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A SURVEY OF SARMATIAN MOLLUSCS OF THE “*TROCHUS PODOLICUS*” GROUP (GASTROPODA, TROCHOIDEA)

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A Survey of Sarmatian Molluscs of the “*Trochus podolicus*” Group (Gastropoda, Trochoidea). Anistratenko O. Yu., Anistratenko V. V. — The Middle to Late Miocene (Sarmatian) species of the “*Trochus podolicus*” group are a heterogeneous assemblage which is here divided in the *Gibbula podolica* group (6 species) and *Calliostoma podoliciformis* group (4 species), in the families Trochidae and Calliostomatidae, respectively. New data on the biostratigraphy of *C. podoliciformis* (Kolesnikov, 1935) and on the biogeography of *G. laevigatopodolica* (Kolesnikov, 1930), *G. cordieriana* (Orbigny, 1844), *C. hommairei* (Orbigny, 1844) and *C. beaumontii* (Orbigny, 1844) are given. A phylogenetic scheme reflecting the relationships of the species discussed here is proposed. Interpopulation differences for some species are described; they are interpreted as a result of palaeo-environmental differences between the Halician and Borysthenian Gulfs of the Sarmatian Sea.

Key words: Gastropoda, Trochidae, Sarmatian, Ukraine, taxonomy, paleobiogeography.

Обзор сарматских моллюсков группы «*Trochus podolicus*» (Gastropoda, Trochoidea). Анистратенко О. Ю., Анистратенко В. В. — Средне–позднемиоценовые (сарматские) виды группы «*Trochus podolicus*» являются гетерогенным конгломератом видов, который подразделен здесь на группы *Gibbula podolica* (6 видов) и *Calliostoma podoliciformis* (4 вида) в составе семейств Trochidae и Calliostomatidae соответственно. Приведены новые данные по биостратиграфии *C. podoliciformis* (Kolesnikov, 1935) и биогеографии *G. laevigatopodolica* (Kolesnikov, 1930), *G. cordieriana* (Orbigny, 1844), *C. hommairei* (Orbigny, 1844) и *C. beaumontii* (Orbigny, 1844). Предложена филогенетическая схема, отражающая родственные связи обсуждаемых видов. Описаны межпопуляционные отличия некоторых видов; они интерпретируются как результат различия палеоэкологических условий в Галицийском и Борисфенском заливах Сарматского моря.

Ключевые слова: Gastropoda, Trochidae, Сармат, Украина, таксономия, палеобиогеография.

Introduction

Many species of the superfamily Trochoidea Rafinesque, 1815 lived in the Sarmatian Basin of south-eastern Europe. Unfortunately, they are investigated insufficiently up to date, though they are very important for biostratigraphy, and for the phylogeny of the Archaeogastropoda. A critical review of relevant published data, in particular in the works of E. Eichwald (1830, 1853), M. Hörnes (1856), V. P. Kolesnikov (1930 a, b, 1935) and others, and their comparison with modern faunal, systematic and taxonomic data is also required.

Material and methods

The present investigation is mainly based on material deposited at the Institute of Geological Sciences of the National Academy of Sciences of the Ukraine (Kyiv). Also some personal collections are examined and a few lots provided by our colleagues. The investigated material was gathered from outcrops and boreholes of Middle Sarmatian (Bessarabian) deposits in western and southern Ukraine (fig. 1). Altogether more than hundred specimens of the “*Tr. podolicus*” group species identified in studied samples. The distribution of species by locality is given in table 1.

Table 1. Distribution of species by locality
Таблица 1. Распределение видов по местонахождениям

Species	Localities										
	Halician Gulf (West Ukraine)							Borysthenian Gulf (SE Ukraine)			
	LET	ANT	TER	VER	SNI	SUS	IZA	VTA	VBZ	MIH	NIK
<i>Gibbula podolica</i> (Dubois de Montpereux, 1831)	+	+	+	+	+		+	+	+		
<i>G. sulcatopodolica</i> (Kolesnikov, 1930)	+	+	+					+			
<i>G. laevigatopodolica</i> (Kolesnikov, 1930)	+										
<i>G. bargi</i> O. Anistratenko, 1999								+			
<i>G. cordieriana</i> (Orbigny, 1844)											+
<i>G. insperata</i> (Kolesnikov, 1930)	+		+				+	+			
<i>Calliostoma podolicoformis</i> (Kolesnikov, 1935)	+						+				
<i>C. beaumontii</i> (Orbigny, 1844)				+				+			
<i>C. hommairei</i> (Orbigny, 1844)		+									
Number of species in each locality	5	3	3	2	1	2	2	4	1	1	1

Shell characters were studied with an optical stereomicroscope. The comparatorial method has been used as additional method (Shikov, Zatravkin, 1991)¹. It allows comparing independently all of Raup's parameters of the shell tube growth (Raup, 1966).

The comparison of apical angles is also a quite simple and convenient method to distinguish the species treated here. Where a large difference in this character exists in different species of one group, no overlap has been observed. Apical angles proved to be a simple and easy parameter to distinguish species. Often large differences without overlaps were found between closely related species.

LET – quarry 1 km NE of Letichev town, Khmelnytsky region; ANT – quarry NE of Antonovka village, Letichev district, Khmelnytsky region; TER – quarry in N suburb of Terlovka village, Letichev district, Khmelnytsky region; VER – outcrop near Verbka village, Letichev district, Khmelnytsky region; SNI – outcrop near Snitovka village, Letichev district, Khmelnytsky region; SUS – outcrop near Suslovtsy village, Letichev district, Khmelnytsky region; IZA – precipice on the bank of river Goryn, vicinity of Izyaslav town, Khmelnytsky region; VTA – outcrop on the bank of Kakhovsky reservoir near Vishchetarsovka village, Tomakovka district, Dnepropetrovsk region; VBZ – borehole 0154 near Velikaya Belozurka village, Zaporozhskaya region; MIH – borehole 0155 near Mihailovka town, Zaporozhskaya region; NIK – borehole 0359 in Nikopol district, Dnepropetrovsk region

Nomenclatural notes

The species known for a long time as "*Trochus podolicus*" was described by Dubois de Montpereux in 1831. The original description was very short. It only indicated that the surface of the shells is covered by something like furrows or wrinkles. The figures are of very low quality (Dubois de Montpereux, 1831: 42, tabl. 3, fig. 1–3). Dubois identified his species with *Trochus conulus* Eichwald, 1830, but, as this name is preoccupied by *Trochus conulus* Linnaeus, 1758, he proposed the substitution name *Trochus*

