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CHELONOLOGICAL STUDIES OF L.I. KHOSATZKY WITH HIS ANNOTATED BIBLIOGRAPHY ON TURTLES

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ABSTRACT

This paper presents a review of the chelonological research of L.I. Khosatzky (1913–1992), a well-known Soviet zoologist-herpetologist and paleontologist from Leningrad (now Saint Petersburg). It provides an annotated bibliography of his 115 publications on turtles. Khosatzky's turtle research was devoted to the origin of turtles, systematics, phylogeny and biogeography of fossil and recent turtles, biomechanics, morphology and evolution of the turtle shell, and the ecological physiology of turtles. Khosatzky supervised numerous student works (course projects, graduate and candidate theses) on different aspects of turtle biology, the results of which were only partially published. Some of Khosatzky's students became well-known specialists on turtles.

Key words: biogeography, biomechanics, ecological physiology, evolution, history of science, morphology, origin, phylogeny, shell, systematics, turtles

ХЕЛОНОЛОГИЧЕСКИЕ ИССЛЕДОВАНИЯ Л.И. ХОЗАЦКОГО С ЕГО АННОТИРОВАННОЙ БИБЛИОГРАФИЕЙ ПО ЧЕРЕПАХАМ

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РЕЗЮМЕ

Эта статья представляет обзор хелонологических исследований Л.И. Хозацкого (1913–1992), известного советского зоолога-герпетолога и палеонтолога из Ленинграда (ныне Санкт-Петербург), и аннотированную библиографию его 115 публикаций по черепахам. Исследования Хозацкого по черепахам были посвящены происхождению черепах, систематике, филогении и биogeографии ископаемых и современных черепах, биомеханике, морфологии и эволюции панциря черепах, и экологической физиологии черепах. Хозацкий руководил многочисленными студенческими работами (курсовые работы, дипломы и кандидатские диссертации) по различным аспектам биологии черепах, результаты которых были опубликованы лишь частично. Некоторые из студентов Хозацкого стали известными специалистами по черепахам.

Ключевые слова: биogeография, биомеханика, экологическая физиология, эволюция, история науки, морфология, происхождение, филогения, панцирь, систематика, черепахи

INTRODUCTION

Lev Isaakovich Khosatzky (1913–1992) was a well-known Soviet zoologist-herpetologist and paleontologist from Leningrad (now Saint Petersburg), who made an especially large contribution to the chelonology (i.e. study of fossil and living turtles) of the USSR and adjacent countries. In addition to turtles, Khosatzky's research was devoted to the systematics, morphology, paleontology, ecology and physiology of other groups of vertebrates, especially amphibians and reptiles, the theory of evolution, and the history and methodology of science. The biography of Khosatzky and his bibliography were published by Borkin (1999, 2003, 2004, 2011, 2013) in Russian. In addition, short notes about Khosatzky were published by Ananjeva (2005) and Adler (2012) in English. Borkin emphasized a wide scope of Khosatzky's scientific interests and studies and noted that "it would be interesting to trace development of Khosatzky's (and his students') studies on modern and extinct turtles" (Borkin 2003, p. 10), because turtles were his main object of study. Khosatzky published at least 268 publications (Borkin [2003, 2004, 2013] indicated 267 publications, but one more publication [Khosatzky et al. 2013] is included in this volume), of which 115 are devoted to or contain original data on turtles (Appendix 1). In addition, at least four publications by other authors contain descriptions of turtles named by Khosatzky or were written by him (Appendix 2). The turtle publications of Khosatzky include studies on the origin of turtles, systematics of fossil and living turtles, biomechanics, morphology and evolution of the turtle shell, as well as ecological physiology of turtles. For a long time (1940s–1960s) Khosatzky was the leading expert on turtles of the USSR and adjacent countries. He named 44 turtle taxa, including two subfamilies, 11 genera/subgenera, and 32 species/subspecies (Table 1). The temporal and geographic "distribution" of some Khosatzky's publications on turtles is summarized in Table 2. Khosatzky was not only a good scientist, but also a great teacher and brilliant lecturer at the Leningrad (now Saint Petersburg) State University (hereinafter LSU), where he worked as a docent at the Faculty of Biology and Soil Sciences, Department of Vertebrate Zoology (hereinafter DVZ), from 1948 to 1983 when he retired. At the DVZ Khosatzky taught lecture courses on vertebrate zoology, comparative vertebrate anatomy, vertebrate paleontology (from

1951 to 1983) and chordate phylogeny. From 1963 to 1981 Khosatzky also taught the lecture course on vertebrate paleontology at the Department of Paleontology (hereinafter DP) of the Geological Faculty of the LSU. Before Khosatzky, the course on vertebrate paleontology at the DVZ and DP was taught by famous anatomist, paleontologist and artist Alexey Petrovich Bystrov (1899–1959; see Kolchinsky 2011). Khosatzky taught several generations of zoologists and paleontologists and supervised and reviewed numerous student works, many of which were devoted to turtles (Table 3). Some photos of L.I. Khosatzky and his teachers, colleagues and students are presented on Plates 1 and 2 (see pages 372–375).

Most of Khosatzky's publications were published in Russian and in journals, books, and conference abstract volumes that are not readily accessible. As a result only a few Khosatzky's publications are known by scientists outside Russia. For instance, the Google Scholar researcher profile for Lev Isaakovich Khosatzky was only able to retrieve seven of Khosatzky's publications, all taxonomic in nature, and 98 citations of these publications (search conducted 7 December 2013). Under those circumstances, it is not surprising that although Khosatzky studied the biomechanics of the turtle shell extensively, his publications were not recognized in at least one of the most recent publications on this subject (Magwene and Socha 2013). Therefore, the goal of this paper is to make Khosatzky's research available to researchers outside Russia and to highlight the wide scope of his various studies on turtles.

In this paper we provide a review of the chelonological studies of Khosatzky and an annotated bibliography of his publications on turtles (see Appendices 1 and 2). First, we give a brief historical account of Khosatzky's turtle research. Then, we review his studies and ideas about the origin of turtles, systematics, phylogeny and biogeography of fossil and recent turtles, biomechanics, morphology and evolution of the turtle shell, and ecological physiology of turtles. We also comment on the current taxonomic status of the turtle taxa and material described or reported by Khosatzky. This study is based on original publications of Khosatzky, publications by Borkin (1999, 2003, 2004, 2011) about Khosatzky, and materials from the archive of Khosatzky, which are kept at the Department of Herpetology, Zoological Institute of the Russian Academy of Sciences (hereinafter ZIN)

Table 1. Turtle taxa established by L.I. Khosatzky. For references, see text.

No.	Original name	Original familial or other attribution	Current name/status	Current familial or other attribution
1	<i>Adocus foveatus</i> Nessov et Khosatzky in Khosatzky et Nessov, 1978	Adocidae	Unchanged	Unchanged
2	<i>Agrionemys</i> Khosatzky et Mlynarski, 1966	Testudinidae	Unchanged or synonym of <i>Testudo</i>	Unchanged
3	<i>Amyda orlovi</i> Khosatzky, 1976	Trionychidae	Member of a new genus	Unchanged
4	<i>Anatolemys</i> Khosatzky et Nessov in Nessov, 1977	Toxochelyidae	Unchanged	Macrobaenidae/Sinemydidae
5	<i>Anatolemys maximus</i> Khosatzky et Nessov in Nessov, 1977	Toxochelyidae	Unchanged	Macrobaenidae/Sinemydidae
6	<i>Anatolemys oxensis</i> Nessov in Khosatzky et Nessov, 1977	Toxochelyidae	Unchanged	Macrobaenidae/Sinemydidae
7	<i>Baicalemys</i> Khosatzky in Khosatzky et Chkhikvadze, 1993	Emydidae	Unchanged	Unchanged
8	<i>Baicalemys elegans</i> Khosatzky in Khosatzky et Chkhikvadze, 1993	Emydidae	Unchanged	Unchanged
9	<i>Chelonia aralis</i> Khosatzky, 1945	Cheloniidae	Nomen dubium	Unchanged
10	<i>Clemmys iliensis</i> Khosatzky et Kuznetsov, 1977	Emydidae	<i>Ocadia iliensis</i> (Khosatzky et Kuznetsov, 1977)	Geoemydidae
11	<i>Clemmys kazachstanica</i> Khosatzky, 1947	Emydidae	" <i>Clemmys</i> " <i>kazachstanica</i> Khosatzky, 1947	Unclear
12	<i>Clemmys pidoplichkai</i> Khosatzky, 1946	Emydidae	" <i>Melanochelys</i> " <i>pidoplichkoi</i> (Khosatzky, 1946)	Geoemydidae
13	<i>Clemmys riabinini</i> Khosatzky, 1946	Emydidae	<i>Sakya riabinini</i> (Khosatzky, 1946)	Geoemydidae
14	<i>Emys orbicularis antiqua</i> Khosatzky, 1956	Emydidae	Unchanged	Unchanged
15	<i>Ferganemys</i> Nessov et Khosatzky, 1977	Adocidae	Unchanged	Unchanged
16	<i>Ferganemys verzilini</i> Nessov et Khosatzky, 1977	Adocidae	Unchanged	Unchanged
17	<i>Geislemys</i> Khosatzky et Mlynarski, 1966 (subgenus)	Emydidae	<i>Geislemys</i> Khosatzky et Mlynarski, 1966 (genus)	Geoemydidae
18	<i>Geochelone devjatkini</i> Khosatzky et Narmandakh, 1973	Testudinidae	Junior synonym of <i>Protestudo darewskii</i> Chkhikvadze, 1971	Unchanged
19	Kirgizemyinae Nessov et Khosatzky, 1973	Toxochelyidae	Junior synonym of Macrobaenidae Sukhanov, 1964	Macrobaenidae/Sinemydidae
20	<i>Kirgizemys</i> Nessov et Khosatzky, 1973	Toxochelyidae	Unchanged	Macrobaenidae/Sinemydidae
21	<i>Kirgizemys dmitrievi</i> Nessov et Khosatzky, 1981	Toxochelyidae	Unchanged	Macrobaenidae/Sinemydidae
22	<i>Kirgizemys exaratus</i> Nessov et Khosatzky, 1973	Toxochelyidae	Unchanged	Macrobaenidae/Sinemydidae
23	<i>Lindholmemys gravis</i> Nessov et Khosatzky, 1980	Dermatemydidae	Unchanged	Lindholmemydidae

Table 1. Continued.

No.	Original name	Original familial or other attribution	Current name/status	Current familial or other attribution
24	<i>Melanochelys etuliensis</i> Khosatzky et Redkozubov, 1986	Emydidae	" <i>Melanochelys</i> " <i>etuliensis</i> Khosatzky et Redkozubov, 1986	Geoemydidae
25	<i>Mongolemys</i> Khosatzky et Mlynarski, 1971	Dermatemydidae	Unchanged	Lindholmemydidae
26	<i>Mongolemys elegans</i> Khosatzky et Mlynarski, 1971	Dermatemydidae	Unchanged	Lindholmemydidae
27	<i>Mongolochelys</i> Khosatzky, 1998	Group Kayentachelydia	Unchanged	Clade Meiolaniformes
28	<i>Mongolochelys efremovi</i> Khosatzky, 1998	Group Kayentachelydia	Unchanged	Clade Meiolaniformes
29	Shachemydinae Khosatzky in Nessov et Khosatzky, 1977	Adocidae	Unchanged	Unchanged
30	? <i>Sinemys efremovi</i>	Sinemydidae	<i>Wuguia efremovi</i> (Khosatzky, 1996)	Macrobaenidae/Sinemydidae
31	<i>Spinemys</i> Khosatzky et Mlynarski, 1966	Emydidae	Unclear	Geoemydidae
32	<i>Testudo aralensis</i> Khosatzky, 1945	Testudinidae	Nomen nudum	Unchanged
33	<i>Testudo černovi</i> Khosatzky, 1948	Testudinidae	<i>Testudo černovi</i> Khosatzky, 1948	Unchanged
34	<i>Testudo eldarica</i> Khosatzky et Alekperov in Alekperov, 1978	Testudinidae	Unchanged	Unchanged
35	<i>Testudo graeca binagadensis</i> Khosatzky in Alekperov, 1978	Testudinidae	Unchanged	Unchanged
36	<i>Testudo graeca pontica</i> Khosatzky, 1987	Testudinidae	Nomen nudum	Unchanged
37	<i>Testudo kegenica</i> Khosatzky in Bazhanov et Pigulevsky, 1955	Testudinidae	<i>Agrionemys (Protagrionemys) kegenica</i> (Khosatzky in Bazhanov et Pigulevsky, 1955)	Unchanged
38	<i>Testudo kuchurganica</i> Khosatzky, 1948	Testudinidae	<i>Testudo kuchurganica</i> Khosatzky, 1948	Unchanged
39	<i>Testudo tekessa</i> Khosatzky et Kuznetsov in Khosatzky et al., 1974	Testudinidae	<i>Agrionemys (Protagrionemys) tekessa</i> (Khosatzky et Kuznetsov in Khosatzky et al., 1974)	Unchanged
40	<i>Toxocheloides</i> Nessov et Khosatzky, 1981	Toxochelyidae	Nomen dubium	Xinjiangchelyidae
41	<i>Toxocheloides narynensis</i> Nessov et Kaznyshkin, 1985	Toxochelyidae	Nomen dubium	Xinjiangchelyidae
42	<i>Trionyx (Amyda) capellinii bulgaricus</i> Khosatzky in Khosatzky et al., 1983	Trionychidae	Unchanged	Unchanged
43	<i>Trionyx moldaviensis</i> Khosatzky, 1986	Trionychidae	" <i>Trionyx</i> " <i>moldaviensis</i> Khosatzky, 1986	Unchanged
44	<i>Trionyx zakhidovi</i> Khosatzky, 1966	Trionychidae	Nomen dubium	Unchanged

Table 2. Temporal and geographic “distribution” of some of Khosatzky’s publications on turtles.

	Bulgaria	USSR in general	European Russia and Caucasus	Moldavia	Ukraine	Siberia and Far East	Kazakhstan	Middle Asia	China	Mongolia	Total
Quaternary -Recent		Khosatzky 1948c; Khosatzky and Alekperov 1958; Khosatzky 1972; Khosatzky 1987			Khosatzky 1946a	Khosatzky and Nesson 1979b, 1981		Turdakov et al. 1967; Khosatzky 1987; Khosatzky et al. 2013	Khosatzky 1945d		15
Neogene		Khosatzky 1949a,d, 1951, 1957b, 1958c, 1982	Khosatzky 1956	Khosatzky 1966a; Khosatzky and Tarabukin 1970; Khosatzky and Toñan 1970a, b; Khosatzky 1986; Khosatzky and Redkozubov 1986a, b, 1989	Khosatzky 1945b, 1946b, 1947c, 1948b, d, 1949b, 1953	Khosatzky 1965a, 1967a; Ivanjev and Khosatzky 1970; Khosatzky and Chkhikvadze 1993	Khosatzky 1944, 1945c, 1947b, 1957a, 1958a; Borisov et al. 1963; Khosatzky and Kuznetsov 1963; Khosatzky 1965a, 1967a; Khosatzky et al. 1974	Khosatzky 1965a, 1965a; Birman et al. 1968, 1971		Khosatzky and Narmandakh 1973, 1975	38
Paleogene	Khosatzky et al. 1985	Khosatzky 1949a, 1951, 1957b, 1958c				Khosatzky 1965a, 1967a		Khosatzky 1965a; 1967a			13
Cretaceous		Khosatzky 1949a, c, 1951, 1957b, 1958c; Nesson and Khosatzky 1977a; Glickman et al. 1987				Rozhdestvensky and Khosatzky 1965, 1967; Nesson and Khosatzky 1973, 1977b; Khosatzky and Nesson 1978; Nesson and Khosatzky 1981a	Khosatzky 1957a; Rozhdestvensky and Khosatzky 1965, 1967; Verzilim et al. 1970a; Nesson and Khosatzky 1973, 1977b; Khosatzky and Nesson 1978; Nesson and Khosatzky 1980	Khosatzky 1957a, c; Rozhdestvensky and Khosatzky 1965, 1967; Verzilim et al. 1970a; Nesson and Khosatzky 1973, 1977b; Khosatzky and Nesson 1978; Nesson and Khosatzky 1978; Khosatzky and Nesson 1979a; Nesson and Khosatzky 1980		Khosatzky and Mlynarski 1971; Khosatzky 1976, 1998, 1999	26
Jurassic		Khosatzky 1949a, 1951, 1957b, 1958c, 1972; Nesson and Khosatzky 1977a				Rozhdestvensky and Khosatzky 1965, 1967		Verzilim et al. 1970b; Nesson and Khosatzky 1999			10
Total	1	10	5	8	8	9	17	19	2	6	6

and DVZ. The names of taxa in the annotations of Khosatzky's publications are given in their original spelling; their current status is discussed in the text. The authorships of suprageneric taxa, other than those established by Khosatzky or otherwise important for discussion, are not given. For corrected ages of the formations (svitas) and localities mentioned in the annotations see Chkhikvadze (1989, 1990) and Nesson (1997).

A few words should be said about the Soviet postgraduate education system in order to better understand Khosatzky's education. A student who has graduated from a university may become an aspirant, or a person who pursues a Candidate (Kandidat) of Sciences degree. After three years of research, an aspirant must defend a candidate thesis or dissertation in order to receive the degree. The Candidate of Sciences is usually recognized as the equivalent of a Ph.D. in the European and American doctorate system. After completion of a candidate degree, a student may become a doctorant and pursue a second postgraduate degree, the Doctor (Doktor) of Sciences. Receipt of a Doctor of Science requires additional research and production and defence of a second dissertation. It is similar to Habilitation in Western Europe in that successful completion of a Doctor of Sciences program (doktorantura) qualifies a person to be a full professor in Russia.

TURTLE CHAPTERS IN THE SCIENTIFIC BIOGRAPHY OF KHOSATZKY

Before discussing Khosatzky, we should briefly discuss the state of turtle research in the USSR before Khosatzky. Previous studies on recent turtles of the USSR were summarized in the first guide to reptiles and amphibians of the USSR by Terentjev and Chernov (1936). Pavel Viktorovich Terentjev (1903–1970) was a zoologist-herpetologist and docent at the DVZ (later professor and head of the DVZ; see Adler 1989; Kolchinsky 2011). Sergei Aleksandrovich Chernov (1903–1964) was the head of the Department of Herpetology of the ZIN (see Adler 1989; Kolchinsky 2011). Papers on turtle taxonomy were published by Wilhelm Adolfovich Lindholm (1874–1935), a malacologist and herpetologist (see Adler 2012). Fossil turtles of this territory were studied by Anatoliy Nikolaevich Riabinin (1874–1942; see Kolchinsky 2011), the Leningrad geologist and vertebrate paleontologist.

In 1930–1936, Khosatzky was a student at the Biological Faculty of the LSU. The first scientific work of Khosatzky was his graduate thesis (diploma) about snakes entitled “The critical review of the Palearctic representatives of the genus *Natrix*” (1936), which he wrote under the supervision of Chernov. Khosatzky began his studies on turtles when he became an aspirant (postgraduate student) at the DVZ after graduation from LSU. Khosatzky worked on his candidate thesis under supervision of the Russian/Soviet zoologist and ecologist Professor Daniil Nikolaevich Kashkarov (1878–1941; see Kolchinsky 2011), who was head of the DVZ. In his teaching Kashkarov paid particular attention to paleontology. He invited paleontologist Prof. Yuriy Aleksandrovich Orlov (1893–1966; see Kolchinsky 2011), later Academician and director of the Paleontological Institute of the Academy of Sciences of the USSR (hereinafter PIN), to teach the lecture course on vertebrate paleontology. “[It is] No coincidence that at this time several students of Prof. D.N. Kashkarov determined the direction of their future activity in the field of paleontology” (Khosatzky 1977a: 143). The first variant of Khosatzky's thesis entitled “An ecological-morphological study of the evolution of the shell of terrestrial turtles” was partially lost in 1941 during bombing of the Peterhof Biological Institute (where the thesis was kept) by German troops in the summer of 1941. However, abstracts of this thesis were published (Khosatzky 1941b). The second variant of his thesis entitled “A functional-morphological and paleontological study of some turtles” dated 1941–1942 was defended in 1944 at the Leningrad Pediatric Medical Institute (a complete copy of this thesis is kept at the DVZ). This unpublished thesis consists of 534 pages of text and an appendix with 50 plates of figures, and contains four main sections: 1) “A general survey of terrestrial turtles”, where Khosatzky surveys the major taxa of tortoises (subfamily Testudininae of the family Testudinidae); 2) “General characteristics of the shell of terrestrial turtles” which contains original data on the morphology and variation of the shell of some species, and general discussions of the origin and evolutionary development of the turtle shell; 3) “Functional study of the main peculiarities of the shell of terrestrial turtles”, i.e. a biomechanical study of the turtle shell; and 4) “A paleontological study of fossil turtles of the USSR”, which presents a review of fossil turtles known from the USSR, including

descriptions of new materials. In the biomechanical part of his study on the turtle shell Khosatzky was advised by his father Isaak Mikhaylovich Khosatzky (1881–1942) who was a construction engineer and professor at the Belorussian Politechnic Institute (BPI, Minsk). All of the experimental studies on the turtle shell presented in Khosatzky's thesis were conducted in laboratories of the BPI under his father's supervision. For this reason, in his thesis (dedicated to the father) and later publications L.I. Khosatzky regarded the turtle shell as a building construction. Materials for the paleontological chapter of the thesis came from the PIN (Moscow), the Zoobiological Institute of the Ukrainian Academy of Sciences (now I.I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Kiev), the All-Union Geological Research Institute (now A.P. Karpinsky Russian Geological Research Institute, Saint Petersburg) and private collections. Some paleontological materials were received from Riabinin, who was a predecessor of Khosatzky in studies of fossil turtles. Khosatzky (1946b) named one species of fossil turtle in honor of Riabinin, dedicated one paper on fossil turtles to him (1953) and co-authored one paper with him on a fossil shark (Riabinin and Khosatzky 1999). Khosatzky (thesis, p. 15) wrote that “this thesis is a part of a planned larger work on the topic “Ecological-morphological study of the evolution of the shell of terrestrial turtles””. In this future work he planned to write a thesis based on a comparative functional study of the shell of some aquatic turtles, and to generalize paleontological data with other available information on fossil turtles. In addition, he planned to study some turtle species under natural conditions and estimate significance of most important morphological-functional features of the shell of these species in the specific environment to determine their adaptability. The synthesis of all obtained morphological-functional, ecological and paleontological data would reveal the character and patterns of transformation of the turtle shell in its evolutionary development. Later, Khosatzky (1951) formulated the main principle of his research method as an analysis of the stable unity of the main biological triad (form-function-environment) and referred to it as a method of “triple unity”.

Reviewers of Khosatzky's thesis were ichthyologist N.L. Gerbilsky and Terentjev, who was an older colleague of Khosatzky at the DVZ. Altig (2012) erroneously indicated Terentjev as a teacher of Kho-

satzy, whose true teachers were Kashkarov, Chernov, and Orlov (Borkin 2011; see above). Terentjev and Chernov (1940: 3) in the 2nd edition of “The Field Guide of Reptiles and Amphibians of the USSR” noted the active participation of Khosatzky in the preparation of the turtle sections of this book. Later, Khosatzky named one species of fossil turtle (*Testudo černovi*; Khosatzky 1948) in honour of Chernov and coauthored several obituaries of Terentjev (see Adler 1989 for references).

In 1941 Khosatzky became a researcher at the Department of Herpetology of the ZIN, where he had worked as a volunteer since 1931. From 1945 to 1948 Khosatzky was a doctorant in the ZIN where he worked on the thesis for his second (doctoral) degree entitled “Fauna of turtles of the USSR and its origin”. His advisors were Prof. Boris Stepanovich Vinogradov (1891–1958; see Kolchinsky 2011), a Leningrad zoologist-theriologist, and Chernov. This thesis has never been defended. In 1948, Khosatzky became a docent at the DVZ, however, until the end of his life Khosatzky maintained his office at the Department of Herpetology, informally called by colleagues the “turtle room”.

Results of the candidate thesis and later studies of Khosatzky were published in a series of papers on the biomechanics of the turtle shell and papers with descriptions and reviews of fossil turtle material from the USSR (see below). For several decades Khosatzky became a leader of turtle studies in the USSR and adjacent countries and received fossil turtle material for study from other geologists and paleontologists. In the 1950s Khosatzky began his studies on ecological physiology of turtles (see below).

In 1946, 1948 and 1949, the Mongolian Paleontological Expedition of the Academy of Sciences of the USSR led by the famous Leningrad-Moscow vertebrate paleontologist (and science fiction writer) Ivan Antonovich Efremov (1907–1972; see Kolchinsky 2011) collected new materials of fossil turtles from Mongolia. In 1950, or perhaps earlier, Khosatzky was invited to work on these materials, but he delayed this work for decades (Borkin 2004). Khosatzky's descriptions of Mongolian turtle materials were written only after the Polish-Mongolian Paleontological Expedition (1963–1971), which collected additional turtle material. One paper was written in collaboration with Polish paleoherpetologist and turtle expert Marian Młynarski (Khosatzky and Młynarski 1971). Two illustrations for this paper (ibid.: figs. 2 and 7)

were made by Khosatzky's student V.N. Malyshev. One of the illustrations, a reconstruction of a living *Mongolemys elegans*, also exists in a coloured version and was used as a prototype for a Mongolian stamp (Fig. 1). Earlier, Khosatzky published two papers on turtles with Młynarski (Khosatzky and Młynarski 1966a, b; see below). Two publications on Mongolian turtles were written with Pagam Narmandakh (Khosatzky and Narmandakh 1973, 1975), a Mongolian, who was a student at the DP and whose course projects and graduate thesis on fossil turtles of Mongolia were supervised by Khosatzky (see Table 3). Other publications by Khosatzky on Mongolian turtles (1976, 1998, 1999) were published later, two of them posthumously. In one of these papers, Khosatzky (1998) named a fossil turtle (*Mongolochelys efremovi*) in honor of Efremov. Description of another fossil turtle named after Efremov (?*Sinemys efremovi* from China) was published after Khosatzky's death (Khosatzky 1996).

