ISSN 0869-5938, Stratigraphy and Geological Correlation, 2014, Vol. 22, No. 1, pp. 1–27. © Pleiades Publishing, Ltd., 2014.
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Permian Nonmarine Bivalve Zonation of the East European Platform

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Received October 12, 2012

Abstract—New finds and revision of available collections of nonmarine bivalves provided grounds for development of a zonal scale for terrestrial sequences of the Permian System based on species belonging to the genus *Palaeomutela* Amalitzky, 1891, which are characterized by regular changes in the structure of the shell hinge. The scale includes two parallel zonal successions that are based on the stratigraphic distribution and evolutionary trends of two morphological lineages of the genus. The zonal succession based on development of the *P. umbonata* group (dwellers of mobile waters and silty–psammitic substrates) includes 11 range zones: stegocephalum, ovatiformis, umbonata, quadriangularis, krotowi, wohrmani, numerosa, ulemensis, keyserlingi, curiosa, golubevi. The zonal succession based on development of the *P. castor* group (dwellers of calm waters and silty–pelitic substrates) includes eight range zones: larae, castor, olgae, doratioformis, marposadica, fischeri, obunca, amalitzkyi. The proposed zonal units are correlated with scales based on ostracod, fish, and tetrapod fossils. New species *Palaeomutela golubevi* sp. nov. and *P. amalitzkyi* sp. nov. are described with the extended diagnosis of the genus *Palaeomutela*.

Keywords: nonmarine bivalves, zonal scale, Permian, East European Platform

DOI: 10.1134/S0869593814010067

INTRODUCTION

Through the European part of Russia (East European and Timan–Pechora Platforms, Uralian foredeep), nonmarine bivalves are widespread in sequences of the Ufimian, Kazanian, Severodvinian, and Vyatkian stages of the Permian System (Fig. 1). Bivalve shells, casts, and impressions frequently occur together with ostracod, fish, and terrestrial vertebrate remains, i.e., with faunal groups which were recently used for development and/or specification of zonal scales (Golubev, 2000; Molostovskaya, 2005; Kukhtinov et al., 2008; Minikh, A.V. and Minikh, M.G., 2009; Newell et al., 2010).

Despite the wide distribution and sufficient knowledge of these fossils, only several regional (Amalitzky, 1892a; Kanev, 1985, 1994; Gusev, 1990, 1996c) and local (Silantiev, 1996a) zonal scales were proposed on the basis of bivalves during the last 120 years. In most of these works, their authors indicated only species assemblages (paleocoenoses, assemblages, faunas) characteristic of particular stratigraphic units (Nechaev, 1894; Gusev, 1963, 1977a; Kuleva, 1980; Silantiev, 1995, 2001; Silantiev and Kurkova, 2009; etc.).

The development of zonal scales based on nonmarine bivalves encounters difficulties determined by the requirements for such scales: primarily their continuity, unambiguous position of boundaries between zones, and succession of assemblages from contiguous zones through the section (*Stratigraficheskii...*, 2006, Article VII.3). These difficulties are explained by the complex structure of terrestrial formations, some evolutionary conservatism of nonmarine bivalves, their multifunctional variability, and facies control in sections, as well as by different approaches to their taxonomy (Betekhtina, 1974; Gusev, 1990). To solve these problems, a uniform technique was proposed in (Silantiev, 2010) for the study of Late Paleozoic nonmarine bivalves, which takes into consideration all the external, internal, and microstructural features of their shells.

The long-term revision of available collections of nonmarine bivalves from many localities in Russia provides grounds for development of a zonal scale based on this faunal group. In this regard, success may be achieved only on the basis of species from the genus *Palaeomutela* Amalitzky, 1891, whose diversity and stratigraphic distribution most completely satisfy the requirements of the Stratigraphic Code of Russia (*Stratigraficheskii...*, 2006). In this connection, the main tasks of this work were as follows: (1) taxonomic revision of the genus *Palaeomutela*; (2) revelation of main evolutionary lineages in its development; (3) analysis of sections for establishing successions of first appearances of species and their stratigraphic ranges; (4) selection of index species; (5) complex paleontological substantiation of zones; (6) standard description of zonal units.

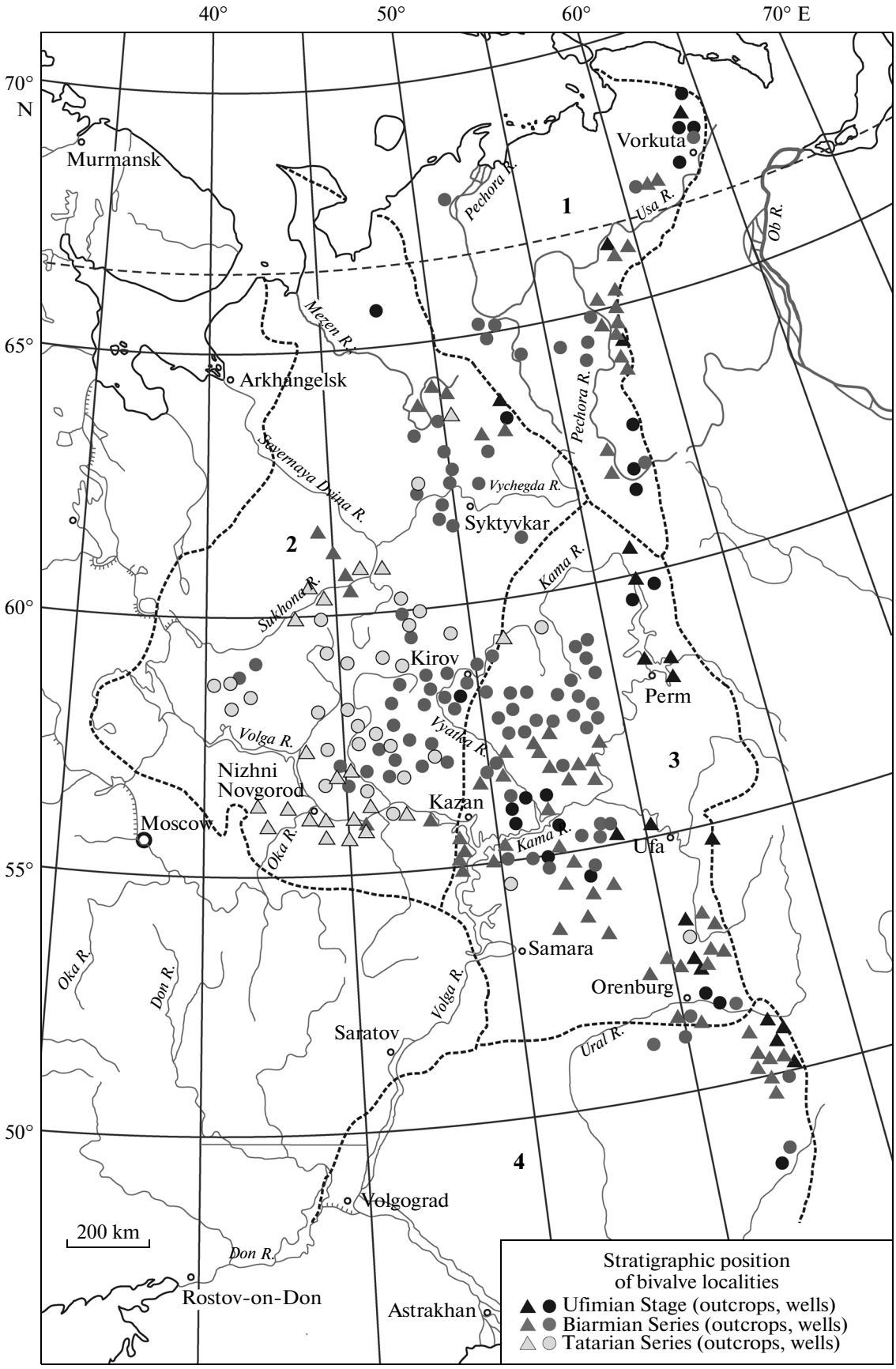

40°
50°
60°
70° E
70° N
65°
60°
55°
50°
45°
Murmansk
Vorkuta
Pechora R.
Usa R.
Ob R.
Mezen R.
Arkhangelsk
Severnaya Dvina R.
Pechora R.
Vychegda R.
Syktyvkar
Kama R.
Sukhona R.
Kirov
Perm
Volga R.
Vyatka R.
Nizhni Novgorod
Kazan
Moscow
Oka R.
Kama R.
Ufa
Samara
Oka R
Don R.
Volga R.
Orenburg
Saratov
Ural R.
Volgograd
200 km
Don R.
Rostov-on-Don
Astrakhan
1
2
3
4
Stratigraphic position of bivalve localities
Ufimian Stage (outcrops, wells)
Biarmian Series (outcrops, wells)
Tatarian Series (outcrops, wells)

Fig. 1. Main localities of nonmarine bivalve finds used for development of the zonal scale.
Numbers designate Permian sedimentary basins (after Gusev, 1977a): (1) Pechora, (2) Dvina–Mezen, (3) Volga–Ural, (4) North Caspian.

MATERIALS AND METHODS

The investigations of terrestrial Permian sections carried out through the region under consideration during the last decades by Moscow, Saratov, and Kazan geologists (*Stratotipicheskii...*, 2001; *Tatarskie...*, 2001; Sennikov and Golubev, 2010; etc.) yielded additional representative collections of nonmarine bivalves and made it possible to specify the stratigraphic distribution of genera and some species, the zonal index forms included. These new stratigraphic data were taken into account in revision of both original (sampled in 1990–2010) materials and monographic collections by E.I. Eichwald and V.P. Amalitzky (St. Petersburg University); A.V. Nechaev and A.K. Gusev (Kazan University); D.M. Fedotov, E.M. Lyutkevich, and V.V. Pogorevich (TsNIGR Museum, VSEGEI, St. Petersburg); M.A. Plotnikov and G.P. Kanev (Institute of Geology, Komi Scientific Center, Syktyvkar); O.A. Betekhtina (Siberian Branch of the Russian Academy of Sciences, Novosibirsk); P.A. Tokareva and Yu.S. Papin (Regional Geological Stocks, Novosibirsk); and others. Only sections or groups of closely spaced sections with at least two to three index species were selected among 900 examined outcrops with nonmarine bivalves.

The taxonomic revision of nonmarine bivalves, primarily including the family Palaeomuteloidea Lahusen, 1897 and genus *Palaeomutela*, was carried out together with many colleagues in the period of 1994–2011. The following taxonomic features were taken into consideration at the family to genus levels: structure of the adductor, ligament, and hinge apparatus of the shell and its microstructure and microornamentation properties (Silantiev, 2010; Silantiev and Carter, 2011). At the species level, the features accepted by Novosibirsk paleontologists (Betekhtina, 1974; Betekhtina and Tokareva, 1988; Silantiev and Chandra, 2011) such as the shape (type) of the initial shell, the degree of shell allometry, and location of shell growth lines were used for taxonomic purposes, in addition to traditional external shell features (Amalitzky, 1892a; Nechaev, 1894; Betekhtina, 1966; Gusev, 1990).

The morphology of the shell hinge margin was analyzed using large-scale photographs of hinges and their schematic sketches that emphasize the shape and location of tooth plates (Fig. 2).

The development of the zonal scale consisted in revealing and substantiating range zones, i.e., beds between first appearances of index species of contiguous zones within the continuous succession (*Stratigraficheskii...*, 2006, Article VII.4.d). When selecting index species, the preference was given to the most widespread well-known species presumably belonging to a single evolutionary lineage. Such an approach provided an approximation of defined range zones to phylozones.

The zonal scale was constructed by the method of the "teilzone synthesis" (Chernykh, 2005) that included the following: (1) determination of stratigraphic ranges of species (teilzones) in sections;

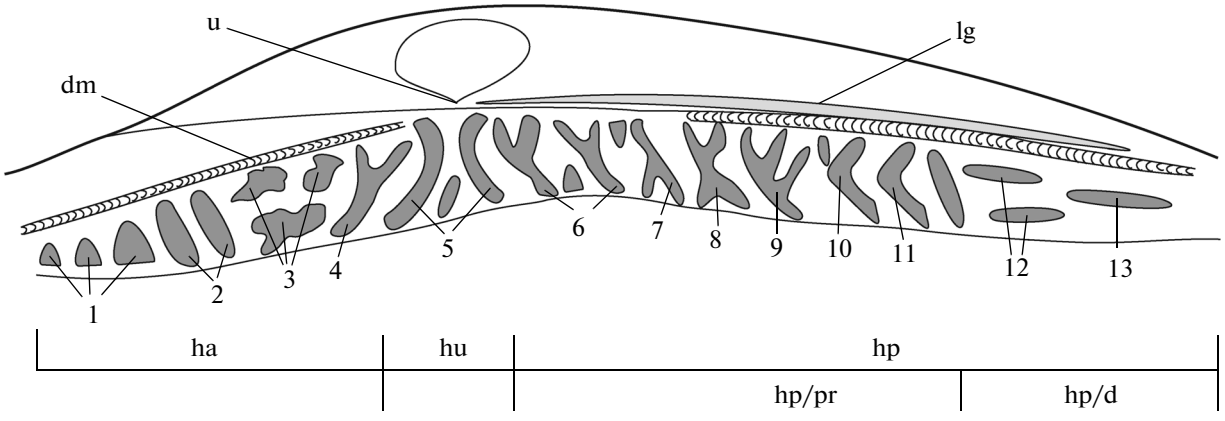


Fig. 2. Schematic structure of the hinge area and shapes of teeth in representatives of the genus *Palaeomutela* Amalitzky, 1891.
Elements of the hinge area: (ha) anterior branch, (hu) umbonal area, (hp) posterior branch, (hp/pr) proximal part of the posterior branch, (hp/d) distal part of the posterior branch. Shapes and arrangement of tooth plates: (1) irregular nodelike uniserial, (2) straight lamellar, (3) irregular nodelike biserial, (4) Y-shaped, (5) curved lamellar, (6) Y-shaped specularly reflected in the vertical plane, (7) λ-shaped, (8) X-shaped, (9) Y-shaped specularly reflected in the vertical plane with additional branching, (10) Y-shaped specularly reflected in the vertical plane with branching fragmentation, (11) herringbone, (12) horizontal biserial, (13) horizontal uniserial. Elements of the valve: (dm) dorsal margin, (lg) ligament furrow, (u) umbo.

(2) summing of these ranges for obtaining the complete stratigraphic range of the biozone; (3) determination of chronological orders of biozones; (4) selection of some biozones to represent scale units; (5) complex paleontological substantiation of each biozone; (6) selection of stratotype sections for zonal units.

When correlating boundaries of nonmarine bivalve bioznes with regional stratigraphic units, biostratigraphic indicators of boundaries and zonal scales based on ostracod, fish, and terapod remains (Golubev, 2000; Molostovskaya, 2005; Kotlyar, 2008; Kukhtinov et al., 2008; Minikh, A.V. and Minikh, M.G., 2009; Newell et al., 2010) were used.

GENUS *Palaeomutela* COMPOSITION AND ITS EVOLUTIONARY LINEAGES

The genus *Palaeomutela* Amalitzky, 1891 is characterized by a *Unio*-shaped shell and "transversely irregularly denticulate" pseudotaxodont hinge (Amalitzky, 1891, p. 1). The author of the genus repeatedly emphasized the high variability of the hinge structure in *Palaeomutela* representatives, which is reflected in reduction of teeth up to their complete disappearance in some species (Amalitzky, 1892a, 1892b, 1895a, 1895b). At the same time, he never indicated criteria for discriminating *Palaeomutela* shells with the reduced hinge from species of other genera with the edentulous hinge. Therefore, representatives of the genus *Palaeomutela* were frequently confused with other genera such as *Palaeanodonta* Amalitzky, 1895 (=*Naiadites* Dawson, 1860 sensu Amalitzky, 1892) (Upper Permian) and *Anthraconaia* Trueman et Weir, 1946 (Carboniferous–Lower Permian).

The revision of the genus *Palaeomutela* based on the microstructural features of the outer, middle, and inner layers of the shell made it possible to solve several general taxonomic problems and specify diagnosis of the genus and compositions of its species (Silantiev, 1995; Silantiev and Carter, 2001). Some of its results appeared to be of stratigraphic significance. They include the following aspects.

(1) Substantiation of the taxonomic significance of microstructural features and introduction of the data on the structure of the outer, middle, and inner layers of the shell into diagnosis of the genus *Palaeomutela* (Silantiev, 1998) allowed the composition of the genus to be widened, attributing to the latter several species which were previously considered as belonging to the genera *Naiadites* Dawson, 1860, *Palaeoanodonta* Amalitzky, 1891, and *Anthraconaia* Trueman et Weir, 1946 (Amalitzky, 1892a; Nechaev, 1894; Gusev, 1990).

(2) Validity of attributing the above-mentioned forms, which were considered as lacking hinge plates (edentulous), to the genus *Palaeomutela* was also confirmed by development of reduced hinges with single teeth or abrasion features (attrition, spalling) of the hinge margin (Silantiev, 2001; Silantiev, 1998).

(3) On the basis of analysis of the hinge margin morphology and microstructural features of shells, some species that were previously included in the genus *Palaeomutela* are attributed to the genera *Redikorella* Silantiev, 1994 (Silantiev, 1994, 1996a), *Palaeoanodonta* Amalitzky, 1895, and *Opo-kiella* Plotnikov, 1949 (Silantiev and Carter, 2010).

The following criteria indicating the evolutionary similarity of species were accepted (in order of priority): (1) similarity of trends in changes of hinge morphology; (2) similarity of microstructural features of shell layers; (3) similarity of external features (initial shells, degree of allometry, and others).

