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NEW DATA ON METHODS FOR PALAEOGEOGRAPHIC RECONSTRUCTIONS OF ANCIENT ENVIRONMENTS USING OSTRACODS (ARTHROPODA, CRUSTACEA)

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New data on methods for palaeogeographic reconstructions of ancient environments using ostracods (Arthropoda, Crustacea). Dykan, N. I. — The full cycle of taphonomic analysis of ostracods, including visual microscopic study of shell fossilisation, as well as statistical, population, ecological, and biostratigraphic analyses, is described. Graphical population analysis is applied to taphonomic studies for the first time and described in detail, allowing the type of ostracod burial to be determined with high accuracy. Diagnostic features of autochthonous and allochthonous (both synchronous and heterochthonous) burials are clarified and illustrated using SEM images. A modified quantitative method for estimating abiotic environmental parameters (water depth, temperature, and salinity), originally designed for fossil ostracods, is also presented.

Key words: Ostracoda, taphonomy, autochthonous, allochthonous, modification method, palaeogeographyc reconstruction.

Introduction

Palaeogeographic reconstruction of ancient environments is a complicated, multifaceted study that requires a comprehensive methodological approach. Current methods either require a specialised laboratory base or operate on a global scale (e. g. warm/cold). Therefore, an important aspect of the study was the refinement of existing methods and the development of new ones for fossil ostracods.

The study aims to test a modified quantitative method for determining the numerical parameters of the aquatic environment (e. g. water depth and temperature), which was initially developed for ostracods. To emphasise the importance of taphonomic analysis of ostracods for the accuracy of palaeogeographical conclusions, the study provides a description of the complete taphonomic analysis cycle of fossil shells, as well as SEM images of the morphological signs of ostracod shells in autochthonous and allochthonous (synchronous and heterochronous) burials.

Material

The factual material comprised the author's collection of fossil and recent ostracods from natural outcrops in continental bodies of water in Ukraine (rivers and lakes), which was collected between 1981 and 2022 (collection no. 2061 is housed at NMNH of NAS of Ukraine; collections no. 2567, 2589, 3000 is housed at the Department of Quaternary Geology, IGN of NAS of Ukraine, Kyiv).

Results

Taphonomic analysis is an important component of palaeogeographic research methods. While micropalaeontologists acknowledge the importance of taphonomic analysis for the accuracy of palaeogeographic and biostratigraphic conclusions, data on the taphonomy of fossil ostracods and their interpretation are scarce in scientific literature. Palaeogeographic and biostratigraphic conclusions are typically accompanied by a catalogue of all the fossil species present in the oryctocenosis, both autochthonous and allochthonous. Principles for the taphonomic analysis of ostracods have been in development since the 1960s. (Mandelstam & Schneider, 1963; Neustroeva, 1975; Karmishina, 1984; Shornikov & Mikhailova, 1990; Kaesler et al., 1993; Horne et al., 2002; Dykan, 2006, 2007, 2008 a, b, 2011, 2016; Dykan et al., 2009; Nogueira et al., 2023) (Tables 1, 2).

The microscopic size of the shells (from 0.2 mm in larvae to 3 mm in adults) does not allow to study all taphonomic signs necessary for the correct interpretation of the actual material in an outcrop (Fig. 1, *a*). Therefore, a complete taphonomic analysis is only possible after laboratory processing of the samples (Shornikov & Mikhailova, 1990; Dykan, 2008 a). The study of shells in their mass burial in rock is carried out in thin sections (Yanin, 1983). The complete cycle of ostracod taphonomic analysis consists of four stages (Dykan, 2008 a, b; Dykan, 2011).

The first stage: visual microscopic examination of the features of shell fossilisation and the degree of shell preservation, their preliminary division into autochthonous (lifetime) and allochthonous (transferred) remains, as well as allochthonous remains into synchronous and heterochronous. The signs of autochthonous (lifetime) burial of ostracods are good preservation of a shell, absence of traces of rounding. There are two types of allochthonous burial: synchronous and heterochronous. Allochthonous shells of the synchronous burial have insignificant lateral transport (within close biotopes) and are determined by mixed signs of autochthonous and allochthonous of fossil ostracods. Signs of autochthonousness in shells of synchronous burial include good preservation of shells, the presence of thin-walled and finely sculptured shells, and the absence of traces of shell rounding. Heterochronous remains have a different geological age than autochthonous remains and are identified by clear signs of prolonged transfer across the area and repeated reburial. Typical signs of the heterochronous burial are poor preservation of the shell, such as

