

HUMBOLDT-UNIVERSITÄT ZU BERLIN



LEBENSWISSENSCHAFTLICHE FAKULTÄT

INSTITUT FÜR BIOLOGIE

MASTERARBEIT

ZUM ERWERB DES AKADEMISCHEN GRADES

MASTER OF SCIENCE

"Körpergrößentrends in fossilen Landschildkröten aus dem Neogen"

"Body size trends in Neogene testudinid tortoises"

vorgelegt von

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geb. am 18.05.1991 in Freudenstadt

angefertigt in der Arbeitsgruppe Paläozoologie

am Institut für Biologie/Museum für Naturkunde

Berlin, im September 2017

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1 Introduction

- Body size as a trait (read Smith, Smith & Lyons) and over time why is it interesting? is there an optimal body size for every organism? how can it be determined? (→ stasis??)
 - evolutionary models (read Gene Hunt's paper and Posada, 2003) → make sense of evolutionary modes: * stasis * unbiased random walk * generalized random walk
 - body size in tortoises (why not use biomass? - not necessary) - distribution of tortoises (?)
- giant tortoises well suited for drifting on ocean currents (Meylan, 2000)
 - OR - mammal megafauna extinctions → giant tortoises
 - human and climatic influence
 - purpose of this work: determine body size trends in tortoises and identify evolutionary mode (if possible). what lead to extinction?

2 Material & Methods

2.1 Data collection

I collected data on body size of fossil testudinids from the Miocene until recent times. The body size data set includes 30 genera, comprising over 100 fossil species. The majority of the data was obtained from the primary literature (Table ??). To find relevant publications, I relied mostly on the references listed in FosFarBase (CITE), PDBD (cite), and "Fossil Turtle Checklist (CITE). Furthermore, the FosFarBase provided fossil occurrences of testudinids all over the world, including their exact localities and age (Table ??), which were used to get an overview over the availability of body size data. For extant taxa, I measured dry material (n = 67) from the collection of the Museum für Naturkunde zu Berlin (MFN). In addition, body size data from the literature was included (Table ??).

2.2 Body size estimation

Body size is reported as straight carapace length (SCL) in mm. Where SCL was not available from the primary literature, it was estimated either from plastron length (PL) or appendicular elements (Table ??). For carapace length estimations based on plastron length, the measurements from the MFN collection material was used to calculate the ratio between SCL and PL. Since the SC/PL ratio was similar for all species and genera, a single general ratio was calculated for all testudinids and hence used for the SCL estimations unless stated otherwise (Table ??). For estimations based on femora and humeri, the ratio provided by Hutterer et al. (1998) and Franz et al. (2001), respectively, were used. A number of publications did not state measurements but instead provided scaled figures of the fossil remains, from which SCL, PL or humeri and femur lengths could be measured.

2.3 Analyses

All subsequent analyses were performed with R (version 3.4.1), including the packages dplyr (cite) to prepare the data for the analysis (???) and ggplot2 (cite) to create figures. Sampling Accumulation Curves were created with the R package vegan (Cite) to see if sample size sufficed. Since the data set relies on literature, references were used as a sampling unit (x-axis). Since genera were much better sampled than species (Fig.) This was repeated on genus

explain
what
species
accu-
mulation
curves

level, since genera of fossil testudinids are relatively well resolved by now whereas determination on the species level is still somewhat obscure in many cases, as some species were based on scarce material.

2.3.1 Distribution and statistics

Histograms and boxplots of the entire data set and several subgroups (fossil vs. modern, insular vs. continental...) were created to explore the distribution of body size. The Wilcoxon Rank Sum Test (unpaired data) was used to test for differences between two subgroups. To be able to compare different subgroups, a subsample (1000 repeats) of the respective larger subgroup was taken to compare equal sample sizes.

2.3.2 Body size trends over time

To investigate trends in body size over time, the R package paleoTS (cite) was used. Data were split into time bins according to stratigraphic stages (Table 1, Fig. 1), although the two stages of the Lower Miocene are considered one time bin, to increase sample size. To decrease influence of sampling bias and because Sampling Accumulation Curves showed that the genus level was well sampled in contrast to species level, the mean SCL per genus was calculated before the timescale analysis. The paleoTS plots were created, which display the mean trait over time and can be fitted to different evolutionary models: stasis, which, generalized random walk (GRW), which or unbiased random walk (URW), which..... . The Akaike Weight Criterion (AICc) indicates which model is best supported → see Catalina's Paper and Hunt's papers

