Colour pattern of white spots, sometimes arranged in diagonal stripes, on brown background, preserved in some specimens.

REMARKS: Only one specimen of *Clanculus* (*Clanculopsis*) *tuberculatus* is present in the SPbGU collection. This specimen (labelled as *Monodonta tuberculata*, SPbGU 3/444) according to Eichwald's label originates from Zalitsi (= Salisze, Zalisce). It was undoubtedly illustrated in Eichwald's atlas (1850, 1851b, 1859, pl. 10, fig. 36a–c). However, the image of the sculpture of the last whorl (pl. 10, fig. 36c) is not accurate. In the illustration, the rows of tubercles are in contact, while the specimen examined (SPbGU 3/444) has the interspaces between them roughly equal to their width.

The second morphological group distinguished by Krach (1981, p. 43) within the subspecies *C. aranis tuberculatus* [see remarks for *C. (C.) krachi* and *C. (C.) robustus* herein] represent “specimens with rounded whorls with a few rows of thick tubercles, 3 on each of the side walls. Sometimes, among them there are rows of secondary tubercles (pl. 12, figs 20, 22–27). Specimens of this group correspond to those described by Friedberg as mut. *tuberculata*” (Krach 1981, p. 43, translated herein). Probably due to a print error, the illustration in Krach (1981, pl. 12, fig. 24) was assigned to this group, although the text above and the description of the plate illustrations refers it to the first morphological group, i.e., ‘*robustus*’. The location ‘Łychów’ is given in the plate captions for the specimen illustrated in Krach (1981, pl. 12, fig. 27) but the original Krach's label indicates the location ‘Węglinek’. Shells assigned by Krach (1981) to the second morphological group are conspecific with Eichwald's specimen of *C. (C.) tuberculatus* (SPbGU 3/444).

As can be seen from the series illustrated (Text-figs 4A–C and 5A–G), *C. (C.) tuberculatus* is interpreted herein as being highly variable in both shape and sculpture. The existence of intermediate forms between the most slender and the most depressed forms does not allow for the separation of the two forms. A similar variation in the shell shape was observed by Chirli (2004, pl. 16, figs 4, 5, 8–10) in *Clanculus corallinus* (Gmelin, 1791) from the Pliocene of Tuscany, Italy.

The slender specimens of *C. (C.) tuberculatus* from Węgliń, Poland (Text-fig. 5A) and Staryi Pochav, Ukraine (Text-fig. 4C) are almost identical

with the specimen identified as *Granulifera pulla* from Węgliń by Anistratenko *et al.* (2003, text-figs 23–25). Only juvenile specimens from the Upper Badenian deposits of Sataniv, Ukraine were described by Anistratenko (2000) as *Granulifera pulla* gen. et sp. n. Later, Anistratenko *et al.* (2003) enriched the information about this taxon by giving a description and illustrations of fully grown individuals and the protoconch of the juvenile shell from Węgliń. A comparative study conducted herein shows *G. pulla* to be a junior subjective synonym of *Clanculus (C.) tuberculatus* (Eichwald, 1830), and thus *Granulifera* is a junior subjective synonym of *Clanculopsis* Monterosato, 1879.

The Badenian specimens from Korytnica identified by Bałuk (2006, pp. 182, 183, pl. 2, fig. 4) as *Granulifera hoernesii* (Doderlein, 1862) are probably juvenile representatives of *Clanculus* sp.

OCCURRENCE: Middle Miocene of the Central Paratethys: Badenian of Austria (Sieber 1946; Mandić *et al.* 2002), Hungary (Csepreghy-Meznerics 1954, 1969b; Strausz 1966), Bulgaria (Kojumdjieva 1960), Poland (Friedberg 1928, 1938; Areń 1962; Krach 1981; Anistratenko *et al.* 2003; and this study), and western Ukraine (Eichwald 1830, 1851a, 1853; Pusch 1837; Friedberg 1928, 1938; Kowalewski 1937; Amitrov 1961; Kulichenko and Sorochan 1968; Anistratenko 2000; Anistratenko and Anistratenko 2001; Anistratenko *et al.* 2003; and this study; for details see Appendix 2).

#### Subfamily Cantharidinae Gray, 1857

REMARKS: The molecular study by Williams *et al.* (2008, 2010) has resulted in changes to the systematic of this subfamily. Some taxa of the Monodontinae Gray, 1857 (e.g., *Oxystele* Philippi, 1847 or *Gibbula* Risso, 1826) have been transferred to the Cantharidinae. The Gibbulinae Stoliczka, 1868, frequently considered a synonym of the Monodontinae, turned out to be synonymous with the Cantharidinae. As a result of these changes, the previous definition of this subfamily based on morphological characters was updated. Unfortunately, radular characters that might be useful for defining Cantharidinae (see Williams *et al.* 2010) are not possible to apply to fossil taxa. Because the shell characters of the Cantharidinae are very differentiated hence not unequivocal and clear, the assignment of fossils to genera of this subfamily may be debateable. The Cantharidinae currently comprises 25 genera (MolluscaBase 2019), two of



them, *Gibbula* and *Jujubinus* Monterosato, 1884, are represented by the species discussed in this paper. The genus *Paroxystele* Schultz, 1969 is known only from fossil record.

This subfamily, usually associated with shallow rocky shores, algae and seagrasses, is mainly a sub-tropical or temperate-water radiation, and is widespread from the Central and Western Indo-Pacific regions to the Mediterranean Sea and the Eastern Atlantic Ocean (Williams *et al.* 2010; Uribe *et al.* 2017a). Such distribution suggests a Tethyan origin of the group (Uribe *et al.* 2017a). Both molecular data and fossil evidence from extant genera imply that Cantharidinae first diversified in the Late Cretaceous (Williams *et al.* 2010). The origin of the Mediterranean and NE Atlantic clade dates back about 47 Ma, its diversification into main lineages, i.e., *Phorcus* Risso, 1826, *Jujubinus*, and various *Gibbula* clades was dated between 38 and 28 Ma, whereas most of the main diversification within each genus started in the middle Miocene at about 14 Ma and again in the Pliocene at about 5 Ma (Uribe *et al.* 2017a).

#### Genus *Gibbula* Risso, 1826

TYPE SPECIES: *Trochus magus* Linnæus, 1758, by subsequent designation by Herrmannsen (1847). Recent, Mediterranean Sea.

REMARKS: The molecular studies of Williams *et al.* (2010), Barco *et al.* (2013), Affenzeller *et al.* (2017) and Uribe *et al.* (2017a) have caused major changes in the concept of the genus *Gibbula* which has turned out not to be monophyletic. Species attributed to *Gibbula* by Uribe *et al.* (2017a) were subdivided into three clades. Accordingly, the clade including the type species *G. magus*, and also *G. ardens* (von Salis Marschlin, 1793), *G. fanulum* (Gmelin, 1791) and *G. guttadauri* (Philippi, 1836) should keep the genus name, while the remaining *Gibbula* clades could be given different generic names. Moreover, Williams *et al.* (2010) and Uribe *et al.* (2017a) have suggested that certain species ascribed to *Gibbula* should probably be assigned to other genera, some of which do not belong in the Cantharidinae. No molecular data can be applied in the interpretation of fossil species, therefore only the use of the shell is possible in this case. When characterising the *Gibbula* shell, Knight *et al.* (1960) stated that its sutures are impressed and the umbilicus is bounded by a ridge. The merits of the use of subgenera within *Gibbula*, as was done in the literature (e.g., Bałuk 1975, 2006; Iljina 1993; Marquet 1998; Landau *et al.* 2003; Chirli 2004),

are not supported by DNA data (Barco *et al.* 2013; Affenzeller *et al.* 2017).

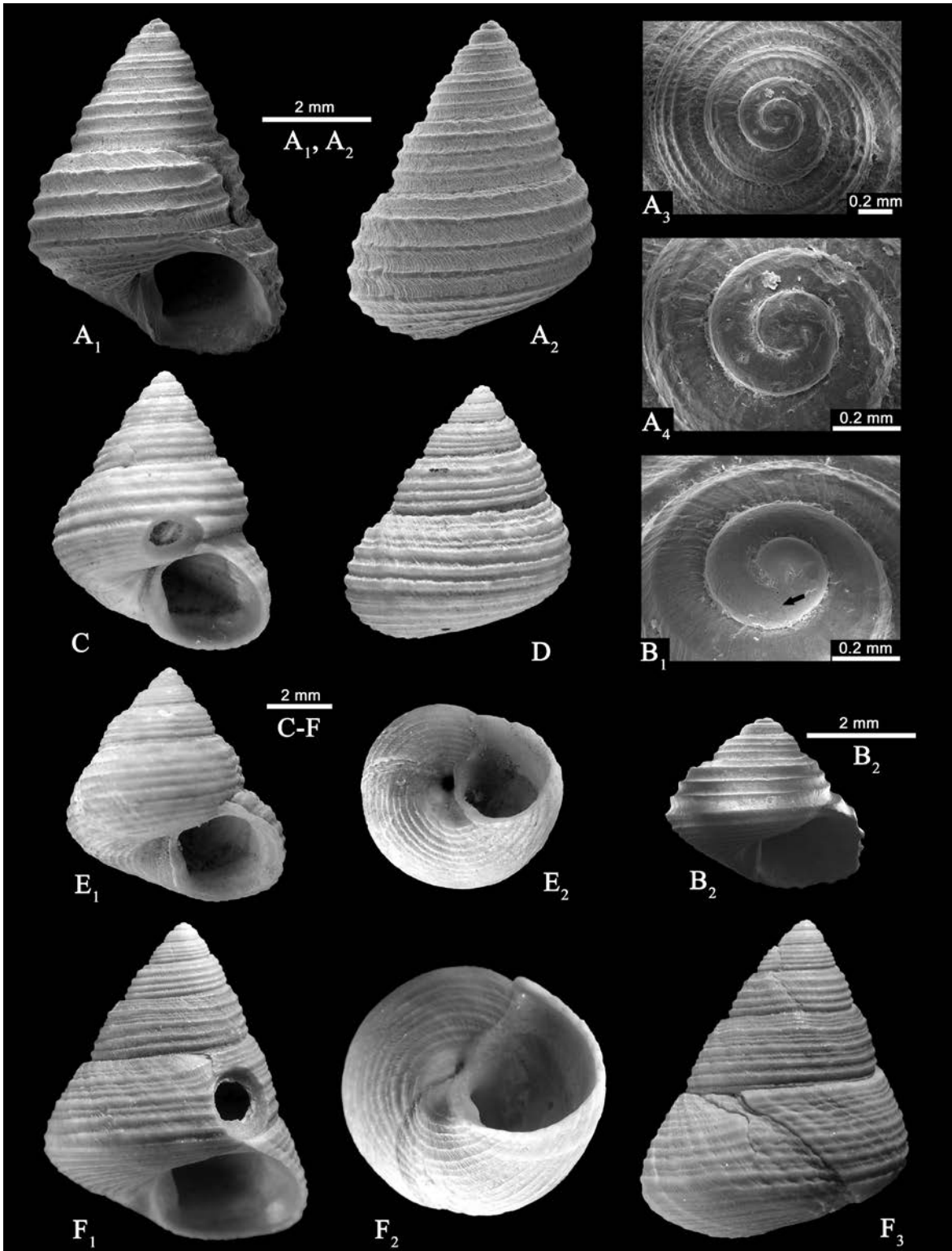
Extant species of the genus *Gibbula* are dominant elements of rocky-shore faunas in the eastern Atlantic and Mediterranean, but they are also associated with marine vegetation and detritic sublittoral bottoms. According to Hickman and McLean (1990), *Gibbula* appeared before the end of the Cretaceous, but the results of the research by Uribe *et al.* (2017a) suggest that the origin of the *Gibbula* clades took place towards the end of the Eocene.

#### *Gibbula affinis* (Eichwald, 1851)

(Text-fig. 6A–F)

1850. [*Trochus affinis* m.]; Eichwald, pl. 9, fig. 16 (atlas) [captions to plates of the atlas were published in Eichwald (1851a, pp. 277–284), therefore, the name *Trochus affinis* was first used in 1851].
- 1851a. *Troch.[us] affinis* m.; Eichwald, pp. 113, 282.
- 1851b. [*Trochus affinis* m.]; Eichwald, pl. 9, fig. 16 (atlas).
1853. *Troch.[us] affinis* m.; Eichwald, pp. 227, 228.
1859. *Trochus affinis*; Eichwald, p. 3, pl. 9, fig. 16 (atlas).
1903. *Trochus affinis* Eichw. var.; Laskarev, pp. 94, 95, pl. 5, figs 18, 19.
1903. *T.[rochus] affinis* Eichw.; Laskarev, pp. 94, 95, pl. 5, figs 20–23.
1903. *Trochus affinis* Eichw.; Mikhailovsky, pp. 68, 69, 227, pl. 4, figs 7, 8, 12–15.
- part 1928. *Gibbula affinis* Eichw.; Friedberg, pp. 489, 490, pl. 30, figs 24–26.
- part 1928. *Gibbula affinis* Eichw. var. *pseudangulata* Boettg.; Friedberg, pp. 491, 492, pl. 31, figs 1–3.
- 1936b. *Gibbula affinis* Eichw.; Kowalewski, p. 15.
1937. *Gibbula affinis* Eichw.; Kowalewski, p. 7.
- part 1938. *Gibbula affinis* Eichw.; Friedberg, p. 54.
- part 1938. *Gibbula affinis* var. *pseudangulata* Boettg.; Friedberg, p. 54.
1950. *Gibbula affinis* Eichw.; Krach, p. 300, pl. 1, fig. 21.
1968. *Gibbula affinis* (Eichwald, 1853); Kulichenko and Sorochan, p. 106.
1970. *Gibbula affinis affinis* (Eichwald); Bałuk, p. 117, pl. 8, fig. 4.
1993. *Gibbula (Colliculus) affinis* (Eichwald, 1850); Iljina, p. 30, pl. 2, figs 23–25.
2001. *Colliculus affinis* (Eichwald, 1853); Anistratenko and Anistratenko, p. 190.

MATERIAL: Sandy facies: Bilozirka (MZ VIII Mg 590, 4535) 72 sh, 6 fp; Yaseniv (MZ VIII Mg 4536) 2



Text-fig. 6. *Gibbula affinis* (Eichwald, 1851) from the Badenian of Ukraine. A, F – Rydomyl'; A – MZ VIII Mg 4542/3, F – MZ VIII Mg 4542/1; B – Zalistsi; MZ VIII Mg 4545/1; C, D, E – Zhukivtsi; C – MZ VIII Mg 641/1, D – MZ VIII Mg 641/2, E – MZ VIII Mg 641/3. A<sub>1</sub>, B<sub>2</sub>, C, E<sub>1</sub>, F<sub>1</sub> – apertural views; A<sub>2</sub>, D, F<sub>3</sub> – lateral views; E<sub>2</sub>, F<sub>2</sub> – umbilical views; A<sub>3</sub> – close-up of the apex in apical view; A<sub>4</sub> – details of juvenile whorls in apical view, B<sub>1</sub> – details of juvenile whorls in oblique view, black arrow indicates demarcation between protoconch and teleoconch. A, B are SEM images.

sh; Korostova (MZ VIII Mg 4537) 1 j; Oles'ko (MZ VIII Mg 4538–4540) 216 sh; Pidhirtsi (MZ VIII Mg 4541) 6 sh; Rydomyl' (MZ VIII Mg 4542) 194 sh; Shushkivtsi (MZ VIII Mg 4543) 48 sh; Vanzhuliv (MZ VIII Mg 4680) 3 sh; Varivtsi (MZ VIII Mg 4681) 15 sh; Zalistsi (MZ VIII Mg 4545) 25 sh; Zalistsi – Zhabiak ravine (MZ VIII Mg 4546) 6 sh, 1 fp; Zhukivtsi (MZ VIII Mg 641) 29 sh. All specimens are from western Ukraine.

**DESCRIPTION:** Shell small, trochiform. Protoconch paucispiral, with apical beak; terminal lip of protoconch simple, not thickened and with no subterminal varix; protoconch/teleoconch boundary clearly defined, fractured. Teleoconch whorls convex to almost flat-sided. Suture impressed, linear. First teleoconch whorl bearing three very fine spiral cords, little further number of spiral cords increases to four, five or six. Cords of equal or variable strength. Interspaces between cords not always of identical width but always with prosocline lamellae, closer spaced towards aperture. Lamellar growth lines sometimes visible also on spiral cords. During ontogeny primary cords dividing into two spiral cords or/and 1–2 secondary cords intercalated in some to all interspaces in some specimens. Last whorl rounded or slightly angular at peripheral cord. Slightly convex shell base bearing primary spiral cords (7 on specimen MZ VIII Mg 4542/3, Text-fig. 6A; 11 on specimen MZ VIII Mg 641/2, Text-fig. 6D), occasionally with weaker spiral cords intercalated in some of the interspaces and prosocline lamellae. Umbilicus open or covered by inner lip. Outer lip with sharp edge, in some specimens bearing an internal ridge running parallel to lip edge and spirally aligned ridges extending far inside aperture. Aperture oval-quadrangle. Columella bearing distinct protuberance. Interior nacreous. Some shells with slightly stepped profile.

**REMARKS:** In the SPbGU collection there are only two specimens (SPbGU 3/426) named by Eichwald as *Trochus affinis*. His original label indicates that these specimens originate from Zhukivtsi (= Shukowze). The specimens have been recognised by the curator of Eichwald's collection as paratypes of *T. affinis*. The drawings of this species somewhat differ in the subsequent editions of Eichwald's atlas (1850, 1851b, 1859, pl. 9, fig. 16). Illustrations of the 1859 version more accurately show the appearance of the shell base and sculpture of the last whorl of *G. affinis*.

The Ukrainian shells of *G. affinis* show high variability in size, outline and sculpture, which is probably the reason why Friedberg (1928) distinguished

the variety *pseudangulata* Boettger, 1907. The species name for the specimens from the Badenian deposits of Coștei, Romania, used by Boettger (1907, p. 181) to designate a new species '*Gibbula (Colliculus) pseudangulata* Boettger, 1907', is preoccupied by the name of the species *Trochus pseudoangulatus* Sincov, 1875, described from the Sarmatian deposits of Chișinău, Moldova (Sincov 1875, pp. 52, 53, pl. 4, figs 17, 18). Iljina (1993, p. 30) recognised Boettger's species name as the junior homonym of the species of the same family, established by Sincov (1875), therefore she replaced it with a new name *boettgeri*. The name was accepted by Bałuk (2006, p. 182). The species *Gibbula boettgeri* Iljina, 1993 is clearly different from *G. affinis* (Eichwald, 1851).

Specimens recognised by Friedberg as *G. affinis* var. *pseudangulata* from different locations, stored in the ZNG PAN collection, belong to different species, including *G. affinis*, *Jujubinus celinae* (Andrzejowski, 1833) and *G. boettgeri*. Only the specimens from Niskowa, Poland (ZNG PAN A-I-50/1619) represent the latter species.

The placement of Hungarian specimens (Strausz 1966, p. 35, pl. 52, figs 14–16) in *G. affinis* is questionable.

**OCCURRENCE:** Lower Miocene of the Proto-Mediterranean Sea: Burdigalian of Iran (Harzhauser *et al.* 2002). Middle Miocene of the Central Paratethys: Badenian of Austria (Sieber 1946; Glibert 1962), Hungary (Kókay 1985), Poland (Liszka 1933; Krach 1950, 1962; Ney 1969; Bałuk 1970; Urbaniak 1974) and western Ukraine (Eichwald 1851a, 1853; Laskarev 1903; Friedberg 1928, 1938; Kowalewski 1936b, 1937; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2); Eastern Paratethys: Tarkhanian of southern Ukraine (Mikhailovsky 1903; Anistratenko and Anistratenko 2001); Konkian of Kazakhstan (Iljina 1993); Paratethys: Sarmatian (= upper Serravallian) of Austria (Papp 1954), western Ukraine (Friedberg 1928; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001), Poland (Friedberg 1928, 1938). ?Upper Miocene of the Proto-Mediterranean Sea: Tortonian of France (Glibert 1962).

*Gibbula biangulata* (Eichwald, 1830)  
(Text-fig. 7A–D)

1830. *T.[rochus] biangulatus*, m.; Eichwald, p. 221.  
1833. *Trochus Andrzejowskii* Pusck.; Andrzejowski, pp. 445, 446, pl. 12, fig. 2.



1837. *Trochus Andrzejowskii* m.; Pusch, p. 108, pl. 10, fig. 12.
1850. [*Trochus biangulatus* m.]; Eichwald, pl. 9, fig. 12 (atlas).
- 1851a. *Troch.[us] biangulatus* m.; Eichwald, pp. 112, 281.
- 1851b. [*Trochus biangulatus* m.]; Eichwald, pl. 9, fig. 12 (atlas).
1853. *Troch.[us] biangulatus* m.; Eichwald, pp. 226, 227.
1856. *Trochus biangulatus* Eichw.; Hörnes, p. 460, pl. 45, fig. 15.
1859. *Trochus biangulatus*; Eichwald, p. 3, pl. 9, fig. 15 (atlas).
1896. [*Gibbula* (*Ph.[orculellus]*) *biangulatus* var. *porella* (De Greg.); Sacco, p. 37, pl. 4, fig. 14.
- non 1917. *Gibbula* (*Colliculus*) *biangulata* [Eichw.]; Cossmann and Peyrot, pp. 124–126, pl. 4, figs 20–22 [= *Gibbula aquitanica* Cossmann and Peyrot, 1917].
- non 1918. *Trochus biangulatus* Eichwald; Cossmann, p. 232 [= *Gibbula aquitanica* Cossmann and Peyrot, 1917].
- non 1918. *Gibbula* (*Colliculus*) *biangulata* [Eichwald]; Cossmann, pl. 8, figs 11, 12 [= *Gibbula aquitanica* Cossmann and Peyrot, 1917].
- 1918. *Tr.[ochus] biangulatus* Eichw.; Cossmann, p. 233.
1928. *Gibbula biangulata* Eichw.; Friedberg, pp. 486, 487, pl. 30, fig. 20.
1938. *Gibbula biangulata* Eichw.; Friedberg, p. 53.
- 1949a. *Gibbula biangulata* Eichwald, sp. 1830; Gilbert, p. 58, pl. 3, fig. 8, excl. reference.
1954. *Gibbula biangulata* Eichw.; Strausz, pp. 8, 77, 89, pl. 6, fig. 136.
- non 1959. *Gibbula biangulata* (Eichwald); Boda, pp. 609, 703, pl. 22, figs 6, 7 [= *Gibbula auingeri* (Fuchs, 1873)].
1962. *Gibbula biangulata* Eichwald; Strausz, p. 127, pl. 52, figs 21–23; pl. 53, figs 1–3.
1966. *Gibbula biangulata* Eichwald, 1830; Strausz, pp. 35, 36, pl. 52, figs 21–23; pl. 53, figs 1–3.
1968. *Gibbula biangulata* (Eichwald, 1830); Kulichenko and Sorochan, p. 107.
- 1969b. *Gibbula* (*Colliculus*) *biangulata* (Eichw.); Csepregy-Meznerics, p. 18, pl. 1, fig. 3.
1975. *Gibbula* (*Gibbula*) cf. *varia* (Linnaeus, 1766); Bałuk, p. 35, pl. 3, fig. 1.
1981. *Gibbula* (*Colliculus*) *biangulata* (Eichwald, 1830); Švagrovský, pp. 106, 107, pl. 32, fig. 8.
1993. *Gibbula* (*Colliculus*) *biangulata* (Eichwald, 1830); Nikolov, p. 66, pl. 1, figs 10, 11.
1996. *Gibbula* cf. *varia* (Linné); Kókay, p. 455, pl. 1, figs 4, 5.
2001. *G.[ibbula] biangulata* (Eichwald, 1830); Anistratenko and Anistratenko, p. 186.
2006. *Gibbula* (*Gibbula*) *varia* (Linnaeus, 1766 [sic]); Bałuk, p. 182, pl. 2, figs 1, 2 [non *Steromphala varia* (Linnæus, 1758)].
- ?part 2017. *Gibbula* (*Gibbula*) *biangulata* (Eichwald, 1830); Sladkovskaya, p. 1517, excl. figs.
2017. *Colliculus biangulatus* (Eichwald, 1830); Landau *et al.*, pp. 102, 103, pl. 27, fig. 1.
2018. *Steromphala biangulata* (Eichwald, 1830); Landau *et al.*, p. 178.

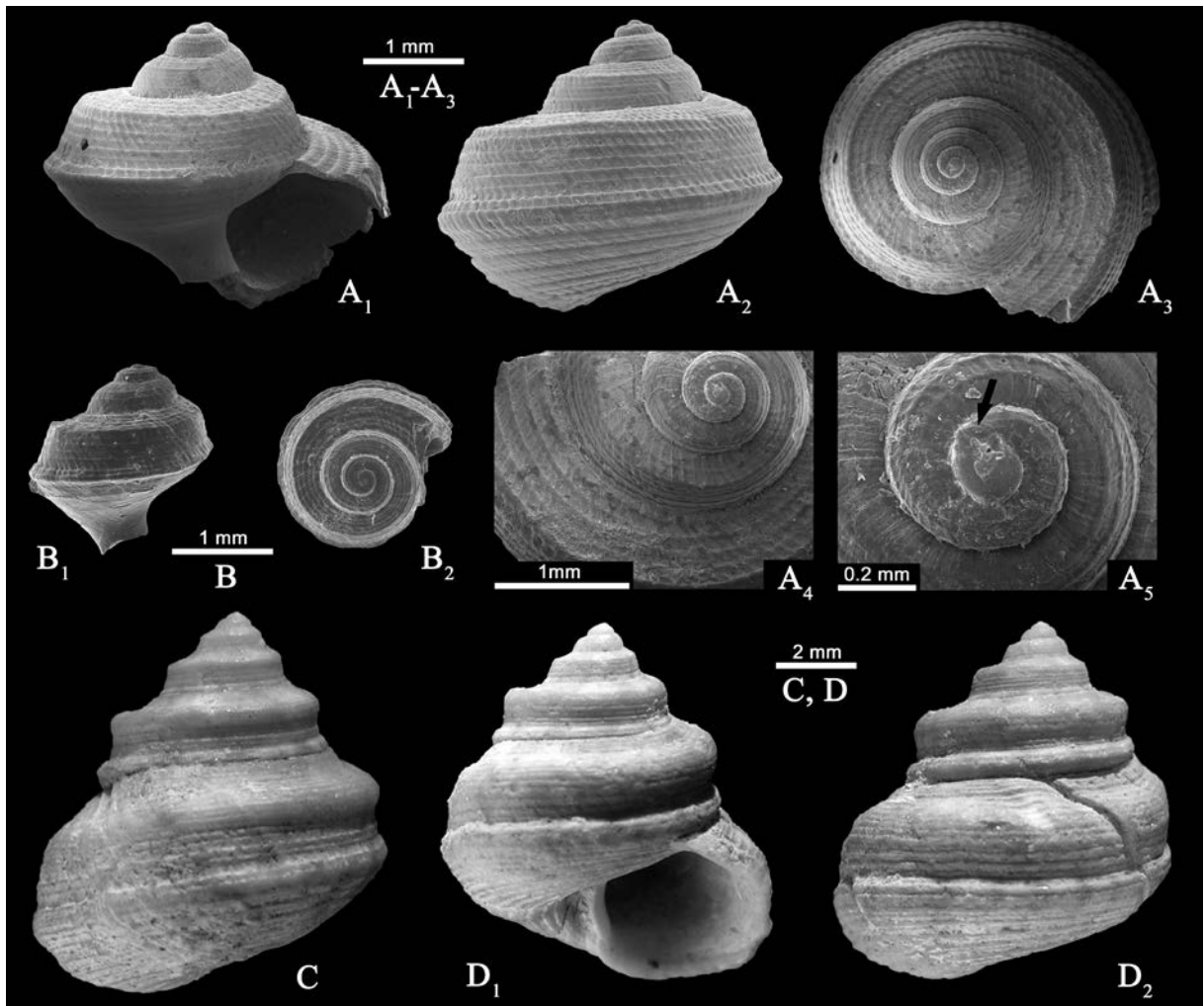
MATERIAL: Sandy facies: Varivtsi (MZ VIII Mg 4682) 1 j; Zalitsi (MZ VIII Mg 4547) 2 j, 8 jf. Carbonate deposits: Staryi Pochaiv (MZ VIII Mg 4548) 4 jf; Zhukivtsi (MZ VIII Mg 4713) 1 jf. All specimens are from western Ukraine.

DESCRIPTION: Shell small, trochiform, with somewhat elevated, scalate spire. Protoconch convex with apical beak and subterminal varix (see Text-fig. 7A<sub>5</sub>). Teleoconch of largest specimen consisting of four whorls, aperture damaged. First teleoconch whorl convex, bearing three spiral cords and relatively strong prosocyrts ribs. Abapically, cords increase in number, closely-set axial prosocline ribs conformable with growth lines gradually become stronger. Spiral cords crossed by oblique ribs forming fine reticulated pattern on last whorl. Typically, shoulder appears in upper part of third whorl and continues on subsequent ones delimiting almost horizontal subsutural platform; whorl profile below flat. Strongly developed, raised peripheral keel delimiting the base; until third teleoconch whorl, keel crenulated forming a wavy appearance of the periphery (see Text-fig. 7B<sub>2</sub>). Base convex, bearing spiral cords crossed by axial ribs, perforate; umbilicus deep, moderately wide, round-edged. Last whorl of specimen MZ VIII Mg 4682 with 25 spiral cords, of variable strength, of which 13 are on the base.

REMARKS: Only one specimen of *Gibbula biangulata* with Eichwald's label is present in the SPbGU collection. This specimen (SPbGU 3/424) originates from Zhukivtsi. Its aperture is damaged. There is no certainty that this is the specimen used by Eichwald to illustrate *Trochus biangulatus* because none of the specimens illustrated (Eichwald 1850, pl. 9, fig. 12; 1851b, pl. 9, fig. 12; 1859, pl. 9, fig. 15) is fully compatible with specimen SPbGU 3/424, although probably all represent the same species.

Comparison of the specimen from Varivtsi (MZ VIII Mg 4682; Text-fig. 7A) with specimen SPbGU 3/424 showed that at the same stage of growth the





Text-fig. 7. *Gibbula biangulata* (Eichwald, 1830) from the Badenian of Ukraine. A – Varivtsi; MZ VIII Mg 4682; B – Staryi Pochaiv; MZ VIII Mg 4548/1; C, D – Zhukivtsi; C – ZNG PAN I-A-50/1590a, D – ZNG PAN I A-50/1590b. A<sub>1</sub>, D<sub>1</sub> – apertural views; A<sub>2</sub>, B<sub>1</sub>, C, D<sub>2</sub> – lateral views; A<sub>3</sub>, B<sub>2</sub> – apical views; A<sub>4</sub> – close-up of the apex in apical view; A<sub>5</sub> – details of juvenile whorls in apical view, black arrow indicates subterminal varix of protoconch. A, B are SEM images.

specimens are very similar to each other. Slight differences are in the axial sculpture, which in specimen SPbGU 3/424 is somewhat finer. Only on the last, sixth whorl of specimen SPbGU 3/424, its shoulder attains the characteristic form of a prominent rounded keel, which is covered with spiral cords. It can be assumed that this feature would have revealed itself on the sixth, not formed, whorl of the specimen from Varivtsi if the shell growth had not been interrupted. On specimens *G. biangulata* from Zhukivtsi (ZNG PAN I-A-50/1590a, b) illustrated herein (Text-fig. 7C, D, respectively), the upper keel near the aperture is flattened. The shell (ZNG PAN I-A-50/1588) illustrated by Friedberg (1928, pl. 30, fig. 20) is not fully

grown. This specimen and two other specimens from the Friedberg collection (ZNG PAN I-A-50/1589, 1591a) have very weak folds on the subsutural ramp, somewhat a wavy appearance of the shoulder and peripheral keel on the last whorl preserved.

The specimens of *G. biangulata* from the MZ collection are incomplete, without the characteristic last whorl. However, SEM images allow the identification of significant differences between species which appear to be similar to each other – *G. biangulata* and *G. podhorcensis* (Friedberg, 1928). It seems that the protoconchs of both species look the same (almost the same width, the presence of apical beak and subterminal varix), but the shape of the teleoconch whorls

and their sculpture are clearly different (compare Text-fig. 7 with Text-fig. 12).

Specimens of other species with the last whorl biangular were included in *G. biangulata*. Cossmann and Peyrot (1917, pl. 4, figs 20–22; 1918, pl. 8, figs 11, 12) illustrated the specimen from the Aquitanian of Mérignac (Aquitaine Basin, France) under the name *G. (C.) biangulata*; it is recorded on the website of the Muséum national d'Histoire naturelle (MNHN.F.J04591). According to Lozouet *et al.* (2001) and Landau *et al.* (2017), the specimen belongs to *Colliculus aquitanicus* (Cossmann and Peyrot, 1917). This decision is followed herein, as these authors probably had the type material at hand to understand the intraspecific variability of *Gibbula aquitanica*. Boda (1959, pl. 22, figs 6, 7) identified a shell from the Sarmatian of Hungary as *G. biangulata*; in fact it represents *Gibbula auingeri* (Fuchs, 1873). Sladkovskaya (2017) considered *G. auingeri* to be a subspecies of *G. biangulata*. I prefer to retain it at full species level. *Gibbula auingeri* differs in being smaller-shelled, with fewer whorls (5.5 in Sladkovskaya 2017, p. 1519 vs. 7 in ZNG PAN I-A-50/1590a, b) and spiral cords, in having stronger, less closely spaced axial ribs and a sharper, more elevated upper keel not covered with spiral cords.

The Badenian specimen of *G. (C.) biangulata* illustrated by Nikolov (1993, pl. 1, figs 10, 11) from Opanec in Bulgaria is very similar to the Badenian specimens from Korytnica identified by Bałuk (2006, p. 182, pl. 2, figs 1, 2) as *Gibbula (Gibbula) varia* (Linnæus, 1758), which was placed by Affenzeller *et al.* (2017) in the genus *Steromphala* Gray, 1847 (Gray 1847b). At the same stage of ontogenetic growth they all are almost the same as specimens of *G. biangulata* (ZNG PAN I-A-50/1590a, b), and vary in having less prominent keels and thus a slightly different shape of the whorls. The specimens from Opanec and Korytnica represent immature forms of *G. biangulata*.

Landau *et al.* (2017, p. 102) placed this species in the genus *Colliculus* Monterosato, 1888. However, the genus was invalidated because, based on genetic data, Affenzeller *et al.* (2017) included *Trochus adansonii* Payraudeau, 1826, the type species of *Colliculus*, in *Steromphala*, a genus validated by them. Therefore, *Colliculus* became a junior synonym of *Steromphala*. Consequently, Landau *et al.* (2018, p. 178) changed the generic assignment of the species *biangulata* to *Steromphala*. However, it should be retained within *Gibbula*, because *G. biangulata* is much closer to *G. magus*, the type species of the genus *Gibbula*, than to *S. cineraria* (Linnæus, 1758), the type species of the genus *Steromphala*. Moreover, *G. biangulata* has weak folds on the subsutural ramp seen in some

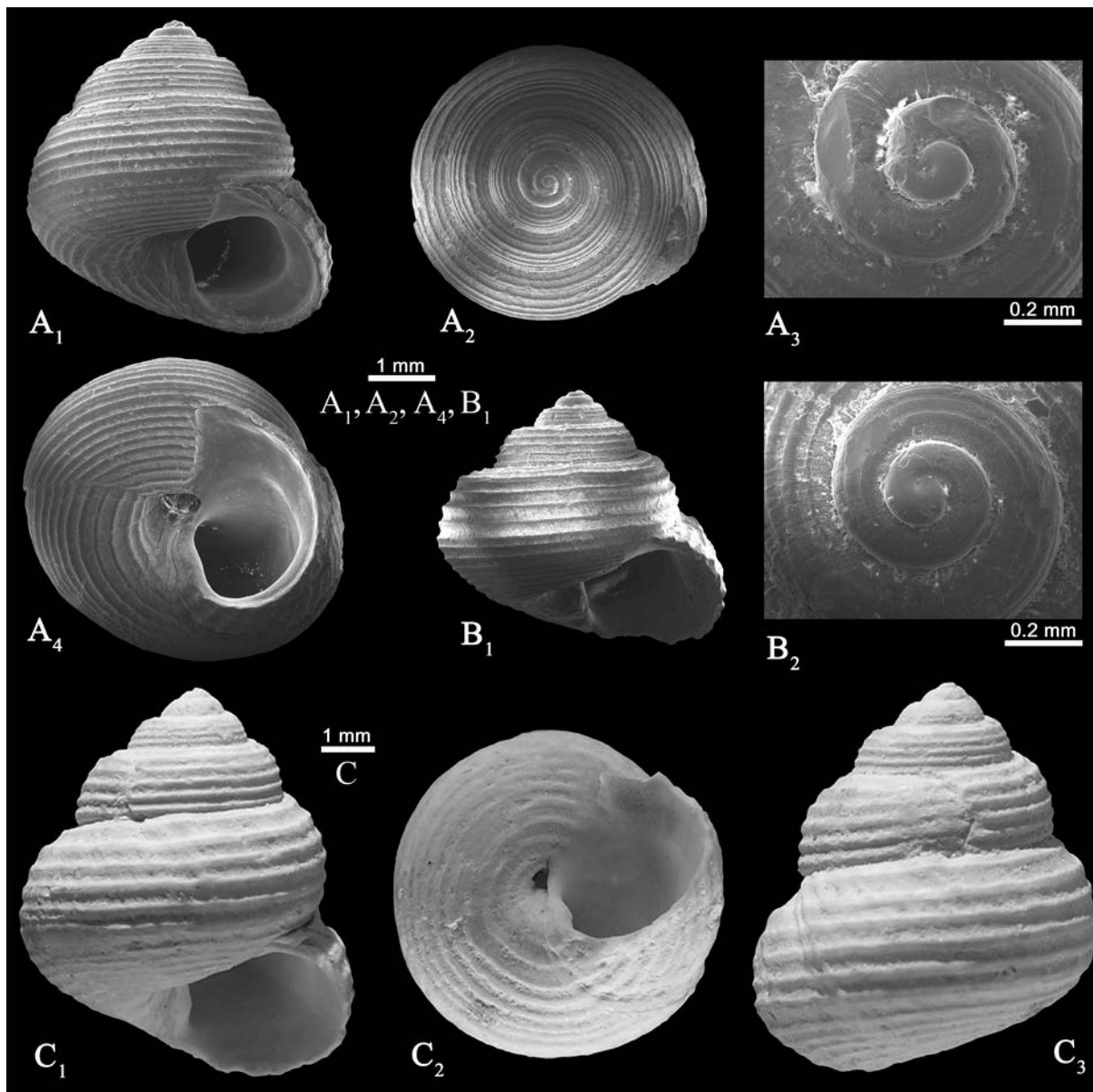
specimens, and the last whorl is biangular with an elevated peripheral keel delimiting base like *G. magus*, which is known from the Pliocene till present (see Ceulemans *et al.* 2016). Such shell characters are not present in *S. cineraria* (see Affenzeller *et al.* 2017, pp. 803, 804, fig. 5).

Dollfus and Dautzenberg (1886, p. 142) and also Peyrot (1938, pp. 27, 28) synonymised *T. biangulatus* Eichwald, 1830 with *T. biangulatus* Dujardin, 1837. It seems that Dujardin (1837, p. 286) introduced exactly the same name for the same species, which he described from the middle Miocene of the Touraine Basin, France, without referring to Eichwald (1830). Probably, he was not aware of Eichwald's publication and the case is an unusual coincidence.

