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

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am Institut für Biologie/Museum für Naturkunde

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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 occurences 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 accumulation 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, wich 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

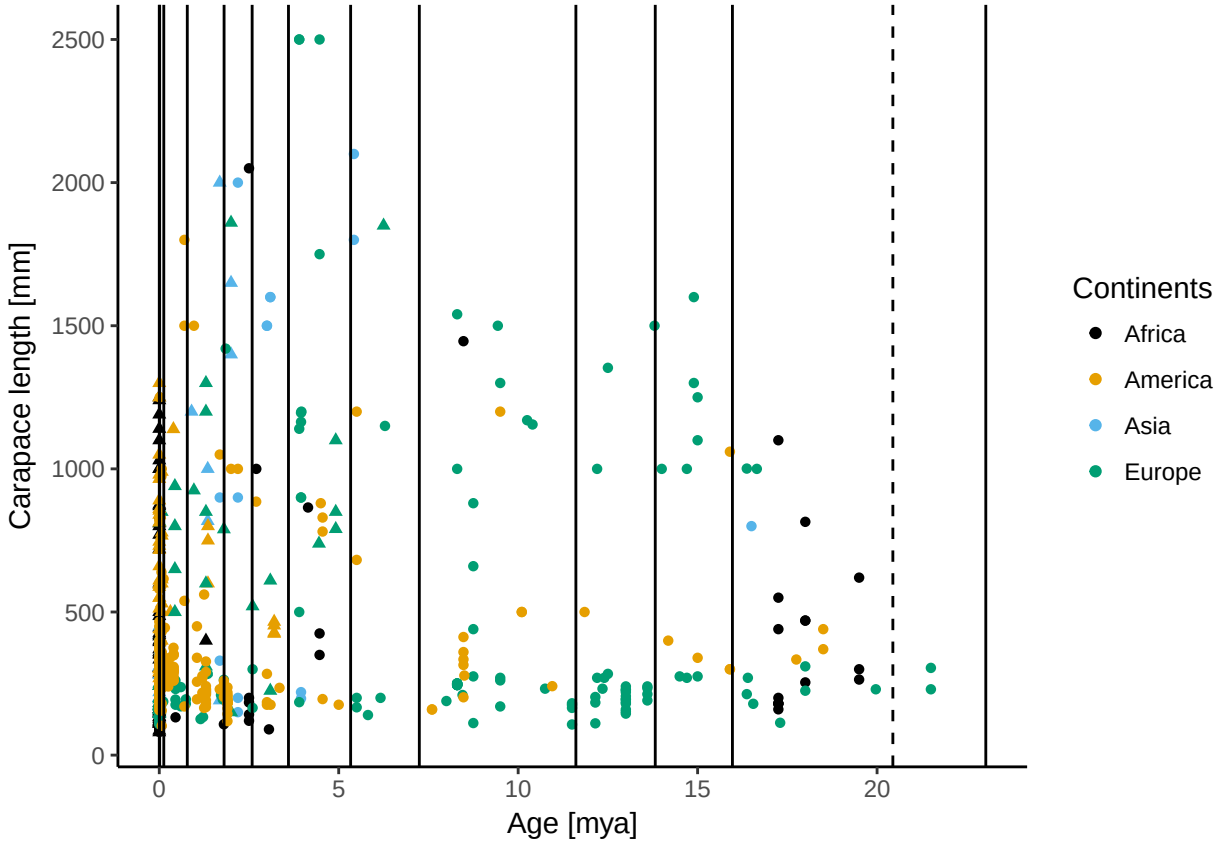


Figure 1: Scatterplot of carapace length over time, indicating insular (triangle) and continental (circles) and colour indicating continents. Lines indicate stratigraphic stages which were used as time bins, the dashed line is the border between the two stages of the Lower Miocene, which were consideres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

