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Genetic variability of abundant littoral species of mesostigmatic mites (Acari, Mesostigmata) with different distributions from the seashores of Eurasia

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Original research

ABSTRACT

The marine littoral acarofauna is of interest both in relation to the history of seas and as biological indicators of water quality, but it remains poorly studied. For the first time, we characterize the molecular genetic variability of four widespread, common and abundant species of littoral mesostigmatic mites: *Phorytocarpais kempersi*, Parasitidae; *Halolaelaps celticus* and *Halolaelaps orientalis*, Halolaelapidae; and *Thinoseius spinosus*, Eviphididae. Based on the nucleotide sequence analysis of nuclear ribosomal repeats (ITS), we studied mite collections from the coasts of the Caspian, Azov, Black, Baltic, White, Barents, Norwegian, Bering, Okhotsk, and Japan seas. The molecular identification of the species studied, based on DNA barcoding using ITS sequences, appears to be clear. We obtained genetic evidence for the separation of *Halolaelaps celticus* and *H. orientalis* as two distinct species, based both on clustering their ITS genotypes (separated by 6 parsimony-informative substitutions) and the geographic distributions of their genotypes. The high genetic similarity of the western and eastern Palaearctic populations in both arctic-adapted species, *Phorytocarpais kempersi* and *Thinoseius spinosus*, is explicable in terms of their rather recent contact on the northern coast of Eurasia during the last interglacial or Holocene climatic optimum. The high genetic similarity of *Halolaelaps orientalis*, a relatively thermophilous species, from the Mediterranean region (the Azov, Black, and Caspian seas) with a sample from the very distant Sea of Japan suggests a recent connection between the European and Pacific populations via the Indian Ocean.

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Introduction

Littoral animal species often show extensive, contour in form (“band” according to Heptner 1936) distribution areas and reliable mechanisms of dispersal. This is also true for a number of mites inhabiting the grounds of the marine intertidal zone and coastal seaweed accumulations (Evans 1962; Lindroth *et al.* 1973; Tikhomirov 1977; Pugh *et al.* 1997; Procheş and Marshall 2001). Mites in general represent the largest group of soil arthropods on Earth in terms of population density (Rosenberg *et al.* 2023), on seashores in particular (Forgie *et al.* 2013). Members of the suborder Mesostigmata are the most diverse and abundant components of coastal acarofauna (Halbert 1920; Luxton 1967; Haynert *et al.* 2017), and their diversity in

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costal habitats at only one locality can reach 40–60 species (Makarova and Bizin 2020; Bizin and Makarova 2022).

Being small organisms (most less than 1 mm in length), mites have enormous potentials for passive dispersal. Thus, mites have been revealed among neuston animals near the Galápagos Islands (Peck 1994). Rafting on different plant residues (seaweeds, logs, grass tussocks) or on ice-floes together with organic debris offers vast dispersion possibilities for littoral mites (Lindroth *et al.* 1973; Schatz 1991), especially during catastrophic tsunami events (Lindo 2020). Their resistance to flooding (Krantz 1974; Schuster 1979; Pugh *et al.* 1987; Avdonin 1999; Makarova and Petrova-Nikitina 2008) and phoresy on other arthropods (Remmert 1956; Evans 1962; Egglshaw 1966; Lindroth *et al.* 1973; Rigby 1996a, b; Pugh *et al.* 1997; Klimov 1998; Avdonin 1999; Takaku 2000; Makarova and Böcher 2009; Gwiazdowicz and Coulson 2010; Halliday 2010; Trach 2016) have been repeatedly demonstrated and could contribute to intense genetic exchanges. However, significant events in the history of the seas (glaciations, isolations etc.) might lead to the segregation of local clusters, which could be reflected in the genetic peculiarity of modern populations. Recently, processing the available data on vertebrates has shown that intraspecies genetic diversity is not related to distribution area size, but regional factors play significant roles instead (Lawrence and Fraser 2020). There seem to be no publications yet concerning the phylogeography of littoral mesostigmatic mites, while interesting results have already been obtained using material of tropical and Arctic species of coastal oribatid mites. For example, a connection between the genetic structure of supraspecific complexes, dispersal capacities and landscape history has been demonstrated, as well as sibling species discoveries (Pfungstl *et al.* 2018, 2019a, b, 2022; Artamonova *et al.* 2023).

Among the littoral mesostigmatic mites of the Holarctic, there are a number of species with extensive distributions (Tikhomirov 1977; Błaszak and Ehrnsberger 1998; Makarova 2015; Makarova and Bizin 2020). Our numerous collections from Eurasia, North America and Greenland reveal that only four species representing different families of the suborder Mesostigmata appear to be especially common and widespread. These are *Phorytocarpais kempersi* (Oudemans, 1902) [= *Parasitus kempersi* Oudemans, 1902 in GenBank; see the new combination in Makarova, 2019, p. 460], Parasitidae; *Halolaelaps celticus* (Halbert, 1915) and *Halolaelaps orientalis* Ishikawa, 1979, Halolaelapidae; and *Thinoseius spinosus* (Willmann, 1939), Eviphididae. It is the complex history of the seas of the Ancient Mediterranean, the regular disruptions of their connections to each other and with the waters of the Atlantic Ocean (Rychagov 1997; Rögl 1999; Svitoch 2008, 2013; Svitoch *et al.* 2010; van Baak *et al.* 2016; Krijgsman *et al.* 2019), as well as the significant climatic diversity of the modern coasts of Eurasia, that has prompted us to analyze the genetic structure of these mesostigmatic species using material from various seas. In this regard, the analysis of their genotypes from the Caspian Sea is of particular interest, because of the exceptionally high level of species endemism of Caspian marine animals (Mordukhai-Boltovskoi 1979; Wesselingh *et al.* 2019), with up to 57–77% in crustacean Amphipoda and fishes (Pjatakova and Tarasov 1996; Naseka and Bogutskaya 2009; Copilaş-Ciocianu and Sidorov 2022).

The modern molecular phylogeny of Mesostigmata is based on the study of the variability of the 18S and 28S rRNA nuclear ribosomal genes and COI mitochondrial gene (Klompen *et al.* 2007; Sourassou *et al.* 2015; Dabert *et al.* 2010; Dowling and O'Connor 2010). The systematics of mites reconstructed on the basis of molecular data are in good agreement with the macrotaxonomic system of mesostigmatic mites proposed by Lindquist *et al.* (2009).

The different domains of a nuclear ribosomal repeat show different rates of accumulation of phylogenetically significant substitutions, allowing them to be used to separate systematic groups of different rank. The 28S rDNA gene is optimal for identifying mites from family to species level, while the variability of intergenic transcribed spacers (ITS) is higher and may be suitable for separating closely related species (Zhao *et al.* 2020; Pérez-Sayas *et al.* 2022). Some authors have proposed the ITS fragment as a basis for DNA barcoding of mite species (Zhao *et al.* 2020).

The present paper provides the first results of DNA barcoding of abundant species of mesostigmatic mites belonging to the genera *Phorytocarpais*, *Halolaelaps*, and *Thinoseius*, all inhabiting the littoral zone of the Eurasian seas, based on a sequence analysis of the ITS ribosomal repeat fragment. On the one hand, taking into account the perfect dispersal mechanisms of littoral mites and, on the other hand, the exceptionally high-level endemism among the marine invertebrates of the Caspian Sea, both the genetic integrity of extensive trans-oceanic mega-populations of our model littoral species and a certain originality of the Caspian genotypes can be proposed as a null hypothesis.

Characteristics of model species

All four model species of mesostigmatic mites are most common on the seashores of Europe and often co-occur in storm debris cast ashore (Halbert 1920; Hyatt 1956; Strenzke 1963; Lindroth *et al.* 1973; Kojumdzhieva 1982; Pugh and King 1985, 1988; Błaszak and Ehrnsberger 1998; Makarova and Petrova-Nikitina 2008; Bolge *et al.* 2018; Makarova and Bizin 2000; Bizin and Makarova 2022). Below we provide descriptions of their habitats and available biological information.

***Phorytocarpais kempersi* (Oudemans, 1902)**

This species was earlier assumed to be cosmopolitan in distribution, although its absence from the shores of the Caspian Sea, the Aral Sea and Arctic Siberia had been reported simultaneously (Tikhomirov 1977). And there still are no records outside the Holarctic. According to our data, *P. kempersi* is an abundant species in sea debris on the shores of the middle and southern parts of the Caspian Sea (O.L.M.: personal observations). It is common everywhere, including the Atlantic and Pacific coasts of North America (Krantz 2016; material from the Canadian National Collection of Insects, Arachnids and Nematodes, accessed 7 October 2020, curator W. Knee; O.L.M. unpublished data). *Phorytocarpais kempersi* appears first in algal emissions, being most abundant in the early stages of their decay succession (Strenzke 1963; Makarova and Petrova-Nikitina 2008; Bizin and Makarova 2022). Phoresy of its deutonymphs on “larger inhabitants of rotting algae carried by water” has also been reported (Tikhomirov 1977), and the possibility of dispersion on sea-washed algal debris in the summer conditions of the North, Black and White seas has been proven experimentally (Pugh and King 1985; Avdonin 1999; Makarova and Petrova-Nikitina 2008). Moreover, in a special experiment conducted in August 2008 in the White Sea, submerged algae were shown to retain about 80% living *P. kempersi* individuals for at least 5 days (O.L.M.: personal observations). The species has the widest diet among the study littoral mite species. Its sharp increase in numbers was observed when feeding on nematodes, Sphaeroceridae larvae and small crustaceans (Avdonin 2002), but *P. kempersi* also consume enchytraeids, dead and living adults of Diptera, juvenile oribatid and mesostigmatic mites, including individuals of their own species (Pugh and King 1985; Avdonin and Striganova 2004). Simultaneously, 4–7 eggs can mature inside the female (O.L.M.: personal observations). Individuals from the White and Black seas successfully interbreed with each other (Avdonin and Striganova 2004).

