NEW *NEUROCYTHERE* AND *TERQUEMULA* (OSTRACODA, CRUSTACEA) FROM THE CALLOVIAN OF THE RUSSIAN PLATE

© 2025 E. M. Tesakova[a,b]

[a]*Lomonosov Moscow State University, Moscow, Russia*

[b]*Geological Institute, Russian Academy of Sciences, Moscow, Russia*

**e-mail: ostracon@rambler.ru*

Received September 06, 2024

Revised September 30, 2024

Accepted September 30, 2024

Abstract. The new species Neurocythere margaritae, N. parva, and Terquemula pseudoflexicosta from Callovian of the Russian Plate are described. The first two form a stratigraphic sequence with N. margaritae occurring in the lower and middle Callovian in the Subpatruus – Jason zones and N. parva in the middle and upper Callovian, Coronatum – Lamberti zones. The morphology of both species is identical, but their sizes are different, which allows us to distinguish these taxa and prove their genetic relationship. The daughter N. parva originated from N. margaritae by gerontomorphosis with minification. The fact that the new species belong to a single lineage allows to establish new homonymous lineage zones for the lower-middle and middle-upper Callovian of the Russian Plate. The species T. pseudoflexicosta is known from the lower Callovian, Koenigi Zone.

Keywords: *new species, evolution, gerontomorphosis, minification, new lineage zones, Middle Jurassic*

DOI: 10.31857/S0031031X250106e9

INTRODUCTION

The present paper is a continuation of the systematic study of the Jurassic ostracods of the Russian Plate, which was started by the author more than 20 years ago. A significant and stratigraphically important component of the fauna is the genus Neurocythere Whatley, 1970, which appeared in Western Europe at the end of the Bajos (Whatley, 1970; Gruendel, 1975), but arrived in the Russian Plate only in the Callovian, starting from the Subpatruus phase (Kolpenskaya, 1999, 2002; Tesakova, 2003, 2013; Tesakova et al., 2009). Russian Kellovian Neurocythere are represented by the species group N. cruciata ssp. [=N. catephracta (Mandelstam in Lyub, 1955)] with subspecies N. cruciata cruciata (Triebel, 1951) and N. c. franconica (Triebel, 1951); N. alata (Whatley, 1970), N. dulcis (Lyubimova, 1955), N. zmeinkensis (Tesakova, 2003), N. flexicosta flexicosta (Triebel, 1951), N. f. lutzei Whatley, 1970 [first erroneously defined by E.M. Tesakova (Tesakova et al, 2017) as N. flexicosta labyrinthos Whatley, Ballent et Armitage, 2001], N. flexicosta ssp. A and N. flexicosta ‘ovata’. In Oxford, N. oxfordiana (Lutze, 1960) is known, and in Kimeridge N. jakovlevae Kolpenskaya in Tesakova et al., 2012 (Lyubimova, 1955; Kolpenskaya, 1999, 2002; Tesakova, 2003, 2008, 2013; Tesakova et al., 2009, 2017; Tesakova et al., 2012, etc.). It is appropriate to explain here that the erroneous attribution of Upper Callovian (Lamberti Zone) specimens of N. flexicosta lutzei from the Mikhailovcement section (Ryazan Region) to N. flexicosta labyrinthos is due to the absolutely identical morphology of these subspecies. They can be distinguished only by their size: if the shell length of N. flexicosta lutzei. flexicosta lutzei varies from 0.71-0.89, while the shell length of N. f. labyrinthos is 0.60-0.69 (Whatley et al., 2001, p. 156), which made the determination difficult.

A similar situation developed with the "flexicosts" from the Callovian of the Russian Platform studied in this article (Tesakova, 2003, 2008, 2013; Tesakova et al., 2009, 2017) – Neurocythere margaritae sp. nov. from the Lower to the lower part of the Middle Callovian is morphologically indistinguishable from N. parva sp. nov. from the upper part of the Middle to Upper Callovian, but has larger dimensions, which allowed establishing two new chronotaxa. Thus, the aim of this article is to revise the Russian ostracods previously assigned to the "flexicosta" group, including those in open nomenclature, as well as to provide systematic descriptions of the new species N. margaritae sp. nov., N. parva sp. nov., and Terquemula pseudoflexicosta sp. nov., identify their ancestors, and reconstruct a phyletic lineage for the first two, based on which new phylozones are proposed to refine the ostracod scale of the Russian Platform.

The following abbreviations are adopted for scientific institutions mentioned in the article: VSU (Voronezh State University), GIN RAS (Geological Institute of RAS, Moscow), MSU (Lomonosov Moscow State University), PIN RAS (Borissiak Paleontological Institute of RAS, Moscow).

MATERIAL AND METHODS

The material for this article consists of ostracods of the genus Neurocythere from the Lower Callovian of Kursk region, from the Mikhailovsky Mining and Processing Plant (GOK) quarry and borehole 7, drilled north of Kursk, 70-80 km east of Zheleznogorsk (Fig. 1). In the open quarry section in the Subpatruus zone, Ch. saratovensis (=Ch. crobyloides) biohorizon, two specimens of females and one male of N. margaritae sp. nov. were found (Tesakova et al., 2009, Table 3, fig. 18, 19), in the Koenigi zone – eight specimens of females and males of the same species (Tesakova, 2003, Table 13, fig. 17). In the Lower Callovian of borehole 7, ostracod zone Praeschuleridea wartae–Pleurocythere kurskensis [corresponding to the upper part of the Subpatruus zone, Saratovensis biohorizon – Middle Callovian, Jason zone (Tesakova, Seltser, 2022)], 312 specimens of females, males, and juveniles of N. margaritae sp. nov. were found (Tesakova, 2013, fig. 6, Table 6, fig. 7).

Specimens of N. parva sp. nov. were studied from the Middle and Upper Callovian of the Zmeinka and Mikhailovcement sections (Ryazan Region) (Fig. 1). In the Mikhailovcement section, 20 specimens were found in the Coronatum zone (Tesakova, 2003, Fig. 3, Table 13, figs. 13, 15) and later another 25 specimens (Tesakova et al., 2017, Fig. 3, Table 3, figs. 14, 15), while 7 specimens were found in the Athleta zone (Tesakova et al., 2017, Fig. 3). In the Zmeinka section, two specimens were found in the Lamberti Zone sediments (Tesakova, 2003, Fig. 4, Table 13, Figs. 14, 16). Descriptions of all the mentioned sections are published in the cited literature.

All material is characterized by good and excellent preservation. Rock samples (clays and siltstones weighing 0.3-0.5 kg) were collected from the Mikhailovsky GOK quarry at different times by L. Guskova (MSU) and D.B. Gulyaev (Commission on the Jurassic System of Russia), from borehole 7 – by A.V. Chereshinsky (VSU), from the Zmeinka and Mikhailovscement sections – by the author of the article. All samples were washed by the author using the standard method of boiling with soda and subsequent washing under water jet on a sieve with a mesh of 0.1 mm. Selection and study of ostracods was carried out under a binocular microscope MBS-9 and under scanning microscopes CamScan and Tescan Vega-2 in the instrumental analytics room of PIN RAS.

Measurements of valves and carapaces were made in the ImageJ program. When measuring the length, the margin was not taken into account, due to the fact that it was not preserved in all specimens and, as a rule, not in full.

Ostracod collections are stored at the Department of Regional Geology and Earth History of Lomonosov Moscow State University (Moscow) under Nos. 300-Ku and 300-Kusk (Mikhailovsky GOK and borehole 7, Kursk region), MS-2 (Mikhailovscement, Ryazan region) and in PIN RAS, No. 4843.

SYSTEMATIC PART

The systematics of suprageneric taxa is adopted according to the "Practical Guide..." (1999) and brought into line with the "International Code" (1999), the terminology of various elements of ostracod carapaces is taken from the "Practical Guide..." (1989). When measuring the parameters of carapaces or individual valves, the following abbreviations are used: L – length, HAE – height of anterior end, HPE – height of posterior end, T – thickness, L/H – ratio of length to maximum height (here – to HAE), juv. – juvenile specimen. Age stages of juveniles are designated from A1 (the last before sexual maturity) to A9 (the first after hatching). Ostracod carapace sizes: small – up to 0.50 mm, medium – from 0.50 to 0.70 mm, large – over 0.70 mm.

