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Molluscs of the alluvial deposits of the Syra River valley (the Middle Urals, the Kama River basin, Russia)

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ABSTRACT. The malacocomplexes studied in alluvial deposits of the Syra River valley formed during the Late Pleistocene to the Middle Holocene. They include 46 species from 15 families (Sphaeriidae, Bithyniidae, Valvatidae, Lymnaeidae, Physidae, Planorbidae, Carychiidae, Succineidae, Cochlicopidae, Valloniidae, Vertiginidae, Discidae, Pristilomatidae, Gastrodontidae, Hygromiidae). Most of the registered freshwater mollusc species tend to inhabit either permanent, weakly flowing or stagnant waterbodies that are overgrown with macrophytes or with signs of swamping; or temporary drying ponds and swamps. Species composition of terrestrial snails indicates the presence of highly humid conditions in their habitats. Perhaps there were temporary swampy waterbodies at the site of the modern riverbed and the composition of the fossil malacofauna along with ecological preferences of found mollusc species represents the specific features of the palaeoecological conditions of past ages.

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Моллюски аллювиальных отложений долины реки Сыры (Средний Урал, бассейн реки Камы)

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РЕЗЮМЕ. Малакокомплексы изученных аллювиальных отложений долины реки Сыры сформировались на рубеже позднего плейстоцена – середины голоцена. Они включают 46 видов из 15 семейств (Sphaeriidae, Bithyniidae, Valvatidae, Lymnaeidae, Physidae, Planorbidae, Carychiidae, Succineidae, Cochlicopidae, Valloniidae, Vertiginidae, Discidae, Pristilomatidae, Gastrodontidae, Hygromiidae). Большинство изученных пресноводных моллюсков обитают либо в постоянных, слабопроточных или стоячих водоёмах, заросших или с признаками заболачивания, либо во временных пересыхающих прудах и болотах. Видовой состав наземных моллюсков свидетельствует о наличии увлажнённых условий в местах их обитания. Возможно, на месте современного русла реки существовали временные заболоченные водоёмы, а состав ископаемой малакофауны и экологические предпочтения изученных моллюсков отражают особенности палеоэкологических условий прошлых эпох.

Introduction

Fossil continental (freshwater and terrestrial) molluscs are known to have significant biostratigraphic value. The sequence of fossil continental malacofaunas can serve as a paleontological basis for detailed sediment stratigraphy [Danukalova, 1990, 2010; Zhidovinov, Kanevskaya, 2013; Silantyev, 2016]. By studying fossil malacofaunas found in sediments, it is possible to reconstruct the paleoclimatic conditions that existed in the study area during past geological periods [Yakovlev *et al*., 2003, 2004; Danukalova *et al*., 2018; Osipova, Danukalova, 2021]. For example, both the species composition and ecology of collected species may reflect climate changes during glacial and interglacial periods [Kuznetsov *et al*., 1998]. Conversely, analysis of the species composition of fossil molluscs may help identify possible pathways for the formation of modern malacofauna in different regions during the postglacial period.

Considering the significant ecosystem and biostratigraphic importance of molluscs, it is relevant to study both recent and fossil malacofaunas of particular regions; as such, research is essential for addressing various problems in biogeography, faunogenesis, stratigraphy, and ecology.

The aim of this study is to investigate the malacocomplexes of alluvial deposits in the Syra River valley (the Middle Urals, the Kama River basin) and to reconstruct the palaeoecological conditions of the studied area in the late Pleistocene – middle Holocene. The data on the fossil Quaternary molluscs of the Syra River valley are practically absent from the literature. Similar research has been conducted in adjacent regions, specifically in the Southern Urals, along the valleys of the Belaya and the Kama River basins [Osipova, 2011]. However, the information on

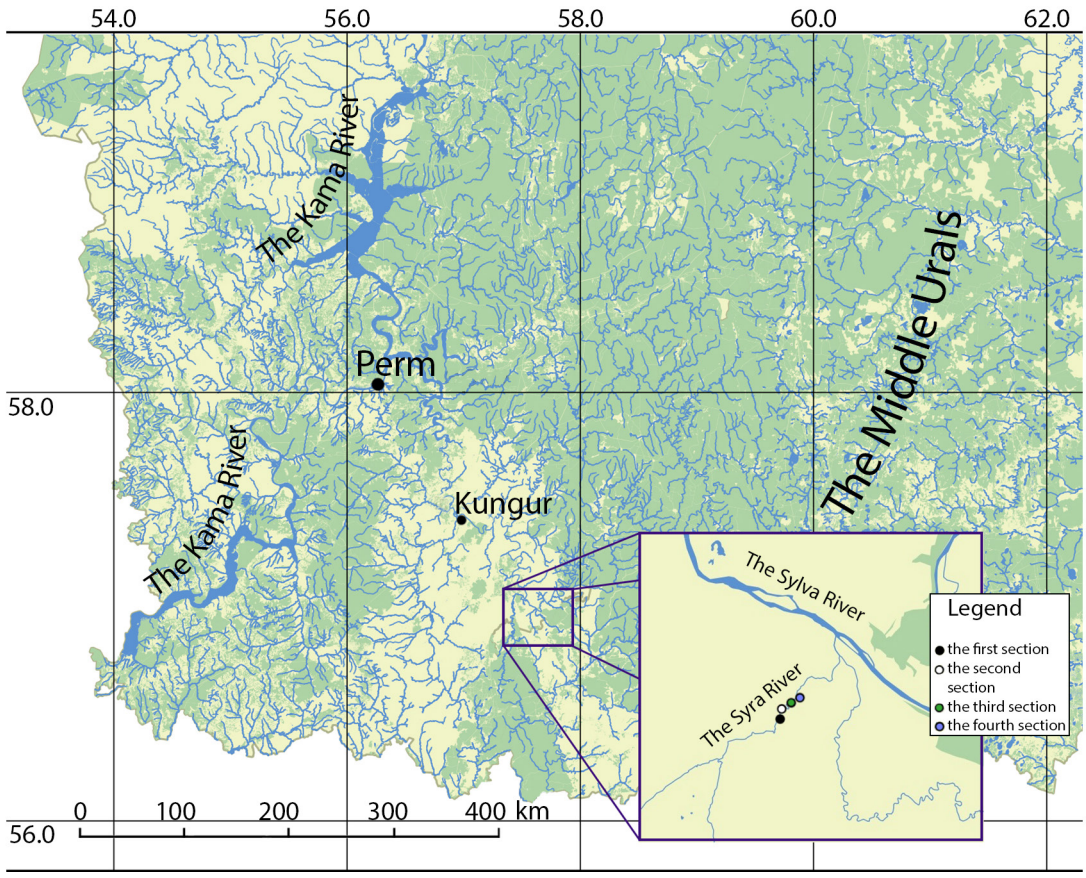

FIG. 1. Map of the studied area, showing the sampling station.