***Halolaelaps celticus* Halbert, 1915**

A North Atlantic species penetrating into Arctic waters up to the Pechora Sea in the east (new records from the shores of the Kola Peninsula, Kanin Peninsula, and Dolgiy Island; O.L.M.: personal observations). Due to the significant variations in “diagnostic” characteristics of females of this and related species (Błaszak and Ehrnsberger 1998; Maslov 2013; O.L.M.: personal observations), only records accompanied by the presence of males can be considered reliable. The records of *H. celticus* from the shores of the Black and Azov seas (Bregetova 1977; Koyumdzhieva 1982; Maslov 2013; Bizin and Makarova 2022) seem to actually concern

H. orientalis Ishikawa, 1979 (? = *Halolaelaps schusteri* Hirschmann, 1966; see below) and require verification. The proper *Halolaelaps celticus* is abundant in the early and middle stages of marine debris decay (Strenzke 1963; Makarova and Petrova-Nikitina 2008). This species withstands flooding with seawater within an algal mass for at least 5 days (O.L.M.: personal observations). This can provide its passive dispersal, although phoresy on Amphipoda has been repeatedly shown for other littoral species of the genus (Willmann 1952; Evans and Till 1979; Pugh *et al.* 1997; Trach 2016).

***Halolaelaps orientalis* Ishikawa, 1979 (? = *Halolaelaps schusteri* Hirschmann, 1966)**

A Palearctic species ranging from the Canary Islands to Japan. There are no records from the shores of the Arctic Ocean, Bering and Okhotsk seas. This species was previously listed as the most common member of the *celticus*-group on the shores of the northern and southern seas of continental Europe, as well as the Canary Islands (Błaszczak and Ehrnsberger 1998).

Since an error in the original description of *Halolaelaps schusteri* (structure of setae *j*₁, *z*₁) has been corrected during the analysis of the type material (Błaszczak *et al.* 2004, p. 2), there are no characters left allowing us to securely distinguish between females of *H. schusteri* and *H. orientalis* (Błaszczak and Ehrnsberger 1998). Therefore, all records of “*H. orientalis*” in the Western Palearctic (Błaszczak and Ehrnsberger 1998; Avdonin 2002; Avdonin and Striganova 2004; Maslov 2013; Bizin and Makarova 2022) probably belong to *H. schusteri*, as possibly does the record from Japan as well. The male of *H. orientalis* has not been described yet. Having analyzed its morphological structures, these two species are highly likely to be synonyms. In marine debris, *H. orientalis* forms “quasi-stationary aggregations” (Avdonin and Striganova 2004). In six districts of the Atlantic coast, including the Canary Islands, this species has been noted to live together with *H. celticus* (Błaszczak and Ehrnsberger 1998). The dispersion of *H. orientalis* with floating algae is possible (Avdonin 1999). It feeds actively on nematodes and copepods (Copepoda) (Avdonin and Striganova 2004); the consumption of damaged enchytraeids and dipteran Sphaeroceridae (larvae and adults) was also recorded (Avdonin 1999, 2002).

Morphological diagnostics of *Halolaelaps* species belonging to the *celticus*-group in general [the subgenus *Halolaelaps* (*Halolaelaps*) sensu Błaszczak and Ehrnsberger 1998] are greatly hampered by the uncritical attitude of the above authors to the asymmetry and intra-population variability of the dorsal idiosomal chaetome. Such cases were revealed by various researchers (Maslov 2013; O.L.M.: personal observations), including Błaszczak and Ehrnsberger (1998, p. 165, 167) themselves, thus leading to doubt the validity of the species they described (Błaszczak and Ehrnsberger 1997, 1998).

***Thinoseius spinosus* (Willmann, 1939)**

A Holarctic littoral species. Its records at distances of dozens or hundreds of kilometers away from a sea coast are of special interest. These are records at chicken farms in Oregon, USA (Volkinburg 1969), as well as on the shores of salt lakes in the south of Western Siberia (GenBank ID: MW367935) and in northern Dagestan, North Caucasus (O.L.M.: personal observation). Generally, *T. spinosus* seems to be the “northernmost” representative of the littoral acarofauna; it lives on Spitsbergen (Gwiązdowicz and Coulson 2010), northern Greenland (Makarova 2015), northern Novaya Zemlya and northern Chukotka (O.L.M.: personal observations). There is no information on nutrition, but for other species of the genus active consumption of nematodes was revealed (Egglisshaw 1966; Rigby 1996a), as well as eating crushed enchytraeids, small dipterans and amphipods (Avdonin 1999, 2002). Deutonymphs of *T. spinosus* are actively dispersed when attached to various brachiceran dipterans, Anthomyiidae, Calliphoridae, Coelopidae, Helomyzidae, Heterocheilidae, Sphaeroceridae (Lindroth *et al.* 1973; Klimov 1998; Makarova and Böcher 2009; Gwiązdowicz and Coulson 2010).

Material and methods

Collections of mites

Targeted collections of the model mite species for genetic studies were carried out in 2016–2022 at 30 localities in Eurasia (Figure 1). At each locality, a mixed sample of marine emissions was usually taken from several coastal plots or a series of 3–5 samples was selected. The samples were wrapped in several layers of newsprint (leaving a layer of air), placed in a plastic bag and delivered to the laboratory. Mites were extracted from sea debris using Tullgren funnels made of thick paper and applying neither special lighting, nor heating until they became completely dry within 7–14 days. Mites were fixed with 96% ethanol. All mites selected for DNA isolation and DNA encoding were preliminarily identified by morphological features and preserved in alcohol until molecular identification was performed. Some individuals of a definite mite species were mounted in permanent slides with Hoyer medium for identification; the other part of the series was used in genetic studies. Voucher specimens or series of model species specimens are stored at the Laboratory of Synecology of the Severtsov Institute of Ecology and Ecology of the Russian Academy of Sciences, Moscow. For DNA barcoding, total DNA was isolated from individual mites from each locality. All nucleotide sequences obtained were deposited in GenBank. The characteristics of the mite collection sites, the results of both morphological identification of species and DNA barcoding following the analysis of variability in the nucleotide sequence of the ribosomal repeat fragment are all presented in Tables 1–3.

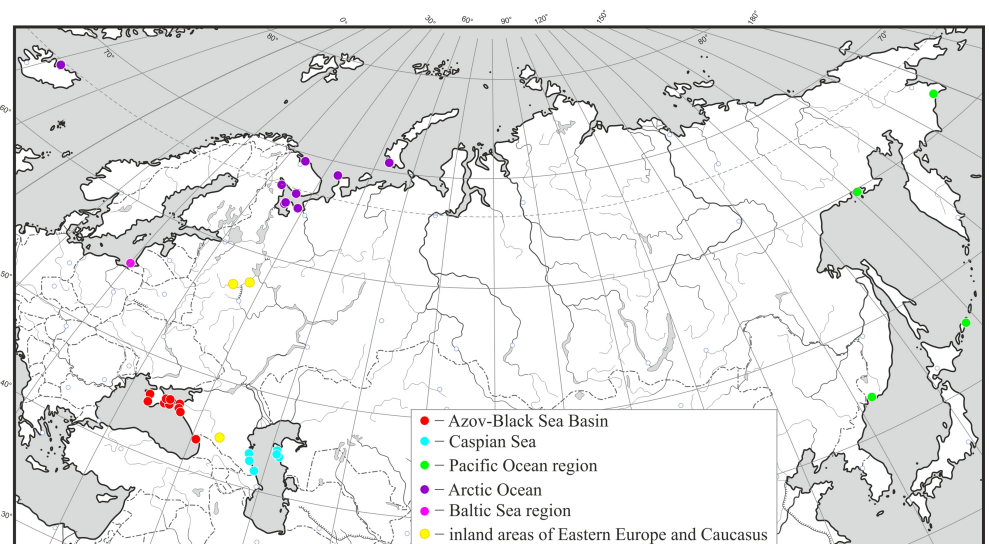


Figure 1 Geographic location of sampling places of coastal mites. See Tables 1–3 for detailed characteristics. Large regions are marked with different colors.

Isolation of total DNA and PCR

Total DNA from individual mites was isolated using the phenol-chloroform method (Maniatis *et al.* 1982). The resulting DNA was dissolved in deionized water. DNA concentration was determined spectrophotometrically utilizing an Implen NanoPhotometer NP80. The DNA concentration in the preparations was adjusted to 4 ng/μl. PCR was carried out in a final volume of 25 μl using EncycloPlus PCR kits (Evrogen, Russia) in accordance with the manufacturer's protocol.

To amplify the ribosomal repeat fragment and sequencing, we used a modified protocol of (White *et al.* 1990, 2013). The primers ITS1F (5'- CTTGGTCATTAGAGGAAGTAA) and

ITS4 (5'-TCCTCCGCTTATTGATATGC-3') were applied to amplify a specific fragment of variable length, formed by a fragment of the 18S rRNA gene; ITS1; 5.8S rRNA gene; ITS2; and a fragment of the 28S rRNA gene. PCR conditions: primary denaturation – 3 min at 94 °C; then 35 cycles: denaturation at 94 °C – 15 s, annealing at 58 °C – 15 s, synthesis at 72 °C – 40 s; and final synthesis at 72 °C – 7 min.

