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New Data on the Terrestrial Gastropods from the Oligocene–Miocene Transition in the Valley of Lakes, Central Mongolia

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Abstract—The Oligocene–Miocene terrestrial gastropod fauna of the Valley of Lakes, Central Mongolia, is described for the first time based on SEM images. These allowed detailed anatomical analyses and resulted in better species delimitation and taxonomic rectifications. The assemblage comprises six pupilloid species of the genera *Gastrocopta, Vallonia,* and *Pupoides*. *Vallonia stworzewiczae* Neubauer, sp. nov. is introduced as a new species. Two samples from the Loh Formation exposed at the Hotuliin Teeg locality have yielded excellently preserved specimens. Based on a small mammal fauna, these samples are proposed to span the interval of the Oligocene–Miocene boundary. A comparison with ecological requirements of modern congeners suggests the presence of rather open but vegetated habitats in the Valley of Lakes during sedimentation of the Loh Formation.

Keywords: terrestrial gastropods, *Gastrocopta, Vallonia,* paleoecology, Mongolia
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INTRODUCTION

The Cenozoic terrestrial gastropod faunas of Mongolia are poorly known. The first taxonomic studies were performed by Prysjazhnjuk (in Prysjazhnjuk et al., 1975) on material from the Valley of Lakes collected in the course of a Joint Soviet–Mongolian Geological and Paleontological Expedition. He described eight taxa from the Hsanda Gol Formation exposed at an unnamed locality 50 km east of the Taatsiin Gol River, 0.5 km east of the mammal site Ulaan Tolgoi, south of the Dzun-Sharo-Ul Mountain (Prysjazhnjuk et al., 1975). Five of these taxa were newly introduced and the remaining ones were only identified at the genus level. Prysjazhnjuk also mentioned unstudied occurrences of terrestrial gastropods in the Taatsiin Gol River valley, 2–3 km north of Tsagaan Ovoo, Hsanda Gol Formation (Prysjazhnjuk et al., 1975). The second and latest work on the fauna of the Valley of Lakes was carried out by Stworzewicz (2007) on the material of the Joint Austrian–Mongolian Expedition (Daxner-Höck et al., 1997, 2010; Höck et al., 1999), which extended the faunal list to a total of 14 taxa. The studied areas and localities are given in the "Geological setting" section.

Apart from these pioneer papers, few studies dealt with the Cenozoic continental gastropods of Mongolia. Devyatkin et al. (1971) studied Pliocene freshwater gastropods of western Mongolia. Tolstikova and Badamgarav (1976) reported the presence of bithyniid opercula (not *Amnicola*, to which some of the taxa are assigned) from the localities in southeastern Mongolia and southeastern Kazakhstan. Tolstikova (1979) subsequently provided more detailed descriptions of terrestrial and freshwater gastropods from these Mongolian localities and proposed a Paleocene age, based on rather doubtful comparisons with North American faunas.

Additional data on terrestrial gastropod faunas from the nearest areas derive from adjacent territories in Russia, Kazakhstan, and China. Steklov (1976) described the fauna from an unnamed locality in Tuva, Russia (between the Alash and Khemchik rivers, near Kyzyl-Mazhalyk, western Tuva, about 50 km north of the Russian–Mongolian border), which is considered roughly coeval to that of the Valley of Lakes. It shares two taxa with the herein described fauna. Steklov and Tsytovich (1967) worked on material from central Kazakhstan (Kostankol valley, presumably Oligocene–Miocene), which also shows potential faunal similarities as discussed in the systematic chapter.

The data from adjacent Chinese regions that are available to us come only from the Pliocene. Chi Ping

(1931) studied freshwater mollusks in Tungur, Inner Mongolia (North China, region adjacent to the southeastern and eastern Mongolian border), which were dated as Pliocene due to co-occurring elephantid remains. About fifty years later, Li Yuntong and Li Zishun (1980) reinvestigated the same formation and described 19 terrestrial gastropods.

The provided illustrations in the taxonomically relevant works on Mongolian terrestrial gastropods range from line drawings to rather poor photographs. In the only case where the illustrations are appropriate (Stworzewicz, 2007), the poor preservation of the material complicates reliable taxonomic comparisons.

Consequently, this study of new material of a Joint Austrian–Mongolian Expedition is the first to provide high-resolution SEM photographs of several species of the terrestrial gastropod fauna from the Valley of Lakes. This allows a detailed documentation of the taxonomically relevant apertural characteristics of gastrocoptid species and provides the first pictures of embryonic shells and, where present, teleoconch microsculpture.

GEOLOGICAL SETTING

The Valley of Lakes is a 500-km-long, west–east extending pre-Altai depression in Central Mongolia, situated between the Mongolian Altai and Gobi Altai mountains in the south and the Khangai Mountains in the north (Fig. 1; Höck et al., 1999; Daxner-Höck and Badamgarav, 2007). The valley is built up from Proterozoic and Paleozoic rocks and is filled with Cretaceous to Quaternary continental sediments. An Oligocene–Miocene sequence with fossiliferous deposits locally intercalated by several basaltic layers is exposed in the areas of Taatsiin Tsagaan Nuur, Khunug Valley, Taatsiin Gol, Tatal-Hsanda Gol, and Ikh Argalatyn Nuruu.

The deposits of the Taatsiin Gol and Taatsiin Tsagaan Nuur areas were studied during a Joint Austrian–Mongolian Project with field trips carried out in the years 1995–1997, 2001, 2004, and 2006. Focus was set on geological mapping, age dating of basaltic layers, sedimentological, paleontological, and stratigraphic studies of the Oligocene and Miocene (Daxner-Höck et al., 1997, 2010; Höck et al., 1999; Daxner-Höck and Badamgarav, 2007). These investigations yielded a great number of fossil remains from 33 localities, covering 289 taxa, including mammals, reptiles, amphibians, and gastropods (for more detail, see faunal lists and references in Daxner-Höck et al., 2010). The rich small mammal assemblages resulted in a well-resolved biostratigraphic framework with subdivision into several biozones (Daxner-Höck et al., 1997, 2010; Daxner-Höck and Badamgarav, 2007). The framework hinges on absolute ages measured from three basalt layers ($^{40}Ar/^{39}Ar$) (Höck et al., 1999). These give a mean age of ca. 31.5 Ma (Early Oligocene) for Basalt I, with measured ages ranging from 30.4 to 32.1 Ma. Basalt II is ca. 28.0 Ma old (early Late Oligocene), with ages ranging from 27.0 to 29.0 Ma. Basalt III deposited at ca. 13.0 Ma (Middle Miocene), ages ranging from 12.2 to 13.2 Ma.

