Invertebrate Zoology, 2025, 22(2): 340–359

Evolutionary traits of planktonic Eucarida

A.A. Lunina, D.N. Kulagin, A.L. Vereshchaka[*]

Institute of Oceanology of Russian Academy of Sciences, Nakhimov Prospekt 36, Moscow 117997 Russia.
Anastasiia Lunina: yalunina@list.ru ORCID https://orcid.org/000-0002-1105-8027
Dmitry Kulagin: kulagin.dima@gmail.com ORCID https://orcid.org/0000-0002-5521-8598
Alexander Vereshchaka: alv@ocean.ru ORCID https://orcid.org/0000-0002-6756-2468
** Corresponding author*

ABSTRACT: The pelagic realm is the most voluminous biome on Earth and a deeper insight into evolutionary traits of dominant planktonic taxa such as Eucarida (Decapoda and Euphausiidae) is indispensable to understanding evolution on our planet. We recorded synapomorphies of all major fully planktonic eucarid groups — Euphausiidae, Oplophoroidea, Pasiphaeoidea, Sergestoidea, and Benthesicymidae — at three clade levels corresponding to families, genera, and species groups. We divided morphological synapomorphies into eight groups and examined which of them provided evolutionary success in the pelagic or benthopelagic biotopes. Morphological diversification was mainly driven by copulatory structures in Benthesicymidae, pereopods and copulatory structures in Euphausiidae and Sergestoidea, carapace, pleon, and mouthparts in Oplophoroidea and Pasiphaeoidea. Proportional contribution of these characters to diversification was unique for each taxon. Morphological characters coevolve as three functional units: copulatory structure (mating); photophores, antennula, and eye (perception and communication); mouthparts, pereopods, pleon, and carapace (feeding and defense). A benthopelagic ambit for a diverged clade may be predicted by the presence of pleon-linked synapomorphies. Species group level clades are characteristic for pelagic biotopes where niche diversity is low and number of habitats is limited due to relatively homogenous environment, which canalizes within-generic evolution through infrageneric taxa such as species groups. In contrast, evolution in the ecologically more diverse benthopelagic biotope occurs through adaptations to ecologically diverse habitats and through speciation without certain infrageneric taxa.

How to cite this article: Lunina A.A., Kulagin D.N., Vereshchaka A.L. 2025. Evolutionary traits of planktonic Eucarida // Invert. Zool. Vol.22. No.2. P.340–359, Suppl. Figs S1–S2, Suppl. Tables S1–S10. doi: 10.15298/invertzool.22.2.09

KEY WORDS: Decapoda, Eucarida, evolutionary traits, morphological analysis, morphological characters, krill, phylogeny, planktonic groups.

Эволюционные тренды планктонных эукарид (Eucarida)

А.А. Лунина, Д.Н. Кулагин, А.Л. Верещака[*]

Институт океанологии им. П.П. Ширшова РАН, Нахимовский проспект, 36, Москва 117997 Россия
** Ответственный за переписку: alv@ocean.ru*

РЕЗЮМЕ: Пелагиаль является самым обширным биомом на Земле, и глубокое понимание эволюционных особенностей доминирующих планктонных таксонов, таких как Eucarida (Decapoda и Euphausiidae), необходимо для понимания эволюции на нашей планете. Мы выявили синапоморфии всех основных полностью планктонных групп эукарид — Euphausiidae, Oplophoroidea, Pasiphaeoidea, Sergestoidea

и Benthesicymidae — на трех уровнях: семейства, рода и групп видов. Мы разделили морфологические синапоморфии на восемь групп и исследовали, какие из них обеспечили эволюционный успех в пелагиали и бентопелагии. Морфологическое разнообразие в исследованных группах обусловлено главным образом копулятивными структурами (Benthesicymidae), либо переоподами и копулятивными структурами (Euphausiidae, Sergestoidea), либо карапаксом, плеоном и ротовым аппаратом (Oplophoroidea, Pasiphaeoidea). Пропорциональный вклад этих признаков в диверсификацию уникален для каждого таксона. Морфологические признаки эволюционируют совместно в составе трех функциональных комплексов: копулятивные структуры (спаривание); фотофоры, антеннулы и глаза (восприятие и коммуникация); ротовой аппарат, переоподы, плеон и карапакс (питание и защита). Среду обитания клады можно предсказать по наличию синапоморфий, связанных с плеоном, что может быть связано с конкретными стратегиями придонного образа жизни. Образование клад на уровне видов характерно для пелагиали, где число биотопов ограничено, а условия среды однородны, что обеспечивает внутриродовую эволюцию. В отличие от этого, эволюция в экологически более разнообразной бентопелагиали происходит за счет адаптаций к разнообразным экологическим средам и через видообразование без участия определенных внутривидовых таксонов.
Как цитировать эту статью: Lunina A.A., Kulagin D.N., Vereshchaka A.L. 2025. Evolutionary traits of planktonic Eucarida // Invert. Zool. Vol.22. No.2. P.340–359, Suppl. Figs S1–S2, Suppl. Tables S1–S10. doi: 10.15298/invertzool.22.2.09

КЛЮЧЕВЫЕ СЛОВА: Decapoda, Eucarida, эволюционные признаки, морфологический анализ, морфологические признаки, криль, филогения, планктонные группы.

Introduction

The pelagic realm is the most voluminous biome on Earth and a deeper insight into evolutionary traits of dominant planktonic taxa is indispensable to understanding evolution on our planet. The crustacean superorder Eucarida, represented by two marine orders Euphausiacea and Decapoda, is one of the most spectacular and evolutionary successful planktonic group. Decapoda encompasses panoceanic superfamilies Oplophoroidea Dana, 1852, Pasiphaeoidea Dana, 1852, Sergestoidea Dana, 1852, and the family Benthesicymidae Wood-Mason in Wood-Mason et Alcock, 1891. All these taxa are planktonic, often dominant in the water column, “shrimp-like”, with elongated carapace and abdomen bearing swimming appendages. They occur either in the pelagic (epi-, meso-, bathy-, and abyssopelagic) or in the benthopelagic (near the bottom, above continental slopes, seamounts, shelves).

The role of eucarids in oceanic plankton is very significant. Euphausiidae, widely known as krill, is probably the most abundant and commercially important group of marine eucarids (e.g., Mauchline, Fisher 1969; Everson, 2000). For example, the krill stock in the Southern Ocean is assessed as 0.38 Gt (wet weight — Atkinson *et al*., 2009) and the catch in earlier times reached 0.53 Gt — Everson, 2000; Nicol *et al*., 2012). Decapods are also notable in the pelagic, especially representatives of the families Sergestidae (belonging to Sergestoidea: Vereshchaka *et al*., 2014; Vereshchaka, 2017) and Acanthephyridae (Oplophoroidea: Kemp, 1939); the latter group makes up the greatest contribution to the global deep-pelagic shrimp biomass that is assessed as 1.7 Gt (Vereshchaka *et al*., 2019b). Overall, total decapod biomass in the pelagic likely lies within the range reported for mesopelagic fishes, i.e., 1–15 Gt (Gjøsaeter, Kawaguchi, 1980; Lam, Pauly, 2005; Irigoien *et al*., 2014).

In addition to the pelagic habitat, a number of planktonic eucarid genera extend their ecological ranges to the near-bottom layer and are linked to the bottom through feeding and\or shelter and thus represent benthopelagic fauna *sensu* Vereshchaka (1995). The adults of twelve genera of Benthesicymidae (except *Altelatipes* and *Gennadas*) live near the bottom permanently. Other genera occur there in the daytime in the course of diurnal vertical migrations (e.g., the pasiphaeoid *Pasiphaea* and the oplophoroid *Janicella*). Colonization of the benthopelagic biotope has resulted in significant morphological changes as shown for individual taxa: lens-bearing photophores in Sergestoidea (Vereshchaka, 2017), abbreviated posterior pleonic somites in Oplophoroidea (Kulagin *et al.*, 2024), simplified copulatory structures in Euphausiidae and Dendrobranchiata (Lunina *et al.*, 2019a, 2024; Vereshchaka *et al.*, 2019a), etc. We hypothesize that planktonic eucarids evolving in benthopelagic habitats have a number of common morphological synapomorphies (derived traits evolved in their most recent common ancestor) and test this hypothesis here; we also try to predict a habitat of a clade (pelagic or benthopelagic) on the basis of synapomorphies supporting the clade.

We focus on the evolutionary traits in Euphausiidae, Oplophoroidea, Pasiphaeoidea, Sergestoidea, and Benthesicymidae and analyze morphological characters providing their evolutionary success in the pelagic and the benthopelagic. In contrast to the rest of eucarid families (e.g., Portunidae, Pandalidae, Penaeidae) that are mostly benthic or benthopelagic with only few truly pelagic species, the five major selected taxa are entirely pelagic or benthopelagic. Their panoceanic distribution, abundance, and dominant role in the plankton mirror their evolutionary success that is expected to be linked to morphological traits to be analyzed here. We answer the following questions:

Which particular characters greater contribute to the morphological diversification within each of individual major taxa?

Which of these characters are similar among the five major taxa and which are different?

Are these characters the same at deeper and more terminal nodes of phylogenetic trees?

Can we predict the principal biotope of a clade (pelagic or benthopelagic) having information of synapomorphies supporting this clade (the 'biotope' hypothesis)?

These objectives have four principal difficulties to overcome. Firstly, such an analysis should be based on statistically supported phylogenetic trees that are confirmed by both molecular and morphological methods. Ideally, phylogenetic trees are expected to include all known representatives of each group in order not to omit important traits. In spite of significant increase of recent phylogenetic analyses of marine groups, only restricted number of publications meets these requirements (Table 1). Sergestoidea have only a morphological tree and there is little chance that a resolved molecular tree including all genera will appear in the foreseeable future due to remote habitats and difficult species identification within this taxon (Vereshchaka, 2000, 2009). Conversely, Pasiphaeoidea have only molecular tree (Liao *et al.*, 2017) but in this case we can fill a morphological gap and examine synapomorphies supporting molecular clades retrieved by Liao *et al.*, (2017) using specimens at hand (Table 2, Suppl. Table S1).

