

RUSSIAN ACADEMY OF SCIENCES
PROCEEDINGS OF THE ZOOLOGICAL INSTITUTE
VOL. 281

ZOOLOGICAL SESSIONS
ANNUAL REPORTS 1998



St. PETERSBURG
1999

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THE ECOLOGICAL TYPES OF TURTLES IN THE LATE CRETACEOUS OF ASIA

There were two turtle faunas in the late Cretaceous of Asia: Middle Asian and Mongolian. These faunas have many families in common (except for Sinemydidae in Mongolia and, probably, Nanhsiungchelyidae in Middle Asia) but their generic composition is extremely different (Table 1). There are just two common genera for these faunas: *Kizylkumemys* for the Cenomanian - early Turonian and *Lindholmemys* for the early Turonian - Santonian. *Mongolemys* was considered as a third common genus for these territories by Nesson and Krassovskaya (1984), based on *Mongolemys occidentalis* from the early Cenomanian of Uzbekistan, but this species was removed to a separate genus, *Khodzhakulemys* (Danilov, 1999), not closely related to *Mongolemys*.

The differences in the taxonomic composition of the turtle faunas has been explained by different environmental conditions in these parts of Asia (Sukhanov, in press) or by absence of direct latitudinal connection between estuaries of the western part of Asia and brackish lakes and estuaries of Mongolia (Nesson, 1984).

Actually, turtle assemblages in Middle Asia and Mongolia also have different age distributions (Jerzykiewicz & Russell, 1991; Nesson, 1997). They are known since early Cenomanian to Santonian - ?early Campanian in the Middle Asia and throughout the whole late Cretaceous (Cenomanian - Maastrichtian) in Mongolia (Table 2). It is important to note that the common genera (*Kizylkumemys* and *Lindholmemys*) belong to the same time intervals in both territories. Despite presence of the common genera there are a number of uncommon genera in the Cenomanian - Santonian of Middle Asia and Mongolia (*Anatolemys*, *Ferganemys*, *Shachemys* in Middle Asia and "*Basilemys*" - in Mongolia). Moreover some genera in Middle Asia existed throughout long time intervals (e.g. *Anatolemys* since early Cenomanian to Santonian), whereas this is not the case in Mongolia. Thus, age differences in faunas could explain their distinction only partially. It is possible however that further investigations of turtle assemblages in the Bainshereen Formation of Mongolia will decrease their distinction from Middle Asian ones.

During the late Cretaceous, Middle Asia is represented by coastal plains and estuaries in the southwestern margin of ancient Asia (Sinitzyn, 1966; Nesson, 1997)

and was characterized by rather stable environmental conditions. According to Nesson (1984, 1997), a big change in the turtle assemblages composition took place in Middle Asia in the early Turonian, when small-sized, thin-shelled turtles were replaced with big and thick-shelled ones. Most turtle genera (e. g. *Kizylkumemys*, *Ferganemys*, *Khodzhakulemys*, *Tienfucheloides*) disappeared and new ones (*Lindholmemys*, *Shachemys*) appeared. Furthermore, there were species changes within the genera *Adocus*, *Anatolemys* and *Trionyx*. These changes are thought to have been caused by a large early Turonian transgression as well as by appearance of a large turtle-eating crocodile (*Shamosuchus*) and large predatory fishes (Ichthyodectidae) (Nesson, 1984). The next noticeable faunal change took place from the late Turonian - Coniacian to Santonian, when species and subspecies were replaced within *Lindholmemys*, *Adocus* and *Shachemys*. Besides the early Turonian turnover, the succession of the turtle assemblages is somewhat gradual on the familial and generic level in the Middle Asia, which could be explained by stable conditions there.

