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The Genus *Glyptocythere* Brand et Malz, 1962 (Ostracoda) in the Late Bajocian and Early Bathonian of the East European Platform. Part 2: Evolution and Stratigraphy

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Abstract—The geological history of the ostracod genus *Glyptocythere*, which flourished in Western Europe during the Bajocian and Bathonian, and on the East European Platform (EEP) during the latest Bajocian to Early Bathonian, is studied. The evolution of Western European lineages characterized by reticulate and costate ornamentation proceeded either through a complete morphogenesis cycle (involving gerontomorphosis during the Bajocian and paedomorphosis during the Bathonian) or through only the initial phase of the cycle (gerontomorphosis during the Bajocian). Their descendants on the East European Platform evolved via paedomorphosis during the terminal Bajocian and Early Bathonian along four parallel lineages. They developed via accelerated male evolution, proceeding at varying intensities and rates. The evolution of sexual dimorphism in the *G. rugosa*–*G. khabarovae* lineage led to its intensification (over time, males became even larger than females). In the *G. tuberodentina*–*G. bathonica* lineage, sexual dimorphism decreased (in the latter species of the lineage, the female and male hardly differed). In the *G. rugosa*–*G. scissa, G. transversa, G. kiklica* lineage, sexual dimorphism remained constant over time (males were consistently larger than females). In contrast, in the *G. concentrica*–*G. tuberosa* lineage, the pattern reversed (females became larger than males). Additional index species have been added for the EEP ostracod zones. For the G. tuberodentina Zone recognized at the end of the Parkinsoni Zone in the Dnieper-Donets Basin, the following index taxa were selected: *G. concentrica, G. losoviensis, G. crassicostata,* and *G. multa*. For the EEP G. aspera Zone (corresponding to the Michalskii Zone and the lower part of the Besnosovi Zone, specifically the *O. mojarowskii* and *O. sciticum* biohorizons), the additional species *G. tuberosa* and *G. praerimosa* were selected. For the G. bathonica Zone of Central Russia, the Volga Region, and Western Kazakhstan (corresponding to the upper part of the Besnosovi Zone and the *O. issae*–*A. excentricum* biohorizons), the species *G. khabarovae, G. scissa, G. transversa*, and *G. kiklica* are proposed as additional markers.

Keywords: Crustacea, Ostracoda, paedomorphosis, gerontomorphosis, differential rates of sex-specific evolution, evolution of sexual dimorphism, *Bathoniella*-subtype sexual dimorphism, congruent sexual dimorphism, paleoecology, paleogeography

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INTRODUCTION

The present work continues the study of ostracods of the genus *Glyptocythere* Brand et Malz from Bajocian–Bathonian deposits of the East European Platform (EEP) (Tesakova, 2026). The first part of the paper presents paleogeographic reconstructions demonstrating the genus's origin in northwestern Germany during the Early Bajocian, its subsequent dispersal across Western Europe during the Bajocian and Bathonian, and the migration of its representatives into the Central Russian Sea during the latest Bajocian via Poland and the Dnieper-Donets Basin (DDB). Reliable records of *G. tuberodentina* Brand et Malz in Brand and Fahrion and *G. concentrica Brand* et Malz (Permyakova, 1970, 1975), species that originated in the Hanover Sea at the end of the Parkinsoni Phase (Brand & Malz, 1966), have made it possible to refine the stratigraphic range of the Ukrainian neo-endemics *G. losoviensis* Permyakova, *G. crassicostata* Permyakova, *G. multa* Permyakova, *G.* aff. *tuberosa* (=*G. regulariformis* sensu Permyakova), *G.* aff. *tuscila*, and *G.* aff. *tenuisulcata*. While M.N. Permyakova previously assigned these species to the Niortense and Garantiana zones (Permyakova, 1970, 1975), the present author has assigned them to the upper part of the Parkinsoni Zone and proposed treating them as characteristic taxa of the G. tuberodentina ostracod Zone, which was widespread across Ukraine at that time. Descendants of the aforementioned Ukrainian *Glyptocythere* species, i.e., *G. aspera* (Khabarova),

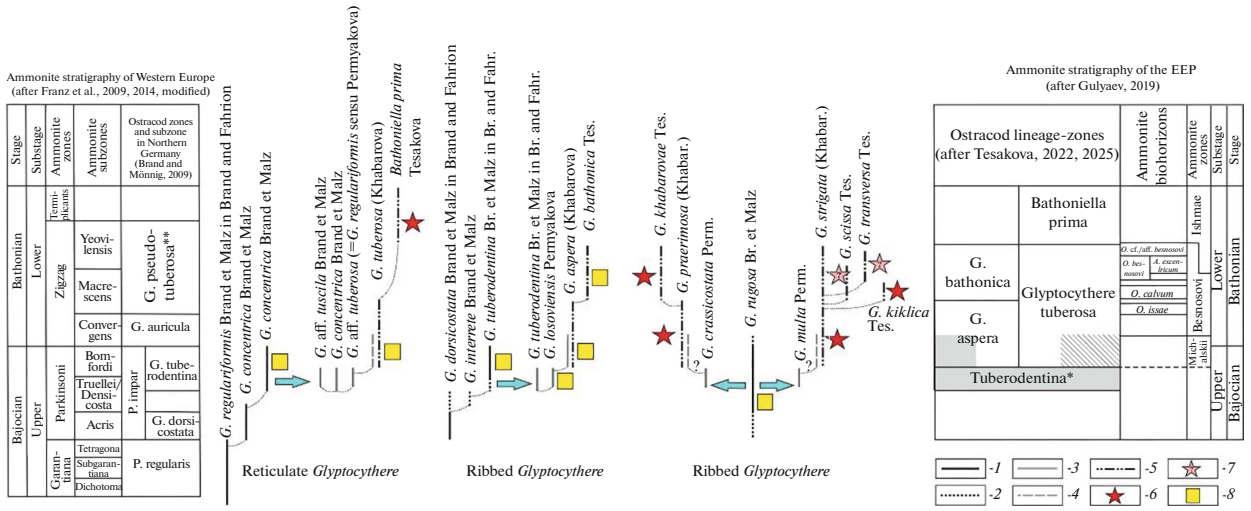

Fig. 1. Distribution of the genus *Glyptocythere* in the Upper Bajocian–Lower Bathonian boundary interval of the EEP and a zonal scale based on the evolution of this genus (from Tesakova, 2022, 2025). (*1*, *2*) Distribution in northern Germany (after Brand & Malz, 1966): (*1*) frequent and abundant occurrences, (*2*) sporadic and single occurrences; (*3*) reliable distribution in the Dnieper-Donets Depression (DDD) (after Permyakova, 1970, 1975, revised by Tesakova); (*4*) inferred distribution in the DDD (author's opinion); (*5*) distribution in Russia (after Khabarova, 1955, 1961; Tesakova, 2022, 2025, 2026); (*6*) *Bathoniella* sexual dimorphism, reliably known in the species; (*7*) supposed *Bathoniella* sexual dimorphism; (*8*) congruent sexual dimorphism in the species. Blue arrows indicate migrations of Western European *Glyptocythere* to the EEP through the DDB; solid gray fill indicates reliable zones, and gray hatching indicates inferred zones distributed in the DDD; the zones not highlighted in color are traced in European Russia; the G. tuberodentina Zone in the DDD smaller stratigraphic range than in Western Europe (Tesakova, 2026); *G. pseudotuberosa*, a replacement name for *G. tuberosa* Brand et Malz, 1966 (Tesakova, 2025).

G. tuberosa (Khabarova), *G. praerimosa* (Khabarova), and *G. strigata* (Khabarova), originated in the Dnieper-Donets Sea during the Michalskii Phase, spread eastward into the Central Russian Sea, and have been proposed as additional index species for the G. aspera ostracod Zone, which has been traced across the East European Platform. In Central Russia, the Volga Region, and Western Kazakhstan, the G. aspera Zone spans a longer time interval than in the Dnieper-Donets Depression, corresponding to the Michalskii Zone and the lower part of the Besnosovi Zone (including the *O. issae* Biohorizon). The upper part of the Besnosovi Zone (the *O. calvum* and *O. besnosovi* biohorizons) is characterized by a subsequent generation of *Glyptocythere* species that inhabited only the Russian seas of the East European Platform: *G. bathonica* Tesakova, *G. khabarovae* Tesakova, *G. scissa* Tesakova, *G. transversa* Tesakova, and G. *kiklica* Tesakova. Thus, the first generation of *Glyptocythere* in East European lineages migrated from the Hanover Basin, via the Polish Sea, into the Dnieper-Donets Sea during the second half of the Parkinsoni Phase. The second generation appeared in the Dnieper-Donets Sea during the Michalskii Phase; it simultaneously colonized the Central Russian Sea and persisted there until the end of the first half of the Besnosovi Phase. The third generation of species originated and evolved exclusively in the Central Russian Sea during the second half of the Besnosovi Phase. Paleogeographic reconstructions involving the migration of *Glyptocythere* onto the East European Platform necessitated a revision of the genus's Eastern European representatives; this resulted in a monographic description of the species originally established by Khabarova (1955) as well as new taxa identified by Tesakova (2026).

Another result of the study, published in the first part of the paper, was the reconstruction of four parallel lineages of the genus *Glyptocythere* that evolved during the Late Bajocian–Early Bathonian interval on the East European Platform (Tesakova, 2026, Fig. 1). However, a comparative analysis of the evolutionary pathways of these lineages is presented in the second part of the article and constitutes its primary objective. A further aim of this paper was to determine the stratigraphic significance of the East European Platform *Glyptocythere* and assess their potential use in biostratigraphy.

