VOLUMINA JURASSICA, 2017, XV: 121–138
DOI: 10.5604/01.3001.0010.6074

Detailed biostratigraphic scales as based on the palaeobiogenetical approach (an example of the Upper Bajocian – Lower Bathonian ostracod scale of the Russian Platform)

Yana A. SHURUPOVA[1], Ekaterina M. TESAKOVA[2,3]

Key words: palaeobiogenetic method, heterochrony, detailed biostratigraphy, ostracods, new species, Bajocian, Bathonian, Saratov Volga Region.

Abstract. Two new species of ostracods of the family Progonocytheridae Sylvester-Bradley *Camptocythere (C.) lateres* Tesakova et Shurupova, sp. nov. and *C. (C.) angustius* Tesakova et Shurupova, sp. nov. from the Michalskii and Besnosovi ammonite zones (Upper Bajocian – Lower Bathonian, Middle Jurassic) of the Sokur section (Saratov) are described. The changes in ontogenesis in the phylogeny of *Camptocythere (C.) lateres* Tesakova et Shurupova in the stratigraphical interval corresponding to the Palaeocytheridea kalandadzei ostracod Zone, and especially to the beds with *C. (C.) lateres*, have been studied. The levels of the change in the predominant type of sculpture (corresponding to evolutionary boundaries) are recognized in the sculpture development among the adult representatives of the species in its phylogeny. This palaeobiogenetic (heterochrony) approach allows subdivision of the beds with *C. (C.) lateres* into three stratigrapical intervals characterized by changes in the type of sculpture.

INTRODUCTION

The biostratigraphic subdivision of sedimentary strata is based either on the evolution of a group of fossils (lineage units of a different rank are distinguished in this case), or a change in the palaeocoenosis associated with various palaeoecological events and depending on regional palaeogeography. Undoubtedly, the most detailed scales not dependent on local conditions have been developed for taxa which evolved quickly, and showed a wide geographical distribution. These include planktonic or nektonic organisms, such as Jurassic or Cretaceous ammonites, or the Upper Cretaceous planktonic foraminifera. Benthic organisms, having either a small or a patchy distribution, evolved much more slowly, so that the units based on them show wide stratigraphical ranges and do not meet the modern requirements for establishing detailed biostratigraphic scales. Nevertheless, various groups of benthic organisms (including ostracods) give a basis for the construction of parallel stratigraphic scales which have been used in the absence of orthostratigraphic groups of fossils (as often happens in boreholes).

Since benthic groups inhabiting shallow epicontinental seas (to a depth of ~50 m) react quickly to changing environmental conditions, the sequences of their palaeocoenosis (ecostratigraphic units) can be recognized in quite large detail. For example, in the stratigraphical scale for the Jurassic ostracods of the East European Platform (Tesakova, 2014), the time-duration of some beds with ostracods is comparable to that of ammonite biohorizons. However, such ecos-

[1] Biological Faculty of Lomonosov Moscow State University, Vorobyovy Gory 1, 119234, Moscow, Russia; shurupova.ya@yandex.ru.

[2] Geological Faculty of Lomonosov Moscow State University, Vorobyovy Gory 1, 119991, Moscow, Russia; ostracon@rambler.ru.

[3] Geological Institute of Russian Academy of Sciences Russia, Pyzhevsky lane 7, 119017, Moscow, Russia.

tratigraphic units, as a rule, are poorly traced over a larger distance, and their direct correlation is extremely difficult. This problem may be solved by identifying the stratigraphic sequences of units for each palaeofacial region (section) separately and their subsequent correlation, rather than by a correlation of one specific zone with another (Nikitenko, 1992, 2009; Shurygin, 2005).

It seems that all the main methodological approaches to the construction and subdivision of biostratigraphic scales are listed above. But in the middle of the XX century, V.E. Livental, a specialist in the Neogene and Quaternary ostracods of Azerbaijan, developed another method, named by him the palaeobiogenetic method (Livental, 1949), which makes it possible to subdivide significantly the biostratigraphic unit. The principle of the method is the recognition of any evolving feature in the ontogenesis of the species and the fixation of the levels with the transition of this feature in the geological section with time (*i.e.*, in the phylogeny of the species). This evolutionary phenomenon is called heterochrony. The stratigraphic levels at which these transitions are noted can be considered as boundaries identified on the basis of the evolution of the taxon. Thus any unit (of phyletic and ecological nature) that a certain species exists in, can be further subdivided into several intervals by evolutionary changes observed in the ontogenesis of this species.

Heterochrony is widely known as one of the ways of speciation, although it cannot be observed as a rule in real time during the study of modern organisms. Heterochrony is studied in fossil groups of organisms (which have existed for a long time) to establish and prove the appearance of new species and to identify family ties within the phyla (Gould, 1977, 1982, 2000; Gould *et al.*, 1979; Alberch, 1982; Fink, 1982; McNamara, 1997, 2012; Arthur, 2000; Zelditch *et al.*, 2003; Webster, Zelditch, 2005; McNamara *et al.*, 2006; Gerber *et al.*, 2008; Gerber, 2011).

However, there are several difficulties in identifying of heterochrony. Firstly, these are associated with the incompleteness of the geological record, which may cause the absence of one or more members and become a reason for the fragmentary preservation of the phyletic branches. Secondly, it is very difficult to investigate ontogeny in fossil organisms with their continual growth: early stages are either not preserved (*e.g.* vertebrates), or if they are preserved (*e.g.* bivalves or cephalopods), there is no precise control over the stages of development, independent of the size of the skeleton. The most convenient group for study of heterochrony are arthropods, which have discrete intervals of growth and grow through molts, like trilobites and ostracods. For example, the study of heterochrony in trilobites of the genus *Arthricocephalus* Bergeron from the Lower Cambrian of China allowed the reconstruction of the lineage of four related species that had paedomorphosis type development (McNamara *et al.*, 2006). A similar study on Ordovican ostracods (from Poland) revealed heterochrony within the genus *Mojczella* Olempska and which made it possible to divide it into three independent chrono-species (Olempska, 1989).

There are many other examples of the study of heterochrony for systematic and evolutionary purposes, but nobody except V.E. Leventhal, has ever used the infraspecific differences in morphological development produced by heterochrony for the elaboration of detailed biostratigraphic scales. He studied the species *Cryptocyprideis bogatchovi* (Liv.) of the Apsheronian (Pliocene) sediments of Azerbaijan. The ontogeny of this species showed the weakening and subsequent reduction of three tubercles placed in the antero-dorsal, postero-dorsal, and postero-ventral areas, well developed only among young specimens (Fig. 1) (Livental, 1949). It turned out that the evolution of this feature (reduction of tubercles) in time (in the phylogeny of the species) has shifted with time to still earlier juvenile stages. Fixation of the boundaries in the section where the evolutionary change from one morphological stage to another took place, allowed the subdivision of the Apsheronian regional stage into three substages which was impossible to achieve with any other biostratigraphic method (Livental, 1949).

Meanwhile, modern geological-prospecting investigations require much more detailed biostratigraphic charts (parallel ones), some already existing and some newly developed, based on different fossil groups. Such a new chart was created by studying the Jurassic ostracods of the Russian Platform (Tesakova, 2014, 2015). The basic subdivisions of this chart were established using palaeogeographic data to provide the necessary resolution. The Middle Jurassic ostracod zones based on the phylogeny of the species of the genus *Palaeocytheridea* Mandelstam have shown fairly wide stratigraphical ranges since speciation in this group occurred relatively slowly.