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the Quaternary continental molluscs of the Middle Urals remains rather fragmentary.

Material and methods

The material for this study was collected by the author in the Suksunsky District of Perm Krai in August 2020 and May 2021. Samples were taken from four sections of the floodplain terrace situated in the lower course of the Syra River (Figs 1, 2).

The fossil molluscs were collected using generally accepted methods [Yakovlev *et al*., 2003; Osipova, Danukalova, 2021] by dry and wet sieving the sediments through sieves with mesh sizes of 0.5, 1.0 and 2.0 mm. A total of 2130 specimens of shells of terrestrial and freshwater molluscs was sampled and examined.

Additionally, peat samples were collected for determination of the absolute age of the deposits using radiocarbon dating (^{14}C). The samples were sent for analysis to the Herzen State Pedagogical University (Saint-Petersburg, Russia). The graphs obtained from the study of peat and wood samples by radiocarbon dating present data on absolute age (BP – before present). This value is derived from measuring the concentration of the radioactive isotope ^{14}C in the sample and is expressed in years before 1950, which is used as the reference point [Mook, Streurman, 1983; Zazovskaya, 2016].

Taxonomic identification of sampled fossil molluscs was made using keys and information of several works [Likharev, Rammelmeier, 1952; Strauch, 1976; Schileyko, 1984; Schileyko, Likharev, 1986; Korniushin, 1996; Sysoev, Schileyko, 2009; Balashov, 2016; Bogatov, Kijashko, 2016; Kijashko *et al*., 2016; Aksenova *et al*., 2018; Glöer, 2019; Bespalaya *et al*., 2024]. Some materials examined during this study were compared with previously identified specimens kept in the collection of terrestrial and freshwater molluscs maintained at the Zoological Institute of the Russian Academy of Sciences (ZIN RAS, Saint-Petersburg).

The morphology of shells was examined and shell photos were made under a Nikon SMZ25 stereoscopic microscope (ZIN RAS). The size and clarity of shell images was adjusted by using Adobe Photoshop 23.4.2. software. The same software was applied for assembling separate images into plates. The studied specimens of fossil shells are stored in the ZIN RAS.

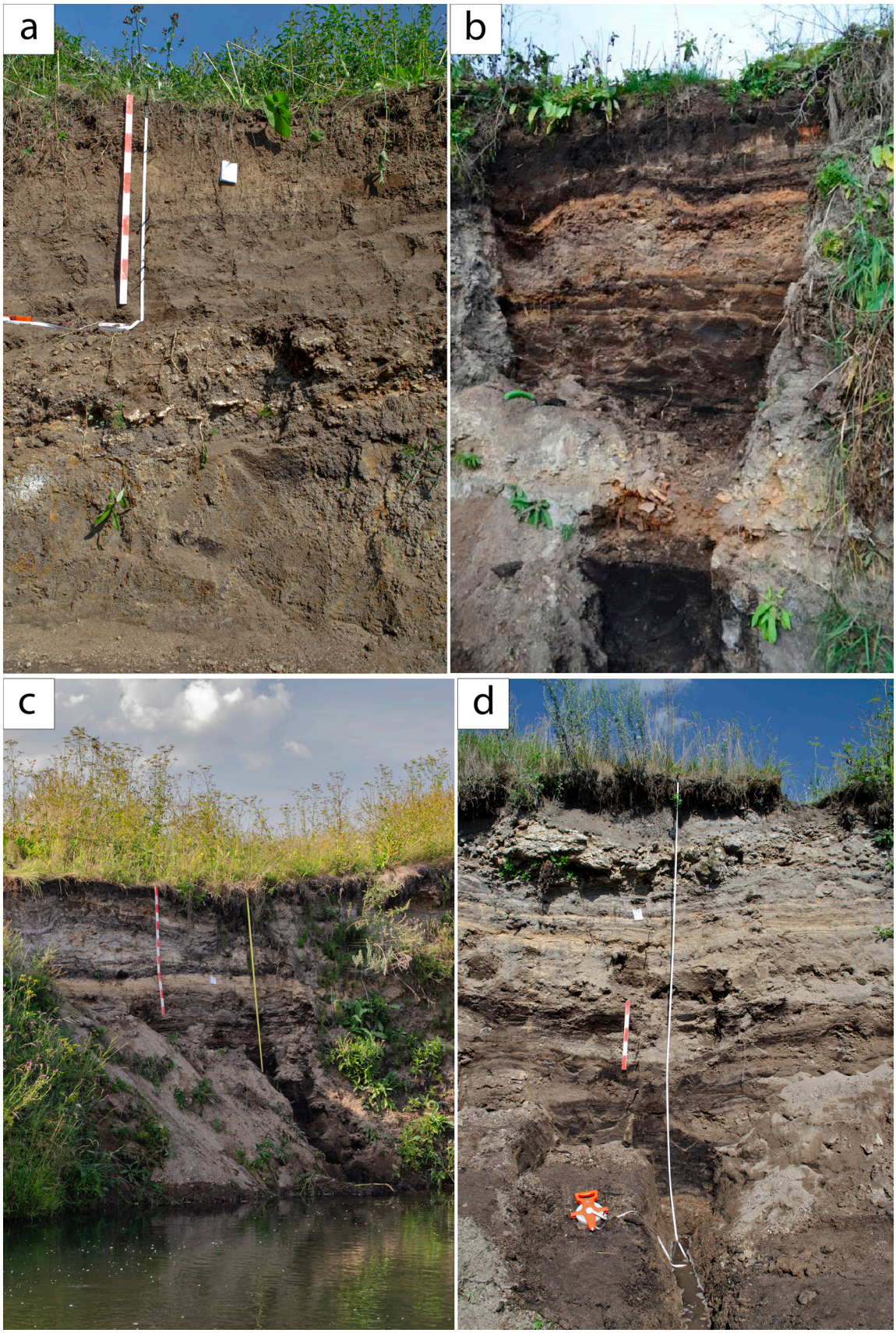

FIG. 2. Photos of the studied sections of the floodplain terrace of the Syra River: a – the first section; b – the second section; c – the third section; d – the fourth section.

