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Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications

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2. Molluscan fauna (Gastropoda: Pulmonata: Pupilloidea): a systematic review

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(With 1 plate)

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Abstract

Oligocene terrestrial gastropods from the Valley of Lakes, Mongolia, were found together with mammal remnants during field work carried out by a joint Austrian-Mongolian Expedition. They are represented by 11 taxa of Pupilloidea belonging to 5 genera: *Vertigo*, *Gastrocopta*, *Pupoides*, *Strobilos* and *Vallonia*. The shells and internal moulds were mainly collected in two horizons of the Hsanda Gol Formation recognized as being of Early Oligocene and Late Oligocene ages and correlated with mammalian associations A and C, respectively. The younger horizon of Early Miocene age, correlated with the rodent association D, yielded only a few shells. Most of the gastropod taxa were already known, but *Gastrocopta valentini* and *Vallonia tumida* are described here as new species. Previously known species are partly revised and new and better preserved specimens are illustrated.

Key words: Terrestrial gastropods, Pupilloidea, Oligocene, Mongolia

Introduction

Although the studies of the Oligocene Hsanda Gol Formation and its fauna were initiated more than eighty years ago, the first and the only information on terrestrial gastropods comes from PRYSJAZHNJK (PRYSJAZHNJK et al. 1975). Based on material collected by the joint Soviet-Mongolian Geological Expeditions and the joint Soviet-Mongolian Paleontological Expeditions, PRYSJAZHNJK described 8 taxa of terrestrial gastropods, including 5 new species. Earlier data on the fossil malacofauna from the area of Mongolia pertain to the Mesozoic continental deposits and to much younger sediments, of Pliocene age. In both cases, freshwater gastropods and bivalves were found, with the exception of a new *Succinea* species from the Pliocene of Tungur (PING 1931).

The Cenozoic terrestrial gastropods are known from other Central Asian localities adjacent to Mongolia, namely from Touva (STEKLOV 1967), Kazakhstan (STEKLOV &

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TZTOVICH 1967) and China (YEN 1943, LI YUNTONG & LI ZISHUN 1980). A comparison of the gastropod fauna from the Valley of Lakes in Mongolia with faunas from these areas reveals some similarities, but they differ in being much more diverse.

In 1970–1971, the first Oligocene terrestrial gastropods were found in two sites of the Valley of Lakes. In the first site the fossils were collected by D. BADAMGARAV, E.V. DEVYATKIN and I.G. LISKUN from the red beds of the Hsanda Gol clays just below the basaltic layers, on the right bank of the Taatsin Gol river (PRYSJAZHNJK et al. 1975). The second locality was 50 km eastward, near the site with Miocene mammal fossils, in the area of Ulaan Tolgoi. In this case as well, the snail shells were found in the red clay and sand below the basaltic layers. The material from the latter site was investigated by PRYSJAZHNJK.

The present paper describes fossil gastropods collected recently during the field work carried out by a joint Austrian – Mongolian Expedition. The shells and moulds were mainly found in two horizons of the Hsanda Gol and Loh Formations recognized as being of Early Oligocene and Late Oligocene ages and correlated with mammalian associations A and C, respectively (DAXNER-HÖCK et al. 1997, HÖCK et al. 1999). Since the sediments are intercalated with basalts which were dated by $^{40}\text{Ar}/^{39}\text{Ar}$, the ages of the basalt eruptions are defined. Consequently, the faunal association A below basalt I is at least 31.5 Ma, whereas the fossils of biozone C below and above basalt II are dated at around 28 Ma. The younger horizon of Early Miocene age, correlated with the rodent association D, yielded only a few shells. Further, comprehensive information on the geological setting of the Hsanda Gol Formation, its lithology and stratigraphy is presented in the above-cited papers.

On the whole, the fossil gastropods are poorly preserved, many specimens being preserved as internal moulds, deformed by lateral compaction, without remnants of actual shells. The remaining, uncompressed specimens with completely preserved shells have their apertures filled with calcite, which is difficult to remove, precluding precise identification.

Eleven species of Pupilloidea representing 5 genera – *Vertigo*, *Gastrocopta*, *Pupoides*, *Strobilos* and *Vallonia* – were identified, and some gastropod eggs were also found. All genera represented in Hsanda Gol sediments are still extant not only in Central Asia, but also in more remote parts of world.

The specimens are stored in the collection of the Natural History Museum, Department of Geology and Palaeontology, Vienna, Austria.

The following abbreviations in the text below denote shell parameters: H – shell height, W – shell width, h – aperture height, w – aperture width, bwh – body whorl height, NW – number of whorls, D – max. diameter, d – min. diameter.

All measurements were taken with a Nikon measurescope MM-11, accuracy 0.01 mm; whorls were counted according to EHRMANN's (1933) method. Photographs of shells were taken with a Nikon DS-5Mc digital camera and Lucia Net program.

Systematic palaeontology

Class: Gastropoda

Subclass: Pulmonata

Order: Stylommatophora

Family: Vertiginidae FITZINGER, 1833

Genus: *Vertigo* O.F. MÜLLER, 1774

Vertigo cf. bicolumellata STEKLOV, 1967

Pl. 1, Fig. 1

1967 *Vertigo (Angustella) bicolumellata* STEKLOV (in STEKLOV & TSYTOVICH): 116, Fig. 9.

L o c a l i t y / S t r a t i g r a p h y : Abzag Ovoo (ABO-A/3) – early Late Oligocene (biozone C): Loh Fm.

M a t e r i a l : 1 shell with broken aperture – ABO-A/3; Inv. Nr. 2006z0196/0001

M e a s u r e m e n t s (in mm): H = 1.75; W = 1.08; h = 0.58; w = ca 0.57; bwh = 1; NW = 5.3

The single shell is ovate with moderately convex whorls, very finely punctate and, except juvenile whorls, covered with weak but well visible striae. Body whorl narrowed at its base and bluntly keeled, crest weakly developed, umbilicus slit-like. There are two weakly visible grooves in the outer surface of the body whorl, marking the position of palatal teeth (tooth). Aperture slightly heart-shaped (its palatal margin is broken), with 6 (5) teeth. Angular tooth thin lamellate; parietal slightly stouter, situated somewhat deeper than the angular (but its position is difficult to ascertain because the parietal callus is destroyed); upper palatal does not reach the palatal margin, its inner part embedded in calcite; "lower" palatal shorter and deeper situated (judging from the grooves on the surface of the body whorl). According to STEKLOV (in STEKLOV & TSYTOVICH 1967: 116) there are two teeth on the columella – columellar, short but thick lamellate, with its inner part slightly deflected downwards, and subcolumellar, smaller and deeper situated. Of them, only the columellar tooth is well visible in the specimen examined; the subcolumellar (if present at all) is covered with calcite.