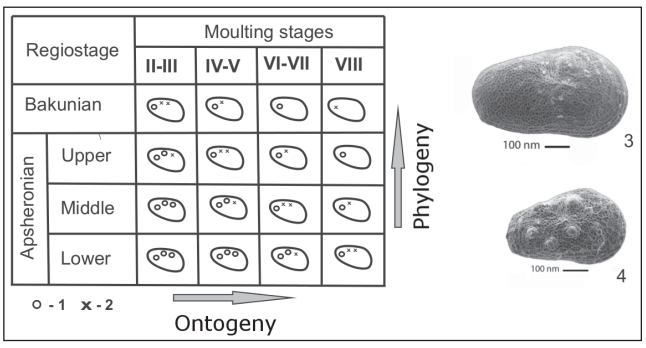


Fig. 1. Ontogeny and phylogeny of *Cryptocyprideis bogatschovi* (Livental, 1929) from Pliocene of Azerbajan (after Livental, 1949)

1 – well developed tubercle; 2 – poorly developed tubercle; *C. bogatschovi* from Meotian, Zheleznyi Rog, Taman' (by Dykan, 2016): 3 – spec. No. 2567–8/4, RV ad. male; 4 – spec. No. 2567–9/4, RV juv. 2

In the Upper Bajocian (Michalskii ammonite Zone) – Lower Bathonian (Besnosovi ammonite Zone) of the interval studied the following stratigraphical units based on ostracods were established: the Palaeocytheridea kalandadzei Lineage Zone, and independently several ecostratigraphic units, corresponding to the alternation of warm and cooler environments – such as beds with *Procytheridea concinna*, beds with *P. ljubimovae*, beds with *Camptocythere (C.) lateres*, beds with *Pseudohutsonia*, beds with *Camptocythere (C.) angustius* and the Fuhrbergiella (Praefuhrbergiella) kizilkaspakensis Subzone. Inside the F. kizilkaspakensis Subzone occurs an interval corresponding to the West Siberian Camptocythere (Anabarocythere) arangastachiensis ostracod Zone, marking the first contact of the Middle Russian and Pechora-Greenland seas at the beginning of the Bathonian. The indicator of comparatively low temperatures in the lower horizons of the section is the Euroboreal subgenus *Camptocythere* (*Camptocythere*) Triebel represented by two species. The appearance of these species in the section has been interpreted by us as a significant paleoecological event. Their first occurrence is indicative of the base of the succession of beds as discussed above.

Both species in question of this subgenus (*i.e. Camptocythere lateres* and *C. angustius*) are new, and their descriptions are given below in this study.

Another goal of this study is to detail the Upper Bajocian and Lower Bathonian strata of this scale using the palaeobiogenetic method, *i.e.* the study of ontogeny for identification of heterochrony in the evolution of the index species most commonly occurring and showing the widest stratigraphical distribution.

MATERIAL AND METHODS

The material studied includes ostracod collections from the Upper Bajocian (Michalskii Zone) and the Lower Bathonian (Besnosovi Zone) from the Sokur section (the borehole and neighbouring quarry) to the north-west of Saratov (Fig. 2). The thickness of the deposits in the section is about 60 m: 135 levels have been sampled of which 105 yielded ostracod faunas (more than 20 species) (Fig. 3).

Relatively abundant associations of the species *Camptocythere (C.) lateres* Tesakova, Shurupova sp. nov. were found in almost every sample in the interval studied corresponding to beds with *C. (C.) lateres* (38 levels) and higher in the section (to the end of the Michalskii Zone and the lower part of the Besnosovi Zone – in four samples more) which allowed the study of the ontogeny of the species on many levels.

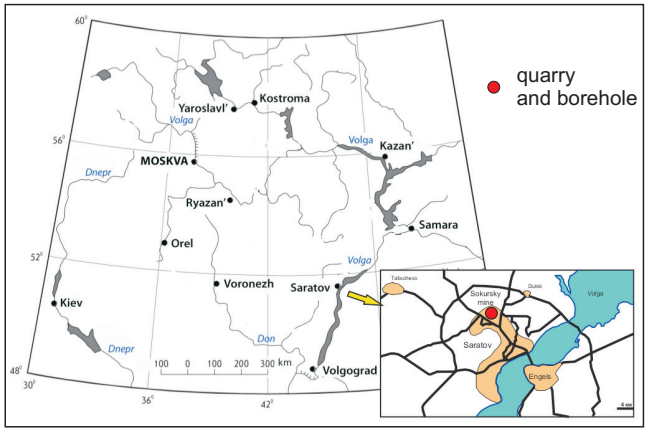


Fig. 2. Geographical location of the Sokur section

Ostracods usually moult 8 times during their life cycle, so we can distinguish 9 age stages respectively. The first stage is the youngest, and stages 1–8 correspond to the juvenile forms, the ninth is the adult. Thus each type of carapace of a different ontogenetic stage clearly varies in size, shape and development of internal structures, as well as in sculpture (in ornamented taxa).

We have studied a total of 223 specimens of the species *C.* (*C.*) *lateres* (whole shells and individual valves) of good and satisfactory preservation from the Michalskii and Besnosovi ammonite zones (Sokur sections).

Each valve was photographed using a Scanning Electron Microscope (CamScan) and studied both from the external and internal side (both lateral sides were photographed and studied on carapaces). The adult status of valves was determined by the degree of development of the pore-canal zone, which is fully developed only in adult ostracods (Pl. 1: 2g). Additional evidence was obtained from the valve thickness, the degree of height of the posterior end and the length/ height ratio (L/H) of the specimens studied (the maximal values of all these parameters are in adults).

The single valves and complete shells of adult males and females of the studied species are easily distinguishable by their length. Males have a greater length and the L/H ratio is higher (Fig. 4; Tab. 1; Pl. 1: 3, 4g; Pl. 2: 1, 2, 4–8). It should be said that both right and left valves were studied separately in the complete carapaces, as they are not completely symmetrical and differ in size. Only whole specimens were analyzed using the morphometric method (Fig. 4); broken valves and shells of both adults and juveniles were not analyzed.

Sexual dimorphism in juvenile shells was not observed, therefore, the ratio L/H depends only on the attainment of maturity. First of all, the L/H ratio for juveniles *C.* (*C.*) *lat-*

