

Genetic similarity between *Pagurus gracilipes* (Stimpson, 1858) (Decapoda: Paguroidea) and another pagurid and diogenid hermit crabs from Russian waters of the Sea of Japan

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ABSTRACT: Biochemical genetic approach was applied to clarify the taxonomic status of the hermit crab *Pagurus gracilipes* which was compared with five species of the family Paguridae (*P. brachiomastus*, *P. ochotensis*, *P. middendorffii*, *P. proximus*, *P. minutus*) and with two species of the family Diogenidae (*Diogenes nitidimanus* and *Stratiotes nigroapiculus*) using 18 allozyme loci. Genetic identity values between *P. gracilipes* and species of the family Paguridae (from 0.611 ± 0.117 for *P. gracilipes* vs *P. proximus*, to 0.249 ± 0.102 for *P. gracilipes* vs *P. middendorffii*) suggest that this species should retain its position in the genus *Pagurus*. This conclusion is supported by similar average identity value between other species of the genus *Pagurus* ($I=0.444 \pm 0.110$) and low genetic similarity between the genera *Diogenes* and *Stratiotes* ($I=0.167 \pm 0.084$) and between the families Paguridae and Diogenidae ($I=0.102 \pm 0.005$).

KEY WORDS: Decapoda; hermit crab; allozyme electrophoresis; genetic similarity; Sea of Japan.

Генетическое сходство между *Pagurus gracilipes* (Stimpson, 1858) (Декапода: Пагуриоидея) и другими видами раков-отшельников из российских вод Японского моря

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РЕЗЮМЕ: Для уточнения таксономического статуса *Pagurus gracilipes* использованы методы биохимической генетики. Этот вид сравнили с пятью видами семейства Paguridae (*P. brachiomastus*, *P. ochotensis*, *P. middendorffii*, *P. proximus*, *P. minutus*) и двумя видами семейства Diogenidae (*Diogenes nitidimanus* и *Stratiotes nigroapiculus*)

по 18 аллозимным локусам. Значения генетического сходства, полученные при сравнении *P. gracilipes* с другими видами семейства Paguridae (от 0.611 ± 0.117 с *P. proximus* до 0.249 ± 0.102 с *P. middendorffii*), свидетельствуют о принадлежности этого вида к роду *Pagurus*. Этот вывод подтверждается близкими значениями генетического сходства между другими видами рода *Pagurus* (в среднем $I=0.444 \pm 0.110$) и низкими значениями генетического сходства между родами *Diogenes* и *Stratiotes* ($I=0.167 \pm 0.084$), а также семействами Paguridae и Diogenidae ($I=0.102 \pm 0.005$).

КЛЮЧЕВЫЕ СЛОВА: Декапода; раки-отшельники, аллозимный электрофорез, генетическое сходство, Японское море.

Introduction

The hermit crab *Pagurus gracilipes* (Stimpson, 1858) is known from the northern Japan, including Hokkaido and northeastern Honshu, and from the continental coast of the Russian Far East, where it inhabits subtidal zones to 42 m depth (Komai, 1998).

The taxonomic position of this species is subject to scientific discussion. A new genus *Parapagurodes* has been established by McLaughlin and Haig (1973). In 1998, four Japanese species of *Pagurus*, including *P. gracilipes*, have been transferred to *Parapagurodes* on the basis of morphology of sexual tubes in males (Komai, 1998). However, later *P. gracilipes* has been returned to *Pagurus* (McLaughlin, Asakura, 2004).

Allozyme electrophoresis was successfully used in resolving taxonomy of decapod crustacean species (Hedgecock et al., 1982; Fuseya, Watanabe, 1996; Stewart, Cook, 1998; Mia et al., 1999; Gouws, Stewart, 2000; Austin, Ryan, 2002).

The aim of this study was to apply biochemical genetics to clarify the taxonomic position of *P. gracilipes* among the Paguridae. To evaluate the degree of genetic difference/similarity between species within a genus, genera within a family and between families, five pagurid and two diogenid species inhabiting Peter the Great Bay (Sea of Japan) and having the stable taxonomic position were also analyzed using enzyme electrophoresis.