In 1951 Khosatzky published a paper entitled "Paleontological and stratigraphical significance of fossil turtles", where he discussed this subject, briefly reviewed findings of fossil turtles on the territory of the USSR, and gave instructions how to collect fossil turtles and a key for determination of some turtle groups. Colleagues facetiously named this paper "How to collect turtles for Khosatzky" (Borkin 1999: 18).

In 1953 Khosatzky became an informal supervisor of Valentin Vasilievich Kuznetsov (1923–2006) from the Institute of Zoology of Kazakhstan (Alma-Ata) for his work on fossil turtles of Kazakhstan (Borkin 2004; Tleuberdina and Danilov 2007; Adler 2012). Later, Khosatzky and Kuznetsov published a series of joint papers on fossil turtles of Kazakhstan (Khosatzky and Kuznetsov 1963, 1971; Khosatzky et al. 1974).

In the mid-1950s Khosatzky was invited to write a section about turtles for the multivolume edition "Osnovy paleontologii" (Fundamentals of Paleontology). According to Borkin (2004), he failed to complete this work, which was finally finished by the then-young (born in 1933) Moscow vertebrate morphologist and paleontologist Vladimir Borisovich Sukhanov (1964). In fact, Khosatzky prepared a manuscript for "Osnovy paleontologii" dated 1956 (ZIN). This manuscript consists of 58 typewritten pages, of which 43 pages are text. There are also two handwritten pages with lists of drawings of 28 turtle taxa for this manuscript which were given (not later than

1956) to Anatoliy Konstantinovich Rozhdestvensky (1920–1983), a Moscow dinosaur paleontologist, who was one of the editors of the "Amphibians, Reptiles and Birds" volume of "Osnovy paleontologii". Some of these drawings were made by an artist S.M. Steinberg and Khosatzky (see Nessov and Khosatzky 1980). The systematic arrangement of turtles used by Khosatzky in his manuscript is given in Appendix 3. For unknown reasons, Khosatzky's manuscript was rejected and the work was entrusted to Sukhanov by Efremov in 1958 (Sukhanov pers. com. to IGD 2013). In his chapter, Sukhanov (1964) used one of the Steinberg/Khosatzky's drawings (ibid., fig. 392: shell of *Lindholmemyx elegans*; see Nessov and Khosatzky 1980). Another such drawing was published by Sukhanov much later (2000, fig. 17–31: ventral shell of *Mongolemys elegans*). Sukhanov's (1964) chapter is much larger than Khosatzky's manuscript and contains a lot of data, which was absent from Khosatzky's manuscript. Khosatzky and Sukhanov (1973) later published a short paper on morphometric parameters of the turtle shell. Starting in 1974, Sukhanov began to work on fossil turtles from Mongolia.

In the 1950s Khosatzky began to work with Abdulla Mustafaevich Alekperov (1912–1981), a zoologist from Azerbaijan who was, like Khosatzky, a student of Kashkarov and a doctorant of Chernov in the ZIN (Adler 2007; N.L. Orlov, pers. com. to IGD 2013). Together they published a series of publications on Caucasian turtles (Khosatzky and Alekperov 1958; Alekperov and Khosatzky 1972). Later, Alekperov (1978) published a monograph on amphibians and reptiles of Azerbaijan, where he described and figured some of the fossil turtles material studied by Khosatzky.

In the 1950s and 1960s new fossil turtle material was collected from the Late Cretaceous localities of Kazakhstan and Tajikistan by expeditions of the PIN led by Rozhdestvensky. Preliminary determinations of these materials were presented in two reviews of terrestrial vertebrates (including turtles) of the Late Mesozoic of the USSR (Rozhdestvensky and Khosatzky 1965, 1967). The results of study of this turtle material were partially reflected in unpublished works of Khosatzky's students V.P. Telepneva and S.V. Levinson (see Table 3; Danilov et al. 2007) and published later (Nessov and Khosatzky 1977a; Khosatzky and Nessov 1978, 1979a; Nessov and Khosatzky 1980). Khosatzky and Nessov named one turtle genus (*Anatolemys*) in honor of Anatoliy



Fig. 1. A reconstruction of a living *Mongolemys elegans* Khosatzky et Mlynarski, 1971 from the Late Cretaceous of Mongolia. Painting by V.N. Malyshev. In the right corner, a Mongolian stamp with *M. elegans*.

K. Rozhdestvensky (Nessov 1977a).

In the mid-1960s Khosatzky (1966a) published his first report on fossil turtles of Moldavia. Even earlier, a publication of his student Telepneva (1964) had appeared, but that publication was actually written by Khosatzky (see Appendix 2). Specimens of fossil turtles of Moldavia were collected by Khosatzky himself and by his students over the course of several seasons in 1960s and in later years. At this time Khosatzky supervised the candidate thesis of Vasiliy Efimovich Tofan “Fauna of amphibians and reptiles of Moldavia”, which contained data about fossil and modern turtles (see Table 3). These and other data on turtles from Moldavia were published in collaboration with Tofan (Khosatzky and Tofan 1970a, 1970b) and B.A. Tarabukin (Khosatzky and Tarabukin 1970). In the mid-1980s, Khosatzky supervised the candidate work of Oleg Igorevich Redkozubov from the Institute of Zoology and Physiology of the Academy of Sciences of the Moldavian SSR (Kishinev) entitled “Neogene reptiles of Moldavia”; Table 3). Together, they published two papers and a monograph on the Neogene turtles of Moldavia (Khosatzky and Redkozubov 1986a, b; 1989). In addition, several unpublished works of Khosatzky’s students were devoted to the study of fossil turtle materials from Moldavia (see Table 3).

At the end of 1960s new materials of fossil turtles were collected from the Jurassic and Early Cretaceous of Kirghizia by Leningrad geologists (expeditions led by N.N. Verzhilin). Preliminary study of these materials resulted in two publications on biostratigraphic dating of deposits of the Fergana deposits (Verzhilin et al. 1970a, b). Those materials were studied in detail by the Khosatzky’s student Lev Aleksandrovich Nessov (1947–1995; see Averianov 1996), later a famous Leningrad paleontologist and turtle expert. Nessov defended his candidate thesis on Mesozoic turtles of the USSR (see Table 3) and published numerous publications on the subject in collaboration with Khosatzky (Nessov and Khosatzky 1973, 1975a, b, 1977a, b; Khosatzky and Nessov 1978; Nessov and Khosatzky 1978; Khosatzky and Nessov 1979a; Nessov and Khosatzky 1980, 1981a, b; Glickman et al. 1987; Nessov and Khosatzky 1999). They also published two papers with Verzhilin and others on the distribution of rare elements in osteological remains of Mesozoic and Cenozoic turtles (Verzhilin et al. 1975, 1976). In addition, Khosatzky and Nessov (1979b, 1981) published two papers on the distribution, ecol-

ogy and conservation of modern soft-shelled turtles in the Far East of the USSR.

According to Borkin (2004), for his entire life Khosatzky collected materials for a big faunal monograph on the fossil and modern turtles of the USSR, which was planned for publication in a famous ZIN serial publication “Fauna SSSR” [The Fauna of USSR]. Unfortunately, this monumental work was never completed. Similarly, Khosatzky never completed another monograph on the morphology, physiology and natural history of the Far Eastern turtle (current name *Pelodiscus maackii* Brandt, 1857), which he planned publish with V.T. Tagirova (Khabarovsk).

During his long scientific life Khosatzky published many publications on turtles and made important contribution to different aspects of turtle biology. He greatly improved the work started by his predecessors. For a long time Khosatzky was the leading expert on turtles of the USSR and adjacent countries and taught numerous students. By the end of Khosatzky’ life there were nine turtle experts (besides Khosatzky) in the USSR and adjacent countries (G.O. Cherepanov, V.M. Chkhikvadze, E.G. Kordikova, M.N. Kaznyshkin, V.V. Kuznetsov, P. Narmandakh, L.A. Nessov, O.I. Redkozubov, V.B. Sukhanov), four of which (Kuznetsov, Narmandakh, Nessov, and Redkozubov) were former students of Khosatzky, and two others (G.O. Cherepanov and M.N. Kaznyshkin) were students of Khosatzky’s student Nessov.

KHOSATZKY’S TURTLE STUDIES

Origin of turtles

Only a few publications of Khosatzky reflect his ideas about the origin and systematic position of turtles. Khosatzky (1977) thought of turtles as a subclass (Testudinata = Chelonia) of the class Anapsida within superclass Sauropsida. He hypothesized that turtles could be derivatives of Procolophonina (another subclass of Anapsida). He also considered the hypothesis that they could have evolved from Captorhinia (members of the superclass Theropsida). The hypothesis of a close relationship between turtles and procolophonids was first proposed by Romer (1968), whereas the relationships of turtles with Captorhinae were suggested by Gaffney and McKenna (1979). See Carroll (2012) for the latest review of the debate about origin of turtles.

Khosatzky (1979b) argued against a close relationship between turtles and *Eunotosaurus* Seeley, 1892, a problematic reptile from the Middle–Late Permian of South Africa. *Eunotosaurus* was long considered a transitional link between cotylosaurs and turtles (Watson 1914) and was even placed within Testudinata by some authors (Romer 1956; Sukhanov 1964). Khosatzky (1979b) assigned *Eunotosaurus* to cotylosaurs and, probably, to captorhinomorphs following the opinion of Cox (1969). Recently the idea of *Eunotosaurus*-turtle relationships was resurrected and *Eunotosaurus* was placed within parareptiles (see Lyson et al. 2010, 2013).

Khosatzky (1965c) supported the hypothesis of a terrestrial origin of turtles, because he thought that the shell evolved as a protective construction. The terrestrial hypothesis was recently supported by analysis of limb morphology and histology of basal turtles (Joyce and Gauthier 2004; Scheyer and Sander 2007). The opposing hypothesis of an aquatic origin of turtles is partially supported by data on *Odontochelys semitestacea* Li et al., 2008, one of the oldest turtles from the Late Triassic of China (Li et al. 2008).

Systematics, phylogeny and biogeography of turtles

The only version of the “complete” systematic arrangement of turtles accepted by Khosatzky was presented in his unpublished manuscript prepared for “Osnovy paleontologii” (see Appendix 3). In this manuscript turtles were thought to rank as a subclass called Chelonia (Testudinata) with a single order Chelonia (Testudinata), which was divided into four suborders: Amphichelydia, Pleurodira, Cryptodira and Trionychoidea. Later, Khosatzky used different numbers of orders: Amphichelydia, Chelonioidea, Dermochelyoidea, Trionychoidea, Cryptodira and Pleurodira (Verzilin et al. 1970b; Khosatzky 1975) or Atheca and Thecophora (Khosatzky 1977). Nessov and Khosatzky (1981b) also mentioned the superfamily Testudinoidea. Atheca corresponds to Dermochelyoidea and Thecophora to all other turtles. The division of turtles into Atheca and Thecophora was proposed by Cope (1868) and had been rejected by the end of the 1970s by most specialists (see Romer 1956; Sukhanov 1964; Mlynarski 1976). Amphichelydia were revised by Gaffney (1975) and generally correspond to basal turtles in the modern system (Joyce 2007). Cryptodira and Pleurodira are

recognized as subdivisions (of various ranks) of turtles (Testudines). Chelonioidea and Trionychoidea, as superfamilies of Cryptodira, Dermochelyoidea (as Dermochelyidae) are placed within Chelonioidea (see Danilov 2005). Below we give an account of the turtle groups studied by Khosatzky.

Amphichelydia as conceptualized by Khosatzky included Amphichelydia gen. et sp. indet. and the families Pleurosternidae, Baënidae, Plesiochelyidae and Thalassemydidae. Remains of Amphichelydia gen. et sp. indet. from the Late Cretaceous of Mongolia were reported by Khosatzky and Mlynarski (1971). The same remains were earlier mentioned by Efremov (1954) as Pleurosternidae, probably, based on identifications by Khosatzky. Later these remains were attributed to *Mongolochelys efremovi* Khosatzky, 1998, which was established within the unranked group Kayentachelydia (Khosatzky 1998). Recent phylogenetic studies have shown that *M. efremovi* belongs to the clade Meiolaniformes (Sterli and Fuente 2013).

Baënidae from the Cretaceous and Paleogene of Kazakhstan and Middle Asia were mentioned by Khosatzky (1958c). He, probably, meant specimens of Baenidae? gen. et sp. indet. reported by Riabinin (1938) from the Late Cretaceous of Kazakhstan (Kyrkuduk I = Sary Agach; see Nessov 1997). Nessov (1997) identified this material as *Lindholmemyx* sp. (Lindholmemydidae; see Vitek and Danilov 2012). Multiple turtles from the Late Cretaceous of Mongolia were mentioned as *Baena* by Rozhdestvensky (1957). This determination was based on “*Baena mongolica* Khos.”, a tentative name of the turtle species later described as *Mongolemys elegans* Khosatzky et Mlynarski, 1971 in the family Dermatemydidae (Danilov unpublished data; see below). The idea that Baenidae were present in the Mesozoic and Paleogene of Asia was also shared by other authors (e.g. Young and Chow 1953) and influenced the establishment of the family Macrobaenidae Sukhanov, 1964 which is “close to some Toxochelyinae, and with a skull typical for Baenidae” (Sukhanov 1964: 391). Later, Baenidae was shown to be a branch of fossil turtles restricted to North American (Gaffney 1972).

Pleurosternidae. Material of Pleurosternidae (*Glyptops* sp.) was reported from the Callovian (Middle Jurassic) of Kirghizia (Verzilin et al. 1970b; Khosatzky 1972). Later this material was assigned to the family Xinjiangchelyidae (Kaznyshkin et al. 1990).

Plesiochelyidae and Xinjiangchelyidae. Material of Plesiochelyidae was mentioned in seven publications of Khosatzky (Verzilin et al. 1970a, b; Nessov and Khosatzky 1977, 1978, 1981a, b; Glickman et al. 1987). This material includes *Plesiochelys* from the Late (now Middle) Jurassic of Kirghizia, Plesiochelyidae from the Aptian of Karakalpakia, *Tienfucheloides* (Plesiochelyidae) from the Cenomanian and Turonian of Karakalpakia (Nessov and Khosatzky 1977), and ?Plesiochelyidae gen. et sp. indet. from the Early Cretaceous of Transbaikalia (Nessov and Khosatzky 1981a). Plesiochelyidae were considered to be the ancestors of the Toxochelyidae as well as other Chelonioidea and Thalassemydidae (Nessov and Khosatzky 1978). Later, most of Asiatic *Plesiochelys* were assigned to the family Xinjiangchelyidae (see Tong et al. 2012a, b). The material of *Xinjiangchelys* cf. *latimarginalis* (Young et Chow, 1953) described from the Middle Jurassic of Sarakamyshsai locality of Kirghizia (Nessov and Khosatzky 1999) probably belong *Xinjiangchelys tianshanensis* Nessov, 1995, a species described from the same locality (Nessov 1995). The genus *Tienfucheloides* Nessov 1978 was considered either Testudinata incertae sedis or closely related to Sinemydidae (Nessov 1978, 1987; Brinkman and Peng 1993).

Thalassemydidae. The only member of Thalassemydidae mentioned by Khosatzky was *Yaxartemys* Riabinin, 1948 from the Late Jurassic of Kazakhstan (see Nessov and Khosatzky 1977a). *Yaxartemys longicauda* Riabinin, 1948 was also mentioned in Khosatzky's reviews of fossil turtles of the USSR, usually without familial attribution (Khosatzky 1945a [as *Iaxartemys longicauda*], 1949a, 1951, 1958c, 1972). The attribution of this species to Thalassemydidae was proposed for this genus by Riabinin (1948) and followed by many authors (see Sukhanov 1964; Młynarski 1976). Later it was considered to be a member of Sinemydidae, Plesiochelyidae or Xinjiangchelyidae (see Chkhikvadze 1987; Nessov 1995; Karl et al. 2012).

Pleurodira. In Khosatzky's earlier systematic arrangement of turtles (see Appendix 3), Pleurodira united the families Plesiochelyidae, Thalassemydidae, Meiolaniidae (as Miolaniidae), Pelomedusidae, Bothremydidae, and Chelidae (as Chelyidae). Khosatzky (1949c) mentioned *Lindholmemys elegans* Riabinin, 1935 from the Late Cretaceous of Kyzylkum as a member of Pleurodira and Pelomedusidae. Riabinin (1935), who described this taxon, placed

it close to Dermatemydidae or Emydidae within Cryptodira. Later, Khosatzky placed *Lindholmemys* within Dermatemydidae (see below) and considered Plesiochelyidae and Thalassemydidae within Amphichelydia (Verzilin et al. 1970b; Khosatzky 1972). Pelomedusidae, Chelidae and Meiolaniidae were discussed in two of Khosatzky's publications that were devoted to the paleobiogeography of turtles (Nessov and Khosatzky 1975a, 1981b).

Cryptodira. In Khosatzky's earlier systematic arrangement of turtles (see Appendix 3), Cryptodira united all turtle groups other than Amphichelydia and Pleurodira. Later, Cryptodira were considered in a stricter sense, i.e., not including Chelonioidea, Dermochelyoidea and Trionchoidea (Khosatzky 1975).

Chelonioidea was divided by Khosatzky into Toxochelyidae, Protostegidae and Cheloniidae (Nessov and Khosatzky 1981b) similar to the systematic arrangement of some other authors (see Sukhanov 1964). The following records of Chelonioidea were mentioned or described by Khosatzky: a small sea turtle from the Kiev marl and a sea turtle from the Eocene of the Crimea (Khosatzky 1951); remains of sea turtles from the Eocene of Ukraine, Oligocene-Miocene of Azerbaijan, Paleogene of Povolzhye and Chelonioidea from the middle Eocene of Kokturnak, Kazakhstan (Khosatzky 1975); *Oxemys* Nessov, 1977 from the Cenomanian of Karakalpakia and Chelonioidea from the Late Cretaceous of Saratov (Nessov and Khosatzky 1977); ?Chelonioidea fam., gen. et sp. indet. from the Early Cretaceous of Transbaikalia (Nessov and Khosatzky 1981a); a large-sized Desmatochelyidae from the Late Cretaceous of Kazakhstan (Glickman et al. 1987). All of those records were reviewed by Averianov (2002), who considered them Chelonioidea indet. Danilov (2004) assumed that *Oxemys* belonged to Xinjiangchelyidae, Macrobaeniidae or Lindholmemydidae.

Toxochelyidae described by Khosatzky include the subfamily Kirgizemyinae Nessov et Khosatzky, 1973, the genus *Kirgizemys* Nessov et Khosatzky, 1973 including *K. exaratus* Nessov et Khosatzky, 1973 from the Early Cretaceous of Kirghizia and *K. dmitrievi* Nessov et Khosatzky, 1981 from the Early Cretaceous of Transbaikalia, and the genus *Anatol-emys* Khosatzky et Nessov in Nessov, 1977 including the species *A. maximus* Khosatzky et Nessov in Nessov, 1977 from the Late Cretaceous of Tajikistan and *A. oxensis* Nessov et Khosatzky in Nessov, 1977 from the Late Cretaceous of Uzbekistan; material of *Ana-*

tolemys sp. was described from the Late Cretaceous of Kazakhstan (Nessov and Khosatzky 1973; Nessov 1977a; Nessov and Khosatzky 1978; Khosatzky and Nessov 1979). Three species of *Osteopygis* described by Bohlin (1953) from the Cretaceous of China were assigned to *Kirgizemys* (Nessov and Khosatzky 1978). Soon after being established, the name *Kirgizemyinae* Nessov et Khosatzky, 1973 was placed into synonymy with *Macrobaeninae* Sukhanov, 1964 (Nessov and Khosatzky 1978). In addition to the taxa mentioned above, *Macrobaeninae* included genera *Hangaemys* Sukhanov et Narmandakh, 1974, *Macrobaena* Tatarinov, 1959, and *Toxocheloides* Nessov et Khosatzky, 1981 (Nessov and Khosatzky 1978; Nessov and Khosatzky 1981b). *Toxocheloides* was based on *Plesiochelys kwanganensis* Yeh, 1973 from the Late Jurassic of China (Nessov and Khosatzky 1981b). Finally, Verzilin et al. (1976) mentioned *Asiachelys* (nomen nudum; a tentative name for *Anatolemys*) of *Toxochelyidae* from the Late Cretaceous of Tajikistan. In the modern system, the “*Macrobaeninae*” correspond to the basal eucryptodiran assemblage of taxa including “*Macrobaenidae*” and “*Sinemydidae*” (see Joyce 2007). The genera *Kirgizemys* and *Hangaemys* were synonymized by Danilov et al. (2006). *Plesiochelys kwanganensis* (type of the genus *Toxocheloides*) is considered to be nomen dubium by Tong et al. (2012b). The name “*Asiachelys*” was later used for *Asiachelys perforata* Sukhanov et Narmandakh, 2006, a macrobaenid turtle from the Late Cretaceous of Mongolia (Sukhanov 2000; Sukhanov and Narmandakh 2006).

Protostegidae, as “*Chelospharginae* (*Teguliscapha*)”, were reported by Glickman et al. (1987: 258). The genus and species *Teguliscapha rossica* Nessov in Nessov et al., 1988 was described from the late Albian–early Cenomanian of European Russia (Nessov et al. 1988).

Cheloniidae described by Khosatzky include a single species *Chelonia aralis* Khosatzky 1945 from the Oligocene of Kazakhstan (Khosatzky 1945a). In addition, several other forms were mentioned in a review of Paleogene turtles of the USSR (Khosatzky 1975). Finally, a costal or plastral fragment of ?*Cheloniidae* from the middle Miocene of Stavropol Region (Belomechetskaya) studied by Khosatzky was described and figured by Alekperov (1978). In the latest review of sea turtles of the USSR (Averianov 2002) material of *Chelonia aralis* was re-identified as *Cheloniidae* indet. (i.e. *Chelonia aralis* was con-

sidered a nomen dubium), whereas material from Belomechetskaya was referred to *Chelonioides* indet.

Trionychoidea of Khosatzky (unpublished manuscript prepared for “*Osnovy paleontologii*”) included the families *Carettochelyidae* and *Trionychidae*, similar to the systematic arrangement of Sukhanov (1964). *Trionychoidea* from the middle Miocene of Stavropol Region (Belomechetskaya) studied by Khosatzky were described and illustrated by Alekperov (1978). Later, these remains were assigned to *Trionyx danovi* Chkhikvadze, 1988 (Chkhikvadze 1988).

Carettochelyidae were mentioned in five of Khosatzky’s publications (Nessov and Khosatzky 1975a, 1975b, 1977a, 1981b, Glickman et al. 1987), based on the results of Nessov’s original (1976, 1977b) studies on this group.

Trionychidae. Numerous publications of Khosatzky contain information about the systematics and distribution of fossil and modern trionychids. Seven publications of Khosatzky were completely devoted to fossil trionychids (Khosatzky 1945b, 1957, 1966, 1976; Khosatzky et al. 1983; Khosatzky 1986, 1999). These are a description of remains of *Trionyx* sp. from the Pliocene of Ukraine (Kuchurgan; Khosatzky 1945b), a review of fossil trionychids of Kazakhstan (Khosatzky 1957); a description of a new species *Trionyx zakhidovi* Khosatzky, 1966 from the Late Cretaceous of southern Kazakhstan (Khosatzky 1966); a description of a new species *Amyda orlovi* Khosatzky, 1976 from the Late Cretaceous of Mongolia (Khosatzky 1976); a description of a new subspecies *Trionyx (Amyda) capellini bulgaricus* Khosatzky in Khosatzky et al., 1983 from the late Eocene of Bulgaria (Khosatzky et al. 1983), a description of a new species *T. moldaviensis* Khosatzky, 1986 from the late Miocene (middle Sarmatian) of Moldavia (Khosatzky 1986), and a review of Cretaceous trionychids of Mongolia (Khosatzky 1999).

The material of *Trionyx* sp. from Kuchurgan was assigned to *Chelydridae* by Khosatzky (1982) and to *Chelydropsis nopcsai* Szalai, 1934 (*Chelydridae*) by Chkhikvadze (1982, 1983). Neither Khosatzky (1945), nor Chkhikvadze (1982, 1983) figured this material.

A later review of material of *Trionyx zakhidovi* showed that it should be considered a nomen dubium, whereas the second specimen of *T. zakhidovi* (the posterior part of a carapace) has been referred to “*T. kansaiensis* Vitek et Danilov, 2010 (see Vitek and Danilov 2012).

Khosatzky's (1976) description of *Amyda orlovi* lacked illustrations; those were not published until much later (Sukhanov 2000: fig. 17.27). According to Danilov et al (in press), this species belongs to a new genus of trionychids. See the latter paper for the latest revision of the materials of Cretaceous trionychids of Mongolia reported by Khosatzky (1999).

Trionyx moldaviensis was first mentioned as *Trionyx* sp. by Khosatzky and Tofan (1970a). Chkhikvadze (1983) considered this trionychid to be identical to *T. brunhuberi* Ammon, 1911 from the Sarmatian of Germany. That idea was rejected by Khosatzky (1986; Khosatzky and Redkozubov 1989). Chkhikvadze (1989) argued that all differences between *T. moldaviensis* and *T. brunhuberi* were due to ontogenetic and individual variation. In our opinion, this species should be referred to as "*Trionyx*" *moldaviensis*, because it is not synonymous with *T. brunhuberi* but its generic attribution is unclear.