STEKLOV (in STEKLOV & TSYTOVICH 1967) regarded palatal teeth in *V. bicolumellata* as two separate structures, the upper palatal and the lower palatal. However, it seems very likely that there is only one, divided, upper palatal tooth. A similar modification of the upper palatal tooth was observed in *Vertigo angulifera* O. BOETTGER, 1884 from the Lower Miocene of the Czech Republic (ČEJCHAN 1985).

The specimen is no doubt identical or very close to *V. bicolumellata*, which was placed by STEKLOV in a separate subgenus *Angustella*, regarded afterwards as unjustifiable (POKRYSZKO & STWORZEWCZ 2001).

V. bicolumellata was hitherto known only from the mid-Miocene deposits of Kazakhstan; hence, its occurrence in the ABO-A/3 profile from the Valley of Lakes in Mongolia extends its stratigraphic range to the Late Oligocene.

Family: Chondrinidae STEENBERG, 1925

Genus: *Gastrocopta* WOLLASTON, 1878

***Gastrocopta cf. mongolica* PRYSJAZHNJK, 1975**

Pl. 1, Figs. 2–3

1975 *Gastrocopta (Albinula) mongolica* PRYSJAZHNJK (in PRYSJAZHNJK et al.): 169, pl. 1, figs. 1–3.

L o c a l i t i e s / S t r a t i g r a p h y : Abzag Ovoo (ABO-A/3) – early Late Oligocene (biozone C): Loh Fm.

Taatsiin Gol right (TGR-A/14) – Early Oligocene (biozone A): Hsanda Gol Fm.

M a t e r i a l : 1 shell fragment (1.5 of somewhat damaged last whorls with aperture) – ABO-A/3: Inv. Nr. 2006z0197/0001; 1 shell fragment (2 last whorls with aperture) – TGR-A/14: Inv. Nr. 2006z0198/0001.

M e a s u r e m e n t s (in mm): W = 1.69, 1.66; h = 0.80, 0.88; w = 0.90, 0.95

Body whorl strongly narrowed at its base, with slit-like umbilicus and distinct crest on outer surface of the palatal and basal wall, parallel to aperture margin. There is a gutter-like depression behind the crest and a distinct sulcus behind it. Aperture rounded-triangular with poorly reflexed lip and very thin parietal callus. In one specimen the aperture is filled with calcite sediment, difficult to remove, hence not all apertural barriers are well visible. In fact, only a solid, lamellate parietoangular tooth and a palatal tooth are partially identifiable; their inner ends are invisible. The outer part of the short and arcuate angular portion of the parietoangular tooth is connected with the upper part of the palatal margin. The angular and parietal portions are separated by a shallow groove. Visible part of parietal portion high lamellate but its inner end is embedded in sediment; in front view its free tip is bent palatalwards. Upper palatal tooth very small, thin and low, elongate tubercular, standing on a thickened ridge representing an exterior sulcus.

In his description of *G. mongolica*, PRYSJAZHNJK (in PRYSJAZHNJK et al. 1975: 169) presented two further teeth: columellar and basal. Columellar large, ear-shaped, vertical. It is visible in the shell from TGR-A/14 only. Basal is lamellate, deeply placed and diagonally situated, and together with the palatal tooth it forms, acc. to PRYSJAZHNJK, a T-shaped structure (though the palatal tooth does not reach the basal). Actually, this "basal" is not visible in the specimen from ABO-A/3 in front view but it is very well marked on the surface of the body whorl in side view. On the other hand, in the specimen from TGR-A/14 this diagonal tooth is very well visible, but does not form a T-shaped structure, being displaced adaxially.

In my opinion the diagonal tooth is the lower palatal rather than the basal, and was incorrectly interpreted by PRYSJAZHNJK.

According to PRYSJAZHNJK (in PRYSJAZHNJK et al. 1975: 170), the form of parietoangular and columellar teeth in *G. mongolica* resembles that of the modern American *Gastrocopta contracta* SAY, 1822. Moreover, the latter species has a lower palatal tooth, transversely and deeply placed, similar to that presented by PRYSJAZHNJK as a "basal" tooth.

G. mongolica at first glance is also similar to *G. (Albinula) krestnikovi* STEKLOV, 1967, described from Mid-Miocene deposits of Touva. However, the structure of the columellar tooth, which in the latter species is long, thin lamellate and prolonged toward the aperture margin, easily separates the two species.

STEKLOV (1967: 274) also regarded his species as a direct ancestor of *G. contracta*; nonetheless, the columellar tooth of recent American *G. contracta* is subvertical and very deeply placed (PILSBRY 1916–1918), like in PRYSJAZHNJUK's *G. mongolica*.

G. mongolica is known from the Valley of Lakes in Mongolia only.

***Gastrocopta devjatkini* PRYSJAZHNJUK, 1975**

Pl. 1, Fig. 4

1975 *Gastrocopta (Kazachalbinula) devjatkini* PRYSJAZHNJUK (in PRYSJAZHNJUK et al.): 170, pl. 1, figs. 7–8.

Localities / Stratigraphy: Abzag Ovoo (ABO-A/3) – early Late Oligocene (biozone C): Loh Fm.

GRAB-II – Early Oligocene (biozone A): Hsanda Gol Fm.

Taatsiin Gol right (TGR-A/14) – Early Oligocene (biozone A): Hsanda Gol Fm.

Material: 1 shell + 1 fragment – ABO-A/3: Inv. Nr. 2006z0199/0001; 1 shell – GRAB-II: Inv. Nr. 2006z0238/0000; 45 shells (partially calcified and squashed) + many fragments – TGR-A/14: Inv. Nr. 2006z0237/0000.

Measurements (in mm) of specimens from ABO-A/3 and GRAB-II, respectively: H = 1.95, 2.07; W = 1.19, 1.2; h = 0.72, 0.9; w = 0.69, 0.8; bwh = 1.14, 1.3; NW = 5.3, 5.3.

Shells ovate-conical with moderately convex or even somewhat flattened whorls, covered with very fine, irregular striae (sculpture visible in two uncalcified specimens only). Body whorl narrowed and keeled at its base. There is a distinct crest on its outer surface, parallel to the aperture margin and with a gutter-like depression behind. Only one shell is more elongate, with a somewhat weaker crest. Umbilicus, if visible, slit-like. Aperture rounded-triangular, with moderately reflexed lip (in some specimens broken) and very thin parietal callus.