**OCCURRENCE:** Lower Miocene of the Western and Central Paratethys: Burdigalian of Switzerland (Mayer 1872), ?Austria (Steininger 1963). Lower to upper Miocene of the Proto-Mediterranean Sea: Burdigalian and Tortonian of Italy (Sacco 1896). Middle Miocene of the northeastern Atlantic in France (Dujardin 1837; Mayer 1862; Dollfus and Dautzenberg 1886; Cossmann 1918; Peyrot 1938; Glibert 1949a, 1962); Central Paratethys: Badenian of Austria (Hörnnes 1856; Sieber 1946; Mandic *et al.* 2002), Czech Republic (Hörnnes 1856), Hungary (Csepregy-Meznerics 1954, 1969b; Strausz 1954, 1962, 1966; Kókay 1996; Katona *et al.* 2011), Bulgaria (Nikolov 1993), Romania (Boettger 1902), Slovakia (Švagrovský 1981), Poland (Friedberg 1928; Liszka 1933; Areń 1962; Urbaniak 1974; Bałuk 1975, 2006) and western Ukraine (Eichwald 1830, 1851a, 1853; Andrzejowski 1833; Pusch 1837; Hörnnes 1856; Friedberg 1928, 1938; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2); Paratethys: Sarmatian (= upper Serravallian) of western Ukraine (Anistratenko and Anistratenko 2001). Upper Miocene of the northeastern Atlantic: Tortonian of France (Landau *et al.* 2017).

*Gibbula dzieduszyckii* Friedberg, 1928  
(Text-fig. 8A–C)

1928. *Gibbula Dzieduszyckii* Friedb.; Friedberg, pp. 492, 493, pl. 31, figs 4–6.  
 1938. *Gibbula Dzieduszyckii* Friedb.; Friedberg, p. 54.  
 1968. *Gibbula dzieduszyckii* Friedberg, 1928; Kulichenko and Sorochan, p. 108.  
 non 1970. *Gibbula dzieduszyckii* Friedberg; Bałuk, p. 117, pl. 8, fig. 6 [= *Gibbula mimula* Boettger, 1907].  
 1977. *Gibbula dzieduszyckii* Friedberg, 1928; Jakubowski, p. 107, pl. 13, figs 12, 13.



Text-fig. 8. *Gibbula dzieduszyckii* Friedberg, 1928 from the Badenian of Ukraine. A, B – Zalistsi – Zhabiak ravine; A – MZ VIII Mg 4567/2, B – MZ VIII Mg 4567/1; C – Oles’ko; MZ VIII Mg 4566/1. A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub> – apertural views; A<sub>2</sub> – apical view; A<sub>3</sub>, B<sub>2</sub> – details of juvenile whorls in apical views; A<sub>4</sub>, C<sub>2</sub> – umbilical views; C<sub>3</sub> – lateral view. A, B are SEM images.

2001. *C.[olliculus] dzieduszyckii* (Friedberg, 1928); Anistratenko and Anistratenko, p. 190.

**MATERIAL:** Sandy facies: Yaseniv (MZ VIII Mg 4565) 4 sh; Oles’ko (MZ VIII Mg 4566) 47 sh; Zalistsi – Zhabiak ravine (MZ VIII Mg 4567) 4 sh. All specimens are from western Ukraine.

**DESCRIPTION:** Shell small, somewhat barrel-like, with convex whorls. Sculpture consisting of spiral

cords with pustules in the interspaces and fine pro-socline growth lines, closer spaced towards aperture. Protoconch paucispiral, with apical beak. Junction with teleoconch marked by beginning of spiral sculpture. On first teleoconch whorl sculpture of four relatively strong spiral cords, increasing in number to six, occasionally five or seven on lateral flank of last whorl; sometimes some of the primary cords bifid or triple, a single spiral thread developed in some of the interspaces. Narrow sutural ramp developed on third,



fourth, sometimes also on fifth teleoconch whorl in many specimens, disappearing with ontogeny; second, occasionally first, primary cord forming shoulder. Suture linear, impressed. Last whorl rounded at periphery in adult specimens, somewhat angulated in juveniles. Base convex, bearing spiral cords of irregular strength and position (9 on specimen MZ VIII Mg 4566/1, Text-fig. 8C; 12 on specimen MZ VIII Mg 4567/2, Text-fig. 8A). Umbilicus deep, completely open or partly covered by inner lip. Aperture circular; outer lip with bevelled edge. Columella bearing weak swelling. Colour pattern of vertical flammules preserved in some specimens.

REMARKS: The syntypes of *G. dzieduszyckii* from the Badenian deposits of Oles'ko, Ukraine are present in the ZNG PAN collection (ZNG PAN A-I-50/1625–1627). When introducing this species, Friedberg (1928, pl. 31, figs 4–6, figures of poor quality) illustrated three specimens, indicating some variability in sculpture and shell outline. A reinvestigation of the syntypes showed that fig. 4 of Friedberg (1928; ZNG PAN A-I-50/1625) shows a specimen with six spiral cords and one or two threads in some of the interspaces on the lateral flank of the last whorl; the most adapical and peripheral cords are triple, there are four intermediate cords on the lateral flank and four cords (out of eleven) on the upper half of the base are bifid; fig. 5 of Friedberg (1928; ZNG PAN A-I-50/1626a) shows a shell, in which the first preserved teleoconch whorl bears four spiral cords of almost equal strength separated by interspaces of unequal width. At the beginning of the second whorl the adapical cord strengthens to form a shoulder, and a relatively wide, horizontal sutural ramp becomes steeper abapically while the shoulder fades; on third whorl a fifth weak cord appears close to the adapical suture, gaining in strength, and the sixth cord is partially hidden in the abapical suture; on the lateral flank of the last convex whorl there are six spiral cords and two spiral threads not clearly visible in the adapical interspace; the doubleness and triple character of some cords are very poorly visible and only seen in some of their parts; fig. 6 of Friedberg (1928; ZNG PAN A-I-50/1626b) shows a shell with the protoconch and two first teleoconch whorls with an eroded surface, and with six spiral cords on the lateral flank of the last whorl, from which only the second and peripheral cords and also the fourth out of eight cords on the base are bifid.

Friedberg (1938, p. 54) himself was unsure if this was a distinct species or variety of *G. affinis*. Indeed, the shells identified here as *G. dzieduszyckii* are very similar to those of *G. affinis* with relatively convex

whorls. However, *G. dzieduszyckii* differs from *G. affinis* in its sculpture of the early teleoconch whorls and aperture outline, in having a round shell profile and spherical last whorl, therefore both taxa can be separated at species level.

OCCURRENCE: Middle Miocene of the Central Paratethys: Badenian of Poland (Ney 1969; Jakubowski 1977) and western Ukraine (Friedberg 1928, 1938; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2).

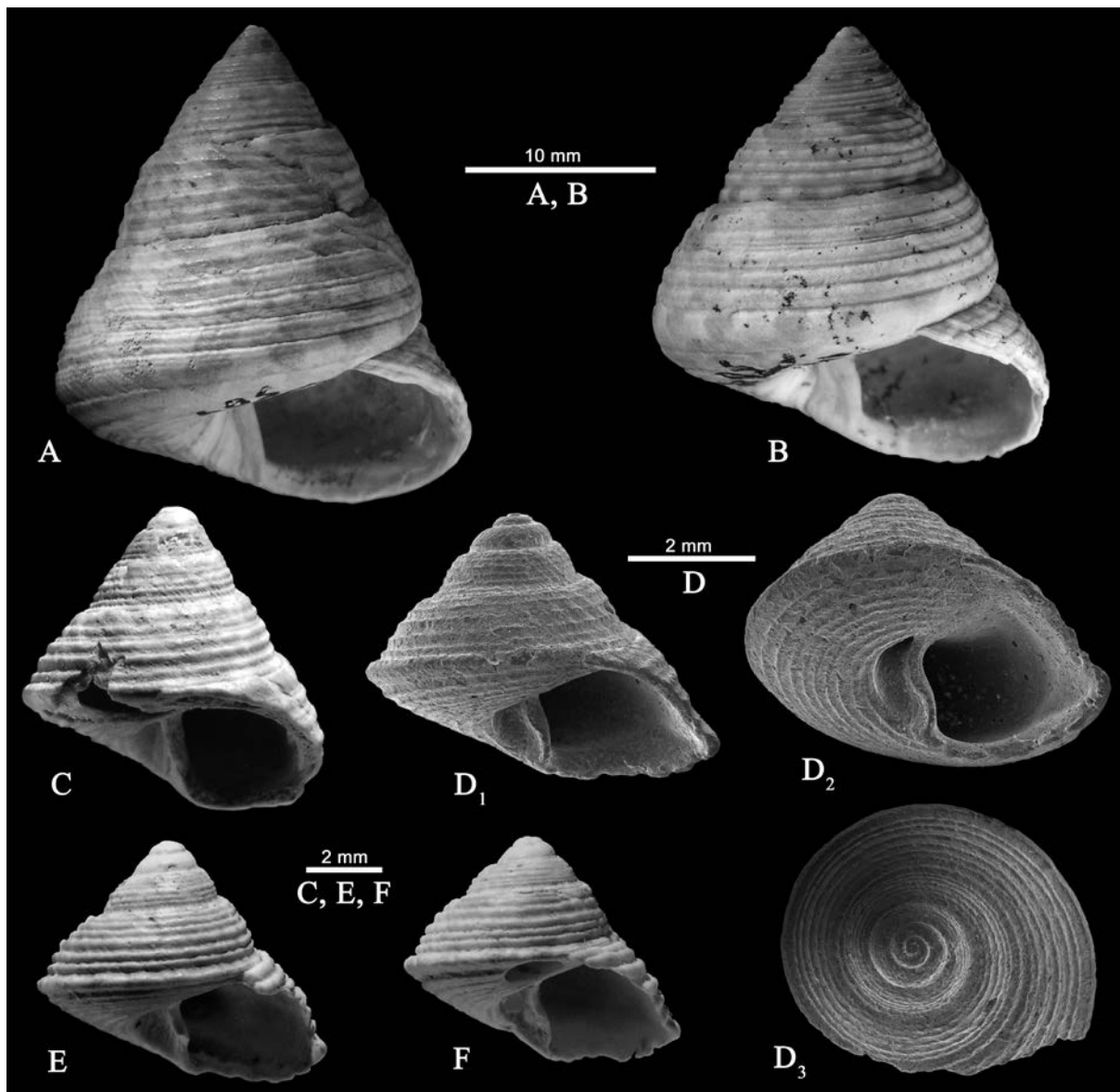
*Gibbula miocaenica* (Mayer, 1853)  
(Text-fig. 9A–F)

1837. *Trochus incrassatus*. Duj.; Dujardin, pp. 285, 286 [non Lamarck, 1822 = *Trochus stellatus* Gmelin, 1791; after MolluscaBase 2019].
- 1853. *Trochus miocenicus*, May.; Mayer, p. 98 [nom. nov. pro *Trochus incrassatus* Dujardin, 1837, non Lamarck, 1822].
1938. *Monodonta (Osilinus) miocenicus* Mayer; Peyrot, pp. 22, 23, pl. 1, figs 17–19.
1938. *Monodonta [(Osilinus)] miocenicus* May., var. *pyramidata* Peyr.; Peyrot, p. 23, pl. 1, fig. 33 [non figs 41, 42 = *Pyrgulina (Chrysallida) pulcherrima* Peyrot, 1938].
- part 1938. *Gibbula novemcincta* de Buch; Friedberg, p. 51.
- 1949a. *Monodonta (Osilinus) miocænica* Mayer, sp. 1853; Glibert, pp. 61, 62, pl. 3, fig. 11.
1961. *Gibbula sytovae* Amitrov, sp. nov.; Amitrov, pp. 41–48, pl. 6, figs 1–4.
1968. *Gibbula sytovae* Amitrov, 1961; Kulichenko and Sorochan, p. 112.
- part 1981. *Oxystele orientalis* Cossmann – Peyrot 1917; Krach, p. 45, pl. 13, figs 3, 4.
2001. *G.[ibbula] sytovae* Amitrov, 1961; Anistratenko and Anistratenko, p. 189.

MATERIAL: Sandy facies: Yaseniv (MZ VIII Mg 4568) 7 j; Kalaharivka (MZ VIII Mg 4686) 1 j; Oles'ko (MZ VIII Mg 4569, 4570) 1 af, 1 j; Sataniv (MZ VIII Mg 4687) 6 sh; Zalistsi (MZ VIII Mg 4571) 2 a. All specimens are from western Ukraine.

DESCRIPTION: Amitrov (1961, pp. 41–48) provided a detailed description of specimens from Sataniv, Ukraine. The juvenile specimen from Yaseniv (Text-fig. 9D) differs from the specimen from Sataniv (Text-fig. 9C) in being less slender and in having a finer sculpture, but its shape is similar to that of the French shell (Text-fig. 9E). These differences are





Text-fig. 9. *Gibbula miocaenica* (Mayer, 1853) from the middle Miocene of Ukraine and France. A, B, C – Sataniv, Ukraine; A – MZ VIII Mg 4687/1, B – MZ VIII Mg 4687/2, C – MZ VIII Mg 4687/3; D – Yaseniv, Ukraine, MZ VIII Mg 4568/1; E, F – Ferrière-Larçon, France; E – MZ VIII Mg 2707/1, F – MZ VIII Mg 2707/2. A, B, C, D<sub>1</sub>, E, F – apertural views; D<sub>2</sub> – oblique umbilical view, D<sub>3</sub> – apical view. D<sub>1</sub>–D<sub>3</sub> are SEM images.

considered to be caused by intraspecific variation. Colour pattern of reddish irregular, elongate blotches is preserved in some of the Ukrainian and French specimens.

REMARKS: *Trochus incrassatus* Dujardin, 1837 is a junior homonym of the extant Indo-Pacific *Trochus incrassatus* Lamarck, 1822 (now accepted as *Trochus stellatus* Gmelin, 1791), therefore Mayer (1853) proposed *Trochus miocaenicus* as the replacement name. Dujardin (1837) provided only a diagnosis and de-

scription, without any illustration, of his *T. incrassatus* from the middle Miocene of the Loire Basin, France. Dujardin's collection could not be located during this study. Fortunately, the photographs of the middle Miocene shells of the species from the Loire Basin published by Peyrot (1938) and Glibert (1949a) are of good quality.

Later, Amitrov (1961) established a new species *Gibbula sytovaе* based on the Badenian shells from Sataniv, Ukraine. The type material, including the holotype (PIN 1467/500), of the species is present in the

PIN collection. With the courtesy of the late Lubov B. Iljina (PIN), the MZ collections were made available with six specimens from Sataniv (MZ VIII Mg 4687, former number PIN 1467/504), identified by the late O.V. Amitrov (PIN) as the paratypes of *G. sytovae*.

Some specimens from the Badenian of Łychów and Węglinek (Roztocze Hills, Poland) identified by Krach (1981) as *O. orientalis* have turned out to be conspecific with '*G. sytovae*'. The illustrated shells from Węglinek (Krach 1981, pl. 13, figs 3, 4) are poorly preserved, with their last whorls detached. Because of the incorrect magnification value in the plate caption, the measurements of these specimens (ZNG PAN A-I-87/82a.1 and ZNG PAN A-I-87/82a.2, respectively) are provided in Appendix 1. Three specimens from Łychów (ZNG PAN A-I-87/82b.1–3) consisting of about the last two whorls are from 29 to 31 mm wide.

The Ukrainian and Polish specimens examined have fine spiral threads in interspaces between primary spiral cords on later teleoconch whorls, not seen in the French specimens. However, Amitrov's (1961, p. 42) description shows that they are not always present in his species.

The very large similarity of the Ukrainian and Polish specimens with specimens of *G. miocaenica* from Ferrière-Larçon (Loire Basin, France) – MZ VIII Mg 2684, 2707 and illustrated by Glibert (1949a, pl. 3, fig. 11) – suggests that they represent a single highly variable species, and consequently *G. sytovae* should be considered as a junior subjective synonym of *G. miocaenica*.

**OCCURRENCE:** Lower Miocene of the Western Paratethys: Burdigalian of Germany (Mayer 1853), Switzerland (Mayer 1872), France (Locard 1878). Middle Miocene of the northeastern Atlantic of France (Dujardin 1837; Mayer 1862; Dollfus and Dautzenberg 1886; Peyrot 1938; Glibert 1949a, b, 1962; and this study); Central Paratethys: Badenian of Poland (Krach 1981) and western Ukraine (Friedberg 1938; Amitrov 1961; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2).

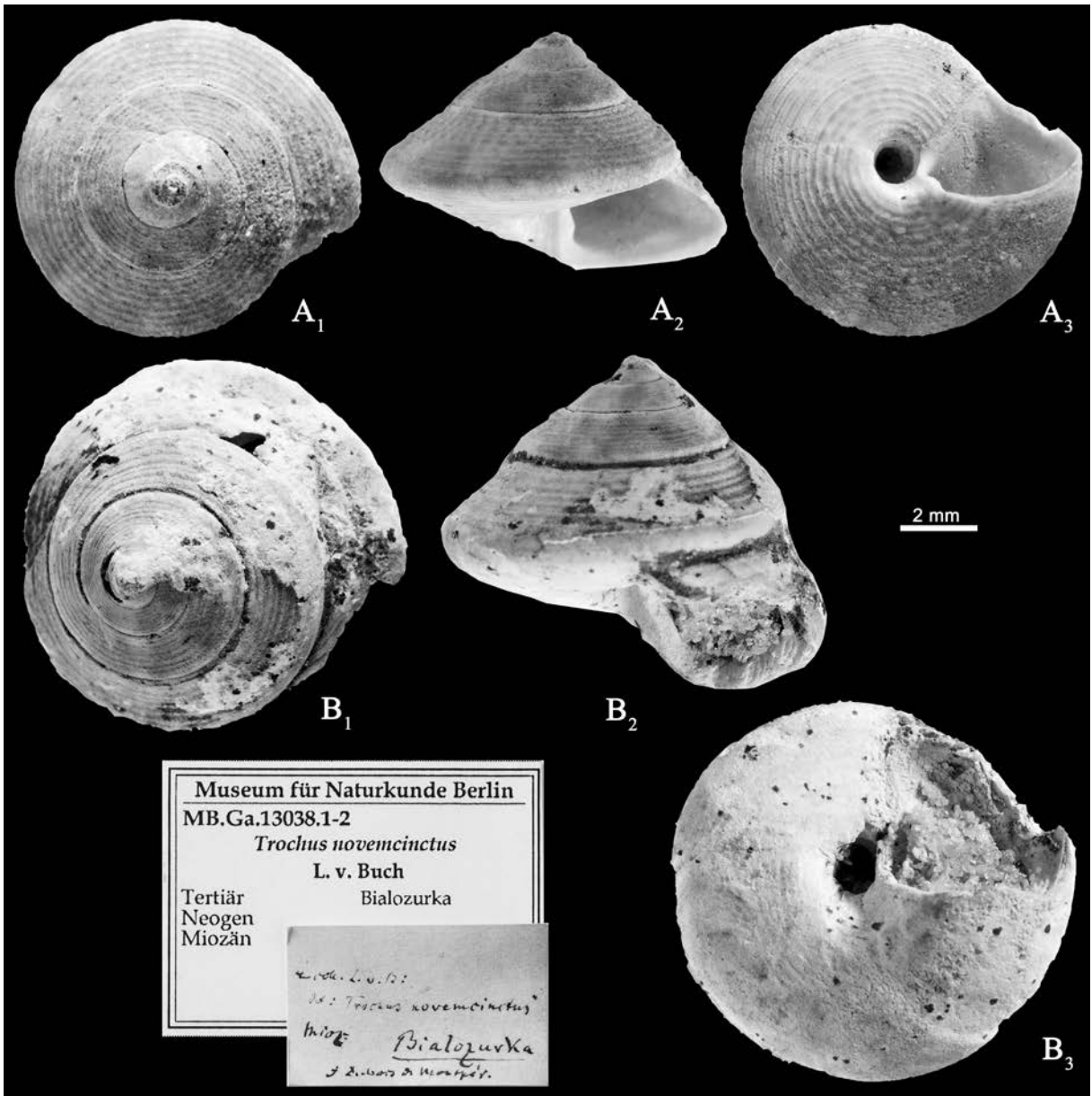
*Gibbula novemcincta* (von Buch, 1830)  
(Text-figs 10A–B and 11A–G)

1830. *Trochus novemcinctus* nov.; von Buch, p. 132.  
 1831. *Trochus novemcinctus*, de Buch; du Bois de Montpéreux, p. 39, pl. 3, figs 17–19.  
 1928. *Gibbula novemcincta* de Buch.; Friedberg, pp. 497, 498, pl. 31, figs 13, 14.

1928. *Gibbula volhynica* Friedb.; Friedberg, pp. 496, 497, pl. 31, figs 9–11.  
 1937. *Gibbula volhynica* Friedb.; Kowalewski, p. 8.  
 1937. *Gibbula novemcincta* de Buch; Kowalewski, p. 8.  
 part 1938. *Gibbula volhynica* Friedb.; Friedberg, p. 51.  
 part 1938. *Gibbula novemcincta* de Buch; Friedberg, p. 51.  
 1968. *Gibbula novemcincta* [(Buch) Dubois de Montpéreux, 1831]; Kulichenko and Sorochan, p. 109, pl. 29, figs 14, 15 [figures from Friedberg 1928, pl. 31, fig. 13a–b].  
 1968. *Gibbula volhynica* Friedberg, 1928; Kulichenko and Sorochan, p. 113, pl. 30, fig. 12 [figure from Friedberg 1928, pl. 31, fig. 9].  
 1968. *Gibbula (Colliculus) volhynica* Friedberg, 1928; Hinculov, p. 119.  
 •1969. *G.[ibbula] volhynica* Friedb.; Ney, 61.  
 2001. *Steromphala novemcincta* (Buch in Dubois de Montpéreux); Anistratenko and Anistratenko, p. 192.  
 2001. *S.[teromphala] volhynica* (Friedberg, 1928); Anistratenko and Anistratenko, p. 192.

**MATERIAL:** Sandy facies: Bilozirka (MZ VIII Mg 591, 4572) 53 sh; Korostova (MZ VIII Mg 4573) 1 a; Ohryzkivtsi (MZ VIII Mg 4574) 1 a; Oles'ko (MZ VIII Mg 4575) 1 a; Shushkivtsi (MZ VIII Mg 4576) 3 a; Vyshhorodok (MZ VIII Mg 4577) 1 sa; Zalistsi (MZ VIII Mg 4578, 4579) 7 sh. All specimens are from western Ukraine.

**DESCRIPTION:** Shell trochiform, with depressed to somewhat elevated conical spire. Protoconch with apical beak. Apical whorls surface badly preserved; protoconch/teleoconch boundary not visible. Suture linear, impressed. Teleoconch whorls with periphery at abapical suture, first two to three whorls weakly convex, subsequent whorls flat-sided to concave. Periphery of later whorls usually marked by swell which overhangs suture. Sculpture of earliest teleoconch whorls not preserved. Later teleoconch whorls bearing 7–9 spiral cords of equal or different strength; occasionally a single spiral thread intercalated in some of the interspaces on the last two teleoconch whorls; peripheral spiral threads visible only on better preserved specimens. Whole whorl surface and cords covered with very fine, closely-set, strongly prosocline growth lines. Almost flat conical base bearing concentric cords of unequal thickness (13 in specimen MZ VIII 4578/2, Text-fig. 11E; 19 in specimen MZ VIII Mg 4573, Text-fig. 11G). Umbiliculus deep, more or less wide. Aperture sub-quadrangular; outer lip with sharp edge, angled at periphery, joining penultimate whorl below pe-



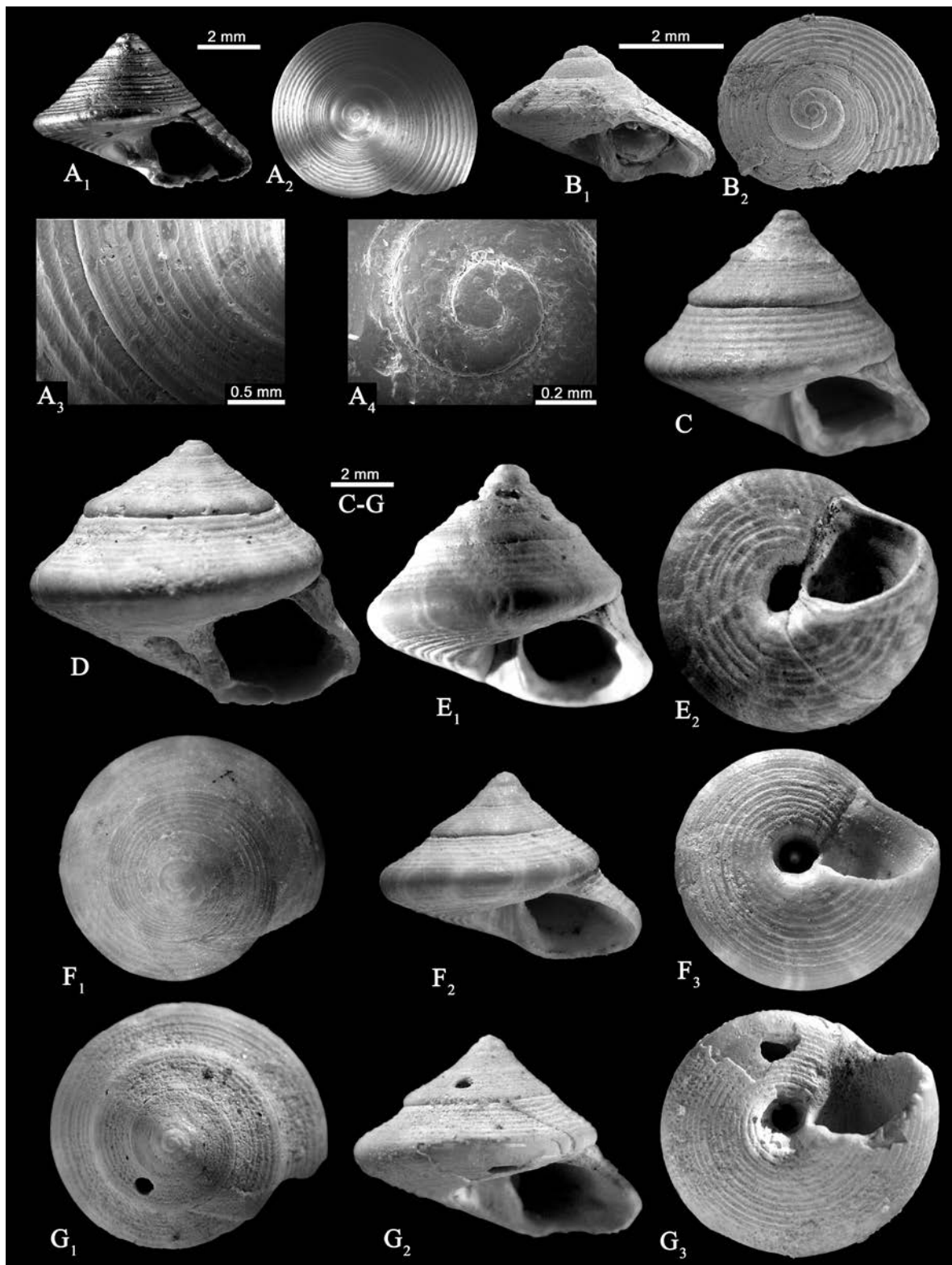
Text-fig. 10. Syntypes of *Gibbula novemcincta* (von Buch, 1830) from the Badenian of Bilozirka, Ukraine. A – MB.Ga.13038.1, B – MB.Ga.13038.2. A<sub>1</sub>, B<sub>1</sub> – apical views; A<sub>2</sub>, B<sub>2</sub> – apertural views; A<sub>3</sub>, B<sub>3</sub> – umbilical views. Illustrated are also the original and contemporary museum labels. Photographs by A. Abele.

riphery. Columella straight, bearing a protuberance. Colour pattern consisting of fine, axial, single wavy stripe between almost semicircular blotches adjacent to abapical suture (this pattern continuing onto base of the last whorl) and dots on the upper cords preserved in some specimens (Text-fig. 11E, F).

REMARKS: This species was described by von

Buch (1830, p. 132) referring to shells collected by du Bois de Montpéreux at Bilozirka, Volhynia in the Ukraine. Two syntypes of *Trochus novemcinctus* (MB.Ga.13038.1–2; Text-fig. 10A, B herein) are present in the MfN collection. In 1929 Friedberg saw the du Bois de Montpéreux’s molluscan collection from Volhynia, housed in the ETHZ. As a result, in the commentary to *T. novemcinctus* from the col-





Text-fig. 11. *Gibbula novemcincta* (von Buch, 1830) from the Badenian of Ukraine. A, C, E – Zalistsi; A – MZ VIII Mg 4578/1, C – MZ VIII Mg 4579/1, E – MZ VIII Mg 4578/2; B – Bilozirka; MZ VIII Mg 4572/1; D – Shushkivtsi; MZ VIII Mg 4576/2; F – Vyshhorodok; MZ VIII Mg 4577; G – Korostova; MZ VIII Mg 4573. A<sub>1</sub>, B<sub>1</sub>, C, D, E<sub>1</sub>, F<sub>2</sub>, G<sub>2</sub> – apertural views; A<sub>2</sub>, B<sub>2</sub>, F<sub>1</sub>, G<sub>1</sub> – apical views; A<sub>3</sub> – close-up of teleoconch surface; A<sub>4</sub> – apex in apical view; E<sub>2</sub>, F<sub>3</sub>, G<sub>3</sub> – umbilical views. A<sub>2</sub>–A<sub>4</sub>, B are SEM images.



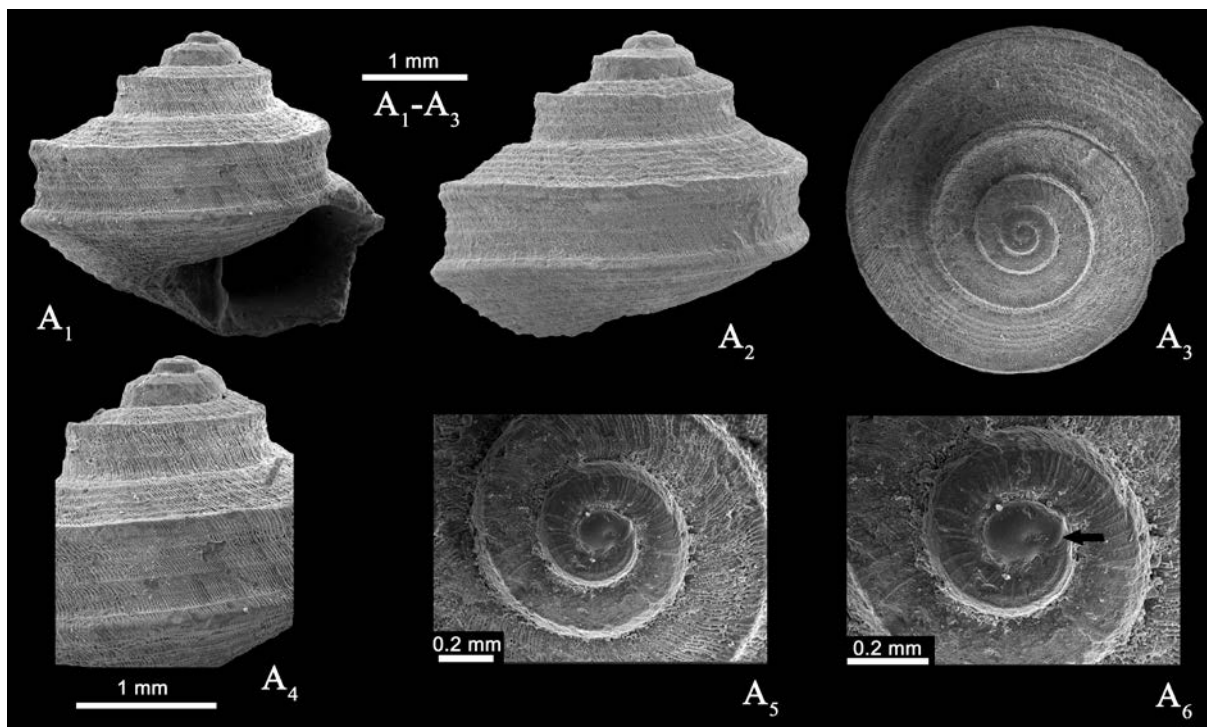
lection of du Bois de Montpéroux (1831), Friedberg (1930, p. 368) said that among eight specimens from Shushkivtsi, in addition to typical lower specimens, there are also more slender specimens, which correspond to his species *Gibbula volhynica*, described from the same locality. Later, in the catalog of his collection, Friedberg (1938, p. 51) stated, with regard to *G. volhynica*, that perhaps this form should be considered only as a variety of *G. novemcincta*. This view was also shared by Kowalewski (1937, p. 8). The collection of du Bois de Montpéroux (1831) was not found in the ETHZ (Andreas Müller, pers. comm. 2019) and is most probably lost. Of syntypes of *G. volhynica* (ZNG PAN A-I-50/1639, 1640), Friedberg (1928, pl. 31, figs 9–11) provided illustrations of only two and not three specimens of his species, as it might seem from their numbering on the plate. His figs 9 and 10a show specimen ZNG PAN A-I-50/1639a, and figs 10b and 11 show specimen ZNG PAN A-I-50/1639b.

Friedberg's doubts about the separateness of his species seem fully justified. The specimens examined both in the Friedberg collection in ZNG PAN and the MZ collection are only different forms of a single species and, consequently, *G. volhynica* is a junior subjective synonym of *G. novemcincta*.

**OCCURRENCE:** Middle Miocene of the Central Paratethys: Badenian of Poland (Ney 1969), Romania (Hinculov 1968) and western Ukraine (von Buch 1830; du Bois de Montpéroux 1831; Mikhailovsky 1903; Friedberg 1928, 1938; Kowalewski 1937; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2).

*Gibbula podhorcensis* (Friedberg, 1928)  
 (Text-fig. 12A)

- 1928. *Pseudonina* (?) *podhorcensis* Friedb.; Friedberg, pp. 519, 520, pl. 33, fig. 9 (holotype).
- 1937. *Pseudonina* (?) *podhorcensis* Friedb.; Kowalewski, p. 8.
- 1938. *Pseudonina* (?) *podhorcensis* Friedb.; Friedberg, p. 49.
- ?1969a. *Gibbula* (*Colliculus*) *biangula obtusata* n. ssp.; Csepregy-Meznerics, p. 67, pl. 1, figs 1, 5, 8.
- ?1969b. *Gibbula* (*Colliculus*) *biangulata obtusata* n. ssp.; Csepregy-Meznerics, p. 18, pl. 1, figs 2, 6, 7.
- 1975. *Gibbula* (*Gibbula*) *podhorcensis* (Friedberg, 1928); Bałuk, p. 34, pl. 3, figs 2, 3.
- 2001. *G.[ibbula]* *podhorcensis* (Friedberg, 1928); Anistratenko and Anistratenko, p. 187.



Text-fig. 12. *Gibbula podhorcensis* (Friedberg, 1928) from the Badenian of Varivtsi, Ukraine; MZ VIII Mg 4688. A<sub>1</sub> – apertural view; A<sub>2</sub> – lateral view; A<sub>3</sub> – apical view; A<sub>4</sub> – close-up of teleoconch in lateral view; A<sub>5</sub>, A<sub>6</sub> – details of juvenile whorls in apical views. Black arrow indicates subterminal varix of protoconch. SEM images.

**MATERIAL:** Sandy facies: Pidhirtsi (MZ VIII Mg 4580) 2 jf, 2 fp; Varivtsi (MZ VIII Mg 4688) 1 j; Zalistsi (MZ VIII Mg 4544) 1 jf. All specimens are from western Ukraine.

**DESCRIPTION:** Shell small, trochiform, with depressed, scalate spire, base weakly convex, perforate, suture linear. Sculpture consists of numerous spiral cords crossed by lamellar, closely-set prosocline growth lines. Protoconch smooth, with prominent subterminal varix and apical beak (Text-fig. 12A<sub>6</sub>). First teleoconch whorl convex, bearing three spiral cords and slightly curved axial ribs. On second teleoconch whorl axial ribs disappear. On subsequent whorls, strongly developed, raised, spiral cord delimiting horizontal to slightly inclined subsutural platform, whorl profile below vertical. Last whorl strongly biangular, a raised peripheral keel delimiting base; whorl profile between keels somewhat concave. Last whorl of specimen MZ VIII Mg 4688 with 38 spiral cords, of which 17 on base. Base slightly convex, with a deep, open umbilicus. Aperture oblique, oval. Columella bearing single, prominent, basal columellar tooth.

**REMARKS:** The specimen from Varivtsi (MZ VIII Mg 4688; Text-fig. 12A) agrees with the holotype of *Pseudonina* (?) *podhorcensis* described by Friedberg (1928, pp. 519, 520, pl. 33, fig. 9) from Pidhirtsi, Ukraine (ZNG PAN A-I-50/1742). Friedberg (1928) had only a juvenile shell, so he was not certain of its generic position. Bałuk (1975) placed this species in the genus *Gibbula* based on adult specimens from the Badenian of Korytnica, Poland.

*Gibbula podhorcensis* from the middle Miocene Langhian deposits of Ferrière-Larçon (MZ VIII Mg 2704, 2917) and Pontlevoy (MZ VIII Mg 379) in the Loire Basin, France, and also Korytnica (MZ VIII Mg 4705) shows some variability in the slenderness of the shell and strength of the keels.

This species is similar in shell profile to the middle and late Miocene *Trochus insignis* Millet, 1854 from France (see Landau *et al.* 2017, pl. 28, fig. 1), which differs in having: a much stronger developed shoulder and peribasal cords; less numerous, coarser spiral cords between the angulations and on the subsutural platform; and a far stronger, less dense axial sculpture.

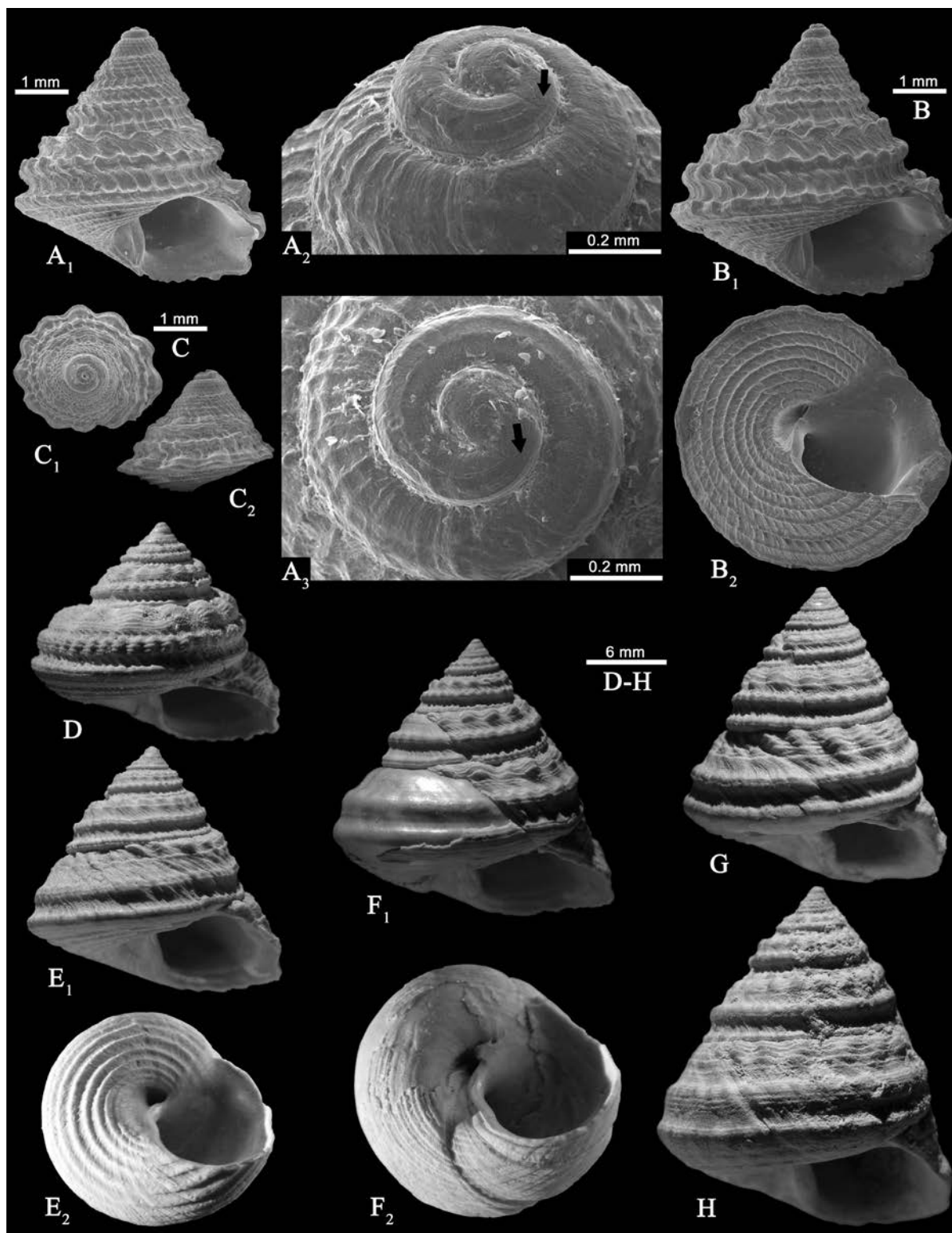
*Gibbula podhorcensis* is also similar to *G. biangulata*, but differs in having a columellar tooth, a lower spire and closer-set axial sculpture (compare Text-fig. 12 with Text-fig. 7).