In addition to the publications mentioned above, trionychids were discussed in other papers of Khosatzky (1948d; 1957c; Borisov et al. 1963; Khosatzky 1965a; 1967a; Khosatzky and Tofan 1970a; Verzilin et al. 1970a; Khosatzky and Młynarski 1971; Khosatzky 1975; Nessov and Khosatzky 1975a, b, 1977a; Khosatzky and Nessov 1979a; Nessov and Khosatzky 1981b; Glickman et al. 1987; Khosatzky and Redkozubov 1989). These are descriptions of shell fragments of *Trionyx* sp. from the Sarmatian of Sevastopol (Khosatzky 1948d); a report on *Amyda* and *Aspideretes* from the Late Cretaceous of Fergana (Khosatzky 1957c); a review of fossil trionychids of the USSR (Khosatzky 1958c); data on trionychids from the Paleogene and Neogene of the Zaysan Depression of Kazakhstan (Borisov et al. 1963); reviews of trionychids from the Cenozoic of the Asiatic part of the USSR (Khosatzky 1965a, 1967a) and from the Neogene of Moldavia (Khosatzky and Tofan 1970a); data on trionychids from the Early Cretaceous of Fergana (Verzilin et al. 1970a); descriptions of trionychids from the Late Cretaceous of Mongolia (Khosatzky and Młynarski 1971); a review of trionychids from the Paleogene of the USSR (Khosatzky 1975); discussions of the paleobiogeography of trionychids (Nessov and Khosatzky 1975a, b, 1981b); a review of fossil trionychids from the Mesozoic of the USSR (Nessov and Khosatzky 1977a); a report on trionychids from the Late Cretaceous of Tajikistan (Kansai; Khosatzky and Nessov 1979a); reviews of trionychids from the Cretaceous of the USSR (Glickman et al.

1987) and from the Neogene of Moldavia (Khosatzky and Redkozubov 1989).

For the most recent reviews of all of those records of trionychids see the publications of Chkhikvadze (1989, 1990), Kordikova (1994), Nessov (1997), Danilov and Vitek (2012) and Danilov et al. (in press).

Three publications of Khosatzky (Turdakov et al. 1967; Khosatzky and Nessov 1979b, 1981) were devoted to the extant trionychid of the USSR, *Trionyx sinensis* Wiegmann, 1834 (current name *Pelodiscus maackii* Brandt, 1857; see Fritz and Havas 2007). Turdakov et al. (1967) reported new records of this species in Kirghizia, which was considered a result of introduction. Khosatzky and Nessov (1979b, 1981) discussed the distribution, ecology and conservation of this species in the Far East.

Finally, several works of Khosatzky's students contain data on fossil Trionychidae (Table 3).

Testudinoidea was discussed by Nessov and Khosatzky (1981b) as a group with the family Dermatemydidae at its base. This view corresponds to the Testudinoidea sensu lato of Williams (1950) and other authors (see Sukhanov 1964). Cryptodira sensu Khosatzky (1975) partially corresponds to this group and is very different from those in his earlier system (see Appendix 3). The following groups of Testudinoidea were studied by Khosatzky: Chelydriidae, Dermatemydidae, Emydidae and Testudinidae. Later, part of Dermatemydidae was recognized as Adocidae (Nessov and Khosatzky 1977a).

Chelydriidae. Seven publications of Khosatzky (1944, 1949b, 1966a, 1967, 1982; Khosatzky and Redkozubov 1986a, 1989) contain information about fossil Chelydriidae. The material of this group was primarily described erroneously as "giant *Testudo*" from the Pliocene of Kazakhstan (Betekey River; Khosatzky 1944) and Ukraine (Kuchurgan; Khosatzky 1949b) and as *Trionyx* sp. from the Pliocene of Ukraine (Kuchurgan; Khosatzky 1945b). Later, Khosatzky (1966a, 1967a, 1982) referred to these materials as *Chelydra* or Chelydriidae. *Chelydra* was also reported from the Pliocene of Moldavia (Khosatzky 1966a; Khosatzky and Tofan 1970a, b). Chkhikvadze and Gaiduchenko (1985) assumed that the material from the Pliocene of Kazakhstan belonged to *Chelydropsis kuznetsovi* Chkhikvadze in Gaiduchenko et Chkhikvadze, 1985. Material from the Pliocene of Ukraine was assigned to *Chelydropsis* (orig. *Trionyx*) *nopcsai* (Szalai, 1934) (see Chkh-

ikvadze 1983). Khosatzky and Redkozubov (1986a, 1989) described turtle dentaries from the Pliocene of Moldavia, which were attributed to the chelydrid *Macrocephalochelys pontica* Pidoplichko et Tarashchuk, 1960 (known from two partial skulls from the Late Miocene [Pontian] of Ukraine; Pidoplichko and Tarashchuk 1960; Tarashchuk 1971). Shell and other postcranial material from the middle Sarmatian of Moldavia (Buzhory) was assigned to *Chelydropsis* cf. *murchisoni* Mlynarski, 1980, whereas shell material from the middle Pliocene of Moldavia (several localities) was attributed to *Ch. nopcsai* (Khosatzky and Redkozubov 1989). Thus, Khosatzky and Redkozubov (1986a, 1989) recognized two forms of chelydrids in the Pliocene of Moldavia (and Europe). This idea was criticized by Chkhikvadze (1989), who considered that interpretation of the dentary material to be erroneous and placed *M. pontica* in junior synonymy with *Ch. nopcsai*.

Dermatemydidae. In his earlier publications, Khosatzky accepted a broad conception of the Dermatemydidae (e.g. Khosatzky 1957c; 1958c; Borisov et al. 1963; Rozhdstvensky and Khosatzky 1965; Verzhilin et al. 1970a; Khosatzky and Mlynarski 1971; Verzhilin et al. 1976; Nessov and Khosatzky 1981b), which was used as a wastebasket taxon for many primitive cryptodires (see Sukhanov 1964). Khosatzky (1957c) mentioned representatives of the genera *Adocus* Cope, 1869, *Basilemys* Hay, 1902 and *Compsemys* Leidy, 1856 as Dermatemydidae from the Late Cretaceous of Fergana. Later, none of these determinations were supported (Nessov 1997: 118). Verzhilin et al. (1970a) mentioned a member of Dermatemydidae similar to *Adocus* and a turtle similar to “*Sinemys* (?Dermatemydidae)” from the Early Cretaceous (Albian) of Kirgizia. Later, these turtles were described as *Ferganemys verzhilini* Nessov et Khosatzky, 1977 (Adocidae; see below) and *Kirgizemys exaratus* (Toxochelyidae; see above), respectively. Khosatzky and Mlynarski (1971) attributed to the Dermatemydidae such genera as *Adocus*, *Anosteira* Leidy, 1871, *Mongolemys* Khosatzky et Mlynarski 1971, *Tretosternon* Owen, 1842 and *Tsaotanemys* Bohlin, 1953. *Anosteira* had already been moved from Dermatemydidae to Carettochelyidae by Williams (1950). By the end of the 1970s many representatives of Dermatemydidae sensu lato had been assigned to the families Adocidae, Dermatemydidae (sensu stricto), Lindholmemydidae, Nanhsiungchelyidae, Sinemydidae and Sinochelyidae (see Yeh 1963;

Chkhikvadze 1973; Nessov 1977c; Shuvalov and Chkhikvadze 1975). Verzhilin et al. (1976) mentioned “Dermatemydidae (*Anatolemys*)” from the Late Cretaceous of Fergana (see Adocidae). Nessov (1977c, 1986) divided Dermatemydidae into the subfamilies Dermatemydinae (sensu stricto) and Lindholmemydinae. Khosatzky accepted the recognition of Adocidae as a group separate from Dermatemydidae (Nessov and Khosatzky 1977a, b; Khosatzky and Nessov 1978; see below). Probably, Khosatzky also shared Nessov’s point of view about Lindholmemydinae, because in Nessov and Khosatzky (1981b) *Lindholmemydinae* Riabinin, 1935 (type genus of Lindholmemydidae) is considered to represent a special Late Cretaceous branch of Dermatemydidae. The material of the following taxa of Lindholmemydinae were described by Khosatzky: the new genus and species *Mongolemys elegans* Khosatzky et Mlynarski 1971 and *Tsaotanemys* cf. *rugosa* Bohlin, 1953 from the Late Cretaceous of Mongolia (Khosatzky and Mlynarski 1971), *Lindholmemydinae elegans* Riabinin, 1935 and *Lindholmemydinae* sp. from the Late Cretaceous of Uzbekistan, and *L. gravis* Nessov et Khosatzky, 1980 from the Late Cretaceous of Kazakhstan and Tajikistan (Nessov and Khosatzky 1980). Currently, all these taxa are considered to be members of the family Lindholmemydidae or basal Testudinoidea (see Danilov and Sukhanov 2013).

Adocidae. Members of Adocidae were long placed in Dermatemydidae sensu lato (Khosatzky 1957c; Verzhilin et al. 1970a, 1976; see above). The following were described as new taxa of Adocidae by Khosatzky: the subfamily Shachemydinae Khosatzky in Nessov et Khosatzky, 1977 (Nessov and Khosatzky 1977a), the genus and species *Ferganemys verzhilini* Nessov et Khosatzky, 1977 from the Early Cretaceous of Kirghizia (Nessov and Khosatzky 1977b) and the species *Adocus foveatus* Nessov et Khosatzky in Khosatzky et Nessov, 1978 from the Late Cretaceous of Tajikistan (Khosatzky and Nessov 1978). It is known that Khosatzky prepared a manuscript (dated 1976) with description of one more genus and species of this group based on abundant material from the Late Cretaceous of Kansai (Tajikistan) and Shakh Shakh (Kazakhstan) (see Danilov et al. 2007). This turtle was tentatively named “*Anatolemys*” (Verzhilin et al. 1976). However, Kuznetsov (1976), who knew about Khosatzky’s work, described this new turtle as *Shachemys baibolatika* Kuznetsov, 1976 based on much less abundant and fragmentary

material from Shakh Shakh. The next year *Shachemys* was used as the type genus for the subfamily Shachemydinae (Nessov and Khosatzky 1977a) and the name *Anatolemys* was applied to another turtle (see Toxochelyidae). Nessov (1977) placed Adocidae in the superfamily Testudinoidea. This opinion was probably shared by Khosatzky, who supervised Nessov's candidate thesis. Later, phylogenetic studies placed Adocidae either within Trionychoidea (see Meylan and Gaffney 1989) or in its own superfamily Adocoidea Cope, 1870 (Danilov and Syromyatnikova 2009a). Nessov and Khosatzky (1981b) placed *Plesiochelys tatsuensis* Yeh, 1963 from the Late (or Middle) Jurassic of China in the genus *Ferganemys*. Later, this species was put in its own genus *Yehguia* Danilov et Parham, 2006 considered to be closely related to or within the Adocidae (Danilov and Parham 2006; Danilov and Syromyatnikova 2009a, b), but recently synonymized with *Sinaspideretes wimani* Young et Chow, 1953 from the Late Jurassic of China and placed among basal Trionychoidea, outside the Adocidae (Tong et al. 2013).

Emydidae of Khosatzky's systematic arrangement of turtles (see Appendix 3) correspond to Emydidae of Mertens and Wermuth (1955; hereinafter Emydidae sensu lato), which correspond to Emydidae + Geoemydidae in the modern system (see Danilov 2005).

Khosatzky's first emydid paper (1945d) was devoted to *Pseudocadia* (orig. *Testudo*) *anyangensis* (Ping, 1930) from the Annyang Hsien archaeological ruins (about 3500 years BP), Henan Province, China. Currently, *P. anyangensis* is considered to be a junior synonym of the extant species *Mauremys* (or *Ocadia*) *sinensis* (Gray, 1834) of the family Geoemydidae (Fritz and Havas 2007).

Four of Khosatzky's publications were completely devoted to representatives of the genus *Emys* Duméril, 1806. These are descriptions of remains of *Emys orbicularis* (Linnaeus, 1758) from the Paleolithic Shan Koba Cave, Crimea (Khosatzky 1946a); a description of a new subspecies *Emys orbicularis antiqua* Khosatzky, 1956 from the Pliocene of Stavropol, European Russia (Khosatzky 1956); and data from a comparative morphological study of several modern populations of *Emys orbicularis* (Khosatzky 1987; Khosatzky and Ivanov 1990). Later, *E. orbicularis antiqua* was considered a distinct species of the genera *Emydoidea* Gray, 1870 (Chkhikvadze 1983) or *Emys* (Chkhikvadze 1989, 2007, 2010). The specific status of this taxon (within *Emys*) was accepted by

Khosatzky and Redkozubov (1989). However, Fritz (1995) returned it back to its status as a subspecies of *Emys orbicularis* (Emydidae).

One paper by Khosatzky (1946b) was devoted to the description of new species *Clemmys pidopličkai* Khosatzky, 1946 and *Cl. riabinini* Khosatzky, 1946 from the Pliocene of Ukraine (Kuchurgan). In subsequent studies *Clemmys pidopličkai* was placed within the genera *Geoemyda* Gray, 1834 or *Melanochelys* Gray, 1869, whereas *Cl. riabinini* was placed in the genus *Sakya* Bogachev, 1960 (Khosatzky and Mlynarski 1966b; Chkhikvadze, 1983). All three genera belong to the family Geoemydidae in the modern system. The name *pidopličkai* was changed to *pidopličkoi* by Telepneva (1964) and to *pidoplichkoi* by Chkhikvadze (2007).

Three papers of Khosatzky (1947b; Borisov et al. 1963; Khosatzky and Kuznetsov 1971) described or reported fossils of Emydidae sensu lato from Kazakhstan. These include descriptions of *Clemmys kazachstanica* Khosatzky 1947 from the late Oligocene or early Miocene of Kazakhstan (Khosatzky 1947b); a report on various taxa (*Echmatemys* Hay, 1906, Emydidae, and *Trachemys* Agassiz, 1857) from the Paleogene and Neogene of the Zaysan Depression of Kazakhstan (Borisov et al 1963); and a description of *Cl. iliensis* Khosatzky et Kuznetsov, 1971 from the early Miocene of Kazakhstan (Khosatzky and Kuznetsov 1971). Material of *Cl. kazachstanica* was not figured until a later publication of Kuznetsov (1978), who also illustrated additional material of this species. *Clemmys kazachstanica* was assigned first to *Melanochelys* (Chkhikvadze 1973), but later (Chkhikvadze, 1990) to *Ocadia* Gray, 1870 (Geoemydidae). Finally, Chkhikvadze (2001, 2007) assigned the holotype of *Cl. kazachstanica* to the genus *Baicalemys* (Emydidae, see below), whereas other specimens were assigned to *Ocadia* cf. *turgaica* Kuznetsov et Chkhikvadze, 1977 and to the family Chelydridae. The Emydidae from the Zaysan Depression of Kazakhstan were assigned to various genera by Chkhikvadze (Chkhikvadze 1973, 1989, 1990). *Clemmys iliensis* was mentioned as *Mauremys iliensis* by Chkhikvadze (1973), but later considered as *Ocadia iliensis* (Chkhikvadze 1989), and finally was synonymized with *Ocadia perplexa* Gilmore, 1931 from the Miocene of China (Chkhikvadze 2007, 2010).

One paper (Khosatzky 1948d) described remains of *Clemmys* sp. from the Sarmatian deposits of Sevastopol (Crimea). Later, those specimens were referred

to as Emydidae indet. (Chkhikvadze 1983) or Geoemydidae indet. (Danilov et al. 2012).

One of Khosatzky's papers (Khosatzky and Mlynarski 1966b) was devoted to a revision of the fossil turtles of the genus *Geoemyda* sensu lato of Europe, including the description of two subgenera of the genus *Geoemyda*–*Geiselemys* Khosatzky et Mlynarski, 1966 (type species – *Geoemyda ptychogastroides* Hummel, 1935 from the middle Eocene of Germany) and *Spinemys* Khosatzky et Mlynarski, 1966 (type species – *Clemmys pidoplichkai*). *Geiselemys* is considered valid genus of Geoemydidae (see Danilov 2005). *Geoemyda* (*Spinemys*) was placed into synonymy with the genus *Sakya* (Chkhikvadze 1973). However, as was discussed by Borkin (1999), this synonymization is incorrect because the type species of *Spinemys* is *Clemmys pidoplichkai*, i.e. member of *Melanochelys* sensu Chkhikvadze, 1973 (Geoemydidae).

Material of fossil *Clemmys* sp. and *Emys orbicularis* from the Neogene and Quarternary of the Caucasus studied by Khosatzky was reviewed by Alekperov (1978). Later, specimens of *Clemmys* sp. were assigned to *Mauremys sarmatica* (Purschke, 1885), *Melanochelys pidoplichkai*, and *Sakya riabinini* (Chkhikvadze 1983, 1989).

Five of Khosatzky's publications (1966a; Khosatzky and Tofan 1970a, b; Khosatzky and Redkozubov 1986b, 1989) contain information about Emydidae sensu lato from the Neogene of Moldavia. Khosatzky (1966a) and Khosatzky and Tofan (1970a, b) mentioned species of the genera *Clemmys*, *Emys*, and *Geoemyda* from the Neogene of Moldavia. Khosatzky and Redkozubov (1986b) described a new species *Melanochelys etuliensis* Khosatzky et Redkozubov, 1986 from the middle Pliocene of Moldavia. Later (Khosatzky and Redkozubov 1989) they reviewed all of the taxa of this group known from the Neogene of Moldavia, synonymized *M. mossoczyi* (Mlynarski, 1964) with *Geoemyda* (*Heosemys*) *boristhenica* Tarashchuk, 1971 and published new shell material of *M. pidoplichkoi* and *Sakya riabinini* from several middle Pliocene localities. *Melanochelys etuliensis* is considered by Chkhikvadze (1989, 2007, 2010) a synonym of *Sakya riabinini* or *Sakya etulienensis*, or *Sarmatemys etuliensis*. Danilov et al. (2012) mentioned this species as "*Melanochelys*" *etuliensis*. *Geoemyda* (*Heosemys*) *boristhenica* is considered a valid species *Melanochelys boristhenica* by Chkhikvadze (1983 and later publications).

Three of Khosatzky's publications (1967; Ivanjev and Khosatzky 1970; Khosatzky and Chkhikvadze 1993) reported and described a new turtle from the late middle or early late Miocene of Baikal (Russia). The first mention of this turtle was a nomen nudum (*Baicalemys gracilis*; Khosatzky 1967; Ivanjev and Khosatzky 1970) and it was only later described (Khosatzky and Chkhikvadze 1993) as a member of a new genus *Baicalemys* Khosatzky in Khosatzky et Chkhikvadze, 1993 with the type species *B. elegans* Khosatzky in Khosatzky et Chkhikvadze, 1993. Three other species, *B. moschifera* Chkhikvadze in Khosatzky et Chkhikvadze, 1993 from the early late Miocene of Zaysan Depression of Kazakhstan, *Chrysemys lavrovi* Kusnetsov et Chkhikvadze, 1977 from the late Oligocene of Kazakhstan and *Zaisanemys jegalloi* Chkhikvadze, 1973 from the late early–early middle Miocene of Zaysan Depression of Kazakhstan, were assigned to this genus (Khosatzky and Chkhikvadze 1993). The genus *Baicalemys* was established within the tribe Chrysemydini sensu Chkhikvadze, 1983 (= Deirochelyinae in the modern system; see Gaffney and Meylan 1988). Chkhikvadze (2001, 2007) assigned the holotype of *Clemmys kazachstanica* to *Baicalemys* (see Khosatzky 1947b). Other authors restricted *Baicalemys* to the type species and assigned this genus to the subfamily Emydinae (see Syromyatnikova et al. 2012).

Different taxa of fossil and modern Emydidae were also mentioned in the reviews of the turtles of the USSR (Khosatzky 1949a, 1951, 1957b, 1958c, 1982). Finally, several unpublished works of Khosatzky's students contain data about fossil and modern Emydidae (Table 3).

Testudinidae. Many of Khosatzky's papers were devoted to the description of new (fossil and recent) taxa of testudinids. Eight papers of Khosatzky (1944, 1945a; Khosatzky 1951; Bazhanov and Pigulevskiy 1955; Khosatzky 1958a, b; Borisov et al. 1961; Khosatzky and Kuznetsov 1963; Khosatzky et al. 1974) contain data about fossil testudinids from Kazakhstan. These include a report on a "giant *Testudo*" from the Pliocene of Kazakhstan (Betekey River), mention of *Testudo aralensis* Khosatzky, 1945 (nomen nudum) from the Oligocene of Kazakhstan (Agyspe) (Khosatzky 1945a), report and descriptions of *Testudo kegenica* Khosatzky in Bazhanov et Pigulevskiy, 1955 from the middle-late Miocene of Kazakhstan (Khosatzky 1951; Bazhanov and Pigulevskiy, 1955; Khosatzky 1958a; Khosatzky and Kuznetsov 1963), a

description of *Testudo* sp. from the ?late Oligocene of Kazakhstan (Khosatzky 1958b); reports on testudinids (*Testudo*) from the Paleogene-Neogene of Zaysan Depression (Borisov et al. 1961); and a description of *T. tekessa* Khosatzky et Kuznetsov in Khosatzky et al., 1974 from the middle Miocene of Kazakhstan (Khosatzky et al. 1974). The “giant *Testudo*” from the Pliocene of Kazakhstan appeared to be a member of Chelydridae (see above). *Testudo aralensis* was mentioned by many authors, but the material has never been described (see Chkhikvadze 1990, 2007). The generic attribution of *Testudo kegenica* varies considerably among authors (see Chkhikvadze 1989); the most current of them is *Agrionemys (Protagrionemys) kegenica* (Chkhikvadze 2010). The testudinids from Zaysan have been assigned to several genera by Chkhikvadze (1973, 1989, 1990). *Testudo tekessa* also has variable generic attributions (see Chkhikvadze 1989); the most current of them is *Agrionemys (Protagrionemys) tekessa* (Chkhikvadze 2010).

One of Khosatzky's paper (1948c) discussed data on reports of the modern testudinids *Testudo graeca* Linnaeus, 1758 and *T. horsfieldi* Gray, 1844 in the European part of the USSR, which was outside of their known ranges.

Two of Khosatzky's publications (1948b, 1949b) were devoted to description of fossil testudinids from the Pliocene of Ukraine (Kuchurgan). These were descriptions of two new species, *Testudo černovi* Khosatzky, 1948 and *T. kučurganica* Khosatzky, 1948, and description of remains of a “giant *Testudo*” (Khosatzky 1949b). *Testudo černovi* and *T. kučurganica* were later synonymized (see Chkhikvadze 1983). However, Khosatzky and Redkozubov (1989) indicated additional differences between these species. Chkhikvadze (2006) replaced the species names *černovi* and *kučurganica* to *chernovi* and *kuchurganica* respectively. Both species belong to the genus *Testudo* sensu stricto (see Chkhikvadze, 1989; Khosatzky and Redkozubov 1989). The “giant *Testudo*” from Kuchurgan appeared to be a member of Chelydridae (see above).

Three of Khosatzky's papers (1947c, 1948d, 1953) contain data on fossil testudinids of the Crimea. Two of these papers (Khosatzky 1947c, 1953) described new specimens (two shells) of *Testudo bosporica* Ribinin, 1945 from the Maeotian of Opuk Mountain and Adzhi Mushkay Village, Kerch Peninsula. The third paper (Khosatzky 1948d) described material of *Testudo* sp. from the Late Miocene (Sarmatian) of Sevastopol. Later, *Testudo* sp. from Sevastopol was

referred to as Testudinidae (Chkhikvadze 1983) or Testudinidae indet. (Danilov et al. 2012).

Four of Khosatzky's publications were devoted to modern testudinids of the Caucasus (Khosatzky and Alekperov 1958; Khosatzky 1968b; Alekperov and Khosatzky 1972; Khosatzky 1987). Khosatzky and Alekperov (1958) described shells of *Testudo graeca* of the Bronze Age from the archeological sites of Mingechaur (Azerbaijan) and discussed differences between population of *T. graeca* inhabiting Western and Eastern Caucasus. These differences were also discussed in the other publications cited above. Khosatzky (1987) named one of these populations (from Western Caucasus) *Testudo graeca pontica*, but this name appeared to be nomen nudum (see Borkin 1999). Later, populations of *T. graeca* from the Western and Eastern Caucasus were recognized as *Testudo graeca nikolskii* Chkhikvadze et Tuniyev, 1986 and *T. g. pallasi* Chkhikvadze et Bakradze, 2002 respectively (Chkhikvadze and Tuniyev 1986; Chkhikvadze and Bakradze 2002). According to results of a molecular study of the *Testudo graeca* complex, *T. graeca nikolskii* is a junior synonym of *T. ibera*, whereas *T. g. pallasi* is a junior synonym of *T. g. armeniaca* Chkhikvadze et Bakradze, 1991 (Fritz et al. 2007). Another extant species of questionable validity, *T. dagestanica* Chkhikvadze et al., 2011, was recently described from Southern Dagestan (Chkhikvadze et al., 2011).

The material of fossil testudinids from the Neogene and Quarternary of the Caucasus studied by Khosatzky was reviewed by Alekperov (1978). These are descriptions of *Testudo eldarica* Khosatzky et Alekperov in Alekperov, 1978 based on shell fragments (syntypes) from the late Miocene of Azerbaijan and *T. graeca binagadensis* Khosatzky in Alekperov, 1978 based on shell fragments from the middle Pleistocene of Azerbaijan, as well as remains (mainly shell fragments) of other *Testudo* sp. and *T. graeca*. See Chkhikvadze (1983, 1989) and Gabashvili et al. (2000) for latest accounts of these material and taxa.