Apertural barriers large and occlude almost entire aperture. Parietal part of parietoangular hardly visible (situated very deeply), remaining teeth very characteristic and fully correspondind to PRYSJAZHNJUK's description. Angular part thick lamellate, arcuate and united with palatal margin of aperture. Its inner end declines wholly and, according to PRYSJAZHNJUK (in PRYSJAZHNJUK et al. 1975: 171), it should reach the transversely situated parietal part, but it is poorly visible in the two better-preserved shells from ABO-A/3 and GRAB-II. Infraparietal tooth is the most specific – massive, deeply situated and horse-shoe-shaped, rarely V-shaped, opened inwards. Right portion (closer to palatal wall) usually longer. Columellar tooth deeply situated, subvertical and ear-shaped. There are three palatal teeth placed on a very well-marked callus. Suprapalatal tooth very small, tapered knob-shaped, the upper palatal tooth triangular, tapering and becoming lower inside the aperture. Lower palatal tooth very strong and long, near mid-length deflected abaxially. A tiny basal tooth mentioned by PRYSJAZHNJUK (in PRYSJAZHNJUK et al. 1975: 171) is marked neither in the specimens examined nor in the three specimens from PRYSJAZHNJUK's collection at my disposal.

G. devjatkini is known from the Valley of Lakes in Mongolia only.

***Gastrocopta shandgolica* PRYSJAZHNJK, 1975**
Pl. 1, Fig. 5

1975 *Gastrocopta (Kazachalbinula) shandgolica* PRYSJAZHNJK (in PRYSJAZHNJK et al.): 172, pl. 1, figs. 9-11.

L o c a l i t i e s / S t r a t i g r a p h y : Abzag Owoo (ABO-A/3) – early Late Oligocene (biozone C): Loh Fm.

Taatsiin Gol right (TGR-A/14) – Early Oligocene (biozone A): Hsanda Gol Fm.

M a t e r i a l : 2 shells + 3 fragments – ABO-A/3: Inv. Nr. 2006z0239/0001, 2006z0239/0000; 4 deformed shells – TGR-A/14: 2006z0240/0000.

M e a s u r e m e n t s (in mm): H = 1.64, 1.59; W = 0.93, 0.91; h = 0.62, 0.61; w = 0.61, 0.57; bwh = 1.0, 0.99; NW = 5.0, 5.0.

Shells more cylindrical than ovate, consisting of 5 weakly convex whorls, covered with very fine striae. Body whorl distinctly exceeding half of shell height, provided with very strong crest parallel to the aperture margin. Behind the crest a gutter-like concavity corresponding to the lower palatal tooth. Umbilicus slit-like. Aperture triangular and, like that described by PRYSJAZHNJK (in PRYSJAZHNJK et al. 1975: 172), extended at the angle of 45° relative to the shell axis. Peristome reflexed moderately, parietal callus thin but distinct.

Apertural barriers very well developed, occluding almost the entire aperture. Angular portion of lamellate parietoangular tooth rather solid and slightly arcuate. Its outer end reaches the parietal callus-palatal margin junction; the inner end becomes somewhat lower and passes into a deep-reaching parietal portion, which curves adaxially. Two infraparietal teeth: the right (close to angular) thin but longer and deeper situated, the left stumpy. In one shell the teeth are closely adjoining. Columellar tooth very characteristic for the species: a long, low and sinuous ridge beginning usually on the parietal-columellar margin junction, subhorizontal in its mid part and descending spirally to the base of columella. Basal tooth prominent, in columellar/basal position, the subcolumellar not always present. Of three palatal teeth the suprapalatal is the smallest, knob-shaped; the upper palatal is higher in front and gently descends inside, the lower palatal is twice as large and strong, in one specimen it is flattened on the upper surface with a depression in the mid part.

Gastrocopta shandgolica is known from the Valley of Lakes in Mongolia only.

***Gastrocopta valentini* sp. nov.**
Pl. 1, Figs. 6–7

? 1975 *Gastrocopta (Sinalbinula?)* sp. PRYSJAZHNJK (in PRYSJAZHNJK et al.): 173, pl. 1, figs. 12, 16.

D i a g n o s i s : Based on the separation of the angular and parietal portions of the parietoangular tooth the new species is somewhat similar to the *G. fissidens* (SANDBERGER, 1858) group, but differs in the following characters: 1. shell oviform (not ovate-cylindrical), 2. anterior end of parietal portion of parietoangularis tooth overlaps the posterior end of angular portion and a thin callus joins the two parts (in the *G. fissidens* group the two parts are nearly parallel), 3. apertural barriers stouter, resulting in a very much occluded aperture.

D e r i v a t i o n o m i n i s : in honour of Dr. Valentin A. PRYSJAZHNJUK, Institute of Geological Sciences, Ukrainian Academy of Sciences, Kiev, who described some new species from the Valley of Lakes in Mongolia and presented a single shell and one fragment with aperture as *Gastrocopta (Sinalbinula?)* sp., probably conspecific with *Gastrocopta valentini*.

H o l o t y p e : Inv.Nr. 2006z0241/0001, TGR-A/14; Fig. 6

P a r a t y p e s : 1 shell Inv. Nr. 2006z0241/0002 (TGR-A/14) (Fig. 7); 21 shells mostly deformed + calcified fragments Inv. Nr. 2006z0241/0000(TGR-A/14)

O t h e r m a t e r i a l : 3 shells badly preserved Inv. Nr. 2006z0242/0000 (TGR-A/13)

C o l l e c t i o n : Natural History Museum, Department of Geology and Palaeontology, Vienna, Austria.

T y p e l o c a l i t y : Taatsiin Gol right (TGR-A/14), Valley of Lakes, Central Mongolia.

S t r a t i g r a p h y : Early Oligocene; lower part of the Hsanda Gol Formation; silt and clay below basalt I (31.5 Ma); biozone A (HÖCK et al. 1999).

M e a s u r e m e n t s of holotype (**H**) and 2 paratypes (in mm): H = 1.98, 2.02, 2.11 (**H**); W = 1.14, 1.17, 1.27 (**H**); h = 0.75, 0.80, 0.80 (**H**); w = 0.73, 0.78, 0.85 (**H**); bwh = 1.19, 1.23, 1.30 (**H**); NW = 4 $\frac{3}{4}$ -5

D e s c r i p t i o n of the holotype: Shell oviform with weakly convex whorls and moderately deep suture. Surface sculpture of delicate, thin striae. Body whorl exceeding half of shell height, narrowed at base, ascending before aperture. Crest very strongly developed, parallel to the aperture margin, with a very distinct concavity behind, and with a groove corresponding to the lower palatal tooth. Umbilicus open, drop-shaped, partly covered by the body whorl. Aperture rounded-triangular, with reflexed lip and a weak parietal callus.