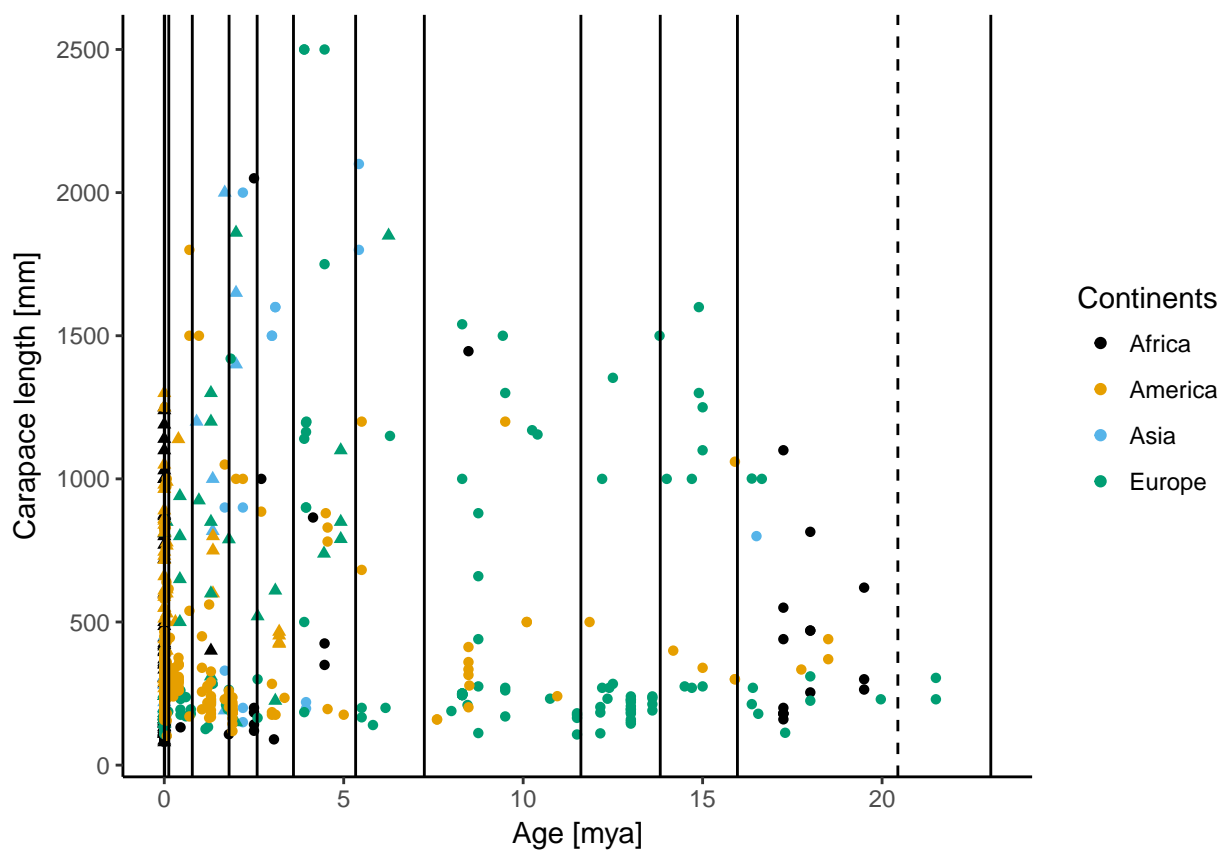


Figure 1: Scatterplot of carapace length over time, indicating insular (triangle) and continental (circles) and colour indicating continents. Lines indicate stratigraphic stages which were used as time bins, the dashed line is the border between the two stages of the Lower Miocene, which were considered as one time bin.

3 Results

Table 1: Time ranges, mean age per bin, corresponding stratigraphic stages and epochs, and respective sample sizes (on individual, species and genus level).)

Age Range [mya]	Mean Age [mya]	Stages	Epochs	n (Individuals)	n (Species)	n (Genera)
0 - 0.0117	0.00585	Modern	Modern	254	66	18
0.0117 - 0.126	0.06885	Upper Pleistocene	Upper Pleistocene	50	18	8
0.126 - 0.781	0.45350	Middle Pleistocene	Middle Pleistocene	53	13	7
0.781 - 1.81	1.29350	Lower Pleistocene	Lower Pleistocene	57	27	12
1.81 - 2.59	2.19700	Gelasian	Lower Pleistocene	33	15	9
2.59 - 3.6	3.09400	Piacencian	Upper Pliocene	24	15	10
3.6 - 5.33	4.46600	Zanclean	Lower Pliocene	31	17	8
5.33 - 7.25	6.28900	Messinian	Upper Miocene	12	9	6
7.25 - 11.6	9.42700	Tortonian	Upper Miocene	46	20	9
11.6 - 13.8	12.71400	Serravallian	Middle Miocene	27	8	6
13.8 - 16	14.89500	Langhian	Middle Miocene	18	14	9
16 - 23	19.50000	Burdigalian/Aquitanian	Lower Miocene	31	15	9