Table 1. **Study of taphonomic signs of fossil ostracods (Mandelstam, Schneider, 1963; Neustroeva, 1975; Karmishina, 1984; Shornikov, Mikhailova, 1990)**

Autochthonous type of burial			
Biotope	Features of the composition of palaeocommunities	Morphological features of shells	Distribution of shells in the rock
Relatively deep-water	Bitaxon and polytaxon communities of marine and brackish water species	Small; thin-walled, thinly sculptured; white, rarely black, often filled with pyrite	Evenly or unevenly scattered
Shallow water	Polytaxon communities of euryhaline marine and brackish water species	Large; smooth and sculptured; white, brown; sometimes covered with carbonate crust, filled with limonite, rarely pyrite	Evenly or unevenly scattered; concentrated on the planes of the layering
Upper sublittoral zone with periodic intensification of wave movements	Not studied	Individual valves are well preserved	A layer of valves oriented convex upwards lies between the layers
Coastal	Monotaxon and bitaxon communities of mostly brackish-water, rarely euryhaline marine species	Thick-walled, sometimes rounded; white, brown	Evenly or unevenly scattered; concentrated on the planes of the layering
Shallow water zone with constantly high hydrodynamics	Not studied	"Valve in a valve"; thick-walled shells and fragments, sometimes with holes on the surface; white, brown	Not studied
Delta	Monotaxon, bitaxon, and rarely polytaxon communities of brackish water, euryhaline marine and freshwater species	Thin-walled (in calm areas of the delta) and thick-walled; white, brown	Lens-shaped
Allochthonous type of burial	Synchronous subtype		Heterochronous subtype
Morphological signs of shells	Shell with round, oval-irregular holes 0.1–0.3 mm in diameter, fragments with uneven edges		Heavy rounded, cavernousness, partial destruction, fragments with uneven edges, frost pattern, crushing, false overlapping, sorting by size
Distribution of shells in the rock	concentrated on the planes of the layering or scattered		Scattered, rarely concentrated on the planes of the layering
Transport routes	Sea currents, digestive activity of fish and other animals. Movement within close biotopes along longitudinal and transverse profiles of the bottom		Repositioning from deposits of different ages

Table 2. **Taphonomic signs of fossil ostracods of autochthonous and allochthonous (synchronous, heterochthonous) type of burial (Dykan, 2007, 2008 a, b; Dykan, 2016; Dykan et al., 2009; Dykan, 2011)**

Type of burial	Autochthonous	Alochthonous (Synchronous)	Alochthonous (Heterochronous)
Morphological signs and degree of shell preservation	Good preservation of thin-walled and sculptured shells (external and internal morphological elements), absence of fragments and traces of shell rounding, traces of biological damage (drilling, etc.), pyritization, ”valve in valve” as an indicator of hydrodynamics	Good preservation of thin-walled and finely sculptured shells, absence of traces of shell rounding, possible traces of biological damage (drilling, etc.) and hatching, pyritization,“valve in valve“as an indicator of hydrodynamics	Poor preservation of shells: strong roundness, calcitisation, traces of corrosion and drilling, crushing, hatching, silicification, phosphoritization leaching, mineralization with salts, complete or partial leveling of the shell sculpture
Composition of oryctocenosis	Presence of whole (unopened) shells, absence of sorting of shells by size, equal or close number of right and left valves of the same species	The species is represented by a single shell (valve) or a different number of right and left valves; sorting by size, absence of small forms	only single valve or shell
Population composition	Presence of females and males, adult and larvae, larvae of different ontogenetic stages	Incomplete composition of the population (female or male, adult or larve), absence of ontogenetic series	only single valve or shell (female or male, adult or larva)
Population dynamics along the vertical section	Synchronous change in the number of adults/larvae in a population of one species. Synchronous development of populations of all species from one location	The number of adults and larvae varies asynchronously in species of the same association.	only single shell or valve
Ecological specialization	Close ecological specialization in species of one association	Different ecological specialization in species of one association	different ecological specialization with autochthonous
Stratigraphic range	Common stratigraphic range in all species of the association	Common stratigraphic range in all species of the association	A different stratigraphic range than that of the association species

strong roundness and calcitisation of the shell, the presence of hatching and traces of corrosion on the shell surface (Figs 1, 2).