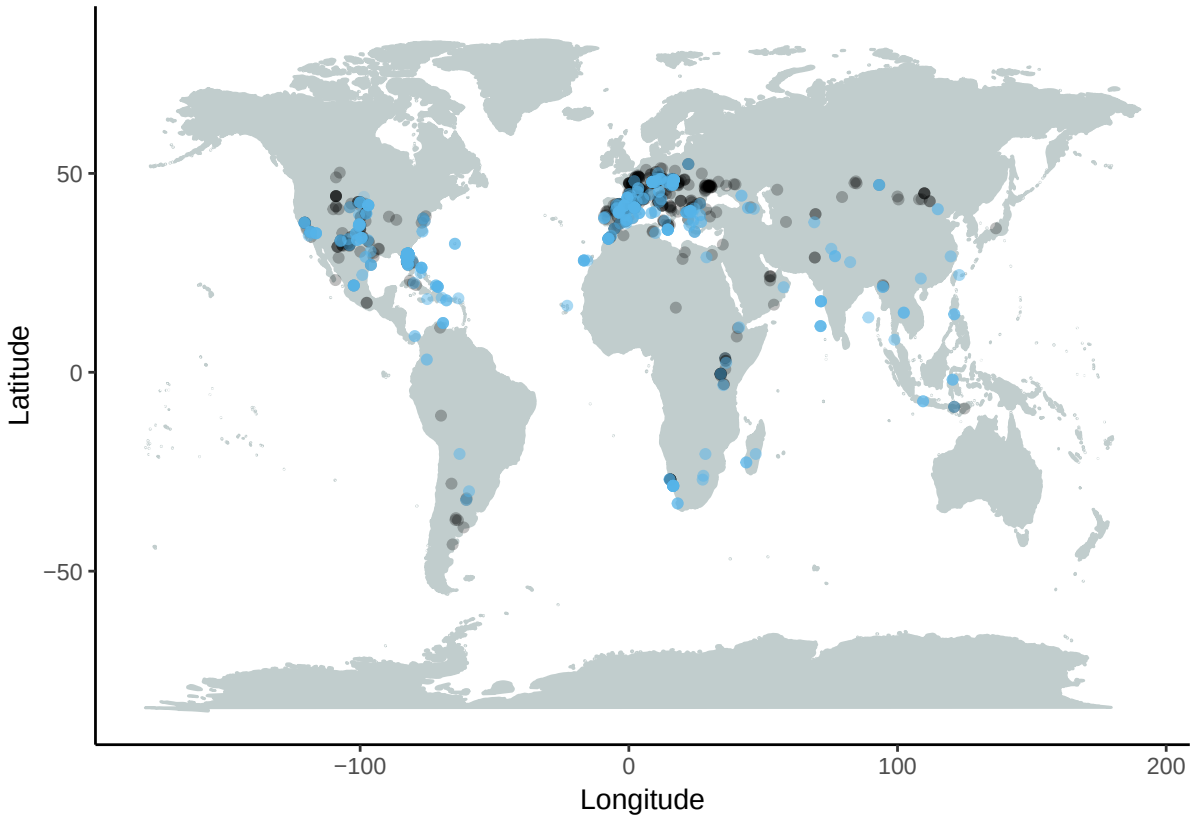


Figure 2: Map displaying all fossil occurrences of testudinids, with color indicating whether body size data was available (blue) or not (black).

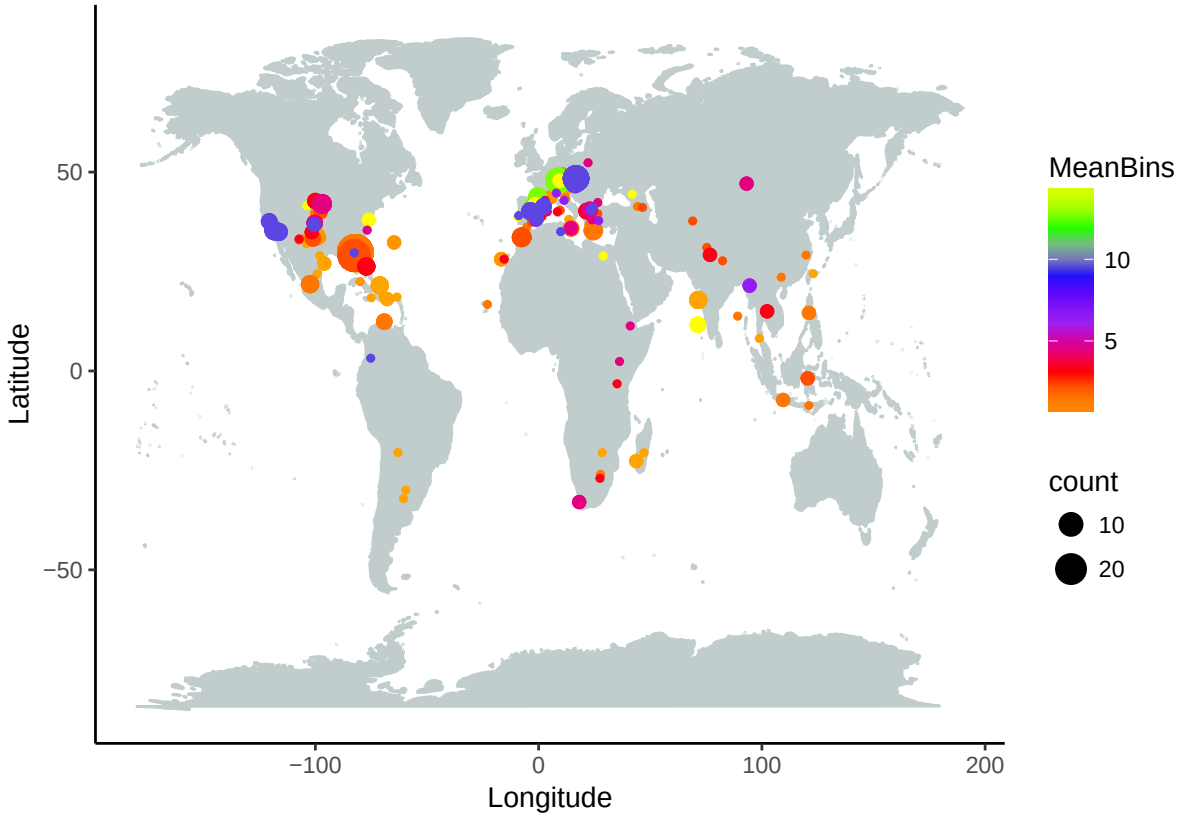


Figure 3: Map displaying all localities for which body size data for testudinids was available in the literature. Size of points denotes sample size, color denotes approximate age.