Material and methods

Sample collection

Samples of *Pagurus gracilipes* (Stimpson, 1858) as well as *P. ochotensis* Brandt, 1851, *P. brachiomastus* (Thallwitz, 1892), *P. proximus* Komai, 2000, *P. minutus* Hess, 1865, *P. middendorffii* Brandt, 1851 (Paguridae), *Diogenes nitidimanus* Terao, 1913, and *Stratiotes nigroapiculatus* Komai, 2009 (Diogenidae) were collected at depths from 0.5 to 5 m in Vostok Bay (Peter the Great Bay, Sea of Japan) in June 2008. Sample sizes are given in Table 1.

Enzyme electrophoresis

Two tissues (liver and muscle) from each animal were homogenized together in one vial, and were further used for electrophoretic analysis. Horizontal electrophoresis was carried out using 13% starch gels as described in Zaslavskaya (1989). Three continuous buffer systems were used to resolve 13 enzymes: (1) TEB (tris-EDTA-boric acid, pH 8.5), (2) TC (tris-citric acid, pH 7.0) and (3) TM (tris-maleic acid, pH 7.4). Electrophoretic buffer systems and enzyme systems used in the analysis are listed below (enzyme abbreviations, enzyme classification numbers, and isozyme locus standard abbreviations are given in parentheses). TEB was used to resolve vial glucose phosphate isomerase (GPI; EC 4.3.1.5, *Gpi*), glutamate pyruvate transaminase (GPT; EC 2.6.1.2, *Gpt*), glutation reductase (GR; EC 1.6.4.2, *Gr*), hexo-

Table 1 (contituing)
Таблица 1 (продолжение)

1	2	3	4	5	6	7	8	9	10
<i>Mdh-1</i>									
	(N)	18	17	19	18	26	18	20	8
	1	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
	2	1.000	1.000	1.000	1.000	0.000	1.000	0.175	0.000
	3	0.000	0.000	0.000	0.000	0.000	0.000	0.775	0.000
	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
	5	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.000
<i>Mdh-2</i>									
	(N)	10	9	11	10	19	10	8	8
	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	2	0.000	0.000	0.000	1.000	1.000	0.000	0.000	0.000
	3	1.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
	4	0.000	1.000	0.000	0.000	0.000	1.000	0.000	0.000
	5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
	6	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
<i>Got-1</i>									
	(N)	18	17	19	18	29	18	20	8
	1	0.000	0.000	0.000	0.167	0.000	0.000	0.000	0.000
	2	0.000	0.000	0.000	0.000	0.000	0.000	0.950	0.000
	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.938
	4	0.194	0.000	0.026	0.000	0.000	0.000	0.000	0.000
	5	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
	6	0.806	0.971	0.974	0.000	1.000	0.000	0.050	0.000
	7	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.062
	8	0.000	0.000	0.000	0.833	0.000	0.000	0.000	0.000
<i>Got-2</i>									
	(N)	18	17	19	18	29	18	20	8
	1	1.000	0.971	1.000	0.000	0.000	0.000	0.000	1.000
	2	0.000	0.029	0.000	1.000	1.000	1.000	0.000	0.000
	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	4	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
<i>Gr</i>									
	(N)	18	17	19	18	29	18	20	8
	1	0.000	0.000	0.000	0.000	0.000	1.000	1.000	0.938
	2	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.062
	3	0.000	0.000	0.000	0.972	0.000	0.000	0.000	0.000
	4	0.000	1.000	1.000	0.028	1.000	0.000	0.000	0.000
<i>Pgm</i>									
	(N)	18	17	19	18	29	18	20	8
	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
	2	0.000	0.000	0.000	0.027	0.586	0.000	0.000	0.000
	3	0.000	0.000	0.027	0.000	0.000	0.056	0.000	0.000
	4	0.000	0.000	0.000	0.000	0.000	0.944	0.100	0.000
	5	0.000	0.000	0.000	0.056	0.414	0.000	0.000	0.000
	6	1.000	0.971	0.947	0.0917	0.000	0.000	0.000	0.000
	7	0.000	0.029	0.026	0.000	0.000	0.000	0.900	0.000