Purification of and sequencing the PCR fragments

The fragments obtained as a result of amplification were fractionated in a 1.5% agarose gel. Elution of fragments from the gel was carried out using the Cleanup Mimi elution kit (Evrogen, Russia) in accordance with the manufacturer’s protocol. The nucleotide sequence of PCR fragments was determined from forward and reverse primers on a 3500 Genetic Analyzer using the BigDye®Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, USA) according to the manufacturer’s recommendations.

Table 1 Description of the collections of mites belonging to the family Parasitidae with genotypes characterized by ITS. Each row of the table contains a description of a genotype that differs from other genotypes either by nucleotide sequence or by mite collection site. The number after the dash in the genotype name is the number of mite individuals processed; the Roman number in the parentheses is the digital name of the genotype. Abbreviations: AB – Azov-Black Sea basin, AO – Arctic Ocean, B – Baltic region, C – Caspian region, PO – Pacific Ocean.

#	ITS isolate (genotype)	Region	District	Biotope	Collector and date	Latitude, longitude	GenBank ID (this study)
<i>Phorytocarpais kempersi</i> (Oudemans, 1902)							
1	Pa10-2_Derbent (I)	C	Caspian Sea, Derbent	Sandy beach, seaweeds	Makarova O., Zavyazkina L., 05 Jan. 2020	42.057012 N, 48.309910 E	PP317488
2	Pa10-3_Derbent (II)	C	Caspian Sea, Derbent	Sandy beach, seaweeds	Makarova O., Zavyazkina L., 05 Jan. 2020	42.057012 N, 48.309910 E	PP317489
3	Pa11-4_Novorossiysk (II)	AB	Black Sea, Novorossiysk	Pebbly beach, seaweeds	Ivanova T., 04 Nov. 2016	44.715625 N, 37.785636 E	PP317490
4	Pa12-8_Makhachkala (I)	C	Caspian Sea, Makhachkala	Sandy beach, sea debris	Makarova O., Zavyazkina L., 11 Jun. 2021	42.968213 N, 47.548986 E	PP317491
5	Pa13-1_Izberbach (I)	C	Caspian Sea, Izberbash	Sandy beach, sea debris	Makarova O., Makarov K., 02 May 2022	42.605582 N, 47.829103 E	PP317492
6	Pa15-1_Karagach (I)	AB	Black Sea, Karadag	Pebble beach, seaweeds	Rapoport I., 01 Oct. 2020	44.911664 N, 35.202299 E	PP317493
7	Pa16-1_Solt (I)	AB	Azov Sea, Solyanoec	Shelly soil on seacoast	Potapov M., Kuznetsova N., 26 Sep. 2021	45.339000 N, 35.399000 E	PP317494
8	Pa17-5_Aktau_L (III)	C	Caspian Sea, Aktau	Sandy beach, sea debris	Makarova O., Bizin M., 07 Jun. 2022	43.475186 N, 51.311233 E	PP317495
9	Pa18-32_Aktau-S (I)	C	Caspian Sea, Aktau	Stony beach, seaweeds	Makarova O., Bizin M., 05 Jun. 2022	43.648634 N, 51.143032 E	PP317496
10	Pa18-4_Aktau-S (IV)	C	Caspian Sea, Aktau	Stony beach, seaweeds	Makarova O., Bizin M., 05 Jun. 2022	43.648634 N, 51.143032 E	PP317497
11	Pa19-4_Aktau-V (III)	C	Caspian Sea, Aktau	Stony beach, seaweeds	Makarova O., Bizin M., 06 Jun. 2022	43.702758 N, 51.108390 E	PP317498
12	Pa1-1_Kazantip (VI)	AB	Azov Sea, Kazantip	Shelly soil on seacoast	Potapov M., Kuznetsova N., 27 Sep. 2021	45.445589 N, 35.828001 E	PP317499
13	Pa3-2_New_Afon (II)	AB	Black Sea, New Afon	Sandy beach, seaweeds	Kovaleva E., 06 Jan. 2021	43.076640 N, 40.860496 E	PP317500
14	Pa4-4_Solt (I)	AB	Azov Sea, Solyanoec	Shelly soil on coast	Potapov M., Kuznetsova N., 26 Sep. 2021	45.339000 N, 35.399000 E	PP317501
15	Pa5-10_Anapa (II)	AB	Black Sea, Anapa	Stony beach, sea debris	Artamonova V., Makhrov A., 28 Jun. 2021	44.896421 N, 37.298307 E	PP317502
16	Pa5-11_Anapa (VI)	AB	Black Sea, Anapa	Stony beach, sea debris	Artamonova V., Makhrov A., 28 Jun. 2021	44.896421 N, 37.298307 E	PP317503
17	Pa5-14_Anapa (II)	AB	Black Sea, Anapa	Stony beach, sea debris	Artamonova V., Makhrov A., 28 Jun. 2021	44.896421 N, 37.298307 E	PP317504
18	Pa6-2_Anapa (II)	AB	Black Sea, Anapa	Sandy beach, seaweeds	Lukashevich R., 10 Dec. 2020	45.069801 N, 37.023375 E	PP317505
19	Pa7-2_Enikale (I)	AB	Azov Sea, Kerch	Sandy beach, seaweeds	Artamonova V., Makhrov A., 29 Jun. 2021	45.359171 N, 36.605753 E	PP317506
20	Pa8-5_Derbent (II)	C	Caspian Sea, Derbent	Sandy beach, seaweeds	Makarova O., Zavyazkina L., 05 Jan. 2020	42.057012 N, 48.309910 E	PP317507
21	Pa9-8_Makhachkala (I)	C	Caspian Sea, Makhachkala	Sandy beach, sea debris	Makarova O., Zavyazkina L., 06 Jan. 2020	42.968956 N, 47.544533 E	PP317508
22	Pa-b1-5_Kaliningrad (I)	B	Baltic Sea, Kaliningrad	Sandy beach, seaweeds	Potapov M., 05 Sep. 2022	54.703544 N, 19.947358 E	PP317509
23	Pa-k1-1_Kanin_nos (I)	AO	Barents Sea, Kanin Peninsula	Stony beach, sea debris	Przhobor A., 29 Jul. 2018	68.659501 N, 43.287568 E	PP317510
24	Pa-a1-1_Taman (I)	AB	Azov Sea, Taman Peninsula	Sandy beach, sea debris	Artamonova V., Makhrov A., 19 Aug. 2022	45.353911 N, 37.119178 E	PP317511
25	Pa-i1-1_Iceland (V)	AO	Norwegian Sea, Iceland	Stony marine coast, seaweeds	Babenko A., 31 Jul. 2016	66.041381 N, 17.333029 W	PP317512
26	Pa-it1-1_Itrup (II)	PO	Sea of Okhotsk, Kuriles	Sandy beach, seaweeds	Popov I., 15 Sep. 2022	45.228286 N, 147.875447 E	PP317513
27	Pa-t1-1_Teriberka (I)	AO	Barents Sea, Teriberka	Stony beach, seaweeds	Nekhaeva A., 26 Jun. 2019	69.167639 N, 35.142228 E	PP317514
28	Pa-sol1-4 (II)	AO	White Sea, Solovetsky Is.	Sandy beach, sea debris	Makarova O., 16 Jul. 2014	65.018832 N, 35.878603 E	PP317515
29	Pa-akt1-1 (VII)	C	Caspian Sea, Aktau	Stony beach, seaweeds	Makarova O., Bizin M., 05 Jun. 2022	43.648634 N, 51.143032 E	PP317516
30	Pa-akt2-3 (I)	C	Caspian Sea, Aktau	Stony beach, seaweeds	Makarova O., Bizin M., 05 Jun. 2022	43.648634 N, 51.143032 E	PP317517
31	Pa-mag1-2 (I)	PO	Sea of Okhotsk, Magadan	Stony beach, seaweeds	Makarova O., 22 Sep. 2018	59.569581 N, 151.231224 E	PP317518
32	Pa-mag2-2 (I)	PO	Sea of Okhotsk, Magadan	Stony beach, seaweeds	Makarova O., 22 Sep. 2018	59.569581 N, 151.231224 E	PP317519
33	Pa-pom1-3 (I)	AO	White Sea, Pomorsky Coast	Sandy beach, seaweeds	Timireva S., Kononov Yu., 04 Aug. 2020	66.319751 N, 36.185190 E	PP317520
34	Pa-pom2-1 (I)	AO	White Sea, Pomorsky Coast	Sandy beach, seaweeds	Timireva S., Kononov Yu., 04 Aug. 2020	66.319751 N, 36.185190 E	PP317521
35	Pak12-4_Solovki (I)	AO	White Sea, Solovetsky Is.	Stony beach, seaweeds	Makhrov A., 30 Jun. 2022	65.03418 N, 35.68567 E	PP503298
<i>Pergamasus crassipes</i> (Linnaeus, 1758)							
36	Pec7-3_Kislovodsk	Caucasus	North Caucasus, Kislovodsk	Spruce forest litter	Makarova O., 04 Jan. 2024	43.897359 N, 42.729707 E	PP503293
<i>Pergamasus longicornis</i> (Berlese, 1906)							
37	Pe18-4_Severodvinsk	AO	White Sea, Severodvinsk	Seaweed emissions	Makarova O., 21 Aug. 2018	64.65145 N, 39.82780 E	PP503294

Bioinformatic analysis

Chromatogram analysis was carried out using CromasPro 13.3 software (Technelysium, Australia). Alignment of the sequences obtained in this study with the sequences deposited in GenBank databases was performed using resources from NCBI (<http://www.ncbi.nlm.nih.gov>).