Aperture bearing 7 teeth. Lamellate angular and parietal portions of parietoangular tooth appear not to be joined, but are in fact connected by a thin callus. Angular portion low but robust, arcuate, its anterior end reaches the parietal callus-palatal margin junction. Parietal portion situated deeply, closer to columella, its anterior end overlaps the posterior end of angular portion and a thin callus joins the two parts. Infraparietal tooth elongated-knob-shaped, deeply placed, more or less in line with the parietal portions of parietoangular. Columellar tooth low-lamellate, subhorizontal, situated on the upper part of columellar margin, its inner end somewhat deflected downwards and around columella. Basal tooth in the form of low convexity, in columellar/basal position. Lower and upper palatal teeth lamellate – the lower solid and longer than the upper one, near mid-length deflected abaxially; foremost part of upper palatal tooth set on a thickened callus together with a very small and tapered suprapalatal.

D e s c r i p t i o n of paratypes: Almost all specimens are crushed and deformed, making the shell shape and dimensions difficult to determine. In most specimens the knob-shaped infraparietal tooth is situated as deep as the parietal portion of the parietoangular, but in some specimens it is placed somewhat deeper. Suprapalatal tooth generally separated from the upper palatal although their bases are connected by a thickened callus. In the single specimen described by PRYSJAZHNJUK (in PRYSJAZHNJUK et al. 1975: 174) and regarded here as conspecific with the new species, the suprapala-

tal and upper palatal teeth are wholly fused and in front view look like an abnormally broad upper palatal.

PRYSJAZHNJK compared his specimen to *Ptychalaea flexidens* (REUSS, 1861) and *Gastrocopta fissidens* (SANDBERGER, 1858) from the Oligocene and Miocene of Europe based on the weak connection between the angular and parietal teeth. However, in both species the angular and parietal teeth are strong and not as deeply placed as in *G. valentini*. On the other hand, there is a group of Far Eastern recent species with similarly developed teeth on the parietal wall, particularly *G. chichijimana* PILSBRY, 1916 and *G. boninensis* PILSBRY, 1916 from Bonin Island. Like the new species, they have a parietal tooth more deeply placed than the angular and connected with the latter by a low callus at its outer end. There is also a whole series of Australian gastrocoptines in which angular and parietal portions of the parietoangular tooth may appear separate in front view (POKRYSZKO 1996).

The newly described species is known from the Oligocene of Mongolia only, but most probably the single specimen presented by STEKLOV (1967: 276) from the Miocene of Touva as *Gastrocopta (Sinalbinula)* sp. No. 2 represents *G. valentini*.

Gastrocopta tuvaense STEKLOV, 1967

Pl. 1, Figs. 8–9

1967 *Gastrocopta tuvaense* STEKLOV: 275, fig. 6.

Locality / Stratigraphy : Abzag Ovoo (ABO-A/3) – early Late Oligocene (biozone C): Loh Fm.

Material : ABO-A/3 – 1 shell: Inv. Nr. 2006z0243/0001, 1 shell: Inv. Nr. 2006z0243/0002, 47 shells + numerous fragments: Inv. Nr. 2006z0243/0000

Measurements (in mm) of 10 specimens: H = 2.08–2.43; W = 1.29–1.42; h = 0.79–0.88; w = 0.78–0.90; bwh = 1.28–1.42; NW = 5½–5½

Shells oviform with weakly convex whorls and rather shallow suture. Surface sculpture of very thin striae. Body whorl exceeding half of shell height, narrowed at base, with rather prominent, sharp crest behind aperture and very distinct groove corresponding to the lower palatal tooth. Umbilicus open but very narrow. Aperture semioval with somewhat flattened palatal margin, poorly reflexed lip and a weak parietal callus.

Aperture bears 6–8 teeth. Lamellate angular and parietal portions of parietoangular tooth fully concrescent, the angular thinner, its free tip more or less bent palatalwards. Infraparietal tooth ranging from prominent (rarely) to small, vestigial or even absent. Columellar tooth lamellate, horizontal. The basal tooth in the form of a low convexity, in columellar/basal position. There are 3–4 teeth on the palatal margin: besides lower, upper and suprapalatal, some specimens also have an interpalatal tooth.

STEKLOV (1967: 275) regarded *G. tuvaense* as especially close to *G. nouletiana* (DUPUY, 1850) from the Neogene of Europe. Like the latter, *G. tuvaense* is very variable in shell shape and tooth number; the interpalatal tooth is present in some shells (cf. STWORZEWICZ 1999). It differs from *G. nouletiana* by having distinctly less convex whorls and a shallow suture, stronger crest and somewhat different aperture shape.

Family: Pupillidae TURTON, 1831

Genus: *Pupoides* PFEIFFER, 1854

***Pupoides steklovi* PRYSJAZHNJK, 1975**

Pl. 1, Fig. 10

1975 *Pupoides steklovi* PRYSJAZHNJK (in PRYSJAZHNJK et al.): 175, pl. 1, figs. 13-14.

L o c a l i t i e s / S t r a t i g r a p h y : Abzag Ovoo (ABO-A/3) – early Late Oligocene (biozone C): Loh Fm.

Taatsiin Gol right (TGR-A/13) – Early Oligocene (biozone A): Hsanda Gol Fm.

Taatsiin Gol right (TGR-A/14) – Early Oligocene (biozone A): Hsanda Gol Fm.

Taatsiin Gol left (TGL-A/2) – Early Oligocene (biozone A): Hsanda Gol Fm.

M a t e r i a l : 1 incomplete shell – ABO-A/3: Inv. Nr. 2006z0244/0000; 2 fragments – TGR-A/13: Inv. Nr. 2006z0246/0000; 1 somewhat deformed shell – TGR-A/14: Inv. Nr. 2006z0245/0001; 9 deformed, incomplete shells + some fragments – TGR-A/14: Inv. Nr. 2006z0245/0000; 6 fragments – TGL-A/2: Inv. Nr 2006z0247/0000.

M e a s u r e m e n t s (in mm) of the best-preserved specimen, somewhat crushed vertically: H = 3.58; W = 2.16; h = 1.78; w = 1.50; bwh = 2.45; NW = 6

Almost all shells are in very bad condition – in the form of internal moulds, not only laterally but also vertically flattened, therefore their precise shape and dimensions are difficult to define. Generally, they are elongate, conical with weakly convex whorls; on some better-preserved specimens very minute striation is visible. The body whorl is huge and solid with narrowed base and drop-shaped umbilicus. Aperture horseshoe-shaped with broadly reflexed margin and thickened lip. There is a nodulous angular tooth just below the point of parietal callus/palatal margin junction.