Two groups of species are defined among the representatives of the genus *Palaeomutela*: *P. umbonata* and *P. castor* groups, which differ from each other in morphological features in the structure of the hinge (Fig. 2) and tendencies in its development (Fig. 3).

The *P. umbonata* group includes species characterized by thick shells and well-developed hinges with many (20–50) curved platy and node-like teeth. By analogy with recent molluscan species, they are considered to represent likely dwellers of highly mobile waters saturated with silty particulate matter (Eagar et al., 1984; Gusev, 1990).

The *P. castor* group is formed by species with thin shells and reduced hinges, which likely preferred calm and pure hydrodynamic environments (Gusev, 1977b, 1990).

At present, the following regularities in common are defined for species of the *P. umbonata* group. From the beginning of the Ufimian Age until the first half of the Severodvinian Age, the number of tooth plates in the hinge increases with simultaneous ordering in their shapes and gradual differentiation of the hinge into the anterior branch, posterior (with proximal and distal parts) branch (series), and umbonal area differing from each other in shapes, sizes, and positions of tooth plates. The maximal differentiation of the hinge, which allows pseudocardinal teeth in the umbonal area and pseudolateral teeth in the distal part of the posterior branch to be discriminated, is observable in species that existed in the late Severodvinian time. From the second half of the Severodvinian Age until the Vyatkian Age, differentiation of the hinge remains high, although the number of tooth plates in the hinge decreases and the ligament thickness increases. The detailed changes of the hinge in different-age species of the *P. umbonata* group are considered below together with description of zones.

In the *P. castor* group, stratigraphically higher species demonstrate generally lower differentiation with the simultaneous decrease in the number of teeth (up to their complete disappearance) and their sizes. Since the Kazanian Age, teeth in the distal part of the posterior branch of the hinge strive for acquiring the horizontal position similar to that of pseudolateral teeth in species of the first group. The transition between the

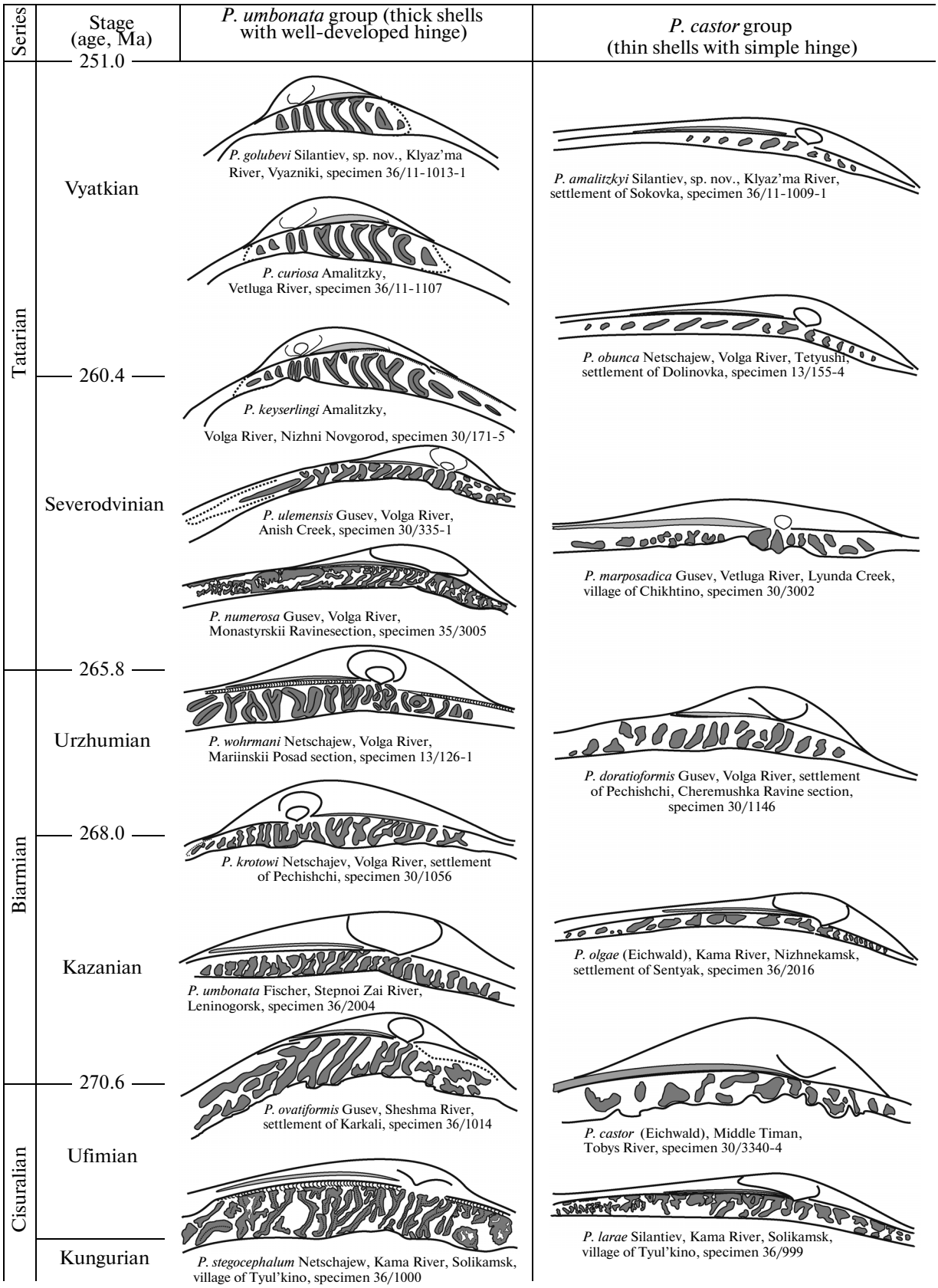


Fig. 3. Changes in morphology of the hinge in representatives of two *Palaeomutela* groups. Magnified.

Urzhumian and Severodvinian ages is marked by the appearance of the group of species with a reduced, although well differentiated, hinge (Fig. 3, *P. marposadica*), where both pseudolateral and pseudodistal tooth plates are readily definable.

Figure 4 demonstrates the recent summarized development of phylogenetic lineages of the genus *Palaeomutela* and main accompanying groups of nonmarine bivalves in the region under consideration during the Biarmian and Tatarian epochs of the Permian Period.

TYPE (REFERENCE) SECTIONS OF ZONAL UNITS

Many works which mention finds of nonmarine bivalves contain a description and paleontological characteristics of sections that are accepted to serve as reference successions for development of the zonal scale based on this group of fossils. The reference sections of the Ufimian Stage are located along the Kama and, further south, Belaya rivers in the central part of the Solikamsk depression (Silantiev, 1995, 1996a, 1996b). The reference sections of the Kazanian and Urzhumian stages are examined in the eastern and northern parts of the East European Platform: along the Sheshma River near the settlement of Karkali (Silantiev et al., 1998, 2007b); along the Kama River near Elabuga and the settlement of Sentyak (Silantiev et al., 1998); along the Volga River in the Cheremushka Ravine near the settlement of Pechishchi (Gusev, 1996a; Silantiev et al., 2007d); along the Vym River in the Pomras River basin (Silantiev and Kurkova, 2009). The reference sections of the Seerodvinian and Vyatkian stages are established in the Monastyrskii and Il'inskii ravines along the Volga River in the Middle Volga region (Silantiev and Esin, 1993; Gusev, 1996b; Silantiev et al., 2007a), along the Vyatka River (Silantiev, 2001), and along the Oka River near Nizhni Novgorod and Gorbatov (Amalitzky, 1892a; Gusev, 1990). The outcrops along the Klyaz'ma River near Vyazniki are accepted to serve as the reference section for the terminal part of the Permian System (Newell et al., 2010; Sennikov and Golubev, 2010).

ZONAL UNITS OF THE PERMIAN SYSTEM

The scale includes two parallel zonal successions that are based on the stratigraphic distribution and evolutionary trends of two morphological lineages of the genus *Palaeomutela*. The zonal succession based on development of species from the *P. umbonata* group (dwellers of mobile waters and silty–psammitic substrates) includes 11 range zones: stegocephalum, ovatiformis, umbonata, quadriangularis, krotowi, wohrmani, numerosa, ulemensis, keyserlingi, curiosa, golubevi. The zonal succession based on development of the *P. castor* group (dwellers of calm waters and silty–pelitic substrates) includes eight range zones: larae, castor, olgae, doratioformis, marposadica, fischeri, obunca, amalitzkyi. The proposed zonal scale is correlated with scales based on ostracod, fish, and tetrapod fossils (Fig. 5).

Zonal Succession Based on Development of the *P. umbonata* Group

Palaeomutela stegocephalum Zone

Index species: *Palaeomutela stegocephalum* Netschajew, 1894 (Plate I, figs. 1, 2). Lectotype (Gusev, 1990, p. 65): Kazan, Geological Museum of Kazan Federal University (GM KFU), specimen 13/124 (Nechaev, 1894, plate IX, fig. 62); Perm region, Usol'e; Ufimian Stage, Solikamsk Horizon.

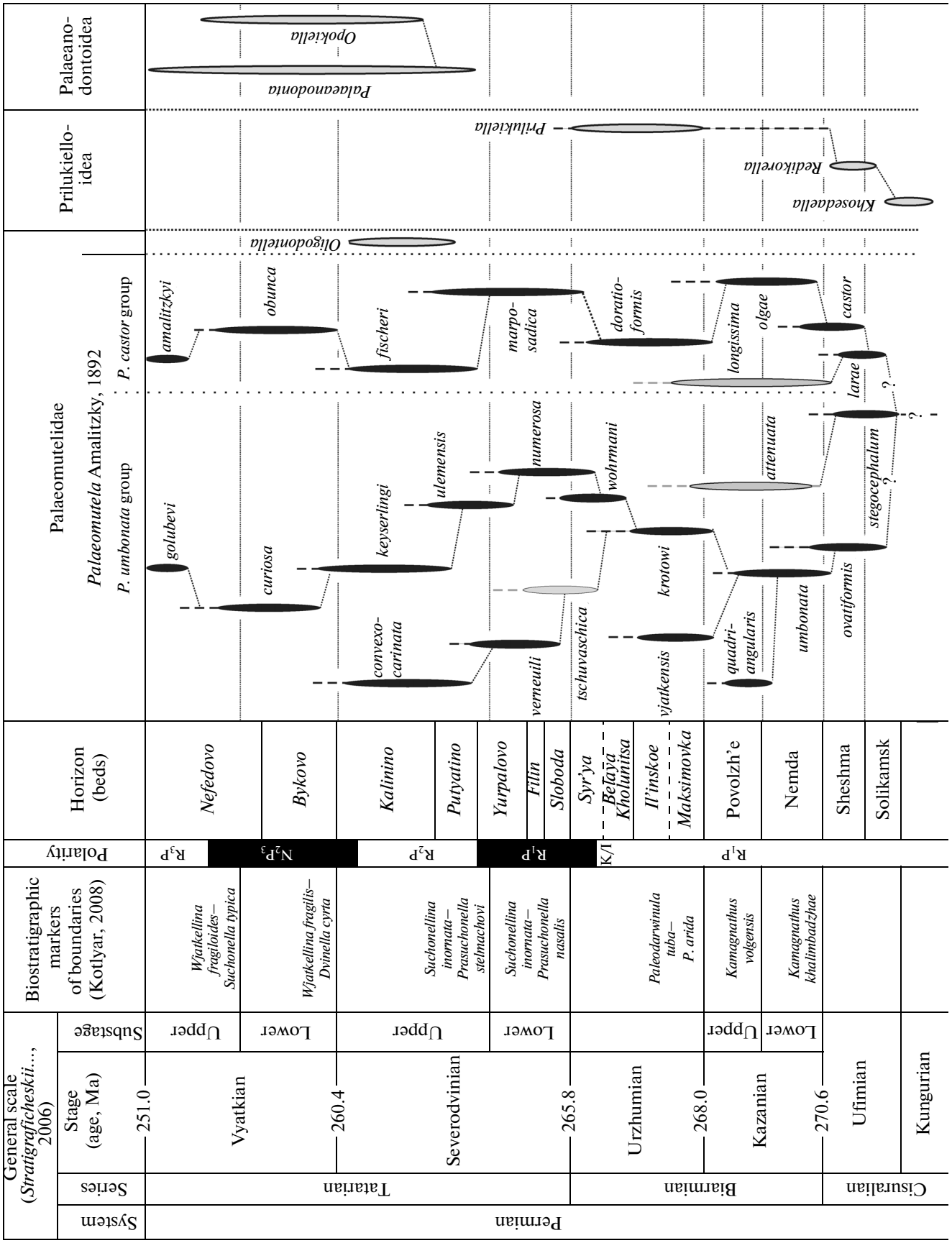
Gusev (1990) was the first to define this unit as a phylozone that comprises the Ufimian and Kazanian stages. Subsequently, this author used the index species for defining the Palaeomutela stegocephalum–Concinella concinnaeformis concurrent range zone corresponding to the Solikamsk Horizon (Gusev, 1996c). Simultaneously, the Palaeomutela stegocephalum ecozone corresponding to the lower part of the Solikamsk Horizon was proposed (Silantiev, 1996a).

Stratotype of the zone was chosen in the Well 51 section (Solikamsk depression, village of Tyul'kino), depth of 272.0 m, lower Solikamsk Subformation (Fig. 6). The lower and upper boundaries of the unit are marked by first appearances of *P. stegocephalum* Netsch. and *P. ovatiformis* Gusev, respectively. The index species is accompanied by *P.* cf. *attenuata* Gusev.

Remarks. The hinge in representatives of *Palaeomutela stegocephalum* exhibits no distinct differentiation to the anterior and posterior branches (Plate I, fig. 2). The umbonal area is defined provisionally on the basis of changes in orientation of tooth plates that diverge in some specimens in a fan manner from the umbo. Proximal areas of the anterior and posterior branches bear branching γ-, λ-, and χ-shaped tooth plates with narrowed and widened segments and characterized by uneven curved lateral surfaces. In the posterior branch of the hinge, the main (longest) shoulders of tooth plates are inclined toward the umbo, while shorter branches are oppositely oriented. In the anterior branch, tooth plates are inclined both toward the umbo and away from it. Linear nonbranching relatively straight or randomly curved tooth plates and

Fig. 4. Schematic phylogenetic development of main nonmarine bivalve groups in the East European Platform during the Biarmian and Tatarian epochs of the Permian Period.

Gray color designates the distribution of taxa from the family Palaeomutelidae, diagnoses and stratigraphic positions of which need further specification. Paleomagnetic chrons are given after (Newell et al., 2010).


General scale (Stratigraficheskii..., 2006)
System
Series
Substage
Stage (age, Ma)
Biostratigraphic markers of boundaries (Kotlyar, 2008)
Polarity
Horizon (beds)
Permian
Tatarian
Biarmian
Cisuralian
Upper
Lower
Upper
Lower
Upper
Lower
251.0
260.4
265.8
268.0
270.6
Vyatkian
Severodvinian
Urzhumian
Kazanian
Ufimian
Kungurian
Wjatkellina fragiloides–Suchonella typica
Wjatkellina fragilis–Dvinella cyrta
Suchonellina inornata–Prasuchonella stelmachovi
Suchonellina inornata–Prasuchonella nasalis
Paleodarwinula tuba–P. arida
Kamagnathus volgensis
Kamagnathus khalimbadzhae
R3P
N2P3
R2P
R1P
K/T
R1P
Nefedovo
Bykovo
Kalinino
Putyatino
Yurpalovo
Filin
Sloboda
Syr'ya
Belaya Kholunitsa
Il'inskoe
Maksimovka
Povolzh'e
Nemda
Sheshma
Solikamsk
Palaeomutelidae
Palaeomutela Amalitzky, 1892
P. umbonata group
P. castor group
golubevi
curiosa
keyserlingi
ulemensis
numerosa
wohrmani
krotowi
vjatkensis
tschuvaschica
verneuili
convexo-carinata
quadri-angularis
umbonata
ovatiformis
stegocephalum
?
?
?
larae
castor
olgae
longissima
atenuata
doratio-formis
marpo-sadica
fischeri
obunca
amalitzkyi
Oligodontella
Prilukiellidae
Prilukiella
Redikorella
Khosedaella
Palaeanodontoidea
Palaeanodonta
Opokiella

