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DIFFERENCES IN SKULL SIZE OF HARBOUR PORPOISES, *PHOCOENA PHOCOENA* (CETACEA), IN THE SEA OF AZOV AND THE BLACK SEA: EVIDENCE FOR DIFFERENT MORPHOTYPES AND POPULATIONS

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Differences in Skull Size of Harbour Porpoises, *Phocoena phocoena* (Cetacea), in the Sea of Azov and the Black Sea: Evidence for Different Morphotypes and Populations. Goldin, P. E., Vishnyakova, K. A. — There are two porpoise stocks in the northern Black Sea: the north-western (Odessa Gulf) and north-eastern (Crimean and Caucasian waters); in addition, another stock is in the Sea of Azov. The Azov porpoises are distinct in their body size and biology. This research was conducted on the skulls of stranded sexually mature porpoises from the north-eastern Black Sea, north-western Black Sea and the Sea of Azov. In the north-eastern Black Sea samples, both present-day and old-time, the sexual dimorphism of the skull size was not significant, whereas in the Sea of Azov the females were significantly larger than males. The Azov skulls were strongly different from those from the Black Sea: they were larger, proportionally wider and had the wider rostra; also, there was no significant chronological variation within the Black Sea. The Azov and Black Sea samples were classified with the 100 % success with four variables. The north-western Black Sea skulls were somewhat intermediate in their characteristics between the Azov and north-eastern Black Sea samples, but they were classified together with other Black Sea specimens. The difference between the Azov and Black Sea skulls was greater than between many North Atlantic populations, despite the extreme geographical proximity of the two stocks. The low variation within the Black Sea supports the earlier conclusions on the lack of genetic variation: all the Black Sea stocks are expected to be genetically similar sub-populations, whereas the Azov and Marmara stocks possibly represent the genetically distant populations. The porpoises from the Black Sea and the Sea of Azov equally show the traits which characterize the subspecies *Phocoena phocoena relicta*, but the Black Sea porpoises appear to be more paedomorphic in terms of ontogenetic trajectories.

Key words: *Phocoena phocoena,* craniometry, variation, sexual dimorphism.

Различия в размерах черепа морских свиней, *Phocoena phocoena* (Cetacea), в Азовском и Чёрном морях: подтверждение существования различных морфотипов и популяций. Гольдин П. Е., Вишнякова К. А. — В северной части Чёрного моря обитает два стада морской свиньи — северо-западное (Одесский залив) и северо-восточное (крымские и кавказские воды); помимо этого, ещё одно стадо обитает в Азовском море. Азовские морские свиньи отличаются размерами тела и особенностями биологии. Данное исследование было проведено по черепам выброшенных на побережье половозрелых морсиих свиней из северо-восточной и северо-западной частей Чёрного моря и из Азовского моря. В выборках из северо-восточной части Чёрного моря (как в современных, так и в старых сборах) половой диморфизм размеров черепа был незначительным, в то время как в Азовском море самки были существенно крупнее самцов. Азовские черепа существенно отличались от черноморских крупными размерами, относительно большей шириной и широким рострумом; в пределах Чёрного моря не выявлено явной временной изменчивости. Азовская и черноморская выборки классифицируются со 100 %-ной точностью с помощью четырёх переменных. Черепа из северо-западной части Чёрного моря занимают по некоторым признакам промежуточное положение между азовской и северо-восточной черноморской выборками, однако классифицируются как черноморские. Различия между азовскими и черноморскими черепами необычно велики (по сравнению со многими популяциями северной Атлантики), несмотря на крайнюю географическую близость двух стад. Слабая изменчивость черноморских черепов подтверждает выводы предыдущих исследований о малом генетическом разнообразии: предположительно, все черноморские стада — это генетически сходные субпопуляции, в то время как стада в Азовском и Мраморном морях, возможно, представляют собой более удалённые в генетическом отношении популяции. Морские свиньи и из Чёрного, и из Азовского морей в равной степени обладают признаками, характерными для подвида *Phocoena phocoena relicta*, однако черноморские животные оказываются более педоморфными по своей онтогенетической траектории.

Ключевые слова: *Phocoena phocoena,* краниометрия, изменчивость, половой диморфизм.

