



LATE MIOCENE (EARLY TUROLIAN) VERTEBRATE FAUNAS AND ASSOCIATED BIOTIC RECORD OF THE NORTHERN CAUCASUS: GEOLOGY, TAXONOMY, PALAEOENVIRONMENT, BIOCHRONOLOGY

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Abstract: Late Miocene continental deposits overlying the Khersonian marine sediments near the city of Maikop bordering the Belaya River (North Caucasus) yielded a diverse biotic record including palynology, ostracods, fresh-water and terrestrial molluscs, fishes, amphibians and reptiles, birds, and mammals. The obtained data indicate predominantly wooded landscapes along the banks of a large fresh-water estuarine or lagoonal basin with occasional connection with the sea. The basin existed in a warm temperate to subtropical climate with a high humidity and an estimated mean annual precipitation above 800 mm. The mammalian assemblage with *Hipparion* spp., *Alilepus* sp., *Paraglitirulus schultzi*, *Eozapus intermedius*, *Parapodemus lugdunensis*, *Collimys caucasicus* sp. nov., *Neocricetodon* cf. *progressus*, etc. is referable to the early Turolian, MN 11. The data regarding composition and stage of evolution of the small mammal content combined with mostly normal polarity of the fossiliferous deposits, and the age estimates of the upper Khersonian boundary as between 8.6 and 7.9 Ma indicate a plausible correlation with Chron C4n and an age range between 8.1–7.6 Ma.

Key words: mammals, birds, amphibians, reptiles, fishes, molluscs, ostracods, palynology, biochronology, Late Miocene, North Caucasus, Russia

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Introduction

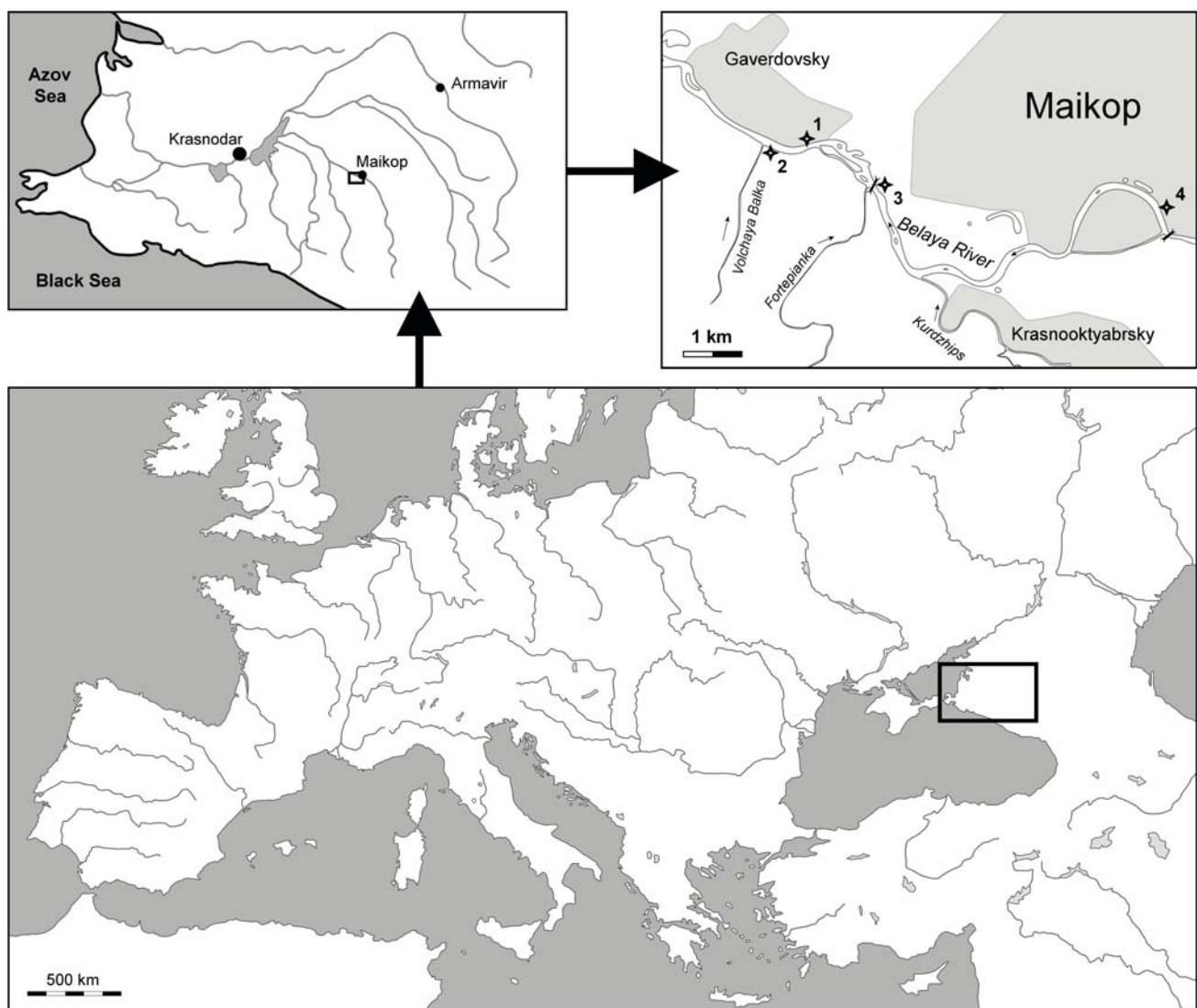
Late Miocene deposits in the Northern Caucasus are widespread and have been thoroughly studied. The Miocene sequence represents consequent development stages of marine basins of the Eastern Paratethys that covered a considerable area of the region. The Late Miocene interval (Tortonian and Messinian) is represented by Bessarabian and Khersonian (= Chersonian) (Middle and Late Sarmatian sensu Andrussov), Maeotian, and Pontian regional ages/

stages and marine basins. The general geological structure of the Northern Caucasus is formed by the north trending monocline of the northern slope of the Caucasus submerging into the Indol-Kubanian branch of the Ciscaucasian foredeep. Regional palaeogeography of the Late Miocene was defined by the northern coast of the large Caucasian island or peninsula (starting from Khersonian time) complicated by the protruding flange of the Stavropolitan land mass (Kolesnikov 1940, Safronov 1972, Popov et al.

2006). The predominance of shallow marine sedimentation is not favourable for the formation of terrestrial vertebrate localities which are rare in the region. The important stages of continental sedimentation occurred prior to the onset of the marine transgression of the Khersonian and during a drastic terminal regression of this basin. The Belaya River exposes this marine-continental transition of the Late Khersonian transecting the monoclinial, north dipping sequence of Late Miocene deposits in the vicinity of the city of Maikop (North Caucasus, Republic of Adygea, Russia). On top of the shallow marine Khersonian deposits with monotonous molluscan assemblages of *Mastra* spp., the so-called sandy-ocherous terrigenous suite occurs. These deposits were first described by Czarnocki (1911) during geological mapping of the Maikop area. Later, the geology and biostratigraphy of the marine-terrigenous transition, and especially the sandy-ocherous deposits of the Belaya River near Maikop, were studied by Grigorovich-Berezovsky (1935a, b), Buryak (1959), Velikovskaya (1960, 1964), and Steklov (1966). The age assignments of these deposits varied from Khersonian to Maeotian. Recently the sandy-ocherous were defined as the

Gavardovsky Formation with a broad estimated age spanning the Late Khersonian, Maeotian, and Pontian (Beluzhenko and Burova 2000), and the underlying Khersonian deposits were defined as the regional Blinov Formation (Beluzhenko 2002). Coarse gravels of the Quaternary Belorechensk Fm (Beluzhenko 2006) overly the Miocene deposits with an erosional unconformity.

The palaeontological record of the marine-continental transition near Maikop is known based on the studies of terrestrial snails, freshwater herpetofauna, cetaceans and pinnipeds, and occasional records of land mammals. Land snails from the Late Miocene terrestrial sequence of the Belaya River near Maikop were monographically described by Steklov (1966) from two main localities, the lacustrine fresh-water deposits at the present day Maikop city park, assigned either to late Bessarabian (Steklov 1966, Beluzhenko 2002) or to Khersonian (Grigorovich-Berezovsky 1935a, and our choice) and from calcareous sandstones in the sandy-ocherous terrigenous sequence overlying Khersonian marine deposits. Both localities yielded a limited number of small vertebrate bones. The



Text-fig. 1. Geographic location of the studied sections. 1. Gavardovsky, 2. Volchaya Balka, 3. Tuapse highway bridge, 4. Maikop city park.

herpetofauna of the Maikop city park was described by Estes and Darevsky (1977) revealing a remarkable diversity of amphibians including the first European record of *Mioproteus*. Two small mammal specimens from this site, listed as Muridae gen. and Vespertilionidae gen. (Steklov 1966), remain undescribed. Bessarabian and Khersonian deposits near Maikop also yielded remains of Cetacea, Pinnipedia and *Deinotherium* (Spasskii 1951, Tarasenko and Lopatin 2012, Tarasenko et al. 2015, etc.). The Late Khersonian shallow water deposits along Fortepianka River, the left tributary below Maikop, yielded scattered remains of marine fishes, trionychid turtle, goose, marine (pinnipeds, cetaceans) and land mammals representing hipparionine horses, the castorid *Trogotherium*, and an undetermined carnivoran (Tarasenko et al. 2014, Tarasenko and Lavrov 2017). The sandy-ocherous deposits of the Gaverdovsky Fm, apart from palynological finds, contained diatoms, and ostracods as reported and briefly reviewed by Beluzhenko and Burova (2000). It also yielded sporadic remains of large mammals *Mastodon borsoni* and *Deinotherium* sp. from the upper part of the formation near the Khanskaya settlement downstream from Maikop (Alexeeva 1959, Titov and Tesakov 2013).

The first two authors made a short visit to the Maikop area in 2003, prospecting for land mammal sites based on the data of Steklov (1966). By that time the locality near the Maikop city park was inaccessible due to the construction of concrete embankment, but the sections of the sandy-ocherous deposits downstream from Maikop were clearly exposed and yielded shells of land snails. In 2011 – 2013, 2017 the joint field team from the Geological Institute RAS (Moscow) and Institute of arid zones SSC RAS (Rostov-on-Don) studied the geology and palaeontology of the area based on three sections (Text-fig. 1) exposing the top of the Khersonian marine deposits and the lower part of the sandy-ocherous terrestrial deposits of the Gaverdovsky Formation (Tesakov et al. 2013, Titov et al. 2013). This contribution reviews the biotic records and their geological and biochronological settings.

Material and methods

The co-authors of this paper made the following contributions: A. S. Tesakov and V. V. Titov studied most small and large mammals, and coordinated the project, M. V. Sotnikova studied remains of carnivorans, S. V. Kruskop studied chiropterans and made drawings of palaeoenvironmental reconstructions, A. N. Simakova worked on palynology, S. V. Kurshakov studied fishes, E. V. Syromyatnikova studied herpetofauna, P. D. Frolov studied most molluscs, D. M. Palatov studied fresh-water bivalve molluscs, E. M. Tesakova studied ostracodes, Ya. I. Trikhunkov performed palaeomagnetic sampling and analysis, N. V. Zelenkov and N. V. Volkova studied bird remains. All team members provided data for the palaeoenvironmental and biochronological sections of the study.

Palaeomagnetic samples were taken manually from steep subvertical walls of the studied sections using a single rope climbing technique. Sampling was preceded by careful cleaning of the outcrops to reach fresh, unweathered

sediments. The oriented samples were collected using digging tools, diluted silicate glue, and a magnetic compass. In the laboratory the oriented rock blocks were cut into the cubic samples. The samples were subjected to stepwise demagnetization by an alternating magnetic field with an additional device to cryogenic magnetometer 2G Enterprise in the Laboratory of the main geomagnetic field and petromagnetism in the Institute of Physics of the Earth of the Russian Academy of Sciences, Moscow (IPE RAS). Magnetic cleaning was performed in 7 steps up to 130 MT, with a gradual increase in pitch. Processing of the results was carried out using the Remasoft computer program (Chadima and Hrouda 2006).

Fossils reviewed and described in this paper were excavated using mass screen-washing operations using hand sieves with mesh size 0.5 mm. More than two tons of sediments in total were washed, dried, and separated into size fractions of 0.2–0.5, 0.5–1, 1–2, 2–3, >3 mm. Larger size fractions were processed in the field, smaller fractions were sorted in the lab by A. S. Tesakov, E. V. Syromyatnikova, P. D. Frolov, and S. V. Kurshakov. The bulk of the fossils came from the localities Gaverdovsky (Gvd) and Volchaya Balka (Vlb) on the right and left banks of the Belaya River downstream from the city of Maikop (Text-fig. 1). Most fossils are housed in the Geological Institute of the Russian Academy of Sciences (GIN RAS), Moscow, collections GIN-1140 (molluscs, 1140/G: Gaverdovsky; 1140/F: Volchaya Balka); GIN-1143 (Volchaya Balka), GIN-1144 (Gaverdovsky) (ostracods, herpetofauna, small mammals); bird remains are stored in collection no. 5528 of the Paleontological Institute RAS (PIN RAS), Moscow; large mammals and fishes are in the collection SSC RAS G of the Southern Scientific Centre RAS (SSC RAS), Rostov-on-Don.

Photos of fossils were taken using CamScan and Tescan SEM microscopes (Paleontological Institute RAS, Geological Institute RAS).

Abbreviations

GIN, Geological Institute of the Russian Academy of Sciences; PIN, Paleontological Institute of the Russian Academy of Sciences; SSC-RAS, Southern Scientific Centre of the Russian Academy of Sciences.

Sections and localities

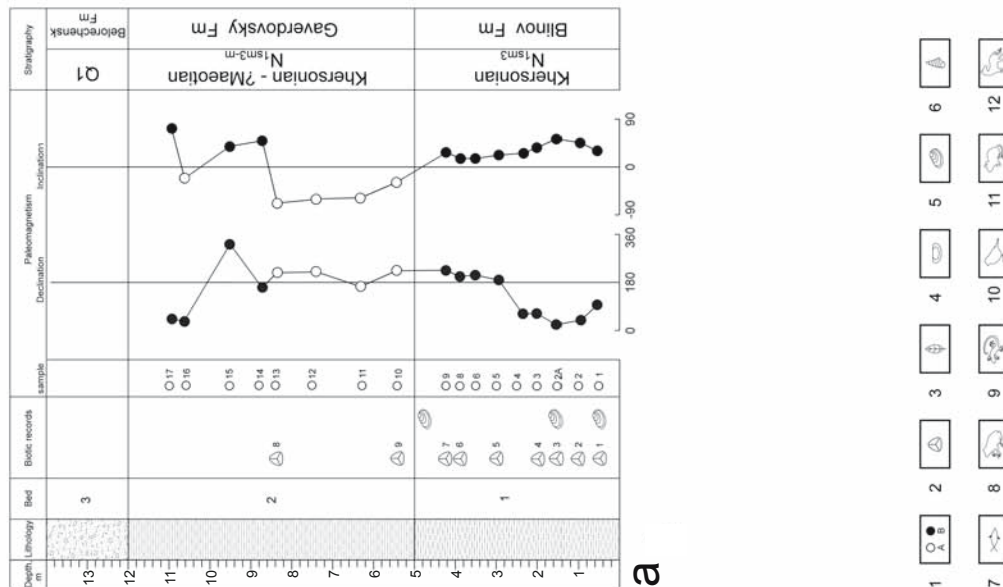
Tuapse highway bridge section (N 44°35'56", E 40°02'49")

The section is situated on the right bank of the Belaya River, 200 m upstream from the new Tuapse highway bridge (Text-figs 1 (loc. 3), 2a). The total thickness of the exposed section is about 15 m. The steep cliff here exposes the following section upwards from the mid-summer water level:

Bed 1. Clayey silts to fine-grained sands grey and bluish-grey with interlayers enriched with compressed *Macra* spp. shells. 5 m.

Bed 2. Sands yellow fine- to medium-grained, with lenses of coarse grained sands and thin interlayers of silts and clays, with ferruginate spots locally. 7 m.

Bed 3. Terrace pebbles. >2 m.



Text-fig. 2. Geological sections and palaeomagnetic record of Late Miocene deposits near Maikop. a. Tuapse highway bridge. b. Gavardovsky. c. Volchaya Balka. 1. palaeomagnetic samples, A: normal polarity, B: reversed polarity; 2. palynological samples; 3. plant remains; 4. ostracods; 5. bivalve molluscs; 6. gastropods; 7. fish remains; 8. amphibians; 9. reptiles; 10. birds; 11. small mammals; 12. large mammals.

According to Beluzhenko and Burova (2000), the boundary between beds 1 and 2 corresponds to the boundary of the Khersonian marine deposits of the Blinov Formation (bed 1) which are overlain by the base of the terrestrial Gaverdovsky Formation (bed 2).

Gaverdovsky section (N44°36'23", E40°01'56")

The section is exposed in right bank cliff of Belaya River at the Gaverdovsky settlement (Text-figs 1 (loc. 1), 2b). From the mid-summer low water level (2011 – 2013) upsection the following beds outcrop:

Bed 1. Clays and clayey silts bluish-grey, laminated, with sandy micaceous interlayers at the top and sporadic concentration of plant detritus and leaf imprints. The observed thickness 1.4 m.

Bed 2. Sands yellow-grey, fine-grained, layered with zones and spots of ferrugination and lenses of coarse sands. 2 m.

Bed 3. Sands yellow, fine-grained, micaceous, clotted, ferruginated. 0.6 m.

Bed 4. Sands yellow to orange, fine-grained, locally cross-bedded. Contain thin (0.01 m) interlayers of silts and interlayers of greenish-grey and beige sands. 1.8 m.

Bed 5. Sands medium-grained, cross-bedded, micaceous. 3.1 m.

Bed 6. Sands yellow-grey, fine-grained, clayey. 1.3 m.

Bed 7. Clayey silts grey-blue, at the bottom hardened by carbonate cement. The bed contains abundant shells of freshwater molluscs (*Lymnaea*, *Planorbarius*, etc.), ostracods, and vertebrate remains. 0.8 m.

Bed 8. Alternating platy sandstones and yellow-brown, locally micaceous sands with occasional clayey interlayers. Protrude in the cliffs as ledges. Contain abundant shells of *Pomatias* land snails and occasional vertebrate bones. A thin interbed at the base ("fish lens") yielded several thousands of poorly preserved fish remains and sporadic bones of turtles and large mammals that occurred as 1 m long and 0.3 m thick lens-like accumulation. 3.2 m.

Bed 9. Sands medium-grained, orange-yellow. 2.5 m.

Bed 10. Pebble deposits of the Pliocene-Quaternary terrace. >2 m.

The interlayers of the middle sandy member of the section (beds 1–6) are variable along the strike in thickness, colour and coarseness. The clayey silts of bed 7 decrease in thickness upstream grading into a thin (0.1 m) layer of bluish-grey silty sands with shell detritus.

Volchaya Balka section (N 44°36'22", E 40°01'25")

The section is exposed on the steep left bank of the Belaya River in front of the south-eastern margin of the Gaverdovsky settlement (Text-figs 1 (loc. 2), 2c). The total thickness of the exposed section varies from the maximum 21–22 m in the large landslide cirque to about 11–12 m in the river washed vertical cliff downstream, with the upper part of section reduced by the present day relief. The following sequence is described upsection from the mid-summer water level of the Belaya River:

Bed 1. Sands grey and yellowish grey, micaceous, with occasional layers enriched with plant detritus. 3.5–4 m.

Bed 2. Sands fine to medium-grained, with occasional lenses of loose sandstones grey and yellowish grey. 6.5 m.

Bed 3. Silts clayey, bluish-grey grading at the top into alternation of grey silts and yellow sands, with lens-like accumulations of fresh-water molluscs and bones of small vertebrates. 1.0–1.5 m.

Bed 4. Sandstones platy, interbedded with sands, greyish yellow, locally ferruginate, with occasional accumulations of land snail shells dominated by *Pomatias* and sporadic vertebrate bones. 5.0 m.

Bed 5. Sands and silts grey and yellowish-grey. 5.5 m.

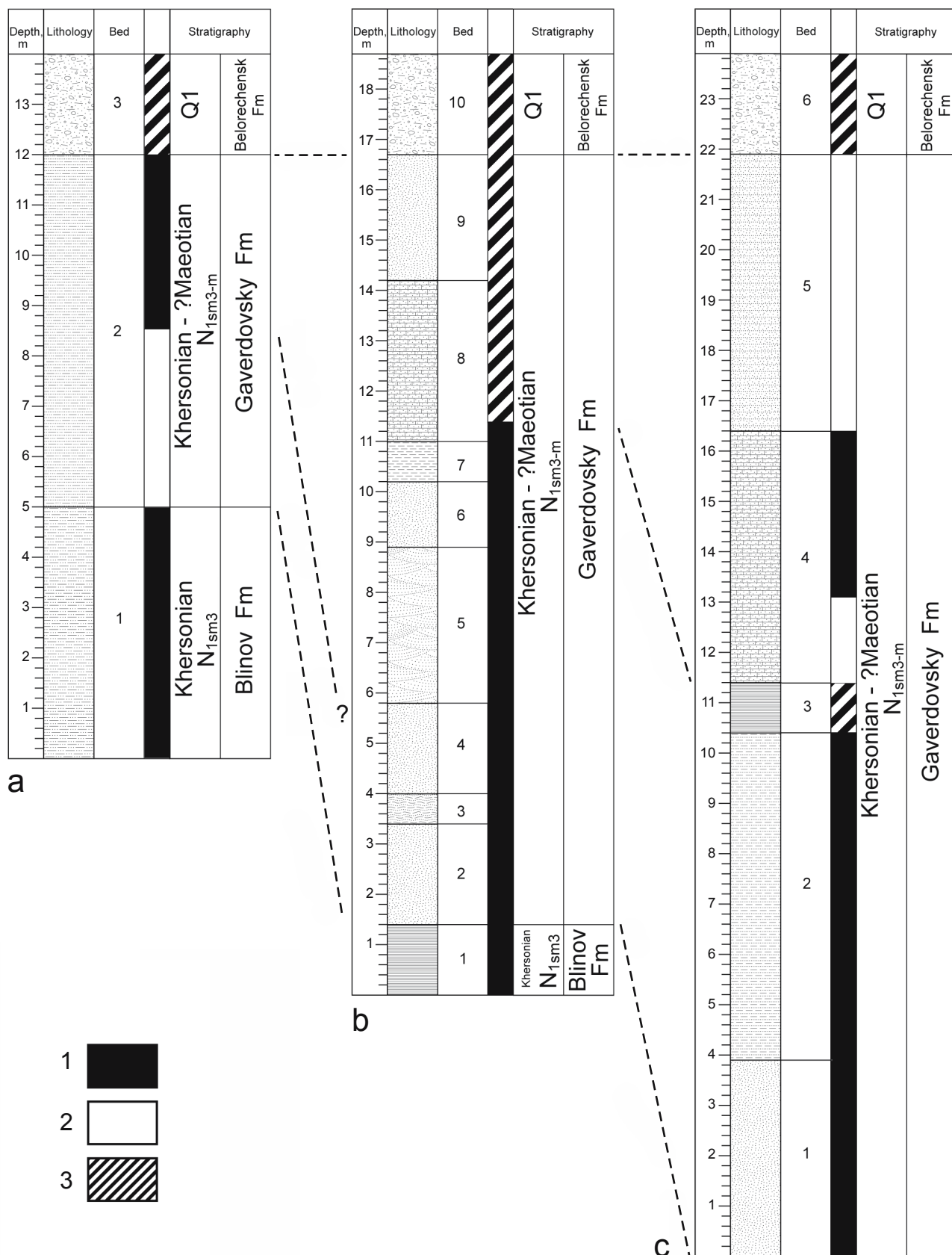
Bed 6. Terrace pebbles. >2 m.

Palaeomagnetism

Palaeomagnetic samples were collected from three sections in the middle reaches of the river Belaya near the city of Maikop: Volchaya Balka, Gaverdovsky, Tuapse highway bridge (Text-figs 1, 2). Sampling was focused on the fine-grained facies, while coarse deposits were generally omitted. Most of the samples were extracted from grey sandy clayey shallow marine deposits of the Khersonian (Blinov Formation) and the layered, dense, relatively well-sorted ocherous sands, interpreted as an estuarine fluvial sequence (Gaverdovsky Formation). In the 22 meters thick Volchaya Balka section (Gaverdovsky Formation) 11 samples from five beds of sandy and silty continental sediments were collected. The 17 meters thick Gaverdovsky section consists of the Blinov Fm of marine clayey-silty deposits (two samples) and the overlying Gaverdovsky Fm of mainly sandy deposits (two samples), covered by pebbly deposits of the Belorechensk Formation (unsuitable for palaeomagnetic measurements). The Tuapse highway bridge section also exposes three members: clayey marine Blinov Fm (nine samples), sandy continental Gaverdovsky Fm (eight samples) and pebbly Belorechensk Fm.

The average sampling interval in the Volchaya Balka section is 1.3 m and ranges from 5 cm and 3.5 m, excluding the two gaps that occurred at the depths 0.40 m – 4 m and 4.4 m – 8.3 m due to poor sediments conditions (very soft material, the samples did not survived the processing). Sampling increments in the Tuapse highway bridge section were set at 0.6 meters. Three samples from the middle part of the section were lost during laboratory processing.

The studied sections are situated along the general dip line of the Late Miocene sequence with the stratigraphically older levels (such as the top of the Khersonian deposits) gradually submerging below the water table of the river downstream. The laboratory analyses revealed the normal magnetization of the Khersonian deposits (Blinov Fm) and a zone of normal polarity at the base of the Gaverdovsky Fm above (Text-fig. 2a). The polarity change is coincident with a sharp change of lithology, which indicates a stratigraphic hiatus here. The uppermost part of the Gaverdovsky Fm deposits in this section are reversely polarised. In the Gaverdovsky section 1.5 km downstream, a relatively loose sampling showed normal polarity at the top of the Khersonian at the base of the section, and normal polarity in higher levels, including the fossiliferous bed 7 (Text-fig. 2b). The Volchaya Balka section about 0.5 km downstream generally showed normal



Text-fig. 3. Correlation model of the studied sections of Late Miocene deposits. a. Tuapse highway bridge. b. Gaverdovsky. c. Volchaya Balka. 1. reversed polarity; 2. normal polarity; 3. unstudied interval.

polarity in the Gaverdovsky Fm deposits with two normal zones, above the fossiliferous level of bed 3, and at the top

of the section (Text-fig. 2c). The correlation model of the studied sections is shown in Text-fig. 3.

Biotic records

Palynology of the Late Miocene sections along Belaya River

Studied sections

Three sections were studied palynologically (Text-fig. 4): Tuapse highway bridge, Gaverdovsky, and Volchaya Balka. Our study continues the pioneer work of Zh. V. Burova (Beluzhenko and Burova 2000, Beluzhenko 2002) but in more detail and denser sampling.

Tuapse highway bridge

Two pollen zones are defined in this section (Text-fig. 4a): palynozone I (seven samples from lower clays) and palynozone II (two samples from clayey interlayers in the upper sandy member below the pebbles of the Plio-Pleistocene terrace).

Palynozone I shows spectra dominated by the pollen of gymnosperms *Pinus* (up to 70%) and *Abies* (15%), and sporadic grains of Taxodiaceae, *Ginkgo*, *Tsuga*, *Podocarpus*, *Sequoia*, *Picea*, *Pinus microalatus* R. POT. Broad-leaved trees are dominated by Juglandaceae (*Juglans*, *Carya*, *Pterocarya*), Ulmaceae and Fagaceae. Sporadic records indicate the presence of *Corylus*, *Quercus*, *Carpinus*, *Liquidambar*, *Nyssa*, and *Ephedra*. Herbs are represented by single grains of Chenopodiaceae, Polygonaceae, Asteraceae. Dominant coniferous-deciduous forests are reconstructed for this interval.

Palynozone II shows spectra dominated by the pollen of gymnosperms *Pinus* (up to 60%) and *Abies* (up to 7%). Also recorded are singular grains of *Pseudotsuga*, Taxodiaceae, *Ginkgo*, *Cedrus*, *Picea*, and *Pinus microalatus* R. POT. Broad-leaved trees are mainly represented by the pollen of *Ulmus*, *Fagus*, Juglandaceae, and singular grains of *Corylus*, *Quercus*, *Carpinus*, *Myrica*, *Nyssa*. Herbs are represented by single grains of Chenopodiaceae, Onagraceae, and Asteraceae. Pollen of *Typha* is also found here. The area was covered by coniferous-deciduous forests.

The presence of riparian plants and redeposited dinoflagellata indicates the fluvial origin of the upper (sandy) member of the section.

Gaverdovsky section

Based on 13 samples the section is subdivided into five palynological zones (I–V; Text-fig. 4b).

Palynozone I is defined for the lower clayey bed at the base of the section (bed 1). The spectrum is dominated by pollen of gymnosperms *Pinus* (57%) and *Abies* (11%). Singular records of Taxodiaceae, *Picea*, *Pinus microalatus* R. POT., *P. peuceformis* ZAKL. are also found. The significant role of Juglandaceae (*Juglans*, *Carya*, *Pterocarya*) and Ulmaceae should be noted. Singular grains of *Corylus*, *Quercus*, *Carpinus*, *Liquidambar*, *Fagus*, *Nyssa*, and *Ephedra* were recorded. The landscapes were dominated by coniferous and deciduous forests with meadow-steppe plant associations in the watershed areas.

Palynozone II (sandy bed 2) The spectrum shows the prevailing angiosperm pollen (61%) with an increased proportion of Juglandaceae (*Juglans*, *Carya*, *Pterocarya*,

Platycarya, *Engelhardtia*). Taxodiaceae, *Fagus*, and *Nyssa* are missing. The percentage of herbs is as high as 20% (Chenopodiaceae, Poaceae, Onagraceae, Caryophyllaceae, Campanulaceae). The reconstructed terrain is a combination of broad-leaved and coniferous forests with meadow plant associations under conditions of a notable climatic aridisation.

Palynozone III (the base of the Gaverdovsky microvertebrate fossiliferous bed 7). Gymnosperms are strongly predominant. The pine pollen shows a drastic increase up to 70%. Also present are diverse gymnosperms Taxodiaceae, *Dacridium*, *Cedripites*, *Podocarpus*, *Cathaya*. The dominance of pine forests reflects a significant cooling and increased humidity.

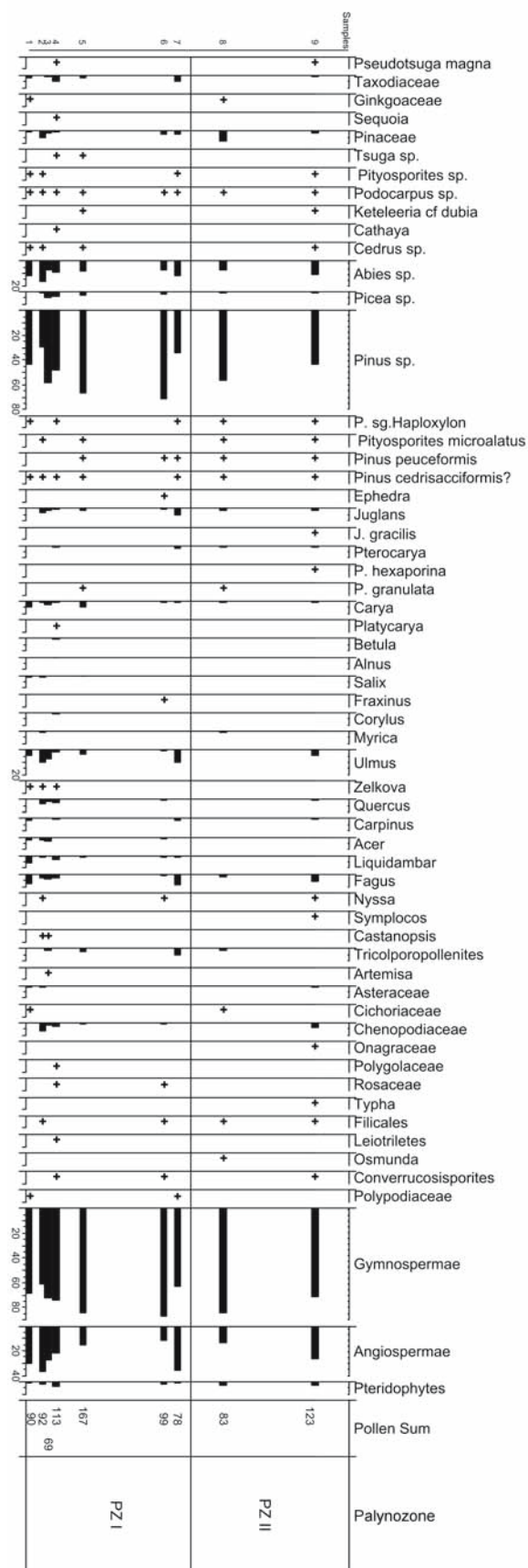
Palynozone IV (the core of fossiliferous bed 7 and clayey interbeds of bed 8 above, including the “fish lens”). The spectra show a high percentage of fir (*Abies*, up to 29%) and increased diversity of conifers *Sciadopites*, Taxodiaceae, Ginkgoaceae, *Tsuga*, *Dacridium*, abnormal *Pityosporites*, *Podocarpus* sp., *Keteleeria*, *Cathaya*, *Cedripites*, *Picea*. The number and diversity of broad-leaved trees *Juglans*, *Pterocarya*, *Carya*, *Platycarya*, Ulmaceae, *Carpinus*, *Liquidambar*, and *Fagus* is generally high but variable. Higher humidity and a warmer climate is reflected in the broad development of conifers (pine, fir) and deciduous (*Ulmus*-*Juglans*) forests. The spectrum of the fish lens with the high content of gymnosperms (*Picea*, 24%) and missing broad-leaved forms may correspond to a colder climatic oscillation.