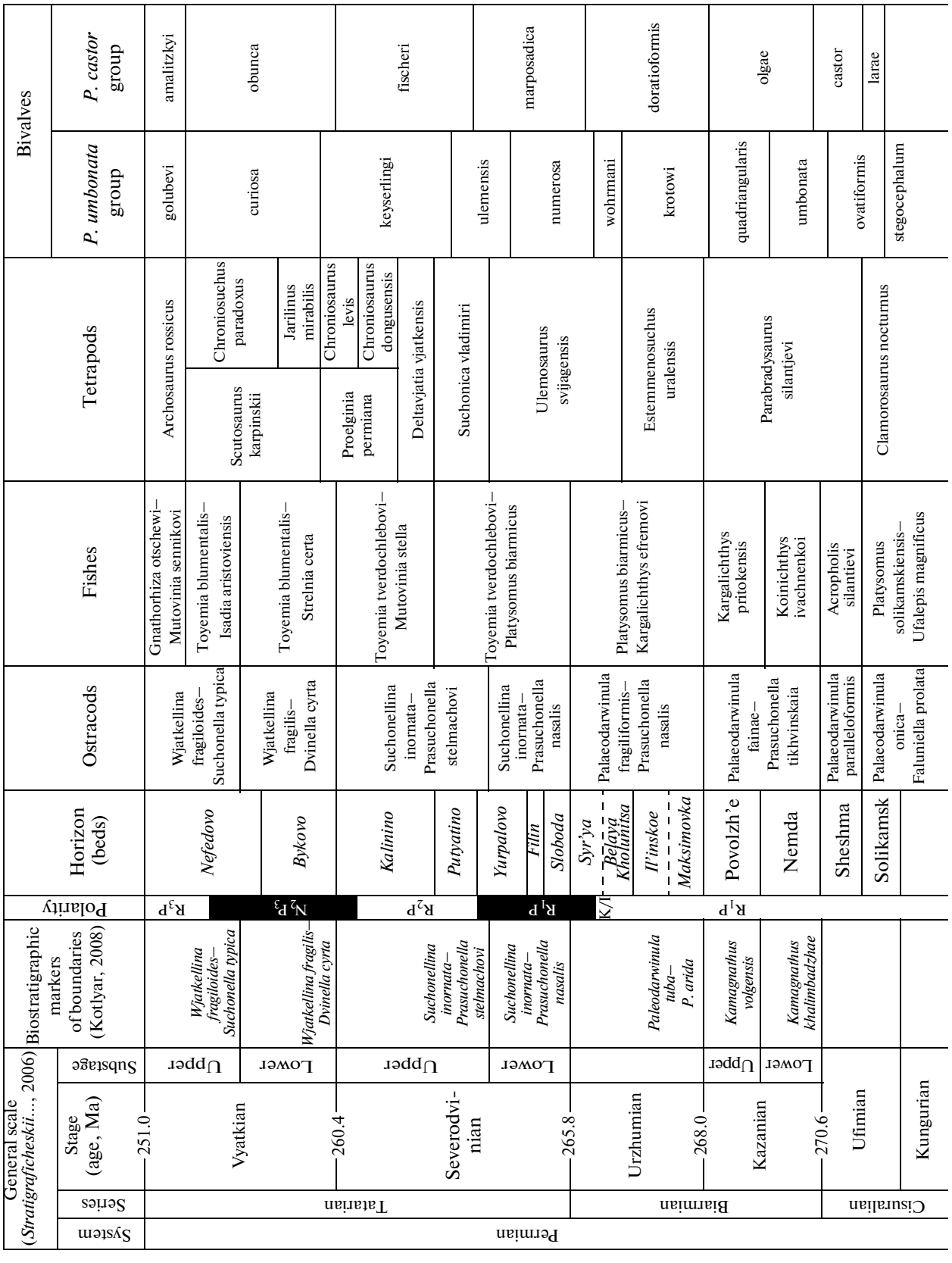


Fig. 5. The proposed Permian zonal scale of the East European Platform based on nonmarine bivalves and its correlation with ostracod, fish, and tetrapod zonal scales (Newell et al., 2010). Paleomagnetic chrons are given after (Newell et al., 2010).

nodelike teeth occupy spaces between branching teeth and distal areas of the hinge.

The Palaeomutela stegocephalum Zone is the most complete in the Solikamsk depression of the Middle Ural region and in the Upper Pechora depression of the Uralian foredeep. On the basis of occurrence of the index species, this unit may provisionally be correlated with the Palaeomutela markini Zone of the Ufimian Stage in the Kuznetsk basin (Betekhtina and Tokareva, 1988).

Palaeomutela ovatiformis Zone

Index species: *Palaeomutela ovatiformis* Gusev, 1990 (Plate I, fig. 3). Holotype: Kazan, GM KFU, specimen 30/1654 (Gusev, 1990, plate I, fig. 8); South Ural region, Ilek River, settlement of Petropavlovka of the Rodniki district of Aktyubinsk oblast; Blagodarnyi Formation, Sheshma Horizon, Ufimian Stage.

Gusev (1990) was the first to define this unit as a biozone comprising the Ufimian Stage and lower part of the Kazanian Stage. Subsequently, this author used the index species for defining the Anthraconaia longissima–Palaeomutela ovatiformis concurrent range zone corresponding to the Sheshma Horizon (Gusev, 1996c).

Stratotype of the zone (Fig. 6) is located in the Solikamsk depression of the Middle Ural region on the right side of the Kama River 2.5 km upstream of the village of Tyul'kino, Outcrop S1, Bed 1, Sample 5 (Silantiev, 1996a). The lower and upper boundaries of the zone are placed at the first appearance levels of *P. ovatiformis* Gusev and *P. umbonata* Gusev, respectively.

Characteristic bivalve species: *P. stegocephalum* Netsch., *P.* cf. *attenuata* Gusev, *P. castor* (Eichw.), *P. opima* (Kanev), *P. markini* Betekht., *P. larae* Silant., *Redikorella kanevi* Silant., *R. starobogatovi* (Kanev), *R. alta* (Pogor.), *R. explanata* (Kanev), *Concinnela (?) concinnaeformis* Pogor., *C. (?) komiensis* (Kanev), *C. (?) trapezoidalis* (Krotow), *C. (?) declivae* (Kanev).

Remarks. In the Palaeomutela ovatiformis Zone, the hinge in representatives of the genus *Palaeomutela* becomes distinctly differentiated into the anterior (short and narrow) and posterior (long and wide) branches. The umbonal area is characterized by small local concavities of the hinge at its conjunction with the anterior and posterior branches. Branching tooth plates are largely located in the proximal area of the posterior branch, being characterized by γ- and λ-shaped outlines; lateral surfaces of plates are more even and bear moderate compressions. On the posterior and anterior branches of the hinge, the main shoulders of tooth plates are inclined toward the umbo.

The ovatiformis Zone is observable in the Uralian foredeep (Upper Pechora, Solikamsk, Yuryuzan–Sylva, and Belaya depressions) and eastern part of the Volga–Ural basin. It is correlated with the Palaeomutela markini Zone of the Ufimian Stage in the Kuznetsk basin (Betekhtina and Tokareva, 1988) on the basis of species in common belonging to the genera *Palaeomutela, Redikorella*, and *Concinella* (?). The species in common from the two last genera allow the ovatiformis Zone to be correlated with the stratigraphic interval corresponding to the Khosedaella alta–Khosedaella permica and Palaeomutela starobogatovi zones defined in the Ufimian Stage of the Pechora basin (Kanev, 1985, 1994).

Palaeomutela umbonata Zone

Index species: *Palaeomutela umbonata* (Fischer, 1840) (Plate 1, fig. 4). Lectotype (Gusev, 1990, p. 73): St. Petersburg, Paleontological–Stratigraphic Museum of St. Petersburg State University (PSM SPGU), specimen 1/871 (Eichwald, 1861, plate XVIII, fig. 21); Ik River basin, Belebei; Kazanian Stage.

Gusev (1990) was the first to define this unit corresponding to the Ufimian (Sheshma Horizon) and Kazanian stages. Subsequently, the index species was used for defining the *Anthraconaia kamae–Palaeomutela umbonata* concurrent range zone corresponding to the Kazanian Stage (Gusev, 1996c).

Stratotype of the zone is located on the right bank of the Kama River near Elabuga, Elabuga Outcrop, Bed 6, lower member of clayey siltstones (Silantiev et al., 1998) (Fig. 7). The lower and upper boundaries of the unit are marked by the first appearances of *P. umbonata* (Fischer) and *P. quadriangularis* Gusev, respectively.

Characteristic bivalve species: *P. pseudoumbonata* Gusev, *P. longissima* (Netsch.), *P. rhomboidea* (Netsch.), *P. olgae* Gusev, *P. attenuata* Gusev, *P.* aff. *attenuata* Gusev.

Remarks. In the Palaeomutela umbonata Zone, tooth plates in representatives of the genus *Palaeomutela* become straighter (less sinuous), teeth on the anterior branch of the hinge are arranged in a uniserial manner, and they are less split.

The umbonata Zone is observable through the Volga–Ural and North Caspian basins of the East European Platform.

Palaeomutela quadriangularis Zone

Index species: *Palaeomutela quadriangularis* Netschajew, 1894) (Plate I, figs. 5, 6). Lectotype (Gusev, 1990, p. 105): Kazan, GM KFU, specimen 13/154 (Nechaev, 1894, plate IX, fig. 37); Sheshma River, settlement of Arkhangel'skoe, Chistopol district, Tatarstan; Kazanian Stage.

The stratigraphic unit is proposed for the first time.

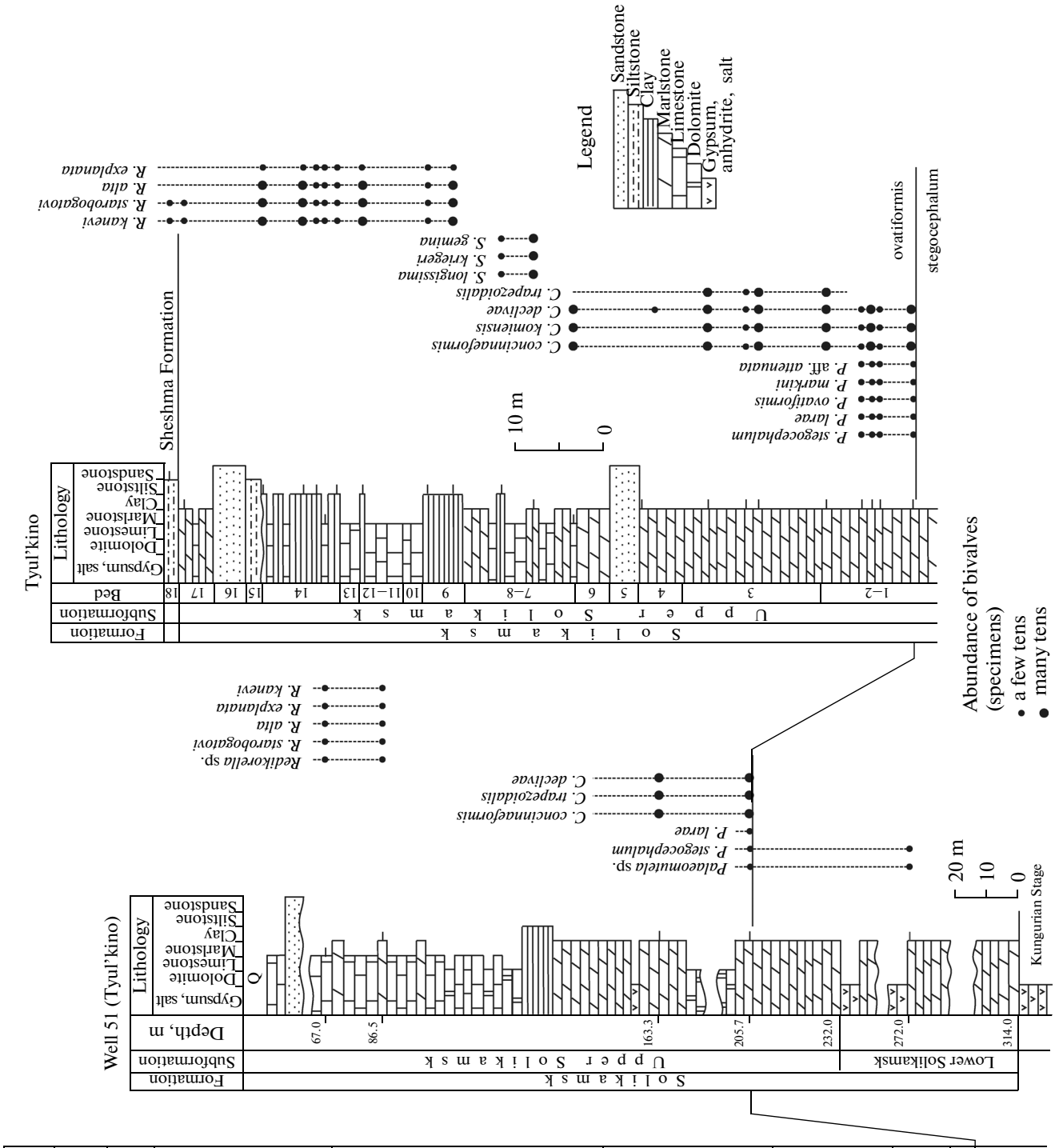


Fig. 6. Distribution of nonmarine bivalves in reference section of the Ufimian Stage in the Solikamsk depression.

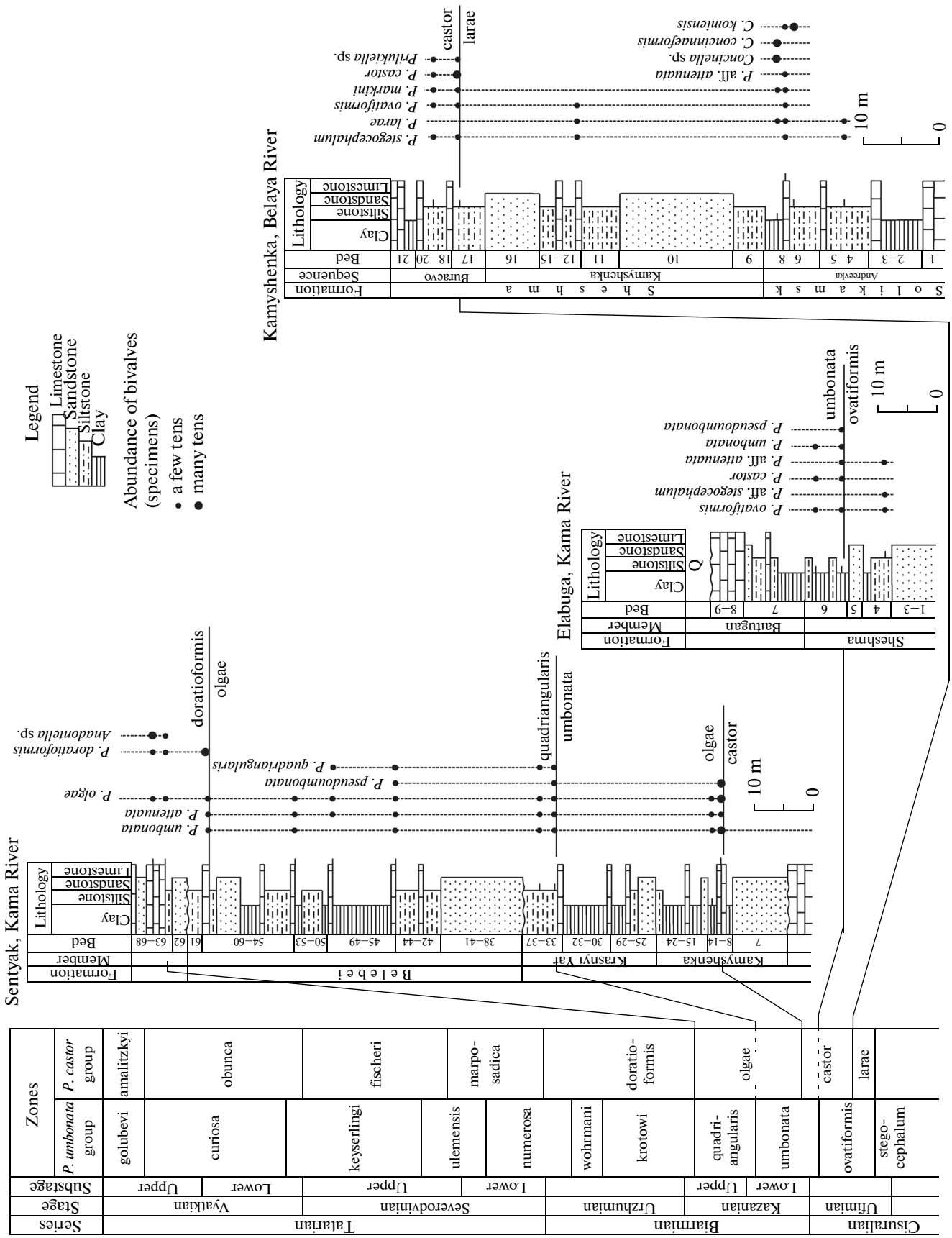


Fig. 7. Distribution of nonmarine bivalves in reference section of the Ufimian and Kazanian stages in the Belaya and Kama river basins.

Stratotype of the zone is located on the right bank of the Kama River, near Nizhnekamsk, Sentyak Section, Bed 33 (Silantiev et al., 1998) (Fig. 7). The lower and upper boundaries of the zone are placed at the first appearance levels of *P. quadriangularis* (Netsch.) and *P. krotowi* Netsch., respectively.

Characteristic bivalve species: *P. kamae* (Gusev), *P. umbonata* Gusev, *P. longissima* (Netsch.), *P. rhomboidea* (Netsch.), *P. olgae* Gusev.

Remarks. In the quadriangularis Zone, the hinge in representatives of the genus *Palaeomutela* was characterized by features observable in them through the umbonata Zone. The unit under consideration is recorded in the Volga–Ural and North Caspian basins of the East European Platform.

Palaeomutela krotowi Zone

Index species: *Palaeomutela krotowi* Netschajew, 1894 (Plate I, fig. 7). Lectotype (Gusev, 1990, p. 84): Kazan, GM KFU, specimen 13/129 (Nechaev, 1894, plate IX, fig. 61); right bank of the Vyatka River 10 km upstream of the Cheptsa River mouth near the settlement of Chirki, Slobodka district, Kirov oblast; Maksimovo Formation, lower beds (limestone), Urzhumian Stage.

The nominal zone is proposed for the first time.