① ORDER PODOCOPIDA

① SUBORDER CYTHEROCOPINA

② SUPERFAMILY PROGONOCYTHERACEA SYLVESTER-BRADLEY, 1948

③ FAMILY NEUROCYTHERIDAE GRUENDEL, 1975

④ Genus Neurocythere Whatley, 1970

⑤ Neurocythere margaritae Tesakova, sp. nov.

⑥ Table VII, fig. 1–15

Lophocythere flexicosta flexicosta: Permyakova, 1975, p. 108, Table pl. 1, fig. 5 a, b (part.).

Crucicythere flexicosta: Pyatkova, Permyakova, 1978, p. 146, Table 62, fig. 1 a–g (part.).

Neurocythere flexicosta flexicosta: Tesakova et al., 2009, Table 3, fig. 18, 19 .

Neurocythere flexicosta ssp. A: Tesakova, 2013, Table 6, fig. 7.

Species name – in honor of micropaleontologist M.N. Permyakova.

Holotype – MSU, № 300-Ku-1-97, left valve of female; Kursk region, borehole 7, depth 135 m; Lower Callovian, ostracod zone Wartae – Kurskensis (pl. VII, fig. 1).

Description. The shell is medium to large, moderately convex, trapezoidal when viewed from the dorsal side, isometric and oval when viewed from the side (females; Table VII, fig. 1, 2, 4, 5, 7, 8) or elongated and rounded-rectangular (males; Table VII, fig. 10, 11, 13, 14). The left valve is larger than the right one, overlapping it at the anterior and posterior-dorsal angles, slightly along the dorsal margin. The greatest length is just below the middle of the height, the greatest height is in the anterior third, the greatest thickness is in the posterior-ventral part of the shell. The dorsal margin is straight when viewed from inside, and slightly concave in the central part when viewed from outside due to developed cardinal angles (especially on the left valve). On the left valve, it transitions to the anterior and posterior margins through rounded cardinal angles (the posterior angle is more obtuse than the anterior), on the right valve - through distinct ledges. The ventral margin, when viewed from outside, is straight (in males) or slightly convex (in females) due to a wide ventral rib overhanging it; and concave in the middle when viewed from inside. It connects smoothly with the anterior and posterior margins; it is not parallel to the dorsal margin and converges toward the posterior end. The anterior end is high, evenly arcuately rounded, slightly oblique from above on the left valves, more so on the right ones; widely flattened. The posterior end is lower than the anterior, rounded-triangular on the left valves and more pointed on the right ones, more oblique from above; widely flattened.

On the valve surface, there are four large ridge-like longitudinal ribs and one thin subvertical rib in the upper half of the anterior end. The long dorsal rib, slightly convex in the posterior and middle parts, sharply deviates downward and crosses the anterior end at an angle of approximately 45°; at the anterior end, it merges with the upper of the ventral ribs. From their merging point, a short oblique rib begins, which crosses the anterior end and reaches its edge below the middle of the height. At the junction of the dorsal and ventral ribs, a triangular figure of three large cells is formed. The ventral rib is slightly convex, longer than the dorsal one, and, unlike it, crosses the posterior end and reaches the posterior edge. The lower of the ventral ribs is equally long and slightly convex, overhangs the ventral margin, overlaps it when viewed from the side, and can reach the anterior and posterior edges. Between it and the ventral margin, on the ventral surface, several thin longitudinal riblets are developed. The median rib (the shortest of the longitudinal ones) extends almost horizontally; in the posterior part, it smoothly connects with the dorsal rib, forming a rounded loop, and in the anterior part, it deviates downward and terminates below the middle of the height. The subvertical short rib, developed at the anterior end and parallel to its edge, begins near the anterodorsal angle, can be traced on the dorsal side (in the anterior half), and its lower end abuts the oblique rib crossing the anterior end, where it may connect with the lower of the ventral ribs. The entire interribbed surface is covered with large four-to-five-sided cells with low thin muriae. On the flattened and smooth parts of the anterior and posterior ends, the cells are largest and least noticeable due to the thread-like thickness of the muriae. The entire surface of the valve: flat anterior and posterior ends, cell bottoms, surface of thin muriae and large ribs, walls of conuli – are covered with numerous small granules, except for the eye spot. A large rounded slightly convex eye spot is located under the anterodorsal cardinal angle.

In many cells, small eccentric sieve-like pores can be distinguished, often raised on conuli.

The lock of the right valve of the female is represented by large marginal teeth, divided into seven (anterior) and eight (posterior) narrow denticles and a narrow median groove, widening in the anterior part and complicated by pits and pit groups – dental formula 7[1+ 4:2 +5-7]8[1]. Pore-canal zone is wide, without vestibule. The adductor is expressed by a subvertical row of four rounded slightly elongated scars with two large mandibular (rounded) and antennal (cordate) imprints in front of them.

Sexual dimorphism is expressed in larger and longer carapaces of males. The ventral margin when viewed from the outside is straight in males and slightly convex in females (due to the overhanging ventral edge). Additionally, males lack the oblique filiform ridge in the posterodorsal part of the carapace, which is distinguishable in females.

Dimensions in mm:	L	HAE	HPE	H/L
holotype MSU, № 300-Ku-1-97 (female)	0.60	0.36	0.26	1.67
MSU, № 300-Kusk-149 (female)	0.58	0.31	0.21	1.87

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[1] In the hinge description, a dental formula is used, where the first number corresponds to the number of sequences of the anterior tooth [in square brackets, the structure of the groove is characterized: underlined numbers indicate the number of socket groups (first number) and the number of grouped sockets (number after the colon), non-underlined numbers indicate single sockets located before and after the socket groups], the last number indicates the number of sequences of the posterior tooth.

MSU, № 300-Kusk-150 (juv. A1-A2)	0.55	0.33	0.20	1.67
MSU, № 300-Ku-2-27 (female)	0.60	0.37	0.26	1.62
MSU, № 300-Ku-1-100 (female)	0.59	0.31	0.21	1.90
MSU, № 300-Kusk-147 (juv. A1-A2)	0.57	0.30	0.21	1.90
MSU, № 300-Ku-1-96 (female)	0.57	0.35	0.23	1.63
MSU, № 300-Ku-2-30 (female)	0.59	0.36	0.23	1.64
MSU, № 300-Ku-1-108 (juv. A3-A4)	0.51	0.28	0.17	1.82
MSU, № 300-Ku-1-103 (male)	0.65	0.33	0.24	1.97
MSU, № 300-Ku-1-104 (male)	0.65	0.30	0.23	2.17
MSU, № 300-Ku-2-28 (juv. A3-A4)	0.50	0.28	0.15	1.79
MSU, № 300-Ku-2-29 (male)	0.64	0.35	0.20	1.83
MSU, № 300-Ku-2-31 (male)	0.71	0.34	0.23	2.09
MSU, № 300-Ku-2-18 (juv. A5-A6)	0.42	0.23	0.13	1.83

Variability. Length of females varies within 0.57-0.64 mm, males – 0.65-0.71 mm, L/H ratio in females 1.62-1.94, in males – 1.67-2.17. The median rib is typically straight (for example, Table VII, fig. 1, 6, 8), but can weakly (Table VII, fig. 5, 13) or strongly (Table VII, fig. 7) undulate or even be interrupted (Table. VII, fig. 4). In its anterior part, at the point of downward inflection or before it, a short weak riblet can develop, directed upward perpendicular to the descending branch of the dorsal rib (Table VII, fig. 2, 6, 11) and sometimes connecting with it (Table VII, fig. 10). The dorsal rib (its horizontal part) may have a saddle in the middle (Table VII, fig. 7), as observed in juvenile stages A5-A6 and A3-A4 (Table VII, fig. 9, 12, 15). In the posterior third of the carapace, between the dorsal and median ribs, muri sometimes form a filiform riblet – short straight (Table VII, fig. 1, 3) or long oblique, reaching the posterior end of the median rib (Table VII, fig. 4, 7). This filiform riblet is most noticeable on juvenile specimens (Table VII, fig. 9, 12, 15); in females it becomes barely distinguishable, and in males it is not expressed at all.