Prior to cladistic analyses, nucleotide sequences were aligned using the ClustalW algorithm (Thompson *et al.* 1994) and MEGA X software (Kumar *et al.* 2018) to obtain a set of sequences of equal length. Cladistic analyses were performed in MEGA7 (Kumar *et al.* 2016). Cladograms were constructed using the neighbour-joining method. Substitution model – due to Maximum Composite Likelihood. Treatment of gaps/missing data – due to Pairwise Deletion.

Table 2 Description of the collections of mites belonging to the family Halolaelapidae, *Halolaelaps* species of the *celticus*-group and *Halolaelaps punctulatus*, with genotypes characterized by ITS. ITS isolate name decoding and regions abbreviations - as in Table 1.

#	ITS isolate (genotype)	Region	District	Biotope	Collector and date	Latitude, longitude	GenBank ID
<i>Halolaelaps orientalis</i> Ishikawa, 1979							
1	Ha1-4_Sevastopol (IV)	AB	Black Sea, Sevastopol	Pebble beach, seaweeds	Makhrov A., 13 Sep. 2021	44.612577 N, 33.502702 E	PP317523
2	Ha2-3_Crimea_Solt (VI)	AB	Azov Sea, Solyanoe	Slime and shelly soil on coast	Potapov M., Kuznetsova N., 26 Sep. 2021	45.339000 N, 35.399000 E	PP317524
3	Ha3-1_New_Afon (III)	AB	Black Sea, New Afon	City beach, storm debris	Makarova O., 14 Aug. 2022	43.083070 N, 40.822061 E	PP317525
4	Ha5-4_Makhachkala (VI)	C	Caspian Sea, Makhachkala	Sandy beach, <i>Enteromorpha</i> emissions	Makarova O., Zavyazkina L., 11 Jun. 2021	42.968220 N, 47.548797 E	PP317527
5	Ha6-1_Izberbach (V)	C	Caspian Sea, Izberbash	Sandy-stony shore, <i>Enteromorpha</i> emissions	Makarova O., Makarov K., 03 May 2022	42.553070 N, 47.903560 E	PP317528
6	Ha7-1_Crimea_Solt (II)	AB	Azov Sea, Solyanoe	Shelly soil on the seacoast	Potapov M., Kuznetsova N., 26 Sep. 2021	45.339000 N, 35.399000 E	PP317529
7	Hao3-4_Eupatoria (I)	AB	Black Sea, Eupatolia	Beach seaweeds	Morozova N., 09 Dec. 2023	45.17889 N, 33.32977 E	PP503289
8	Hao9-2_Vladivostok (I)	PO	Japan Sea, Vladivostok	Algae emissions	Makarov K., 28 May 2022	42.66749 N, 131.21514 E	PP503295
<i>Halolaelaps</i> sp.1 [“ <i>gracilis</i> ”]							
9	Ha4-2_Anapa	AB	Black Sea, Anapa	Stony beach, sea debris	Artamonova V., Makhrov A., 28 Jun. 2021	44.896421 N, 37.298307 E	PP317526
<i>Halolaelaps</i> sp.2 [“ <i>elongatus</i> ”]							
10	Ha-it1-1_Iturup	PO	Sea of Okhotsk, Kuriles	Sandy beach, seaweeds	Popov I., 15 Sep. 2022	45.228286 N, 147.875447 E	PP317532
<i>Halolaelaps</i> sp.3 [“ <i>extremiorientis</i> ”]							
11	Ha-ch1-1_Chukotka	PO	Bering Sea, Meinypilgyno	Stony beach, sea debris	Rybalov L., 12 Jul. 2022	62.533574 N, 177.034421 E	PP317530
<i>Halolaelaps celticus</i> Halbert, 1915							
12	Hai1-1_Iceland	AO	Norwegian Sea, Iceland	Stony beach, seaweeds	Babenko A., 31 Jul. 2016	66.041381 N, 17.333029 W	PP317531
13	Ha-k2-2_Kanin nos	AO	Barents Sea, Kanin Peninsula	Sandy beach, sea debris	Przhborov A., 29 Jul. 2018	68.659501 N, 43.287568 E	PP317533
14	Ha-t1-1_Teriberka	AO	Barents Sea, Teriberka	Stony beach, seaweeds	Nekhaeva A., 26 Jun. 2019	69.167639 N, 35.142228 E	PP317534
15	Ha-w1-1_White_Sea	AO	White Sea, Kandalaksha	Sandy beach, sea debris	Leonov V., 25 May 2019	66.553709 N, 33.103388 E	PP317535
16	Hac10-5_Solovki	AO	White Sea, Solovetsky Is.	Stony beach, seaweeds	Makhrov A., 30 Jun. 2022	65.03418 N, 35.68567 E	PP503296
<i>Halolaelaps punctulatus</i> (Leitner, 1946)							
17	Hap1-1_Uglich	Europe	Middle Volga, Uglich	River beach debris	Kuznetsova N., Potapov M., 12 Oct. 2023	57.51674 N, 38.25130 E	PP503286
18	Hap1-3_Uglich	Europe	Middle Volga, Uglich	River beach debris	Kuznetsova N., Potapov M., 12 Oct. 2023	57.51674 N, 38.25130 E	PP503287
19	Hap2-2_Tver	Europe	Middle Volga, Tver	River beach debris	Kuznetsova N., Potapov M., 14 Aug. 2023	57.52346 N, 34.40483 E	PP503288

Trees are drawn to scale, with branch lengths in units of the number of base substitutions per site. The statistical significance of the resulting clustering of taxa was assessed using bootstrap support. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is shown next to the branches.

The median ITS genotype network was constructed in PopART (Leigh *et al.* 2015) using the TCS algorithm (Clement *et al.* 2000). Population statistics, namely: nucleotide diversity (Pi), genotype diversity (Hd), their standard deviation, number of variable sites and Tajima's D test for selective neutrality, were obtained with the DnaSP program (Rozas *et al.* 2017).

Results

Phorytocarpais kempersi

Among the species we studied, *P. kempersi* is the most widespread and common mite species found in all five larger regions (Azov-Black Sea Basin, Caspian Sea region, Pacific Ocean region, Arctic Ocean, Baltic Sea region). Of all 154 mite specimens used, 35 sequences of ITS gene fragments were obtained, representing 7 genotypes (Table 1). The variability of ITS genotypes of *P. kempersi* is presented in Figure 2. Other mite species from the family Parasitidae with known ITS sequences (representatives of the genera *Pergamasus* Berlese, 1903 and *Poecilochirus* G. & R. Canestrini, 1882) are separated from *P. kempersi* by a hiatus. The bootstrap values at the node separating the ITS sequences of *P. kempersi* from the representatives of the closest genera *Pergamasus* and *Poecilochirus* are 99% (Figure 2). At the same time, the intraspecific variability of *P. kempersi* across a huge part of its distribution (from Iceland to the Kuril Islands) does not exceed 1%, allowing an unambiguous identification of the species. To characterize the intraspecific variation of *P. kempersi* and to compare data from geographically distant parts of its range, we obtained a median network of genotypes (Figure

Table 3 Description of the collections of mites belonging to the family Eviphididae with genotypes characterized by ITS. ITS isolate name decoding and regions abbreviations - as in Table 1.