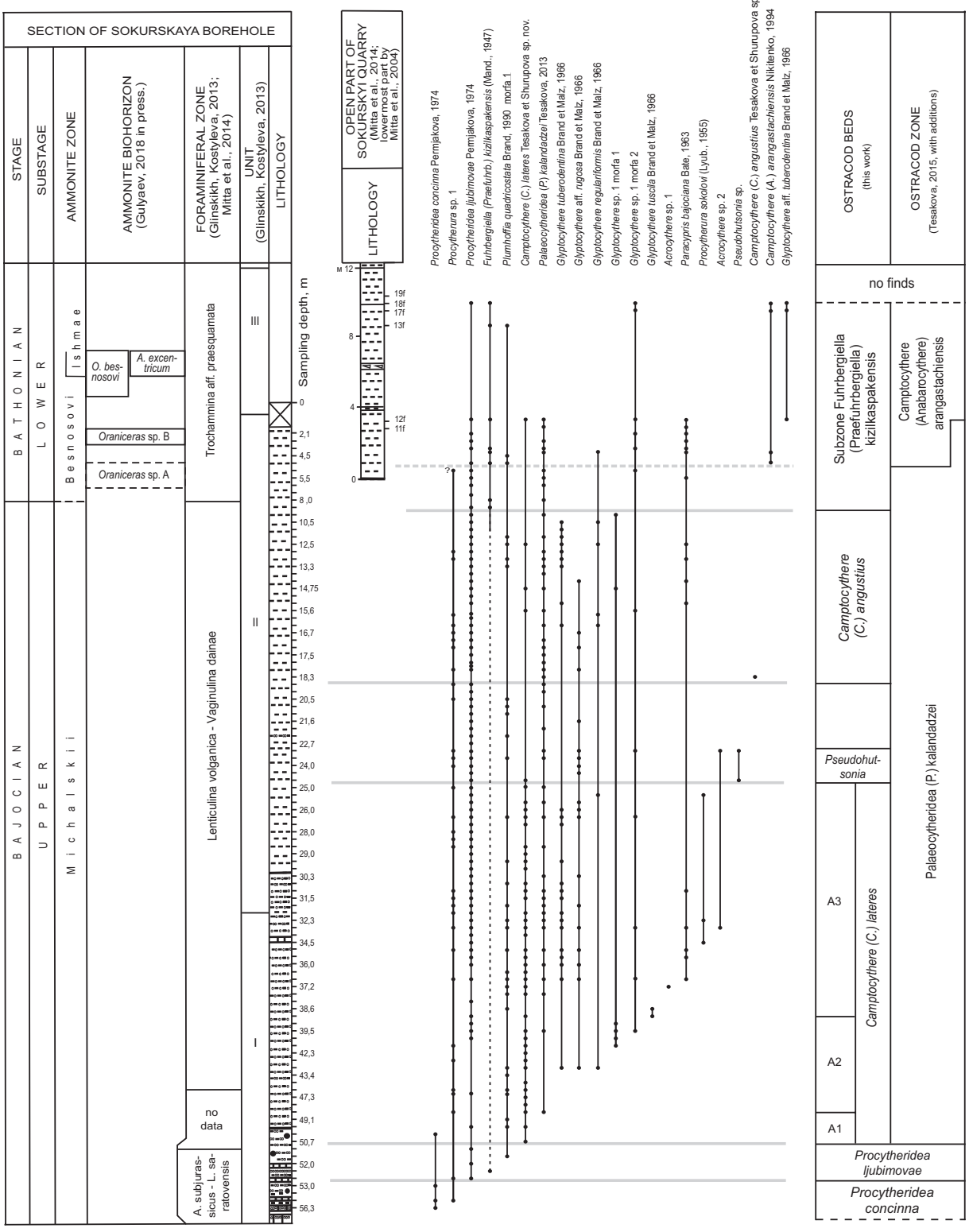


Fig. 3. Ostracod stratigraphy of the deposits from Sokur section (quarry and borehole)

Intervals A1–A3 created by evolutionary changes of sculptural types of adults *Camptocythere* (*C.*) *lateres* Shurupova et Tesakova sp. nov.; A1 – specimens with dominance of sculptural type I prevail; A2 – specimens with a predominance of sculptural type II appear; A3 – specimens with the predominant sculptural type III appear

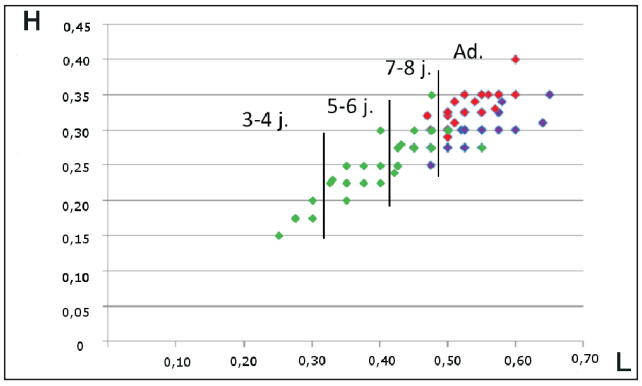


Fig. 4. The ratio of height (H) to length (L) (in mm) for all adult males (purple), adult females (red) and juveniles (green) of *Camptocythere* (*C.*) *lateres* Tes. et Shur. sp. nov.

3–4, 5–6, 7–8 successive age stages of juveniles, Ad – adult specimens

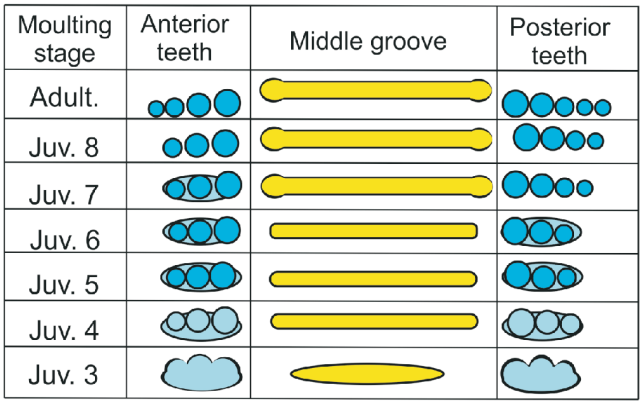


Fig. 5. Ontogeny of the hinge structures of *Camptocythere* (*C.*) *lateres* Tesakova, Shurupova, sp. nov.

eres graphs were plotted separately for each studied level of the section. Three size clusters, corresponding to different age stages of individuals were identified (3–4, 5–6 and 7–8). Then, the variations in the size of specimens across the entire section were traced for each cluster. The variations appeared to fit a normal distribution, and there was no significant difference in the size of the juvenile stages in the phylogeny of *C.* (*C.*) *lateres*. Therefore, a general L/H ratio graph was made for all juveniles (Fig. 4).

Another feature that changes in ontogeny is the hinge. The evolution of its morphology from the earliest juvenile stages to the adult in *C.* (*C.*) *lateres* has been studied using SEM photos of the details (Fig. 5; Pl. 1: 1, 2).

Apparently the most variable species characteristic of ostracods is the mesosculpture. Its variations may reflect species variability, but variation also may be related to the environmental conditions. The evolution of the sculpture of *C.* (*C.*) *lateres* in ontogeny and phylogeny has been also studied using SEM photographs (Pl. 1: 3, 4; Pl. 3: 1–3). The sculpture consists of separate pits (sculptural type I), or pits grouped into rows (sculptural type II), or rosettes (sculptural type III). The occurrence of the various sculptural types and the degree of their predominance was recorded for each studied specimen (both adult and juvenile). The predominance of any one sculpture type was determined by measuring the total area of the pits of each type. It was calculated in the ImageJ program for the most typical specimens (Tab. 2a, b, c; Pl. 3).

Thus, change of three different features – dimensions, hinge and sculpture was traced in the ontogeny and phylogeny of *C.* (*C.*) *lateres*.

Table 1

The morphometric indices of adult and juvenile specimens *Camptocythere* (*C.*) *lateres* Tes. et Shur. sp. nov.

	Male (27 spec.)	Female (40 spec.)	Juvenile (67 spec.)
Length (L) [mm]	0.48–0.65	0.45–0.60	0.25–0.55
Height (H) [mm]	0.28–0.35	0.25–0.40	0.15–0.35
Ratio L/H	1.57–2.06	1.47–1.92	0.33–1.96
Ratio L/H (mean value)	1.78	1.63	1.60

RESULTS

The dimensions. In the material of *Camptocythere (C.) lateres* species the last 7 stages of growth (the first and the second are absent) are represented. A cluster of adult specimens stands out well (Fig. 4). The small spread in sizes observed in Fig. 4 fits into the normal Gauss-Laplace distribution and is not associated with speciation. Separate small or large representatives of the species were encountered in association with medium-sized specimens both in the lower and upper parts of the section. This is in good agreement with the data of juveniles, where no heterochrony was recognized.

Thus, all studied specimens of *Camptocythere* belong to the same species, and all the evolutionary changes in sculpture described below (heterochrony) are part of the microevolution, *i. e.* evolution within one species.

The hinge is of hemimerodont type, represented by a smooth middle groove in the right valve of the mature individual, which is dipping at both ends, and also by margin elements, composing of 4 (anterior) and 5 (posterior) tiny rounded teeth, the size of which is diminished at the margin (Fig. 5; Pl. 1: 1). In the ontogeny of *C. (C.) lateres*, the marginal elements are modified (Fig. 5; Pl. 1: 2). The 3th juvenile stage has a bar-like tooth, this element becomes subdi-

