

New findings of neogene tortoises *Titanochelon kayadibiensis* sp. nov. and *Protestudo bessarabica* (Riabinin, 1918) (Testudinidae) from the Miocene of western Turkey, with a review of fossil turtles of Turkey

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Abstract

Fossil remains of turtles were discovered in various localities of Lower to Upper Miocene within the western part of Turkey. We revised the taxonomic position and describe the systematic paleontology, distribution, phylogeny and palaeo-environments of two Neogene taxa *Titanochelon kayadibiensis* sp. nov. and *Protestudo bessarabica* (Testudinidae) of Western Turkey and give an updated list of fossil turtles of Turkey which include *Trionyx triunguis* (Forskål, 1775), *Mauremys aristotelica* Vlachos et al., 2019, *Testudo marmorum* Gaudry, 1862, *Protestudo bessarabica* Riabinin, 1918 and *Titanochelon kayadibiensis* sp. nov.

Keywords: *Titanochelon kayadibiensis* sp. nov.; *Protestudo bessarabica*; Testudinidae; taxonomy; Miocene; Turkey.

1. Introduction

The Miocene period was an important paleontological time interval for vertebrate faunas, as it witnessed major dispersal events especially in Africa and Asia, and also important climatic changes characterized by higher temperatures, all resulting in the emergence of new palaeo-environments, extinction events, and drastic faunal turnovers (Rögl, 1999; Böhme, 2003). The most important studies about these Miocene events have so far focused primarily on mammals (Koufos, 2013), contrary the knowledge of the respective coeval herpetofauna is far more limited and poorly documented (Delfino et al., 2003; Čerňanský et al., 2015; Georgalis et al., 2017; Ivanov et al., 2017; Danilov et al., 2017). The situation is even more puzzling for the southeastern portions of Europe and Western Asia, where the known early Miocene herpetofauna is limited to only a few sporadic occurrences (Đurić, 2016; Georgalis et al., 2016 and 2017; Vasileiadou et al., 2017). A joint technical cooperation project between the German Geological Survey, Hannover (Today: Federal Institute for Geosciences and Raw Materials, BGR) and the Turkish Mineral Research and Exploration Institute (Maden Tetkik ve Arama Enstitüsü, MTA) was carried out during period of 1965-1975 in the large areas of western Turkey, which are dominated by Neogene deposits. The first part of this project focused on the prospecting of lignite and the development of a stratigraphic structure of the continental Cenozoic Era. In its course many vertebrate sites were unearthed, in which, among other fossils, turtle remains were often found. The scientific processing of the tortoise fossils was started, and an interim result presented by Staesche (1975) at that time. Later on the fossil turtle remains have been primarily revised and taxonomically analyzed by Staesche et al. (2007) and deposited in the collections of the Geological Survey of Lower Saxony, Hannover (today: State Office for Mining, Energy and Geology, LBEG) under the Original-Numbers Ma-13580 until Ma-13591). The large-scales shell material was assigned to *Cheirogaster* sp. cf. *bolivary* Hernández-Pacheco, 1917, due to similarities with this species, although the zoogeographical distance was considerable. The revision of the poorly diagnosed "*Testudo bolivary*" and the proposal of a new genus *Titanochelon* gen. nov. by Perez-García & Vlachos (2016) is of paramount importance. It includes nearly all of the large tortoises of the Miocene and Pliocene of Europe (de Lapparent de Broin, 2001, 2002, 2008). Large testudinids were abundant and diverse also in the European Neogene record, ranging from the early Miocene of France to the Pleistocene of Greece and some Mediterranean islands. More than 10 potentially valid species are generally recognized (de Lapparent de Broin, 2001, 2002). In contrast to the taxa found in the Palaeogene of Europe, the size of these Neogene forms was greater than one meter with specimens reaching truly gigantic lengths close to two meters (e.g. the indeterminate species from Las Higuieruelas, in Spain, and from Lesvos and Samos, in Greece; see Jiménez Fuentes, 1994, 2000, and de Lapparent de Broin, 2002). Despite the abundant postcranial remains of these tortoises, many of the nominated taxa are relatively poorly known (Gmira et al., 2013). The incompleteness of the fossil record of the large tortoises only allows comparisons of the known material from the Neogene of Turkey with those of medium-sized tortoises from the Palaeogene, based on detailed analysis of their shells.

In this study, we present relatively complete material which improves our knowledge of the Neogene fossil record of the Turkish large tortoises. The currently available information on the shells of these taxa is limited. The shell material of a single species is represented by the most complete shells, i.e. the plastron of the holotype, belonging to a juvenile individual. In addition, there are several Neogene species without known elements of the shell, such as the late Miocene '*Testudo schafferi* Szalai, 1931, and taxa named from several Mediterranean islands. The type species of the genus *Protestudo* Chkhikvadze, 1970 of the family Testudinidae Batsch, 1788, is *Testudo bes-sarabica* Riabinin, 1918. Turtles of this species differ from other species of *Protestudo* in having a precentral scale and a strongly elongated, though not pointed, gular projection (Danilov et al., 2017). They are known from the Maeotian (Middle Turolian) of Moldova, Russia, and Ukraine. The species was first described from several incomplete shells and one internal mold from the Maeotian of Moldova (Taraklia and Todorovo localities: Riabinin, 1918).

The present study is an attempt to identify these Neogene fossils of Testudinidae. All the related taxa involved are compared here, and a detailed study of the Neogene forms from western Turkey is performed. Therefore, in addition to reviewing specimens corresponding to all taxa of large Testudinidae so far described in the Neogene of Turkey, we include information and revise the taxonomic description of these studied Neogene tortoises. No hypothesis on the phylogenetic relationships amongst these Neogene forms had been hitherto proposed. Here, the data of the Miocene taxa under consideration are incorporated for the first time in a taxon-character matrix, so that a hypothesis on their phylogenetic relationship is justified. Clarification of the morphology and status of the genus *Protestudo* is performed here. The study identifies the large Testudinidae from the Neogene of Turkey as belonging to a monophyletic clade, assigned to the new species of the genus *Titanochelon*.