**OCCURRENCE:** Middle Miocene of the northeastern Atlantic: Langhian of France (this study); Central

Paratethys: Badenian of ?Hungary (Csepregy-Meznerics 1969a, b), Poland (Bałuk 1975 and this study) and western Ukraine (Friedberg 1928, 1938; Kowalewski 1937; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2). *Gibbula cf. podhorcensis* was recorded from the lower Miocene Burdigalian of the Proto-Mediterranean Sea in Italy (Zunino and Pavia 2009).

*Gibbula puschii* (Andrzejowski, 1830)  
(Text-fig. 13A–H)

- 1830a. *Trochus Puschii* Nobis.; Andrzejowski, p. 99, pl. 5, fig. 1.  
 1830. *T.[rochus] catenularis*, m.; Eichwald, p. 221.  
 1830. *Trochus annulatus* nov.; von Buch, p. 132 [non *Trochus annulatus* Lightfoot, 1786 = *Calliostoma annulatum* (Lightfoot, 1786)].  
 1831. *Trochus Buchii*. Nov.; du Bois de Montpéreux, pp. 39, 40, pl. 3, figs 9–12 [nom. nov. pro *Trochus annulatus* von Buch, 1830 non Lightfoot, 1786].  
 •1832b. *Trochus Puschii* Nob.; Andrzejowski, p. 563.  
 1837. *Trochus Buchii* Dubois; Pusch, p. 109.  
 1840. *Tr.[ochus] catenularis*; Eichwald, p. 11.  
 1850. [*Trochus catenularis* m.]; Eichwald, pl. 9, fig. 6 (atlas).  
 1851a. *Troch.[us] catenularis* m.; Eichwald, pp. 110, 281.  
 1851b. [*Trochus catenularis* m.]; Eichwald, pl. 9, fig. 6 (atlas).  
 1853. *Troch.[us] catenularis* m.; Eichwald, p. 218.  
 1856. *Trochus fanulum* Gmel.; Hörnes, pp. 446, 447, pl. 45, fig. 1 [non *Gibbula fanulum* (Gmelin, 1791)].  
 1859. *Trochus catenularis*; Eichwald, p. 3, pl. 9, fig. 6 (atlas).  
 1882. *Trochus Buchii* du Bois.; Hilber, pp. 10, 11, pl. 1, fig. 22.  
 1907. *Gibbula (Forskalia) fanulum* (Gmel.) var. *cingulifera* Bronn.; Boettger, pp. 182, 183, No. 630.  
 1928. *Gibbula Buchi* Dub.; Friedberg, pp. 480–483, pl. 30, figs 8–14.  
 1936b. *Gibbula Buchi* Dub.; Kowalewski, p. 15.  
 1937. *Gibbula Buchi* Dub.; Kowalewski, p. 7.  
 1938. *Gibbula Buchi* Dub.; Friedberg, p. 51.  
 1950. *Gibbula buchii* Dub ?; Krach, p. 299, pl. 1, fig. 23.  
 1954. *Gibbula buchii* Dub.; Strausz, pp. 8, 77, 89, pl. 6, fig. 137.  
 1954. *Gibbula (Forskalia) buchii* Dubois; Csepregy-Meznerics, p. 13, pl. 1, fig. 12.  
 1955. *Gibbula (Gibbula) buchii* Dub.; Korobkov, pl. 5,



Text-fig. 13. *Gibbula pushtii* (Andrzejowski, 1830) from the Badenian of Ukraine. A, B, G – Rydomyl'; A – MZ VIII Mg 4558/1, B – MZ VIII Mg 4558/2, G – MZ VIII Mg 4558/3; C – Vyshhorodok; MZ VIII Mg 4560/1; D – Shushkivtsi; MZ VIII Mg 4559/1; E, F – Zalistsi; E – MZ VIII Mg 4562/1, F – MZ VIII Mg 4562/2; H – Zalistsi – Zhabiak ravine; MZ VIII Mg 4564/1. A<sub>1</sub>, B<sub>1</sub>, D, E<sub>1</sub>, F<sub>1</sub>, G, H – apertural views; A<sub>2</sub> – apex in oblique view; A<sub>3</sub> – apex in apical view; B<sub>2</sub>, E<sub>2</sub>, F<sub>2</sub> – umbilical views; C<sub>1</sub> – apical view, C<sub>2</sub> – lateral view. Black arrows indicate demarcation between protoconch and teleoconch. A–C are SEM images.



- figs 19–22 [figures from Friedberg 1928, pl. 30, figs 10, 11, 13b, 14].
- non 1961. *Gibbula (Gibbula) buchi* Dub.; Florei, p. 681, pl. 6, figs 38, 39 [= *Modulus basteroti* Benoist, 1874].
1962. *Gibbula buchi* Dubois; Strausz, p. 127, pl. 53, figs 4–9.
1966. *Gibbula buchi* Dubois, 1831; Strausz, p. 37, pl. 53, figs 4–9.
1968. *Gibbula buchii* (Dubois de Montpereux, 1831); Kulichenko and Sorochan, p. 107, pl. 29, fig. 6 [figure from Friedberg 1928, pl. 30, fig. 11].
- 1969b. *Gibbula (Forskalea) buchi* Dub.; Csepregy-Meznerics, p. 18, pl. 1, fig. 17.
1975. *Gibbula (Gibbula) buchi* (Dubois, 1831); Bałuk, pp. 32–34, pl. 4, figs 4, 5.
- non 1978. *Gibbula (G.) buchi* Dubois, 1831; Calzada Badía, p. 300, fig. 1.7 [= *Gibbula fanulum* (Gmelin, 1791)].
1981. *Gibbula (Gibbula) buchii* (Dubois 1831); Krach, pp. 43, 44, pl. 13, figs 11–14.
1993. *Gibbula (Gibbula) buchi* (Dubois, 1831); Iljina, pp. 24, 25, pl. 1, figs 15–18.
2001. *G.[ibbula] buchii* (Dubois de Montpereux, 1831); Anistratenko and Anistratenko, p. 186.
2002. *Gibbula buchi* (Dubois, 1831); Harzhauser and Kowalke, p. 64, pl. 12, figs 7, 8, 13.
2005. *Gibbula buchi* (Dubois); Piller and Harzhauser, p. 452, fig. 4.8.
2013. *Gibbula catenularis* (Eichwald, 1830); Landau *et al.*, pp. 27, 28, pl. 1, fig. 7.

**MATERIAL:** Sandy facies: Bilozirka (MZ VIII Mg 592, 4549) 6 j; Yaseniv (MZ VIII Mg 4550) 4 sa, 13 j; Oles'ko (MZ VIII Mg 4551–4555) 7 sa, 44 j, 1 fp; Pidhirtsi (MZ VIII Mg 4556, 4557) 2 sa, 6 j; Rydomyl' (MZ VIII Mg 4558) 160 sh; Shushkivtsi (MZ VIII Mg 4559) 7 j, 1 a; Vanzhuliv (MZ VIII Mg 4683, 4714) 5 a, 7 sa, 5 j; Varivtsi (MZ VIII Mg 4684) 9 a, 14 j; Vyshhorodok (MZ VIII Mg 4560) 1 sa, 4 j; Zalistsi (MZ VIII Mg 4561, 4562) 17 a, 11 j; Zalistsi – Zhabiak ravine (MZ VIII Mg 4563, 4685) 5 sa, 3 j. Carbonate deposits: Zalistsi – Zhabiak ravine (MZ VIII Mg 4564) 4 a, 2 sa; Zhukivtsi (MZ VIII Mg 4715) 1 a, 2 sa. All specimens are from western Ukraine.

**DESCRIPTION:** Shell big, medium thickness, with relatively tall, somewhat scalate spire, rugose sculpture, suture superficial to weakly impressed linear or undulating. Protoconch paucispiral with apical beak. Protoconch/teleoconch demarcation clearly visible; terminal lip of protoconch sinuous, not thickened and with no subterminal varix. Teleoconch starting with

four spiral cords with growth lines and pustules in each interspace. Later whorls bearing five spiral cords and prosocline axial ribs, occasionally with nodes developed at intersections. From fourth whorl, three spiral rows of prominences separated by two spiral furrows with very prominent oblique axial lamellae. Surface of prominences and spaces between them covered by spiral cords. Apicalmost row consisting of the greatest extended oblique prominences (17 on the last whorl of specimen MZ VIII Mg 4559/1; Text-fig. 13D). Middle row, narrower than the upper, consisting of much smaller and more numerous prominences (40 on the last whorl of specimen MZ VIII Mg 4559/1). Row of prominences adjoining to abapical suture on later teleoconch whorls transforming into strong spiral cord, forming the periphery on last whorl. Spiral sculpture crossed by prosocline lamellae, particularly strongly developed in spiral furrows. Shell base covered by spiral cords (most often 7–9), separated by usually deep grooves, with sharp growth lines; spiral cords bifid or triple in some specimens. Umbilicus rather narrow, very deep, partially covered by inner lip; columella bearing a relative well-developed fold. Interior nacreous. Very young specimens with strongly developed row of prominences forming on last whorl an acutely angular periphery to base (see Text-fig. 13C). There is some variation in slenderness of shell, whorl profile and sculpture, as seen in the series illustrated (Text-fig. 13D–H).

**REMARKS:** In 1830, this species was independently described as new under three different names by three different authors, based on the middle Miocene material from the same area of the Fore-Carpathian Basin now located in Ukraine. Andrzejowski (1830a, p. 99, pl. 5, fig. 1) described and illustrated the species as *Trochus puschi* in the *Bulletin Société Imperiale des Naturalistes de Moscou* that is dated 1<sup>st</sup> February, 1830. Eichwald (1830, p. 221) provided a description of this species under the name *Trochus catenularis* only in a footnote. Andrzejowski's species name takes precedence because the work of Eichwald (1830) was published later. This is evidenced by a postscript, in which Eichwald (1830, pp. 253, 254) commented on the publication of Andrzejowski (1830a) in question and on another Andrzejowski's paper (1830b) published in May. This species was also described by von Buch (1830, p. 132) under the name *Trochus annulatus*, referring to shells collected by du Bois de Montpéroux at Bilozirka in Ukraine. Two syntypes of *T. annulatus* (MB.Ga.12703.1–2) present in the MfN collections are poorly preserved. The *Archiv für Mineralogie, Geognosie, Bergbau und Hüttenkunde*,



in which von Buch's paper (1830) was published, was probably issued later than the Eichwald publication mentioned above. An indirect proof is the date of a letter to the editor of this magazine – 20<sup>th</sup> June 1830 (p. 373). The exact date of publication is not relevant because the name was preoccupied for a Recent species *Calliostoma annulatum* (Lightfoot, 1786), which was originally credited to Martyn (1784), however his work was invalidated by ICZN (1957, Opinion 456). Therefore, du Bois de Montpéroux (1831, pp. 39, 40, pl. 3, figs 9–12) proposed *Trochus buchii* as the new name for the specimens described by von Buch. Pusch (1837) placed *T. annulatus* von Buch and *T. puschiei* Andrzejowski in the synonymy of *Trochus Buchii* du Bois de Montpéroux. Eichwald again described *Trochus catenularis* in 1851a and 1853, and illustrated this species in 1850, 1851b and 1859. The drawings of the two earlier editions of the atlas: 1850, 1851b, pl. 9, figs 6a–c differ in detail from the drawings from 1859, pl. 9, figs 6a–c. Eichwald (1851a, 1853) placed *Trochus buchii* du Bois de Montpéroux, 1831, *Trochus annulatus* von Buch 1830, *Trochus puschiei* Andrzejowski, 1830 in the synonymy of *T. catenularis*.

In the SPbGU collection there is one specimen of *T. catenularis* (SPbGU 3/405) recognised by the curator of Eichwald's collection as a paratype. According to Eichwald's label, it originates from Zhukivtsi. Photographs of syntypes of *T. annulatus*, provided kindly by Andreas Abele (NfM), and also descriptions and illustrations of *T. puschiei* given by Andrzejowski (1830a) (the type material of *T. puschiei* is probably housed in the KNUISH, see introduction) and *T. buchii* given by du Bois de Montpéroux (1831) have confirmed that the names are synonyms of *Trochus catenularis* Eichwald, 1830. The same opinion was also shared by Friedberg (1928), Kulichenko and Sorochan (1968), Krach and Brzezińska (1977), Krach (1981), Landau *et al.* (2013), and also Hilber (1882), however with some doubts.

This species is widely accepted as *Gibbula buchii* (du Bois de Montpéroux, 1831) and has been mentioned frequently in various papers, listed in synonymy above. However, the first available name for this species is *Trochus puschiei* Andrzejowski, 1830, which referred to shells from Zhukivtsi and Varivtsi in Ukraine. Though it might be desirable to treat *Gibbula buchii* as a *nomen protectum*, the use of *Trochus Puschiei* and also *Trochus catenularis* and *Trochus buchii* by Mikhailovsky (1903), while discussing the Tarkhanian *Trochus (Forskalia) fanulum* Gmelin, 1791 (his pp. 65, 66, 225, 226) and the inclusion of the names in the list of the middle Miocene molluscs of Podolia, Volhynia and Bessarabia (his

p. 115) prevents the treatment of *Trochus Puschiei* as a *nomen oblitum*. Therefore, *Trochus puschiei* is declared a *nomen protectum*, and it is a recombinant as *Gibbula puschiei* (Andrzejowski, 1830).

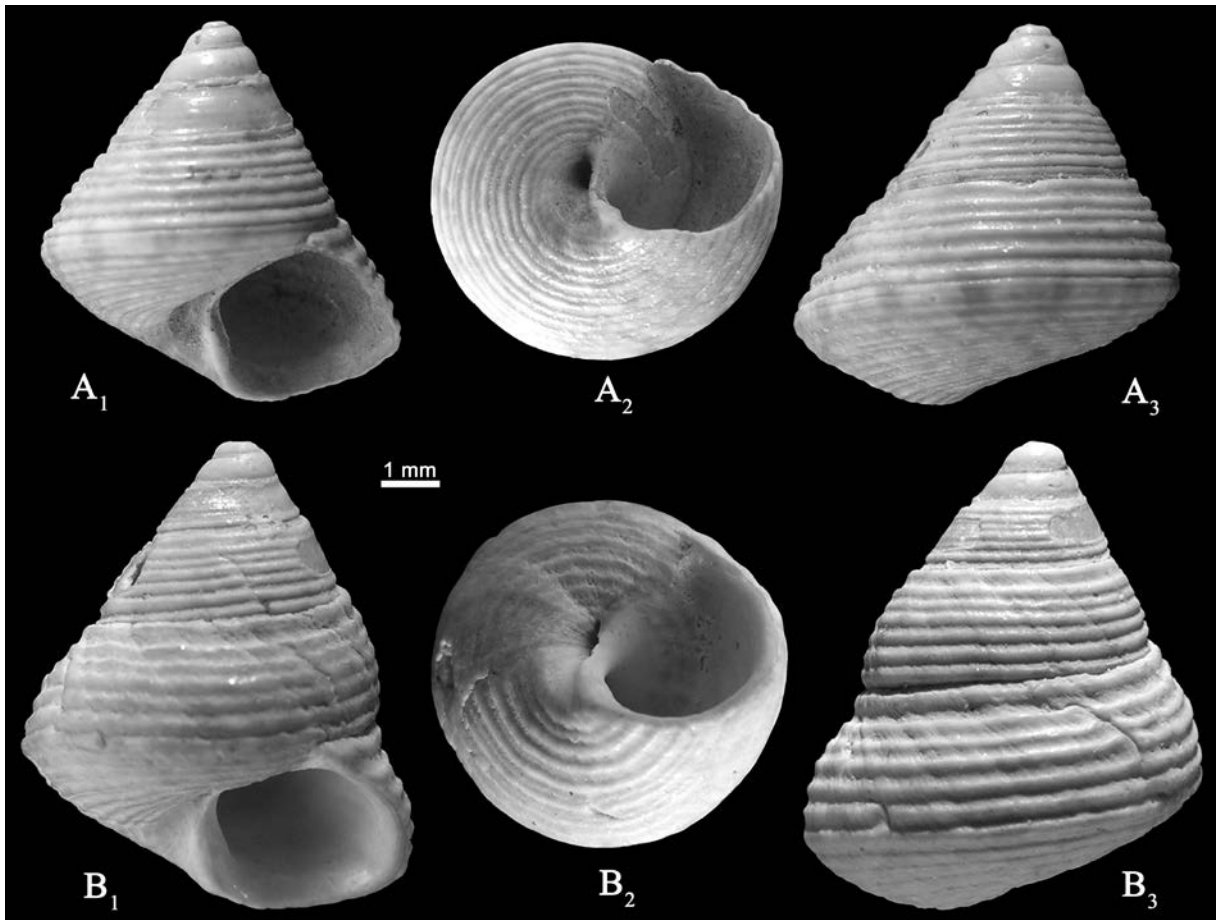
Landau *et al.* (2013), based on an erroneous premise (10<sup>th</sup> January 1830 – the date of censor's approval for printing of the *Naturhistorische Skizze...* was erroneously accepted as the date of publication) resurrected the name *T. catenularis*. The species name, however, has no priority, as shown above.

*Gibbula puschiei* is similar to *Gibbula fanulum* (Gmelin, 1791), which is known from the upper Miocene Tortonian of NW France (Landau *et al.* 2017) to the Pliocene and present-day of the Mediterranean (Landau *et al.* 2003); it was also described from the Tarkhanian of Eastern Paratethys (Mikhailovsky 1903). The differences between the shells of these species were discussed by Landau *et al.* (2013, p. 28).

OCCURRENCE: Lower to middle Miocene of the Proto-Mediterranean Sea: Burdigalian of Iran (Harzhauser *et al.* 2002); upper Serravallian of Turkey (Landau *et al.* 2013); Central Paratethys: Karpatian of Hungary (Harzhauser 2003); Badenian of Poland (e.g., Bałuk 1975; Krach 1981; MZ collection), Czech Republic (Hörnès 1856), Austria (Hörnès 1856; Sieber 1953; Glibert 1962; Mandić *et al.* 2002; Zuschin *et al.* 2006, 2007), Hungary (Csepregy-Meznerics 1954, 1969b; Strausz 1954, 1962, 1966; Katona *et al.* 2011), Romania (Boettger 1907) and western Ukraine (Andrzejowski 1830a, 1832b; von Buch 1830; Eichwald 1830, 1851a, 1853; du Bois de Montpéroux 1831; Hilber 1882; Łomnicki 1895; Friedberg 1928, 1938; Kowalewski 1936b, 1937; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; this study; for details see Appendix 2); Eastern Paratethys: Tarkhanian of southern Ukraine (Iljina 1993; Anistratenko and Anistratenko 2001), Konkian of Russia (western Ciscaucasia), Georgia, Kazakhstan and Turkmenistan (Iljina 1993); Paratethys: Sarmatian (= upper Serravallian) of Austria (Harzhauser and Kowalke 2002; Latal *et al.* 2004; Piller and Harzhauser 2005) and western Ukraine (Friedberg 1928, 1938).

*Gibbula teisseyrei* Friedberg, 1928  
(Text-fig. 14A, B)

1928. *Gibbula Teisseyrei* Friedb.; Friedberg, pp. 494, 495, pl. 31, fig. 8.  
 1938. *Gibbula Teisseyrei* Friedb.; Friedberg, p. 54.  
 1968. *Gibbula teisseyrei* Friedberg, 1928; Kulichenko and Sorochan, p. 112.



Text-fig. 14. *Gibbula teisseyrei* Friedberg, 1928 from the Badenian of Ukraine. A – Zalistsi; MZ VIII Mg 4585/1; B – Oles'ko; MZ VIII Mg 4583/1. A<sub>1</sub>, B<sub>1</sub> – apertural views; A<sub>2</sub>, B<sub>2</sub> – umbilical views; A<sub>3</sub>, B<sub>3</sub> – lateral views.

2001. *C.[olliculus] teisseyrei* (Friedberg, 1928); Anistratenko and Anistratenko, p. 191.

**MATERIAL:** Sandy facies: Bilozirka (MZ VIII Mg 4581) 1 sa; Oles'ko (MZ VIII Mg 4582, 4583) 5 sh; Pidhirtsi (MZ VIII Mg 4584) 1 fp; Zalistsi (MZ VIII Mg 4585) 2 sh. All specimens are from western Ukraine.

**DESCRIPTION:** Shell small, of medium thickness, conical. Protoconch not preserved. Teleoconch whorls flat or slightly convex. Suture weakly impressed, linear. Surface eroded on early teleoconch whorls. Sculpture on further whorls consisting of 7–8 spiral cords, slightly varying in strength; occasionally abapical cord strengthened, forming a triple peripheral band, delimiting base. Axial sculpture restricted to fine, closely-set, prosocline growth lines. Base slightly convex, bearing 9–13 concentric cords of

varying strength, narrow umbilicus partially covered by inner lip. Aperture sub-quadrate, outer lip angled at periphery. Columella with or without a very weak columellar swelling. Interior nacreous. Colour pattern of blotches at the periphery of whorls and on base preserved in some specimens (Text-fig. 14A).

**REMARKS:** Friedberg (1928) established this species based on five specimens from the Badenian of Zboriv, Ukraine, which are present in the ZNG PAN collection. The syntypes (ZNG PAN A-I-50/1631, 1632) are poorly preserved, their protoconch and the surface of early teleoconch whorls eroded. It is doubtful whether all Friedberg's specimens are conspecific. In his description, Friedberg (1928) said that the whorls of this species are flat-sided. However, the illustrated syntype (Friedberg 1928, pl. 31, fig. 8; ZNG PAN A-I-50/1631) consists of slightly convex whorls; moreover, some of its spiral cords become bifid on

the last whorl, the peripheral cord is triple, the outer lip is sharp. The specimen bears three scars after repairing damage to the shell on the last two whorls. When describing this species, Friedberg (1928) did not give these details.

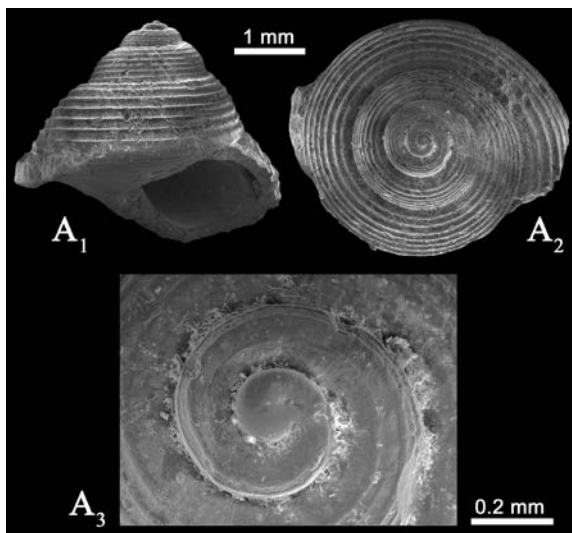
**OCCURRENCE:** Middle Miocene of the Central Paratethys: Badenian of western Ukraine (Friedberg 1928, 1938; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2).

*Gibbula zboroviensis* Friedberg, 1928  
(Text-fig. 15A)

1928. *Gibbula zboroviensis* Friedb.; Friedberg, pp. 493, 494, pl. 31, fig. 7.  
 1938. *Gibbula zboroviensis* Friedb.; Friedberg: p. 54.  
 1968. *Gibbula zboroviensis* Friedberg, 1928; Kulichenko and Sorochan, p. 113.  
 1968. *Gibbula (Colliculus) zboroviensis* Friedberg, 1929; Hinculov, p. 119, pl. 26, figs 13, 14.  
 1977. *Gibbula zboroviensis* Friedberg, 1928; Jakubowski, p. 107, pl. 13, figs 8, 9.  
 2001. *C.[olliculus] zboroviensis* (Friedberg, 1928); Anistratenko and Anistratenko, p. 191.

**MATERIAL:** Sandy facies: Varivtsi, Ukraine (MZ VIII Mg 4689) 1 jf.

**DESCRIPTION:** Shell small, solid, trochiform, with weakly stepped spire. Protoconch very convex with



Text-fig. 15. *Gibbula zboroviensis* Friedberg, 1928 from the Badenian of Varivtsi, Ukraine; MZ VIII Mg 4689. A<sub>1</sub> – apertural view, A<sub>2</sub> – apical view, A<sub>3</sub> – apex in apical view. SEM images.

apical beak. First three whorls convex, last preserved whorl almost flat. Suture linear, impressed. Three spiral cords of similar strength with micropustules in the interspaces, appearing at beginning of teleoconch. Additional weaker spiral cords appearing in latter part of first teleoconch whorl between primary cords and near adapical and abapical sutures resulting in seven spiral cords, almost equal in strength and spacing, on second and later whorls. Peripheral, indistinctly-bifid cord on last whorl. Narrow, closely-set prosocline growth lines visible in interspaces between cords. Shell base bearing eight cords, first and second ones bifid. Umbilicus narrow, deep. Aperture destroyed.

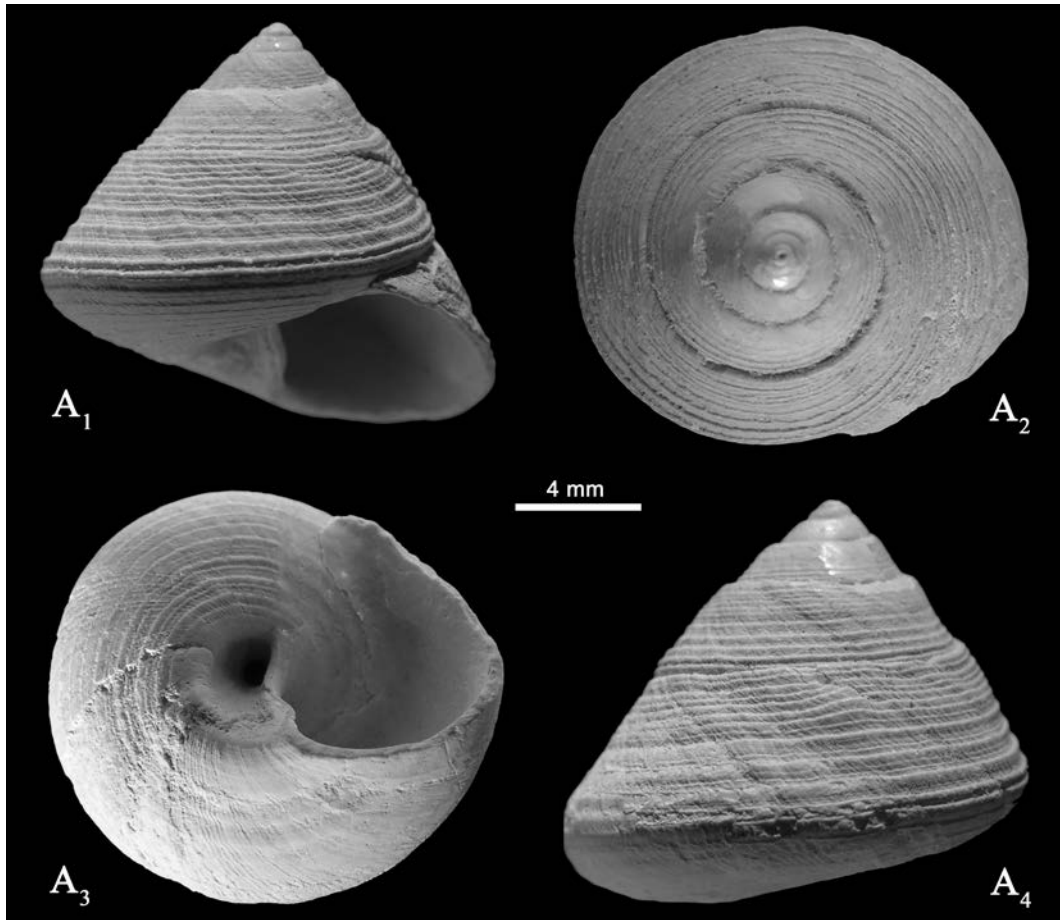
**REMARKS:** Comparative studies of specimens of several species from the Friedberg collection allow the conclusion that the shell described here belongs to *G. zboroviensis*. Friedberg (1928) established this species based on six specimens (ZNG PAN A-I-50/1629, 1630) from the Badenian of Zboriv, Ukraine, which are present in the ZNG PAN collection. The type material at hand allows the making of observations not included in the original description. The syntype illustrated by Friedberg (1928, pl. 31, fig. 7, ZNG PAN A-I-50/1629) has the protoconch and surface eroded on the first two teleoconch whorls preserved, 7 spiral cords on the last two whorls, of which the adapical two cords and the peripheral cord become bifid on the last whorl, and the base bears 11 cords. The syntypes differ in the details of their sculpture, e.g., the number of spiral cords varies from 6 to 8 on the penultimate whorl. One of the syntypes has an umbilicus completely closed by a columellar callus.

**OCCURRENCE:** Middle Miocene of the Central Paratethys: Badenian of Poland (Jakubowski 1977) and western Ukraine (Friedberg 1928, 1938; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2); Paratethys: Sarmatian of Romania (Hinculov 1968).

*Gibbula* sp.  
(Text-fig. 16A)

**MATERIAL:** Sandy facies: Zalistsi – Zhabiak ravine (MZ VIII Mg 4586) 1 sa; Zalistsi (MZ VIII Mg 4587) 1 af. All specimens are from western Ukraine.

**DESCRIPTION:** Shell large, relatively thin-shelled, with weakly scalate spire. Protoconch not preserved. First three teleoconch whorls convex, subsequent whorls flat or slightly concave. Suture linear, im-



Text-fig. 16. *Gibbula* sp. from the Badenian of Zalistsi – Zhabiak ravine, Ukraine; MZ VIII Mg 4586. A<sub>1</sub> – apertural view, A<sub>2</sub> – apical view, A<sub>3</sub> – umbilical view, A<sub>4</sub> – lateral view.

pressed. Spiral sculpture consisting of numerous cords and theards; four widely spaced stronger cords, with threads intercalated in each of the interspaces, placed at abapical part of the whorls. Axial sculpture of strongly prosocline growth lines, finely beading spiral cords on the last two whorls. Last whorl slightly angular at peripheral cord, base weakly convex, bearing concentric cords, threads and closely-set prosocline growth lines. Aperture sub-quadrangular, outer lip not thickened. Umbilicus narrow, deep. Columella bearing a small denticle. Colour pattern of axial flammules preserved.

REMARKS: These specimens, belonging to the genus *Gibbula*, differ from all other western Ukraine congeners in their shape and ornamentation. No similar specimens may be found in the available literature. Better preserved shells are required before a formal description of this probable new species.

#### Genus *Jujubinus* Monterosato, 1884

TYPE SPECIES: *Trochus matonii* Payraudeau, 1826 (= *Trochus exasperatus* Pennant, 1777), by subsequent designation of Crosse (1885). Recent, Mediterranean Sea.

REMARKS: The genus *Jujubinus* was sometimes used as a subgenus of *Cantharidus* Montfort, 1810. Williams *et al.* (2010) did not think this to be correct because *Cantharidus* was a mainly a New Zealand radiation that excludes *Jujubinus*. Donald and Spencer (2016) recognised *Cantharidus* as an endemic genus from New Zealand. *Jujubinus* includes 36 contemporary species (MolluscaBase 2019); these live mostly in the sea from extreme low tide to 200 m depths, on seaweeds and gravel bottoms in the northeastern Atlantic and Mediterranean (Poppe and Goto 1991). The taxonomy and exact distribution of this genus



are still unresolved (Smriglio *et al.* 2014), but the molecular studies of Uribe *et al.* (2017a) support the monophyly of *Jujubinus*.

Knight *et al.* (1960) assumed a Late Cretaceous origin of the genus, which was seemingly supported by a description by Abbass (1963 after Sohl 1998, p. 72). Nevertheless, molecular clock evidence suggests that *Jujubinus* originated towards the end of the Eocene (Uribe *et al.* 2017a).

The shell of *Jujubinus* has a relatively high spire. A columellar tooth or fold may be present or absent. The shell surface is mostly sculptured, with a predominance of closely spaced spiral elements, often beaded. Interior nacre is well developed.

*Jujubinus celinae* (Andrzejowski, 1833)  
(Text-fig. 17A–E)

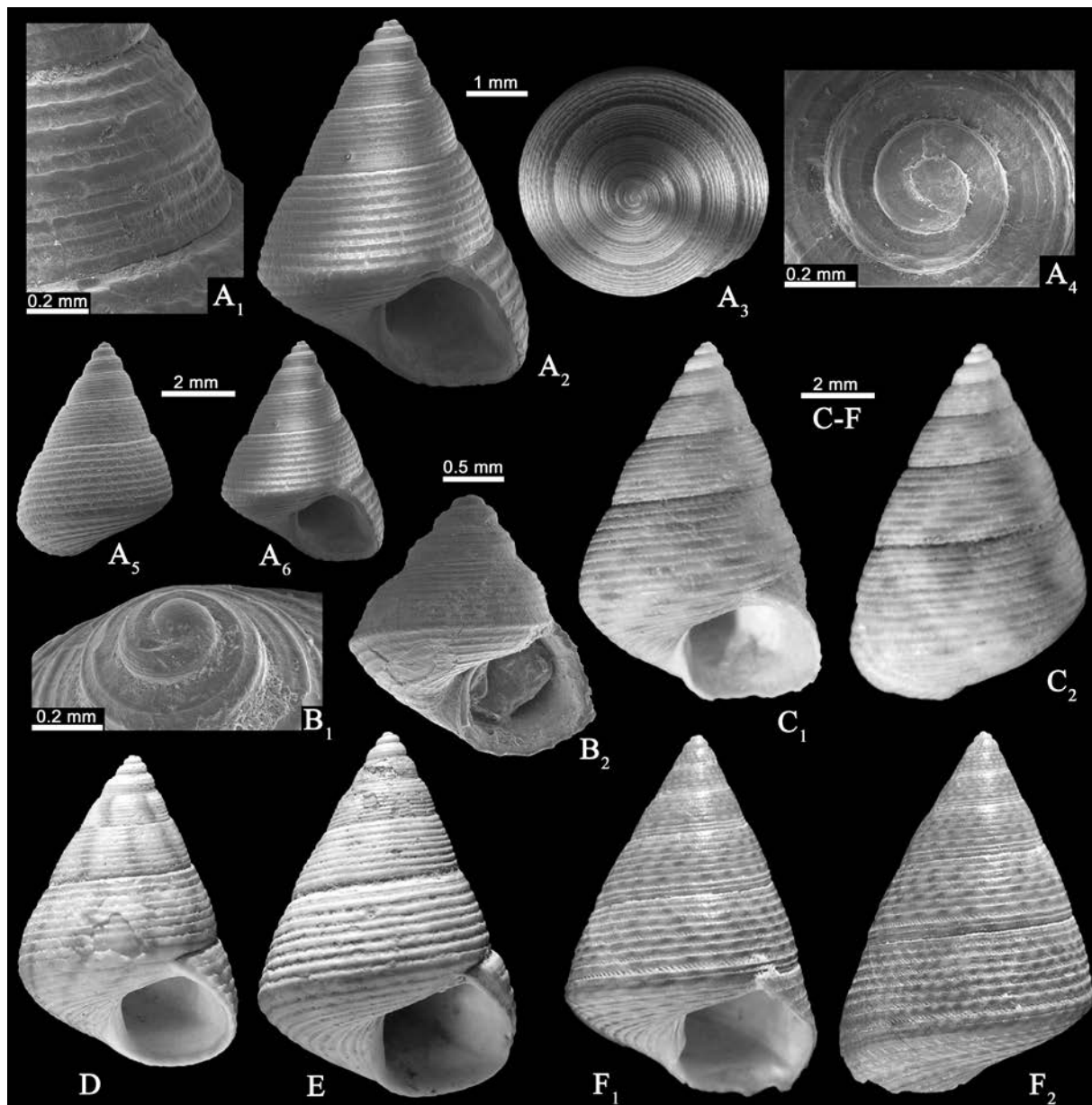
1831. *Trochus turgidulus*. Brocchi; du Bois de Montpereux, p. 40, pl. 2, figs 29, 30 [non *Trochus turgidulus* Brocchi, 1814].
1833. *Trochus Celinae*; Andrzejowski, pp. 443, 444, pl. 13, fig. 1.
- 1851a. *Turbo Celinae* Andr.; Eichwald, p. 117.
1853. *Turb.[o] Celinae* Andr.; Eichwald, p. 241.
- part 1856. *Trochus Celinae* Andr.; Hörnes, pp. 450, 451 [non pl. 45, fig. 4 = *Jujubinus puber* (Eichwald, 1851)].
1903. *Trochus striatus* L. var. *Celinae* Andr.; Laskarev, pp. 93, 94, pl. 5, figs 7–10.
- part 1928. *Gibbula affinis* Eichw. var. *pseudangulata* Boettg.; Friedberg, pp. 491, 492, excl. figs.
1928. *Callistoma pseudoanceps* Friedb.; Friedberg, pp. 500, 501, pl. 31, fig. 19.
- non 1928. *Callistoma Celinae* Andr.; Friedberg, pp. 508, 509, pl. 32, fig. 8 [= *Jujubinus puber* (Eichwald, 1851)].
- part 1928. *Callistoma puberum* Eichw.; Friedberg, pp. 510, 511, excl. figs.
- 1936b. *Callistoma puberum* Eichw.; Kowalewski, p. 15.
- non 1936b. *Callistoma Celinae* Andr.; Kowalewski, p. 15 [= *Jujubinus puber* (Eichwald, 1851)].
1937. *Callistoma puberum* Eichw.; Kowalewski, p. 8.
- part 1938. *Gibbula affinis* Eichw. var. *pseudangulata* Boettg.; Friedberg, p. 54.
- part 1938. *Callistoma puberum* Eichw.; Friedberg, p. 55.
- part 1938. *Callistoma Celinae* Andr.; Friedberg, p. 57.
1969. *Calliostoma puber* (Eichwald); Kojumdgieva, p. 76, pl. 28, fig. 1.
- non 1975. *Jujubinus (Strigosella) celinae* (Andrzejowski, 1833); Batuk, pp. 41, 42, pl. 4, figs 11–15 [= *Jujubinus puber* (Eichwald, 1851)].

1977. *Calliostoma cf. celinae* (Andrzejowski, 1833); Jakubowski, p. 108, pl. 13, figs 20, 21.
- non 1981. *Calliostoma celinae* (Andrzejowski 1833); Krach, p. 44, pl. 14, figs 11–14 [= *Jujubinus puber* (Eichwald, 1851)].
- non 2013. *Jujubinus celinae* (Andrzejowski, 1833); Landau *et al.*, pp. 25, 26, pl. 1, figs 4, 5 [= *Jujubinus puber* (Eichwald, 1851)].

MATERIAL: Sandy facies: Bilozirka (MZ VIII Mg 4613) 30 sh; Yaseniv (MZ VIII Mg 4614) 1 sa; Korostova (MZ VIII Mg 4615) 3 fp; Oles'ko (MZ VIII Mg 4616) 1 j; Rydomyl' (MZ VIII Mg 4617) 76 sh; Shushkivtsi (MZ VIII Mg 4618) 22 sh; Varivtsi (MZ VIII Mg 4696) 18 sh; Zalistsi (MZ VIII Mg 4619, 4620) 1 a, 10 j; Zalistsi – Zhabiak ravine (MZ VIII Mg 4621) 4 a, 9 sa; Zhukivtsi (MZ VIII Mg 4622) 1 fp. All specimens are from western Ukraine.