Secondly, external morphology of the five clades belonging to different orders is not always completely homological, some groups of organs may be present or absent. For example, thoracopods in Euphausiidae (second to eight thoracic segments) and pereopods in Decapoda (fourth to eight thoracic segments), albeit not linked to identical segments, have the same function (catching prey and movement). Furthermore, elaborated copulatory structures (petasmata in males and thelyca in females) may be present in Euphausiidae, Sergestoidea, and Benthesicymidae but absent in the rest of the groups. In addition, photophores may be visible and easy to codify in

Table 1**.** Literature sources of phylogenetic trees and supporting synapomorphies.
Таблица 1. Литературные источники филогенетических деревьев и синапоморфий.

Taxa	**Sources**	**Figures**
Euphausiidae	Vereshchaka *et al.*, 2019a	5–9
Benthesicymidae	Vereshchaka *et al.*, 2021	2–3, 5–6
Sergestoidea	Vereshchaka, 2017	3
Oplophoroidea	Lunina *et al.*, 2019a	5
	Lunina *et al.*, 2021	5
	Lunina *et al.*, 2024	5
Pasiphaeoidea	Liao *et al.*, 2017	2–3

Euphausiidae and Sergestoidea or hardly (if at all) visible and uncertain in most alcohol-preserved Benthesicymidae and Oplophoroidea. We, therefore, combined morphological characters into several groups and analyzed distribution of these group-linked synapomorphies across the trees (Fig. 1A).

In our analyses we use a combination of Hennigian and Linnaean taxonomic approaches representing different concepts in biological classification (e.g., Williams, Lee, 2014). A Hennigian clade is a group of organisms that includes a common ancestor and all its descendants and mirrors the branching patterns of evolutionary history. Phylogenetic trees of five major taxa under consideration inevitably have different topology and branching of Hennigian clades. In order to standardize level of these clades, we

Table 2. Morphological synapomorphies (our data: Suppl. Table S1) supporting molecular clades of Pasiphaeoidea (Liao *et al*., 2017).
Таблица 2. Морфологические синапоморфии (наши данные: Табл. S1), поддерживающие молекулярные клады Pasiphaeoidea (Liao *et al*., 2017).

Clade	**Synapomorphies**	**Absence/ presence**
Pasiphae	Carapace, ratio maximal width two of postsinusial width 2.1±0,2	present
	Carapace, branchiostegal sinus distinct and deep	absent
	Rostrum reaching/overreaching distal part of cornea	absent
	Maxilla II, endites separate	absent
	Maxilliped I, endites fused with basis, endopod developed or reduced	present
	Pereopod I, distal part of basis unarmed	absent
	Pereopod I, distal part of basis with acute tooth on outer margin	present
	Pereopods II, equal spines of chela's fingers	present
	Pereopods III filiform	present
	Pereopods IV shorter than Pereopods V	present
	Pereopod IV, propodus, brush of short setae	present
	Pereopod IV, dactylus, row of short setae	present
	Telson, dorsolateral spines	absent
Eupasiphae	Carapace, orbital spine	present
	Carapace, orbital and branchiostegal spines	present
	Carapace, orbital spine proceeding in postorbital ridge	present
	Postorbital carina (ridge)	present
	Telson, 5–6 pairs of terminal spines	present
Parapasiphae	Rostrum not reaching proximal part of cornea	present
	Orbital stalk with terminal appendage or second eye field	present
	Eyestalk wider than cornea	present
	Elevation of dorsal carina on rostrum or proximal part of carapace	present
	Low dorsal carina elevation on rostrum or proximal part of carapace	present
	Carapace, branchiostegal spine	absent
	Pereopod I, distal part of basis laterally expanded	present
	Abdomen, carina on II segment	absent
	Abdomen, carina on III segment	absent
	Abdomen, carina on IV segment	absent

Table 2 (continued).
Таблица 2 (продолжение).

Clade	**Synapomorphies**	**Absence/ presence**
Leptochela	Carapace, breeding female, dorsal carina and pair depressions along midline	present
	Mandible, palp 1-segmented	present
	Mandible, palp rounded	present
	Maxilliped I, endopod developed or reduced, endites well-developed	present
	Pereopod II, merus, 2–10 spines	present
	Pereopod II, ischium, armament	present
	Pleon, VI somite, posterior part distinctly wider than anterior	present
	Pleon, VI somite, ventrolateral margin armed with 1 spine in posterior part	present
	Telson, mesial spines in the anterior part	present
	Telson, ‘Leptochela’ type armament of the tip	present
	Telson, 5–6 pairs of terminal spines	present
	Telson equal to uropods in length	present
	Uropod, endopod, movable spines	present
	Uropods exopod, movable spines	present
Psathyrocaris	Mandible, palp 2-segmented	present
	Mandible, palp leaf-like	present
	Mandible, palp longer than mandible	present
	Pereopod III, exopod longer than or subequal to endopod	present
	Pereopods IV, exopod longer than or subequal to endopod	present
	Pereopods V, exopod longer than or subequal to endopod	present
	Pleopods I–V subequal or equal to carapace in length	present
	Telson longer than VI pleonic somite	absent

Eupasiphae and *Parapasiphae* considered here as separate genera because (1) monophyly on molecular tree of *Eupasiphae* was rejected by the Bayes factor test but not by the AU one in Liao *et al*., (2017) and (2) both genera are supported by a set of distinct morphological synapomorphies. *Glyphus* not included because supporting synapomorphies were not found.

further use Linnaean approach (hierarchical categories used to organize and classify organisms). We group the clades into ranked groups such as species groups, genera, subfamilies, families and ignore intermediate branching episodes (for example, between genus and species group level clades). Euphausiidae and Benthesicymidae have monophyletic subfamilies absent in the rest of the taxa that, instead, encompass monophyletic families. We compared the subfamily level clades of these taxa with the family level clades of the rest of the eucarids in a common pool (hereafter, family level clades).

Fourthly, a pelagic or a benthopelagic habitat for a taxon is not always obvious. In most cases benthopelagic eucarids may be identified (see details in Vereshchaka, 1995) on the basis of their distribution (high abundances over shelves, seamounts, continental slopes coupled with only occasional occurrence in the open ocean), behavior (burial in a ground instead of swimming around), and feeding (regular presence of benthic prey in gut content). Information of the gear type may also be helpful: high abundances in benthic trawls (especially in the daytime) coupled with aggregation in the water column

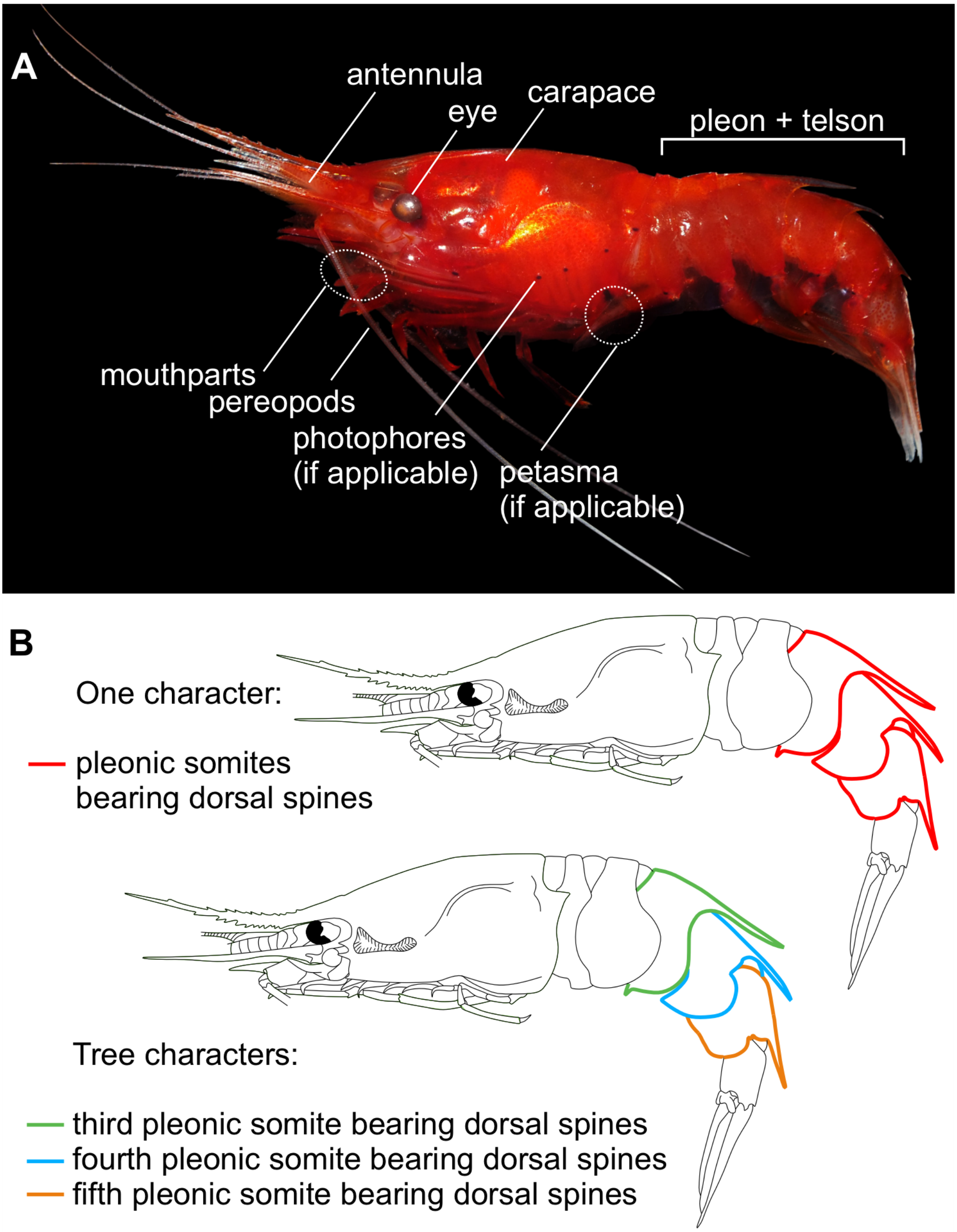

Fig. 1. Character grouping in Eucarida: A — *Systellaspis debilis*, B — various ways of codification of the same characters exemplified by *Oplophorus spinosus*.

Рис. 1. Группировка признаков у Eucarida: A — *Systellaspis debilis*; B — различные способы кодификации тех же признаков на примере *Oplophorus spinosus*.

at night suggest benthopelagic habitat. Overall, on the basis of this integrative information, we can designate planktonic eucarids as pelagic or benthopelagic with reasonable certainty.