Age-related changes are manifested in the shape of juvenile carapaces: the younger the specimen, the lower the posterior end, and the outlines become more triangular (Table VII, fig. 3, 6, 9, 12, 15). The sculpture in ontogenesis hardly changes, except for the dorsal rib: with a saddle in the middle in individuals not older than A5-A6 (Table VII, fig. 15), "humped" in the posterior half in individuals not older than A3-A4 (Table VII, fig. 9, 12, 15) and straightening at stages A1-A2 (Table VII, fig. 3, 6).

Comparison. It differs from the morphologically indistinguishable daughter taxon N. parva by the greater length of the carapace with the same height: while in females of N. margaritae L=0.57-0.64 mm, in females of N. parva L=0.54-0.56 mm (anterior height in N. margaritae 0.30-0.37, in N. parva 0.30-0.35), and by a larger L/H ratio: in N. margaritae 1.62-1.94, and in N. parva 1.60-1.80.

It differs from the most similar in shell shape and rib arrangement N. caesa caesa (Triebel, 1951) (pl. VIII, fig. 14), known from the Bathonian and Callovian of Germany, England, Paris Basin, Poland and Canada (Triebel, 1951, p. 96, Table 48, fig. 42-45; Lutze, 1960, p. 431, Table 35, fig. 7; Malz, 1962, Table 24, fig. 6e; Dépêche, 1969, p. 271, Table 3, fig. 1, 2.; Ascoli, 1976, Table 8, fig. 1; Herngreen et al., 1983, Table 3, fig. 6, 7; Bielecka et al., 1988, p. 170, Table 66, fig. 5; Whatley, Ballent, 2004, p. 100; Franz et al., 2009, p. 145, Table 5, fig. 4; Wilkinson, Whatley, 2009, Table 7, fig. 13, 14), by having a more isometric (less elongated) shell, smaller size (N. caesa caesa has L=0.78-0.90 mm; Triebel, 1951, p. 98), a filiform oblique rib made of high muriae located between the dorsal and median ribs in the posterior third instead of a well-developed rib in the compared species, as well as by the connection of the dorsal rib with the median rib at the posterior end and with the ventral rib at the anterior end.

It differs from the similar in sculpture N. caesa warei Whatley, Ballent et Armitage, 2001 (Table VIII, fig. 15) from the middle Callovian, Jason Zone, northern Germany (Lutze, 1960, p. 431, Table 36, fig. 1) and upper Callovian, Athleta Zone, Oxford Clay from the Calvert brickyard

(Buckinghamshire, England) (Whatley et al., 2001, p. 152, Table 4, fig. 16-18, Table 5, fig. 1-3) by its smaller size (females of N. caesa warei have L=0.67-0.73) and isometric, oval shell in side view (instead of elongated-rectangular in N. caesa warei), as well as by a well-developed dorsal rib throughout its entire length (connected with the median and ventral ribs) and by the absence of a short subhorizontal rib in the posterior third of the shell between the median rib and the dorsal margin (as in N. caesa warei).

It differs from the similar in shell shape, sculpture and size N. cuvillieri (Dépêche) (Table VIII, fig. 13) from the middle Callovian of Lorraine (Paris Basin) (Dépêche, 1969, p. 273, Table 1, fig. 8, 9) by its well-developed median rib, as well as by a rounded and symmetrical (less oblique in the upper part) anterior end and posterior end without a pronounced ledge (more rounded).

From N. rimosa (Dépêche, 1973) (Fig. 2, *a*) from the terminal Bajocian and Bathonian of the Paris Basin, Southern England and Germany (Dépêche, 1973, p. 218, Table 1, fig. 9–14; 1985, Table 30, fig. 2; Sheppard, 1981, p. 83, Table 13, fig. 2–5; Bate, 2009, Table 2, fig. 7–9; Wilkinson, Whatley, 2009, Table 2, fig. 7; Franz et al., 2014, fig. 13 *p*), as well as the Lower Callovian, Calloviense Zone of Dagestan (Tesakova, Glinskikh, 2020, fig. 2; Glinskikh, Tesakova, 2021, Table 7, fig. 9), which is similar in number and arrangement of ribs, it differs by clearly defined ridge-like ventral ribs (N. rimosa has large cells in two rows in the ventral part, and ribs only in front and behind the cells), absence of a rhomboid figure on the median rib, symmetric and rounded anterior end (in N. rimosa it is more elongated forward and oblique from above) and a shorter posterior end.

From N. bessinensis (Dépêche, 1973) (Fig. 2, *b*) from the Lower and Middle Bathonian (Zigzag–Morrisi zones) of England and Normandy (Paris Basin) (Dépêche, 1973, p. 217, Table 1, fig. 3–8; 1985, Table 30, fig. 3; Wilkinson, Whatley, 2009, Table 2, fig. 10), which has similar sculpture, it differs by well-developed ventral ribs (N. bessinensis has large cells on the ventral side), by the dorsal rib connecting with the median rib (posteriorly) and ventral rib (anteriorly), by the presence of a triangular figure at the junction of the dorsal and ventral ribs, by a shorter median rib, as well as by a symmetric and rounded anterior end (in N. bessinensis it is more elongated forward and oblique from above) and a shorter posterior end.

Remarks. (1) From the synonymy, it is evident that N. margaritae has been regularly associated with the flexicosta species group due to the number and arrangement of ribs on the valve, but without considering the shape of the ribs and shell. Initially, the species N. flexicosta with roller-shaped ribs and an elongated rounded-rectangular shell (Table VIII, fig. 17, 18) was attributed by E. Triebel to the genus Lophocythere Sylvester-Bradley, 1948 (Triebel, 1951), which was supported by many authors (Lutze, 1960; Brand, Fahrion 1962; Malz, 1962; Oertli, 1963; Wienholz, 1967; Permyakova, 1975; Bielecka et al., 1988; Kaever et al, 1994). Subsequently, due to its inconsistency with the ridge-shaped ribs characteristic of Lophocythere, the species was transferred by R. Whatley to the new subgenus Neurocythere (Whatley, 1970), and later to the nominative genus (Whatley et al., 2001). Additionally, N. flexicosta was identified as part of Crucicythere Malz, 1975 (Pyatkova, Permyakova, 1978; Gerasimov et al., 1996) and Nophrecythere Gruendel, 1975 (Tesakova, 2003) – genera that were synonymized with Neurocythere (Whatley, Ballent, 2004). Currently, the species flexicosta is considered to belong to the genus Terquemula Blaszyk et Malz, 1965 (Dépêche, 1985; Whatley, Ballent, 2004; Franz et al., 2009; present work).

The main distinguishing features of the genera Neurocythere and Terquemula are the shape of the shell and ribs (ridge-shaped in the former and roller-shaped in the latter) (Whatley, Ballent, 2004, p. 84), which is why we attribute the species margaritae to the former. However, its sculpture is so similar to that of T. flexicosta that it is possible that N. margaritae was genetically closer to T. flexicosta than to all Neurocythere with which it has been compared. Therefore, it is advisable to also compare the new species with the flexicostas and discuss the possibility of its origin from them.

(2) From the similar in sculpture (especially in number and arrangement of ribs) Terquemula flexicosta flexicosta (Triebel, 1951) (Table VIII, fig. 17, 18) from the Upper Bathonian - Middle Callovian of Germany (Triebel, 1951, p. 97, Table 48, fig. 46-48; Lutze, 1960, p. 428, Table 35, fig.