Two formations were of particular interest because of their fossil content and contact to the basalts, i.e., the Hsanda Gol Formation and the Loh Formation (following descriptions after Höck et al., 1999). The Hsanda Gol Formation is made up of fine clastic brick red beds below and above Basalt I, indicating an Early Oligocene to early Late Oligocene age. The highly fossiliferous sediments commonly consist of massive, horizontally bedded layers with nonerosive boundaries. Based on the occurrence of caliche horizons, the depositional setting of the formation was interpreted as arid to semiarid (Höck et al., 1999). The total thickness varies strongly and increases towards the center of the Valley of Lakes, where it attains up to 70 m. The Loh Formation comprises usually brighter colored, cross-bedded sands and gravels, intercalated by fluvial silts and clays. The total thickness reaches up to 150 m, including Basalt II and Basalt III, which suggest a Late Oligocene to Late Miocene age for the Loh Formation. The depositional environment was interpreted as floodplains of braided to meandering rivers with ephemeral lakes that had formed under a more humid climate with denser vegetation (Höck et al., 1999).

MATERIAL AND METHODS

In the course of earlier studies, terrestrial gastropods were found in several localities of the Hsanda Gol Formation and the Loh Formation. The following localities were studied by Stworzewicz (2007): Taatsiin Gol (Hsanda Gol Formation, Biozone A, Early Oligocene; Hsanda Gol Formation, Biozone C, early Late Oligocene), Ikh Argalatyn Nuruu (Hsanda Gol Formation, Biozone A, Early Oligocene; Hsanda Gol Formation, Biozone C1, latest Oligocene), Abzag Ovoo (Loh Formation, Biozone C, early Late Oligocene), Toglorhoi (Loh Formation, Biozone C, early Late Oligocene), Luugar Khudag (Loh Formation, Biozone D, Early Miocene), and Unkheltseg (Loh Formation, Biozone D, Early Miocene) (Figs. 1, 2).

The current investigation examines to date unknown material from Hotuliin Teeg, located west of Taatsiin Gol (45°28′53.2″ N, 101°11′34.9″ E), and Tatal Gol (45°18′08.2″ N, 101°37′09.3″ E) (Fig. 1). The fossils were obtained during the 2011 field trip in the course of a Joint Austrian–Mongolian Project (project leader G. Daxner-Höck). Three horizons yielded terrestrial gastropods in variable number and preservation. Samples HTS-056/2 and HTS-056/3 from Hotuliin Teeg are taken from the red beds of the Loh Formation above Basalt II and contain excellently

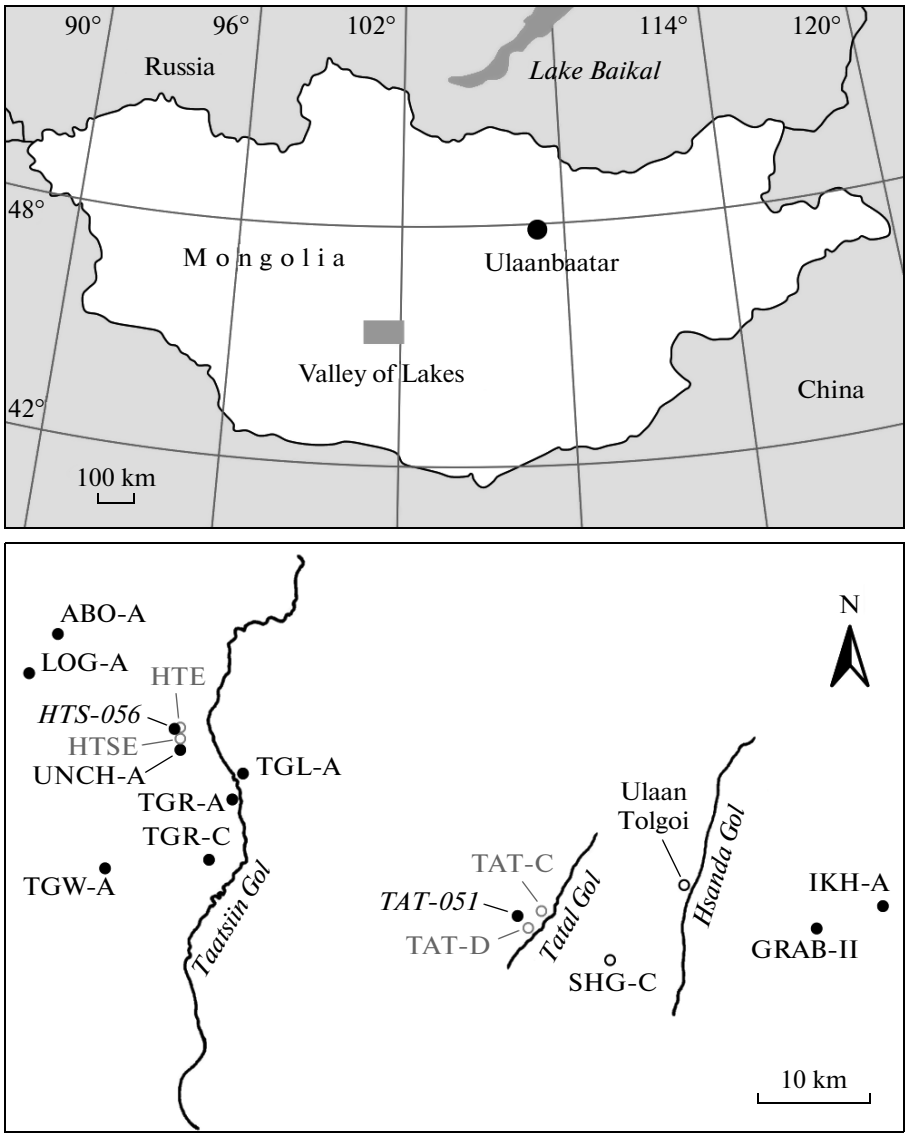


Fig. 1. Schematic position of terrestrial gastropod localities in the Valley of Lakes, central Mongolia (after Höck et al., 1999; Daxner-Höck and Badamgarav, 2007, modified). The samples studied herein are given in italic. Samples marked gray with open circles were studied by Daxner-Höck and Badamgarav (2007) and are here indicated for easier comprehension of the geographic relations. Remaining sample numbers indicated by full circles refer to those investigated by Stworzewicz (2007). The sample SHG-C from locality Hsanda Gol yielded few gastropod remains that were not published (Stworzewicz, unpublished data). The gastropods recorded by Prysjazhnjuk et al. (1975) derive from an unnamed locality 0.5 km east of Ulaan Tolgoi (geographic position after Daxner-Höck and Badamgarav, 2007; see text for details).

preserved mollusks, including several complete specimens and numerous fragments. The small mammal assemblages from these layers indicate Oligocene–Miocene boundary age (Biozone C1/Biozone D). Originally, the deposits at Hotuliin Teeg were partly assigned to the Tsagaan Ovoo Formation (Höck et al., 1999). Recent faunal analyses, however, proved their affiliation with the Loh Formation.