Table 1 (contituing)
Таблица 1 (продолжение)

1	2	3	4	5	6	7	8	9	10
<i>Aldh</i>									
	(N)	12	12	14	13	24	12	15	8
	1	0.000	0.000	0.000	1.000	0.000	0.000	1.000	0.000
	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
	3	0.000	0.000	0.071	0.000	0.062	0.000	0.000	0.000
	4	0.917	1.000	0.929	0.000	0.938	0.000	0.000	0.000
	5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	6	0.083	0.000	0.000	0.000	0.000	0.042	0.000	0.000
	7	0.000	0.000	0.000	0.000	0.000	0.958	0.000	0.000
<i>Hk</i>									
	(N)	8	8	8	8	10	8	10	8
	1	0.000	0.000	0.000	0.000	0.050	0.875	0.850	1.000
	2	1.000	1.000	1.000	1.000	0.950	0.125	0.000	0.000
	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	4	0.000	0.000	0.000	0.000	0.000	0.000	0.150	0.000
<i>Ac-1</i>									
	(N)	8	8	8	8	10	8	10	8
	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
	2	0.000	1.000	1.000	1.000	1.000	1.000	0.000	0.000
	3	0.000	0.000	0.000	0.000	0.000	0.000	0.300	0.000
	4	0.000	0.000	0.000	0.000	0.000	0.000	0.700	0.000
	5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	6	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Ac-2</i>									
	(N)	8	8	8	8	10	8	10	8
	1	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
	2	0.000	0.062	0.000	0.000	0.000	0.000	0.000	0.000
	3	0.000	0.938	1.000	1.000	1.000	1.000	0.000	0.000
	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
	5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	6	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Lap</i>									
	(N)	14	17	18	17	28	18	10	8
	1	0.000	0.000	0.056	0.000	0.018	0.000	1.000	0.000
	2	0.000	0.000	0.111	0.000	0.803	0.000	0.000	0.000
	3	0.000	0.000	0.694	0.000	0.000	0.000	0.000	0.000
	4	0.000	0.000	0.000	0.000	0.179	0.000	0.000	0.000
	5	0.000	0.676	0.139	0.118	0.000	0.611	0.000	0.000
	6	0.036	0.324	0.000	0.000	0.000	0.361	0.000	0.000
	7	0.357	0.000	0.000	0.000	0.000	0.028	0.000	0.812
	8	0.607	0.000	0.000	0.676	0.000	0.000	0.000	0.188
	9	0.000	0.000	0.000	0.206	0.000	0.000	0.000	0.000
<i>Est-1</i>									
	(N)	8	8	8	9	14	8	10	8
	1	1.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
	2	0.000	0.000	1.000	0.833	0.000	0.063	0.000	0.000

Table 1 (contituing)
Таблица 1 (продолжение)

1	2	3	4	5	6	7	8	9	10
	3	0.000	0.000	0.000	0.167	1.000	0.063	0.000	0.000
	4	0.000	0.000	0.000	0.000	0.000	0.874	0.000	0.000
	5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063
	6	0.000	0.000	0.000	0.000	0.000	0.000	0.600	0.874
	7	0.000	0.000	0.000	0.000	0.000	0.000	0.400	0.063
<i>Est-2</i>									
	(N)	8	8	8	9	14	8	10	8
	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	2	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	3	0.000	0.812	1.000	1.000	1.000	1.000	0.000	0.000
	4	0.000	0.188	0.000	0.000	0.000	0.000	0.000	0.000
	5	0.000	0.000	0.000	0.000	0.000	0.000	0.600	0.000
	6	0.000	0.000	0.000	0.000	0.000	0.000	0.400	0.000
	7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
<i>Est-3</i>									
	(N)	10	9	11	10	19	10	10	8
	1	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
	2	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
	3	1.000	1.000	1.000	0.000	1.000	0.000	0.000	1.000
	4	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000