The second stage: the statistical and population analysis of fossil ostracods, which allows determining the autochthonous/synchronous type of ostracod burial with a high degree of accuracy.

Statistical analysis is performed for all ostracod remains in the samples and includes counting of the total number of valves/shells, right/left valves, adults/larvae, females/males, larvae of different ontogenetic stages.

Population analysis is based on the results of statistical analysis and includes analysis of population density (total number of adults/larvae) and age structure of the population

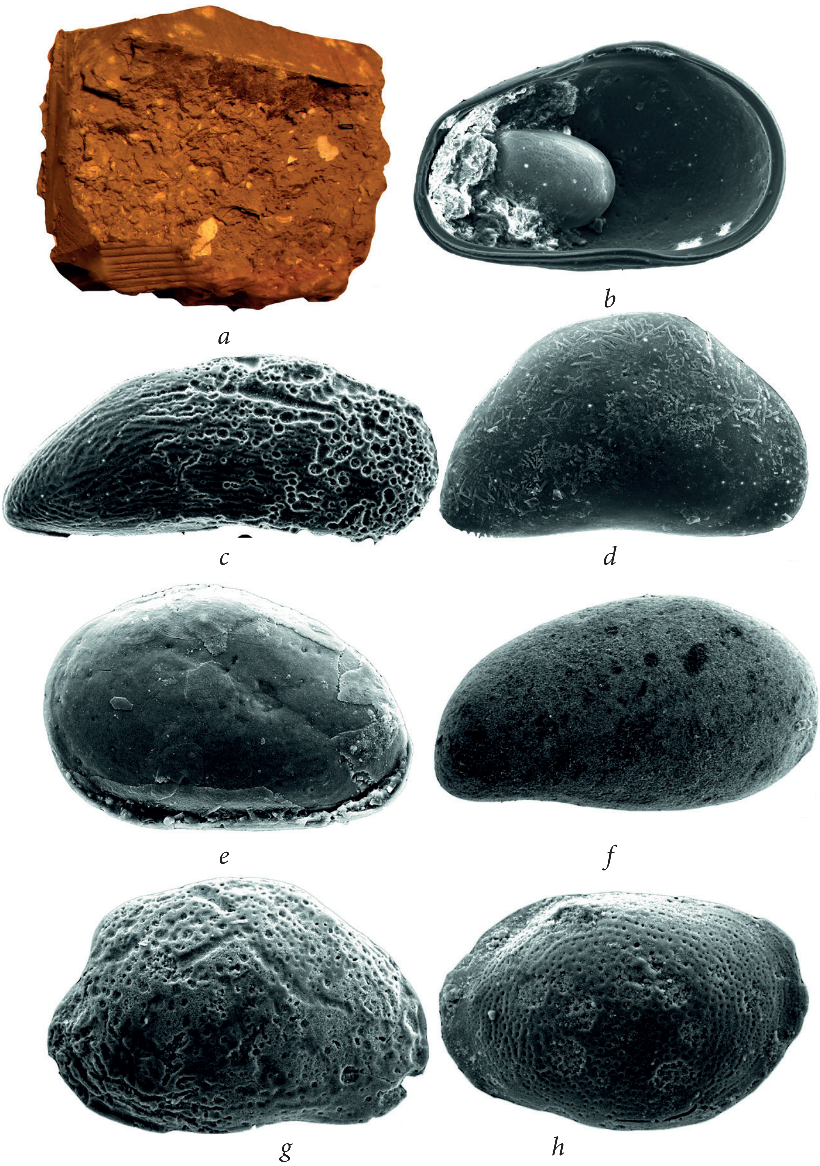

Fig. 1. Taphonomic signs of allochthonous (heterochronous, synchronous) burial of fossil ostracods: *a* — Miocene rock with ostracod shell imprints (Black Sea, Taman Peninsula, Zaliznyi Rih section). Sign of allochthonous burial: *b* — “valve in valve”, *Cyprideis torosa* (Jones, 1850) (Black Sea, Taman Peninsula, Zhaliznyi Rih section, Upper Miocene, Tortonian/Meotian; Dykan, 2016). Signs of heterochronous burial: *c* — leaching traces, *Pontoniella acuminata* (Zalányi, 1929) (Black Sea, Taman Peninsula, Zaleznyy Rog section, Upper Miocene, Meccinian/Pontian; Dykan, 2016); *d* — mineralization with salts, *Advenocypris cenropunctata* (Suzin, 1956) (Black Sea, Taman Peninsula, Popov Kamen section, Upper Miocene, Tortonian/Meotian; Dykan, 2016); *e* — silicification, *Cytherella* sp. (Ukraine, Ukrainian Shield, Boltyschka impact structure, Paleogene; Dykan et al., 2018); *f* — calcification, *Cytheridea* sp. (Western Ukraine, Podolia Upland, Scala Podilska section, Middle Miocene, Serravalian/Sarmatian; Dykan, 2008 b); *g* — corrosion marks, *Tyrrhenocythere* sp. 1 (Western Ukraine, Podolia Upland, Scala Podilska section, Middle Miocene, Serravalian/Sarmatian; Dykan; 2008 b); *h* — corrosion marks, *Loxoconcha rhombovalis* Pokorny, 1952 (Western Ukraine, Podolia Upland, Scala Podilska section, Middle Miocene, Serravalian/Sarmatian; Dykan, 2008 b)

