ISSN 0869-5938, Stratigraphy and Geological Correlation, 2020, Vol. 28, No. 4, pp. 402–415. © Pleiades Publishing, Ltd., 2020.
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Callovian Ostracods of Central Dagestan: Biostratigraphy, Paleoecology, and Chorology

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Received August 23, 2019; revised November 17, 2019; accepted November 20, 2019

Abstract—Analysis of the distribution of ostracods from the Armkhi Formation (Callovian) of the Tsudakhar section (Central Dagestan) enabled the identification of a stratigraphic sequence of six assemblages determined by paleoecological conditions and the first ostracod-based biostratigraphic zonation of the Callovian of Dagestan. Beds with *Pleurocythere khapissovi* and the Neurocythere cruciata intermedia Zone of the European ostracod scales were identified in the middle Callovian; this facilitated the interregional correlation for ostracods. Paleoecological analysis demonstrated the formation of the lower part of the section (beds with *P. khapissovi* and the N. cruciata intermedia Zone) in the coastal zone of the upper subtidal with normal marine salinity, good aeration, and low sedimentation rates. Sediments of the upper part of the section (paleoecological intervals with *Schuleridea translucida–Cytherella perennis* and with *C. perennis*) accumulated in the lower zone of the upper subtidal with a high sedimentation rate, high (and constantly increasing) eutrophication, and lowered pH values. Analysis of the paleogeographic distribution of the species studied revealed the connections of the Caucasus Sea to Western and Eastern Europe and to Central Asia.

Keywords: ostracods, biostratigraphy, paleoecology, chorology, Middle Jurassic, Callovian, Central Dagestan

DOI: 10.1134/S0869593820040097

INTRODUCTION

In the stratigraphic aspect, any microfauna group has its advantages and limitations, which are related to biological features and the nature of the skeleton. For example, Jurassic marine ostracods are not as widespread in various spectra of sedimentary facies as foraminifera and are much less abundant and diverse. This for a long time delayed the use of ostracods in biostratigraphy (especially in the Soviet Union), although their stratigraphic potential is often higher than that of Protista (Tesakova, 2010). For instance, this group is commonly used for Jurassic stratigraphy of Germany, because foraminifera do not provide the same degree of detail (see, for example, Franz et al., 2009; Schudack, 1994; Schudack, U. and Schudack, M.E., 2000). Ostracod-based stratigraphy of the Lower Cretaceous section on Kolguyev Island (Barents Sea) (Kupriyanova, 2000) and the Upper Jurassic of Mikhalenino section (Kostroma Region) (Tesakova et al., 2012) also turned out more detailed. These organisms were faster to react to the paleoevents, and therefore the lower boundaries of ostracod strata were observed lower in a section than the boundaries of foraminifera strata, and the boundaries of both fauna assemblages coincided only in the presence of breaks (conspicuous or hidden).

In foreign countries, Jurassic ostracods have been used in biostratigraphy since the 1930s and in zonal scale construction since the 1960s. Such scales were developed for the marine Jurassic of Northern France (Bodergat, 1997), Scotland and England (Bate, 2009; Wilkinson and Whatley, 2009), Northern Germany (Brand, 1990; Schudack, 1994; Triebel, 1951; Wienholz, 1967), and Poland (Bielecka et al., 1988a, 1988b). The ostracod scales of Siberia (Nikitenko, 2009) and the Russian Plate (Kolpenskaya, 1999; Tesakova, 2014a, 2015; Tesakova et al., 2017) were developed much later. The stratigraphic and correlation potential of such scales is quite high in each of the countries listed, but direct comparison of the scales is extremely difficult, because the ostracod faunas are characterized to varying degrees and the principles used in delineation of zones vary. A partial correlation between the Western and Eastern European scales mentioned above (in the Middle Jurassic interval) has recently become possible owing to the use of pan-European migratory levels established for cosmopolitan species that propagated with transgressions (Tesakova, 2014a, 2015;

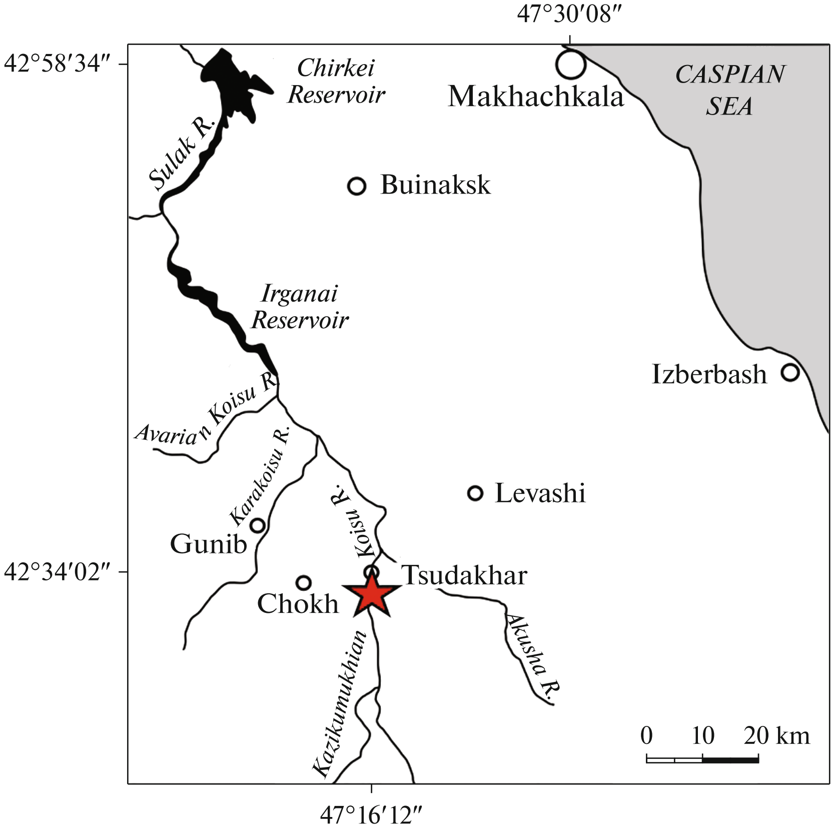

Fig. 1. Schematic map of the location of Tsudakhar section (marked by an asterisk).

Tesakova et al., 2017). Phylogenetic sequences based on the evolution of genera *Lophocythere* Sylv.-Bradley, 1948, *Camptocythere* Triebel, 1950, and *Palaeocytheridea* Mandelstam, 1947 widely spread in Europe are developed for the same purpose (Shurupova and Tesakova, 2017a, 2017b, 2019; Tesakova, 2013b, 2014a, 2014b).

The scales for Southern Germany and Switzerland (Beher et al., 2010; Dietze et al., 2017; Franz et al., 2009; Schudack, U. and Schudack, M.E., 2000; Schudack et al., 2013) differ considerably from those listed above. For example, the area distribution of some zonal taxa is limited only to the Swabian Alb, and the first appearance of pan-European zonal index species in the sections of the southern part of Western Europe occurs earlier than in its northern part. Therefore, the correlation for ostracods of the northern and southern parts of Western Europe has not yet been traced, even for individual levels.