Table 2

The detailed measurement of the areas of various sculptural types (I–III) in the ImageJ program for three specimens of *Camptocythere* (*C.*) *lateres* Tes., Shur., sp. nov., representative of the particular intervals of the succession studied (A1, A2, and A3 in Fig. 3); adult females

a

Sculptural type	Total area [μm]	%
I	6465.5	50.5
II	364.5	2.8
III	6035.6	46.7

No.	Sculptural type	Area [μm]
1	III	563.608
2	III	447.842
3	III	1004.156
4	III	857.274
5	III	401.329
6	III	263.278
7	III	366.121
8	III	793.068
9	III	657.718
10	III	307.122
11	III	374.046
12–14	II	364.488
15	I	228.021
16	I	194.382
17	I	308.821
18	I	237.838
19	I	310.713
20	I	285.532
21	I	323.134
22	I	799.877
23	I	445.902
24	I	104.460
25	I	330.557
26	I	178.500
27	I	188.058
28	I	284.416
29	I	302.707
30	I	253.623
31	I	188.252
32	I	120.472
33	I	466.506
34	I	394.747
35	I	131.404
36	I	120.617
37	I	146.332
38	I	120.601
Total		**12865.522**

b

Sculptural type	Total area [μm]	%
I	2593.9	19.0
II	8302.6	62.0
III	2558.2	19.0

No.	Sculptural type	Area [μm]
1	II	816.231
2	II	275.459
3	II	929.317
4	II	493.349
5	II	502.096
6	II	593.880
7	II	427.007
8	II	406.318
9	II	403.043
10	II	503.254
11	II	421.655
12	II	250.469
13	II	313.416
14	II	538.509
15	II	542.370
16	I	166.926
17	I	230.964
18	I	169.482
19	I	197.467
20	I	155.37
21	I	113.645
22	I	43.030
23	I	218.876
24	I	232.416
25	I	119.756
26	I	178.056
27	I	159.577
28	I	101.104
29	I	107.361
30	I	116.574
31	I	56.343
32	I	226.997
33	III	215.441
34	III	405.879
35	III	398.490
36	III	282.581
37	III	446.046
38	III	322.962
39	III	486.799
40	II	310.473
41	II	253.265
42	II	322.522
Total		**13454.775**

c

Sculptural type	Total area [μm]	%
I	1742.0	17.0
II	2601.0	25.0
III	5952.5	58.0

No.	Sculptural type	Area [μm]
1	III	683.484
2	III	539.646
3	III	436.861
4	III	717.223
5	III	332.831
6	III	164.452
7	III	310.433
8	III	545.846
9	III	340.427
10	III	388.514
11	III	517.085
12	III	416.626
13	III	185.649
14	III	373.452
15	II	750.453
16	II	245.152
17	II	264.402
18	II	189.198
19	II	737.501
20	II	238.497
21	II	175.835
22	I	171.182
23	I	206.869
24	I	229.981
25	I	323.883
26	I	129.296
27	I	226.800
28	I	95.265
29	I	43.001
30	I	206.782
31	I	109.050
Total		**10295.676**

RV: a – spec. No. S-57, dp. 50.3 m; b – spec. No. S-68, dp. 44.6 m; c – spec. No. Sokur-Ya-012, dp. 37.4 m

vided into rows of separate small teeth when the mature individual reaches the 8th growth stage. The ontogenesis of this attribute is stable during the entire Michalskii ammonite Zone.

The results of the ontogenetic analysis of the ***sculpture*** appear to be much more promising. This species has a moderately convex carapace, with flat lateral sides; the surface of the wing slopes steeply (almost at right angles) to the anterior margin and more gently to the posterior (Pl. 2: 1–3). Both edges along the contour are flattened. The sculpture itself is represented by pits of variable size and shape, merging together on the flattened area of the lateral sides. On the sloping parts of the valve, pits are always separated (sculpture type I) (Pl. 1: 3). The sculpture varies in the arrangement of lateral pits, these being in irregular rows (type II) (Pl. 1: 3) and rosette (type III) (Pl. 1: 3). Between the pits the surface is convex, robust.

In the ontogeny of *C. (C.) lateres*, the development of the sculpture follows from type I to type III (Pl. 1: 4a–g). This is expressed by a change in the predominant type in different ontogenetic stages. The same trend is distinguished in the phylogeny of this species during the Michalskii and Besnosovi ammonite Zones.

Juveniles of 2(?) – 4 stages have sculptural types I + II on the flat parts of the valve throughout the section. Sculptural types I + II + III are observed on the flat parts of the shells of juveniles of 5–8 stages in equal proportions throughout the section. The predominance of any of them could not be detected at selected intervals. All three sculptural types are also recognized on adult specimens. But the percentages of their areas vary in different parts of the section studied (Fig. 3). In the lower part – interval A1 (50.7–50.3 m) – specimens with dominance of sculptural type I prevail (type I – 50,5%, type II – 2,8%, type III – 46,7 %) (Tab. 2a; Pl. 3: 1); in the interval A2 (47.6–42.3 m) – specimens with a predominance of sculptural type II occur (type I – 19%, type II – 62%, type III – 19%.) (Tab. 2b; Pl. 3: 2); in the interval A3 (38.8–12.5 m) – specimens with the predominant sculptural type III occur (type I – 17%, type II – 25%, type III – 58 %) (Tab. 2c; Pl. 3: 3); their number increases gradually up the section.

SYSTEMATIC PALAEONTOLOGY

The systematics of suprageneric taxa is adopted from that in the Prakticheskoe rukovodstvo po mikrofaune (Practical Handbook on the Microfauna) (Andreev *et al.*, 1999).

Order Podocopida Sars, 1865

Superfamily Progonocytheracea Sylvester-Bradley, 1948

Family Progonocytheridae Sylvester-Bradley, 1948

Subfamily Progonocytherinae Sylvester-Bradley, 1948

Genus *Camptocythere* Triebel, 1950

Subgenus *Camptocythere* Triebel, 1950

Camptocythere (*Camptocythere*) *lateres*
Tesakova et Shurupova, sp. nov.
Pl. 1: 1–4; Pl. 2: 1–9; Pl. 3: 1–3; Tab. 3

2016. *Camptocythere sp.*: Shurupova *et al*., pl. 1, fig. 1.

Etymology. – The name is given because the carapace is shaped similar to a brick, *lateres* (*Latin*.) – brick.

Holotype. – Pl. 2: 4; MSU Sokur-Ya-049, right valve of a female, the NW outskirts of Saratov, borehole in Sokur quarry, depth 42.3 m, Upper Bajocian, Michalskii ammonite Zone, Lenticulina volganica – Vaginulina dainae foraminifera Zone, Palaeocytheridea kalandadzei ostracod Zone.

Description. – Carapace of median size, rounded rectangular outline on the side, moderately convex, with parallel lateral sides and flattened anterior and posterior ends. The left valve slightly overlaps the right valve at the anterodorsal and anteroventral corners, the right valve overlaps the left on the dorsal end. The maximum length is in the middle of the height or slightly above it. The valves, except for the ends, all along their length have almost the same height; on the females valve anterior ends are insignificantly higher; on the male valve both ends are of equal height or posterior is higher. Respectively, the maximum height of female valve is located in its anterior third, of male valve – in posterior. The maximum thickness is in the posteroventral part and better visible on the valves of males and juveniles, the thickness of the valve of adult females is almost the same throughout. The dorsal margin is straight, slightly convergent towards the posterior end in females and strictly horizontal in males; in the anterior and posterior ends of the dorsal margin the carapace terminates smoothly on the right valve, with the formation of rounded obtuse angles on the left. The ventral margin is straight, concave near the middle, but closer to anterior end; the anterior and posterior ends of the ventral margin terminate smoothly on both valves. The anterior end is high, roundly arcuate, somewhat oblique on the top, a feature more noticeable on the right valve, and flattened along the edge. The posterior end is below the anterior in the females and higher in the males; roundly triangular; evenly rounded in the lower part and beveled at the top, and while on the left valve this skewed part is slightly convex, but on the right it is distinctly concave; along the margin it is flattened. The eye tubercle and muscle scar on the surface of the valve are absent. The pores are rare, simple.

The hinge, as in the genus, is tripartite. On the right valve are present narrow elongated marginal teeth, between which is a long smooth groove. The anterior tooth is dissected into 4 rounded parts, their size is decreasing towards the anterior margin; the posterior tooth is dissected into 5 similar parts, also is decreasing to the posterior margin. The groove has slits in the places of contact with both teeth. The adductor scar is represented by an uneven vertical row of four elongated spots; two lower spots are oval, two top – are oval-triangular, and their position is somewhat higher of the general range. The mandibular scar, which is located in front of the adductor, has a rounded shape. The pore-canal zone is wide, well developed at both ends. Often a narrow selvage is preserved along the margin.

The surface of the valve, except the flattened and smooth part of both ends, is covered with numerous round pits, often combined into subvertical series or groups of 2–3 (pit-groups). The size of the pits is approximately the same on the entire surface and decreases only along the periphery. The walls of the pits merge and form a network of low, smoothed, weakly expressed ribs. The most clearly defined is the oblique rib, it extends from the middle of the dorsal margin to the middle of the anterior end. In the area of the anterodorsal corner, above the visual organ, the surface of the valve is smooth.