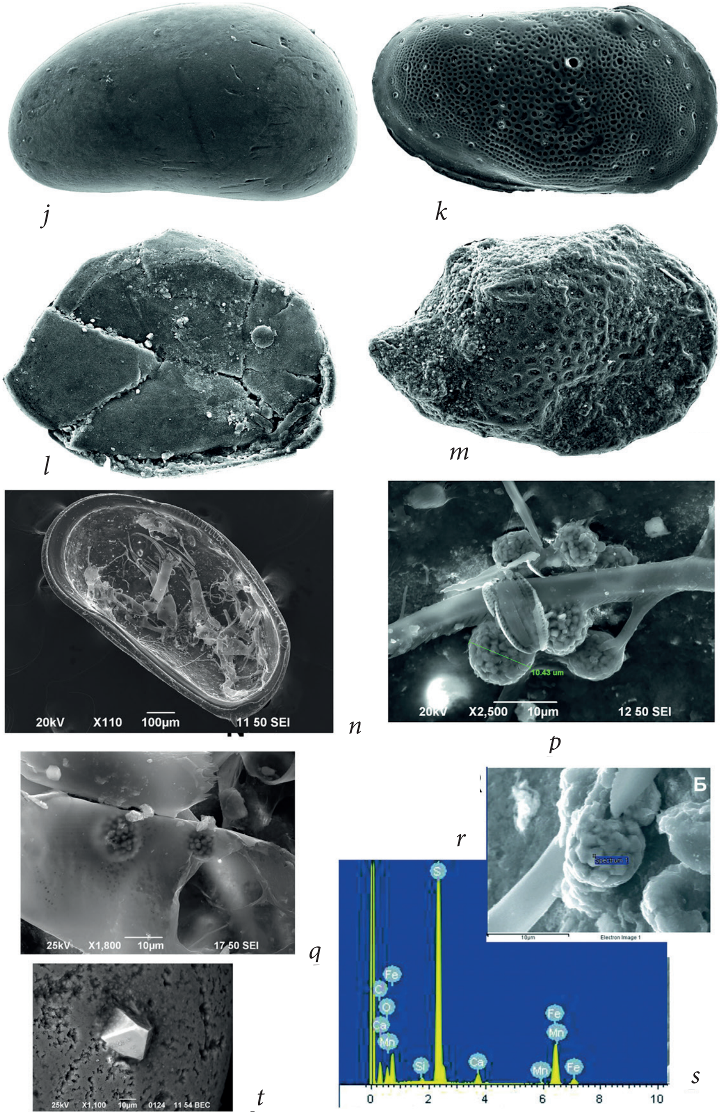

Fig. 2. Taphonomic signs of allochthonous (heterochronous, synchronous) burial of fossil ostracods: *j* — traces of hatching, *Candona* sp. shell of synchronous burial (Western Ukraine, Podolia Upland, Scala Podilska section, Lower Pleistocene, Calabrian, Eburonian/Berezanian; Dykan, 2008 b); *k* — traces of drilling, *Loxoconchissa* (L.) *praeimmodulata* shell of synchronous burial (Black Sea, Taman Peninsula, Popov Kamen section, Upper Miocene, Tortonian/Meotian; Dykan, 2016); *l* — crushing, of *Cytherella temporalis* Mand., 1960 shell of heterochronous burial (Ukraine, Ukrainian Shield, Boltyschka impact structure, Paleogene; Dykan et al., 2018); *m* — partial leveling of the sculpture, *Neomoceratina* sp. shell of heterochronous burial (Western Ukraine, Podolia Upland, Scala Podilska section, Middle Miocene, Serravalian/Sarmatian; Dykan, 2008 b); *n* — pyritization of the inner surface of the valve and soft body remains