Tsudakhar, the reference section for the Callovian of Central Dagestan (Fig. 1) (Gavrilov et al., 2015), is one of the outcrops that have great potential for such correlations: ostracods were discovered in the section along with various invertebrates, including ammonites (Fig. 2). Jurassic ostracods of this region remained virtually uncharacterized until recently. The systematic composition of these organisms was characterized (with images published) and a full description of a new species was given in the previous article by the authors (Glinskikh and Tesakova, 2020). The present work is devoted to ostracod biostratigraphy and paleoecology in the same section. The objectives of this article also include analysis of the correlation potential of Tsudakhar ostracods and paleogeographic (chorological) analysis of these organisms.

The Tsudakhar section is represented by the Armkhi Formation (upper part of the lower Callovian to lower part of the upper Callovian: Calloviense, Jason, Coronatum, and Athleta ammonite zones); the Tsudakhar Formation (upper Bajocian–Bathonian) is the non-concordant underlying stratum, and the Iron Formation (Upper Jurassic) overlies the Armkhi Formation. A detailed description of lithology and fossil assemblages (ammonites, belemnites, and bivalves) and the biostratigraphy, as well as the images of characteristic foraminifers and sedimentological interpretation, are presented in (Gavrilov et al., 2015, pp. 81–105).

A detailed description of the material used for the present study is presented in (Glinskikh and Tesakova, 2020).

The collection (no. DZ-19) is stored at the micropaleontology laboratory of the Trofimuk Institute of Petroleum Geology and Geophysics, Siberian Branch, Russian Academy of Sciences.

BIOSTRATIGRAPHY AND CORRELATION

The extremely nonuniform distribution of ostracods along the Tsudakhar section allowed for the identification of six assemblages (Fig. 2) that characterize different stratigraphic intervals revealed by the analysis of ammonites performed by M.A. Rogov and D.B. Gulyaev (Gavrilov et al., 2015). The assemblages are described in the order of decreasing depth.

Assemblage I is identified in the lower Callovian (Calloviense Zone, Enodatum Subzone) and encompasses beds 1–7. Its systematic composition (*Cytherella perennis* Błaszyk, 1967 s.l., *Praeschuleridea wartae* Błaszyk, 1967 s.l., *Schuleridea translucida* (Lyubimova, 1955) s.l., *Pleurocythere khapissovi* Glinskikh et Tesakova, 2020, and *Neurocythere rimosa* (Dépêche, 1973)) is almost entirely transferred to the overlying assemblage, except for *Neurocythere rimosa*, for which the only specimen was found at the base of assemblage I. It was most likely redeposited from the Bathonian beds that underlie the lower Callovian beds with a large break. The allochthony of *N. rimosa* is evident from the confinement of this taxon to exactly the Bathonian (the entire Bathonian of Southern England and lower and middle Bathonian of Northwest France and Southern Germany; Table 1).

The stratigraphic distribution of other ostracods (Table 1) does not contradict the early Callovian age of assemblage I. The species *C. perennis*, *P. wartae*, and *S. translucida* are the reference species most abundant in the section (Figs. 3a and 3b) and are obligate in the association with *P. khapissovi* found in assemblages I, II, and III.

Assemblage II was identified in the middle Callovian (Jason and Coronatum zones, with the ?Medea–Jason subzones and the lower part of the Obductum Subzone) in beds 9–12. It is distinguished from the underlying assemblage by the presence of three new taxa: *Bairdia pumicosa* Sheppard in Franz et al., 2009, *Neurocythere cruciata intermedia* (Lutze, 1960), and *Palaeocytheridea* (*P.*) sp.; the appearance of these taxa marks the lower boundary of assemblage II. The appearance of the zonal index species *N. cruciata intermedia* (see below) marks the beginning of the middle Callovian in the section.

Assemblage III was identified in beds 13–26 of the middle Callovian (Coronatum Zone, the upper part of the Obductum Subzone, and the lower part of the Grossouvrei Subzone). Its composition is almost identical to that of the previous assemblage, except for the disappearance of *B. pumicosa* from the section near the lower boundary of the assemblage and the detection of a single *Cytheropteron* sp. specimen, which is important from the point of view of paleoecology. Another paleoecological feature, the change of dominants from schulerideids to cytherellids, which marks the first manifestation of the *Cytherella* signal (see below), is the main distinctive feature of the assemblage.

Assemblage IV was detected in beds 28–30 (Coronatum Zone, middle part of the Grossouvrei Subzone). Its systematic composition is twofold poorer, with relatively abundant *C. perennis* and *P. wartae* and the only *P.* (*P.*) sp. specimen found in the upper part of the stratum.

Assemblage V was detected in the same stratigraphic interval, in bed 36; it includes two species, the scarce *C. perennis* and isolated *S. translucida* finds.

Assemblage VI is a monospecies assemblage. It consists of *C. perennis*, overlaps a wide interval (beds 48–58) in the section, and dates to the top of the Coronatum Zone (upper part of the Grossouvrei Subzone) of the middle Callovian and the Athleta Zone of the upper Callovian (Phaeinum Subzone and the lower part of Proniae + Spinosum).

The distribution of ostracods along the section Tsudakhar (Fig. 2) clearly divides it into the lower part (assemblages I–III) and the upper part (assemblages IV–VI) if variations in species diversity, organism numbers, and change of dominants (Figs. 3a and 3b) are taken into account. The lower part fully corresponds to the beds with *Pleurocythere khapissovi*, which are determined by the distribution of the index species and are identified for the first time in this work. The index species may acquire zonal status in the future, because it is a part of the currently uncharacterized branch on the phylogenetic tree of *Pleurocythere*. The stratigraphic volume of the layers is the lower–middle Callovian (Calloviense–Coronatum zones), and their geographical distribution is currently limited to Central Dagestan.

Moreover, the N. cruciata intermedia ostracod Zone was identified in the lower part of the section (it