DESCRIPTION: Shell of medium size, with high conical spire, convex base. Protoconch paucispiral, convex, with apical beak; terminal lip of protoconch seems to be sinuous (see Text-fig. 17B<sub>1</sub>). Spiral sculpture starting with 5–6 cords, two stronger than the others; interspaces between cords covered by small pustules. Single secondary cord appearing in some interspaces, on third teleoconch whorl; these cords gaining in strength and almost equal to the primary cords, resulting in 7–10 (most often 8–9) flattened, strap-like cords of strength, almost the width of their interspaces, a single spiral thread intercalated in some of the interspaces, on last whorl. Axial sculpture restricted to closely-set prosocline growth lines, clearly visible in interspaces. Whorl profile weakly convex to straight. Suture linear, weakly indented. Last whorl roundly angled at periphery. Base weakly convex, imperforate, bearing spiral cords of equal or irregular strength, and prominent axial growth lines. Outer lip with bevelled edge. Columella with or without weak fold. Juvenile specimens with sharply angled last whorl, and sometimes with umbilical chink. Colour pattern of brown spots (Text-fig. 17C) or vertical flammules (Text-fig. 17D) is preserved in many specimens, especially from Rydomyl'.

REMARKS: The location of Andrzejowski's original material is unknown; it could be in the KNUSH, but no answer from the curator was obtained. In his diagnosis and description of *Trochus celinae* from Bilozirka and Katerynivka, Ukraine, Andrzejowski (1833) pointed to eight spiral striations per whorl, typical of this species. However, the inaccurate illustrations of *Trochus celinae* given by Andrzejowski



Text-fig. 17. Fossil and Recent representatives of *Jujubinus* Monterosato, 1884. A–E – *Jujubinus celinae* (Andrzejowski, 1833) from the Badenian of Ukraine. A, C, D – Rydomyl'; A – MZ VIII Mg 4617/1, C – MZ VIII Mg 4617/2, D – MZ VIII Mg 4617/3; B – Zalistsi; MZ VIII Mg 4619/1; E – Zalistsi – Zhabiak ravine; MZ VIII Mg 4621/1. A, B are SEM images. F – Recent *Jujubinus striatus* (Linnaeus, 1758) from Messina (Sicily), Italy; MZ VIII Mg 4456/1. A<sub>1</sub> – details of the teleoconch ornamentation at the fourth whorl; A<sub>2</sub>, A<sub>6</sub>, B<sub>2</sub>, C<sub>1</sub>, D, E, F<sub>1</sub> – apertural views; A<sub>3</sub> – apical view, A<sub>4</sub> – close-up of juvenile whorls in apical view; A<sub>5</sub>, C<sub>2</sub>, F<sub>2</sub> – lateral views; B<sub>1</sub> – apex in oblique view.

(1833, pl. 13, fig. 1a, b) have caused much confusion in the palaeontological literature in the understanding of this species. This name is most often applied to smooth specimens or those with very numerous fine spiral elements of sculpture. Such specimens should be identified as *Jujubinus puber* (Eichwald, 1851), a species discussed below.

Unfortunately, the juvenile specimens described, but not illustrated, by Eichwald (1851a, 1853) as '*Turbo celinae* Andrzejowski' from the vicinity of Novokonstantyniv are not present in the SPbGU collection.

Hörnès (1856, pl. 45, fig. 4) illustrated a specimen from Steinabrunn, Austria, as *Trochus celinae*,

which in fact represents *J. puber*. However, he considered *T. puber* as a junior synonym of *T. celinae* (Hörnnes 1856, p. 450). This is not correct because these names refer to a completely different forms (compare remarks for *J. puber*).

Laskarev (1903) recognised specimens from Domanenka, Ukraine (pl. 5, figs 7–10) as '*Trochus striatus* Linnæus var. *celinae* Andrzejowski'. They are almost identical to the specimens presented herein. He proved in a footnote (Laskarev 1903, pp. 93, 94) that it is correct to leave the name *T. celinae* Andrzejowski for grooved forms, which he regarded as a variety of *T. striatus*.

*Jujubinus striatus* (Linnæus, 1758) was reported from the early and middle Miocene of the Aquitaine Basin (Cossmann and Peyrot 1917, pp. 162–164, pl. 5, figs 28–30), and from the middle Miocene of the Loire Basin (Peyrot 1938, pp. 33, 34) under the name '*Callistoma (Strigosella) striatum* (Linnæus)', as well as from the late Miocene Tortonian, Pliocene and Pleistocene of the northeastern Atlantic and (Proto-) Mediterranean (see e.g., Chirli 2004; Ceulemans *et al.* 2016; Landau *et al.* 2017). Today it occurs in an area from the Isle of Man to the Azores, the Canary Islands and the Mediterranean (Poppe and Goto 1991). Despite the superficial similarity of the specimens of *J. celinae* to those of *Jujubinus striatus* (compare Text-fig. 17A–E and Text-fig. 17F – specimen MZ VIII Mg 4456/1), I believe that they should be treated as separate species, for example because of different sculpture on the early teleoconch whorls of these species. *Jujubinus striatus* most often has four very narrow spiral grooves separating five, almost equal in width, flattened cords on the third teleoconch whorl; the increase in the number of cords on the next whorl is made by splitting some of the cords into two subcords.

The specimens from Ukraine, which Friedberg (1928, pp. 508, 509, pl. 32, fig. 8) erroneously identified as *celinae*, are considered to represent *J. puber*. The consequence of Friedberg's error is that Kowalewski (1936b, p. 15 and his museum labels; in relation to specimens from Rydomyl', Bilozirka, Oles'ko and Zalisti – Zhabiak ravine, which are the subject of this study), Bałuk (1975) and Krach (1981) wrongly used the name *celinae* instead of *puber*. On the other hand, specimens from Rydomyl' (Kowalewski 1936b, p. 15), Korostova and Shushkivtsi identified herein as *J. celinae*, were reported as *Callistoma puberum* by Kowalewski (1937, p. 8).

OCCURRENCE: Lower to middle Miocene of the Central Paratethys: ?Karpatian of Austria (Harzhauser

2003); Badenian of Austria (Hörnnes 1856), Hungary (Hörnnes 1856; ?Saint Martin *et al.* 2000), Poland (Jakubowski 1977), and western Ukraine (du Bois de Montpereux 1831; Andrzejowski 1833; Eichwald 1851a, 1853; Laskarev 1903; Friedberg 1928, 1938; Kowalewski 1936b, 1937; Kojumdgieva 1969; and this study; for details see Appendix 2).

The presence of *J. celinae* in the Badenian deposits of western Ukraine was also reported by Kulichenko and Sorochan (1968, p. 116), as well as by Anistratenko and Anistratenko (2001, p. 192). However, on the basis of synonymy given by those authors, it is not possible to determine which form was assigned to that name.

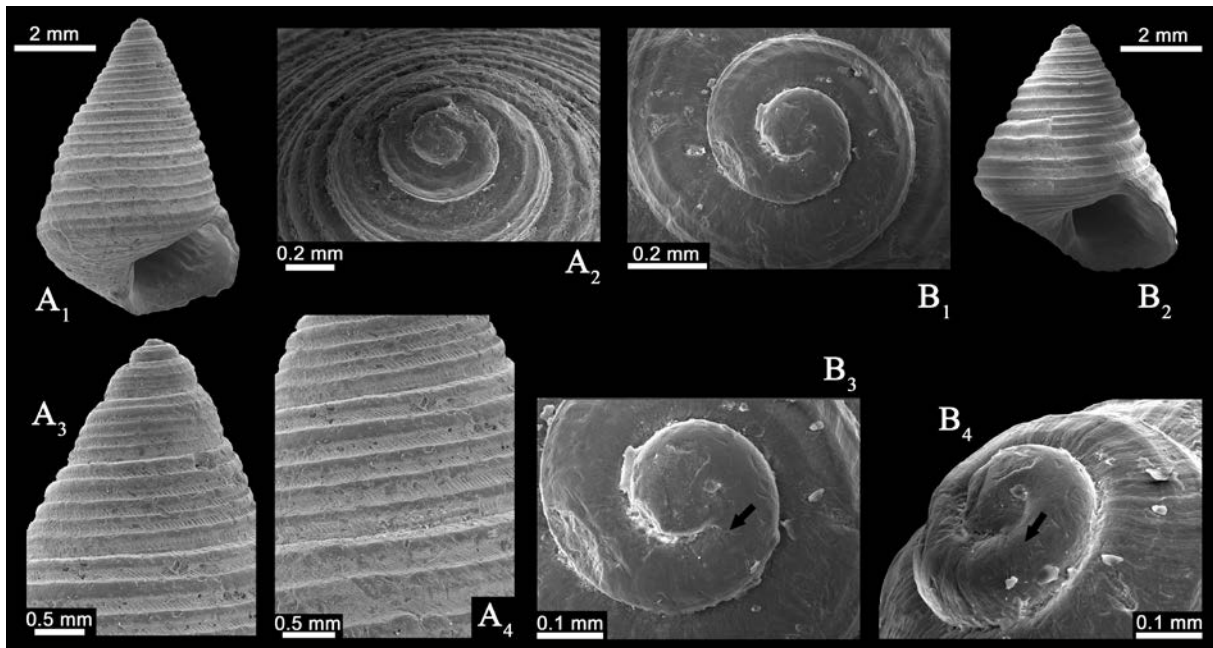
*Jujubinus planatus* (Friedberg, 1928)  
(Text-fig. 18A, B)

1928. *Callistoma planatum* Friedb.; Friedberg, p. 502, pl. 31, fig. 23.  
 1928. *Callistoma planatum* Friedb. var. *crassior*; Friedberg, p. 503, pl. 31, fig. 24.  
 1938. *Callistoma planatum* Friedb.; Friedberg, p. 56.  
 1938. [*Callistoma planatum*] var. *crassior* Friedb.; Friedberg, p. 56.  
 non 1940. *Trochus planatus* Friedb., var. *crassior* Friedb.; Simionescu and Barbu, p. 41, pl. 5, figs 76–78.  
 part 1957. *Calliostoma planata striatella* n. ssp.; Švagrovský, pp. 210–212, pl. 2, figs 1–3 [non fig. 4 = *C. guttenbergi* (Hilber, 1897)].  
 1968. *Calliostoma planata* Friedberg, 1928; Kulichenko and Sorochan, p. 118.  
 part 1969. *Calliostoma guttenbergi* (Hilber, 1897); Kojumdgieva, p. 76, pl. 28, fig. 4 [non figs 2, 3].  
 1971. *Calliostoma planatum striatellum* Švagrovský, 1957; Švagrovský, pp. 211–213, pl. 26, figs 10–12, pl. 27, figs 1–3.  
 1981. *Calliostoma planatum* Friedberg 1928; Krach, p. 45, pl. 13, figs 15–18, pl. 14, fig. 1.  
 2001. *C.[alliostoma] planata* Friedberg, 1928; Anistratenko and Anistratenko, p. 182.  
 2017. *Jujubinus planatum* Friedberg, 1928; Sladkovskaya, pp. 1563, 1564, pl. 7, figs 6, 7.  
 2017. *Jujubinus planatum striatellum* (Švagrovsky, 1957); Sladkovskaya, p. 1564, pl. 7, figs 6, 7.

MATERIAL: Sandy facies: Yaseniv (MZ VIII Mg 4623) 18 j; Oles'ko (MZ VIII Mg 4624–4626) 10 a, 6 j; Pidhirtsi (MZ VIII Mg 4627, 4628) 23 sh. All specimens are from western Ukraine.

DESCRIPTION: Shell of medium size, thick, with conical spire. Teleoconch whorls flat-sided to weakly





Text-fig. 18. *Jujubinus planatus* (Friedberg, 1928) from the Badenian of Ukraine and Poland. A – Pidhirtsi, Ukraine; MZ VIII Mg 4628/1; B – Węgliń, Poland; MZ VIII Mg 4706. A<sub>1</sub>, B<sub>2</sub> – lateral views; A<sub>2</sub> – apex in latero-apical view; A<sub>3</sub> – juvenile whorls in lateral view; A<sub>4</sub> – details of teleoconch ornamentation; B<sub>1</sub> – close-up of apex; B<sub>3</sub> – close-up of protoconch; B<sub>4</sub> – close-up of juvenile whorls. Black arrows indicate demarcation between protoconch and teleoconch. SEM images.

convex. Suture linear, superficial. Protoconch not well preserved, with apical beak (Text-fig. 18A<sub>2</sub>). Protoconch/teleoconch boundary barely visible, sinuous?, fractured (seen in the specimen from Węgliń, Poland; Text-fig. 18B<sub>3</sub>, B<sub>4</sub>). Sculpture on first teleoconch whorl of three spiral cords and micropustules placed adjacent to adapical suture. Second teleoconch whorl bearing most often five cords, not equal in strength. Later whorls with 4–6 spiral cords, of which second or first and second ones are sometimes slightly stronger than the others. Single secondary cord intercalated in some interspaces between primaries, especially on the last whorl, in some specimens. Fine, prosocline growth lines visible in interspaces between cords on spire whorls, crossing spiral elements on last whorl, closer-set towards aperture (see Text-fig. 18A<sub>4</sub>). Last whorl slightly angular at peripheral cord, occasionally bifid or triple. Shell base weakly convex, bearing concentric cords of irregular strength and position (10 cords on the base of specimen MZ VIII Mg 4628/1; Text-fig. 18A) and axial growth lines. Aperture sub-quadrangular, outer lip with bevelled edge. Small umbilical chink, weak columellar swelling, irregularly spaced ridges within the outer lip are present in some specimens.

REMARKS: Friedberg (1938, p. 56) was not sure about the status of his new species due to the small number of specimens. He distinguished larger shells of *Calliostoma planatum*, with a wider apical angle, as a new variety *crassior*. The specimens of this species are present in the ZNG PAN collection (ZNG PAN A-I-50/1658–1662).

Based on the large number of Badenian shells from the carbonate deposits of Roztocze Hills, Poland, in the MZ collection, I consider *J. planatus* to be a very variable species. The shells of this species show a wide range of intraspecific variability in apical angle, shape, size, and sculpture. Most of the specimens have a spiral sculpture consisting of an adapical fine cord and four cords below, more strongly developed. Between the extremes there are intermediate forms. Therefore, the introduction of the new variety *Calliostoma planatum* var. *crassior* by Friedberg (1928) is not justified.

The Ukrainian shells fall well within the wide range of variability seen in specimens from Roztocze Hills. Therefore, due to the relatively good state of preservation one specimen from Węgliń (MZ VIII Mg 4706) was used to illustrate the protoconch of this species (see Text-fig. 18B).

Švagrovský (1957, 1971) considered the middle Miocene Sarmatian shells from eastern Slovakia to be a separate subspecies, i.e., *C. planatum striatellum*, differing from the Badenian shells in having a more slender shell with a stronger peripheral keel on the last whorl, and in having sculpture composed of more numerous, finer spiral cords.

Previous authors (except Sladkovskaya 2017) placed the species *planatus* in the genus *Calliostoma* Swainson, 1840. This identification is incorrect, because of the protoconch, which has not the typical honeycomb-like microsculpture of *Calliostoma* (see the protoconch of *Calliostoma trigonum* (Eichwald, 1830) illustrated below in Text-fig. 24B<sub>2</sub>, B<sub>3</sub>).

**OCCURRENCE:** Middle Miocene of the Central Paratethys: Badenian of Poland (Krach 1962, 1981; Ney 1969; Pisera 1985; this study), Hungary (Kóráy 1985) and western Ukraine (Friedberg 1928, 1938; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2); Paratethys: Sarmatian (= upper Serravallian) of Slovakia (Švagrovský 1957, 1971; Iljina 1998; Sladkovskaya 2017), Bulgaria (Kojumdgieva 1969; Iljina 1998; Sladkovskaya 2017), Austria, Czech Republic, Moldova (Iljina 1998; Sladkovskaya 2017), Poland, and western Ukraine (Sladkovskaya 2017).

*Jujubinus puber* (Eichwald, 1851)  
(Text-fig. 19A–C)

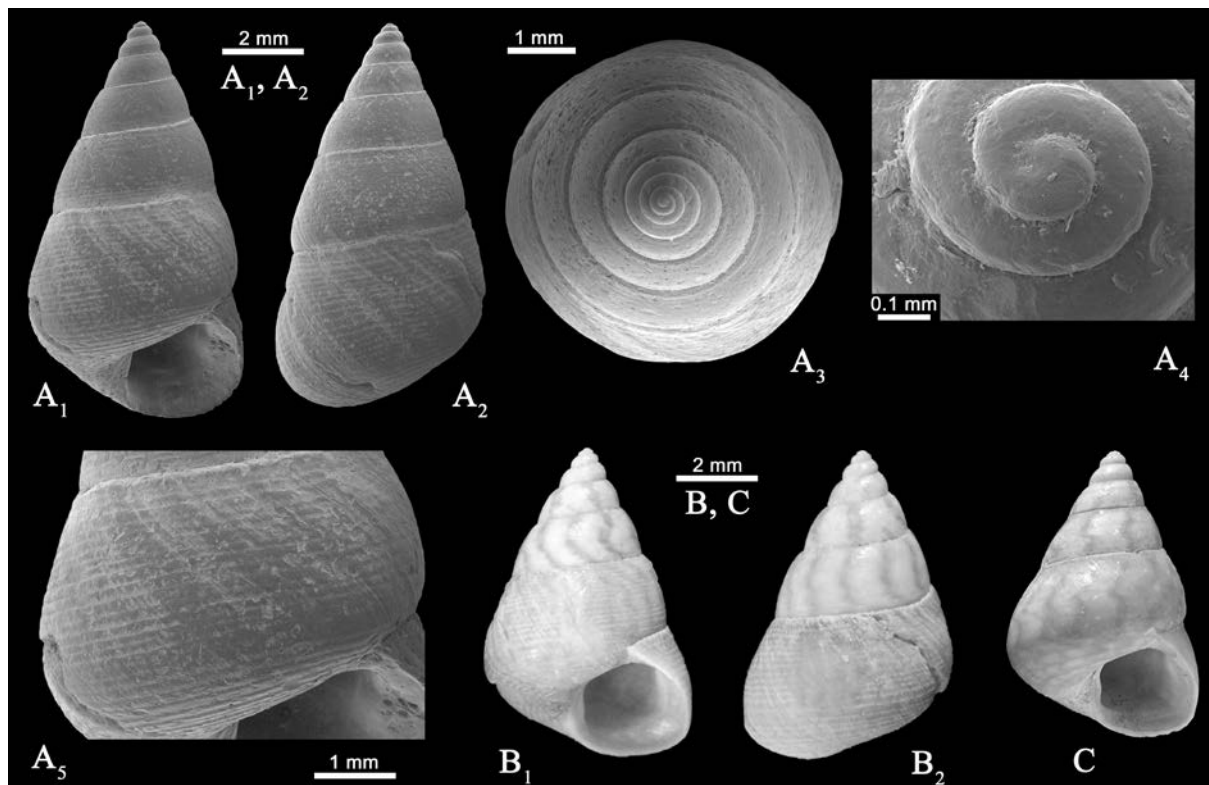
1850. [*Trochus puber* m.]; Eichwald, pl. 9, fig. 20 (atlas).  
1851a. *Troch.[us] puber* m.; Eichwald, pp. 114, 115, 282.  
1851b. [*Trochus puber* m.]; Eichwald, pl. 9, fig. 20 (atlas).  
1853. *Troch.[us] puber* m.; Eichwald, p. 231.  
part 1856. *Trochus celinae* Andr.; Hörnes, pp. 450, 451, pl. 45, fig. 4.  
1859. *Trochus puber*; Eichwald, p. 3, pl. 9, fig. 20 (atlas).  
1903. *T.[rochus] puber* Eichw.; Laskarev, pp. 93, 94, pl. 5, figs 11–13.  
1928. *Calliostoma Celinae* Andr.; Friedberg, pp. 508, 509, pl. 32, fig. 8.  
non 1928. *Calliostoma puberum* Eichw.; Friedberg, pp. 510, 511, pl. 32, figs 9–12.  
1936b. *Calliostoma Celinae* Andr.; Kowalewski, p. 15.  
non 1936b. *Calliostoma puberum* Eichw.; Kowalewski, p. 15 [= *Jujubinus celinae* (Andrzejowski, 1833)].  
non 1938. *Calliostoma puberum* Eichw.; Friedberg, p. 55.

1938. *Calliostoma Celinae* Andr.; Friedberg, p. 57.  
part 1956. *Calliostoma puberum* (Eichwald); Csepregy-Meznerics, p. 377, pl. 1, figs 1, 2.  
part 1962. *Calliostoma puberum* Eichwald; Strausz, p. 53, pl. 13, fig. 4 [figure from Csepregy-Meznerics 1956, pl. 1, fig. 1].  
part 1966. *Calliostoma puberum* Eichwald, 1853; Strausz, p. 34, pl. 13, fig. 4 [figure from Csepregy-Meznerics 1956, pl. 1, fig. 1].  
1968. *Calliostoma celinae* (Andrzejowski, 1833); Kulichenko and Sorochan, p. 116.  
non 1968. *Calliostoma puberum* (Eichwald, 1853); Kulichenko and Sorochan, p. 120, pl. 32, fig. 3 [figure from Friedberg 1928, pl. 32, fig. 9].  
non 1969. *Calliostoma puber* (Eichwald); Kojumdgieva, p. 76, pl. 28, fig. 1 [= *Jujubinus celinae* (Andrzejowski, 1833)].  
1970. *Calliostoma subturriculoides* (Sinzow); Bałuk, p. 117, pl. 8, fig. 8.  
1975. *Jujubinus (Strigosella) celinae* (Andrzejowski, 1833); Bałuk, pp. 41, 42, pl. 4, figs 11–15.  
1981. *Calliostoma celinae* (Andrzejowski 1833); Krach, p. 44, pl. 14, figs 11–14.  
2013. *Jujubinus celinae* (Andrzejowski, 1833); Landau *et al.*, pp. 25, 26, pl. 1, figs 4, 5.

**MATERIAL:** Sandy facies: Bilozirka (MZ VIII Mg 4629) 5 sh; Yaseniv (MZ VIII Mg 4630) 1 j; Oles'ko (MZ VIII Mg 4631–4633) 13 sh; Pidhirtsi (MZ VIII Mg 4634) 1 sa, 2 j; Rydomyl' (MZ VIII Mg 4635) 81 sh; Zalistsi (MZ VIII Mg 4636) 2 sa, 11 j; Zhukivtsi (MZ VIII Mg 4637) 2 j. Carbonate deposits: Lidykhiv (MZ VIII Mg 4638) 1 a; Staryi Pochoiv (MZ VIII Mg 4639) 1 j; Zalistsi – Zhabiak ravine (MZ VIII Mg 4640) 4 sh. All specimens are from western Ukraine.

**DESCRIPTION:** Shell of medium size, with high conical spire. Protoconch with apical back, protoconch surface abraded. First three teleoconch whorls more convex than subsequent ones. Suture linear, weakly impressed. Three fine spiral cords sometimes visible on first teleoconch whorl. Later whorls smooth or with many narrow spiral grooves (18–20 in specimen MZ VIII Mg 4635/1; Text-fig. 19A) causing spiral ribbed mostly on the two last whorls. Last whorl rounded or slightly angled at periphery. Outer lip with bevelled edge. Shell base convex, bearing spiral cords (11 in specimen MZ VIII Mg 4635/1). Columella with or without weak columellar fold. Umbilicus absent in adults. Juvenile specimens with slit-like umbilicus and sharply angled last whorl.

Colour pattern is the same as that of specimens from Korytnica (see Bałuk 1975, p. 41, pl. 4, figs



Text-fig. 19. *Jujubinus puber* (Eichwald, 1851) from the Badenian of Rydomyl', Ukraine. A – MZ VIII Mg 4635/1, B – MZ VIII Mg 4635/2, C – MZ VIII Mg 4635/3. A<sub>1</sub>, B<sub>1</sub>, C – apertural views; A<sub>2</sub>, B<sub>2</sub> – lateral views; A<sub>3</sub> – apical view; A<sub>4</sub> – apex in apical view; A<sub>5</sub> – details of late teleoconch ornamentation. A<sub>1</sub>–A<sub>5</sub> are SEM images.

11–15), Węglińek and Łychów (see Krach 1981, p. 44, pl. 14, figs 11–14), or somewhat different, consisting of combined horizontal chevrons forming the axial wavy stripes (see Text-fig. 19B, C).

This species is very variable in the slenderness of shell, whorl convexity and strength of spiral sculpture.

REMARKS: Shells collected and described by Eichwald (1851a) as *Trochus puber* are not present in the SPbGU collection. Because the first description of *T. puber* is brief (Eichwald 1851a, pp. 114, 115), the present author follows Eichwald (1850, 1851b, 1859, pl. 9, fig. 20; 1853, p. 231) and Laskarev (1903, pp. 93, 94, pl. 5, figs 11–13) in identifying specimens of this species. In his description, Eichwald (1853, p. 231) stated that: the whorls are almost smooth or spirally striated; the fine striations are very numerous, with 15–16 on spire whorls, more than 20 on the last whorl. However, the illustrations in Eichwald's atlas are sketchy, while the figures of the Badenian specimens of *T. puber* from Zalistsi in Laskarev (1903, pl. 5, figs 11–13) are of good quality. The footnote on pp.

93, 94 shows that he had seen the syntype described by Eichwald (1851a) from Zhukivtsi. Therefore, one can be sure that he properly recognised and illustrated this species.

I have identified as *J. puber* a specimen illustrated by Hörnes (1856, pl. 45, fig. 4) as *T. celinae*. Laskarev (1903, p. 94) noted that in the Vienna Museum the name *celinae* was applied to various forms, and the illustrations of the original given by Hörnes are not fully consistent with the appearance of this specimen. Hörnes (1856) synonymised *Trochus celinae* Andrzejowski, 1833 with *Trochus puber* Eichwald, 1851. This is incorrect, as differences between *puber* and *celinae* are sufficient to consider them as separate species (compare Text-fig. 19 with Text-fig. 17).

Friedberg (1928, pp. 508, 509, pl. 32, fig. 8) misinterpreted Andrzejowski's species *celinae* and, consequently, applied the name to the specimens that in my opinion should be identified with the discussed species *J. puber*. Friedberg's error was repeated by Kowalewski (see remarks for *J. celinae*), Kulichenko and Sorochan (1968), Bałuk (1975), Krach (1981),



Anistratenko and Anistratenko (2001) and recently also Landau *et al.* (2013). It should be noted that the specimens from Korytnica (Bałuk 1975, pp. 41, 42, pl. 4, figs 11–15) differ from the Ukrainian ones in having a more pronounced sculpture and the presence of the umbilicus in adults.

**OCCURRENCE:** Middle Miocene of the Central Paratethys: Badenian of Austria (Hörnes 1856), Hungary (Hörnes 1856; Csepregy-Meznerics 1956; Strausz 1962, 1966), Poland (Eichwald 1853; Bałuk 1970, 1975; Krach 1981; MZ collection), western Ukraine (Eichwald 1851a, 1853; Laskarev 1903; Friedberg 1928, 1938; Kowalewski 1936b; and this study; for details see Appendix 2); Paratethys: Sarmatian (= upper Serravallian) of western Ukraine (Laskarev 1903); Proto-Mediterranean Sea: upper Serravallian of Turkey (Landau *et al.* 2013).

The occurrence of *Calliostoma puberum* in the Badenian and Sarmatian of western Ukraine was also reported by Anistratenko and Anistratenko (2001, p. 183). However, based on the synonymy given by these authors, it is considered that this name was assigned to specimens not belonging to *J. puber*.

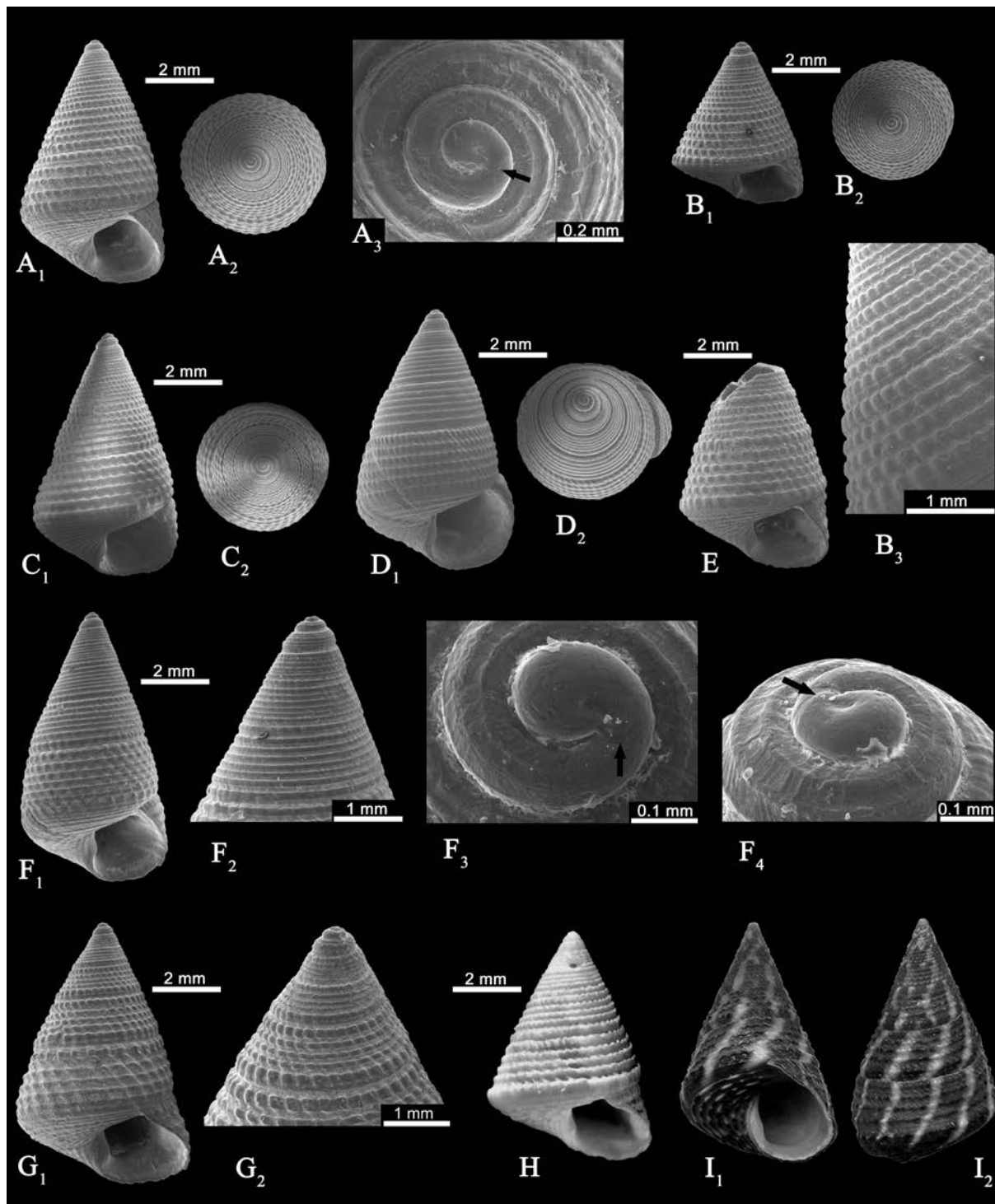
*Jujubinus turricula* (Eichwald, 1830)  
(Text-fig. 20A–H)

1830. *T.[rochus] turricula*, m.: Eichwald, pp. 220, 221.
1833. *Trochus granulato-striatus*; Andrzejowski, p. 444, pl. 13, fig. 3.
1837. *Trochus granulato-striatus* Andrz.; Pusch, p. 109.
1850. [*Trochus turricula* m.]; Eichwald, pl. 9, fig. 15 (atlas).
- 1851a. *Troch.[us] turricula* m.; Eichwald, pp. 113, 282.
- 1851b. [*Trochus turricula* m.]; Eichwald, pl. 9, fig. 15 (atlas).
1853. *Troch.[us] turricula* m.; Eichwald, pp. 229, 230.
1856. *Trochus turricula* Eichw.; Hörnes, pp. 451, 452, pl. 45, fig. 6.
1859. *Trochus turricula*; Eichwald, p. 3, pl. 9, fig. 18 (atlas).
1896. [*Calliostoma* (] *J.[ujubinus]*) *turricula* var. *laevigranosa* Sacc.; Sacco, p. 47, pl. 4, fig. 54.
1896. [*Calliostoma* (*Jujubinus*) *turricula*] var. *hoernesiana* Sacc.; Sacco, p. 48.
1907. *Calliostoma* (*Jujubinus*) *turricula* (Eichw.) var. *hoernesiana* Sacco; Boettger, p. 184, No. 633.
- part 1917. *Calliostoma* (*Strigosella*) *turricula* [Eichwald]; Cossmann and Peyrot, pp. 158–160, pl. 5, figs 19–21, non pl. 5, figs 16–18.

1928. *Callistoma turricula* Eichw.; Friedberg: pp. 507, 508, pl. 32, figs 5–7.
- 1936b. *Callistoma turricula* Eichw.; Kowalewski, p. 15.
1937. *Callistoma turricula* Eichw.; Kowalewski, p. 8.
1938. *Callistoma turricula* Eichw.; Friedberg, p. 57.
- 1949a. *Calliostoma turricula* (Eichwald); Glibert, p. 43, pl. 3, fig. 1.
1950. *Callistoma turricula* Eichw.; Krach, p. 300, pl. 1, fig. 28.
1955. *C.[antheridus]* (*Jujubinus*) *turriculus* Eichw.; Korobkov, p. 100.
1955. *Cantharidus* (*Jujubinus*) *turricula* Eichw.; Korobkov, pl. 5, figs 3–5 [figures from Friedberg 1928, pl. 32, figs 5–7].
1968. *Jujubinus turricula* (Eichwald, 1830); Kulichenko and Sorochan, p. 105, pl. 28, figs 17, 18 [figures from Friedberg 1928, pl. 32, figs 5, 6].
1975. *Jujubinus* (*Jujubinus*) *turricula hoernesiana* Sacco, 1896; Bałuk, pp. 39, 40, pl. 4, figs 2, 3.
1975. *Jujubinus* (*Jujubinus*) *turricula turricula* (Eichwald, 1850); Bałuk, p. 40, pl. 4, fig. 1.
1977. *Calliostoma turricula* (Eichwald, 1830); Jakubowski, p. 108, pl. 13, figs 18, 19.
1981. *Calliostoma* (*Ampullotrochus*) *trigonum* (Eichwald, 1830); Švagrovský, p. 108, pl. 33, figs 4–6.
1981. *Calliostoma turricula* (Eichwald 1830); Krach, p. 44, pl. 13, figs 5, 6.
2001. *J.[ujubinus] turricula* (Eichwald, 1830); Anistratenko and Anistratenko, p. 192.
2002. *Jujubinus turriculus* (Eichwald, 1851); Harzhauser and Kowalke, p. 64, pl. 12, figs 4–6, 9.
2013. *Jujubinus hoernesianus* Sacco, 1896; Landau *et al.*, p. 26, pl. 1, fig. 6.

**MATERIAL:** Sandy facies: Nadrichne (MZ VIII Mg 4641) 9 j.; Yaseniv (MZ VIII Mg 4642) 1 j, 2 fp; Korostova (MZ VIII Mg 4643) 2 a; Oles'ko (MZ VIII Mg 4644) 4 fp; Rydomyl' (MZ VIII Mg 4645) 187 sh; Shushkivtsi (MZ VIII Mg 4646) 6 sh, 3 fp; Varivtsi (MZ VIII Mg 4697) 1 a, 2 j; Vyshhorodok (MZ VIII Mg 4647) 1 jf; Zalistsi (MZ VIII Mg 4648) 5 a, 35 j; Zalistsi – Zhabiak ravine (MZ VIII Mg 4649) 2a, 3j; Dzvyntsiacha (MZ VIII Mg 4650) 1 fp; Zhukivtsi (MZ VIII Mg 517, 4651) 16 sh. Carbonate deposits: Lidykhiv (MZ VIII Mg 4652) 6 fp; Saryi Pochaiv (MZ VIII Mg 4653) 4 j, 2 fp; Zalistsi – Zhabiak ravine (MZ VIII Mg 4654) 6 fp. All specimens are from western Ukraine.

**DESCRIPTION:** Shell of medium size, with high conical spire. Protoconch paucispiral, with apical beak,



Text-fig. 20. Fossil and Recent representatives of *Jujubinus* Monterosato, 1884. **A–H** – *Jujubinus turricula* (Eichwald, 1830). **A**, **B**, **C** – Badenian of Rydomyl', Ukraine; **A** – MZ VIII Mg 4645/1, **B** – MZ VIII Mg 4645/2, **C** – MZ VIII Mg 4645/3); **D**, **G** – Badenian of Zalistsi – Zhabiak ravine, Ukraine; **D** – MZ VIII Mg 4649/1, **G** – MZ VIII Mg 4649/2; **E** – Badenian of Staryi Poचाiv, Ukraine, MZ VIII Mg 4653/1; **F** – Badenian of Zalistsi, Ukraine, MZ VIII Mg 4648/1; **H** – Pleistocene of Ireon, Greece, MZ VIII Mg 3353/1. **A–G** are SEM images. **I** – Recent *Jujubinus exasperatus* (Pennant, 1777) from Pellestrina (Venice), Italy; Liceo Classico 'Marco Foscarini' – Venezia, 24.07.2017. **A<sub>1</sub>**, **B<sub>1</sub>**, **C<sub>1</sub>**, **D<sub>1</sub>**, **E**, **F<sub>1</sub>**, **G<sub>1</sub>**, **H**, **I<sub>1</sub>** – apertural views; **A<sub>2</sub>**, **B<sub>2</sub>**, **C<sub>2</sub>** – apical views; **A<sub>3</sub>**, **F<sub>3</sub>** – apices in apical view, black arrows indicate demarcation between protoconch and teleoconch; **B<sub>3</sub>** – close-up of teleoconch surface; **D<sub>2</sub>** – oblique apical view; **F<sub>2</sub>**, **G<sub>2</sub>** – apices in lateral view; **F<sub>4</sub>** – apex in oblique view, black arrow indicates subterminal varix of protoconch; **I<sub>2</sub>** – lateral view.

subterminal varix (see Text-fig. 20A<sub>3</sub>, F<sub>4</sub>) and terminal lip sinuous (see Text-fig. 20A<sub>3</sub>, F<sub>3</sub>). Teleoconch consisting of slightly more than seven whorls, of which first two strongly convex, the other ones slightly convex or quite flat-sided. Slight concavity of third, fourth and fifth teleoconch whorl visible in some specimens. Suture linear, superficial. Last whorl rounded at periphery in most specimens, roundly angled in others. Umbilicus absent in adult specimens. Angularity at base and umbilical chink present in not fully grown shells (Text-fig. 20B<sub>1</sub>). Shell base flattened or slightly convex bearing prosocline growth lines and smooth or scabrous spiral cords (most often eight), irregular in strength and position in some specimens. Outer lip with bevelled edge. Columella bearing fold.

*Variation of ornamentation.* Sculpture on first teleoconch whorl of three smooth cords, a single weaker cord intercalated in some to all interspaces and above abapical suture on second whorl; these cords rapidly gaining in strength, resulting in 5–6 beaded spiral cords per whorl, separated by grooves. Occasionally, the presence of 5–6 strong cords is made by splitting primary cords into two or two fine cords, united or not, appear just above abapical suture. The order of appearance of the secondary cords is variable. Seven cords developed in a few specimens (e.g., on specimen MZ VIII Mg 4648/1; Text-fig. 20F, seventh cord appearing between cords 4 and 5 from third teleoconch whorl). Spiral cords of equal strength and rounded on some specimens, flattened in others. Only abapical cord or both abapical and adapical cords bordering the suture more strongly developed in some specimens. Most abapical cord bifid on later whorls in many specimens, forming periphery on last whorl. A single spiral thread intercalated in some of the interspaces on last whorl in some specimens. Beads on spiral cords appearing from third teleoconch whorl in most specimens, from later whorl in others, in a few specimens beads on cords developed only on whorls 6 and 7. Beads closely-set and of medium to weak strength, strongest on abapical cord in some specimens; arranged in oblique axial rows that follow prosocline growth lines. Spiral beaded cords weaker developed, narrower than their interspaces, on last whorl in some specimens.