8 a-c; Malz, 1962, Table 24, fig. 6d; Brand, Fahrion, 1962, p. 149, Table 21, fig. 34; Kaever et al., 1976, p. 63, Table 9, fig. 7; Whatley, Ballent, 2004, p. 83; Franz et al., 2009, p. 149, Table 5, fig. 5), Lower-Upper Callovian of France (Dépêche, 1985, Table 6) and Poland (Bielecka et al., 1988, p. 171, Table 67, fig. 3), N. margaritae differs by an isometric and oval, rather than elongated rounded-rectangular female carapace, as well as ridge-like rather than roll-like ribs, the absence of short oblique ribs in the upper posterior part of the left valve, and smaller size (T. flexicosta flexicosta has L=0.78-0.90 mm; Triebel, 1951, p. 98).

From T. flexicosta labyrinthos (Whatley, Ballent et Armitage, 2001) (Table VIII, fig. 16) from the Upper Callovian, Athleta Zone of the brick pit at Calvert (Buckinghamshire, England) (Whatley et al., 2001, p. 154, Table 5, fig. 10-17), which is very similar in number and arrangement of ribs, the new species differs by its smaller size (female T. flexicosta labyrinthos has L=0.64-0.69 mm), carapace shape (shorter and oval, with a higher posterior end), as well as convex rather than horizontal dorsal and ventral ribs, which converge at the anterior end at an angle forming a triangular figure of three cells. The same features of carapace shape and sculpture distinguish it from T. flexicosta lutzei (Whatley, 1970) from the Middle Callovian, Coronatum Zone of Scotland; Upper Callovian, Athleta and Lamberti Zones of England (Whatley, 1970, p. 341, Table 12, fig. 1-12), as well as Upper Callovian, Athleta Zone of Northern Germany (Brand, Fahrion, 1962, p. 149, Table 21, fig. 41; Wienholz, 1967, Table 5, fig. 57) and Lower Callovian of France (Oertli, 1963, Table 34, fig. 1, 2, Table 35, fig. 1; Dépêche, 1985, Table 32, fig. 19), and also by even smaller size - female T. flexicosta lutzei has L=0.71-0.89 (Whatley et al., 2001, p. 156).

(3) Ostracods from the Dnieper-Donets Depression, attributed by M.N. Permyakova to the species flexicosta, were indicated by her from deposits of both the Lower and Middle Callovian. This can only mean one thing – the Early Callovian specimens should be identified as N. margaritae (this includes the specimen from: Permyakova, 1975, Table 1, fig. 5 a, b), and the Middle Callovian ones – in the absence of zonal division – as N. margaritae-parva (or N. margaritae s.l.). Unfortunately, the

stratigraphic reference of the specimen illustrated in: Pyatkova, Permyakova (1978, Table 62, fig. 1 a-g) is too vague – "Callovian," and its size is not indicated, so it is unclear to which of the new species it should be attributed.

Distribution. Lower and lower part of the Middle Callovian, ammonite zones Subpatruus (biohorizon Ch. saratovensis) – Jason, ostracod zone Praeschuleridea wartae – Pleurocythere kurskensis, Kursk Region; Lower-Middle Callovian of the Dnieper-Donets Depression.

Material. 322 specimens (separate valves and complete carapaces of females, males, and juveniles) of good and excellent preservation from Lower Callovian deposits (Subpatruus zone, Ch. saratovensis biohorizon) of the Mikhailovsky GOK and Lower-Middle Callovian (ostracod zone P. wartae – Pl. kurskensis) from borehole 7 of the Kursk Region.

⑤ Neurocythere parva Tesakova, sp. nov.

⑥ Table VIII, fig. 1-11

Lophocythere flexicosta flexicosta: Permyakova, 1975, p. 108, Table 1, fig. 5 a, b (part.).

Crucicythere flexicosta: Pyatkova, Permyakova, 1978, p. 146, Table 62, fig. 1 a-g (part.).

Nophrecythere flexicosta: Tesakova, 2003, p. 197, Table 13, fig. 13-16.

Neurocythere flexicosta ssp. A: Tesakova et al., 2017, Table 3, fig. 14, 15; Tesakova, Shurupova, 2018, Table 10, fig. 7.

Species name parva *Lat.* – small, little.

Holotype – MSU, № MC2-7, left valve of female; Ryazan Region, Mikhailovcement section; Middle Callovian, Coronatum zone, Grossouvrei subzone and biohorizon (Table VIII, fig. 1).

Description. Morphologically, this species does not differ from N. margaritae sp. nov., so see the description of the latter. But it should be clarified that specimens of N. parva sp. nov. belong to the medium size category.

Internal features, such as the hinge, muscle scars, and pore-canal zone, are the same as in N. margaritae sp. nov. (Table VIII, fig. 11).

Sexual dimorphism was not revealed in the studied material.

Dimensions in mm:	L	HRV	HLV	L/H
holotype MSU, № MC2-7 (female)	0.56	0.35	0.21	1.60
spec. MSU, № MC2-3 (female)	0.54	0.30	0.21	1.80
spec. MSU, № MC2-62 (female)	0.55	0.35	0.18	1.57
spec. MSU, № MC2-4 (juv. A3-A4)	0.44	0.26	0.16	1.71
spec. MSU, № MC2-5 (juv. A5-A6)	0.40	0.24	0.12	1.67
spec. MSU, № MC2-60 (juv. A5-A6)	0.37	0.22	0.12	1.68
spec. MSU, № MC2-64 (juv. A3-A4)	0.44	0.24	0.13	1.83
spec. MSU, № MC2-6 (juv. A5-A6)	0.37	0.20	0.12	1.70
spec. MSU, № MC2-58 (juv. A5-A6)	0.35	0.20	0.11	1.80
spec. MSU, № MC2-63 (female)	0.56	0.32	0.21	1.75

Variability. The length of females of the new species varies within 0.54 - 0.56 mm, the L/H ratio – 1.60 - 1.80. The variability of sculpture in adult females is the same as in N. margaritae sp. nov. In ontogeny, the dorsal rib is characterized by a central saddle at stages A5-A6 (Table VIII, fig. 5, 6, 8, 9), "humps" in front and behind it at stages A3-A4 (Table VIII, fig. 4, 7), and a straight middle part starting from stages A1-A2.

Comparison. For comparison with the most similar N. margaritae, see its description above.

Distribution. Middle and Upper Callovian, Coronatum–Lamberti zones, Ryazan region; Middle Callovian of the Dnieper-Donets Basin.

Material. 54 specimens of well and excellently preserved females and juveniles from the Middle and Upper Callovian of the Ryazan region: 45 specimens from the Coronatum zone, seven specimens from the Athleta zone of the Mikhailovcement section; two specimens from the Lamberti zone of the Zmeinka section.

⑤ **Terquemula pseudoflexicosta Tesakova, sp. nov.**

⑥ Table VIII, fig. 12

Nophrecythere flexicosta: Tesakova, 2003, p. 197, Table 13, fig. 17.

Species name from pseudēs *Greek.* – false and the most similar species T. flexicosta.

Holotype – PIN, № 4843/301, left valve of male(?); Kursk region, Mikhailovsky GOK section, sample 95-5; lower Callovian, Koenigi zone (Table VIII, fig. 12).