The shell form places *P. steklovi* in the group of Oriental and Ethiopian members of *Pupoides*. Recently, they are mainly tropical and subtropical species of arid regions or dry places in humid areas. As fossils, the group is insufficiently known; the species originally described as *Pupoides* were later transferred to *Microstele* (ex. *Pupoides wenzi* FISCHER, 1920 and *Pupoides pilsbryi* DALL, 1915) (PILSBRY 1920-1921).

Family: Valloniidae MORSE, 1864

Genus: *Vallonia* RISSO, 1826

***Vallonia cf. lepida* (REUSS, 1849)**

Pl. 1, Figs. 11-12

1849 *Helix lepida* REUSS: 24, pl. 2, fig. 4.

L o c a l i t i e s / S t r a t i g r a p h y : Taatsiin Gol right (TGR-A/13) – Early Oligocene (biozone A): Hsanda Gol Fm.

Taatsiin Gol right (TGR-A/14) – Early Oligocene (biozone A): Hsanda Gol Fm.

Taatsiin Gol right (TGR-C/1) – Late Oligocene (biozone C): Hsanda Gol Fm.

Taatsiin Gol right (TGR-C/5) – Late Oligocene (biozone C): Hsanda Gol Fm.

M a t e r i a l : numerous fragments – TGR-A/13: 2006z0249/0000; 1 shell – TGR-A/14: Inv. Nr. 2006z0248/0001; 1 shell – TGR-A/14: Inv. Nr. 2006z0248/0002; 83 shells + fragments – TGR-A/14: 2006z0248/0000; 10 shells – TGR-C/1: Inv. Nr. 2006z0250/0000; 4 shells + fragments – TGR-C/5: Inv. Nr. 2006z0251/0000.

M e a s u r e m e n t s of 10 specimens (D x d, in mm): 2.31x2.07, 2.34x1.98, 2.45x1.96, 2.48x2, 2.48x2.05, 2.48x2.08, 2.52x2.26, 2.65x2.16, 2.67x2.07, 2.71x2.17.

Most specimens very badly preserved – deformed and mineralised. Some retained shell fragments with partially visible surface sculpture. As a rule, protoconch or early whorls pressed in the body whorl, making shell height hard to establish. Although not a single specimen is complete, based on the few best specimens certain shell characters correspond to *Vallonia lepida*. GERBER (1996) described particular variability of the species, which is also visible in the Hsanda Gol material.

The few less damaged shells are either more or less depressed or with distinctly elevated spire. Whorls (about 3½) increase regularly, the body whorl expanding towards the aperture and moderately descending. Aperture almost circular, oblique, with well-expanded and thickened peristome. Umbilicus generally wide and perspective, about one-third minor width, but generally difficult to define because of shell deformation. Surface sculpture visible in few specimens only; it consists of delicate, regular, not very closely spaced ribs.

V. lepida was also recorded as *Vallonia* sp. N 1 by PRYSJAZHNJUK et al. (1975: 176), who regarded it as close to *V. sandbergeri* (DESHAYES, 1863) and to *V. moguntiaca* WENZ, 1915 (included to *V. lepida* by GERBER).

Although the species is known from the Oligocene (only from three sites in Germany), it was particularly widespread in the Miocene, not only in Europe; it was also recorded from China (GERBER 1996).

Vallonia subcyclophorella (GOTTSCHICK, 1911)

Pl. 1, Figs. 13–15

1911 *Helix (Vallonia) subcyclophorella* GOTTSCHICK: 503, pl. 7, fig. 2.

L o c a l i t i e s / S t r a t i g r a p h y :

Abzag Ovoo (ABO-A/3) – early Late Oligocene (biozone C): Loh Fm.

Taatsiin Gol right (TGR-A/14) – Early Oligocene (biozone A): Hsanda Gol Fm.

Taatsiin Gol left (TGL-A/2) – Early Oligocene (biozone A): Hsanda Gol Fm.

M a t e r i a l : 1 shell – ABO-A/3: Inv. Nr. 2006z0252/0001; 6 shells – ABO-A/3: Inv. Nr. 2006z0252/0000; 4 shells – TGR-A/14: Inv. Nr. 2006z0253/0000; 15 shells + fragments – TGL-A/2: Inv. Nr. 2006z254/0000.

M e a s u r e m e n t s of 7 specimens (D x d, H, in mm.): 1.81x1.62, 0.96; 1.83x1.56, 1.05; 1.88x1.57, 0.95; 1.88x1.63, 0.92; 1.90x1.60, 0.86; 1.95x1.55, 0.97; 1.95x1.61, 0.93.

Shells small, depressed, consisting of 3¼ rounded whorls, separated by rather deep suture. Body whorl expanding towards the aperture and moderately descending. Aperture more oval than circular, with somewhat expanded and poorly thickened peristome. Umbilicus generally wide and regularly decolling, but last third of the whorl decolling

more rapidly. Surface sculpture of regular, delicate, radial ribs and hardly visible irregular striae between them.

V. subcyclophorella is known from the numerous sites in Europe from the Early Miocene to Late Miocene (GERBER 1996), but there is also a record from the Miocene of Kazakhstan (STEKLOV & TSYTOWICH 1967).

***Vallonia tumida* sp. nov.**

Pl. 1, Figs. 16–18

D i a g n o s i s : One of the biggest *Vallonia* species. It differs at first glance from all its congeners in the rounded, somewhat tumid, as if "swollen" shell and distinctly narrow umbilicus.

D e r i v a t i o n o m i n i s : Latin, *tumidus*, tumid, swollen.

H o l o t y p e : Inv.Nr. 2006z0255/0001, ABO-A/3; Figs. 16-18

P a r a t y p e s : 8 + fragments – Inv. Nr. 2006z0255/0000 (ABO-A/3)

O t h e r m a t e r i a l : 17 – Inv. Nr. 2006z0256/0000 (TGR-A/14); 9 – Inv. Nr. 2006z0257/0000 (TGL-A/2)

C o l l e c t i o n : Natural History Museum, Department of Geology and Palaeontology, Vienna, Austria.

T y p e l o c a l i t y : Abzag Ovoo (ABO-A/3), Valley of Lakes, Central Mongolia.

S t r a t i g r a p h y : Loh Formation below basalt II (28 Ma); biozone C (HÖCK et al. 1999).