2. Materials and methods

The fossil bone material studied here was collected from several localities in Turkey. A joint technical cooperation project between the German Geological Survey, Hannover (Today: Federal Institute for Geosciences and Raw Materials, BGR) and the Turkish Mineral Research and Exploration Institute, Ankara, (Maden Tetkik ve Arama Enstitüsü, MTA) was carried out during period of 1965-1975 in the large areas of western Turkey, which are dominated by Neogene deposits. The first part of this project focused, in connection with the prospecting of lignite, the development of a stratigraphic structure of the continental Cenozoic era. In its course many vertebrate sites were unearthed, in which, among other fossils, turtle remains were often found. The scientific processing of the tortoise fossils was started, and an interim result presented by Staesche (1975) at that time. Later on the fossil turtle remains have been primarily revised and taxonomically analyzed by Staesche et al. (2007). The large-scales shell material was assigned to *Cheirogaster* sp. cf. *bolivari* Hernández-Pacheco, 1917, due to similarities with this species, although the zoogeographical distance was considerable. The bone material was prepared in the laboratory of the German Geological Survey, Hanover and deposited in the sample archive under the inventory numbers given in the text. The terminology of the turtle shell used in this study is shown in fig. 1.

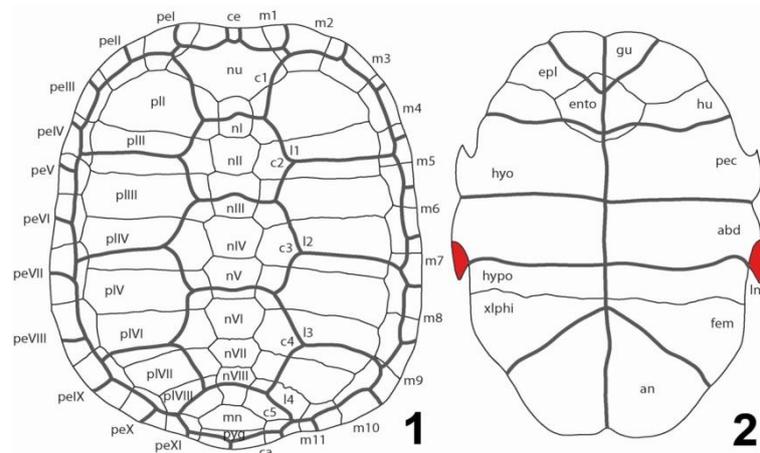


Fig. 1: Terminology of the carapace and plastron of an emydid turtle *Emys orbicularis* (1-2).

The testudine fossils which are discussed here, found in the following localities of western Turkey (Figures 2 & 3):

CA — Ankara-Kalecik-Çandır-faunal group, MN 6, (lower) Astaracian /7 (highest) Burdigalian to Langhian, Lower to Central Miocene. Vlachos et al. (2020: fig. 1) added --löschen

Environments: Bones in several layers or lenses of limnic-fluviatile sediments. The main bone bed is a carnivore-eating place. Largely open landscape, savannah and bush steppe, partly plain or gallery forest, semi-arid climate.

IK — İstanbul-Küçükçekmece

Initial processing of this site by Malik & Nafiz (1933). Classification not quite certain, probably Kayadibi-faunal group, MN 11, (deeper) Turolian 7/ (middle) Tortonian, Upper Miocene.

Environments: Deposits in a limnic to brackish-marine environment. Another site "İstanbul-Küçük-Çekmece" was briefly described by Nicolas (1978). In terms of facies and fossil content, it corresponds very precisely to the older site.

KB = KBS = KD — Konya-Hatunsaray-Kayadibi

Kayadibi-Fauengruppe, MN 11, (deeper) Turolian 7/ (middle) Tortonian, Upper Miocene.

Environments: Terrestrial deposits, bone remains washed up by periodic mud flows. In the surroundings dry bush steppe and bush forest, with rivers and gallery forest.

MC — Muğla-Yerkesik-Çatakbağyaka

Yeni Eskişehir or Sofça-faunal group, MN 7+8, (higher) Astaracian /7 Serravallian to (lower) Tortonian, Middle Miocene to Upper Miocene.

Environments: Deposits in small creeks.

SaG — Afyon-Sandikli-Garkin

Garkin-faunal group, MN 11, (middle) Turolian II (highest) Tortonian to (deeper) Messinian, Upper Miocene.

Environments: Bone finds in terrestrial deposits, washed together by periodic mud flows. Steppe with larger areas of dry bush.

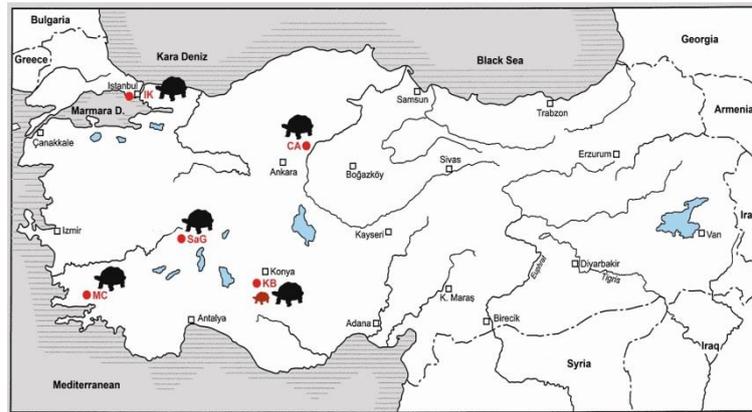


Fig. 2: Geographical position of the Western Turkish localities where the Neogene tortoises were discovered.