of *Cyprideis torosa* (Jones, 1850) of synchronous burial (Black Sea, Dnipro-Bug estuary, Upper Pleistocene, Weichselanian/Novoevksinian; Dykan et al., 2009); *p* — spherical formations of framboidal iron disulfide (pyrite, Fe_2S), structurally related to the soft body remains (plumose setae; Dykan et al., 2009); Q — the iron disulfide framboids are located insite the mummified remains (Dykan et al.,2009); *r* — area of X-ray analysis; *s* — X-ray spectrum of the iron disulfide framboid; *t* — pyrite crystal on the surface of a *Cyprideis torosa* (Jones, 1850) shell from heterochronous burial (Black Sea, Taman Peninsula, Popov Kamen section, Upper Miocene, Tortonian/Meotian; Dykan, 2016)

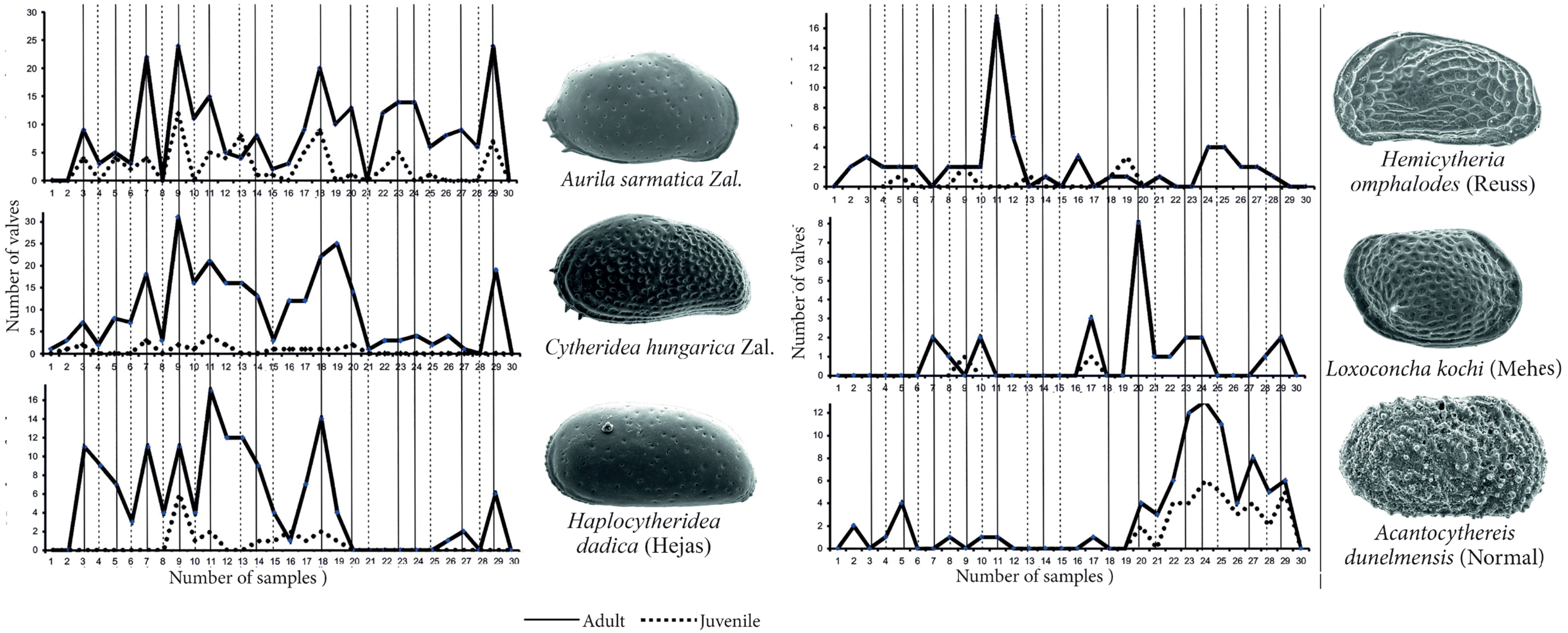

Fig. 3. Graph showing the population density of fossil ostracods from a single oryctocenosis of autochthonous burial type (Western Ukraine, Podolia Upland, Scala Podilska section, Middle Miocene, Serravalian/Sarmatian) (Dykan, 2008 b)