REMARKS: The syntypes of Eichwald (1830) are probably in the KNUSH collection (see above). Unfortunately, specimens of this species are not present in Eichwald's collection stored in the SPbGU. However, abundant material at hand from the type localities (e.g., Zalisti, Zhukivtsi, Saryi Pochaiv) allows the understanding of the variation of the shape

of the shell, the degree of convexity of the teleoconch whorls and the sculpture. The figure in Eichwald (1850, 1851b, pl. 9, fig. 15) shows a specimen of *T. turricula* with flat-sided whorls, the last whorl roundly angled at periphery and with sculpture consisting of finely beaded spiral cords. However, the specimen illustrated in Eichwald (1859, pl. 9, fig. 18) has clearly convex whorls, with the last whorl rounded at periphery and distinctly-beaded spiral cords. Eichwald (1853, p. 229) in his species description said that the whorls are flat-sided (this is contrary to the illustrations in Eichwald 1859, pl. 9, fig. 18a, b) and sculptured by 5–6 nodular cords of equal strength. Eichwald's illustrations and material in the MZ collection show the high variability of *J. turricula*.

Among the Badenian specimens from Korytnica, on the basis of, *inter alia*, the number of spiral granular ribs, Bałuk (1975) distinguished the subspecies *Jujubinus (Jujubinus) turricula hoernesiana* Sacco, 1896 (six ribs per whorl) and *Jujubinus (Jujubinus) turricula turricula* (Eichwald, 1850) [sic] (five ribs per whorl). Because both forms are present together, a subspecies rank is impossible. Consequently, Landau *et al.* (2013) separated them at the species level into *J. turricula* and *J. hoernesianus*.

Comparison of *J. turricula* specimens from different locations shows differences between populations and allows for a conclusion that ornamentation depends on facies. Accordingly, the specimens from Korytnica (clays) and Roztocze (Węglin, Węglinek; marl and reef sediments) are dominated by those with a relatively finer spiral sculpture consisting of six cords per whorl. In the Ukrainian material, shells of the species from Rydomyl' (sands) are the most abundant and in a very good state of preservation. Among them the largest number of specimens has five spiral cords per whorl (174; Text-fig. 20A); other specimens (13) have six cords (Text-fig. 20C). The colour pattern of alternating brown and white, sometimes zig-zag axial stripes and spots on the base of the last whorl is clearly preserved in the shells.

The material from Varivtsi and Zalisti is different, because the beads on the spiral cords appear on the late teleoconch whorls in many shells. In specimens from Shushkivtsi and Zhukivtsi the spiral cords are of equal strength or vary slightly. In turn, in two specimens from Saryi Pochaiv the cord adjacent to the abapical suture is more prominent than the others (Text-fig. 20E).

Specimens from the Pleistocene of Ireon, Greece have a sculpture consisting of five beaded cords, of which the adapical and abapical ones are usually stronger than the others (Text-fig. 20H).



Setting a boundary between the extreme forms of *J. turricula* that look quite unlike is impossible because of the existence of transitional morphs. This was also noted by Hörnes (1856, p. 452), who observed the great variability in the shell sculpture of this species in the collection from the Vienna Basin.

Juvenile specimens of *J. turricula* were also found in the Sarmatian deposits of St. Margarethen, Austria (Harzhauser and Kowalke 2002). The amazing thing is that despite the conformity of the specimens described by the authors (6–8 spiral ribs on later whorls) with *J. (J.) turricula hoernesiana* of Bałuk (1975) they have, in their synonymy, taken into account only the subspecies *J. (J.) turricula turricula* of Bałuk (1975), which is characterised by the presence of five spiral ribs per whorl. Harzhauser and Kowalke (2002) amended the name to *J. turriculus*. They considered the word *turricula* an adjective, consequently replaced the grammatical ending for the female gender ‘-a’ with the masculine ending ‘-us’, creating in some measure an agreement in gender between the noun *jubinus* and the adjective ‘\**turriculus*’. In fact, the name *Jubinus turricula* is a compound of two nouns, between which there is no agreement in gender; these are two nouns in the nominative case related only by a logical connection. *Turricula* to *jubinus* is an attribute of substantive noun. Furthermore, The Lewis and Short Latin Dictionary and the Oxford Latin Dictionary note only the noun of *turricula*, -ae (fem.), but neither the adjective \**turriculus* nor a verb, from which the corresponding participle could be created. Therefore, the only possible conclusion is to consider the name *Jubinus turricula* as a logical combination of two nouns that retain their proper gender (i.e., masculine and feminine, respectively).

Previous authors (Andrzejowski 1833; Eichwald 1853; Hörnes 1856) pointed to the similarity of the discussed species to the very variable *Jubinus striatus* (Linnæus, 1758) (see e.g., Giannuzzi-Savelli *et al.* 1994, figs 303–315; Text-fig. 17F herein). Specimens most similar to *J. striatus* are those of *J. turricula*, which on the majority of the whorls have smooth cords, and indistinctly-beaded cords on the last two whorls.

Eichwald (1853, p. 230) discussed the similarity with *Trochus crenulatus* Brocchi, 1814 but clearly pointed out the differences. Specimens with abapical and often also adapical cords strengthened are indeed very similar to the holotype of *T. crenulatus*. The holotype of Brocchi’s species, from the ‘Quaternary (?)’ of the island of Ischia, Italy, was reillustrated by Pinna and Spezia (1978, pl. 56, fig. 2).

According to Rossi Ronchetti (1951, p. 6) and

Chirli (2004, p. 79) the name *Trochus crenulatus* Brocchi, 1814 is a junior subjective synonym of *Jubinus exasperatus* (Pennant, 1777). Today, *J. exasperatus* occurs in the area from the west coast of Scotland south to the Canary Islands, Madeira, Azores, and in the Mediterranean (Poppe and Goto 2001). This species is extremely variable in shape and coloration (see e.g., Giannuzzi-Savelli *et al.* 1994, figs 289–302). Molecular studies have shown that *J. exasperatus* is split into two distinct biogeographic lineages (NE Atlantic lineage and Mediterranean lineage), suggesting a cryptic diversity within this species (Uribe *et al.* 2017a).

Some specimens of *J. turricula* are very similar to the modern specimen labeled as *J. exasperatus* from Pellestrina (Venice), in the Adriatic Sea (see Text-fig. 20I; shell height 12.0 mm, shell width 8.0 mm). This fact and the occurrence of *J. turricula* in the Pleistocene of Greece suggest that this species may still exist today, but specimens of the species are identified as *J. exasperatus* by malacologists. The protoconch could be useful in separating the two species. Illustrations of Recent juvenile specimens of *J. exasperatus* given by Bandel (1975, pp. 85–88, pl. 1, figs 1–3, 7) show that, in contrast to *J. turricula*, it does not have a subterminal varix and a sinuous terminal lip.

Bałuk (2006, pp. 181, 182, pl. 2, fig. 3) identified seven specimens from the Badenian of Korytnica as *J. exasperatus*. Of the specimens at hand, two (including the illustrated specimen) have a protoconch with partially preserved sculpture, which is a hexagonal network of fine ridges (honeycomb pattern). This protoconch sculpture excludes the placement in *Jubinus* but is typical for *Calliostoma* (Hickman and McLean 1990, p. 109). The Korytnica specimens most likely represent a new, as yet unnamed species.

There is some similarity between specimens of *J. turricula* with five spiral beaded cords and *J. proximus* (Millet, 1865), a species known from the Tortonian of northwestern France (see Landau *et al.* 2017, pl. 22, figs 1–3), which also has five beaded cords per whorl. *Jubinus turricula* has a protoconch with a subterminal varix and a sinuous terminal lip, whereas these protoconch characters have not been observed in *J. proximus*. Moreover, *J. turricula* differs in being smaller-shelled (maximum shell height 13.5 mm for *J. turricula*; Friedberg 1928, p. 507 vs. 21.1 mm for *J. proximus*; Landau *et al.* 2017, p. 98) and having a much more variable surface sculpture.

OCCURRENCE: Middle Miocene of the Central Paratethys: Badenian of Poland (e.g., Bałuk 1975; Jakubowski 1977; Krach 1981; this study), Austria

(Hörnnes 1856; Glibert 1949a, 1962; Mandić *et al.* 2002), Romania (Boettger 1907), Slovakia (Švagrovský 1981) and western Ukraine (Eichwald 1830, 1851a, 1853; Andrzejowski 1833; Pusch 1837; Łomnicki 1895; Teisseyre 1900; Friedberg 1928, 1938; Kowalewski 1936b, 1937; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2); Paratethys: Sarmatian (= upper Serravallian) of Austria (Harzhauser and Kowalke 2002; Piller and Harzhauser 2005), western Ukraine (Teisseyre 1900; Friedberg 1938); north-eastern Atlantic: Serravallian of France (Cossmann and Peyrot 1917); Proto-Mediterranean Sea: upper Serravallian of Turkey (Landau *et al.* 2013). Upper Miocene of the Proto-Mediterranean Sea: Tortonian of Italy (Sacco 1896). Pleistocene of the Mediterranean Sea in Greece (this study).

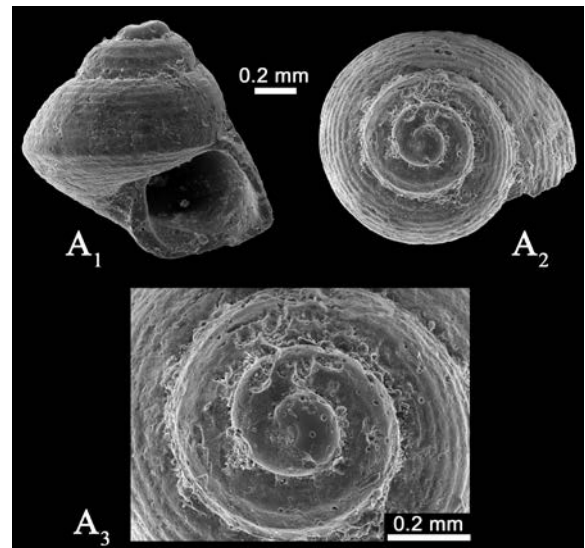
*Jujubinus vexans* (Boettger, 1907)  
(Text-fig. 21A)

1907. *Calliostoma (Strigosella) vexans* n. sp.; Boettger, p. 185, No. 636.  
1934. *Cantharidus (Jujubinus) vexans* (Boettger); Zilch, p. 202, pl. 2, fig. 34 (lectotype).  
1975. *Jujubinus (Strigosella) vexans* (Boettger); Bałuk, p. 42, pl. 4, figs 8–10.  
1981. *Jujubinus (Strigosella) vexans* (Boettger, 1907); Švagrovský, pp. 105, 106, pl. 33, fig. 10.  
1982. *Jujubinus (Strigosella) aff. vexans* (Boettger, 1907); Švagrovský, p. 8, pl. 1, fig. 5.  
2001. *Jujubinus vexans* (Boettger, 1907); Anistratenko and Anistratenko, p. 192.

**MATERIAL:** Sandy facies: Nadrichne, Ukraine (MZ VIII Mg 4655) 2 j.

**DESCRIPTION:** Shell small, trochiform, with low conical spire. Protoconch convex with apical back, abraded. Teleoconch whorls weakly convex to nearly flat-sided. Suture linear, impressed. Spiral sculpture consisting of closely-set, narrow cords, four on first teleoconch whorl, nine on last whorl; peripheral cord on last whorl slightly stronger. Spiral cords separated by narrow grooves. Prosocline growth lines hardly visible. Last whorl roundly angled at base. Base flattened, perforate, bearing eleven close-set spiral cords. Umbilicus narrow, with rounded edge. Inner lip without columellar fold. Aperture square in outline.

**REMARKS:** The two juvenile specimens, although poorly preserved, evidently belong to the indicated



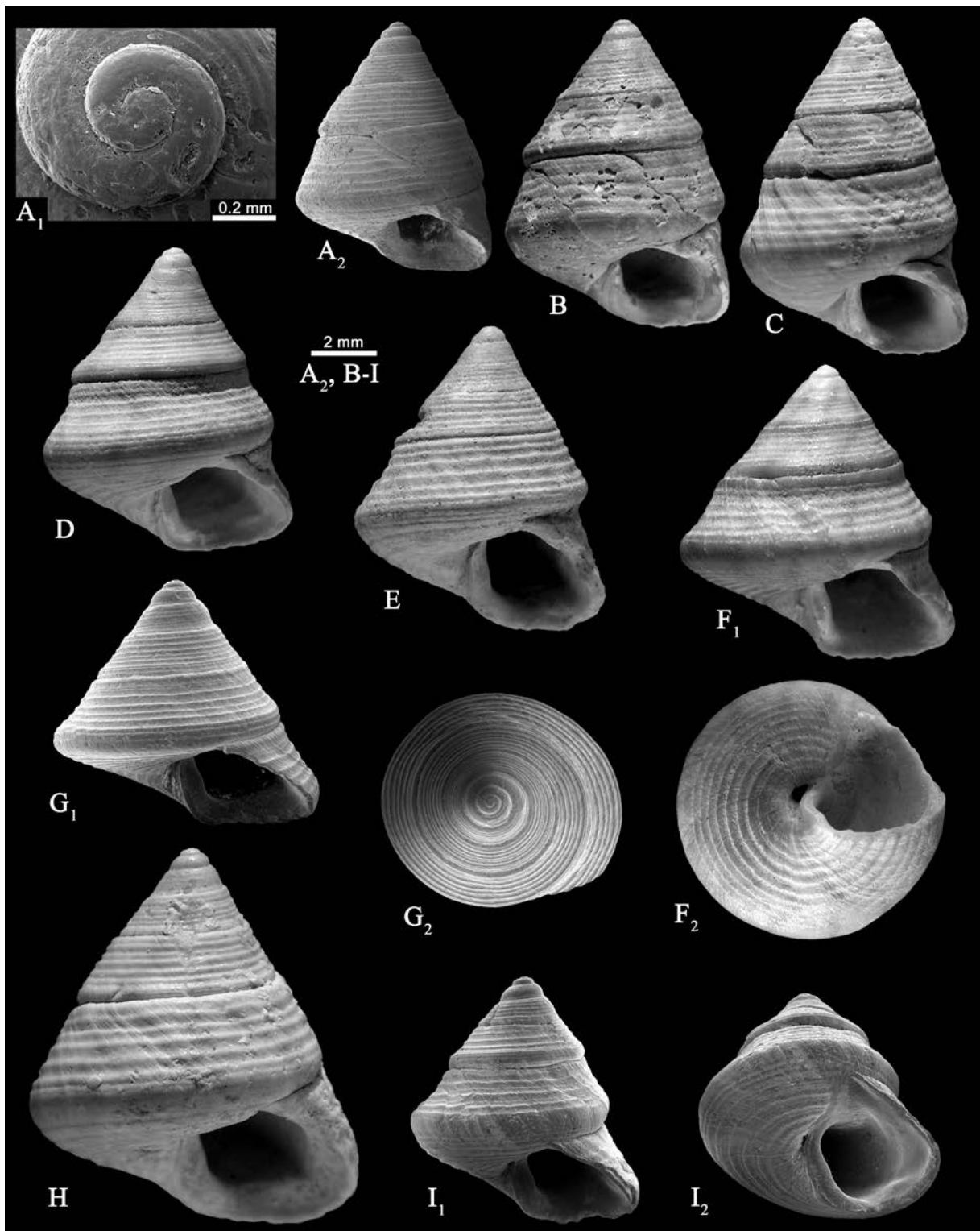
Text-fig. 21. *Jujubinus vexans* (Boettger, 1907) from the Badenian of Nadrichne, Ukraine; MZ VIII Mg 4655/1. A<sub>1</sub> – apertural view, A<sub>2</sub> – apical view, A<sub>3</sub> – apex in apical view. SEM images.

species. They are at the same growth stage, almost fully concordant both with the lectotype from the Badenian of Coștei, Romania (see Zilch 1934, pl. 2, fig. 34, SMF XII 2514 a; not seen) and specimens from Korytnica, Poland (MZ VIII Mg 4711, 4712). The Ukrainian specimens of *J. vexans* are very similar in shape and sculpture to *Calliostoma veliscense* Friedberg, 1938 from the Badenian salt of Wieliczka, Poland (Friedberg 1938, p. 55). However, the specimens of *C. veliscense* (ZNG PAN A-I-23/37) at hand have a flat protoconch and their spiral sculpture appears at a later growth stage than in *J. vexans*.

**OCCURRENCE:** Middle Miocene of the Central Paratethys: Badenian of Romania (Boettger 1907; Zilch 1934), Slovakia (Švagrovský 1981, 1982), Poland (Bałuk 1975; and this study) and western Ukraine (Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2).

*Jujubinus zukowcensis* (Andrzejowski, 1833)  
(Text-fig. 22A–I)

1833. *Trochus Zukowcensis* Pusch.; Andrzejowski, pp. 444, 445, pl. 13, fig. 2.  
1928. *Gibbula volhynica* Friedb. var.; Friedberg, p. 497, pl. 31, fig. 12.  
1928. *Callistoma Żukowcense* Andr.; Friedberg, pp. 511, 512, pl. 32, figs 13–17.  
1936b. *Callistoma żukowcense* Andr.; Kowalewski, p. 15.



Text-fig. 22. *Jujubinus zukowcensis* (Andrzejowski, 1833) from the Badenian of Ukraine and Poland. A, C – Pidhirtsi, Ukraine; A – MZ VIII Mg 4663/1, C – MZ VIII Mg 4663/2; B – Yaseniv, Ukraine, MZ VIII Mg 4657; D, F – Rydomyl', Ukraine; D – MZ VIII Mg 4664/1, F – MZ VIII Mg 4664/2; E – Zhukivtsi, Ukraine, MZ VIII Mg 4668/1; G – Zalistsi, Ukraine, MZ VIII Mg 4666/1; H – Oles'ko, Ukraine, MZ VIII Mg 4659/1; I – Węgliń, Poland, MZ VIII Mg 4707. A<sub>1</sub> – apex in apical view; A<sub>2</sub>, B, C, D, E, F<sub>1</sub>, G<sub>1</sub>, H, I<sub>1</sub> – apertural views; F<sub>2</sub> – umbilical view; G<sub>2</sub> – apical view; I<sub>2</sub> – oblique umbilical view. A, G, I are SEM images.



- 1937. *Calliostoma Żukowcense* Andr.; Kowalewski, p. 8.
- 1938. *Calliostoma żukowcense* Andr.; Friedberg, p. 55.
- 1968. *Calliostoma zukowcense* (Andrzejowski, 1833); Kulichenko and Sorochan, p. 122, pl. 32, figs 16, 17 (figures from Friedberg 1928, pl. 32, figs 14, 15).
- 1981. *Calliostoma żukowcense* (Andrzejowski 1833); Krach, pp. 44, 45, pl. 14, figs 2–10.
- 2001. *C.[olliculus] zukowcensis* (Andrzejowski, 1833); Anistratenko and Anistratenko, p. 192.

**MATERIAL:** Sandy facies: Bilozirka (MZ VIII Mg 4656) 1 fp; Yaseniv (MZ VIII Mg 4657) 1 a; Kalaharivka (MZ VIII Mg 4698) 1 a, 2 fp; Korostova (MZ VIII Mg 4658) 2 af, 7 j; Oles'ko (MZ VIII Mg 4659–4661, 4699) 13 a, sa, 14 j; Pidhirtsi (MZ VIII Mg 4662, 4663, 4700) 83 sh; Rydomyl' (MZ VIII Mg 4664) 7 a, sa; Vanzhuliv (MZ VIII Mg 4701) 1 a, 1 af; Zalistsi (MZ VIII Mg 4665, 4666) 1 a, 1 sa, 5 j; Zalistsi – Zhabiak ravine (MZ VIII Mg 4667) 2 a; Zhukivtsi (MZ VIII Mg 4668) 2 a. Carbonate deposits: Lidykhiv (MZ VIII Mg 4669) 24 a and sa, 2 jf; Staryi Pochaiv (MZ VIII Mg 4670) 15 a and sa. All specimens are from western Ukraine.

**DESCRIPTION:** Shell of medium size, thick, conical. Suture linear, impressed. Surface covered with fine, irregular spiral cords and threads crossed by closely-set prosocline growth lines. Protoconch abraded, apical beak visible in some specimens. Sculpture on first teleoconch whorl of four rounded spiral cords, increasing in number to ten on second teleoconch whorl. On later whorls number of primary cords variable, six to seven, rarely eight, usually five on lateral flank of last whorl. Spiral cord adjacent to adapical suture strengthened in some specimens. Teleoconch whorls with periphery at abapical suture, first three whorls convex, later whorls concave, rarely flat-sided. Periphery of later whorls usually marked by swell, which overhangs suture. Base bearing flattened spiral cords (eleven on specimen MZ VIII Mg 4657, Text-fig. 22B; seven on specimen MZ VIII Mg 4663/2, Text-fig. 22C). Umbiliculus absent or slit-like; in juvenile specimens always present. Oblique aperture in quadrangle form, lower part of peristome thickened, outer lip with bevelled edge. Columella bearing swelling in some specimens. Interior nares. Colour pattern of fine, diagonal stripes preserved in many shells (see Text-fig. 22F).

**REMARKS:** The type material of *T. zukowcensis* is probably present in the KNUSH collection, from Zhukivtsi, Ukraine. This species has been placed by most authors in the genus *Calliostoma*. However, the

placement of this species within the genus *Jujubinus* seems more appropriate. Unfortunately, the protoconch is not well preserved in the studied specimens, but they do not seem to have a protoconch typical for *Calliostoma* (see below).

The abundant material at hand of *J. zukowcensis* from the Badenian of western Ukraine in the MZ and ZNG PAN collections shows great variability in shell shape, size and sculpture.

As seen in the series illustrated, the shells can be squat (Text-fig. 22F, G) to relatively slender (Text-fig. 22C). The height/width ratio of measured Ukrainian specimens of *J. zukowcensis* is 1.01–1.47. The squat specimens of this species are very similar to slender specimens of *G. novemcincta*, presented herein, but differ from them primarily in the size of the umbiliculus as well as the colour pattern.

Krach (1981, pp. 44, 45, pl. 14, figs 2–10) showed the variation within the population *J. zukowcensis* from the carbonate facies of Roztocze, Poland. Among several hundred specimens from there in the MZ collection, specimens with the swollen whorl periphery which overhangs the suture (see Text-fig. 22I) are few.

Some specimens of *J. zukowcensis* (e.g., Text-fig. 22F) are similar to *Jujubinus pigeonblancensis* Ceulemans, Van Dingenen and Landau, 2016 from the early Pliocene of northwestern French Atlantic (see Ceulemans *et al.* 2016, pl. 3, figs 2–4), but differ in having fewer and stronger spiral cords, which are not beaded.

**OCCURRENCE:** Middle Miocene of the Central Paratethys: Badenian of Poland (Krach 1962, 1981; this study) and western Ukraine (Andrzejowski 1833; Friedberg 1928, 1938; Kowalewski 1936b, 1937; Amitrov 1961; this study; for details see Appendix 2).

#### Genus *Paroxystele* Schultz, 1969

**TYPE SPECIES:** *Trochus patulus* Brocchi, 1814, by original designation. Neogene, Italy.

**REMARKS:** The subgenus *Paroxystele* established by Schultz (1969) in the genus *Diloma* Philippi, 1845, was raised to generic rank by Anistratenko and Anistratenko (2001), Lozouet *et al.* (2001), Harzhauser (2002), Landau *et al.* (2003, 2013, 2017), Ceulemans *et al.* (2016) and Thivaiou *et al.* (2019). *Paroxystele* was again included within the genus *Diloma* by Mikuž (2009). Nevertheless, the Recent *Diloma nigerrimum* (Gmelin, 1791), the type species of *Diloma*

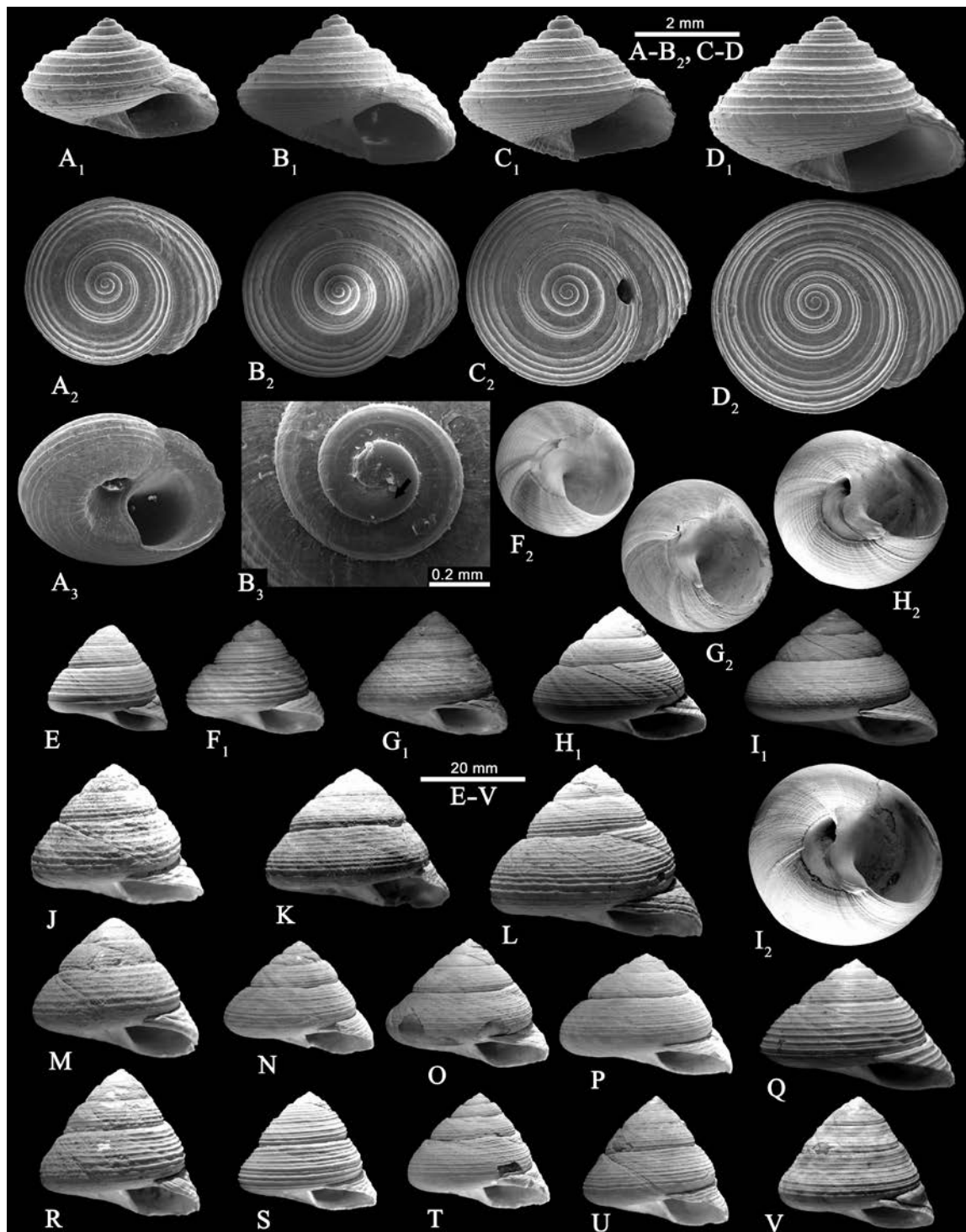
(Monodontinae), has a completely different shell from European representatives of *Paroxysteles*. Moreover, the speciose nature of *Diloma* in New Zealand and its wide distribution in the Pacific (Donald *et al.* 2005) implies that *Paroxysteles* should not be combined with this genus. Schultz (1969, 1971) found that *Paroxysteles* in modern seas is represented by *Diloma (Paroxysteles) sauciata* (Koch in Philippi, 1845). Based on molecular evidence, the species *sauciata* has recently been moved into the genus *Phorcus* Risso, 1826 (Donald *et al.* 2012; MolluscaBase 2019), which is placed in the subfamily Cantharidinae (Williams *et al.* 2010; Donald *et al.* 2012; Uribe *et al.* 2017a). Therefore, placement of *Paroxysteles* in the subfamily Umboniinae by Lozouet *et al.* (2001) and Harzhauser (2002) or in the Trochinae by Landau *et al.* (2003, 2013) seems inappropriate, especially because only one umboniine species lives in European seas. This is *Umbonium vestiarium* (Linnæus, 1758) occurring in the Eastern Mediterranean where it was introduced via the Suez Canal (Poppe and Goto 1991) from the Indo-West Pacific. Recently, Ceulemans *et al.* (2016) and Landau *et al.* (2017) placed *Paroxysteles* in the subfamily Cantharidinae, without further comment.

According to Schultz (1969, p. 218), the shell characters of *Paroxysteles* are: “Spiralskulptur auch auf dem letzten Umgang” and “zumindest juvenil genabelt; auch adult meist mit Hohlspindel, die zum Teil durch den Spindelkallus ausgefüllt wird”. Schultz (1971) listed many species and subspecies of the subgenus *Paroxysteles* from the Neogene deposits of Europe and showed their stratigraphic range and palaeogeographic distribution. *Paroxysteles* is known from the Miocene of both the northeastern Atlantic and the Proto-Mediterranean Sea, and also of both the Central and Eastern Paratethys, from the Pliocene of both the northeastern Atlantic and Proto-Mediterranean Sea, and from the Pleistocene of the Mediterranean (see e.g., Schultz 1971; Iljina 1993; Landau *et al.* 2003). It seems that the genus *Paroxysteles* was already present during the late Oligocene in European faunas (Lozouet 1986 after Landau *et al.* 2013). *Paroxysteles* is not associated with any particular facies. Various species of this genus were recorded from clay (e.g., Bałuk 1975), sandy (e.g., Katona *et al.* 2011) and carbonate deposits (e.g., Krach 1981; Saint Martin *et al.* 2000).

*Paroxysteles orientalis* (Cossmann and Peyrot, 1917)  
(Text-fig. 23A–V)

1830. *T.[rochus] sulcatus*, m; Eichwald, p. 221 [non *Trochus sulcatus* Lightfoot, 1786].

1830. *Trochus carinatus*; von Buch, p. 130 [non *Trochus carinatus* Borson, 1821].
1830. *Trochus patulus*; von Buch, p. 132 [non *Paroxysteles patulum* (Brocchi, 1814)].
1831. *Trochus patulus*. Brocchi.; du Bois de Montpéroux, p. 39, pl. 2, figs 31–33 [non *Paroxysteles patulum* (Brocchi, 1814)].
1837. *Tr.[ochus] patulus* Brocchi; Pusch, p. 109 [non *Paroxysteles patulum* (Brocchi, 1814)].
1850. [*Trochus patulus* Brocchi]; Eichwald, pl. 9, fig. 5 (atlas) [non *Paroxysteles patulum* (Brocchi, 1814)].
- 1851a. *Troch.[us] patulus* Brocchi; Eichwald, pp. 110, 281 [non *Paroxysteles patulum* (Brocchi, 1814)].
- 1851b. [*Trochus patulus* Brocchi]; Eichwald, pl. 9, fig. 5 (atlas) [non *Paroxysteles patulum* (Brocchi, 1814)].
1853. *Troch.[us] patulus*. Brocchi.; Eichwald, pp. 216–218 [non *Paroxysteles patulum* (Brocchi, 1814)].
1856. *Trochus patulus* Brocc.; Hörnes, pp. 458–460, pl. 45, fig. 14 [non *Paroxysteles patulum* (Brocchi, 1814)].
1859. *Trochus patulus* Brocchi; Eichwald, p. 3, pl. 9, fig. 5 (atlas) [non *Paroxysteles patulum* (Brocchi, 1814)].
1867. *Tr.[ochus] patulus* Brocchi.; Reuss, p. 162 [non *Paroxysteles patulum* (Brocchi, 1814)].
1903. *Trochus patulus* Brocchi.; Mikhailovsky, pp. 69, 228, pl. 4, figs 5, 6 [non *Paroxysteles patulum* (Brocchi, 1814)].
1912. *Trochus (Oxysteles) Amedei* Brongniart.; Schaffer, p. 171, pl. 54, figs 36–39 [non *Paroxysteles amadei* (Brongniart, 1823)].
1917. *O.[xysteles] orientalis* C. et P.; Cossmann and Peyrot, p. 102.
1918. *Oxysteles orientalis* Cossm. et Peyr.; Cossmann, p. 213, pl. 8, figs 9, 10.
1928. *Oxysteles orientalis* Cossm. et Peyr.; Friedberg, pp. 516–518, pl. 33, figs 4–7.
- 1936b. *Oxysteles orientalis* Cossm. i Peyr.; Kowalewski, p. 15.
1937. *Oxysteles orientalis* Cossm.; Kowalewski, p. 8.
1938. *Oxysteles orientalis* Cossm. et Peyr.; Friedberg, p. 58.
1955. *Oxysteles orientalis* Cossm. et Peyrot; Korobkov, p. 98, pl. 4, figs 16–18 [figures from Friedberg 1928, p. 98, pl. 33, figs 4, 5, 7b].
1960. *Oxysteles orientalis* Cossmann et Peyrot 1917; Kojumdgieva, p. 87, pl. 29, fig. 1.
1961. *Oxysteles orientalis* Cosm. et Peyr.; Florei, p. 680, pl. 6, fig. 36.
1962. *Oxysteles patula orientalis* Cossmann & Peyrot; Strausz, p. 126, fig. 150a.



Text-fig. 23. *Paroxystele orientalis* (Cossmann and Peyrot, 1917) from the Badenian of Ukraine. A – Yaseniv; MZ VIII Mg 4591/1; B–D, F, G – Rydomyl'; B – MZ VIII Mg 4604/1, C – MZ VIII Mg 4604/2, D – MZ VIII Mg 4604/3, F – MZ VIII Mg 4604/4, G – MZ VIII Mg 4604/5; E – Chepeli; MZ VIII Mg 4589/1; H, I, M–P, R–U – Zalistsi; H – MZ VIII Mg 4608/1, I – MZ VIII Mg 4608/2, M – MZ VIII Mg 4609/8, N – MZ VIII Mg 4609/3, O – MZ VIII Mg 4609/1, P – MZ VIII Mg 4609/2, R – MZ VIII Mg 4609/7, S – MZ VIII Mg 4609/6, T – MZ VIII Mg 4609/5, U – MZ VIII Mg 4609/4; J–L, Q – Varivtsi; J – MZ VIII Mg 4694/1, K – MZ VIII Mg 4694/2, L – MZ VIII Mg 4694/3, Q – MZ VIII Mg 4694/4; V – Zalistsi – Zhabiak ravine; MZ VIII Mg 4695/1. A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub>, D<sub>1</sub>, E, F<sub>1</sub>, G<sub>1</sub>, H<sub>1</sub>, I<sub>1</sub>, J–V – apertural views; A<sub>2</sub>, B<sub>2</sub>, C<sub>2</sub>, D<sub>2</sub> – apical views; A<sub>3</sub> – shell base in oblique view; B<sub>3</sub> – details of juvenile whorls in apical view, black arrow indicates demarcation between protoconch and teleoconch; F<sub>2</sub>, G<sub>2</sub>, H<sub>2</sub>, I<sub>2</sub> – umbilical views. A–D are SEM images.



1966. *Oxystele patula orientalis* Cossmann & Peyrot, 1917; Strausz, p. 40, fig. 24.
1968. *Oxystele orientalis* Cossmann et Peyrot, 1917; Kulichenko and Sorochan, p. 105, pl. 28, figs 15, 16 [figures from Friedberg 1928, pl. 33, figs 4a, 7a].
1968. *Diloma (Oxystele) orientalis* (Cossmann et Peyrot, 1917); Hinculov, p. 119, pl. 27, figs 1–5.
1970. *Oxystele orientalis* Cossmann et Peyrot; Bałuk, p. 117, pl. 8, fig. 7.
1971. *Oxystele orientalis* Cossmann et Peyrot; Eremija, p. 65, pl. 6, fig. 9.
1975. *Diloma (Paroxystele) amedei* (Brongniart, 1823); Bałuk, p. 31, pl. 6, fig. 8.
1975. *Diloma (Paroxystele) orientalis* (Cossmann et Peyrot, 1917); Bałuk, p. 32, pl. 6, fig. 9.
1981. *Diloma (Paroxystele) orientale* (Cossmann et Peyrot, 1916); Švagrovský, pp. 104, 105, pl. 32, figs 5–7.
- part 1981. *Oxystele orientalis* Cossmann et Peyrot 1917; Krach, p. 45 [non pl. 13, figs 3, 4 = *Gibbula miocaenica* (Mayer, 1853)].
1993. *Diloma (Paroxystele) orientalis* (Cossmann et Peyrot, 1917); Iljina, p. 32, pl. 1, figs 10–14.
2001. *Paroxystele orientalis* (Cossmann et Peyrot, 1917); Anistratenko and Anistratenko, p. 192.
2009. *Diloma (Paroxystele) orientalis* (Cossmann & Peyrot, 1916); Mikuž, p. 8, pl. 1, fig. 1.
2013. *Paroxystele orientale* (Cossmann et Peyrot, 1917); Landau *et al.*, pp. 28, 29, pl. 1, fig. 8.
2019. *Paroxystele orientale* (Cossmann et Peyrot, 1917); Thivaoui *et al.*, p. 327, fig. 3A1–A4.

**MATERIAL:** Sandy facies: Bilozirka (MZ VIII Mg 523, 4588) 1 sa, 13 j; Chepeli (MZ VIII Mg 4589) 25 sh; Nadrichne (MZ VIII Mg 4590) 4 sh; Yaseniv (MZ VIII Mg 4591, 4592) over 100 sh; Kalaharivka (MZ VIII Mg 4690) 1 a, 1 sa; Korostova (MZ VIII Mg 4593) 2 j; Ohryzkivtsi (MZ VIII Mg 4594) 1 j; Oles'ko (MZ VIII Mg 4595–4600, 4691) over 100 sh; Pidhirtsi (MZ VIII Mg 4601–4603, 4692) over 100 sh; Rydomyl' (MZ VIII Mg 4604) over 100 sh; Shushkivtsi (MZ VIII Mg 4605) over 100 sh; Vanzhuliv (MZ VIII Mg 4693, 4606) 53 sh; Varivtsi (MZ VIII Mg 4694) 58 sh; Vyshhorodok (MZ VIII Mg 4607) 1 j; Zalistsi (MZ VIII Mg 521, 4608, 4609) over 100 sh; Zalistsi – Zhabiak ravine (MZ VIII Mg 2860, 4695) 42 sh; Dzvyniacha (MZ VIII Mg 4610) 1 j; Zhukivtsi (MZ VIII Mg 522) 8 j. Carbonate deposits: Lidykhiv (MZ VIII Mg 4611) 2 j; Staryi Pochaiv (MZ VIII Mg 4612) 1 j. All specimens are from western Ukraine.

**DESCRIPTION:** Shell large, trochiform, with high

or slightly depressed spire and flattened base. Spiral sculpture of closely-set cords and threads of irregular strength and position. Protoconch with apical beak. Protoconch/teleoconch boundary barely visible, sinuous?, fractured. Teleoconch starting with growth lines. Three to four spiral cords appearing in latter part of first teleoconch whorl. Number of spiral cords of variable strength meaningfully increasing with ontogeny. Micropustules present close to adapical suture on early teleoconch whorls. Axial sculpture restricted to fine, strongly prosocline growth lines, more closely-set towards aperture. Teleoconch whorls weakly convex, flat or sometimes concave. Narrow ramp in the adapicalmost part of whorls present in the same specimens. Suture linear, impressed. Last whorl depressed, roundly angled at periphery. Base almost flat with fine concentric cords, sometimes nearly smooth. Aperture quadrangular; outer lip sharp edged, joining penultimate whorl below periphery. Columella oblique. Umbilicus filled with large callus with a slit-like orifice on the rim. Juvenile specimens with open, deep umbilicus with crenated margin. Interior nacreous. Some specimens almost completely brown, others with colour pattern of vertical stripes or small spots, or irregular broad flammules.