MATERIAL AND METHODS

The material used in this study and the methods employed for its processing and examination are described in detail in the first part of the paper (Tesakova, 2026).

Ostracod collections are housed at the Department of Regional Geology and Earth History, Lomonosov Moscow State University (Moscow), coll. nos. MSU Sokur, MSU Sokur-Ya, and MSU Sokur-LG (Saratov Region; composite section of the Sokur Borehole and the exposed part of the Sokur Quarry; Upper Bajocian–Lower Bathonian, Michalskii and Besnosovi

zones, G. aspera and G. bathonica ostracod zones); MSU Pnz-1, MSU Pnz-2, and MSU Pnz-3 (=MSU Pnz-12) (Penza Region; sections of the Krylovka, Kochaleyka, and Obval boreholes, respectively; Lower Bathonian, upper part of the Besnosovi Zone, G. bathonica ostracod Zone); and MSU ISSA (Penza Region; Pletnevka Quarry section).

The terminology used to describe heterochrony in the studied ostracods follows Kiselev (2023).

RESULTS AND DISCUSSION

Evolution of Glyptocythere on the East European Platform

The intensity and rate of evolution of *Glyptocythere* in each of the four East European Platform lineages were assessed based on the following parameters, measured separately for females and males: marginal figure (carapace outline in dorsal view), linear dimensions, and morphology (carapace shape and ornamentation). In other words, sexual dimorphism was examined within each lineage, and the degree of its expression, as well as the rate and intensity of the evolutionary changes leading to its intensification or reduction, were determined. These parameters evolved differently in each lineage, proceeding at varying rates and times for females and males (or remaining unchanged altogether). Heterochronies of individual traits in each lineage are described below, followed by a comparative analysis.

These parameters for the Upper Bajocian–Lower Bathonian *Glyptocythere* of the East European Platform were studied using the author's collections; for *Glyptocythere* from Western Europe, they were assessed based on published data (Brand & Malz, 1966, etc.), and for those from the Dnieper-Donets Depression, based on Permyakova (1970) and Pyatkova & Permyakova (1978).

Marginal figure. A congruent subtype of sexual dimorphism has been established for all Western European *Glyptocythere* (Tesakova, 2026, Table 1) analyzed using photographs from Bate (1963, 1965, 1967, 1969, 2009), Bate & Mayes (1977), Brand & Malz (1966), Lutze (1966), Błaszyk (1967, 1972), and Sheppard (1981). Congruent sexual dimorphism is recognized when the marginal figures in both females and males correspond to the same geometric shape (e.g., trapezoidal or ellipsoidal) and differs between the sexes only in size (Tesakova, 2024). Its counterpart—the *Bathoniella* subtype, in which the marginal figure of females and males differ not only in size but also in shape (e.g., trapezoidal in females versus ellipsoidal or lenticular in males), has been occurs in three *Glyptocythere* lineages that evolved on the East European Platform (Table 1, Fig. 1). The transition from the congruent subtype to the *Bathoniella* subtype occurred at different times in different *Glyptocythere*. For instance, in the *G. concentrica – Bathoniella ultima* Tesakova ostracod lineage, this transition is observed in the Early Bathonian at the boundary between the Besnosovi and Ishmae phases in the species *Bathoniella prima* Tesakova and persists in all subsequent *Bathoniella* species. However, in the *G. rugosa – G. khabarovae* and *G. rugosa – G. scissa, G. transversa*, and *G. kiklica* lineages, it appeared much earlier, during the latest Bajocian at the onset of the Michalskii Phase. *Bathoniella*-subtype dimorphism is reliably documented in *G. praerimosa, G. khabarovae, G. strigata,* and *G. kiklica*, species for which both females and males have been studied. In the case of *G. scissa* and *G. transversa*, which were described based on female specimens, this subtype of dimorphism is inferred due to their close affinity with *G. strigata* and *G. kiklica*.

In contrast, no *Bathoniella*-subtype sexual dimorphism was observed in the *G. tuberodentina–G. bathonica* lineage; instead, the congruent subtype persisted throughout its evolutionary history. The marginal figure in males of *G. aspera* and *G. bathonica* was rectangular, just as in females. Apparently, this lineage did not undergo the major restructuring of the male reproductive organs, inferred from the indirect evidence of the marginal figure observed in other groups. Sexual dimorphism either did not develop in these forms or evolved more slowly than in the males of G. *praerimosa, G. khabarovae, G. strigata, G. kiklica*, presumably *G. scissa,* and *G. transversa*, and all species of *Bathoniella* (sensu Tesakova).

Sexual dimorphism, manifested not in marginal figures but in the linear dimensions of female and male shells, is described below.

Linear dimensions. The *Glyptocythere* species that evolved in the Central Russian Sea fall into large, medium, and small size categories. Large-sized ostracods, with carapace lengths of 0.71–0.88 mm (females) and 0.76–0.88 mm (males), include the species *G. aspera* and *G. bathonica* (Table 2). Medium-sized species—including *G. strigata, G. kiklica, G. transversa*, and *G. scissa* (Table 3), have carapace lengths of 0.54–0.63 mm (females) and 0.63–0.65 mm (males). Small-sized ostracods, with carapace lengths of 0.37–0.53 mm (females) and 0.48–0.6 mm (males), include *G. tuberosa, G. praerimosa*, and *G. khabarovae* (Table 4), as well as representatives of another lineage, *G. concentrica* and *G. tuberosa* (Table 5).

Shell length measurements for females and males of species belonging to various lineages known from the East European Platform are presented below. The species lists in Tables 2–5 are arranged in stratigraphic order and should therefore be read from bottom to top.

The measurements for the German specimens are taken from Brand and Malz (1966), and those for the Ukrainian specimens from Permyakova (1970). Unfortunately, M.N. Permyakova did not specify whether the measurements for particular species referred to females or males, even though she clearly distinguished the sexes of the *Glyptocythere* in her

Table 1. Sexual dimorphism and marginal figures of females and males of the genera *Glyptocythere* and *Bathoniella* on the East European Platform

Species	Subtype of sexual dimorphism	Female marginal figure	Male marginal figure
G. strigata	*Bathoniella*	Trapezoidal (Tesakova, 2026, pl. II, fig. 4b)	Lenticular
G. kiklica		Trapezoidal	Lenticular
G. transversa		Trapezoidal	? Lenticular
G. scissa		Trapezoidal	? Lenticular
B. prima		Trapezoidal (Tesakova, 2024, pl. I, fig. 8b)	Lenticular
G. praerimosa		Trapezoidal (Tesakova, 2026, pl. V, fig. 7a)	Lenticular (Tesakova, 2026, pl. V, fig. 6)
G. khabarovae		Trapezoidal	Lenticular
G. tuberosa	Congruent	Trapezoidal	Trapezoidal
G. aspera		Rectangular (Pl. I, fig. 15; Tesakova, 2022, pl. XII, fig. 4)	Rectangular
G. bathonica		Rectangular (Pl. I, fig. 17b; Tesakova, 2022, pl. XII, fig. 6b)	Rectangular

material. The author of the present paper has assigned the lengths of the Ukrainian taxa to the female and male columns based on the illustrations in Permyakova's paper (1970).

It is noteworthy that the evolution of linear dimensions in females and males within the *G. tuberodentina – G. bathonica* lineage followed divergent paths. While shell length in females increased continuously from species to species (magnification), it decreased in males (minification). Consequently, the shell sizes of females and males converged in the final species, making it impossible to distinguish the sexes of *G. bathonica* based on this trait. In other words, evolution in this lineage "tended to equalize" the sexes: females grew larger while males became smaller, reducing sexual dimorphism to near-zero levels.

Unfortunately, too little is known about the size of males in the *G. rugosa–G. scissa, G. transversa*, and *G. kiklica* ostracod lineage to draw conclusions regarding the evolution of this trait. However, data on female carapace length are complete, revealing the following patterns. Upon the immigration of the German taxon *G. rugosa* into the DDB and the subsequent formation of the neoendemic species *G. multa* (Late Bajocian, Parkinsoni Zone), carapace size increased. The lineage's subsequent evolution was marked by a significant reduction in size among all Central Russian representatives. Specifically, the sizes of *G. strigata* (from the Michalskii Zone to the lower part of the Besnosovi Zone) and *G. scissa* (from the upper part of the Besnosovi Zone) are virtually identical, whereas *G. transversa* and *G. kiklica* are slightly smaller than their ancestor, *G. strigata*. Overall, males in this lin-

Table 2. Large-sized ostracods of the lineage *G. tuberodentina* → *G. losoviensis* → *G. aspera* → *G. bathonica* in the EEP

Complete lineage	Male length, mm	Female length, mm
G. bathonica	0.84–0.88	0.74–0.88
G. aspera	0.76–0.85	0.71–0.79
G. losoviensis	0.92–0.95	?
G. tuberodentina	1.00–1.09	0.66–0.75

Table 3. Medium-sized ostracods of the *G. rugosa* → *G. multa* → *G. strigata* → *G. scissa, G. transversa,* and *G. kiklica* lineage on the EEP

Complete lineage	Male length, mm	Female length, mm
G. transversa	?	0.54–0.55
G. kiklica	0.63	0.55–0.58
G. scissa	?	0.56–0.63
G. strigata	0.65	0.56–0.60
G. multa	?	0.77–0.95
G. rugosa	0.92–1.00	0.71–0.82

Table 4. Small-sized ostracods of the lineage *G. rugosa* → *G. crassicostata* → *G. praerimosa* → *G. khabarovae* on the EEP

Complete lineage	Male length, mm	Female length, mm
G. khabarovae	0.62–0.67	0.42–0.48
G. praerimosa	0.47–0.60	0.41–0.50
G. crassicostata	0.98	0.90–0.95
G. rugosa	0.92–1.00	0.71–0.82

Table 5. Small-sized ostracods of the *G. concentrica* Brand et Malz, 1966 → *G.* aff. *tuberosa* (=*G. regulariformis* sensu Permyakova) → *G. tuberosa* lineage (excluding *Bathoniella*) on the EEP.