Variability. – The species has a stable set of characteristics: variability is expressed in minor variations in the size (Tab. 3) and number of pits, and their configuration. The strength of the ribs (reticulum) directly depends on the number of merged pits. Specimens also occur which have a cellular sculpture (not pitted, as in the majority).

Sexual dimorphism is expressed in differences in the shape and size of the carapace of females and males. The carapace of females is shorter, and the anterior end is higher than the posterior end.

The age variability is manifested in a decrease in the size of the carapace. In addition, the younger the age stage, the more the shape of the carapace approaches triangular, but the less the pits are developed on the surface, and the weaker the ribs are expressed (until they are completely absent).

Comparison. – Comparison with the closest species *C. (C.) angustius* Tesakova et Shurupova, sp. nov. from the Upper Bajocian of the same section is given at the description of the latter.

The new species *C. (C.) lateres* shows a form of the carapace (with parallel lateral sides) and a pit-shaped sculpture similar to those of the species group *Camptocythere* such as (*C.*) *foveolata foveolata* Triebel, 1950 (Triebel, 1950, p. 202, pl. 2, fig. 16–21; Plumhoff, 1963, p. 43, pl. 9, fig. 132–137), *C.* (*C.*) *foveolata prima* Plumhoff, 1963 (Plumhoff, 1963, p. 44, pl. 9, fig. 138–140), *C.* (*C.*) *foveolata brevis* Plumhoff, 1963 (Plumhoff, 1963, p. 44, pl. 9, fig. 141–143) and the species *Camptocythere* (*C.*) *obtusa* Triebel, 1950 (Triebel, 1950, p. 204, pl. 3, fig. 22–24; Plumhoff, 1963, p. 45, pl. 9, fig. 144–147) from the Upper Aalenian of Northern Germany; the new ostracod species differs however in having a lower anterior end, significantly smaller coverage of the right valve by the dorsal margin, and lack of coverage of the left valve along the ventral margin. Moreover, *C. (C.) lateres* differs from *C. (C.) foveolata*, from the Lower Aalenian of Western Siberia (Nikitenko, 2009, plate O-2, fig. 5) in its larger pits and smaller carapace thickness, and from *C. (C.) obtusa* in having much larger pits and the presence of ribbing.

The representatives of the subgenus *Camptocythere* which are widely distributed in the Middle Jurassic sediments of the north of Siberia and the Timan-Pechora region, are less similar to the newly described species than the North German forms, because of their uniformly convex carapace, with nonparallel lateral sides. Apparently, the closest species, with a similar well-developed pitted sculpture, is *C.* (*C.*) *scrobiculataformis* Nikitenko, 1994 from the Lower Bathonian of the north of Siberia and the Timan-Pechora region (Nikitenko, 1994. p. 51, plate 1, fig. 16–19; Nikitenko, 2009, plate O-4, fig. 11–15). The species *C.* (*C.*) *lateres* shows, however, a different arrangement of pits, with a smaller number and a tendency to the formation of pit-groups (2–3), as well as having parallel sides to the carapace.

Occurrence. Upper Bajocian (the Michalskii ammonite Zone, Lenticulina volganica – Vaginulina dainae foraminifera Zone, Palaeocytheridea kalandadzei ostracod Zone) and Lower Bathonian (Besnosovi ammonite Zone, Trochammina aff. praescuamata foraminifera Zone, Camptocythere arangastachiensis ostracod Zone) from Saratov and Penza region, Russia.

Material. – More than two hundred single valves and whole carapaces, both adults and juveniles, good and beautifully preserved from the Upper Bajocian (Michalskii ammonite Zone, Lenticulina volganica – Vaginulina dainae foraminifera Zone, Palaeocytheridea kalandadzei ostracod

Table 3

***Camptocythere (Camptocythere) lateres*: size of selected specimens**

Spec. No.	Length (mm)	Height (mm)
Holotype MSU Sokur-Ya-049	0.40	0.25
MSU Sokur-Ya-048	0.43	0.23
MSU S-22	0.48	0.29
MSU S-51	0.41	0.25
MSU S-28	0.41	0.21
MSU S-82	0.31	0.20

Zone) and Lower Bathonian (Besnosovi ammonite Zone, Trochammina aff. praescuamata foraminifera Zone, Camptocythere (Anabarocythere) arangastachiensis ostracod Zone) from Saratov and Penza region

Camptocythere (*Camptocythere*) *angustius*
Tesakova et Shurupova, sp. nov.
Pl. 2: 10–15; Tab. 4

The name is given because of the characteristic form of the posterior end of the carapace, *angustius (Latin*.) – narrower.

Holotype. – Pl. 2: 14; MSU Sokur-Ya-193, left valve of a female, the NW outskirts of Saratov, borehole in Sokur quarry, depth 18.3 m, Upper Bajocian, Michalskii ammonite Zone, Lenticulina volganica – Vaginulina dainae foraminifera Zone, Palaeocytheridea kalandadzei ostracod Zone.

Description. – Carapace of median size, elongated, somewhat irregularly quadrangular in outline from the side, moderately convex, with parallel lateral sides and with a narrow flattened part along the anterior and posterior ends. The left valve slightly overlaps the right valve at the anterodorsal and anteroventral corners, the right valve is low overlapping the left at the dorsal end. The maximum length is in the middle of the height; the maximum height in the anterior third; the maximum thickness in the posterolateral part of the valve. The dorsal margin is straight, distinctly convergent towards the posterior end, a feature which is more noticeable on the right valve; towards the anterior end of the dorsal margin the carapace continues smoothly on the left valves, but on the right valves there is a pronounced inflection; the posterior end matches smoothly on the right valve but there is the formation of a small ledge on the left. The ventral margin is straight, concave nearly in the middle; the anterior and posterior ends terminate smoothly on both valves. The anterior end of the ventral margin is high, roundly arcuate, somewhat oblique on the top, a feature more noticeable on the right valve; it is narrowly flattened along the edge. The posterior end is below the anterior; triangular in outline, almost symmetrical, and very slightly sloping at the top; along the edge it is narrowly flattened. The eye tubercle and muscle scar on the surface of the valve are absent. The pores are rare, simple.

The hinge of the right valve is represented by narrow elongated incised marginal teeth, between which is a long smooth groove. The anterior tooth is dissected into 4 rounded parts, their size is decreasing towards the anterior margin; the posterior tooth is dissected into 5 similar parts, also is decreasing towards the posterior margin. The groove has slits in the places of contact with both teeth. The muscle scar is as in the genus. The pore-canal zone is wide, well developed at both ends. A narrow selvage occurs along the margins.

The surface of the valve is covered with rounded pits, the size of which decreases from the center to the periphery; the peripheral part of the carapace - at the anterior and posterior ends and along the dorsal margin – smooth. In the central part of the valve the pits can be grouped into a few in each set. The walls of the pits, merging, form a lumpy robust sculpture, among which a slightly developed diagonal rib is projected from the middle of the dorsal to the middle of the anterior margin.

Variability. – Slightly expressed in variations in the size (Tab. 4) and number of pits, as well as in the degree of robustness of the sculpture and the distinctness of the diagonal rib.

Comparison. – The shape of the carapace and sculpture is most similar to that of *C.* (*C.*) *lateres* sp. nov., from which the species described differs in its somewhat irregularly quadrangular carapace, in contrast to the round-rectangular carapace of the former species; moreover *C.* (*C.*) *angustius* has a lower, triangular, symmetrically cut from above and below the posterior end; and in the sculpture: the pits of *C. (C.) angustius* are more rare and rapidly diminish in size from the center to the periphery, the ribbing formed by the merged walls of the pits, characteristic of *C.* (*C.*) *lateres*, is practically not seen in the species described.