РИС. 2. Фото изученных разрезов пойменной террасы реки Сыры: a – первый разрез; b – второй разрез; c – третий разрез; d – четвертый разрез.

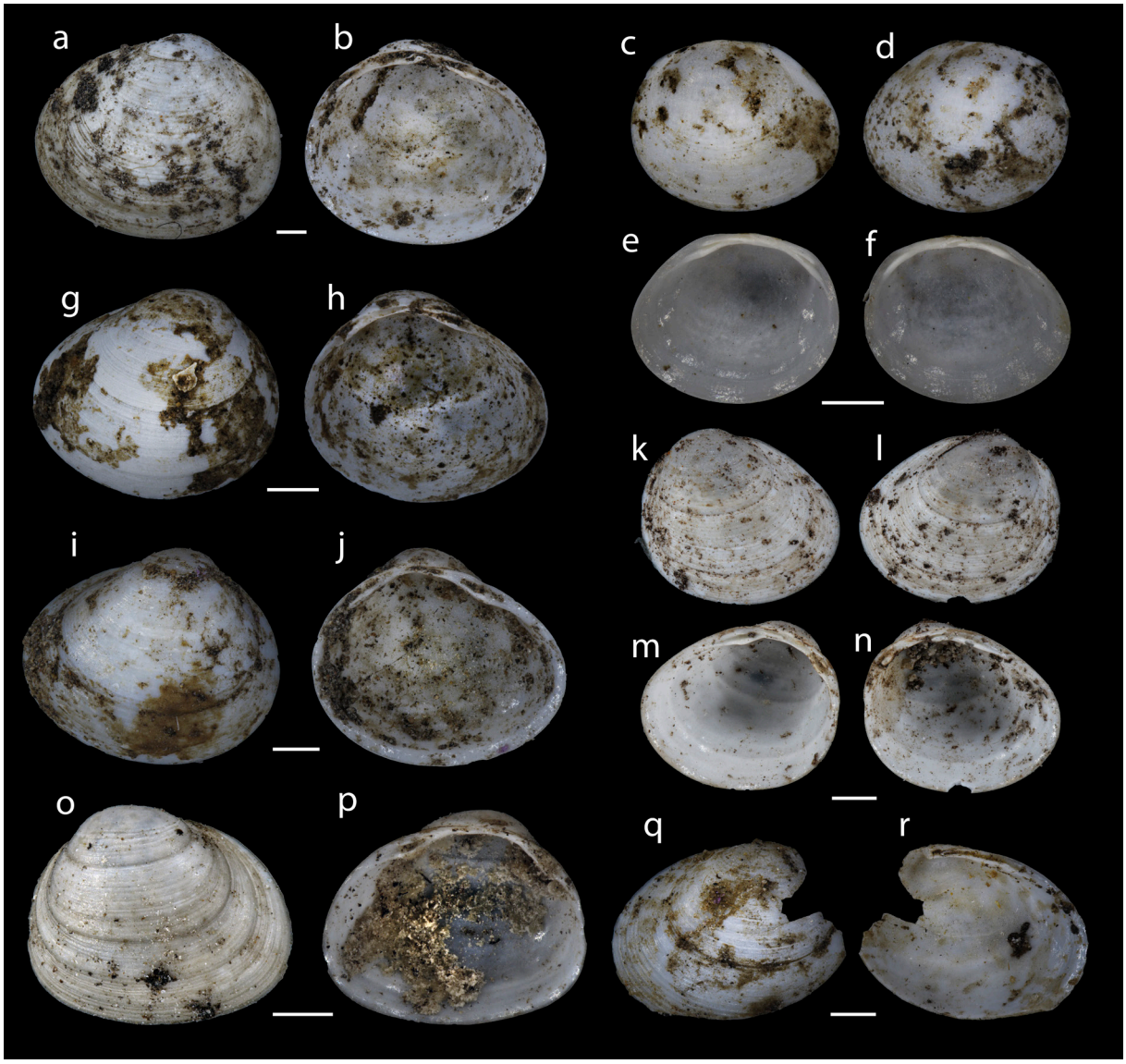

FIG. 3. Molluscs of Sphaeriidae family of alluvial deposits of the Syra River valley: *Euglesa casertana* (a, b); *E. nitida* (c-f); *E. obtusalis* (g, h); *E. lilljeborgii* (i, j); *E. subtruncata* (k-n); *E. milium* (o, p), *E. pseudosphaerium* (q, r). Scale bar 0.5 mm.

РИС. 3. Моллюски семейства Sphaeriidae аллювиальных отложений долины реки Сыры: *Euglesa casertana* (a, b); *E. nitida* (c-f); *E. obtusalis* (g, h); *E. lilljeborgii* (i, j); *E. subtruncata* (k-n); *E. milium* (o, p), *E. pseudosphaerium* (q, r). Шкала 0.5 мм.

The mapping of sampling sites of molluscs was realized using software QGIS 2.18.25 «Las Palmas» on the cartographic basis taken from http://nextgis.ru/.

The delineation of ecological groups of molluscs is based on following works [Korniushin, 1996; Khokhutkin *et al*., 2000; Bogatov, Kijashko, 2016; Kijashko *et al*., 2016; Shikov, 2025] and our own observations.

Stacked charts were constructed using Past 4.16c software [Hammer *et al*., 2001], with subsequent editing in Inkscape 1.4.2. software.

Results

The list of the fossil molluscs identified in the Syra River valley deposits comprises 46 species, among them: 29 freshwater species from six families and 13 genera; and 17 terrestrial species from 9 families and 11 genera.

Freshwater molluscs are represented by the families Sphaeriidae (Fig. 3): *Euglesa casertana* (Poli, 1791), *E. nitida* (Jenyns, 1832), *E. obtusalis* (Lamarck, 1818), *E. lilljeborgii* (Clessin, 1886), *E. subtruncata* (Malm, 1855), *E. milium* (Held, 1836), *E. pseudosphaerium* (Ehrmann, 1933); Bithyniidae (Fig. 4): *Bithynia troschelii* (Paasch, 1842); Valvatidae (Fig. 4): *Valvata cristata* O.F. Müller, 1774, *V. macrostoma* Mörch, 1864, *V. studeri* Boeters et Falkner, 1998, *V. piscinalis* O.F. Müller, 1774, *V. ambigua* Westerlund, 1873; Lymnaeidae (Fig. 4): *Stagnicola palustris* (O.F. Müller, 1774), *S. cal-*