IK- Istanbul-Küçük-Çekmece. CA- Ankara-Kabecik-Eandir-faunal group, MN 6, (lower) Astaracian /7 (highest) Burdigalian to Langhian, Lower to Central Miocene. SaG- Afyon-Sandikli-Garkin. MC- Muğla-Yerkesik-Çatakağyaka. KB- KBS = KD— Konya-Hatunsaray-Kayadibi, Also the finding place of *Protestudo bessarabica* (Riabinin, 1918). (Map adapted from Staesche, Karl & Staesche (2007).

Eonothem/ Eon	Erathem/ Era	Series/ Period	Stage/ Age	MY	Localities
Phanerozoic	Cenozoic	Pliocene	Piacencian	2.58-3.6	
			Zanclean	3.6-5.333	
		Miocene	Messinian	5.333-7.246	SaG
			Tortonian	7.246-11.63	IK, KB
			Serravallian	11.63-13.82	MC
			Langhian	13.82-15.97	
			Burdigalian	15.97-20.44	CA
Aquitainian	20.44-23.03				

Fig. 3: Stratigraphic position of the Turkish land tortoises localities according to figure 2 (explanations in the text). International Chronostratigraphic Order according to International Commission on Stratigraphy (ICS) 2015.

3. Systematic palaeontology

Subclass Testudinata Klein, 1760,

Order Testudines Batsch, 1788,

Infraorder Cryptodira Cope, 1868,

Superfamily Testudinoidea Batsch, 1788,

Family Testudinidae Batsch, 1788,

Subfamily Testudininae Batsch, 1788.

Genus *Titanochelon* (Pérez-García and Vlachos, 2014)

Type species: *Titanochelon bolivari* Hernández-Pacheco, 1917

Type material: See Pérez-García and Vlachos 2014: 658.

Type locality and horizon: According to Pérez-García and Vlachos (2014) Cerro del Viso, in Alcalá de Henares (Madrid, Spain). MN6 zone (late Aragonian, Serravallian) of the Intermediate Unit of the Madrid Basin, belonging to the Tagus Basin.

Diagnosis of the Genus: Member of *Titanochelon* differing from the other species of this genus by the following features: presence of medially short and laterally long prefrontals, with medially long and laterally short frontals; crista supraoccipitalis elevated upwards; omegashaped femoro-anal sulcus and deep anal notch of the females; males with trapezoidal posterior lobe, showing a wide and very shallow anal notch, and with a pair of lateroposterior protrusions, well developed in adult specimens; asymmetric shape of the distal end of the humerus; elongated and narrow glenoid fossa of the scapula; long neck of the coracoid; wide and short femoral head with a well-developed neck; narrow and elongated fused astragalocalcaneum. In addition, it differs from all other species of *Titanochelon* in the following exclusive combination of characters: thin zygomatic arch; very shallow nuchal notch; nuchal as wide as long; first neural lacking a dorsal bump; absence of subhorizontal anterior peripherals; highly variable morphology of the anterior plastral lobe (e.g. subrounded, trilobed, trapezoidal); lacking or poorly developed gular pocket; gulars covering the anterior part of the entoplastron; narrow entoplastron in relation to the width of the anterior plastral lobe; posterior border of the entoplastron located anterior to the humeropectoral sulcus or in contact with it; low angle (< 120°) between the scapula and the acromion; medial articular surface of the intermedium contacting the radius; femoral head at an angle to the diaphysis.

Distribution of the genus: Neogene (Early Miocene to early Pleistocene) of Europe (Portugal, Spain, France, Switzerland, Germany, Austria, Greece, Bulgaria), European and Anatolian Turkey. This taxon may also be present in the Pleistocene deposits of some Mediterranean Islands (Balearic Islands and Malta).

Titanochelon kayadibiensis sp.nov. (Plate 1; Fig. 4)

Synonyms:

- *Testudo* sp. Riesenschildkröte und *Geochelone* sp.: Staesche, 1975: 117—118.
- *Cheirogaster* sp. cf. *bolivari* Hernández-Pacheco, 1917: Staesche et al., 2007: 103; figures 3, 8, 9, plate 1—3.

Holotype: KB 50 (Staesche et al., 2007: Abb. 3, Tab. 1).

Diagnosis: Member of the genus *Titanochelon* with a very large entoplastron without gular sulci; very small pectorals with extremely blunt notch. The entoplastron is hexagonal, strongly rounded and extensive. The entoplastron is covered only by the humerals. Epiplastral hump develop to dorsal side.

Description of the holotype: Six large connected plastron remains, including a large part of the left hyoplastron with the humeropectoral sulcus and pectoro-abdominal sulcus, as well as the axillary pillar and axillary notch, as well as a large part of the hypoplastron with portions of the inguinal notch (Staesche et al., 2007: plate 1: 1). The height of the bridge-peripherals is about 245 mm. The epiplastral cavity has a height of 33 mm and a depth of 17 mm. Behind this is a strong V-shaped entoplastral hump. The visceral length of the gular sulcus is 180 mm. The synostosis/ kyphosis between the plates is well advanced. Reconstruction of shell dimensions: CL = ca. 1300 mm, PL = 1140 mm, PB = 980 mm.

Type locality and horizon: Konya-Hatunsaray-Kayadibi, Kayadibi-Frauengruppe, MN 11, (deeper) Turolian 7/ (middle) Tortonian, Upper Miocene (Figure 2 = KB).