Sample TAT-051/2 from Tatal Gol is taken from the Hsanda Gol Formation and contains few fragmentary and poorly preserved molds. The small mammal fauna unambiguously classified the layers as belonging to Biozone C1 (latest Oligocene).

Samples were wet-sieved and fossils picked from dry residues. Where the apertures of gastrocoptids, bearing taxonomically important features, were filled with sediment, an ultrasonic device was used to clean the shells. To avoid double counting, the part bearing the aperture was counted for gastrocoptids and the apical region for valloniids. The stratigraphic chart

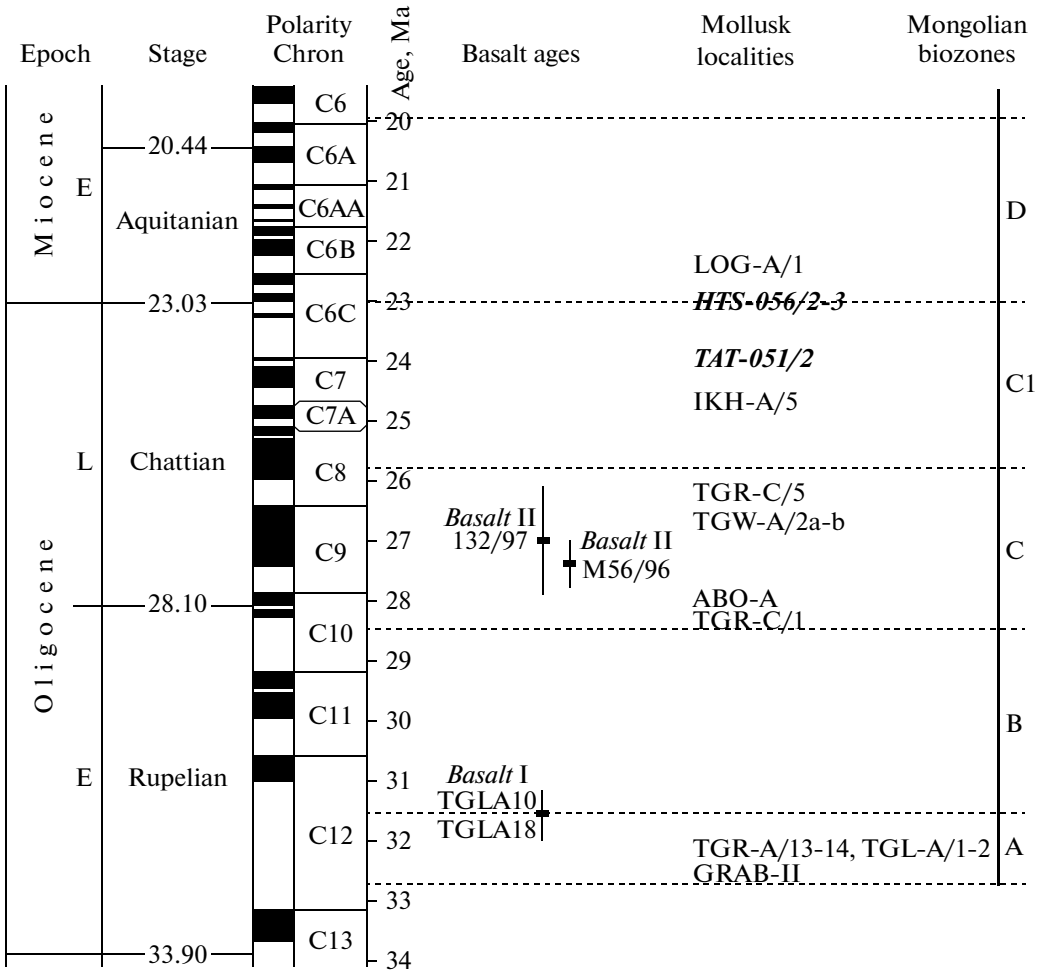


Fig. 2. Stratigraphic chart indicating ages of the samples studied (bold italic) and those studied by Stworzewicz (2007), including ages of the basaltic layers (Höck et al., 1999), and the biozones based on small mammal faunas (Daxner-Höck et al., 2010).

(Fig. 2) was created using Time Scale Creator 6.0 (Ogg and Lugowski, 2012), following the age model in Gradstein et al. (2012).

FAUNAL COMPOSITION AND PALEOECOLOGY

Previous studies of fossil terrestrial gastropods from the Valley of Lakes documented up to 14 taxa in total (including those not determined at the species level). The present investigation yielded six gastropod taxa, one of which is new to science. These are *Pupoides* cf. *steklovi* Prysjazhnjuk in Prysjazhnjuk et al., 1975, *Vallonia stworzewiczae* Neubauer, sp. nov., *V. tumida* Stworzewicz, 2007, *Gastrocopta devjatkini* Prysjazhnjuk in Prysjazhnjuk et al., 1975, *G. tuvaense* Steklov, 1967, and *G. valentini* Stworzewicz, 2007.

The reason for the rather small spectrum detected in this study results from the low availability of fossil-bearing horizons and the generally low number of mollusk fossils in the area. Of the three samples studied, only two contained well-preserved shells that could be determined at the species level.

Sample HTS-056/2 yielded the greatest number of fossils, including specimens of all six species. *Gastrocopta valentini* is the most common species, followed by *Vallonia tumida, V. stworzewiczae* Neubauer, sp. nov., and *G. tuvaense*. Additionally, a few fragments of *G. devjatkini* and a single fragment of *Pupoides* cf. *steklovi* occur. In sample HTS-056/3, three taxa are found, with *V. tumida* as the most common fossil, accompanied by a few and mostly fragmented specimens of *G. valentini* and *G. tuvaense*. Sample TAT-051/2 consists of unidentifiable internal molds of *Vallonia* sp.

Apart from that, several species previously described for the Valley of Lakes are not detected in the present study: *Gastrocopta mongolica* Prysjazhnjuk in Prysjazhnjuk et al., 1975, *G. primitiva* Prysjazhnjuk in Prysjazhnjuk et al., 1975, *G. shandgolica* Prysjazhnjuk in Prysjazhnjuk et al., 1975, *Vertigo* cf. *bicolumellata* Steklov in Steklov and Tsytovich, 1967, *Vallonia*

cf. *lepida* (Reuss, 1852), *?Strobilops* sp. (Stworzewicz, 2007). All of these taxa are claimed to be generally rare (Prysjazhnjuk et al., 1975; Stworzewicz, 2007).