Stratotype of the zone is located on the right bank of the Volga River 1.5 km west of the settlement of Pechishchi, Cheremushka Ravine, Outcrop, Bed 19 (Silantiev et al., 2007d) (Fig. 8). The lower and upper boundaries of the zone correspond to the first appearance levels of *P. krotowi* Netsch.) and *P. wohrmani* Netsch., respectively.

Characteristic bivalve species: *P. vjatkensis* Gusev, *P. doratioformis* Gusev, *Anadontella volgensis* (Gusev), *Prilukiella lata* (Netschajew).

Remarks. Beginning from the krotowi Zone, the hinge in representatives of the genus *Palaeomutela* is distinctly differentiated into the anterior branch, posterior branch, and umbonal area. The krotowi Zone is registered in the Volga–Ural, North Caspian, and Dvina–Mezen basins. On the basis of the occurrence of the index species, this unit may be correlated with the Palaeomutela visenda–Palaeomutela meraca Zone established in the Tal'bei Formation of the Pechora basin (Kanev, 1985, 1994).

Palaeomutela wohrmani Zone

Index species: *Palaeomutela wohrmani* Netschajew, 1894 (Plate I, fig. 8). Lectotype (Gusev, 1990, p. 93): Kazan, GM KFU, specimen 13/126 (Nechaev, 1894, plate IX, fig. 35); Volga River basin, Sundyr River 11 km southeast of Mariinskii Posad, Chuvash Republic; Urzhumian Stage.

Gusev (1990) was the first to define this unit as a biozone corresponding to the Severodvinian Horizon. Subsequently, the index species was used for defining the Palaeomutela wohrmani–Anthraconaia trapezoidalis concurrent range zone correlative with the lower half of the Severodvinian Horizon (Gusev, 1996c).

Stratotype of the zone is located on the right bank of the Volga River 1.5 km west of the settlement of Pechishchi, Cheremushka Ravine Outcrop, Member 8, Bed 66 (Silantiev et al., 2007d) (Fig. 8). The lower and upper boundaries of the unit under consideration correspond to the first appearance levels of *P. wohrmani* Netsch. and *P. numerosa* Gusev, respectively.

Characteristic bivalve species: *P. krotowi* Netsch., *P. extensiva* Gusev, *P. doratioformis* Gusev, *Anadontella uslonensis* (Gusev), *A. volgensis* (Gusev), *A. tscherdinzewi* (Gusev), *Prilukiella janischewskyi* Plotnikov, *Pr. subovata* (Jones), *Pr. nitida* Gusev, *Pr. mirabilis* Gusev, *Pr. pugnatoria* Gusev.

Remarks. Beginning from the wohrmani Zone, the hinge in the *Palaeomutela* representatives acquires subhorizontal plates located at the distal part of the posterior branch and resembling lateral teeth of heterodont hinges. In *P. wohrmani*, such subhorizontal plates are arranged in two rows. The subvertical orientations of tooth plates are retained in the proximal areas of the posterior and anterior branches.

The wohrmani Zone is documented in the Volga–Ural and Dvina–Mezen basins. The *Anadontella* and *Prilukiella* species in common allow this unit to be correlated with the Palaeomutela visenda–Palaeomutela meraca Zone established in the Tal'bei Formation of the Pechora basin (Kanev, 1985, 1994). The Anadontellidae and Prilukielloidea representatives characteristic of the wohrmani Zone are close to morphotypes of these taxa from the Anadontella supraphillipsii–Terciella certa Zone corresponding to the Leninsk Horizon of the Kuznetsk basin (Betekhtina and Tokareva, 1988). This feature allows the stratigraphic units in question to be considered as conditionally synchronous.

Palaeomutela numerosa Zone

Index species: *Palaeomutela numerosa* Gusev, 1990 (Plate I, figs. 9, 10). Holotype: Kazan, GM KFU, specimen 30/3130 (Gusev, 1990, plate III, fig. 12); right bank of the Volga River 12 km northeast of Tetyushi: Monastyrskii Ravine Section, Urzhumian Stage.

Gusev (1990) was the first to define this unit as a biozone corresponding to the upper part of the Urzhumian and lower part of the Severodvinian horizons.

Stratotype of the zone is located on the right bank of the Volga River 1.5 km west of the settlement of Pechishchi, Cheremushka Ravine Outcrop, Member 13, Bed 138 (Silantiev et al., 2007c) (Fig. 8). The lower and upper boundaries of the unit under consideration correspond to the first appearance levels

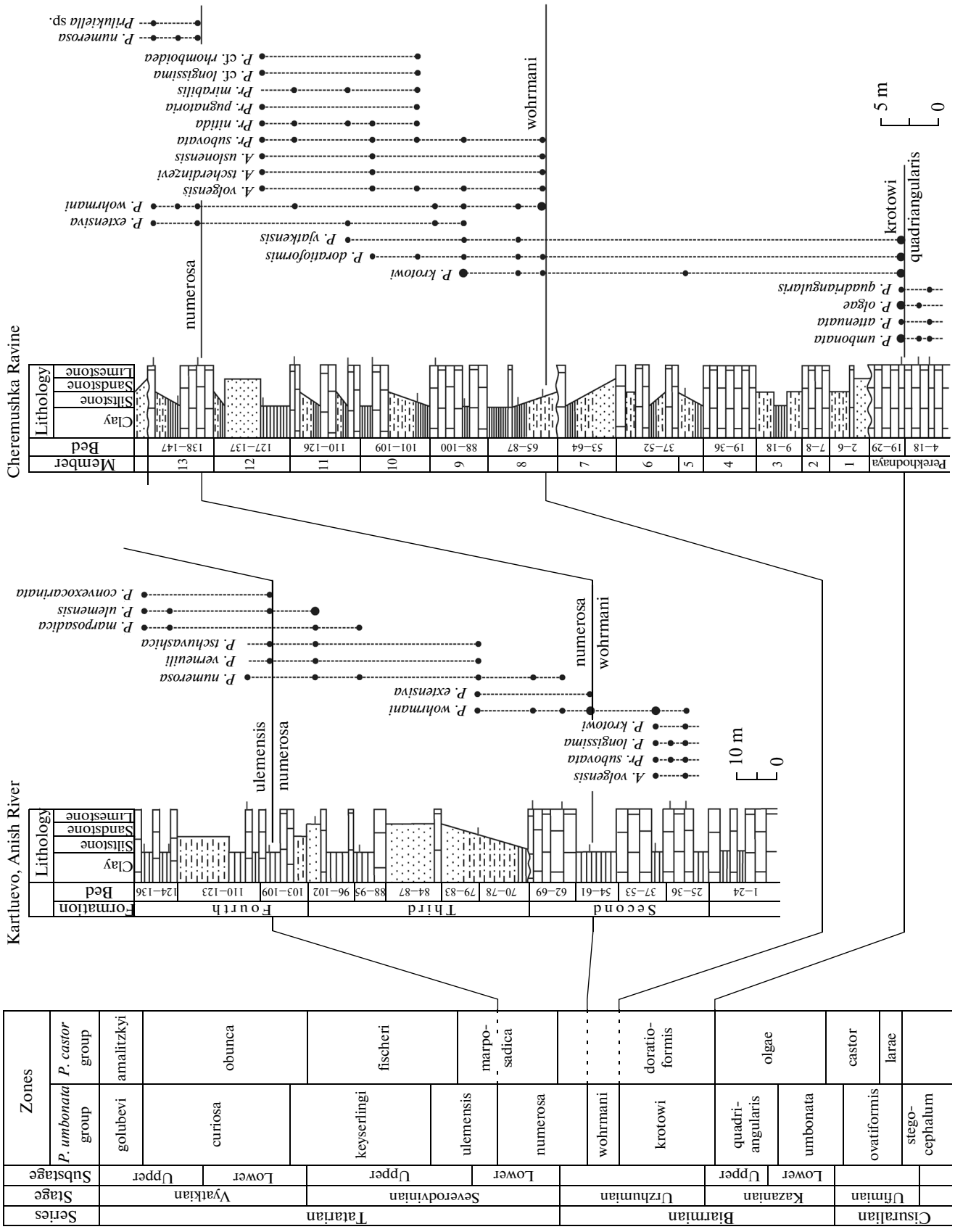


Fig. 8. Distribution of nonmarine bivalves in reference section of the Urzhumian and Severodvinian stages in the Middle Volga region. For legend, see Fig. 7.

of *P. numerosa* Gusev and *P. keyserlingi* Amalitzky, respectively.

Characteristic bivalve species: *P. verneuili* Amal., *P. semilunulata* Amal., *P. solenoides* Amal., *P. subparallela* Amal., *P. marposadica* Gusev, *P. rectodorsala* Gusev, *P. tschuvaschica* (Gusev).

Remarks. Through the numerosa Zone, the hinge in the *Palaeomutela* representatives is characterized by the most complex structure. The anterior branch of the hinge is widened and bears many thin tooth plates and thickened nodes; the main shoulders of tooth plates are inclined by their upper ends away from the umbo. The umbonal area is thickened and separated from conjugate branches by distinct depressions of the hinge with more or less expressed subvertical tooth plates ("pseudocardinal" teeth). The proximal area of the posterior branch bears thin platy slightly branching teeth inclined toward the umbo. The distal area of the posterior is complicated by two to three pairs of biserial (parallel to each other) "pseudolateral" teeth located successively and formed by intergrown nodelike teeth.

The zone is recorded in the Volga–Ural and Dvina–Mezen basins of the East European Platform.

Palaeomutela ulemensis Zone

Index species: *Palaeomutela ulemensis* Gusev, 1990 (Plate I, fig. 11). Holotype: Kazan, GM KFU, specimen 30/173 (Gusev, 1990, plate III, fig. 6); Volga River basin, Anish River, village of Kartluevo, Kozlovsk district, Chuvash Republic; Severodvinian Stage, Yurpalov Beds. The index species was subsequently used for defining the Palaeomutela ulemensis–Anthraconaia castor concurrent range zone corresponding to the upper half of the Urzhumian Horizon (Gusev, 1996c).

Stratotype of the zone is selected in the Kartluevo Section, Bed 108; Anish River, Chuvash Republic (Fig. 8). The lower and upper boundaries of the unit are placed at the first appearance levels of *P. ulemensis* Gusev and *P. keyserlingi* Amalitzky, respectively.

Characteristic bivalve species: *P. convexocarinata* Netsch., *P. marposadica* Gusev, *P. verneuili* Amal., *P. solenoides* Amal., *P. subparallela* Amal.

Remarks. The general structure of the hinge characteristic of *Palaeomutela* representatives is retained also in the ulemensis Zone; at the same time, shells in the latter exhibit a narrowed (reduced) anterior branch of the hinge and simpler posterior branch. The anterior branch bears a single row of node-like teeth, which are locally intergrown into a "pseudolateral" tooth. The "pseudocardinal" tooth of the umbonal area strongly protrudes forward relative to contiguous teeth of the posterior and anterior branches. The distal area of the posterior branch bears one to three "pseudolateral" teeth arranged in a single row. In this zone, the genus *Palaeomutela* gives birth to the genus *Oligodontella* Gusev, 1963, which is characterized by reduced anterior and posterior branches of the hinge and increased number of thickened "pseudocardinal" teeth. The ulemensis Zone is documented through the Volga–Ural and Dvina–Mezen basins of the East European Platform.

Palaeomutela keyserlingi Zone

Index species: *Palaeomutela keyserlingi* Amalitzky, 1892 (Plate I, fig. 12). Lectotype (Gusev, 1990, p. 116): St. Petersburg, SPGU, specimen 11/130 (Amalitzky, 1892a, plate III, fig. 9; Amalitzky, 1892b, plate XXI, fig. 9); right bank of the Oka River near Nizhni Novgorod, Yaril'skii Ravine Section; Severodvinian Stage.

This biostratigraphic unit was first defined by Gusev (1990) as a phylozone corresponding to the Severodvinian and Vyatkian stages.

Stratotype of the zone (Fig. 9) is located on the right bank of the Oka River near Nizhni Novgorod; Yaril'skii Ravine Section, Bed 188. The lower and upper boundaries of the unit are drawn at the first appearance levels of *P. keyserlingi* Amal. and *P. curiosa* Amal., respectively.

Characteristic bivalve species: *P. orthodonta* Amal., *P. ovalis* Amal., *P. parallela* (Amal.), *P. subcastor* (Amal.), *P. fischeri* (Amal.) *P. convexocarinata* (Netsch.), *Oligodontella zitteli* (Amal.), *O. geinitzi* (Amal.), *Palaeanodonta novoculchumica* (Kuleva), *Opokiella tschernyschewi* Plotnikov.

Remarks. Beginning from the keyserlingi Zone, the hinge in the *Palaeomutela* representatives becomes shorter, while the thickness of the ligament increases by two to three times. The anterior branch of the hinge becomes reduced and bears the whole interior "pseudolateral" tooth or single horizontal plates and/or nodes. The "pseudocardinal" tooth consists of two to four tooth plates variably intergrown with each other. The posterior branch of the hinge is thickened, wide, with nonbranching γ-shaped and herringbone teeth in its proximal part; the distal part bears a row of "pseudolateral" teeth arranged from one to four in a uniserial manner.

The keyserlingi Zone is registered through the Volga–Ural and Dvina–Mezen basins of the East European Platform.

Palaeomutela curiosa Zone

Index species: *Palaeomutela curiosa* Amalitzky, 1892 (Plate I, fig. 13). Lectotype (Gusev, 1990, p. 108): St. Petersburg, SPGU, specimen 11/122 (Amalitzky, 1892a, plate I, fig. 22); right bank of the Oka River near Gorbatov in Nizhni Novgorod oblast; Vyatkian Stage.

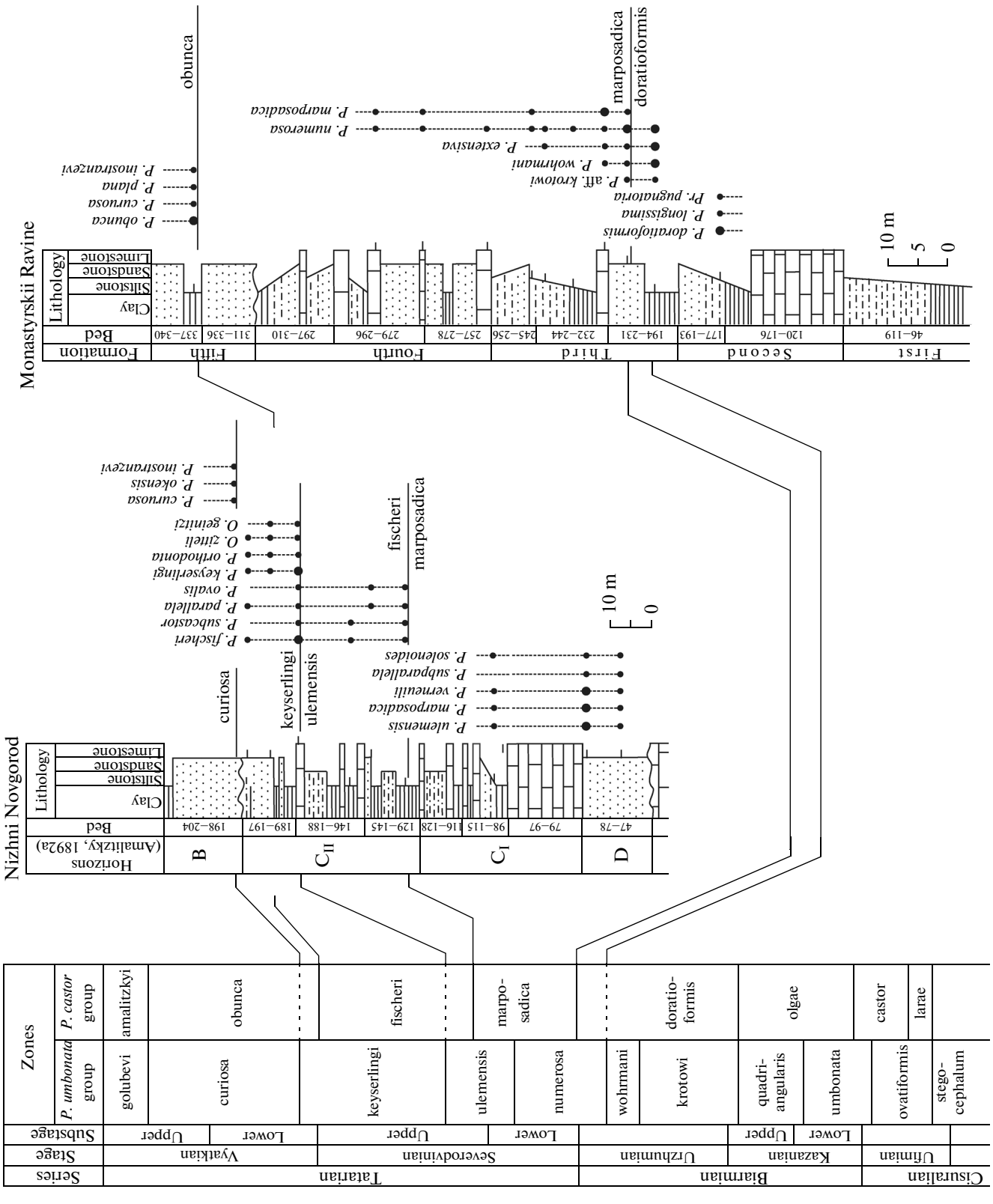


Fig. 9. Distribution of nonmarine bivalves in reference section of the Urzhumian, Severodvinian, and Vyatkian stages in the Nizhni Novgorod and Tetyshi Volga region. For legend, see Fig. 7.