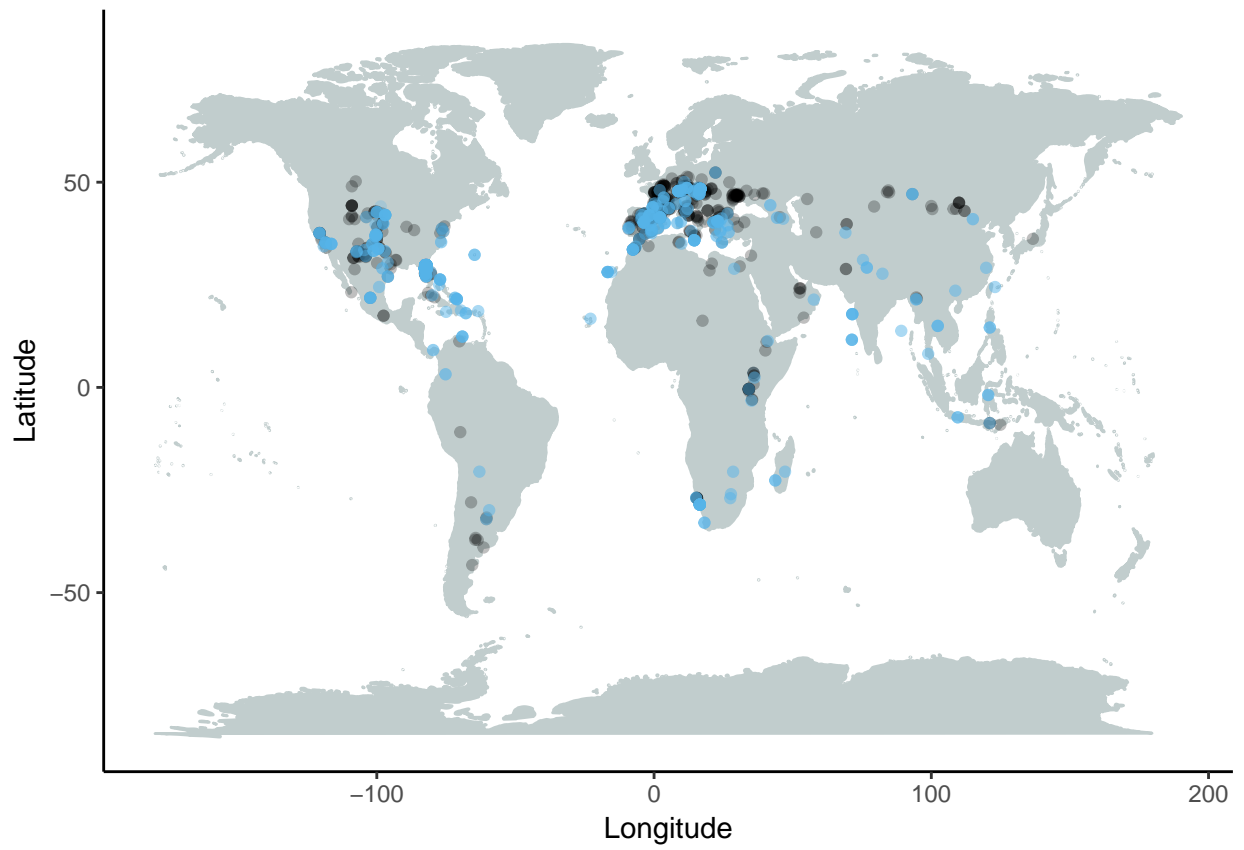


Figure 2: Map displaying all fossil occurrences of testudinids, with color indicating whether body size data was available (blue) or not (black).

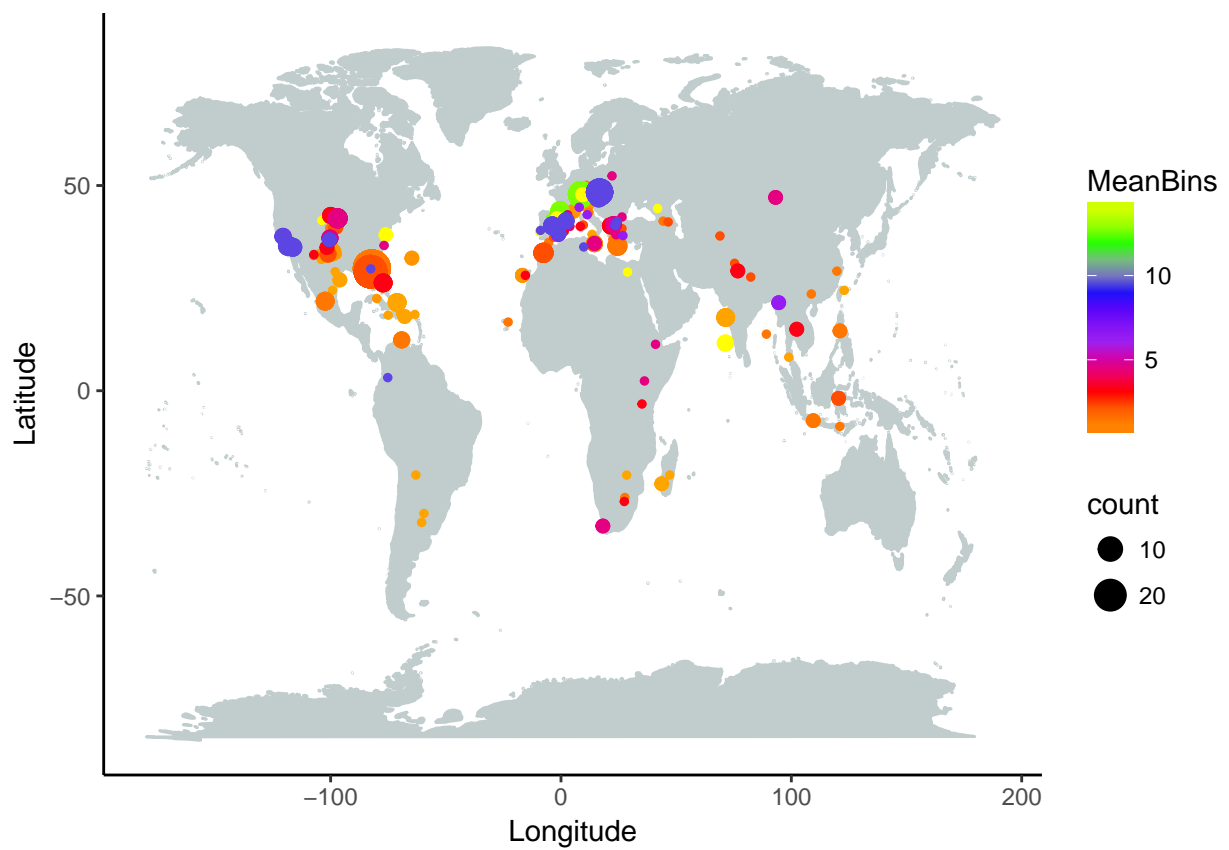


Figure 3: Map displaying all localities for which body size data for testudinids was available in the literature. Size of points denotes sample size, color denotes approximate age.