Description. Shell large, rounded-rectangular from the lateral side, trapezoidal from the dorsal side, moderately convex. The greatest length is in the middle of the height, the greatest height is at the beginning of the anterior end, the greatest thickness is in the posterioventral part of the valve. The dorsal margin is straight, transitioning to the anterior margin through a small hinge ear, and to the posterior margin through a weakly visible ledge. The ventral margin is straight, parallel to the dorsal one, concave in the anterior third, smoothly connecting with the anterior and posterior margins. The anterior end is high, smoothly rounded, oblique from above, slightly flattened. The posterior end is lower than the anterior, rounded-triangular, symmetrical, evenly sloped from above and below, widely flattened along the edge. On the lateral surface of the valve, four long ridge-like longitudinal ribs and a short thin subvertical one, parallel to the anterior margin, are developed. The dorsal rib – the longest – extends along the dorsal margin (in this part it undulates, with a small saddle), anteriorly deviates downward and diagonally crosses the anterior end, reaching its edge at a point below the middle of the height. The median rib – the shortest – is developed in the posterior two-thirds of the valve and weakly undulates, reaches the flattened part of the posterior end, but does not cross it. The upper of the two ventral ribs develops parallel to the ventral margin; at the anterior end it connects with the dorsal rib at an acute angle, and at their junction a large rounded cell is isolated; at the opposite end it crosses its flat part and reaches the posterior margin below the middle of the height. Below is the second ventral rib, which in the posterior half somewhat overhangs the ventral margin and masks it; it crosses both ends and reaches the anterior and posterior margins. On the ventral surface there are several thin longitudinal riblets, not visible from the side view. In the upper half of the anterior end, a thin transverse rib is developed, originating from a large low eye spot and abutting the junction of the dorsal and ventral ribs. The entire interrib surface, except for the flattened parts of both ends and along the dorsal margin, is covered with large irregular cells with thin low muri, rounded in cross-section.

In many cells, including on the flat parts of both ends and along the dorsal margin, conuli with small sieve-like (?) pores at the top are developed.

It was not possible to observe the hinge, muscle scars, and pore canal zone.

Dimensions, in mm:	L	H	T
holotype PIN, No. 4843/301	0.74	0.41	0.35

Comparison. It differs from the most similar in number, shape and arrangement of ribs T. flexicosta flexicosta (Table VIII, fig. 17, 18) by smaller size (T. flexicosta flexicosta has L=0.78–0.90 mm), more oblique anterior end at the top and longer posterior end, low and poorly developed anterior hinge ear, unconnected dorsal and median ribs in the posterior part, and the absence of oblique riblets between the dorsal and median ribs in the posterior part on the left valve.

It differs from T. flexicosta lutzei and T. flexicosta labyrinthos by parallel dorsal and ventral margins not converging toward the posterior end, more elongated anterior and posterior ends, the absence of connection between the dorsal and median ribs at the posterior end, the connection of dorsal and ventral ribs at an acute angle at the anterior end (unlike the smooth conjugation in the compared subspecies), and the absence of vertical filiform riblets between the dorsal and median, as well as median and ventral ribs; additionally, it differs from T. flexicosta labyrinthos (L=0.60–0.69) by larger size.

Remarks. It differs from the most similar in elongated shell and size characteristic of males Neurocythere margaritae sp. nov. (Table VII, fig. 10, 13), and the arrangement of ribs in this species by a longer and more symmetrical posterior end, evenly oblique both from above and below; asymmetrical anterior end, oblique from above; unconjugated dorsal and median ribs at the posterior end (there is no rounded open loop in the posterior third of the valve); ridge-like rather than crest-like ribs and low muri (weakly expressed cells).

Based on the characteristic features of the sculpture, this specimen cannot be assigned to any known species, but the lack of material does not allow reliable determination of the sex of the described specimen. Based on the large size of the specimen, similar to that of males of N. margaritae, the author suggests that the valve is most likely of a male, but there is no complete certainty in this.

Material. Holotype.

PHYLOGENETIC RELATIONSHIPS AND EVOLUTION OF THE DISCUSSED TAXA

The evolutionary relationships of the new species Neurocythere margaritae, N. parva, and Terquemula pseudoflexicosta with the most similar species from Western Europe are not entirely clear (Fig. 2). The characteristics used for their comparison and available for evolutionary analysis from published photographs include carapace size and shape, as well as the number and relative arrangement of ribs on the valve and microsculpture. Other features, such as the hinge structure (especially the median element), the shape of muscle scars (particularly mandibular and antennal), and the pore canal zone with radial canals were not compared due to insufficient characterization in the literature (Triebel, 1951, p. 97; Dépêche, 1969, p. 272; 1973, pp. 217, 218). It should be emphasized that the shape of the carapace and ribs in the species margaritae and parva resembles Neurocythere, while the number and arrangement of ribs are similar to Terquemula flexicosta. Moreover, the literature lacks information on the ontogenesis of the species (and corresponding subspecies) T. flexicosta, N. caesa, N. cuvillieri, N. rimosa, and N. bessinensis, which could be compared with those of N. margaritae and N. parva.

The reconstruction of the phylogenetic lineage T. flexicosta flexicosta (D=0.78–0.90 mm) → T. flexicosta lutzei (D=0.71–0.89 mm) → T. flexicosta labyrinthos (0.60–0.69 mm) is based on morphological similarity of subspecies and stratigraphic position and raises no doubts, as well as the short lineages N. caesa caesa (D=0.78–0.90 mm) → N. caesa warei (D=0.67–0.73 mm) and N. caesa caesa → N. caesa subsp. A Wilkinson et Whatley, 2009 (Fig. 2). Here it should be mentioned again that the differences between T. flexicosta lutzei and T. flexicosta labyrinthos, which possess shells identical in form, proportions, and ornamentation, consist only in their sizes (Whatley et al., 2001, p. 156). The reduction in size of specimens of the descendant species while maintaining the morphology of the ancestor species is characteristic of evolution through gerontomorphosis with minification (according to: Kiselev, 2023). A similar pattern is observed in the development of English Neurocythere. Among specimens of N. caesa from the Upper Callovian and Lower Oxfordian of England, differences in size and minor variations in microsculpture were revealed. Thus, ostracods from the Athleta and Lamberti zones were characterized by larger sizes and were assigned to the subspecies N. caesa caesa (Triebel) (Wilkinson, Whatley, 2009, Table 7, fig. 13, 14). Smaller ostracods from the Athleta – Cordatum zones, which partially coexisted with the nominative subspecies, were designated as a new subspecies N. caesa subsp. A (Wilkinson, Whatley, 2009, Table 7, fig. 15, 16) and additionally differed from the ancestral taxon by less parallel sides converging toward the posterior end, and finer muri of the intercostal cells (which is characteristic of juveniles of penultimate stages). This is also evolution that proceeded through gerontomorphosis with minification.

The origin of N. cuvillieri is not so obvious. Its distribution in the Middle Callovian of Lorraine (Paris Basin) geographically associates it with similar species N. rimosa (Fig. 2, *a*) (terminal Bajocian and Bathonian) and N. bessinensis (Fig. 2, *b*) (Lower-Middle Bathonian). The ranges of the latter are wider – Normandy, Southern England, and for N. rimosa also Dagestan, where it is found in the Lower Callovian (Calloviense zone). This reduces the stratigraphic gap between it and N. cuvillieri, but in the Paris Basin, N. rimosa is not found above the Upper Bathonian. However, morphologically N. cuvillieri is more similar to N. bessinensis, with which the temporal gap is very significant (Upper Bathonian and Lower Callovian). All this creates difficulties for deriving N. cuvillieri directly either from the most similar N. bessinensis or from the temporally closest N. rimosa and suggests an intermediate link between them. But with equal success, N. cuvillieri could have descended from N. caesa caesa – there is no stratigraphic contradiction and there is morphological similarity. Thus, it is impossible to make a firm choice between the ancestral species for it (until their ontogenies are studied).

Similarly, a problem arose with the ancestors for N. margaritae sp. nov. and N. parva sp. nov. First, the taxonomic weight of such features as shell and rib shape, as well as the number and arrangement of ribs, should be clarified. Depending on how these features developed in the ontogeny of the presumed predecessors (T. flexicosta flexicosta, N. caesa caesa, N. rimosa or N. bessinensis), it might be possible to determine the ancestral group. Second, knowledge of evolutionary trends and heterochronies in the discussed lineages would be very helpful. But this requires studying the ontogenies of all the listed species and subspecies, which, unfortunately, are absent in the author's material (as they did not extend to Eastern Europe, including the waters of the Middle Russian Sea and the Dnieper-Donets Basin).

Similarly, there is no complete clarity about the ancestors of T. pseudoflexicosta sp. nov. Morphologically, this species is most and equally close to both T. flexicosta flexicosta and N. caesa caesa (Table VIII, Fig. 14, 17). The lack of sufficient original material, including juveniles of the new species, and the inability to trace ontogenies in the latter two prevent the resolution of this issue.