This biostratigraphic unit was first defined by Gusev (1990) as a phylozone corresponding to the Vyatka Horizon.

Stratotype of the zone is located on the right bank of the Oka River near Nizhni Novgorod, Yaril'skii Ravine Section, Bed 198 (Fig. 9). The lower and upper boundaries of the unit are placed at the first appearance levels of *P. curiosa* Amalitzky and *P. golubevi* Silantiev, sp. nov., respectively.

Characteristic bivalve species: *P. inostranzevi* Amal., *P. obunca* Netsch., *P. crassa* Amal., *P. parva* Amal., *P. plana* Amal., *P. okensis* (Amal.), *Opokiella ignatjevi* Gusev, *O. pakhtusovi* Gusev.

Remarks. Beginning from this zone, the hinge in the *Palaeomutela* representatives begins reducing. The anterior branch bears single nodes. The "pseudocardinal" tooth consists of one to two vertical tooth plates. The posterior branch of the hinge is thickened, wide, with herringbone tooth plates in the proximal part; the distal part bears a single short "pseudolateral" tooth.

The zone is documented in the Volga–Ural and Dvina–Mezen basins of the East European Platform.

Palaeomutela golubevi Zone

Index species: *Palaeomutela golubevi* Silantiev, sp. nov. (Plate I, figs. 14–16). Holotype: GM KFU, specimen 36/11-1107, Vetluga River, Well 10, depth 89 m; upper Vyatkian Substage.

This biostratigraphic unit is proposed for the first time.

Stratotype of the zone is located on the right bank of the Klyaz'ma River southwest of Gorokhovets; Zhukov Ravine Section, Outcrop 1027A, Bed 1 (Sennikov and Golubev, 2010) (Fig. 10). The lower boundary of the unit is placed at the first appearance level of *P. golubevi* Silantiev, sp. nov.; its upper boundary is unknown.

Characteristic bivalve species: *P.* aff. *keyserlingi* (Amal.), *P.* aff. *obunca* (Netsch.), *P. amalitzkyi* Silantiev, sp. nov., *Palaeanodonta* sp. nov.

The *Palaeomutela* forms from this zone exhibit further reduction of the hinge. In the index species, the anterior branch of the hinge bears single poorly expressed nodes; the "pseudocardinal" tooth is indistinct. The posterior branch of the hinge is wide, with herringbone tooth plates on the proximal part; the distal part bears single nodelike teeth.

The golubevi Zone is documented in the Volga–Ural and Dvina–Mezen basins of the East European Platform.

Zonal succession based on development of the *P. castor* group

Palaeomutela larae Zone

Index species:*Palaeomutela larae* Silantiev, 1995 (Plate II, figs. 1, 2). Holotype: Kazan, GM KFU, specimen 36/1014 (Silantiev, 1995, drawing 5, fig. 1); Perm region, Solikamsk depression, right bank of the Kama River, 2.5 km upstream of the village of Tyul'kino; Ufimian Stage, Solikamsk Horizon.

The zone was first defined for the Solikamsk depression as corresponding to the middle part of the Solikamsk Horizon (Silantiev, 1996a). Simultaneously, Gusev (1996c) proposed the *P. larae* Biozone comprising the entire Solikamsk Horizon of the Ufimian Stage for the European part of Russia.

Stratotype of the zone is located on the right bank of the Kama River 2.5 km upstream of the village of Tyul'kino, Outcrop S1, Bed 1, samples 3–5 (Fig. 6) (Silantiev, 1996a). The lower and upper boundaries of this biostratigraphic unit are marked by the first appearance of *P. larae* Silantiev and *P. castor* (Eichwald), respectively.

Characteristic bivalve species: *P. stegocephalum* Netsch., *P.* cf. *attenuata* Gusev, *P. opima* (Kanev), *P. markini* Betekht., *Redikorella kanevi* Silant., *R. starobogatovi* (Kanev), *R. alta* (Pogor.), *R. explanata* (Kanev), *Concinella* (?) *concinnaeformis* Pogor., *C.* (?) *komiensis* (Kanev), *C.* (?) *trapezoidalis* (Krotow), *C.* (?) *declivae* (Kanev).

Remarks. The larae Zone is marked by the appearance of species from the *Palaeomutela castor* group characterized by a thin-walled shell, narrow hinge area, and reduced hinge. The narrow hinge area has no distinct differentiation into the anterior and posterior branches (Plate II, fig. 2) and bears slightly branching γ-shaped or nodelike tooth plates. In the posterior branch of the hinge, the main (longest) shoulders of tooth plates are inclined both toward the umbo and in the opposite direction. In the anterior branch, the main shoulders of tooth plates are inclined away from the umbo. The node-like teeth occupy distal parts of the hinge area.

The larae Zone is the most complete in the Solikamsk depression of the Middle Ural region. It is also traceable in the Upper Pechora depression of the Uralian foredeep and in the eastern part of the East European Platform up to the latitude of the Vyatka River mouth.

Palaeomutela castor Zone

Index species: *Palaeomutela castor* (Eichwald) (Plate II, figs. 3, 4). Lectotype (Gusev, 1990, p. 164): St. Petersburg, SPGU, specimen 1/837 (*Unio castor*: Eichwald, 1860, p. 1003, plate XXXIX, fig. 20); Volga River basin, Aktai River, settlement of Burakovo, Spassk district, Republic of Tatarstan; Urzhumian Stage. The index species was subsequently used by Gusev (1996c) for defining the Palaeomutela ulemensis–Anthraconaia castor concurrent range zone corresponding to the upper half of the Urzhum Horizon. Examination of many collections revealed the reduced hinge in representatives of this species, which

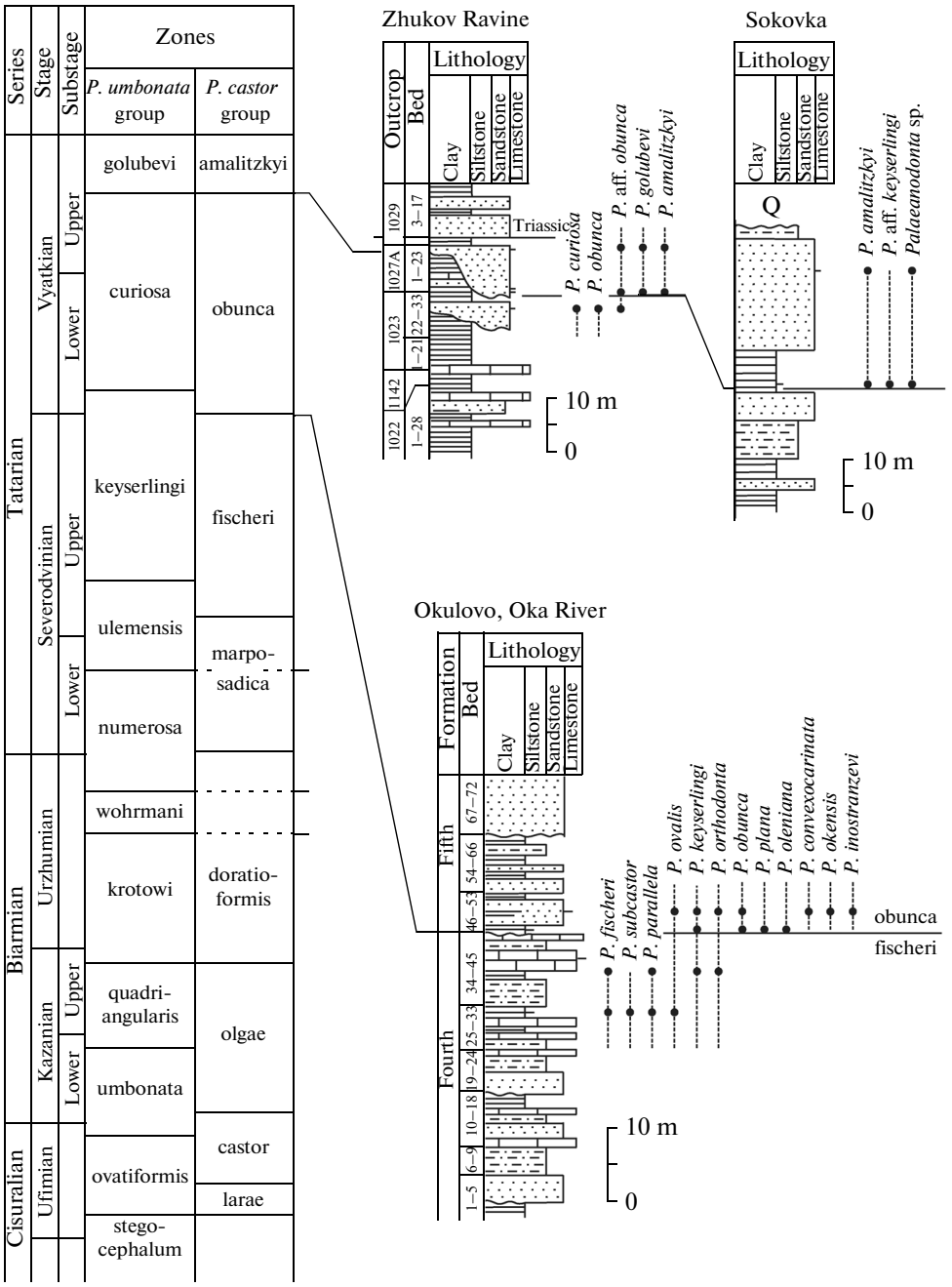


Fig. 10. Distribution of nonmarine bivalves in reference section of the Vyatkian Stage in the Oka and Klyaz'ma river bains. For legend, see Fig. 7.

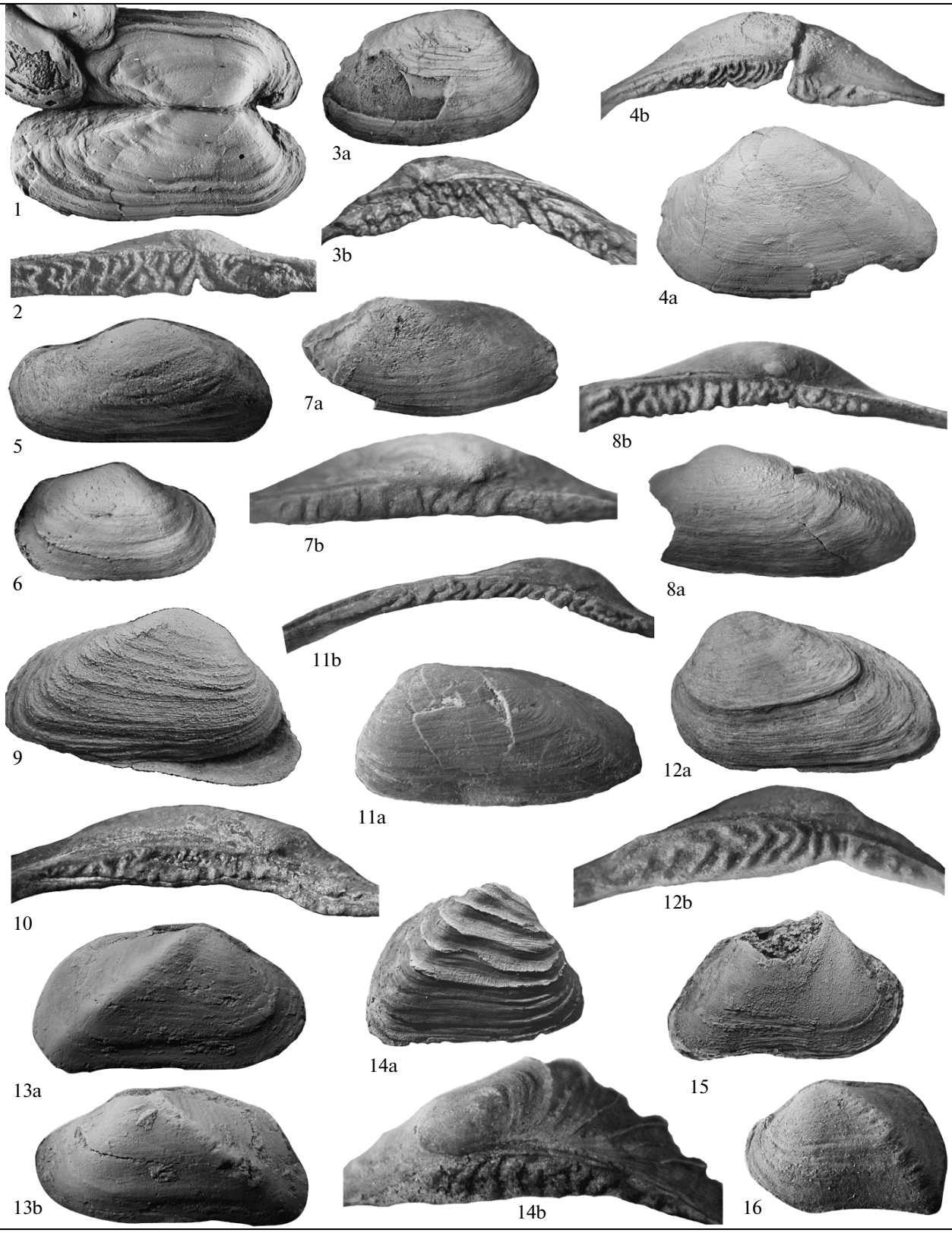
provided grounds for attributing it to the genus *Palaeomutela*.

Stratotype of the zone (Fig. 7) is located on the right bank of the Belaya River 1.0–3.0 km downstream of the village of Kamyshenka, Kamyshenka Outcrop, Bed 17 (upper part) (Silantiev, 1996b). The lower and upper boundaries of this biostratigraphic unit correspond to the first appearance levels of *P. castor* (Eichw.) and *P. olgae* Gusev, respectively.

Characteristic bivalve species: *P. stegocephalum* Netsch., *P.* cf. *attenuata* Gusev, *P. markini* Betekht., *P. ovatiformis* Gusev, *Prilukiella* sp.

Remarks. The representatives of the species from the castor Zone are characterized by the hinge differentiated into the anterior (shorter and narrower) and posterior (longer and wider) branches. In the umbonal area, the hinge is narrowed at the junction of anterior and posterior branches and exhibits a subvertical position of tooth plates. In the posterior and ante-

Plate I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16

rior branches of the hinge, the main shoulders of tooth plates are inclined toward the umbo.

The castor Zone is documented in the Upper Pechora, Solikamsk, Yuryuzan–Sylva, and Belaya depressions of the Uralian Foredeep and Volga–Ural basin of the East European Platform.

Palaeomutela olgae Zone

Index species: *Palaeomutela olgae* Gusev, 1990 (Plate II, figs. 5, 6). Holotype: Kazan, GM KFU, specimen 30/3311 (Gusev, 1990, plate II, fig. 23); Sheshma River, Outcrop 1212, settlement of Tatarskie Tukmakly 25 km southeast of Chistopol, Republic of Tatarstan; Kazanian Stage. Gusev (1996c) used the index species for defining the Anthraconaia trapezoidalis–Palaeomutela olgae concurrent range zone corresponding to the lower half of the Urzhumian Stage.

Stratotype of the zone (Fig. 7) is located on the right bank of the Kama River near Nizhnekamsk, Sentyak Section, Bed 11 (Silantiev et al., 1998). The lower and upper boundaries of the unit are placed at the first appearance levels of *P. olgae* Gusev and *P. doratioformis* Gusev, respectively.

Characteristic bivalve species: *P. umbonata* (Fischer), *P. pseudoumbonata* Gusev, *P. quadriangularis* (Netsch.), *P. longissima* (Netsch.), *P. rhomboidea* (Netsch.), *P. kamae* (Gusev), *P. attenuata* Gusev, *P.* cf. *attenuata* Gusev.

Remarks. The anterior branch of the hinge with small nodelike teeth arranged in a single row becomes narrow in *Palaeomutela* representatives from the olgae Zone; the distal part of the posterior branch acquires subhorizontal plates resembling lateral teeth of heterodont hinges.

The olgae Zone is registered in the Volga–Ural and North Caspian basins of the East European Platform.

Palaeomutela doratioformis Zone

Index species: *Palaeomutela doratioformis* Gusev, 1990 (Plate II, figs. 7, 8). Holotype: Kazan, GM KFU, specimen 30/3139 (Gusev, 1990, plate II, fig. 23); Kama River basin, Nechkina River, 3.0 km south of the settlement of Nechkino, Sarapul district, Udmurt Republic; Kazanian Stage.

The biostratigraphic unit is defined for the first time.

Stratotype of the zone (Fig. 7) is located on the right bank of the Kama River near Nizhnekamsk, Sentyak Section, Bed 60 (Silantiev et al., 1998). The lower and upper boundaries of the unit are placed at the first appearance levels of *P. doratioformis* Gusev and *P. marposadica* Gusev, respectively.

Characteristic bivalve species: *P. vjatkensis* Gusev, *P. extensiva* Gusev, *P. krotowi* Netsch., *P. wohrmani* Netsch., *Anadontella volgensis* (Gusev), *A. uslonensis* (Gusev), *A. tscherdinzewi* (Gusev), *Prilukiella lata* (Netschajew), *Pr. janischewskyi* Plotnikov, *Pr. subovata* (Jones), *Pr. nitida* Gusev, *Pr. mirabilis* Gusev, *Pr. pugnatoria* Gusev.

Remarks. The *Palaeomutela* representatives from this zone are characterized by the widened posterior branch of the hinge and biserial arrangement of nodelike teeth in its distal part. In the posterior branch of the hinge, the main shoulders of tooth plates are inclined toward the umbo and their counterparts in the anterior branch are inclined away from the latter.