The new species is similar in shape of carapace with parallel lateral sides, and a triangular posterior end, as well as in pit sculpture to the North German species of the Upper Aalenian, such as *Camptocythere* (*C.*) *foveolata prima* Plumhoff, 1963 (Plumhoff, 1963, p. 44, pl. 9, fig. 138–140) and *C.* (*C.*) *obtusa* Triebel, 1950 (Triebel, 1950, p. 204, pl. 3, fig. 22–24; Plumhoff, 1963, p. 45, pl. 9, fig. 144–147). It differs however in its lower and elongated posterior end, lack of strong coverage of the right valve along the dorsal margin, larger ratio of length to height; and, in additionally, it is distinguished from the species *C. (C.) obtusa* in its even greater number and size of pits. From *C.* (*C.*) *foveolata foveolata* Triebel, 1950 of the Upper Aalenian of Northern Germany (Triebel, 1950, p. 202, pl. 2, fig. 16–21; Plumhoff, 1963, p. 43, pl. 9, fig. 132–137) and the Lower Aalenian of Western Siberia (Nikitenko, 2009, plate O-2, fig. 5), and *C.* (*C.*) *foveolata brevis* Plumhoff, 1963 of the Upper Aalenian of Northern Germany (Plumhoff, 1963, p. 44, pl. 9, fig. 141–

Table 4
***Camptocythere (Camptocythere) angustius*: size of selected specimens**

Spec. No.	Length (mm)	Height (mm)
Holotype MSU Sokur-Ya-193	0.42	0.24
MSU Sokur-Ya-190	0.39	0.23
MSU Sokur-Ya-191	0.42	0.24
MSU Sokur-Ya-192	0.38	0.22

143), except for the features in common, characteristic of the whole *C. (C.) foveolata* group, the newly described species differs in having a triangular shape to the posterior end of the carapace.

Occurrence. – The Upper Bajocian (the Michalskii ammonite Zone, Lenticulina volganica – Vaginulina dainae foraminifera Zone, Palaeocytheridea kalandadzei ostracod Zone) from Saratov region.

Material. – Four valves of good preservation from the Upper Bajocian (the Michalskii ammonite Zone, Lenticulina volganica – Vaginulina dainae foraminifera Zone, Palaeocytheridea kalandadzei ostracod Zone) from Saratov Region, borehole in the Sokur section.

CONCLUSION

Two new species of ostracod of the family Progonocytheridae Sylvester-Bradley *Camptocythere (C.) lateres* Tesakova et Shurupova, sp. nov. and *C. (C.) angustius* Tesakova et Shurupova, sp. nov. from the Michalskii and Besnosovi ammonite zones (Upper Bajocian – Lower Bathonian, Middle Jurassic) of the Sokur section (Saratov) are described.

Detailed subdivision of the ostracod scale for the Upper Bajocian (Michalskii Zone) in the Sokur section (Saratov) became possible using the palaeobiogenetic approach. The successive levels of evolutionary changes in the type of sculpture identified in the phylogeny of the species *Camptocythere* (*C.*) *lateres* Tes., Shur., sp. nov. allowed the subdivision of the beds with *C. (C.) lateres* into 3 intervals: interval A1 (50.7–50.3 m) – specimens with dominance of sculptural type I prevail; A2 (47.6–42.3 m) – specimens with a predominance of sculptural type II occur; A3 (38.8–12.5 m) – specimens with the predominant sculptural type III occur.

Acknowledgements. The authors are grateful to Ivan Kuzmin (Moscow), Maria Karpuk (Moscow) for their help with English translation of this paper, Dmitriy Mamontov for their help with ImageJ program. Authors are also thankful to Ewa Olempska, Andrzej Wierzbowski and anonymous reviewer for constructive discussion of the results of the article. The research was carried out within the framework of the state task 0135-2014-0070 (GIN RAS) and AAAA-A16-116033010096-8 (MSU), with partial financial support of the Russian Foundation for Basic Research No. 15-05-03149.

REFERENCES

ANDREEV J.N., KOLPENSKAYA N.N., KUPRIYANOVA N.V., KUCHTINOV D.A., LYUBIMOVA P.S., NEUSTRUEVA I.Y., NIKOLAEVA I.A., SINICA S.M., SKOBLO V.M., STAROZHILOVA N.N., EVDOKIMOVA I.O., 1999 – Prakticheskoe rukovodstvo po microfaune,7. Ostrakody mezozoya. VSEGEI, Sankt-Peterburg, 244 pp. (in Russian).

ALBERCH P., 1982 – Developmental constraints in evolutionary processes. *In*: Evolution and Development, Dahlem Konferenzen (ed. J.T. Bonner), Springer-Verlag, Berlin: 313–332.

ARTHUR W., 2000 – The concept of developmental reprogramming and the quest for an inclusive theory of evolutionary development. *Evolution and Development*, **2**: 49–57.

DYKAN N.I., 2016 – Neogene-quaternary ostracodes of the northern part of the Black Sea. Publishing House "Chetverta Hvylja", Kyiv, 272 pp. (in Russian).

FINK W.L., 1982 – The conceptual relationship between ontogeny and phylogeny. *Paleobiology*, **8**: 254–264.

GERBER S., 2011 – Comparing the differential filling of morphospace and morphometric space through time: the morphological and developmental dynamics of Early Jurassic ammonoids. *Paleobiology*, **37**: 369–82.

GERBER S., EBLE G.J., NEIGE P., 2008 – Allometric space and allometric disparity: a developmental perspective in the macroevolutionary analysis of morphological disparity. *Evolution*, **62**: 1450–1457.

GLINSKIKH L.A., KOSTYLEVA V.A., 2013 – The micropalaeontological and sedimentological evidence of the boreal transgression in the Bajocian-Bathonian of the vicinity of Saratov. *In:* Jurassic system of Russia: problems of stratigraphy and paleogeography (ed. V. A. Zakharov). The Fifth All-Russian Conference. Scientific materials: 44–46, Ekaterinburg (in Russian).

GOULD S.J., 1977 – Ontogeny and Phylogeny. Harvard University Press, Cambridge, Mass. and London.

GOULD S.J., 1982 – Change in developmental timing as a mechanism of macroevolution. *In*: Evolution and Development, Dahlem Konferenzen (ed. J.T. Bonner), Springer-Verlag, Berlin: 333–346.

GOULD S.J., 2000 – Of coiled oysters and big brains: how to rescue the terminology of heterochrony, now gone astray. *Evolution and Development*, **2**: 241–248.

GOULD S.J., OSTER G.F., WAKE D.B., 1979 – Size and shape in ontogeny and phylogeny. *Paleobiology*, **5**: 296–317.

GULYAEV D.B., 2018 – The ammonites and stratigraphy of the Upper Bajocian – Lower Bathonian of the Central and South parts of the East European Platform. *Stratigraphy. Geological correlation* [in press] (in Russian).

LIVENTAL V.E., 1949 – Palaeobiogenetic method of stratigraphic subdivision of strata. *Doklady AN SSSR*, **64,** 1: 111–112 [in Russian].

McNAMARA K.J., 1997 – Shapes of time: the evolution of growth and development. Johns Hopkins University Press, Baltimore.

McNAMARA K.J., 2012 – Heterochrony: the Evolution of Development. *Evolution: Education and Outreach*, **5**: 420.

McNAMARA K.J., YU F., ZHOU Z., 2006 – Ontogeny and heterochrony in the oryctocephalid trilobites *Changaspis, Duyunaspis* and *Balangia* from the Lower Cambrian of China. *Palaeontology*, **48**: 1–19.

MITTA V.V., BARSKOV I.S., GRÜNDEL J., ZAKHAROV V.A., SELTZER V.B., IVANOV A.V., ROSTOVTSEVA J.A., TARASOVA L.O., 2004 – The Upper Bajocian and Lower Bathonian

in the section near Saratov. *Vernadsky Museum-Novitates*, **12**: 39 pp. (in Russian).

MITTA V., KOSTYLEVA V., DZYUBA O., GLINSKIKH L., SHURYGIN B., SELTZER V., IVANOV A., URMAN O., 2014 – Biostratigrahy and sedimentary setting of the Upper Bajocian – Lower Bathonian in the vicinity of Saratov (Central Russia). *Neues Jahrbuch für Geologie und Paläontologie. Abh.*, **271**, 1: 95–121.

NIKITENKO B.L., 1992 – Zonal scale of Lower and Middle Jurassic in the north of Siberia by foraminifera. *Geology and Geophysics*, **1**: 3–14 (in Russian).