In general, the palynological data from the Gaverdovsky section show a marked predominance of forest vegetation. The proportion of herbaceous plant pollen and spores rarely exceeds 5%. Coniferous forests dominant in palynozone III are likely an indications of a climatic cooling. The most arid interval marked by the expansion of meadow cenoses and increase of broad-leaved species is recorded in the palynozone II. The optimal conditions for coniferous and deciduous forests are signaled by the palynospectra of zone IV. The deposits from the lower part of the section were formed in freshwater conditions as indicated by purely freshwater plants (*Zygnema* type, *Spirogyra*, *Azolla bohemica* PAKLT.), and possibly, under slightly brackish-water conditions (above 10 m from the base of the section, in the upper part of the fossiliferous bed) as indicated by spores of colonial algae *Pediastrum simplex*, *P. duplex*, *P. boranum*, *Botryococcus braunii* that can tolerate a salinity up to 8‰ (Mudie et al. 2010, 2011). The uppermost sandy part of the section is extremely poor in pollen. The entire sequence studied shows the occurrence of redeposited Cretaceous and Paleogene dinocysts and pollen (*Achomosphaera* cf. *alcicornu*, *Deflandrea*, *Lingulodinium*, *Spiniferites*, *Wetzeliiella*, *Wilsonidinium lineidentatum*, cf. *Oculopollis praedicatus* WEIL et KRIEG, *Impardecispora trioreticulosa* (COOKSON et DETTMANN) VENKATACHALA).

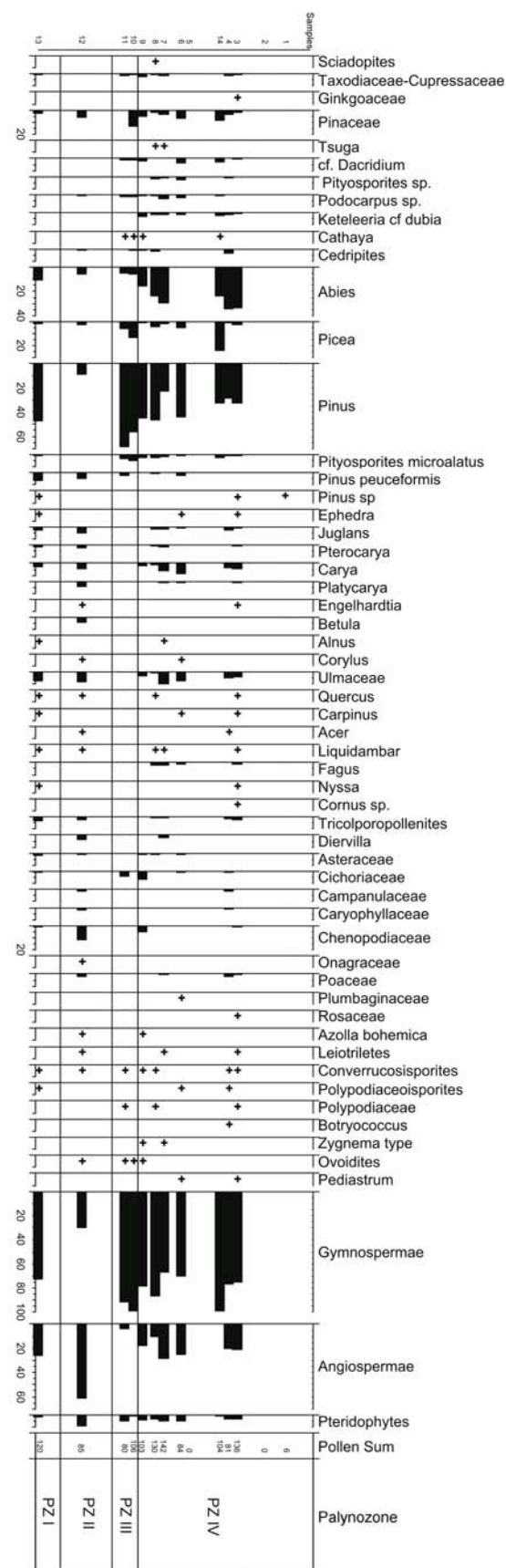
Volchaya Balka section

Four palynological zones are defined based on 20 samples from the section (Text-fig. 4c). Most levels show the presence of fresh-water algae *Ovoidites*, *Pseudoschizaea*, and *Pediastrum*.

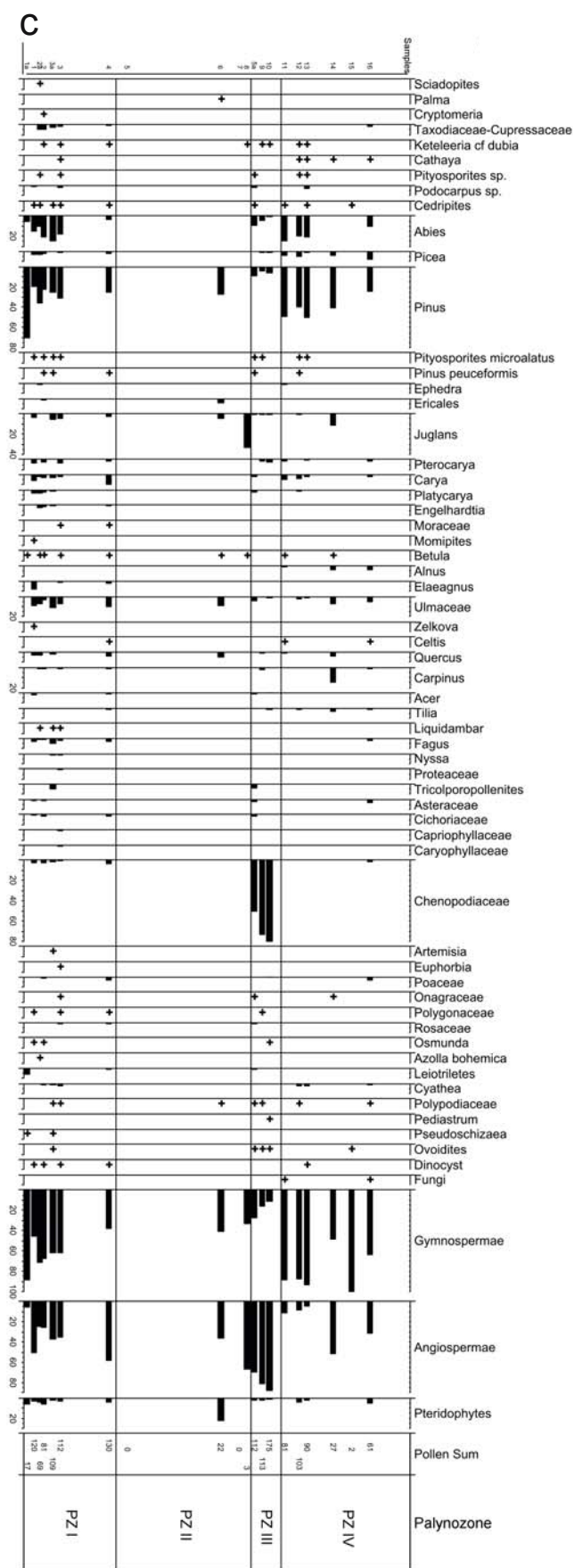
a



b



Text-fig. 4. Palynological diagrams of Late Miocene deposits, North Caucasus. a. Tuapse highway bridge. b. Gaverdovsky. c. Volchaya Balka.



Text-fig. 4. continued.

Palynozone I is characterized by a high percentage of gymnosperm pollen. The spectrum of the lowermost sample near the base of the section displays a dominant proportion of pine (69%), fir (6%), and birch (6%). Also present is Taxodiaceae, *Fagus*, and *Nyssa*. Herb pollen does not exceed 10% and includes Chenopodiaceae, Poaceae, Onagraceae, Caryophyllaceae, Campanulaceae. Coniferous – small-leaved forests growing under conditions of climatic cooling are indicated for this interval.

Palynozone II is based on a single pollen spectrum with reduced gymnosperms (*Pinus*, 25%), and an increased proportion of angiosperms dominated by *Juglans*, *Ulmus*, and *Quercus*.

Palynozone III (bluish silts and clays of the Volchaya Balka microvertebrate fossiliferous level). The representative spectra of this zone show a sharp increase (50%) in Chenopodiaceae, and lack of Taxodiaceae, *Corylus*, *Quercus*, *Fagus*, and *Nyssa*. Meadow and steppe vegetation spread widely in this time interval as a result of considerable climatic aridisation.

Palynozone IV. The proportion of gymnosperm pollen is high within the total composition of the spectra. The percentage of pollen of fir and spruce considerably increased. The spectra show the re-occurrence of Taxodiaceae and *Cedripites*. Dominant among angiosperms are *Juglans*, *Pterocarya*, *Carya*, *Ulmus*, *Quercus*, *Carpinus*, and *Tilia*. Herbs are represented by the Asteraceae, Poaceae, and Chenopodiaceae. During this interval broad-leaved – coniferous forests dominated in a humid climate. Forests became more mesophilic.

Correlation of the studied sections

Late Sarmatian (Khersonian) bluish clays from the Tuapse highway bridge and Gaverdovsky sections show a partial overlap of the lower palynozones with a predominance and high diversity of conifers (Gvd I equals the upper part of Thb I). The second palynozone of the Thb section with a dominance of conifers has no known equivalent in the Gvd section, and may be partially correlated or capped by the lower palynozone of the Volchaya Balka section (Vlb I) indicating a high percentage of conifers although decreasing upsection. Palynozones Gvd II and Vlb II share decreased proportion of gymnosperms. A possible continuation of this biotope trend is reflected by the third palynozone of the Volchaya Balka section (Vlb III) with a sharp increase of meadow and steppe vegetation. This stage is unmatched in the palynological sequence of the Gaverdovsky section. Using this model, the microvertebrate bed of Volchaya Balka slightly predates the bone bearing bed in the Gaverdovsky section. Both small vertebrate faunas are very similar but not identical in composition (see below). The pollen assemblage of the lower part of the Gaverdovsky fossiliferous bed, Gvd III, with a high content of gymnosperms, with dominant *Pinus* and subdominant *Abies*, most likely predates the lower part of the extensive palynozone Vlb IV. Bearing in mind that the upper part of the Volchaya Balka section stratigraphically equals the top of the Gaverdovsky section and obviously crowns it, the palynozone Gvd IV with dominant conifers and varying content of angiosperms, correlates to the lower part of Vlb IV.

Table 1. Correlation of palynological assemblages of the three studied sections.

Tuapse highway bridge (Thb)	Gavardovsky (Gvd)	Volchaya Balka (Vlb)	Vegetation
–	–	Pz IV	<i>Pinus-Picea-Abies</i> forests coniferous <i>Pinus-Abies</i> and broadleaf <i>Ulmus-Juglandaceae</i> forests
–	Pz IV	–	
–	Pz III	–	pine forests
–	–	Pz III	meadow and steppe vegetation
–	Pz II	Pz II	broadleaf-coniferous forest and meadow vegetation associations pine-broadleaf forests
Pz II	–	Pz I	pine and coniferous-broadleaf forests
Pz I	Pz I	–	coniferous-broadleaf forest with meadow-steppe vegetation

See Table 1 for correlation of palynological assemblages from studied sections. Characteristic palynomorphs from the studied sections are shown in the Text-fig. 5.

Previous studies and comparison with different regions of Europe and western Asia

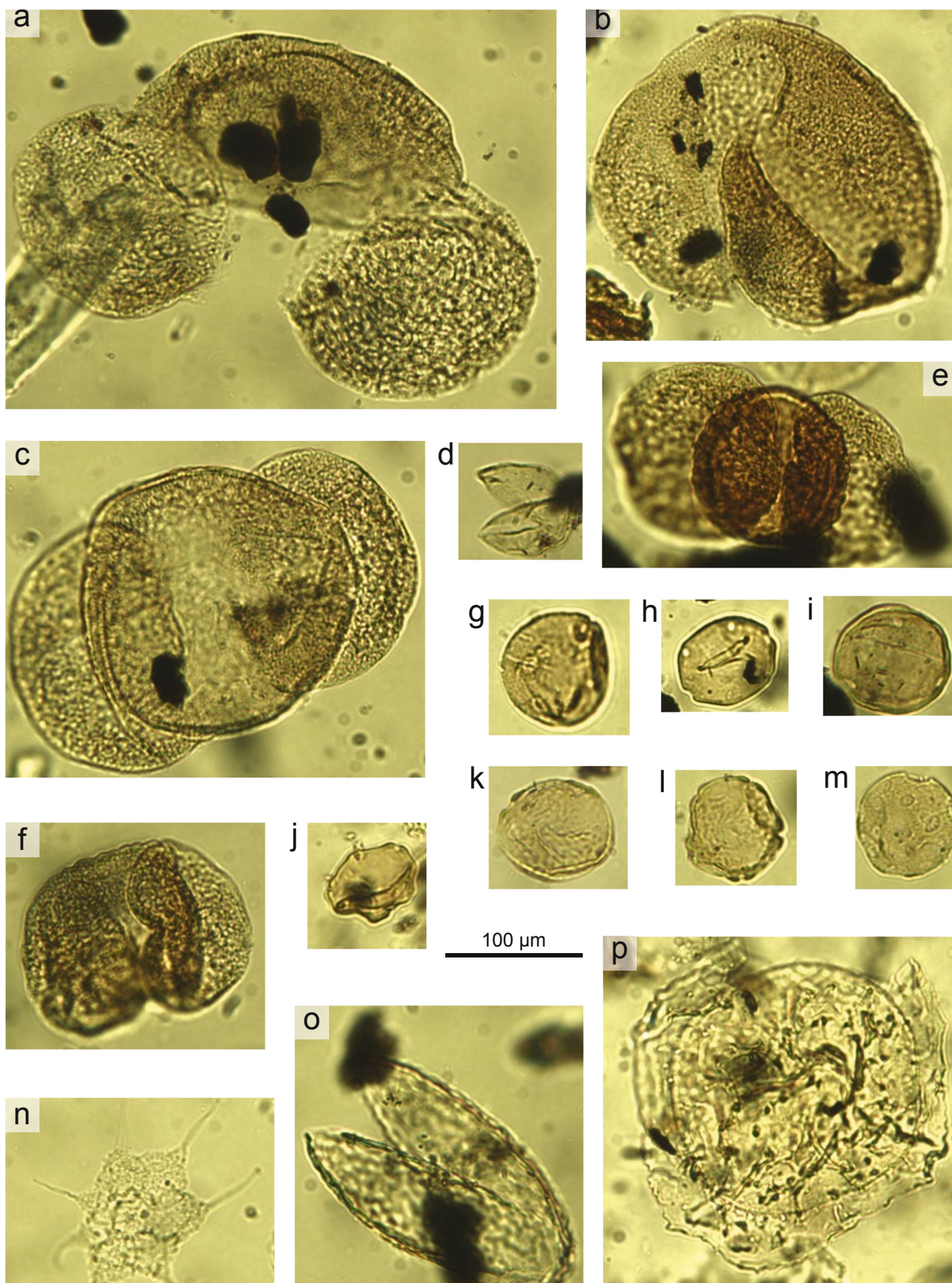
The palynological data on the transition from the marine Late Sarmatian (Khersonian) to continental sediments of Gavardovsky Fm in the sections along the Belaya River downstream from Maikop were first obtained by Beluzhenko and Burova (2000) with quite wide-spaced sampling. The bluish clays and sands from the right bank section in front of the Fortepianka River mouth (= our Tuapse highway bridge section, Pz I) yielded palynological spectra characterizing forest vegetation dominated by conifers *Pinus*, *Abies*, *Picea*, and subdominant broad-leaved trees *Ulmus*, *Carya*, *Juglans* in combination with areas of meadow vegetation (Beluzhenko and Burova 2000, Beluzhenko 2002). The next level upsection, in the continental sequence of the Gavardovsky Fm, was sampled from the greenish-grey clays in 8–10 m above the sandstone member containing shells of *Pomatias* (bed 10 of Beluzhenko and Burova, equates to the uppermost part of the Volchaya Balka section or is out of the range of our sections). This level yielded the spectrum with *Pinus*, *Abies*, *Carya*, *Ulmus*, *Chenopodiaceae* (Beluzhenko and Burova 2000). The still higher clayey-sandy level (10–15 m upsection, bed 11) at the top of the lower subformation of the Gavardovsky Fm produced a palynospectrum showing a dominance of coniferous trees with the largest proportion being *Abies* (Beluzhenko and Burova 2000). The upper, mostly clayey, part of the Gavardovsky Fm yielded palynological spectra with a significant content of angiosperm pollen, including increasing amounts of herbaceous vegetation pollen. This part of the sequence was correlated to the Late Maeotian and Pontian (Beluzhenko and Burova 2000).

Two sets of quality palynological data on the Late Miocene of the Caucasian Island/Peninsula come from its northwestern (Taman Peninsula, Russia) and southwestern (Georgia) parts.

The excellent and thoroughly studied geological record of the nearly continuous Late Miocene sequence

of the neighbouring Taman Peninsula gives an important reference point for the Khersonian-Maeotian transition. The palynological data by Filippova (Popov et al. 2016) present very similar pollen assemblages for the Late Sarmatian to Early Maeotian interval in the Panagia and Zheleznyi Rog sections. The spectra of the Late Sarmatian show a predominance of conifers *Pinus*, *Taxodiaceae*, *Abies*, *Picea*. The deciduous taxa are dominated by *Carya*, *Juglans*, *Pterocarya*, *Ulmaceae*, *Carpinus*, *Corylus*, *Alnus*, *Betula*, *Moraceae*, *Liquidambar*, *Nyssa*, *Quercus*, *Acer*, *Salix*, *Tilia*, and *Oleaceae* are present. Pollen of herbaceous plants is less frequent and mainly represented by *Chenopodiaceae*. The spectra of Early Maeotian are dominated by *Pinus* and mountain conifers *Abies*, *Picea*, *Tsuga*, *Taxodiaceae*. The broad-leaved taxa are represented by *Juglandaceae*, *Carya*, *Ulmaceae*, *Quercus*, *Carpinus*, and *Liquidambar*. Rare dwarf shrub xerophytes are represented by *Chenopodiaceae*, *Artemisia*, and sporadic *Ephedra* (Popov et al. 2016). In general, the Taman record shows a spread of mesoxerophytic vegetation at the very end of the Late Sarmatian, followed by a predominance of coniferous forest communities in the Early Maeotian with a moderately mesic appearance of the vegetation. The record of the Late Maeotian evidences a significant climate aridisation and increase of open landscape vegetation (Popov et al. 2016).

The Late Sarmatian of Western Georgia is characterized by the stable presence of a diverse coniferous association whereas in Eastern Georgia the open landscape vegetation strongly expanded during this period. Arboreal vegetation edified floodplain forests and woodlands that consisted of warm temperate and subtropical plants. Pines were predominant in the upper mountain belts. The Maeotian flora of Western Georgia shows a high diversity of coniferous trees. Compared to the Sarmatian forests, most of the conifers, such as *Abies*, *Picea*, and *Tsuga*, were ecologically associated with a temperate climatic zone. Subtropical conifers *Podocarpus*, *Dacrydium*, *Cathaya*, *Araucaria*, *Keteleeria* survived into the Maeotian (Shatilova et al. 2011). The general features of the Late Miocene palynological record of Georgia shows a strongly pronounced period of forest vegetation in the middle Sarmatian (Bessarabian),



Text-fig. 5. Palynomorphs from Late Miocene deposits. Gaverdovsky section, North Caucasus. a – *Abies minor* ANANOVA; b – *Picea* sp.; c – *Keteleeria* cf. *dubia* CHLONOWA; d – *Taxodiaceae* gen.; e – *Podocarpidites podocarpoides* (THIERGART) KRUTZSCH; f – *Pinus labdaca* KRUTZSCH; g – *Fagus* cf. *tenella* PAN.; h – *Juglans gracilis* ANANOVA; i – *Carya* cf. *spackmania* TRAV.; j – *Pterocarya* sp.; k – *Ulmus* sp.; l – *Zelkova* cf. *miocenica* ANANOVA; m – *Liquidambar* sp.; n – *Pediastrum simplex* MEYEN; o – *Spirogyra* sp.; p – re-deposited Palaeogene dinocyst *Wilsonidinium lineidentatum* (DEFLANDRE et COOKSON, 1955) LENTIN et WILLIAMS, 1976. Scale bar 40 μm for all photographs.

a trend towards expansion of meadow vegetation in the Late Sarmatian, another strong forest maximum in Early Maeotian, and a significant restructuring of the late Early Maeotian with a reduction of the area of polydominant forests and more dynamic fluctuations in the assemblages (Shatilova et al. 1999, 2011).

Outside the Caucasus, it is worth mentioning the palynological sequence of western Ukraine. In the Pannonian of the cis-Carpathian region the main edifiers of forest communities at low and medium altitudes were species of the genus *Carya* in association with *Juglans*, *Quercus*, *Acer*, *Tilia*, *Ulmus*, *Celtis*, rare *Engelhardtia*, and *Castanea*. The coniferous forests were dominated by *Pinus* with small proportions of *Abies* and *Picea*. By the end of the Miocene (the Pontian), the coniferous forests had expanded in the mountains shifting the broad-leaved deciduous forests to lower elevations. Subtropical species almost disappeared (Syabryaj et al. 2007).

The palynospectra of the Late Sarmatian in the south of the Russian Plain and Ukraine reflect the restructuring of the assemblages with an increase in the role of broad-leaved trees and herbaceous vegetation, mainly represented by *Chenopodiaceae* and *Artemisia* (Ananova 1974, Shchekina 1979). At the end of the Late Sarmatian, the entire northern Black Sea region, with the exception of the southern Crimea, transformed into a steppe plain. In the Early Maeotian, the areas of forest vegetation expanded resulting in a co-occurrence of open and wooded landscapes. Forests at that time were edified by deciduous broad-leaved trees including *Quercus*, *Ulmus*, *Alnus*, *Salix*, *Moraceae*, as well as *Fagus*, *Acer*, *Tilia*, *Carpinus*, *Betula*, with the presence of *Juglandaceae*, *Ostrya*, *Parottia*, *Liquidambar*, *Picea*, and *Pinus*. The herbaceous communities were composed of *Chenopodiaceae*, *Brassicaceae*, *Poaceae*, and *Fabaceae*. The end of the Maeotian evidences predominant communities of open and semi-open landscapes (Kritskaya 2010, Syabryaj et al. 2007). Thus, the similarity of the Late Sarmatian and Early Maeotian spectra reflecting a general wooded appearance of the environment contrasts to the assemblages of Late Maeotian and Pontian with the predominance of non-arboreal pollen (Ananova 1974).

In central Anatolia, mesophytic forests with *Ulmus*, *Quercus*, *Castanea*, *Alnus*, and *Sambucus* were widespread at the beginning of the Tortonian. Swamp (*Taxodiaceae* and *Myricaceae*) and mountain pine forests had a much more restricted distribution. The vegetation of open landscapes increased from early to Middle Tortonian when it reached its maximum (Akgün et al. 2007).

In southeastern Europe, the northeastern Mediterranean, and the Central Paratethys (Pannonian Basin) the evergreen broad-leaved forest elements show a decrease in diversity from the late Middle to Late Miocene. On the contrary, forests were gradually enriched with deciduous mesothermic elements such as *Quercus*, *Fagus*, *Alnus*, *Tilia*, *Ulmus*, and *Acer*. Forests at medium elevations were dominated by *Cathaya*, *Tsuga*, *Cedrus*, and by *Picea* and *Abies* in the highlands. Vegetation proxies also show a directed trend towards a decrease in mean annual temperatures. The north-south climatic differentiation became obvious in the Late Miocene. More stable and higher humidity values in the Pannonian realm contrasts with the increasing seasonality and alternation of more humid and more arid phases in

southern areas of Eastern Europe (Jimenez-Moreno et al. 2007, Ivanov et al. 2011, Utescher et al. 2017).

The reconstructed vegetation dynamics in the studied sections shows a cyclic trend from wooded landscapes through more open biotops and back to the wooded conditions again (Tab. 1). The period of relative expansion of open landscapes recorded in the palynozones Gvd II and Vlb III may correspond to a noticeable climatic aridisation in the Middle Tortonian correlated with the Late Sarmatian and the beginning of Early Maeotian. This event (or a series of events) is recorded in the palynological data in the Caucasus, northern Black Sea region, Turkey, and eastern Mediterranean (Ananova 1974, Shchekina 1979, Shatilova et al. 1999, Akgün et al. 2007, Syabryaj et al. 2007, Kritskaya 2010, Ivanov et al. 2011, Shatilova et al. 2011, Popov et al. 2016).

Summing up the reviewed data, the age of the studied sections based on their palynological content, is defined as latest Sarmatian (Khersonian) – Early Maeotian.

Ostracods from Gaverdovsky and Volchaya Balka

Ostracod remains were collected from the microvertebrate fossiliferous beds in the sections of Gaverdovsky (bed 7), and Volchaya Balka (bed 3) by manual sorting of the smallest size fractions of the bone concentrate (1.0–0.5 mm and 0.5–0.2 mm). Even though a comparable amount of sediment was from both localities, the amount of ostracod material from Gaverdovsky was much greater ($n > 400$) than that from Volchaya Balka ($n = 10$) (Tab. 2).

Ostracod assemblages from Volchaya Balka and Gaverdovsky have certain similarities but nevertheless, are very different and indicate dissimilar environmental conditions. Both assemblages are quite poor in species composition (four species in Volchaya Balka, and seven species in Gaverdovsky), and share taxa of freshwater ostracods *Candona*, *Ilyocypris*, and *Cyprinotus*, although represented by single and sporadic records (see the species lists). These fresh-water forms prevail in the small collection from Volchaya Balka thus indicating freshwater continental conditions in this site.

On the contrary, the Gaverdovsky assemblage is strongly dominated ($n > 400$) by the species *Cyprideis torosa* (JONES, 1850), a well known Neogene and Quaternary indicator of a variable and abnormal salinity ranging from estuarine and lagoonal brackish environments to hypersaline waters of the Dead Sea. This species shows great variability correlated with hydrochemical features of the water basins. Its shell sculpture is salinity-sensitive and at salinity levels below 5 ‰ develops asymmetric nodes that are more numerous as the salinity decreases. For this reason, this species is widely used in palaeontology as an indicator of brackish water environments (Sandberg 1964, Vesper 1972, Karmishina 1975, and others). This is due to inability of this crustacean to regulate the increasing osmotic pressure during moulting in conditions of low salinity and/or lack of calcium (Keyser 2005). None of the specimens of *C. torosa* found in Gaverdovsky, including juveniles, showed any nodes, thus indicating that the salinity exceeded 5 ‰.

It is also known that the pitted sculpture is characteristic for the representatives of *C. torosa* from oligohaline settings

(5–18 ‰), while smooth forms occur in hyperhaline biotopes (>40 ‰) (Bodergat 1985). In addition, the pitted sculpture of the valves is directly proportional to the Mg/Ca ratio in the shells of this species. The pitted sculpture gets stronger and the nodes begin to develop with an increased content of barium in shells (Bodergat 1983). The specimens studied showed well-defined pitted sculpture characteristic of oligohaline conditions.

Another sensitive indicator of salinity in shell morphology of *C. torosa* is the shape of the sieve pores. A strong relationship between the salinity and the shape of the sieve pores (which can range from round to elliptical and irregular) in the valves of the *C. torosa* was revealed in the study of associations from water bodies with different salinity (from drainage ditches periodically flooded with sea water to the Dead Sea) along the geographic transect from northern Germany and Denmark to Israel (Rosenfeld and Vesper 1977). An inverse relationship was established between the percentage of round pores and the increase in salinity. The shells from fresh waters mainly developed round pores, whereas irregular shaped pores dominate in hypersaline environments. Ellipsoidal pores occupy an intermediate position along the spectrum with their number also increasing with greater salinity.

The study of the sieve pores *C. torosa* shells from Gaverdovsky showed the dominance of ellipsoidal shaped pores in combination with round pores (Pl. 2, Figs 4–14), whereas irregularly shaped pores were sporadic (Pl. 2, Figs 15, 16). Therefore, the morphology of sieve pores also indicates oligohaline conditions, with salinity in the range of 10–20 ‰.

The dominating presence of *C. torosa* in the sample in combination with a low diversity freshwater association clearly indicates a transitional condition from continental to marine, possibly an upper estuary. The abundance of *C. torosa*, the most salinity tolerant from the known ostracod species, indicates a weak and most likely periodic (irregular) marine influence. It is supported by the lack of other ostracods commonly co-occurring in brackish environments (such as, for example, *Leptocythere*, *Caspiolla*, *Caspiocypris*, *Bakunella*, *Pontoniella*, *Loxoconcha*, *Xestoleberis*, etc.). The only specimen of *Leptocythere* sp. (a brackish-water taxon) is represented by a juvenile valve probably pointing to an unfavourable biotope with insufficient or unstable salinity.

A different biotopic model may be considered with a shift from full fresh-water conditions to a brackish-water basin, a lagoon, partially isolated from the sea with a presumed salinity of 10–20 ‰ and with a mass development of *C. torosa* but unfavourable for fresh-water ostracods and molluscs. Indirectly it may be supported by several occurrences of abundant *C. torosa* shells inside the shells of fresh-water gastropods. In this model fresh-water forms in the burial are not synchronous with (but precede) brackish-water ostracods.

All studied ostracods, except the juvenile valve of *Leptocythere* sp. that was destroyed during preparation, are illustrated in Plates 1 and 2.

Previous studies

Previous studies of the Late Miocene sections along the Belaya River produced the first data on ostracods during research carried out in the 1960 – 1970s and during the geological mapping of the early 2000s. We present these lists in their original form. The stratigraphically lowermost level of the initial fresh-water stage of the Late Sarmatian (Khersonian) on the right bank of the Belaya River near Maikop city park yielded an exclusively fresh-water association with *Herpetocypris reptans* BAIRD, *Paracandona euplectella* BR. et NORM., *Cyprinotus* sp., *Candoniella albicans* BRADY, *Cyclocypris laevis* SARS, *Candona compressa* KOCH. (determinations by G. F. Schneider in Steklov 1966) from bed 5 (freshwater lacustrine marl).

Velikovskaya (1960) described a section of the sandy ocherous formation on the left bank exposures of the Belaya River in front of Gaverdovsky settlement. She listed an ostracod association, determined by N. N. Naidina, including *Cypridopsis* ex gr. *vidua* (O. F. MUELLER), *Cypridopsis* sp. (1), *Cyprinotus* sp. (1), *Cyprideis littoralis* (BRADY), *C. torosa* (JONES), *C. punctillata* (BRADY) from a bed of dark grey clay with abundant *Hydrobia*, plant detritus and imprints of leaves and fish scales. According to the description, this bed corresponds to beds 1 and 2 of our Volchaya Balka section. The listed ostracod association combining fresh- and brackish-water forms is similar to our assemblage from the Gaverdovsky section.