Complete lineage	Male length, mm	Female length, mm
G. tuberosa	0.48	0.37–0.53
G. aff. *tuberosa*	?	?
G. concentrica	0.92–1.00	0.78–0.89

eage are larger than females; linear dimensions in both sexes evolved in the same direction, and sexual dimorphism remained pronounced throughout the existence of the lineage.

As in the *G. rugosa* – *G. scissa, G. transversa,* and *G. kiklica* lineage, an increase in size within the *G. rugosa* – *G. khabarovae* lineage occurred with the emergence of a neoendemic species in the DDB during the Parkinsoni Phase, followed by a sharp reduction in the size of Central Russian ostracods during the Michalskii and Besnosovi phases. However, there are differences. While the sizes of females of *G. praerimosa* (from the Michalskii Zone and the lower part of the Besnosovi Zone) and *G. khabarovae* (from the upper part of the Besnosovi Zone) are virtually identical, the males of the latter lineage representative showed a significant increase in size. In other words, the linear dimensions of females of the Central Russian species remained unchanged over time, whereas the males, conversely, exhibited size enlargement, leading to an even more pronounced sexual dimorphism.

The least is known about size evolution within the *G. concentrica* – *G. tuberosa* lineage. It can only be stated that the Central Russian *Glyptocythere* are significantly smaller than their distant German ancestors. However, one circumstance radically distinguishes this *Glyptocythere* lineage from the other three: the females ultimately became larger than the males, and the sexual dimorphism was, in a sense, "reversed".

To summarize this section, it should be noted that the four lineages of *Glyptocythere* that evolved via paedomorphosis followed distinctly different evolutionary paths. Each lineage exhibited either a trend toward size reduction (progenesis) or size increase (magnification) in females and males, or else size stasis. In some instances, the evolutionary trajectories of males and females diverged. For example, in the *G. tuberodentina* – *G. bathonica* lineage, females evolved toward magnification, whereas males evolved toward progenesis. Consequently, the body sizes of the two sexes in the terminal species *G. bathonica* converged, resulting in minimal sexual dimorphism regarding this trait. In the *G. rugosa* – *G. scissa, G. transversa*, and *G. kiklica* lineage, both sexes showed a tendency toward progenesis, leading to a slight reduction in size over time. Nevertheless, males remained larger than females, and sexual dimorphism remained pronounced. The *G. rugosa* – *G. khabarovae* lineage was characterized by size stasis in females, while males evolved toward magnification; this resulted in an intensification of sexual dimorphism from ancestral to descendant forms. Finally, in the *G. concentrica* – *G. tuberosa* lineage, progenesis primarily affected the males, while the size reduction in females was less pronounced. As a result, females of the terminal species became larger than males, leading to the development of "reversed" sexual dimorphism.

Upon the immigration of ancestral Western European species into the Dnieper-Donets Sea, different lineages exhibited distinct adaptive strategies. For instance, a marked reduction in size (progenesis) occurred during the transition from *G. tuberodentina* to *G. losoviensis* (and possibly from *G. concentrica* to *G.* aff. *tuberosa*). In contrast, an increase in size (magnification) was observed in the *G. rugosa* – *G. multa* and *G. rugosa* – *G. crassicostata* lineages. However, during their subsequent dispersal from the Dnieper-Donets Basin into the Central Russian Sea, all four lineages independently evolved toward progenesis, resulting in a significant reduction in size.

Ornamentation. The main (reticulate) ornamentation of *Glyptocythere*, which first appeared in the Early Bajocian, is based on primary cells defined by low, thin muri formed along the walls of the epidermal cells that secreted the shell. The genus's development and diversification led to the emergence of two additional sculptural patterns—costate and rugose—at the beginning of the late Bajocian. Consequently, from the early Late Bajocian through the end of the Bathonian (Bate, 1963; Brand & Malz, 1966; Błaszyk, 1967, 1972; etc.)—or extending to the end of the Early Callovian if one includes the direct descendants of reticulate *Glyptocythere* on the EEP, namely *Bathoniella* (Tesakova, 2024, 2026), the genus evolved along three parallel lineages. One of these, characterized by rugose ornamentation, did not develop on the EEP at all; conversely, the costate form flourished in the Central Russian Sea, evolving there during the Late Bajocian and Early Bathonian along three parallel lineages (Fig. 1): *G. tuberodentina* – *G. bathonica* (characterized by both reticulate and costate ornamentation) (Fig. 2, Pl. I); *G. rugosa* – *G. scissa, G. transversa, G. kiklica* (with sculpture consisting of straight ribs) (Fig. 3); and *G. rugosa* – *G. khabarovae* (with sculpture consisting of arcuate and concentric ribs) (Fig. 4).

The longest-lived lineage comprises forms with reticulate ornamentation: *G. plicata* Brand et Malz → *G. sowerbyi* Brand et Malz → *G. tuscila* Brand et Malz → *G. regulariformis* Brand et Malz (in Brand and Fahrion) → *G. perpolita* Brand et Malz → *G. concentrica* Brand et Malz → *G. comes* Brand et Malz → *G. obtusa* Lutze, and the branch *G. concentrica* – *B. ultima*. This lineage originated in the early Early