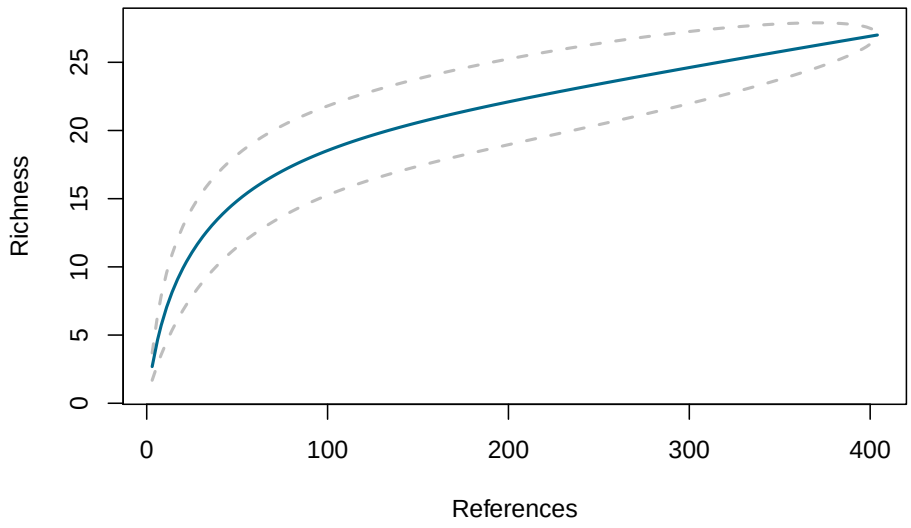


Figure 4: Sampling Accumulation Curve of fossil genera per reference.

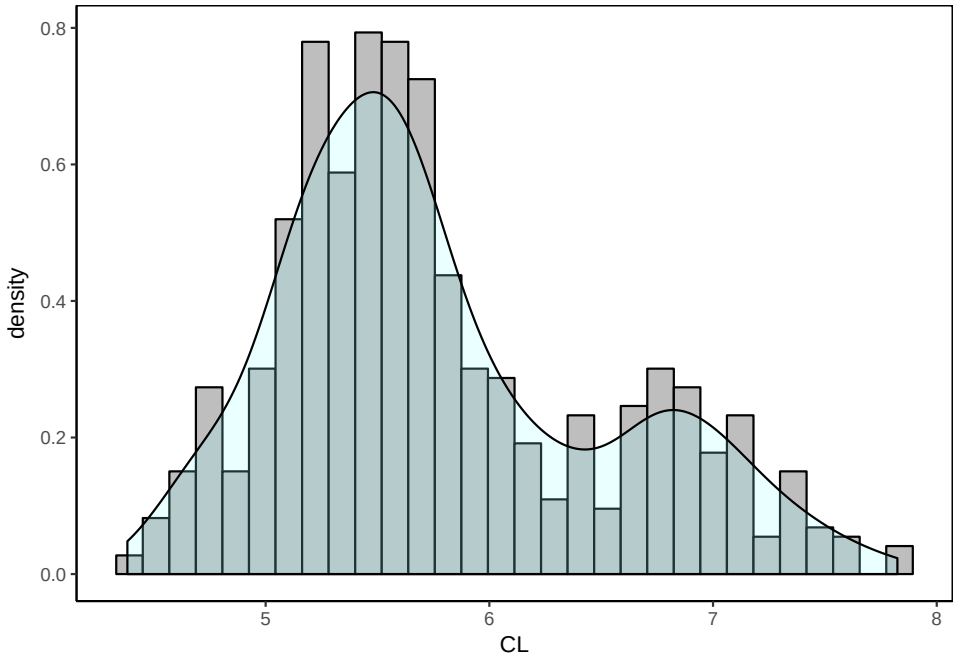
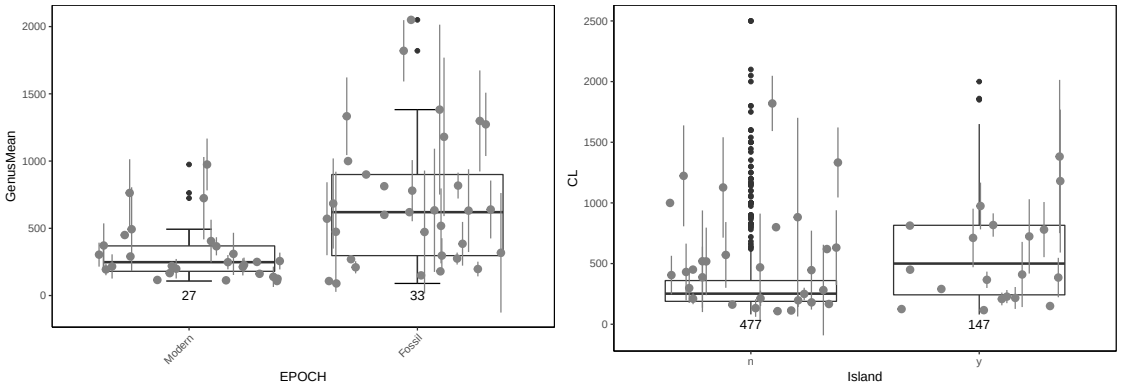


Figure 5: Body size distribution. Bimodally distributed.