Material and methods

MATERIAL. We analyzed morphological synapomorphies of all five major planktonic taxa belonging to Euphausiidae and Decapoda. We summarized published from recent phylogenetic analyses of three taxa (Euphausiidae, Benthesicymidae, and Oplophoroidea) based on simultaneous use of molecular and morphological methods, analyses of Sergestoidea based on morphological characters, and analyses of Pasiphaeoidea based on molecular methods (Table 1). For all taxa except Pasiphaeoidea synapomorphies were previously retrieved using the outgroup analyses (see details in Table 1); for Pasiphaeoidea we used molecular tree by Liao *et al*. (2017) and recorded morphological synapomorphies supporting molecular clades using material at hand and suggesting that the synapomorphies evolved *de novo* within the clades (Suppl. Table S1). Synapomorphies were recorded only for the clades of three distinct taxonomic levels (Suppl. Tables S2–S6):

– family level in Oplophoroidea, Pasiphaeoidea, and Sergestoidea and subfamily level in Euphausiidae and Benthesicymidae (‘family level’),

– genus level,

– species group level (if species groups were previously designated in the papers referred to in Table 1).

We considered Leptochelidae and Psathyrocarididae as family level clades (without formal erecting here these taxonomic names) in Pasiphaeoidea; the status of both clades is currently under question but the nodes separating both clades are much deeper than those of the rest of the Pasiphaeoidea genera (e.g., Liao *et al*., 2017). Four clades corresponding to the families Petalidiumidae, Sicyonellidae, Leptochelidae and Psathyrocarididae encompassed a single genus each; in this case we considered supporting synapomorphies both as family level and genus level supporting synapomorphies.

CONTRIBUTION OF CHARACTER GROUPS TO MORPHOLOGICAL DIVERSIFICATION. We divided all morphological characters into eight groups (Fig. 1A) associated with: (1) the carapace, (2) the pleon and the telson (hereafter ‘pleon’), (3) the eye, (4) the antennula, (5) the mouthparts, (6) the pereopods in Decapoda or thoracopods in Euphausiidae, (7) the photophores, and (8) the copulatory structures. As some morphological characters may be coded subjectively (several synapomorphies may be coded separately or combined into a single synapomorphy: e.g., Fig. 1B), we considered number of supporting synapomorphies as binary parameters, i.e., either absent or present.

For each clade we recorded the clade level (family, genus, or species group) and the presence or absence of synapomorphies supporting this clade. Synapomorphies for Pasiphaeoidea (“in-group” analysis) are listed in Table 2, synapomorphies for the rest of the groups were collected from the papers and figures listed in Table 1. The contribution of each character group (C_i) to the clade diversification was calculated as $C_i = N_i / N_{tot}$, where N_i was a binary character (0=absent, 1=present) and N_{tot} was a sum of binary characters supporting the clade. Since the contribution C_i was normalized (divided by N_{tot}), we expected that this value did not depend on a number of recorded synapomorphies within each of the character groups. Three-D histograms were then made for each of five major taxa.

In order to assess contribution of character groups to diversification of the planktonic eucarid clades in detail, we combined results in a common pool and ran Principal Component Analysis (PCA) using Kulczynski (binary) similarity index. PCA was aimed to assess contribution of various morphological characters to diversification among the major eucaridean groups.

We generated three datasets:

(1) all character groups and Clade Level included (Taxon as a target): this analysis was designed to show comparative impact of the Clade Level and all various morphological characters on diversification in major taxa;

(2) all character groups included (Taxon as a target, Clade Level excluded): this analysis was expected to result in a clearer picture and reveal contribution of individual character groups to diversification of the planktonic eucarids in major taxa regardless Clade Level;

(3) all character groups included (Clade Level as a target): this analysis was aimed to unveil morphological characters whose impact on diversification depend on the Clade Level.

ANALYSIS OF COEVOLUTION. We further assessed possible contribution of various groups of morphological characters to the pelagic eucarid evolution using the same eight character groups as in the previous section. For each of the selected clades we considered every node as an evolutionary event and recorded which character groups supported the clade (following, e.g., Vereshchaka *et al*., 2019a). In the case of Pasiphaeoidea (only a molecular tree was available, from Liao *et al*., 2017), we examined representatives of supported clades morphologically (Suppl. Table S1) and recorded morphological characters supporting each of these clades. We finally had a matrix with rows listing the supported clades (family, genus, and species group level) and columns indicating presence/absence of synapomorphies that supported each branch (Suppl. Tables S2–S6).

Robust clustering of character groups (similar results retrieved by various settings) suggests their most possible co-evolution (Vereshchaka *et al.*, 2019a); we ran hierarchical clustering with several settings and further compared resulting dendrograms. We used Ward's Method (Clusters are joined in such a way that increase in within-group variance is minimized) and Complete Linkage Method (each element is in a cluster of its own; the clusters are then sequentially combined into larger clusters until all elements end up being in the same cluster) and measured intervals using Euclidean, Squared Euclidean and Minkovski distances in each method.

TESTING A 'BIOTOPE' HYPOTHESIS. We tested a hypothesis that morphological diversification is tightly linked to the biotope inhabited by the clade. If so, we can predict a major oceanic biotope (pelagic or benthopelagic) inhabited by a clade with a knowledge of (1) morphological synapomorphies supporting the clade and (2) the clade level (family, genus, species group). We ran Generalized Linear Mixed Models (GLMMs), used multinomial logistic regressions with Habitat (pelagic or benthopelagic) as a target and the following variables (presence or absence of synapomorphies linked to the character groups below) as fixed factors: (1) Carapace, (2) Pleon, (3) Antennula, (4) Eye, (5) Mouthparts, (6) Pereopods, (7) Photophores, (8) Copulatory structures, and (9) Clade Level.

For eight groups of morphological characters (factors 1–8) and for each particular clade we used '0' if synapomorphies were absent and '1' is present. Clade Level (factor 9) was '1' for families, '2' for genera, and '3' for species groups. The input matrix was based on the data of Tables S2–S6.

We additionally calculated tetrachoric correlations between biotope (binary) and each of binary variables linked to morphological synapomorphies using an approximation after Bonett & Price (2005), which is appropriate for our binary dataset. These correlations were designed to independently show correlations between Habitat (set as: pelagic=1, benthopelagic=0) and each of character types.

We used Microsoft Excel 2010 software for handling data and IBM SPSS Statistics 26 (https://www.ibm.com/support/pages/downloading-ibm-spss-statistics-26) for statistical analyses.

Results

CONTRIBUTION OF CHARACTER GROUPS TO MORPHOLOGICAL DIVERSIFICATION OF INDIVIDUAL CLADES: SIMPLE VISUALIZATION. Contribution of character groups to morphological diversification of families, genera and species groups (C_i) is shown in Fig. 2, we further consider the morphological contribution significant if $C_i \geq 0.1$.

Carapace-linked characters are notable everywhere (especially in Oplophoroidea in which their contribution exceeds 0.5 at the species-group level) except species groups of Benthesicymidae.

Pleon-linked characters are always important in Oplophoroidea, Pasiphaeoidea, and Sergestoidea as well as in species group clades of Euphausiidae, in family and genus level clades of Benthesicymidae.

Both antenna and eye contribute only in genus level clades of Euphausiidae, the antenna contributes to family level clades of Sergestoidea (antenna), and the eye contributes to the genus level clades of Pasiphaeoidea.

Mouthparts are always important in Sergestoidea and (0.22) especially in Oplophoroidea (0.33) and Pasiphaeoidea (0.30) as well as in family level clades of Benthesicymidae (0.25).

Contribution of pereopod-linked characters was significant everywhere except Benthesicymidae (all clades) and species group clades of Oplophoroidea.

Copulatory structures are very important in the taxa with elaborate copulatory structures (petasmata in males and thelyca in females), these organs explain most of morphological diversification in Euphausiidae, Sergestoidea, and Benthesicymidae; their contribution increases from the family level clades to the genus level clades and to species group level clades. In Benthesicymidae, synapomorphies linked to copulatory structures dominate absolutely: from 0.5 in the family-level clades to 1.0 in the species group level clades.

Photophores make contribution only to diversification of generic clades of Sergestoidea.

Overall, simple visualization shows that contribution of various character groups to diversification greatly depends on the clade level and on individual taxon. Carapace-, pleon-, mouthparts-, and pereopod-linked synapomorphies are the most widely distributed across the taxa and clades but their contribution usually is not so great. Conversely, copulatory structures, albeit recorded only in three taxa, significantly contribute to their morphological diversification, especially in Benthesicymidae.