Introduction

The geographically isolated subspecies of harbour porpoise, *Phocoena phocoena relicta* Abel, 1905, inhabits the Sea of Azov, the Black Sea and adjoining north-eastern Mediterranean waters; it greatly differs from the Atlantic porpoises in body size (Gol'din, 2004), as well as in skull size, proportions and shape (Gol'din, 2004 a, 2007; Viaud-Martínez et al., 2007; Galatius, Gol'din, 2011). There are a few distinct porpoise stocks within the Black Sea, and two of them are in the northern Black Sea: the north-western stock (Odessa Gulf region) and north-eastern stock (Crimean and Caucasian waters) (Mikhalev, 2005); in addition, another stock was found in the Sea of Azov (Gol'din, 2004). The Azov porpoises are larger than the animals in the Black Sea (Gol'din, 2004), and they differ from the Black Sea stocks in the summer diet (Zalkin, 1940; Tonay et al., 2007) and the reproductive seasonality: their peak of births falls in late June to early July, rather than in May to June as seen in the Black Sea (Vishnyakova, Gol'din, in press). In summer the Azov porpoises inhabit the Sea of Azov and possibly the Kerch Strait, the north-eastern Black Sea stock occupies the most part of Crimean Black Sea coastal waters, and the north-western stock is located in the Odessa Gulf (Mikhalev, 2005).

Here we present the first results of comparative analysis of skull morphometry of the porpoises from the northern Black Sea and the Sea of Azov and its implications for population identity and for further studies of population genetics of the Black Sea porpoises.

Institutional abbreviations: MSU, Zoological Museum of the Lomonosov Moscow State University, Moscow; ONU, Zoological Museum of the Mechnikov Odessa National University, Odessa; TNU, Zoological Museum of the Vernadsky Taurida National University, Simferopol.

Material and methods

The research was conducted on the skulls of stranded sexually mature porpoises from the geographical ranges of the north-eastern Black Sea stock (south-western and south-eastern coast of Crimea; n = 29: 10 females and 19 males; MSU and TNU), north-western Black Sea stock (Odessa Gulf; n = 2: 1 female and 1 male; ONU) and Azov stock (Azov coast of Crimea; n = 37: 23 females and 14 males; TNU). Within the north-eastern Black Sea sample there were recent findings, as well as the MSU specimens which were harvested and taken in 1948 and described by Kleinenberg (1956).

The age was determined as the number of growth layer groups in the dentine of thin haematoxylin-stained longitudinal sections of teeth. Neonates were considered as animals with healing umbilicus, non-erupted teeth, and no neonatal line in the dentine. The sexual maturity of females was identified from the presence of corpora lutea or corpora albicantia in the ovaries, evidences for recent delivery, pregnancy or lactation; in addition, all females of 4 years and older were classified as sexually mature (Vishnyakova, Gol'din, in press).

Twelve measurements were taken from each skull using vernier calipers (fig. 1): 1 — condylobasal length (CBL); 2 — rostrum length (the perpendicular line from tip of the rostrum to the line along the Measurement 6); 3 — zygomatic width (ZW); 4 — orbital width; 5 — parietal width (PAR); 6 — rostrum width at the base; 7 — rostrum width at the mid-point (RWM); 8 — length of basioccipitale (distance from the tip of the condyle to the posterior point of the vomer); 9 — condylar width; 10 — condylar height (left); 11 — length of the prenarial region; 12 — preorbital width (PRO).

Measurements were taken point to point on the left side, according to the protocol of Kleinenberg (1956) with the modifications by Perrin (1975) and Gol'din (2007). The measurements were selected as the best characteristics of the skull size, which were not duplicating and the least subject to the measurement errors: for the last reason, we did not use such measurements as skull height and orbit length.

Differences between samples were estimated using MANOVA with the sex (female; male), region (Black Sea; the Sea of Azov) and sample (NE Black Sea, present-day; Azov, present-day; NE Black Sea, 1948; NW Black Sea) as independent variables; and the Tukey's honest significant difference test was used for the post-hoc analysis of all measurements. Sexual differences within each sample were estimated using *U* Mann-Whitney test. Discriminant function analysis was performed using the Mahalanobis distances; group assignment was cross-validated using the jackknifing procedure (Hammer et al., 2001).

Results

The descriptive statistics for four samples is summarized in the table 1. Overall skull size (represented by the condylobasal length) varied within 223–274 mm; no age variation in the skull length was found within the samples of sexually mature animals (Gol'din, 2007).