(a) Fossil vs. modern

(b) Continental vs. insular

Wilcoxon Rank Sum Test (unpaired data):

modern < fossil (P = 2.6739885×10^{-7})

Wilcoxon Rank Sum Test (unpaired data):

continental < insular (P = 1.5123×10^{-6})

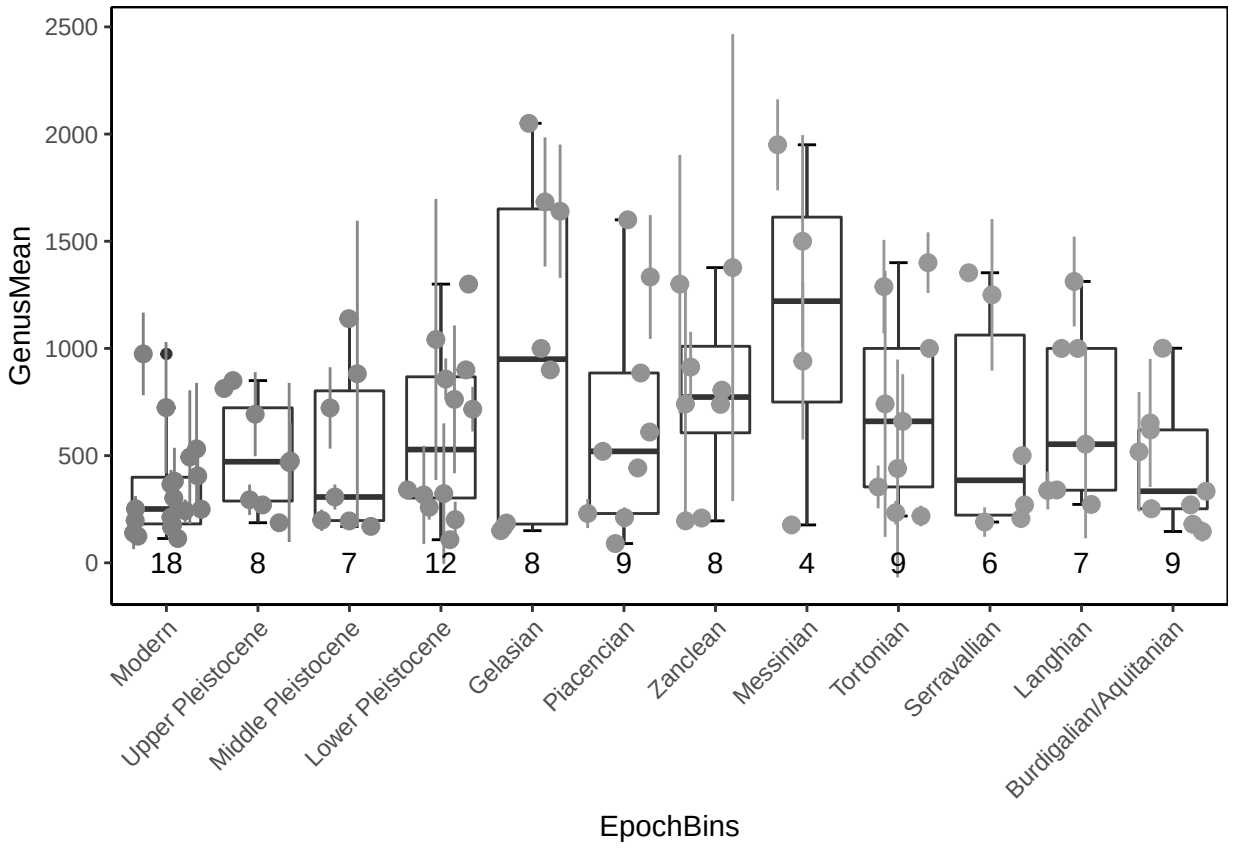


Figure 6: Boxplots of mean CL per time bin, including mean and sd CL for each genus (as pointrange).

4. paleoTS analysis

4.1. all (continental and insular)

Table 2: paleoTS object, all data

tt	mm	vv	nn
0.0000005	401.9641	102306.64	4
0.0058500	314.1859	42607.58	18
0.0688500	506.3265	64620.11	8
0.4535000	516.4053	155241.85	7
1.2935000	593.8669	147507.20	12
2.1970000	971.8850	580540.76	8
3.0940000	658.0826	271043.73	9
4.4660000	785.0792	187937.61	8
6.2890000	1141.9375	584378.85	4
9.4270000	703.9570	195766.19	9
12.7140000	628.3020	285258.36	6
14.8950000	687.9619	169914.58	7
19.5000000	441.5420	78467.65	9

Table 3: Model-fitting results for testudinidae, genera, all

	logL	K	AICc	Akaike.wt
GRW	-81.31790	2	167.9691	0.161
URW	-82.05721	1	166.5144	0.332
Stasis	-80.16802	2	165.6694	0.507