The record of *V. lepida* should be discussed in more detail. The species was originally described from the late Early Miocene of the Czech Republic by Reuss (1852). Based on literature review, Gerber (1996) gave its temporal range as Oligocene–Pliocene for a territory extending from Europe to China. This implies an extremely wide stratigraphical and geographical distribution, both of which are biologically unrealistic (Harzhauser et al., in press). Anyway, the Mongolian record of *V. lepida* is based upon poorly preserved molds that cannot be reliably assigned to any species.

So far, the mollusk fauna of the Valley of Lakes was mainly documented for the Oligocene biozones A and C (Fig. 2). Stworzewicz (2007) recorded only *Vallonia* sp. for the Biozone C1 and *Vallonia* sp. and *?Strobilops* sp. for the Biozone D. Now we can add additional taxa for this period, spanning the Oligocene–Miocene boundary (Biozone C1/Biozone D). Many of these, such as *Gastrocopta valentini, G. devjatkini, Vallonia stworzewiczae*, and *V. tumida* were reported by Stworzewicz (2007) from the Biozone A (older than 31.5 Ma), while our records are about 8.5 m.y. younger. This might be a hint for rather low species turnover rates among terrestrial gastropods in central Mongolia during the Oligocene. Such a pattern differs considerably from the rapid succession of mammal faunas, which are the basis for the biozones (Daxner-Höck et al., 1997, 2010; Daxner-Höck and Badamgarav, 2007). An explanation might be the higher degree of adaptability of the mollusk species and (or) the lack of immigration events and subsequent replacement typical for mammal faunas.

Paleoecology

All identifiable fossils come from the samples of the Hotuliin Teeg locality, which is assigned to the Loh Formation. Extant representatives of the occurring genera dwell in a great variety of habitats, complicating any reliable paleoecological reconstruction. Nevertheless, their ecological requirements can be outlined to give at least a broader impression of the possible ecological setting of the fossil assemblage.

Extant European representatives of the genus *Vallonia* are calciphilous, ground-near living animals of open habitats (Gerber, 1996). Kerney et al. (1979) give a wide variety of open habitats for European representatives of the genus, including dry and calcareous habitats, dry meadows, humid meadows or swamps, sand dunes, and pebbles (see also Fechter and Falkner, 1990). They are rarely found in forested areas (Gerber, 1996; Frank, 2006).

The fossil record of gastrocoptids in Europe ranges up to the Pliocene; they are not recorded for Quaternary deposits (Ložek, 1964). Nowadays, their distribution area encompasses North America, South America, Central and East Asia. Recent *Gastrocopta theeli* (Westerlund, 1877) lives in Middle and East Asia, under leaves and stones on warm, sunlit hillsides (Ložek, 1964). In the United States, the genus is represented by numerous well-documented species (ecological data from Franzen and Leonard, 1947; Taylor, 1960; Nekola and Coles, 2001). *G. armifera* (Say, 1821), a common species in the United States, occurs on wooded slopes near streams, under leaves, dead wood, limestone rocks, or in moist grass. *G. procera* (Gould, 1840), *G. holzingeri* (Sterki, 1889), and *G. cristata* (Pilsbry et Vanatta, 1900) are all commonly found on timbered slopes of streams. *G. procera* and *G. holzingeri* also frequents the Midwest of the United States, suggesting that they can withstand periods of summer droughts. Due to its geographical distribution, *G. holzingeri* is considered to prefer cooler climates. *G. rogersensis* Nekola et Coles, 2001 is limited to xeric or dry–mesic calcareous rock outcrops.

The North American species *Pupoides albilabris* (Adams, 1841) lives at grass roots or under stones of well-drained, often sunny places (Pilsbry, 1948; Taylor, 1960).

In summary, extant representatives of the occurring genera display a wide variety of potential habitats, including open to forested, dry/xeric to humid or swampy sites. Nevertheless, some restrictions can be made: (1) the presence of valloniids and *Pupoides* argues for open habitats; (2) the majority of the above outlined species need some degree of vegetation. This fits well to the reconstruction based on sedimentary facies of the Loh Formation (Höck et al., 1999). These deposits are interpreted to derive from a more humid setting with a dense vegetation cover near a braided to meandering river, floodplain and (or) ephemeral lakes.

In contrast, the Hsanda Gol Formation is interpreted to derive from an ephemeral lake and (or) dust deposits; episodic droughts and occasionally following heavy rainfalls might have shaped the landscape during that period (Höck et al., 1999). Therefore, the valloniids of the Tatal Gol sample may represent aridity-adapted species.

SYSTEMATIC PALEONTOLOGY

Systematic classification follows Bouchet and Rocroi (2005) and Jörger et al. (2010). The latter study, based on molecular data, reordered and newly established several clades within the traditional "Pulmonata". No rank has been assigned to most of these categories yet. Terminology of apertural folds and lamellae in *Gastrocopta* species follows Moore (1960). The studied specimens are stored in the Natural History Museum of Vienna (NHMW) (collection no. 2012/0179). The fauna studied was compared with

the material described by Stworzewicz (2007), stored in the same museum (collection no. 2006/0196).

CLASS GASTROPODA CUVIER, 1795

SUBCLASS ORTHOGASTROPODA PONDER ET LINDBERG, 1997

Superorder Heterobranchia Gray, 1840

CLADE EUTHYNEURA SPENGEL, 1881

CLADE PANPULMONATA JÖRGER ET AL., 2010

CLADE EUPULMONATA HASZPRUNAR ET HUBER, 1990

CLADE STYLOMMATOPHORA SCHMIDT, 1855

CLADE ORTHURETHA PILSBRY, 1900

Superfamily Pupilloidea Turton, 1831

Family Valloniidae Morse, 1864

Subfamily Valloniinae Morse, 1864

Genus *Vallonia* Risso, 1826

Type species. *Vallonia rosalia* Risso, 1826 [= *Vallonia pulchella* (Müller, 1774)], Recent, France.

***Vallonia stworzewiczae* Neubauer, sp. nov.**

Plate 4, figs. 4–7

Vallonia subcyclophorella: Stworzewicz, 2007, p. 34, pl. 1, figs. 13–15.

Etymology. In honor of our colleague Ewa Stworzewicz (Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow), who greatly contributed to the knowledge of Mongolian fossil land snails.

Holotype. NHMW, no. 2012/0179/0001; shell (Pl. 4, fig. 4) from sample HTS-056/2; Hotuliin Teeg, Valley of Lakes, central Mongolia; Loh Formation, Late Oligocene–Early Miocene, Biozone C1–Biozone D.