Plate I. Zonal species of nonmarine bivalves from the *P. umbonata* group. All specimens illustrated in Plates I and II are stored at the Geological Museum of Kazan Federal University (GM KFU).
(1, 2) *Palaeomutela stegocephalum* Netschajew, 1894: (1) specimen 36/996-1 (×2), open shell with the fragment of the open shell of *Palaeomutela larae* Silantiev, 1995 in the left upper corner; (2) specimen 36/996-2 (×7), hinge of the left valve; Solikamsk depression, Well 1542 section, depth 112 m, Ufimian Stage, Palaeomutela larae Zone; (3) *Palaeomutela ovatiformis* Gusev, 1990, specimen 36/1014-2: (3a) right valve (×2), (3b) hinge (×7); Udmurt Republic, Cheptsa River basin, Balezino Settlement, Well 7, depth 240 m, Ufimian Stage, Palaeomutela ovatiformis Zone; (4) *Palaeomutela umbonata* (Fischer, 1840), specimen 36/3164: (4a) left valve (×2), (4b) hinge (×7); South Ural region, Zhaksy-Kargala River, Kazanian Stage, Palaeomutela umbonata Zone; (5, 6) *Palaeomutela quadriangularis* Netschajew, 1894: (5) lectotype, specimen 13/154 (×3), cast of the left valve, Middle Volga region, Sheshma River, settlement of Arkhangel'skoe, Kazanian Stage, Palaeomutela quadriangularis Zone; (6) specimen 30/2094 (×4), cast of the right valve, Vyatka River basin, Lubyanka River, stratigraphic position the same; (7) *Palaeomutela krotowi* Netschajew, 1894, lectotype, specimen 13/129: (7a) left valve (×2), (7b) hinge (×7); Vyatka River, right bank near the settlement of Chirki, Urzhumian Stage, Palaeomutela krotowi Zone; (8) *Palaeomutela wohrmani* Netschajew, 1894, lectotype, specimen 13/126-1: (8a) left valve (×3), (8b) hinge (×8); Volga River basin, Sundyr River, settlement of Sotnikovo, Urzhumian Stage, Palaeomutela wohrmani Zone; (9, 10) *Palaeomutela numerosa* Gusev, 1990: (9) holotype, specimen 30/3130 (×2), closed shell; (10) specimen 30/1025-4 (×7), hinge of the left valve; Volga River, settlement of Monastyrskoe, Monastyrskii Ravine section, Urzhumian Stage, Palaeomutela numerosa Zone; (11) *Palaeomutela ulemensis* Gusev, 1990, specimen 30/335: (11a) left valve (×3), (11b) hinge (×10); Volga River, Tetyushi, Urzhumian Stage, Severodvinian Stage, Palaeomutela ulemensis Zone; (12) *Palaeomutela keyserlingi* Amalitzky, 1892, specimen 30/171-23: (12a) left valve (×3.5), (12b) hinge (×12); Oka River, Nizhni Novgorod, Yaril'skii Ravine section, Severodvinian Stage, Palaeomutela keyserlingi Zone; (13) *Palaeomutela curiosa* Amalitzky, 1892, specimen 13/136-2 (×3.5), cast of the right (13a) and left (13b) valves of the open shell, Vyatka River basin, Kobra River, settlement of Kobra, Vyatkian Stage, Palaeomutela curiosa Zone; (14–16) *Palaeomutela golubevi* Silantiev, sp. nov.: (14) holotype, specimen 36/11-1107: (14a) right valve (×3), (14b) hinge (×9), Vetluga River, Well 10, depth 89 m; (15) specimen 36/11-1013-1 (×3), cast of the right valve, Klyaz'ma River, Gorokhovets, Zhukov Ravine section; (16) specimen 36/11-136-3 (×3) cast of the left valve, Oka River, village of Konstantinovo, Well 14 section, depth 54 m, Vyatkian Stage, Palaeomutela golubevi Zone.

The doratioformis Zone is recorded in the Volga–Ural and North Caspian basins of the East European Platform.

Palaeomutela marposadica Zone

Index species: *Palaeomutela marposadica* Gusev, 1990 (Plate II, fig. 9). Holotype: Kazan, GM KFU, specimen 30/336 (Gusev, 1990, plate III, fig. 13); Volga River, eastern outskirts of Mariinskii Posad, Chuvash Republic; Severodvinian Stage, Slobodka Beds. Subsequently, Gusev (1996c) used the index species for defining the Palaeanodonta fischeri–Palaeomutela marposadica concurrent range zone corresponding to the upper half of the Severnaya Dvina Horizon.

Stratotype of the zone (Fig. 9) is located on the right bank of the Volga River upstream of Tetyushi, Monastyrskii Ravine Outcrop, Bed 226, samples 9, 10 (Silantiev et al., 2007a). The lower and upper boundaries of the unit correspond to the first appearance levels of *P. marposadica* Gusev and *P. fischeri* (Amal.), respectively.

Characteristic bivalve species: *P. numerosa* Gusev, *P. extensiva* Gusev, *P. verneuili* Amal., *P. solenoides* Amal., *P. subparallela* Amal., *P. semilunulata* Amal., *P. rectodorsala* Gusev, *P. tschuvaschica* (Gusev).

Remarks. The *Palaeomutela* representatives from the marposadica Zone exhibit the most complex differentiated hinge as compared with its other species that form the *P. castor* group (Fig. 3). Distinct depressions in the hinge separate the umbonal area that is characterized by the subvertical positions of tooth plates in the anterior and posterior branches of the hinge. In the posterior and anterior branches of the hinge, the main shoulders of tooth plates are inclined toward the umbo. The distal part of the posterior branch bears rare subhorizontal plates resembling lateral teeth of heterodont hinges.

The marposadica Zone is documented through Volga–Ural and North Caspian basins of the East European Platform.

Palaeomutela fischeri Zone

Index species: *Palaeomutela fischeri* (Amalitzky, 1892b) (Plate II, fig. 10). Lectotype (Gusev, 1990, p. 192): St. Petersburg, SPGU, specimen 11/141 (Amalitzky, 1892a, plate 4, fig. 34; Amalitzky, 1892b, plate XXII, fig. 34); right bank of the Oka River near Nizhni Novgorod, Yaril'skii Ravine Section, Severodvinian Stage, Putyatino Beds. Subsequently, Gusev (1996c) used the index species for defining the Palaeanodonta fischeri–Palaeomutela marposadica concurrent range zone corresponding to the upper half of the Severodvinian Stage.

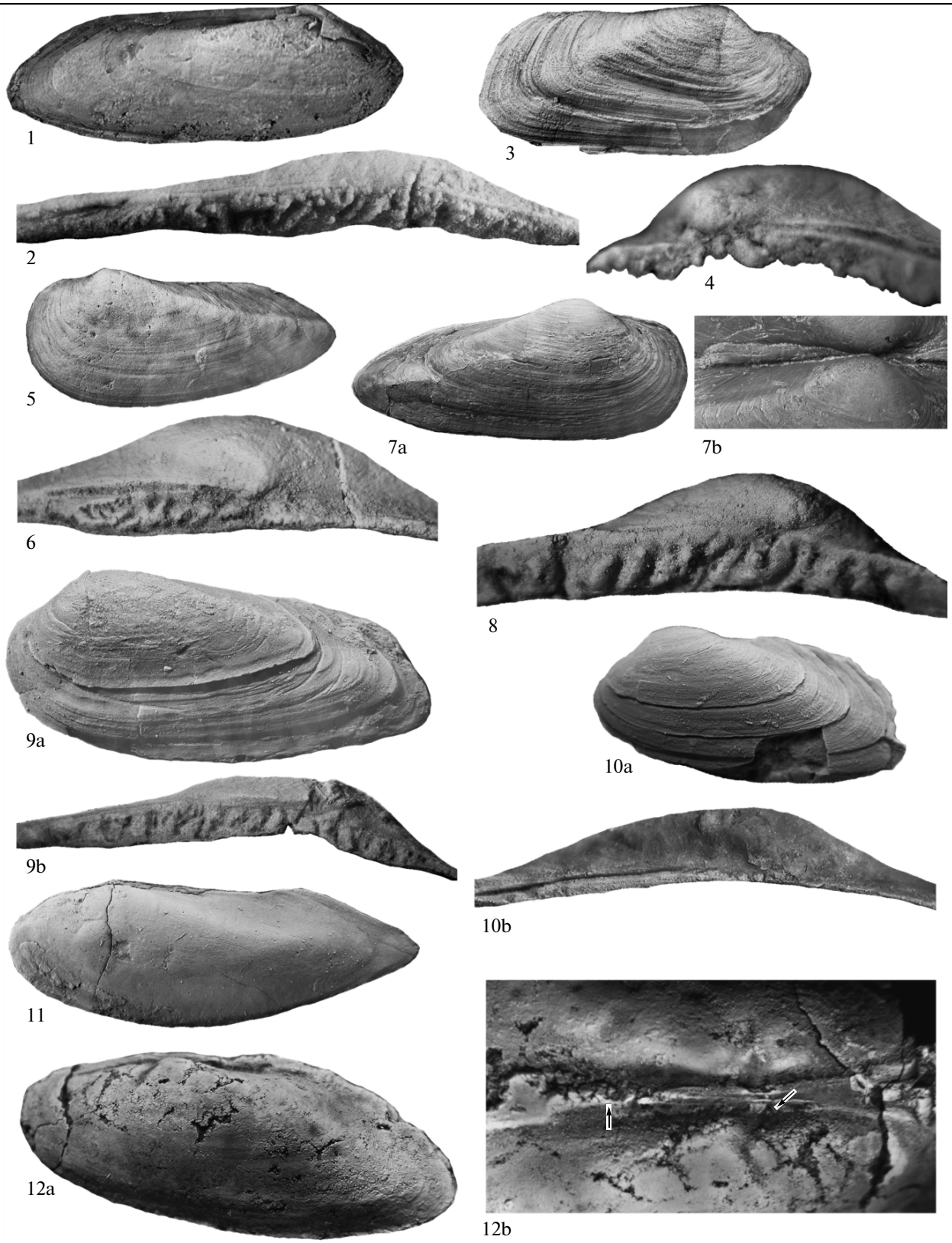
Stratotype of the zone is located on the right bank of the Oka River near Nizhni Novgorod, Yaril'ski Ravine Section, Bed 132 (Fig. 9). The lower and upper boundaries of the unit are placed at the first appearance levels of *P. fischeri* (Amal.) and *P. obunca* Netsch., respectively.

Characteristic bivalve species: *P. keyserlingi* Amal., *P. ovalis* Amal., *P. orthodonta* Amal., *P. parallela* (Amal.), *P. subparallela* Amal., *P. subcastor* (Amal.), *P. convexocarinata* (Netsch.), *P. solenoides* Amal., *Oligodontella zitteli* (Amal.), *O. geinitzi* (Amal.), *Palaeanodonta novoculchumica* (Kuleva), *Opokiella tschernyschewi* Plotnikov.

Remarks. The *Palaeomutela* forms from the *P. castor* group in the fischeri Zone are characterized by the most reduced hinge. Single small node-like teeth are retained in the umbonal area and in the posterior branch of the hinge (Plate II, fig. 10b). The reduction of the hinge in representatives of the genus *Palaeomutela* up to the complete disappearance of teeth was discussed in detail by the author of this genus and served the basis for attributing such forms to the genus *Naiadites* Dawson, 1860 (Amalitzky, 1892a, pp. 65–66; Amalitzky, 1892b, p. 160) and, subse-

Plate II. Zonal nonmarine bivalve species of the *P. castor* group.
(1, 2) *Palaeomutela larae* Silantiev, 1995: (1) specimen 36/1010 (×3), cast of the right valve, Solikamsk depression, Tyul'kino section, (2) specimen 36/999 (×14), hinge of the left valve, Solikamsk depression, Well 214 section, depth 76, Ufimian Stage, Palaeomutela larae Zone; (3, 4) *Palaeomutela castor* (Eichwald, 1861): (3) specimen 30/3340-3 (×3) open shell, (4) specimen 30/3340-3 (×14), hinge of the right valve; Pechora River basin, Tobys River, Ufimian Stage, Palaeomutela castor Zone; (5, 6) *Palaeomutela olgae* Gusev, 1990: (5) specimen 30/7013 (×2.5), cast of the left valve, lower reaches of the Kama River, settlement of Sentyak, Kazanian Stage, Palaeomutela olgae Zone; (6) specimen 36/11-1101 (×14), hinge of the left valve, Vyatka River basin, village of Maksimovtsy, Urzhumian Stage, Palaeomutela doratioformis Zone; (7, 8) *Palaeomutela doratioformis* Gusev, 1990: (7) holotype, specimen 30/3139: (7a) right valve of the closed shell (×2), (7b) dorsal view of the hinge margin with preserved outer opisthodetic parivincular ligament (×6); middle reaches of the Kama River, Nechkinka River, settlement of Nechkino; (8) specimen 30/1146 (×14), hinge of the left valve, lower reaches of the Kama River, settlement of Sentyak, Kazanian Stage, Palaeomutela doratioformis Zone; (9) *Palaeomutela marposadica* Gusev, 1990, holotype, specimen 30/336: (9a) left valve (×3), (9b) hinge (×12); Volga River, Mariinskii Posad, Severodvinian Stage, Palaeomutela marposadica Zone; (10) *Palaeomutela fischeri* Amalitzky, 1892, specimen 11/141 (Amalitzky, 1892a, plate IV, fig. 34): (10a) left valve (×4), (10b) reduced hinge with single nodelike teeth (×14); Oka River, Nizhni Novgorod, Yaril'skii Ravine section, Severodvinian Stage, Palaeomutela fischeri Zone; (11) *Palaeomutela obunca* Netschajew, 1894, lectotype, specimen 13/155, cast of the left valve (×3), Volga River, village of Danilovka, Vyatkian Stage, Palaeomutela obunca Zone; (12) *Palaeomutela amalitzkyi* Silantiev, sp. nov., holotype, specimen 36/11-1012-1: (12a) cast of the left valve of the open shell (×4), (12b) dorsal view of the hinge with white arrows indicating single nodelike teeth (×12); Klyaz'ma River, Gorokhovets, Zhukov Ravine section, Vyatkian Stage, Palaeomutela amalitzkyi Zone.

Plate II



quently, to the genus *Palaeanodonta* Amalitzky (Amalitzky, 1895a, 1895b). The study of the shell material structure in plesiotypes of *Unio castor* Eichwld, 1861 (type species of the genus *Palaeanodonta*) and many species close to *Naiadites fischeri* Amalitzky, 1892 revealed its dominant complex crossed-lamellar patterns characteristic of the genus *Palaeomutela* Amalitzky, 1891. On the basis of this feature, the species under consideration, previously assigned to the genera *Naiadites* or *Palaeanodonta*, are attributed to the genus *Palaeomutela* Amalitzky, 1891 (Silantiev and Carter, 2010). At the same time, reduction patterns of the hinge allows *P. fischeri* Amalitzky, 1892 and close species to be considered as forming a peculiar group with a different tendency in development of the hinge as compared with that in the *P. castor* group (Fig. 3).

The fischeri Zone is recorded through Volga–Ural and Dvina–Mezen basins of the East European Platform.

Palaeomutela obunca Zone

Index species: *Palaeomutela obunca* Netschajew, 1894 (Plate II, fig. 11). Lectotype: Kazan, GM KFU, specimen 13/155 (Nechaev, 1894, p. 291, fig. 22); right bank of the Volga River near the settlement of Dolinovka, 20 km south of Tetyushi, Republic of Tatarstan; Vyatkian Stage.

This biostratigraphic unit is proposed for the first time.

Stratotype of the zone is located on the right bank of the Oka River near the settlement of Okulovo, Outcrop 12, Bed 46 (Fig. 10). The lower and upper boundaries of the unit are drawn at the first appearance levels of *P. obunca* Netschajew and *P. amalitzkyi* Silantiev, sp. nov., respectively.

Characteristic bivalve species: *P. curiosa* Amal., *P. inostranzevi* Amal., *P. crassa* Amal., *P. parva* Amal., *P. plana* Amal., *P. oleniana* Gusev, *P. okensis* (Amal.), *Opokiella ignatjevi* Gusev.

Remarks. Beginning from the obunca Zone, the previously reduced anterior branch of the hinge in species of the *P. castor* group becomes restored. Some platy teeth in the posterior branch acquire the subhorizontal position.

The obunca Zone is registered in the Volga–Ural basin.

Palaeomutela amalitzkyi Zone

Index species: *Palaeomutela amalitzkyi* Silantiev, sp. nov. (Plate II, fig. 12). Holotype: Kazan, GM KFU, specimen 36/11-1012-1; right bank of the Klyaz'ma River 2 km southwest of Gorokhovets, Zhukov Ravine Section; Vyatkian Stage

This biostratigraphic unit is proposed for the first time.

Stratotype of the zone is located on the right bank of the Klyaz'ma River 2 km southwest of Gorokhovets, Zhukov Ravine Section, Outcrop 1027A, Bed 1 (Sennikov and Golubev, 2010). The lower boundary of the unit is placed at the first appearance level of *P. amalitzkyi* Silantiev, sp. nov.; its upper boundary is unknown.

Characteristic bivalve species: *P.* aff. *keyserlingi* (Amal.), *P.* aff. *obunca* (Netsch.), *P. golubevi* Silantiev, sp. nov., *Palaeanodonta* sp. nov.

Remarks. Through the amalitzkyi Zone, species of the *P. castor* group are characterized by a narrow hinge with small nodelike teeth, the number of which never exceeds ten.