kinase (Hk; EC 2.7.1.1, *Hk*), inorganic pyrophosphatase (IPP; EC 3.6.1.1, *Ipp*), nonspecific esterases (EST; EC 3.1.1..., *Est-1*, *Est-2*, *Est-3*). TC was used to resolve acid phosphatase (Ap; EC 3.1.3.2, *Ac-1*, *Ac-2*), leucine aminopeptidase (LAP; EC 3.4.11.1, *Lap*), malate dehydrogenase (MDH; EC 1.1.1.37, *Mdh-1*, *Mdh-2*), glutamate oxaloacetate transaminase (GOT; EC 2.6.1.1, *Got-1*, *Got-2*). TM was used to resolve alanopine dehydrogenase (ALPDH; EC 1.5.1.17, *Aldh*), mannose phosphate isomerase (MPI; EC 5.3.1.8, *Mpi*), phosphoglucomutase (PGM; EC 2.7.5.1, *Pgm*). Genetic interpretation of electrophoretic data was based on specific patterns of enzyme bands on zymograms (Harris, Hopkinson, 1976; Manchenko, 1994).

Data analysis

Allele frequencies were calculated using the program BIOSYS (Swofford, Selander, 1981). Nei's (1978) unbiased genetic identity (*I*) and genetic distance (*D*) coefficients, estimation of their standard error were calculated using the program DBOOT (Pudovkin et al., 1996). Phe-

nogram was constructed by the unweighted pair group method from estimates of Nei's (1978) genetic similarity using software package NTSYS (Rohlf, 1988).

Results and discussion

Allele frequencies at 18 allozyme loci coding for 13 enzyme systems calculated for all species are given in Table 1. When it was possible to test fits to Hardy-Weinberg equilibria, no significant deviations from expectations were found. Nei's (1978) genetic similarity and distance are shown in Table 2.

Figure 1 shows the dendrogram of genetic relationships between all studied species. All six species of the genus *Pagurus* (including *P. gracilipes*) form a cluster with an average *I*-value of 0.444 ± 0.110 . Two genera, *Diogenes* and *Stratiotes*, and two families, Paguridae and Diogenidae, exhibited much lower values of genetic identity ($I=0.167 \pm 0.084$ and $I=0.102 \pm 0.005$, respectively). Among the pagurids, *P. gracilipes* is rather closely related to *P. proxi-*

Table 2. Nei's (1978) genetic similarity (above diagonal) and distance (below diagonal) among eight hermit crabs inhabiting Peter the Great Bay.

Таблица 2. Значения генетического сходства (выше диагонали) и расстояния (ниже диагонали) (Nei, 1978) для 8 видов раков-отшельников, обитающих в заливе Петра Великого.

Species	1	2	3	4	5	6	7	8
1. <i>Pagurus middendorffii</i>	****	0.577	0.506	0.287	0.249	0.084	0.033	0.190
2. <i>Pagurus proximus</i>	0.549	****	0.700	0.495	0.611	0.439	0.027	0.159
3. <i>Pagurus ochotensis</i>	0.682	0.356	****	0.486	0.539	0.379	0.024	0.200
4. <i>Pagurus brachiomastus</i>	1.249	0.704	0.722	****	0.501	0.439	0.092	0.072
5. <i>Pagurus gracilipes</i>	1.392	0.493	0.618	0.692	****	0.372	0.007	0.123
6. <i>Pagurus minutus</i>	2.473	0.823	0.972	0.824	0.988	****	0.131	0.170
7. <i>Diogenes nitidimanus</i>	3.410	3.613	3.715	2.390	4.942	2.035	****	0.167
8. <i>Stratiotes nigroapiculus</i>	1.663	1.839	1.611	2.627	2.099	1.772	1.790	****

