



A taxonomic reassessment of the Upper Pliocene Pond turtle, *Melanochelys mossoczyi wetterauensis*, from the lignite coal mines of Wetterau, Hesse, Germany

Hans-Volker Karl^{1*}, Amtyaz Safi², Gottfried Tichy³

¹Department of Prehistory and Early History, Friedrich Schiller University, Löbdergraben 24a, Jena 07743, Germany, <https://orcid.org/0000-0003-1924-522X>

²Department of Zoology (Wildlife Section), University of Karachi 75270, Pakistan, <https://orcid.org/0000-0002-4484-3224>

³Department of Geography and Geology, Paris Lodron University of Salzburg, Hellbrunnerstrasse 34, 5020, Austria

*Email: hvkarl@icloud.com

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Abstract

An overview description of the taxonomical feature of the Upper Pliocene turtle's remains from the Wölfersheim brown coal deposit in the Wetterau, Hesse, Germany is given here. The original material came from the former "Natural Science Collections" in Meiningen (1950-1960) as an exchange sample and is now preserved as a holotype "MSB IB k 314" in the "Museum of Natural History" Schleußingen, Thuringia, Germany. The material was scientifically described previously as a member of the genus *Geoemyda* and is reviewed again here. This taxon is reassessed and re-identified as being in close relationship with the European taxon of *Melanochelys mossoczyi* (Previously referred to as *Geoemyda mossoczyi*).

Keywords: *Melanochelys*, Upper Pliocene, Wetterau, Hesse, Germany

Introduction

Testudines (Chelonii) are among the most common and well-preserved fossilized organisms, these are useful paleo-biogeographical indicators as their exoskeletons include shell elements that are durable and amenable to fossilization and allow clear inferences about their strong phylogenetic relationships to other members. Detailed studies of the paleo-biogeographic patterns can be developed by comparing fossils of different eras and areas. Resolving the phylogeny of extinct turtle remains is one of the unique challenges in the fields of evolution and paleontology. Equivocal reconstructions of turtles remain to find the evolutionary and

paleo-climatic data with phylogenetic hypotheses are important for prehistoric turtle fossil remains (Karl et al., 2024). Keeping this advantage in mind, we have been re-investigating the taxonomic status and phylogenetic affinities of fossil terrestrial turtles which were discovered in the upper Pliocene era, from the lignite coal mines of Wetterau, Germany (Fig. 1a & 1b) by making detailed comparisons Karl (1983) named it as *Geoemyda mossoczyi*. Here, we briefly review the fossil remains of a turtle and discuss its taxonomic status and its paleo-biogeographic implications, however, due to the paucity of appropriate comparisons most of the taxonomic status and phylogenetic affinities of most of the fossils remain are uncertain (Takahashi et al., 2007; 2008). Wölfersheim is located in the former Wetterau lignite mining area; the former coaling basin is now the Wölfersheimer (Lake Wölfersheim). It was operated from 1913 to 1991 by Preußische Electricity AG brown coal mining has been going on since the beginning of the 19th century; from 1962 onwards, the coal for the power plant was only mined in opencast mines. The original material came to the former Natural Science Collections in Meiningen in the 1950s and 1960s by Johannes Friedemann Schaarschmidt (1934-2005) as an exchange sample and is now in the collection of the Museum of Natural History Schleußingen, Thuringia, Germany. The material was scientifically described for the first time by Karl (1983) as a member of the genus *Geoemyda/ Melanochelys* and is reviewed here again. We provide an extensive description and diagnosis of *Geoemyda* based on the re-examination of the holotype. The phylogenetic analysis concludes that this taxon is a member of the Geoemydidae family (Formerly Bataguridae), which includes freshwater hard-shell turtles. The Geoemydidae are one of the largest and most diverse families in the order Testudines (turtles), with about more than 70 species. The family includes the Eurasian pond and river turtles and Neotropical wood turtles. We also provide an updated account of the paleoecology and biogeography of the group, including both extinct and extant species. These are now considered distinct and placed in the genera *Heosemys*, *Leucocephalon*, *Melanochelys*, *Siebenrockiella/ Panayanemys*, and *Vijayachelys*. The genus *Geoemyda/ Melanochelys* had once accommodated various extant and extinct lineages as a “Catchall taxon” (Wermuth & Mertens, 1961; Takahashi et al., 2007; 2008), but recent taxonomic and phylogenetic studies established the consensus that this genus consists of only two living species (*Geoemyda japonica*, and *Geoemyda spengleri*), all other are extinct species (TTWG (2021).

1. Ryukyu black-breasted leaf turtle, *Geoemyda japonica*, (Fan 1931)
2. Black-breasted leaf turtle, *Geoemyda spengleri* (Gmelin, 1789). All other species of this genus are considered as extinct;

3. *Geoemyda amamiensis* (Takahashi et al., 2007), Amami Leaf Turtle; This species was probably terrestrial and is most closely related to modern *Geoemyda japonica*, a terrestrial species that occurs in the Ryukyu Archipelago (TEWG, 2015).
4. Another extinct species is *Geoemyda eureia* (Wegner), discovered in Poland.
5. *Geoemyda* (*Geoliemys*) Matsumoto 1929:
6. *Geoemyda headonensis* Hooley 1905,
7. *Geoemyda malustensis* Macarovici and Vanca 1960,
8. *Geoemyda mossoczyi* Mlynarski 1964,
9. *Geoemyda pidoplickai* Khosatzky 1946,
10. *Geoemyda ptychogastroides* Hummel 1935 (Synonym of *Geislemys* Khosatzky & Mlynarski 1966, 1976),
11. *Geoemyda striata* Deraniyagala 1969.



Fig 1a. Schematic map of Central Europe with the extent of the Hessian brown coal mining area.