All examined factors (region, sex and sample) were found to be significant in determining the skull measurements ($p < 0.05$ for all Pillai's traces and Wilks' lambdas), as well as all combinations of factors involving the region (Black Sea vs Azov).

S e x u a l d i m o r p h i s m. Female skulls were on average as large as the male skulls or absolutely larger in all dimensions in all samples, except the condylar height in the north-eastern Black Sea sample. However, the extant of dimorphism strongly varied between porpoises from the Black Sea and the Sea of Azov. In the north-eastern Black Sea samples, both recent and old-time, the sexual dimorphism was weakly pronounced and not significant: for example, the rostrum was on average only 0.4 mm longer in females. None of the measurements showed statistically significant sexual differences. On the contrary, 10 of 12 skull measurements (all but parietal width and prenarial length) in porpoises from the Sea of Azov showed statistically significant ($p < 0.05$) sexual dimorphism (Gol'din, 2007): for example, the rostrum was on average 7.8 mm longer in females. The female skulls were on average 6 % longer in the Azov sample, and most of measurements determining the skull size were proportionally greater, while the rostra were especially elongated (table 1). Interestingly, among the skulls of the north-western Black Sea porpoises the female was distinctly larger than the male; however, no conclusions could be drawn because of the small sample size.

D i f f e r e n c e s b e t w e e n t h e B l a c k S e a s a m p l e s. North-eastern Black Sea porpoises from the modern sample were significantly ($p < 0.05$) larger than those studied by Kleinenberg (1956) in the basioccipital length and condylar width, as well as the condylobasal length. However, even in these cases the differences in absolute size were small: the condylobasal length on average was greater in 5.5 mm (2.4 %). The other nine measurements, including most of width dimensions, did not differ. Both specimens from the north-western Black Sea generally fitted the size range of the north-eastern Black Sea animals: however, the male had slightly greater rostrum width at the mid-point (44 vs 42 mm, the widest north-eastern record), and the female had greater condylar width and condylar height (61 vs 59 mm and 38 vs 36.5 mm).

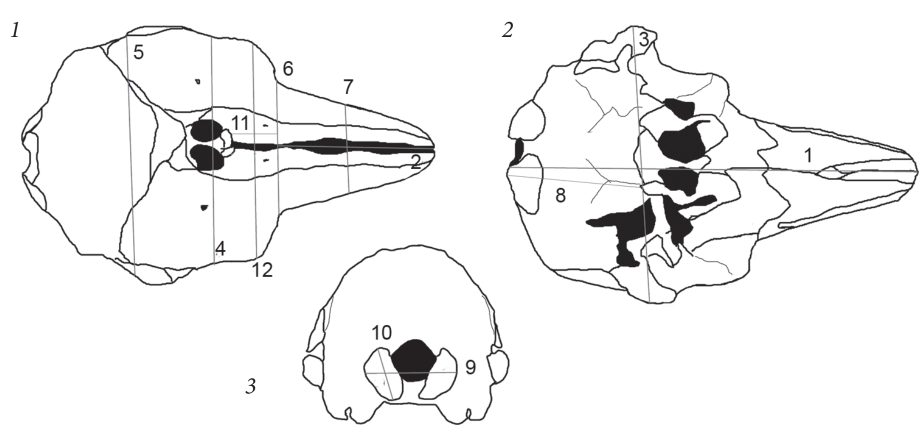


Fig. 1. Cranial measurements of the harbour porpoises (*Phocoena phocoena*): *1* — dorsal view; *2* — ventrolateral view; *3* — posterior view.

Рис. 1. Промеры черепа морских свиней (*Phocoena phocoena*): *1* — вид сверху; *2* — вид вентролатерально; *3* — вид сбоку.

Table 1. Skull measurements of the harbour porpoises, *Phocoena phocoena relicta*, from the Black Sea and the Sea of Azov

Таблица 1. Промеры черепа морских свиней, *Phocoena phocoena relicta*, из Чёрного и Азовского морей