Hitherto known distribution of *Titanochelon kayadibiensis* sp.nov: The land tortoise fossils are discussed here, found in the following localities of western Turkey (Figures 2 & 3): CA — Ankara-Kalecik-Çandır-faunal group, MN 6, (lower) Astaracian /7 (highest) Burdigalian to Langhian, Lower to Central Miocene. Vlachos et al. (2020: fig. 1) added --löschen. Environments: Bones in several layers or lenses of limnic-fluviatile sediments. The main bone bed is a carnivore-eating place. Largely open landscape, savannah and bush steppe, partly plain or gallery forest, semi-arid climate; IK — İstanbul-Küçükçekmece. Initial processing of this site by Malik & Nafiz (1933). Classification not quite certain, probably Kayadibi-faunal group, MN 11, (deeper) Turolian 7/ (middle) Tortonian, Upper Miocene. Environments: Deposits in a limnic to brackish-marine environment. Another site "İstanbul-Küçük-Çekmece" was briefly described by Nicolas (1978). In terms of facies and fossil content, it corresponds very precisely to the older site; KB = KBS = KD — Konya-Hatunsaray-Kayadibi, Kayadibi-Frauengruppe, MN 11, (deeper) Turolian 7/ (middle) Tortonian, Upper Miocene. Environments: Terrestrial deposits, bone remains washed up by periodic mud flows. In the surroundings dry bush steppe and bush forest, with rivers and gallery forest; MC — Muğla-Yerkesik-Çatakağyaka, Yeni Eskihsar or Sofça-faunal group, MN 7+8, (higher) Astaracian /7 Serravallian to (lower) Tortonian, Middle Miocene to Upper Miocene. Environments: Deposits in small creeks; SaG — Afyon-Sandikli-Garkin, Garkin-faunal group, MN 11, (middle) Turolian II (highest) Tortonian to (deeper) Messinian, Upper Miocene. Environments: Bone finds in terrestrial deposits, washed together by periodic mud flows. Steppe with larger areas of dry bush.

Other material from Turkey:

CA: one pleural fragment very large and three fragments indet.; CA 1/ v 49: one humerus fragment proximal and one undetermined fragment; MC 186 1: one left hyoplastron fragment 7/ 214 III: one plastron fragment; SaG 7-1/51: one Neural (VI). 7/ 1/82: one pleural fragment. 7/ 1/122: one Axillary buttress; fragment of the right side 7/ 1/157: one carapace fragment indet.; IK: Thick plate fragments of the plastron (hypoplastron) and osteoderm bone. CA: Juvenile specimen of a right peripheral VII with transition from the bridge to the free rear edge and the alternation site of the inguinal fortification. Height from the bridge ridge to the proximal ending 50 mm, length proximal 31 mm, length distal 37 mm. Estimated carapace length approx. 300-360 mm.

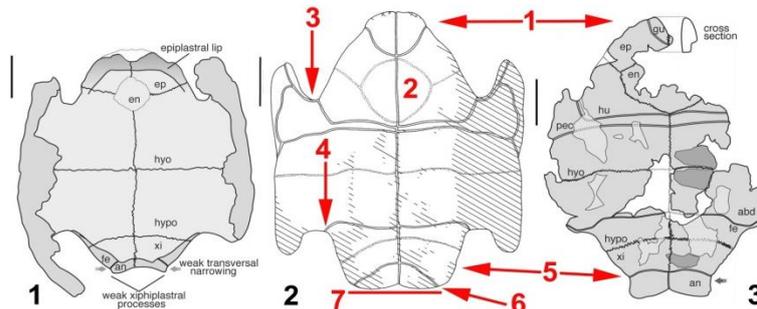


Fig. 4: Schematic illustration of the holotype of *Titanochelon kayadibiensis* n. spec., BGR — KB without number; comparison of the plastron characters of *Titanochelon bacharidisi*: 1 - Visceral, 3 - Ventral and *Titanochelon kayadibiensis* n. spec.: 2 - Ventral (explanations in the text), figures 1 and 3 adapted by Vlachos, Tsoukala and Corsini (2014), Figure 2 by Staesche, Karl & Staesche (2007). Scale bar 5 cm.

Differential diagnosis: Luján et al. (2017) refer the "*Testudo*" *gymnesica* Bate, 1914 tentatively as aff. *Titanochelon gymnesica*. To clarify the taxonomic status and phylogenetic position of this species the authors describe and figure in detail in their paper the type material from Minorca (lectotype and paralectotypes), together with some unpublished specimens not included in the original description. Březina et al. (2019) revised on historical finding (carapace and plastron remains) the giant turtle *Titanochelon* from the Brno Sand (Middle Miocene, Lower Badenian) of the locality Královo Pol (Kostelní Zmola) in the city of Brno (South Moravia, Czech Republic). According to Staesche et al. (2007): Large Eurasian species without cervical scute, with "geochelonid" pygal region and pectoralia as well as progressive evolution of the epiplastral hump. According to Pérez-Garzá and Vlachos (2014) western Euroasiatic (from Western Europe to Asia Minor) Neogene large Testudinidae (shell from more than one meter up to two meters long) based on several exclusive characters such as the alternating pattern of the costals, reduced proximal region of the ribs, presence of a thickened epiplastral lip, and fused trochanters of the femur. It is diagnosed by the presence of frontals narrower than prefrontals, causing a gentle constriction of the frontals in dorsal view, and by the following exclusive character combination: long crista supra-occipitalis (not shared in *Centrochelys sulcata*), but shared with *Ergilemys brunetti*; presence of an elliptical to circular pre-maxillary pit (not in *Centrochelys sulcata*); relatively low carapace (shared with *Centrochelys sulcata*, but not with *Cheirogaster maurini* or *Chelonoidis* spp.); wide shell (not in *Cheirogaster maurini*); nuchal plate as wide as long or wider than long (shared with '*A.*' *cassouleti*, but not with *Ch. maurini* or *Ce. sulcata*); eight neural plates, the first one being rectangular; longer than wide first neural, the second and fourth neurals octagonal, with the greatest width of the second one situated in its rear half, the third and fifth neurals rectangular, wider than long, and the sixth to eighth neurals hexagonal, the length of their latero-anterior margins being similar to that of the lateroposterior ones (this neural pattern is shared with '*Ergilemys brunetti*', but not with '*A.*' *cassouleti*, '*Hadrianus*' *castrensis*, *Ch. maurini*, or *Ce. sulcata*); absence of pointed tips in the carapacial rim in the region of contact of the sulci between the marginal scutes and the lateral border of the anterior and posterior peripherals (shared with '*H.*' *castrensis* and *Ch. maurini*, but not with '*A.*' *cassouleti*); two suprapygals, the first dorso-laterally surrounding the lenticular second one (shared with '*Ergilemys brunetti*', but not with '*A.*' *cassouleti*, '*H.*' *castrensis*, and *Ch. maurini*); longer than wide pygal (shared with *Ce. sulcata*, but not with '*H.*' *castrensis* or '*A.*' *cassouleti*); absence of cervical scute (not in '*A.*' *cassouleti*, '*H.*' *castrensis*, or '*Ergilemys brunetti*); coincidence between the medial margins of all the marginals and the suture between the costal and peripheral plates