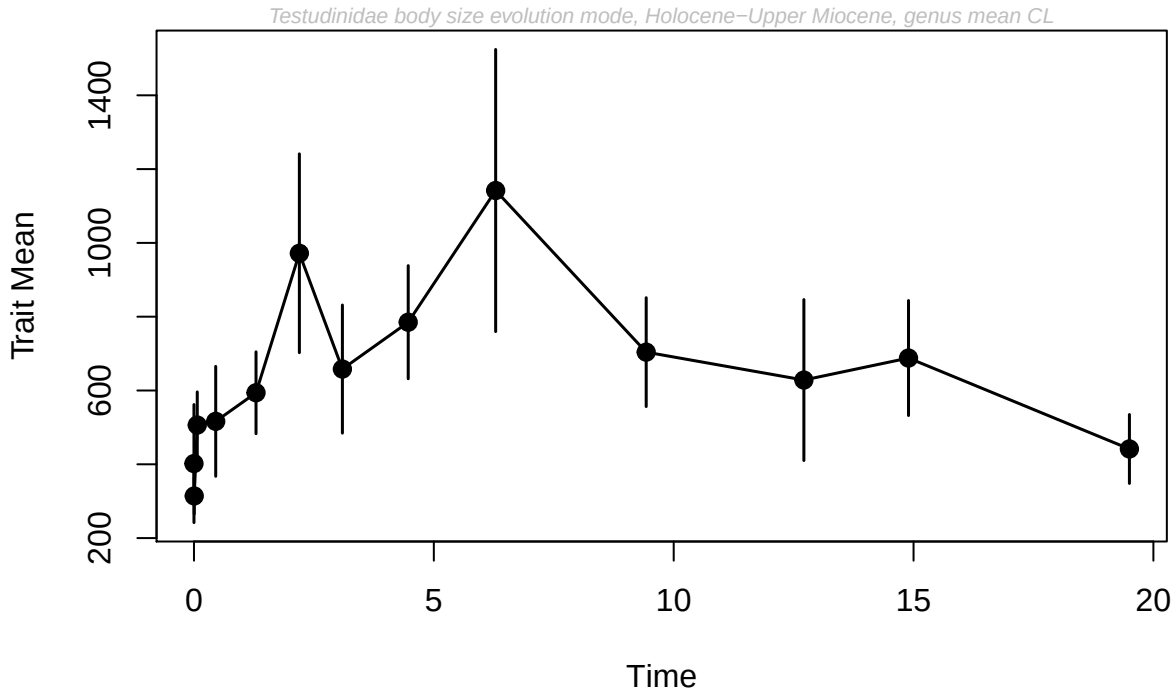


Figure 7: paleoTS plot with genus mean, all

4.2. continental (excluding insular species)

Table 4: paleoTS object, continental

tt	mm	vv	nn
0.0000005	233.1680	8331.753	3
0.0058500	241.7917	13004.928	15
0.0688500	397.4606	50619.392	6
0.4535000	416.9341	200982.124	5
1.2935000	346.8484	66240.066	7
2.1970000	1103.1067	595507.933	7
3.0940000	725.4156	414253.291	6
4.4660000	771.3833	259173.082	6
6.2890000	1054.4375	531455.932	4
9.4270000	703.9570	195766.185	9
12.7140000	628.3020	285258.362	6

tt	mm	vv	nn
14.8950000	687.9619	169914.577	7
19.5000000	441.5420	78467.646	9

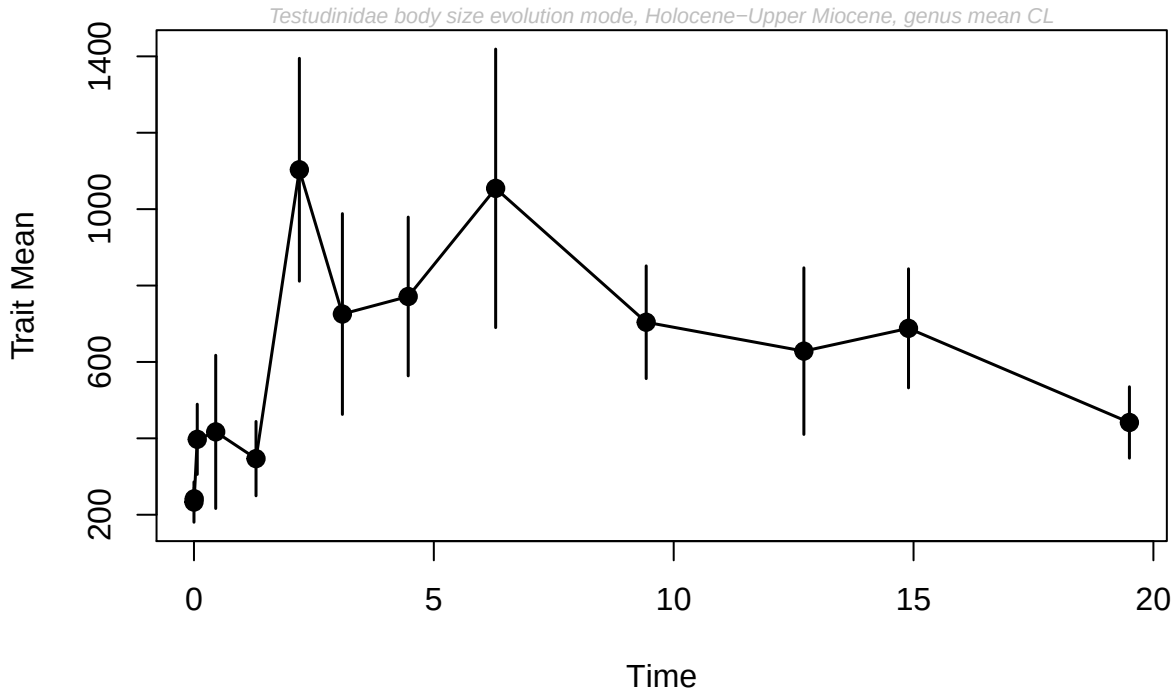


Figure 8: paleoTS plot with genus mean, continental

Table 5: Model-fitting results for testudinidae, genera, continental

	logL	K	AICc	Akaike.wt
GRW	-82.26287	2	169.8591	0.300
URW	-83.12577	1	168.6515	0.548
Stasis	-82.93984	2	171.2130	0.152