¹ The main idea of the comparatorial method is to use a "camera lucida" for the direct comparison of shells which are observed in a standard orientation through stereoscopic microscope oculars, and directly compared with the outlines of reference specimens, usually the type specimens of other species in the same orientation. In many cases (but not always) specific distinctness of the forms can be concluded almost exclusively from the coincidence or non-coincidence of the outlines. The method is widely used by malacologists in the former USSR. We often use it as an additional method. Full description of the method was published in English only by Shikov, Zatravkin (1991). In this paper the method is called "comparatory", but Starobogatov himself proposed (in additional remarks to this paper) to use the word "comparatorial" to emphasize that method based not on ordinary morphological comparison, but on using of "comparator" i. e. camera lucida.

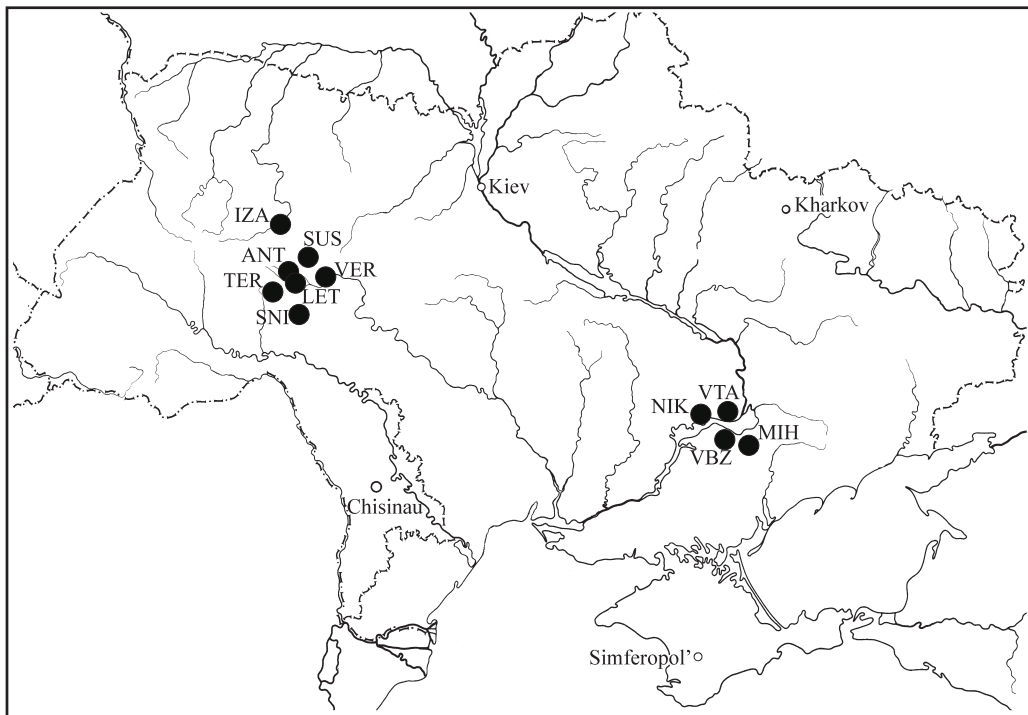


Fig. 1. Localities in West and South Ukraine mentioned in this paper (with abbreviations used).

Рис. 1. Местонахождения в Западной и Южной Украине, упоминаемые в тексте (с принятыми сокращениями).

podolicus. E. Eichwald (1850) agreed with Dubois' suggestion. Later (Eichwald, 1853: 220–221) he split¹ *Trochus podolicus* into 7 “variétés”:

1. Variétés en forme de cône alongé:
 - a) *Trochus podolicus* var. *Trochus beaumontii* d’Orb.
 - b) *Trochus podolicus* var. *Trochus hommairei* d’Orb.
2. Variétés en forme de cône déprimé:
 - c) *Trochus podolicus* Dub.
 - d) *Trochus podolicus* var. *Turbo omaliusii* d’Orb.
 - e) *Trochus podolicus* var. *Trochus cordierianus* d’Orb.
 - f) *Trochus podolicus* var. *Turbo beaumontii* d’Orb.
 - g) *Trochus podolicus* var. *caucasica*”.

Further, M. Hörnes included *Trochus anceps* Eichwald, 1850 and *Trochus sannio* Eichwald, 1853 in the synonymy of *Trochus podolicus*, but gave drawings of very insufficient quality (Hörnes, 1856: pl. 45, fig. 2, a-c). W. Friedberg (1928) attributed *Trochus anceps* and *Trochus sannio* as separate species to *Calliostoma*.

Sarmatian “Trochidae” from Moldova and Ukraine have been studied in details by V. P. Kolesnikov (1930). He distinguished, beside the nominotypical form, “variétés” of “*Trochus podolicus*” on the basis of sculpture characters and shell shape analysis: var. *laevigatopodolicus* Kolesnikov, 1930, var. *sulcatopodolicus* Kolesnikov, 1930, var. *hommairei* Orbigny, 1844, var. *caucasica* Eichwald, 1853.

¹ All these “variétés” are currently considered as species, some of which (*beaumontii*, *hommairei*, *caucasica*) are placed in *Calliostoma*, others (*cordierianus*) in *Gibbula*. V. P. Kolesnikov (1935) attributed *Trochus podolicus* var. *Turbo omaliusii* d’Orb to *Barbotella*. *Calliostoma caucasica* (Eichwald, 1853) is not discussed here, as it belongs to another species group than “*podolica*”. Altogether in the present paper we discuss not all Trochoidea species of the Sarmatian, but only part of them, i.e. belonging to the “*Trochus podolicus*” group.