Measurement	Males n	Males lim	Males $\bar{x}$	Males s_x	Females n	Females lim	Females $\bar{x}$	Females s_x
North-eastern Black Sea (present-day)								
1	11	228–244	235.7	5.8	8	231–258	240.6	9.4
2	11	98–112	103.5	4.7	8	97–114	103.9	5.2
3	10	126–138	131.6	3.8	8	123–141	133.2	6.1
4	11	98–116.0	107.7	5.0	8	103–120	111.5	5.2
5	10	106–118	113.0	3.2	8	111–117	114.4	2.5
6	11	61–73	65.3	3.7	8	60–68	64.0	3.0
7	11	35–41	38.3	2.1	8	34–43	38.8	3.3
8	11	54–71	66.3	4.7	8	57–75	66.4	4.5
9	11	49–58	55.3	2.8	8	53–59	55.4	1.7
10	11	31–37	34.0	1.9	8	31–36	33.7	1.8
11	11	29–36	31.8	2.5	8	27–35	32.4	2.5
12	11	95–109	101.5	4.6	8	94–113	105.0	6.7
North-eastern Black Sea (1948)								
1	8	223–239	230.9	4.9	2	233–243	238.0	7.1
2	8	96–107	102.5	3.4	2	102–108	105.0	4.2
3	8	127–142	131.6	4.8	2	131–132	131.5	0.7
4	8	104–119	109.5	4.6	2	110	110.0	0
5	8	106–116	112.6	3.5	2	113–114	113.8	0.4
6	8	61–69	64.6	2.5	2	66–70	68.0	2.8
7	8	35–42	37.8	2.3	2	38–39	38.5	0.7
8	8	56–62	57.9	2.3	2	56–61	58.5	3.5
9	8	50–54	51.8	1.6	2	51–55	53.0	2.8
10	8	32–34	33.4	0.7	2	33–34	33.5	0.7
11	8	24–35	28.5	3.3	2	29–35	32.0	4.2
12	8	96–114	103.3	5.4	2	107	107.0	n/a

Measurement	Males n	Males lim	Males $\bar{x}$	Males s_x	Females n	Females lim	Females $\bar{x}$	Females s_x
North-western Black Sea								
1	1	235	235.0	n/a	1	252	252.0	n/a
2	1	104	104.0	n/a	1	111	111.0	n/a
3	1	139	139.0	n/a	1	139	139.0	n/a
4	1	114	114.0	n/a	1	114	114.0	n/a
5	1	117	117.0	n/a	1	113	113.0	n/a
6	1	69	69.0	n/a	1	67	67.0	n/a
7	1	44	44.0	n/a	1	43	43.0	n/a
8	1	66	66.0	n/a	1	67	67.0	n/a
9	1	52	52.0	n/a	1	61	61.0	n/a
10	1	32	32.0	n/a	1	38	38.0	n/a
11	1	26	26.0	n/a	1	33	33.0	n/a
12	1	108	108.0	n/a	1	107	107.0	n/a
Sea of Azov								
1	14	236–258	246.6	5.8	23	251–274	261.3	5.8
2	14	101–115	107.2	3.8	23	106–124	116.0	4.2
3	13	139–149	145.3	3.2	23	146–164	154.7	4.7
4	14	111–123	119.0	3.3	23	122–135	127.4	3.9
5	13	117–126	121.7	2.4	23	114–131	122.9	3.5
6	13	66–74	70.5	2.6	22	71–84	77.9	3.8
7	14	41–53	46.2	2.7	23	47–59	51.6	3.0
8	12	65–74	69.5	2.6	23	66–78	73.4	2.2
9	14	52–63	57.2	3.1	23	58–65	61.0	1.9
10	14	32–38	35.0	1.7	23	35–41	37.7	1.5
11	14	21–37	31.4	4.3	23	25–40	33.3	4.2
12	12	101–110	106.3	2.9	20	108–122	115.6	4.1

D i f f e r e n c e s b e t w e e n t h e B l a c k S e a a n d t h e S e a o f A z o v. The skulls from the Azov sample were significantly ($p < 0.05$) larger than the skulls from the Black Sea, pooled together or divided by samples, regardless of the time of collection, in all measurements except the prenarial length. For example, the condylobasal length and zygomatic width of the Azov porpoises were on average 19 mm greater than of the Black Sea ones (pooled samples); the similar differences are observed in comparison between the Azov sample and separate Black Sea samples (table 1).

Significant statistical differences ($p < 0.05$) in skull proportions was found in the zygomatic width and rostrum width at the base and at the mid-point: all these measurements took significantly greater portion of the condylobasal length in the Azov sample (fig. 2). For example, the rostrum width at the mid-point took 17–22 % of the condylobasal length in the Azov sample and only 15–18 % in the north-eastern Black Sea sample, and notably, it was 17–19 % in the skulls from the north-western Black Sea. Thus, the Azov skulls were relatively wider than the Black Sea ones, and the north-western Black Sea skulls had intermediate proportions between the eastern Black Sea and the Azov stocks (fig. 2).