4.3. insular (excluding continental)

Table 6: paleoTS object, insular

tt	mm	vv	nn
0.0000005	860.9268	0.00	1
0.0058500	379.5354	68570.44	12
0.0688500	727.5938	14997.58	4
0.4535000	748.8333	142649.08	3
1.2935000	829.6744	112964.44	6
2.1970000	1178.3333	821158.33	3
3.0940000	449.4375	27058.77	4
4.4660000	826.1667	15196.06	2
6.2890000	1850.0000	0.00	1

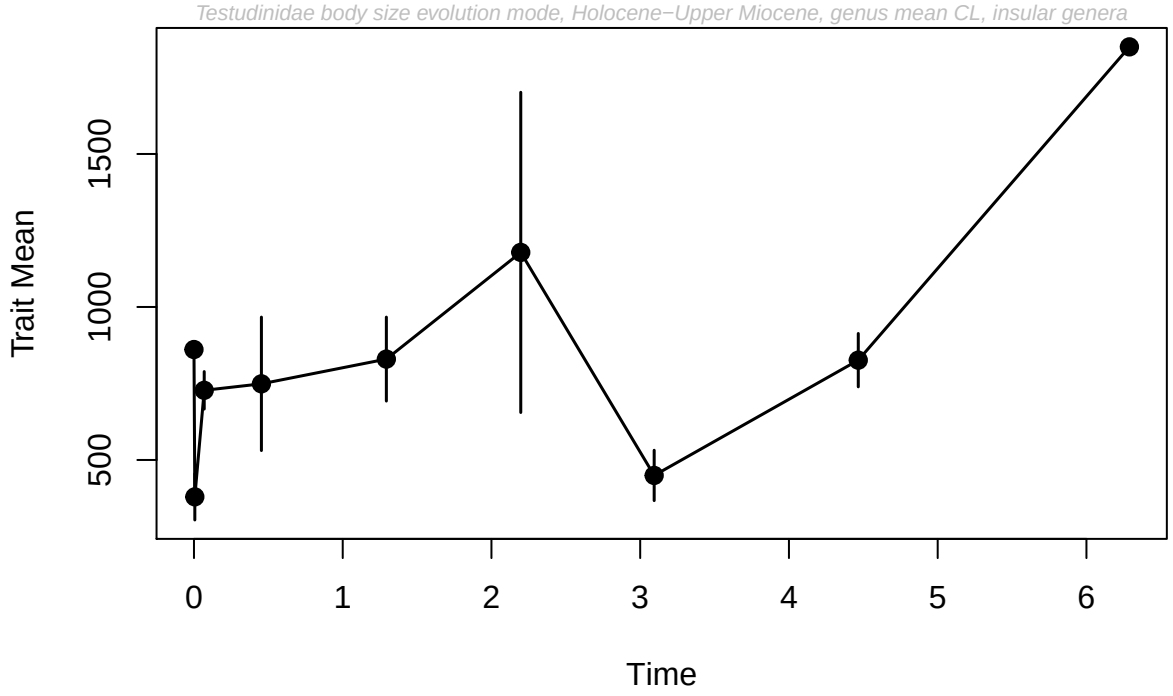


Figure 9: paleoTS plot with genus mean, insular

Table 7: Model-fitting results for testudinidae, genera, insular

	logL	K	AICc	Akaike.wt
GRW	-68.57344	2	143.5469	0
URW	-75.76576	1	154.1982	0
Stasis	-60.41581	2	127.2316	1

4.4. per continent

4.4.1. Europe, genera

Table 8: paleoTS object, Europe

mm	nn	vv	tt
148.8559	2	3338.406	0.00585
616.6667	3	138802.333	0.06885
377.8167	3	89203.953	0.45350
697.3717	5	218431.974	1.29350
895.0000	2	1110050.000	2.19700
453.3333	3	39433.333	3.09400
1215.8667	5	159317.256	4.46600
838.3750	2	875495.281	6.28900
800.0508	6	263434.389	9.42700
653.9625	5	351634.528	12.71400
772.0000	5	223154.375	14.89500
533.8533	5	183706.682	19.50000

Table 9: Model-fitting results for testudinidae, genera, Europe

	logL	K	AICc	Akaike.wt
GRW	-84.14010	2	173.7802	0.006
URW	-85.90727	1	174.2590	0.005
Stasis	-79.01365	2	163.5273	0.990