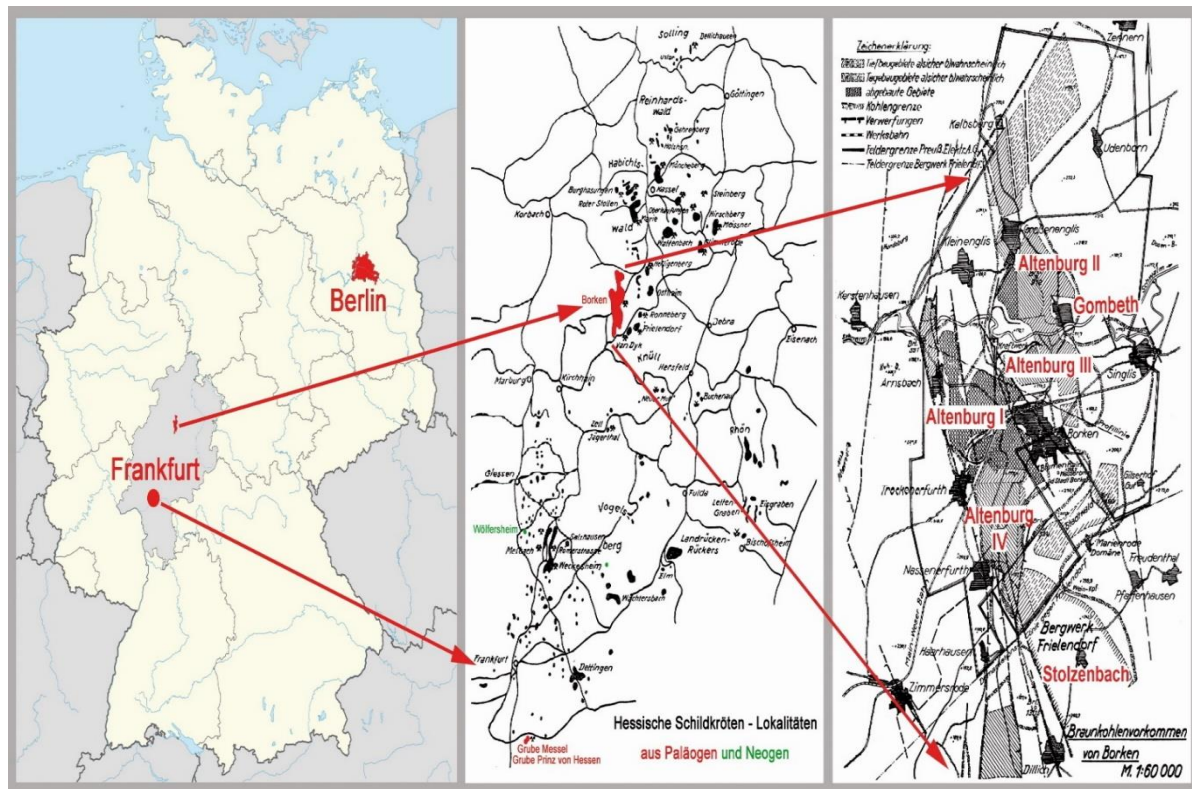


Fig 1b. 1 = Location of the state of Hesse in Germany and position of Frankfurt am Main. 2 = Detail of the area of North Hesse and the former lignite deposits about other turtle localities, red = Paleogene (Messel and Prinz von Hesse mines and green = Neogene (Wölfersheim, Wetterau lignite mining area). 3 = Brown coal deposits from Borken with the turtle locations Altenburg IV and Gombeth. 1 = according to the map “NordNordWest, License: Creative Commons by-a-3.0 de”, 2 and 3 according to Steckhan (1952). The discovery of the Neogene turtle material from Wölfersheim is in the economic context of the Paleogene Lower Hesse brown coal mining area around Borken.

Material and methods

The fossil terrapin described herein was discovered from the Upper Pliocene turtle remains from the Wölfersheim brown coal deposit in Wetterau, Hesse, Germany. This study is based on turtle shell fragments from this locality. Wölfersheim is located in the former Wetterau lignite mining area; the former coaling basin is now the Wölfersheimer (Lake Wölfersheim). It was operated from 1913 to 1991 by Preußische Electricity AG brown coal mining has been going on since the beginning of the 19th century; from 1962 onwards, the coal for the power plant was only mined in opencast mines. The original material came to the former Natural Science Collections in Meiningen in the 1950s and 1960s by Johannes Friedemann Schaarschmidt (1934-2005) as an exchange sample and is now in the collection of the Museum of Natural History Schleußingen, Thuringia, Germany. The material was scientifically described for the first time by Karl (1983) as a member of the genus *Geoemyda* and is reviewed here again. Here, the fossils are prefixed by the acronym B, followed by a collection number. These comprise the

isolated elements collected by screen-washing or surface prospecting. All material was photographed using a Nikon D 90 camera, and the standard anatomical orientation system is used throughout this paper.

Terminology on the shell of a pond turtle (Fig 2, 5-6; Plate 1-2):

Anatomical terms of the shell follow those of Zangerl (1969). The terminology of the carapace of a turtle is shown in the individual figures according to Karl & Paust (2014). The following correspond: Carapace plates (bones): nuchal = nu, neurals = n I to n VIII, pleurals = pl I to VIII, peri-pheralals = pe I to pe XI, meta-neurals = mn I to II, pygal = pyg. Carapace shields (horn): cervical = ce, centrals = c 1 to c 5, laterals = l 1 to l4, caudal = ca. Plastron plates (bones): epiplastrals = epi, entoplastron = ento, hyoplastrals = hyo, hypoplastrals = hypo, xiphiplastrals = xiphi. Plastron shields (horn): Gulars = gu, Humerals = hu, Pectorals = pec, Abdominals = ab, Femorals = fe, Anals = an.