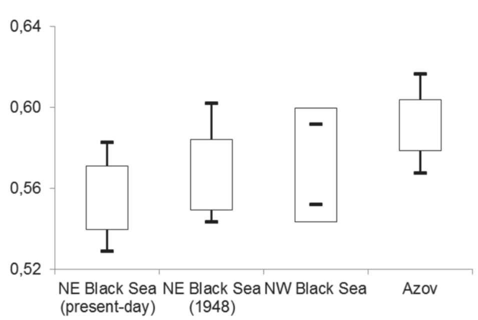
D i s c r i m i n a n t a n a l y s i s. The Azov and Black Sea samples (including the north-western Black Sea ones) were discriminated and classified with the 100 success. Four variables were enough for the discrimination by region: zygomatic width; parietal width; rostrum width at the mid-point; and preorbital width; the discriminant function is expressed as the following equation:

$$DF = 0.140ZW + 0.117PAR + 0.245RWM - 0.188PRO - 24.260$$

The breakpoint between the Azov and Black Sea specimens was at the $DF = 0$: all the Azov specimens had the positive *DF* scores, and all the Black Sea specimens had the negative ones.

Most of specimens are successfully classified with combinations of just two parameters contributing to the discriminant function: for example, the Azov and Black Sea specimens well differed in plots of the parietal width or zygomatic width against the rostrum width at the mid-point (fig. 3). On the contrary, two north-eastern Black Sea samples completely overlapped, leaving no way for their discrimination. The north-western Black Sea specimens occupied the border zone of the Black Sea samples.

1



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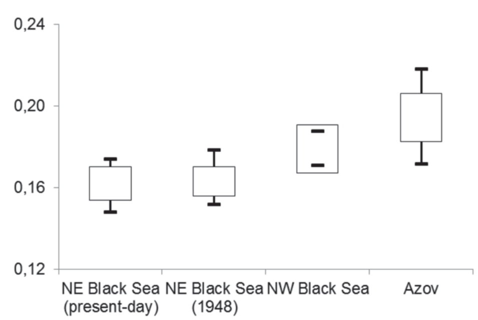

Fig. 2. Skull proportions of the harbour porpoises from the Sea of Azov and the Black Sea (mean ± standard deviation is presented as the box, upper and lower limits as the lines): *1* — zygomatic width as the CBL percentage; *2* — rostrum width at the mid-point as the CBL percentage.

Рис. 2. Пропорции черепа морских свиней из Азовского и Чёрного морей (среднее ± стандартное отклонение показано в прямоугольнике, предельные значения — линиями): *1* — скуловая ширина в виде доли КБД; *2* — ширина рострума на середине в виде доли КБД.

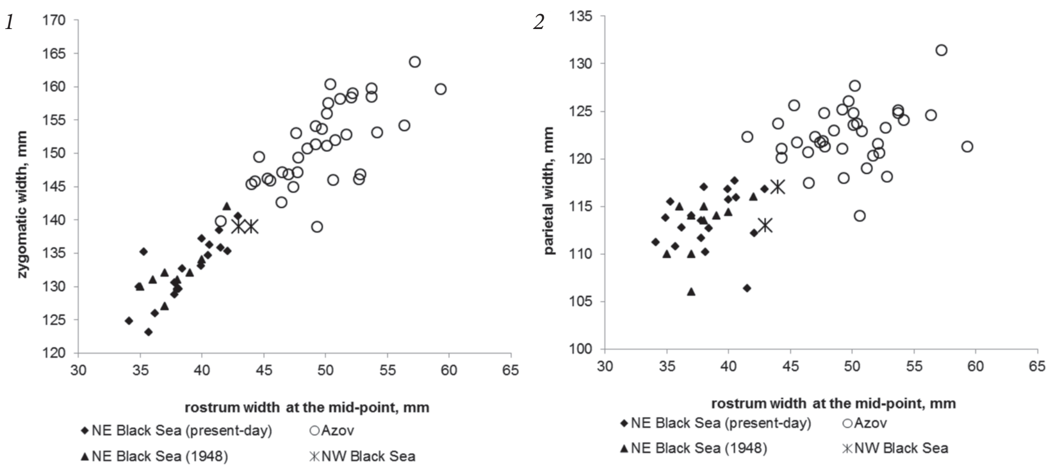

Fig. 3. The skull measurements of the harbour porpoises from the Sea of Azov and the Black Sea: *1* — zygomatic width vs rostrum width at the mid-point; *2* — parietal width vs rostrum width at the mid-point.