Steklov (1966) listed *Cyprideis littoralis* BRADY, *C. punctillata* BRADY, *Cypridopsis* sp., *Cyprinotus* sp., *Candoniella albicans* BRADY, *C. suzini* SCHN., *Cypria*

Table 2. Ostracod material studied (lv, left valve; rv, right valve; c, carapace; ad., adult; juv., juvenile; ♀, female; ♂, male).

Volchaya Balka	Gaverdovsky
<i>Candona neglecta</i> SARS, 1887: 1 lv ad.	<i>Cyprideis torosa</i> (JONES, 1850): ♀: 140 lv + rv + 103 c = 344 ad.; ♂: 10 c + 31 lv + rv = 51 ad.; juv.: 9 lv + rv + 7 c = 23 juv. Total: 420 valves.
<i>Ilyocypris gibba</i> (RAMDOHR, 1808): 4 lv + 1 rv = 5 ad.	<i>Leptocythere</i> sp.: 1 rv juv.
<i>Cyprinotus vialovi</i> SCHNEIDER, 1961: 1 rv ad.	<i>Cyprinotus vialovi</i> SCHNEIDER, 1961: 1 c + 1 lv = 3 ad.
<i>Cyprinotus</i> aff. <i>speciosus</i> MANDELSTAM, 1963: 2 lv + 1 rv = 3 ad.	Gen. sp. 3: 1 c, with shifted valves.
	<i>Cyprinotus formalis</i> SCHNEIDER, 1963: 2 lv + 2 c = 6 juv. + ad.
	<i>Candona combibo</i> LIVENTAL, 1939: 1 rv fragment.
	<i>Candoniella suzini</i> SCHNEIDER in SUZIN, 1956: 6 c + 4 lv + rv = 14 ad.
	<i>Cyprinotus baturini</i> SCHNEIDER, 1961: 3 c.

sp. from the sandstone member with abundant terrestrial snails *Pomatias*. This level coincides with our bed 8 of the Gaverdovsky section and bed 4 of the Volchaya Balka section. The association combines fresh water species and the brakish water indicator *Cyprideis littoralis* (= *C. torosa*) and resembles the association from bed 3 of the Gaverdovsky section.

Velikovskaya (1964) gave a generalised description of the terrestrial formation overlying Khersonian marine deposits exposed in the valleys of the Belaya and Pshekha rivers, and listed an ostracod association with *Cyprideis torosa littoralis* BRADY, *Loxoconcha maeotica* VOROSH., *L. aff. tamarindus* JONES, *L. trapezoides* VOROSH., *Xestoleberis goretskii* GOLOW., *X. jatskoi* GOLOW., *X. maeotica* SUZ., *Leptocythere sulakensis* SUZ., *L. maeotica* LIV. (identified by N. N. Naidina) but without giving an accurate stratigraphic position. This strongly marine association of ostracods was correlated with Maeotian, however it has a very dissimilar composition with the Maeotian associations of the Taman Peninsula studied by Dykan (Popov et al. 2016). The association listed by Velikovskaya (1964) lacks genera *Caspiocypris*, *Pontoniella*, *Bacunella*, *Camptocypris*, *Amnicocythere*, *Euxinocythere*, *Pontoleberis*, *Cryptocyprideis*, *Candona*, etc., which are characteristic for the Maeotian of the Taman sections. We therefore question its unambiguous correlation with the Maeotian. These data, however, gave a clear evidence of levels with a stronger marine influence in the sequence of the sandy ocherous deposits of the Gaverdovsky Fm.

Stratigraphic distribution of the studied ostracods and their biotopes

Candona combibo LIVENTAL, 1939 (Pl. 1, Fig. 1), a freshwater taxon common in the Pliocene and Pleistocene of the Caucasus, the Volga region, the Caspian Sea, Bashkortostan, Azerbaijan, and Turkmenistan (Agalarova et al. 1961: 58, pl. 31, fig. 1, pl. 32, fig. 1, pl. 33, fig. 4; Livental 1929: 52, pl. 2, figs 40, 41; Mandelstam et al. 1962: 127, pl. 13, figs 1–4; Mandelstam and Schneider 1963: 149, pl. 23, figs 1, 2; Popova-Lvova 1965: 253, pl. 5, fig. 7; Suzin 1956: 30, pl. 14, figs 5, 6).

Candona neglecta SARS, 1887 (Pl. 1, Fig. 2), a freshwater taxon widely distributed in Eurasia from the Miocene to the present, including the Caucasus, Central Asia, western Kazakhstan, Lower Volga region, Caspian Sea, Bashkortostan (Agalarova et al. 1961: 58, pl. 34, fig. 1; Dykan 2009: pl. 1, fig. 4; 2016: 182, pl. 27, figs 1–12; Mandelstam et al. 1962: 127, pl. 12, fig. 12; Mandelstam and Schneider 1963: 154, pl. 24, figs 6, 9; Negadaev-Nikonov 1968: 25, pl. 3, figs 1, 5, pl. 9, fig. 3; Popova-Lvova 1965: 243, pl. 3, figs 4, 6; 1972: 76, fig. 4, fig. 6; 1977: 90, pl. 24, figs 1–3, 5, pl. 25, fig. 1; Suzin 1956: 29, pl. 14, figs 16, 17).

Candoniella suzini SCHNEIDER in SUZIN, 1956 (Pl. 1, Figs 3–5): a species known from the Maeotian, Pliocene, and Akchagylian of the northern Caucasus (Mandelstam and Schneider 1963: 161, pl. 27, fig. 8; Suzin 1956: 36, pl. 13, figs 19–21). A similar form was determined as *Herpetocypris reptans* (BAIRD) from the Middle and Late Miocene (Karaganian and Sarmatian) of the western Ciscaucasia (Schneider 1949: 122, pl. 6, fig. 3).

Ilyocypris gibba (RAMDOHR, 1808) (Pl. 1, Figs 6–8): the species is widespread in modern freshwater basins of Eurasia and America. Fossil records are known from Miocene – Pleistocene deposits of the Volga area, Bashkortostan, Caspian Sea, Crimea, Caucasus, Azerbaijan, Turkmenistan, western Kazakhstan, Central Asia, and Siberia (Agalarova et al. 1961: 50, pl. 20, figs 2–4, pl. 21, fig. 1, pl. 48, figs 5–6; Dykan 2016: 197, pl. 29, figs 13–18; Mandelstam et al. 1962: 93, pl. 6, figs 3, 4; Mandelstam and Schneider 1963: 124, pl. 17, fig. 9, pl. 18, fig. 6; Negadaev-Nikonov 1968: 20, pl. 2, fig. 3; Popova-Lvova 1965: 234, pl. 1, fig. 7; 1972: 72, pl. 3, fig. 3; Suzin 1956: 40, pl. 15, figs 2, 3; Shveyer 1949: 56, pl. 5, fig. 8; Guillaume et al. 1985: pl. 98, figs 1, 2, pl. 112, figs 8, 9).

Cyprinotus: An exclusively freshwater genus, inhabits modern water basins of Europe and Asia. Fossil forms are known from freshwater deposits of the Miocene and Pliocene of Bashkortostan, Caucasus, and Central Asia.

Cyprinotus baturini SCHNEIDER, 1961 (Pl. 1, Figs 9, 11): fresh water species described from the Pliocene of the Ily valley in eastern Kazakhstan (Mandelstam and Schneider 1963: 206, pl. 37, fig. 2).

Cyprinotus formalis SCHNEIDER, 1963 (Pl. 1, Figs 10, 14–16): the species described from the Miocene-Pliocene molasses of Dzungaria (Mandelstam and Schneider 1963: 202, pl. 20, fig. 9).

Cyprinotus vialovi SCHNEIDER, 1961 (Pl. 1, Figs 12, 13): a fresh-water species from the Pliocene of Kazakhstan, Uzbekistan, and Fergana valley (Mandelstam and Schneider 1963: 203, pl. 38, fig. 2). A similar form was described by Suzin from the Late Sarmatian (Khersonian) of Ossetia in the Northern Caucasus as *Cypridopsis* ex gr. *vidua* (O. F. MULLER) (Suzin 1956: 43, pl. 15, figs 12, 13).

Cyprinotus aff. *speciosus* MANDELSTAM, 1963 (Pl. 2, Figs 1–3): fresh-water deposits of the Miocene and Pliocene of Dzungaria in eastern Kazakhstan (Mandelstam and Schneider 1963: 204, pl. 38, fig. 6).

Cyprideis torosa (JONES, 1850) (Pl. 2, Figs 4–16): the species most tolerant to salinity. It inhabits a wide range of biotopes from estuaries with a large freshwater component and lagoons to the hypersaline waters of the Dead Sea. This form is considered as a brakish water species occurring from the Miocene to recent (Agalarova 1967: 106, pl. 16, figs 1–3; Agalarova et al. 1961: 132, pl. 77, fig. 1, pl. 78, figs 1–4; Bronstein 1947: 296, pl. 14, figs 6, 7; Dykan 2009: pl. 1, fig. 6; 2016: 33, pl. 1, figs 1–28; Lyubimova et al. 1960: 167, pl. 16, figs 1, 2; Karmishina 1975: p. 123, pl. 15, figs 3–5, pl. 16, figs 1–3; Livental 1929: 41, pl. 2, figs 19–21; Mandelstam et al. 1962: 281, pl. 45, fig. 13, pl. 46, figs 1–4; Negadaev-Nikonov 1968: 53, pl. 7, figs 1, 2; Popova-Lvova 1965: 282, pl. 11, figs 6, 7; 1972: 84, pl. 8, fig. 7; Suzin 1956: 121, pl. 9, figs 1, 2; Shveyer 1949: 40, pl. 7, figs 1–3; Schneider 1949: 153, pl. 10, fig. 9; Guillaume et al. 1985: pl. 99, figs 1, 2).

The wide variation in the sculpture of this eurytopic species, in combination with pronounced sexual dimorphism and differences in the shape of shells and sculpture of adults and juveniles, resulted in the usage of multiple names for this species in the literature (primarily *C. torosa* and *C. littoralis*, and also *C. punctillata*, *C. pannonica*, and *C. rahimica*).

Molluscs

Systematic studies of continental molluscs of Ciscaucasia started in the middle of the 20th century. Several contributions devoted mainly to terrestrial forms were published by Volkova (1956) and Likharev (1962). The only major monographic study published so far is the now classic work “Terrestrial Neogene mollusks of Ciscaucasia and their stratigraphic importance” by Steklov (1966). Some data on freshwater molluscs of the Caucasus, almost exclusively on the families Viviparidea and Unionidae, can be found in papers by Bogachev (1924, 1961). A series of publications devoted to Miocene terrestrial and freshwater molluscs of southern Eastern Europe were published by Ukrainian malacologists (Prisyazhnyuk 1975, Gozhyk and Prisyazhnyuk 1978 and many others). No specific studies of the Miocene continental molluscs of Ciscaucasia have been conducted in recent decades. Some species lists from older publications were reproduced in Beluzhenko (2002). Recently a new species of *Lymnaea* from the Volchaya Balka and Gaverdovsky localities was described by Vinarsky and Frolov (2017).

The molluscan assemblage from the ?early Late Sarmatian fresh-water marl of the Maikop city park was listed by Steklov (1966). In addition to the dominant fresh-water forms *Limnaea stagnalis*, *L. cf. glabra*, *Planorbarius corneus*, *Gyraulus riparius*, *G. sp.*, *Anisus aff. vortex*, *A. vorticulus*, *A. septemgyratus*, *A. sp.*, *Armiger crista*, *Segmentina aff. nitida*, *Hippeutis aff. complanatus*, *Viviparus sp.*, more rare land snails *Carychium plicatum*, *Succinea sp.*, *Gastrocopta (Albinula) acuminata*, *G. (Sinalbinula) nouletiana*, *Vertigo (Vertigo) antivertigo callosa*, *Vallonia lepida steinheimensis*, *Euxinophaedusa volkovae*, *Monacha (?) externa*, and *Caucasotachea andrussovi* are also present in the assemblage.

Most forms in this list, except *Succinea sp.*, *Monacha (?) externa*, and *Caucasotachea andrussovi*, also occur in our material. This difference may be due to the older geological age or to the screen washing method we used, which is not gentle to a collection of large shells. Other molluscs from the Maikop city park association have a wide stratigraphic distribution (*Carychium plicatum*, *Gastrocopta (Albinula) acuminata*, *Gastrocopta (Sinalbinula) nouletiana*, *Vertigo callosa*) or are known from Bessarabian – Maeotian localities in Ciscaucasia (Steklov 1966).

The new material reviewed below comes from two levels of the Gaverdovsky and Volchaya Balka sections. The Gaverdovsky section is the type locality for three species of terrestrial and one species of freshwater gastropods: *Caspicyclotus praesiversi*, *Carychium marinae*, *Strobilops (Eustrobilops) caucasica* (all in Steklov 1966) and the recently described *Lymnaea (Lymnaea) bogatschevi*, the form similar to extant *L. stagnalis* (LINNAEUS, 1758) but distinct in a peculiar groove-like suture that penetrates deep into the shell matter. This structure may be traced in protoconchs and juvenile shells with 3–4 whorls (Vinarsky and Frolov 2017). Gaverdovsky and Volchaya Balka are the reference localities for biostratigraphy of Late Miocene deposits of the Western Ciscaucasia. The study of the malacofauna from these sections contributes to knowledge on the biodiversity of terrestrial and freshwater molluscan

communities and the palaeoenvironmental conditions in the study region.

The molluscan associations from Volchaya Balka and Gaverdovsky localities can be divided into three assemblages:

Assemblage 1 (fresh-water) comprises predominately freshwater, stagnophilic forms with an overwhelming predominance of the genera *Lymnaea*, *Planorbarius*, and *Gyraulus*. In addition, sporadic shells of land molluscs are found here. The assemblage is confined to bluish clayey silts of Gaverdovsky bed 7 and Volchaya Balka bed 4.

Assemblage 2 (with *Melanopsis*) is defined for molluscs of the so called “fish lens” in the lower part of bed 8 in the Gaverdovsky section. In fact, it is nearly identical with Assemblage 3. We define it separately because it includes mesophilous landsnails *Pomatias* and *Caspicyclotus*, and, importantly, the aquatic gastropod *Melanopsis* which is not found elsewhere in the studied sections.

Assemblage 3 (terrestrial) is characterized by a large number of terrestrial species, with an admixture of freshwater forms. It is worth noting that some of the latter and few landsnails are recrystallized or represented as internal nuclei. These are possibly redeposited from the underlying fresh-water level yielding Assemblage 1.

Description of the assemblages

Assemblage 1

This assemblage mainly includes freshwater molluscs with a small number of terrestrial species, including the rare *Pomatias rivulare*, fragments of Pupillidae, apical parts of shells of Clausiliidae, and several species referred to the genus *Limax*. Land slugs in the Miocene sediments of Ciscaucasia are represented by vestigial shells obviously belonging to several species and possibly genera. They are conventionally attributed to the genus *Limax* because the modern systematics of slugs is based on the structure of a soft body whereas the shells are still little studied (Steklov 1966). Freshwater molluscs include *Lymnaea bogachevi*, *Galba cf. turrita*, *G. aff. dupuyana* (Pl. 3, Fig. 9), *Planorbarius mantelli*, *P. cf. thiollerei* (Pl. 3, Figs 14–16), *Anisus (Odontogyrorbis) krambergeri*, *Gyraulus cf. kleini*, *G. cf. applanatus*, *G. cf. solenoides* (Pl. 4, Fig. 21), *Armiger nautiliformis* (Pl. 4, Fig. 13), *Armiger cf. cristaeformis* (Pl. 4, Figs 9–12), and *Pisidium (Cingulipisidium) cf. nitidum*. The latter form is the only taxon of bivalve molluscs found in our material. It is represented by juvenile shells referable to *Pisidium (Cingulipisidium) cf. nitidum* JENYNS, 1832 based on the umbones being separated by several sharp ribs (in juvenile shells they are located along the lower edge of the shell), the cardinal teeth of the left valve being almost parallel, and the imprints of mantle muscles not separated from the mantle line (Pl. 6, Figs 20–23).

The fauna of Volchaya Balka also includes poorly preserved shells of Viviparidae with the characteristic pointed apex and a keel in the middle of the last whorl (Pl. 3, Fig. 4), the features characterising the subfamily Bellamyinae. The modern range of the group includes Africa and east Asia. Early Pleistocene finds of Bellamyinae were reported from Israel (Tchernov 1975). Recent records are assumed for Syria and Yemen (Brown 2005).

Nearly all forms of the families Lymnaeidae and Planorbidae are here referred to in open nomenclature because of the lack of any previous studies on the Miocene freshwater fauna of the Ciscaucasus. We used the descriptions of Miocene freshwater molluscs from Ukraine (Gozhik and Prisyazhnyuk 1978), Hungary (Kokay 2006), Austria (Binder 2004, Harzhauser and Binder 2004, Harzhauser et al. 2014a, b), Germany (Salvador 2013, Salvador and Rasser 2014), and others.

Some of these publications attribute the fossil *Gyraulus* to a group of species near the Early and Middle Miocene *Gyraulus dealbatus*. Currently three species are accepted as valid: *Gyraulus dealbatus*, *Gyraulus applanatus*, and *Gyraulus kleini* (Harzhauser et al. 2014a), but given their high variability, a determination of fossil forms to the species is problematic (Pl. 3, Figs 17–21).

The form of *Planorbarius* in our material according to the protoconch structure, shape, and size of shells is assigned to *P. mantelli* (Pl. 3, Figs 12–13). Adult shells of this species are very similar to the extant *P. corneus* (LINNAEUS, 1758), but differ in the protoconch which is formed by an inflated initial cap (Harzhauser and Binder 2004). From Middle Miocene *P. cornu* (BRONGNIART, 1810) they differ in the less bulbous whorls (Harzhauser et al. 2014a). From contemporaneous *P. thiollierei* (MICAUD, 1855), they differ in their smaller sizes, more flatten whorls (Sauerzopf 1953), and protoconch formed by an inflated initial cap.

Most of the studied molluscs belong to a group of freshwater limnophilous forms preferring water basins with rich vegetation and weak currents. Some of the freshwater species can tolerate a weak salinity. For example, *Lymnaea stagnalis*, can withstand a salinity up to 7 ‰, but other member of the assemblage, *Planorbarius*, *Gyraulus*, and *Galba* aff. *dupuyana* are considered to be purely freshwater forms (Kokay 2006).

This species complex is somewhat similar to the assemblages from the Middle – Late Miocene faunas of central Europe: Öcs (Schlickum 1978), Richardhof, Eichkogel (Harzhauser and Binder 2004), Oggenhausen (Salvador and Rasser 2016), the Late Pannonian of Hungary (Várpalota Basin) (Kokay 2006), and several others. From Eastern Europe, it can only be compared with the Sarmatian – Maeotian faunas from the right-bank Ukraine (Zhdanovo, Novobogdanovka, Mikhailovo). As noted by Gozhik and Prisyazhnyuk (1978), one of the most characteristic forms of the Late Sarmatian assemblage is *Anisus* (*Odontogyrorbis*) *krambergeri*. The adult shells of this planorbid species bear three to four enlarged teeth in the aperture (Pl. 4, Figs 1–4). In the case of a damaged aperture they are nearly indistinguishable from common forms of the genus *Anisus*. This form is unknown in pre-Late Sarmatian (Khersonian) faunas. The continental Maeotian molluscan association is distinct from that of the Late Sarmatian only in the rheophilic species, whereas the pulmonate snails are identical in both assemblages (Gozhik and Prisyazhnyuk 1978).

The freshwater assemblages from Gaverdovsky and Volchaya Balka are nearly identical. The obvious differences are only in higher frequencies of *Armiger* in Volchaya Balka than in Gaverdovsky, and the presence of Bellamyinae only in Volchaya Balka.

Assemblage 2

The second assemblage contains shells of the terrestrial snails *Pomatias rivulare* and *Caspicyclotus praesiversi*, mesophilic forest elements inhabiting biotopes with medium humidity (Stoyko and Bulavkina 2010). Shells of *Melanopsis* ex gr. *praemorsa* group (Bandel 2000), were also found here (Pl. 3, Fig. 2). This is the only record of *Melanopsis* in the studied sections and it is not accompanied by any other freshwater molluscs. Because Melanopsidae can tolerate brackish water conditions, proximity to the sea can be assumed for this level.

Assemblage 3

This association mainly contains shells of land molluscs with predominant inhabitants of forest litter (*Gastrocopta*, *Negulus*, *Strobilops*). Modern species of these genera are mainly known in south and southeastern Asia, and in North and South America. Modern *Negulus* is only known from Africa (Bruggen 1994). Species of the genera *Vertigo*, *Pupilla*, *Vallonia*, *Truncatellina*, *Oxychilus*, and others also inhabit the forest litter and prefer relatively humid conditions. Also present are other mesophilic forms such as *Pomatias rivulare* (Pl. 3, Fig. 1), *Caspicyclotus*, cf. *Caucasotachea* (Pl. 6, Fig. 19).

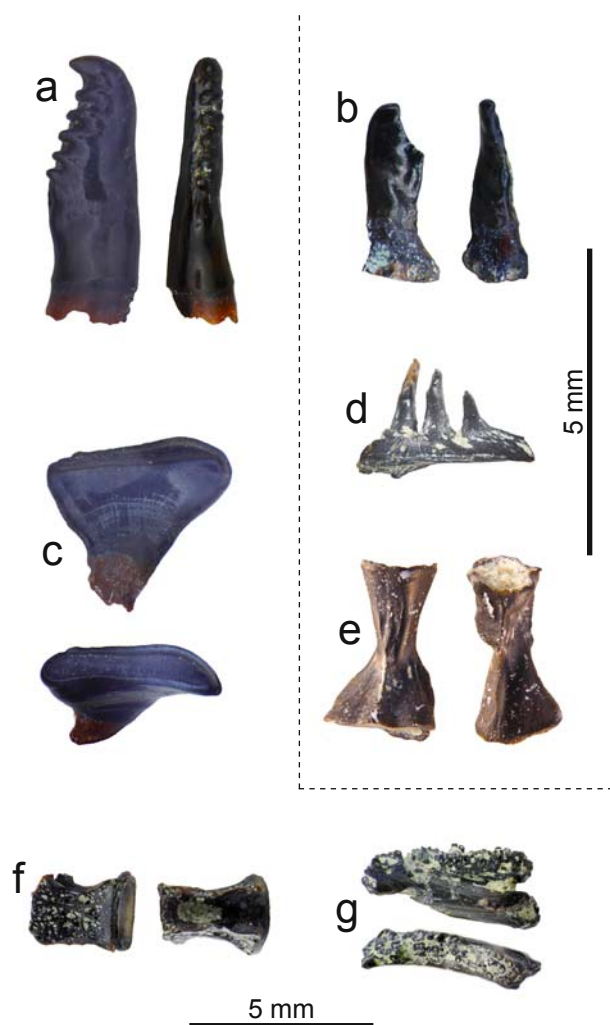
The composition of this assemblage indicates a humid, warm temperate to subtropical climate and dominant forests with moist soil and deciduous litter. Rare finds of Enidae indet. (Pl. 6, Fig. 18) indicate a local presence of mesoxerophilic biotopes.

Many of the species found have a fairly wide stratigraphic range. For example, *Vertigo protracta* (Pl. 5, Figs 7–8) is known from the Late Oligocene to the Late Miocene. *Gastrocopta* (*Albinula*) *acuminata* (Pl. 5, Figs 1–2), *Gastrocopta* (*Sinalbinula*) *nouletiana* (Pl. 5, Figs 3–4), and *Vertigo callosa* (Pl. 5, Figs 5–6) are found in localities of Bełchatów-B (Poland, MN 5), Vračević (Serbia, MN 7 + 8), Eichkogel (Austria, MN 11), as well as in a number of localities of intermediate age (Steklov 1966, Gozhik and Prisyazhnyuk 1978, Lueger 1981, Stworzewicz 1999, Harzhauser and Binder 2004, Salvador and Rasser 2016, Neubauer et al. 2016). *Vertigo* (*Vertilla*) *oecensis* is found only in the age range MN 9 – MN 11 in localities Richardhof, Eichkogel (both Austria), Bełchatów – A (Poland), and others (Stworzewicz 1999, Harzhauser and Binder 2004). Some species are currently known exclusively from Ciscaucasia: *Caspicyclotus praesiversi*, *Pupilla mutabilis*, *Euxinophaedusa* aff. *volkovae*, *Quadriplicata farsica*, and *Hawaiiia antiqua* (Pl. 6, Figs 15–17). They have a general age range from the Middle Sarmatian (Bessarabian) to Maeotian. *Pontophaedusa praefuniculum* is known only from the continental Maeotian locality on the Fortanga River (Chechen Republic, Russia) and in Gaverdovsky. Two species of *Carychium marinae* (Pl. 4, Fig. 22) and *Strobilops* (*Eustrobilops*) *caucasica* (Pl. 6, Figs 6–8) are known only from the studied site (Steklov 1966).

Based on this brief stratigraphic analysis, we can assume the age of the studied sequence to be within the MN 10 – MN 11 zones, because some of the forms found are not known outside the range of the Late Sarmatian (Khersonian) and Maeotian.

All molluscs of Assemblage 3 encountered in Gaverdovsky (bed 8) were also found in the corresponding bed 4 of the Volchaya Balka section. The amount of material in Volchaya Balka, however, is much larger due to the easier accessibility of the sandstone member here.

Based on the composition of the malacofauna, all three defined assemblages are almost synchronous and are dated to Late Sarmatian (Khersonian) – Maeotian interval. These data indicate the presence of a fresh-water basin with rich water vegetation and wooded shores. Periodic sea influxes could affect the freshwater molluscan fauna as indicated by the presence of *Melanopsis* and lack of any other fresh-water forms in Assemblage 2. Climatic conditions were warm temperate to humid subtropical.



Text-fig. 6. Fish remains from Volchaya Balka locality (Late Miocene, North Caucasus). a – *Scardinius* sp., SSC-RAS G-2/1, pharyngeal tooth of the first row, side view, occlusal view; b – *Abramis* cf. *bjoerkna*, SSC-RAS G-2/2, pharyngeal tooth of the first row: top – side view, bottom – occlusal view; c – *Carassius* sp., SSC-RAS G-2/3, pharyngeal tooth of the first row: top – side view, bottom – occlusal view; d – *Alburnus* sp., SSC-RAS G-2/4, fragment of pharyngeal bone (os pharyngicus inferior), medial view; e – *Acipenser* sp., SSC-RAS G-2/5, left hyomandibular: left – medial view, right – proximal view; f – Gobiidae gen. indet., SSC-RAS G-2/6, tail vertebra: left – lateral view, right – dorsal view; g – Gobiidae gen. indet., SSC-RAS G-2/7, dentary: top – medial view, bottom – dorsal view.

Fishes

In the previous studies of Late Miocene sections near the city of Maikop fish remains were rarely listed. The only level with fish remains mentioned in continental sandy ocherous deposits downstream from Maikop was the record of fish scales in a clay bed with abundant *Hydrobia* shells, about 20 m above the Khersonian clays containing *Macra* shells (Steklov 1966: 58). We could not re-locate this level. Fish remains in the underlying Khersonian deposits along the Fortepianka River were listed by Tarasenko et al. (2014) and include marine forms of the families Scombridae and Sparidae.

Fish remains in the studied sections are unevenly distributed. The most numerous is the assemblage from the bed 3 of the Volchaya Balka section (the bed containing shells of fresh-water molluscs). Surprisingly, the fresh-water bed 7 of the Gaverdovsky section is very poor in fish remains with only a few vertebrae of cyprinid fishes found. At the same time, a sandy lens (“fish lens”) at the base of the sandstone member (bed 8) in Gaverdovsky yielded abundant remains of fresh-water fishes.

Fish fauna of the Volchaya Balka (Text-fig. 6) is represented by *Acipenser* sp., *Abramis* cf. *bjoerkna* L., *A. aff. sapa* PALLAS, *Scardinius* sp., *Alburnus* sp., *Carassius* sp., *Sander* sp., Gobiidae gen. indet. The material largely consists of vertebrae fragments (n = 1,917) accounting for more than 85% of the bone sample. The majority (ca. 70%) of vertebrae belongs to the Gobiidae family. Remains of cyprinid fishes (family Cyprinidae) are represented by pharyngeal teeth (n = 18). Most pharyngeal teeth belong to *Carassius* sp. (n = 12). The identified taxa are typical of the modern Aralo-Ponto-Caspian province (Berg 1949) and belong to four families (Acipenseridae, Cyprinidae, Percidae, Gobiidae).

The studies by Sychevskaya (1989, and many others) and Kovalchuk (2015) showed that most modern taxa characteristic for this province have occurred in the fossil record since Miocene. Our data for North Caucasus confirm this concept. On the other hand, the studied assemblages, possibly due to environmental limitations and/or sampling bias, are less diverse than the ichthyofauna of the north-western Black Sea region (Kovalchuk 2015), and Middle to Late Miocene fauna of the Central Asian region (Sychevskaya 1989).

The “fish lens” (base of bed 8) in the Gaverdovsky section contains abundant remains of *Scardinius* sp., *Esox* sp., *Sander* sp., and Gobiidae gen. The presence of rudd (*Scardinius* sp.) and pike (*Esox* sp.) indicates a fresh-water basin.

The taxonomic composition of the fish assemblage indicates a fresh-water, or strongly fresh water biased, basin. The presence of pike-perch (*Sander* sp.) evidences a well aerated water body. The record of sturgeon, *Acipenser* sp., indicates a connection either with a sea or a river. But the impoverished species composition and the presence of *Carassius* sp. and rudd (*Scardinius* sp.), which prefer stagnant water basins with an oozy bottom, may indicate an isolated lake-like water basin with periodic connections either with the sea or with fresh-water basins from which sturgeons could penetrate into it. Gobies (Gobiidae), predominant in the Volchaya Balka material, are not necessarily indicative

of a connection with the sea. In the Ponto-Caspian region *Gobius* species also inhabit isolated freshwater basins.

Amphibia and Reptilia

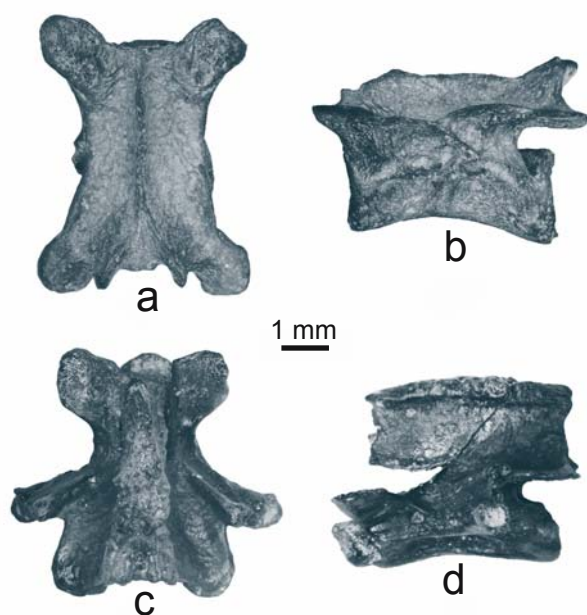
The Volchaya Balka and Gaverdovsky localities yielded 14 taxa of amphibians and 12 taxa of reptiles: *Mioproteus caucasicus* ESTES et DAREVSKY, 1977 (Proteidae), *Chelotriton paradoxus* POMEL, 1853, *Triturus cristatus* (LAURENTI, 1768), *Triturus* cf. *marmoratus* (LATREILLE, 1800), *Lissotriton* sp. (Salamandridae), *Latonia* sp. (Alytidae), *Bombina* cf. *bombina* (LINNAEUS, 1761) (Bombinatoridae), *Hyla* sp. (Hylidae), *Palaeobatrachus* sp. (Palaeobatrachidae), *Pelobates* sp. (Pelobatidae), *Bufotes viridis* (LAURENTI, 1768), *Bufo* sp. (Bufonidae), *Rana* sp., *Pelophylax* sp. (Ranidae), *Emys* cf. *tarashchuki* (CHKHIKVADZE, 1980) (Emydidae), cf. *Sakya* sp. (Geoemydidae), Testudinidae indet., *Testudo* s. s. (Testudinidae), *Pseudopus pannonicus* (KORMOS, 1911), *Anguis* sp. (Anguidae), Lacertidae indet. (Lacertidae), *Coronella* sp., *Natrix* cf. *longivertebrata* SZYNDLAR, 1984, *Natrix* sp., Colubrinae indet. (Colubridae), and Viperidae indet. (Viperidae).