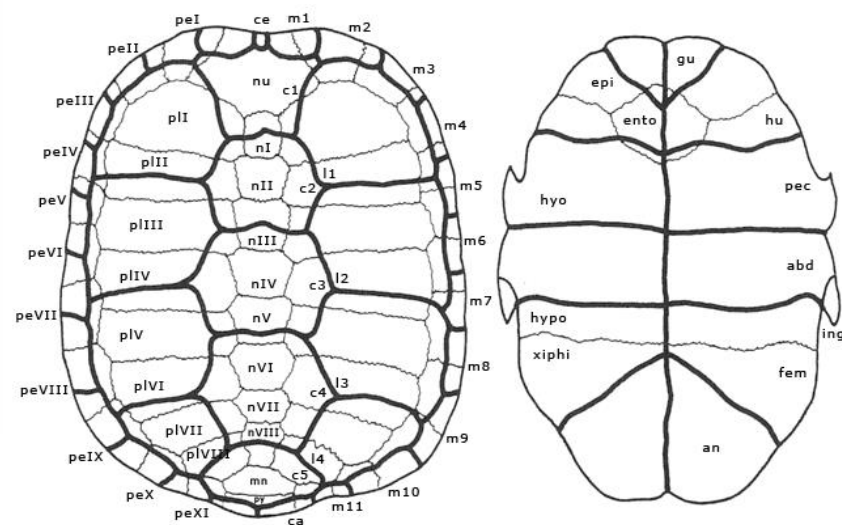


Fig 2. Terminology on the shell of a pond turtle.

Anatomical terms in the text follow Zangerl (1969) and are abbreviated in the figures as:

Ab = abdominal scute, An = anal scute, Ce = cervical scute, co = costal bone, ento = entoplastron
 epi = epiplastron, Fe = femoral scute, fo = fontanelle, Gu = gular scute, Hum = humeral scute
 hyo = hyoplastron, hypo = hypoplastron, lg = inguinal scute, Ma = marginal scute, mdf = musk duct foramina
 ne = neural bone, nu = nuchal bone, Pe = pectoral scute, per = peripheral bone, Pl = pleural scute
 py = pygal bone, spy = suprapygal bone, Ve = vertebral scute, xi = xiphiplastron

Systematic palaeontology (Fig 3)

Geoemydidae Theobald 1868

Geoemydinae Theobald 1868

Geoemyda Gray 1834b

Geoemyda mossoczyi/Melanochelys mossoczyi (Młynarski 1964)

(Late Miocene to Early Pleistocene) Mossoczy's Pond Turtle.

Synonyms: *Geoemyda mossoczyi* Młynarski 1964: 335 [Pliocene to Pleistocene, Poland]; *Geoemyda (Heosemys) mossoczyi*, *Sakya mossoczyi*, *Clemmydopsis mossoczyi*, *Melanochelys mossoczyi*, *Geoemyda (Heosemys) boristhenica* Tarashchuk 1971: 56 [Middle-Upper Pliocene, Ukraine]; *Geoemyda (Heosemys) mossoczyi wetterauensis* Karl 1983: 375, *Melanochelys mossoczyi wetterauensis* (Karl 1983 in part.) [Upper Pliocene, Wetterau, Hesse, Germany]. According to TEWG (2015), *Geoemyda m. wetterauensis* is also listed under *Melanochelys mossoczyi*.

Type material: NWSM¹ IE k 313; Fragmentary remains of an approximately 8 cm long animal consisting of an entoplastron (plate 2, figure 1), neural V (plate 2, figure 2), hyoplastron fragment (sin.) (plate 2, figure 12-12a), a peripheral (fragm.) from the caudal area (plate 2, figure 3), eight various pleural fragments (plate 2, figure 4-11) and two plastron fragments (indet.) (plate 2, figure 13-14) Karl (1983).

Further material: NWSM IE k 314 (plate 3); fragmentary remains of an approximately 15 cm long animal including a fragmentary peripheral, an epiplastron fragment, an incomplete hyoplastron (dex.) with the attachment of the axillary support, a fragment of a hyo- or hypoplastron from the area of the hyo-hypoplastral suture as well as two further plastron fragments from the edge area and two humerus or femur fragments (see plate 3), Karl (1983).

Geographical and stratigraphic distribution: Wölfersheim, Wetterau, Hesse. Upper Pliocene, Piacenzian MN 16: Layer of the Pliocene lignite seam from a level lying between the Montpellier-Roussillon faunas of Val d'Arno, Seneze, Pardines, Roccaneyra, and Tegelen (Tobien 1952; Karl 1983).

Type localities: Poland, Moldavia, Russia, Slovakia, Ukraine, Germany

Size: CL ca. 20 cm

Synonyms: *Geoemyda mossoczyi* † Młynarski 1964:335 [Pliocene to Lower Pleistocene, Poland], *Geoemyda (Heosemys) mossoczyi*, *Sakya mossoczyi*, *Clemmydopsis mossoczyi*, *Melanochelys mossoczyi*, *Geoemyda (Heosemys) boristhenica* † Tarashchuk, 1971:56 [Middle to Late Pliocene, Ukraine]

Geoemyda (Heosemys) mossoczyi wetterauensis † Karl 1983:375 [Late Pliocene, Wetterau, Hesse, Germany], *Melanochelys mossoczyi wetterauensis*

Comments and referred materials: Lapparent de Broin (2001) indicated that this taxon from the Plio-Pleistocene boundary might be referred to either *Sakya* Bogachev 1960 or

Clemmydopsis Boda 1927. It was referred to as *Melanochelys* by Chkhikvadze (1989) and Danilov et al. (2012, 2013). Generic placement uncertain, sometimes referred to as “*Melanochelys*”. The Late Pliocene taxa *Geoemyda boristhenica* and *Geoemyda wetterauensis* may or may not be distinct, but are tentatively listed for now as synonyms under *M. mossoczyi* (TEWG, 2015).