Рис. 3. Промеры черепа морских свиней из Азовского и Чёрного морей: *1* — скуловая ширина и ширина рострума на середине; *2* — теменная ширина и ширина рострума на середине.

Discussion

Overall skull size and sexual dimorphism. The skull sizes found here concur with the earlier data reported by Barabash-Nikiforov (1940) for the Black Sea (e. g., CBL = 216–257 mm) and by Zalkin (1938) for the Sea of Azov (CBL = 238–293 mm, only sexually mature animals). These skulls are significantly smaller than the skulls of the North Atlantic and Pacific porpoises; this is typical for the Black Sea subspecies *Phocoena phocoena relicta* (Tomilin, 1957; Gol'din, 2004 a; Viaud-Martinez et al., 2007). Thus, this study confirms the Black Sea porpoises as not only the smallest living cetaceans (Gol'din, 2004) but also the cetaceans with the very short skulls, which are almost as short, as in vaquita, *Phocoena sinus*, 210–243 mm (Brownell, 1983) (while the narrowest skulls are observed in *Pontoporia* (Ramos et al., 2002)). As in the most populations of harbour porpoises (Amano, Miyazaki, 1992; Galatius, 2005), the sexual dimorphism is reverted in comparison with the most delphinoids: females are on average larger than males (Gaskin and Blair, 1977). However, the geographical variation of skull size between the examined samples (to say nothing of the more distantly related North Atlantic populations) is manifestly greater than the sexual dimorphism within any of them. Moreover, strong geographical variation of the sexual dimorphism is notable: in the Sea of Azov it is pronounced to such extent that gender can even be visually identified without further measurements (fig. 4), while in the Black Sea it is barely seen, similar to that in the North Atlantic populations (Noldus, de Klerk, 1984; Gao, Gaskin, 1996; Börjesson, Berggen, 1997).

Geographical variation. The skulls of porpoises from the Sea of Azov strikingly differ from those from the Black Sea, and they can be easily visually distinguished (fig. 4). In particular, the Azov skulls are larger, proportionally wider, and have unusually wide rostra. The skulls from the northern Black Sea, on the contrary, show little spatial or temporal variation, except for some Azov-like traits in the north-western Black Sea skulls. Interestingly, this difference is likely to have existed 60–80 years ago, which explains the different size estimates in earlier studies: Barabash-Nikoforov (1940) and Kleinenberg (1956) dealt with the Black Sea samples, whereas Zalkin (1938) and Tomilin (1957) with the Azov specimens.

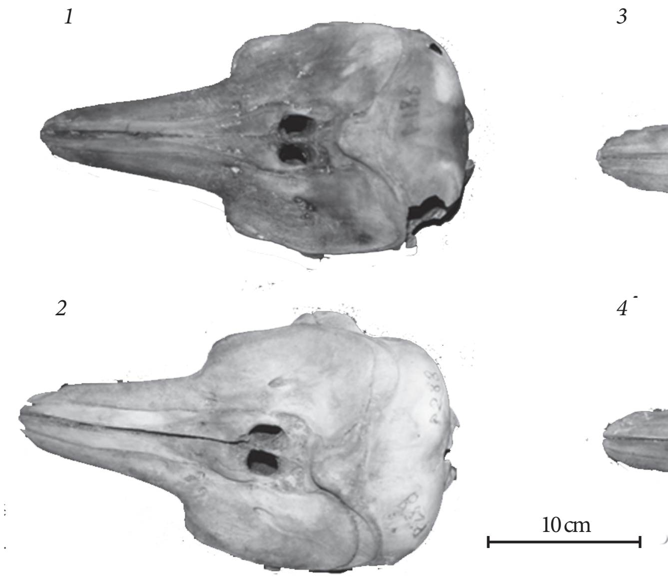

Fig. 4. Dorsal views of skulls of the harbour porpoises *Phocoena phocoena relicta* from the Sea of Azov and the Black Sea: *1* — Azov Sea, male; *2* — Azov Sea, female; *3* — Black Sea, male; *4* — Black Sea, female. Photo by M. Chopovdya.