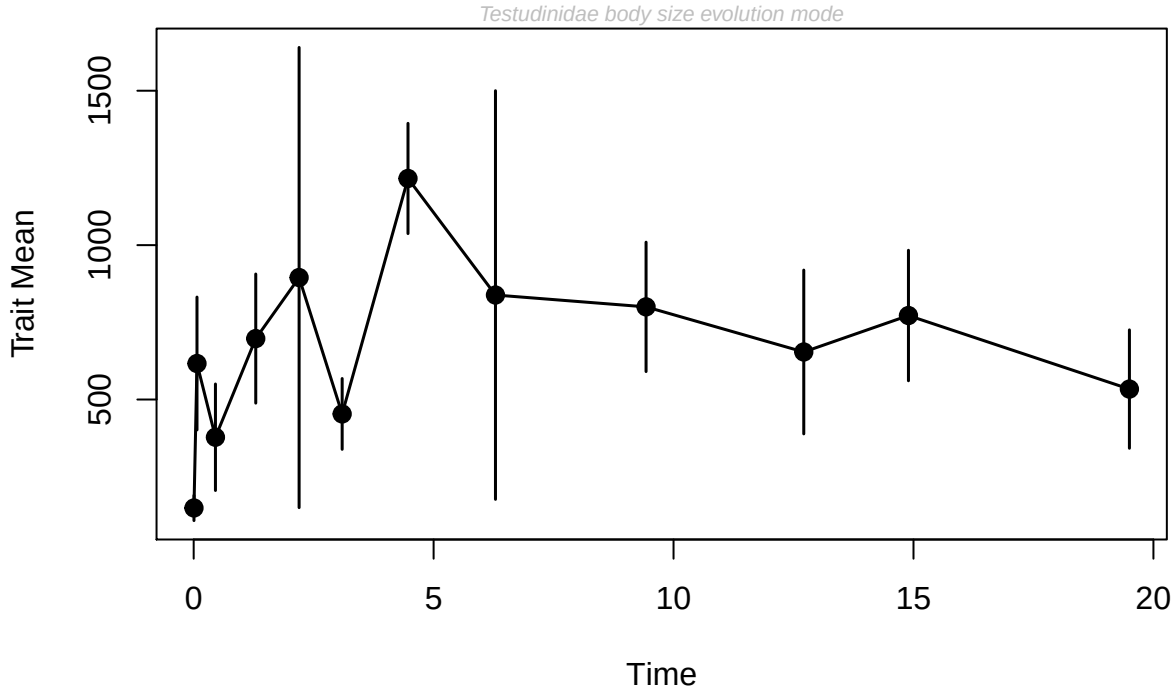


Figure 10: Genera, Europe

Table 10: paleoTs object, Europe, continental

mm	nn	vv	tt
149.5381	2	3450.8267	0.00585
187.0000	1	0.0000	0.06885
205.4750	2	198.0050	0.45350
204.9292	2	23.1767	1.29350
1420.0000	1	0.0000	2.19700
232.5000	1	0.0000	3.09400
1475.6667	3	57926.3333	4.46600
663.3750	2	473607.7812	6.28900
800.0508	6	263434.3893	9.42700
653.9625	5	351634.5281	12.71400
772.0000	5	223154.3750	14.89500
533.8533	5	183706.6821	19.50000

Table 11: Model-fitting results for testudinidae, genera, Europe, continental

	logL	K	AICc	Akaike.wt
GRW	-87.93137	2	181.3627	0.009
URW	-92.56882	1	187.5821	0.000
Stasis	-83.21073	2	171.9215	0.991

Europe, genera, continental

Table 12: paleoTs object, Europe, insular

mm	nn	vv	tt
187.5077	1	0.00	0.00585
831.5000	2	684.50	0.06885
722.5000	1	0.00	0.45350
835.0833	4	168423.36	1.29350
1005.0000	2	1462050.00	2.19700
451.6667	3	40558.33	3.09400
826.1667	2	15196.06	4.46600
1850.0000	1	0.00	6.28900

Table 13: Model-fitting results for testudinidae, genera, Europe, insular

	logL	K	AICc	Akaike.wt
GRW	-67.12192	2	141.2438	0.000
URW	-57.51634	1	117.8327	0.074
Stasis	-52.89638	2	112.7928	0.926