In his later monograph, V. P. Kolesnikov (1935) raised all aforementioned varieties to species rank. Still later, V. P. Kolesnikov (1939) allocated these species between the genera *Gibbula* and *Calliostoma*. In these genera V. P. Kolesnikov proposed several sections, viz. in *Gibbula*, *Robur* (type species *Trochus robur* Davidashvili, 1932), *Rollandiana* (type species *Trochus rollandianus* Orbigny, 1844) and *Pictiformes* (type species *Monodonta mamilla* Andrzejowski, 1830); and in *Calliostoma* s. str., *Sarmates* (type species *Trochus sarmates* Eichwald, 1850), *Feneoniana* (type species *Trochus feneonianus* Orbigny, 1844), *Anceps* (type species *Trochus anceps* Eichwald, 1850). A description of these sections was not given by V. P. Kolesnikov, but species were attributed to them, and type species were designated. I. A. Korobkov (1955) kept most of the sections proposed by V. P. Kolesnikov. V. P. Kolesnikov (1930) had regarded *Trochus cordierianus* and *Trochus omaliosii* as closely related to *Trochus podolicus*. To *Trochus omaliosii* he attributed some varieties, which he later (Kolesnikov, 1935) raised to species rank, and simultaneously moved them to the genus *Barbotella* Cossmann, 1918.

These publications practically exhaust the works of a systematic character devoted to this group of 'trochids'. Recently the species conglomerate of "*Trochus podolicus*" was divided into the *Gibbula podolica* (= "*Trochus podolicus*" s. str.) Group and the *Calliostoma podolicoformis* Group (Anistratenko, 1999, 2000). As the figure of *Trochus podolicus* s. str., which corresponds best to the original and subsequent descriptions, we accept the figure of the shell represented by V. P. Kolesnikov (1930: tabl. 1, fig. 30).

Because V. P. Kolesnikov never designated types for his species, the lectotypes for four Kolesnikov's species were selected and designated by O. Anistratenko (1999, 2000) on the basis of images according to article 74.4 ICZN (1999). O. Anistratenko (1999) designated the lectotypes for two *Gibbula* species, and in 2000 she also designated the lectotypes for two *Calliostoma* species (tabl. 2).

Class GASTROPODA Cuvier, 1767

Superfamily TROCHOIDEA Rafinesque, 1815

Family TROCHIDAE Rafinesque, 1815

Genus *Gibbula* Risso, 1826

Gibbula podolica (Dubois de Montpereux, 1831) (fig. 2, 1 a, 1 b; fig. 3, 1 a, 1 b)

Syn.: – *conulus* Eichwald, 1830: 221 (*Trochus*) [non Linnaeus 1758]; – *podolicus* Dubois de Montpéroux, 1831: 42, pl. 3, fig. 1–3 (*Trochus*) [nom. nov. pro *Trochus conulus* Eichwald, 1830]; – *podolica* Dubois de Montpéroux – Kolesnikov, 1939: 702 (*Calliostoma*); – *podolica* Dubois de Montpéroux – Anistratenko, 1999: 68–70, fig. 2 a, b (*Gibbula*).

Material examined. 6 (LET); 9 (ANT); 13 (TER); 1 (VER); 1 (SNI); 1 (IZA); 22 (VTA); 2 (VBZ); 1 (MIH).

Description. Shell large, sturdy, peg-top shaped, with 6–7 stepped whorls. Protoconch of up to 1,5 smooth, convex whorls. Initial whorls of the teleoconch with

Table 2. Lectotypes for species assigned to "*Trochus podolicus*" group

Таблица 2. Лектотипы видов группы «*Trochus podolicus*»

Species	Original shell images
<i>Gibbula sulcatopodolica</i> (Kolesnikov, 1930)	Kolesnikov, 1930, pl. 2, fig. 54 (<i>Trochus podolicus</i> var. <i>sulcatopodolica</i>)
<i>Gibbula laevigatopodolica</i> (Kolesnikov, 1930)	Kolesnikov, 1930, pl. 2, fig. 46 (<i>T. podolicus</i> var. <i>laevigatopodolica</i>)
<i>Calliostoma podolicoformis</i> (Kolesnikov, 1935)	Kolesnikov, 1935, pl. 23, fig. 1 (<i>Trochus podolicoformis</i>)
<i>Calliostoma pseudohommairei</i> (Kolesnikov, 1935)	Kolesnikov, 1935, pl. 23, fig. 15 (<i>Trochus pseudohommairei</i>)