Two of Khosatzky's publications (Khosatzky and Narmandakh 1973, 1975) were devoted to description of *Geochelone devjatkini* Khosatzky et Narmandakh, 1973 from the middle-late Miocene of Mongolia. Chkhikvadze (1989) considered this species a junior synonym of *Protestudo darewskii* Chkhikvadze, 1971, a species originally described from the middle Miocene of Kazakhstan (Zaysan Depression).

Nine of Khosatzky's publications (Khosatzky 1949a, d; Khosatzky and Młynarski 1966a; Birman

et al. 1968, 1971; Khosatzky 1982, 1987, 1991; Khosatzky et al. 2013) were devoted to or contained data on the Horsfield's tortoise, *Testudo horsfieldi* Gray, 1844. Khosatzky and Mlynarski (1966a) used this species as the type of the genus *Agrionemys* Khosatzky et Mlynarski, 1966. Birman et al. (1968, 1971) reported discoveries of *T. horsfieldi* from the Pliocene of Eastern Kopetdag (Turkmenia). Khosatzky (1982) noted that it may be more accurate to consider *Agrionemys* a subgenus of *Geochelone* (not *Testudo*). In this and in another earlier publication (Khosatzky 1949a), it was assumed that *T. horsfieldi* came to Middle Asia and Kazakhstan from non-Palearctic regions of Africa via Western Asia sometime around the boundary between Neogene and Anthropogene. Khosatzky (1982) briefly mentioned *T. (Agrionemys) horsfieldi* from the Mousterian (middle Paleolithic) of Aman Kutan (Uzbekistan) and Mesolithic or Mousterian Ogzi Kichik (Tajikistan) archeological sites. Khosatzky (1987) published more information about a mass accumulation of *Agrionemys horsfieldi* from Ogzi Kichik (10000–20000 BP). The latest publication about this accumulation is Khosatzky et al. (2013). *Agrionemys* was considered a subgenus of *Testudo* (sensu lato) by Auffenberg (1974). Some modern authors do not recognize *Agrionemys* and consider its living representatives as a single species (*Testudo horsfieldi*) within *Testudo* sensu lato (see Fritz and Havas, 2007; Rhodin et al., 2008). Other modern authors (mainly paleontologists) recognize *Agrionemys* as a distinct genus, but propose a different set of included taxa (Gmira 1995; Chkhikvadze 2006, 2007; Lapparent de Broin et al. 2006a, b). Material from Ogzi Kichik was described by Sharapov et al. (1989) and considered to be Upper Paleolithic in age. One publication of Khosatzky's (1991), devoted to "double monsters" (conjoined twins) in reptiles, contains description of two fused individuals of *Agrionemys horsfieldi* from Tajikistan.

Five of Khosatzky's publications contain information about Testudinidae from the Neogene of Moldavia (Khosatzky 1966a; Khosatzky and Tarabukin 1970; Khosatzky and Tofan 1970a, b; Khosatzky and Redkozubov 1989). Khosatzky (1966a) and Khosatzky and Tofan (1970a) mentioned different forms of *Testudo* from the Neogene of Moldavia. Khosatzky and Tarabukin (1970) described two incomplete shells of *Testudo bessarabica* Riabinin, 1918 from the late Miocene of Moldavia. In another publication (Khosatzky and Tofan 1970a), synonymy of this

species with *T. tarakliensis* Riabinin, 1918 from the late Miocene of Moldavia was suggested and other findings of *Testudo* from the Neogene of Moldavia were mentioned. The same year *Testudo bessarabica* was used as a type species of the genus *Protestudo* Chkhikvadze, 1970 (Chkhikvadze 1970). Other authors referred to this species as *Geochelone bessarabica* (Auffenberg 1974), "*Protestudo*" *bessarabica* or *Agrionemys bessarabica* (Lapparent de Broin et al. 2006a, b). Khosatzky and Redkozubov (1989) described new shell material of *Protestudo csakvarensis*, *P. bessarabica*, *Testudo cernovi* and *T. kucorganica*.

Different taxa of fossil Testudinidae were also mentioned in the reviews of turtles of the USSR (Khosatzky 1949a, 1951, 1957b, 1958c, 1982). Finally, several unpublished works of Khosatzky's students contain data about fossil and modern Testudinidae (Table 3).

Cryptodira incertae sedis. Sinemydidae. Sinemydidae are placed in Cryptodira incertae sedis, because their position within Khosatzky's system is unclear. The genus *Sinemys* Wiman, 1930 (type of the family Sinemydidae) was questionally placed in the Dermatemydidae in the publication of Verzilin et al. (1970a). In a later publication (Nessov and Khosatzky 1978) considered Sinemydidae as not closely related to Macrobaeninae (Toxochelyidae), contrary to the opinion of Chkhikvadze (1977 and others), who united these groups. Khosatzky (1996) described a new species *?Sinemys efremovi* Khosatzky, 1996 from the Early Cretaceous of China. Danilov and Sukhanov (2006) assigned this species to the genus *Wuguia* Matzke et al., 2004.

To summarize this section, Khosatzky reported and/or described original material on the following turtle groups (modern attributions of this material are given in parentheses): Amphichelydia (Meiolaniformes), Baëniidae (Lindholmemydidae), Pleurosternidae (Xinjiangchelyidae), Plesiochelyidae and Xinjiangchelyidae (both Xinjiangchelyidae), Toxochelyidae (Macrobaenidae/Sinemydidae), Cheloniidae (Cheloniidae), Trionychidae (Trionychidae), Chelydridae (Chelydridae), Dermatemydidae sensu lato (Lindholmemydidae), Adocidae (Adocidae), Emydidae sensu lato (Emydidae and Geoemydidae), Testudinidae (Testudinidae) and Sinemydidae (Macrobaenidae/Sinemydidae). Most of Khosatzky's publications on the systematics, phylogeny and biogeography of turtles were devoted to turtles of the families Testudinidae, Trionychidae and

Emydidae. Table 1 summarizes data on 44 turtle taxa named by Khosatzky, including their original and current names/status and familial or other attributions. Of these taxa, 35 are valid, two are considered to be junior subjective synonyms of other taxa (*Geochelone devjatkini*, Kirgizemyinae), four are nomina dubia (*Chelonia aralis*, *Toxocheloides*, *Toxocheloides narynensis*, *Trionyx zakhidovi*), two are nomina nuda (*Testudo aralensis* and *T. graeca pontica*), and status of one taxon is unclear (*Spinemys*).

Turtle faunas. The turtle publications of Khosatzky contain information on past and/or present (from the Middle Jurassic to the Quarternary/Recent) turtle faunas of Bulgaria, USSR (in general), European Russia and Caucasus, Moldavia, Ukraine, Siberia and Far East, Kazakhstan, Middle Asia, China, and Mongolia. The temporal and geographic "distribution" of some Khosatzky's publications on turtles is summarized in Table 2. Geographically, most publications were devoted to turtles of Middle Asia (19) and Kazakhstan (17), and temporally, to turtles of the Neogene (38) and the Cretaceous (26).

Biomechanics, morphology and evolution of the turtle shell

The biomechanics of the turtle shell was one of the primary interests of Khosatzky, which occupied him for his entire scientific life (Khosatzky 1941, 1947a, 1948a, 1959a, 1964, 1965c, 1968a, 1969; Masharskiy and Khosatzky 1969; Avelev et al. 1992; Khosatzky and Avelev 1992). His first studies on the biomechanics of the turtle shell were presented in his candidate thesis and reflected in the abstract of this thesis (Khosatzky 1941b) and two papers (Khosatzky 1947a, 1948a). In the first of these papers Khosatzky (1947a) presented data of experiments on shell resistance to destruction in turtles with convex (*Testudo graeca*) and flattened (*Agrionemys horsfieldi*) shells. In the second paper Khosatzky (1948a) discussed (partially based on experimental data) the role of some constructive details of the bony shell (vertebral column, external keels, rib thickenings, plastral buttresses) and shape of its individual elements in the reinforcement of the shell, the role of bony sutures as shock absorbers and damage limiters as well as the mechanical role of the horny shell in different turtles. The biomechanics of the turtle shell, including its hydrodynamic properties, were also discussed by Khosatzky (1969). Later, Khosatzky's biomechanical

studies were continued by vibrometric analysis of the shells of aquatic and terrestrial turtles (Masharskiy and Khosatzky 1969) and study of the influence of high frequency electromagnetic fluctuations on live turtles and prepared shells of *Emys orbicularis* (Avelev et al. 1992). In this connection the seismoprognostic abilities of turtles (and other reptiles) were discussed (Khosatzky and Avelev 1992).

Three of Khosatzky's publications (1959a, c, 1964, 1965c) discussed the significance of certain features of turtles (particularly, of their shell) important for ecological functional analysis of their morphology and reconstruction of their phylogeny. One paper (Khosatzky 1968a) focused on oligomerization (i.e. decrease in the number of morphofunctional units of a system) as the main tendency in the evolution of the turtle shell. Anomalies of the shell connected with the appearance of additional plates were considered recapitulations of the primitive shell morphology.

Concerning the nature of the bony shell of turtles, Khosatzky supported the hypothesis of its complex origin from fusion of superficial thecal ossifications with basal skeletal elements (vertebrae, ribs, gastralia etc.). However, this hypothesis was only mentioned in passing in one of his publications (Khosatzky 1968a). Despite the results of morphogenetic studies of his student's and colleague's refuting this hypothesis (Borkhvardt 1978; Cherepanov 1989), Khosatzky's opinion on the matter did not change.

One of Khosatzky's publications (1978) was devoted to the comparative study of the dermal bone microstructure in stegocephalian amphibians and trionychid turtles. It is assumed that the pit-ridge sculpturing of the shell bones of trionychid turtles provides them additional mechanical strength and more tight connection with soft skin, reducing the risk of rupture of blood vessels.

In addition to the publications mentioned above, Khosatzky supervised and reviewed numerous student works on the biomechanics, morphology and evolution of the turtle shell (see Table 3).

Ecological physiology of turtles

Khosatzky's studies on the ecological physiology of turtles began in 1957, when he supervised the graduate thesis of his student N.V. Tolmacheva (see Table 3). However, Khosatzky's interest in the physiology of reptiles was demonstrated much earlier in one of his early papers devoted to skin respiration in reptiles

Table 3. Data on unpublished student works (CP – course project; CT – candidate thesis; GT – graduate thesis) supervised (S) and reviewed (R) by Khosatzky and devoted to turtles or containing original data about turtles with references to corresponding publications. DH – Department of Hydroaerodynamics, Faculty of Mathematics and Mechanics. See text for other abbreviations.

No.	Name	Year	Title	Place of defence	Type of work	S/R	References
1	Ananjeva N.B.	1967	Manifestation of oligomerization in the evolution of turtle shell and variations of its morphology	DVZ	CP	S	–
2	Ananjeva N.B.	1968	Peculiarities of innervation and vascularization of the turtle shell	DVZ	GT	S	–
3	Borkin L.J.	1969	Pliocene turtles of Moldavia and Ukraine	DVZ	CP	S	–
4	Borkin L.J.	1970	Ecology of the Greek tortoise	DVZ	CP	S	Borkin et al. 1979
5	Borkin L.J.	1971	[Morphology of the turtle shell]	DVZ	GT	S	Borkin 1973
6	Desyatskov V.L.	1973	Experimental study of thermoreceptor sites of the turtle shell	DVZ	CP	S	Khosatzky 1981
7	Desyatskov V.L.	1974	Some peculiarities of the thermoregulation of turtles	DVZ	GT	S	Khosatzky 1981
8	Ivanov A.O.	1981	Soft-shelled turtles of the Late Cretaceous of Kyzylkum	DP	CP	S	–
9	Ivanov A.N.	1981	Variation of the shell of the European pond turtle <i>Emys orbicularis</i>	DVZ	GT	S	Khosatzky 1987; Khosatzky and Ivanov 1990
10	Golubyatnikova M.M.	1959	A comparative-anatomical study of parts of the internal skeleton of some turtles	DVZ	GT	S	–
11	Khusnetdinova R.M.	1987	Some peculiarities of heat exchange and thermoregulation of soft-shelled turtles	DVZ	CP	S	–
12	Kryuchkov B.	1955	Shell of the European pond turtle	DVZ	CP	S	–
13	Levinson S.V.	1974	Some peculiarities of the correlation of the vertebrate column and shell in terrestrial turtles	DVZ	CP	S	–
14	Levinson S.V.	1976	New freshwater turtles of the Cretaceous of Fergana and Kyzylkum	DVZ	GT	S	Danilov et al. 2007
15	Levshakova I.Yu.	1980	Soft-shelled turtles (trionychids) of the Late Cretaceous of Fergana	DP	CP	S	Vitek and Danilov 2010
16	Levshakova I.Yu.	1981	Trionychids of the Cretaceous and Paleogene of Mongolia	DP	CP	S	Khosatzky 1999
17	Levshakova I.Yu.	1982	Trionychids of the Cretaceous and Cenozoic of Middle Asia and Mongolia	DP	GT	S	Khosatzky 1999; Vitek and Danilov 2010
18	Malyshev V.N.	1968	Russilion fauna of vertebrates of the Lucheshty locality	DVZ	CP	S	–
19	Malyshev V.N.	1969	Late Cretaceous trionychid turtles of Fergana	DVZ	CP	S	–
20	Narmandakh P.	1967	Freshwater turtles of the Late Cretaceous of Mongolia	DP	CP	S	–
21	Narmandakh P.	1968	Materials on fauna of turtles of the Mesozoic and Cenozoic of Mongolia	DP	CP	S	Khosatzky and Narmandakh 1973, 1975

Table 3. *Continued.*

No.	Name	Year	Title	Place of defence	Type of work	S/R	References
22	Narmandakh P.	1969	Turtles of the Mesozoic and Cenozoic of Western Mongolia	DP	CP	S	Khosatzky and Narmandakh 1973, 1975
23	Nessov L.A.	1968	Freshwater turtles of the Early Cretaceous of Fergana Depression	DP	CP	S	Verzilin et al. 1970a; Nessov and Khosatzky 1973, 1977b; Nessov and Khosatzky 1978; Nessov 1995
24	Nessov L.A.	1977	Phylogeny and systematics of Mesozoic turtles of the USSR and their relations with modern groups	LSU	CT	S	Verzilin et al. 1970a; Nessov and Khosatzky 1973, 1975a, b; Nessov 1976, 1977a, b; Nessov and Khosatzky 1977a, b, 1978; Nessov 1978; Nessov and Khosatzky 1978; Khosatzky and Nessov 1979a; Nessov and Khosatzky 1980, 1981a, b; Nessov 1986; Glickman et al. 1987; Nessov 1987, 1995; Nessov and Khosatzky 1999
25	Obrezkova I.V.	1976	A morphometric study of the skeleton of limbs and girdles of the Greek tortoise	DVZ	CP	S	–
26	Obrezkova I.V.	1977	A comparative-anatomical study of limbs of the Greek and Horsfield's tortoises	DVZ	GT	S	–
27	Paevskaya E.B.	1969	A correlation analysis of the shell construction of terrestrial turtles	DVZ	GT	S	Khosatzky 1987
28	Potselueva T.A.	1974	A comparative-anatomical study of the skull of terrestrial turtles of the fauna of the USSR	DVZ	GT	S	–
29	Pronenko Yu.A.	1983	Aerohydrodynamic study of the structural properties of the shell of aquatic turtles	DH	GT	R	–
30	Pystina M.V.	1976	The development of the carapace in the ontogenesis of the Greek tortoise	DVZ	CP	S	–
31	Pystina M.V.	1977	The development of the bony and horny shell in the ontogenesis of the Greek tortoise	DVZ	GT	S	–
32	Redkozubov O.I.	1991	Neogene reptiles of Moldavia	PIN	CT	S	Khosatzky and Redkozubov 1986a, b; 1989
33	Rumyantseva I.F.	1958	Microstructure of the shell of vertebrates (a comparative-anatomical study)	DVZ	GT	S	–
34	Seletskiy O.B.	1966	Lucheshty locality of the Pliocene fauna of Moldavia	DP	GT	S	Khosatzky and Tofan 1970a
35	Shkalinskaya L.B.	1979	Peculiarities of respiration of turtles on land and under water	DVZ	CP	S	–
36	Sokolova A.I.	1978	A comparative study of the microstructure of the skin of some reptiles	DVZ	GT	S	–
37	Stankevich S.E.	1985	A craniological study of terrestrial turtles of the fauna of the USSR	DVZ	GT	S	–

Table 3. Continued.

No.	Name	Year	Title	Place of defence	Type of work	S/R	References
38	Telepneva V.P.	1962	Constructive peculiarities of the shell microstructure of extinct and modern turtles	DVZ	CP	S	–
39	Telepneva V.P.	1965	Turtles of the Mesozoic of Fergana	DVZ	GT	S	Danilov et al. 2007
40	Tofan V.E.	1967	Fauna of amphibians and reptiles of Moldavia	LSU	CT	S	Khosatzky and Tofan 1970a, b
41	Tolmacheva N.V.	1955	Constructive peculiarities and growth regularities of the shell of the Caspian turtle	DVZ	CP	S	–
42	Tolmacheva N.V.	1956	Fossil turtles from the Pliocene deposits of Northern Priazovye	DVZ	CP	S	–
43	Tolmacheva N.V.	1957	A comparative ecological-physiological study of terrestrial and freshwater turtles	DVZ	GT	S	Khosatzky and Tolmacheva 1959; Shcheglova et al. 1977
44	Trusova V.K.	1968	[“ <i>Chelydra</i> ” from the Pliocene of Moldavia]	DVZ	GT	S	Khosatzky and Tofan 1970a
45	Yurgelevich V.I.	1963	Sexual dimorphism of the shell of the Horsfield's tortoise	DVZ	CP	S	–
46	Yurgelevich V.I.	1968	Peculiarities of shell morphology of the Horsfield's tortoise	DVZ	GT	S	Khosatzky et al. 2013
47	Zhdanukhin V.I.	1962	[Intraspecific variation of the shell of the Greek tortoise]	DVZ	GT	S	–
48	Zherekhova I.E.	1974	A morphometric study of historical changes of the shell of the Horsfield's tortoise	DVZ	GT	S	Khosatzky 1987; Khosatzky et al. 2013
49	Zolotarev O.B.	1969	Peculiarities of vascularization of the skin of aquatic and terrestrial turtles	DVZ	CP	S	–

(Khosatzky 1941a). This interest was influenced in part by Khosatzky's teacher in ecology D.N. Kaskarov and in part by Khosatzky's wife Aleksandra Ivanovna Shcheglova, who was a physiologist. All in all, from 1959 to 1990 Khosatzky wrote twelve publications on the ecological physiology of turtles in collaboration with his students and wife (Khosatzky 1959b; Khosatzky and Tolmacheva 1959; Khosatzky 1965b, 1967b, 1968c; Khosatzky et al. 1970; Trusova and Khosatzky 1970; Shcheglova et al. 1977; Khosatzky 1979a, 1981; Khosatzky and Maslennikova 1989; Maslennikova and Khosatzky 1990).

Khosatzky's first publications on the thermobiology of turtles appeared in 1959 (Khosatzky 1959b; Khosatzky and Tolmacheva 1959). The first of these two publications presented results of a study of surface temperature of four turtle species (*Agrionemys horsfieldi*, *Emys orbicularis*, *Mauremys caspica*, and *Testudo graeca*), whereas the latter one reported results of an experimental study of hydrotactic and

thermotactic optima in the same species. These and later publications (Khosatzky 1965b; Trusova and Khosatzky 1970) demonstrated the key role of the shell in the thermoregulation of turtles. The shell was considered a powerful thermal insulator that allowed turtles to withstand considerable fluctuations in the thermal conditions of the environment. He hypothesized that the turtle shell could evolve as a protection not only from enemies, but also from unfavourable environmental factors (Khosatzky 1965b).

Later, *Pelodiscus maackii* (then called *Trionyx sinensis*) became the preferred study organism for Khosatzky's thermobiological studies (Khosatzky 1981; Khosatzky and Maslennikova 1989; Maslennikova and Khosatzky 1990). These publications presented experimental data on the internal (rectal) and external (skin) temperature of this species. It was shown that the body temperature of these turtles exceeds the ambient temperature, suggesting a high metabolic

level connected with intensive skin respiration and an active lifestyle. In addition to physical thermoregulation, *P. maackii* has chemical thermoregulation. In the zone of low ambient temperatures, the sharp increase in metabolic rate provides a mechanism for the retention of the body heat (effect of endothermy).

Other directions of ecological-physiological investigations of Khosatzky were studies of skin respiration (Khosatzky 1967b, 1968c, 1979a) and water metabolism in turtles (Khosatzky et al. 1970; Shcheglova et al. 1977). The main experimental organism for his studies on skin respiration was *Pelodiscus maackii*. It was experimentally shown that when under water, these turtles use a buccal-pharyngeal apparatus and their skin for respiration. These features are connected with the active lifestyle of these turtles and make it possible for them to stay under water for a long time (Khosatzky 1967b). Morphologically, this ability is conferred by the distinctive structure of the exterior of trionychids—the lack of keratinous scutes, thin epidermis and vascularization of the dermal skin layer. The study of microstructure of shell bones of trionychids revealed presence of a rich net of blood vessels, similar to those in exoskeleton of ancient amphibians—stegocephalians (Khosatzky 1978). For this reason, trionychids were called “amphibious reptiles” (Khosatzky 1979a). Water metabolism was studied in *Mauremys caspica* (Khosatzky et al. 1970; Shcheglova et al. 1977). It was shown that these freshwater turtles can consume and lose (due to evaporation) water through the skin.

In addition to the mentioned publications, Khosatzky supervised several student works on the ecological physiology of turtles (see Table 3).

Other turtle studies

Other turtle studies of Khosatzky include several “geological” publications. Two publications co-authored by Khosatzky were devoted to biostratigraphic dating of the Jurassic and Cretaceous deposits of Fergana based on fossil turtles (Verzilin et al. 1970a, b). Two other papers coauthored by Khosatzky were devoted to the study of distribution of rare elements in osteological remains of different Mesozoic and Cenozoic turtles of the USSR (Verzilin et al. 1975, 1976). Finally, one paper described turtle-like concretions (turtle stones) from Kyurendag in Turkmenia and discussed other discoveries of this kind (Khosatzky et al. 1985).

Unpublished turtle works of Khosatzky’s students

Table 3 lists 49 unpublished works supervised (48) and reviewed (1) by Khosatzky and devoted to turtles or containing original data about turtles. Of these works, 24 are course projects, 22 are graduate theses, and three are candidate theses. Most of these works (36) were defended at the DVZ, 9 at the DP, one at the Department of Hydroaerodynamics (Faculty of Mathematics and Mechanics, LSU), two in the LSU and one in the PIN. Results of at least 21 of these works were published by Khosatzky and/or his students or mentioned in publications of other authors (see Table 3 for references). Although we have not included annotations of these works, even their titles provide an idea of the wide scope of Khosatzky’s studies and interests. Some of turtle students of Khosatzky became well-known herpetologists (N.B. Ananjeva, L.J. Borkin, V.E. Tofan), ichthyologists (V.P. Telepneva [Prirodina]), and paleontologists (A.O. Ivanov, L.A. Nesson, P. Narmandakh, and O.I. Redkozubov). Ananjeva, Borkin, Nesson, Narmandakh, Redkozubov and Tofan published works on turtles.

CONCLUSIONS

The main avenues of Khosatzky’s turtle research were laid in his candidate thesis and realized in his later life. These directions include the biomechanics, morphology and evolution of the turtle shell and the paleontology of turtles of the USSR. Later, the ecological physiology of turtles joined these avenues. His studies on paleontology of turtles were also expanded to include the territories outside the USSR (Eastern and Western Europe and Mongolia). In terms of the paleontology of turtles, most of Khosatzky’s contributions were devoted to the study of fossil testudinids, trionychids and emydids. Geographically, most of his publications were devoted to turtles of Middle Asia and Kazakhstan, and temporally, a majority of publications were devoted to turtles of the Neogene and the Cretaceous. Of the 44 turtle taxa named by Khosatzky, 36 are considered to be valid in the modern system, although the taxonomic status of some of them has been changed. Khosatzky supervised numerous student works on turtles, results of which were only partially published. Some of Khosatzky’s students became well-known turtle experts. Although many turtle projects of Khosatzky were not completed, he defined important directions of research for future generations of chelonologists.

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Appendix 1. Annotated bibliography of publications concerning turtles by L.I. Khosatzky. See text for comments and discussion.

- 1. Khosatzky L.I. 1941b.** An ecological-morphological study of the evolution of the shell of terrestrial turtles. Abstract of the thesis of the Candidate of Biological Sciences. Leningrad State University, 7 p. [In Russian]

This paper analyses the main features of the shell morphology of tortoises (Testudininae sensu Williams, 1950) and discusses adaptive significance of their shell based on ecological and functional data. The design quality of the shell as a mechanical construction was investigated in a laboratory for testing materials. It was found, that species with convex carapaces withstand heavy loads (both strikes and evenly distributed loads) than species with flat shells. The thickness of the shell bones is connected with the degree of carapace convexity: high-domed *Testudo elephantopus* have a relatively thin shell. The wedge-shaped costals and serrated bony sutures significantly enhance the mechanical strength of the shell through the establishment of maximum effect of friction between the neighboring plates of the shell. Species of Testudininae can be grouped into two ecological groups: the inhabitants of open landscapes and inhabitants of the forest and scrub. Members of the first group sometimes utilize burrows (*Testudo horsfieldi*, *Gopherus polyphemus*) and have a flattened shell. Members of the second group have stronger and more convex shell. The study of fossil material showed that early representatives of *Testudo* had relatively unspecialized shell. Later, the shell became more convex because turtles lived in areas rich in vegetation that were not conducive to a burrowing lifestyle. Even later, climate change has led to the spread of open landscapes (steppes and deserts) where turtles adapted to digging and life in burrows that resulted in the flattening of their shells.