The amalitzkyi Zone is recorded in the Volga–Ural basin.

PALEONTOLOGICAL DESCRIPTION

ORDER ACTINODONTIDA DESCHASEAUX, 1952

SUPRAFAMILY PALAEOMUTELOIDEA LAHUSEN, 1897

FAMILY PALAEOMUTELIDAE LAHUSEN, 1897

Genus *Palaeomutela* Amalitzky, 1891 emend Silantiev, herein

Anthracosia: Krotow, 1888, p. 490; Amalitzky, 1892a, p. 52 (pars); Amalitzky, 1892b, p. 153 (pars).

Palaeanodonta: Amalitzky, 1891, p. 2 (pars); Amalitzky, 1895a, p. 10 (pars); Amalitzky, 1895b, p. 346 (pars).

Palaeomutela: Amalitzky, 1891, p. 1; Amalitzky, 1892a, p. 63; Amalitzky, 1892b, p. 142; Nechaev, 1894, p. 252; Laguzen, 1897, p. 355; Chernishev, 1943, p. 14; Lyutkevich and Lobanova, 1960, p. 37 (pars); Betekhtina, 1966, p. 134; Betekhtina, 1974, p. 125; Betekhtina et al., 1987, p. 37; Gusev, 1990, p. 61; Silantiev, 1998, p. 440.

Palaeopleiodon: Amalitzky, 1891, p. 1; Betekhtina et al., 1987, p. 38.

Carbonicola: Amalitzky, 1892a, p. 33; Amalitzky, 1892b, p. 142.

Rectodontia: Chernishev, 1943, p. 17; Betekhtina et al., 1987, p. 39.

Hinganodon: Liang, 1982, p. 138; Fang et al., 2009, p. 86.

Solonodon: Liang, 1982, p. 136; Fang et al., 2009, p. 86.

Type species: *Palaeomutela verneuili* Amalitzky, 1892, Middle–Upper Permian, Urzhumian and Severodvinian stages of the East European Platform.

Diagnosis. Shells are small to large (from 5 mm to 10 cm long, averaging 2 cm across), oval, *Unio*-like, lanceolate, variably elongated, equivalve, unequilateral. Ligament is external, opisthodetic, with a distinct furrow. Ornamentation is represented by thin dichotomizing growth lines and rougher growth folds. Thick-walled shells (1.5–3.0 mm thick) are provided with the well-developed pseudotaxodont hinge with many (20–50) curved platy and nodelike teeth. The hinge is differentiated into the anterior and posterior (with proximal and distal parts) branches (series) and umbonal area, each differing from others in shapes, dimensions, and arrangement of tooth plates. Maximal differentiation of the hinge is reflected in development of pseudocardinal teeth in the umbonal area and

pseudolateral teeth in the distal part of the posterior branch of the hinge. Thin-walled shells (<1.5 mm) exhibit a less differentiated hinge; the number of teeth never exceeds 20 and may decrease up to their total disappearance.

Unaltered shells are largely composed of aragonite; calcite is registered only in the thin upper part of the outer layer that is characterized by a simple prismatic structure. The following crossed-lamellar microstructure varieties are dominant: comarginally oriented branching (largest part of the outer layer), radial (middle layer), and irregular complex (inner layer).

Comparison. The genus under consideration differs from the closest genus *Oligodontella* Gusev, 1963 with a short downward oriented hinge, which is also attributed to the family Palaeomutelidae, by a longer differentiated hinge area and variable shapes of tooth plates. From externally similar shales of the Carboniferous genera *Anthracosia* King, 1856 and *Carbonicola* McCoy in (Sedgwick and McCoy, 1855) that are characterized by the presence of single or several cardinal teeth, it differs by the pseudotaxodont hinge. From the Carboniferous genera *Naiadites* Dawson, 1860 and *Anthraconaia* Trueman et Weir, 1946 with the duplivincular slightly amphidetic ligament and edentuluos hinge area, representatives of the genus *Palaeomutela* differ by the external opisthodetic ligament and pseudotaxodont hinge.

Composition. Approximately 100 species described from the Permian sections of the East European Platform (Amalitzky, 1892a, 1892b; Nechaev, 1894, Kuleva, 1967; Gusev, 1990; Silantiev, 1995), Kuznetsk and Tungus basins (Betekhtina, 1966), Norvik area of the North Siberian Lowland (Lyutkevich and Lobanova, 1960), Tsilyangshan fold belt (Lu, 1986), northeastern China and Inner Mongolia (Liang, 1982), and Main Karoo basin (Sharpe, 1852; Jones, 1890a, 1890b; Amalitzky, 1895b). The taxonomic affinity of some forms with the genus *Palaeomutela* needs to be specified. Such forms are established in the Tarim (Fong, 1996), Dzhungar (Zhao and Tang, 2000), and Turpan (Brand et al., 1993) basins of China; Raniganj and Jaraya basins of India (Chandra and Betekhtina, 1990), Salt Range of Pakistan (Reed, 1939); Ruhuhu basin and Kilombero rift valley of Tanzania (Cox, 1932, 1936), Zambia (Bond, 1954); Zimbabwe (Hind, 1903; Bond, 1946); Parana basin of Brazil (Simoes et al., 1998); and Mexico (Silva-Pineda et al., 2003).

Remarks. The taxonomic history of the genus *Palaeomutela* and compliance of its type species *Palaeomutela verneuili* Amalitzky, 1892 with requirements of the International Code of Zoological Nomenclature are discussed in detail in the special publication (Betekhtina et al., 1987). The nomenclature inferences of these authors are taken into account in this work. The alternative standpoint on the *Palaeomutela* type species is proposed in (Gusev, 1990). In Gusev's opinion, the genus *Rectodontia* Chernyshev, 1943 with the type species *Palaeomutela rectodonta* Amalitzky, 1892 should unite *Palaeomutela* species with the hinge characteristic of bivalve species from the keyserlingi Zone. Most researchers either ignore the genus *Rectodontia* or consider it as a junior synonym of the genus *Palaeomutela* (Weir, 1969; Gusev, 1990). The genus *Palaeopleiodon* defined by Amalitzky (1891) without indication of its type species and species composition was introduced into the nomenclature (Betekhtina et al., 1987) by including *Palaeomutela subovalis* Amalitzky, which is also characterized by the hinge characteristic of forms from the Palaeomutela keyserlingi Zone, as the type species in this genus. The genus *Palaeopleiodon* is considered as a junior synonym of *Palaeomutela* (Weir, 1969). The genera *Hinganodon* Liang, 1982 and *Solonodon* Liang, 1982 substantiated by limited material from the Upper Permian section of northeastern China and Inner Mongolia are also considered now as probable junior synonyms of *Palaeomutela* (Fang et al., 2009). The *Palaeomutela* representatives with the reduced hinge externally resemble some species of the Late Permian genus *Palaeanodonta* Amalitzky, 1891, which are characterized either by edentulous hinge or single pseudotaxodont teeth. The remarkable feature of *Palaeanodonta* shells is their microstructure: their outer layer is characterized by an inclined irregular simple prismatic structure, while the middle and inner layers are mostly homogenous (Silantiev and Carter, 2010).

***Palaeomutela golubevi* Silantiev, sp. nov.**

Plate I, figs. 14–16

Name. In honor of paleontologist V.K. Golubev.

Holotype: GM KFU, specimen 36/11-1107, Vetluga River, Well 10, depth 89; upper Vyatkian Substage, Palaeomutela golubevi Zone; Plate I, fig. 14.

Description. Shell is small (up to 20 mm across), subtrapezoid; the height/length value varies from 0.65 to 0.75, averaging 0.70. The upper margin is straight in small specimens, becoming slightly rounded in larger specimens, and is separated from the straight posterior margin by a distinct bend at an angle of approximately 140°. The lower margin in small specimens is slightly rounded, becoming straighter or slightly concave in more adult specimens. The anterior margin is convex, becoming relatively shorter with the growth of the lower posterior margin of the shell. The initial shell is suboval, with small subcentral umbo, which never towers above the upper margin. Keel is distinct, slightly convex, elevated, emphasized by ornamentation of the valve. The maximal convexity is characteristic of the middle part of the keel elevation. The surface of the valve is slightly concave in front of the keel and goes sharply down behind the latter. Ornamentation is represented by many thin dichotomizing ridges and imbricate or stepped growth folds. Growth folds are separated from each other by thin

(0.3 mm) radial ridges. The hinge is lenticular with maximal width in the umbonal area. The anterior branch bears single poorly expressed nodes; the "pseudocardinal" tooth is indistinct; the posterior branch of the hinge is wide with herringbone tooth plates in the proximal part; the narrow distal part bears single node-like teeth.

Comparison. The species under consideration differs from *P. curiosa* Amalitzky, 1892, which is also subtrapezoid in shape, by the higher shell (height/length value in *P. curiosa* averages 0.55) and more flattened hinge. From *P. ovalis* Amalitzky, 1892 (height/length value averages 0.60), *P. golubevi* differs by the well-developed keel and subtrapezoid shape of valves with a distinct bend between upper and posterior margins.

Material. In total, 20 specimens originating from wells located in the Oka and Vetluga river basins: Zhukov Ravine locality at the Klyaz'ma River near Gorokhovets (collections by V.K. Golubev and A.G. Sennikov, 2008) and the Savvatii locality at the Malaya Severnaya Dvina River (collections by M.P. Aref'ev, 2011; upper Vyatkian Substage, P. golubevi Zone.

***Palaeomutela amalitzkyi* Silantiev, sp. nov.**

Plate II, fig. 12

Name. In honor of paleontologist V.P. Amalitzky.

Holotype: GM KFU, specimen 36/11-1012-1, right bank of the Klyaz'ma River, 2 km southwest of Gorokhovets; Zhukov Ravine Section, Vyatkian Stage, Palaeomutela amalitzkyi Zone; Plate II, fig. 12.

Description. Shell is small (up to 20 mm across), subtrapezoid; the height/length value in young shells averages 0.35. In more adult shells, the lower posterior margin becomes gradually wider and they acquire subtriangular outlines with the height/length value increasing to 0.40 on average. The upper margin is short (never exceeding half of the shell length), straight, grading into narrowly rounded anterior and widely rounded posterior margins. With shell maturation, the angle between the upper and posterior margins increases from 130° to 160°. The lower margin is slightly rounded. Keel is poorly developed, being notable only near the umbo in large specimens. The maximal convexity is confined to the lower part of the keel elevation. The hinge is reduced: the hinge area is narrow, short; teeth in the anterior and posterior branches are represented by small nodes, the number of which never exceeds ten.

Comparison. *Palaeomutela amalitzkyi* differs from all the known *Palaeomutela* species by its subtriangular shell in adult specimens. Small specimens (5–12 mm across) are similar to shells of *Palaeomutela obunca* Netschajew, 1894 differing from them by the less widened middle part of the shell and more obtuse posterior end, which is tapered downward.

Remarks. Available material is represented only by inner casts. No data on the structure of initial shell, umbo, and ornamentation are available.

Material. Eight specimens from the Zhukov Ravine locality near Gorokhovets and Sokovka locality near Vyazniki at the Klyaz'ma River (collections by V.K. Golubev and A.G. Sennikov, 2008); upper Vyatkian Substage, Palaeomutela amalitzkyi Zone.

CONCLUSIONS

The analysis of the stratigraphic distribution of nonmarine bivalves in the Permian sections of the East European Platform revealed that the bivalve zonation should be based on representatives of the genus *Palaeomutela* that occur in the Ufimian to Vyatkian strata. The study of external, internal, and microstructural features of shells allowed the composition of the genus *Palaeomutela* to be specified: several species which were previously attributed to the genera *Naiadites, Palaeanodonta*, and *Anthraconaia* were included in this taxon, while other forms belonging to the genera *Redikorella, Palaeanodonta*, and *Opokiella* were excluded from the latter.

On the basis of the detailed examination of hinge morphology in *Palaeomutela* representatives, its structure is revised: (1) the anterior branch, umbonal area, and posterior branch with the proximal and distal parts are defined; (2) tooth plates are subdivided into several elements confined to particular parts of the hinge and becoming gradually more complex; (3) isolated subvertical ("pseudocardinal") and horizontal ("pseudolateral") teeth are defined in the umbonal area and distal part of the posterior branch, respectively, observable in species with the maximal differentiation of the hinge; (4) two groups of species with different hinge morphologies are definable in the genus *Palaeomutela*: *P. umbonata* (thick-walled shell, well-developed hinge) and *P. castor* (thin-walled shell, reduced hinge) groups. Changes in morphology of the hinge in different-age species from these groups provided grounds for defining phylogenetic lineages in the genus *Palaeomutela* evolution.

The results of revision of the *Palaeomutela* taxonomic composition and its stratigraphic distribution provided grounds for development of a zonal scale which includes two parallel successions of range zones based on evolutionary trends of the *P. umbonata* (dwellers of silty–psammitic substrates) and *P. castor* (dwellers of pelitic–silty substrates) groups. The first appearance levels of nonmarine bivalve index species are mostly inconsistent with boundaries of regional stratigraphic units substantiated by ostracods. Stratigraphic ranges of bivalve-based zones are different. Some of them characterize relatively narrow intervals of the section (stegocephalum, larae, wohrmani, ulemensis, obunca, golubevi, and amalitzkyi zones); others correspond to substages. The bivalve zones are usu-

ally comparable in their ranges with zones based on ostracod, fish, and tetrapod fossils.

ACKNOWLEDGMENTS

I am grateful to M.P. Aref'ev (Geological Institute, Russian Academy of Sciences) and V.V. Bulanov, V.K. Golubev, and A.G. Sennikov (Paleontological Institute, Russian Academy of Sciences) for donated collections and assistance in determining the stratigraphic positions of samples, and A.S. Alekseev (Moscow State University), A.S. Byakov (Northeast Complex Research Institute), and G.V. Kotlyar (VSEGEI) for valuable recommendations which made it possible to specify some stratigraphic aspects and improve the manuscript. This work was supported by the Russian Foundation for Basic Research, projects nos. 11-05-00252 and 13-05-00642.

Reviewer A.S. Alekseev

REFERENCES

Amalitzky, V.P., About the ancient age of *Unionidae*, in *Protokoly zasedanii sektsii biologii Varshavskogo o-va estestvoispytatelei* (Proc. Warsaw Soc. Naturalists. Biol. Sect.), 1891, Iss. 2, no. 7, pp. 1–5.

Amalitzky, V.P., The data on the fauna of the permian system of Russia. 1. Marly-sandy deposits of the Oka–Volga basin. *Anthracosidae*, *Proc. Warsaw Univ.*, 1892a, nos. 2–5, 7–8, pp. 1–150.

Amalitzky, V.P., Über die Anthracosien der Permformation Russlands, *Palaeontographic,* 1892b, vol. 39, nos. 4–6, pp. 125–214.

Amalitzky, V.P., Several remarks on the Upper Permian continental deposits of Russia and South Africa, *Proc. Warsaw Soc. Naturalists*, 1895a, no. 6, pp. 1–10.

Amalitzky, V.P., A comparison of the Permian freshwater *Lamellibranchiata* from Russia with those from the Karoo system of South Africa, *J. Geol. Soc. London*, 1895b, vol. 51, nos. 1–4, pp. 337–351.

Betekhtina, O.A., *Verkhnepaleozoiskie nemorskie peletsipody Sibiri i Vostochnogo Kazakhstana* (The Upper Paleozoic non-Marine Pelecypoda of Siberia and Eastern Kazakhstan), Moscow: Nauka, 1966 [in Russian].

Betekhtina, O.A., *Biostratigrafiya i korrelyatsiya uglenosnykh otlozhenii pozdnego paleozoya po nemorskim dvustvorkam* (Biostratigraphy and Correlation of Late Paleozoic Coal-Bearing Deposits Based on Non-Marine Bivalves), Novosibirsk: Nauka, 1974 [in Russian].

Betekhtina, O.A., Starobogatov, Ya.I., and Yatsuk, N.E., Some problems in the nomenclature and taxonomy of Late Paleozoic nonmarine bivalve mollusks, in *Sistema i filogeniya iskopaemykh bespozvonochnykh* (Taxonomy and Phylogeny of Invertebrata), Moscow: Nauka, 1987, pp. 37–49.

Betekhtina, O.A. and Tokareva, P.A., Non-marine bivalves, in *Verkhnii paleozoi Angaridy. Fauna i flora* (The Upper Paleozoic of Angarida. Fauna and Flora), Novosibirsk: Nauka, 1988, pp. 59–71.

Bond, G., A lower Beaufort (Karroo) invertebrate fauna from Southern Rhodesia, *Trans. R. Soc. South Africa*, 1946, vol. 31, no. 2, pp. 125–131.

Bond, G., *Lamellibranchia* and plants from the Lower Karroo Beds of Northern Rhodesia, *Geol. Mag.,* 1954, vol. 91, pp. 189–192.

Brand, U., Yochelson, E.L., and Eagar, R.M., Geochemistry of Late Permian non-marine bivalves: implications for the continental paleohydrology and paleoclimatology of northwestern China, *Carbonates and Evaporites*, 1993, vol. 8, no. 2, pp. 199–212.

Chandra, S.K. and Betekhtina, O.A., Bivalves in the Indian Gondwana Coal Measures, *Indian J. Geol.*, 1990, vol. 62, no. 1, pp. 18–26.

Chernyshev, B.I., *Do sistematiki verkhn'o-paleozoiskikh Taxodonta* (The Taxonomy of Upper Paleozoic Taxodonta), Moscow: Bid. Akad. nauk URSR, 1943 [In Ukranian].