(not in 'A.' *cassouleti*, 'H.' *castrensis*, or *Ch. maurini*); significant distance between the second pair of marginals and the nuchal plate; fourth to sixth marginals in contact with the second pleural scute (shared with 'A.' *cassouleti*, 'H.' *castrensis*, and *Ce. sulcata*, but not with *Ch. maurini*); presence of a supracaudal scute (not in 'A.' *cassouleti* or 'H.' *castrensis*); second suprapygal crossed by the vertebro-supracaudal sulcus (shared with *Ch. maurini*, but not with 'A.' *cassouleti* or 'H.' *castrensis*); absence of plastral hinges (shared with 'A.' *cassouleti*, 'H.' *castrensis*, *Ch. maurini*, and *Ce. sulcata*, but not with 'Ergilemys' *bruneti*); wide plastral lobes, at least in the region of contact with the plastral bridge (not in *Ch. maurini*); anterior plastral lobe longer than the posterior lobe (not in *Ch. maurini*); convex to flat dorsal lip of the epiplastra (not in 'A.' *cassouleti*, 'H.' *castrensis*, or *Ce. sulcata*); absence of ventral relief in the area covered by the gular scutes (present in 'H.' *castrensis*, but not in 'Ergilemys' *bruneti*); angle between the sagittal axis and the gular-humeral sulcus of 45° or more acute (shared with *Ce. sulcata*, but not with 'A.' *cassouleti*, 'H.' *castrensis*, or *Ch. maurini*); humeropectoral sulcus perpendicular to the axial plane in the medial region, but with a well-developed lateral change of curvature (shared with *Ce. sulcata*, but not with 'A.' *cassouleti*, 'H.' *castrensis*, or *Ch. maurini*); very short pectoral scutes in the sagittal plane, but markedly expanded, towards the anterior region, laterally (not in 'A.' *cassouleti*, 'H.' *castrensis*, or *Ch. maurini*); presence of a single pair of inguinal scutes (not in *Manouria emys*); males with a well-developed ventral thickening in the area covered by the anal scutes (not shared with *Ce. sulcata*); curved diaphysis of the humerus and femur (not in 'A.' *cassouleti*); fused astragalus and calcaneum (not shared with *Chelonoidis* spp., but shared with *Ce. sulcata*). Other specimens attributed to this taxon see Pérez-García and Vlachos (2014).

Differences between *Titanochelon kayadibiensis* and *Titanochelon bacharidisi*:

1) Clearly extended gular region, beak formed, not rounded, with very strongly formed gular hump extended of the entoplastron; 2) the rounded shape of the entoplastron; 3) humero-pectoral sulcus runs along the axillar buttresses and does not flow into the axillar notch; 4) abdomino-femoral sulcus flows into the inguinal section and does not run along the inguinal buttress; 5) side edges of the caudal lobe almost straight, without insertion on the analia; 6) analia trigonal and not tetragonal and 7) anal notch extremely blunt-angled.

Titanochelon kayadibiensis sp. nov. shared: (Plate 1)

- 1) the flat anal notch and the pointed-angled anal sulcus with *Titanochelon bolivari* (Staesche et al., 2007): fig. 5) and larger *Titanochelon perpiniana* as well as the shallow rounded posterior xiphiplastral ends with *Titanochelon* cf. *schafferi* of Pikermi; 2) the rounder entoplastron with *Testudo meschetica*; 3) the missing gularia sulci on the entoplastron with *Testudo meschetica*, *Titanochelon perpiniana* and *Ergilemys insolitus*; 4) the position of the humero-pectoral-sulcus with *Titanochelon bolivari*, where in with the peripherals a hump-shaped excitation is formed. As with all other forms compared by Staesche et al., (2007), an offshoot of this sulcus approaches the axillary section as well as with *Titanochelon bolivari* the axillary on the left (Staesche et al., 2007): Fig. 5); compared to the African mainland species of giant tortoises described so far or approximately the same size is different from *Titanochelon kayadibiensis*: 5) *Geochelone stromeri* and *G. namaquensis* due to the stronger shape of the gular cave, the much clearer beak shape of the gular region and the lack of cervical; 6) *Aldabrachelys laetoliensis* and *Geochelone brachygularis* also by the more extensive gular region and the position of the highest shell elevation in the middle and not in the back half; furthermore, the characteristic dorsal hump for the latter are missing; added to this is the relatively larger entoplastron in *Titanochelon kayadibiensis*; 7) There is no relationship with the relatively large species *Impregnochelys pachytestys*. This shows features of the genus *Kinixys*.