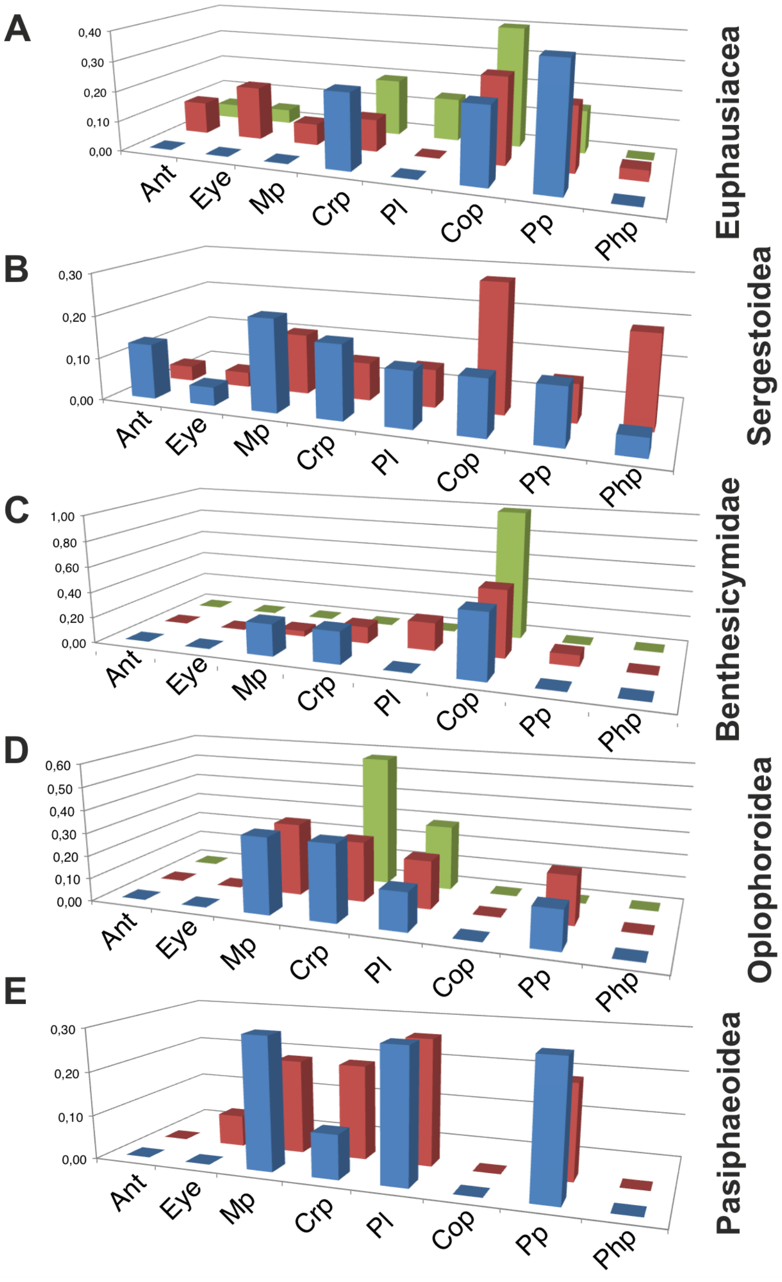

Fig. 2. Contribution of various character groups in morphological diversification of major planktonic groups of Eucarida in family level clades (anterior rows), genus level clades (intermediate rows), and species group level clades (posterior rows). Mp — mouthparts, Crp — carapace, Pl — pleon, Cop — copulatory structures, Pp — pereopods, Php — photophores.

Рис. 2. Вклад различных групп признаков в морфологическое разнообразие основных планктонных групп Eucarida в кладах уровня семейства (передние ряды), кладах уровня рода (промежуточные ряды) и кладах уровня групп видов (задние ряды). Ant — антенна, Eye — глаза, Mp — ротовые конечности, Crp — карапакс, Pl — плеон, Cop — копуляторные структуры, Pp — переоподы, Php — фотофоры.

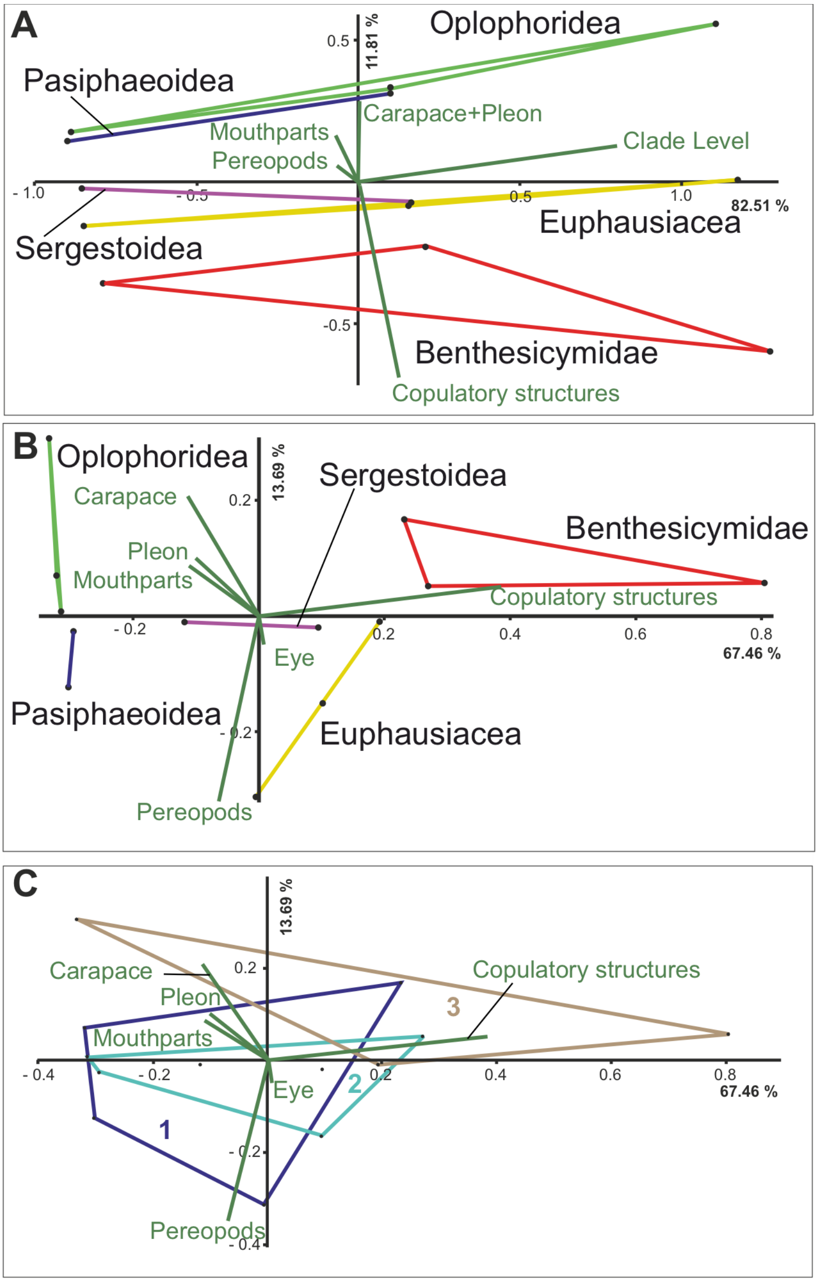

Fig. 3. Results of Principal Component Analyses: A — with all character groups and Clade Level included, grouped by Taxon; B — all character groups included and Clade Level excluded, grouped by Taxon; C — all character groups included, grouped by Clade Level. Only notable vectors corresponding character groups included (green).

Рис. 3. Результаты анализа главных компонентов (PCA): A — включены все группы признаков и уровни клад, сгруппированы по таксону; B — включены все группы признаков и исключен уровень клады, сгруппированы по таксону; C — включены все группы признаков, сгруппированы по уровню клады. Включены только известные векторы, соответствующие группам признаков (обозначены зеленым цветом).

CONTRIBUTION OF CHARACTER GROUPS TO MORPHOLOGICAL DIVERSIFICATION WITHIN THE COMMON EUCARID POOL: PCA APPROACH. PCA analysis with all character groups and Clade Level included show that diversification may be perfectly (94% of variance) explained by two principal components (Fig. 3A). The first one accounted for 83% of variance and was mainly associated with the Clade Level. The second component (12% of variance) was primarily linked to the copulatory structures and the carapace+pleon (both combined due to their collinearity). Diversification of Dendrobranchiata (Sergestoidea and Benthesicymidae) and Euphausiidae was mainly driven by characters linked to the copulatory structures, whereas diversification of Caridea (Oplophoroidea and Pasiphaeoidea) was driven by the carapace, the pleon, and the mouthparts.

When we excluded the most important factor (Clade Level) from the PCA, 81% of variance still was explained (Fig. 3B). The first component accounted for 67% of variance and was mainly associated with the copulatory structures. The second component (14% of variance) was primarily linked to the pereopods and the carapace. Diversification of Benthesicymidae and, to a lesser extent, Euphausiidae was mainly driven by characters linked to the copulatory structures, whereas diversification of Caridea was driven by the carapace, the pleon, and the mouthparts. Diversification of Sergestoidea and, partly, Euphausiidae was also explained by the pereopods.

When we used the clade level as a target in the PCA, 81% of variance was explained (Fig. 3C). The first component accounted for 67% of variance and was mainly associated with the copulatory structures. The second component (14% of variance) was primarily linked to the pereopods and the carapace. Data for family and genus level clades were centered at zero, diversification at these levels were dominated by various characters depending on the taxon (mainly pereopods and carapace); diversification of the species group level clades was driven by the copulatory structures (Dendrobranchiata and Euphausiidae) and the carapace-, pleon-, and mouthparts-linked characters (Caridea).

Overall, diversification of planktonic eucarids is mainly driven by the copulatory structures (Euphausiidae, Sergestoidea, and Benthesicymidae) and by a complex of the carapace-, pleon-, and mouthparts-linked synapomorphies (Oplophoroidea and Pasiphaeoidea). Morphological diversification differs at deeper and terminal nodes (greatly depends on Clade Level: Fig. 3A): diversification at species group level is primarily driven by copulatory structures in Euphausiidae and Benthesicymidae and the carapace-, pleon-, and mouthparts-linked characters in Oplophoroidea (Fig. 3C). Diversification drivers of the family and genus level clades depended on the taxon.

COEVOLUTION OF CHARACTER GROUPS: HIERARCHICAL CLUSTERING. Hierarchical clustering based on Ward's Method and Complete Linkage Method (each with intervals measured using Euclidean, Squared Euclidean and Minkovski distances) retrieved six similar dendrograms (Suppl. Fig. S1), one shown on Fig. 4 as an example. All dendrograms share the same topology with three principal branches and same distances of branching (DB) which mirror co-evolution of character groups within pelagic eucarids:

– copulatory structures (DB = 25) represented a separate branch most distant from the rest of morphological characters;

– antennula+eye+photophores (DB = 16) further divided into the branches antennula+eye (DB = 1) and photophores (DB = 5);

– mouthparts+pereopods+pleon+carapace (DB = 16) further divided into the branches mouthparts+pereopods (DB = 7), pleon (DB = 8), and carapace (DB = 11).