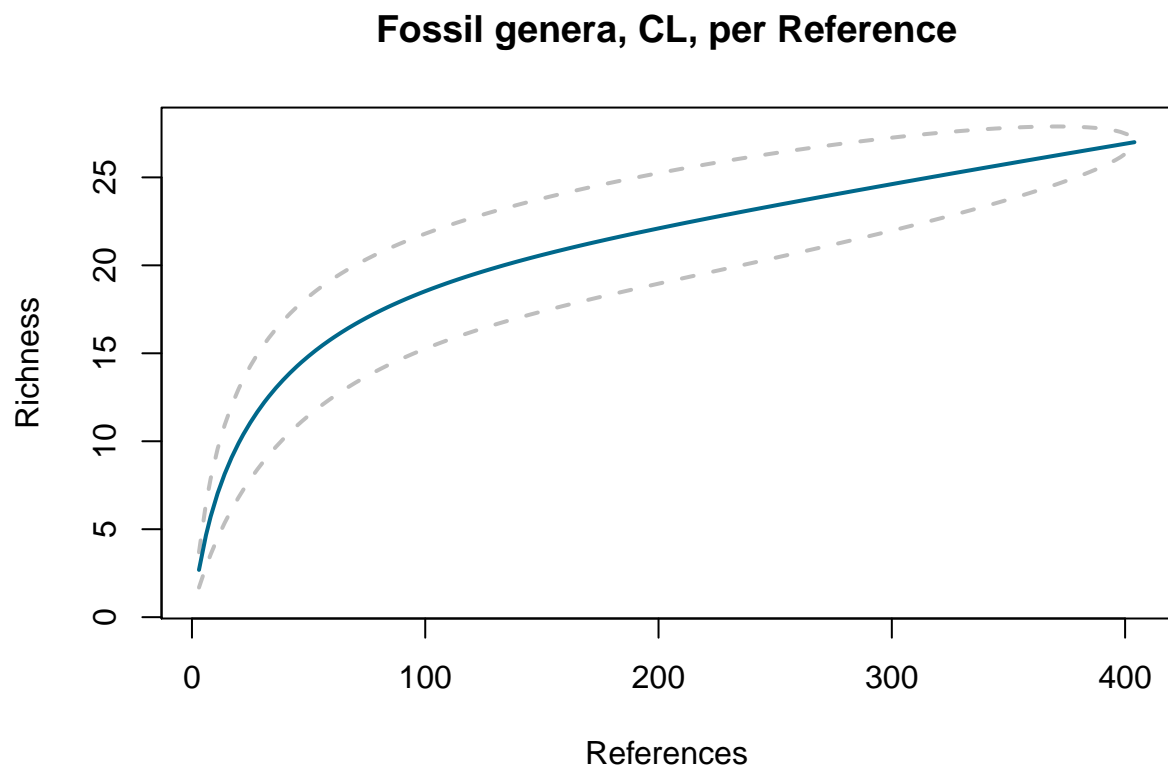


Figure 4: Sampling Accumulation Curve of fossil genera per reference

Sampling Accumulation Curves

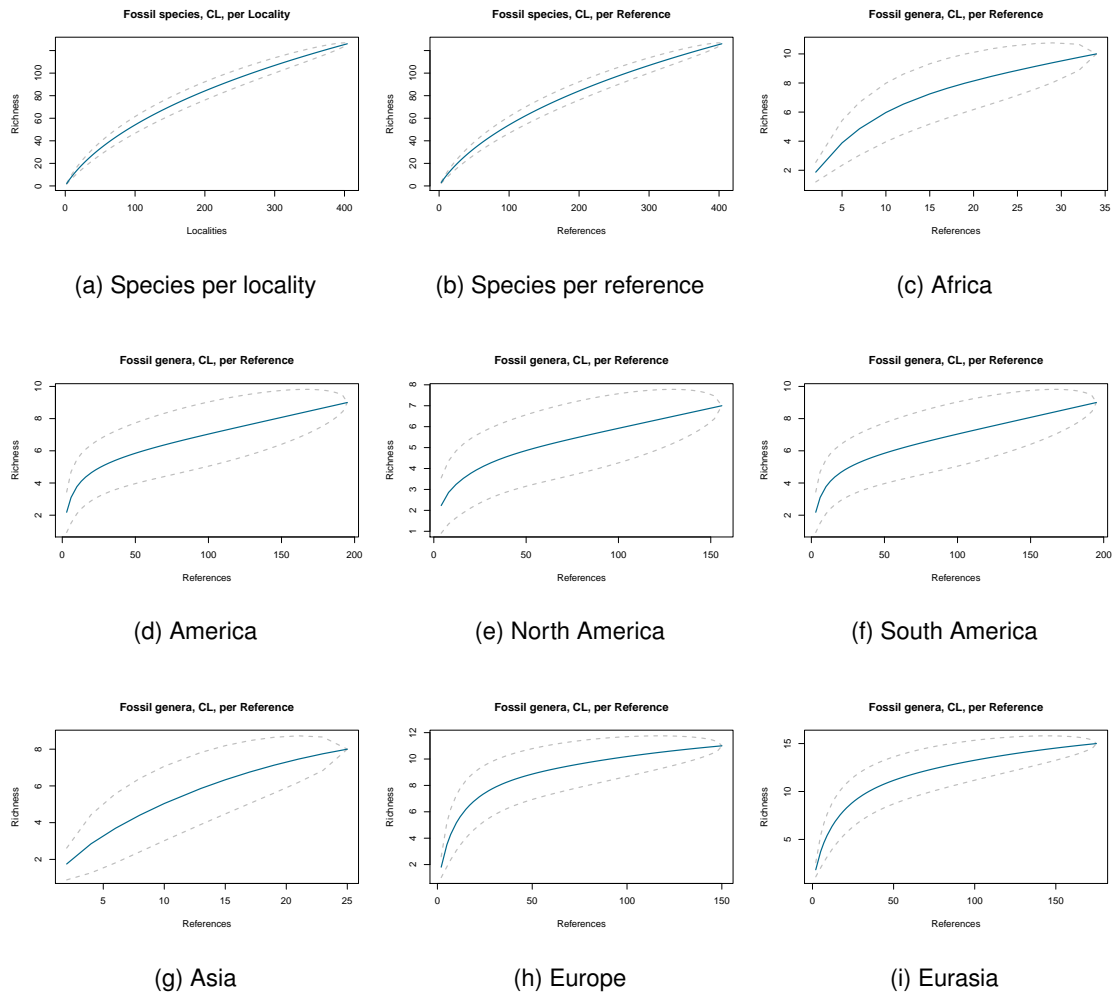


Figure 5: Sampling Accumulation Curves: (a) - (b) Species are not sufficiently sampled, regardless of sampling unit. (c) - (i) Sampling Accumulation Curves on generic level per continent. Only Europe (h) and Eurasia (i) are sufficiently sampled.

Histograms

Boxplots

Random Sampling

Tables

Table 2: Overview over fossil species per time bin, with sample size and mean CL.