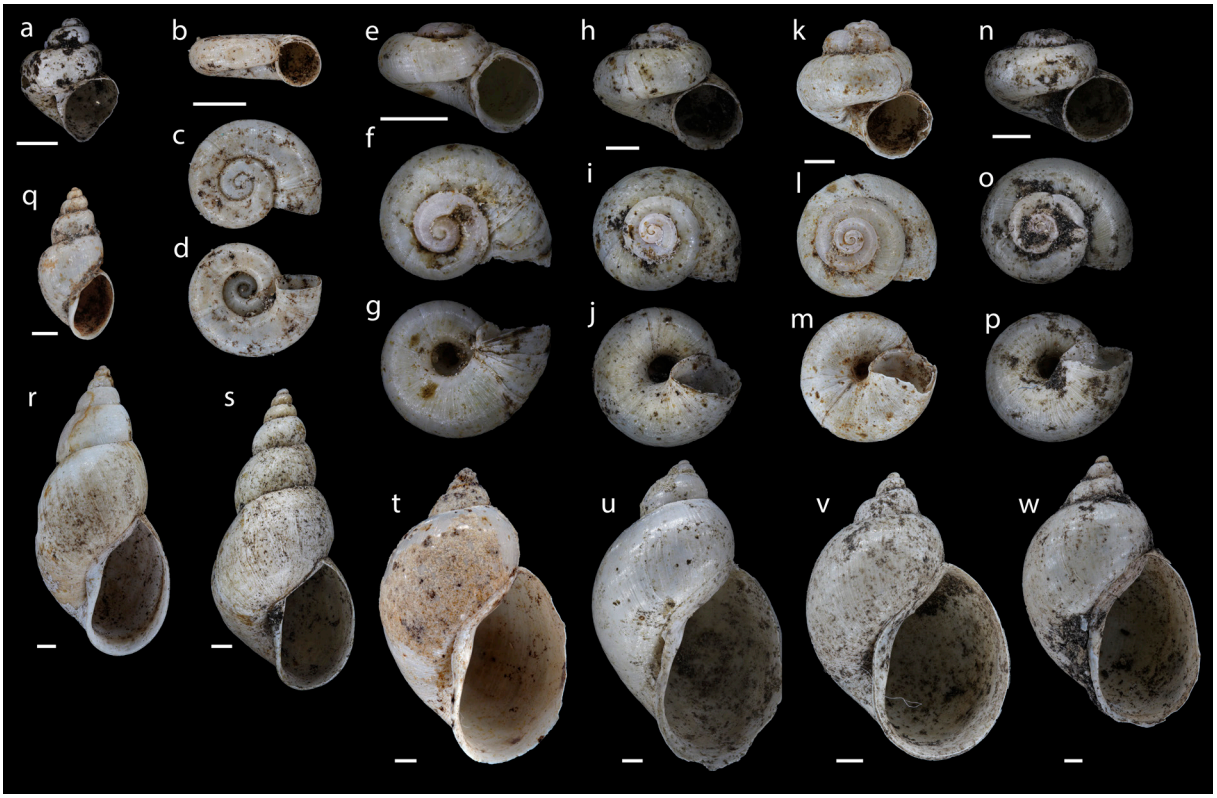

FIG. 4. Molluscs of Bithyniidae, Valvatidae and Lymnaeidae families of alluvial deposits of the Syra River valley: *Bithynia troschelii* (a), *Valvata cristata* (b-d), *V. macrostoma* (e-g), *V. studeri* (h-j), *V. piscinalis* (k-m), *V. ambigua* (n-p), *Galba truncatula* (q), *Stagnicola palustris* (r), *S. callomphala* (s), *Peregriana peregra* (t), *Ampullaceana balthica* (u), *A. intermedia* (v), *A. lagotis* (w). Scale bar 1 mm.

РИС. 4. Моллюски семейств Bithyniidae, Valvatidae и Lymnaeidae аллювиальных отложений долины реки Сыры: *Bithynia troschelii* (a), *Valvata cristata* (b-d), *V. macrostoma* (e-g), *V. studeri* (h-j), *V. piscinalis* (k-m), *V. ambigua* (n-p), *Galba truncatula* (q), *Stagnicola palustris* (r), *S. callomphala* (s), *Peregriana peregra* (t), *Ampullaceana balthica* (u), *A. intermedia* (v), *A. lagotis* (w). Шкала 1 мм.

lomphala (Servain, 1881), *Galba truncatula* (O.F. Müller, 1774), *Peregriana peregra* (O.F. Müller, 1774), *Ampullaceana balthica* (Linnaeus, 1758), *A. intermedia* (Lamarck, 1822), *A. lagotis* (Schrank, 1803); Physidae (Fig. 5): *Aplexa hypnorum* (Linnaeus, 1758); Planorbidae (Fig. 5): *Anisus vortex* (Linnaeus, 1758), *Armiger crista* (Linnaeus, 1758), *Bathyomphalus contortus* (Linnaeus, 1758), *B. crassus* (Da Costa, 1778), *B. dispar* (Westerlund, 1871), *Gyraulus albus* (O.F. Müller, 1774), *G. acronicus* (Férussac, 1807), *Planorbarius corneus* (Linnaeus, 1758).

The highest taxonomic richness of freshwater molluscs is recorded for the second and fourth sections, slightly lower – for the first section, and the lowest – for the third section (Fig. 8). The families Lymnaeidae, Planorbidae, and Sphaeriidae are the most numerous in most sections. Valvatids are somewhat fewer in number, and the fewest taxa belonged to the families Physidae and Bithyniidae. The latter families are present only in the second and fourth sections, respectively.

The following families and species of terrestrial molluscs have been identified: Carychiidae (Fig. 6): *Carychium tridentatum* (Risso, 1826); Succineidae (Fig. 6): *Succinea putris* (Linnaeus, 1758), *Succinella oblonga* (Draparnaud, 1801), *Oxyloma elegans* (Risso, 1826), *O. sarsii* (Esmark, 1886); Cochlicopidae (Fig. 6): *Cochlicopa lubrica* (O.F. Müller, 1774), *C. nitens* (Gallenstein, 1852); Valloniidae (Fig. 6): *Vallonia costata* (O.F. Müller, 1774), *V. pulchella* (O.F. Müller, 1774), *V. tenuilabris* (Al. Braun, 1843); Vertiginidae (Fig. 7): *Vertigo antivertigo* (Draparnaud, 1801), *V. modesta* (Say, 1824), *V. angustior* (Jeffreys, 1830); Discidae (Fig. 7): *Discus ruderatus* (W. Hartmann, 1821); Pristilomatidae (Fig. 7): *Vitrea crystallina* (O.F. Müller, 1774); Gastrodontidae (Fig. 7): *Aegopinella minor* (Stabile, 1864); Hygromiidae (Fig. 7): *Trochulus hispidus* (Linnaeus, 1758).