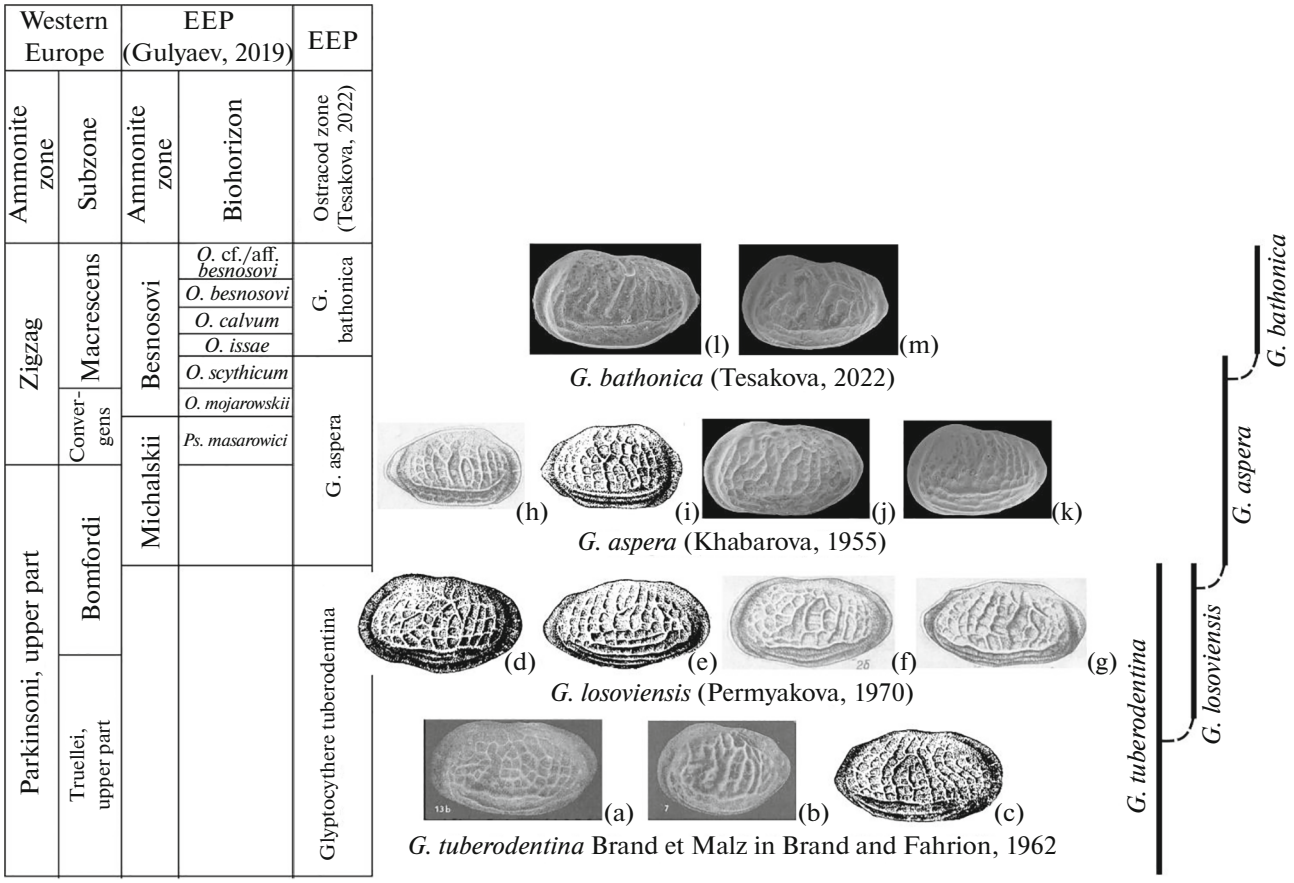

Fig. 2. Evolution of the *G. tuberodentina* → *G. losoviensis* → *G. aspera* → *G. bathonica* lineage on the East European Platform during the Late Bajocian and Early Bathonian. Here and in Figs. 3–5: (1) all North German ostracods originate from the Fuhrberg petroleum province, Upper Bajocian, Parkinsoni Zone (Brand & Malz, 1966); (2) all Ukrainian ostracods come from Upper Bajocian deposits of the DDB and are illustrated in (Permyakova, 1970; Pyatkova & Permyakova, 1978) without collection numbers or measurements. (3) all Russian ostracods from the Sokur Borehole (Saratov) and borehole sections in the Penza Region were previously published (Tesakova, 2022, 2026). The ostracods (k, l, n) come from the Saratov Region, Sokur Borehole section: (k, l) from the Michalskii ammonite Zone / lower part of the Besnosovi Zone (*O. mojarowskii* and *O. scythicum* biohorizons), G. aspera ostracod Zone; (n) from the upper part of the Besnosovi ammonite Zone (*O. issae–A. excentricum* biohorizons), G. bathonica ostracod Zone. Abbreviations: CC – complete carapace, RV – right valve, LV – left valve, juv. – juvenile specimen. (a–c) *G. tuberodentina* Brand et Malz in Brand and Fahrion, 1962, upper part of the Parkinsoni Zone: (a) specimen Xe 43055, male LV, L = 1.04 mm, Fuhrberg-Ost Borehole, depth 439 m; (b) specimen Xe 4302, female LV, L = 0.81 mm, Fuhrberg 148 Borehole, depth 427–430 m (Brand & Malz, 1966, pl. 52, figs. 7, 13b); (c) male RV (Pyatkova & Permyakova, 1978, pl. 58, fig. 3a); (d–g) *G. losoviensis* Permyakova, 1970: (d) male LV; (e) male RV (Pyatkova & Permyakova, 1978, pl. 57, figs. 1a, 2); (f) male LV; (g) male RV (Pyatkova, 1970, pl. 1, figs. 2a, 2b); (h–k) *G. aspera* (Khabarova, 1955): (h) female RV (Permyakova, 1970, pl. 1, fig. 5a); (i) female RV (Pyatkova & Permyakova, 1978, pl. 56, fig. 2a); (j) specimen MSU Sokur-Ya-111, male LV, L = 0.80 mm, depth 32.3 m; (k) neotype MSU Sokur-Ya-138, female CC (left view), L = 0.76, depth 42.9 m (Tesakova, 2022, pl. XI, figs. 1, 6); (l–m) *G. bathonica* Tesakova, 2022: (m) specimen MSU PNZ-12-02, male LV, L = 0.84 mm, Penza Region, Obval Borehole, depth 332.6–332.8 m, G. bathonica ostracod Zone; (n) specimen MSU SOK-LG-01, female RV, L = 0.88 mm, sample 12f (Tesakova, 2022, pl. XII, figs. 6a, 12).

Bajocian and persisted until the end of the Bathonian or the Early Callovian through its descendants, *Bathoniella* (Brand & Malz, 1966, table 1; Tesakova, 2025, fig. 1). All reticulate (and costate) *Glyptocythere* species possess well-developed longitudinal ribs on the ventral side; therefore, these features are not discussed further below in the analysis of ornamentation evolution. During the Early Bajocian, the Discites–Laeviuscula/Sauzei phases, the ostracod valves initially had small reticulate cells (*G. plicata*), which subsequently increased in size (*G. sowerbyi*); by the Humphriesianum Phaze, these reticulate cells had become not only large but also complex, featuring small subvertical and oblique riblets in the upper half of the shell (*G. tuscila*). Thus, the trait of ornamentation (ribbing) first appeared in the evolution of *Glyptocythere* ornamentation. During the Late Bajocian, the Niortense, Garantiana (*G. regulariformis*), and Parkinsoni (*G. perpolita, G. concentrica*) phases, ribbed ornamentation on the carapace surface intensified progressively, whereas at

the onset of the Bathonian age, it became subdued (*G. comes*) and eventually disappeared entirely (*G. obtusa*). Consequently, the evolution of the *G. plicata* – *G. obtusa* lineage underwent gerontomorphosis (acceleration) during the Late Bajocian, whereas in the Bathonian it was replaced by paedomorphosis (retardation). The *G. concentrica* – *B. ultima* lineage also evolved via paedomorphosis, accompanied by progenesis (Tesakova, 2025).

The appearance of ribs in reticulate *Glyptocythere* species led to the emergence, at the beginning of the Late Bajocian (Niortense Phase), of two new ribbed phyletic lineages that persisted in Western Europe until the Early Bathonian. The first lineage, which existed until the start of the Zigzag Phase, comprises the species *G. praecursor* Brand et Malz → *G. hieroglyphica* Brand et Malz → *G. rugosa* Brand et Malz. The second lineage, which lasted until the end of the Zigzag Phase, is represented by the sequence: *G. praecursor* → *G. dorsicostata* Brand et Malz (in Brand and Fahrion) → *G. interrete* Brand et Malz → *G. tuberodentina* Brand et Malz (in Brand and Fahrion) → *G. auricula* Brand et Malz (in Brand and Fahrion) (Brand et Malz, 1966). The evolution of ornamentation differed between these two lineages. In *G. praecursor* (the progenitor of both lineages) the ornamentation combined reticular cells and ribs. However, as early as the Parkinsoni Phase, the reticulum disappeared completely in *G. hieroglyphica* and *G. rugosa* (the first lineage), leaving only the ribs. Ornamentation evolution was more complex in the second lineage. In the immediate descendant *G. dorsicostata* (beginning of the early Parkinsoni Phase), the cells also gave way to ribs. Subsequently, however, in *G. interrete* (end of the early Parkinsoni Phase), the reticulum reappeared on the posterior end of the shell, and in *G. tuberodentina* (late Parkinsoni Phase), it covered the entire intercostal surface. At the beginning of the Bathonian (Zigzag Phase), the reticulum disappeared a second time in *G. auricula*, and the ornamentation once again became purely costate.

The wrinkled lineage known in Western Europe, did not penetrate the East European Platform and is therefore not discussed in this paper.

The evolution of the ornamentation of East European ribbed *Glyptocythere* species, derived from *G. rugosa* and *G. tuberodentina*, is described below.

Glyptocythere with a Costate Ornamentation Pattern

G. tuberodentina–*G. bathonica lineage*. The costate pattern of this lineage consists of longitudinal and transverse ribs that originated from primary cells. In early juvenile stages of each species, the vertical (transverse) ribs were particularly well-developed; consequently, all of them were characterized by transverse ribbing (Table 6). In juveniles, the longitudinal ribs initially appeared as thin muri walls, later developed as connecting bars between the transverse ribs, and finally, at the latest ontogenetic stages, manifested as fully formed longitudinal ribs (Pl. I, figs. 7, 8, 12).

This pattern was observed during the early stages of ontogeny in all species of the lineage (Table 6). However, during the late juvenile stages, *G. losoviensis* and *G. aspera* exhibited a reticulate (basal) pattern characteristic of the ancient—Early Bajocian—ancestors of this lineage, representing a reversion to the ancestral state. Notably, this trait first appeared in males of *G. tuberodentina* (Pl. I, fig. 5), whereas females of the species retained the ribbed ornamentation (Pl. I, fig. 6) characteristic of juveniles (Pl. I, figs. 7, 8). Subsequently, reticulate ornamentation developed in males of *G. losoviensis* (Pl. I, fig. 9) and, presumably, in juve-

Plate I. Representatives of *Glyptocythere* are from: **Figs. 1–8.** Northern Germany, Fuhrberg, Upper Bajocian, Parkinsoni ammonite Zone (after: Brand & Malz, 1966, pl. 52, figs. 6, 7, 8a, 9, 13b; text-figs. 32, 33a, 33b); **Figs. 9, 10.** DDD (Dnieper-Donets Depression), Upper Bajocian, upper part of the Parkinsoni Zone (after: Permyakova, 1970, pl. 1, fig. 2b; Pyatkova & Permyakova, 1978, pl. 57, fig. 1c); **Figs. 11–15.** Sokur Borehole section (Saratov Region), Michalskii ammonite Zone – lower part of the Besnosovi Zone (*O. mojarowskii* and *O. scythicum* biohorizons), Lenticulina volganica–Vaginulina dainae foraminiferal Zone, Glyptocythere aspera ostracod Zone; **Fig. 16.** Obval Borehole section (Penza Region), G. bathonica ostracod Zone; **Fig. 17.** Upper part of the Besnosovi Zone (*O. issae–A. excentricum* biohorizons), Trochammina jakovlevae foraminiferal Zone, G. bathonica ostracod Zone (after: Tesakova, 2022, pl. 11, figs. 6, 9, 12, 16; pl. 12, figs. 4, 6a, 6b, 12). Abbreviations: CC – complete carapace, RV – right valve, LV – left valve, juv. – juvenile specimen; I–II – juvenile age stage preceding sexual maturity; III–IV – early juvenile stage. Scale bar (Figs. 11–17) 100 μm. (1–3) *G. interrete* Brand et Malz, 1966, Vordorf-4 Borehole, depth 448.2–451.3 m, lower part of the Parkinsoni Zone: (1) specimen Xe 5578, male LV, L = 0.82 mm; (2, 3) holotype Xe 5577, female CC, L = 0.67 mm: (2) left view, (3) dorsal view; (4–8) *G. tuberodentina* Brand et Malz in Brand and Fahrion, 1962: Fuhrberg-148 Borehole, depth 427–430 m, upper part of the Parkinsoni Zone: (4) specimen Xe 4303, female CC, dorsal view, L = 0.80 mm; (5) specimen Xe 4305, male LV, L = 1.04 mm, Fuhrberg-East-22 Borehole, depth 439 m; (6) specimen Xe 4302, female LV, L = 0.81 mm; (7) specimen Xe 4302, LV juv., L = 0.65 mm; (8) specimen Xe 4302, RV juv., L = 0.72 mm; (9, 10) *G. losoviensis* Permyakova, 1970: (9) (presumably) holotype IGN AS UkrSSR no. 16-21, male RV; Kharkiv Region, Lozovaya District, village of Krasnopavlovka; (10) specimen number unknown, female LV, dorsal view; (11–15) *G. aspera* (Khabarova, 1955): (11) specimen Sokur-Ya-137, LV juv. I–II, L = 0.67 mm, depth 42.9 m; (12) specimen Sokur-Ya-093, LV juv. III–IV, L = 0.63 mm, depth 13.3 m; (13) specimen Sokur-Ya-053, male LV, L = 0.81 mm, depth 37.0 m; (14) neotype Sokur-Ya-138, female CC, left view, L = 0.76 mm, depth 42.9 m; (15) specimen Sokur-Ya-147, female CC, dorsal view, L = 0.75 mm, depth 31.5 m; (16, 17) *G. bathonica* Tesakova, 2022: (16) specimen PNZ-12-02, male LV, L = 0.84 mm, depth 332.6–332.8 m; (17) specimen SOK-LG-01, female CC, L = 0.88 mm, sample 12f: (17a) left view, (17b) dorsal view.