A related referred species of Sub-Family Geoemydinae Theobald 1868, *Melanochelys trijuga*, Gray, 1869: (Fig. 4)

Type species: *Emys trijuga* Schweigger 1812 (Schweigger 1812).

Holotype: According to Iverson (1992, 2022) in the MNHN, without further information.

Diagnosis: See Das (1991, 1998)

Further species: *Melanochelys etulensis* Khosatzky & Redkozubov 1986 (Lower Pliocene-Lower Pleistocene, Moldavia), *Melanochelys pidoplickoi* (Khosatzky 1946) (Lower Pliocene-Lower Pleistocene of Ukraine, Moldova and Russia), *Melanochelys sinhaleyus* Deraniyagala 1953 (Late Pleistocene, Sri Lanka), *Melanochelys tricarinata* (syn. *Nicoria tricarinata* Lydekker, 1889, *Nicoria tricarinata sivalensis* Lydekker 1889).

Description

Geoemyda is now considered distinct and placed in the genera *Heosemys*, *Leucocephalon*, *Melanochelys*, *Siebenrockiella*/ *Panayanemys*, and *Vijayachelys*, this contains two living species: Ryukyu black-breasted leaf turtle, *G. japonica*, and Black-breasted leaf turtle, *G. spengleri* (TTWG (2021), which are found in East and Southeast Asian countries, while most of the fossil remains from extinct species are discovered from Europe. These fossils recorded species are Genus *Geoemyda* (*Geoliemys*) Matsumoto 1929: *Geoemyda amanuensis* Takahashi et al. 2008, *Geoemyda eureia* Wegner 1913, *Geoemyda headonensis* Hooley 1905, *Geoemyda malustensis* Macarovici and Vanca 1960, *Geoemyda mossoczyi* Mlynarski 1964, *Geoemyda pidoplickai* Khosatzky 1946, *Geoemyda ptychogastroides* Hummel 1935 (synonym of *Geislemys* Khosatzky & Mlynarski 1966, 1976), and *Geoemyda striata* Deraniyagala 1969.

Entoplastron has the outline of a rhombus, somewhat blunted in the frontal area and rounded in the caudal area, humero-pectoral suture divides the entoplastron exactly in the middle, middle suture and the ends of the gular sutures that converge at it are present on the entoplastron; Neural III or V divided into almost equal halves by horizontal suture of the Centralia, the shape of this neural typical geoemydal. without signs of keel formation or sculpting; Inguinal and axillary supports weakly developed, sculpting on the plastron concentric but very delicately developed, fine-grained, areoles on the plastron form characteristic figures, lateral caudal

peripherals slightly protruding, comma-shaped in cross-section, gular ridges strongly developed, caudal plastral part mobile (Karl 1983).

Remarks: The Mossoczy's forest turtle is known from the Upper Miocene to the Lower Pleistocene from Poland, Moldova, Russia, Slovakia, Ukraine, and Germany. Bachmayer & Mlynarski (1984) believe, contrary to Ckhikvasze (1973, 1983), that all these fossil species do not belong to *Melanochelys* Gray, 1869. In their opinion, these turtles did not occur in the European Tertiary. The turtles discussed include some specific characteristics of the two subgenera *Geoemyda* and *Melanochelys*, but not of *Heosemys*, as had been thought until then. According to Lapparent de Broin (2001), this taxon from the Plio-Pleistocene boundary also shows similarities to the genera *Sakya* Bogachev 1960 and *Clemmydopsis* Boda 1927. Chkhikvadze (1989) and Danilov et al. (2012, 2013, 2017) referred to the genus *Melanochelys*, in the latter work, these are listed in open nomenclature under *Geoemyda*. No relevant section remains are preserved in either sample besides from the confirmed ectoplasm (Plate 3).

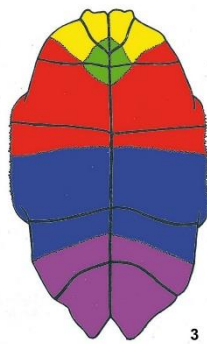


Fig 3. *Melanochelys mossoczyi*, schematic plastron view according to Młynarski: epiplastrals = yellow, entoplastron = green, hyoplastrals = red, hypoplastrals = blue, xiphiplastrals = violet.



Fig4. *Melanochelys trijuga* (Schweigger, 1812), plastral view according <https://indiabiodiversity.org/species/show/238667> detected on 24.01.2024, 7.44 pm.