**REMARKS:** Eichwald introduced two species names for a single new species from the Miocene of Ukraine, *Trochus carinatus* and *Trochus sulcatus*, which were preoccupied for two other species (see Eichwald 1851a, 1853 and the synonymy above). According to Eichwald (1853, pp. 216, 217, footnote), *T. carinatus* is the oldest name for this species. However, this species name was published by von Buch (1830), somewhat later than the species name *T. sulcatus* introduced by Eichwald (1830) (for exact publication dates see remarks for *G. puschii*). Later, Eichwald (1851a, p. 110) considered the Ukrainian Miocene specimens to be conspecific with the Pliocene species *Trochus patulus* Brocchi, 1814, but with some doubts. Cossmann and Peyrot (1917) recognised that specimens described by Eichwald (1851a, 1853) and Hörnes (1856) as *T. patulus* were distinctly different from those from the Pliocene and represent separate species. Consequently, they proposed *Oxystele orientalis* as a new species name for specimens from the Miocene of the Paratethys.

The discussed species was placed by many authors in *Oxystele* (see synonymy above), but it seems inappropriate because Donald *et al.* (2005) showed that this genus is endemic to southern Africa.

*Paroxystele orientalis* is a very common species in European Miocene sediments. The shells of this

species show a wide range of intraspecific variability. Iljina (1993, pl. 1, figs 10–12) illustrated the considerable variation in the slenderness of the shells of discussed species from the Konkian (middle Miocene) of the Molkuduk (Ustyurt Plateau, Kazakhstan). Bałuk (1975), however, having only two specimens from the Badenian of Korytnica, Poland identified the less slender shell with convex whorls as *Diloma (Paroxystele) amedei* (Brongniart, 1823), while the slimmer shell and somewhat tierlike in outline with flattened whorls as *Diloma (Paroxystele) orientalis* (Cossmann and Peyrot, 1917). I have examined a large number of specimens and found that apart from the shells that correspond to the above-described forms, many intermediate shells are also present. In addition, the specimens show a wide range of variability in the spiral sculpture. Apart from specimens with relatively few strong spiral cords (Text-fig. 23J) there are specimens with very numerous fine spiral cords (Text-fig. 23H). Moreover, in some specimens, among others from Oles'ko and Rydomyl', there is no slit-like orifice on the callus rim. The same range of shell variability as seen in the series illustrated herein, is also seen in Eichwald's and Friedberg's collections. The enormous degree of variability of *P. orientalis* is of no exception. It has also been observed in the shells of other *Paroxystele* species. A highly polymorphic shell occurs in the Plio–Pleistocene *Paroxystele patulum* (Brocchi, 1814) (Landau *et al.* 2003, p. 51). The differences between the shells of *P. orientalis* and other Miocene *Paroxystele* species were discussed by Landau *et al.* (2013).

Specimens of the species *P. orientalis* in the SPbGU collection were labeled by Eichwald as *Trochus patulus* Br. – *sulcatus* m. According to the labels, five specimens (SPbGU 3/397, 3/398, 3/399, 3/400, 3/402) are from Zhukivtsi and two specimens (SPbGU 3/343, 3/404) are from Poczajów. The latter locality, with regard to species discussed herein, is not listed in Eichwald (1830, 1851a, 1853).

**OCCURRENCE:** Lower Miocene of the Proto-Mediterranean Sea: Aquitanian of Greece (Thivaïou *et al.* 2019); Central Paratethys: Eggenburgian of Austria (Schaffer 1912). Middle Miocene of the Central Paratethys: Badenian of Poland (e.g., Bałuk 1975; Krach 1981; MZ collection), Austria (Hörnès 1856; Cossmann 1918; Glibert 1962; Zuschin *et al.* 2007), Czech Republic (Hörnès 1856), Slovakia (Hörnès 1856; Švagrovský 1981), Bulgaria (Kojumdgieva 1960), Romania (Florei 1961; Hinculov 1968), Hungary (Csepregy-Meznerics 1954, 1969b; Strausz 1966), Slovenia (Mikuž 2009), Bosnia and Herzegovina

(Eremija 1971), Moldova (Iljina 1993; Anistratenko and Anistratenko 2001), and western Ukraine (von Buch 1830; du Bois de Montpéreux 1831; Eichwald 1830, 1851a, 1853; Friedberg 1928, 1938; Kowalewski 1936b, 1937; Kulichenko and Sorochan 1968; Iljina 1993; Anistratenko and Anistratenko 2001; and this study; for details see Appendix 2); Eastern Paratethys: Tarkhanian of southern Ukraine (Mikhailovsky 1903; Anistratenko and Anistratenko 2001), Konkian of Russia (western Ciscaucasia), Georgia, Kazakhstan (Iljina 1993; Anistratenko and Anistratenko 2001); Paratethys: Sarmatian (= upper Serravallian) of western Ukraine and Moldova (Anistratenko and Anistratenko 2001); Proto-Mediterranean Sea: upper Serravallian of Turkey (Landau *et al.* 2013).

#### Family Calliostomatidae Thiele, 1924 (1847)

**REMARKS:** Calliostomatines were treated for a long time as a subfamily of Trochidae (e.g., Wenz 1938; Knight *et al.* 1960; Hickman and McLean 1990; Sladkovskaya 2017). Nevertheless, some authors have raised them to familial rank (e.g., Golikov and Starobogatov 1975; Marshall 1995; Bouchet *et al.* 2005) and this status was confirmed by the molecular studies of Williams *et al.* (2008, 2010) and Williams (2012). According to Bouchet *et al.* (2017) and the MolluscaBase (2019), the Calliostomatidae includes five Recent subfamilies, of which only the Calliostomatinae Thiele, 1924 (1847) are represented by the species described herein.

In almost all Calliostomatidae genera, the protoconch has a honeycomb pattern; exceptions include e.g., *Margarella* Thiele, 1893 (see Williams 2012 and references therein) and *Xeniostoma* McLean, 2012 (see McLean 2012). The research carried out by Marshall (1995, p. 83) showed that “calliostomatid shell morphology tends to become more variable with increasing size/age, so that species with dissimilar early teleoconchs can be superficially similar at maturity and vice versa.”

This family comprises about 250 extant species, which are distributed in all oceans (Marshall 1995), from tropics to polar latitudes, but many of them exhibit distinct local endemism (Marshall 1988, 1995). They occur from the intertidal to bathyal depths, mostly on rocky ground (Marshall 1995). Species of Calliostomatidae are carnivores, feeding on coelenterates, sponges, tunicates (Hickman and McLean 1990), possibly even small molluscs (Dornellas and Simone 2011) and also carrion (Marshall 1995). The exception, taking into account the diet, is *Xeniostoma*

*inexpectans* McLean, 2012 whose radular morphology indicates detritivory. This family is recognised in a strict sense in the Late Cretaceous (Hickman and McLean 1990), but according to Williams *et al.* (2008) diversified at 41 Ma (Eocene).

#### Subfamily Calliostomatinae Thiele, 1924 (1847)

REMARKS: The subfamily Calliostomatinae includes 18 accepted Recent genera (MolluscaBase 2019). Most of them occur in Australia and New Zealand, so in this region, the Calliostomatinae show great morphological diversity. On the other hand, only one genus, namely *Calliostoma*, was recognised in European seas (see Poppe and Goto 1991).

Calliostomatinae shells were characterised in detail by Hickman and McLean (1990). However, it is noteworthy that, although the calliostomatine shell is very similar to that of the Thysanodontinae, it is distinguishable by having three or four primary spirals of similar sizes on the first teleoconch whorls, unlike thysanodontines in which shells have a strong carina on the first 1.5 to 2.5 whorls (Marshall 1988). The first report of the Thysanodontinae in European faunas was provided by Landau *et al.* (2017).

Calliostomatine-like shells are present in Triassic and Jurassic faunas, but this subfamily is not recognised in a strict sense until the Late Cretaceous (Hickman and McLean 1990).

#### Genus *Calliostoma* Swainson, 1840

TYPE SPECIES: *Trochus conulus* Linnæus, 1758 by subsequent designation of Herrmannsen (1846). Recent, north-eastern Atlantic, Mediterranean Sea.

REMARKS: *Calliostoma* is diagnosed as the subfamily Calliostomatinae by anatomical and radular characters (for details see Hickman and McLean 1990; Willan 2002) and by shells that were described (Willan 2002, p. 9) as follows: “conical (shaped like a spinning top) as is generally characteristic for all trochoideans with an oblique aperture and all have an oblique angle where the relatively straight columella meets the lower section of the outer lip. The outer lip is generally not thickened and is never denticulate. There is generally a sharp peripheral demarcation, which may be reinforced with a thickened spiral cord, between the spire and the base of the shell. Spiral cords, either smooth or ornamented with regular nodules, are the predominant sculptural component on the exterior of the shell. The honeycomb-like microsculpture on the protoconch of

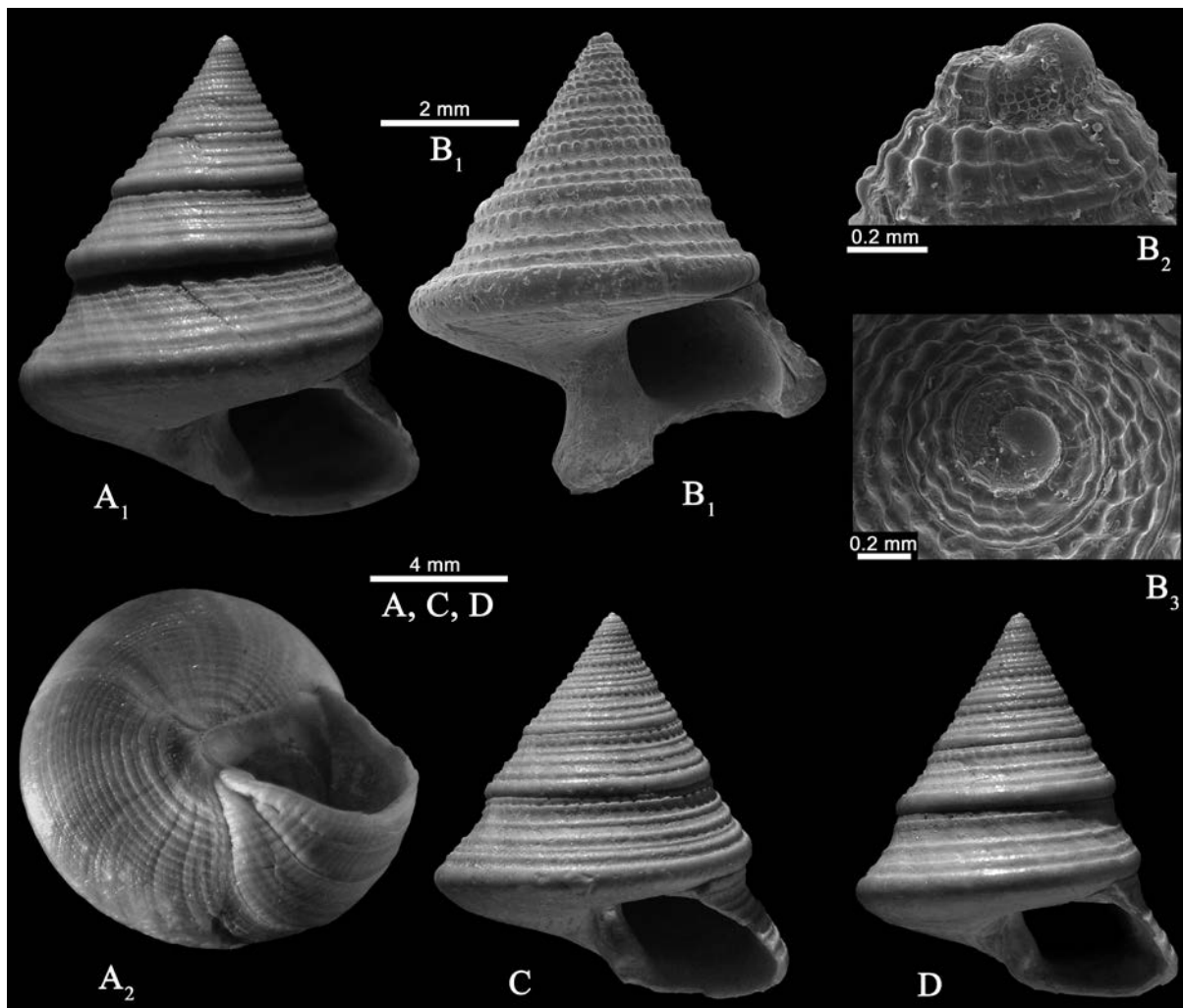
the shell is a derived character diagnosing the family”. Photographs of *Calliostoma* protoconchs have been presented by e.g., Bandel (1982), Cretella *et al.* (1990), Hickman and McLean (1990), Hickman (1992), Marshall (1995), Marquet (1998), Sasaki (1998), Landau *et al.* (2003, 2017) and Ceulemans *et al.* (2016).

*Calliostoma* is distributed worldwide, from shallow waters to bathyal depths. Species of this genus occur mainly on hard substrates, although Japanese species have been found also on sandy bottoms (Williams *et al.* 2010). Almost 100 valid Recent species of *Calliostoma* are known from the western Atlantic, 36 species occur in the eastern Pacific (Quinn 1992), and only 13 species were mentioned by Poppe and Goto (1991) from European seas – recently, two of them, i.e., ‘*Calliostoma wiseri*’ (Calcara, 1842) and ‘*Calliostoma miliaris*’ (Brocchi 1814) were transferred to other genera (see MolluscaBase 2019).

*Calliostoma s.l.* was identified in the Early Cretaceous, however this genus is identified in a strict sense only since the Late Cretaceous (Hickman and McLean 1990). According to Hickman and McLean (1990), *Calliostoma* is well represented in Palaeogene and Neogene faunas. Recently, many *Calliostoma* species were described from the upper Miocene (Landau *et al.* 2017, 22 species) and the lower Pliocene (Ceulemans *et al.* 2016, 6 species) deposits of northwestern France. Anistratenko and Anistratenko (2001) listed as many as 43 species of *Calliostoma* from the Miocene of Ukraine. Later, however, Anistratenko and Anistratenko (2012) transferred almost all Sarmatian species which were previously assigned to *Calliostoma* to the genus *Gibbula*, without further comment. Sarmatian Trochidae from the Eastern Paratethys were revised recently by Sladkovskaya (2017), who continued to include there the subfamilies Trochinae and Calliostomatinae. As a result, out of 42 described species, Sladkovskaya (2017) assigned only one species to the genus *Calliostoma*, but with doubt, because she did not have any information on its protoconch. She did not provide any protoconch illustrations, but noted that “Sarmatian trochids have homeostrophic oligospiral (about one and a half whorls) protoconchs with the rounded convex smooth whorls seen in a light microscope” (Sladkovskaya 2017, p. 1462).

Some fossil species considered as belonging to *Calliostoma* should be reviewed with special emphasis on the protoconch sculpture. This problem is well illustrated by ‘*Trochus miliaris*’ Brocchi, 1814, known from the early Miocene to Recent (see





Text-fig. 24. *Calliostoma trigonum* (Eichwald, 1830) from the Badenian of Rydomyl', Ukraine; A – MZ VIII Mg 4674/1, B – MZ VIII Mg 4674/2, C – MZ VIII Mg 4674/3, D – MZ VIII Mg 4674/4). A<sub>1</sub>, B<sub>1</sub>, C, D – apertural views; A<sub>2</sub> – basal view; B<sub>2</sub> – apex in lateral view; B<sub>3</sub> – apex in apical view. B<sub>1</sub>–B<sub>3</sub> are SEM images.

Landau *et al.* 2013); it is often referred to *Calliostoma* (e.g., Glibert 1962; Landau *et al.* 2003, 2013), but its smooth protoconch (see Cretella *et al.* 1990, fig. 13) indicates that the species does not belong in this genus. Cretella *et al.* (1990) have assigned the taxon to *Clelandella* Winckworth, 1932 (now allocated to Cantharidinae), and this status is accepted by Gofas (2005) and MolluscaBase (2019).

So far, only two species from the Badenian of the Fore-Carpathian Basin belonging to the genus *Calliostoma* have been confirmed by protoconch sculpture. They are: *Calliostoma trigonum* (Eichwald, 1830), the species described below, and possibly a new, yet unnamed species whose specimens were identified by Bałuk (2006) as *Jujubinus exasperatus* (see remarks for *J. turricula*).

*Calliostoma trigonum* (Eichwald, 1830)  
(Text-fig. 24A–D)

1830. *T.[rochus] trigonus*, m.; Eichwald, p. 220.  
 1831. *Trochus semigranulatus*. nov.; du Bois de Montpèreux, pp. 40, 41, pl. 3, figs 7, 8.  
 1837. *Trochus semigranulatus* Dubois Var.  $\beta$  m.; Pusch, p. 108, pl. 10, fig. 10.  
 1850. [*Trochus trigonus* m.]; Eichwald, pl. 9, fig. 21 (atlas).  
 1851a. *Troch.[us] trigonus* m.; Eichwald, pp. 115, 282.  
 1851b. [*Trochus trigonus* m.]; Eichwald, pl. 9, fig. 21 (atlas).  
 1853. *Troch.[us] trigonus* m.; Eichwald, pp. 231, 232.  
 1859. *Trochus trigonus*; Eichwald, p. 3, pl. 9, fig. 21 (atlas).

- part 1928. *Callistoma trigonum* Eichw.; Friedberg, pp. 506, 507, pl. 32, figs 1–4.
- 1936b. *Callistoma trigonum* Eichw.; Kowalewski, p. 15.
1937. *Callistoma trigonum* Eichw.; Kowalewski, p. 8.
- part 1938. *Callistoma trigonum* Eichw.; Friedberg, p. 54.
1962. *Calliostoma trigonum* Eichwald; Strausz, pp. 53, 54, pl. 13, figs 8, 9.
1966. *Calliostoma trigonum* Eichwald, 1830; Strausz, p. 34, pl. 13, figs 8, 9.
1968. *Calliostoma trigona* (Eichwald, 1830); Kulichenko and Sorochan, p. 121, pl. 32, figs 11, 12 [figures from Friedberg 1928, pl. 32, figs 2, 3].
- part 1977. *Calliostoma trigonum* (Eichwald, 1830); Jakubowski, p. 107, pl. 13, figs 14, 15 [non pl. 13, figs 16, 17].
- non 1981. *Calliostoma (Ampullotrochus) trigonum* (Eichwald, 1830); Švagrovský, p. 108, pl. 33, figs 4–6 [= *Jujubinus turricula* (Eichwald, 1830)].
2001. *[Calliostoma] trigonum* (Eichwald, 1830); Anistratenko and Anistratenko, p. 184.

**MATERIAL:** Sandy facies: Bilozirka (MZ VIII Mg 4671) 1 jf; Nadrichne (MZ VIII Mg 4672) 1 j; Oles'ko (MZ VIII Mg 4673) 1 j; Rydomyl' (MZ VIII Mg 4674) 115 sh; Shushkivtsi (MZ VIII Mg 4675) 1 af, 5 jf; Varivtsi (MZ VIII Mg 4702) 1 af, 8 jf; Zalistsi (MZ VIII Mg 4676) 3 jf; Zalistsi – Zhabiak ravine (MZ VIII Mg 4677) 3 af, 1 j, 1 jf. All specimens are from western Ukraine.

**DESCRIPTION:** Shell of medium size, with conical spire. Convex, paucispiral protoconch forming angle to teleoconch, exhibiting heterostrophic appearance. Protoconch bearing honeycomb surface microsculpture. Junction with teleoconch marked by axial ridge. Five to six finer horizontal ribs present in the interspaces between this ridge and between two or three further equally strong axial ribs. Axial ribs weakening during ontogeny, while three spiral cords becoming predominant. A single secondary spiral thread intercalated in each interspace, but the threads disappear rapidly. Axial ribs crossing cords forming beads at intersections; adapical beaded cord, adjacent to suture gaining in strength, becoming predominant. On second or third teleoconch whorl the fourth cord emerging from abapical suture. At the beginning it is indistinctly-beaded, further becoming smooth, swollen and elevated, overhanging abapical suture, giving the shell a scalate profile, and forming periphery on last whorl. On later whorls beads on cords disappear (the longest in ontogenesis, they remain on adapical cord, placed a short distance below suture), and single fine secondary spiral cord often appearing

in interspaces between cords 1 and 2, and 2 and 3, with further even weaker tertiary cords developed in some interspaces. Surface covered by prosocline growth lines. Early teleoconch whorls straight-sided, later whorls straight-sided to concave. Suture linear, impressed. Last whorl angled at base. Flat to slightly convex, imperforate base bearing irregular spiral cords (20 in specimen MZ VIII Mg 4674/1; Text-fig. 24A), strengthening and wider-set towards centre, crossed by opisthocyrt growth lines. Aperture oblique, subquadrate; outer lip sharp edged, angled at periphery. Columella thickened, with basal columellar tooth, meeting lower lip at distinctly obtuse angle.

**REMARKS:** The syntypes of *T. trigonus* are probably present in the KNUSH collection, from Bilka and Medzhybizh. However, two juvenile specimens identified by the present author as *Calliostoma trigonum* are in Eichwald's collection stored in the SPbGU. A larger specimen consists of about six whorls (height 5.0 mm, width 5.4 mm). Unfortunately, these specimens are not labeled. Eichwald's collection, during its long history, has been examined by many people, so it happens that sometimes labels do not match the specimens. This also applies to the original Eichwald's label with the species name *Trochus trigonus* and a provenance of the fossils as Bilka that have been mistakenly assigned to four specimens with inventory number SPbGU 3/433, which certainly do not belong to this species.

The illustrations in Eichwald (1850, 1851b and 1859) show immature specimens of *T. trigonus*. The shell illustrated by Eichwald in 1859 (pl. 9, fig. 21a) has a concave profile and the last whorl with spiral cords but only one of them, adjacent to the posterior suture, is clearly beaded (Eichwald 1859, pl. 9, fig. 21c). However, in the atlas (Eichwald 1850, 1851b, pl. 9, figs 21a and 21c), the shell profile is nearly flat, and on the last whorl two of the cords are coarsely beaded, one placed near the adapical suture and second one approximately in the middle of the whorl. These different illustrations reflect the intraspecific variability of this species, which can also be observed in the studied material. In addition, adult specimens have on the lateral flank of the last whorl a variable number of cords, from 4 to 11, including a peripheral cord, of variable strength. The slenderness of the shells is also variable.

So far, the largest specimen of this species is from Saryi Pochaiv (ZNG PAN A-I-50/1677a, this shell has the last whorl damaged).

The distinctive sculpture and shape of the shell make the recognition of this species in Miocene

gastropod fauna easy. Teleoconch features and protoconch with typical honeycomb-like microsculpture indicate that the species belongs to the genus *Calliostoma*.

**OCCURRENCE:** Middle Miocene of the Central Paratethys: Badenian of Hungary (Strausz 1962, 1966), Austria (Mandic *et al.* 2002), Poland (Liszka 1933; Krach 1962; Urbaniak 1974; Jakubowski 1977), and western Ukraine (Eichwald 1830, 1851a, 1853; du Bois de Montpereux 1831; Pusch 1837; Friedberg 1928, 1938; Kowalewski 1936b, 1937; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001; this study; for details see Appendix 2).

## CONCLUSIONS

Taxonomic studies of the Trochoidea are not easy, being hampered by the fact that only few taxa of the superfamily show determinate growth, which is understood as “a pattern of ontogeny wherein adult forms cease growth in body size and change in shape” (Vermeij and Signor 1992, p. 233). In the Trochidae, determinate growth is visible e.g., in *Clanculus*, being expressed by the appearance of all the characteristic elements of the columella and the aperture. In many other genera it is difficult to determine whether the shell has reached final growth, resulting in potential taxonomic mistakes, such as treating the juvenile specimens of known species as new taxa. The study is also impeded by the fact that the species inhabiting shallow-water environments have diversified characteristics of the late teleoconch. In such cases, the protoconch and early teleoconch, exhibiting less variability than the late teleoconch whorls, are much more useful in taxonomic analyses.

Despite from being derived from high-energy, shallow-marine sandy and carbonate deposits, usually preventing the preservation of delicate structures of the mollusc shell, many specimens of the Trochoidea, which are the subject of this study, are very well-preserved so that it was possible to describe and illustrate the shells of most species at an early stage of ontogenetic development (including the protoconch), some of them for the first time.

Twenty-one species belonging to five different genera representing two families have been identified in the examined material (over 3,000 specimens). The genus *Paroxystele* is known only from the fossil record. Twenty species were known earlier, mainly from the middle Miocene deposits of the Fore-Carpathian Basin, and one of them is de-

scribed as *Clanculus (Clanculopsis) krachi* sp. nov. One *Gibbula* species is left in open nomenclature.

Of 606 species of gastropods recognised in the Late Badenian assemblages of the Central Paratethys (Harzhauser and Piller 2007), the Trochoidea described in this paper represent almost 3.5%.

*Paroxystele orientalis* is the most abundant species in the examined collection from western Ukraine, being represented by over 750 specimens. The rarest species are recorded by only one or two specimens, i.e., for *Clanculus (Clanculopsis) krachi* sp. nov., *Gibbula zboroviensis*, *Gibbula* sp. and *Jujubinus vexans*.

The protoconchs of 17 of the 21 examined species are described herein. The protoconch is generally paucispiral ( $\pm 1.25$  whorls). In the Trochidae, it reaches a maximum width of 0.20–0.28 mm, while in *Calliostoma trigonum* it is 0.35 mm. The microsculpture of the protoconch is preserved only in *C. trigonum*. It consists of fine threads in a pattern of interconnected hexagons (honeycomb-like pattern). Besides, only in the latter species the protoconch exhibits a heterostrophic appearance. All protoconchs have a small and pointed tip (= apical beak), which reflects the original small ovum, from which the larva developed (Bandel 1982). A sinuous terminal lip occurs on the protoconchs of *Gibbula puschiei*, *Jujubinus turricula* and probably in *Jujubinus celinae*, *Jujubinus planatus* and *P. orientalis*. The subterminal varix of the protoconch was observed in *Gibbula biangulata*, *Gibbula podhorcensis* and *J. turricula*. An axial ridge marks the protoconch-teleoconch boundary in *C. trigonum*. The size and shape of the studied protoconchs indicate some yolk reserves and lecithotrophic larval development of the species studied (Bandel 1982; Hickman 1992). Unfortunately, the protoconch was not observed in *Clanculus (Clanculopsis) robustus*, *Gibbula mio-caenica*, *Gibbula teisseyreii* and *Gibbula* sp.

Among the species studied, *Gibbula affinis*, *G. biangulata*, *P. orientalis* and *J. turricula* have the widest stratigraphic ranges (see Appendix 3 for the occurrences of the studied western Ukrainian trochoidean species in the Miocene and Pleistocene of the north-eastern Atlantic, (Proto-)Mediterranean and Paratethyan regions). The first two species are known from the Burdigalian (early Miocene) to the Tortonian (late Miocene), *P. orientalis* ranges from the Aquitanian (early Miocene; Thivaoui *et al.* 2019) to the Serravallian (middle Miocene), and *J. turricula* occurs from the Langhian to the Pleistocene.

*Paroxystele orientalis*, a common middle Miocene species, dwelled both in the Central and Eastern



Paratethys. Its geographic range, as well as that of *G. affinis* and *G. puschii*, reached as far as the modern Ustyurt Plateau between the Caspian and Aral seas (Iljina 1993) and the eastern Proto-Mediterranean Sea (Harzhauser *et al.* 2002; Landau *et al.* 2013). *Jujubinus turricula* originated in the middle Miocene; this species is known already from the Mid Badenian *sensu* Hohenegger *et al.* 2014 of the Central Paratethys (e.g., Mandić *et al.* 2002). Later it spread to the Atlantic (Serravallian; Cossmann and Peyrot 1917) and Mediterranean regions (late Serravallian, Landau *et al.* 2013; Tortonian, Sacco 1896; Pleistocene, MZ collection). *Gibbula miocaenica* most likely developed during the Burdigalian (early Miocene) in the Western Paratethys (e.g., Mayer 1853). In the middle Miocene, it dwelled in the north-eastern Atlantic and the Central Paratethys Sea (listed so far only from the Badenian of the Fore-Carpathian Basin under the names *Gibbula sytovae* and *Gibbula novemcincta* by Amitrov 1961 and Friedberg 1938, respectively).

Species that have been listed solely from the Badenian of the Central Paratethys include: *Clanculus (Clanculopsis) tuberculatus*, *C. trigonum*, *J. vexans*, *G. novemcincta*, *G. dzieduszyckii*, *G. teisseyrei*, *Jujubinus zukowcensis*, *C. (C.) krachi* sp. nov. and *Gibbula* sp. Apart from the first four taxa, the other ones were quoted so far only from the Polish–Ukrainian part of the Fore-Carpathian Basin. This points to the development of local endemics, as seen in the Nassariidae (see Harzhauser and Kowalke 2004), due to partial isolation of this basin.

Of the 21 species of the Trochoidea, described herein, that inhabited the Late Badenian Central Paratethys, 9 (42.8%) taxa are known to have survived into the Sarmatian, most of them mainly in the Fore-Carpathian Basin.

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## REFERENCES

- Abbass, H. L. 1963. Monograph on the Egyptian Cretaceous gastropods. Paleontological series (Geological Museum, Cairo), Monograph 2, 146 pp. General Organization for Government Printing Office; Cairo.
- Affenzeller, S., Haar, N. and Steiner, G. 2017. Revision of the genus complex *Gibbula*: an integrative approach to delimiting the Eastern Mediterranean genera *Gibbula* Risso, 1826, *Steromphala* Gray, 1847, and *Phorcus* Risso, 1826 using DNA-barcoding and geometric morphometrics (Vetigastropoda, Trochoidea). *Organisms Diversity & Evolution*, **17** (4), 789–812.
- Amitrov, O.W. 1961. On the age changes in a new trochid species. *Palaeontological Journal*, **4**, 40–49. [In Russian]
- Andreyeva-Grigorovich, A.S., Kulchitsky, Y.D., Gruzman, A.D., Lozynyak, P.Yu., 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 of Neogene formations of the Central Paratethys in the Ukraine. *Geologica Carpathica*, **48** (2), 123–136.
- Andreyeva-Grigorovich, A.S., Oszczytko, N., Ślącza, A., Oszczytko-Clowes, M., Savitskaya, N.A. and Trofimovicz, N. 2008. New data on the stratigraphy of the folded Miocene Zone at the front of the Ukrainian Outer Carpathians. *Acta Geologica Polonica*, **58**, 325–353.
- Andrzejowski, A. 1830a. Notice sur quelques coquilles fossiles de Volhynie, Podolie etc. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **2**, 90–104.
- Andrzejowski, A. 1830b. Dalszy ciąg postrzeżeń czynionych w podrózach botanicznych w roku 1823 i 1824. *Dziennik Wileński. Umiejętności i sztuki*, **5** (May), 125–183.
- Andrzejowski, A. 1832a. Remarques sur l'ouvrage de M, Frédéric Du Bois de Montpireux, ayant pour titre; Conchyliologie fossile, ou Aperçu géognostique des formations du Plateau Volhynie-Podolien; in 4 Berlin 1830. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **4**, 513–558.
- Andrzejowski, A. 1832b. Catalogue des Coquilles fossiles du Plateau Volhynie-Podolien de la Collection du Lycée de Volhynie. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **4**, 559–567.
- Andrzejowski, A. 1833. Coquilles fossiles de Volhynie et de Podolie. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **6**, 437–451.
- Anistratenko, O.Yu. 2000. *Granulifera pulla* gen. et sp. n. (Gastropoda, Pectinibranchia, Trochidae) from Middle Miocene of the Western Ukraine. *Vestnik zoologii*, **34** (3), 3–6. [In Russian]
- Anistratenko, O. and Anistratenko, V. 2012. Zoogeography and ecology of the Middle Sarmatian Gastropods of the Eastern Paratethys. *Ruthenica*, **22** (2), 115–134. [In Russian with English abstract]
- 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.
- Anistratenko, V.V. and Anistratenko, O.Yu. 2001. Fauna Ukraine in 40 volumes. Mollusca. Fasc. 1. B. 1: Class Polyplacophora or Chitons, Class Gastropoda – Cyclobranchia, Scutibranchia and Pectinibranchia (part). Volume 29, 240 pp. Veles; Kyiv. [In Russian with English summary]
- Anistratenko, V.V., Bandel, K. and Anistratenko, O.Yu. 2003. On some rare trochoidean gastropods from the Miocene of the West Ukraine. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **87**, 99–113.
- Anton, H.E. 1838 [1839]. Verzeichniss der Conchylien welche sich in der Sammlung von Herrmann Eduard Anton befinden. Herausgegeben von dem Besitzer. Halle: Anton. 110 pp. [Title page dated 1839, but volume actually published in 1838; see W.O. Cernohorsky, 1978, *The Veliger* 20 (3), p. 299].
- Areń, B. 1962. The Miocene of the Lublin Roztocze Range between the Sanna and Tanew Rivers. *Prace Instytutu Geologicznego*, **30**, 5–77. [In Polish with Russian and English summary]
- Bałuk, W. 1970. The Lower Tortonian at Niskowa near Nowy Sącz, Polish Carpathians. *Acta Geologica Polonica*, **20**, 101–157. [In Polish with English summary]
- Bałuk, W. 1975. Lower Tortonian gastropods from Korytnica, Poland; Part I. *Palaeontologia Polonica*, **32**, 1–186.
- Bałuk, W. 2006. Middle Miocene (Badenian) gastropods from Korytnica, Poland; Part V Addenda et corrigenda ad Prosobranchia. *Acta Geologica Polonica*, **56**, 177–220.
- Bałuk, W. and Radwański, A. 1968. Lower Tortonian sands at Nawodzice (southern slopes of the Holy Cross Mts.), their fauna and facial development. *Acta Geologica Polonica*, **18**, 447–470. [In Polish with English summary]
- Bandel, K. 1975. Das Embryonalgehäuse mariner Prosobranchier der Region von Banyuls-sur Mer. I. Teil. *Vie et Milieu*, **25** (1), 83–118.
- Bandel, K. 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies*, **7**, 1–198.
- Bandel, K. 2009. The slit bearing nacreous Archaeogastropoda of the Triassic tropical reefs in the St. Cassian Formation with evaluation of the taxonomic value of the selenizone. *Berliner paläobiologische Abhandlungen*, **10**, 5–47.
- Barco, A., Evans, J., Schembri, P.J., Taviani, M. and Oliverio, M. 2013. Testing the applicability of DNA barcoding for Mediterranean species of top-shells (Gastropoda, Trochidae, Gibbula s.l.). *Marine Biology Research*, **9** (8), 785–793.
- 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.
- Basterot, B. de 1825. Description géologique du Bassin tertiaire du Sud-Ouest de la France. *Mémoires de la Société d'Histoire Naturelle de Paris*, **2** (1), 1–100.
- Benoist, E.A. 1874. Catalogue synonymique et raisonné des testacés fossiles recueillis dans les faluns miocènes des communes de La Brède et de Saucats. *Actes de la Société Linnéenne de Bordeaux*, **29**, 265–460.
- Boda, J. 1959. Das Sarmat in Ungarn und seine Invertebraten-Fauna. *A Magyar Állami Földtani Intézet Évkönyve*, **47** (3), 569–862. [In Hungarian and German]
- Boettger, O. 1902. Zur Kenntnis der Fauna der mittelmiozänen Schichten von Kostej im Krassó-Szörényer Komitat. Mit einem Situationsplan der Fundpunkte, 2. *Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, **51**, 1–200 (1901).