Plate 1



Table 6. Evolutionary pathways of sculptural patterns in the *G. interrete* → *G. tuberodentina* → *G. losoviensis* → *G. aspera* → → *G. bathonica* lineage

Species	Ornamentation pattern				Evolution of ornamentation
	Early juvenile stages	Late juvenile stages	Males	Females	
G. bathonica	Ribs	Ribs	Ribs	Ribs	Paedomorphosis
G. aspera	Ribs	Reticulum	Ribs	Reticulum	
G. losoviensis	Ribs	? Reticulum	Reticulum	? Reticulum	
G. tuberodentina	Ribs	Ribs	Reticulum	Ribs	
G. interrete	Ribs	? ribs	Ribs	Ribs	Gerontomorphosis

Table 7. Evolution of ornamentation patterns in the *G. rugosa* → *G. multa* → *G. strigata* → *G. scissa, G. transversa, G. kiklica* lineage on the EEP

Complete lineage	Males	Females	Evolution of ornamentation
G. transversa	Ribs and ? reticulum	Ribs and reticulum	Paedomorphosis
G. kiklica	Ribs and reticulum	Ribs and reticulum	
G. scissa	Ribs and ? reticulum on the anterior end	Ribs and reticulum on the anterior end	
G. strigata	Ribs and reticulum	Ribs and reticulum	
G. multa	Ribs and ? reticulum on the anterior end	Ribs and reticulum on the anterior end	
G. rugosa	Only ribs	Only ribs	

niles and females of the species. In *G. aspera*, the reticulate pattern persisted into the late juvenile stages (Pl. I, fig. 11) and in females (Pl. I, fig. 14); however, males of this species reverted to the ribbed pattern characteristic of all early juveniles in the lineage (Pl. I, fig. 13), including those of *G. aspera* (Pl. I, fig. 12). Finally, in the last species of the lineage, *G. bathonica*, the costate ornamentation became identical in both females and males (Pl. I, figs. 16–17), reverting to the ancestral state characteristic of the lineage's founding species, *G. interrete* (Pl. I, figs. 1–3).

To summarize the above, it should be noted that males were the first to be involved in the evolutionary process of this lineage, whereas evolutionary change was more delayed in females. This resulted in intraspecific heterochrony, manifested as differences in ornamentation between males and females in species such as *G. aspera* and *G. tuberodentina*. In contrast, the species *G. interrete, G. losoviensis*, and *G. bathonica* exhibited uniform ornamentation across both sexes but differed between species—a pattern consistent with interspecific heterochrony. Thus, the accelerated evolution of males led to intraspecific heterochrony, allowing for the distinction of a greater number of species and resulting in more detailed biostratigraphy. In other words, recognition of different evolutionary rates between the sexes enables higher resolution in biostratigraphic scales.

Furthermore, the appearance of an ancestral trait in adult *G. tuberodentina* specimens, followed by its shift to later developmental stages in juvenile *G. losoviensis*, indicates that the evolution of species within the *G. interrete* → *G. tuberodentina* → *G. losoviensis* lineage proceeded via gerontomorphosis. In contrast, the *G. losoviensis* → *G. aspera* → *G. bathonica* segment of the lineage evolved in the opposite direction—through paedomorphosis. In this instance, the evolving trait—which persisted into later stages in females and juveniles—failed to appear in males and subsequently disappeared entirely from the ontogeny of adults of both sexes.

The G. rugosa – G. scissa, G. transversa, G. kiklica lineage. It was not possible to examine males of the species *G. multa, G. scissa*, and *G. transversa*; however, in *G. rugosa, G. strigata,* and *G. kiklica*, the ornamentation of females and males did not differ, with sexual dimorphism manifesting instead in the shape, marginal figure, and size of the shells. Thus, no evidence of precocious male evolution was found in this lineage; only interspecific heterochronies were observed.

All representatives of this lineage characterized by a ribbed ornamentation pattern exhibit a well-developed intercostal reticulate mesosculpture (reticulum), which persists to varying degrees across different ontogenetic stages. In the sequence *G. strigata* → *G. transversa, G. kiklica*, the reticulum remains well-developed across the entire intercostal surface up to the sexually mature stage in both sexes (Figs. 3e–3g, 3j–3m; Table 7; Tesakova, 2026, pls. II, III). In contrast, in the species *G. rugosa, G. multa,* and *G. scissa* (Figs. 3a–3e, 3h, 3i), the reticulum becomes attenuated and obscured at the adult stage, even though their early juvenile stages (e.g., in *G. scissa*: Tesakova, 2026, pl. IV, figs. 3–4) display the same reticulate pattern