The highest taxonomic diversity of terrestrial molluscs is recorded for the second and fourth sections, slightly lower – for the first section, and the lowest – for the third section (Fig. 9). The families Succineidae and Valloniidae are the most abundant in most sections. Slightly fewer taxa are represented in the family Cochlicopidae, and the smallest number

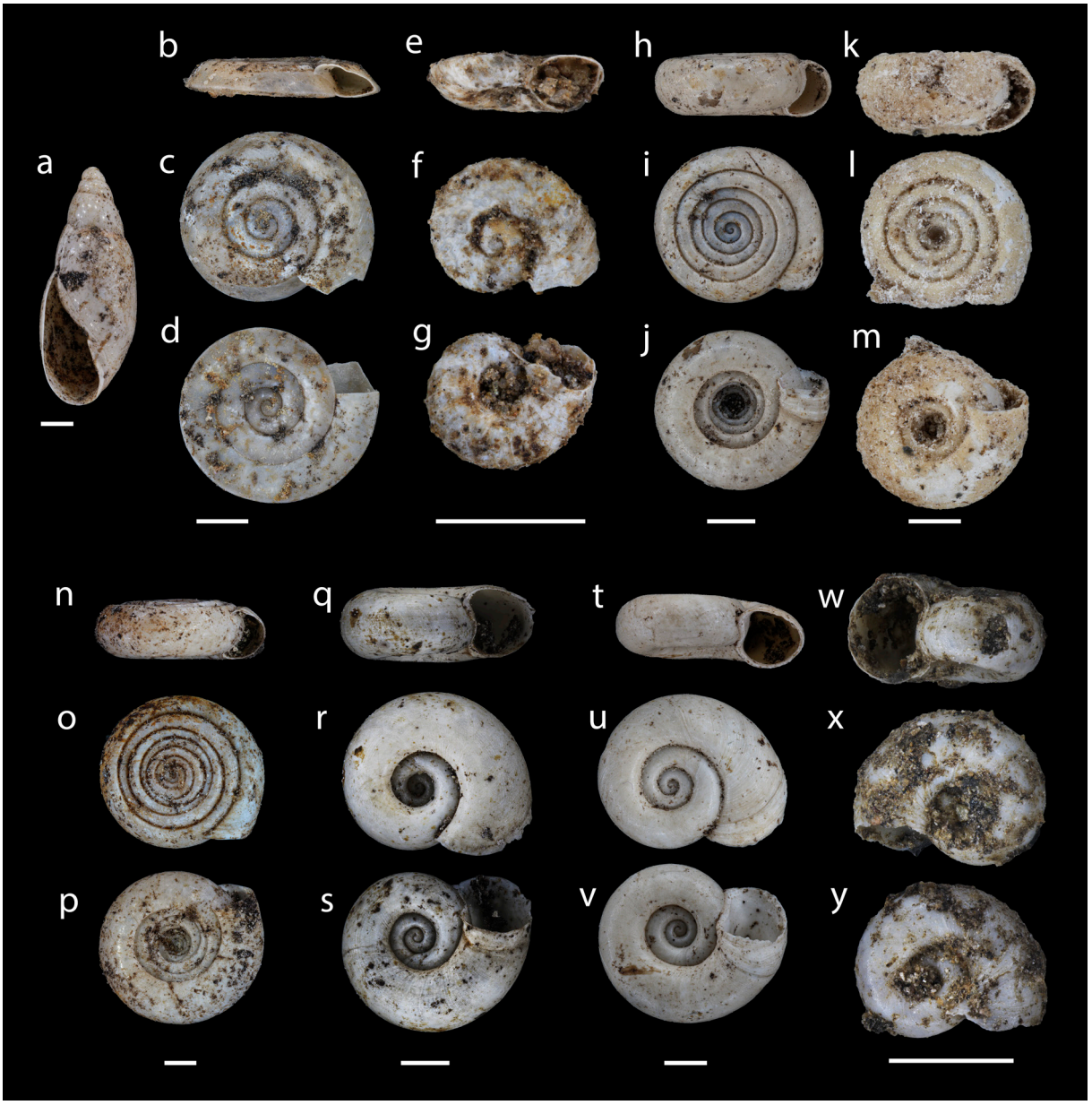

FIG. 5. Molluscs of Physidae and Planorbidae families of alluvial deposits of the Syra River valley: *Aplexa hypnorum* (a), *Anisus vortex* (b-d), *Armiger crista* (e-g), *Bathyomphalus contortus* (h-j), *B. crassus* (k-m), *B. dispar* (n-p), *Gyraulus albus* (q-s), *G. acronicus* (t-v), *Planorbarius corneus* (w-y). Scale bar 1 mm.

РИС. 5. Моллюски семейств Physidae и Planorbidae аллювиальных отложений долины реки Сыры: *Aplexa hypnorum* (a), *Anisus vortex* (b-d), *Armiger crista* (e-g), *Bathyomphalus contortus* (h-j), *B. crassus* (k-m), *B. dispar* (n-p), *Gyraulus albus* (q-s), *G. acronicus* (t-v), *Planorbarius corneus* (w-y). Шкала 1 мм.

of taxa is registered among Carychiidae, Discidae, Pristilomatidae, Gastrodontidae, Hygromiidae, each of which is represented by one genus/species.

The third section is characterized by the lowest taxonomic richness of freshwater and terrestrial molluscs. This can be probably explained by acidic environmental conditions, as evidenced by the presence of a substantial peat layer with a thickness of 125–285 cm. Under such conditions, the shells could have either not been preserved or become unsuitable for subsequent identification. Furthermore, most horizons in the third section contained mostly shell fragments, complicating further taxonomic identification.

The registered freshwater mollusc species are associated with various habitat conditions. We identified five groups of species, which prefer: predominantly permanent waterbodies; predominantly temporary waterbodies; swampy waterbodies, slow-flowing streams, small rivers and ditches; and permanent flowing and non-flowing waterbodies.