TESTING THE 'BIOTOPE' HYPOTHESIS: GLMMS AND TETRACHORIC CORRELATIONS ASSESS PREDICTION POWER OF MORPHOLOGICAL SYNAPOMORPHIES. Analysis 1. We run a generalized linear mixed model (GLMM) with Habitat (pelagic or benthopelagic) as a target and all nine fixed factors: (1) Carapace, (2) Pleon, (3) Antennula, (4) Eye, (5) Mouthparts, (6) Pereopods, (7) Photophores, (8) Copulatory structures, and (9) Clade Level. The model (Suppl. Tables S8–S9, Fig. S2) was significant at $p = 0.036$, two factors were statistically significant: pleon (negative effect, $p=0.003$) and Clade Level (positive effect, $p= 0.026$). This analysis shows that the biotope type (benthopelagic) may be predicted by the presence/absence of pleon-linked morphological

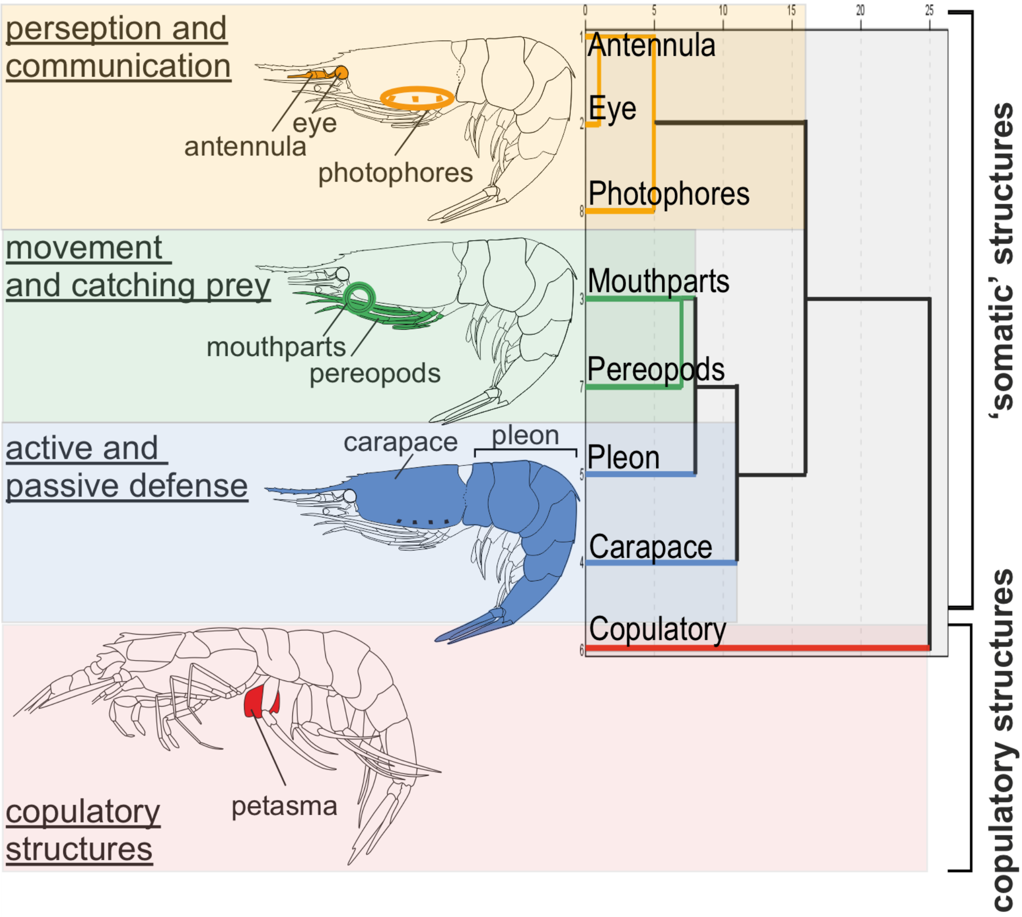

Fig. 4. Hierarchical dendrogram retrieved using Ward's Method and Squared Euclidean Distance (right) and coevolving character groups (left). The rest of dendrograms are shown in Suppl. Fig. S1.
Рис. 4. Иерархическая дендрограмма, полученная с использованием метода Уорда и Квадрата евклидова расстояния (справа) и совместно развивающихся групп признаков (слева). Остальные дендрограммы показаны на рис. S1 (Suppl. Fig. S1).

synapomorphies and by the Clade (Suppl. Fig. S2). Particular pleon-linked synapomorphies are listed in Table 3.

Analysis 2. We left only the most powerful predictor, i.e., the Pleon, and used this as the only fixed factor. The model (Suppl. Tables S8–S9, Fig. S2) was robust (the factor was negative, p=0.008).

Analysis 3. We left the second statistically significant factor, the Clade Level, and used this as the only fixed factor. The model (Suppl. Tables S8–S9, Fig. S2) was less robust but still significant (the factor was positive, p=0.035).

Analysis 4. We combined both statistically significant factors, the Pleon and the Clade Level, and used them as fixed factors. The model (Suppl. Tables S8–S9, Fig. S2) was significant (p=0.010); the Pleon was a negative factor, the Clade Level was a positive factor.

Independent proof of the morphological synapomorphies prediction power was obtained using tetrachoric correlations between all parameters of our dataset and Habitat (set as: pelagic=1, benthopelagic=0). Table (Suppl. Table S10) shows that both factors, the Pleon (p=0.002) and the Clade Level (p=0.007), are significantly correlated with Habitat, the former negatively, the latter positively.

Table 3. Pleon-linked synapomorphies of Euphausiidae, Benthesicymidae, Oplophoroidea and Sergestoidea.
Таблица 3. Связанные со строением плеона синапоморфии Euphausiidae, Benthesicymidae, Oplophoroidea и Sergestoidea.

Euphausiidae	**Benthesicymidae**	**Oplophoroidea**	**Sergestoidea (in male)**
Somite IV, mid-dorsal spine present	Somite III, a short posteromedian spine present	Somite I, anterior margin armed with a barb or tooth	Somite VI with two ventral processes
Somite IV, additional pair of dorsal teeth present	Somite IV, posterolateral margin crenate	Somite II, strong posteromesial tooth present	Somite VI with not tapering, obtuse posterior ventral process
Somite IV, three short rows of integumental pits in depressed grooves which have elevated keel-like borders present	Somite VI, dorsolateral carina present	Somite IV, sulcus present	Somite VI with tapering, acute posterior ventral process
Somite IV, mid-dorsal spine present	Somite VI, ventrolateral carina present	Somite V, dorsal carina present	Somite VI with straight posterior ventral process
Somite V, mid-dorsal spine present	Somite VI greatly elongate,>2.5 times as long as somite V	Somite V, spinules on lateral margin present	Somite VI with curved posterior ventral process
Somite V, additional pair of dorsal teeth present	Somite VI, posteromedian margin curved upward	Somite VI, dorsal carina present	
Somite VI short (nearly as long as somite V)			

Overall, both GLMMs and tetrachoric correlations show that the habitat may be confidently predicted with the use of the information of presence/absence of the pleon-linked synapomorphies, of the Clade level, or of their combination. The absence of the pleon-linked synapomorphies indicates that the clade does not colonize the benthopelagic (i.e., remains pelagic), the species group level clade level suggests that the clade is pelagic.

Discussion

CONTRIBUTION OF MORPHOLOGICAL CHARACTERS TO DIVERSIFICATION OF PLANKTONIC EUCARIDS. In spite of ostensible heterogeneity in distribution of morphological characters supporting diversification within individual taxa, some common patterns are clear.

First of all, patterns of morphological diversification depend on the clade level (the first principal component in Fig. 3A), i.e., diversification at deeper and more terminal nodes involves different character groups. This difference is visible in the contribution of copulatory structures which increases from the deeper to terminal nodes on phylogenetic trees, i.e., from family level to species group level clades (Figs 2; 3C). This finding mirrors a standard model for evolution (e.g., Matute, Cooper, 2021): initially, isolated populations are more likely to diverge only in their secondary sex characters so that there is no mixing among the isolates. As isolation continues, structures involved with feeding and/or locomotion etc. are likely to begin to diverge. Thus the relative importance of the secondary sex characters to overall morphological divergence is reduced from terminal to deeper nodes on the phylogenetic tree. Significance of these organs in the colonization of the pelagic realm has been recognized previously for the decapods in general (Lunina, Vereshchaka, 2017) and further considered in detail for individual taxa (Vereshchaka *et al*., 2017, 2021). These organs account for the main bulk of morphological diversification, especially in Benthesicymidae and Euphausiidae