NIKITENKO B.L., 1994 – Early and Middle Jurassic ostracods of the north of Siberia: the basic laws of evolution and the zonal scale. *Stratigraphy. Geological correlation*, **2,** 4: 38–55 (in Russian).

NIKITENKO B.L., 2009 – Jurassic Stratigraphy, Palaeogeography and Biofacies of Siberia on Microfauna (Foraminifers and Ostracodes). Publishing House "Parallel", Novosibirsk, 680 pp. [in Russian].

OLEMPSKA E., 1989 – Gradual evolutionary transformations of ontogeny in an Ordovician ostracod. *Lethaia*, **22**: 159–168.

PLUMHOFF F., 1963 – Ostracoden des Oberaalenium und tiefen Unterbajocium (Jura) des Gifhorner Troges, Nordwestdeutschland. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **503**: 100.

SHURUPOVA Y.A., TESAKOVA E.M., KOLPENSKAYA N.N., SELTZER V.B., IVANOV A.V., 2016 – Saratov Volga region in the Late Bajocian (Middle Jurassic). Paleogeography reconstructed by the ostracods. *Life of the Earth*, **38**, 1: 22–37 (in Russian).

SHURYGIN B.N., 2005 – Biogeography, facies and stratigraphy of Lower and Middle Jurassic of Siberia on bivalves. Publishing House of SB RAS, Department "Geo", Novosibirsk, 154 pp. (in Russian).

TESAKOVA E.M., 2014 – Jurassic ostracods of the Russian Plate: stratigraphy, paleoecology and paleogeography. Dissertation Doct. Geol.-min. Science, Moscow [in Russian]. Gorky Scientific Library of the Lomonosov Moscow State University at the Geological Faculty [unpubl.].

TESAKOVA E.M., 2015 – Correlation of the Middle-Late Jurassic ostracod Scales of Western and Eastern Europe. *In:* Materials of the Sixth All-Russian meeting "Jurassic System of Russia: Problems of stratigraphy and paleogeography", held in Makhachkala, September 15–20 2015 (eds. V.A. Zakharov *et al*): 268–272, Makhachkala (in Russian).

TRIEBEL E., 1950 – *Camptocythere*, eine neue Ostracoden-Gattung aus dem Dogger Norddeutschlands. *Senckenbergiana*, **31**: 197–208.

WEBSTER M., ZELDITCH M.L., 2005 – Evolutionary modifications of ontogeny: heterochrony and beyond. *Paleobiology*, **31**: 354– 372.

ZELDITCH M.L., SHEETS H.D., FINK W.L., 2003. – The ontogenetic dynamics of shape disparity. *Paleobiology,* **29**: 139–156.

PLATE 1

All ostracods shown belong to the species *Camptocythere* (*C.*) *lateres* Tesakova, Shurupova, sp. nov. from Upper Bajocian (Michalskii Zone) of Sokur section (Saratov, Russia)

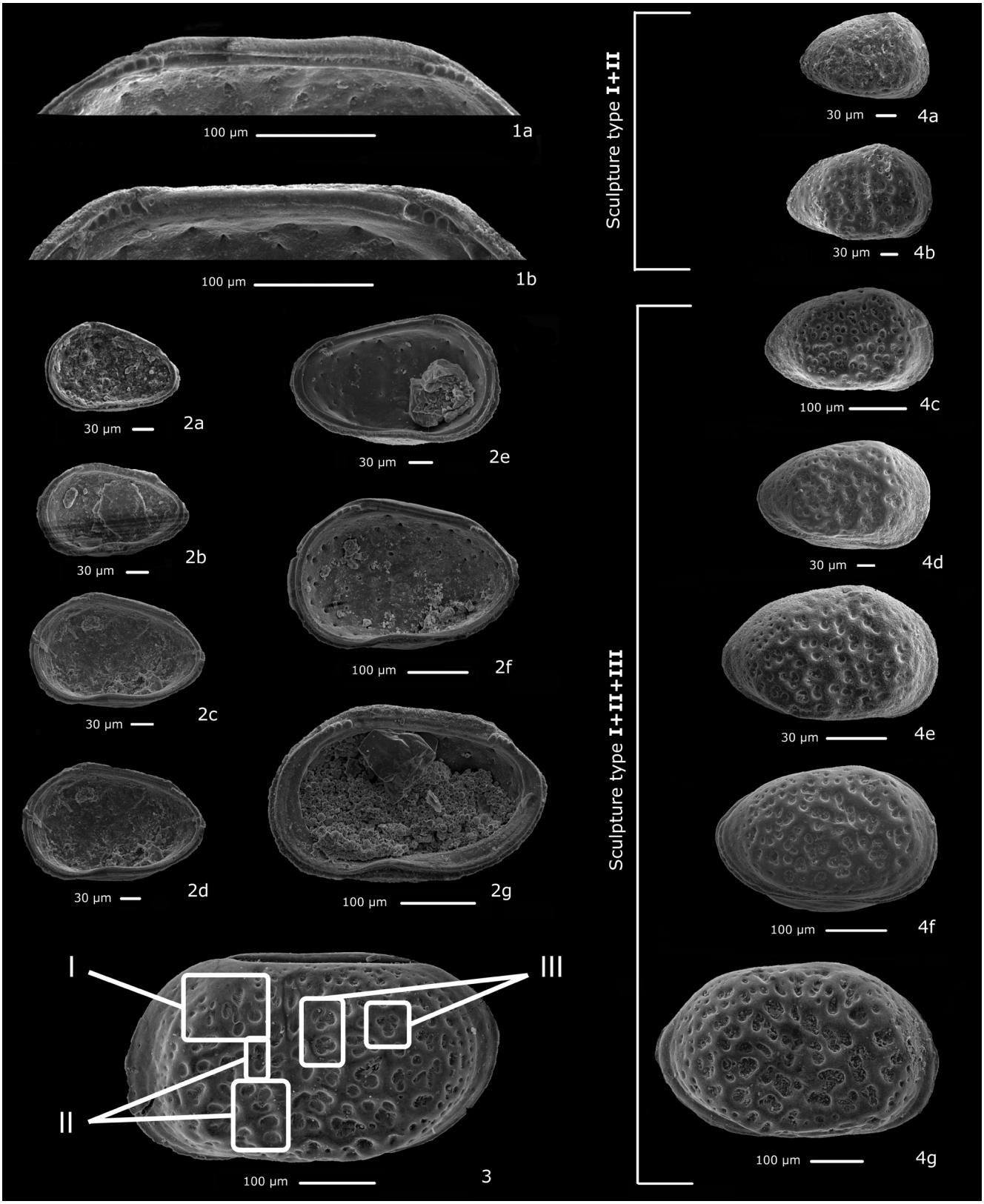
Fig. 1. The hinge (inside): a – spec. MSU Sokur-48, RV ad. male, dp. 42.3 m; b – spec. MSU S-64, LV ad. male, dp. 37.0 m

Fig. 2. Ontogeny of the hinge (inside): a – spec. MSU S-21, RV juv. 3, dp. 26.0 m; b – spec. MSU S-87, RV juv. 4, dp. 33.0 m; c – spec. MSU S-34, RV juv. 5, dp. 29.4 m; d – spec. MSU S-34, RV juv. 6, dp. 29.4 m; e – spec. MSU Sokur-64, LV juv. 7, dp. 33.6 m; f – spec. MSU Sokur-Ya-229, RV juv. 8, dp. 27.8 m; g – spec. MSU S-62, RV ad. female, dp. 37.0 m

Fig. 3. Sculptural types (I, II, III – see text); spec. MSU Sokur-13, C from the left ad. male, dp. 47.6 m

Fig. 4. Ontogeny of the sculpture: a – spec. MSU S-21, RV juv. 3, dp. 26.0 m; b – spec. MSU S-14, RV juv. 4, dp. 42.9 m; c – spec. MSU S-45, RV juv. 5, dp. 42.3 m; d – spec. MSU S-2, C from the right, juv. 6, dp. 29.0 m; e – spec. MSU S-15, RV juv. 7, dp. 42.9 m; f – spec. MSU S-47, C from the right, juv. 8, dp. 31.5 m; g – spec. MSU Sokur-15, RV ad. female, dp. 47.6 m

Abbreviations: C – carapace, LV – left valve, RV – right valve, dp. – depth. Ontogeny stages: juv. 3–8; adult – ad.