Description. The shell is low trochiform, comprising up to 3.2 whorls. The protoconch consists of 1.2–1.25 whorls, distinctly demarcated from the teleoconch, its initial part is immersed, the surface is smooth. The early whorls are weakly convex, producing a slightly stepped spire. The whorls are rapidly expanding in diameter. The sutures are moderately incised. The last whorl is highly convex, with the maximum convexity slightly above the midheight of the whorl, attaining about 80–85% of the total shell height and 1.7 times the width of the penultimate whorl. The last portion of the last whorl is deflected abapically. The aperture is round, with regularly convex outer lip and slightly convex inner lip. The peristome is strongly extended and everted in fully grown specimens. The inner surface of the peristome is weakly granulated. The umbilicus is deep and wide, leaving parts of the penultimate whorl visible (about 30% of the shell diameter). The shell is ornamented with distinct prosocline to slightly sigmoidal growth lines; every third to fourth line forms a delicate riblet. The growth lines are stronger on the apical side; the riblets are equally expressed all around. Expression of the riblets and regularity of interspaces seem to increase with ontogeny in some specimens.

Measurements, in mm:

Specimen NHMW, no.	Shell diameter	Shell height
2012/0179/0001 (holotype)	2.3	1.2
2012/0179/0002 (paratype 1)	1.9	1.2
2012/0179/0003 (paratype 2)	2.3	1.1
2012/0179/0004	2.1	1.2

Comparison. The first determination of this species by Stworzewicz (2007) as *Vallonia subcyclophorella* (Gottschick, 1911) is problematic. This taxon is described from the Middle Miocene of the Steinheim Basin (south Germany). Both the wide geographic separation (about 6400 km) and stratigraphic gap (about 8 m.y.) of the German and Mongolian records make this identification unlikely. Nevertheless, both taxa are indeed quite similar in morphology. The size, number of whorls, and mode and strength of sculpture are almost identical, although comparable features are typically found in other valloniids too (see Gerber, 1996). However, they differ slightly in shape. *Vallonia subcyclophorella* has a lower spire, often slightly irregular growth, and a pronounced convexity above the midheight of the last whorl (Gerber, 1996). Maybe also the record of "*V. subcyclophorella*" from central Kazakhstan (Steklov and Tsytovich, 1967) has to be synonymized with *V. stworzewiczae*, but without a study of the original material a reliable determination is impossible. *Vallonia stworzewiczae* can easily be distinguished from the co-occurring *V. tumida* Stworzewicz, 2007 by its smaller size, the lower spire, and the presence of riblets.

Occurrence. Central Mongolia, Valley of Lakes: Taatsiin Gol, Hsanda Gol Formation, Early Oligocene, Biozone A; Abzag Ovoo, Loh Formation, early Late Oligocene, Biozone C (Stworzewicz, 2007).

Material. Five complete shells and several fragments from sample HTS-056/2.

***Vallonia tumida* Stworzewicz, 2007**

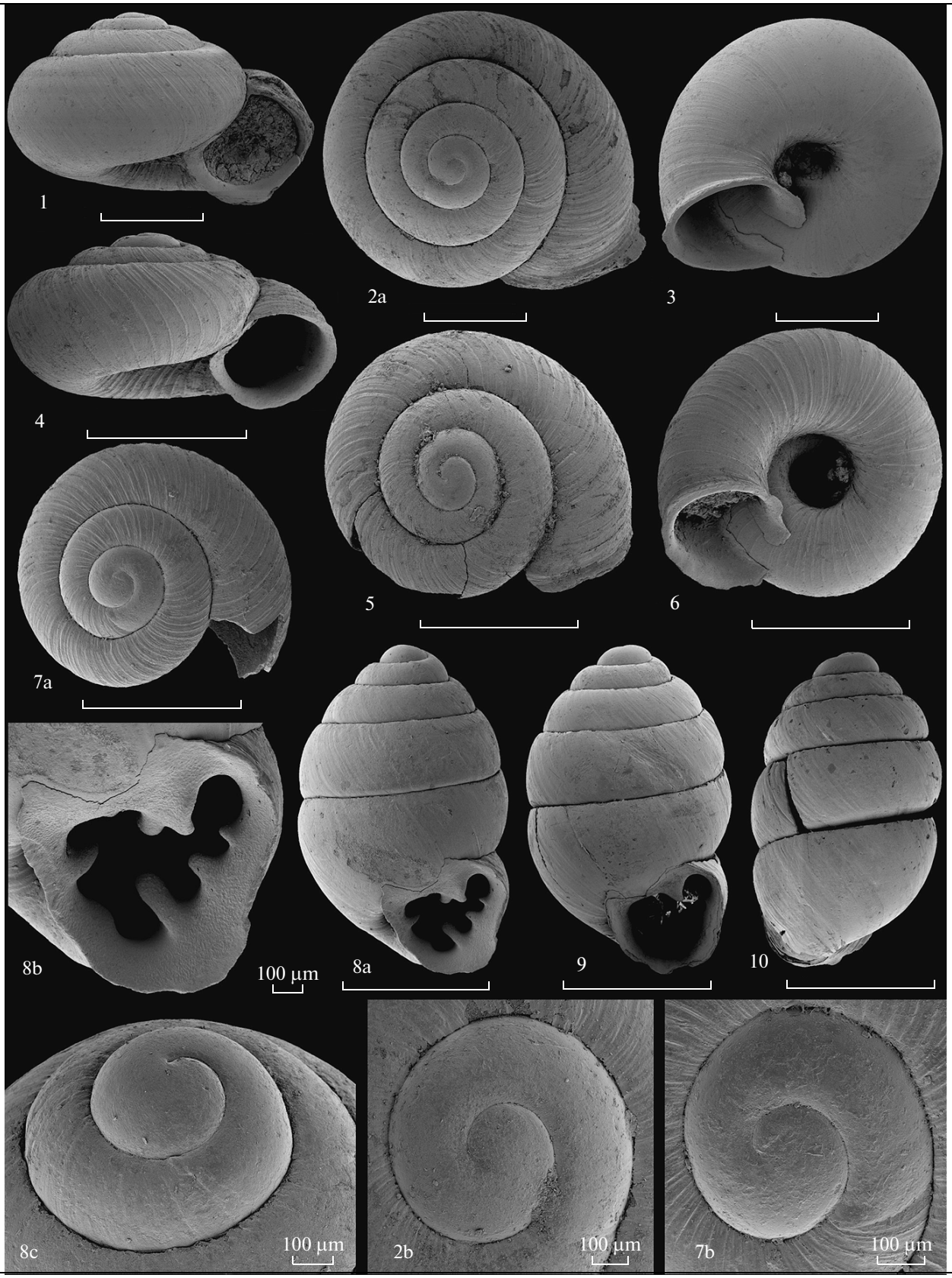
Plate 4, figs. 1–3

Vallonia tumida: Stworzewicz, 2007, p. 35, pl. 1, figs. 16–18.

Holotype. NHMW, no. 2006/0255/0001, shell; Abzag Ovoo, Valley of Lakes, central Mongolia; Loh Formation, Late Oligocene, Biozone C.