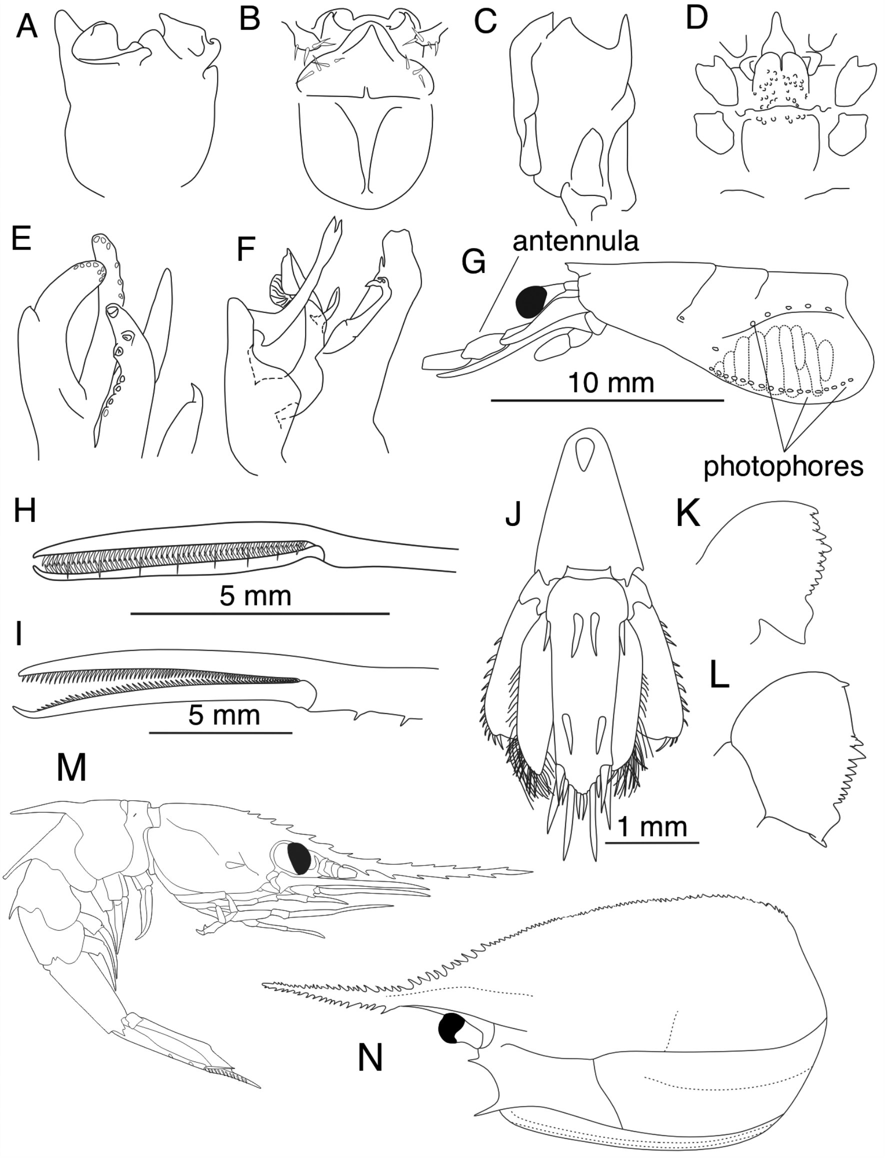

Fig. 5. Examples of synapomorphies supporting phylogenetic clades of Eucarida. A — *Gennadas parvus*, petasma; B — *G. parvus*, thelycum; C — *Trichocaris tirmiziae*, petasma; D — *T. tirmiziae*, thelycum; E — *Phorcosergia filicta*, petasma; F — *Euphausia vallentini*, petasma; G — *Prehensilosergia prehensilis* side view; H — chela of pereopod II in *Psathyrocaris infirma*; I — chela of pereopod II of *Eupasiphae paucidentata*, J — sixth pleonic somite and telson of *Leptochela soelae*; K — mandible of *Acanthephyra brevicarinata*; L — mandible of *Ephyrina bifida*; M — *Oplophorus spinosus*, lateral view; N — *Notostomus elegans*, lateral view of carapace.

Рис. 5. Примеры синапоморфий, подтверждающих филогенетические клады Eucarida. A — *Gennadas parvus*, петазма; B — *G. parvus*, теликум; C — *Trichocaris tirmiziae*, петазма; D — *T. tirmiziae,* теликум; E — *Phorcosergia filicta*, петазма; F — *Euphausia vallentini*, теликум; G — *Prehensilosergia prehensilis*, вид сбоку; H — клешня переопода II у *Psathyrocaris infirma*; I — клешня переопода II у *Eupasiphae paucidentata*, J — шестой плеонический сомит и тельсон у *Leptochela soelae*; K — мандибула *Acanthephyra brevicarinata*; L — мандибула *Ephyrina bifida*; M — *Oplophorus spinosus,* вид сбоку; N — *Notostomus elegans*, карапакс, вид сбоку.

(Fig. 3A, B). Morphological diversification and its contribution to diversification are well documented for the males whose petasmata are very diverse and spectacular (see examples in Fig. 5A–F); in contrast, female structures, the thelyca, are more uniform in Euphausiidae and Sergestoidea and vary only in Benthesicymidae. In the latter group, petasmata and thelyca co-evolve in males and females (Vereshchaka *et al*., 2017). The petasma provides a selective mechanism (sexual selection by female choice) on the morphology of males and simplifies the chance of correct sexual selection (Bauer, 1986, 1991, 1994). Another function of the petasma is to touch and prod the female, providing key stimulation (Bauer, 1986, 1991, 1994), and the elaborate petasma facilitates this function. (Lunina, Vereshchaka, 2017). Interestingly, copulatory structures are not so important in two caridean families but the absence of elaborated structures, at least in some Oplophoridae, may be partly balanced by a species-specific spination of fifth pereopods that likely participate in mating (Lunina *et al*., 2019a).

Pereopods is the second (after copulatory structures) morphological factor explaining diversification of the eucarid planktonic clades (Fig. 3B). Albeit widely distributed across the eucarid taxa (Fig. 2), these synapomorphies are not specific for any particular taxon or clade level (although rarely support species group clades: Fig. 3C).

Synapomorphies linked to the carapace, the pleon, and the mouthparts are widely distributed across the analyzed taxa and clades (Fig. 2) and are especially important for morphological diversification of caridean shrimps (Fig. 3A, B). They are also more important for the species group level clades than for the genus and family level clades (Fig. 3C), although this dependence is not as clear as for the copulatory structures.

Last but not least, each major taxon has its own space on the PCA plot. Fig. 3A, B show that all five taxa are isolated (convex hulls do not even overlap), i.e., diversification of each taxon is driven by a unique combination of morphological characters at family, genus, and species group levels. That means that in the multidimensional space each taxon shows its own diversification pattern that is projected on the two-dimensional plane as non-overlapping contours. In particular, Fig. 3B shows that morphological diversification of Benthesicymidae, Euphausiidae, and Caridea is manly driven by different characters: copulatory structures (Benthesicymidae), pereopods and copulatory structures (Euphausiidae), carapace, pleon, and mouthparts (Oplophoroidea and Pasiphaeoidea). Proportional contribution of these characters to diversification is unique for each taxon and also depends on the taxon level. From a practical standpoint that means that we can likely solve an inverse problem: with information of contribution that morphological characters make to a clade diversification we can recognize a taxon regardless hierarchical level of the clade. We invite researchers to test this hypothesis on other taxonomic groups.

CHARACTER GROUPS AS COEVOLVING FUNCTIONAL UNITS. Morphological characters showed definite coevolution between characters groups linked to different functions. Dendrograms (Fig. 4) mirror three principal functional groups.

Mating function that is primarily provided by copulatory characters (Fig. 5A–F). These structures evolve independently of the rest of the characters that are not involved in mating directly. In Benthesicymidae, male and female organs are very diverse and show strong coevolution (Vereshchaka *et al*., 2017), whereas in Euphausiidae and Sergestoidea only male organs are vary greatly while the female organs remain more or less uniform (Vereshchaka *et al*., 2014, 2019a; Vereshchaka, 2017).

The photophores, the antennula, and the eye (Fig. 5G) serve a sensory and communicative function. These structures form the second major branch of the dendrogram as a coevolved as an integrated evolutionary unit. The antennula and the eye are the most tightly coupled in the eucarid evolution (Fig. 4). Photophores are separated a bit more on the dendrograms: they are more developed in swarming eucarids, possibly owing to their communicative function in swarming species and recognizing mates (Vereshchaka, 2017) or perhaps in the identification of mates.

Feeding and defense function is provided by the mouthparts, the pereopods, the pleon, and the carapace that created the third major branch on the dendrogram and also coevolved as an integrated evolutionary unit. Within this branch, the mouthparts and the pereopods (Fig. 5H–L) created the most tightly coevolving group linked to the feeding function. Pursuing, catching and crushing (carnivores) or filtering and grazing (omnivores and herbivores) — all these actions are done with the mouthparts and the pereopods (e.g., Bauer, 2023) (Fig. 5H–L). The carapace and the pleon (including the telson) provide defense, either passive or active. Passive defense (protection of eucarids from carnivores) is primarily linked to the acute rostrum as well as to long and sharp teeth on the carapace and pleon (Fig. 5M, N). Firm and large dorsal spines are especially large and firm in Oplophoroidea (*Notostomus*, *Oplophorus* in Oplophoroidea: Fig. 5M) and Euphausiidae (*Thysanopoda tricuspidata* in Euphausiidae). Armament and shape of the telson (Fig. 5J) coupled with comb-like carina and lappet on the posterior pleonic somites in *Leptochela* (Pasiphaeoidea) may help in anchorage on the rocky bottom and macrophytes. Conversely, sandy or oozy ground cause such adaptations as spatulate rostrum in *Pseudeuphausia* (Euphausiidae) or spatulate endpiece on the telson (part of *Systellaspis* and *Hymenodora* in Oplophoroidea) that likely serve in bedding into loose sediments (Vereshchaka *et al.*, 2019a; Lunina *et al.*, 2024) as well as spatulate rostrum and telson of *Lophogaster* and *Paralophogaster* favour them to dig into sediments in aquaria (Vereshchaka, 1995).

Active defense (escapement from predators) is primarily linked to the pleon. Pelagic eucarideans have more elongated last pleonic somites providing more effective backward escapement flips (e.g., '*Acanthephyra pelagica*' species group: Kulagin *et al.*, 2024). Such adaptations as serration of the pleurae may acts like a spoiler on a hydrofoil, whereas various keels or sulci provide additional support and better rudder control during the flips (Oplophoroidea: Lunina *et al.*, 2019a). Elongated rostrum (respective to those in benthopelagic relatives) in pelagic *Acanthephyra* and *Oplophorus* (Oplophoroidea) or *Eupasiphae* and *Parapasiphae* (Pasiphaeoidea) provide additional rudder control. Such functions cannot be proven by direct observations in planktonic organisms but are well known and currently studied in detail by undersurface vessel engineers (e.g., Liu *et al.*, 2023).

THE 'BIOTOPE' HYPOTHESIS: THE PLEON AND THE CLADE LEVEL AS PREDICTORS OF PELAGIC OR BENTHOPELAGIC HABITAT OF THE CLADES. Both GLMMs and tetrachoric correlations show that we may predict a principal biotope type (pelagic or benthopelagic) inhabited by a specific clade if we have information about the presence or absence of the pleon-linked synapomorphies (Suppl. Tables S2–S6, examples listed in Table 3) or the clade level (Suppl. Tables S2–S6, model-assessed and cannot be listed). This is one of the most interesting outcomes of our analyses.

The first predictor, the absence of the pleon-linked synapomorphies suggests that the clade is pelagic, whereas the presence of these synapomorphies indicates the benthopelagic habitat. In order to explain this, we suggest that diversification within the pelagic realm usually excludes morphological changes in the pleon, i.e., the pleon is the most conservative structure in the water column. As the pleon in the planktonic eucarids is mainly linked to active or passive defense (see previous section), the pleon-linked characters are likely always perfectly adapted to the pelagic lifestyle and any change in these structures may be "safety-critical". Conversely, benthopelagic habitat that is greatly more diverse in ecological niches 'offers' a number of opportunities for morphological diversification in the pleon to fit particular habitats (oozy or sandy grounds, rocks, macrophytes, etc.).