O t h e r l o c a l i t i e s / S t r a t i g r a p h y :

Taatsiin Gol right (TGR-A/14) – Early Oligocene (biozone A): Hsanda Gol Fm.

Taatsiin Gol left (TGL-A/2) – Early Oligocene (biozone A): Hsanda Gol Fm.

M e a s u r e m e n t s o f h o l o t y p e (H) and 2 paratypes (D x d, H, in mm): (H) 3.23x2.70, 1.95; 2.99x2.41, 1.72; 2.53x2.12, 1.59.

Shell rounded (H/D ratio ca. 1.6), of 4 – 4¼ moderately convex whorls; suture moderately deep. Body whorl not much wider than the penultimate, rapidly widening toward the aperture in the last fourth of whorl and distinctly descending before it. Aperture nearly circular with expanded and thickened peristome. Umbilicus rather narrow, about ⅓ of minimum shell diameter, partly covered by expanded peristome. Embryonic whorls smooth, definitive whorls finely, somewhat irregularly striated; the striae are more delicate on the base.

The new species is well characterized by having a very elevated spire, much more so than in all other members of the genus, as if swollen, and by a strikingly narrow umbilicus.

***Vallonia* sp.**

Some shells of *Vallonia* were also found in different localities, but they are unidentifiable because of very bad preservation.

Localities / Stratigraphy : Taatsiin Gol right (TGR-C/2) – Late Oligocene (biozone C): Hsanda Gol Fm.

Toglorhoi (TGW-A/2b) – Late Oligocene (biozone C): Loh Fm.

Ikh Argalatyn Nuruu (IKH-A/5) – Late Oligocene (biozone C1): Hsanda Gol Fm.

Luugar Khudag (LOG-A/1) – Early Miocene (biozone D): Loh Fm.

Material : 11 shells – TGR-C/2: Inv. Nr. 2006z0294/0001; 12 shells – TGW-A/2b: Inv. Nr. 2006z0295/0000; 1 shell – IKH-A/5: Inv. Nr. 2006z0296/0001; 1 shell – LOG-A/1: Inv. Nr. 2006z0297/0001.

Family: Strobilosidae PILSBRY, 1918

Genus: *Strobilops* PILSBRY, 1892

? *Strobilops* sp.

Pl. 1, Fig. 19

Locality / Stratigraphy : Unkheltseg (UNCH-A/3) – Early Miocene (biozone D): Loh Fm.

Material : 1 shell – UNCH-A/3: Inv. Nr. 2006z0292/0001

Measurements : H = 2.08; W = 3.02; NW = ca. 4 ½

A single specimen with destroyed and calcified a final part of the body whorl and aperture. Shell coniform, surface sculpture of narrow, obliquely radial ribs, weakening at the base; the sculpture of protoconch unknown. Umbilicus rather narrow, regularly decoiling. Aperture, or properly speaking the cross-section of the body whorl before aperture, broadly lunate.

This incomplete shell probably belongs to the genus *Strobilops* but the impossibility to observe the aperture and apertural barriers makes the assignation uncertain.

Strobilosids were widespread in the Tertiary of the Northern Hemisphere, including Europe, where they became extinct at the end of Pliocene. Some species were recorded also from areas adjacent to Mongolia (STEKLOV 1967, WEN et al. 1982).

Gastropod eggs

Pl. 1, Fig. 20

Localities / Stratigraphy : Toglorhoi (TGW-A/2a) – Late Oligocene (biozone C): Loh Fm.

Taatsiin Gol left (TGL-A/1) – Early Oligocene (biozone A): Hsanda Gol Fm.

Taatsiin Gol left (TGL-A/2) – Early Oligocene (biozone A): Hsanda Gol Fm.

Material : 5 – TGW-A/2a: Inv. Nr. 2006z0293/0001; 115 – TGW-A/2a: Inv. Nr. 2006z0293/0000; 2 – TGL-A/1: Inv. Nr. 2006z0258/0000; 181 – TGL-A/2: Inv. Nr. 2006z0259/0000.

In three samples, more than 300 gastropod eggs were found. They are oblate spheroid, wholly calcified and nearly the same in size. Dimensions of 10 specimens vary from 0.67–0.81 mm (D) and 0.53–0.63 mm (d). Fossil terrestrial gastropod eggshells of similar age were examined before by PIERCE (1993). The author analysed two eggshell forms found in the Late Oligocene-Early Miocene sediments of Cabbage Patch (Western Montana) and attempted to correlate them with taxa of associated terrestrial gastropods. The minor form was correlated with a *Vallonia* species and attributed to *Vallonia berryi* PIERCE, 1992 from the same locality. Its dimensions (10 specimens) were: 0.72–0.80 mm. and 0.55–0.60 mm.

The eggs from Hsanda Gol Formation correspond very well to those described by PIERCE, but from among three *Vallonia* species found there, only *V. cf. lepida* is similar in size to *V. berryi*. The remaining species are either smaller (*V. subcyclophorella*) or bigger (*V. tumida* sp.nov.). Snails of the genera accompanying *Vallonia*, namely *Vertigo*, *Gastrocopta*, *Pupoides* and *Strobilops*, do not form calcified eggs (TOMPA 1976).

Conclusions

Most of the identified snail taxa occur both in biozone A and biozone C, which indicates that during the Oligocene in the area of Central Mongolia the pupilloid assemblage did not change significantly. Being mostly long-lived, terrestrial gastropods only rarely allow stratigraphic conclusions, in contrast with rodent faunas; the biostratigraphy based on rodent assemblages was adopted here. On the other hand, gastropods are useful for palaeoecological considerations.

Disregarding the single incomplete shell of *Vertigo* found in the sediments of biozone C, two species of *Gastrocopta* occur only in one biozone each: *Gastrocopta tuvaense* in sediments of early Late Oligocene age (biozone C) and *Gastrocopta valentini* in the Early Oligocene deposits (biozone A) (Tab. 1).