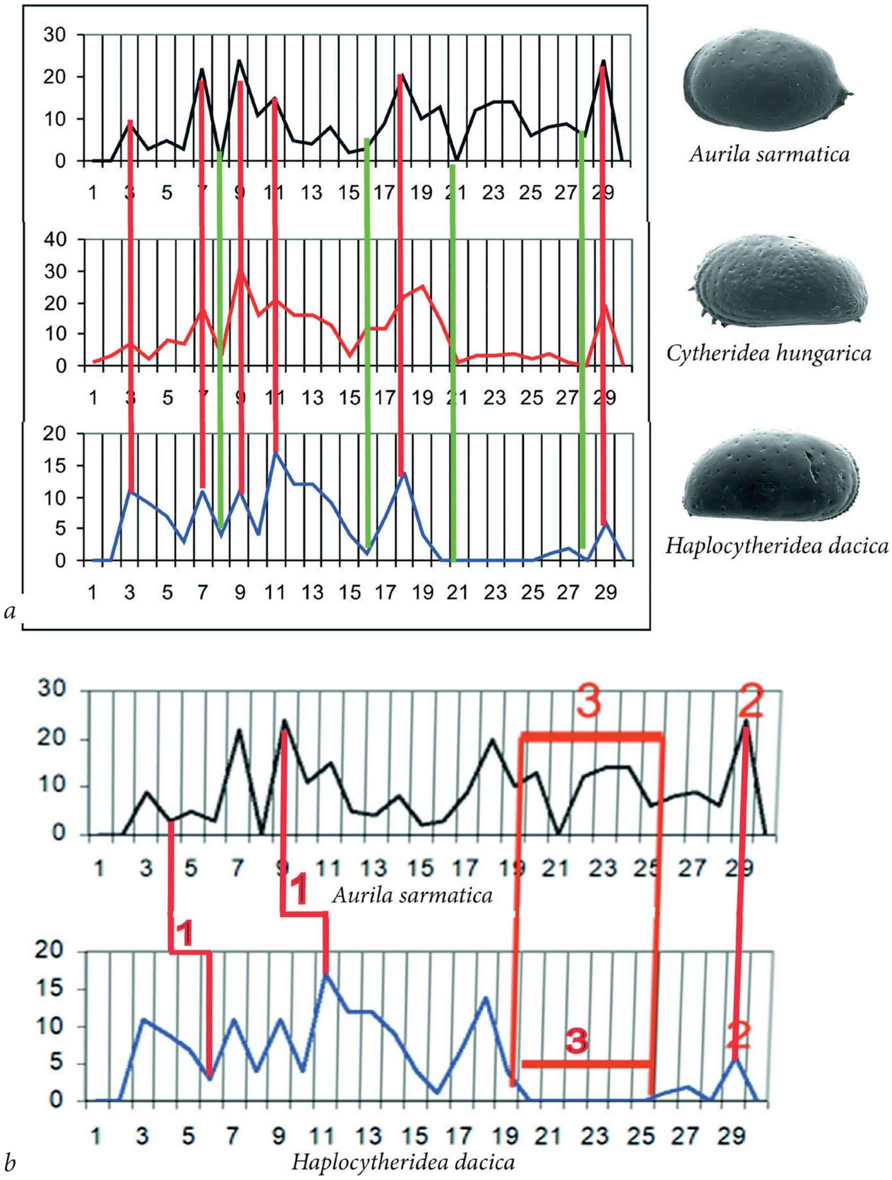

Fig. 4. Graphical analysis of the synchronous development of fossil ostracod populations of one oryctocenosis. *a* — synchronous development of ostracod populations as a sign of autochthonous burial type. *b* — analysis of the peculiarities of individual development and adaptive response of ostracods: 1 — shift of positive and negative peaks; 2 — coincidence of positive and negative peaks; 3 — presence/number of additional fluctuations or their absence (Western Ukraine, Podolia Upland, Scala Podilska section, Middle Miocene, Serravalian/Sarmatian) (Dykan, 2008 b)