#	ITS isolate (genotype)	Region	District	Biotope	Collector and date	Latitude, longitude	GenBank ID (this study)
<i>Thinoseius spinosus</i> (Willmann, 1939)							
1	Th10-4_Aktau_C (I)	C	Caspian Sea, Aktau	Stony beach, seaweeds	Makarova O., Bizin M., 05 Jun. 2022	43.648634 N, 51.143032 E	PP296393
2	Th3-1_New_Afon (I)	AB	Black Sea, New Afon	Sandy beach, seaweeds	Kovaleva E., 06 Jan. 2021	43.076640 N, 40.860496 E	PP296394
3	Th4-2_Makhachkala (I)	C	Caspian Sea, Makhachkala	Sandy beach, sea debris	Makarova O., 11 Jun. 2021	42.968213 N, 47.548986 E	PP296395
4	Th5-1_Izberbash (I)	C	Caspian Sea, Izberbash	Sandy beach, sea debris	Makarova O., Makarov K., 02 May 2022	42.605582 N, 47.829103 E	PP296396
5	Th6-1_Kerch (I)	AB	Azov Sea, Kerch	Sandy beach, seaweeds	Artamonova V., Makhrov A., 29 Jun. 2021	45.359171 N, 36.605753 E	PP296397
6	Th7-5_Aktau-H (I)	C	Caspian Sea, Aktau	Sandy beach, seaweeds	Makarova O., Bizin M., 07 Jun. 2022	43.656724 N, 51.161292 E	PP296398
7	Th8-5_Aktau-V (I)	C	Caspian Sea, Aktau	Stony beach, seaweeds	Makarova O., Bizin M., 06 Jun. 2022	43.702758 N, 51.108390 E	PP296399
8	Th9-5_Aktau-L (I)	C	Caspian Sea, Aktau	Sandy beach, sea debris	Makarova O., Bizin M., 07 Jun. 2022	43.475186 N, 51.311233 E	PP296400
9	Thb1-4_Kaliningrad (I)	B	Baltic Sea, Kaliningrad	Sandy beach, seaweeds	Potapov M., 05 Sep. 2022	54.458107 N, 52.309238 E	PP296401
10	Th-ch1-5_Chukotka (II)	PO	Bering Sea, Meinypil-gyno	Sandy beach, sea debris	Rybalov L., 12 Jul. 2022	62.533574 N, 177.034421 E	PP296402
11	Th-i1-1_Iceland (I)	AO	Norwegian Sea, Iceland	Stony beach, seaweeds	Babenko A., 31 Jul. 2016	66.041381 N, 17.343029 W	PP296403
12	Th-i1-2_Iceland (III)	AO	Norwegian Sea, Iceland	Stony beach, seaweeds	Babenko A., 31 Jul. 2016	66.041381 N, 17.343029 W	PP296404
13	Th-z1-5_New_Land (I)	AO	Barents Sea, Novaya Zemlya	Sandy beach, seaweeds	Krashennnikov A., 30 Jul. 2015	71.548107 N, 52.309238 E	PP296407
14	Th-sol1-4 (I)	AO	White Sea, Solovetsky Is.	Stony beach, sea debris	Makarova O., 16 Jul. 2014	65.018832 N, 35.878603 E	PP296408
15	Th-pom1-1 (IV)	AO	White Sea, Pomor Coast	Stony beach, seaweeds	Timireva S., Kononov Yu., 04 Aug. 2020	66.319751 N, 36.185190 E	PP296409
16	Th-pom2-2 (I)	AO	White Sea, Pomor Coast	Stony beach, seaweeds	Timireva S., Kononov Yu., 04 Aug. 2020	66.319751 N, 36.185190 E	PP296410
17	Ths11-4_Eupatoria (I)	AB	Black Sea, Eupatoria	Seaweed emissions	Morozova N., 09 Dec. 2023	45.17889 N, 33.32977 E	PP503297
<i>Thinoseius occidentaliapacificus</i> Klimov, 1998							
18	Th-oxi1-5_Iturup	PO	Sea of Okhotsk, Kuriles	Sandy beach, seaweeds	Popov I., 15 Sep. 2022	45.228286 N, 147.875447 E	PP296406
19	Tho4-5_Vladivostok	PO	Japan Sea, Vladivostok	Sandy beach, seaweed emissions	Makarov K., 28 May 2022	42.66749 N, 131.21514 E	PP503290
<i>Thinoseius fucicola</i> (Halbert, 1920)							
20	Th-k1-5_Kanin_nos	AB	Barents Sea, Kanin Peninsula	Stony beach, sea debris	Przhboro A., 29 Jul. 2018	68.659501 N, 43.287568 E	PP296405
<i>Thinoseius cf. kargi</i> Hirschmann, 1966							
21	Th1-4_Anapa	AB	Black Sea, Anapa	Pebble beach, seaweeds	Lukashevich R., 10 Dec. 2020	44.882203 N, 37.305167 E	PP296392
<i>Eviphis ostrinus</i> (C.L. Koch, 1836)							
22	Evo6-4_Kislovodsk	Caucasus	North Caucasus, Kislovodsk	Spruce forest litter	Makarova O., 04 Jan. 2024	43.897359 N, 42.729707 E	PP503292

3). There the central position is occupied by the genotype marked with the Roman numeral (I), found in four large regions. All this allows us to consider it ancestral. All other genotypes appear to be associated with it, directly or indirectly. The closely related genotype (II), found in five large regions, is the most common one in the Caspian Sea region. The remaining genotypes are found only in particular regions. The genotypic diversity of the entire sample of *P. kempersi* and local populations of this species in individual large regions are presented in Tables 4 and 5. In the most remote, Far Eastern populations (Pacific coast), only two widespread genotypes were found.

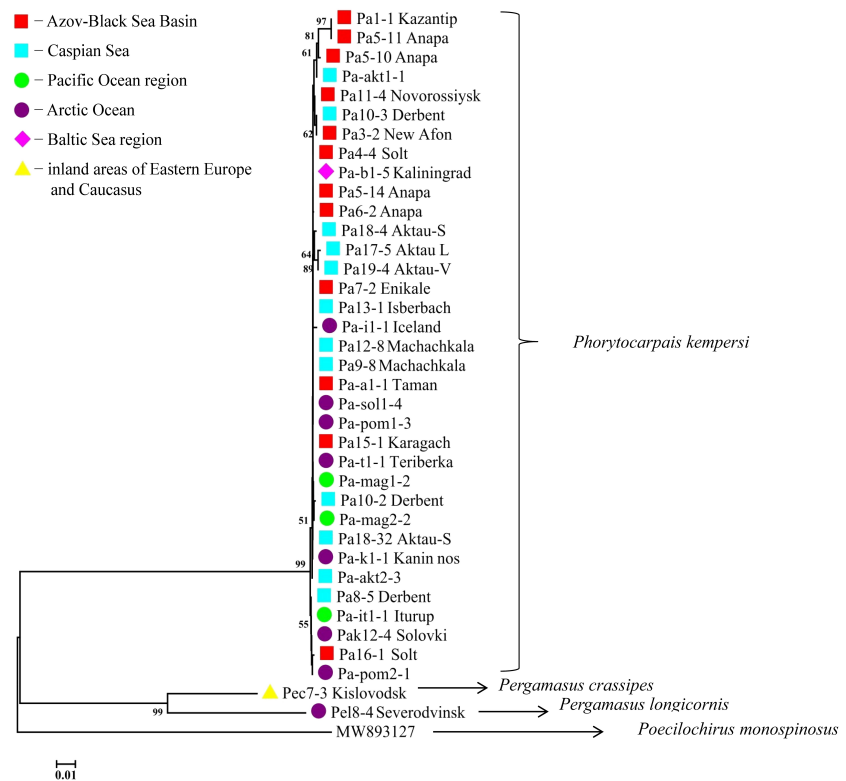


Figure 2 NJ cladogram of ITS genotypes of the littoral mite, *Phorytocarpais kempersi*. ITS genotypes of two members of the genus *Pergamasus*, Parasitidae, and *Poecilochirus monospinosus* Wise, Hennessey & Axtell, 1988, Parasitidae, were used as out-groups to root the tree. The sequence taken from GenBank is marked with GenBank ID number. The length of the aligned sequences is 575 nucleotide sites. The newly obtained sequences are denoted by color labels according to large regions. Sample characteristics are given in Table 1.

Genotypes (III), (IV) and (VII) are revealed only on the shores of the Caspian Sea, and genotype (V) only in the Iceland region (Table 1). The greatest divergence from the ancestral genotype is observed in mites with genotype (VI). As this genotype was found in closely located areas on the coast near the town of Anapa, Black Sea and on Cape Kazantip, Azov Sea, the early formation of a locally adapted population seems to take place. If adaptation does occur, it occurs at a very early stage, since the value of the test (Tajima's D) for selective neutrality corresponds to the model of random accumulation of mutations in the absence of selective pressure on the population (Table 4). A comparison of *P. kempersi* populations from different geographic regions shows the absence of fixed region-specific nucleotide substitutions (Figure 3), this also being consistent with the model of random accumulation of mutations.

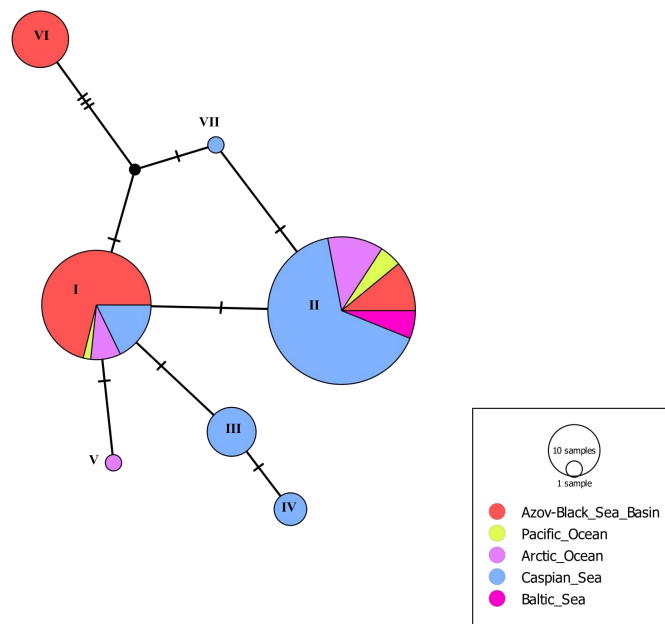


Figure 3 Median network of ITS genotypes of the littoral mite, *Phorytocarpais kempersi*. The size of the circles is proportionate to the number of individuals of given genotype. The dashes indicate mutations separating the genotypes. The length of the aligned sequences is 538 nucleotide sites. Number of segregating sites 8. The numbers in the circles indicate the different genotypes of *P. kempersi*. Sample characteristics are given in Table 1.

Halolaelaps orientalis* and *H. celticus

When analyzing the sequences of 20 specimens of *H. orientalis*, six ITS genotypes were obtained (Table 2). However, based on morphological characters, we have discovered three possible cryptic species close to *H. orientalis*. They were revealed in the Black Sea (sp. 1) and the seas of the Pacific Ocean (sp. 2, 3) and have some genetical distinctions (Figure 5).