EpochBins	Taxon	n	meanCL
Upper Pleistocene	Centrochelys robusta	1	850.0000
Upper Pleistocene	Chelonoidis denticulata	1	616.0000
Upper Pleistocene	Chelonoidis lutzae	1	830.0000
Upper Pleistocene	Chelonoidis marcanoi	4	672.2500
Upper Pleistocene	Chelonoidis monensis	1	500.0000
Upper Pleistocene	Chelonoidis sombreroensis	1	990.0000
Upper Pleistocene	Chelonoidis sp.	3	666.6667
Upper Pleistocene	Eurotestudo hermanni	1	187.0000
Upper Pleistocene	gen. indet.	1	813.0000
Upper Pleistocene	Geochelone sp.	2	475.0000
Upper Pleistocene	Gopherus agassizi	1	252.0000
Upper Pleistocene	Gopherus polyphemus	20	292.9700
Upper Pleistocene	Gopherus praecedens	1	360.0000
Upper Pleistocene	Hesperotestudo crassiscutata	6	435.1667
Upper Pleistocene	Hesperotestudo incisa	1	232.7600
Upper Pleistocene	Hesperotestudo sp.	2	806.5000
Upper Pleistocene	Hesperotestudo wilsoni	1	226.0000
Upper Pleistocene	Indotestudo elongata	1	270.0000
Middle Pleistocene	Centrochelys burchardi	4	722.5000
Middle Pleistocene	Chelonoidis cubensis	1	1139.0000
Middle Pleistocene	Eurotestudo aff. hermanni	2	187.0000
Middle Pleistocene	Eurotestudo hermanni	2	204.0500

EpochBins	Taxon	n	meanCL
Middle Pleistocene	<i>Geochelone</i> sp.	1	170.0000
Middle Pleistocene	<i>Gopherus agassizi</i>	1	445.0000
Middle Pleistocene	<i>Gopherus laticaudatus</i>	1	375.0000
Middle Pleistocene	<i>Gopherus polyphemus</i>	31	300.4316
Middle Pleistocene	<i>Hesperotestudo bermudae</i>	2	385.0000
Middle Pleistocene	<i>Hesperotestudo equicomis</i>	1	340.0000
Middle Pleistocene	<i>Hesperotestudo</i> sp.	2	1650.0000
Middle Pleistocene	<i>Testudo kenitrensis</i>	1	132.0000
Middle Pleistocene	<i>Testudo lunellensis</i>	4	215.4250
Lower Pleistocene	<i>Centrochelys atlantica</i>	1	400.0000
Lower Pleistocene	<i>Centrochelys robusta</i>	3	883.3333
Lower Pleistocene	<i>Cheirogaster</i> cf. <i>gymnesica</i>	1	789.0000
Lower Pleistocene	<i>Cheirogaster</i> sp.	1	925.0000
Lower Pleistocene	<i>Chelonoidis</i> sp.	3	716.6667
Lower Pleistocene	<i>Eurotestudo globosa</i>	1	263.0000
Lower Pleistocene	<i>Eurotestudo hermanni</i>	2	205.0000
Lower Pleistocene	gen. indet.	1	900.0000
Lower Pleistocene	<i>Geochelone</i> sp.	1	340.0000
Lower Pleistocene	<i>Gopherus berlandieri</i>	2	225.6500
Lower Pleistocene	<i>Gopherus flavomarginatus</i>	1	450.0000
Lower Pleistocene	<i>Gopherus pertenuis</i>	1	1050.0000
Lower Pleistocene	<i>Gopherus polyphemus</i>	3	254.4667
Lower Pleistocene	<i>Gopherus</i> sp.	6	233.9667
Lower Pleistocene	<i>Hesperotestudo crassiscutata</i>	5	285.6000
Lower Pleistocene	<i>Hesperotestudo incisa</i>	7	234.6286
Lower Pleistocene	<i>Hesperotestudo mlynarskii</i>	2	184.2500
Lower Pleistocene	<i>Hesperotestudo</i> sp.	1	1500.0000
Lower Pleistocene	<i>Hesperotestudo turgida</i>	1	230.0000
Lower Pleistocene	<i>Megalochelys sondaari</i>	2	909.0000
Lower Pleistocene	<i>Megalochelys</i> sp.	3	1130.4667

EpochBins	Taxon	n	meanCL
Lower Pleistocene	<i>Psammobates antiquorum</i>	1	107.8000
Lower Pleistocene	<i>Testudo changshanesis</i>	1	330.0000
Lower Pleistocene	<i>Testudo graeca</i>	1	195.0000
Lower Pleistocene	<i>Testudo hermanni</i>	2	176.5500
Lower Pleistocene	<i>Testudo marginata</i>	3	270.0000
Lower Pleistocene	<i>Titanochelon gymnesica</i>	1	1300.0000
Gelasian	<i>Centrochelys marocana</i>	1	2050.0000
Gelasian	<i>Eurotestudo cf. hermanni</i>	1	150.0000
Gelasian	<i>Gopherus</i> sp.	15	185.7467
Gelasian	<i>Hesperotestudo campester</i>	1	1000.0000
Gelasian	<i>Hesperotestudo</i> sp.	1	1000.0000
Gelasian	<i>Manouria punjabiensis</i>	1	900.0000
Gelasian	<i>Megalochelys atlas</i>	3	1683.3333
Gelasian	<i>Testudo aff. kenitrensis</i>	1	142.0000
Gelasian	<i>Testudo oughlamensis</i>	1	120.0000
Gelasian	<i>Testudo ranovi</i>	1	200.0000
Gelasian	<i>Testudo</i> sp.	2	192.0000
Gelasian	<i>Testudo transcaucasia</i>	1	150.0000
Gelasian	<i>Titanochelon aff. schafferi</i>	1	1860.0000
Gelasian	<i>Titanochelon</i> sp.	1	1420.0000
Piacencian	" <i>Aldabrachelys</i> " <i>laetoliensis</i>	1	1000.0000
Piacencian	<i>Aldabrachelys</i> ? sp.	2	1500.0000
Piacencian	<i>Centrochelys vulcanica</i>	1	610.0000
Piacencian	<i>Chelonoidis alburyorum</i>	4	442.7500
Piacencian	<i>Gopherus canyonensis</i>	1	885.5000
Piacencian	<i>Hesperotestudo johnstoni</i>	1	235.0000
Piacencian	<i>Hesperotestudo oelrichi</i>	1	283.8000
Piacencian	<i>Hesperotestudo riggsi</i>	2	180.5000
Piacencian	<i>Hesperotestudo</i> sp.	1	176.0000
Piacencian	<i>Homopus fenestratus</i>	1	90.0000