(ratio of adults/larvae). A linear graph of population density dynamics graph is constructed for adults and larvae of all species of oryctocenosis along a vertical geological section. Positive peaks of the maximum population density on the graph correspond to optimal conditions for the ostracod's existence. Negative peaks of the low population density correspond to pessimistic conditions of existence when larval development slows down or stops, and the number of adult decreases. Straight lines correspond to periods of

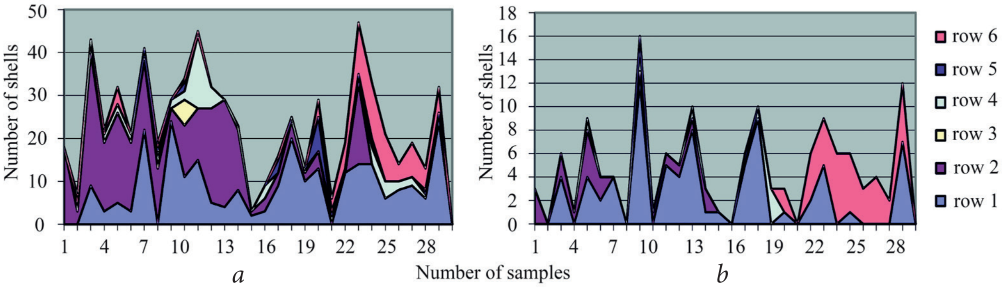

Fig. 5. Graph of the synchronous development of adults (*a*) and larvae (*b*) in populations of autochthonous ostracods of a single oryctocenosis: row 1 — *Aurila sarmatica*; row 2 — *Cytheridea hungarica*; row 3 — *Haplocytheridea dacica*; row 4 — *Hemicytheria omphalodes*; row 5 — *Loxoconcha kochi*; row 6 — *Acantocythereis dunelmensis* (Western Ukraine, Podolia Upland, Scala Podilska section, Middle Miocene, Serravalian/Sarmatian) (Dykan, 2008 b)

stabilization of abiotic characteristics in the basin (Fig. 3). Features of individual development and adaptive reaction of ostracods are recorded on the graph by the displacement of positive and negative peaks, the difference in the amplitude of their fluctuations, and the presence and number of additional fluctuations on the graph (Fig. 4). The coincidence of positive and negative peaks is an indicator of the species composition of the lifetime association of ostracods and their synchronous development in the biotope, as well as evidence of autochthonous burial (Fig. 5).

The third stage: ecological analysis of ostracods to determine the ecological compatibility of species within a single association, based on the principle of coexistence of ecologically similar species ("...a biotope is inhabited by species with similar ecological specialization"; Reymers, 1994). Ostracods of synchronous burial have a different type of ecological specialization than autochthonous species.

The fourth stage: stratigraphic analysis to determine and compare the stratigraphic position of all fossil species in the oryctocenosis. Ostracods of synchronous burial type have same stratigraphic range autochthonous ostracods. Ostracods of heterochronous burial type have a different stratigraphic range than autochthonous ostracods (Dykan, 2007, 2008 a).

Conclusions

A main sign of ostracod autochthonousness is the synchronous change in the number of adults and larvae in a population of one species, as well as the synchronous development of the populations of all the species from one location. Visual signs of autochthonous (lifetime) burial of ostracods are good preservation of a shell, absence of traces of rounding, full population composition (females and males, larvae of different stages of development). Autochthonous ostracods are the main group for determining the geological age of deposits and palaeogeographic reconstructions.

General signs of allochthonous (transferred) type of ostracod burial: the species is represented by a single valve or shell, population composition incomplete (females or males, adults or larvae), sorting the shells by size. There are two types of allochthonous burial: synchronous and heterochronous. Allochthonous of the synchronous burial type exhibit both autochthonous and allochthonous characteristics.

Signs of autochthonousness include good preservation of shells, the presence of thin-walled and finely sculptured shells, and the absence of traces of shell rounding, shared stratigraphic range and a similar but different ecological specialisation to autochthons. Allochthonous of the synchronous burial type are of the same age as autochthons and have biostratigraphic significance. Their lateral transfer along the longitudinal and transverse profiles of the water basin occurs both within close biotopes and over significant distances by sea currents, mechanically (by fish, birds, algae), and by bottom sediments under the influence of geological and geomorphological processes. Therefore, ostracods of synchronous burial type cannot be used for local reconstructions (biotopes), but only for regional palaeogeographic reconstructions (lake, river, part of the sea area).