Amphibia LINNAEUS, 1758

The Amphibia are represented by the Anura and Urodela. The tailed amphibians (Urodela) are represented by relatively large forms such as *Mioproteus* and *Chelotriton* and several smaller forms of *Triturus sensu lato*. Remains of *Mioproteus caucasicus* are relatively rare and represented by eleven vertebrae (Text-fig. 7a, b). Their overall morphology is consistent with *M. caucasicus* described from the same area (Maikop city park), but from slightly older deposits, in the shape of the forking processes on the dorsoposterior region of the neural arch and other characters (Estes and Darevsky

1977). *Chelotriton* is more frequent than *Mioproteus* and documented by about 40 cranial and postcranial (vertebrae) elements (Text-fig. 7c, d). It is assigned to *Ch. paradoxus* POMEL, 1853 (according to Schoch et al. 2015) based on the heavily ossified skull bones and extensive tubercular ornamentation.

Triturus sensu lato is the most abundant tailed amphibian in Volchaya Balka and Gaverdovsky (several hundred vertebrae and skeletal elements) and represented by at least three forms. These are relatively large size *Triturus cristatus* (Pl. 7, Fig. 1a, b) and *Triturus* cf. *marmoratus* (Pl. 7, Fig. 2a, b) which differ in the length of the neural arch (long in *T. cristatus* and short in *T. cf. marmoratus*) and height of the neural spine (low in *T. cristatus* and high in *T. cf. marmoratus*), and smaller *Lissotriton* sp. (Pl. 7, Fig. 3a, b) with a very high neural spine. Additionally, two fragmentary opisthocoelous vertebrae which are different from *Chelotriton* in the absence of ornamentation and from *Triturus* s. str. and *Lissotriton* in its relatively large size and flattened posterior part of neural arch and, thus, indicate the presence of another salamandrid taxon. *Bombina* is very rare in the material and represented by seven elements. It is indicated by the opisthocoelous presacral vertebrae, posterior position of tuber superior of the ilia and poorly developed pars descendens (Pl. 7, Figs 4, 5). The Caucasian *Bombina* shows the presence of a prominent tuber superior and preacetabular fossa which is characteristic of *B. bombina* rather than *B. variegata* (Böhme 1977, Sanchíz and Młynarski 1979). One of the most common anurans was *Latonia* which is represented by 70 cranial and postcranial elements (Pl. 7, Fig. 6). It differs from *Latonia gigantea* (LARTET, 1851), the most widespread species in the Late Miocene of Europe (Rage and Roček 2003), in the maxilla lacking any sculpture. Caucasian *Latonia* also differs from other existing *Latonia* species in shape of sacral transverse processes and possibly belongs to a separate species. *Hyla* is extremely rare and represented by four ilia and a single sacral vertebra (Pl. 7, Fig. 7). Its presence is confirmed by the morphology of the ilia, i.e., thin and expanded anteriorly anteroventral margin of the pars descendens. The tuber superioris is prominent and projects anteriorly. It is nearly oval in shape, which allows distinguishing between *Hyla arborea* (with an oval tuber superior) and *H. meridionalis* (with a rounded tuber superior) (Holman 1992, Bailon 2000). Because the osteological characters of *Hyla savignyi* are not known, the Caucasian *Hyla* can only be identified to the genus. Another common anuran is *Palaeobatrachus* which is represented by 50 cranial and postcranial elements (Pl. 7, Figs 8, 9). Among the other palaeobatrachids it clearly differs from the older (Oligocene – Early Miocene) *Palaeobatrachus* species and is most similar to the Plio-Pleistocene species (*P. eurydices* and *P. langhae*) in the reduction of premaxillar and maxillar teeth. The Pelobatidae, which are predominantly fossorial (burrowing) frogs are fairly rare here (about 15 cranial bones, vertebrae and ilia; Pl. 7, Fig. 10). Most available remains were assigned to the extant genus *Pelobates*. As in the other *Pelobates*, it is characterized by missing dorsal crests on the iliac shafts and striated scars on the postero-mesial border of the ilia. As in the Miocene *Pelobates* it has a small interiliac tubercle (Rage and Hossini 2000). In addition to *Pelobates*, the material from Volchaya Balka also includes several



Text-fig. 7. Fossil urodelans from studied localities. a, b – *Mioproteus caucasicus*, trunk vertebra, dorsal (a) and lateral (b) views; c, d – *Chelotriton paradoxus*, trunk vertebra, dorsal (c) and lateral (d) view. Scale bar 1 mm.

remains of the fossil genus *Eopelobates* with characteristic pit-and-ridge sculpture on frontoparietals (Syromyatnikova 2017). Bufonidae are documented by toothless premaxilla and lateral position of the olecranon scar on the humerus and several fragmentary ilia. The presence of small bulges on the lateral side of the tuber superior on the ilium and preacetabular fossa indicates the toad species *Bufo viridis* (Pl. 7, Fig. 11). In the material it is represented by the less than 10 bones. The single humerus which is assigned here to *Bufo* sp. can be distinguished from the former species by its larger size (about twice as big as *B. viridis*). Ranidae are the most numerous in the amphibian material and are represented by more than 300 cranial and postcranial elements (Pl. 7, Figs 12, 13). Some specimens exhibit characters typical for brown frogs *Rana* (*Rana temporaria* group), i.e., lateral position of the parietal eminence of the frontoparietal, dorsally inflected medial and lateral crests of humerus, presence of tubercles on tuber superior of the ilia (Böhme 1977, Ratnikov 2001). Most of the ranid bones exhibit characters typical for green frogs *Pelophylax* (*Rana esculenta* group) (Pl. 7, Fig. 14), i.e., elongate external mandibular ridge of angular, extremely expanded and flattened pars epicoracoidalis and slender middle part of coracoid, high dorsal crest (much higher than iliac shaft) of ilium, laterally flattened tuber superior and its position close to the front of the anterior edge of the acetabulum (Böhme 1977, Böhme and Günther 1979, Rage 1984, Ratnikov 2001). Extant ranid species are mainly distinguished by external morphological characters. Thus, the described material of *Rana* sp. and *Pelophylax* sp. is not assigned here to extant species.

Reptilia McCARTNEY, 1802

Turtles are not numerous in the studied localities and are preserved as isolated shell plates. Six species are present belonging to the three families: Emydidae, Geoemydidae and Testudinidae. The majority of turtle specimens belong to the emydids. Some are similar to *Emys tarashchuki* (described from the Late Miocene of Ukraine) in the position of skin-scale sulcus on the epiplastron, which is relatively distant from the free edge of the bone. Geoemydidae are represented by *Sakya* sp., which was identified based on the peculiar shield configurations, i.e., having an extra number of vertebral, pleural and marginal scutes on the carapace (Chkhikvadze 1983). Testudinidae are represented by a fragment of the anterior lobe of the plastron (epi+entoplastron) from the Gaverdovsky locality and several isolated shell plates. Some fragments of xiphiplastra indicate the presence of a hypoxiphiplastral hinge and can be referred to *Testudo* s. s.

Remains of squamates document the presence of at least six taxa. The anguids are represented, first of all, by *Pseudopus pannonicus* (Pl. 7, Fig. 15), the species common in the European Late Miocene. The remains of this lizard are abundant and include a posterior part of the braincase, i.e., a diagnostic element within the genus, vertebrae and osteoderms. *Anguis* are slightly more frequent than *Pseudopus* and recognized on the basis of the frontal morphology, presence of curved and widely-spaced teeth and non-rectangular osteoderms without keels (Pl. 7, Figs 16, 17). Lacertids are represented by a limited quantity of small fragments of lower jaws and vertebrae which does

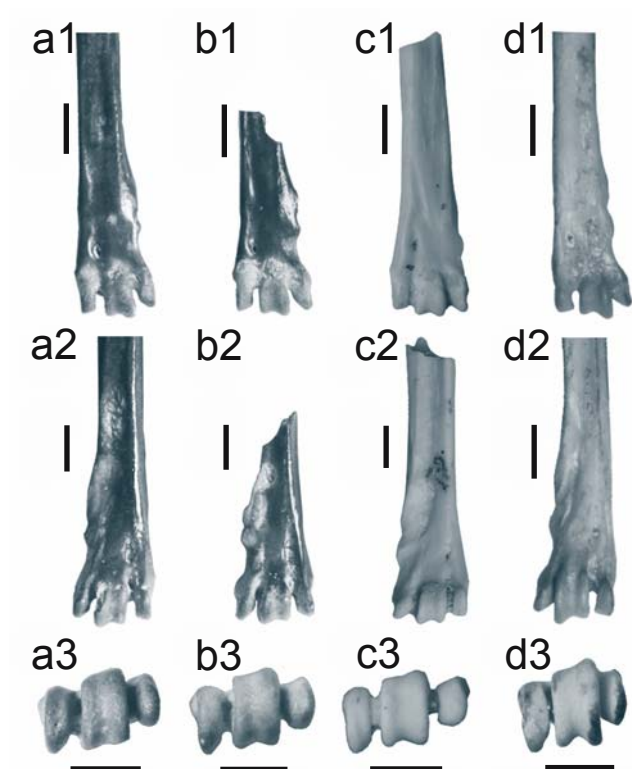
not permit an accurate identification of genus and species (Pl. 7, Fig. 18). *Coronella* sp. is represented by several small size vertebrae with a dorso-ventrally flattened neural arch and weakly developed haemal keel (Pl. 7, Fig. 19). The Caucasian *Coronella* is most similar to *C. miocaenica* VENCZEL, 1998 (Middle Miocene, MN 8, Romania and Late Miocene, MN 13, Hungary) in its less depressed neural arch (Venczel 1998), however its centrum length/width ratio is 1.44, which corresponds to *C. austriaca* rather than *C. miocaenica* (Szyndlar 1991a). Three fragmentary vertebrae document the presence of another colubrine which differs from *Coronella* in a larger size and vaulted neural arch. The four fragmentary vertebrae are assigned to *Natrix* cf. *longivertebra*, a widely distributed species in the European Neogene (Szyndlar 1991b), based on their elongate and narrow centra with strong subcentral ridges. Another taxon of *Natrix* is characterized by its relatively small size and centrum length/centrum width ratio of 1.38 (Pl. 7, Fig. 20). It is most similar to *N. rudabanyaensis* SZYNDLAR, 2005 (Middle – Late Miocene, MN 6–9, Hungary and Romania) in its moderately developed subcentral ridges, centrum length/width ratio and, rounded distal hypapophyseal tip (Szyndlar 2005). The single fragmentary trunk vertebra is assigned to the Viperidae, however, due to the limited amount of the material, the identification is possible to the family rank only.

Birds

Birds are not at all well known in the Late Miocene deposits near Maikop. The only form previously reported from the Khersonian (Late Sarmatian) deposits of the neighboring Fortepianka River is a record of the goose *Anser* sp. (Tarasenko et al. 2014).

In the Gaverdovsky locality, two bird remains were identified: a poorly preserved partial distal radius of an owl referable to Strigidae gen. indet. similar in size and general morphology to the extant long-eared owl *Asio otus*; and a fragmental tarsometatarsus of a perching bird (order Passeriformes).

Three fragmentary avian bones were found in the Volchaya Balka locality, the distal part of a left tibiotarsus and two distal parts of right tarsometatarsi, belonging to perching birds (order Passeriformes) the size of modern *Sylvia borin*. The latter two specimens have diagnostic anatomical features and are morphologically similar to modern Sylvioidea (Alstrom et al. 2006), a taxonomically rich and globally distributed clade which includes small- and medium-sized birds with diverse ecologies. The two tarsometatarsi are closer in overall morphology to modern Old World warblers of the family Sylviidae s. s. (Text-fig. 8), but they still display several anatomical features which preclude their assignment to any of the examined Palaearctic families (Acrocephalidae, Locustellidae, Phylloscopidae, Sylviidae s. s., Cisticolidae, Cettidae). It is possible that warblers from Volchaya Balka represent one of the families which today inhabit sub-Saharan Africa (largely unavailable for comparisons), because several modern bird taxa characteristic of the Sahel zone (e.g., ostrich, *Ortyxelos* buttonquails, hornbills) were found in the Late Miocene of Europe (Mlíkovský 2002, Boev and Kovachev 2007, Zelenkov et al. 2016).



Text-fig. 8. Tarsometatarsi of fossil and Recent Sylvioidea. **a** – PIN, № 5528/3 from Volchaya Balka; **b** – PIN № 5528/4 from Volchaya Balka; **c** – *Sylvia intermedia* KESSLER, 2013; **d** – *Sylvia borin* (BODDAERT, 1783). **a1–d1** – dorsal view; **a2–d2** – plantar view; **a3–d3** – distal view. Scale bars 1 mm.

It is notable that the tarsometatarsi from Volchaya Balka are quite similar to a tarsometatarsus from the Late Miocene (MN 13) locality Polgárdi 4 (Hungary) referred to as *Sylvia intermedia* (Text-fig. 8; Kessler 2013). The allocation of the tarsometatarsus from Polgárdi 4 to the modern genus *Sylvia* is questionable. The Hungarian specimen and bones from Volchaya Balka apparently belong to closely related taxa whose phylogenetic position within the Sylvioidea remains unclear.

Mammals

Small mammals

Mammalian associations of Gaverdovsky (bed 7) and Volchaya Balka (bed 3) are shown in the Table 3.

The two small mammal assemblages are quite similar in composition. The notable exception is the presence of lagomorphs in the fauna of Gaverdovsky and different dominant small cricetines: *Pseudocricetus* in Gaverdovsky and *Neocricetodon* in Volchaya Balka. Other differences, such as the presence of eomyids and dipodids in Gaverdovsky and their absence in Volchaya Balka and the occurrence of squirrels only in Vlb, may be due to a sampling bias. In addition to two main mammalian samples from beds with fresh-water molluscs, scanty material on small mammals comes from the sandstone member (bed 4) of Volchaya Balka in association with land snails of the molluscan Assemblage 3. This material includes bones of Talpidae, *Pseudocricetus* sp., and, most important, *Trogotherium* (*Euroxenomys*) *minutum*, the only record of beavers in the Gaverdovsky Fm.

Table 3. Composition of Late Miocene small mammals of the Gaverdovsky Fm.

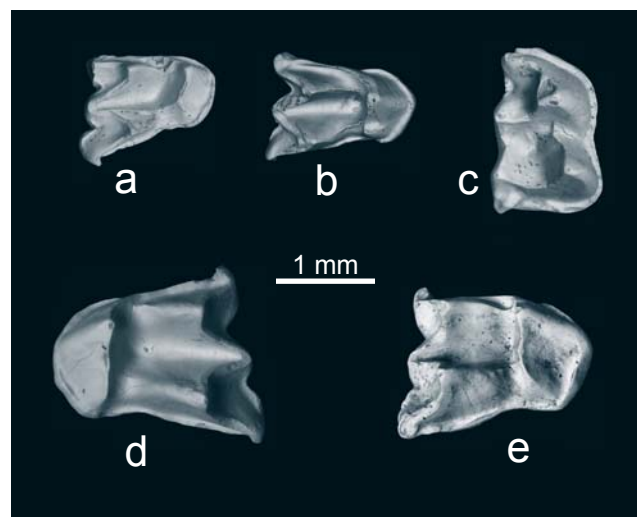
Taxon	Gaverdovsky	Volchaya Balka
<i>Myotis</i> sp. 1	2	–
<i>Myotis</i> sp. 2	–	2
<i>Eptesicus</i> sp.	–	1
<i>Talpa</i> sp.	20	33
<i>Desmanella</i> sp.	6	4
<i>Blarinella</i> cf. <i>dubia</i> (BACHMAYER et WILSON)	7	6
<i>Paenelimnoecus repenningi</i> (BACHMAYER et WILSON)	5	4
<i>Amblycoptus oligodon</i> KORMOS	4	18
<i>Prolagus</i> cf. <i>crusafonti</i> LÓPEZ MARTÍNEZ	1	–
<i>Ochotona</i> sp.	13	–
<i>Alilepus</i> sp.	2	–
cf. <i>Miopetaurista</i> sp.	–	2
<i>Neopetes</i> cf. <i>hoeckarum</i> (DE BRUIJN)	–	8
<i>Trogotherium minutum</i> (VON MEYER)	–	1 (bed 4)
<i>Ramys</i> vel <i>Vasseuromys</i>	16	3
<i>Paraglitulus schultzi</i> DAXNER-HÖCK et HÖCK	1	5
<i>Muscardinus pliocaenicus</i> KOWALSKI	4	5
<i>Keramidomys</i> sp.	6	–
<i>Eozapus intermedius</i> (BACHMAYER et WILSON)	7	–
<i>Sicista</i> sp.	1	–
<i>Neocricetodon</i> cf. <i>progressus</i> (TOPACHEVSKY et SCORIK)	3	45
<i>Pseudocricetus</i> ex gr. <i>antiquus</i> TOPACHEVSKY et SCORIK	33	–
<i>Collimys caucasicus</i> sp. nov.	6	4
<i>Parapodemus lugdunensis</i> SCHAUB	38	34
Total	175	205

Bats are relatively common and taxonomically diverse in European fossil sites from Early and Middle Miocene (Storch 1999, Rosina and Rummel 2012). The geologically oldest bat record for the Caucasus was reported from the early Middle Miocene fauna of Belomechetskaya, *Scotopilus* sp. and *Tadarida* sp. (Gabunia and Bendukidze 1984). But for the Late Miocene only a low number of fossil sites with bat remains are known and the diversity of the bats is limited. For example, only about 5 – 6 species representing modern Vespertilionid genera are known from the early and middle Turolian of southern Ukraine (Rosina and Sinitsa 2014); the early Turolian (MN 11) fauna of Eichkogel in Austria documents the single species, *Paleptesicus* cf. *noctuloides* (Zeigler 2006). In Russia, the only described record of a Late Miocene bat, identified as *Vespertilio* cf. *villanyiensis*, comes from the fauna of Morskaya 2 (late Turolian, MN 13) (Rossina et al. 2006).

Our new bat material originated from two distinct sites, Volchaya Balka and Gaverdovsky. Both sites are non-karstic, which in general rarely contain bat remains (Sigé and Legendre 1983, Rosina et al. 2015). Bats are represented by five isolated cheek teeth: one left M1 or M2, three right M2 and one right m1 or m2. All specimens have partly damaged roots, but the cusps are preserved quite well; only one specimen (Text-fig. 9a) has a partly broken parastyle.

For identification of material we compared it with museum specimens of modern bats from different families and genera, taken from the collection of Moscow Zoological Museum (ZMMU). List of species used for comparison includes: *Rhinolophus fumigatus*, *Hipposideros abae*, *Chaerephon pumila*, *Ch. nigeriae*, *Miniopterus schreibersi*, *Kerivoula kachinensis*, *Myotis alcathoe*, *M. annectans*, *M. blythii*, *M. dasycneme*, *M. daubentonii*, *M. indochinensis*, *M. montivagus*, *M. muricola*, *M. mystacinus*, *M. nattereri*, *M. welwitchii*, *Plecotus auritus*, *P. turkmenicus*, *Pipistrellus kuhlii*, *Nyctalus noctula*, *N. leisleri*, *Vespertilio murinus*, *V. sinensis*, *Eptesicus serotinus*, *E. nilssonii*, *Hesperoptenus tickelli*, *Arielulus circumdatus*, and *Scotophilus kuhlii*. First of all, from that comparison we came to conclusion that all the five specimens represent the family Vespertilionidae.

The specimen in Text-fig. 9d (left M1 or M2) from Volchaya Balka in morphology and proportions (shape of protocone, stage of hypocone reduction, almost open trigon basin with deep fossa, proportionally unwidened stylar shelf) is mostly similar to large serotines of the genus *Eptesicus* (especially with M2 of *E. serotinus*). In size (L = 1.85, W = 1.95 mm), this molar also corresponds to *E. serotinus*. According to direct comparison, in proportions the fossil molar somewhat differs from the teeth of *Vespertilio* and small serotines, such as *E. nilssonii*; other large nycticeines, such as *Arielulus* and *Hesperoptenus*, have different proportions and shape of the protocone and a more shallow fossa in the trigon basin. The Late Miocene fauna of Eichkogel in Austria (Ziegler 2006), similar in age to the faunas under study, yielded the single nycticeine, *Miostrellus noctuloides*. This form, as well as other *Miostrellus*, is definitely smaller than *E. serotinus* (Rosina and Rummel 2012) and our specimen. Another Late Miocene European serotine, *E. campanensis*, is similar



Text-fig. 9. Bats from Late Miocene deposits, North Caucasus. a – *Myotis* sp. 1, right M2, GIN-1143-411; b – *Myotis* sp. 1, M2, dex, GIN-1143-412; c – *Myotis* sp. 2, m1 or m2, dex, GIN-1144-311; e – *Myotis* sp. 2, M2, dex, GIN-1144-312; d – *Eptesicus* sp., M1 or M2, sin, GIN-1143-413. a, b, d – Volchaya Balka; c, e – Gaverdovsky.

to modern *E. serotinus* in both size and proportions. This fossil species was described from France and later found in several sites across Europe (Rosina and Sinitsa 2014). *Eptesicus kowalskii*, which occurred sympatrically and synchronously, has a similar morphology but is somewhat smaller (ibid.).

Other upper teeth we identified as belonging to *Myotis* spp. The only lower molar (Text-fig. 9c) does not show features which exclude its affiliation to *Myotis*. According to its size, it may represent the same species as the upper molar in Text-fig. 9e, found in the same locality (Gaverdovsky). Smaller *Myotis* teeth, Text-fig. 9a and 9b from Volchaya Balka, are similar in size, shape and morphology and likely belong to the same species. All three upper molars tentatively assigned to *Myotis* have relatively well developed hypocones and postprotocrysts, and lack paraconules. We did not find this combination in European myotines, but it occurs in some South-East Asian bats from *muricola* and *montivagus* species groups. The dimensions of the teeth (Text-fig. 9a, b) are L = 1.1 and 1.15, W = 1.4 and 1.5 mm, respectively. In size they are similar to smaller modern *Myotis*, in particular to *M. muricola*. They are morphologically specific in the more concave posterior edge. The cingulum is almost interrupted in this concavity while in all inspected modern *Myotis* there is no cingulum break or even a significant constriction in the same place. Specimens in Text-fig. 9e and, probably, Text-fig. 9c from Gaverdovsky belong to a definitely larger bat with the upper molar size, L = 1.6, W = 1.85, and the lower molar, L = 1.7, Wtrd = 1.0, Wtld = 1.15 mm. This is comparable to larger members of the *montivagus* species group (almost identical in size to cheek teeth of *M. indochinensis*), with which the specimen Text-fig. 9e has a certain morphological similarity. Of the European fossil mouse-eared bats, *M. podlesicensis* from the Early Pliocene of Poland is most similar in size (Ziegler 2003, Rosina and Kruskop 2011).

All the available teeth were found in deposits of a shallow water basin. It is known that *E. campanensis* was described from similar deposits (Bonis et al. 1999, Rosina and Sinitsa 2014). The foraging activity of many modern *Myotis* is also closely linked to water pools or directly with the water surface (e.g., Findley 1993). It is thus possible that a similar behavior could have been inherent in the fossil species. Judging from the absence of wear signs and the very sharply pronounced tips and crests on all five teeth, they belong to young individuals, which became independent only shortly before fossilisation. This may imply that both Late Miocene burials at Volchaya Balka and Gaverdovsky were situated near sites favourable for roosting and reproduction of insectivorous bats.

Order Eulipotyphla WADDELL, OKADA et HASEGAWA, 1999

The insectivoran assemblage is identical for both sites and is not very diverse. It includes *Talpa* sp., *Desmanella* sp., *Blarinella dubia* (BACHMAYER et WILSON, 1970), *Paenelimnoecus repenningi* (BACHMAYER et WILSON, 1970), and *Amblycoptus oligodon* KORMOS, 1926. The assemblage is dominated by remains of Talpidae. Most abundant are remains of *Talpa* sp., a medium-size mole smaller in dental and humeral structure than the modern species of the genus *Talpa*. Among soricids, common in both sites are remains of *Amblycoptus oligodon* with the typical basal features in dentition (Text-fig. 10) including the lack of cusp-like parastyle and moderately developed protocone in A1, well protruding parastyle and strong posterior emargination in P4, and poorly developed mesostyle in M1. Morphologically the Caucasian forms are very similar to forms from Hungarian karstic sites Polgárdy 2 and Tardosbanya (Kormos 1926, Meszaros 1998) attributed to late and middle Turolian. Recently records of *Amblycoptus* were reported from late

Vallesian/early Turolian sites in Moldova and Ukraine (Nesin and Nadachowski 2001, Rzebik-Kowalska and Lungu 2009, Rzebik-Kowalska and Nesin 2010, Sinitsa 2012). Smaller soricid from both sites clearly correspond with the morphology of *Paenelimnoecus repenningi*, with well developed entoconid and lack of entoconid crest in m1, condylar structure, etc.

Order Lagomorpha BRANDT, 1855

Lagomorph remains were unearthed only in the Gaverdovsky locality. Three forms were identified: *Prolagus* ex gr. *crusafonti*, *Ochotona* sp., and *Alilepus* sp., with *Ochotona* being the most abundant.

Family Prolagidae GUREEV, 1960

Genus *Prolagus* POMEL, 1853

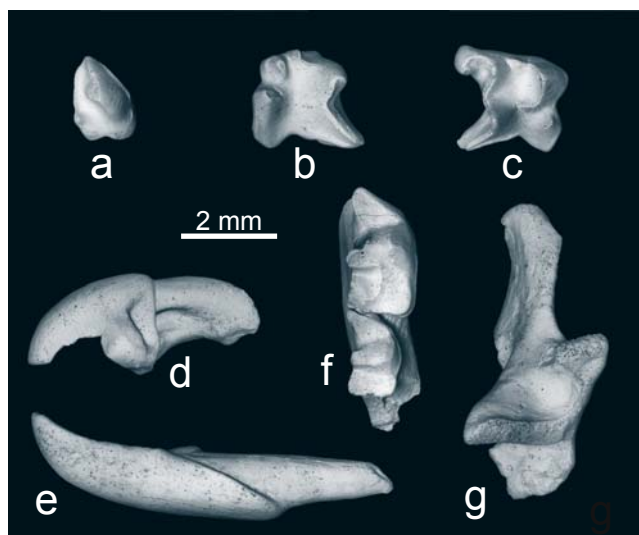
Prolagus ex gr. *crusafonti* LÓPEZ MARTÍNEZ, 1975

Text-fig. 11a

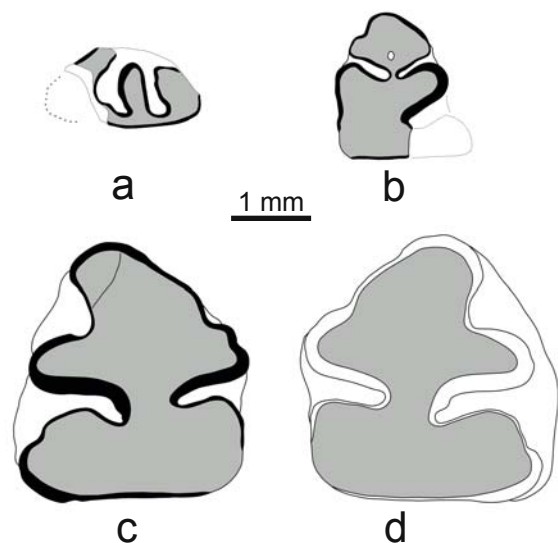
Material. 1 P2 (1.7 × 1.0 mm).

Description. A slightly damaged premolar showing a characteristically short hyperloph only slightly extending labially as is known for geologically older, Middle – Late Miocene species from Western Europe (López Martínez and Thaler 1975). Most later Miocene and Plio-Pleistocene species show a well developed hyperloph strongly extended labially.

Comments. This rare record from Gaverdovsky seems to be the easternmost European record. Other broadly synchronous records from Eastern Europe include *P. cf. crusafonti* or *Prolagus* sp. listed from a number of early Turolian faunas in southern Ukraine, e.g.:



Text-fig. 10. *Amblycoptus oligodon*, Late Miocene deposits, North Caucasus. a – A1, sin, GIN-1143-182; b – P4, sin, GIN-1143-183; c – M1, dex, GIN-1143-184; d – I sup, sin, labial view, GIN-1143-181; e – i inf, sin, labial view, GIN-1143-186; f – fragment of mandible with m1–m2, dex, occlusal view, GIN-1144-181; g – fragment of mandible, dex, condilar view, GIN-1143-185.



Text-fig. 11. Lagomorphs from Gaverdovsky, Late Miocene, North Caucasus. a – *Prolagus* ex gr. *crusafonti*, P2, sin, GIN-1144-500; b – *Ochotona* sp., p3, dex, GIN-1144-501; c, d – *Alilepus* sp., p3, sin, in occlusal (c) and root (d) views, GIN-1144-521.

Novoelizavetovka 3 (Nesin 2013), Popovo 3 (Rekovets and Pashkov 2009), Palievo (Sinita 2012). In most of these faunas *Prolagus* is a rare admixture to strongly dominant *Ochotona* species.

Family Ochotonidae THOMAS, 1897

Genus *Ochotona* LINK, 1795

Ochotona sp.

Text-fig. 11b

Material. 1 fragmental p3 (1.81 × ca. 1.7 mm), 12 lower and upper teeth.

Description. The single slightly damaged p3 shows the generalized morphology of the genus. Noteworthy is the antero-internal indentation of the anterocid filled with cement.

Comments. *Ochotona* species are common in late Vallesian and early Turolian faunas of Eastern Europe and Anatolia (Sen 2003, 2016, Čermák 2016). The form from Gaverdovsky is distinct in a stronger separation of anterocid by equally deep, obliquely inclined paraflexid and protoflexid.

Family Leporidae GRAY, 1821

Genus *Alilepus* DICE, 1931

Alilepus sp.

Text-fig. 11c, d

Material. 1 P2, 1 p3 (occlusal 3.2 × 3.1 mm, alveolar 3.3 × 3 mm).

Description. Small size leporid. Lower premolar shows a subtriangular trigonid with wavy anter-internal margin and a well developed antero-external reentrant.

Comments. Recent review of European *Alilepus* by Čermák et al. (2015) characterized early species of the genus *A. lasearevi* from the mid Turolian fauna of Taraklia (Moldova) and Egorovka 2 (Ukraine). Still older, scanty remains of leporids tentatively referred to *Alilepus* from faunas of Keinar (= Cainari) in Moldova and Palievo in Ukraine can be correlated with the late Vallesian/early Turolian. The burial of Keinar is associated with Khersonian deposits (Lungu 1980), Palievo may also be correlated with the Khersonian (Sinita 2012). Thus, *Alilepus* from the fauna of Gaverdovsky, which has a similar age, is among the oldest records of *Alilepus* in Europe.

Order Rodentia BOWDICH, 1821

The remains of rodents account for more than 60% of the small mammal associations in both sites. Both assemblages are co-dominated by *Parapodemus* (about 30%) and cricetines, *Pseudocricetus* in Gaverdovsky (ca. 30%) and *Neocricetodon* in Volchaya Balka (42%). Noteworthy are the significant proportions of dormice 18% (Gvd) and 13% (Vlb). Other similarities and distinctions are not significant due to small sample size in both assemblages.

Family Muridae ILLIGER, 1811

Genus *Parapodemus* SCHAUB, 1938

Comments. The common practice of attributing all *Apodemus*-like fossil murids regardless of the degree of development of t7 to the genus *Apodemus* may appear logical if it had not been for the deep split between the recent crown groups of *Apodemus* s. l. into several obviously genus-rank taxa. Most of European Late Miocene and Plio-Pleistocene apodemyines could belong to the genera *Sylvaemus* and *Karstomys*. Therefore we prefer to use *Parapodemus* for the earliest (late Vallesian and early Turolian) and morphologically primitive forms not yet manifesting affinities to any particular group of recent apodems and conforming to the diagnosis presented by de Bruijn et al. (1999).