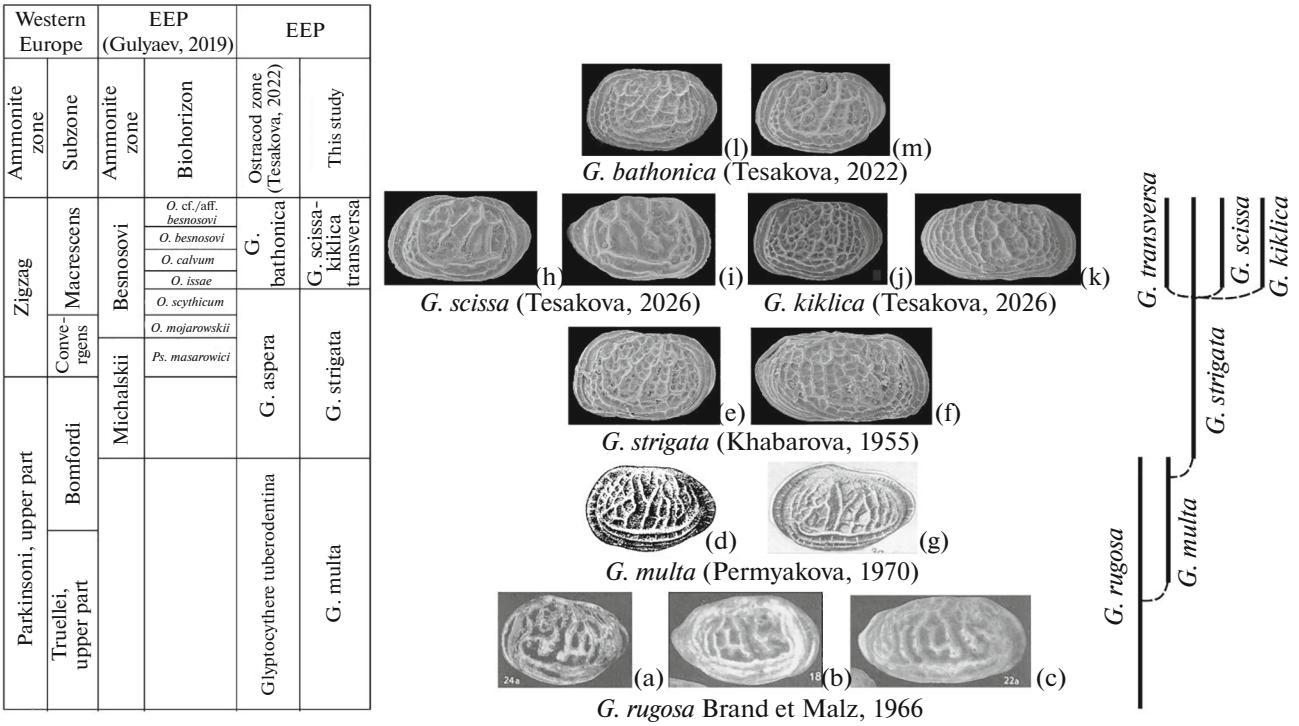

Fig. 3. Evolution of the *G. rugosa* → *G. multa* → *G. strigata* → *G. scissa*, *G. kiklica*, *G. transversa* lineage on the East European Platform during the Late Bajocian and Early Bathonian. (a–c) *G. rugosa* Brand et Malz, 1966: (a) holotype Xe 4312, female LV, L = 0.78 mm, Fuhrberg 7 Borehole, depth 175 m, upper part of Parkinsoni Zone; Schneflingen 5 Borehole, depth 581.9–591 m, lower part of Parkinsoni Zone: (b) specimen Xe 4314, female RV, L = 0.74 mm; (c) specimen Xe 4317, male RV, L = 0.96 mm (Brand & Malz, 1966, pl. 53, figs. 22a, 24a); (d, e) *G. multa* Permyakova, 1970: (d) female LV (Pyatkova & Permyakova, 1978, pl. 57, fig. 3a); (e) female LV (Permyakova, 1970, pl. 1, fig. 3a); (f, g) *G. strigata* (Khabarova, 1955), Saratov Region, Sokur Borehole: (f) specimen MSU Sokur-31, female LV, L = 0.60 mm, depth 39.3 m, Upper Bajocian–Lower Bathonian, Michalskii Zone–lower part of Besnosovi Zone, G. aspera ostracod Zone; (g) specimen MSU Sokur-164, male CC, right view, L = 0.65 mm, depth 4.4 m, Lower Bathonian, upper part of the Besnosovi Zone, G. bathonica ostracod Zone (Tesakova, 2026, pl. II, figs. 1, 6a); (h, i) *G. scissa* Tesakova, 2026, Penza Region, Obval Borehole, depth 340.3–340.5 m, Lower Bathonian, G. bathonica ostracod Zone: (h) holotype MSU Pnz-3-22, female LV, L = 0.62 mm; (i) specimen MSU Pnz-3-18, RV juv., L = 0.47 mm (Tesakova, 2026, pl. III, figs. 10, 12); (j, k) *G. kiklica* Tesakova, 2026, Penza Region, Lower Bathonian, G. bathonica ostracod Zone: (j) holotype MSU Pnz-3-45, female LV, L = 0.56 mm, Obval Borehole, depth 351.0–351.2 m; (k) specimen MSU Pnz-1-6, male RV, L = 0.63 mm, Krylovka Borehole, depth 279.1 m (Tesakova, 2026, pl. III, figs. 1, 4); (l, m) *G. transversa* Tesakova, 2026, Penza Region, Obval Borehole, depth 347.0–347.2 m, Lower Bathonian, G. bathonica ostracod Zone: (l) specimen MSU Pnz-3-38, female? LV, L = 0.55 mm; (m) holotype MSU Pnz-3-39, female LV L = 0.55 mm (Tesakova, 2026, pl. III, figs. 7, 8).

seen on the adult shells of *G. strigata, G. transversa,* and *G. kiklica*. However, during the final stages of ontogeny in all members of this lineage, the transverse elements of the reticulum became dominant, resulting in the formation of distinct, straight vertical and oblique ribs on the shells. These ribs are most pronounced in the species where the reticulum is obscured—namely *G. rugosa, G. multa,* and *G. scissa*.

The species *G. rugosa* is not only the founder species of the lineage on the East European Platform but also the final representative of the Western European *G. praecursor* – *G. rugosa* lineage. In the Late Bajocian, a juvenile trait (the reticulum) persisted to varying degrees in young *G. rugosa* individuals, with its disappearance or obscuration occurring only at the sexually mature stage (Figs. 4a, 4b). Thus, this species emerged as a result of gerontomorphosis within the Western European lineage. Given that the reticulum—lost during the adult stage in *G. rugosa*, reappears in its descendant *G. multa* (at the anterior end) and subsequently extends across the entire intercostal surface in *G. strigata, G. transversa,* and *G. kiklica*, this sequence represents a classic example of evolution via paedomorphosis.

An analysis of the morphology and arrangement of ribs on the shells of *G. strigata* and *G. scissa* (Tesakova, 2026) points to the same conclusion. *G. scissa* exhibits a reversion to an ancestral trait (an obscured reticulum)—a feature lost in its immediate ancestor, *G. strigata*, but present in earlier representatives of the lineage (such as *G. rugosa* and *G. multa*). During the early juvenile stages, *G. scissa* (Tesakova, 2026, pl. IV, figs. 3, 4) displayed characteristics of both species: the reticulate intercostal surface typical of *G. strigata* and the open junction between the transverse oblique ribs and the upper longitudinal rib characteristic of *G. scissa*. As the organism matured, the ancestral trait (reticulation) became less pronounced, whereas the

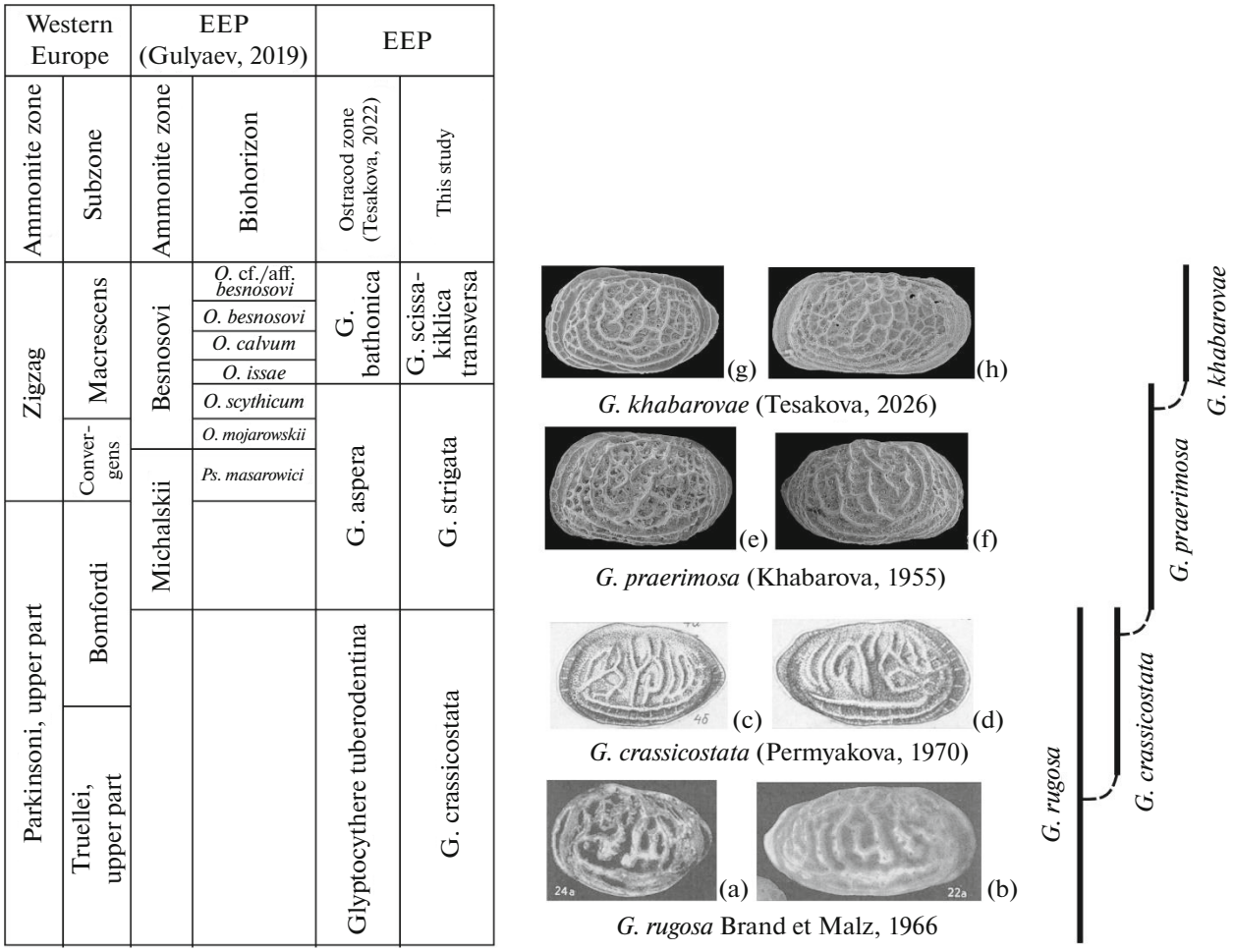

Fig. 4. Evolution of the *G. rugosa* → *G. crassicostata* → *G. praerimosa* → *G. khabarovae* lineage on the EEP during the Late Bajocian and Early Bathonian. (a, b) *G. rugosa* Brand et Malz, 1966: (a) holotype Xe 4312, female LV, L = 0.78 mm, Fuhrberg 7 Borehole, depth 175 m, upper part of Parkinsoni Zone; (b) specimen Xe 4317, male RV, L = 0.96 mm, Schneflingen 5 Borehole, depth 581.9–591 m, lower part of Parkinsoni Zone (Brand & Malz, 1966, pl. 53, figs. 22a, 24a); (c, d) *G. crassicostata* Permyakova, 1970: (c) female LV, (d) male RV (Permyakova, 1970, pl. 1, figs. 4a, 4b); (e, f) *G. praerimosa* (Khabarova, 1955), Saratov Region, Sokur Borehole, Upper Bajocian–Lower Bathonian, Michalskii Zone–lower part of Besnosovi Zone (**O. mojarowskii* and *O. scythicum* biohorizons), G. aspera ostracod Zone: (e) specimen MSU Sokur-129, female LV, L = 0.41 mm, depth 17.2 m; (f) specimen MSU Sokur-Ya-209, female RV, L = 0.48 mm, depth 27.0 m (Tesakova, 2026, pl. 5, figs. 1, 12); (g, h) *G. khabarovae* Tesakova, 2026, Penza Region, Obval Borehole, Lower Bathonian, G. bathonica ostracod Zone: (g) specimen MSU Pnz-3-08, female LV, L = 0.44 mm, depth 337.9–338.5 m; (h) specimen MSU Pnz-3-47, male LV, L = 0.67 mm, depth 351.0–351.2 m (Tesakova, 2026, pl. V, figs. 2, 4).

specific trait of *G. scissa* (the open rib junction) persisted (Tesakova, 2026, pl. IV, figs. 1, 2).