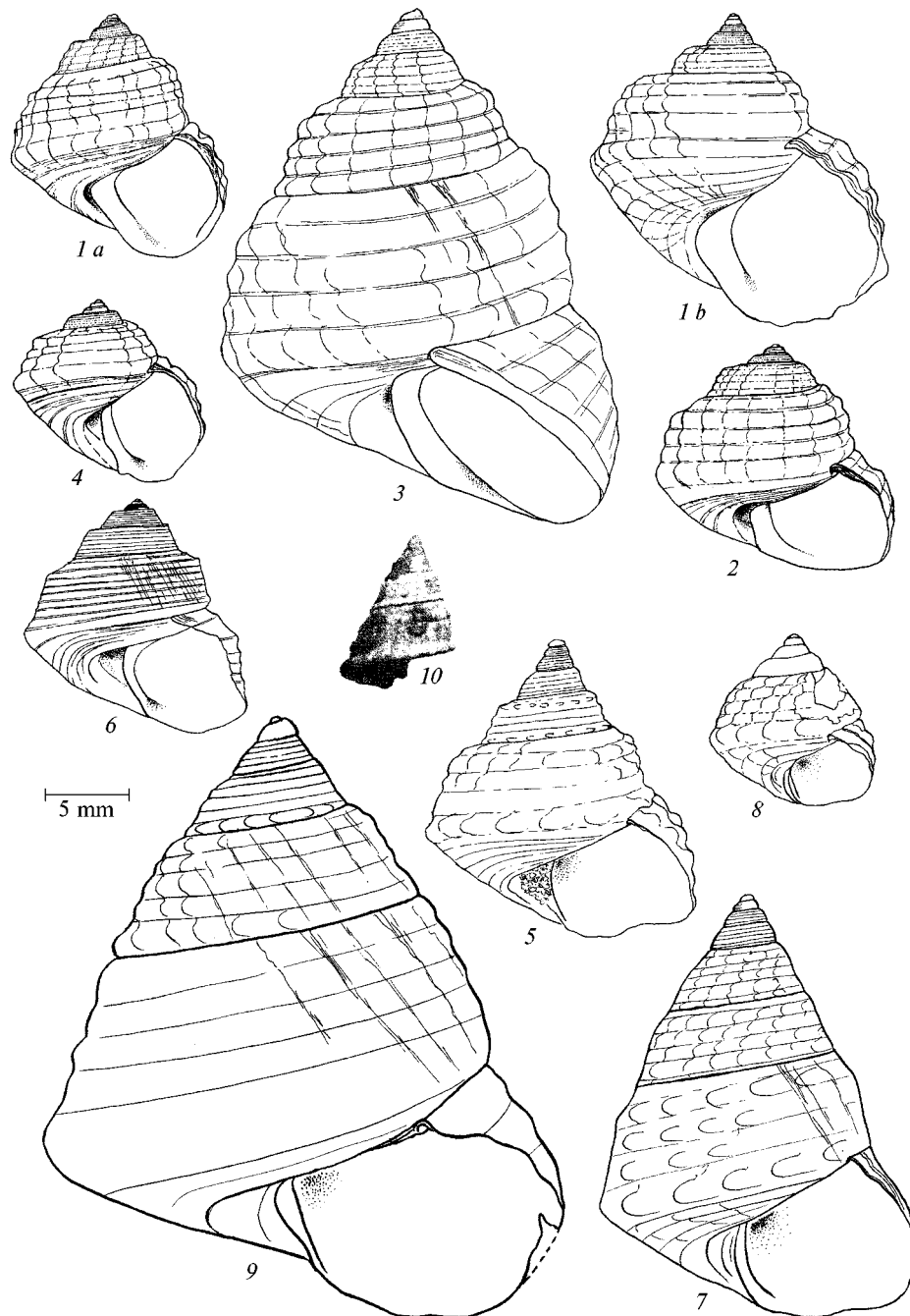


Fig. 2. Shells of the "Trochus podolicus" group species: 1 a, 1 b – *Gibbula podolica* (1 a – shell from Borysthenian Gulf, 1 b – from Halician Gulf); 2 – *G. sulcatopodolica*; 3 – *G. laevigatopodolica*; 4 – *G. bargi* (holotype); 5 – *G. insperata*; 6 – *G. cordieriana*; 7 – *Calliostoma podoliciformis*; 8 – *C. beaumontii*; 9 – *C. hommairei*; 10 – *C. pseudohommairei*. Figures 1–9 – original drawings, 10 – after Kolesnikov (1935).

Рис. 2. Раковины видов группы «Trochus podolicus»: 1 a, 1 b – *Gibbula podolica* (1 a – раковина из Борисфенского залива, 1 b – из Галицийского залива); 2 – *G. sulcatopodolica*; 3 – *G. laevigatopodolica*; 4 – *G. bargi* (голотип); 5 – *G. insperata*; 6 – *G. cordieriana*; 7 – *Calliostoma podoliciformis*; 8 – *C. beaumontii*; 9 – *C. hommairei*; 10 – *C. pseudohommairei*. Фигуры 1–9 – оригинальные рисунки, 10 – по Колесникову (1935).