Parapodemus lugdunensis SCHAUB, 1938

Pl. 8, Text-fig. 12

Material. 15 m1, 8 m2, 3 m3, 9 M1, 4 M2, 3 M3: Gaverdovsky; 9 m1, 6 m2, 5 m3, 8 M1, 2 M2, 1 M3: Volchaya Balka.

Description. **m1.** The molar is composed of the tma, and usually connected anteroconid and metaconid-protoconid chevrons, and the posterior hypoconid-entoconid chevron. The anterior cusp (tma) is relatively large, elevated to the level of the anterior chevron of the anteroconid, and always present. The cusps of the labial cingulum are well developed. There are from two to four (most often three) accessory cusps anteriorly of c1. In one specimen, an accessory cusp lingual to interanteroconid is present. The posterior heel (posteroconid) is expressed as an oval cusp. Two roots.

m2. The molar is composed of equally developed metaconid-protoconid and hypoconid-entoconid chevrons.

Table 4. Measurements of *Parapodemus lugdunensis* (in mm).

Tooth	Length					Width				
	n	min–max	mean	SD	CV	n	min–max	mean	SD	CV
m1	17	1.56–1.9	1.73	0.104	6.02	16	0.9–1.22	1.04	0.101	9.72
m2	13	1.2–1.45	1.32	0.079	5.98	14	0.86–1.22	1.08	0.103	9.58
m3	8	0.97–1.15	1.05	0.067	6.37	8	0.85–1.02	0.93	0.069	7.45
M1	12	1.7–2.07	1.86	0.105	5.66	16	1.05–1.25	1.15	0.053	4.65
M2	6	1.1–1.47	1.29	0.145	11.20	6	1.05–1.27	1.18	0.084	7.11
M3	4	0.85–1.1	0.96	0.120	12.52	4	0.82–1	0.89	0.079	8.84

In two specimens, the chevrons are connected by a low central ridge. The cingular cusps are variably developed. There are from 0 to 3 accessory cusps between c1 and the antero-labial cusp. Posterior heel (posteroconid) is expressed as an oval cusp, but may be reduced to a low posterior ridge closing the posterosinusid. In one specimen c1 is not expressed. Two roots.

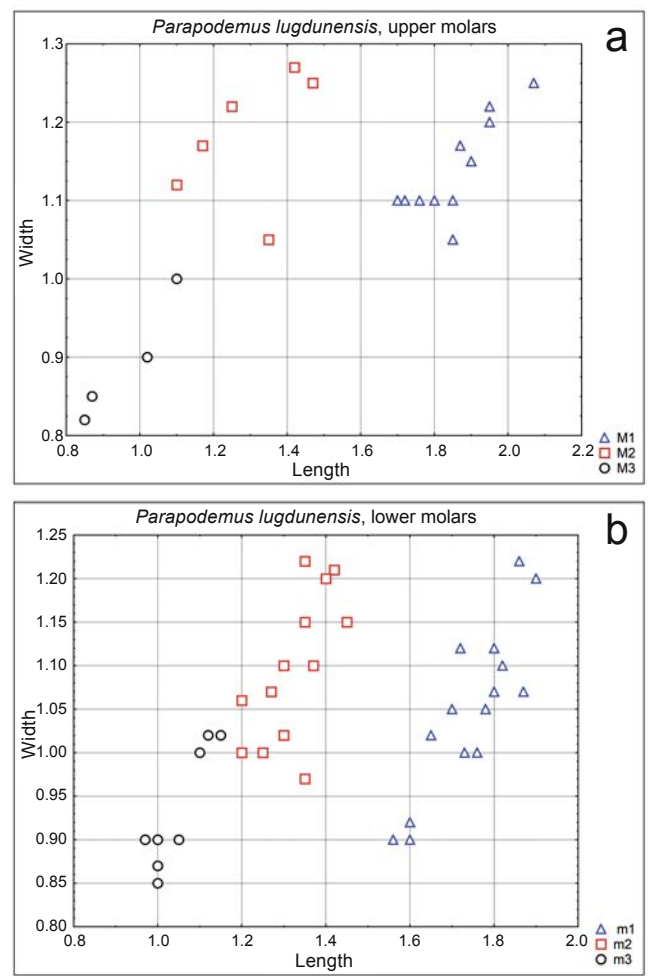
m3. The molar is composed of the metaconid-protoconid chevron, and the posterior cusp. They may be connected by a very low lingual ridge. The antero-labial cusp is weakly developed. No conspicuous accessory cusps are present except for a minuscule swelling on the labial side of the protoconid in one specimen. Two roots.

M1. The molar is composed of the anterior transverse chevron (t1-t2-t3) and posterior cusp ring with t4-t5-t6, t8-t9, and t12. The antero-lingual cusp (t1) is shifted more posteriorly relative to t2-t3 block. In some specimens t1 may connect to t2-t3 at a right angle (Pl. 8, Fig. 9) resembling the *Progonomys* condition. A very small t1bis is present in 2 out of 13 complete specimens. A prestile at the base of t2 is present in one molar (Pl. 8, Fig. 8). There is a posterior ridge in t3 (n = 8 out of 16). The t4 and t8 connection (Pl. 8, Figs 8–11) ranges from a direct contact without any swellings (n = 6/16), an elevated ridge sometimes turning with wear into a small swelling (n = 8/16), or a small cusp (t7) on the ridge between t4 and t8 (2/16). Cusps t6 and t9 are always connected. The postero-labial cusp t12 is well developed and may be expressed as a large circular cusp (Pl. 8, Figs 9, 10). Three roots. The lingual root may be flattened and show weak signs (longitudinal groove) of separation into two roots.

M2. The molar structure is similar to that of M1 except for the absence of t2. The cusp t1 is oval in shape with the long axis running somewhat postero-lingually. In one specimen (n = 1/5) the t1 is subdivided into two cusps (Pl. 8, Fig. 13). The cusp t3 is smaller than t1. In one specimen it is strongly reduced. The connection between t4 and t8 can appear as a high ridge (n = 3/5), or as a small t7 (2/5). Three roots (n = 3). In one specimen the lingual root is strongly flattened and slightly bifid at the apex.

M3. The molar is subtriangular. In the smaller (L = 0.87) of the two moderately used teeth, t1 is drop-shaped with a horizontally oriented long axis, t3 is missing, t4-t5-t6 broadly fused, t8 communicates with t6 and with a ridge-like connection with t4 (Pl. 8, Fig. 15). The larger molar (L = 1.1) has a much more complex structure with cusplet-like t3, large crescent obliquely oriented t1, discernable t9, low ridge-like connection between t4 and t8, and even a notch-like t12 on the posterolabial side of t8 (Pl. 8, Fig. 16). Three roots.

Comments. The Caucasian form shows slightly larger size values in the upper part of the observed variation range and has a higher percentage of weak t7 formation in M1 (but less than 50%) than in *P. lugdunensis* from the late Vallesian and early Turolian sites of Central Europe (Schernham, Kohfidisch, Eichkogel) and Iberia (Los Aguanaces 3, Crevillente 2 and 4B) (Daxner-Höck 1977, van de Weerd 1976, van Dam 1997, Martín Suárez and Freudenthal 1993, Wöger 2011, Daxner-Höck and Höck 2015) but lower than in the Anatolian site of Düzyayla (de Bruijn et al. 1999) attributed to the middle Turolian. This can be taken as an indication of a late early Turolian age for



Text-fig. 12. Scatter diagrams of upper (a) and lower (b) molars of *Parapodemus lugdunensis*, Gaverdovsky and Volchaya Balka, Late Miocene, North Caucasus.

the Caucasian form. Nesin (2011) described a small species *Apodemus alae* diagnosed on the presence of t7 in less than 50% of specimens from the early and middle Turolian faunas in south Ukraine. The large sample from the type locality, the middle Turolian fauna of Cherevichnoe 3, shows t7 in approximately 20–30% of M1–2 (Nesin 2013). This species is likely to be a younger synonym of *P. lugdunensis*.

The size distribution is quite continuous in most molar types (Text-fig. 12), except for M3. In this latter case the sample size (n = 4) is very low therefore impeding any reliable conclusions. The very different morphology of two moderately worn M3 may indicate a considerable morphotype variation within a single species (as illustrated for *P. lugdunensis* from Kohfidisch by Wöger 2011) or alternatively, a co-occurrence of a smaller and larger species. This hypothetical large form would then be represented by only a few specimens. A possible admixture of a larger form may also be signalled by somewhat high CV values for some molar types (Tab. 4). At the same time the largest M1 (Pl. 8, Fig. 8) shows outlines similar to that of smaller specimens (Pl. 8, Figs 9–12) and does not show any variation towards larger W/L values in M1 known for *P. barbarae*, the larger species commonly co-occurring with *P. lugdunensis* in the middle Turolian of Spain (Los Mansuetos) and Ukraine

(Cherevichnoe 3). Only a larger sample can shed light on this issue.

Family Cricetidae FISCHER, 1817

Genus *Pseudocricetus* TOPACHEVSKY et SCORIK, 1992

Pseudocricetus cf. *antiquus* TOPACHEVSKY et SCORIK, 1992 Pl. 9, Figs 1–6

Material. 5 m1, 9 m2, 4 m3, 3 M1, 7 M2, 5 M3: Gaverdovsky.

Description. A smaller hamster (Tab. 5) with a typical cricetine dental pattern with strongly reduced

short sloping ridge (Pl. 9, Fig. 3). The posterosinusid forms a fossetid after moderate wear. Two roots.

M1. The anterocon is significantly divided. Equally developed lingual and labial anterolophules connect the anterocon with protocon-paracone region and delimit a small anterocon fossette. Deep anterior and posterior basins are delimited by high proto- and metalophs. Mesolophs are not present. Posteroloph connects to metacone posteriorly, posterior metalophule is not present ($n = 3$). Two of three available molars show four roots with distinctly separated lingual roots.

M2. The anteroloph is well developed, its lingual branch delimits a moderately developed protosinus. As in M1, high

Table 5. Measurements of *Pseudocricetus* cf. *antiquus* (in mm).

Tooth	Length					Width				
	n	min–max	mean	SD	CV	n	min–max	mean	SD	CV
m1	3	1.85–2.03	1.97	0.101	5.14	4	1.01–1.22	1.11	0.095	8.61
m2	9	1.65–1.77	1.71	0.044	2.55	9	1.27–1.4	1.31	0.043	3.25
m3	4	1.6–1.8	1.67	0.087	5.17	4	1.18–1.3	1.24	0.064	5.14
M1	3	2.00–2.26	2.16	0.142	6.57	3	1.4–1.45	1.42	0.025	1.77
M2	7	1.52–1.75	1.66	0.071	4.33	7	1.2–1.45	1.34	0.093	6.92
M3	5	1.27–1.42	1.31	0.060	4.62	5	1.1–1.2	1.14	0.040	3.55

additional elements. Lower and upper incisors are oval in transverse section with a marked smoothed ledge on the anterior surface. The enamel does not extend to the medial side of the incisors.

m1. Cusps of the anteroconid are well defined and separated by anterior and posterior valleys ($n = 3$). An anterostylid is present in one specimen (Pl. 9, Fig. 1). The anteroconid connects to the protocone-metacone pair by an anterolophulid with its two almost completely fused branches enclosing a small anterofossetid. Mesolophid is strongly reduced and expressed as a short sloping ridge reaching at maximum the mid-depth of mesosinusid. Two roots.

m2. Labial anterolophid is well developed, running to the base of protoconid but never closing the protosinusid. The lingual anterolophid is weakly developed, not forming an enamel-dentine ridge with wear, and in most cases appearing as a shallow basin on the anterointernal side of the metaconid. Mesolophids are absent ($n = 4$), or present only as a short swelling ($n = 4$) sometimes with a sloping ridge nearly reaching mid-depth of the mesosinusid. A weakly developed ectomesolophid ($n = 1$) and ectostylid ($n = 2$) may be present (Pl. 9, Fig. 2). A distinct posterior notch between hypoconid and posteroloph is present in all specimens. The posterosinusid remains open regardless of wear. Two roots. The posterior root is strongly built, wide and flattened with a concave anterior face. The anterior root is much thinner, with an oval cross-section.

m3. Anterolophid expression as in m2, the lingual branch is present but weakly developed, never forming a lophid with wear. The mesolophid is strongly reduced but always expressed as a distinct bulge on the ectolophid or even a

proto- and metalophs close anterior and posterior basins with early wear. Posterior metalophule is present in two specimens. Four roots.

M3. The labial anteroloph is strong and forms a ridge after wear. The lingual anteroloph is weakly expressed. Two fossae are formed after slight wear, similar to M1–2. The mesoloph is usually significantly reduced. It is present ($n = 4$) as a short, anteriorly directed bulge on the anterior metalophule or as a long ridge reaching the paracone ($n = 1$). The posterior basin may be crossed by a tiny posterior metalophule ($n = 1$; Pl. 9, Fig. 6). Three roots.

Comments. The middle and late Turolian cricetines with a simple dental pattern in Eastern Europe are traditionally attributed to the genus *Pseudocricetus* TOPACHEVSKY et SCORIK, 1992. The sequence of *P. antiquus*–*P. orienteuropaeus* (MN 12)–*P. kormosi* (MN 13) was shown to manifest a reduction of mesolophs/mesolophids and size increase. The early Turolian faunas from the northern Black Sea region mostly contain abundant *Neocricetodon* and rare *Stylocricetus* (Topachevsky and Scorik 1992, Nesin 2013). In all hitherto known faunas in the region the cricetines form monodominant assemblages with either *Pseudocricetus* or *Neocricetodon*. Sinitsa (2010) showed that presumably chronoclineal characters, such as a degree of mesoloph/mesolophid reduction, may be variable and mosaic in different samples of *Pseudocricetus* from early and middle Turolian. If related to *Pseudocricetus*, the early Turolian cricetine from North Caucasus may represent one of its geologically oldest populations or belong to a basal radiation of this group of hamsters. The small sample size hampers the clear understanding of the variability

in the Caucasian form. On the other hand, its comparison with early – middle Turolian forms from Ukraine shows obviously basal characters in the Caucasian form. These include well expressed mesolophids in m1 in half of the specimens (Pl. 9, Fig. 1), occasional ectomesolophid in m2 (Pl. 9, Fig. 2) and, in a reduced form, in m1, weakly expressed lingual branches of the anterolophid in m2 – m3, and labial branches of anteroloph in M2 – M3, occasional presence of a posterior ridge of the metacon (posterior metalophule) in M1 – M2. The length of lower m3 equals or exceeds that of m2, which is typical for *Pseudocricetus*. Apparent increased hypsodonty of some ontogenetically younger molars, especially upper ones, may represent a regional specific feature. More material is needed to refine the taxonomic placement of the described sample of *P. cf. antiquus*.

Genus *Neocricetodon* SCHAUB, 1934
= *Kowalskia* FAHLBUSCH, 1969

Neocricetodon cf. progressus
(TOPACHEVSKY et SCORIK, 1992)
 Pl. 9, Figs 7–13

Material. 4 m1, 7 m2, 6 m3, 11 M1, 9 M2, 6 M3: Volchaya Balka; 2 m1, 1 M2: Gaverdovsky.

enclosing a shallow posterosinusid. A notch between the posterolophid and hypoconid is well expressed.

m3. The lingual anteroloph is small but well expressed, turning into a tiny ridge with wear. The short mesolophid reaches mid-depth of the mesosinusid. The crescentic posteroloph connects to a stylid-like metaconid and closes a deep posterosinus.

M1. The anterocone cusps are separated by a shallow anterior depression and a deeper groove or a rounded basin of the anterosinus distally (Pl. 9, Figs 12–13). The well developed lingual anterolophule may be a single connection between the anterocon and the protocone-paracone region (n = 5), or may be accompanied by a much weaker labial anterolophule connecting to the labial spur of the anterolophule (anteromesoloph) (n = 3), or to the distal part of the lingual anterolophule (n = 1). An anteromesoloph is commonly present (n = 6), being long (n = 2), not reaching labial cingulum (n = 4), or absent (n = 1). The mesoloph extends for 2/3 of the mesosinus depth (n = 9) but does not reach the mesostyle. The posterior metaloph often closes a small posterosinus (n = 7). Most molars show a three rooted condition with a flattened but integer lingual root (n = 8). In one specimen the lingual roots are subdivided into two closely spaced roots.

M2. A well developed lingual anteroloph is a normal condition. A mesoloph is present in all specimens (n = 6). It

Table 6. Measurements of *Neocricetodon cf. progressus* (in mm).

Tooth	Length					Width				
	n	min–max	mean	SD	CV	n	min–max	mean	SD	CV
m1	5	1.81–2.05	1.91	0.096	5.2	5	1.00–1.20	1.14	0.084	7.36
m2	6	1.56–1.72	1.65	0.051	3.10	7	1.26–1.45	1.34	0.058	4.40
m3	5	1.42–1.67	1.55	0.095	6.15	6	0.95–1.27	1.19	0.121	10.13
M1	9	2.00–2.21	2.11	0.076	3.59	11	1.3–1.47	1.39	0.063	4.53
M2	9	1.45–1.65	1.56	0.060	3.82	9	1.25–1.5	1.40	0.084	5.99
M3	6	1.27–1.45	1.36	0.069	5.07	6	1.1–1.4	1.3	0.114	8.77

Description. **m1.** Anteroconid cusps are closely spaced. The anterior surface is undivided and rounded (Pl. 9, Figs 7–9). Posteriorly anterocon cusps are weakly subdivided by a shallow groove. Anterolophulid is represented by its labial only (n = 2) or both branches (n = 3) delimiting a very small anterofossetid basin. The mesolophid is long and well developed (n = 4) or short not reaching mid-depth of the mesosinusid. A small bulge representing the mesostylid is present in most specimens. Ectomesolophid (n = 1) and ectostylid (n = 3) are occasionally present. The posterolophid connects to the very base of the entoconid leaving the sinusid open till latest wear stages. Two roots.

m2. The lingual anteroloph is very small, expressed as a shallow basin on the antero-lingual side of the metaconid, never becoming a ridge regardless of wear stages. The mesolophid is long (n = 6) but may be strongly obliterated in advanced wear stages (n = 2; Pl. 9, Fig. 10), or reaching mid-depth of the mesosinusid (n = 1). Long mesolophids usually connect with expanded mesostylid. The posterolophid usually connects to the posterior side of the entoconid

may be long (n = 2), medium length and ending very shortly before the mesostylar margin (n = 5) as in M1, or short, reaching the mid-depth of mesosinus. A posterior metaloph is present in all specimens in the early or medium wear stages (n = 7) enclosing a small posterosinus. Four roots.

M3. A lingual anteroloph is present becoming a small ridge with moderate wear (Pl. 9, Fig. 13). A reduced mesoloph is present in most specimens as a laterally or anteriorly directed short bulge or ridge on the metaconal ridge. Three roots.

See Table 6 for measurements.

Comments. Late Miocene faunas of south Eastern Europe show a transition from *Neocricetodon* dominated faunas in the late Vallesian and early Turolian to *Pseudocricetus* dominated faunas in the middle – late Turolian (Topachevsky and Scorik 1992, Sinita 2012). This shift probably reflects a transformation from more closed to more open landscapes. The two synchronous faunas from the North Caucasus, alternatively dominated by one of the two genera,

support a strict biotopic separation of these two lineages of hamsters. The morphological appearance of the Caucasian *Neocricetodon* represents a combination of characters of *N. moldavicus* (LUNGU, 1981) and *N. progressus*. With the former species recently revised by Sinita and Delinschi (2016) the described form shares a weak differentiation of anteroconid in m1, frequencies and manifestation degree of mesolophs, predominance of three-rooted M1. On the other hand, it resembles *N. progressus* in the comparable development of the anteromesoloph in M1 and mesolophs in upper molars, predominant development of a lingual anterolophule in M1, and the moderate development of lingual anterolophids in m2 – m3 and lingual anterolophs in the upper molars. It, however, appears more basal than both the type population from Novoelizavetovka 2 and the somewhat less derived form from Palievo (Sinita 2012). From most Late Miocene central European species the described form differs by the less developed elements of dental complexity. Specifically, from the Vallesian Austrian species (Daxner-Höck and Höck 2015) it differs in the relatively short m3 and M3 (from *Kowalskia* sp. A and B), in the three-rooted M1 (from *Kowalskia* sp. C), and in double anteroconid (from *Kowalskia* sp. B and C). From the early Turolian *N. falhbuschi* (BACHMAYER et WILSON, 1970) it differs in smaller size, three-rooted M1, and relatively shorter m3/M3. From otherwise similar *N. skofleki* (KORDOS, 1987) (Daxner-Höck 1972, Kordos 1987, Freudenthal and Kordos 1989) it also differs in having a double-cusped anteroconid. We tentatively assign our form to *N. cf. progressus*.

Steklov (1966) studied the same sections near Maikop and found a single cricetine molar from the sandy beds with abundant shells of terrestrial snails dominated by *Pomatias*. We studied this molar (Steklov's specimen 3044) in the collections of the Zoological Institute in Saint-Petersburg. The M1 (2.16 × 1.39) is identical in morphology (strong lingual anterolophule, long anteromesoloph, medium long mesoloph not reaching the mesostyle, posteroloph with defined posterosinus, three roots) to *Neocricetodon* from the Volchaya Balka sample.

Genus *Collimys* DAXNER-HÖCK, 1972

Collimys caucasicus TESAKOV, sp. nov.

Pl. 10, Text-fig. 13f, g

Holotype. Right m1, GIN-1143-001, 1.85 × 1.17 mm (Pl. 10, Fig. 1), housed in the collection of Geological Institute of the Russian Academy of Sciences.

Type locality. Volchaya Balka, bed 7, Late Miocene, North Caucasus, Russia.

Etymology. After the geographic provenance of the new taxon.

Diagnosis. Hypsodont *Collimys* preserving short mesolophs/mesolophids.

Differential diagnosis. *C. caucasicus* sp. nov. differs from most congeneric species in higher hypsodonty (Text-fig. 13) and strong reduction of mesoloph/mesolophids. From *Pseudocollimys steiningeri* DAXNER-HÖCK, 2004 it differs in larger size (Tab. 7), lower hypsodonty, and less reduced mesolophs/mesolophids.

Additional material. 1 m1, 1 M3: Volchaya Balka; 1 m1, 1 m2, 1 M1, 1 M2, 2 M3: Gaverdovsky.

Description. The hypsodont cricetine with alternating dental prisms, deep reentrant synclines, flat occlusal surface after a slight wear, and thick enamel wall. Molars with two roots in the lower jaw and three roots in the upper dentition.

m1. The molar is composed of a posterior loop integrating a hypoconid and broad posterolophid, alternating entoconid, protoconid, and metaconid, and anteroconid. Tips of lingual anticlines are squared in contrast with the more rounded labial ones. The mesolophid is reduced in size (Pl. 10, Figs 1–2) and becomes an indistinct sloping spine reaching the side of the molar. An ectostylid is present in two of the three specimens, in one case it is doubled (Pl. 10, Fig. 3). A rounded anteroconid is broadly fused with the metaconid. In the less worn specimen it is slightly bifid anteriorly (Pl. 10, Fig. 1). The rounded lingual side contrasts with the labial which is expanded by a well-developed anterolophid. The anteroconid of the type specimen bears two strongly obliterated enamel islets indicating its initial complex structure of three lobes subsequently fused by wear.

m2. The only available molar is heavily worn (Pl. 10, Fig. 4).

M1. The molar is composed of alternating loops of anterocone, protocone, paracone, hypocone, and metacone. The mesoloph is well developed but does not reach the labial side of the molar; at the current stage of wear (Pl. 10, Fig. 5) it is fused with the metacone thus closing a fossette. The anteromesoloph is reduced in length and fused with the anterocone.

Table 7. Measurements of *Collimys caucasicus* sp. nov. (in mm).

Specimen	Coll. number	Length	Width
m1, dex, type	1143-001	1.85	1.17
m1, sin	1143-002	1.87	1.17
m1, sin	1144-001	1.95	–
m2, sin	1144-002	1.45	1.29
M1, sin	1144-003	1.96	1.35
M2, dex	1144-004	1.59	1.31
M3, dex	1143-003	1.10	1.13
M3, sin	1144-005	1.13	1.02
M3, sin	1144-006	1.14	1.07

M2. The molar is composed of four main cusps, and a moderately developed anterocone on a long labial anteroloph (Pl. 10, Fig. 6). The mesoloph is short, with wear its tip fuses with the anterior face of the metacone enclosing a fossette. The posterior metalophule is prominent and delimits a shallow posterosinus.

M3. The anterior part of the molar is composed of a large protocone and labial anteroloph. The large paracone connects to the protocone after considerable wear (Pl. 10, Fig. 7). The anterosinus tends to be closed forming a fossette by the anterior lophule (protolophule I) (Pl. 10, Figs 8–9). The mesoloph is long and reaches the labial margin of the crown. The paracone spur may reach the mesoloph and close a fossette in the anterior part of the mesosinus. With only slight wear the mesoloph, hypocone, posteroloph and a small, cusplet-like metacone delimit a fossette in the posterior part of the mesosinus. When in an unworn condition, the posterosinus contains a minute basin (Pl. 10, Fig. 7) which becomes a very small fossette when worn (Pl. 10, Fig. 9).

Comparison. In comparison with late Middle Miocene (“MN 7”) forms from south Germany, *C. transversus* HEISSIG, 1995 from Steinheim and *C. gudrunae* RUMMEL et PRIETO, 2009b from Petersbuch 31, the Caucasian *Collimys* is significantly more hypsodont, and shows a large reduction of mesolophs(ids) and ectomesolohids in m1, and a nearly complete reduction of anteromesoloph in M1, and

lacks a lingual anteroloph in M2. It is also larger than *C. transversus*.

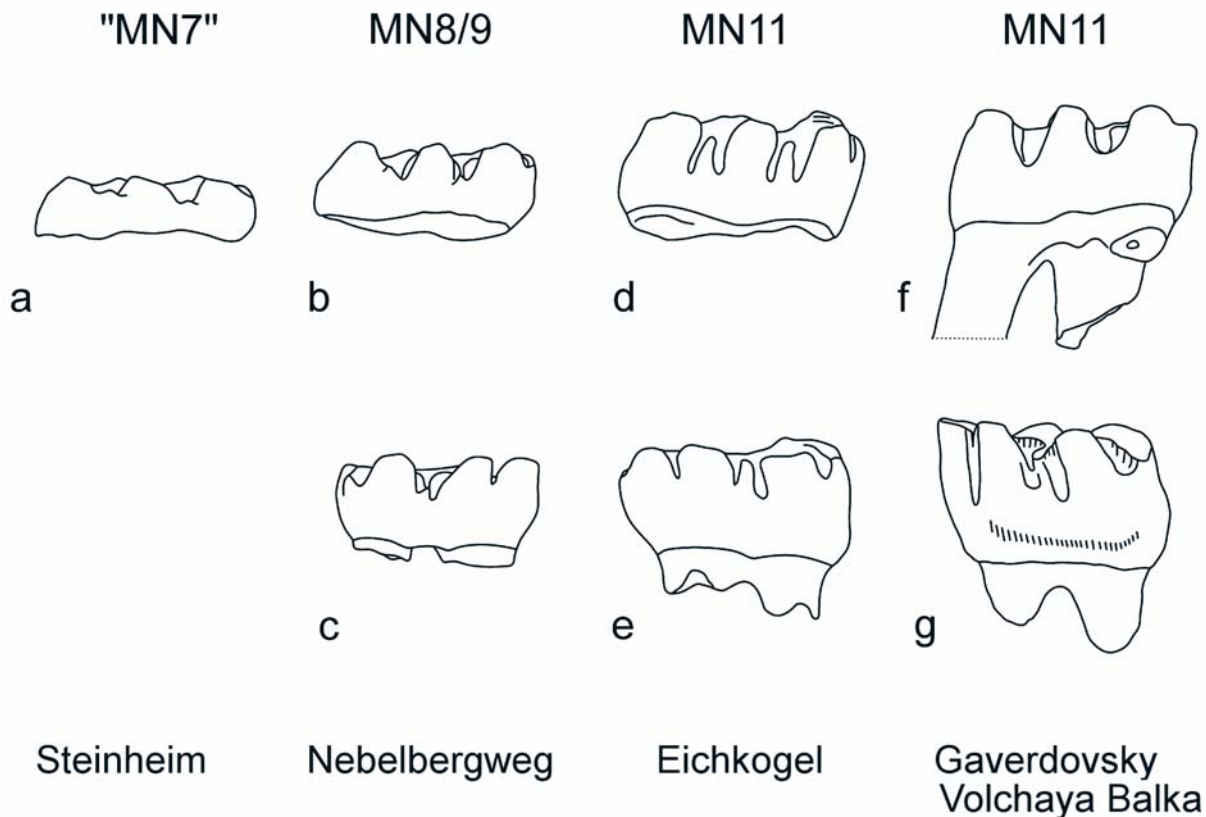
In comparison with the group of forms from faunas of the Astaracian-Vallesian transition in south Germany, Switzerland, and Hungary (“MN 8”/MN 9), *C. hiri* PRIETO et RUMMEL, 2009 from Hammerschmiede, *C. longidens* KÄLIN et ENGESSER, 2001 from Nebelbergweg, and *C. dobosi* HIR, 2005 from Felsőtárkány 3/2, *C. caucasicus* sp. nov. differs in higher hypsodonta, a single anterolophulid in m1, stronger reduction of mesolophs(ids) and other elements of dental complexity.

From *C. primus* DAXNER-HÖCK, 1972 from Kohfidisch and Eichkogel (MN 11) and Richardhof-Wald (MN 10) it differs in its slightly higher hypsodonta (Text-fig. 13), a flatter occlusal surface, and strong reduction of mesolophs(ids) and anteromesolophs in M1.

From *C. cf. primus* from Dorn-Dürkheim (Franzen and Storch 1975) it differs in having a less reduced mesolophid in m1, and mesoloph in M2. Otherwise, this form is the best morphological match for the described species.

From *Colloides xiaomingi* from Vallesian – early Turolian correlated faunas of northern China (Qiu and Li 2016) it differs in smaller and less divided anteroconids in m1, and less reduced mesolophs (-lophids).

Comments. After the first description of the peculiar hypsodont hamsters of the genus *Collimys* in Late Miocene deposits of the Vienna basin (Daxner-Höck 1972), the group



Text-fig. 13. Hypsodonta in different *Collimys* species. a, b, d, f – M1, labial view; c, e, g – m1, lingual view; a – *C. transversus*, Steinheim, late Middle Miocene (“MN 7”); b, c – *C. longidens*, Nebelbergweg, Middle-Late Miocene transition, MN 8/9; d, e – *C. primus*, Eichkogel, Late Miocene, MN 11; f, g – *C. caucasicus* sp. nov., Gaverdovsky (f) and Volchaya Balka (g, holotype), Late Miocene, MN 11. a–e – modified after Kälin and Engesser (2001).

was recognised in multiple late Middle Miocene (Heissig 1995, Kálin and Engesser 2001, Hír 2005, Prieto and Rummel 2009a, b) and Late Miocene (Franzen and Storch 1975) localities in central Europe. Probably descending from *Democricetodon* (Heissig 1995), the group splits into separate phyletic lineages all demonstrating trends towards higher hypsodonty and larger dimensions, and different degrees of reduction in elements of molar complexity. The largest so far known sample of *Collimys* (*C. dobosi*) described by Hír (2005) from latest Middle Miocene of Hungary showed a considerable amount of morphological variation in dental characters thus emphasizing the risk of coining taxa based on minor differences in small samples. The description of *Pseudocollimys* from the late Vallesian locality of Schernham (Daxner-Höck 2004a) showed that some of these lineages could develop a notable hypsodonty and almost completely reduce the mesolophids (-ids) and other smaller elements. The rank of genus for *Pseudocollimys* is questioned here. Two other records referable to *Pseudocollimys* originated from the MN 10 correlated locality of Suchomasty in the Czech Republic (labeled as “Cricetidae aff. *Pseudomeriones* gen. et sp. indet.” in Fejfar 1990: fig. 14: 1–3) and the MN 11 locality of Dorn-Dürkheim in Germany (Franzen and Storch 1975). One specimen of an incomplete M1 from the latter site (Franzen and Storch 1975: taf. 5, fig. 41) more closely corresponds with the morphology of *Collimys primus*. This broadly synchronous form, the type species *Collimys primus* from late Vallesian to early Turolian (MN 10 – MN 11) of Austria, shows a much less derived morphology (Daxner-Höck 1972, Daxner-Höck and Höck 2015) and apparently represents a Late Miocene survivor of a distinct and more conservative lineage/species group, most likely that of *C. hiri*-*C. dobosi* – (MN 9) of Prieto and Rummel (2009b). In addition to the original type series of *Collimys primus* from Eichkolgel, Daxner-Höck and Höck (2015) illustrated supplementary material on *C. primus* (M1, M2) from Kohfidisch (MN 11), and m2 from Richardhof-Wald (“MN 10a”). The latter locality is believed to be older than the latest Vallesian fauna of Schernham (“MN 10b”; Daxner-Höck et al. 2016) that yielded *Pseudocollimys*. These data indicate a co-existence of two collimyine lineages in the late Vallesian of Austria. This co-occurrence could possibly have continued into the early Turolian as likely indicated by the material from Dorn-Dürkheim.