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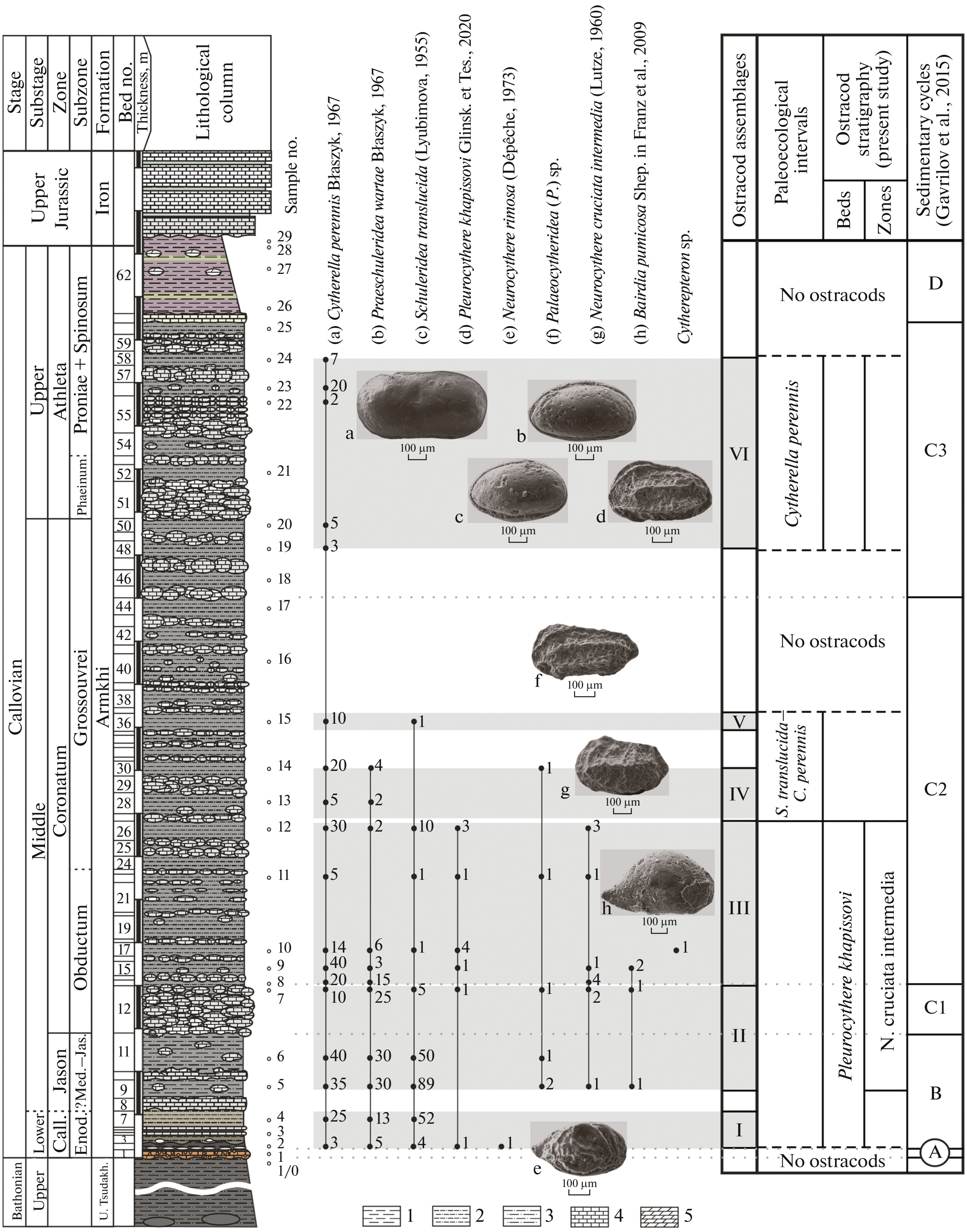
Fig. 2. Ostracod distribution in the Tsudakhar section. Lithological columns and ammonite stratigraphy after (Gavrilov et al., 2015, with modifications). Legend: 1—clay, 2—silt clay, 3—siltstone, 4—limestone, 5—marl. The numbers next to the black circles indicate the number of specimens of a certain species at a given level in the section. (a–h) Ostracod photographs: (a) *Cytherella perennis* Błaszyk, 1967 s.l., specimen no. DZ-19/1, c (complete shell) of a female viewed from the left, bed 17, Coronatum Zone; (b) *Praeschuleridea wartae* Błaszyk, 1967 s.l., specimen no. DZ-19/4, male c from the right, bed 7, Calloviense Zone; (c) *Schuleridea translucida* (Lyubimova, 1955) s.l., specimen no. DZ-19/7, male c from the right, bed 7, Calloviense Zone; (d) *Pleurocythere khapissovi* Glinskikh et Tesakova, 2020, holotype No. DZ-19/13, female c from the left, bed 2, Calloviense Zone; (e) *Neurocythere rimosa* (Dépêche, 1973), specimen no. DZ-19/9, c from the right, bed 2, Calloviense Zone; (f) *Palaeocytheridea (P.)* sp., specimen no. DZ-19/12, c from the left, bed 9, Jason Zone; (g) *Neurocythere cruciata intermedia* (Lutze, 1960), specimen no. DZ-19/11, female c from the left, bed. 13, Coronatum Zone; (h) *Bairdia pumicosa* Sheppard in Franz et al., 2009, specimen no. DZ-19/6, female c from the right, bed 9, Jason Zone. Abbreviations: U. Tsudakh.—Upper Tsudakhar, Call.—Calloviense, Enod.—Enodatum.


Stage
Substage
Zone
Subzone
Formation
Bed no.
Thickness, m
Lithological column
Sample no.
Upper Jurassic
Iron
Callovian
Middle
Upper
Lower
Athleta
Proniae + Spinosum
Phaeinum
Coronatum
Grossouvrei
Obductum
Jason
Med.–Jas.
Call.
Enod.?
Armkhi
Bathonian
Upper
U. Tsudakh.
62
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(a) *Cytherella perennis* Błaszyk, 1967
(b) *Praeschuleridea wartae* Błaszyk, 1967
(c) *Schuleridea translucida* (Lyubimova, 1955)
(d) *Pleurocythere khapissovi* Glinsk. et Tes., 2020
(e) *Neurocythere rimosa* (Dépêche, 1973)
(f) *Palaeocytheridea* (*P.*) sp.
(g) *Neurocythere cruciata intermedia* (Lutze, 1960)
(h) *Bairdia punicosa* Shep. in Franz et al., 2009
Cytherepteron sp.
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f
g
h
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Ostracod assemblages
Paleoecological intervals
Ostracod stratigraphy (present study)
Beds
Zones
Sedimentary cycles (Gavrilov et al., 2015)
No ostracods
VI
V
IV
III
II
I
Cytherella perennis
S. translucida–*C. perennis*
Pleurocythere khapissovi
N. cruciata intermedia
D
C3
C2
C1
B
A
1
2
3
4
5

Table 1. Paleogeographic distribution of Tsudakhar ostracods (see Fig. 5)