EpochBins	Taxon	n	meanCL
Piacencian	Megalochelys atlas	2	1600.0000
Piacencian	Testudo brevitesta	2	232.5000
Piacencian	Testudo pecorinii	1	225.0000
Piacencian	Titanochelon sp.	1	520.0000
Zanclean	Caudochelys rexroadensis	2	805.5000
Zanclean	Centrochelys robusta	3	913.3333
Zanclean	Cheirogaster gymnesica	1	739.0000
Zanclean	Ergilemys oskarkuhni	2	209.0000
Zanclean	Geochelone crassa	1	865.0000
Zanclean	Geochelone s. l.	1	1750.0000
Zanclean	Geochelone sp.	2	528.0000
Zanclean	Geochelone stromeri	2	387.5000
Zanclean	Hesperotestudo riggsi	1	195.8000
Zanclean	Testudo cf. graeca	1	185.0000
Zanclean	Testudo sp.	4	1675.0000
Zanclean	Titanochelon bacharidisi	4	1040.0000
Zanclean	Titanochelon perpiniana	1	1140.0000
Zanclean	Titanochelon schafferi	1	2500.0000
Messinian	Hesperotestudo orthopygia	2	941.0000
Messinian	Megalochelys atlas	2	1950.0000
Messinian	Testudo amiatae	1	140.0000
Messinian	Testudo graeca	2	183.5000
Messinian	Testudo sp.	1	200.0000
Messinian	Titanochelon bolivari	1	1150.0000
Messinian	Titanochelon schafferi	1	1850.0000
Tortonian	“Hadrianus sp.”	1	1000.0000
Tortonian	Cheirogaster richardi	1	1155.0000
Tortonian	Cheirogaster sp.	2	1355.0000
Tortonian	gen. indet.	3	660.0000
Tortonian	Geochelone hesterna	1	278.0000

EpochBins	Taxon	n	meanCL
Tortonian	Geochelone sp.	2	973.0000
Tortonian	Gopherus ? sp.	1	500.0000
Tortonian	Gopherus mohavetus	5	324.8000
Tortonian	Hesperotestudo alleni	1	240.9000
Tortonian	Hesperotestudo riggsi	2	159.5000
Tortonian	Hesperotestudo sp.	1	1200.0000
Tortonian	Paleotestudo sp.	3	233.6667
Tortonian	Testudo burgenlandica	2	193.5000
Tortonian	Testudo catalaunica	4	157.0000
Tortonian	Testudo cf. promarginata	5	250.0000
Tortonian	Testudo graeca	1	210.0000
Tortonian	Testudo s. s.	1	189.0000
Tortonian	Testudo sp.	7	243.1571
Tortonian	Titanochelon bolivari	1	1300.0000
Tortonian	Titanochelon cf. bolivari	1	1500.0000
Serravallian	Cheirogaster sp.	2	1250.0000
Serravallian	gen. indet.	1	270.0000
Serravallian	Gopherus ? sp.	1	500.0000
Serravallian	Paleotestudo antiqua	18	203.0556
Serravallian	Paleotestudo cf. sp.	1	270.0000
Serravallian	Testudo catalaunica	1	232.0000
Serravallian	Testudo steinheimensis	2	169.3500
Serravallian	Titanochelon bolivari	1	1353.0000
Langhian	Caudochelys ducateli	1	339.9000
Langhian	Chelonoidis sp.	3	553.3333
Langhian	Ergilemys sp.	1	1000.0000
Langhian	gen. indet.	1	1000.0000
Langhian	Paleotestudo antiqua	1	275.0000
Langhian	Paleotestudo cf. sp.	1	270.0000
Langhian	Testudo kalksburgensis	1	275.0000

EpochBins	Taxon	n	meanCL
Langhian	Testudo sp.	1	400.0000
Langhian	Titanochelon bolivari	2	1175.0000
Langhian	Titanochelon cf. bolivari	2	1450.0000
Burdigalian/Aquitania	Caudochelys williamsi	1	334.0000
Burdigalian/Aquitania	gen. indet.	1	270.0000
Burdigalian/Aquitania	Geochelone sp.	2	900.0000
Burdigalian/Aquitania	Geochelone tedwhitei	2	405.0000
Burdigalian/Aquitania	Impregnochelys pachytectis	1	620.0000
Burdigalian/Aquitania	Mesocherus orangeus	5	180.0000
Burdigalian/Aquitania	Namibchersus aff. namaquensis	3	696.6667
Burdigalian/Aquitania	Namibchersus namaquensis	6	428.8333
Burdigalian/Aquitania	Paleotestudo cf. antiqua	1	113.0000
Burdigalian/Aquitania	Paleotestudo sp.	1	179.3000
Burdigalian/Aquitania	Testudo kalksburgensis	2	227.5000
Burdigalian/Aquitania	Testudo promarginata	3	281.5667
Burdigalian/Aquitania	Testudo rectogularis	1	213.0000
Burdigalian/Aquitania	Titanochelon cf. perpiniana	1	1001.0000

Table 3: General overview over fossil species, with sample size and mean CL

Taxon	n	meanCL
“Aldabrachelys” laetoliensis	1	1000.0000
“Hadrianus sp.”	1	1000.0000
Aldabrachelys ? sp.	2	1500.0000
Caudochelys ducатели	1	339.9000
Caudochelys rexroadensis	2	805.5000
Caudochelys williamsi	1	334.0000
Centrochelys atlantica	1	400.0000
Centrochelys burchardi	4	722.5000
Centrochelys marocana	1	2050.0000
Centrochelys robusta	7	891.4286