The Caucasian form shows a notable similarity to *Pseudocollimys steiningeri*, but although being slightly larger, it demonstrates less advanced states of most dental characters. The striking difference is in the well developed mesolophids/mesolophids resembling a condition of less hypsodont *Collimys* species. Thus being dentally intermediate between the two Late Miocene collimyines from Central Europe, the Caucasian form is most likely the youngest of them. This mosaic of different stages of dental complexity and hypsodonty not forming a chronological sequence probably indicates a separate position of *C. caucasicus* sp. nov., as an advanced stage of a distinct lineage of collimyines in the Caucasus, or a direct successor of *C. primus*. It can be hypothesized that *Pseudocollimys steiningeri* with a reduced depth of anterolingual synclines in M1 may be derived from brachyodont *Collimys* showing this character, such as *C. transversus* from Petersburg 26 (Prieto

and Rummel 2009b: fig. 2d). The limited material hampers evaluation of this character, moreover *C. transversus* from the type locality of Steinheim does not show any reduction in the depth of this syncline (Heissig 1995: taf. I, figs 5, 7, Kálin and Engesser 2001: fig. 36d).

The recent find of collimyine hamsters in Late Miocene faunas of northern China (Qiu and Li 2016) reveals a previously unrecognised vast distribution area of this group in Eurasia. The Caucasian form shows a similarity to *Colloides xiaomingi* from the Vallesian-early Turolian correlated faunas of northern China (Qiu and Li 2016) in size and hypsodonty level and overall dental structure of a medium-hypsodont collimyine. It is, however, markedly different in the less reduced mesolophids (-lophs) and smaller anteroconid in m1. The teeth described as M3 in Chinese form may actually represent M2. The genus rank status of the Chinese form is due to a discussion. A series of forms with a gradually increasing hypsodonty may suggest the attribution of *Colloides xiaomingi* to the genus *Collimys*.

The hypsodonty and alternating dental elements with transverse enamel ridges indicate propalinal mastication and probably mark an early stage of obligate herbivory in at least advanced forms of *Collimys*. The similar biomechanical constraints on dentition with propalinal movements in muroid rodents form vole-like prismatic molars in many independent lineages in the Middle – Late Miocene (Fejfar et al. 2011).

Family Gliridae THOMAS, 1897

Pl. 11, Figs 10–18

Comments. Glirids are represented by three forms: *Ramys* vel *Vasseuromys*, *Muscardinus*, and *Paraglrulus schultzi*. The glirid association is indicative of wooded landscape. Its composition is peculiar for Eastern Europe combining the widespread European *Muscardinus pliocaenicus* (Pl. 11, Figs 17–18) typical for early Turolian of Central Europe and *Paraglrulus*, the common European dormouse of Middle and early Late Miocene. In particular, *P. schultzi* with its specific extra ridges (Pl. 11, Figs 10–13) has been so far known from the late Vallesian site of Schernham in Austria (Daxner-Höck and Höck 2009), and possibly in the coeval Suchomasty locality in the Czech Republic (Fejfar 1990). The Caucasian record of *Paraglrulus* is the first evidence that this genus survived into the early Turolian. *Ramys/Vasseuromys* is dominant among dormice in Gaverdovsky and sub-dominant in Volchaya Balka. This form resembles early Vallesian *Ramys* from Central and Eastern Europe but also shows a variability of the dental pattern reminiscent of *Vasseuromys* (Pl. 11, Figs 14–16).

Family Castoridae HEMPRICH, 1822

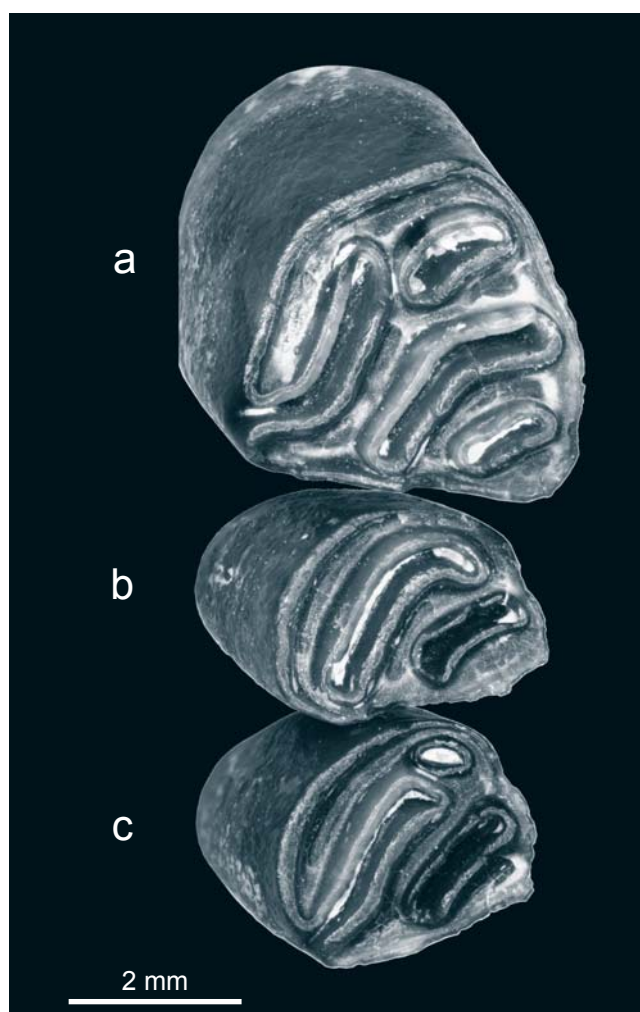
Genus *Trogotherium* FISCHER, 1809

Subgenus *Euroxenomys* RADULESCO et SAMSON, 1973

Trogotherium minutum (VON MEYER, 1838)

Text-fig. 14

Comments. The maxillar fragment with P4 – M2 comes from sandstones of the bed 4 in the Volchaya Balka section. In size (P4: 4.25 × 4.25; M1: 3.05 × 3.0; M2: 2.85 × 3.2) and morphology this form is very close to numerous



Text-fig. 14. *Trogontherium (Euroxenomys) minutum*. Volchaya Balka. Late Miocene deposits, North Caucasus. a – P4, b – M1, c – M2, GIN-1143-131, occlusal view.

records of small trogontheriine beavers from the Middle and Late Miocene of Europe.

Family Sciuridae FISCHER, 1817

Pl. 11, Figs 19–21

Comments. There were very few squirrels in the studied material. All available specimens represent pteromyines. They originated from the Volchaya Balka site. *Neopetes* cf. *hoeckarum* shows typical morphology with generally smooth occlusal surface of molars, smooth, oblique and subparallel proto- and metalophs in the upper molars, well developed entoconid and mesostylid in lower molars (Pl. 11, Figs 19–20). This is the first record of this medium size flying squirrel in the Caucasus. In central Europe, this form occurs from Early to Late Miocene and shows a notable morphological stability (Daxner-Höck 2004b, Daxner-Höck and Höck 2015). M1–2: 1.93×2.04 ; m1: 2.27×2.12 .

A fragment of heavily worn upper molar (P4 or M1–2) of a large ($W > 3.6$ mm) sciurid with preserved rugged protocone and part of the central basin and metaloph (Pl. 11, Fig. 21) is tentatively assigned to *?Miopetaurista* sp. This large flying squirrel was reported from a number of Vallesian and early

Turolian sites in Central Europe (Daxner-Höck 2004b), and in southern Ukraine (Nesin 2013). In the North Caucasus *Miopetaurista* was previously listed from a poorly known Early Pleistocene (?Gelasian) site Zhukovskoe (Derevyanko et al. 2010).

Family Eomyidae DEPÉRET et DOUXAMI, 1902

Pl. 8, Figs 5–9

Comments. The first record of eomyids in the Late Miocene of the Caucasus is only the third find of this family in Russia. Previously known records originated from the Early and Late Pliocene levels in the Obukhovka locality in the Sea of Azov area (*Estramomys* sp.; Topachevsky et al. 1988) and the late Early Miocene Tagay fauna from the Baikal area (*Keramidomys* sp. and *Leptodontomys* sp.; Daxner-Höck et al. 2013). The few records of eomyids from the Late Miocene of the northern Black Sea area date back to Vallesian of Ukraine and Moldova and are reported to include *Keramidomys* and *Leptodontomys* sp. from the fauna of Gritsev (Nesin 2013) and *Keramidomys* sp. and *Eomyops* aff. *catalunicum* (HARTENBERGER, 1967) from Buzhor (Lungu and Rzebik-Kowalska 2011), plus undetermined eomyids from the late Turolian fauna of Andreevka in Ukraine (Topachevsky 1971). The *Keramidomys* sp. from the Caucasus fits the characteristic morphology of the genus (Pl. 8, Figs 5–9) but looks quite simplified (reduction of mesolophids and mesolophs) even in comparison with the late Turolian form from Maramena (de Bruijn 1995). No affinities with *Estramomys*, e.g., no trends to the formation of the sigmoid ridge pattern in upper molars, are obvious. More material is needed for a clear definition of the systematic position of this form.

Superfamily Dipodoidea FISCHER, 1817

Pl. 11, Figs 1–4

Comments. Two forms are represented in the fauna of Gaverdovsky: the zapodid *Eozapus intermedius* ($n = 7$) and the smynthid *Sicista* sp. ($n = 1$). *Eozapus* is a common member of European faunas of late Vallesian and Turolian. The Caucasian sample of *E. intermedius* closely corresponds to the morphology and size of the species (Pl. 11, Fig. 2–4).

This first record of *Sicista* in Miocene of Europe is remarkable. The earliest true *Sicista*, *S. primus* is recorded in Eurasia as early as the Early Miocene of North China (Kimura 2011). Scanty late Early and Middle Miocene record of *Sicista* in Asia has recently become known (Qiu and Li 2016). It thus bridges the gap between the Early Miocene finds and the rich records from Late Miocene (Turolian) of Kazakhstan (Savinov 1970) and Early Pliocene of North China (Qiu and Storch 2000). The Caucasian record shows that birch mice were already present in wooded biotopes of the eastern margin of Europe by the early Turolian. The morphology of the single m1 fits a simple dental pattern, but shows an unusually long lingual branch of posterolophid (Pl. 11, Fig. 1).

Large mammals

The previous records of large land mammals remains from the Late Miocene deposits near Maikop are very

Table 8. Large mammal remains from the Late Miocene deposits of the Gaverdovsky Fm, North Caucasus.

Taxa	Gaverdovsky	Volchaya Balka
<i>Hipparion</i> aff. <i>gromovae</i> GABUNIA, 1959	1	–
<i>Hipparion</i> cf. <i>moldavicum</i> GROMOVA, 1952	1	–
<i>Hipparion</i> sp.	–	2
<i>Procapreolus</i> sp.	1	–
<i>Microstonyx</i> aff. <i>major</i> (GERVAIS, 1848)	–	1
Cervidae gen. indet (small size form)	–	2
Bovidae gen. indet (middle size form)	2	2
<i>Promephitis maeotica</i> ALEXEJEV, 1915	1	–
Procyonidae? gen.	–	2

scarce. The coarse sandy gravels of the upper part of the Gaverdovsky Fm near the Khanskaya village, downstream from the city of Maikop, yielded remains of *Mammot* cf. *borsoni*, *Anancus arvernensis* cf. *turolensis*, *Deinotherium proavum*, cf. *Procapreolus* (Titov and Tesakov 2013). These finds are mostly stored in the National Museum of the Republic of Adygea (Maikop, Russia). The mandible of zygodont mastodon *Mammot* cf. *borsoni* (HAYS, 1834) is partially coated with cemented clayey sand (Alexeeva 1955). The size and morphology of m3 are similar to those of the zygodont mastodons from middle/late Turolian sites of the Sea of Azov and the northern Black Sea region: Obukhovka-Yanovka and Morskaya 2 (Titov et al. 2006, 2013).

Both size and primitive morphology of the isolated m3 of *Anancus arvernensis* cf. *turolensis* GAZIRY, 1997 are similar to Late Miocene *Anancus* from Dorn-Dürkheim 1 (Germany, MN 11) and Develi (Turkey, MN 13) (Gaziry 1997, Mayda et al. 2014).

The lower molars of deinotheres are similar to the teeth of the largest form of the genus, *Deinotherium proavum* (EICHWALD, 1831) from early – middle Turolian localities Dorn-Dürkheim 1 (Germany, MN 11) and Obukhovka (Russia, Lower Don area, MN 12) (Bajgusheva and Titov 2006, Pickford and Pourabrishami 2013).

Recently an isolated molar of *Deinotherium* cf. *proavum* was also found in the shallow marine Khersonian deposits underlying the sandy-ocherous continental sediments (Tarasenko et al. 2015).

Large mammal remains in the studied localities Gaverdovsky and Volchaya Balka are very rare (Tab. 8). They are represented by detached teeth and rare postcranial bones of ungulates and carnivores.

Order Perissodactyla OWEN, 1848

Family Equidae GRAY, 1821

Genus *Hipparion* DE CHRISTOL, 1832

Hipparion cf. *moldavicum* GROMOVA, 1952

Text-fig. 15a

Material. M1–2 dex, Gaverdovsky (bed 7).

Description. M1–2 (22.1 × 21.6 mm) belongs to a medium-sized hipparion. The tooth shows a small suboval protocone (protocone length is 25.8 mm), relatively wide unsplit mesostyle, wide and forked parastyle, numerous

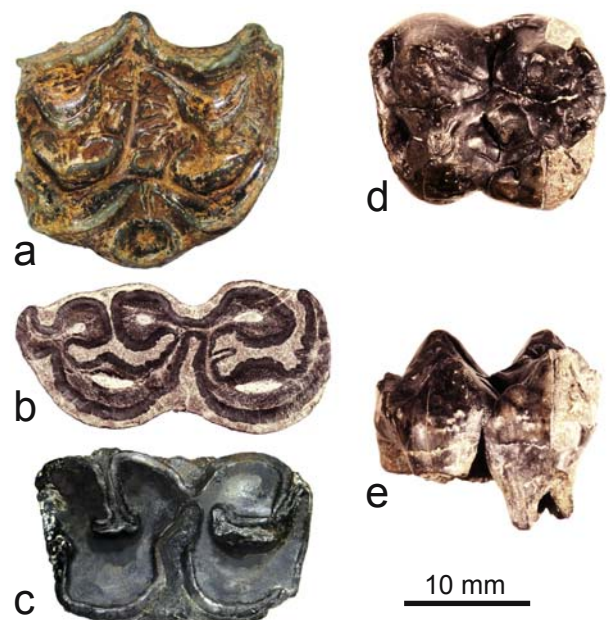
enamel folds on the prefossette and postfossette, and a single pli caballin. In combination of these features, the molar is similar to *H. moldavicum*, occurring in the Late Miocene (Early to Middle Maeotian) of Eastern Europe (Gromova 1952, Krakhmalnaya 1996).

Hipparion aff. *gromovae* GABUNIA, 1959

Text-fig. 15b

Material. m3 dex, Gaverdovsky (bed 7).

Description. The weakly worn m3 (27.6 × 11.9 mm) belongs to a medium-large hipparion. In the upper third section of the tooth crown, the double knot shows relatively equal lobes, a wide linguaflexid, and with suboval metaconid and metastylid. The outer valley of the ectoflexid



Text-fig. 15. Large mammal remains from Gaverdovsky and Volchaya Balka, Late Miocene, North Caucasus. a – *Hipparion* cf. *moldavicum*, SSC-RAS G-1/1, upper right M1–2, occlusal view, Gaverdovsky; b – *Hipparion* aff. *gromovae*, SSC-RAS G-1/2, lower right m3, occlusal view, Gaverdovsky; c – *Hipparion* sp., SSC-RAS G-1/4, lower right m1, occlusal view, Volchaya Balka; d–e – *Microstonyx* aff. *major*, SSC-RAS G-1/3, upper left dP4, d – occlusal view, e – lingual view, Volchaya Balka.

penetrates deeply into the neck of the double knot isthmus. The valley almost connects with the linguaflexid. The enamel folding on the preflexid and postflexid is weak. In size and weak folding of the enamel, the tooth resembles that of *H. gromovae*, characteristic of the Early Maeotian of Eastern Europe (Gabunia 1959).

Order Artiodactyla OWEN, 1848

Family Suidae GRAY, 1821

Genus *Microstonyx* PILGRIM, 1926

***Microstonyx* aff. *major* (GERVAIS, 1848)**

Text-fig. 15d, e

Material. dP4 sin, Volchaya Balka (bed 3).

Comments. The deciduous premolar dP4 (19.5 × 17.3 mm) is generally larger than in *Propotamochoerus*, but similar to *Microstonyx*. The size and shape of the specimen coincide with those of *Microstonyx major* from Samos and Nikiti 1 (Greece) (Kostopoulos 1994). The widespread European species *Microstonyx major* is fairly widespread in the Late Miocene of Europe (MN 10 through MN 12) (van der Made and Moya-Sola 1989, van der Made 1990).

Family Cervidae GRAY, 1821

Genus *Procapreolus* SCHLOSSER, 1924

***Procapreolus* sp.**

Comments. Remains of medium-sized deer are represented in the Gaverdovsky fauna (bed 7) by bones of an incomplete forelimb of a single individual, and an isolated premolar and fragments of molars. The morphology of the bones of the extremities is similar to that of the modern roe deer. The dimensions of the teeth coincide with that of the genus *Procapreolus*. The lack of diagnostic remains precludes a precise species definition. *Procapreolus* was common in Late Miocene faunas of Europe from the late Vallesian to Ruscinian (Korotkevich 1970, Valli 2010).

Order Carnivora BOWDICH, 1821

Superfamily Musteloidea SWAINSON, 1835

Family Mephitidae BONAPARTE, 1845

Genus *Promephitis* GAUDRY, 1861

***Promephitis maeotica* ALEXEJEW, 1915**

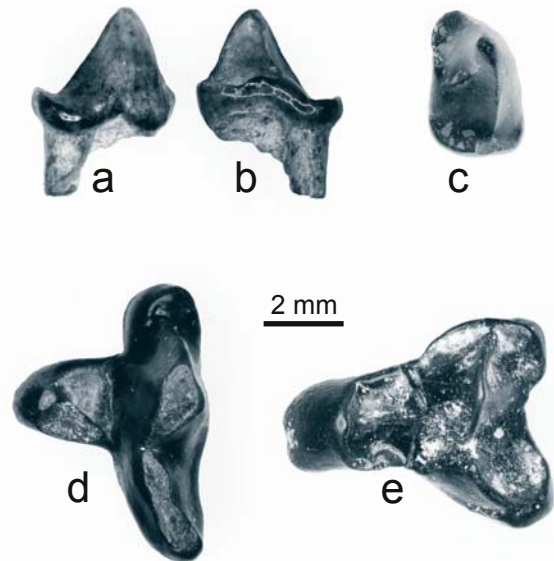
Text-figs 16a–c, 17

Material. p4 dex (GIN-1144-302): Gaverdovsky.

Description. The fourth lower premolar corresponds in size ($L \times W = 3.8 \times 2.5$) and shape to p4 of the fossil skunk *Promephitis* from the European Turolian (Text-fig. 16a–c). As in other *Promephitis*, the high crowned p4 has an almost triangular occlusal outline with significant distal broadening of the crown. It also corresponds with Turolian skunks in the presence of two roots and a single tall main cusp with a well developed posterior cingular cusp(id) as well as in the presence of a weak anterior and more distinct posterior cingulae. In addition, the main cuspid of p4 from Gaverdovsky bears mesial and distal ridges and a prominent lingual crest. A well developed lingual cingulum which

forms a bulge at the junction of the lingual crest with the base of the crown is also present.

Comparison and discussion. Among European taxa, p4 from Gaverdovsky is larger than in *Promephitis majori* and lies within the variability range of the Turolian species *P. maeotica* and *P. lartetii* (Text-fig. 17). A variety of views on the systematics of these two species have been recently published. Therefore it is worth discussing their taxonomic position before any morphological comparison is made.



Text-fig. 16. Carnivorans from Gaverdovsky and Volchaya Balka, Late Miocene, North Caucasus. a–c – *Promephitis maeotica*, p4, dex, GIN-1144-302, a – labial, b – lingual, c – occlusal view; d–e – ?Procyonidae gen., occlusal view; d – dP3, sin, GIN-1143-401, e – dP4, sin, GIN-1144-301.

Fossil skunks *Promephitis* were common elements of the Turolian carnivoran assemblages. They were widespread in Late Miocene of Eurasia and survived till the Pliocene in Asia. The genus includes about ten species with some of them being poorly defined thus leading to an ongoing discussion on the taxonomic composition of the genus (Wang and Qiu 2004, Koufos 2006, Geraads and Spassov 2016).

Werdelin (1996) recognised four species among European *Promephitis*: *P. pristinidens*, *P. maeotica*, *P. lartetii*, and *P. brevirostris*. According to Ginsburg's (1999) concept, Europe was inhabited by only three species, the Vallesian *P. gaudryi* and *P. pristinidens*, and Turolian *P. lartetii*, while *P. majori* and *P. maeotica* were considered as synonyms of the latter species.

In a recent revision Geraads and Spassov (2016) questioned the affiliation of the Vallesian species *P. gaudryi* and *P. pristinidens* to *Promephitis*, listed two other taxa *P. brevirostris* and *P. malustenensis* as problematic and found that Turkish species *P. hootoni* is a synonym of *P. lartetii*.

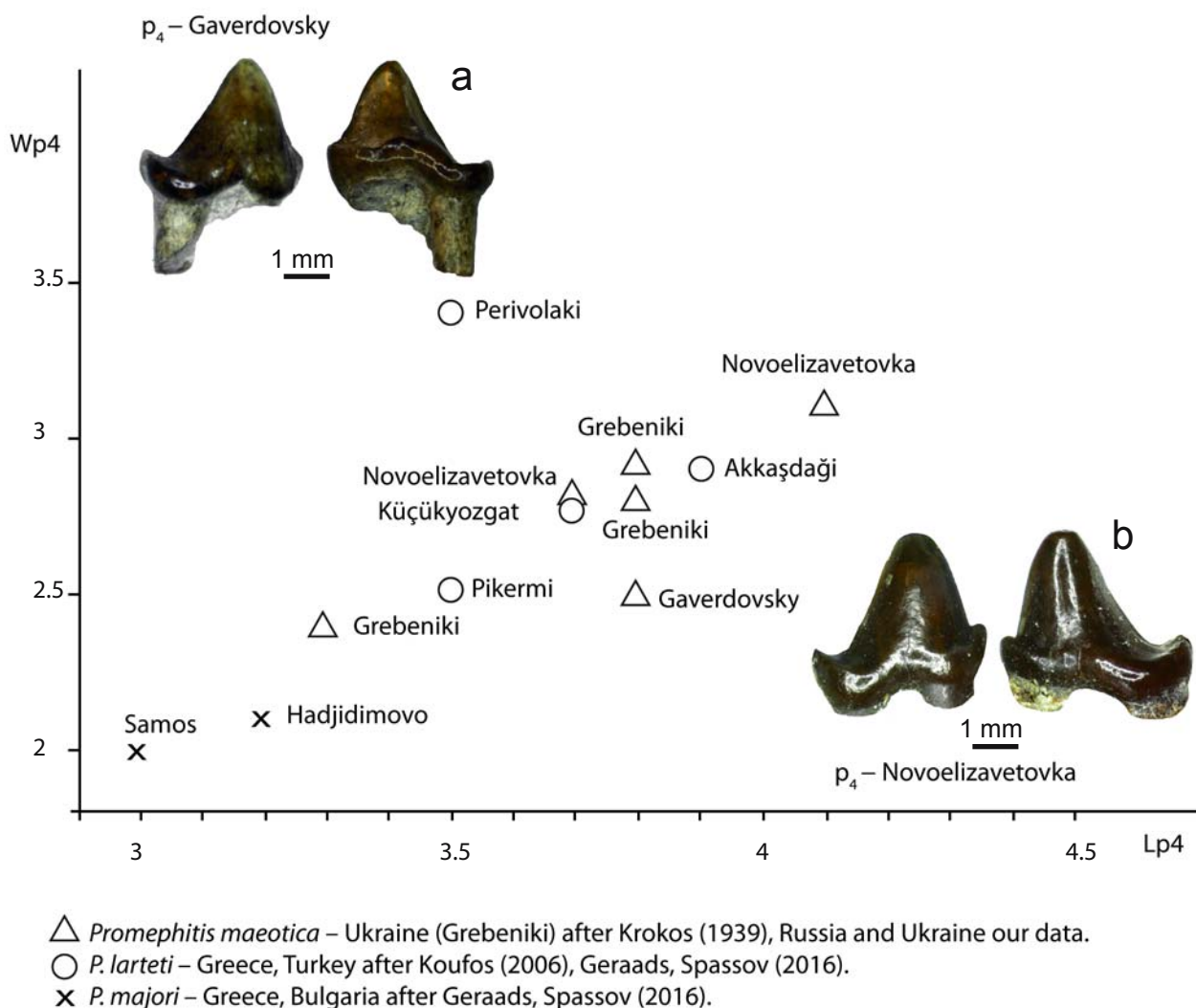
Finally they recognized only three species in the Turolian of Western Eurasia: the largest being *P. maeotica* from Novoelizavetovka (Ukraine) (MN 12), the slightly smaller *P. lartetii* (= *P. hootoni*) from Pikermi, Perivolaki (Greece), Küçükoyzgat, Akkaşdağı (Turkey), Hadjidimovo, and Kalimantsi (Bulgaria) (MN 11–12), and the notably smaller *P. majori* from Samos (Greece) and Hadjidimovo (Bulgaria) (MN 11–12).

Thanks to the new finds from Greece and Bulgaria, the cranial-based distinctions between *P. lartetii* and *P. maeotica* finally excluded their synonymy (Koufos 2006, Geraads and Spassov 2016). The important derived feature of *P. maeotica* from different stratigraphical levels of Turolian is the long m1. The length range of p4 in the three discussed species is quite narrow (3.0–4.0 mm, n = 11; Text-fig. 16) while the length difference between m1 of *P. maeotica* (9.5–10.8 mm, n = 6) and *P. majori* and *P. lartetii* (7.9–9.3 mm, n = 11) is considerable and the values do not overlap.

As noted above the p4 of Turolian skunks do not significantly differ in linear dimensions, but their L/W ratio

is not a stable characteristic (Text-fig. 16). The skunk from Gaverdovsky has a relatively long and narrow p4 that is more similar to *P. majori* than to other discussed taxa. Wang and Qiu (2004) speculated that the broadening of p4 is a derived condition shared by advanced species of *Promephitis* and concluded that *P. majori* is the most plesiomorphic taxon among the discussed forms. From this point of view *P. maeotica* from Novoelizavetovka and Grebeniki as well as all specimens assigned to *P. lartetii* are derived relative to the Gaverdovsky skunk. Text-fig. 17 however shows the wide variability range of the character which therefore questions its reliability as a taxonomic marker.

Unfortunately, the morphology of p4 in *Promephitis* is insufficiently known. Nevertheless, none of the students described the presence of the strong lingual cingulum plus crest and bulge on the internal wall of p4 in *P. majori* and *P. lartetii*, which are present on the Gaverdovsky tooth. On the other hand, Krokos (1939) noted the presence of a strong lingual cingulum in p3 and p4 of the early Turolian skunk from Grebeniki. Our examination of the material from



Text-fig. 17. Scatter diagram of length and width of *Promephitis* species from Late Miocene faunas of southern Europe and western Asia. a – *Promephitis maeotica*, p4, dex, Gaverdovsky, GIN-1144-301: labial (left) and lingual (right) views. b – *P. maeotica*, p4, sin, reversed, Novoelizavetovka, PIN-355: labial (left) and lingual (right) views. Scale 1 mm.

the middle Turolian site of Novoelizavetovka showed the presence of cingula in lower premolars, though somewhat less expressed in premolars of the specimen PIN-355. It is therefore possible to assign the skunk from Gaverdovsky to *P. maeotica*. The specific morphological features of the described form, such as the complex structure of the lingual wall and lack of the anterior cingular cusp characterise a somewhat more basal morphotype of p4 that most likely fits the early Turolian age of the fauna.

Family ?Procyonidae GRAY, 1825

Text-fig. 16d, e

Material. Left dP3 (GIN-1143-401): Volchaya Balka; left dP4 (GIN-1144-301): Gaverdovsky.

Description. The left dP3 ($L \times W = 6.9 \times 4.6$ mm) has a mesiodistally elongated and narrow profile and transversally positioned long protocone (Text-fig. 16d). The parastyle is a low conical cusp separated from the paracone by a small shallow basin and located directly mesially to the paracone. The heavily worn metastyle is elongated mesiodistally and transversely compressed, but is slightly shorter than the paracone. It is separated from the paracone by the carnassial notch. The protocone is significantly longer than the parastyle and is positioned lingually to the central part of the paracone. A distinct preparacrista and less pronounced lingual crest run down to the mesial and lingual base of the paracone respectively.

The transversely elongated left dP4 with $L \times W = 6.7 \times 5.1$ has a buccal length twice longer than the lingual length (Text-fig. 16e). Their ridge-like paracone and metacone are located at an angle to each other. The paracone is slightly taller and longer than the metacone but bears a central conule. The styler shelf is developed between the parastyle and paracone mesially and is less expressed between the metacone and metastyle distally. An asymmetric ectoflexus is present, with its deepest point buccal to the distal half of the paracone. The meta- and paraconules are small and located closer to the protocone than to the paracone and metacone. The pre- and postprotocristae surround the nearly vertical lingual wall of the tooth and connect their central conules with the protocone apex.