Species	Distribution
B. pumicosa Sheppard in Franz et al., 2009	Bathonian and Callovian of Southern Germany (Buck, 1954; Schudack and Schudack, 2000, p. 102, fig. 6; Franz et al., 2009, p. 132, pl. 1, fig. 8; pl. 6, fig. 12; 2014, fig. 15r; Beher et al., 2010, p. 50, text-fig. 3); Bathonian of Normandy (Sheppard, 1981a, pl. 2, fig. 8; 1981b, p. 44, pl. 4, figs. 1–7; Dépêche, 1984, pl. 3, figs. 3 and 4; 1985, pl. 29, fig. 1), lower Bathonian of Dorset (Sheppard, 1981a, pl. 2, fig. 8; 1981b, p. 44, pl. 4, figs. 1–7); lower Bathonian and lower Callovian of Poland (Tesakova et al., 2008, pl. 1, fig. 3).
N. cruciata intermedia (Lutze, 1960)	Lower Callovian (starting from the Koenigi Zone)–lower Oxfordian of Southern Germany (Buck, 1954; Huber et al., 1987, fig. 3; Franz et al., 2009, p. 147, pl. 5, fig. 8; 2014, fig. 15p; Beher et al., 2010, p. 51, pl. 2, fig. 9; Dietze et al., 2017, pl. 12, fig. k); middle Callovian of the eastern Netherlands and the Dnieper-Donets Basin (Pyatkova and Permyakova, 1978, p. 146, pl. 62, figs. 3–4; Herngreen et al., 1983, pl. 3, figs. 1–5); middle and upper Callovian of Northeastern Germany (Lutze, 1960, p. 423, pl. 34, figs. 5–6); middle–upper Callovian and lower Oxfordian (Coronatum–Cordatum zones) of Scotland and England (Whatley, 1970, p. 338, pl. 10, figs. 6, 7, and 9–21; pl. 11, figs. 1 and 4; Kilenyi, 1978, pl. 11, figs. 9–12; Whatley et al., 2001, p. 153, pl. 5, figs. 4–9; Whatley and Ballent, 2004, p. 100; Wilkinson and Whatley, 2009, pl. 8, figs. 8–11); upper Callovian of the Paris Basin and Poland (Oertli, 1963, pl. 34, fig. 1f; pl. 35, figs. 1f and 2f; Bielecka et al., 1988a, p. 171, pl. 67, fig. 1; Olempska and Błaszyk, 2001, p. 568, figs. 9A–9H).
N. rimosa (Dépêche, 1973)	Lower–middle Bathonian of Normandy and the entire Bathonian of Southern England (Dépêche, 1973, p. 218, pl. 1, figs. 9–14; 1984, p. 241, pl. 10, figs. 1–3; 1985, pl. 30, fig. 2; Sheppard, 1981b, p. 83, pl. 13, figs. 2–5; Bate, 2009, pl. 2, figs. 7–9); lower–middle Bathonian (Macrescens Subzone of Zigzag Zone–Morrisi Zone) of Southern Germany (Franz et al., 2014, fig. 13p).
C. perennis Błaszyk, 1967 s.l.	Bajocian and Bathonian of Poland (Błaszyk, 1967, p. 16, pl. 2, figs. 1–11; pl. 3, figs. 6 and 7; Bielecka et al., 1988a, p. 169, pl. 65, fig. 3; Tesakova et al., 2008, pl. 1, fig. 1); upper Bajocian of the Dnieper-Donets Basin (Pyatkova and Permyakova, 1978, p. 122, pl. 45, fig. 1); lower–middle Callovian of the Paris Basin (Lorraine, France) (Dépêche, 1969, p. 264, pl. 3, figs. 7 and 8); middle Callovian–middle Oxfordian of European Russia (Gerasimov et al., 1996, pl. 3, fig. 2–3; Tesakova, 2003, p. 157, pl. 1, figs. 7–9; 2008, fig. 2 (2); Tesakova et al., 2017, pl. 2, fig. 2).
P. wartae Błaszyk, 1967 s.l.	Bathonian of Poland (Błaszyk, 1967, p. 43, pl. 12, figs. 1–2; Bielecka et al., 1988a, p. 176, pl. 72, fig. 3); lower Callovian of Belarus (Makhnach and Tesakova, 2015, pl. 3, figs. 14–18); lower–middle Callovian (Gowerianus–Jason zones) of European Russia (Tesakova, 2003, pl. 10, figs. 1–4; 2013a, pl. 6, fig. 17; Tesakova et al., 2009, pl. 2, figs. 1–4.
S. translucida (Lyubimova, 1955) s.l.	Lower Callovian of the Dnieper-Donets Basin (Pyatkova and Permyakova, 1978, p. 138, pl. 53, figs. 10–11); middle–upper Callovian of European Russia (Lyubimova, 1955, p. 97, pl. 11, fig. 1; 1956, p. 564, pl. 3, figs. 7–8; Gerasimov et al., 1996, pl. 3, fig. 5; Tesakova, 2003, p. 186, pl. 9, fig. 15 (non figs. 12–14 and 16); 2008, fig. 3 (12); Tesakova et al., 2017, pl. 4, figs. 16–17).

corresponds to assemblages II and III). The zonal species or the species characteristic of an analog of his zone (Fig. 4) appears almost everywhere in Western Europe from the middle Callovian, with the exception of Southern Germany, where it is recorded earlier, starting from the middle of the lower Callovian (Franz et al., 2009). The eponymous ostracod zone in Southern Germany corresponds to the interval of the Koenigi–Lamberti ammonite zones (Dietze et al., 2017).

N. cruciata intermedia is used as a characteristic concomitant species of the English Lophocythere interrupta interrupta Zone (Fig. 4), which corresponds to the Coronatum–Lamberti ammonite zones (Kilenyi, 1978; Wilkinson and Whatley, 2009), in Boreal ostracod stratigraphy. The same L. interrupta interrupta Zone with almost the same volume (Jason–Lamberti) was identified in the Paris Basin (Bodergat, 1997), but Bodergat did not mention *N. cruciata inter-*

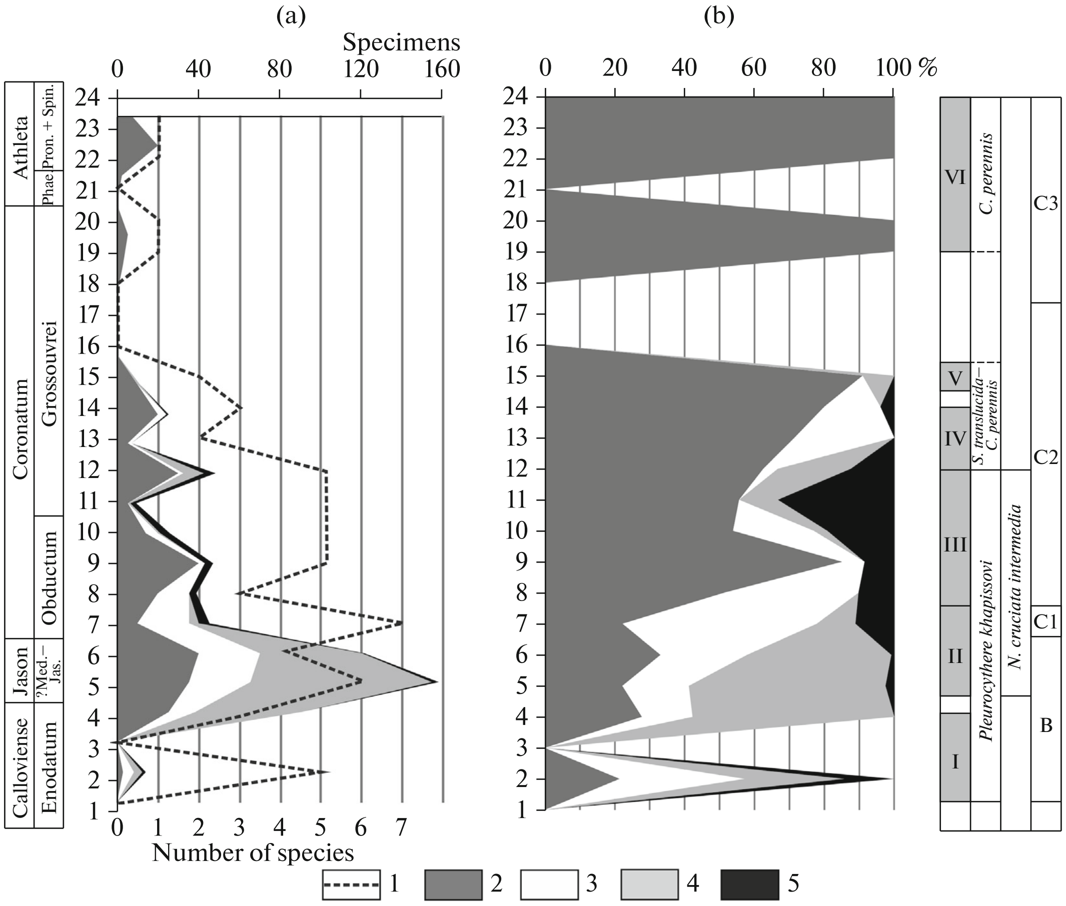

Fig. 3. The ratio of dominant species: (a) numbers of specimens (total numbers = abundance) and (b) percentages. Legend: 1—species diversity, 2—*C. perennis*, 3—*P. wartae*, 4—*S. translucida*, 5—all other taxa (*B. pumicosa*, *N. cruciata intermedia*, *N. rimosa*, *P. khapissovi*, *Palaeocytheridea* (*P.*) sp., and *Cytheropteron* sp.). Abbreviations: Med.–Jas.—Medea–Jason, Phae.—Phaeinum, Pron. + Spin.—Proniae + Spinosum.