- Boettger, O. 1907. Zur Kenntnis der Fauna der mittelmiozänen Schichten von Kostež im Krassó-Szörényer Komitat. Gastropoden und Anneliden, 3. *Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, **55**, 101–217 (1905).
- Bois de Montpéroux, F. du 1831. Conchiologie fossile et aperçu géognostique des formations du plateau Wolhyni-Podolien, 76 pp. Simon Schropp et Comp.; Berlin.
- Borson, S. 1821. Continuazione del Saggio di oritografia Piemontese. *Memorie della Reale Accademia delle Scienze di Torino*, **26**, 297–364.
- Bouchet, P., Frýda, J., Hausdorf, B., Ponder, W., Valdés, Á. and Warén, A. 2005. Working Classification of the Gastropoda. In: Bouchet, P. and Rocroi, J.-P. (Eds), Classification and Nomenclator of Gastropod Families. *Malacologia*, **47** (1–2), 239–283.
- Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, H. and Strong, E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, **61** (1–2), 1–526.
- Brocchi, G. 1814. Conchiologia fossile subapennina, con osservazioni geologiche sugli Apennini e sul suolo adiacente, 2, 241–712. Stamperia Reale; Milano.
- Brongniart, A. 1823. Mémoire sur les terrains de sédiment supérieurs calcaréo-trappéens du Vicentin, et sur quelques terrains d'Italie, de France, d'Allemagne, etc., qui peuvent se rapporter à la même époque, 86 pp. F.G. Levrault; Paris.
- Buch, L. von 1830. Nachschrift. *Archiv für Mineralogie, Geognosie, Bergbau und Hüttenkunde*. Hrsg. von Dr. C.J.B. Karsten, **2**, 126–134.
- Calcara, P. 1842. Nuove ricerche ed osservazioni sopra vari molluschi Siciliani. Nuove specie di Calyptra. *Il Maurolico, Giornale del Gabinetto Letterario di Messina*, **13**, 1–14.
- Calzada Badía, S. 1978. Gasterópodos tortonienses de Archena (Murcia). *Estudios Geológicos*, **34**, 299–307.
- Ceulemans, L., Van Dingenen, F. and Landau, B.M. 2016. The lower Pliocene gastropods of Le Pigeon Blanc (Loire-Atlantique, Northwest France). *Patellogastropoda and Vetigastropoda*. *Cainozoic Research*, **16** (1), 51–100.
- Chirli, C. 2004. Malacofauna Pliocenica Toscana. Vol. 4. Polyplacophora Gray J.E., 1821, Monoplacophora Odhner, 1940, Archaeogastropoda Thiele, 1925, 113 pp., 41 Plates. [Private edition, without indication of any Publisher]; Firenze.
- Collin, R. and Voltzow, J. 1998. Initiation, Calcification, and Form of Larval “Archaeogastropod” Shells. *Journal of Morphology*, **235**, 77–89.
- Cossmann, M. 1918. Essais de paléoconchologie comparée, 11, 388 pp. Chez l’auteur; Paris.
- Cossmann, M. and Peyrot, A. 1917. Conchologie néogénique de l’Aquitaine. Extrait des *Actes de la Société Linnéenne de Bordeaux*, **3** (1), 1–384.
- Cretella, M., Scillitani, G. and Picariello, O. 1990. The systematic position of “*Trochus*” *miliaris* Brocchi, 1814 (Gastropoda: Trochidae); morphological and biochemical evidences. *Lavori, Società Italiana di Malacologia*, **23**, 51–81.
- Crosse, H. 1885. Nomenclatura generica e specifica par le marquis de Monterosato. *Journal de Conchyliologie*, **33**, 139–142.
- Csepregy-Meznerics, I. 1954. Helvetische und tortonische Fauna aus dem östlichen Cserhátgebirge. *A Magyar Állami Földtani Intézet Évkönyve*, **41** (4), 1–185. [In Hungarian with German summary]
- Csepregy-Meznerics, I. 1956. Die Molluskenfauna von Szob und Letkés. *A Magyar Állami Földtani Intézet Évkönyve*, **45** (2), 363–477. [In Hungarian with German summary]
- Csepregy-Meznerics, I. 1969a. Nouvelles Gastropodes et Lamellibranches pour la faune hongroise des gisements tortonien-inférieurs de la Montagne de Bükk. *Annales Historico-Naturales Musei Nationalis Hungarici, Pars Mineralogica et Palaeontologica*, **61**, 63–127.
- Csepregy-Meznerics, I. 1969b. La faune tortonienne-inférieure des gisements tufiques de la Montagne de Bükk: Gastropodes I. *Különlenyomat az Egri Múzeum Évkönyvé – Annales Musei Agriensis* **7**, 17–34.
- Cuvier, G. 1795. Second Mémoire sur l’organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d’Histoire Naturelle de Paris, le 11 prairial an troisième. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, **2**, 433–449.
- Defrance, M.J.L. 1824. Monodonte perlée; *Monodonta baccata*, Def. In: Cuvier, F. (Ed.), Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différents êtres de la nature, considérés soit en eux-mêmes, d’après l’état actuel de nos connoissances, soit relativement à l’utilité qu’en peuvent retirer la médecine, l’agriculture, le commerce et les arts. Suivi d’une biographie des plus célèbres naturalistes. Ouvrage destiné aux médecins, aux agriculteurs, aux commerçants, aux artistes, aux manufacturiers, et à tous ceux qui ont intérêt à connoître les productions de la nature, leurs caractères généraux et spécifiques, leur lieu natal, leurs propriétés et leurs usages, 32, p. 475. F.G. Levrault; Strasbourg & Le Normant; Paris.
- Doderlein, P. 1862. Cenni geologici intorno la giacitura dei terreni miocenici superiori dell’Italia centrale. Estratto dagli Atti del X° Congresso degli Scienziati Italiani, 1862, Siena, 25 pp. Also published as: 1864, Atti del Decimo Congresso degli Scienziati Italiani, pp. 83–107, 223 (errata).
- Dollfus, G. and Dautzenberg, P. 1886. Étude préliminaire des coquilles fossiles des faluns de la Touraine. *Feuille des Jeunes Naturalistes*, **192**, 138–142.
- Donald, K.M., Kennedy, M. and Spencer, H.G. 2005. The phylogeny and taxonomy of austral monodontine topshells (Mollusca: Gastropoda: Trochidae), inferred from DNA



- sequences. *Molecular Phylogenetics and Evolution*, **37**, 474–483.
- Donald, K.M., Preston J., Williams, S.T., Reid, D.G., Winter, D., Alvarez, R., Buge, B., Hawkins, S.J., Templado, J. and Spencer, H.G. 2012. Phylogenetic relationships elucidate colonization patterns in the intertidal grazers *Osilinus Philippi*, 1847 and *Phorcus Risso*, 1826 (Gastropoda: Trochidae) in the northeastern Atlantic Ocean and Mediterranean Sea. *Molecular Phylogenetics and Evolution*, **62**, 35–45.
- Donald, K.M. and Spencer, H.G. 2016. Phylogeographic patterns in New Zealand and temperate Australian cantharidines (Mollusca: Gastropoda: Trochidae: Cantharidinae): Trans-Tasman divergences are ancient. *Molecular Phylogenetics and Evolution*, **100**, 333–344.
- Dornellas, A.P.S. and Simone, L.R.L. 2011. Bivalves in the stomach contents of *Calliostoma coppingeri* (Calliostomatidae: Gastropoda). *Strombus*, **18** (1–2), 10–12.
- Dujardin, F. 1837. Mémoire sur les couches du sol en Touraine, et description des coquilles de la craie et des faluns. *Mémoires de la Société géologique de France*, **2**, 211–311.
- Eichwald, E. 1829. Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum, et Poloniae in specie, in usum lectionum publicarum in Universitate caesarea Vilnensi. Pars prior pro-paedeuticam zoologiae atque specialem Heterozoorum expositionem continens. Cum icone tituli et quinque aliis lithographicis, 314 pp., 5 plates. Joseph Zawadzki; Vilnae.
- Eichwald, E. 1830. Naturhistorische Skizze von Lithauen, Volhynien und Podolien in geognostisch-mineralogischer, botanischer und zoologischer Hinsicht, 256 pp. Joseph Zawadzki; Wilna.
- Eichwald, E. 1840. Einige Berichtigungen der vom Herrn Münzmeister Pusch bestimmten Schalthiere des volhynisch podolischen Tertiaerbeckens. *Bulletin Scientifique, L'Académie Impériale des Sciences de Saint-Petersbourg*, **6**, 1–25.
- Eichwald, E. 1850. Atlas to Palaeontology of Russia. New period, 14 plates. Saint Petersburg. [In Russian]
- Eichwald, E. 1851a [‘1850’] Palaeontology of Russia. Descriptions of marine and alluvial formations of Russia, based on material preserved in the Museum of the Imperial Medical-Surgical Academy. New period, 284 pp. Édouard Prace; Saint Petersburg [Despite the fact that on the title page is given the year 1850 date of publication was adopted on the basis of a note on the back of the title page]. [In Russian]
- Eichwald, E. 1851b. Atlas to Palaeontology of Russia, 14 plates. Saint Petersburg. [In Russian]
- Eichwald, E. 1853. Lethaea Rossica ou Paléontologie de la Russie, dernière période, 533 pp. E. Schweizerbart; Stuttgart.
- Eichwald, E. 1859. Lethaea Rossica ou Paléontologie de la Russie. Période moderne. Atlas, 4 pp., 14 plates. E. Schweizerbart; Stuttgart.
- Eremija, M. 1971. Miozänische Mollusken im Bassin Prnjavor (Bosnien). *Annales Géologiques de la Péninsule Balkanique*, **36**, 51–85. [In Serbian with German summary]
- Florei, N. 1961. Nouvelles données sur la faune miocène de Zorlențul-Mare (Banat). *Studii și Cercetări de Geologie*, **6** (4), 667–698. [In Romanian with French summary]
- Friedberg, W. 1911–1928. Mollusca miocaenica Poloniae. Pars I – Gastropoda et Scaphopoda, 1–631 [issued in parts: **1**, 1–112 (1911); **2**, 113–239 (1912); **3**, 240–360 (1914); **4**, 361–440 (1923); **5**, 441–631 (1928)]. Muzeum imienia Dzieduszyckich we Lwowie; Lwów, Poznań. [In Polish]
- Friedberg, W. 1930. Wołyńskie zbiory miocénskie Fryderyka Dubois’a de Montpéroux. In: Miocänstudien in Polen, VI Teil. *Kosmos*, seria A, **55**, 364–370.
- Friedberg, W. 1934–1936. Mollusca miocaenica Poloniae. Pars II – Lamellibranchiata, 1–274 [issued in parts: **1**, 1–158 (1934), **2**, 159–274 (1936)]. Polskie Towarzystwo Geologiczne; Kraków. [In Polish]
- Friedberg, W. 1938. Katalog meiner Sammlung der Miozänmollusken Polens. *Mémoires de l’Académie Polonaise des Sciences et des Lettres, Classe des Sciences Mathématiques et Naturelles, Série B, Sciences Naturelles*, **12**, 1–164.
- Fuchs, T. von 1873. Beiträge zur Kenntniss fossiler Binnenfaunen. VI. Neue Conchylienarten aus den Congerien-Schichten und aus Ablagerungen der sarmatischen Stufe. *Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt*, **23** (1), 19–26.
- Garbowska, J. 1993. Geological sciences at the higher schools of Vilnius and Krzemieniec in the years 1781–1840. *Prace Muzeum Ziemi*, **42**, 5–112. [In Polish with English summary]
- Garbowska, J. 2005. Antoni Andrzejowski – investigator of Volhynia and Podolia. *Prace Muzeum Ziemi*, **48**, 19–27. [In Polish with English summary]
- Gataulina, G.M. and Arcadieiev, V.V. 2010. History of paleontological collection of E.I. Eichwald to monograph “Palaeontology of Russia”. *Vestnik of Saint Petersburg University. Series 7: Geology, Geography*, **3**, 48–58. [In Russian]
- Geiger, D.L. and Thacker, C.E. 2005. Molecular phylogeny of Vetigastropoda reveals non-monophyletic Scissurellidae, Trochoidea, and Fissurelloidea. *Molluscan Research*, **25** (1), 47–55.
- Giannuzzi-Savelli, R., Pusateri, F., Palmeri, A. and Ebreo, C. 1994. Atlante delle conchiglie marine del Mediterraneo. Atlas of the Mediterranean sea shells, vol. 1 (Archaeogastropoda), 125 pp. La Conchiglia; Roma.
- Glibert, M. 1949a. Gastropodes du Miocène moyen du Bassin de la Loire. *Mémoires de l’Institut royal des Sciences naturelles de Belgique, Série 2*, **30**, 1–240.
- Glibert, M. 1949b. Gastropodes du Miocene moyen du Bassin de la Loire. Rectifications de nomenclature. *Bulletin de l’Institut royal des Sciences naturelles de Belgique*, **25** (34), 1–36.
- Glibert, M. 1962. Les Archaeogastropoda fossiles du Cénozoïque Étranger des collections de L’Institut Royal des Sci-

- ences Naturelles de Belgique. *Mémoires de Institut royal des Sciences naturelles de Belgique*, **68**, 1–131.
- Gmelin, J.F. 1791. Caroli a Linné. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vermes testacea. Editio decima tertia, aucta, reformata, cura J.F. Gmelin, **1** (6), 3021–4120. G.E. Beer; Lipsiae.
- Gofas, S. 2005. Geographical differentiation in *Clelandella* (Gastropoda: Trochidae) in the northeastern Atlantic. *Journal of Molluscan Studies*, **71**, 133–144.
- Golikov, A.N. and Starobogatov, Y.I. 1975. Systematics of prosobranch Gastropods. *Malacologia*, **15** (1), 185–232.
- Golovina, L., Bylinskaya, M., Goncharova, I., Popov, S. and Palcu, D. 2019. Towards solving the problem of volume and boundaries of the Tarkhanian regional stage of the Eastern Paratethys. In: Studencka, B. (Ed.), NCSEE 2019, 8<sup>th</sup> International Workshop on Neogene of Central and South-Eastern Europe, 27th–31st May 2019, Chęciny, Poland, 38–40. University of Warsaw, Faculty of Geology; Warsaw.
- Gozhyk, P., Semenenko, V., Andreeva-Grigorovich, A. and Maslun, N. 2015. The correlation of the Neogene of Central and Eastern Paratethys segments of Ukraine with the International Stratigraphic Chart based on planktonic microfossils. *Geologica Carpathica*, **66** (3), 235–244.
- Gray, J.E. 1847a. On the classification of the British Mollusca by W.E. Leach. *Annals and Magazine of Natural History*, ser. 1, **20**, 267–273.
- Gray, J.E. 1847b. A list of the genera of recent Mollusca, their synonyms and types. *Proceedings of the Zoological Society of London*, **15**, 129–219.
- Gray, J.E. 1857. Guide to the Systematic Distribution of Mollusca in the British Museum, 1, 230 pp. Taylor & Francis; London.
- Grishkevich, G.N. 1970. The Buglovian Beds and their stratigraphic position. In: Vialov, O.S. (Ed.), The Buglovian Beds of Miocene, 19–68. Naukova Dumka; Kiev. [In Russian]
- Hadfield, M. and Strathmann, M.F. 1990. Heterostrophic shells and pelagic development in trochoideans: implications for classification, phylogeny and palaeoecology. *Journal of Molluscan Studies*, **56**, 239–256.
- Harzhauser, M. 2002. Marine und brachyhaline Gastropoden aus dem Karpatium des Korneuburger Beckens und der Kreuzstettener Bucht (Österreich, Untermiozän). *Beiträge zur Paläontologie*, **27**, 61–159.
- Harzhauser, M. 2003. Marine Gastropods, Scaphopods and Cephalopods of the Karpatian in the Central Paratethys. In: Brzobohatý, R., Cicha, I., Kováč, M. and Rögl, F. (Eds), The Karpatian – a Lower Miocene Stage of the Central Paratethys, 193–201. Masaryk University; Brno.
- Harzhauser, M. and Kowalke, T. 2002. Sarmatian (Late Middle Miocene) Gastropod Assemblages of the Central Paratethys. *Facies*, **46**, 57–82.
- Harzhauser, M. and Kowalke, T. 2004. Survey of the Nassariid Gastropods in the Neogene Paratethys (Mollusca: Caenogastropoda: Buccinoidea). *Archiv für Molluskenkunde International Journal of Malacology*, **133** (1/2), 1–63.
- Harzhauser M. and Landau B. 2016. A revision of the Neogene Conidae and Conorbidae (Gastropoda) of the Paratethys Sea. *Zootaxa*, **4210** (1), 1–178.
- 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.
- Harzhauser, M., Piller, W.E. and Steininger, F.F. 2002. Circum-Mediterranean Oligo-Miocene biogeographic evolution – the gastropods’ point of view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **183**, 103–133.
- Herbert, D.G. 1992. Revision of the Umboniinae in southern Africa and Mozambique (Mollusca: Prosobranchia: Trochidae). *Annals of the Natal Museum*, **33** (2), 379–459.
- Herbert, D.G. 1993. Revision of the Trochinae, tribe Trochini (Gastropoda: Trochidae) of southern Africa. *Annals of the Natal Museum*, **34** (2), 239–308.
- Herrmannsen, A. N. 1846–1847. Indicis Generum Malacozorum primordia. Nomina subgenerum, generum, familiarum, tribuum, ordinum, classium: adjectis auctoribus, temporibus, locis systematicis atque literariis, etymus, synonymis. Praetermittuntur Cirripedia, Tunicata et Rhizopoda, 1, 105–232 (1846), 361–488 (1847). Fischer; Cassel.
- Hickman, C.S. 1992. Reproduction and Development of Trochacean Gastropods. *The Veliger*, **35** (4), 245–272.
- Hickman, C.S. and McLean, J.H. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Science Series of Natural History Museum of Los Angeles County*, **35**, 1–169.
- Hilber, V. 1882. Neue und wenig bekannte Conchylien aus dem ostgalizischen Miocän. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, **7**, 1–35.
- Hilber, V. 1897. Die sarmatischen schichten vom Waldhof bei Wetzelsdorf, Graz SW. *Mittheilungen des Naturwissenschaftlichen Vereines für Steiermark*, **33**, 182–204.
- Hinculov, L. 1968. II-e Partie. Faune Miocène dans le bassin de Mehădia. In: Iliescu, O., Hinculov, A. and Hinculov L., Bazinul Mehădia. Studiu geologic și paleontologic. *Memorii*, **9**, 75–201. [In Romanian with French summary]
- Hohenegger, J., Ćorić, S. and Wägrich, M. 2014. Timing of the Middle Miocene Badenian Stage of the Central Paratethys. *Geologica Carpathica*, **65** (1), 55–66.
- Hörnes, M. 1856. Die fossilen Mollusken des Tertiär-Beckens von Wien; I. Univalven. *Abhandlungender kaiserlich-königlichen Geologischen Reichsanstalt*, **3**, 1–736.
- Iļjina, L.B. 1993. Handbook for identification of the marine Middle Miocene gastropods of Southwestern Eurasia. *Transactions of the Paleontological Institute, Russian Academy of Sciences*, **255**, 1–149. [In Russian]

- Iljina, L.B. 1998. Zoogeography of Sarmatian Gastropods. *Paleontologicheskii Zhurnal*, **4**, 22–30. [In Russian]
- International Commission on Zoological Nomenclature. 1957. Opinion 456. *Opinions and Declarations rendered by the International Commission on Zoological Nomenclature*, **15** (22), 393–418.
- International Commission on Zoological Nomenclature 1999. International Code of Zoological Nomenclature. Fourth Edition, 306 pp. International Trust for Zoological Nomenclature; London.
- Jablonski, D. and Lutz, R.A. 1980. Molluscan Larval Shell Morphology: Ecological and Paleontological Applications. In: Rhoads, D.C. and Lutz, R.A. (Eds), *Skeletal Growth of Aquatic Organisms*, 323–377. Plenum Press; New York and London.
- Jakubowski, G. 1977. Part II – Palaeontology. In: Jakubowski, G. and Musiał, T., *Lithology and fauna from the Upper Tortonian sands of Monastyrz and Długi Goraj (Southern Roztocze – Poland)*. *Prace Muzeum Ziemi*, **26**, 74–126.
- Jasionowski, M., Górka, M., Studencka, B. and Poberezhskyy, A. 2006. Miocene of Medobory Hills (Podillya, West Ukraine). In: Wysocka, A. and Jasionowski, M. (Eds), *Przebieg i zmienność sedymentacji w basenach przedgórskich. Materiały konferencyjne: Przewodnik sesji terenowych, streszczenia referatów i posterów. II Polska Konferencja Sedymentologiczna Pokos2, IX Krajowe Spotkanie Sedymentologów. Zwierzyniec 20–23.06.2006*, pp. 53–65. Instytut Geologii Podstawowej, Wydział Geologii UW; Warszawa. [In Polish with English summary]
- Katona, L.T., Kókay, J. and Berta, T. 2011. Badenian mollusc fauna from Várpalota (Faller street). *Földtani Közletemény*, **141** (1), 3–22 [In Hungarian with English abstract].
- Keen, A.M. 1958. *Sea shells of tropical West America*, 624 pp. Stanford University Press; Stanford.
- Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. and Robertson, R., 1960. Systematic descriptions. In: Knight, J.B., Cox, L.R., Keen, A.M., Smith, A.G., Batten, R.L., Yochelson, E.L., Ludbrook, N.H., Robertson, R., Yonge, C.M. and Moore, R.C. (Eds), *Treatise on Invertebrate Paleontology. Part I. Mollusca 1*, 169–351. Geological Society of America, Inc. and University of Kansas Press; Lawrence.
- Kojumdgieva, E. 1960. Le Tortonien du type viennois. In: Kojumdgieva, E. and Strachimirov, B., *Les fossiles de Bulgarie*, **7**, Tortonien, 13–246. Académie des Sciences de Bulgarie; Sofia. [In Bulgarian with French summary]
- Kojumdgieva, E. 1969. *Les fossiles de Bulgarie*, **8**, Sarmatien, 223 pp. Académie Bulgare des Sciences; Sofia. [In Bulgarian with French summary]
- Kókay, J. 1985. Central and Eastern Paratethyan interrelations in the light of Late Badenian salinity conditions. *Geologica Hungarica series Palaeontologica*, **48**, 7–95.
- Kókay, J. 1996. Palaeontological and geological revision of the Badenian mollusc fauna from Illés street, Budapest. *Földtani Közletemény*, **126** (4), 447–484. [In Hungarian with English abstract and summary]
- Koken, E. 1889. Ueber die Entwicklung der Gastropoden vom Cambrium bis zur Trias. *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie, Beilage Band*, **6**, 305–484.
- Korobkov, I.A. 1955. Handbook and Methodical Guide to the Tertiary Mollusca. Gastropoda, 795 pp. Gostoptekhizdat; Leningrad. [In Russian]
- Kováč, M., Andreyeva-Grigorovich, A., Bajraktarević, Z., Brzobohatý, R., Filipescu, S., Fodor, L., Harzhauser, M., Nagymarosy, A., Oszczytko, N., 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** (6), 579–606.
- Kováč, M., Halássová, E.V.A., Hudáčková, N., Holcová, K., Hyžný, M., Jamrich, M. and Ruman, A. 2018. Towards better correlation of the Central Paratethys regional time scale with the standard geological time scale of the Miocene Epoch. *Geologica Carpathica*, **69** (3), 283–300.
- Kováč, M., Hudáčková, N., Halássová, E., Kováčová, M., Holcová, K., Oszczytko-Clowes, M., Báldi, K., Less, Gy., Nagymarosy, A., Ruman, A., Klučiar, T. and Jamrich, M. 2017. The Central Paratethys palaeoceanography: a water circulation model based on microfossil proxies, climate, and changes of depositional environment. *Acta Geologica Slovaca*, **9** (2), 75–114.
- Kowalewski, K. 1936a. Nouvelles données concernant la stratigraphie et l'âge de la formation lignitifère en Volhynie. *Posiedzenia Naukowe Państwowego Instytutu Geologicznego*, **45**, 73–78. [In Polish]
- Kowalewski, K. 1936b. Sur la faune tortonienne à Rydoml, en Volhynie. *Posiedzenia Naukowe Państwowego Instytutu Geologicznego*, **46**, 12–18. [In Polish]
- Kowalewski, K. 1937. Sur la faune des couches de Buhlów en Volhynie, en rapport avec l'âge des sables de Szuszkowce. *Posiedzenia Naukowe Państwowego Instytutu Geologicznego*, **47**, 4–13. [In Polish]
- Kowalewski, K. 1950. Le Miocène des environs de Rybnica près de Klimontów. *Acta Geologica Polonica*, **1**, 41–51. [In Polish with French summary]
- Kowalke, T. 2006. Ecological implications of molluscan ontogenetic strategies – examples from aquatic ecosystems of the Cenozoic Iberian Peninsula. *Lethaia*, **39** (3), 195–209.
- Kowalke, T. and Harzhauser, M. 2004. Early ontogeny and palaeoecology of the Mid-Miocene rissoid gastropods of the Central Paratethys. *Acta Palaeontologica Polonica*, **49**, 111–134.
- Krach, W. 1950. Matériaux pour la connaissance du Miocène des environs de Lublin. *Rocznik Polskiego Towarzystwa Geologicznego*, **19** (2), 293–313. [In Polish with French summary]



- Krach, W. 1962. Stratigraphy and fauna of the Miocene in the vicinity of Zaklików and Modliborzyce, Lublin Upland. *Prace Instytutu Geologicznego*, **30** (3), 417–445. [In Polish with English and Russian summary]
- Krach, W. 1981. The Baden reef formation in Roztocze Lubelskie. *Prace Geologiczne*, **121**, 5–115. [In Polish with English summary]
- Krach, W. and Brzezińska, M. 1977. Gastropoda. In: Czerwiński, J. (Ed.), *Budowa Geologiczna Polski, Tom II, Katalog skamieniałości. Część 3a: Kenozoik, trzeciorzęd*, 70–94. Wydawnictwa Geologiczne; Warszawa.
- Kudrin, L.N. 1966. Stratigraphy, facies and ecological analysis of Paleogene and Neogene faunas of the Fore-Carpathian sequences, 174 pp. Lvov University Press; Lvov. [In Russian]
- Kulichenko, V.G. and Sorochan, E.A. 1968. Neogene Gastropods. In: Zelinskaya, V.A., Kulichenko, V.G., Makarenko, D.E. and Sorochan, E.A., *Palaeontological guide-book. Volume II: Palaeogene and Miocene gastropods and scaphopods from the Ukraine*, 95–241. Naukova Dumka; Kiev. [In Russian]
- Lamarck, J.B.P.A. de M. 1822. Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s’y rapportent; précédée d’une Introduction offrant la détermination des caractères essentiels de l’Animal, sa distinction du végétal et des autres corps naturels; enfin, l’exposition des principes fondamentaux de la Zoologie, 7, 711 pp. De Lamarck; Paris.
- Landau, B.M., Ceulemans, L. and Van Dingenen, F. 2018. The upper Miocene gastropods of northwestern France, 2. Caenogastropoda. *Cainozoic Research*, **18** (2), 177–368.
- Landau, B.M., Van Dingenen, F. and Ceulemans, L. 2017. The upper Miocene gastropods of northwestern France, 1. Patellogastropoda and Vetigastropoda. *Cainozoic Research*, **17** (2), 75–166.
- Landau, B.M., Harzhauser, M., İslamoğlu, Y. and Silva, C.M. da 2013. Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin, Turkey. *Cainozoic Research*, **11-13**, 3–576.
- Landau, B., Marquet, R. and Grigis, M. 2003. The Early Pliocene Gastropoda (Mollusca) of Estepona, Southern Spain. Part 1: Vetigastropoda. *Palaeontos*, **3**, 1–87.
- Laskarev, V. 1903. Fauna from the Buglovan Beds of Volhynia. *Transactions of the Geological Committee*, New series, **5**, 1–127. [In Russian]
- Latal, C., Piller, W.E. and Harzhauser, M. 2004. Palaeoenvironmental reconstructions by stable isotopes of Middle Miocene gastropods of the Central Paratethys. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **211**, 157–169.
- de Leeuw, A., Bukowski, K., Krijgsman, W. and Kuiper, K.F. 2010. Age of the Badenian salinity crisis, impact of Miocene climate variability on the circum-Mediterranean region. *Geology*, **38** (8), 715–718.
- de Leeuw, A., Tulbure, M., Kuiper, K.F., Melinte-Dobrinescu, M.C., Stoica, M. and Krijgsman, W. 2018. New 40Ar/39Ar, magnetostratigraphic and biostratigraphic constraints on the termination of the Badenian Salinity Crisis: evidence for tectonic improvement of basin interconnectivity in Southern Europe. *Global and Planetary Change*, **169**, 1–15.
- Lightfoot, J. 1786. A catalogue of the Portland Museum, lately the property of the Duchess Dowager of Portland, deceased: Which will be sold by auction by Mr. Skinner and Co. On Monday the 24<sup>th</sup> of April, 1786, and the thirty-seven following days (...) at her late dwelling-house, in Privy-Garden, Whitehall, by order of the Acting Executrix, 194 pp. Skinner; London.
- Lindberg, D.R. 1985. Shell sexual dimorphism of *Margarites vorticifera*: multivariant analysis and taxonomic implications. *Malacological Review*, **18** (1–2), 1–8.
- Linnæus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 1, 824 pp. Editio decima, reformata. Laurentii Salvii; Holmiae.
- Liszka, S. 1933. Fauna der Bugucicer Sande in der Umgegend von Wieliczka. *Rocznik Polskiego Towarzystwa Geologicznego*, **9**, 184–196. [In Polish with German summary]
- Locard, A. 1878. Description de la Faune de la Mollasse marine et d’eau douce du Lyonnais et du Dauphiné. *Archives du Muséum d’histoire naturelle de Lyon*, **2**, 1–284.
- Lozouet, P. 1986. Les gastéropodes prosobranches de l’Oligocène supérieur du Bassin de l’Adour (systématique, paléoenvironnements, paléoclimatologie, paléobiogéographie). Unpublished diploma thesis, 475 pp. École Pratique des Hautes Études; Paris.
- Lozouet, P., Lesport, J.F. and Renard, P. 2001. Révision des Gastropoda (Mollusca) du Stratotype de l’Aquitainien (Miocène inf.): site de Saucats “Laricy”, Gironde, France. *Cossmanniana*, Hors série **3**, 1–189.
- Łomnicki, A.M. 1895. Atlas Geologiczny Galicyi. Tekst do zeszytu siódmego, 128 pp. Wydawnictwo Komisji Fizyograficznej Akademii Umiejętności; Kraków.
- Mandic, O., Harzhauser, M., Spezzaferri, S. and Zuschin, M. 2002. The paleoenvironment of an early Middle Miocene Paratethys sequence in NE Austria with special emphasis on paleoecology of mollusks and foraminifera. *Geobios*, **24**, 193–206.
- Mandic, O., Sant, K., Kallanxhi, M.-E., Čorić, S., Theobalt, D., Grunert, P., de Leeuw, A., and Krijgsman, W. 2019. Integrated bio-magnetostratigraphy of the Badenian reference section Ugljevik in southern Pannonian Basin – implications for the Paratethys history (middle Miocene, Central Europe). *Global and Planetary Change*, **172**, 374–395.
- Marquet, R. 1998. De Pliocene Gastropodenfauna van Kallo

- (Oost-Vlaanderen, België). Belgische *Vereniging voor Paleontologie v.z.w.*, **17**, 1–246.
- Marshall, B.A. 1988. Thysanodontinae: a new subfamily of the Trochidae (Gastropoda). *Journal of Molluscan Studies*, **54**, 215–229.
- Marshall, B.A. 1995. A Revision of the Recent *Calliostoma* Species of New Zealand (Mollusca: Gastropoda: Trochoidea). *The Nautilus*, **108** (4), 83–127.
- Marshall, B.A. 1999. A Revision of the Recent Solariellinae (Gastropoda: Trochoidea) of the New Zealand Region. *The Nautilus*, **113** (1), 4–42.
- Martyn, T. 1784. The Universal Conchologist, 1, pls 1–40. Published by the author; London.
- 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. *Bulletin of the Academy of Sciences of the USSR, series Geology*, **1958** (12), 73–93. [In Russian]
- Mayer, K. 1853. Verzeichniss der in der marinen Molasse der schweizerisch-schwäbischen Hochfläche enthaltenen fossilen Mollusken. *Mitteilungen der Naturforschenden Gesellschaft Bern*, **1853**, 76–106.
- Mayer, M.C. 1862. Description de Coquilles fossiles des terrains tertiaires supérieurs (suite). *Journal de Conchyliologie*, **10**, 261–275.
- Mayer, K. 1872. Systematisches Verzeichniss der Versteinerungen des Helvetian der Schweiz und Schwabens. *Beiträge zur geologischen Karte der Schweiz*, **11**, 477–511.
- McLean, J.H. 2012. Detrital feeding in *Xenostoma inexpectans*, new genus, new species, and new subfamily Xenostomatinae of Calliostomatidae (Gastropoda: Vetigastropoda), hosted by hexactinellid sponges of the Aleutian Islands, Alaska. *The Nautilus*, **126** (3), 89–97.
- Mikhailovsky, G. 1903. Die Mediterran-Ablagerungen von Tomakowka (Gouvernement Jekaterinoslaw). *Mémoires du Comité Géologique*, **13** (4), 1–311. [In Russian and German]
- Mikuž, V. 2009. Miocene gastropods from the vicinity of Šentjernej and from other localities in the Krka Basin, Slovenia. *Folia Biologica et Geologica*, **50** (2), 5–69.
- Millet [de la Turtaudière], P.-A. 1854. Paléontologie de Maine et Loire: comprenant, avec des observations et l'indication des diverses formations géologiques du département de Maine et Loire, un relevé des roches, des minéraux et des fossiles qui se rapportent à chacune d'elles, 187 pp. Cosnier et Lachèse; Angers.
- MolluscaBase 2019. <http://www.molluscabase.org> accessed on 15<sup>th</sup> September 2019.
- Monterosato, T.A. di 1879. Notizie intorno ad alcune conchiglie delle coste d'Africa. *Bullettino della Società Malacologica Italiana*, **5**, 213–233.
- Monterosato, T. di 1884. Nomenclatura generica e specifica di alcune conchiglie mediterranee, 152 pp. Virzi; Palermo.
- Montfort, D. de 1810. Conchyliologie systématique, et classification méthodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des Coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées, 676 pp. F. Schoell; Paris.
- Ney, R. 1969. Structural stages in the north-eastern border of the Carpathian fore-deep. *Prace Geologiczne*, **53**, 5–106. [In Polish with English summary]
- Nikolov, P.I. 1993. Some molluscs from the Badenian (Middle Miocene) west of Pleven (Central Northern Bulgaria). I. Gastropoda: orders Archaeogastropoda and Mesogastropoda. *Geologica Balcanica*, **23** (6), 61–72.
- Nikula, R., Spencer, H.G. and Waters J.M. 2012. Passive rafting is a powerful driver of transoceanic gene flow. *Biology Letters*, **9** (1), 20120821.
- Palcu, D.V., Tulbure, M., Bartol, M., Kouwenhoven, T.J. and Krijgsman, W. 2015. The Badenian–Sarmatian Extinction Event in the Carpathian foredeep basin of Romania: paleogeographic changes in the Paratethys domain. *Global and Planetary Change*, **133**, 346–358.
- Palcu, D.V., Golovina, L.A., Vernyhorova, Y.V., Popov, S.V. and Krijgsman, W. 2017. Middle Miocene paleoenvironmental crises in Central Eurasia caused by changes in marine gateway configuration. *Global and Planetary Change*, **158**, 57–71.
- Palcu, D.V., Popov, S.V., Golovina, L.A., Kuiper, K.F., Liu, S. and Krijgsman, W. 2019. The shutdown of an anoxic giant: magnetostratigraphic dating of the end of the Maikop Sea. *Gondwana Research*, **67**, 82–100.
- Papp, A. 1954. Die Molluskenfauna im Sarmat des Wiener Beckens. *Mitteilungen der Geologischen Gesellschaft in Wien*, **45**, 1952, 1–112.
- Passendorfer, E. 1938. Rzut oka na dotychczasową działalność Towarzystwa Muzeum Ziemi. *Wiadomości Muzeum Ziemi*, **1** (2–3), 72–80.
- Payraudeau, B.C. 1826. Catalogue descriptif et méthodique des annélides et des mollusques de l'île de Corse, 218 pp. Béchét; Paris.
- Pennant, T. 1777. The British zoology, 4. Crustacea, Mollusca, Testacea, 154 pp. Benjamin White; London.
- Petryczenko, O.I., Panow, G.M., Peryt, T.M., Srebrodolski, B.I., Poberežski, A.W. and Kowalewicz, W.M. 1994. Outline of geology of the Miocene evaporite formations of the Ukrainian part of the Carpathian Foredeep. *Przegląd Geologiczny*, **42** (9), 734–737. [In Polish]
- Peyrot, A. 1938. Les mollusques testacés univalves des dépôts Helvétiens du Bassin Ligérien. Catalogue critique, descriptif et illustré. *Actes de la Société Linnéenne de Bordeaux*, **89**, 1–361.
- Philippi, R.A. 1836. Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, quae in itinere suo observavit. Vol. 1, 268 pp. Schropp; Berolini.

- Philippi, R.A. (Ed.) 1845. Abbildungen und Beschreibungen neuer oder wenig gekannter Conchilien unter Mithilfe mehrerer deutscher Conchyliologen. Volume I, 187–204. Fischer; Cassel.
- Philippi, R.A. 1847. Versuch einer systematischen Eintheilung des Geschlechtes Trochus. *Zeitschrift für Malakozoologie*, **4**, 17–26.
- Piller, E.W. and Harzhauser, M. 2005. The myth of the brackish Sarmatian Sea. *Terra Nova*, **17** (5), 450–455.
- Piller, W.E., Harzhauser, M. and Mandic, O. 2007. Miocene Central Paratethys stratigraphy: current status and future directions of stratigraphy. *Stratigraphy*, **4**, 151–168.
- Pinna, G. and Spezia, L. 1978. Catalogo dei Tipi del Museo Civico di Storia Naturale di Milano; V. I Tipi dei Gastropodi fossili. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **119** (2), 125–180.
- Pisera, A. 1985. Paleoecology and lithogenesis of the Middle Miocene (Badenian) algal-vermetid reefs from the Roztocze Hills, south-eastern Poland. *Acta Geologica Polonica*, **35**, 89–155.
- Popov, S.V., Rögl, F., Rozanov, A.Y., Steininger, F.F., Shcherba, I.G. and Kováč, M. 2004. Lithological-Paleogeographic maps of Paratethys. 10 maps Late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg*, **250**, 1–46.
- Poppe, G.T. and Goto, Y. 1991. European Seashells. Volume I (Polyplacophora, Caudofoveata, Solenogastera, Gastropoda), 352 pp. Verlag Christa Hemmen; Wiesbaden.
- Pusch, G.G. 1837. Polens Paläontologie oder Abbildung und Beschreibung der vorzüglichsten und der noch unbeschriebenen Petrefakten aus den Gebirgsformationen in Polen, Volhynien und den Karpathen nebst einigen allgemeinen Beiträgen zur Petrefaktenkunde und einem Versuch zur Vervollständigung der Geschichte des Europäischen Auer-Ochsen, 218 pp. Schweizerbart; Stuttgart.
- Quinn, J.F. 1992. New Species of *Calliostoma* Swainson, 1840 (Gastropoda: Trochidae), and Notes on Some Poorly Known Species from the Western Atlantic Ocean. *The Nautilus*, **106** (3), 77–114.
- Rafinesque, C.S. 1815. Analyse de la nature, ou tableau de l'univers et des corps organisés, 224 pp. Jean Barravecchia; Palerme.
- Reuss, A.E. 1867. Die fossile Fauna der Steinsalzablagerung von Wieliczka in Galizien. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftlichen Classe*, **55**, 17–183.
- Risso, A. 1826. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, 4, Mollusques, 439 pp. F.-G. Levrault; Paris.
- Rögl, F. 1998. Palaeogeographic Considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien*, **99A**, 279–310.
- Rögl, F. 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geologica Carpathica*, **50** (4), 339–349.
- Rossi Ronchetti, C. 1951. I Tipi della “Conchiologia fossile subappennina” di G. Brocchi. *Rivista Italiana di Paleontologia e Stratigrafia*, **5** (1), 1–89.
- Sacco, F. 1896. I Molluschi dei terreni terziarii del Piemonte e della Liguria, Parte 21. (Naricidae, Modulidae, Phasianellidae, Turbinidae, Trochidae, Delphinulidae, Cyclostrematidae e Tornidae), 65 pp. Carlo Clausen; Torino.
- Saint Martin, J.P., Müller, P., Moissette, P. and Dulai, A. 2000. Coral microbialite environment in a Middle Miocene reef of Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **160**, 179–191.
- Salis Marschlins, C.U. von 1793. Reisen in verschieden Provinzen den Königreichs Neapel. Volume I, 442 pp. Ziegler; Zurich and Leipzig.
- Salvini-Plawen, L. 1980. A reconsideration of systematic in the Mollusca (Phylogeny and higher classification). *Malacologia*, **19** (2), 249–278.
- Sant, K., Palcu, D., Mandic, O. and Krijgsman, W. 2017. Changing seas in the Early–Middle Miocene of Central Europe: a Mediterranean approach to Paratethyan stratigraphy. *Terra Nova*, **29**, 273–281.
- Sant, K., Palcu, D.V., Turco, E., Di Stefano, A., Baldassini, N., Kouwenhoven, T., Kuiper, K.F. and Krijgsman, W. 2019. The mid-Langhian flooding in the eastern Central Paratethys: integrated stratigraphic data from the Transylvanian Basin and SE Carpathian Foredeep. *International Journal of Earth Sciences*, **108**, 2209–2232.
- Sasaki, T. 1998. Comparative anatomy and phylogeny of the Recent Archaeogastropoda (Mollusca: Gastropoda). *The University Museum, The University of Tokyo, Bulletin*, **38**, 1–223.
- Schaffer, F.X. 1912. Das Miocän von Eggenburg. Die Fauna der ersten Mediterranstufe des Wiener Beckens und die geologischen Verhältnisse der Umgebung des Manhartsberges in Niederösterreich. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, **22**, 127–193.
- Schulz, H.-M., Bechtel, A. and Sachsenhofer, R.F. 2005. The birth of the Paratethys during the Early Oligocene: From Tethys to an ancient Black Sea analogue? *Global and Planetary Change*, **49**, 163–176.
- Schultz, O. 1969. Die Vertreter von *Diloma* (*Paroxystele* nov. subgen.) (Trochidae, Gastropoda) im Neogen Europas. *Anzeiger der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse*, **106** (12), 217–220.
- Schultz, O. 1971. Zur Phylogenie und Paläogeographie von *Diloma* (*Paroxystele* Schultz, 1969) (Trochidae, Gastropoda) im Jungtertiär Europas. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **5**, 306–313.
- Shuto, T. 1974. Larval ecology of prosobranch gastropods and its



- bearing on biogeography and paleontology. *Lethaia*, **7** (3), 239–256.
- Sieber, R. 1946. Eine Fauna der Grunder Schichten von Gunterdsdorf und Immendorf in Niederösterreich (Bezirk Hollabrunn). *Verhandlungen der Geologischen Bundesanstalt*, **1946** (7–9), 107–122.
- Sieber, R. 1953. Die Tortonfauna von Pötzleinsdorf (Wien, 18. Bezirk). *Verhandlungen der Geologischen Bundesanstalt*, **1953** (3), 184–195.
- Simionescu, I. and Barbu, I.Z. 1940. La faune sarmatienne de Roumanie. *Memoriile Institutului Geological României*, **3**, 1–194.
- Sincov, I. 1875. Description of new and poorly studied forms of shells from Tertiary formations of Novorossia. Article 2. *Zapisok Novorossijskago Obshestva Estestvoispytatelej, Odessa*, **3**, 41–59. [In Russian]
- Sladkovskaya, M.G. 2017. Trochidae (Gastropoda) from the Sarmatian Basin of the Eastern Paratethys. *Paleontological Journal*, **51** (14), 1453–1583.
- Smriglio, C., Di Giulio, A., Mariottini, P. 2014. Description of two new *Jujubinus* species (Gastropoda: Trochidae) from the Sicily Channel, with notes on the *Jujubinus curinii* species complex. *Zootaxa*, **3815** (4), 583–590.
- Sohl, N.F. 1998. Upper Cretaceous Trochacean Gastropods from Puerto Rico and Jamaica. *Palaeontographica Americana*, **60**, 1–109.
- Spadini, V. 2006. Il genere *Clanculus* Monfort, 1810 (Gastropoda: Trochidae) nel Pliocene senese (Toscana, Italia). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, **147** (II), 211–237.
- Steininger, F. 1963. Die Molluskenfauna aus dem Burdigal (Unter-Miozän) von Fels am Wagram in Niederösterreich. *Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Denkschriften*, **110** (5), 1–88.
- Stoliczka, F. 1868. The Gastropoda. Cretaceous Fauna of Southern India. *Palaeontologia Indica*, being figures and descriptions of the organic remains procured during the progress of the geological Survey of India. *Memoirs of the Geological Survey of India*, ser. 5, **2** (7–10), 285–498.
- Strausz, L. 1954. Les gastropodes du méditerranéen supérieur (tortonien) de Várpálot. *Geologica Hungarica, series palaeontologica*, **25**, 1–150. [In Hungarian with French summary]
- Strausz, L. 1962. Magyarországi miocén-mediterrán csigák határozója, 371 pp. Akadémiai Kiadó; Budapest.
- Strausz, L. 1966. Die miozän-mediterranen Gastropoden Ungarns, 693 pp. Akadémiai Kiadó; Budapest.
- 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., Gontsharova, I.A. and Popov, S.V. 1998. The bivalve faunas as a basis for reconstruction of the Middle Miocene history of the Paratethys. *Acta Geologica Polonica*, **48**, 285–342.
- 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 Popov, S.V. 1996. Genus *Acanthocardia* (Bivalvia) from the Middle Miocene of the Paratethys. *Prace Muzeum Ziemi*, **43**, 17–37.
- Swainson, W. 1840. A treatise on malacology or shells and shell-fish, 419 pp. Longman; London.
- Śliwiński, M., Bąbel, M., Nejbort, K., Olszewska-Nejbort, D., Gąsiewicz, A., Schreiber, B.Ch., Benowitz, J.A. and Layer, P. 2012. Badenian–Sarmatian chronostratigraphy in the Polish Carpathian Foredeep. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **326–328**, 12–29.
- Švagravský, J. 1957. Einige neue miozäne Vertreter der Familie Trochidae. *Geologický Sborník*, **8** (2), 204–225. [In Slovak with German summary]
- Švagravský, J. 1971. Das Sarmat der Tschechoslowakei und seine Molluskenfauna. *Acta Geologica et Geographica Universitatis Comenianae. Geologica*, **20**, 1–476.
- Švagravský, J. 1981. Lithofazielle Entwicklung und Molluskenfauna des oberen Badeniens (Miozän M<sub>4d</sub>) in dem Gebiet Bratislava–Devínska Nová Ves. *Západné Karpaty, série paleontológia*, **7**, 5–204.
- Švagravský, J. 1982. Gastropoda, Prosobranchia Teil. I: Archaeogastropoda und Mesogastropoda des oberen Badeniens von Borský Mikuláš (NO–Teil des Wiener Beckens) und ihre stratigraphische Bedeutung. *Geologický Zborník, Geologica Carpathica*, **33** (1), 3–50.
- Teisseyre, W. 1900. Atlas Geologiczny Galicyi. Tekst do zeszytu ósmego, 330 pp. Wydawnictwo Komisji Fizyograficznej Akademii Umiejetności; Kraków.
- Thiele, J. 1893. Das Gebiss der Schnecken zur Begründung einer Natürlichen Classification. Untersuch von Professor Dr. F.H. Troschel, Fortgesetzt von Dr J. Thiele, **2** (8), 337–409. Nicolaische Verlags-buchhandlung R. Stricker; Berlin.
- Thiele, J. 1924. Revision des Systems der Trochacea. *Mitteilungen aus dem Zoologischen Museum in Berlin*, **11**(1), 49–72.
- Thivaoui, D., Harzhauser, M. and Koskeridou, E. 2019. Early Miocene Gastropods from the Felli Section (Proto-Mediterranean Sea, NW Greece). *Geodiversitas*, **41** (8), 323–366.
- Turton, W.H. 1932. Marine Shells of Port Alfred, S. Africa, 331 pp. Humphrey Milford; London.
- Urbaniak, J. 1974. Stratigraphy of Miocene beds in the valley Dunajec near Tarnów. *Prace Geologiczne*, **86**, 1–89. [In Polish with Russian and English summary]
- Uribe, J.E., Williams, S.T., Templado, J., Buge, B. and Zardoya R. 2017a. Phylogenetic relationships of Mediterranean and North-East Atlantic Cantharidinae and notes on Stomatellinae (Vetigastropoda: Trochidae). *Molecular Phylogenetics and Evolution*, **107**, 64–79.