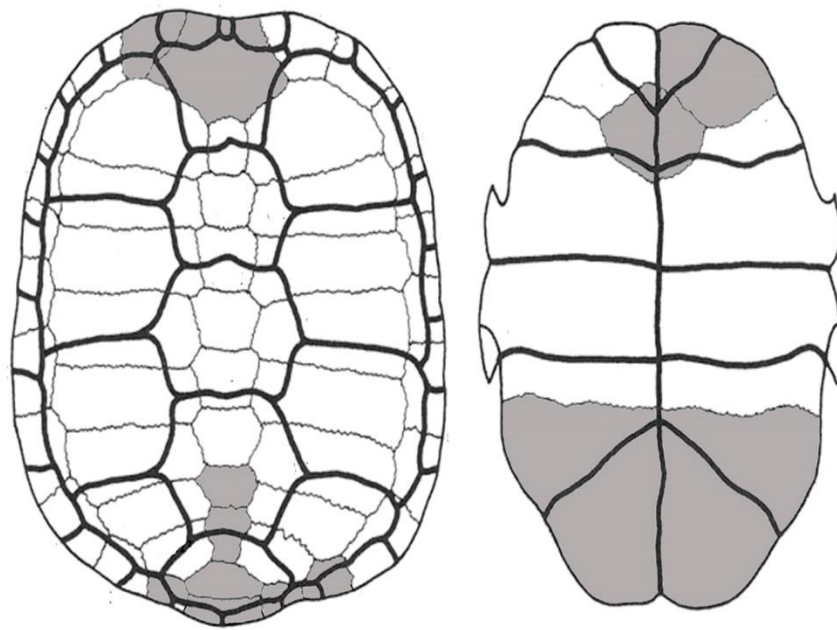


Fig 5. Schematic representation of the shell of a pond turtle as in Figure 2 shows the distribution of the preserved shell parts of the original material of *G. mossoczyi*.

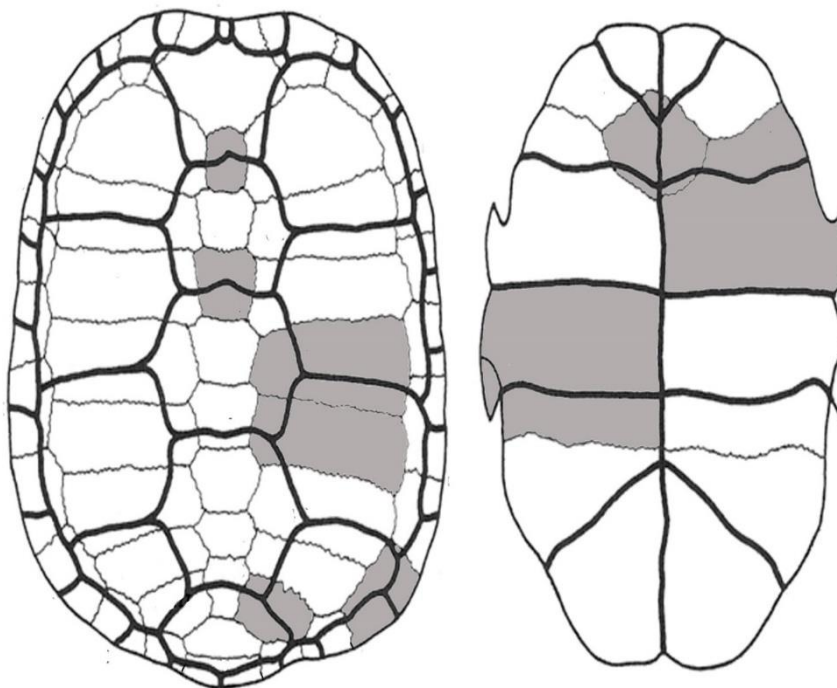


Fig 6. Schematic representation of the shell of a pond turtle as in Figure 2 shows the distribution of the preserved shell parts of the original material of *G. m. wetterauensis*.