Tab. 1: Occurrences of land snail taxa in particular biozones established based on rodent assemblages (DAXNER-HÖCK et al. 1997)

Species	biozone A	biozone C	biozone C1	biozone D
<i>Vertigo cf. bicolumellata</i> STEKLOV	–	+	–	–
<i>Gastrocopta mongolica</i> PRYSJAZHNJK	+	+	–	–
<i>Gastrocopta devjatkini</i> PRYSJAZHNJK	+	+	–	–
<i>Gastrocopta shandgolica</i> PRYSJAZHNJK	+	+	–	–
<i>Gastrocopta valentini</i> sp. nov.	+	–	–	–
<i>Gastrocopta tuvaense</i> STEKLOV	–	+	–	–
<i>Pupoides steklovi</i> PRYSJAZHNJK	+	+	–	–
<i>Vallonia cf. lepida</i> (REUSS)	+	+	–	–
<i>Vallonia subcyclophorella</i> (GOTTSCHICK)	+	+	–	–
<i>Vallonia tumida</i> sp. nov.	+	+	–	–
<i>Vallonia</i> sp.	–	+	+	+
? <i>Strobilops</i> sp.	–	–	–	+

G. tuvaense, known previously only from the Miocene of Touva, and similar to *G. nouletiana*, is apparently closer to modern gastrocoptines than the remaining species from the Hsanda Gol Formation. Considering this, its presence limited to the younger fossil horizon associated with biozone C is understandable. On the other hand, *G. valentini*, which appears to be more plesiomorphic in having parietal and angular teeth almost separate, was found only in the Early Oligocene horizon.

All genera represented in Hsanda Gol sediments are still extant and rather widespread. Among them, *Gastrocopta* and *Pupooides* are at present distributed in tropical and temperate zones of nearly all continents except Europe, whereas *Vertigo*, *Strobilops* and *Vallonia* occur chiefly in the Northern Hemisphere.

Ecological and climatic preferences of recent members of the genera represented in Hsanda Gol sediments provide a basis for inferences about the environment that existed in the area of present-day Central Mongolia at the time of deposition. Extant members of *Gastrocopta*, the most diverse genus in Hsanda Gol deposits, live mainly in limestone areas, both in moderately humid forests and in sunny places, in leaf-litter, under stones and decaying logs. *Vallonia* are mostly open landscape dwellers but are also found in habitats similar to those of *Gastrocopta*. Species of *Pupooides* today inhabit dry areas where they shelter under stones and among grass roots. Although fossil plants were not found in the sediments of Valley of Lakes, remnants of plant-eating mammals indicate the existence of a rich vegetation.

Being very small, shells of *Gastrocopta*, *Vallonia* or *Vertigo* are often washed into streams in great numbers, making them very common in flood debris. In Hsanda Gol sediments, such a scenario of fossil accumulation, as a result of heavy rainfalls and floods, was very likely (HÖCK et al. 1999).

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References

- ČEJCHAN, P. (1985): *Vertigo (Vertilla) angulifera angulifera* (Gastropoda, Euthyneura) from the Lower Miocene of Czechoslovakia. – *Vestnik ústředního ústavu geologického*, **60**/3: 175-178. – Prag.
- DAXNER-HÖCK, G., HÖCK, V., BADAMGARAV, D., FURTMÜLLER, G., FRANK, W., MONTAG, O. & SCHMID, H.P. (1997): Cenozoic stratigraphy based on a sediment-basalt association in Central Mongolia as requirement for correlation across Central Asia. – In: AGUILAR, J.-P., LEGENDRE, S. & MICHAUX, J. (Eds.): *Actes du Congrès BiochroM'97*. – Mém. Trav. E.P.H.E., Institut Montpellier, **21**: 163-176.

- EHRMANN, P. (1933): Mollusken (Weichtiere). – In: BROHMER, P., EHRMANN, P. & ULMER, G. (Eds.): Die Tierwelt Mitteleuropas **2**: 1-264. – Leipzig (Quelle & Meyer).
- GERBER, J. (1996): Revision der Gattung *Vallonia* Risso 1826 (Mollusca: Gastropoda: Valloniidae). – Schriften zur Malakozoologie aus dem Haus der Natur, **8**: 1-227. – Cismar.
- GOTTSCHICK, F. (1911): Aus dem Tertiärbecken von Steinheim a. A. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **67**: 496-534. – Stuttgart.
- HÖCK, V., DAXNER-HÖCK, G., SCHMID, H.P., BADAMGARAV, D., FRANK, W., FURTMÜLLER, G., MONTAG, O., BARSBOLD, R., KHAND, Y. & SODOV, J. (1999): Oligocene-Miocene sediments, fossils and basalts from the Valley of Lakes (Central Mongolia). An integrated study. – Mitteilungen der Österreichischen Geologischen Gesellschaft, **90** (1997): 83-125. – Wien.
- LI YUNTONG & LI ZISHUN (1980): Gastropods from the "Xuchuashan Formation" in the Jingxing District, Hebei Province and their stratigraphical significance. – Acta Geologica Sinica, **54/4**: 260-274.
- PIERCE, G.H. (1993): On the Identification of Fossil Terrestrial Gastropod Eggshells. – The Nautilus, **107**: 79-80.
- PILSBRY, H. (1916–1918): Manual of Conchology: Pupillidae (Gastrocoptinae), **24**: 1-380, 49 Tab.
- (1920–1921): Manual of Conchology: Pupillidae, **26**: 1-254, 24 Tab.
- PING, C. (1931): On some new fossil molluscs of Mongolia. – Bulletin of the Geological Society of China, **10**: 229-246.
- POKRYSZKO, B.M. (1996): The Gastrocoptinae of Australia (Gastropoda: Pulmonata: Pupilloidea): Systematics, Distribution and Origin. – Invertebrate Taxonomy, **10**: 1085-1150.
- & STWORZEWICZ, E. (2001): On the subgeneric classification of *Vertigo* O.F. MÜLLER, 1774 (Gastropoda: Pulmonata: Vertiginidae). – Folia malakologica, **9/1**: 27-35. – Poznań.
- PRYSJAZHNJK, V.A., DEVIATKIN, E.W., BADAMGARAV, D. & LISKUN, I.G. (1975): Piervyje nahodki nazemnykh mollyuskov v oligocene Mongolii. – The Joint Soviet-Mongolian Paleontological Expedition, Transactions **2**: 167-177. – Moscow. [in Russian].
- REUSS, A.E. (1849): Beschreibung der fossilen Ostracoden und Mollusken der tertiären Süßwasserschichten des nördlichen Böhmens. – Palaeontographica, **2**: 16-42. – Cassel.
- STEKLOV, A.A. (1967): Land Molluscs from the Neogene of Touva. – In: B.E. BYKHOVSKIY (Ed.): Molluski i ikh rol v biocenozakh i formirovaniy faun. – Trudy Zool. Inst., **42**: 1-315. – Leningrad. [in Russian].
- & TSYTOVICH, M.W. (1967): O nakhodke neogenovykh nazemnykh mollyuskov v Doline Kostankol v Tsentralnom Kazakhstane. [On a finding of Neogene terrestrial mollusks in the Kostankol valley in Central Kazakhstan]. – Byull. Mosk. Obshch. Ispyt. Prir., Otd. Geol. **3**: 108-119. – Moscow. [in Russian].
- STWORZEWICZ, E. (1999): Miocene land snails from Bełchatów (Central Poland). IV: Pupilloidea (Gastropoda Pulmonata). Systematic, biostratigraphic and palaeoecological studies. – Folia Malacologica, **7/3**: 133-170.
- TOMPA, A. (1976): A comparative study of the ultrastructure and mineralogy of calcified land snail eggs (Pulmonata: Stylommatophora). – Journal of Morphology, **150/4**: 861-888.
- WEN, Y., HUAZHANG, P. & HUIJI, W. (1982): Late Cretaceous and Early Tertiary non-marine Gastropods from Southern Anhui. – Memoirs of Nanjing Institute of Geology and Palaeontology, **17**: 1-36.