Table 1

Composition of the turtle faunas in the late Cretaceous of Middle Asia and Mongolia

Family	Middle Asia	Mongolia
Lindholmemydidae	<i>Lindholmemys</i> , <i>Khodzhakulemys</i>	<i>Lindholmemys</i> , <i>Gravemys</i> , <i>Mongolemys</i>
Adocidae	" <i>Adocus</i> ", <i>Ferganemys</i> , <i>Shachemys</i>	<i>Adocoides</i> , <i>Mlynarskiella</i>
Nanhsiungchelyidae	? " <i>Basilemys</i> "	<i>Zangerlia</i> , <i>Charitonyx</i>
Macrobaenidae	<i>Anatolemys</i> , ? <i>Kirgizemys</i>	? <i>Kirgizemys</i> sp.
Carettochelyidae	<i>Kizylkumemys</i>	<i>Kizylkumemys</i>
Trionychidae	several genera	several genera
M. fam. n.*		<i>Mongolochelys</i>
?Sinemydidae	<i>Tienfucheloides</i>	
Testudines inc. sedis	<i>Oxemys</i> , <i>Parathalassemys</i>	

* description of this family is in press by V. B. Sukhanov.

Mongolia demonstrated more variable environmental conditions throughout the late Cretaceous than did Middle Asia (Osmolska, 1980; Jerzykewicz & Russell, 1991; Jerzykewicz, 1995). During the Bainshirenian "Age", diverse turtle assemblages existed in eastern Mongolia. As in Middle Asia, one turtle assemblage characterized by the presence of *Kizylkumemys* is replaced by another characterized by *Lindholmemys*. Environments there were probably similar to the coastal plains and estuaries of the Middle Asia. During the Djadokhta "Age", there was aridization in the central part of Mongolia. Vertebrates from these assemblages were representative of a community adapted to living in arid environments (Osmolska, 1980). Turtles are represented there by *Zangerlia* and *Gravemys*. The Nemegtian "Age" reflects the local onset of a relatively more humid climatic regime

and the development of integrated drainage systems. During this time the central parts of Mongolia were penetrated by the giant *Mongolochelys* (Khosatzky, 1997) and the middle-sized *Mongolemys*, which are the most characteristic elements of the turtle fauna of the end of the late Cretaceous.

Table 2

Turtle assemblages in the late Cretaceous of Middle Asia and Mongolia

	Middle Asia	Mongolia
Maastrichtian		<i>Mongolemys elegans</i> <i>Mongolemys sp. n.</i> <i>Mongolochelys efremovi</i> <i>Mongolochelys sp. n. *</i> "Amyda" <i>meneri</i> <i>Platypteltis sp. n. *</i>
Campanian		<i>Zangerlia sp. n. *</i> <i>Zangerlia testudinimorpha</i> <i>Gravemys barsboldi</i>
		<i>Trionyx sp.</i>
Santonian	<i>Anatolemys maximus</i> <i>Shachemys baibolatica baibolatica</i> "Adocus" <i>foveatus</i> <i>Lindholmemys gravis</i> ? <i>Axestemys riabtnini</i> <i>Paraplastomenus riabtnini</i>	<i>Kizylkumemys sp.</i> "Amyda" <i>orlovi</i>
upper Turonian - Coniacian	<i>Anatolemys sp. cf. A. maximus</i> <i>Shachemys baibolatica ancestralis</i> "Adocus" <i>aksary</i> <i>Lindholmemys elegans</i> <i>Khunnuchelys kizylkumensis</i> <i>Palaeotrionyx sp.</i>	<i>Lindholmemys martinsoni</i> <i>Adocooides amtgai</i> <i>Mlynarskiella mariani</i>
lower Turonian	<i>Lindholmemys sp.</i> <i>Shachemys sp.</i> <i>Kirgizemys sp.</i> <i>Kizylkumemys sp.</i>	<i>Gravemys sp. n. *</i> <i>Zangerlia sp.</i> <i>Charitonox tajanikolaevae</i>
	<i>Anatolemys oxensis</i> <i>Ferganemys itemirensis</i> <i>Kizylkumemys shultzi</i> <i>Khodzhakulemys occidentalis</i>	<i>Kizylkumemys sp.</i> "Adocus" <i>sp.</i> ? <i>Kirgizemys sp.</i>
Cenomanian	<i>Tierfucheloides undatus</i> <i>Kirgizemys sp.</i> <i>Oxemys sp.</i> "Adocus" <i>sp.</i> ? "Basilemys" <i>sp.</i> <i>Palaeotrionyx sp.</i> <i>Parathalassemys cava</i>	

* Description of these species are in press by V. B. Sukhanov.