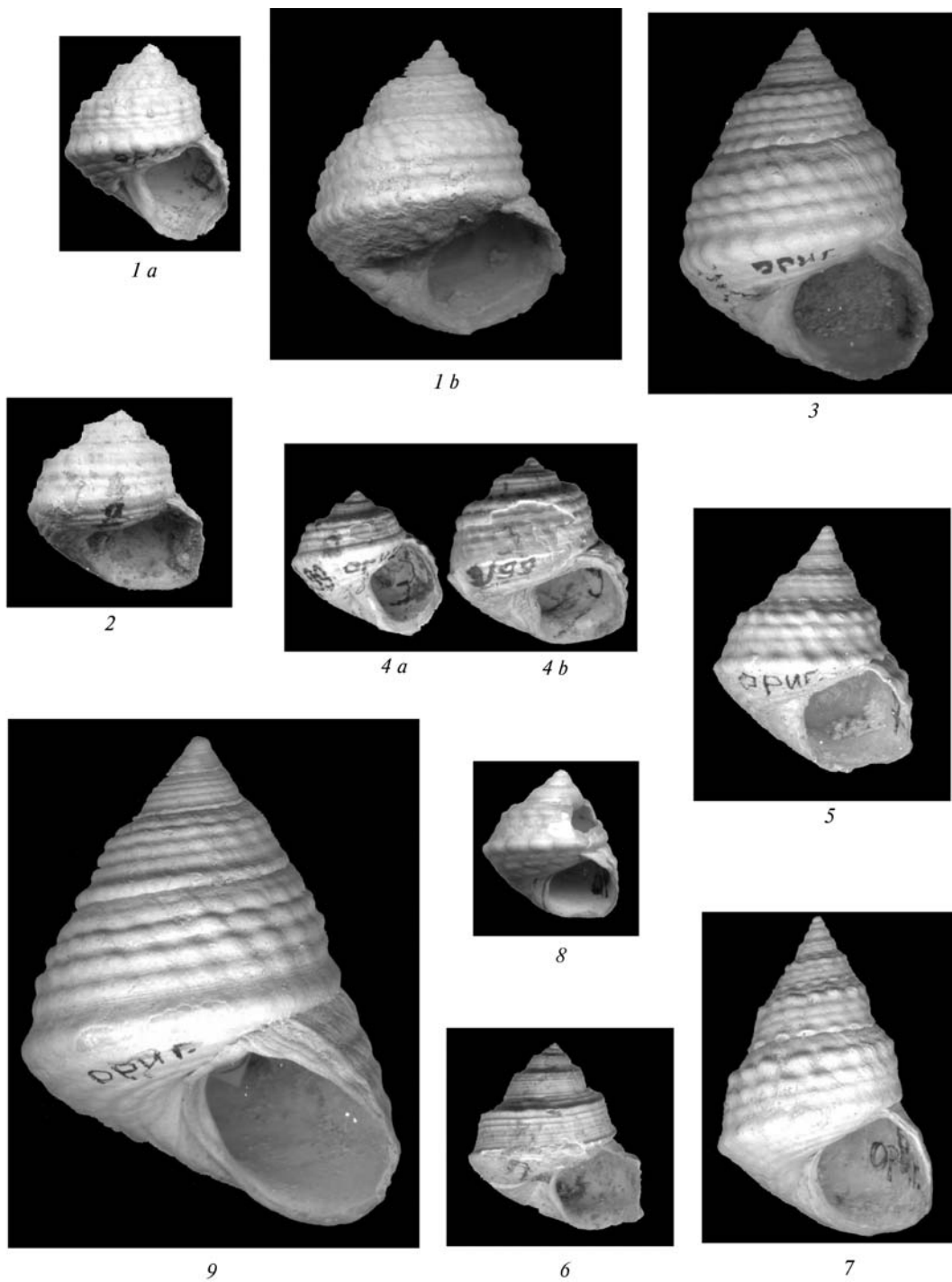


Fig. 3. Shells of the "*Trochus podolicus*" group species: 1 a, 1 b – *Gibbula podolica* (1 a – shell of Borysthenian Gulf, 1 b – of Halician Gulf); 2 – *G. sulcatopodolica*; 3 – *G. laevigatopodolica*; 4 a, 4 b – *G. bargi* (4 a – holotype, 4 b – paratype); 5 – *G. insperata*; 6 – *G. cordieriana*; 7 – *Calliostoma podoliciformis*; 8 – *C. beaumontii*; 9 – *C. hommairei*.

Рис. 3. Раковины моллюсков группы «*Trochus podolicus*»: 1 a, 1 b – *Gibbula podolica* (1 a – раковина из Борисфенского залива, 1 b – из Галицийского залива); 2 – *G. sulcatopodolica*; 3 – *G. laevigatopodolica*; 4 – *G. bargi* (4 a – голотип, 4 b – паратип); 5 – *G. insperata*; 6 – *G. cordieriana*; 7 – *Calliostoma podoliciformis*; 8 – *C. beaumontii*; 9 – *C. hommairei*.

3–5 spiral ribs, grading into 5 thick ribs with large tubercles. Between the ribs are frequently very fine spiral threads. Between the suture and the upper keel (formed by a stronger developed spiral row of tubercles) a subhorizontal shoulder is formed, on which frequently there is an additional row of tubercles. Abapical keel strongly developed, with rounded tubercles. Apical angle 70–75°, the tangent-line (= “profile of spire” of some authors) straight or slightly convex. Basis of the last whorl convex, covered by 4–6 smooth or slightly tuberculate spiral ribs, sometimes with spiral threads between them. Aperture ovate, in juveniles angular where crossed with keel.

Measurements (in mm). Height of shell (HS) – up to 31; width of shell (WS) – up to 28; height of the last (body) whorl (HBW) – up to 26; height of aperture (HA) – up to 18; width of aperture (WA) – up to 18; no. of whorls (NW) – up to 7.

Remarks. The shells from western localities in Ukraine are larger than those from the south.

Distribution. Very common species in the entire area of Middle Sarmatian deposits – from Central Europe (including Vienna Basin) to Mangyshlak (Kazakhstan).

Gibbula sulcatopodolica (Kolesnikov, 1930) (fig. 2, 2; 3, 2)

Syn.: – *podolicus* Orbigny, 1844: 445, pl. 3, fig. 15, 16 (*Trochus*) [non Dubois de Montpéroux 1831]; – *podolicus* Dubois var. *sulcatopodolicus* Kolesnikov, 1930 a: 52–55, tabl. 2, fig. 49–55 (*Trochus*); – *sulcatopodolicus* – Kolesnikov, 1935: 169, tabl. 23, fig. 3–6 (*Trochus*); – *sulcatopodolica* – Kolesnikov, 1939: 702 (*Calliostoma*); – *sulcatopodolicus* Kolesnikov – Korobkov, 1955: tabl. 7, fig. 2, 3 *Gibbula* (*Gibbula*, sect. *Robur*); – *sulcatopodolica* Kolesnikov – Zelinskaya et al., 1968: 114, tabl. 30, fig. 15 (*Astele*); – *sulcatopodolica* Kolesnikov – Anistratenko, 1999: 70, fig. 2 c (*Gibbula*).

Material examined. 1 (LET); 2 (TER); 1 (ANT); 8 (VTA).

Description. Shell relatively large, sturdy with 6–7 stepped whorls. Sculpture similar to that of *Gibbula podolica*. Apical angle 90–95°, the tangent-line straight or slightly convex. Basis of the last whorl convex with 4–6 smooth or tuberculate thick spiral ribs. Aperture ovate-quadrangular, slightly extended horizontally. Abapical keel very broad and high, rounded, tubercles obsolete.

Measurements (in mm). HS – up to 31; WS – up to 31; HBW – up to 25; HA – up to 13,7; WA – up to 18; NW – up to 7.

Remarks. Differs from *Gibbula podolica* in having a lower spire and from *G. bargi* by its higher spire.

Distribution. As for *Gibbula podolica*.

Gibbula laevigatopodolica (Kolesnikov, 1930) (fig. 2, 3; 3, 3)

Syn.: – *laevigatopodolicus* Kolesnikov, 1930 a: 50, tabl. 2, fig. 41–48 (*Trochus podolicus* Dubois de Montpéroux var.); – *laevigatopodolica* – Kolesnikov, 1939: 702 (*Calliostoma*); – *laevigatopodolica* Kolesnikov – Anistratenko, 1999: 70–71, fig. 2 e (*Gibbula*).

Material examined. 3 (LET).

Description. Shell large, relatively high, thick-walled with 6–7 slightly convex, weakly stepped whorls. Protoconch of up to 1,5 smooth, convex whorls. Initial whorls of the teleoconch with 4–5 spiral ribs, which become stronger on later whorls and are covered by large tubercles. The whorls have keels near the adapical and abapical sutures, which in the last whorl become rounded. Apical angle about 60°, the tangent-line straight or slightly convex. Basis of the last whorl covered by 3–4 thick and broad spiral ribs with very low tubercles. Aperture oblique, ovately quadrangular, more angular in juvenile individuals. Umbilicus closed or rarely slit-like.

Measurements (in mm). HS – up to 32; WS – up to 29; HBW – up to 21; HA – up to 10; WA – up to 10; NW – up to 7.

Remarks. The shell of *Gibbula laevigatopodolica* has the highest spire of all *Gibbula* species discussed here. This species is here reported from the western Ukraine for the first time; it was noted only from Moldova before (Kolesnikov 1930, 1935).

Distribution. Middle Sarmatian of Western Ukraine and Moldova.

Gibbula bargi O. Anistratenko, 1999 (fig. 2, 4; 3, 4 a, 4 b)

Syn.: — *bargi* O. Anistratenko, 1999: 71, fig. 2 d (*Gibbula*).