In this article, one can only state the following. In three short phyletic lineages: N. margaritae → N. parva, T. flexicosta lutzei → T. flexicosta labyrinthos, and N. caesa caesa → N. caesa subsp. A, evolution primarily affected the size (descendant taxa are smaller). This pathway can be attributed to gerontomorphosis with minification (according to: Kiselev, 2023).

The justification of the phyletic lineage N. margaritae → N. parva, in principle, allows the identification of new eponymous phylozones: the first in the Lower-Middle Callovian, Subpatruus-Jason zones, the second in the Middle-Upper Callovian, Coronatum-Lamberti zones; both are distributed in Central Russia and the Dnieper-Donets Basin. The section of the Mikhailovsky Mining and Processing Plant in Kursk Region is proposed as the type section for the N. margaritae phylozone, and Mikhailovcement in Ryazan Region for the N. parva phylozone.

CONCLUSION

Species from the Callovian of Eastern Europe that were referred to in literature as Neurocythere flexicosta, N. flexicosta flexicosta, N. flexicosta "ovata" and N. flexicosta ssp. A have been revised. They have been divided into three new species: N. margaritae sp. nov., N. parva sp. nov., and Terquemula pseudoflexicosta sp. nov., which are substantiated and described in this article.

The species Neurocythere margaritae and N. parva form a single phyletic lineage that developed along the path of gerontomorphosis with minification. The same evolutionary trends were traced in the lineages Neurocythere caesa caesa → N. caesa subsp. A and Terquemula flexicosta lutzei → T. flexicosta labyrinthos.

It was not possible to identify ancestors for the new taxa. Presumably, they could have been the species N. caesa caesa, N. rimosa, N. bessinensis, or T. flexicosta flexicosta (Fig. 2).

The species N. margaritae and N. parva are proposed as indices of new eponymous phylozones. The first for the Lower-Middle Callovian (Subpatruus-Jason zones), the second for the Middle-Upper Callovian (Coronatum-Lamberti zones); both within Eastern Europe (Central Russia and the Dnieper-Donets Basin). The species T. pseudoflexicosta sp. nov. is distributed in the Lower Callovian (Koenigi zone) of Kursk Region.

ACKNOWLEDGEMENTS

The author expresses sincere gratitude to L. Guskova (Moscow State University), D.B. Gulyaev (Commission on the Jurassic System of Russia), M.A. Rogov (GIN RAS), V.V. Mitta (PIN RAS), A.G. Olferyev (PIN RAS), and A.V. Chereshinsky (VSU) for their help in collecting and dating material from open sections using ammonites and for providing samples from boreholes. Special thanks to M.A. Rogov for assistance with preparing the figures and R.A. Rakitov (PIN RAS) for help with scanning electron microscope work. The author is deeply grateful to reviewers L.M. Melnikova (PIN RAS) and D.N. Kiselev (YaSPU) for comprehensive discussion of the manuscript and valuable advice on its improvement.

FUNDING

This work was carried out within the framework of state assignment topics No. 0135-2019-0062 (Geological Institute of the Russian Academy of Sciences) and AAAA-A16-116033010096-8 (Lomonosov Moscow State University).

CONFLICT OF INTERESTS

The author of this work declares that he has no conflict of interest.

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Figure Captions

Fig. 1. Location scheme of the studied sections (marked with asterisks).

Fig. 2. Distribution of new Neurocythere and Terquemula and their presumed ancestors in Western and Eastern Europe and their stratigraphic significance. Legend: *a* – N. rimosa (Dépêche, 1973), specimen OS 9064, LS female (L=0.54 mm) from the Lower Bathonian, Lower Fuller's Earth of Bath (Somerset, England) (Wilkinson, Whatley, 2009, Table 2, fig. 7); *b* – N. bessinensis (Dépêche, 1973) specimen OS 9061, LS female (L=0.60 mm), same location and age (Wilkinson, Whatley, 2009, Table 2, fig. 10). Subdivisions of the Subpatruus zone, biohorizons (after: Gulyaev, 2015): 1 – C. surensis, 2 – C. subpatruus, 3 – C. uzhovkensis, 4 – Ch. saratovensis.

Explanation to Table VII

All illustrated specimens are from borehole 7, Kursk region (Tesakova, 2013, fig. 6): specimens in figs. 1, 5, 7, 9–11 – depth 135 m; 2, 3 – depth 128 m; 4, 8, 12–15 – depth 136 m; 6 – depth 127 m; Lower Callovian, ostracod zone Wartae–Kurskensis. Abbreviations used for Table VII and VIII: CR – complete carapace, RV – right valve, LV – left valve, juv. – juvenile specimen.

Fig. 1–15. Neurocythere margaritae sp. nov.: 1 – holotype MSU, № 300-Ku-1-97, left valve of female; 2 – spec. MSU, № 300-Kusk-149, right valve of female; 3 – spec. MSU, № 300-Kusk-150, left valve juv. A1-A2 (from: Tesakova, 2013, Table 6, fig. 7, where it was identified as female N. flexicosta ssp. A); 4 – spec. MSU, № 300-Ku-2-27, left valve of female; 5 – spec. MSU, № 300-Ku-1-100, right valve of female; 6 – spec. MSU, № 300-Kusk-147, right valve juv. A1-A2; 7 – spec. MSU, № 300-Ku-1-96, left valve of female; 8 – spec. MSU, № 300-Ku-2-30, left valve of female; 9 – spec. MSU, № 300-Ku-1-108, left valve juv. c; 10 – spec. MSU, № 300-Ku-1-103, left valve of male; 11 – spec. MSU, № 300-Ku-1-104, right valve of male; 12 – spec. MSU, № 300-Ku-2-28, left valve juv. A3-A4; 13 – spec. MSU, № 300-Ku-2-29, left valve of male; 14 – spec. MSU, № 300-Ku-2-31, right valve of male; 15 – spec. MSU, № 300-Ku-2-18, right valve juv. A5-A6. Scale bar is 100 μm.

Explanation to Table VIII

Specimens in fig. 1–10 are from the Mikhailovtsement section, Ryazan region (Tesakova et al., 2017, fig. 3): spec. in fig. 1, 2, 4, 5, 8 from sample 8; spec. in fig. 3, 6, 7, 9, 10 from sample 9; all spec. from the Upper Callovian, Athleta Zone, Phaeinum Subzone. Spec. fig. 1 and 2 from: Tesakova et al. (2017, Table 3, fig. 14, 15), where they were identified as Neurocythere flexicosta (Triebel) ssp. A.

Fig. 1–11. Neurocythere parva sp. nov.: 1 – holotype MSU, № MC2-7, left valve of female; 2 – spec. MSU, № MC2-3, right valve of female; 3 – spec. MSU, № MC2-62, left valve of female; 4 – spec. MSU, № MC2-4, left valve juv. A3-A4; 5 – spec. MSU, № MC2-5, left valve juv. A5-A6; 6 – spec. MSU, № MC2-60, left valve juv. A5-A6; 7 – spec. MSU, № MC2-64, right valve juv. A3-A4; 8 – spec. MSU, № MC2-6, right valve juv. A5-A6; 9 – spec. MSU, № MC2-58, right valve juv. A5-A6; 10 – spec. MSU, № MC2-63, right valve of female; 11 – spec. PIN, № 4843/265, left valve of female from inside (L–0.65 mm, H–0.34 mm, W–0.30 mm); Mikhailovtsement section, sample 94-22; Middle Callovian, Coronatum Zone (from: Tesakova, 2003, Table 13, fig. 13, where it was identified as Nophrecythere flexicosta);

Fig. 12. Terquemula pseudoflexicosta sp. nov., holotype PIN, № 4843/301, left valve (L–0.74 mm, H–0.41 mm, W–0.35 mm); section of Mikhailovsky GOK, sample 95-5; Lower Callovian, Koenigi Zone (from: Tesakova, 2003, Table 13, fig. 17, where it was identified as Nophrecythere flexicosta).