YEN, T.-C. (1943): Review and summary of Tertiary and Quaternary non-marine molluscs of China. – Proceedings of the Academy of Natural Sciences of Philadelphia, **95**: 267-309.

Plate 1

Fig. 1: *Vertigo cf. bicolumellata* STEKLOV. H = 1.75 mm (ABO-A/3).

Figs. 2–3: *Gastrocopta mongolica* PRYSJAZHNJUK. 2 – W = 1.69 mm (TGR-A/14); 3 – side view, arrow points a trace of tooth (ABO-A/3).

Fig. 4: *Gastrocopta devjatkini* PRYSJAZHNJUK. H = 1.95 mm (ABO-A/3).

Fig. 5: *Gastrocopta shandgolica* PRYSJAZHNJUK. H = 1.64 mm (ABO-A/3).

Figs. 6–7: *Gastrocopta valentini* sp. nov. 6 – Holotype, H = 2.11 mm; 7 – Paratype, in umbilical view.

Figs. 8–9: *Gastrocopta tuvaense* STEKLOV (ABO-A/3). 8 – H = 2.37 mm; 9 – H = 2.36 mm.

Fig. 10: *Pupoides steklovi* PRYSJAZHNJUK. H = 3.58 mm (TGR-A/14).

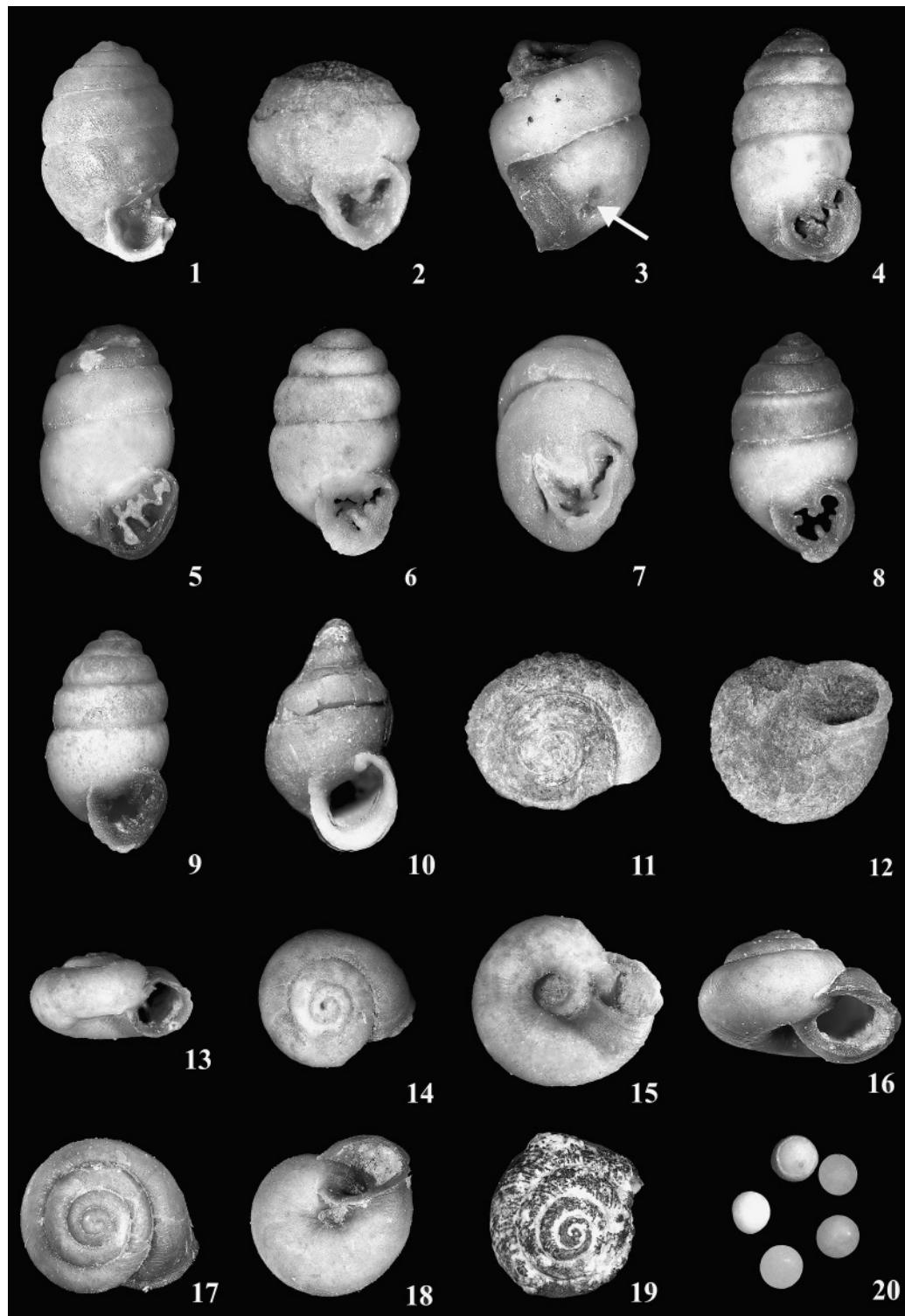
Figs. 11–12: *Vallonia cf. lepida* (REUSS) (TGR-A/14). 11 – in top view, D = 2.52 mm; 12 – in umbilical view, D = 2.48 mm.

Figs. 13–15: *Vallonia subcyclophorella* (GOTTSCHICK) (ABO-A/3), D = 1.83 mm. 13 – in side view; 14 – in top view; 15 – in umbilical view.

Figs. 16–18: *Vallonia tumida* sp. nov. (ABO-A/3), D = 3.23 mm. 16 – in side view; 17 – in top view; 18 – in umbilical view.

Fig. 19: ?*Strobilos* sp. (UNCH-A/3), W = 3.02 mm.

Fig. 20: Gastropod eggs.



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