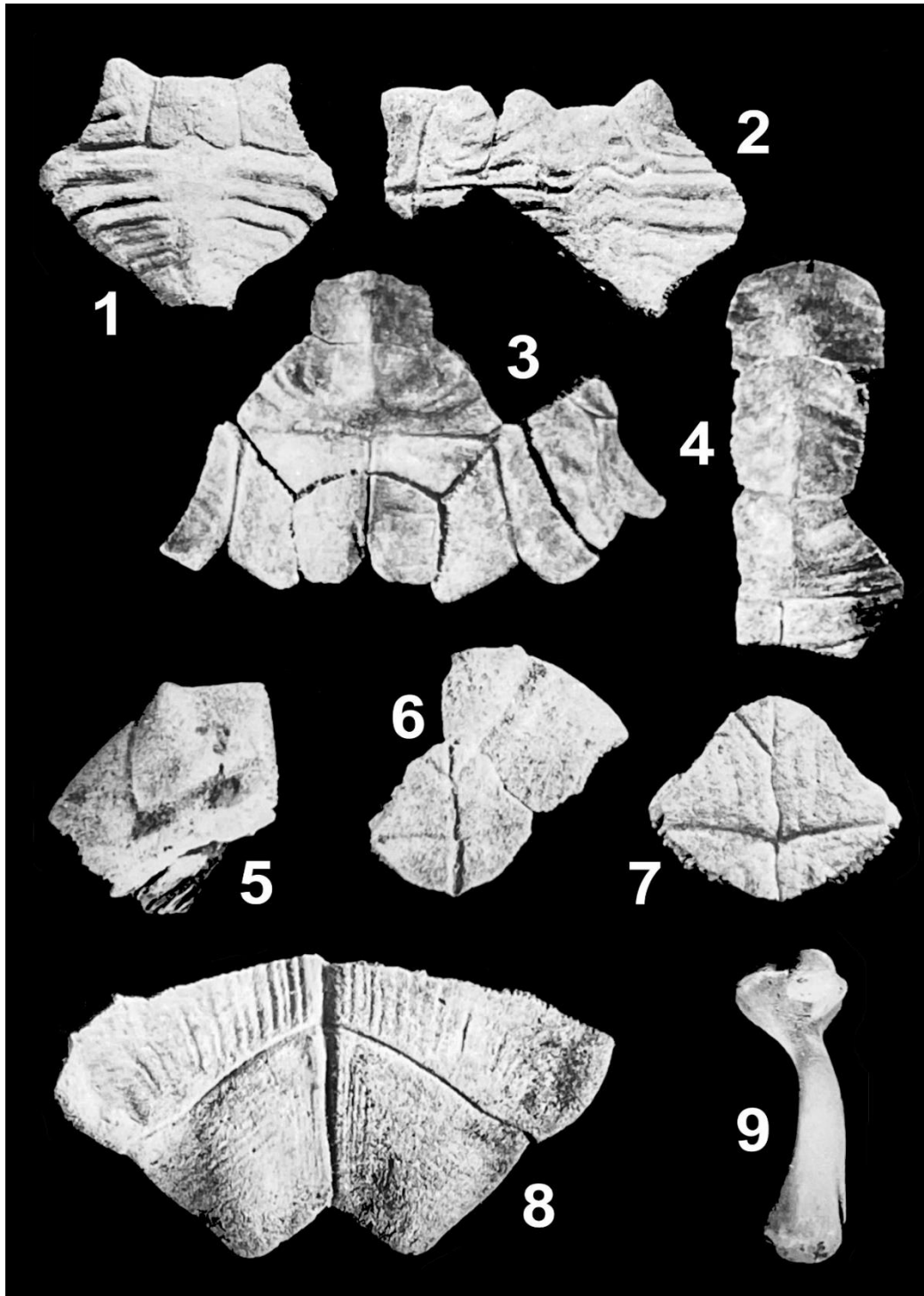


Plate 1: *Melanochelys mossoczyi*, original material according Młynarski (1964): 1 = nuchal plate, adult (length 27 mm, width 31 mm); 2 = nuchal plate fragment with left first peripheral fragment, adult (length 23.3 mm, width 33.2 mm); 3 = pygal part of the carapace with metaneurals I-II, pygal, right peripheral X and both XI, adult (length 36 mm, width 56 mm); 4 = last neural plate with metaneural I, adult (length 37.8 mm); 5 = epiplastral plate visceral, adult (length 43.4 mm, width 22.1 mm); 6 = epiplastral plate and entoplastron, juvenile (length 25.6 mm); 7 = entoplastron, adult (length 19.8 mm); 8 = both xiphiplastrals, adult (length 47 mm, width 73 mm); 9 = left humerus, juvenile (length 19.8 mm).

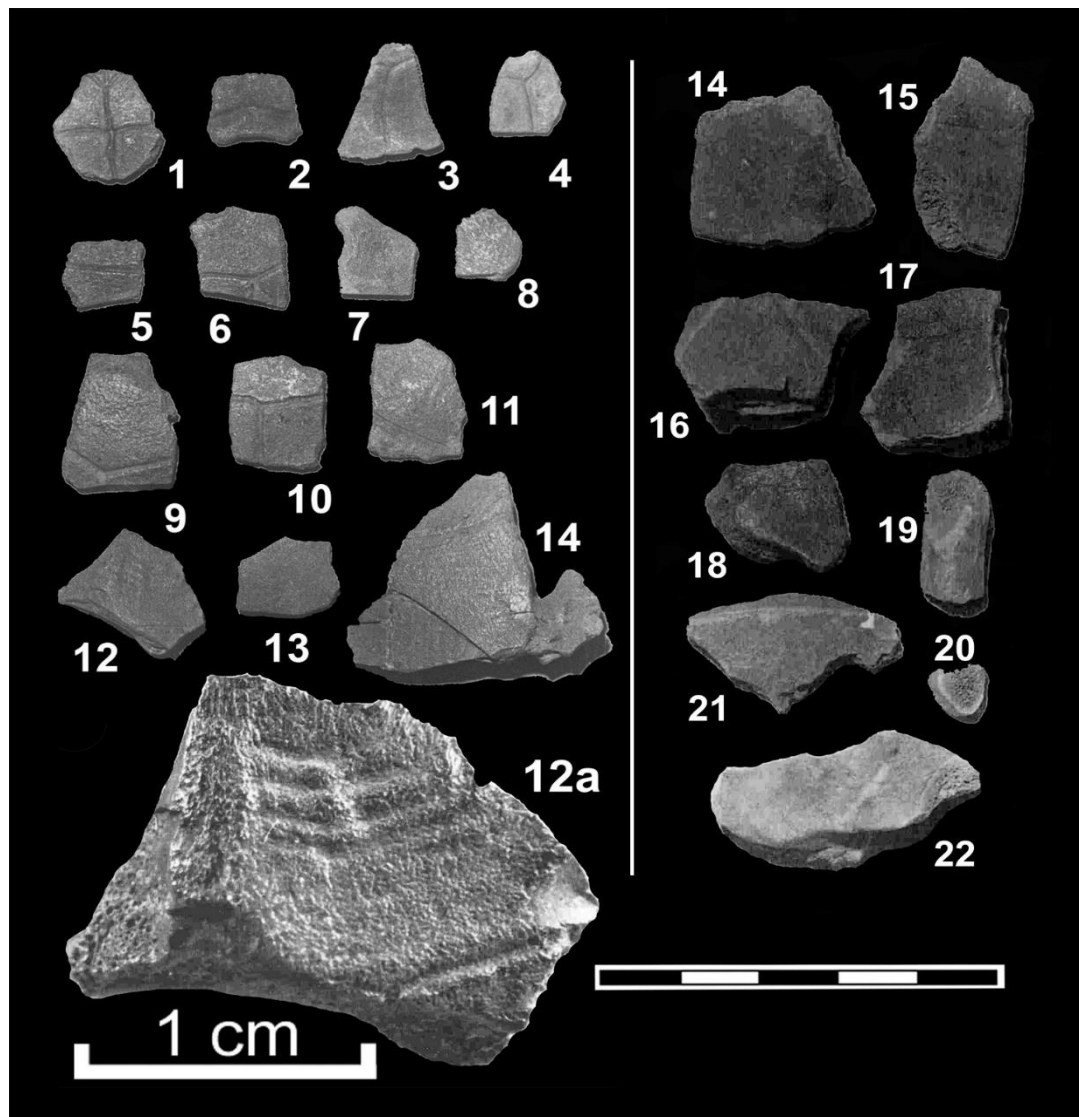


Plate 2: *Melanochelys mossoczyi* (syn. ssp. *wetterauensis*): MSB IB k 313, original material to Karl (1983), explanations in the text, scale 5/ 1 cm.