- 2. Khosatzky L.I. 1944.** Finding of remains of a giant tortoise in the Pliocene deposits of Northern Kazakhstan. *Priroda*, **1**: 80–82. [In Russian]

This short paper describes and illustrates a single peripheral plate from the Pliocene of Northern Kazakhstan (Betekey River) attributed to a giant representative of testudinids of the genus *Testudo* (sensu lato) as *Testudo* sp. In addition, this paper reviews other discoveries of giant representatives of *Testudo* and giant testudinids in general.

- 3. Khosatzky L.I. 1945a.** Remains of a sea turtle discovered in Oligocene deposits of the near-Aral region. *Comptes Rendus (Doklady) de l'Academie des Sciences de l'URSS*, **49**(1): 52–54. [Original Russian text was published in *Doklady Akademii Nauk*, **49**(1): 53–55].

This paper describes and illustrates fragmentary material, including a partial costal, two peripherals (not figured) and a distal portion of the coracoid from the Oligocene of Kazakhstan (Agyspe) attributed to Cheloniidae as a new species *Chelonia aralis* Khosatzky. In addition *Testudo aralensis* (nomen nudum) is mentioned from the same locality.

- 4. Khosatzky (Khosatsky) L.I. 1945b.** Discovery of the representatives of Trionychoidea (Testudines, Reptilia) in the Pliocene of the Ukraine. *Comptes Rendus (Doklady) de l'Academie des Sciences de l'URSS*, **49**(6): 445–446. [Original Russian text was published in *Doklady Akademii Nauk*, **49**(6): 455–457].

This paper describes fragmentary shell material attributed to *Trionyx* sp. from the Pliocene of Kuchurgan locality, Ukraine. In addition, this paper lists other findings of trionychids from the Neogene of Ukraine and Moldavia, and from the Paleogene and Cretaceous of the USSR, and discusses paleogeographic distribution of this group.

- 5. Khosatzky L.I. 1945c.** [About giant turtles]. *Paleontologicheskoe Obozrenie*, **5**: 80–81 [In Russian]

This is a short report about new discoveries of fossils of giant turtles from Kazakhstan. The fossils were described in separate publications (Khosatzky 1944, 1945a).

- 6. Khosatzky L.I. 1945d.** [About *Pseudocadia anyangensis*]. *Paleontologicheskoe Obozrenie*, **5**: 81–82. [In Russian]

This is a short note about *Pseudocadia* (orig. *Testudo*) *anyangensis* (Ping, 1930), a species based on a single shell from Annyang Hsien archaeological ruins (about 3500 years BP), Henan Province, China. A large series of shell fragments of this species from Annyang stored in the collection of the Hermitage (Leningrad) is mentioned.

- 7. Khosatzky L.I. 1946a.** Remains of freshwater turtle *Emys orbicularis* L. from the Quarternary deposits of the Crimea. *Byulleten' Komissii po Izucheniyu Chetvertichnogo Perioda*, **8**: 78–81. [In Russian with English summary].

This paper describes fragmentary remains (parts of humeral and femoral bones; not figured) of *Emys orbicularis* from the Paleolithic deposits of Shan Koba Cave, Crimea.

- 8. Khosatzky (Khosatsky) L.I. 1946b.** Some new species of the genus *Clemmys* Ritgen (Testudines, Reptilia) from the Pliocene of the Ukraine. *Comptes Rendus (Doklady) de l'Academie des Sciences de l'URSS*, **52**(7):

617–620. [Original Russian text was published in *Doklady Akademii Nauk*, 52(7): 617–620].

This paper describes two turtle species attributed to the genus *Clemmys* Ritgen, 1828 (*Clemmys pidoplichkai* Khosatzky and *Cl. riabinini* Khosatzky) based on a series of shell fragments from the Pliocene of Kuchurgan River valley, Ukraine. In addition to the descriptions, this paper contains reconstructions of the plastra of these species.

9. Khosatzky L.I. 1947a. Biomechanics of the turtle shell. Part I. The correlation between shape of the shell and its strength. *Izvestiya Akademii Nauk SSSR. Seriya Biologicheskaya*, 5:707–719. [In Russian]

This paper presents general rules of structural mechanics as a basis for studying of the strength of the turtle shell construction. The data from experiments studying the resistance of the shells of *Testudo graeca* (convex shell) and *Testudo horsfieldi* (flattened shell) to destruction due to a gradual increase in pressure versus precise strikes are given. Significantly less force is required to destroy the shell through a strike as opposed to evenly distributed pressure. In general, the turtle shell is considered a strong mechanical construction. A direct correlation between an increase in the height of the shell arch and an increase of the shell's resistance to crushing is mathematically proven.

10. Khosatzky L.I. 1947b. Turtles of the genus *Clemmys* of the Tertiary fauna of Kazakhstan. *Izvestiya Akademii Nauk Kazakhskoy SSR*, 36, Seriya Zoologicheskaya, 6: 125–129. [In Russian]

This paper describes a new species *Clemmys kazakhstanica* Khosatzky, based on the isolated xiphiplastron (holotype) and hyoplastron from the upper Oligocene or lower Miocene of Askansor locality in Kazakhstan. The hypothesis that this species may belong to the genus *Echmatemys* is considered.

11. Khosatzky L.I. 1947c. A tortoise from the Maeotian deposits of the Crimea. *Doklady Akademii Nauk SSSR*, 58(9): 2059–2062. [In Russian]

This paper describes and illustrates the second specimen (a complete shell) of *Testudo bosporica* Riabinin, 1945 from the Maeotian (Late Miocene) deposits of Opuk Mountain, Kerch Peninsula, Crimea (type locality of this species). Potential routes of immigration of tortoises to the Crimea in the Miocene and reasons for their later extinction there are discussed.

12. Khosatzky L.I. 1948a. Biomechanics of the turtle shell. Part II. *Izvestiya Akademii Nauk SSSR. Seriya Biologicheskaya*, 1: 37–52. [In Russian]

This paper continues a series of publication by Khosatzky (1947a) on the biomechanics of the turtle shell. It discusses longitudinal and transverse reinforcement of the carapace. It is shown that the vertebral column in turtles with flattened shells (*Emys*, experimental data) and external keels in some freshwater turtles (*Staurotypus*, *Geoclemys*, *Geoemyda* and others) act as stiffeners that reinforce the carapace in a longitudinal direction. Rudiments of trunk ribs (rib thickenings), which reinforce the costal plates of the carapace, contribute to the consolidation of the shell in a transverse direction. A considerable role in the mechanical reinforcement of the carapace is played by uprights on the hyo- and hypoplastra (axillary and inguinal buttresses), which oppose inclined pressure. The constructional significance of some shell plates, such as the wedge-

shaped costals of testudinids, and the role of bony sutures as shock absorbers and damage limiters (experimental data), as well as the mechanical role of the keratinous shell, are discussed.

13. Khosatzky L.I. 1948b. New species of the genus *Testudo* Linne (Testudines, Reptilia) from the Pliocene of Ukraine. *Byulleten' Komissii po Izucheniuyu Chetvertichnogo Perioda*, 11: 92–96. [In Russian]

This paper describes and illustrates two new species of the genus *Testudo* Linne: *T. černovi* Khosatzky, based on the anterior part of the shell, and *T. kuchurganica* Khosatzky, based on shell fragments from the late Pliocene Kuchurgan locality of Ukraine.

14. Khosatzky L.I. 1948c. About finding of tortoises in the European part of the USSR. *Priroda*, 4: 59–60. [In Russian]

This short paper analyses data on discoveries of modern tortoises (*Testudo graeca* L. and *T. horsfieldi* Gray) in the European part of the USSR, outside their previously reported ranges. It is concluded that all such findings, probably, are the result of introduction by humans.

15. Khosatzky L.I. 1948d. About remains of turtles from the Sarmatian of the Crimea. *Byulleten' Moskovskogo Obshchestva Ispytateley Prirody. Otdel geologii*, 23(3): 17–22. [In Russian]

This paper describes and illustrates turtle shell fragments from the Sarmatian deposits of Sevastopol (Crimea). These fragments are identified as *Trionyx* sp., *Clemmys* sp. and *Testudo* sp.

16. Khosatzky L.I. 1949a. The history of the fauna of turtles of the USSR in light of paleogeography. In: Trudy Vtorogo Vsesoyuznogo geograficheskogo s'ezda. T. 3. Gosudarstvennoe izdatel'stvo po geograficheskoy literature, Moskva: 221–230. [In Russian]

This paper presents a review of discoveries of fossil turtles in the USSR and discusses the history of the formation of the modern turtle fauna of this territory. The best known is the history of the fossil turtles of Ukraine, Moldavia and the Crimea. These turtle fossils include a sea turtle from the Eocene of Ukraine, *Testudo bessarabica* Riab. from the Miocene of Bessarabia, a new species of *Testudo* from the Maeotian of Ukraine (Odessa Province), representatives of the Pliocene Kuchurgan fauna (*Trionyx* sp., several species of *Clemmys* and *Testudo*), the Pliocene fauna of Morskaya Station (near Taganrog, Sea of Asov coast; new species of the genus *Clemmys* close to *Clemmys riabinini* Khoz.), and the Pliocene fauna of Kosyakino Quarry (near Stavropol; same taxa as in Kuchurgan plus *Emys*), representatives of *Testudo* from the Upper Pliocene of Grozny, remains of a sea turtle from the Eocene of the Crimea, representatives of the Sarmatian Sevastopol fauna (*Trionyx*, *Testudo*, *Clemmys*), *Testudo bosporica* Riab. from the Maeotian of the Kerch Peninsula, *Emys orbicularis* from the Shan-Koba Paleolithic site, sea turtles from the Lower Oligocene of Dzauzhikau (Vladikavkaz), *Testudo* aff. *graeca* L. from the Pleistocene of Apsheron Peninsula, subfossil *Testudo graeca* from Taman Peninsula, and *Clemmys* close to *Cl. caspica* from Pliocene of Zangi River (Armenian SSR). Fossil turtles from the Asiatic part of the USSR are represented by members of Trionychoidea, Cryptodira and Pleurodira of the Late Cretaceous age, Oligocene–Miocene terrestrial and freshwater turtles, and large Oligocene sea turtles. The oldest sea turtle from the territory of the USSR is *Yaxartemys longicauda* Riab. from the

Jurassic deposits of the Kara-Tau Ridge (southern Kazakhstan). *Testudo* is known from the Pliocene of Kazakhstan. Ancestors of *Testudo horsfieldi* arrived in the species' modern range from Africa via Western Asia, probably, only in the Quarternary.

- 17. Khosatzky L.I. 1949b.** About gigantic turtles of the Pliocene of Ukraine. *Doklady Akademii Nauk SSSR*, **64**(3): 387–389. [In Russian]

This paper describes and partially illustrates fragments of large peripherals of a turtle shell from the Pliocene Kuchurgan locality of Ukraine. These plates are identified as *Testudo* sp. and considered to belong to a giant representative of this genus.

- 18. Khosatzky L.I. 1949c.** Class Reptilia. Reptiles. In: Atlas rukovodyashchikh form iskopaemykh faun SSSR. Tom XI. Verkhniy otdel melovoy sistemy. Gosudartstvennoe izdatel'stvo geologicheskoy literatury, Moscow: 268–281. [In Russian]

This paper reviews Late Cretaceous reptiles of the USSR, including turtles (subclass Chelonia), which are represented by *Lindholmemys elegans* Riabinin, 1935 (Pleurodira: Pelomedusidae) from the Cenomanian of Kyzylkum. The paper contains diagnoses of *Lindholmemys* and *L. elegans* and a figure of the lateral view of the shell of *L. elegans*.

- 19. Khosatzky L.I. 1949d.** Class Reptilia. Reptiles. In: Atlas rukovodyashchikh form iskopaemykh faun SSSR. Tom XIII. Neogen. Gosudartstvennoe izdatel'stvo geologicheskoy literatury, Moscow: 361–365. [In Russian]

This paper reviews Neogene reptiles of the USSR, including turtles (subclass Testudines), which are represented by *Testudo* Linné, 1758: *Testudo turgaica* Riabinin, 1926 (middle Miocene of Kazakhstan), *T. bessarabica* Riabinin, 1918 (Maotian of Bessarabia), *T. cernovi* Khosatzky and *T. kucurganica* Khosatzky (both from the upper Pliocene of Ukraine); *Clemmys* Ritgen, 1828: *C. pidoplichkai* Khosatzky and *C. riabinini* Khosatzky (both from the upper Pliocene of Ukraine). Diagnoses and illustrations are given for all these taxa.

- 20. Khosatzky L.I. 1951 (1950).** Paleontological and stratigraphical significance of fossil turtles. In: Voprosy Paleontologii. T. 1. Leningrad State University, Leningrad: 20–31. [In Russian]

This paper discusses the significance of fossil turtles for paleontology and stratigraphy. It contains a brief review of discoveries of fossil turtles in the territory of the USSR. Among previously unreported findings are *Testudo kegenica* Khos. from the Miocene of the Asiatic part of the USSR, a small sea turtle from the Kiev marl and a sea turtle from the Eocene of the Crimea. This paper also provides instructions for collecting fossil turtles and an identification key for some turtle groups (orders Trionychoidea and Cryptodira, genera *Emys*, *Clemmys* and *Testudo*).

- 21. Khosatzky L.I. 1953.** About Maeotian turtles of the Kerch Peninsula. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **14** (for 1948–1953): 237–256. [In Russian]

This paper describes and illustrates the third specimen (complete shell) of *Testudo bosporica* Riabinin, 1945, found in 1934 in marine Maeotian limestone in quarries of the Kerch Metallurgical Plant in vicinities of Adzhi Mushkay Village (5 km NE from Kerch), Crimea. The history of Maeotian turtles of the Kerch Peninsula is discussed in connection with its paleogeography.

- 22. Khosatzky L.I. 1956.** Remains of the European pond turtle from the Pliocene of Stavropolye. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **15** (for 1954–1955): 321–327. [In Russian]

This paper describes and illustrates material (posterior part of the plastron) of a new subspecies of the European pond turtle *Emys orbicularis antiqua* Khosatzky from the Pliocene of Kosytkino Quarry, 12 km from Stavropol. Material described by Szalai (1934) as *E. orbicularis* from Köpec [Romania] and Hajnáčka [Slovakia] is also assigned to the new subspecies.

- 23. Khosatzky L.I. 1957a.** On the history of trionychid turtles in Kazakhstan. *Izvestiya Akademii Nauk Kazakhskoy SSR. Seriya Biologicheskaya*, **2**: 15–30 [In Russian]

This paper reviews discoveries of fossil soft-shelled turtles (Trionychidae) from Kazakhstan and adjacent territories. All these findings come from the Upper Cretaceous and Tertiary (Eocene–Miocene) deposits of about 30 localities and represented mainly by fragmentary shell remains collected by Russian/Soviet geologists in the first half of 20th century. The reduction of the range of trionychids in Kazakhstan during the Cenozoic and their extinction there by the end of the Miocene is hypothesized to be caused by progressive climate change (aridification).

- 24. Khosatzky L.I. 1957b.** Peculiarities of the past and present distribution of turtles on the territory of the USSR. In: Materialy k soveshchaniyu po voprosam zoogeografii sushy. Tezisy dokladov (1–9 June 1957, Lvov). Lvov University, Lvov: 158–160. [In Russian]

This is an abstract version of the paper of Khosatzky (1958c).

- 25. Khosatzky L.I. 1957c.** Freshwater turtles of the Upper Cretaceous of Fergana. *Doklady Akademii Nauk Tadzhikskoy SSR*, **22**: 19–21. [In Russian]

This short paper reports fossil turtle material from the Upper Cretaceous (lower Senonian) deposits of Fergana (territory of Tajik SSR and adjacent areas of Kirghiz SSR and Uzbek SSR, localities Kan, Kizyl-Pilyal' and Shurab) collected by geologists M.A. Zaprudskaya. This material consists of about 150 fragmentary shell remains belonging to two or three forms of the genera *Amyda* and *Aspideretes* (Trionychidae) and several different forms, which are similar to the genera *Adocus*, *Basilemys* and *Compsemys* (Dermaptemydidae).

- 26. Khosatzky L.I. 1958a.** A tortoise of the Neogene of the Northern Tian Shan. In: Materialy po istorii fauny i flory Kazakhstana. T. 2. Academy of Sciences of the Kazakh SSR, Alma-Ata: 39–54. [In Russian]

This paper presents a detailed description and illustration of a new species *Testudo kegenica* based on two shells from the middle–upper Miocene of the upper reaches of the Kegen' River, Chul'adry Ridge, Kegen' District, Alma-Ata Province, Kazakhstan.

Remarks. See Bazhanov and Pigulevskiy 1955 (Appendix 2).

- 27. Khosatzky L.I. 1958b.** A rare case of preservation of remains of fossil turtle. In: Materialy po istorii fauny i flory Kazakhstana. T. 2. Academy of Sciences of the Kazakh SSR, Alma-Ata: 55–59. [In Russian]

This paper presents a description of the imprint of several carapacial scutes of *Testudo* sp. from the ?upper Oligocene clays of

Erzhilansay, right bank of the upper reaches of Ully-Dzhilanchik River, Turgai Depression, Karaganda Province, Kazakhstan.

28. Khosatzky L.I. 1958c. Present and past distribution of turtles in the USSR. In: Problemy zoogeografii sushhi. Materialy soveshchaniya. Lvov University, Lvov: 319–324. [In Russian]

This short paper reviews present and past distributions of turtles in the USSR. Remains of fossil marine turtles are known from Mesozoic and Paleogene deposits of both European and Asiatic parts of the USSR. Remains of non-marine Mesozoic and Paleogene turtles are known from Asiatic part of the USSR, whereas Neogene species are known predominantly from the European part and some regions of Kazakhstan. The following turtle groups of turtles are discussed: *Yaxartemys longicauda* (Late Jurassic of Kazakhstan); Trionychidae (Cretaceous of the Asiatic part of the USSR; Paleogene of Kazakhstan; Neogene of the European part of the USSR; Present of Far East); Emydidae (*Clemmys*, Neogene-Present of the European part of the USSR and Turkmenia; several genera close to *Clemmys* and *Echmatemys*, Paleogene and Neogene of Kazakhstan, Paleogene of Primorye and Neogene of Baikal; *Emys*, Neogene-Present of the European part of the USSR, Present of Kazakhstan and Middle Asia); Dermatemydidae and Baënidæ (from the Cretaceous and Paleogene of Kazakhstan and Middle Asia); and Testudinidae (*Stylemys*, Oligocene-Miocene of Kirghizia; *Testudo*, Oligocene of Kazakhstan, Neogene-Present of the European part of the USSR, Kazakhstan, and Middle Asia).

29. Khosatzky L.I. and Alekperov A.M. 1958. Shells of turtles from the archeological excavations in Mingechaur. *Uchenye Zapiski Azerbaydzhanskogo Gosudarstvennogo Universiteta*, 12 (for 1957): 101–112. [In Russian]

This paper reports discoveries of turtle shells of *Testudo graeca* of the Bronze Age from the archeological sites of Mingechaur (Azerbaijan). Several mostly complete shells are described and illustrated. These shells differ from modern *T. graeca* of Azerbaijan in relative height of the shell, degree of convexity of the carapaces and the egg-like shape (narrowed posteriorly) of the carapace discus (without peripherals) in dorsal view. On the other hand, in these and some other characters, Mingechaur turtles are similar to a West Caucasian form of *T. graeca*. Based on these observations, it is concluded that Mingechaur turtles lived in forest or forest-bush biotopes like modern *T. graeca* from Western Caucasus. In contrast, modern *T. graeca* of Azerbaijan live in more open habitats.

30. Khosatzky L.I. 1959a. Paleontological significance of fossil remains of turtles. In: Voprosy biostratigrafii kontinental'nykh tolshch. Trudy III sessii Vsesoyuznogo paleontologicheskogo obshchestva. Gosudarstvennoe nauchno-tekhnicheskoe izdatelstvo literatury po geologii i okhrane nedr, Moscow: 104–107. [In Russian]

This short paper briefly discusses significance of some features of turtles important for ecological-functional analyses of their morphology and for reconstruction of the historical sequence of the appearance of different turtles in the course of evolution. These features are size of the body, shape of the shell and thickness of its bones, development of hinges, and reduction of the shell elements, strengthening of the shell by keels and thickenings, and general patterns of the mosaics of shell elements.

31. Khosatzky L.I. 1959b. The body surface temperature of some amphibians and reptiles. *Vestnik Leningradsk-*

ogo Universiteta. Seriya Biologicheskaya, 21(4): 92–105. [In Russian]

This paper presents the results of the study of surface temperature in different parts of the body of some amphibians and reptiles, including four species of turtles: *Testudo graeca*, *T. horsfieldi*, *Emys orbicularis*, and *Clemmys caspica*. In *T. graeca* and *T. horsfieldi*, the general pattern of distribution of the body surface temperature at 14 measurement points was similar and 0.4–1.5 °C above ambient temperature. In *E. orbicularis*, the body surface temperatures did not much differ from air temperature, being 0.1–0.2 °C above the latter (in *T. graeca* and *T. horsfieldi* this value is 1.0–0.5 °C). The lowest body surface temperatures were recorded in *C. caspica*, and were 0.5–1.0 °C below ambient temperatures on the non-shell parts of the body (excluding the head). It is hypothesized that the relatively low body surface temperature of freshwater turtles is connected with their ability of their evaporate water through their skin. The turtle shell plays an important role in thermoregulation by acting as a kind of thermos, preventing the body from rapid overheating and cooling and allowing turtles to stay in high temperatures longer than other reptiles. It is hypothesized that the turtle shell could have evolved as a protection not only from enemies, but also from adverse climatic factors.

32. Khosatzky L.I. 1959c. The doctrine about life forms of extinct and modern organisms. In: Voprosy paleobiologii i biostratigrafii. Trudy II sessii Vsesoyuznogo paleontologicheskogo obshchestva. Gosudarstvennoe nauchno-tekhnicheskoe izdatelstvo literatury po geologii i okhrany nedr, Moscow: 145–157. [In Russian]

This paper is devoted to the doctrine about life forms of extinct and modern organisms. Among other things, the paper contains examples of life forms of modern and extinct turtles. These life forms are distinguished by different sizes and shapes of the plastron in relation to the carapace and presence/absence of hinges in the plastron and correspondingly different levels of protection and activity.

33. Khosatzky L.I. and Tolmacheva N.V. 1959. Peculiarities of ecological-physiological specializations of freshwater and terrestrial turtles. In: Soveshchanie po ekologicheskoy fiziologii. Tezisy dokladov. Moscow-Leningrad. Publishers of the Academy of Sciences of the USSR: 116–119. [In Russian]

This short paper presents data on ecological-physiological features of freshwater (*Emys orbicularis*, *Clemmys caspica*) and terrestrial (*Testudo graeca*, *T. horsfieldi*) turtles. It is shown that the hydro-tactic optimum in the freshwater species is considerably higher than in the terrestrial ones. The freshwater species preferred sand with 20–30% humidity, whereas the terrestrial ones, which preferred 5–10%. The level of gas exchange in the terrestrial species is somewhat higher than in the freshwater ones. The same is true about levels of haemoglobin (*T. graeca*–75, *T. horsfieldi*–60, *E. orbicularis*–52, *C. caspica*–35). The body temperature of the examined turtle species exceeds the ambient temperature for 1.2–0.6 °C. The turtle shell, having thermal insulation properties, protects turtles from overly rapid heating or cooling. The thermotactic optimum equals in average: 29 °C (*T. horsfieldi*), 23 °C (*T. graeca*), 20 °C (*C. caspica*), and 18 °C (*E. orbicularis*). Terrestrial turtles adapted to arid climates are more tolerant of low humidity and high temperature.

34. Borisov B.A., Il'inskaya I.A., Martinson G.G. and Khosatzky L.I. 1963. The Upper Cretaceous and Paleogene-Neogene of Zaysan Depression. In: Mate-

rialy po regional'noy stratigrafii SSSR. Gosudarstvennoe nauchno-tekhnicheskoe izdatelstvo literatury po geologii i okhrane nedr SSSR: 240–251. [In Russian]

This paper presents preliminary results of a study of fossil material collected from the Upper Cretaceous and Paleogene-Neogene deposits of Zaysan Depression (Eastern Kazakhstan) in 1958–1960. The turtle material (shell fragments) comes from the following svitas (formations): middle Eocene: Obayala Formation: Emydidae, *Testudo*, Trionychidae; lower Oligocene: lower Aksyir Formation (Dermatemydidae, Emydidae, *Testudo*, Trionychidae); upper Aksyir Formation (Emydidae, genus close to *Trachemys*, Trionychidae); middle Oligocene: Kusto Formation (genera close to *Echmatemys* and *Trachemys*; Trionychidae); lower–middle Miocene: Akzhara Formation (*Echmatemys*, Emydidae, *Testudo*); middle–upper Miocene: Sarybulak Formation (*Testudo*).

35. Khosatzky L.I. and Kuznetsov V.V. 1963. A new finding of the Neogene turtle in Northern Tian Shan. In: Materialy po istorii fauny i flory Kazakhstana. T. 4. Academy of Sciences of the Kazakh SSR, Alma-Ata: 3–11. [In Russian]

This paper describes and illustrates an imprint of the plastron of *Testudo hegenica* from the middle–upper Miocene of Karkara River valley, Chul'adyr Ridge, Kegen District, Alma-Ata Province, Kazakhstan. Examination of the three available specimens of this species allows determination their ages (based on growth rings) and analysis of ontogenetic features of this species.