The variability of the ITS fragment of all five distinguished members of the *celticus*-group analyzed, and of the congeneric *Halolaelaps punctulatus* (Leitner, 1946), is presented in Figure 4. Three clades with 99% and 100% bootstrap support correspond to the species: *H. celticus*, *H. punctulatus* and a complex of closely related species, *Halolaelaps* spp., related to *H. orientalis*. To analyze the genetic structure of this complex of close species, we constructed a median network of genotypes (Figure 5). This median network is star-shaped, this being characteristic of species that may have relatively recently gone through a stage of an explosive range expansion. The central position in this median network of genotypes is occupied by genotype (I), which is found in the Azov-Black Sea region and in the Pacific region and belongs to *H. orientalis* proper. The remaining genotypes have a narrower geographic distribution and are likely to have derived from genotype (I). Among the intertidal mite species we studied, *H. orientalis* is the most variable (Table 4). As in the case of *Phorytocarpais kempersi*, the value of the selective neutrality test (Tajima's D) fails to indicate the presence of any discriminatory pressure on its modern population. We found numerous demes of *H. orientalis* on the coasts of the Mediterranean, Azov and Black seas, as well as the Russian Far East (Sea of Japan).

H. orientalis was not found on the coasts of the Arctic Ocean seas, where it is replaced by the closely related species, *H. celticus*. We were able to obtain genetic material of *H. celticus* from remote populations: the shores of Iceland, Solovetsky Islands, Kola Peninsula, and Kanin Peninsula. The ITS fragment studied turned out to be monomorphic in our sample of *H. celticus* (10 specimens from five localities), but separated from *H. orientalis* by six phylogenetically significant substitutions.

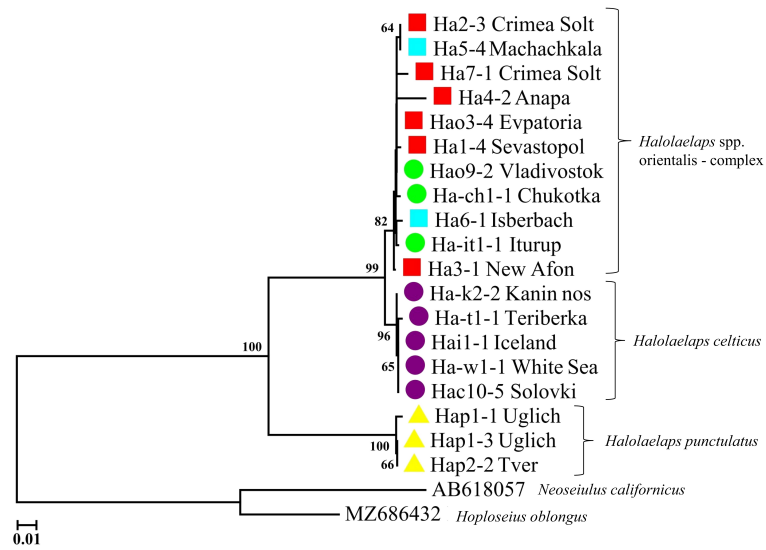


Figure 4 NJ cladogram of ITS genotypes of mites of the genus *Halolaelaps*. ITS genotypes of *Neoseiulus californicus* (McGregor, 1954), Phytoseiidae, and *Hoploseius oblongus* Masan and Halliday, 2016, Blattisociidae, were used as out-groups to root the tree. The sequence taken from GenBank is marked with GenBank ID number. The length of the aligned sequences is 655 nucleotide sites. The newly obtained sequences are denoted with color labels. The legend for color labels is given in Figure 2.

So, besides well distinguished species *H. orientalis* and *H. celticus*, some probably new species were found within the *celticus*-group, namely: *Halolaelaps* sp. 1 [“gracilis”] from the northeastern Black Sea coast, *Halolaelaps* sp. 2 [“elongatus”] from Iturup Island, *Halolaelaps* sp. 3 [“extremiorientis”], from the southern coast of Chukotka and Kamchatka peninsulas. All these forms have unique ITS genotypes (Figure 5). The genetic evidence, together with some morphological differences, support the assumption of species rank status for these three species. Further data are required to clarify this proposal. Carriers of ITS genotypes I–VI, on the contrary, showed no clear morphological differences.

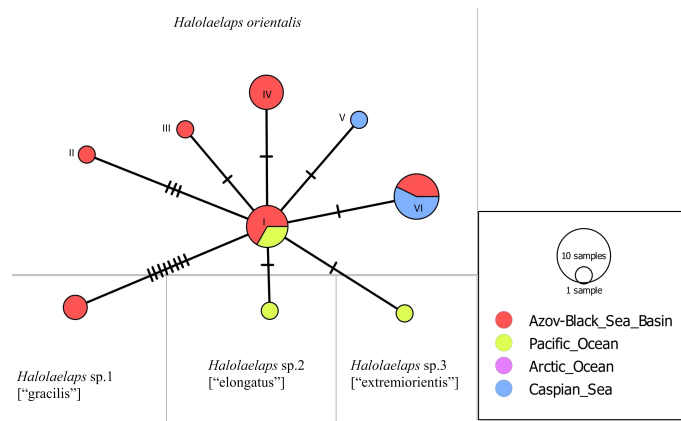


Figure 5 Median network of ITS genotypes of littoral mites of the genus *Halolaelaps* belonging to the *orientalis*-complex of the *celticus*-group. The size of the circles is proportionate to the number of individuals of given genotype. The dashes indicate mutations separating the genotypes. The length of the aligned sequences is 544 nucleotide sites. Number of segregating sites 17. The numbers in the circles indicate the different genotypes of *H. orientalis*. Sample characteristics are given in Table 2.

Thinoseius spinosus and other species of the genus

In addition to the widespread Holarctic species *T. spinosus*, further three species of the genus *Thinoseius* with narrower geographic distributions have been found in the littoral zones of Eurasia: *T. fucicola* (Halbert, 1920), *T. occidentalis* Klimov, 1998; and *Thinoseius* cf. *kargi* Hirschmann, 1966. The variability of ITS fragments of all four species is presented in Figure 6. Distinguishing the species is not difficult. Three clades are observed with good bootstrap support. Two clades correspond to the species *T. spinosus* and *T. occidentalis*. The third clade combines ITS sequences of *T. fucicola* and *Thinoseius* cf. *kargi*. *Thinoseius occidentalis* mites are known from the Pacific region (Klimov 1998; Takaku 2000; Makarova 2019), *T. fucicola* from the shores of the northern and southern seas of Europe (Remmert 1956; Evans 1969; Bregetova 1977), and *T. cf. kargi* from the coasts of the Mediterranean and Black seas (Hirschmann 1966; Avdonin 2002). Both latter species show a single genotype of the ITS fragment, one different from other genotypes found among *Thinoseius* species.

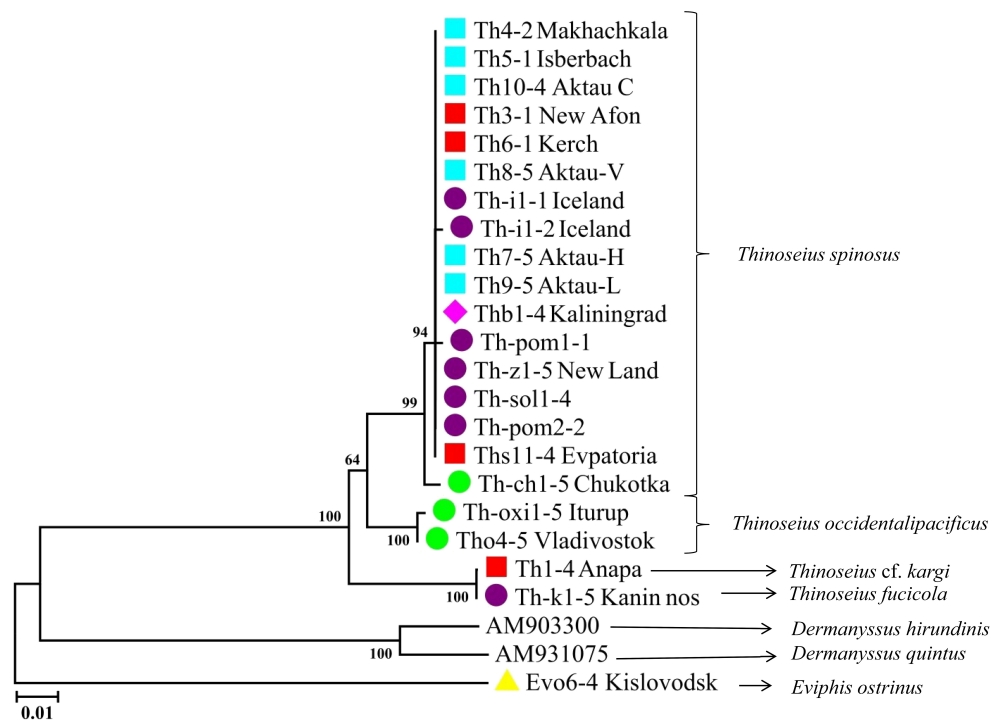


Figure 6 NJ cladogram of ITS genotypes of the genus *Thinoseius*. ITS genotypes of two members of the genus *Dermanyssus* (Dermanyssidae) and *Eviphis ostrinus* (Eviphididae) were used as out-groups to root the tree. The sequence taken from GenBank is marked with GenBank ID number. The length of the aligned sequences is 669 nucleotide sites. The newly obtained sequences are denoted with color labels. The legend for color labels is given in Figure 2.