media in the description of this zone. However, this species was previously mentioned as stratigraphically significant for the upper Callovian of the Paris Basin (Dépêche, 1985, Plate 6) and assigned to the proposed lineage of *N. cruciata cruciata* (Triebel, 1951)–*N. cruciata intermedia*–*N. cruciata oxfordiana* (Lutze, 1960)–*N. cruciata kimmeridgiensis* (Guyader, 1967) (Dépêche, 1985, p. 121). The appearance of *N. cruciata intermedia* only since the upper Callovian of France seems to be associated with the insufficient amount of research or the deterioration of living conditions of ostracods in the middle Callovian, because only a few stratigraphically significant species were detected in this interval in the Paris Basin (Dépêche, 1985, Plate 6). Analysis of the stratigraphic distribution of ostracods in the Jurassic of Poland (Bielecka et al., 1988a; Olempska and Błaszyk, 2001; Tesakova et al., 2008) enabled Tesakova (2014a, 2015) to propose an ostracod-based zonal division of the Jurassic deposits of Poland. The three characteristic species *N. cruciata intermedia*, *Lophocythere karpinskyi* (Mand. in Lyub., 1955), and *Neurocythere caesa* (Triebel, 1951) appear starting from the Jason Zone. The second taxon was selected as the zonal species for the Jason–lower half of the Pollux [= Coronatum] interval, but the appearance of *N. cruciata intermedia* can also be considered a marker of the lower boundary of the middle Callovian in Poland. *N. cruciata intermedia* was not included in the zonal schemes of Northern Germany (Brand, 1990; Schudack, 1994; Triebel, 1951; Wienholz, 1967), but it was exactly Saxony where the species was first described, and it was exactly the middle Callovian (the Castor et Pollux Zone, upper part of Jason–lower part of Coronatum (Lutze, 1960)) when the species appeared in a Jurassic section of Germany. This species is also registered in the Callovian of the Dnieper–Donets basin starting from the middle Callovian (Pyatkova and Permyakova, 1978), but it was not found on the territory of the Russian Plate (Tesakova, 2014a).

Thus, the N. cruciata intermedia ostracod Zone corresponds to the Koenigi–Lamberti a-zones in the southern part of Western Europe and to the interval of the Jason–Lamberti zones in the northern part of Western Europe.

The interval of the N. cruciata intermedia Zone in the Tsudakhar section is strictly dated to the lower part of the Jason ammonite zone (the index species was not found in the Calloviense Zone)—the middle part of the Coronatum Zone.

Four phylozones for ostracods of the subgenus *Palaeocytheridea* (*Palaeocytheridea*) Mandelstam, 1947 were identified earlier in the middle Jurassic of Europe (Tesakova, 2014a, 2014b). One of the zonal species, *P.* (*P.*) *carinilia* (Sylvester-Bradley, 1948), is known from the lower Bathonian–lower Callovian of Northern France and England (Dépêche, 1969, 1973, 1984; Sheppard, 1981b; Sylvester-Bradley, 1948) and the middle Bathonian of Southern Germany (Malz, 1975; Liebau, 1987). Another species, *P.* (*P.*) *pavlovi* (Lyubimova, 1955), is found in the lower Callovian of the Volga region (Lyubimova, 1955; Tesakova, 2013b, 2014a, 2014b). Unfortunately, the poor preservation of the Dagestan material precluded the species identification of the *P.* (*P.*) sp. specimens from assemblages II–IV, and we were not able to compare this interval of section with the West European *Palaeocytheridea* scales, including the ostracod scale of the Russian Plate.

The systematic composition of ostracods in the upper part of the Tsudakhar section is characteristically poor. Assemblages IV and V are combined in the paleoecological interval with *S. translucida–C. perennis*, which is uninformative from the point of view of stratigraphy, since the vertical range of the index species is unjustifiably wide (Table 1), which is apparently due to the use of composite taxa (Glinskikh and Tesakova, 2020). This interval is put into correspondence with the Grossouvrei Subzone of the Coronatum ammonite zone of the middle Callovian. It covers the transition to the monospecies assemblage VI, which corresponds to the paleoecological interval with *Cytherella perennis*. The latter is also dated to the interval from the upper Grossouvrei Subzone of the Coronatum Zone of the middle Callovian to the Phaeinum and Proniae + Spinosum ammonite subzones of the upper Callovian.

Stratigraphic insufficiency of intervals with *S. translucida–C. perennis* and with *C. perennis* is compensated by their high paleoecological value (see below).

PALEOECOLOGY

Analysis of the cyclic structure of the Callovian stratum enabled Yu.O. Gavrilov (Gavrilov et al., 2015, pp. 91–94) to reconstruct three large sedimentation cycles in Tsudakhar; one cycle was complete and two were reduced (Fig. 2). The reduced cycles B and D correspond to the basal (extremely shallow) phase of the transgression; the higher part denuded during the