In all sections, the major part of freshwater species found are inhabitants of permanent waterbodies

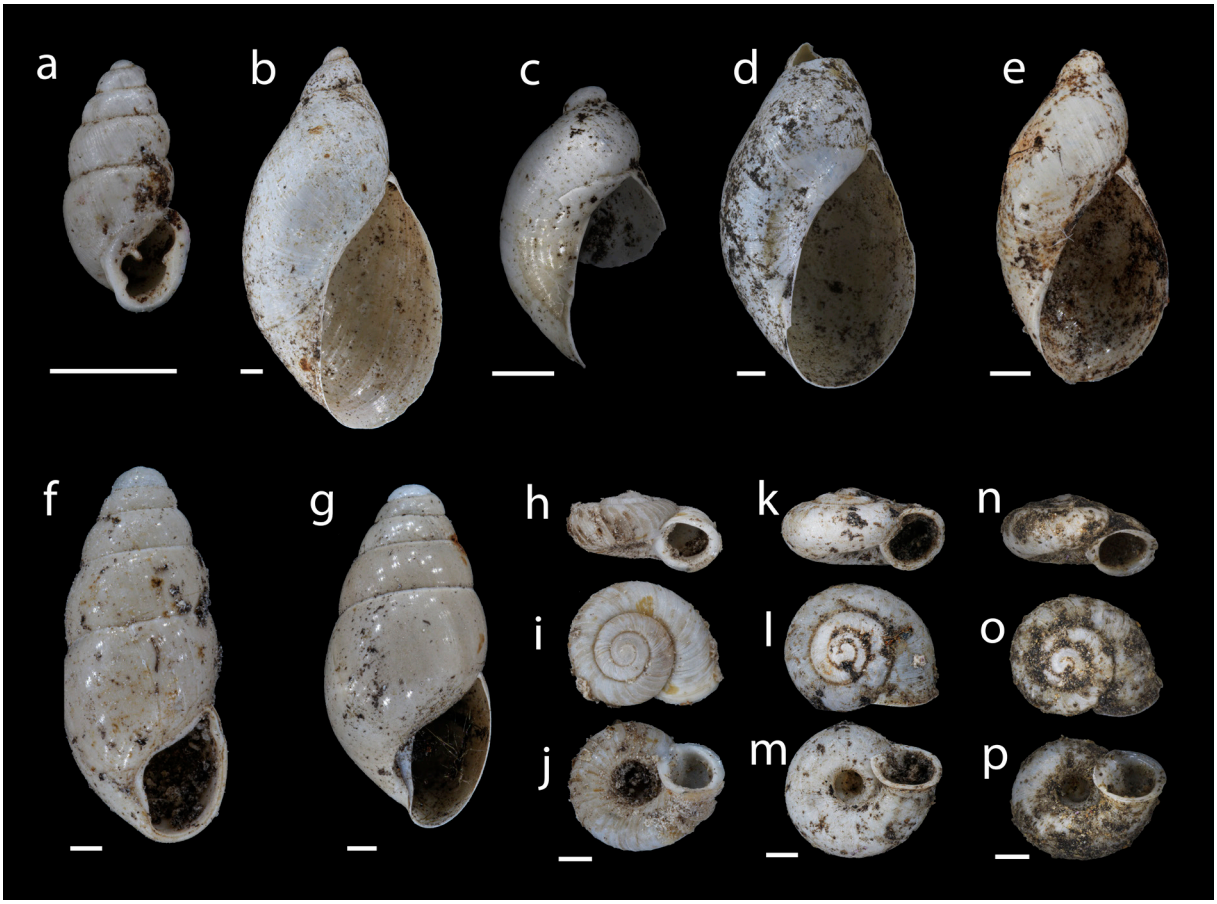

FIG. 6. Molluscs of Carychiidae, Succineidae, Cochlicopidae and Valloniidae families of alluvial deposits of the Syra River valley:*Carychium tridentatum* (a), *Succinea putris* (b), *Succinella oblonga* (c), *Oxyloma elegans* (d), *O. sarsii* (e), *Cochlicopa lubrica* (f), *C. nitens* (g), *Vallonia costata* (h-j); *V. pulchella* (k-m); *V. tenuilabris* (n-p). Scale bars: 1 mm (a-e), 0.5 mm (f-p).

РИС. 6. Моллюски семейств Carychiidae, Succineidae, Cochlicopidae и Valloniidae аллювиальных отложений долины реки Сыры: *Carychium tridentatum* (a), *Succinea putris* (b), *Succinella oblonga* (c), *Oxyloma elegans* (d), *O. sarsii* (e), *Cochlicopa lubrica* (f), *C. nitens* (g), *Vallonia costata* (h-j); *V. pulchella* (k-m); *V. tenuilabris* (n-p). Шкалы 1 мм (a-e), 0.5 мм (f-p).

(rivers, lakes, with varying flow velocities and degrees of macrophyte overgrowth) (Fig. 10). Second place goes to species that primarily inhabit temporary bodies of water. These include almost all recorded species of Lymnaeidae family, two species of the Valvatidae, and *Aplexa hypnorum* (Physidae). Of particular note here is the amphibiotic species *Galba truncatula* (Lymnaeidae), which occurs in the coastal zones of lakes, in splash zones, as well as in puddles, hollows and on wet meadow lands. The following are species that can exist in swampy conditions and in heavily overgrown waterbodies. Some of these species serve as indicators of swamping (several species of the genus *Euglesa*; *Bithynia troschelii* and *Anisus vortex*. Species that inhabit only permanent flowing or non-flowing waterbodies were found in certain horizons of the first and fourth sections. Their absolute numbers and proportion relative to the total number of specimens in horizons are insignificant.

The major part of the recorded terrestrial snails are mesophiles (*Succinea oblonga*, *Cochlicopa nitens*, *Vallonia costata*, *Vallonia pulchella*, *Vallonia tenuilabris*, *Vertigo antivertigo*, *Vertigo modesta*, *Vertigo angustior*, *Discus ruderatus*, *Vitrea crystallina*, *Aegopinella minor*) that prefer wet biotopes, such as swamps, wet meadow lands, river banks, as well as damp leaf litter in mixed and broad-leaved forests. Some of the encountered species are capable of inhabiting both wet and dry conditions (*Carychium tridentatum*, *Succinea putris*, *Oxyloma elegans*, *Oxyloma sarsi*, *Cochlicopa lubrica*, *Trochulus hispidus*). We classify them as psychrophiles.