When studying the ITS sequences of 52 specimens of *T. spinosus* from 17 localities, four genotypes were found (Table 3). To analyze the intraspecific variability of this species, we constructed a median network of genotypes (Figure 7). Intraspecific variability of *T. spinosus* is again star-shaped. The most abundant genotype, marked with number (I), occupies the central position in the median network of genotypes and thus it is considered ancestral, at least so for the modern European super-population. We found genotype (I) in four of five larger regions, except for the Pacific region, where it is replaced by genotype (II).

Special genotypes of *T. spinosus* different from the central genotype (I) are found only in the regions of the Pacific and Arctic oceans, while across the vast areas covering the shores of the Baltic, Black, Azov and Caspian seas *T. spinosus* appears to be monomorphic. The value of

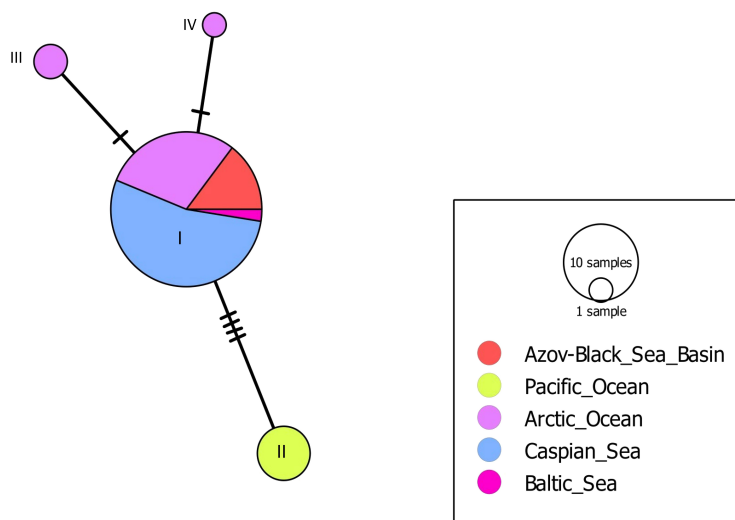


Figure 7 Median network of ITS genotypes of the littoral mite, *Thinoseius spinosus*. The size of the circles is proportionate to the number of individuals of given genotype. The dashes indicate mutations separating the genotypes. The length of the aligned sequences is 663 nucleotide sites. Number of segregating sites 6. The numbers in the circles indicate the different genotypes of *T. spinosus*. Sample characteristics are given in Table 3.

the selective neutrality test (Tajima’s D) does not reveal any selection effect on the *T. spinosus* population (Table 4).

Discussion

Suitability of the ITS fragment for phylogenetic analysis

At present, the following data are available for the molecular comparison of the littoral mites studied in this work. DNA barcode fragments of mites from the genus *Phorytocarpais* Athias-Henriot, 1979 (formerly, partly *Parasitus* Latreille, 1795) have been obtained from a few species. The DNA barcode fragment of the COI gene is known for the following species: *Phorytocarpais fimetorum* (Berlese, 1903) (NC_061975), *Parasitus loricatus* (Wankel, 1861) (MN906455), *Parasitus hyalinus* (Willmann, 1949) (MH983860), and *Parasitus wangdunqingi* Ma, 1995 (MK270528). Fragments of ribosomal nucleotide sequences of the RNA 18S and 28S genes used for DNA barcoding are known only for *P. fimetorum* (GenBank Accession: AY626653, AY626616, AY620935) (Klompen *et al.* 2007).

No DNA barcode fragments of mites belonging to the genus *Halolaelaps* Berlese et Trouessart, 1889 have heretofore been obtained.

Table 4 Overall mean population variance of the set of ITS sequences in model littoral mite species.

Estimated character	<i>Phorytocarpais kempersi</i>	<i>Thinoseius spinosus</i>	<i>Halolaelaps orientalis</i>
Number of sites	538	645	544
Number of variable sites, S	7	6	8
Number of sequences	154	52	20
Genotype diversity, Hd (standard deviation of genotype diversity, σ)	0.237 ($\sigma=0.044$)	0.278 ($\sigma=0.078$)	0.779 ($\sigma=0.055$)
Nucleotide diversity (per site), Pi (standard deviation of Pi, σ)	0.00133 ($\sigma=0.00029$)	0.00128 ($\sigma=0.00042$)	0.00264 ($\sigma=0.00055$)
Neutrality Test, Tajima's D	-1.00232, not significant, P > 0.10	-0.96070, not significant, P > 0.10	-1.25425, not significant, P > 0.10

Table 5 Regional comparison of population variance of the set of ITS sequences in model littoral mite species. "N" – number of individuals those sequences were studied, "Pi(JC)" – nucleotide diversity with Jukes and Cantor, "σ" – standard deviation of Pi(JC) Jukes and Cantor; "–" – species absent from the region; "0" – ITS of species monomorphic in the region.

Mite species	Sampling parameters	Region		
		Caspian Sea	Azov-Black Sea basin	Arctic Ocean
<i>Phorytocarpais</i>	N	75	52	15
<i>kempersi</i>	Pi(JC) (σ)	0.00025 (0.0001)	0.00291 (0.0005)	0.00026 (0.00022)
<i>Thinoseius</i>	N	22	6	15
<i>spinosus</i>	Pi(JC) (σ)	0	0	0.00059 (0.00025)
<i>Halolaelaps</i>	N	5	13	–
<i>orientalis</i>	Pi(JC) (σ)	0.00225 (0.00133)	0.00273 (0.00069)	–

DNA barcode fragments of members of the genus *Thinoseius* Halbert, 1920 are so far known for only one species. As a fragment of the mitochondrial COI gene was studied in a single specimen of *Thinoseius spinosus* (Willmann, 1939) (GenBank ID: MW367935; found on a salt lake shore in Western Siberia), neither intraspecific variations nor the utility of DNA barcoding for the identification of this species can be assessed.

In this study, based on ITS ribosomal repeat fragment sequence analysis, we present results of effective DNA barcoding of abundant mite species inhabiting the littoral zone of Eurasian seas: *P. kempersi*, *Halolaelaps* spp. *orientalis* - complex, *H. celticus* and *T. spinosus*.

The molecular diagnostics of almost all mite species studied here based on the analysis of the ITS ribosomal repeat gene fragment turns out to be suitable for using this marker in new generation biomonitoring technologies (Makiola *et al.* 2020). Only distant populations of *Thinoseius fucicola* (Barents Sea) and *Thinoseius cf. kargi* (Black Sea) failed to be distinguished from each other using this marker, but this must be studied in more detail. At present, it is not possible to assess the effectiveness of ITS as a marker for distinguishing closely related *Halolaelaps* species: *Halolaelaps* sp. 1 ["gracilis"], *Halolaelaps* sp. 2 ["elongatus"] and *Halolaelaps* sp. 3 ["extremiorientis"].

ITS fragment sequences variation in individual model species are provided with high bootstrap support, 94–100%. At the same time, the results of the test for selective neutrality (Tajima's D) correspond to the model of random accumulation of mutations in the absence of a discriminatory pressure on the population.

A likely explanation for this type of variability is the relative stability of the ecological conditions of littoral mite species during the period of their dispersal across their modern range and intensive intrapopulation genetical exchange due their dispersal mechanisms. A possible explanation as well can be the vastness of the ranges of these species, so that abrupt climatic changes associated with Pleistocene glacial cycles did not lead to the extinction of mite populations, but only to fluctuations in their boundaries.

The sample of the North Atlantic species, *Halolaelaps celticus*, containing specimens from Iceland in the west to the Kanin Peninsula in the east, turned out to be monomorphic, based on the ITS marker. All the area is known to have been covered with ice during the Last Glacial Maximum (20,000 yr BP) (Gowan *et al.* 2021; Mangerud *et al.* 2023). Following ice melting, in the Holocene, the spread of *H. celticus* from a southern refugium can be assumed to have rapidly occurred. In a similar way, across the vast territories along the shores of most European seas, a single genotype (I) of *Thinoseius spinosus* has become widespread. Its derivatives differing by single nucleotide substitutions in the ITS fragment (genotypes III and IV), occur on the coasts of Iceland and the White Sea. The Pacific population of this species is more strongly separated, differing by four substitutions [genotype (II)]. It seems very likely that the integrity of its European super-population is largely ensured by intense phoresy on dipterans, these latter being represented by a whole range of taxa (see above the section "Characteristics of model species").

Triviality of Caspian genotypes

According to the modern classification of seas (Briggs 1974), the tideless Caspian Sea is the eastern outpost of the Mediterranean-Atlantic littoral biogeographic region. During its history, it has undergone and is still undergoing large-scale changes in area and salinity, as well as periods of destruction and restoration of connections to the Azov-Black Sea basin (Rychagov 2011; Svitoch 2008, 2013; Krijgsman *et al.* 2019). Long periods of isolation and desalination must have resulted in high-level species endemism of the Caspian marine fauna (Mordukhai-Boltovskoi 1979; Naseka and Bogutskaya 2009). However, our pioneering studies on its littoral mites did not reveal previously unknown species, and the list of littoral mite species of the Caspian Sea appears to be extremely poor compared to the Black Sea shores (unpublished new data). Moreover, the genotypes of the study model species that dominate the Caspian shores belong to the most trivial ones, while the rare “endemic” variants of *Phorytocarpais kempersi* may differ only in one nucleotide substitution, that might reflect their recent origins. The same is true for the rare “endemic” variants of *Halolaelaps orientalis*.