For example, such pleonic characters as proportions of the posterior somites differ in phylogenetically related pelagic and benthopelagic taxa: somites are longer and thinner in pelagic groups and thicker and shorter in diverged benthopelagic groups (Vereshchaka *et al.*, 2022). This trend may be exemplified by the panoceanic shrimp genus *Acanthephyra*. Three benthopelagic species of the '*Acanthephyra smithi*' clade have the shortest and the most ponderous 6th somites (Kulagin *et al.*, 2024: fig. 4B). The pelagic '*Acanthephyra pelagica*' clade has more elongated and thinned somite likely providing more effective tail flips and more efficient escape from predators. Finally, the clade "*A. kingsleyi* + *A. quadrispinosa* + *A. purpurea*' has the longest and thinnest 6th pleonic somites that may provide the best chance to escape from carnivores feeding on these shrimps. The elongation of the last pleonic somites results in a successful colonization of the pelagic realm because the last three species dominate at least in the Atlantic waters (Judkins, 2014). The posterior pleonic somites serve as an engine, whereas proportions between the somites may significantly drive efficiency and trajectory of the backward flips through different types of rudder control as in other Acanthephyridae (Lunina *et*

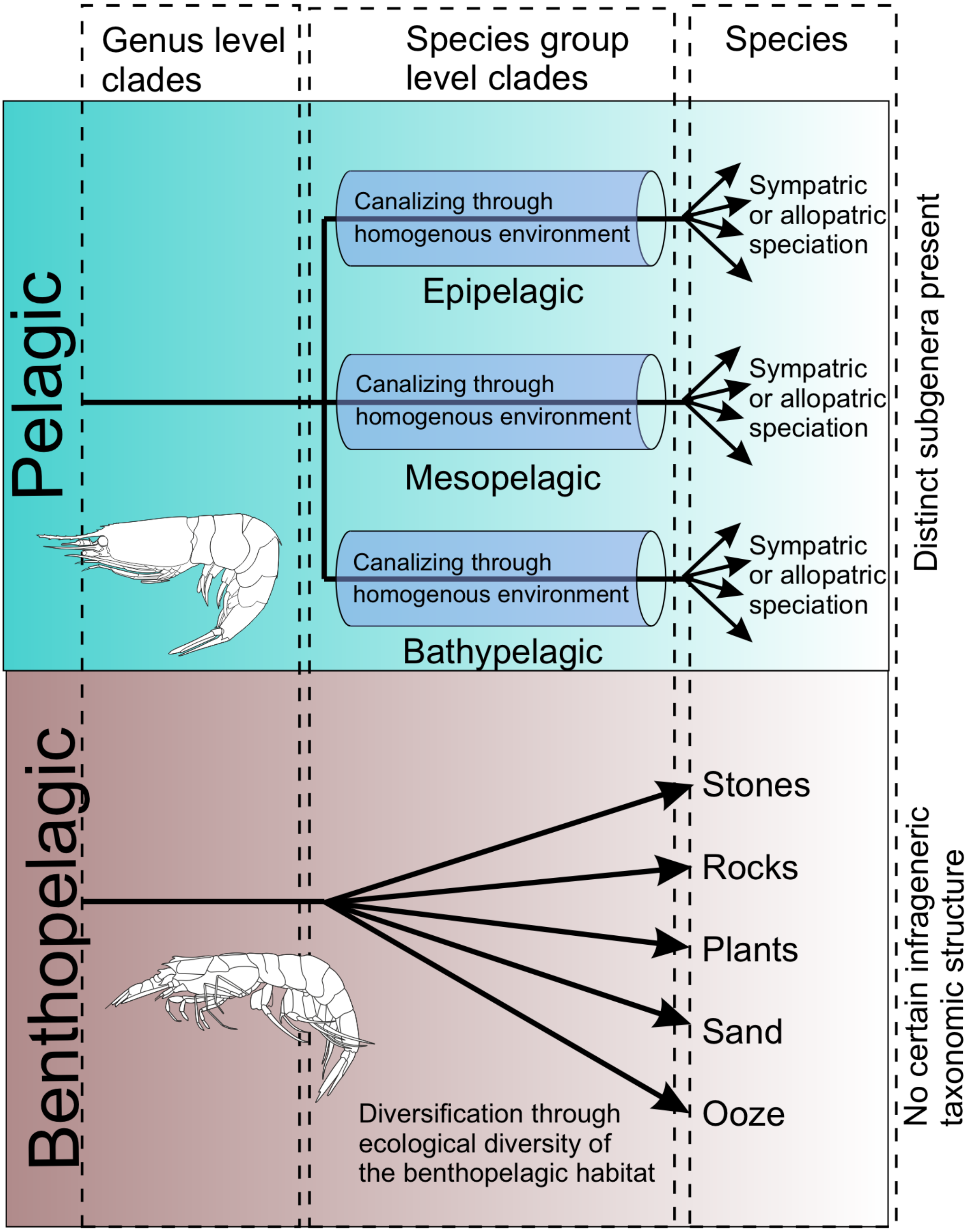

Fig. 6. Schematic evolution of planktonic eucarids in the pelagic (infrageneric speciation canalized into species groups) and benthopelagic (no species groups).
Рис. 6. Схема эволюции планктонных эукарид в пелагических и бентопелагических местообитаниях.

al., 2021; Vereshchaka *et al*., 2022) as shown by marine engineers (e.g., Liu *et al*., 2023). As the posterior pleonic somites (along with the tail fan) serve as an engine during the backward flips, thinner and longer somites provide higher speed and a longer escaping path (Lunina *et al*., 2021; Vereshchaka *et al*., 2022; Kulagin *et al*., 2024), which is important in the pelagic. Conversely, benthopelagic eucarideans may conceal in nearby shelter, which shortens the escapement path and makes elongate posterior pleonic somites redundant. Instead, shorter and more massive somites, especially if coupled with spatulate endpiece on the telson (e.g., *Hymenodora acanthitelsonis* Wasmer, 1972, *Hymenodora chacei* Wasmer, 2022 or *Janicella* Chace, 1986) are advantageous near the bottom because they are more successful in digging in sediments during the daytime as shown in aquaria observations on lophogastrids (Vereshchaka, 1995).

The second predictor is the clade level. Species group level clades are pelagic (the only possible exception is the '*Acanthephyra armata*' species group), whereas benthopelagic clades are nearly all genus level clades. That suggests that colonization of the benthopelagic usually occurs at the genus level and further diversification within this habitat is limited to the species level and does not result in formation of species group clades. The benthopelagic *Pasiphaea* is only an ostensible exception from this rule because species groups proposed by Hayashi (1999, 2004, 2006) have not been supported by resent molecular analyses (Liao *et al*., 2017) and we do not consider them here.

Depending on the bottom characteristics, the benthopelagic 'offers' a lot of very diverse ecological niches to colonize depending on substrate type and near-bottom hydrography (Vereshchaka, 1995) and the genus clade diversification cannot be canalized into a restricted number species groups dwelling in a restricted number of habitats (Fig. 6). Instead, diversification occurs through adaptation to ecologically diverse habitats and through speciation without certain infrageneric taxa such as species groups. Conversely, pelagic biotope favours further diversification at the species group level because it encompasses a lower niche variation and a limited number of habitats (e.g., Dickey-Collas *et al*., 2017) with respectively homogenous environmental conditions (Fig. 6). Infrageneric diversification is, therefore, channelized into numerous species group-level clades in the mesopelagic (e.g., '*Acanthephyra purpurea*' in Decapoda (Vereshchaka *et al*., 2024), '*Thysanoessa gregaria*' in Euphausiidae (Vereshchaka *et al*., 2019)) or the bathypelagic ('*Acanthephyra tenuipes*' in Oplophoroidea (Vereshchaka *et al*., 2024), '*Thysanopoda cornuta*' in Euphausiidae (Vereshchaka *et al*., 2019)), etc.

Supplementary data. The following materials are available online.

Fig. S1. A–C — hierarchical dendrograms retrieved using Ward's; D–F — Complete Linkage Methods. Interval measure: Squared Euclidean (A, D), Euclidean (B, E), and Minkovski (C, F).

Fig. S2. Visualized GLMMs with Habitat (pelagic or benthopelagic) as a target. Analysis 1: all nine fixed factors included: (1) Carapace, (2) Pleon, (3) Antennula, (4) Eye, (5) Mouthparts, (6) Pereopods, (7) Photophores, (8) Copulatory structures, and (9) Clade Level. Analysis 2: only Pleon included as a fixed factor. Analysis 3: only Clade Level included as a fixed factor. Analysis 4: both Pleon and Clade Level included as fixed factors.

Table S1. Specimens of Pasiphaeoidea morphologically examined for current analyses. NMHN — National Museum of Natural History, France; ZMMU — Zoological Museum Moscow State University; LACM — Natural History Museum of Los Angeles County, USNM — Smithsonian National Museum of Natural History.

Table S2. Morphological synapomorphies supporting Benthesicymidae clades and their habitat, pelagic (P) or benthopelagic (BP).

Table S3. Morphological synapomorphies supporting Euphausiidae clades and their habitat, pelagic (P) or benthopelagic (BP).

Table S4. Morphological synapomorphies supporting Oplophoroidea clades and their habitat, pelagic (P) or benthopelagic (BP). '*Hymenodora glacialis*' and '*Hymenodora gracilis*' complexes (Lunina *et al*., 2024), '*Systellaspis braueri*', '*Systellaspis debilis*', '*Systellaspis cristata*', and '*Systellaspis lanceocaudata*' species groups (Lunina, 2019a) are considered as genus-level clades owing to genus-level molecular and morphological differenced among them (Vereshchaka *et al*., 2025).

Table S5. Morphological synapomorphies supporting Sergestoidea clades and their habitat, pelagic (P) or benthopelagic (BP).

Table S6. Morphological synapomorphies supporting Pasiphaeoidea clade and their habitat, pelagic (P) or benthopelagic (BP). *Eupasiphae* and *Parapasiphae* considered here as separate genera because (1) monophyly on molecular tree of *Eupasiphae* was rejected by the Bayes factor test but not by the

AU one in Liao *et al*. (2017) and (2) both genera are supported by a set of distinct morphological synapomorphies. *Glyphus* not included because supporting synapomorphies were not found.

Table S7. Contribution (C_i) of various synapomorphies to diversification of planktonic eucarids.

Table S8. Results of GLMMs with Habitat (pelagic or benthopelagic) as a target. Analysis 1: all nine fixed factors included: (1) Carapace, (2) Pleon, (3) Antennula, (4) Eye, (5) Mouthparts, (6) Pereopods, (7) Photophores, (8) Copulatory structures, and (9) Clade Level. Analysis 2: only Pleon included as a fixed factor. Analysis 3: only Clade Level included as a fixed factor. Analysis 4: both Pleon and Clade Level included as fixed factors.