Fig. 4. Черепа морских свиней, *Phocoena phocoena relicta,* из Азовского и Чёрного морей, вид сверху: *1* — Азовское море, самец; *2* — Азовское море, самка; *3* — Чёрное море, самец; *4* — Чёрное море, самка. Фото М. П. Чоповди.

There are a few unusual aspects of this observation. First, the difference between the Azov and the Black Sea samples is surprisingly great: the neighbouring populations are usually far more similar and hardly classified: the well-studied example is the population structure of porpoises in the Baltic and North Seas where there are minor (although statistically significant) inter-population differences in the skull measurements (Börjesson, Berggen, 1997; Huggenberger et al., 2002), which are better described in terms of the skull shape (Galatius et al., 2012).

Second, the Azov and the north-eastern Black Sea stocks are bordering with each other: many of examined specimens from the southern Sea of Azov stranded only 50 km away from porpoises from the north-eastern Black Sea region. The Azov porpoises in winter inhabit the waters where the north-eastern Black Sea porpoises spend summer season (Vishnyakova et al., 2013), and there are summer movements between the two regions (Vishnyakova, Gol'din, in press); thus, the two populations are expected to contact in one way or another. However, their differences in skull anatomy seem to be greater than inter-population differences in the North Atlantic. In combination with other differences in morphology, ecology, migration patterns and life history (see Introduction); this leads to the conclusion of co-existence of the two deeply diverged populations with different morphological types in neighbouring sea areas. The question of the genetic or epigenetic mechanism underlying these differences, as well as its ecological significance, is left open. It is suggested that broad rostrum can be an advantage for porpoises, which forage near the sea floor (Galatius, Gol'din, 2011), as Azov and possibly north-western Black Sea animals do (Zalkin, 1940), whereas pelagic porpoises often have slender rostra (Galatius, Gol'din, 2011).

Third, notable is the low variation within the north-eastern Black Sea samples and their similarity with the north-western specimens. This variation supports the earlier concerted conclusions from genetic studies which did not find any significant variation within the Black Sea (Fontaine et al., 2007; Viaud-Martinez et al., 2007; Tonay et al., 2012). Thus, all the present-day Black Sea stocks are expected to be genetically similar sub-populations. On the contrary, the Azov and Marmara stocks (for the latter one, see Tonay et al., 2012) should be further tested for genetic uniqueness and are likely to represent genetically distant populations. A possible exception within the Black Sea can still be the north-western stock: few skulls from this region show some similarities to the Azov skulls and need further detailed morphometric and genetic examinations. Interestingly, this pattern of geographical variation concurs with the population structure of the anchovy *Engraulis encrasicolus* (Linnaeus, 1758), which forms two genetically different forms in the Sea of Azov and the Black Sea; however, the north-western Black Sea stock also shows genetic similarities with the Azov anchovies (Kalnina, Kalnin, 1984).

Finally, the porpoises from the Black Sea and the Sea of Azov equally show the skull size and proportions which characterize the subspecies *Phocoena phocoena relicta* and distinguish them from the North Atlantic and North Pacific subspecies (fig. 4): the relatively long and very wide rostrum (length: 42–47 % of CBL; width: 27–31 % of CBL and 46–55 % of ZW) and small condylar width (21–25 % of CBL) (see also Abel, 1905; Tomilin, 1957; Gol'din, 2004 a; Viaud-Martinez et al., 2007). These traits are partly owing to the specific skull shape with more ventrally directed rostrum and ventrally shifted foramen magnum (Galatius, Gol'din, 2011). The Azov porpoises were also reported to have the most paedomorphic skull anatomy among the harbour porpoises, with the greatest amount of juvenile features (Galatius, Gol'din, 2011). In this regard, the skulls of the Black Sea porpoises are more paedomorphic than the Azov ones: they are smaller and narrower, with smaller rostra (which are still relatively large in comparison with other subspecies), and their lack of sexual dimorphism can be also considered a juvenile trait, since all these features develop in the course of postnatal ontogeny (Gol'din, 2007). Further comparative studies of the skull shape would provide an insight into the pathways of morphological differentiation within the Azov-Black Sea porpoises and their possible evolutionary and ecological mechanisms.

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