Discussion

The species found in the studied samples are currently typical for most waterbodies and territories of Perm Prikamye [Ovchankova, 2021; Tartmina, Ovchankova, 2022]. However, large bivalves from the family Unionidae and clams of the genus *Sphaerium* were not registered within the studied malacocomplex. In modern conditions these bivalves

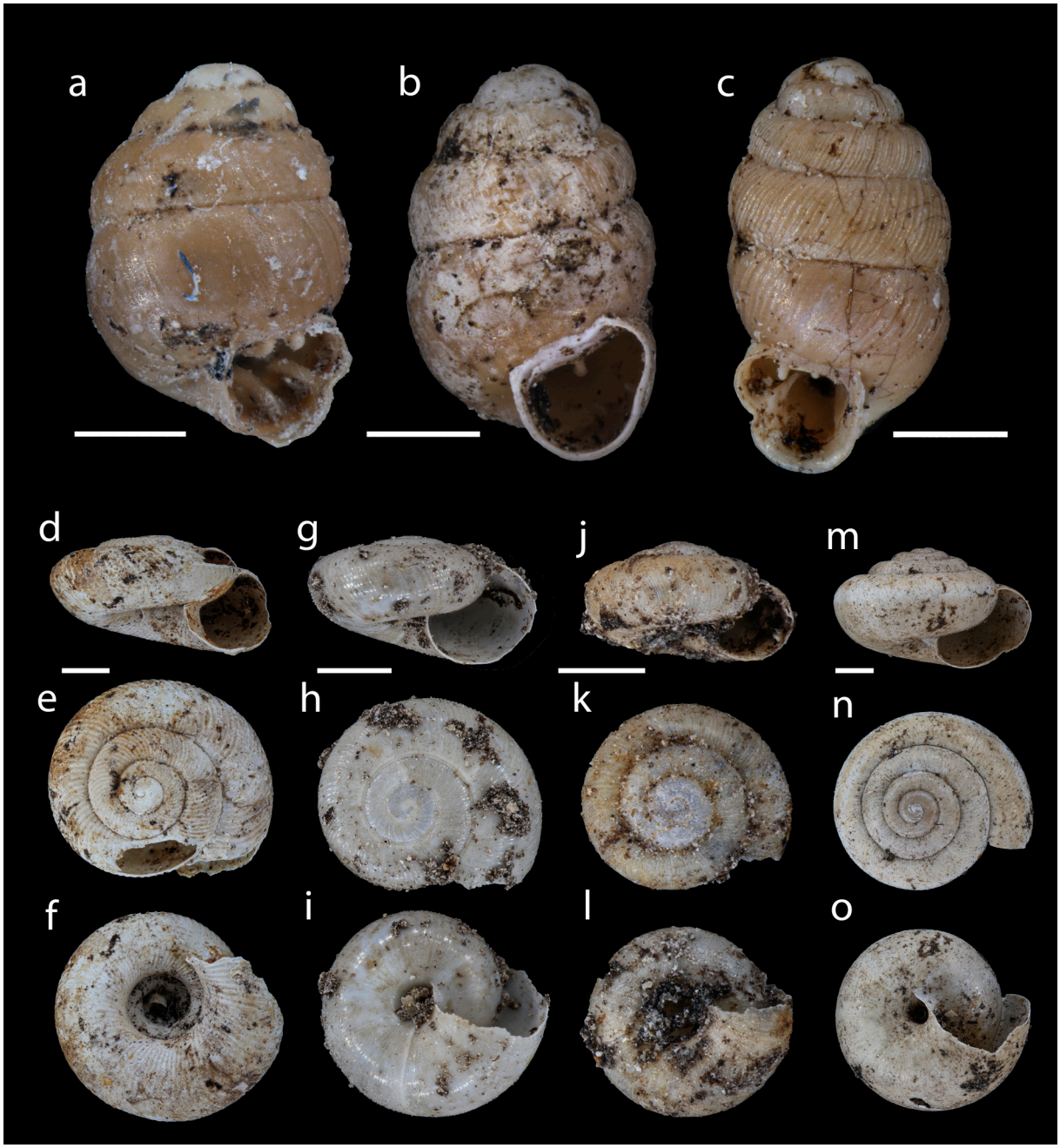

FIG. 7. Molluscs of Vertiginidae, Discidae, Pristilomatidae, Gastrodontidae and Hygromiidae families of alluvial deposits of the Syra River valley: *Vertigo antivertigo* (a), *V. modesta* (b), *V. angustior* (c), *Discus ruderatus* (d-f), *Vitrea crystallina* (g-i), *Aegopinella minor* (j-l), *Trochulus hispidus* (m-o). Scale bars: 1 mm (d-i, m-o), 0.5 mm (a-c), 0.1 mm (j-l).

РИС. 7. Моллюски семейств Vertiginidae, Discidae, Pristilomatidae, Gastrodontidae и Hygromiidae аллювиальных отложений долины реки Сыры: *ertigo antivertigo* (a), *V. modesta* (b), *V. angustior* (c), *Discus ruderatus* (d-f), *Vitrea crystallina* (g-i), *Aegopinella minor* (j-l), *Trochulus hispidus* (m-o). Шкалы 1 мм (d-i, m-o), 0.5 мм (a-c), 0.1 мм (j-l).

are predominantly found in major watercourses or large lakes. Their absence in the Syra valley deposits may be due to the habitat conditions that existed in the studied area in the past. The absolute age of peat samples taken from peat layers of the second and the fourth sections ranged from 4718±139 to 14507±261 radiocarbon years. It is evident that the peat horizons formed during the Late Pleistocene to the Middle Holocene under conditions of hydromorphism with stagnant moisture or minimal fluvial activity of the river. It is possible that waterbodies became overgrown with macrophytes and plant remains accumulated. Fauna can change during the development of floodplains and the formation of floodplain waterbodies. The swamping of low-lying areas leads to the gradual decline of rheophilic spe-

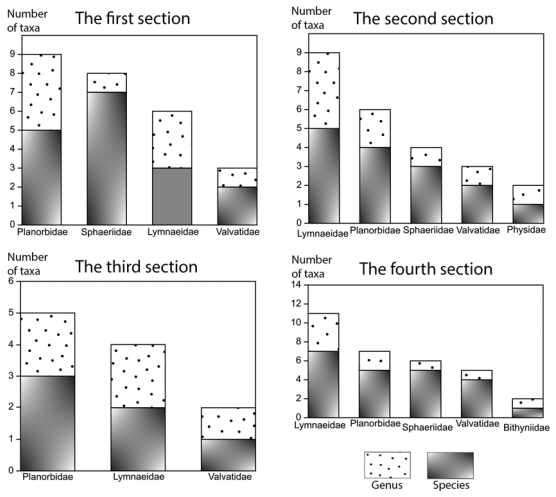

FIG. 8. Taxonomic structure of freshwater molluscs. The families are arranged along the x-axis.