36. Khosatzky L.I. 1964. Biomechanics of the shell of amphibians and reptiles. Voprosy gerpetologii. Materialy herpetologicheskoy konferentsii (12–14 October 1964, Leningrad). Leningrad State University, Leningrad: 72–74. [In Russian]

This abstract discusses biomechanics of the shell (armor) of amphibians and reptiles, including turtles. The mechanical protection and support of the body are considered to be the main roles of the shell. These functions are dependent on the mechanical properties of the shell as a whole, on the mechanical properties of its parts, and on the microstructure and materials of which the shell is constructed. The mechanical properties of the shell as a whole are largely determined by its shape. Turtles are used as an example of various shell designs that are correlated with natural history and locomotory style. The trade-offs between the evolution of the shell in terms of passive protection, reduced mobility of the body, and increased energy costs are discussed.

37. Khosatzky L.I. 1965a. Terrestrial reptiles of the Cenozoic of Soviet Asia. In: Tezisy dokladov k mezhdovomstvennomu soveshchaniyu po kontinental'nym otlozheniyam mezozoya i kaynozoya sovetskoy Azii i ikh biostratigrafiya (3–5 February 1965). Leningrad: 35–37. [In Russian]

This is an abstract version of the paper of Khosatzky (1967a).

38. Khosatzky L.I. 1965b. Some peculiarities of the heat exchange in turtles. In: Gerpetologiya. Nauka, Tashkent: 36–39. [In Russian]

This paper presents results of the experimental study of the thermal insulation properties of the shell of tortoises *Testudo graeca* and *T. horsfieldi*. It is shown that at an air temperature of 20–23 °C,

the body surface temperature in different parts, including shell, exceeds that temperature by 0.1–0.6 °C. As air temperature increases up to 30–32 °C, the body surface temperature on the limbs, head, and tail exceeds air temperature by 3–5.5 °C, while temperature at the shell is lower than ambient temperature by 1–6 °C. Thus the shell acts as a powerful thermal insulator that allows turtles to withstand considerable fluctuations in the thermal conditions of the environment relatively easily.

39. Khosatzky L.I. 1965c. Phylogenetic significance of the turtle shell construction. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, 17: 196–227. [In Russian]

This paper presents results of an ecological-functional analysis of the morphological features of the turtle shell. The following constructional features of the shell were examined in multiple turtle species: shape (outline) of the carapace and plastron; height/length ratio, size of the axillary and inguinal notches, presence of movable elements, spikes and projections. In accordance with the provisions of structural mechanics, a constructional function for the shell characteristics of various turtles that determine their resistance to mechanical stress is demonstrated. It is shown that these morphological characters are connected with features of turtle ecology and natural history. It is stated that since the shell is the most important element of the organization of turtles, evolutionary changes affect this particular structure. Based on the design of the shell, a hypothesis of the terrestrial origin of turtles is suggested. According to this hypothesis, the turtle shell appeared in terrestrial conditions as a protection from predatory reptiles. A complete shell, like those of primitive turtles, is characteristic for terrestrial turtles, including modern ones. With the advent of carnivorous mammals and birds, the shell has lost its exceptional significance. This has led to multiple transitions of various turtles from terrestrial to aquatic environment and resulted in considerable reduction of the shell.

40. Rozhdestvensky A.K. and Khosatzky L.I. 1965. Terrestrial vertebrates of the Late Mesozoic of the Soviet Asia. In: Tezisy dokladov k mezhdovomstvennomu soveshchaniyu po kontinental'nym otlozheniyam mezozoya i kaynozoya sovetskoy Azii i ikh biostratigrafiya (3–5 February 1965). Leningrad: 12–15. [In Russian]

This is an abstract version of the paper of Rozhdestvensky and Khosatzky (1967).

41. Khosatzky L.I. 1966a. New data on the fauna of reptiles of the Pliocene of Moldavia. In: Materialy nauchnoy konferentsii po itogam issledovatel'skoy raboty za 1965 god. Kartya moldovenyaskie, Kishinev: 129–131. [In Russian]

This abstract reports new discoveries of reptiles from the Pliocene of Moldavia, including different forms of terrestrial and freshwater turtles. These are several species of the genus *Testudo*, species of the genera *Clemmys*, *Geoemyda*, *Emys* and *Chelydra* (also reported from the Pliocene of Ukraine). A new discovery of *Chelydra* from Lucheshty (Moldavia) is represented by the anterior part of the carapace. A semi-hinged connection between the posterior part of the plastron and the anterior part of the plastron and carapace is reported for *Geoemyda* (probably females).

42. Khosatzky L.I. 1966b. About a gigantic Mesozoic representative of trionychids and several features of

the shell of these turtles. In: Pozvonochnye zhivotnye Sredney Azii. Fan, Tashkent: 150–157. [In Russian]

This paper presents a description of a new species of trionychid, *Trionyx zakhidovi* Khosatzky, based on a giant, approximately 20 cm long femur (the holotype) and a referred, posterior part of a large trionychid carapace with an estimated length of about 70 cm from the Upper Cretaceous (Turonian) deposits near Kyrkkuduk Well, southern Kazakhstan.

- 43. Khosatzky [Khozatsky] L.I. et Mlynarski M. 1966a.** *Agrionemys*—nouveau genre de tortues terrestres (Testudinidae). *Bulletin de l'Academie Polonaise des Sciences. Serie des sciences biologiques*, **14**(2): 123–125.

This paper establishes a new genus *Agrionemys* for *Testudo horsfieldi* Gray, 1844.

- 44. Khosatzky L.I. and Mlynarski M. 1966b.** Fossil tortoises of the genus *Geoemyda* Gray, 1834 (s. lat.) of Europe. *Acta Zoologica Cracoviensia*, **11**(13): 397–421.

This paper presents a revision of the fossil turtles of the genus *Geoemyda* sensu lato (Emydidae) of Europe based on examination of collections in Germany, Czechoslovakia, Hungary, Romania and the USSR. *Geoemyda* sensu lato is divided into five subgenera (two of which are new): new subgenus *Geiselemys* Khosatzky et Mlynarski (type species—*Geoemyda ptychogastroides* Hummel, 1935); *Geoemyda* Gray, 1854; *Heosemys* Stejneger, 1902, *Rhinoclemys* Gray, 1863, and new subgenus *Spinemys* Khosatzky et Mlynarski (type species—*Geoemyda pidoplickai* (Khosatzky, 1946)). The *Geoemyda* sensu lato of Europe are distributed among subgenera *Geiselemys* (*G. ptychogastroides* and *G. saxonica* Hummel, 1935, both from the Middle Eocene of Germany), *Heosemys* (*G. eureia* (Wegner, 1913), Upper Miocene of Poland; *G. mossoczyi* Mlynarski, 1964, Upper Pliocene of Poland), and *Spinemys* (*G. pidoplickai*, Upper Pliocene of Ukraine; and *G. malustensis* (Macarovici et Vanca, 1960), Upper Pliocene of Romania). *Geoemyda headonensis* (Hooley, 1905) from the Middle Eocene of England and *Clemmydopsis sopronensis* Boda, 1927 from the Lower Pliocene of Hungary are considered as a species of doubtful systematic position. In addition, possible ecological and climatic adaptations of fossil *Geoemyda* sensu lato as well as their phylogenetic position are discussed.

- 45. Khosatzky L.I. 1967a.** Cenozoic terrestrial reptiles of the Asiatic part of the USSR. In: Stratigrafiya i paleontologiya mesozoyskikh i paleogen-neogenovykh kontinental'nykh otlozheniy aziatskoy chasti SSSR. Nauka, Leningrad: 215–218. [In Russian]

This paper presents a review of discoveries of terrestrial reptiles from the Cenozoic of the Asiatic part of the USSR, including turtles from the Paleogene of Kazakhstan (Zaysan Depression; Aral-Turgay Depression: Emydidae, Trionychidae and Testudinidae) and Central Kyzylkum (Altyn Tau), early Oligocene of Kazakhstan (Aktau: Emydidae and Trionychidae), Oligocene of Kirghizia (Issyk Kul' Lake: *Stylemys*), late Oligocene to early Miocene of Kazakhstan (Askazansor, Beleutty, Chu, Karakoin, Sary Su: Emydidae and Trionychidae; Agyspe: *Chelonia* and *Testudo*), Eocene of Primorye (Artem: Emydidae), Neogene of Kazakhstan (Zaysan Depression: freshwater and terrestrial turtles); Miocene of Kazakhstan (Betekey: *Chelydra*; Betekey, Kegen, Kushuk, Turme: *Testudo*; Pavlodar: Trionychidae and other freshwater turtles; Ustyurt: Testudinidae), Tajikistan (Magian: *Testudo*), Baikal (Olkhon: Emydidae).

- 46. Khosatzky L.I. 1967b.** Skin respiration in aquatic turtles. In: Vidovyye i prirodno-klimaticheskiye adaptatsii organizma zhivotnykh. Fiziologo-geneticheskiye issledovaniya. Referaty dokladov k III Vsesoyuznomu soveshchaniyu po ekologicheskoy fiziologii, biokhimi i morfologii. Institute of Cytology and Genetics of the Siberian Branch of the Academy of Sciences of the USSR, Novosibirsk: 135–138. [In Russian]

This short paper presents the results of a study of gas exchange and skin morphology in some aquatic turtles. It is shown that adult individuals of *Trionyx sinensis* use the buccal-pharyngeal apparatus and their skin for respiration when under water. During one hour they consume 1.23–1.57 mg of O₂ per liter of water, of which 0.76–0.96 mg of O₂ are consumed via the skin. It is assumed that the intensification of the skin respiration is connected with an active way of life of these carnivorous turtles and results in their ability to stay under water for a long time. Morphologically, this ability is conferred by the special structure of the skin—the lack of horny scutes, thin epidermis and vascularization of the dermal skin layer.

- 47. Rozhdestvensky A.K. and Khosatzky L.I. 1967.** Late Mesozoic terrestrial vertebrates of the Asiatic part of the USSR. In: Stratigrafiya i paleontologiya mesozoyskikh i paleogen-neogenovykh kontinental'nykh otlozheniy aziatskoy chasti SSSR. Nauka, Leningrad: 82–92. [In Russian]

This paper presents a review of discoveries of Late Mesozoic vertebrates of the Asiatic part of the USSR, including turtles from the Late Jurassic of Kazakhstan (*Yaxartemys*), Early Cretaceous of Transbaikalia, Late Cretaceous of Kazakhstan (Shakh-Shakh: Dermatemydidae, Trionychidae), Central Kyzylkum (Dzharakuduk) and Western Fergana (Kansai: Dermatemydidae, Trionychidae and others).

- 48. Turdakov F.A., Toktosunov A.T. and Khosatzky L.I. 1967.** About finding of a soft-shelled turtle in the Chuy Valley of Kirghizia. *Trudy Kirgizskogo Gosudarstvennogo Universiteta. Seriya Biologicheskije Nauki*: 103–114. [In Russian]

This paper presents description of a trionychid specimen (probably, *Trionyx sinensis*), caught in 1961 on the territory of Kirghizia (18 km North from Frunze). It is hypothesized that this turtle was introduced to Kirghizia from the Far East. However, there is also some evidence of possible natural habitats of trionychids in Kirghizia at the beginning of the 20th century.

- 49. Birman A.S., Zhegallo V.I., Rastsvetaev L.M., Khosatzky L.I. and Shevyreva N.S. 1968.** To the history of the fauna of vertebrates of Eastern Kopetdag. *Byulleten' Moskovskogo Obshchestva Ispytateley Prirody. Otdel Geologicheskij*, **43**(1): 159–160. [In Russian]

This is a short version of the paper of Birman et al. (1971).

- 50. Khosatzky L.I. 1968a.** Oligomerization in the evolution of the shell of vertebrates. *Ezhgodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **18**: 367–369. [In Russian]

This paper is devoted to the discussion of general problems of oligomerization (i.e., the decrease in the number of morpho-

functional units in a system) of armor structures in vertebrates, including turtles. It is demonstrated that the oligomerization is the main tendency in the evolution of the turtle shell. In the more specialized aquatic turtles, this process was more intense and has been almost completed. In the more primitive and conservative terrestrial turtles this process is continuing. This explains higher frequency of occurrence of anomalies of bony plates in terrestrial turtles, than in aquatic ones. These anomalies are manifested in the appearance of additional plates that, probably, recapitulate the ancestral condition.

51. Khosatzky L.I. 1968b. A species and intraspecies divisions in amphibians and reptiles. In: *Gerpetologiya Sredney Azii*. Fan, Tashkent: 5–7. [In Russian]

The author suggests distinguishing three gradations of intraspecies diversity: 1) ecological forms, which have only ecological differences; 2) biological forms, which have ecological-physiological differences; 3) subspecies, which have morphological differences within species. Based on the ecological-morphological differences, two populations of *Testudo graeca*, living in the Black Sea coast and in the Caspian Sea coast, are considered to be subspecies.

52. Khosatzky L.I. 1968c. Skin respiration of some reptiles. In: *Gerpetologiya Sredney Azii*. Fan, Tashkent: 22–24. [In Russian]

This short paper reviews data on skin respiration in reptiles, including soft-shelled turtles.

53. Khosatzky L.I. 1969. The structure of the shell of vertebrates in light of bionics. In: *Primeneniye matematicheskikh metodov v biologii*. T. 4. Leningrad State University, Leningrad: 116–118. [In Russian]

This abstract discusses morphology of the shell of vertebrates, including turtles. The vaulted carapace provides basic mechanical protection, whereas the plastron plays a role of supports for it. The strongest shells are characterized by rounded arches or parabolic outlines. However such arches are less stable. Low shells have reduced strength, but they have more aero- and hydrodynamic. The mechanical strength of the shell depends on the type of connection (sutures) between the plates. The sutures play the role of shock absorbers and dampeners of harmful effects.

54. Masharskiy E.A. and Khosatzky L.I. 1969. A vibrometric analysis of the constructive heterogeneity of the turtle shell. In: *Primeneniye matematicheskikh metodov v biologii*. T. 4. Leningrad State University, Leningrad: 118–120. [In Russian]

This abstract presents results of a vibrometric study of the shells of aquatic and terrestrial turtles. It is shown that in different parts of the shell, the elastic response to vibration is different and shows a mosaic pattern of distribution. The highest values of elastic response were observed in the dome part of the carapace. The morphological heterogeneity of the bony and keratinous basis of the shell causes unequal distribution of mechanical vibration and ensures their rapid dampening.

55. Ivanjev L.I. and Khosatzky L.I. 1970. Remains of Neogene reptiles and amphibians of Olkhon Island of Baykal Lake. *Izvestiya Vostochno-Sibirskogo Otdela Geograficheskogo Obshchestva SSSR*, **67**: 153–158. [In Russian]

This paper reports discoveries of amphibians and reptiles from the Neogene deposits of Tagay locality in Olkhon Island of Baykal

Lake. The diagnostic turtle material from this locality includes more than 200 plates of the shell and bones of non-shell postcrania. The analysis of this material shows that it belongs to a new genus and species of Emydidae, provisionally named *Baicaemyd gracilis* Khos.

56. Khosatzky L.I. and Tarabukin B.A. 1970. About shells of Maeotian turtles found in the MSSR. *Uchenye Zapiski Tiraspol'skogo Gosudarstvennogo Pedagogicheskogo Instituta*, **17**: 64–70. [In Russian]

This paper describes and illustrates two incomplete shells of *Testudo bessarabica* Riabinin, 1918 from the Maeotian locality Chimishliya of Moldavia. Other undescribed specimens of this species from different localities in Moldavia and Ukraine are also mentioned.

57. Khosatzky L.I. and Tofan V.E. 1970a. Past and present state of the herpetofauna of Moldavia. *Uchenye Zapiski Tiraspol'skogo Gosudarstvennogo Pedagogicheskogo Instituta*, **20**: 157–181.

This paper reviews data on modern and extinct amphibians and reptiles of Moldavia, including old and new discoveries of turtles. These turtle discoveries come from the following localities: Kalfa (middle Sarmatian; new species of *Testudo*, Emydidae, *Trionyx* sp.); Lapushna (middle Sarmatian; *Chelydra* sp., *Clemmys* sp., *Testudo* sp.); Raspopena (middle or late Sarmatian; *Testudo* sp.); Varnitsa (middle or late Sarmatian; *Clemmys*, *Testudo*); Chimishliya (Maeotian; *T. bessarabica*); Chobruchi (Maeotian; *Clemmys* sp., *Testudo bessarabica* = *T. tarakliensis*); and Pliocene localities (*Chelydra*, *Clemmys*, *Emys*, *Geoemyda*, *Testudo*). The only modern turtle species in the fauna of Moldavia is *Emys orbicularis*.

58. Khosatzky L.I. and Tofan V.E. 1970b. History and ways of formation of the herpetofauna of Moldavia. In: *Materialy dokladov Pervoy respublikanskoy mezhvuzovskoy nauchno-prakticheskoy konferentsii*. Tiraspol State Pedagogical Institute, Kishinev: 176–179. [In Russian]

This short paper is devoted to the history of the herpetofauna of Moldavia, including turtles, which are represented by the following forms: *Emys orbicularis* in the modern herpetofauna; *Trionyx*, *Chelydra*, *Clemmys* and *Testudo* in Kalfa and Varnitsa faunistic assemblages (Sarmatian); *Clemmys* and *Testudo bessarabica* Riab. in the Maeotian; several forms of *Testudo*, including the subgenus *Geochelone*, which also includes some Miocene species, *Chelydra*, *Clemmys*, *Geoemyda*, *Emys* in the Pliocene (fauna of the Russian type).

59. Khosatzky L.I., Tolmacheva N.V. and Shcheglova A.I. 1970. Some peculiarities of the water metabolism in turtles. In: *Adaptatsiya organizma cheloveka i zhivotnykh k ekstremal'nym prirodnym faktoram sredy*. Materialy Symposiuma (12–17 October 1970). Adaptatsiya k aridnoy zone. Zimnyaya spyachka. Institute of Physiology of the Siberian Branch of the Academy of Sciences of the USSR: 127–129. [In Russian with English summary]

This abstract presents results of an experimental study of water metabolism (evaporation and consumption of water through the skin) in *Clemmys caspica*. Two groups of animals were kept under

different conditions for 15 days. The first ("dry") group was kept without water, whereas the second ("water") group was kept permanently in water. Both groups were deprived of food. The "dry" group turtles lost 300 g of their weights, which was caused by evaporation of water through the skin. In the "water" group of turtles body weight increased within this period by 100 g, which was due to the absorption of water by the skin. The metabolic rate in both groups did not change significantly from the initial rate.

60. Trusova V.K. and Khosatzky L.I. 1970. The role of the shell in thermoregulation of turtles. In: *Adaptatsiya organisma cheloveka i zhivotnykh k erestremal'nym prirodnyim faktoram sredy. Materialy Simposiuma (12–17 October 1970). Teploobrazovanie i termoregulyatsia. Adaptatsiya k kholody.* Institute of Physiology of the Siberian Branch of the Academy of Sciences of the USSR: 120–122. [In Russian with English summary]

This abstract presents results of an experimental study of the role of the turtle shell in thermoregulation using *Agrionemys horsfieldi*, *Testudo graeca*, *Emys orbicularis* and *Clemmys caspica*. In all turtles the shell better protects the organism from overcooling than overheating. Terrestrial turtles are better able to withstand the effects of high temperatures and fluctuations of ambient temperatures than freshwater turtles. In freshwater turtles at rest the body temperature only slightly exceeds the ambient temperature, due to poorer heat retention of their shells as compared with terrestrial turtles, and also due to some evaporation of water from the non-shell parts of the body surface. This evaporation during their stay on land results in a decrease in body temperature. In terrestrial turtles such evaporation is negligible and their thermal balance is not subjected to considerable fluctuations under conditions of variable humidity. For this reason, terrestrial turtles are able to endure considerable drought under high ambient temperature. During exposure to the sun, the increase of body temperature is slower in terrestrial turtles than in freshwater ones.

61. Verzilin N.N., Khosatzky L.I., Vu Din' Li and Nessov L.A. 1970a. New paleontological data about border between the Lower and Upper Cretaceous in Fergana. *Vestnik Leningradskogo Universiteta*, **18** (Geologiya, Geografiya, 3): 43–50. [In Russian]

In this paper new paleontological data about turtles are used for establishing the boundary between the Lower and Upper Cretaceous in Fergana. These turtles come from the Albian Alamyshik Formation near Klauzlin settlement, South-Eastern Fergana, Kirghiz SSR and represented by *Trionyx* (Trionychidae), a member of Dermatemydidae similar to *Adocus*, and a turtle similar to genera *Sinemys* (?Dermatemydidae), *Osteopygis* (Toxochelyidae) and *Plesiochelys* (Plesiochelyidae).

62. Verzilin N.N., Martinson G.G. and Khosatzky L.I. 1970b. New data on paleontological dating of Upper Jurassic deposits of Fergana Depression. *Doklady Akademii Nauk SSSR*, **191**(2): 407–409. [In Russian]

This paper reports new paleontological material that is important for dating Upper Jurassic deposits of the Fergana Depression (Kirghiz SSR). These materials include fragmentary remains of primitive turtles of the order Amphichelydia from the middle part of the Balabansai Formation on the left bank of Naryn River, near town of Tashkumyr, in the area of Sarakamyshsai. This turtle material

belongs to the genus *Glyptops* (Pleurosternidae) and to the family Plesiochelyidae.

63. Birman A.S., Zhegallo V.I., Rastsvetaev L.M., Khosatzky L.I. and Shevyreva N.S. 1971. About finding of Pliocene vertebrates in the molasse deposits of Eastern Kopetdag. *Byulleten' Moskovskogo Obshchestva Ispytateley Prirody. Otdel Geologii*, **46**(2): 99–106. [In Russian]

This paper reports discoveries of Pliocene vertebrates from the molasse deposits of Eastern Kopetdag, Turkmenia. Among these findings is a single turtle specimen (a part of the carapace and a fragment of caudal peripheral plate) of *Testudo horsfieldi*.

64. Khosatzky L.I. and Kuznetsov V.V. 1971. A freshwater turtle of the Oligocene of the Dzungarian Alatau. In: *Materialy po istorii fauny i flory Kazakhstana. T. 5.* Nauka, Alma-Ata: 34–51. [In Russian]

This paper describes a new species of turtle of the family Emydidae—*Clemmys iliensis* Khosatzky et Kuznetsov based on an anterior part of the shell and numerous shell fragments from Aktau locality (Dzungarian Alatau, Kazakhstan, upper part of the Aktau Formation, early Miocene).

65. Khosatzky L.I. and Mlynarski M. 1971. Chelonians from the Upper Cretaceous of the Gobi Desert Mongolia. *Palaentologia Polonica*, **25**: 131–144.

This paper is devoted to the description of some turtle material collected by Polish-Mongolian Paleontological Expeditions (1963–1965) and by earlier Soviet Expeditions (1946, 1948, 1949) from the Upper Cretaceous deposits of the Gobi Desert, Mongolia. The material is attributed to the following turtle taxa: *Mongolemys elegans* Khosatzky et Mlynarski (a new genus and species of Dermatemydidae), *Trionyx* sp. a (Trionychidae) and Amphichelydia gen. et sp. indet. from Tsagan Khushu, *Tsaotanemys* cf. *rugosa* Bohlin, 1953 (Dermatemydidae) and *Trionyx* sp. from Ulan Bulak and a large form of *Trionyx* sp. from Khar Teg. The authors discuss the composition of the family Dermatemydidae, from which they exclude genera such as *Adocus* Cope, 1868, *Tretosternon* Owen, 1842 and *Anosteira* Leidy, 1871 and conclude that *Mongolemys* in some respects is intermediate between the Dermatemydidae and Emydidae and stays close to the ancestral forms of the extant predominant group Neochelydia. *Mongolemys elegans* is considered to be a herbivorous turtle based on the similarity of its jaws with *Dermatemys* Gray, 1847 (type genus of the Dermatemydidae). It is assumed, that *Mongolemys* lived in shallow, warm basins overgrown by exuberant vegetation, whereas the trionychids and Amphichelydia gen. et sp. indet. lived in deeper basins.

66. Alekperov A.M. and Khosatzky L.I. 1972. Constructive features of the shell of the Greek tortoise. *Uchenyye Zapiski Azerbaydzhanskogo Gosudarstvennogo Universiteta. Seriya Biologicheskikh Nauk*, **4** (for 1971): 43–49. [In Russian]

This paper presents a comparative analysis of the constructional features of the shell of *Testudo graeca* from the western (Black Sea coast) and eastern (Caspian Sea coast) parts of the Caucasus. The eastern form most closely matches the characteristics of *T. graeca ibera* Pallas, 1814, whereas the western form looks more similar to *T. graeca graeca* and differs from the eastern form in its more vaulted carapace and relatively short plastron. In addition, these

two forms demonstrate statistically significant differences in the shape of the nuchal, suprapygial, costal, peripheral and plastral plates of the shell. The evolution of the distinctive features of *T. graeca iberica* was probably connected with arid conditions in its habitats in the Eastern Caucasus and a transition to a more burrowing lifestyle. Finally, anomalies of the bony and keratinous shell of both forms of *T. graeca* are reported.

- 67. Khosatzky L.I. 1972.** Reptiles. In: Stratigrafia SSSR. Yurskaya sistema. Nedra, Moscow: 440–442. [In Russian]

This paper briefly reviews Jurassic reptiles from the USSR, including two records of turtles (Amphichelydia): *Yaxartemys* (Thalassemydidae) from the Late Jurassic of Karatau (Southern Kazakhstan) and a representative of the genus *Glyptops* (Pleurosternidae) from Tashkumyr (Fergana).