Description. The shell is generally low trochiform, but higher as in other species of the genus, composed of up to 4.25 whorls. The protoconch consists of 1.1 whorls, distinctly demarcated from the teleoconch, its initial part is slightly immersed; the surface is smooth. The whorls are weakly but regularly convex, forming a slightly stepped outline. The whorls expansion rate is constant. The sutures are moderately

Plate 4



incised. The last whorl has a semicircular outline, attains 75–80% of the total shell height and 1.6 times the width of the penultimate whorl. The aperture is inclined, circular, with regularly rounded outer lip and slightly concave inner lip; it is distinctly deflected in the latest ontogeny. The peristome is strongly thickened, ringlike, and everted. The inner surface of the peristome is weakly granulated. The umbilicus is narrow and deep. The shell is ornamented with densely spaced, prosocline to slightly sigmoidal moderately prominent growth lines, which are stronger on the apical side and almost reduced on the umbilical side.

Measurements, in mm:

Specimen NHMW, no.	Shell diameter	Shell height
2012/0179/0006	3.2	1.8
2012/0179/0007	3.3	2.3
2012/0179/0008	3.0	2.3

Comparison. As already stated by Stworzewicz (2007), the most characteristic features of this species are the relatively high spire and the very narrow umbilicus, resulting in a compact coiling, which is uncommon for valloniids (Gerber, 1996). The only similar species from this region is *V. gigantea* Steklov in Steklov et Tsytovich, 1967 from central Kazakhstan. This taxon also exposes a slightly elevated spire and a distinctly inclined and deflected aperture. However, its umbilicus is markedly wider than in *V. tumida*.

Occurrence. Central Mongolia, Valley of Lakes: Taatsiin Gol, Hsanda Gol Formation, Early Oligocene, Biozone A; Abzag Ovoo, Loh Formation, early Late Oligocene, Biozone C (Stworzewicz, 2007).

Material. Forty-two partly fragmented shells and numerous additional whorl fragments from samples HTS-056/2 and HTS-056/3.

Family Vertiginidae Fitzinger, 1833

Subfamily Gastrocoptinae Pilsbry, 1916

Genus *Gastrocopta* Wollaston, 1878

Type species. *Pupa acarus* Benson, 1856, Recent, Cape Verde Islands.

Gastrocopta devjatkini Prysjazhnjuk in Prysjazhnjuk et al., 1975

Plate 5, figs. 6 and 7

Gastrocopta (Kazachalbinula) devjatkini: Prysjazhnjuk et al., 1975, p. 170, pl. 1, figs. 5–8.

Gastrocopta devjatkini: Stworzewicz, 2007, p. 29, pl. 1, fig. 4.

Holotype. Institute of Geological Sciences of National Academy of Sciences of Ukraine (Kiev), no. 504, shell; unnamed locality 50 km east of the Taatsiin Gol River, 0.5 km east of the mammal site Ulaan Tolgoi, south of Dzun-Sharo-Ul Mountain, Valley of Lakes, central Mongolia; Hsanda Gol Formation, Oligocene.

Description. Since only the last whorl is preserved in all our specimens, the shape and protoconch characteristics cannot be given. Following the original description (Prysjazhnjuk et al., 1975), the shell is broadly ovoid, comprising up to 5 whorls; occasionally, more slender specimens occur (Stworzewicz, 2007). The base is straight to weakly convex. The umbilicus is narrow, slitlike. The aperture is wide, round to bluntly triangular. The peristome is strongly sheetlike expanded, its surface is distinctly granulated. The infraparietal lamella is most prominent, forming a massive trapezoid block with weakly split distal portion. The parietal portion of the parietoangular lamella is hardly discernible, situated more internally; the angular portion is strong, triangular, approximately as long as the infraparietal lamella. The columellar lamella is not visible in the available material, but stated to be deeply situated and ear-shaped (Stworzewicz, 2007). The lower palatal fold forms a low, very broad bulge; occasionally, specimens with a stronger, thinner fold occur (Stworzewicz, 2007). The upper palatal fold is small, broadly triangular. The suprapalatal fold is slightly smaller, narrow triangular. The prosocline growth lines ornament the shell.

Comparison. Although no complete shell is preserved in the available material, the determination of the fragments is unambiguous due to the uniquely formed infraparietal lamella. This prevents confusion with any other *Gastrocopta* species from this region.

Occurrence. Central Mongolia, Valley of Lakes: Taatsiin Gol Hsanda Gol Formation, Early Oligocene, Biozone A; Grab-II (Ikh Argalatyn Nuruu), Hsanda Gol Formation, Early Oligocene, Biozone A; Abzag Ovoo, Loh Formation, early Late

Explanation of Plate 4

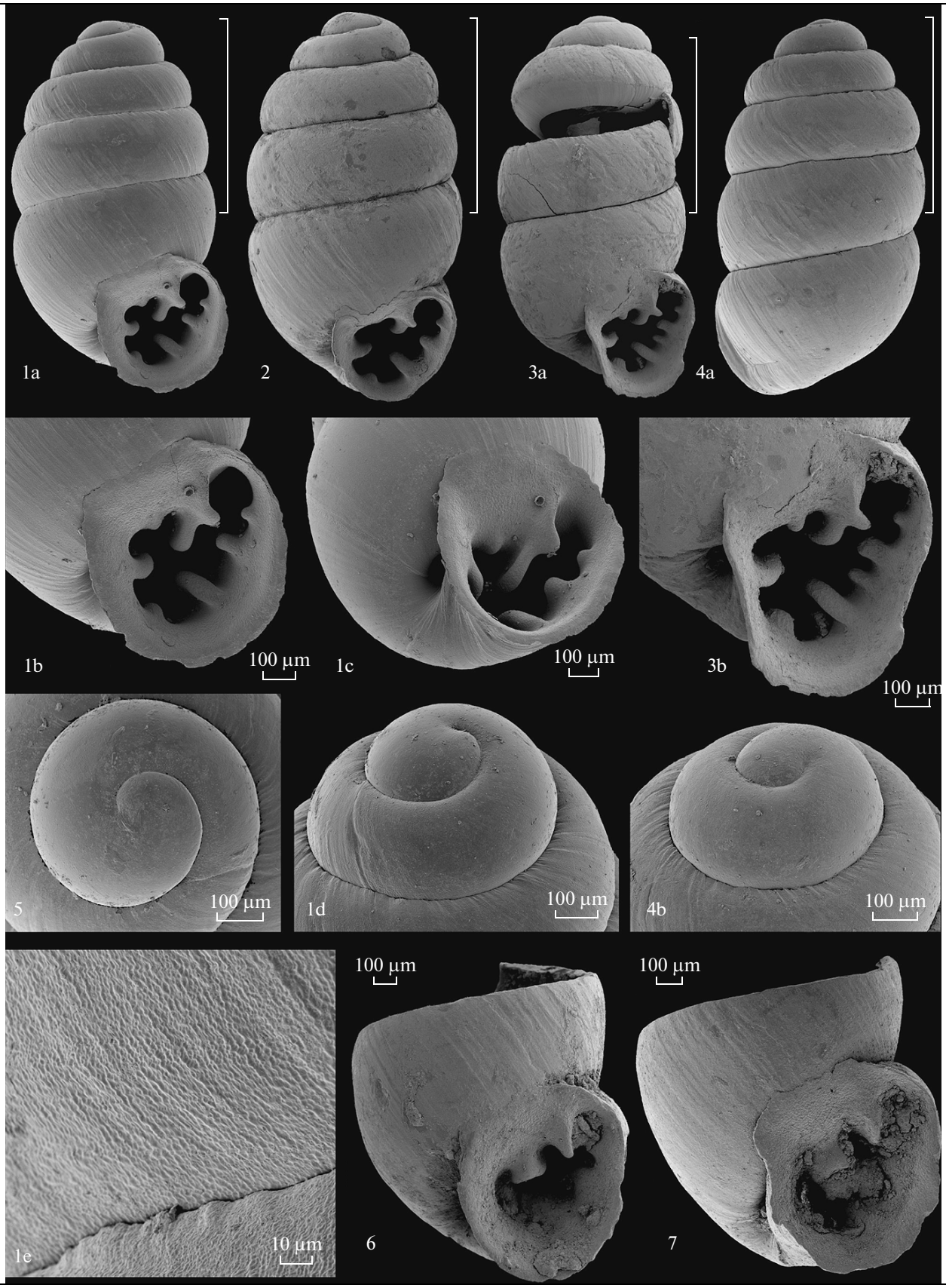
Scale bar, 1 mm (except figs. 2b, 7b, 8b, 8c).