Comments. There is the significant difference between posterior milk premolars and their permanent analogues in carnivorans. As a rule, deciduous teeth are smaller in size, lower crowned, transversely more narrow, and do not duplicate the structure of the permanent teeth. These features hamper an unambiguous taxonomic assignment of the studied material. Judging by the long talon and a carnassial notch in dP3, and the occlusal surface of dP4, the studied deciduous teeth belong to Musteloidea. The size ($L \times W$) of dP3 from Volchaya Balka is 6.9×4.6 mm. Using measurements from Baryshnikov and Averianov's (1990) review, the size of the studied musteloid may be estimated as ranging between *Martes martes*, with the dP3 $L \times W$ upper limit being 6.6×4.2 mm, and *Taxidea taxus*, with the $L \times W$ lower limit being 6.8×5.0 mm. Deciduous molars of Miocene carnivorans have been insufficiently studied. Similar morphotypes of dP3 and dP4 are known from the Early Miocene European procyonid carnivore *Stromeriella*

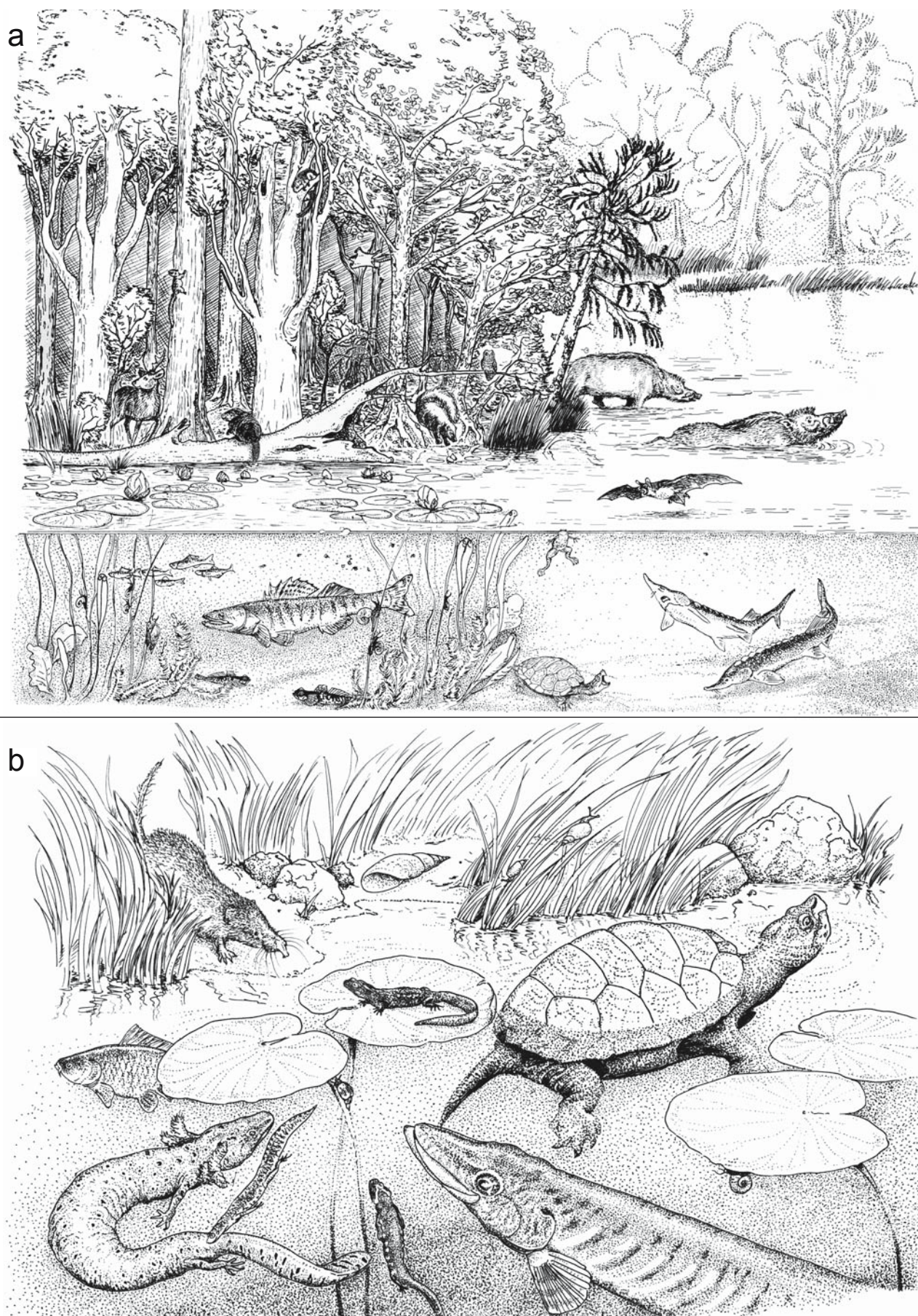
franconica. This form is also similar in size (dP3 $L \times W = 6.3 \times 4.3$) to the described form (Dehm 1950: 107, figs. 209–210).

Palaeoenvironmental implications

The biotic proxies of both studied Late Miocene localities qualitatively unequivocally indicate considerable role played by forested and humid biotopes (e.g., flying squirrels, dormice, etc.; Text-fig. 18a). At the same time the fauna of Gaverdovsky also contains a number of taxa indicating open landscapes (lagomorphs). The vertebrate fauna of Volchaya Balka lacks these and shows a higher diversity of herpetofauna, and also a higher number of landsnails. The pollen record shows predominantly forested biotopes in Gaverdovsky, and a notable role of open landscapes vegetation in Volchaya Balka. Ostracods point to an increased salinity basin during the formation of the Gaverdovsky burial and fresh-water conditions in Volchaya Balka. It is clear that these mosaic differences for two closely spaced and obviously almost synchronous sites formed in the same fresh-water basin reflect palaeolandscape differentiation of its shores both laterally and over a small-scale chronological time span. The correlation of pollen zones in the studied sections (Tab. 1), if accurately interpreted as a climatic/landscape cycle of humid – more arid – humid conditions, tentatively indicate that among the vertebrate faunas of beds with freshwater molluscs, the fauna of Volchaya Balka (bed 3) may slightly predate the fauna of Gaverdovsky (bed 7).

The diverse early Turolian biota of the Northern Caucasus provides a means of evaluation of the environmental parameters, specifically the level of precipitation and general palaeoclimatic assessment. Four climate-sensitive proxies supported by sufficient data are available in our results: the palynological spectra, mollusc assemblages, terrestrial and aquatic herpetofauna, and small mammal assemblage. The molluscan assemblage shows warm temperate or subtropical climatic conditions.

Volchaya Balka and Gaverdovsky represent one of the most diverse and well-documented Late Miocene herpetological assemblages. The all revealed taxa are found in both localities, no significant faunal differences between localities are apparent. However, in Gaverdovsky remains of *Anguis* are more abundant than in Volchaya Balka. The amphibian and reptile assemblage contains a diverse (26 taxa) fauna, which shows adaptations to aquatic environments. The aquatic fauna is characterized by abundant remains of the three species of *Triturus* s. l. (*Triturus cristatus*, *T.* cf. *marmoratus*, and *Lissotriton* sp.) belonging to peri- and semi-aquatic groups. Another abundant aquatic form here is *Pelophylax* sp. which spends a significant part of its life in the water. The fully aquatic *Mioproteus caucasicus*, *Palaeobatrachus* sp., and *Emys* cf. *tarashchuki* are indicators of a long-term permanent water-body. *Mioproteus*, which is ecologically related to the North American *Necturus* (stream habitats), is mostly found only in localities of fluvial origin and absent in pond, pool or stagnant lake environments. The low numbers of fossorial spadefoot toads (*Pelobates* sp.) may indicate a limited presence of open landscapes and well drained soils. This



Text-fig. 18. Landscape reconstruction of the Late Miocene localities of the North Caucasus studied. **a** – general view of the reconstructed riparian biotope; **b** – periaquatic fauna. Drawings by S. Kruskop.

can be confirmed by the sparse remains of *Bufo viridis* which avoid wooded areas and are usually found in open habitats (Kuzmin 1999). Other heliophil taxa (*Testudo* s. str., *Pseudopus pannonicus*, Lacertidae indet.) which exploit open environments are relatively rare in both localities. The high number of *Anguis* remains in Gaverdovsky suggests a stronger development of wooded habitats in the vicinity of the burial when compared to the Volchaya Balka locality.

The dominance of fully aquatic, semi-aquatic, and peri-aquatic forms over heliophil taxa suggests a wet and humid climate. The abundant herpetofaunal remains allow reconstruction of the palaeoprecipitation for Volchaya Balka and Gaverdovsky using methods of Böhme et al. (2006). For an estimation of the palaeoprecipitation value, 19 recorded taxa of amphibians and reptiles (excluding the non-fossorial snakes, and *Eopelobates* with not reliably known palaeoenvironmental preferences) are grouped according to their ecologic adaptations into five ecophysiological groups (Tab. 9). Using the mean of the ecophysiological indices and equation 6 in Böhme et al. (2006) results in a mean annual precipitation value (MAP) of 858 mm (Tab. 9). The present precipitation value for the area (Maikop) is 772 mm. The Late Miocene MAP value is thus close or slightly exceeds the present day precipitation.

The faunal composition at Volchaya Balka and Gaverdovsky suggests the presence of warm, wet and mainly forested environments with a permanent water-body. The herpetofauna of Volchaya Balka and Gaverdovsky includes taxa common for Late Miocene European assemblages. This fauna is similar in composition to the Early Khersonian

assemblage of the Maikop city park (MN 10?) which includes the following taxa: Emydidae indet., “*Trionyx*” *khosatzkyi*, *Mioproteus caucasicus*, *Triturus* sp. cf. *T. marmoratus*, Discoglossidae indet., unidentifiable procœlous frog, *Lacerta* sp. However, a detailed description is impossible due to scarcity of fossils from this locality. The only obvious difference is the lack of trionychid remains in Volchaya Balka and Gaverdovsky. The absence of trionychids in the studied faunas can be either controlled by different environmental filters or, most likely, by the different stratigraphic position of the localities. Trionychids almost disappeared in Western Europe in the early Late Miocene (MN 9–10), except in Romania where they survived until MN 13 (Vremir 2004). The faunal composition of Volchaya Balka and Gaverdovsky is very similar to some Late Miocene faunas of Central Europe. For example, they share 57% of taxa with the herpetofauna of Kohfidisch (MN 11). This is the only Late Miocene locality (together with Volchaya Balka and Gaverdovsky) documenting the co-occurrence of *Anguis* and *Pseudopus*.

The quantitative criteria for evaluation of mean precipitation based on Neogene micromammals were recently elaborated by van Dam (van Dam 2006, van Dam and Utescher 2016). These analyses based on a large set of actualistic data were applied to numerous well studied micromammalian faunas of the European Neogene ranged in MN units. For the early Turolian (MN 11) time slice of the Late Miocene this analysis revealed two relatively arid zones, with a mean annual precipitation (MAP) of 400–500 mm, in the west (Iberia) and east (south of Eastern Europe) of the continent, separated by a much wetter region in the so

Table 9. Amphibian and reptile taxa from Volchaya Balka and Gaverdovsky, their supposed ecophysiological groups, and calculation details for the estimation of palaeoprecipitation (according to Böhme et al. 2006).

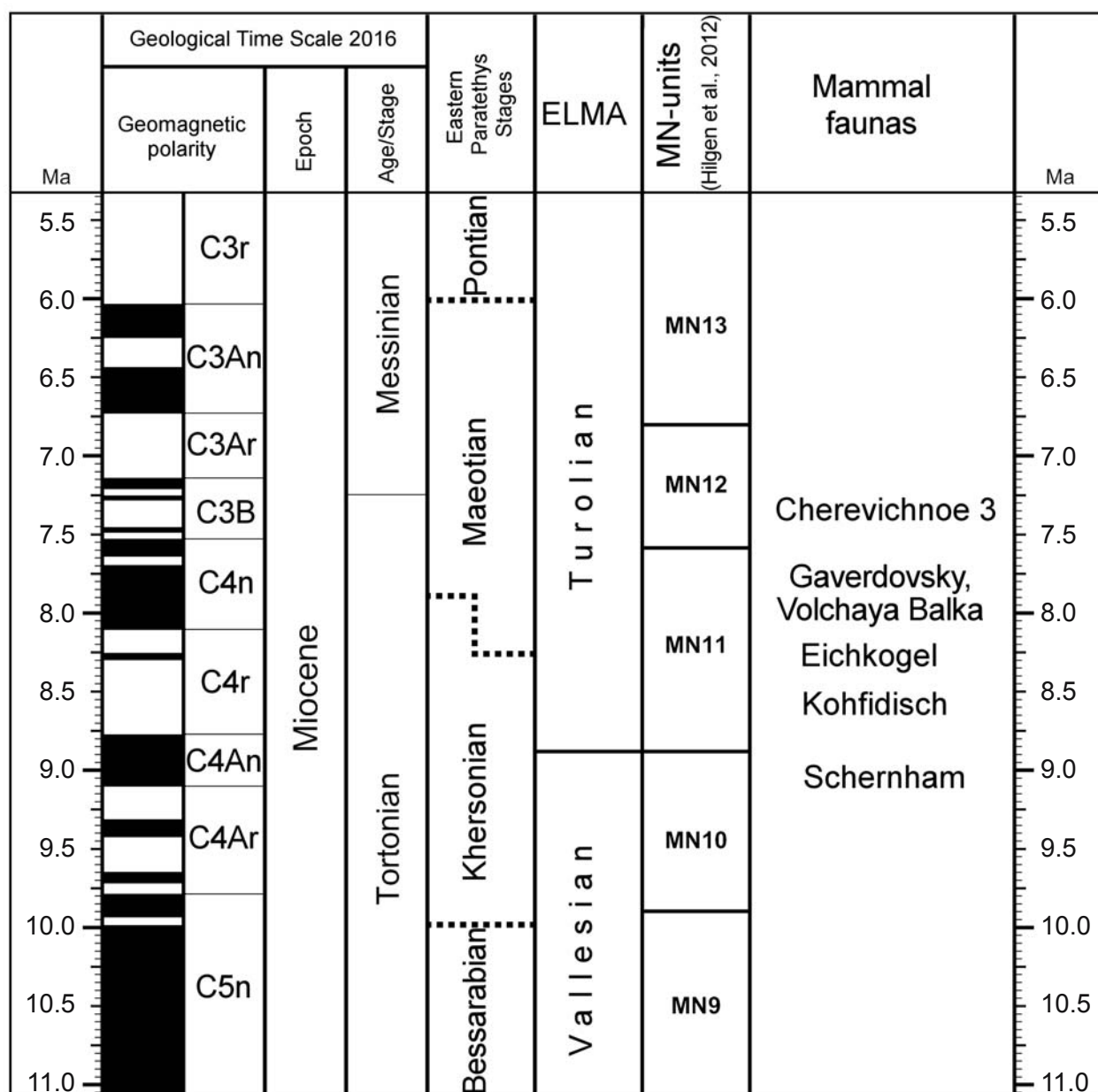
Taxon	Ecophysiological group	Index
<i>Mioproteus caucasicus</i>	Fully aquatic	1
<i>Chelotriton paradoxus</i>	Peri-aquatic	0.3918
<i>Triturus cristatus</i>	Peri-aquatic	0.3918
<i>Triturus</i> cf. <i>marmoratus</i>	Semi-aquatic	0.513
<i>Lissotriton</i> sp.	Peri-aquatic	0.3918
<i>Latonia</i> sp.	Peri-aquatic	0.3918
<i>Bombina</i> cf. <i>bombina</i>	Semi-aquatic	0.513
<i>Hyla</i> sp.	Peri-aquatic	0.3918
<i>Palaeobatrachus</i> sp.	Fully aquatic	1
<i>Pelobates</i> sp.	Fossorial	0.0917
<i>Bufo viridis</i>	Heliophil	0
<i>Rana</i> sp.	Peri-aquatic	0.3918
<i>Pelophylax</i> sp.	Semi-aquatic	0.513
<i>Emys</i> cf. <i>tarashchuki</i>	Fully aquatic	1
Testudinidae indet.	Heliophil	0
<i>Testudo</i> s.s.	Heliophil	0
<i>Anguis</i> sp.	Fossorial	0.0917
<i>Pseudopus pannonicus</i>	Heliophil	0
Lacertidae indet.	Heliophil	0
Ecophysiological index		0.3723
Mean annual precipitation (mm)		858

called European Temperate Wet Zone (ETWZ) with MAP in the range of 800–1200 mm. The Caucasian region was not included in the analysis due to the scarcity of data on fossil micromammals at that time. The analysis of climate-related hypsodonty data for large herbivores showed a predominance of high-crowned plant-eating large mammals interpreted as an indicator of aridity for the easternmost Europe and western Asia (Fortelius et al. 2006). Using van Dam's (2006) methodology for estimating MAP based on data regarding the percentage of arboreal and invertivorous mammals, the MAP value for the combined Gaverdovsky and Volchaya Balka fauna, with arboreal and invertivorous groups each represented by six species (i.e., each amounting to 30% of the fauna), is 966 or 942 mm/year depending on the use of linear (van Dam 2006) or improved non-linear (van Dam and Utescher 2016) equations. Taking into account

an accuracy of approximately ± 200 –400 mm inferred by van Dam (2006), this estimate closely agrees with that based on the herpetofauna (858 mm, see above). The pollen record, with the presence of *Engelhardia* and other humidity indicators, also points to precipitation above 700–800 mm (Eronen et al. 2011, van Dam and Utescher 2016). Therefore, our data sets clearly indicate a relatively high level of annual precipitation along the northern coast of the Caucasian Peninsula in the early Turolian, not previously recognised in European-wide quantitative palaeoenvironmental analyses.

Biochronological discussion

The most important for assessing the biochronological position of the studied sequences is the resulting data on



Text-fig. 19. Position of the studied faunas correlated to chronostratigraphic and biochronological charts.

composition and evolutionary levels of mammals. Both studied faunas have a typical Turolian appearance with the dominance of murids and advanced cricetines. In comparison to Central and Western European faunas of the Vallesian-Turolian transition (e.g., Mein 1999, Daxner-Höck et al. 2016) the somewhat lower diversity of the Caucasian faunas is apparent even taking into account a limited amount of material ($n = \text{ca. } 380$). This may be due to specific taphonomic and regional biotopic factors with poor representation of species from flowing waters (absent are desmans and beavers) and open biotopes in combination with a sampling bias. The relatively poor composition of the insectivore assemblage, lacking typical Vallesian elements, is also indicative of the Turolian. The presence of basal *Amblycoptus* and the absence of *Crusafontina*, may have the same significance although it could also be regarded as a regional feature. The almost identical soricid assemblage is known from the early Turolian fauna Hayranlı 1 (Furió et al. 2014) from central Anatolia.

The rodent fauna strongly resembles early Turolian faunas of Eastern and Central Europe and Anatolia. The evolutionary level of *Parapodemus* with about half of the specimens showing weak signs of $t7$ in upper molars M1–2 corresponds to the early Turolian samples, but possibly postdates the earliest MN 11 faunas such as Kohfidisch with very low frequencies of $t7$ (Wöger 2011). The fauna Hayranlı 1, Anatolian zone J correlated to MN 11, documenting a murid with a mixture of *Parapodemus*/*Apodemus*/*Progonomys* morphotypes (de Bruijn et al. 2013), is another biochronological match with the Caucasian faunas. The presence of the glirid *Paraglrulus schultzi* previously known in the single late Vallesian fauna of Schernham in Austria (Daxner-Höck and Höck 2009) does not exclude the possibility of survival of this lineage into early Turolian in the North Caucasus. The hypsodont collimyine hamster *Collimys caucasicus* sp. nov., less advanced than the peculiar *Pseudocollimys* of Schernham (MN 10), may represent an independent conservative lineage of these hamsters, and in particular be the immediate successor of the early Turolian *Collimys primus* of Kohfidisch and Eichkogel thus also favouring the late early Turolian age. The overall similarity of the studied faunas from the Caucasus is obvious with the fauna of Dorn-Dürkheim 1 in Germany (Franzen and Storch 1975), the classical early Turolian (MN 11) assemblage of Central Europe. The unusual diversity of this fauna, e.g., with five co-occurring species of beavers and proboscideans, however, fuels the discussion of its taphonomic mixing (Costeur et al. 2013, personal communications of S. Mayda and M. Böhme 2017).

The lower limit of the age estimate of the North Caucasian faunas is provided by the timing of several important event datums, e.g., the appearance of Leporidae and *Parapodemus*. The Late Miocene appearance of leporids in Eurasia was estimated at around 8 Ma (Flynn et al. 2014), although the records of the earliest European leporid in sites occurring in Khersonian deposits, such as Keinar and Palievo (Čermák et al. 2015) are obviously older than 8 Ma (see below).

The lower boundary of MN 11 is dated within the range of 8.7–8.9 Ma (Steininger 1999, Hilgen et al. 2012). The first appearance of the murid *Parapodemus lugdunensis* (the criterion defining the lower boundary of MN 11) was

estimated to occur around 8.9 Ma (Hilgen et al. 2012). The appearance of the genus *Parapodemus* was recently shown to be diachronous in neighbouring sedimentary basins in Spain, with a 9.25 Ma level for a primitive form in Valles-Penedes Basin predating the conventional 8.9 Ma for *P. lugdunensis* in Teruel Basin (Casanovas-Vilar et al. 2016). The earliest *Parapodemus* in Central Europe were also found in late Vallesian sites, such as Suchomasty and Schernham (Fejfar 1990, Daxner-Höck and Höck 2015). The upper boundary of the MN 11 unit is estimated between 8.0 Ma (Steininger et al. 1999) and 7.6 Ma (Hilgen et al. 2012).

Further refining of the age of Caucasian faunas comes from chronology of the regional stages of the Eastern Paratethys and palaeomagnetic record of the studied sections. The age of the upper Khersonian boundary, to which the studied faunas are close, is bracketed within the range 8.6–8.2 Ma (Vasiliev et al. 2011) or dated at 7.9 Ma (Radionova et al. 2012). The older estimates around 9.6 Ma (Vangengeim and Tesakov 2013), based on an apparent miscorrelation of the thick normally magnetized zone in the Khersonian section of Eldari (Georgia) with the Chron C5n, cannot be currently accepted as reliable. The time interval between 9 and 8 Ma contains three main chrons of normal (C4An), reversed (C4r), and normal (C4n) polarity. These chrons of the magnetostratigraphic scale are dated within the range 9.1–8.77 Ma (C4An), 8.77–8.1 Ma (C4r), and 8.1–7.53 Ma (C4n) (Hilgen et al. 2012). The lower part of the Gaverdovsky formation including the studied localities shows predominantly normal magnetisation (Text-fig. 3). Sediments in the upper part of the marine Khersonian are also normally polarised but a stratigraphic gap is predicted at the boundary between the marine deposits of the Khersonian and the terrestrial Gaverdovsky Fm. Taking into consideration the above reviewed constraints provided by biochronology, we favour a correlation of the top Khersonian with Chrons C4An or C4r.2n or C4r.1n, and we correlate the Gaverdovsky sandy-ocherous deposits with lower part of Chron C4n (Text-fig. 19). Thus mammalian faunas Gaverdovsky and Volchaya Balka are correlated to the Late Tortonian, and their age is estimated in the the range of 8.1–7.6 Ma.

Conclusion

This study reviews the Late Miocene biotic record of the stratigraphic transition from the marine Late Sarmatian (Khersonian) to a terrestrial environment of fresh-water basins that framed the northern shore of the Caucasian Peninsula after the regression of the Khersonian sea, correlated to Late Tortonian. The sections along the Belaya River in the North Caucasus yielded data on palynology, ostracods, fresh-water and terrestrial molluscs, fishes, amphibians and reptiles, birds, and mammals. Palynological study evidences landscapes with dominant warm temperate to subtropical broad-leaved and coniferous forests. A climatic phase with more open biotopes added to the wooded ones has also been detected. Ostracod assemblages indicated dissimilar environmental conditions during the formation of the two studied vertebrate localities. The burial of Volchaya Balka was formed in a fresh-water basin with a pollen-indicated mixture of wooded and open biotopes,

whereas the Gaverdovsky locality was formed under conditions of a marked marine water influx into a basin with densely forested shores. Therefore, the Gvd and Vlb faunas, although located only ca. 1 km from each other in identical stratigraphic settings and featuring very similar taxonomic composition, do not represent the same local sedimentary interval, but are slightly diachronous. The molluscan assemblages of the studied localities document a diverse aquatic fauna combining common European Neogene forms with large time and geographic ranges and local endemic forms of the Caucasian provenance. The fish assemblage of the Vlb site contains fresh-water forms with dominant Gobiidae and forms most likely indicating an occasional connection to the sea (sturgeons). Diverse and abundant amphibians and reptiles show the strong dominance of aquatic forms over heliophilic ones. The scarce large mammal assemblage includes common Late Miocene forms of ungulates and carnivores (hipparions, deer, suid, skunk, and undefined procyonid). The small mammal assemblages include predominant forms of wet and forested biotopes (Vlb) with some addition of open landscape dwellers (Gvd). Many species are shared with late Vallesian and especially early Turolian faunas of Central Europe and western Asia. The biotic records of the lower part of the Gaverdovsky Fm near Maikop evidence its correlation with Late Khersonian – Early Maeotian transition, Late Tortonian, and the MN 11 unit. The obtained data for the first time elucidated faunal composition of the Late Miocene terrestrial biota in the Northern Caucasus at around the transition from Vallesian to Turolian Land Mammal Ages of the European biochronological scale.

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Explanations of the plates

PLATE 1

Ostracods from Late Miocene deposits of Gaverdovsky and Volchaya Balka, North Caucasus.

Candona combibo LIVENTAL, 1939

1. rv, female, int., GIN-1144-443; Gaverdovsky.

Candona neglecta SARS, 1887

2. lv, female, GIN-1143-501; Volchaya Balka.

Candoniella suzini SCHNEIDER in SUZIN, 1956

3. c, female, vent., GIN-1144-451; Gaverdovsky.
4. c, female, dex, GIN-1144-449; Gaverdovsky.
5. lv, female, int., GIN-1144-448; Gaverdovsky.

Ilyocypris gibba (RAMDOHR, 1808)

6. lv, female, GIN-1143-502; Volchaya Balka.
7. lv, female, GIN-1143-503; Volchaya Balka.
8. rv, female, GIN-1143-504; Volchaya Balka.

Cyprinotus baturini SCHNEIDER, 1961

9. c, female, dex, GIN-1144-436; Gaverdovsky.
11. c, female, dors., GIN-1144-437; Gaverdovsky.

Cyprinotus formalis SCHNEIDER, 1963

10. c, female, dors., GIN-1144-441; Gaverdovsky.
14. rv, female, GIN-1144-432; Gaverdovsky.
15. c, female, dex, GIN-1144-438; Gaverdovsky.
16. lv, female, int., GIN-1144-446; Gaverdovsky.

Cyprinotus vialovi SCHNEIDER, 1961

12. c, female, dors., GIN-1144-433; Gaverdovsky.
13. rv, female, GIN-1143-505; Volchaya Balka.

Abbreviations: rv – right valve, lv – left valve, c – carapace, int. – internal view, dors. – dorsal view, vent. – ventral view, dex – right side view.

PLATE 2

Ostracods from Late Miocene deposits of Gaverdovsky (1144) and Volchaya Balka (1143), North Caucasus.

Cyprinotus aff. *speciosus* MANDELSTAM, 1963

1. rv female, GIN-1143-506.
2. lv, female, GIN-1143-507.
3. lv female, int., GIN-1144-435.

Cyprideis torosa (JONES, 1850)

4. c, male, dors, GIN-1144-431.
5. c, female, dors, GIN-1144-419.
6. rv, female, GIN-1144-416.
7. c, female, dex, GIN-1144-421.
8. rv female, int., GIN-1144-435.
9. lv, female, GIN-1144-414.
10. lv, male, GIN-1144-422.
11. lv, female, int., GIN-1144-412.
12. lv, male, int., GIN-1144-422.
13. c, male, dex, GIN-1144-430.
14. lv, male, GIN-1144-426.
15. lv, female, GIN-1144-414, sieve pores.
16. lv, female, GIN-1144-414, sieve pores.

Abbreviations: rv – right valve, lv – left valve, c – carapace, int. – internal view, dors. – dorsal view, vent. – ventral view, dex – right side view.

PLATE 3

Molluscs from Late Miocene deposits of Gaverdovsky and Volchaya Balka, North Caucasus

1. *Pomatias rivulare* (EICHWALD, 1829); Volchaya Balka, Association 3.
2. *Melanopsis praemorsa* group; Gaverdovsky, Association 2.
3. *Caspicyclotus praesiversi* STEKLOV, 1966; Volchaya Balka, Association 1.
4. Bellamyinae gen.; Volchaya Balka, Association 1.
5. *Pseudamnicola* sp.; Volchaya Balka, Association 1.
- 6, 7. *Bithynia* sp. Volchaya Balka, Association 1.
8. *Pseudamnicola* sp.; Volchaya Balka, Association 1.
9. *Galba* aff. *dupuyana* (NOULET, 1854); Gaverdovsky, Association 1.
10. *Lymnaea* aff. *turrita* (KLEIN, 1855); Volchaya Balka, Association 1.
11. *Stagnicola* aff. *praebouilleti* SCHLICKUM, 1970; Volchaya Balka, Association 1.
- 12, 13. *Planorbarius mantelli* (DUNKER, 1848); Volchaya Balka, Association 1; Fig. 13 shows protoconch of specimen figured in Fig. 12.
- 14–16. *Planorbarius* cf. *thiollierei* (MICAUD, 1855); Volchaya Balka, Association 1.

PLATE 4

Molluscs from Late Miocene deposits of Gaverdovsky and Volchaya Balka, North Caucasus

- 1–4. *Anisus* (*Odontogyrorbis*) *krambergeri* (HALAVÁTS, 1903); Volchaya Balka, Association 1; Fig. 4 shows protoconch of specimen figured in Fig. 1.
- 5–8. *Armiger* sp.; Volchaya Balka, Association 1; Fig. 8 shows protoconch of specimen figured in Fig. 5.
- 9–12. *Armiger* cf. *cristaeformis* GOZHIK et PRYSJAZHNJUK, 1978; Volchaya Balka, Association 1; Fig. 12. shows protoconch of specimen figured in Fig. 9.
13. *Armiger* cf. *nautiliformis* GOZHIK et PRYSJAZHNJUK, 1978; Volchaya Balka, Association 1.
- 14–16. *Gyraulus* sp.; Volchaya Balka, Association 1.
17. *Gyraulus* cf. *applanatus* (THOMAE, 1845); Volchaya Balka, Association 1.
- 18–20. *Gyraulus* cf. *kleini* (GOTTSCHICK et WENZ, 1921); Volchaya Balka, Association 1.
21. *Gyraulus* cf. *solenoides* (LÖRENTHEY, 1902); Volchaya Balka, Association 1.
22. *Carychium* *marinae* STEKLOV, 1966; Volchaya Balka, Association 3.
- 23–24. *Carychium* *plicatum* STEKLOV, 1966; Volchaya Balka, Association 3.
25. *Carychium* sp.; Volchaya Balka, Association 3.
26. *Cochlicopa* sp.; Volchaya Balka, Association 3.

PLATE 5

Molluscs from Late Miocene deposits of Gaverdovsky and Volchaya Balka, North Caucasus

- 1–2. *Gastrocopta* (*Albinula*) *acuminata* (KLEIN, 1846); Volchaya Balka, Association 3.
- 3–4. *Gastrocopta* (*Sinalbinula*) *nouletiana* (DUPUY, 1850); Volchaya Balka, Association 3.
- 5–6. *Vertigo* *callosa* (REUSS, 1852); Volchaya Balka, Association 3.
- 7–8. *Vertigo* *protracta* SANDBERGER, 1874; Volchaya Balka, Association 3.
- 9–10. *Pupilla* *mutabilis* STEKLOV, 1966; Volchaya Balka, Association 3.
11. *Truncatellina* sp; Volchaya Balka, Association 3.
12. *Truncatellina* sp; Volchaya Balka, Association 3.
13. *Negulus* *gracilis* GOTTSCHICK et WENZ, 1919; Volchaya Balka, Association 3.
- 14–16. *Vallonia* *subcyclophorella* (GOTTSCHICK, 1911); Volchaya Balka, Association 3; Fig. 16 shows protoconch of specimen figured in Fig. 15.

PLATE 6

Molluscs from Late Miocene deposits of Gaverdovsky and Volchaya Balka, North Caucasus

- 1–2. *Euxinophaedusa* cf. *volkovae* LIKHAREV, 1962; 1. Volchaya Balka, Association 1; 2. Volchaya Balka, Association 3.
3. *Pontophaedusa* *praefuniculum* LIKHAREV, 1962; Volchaya Balka, Association 3.
4. *Quadriplicata* *farsica* LIKHAREV 1962; Volchaya Balka, Association 3.
5. *Cecilioides* cf. *aciculella* (SANDBERGER, 1874); Volchaya Balka, Association 3.
- 6–8. *Strobilops* (*Eustrobilops*) *caucasica* STEKLOV, 1966; Volchaya Balka, Association 3.
- 9–11. *Strobilops* (*Strobilops*) *costata* (CLESSIN, 1877); Volchaya Balka, Association 3.
- 12–14. *Helicodiscus* *depressus* (EICHWALD, 1830); Volchaya Balka, Association 3; Fig. 14 shows protoconch of specimen figured in Fig. 13.
- 15–17. *Hawaiiia* *antiqua* RIEDEL, 1963; Volchaya Balka, Association 3; Fig. 17 shows protoconch of specimen figured in Fig. 16.
18. Enidae indet.; Volchaya Balka, Association 3.
19. *Caucasotachea* sp.; Volchaya Balka, Association 3.
- 20–23. *Pisidium* (*Cingulipisidium*) cf. *nitidum* JENYNS, 1832, juvenile specimen; Gaverdovsky, Association 1; 21, 23 left valve, 22 right valve.