Fig. 13. Neurocythere cuvillieri (Dépêche, 1969), spec. FDO-14, left valve of female from Lorraine (Paris Basin), borehole Chonville-1, depth 314 m; Middle Callovian (from: Depeche, 1969, Table 1, fig. 8, where it was identified as Lophocythere cuvillieri).

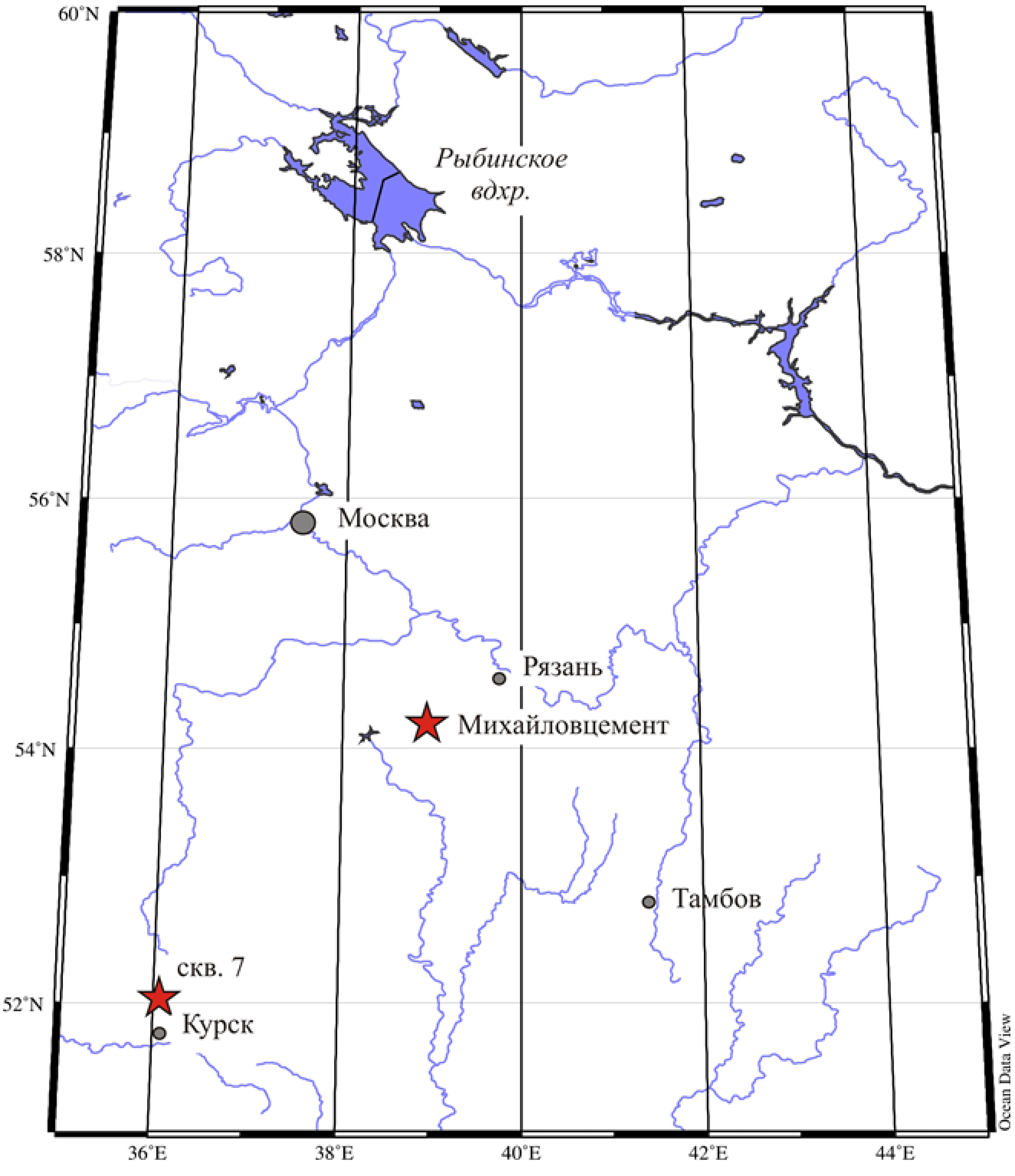
Fig. 14. Neurocythere caesa caesa (Triebel, 1951), holotype Xe 1799, left valve of female from borehole Furberg 148 (Northern Germany), depth 363-367 m; Lower Callovian (from: Triebel, 1951, Table 48, fig. 42-43, where it was identified as Lophocythere caesa).

Fig. 15. Neurocythere caesa warei Whatley, Ballent et Armitage, 2001, holotype OS 15837, left valve of female (L=0.70, H=0.39) from Oxford Clay of Calvert Brick Pit (Buckinghamshire, England); Upper Callovian, Athleta Zone (from: Whatley et al., 2001, Table 4, fig. 16).

Fig. 16. Terquemula flexicosta labyrinthos Whatley, Ballent et Armitage, 2001, holotype OS 15844, left valve of female (L=0.64, H=0.37); location and age are the same (from: Whatley et al., 2001, Table 5, fig. 10).

Fig. 17, 18. Terquemula flexicosta flexicosta (Triebel, 1951) from Lower Callovian of Northern Germany (from: Triebel, 1951, Table 48, fig. 46, 47, where they were identified as Lophocythere flexicosta): 17 – paratype Xe 1807, left valve of female, Dögerode bei Echte section; 18 – holotype Xe 1806, complete carapace of female from right side, borehole Furberg 148, depth 380-384 m.

Images in fig. 1-10 are shown at the same scale, scale bar length is 100 μm. Dimensions of specimens in fig. 11, 12, 15, 16 are given in brackets. Dimensions of specimens in fig. 13, 14, 17, 18 can be found in the tables of the cited publications.


60°N
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38°E
40°E
42°E
44°E
Рыбинское
вдхр.
Москва
Рязань
Михайловцемент
Тамбов
скв. 7
Курск
Ocean Data View