Figs. 1–3. *Vallonia tumida* Stworzewicz, 2007, shells from sample HTS-056/3: (1) specimen NHMW, no. 2012/0179/0006, apertural view; (2) specimen NHMW, no. 2012/0179/0007: (2a) apical view, (2b) protoconch; (3) specimen NHMW, no. 2012/0179/0008, umbilical view.

Figs. 4–7. *Vallonia stworzewiczae* Neubauer, sp. nov., shells from sample HTS-056/2: (4) holotype NHMW, no. 2012/0179/0001, apertural view; (5) specimen NHMW, no. 2012/0179/0004, apical view; (6) paratype 1, NHMW, no. 2012/0179/0002, umbilical view; (7) specimen NHMW, no. 2012/0179/0005: (7a) apical view, (7b) protoconch.

Figs. 8–10. *Gastrocopta tuvaense* Prysjazhnjuk in Prysjazhnjuk et al., 1975, shells from sample HTS-056/2: (8) specimen NHMW, no. 2012/0179/0011: (8a) apertural view, (8b) apertural morphology (infraparietal lamella is present, but hardly visible due to its deep position inside the aperture), (8c) initial whorls with protoconch; (9) specimen NHMW, no. 2012/0179/0012, apertural view (teeth the same as in Fig. 8, but indistinguishable due to a SEM static charge); (10) specimen NHMW, no. 2012/0179/0013, abapertural view.

Pkate 5


1a
2
3a
4a
1b
100 μm
1c
100 μm
3b
100 μm
5
100 μm
1d
100 μm
4b
100 μm
1e
10 μm
100 μm
6
100 μm
7

Oligocene, Biozone C (Stworzewicz, 2007); east of Ulaan Tolgoi, Hsanda Gol Formation (?), Middle to Late Oligocene (?) (Prysjazhnjuk et al., 1975).

Material. Four fragments, including the last whorl from sample HTS-056/2.

***Gastrocopta tuvaense* Steklov, 1967**

Plate 4, figs. 8–10

Gastrocopta (Sinalbinula) tuvaense: Steklov, 1967, p. 275, pl. 1, fig. 6.

Gastrocopta tuvaense: Stworzewicz, 2007, p. 32, pl. 1, figs. 8 and 9.

Holotype. Zoological Institute of the Russian Academy of Sciences (St. Petersburg), no. 705, shell; unnamed locality between the Alash and Khemchik rivers, near Kyzyl-Mazhalyk, Western Tuva, about 50 km north of the Russian–Mongolian border; Miocene (?).

Description. The shell is globose-ovoid, consists of up to 5 whorls. The protoconch is composed of 1.0 whorl, its border with the teleoconch is marked by a weak growth rim and onset of weak, prosocline growth lines. The initial part of the protoconch is immersed and inflated, the surface is weakly granulated. The whorls are weakly convex, forming an almost regularly rounded shell outline. The sutures are moderately incised. The last whorl attains about 55% of the total shell height, passing into a straight base. The umbilicus is narrow, slitlike. The aperture is bluntly triangular, with a straight parietal margin, a weakly indented palatal margin, and a slightly convex columellar margin. The palatal and columellar margins meet at a regularly rounded basal margin. The peristome is sheetlike expanded, its surface is distinctly granulated. Dentition includes 7 or 8 teeth (6–8 according to Stworzewicz, 2007). The parietal and angular portions of the parietoangular lamella are roughly of equal strength, meeting at an angle of 90°. The angular portion is oriented perpendicular to the palatal margin; the parietal portion is more deeply placed. The infraparietal lamella is very small ("small to rarely prominent" according to Stworzewicz, 2007). The columellar lamella is thin but very distinct. The basal fold forms a small, broad convexity, lying in the subcolumellar position. The teeth of the palatal margin are decreasing consistently in strength in the adapical direction. The lower palatal fold is the most prominent, forming a thin, bladelike crest with parallel margins. The upper palatal fold is subtriangular, about half as high as the lower palatal fold. The interpalatal fold is occasionally present as a small, thin denticle. The suprapalatal fold is small, spiky, and subtriangular.

Measurements, in mm:

Specimen NHMW, no.	Shell diameter	Shell height
2012/0179/0011	1.4	2.2
2012/0179/0012	1.4	2.2
2012/0179/0013	1.3	2.1

Comparison. The available shells perfectly correspond to the material illustrated by Steklov (1967) and Stworzewicz (2007) regarding the shell shape, whorl convexity, and dentition. *G. subtuvaense* Steklov in Steklov et Tsytovich, 1967 is an extremely similar species from central Kazakhstan. Both species share the broad ovoid shape with low convex whorls and the general dentition pattern. *G. subtuvaense* slightly differs in its broader shell and the stronger parietoangular lamella. Because of these only minor differences, both taxa might be conspecific. A review of the type material of both species is necessary to solve this issue.