Yana A. SHURUPOVA, Ekaterina M. TESAKOVA – Detailed biostratigraphic scales as based on the palaeobiogenetical approach (an example of the Upper Bajocian – Lower Bathonian ostracod scale of the Russian Platform)

PLATE 2

Fig. 1–9 *Camptocythere* (*C.*) *lateres* Tesakova et Shurupova, sp. nov.: 1 – spec. MSU Sokur-45, C dorsal view ad. female, dp. 38.8 m; 2 – spec. MSU Sokur-14, C dorsal view ad. male, dp. 47.6 m; 3 – spec. MSU Sokur-19, C dorsal view juv.6, dp. 47.6 m; 4 – Holotype MSU Sokur-Ya-049, RV ad. female, 42.3 m; 5 – spec. 345 MSU Sokur-Ya-048, RV ad. male, 42.3 m; 6 – spec. MSU S-22, C from the left ad. female, 29.0 m; 7 – spec. MSU S-51, C from the left ad. female, 31.5 m; 8 – spec. MSU S-28, C from the left ad. male, 36.0 m; 9 – spec. MSU S-82, RV juv. 7, 33.0 m

Fig. 10–15 *Camptocythere* (*C.*) *angustius* Tesakova et Shurupova, sp. nov.: 10 – spec. MSU-Sokur-Ya-190, RV juv., 18.3 m; 11 – spec. MSU Sokur-Ya-191, RV ad. female, 18.3 m; 12 – the same spec. inside; 13 – spec. MSU Sokur-Ya-192, LV juv., 18.3 m; 14 – Holotype MSU Sokur-Ya-193, LV ad. female, 18.3 m; 15 – the same spec. inside

Abbreviations: C – carapace, LV – left valve, RV – right valve, dp. – depth. Ontogeny stages: juv. 3–8; adult – ad.

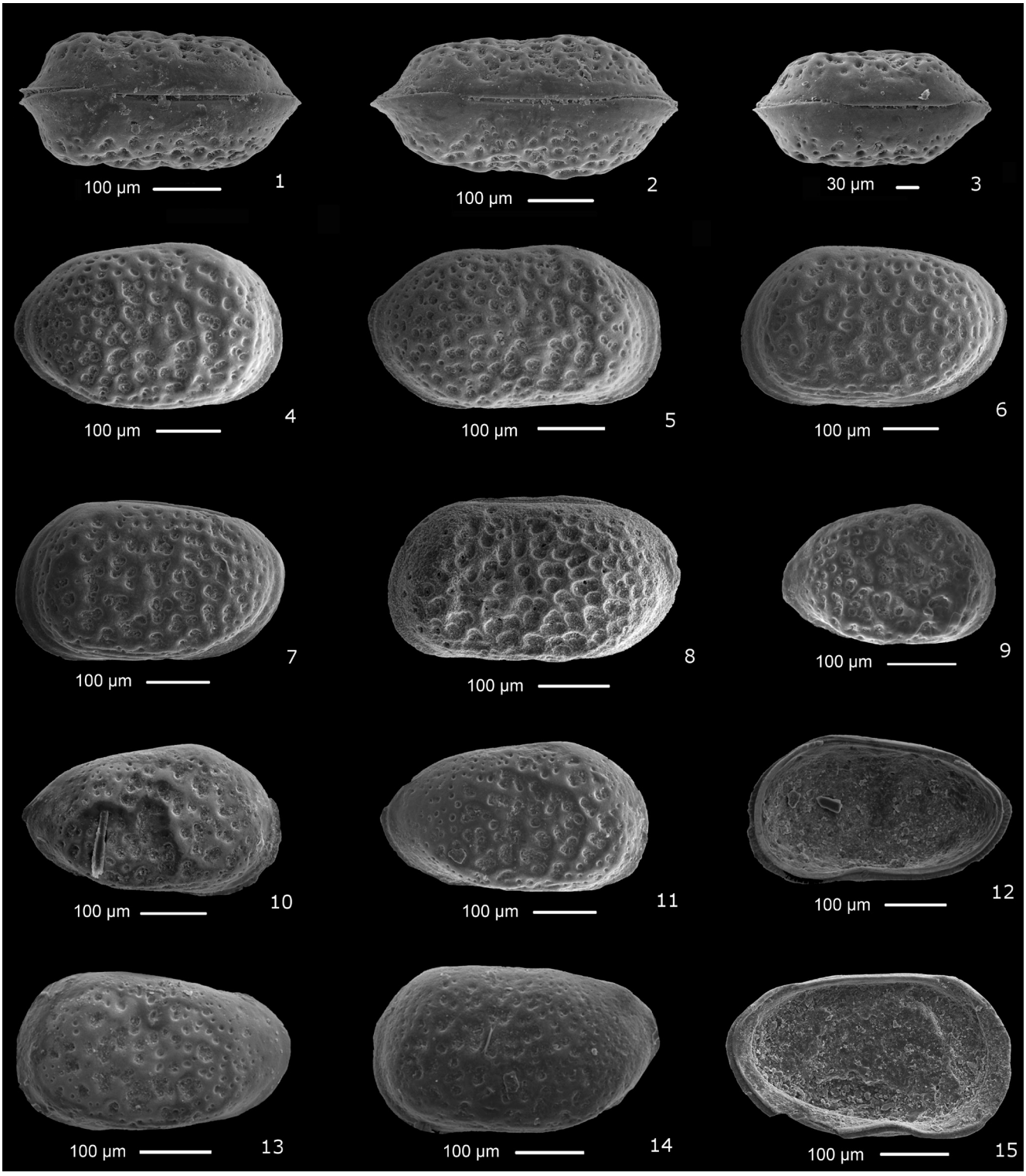
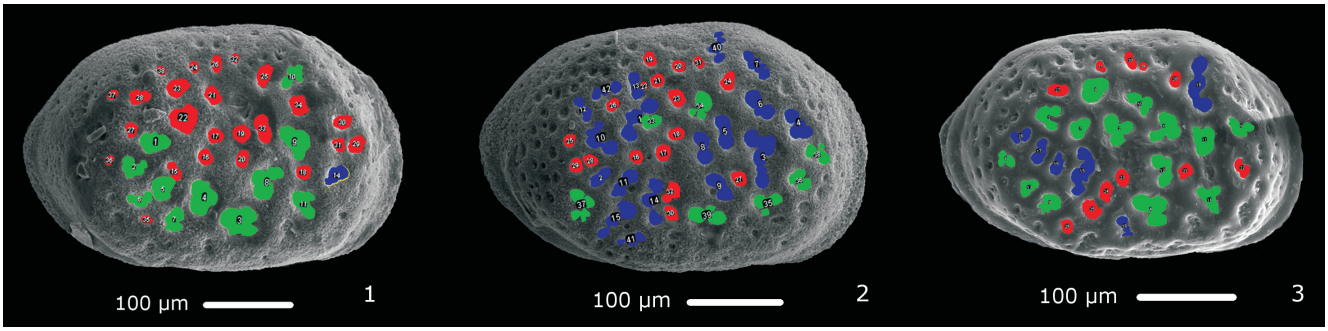

100 µm
1
100 µm
2
30 µm
3
100 µm
4
100 µm
5
100 µm
6
100 µm
7
100 µm
8
100 µm
9
100 µm
10
100 µm
11
100 µm
12
100 µm
13
100 µm
14
100 µm
15

PLATE 3

Fig. 1–3 *Camptocythere* (*C.*) *lateres* Tesakova, Shurupova, sp. nov., adult female, RV; Upper Bajocian (Michalskii Zone), Sokur section (Saratov, Russia): 1 – spec. MSU S-57, dp. 50.3 m (the dominant sculpture type I – red); 2 – spec. MSU S-68, dp. 44.6 m (the dominant sculpture type II – blue); 3 – spec. MSU Sokur-Ya-012, dp. 37.4 m (the dominant sculpture type III – green)

Abbreviations: C – carapace, LV – left valve, RV – right valve, dp. – depth. Ontogeny stages: juv. 3–8; adult – ad.


100 µm
1
100 µm
2
100 µm
3