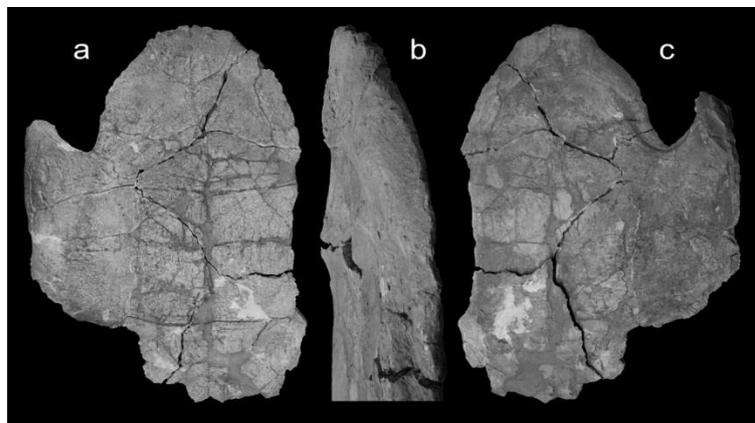


Plate 1: Photographs of the holotype of *Titanochelon kayadibiensis* n. spec. BGR — KB without number: A - Plastron in ventral view, B - in lateral view, C - Plastron in dorsal view (Scale bar 10 cm).

Genus *Protestudo* Chkhikvadze, 1970 (See Danilov et al., 2017)

Type: *Protestudo bessarabica* (Riabinin, 1918: Plate 2-3; Fig. 5-6)

PaleoDB taxon number: 399540

Synonyms: See Riabinin (1918), Luján et al. (2016), Syromyatnikova et al. (2019) [*Agrionemys bessarabica*, *Protestudo bessarabica*, *Testudo bessarabica*, *Testudo tarakliensis*].

Lectotype: PIN 1451, shell.

Description: See Riabinin, 1918; Danilov et al., 2017; Syromyatnikova et al. (2019).

Distribution: Type locality: Meotian, MN 12, Bessarabia (Moldavia); Middle Sarmatia (7.75 to 7.246 Ma), Miocene of Moldova, Ukraine, Kazakhstan and Konya (Turkey).

Environments: Floodplain, lagoonal and fluvial-lacustrine.

Character comparison with the Turkish material:

Material: KD (Fig. 8, 9, Tab. 2, 3): A juvenile specimen, anterior part destroyed. "Geochelonide"; no cervical; Caudale undivided; axillary and inguinals present; Gularia taking over 2/3 of the length of the entoplastron; entoplastron strongly rounded hexagonal, longer than wide; visceral epiplastral hump not pronounced; clear epiplastral bead developed in the formation of a gular cavern, visceral gular sulcus 35 mm long, cavern depth 10 mm; anal notch about right angle; the juvenile condition of the specimen is particularly evident in the entire plate seams, which do not show synosteoses at any point. An associated left scapula (Taf. 3: u. 4) is blunt-angled, length of the processus scapularis = 50 mm, Processus acromialis incomplete, strongly curved. Shell dimensions: CL approx. 190 mm, PL = 162 mm, PB = 146 mm, H = 108 mm, BL = 90 mm.

Characters for analysis using data by Syromyatnikova et al. (2019): 1) Number of neurals: 8 - (0) or 7 - (1); 2) Neural formula: last neurals 6-6 (0) or 6-4 - (1); 3) Peripheral I (ratio of the medial margin length to the free margin length): 0.5-0.6 - (0) or 0.7-0.8 - (1); 4) Shape of the cervical: very narrow trapezoid, slightly expanded posteriorly - (0) or normally developed, trapezoid, strongly expanded posteriorly - (1); 5) Anal notch: narrow - (0) or wide (1); 6) Midline sulcus: weakly sinuous - (0) or straight (1); 7) Analia posterior pointed out - (0) or analia rounded, notch rounded - (1).

Data matrix: NMNHU-P48-7118-0010100/ NMNHU-P48-7116-0010??/?/ NMNHU-P48-7117-0011??/?/ PIN 1451-1001110/ GLIU no number-0001110/ GKM 8027-1001110/ TKM KL 8659/EI-I-????100/ KD no number-01??011.

Out trees by PARS: (TKM KL 8659 Nedvigovka:0.00,(BGR-KD Konya-Hatunsaray-Kayadibi:3.00,GLIU Cioburciu:0.00,(GKM 8027 Cimisia:0.00,PIN 1451 Tudorovo:0.00):1.00):2.00,NMNHU-P48-7117:0.00):1.00,NMNHU-P48-7116:0.00,NMNHU-P48-7118:0.00)[0.5000];

(TKM KL 8659 Nedvigovka:0.00,(BGR-KD Konya-Hatunsaray-Kayadibi:3.00,GLIU Cioburciu:0.00,(GKM 8027 Cimisia:0.00,PIN 1451 Tudorovo:0.00):1.00):1.50,NMNHU-P48-7117:0.00):1.50,NMNHU-P48-7116:0.00,NMNHU-P48-7118:0.00)[0.5000];