- Uribe, J.E., Williams, S.T., Templado, J., Abalde, S. and Zardoya, R. 2017b. Denser mitogenomic sampling improves resolution of the phylogeny of the superfamily Trochoidea (Gastropoda: Vetigastropoda). *Journal of Molluscan Studies*, **83** (1), 111–118.
- Vermeij, G.J. and Signor, P.W. 1992. The geographic, taxonomic and temporal distribution of determinate growth in marine gastropods. *Biological Journal of the Linnean Society*, **47**, 233–247.
- Wenz, W. 1938. Gastropoda. Teil 1: Allgemeiner Teil und Probranchia. In: Schindewolf, O.H. (Ed.), *Handbuch der Paläozoologie*, **6** (3), 241–480. Gebrüder Borntraeger; Berlin.
- Willan, R.C. 2002. Description of a new bathyal species of *Calliostoma* (Mollusca: Trochoidea: Calliostomatidae) from the Arafura seaway. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory*, **18**, 9–14.
- Williams, S.T. 2012. Advances in molecular systematics of the vetigastropod superfamily Trochoidea. *Zoologica Scripta*, **41** (6), 571–595.
- Williams, S.T., Donald, K.M., Spencer, H.G. and Nakano, T. 2010. Molecular systematics of the marine gastropod families Trochidae and Calliostomatidae (Mollusca: Superfamily Trochoidea). *Molecular Phylogenetics and Evolution*, **54**, 783–809.
- Williams, S.T., Karube, S. and Ozawa, T. 2008. Molecular systematics of Vetigastropoda: Trochidae, Turbinidae and Trochoidea redefined. *Zoologica Scripta*, **37** (5), 483–506.
- Winckworth, R. 1932. The British marine mollusca. *Journal of Conchology*, **19** (7), 211–252.
- Wood, S.V. 1842. A catalog of shells from the Crag. *The Annals and Magazine of Natural History*, **9** (61), 527–544.
- Wysocka, A. and Jasionowski, M. (Eds) 2006. Przebieg i zmienność sedymentacji w basenach przedgórkich. Materiały konferencyjne: Przewodnik sesji terenowych, streszczenia referatów i posterów. II Polska Konferencja Sedymentologiczna Pokos2, IX Krajowe Spotkanie Sedymentologów. Zwierzyniec 20–23.06.2006, 178 pp. Instytut Geologii Podstawowej Wydział Geologii UW; Warszawa. [In Polish, some articles with English summary]
- Wysocka, A., Radwański, A., Górka, M., Bąbel, M., Radwańska, U. and Złotnik, M. 2016. The Middle Miocene of the Fore-Carpathian Basin (Poland, Ukraine, Moldova). *Acta Geologica Polonica*, **66**, 351–401.
- Yochelson, E.L. 1956. Permian Gastropoda of the southwestern United States. 1. Euomphalacea, Trochonematacea, Pesudophoracea, Anomphalacea, Craspedostomatacea, and Platyceratacea. *Bulletin of the American Museum of Natural History*, **110** (3), 173–276.
- Zelinskaya, V.A., Kulichenko, V.G., Makarenko, D.E. and Sorochan, E.A. 1968. Palaeontological guide-book. Volume I: Palaeogene and Miocene bivalves from the Ukraine, 297 pp. Naukova Dumka; Kiev. [In Russian]
- Zilch, A. 1934. Zur Fauna des Mittel-Miocäns von Kostež (Banat). Typus-Bestimmung und Tafeln zu O. Boettger's Bearbeitungen. *Senckenbergiana*, **16** (4–6), 193–302.
- Zunino, M. and Pavia, G. 2009. Lower to Middle Miocene mollusc assemblages from the Torino Hills (NW Italy): synthesis of new data and chronostratigraphical arrangement. *Rivista Italiana di Paleontologia e Stratigrafia*, **115** (3), 349–370.
- Zuschin, M., Harzhauser, M. and Mandic, O. 2007. The stratigraphic and sedimentologic framework fine-scale faunal replacements in the Middle Miocene of the Vienna Basin (Austria). *Palaios*, **22**, 285–295.
- Zuschin, M., Harzhauser, M. and Sauermoser, K. 2006. Patchiness of local species richness and its implication for large-scale diversity patterns: an example from the middle Miocene of Paratethys. *Lethaia*, **39**, 65–78.

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## APPENDIX 1

Parameters of the specimens studied. All specimens are from the Badenian and Langhian (middle Miocene) of western Ukraine (U), Poland (P) and France (F), unless stated otherwise. NWS – number of shell whorls, HS – shell height, WS – shell width, WP – width of protoconch, \* – shell without preserved protoconch or shell without preserved protoconch and the first teleoconch whorls.

Species	Locality and age	Repository and inventory number	Illustrated herein	NWS	HS [mm]	WS [mm]	WP [mm]
<i>Clanculus (Clanculopsis) baccatus</i>	Pontlevoy (F)	MZ VIII Mg 451/1	Text-fig. 3D	5.5*	11.3	11.3	-
<i>Clanculus (Clanculopsis) krachi</i>	Oles'ko (U)	MZ VIII Mg 4522	Text-fig. 2A	5.0*	9.2	9.5	-
<i>Clanculus (Clanculopsis) robustus</i>	Lidykhiv (U)	MZ VIII Mg 4520/1	Text-fig. 3C	5.5*	10.0	10.0	-
	Saryi Pochaiv (U)	MZ VIII Mg 4521/1	Text-fig. 3A	5.5*	10.8	10.5	-
		MZ VIII Mg 4521/2	Text-fig. 3B	5.75*	11.0	11.3	-
	Rybnica (P)	ZNG PAN A-I-50/1557a	-	4.5*	11.0	12.0	-
<i>Clanculus (Clanculopsis) tuberculatus</i>	Zalistsi (U)	MZ VIII Mg 4530/1	Text-fig. 4B	5.5*	9.4	9.7	-
		MZ VIII Mg 4531/1	Text-fig. 4A	5.0*	9.4	9.7	-
		SPbGU 3/444	-	6.0	11.5	11.2	-
	Saryi Pochaiv (U)	MZ VIII Mg 4534/1	Text-fig. 4C	6.25*	11.8	9.2	-
	Węglin (P)	MZ VIII Mg 4704/1	Text-fig. 5A	6.5*	10.5	8.0	-
		MZ VIII Mg 4704/2	Text-fig. 5B	7.0	9.7	8.0	-
		MZ VIII Mg 4704/3	Text-fig. 5C	6.0*	9.4	8.6	-
		MZ VIII Mg 4704/4	Text-fig. 5D	7.0	9.0	9.2	-
		MZ VIII Mg 4704/5	Text-fig. 5E	6.25*	11.5	10.3	-
		MZ VIII Mg 4704/6	Text-fig. 5F	6.25*	9.5	8.3	-
MZ VIII Mg 4704/7		Text-fig. 5G	5.0*	8.5	8.3	-	
<i>Gibbula affinis</i>	Rydomył' (U)	MZ VIII Mg 4542/1	Text-fig. 6F	7.5	9.8	7.8	-
		MZ VIII Mg 4542/3	Text-fig. 6A	6.5	6.2	4.8	0.28
	Zalistsi (U)	MZ VIII Mg 4545/1	Text-fig. 6B	4.75	3.2	3.6	0.26
	Zhukivtsi (U)	MZ VIII Mg 641/1	Text-fig. 6C	7.0	8.6	6.5	-
		MZ VIII Mg 641/2	Text-fig. 6D	7.0	7.8	6.7	-
		MZ VIII Mg 641/3	Text-fig. 6E	6.5	7.2	6.2	-
		SPbGU 3/426.1	-	6.0	6.9	4.7	-
	SPbGU 3/426.2	-	5.0	4.5	4.3	-	
<i>Gibbula biangulata</i>	Saryi Pochaiv (U)	MZ VIII Mg 4548/1	Text-fig. 7B	3.75	1.9	1.8	-
		ZNG PAN I-A-50/1591a	-	6.5	8.0	7.5	-
	Varivtsi (U)	MZ VIII Mg 4682	Text-fig. 7A	5.0	2.9	3.4	0.21
	Zalistsi (U)	ZNG PAN I-A-50/1588	-	6.0	6.5	6.5	-
		ZNG PAN I-A-50/1589	-	5.5	4.5	4.5	-
		SPbGU 3/424	-	6.0	6.6	6.5	-
		Zhukivtsi (U)	ZNG PAN I-A-50/1590a	Text-fig. 7C	7.0	9.5	8.4
	ZNG PAN I-A-50/1590b	Text-fig. 7D	7.0	9.0	8.0	-	
<i>Gibbula dzieduszyckii</i>	Oles'ko (U)	MZ VIII Mg 4566/1	Text-fig. 8C	5.5*	7.3	6.2	-
		ZNG PAN A-I-50/1625	-	5.25*	7.1	6.4	-
		ZNG PAN A-I-50/1626a	-	5.0*	5.9	5.2	-
		ZNG PAN A-I-50/1626b	-	6.0	5.8	5.3	-
	Zalistsi – Zhabiak ravine (U)	MZ VIII Mg 4567/1	Text-fig. 8B	6.0	3.8	4.3	~0.20
	MZ VIII Mg 4567/2	Text-fig. 8A	6.25	4.7	4.6	~0.22	
<i>Gibbula miocaenica</i>	Yaseniv (U)	MZ VIII Mg 4568/1	Text-fig. 9D	5.5	4.2	5.0	-
	Sataniv (U)	MZ VIII Mg 4687/1	Text-fig. 9A	7.0*	25.2	21.3	-
		MZ VIII Mg 4687/2	Text-fig. 9B	7.0*	23.0	19.5	-
		MZ VIII Mg 4687/3	Text-fig. 9C	5.25*	8.0	8.2	-
	Węglinek (P)	ZNG PAN A-I-87/82a.1	-	5.25*	26	23	-
		ZNG PAN A-I-87/82a.2	-	5.75*	24	21	-
	Ferrière-Larçon (F)	MZ VIII Mg 2707/1	Text-fig. 9E	5.0*	6.4	7.5	-
MZ VIII Mg 2707/2		Text-fig. 9F	5.0*	6.0	6.7	-	



Species	Locality and age	Repository and inventory number	Illustrated herein	NWS	HS [mm]	WS [mm]	WP [mm]	
<i>Gibbula novemcincta</i>	Bilozirka (U)	MZ VIII Mg 4572/1	Text-fig. 11B	4.5	2.6	4.6	-	
	Korostova (U)	MZ VIII Mg 4573	Text-fig. 11G	6.5	6.5	8.9	-	
	Shushkivtsi (U)	MZ VIII Mg 4576/1	-	-	5.5*	9.5	11.5	-
		MZ VIII Mg 4576/2	Text-fig. 11D	Text-fig. 11D	5.0*	8.5	10.0	-
		ZNG PAN A-I-50/1639a	-	-	5.0*	9.6	9.6	-
		ZNG PAN A-I-50/1639b	-	-	5.0*	7.9	9.7	-
	Vyshhorodok (U)	MZ VIII Mg 4577	Text-fig. 11F	Text-fig. 11F	6.5	6.3	8.5	-
	Zalistsi (U)	MZ VIII Mg 4578/1	Text-fig. 11A	Text-fig. 11A	6.0	4.8	6.7	-
MZ VIII Mg 4578/2		Text-fig. 11E	Text-fig. 11E	5.0*	8.3	9.0	-	
MZ VIII Mg 4579/1		Text-fig. 11C	Text-fig. 11C	5.5*	7.9	8.7	-	
<i>Gibbula podhorcensis</i>	Varivtsi (U)	MZ VIII Mg 4688	Text-fig. 12A	Text-fig. 12A	5.0	2.9	3.6	0.20
	Pidhirska (U)	ZNG PAN A-I-50/1742	-	-	4.25	1.8	2.5	-
<i>Gibbula puschie</i>	Rydomyl' (U)	MZ VIII Mg 4558/1	Text-fig. 13A	Text-fig. 13A	6.5	4.8	4.7	0.24
		MZ VIII Mg 4558/2	Text-fig. 13B	Text-fig. 13B	6.5	5.1	5.3	0.23
		MZ VIII Mg 4558/3	Text-fig. 13G	Text-fig. 13G	7.0*	22.2	18.6	-
	Shushkivtsi (U)	MZ VIII Mg 4559/1	Text-fig. 13D	Text-fig. 13D	6.5*	16.5	17.5	-
	Vyshhorodok (U)	MZ VIII Mg 4560/1	Text-fig. 13C	Text-fig. 13C	4.0*	2.3	3.0	-
	Zalistsi (U)	MZ VIII Mg 4562/1	Text-fig. 13E	Text-fig. 13E	7.0*	18.3	17.5	-
		MZ VIII Mg 4562/2	Text-fig. 13F	Text-fig. 13F	7.5*	20.8	20.0	-
	Zalistsi – Zhabiak ravine (U)	MZ VIII Mg 4564/1	Text-fig. 13H	Text-fig. 13H	8.0*	25.5	20.7	-
Zhukivtsi (U)	SPbGU 3/405	-	-	~7.0	17.8	17.3	-	
<i>Gibbula teisseyreii</i>	Oles'ko (U)	MZ VIII Mg 4583/1	Text-fig. 14B	Text-fig. 14B	5.0*	8.0	6.1	-
	Zalistsi (U)	MZ VIII Mg 4585/1	Text-fig. 14A	Text-fig. 14A	5.0*	6.5	6.0	-
	Zboriv (U)	ZNG PAN A-I-50/1631	-	-	5.0*	6.3	5.5	-
<i>Gibbula zboroviensis</i>	Varivtsi (U)	MZ VIII Mg 4689	Text-fig. 15A	Text-fig. 15A	5.25	3.2	3.8	0.22
	Zboriv (U)	ZNG PAN A-I-50/1629	-	-	4.25*	4.6	4.7	-
<i>Gibbula</i> sp.	Zalistsi – Zhabiak ravine (U)	MZ VIII Mg 4586	Text-fig. 16A	Text-fig. 16A	6.0	12.9	13.3	-
	Zalistsi (U)	MZ VIII Mg 4587	-	-	2.5*	15.5	17.2	-
<i>Jujubinus celinae</i>	Rydomyl' (U)	MZ VIII Mg 4617/1	Text-fig. 17A	Text-fig. 17A	6.75	6.0	4.5	~0.20
		MZ VIII Mg 4617/2	Text-fig. 17C	Text-fig. 17C	8.0	9.8	6.7	-
		MZ VIII Mg 4617/3	Text-fig. 17D	Text-fig. 17D	6.5*	8.5	6.0	-
	Zalistsi (U)	MZ VIII Mg 4619/1	Text-fig. 17B	Text-fig. 17B	5.0	2.2	2.0	0.22
	Zalistsi – Zhabiak ravine (U)	MZ VIII Mg 4621/1	Text-fig. 17E	Text-fig. 17E	7.0*	10.0	7.3	-
<i>Jujubinus planatus</i>	Oles'ko (U)	MZ VIII Mg 4624	-	-	7.0	9.2	7.2	-
		MZ VIII Mg 4625/1	-	-	6.0*	10.0	8.0	-
	Pidhirska (U)	MZ VIII Mg 4628/1	Text-fig. 18A	Text-fig. 18A	7.25	7.7	5.5	~0.23
	Węglin (P)	MZ VIII Mg 4706	Text-fig. 18B	Text-fig. 18B	6.5	6.2	5.0	0.24
<i>Jujubinus puber</i>	Rydomyl' (U)	MZ VIII Mg 4635/1	Text-fig. 19A	Text-fig. 19A	8.0	9.7	5.4	-
		MZ VIII Mg 4635/2	Text-fig. 19B	Text-fig. 19B	7.0	7.6	5.0	-
		MZ VIII Mg 4635/3	Text-fig. 19C	Text-fig. 19C	7.0	7.3	4.8	-
	Zalistsi – Zhabiak ravine (U)	MZ VIII Mg 4640/1	-	-	6.0*	9.6	6.3	-
<i>Jujubinus striatus</i>	Messina (Sicily), Italy, Recent	MZ VIII Mg 4456/1	Text-fig. 17F	Text-fig. 17F	8.0*	9.9	7.1	-
<i>Jujubinus turricula</i>	Rydomyl' (U)	MZ VIII Mg 4645/1	Text-fig. 20A	Text-fig. 20A	8.0	7.5	4.5	~0.26
		MZ VIII Mg 4645/2	Text-fig. 20B	Text-fig. 20B	7.0	5.0	4.8	-
		MZ VIII Mg 4645/3	Text-fig. 20C	Text-fig. 20C	8.25	7.5	4.6	-
	Zalistsi (U)	MZ VIII Mg 4648/1	Text-fig. 20F	Text-fig. 20F	8.0	8.0	4.8	~0.26
	Zalistsi – Zhabiak ravine (U)	MZ VIII Mg 4649/1	Text-fig. 20D	Text-fig. 20D	8.5	8.2	4.5	0.22
		MZ VIII Mg 4649/2	Text-fig. 20G	Text-fig. 20G	8.25	8.0	5.1	-
	Staryi Pochaiv (U)	MZ VIII Mg 4653/1	Text-fig. 20E	Text-fig. 20E	3.5*	6.4	4.8	-
		MZ VIII Mg 4653/2	-	-	5.75	2.7	2.4	~0.23
Ireon, Greece, Pleistocene	MZ VIII Mg 3353/1	Text-fig. 20H	Text-fig. 20H	8.0	6.8	4.9	-	

Species	Locality and age	Repository and inventory number	Illustrated herein	NWS	HS [mm]	WS [mm]	WP [mm]
<i>Jujubinus vexans</i>	Nadrichne (U)	MZ VIII Mg 4655/1	Text-fig. 21A	3.5	1.1	1.2	-
		MZ VIII Mg 4655/2	-	4.25	1.9	1.7	-
<i>Jujubinus zukowcensis</i>	Yaseniv (U)	MZ VIII Mg 4657	Text-fig. 22B	7.25	9.4	6.8	-
	Oles'ko (U)	MZ VIII Mg 4659/1	Text-fig. 22H	7.5	11.5	9.7	-
	Pidhirtsi (U)	MZ VIII Mg 4663/1	Text-fig. 22A	7.0	8.0	6.2	-
		MZ VIII Mg 4663/2	Text-fig. 22C	7.0*	10.3	7.0	-
	Rydomyl' (U)	MZ VIII Mg 4664/1	Text-fig. 22D	7.5	9.3	7.7	-
		MZ VIII Mg 4664/2	Text-fig. 22F	7.0	9.0	8.2	-
	Zalistsi (U)	MZ VIII Mg 4666/1	Text-fig. 22G	6.0	7.6	7.5	-
	Zhukivtsi (U)	MZ VIII Mg 4668/1	Text-fig. 22E	6.0*	9.3	7.4	-
Węglin (P)	MZ VIII Mg 4707	Text-fig. 22I	7.0	7.5	7.2	-	
<i>Paroxystele orientalis</i>	Chepeli (U)	MZ VIII Mg 4589/1	Text-fig. 23E	7.0*	20.5	22.0	-
	Yaseniv (U)	MZ VIII Mg 4591/1	Text-fig. 23A	5.25	2.3	3.7	~0.26
	Rydomyl' (U)	MZ VIII Mg 4604/1	Text-fig. 23B	5.75	2.9	4.2	0.24
		MZ VIII Mg 4604/2	Text-fig. 23C	5.75	2.8	4.1	0.26
		MZ VIII Mg 4604/3	Text-fig. 23D	6.0	3.4	4.7	~0.26
		MZ VIII Mg 4604/4	Text-fig. 23F	7.0*	22.0	25.0	-
		MZ VIII Mg 4604/5	Text-fig. 23G	7.0*	24.0	28.0	-
	Zalistsi (U)	MZ VIII Mg 4608/1	Text-fig. 23H	8.0*	25.8	30.5	-
		MZ VIII Mg 4608/2	Text-fig. 23I	7.5*	26.5	34.7	-
		MZ VIII Mg 4609/1	Text-fig. 23O	8.0*	25.0	30.0	-
		MZ VIII Mg 4609/2	Text-fig. 23P	7.5*	23.5	30.5	-
		MZ VIII Mg 4609/3	Text-fig. 23N	7.0*	22.0	27.0	-
		MZ VIII Mg 4609/4	Text-fig. 23U	7.5*	25.0	26.0	-
		MZ VIII Mg 4609/5	Text-fig. 23T	7.5*	22.4	25.0	-
		MZ VIII Mg 4609/6	Text-fig. 23S	8.0*	23.0	24.5	-
		MZ VIII Mg 4609/7	Text-fig. 23R	7.25*	28.5	28.0	-
	Varivtsi (U)	MZ VIII Mg 4609/8	Text-fig. 23M	6.0*	27.0	29.2	-
		MZ VIII Mg 4694/1	Text-fig. 23J	7.0*	27.0	29.7	-
		MZ VIII Mg 4694/2	Text-fig. 23K	7.0*	27.0	32.6	-
		MZ VIII Mg 4694/3	Text-fig. 23L	8.0*	33.0	37.5	-
Zalistsi – Zhabiak ravine (U)	MZ VIII Mg 4694/4	Text-fig. 23Q	7.75	25.5	34.0	-	
	MZ VIII Mg 4695/1	Text-fig. 23V	7.0*	25.5	28.5	-	
<i>Calliostoma trigonum</i>	Rydomyl' (U)	MZ VIII Mg 4674/1	Text-fig. 24A	9.0	14.0	11.5	-
		MZ VIII Mg 4674/2	Text-fig. 24B	6.75	6.5	6.1	0.35
		MZ VIII Mg 4674/3	Text-fig. 24C	8.25	11.1	10.3	-
		MZ VIII Mg 4674/4	Text-fig. 24D	9.0	11.2	9.3	-
	Staryi Poचाiv (U)	ZNG PAN A-I-50/1677a	-	9.0	17.8	15.4	-

## APPENDIX 2

Summary of the geographic distribution of the species studied from the Badenian (middle Miocene) deposits of western Ukraine.

Species	Locality	Most important references and this paper
<i>Clanculus (Clanculopsis) krachi</i>	Oles'ko	this study
<i>Clanculus (Clanculopsis) robustus</i>	Lidykhiv, Oles'ko, Pidhirtsi, Shushkivtsi, Saryi Pochaiv, Yaseniv	this study
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Clanculus (Clanculopsis) tuberculatus</i>	Bilka	Eichwald 1830, 1851a, 1853; Pusch 1837
	Hołdy	Friedberg 1928, 1938
	Lidykhiv, Saryi Pochaiv, Vanzhuliv, Vyshhorodok	this study
	Podhirtsi, Yaseniv	Friedberg 1928, 1938; this study
	Oles'ko	Friedberg 1938; this study
	Sataniv	Amitrov 1961; Anistratenko 2000; Anistratenko <i>et al.</i> 2003
	Shushkivtsi	Kowalewski 1937; Friedberg 1938; this study
	Varivtsi	Pusch 1837; this study
	Zalistsi	Eichwald 1830, 1851a, 1853; Pusch 1837; this study
	Zbarazh	Friedberg 1938
	Zhukivtsi	Eichwald 1830, 1851a, 1853; Pusch 1837; Friedberg 1938; this study
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Gibbula affinis</i>	Bilozirka, Korostova	Kowalewski 1937; this study
	Hołdy, Holubytsia, Velyki Birky, Velyki Hlybochok, Zboriv	Friedberg 1928, 1938
	Derman', Stupky	Friedberg 1928
	Domanenka, Plyska	Laskarev 1903
	Oles'ko, Pidhirtsi, Yaseniv, Zalistsi – Zhabiak ravine	Friedberg 1928, 1938; this study
	Rydomyl'	Friedberg 1928; Kowalewski 1936b; this study
	Saryi Pochaiv, Vyshnivets'	Friedberg 1938
	Shushkivtsi	Eichwald 1853; Kowalewski 1937; Friedberg 1938; this study
	Vanzhuliv, Varivtsi, Zalistsi	this study
	Zhukivtsi	Eichwald 1851a, 1853; Friedberg 1928, 1938; this study
not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001	
<i>Gibbula biangulata</i>	Saryi Pochaiv	Friedberg 1928, 1938; this study
	Tarnoruda	Eichwald 1830, 1851a, 1853
	Ternopil'	Hörnes 1856
	Varivtsi, Zalistsi	this study
	Zalistsi – Zhabiak ravine	Friedberg 1928, 1938
	Zhukivtsi	Eichwald 1830, 1851a, 1853; Andrzejowski 1833; Pusch 1837; Friedberg 1938; this study
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Gibbula dzieduszyckii</i>	Oles'ko	Friedberg 1928, 1938; this study
	Velyki Birky	Friedberg 1938
	Yaseniv, Zalistsi – Zhabiak ravine	this study
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001



Species	Locality	Most important references and this paper
<i>Gibbula miocaenica</i>	Kalaharivka, Yaseniv, Zalistsi	this study
	Oles'ko	Friedberg 1938; this study
	Sataniv	Amitrov 1961; this study
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Gibbula novemcincta</i>	Bilozirka	von Buch 1830; Kowalewski 1937; this study
	Korostova	Kowalewski 1937; this study
	Ohryzkivtsi, Vyshhorodok, Zalistsi	this study
	Oles'ko	Friedberg 1938; this study
	Shushkivtsi	du Bois de Montpéroux 1831; Mikhailovsky 1903; Friedberg 1928, 1938; Kowalewski 1937; this study
	Staryi Pochaiv, Vyshnivets', Zhukivtsi	Friedberg 1938
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Gibbula podhorcensis</i>	Pidhirtsi	Friedberg 1928, 1938; this study
	Shushkivtsi	Kowalewski 1937
	Varivtsi, Zalistsi	this study
	not specified	Anistratenko and Anistratenko 2001
<i>Gibbula puschiei</i>	Bilka, Zavadynsi	Eichwald 1830, 1853
	Bilozirka	von Buch 1830; Kowalewski 1937; this study
	Chepeli	Hilber 1882; Łomnicki 1895
	Faschivka, Staryi Pochaiv, Zboriv	Friedberg 1928, 1938
	Holdy	Łomnicki 1895; Friedberg 1928, 1938
	Holubytsia	Hilber 1882; Łomnicki 1895; Friedberg 1928, 1938
	Oles'ko	Hilber 1882; Friedberg 1928, 1938; this study
	Pidhirtsi	Hilber 1882; Łomnicki 1895; Friedberg 1928, 1938; this study
	Rydomyl'	Kowalewski 1936b; this study
	Shushkivtsi	Eichwald 1853; du Bois de Montpéroux 1831; Friedberg 1928, 1938; Kowalewski 1937; this study
	Tarnoruda	Eichwald 1830, 1853; Friedberg 1928, 1938
	Ternopil'	Hilber 1882
	Turivka	Friedberg 1928
	Vanzhuliv, Vyshhorodok	this study
	Varivtsi	Andrzejowski 1830a, 1832b; this study
	Vyshnivets'	Friedberg 1938
	Yaseniv	Łomnicki 1895; Friedberg 1928, 1938; this study
	Zalistsi	Eichwald 1830, 1853; this study
	Zalistsi – Zhabiak ravine	Friedberg 1928, 1938; this study
	Zhukivtsi	Andrzejowski 1830a, 1832b; Eichwald 1830, 1853; Friedberg 1928, 1938; this study
not specified	Eichwald 1851a; Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001	
<i>Gibbula teisseyreii</i>	Bilozirka, Oles'ko, Pidhirtsi, Zalistsi	this study
	Zboriv	Friedberg 1928, 1938
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Gibbula zboroviensis</i>	Varivtsi	this study
	Zboriv	Friedberg 1928, 1938
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Gibbula</i> sp.	Zalistsi, Zalistsi – Zhabiak ravine	this study

Species	Locality	Most important references and this paper
<i>Jujubinus celinae</i>	Bilozirka	Andrzejowski 1833; this study
	Faschivka, Tarnoruda, Velyki Birky, Zboriv	Friedberg 1928, 1938
	Domanenka	Laskarev 1903
	Horodok	Kojumdgieva 1969
	Katerynivka	Andrzejowski 1833
	Korostova	Kowalewski 1937; this study
	Novokostiantyniv	Eichwald 1851a, 1853
	Ohryzkivtsi	Kowalewski 1937
	Oles'ko	Friedberg 1928, 1938; this study
	Rydomył'	Kowalewski 1936b; this study
	Shushkivtsi	du Bois de Montpereux 1831; Friedberg 1928, 1938; Kowalewski 1937; this study
	Saryi Pochaiv	Friedberg 1938
	Varivtsi, Yaseniv, Zalistsi – Zhabiak ravine	this study
	Zalistsi	Laskarev 1903; Friedberg 1938; this study
Zhukivtsi	Friedberg 1938; this study	
<i>Jujubinus planatus</i>	Faschivka, Tarnoruda	Friedberg 1928, 1938
	Oles'ko	Friedberg 1928, 1938; this study
	Pidhirtsi	Friedberg 1928; this study
	Yaseniv	this study
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Jujubinus puber</i>	Bilozirka, Lidykhiv, Oles'ko, Yaseniv	this study
	Domanenka, Pochaiv	Laskarev 1903
	Hołdy, Tarnoruda, Zboriv	Friedberg 1928, 1938
	Pidhirtsi, Saryi Pochaiv, Zalistsi – Zhabiak ravine	Friedberg 1928, 1938; this study
	Rydomył'	Kowalewski 1936b; this study
	Shushkivtsi	Eichwald 1853
	Zalistsi	Laskarev 1903; this study
	Zhukivtsi	Eichwald 1851a, 1853; Laskarev 1903; Friedberg 1938; this study
<i>Jujubinus turricula</i>	Bilka	Eichwald 1830, 1851a
	Dzvyniacha, Lidykhiv, Nadrichne, Varivtsi, Vyshhorodok	this study
	Hołdy, Tarnoruda, Zboriv	Friedberg 1928, 1938
	Holubytisia, Zbarazh	Friedberg 1928
	Korostova	Kowalewski 1937; this study
	Medzhybizh	Eichwald 1830, 1853
	Oles'ko, Yaseniv, Zalistsi – Zhabiak ravine	Friedberg 1928, 1938; this study
	Pidhirtsi	Łomnicki 1895
	Rydomył'	Kowalewski 1936b; this study
	Shushkivtsi	Kowalewski 1937; this study
	Saryi Pochaiv	Eichwald 1830, 1853; Friedberg 1928, 1938; this study
	Turivka	Teisseyre 1900
	Zalistsi	Eichwald 1830, 1851a, 1853; this study
	Zhukivtsi	Eichwald 1830, 1851a, 1853; Andrzejowski 1833; Pusch 1837; Friedberg 1928, 1938; this study
not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001	
<i>Jujubinus vexans</i>	Nadrichne	this study
	not specified	Anistratenko and Anistratenko 2001

Species	Locality	Most important references and this paper
<i>Jujubinus zukowcensis</i>	Bilozirka, Kalaharivka, Korostova, Lidykhiv, Vanzhuliv, Yaseniv, Zalistsi	this study
	Faschivka, Holubytsia	Friedberg 1928
	Hołdy	Friedberg 1928, 1938
	Kabarivtsi, Vyshnivets'	Friedberg 1938
	Ohryzkivtsi	Kowalewski 1937
	Oles'ko, Pidhirtsi, Staryi Pochaiv	Friedberg 1928, 1938; this study
	Rydomył'	Kowalewski 1936b; this study
	Sataniv	Amitrov 1961
	Shushkivtsi	Friedberg 1928, 1938; Kowalewski 1937
	Zalistsi – Zhabiak ravine	Friedberg 1938; this study
	Zhukivtsi	Andrzejowski 1833; Friedberg 1938; this study
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Paroxystele orientalis</i>	Bilka	Eichwald 1830, 1851a, 1853
	Bilozirka	von Buch 1830; Kowalewski 1937; this study
	Chepeli, Dzvyniacha, Kalaharivka, Lidykhiv, Nadrichne, Staryi Pochaiv, Vanzhuliv, Varivtsi, Vyshhorodok	this study
	Hołdy, Holubytsia, Velyki Birky, Zboriv	Friedberg 1928, 1938
	Korostova	Kowalewski 1937; Friedberg 1938; this study
	Kreminna	Eichwald 1830, 1853
	Leworda	Friedberg 1928
	Ohryzkivtsi	Kowalewski 1937; this study
	Oles'ko, Pidhirtsi, Yaseniv, Zalistsi – Zhabiak ravine	Friedberg 1928, 1938; this study
	Rydomył'	Kowalewski 1936b; this study
	Shushkivtsi	du Bois de Montpèreux 1831; Eichwald 1853; Friedberg 1928, 1938; Kowalewski 1937; this study
	Tarnoruda	Eichwald 1853; Friedberg 1928, 1938
	Zalistsi	Eichwald 1830, 1853; this study
	Zhukivtsi	von Buch 1830; Eichwald 1830, 1853; Friedberg 1928, 1938; this study
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001
<i>Calliostoma trigonum</i>	Bilka	Eichwald 1830, 1851a, 1853
	Bilozirka, Nadrichne, Varivtsi, Zalistsi	this study
	Hołdy, Zboriv	Friedberg 1928, 1938
	Holubytsia	Friedberg 1928
	Medzhybizh	Eichwald 1830
	Oles'ko	Friedberg 1928, 1938; this study
	Rydomył'	Kowalewski 1936b; this study
	Shushkivtsi	du Bois de Montpèreux 1831; Eichwald 1853; Kowalewski 1937; this study
	Staryi Pochaiv	Friedberg 1938
	Zalistsi – Zhabiak ravine	Friedberg 1938; this study
	Zhukivtsi	Pusch 1837; Eichwald 1851a, 1853; Friedberg 1938
	not specified	Kulichenko and Sorochan 1968; Anistratenko and Anistratenko 2001

## APPENDIX 3

Palaeogeographic and stratigraphic distribution of the species identified in the Badenian western Ukrainian trochoidean assemblages. \* – Paratethys in the Sarmatian (= late Serravallian) as in Palcu *et al.* (2015, text-fig. 11b). Chronostratigraphic units: A – Aquitanian, Bu – Burdigalian, L – Langhian, Se – Serravallian, To – Tortonian, P – Pleistocene, E – Eggenburgian, Ka – Karpatian, B – Badenian, T – Tarkhanian, K – Konkian, S – Sarmatian = upper Serravallian, M – stage not specified, ? – record unsure.

Species	Northeastern Atlantic		(Proto-) Mediterranean Sea				Western Paratethys	Central Paratethys				Eastern Paratethys	Paratethys*
								Fore-Carpathian Basin					
									Poland	Ukraine			
	Miocene	Miocene	Miocene	Miocene	Pleisto-	Miocene	Miocene	Miocene	Miocene	Miocene	Miocene	Miocene	
middle	upper	lower	middle	upper	cene	lower	lower	middle	middle	middle	middle	middle	
<i>C. (C.) krachi</i>										B	B		
<i>C. (C.) robustus</i>										B	B		S
<i>C. (C.) tuberculatus</i>									B	B	B		
<i>G. affinis</i>			Bu		?To				B	B	B	T, K	S
<i>G. biangulata</i>	M	To	Bu		To		Bu	?Bu	B	B	B		S
<i>G. dzieduszyckii</i>										B	B		
<i>G. miocaenica</i>	M						Bu			B	B		
<i>G. novemcincta</i>									B	B	B		
<i>G. podhorcensis</i>	L								?B	B	B		
<i>G. puschiei</i>			Bu	Se				Ka	B	B	B	T, K	S
<i>G. teisseyrei</i>											B		
<i>G. zboroviensis</i>										B	B		S
<i>Gibbula</i> sp.											B		
<i>J. celinae</i>								?Ka	B	B	B		
<i>J. planatus</i>									B	B	B		S
<i>J. puber</i>				Se					B	B	B		S
<i>J. turricula</i>	Se			Se	To	P			B	B	B		S
<i>J. vexans</i>									B	B	B		
<i>J. zukowcensis</i>										B	B		
<i>P. orientalis</i>			A	Se				E	B	B	B	T, K	S
<i>C. trigonum</i>									B	B	B		