РИС. 8. Таксономическая структура пресноводных моллюсков. По оси абсцисс – семейства.

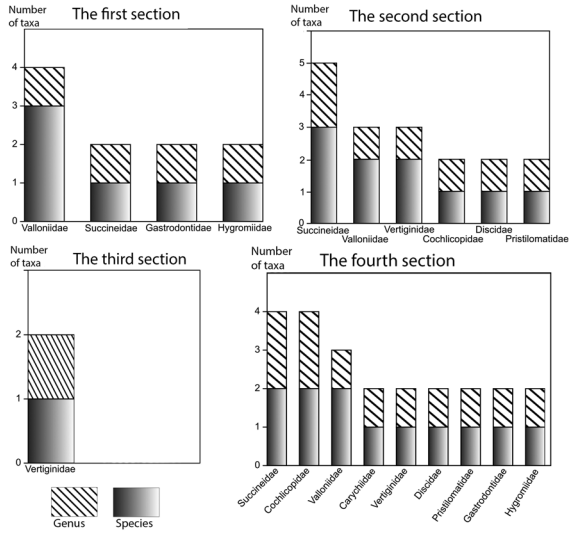

FIG. 9. Taxonomic structure of terrestrial molluscs. The families are arranged along the x-axis.

РИС. 9. Таксономическая структура наземных моллюсков. По оси абсцисс – семейства.

cies (for example, certain representatives of the genus *Sphaerium* and unionid mussels) and their replacement by stagnophilic species (such as some species of the genus *Euglesa*, lymnaeid and valvatid snails).

Most of the detected freshwater mollusc species tend to inhabit either permanent, weakly flowing or stagnant waterbodies that are overgrown with macrophytes or with signs of swamping; or temporary drying ponds and swamps. The composition of terrestrial molluscs, in turn, indicates the presence of highly humid conditions in their habitats.

It is worth mentioning that the lowest number of shells was found predominantly in the floodplain and river alluvium layers in the first and the third sections. In contrast, shells are present in almost every horizon of the second and the fourth sections. Probably, a series of stagnant, heavily overgrown with aquatic vegetation, swampy waterbodies existed at the site of the current riverbed. It is possible that these waterbodies were connected to each other during of the water level increases.

Thus, the composition of the fossil malacofauna and the ecological preferences of the studied molluscs from alluvial deposits reflect the specific features of the probable paleoecological conditions of the Syra River valley during the Late Pleistocene–Middle Holocene. Further studies of the radiocarbon dating of peat from horizons in other sections, as well as analysis of soil and sediment morphogenesis and palynological examinaton, are needed to more fully and accurately reconstruct the environmental conditions of past eras in this region.

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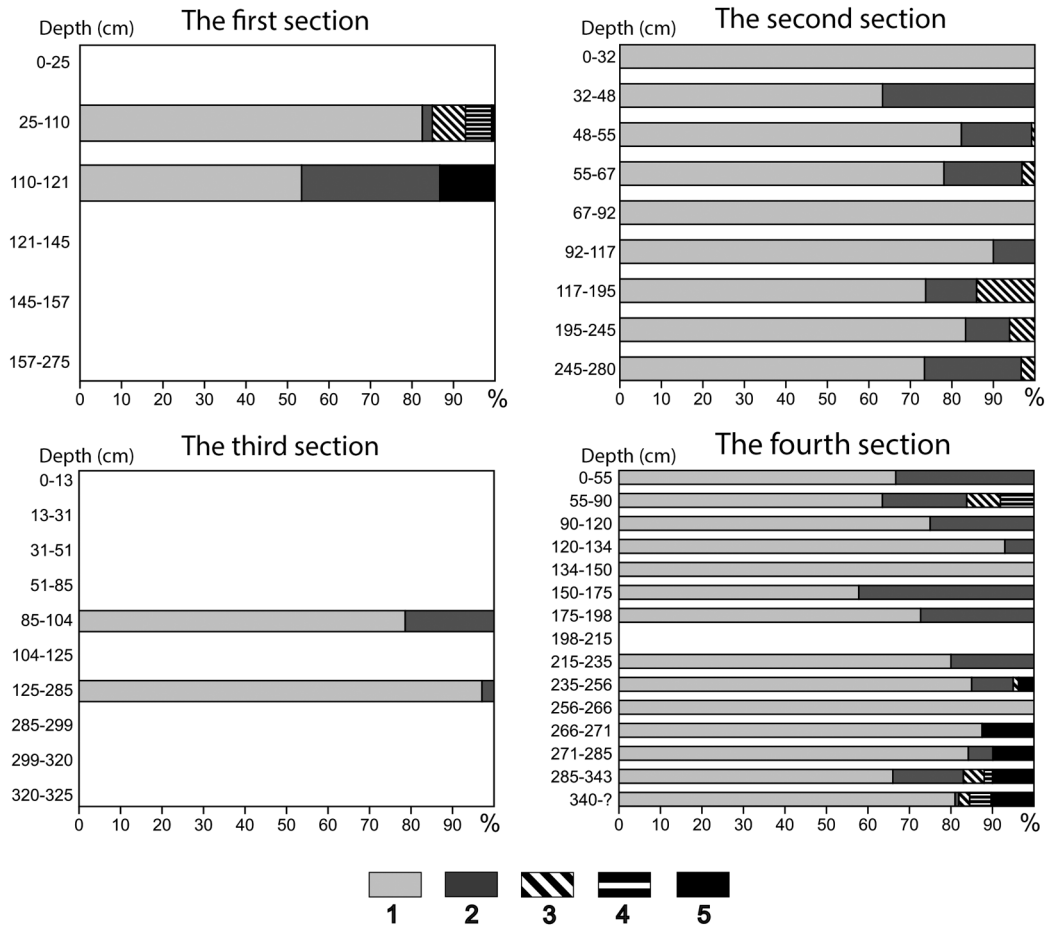

FIG. 10. Ecological preferences of freshwater molluscs: 1 – predominantly permanent waterbodies; 2 – predominantly temporary waterbodies; 3 – swampy waterbodies, slow-flowing streams, small rivers and ditches; 4 – permanent flowing waterbodies; 5 – permanent non-flowing waterbodies.

РИС. 10. Экологические предпочтения пресноводных моллюсков: 1 – преимущественно постоянные водные объекты; 2 – преимущественно временные водоёмы; 3 – заболоченные водоёмы, медленнотекущие ручьи, реки и канавы; 4 – постоянные проточные водные объекты; 5 – постоянные непроточные водоёмы.

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