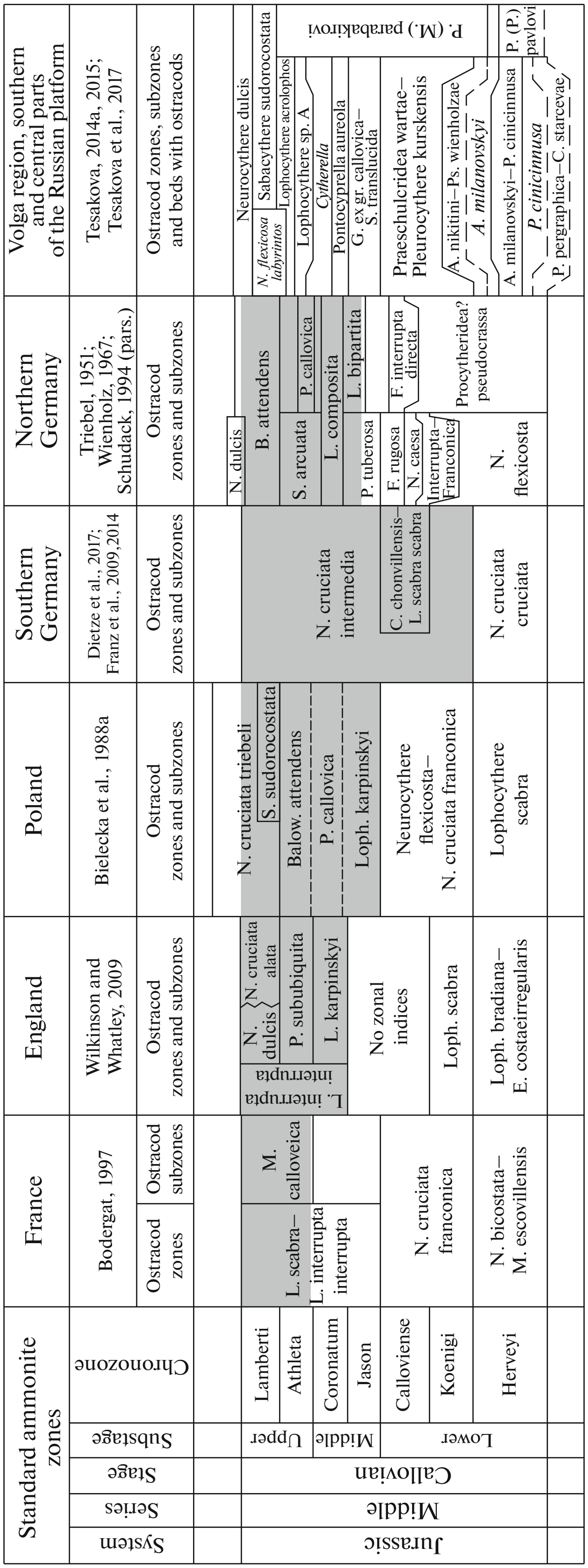

Fig. 4. Ostracod-based zonal scales for the Callovian of Western and Eastern Europe. The interval in which *N. cruciata intermedia* was found is shaded in gray.

sea level drop prior to the next transgressions was not preserved. Both cycles are represented by calcareous sandy-clayey siltstones with several strata of sandy-calcareous rocks. The complete cycle C includes all elements. Slow transgression with alternating accumulation of clay and carbonate rocks in a shallow area corresponds to the initial phase of the cycle (C1). The alternation of these layers (with carbonates predominating) is attributed to frequent sea level fluctuations associated with the Milankovitch precession cycles. The formation of carbonate layers ("debris limestones") occurred during the regressive episodes. The second phase (C2), characterized by predominant accumulation of clay rocks and a reduction in the number and thickness of carbonate interlayers, is associated with rapid transgression and rare short-term episodes of shallowing. This process was accompanied by rapid sedimentation, which prevented a strong deepening of the basin, and an abundant supply of organic matter (OM), which contributed to eutrophication. OM oxidation led to a decrease in pH and could also have accounted for toxic carbon dioxide levels in the bottom water (Gavrilov, 2005). The final stage of the cycle (C3) was marked by a slowdown or stop of the transgression, which led to progressive shallowing of the basin and the formation of a carbonate member.

Let us compare the paleoecological reconstructions based on lithological and ostracod analysis. It is necessary to remember that the ostracod assemblages studied were retrieved from the siltstone, because it is extremely difficult to collect ostracod remains from hard limestone. Moreover, the clearly shallow-water origin of "debris limestones" in an environment with intensive hydrodynamic processes (Gavrilov et al., 2015, pp. 89–91) was not favorable for fossilization of ostracod skeletons (Tesakova and Shurupova, 2018, p. 1565; Zakharov et al., 1988, p. 424).

Cyclic fluctuations in sea level are naturally reflected in the distribution of benthos, including ostracods, on the shelf (Andreev, 1988; Babinot and Lethiers, 1984; Boomer and Eisenhauer, 2002; Kolasa et al., 1998; Pokorný, 1971; Tesakova, 2008, 2013a; Tesakova and Shurupova, 2018; Tesakova et al., 2016). The coastal shallow-water environment (low sea level and closeness to the coast) is characterized by low taxonomic diversity, and the total number of organisms can be small or large depending on the trophic status (large population size is only attained owing to the dominant species). The moderately deep shelf zone (high sea level and a considerable distance from the shore) is usually characterized by high taxonomic diversity and total abundance, but there are no clearly dominant species, even though oxygen-deficient habitats can form an exception.

Accordingly, if the diversity and abundance vary greatly in a certain interval of the section, one can assume that it corresponded to an upper subtidal habitat and evaluate the change in the relative depth within the interval. On the other hand, if the diversity and abundance are stable and high, one can assume that the deposits were formed in the lower subtidal.

The relative depth and its variations can be inferred from the analysis of size clusters of ostracods. A high content (≈80–100%) of large ostracods (shell length of ≈0.48–1.2 mm for the Jurassic forms) in the assemblages is an excellent marker of the upper subtidal. On the contrary, small ostracods (≈0.25–0.32 mm in the Jurassic) significantly prevailed in the lower subtidal. Small variations in the relative abundance of size clusters provide information on the increase/decrease in depth within each of these bionomic zones (Tesakova and Schurupova, 2018).

Another technique was developed for the assessment of the relative depth on the lower subtidal (50–60 m and deeper). The number of taxa with eye tubercles and their total number, as well as the size and the degree of protrusion of the eye tubercles, increase with increasing depth and decreasing bottom illumination on the shelf (Karpuk, 2016).

Other methods, such as analysis of the distribution of cosmopolitan species in the section, morphofunctional analysis of ostracod shells, and analysis of the distribution of index species of various paleoecological environments in the section and the ratio of their dominance can also be used (Shornikov and Mikhailova, 1990; Tesakova and Schurupova, 2018; etc.).

It should be borne in mind that the patterns described and their visual appearance are disrupted upon a deviation from the normal living or entombment conditions for the ostracods (high eutrophication, elevated levels of hydrogen sulfide or carbon dioxide, and the like).

Comprehensive analysis based on some of the methods described above led to the following reconstructions. The beds with *P. khapissovi* (Figs. 2 and 3) are characterized by low taxonomic diversity of marine ostracods (3–7 species) with a periodic increase in the total organism numbers due to 2–3 dominants. The abundance varies over a wide range from 12 to 162 specimens per sample. The features listed are characteristic of the upper subtidal zone, in which the rapid and frequent changes in environmental factors are more common than in the other bionomic zones of the sea.

Moreover, low diversity and high variability of organism numbers are especially pronounced in the lower part of the corresponding graph (assemblages I and II; Fig. 3a), this being indicative of periodic shallowing of the upper subtidal, up to the coast, and completely consistent with sedimentological conclusions about the accumulation conditions for cycles B and C1. The periodic formation of coastal conditions in the interval of assemblages I and II and cycles B and C1 is confirmed by an analysis of the taxonomic structure of the ostracod communities studied, namely, by the distinct dominance of two ubiquitous taxa *P. wartae* and *S. translucida* (Fig. 3b). Schulerideids, which inhabited only the upper subtidal (Malz, 1966; Tesakova et al., 2012), exhibited rapid increases in population sizes in the shallowest areas (Tesakova, 2013a, figs. 2 and 5) due to halotolerance (Wilkinson, 2008), and therefore the predomination of this family (the "Schulerideidae signal") is regarded as a marker of coastal environments in the Middle and Late Jurassic. This is also evidenced by the complete absence of small ostracods, including the taxa with an ocular tubercle (Fig. 2).