- 68. Khosatzky L.I. and Narmandakh P. 1973.** A terrestrial Miocene turtle from Western Mongolia. *Byulleten' Moskovskogo Obshchestva Ispytateley Prirody. Otdel Geologii*, 48(1): 153. [In Russian]

This abstract reports a new species of tortoise *Geochelone devjatkini* Khosatzky et Narmandakh, based on several incomplete shells from the middle–late Miocene of the Oshin Formation of Western Mongolia.

- 69. Khosatzky L.I. and Sukhanov V.B. 1973.** Morphometric parameters of the turtle shell. Voprosy gerpetologii. III Vsesoyuznaya gerpetologicheskaya konferentsiya. Avtoreferaty dokladov (1–3 February 1973, Leningrad). Nauka, Leningrad: 192–195. [In Russian]

This short paper proposes a consistent nomenclature of keratinous and bony elements of the turtle shell, standards for the main measurements of the shell and its elements and some indexes.

- 70. Nessov L.A. and Khosatzky L.I. 1973.** Early Cretaceous turtle from the south-eastern Fergana. Voprosy gerpetologii. III Vsesoyuznaya gerpetologicheskaya konferentsiya. Avtoreferaty dokladov (1–3 February 1973, Leningrad). Nauka, Leningrad: 132–133. [In Russian]

This abstract establishes a new turtle subfamily Kirgizemyinae Nessov et Khosatzky of the family Toxochelyiidae, a new genus *Kirgizemys* Nessov et Khosatzky and a new species *Kirgizemys exaratus* Nessov et Khosatzky, based on nuchal plate (holotype, figured) and about 500 shell fragments from Klauzdzin locality, near Klauzdzin settlement, Kirghiz SSR; upper part of Alamyshik Formation, Albion, Lower Cretaceous. In addition to *K. exaratus*, the new genus includes *K. acutus* (Bohlin, 1953), *K. kansuensis* (Bohlin, 1953), and *K. latilimbata* (Bohlin, 1953) from the Cretaceous of China (Gansu).

- 71. Khosatzky L.I., Kuznetsov V.V. and Leonov A.V. 1974.** A new species of Miocene turtle of the south-east of Kazakhstan. In: Materialy po istorii fauny i flory Kazakhstana. T. 6. Nauka, Alma-Ata: 22–30. [In Russian]

This paper describes a new species of tortoise of the genus *Testudo* sensu lato—*Testudo tekessa* Khosatzky et Kuznetsov based on an incomplete shell from the middle Miocene Kapkasskaya Formation of southern slope of Basulytau mountains, left edge of the Tekess Depression, Kazakhstan.

- 72. Khosatzky L.I. [Khazatsky] 1975.** Amphibians and reptiles. In: Stratigrafiya SSSR. Paleogenovaya sistema. Nedra, Moscow: 439–441. [In Russian]

This paper reviews data on discoveries of amphibians and reptiles from the Paleogene deposits of the USSR, including those of turtles (subclass Chelonia). Cenozoic and Paleogene turtles belong to five orders, of which only three are known from the USSR: Chelonioida, Trionychoidea, and Cryptodira. Chelonioida are reported from the middle Eocene of Kokturnak (Kazakhstan), middle Oligocene of Agyspe (*Chelonia aralis* Khos.; Kazakhstan), lower Oligocene of Ordzhonikidze (*Chelonia caucasica* Riab.), Paleogene deposits of Middle Povolzhye, Eocene deposits of Ukraine and Oligocene–Miocene of Azerbaijan. Trionychoidea are reported from the lower Eocene–middle Oligocene of Zaysan Depression (Kazakhstan), Oligocene deposits of Kazakhstan: Ili Depression (Dzhungarsky Aktau), Betpakdala, right bank of the Sarysu River, in Turgay Depression. Cryptodira are represented by *Clemmys* (Emydidae) from the Far East (near Artem Town; late Eocene–early Oligocene); *Cl. iliensis* Khos. et Kuzn. from Dzhungarsky Alatau (Aktau) and *Cl. turgaica* Kuzn. from Myneske-Suek (both from the middle Oligocene of Kazakhstan); *Cl. kazakhstanica* Khos. from Betpakdala and Kzyl Kiya (Oligocene–Miocene of Kazakhstan); turtles close to genera *Trachemys* and *Deirochelys* (late Oligocene of Zaysan Depression); Chelydridae from the Paleogene and Neogene of Zaysan Depression; Testudinidae: representatives of *Geochelone* and, probably, *Hadrianus* from the lower Eocene of Zaysan Depression; *Stylemys karakolensis* Riab. from the Oligocene–Miocene of Issyk Kul Lake, and *Geochelone meschethica* (Gab. Et Tschikov.) from the middle-late Oligocene of the Georgian SSR.

- 73. Khosatzky L.I. and Narmandakh P. 1975.** A Miocene turtle from Western Mongolia. In: Iskopyemaya fauna i flora Mongolii. Trudy Sovmestnoy sovetskomo-mongol'skoy paleontologicheskoy ekspeditsii. T. 2. Nauka, Moscow: 110–121. [In Russian]

This paper presents a detailed description of material of *Geochelone devjatkini* Khosatzky et Narmandakh, 1973.

- 74. Nessov L.A. and Khosatzky L.I. 1975a.** Peculiarities of the past and present distribution of pig-nosed and soft-shelled turtles. In: Aktual'nye voprosy zoogeografii. VI Vsesoyuznaya zoogeograficheskaya konferentsiya (September 1975). Tezisy dokladov. Shtiintsia, Kishinev: 170. [In Russian]

This abstract reports the presence of the oldest representatives of carettochelyid turtles in the Late Cretaceous (Cenomanian) of Asia and the oldest representative of the trionyhid turtles in the Early Cretaceous (Albian) of Asia and reconstructs the biogeographic history of these groups.

- 75. Nessov L.A. and Khosatzky L.I. 1975b.** Historical ways of distribution of freshwater and terrestrial turtles. Paleontologiya, paleobiogeografiya i mobilizm. Tezisy dokladov XXI sessii Vsesoyuznogo paleontologicheskogo obshchestva (27–31 January 1975). All-Union Geological Institute, Leningrad: 20–22. [In Russian]

This is an abstract version of the paper of Nessov and Khosatzky (1981b).

- 76. Verzilin N.N., Galibin V.A., Nessov L.A. and Khosatzky L.I. 1975.** About rare elements in bone remains of Meso-Cenozoic turtles. *Doklady Akademii Nauk SSSR*, **224**(3): 681–684. [In Russian]

This paper presents results of a study of distribution of rare elements in osteological remains of Mesozoic and Cenozoic turtles based on analysis of 61 bone specimens from the Cretaceous of Fergana (Kirghizia and Tajikistan) and early Oligocene of Zaysan (Kazakhstan). Considerable differences in the distribution of rare elements occur between material from Fergana and Zaysan. These differences are due to different geochemical conditions of the sedimentation and diagenesis.

- 77. Khosatzky L.I. 1976.** A new representative of trionychids from the Late Cretaceous of Mongolia. In: *Gerpetologiya*. Kubanskiy gosudarstvennyy universitet. Nauchnye trudy. Vypusk 218. Krasnodar: 3–19. [In Russian]

This paper describes a new species of trionychid *Amyda orlovi* Khosatzky based on an incomplete carapace from the Upper Cretaceous (Cenomanian) of Bain Shire, Eastern Gobi, lower part of the Bainshire Formation. This paper also presents the new diagnosis of the genus *Amyda* Schweigger, 1809, which is expanded to include members of the genera *Platypeltis* and *Aspideretes*.

- 78. Verzilin N.N., Galibin V.A., Mironenko O.A., Nessov L.A. and Khosatzky L.I. 1976.** Use of data on rare element distribution in bone remains of Mesozoic and Cenozoic turtles in paleogeography and paleosedimentology. *Geokhimiya*, **11**: 1714–1723. [In Russian with English abstract].

This paper presents results of a study of the amounts of 13 rare elements in 237 samples of osteological remains of fossil turtles from different taxonomic groups and from deposits of different ages of the Fergana, Kyzylkum, Moldavia, Mongolia, Tajikistan, Ukraine and Zaysan, which was determined by the quantitative spectrochemical analysis. It is shown that the enrichment of the bone material in rare elements occurs during diagenesis and depends on the geochemical conditions during sedimentation. Manganese, lead, scandium and beryllium accumulate more actively in a humid climate and ytterbium, yttrium, vanadium, lanthanum and chromium—in an arid climate. Bones of freshwater turtles are more enriched with rare elements than those of the terrestrial ones when found in one locality.

- 79. Khosatzky L.I. 1977b.** System of reptiles and ways of its formation. *Voprosy gerpetologii*. IV Vsesoyuznaya gerpetologicheskaya konferentsiya. Avtoreferaty dokladov (1–3 February 1977, Leningrad). Nauka, Leningrad: 215. [In Russian]

This abstract contains the author's conception of the systematics of Reptilia. In this systematic classification, the class Reptilia belongs to the superclass Sauropsida along with classes Dinosauria, Pterosauria and Aves. Turtles are considered subclass Testudinata (= Chelonia) of the class Anapsida. Testudinata are divided into orders Atheca and Thecophora. It is assumed that turtles are probable derivatives of Procolophonina (subclass of Anapsida). However, if turtles derive from Captorhinia (a hypothesis that is not rejected) they have to be moved in the superclass Therapsida.

- 80. Nessov L.A. and Khosatzky L.I. 1977a.** Turtles of the Mesozoic of the USSR. *Voprosy gerpetologii*. IV Vsesoyuznaya gerpetologicheskaya konferentsiya. Avtoreferaty dokladov (1–3 February 1977, Leningrad). Nauka, Leningrad: 157–159. [In Russian]

This abstract reviews data of the Mesozoic turtles of the USSR: Late Jurassic: Fergana: Tashkumyr, Changtsu: *Plesiochelys* (Plesiochelyidae); Kazakhstan: *Yaxartemys* (Thalassemydidae); Early Cretaceous of Transbaikalia: *Kirgizemys* (Macrobaenidae) and Plesiochelyidae; Aptian of Karakalpakia: unnamed turtles; Albanian of Fergana (Klaudzin or Kylodzhun): *Ferganemys* (Adocidae); *Kirgizemys* (Toxochelyidae), *Trionyx* (Trionychidae); Late Cretaceous: Cenomanian of Central and South-Western Kyzylkum: *Lindholmemys* (Dermatemydidae); Early Turonian of Kyzylkum: Adocidae, *Anatolemys* (Toxochelyidae); Cenomanian and Turonian of Karakalpakia: *Kizylkumemys* (Carettochelyidae), *Oxemys* (Chelonioidea), *Tienfucheloides* (Plesiochelyidae); Late Turonian–Santonian of Fergana (Isfara, Kansai) and Turonian–Santonian of Kazakhstan (Shakh Shakh): new species of *Lindholmemys* (Dermatemydidae), *Adocus* (Adocidae); *Shachemys*, which is a type genus of a new subfamily Shachemydinae Khosatzky (diagnosis of this subfamily is given) established within the family Adocidae; new species of *Anatolemys*; Southern Kazakhstan (Kyrkkuduk, Alymtau and others): *Trionyx*. Late Mesozoic of the European part of the USSR (Lysaya Gora near Saratov and other regions of Saratov Povolzhye): Chelonioidea.

- 81. Nessov L.A. and Khosatzky L.I. 1977b.** Freshwater turtle from the Early Cretaceous of Fergana. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **20**: 248–262. [In Russian]

This paper describes and illustrates material of a new genus and species of freshwater turtles of the family Adocidae—*Ferganemys verzilini* Nessov et Khosatzky, based on a plastron (holotype) and about 3000 shell fragments from the Upper Cretaceous (Albian) upper part of Alamyshik Formation of Klaudzin, Kirghiz SSR.

- 82. Shcheglova A.I., Tolmacheva N.V. and Khosatzky L.I. 1977.** The peculiarities of the water metabolism in the Caspian turtles. *Voprosy gerpetologii*. IV Vsesoyuznaya gerpetologicheskaya konferentsiya. Avtoreferaty dokladov (1–3 February 1977, Leningrad). Nauka, Leningrad: 235–236. [In Russian]

This abstract presents results of an experimental study of water metabolism in *Mauremys caspica*. It is shown that these freshwater turtles are able to consume and lose water via the skin. The significance of the skin regulation of the water balance in amphibiotic turtles is discussed.

- 83. Khosatzky L.I. 1978.** Analogous shell microstructures of stegocephalians and trionychids. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **21**: 280–287. [In Russian]

This paper presents results of a comparative study of the dermal bones of stegocephalians, modern and fossil trionychids. It is shown that in trionychids, a rich net of blood vessels in the shell bones and in the skin plays an important role in cutaneous gas exchange, similar to amphibians. The pit-ridge sculpturing of the shell bones provides them additional mechanical strength and a tighter connection with soft skin, reducing the risk of rupture of blood vessels.

- 84. Khosatzky L.I. and Nessov L.A. 1978 (1977).** Turtles of the genus *Adocus* from the Late Cretaceous of the USSR. In: Gerpetologicheskii sbornik (*Trudy Zoologicheskogo Instituta AN SSSR*, **74**): 116–119. [In Russian]

This short paper describes a new species of the genus *Adocus* Cope, 1868 (Adocidae)–*A. foveatus* Nessov et Khosatzky, based on a peripheral 4 plate from the Upper Cretaceous (Turonian–Santonian) Yalovach Formation of Kansai locality, Western Fergana, Tajik SSR. Species of *Adocus* from the Eocene of Kazakhstan and China (Gilmore 1931; Chkhikvadze 1973) differ from Cretaceous *Adocus* in external sculpturing of the shell bones and may be attributed to this genus only conditionally.

- 85. Nessov L.A. and Khosatzky L.I. 1978.** Freshwater turtle of the Early Cretaceous of Kirghizia. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **21**: 267–279. [In Russian]

This paper presents a detailed description and illustration of material of *Kirgizemys exaratus* Nessov et Khosatzky, 1973 from the Early Cretaceous of Kirghizia. The genus *Kirgizemys* demonstrates considerable similarity with the genus *Hangaemys* Sukhanov et Narmandakh, 1974. The authors agree with Sukhanov et Narmandakh (1974) in that *Osteopygis kansuensis*, *O. latilimbata* and *O. acutus*, described from the Cretaceous of China (Bohlin 1953), should be considered a single species *O. kansuensis*, but argue in favor of its attribution to the genus *Kirgizemys*, rather than to *Hangaemys*. In addition, remains of *Kirgizemys* sp. are reported from the Cenomanian of Karakalpakia (Chelpyk, Khodzhakul, Khodzhakulsay). The neural plate with three longitudinal keels attributed to Chelydridae by Chkhikvadze and Shuvalov (1975), probably, also belongs to *Kirgizemys*. The name Macrobaeninae Sukhanov, 1964 is considered to be a senior synonym of Kirgizemyinae Nessov et Khosatzky, 1973. Macrobaeninae (Toxochelyidae) and Sinemydidae are not considered to be close relatives. On the other hand, Toxochelyidae as well as other Chelonioida and Thalassemydidae are considered to be probable derivatives of Plesiochelyidae.

- 86. Khosatzky L.I. 1979a.** Skin respiration in the Far Eastern turtle. In: Gerpetologiya. Kuban State University, Krasnodar: 43–46. [In Russian]

This short paper briefly repeats results of the experimental study of gas exchange in *Trionyx sinensis* (Khosatzky 1967b). The term “amphibious reptiles” is applied for trionychids.

- 87. Khosatzky L.I. 1979b.** Peculiarities of *Eunotosaurus africanus* in the light of the doctrine of specialization. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **22**: 189–198. [In Russian]

The morphology of *Eunotosaurus africanus* Seeley, 1892, a problematic reptile from the Middle–Late Permian of South Africa, is discussed based on data from the published literature. It is emphasized that the observation that this species has osteoderms is erroneous. Particular attention is paid to the morphology of trunk ribs, which are widened and spoon-like. The unusual shape of these ribs with a double curvature is considered to be a highly specialized condition. For this reason (Cope’s rule of descent from non-specialized ancestors), the rib cage of *Eunotosaurus* could not be used as a base for the turtle carapace, which has more simple rib curvature. It is proposed, that *Eunotosaurus* should be assigned to cotylosaurs and, probably, to captorhinomorphs.

- 88. Khosatzky L.I. and Nessov L.A. 1979a.** Large turtles of the Late Cretaceous of Middle Asia. In: Ekologiya i sistematika amfibi i reptiliy (*Trudy Zoologicheskogo Instituta AN SSSR*, **89**): 98–108. [In Russian]

This paper presents a detailed description and illustration of fragmentary shell material of two turtle species of the genus *Anatolemys* Khosatzky et Nessov in Nessov, 1977 (subfamily Macrobaeninae Sukhanov, 1964 [= Kirgizemyinae Nessov et Khosatzky, 1973] of the family Toxochelyidae Baur, 1895): *Anatolemys maximus* Khosatzky et Nessov in Nessov, 1977 from Kansai locality (Tajikistan, Yalovach Formation, early Campanian) and *A. oxensis* Nessov et Khosatzky in Nessov, 1977 from localities of Khodzhakul Formation (Uzbekistan, Cenomanian). In addition, *Anatolemys* sp. is described based on a fragment of a nuchal from Shakh Shakh locality (Kazakhstan, Bostobe Formation, Santonian–early Campanian). Traces of pathological lesions on the shell bones of *Anatolemys* are reported and considered to be caused by bacteria or fungi like those observed in some modern freshwater turtles. *Anatolemys* is considered to be an inhabitant of firths. Other turtles of the Kansai assemblage include *Shachemys* (Shachemydinae, Adocidae), Trionychidae, *Lindholmemydidae* (Dermatemydidae) and *Adocus foveatus* Nessov et Khosatzky in Khosatzky et Nessov, 1978 (Adocidae). The latter species is known only from several shell fragments, some of which are illustrated in this paper. The hypothesis that shell fragments of *Basilemys* sp. described from the Shakh Shakh assemblage by Kuznetsov (1977) belong to the genus *Adocus* is considered.

- 89. Khosatzky L.I. and Nessov L.A. 1979b.** Distribution of the Far-Eastern turtle in Primorye and Priamurye and objectives of its conservation. In: Gerpetologiya. Kuban State University, Krasnodar: 89–93. [In Russian]

This short paper discusses problems of distribution, ecology and conservation of *Trionyx sinensis* in the Far East of the USSR.

- 90. Nessov L.A. and Khosatzky L.I. 1980.** Turtles of the genus *Lindholmemydidae* of the Late Cretaceous of the USSR. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **23**: 250–264. [In Russian]

This paper reports new material of turtles of the genus *Lindholmemydidae* Riabinin, 1935 (Dermatemydidae) from the Late Cretaceous of the USSR. This material includes shell fragments of *L. elegans* Riabinin, 1935 (type species) from the Late Cretaceous (Cenomanian) of Uzbekistan (Bissekty) and shell fragments from the Late Cretaceous (Turonian–Santonian) of Kazakhstan (Shakh Shakh) and Tajikistan (Kansai) assigned to a new species—*L. gravis* Nessov et Khosatzky. In addition, one shell fragment from the late Turonian of Kokcha Ridge of South-Western Kyzylkum (Uzbekistan) was referred to *Lindholmemydidae* sp. The heavy and relatively high shell of *Lindholmemydidae* suggests that these turtles were semi-aquatic.

- 91. Khosatzky L.I. 1981.** Some peculiarities of the thermoregulation of the Far Eastern turtle *Trionyx sinensis* (Wiegmann). In: L.J. Borkin (Ed.). Gerpetologicheskie issledovaniya v Sibiri i na Dal’nem Vostoke. Academy of Sciences of the USSR, Leningrad: 113–117. [In Russian]

This paper presents results of an experimental study of thermoregulation in *Trionyx sinensis* (Trionychidae), based on measurements

of internal (rectal) and external (skin) temperature at different parts of the body. It is demonstrated that external temperatures for this species, as well as rectal temperatures, usually exceed ambient temperature (both air and water) by 0.1–1.0 °C. This indicates a high level of metabolism that is connected such physiological features of trionychids as intensive skin respiration and an active lifestyle. It is assumed that thermoregulation in trionychids is implemented not only due to physical processes, but also due to chemical ones.

- 92. Khosatzky L.I. and Nesson L.A. 1981.** Soft-shelled turtle and its conservation in the Far East. In: Redkie i ischezayushchie zhivotnye sushi Dal'nego Vostoka SSSR (materialy konferentsii). Far East Scientific Center of the Academy of Sciences of the USSR, Vladivostok: 122–124. [In Russian]

This short paper discusses problems of distribution, ecology and conservation of *Trionyx sinensis* in the Far East of the USSR.

- 93. Nesson L.A. and Khosatzky L.I. 1981a.** Turtles of the Early Cretaceous of Transbaikalia. In: L.J. Borkin (Ed.). Gerpetologicheskie issledovaniya v Sibiri i na Dal'nem Vostoke. Zoological Institute of the Academy of Sciences of the USSR, Leningrad: 74–78. [In Russian]

This paper describes and illustrates new discoveries of Early Cretaceous turtles from Transbaikalia (Buryat ASSR) including descriptions of the following taxa: a new species of the genus *Kirgizemys* Nesson et Khosatzky, 1973 – *Kirgizemys dmitrievi* Nesson et Khosatzky, based on a carapace fragment from "Ovrag Dinovavrov" locality, Gusinoe Lake; *Kirgizemys* sp. based on a peripheral plate from the same locality and several shell fragments from near the Shibertuy River; ?Toxochelyidae gen. et sp. indet. and ?Plesiochelyidae gen. et sp. indet. based on shell fragments from "Ovrag Dinovavrov"; ?Chelonioida fam., gen. et sp. indet. based on shell fragments from near the Motnya settlement, right bank of the Khilok River.

- 94. Nesson L.A. and Khosatzky L.I. 1981b.** History of some groups of turtles in connection with fates of the continents. In: Paleontologiya, paleobiogeografiya i mobilizm. Trudy XXI sessii Vsesoyuznogo paleontologicheskogo obshchestva (1975). Magadanskoe knizhnoe izdatel'stvo, Magadan: 153–160. [In Russian]

This paper presents a review of phylogenetic relationships, taxonomy, and past and present distributions of some turtle groups in light of the theory of mobilizm (continental drift). These groups are Dermatemydidae, Carettochelyidae, Trionychidae, Toxochelyidae, Pelomedusidae, Chelyidae, and Meiolaniidae.

In the USSR, the earliest dermatemydid is *Ferganemys verzilini* from the Albian of Kirghizia. *Plesiochelys tatsuensis* from the Late (or Middle) Jurassic of China should be considered the second species of *Ferganemys*. The dermatemydids had a broad distribution in Middle Asia and Kazakhstan during the Cretaceous, especially during the Late Cretaceous. They were also present there in the Paleogene. In addition to *Ferganemys*, dermatemydids include turtles from the Cenomanian–Turonian of Sultanuvays Ridge, the genus *Peltochelys* from the Early Cretaceous of Europe and the North American genera *Adocus* and *Alamosemys*. The genus *Lindholmemys*, previously known only from Kyzylkum, but now

also from Fergana, represents a special Late Cretaceous branch of the dermatemydids. Turtles of this genus, without a doubt, were terrestrial. It is clear, that early stages of the evolution of dermatemydids occurred in Asia. The known distribution of this group suggests the presence of a land connection between Asia and North America in the Late Cretaceous and Paleogene. The early dermatemydids stand at the base of the superfamily Testudinoidea.

Early stages of the evolution of the carettochelyids are connected with Asia, where primitive members of this group (*Kizylkumemys*, Late Cretaceous of Uzbekistan; *Anosteira*, Paleogene) are known; one lineage of the carettochelyids immigrated to Europe, whereas another one immigrated to the Australian region at the beginning of Cenozoic.

Trionychids are also of Asiatic origin, because their oldest reliable representative comes from the Albian of Kirghizia. *Sinaspideretes wimani* from the Early Cretaceous of China does not belong to this group. The radiation of the trionychids took place in the Late Cretaceous and Paleogene of Laurasia. Their appearance in Gondwana was relatively late (in Africa from the beginning of the Miocene; in South America in the middle Pliocene; in New Guinea, recently). However, in India trionychids are known beginning in the Middle Eocene.

The earliest toxochelyids are represented by *Kirgizemys exaratus* and *Hangaemys hoburensis* from the Albian of Fergana and Mongolia respectively. These two genera and *Macrobaena* from the Paleocene of Mongolia are members of a primitive Asiatic, mainly freshwater, branch of toxochelyids (Macrobaeninae Sukhanov, 1964 = Kirgizemyinae Nesson et Khosatzky, 1973). Some other forms of this group are known from the Cretaceous of the Asiatic part of the USSR. *Plesiochelys kwanganensis* Yeh, 1973 from the Late Jurassic of China should be assigned to the Toxochelyidae. A new genus *Toxocheloides* Nesson et Khosatzky is established for this species. Toxochelyidae is thought to have evolved from the Asiatic, rather than the European, turtles of the family Plesiochelyidae.

The oldest representatives of turtles of the families Dermatemydidae, Carettochelyidae, Trionychidae and Toxochelyidae appeared in Asia earlier than in other parts of Laurasia. During the Late Cretaceous, the center of Asia was an area of a broad evolutionary radiation in these groups. From there, they dispersed to other parts of the Northern Hemisphere and appeared in Gondwana relatively late. The center of origin of the Pelomedusidae was placed, probably, on the united territories of Africa, South and North America and Europe, separated from Asia by epicontinental seas. The presence of pelomedusids in Indostan from the Danian to the Pliocene and their absence in other parts of Asia can be considered as evidence for drift of Indostan from Africa to Asia. The Chelyidae and Meiolaniidae probably originated later than the Pelomedusidae in South America. They could not penetrate into North America and Africa, but came to Australia via Antarctica.