Material examined. Holotype (N 1/99) and paratype (N 2/99) (both VTA).

Description. Shell of moderate size, sturdy, peg-top shaped with 5–6 stepped whorls with deep sutures. Height of shell is almost equal to width. Last whorl very large; its height is about 0.85 of the height of the shell. The protoconch consists of 1–1.5 smooth whorls. Periphery of initial 1–1.5 whorls of teleoconch rounded, then with two rounded keels. The abapical one is usually covered by the suture and is seen only in the free part of the last whorl. The sculpture is typical for the “*Trochus podolicus*” group, i. e. with 5–6 spiral ribs, which from the third or fourth teleoconch whorl onwards dissolve into rows of round tubercles. Apical angle about 110°, the tangent-line slightly concave. Basis of the last whorl convex, covered by 6 spiral ribs, which are smooth or covered with flattened tubercles, and have sometimes fine spirals intercalated between them. The entire surface of the teleoconch is covered by very fine growth lines. Aperture ovately quadrangular, with its long axis oriented slightly oblique to the spiral axis. The parietal margin forms a distinct flap, which almost covers the deep slit-like umbilicus. Where the periostracum is peeled off, the brightly coloured nacre layer repeats the general characters of surface sculpture.

Measurements (in mm). Holotype. HS — 12.3; WS — 11.7; HBW — 10.5; HA — 8.0; WA — 6.0; NW — 5. Paratype: HS — 14.3; WS — 14.0; HBW — 12.0; HA — 10.0; WA — 7.5; NW — 5.75.

Etymology. The species named in honour of famous Ukrainian palaeontologist and geologist Prof. Igor. M. Barg (Dnepropetrovsk University) who kindly provided type material.

Remarks. Differs from all species of this group by its highest rate of whorl growth, lowest spire, biggest apical angle and concave tangent line.

Distribution. This species is known only from the type locality — outcrop on the bank of Kakhovsky reservoir near Vishchetarasovka village, Tomakovka district, Dnepropetrovsk region.

Gibbula insperata (Kolesnikov, 1930) (fig. 2, 5; 3, 5)

Syn.: — *insperatus* Kolesnikov, 1930 b: 146, tabl. 3, fig. 19–23 (*Trochus*); — *insperata* Kolesnikov, 1939: 702 (*Calliostoma*); — *insperata* Kolesnikov — Korobkov, 1955: 105 (*Calliostoma (Astele)*, sect. *Insperata*); — *insperatus* Kolesnikov — Korobkov, 1955: tabl. 7, fig. 4, 5 (*Gibbula (Gibbula)*, sect. *Robur*); — *insperata* Kolesnikov — Zelinskaya et al., 1968: 108, tabl. 29, fig. 10 (*Gibbula*).

Material examined. 3 (LET); 7 (SUS); 4 (TER); 3 (IZA).

Description. Shell rather high-conical with 6–7 initially rounded, then distinctly stepped whorls. Sculpture is very similar to *Gibbula podolica*. Apical angle about 55°, the tangent-line straight or slightly convex, becoming concave in very large specimens. Basis of the last whorl flattened, covered by 6–7 flattened broad spiral, sometimes tuberculate, ribs. Aperture ovately-quadrangular, inner lip covers a slit-like umbilicus.

Measurements (in mm). HS — up to 27; WS — up to 25; HBW — up to 19; HA — up to 11; WA — up to 12; NW — up to 7.

Remarks. *Gibbula insperata* combines characters of some *Gibbula* and *Calliostoma*, nevertheless we include it into *Gibbula* group, though its relationship with other

Gibbula is still obscure yet. It differs from *Gibbula podolica* in having a very high spire, from *Calliostoma podolicoformis* by sharp-marked stepped whorls.

Distribution. Middle Sarmatian of Western Ukraine and Moldova (deposits of sublittoral zone).

Gibbula cordieriana (Orbigny, 1844) (fig. 2, 6; 3, 6)

Syn.: – *cordierianus* Orbigny, 1844: 448, pl. 2, fig. 9–12 (*Trochus*); – *carinula* Eichwald, 1853: 235–236, pl. 9, fig. 24 (*Turbo*); – *cordieriana* Orbigny – Kolesnikov, 1939: 702 (*Calliostoma*); – *cordieriana* Orbigny – Zelinskaya et al., 1968: 116, tabl. 31, fig. 5 (*Calliostoma*); – *cordieriana* Orbigny – Anistratenko, 1999: 72, fig. 2 f (*Gibbula*).

Material examined. 1 (NIK).

Description. Shell of moderate to large size, with 6–7 stepped whorls. Sculpture with moderately broad spiral ribs crossed by irregular fine growth lines; tubercles absent. Apical and abapical keels clearly developed. Basis of the last whorl rather convex, covered by spiral ribs. Aperture ovately quadrangular, outer lip thin whereas the inner one is thickened and into forms a column covering the umbilicus partially. Umbilicus slit-like.

Measurements (in mm): HS – up to 31; WS – up to 30; HBW – up to 24; HA – up to 15; WA – up to 15; NW – up to 7.

Remarks. Kolesnikov (1935) considered *Gibbula cordieriana* an ancestral form of the “*Trochus podolicus*” group; a very wide natural habitat of this species is consistent with this supposition. Both species lived in Middle Sarmatian; Kolesnikov probably regarded the development of the sculpture as more primitive than that of *G. podolica*. Shells of *G. cordieriana* differ from *G. podolica* by lacking tubercles on the spiral ribs and in having a thinner apertural margin.

Distribution. Middle Sarmatian of Western Ukraine and Moldova. We found it in southern Ukraine for the first time; it was known before only from Moldova and Crimea (Kolesnikov, 1935 a. o.).

Family CALLIOSTOMATIDAE Thiele, 1924

Genus *Calliostoma* Swainson, 1840

The main characters differentiating these species from previous are: 1) comparatively higher shell shape and 2) comparatively smaller elements of sculpture.

Calliostoma podolicoformis (Kolesnikov, 1935) (fig. 2, 7; 3, 7)

Syn.: – *podolicoformis* Kolesnikov, 1935: 166–168, tabl. 23, fig. 1, 2 (*Trochus*); – *podolicoformis* – Kolesnikov, 1939: 702 (*Calliostoma*); – *podolicoformis* Kolesnikov – Korobkov, 1955: 105 (*Calliostoma* (*Astele*, sect. *Inesperata*)); – *podolicoformis* Kolesnikov – Zelinskaya et al., 1968: 113 (*Astele*).