Signs of heterochronous burial include poor preservation of shells (pitting, calcification, hatching, corrosion marks, etc.), different ecological specialisation of the species with autochthons, long-distance transport over an area. Ostracods of heterochronous burial type have a different geological age from autochthonous ones, having been redeposited from older or younger deposits as a result of weathering or erosion of rock. They have no palaeogeographic or biostratigraphic significance, but can be used to determine areas of erosion and the distance of transport of fossil material.

Modified quantitative method is based on the earlier developed methods of palaeoclimatic reconstruction (arealogram method, Grichuk, 1969; Grichuk et al., 1987; method of quantitative palaeoclimate reconstruction, Mosbrugger & Utescher, 1996; analytical and mathematical method of modeling palaeoclimatic fluctuations, Molchanoff, 2003), developed for fossil flora. For the first time, analytical and mathematical analysis was tested on ostracods as a quantitative modification method (Dykan & Molchanoff, 2006; Dykan, 2012, 2014) but it can also be applied to other faunal groups (molluscs, foraminifera, etc.). Although analytical and mathematical methods were initially developed for ostracods (Dykan & Molchanoff, 2006; Dykan, 2012, 2014), their application can be extended to other faunal groups, including molluscs and foraminifera.The analytical basis is data on the ecology of recent ostracod species and genera.

The method is based on the principle of coexistence of ecologically closely related ostracode species (Reimers, 1994), which does not diverge in principles of palaeoclimatic reconstruction using palaeoflora, hower it has some peculiarities. They are stipulated by a multifactor influence of water environment on the water organisms (the law of equivalence of all living conditions "all environmental factors necessary for life have an equivalent role", Reimers, 1994). At this, the influence of one factor on species individuals can strongly vary depending on other abiotic parameters e.g. salinity, depth (F. Blackman's law of limiting factors "the existence of a species is limited by environmental factors whose values are closest to pessimistic ones"; W. Scheld's law of tolerance: "The limiting factor for the prosperity of species can be either the minimum or the maximum of an environmental factor that determines the species' tolerance to that factor"; Reimers, 1991, 1994). In the moderate latitudes of the Northern Hemisphere, the geographical distribution of species is limited by temperatures, which are necessary for reproduction and restricted to extreme values of summer and winter temperatures of the year (rules of V. Sheldford-T. Park, A. Golikov-O. Skarloto; Reimers, 1991, 1994).

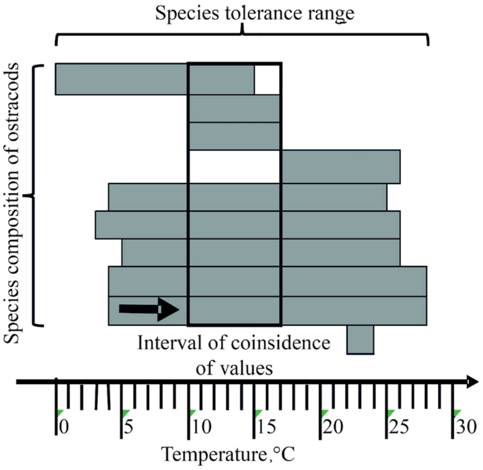

Fig. 6. Determination of numerical values of abiotic parameters of the aquatic environment by the modified quantitative method

The numerical values of abiotic parameters of the aquatic environment (water temperature, °C; water salinity, ‰; depth water of biotope, m) are determined by graphical analysis. The diagram is constructed for each abiotic parameter where the numerical values of the abiotic factor are on the axis of abscissa, and the species composition of ostracods is on the axis of ordinate. Three optimal numerical values exist for species that do not coincide for different species: minimum, maximum, and optimal. The maximum and minimum numerical values determine a diapason of tolerance range to the analysed factor. The interval having the limits of all coincided values represents the diapason of optimal values of abiotic factor for species coexisted in the association (Fig. 6). The reconstruction of the abiotic factor is based on data on the ecology of recent ostracods, analysis of population structure (population density, adult/larvae ratio) for each species association. For the mean month water temperature calculation within year the method trigonometric polynomial was used (Molchanoff, 2003).

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