Taxon	n	meanCL
<i>Centrochelys vulcanica</i>	1	610.0000
<i>Cheirogaster cf. gymnesica</i>	1	789.0000
<i>Cheirogaster gymnesica</i>	1	739.0000
<i>Cheirogaster richardi</i>	1	1155.0000
<i>Cheirogaster sp.</i>	5	1227.0000
<i>Chelonoidis alburyorum</i>	4	442.7500
<i>Chelonoidis cubensis</i>	1	1139.0000
<i>Chelonoidis denticulata</i>	1	616.0000
<i>Chelonoidis lutzae</i>	1	830.0000
<i>Chelonoidis marcanoi</i>	4	672.2500
<i>Chelonoidis monensis</i>	1	500.0000
<i>Chelonoidis sombreroensis</i>	1	990.0000
<i>Chelonoidis sp.</i>	9	645.5556
<i>Ergilemys oskarkuhni</i>	2	209.0000
<i>Ergilemys sp.</i>	1	1000.0000
<i>Eurotestudo aff. hermanni</i>	2	187.0000
<i>Eurotestudo cf. hermanni</i>	1	150.0000
<i>Eurotestudo globosa</i>	1	263.0000
<i>Eurotestudo hermanni</i>	5	201.0200
gen. indet.	8	654.1250
<i>Geochelone crassa</i>	1	865.0000
<i>Geochelone hesternae</i>	1	278.0000
<i>Geochelone s. l.</i>	1	1750.0000
<i>Geochelone sp.</i>	10	626.2000
<i>Geochelone stromeri</i>	2	387.5000
<i>Geochelone tedwhitei</i>	2	405.0000
<i>Gopherus ? sp.</i>	2	500.0000
<i>Gopherus agassizi</i>	2	348.5000
<i>Gopherus berlandieri</i>	2	225.6500
<i>Gopherus canyonensis</i>	1	885.5000

Taxon	n	meanCL
<i>Gopherus flavomarginatus</i>	1	450.0000
<i>Gopherus laticaudatus</i>	1	375.0000
<i>Gopherus mohavetus</i>	5	324.8000
<i>Gopherus pertenuis</i>	1	1050.0000
<i>Gopherus polyphemus</i>	54	295.1144
<i>Gopherus praecedens</i>	1	360.0000
<i>Gopherus</i> sp.	21	199.5238
<i>Hesperotestudo alleni</i>	1	240.9000
<i>Hesperotestudo bermudae</i>	2	385.0000
<i>Hesperotestudo campester</i>	1	1000.0000
<i>Hesperotestudo crassiscutata</i>	11	367.1818
<i>Hesperotestudo equicomes</i>	1	340.0000
<i>Hesperotestudo incisa</i>	8	234.3950
<i>Hesperotestudo johnstoni</i>	1	235.0000
<i>Hesperotestudo mlynarskii</i>	2	184.2500
<i>Hesperotestudo oelrichi</i>	1	283.8000
<i>Hesperotestudo orthopygia</i>	2	941.0000
<i>Hesperotestudo riggsi</i>	5	175.1600
<i>Hesperotestudo</i> sp.	8	1098.6250
<i>Hesperotestudo turgida</i>	1	230.0000
<i>Hesperotestudo wilsoni</i>	1	226.0000
<i>Homopus fenestratus</i>	1	90.0000
<i>Impregnochelys pachytectis</i>	1	620.0000
<i>Indotestudo elongata</i>	1	270.0000
<i>Manouria punjabiensis</i>	1	900.0000
<i>Megalochelys atlas</i>	7	1735.7143
<i>Megalochelys sondaari</i>	2	909.0000
<i>Megalochelys</i> sp.	3	1130.4667
<i>Mesocherus orangeus</i>	5	180.0000
<i>Namibchersus</i> aff. <i>namaquensis</i>	3	696.6667

Taxon	n	meanCL
Namibchersus namaquensis	6	428.8333
Paleotestudo antiqua	19	206.8421
Paleotestudo cf. antiqua	1	113.0000
Paleotestudo cf. sp.	2	270.0000
Paleotestudo sp.	4	220.0750
Psammobates antiquorum	1	107.8000
Testudo aff. kenitrensis	1	142.0000
Testudo amiatae	1	140.0000
Testudo brevitesta	2	232.5000
Testudo burgenlandica	2	193.5000
Testudo catalaunica	5	172.0000
Testudo cf. graeca	1	185.0000
Testudo cf. promarginata	5	250.0000
Testudo changshanesis	1	330.0000
Testudo graeca	4	193.0000
Testudo hermanni	2	176.5500
Testudo kalksburgensis	3	243.3333
Testudo kenitrensis	1	132.0000
Testudo lunellensis	4	215.4250
Testudo marginata	3	270.0000
Testudo oughlamensis	1	120.0000
Testudo pecorinii	1	225.0000
Testudo promarginata	3	281.5667
Testudo ranovi	1	200.0000
Testudo rectogularis	1	213.0000
Testudo s. s.	1	189.0000
Testudo sp.	15	625.7400
Testudo steinheimensis	2	169.3500
Testudo transcaucasia	1	150.0000
Titanochelon aff. schafferi	1	1860.0000

Taxon	n	meanCL
Titanochelon bacharidisi	4	1040.0000
Titanochelon bolivari	5	1230.6000
Titanochelon cf. bolivari	3	1466.6667
Titanochelon cf. perpiniana	1	1001.0000
Titanochelon gymnesica	1	1300.0000
Titanochelon perpiniana	1	1140.0000
Titanochelon schafferi	2	2175.0000
Titanochelon sp.	2	970.0000

Table 4: Overview over genera (modern and fossil) per time bin, with sample sizes and mean CL.