The finds of diverse and sometimes abundant ammonites, bivalves, brachiopods, gastropods, sea urchins, corals, bryozoans, and serpulids in the lower Callovian beds 1–7 (Enodatum Subzone) and the large numbers of ammonites in beds 8–12 confirm our conclusions concerning the very shallow and well aerated normal marine environment (assemblages I and II).

Assemblage III (beds 13–26) probably emerged at greater depths, farther from the coast, as evident from a somewhat increased uniformity of its taxonomic structure. For instance, the contribution of eurybiont dominants not associated with specific substrates and devoid of shell sculpture decreased, and the eurybiont/specialized species ratio shifted toward the latter (Fig. 3b). Moreover, one specimen of a small taxon *Cytheropteron* sp. (Fig. 2) characterized by preference for greater depths appeared in this interval of the section. However, assemblage III was still confined to the upper subtidal, since a single find of *Cytheropteron* sp. does not change the pattern of the absolute predominance of large ostracods and the diversity and abundance curves exhibit peaks and low values.

The decrease in the abundance of ostracods in a fixed-weight rock sample (Fig. 3a) can be due to various reasons, such as the deterioration of living conditions, dissolution of shells during diagenesis, and dilution at a high sedimentation rate (Gavrilov, 2005). The latter appears the most likely, since assemblage III is correlated with the first half of phase C2, that is, the beginning of rapid transgression, during which the amount of incoming terrigenous material increased sharply.

The change of dominants in the assemblages is also very illustrative: Schulerideidae (markers of closeness to the shore) substantially predominated in assemblages I and II, and *Cytherella* spp. assumed the leading dominant role in the assemblage III. Ostracods of the genus *Cytherella* Jones, 1849 settled in various habitats from the lagoons (Omatsola, 1971) to the bathyal (Tesakova and Savel'eva, 2005; Yasuhara et al., 2009; etc.) and withstood a salinity decrease to 16‰ (Wilkinson, 2008). They were also able to drive water through the shell twice as fast as other ostracods, and therefore they proved to be the most adapted to oxygen-deficient environments (Corbari et al., 2005; Whatley et al., 2003). Monospecific associations or significant predominance of this genus in the assemblages is termed the "*Cytherella* signal," which is a marker of eutrophication (with a decrease in the oxygen level as a possible consequence) or desalination. In our case, the *Cytherella* signal can only be associated with eutrophication, which occurred during the rapid transgression phase when a large amount of OM arrived from the coastal marshes.

The inflow of OM and sedimentary material increased in the second half of the C2 phase. The elimination of specialized ostracods and enhancement of the *Cytherella* signal occurred in assemblages IV and V owing to the first factor (Fig. 3b) and a decrease in the number of ostracods in the rock samples (Fig. 3a) occurred owing to the second factor.

No ostracods were found in the overlying beds of the section (beds 40–46); the supposed disappearance of ostracods from the paleobiotopes is associated with elevated carbon dioxide levels in the bottom waters, which could have occurred upon OM oxidation. The dissolution of ostracod skeletons during diagenesis at a high CO_2 level is another putative reason for the disappearance of the shells from the fossil record (Gavrilov, 2005).

The "*Cytherella* signal," a marker of a eutrophic environment, becomes evident again in assemblage VI, but the CO_2 level was apparently normal, and therefore the ostracods were preserved in the section. This is indicative of a decrease in OM inflow and rate of transgression, which is in good agreement with the reconstruction of the sedimentological phase C3.

Let us now evaluate the agreement between the ostracod- and pelecypod-based reconstructions. Biofacial analysis of bivalve mollusks performed by V.A. Zakharov showed that "benthic biota (at least in the middle Callovian) ... existed under relatively shallow conditions, mainly within the limits of action of regular waves (above the level of storm wave penetration), in moderately warm sea water of normal salinity.... The general tendency of the sedimentation process points to a gradual shallowing of the water area during the middle Callovian, a decrease in the distance to the source of terrigenous material inflow, and a gradual replacement of marine conditions with lagoon-marine conditions" (Gavrilov et al., 2015, pp. 89–90).

Thus, the results of ostracod analysis are generally consistent with the findings concerning the shallowness, normal salinity, and good aeration of the Central Dagestan paleobasin in the middle Callovian, but add detail to this reconstruction. First, the situation in the upper (coastal) part of the upper subtidal with the listed environmental conditions is revealed for the early and the beginning of the middle Callovian (beds 2–12, assemblages I and II). Second, the situation of the lower (relatively deep) part of the upper subtidal with gradually increasing eutrophication (beds 13–36, assemblages III, IV, and V) and the dissolution of ostracods during diagenesis (beds 38–46) is demonstrated for the overlying middle Callovian beds. Third, the upper part of the middle Callovian and the lower beds of the upper Callovian (beds 48–58, assemblage VI) are

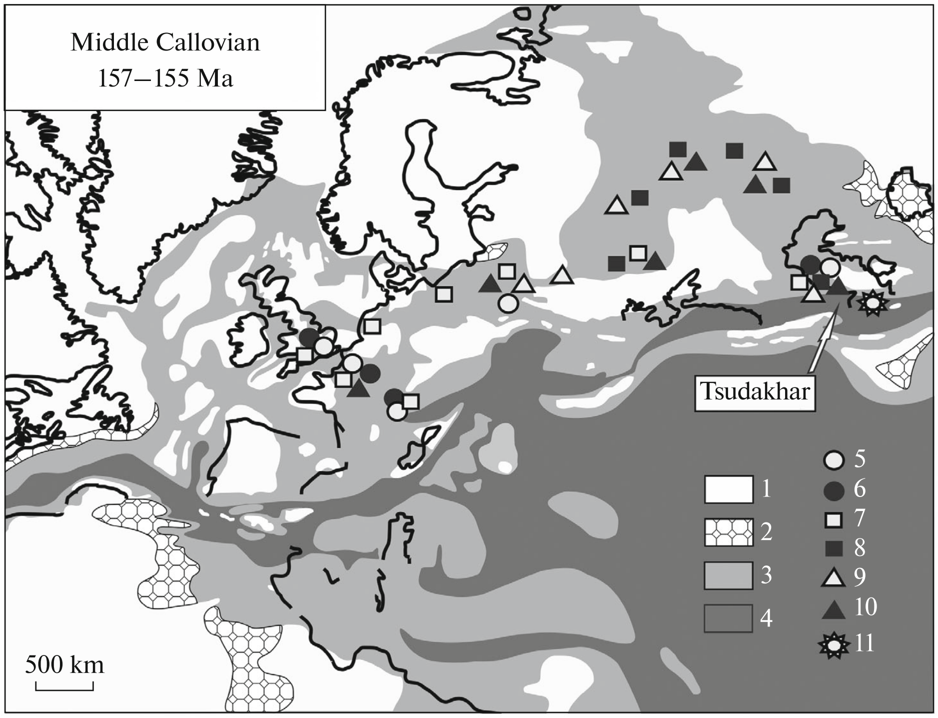

Fig. 5. Paleogeographic scheme of Europe in the middle Callovian (after Thierry, 2000) and the distribution of the ostracod species studied. Legend: 1—eroded land, 2—accumulative land, 3—epicontinental seas, 4—oceanic basin, 5—*B. pumicosa*, 6—*N. rimosa*, 7—*N. cruciata intermedia*, 8—*C. perennis* s.l., 9—*P. wartae* s.l., 10—*S. translucida* s.l., 11—*P. khapissovi*.

characterized by a *Cytherella* signal (high eutrophication), but ostracods cannot be used to estimate the depth of the basin in which this interval of the section was formed and the probability of lagoon formation.