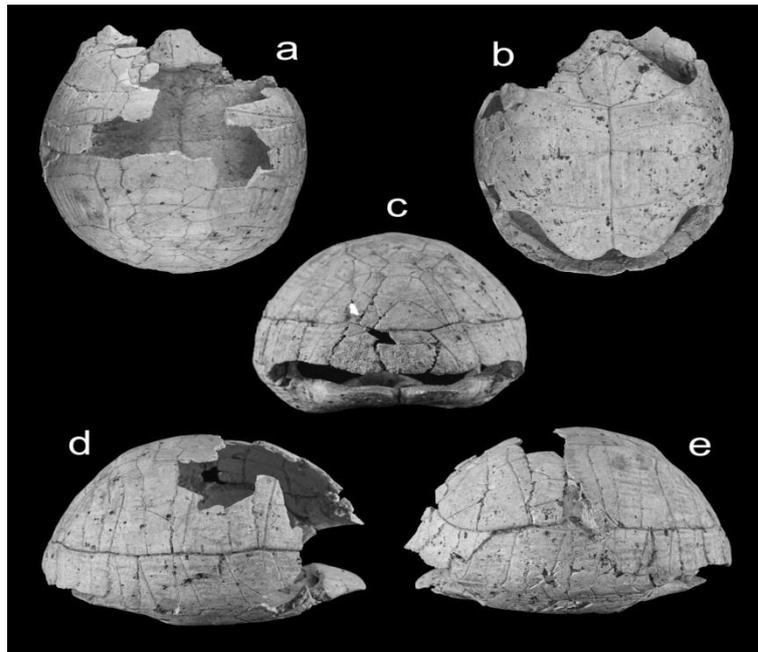


Plate 2: Photographs of the Turkish material of *Protestudo bessarabica* Riabinin 1918, BGR — KB without number: A- Carapace in dorsal view, B - plastron in ventral view, C - Shell in frontal view, D - Shell in right lateral view, E - Shell in left lateral view (Scale bar 10 cm).

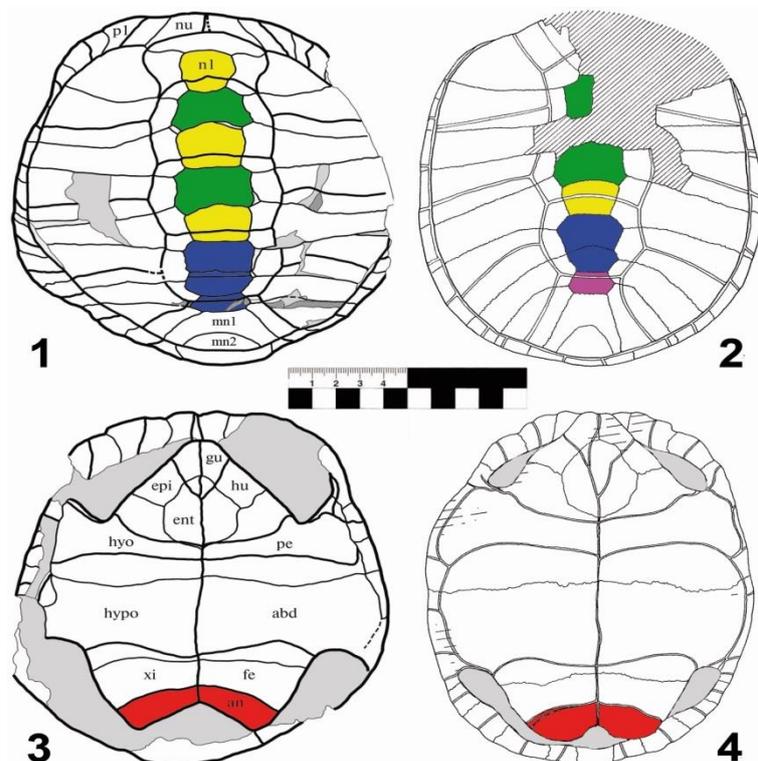


Fig. 5: Comparison of the shell characters of *Protestudo bessarabica*: Carapace dorsal view: 1 - Ukraine, 2 - Turkey; plastron ventral view: 3 - Ventral, Ukraine, 4 - Turkey (Explanations in the Text), Figures 1 and 3 adapted by Syromyatnikova et al. (2019), Figures 2 and 4 by Staesche, Karl & Staesche (2007). Scale bar 10 cm.



Fig. 6: Clusteranalysis of shell characters of *Protestudo bessarabica* from Ukraine and Turkey: Tree by PARS©Joseph Felsenstein Graphically Represented with Treeview©Roderic.

4. Discussion

Hitherto, the follow species are included in the genus *Titanochelon*: *T. bolivari*, *T. eury sternum* Gervais, 1848–1852, *T. ginsburgi* de Broin, 1977, *T. vitodurana* Biedermann, 1862, *T. leberonensis* Depéret, 1890, *T. schafferi* Szalai, 1931, *T. perpiniana* Depéret, 1885 and *T. bacharidisi* Vlachos et al., 2014. *T. kayadibiensis* sp.nov. is presented here. From an unknown Tertiary locality of Turkey, which can no longer be reconstructed, material was described as *Testudo sloani* Lydekker in 1889, which was quite incomplete, but is supposed to show characteristic features. In addition to the incomplete plastron, only the neural and most pleural still exist. The collector of this material, Sir Hans Sloan, described the material as "a petrified common land tortoise, filled with hard chalk, from Turkey". Lydekker (1889) found out that the material shows an extreme armor vault, but only a weak development of the epiplastra. In the former feature, it could roughly match the shell of the Turkish find of *Protestudo*, but not in the case of the epiplastra. The estimated length is given as over 180 mm. It is therefore more likely that the original material of *Testudo sloani* Lydekker, 1889 is a larger specimen of the *Protestudo*. Finally, the name *T. sloani* is a nomen nudum, because it was published without illustration, which was never made up later. *Protestudo bessarabica* specimens from the Belka locality are the first fossils described and figured for this species from Ukraine. Fossil finds of this species mentioned from other localities in Ukraine (Grebenik, Novaya Emetovka 2 (=Kostev ovrage), Novoyeliza-vetovka, Novoukrainka, Cherevichnaya; Danilov et al., 2017) remain undescribed. *P. bessarabica* was likely widely distributed within a narrow time period (end of the Sarmatian to Maeotian). Syromyatnikova et al. (2019) described three incomplete shells of terrestrial turtle *Protestudo bessarabica* (Testudinidae) from the Late Miocene (Maeotian, biozone MN 12) of the Belka locality (Ukraine). Materials from Belka add new data on morphology and variation of the *P. bessarabica* shell in the formula of the neural plates, the shape of the precentral scale and the gular projection. Additionally, materials from Belka confirm the previously known variation of the shell of *P. bessarabica* in other characters. Redkozubov et al (2020) described the new species *Chersine khosatzkyi*, from the early Pliocene of the Musait and Colibasi localities of Moldova, based on an incomplete shell. That species can be distinguished from all other species of *Chersine* by relatively wide posterior lobe of the plastron with nearly parallel lateral borders and presence of additional suprapygal, and show no relations with *Protestudo*.