Material examined. 7 (LET); 2 (SUS).

Description. Shell of moderate to large size, conical with 6–7 whorls. Sculpture in general features and habitus is similar to that of the previous species group. Apical angle about 60°, the tangent-line straight or slightly concave. Basis of the last whorl flatted with 4–5 thick weakly tuberculated spiral ribs. Aperture ovately quadrangular, inner lip covers partly or completely the slit-like umbilicus. Color brownish with white tubercles.

Measurements (in mm). HS – up to 30; WS – up to 21; HBW – up to 20; HA – up to 10; WA – up to 11; NW – up to 7.5–8.

Remarks. Shells of *Calliostoma podolicoformis* differ from those of *C. pseudohom-mairei* in having a larger apical angle and more clearly developed sculpture. This species has been found in Middle Sarmatian deposits for the first time, having been known only from the Early Sarmatian before (Kolesnikov, 1930, 1935). There are clear differences

between Middle Sarmatian and Early Sarmatian specimens; the Middle Sarmatian populations have larger, sturdier and more massive shells with a greater number of whorls than the Early Sarmatian ones. We suggest these differences were caused by differences in environmental conditions in the Halician Gulf in different time periods.

Distribution. Early and Middle Sarmatian of western Ukraine (deposits of the sublittoral zone).

Calliostoma beaumontii (Orbigny, 1844) (fig. 2, 8; 3, 8)

Syn.: – *beaumontii* Orbigny, 1844: 447, pl. 2, fig. 6–8 (*Trochus*); – *beaumontii* Orbigny – Zelinskaya et al., 1968: 115, tabl. 30, fig. 23 (*Calliostoma*).

Material examined. 1 (VER); 1 (VTA).

Description. Shell large, massive, broadly conical with 7–8 whorls. Protoconch of up to 1, 5 convex whorls, smooth. On the first whorl of the teleoconch appear 5 relatively thick spiral ribs, which during growth grade into 6–7 rows of big tubercles. Simultaneously the periphery of the whorls becomes flat and the adapical spiral rib transforms into a keel. Apical angle 88°, the tangent-line straight or slightly concave. Basis of the last whorl flat, covered by 6–7 spiral ribs. Aperture ovately quadrangular, inner lip thickened and bent towards the slit-like umbilicus. Background color brownish with white tubercles.

Measurements (in mm). HS – up to 36; WS – up to 33; HBW – up to 29; HA – up to 15; WA – up to 18; NW – up to 8.

Remarks. Shells of this species differ from all other *Calliostoma* discussed here in having the largest apical angle. This species has been found in southern Ukraine for the first time; it was known before only from western Ukraine (Kolesnikov, 1930, 1935). As is the case with all other Trochoidea, specimens of *C. beaumontii* from the Borysthenian Gulf are smaller than those from the Halician Gulf (Anistratenko, 1999).

Distribution. Middle Sarmatian of western and southern Ukraine.

Calliostoma hommairei (Orbigny, 1844) (fig. 2, 9; 3, 9)

Syn.: – *hommairei* Orbigny, 1844: 445, pl. 2, fig. 1, 2 (*Trochus*); – *hommairei* Orbigny – Kolesnikov, 1930 a: 53, tabl. 2, fig. 58–65 (*Trochus podolicus* Dubois de Montpéroux var.).

Material examined. 1 (ANT).

Description. Shell large, broadly conical with 5–6 whorls. Protoconch of up to 1, 5 smooth convex whorls. Sculpture similar to that of *Calliostoma beaumontii*, but the tubercles are smoother. Apical angle about 70°, the tangent-line straight or slightly concave, near the apex slightly convex. Basis of the last whorl flattened with 3–4 broad, weakly tuberculated spiral ribs, sometimes smooth. Aperture ovately quadrangular, inner lip thickened and bent towards the slit-like or closed umbilicus.

Measurements (in mm). HS – up to 35; WS – up to 31; HBW – up to 24; HA – up to 12; WA – up to 14; NW – up to 6.

Remarks. Differs from *C. beaumontii* in having a smaller apical angle and a more flattened base of the last whorl. This species has been found in western Ukraine for the first time, it was only noted from Moldova before (Kolesnikov, 1930, 1935). The shells from Podolia (i. e. from all western Ukraine localities) possess a well-developed sculpture of the “*Trochus podolicus*” type, but all parameters of shell tube growth (“Raup’s parameters”) are exactly as in specimens of *C. hommairei* from Kishinev where shells are lacking almost any sculptural elements.

Distribution. Middle Sarmatian of western Ukraine and Moldova.

***Calliostoma pseudohommairei* (Kolesnikov, 1935) (fig. 2, 10)**

Syn.: – *pseudohommairei* Kolesnikov, 1935: 170–171, tabl. 23, fig. 14, 15 (*Trochus*); – *pseudohommairei* Kolesnikov – Kolesnikov, 1939: 702 (*Calliostoma*); – *pseudohommairei* Kolesnikov – Zelinskaya et al., 1968: 119, tabl. 32, fig. 1 (*Calliostoma*).

Material examined. None.

Description. Shell slender, high-conical with 7–8 regularly growing whorls. Sculpture similar to that of other species of this group, but abapical spiral strongly thickened. Adapical row of tubercles forms a weak keel. Apical angle about 50°, the tangent-line straight. Base of the last whorl flat or sometimes slightly convex with 5–6 thick spiral ribs. Aperture irregularly quadrangular, inner edge thickened and bent towards the slit-like umbilicus. Background color white, patterned with narrow brown axial stripes.

Measurements (in mm). HS – up to 40; WS – up to 33; HBW – up to 24; HA – up to 10; WA – up to 10; NW – up to 8.

Remarks. Differs from all other species by its most slender shell (apical angle about 50°) and the much flattened or slightly convex base of the last whorl.

Distribution. Middle Sarmatian of western Ukraine (Kolesnikov, 1930 a, b, 1935 a. o.).