G. rugosa – G. khabarovae lineage. A similar pattern is observed in the evolution of the *G. rugosa* → *G. crassicostata* → *G. praerimosa* → *G. khabarovae* lineage (Table 8). In *G. crassicostata* from the late Parkinsoni Phase, reticulate cells appeared at the posterior end in females and, presumably, at the anterior end in males

Table 8. Evolution of ornamentation in the lineage *G. rugosa* → *G. crassicostata* → *G. praerimosa* → *G. khabarovae* on the EEP

Complete lineage	Males	Females	Evolution of ornamentation
G. khabarovae	Ribs and reticulum	Ribs and reticulum	Paedomorphosis
G. praerimosa	Ribs and reticulum	Ribs and reticulum	
G. crassicostata	Ribs and ? reticulum on the anterior end	Ribs and reticulum on the anterior end	
G. rugosa	Only ribs	Only ribs	

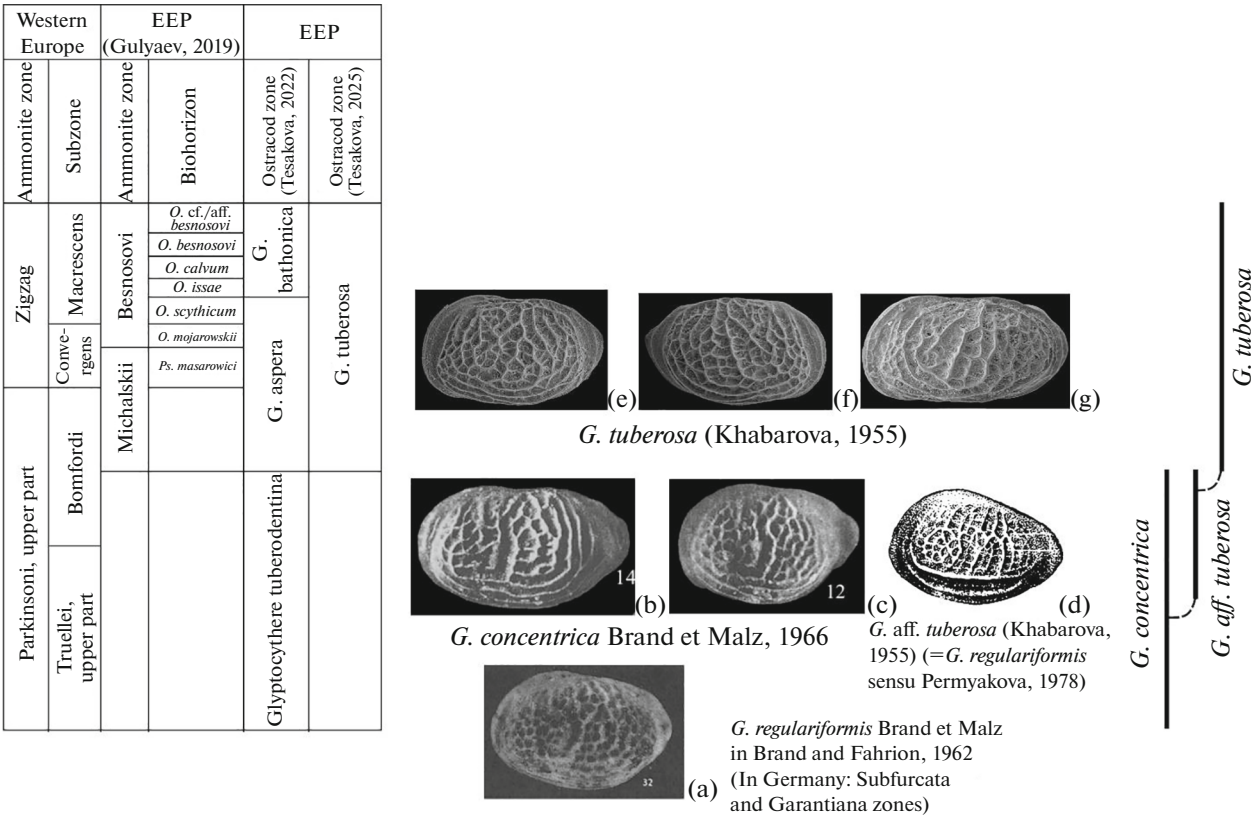

Fig. 5. Evolution of the *G. concentrica* → *G.* aff. *tuberosa* → *G. tuberosa* lineage on the East European Platform during the Late Bajocian and Early Bathonian. (a) *G. regulariformis* Brand et Malz in Brand and Fahrion, 1962, holotype Xe 4336, female LV, L = 0.94 mm, Regina 9 Borehole, depth 587 m, Upper Bajocian, Subfurcata Zone (Brand & Malz, 1966, pl. 55, fig. 32); (b, c) *G. concentrica* Brand et Malz, 1966, Upper Bajocian, upper part of Parkinsoni Zone: (b) holotype Xe 4387, male LV, L = 0.98 mm, Fuhrberg 251 Borehole, depth 267.4–273.2 m (Brand & Malz, 1966, text-fig. 7); (c) specimen Xe 4394, female LV, L = 0.83 mm, Fuhrberg-Ost 22 Borehole, depth 435 m (Brand & Malz, 1966, text-fig. 11); (d) *G.* aff. *tuberosa* (Khabarova, 1955), female LV (= *G. regulariformis*; Pyatkova & Permyakova, 1987, pl. 57, fig. 4a); (e–g) *G. tuberosa* (Khabarova, 1955), Saratov Region, Sokur Borehole, Upper Bajocian–Lower Bathonian, Michalskii Zone: (e) neotype MSU Sokur-Ya-178, female LV, L = 0.40 mm, depth 38.6 m (Tesakova, 2026, pl. I, fig. 4); (f) specimen MSU Sokur-Ya-177, female RV, L = 0.40 mm, depth 38.6 m (Tesakova, 2026, pl. IV, fig. 5); (g) specimen MSU Sokur-Ya-197, male LV, L = 0.48 mm, depth 16.40 m (Tesakova, 2026, pl. IV, fig. 6).

(Fig. 4c, 4d). The appearance of this juvenile trait at the adult stage (especially in females) allows this morphogenetic shift to be viewed as a manifestation of retardation—the first step toward paedomorphosis. In the Bajocian–Bathonian boundary interval (within the Michalskii Zone), another heterochrony is recorded in *G. praerimosa* (Fig. 4e, 4f); this shifted the fully developed reticulum—characteristic of juveniles—to the adult stage in both males and females (Tesakova, 2026, pl. IV, fig. 14; pl. V, figs. 1–13). The next heterochrony in *G. khabarovae* (Fig. 4g, h), involving the morphology and relative arrangement of arcuate and concentric ribs on the valve (Tesakova, 2026, pl. V, figs. 14–15; pl. VI, figs. 1–14), occurred during the Early Bathonian in the Besnosovi Zone. Thus, the development of ornamentation in this lineage followed a paedomorphic pathway starting from the end of the Parkinsoni Phase. At the same time, the lineage's founder species, *G. rugosa*, was simultaneously the final representative of an ancestral lineage that had evolved via gerontomorphosis.

It is interesting to note that the ornamentation of *G. praerimosa* males exhibits features characteristic of the juveniles of this species and the adults of the descendant species, *G. khabarovae.* Conversely, *G. khabarovae* males retain traits characteristic of the females of the ancestral species (Tesakova, 2026). Thus, speciation in this phyletic lineage begins with changes in males, or, in other words, the evolution of males outpaces that of females.

Glyptocythere with a Reticulate Ornamentation Pattern

Lineage G. concentrica – G. tuberosa. Ostracods of this lineage are relatively scarce in the author's material; consequently, it was not possible to establish reliably documented changes in the ornamentation of *G. tuberosa* (Tesakova, 2026, pl. IV, figs. 5–13) across the Michalskii–Besnosovi interval (or to describe a new species from the Bathonian deposits). The evolution of ornamentation from *G. concentrica* (Figs. 5b, 5c) and *G.* aff. *tuberosa* (Fig. 5d) to *G. tuberosa* (Figs. 5e–5g) is

characterized by the weakening of ribs, leading to the dominance of the intercostal reticulum. This pattern aligns with the general evolutionary trend of glyptocytherids on the East European Platform—namely, paedomorphosis—and is further supported by the emergence and development of descendant *Bathoniella* species, which also arose through paedomorphosis (Tesakova, 2025).