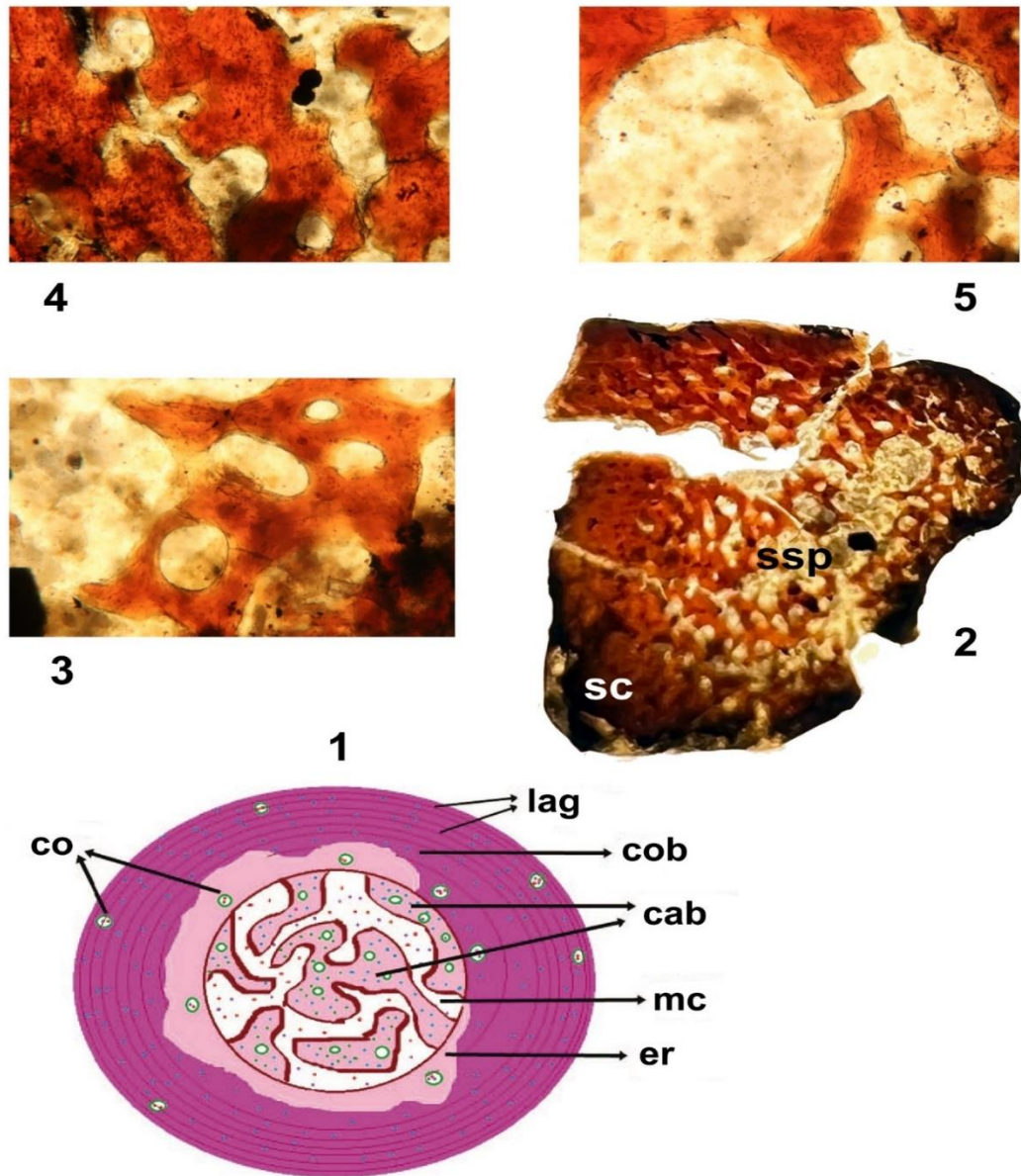


Plate 3: *Melanochelys mossoczyi* (syn. ssp. *wetterauensis*): MSB IB k 314, original material to Karl (1983).

Plate 3.1 - Schematic view of the cross-section of a hypothetical freshwater turtle humerus according to Çiçek et al (2016).

Plate 3.2 - Light micrograph of a thin section of extremity fragment NWSM IE k 314.

Plate 3.3-3.5 - Enlarged sections of the substantia spongiosa.

Abbreviations: so - secondary osteon, lag - lines of arrested growth, cob - compact bone, cab - cancellous bone, mc - marrow cavity, er - endosteal resorption, sc - substantia compacta, ssp - substantia spongiosa. Photos Ivonne Przemuß, Friedrich-Schiller-Universität Jena.

¹ NWSM=Natural Science Collections Meiningen (old)

Dataset for plastral character analysis with PARS: 1- ento l<b, 2 - ento l=b, 3 - ento l>b, 4 - gular suture anterior, 5 - gular suture medial, 6 - hum-pect posterior, 7 - hum-pect medial, 8 - Sculpture present, 9 - Gularzack present, 19 - fusions of horn shields present, 11 - movable shell elements present.

Mauremys caspica 10010100000/ *Geoemyda eureia* 01010011101/ *Geoemyda mossozcyi* 01010011101/ *Geoemyda wetterauensis* 01010011?01/ *Geoemyda malustensis* 01010011?01/ *Clemmydopsis sopronensis* 10010101010/ *Sakya pontica* 10001010010/ *Emys orbicularis* 10010100001/ *Ptychogaster emydoides* 00100100101/ *Testudo marginata* 10010001000 using Macarovici & Vancea (1960).