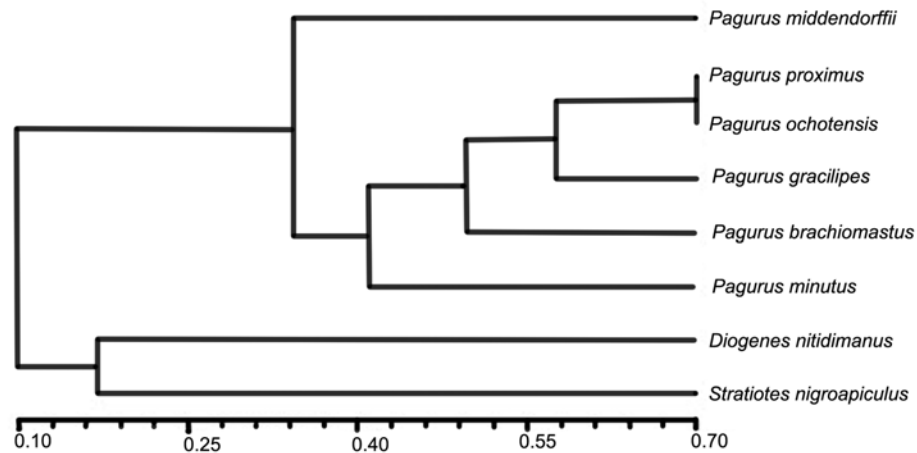


Fig. 1. UPGMA tree constructed on the base of genetic similarity (Nei, 1978) showing genetic relationships among eight hermit crab species.

Рис. 1. UPGMA-дерево, построенное на основе индексов генетического сходства (Nei, 1978), демонстрирующее генетические связи между 8 видами раков-отшельников.

mus ($I=0.611\pm 0.117$), *P. ochotensis* ($I=0.539\pm 0.121$) and *P. brachiomastus* ($I=0.501\pm 0.117$).

It was shown that the average genetic similarity between the pagurid species inhabiting Peter the Great Bay is lower than the average genetical identity obtained by Hedgecock et al. (1982) for 26 pairs of congeneric decapod species ($I=0.66\pm 0.15$) and values obtained by Mulley and Latter (1980) for the genera *Metapenaeus* ($I=0.69\pm 0.08$) and *Penaeus* ($I=0.65\pm 0.08$) and within the genus *Scylla* (Gao, Watanabe, 1998). Earlier, we have found that two spider crabs (*Pisoides bidentatus* and *Pugettia*

quadridens) and two intertidal crabs (*Hemigrapsus sanguineus* and *H. penicillatus*) were also very similar genetically (Zaslavskaya et al., 2007). Genetic identity values between these pairs of species were high ($I=0.758\pm 0.092$ and $I=0.821\pm 0.078$, respectively). Fairly low genetic identity among the pagurid species is in line with the observed variability in morphology among adults and among larvae within the genus *Pagurus*. This genus contains more than a 100 species (Ingle, 1985). Because of their recognized heterogeneity, species of the genus *Pagurus* were repeatedly divided into informal

groups based on either adult or larval morphology. For example, four groups (A–D) were distinguished based on the similarities of larval characters (see Roberts, 1970; McLaughlin, Gore, 1988).

According to larval characters, most of the pagurids inhabiting Russian waters of the Sea of Japan (*P. brachiomastus*, *P. ochotensis*, *P. middendorffii*, *P. proximus* and *P. minutus*) are members of Group A (typical representative is *Pagurus bernhardus*) (Kornienko, Korn, 2006). Larval characters of *P. gracilipes* considerably differ from larval characters of these pagurids (Kornienko, Korn, 2007). Detailed description indicated that this species should rather be placed in Group C (typical representative is *Pagurus anachoretus*). Therefore, larval morphology confirms that *P. gracilipes* differs from the other pagurids living in Peter the Great Bay.

However, according to genetic relationships, *P. gracilipes* undoubtedly belongs to the genus *Pagurus*. This conclusion is supported by similar identity values between other species of the genus *Pagurus* and much lower genetic similarities between the genera *Diogenes* and *Stratiotes* and between the families Paguridae and Diogenidae. Genetic identity values among the pagurid species in our study are close to interspecific values obtained in electrophoretic studies of other invertebrates. These studies suggest that 85% of *I*-values between congeneric species exceed 0.35, while between genera fall below 0.35 (Thorpe, 1982; Thorpe, Solé-Cava, 1994).

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