Table S9. Fixed coefficients in GLMMs with Habitat (BP=benthopelagic) as a target. Analysis 1: all nine fixed factors included: (1) Carapace, (2) Pleon, (3) Antennula, (4) Eye, (5) Mouthparts, (6) Pereopods, (7) Photophores, (8) Copulatory structures, and (9) Clade Level. Analysis 2: only Pleon included as a fixed factor. Analysis 3: only Clade Level included as a fixed factor. Analysis 4: both Pleon and Clade Level included as fixed factors.

Table S10. Tetrachoric correlations between Habitat, absence (0) /presence (1) of synapomorphies in morphological characters, Clade Level, and major biotope (pelagic=1, benthopelagic=0). Statistically significant values are in bold.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

Data availability statement

The data that support this study are available in the article and accompanying online supplementary material.

Acknowledgements. We would like to express our sincere gratitude to Dr. F. Ferrari for his invaluable feedback, which has significantly contributed to the improvement of this manuscript.

This research was supported by the Russian Science Foundation under Project numbers 22-14-00187 (molecular and morphological analyses) and 22-17-00154 (material collection).

References

Atkinson A., Siegel V., Pakhomov E.A., Jessopp M.J., Loeb V. 2009. A re-appraisal of the total biomass and annual production of Antarctic krill // Deep Sea Research Part I: Oceanographic Research Papers. Vol.56. P.27–740.

Bauer R.T. 1986. Sex change and life history pattern in the shrimp *Thor manningi* (Decapoda: Caridea): a novel case of partial protandric hermaphroditism // The Biological Bulletin. Vol.170. P.11–31.

Bauer R.T. 1996. A test of hypotheses on male mating systems and female molting in decapod shrimp, using *Sicyonia dorsalis* (Decapoda: Penaeoidea) // Journal of Crustacean Biology. Vol.16. P.429-436.

Bauer R.T. 1991. Sperm transfer and storage structures in penaeoid shrimps: a functional and phylogenetic perspective // Crustacean Sexual Biology. New York, NY, USA: Columbia University Press. P.183–207.

Bauer R.T. 1994. Usage of the terms thelycum and spermatheca in the reproductive morphology of the Decapoda, with special reference to the Penaeoidea // Journal of Crustacean Biology. Vol.14. P.715–721.

Bauer R.T. 2023. Shrimps: their diversity, intriguing adaptations and varied lifestyles // Cham: Springer International Publishing. Vol.42. 720 p.

Bonett D.G., Price R.M. 2005. Inferential methods for the tetrachoric correlation coefficient // Journal of Educational and Behavioral Statistics. Vol.30. P.213–225.

Dickey-Collas M., McQuatters-Gollop A., Bresnan E., Kraberg A.C., Manderson J.P., Nash R.D., Trenkel V.M. 2017. Pelagic habitat: exploring the concept of good environmental status // ICES Journal of Marine Science. Vol.74. P.2333–2341.

Everson I. 2000. Krill: biology, ecology and fisheries. London, UK: Blackwell Science. 348 p.

Gjøsaeter J., Kawaguchi K. 1980. A review of the world resources of mesopelagic fish // Food Agriculture Org. P.193–199.

Hayashi K.-I. 1999. Crustacea Decapoda: revision of *Pasiphaea sivado* (Risso, 1816) and related species, with descriptions of one new genus and five new species (Pasiphaeidae) // A. Crosnier (ed.). Résultats des Campagnes MUSORSTOM. Muséum National d'Histoire Naturelle, Paris. P.267–302.

Hayashi K.-I. 2004. Revision of the Pasiphaea cristata Bate, 1888 species group of *Pasiphaea savigny*, 1816, with descriptions of four new species, and referral of *P. australis* Hanamura, 1989 to *Alainopasiphaea* Hayashi, 1999 (Crustacea: Decapoda: Pasiphaeidae) // B.A. Marshall, B. Richer de Forges (eds.). Tropical Deep-sea Benthos. Muséum National d'Histoire Naturelle, Paris. P.319–373.

Hayashi K.-I. 2006. Revision of the *Pasiphaea alcocki* species group (Crustacea, Decapoda, Pasiphaeidae) // B. Richer de Forges, J.L. Justine (eds.). Tropical Deep-sea Benthos. Muséum National d'Histoire Naturelle, Paris. P.193–241.

Irigoien X., Klevjer T.A., Røstad A., Martinez U., Boyra G., Acuña J.L., ... Kaartvedt S. 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean // Nature Communications. Vol.5. Art.3271.

Judkins D.C. 2014. Geographical distribution of pelagic decapod shrimp in the Atlantic Ocean // Zootaxa. Vol.3895. P.301–345.

Kemp S. 1939. On *Acanthephyra purpurea* and its allies (Crustacea Decapoda: Hoplophoridæ) // Annals and Magazine of Natural History. Vol.4. P.568–579.

Kulagin D.N., Lunina A.A., Simakova U.V., Vedenin A.A., Vereshchaka A.L. 2024. Revision of the 'Acanthephyra purpurea' species complex (Crustacea: Decapoda), with an emphasis on species diversification in the Atlantic // Molecular Phylogenetics and Evolution. Vol.195. Art.108070.

Lam V., Pauly D. 2005. Mapping the global biomass of mesopelagic fishes // Sea Around Us Project Newsletter. Vol.3. P.4.

Liao Y., De Grave S., Ho T.W., Ip B.H., Tsang L.M., Chan T.Y., Chu K.H. 2017. Molecular phylogeny of Pasiphaeidae (Crustacea, Decapoda, Caridea) reveals systematic incongruence of the current classification // Molecular Phylogenetics and Evolution. Vol.115. P.171–180.

Lunina A.A., Vereshchaka A.L. 2017. The role of the male copulatory organs in the colonization of the pelagic by shrimp-like eucarids // Deep Sea Research Part II: Topical Studies in Oceanography. Vol.137. P.327–334.

Lunina A.A., Kulagin D.N., Vereshchaka A.L. 2024. The taxonomic status of *Hymenodora* (Crustacea: Oplophoroidea): morphological and molecular analyses suggest a new family and an undescribed diversity deep in the sea // Zoological Journal of the Linnean Society. Vol.200. P.336–351.

Lunina A.A., Kulagin D.N., Vereshchaka A.L. 2019a. Oplophoridae (Decapoda: Crustacea): phylogeny, taxonomy and evolution studied by a combination of morphological and molecular methods // Zoological Journal of the Linnean Society. Vol.186. P.213–232.

Lunina A.A., Kulagin D.N., Vereshchaka A.L. 2019b. A hard-earned draw: phylogeny-based revision of the deep-sea shrimp *Bentheogennema* (Decapoda: Benthesicymidae) transfers two species to other genera and reveals two new species // Zoological Journal of the Linnean Society. Vol.178. P.15–32.

Lunina A.A., Kulagin D.N., Vereshchaka A.L. 2021. Phylogenetic revision of the shrimp genera *Ephyrina, Meningodora* and *Notostomus* (Acanthephyridae: Caridea) // Zoological Journal of the Linnean Society. Vol.193. P.1002–1019.

Matute D.R., Cooper B.S. 2021. Comparative studies on speciation: 30 years since Coyne and Orr // Evolution. Vol.75. P.764–778.

Mauchline J., Fischer L.R. 1969. The biology of euphausiids // Advances in Marine Biology. Vol.7. P.1–454.

Nicol S., Foster J., Kawaguchi S. 2012. The fishery for Antarctic krill – recent developments // Fish Fish. Vol.13. P.30–40.

Vereshchaka A.L. 1995. Macroplankton in the near-bottom layer of continental slopes and seamounts // Deep Sea Research Part I: Oceanographic Research Papers. Vol.42. P.1639–1668.

Vereshchaka A.L. 2000. The genus *Sergia*: taxonomy, systematics, and distribution // Galathea Report. Vol.19. 207 p.

Vereshchaka A.L. 2009. Revision of the genus *Sergestes* (Decapoda: Dendrobranchiata: Sergestidae): taxonomy and distribution // Galathea Report. Vol.22. P.7–104.

Vereshchaka A.L. 2017. The shrimp superfamily Sergestoidea: a global phylogeny with definition of new families and an assessment of the pathways into principal biotopes // Royal Society Open Science. Vol.4. Art.170221.

Vereshchaka A.L., Olesen J., Lunina A.A. 2014. Global diversity and phylogeny of pelagic shrimps of the former genera *Sergestes* and *Sergia* (Crustacea, Dendrobranchiata, Sergestidae), with definition of eight new genera // PloS One. Vol.9. Art.e112057.

Vereshchaka A.L., Lunina A.A., Olesen J. 2017. The genus *Gennadas* (Benthesicymidae: Decapoda): morphology of copulatory characters, phylogeny and coevolution of genital structures // Royal Society Open Science. Vol.4. Art.171288.

Vereshchaka A.L., Kulagin D.N., Lunina A.A. 2019a. A phylogenetic study of krill (Crustacea: Euphausiacea) reveals new taxa and co-evolution of morphological characters // Cladistics. Vol.35. P.150–172.

Vereshchaka A.L., Lunina A.A., Sutton T. 2019b. Assessing deep-pelagic shrimp biomass to 3000m in the Atlantic Ocean and ramifications of upscaled global biomass // Scientific Reports. Vol.9. Art.5946.

Vereshchaka A.L., Kulagin D.N., Lunina A.A. 2021. Across the benthic and pelagic realms: a species-level phylogeny of Benthesicymidae (Crustacea: Decapoda) // Invertebrate Systematics. Vol.35. P.776–796.

Vereshchaka A.L., Kulagin D.N., Lunina A.A. 2022. Discovery of a new species provides a deeper insight into taxonomic grouping of the deep-sea genus *Acanthephyra* (Crustacea: Decapoda) // Diversity. Vol.14. Art.907.

Vereshchaka A.L., Kulagin D.N., Lunina A.A., Shatravin A.V. 2024. A global revision of Oplophoroidea (Caridea: Decapoda) with a novel approach for visualizing genetic differences between species // Organisms Diversity & Evolution. Vol. 24. P.507–532.

Williams D.M., Lee M.J.C.R.J. 2014. Principles of Cladistics. Cambridge University Press.

Responsible editor V.N. Ivanenko