It is proposed here that environmental conditions in different parts of Asia must be reflected in the different ecological adaptations of turtles. Ideas about the ecological types of late Mesozoic turtles from Middle Asia were provided by Nessov (1984), who thought the trionychids to be mainly fish-eaters, adocids - gatherers, and *Lindholmemys* to be gatherers or plant eating forms. The latter genus has been considered a terrestrial or bottom-walking form of calm and shallow reservoirs (Nessov & Khosatzky, 1980; Nessov, 1984). In contrast, *Anatolemys* is thought to have inhabited the open parts of estuaries (Nessov & Khosatzky, 1980). Finally, nanhsiungchelyids were thought to have used their claws and plastrons for anchoring against the current on channel bottoms (Nessov, 1984). Most ideas of this kind have little evidence.

For instance, the idea that *Lindholmemys* was a terrestrial or bottom walking turtle with weak swimming abilities was based on its heavy, relatively high shell. Nessov and Khosatzky (1980) hypothesized that the narrow shell openings restricted limb movements and that the strongly developed plastral buttresses played a protective role in terrestrial conditions. Later Nessov (1997) considered *Lindholmemys* as a bottom-walking turtle of shallow waters.

It is noteworthy that plastral buttresses similar to those in *Lindholmemys* are known in some recent batagurids like *Batagur*, *Callagur* and *Kachuga*. These species are well-adapted to diving to considerable depth and are good swimmers. The buttresses in these turtles restrict the pulmonary cavities within carapace, thus forming lung chambers which enable their lungs to withstand extreme pressure (Obst, 1986). These turtles inhabit big rivers and estuaries of south-east Asia and are known to invade brackish waters (Ernst & Barbour, 1989). Thus, it seems more probable that *Lindholmemys* were an analogue of recent batagurs and callagurs in late Cretaceous time, than a bottom dweller. Like *Batagur* and *Callagur*, *Lindholmemys* could reach considerable size (a shell of a juvenile with fontanelles in carapace has about 20 cm in length). The proposed ecology for this turtle is consistent with a reconstruction of its habitat based on geological data (Archibald *et al.*, 1998). The replacement of *Kizylkumemys* with *Lindholmemys* in the early Turonian could be explained by competition as they probably shared a similar ecology.

Tatarinov (1998) expressed doubt about Nessov's (1997) idea that the heavy shelled *Lindholmemys* would have been unable to use the surface and inhale air, and so must acquired energy via glycolysis. Instead it is proposed here that *Lindholmemys* could have well-developed accessory respiratory structures.

Mongolemys represents another ecological type of turtle in the late Cretaceous of Asia. Khosatzky and Mlynarski (1971) thought *M. elegans* was associated with fresh-water environments, shallow, flooded areas, old river-beds, interconnected lakes or ponds with a soft, sandy-muddy bottom and exuberant vegetation. Such considerations were based on the supposed relationships between *Mongolemys* and *Dermatemys* as well as the mud and musk turtles. However, I

propose that *Mongolemys* is ecologically similar to some recent Australian chelids (e. g. *Chelodina*, *Elseya*, *Emydura*) based on the overall shape of the shell. Chelids are highly aquatic, some of them (e. g. *Chelodina*) only leave water to lay eggs and rarely to bask (Legler & Georges, 1993). Some species of *Chelodina* inhabit permanent waters whereas others occupy more ephemeral waterbodies. These latter species migrate overland to more permanent waters when the floodplains recede. If permanent water is not available they may burrow and aestivate. The highly aquatic habits of *Mongolemys* are supported by a well-ossified hyoid apparatus which indicates a considerable amount of bucco-pharyngeal respiration. This hypothesis is also consistent with data about climate and habitats during the Nemegtian "Age" in Mongolia (Osmolska, 1980; Jerzykiewicz, 1995). This time is characterized by a seasonal climate and therefore the presence of ephemeral water bodies. The taphonomy suggests that turtles were concentrated in diminishing pools and lakes and died when water bodies became completely dry. The presence of a fine net of branching sulci from blood vessels on the surface of the shell of *Mongolemys elegans* (Khosatzky & Mlynarski, 1971) may be explained by a specific method of thermoregulation, water basking.