It seems very likely that the simplicity of the Caspian fauna of littoral mites (mainly soil-dwellers) is determined both by their less strong association with the so variable marine environment, as well as the recent contact of the Caspian and Azov seas during the Early Khvalynsk transgression. Its chronology has been the subject of discrepancies and debate for many years, the age of this transgression being dated a wide range, from 71,000 to 7,000 years ago (Tudryn *et al.* 2013; Koriche *et al.* 2022; Makshaev and Tkach 2023). However, most authors presently admit that the last contact of the Caspian and Black seas (an overflow from the former to the latter basin through the Kuma-Manych Strait and the Sea of Azov) could have occurred not earlier than 17,000–14,000 years ago (Svitoch *et al.* 2010; Sorokin 2011; Arslanov *et al.* 2016; Krijgsman *et al.* 2019; Kurbanov *et al.* 2023; Gelfan *et al.* 2024). Taking into account the low rate of evolution of nuclear ribosomal genes in the Class Acari (Murrell *et al.* 2005; Klompen *et al.* 2007), the integrity of the genetic structure by this marker of the populations of the Azov-Black Sea basin and the Caspian Sea is hardly surprising. Yet, the significant sample size for *Phorytocarpais kempersi* (154 mite sequences) has made it possible to reveal a clear predominance of different genotypes in its populations from these regions. The contribution of historical and/or modern (climatic and other) factors responsible for these differences remains to be studied.

It still seems premature to analyze the reasons for the poverty of the Caspian littoral acarofauna. The complete isolation of this sea-lake from the Azov-Black Sea basin is, according to the most maximum estimates, dates back to more than 35,000 – 42,000 years (Sorokin 2011; Krijgsman *et al.* 2019). It is impossible to exclude the absence of a two-way exchange during the last contact of these seas because the current was directed towards the Black Sea, and the Caspian waters were significantly desalinated (Krijgsman *et al.* 2019), and then the reasons for the deterioration of the Caspian littoral fauna could be sought in its more ancient history.

Uniqueness of the genotypes of the Azov-Black Sea region

Unlike the Caspian Sea, the shores of the Black and Azov seas support both common and unique genotypes of mites. Thus, in a large sample of *Phorytocarpais kempersi*, genotype (VI) with three nucleotide substitutions has been identified, whose carriers were found in closely located areas on the coasts of the Azov Sea (Cape Kazantip) and the Black Sea (Anapa). This may reflect the early evolution of a locally adapted population due to the fixation of random mutations. However, the value of the selective neutrality test (Tajima's D) corresponds to the model of random accumulation of mutations in the absence of discriminatory pressure on the population, which contradicts local adaptation.

Members of the genus *Halolaelaps* from the vicinity of Anapa, initially identified as *H. orientalis*, upon a more profound analysis of its morphology and ITS marker, appear to represent a new species, *Halolaelaps* sp. 1 (“gracilis”), separated from *H. orientalis* by eight

nucleotide substitutions. We have also found this species in the surroundings of the town of Tuapse (160 km south of Anapa). It cannot be ruled out that the genetic peculiarity of *P. kempersi* and *Halolaelaps* sp. 1 in this region (Kerch-Taman mud volcano province) may be somehow associated with the history of its biota. This region is characterized by massive manifestations of mud volcanism (terrestrial and marine) caused by the special tectonics of the West Kuban trough (Kopf 2002).

It seems noteworthy that the overall nucleotide diversity of the ITS fragment in *Phorytocarpais kempersi* mites from the Azov-Black Sea population is significantly (by an order of magnitude) higher compared to the Caspian and Arctic regions (Table 5), indicating its ancestral nature at least in terms of the European part of this species' modern distribution.

Similarities between European and East Asian populations of model species

A number of intertidal mite species show extensive distributions (Schulte 1975; Procheş and Marshall 2001), including our model species (see above the section “Characteristics of Model Species”). The wide physiological valence of the inhabitants of sea coasts, on the one hand, and the similarity of key environmental factors over the vast range of the sea littorals, on the other, are believed the main reasons why they are not affected by species differentiation (Procheş and Marshall 2001). This may be especially pronounced in the Holarctic, whose natural environments have changed dramatically during the Quaternary and must have led and still lead to large-scale species migrations that eliminate possible inter-population differences (Coop 2004). When analyzing a large dataset on vertebrates, the relationship between range size and genetic diversity turns out to be quite ambiguous (Lawrence and Fraser 2020).

In mesostigmatic mites, the higher average divergence level is shown in comparison with all other chelicerates (Klompen *et al.* 2007). Their significantly faster rates of nucleotide substitution as compared to other parasitiform mites have been suggested to possibly be related to their shorter lifespan and higher metabolic rate (Murell *et al.* 2005). However, no significant differences in the ITS marker have been revealed between populations of any studied species from the coasts of the Atlantic and Pacific basins. Nowhere did these differences exceed 1%. This genetic integrity was also shown in *Phorythocarpais kempersi* mites from the White and Black Sea populations, freely crossing and traced to F2 (Avdonin and Striganova 2004). At present, the presence of an original genotype on the shores of the Pacific, distinguished by four substitutions in the ITS fragment, has been proven only for *Thinoseius spinosus*.

All our studied species are common and widespread inhabitants of seaweeds on the Palaearctic marine coasts. However, they have never been recorded from the coasts of the boreal seas of Central and Eastern Siberia, with the exception of *Thinoseius spinosus* that also lives in the north of Chukotka (O.L.M.: personal observations). Therefore, a direct contact of their western and eastern Palaearctic populations across the Arctic seaway is currently absent or difficult. Through most of the Pleistocene, opportunities for littoral mite dispersals must have been even worse due to both the repeatedly closing Bering Strait and the severe Arctic climate (Elias and Brigham-Grette 2013). In the case of the rather “Arctic-adapted” *Phorythocarpais kempersi* and *Thinoseius spinosus*, both currently dwelling on the Barents and Kara sea sides (Makarova 2013; O.L.M.: personal observations), the genetic integrity of their amphi-Palaearctic populations seems to indicate rather recent contacts between them in the north of Eurasia during the periods of warming. Thus, during the last Eemian interglacial (Mikulino) (=MIS 5e; 130,000–110,000 years ago), the Arctic summer temperatures could have been 4–6 °C higher than now and occasionally the ocean could have been of ice-free (Velichko *et al.* 1984; Pavlidis *et al.* 1998; Anderson *et al.* 2006). During such times, the tundra biome on the arctic shores of most of the Palaearctic could have been replaced by woodlands (Grichuk 2002). Only some 9,200–9,800 years ago, in the early Holocene, the temperatures during the growing season on the Severnaya Zemlya Archipelago, about 78° N, seem to have been at least 4 °C higher than present-day (Andreev *et al.* 2008).

In the case of the relatively thermophilous *Halolaelaps orientalis* (still no records in the Arctic), a northern transit seems unlikely. Yet, its ITS genotype recorded from the shores of the Sea of Japan is indistinguishable from the most common variant in the Azov-Black Sea basin. The ancient ocean Paratethys, of which the Caspian and Black seas are derivatives, is known to have lost contact to the Indian Ocean in the mid-Miocene, 12–14 million years ago (Popov *et al.* 2004; Palcu *et al.* 2015), and this could be reflected in the genetic structure of amphi-Palaeartic littoral species. We can only assume the existence of genetic exchange in our time between populations of this species on the shores of the seas of the Mediterranean and the Pacific Ocean through the Suez Canal and the coasts of the Indian Ocean. Studies on their intertidal acarofauna have just begun (Kazemi 2020; Moraza *et al.* 2016). It cannot be excluded that the extensive, transoceanic and polyzonal distribution range of *Halolaelaps orientalis* might have determined its high general nucleotide and genotypic diversity, 2–3 times as high as the values obtained for the other species (Table 4).

Conclusions

The approach we used (ITS analysis) has allowed us to confidently identify all studied species (*P. kempersi*, *Halolaelaps* spp. *orientalis*-complex, *H. celticus* and *T. spinosus*), all separated by long barcode gaps from the nearest known relatives.

A comparative analysis of the population variability of *Phorytocarpais kempersi* and *Halolaelaps orientalis* in the regions of the Azov-Black Sea basin and the Caspian Sea basin shows a significantly lower level of intraspecific polymorphism in populations from the latter region. This may be related to long periods of the Caspian Sea isolation from the western seas and Atlantic Ocean during the Pliocene-Pleistocene, coupled with the permanent instability of its size and environments.

The high similarity of the amphi-Palaeartic populations of three of our studied littoral mite species seems to indicate the recent and/or still ongoing genetic exchange between them. In *Phorytocarpais kempersi* and *Thinoseius spinosus*, both known from the Arctic, a recent contact along the northern coast of Eurasia is suggested to have occurred during the last Pleistocene interglacial or Holocene climatic optimum. The current distribution of the relatively thermophilous *Halolaelaps orientalis* may well include the shores of the Indian Ocean.

We believe that this study will contribute to a comprehensive assessment of biological diversity on the Russian and adjacent countries seashores as a whole. The results of the given work can be used in future, more detailed phylogeographic as well as metagenomic bioindication studies.

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