Chernykh, V.V., *Zonal'nyi metod v biostratigrafii. Zonal'naya shkala nizhnei permi po konodontam* (Zonal Method in Biostratigraphy. Zonal Conodont Scale of the Lower Permian in the Urals), Yekaterinburg: IGG UrO RAN, 2005 [in Russian].

Cox, L.R., *Lamellibranchia* from the Karroo Beds of the Ruhuhu Coalfields, Tanganyika territory, *J. Geol. Soc. London*, 1932, vol. 88, pp. 623–633.

Cox, L.R., Karoo *Lamellibranchia* from Tanganyika territory and Madagascar, *J. Geol. Soc. London*, 1936, vol. 92, no. 1, pp. 32–54.

Dawson, J.W., *Supplementary Chapter to Acadian Geology*, Edinburg: Oliver et Boyd, 1860.

Eagar, R.M.C., Stone, N.M., and Dickson, P.A., Correlations between shape, weight and thickness of shell in four populations of Venerupis rhomboids (Pennant), *J. Mollus. Stud.*, 1984, vol. 50, no. 1, pp. 19–38.

von Eichwald, J.K.E.I., *Lethaea Rossica ou Paléontologie de la Russie, Décrite et Figurée par Edouard d'Eichwald.* Stuttgart: E. Schweizerbart, 1860, vol. 1, Ancienne Période.

Fang, Z., Chen, J., Chen, Ch., et al., Supraspecific bivalvia taxa first named, described and published in China (1927–2007), *Univ. Kansas Paleontol. Contrib. N. S.*, 2009, no. 17, p. 157.

Fong, Z.J., Permian non-marine bivalves from Tarim, northwest China, *Acta Palaeontol. Sinica,* 1996, no. 35, pp. 60–79.

Golubev, V.K., *Permskie i triasovye khroniozukhii i biostratigrafiya verkhnetatarskikh otlozhenii Vostochnoi Evropy po tetrapodam* (Permian and Triassic Chronosuchians and Biostratigraphy of the Upper Tatarian Deposits of Eastern Europe by Tetrapods), Moscow: Nauka, 2000 [in Russian].

Gusev, A.K., Importance of bivalves for subdivision and correlation of Upper Permian red deposits of the eastern part of the Russian Platform, *Uch. Zap. Kazan. Gos. Univ.*, 1963, vol. 123, Book 5, pp. 15–25.

Gusev, A.K., Stratigraphic importance of Upper Permian non-marine bivalves for the of the European part of the USSR, in *Materialy po stratigrafii verkhnei permi na territorii SSSR* (Materials on the Upper Permian Stratigraphy in the USSR), Kazan: Izd. Kazan. Univ., 1977a, pp. 94–128.

Gusev, A.K., Taphonomic analysis by the example of fossil non-marine bivalves from Upper Permian sedimentary basins of the Russian Platform, in *Stratigrafiya i paleontologiya paleozoya vostoka Russkoi platformy* (Stratigraphy

and Paleontology of the Paleozoic Sequences of the Eastern Part of the Russian Platform), Kazan: Izd. Kazan. Univ., 1977b, pp. 127–153.

Gusev, A.K., *Nemorskie dvustvorchatye mollyuski verkhnei permi Evropeiskoi chasti SSSR* (Upper Permian Non-Marine Bivalves of the European Part of the USSR), Kazan: Izd. Kazan. Univ., 1990 [in Russian].

Gusev, A.K., The reference section of the Urzhumian Stage in the Cheremushka ravine, in *Stratotipy i opornye razrezy Povolzh'ya i Prikam'ya* (Stratotypes and Reference Sections of the Upper Permian in the Regions of the Volga and Kama Rivers), Kazan: Ekotsentr, 1996a, pp. 113–122.

Gusev, A.K., The reference section of the Tatarian Stage near the Monastyrskoe village, in *Stratotipy i opornye razrezy Povolzh'ya i Prikam'ya* (Stratotypes and Reference Sections of the Upper Permian in the Regions of the Volga and Kama Rivers), Kazan: Ekotsentr, 1996b, pp. 123–140.

Gusev, A.K., Non-marine bivalves. The zonal stratigraphic division of Upper Permian sequences based on different assemblages of flora and fauna, in *Stratotipy i opornye razrezy Povolzh'ya i Prikam'ya* (Stratotypes and Reference Sections of the Upper Permian in the Regions of the Volga and Kama Rivers), Kazan: Ekotsentr, 1996c, pp. 223–226.

Hind, W., Notes on some *Lamellibranchiate* Mollusca obtained by Mr. Molyneux from the Sengwe Coalfield, *J. Geol. Soc. London*, 1903, vol. 59.

Jones, T.R., On some small bivalve shells from the Karoo formation, South Africa, *Geol. Mag.*, 1890a, vol. 7, pp. 409–410.

Jones, T.R., On some fossils from Central Africa, *Geol. Mag.*, 1890b, vol. 7, pp. 553–558.

Kanev, G.P., Zonal division of Permian coal-bearing deposits of the Pechora Basin based on non-marine bivalves, *Tr. Inst. Geol. AN SSSR, Komi Filial*, 1985, Iss. 54, pp. 65–70.

Kanev, G.P., Non-marine bivalve-based correlation of zonal stratigraphic scales of the Russian Platform and the Pechora Basin, *Tr. Inst. Geol. AN SSSR, Komi Filial*, 1994, Iss. 82, pp. 37–44.

King, W., On *Anthracosia*, a fossil genus of the family Unionidae, in *The Annals and Magazine of Natural History*, 1856, vol. 17, no. 97, pp. 51–57.

Kotlyar, G.V., The Permian System, in *Sostoyanie izuchennosti stratigrafii fanerozoya Rossii. Zadachi dal'neishikh issledovanii. Postanovleniya Mezhv. Stratigr. Kom. i ego Postoyan. Kom. Vyp. 38* (The State of Knowledge of the Phanerozoic Stratigraphy of Russia. Further Research Objectives. Resolutions of Interdepartmental Stratigraphic Committee and Its Permanent Commissions. Iss. 38), St. Petersburg: Izd. VSEGEI, 2008, pp. 69–76.

Krotov, P.I., Geological investigations on the western slope of the Solikamsk and Cherdyn Urals, *Tr. Geol. Kom.*, 1888, vol. 6.

Kukhtinov, D.A., Lozovskiy, V.R., Afonin, S.A., et al., Non-marine ostracods of the Permian–Triassic transition from the sections of the East European Platform, *Boll. Soc. Geol. Italiana,* 2008, vol. 127, pp. 717–726.

Kuleva, G.V., New species of bivalves from Upper Kazanian and Tatarian continental deposits of the southern parts of Orenburg and Bashkir Urals, in *Voprosy geologii Yuzhnogo Urala i Povolzh'ya. Vyp. 4. Ch. 1* (Problems in Geology of the Southern Urals and Volga Region, Iss. 3, Pt. 1), Saratov: Izd. Saratov. Inst., 1967, pp. 27–36.

Kuleva, G.V., Upper Permian bivalves and sedimentation conditions, in *Voprosy stratigrafii i paleontologii. Vyp. 5* (Problems in Stratigraphy and Paleontology, Iss. 5), Saratov: Izd. Saratov. Inst., 1980, pp. 22–31.

Laguzen, I., *Kratkii kurs paleontologii. Tom 2. Paleozoologiya* (Short course in paleontology. Vol. 2. Paleozoology), St. Petersburg: Izd. Akad. Nauk, 1897 [in Russian].

Liang, Zh., Some Late Permian bivalvia and related stratigraphical questions of Eastern Nei Mongol and northern-northeastern China, *Bull. Shenyang Inst. Geol. Mineral Resources, Chinese Acad. Geol. Sci.*, 1982, vol. 4, pp. 130–148.

Lu, Y.J., Permian Lamellibranchs from Buha River valley, Tianjun district, Qinghai, *Acta Palaeontol. Sinica*, 1986, vol. 25, no. 4, pp. 463–473.

Lyutkevich, E.M. and Lobanova, O.V., Permian Pelecypods of the Soviet sector of the Arctic, *Tr. VNIGRI*, 1960, no. 149.

Minikh, A.V. and Minikh, M.G., *Ikhtiofauna permi Evropeiskoi Rossii* (The Permian Ichtyofauna in the Eastern Part of Russia), Saratov: Nauchn. Kniga, 2009 [in Russian].

Molostovskaya, I.I., Towards broadening the correlation prospects of the East European stratigraphic scale for the Upper and Middle Permian, *New Mexico Museum of Natural History and Science Bulletin*, 2005, vol. 30, pp. 219–225.

Nechaev, A.V., The Permian Fauna in the eastern part of European Russia, *Tr. O-va Estestvoispyt. Kazan. Univ.*, 1894, vol. 27, iss. 4.

Newell, A.J., Sennikov, A.G., Benton, M.J., et al., Disruption of playa-lacustrine depositional systems at the Permo-Triassic boundary: evidence from Vyazniki and Gorokhovets on the Russian Platform, *J. Geol. Soc. London*, 2010, vol. 167, pp. 695–716.

Plotnikov, M.A., New data on fauna of the Tatarian Stage in the basins of Sukhona and Malaya Severnaya Dvina Rivers, in *Ezhegodnik VPO. T. 13* (Yearbook VPO. Vol. 13), M.–L.: Gosgeoltekhizdat, 1949, pp. 91–98.

Reed, F., Non-marine lamellibranchs, etc., from the Speckled Sandstone Formation (Punjubian) of the Salt Range, *Rec. Geol. Surv. India*, 1939, vol. 74, no. 4, pp. 474–491.

Sedgwick, A. and McCoy, F., *A Synopsis of the Classification of the British Palaeozoic Rocks, with a Systematic Description of the British Palaeozoic Fossils in the Geological Museum of the University of Cambridge*, London: Cambridge Univ. Press, 1855.

Sennikov, A.G. and Golubev, V.K., Permian/Triassic deposits of Gorokhovets–Vyazniki area, Vladimir Region, in *Paleontologiya i stratigrafiya permi i triasa Severnoi Evrazii* (Permian and Triassic Paleontology and Stratigraphy of the North Eurasia), Moscow: PIN RAN, 2010, pp. 102–107.

Sharpe, D., Description of some remains of mollusca from near Graaf Reinet, *Trans. Geol. Soc. London,* 1852, Ser. 2, vol. 7, pp. 225–226.

Silantiev, V.V., Redikorella, a new non-marine bivalve from the Ufimian (Upper Permian) of West Russia, *N. Jb. Geol. Palaont., Mh.*, 1994, no. 11, pp. 692–702.

Silantiev, V.V., Upper Permian non-marine bivalve *Palaeomutela* from the Solikamsk Horizon of the Solikamsk Basin, *Byull. Mosk. O-va Ispyt. Prir., Otd. Geol.*, 1995, vol. 70, no. 5, pp. 73–82.

Silantiev, V.V., The Solikamsk Horizon of the Permian in the Fore-Urals, in *Stratotipy i opornye razrezy Povolzh'ya i Prikam'ya* (Stratotypes and Reference Sections of the Upper Permian in the Regions of the Volga and Kama Rivers), Kazan: Ekotsentr, 1996a, pp. 13–55.

Silantiev, V.V., Solikamsk and Sheshmian Horizons in the reference sections along the Belaya River (Bashkortostan), in *Stratotipy i opornye razrezy Povolzh'ya i Prikam'ya* (Stratotypes and Reference Sections of the Upper Permian in the Regions of the Volga and Kama Rivers), Kazan: Ekotsentr, 1996b, pp. 56–61.

Silantiev, V.V., New data on the Upper Permian bivalve Palaeomutela in European Russia, in *Bivalves—an Eon of Evolution*, Calgary: Univ. Calgary Press, 1998, pp. 437–442.

Silantiev, V.V., Bivalves, in *Stratotipicheskii razrez tatarskogo yarusa na r. Vyatke* (The Reference Section of the Tatarian Stage in the Vyatka River Basin), Moscow: GEOS, 2001, pp. 83–96.

Silantiev, V.V. and Carter, J.G., A Permian non-marine Cardiida genus *Palaeanodonta* Amalitzky, 1985 from European Russia; Systematic position and revised diagnosis, in *Permian and Triassic Paleontology and Stratigraphy of North Eurasia*, Moscow: PIN RAS, 2010, pp. 107–110.

Silantiev, V.V., The current state of the Bivalvia taxonomy, *Byull. Mosk. O-va Ispyt. Prir. Otd. Geol.*, 2010, vol. 85, Iss. 3, pp. 16–28.

Silantiev, V.V. and Chandra, S.K., *The non-Marine Bivalve Molluscs from the Indian Gondwana Coal Measures*, Saarbrucken: Lambert Academic Publishing, 2011.

Silantiev, V.V. and Carter, J.G., On changes in taxonomy of non-marine bivalve mollusks of the Late Paleozoic in the "Treatise on Invertebrate Paleontology," 3rd ed., *Byull. Mosk. O-va Ispyt. Prir., Otd. Geol.*, 2011, vol. 86, no. 1, pp. 14–17.

Silantiev, V.V. and Esin, D.N., The reference section of the Tatarian Stage in the Monastyrskoe ravine near Kazan (Volga Region), *Vestn. Mosk. Univ. Ser. Geol.*, 1993, no. 4, pp. 38–48.

Silantiev, V.V., Golubev, V.K., Kotlyar, G.V., et al., The sequence of Biarmian and Tatarian Stages of the Permian System in the Monastyrskoe and Ilinskoe ravines, in *Geologicheskie pamyatniki prirody Respubliki Tatarstan* (Geological Natural Monuments of the Republic of Tatarstan), Kazan: Akvarel'-Art, 2007a [in Russian].

Silantiev, V.V. and Kurkova, S.V., Non-marine bivalves from the basin of the Vym' River, the southwestern Timan Region, *Uchen. Zap. Kazan. Univ., Ser. Estestv. Nauk*, 2009, vol. 151, Iss. 3, pp. 205–215.

Silantiev, V.V., Kurkova, S.V., and Murav'ev, F.A., The "Perekhodnaya" unit in the Cheremushka ravine, in *Geologicheskie pamyatniki prirody Respubliki Tatarstan* (Geological Natural Monuments of the Republic of Tatarstan), Kazan: Akvarel'-Art, 2007c [in Russian].

Silantiev, V.V., Kotlyar, G.V., Shishlov, S.A., et al., The sequences of Permian deposits near the Shugurovo village and the Karkaly quarry, in *Geologicheskie pamyatniki prirody Respubliki Tatarstan* (Geological Natural Monuments of the Republic of Tatarstan), Kazan: Akvarel'-Art, 2007b [in Russian].

Silantiev, V.V., Morozov, V.P., Krinari, G.A., et al., The reference section of the Urzhumian Stage in the Cheremushka ravine, in *Geologicheskie pamyatniki prirody Respubliki Tatarstan* (Geological Natural Monuments of the Republic of Tatarstan), Kazan: Akvarel'-Art, 2007d [in Russian].

Silantiev, V.V., Zharkov, I.Ya., Sungatullin, R.Kh., et al., *Mezhdunarodnyi simpozium "Verkhnepermskie stratotipy Povolzh'ya." Putevoditel' geologicheskoi ekskursii* (Int. Symp. "Upper Permian Stratotypes of the Volga Region." Guidebook of Geological Excursion), Kazan: Izd. Kazan. Univ., 1998 [in Russian].

Silva-Pineda, A., Buitrón-Sánchez, B.E., Arellano-Gil, J., et al., Continental and marine Permian biota of south-central Mexico, in *Circum-Gulf of Mexico and the Caribbean: Hydrocarbon Habitats, Basin Formation, and Plate Tectonics, Am. Assoc. Geol. Mem.*, 2003, vol. 79, pp. 462–475.

Simoes, M.G., Rocha-Campos, A.C., and Anelli, L.E., Paleoecology and evolution of Permian pelecypod assemblages (Parana Basin) from Brazil, in *Bivalves—an Eon of Evolution*, Calgary: Univ. Calgary Press, 1998, pp. 443–452.

Stratigraficheskii kodeks Rossii. Izdanie tret'e (Stratigraphic Chart of Russia. The 3rd edition), St. Petersburg: Izd. VSEGEI, 2006 [in Russian].

Stratotipicheskii razrez tatarskogo yarusa na reke Vyatka (The Reference Section of the Tatarian Stage in the Vyatka River Basin), Moscow: GEOS, 2001 [in Russian].

Tatarskie otlozheniya reki Sukhony (Tatarian Deposits of the Sukhona River Basin), Molostovskii, E.A. and Minikh, A.V., Eds., Saratov: Nauchn. Kniga, 2001 [in Russian].

Trueman, A.E. and Weir, J., The British carboniferous non-marine *Lamellibranchia*, *Palaeontogr. Soc. Monogr.*, 1946, vol. 99, no. 434, pp. 1–18.

Weir, J., Order *Unionoida*, superfamily *Archanodontacea*, superfamily *Anthracosiacea*, in *Treatise on invertebrate paleontology. Part N. Mollusca, 6(1): Bivalvia*, Moore, R.C. and Cox, L. R., Eds., Lawrence: Geol. Soc. America and Univ. Kansas Press., 1969, pp. N401–N411.

Zhao, X. and Tang, Zh., Lacustrine deposits of the Upper Permian Pingdiquan Formation in the Kelameili Area of the Junggar Basin, Xinjiang, China, in *Lake Basins through Space and Time*, Gierlowski-Kordesch, E.H. and Kelts K.R., Eds. AAPG Studies in Geology, 2000, no. 46, pp. 111–122.

Translated by I. Basov