Concerning the shell shape, *G. tuvaense* is also similar to *G. mongolica* Prysjazhnjuk in Prysjazhnjuk et al., 1975, *G. devjatkini* Prysjazhnjuk in Prysjazhnjuk et al., 1975, and *G. shandgolica* Prysjazhnjuk in Prysjazhnjuk et al., 1975 (all species were previously recorded from the Valley of Lakes), and *G. gemina* Steklov, 1967 (from Tuva, type locality of *G. tuvaense*). Confusion with any of these species is unlikely due to their unique dentition. *G. mongolica* has a thin and highly elongated parietoangular lamella; *G. devjatkini* shows a large, broad, subrectangular infraparietal lamella; *G. shandgolica* has two infraparietal lamellae; *G. gemina* develops an even stronger lower palatal fold, a stronger parietoangular lamella, and an interpalatal fold closer to the lower palatal fold.

Occurrence. Central Mongolia, Valley of Lakes (Abzag Ovoo, early Late Oligocene, Biozone C) (Stworzewicz, 2007); Russia, western Tuva, near Kyzyl-Mazhalyk (Oligocene–Miocene) (Steklov, 1967).

Material. Three complete shells and 12 fragments from sample HTS-056/2 and one fragment from sample HTS-056/3.

Explanation of Plate 5

Scale bar, 1 mm if not indicated otherwise.

Figs. 1–5. *Gastrocopta valentini* Stworzewicz, 2007, shells from sample HTS-056/2: (1) specimen NHMW, no. 2012/0179/0014: (1a) apertural view, (1b) and (1c) apertural morphology, (1d) initial whorls with protoconch, (1e) teleoconch microsculpture; (2) specimen NHMW, no. 2012/0179/0015, apertural view; (3) specimen NHMW, no. 2012/0179/0016: (3a) apertural view, (3b) apertural morphology; (4) specimen NHMW, no. 2012/0179/0017: (4a) abapertural view, (4b) initial whorls with protoconch; (5) specimen NHMW, no. 2012/0179/0018, protoconch.

Figs. 6 and 7. *Gastrocopta devjatkini* Prysjazhnjuk in Prysjazhnjuk et al., 1975, shell fragments from sample HTS-056/2, apertural view: (6) specimen NHMW, no. 2012/0179/0009; (7) specimen NHMW, no. 2012/0179/0010.

***Gastrocopta valentini* Stworzewicz, 2007**

Plate 5, figs. 1–5

Gastrocopta (Sinalbinula) sp. 1: Steklov, 1967, p. 276, pl. 1, fig. 9.

Gastrocopta valentini: Stworzewicz, 2007, p. 30, pl. 1, figs. 6 and 7.

Holotype. NHMW, no. 2006/0241/0001, shell; Taatsiin Gol, Valley of Lakes, central Mongolia; Hsanda Gol Formation, Early Oligocene, Biozone A.

Description. The shell is slender ovoid to barrel-shaped, composed of up to 4.8 whorls. The protoconch consists of 1.1 whorls, its initial part is immersed and inflated; the surface is smooth to weakly granulated, granulation becomes consistently stronger to the distinct demarcation from the teleoconch. The granulation persists on the teleoconch (Pl. 5, fig. 1e). Additionally, the shell surface is ornamented by prosocline growth lines. The whorls are strongly and evenly convex. The sutures are moderately incised. The whorl height increases slowly but constantly; the last whorl attains 50–55% of the total shell height. The base is weakly convex. In the latest stage, an indentation occurs in the lower whorl portion, producing a short and thin furrow parallel to the growth direction. The umbilicus is small and narrow. The aperture is bluntly triangular, with a straight parietal margin, a straight to convex palatal margin (depending on the degree of indentation), and a slightly convex columellar margin. The palatal and columellar margins meet at regularly rounded basal margin. The peristome is sheetlike expanded, slightly everted, with posterior emargination visible in lateral view; its surface is distinctly granulated. The dentition is variable, including 7 or 8 teeth. The parietoangular lamella is prominent; its parietal portion is strong, thin, with more or less parallel margins, extending distinctly internally (Pl. 5, fig. 1c). The angular portion is weaker, bluntly triangular, meeting parietal portion approximately at a right angle. The infraparietal lamella is weak, broadly triangular, rather deeply placed. The columellar lamella is prominent, arcuate, and thin, with subparallel margins. The basal fold is moderately strong, forming a small, thin denticle. The lower palatal fold is very prominent, thin, and bladelike, with parallel margins. The upper palatal fold is equally shaped but about half as high as the lower palatal fold. In some specimens, a small, thin interpalatal fold occurs. The suprapalatal fold forms a weak, thin cusp.

Measurements in mm:

Specimen NHMW, no.	Shell diameter	Shell height
2012/0179/0014	1.1	1.9
2012/0179/0015	1.1	2.0
2012/0179/0017	1.1	1.9

Comparison. *G. valentini* is very similar in shape and dentition to *G. conturbata* Steklov in Steklov et Tsytovich (1967) from Kazakhstan. However, in the latter, the angular portion of the parietoangular lamella is arcuate and stronger as compared to that of *G. valentini*. In addition, the columellar lamella seems to be not as arcuate as it is the case of *G. valentini*. However, a firm taxonomic decision is impossible without reexamination of the type material from Kazakhstan.

Remarks. This taxon is morphologically very variable and, thus, problematic to determine. First, the shell shape varies slightly from slender ovoid to barrel-shaped. Second, the shape of the aperture varies from almost round to more elongate with a slightly concave palatal margin. Third, several specimens show a small interpalatal tooth. Gradual transitions of the features mentioned under the first two points do not allow a proper delimitation of morphotypes. The variability does not depend on the locality or biozone the specimen derive from. The presence of an additional tooth is nothing unusual in *Gastrocopta*, also among extant species (e.g., Taylor, 1960). Thus, all these features are considered to range within the natural intraspecific variability.

The available shells match perfectly with the type material described and illustrated by Stworzewicz (2007). However, this author also assigned more bulky shells to this species (not detected in our material). The difficulties of distinguishing this species from similar taxa have arisen from the poorly preserved and often highly deformed material of the type locality.

Stworzewicz (2007) also regarded *Gastrocopta* sp. 2 in Steklov (1967) from Tuva, Russia, as potentially conspecific. However, it clearly differs in the relatively larger last and penultimate whorls. In contrast, *Gastrocopta* sp. 1 in Steklov (1967) corresponds well to *G. valentini* in its shape and dentition, so that both forms are considered conspecific herein.

Occurrence. Central Mongolia, Valley of Lakes (Taatsiin Gol, Early Oligocene, Biozone A) (Stworzewicz, 2007); Russia, western Tuva, near Kyzyl-Mazhalyk (Oligocene–Miocene) (Steklov, 1967).

Material. Twenty-tree complete shells and many fragments with aperture from sample HTS-056/2, one complete specimen and 4 fragments from sample HTS-056/3.

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in the Neogene and Quaternary of Europe: Gastropod biodiversity, provinciality, and faunal gradients".

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