PARS - Discrete character parsimony algorithm, version 3.6a3, 4 trees in all found

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1 - (*Sakya pontica*:5.00,(*Testudo marginata*:1.00,*Clemmydopsis sopronensis*:1.00):1.00,(*Emys orbicularis*:0.00,(*Ptychogaster emydoides*:2.00,(*Geoemyda mossoczyi*:0.00,*Geoemyda wetterauensis*:0.00,*Geoemyda malustensis*:0.00,*Geoemyda eureia*:0.00):4.00):2.00):1.00,*Mauremys caspica*:0.00)[0.2500];

2 - ((*Testudo marginata*:1.00,*Sakya pontica*:4.00):1.00,*Clemmydopsis sopronensis*:2.00,(*Emys orbicularis*:0.00,(*Ptychogaster emydoides*:2.00,(*Geoemyda mossoczyi*:0.00,*Geoemyda wetterauensis*:0.00,*Geoemyda malustensis*:0.00,*Geoemyda eureia*:0.00):4.00):2.00):1.00,*Mauremys caspica*:0.00)[0.2500];

3 - (*Testudo marginata*:2.00,(*Sakya pontica*:4.00,*Clemmydopsis sopronensis*:1.00):1.00,(*Emys orbicularis*:0.00,(*Ptychogaster emydoides*:2.00,(*Geoemyda mossoczyi*:0.00,*Geoemyda wetterauensis*:0.00,*Geoemyda malustensis*:0.00,*Geoemyda eureia*:0.00):4.00):2.00):1.00,*Mauremys caspica*:0.00)[0.2500];

4 - ((*Ptychogaster emydoides*:4.00,*Emys orbicularis*:0.00):1.00,(*Clemmydopsis sopronensis*:1.00,(*Testudo marginata*:0.00,(*Sakya pontica*:4.00,(*Geoemyda mossoczyi*:0.00,*Geoemyda wetterauensis*:0.00,*Geoemyda malustensis*:0.00,*Geoemyda eureia*:0.00):4.00):1.00):1.00,*Mauremys caspica*:0.00)[0.2500];

Abundance of the vertebrate fauna of Wölfersheim

Tobien (1952) gives the following taxa list for the Wölfersheim fauna, including the mammals: *Anancus arvernensis* (Croizet & Jobert, 1828); *Zygodolophodon borsoni* (Hays, 1834); *Tapirus arvernensis* Croizet & Jobert, 1828; *Dicerorhinus* (syn. *Rhinoceros*) *megarhinus* (De Christol, 1834); *Sus minor*; Cervidae Goldfuss, 1820; *Ursus arvernensis* Croizet & Jobert, 1828; *Pareilurus* Schlosser, 1899; *Pannonictis* Kormos, 1931; *Mustela palermina* Petényi, 1934; *Castor* Linnaeus, 1758; *Trogontherium* Fischer von Waldheim, 1809; Sciuridae Gray, 1821;

Glires Linnaeus, 1758 (=Myoxidae); *Mus* cf. *sylvaticus* Linnaeus, 1758; Cricetidae Kurten & Anderson, 1980 (=Microtinae); *Prolagus* Pomel, 1853; Leporidae Fischer von Waldheim, 1817; *Desmana* Guldenstaedt, 1777; *Galemys* Kaup, 1829; Talpidae Fischer von Waldheim, 1817; Soricidae Fischer von Waldheim, 1814; *Macacca* Lacépède, 1799; furthermore reptiles like Lacertilia Owen, 1842; amphibians like Anura Fischer von Waldheim, 1813 and fishes like Cyprinodontoidae Gill, 1865. The turtle material classified here as the Geoemydid turtle, *Melanochelys* is the only one described from that locality so far. The composition of the complete fauna of upper Pliocene Wölfersheim shows members of a forest biotope around a lake or swamp area which formed a lignite forest (Brown coal).

Summary

The first material belonging to this complex was identified by Wegner (1913), supplemented by Młynarski (1959), newly described by Młynarski (1964), and systematically summarized for the first time by Khosatzky & Młynarski (1966), see also Młynarski (1969, 1976). In 1983, Karl described material from Germany under the name *Geoemyda* (*Heosemys*) *mossoczyi wetterauensis*. In the current version of TEWG (2015) it is listed as a synonym of *Melanochelys mossoczyi* (Młynarski, 1964): (Late Miocene to Early Pleistocene) Mossoczy's Pond Turtle from Poland, Moldavia, Russia, Slovakia, Ukraine, Germany; carapace length ca. 20 cm: *Geoemyda* (*Heosemys*) *mossoczyi wetterauensis*† Karl, 1983 [Late Pliocene, Wetterau, Hesse, Germany], *Melanochelys mossoczyi wetterauensis*; Comment: Lapparent de Broin (2001) indicated that this taxon from the Plio-Pleistocene boundary might be referred to either *Sakya* Bogachev 1960 or *Clemmydopsis* Boda 1927. It was referred to *Melanochelys* by Chkhikvadze (1989) and Danilov et al. (2012, 2013). Generic placement uncertain, sometimes referred to as “*Melanochelys*”. The Late Pliocene taxa *Geoemyda boristhenica* and *Geoemyda wetterauensis* may or may not be distinct, but are tentatively listed for now as synonyms under *M. mossoczyi*. In principle, the material used so far is fragmentary, so we need more complete findings. In all possible trees, the character complexes of *mossoczyi*, *wetterauensis*, *malustensis*, and *eureia* lie close together, which could indicate systematic proximity, at least the belonging of *Mossoczyi* and *wetterauensis* to a common taxon.

Acknowledgments

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