EpochBins	Genus	n	meanCL
Modern	Aldabrachelys	12	974.5833
Modern	Astrochelys	14	366.2143
Modern	Centrochelys	3	493.3333
Modern	Chelonoidis	45	531.5178
Modern	Chersina	15	176.2667
Modern	Cylindraspis	5	724.0000
Modern	Geochelone	8	252.1250
Modern	Gopherus	23	302.4839
Modern	Hesperotestudo	1	250.0000
Modern	Homopus	7	139.2857
Modern	Indotestudo	16	242.9875
Modern	Kinixys	15	213.0667
Modern	Malacochersus	2	166.5000
Modern	Manouria	9	380.7778
Modern	Psammobates	17	113.4118
Modern	Pyxis	16	124.1875
Modern	Stigmochelys	6	405.3333
Modern	Testudo	39	197.5436

EpochBins	Genus	n	meanCL
Upper Pleistocene	Centrochelys	1	850.0000
Upper Pleistocene	Chelonoidis	11	693.1818
Upper Pleistocene	Eurotestudo	1	187.0000
Upper Pleistocene	gen.	1	813.0000
Upper Pleistocene	Geochelone	2	475.0000
Upper Pleistocene	Gopherus	22	294.1545
Upper Pleistocene	Hesperotestudo	10	468.2760
Upper Pleistocene	Indotestudo	1	270.0000
Middle Pleistocene	Centrochelys	4	722.5000
Middle Pleistocene	Chelonoidis	1	1139.0000
Middle Pleistocene	Eurotestudo	4	195.5250
Middle Pleistocene	Geochelone	1	170.0000
Middle Pleistocene	Gopherus	33	307.0721
Middle Pleistocene	Hesperotestudo	5	882.0000
Middle Pleistocene	Testudo	5	198.7400
Lower Pleistocene	Centrochelys	4	762.5000
Lower Pleistocene	Cheirogaster	2	857.0000
Lower Pleistocene	Chelonoidis	3	716.6667
Lower Pleistocene	Eurotestudo	4	201.5250
Lower Pleistocene	gen.	1	900.0000
Lower Pleistocene	Geochelone	1	340.0000
Lower Pleistocene	Gopherus	13	316.8077
Lower Pleistocene	Hesperotestudo	16	323.0562
Lower Pleistocene	Megalochelys	5	1041.8800
Lower Pleistocene	Psammobates	1	107.8000
Lower Pleistocene	Testudo	6	259.1667
Lower Pleistocene	Titanochelon	1	1300.0000
Gelasian	Centrochelys	1	2050.0000
Gelasian	Eurotestudo	1	150.0000
Gelasian	Gopherus	15	185.7467

EpochBins	Genus	n	meanCL
Gelasian	Hesperotestudo	2	1000.0000
Gelasian	Manouria	1	900.0000
Gelasian	Megalochelys	3	1683.3333
Gelasian	Testudo	6	166.0000
Gelasian	Titanochelon	2	1640.0000
Piacencian	Aldabrachelys	3	1333.3333
Piacencian	Centrochelys	1	610.0000
Piacencian	Chelonoidis	4	442.7500
Piacencian	Gopherus	1	885.5000
Piacencian	Hesperotestudo	5	211.1600
Piacencian	Homopus	1	90.0000
Piacencian	Megalochelys	2	1600.0000
Piacencian	Testudo	3	230.0000
Piacencian	Titanochelon	1	520.0000
Zanclean	Caudochelys	2	805.5000
Zanclean	Centrochelys	3	913.3333
Zanclean	Cheirogaster	1	739.0000
Zanclean	Ergilemys	2	209.0000
Zanclean	Geochelone	6	741.0000
Zanclean	Hesperotestudo	1	195.8000
Zanclean	Testudo	5	1377.0000
Zanclean	Titanochelon	6	1300.0000
Messinian	Hesperotestudo	2	941.0000
Messinian	Megalochelys	2	1950.0000
Messinian	Testudo	4	176.7500
Messinian	Titanochelon	2	1500.0000
Tortonian	“Hadrianus”	1	1000.0000
Tortonian	Cheirogaster	3	1288.3333
Tortonian	gen.	3	660.0000
Tortonian	Geochelone	3	741.3333

EpochBins	Genus	n	meanCL
Tortonian	Gopherus	6	354.0000
Tortonian	Hesperotestudo	4	439.9750
Tortonian	Paleotestudo	3	233.6667
Tortonian	Testudo	20	218.3050
Tortonian	Titanochelon	2	1400.0000
Serravallian	Cheirogaster	2	1250.0000
Serravallian	gen.	1	270.0000
Serravallian	Gopherus	1	500.0000
Serravallian	Paleotestudo	19	206.5789
Serravallian	Testudo	3	190.2333
Serravallian	Titanochelon	1	1353.0000
Langhian	Caudochelys	1	339.9000
Langhian	Chelonoidis	3	553.3333
Langhian	Ergilemys	1	1000.0000
Langhian	gen.	1	1000.0000
Langhian	Paleotestudo	2	272.5000
Langhian	Testudo	2	337.5000
Langhian	Titanochelon	4	1312.5000
Burdigalian/Aquitania	Caudochelys	1	334.0000
Burdigalian/Aquitania	gen.	1	270.0000
Burdigalian/Aquitania	Geochelone	4	652.5000
Burdigalian/Aquitania	Impregnochelys	1	620.0000
Burdigalian/Aquitania	Mesocherus	5	180.0000
Burdigalian/Aquitania	Namibchersus	9	518.1111
Burdigalian/Aquitania	Paleotestudo	2	146.1500
Burdigalian/Aquitania	Testudo	6	252.1167
Burdigalian/Aquitania	Titanochelon	1	1001.0000

Table 5: General overview over genera, with sample sizes and mean CL.

Genus	n	meanCL
“Hadrianus”	1	1000.0000
Aldabrachelys	15	1046.3333
Astrochelys	14	366.2143
Caudochelys	4	571.2250
Centrochelys	17	804.1176
Cheirogaster	8	1102.2500
Chelonoidis	67	571.0940
Chersina	15	176.2667
Cylindraspis	5	724.0000
Ergilemys	3	472.6667
Eurotestudo	10	192.5200
gen.	8	654.1250
Geochelone	25	510.2800
Gopherus	114	298.0361
Hesperotestudo	46	465.3296
Homopus	8	133.1250
Impregnochelys	1	620.0000
Indotestudo	17	244.5765
Kinixys	15	213.0667
Malacochersus	2	166.5000
Manouria	10	432.7000
Megalochelys	12	1446.6167
Mesocherus	5	180.0000
Namibchersus	9	518.1111
Paleotestudo	26	210.1269
Psammobates	18	113.1000
Pyxis	16	124.1875
Stigmochelys	6	405.3333
Testudo	99	269.2465

Genus	n	meanCL
Titanochelon	20	1315.2000

Acknowledgements

Declaration of Authorship