The similarity of the jaw structure in *M. elegans* and *Dermatemys* was a basis for the suggested herbivory of the former (Khosatzky & Mlynarski, 1971). In fact, *Mongolemys* has narrow triturating surfaces without ridges and thus is not at all similar to *Dermatemys*. Thus, I would rather propose an omnivorous diet for *Mongolemys*.

Mongolemys seems to be an ecologically specialized aquatic turtle living in a specific environment with a seasonal climate characteristic of the Nemegtian "Age" of Mongolia. This supports my statement, based on morphological data, that the distribution of *Mongolemys* was restricted to the Maastrichtian of Mongolia (Danilov, 1999).

In conclusion, it seems that different environmental conditions in different parts of Asia throughout the late Cretaceous could explain differences of turtle faunas. The specific (extreme) conditions in the late Cretaceous of Mongolia could explain the absence of a gradual succession of turtle assemblages, whereas the more stable environment in the coastal plains of Middle Asia allows such a succession.

ACKNOWLEDGEMENTS

The author is grateful to Dr. V.B. Sukhanov (Paleontological Institute, Moscow) for permission to use manuscript of his paper (Sukhanov, in press) and for loaning material on *Mongolemys elegans*. Dr. A.O. Averianov (Zoological Institute, St. Petersburg) for his help with literature and discussions and to Mr. J. Parham (University of California, Berkeley) for checking the English and valuable discussions.

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ERRATA to Danilov 1999b (never published)

The correct version of Table 2:

Table 2. Turtle assemblages in the late Cretaceous of Middle Asia and Mongolia

	Middle Asia	Mongolia
Maastrichtian		<i>Mongolemys elegans</i> <i>Mongolemys</i> sp. nov. <i>Mongolochelys efremovi</i> <i>Mongolochelys</i> sp.nov.* "Amyda" <i>menneri</i> <i>Platypeltis</i> sp. nov.*
Campanian		<i>Zangerlia</i> sp. nov.* <i>Zangerlia testudinimorpha</i> <i>Gravemys barsboldi</i> <i>Trionyx</i> sp. Nanhsiungchelyidae gen. et sp. nov.*
Santonian	<i>Anatolemys maximus</i> <i>Shachemys baibolatica baibolatica</i> "Adocus" <i>foveatus</i> <i>Lindholmemys gravis</i> ? <i>Axestemys riabinini</i> <i>Paraplastomenus riabinini</i>	" <i>Basilemys</i> " <i>orientalis</i> <i>Kizylkumemys</i> sp. "Amyda" <i>orlovi</i>
Upper Turonian - Coniacian	<i>Anatolemys</i> sp. cf. <i>A. maximus</i> <i>Shachemys baibolatica ancestralis</i> "Adocus" <i>aksary</i> <i>Lindholmemys elegans</i> <i>Khunnuchelys kizylkumensis</i> <i>Palaeotrionyx</i> sp.	<i>Lindholmemys martinsoni</i> "Adocus" <i>amtgai</i> <i>Mlynarskiella mariani</i>
Lower Turonian	<i>Lindholmemys</i> sp. <i>Shachemys</i> sp. <i>Kirgizemys</i> sp. <i>Kizylkumemys</i> sp.	<i>Adocidae</i> gen. et sp. nov.* <i>Gravemys</i> sp. nov.* <i>Zangerlia</i> sp. <i>Charitonyx tajanikolaevae</i>
Upper Cenomanian		<i>Hanbogdemys</i> sp. nov. <i>Kizylkumemys</i> sp. "Adocus" sp. ? <i>Kirgizemys</i> sp.
Lower Cenomanian	<i>Anatolemys oxensis</i> <i>Ferganemys itemirensis</i> <i>Kizylkumemys shultzi</i> <i>Khodzhakulemys occidentalis</i> <i>Tienfucheloides undatus</i> <i>Kirgizemys</i> sp. <i>Oxemys</i> sp. "Adocus" sp. ?" <i>Basilemys</i> " sp. <i>Palaeotrionyx</i> sp. <i>Parathalassemys cava</i>	

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