PLATE 7

Amphibians and reptiles from Late Miocene deposits of Gaverdovsky and Volchaya Balka, North Caucasus

1. *Triturus cristatus* (LAURENTI, 1768), trunk vertebra, dorsal (a) and lateral (b) views.
2. *Triturus* cf. *marmoratus* (LATREILLE, 1800), trunk vertebra, dorsal (a) and lateral (b) views.
3. *Lissotriton* sp., trunk vertebra, dorsal (a) and lateral (b) views.
4. *Bombina* cf. *bombina* (LINNAEUS, 1761), presacral vertebra, dorsal view.
5. *Bombina* cf. *bombina*, fragment of ilium, lateral view.
6. *Latonia* sp., fragment of angular, dorsal view.
7. *Hyla* sp., fragment of ilium, lateral view.
8. *Palaeobatrachus* sp., fragment of maxilla, lingual view.
9. *Palaeobatrachus* sp., fragment of ilium, lateral view.
10. *Pelobates* sp., fragment of ilium, lateral view.
11. *Bufo* cf. *viridis* (LAURENTI, 1768), fragment of ilium, lateral view.
12. *Rana* sp., fragment of frontoparietal, ventral (a) and dorsal (b) views.
13. *Rana* sp., fragment of ilium, lateral view.
14. *Pelophylax* sp., fragment of ilium, lateral view.
15. *Pseudopus* *pannonicus* (KORMOS, 1911), osteoderm, dorsal view.
16. *Anguis* sp., fragment of frontal, dorsal (a) and ventral (b) views.
17. *Anguis* sp., osteoderm, dorsal view.
18. Lacertidae indet., fragment of dental, lingual view.
19. *Coronella* sp., trunk vertebra, dorsal (a), ventral (b), posterior (c), and lateral (d) views.
20. *Natrix* sp., trunk vertebra, dorsal (a), ventral (b), posterior (c), and lateral (d) views.

All specimens, except Figs 15–17 from Gaverdovsky, originated from Volchaya Balka.

PLATE 8

Parapodemus lugdunensis SCHAUB, 1938 from Late Miocene deposits of Gaverdovsky (1144) and Volchaya Balka (1143), North Caucasus

1. m1, dex, GIN-1144-21.
2. m1, sin, GIN-1143-26.
3. m1, dex, GIN-1144-22.
4. m1, dex, GIN-1144-14.
5. m2, dex, GIN-1144-35.
6. m2, sin, GIN-1143-45.
7. m3, dex, GIN-1143-55.
8. M1, sin, GIN-1144-63.
9. M1, dex, GIN-1143-67.
10. M1, sin, GIN-1144-58.
11. M1, dex, GIN-1144-64.
12. M1, dex, GIN-1144-57.
13. M2, dex, GIN-1143-79.
14. M2, sin, GIN-1144-75.
15. M3, dex, GIN-1143-83.
16. M3, dex, GIN-1144-81.

PLATE 9

Pseudocricetus cf. *antiquus* TOPACHEVSKY et SCORIK, 1992 from Late Miocene deposits of Gaverdovsky (1144), North Caucasus

1. m1, sin, GIN-1144-93.
2. m2, sin, GIN-1144-97.
3. m3, sin, GIN-1144-107.
4. M1, sin, GIN-1144-111.
5. M2, sin, GIN-1144-117.
6. M3, sin, GIN-1144-121.

Neocricetodon cf. *progressus* TOPACHEVSKY et SCORIK, 1992 from Late Miocene deposits of Gaverdovsky (1144) and Volchaya Balka (1143), North Caucasus

7. m1, sin, GIN-1143-91.
8. m1, sin, GIN-1144-126.
9. m1, sin, GIN-1144-127.
10. m2, sin, GIN-1143-95.
11. m3, sin, GIN-1143-101.
12. M1, sin, GIN-1143-118.
13. maxillary fragment with M1 – M3, sin, GIN-1143-112.

PLATE 10

Collimys caucasicus sp. nov., from Late Miocene deposits of Gaverdovsky (1144) and Volchaya Balka (1143), North Caucasus

1. m1, dex, GIN-1143-001, holotype.
2. m1, sin, GIN-1143-002.
3. m1, sin, damaged, GIN-1144-00.
4. m2, sin, GIN-1144-002.
5. M1, sin, GIN-1144-003.
6. M2, dex, GIN-1144-004.
7. M3, dex, GIN-1143-003.
8. M3, sin, GIN-1144-005.
9. M3, sin, GIN-1144-006.

PLATE 11

Dipodids, eomyids, glirids, and sciurids from Late Miocene deposits of Gaverdovsky (1144) and Volchaya Balka (1143), North Caucasus.

Sicista sp.

1. m1, dex, GIN-1144-199.

Eozapus intermedius (BACHMAYER et WILSON, 1970)

2. m2, sin, GIN-1144-132.
3. m3, dex, GIN-1144-134.
4. M2, dex, GIN-1144-131.

Keramidomys sp.

5. m1, sin, GIN-1144-191.
6. m1/2, dex, GIN-1144-192.
7. m1/2, dex, GIN-1144-193.
8. M1/2, dex, GIN-1144-194.
9. M3, dex, GIN-1144-195.

Paraglrulus schultzi DAXNER-HÖCK et HÖCK, 2009

10. p4, sin, GIN-1143-132.
11. m1, dex, GIN-1143-133.
12. M1, sin, GIN-1143-134.
13. M3, dex, GIN-1143-135.

Ramys sp. vel *Vasseuromys* sp.

14. m2, sin, GIN-1144-141.
15. m3, sin, GIN-1144-142.
16. M1–2, dex, GIN-1144-143.

Muscardinus pliocaenicus KOWALSKI, 1963

17. m1, sin, GIN-1144-161.
18. M2, sin, GIN-1143-142.

Neopetes cf. *hoeckarum* (DE BRUIJN, 1998)

19. m1, dex, GIN-1143-161.
20. M1–2, dex, GIN-1143-162.

?*Miopetaurista*

21. P4 or M1–2, dex, fragment, GIN-1143-171.

PLATE 1

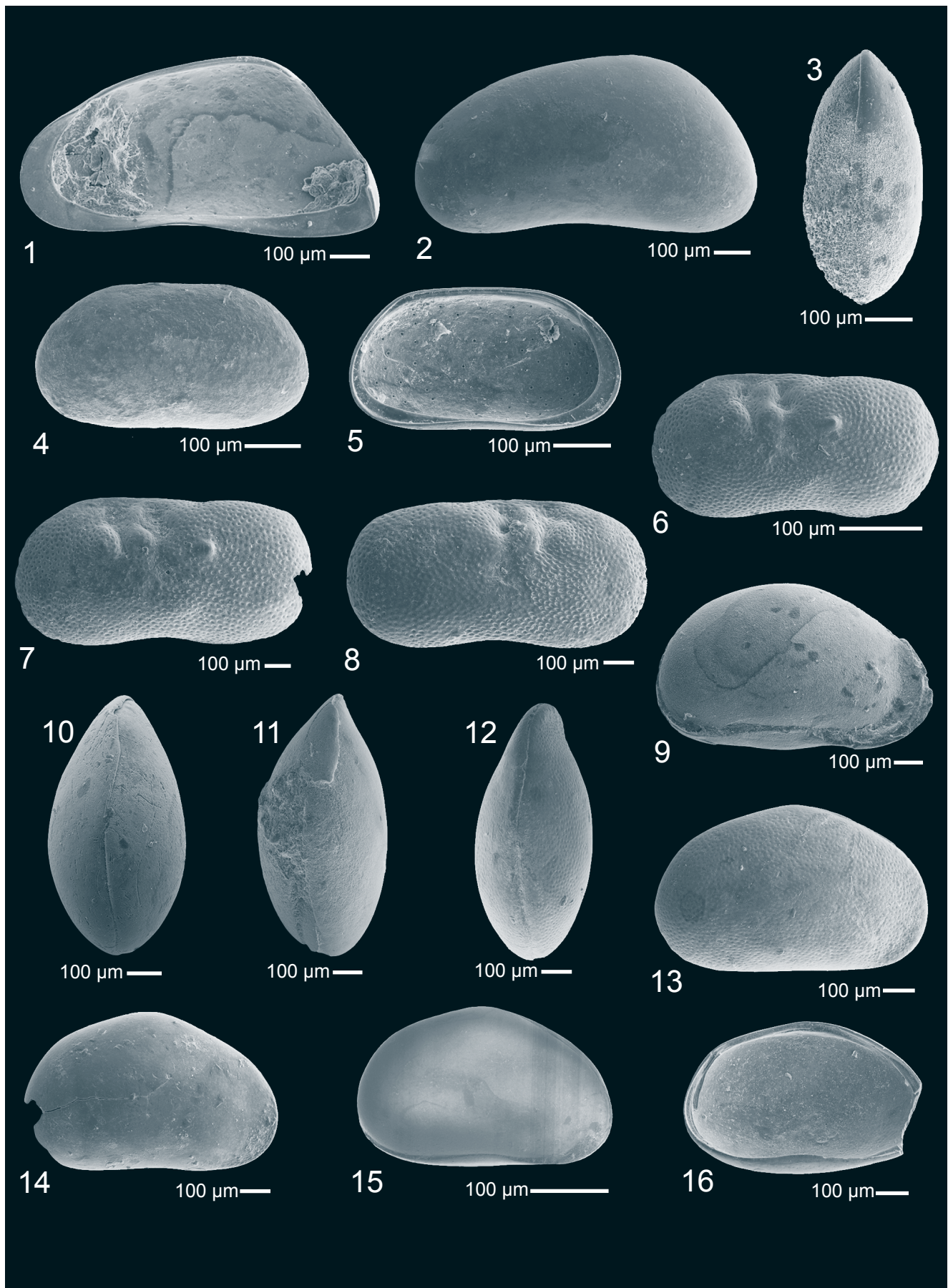
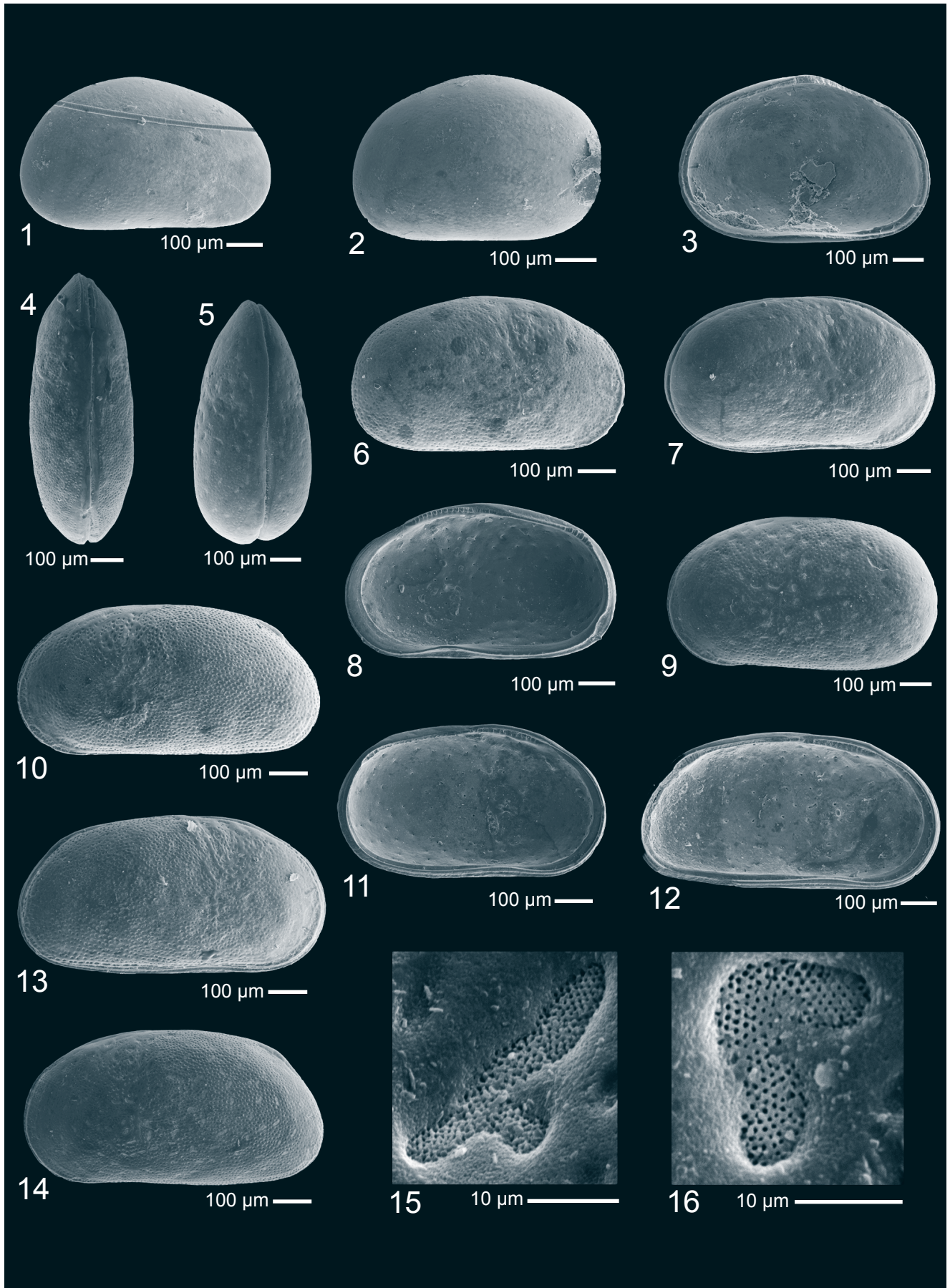
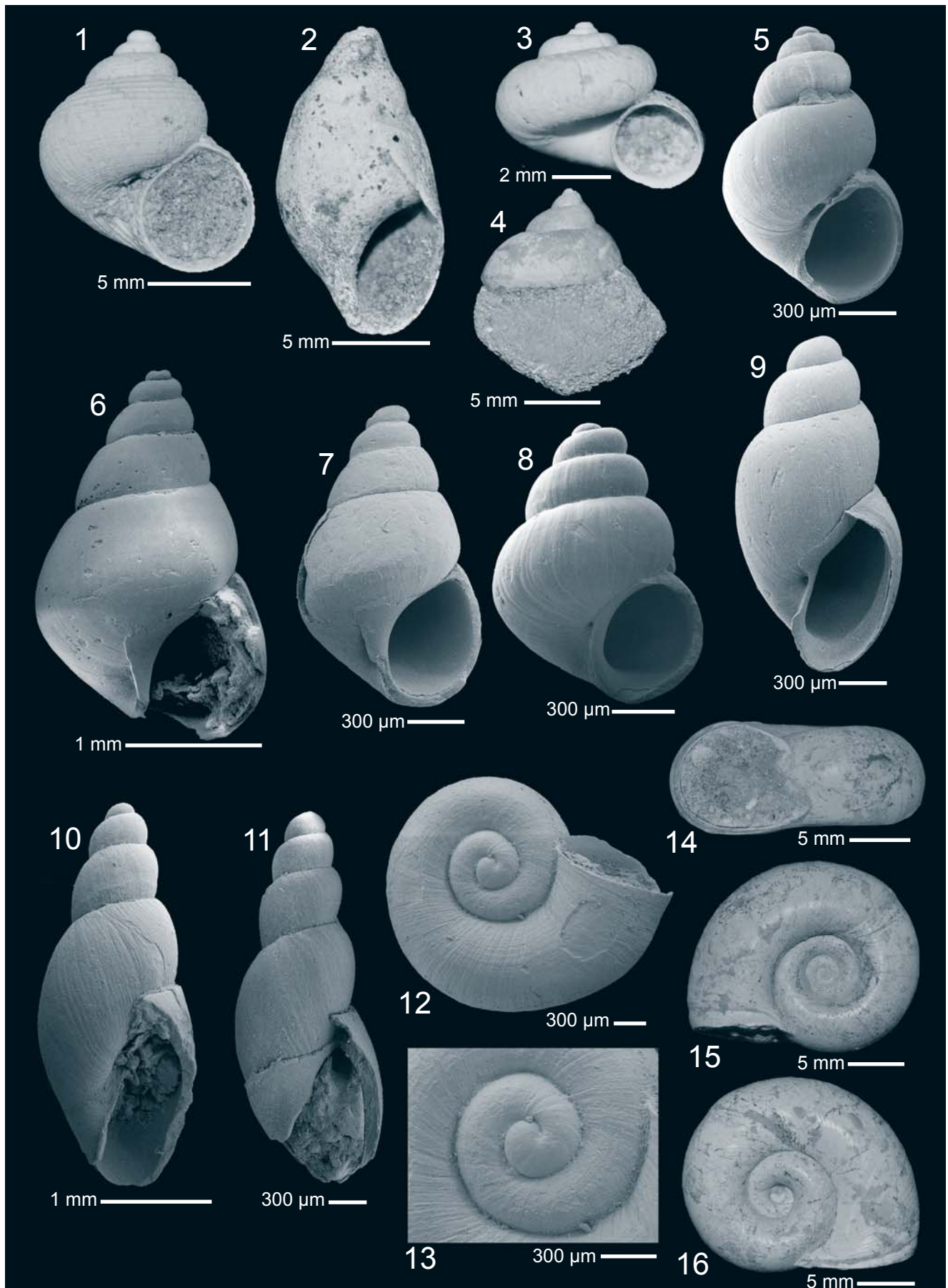
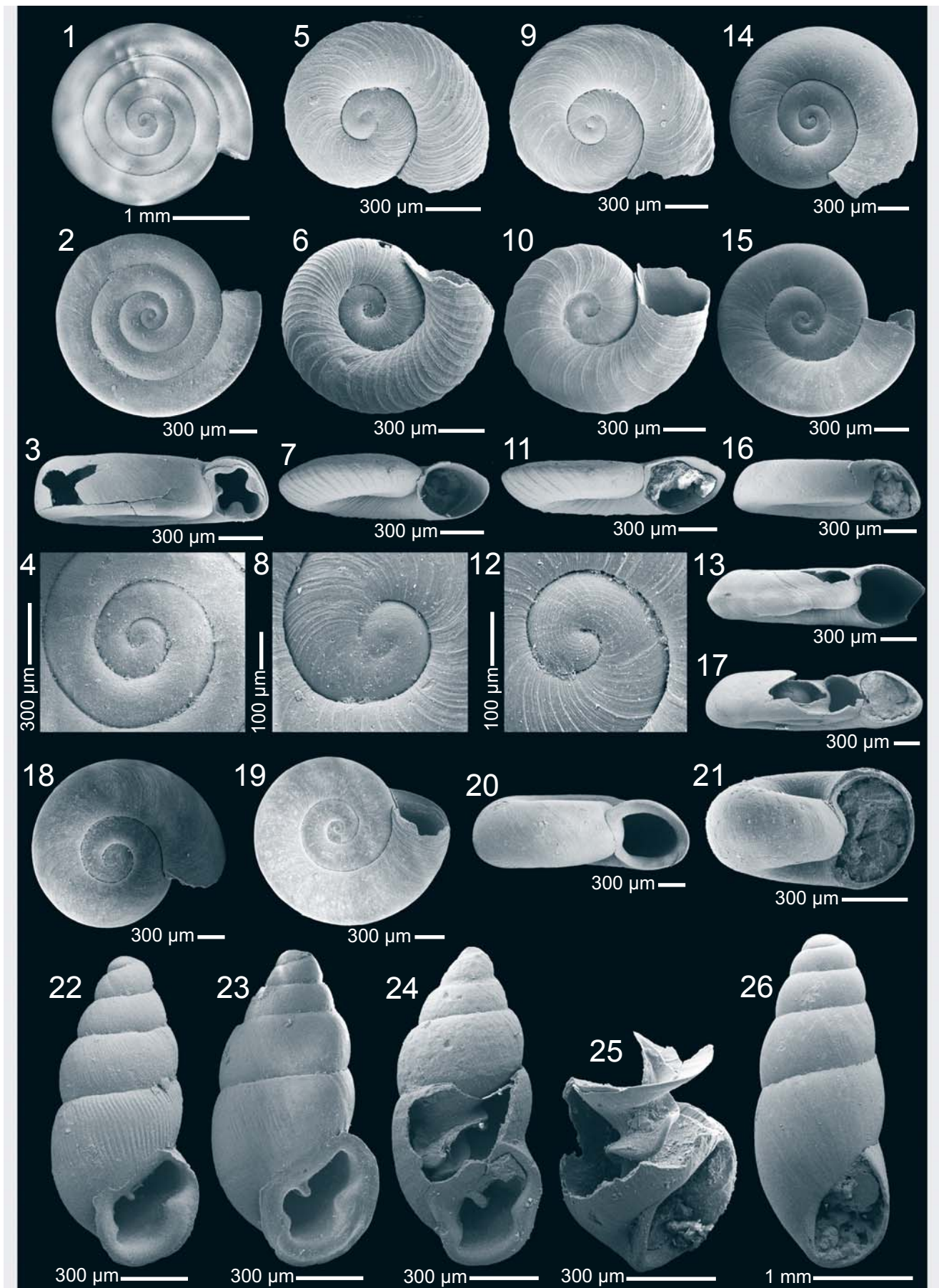


PLATE 2







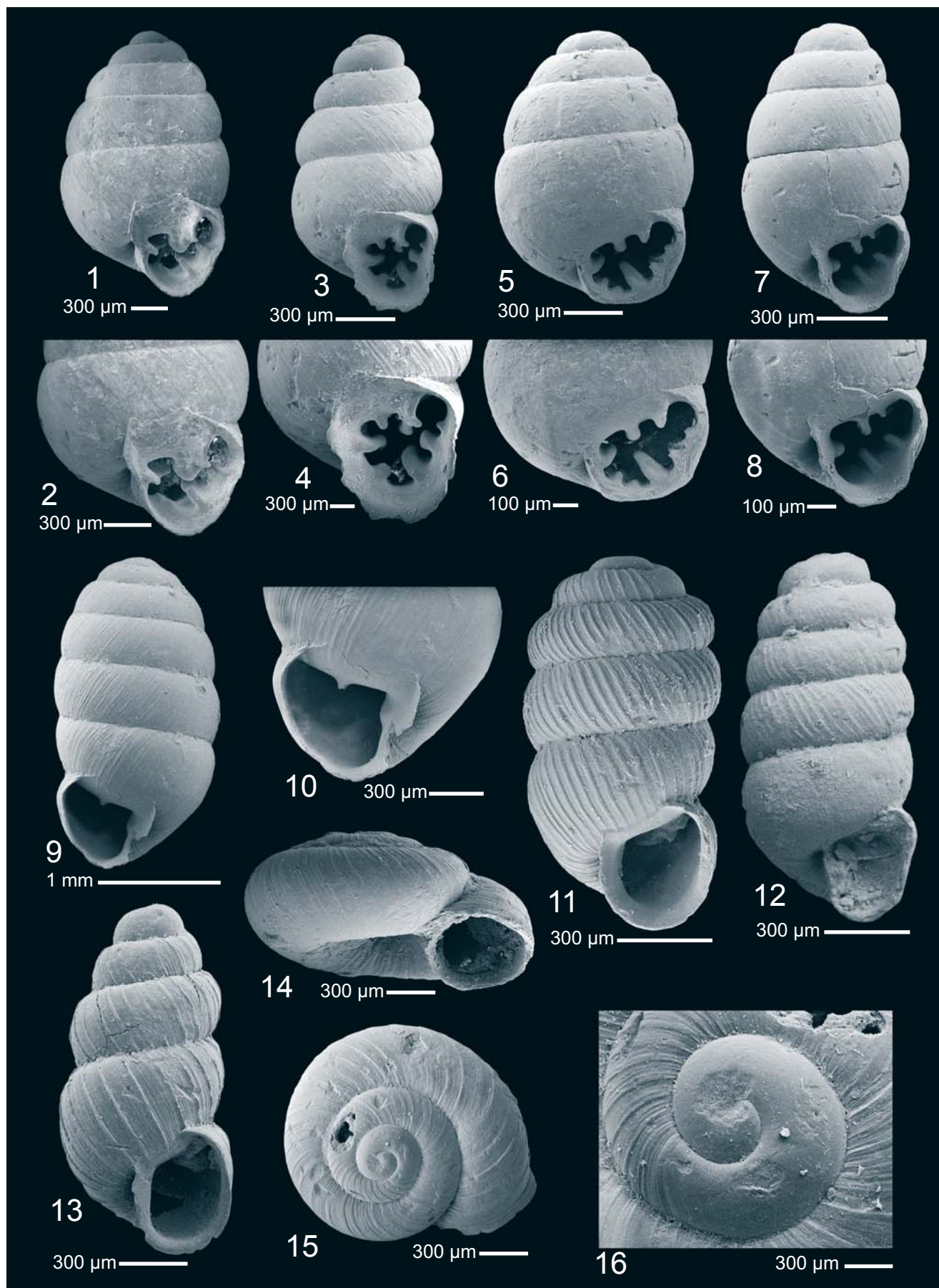
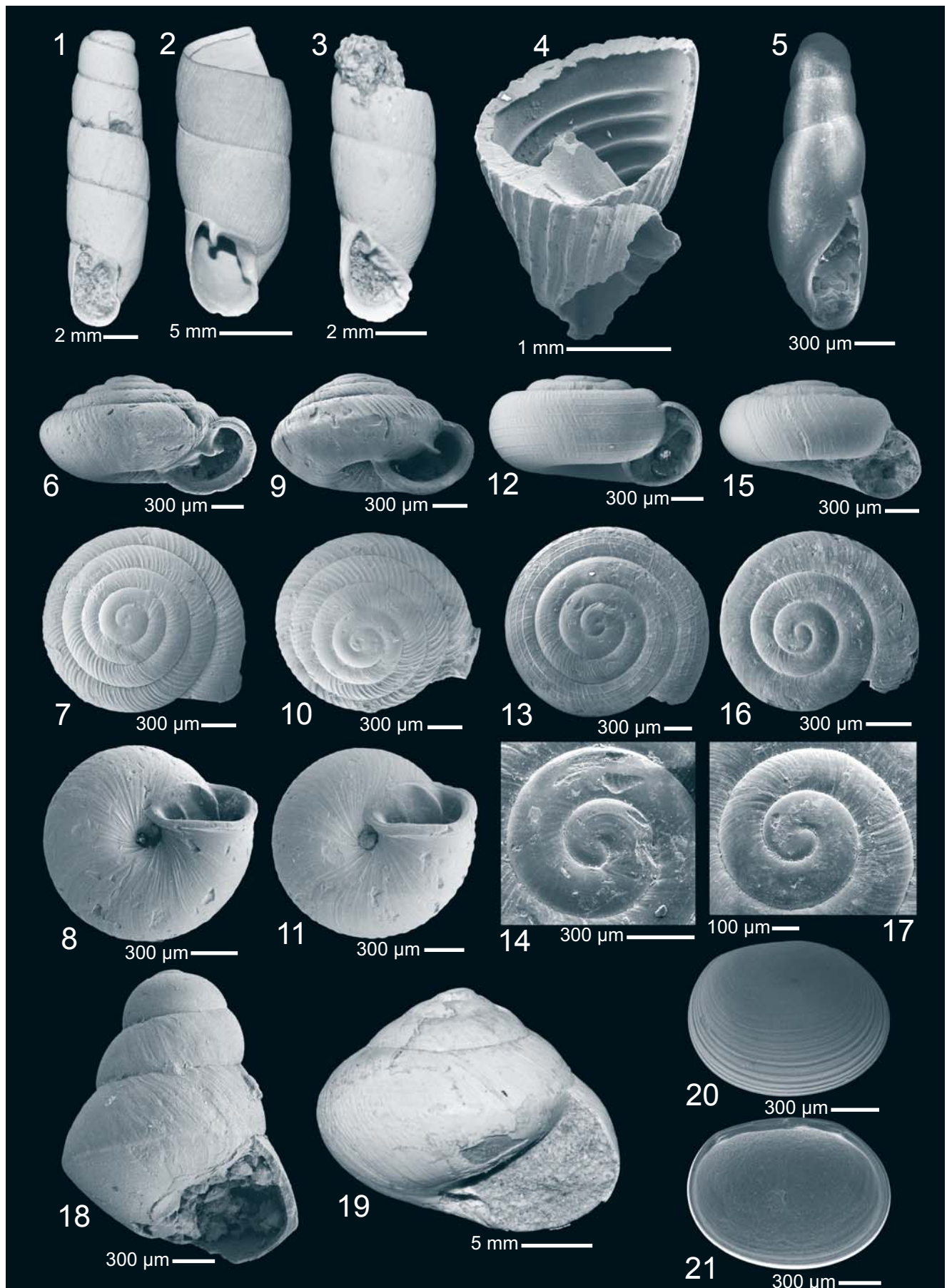


PLATE 6



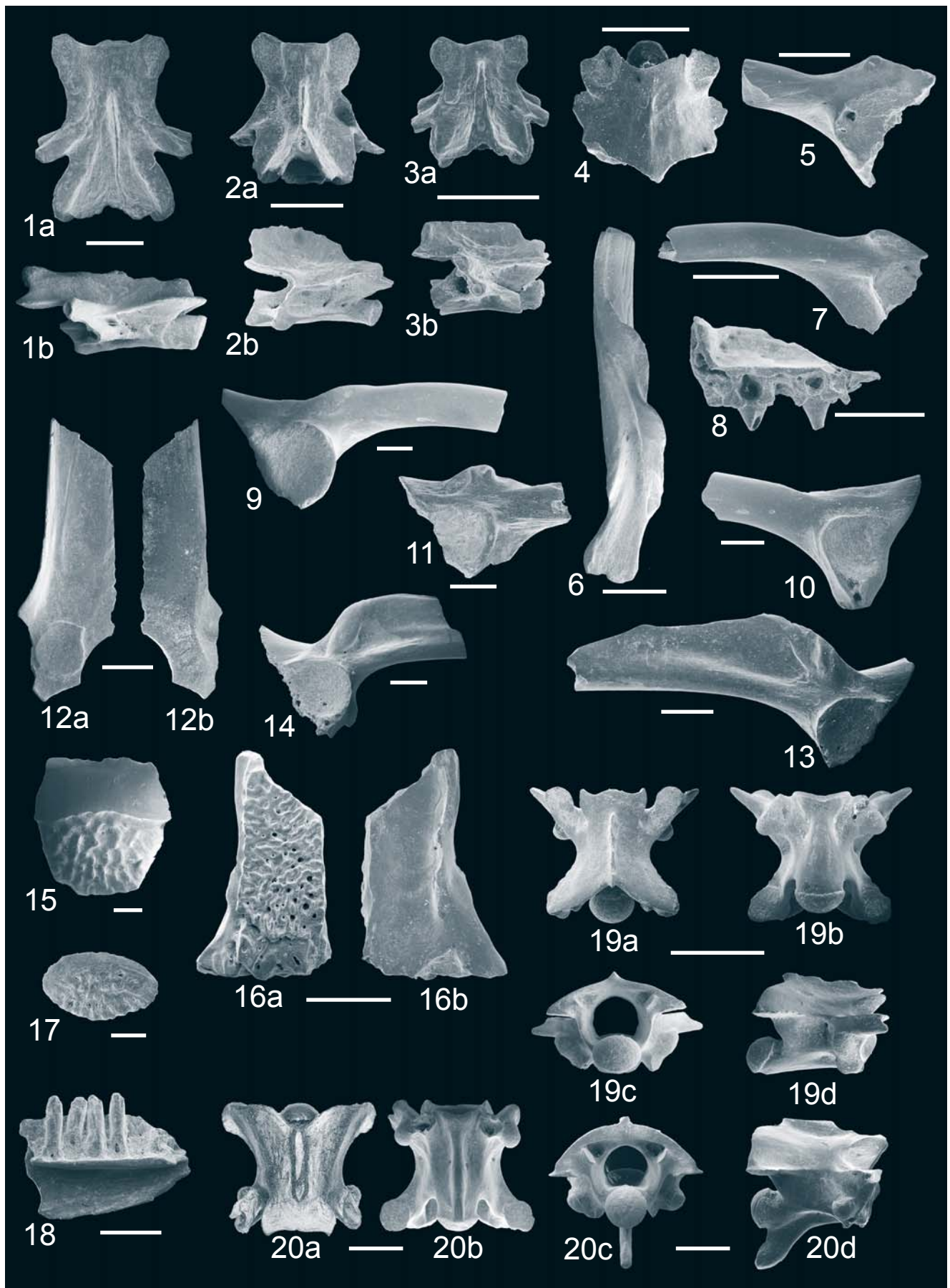


PLATE 8