- 95. Khosatzky L.I. 1982.** Reptiles. In: Stratigrafiya SSSR. Chetvertichnaya sistema. Polutom 1. Nedra, Moscow: 252–262. [In Russian]

This paper reviews data on reptiles from the late Pliocene and Quaternary of the USSR. Turtles are represented by Chelydridae, Emydidae and Testudinidae. Chelydridae are reported from the late Pliocene of Ukraine, Moldavia and Kazakhstan. Some of them were previously described as *Testudo* sp. and *Trionyx* sp. (Khosatzky 1944, 1945b, 1949b). Emydidae are represented by members of *Mauremys* (*Clemmys*), *Geoemyda* and *Sakya* from the late Pliocene (*Geoemyda* also from the Eopleistocene) of Moldavia, Ukraine, and

Northern Caucasus, and *Emys* from the late Pliocene–Holocene of the same territory and late Neolithic sites of Estonia. Testudinidae are represented by members of *Geochelone* from the late Pliocene–early Anthropogene of the USSR and *Testudo* (*T. cernovi* and *T. kucurganica* from the late Pliocene of Moldavia and Ukraine, and *T. cernovi* from the Akchagyl of Georgia). *Testudo graeca* is known from the Pleistocene of Binagady (Azerbaijan), Holocene of Mingechaur (Azerbaijan) and Holocene of Taman Peninsula. *Testudo* (*Agrionemys*) *horsfieldi* is known from the Pliocene of Eastern Kopetdag (Turkmenia), Mousterian (middle Paleolithic) of Aman Kutan (Uzbekistan) and Mesolithic or Mousterian Ogzi Kichik (Tajikistan) archeological sites. *Agrionemys* probably represent a subgenus of *Geochelone* (not *Testudo*). *T. horsfieldi* came to Middle Asia and Kazakhstan from non-Paleartic regions of Africa via Western Asia somewhere at the border between Neogene and Anthropogene.

96. Khosatzky L.J., Christov L. and Nankinov D. 1983. An Eocene soft-shelled turtle from Bulgaria. In: W.-D. Heinrich (Hrsg.). Wirbeltier-Evolution und Faunenwandel in Kanozoikum. Akademie-Verlag, Berlin (Schriftenreihe für geologische Wissenschaften, 19/20): 271–279.

This paper describes a new subspecies *Trionyx* (*Amyda*) *capellinii bulgaricus* Khosatzky based on an incomplete carapace and its imprints from the Upper Eocene of Nikolaevo village, District of Stara Zagora town, Bulgaria. This is the first record of a fossil turtle from Bulgaria.

97. Khosatzky L.I., Shammakov S.Sh. and Semerikov A.A. 1985. About turtle-like concretions from Kyurendag. *Izvestiya Akademii Nauk Turkmenskoy SSR. Seriya Biologicheskikh Nauk*, 3: 32–37. [In Russian]

This paper reports discoveries of turtle-like concretions (turtle stones) in the area of Kyurendag, Turkmenia. Similar discoveries from other parts of Eurasia, including the “oldest turtle” *Archaeochelys pougeti* Bergounioux, 1938 from the Late Permian of France, are discussed.

98. Khosatzky L.I. 1986. A large trionychid from the Sarmatian of Moldavia. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, 29: 158–170. [In Russian]

This paper describes and illustrates a new species of trionychid turtle—*Trionyx moldaviensis* Khosatzky, based on an almost complete carapace from the locality Malye Mileshty, Kutuzov District, Moldavian SSR, middle Sarmatian. This specimen represents the first complete carapace of fossil trionychids known from the USSR. *Trionyx moldaviensis* is considered clearly taxonomically distinct from *Trionyx brunhuberi* Ammon, 1911 from the Sarmatian of Germany. On the other hand, trionychid material described from the Pannonian of Pechvarad (Hungary) and other trionychid remains from the Sarmatian of Moldavia and from Sevastopol (Ukraine), probably, belongs to the species from Moldavia.

99. Khosatzky L.I. and Redkozubov O.I. 1986a. A jaw of the snapping turtle from the Pliocene of Moldavia. In: Pliotsen-antropogonovaya fauna Dnestrovsko-Prutskogo mezhdurech'ya. Shtiintsa, Kishinev: 51–62. [In Russian]

This paper describes three turtle dentaries from the Pliocene of Moldavia attributed to the chelydrid *Macrocephalochelys pontica* Pidoplichko et Tarashchuk, 1960.

100. Khosatzky L.I. and Redkozubov O.I. 1986b. A new species of freshwater turtle from the Pliocene of south of Moldavia. *Izvestiya Akademii Nauk Moldavskoy SSR. Seriya Biologicheskikh i Khimicheskikh Nauk*, 6: 74. [In Russian]

This paper describes a new species of the family Emydidae, subfamily Geoemydinae, genus *Melanochelys* sensu Chkhikvadze, 1983—*Melanochelys etuliensis* Khosatzky et Redkozubov, based on several epiplastra from the middle Pliocene of Moldavia.

101. Glickman L.S., Mertenene L.S., Nessov L.A., Rozhdestvensky A.K., Khosatzky L.I. and Yakovlev V.N. 1987. Vertebrates. In: Stratigrafiya SSSR. Melovaya sistema. Polutom 2. Nedra, Moscow: 255–262. [In Russian]

This book chapter reviews data on Cretaceous vertebrates of the USSR, including turtles, which are represented by the following taxa: *Kirgizemys dmitrievi* (Neocomian of Transbaikalia); probable Plesiochelyidae (late Aptian of Kyzylkum); *Ferganemys verzilini*, *Kirgizemys exaratus*, and archaic *Trionyx* (upper Albian of south-eastern of Fergana); *Adocus kizylkumensis*, *Basilemys*, *Kirgizemys*, *Kizylkumemys*, *Mongolemys*, *Oxemys*, and a middle-sized *Trionyx* (upper Albian of Kyzylkum); Chelospharginae (*Teguliscapha*) (sea of the Albian–Cenomanian); *Anatolemys oxensis*, *Ferganemys itemirensis*, *Kizylkumemys schultzi*, *Mongolemys occidentalis*, *Tienfucheloides* (Cenomanian of Kyzylkum); *Adocus aksary*, *Anatolemys* cf. *maximus*, *Lindholmemys elegans*, *Shachemys bai-bolatica ancestralis*, a large *Trionyx* (late Turonian–Coniacian of Kyzylkum and North-Eastern Aral Sea area). The disappearance of *Kizylkumemys* in the middle Turonian and the appearance of *Lindholmemys elegans* is typical for Middle Asia and Mongolia. In the early Santonian of Fergana, Circum-Tashkent Chul and Aral Sea area, new species and subspecies of *Adocus*, *Lindholmemys*, *Shachemys*, and *Trionyx* appeared. *Anatolemys* is also present; these genera are also traced in the early Campanian of Fergana. Large marine Desmatochelyidae lived in the late Santonian–Campanian of Circum-Tashkent Chul (Alymtau).

102. Khosatzky L.I. 1987. Mesontology—a particular direction in the study of evolution. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, 30: 50–66. [In Russian]

This paper is devoted to mesontology, a name proposed for a special direction in the study of evolution. Mesontology examines micro-evolutionary processes at different boundaries of geological events, including rather old ones. There are several examples of such an examination using subfossil (or semirecent) turtle material.

A mass accumulation of shell fragments of *Agrionemys horsfieldi* comes from the Mesolithic site Ogzi Kichik in southern Tajikistan (10000–20000 BP). This accumulation was formed as a result of Stone-Age human activity. A detailed morphometric study of the main (best preserved) part of this material (in collaboration with I.E. Zherekhova) and comparison with modern populations of *A. horsfieldi* reveals some historical changes in the morphological structure of the shell of this species. These changes include: a) widening of the cranial opening of the shell; b) shortening of the anterior part of the plastron and its mechanical reinforcement; c) convergence of caudal margins of the carapace and plastron; d) some changes in the bony elements of the anterior and posterior parts of the shell; e) a minor decrease in the relative height of the

shell. All these changes are connected with improved burrowing abilities of *A. horsfieldi*. A reconstructed microevolutionary lineage of *A. horsfieldi* includes a specimen from the Pliocene of Eastern Kopetdag (Birman et al. 1971), specimens from Ogzi Kichik and modern forms.

Two modern subspecies are recognized among Caucasian *Testudo graeca* L.: 1) *T. g. graeca* L. (although it is not impossible that this population is a new subspecies, in which case it should be named *T. graeca pontica* Khosatzky) inhabits coast of the Black Sea in the Western Caucasus, lives in the forest zones of subtropical region and is characterized by high, vaulted shells and limbs weakly specialized for burrowing; 2) *T. g. ibera* Pallas, 1814 inhabits Eastern Transcaucasia and Dagestan, lives in semiarid habitats, and is characterized by more flattened shells and a variable number (4 or 5) of digits on the forelimbs. *Testudo graeca* from archeological sites of Mingechaur (about 3000 BP; Khosatzky and Alekperov 1957) are somewhat transitional between Western Caucasian and Eastern Caucasian forms. *Testudo graeca binagadensis* Khosatzky in Alekperov, 1978 from the Pleistocene of Azerbaijan (Binagady and Fat'mai) is considered to be a direct predecessor of the above mentioned modern subspecies of *T. graeca*. *Testudo g. binagadensis* differs from these modern subspecies by such primitive characters as thicker shell bones and a less perfect hinge between the hypoplastra and xiphoplastra.

A comparative study of several modern populations of *Emys orbicularis* (in collaboration with E.B. Payevskaya and A.N. Ivanov) has shown that values of many correlation coefficients are higher in the Dagestanian population of this species than in the Kalmykian one. The lower level of correlation between bone elements of the shell in representatives of the Kalmykian population may be explained by its younger age. Interestingly, the same correlation values appear to be even lower in *E. orbicularis* from the late Pliocene and Pleistocene of Moldavia.

103. Khosatzky L.I. and Maslennikova L.S. 1989. Thermoregulation in soft-shelled turtles. *Voprosy gerpetologii. VII Vsesoyuznaya gerpetologicheskaya konferentsiya. Aftoreferaty dokladov* (26–29 September 1989, Kiev): Naukova Dumka: 271–272. [In Russian]

This abstract presents results of a study of thermoregulation of *Trionyx sinensis*. It is shown that during overheating, the rate of increase in body temperature slows down. This is connected with the increasing metabolic rate (evaporation), probably due to the movement of blood currents from internally towards the skin. In addition to physical thermoregulation, *T. sinensis* has chemical thermoregulation. In the zone of low ambient temperatures, a sharp increase in metabolic rate prevents a decline in body temperature (effect of endothermy). [In Russian]

104. Khosatzky L.I. and Redkozubov O.I. 1989. Neogenovye cherepakhi Moldavii [Neogene turtles of Moldavia]. *Shtiintsa, Kishinev*, 94 p. [In Russian]

This monograph summarizes the results of long-term studies of fossil turtles of Moldavia. It contains a brief summary of the history of paleochelonological investigations in Moldavia (Introduction), a chapter devoted to significance of studies on ancient turtles, a chapter about the role of turtles in the faunal assemblages of the Neogene of Moldavia, a chapter with a review of localities containing fossil turtle remains, a chapter of systematic account and, finally, the history of the development of Moldavian turtle fauna. The systematic account is generally based on the previous

publications, but also presents some new data. It includes the following taxa: Chelydridae: *Chelydropsis* cf. *murchisoni* Mlynarski, 1980: new shell and non-shell postcranial remains from the middle Sarmatian of Buzhory; *Ch. nopscai* (Szalai, 1934): new shell remains of from the Middle Pliocene of Etulia and Lucheshty; *Macrocephalochelys pontica* Pidoplichko et Tarashchuk, 1960; Trionychidae: *Trionyx moldaviensis* Khosatzky, 1986; Emydidae: Emydinae: *Emys antiqua* Khosatzky, 1956: new shell remains of from the Upper Pliocene of Chishmikiy; Geoclemydinae: *Mauremys salciensis* Redkozubov, 1988; Geoemydinae: *Melanochelys moldavica* Chkhikvadze, 1983; *M. mossoczyi* (Mlynarski, 1964) (= *Geoemyda* (*Heosemys*) *boristhenica* Tarashchuk, 1971) and *M. pidoplichkoi* (Khosatzky, 1946): new shell remains of from the Middle Pliocene of several localities; *M. etuliensis* Khosatzky et Redkozubov, 1986; *Sarmatemys lungui* Chkhikvadze, 1983; *Sakya riabinini* (Khosatzky, 1946): new shell material of from the Middle Pliocene of several localities; Testudinidae: *Prottestudo csakvarensis* (Szalai, 1934): new shell material of from the middle Sarmatian of Buzhory and Kalfa; *P. darewskii moldavica* Chkhikvadze et Lungu, 1979; *P. bessarabica* (Riabinin, 1918): new shell from the Maeotian of Chobruchi; *Testudo cernovi* Khosatzky, 1948 and *T. kucurganica* Khosatzky, 1948: new shell remains from the Middle Pliocene of several localities. In addition, diagnoses are given for *M. mossoczyi*, *M. pidoplichkoi*, *T. cernovi* and *T. kucurganica*. The type material of *Geoemyda* (*Heosemys*) *boristhenica* is distributed between *M. mossoczyi* and *M. pidoplichkoi*.

105. Khosatzky L.I. and Ivanov A.N. 1990. A population diversity of the correlation structure of the shell of the European pond turtle. In: *Fenetika prirodnykh populatsiy. Materialy IV Vsesoyuznogo soveshchaniya*. Moscow: 299–300. [In Russian]

This abstract reports results of a correlation analysis of the main morphometric characters of the bony shell in different turtles (terrestrial, freshwater, and marine) and, in particular, in different populations of the European pond turtle (*Emys orbicularis*) from Azov, Krasnodar, Southern Dagestan, Northern Dagestan, Kalmykia and Turkmenia. This analysis shows different degrees of structural consolidation of the shell elements in different turtles. In all turtles, the most consolidated is the carapace, especially its central part. *Emys orbicularis* demonstrates considerable variation in its morphological characters, corresponding to clinal variation. The morphology of the cline of populations mentioned above reflects the history of distribution of this species. For instance, populations from Kalmykia and Turkmenia are comparatively young historically and less specialized. Comparison of the Kalmykian population with the more ancient Dagestanian one shows higher degree of correlation of the shell elements in the latter. Within Dagestan, the population from Southern Dagestan is more stabilized and with higher degree of correlation between shell elements, than the population from the Northern Dagestan.

106. Maslennikova L.S. and Khosatzky L.I. 1990. The evolutionary level of thermoregulation in turtles. *X Vsesoyuznoe soveshchanie po evolyutsionnoy fiziologii, posvyashchennoe pamyati arfдемika L.A. Obeli. Tezisy dokladov* (28–30 November 1990). Nauka, Leningrad: 24. [In Russian]

This abstract states that considerably muted changes in body temperature in comparison to the ambient temperature suggests a peculiar regime of thermoregulation in trionychids. The phe-

nomenon of chemical thermoregulation indicates a high level of metabolism in turtles, which correspond to the rank of Amniota.

- 107. Khosatzky L.I. 1991.** Double monsters in reptiles. *Gerpetologicheskie issledovaniya*. T. 1. LISS, Leningrad: 164–170. [In Russian]

This paper reviews published and original data on double monsters in modern reptiles, including description of two fused individuals of *Agrionemys horsfieldi*, collected in Tadzhikistan in 1975. Mechanisms of formation of double monsters are discussed.

- 108. Avelev V.D., Gal'chenko S.V. and Khosatzky L.I. 1992.** The influence of extremely high frequency electromagnetic fluctuations on the turtle shell. In: *Problemy neyrokibernetiki*. Rostov State University, Rostov-on-Don: 269–270. [In Russian]

This abstract presents results of an experimental study of the influence of high frequency electromagnetic fluctuations on live turtles and prepared shells of *Emys orbicularis*. It is shown that in different parts of the shell the maximum reflectance value is 40–42 GHz, and the minimum is ~50–53 GHz. In general, the pattern of mosaic distribution of the perception of the electromagnetic fluctuations is similar to that observed during vibration influence (see Masharskiy and Khosatzky 1969).

- 109. Khosatzky L.I. and Avelev V.D. 1992.** The perspectives of the study of the seismoprognostic abilities of reptiles. In: *Problemy neyrokibernetiki*. Rostov State University, Rostov-on-Don: 282–283. [In Russian]

This abstract discusses the seismoprognostic abilities (the abilities to predict earthquakes) of reptiles (including turtles). These abilities are expressed in the unusual behavior of the animals for a few hours or days before the earthquake. It is proposed to conduct a detailed study of receptor units specialized in the perception of the vibrations of the environment.

- 110. Khosatzky L.I. and Chkhikvadze V.M. 1993.** New data on Miocene turtles of the genus *Baicalemys*. *Soobshcheniya Akademii Nauk Gruzii*, **148**(3): 155–160. [In Russian]

This paper presents the description of a new genus *Baicalemys* Khosatzky with two new species: *B. gracilis* Khosatzky (type species), based on isolated shell plates from the late middle or early late Miocene of Baikal (Russia), and *B. moschifera* Chkhikvadze based on an incomplete shell and fragments of non-shell postcrania from the early late Miocene of Zaysan Depression (Kazakhstan). In addition, two more species are assigned to this genus: *B. (orig. Chrysemys) lavrovi* (Kusnetsov et Chkhikvadze, 1977), known from shell fragments from the late Oligocene of Kazakhstan and *B. (orig. Zaisanemys) jegalloi* (Chkhikvadze, 1973) known from shell fragments from the late early–early middle Miocene of Zaysan Depression (Kazakhstan). The genus *Baicalemys* is assigned the tribe Chrysemydini sensu Chkhikvadze, 1983 of the family Emydidae.

- 111. Khosatzky [Khozatsky] L.I. 1996.** New turtle from the Early Cretaceous of Central Asia. *Russian Journal of Herpetology*, **3**(1): 89–94.

This paper describes a new turtle species ?*Sinemys efremovi* Khosatzky (Sinemydidae), based on three drawings and one photograph, which are thought to represent three specimens. The material was collected from the Lower Cretaceous (Barremian) of the

Tugulu Group (Hutubin Formation) of the Tukhun Kho locality, Jungarr Basin, Xinjiang Province, China in the early 1940-ies by soviet geologist N.P. Tuavev. The material is considered to be lost.

- 112. Khosatzky L.I. 1998 (1997).** Big turtle of the Late Cretaceous of Mongolia. *Russian Journal of Herpetology*, **4**(2): 148–154.

This paper describes a new genus and species of an archaic turtle *Mongolochelys efremovi* Khosatzky, based on complete skull, carapace, and elements of the plastron, and bones of the non-shell postcrania from the Nemegt Formation (Late Cretaceous Maastrichtian) of Nemegt locality of Southern Mongolia. This material was collected by the Mongolian Paleontological Expeditions (1946–1949). *Mongolochelys* is placed in the group Kayentachelydia Gaffney et al. 1987.

- 113. Khosatzky L.I. 1999.** Turtles-trionychids of the Cretaceous of Mongolia. In: *Voprosy paleontologii*. T. 11. Saint Petersburg: 141–149. [In Russian]

This paper reports new material of trionychids from the Cretaceous of Mongolia collected by Soviet paleontologists and geologists and stored in the Zoological Institute of the Russian Academy of Sciences. This paper gives no taxonomic descriptions, but contains morphological characteristics and drawings of some trionychid specimens.

- 114. Nesson L.A. and Khosatzky L.I. 1999.** A turtle from the Late Jurassic of Northern Fergana. *Trudy Zoologicheskogo Instituta Rossiyskoy Akademii Nauk*, **277**: 119–126. [In Russian]

This paper describes shell fragments of *Xinjiangchelys cf. latimarginalis* from the Middle Jurassic (Callovian) Balabansai Formation of Sarakamyshsay locality of Kirghizia.

- 115. Khosatzky L.I., Ranov V.A. and Stal'makova V.A. 2013.** About Horsfield's tortoise of the Stone Age of Tajikistan. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, **317**(4): 376–381. [In Russian]

See Khosatzky et al. (2013) in this volume.

Appendix 2. Annotated publications of other authors, in which turtle taxa were named by L.I. Khosatzky, or which were written by him.

- Bazhanov V.S. and Pigulevskiy N.A. 1955.** About some peculiarities and age of Tertiary turtles *Testudo kegenica* Choz. In: *Materialy po istorii fauny i flory Kazakhstana*. T. 1. Academy of Sciences of the Kazakh SSR, Alma-Ata: 87–94. [In Russian]

This paper presents description and illustration of a new species of tortoises *Testudo kegenica* Choz.

- Telepneva V.P. 1964.** New data on Pliocene turtles of Moldavia and Ukraine. *Voprosy gerpetologii*. *Materialy gerpetologicheskoy konferentsii* (12–14 October 1964). Leningrad State University, Leningrad: 70. [In Russian]

This abstract reports new materials of late Pliocene turtles of the families Emydidae (*Emys*, *Clemmys* and *Geoemyda*), Chelydridae and Testudinidae (several forms of the genus *Testudo*). This is the first report of *Geoemyda* in the fauna of the USSR. However, a detailed examination of numerous remains of Neogene freshwater turtles collected in different places of the European part of the USSR demonstrates that species of this genus were widely distributed there. An almost complete shell of *Geoemyda* sp. was collected from the eastern part of Khadzhibeysky firth, 0.5 km S from Morozovka Village (Ukraine, Odessa Province). This species is close to *Clemmys pidoplichoi* Khosatzky, 1946 (see Khosatzky 1946b), which should be assigned to the genus *Geoemyda*.

Remarks. According to Telepneva (pers. com. to IGD 2013), this abstract was written by Khosatzky.

Nessov L.A. 1977a. Turtles and some other reptiles of the Cretaceous of Karakalpakia. Voprosy gerpetologii. IV Vsesoyuznaya gerpetologicheskaya konferentsiya. Aftoreferaty dokladov. Nauka, Leningrad: 155–156. [In Russian]

This abstract reports new discoveries of reptiles from the Cretaceous of Karakalpakia. It includes the formal erection of the new genus *Anatolemys* Khosatzky et Nessov with two new species *A. maximus* Khosatzky et Nessov (type species) from the Late Cretaceous of Tajikistan and *A. oxensis* Nessov et Khosatzky from the Late Cretaceous of Uzbekistan.

Alekperov A.M. 1978. Zemnovodnye i presmykayuschiesya Azerbaydzhana [Amphibians and reptiles of Azerbaijan]. Elm, Baku, 264 p. [In Russian]

This monograph, among other things, reviews fossil turtle material from the Neogene and Quaternary of the Caucasus. This review includes descriptions and illustrations of new turtle taxa: *Testudo eldarica* Khosatzky et Alekperov based on shell fragments from the late Miocene (late Sarmatian) of the Eldar Steppe area (Azerbaijan and, possibly, Georgia) and *T. graeca binagadensis* Khosatzky based on shell fragments from the middle Pleistocene of Binagady (Azerbaijan). In addition, this review presents brief descriptions and illustrations of the following turtle materials: a fragment of the left part of the pectoral girdle of *Testudo* sp. from the middle Miocene of Stavropol Region (Belomechetskaya), shell fragments of *Testudo* sp. from the late (may be middle) Pliocene of Ergeni (Rostov Province); shell fragments of *Testudo* sp. from the middle or late Pliocene of Kosyakino Quarry (near Stavropol); a nuchal plate of *Testudo* sp. from the Pliocene (?), 80 km S from Armavir; carapace fragments of *Testudo* sp. from the late Pliocene of Tashkala Mountain, near Grozny; shell fragments of *T. graeca* from the Pleistocene of Fat'mai (Apsheon Peninsula, Azerbaijan); shells of *T. graeca* from Mingechaur (see Khosatzky and Alekperov 1958); subfossil shell fragments of *T. graeca* from the Taman Peninsula; shell fragments of *Clemmys* sp. from the Eldar Steppe (Azerbaijan and Georgia); shell fragments of *Clemmys* sp. and *Emys orbicularis*

antiqua Khosatzky, 1956 from Kosyakino Quarry; shell fragments of *E. orbicularis* from the Pleistocene of Mashuk Mountain (Pyatigorsk); costal fragments of Trionychoidea and ?Cheloniidae from Belomechetskaya.

Remarks. Alekperov (1978: 177) noted that all materials on fossil turtles mentioned in his monograph were under study by Khosatzky, who showed them to Alekperov.

Appendix 3. Systematic arrangement of turtles from the Khosatzky's unpublished manuscript prepared for "Osnovy paleontologii" (see text for discussion).

Subclass Chelonia (Testudinata)

Order Chelonia (Testudinata)

Suborder Amphichelydia

Family Triassochelyidae

Family Proterochersidae

Family Pleurosternidae

Family Baëniidae

Family Kalkokibotiidae

Suborder Pleurodira

Family Plesiochelyidae

Family Thalassemydidae (Acichelyidae)

Family Miolaniidae

Family Pelomedusidae

Family Bothremydidae

Family Chelyidae

Suborder Cryptodira

Family Chelydridae

Family Dermatemydidae

Family Emydidae

Family Testudinidae (Chersidae)

Family Cheloniidae

Family Toxochelyidae

Family Protostegidae

Family Dermochelyidae (Athecae)

Suborder Trionychoidea

Family Carettochelyidae

Family Trionychidae