Staesche et al. (2007) interpreted and described these Turkish samples in detail. They revised and formulated a synopsis on palaeoecological reconstruction based on these forms of Eurasian giant land tortoises. Garcia and Vlachos (2014) described the European Cenozoic taxa on their phylogenetic relationships. They identified the large testudinids from the Neogene of Europe as belonging to a monophyletic clade, assigned to the new genus *Titanochelon*. Its comparison with the other Neogene species allowed a detailed study of the new genus and an analysis of its phylogenetic relationships with the other European taxa. Vlachos et al. (2019) described the Neogene chelonian diversity in northern Greece with the present description of a new species of *Mauremys* (Testudines, Geoemydidae) from the late Miocene to Pliocene of three localities in central Macedonia (Gefira-2, Nea Silata, Allatini). *Mauremys aristotelica* Vlachos et al., 2019 - is characterized by the presence of exceptionally wide vertebral scutes, a trait that is quite rare within *Mauremys* but has evolved independently in other pan-testudinoid non testudinid. Total evidence phylogenetic analysis confirms the placement of the new species within *Mauremys* and reveals that its closest relative is *Mauremys campanii* from the late Miocene of Italy. It is also likely, under parsimony that all geoemydidae with similarly wide vertebral scutes from the Neogene of Eurasia form a clade nested within *Mauremys*. Our results also shed some light on the evolution of Geoemydids.. oder Testudinids ? in the eastern Mediterranean during late Miocene to Pliocene times. The recent advances in our knowledge of the anatomy and taxonomy of the Neogene large testudinids from Europe highlight that the Middle Miocene was an important period for the diversification of this clade. First of all, the tortoises from Europe achieve a large size for the first time in their evolutionary history during the Late Langhian - Middle Serravallian interval (i.e. the Late Orleanian - Middle Astaracian, MN5-MN6) (see Pérez-García & Vlachos, 2014), following a trend toward increased size known from the Eocene (Pérez-García et al., 2016). The materials described herein represent the westernmost records of *Titanochelon* in the European continent, not only for the Middle Miocene but for all the Neogene. Middle Miocene confirmed records of taxa *Titanochelon* and *Protestudo* are known in Turkey. Vlachos et al. (2020) take it for "possibly 'Agrionemys' " but our cluster analysis shows a position within the *Protestudo*-cluster. According to Vlachos et al. (2020) *Testudo marmorum* Gaudry, 1862 the iconic 'marble tortoise,' is known from Greece and the South Balkans and we subordinate to that species our single shell elements of provisorily *Testudo* cf. *graeca* Linnaeus, 1758 correspondingly (Staesche et al., 2007). The same procedure we use with our very pure plate remains of *Mauremys* cf. *caspiica* (Gmelin, 1774) and *Clemmydopsis* cf. *turnauensis* (Meyer, 1847) as synonyms of *Mauremys aristotelica* Vlachos et al., 2019.

Updated list for the fossil turtles of Turkey:

1) Order Testudines Batsch, 1788

Infraorder Cryptodira Cope, 1868

Superfamily Trionychoidea Fitzinger, 1826

Family Trionychidae Fitzinger, 1826

Genus *Trionyx* Geoffroy Saint-Hillaire, 1809

Trionyx triunguis (Forskål, 1775)

• syn. *Trionyx triunguis* (Forskål, 1775) according to Staesche et al., 2007

2) Superfamily Testudinoidea Batsch, 1788

Family Geoemydidae Rafinesque, 1815

Genus *Mauremys* Gray, 1869

Mauremys aristotelica Vlachos, Sterli, Vasileiadou & Syrides, 2019

- syn. *Mauremys* sp. cf. *caspica* (Gmelin, 1774) according to Staesche et al., 2007
- syn. *Clemmydopsis* cf. *turnauensis* (H. v. Meyer, 1847) according to Staesche et al., 2007

3) Family Testudinidae Batsch, 1788

Genus *Testudo* Linnaeus, 1785

Testudo marmorum Gaudry, 1862

- syn. *Testudo* sp. cf. *graeca* ssp. Linnaeus, 1758 according to Staesche et al., 2007

4) Genus *Protestudo* Chkhikvadze, 1970

Protestudo bessarabica Riabinin, 1918

- syn. juvenile *Cheirogaster* spec. cf. *bolivary* Hernández-Pacheco, 1917 according to Staesche et al., 2007

5) Genus *Titanochelon* Pérez-García and Vlachos, 2014

Titanochelon kayadibiensis sp.nov.

- syn. adult *Cheirogaster* spec. cf. *bolivary* Hernández-Pacheco, 1917 according to Staesche et al., 2007.

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