Fig. 1

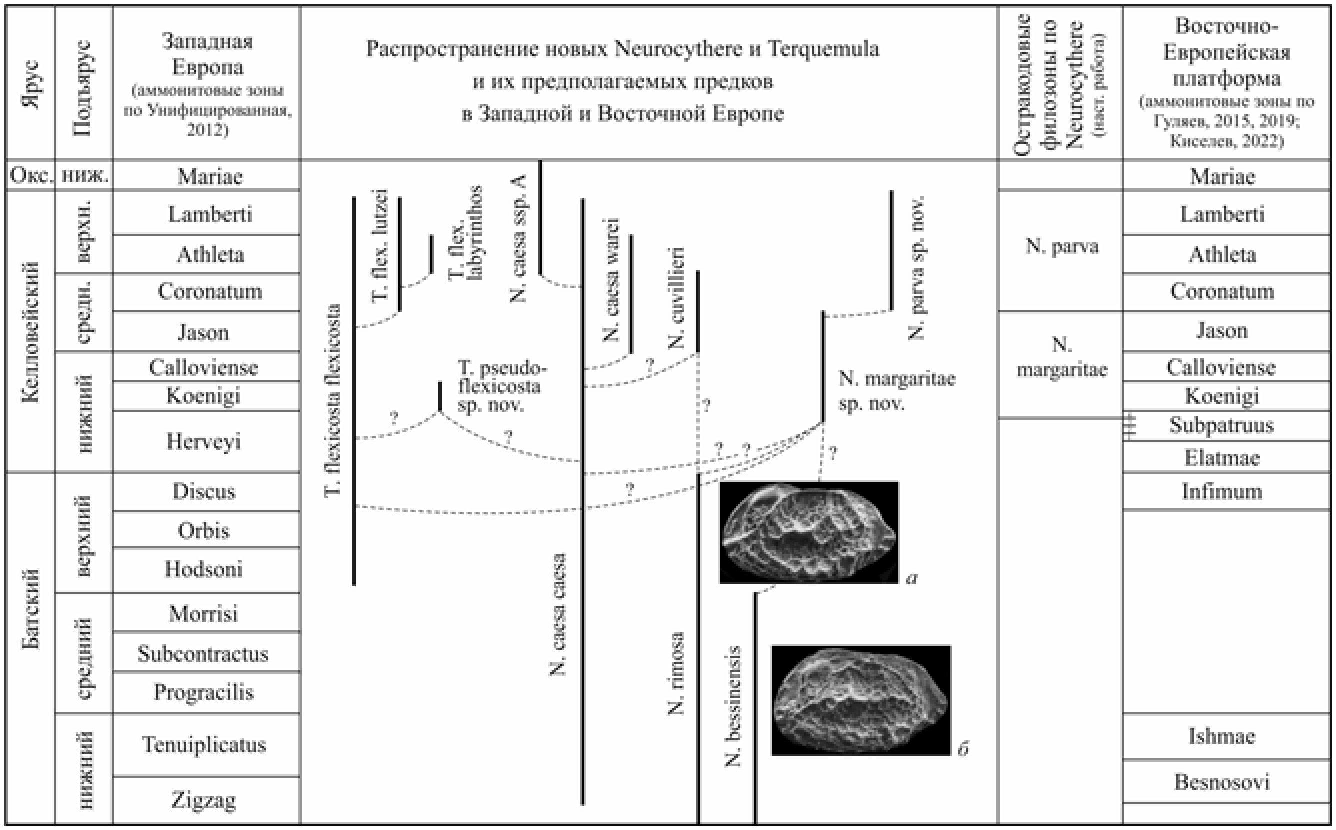
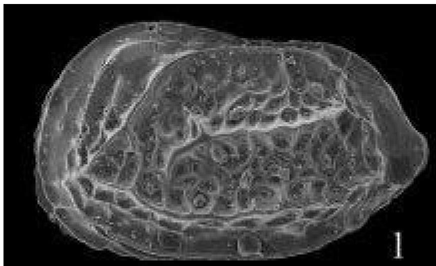

Ярус
Подъярус
Западная Европа (аммонитовые зоны по Унифицированная, 2012)
Распространение новых Neurocythere и Terquemula и их предполагаемых предков в Западной и Восточной Европе
Остракодовые филозоны по Neurocythere (наст. работа)
Восточно-Европейская платформа (аммонитовые зоны по Гуляев, 2015, 2019; Киселев, 2022)
Окс.
ниж.
Mariae
Келловейский
верхн.
Lamberti
Athleta
средн.
Coronatum
Jason
нижний
Calloviense
Koenigi
Herveyi
Батский
верхний
Discus
Orbis
Hodsoni
средний
Morrisi
Subcontractus
Progracilis
нижний
Tenuiplicatus
Zigzag
T. flexicosta flexicosta
T. flex. lutzei
T. flex. labyrinthos
N. caesa ssp. A
N. caesa caesa
N. caesa warei
N. cuvillieri
N. rimosa
N. bessinensis
N. parva sp. nov.
N. margaritae sp. nov.
T. pseudo-flexicosta sp. nov.
?
a
б
N. parva
N. margaritae
Mariae
Lamberti
Athleta
Coronatum
Jason
Calloviense
Koenigi
Subpatruus
Elatmae
Infimum
Ishmae
Besnosovi

Fig. 2

Table VII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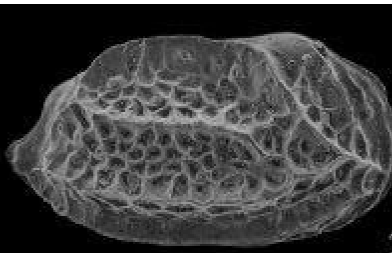
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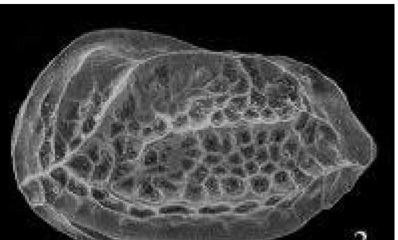
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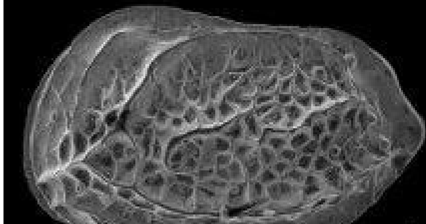
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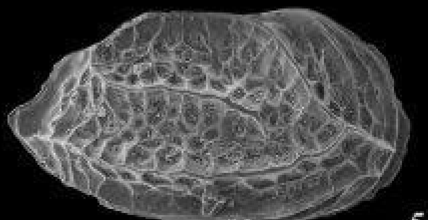
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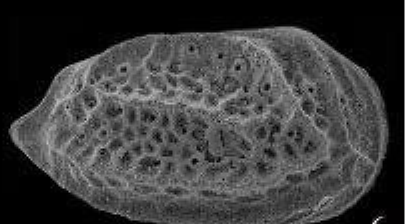
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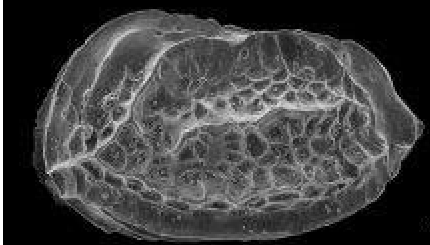
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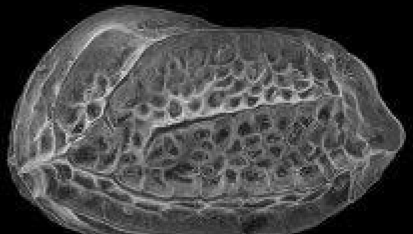
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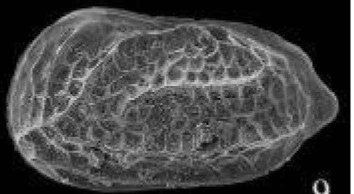
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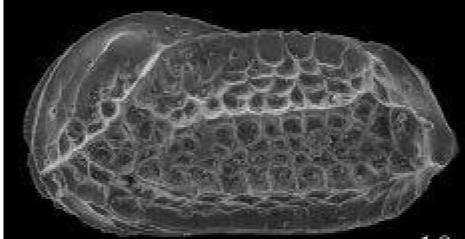
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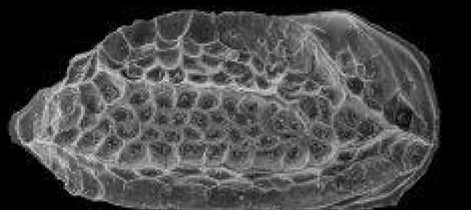
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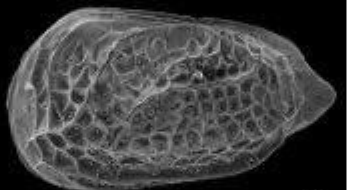
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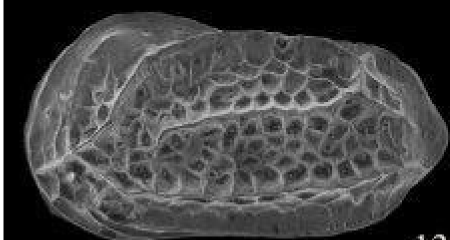
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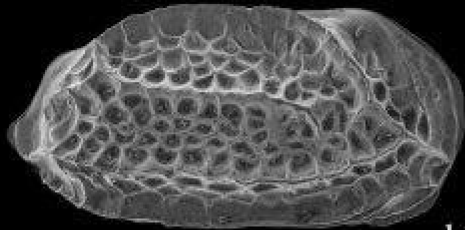
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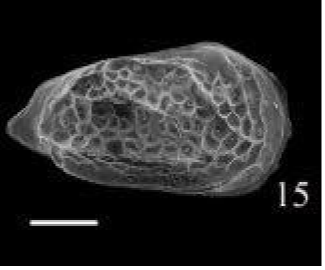
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Table VIII