Paleogeography and interpopulation variation

The distributional data now available show that *G. podolica*, *G. cordieriana*, *G. sulcatopodolica* and *C. beaumontii* had in Middle Sarmatian time a wide area of distribution and lived in both the western, more marine Halician Gulf, and in the south-eastern, less saline Borysthenian Gulf.

In two of those species (*G. podolica* and *G. sulcatopodolica*, represented in our collection by more than single specimens) which occur in the entire area of Sarmatian deposits of the Ukraine (tabl. 3), we noted a clearly expressed interpopulation variability. The adult sizes of Halician populations are much larger than those of Borysthenian ones (fig. 2, 3). The adult specimens differ not only by a greater number of whorls (up to 7–7.5), but also by thicker shells with more massive sculpture elements. In samples from southern Ukraine all species have a smaller number of whorls (5–6), and accordingly smaller sizes, rather thin-walled shells and a weaker, more delicate sculpture. In all samples from western Ukraine the protoconch is larger than in samples of the same species from southern Ukraine. The reduced size of the species from the “*Trochus*

Table 3. Palaeogeography of the “*Trochus podolicus*” species group in Sarmatian deposits of Ukraine

Таблица 3. Палеогеографическое распространение видов группы «*Trochus podolicus*» в сарматских отложениях Украины

Species	Halician Gulf (West Ukraine)	Borysthenian Gulf (SE Ukraine)
<i>Gibbula podolica</i> (Dubois de Montpereux, 1831)	+	+
<i>G. sulcatopodolica</i> (Kolesnikov, 1930)	+	+
<i>G. laevigatopodolica</i> (Kolesnikov, 1930)	+	
<i>G. bargi</i> O. Anistratenko, 1999		+
<i>G. cordieriana</i> (Orbigny, 1844)	+	+
<i>G. insperata</i> (Kolesnikov, 1930)	+	
<i>Calliostoma podolicoformis</i> (Kolesnikov, 1935)	+	
<i>C. beaumontii</i> (Orbigny, 1844)	+	+
<i>C. hommairei</i> (Orbigny, 1844)	+	
<i>C. pseudohommairei</i> (Kolesnikov, 1935)	+	
Total number of species	9	5

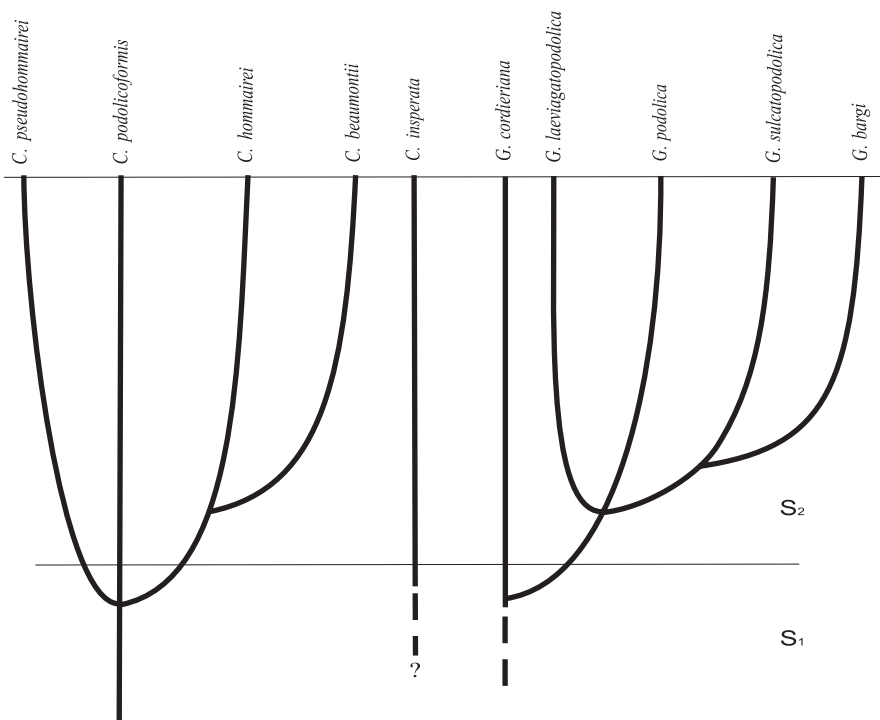


Fig. 4. Possible phylogenetic relationships within the “*Trochus podolicus*” species group.

Рис. 4. Вероятные филогенетические отношения в групп видов «*Trochus podolicus*».

podolicus” species conglomerate which inhabited the Borysthenian Gulf is statistically significant, as shown by L. S. Belokryz (1963) on a large material.

Interpopulation differences in the sizes of the protoconch may be explained by variable amounts of lecithin in the egg capsules, which determines the size of the larva. The lecithin content, in its turn, depends on the environmental conditions to which the parents were exposed (Fretter, Graham, 1963 a. o.).

The interpopulation differences discussed are very characteristic for almost all widely distributed species (at least in Trochoidean gastropods) which have been studied. This fact proves that in the Halician Gulf, especially in a zone of Bryozoan reefs, there were optimal conditions for existence of these and others gastropods (Kolesnikov, 1935; Simionescu, Barbu, 1940; Anistratenko, 2000 a. o.).

Beside the widely distributed species there were others with a more limited distribution, viz. *Gibbula laevigatopodolica*, *G. insperata*, *Calliostoma podoliciformis*, *C. hommairei*, *C. pseudohommairei* in the Halician Gulf only, and *G. bargi*, which was not yet found outside the Borysthenian Gulf.

Our observations on species occurring in the Halician Gulf only, show that shells of *Gibbula laevigatopodolica* and *Calliostoma hommairei* from Kishinev were smooth or nearly smooth but the shells from Podolia and Southern Ukraine usually have a well expressed sculpture. This regularity suggests the existence of sharp local variations of the ecological conditions in Middle Sarmatian time in the southern and northern parts of the Halician Gulf.

The different species assemblages (tabl. 3) and interpopulation variability confirm that in Middle-Sarmatian times ecological conditions differed in the Halician and Borysthenian Gulfs of the Eastern Paratethys.

The study of our materials and analysis of relevant published data enabled us to reconstruct the most probable phylogenetic relationships within the groups discussed

(fig. 4). We reconstruct the phylogeny only by visual analysis and comparison of the similarities of traditional shell characters. The border between Early Sarmatian (S_1) and Middle Sarmatian (S_2) is conditionally shown.

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