ANALYSIS OF PALEOGEOGRAPHIC DISTRIBUTION OF THE SPECIES STUDIED

The combined list of Tsudakhar ostracods includes nine species with the paleogeographic distribution shown in Fig. 5. The species *B. pumicosa*, *N. cruciata intermedia*, and *N. rimosa* are of particular interest, because they were found in Western Europe, both in its northern (Scotland, Southern England, Normandy, Paris Basin, Netherlands, and Northeast Germany), and southern (Southern Germany and Switzerland) parts, as well as in the west of Eastern Europe (Poland and the Dnieper-Donets Basin) (Table 1). Moreover, the first and last appearance of these species in the fossil record is recorded exactly in the southern part of the range, whereas the species spread into the more northern waters of Western Europe at a later time and disappeared from them at an earlier time. They spread over large areas in the seas of Western Europe and the west of Eastern Europe, but did not reach the Central Russian Sea on the Russian Plate. Consequently, we can talk about their origin, resettlement, and migrations within the shallow marginal seas of the northern part of the Tethys Ocean and in the epicontinental basins of Western and partially Eastern Europe, where the temperatures were higher than in the Central Russian Sea.

The species *P. khapissovi* should be considered endemic to Central Dagestan at present, since its morphology (Glinskikh and Tesakova, 2020) is the closest to the morphology of Uzbekistan *Pleurocythere* (Masumov, 1973). It shows less similarity to the *Pleurocythere* of Western and Eastern Europe (Bielecka et al., 1988a; Błaszyk, 1967; Brand, 1990; Brand and Fahrion, 1962; Dépêche, 1984; Liebau, 1987; Oertli, 1963; Pyatkova and Permyakova, 1978; Sheppard, 1981b; Triebel, 1951) and even less similarity to the representatives of this genus from Southern Germany and Switzerland (Beher et al., 2010; Dietze et al., 2017; Franz et al., 2009, 2014, 2018; Ohmert, 2004; Tesakova, 2017). As in the cases described above, it does not have anything in common with the lineages from Central Russia and Belarus (Makhnach and Tesakova, 2015; Tesakova, 2013a; Tesakova, 2014a; Tesakova et al., 2009). This species apparently is a marker of connections to Central Asia.

The taxa *C. perennis*, *P. wartae*, and *S. translucida*, which inhabited the Polish and Central Russian seas more susceptible to boreal influences, should be considered separately.

The complete absence of species common with the Callovian ostracod fauna of the southern coast of the

Tethys, which exhibit high generic endemism, is a very remarkable feature of the Tsudakhar section and Europe as a whole. Exactly this is the reason for not considering the ostracod-based Callovian schemes for Saudi Arabia (Dépéche et al., 1987), Israel (Oertli, 1966), Jordan (Basha, 1980), Syria (Dobrova, 1997; Kuznetsova and Dobrova, 1995, 1997), Tanzania (Bate, 1975, 1977), Congo (Grékoff, 1957), and Madagascar (Grékoff, 1963) in the present article. The paleogeographic separation of the ostracod fauna of the southern and northern coasts of the ocean is due to the biological characteristics of the group. These organisms lacked the planktonic larva ontogenetic stage: therefore, they could spread only by moving along the bottom and only in the bathymetric interval characteristic of each taxon. Relatively large depths, as well as shallow ones, are a natural barrier to migration of shelf ostracods (Tesakova and Shurupova, 2018).

CONCLUSIONS

Analysis of the distribution of ostracods along the section revealed a stratigraphic sequence of six different assemblages. The presence of the *Pleurocythere khapissovi* species, which was used to identify homonymous beds in the lower and middle Callovian (Calloviense–Coronatum ammonite zones, Enodatum–lower Grossouvrei subzones), is the common feature of the first three assemblages. The second and third assemblages belong to the middle Callovian part (Jason–lower part of the Coronatum ammonite zones) of the Neurocythere cruciata intermedia Zone according to the presence of the zonal index species of the ostracod scales of England and Southern Germany. The fourth and fifth assemblages are assigned to the paleoecological interval with *S. translucida–C. perennis* (Coronatum Zone, middle part of the Grossouvrei Subzone), and the sixth assemblage is assigned to the interval with *C. perennis* (upper part of the Coronatum Zone, upper Grossouvrei Subzone–Athleta Zone, Phaeinum and Proniae + Spinosum subzones).

The sedimentation of the Tsudakhar section were reconstructed by clumped ostracod analysis (complex paleoecological analysis with different techniques for ostracods applied independently). The lower Callovian and lower part of the middle Callovian sediments (the lower half of the beds with *P. khapissovi*) were accumulated in the upper (coastal) part of the upper subtidal with normal marine salinity, good aeration, intense hydrodynamic processes, and low sedimentation rates. The upper part of the middle Callovian (upper half of the beds with *P. khapissovi* and the paleoecological interval with *S. translucida–C. perennis*) was formed in the lower (relatively deep) part of the upper subtidal, with a high sedimentation rate, high (and constantly increasing) eutrophication, and lower pH values. The low number of ostracod species and specimens in this interval of the section is explained by dilution of the assemblages in the rock due to high sedimentation rates. The absence of ostracods from the samples may be due to low pH and dissolution during diagenesis. The top of the middle Callovian and lower beds of the upper Callovian (paleoecological interval with *C. perennis*) exhibit the *Cytherella* signal (oxygen depletion), but ostracod-based reconstruction of the basin depth in this interval is complicated.

Chorological analysis of ostracods showed that all species, except *P. khapissovi*, are known from both Western and Eastern Europe. However, the three species (*B. pumicosa*, *N. cruciata intermedia*, and *N. rimosa*) that lived exclusively in the West European waters could have reached the Caucasus Sea only along the northern edge of the Tethys Ocean or through the southern strait of the Polish Sea, as evident from the absence of these species from the sediments of the Russian platform. Three other species (*C. perennis*, *P. wartae*, and *S. translucida*) spread to the Polish, Central Russian, and Caucasian seas through the Caspian basin. Thus, the ostracods listed above used two different migration corridors for biota exchange with Europe: the western corridor stretched along the southern edge of the Ukrainian shield and bypassed the Russian Plate, and the northern corridor passed through the Central Russian Sea. The species *P. khapissovi* apparently is a marker of the southeastern direction of faunistic exchange with Central Asia.

ACKNOWLEDGMENTS

We are deeply grateful to A.P. Ippolitov (Geological Institute, Russian Academy of Sciences) for constructive comments that substantially improved the article.

FUNDING

This work was carried out within the framework of state assignment no. 0135-2019-0062 (Geological Institute, Russian Academy of Sciences) and AAAA-A16-116033010096-8 (Moscow State University) and with partial support from the Russian Foundation for Basic Research (grants 18-05-00501 and 19-05-00130) and FNI project no. 0331-2019-0005.

Reviewed by Yu.O. Gavrilov,
V.A. Zakharov, and A.P. Ippolitov

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Translated by S. Semenova