BIOSTRATIGRAPHY

Previously, the G. tuberodentina, G. aspera, and G. bathonica zones were established for the Upper Bajocian–Lower Bathonian of the East European Platform based on the migration and evolution of the representatives of the *G. tuberodentina–G. bathonica* lineage (Tesakova, 2022). Similarly, the G. tuberosa, B. prima, B. milanovskyi, B. paenultima, and B. ultima zones were established for the Upper Bajocian–Lower Callovian of the EEP based on *the G. concentrica – B. ultima* lineage (Tesakova, 2025). The present study has shown that the phylogenetic species turnover within the *G. rugosa – G. scissa, G. transversa, G. kiklica*, and *G. rugosa – G. khabarovae* sequences occurred at the same stratigraphic horizons as in the previously studied lineages. Consequently, it would be possible to establish new lineage-zones based on these lineages, their stratigraphic ranges and distribution would coincide exactly with those of the G. tuberodentina, G. aspera, and G. bathonica zones. Such duplication would offer no stratigraphic benefit and would not refine local zonal schemes; instead, it could introduce further confusion. Furthermore, defining new parallel ostracod-based units within the Parkinsoni, Michalskii, and Besnosovi zones of the Dnieper-Donets Depression (DDD) and European Russia is considered impractical, as their index species occur much less frequently in sections than the index species of the G. tuberodentina, G. aspera, and G. bathonica zones. Nevertheless, the significant stratigraphic value of ostracods from the *G. rugosa – G. scissa, G. transversa, G. kiklica,* and *G. rugosa – G. khabarovae* lineages was already substantiated in the first part of this paper (Tesakova, 2026). Therefore, additional index species are proposed for the G. tuberodentina, G. aspera, and G. bathonica zones.

The G. tuberodentina Zone first appeared in the Middle Jurassic ostracod zonation scheme for Northern Germany developed by E. Brand, where it corresponded to the uppermost part of the Parkinsoni Zone (Brand & Mönnig, 2009, fig. 23). It was subsequently identified in Poland and the DDD (Tesakova, 2022). In the DDD, its range also corresponds to the upper part of the Parkinsoni Zone, though it is somewhat reduced due to the recognition of the Michalskii Zone—in which *G. tuberodentina* no longer occurs—within the Bajocian-Bathonian boundary interval (Tesakova, 2022, 2026). Additional index species for the G. tuberodentina Zone in the DDD include *G. concentrica, G. losoviensis, G. crassicostata*, and *G. multa*; the last three are endemic to the DDD.

The G. aspera Zone was established by Tesakova (2022) and traced across the Dnieper-Donets Depression, Central Russia, the Volga Region, and Western Kazakhstan. It corresponds to the Michalskii Zone plus the lower part of the Besnosovi Zone (the *O. mojarowskii* and *O. sciticum* biohorizons). Additional index species include *G. tuberosa, G. praerimosa,* and *G. strigata* (in the absence of *G. scissa, G. transversa,* and *G. kiklica*). While the presence of these additional index species in the DDD has not yet been confirmed, it was presumed by Tesakova (2026).

The G. bathonica Zone has also been recognized by Tesakova (2022) and is found across Central Russia, the Volga Region, and Western Kazakhstan. Stratigraphically, it corresponds to the upper part of the Besnosovi Zone (the *O. issae–A. excentricum* biohorizons). Additional index species include *G. khabarovae, G. scissa, G. transversa*, and *G. kiklica*.

CONCLUSIONS

A comparative morphological analysis of ostracods of the genus *Glyptocythere* revealed characters (marginal figure, linear dimensions, and carapace ornamentation) that changed over time, making it possible to trace the evolutionary paths of several parallel lineages. These lineages evolved in Western Europe from the beginning of the Bajocian to the Late Bathonian, and on the East European Platform (in the Central Russian Sea) from the Late Bajocian to the end of the Early Bathonian (or to the end of the Early Callovian, when the descendant genus *Bathoniella* is included). Analysis of the evolution of the studied characters led to the following conclusions.

(1) The appearance of *Bathoniella*-subtype sexual dimorphism in certain lineages at different times reflects varying intensities and rates of evolution among male glyptocytherids of the East European Platform. Judging by the marginal figure of the carapace—which indirectly reflects the structure of male reproductive organs—the evolution of the male reproductive system in the *G. tuberodentina – G. bathonica* lineage either slowed markedly or did not occur at all. In contrast, during the Michalskii Phase, a major restructuring of the reproductive system occurred in males of the *G. rugosa – G. khabarovae* and *G. rugosa – G. strigata, G. transversa,* and *G. kiklica* lineages, as well as in *Bathoniella* of the *G. concentrica – B. ultima* lineage during the Early Bathonian; this restructuring manifested as the emergence of *Bathoniella* sexual dimorphism.

(2) Taxa in four lineages evolved toward either progenesis (size reduction) or magnification (size increase), or their sizes remained stable (stasis). In the *G. tuberodentina – G. bathonica* lineage, females evolved toward magnification while males evolved toward progenesis; consequently, the sizes of the two sexes converged over time, and sexual dimorphism declined almost to zero. In the *G. rugosa – G. scissa, G. transversa*, and *G. kiklica* lineage, both sexes exhibited a trend toward progenesis, resulting in a slight reduction in size over time. Nevertheless, males remained larger than females, and sexual dimorphism remained pronounced. Females of the *G. rugosa – G. khabarovae* lineage exhibited stasis, whereas males evolved toward magnification, leading to a further increase in sexual dimorphism. Only in the *G. concentrica – G. tuberosa* lineage did progenesis primarily affect males, while female size decreased to a lesser extent; as a result, females became larger than males, leading to "reversed" sexual dimorphism.

(3) The evolution of the ornamentation in each of the studied lineages demonstrated either a single phase of the morphogenesis cycle or a complete cycle, characterized by gerontomorphosis at the initial stage of development and paedomorphosis at a later stage. For instance, the West European *G. plicata – G. obtusa* lineage underwent gerontomorphosis throughout the Bajocian, which was succeeded by paedomorphosis in the Bathonian; thus, this lineage completed the full cycle. A complete cycle was also identified in the *G. praecursor – G. auricula* lineage, featuring gerontomorphosis in the Late Bajocian and paedomorphosis in the early Bathonian. The *G. praecursor – G. rugosa* lineage exhibited only the initial phase of the cycle, gerontomorphosis in the Late Bajocian, and did not continue into the Bathonian. Consequently, different West European *Glyptocythere* lineages passed through different stages of the evolutionary cycle, ranging from a complete cycle (involving both gerontomorphosis and paedomorphosis) to an incomplete one (involving only gerontomorphosis).

(4) All lineages on the EEP evolved via paedomorphosis from the Michalskii Phase to the end of the Early Bathonian (Besnosovi Phase: *G. tuberodentina – G. bathonica, G. rugosa – G. khabarovae* and *G. rugosa – G. scissa, G. transversa, G. kiklica*) or up to the Early Callovian (Calloviense Phase: *G. concentrica – B. ultima*).

Thus, among Western European *Glyptocythere*, the shift in the morphogenetic cycle from gerontomorphosis to paedomorphosis occurred at the Bajocian–Bathonian boundary, whereas the *Glyptocythere* of the EEP, following their ancestors from Western European lineages, continued to evolve via paedomorphosis during the Late Bajocian and Early Bathonian. The apparently earlier transition to paedomorphosis observed in East European ostracods is probably attributable merely to the greater stratigraphic resolution of Jurassic deposits on the EEP, does not reflect genuinely earlier evolution of ostracods on the EEP.

(5) The ostracod lineages *G. tuberodentina – G. bathonica* and *G. rugosa – G. khabarovae* were characterized by the precocious evolution of males. In a number of Western European *Glyptocythere* species, the ornamentation of females and males differed—as seen in *G. tuberodentina* and *G. khabarovae* (Brand & Malz, 1966; Tesakova, 2026). This suggests that speciation in other lineages likely also began with the males; however, tracing such details in the fossil record is difficult, as it requires a large number of specimens of both sexes and juveniles spanning a time interval sufficient for the emergence of heterochrony. Only the ostracods of the *G. tuberodentina – G. bathonica* and *G. rugosa – G. khabarovae* lineages met this condition in our material, whereas representatives of the other studied lineages were not sufficiently abundant. This is likely the reason why precocious male evolution was not detected in the *G. rugosa – G. scissa, G. transversa, G. kiklica*, and *G. concentrica – G. tuberosa* lineages.

(6) Analysis of the distribution of *Glyptocythere* species across the Upper Bajocian–Lower Bathonian succession of the East European Platform made it possible to supplement the descriptions of previously established zones with additional index species: for the G. tuberodentina Zone of the DDD (upper part of the Parkinsoni Zone), these are *G. concentrica, G. losoviensis, G. crassicostata*, and *G. multa*; for the G. aspera Zone of the DDB, Central Russia, the Volga Region, and Western Kazakhstan (Michalskii Zone–lower part of the Besnosovi Zone; *O. mojarowskii* and *O. sciticum* biohorizons), these are *G. tuberosa, G. praerimosa*, and *G. strigata* (in the absence of *G. scissa, G. transversa*, and *G. kiklica*); and for the G. bathonica Zone of Central Russia, the Volga Region, and Western Kazakhstan (upper part of the Besnosovi Zone; *O. issae–A. excentricum* biohorizons), these are *G. khabarovae, G. scissa, G. transversa,* and *G. kiklica*.

ABBREVIATIONS AND NOTATION

The following abbreviations are used for the institutions mentioned in the text:

GIN	Geological Institute of the Russian Academy of Sciences, Moscow
IPGG	Trofimuk Institute of Petroleum Geology and Geophysics, Siberian Branch of the Russian Academy of Sciences, Novosibirsk
MSU	Lomonosov Moscow State University

PIN Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow

SNIGU N.G. Chernyshevsky Saratov National Research State University

YSPU K.D. Ushinsky Yaroslavl State Pedagogical University

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CONFLICT OF INTEREST

The author of this work declares that she has no conflicts of interest.

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