Europe, genera, insular

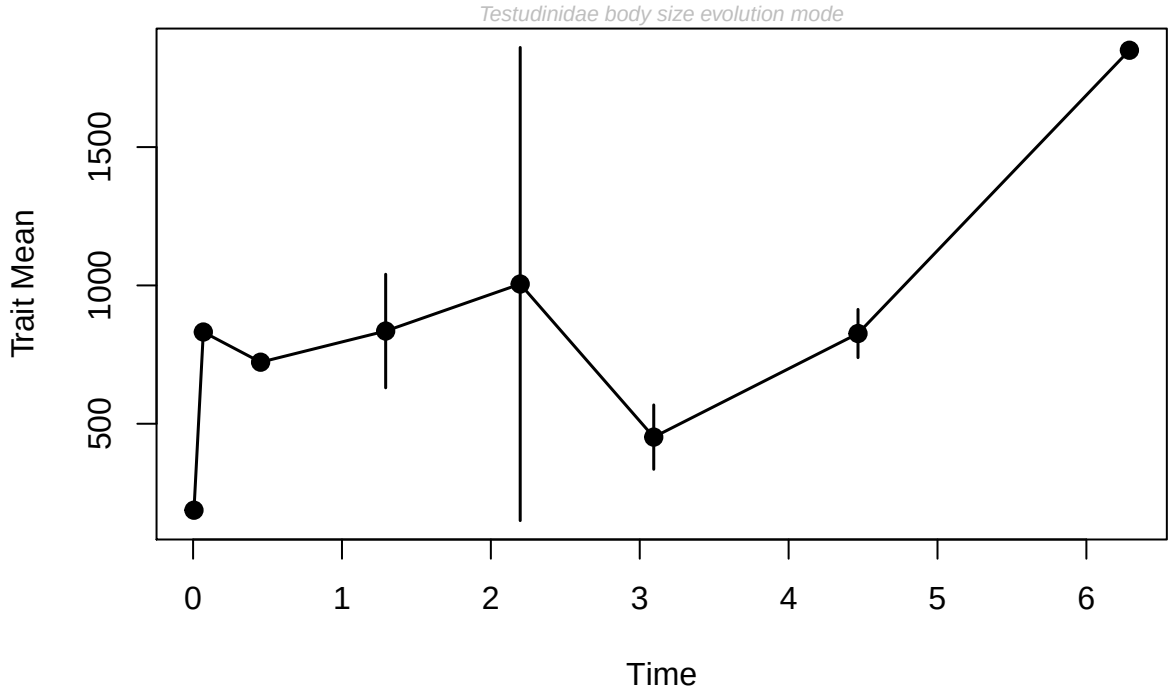


Figure 12: paleoTS, genera, Europe, insular

4.4.2. Eurasia, genera

Table 14: paleoTS object, Eurasia

tt	mm	vv	nn
0.0000005	137.2637	0.000	1
0.0058500	236.8217	9760.467	5
0.0688500	530.0000	122579.333	4
0.4535000	377.8167	89203.953	3
1.2935000	777.5579	162641.142	7
2.1970000	909.6667	562217.222	5
3.0940000	892.0000	381770.000	5
4.4660000	1048.0556	296417.219	6
6.2890000	1208.9167	849651.021	3
9.4270000	800.0508	263434.389	6
12.7140000	653.9625	351634.528	5

tt	mm	vv	nn
14.8950000	772.0000	223154.375	5
19.5000000	513.8533	162399.349	5

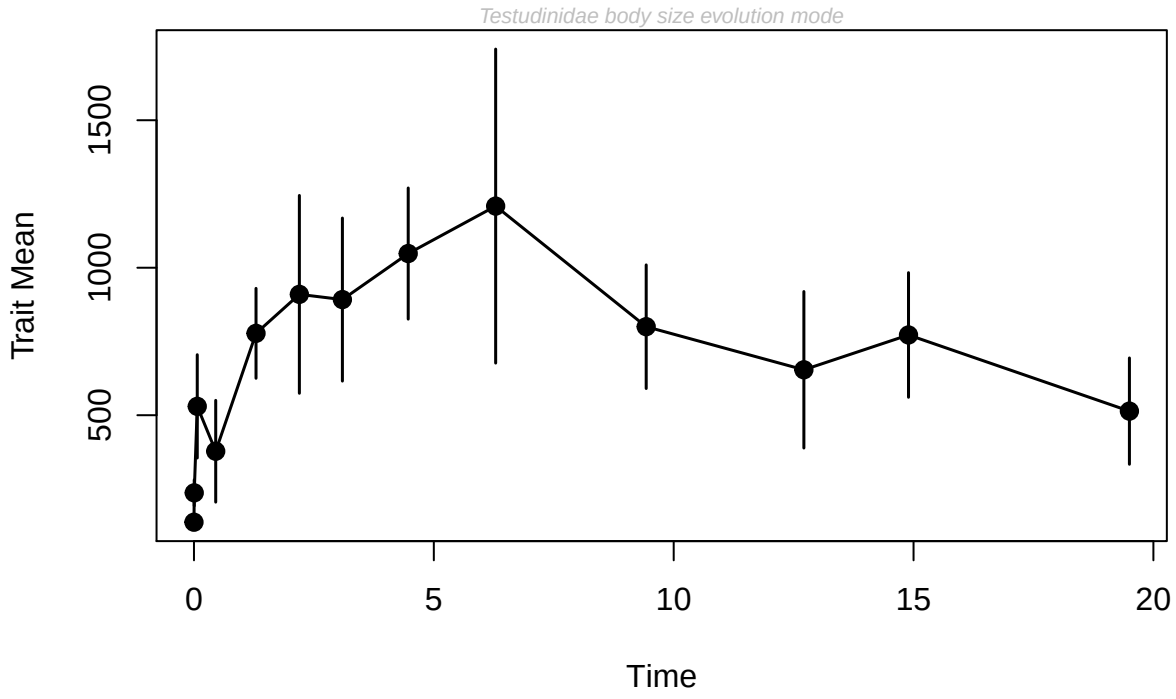


Figure 13: paleoTS, genera, Eurasia

Table 15: Model-fitting results for testudinidae, genera, Eurasia

	logL	K	AICc	Akaike.wt
GRW	-85.25195	2	175.8372	0.149
URW	-85.39072	1	173.1814	0.562
Stasis	-84.58890	2	174.5111	0.289

4.4.3. Eurasia, genera, continental

Table 16: paleoTS object, Eurasia, continental

tt	mm	vv	nn
0.0000005	137.2637	0.000	1
0.0058500	238.0120	9654.865	5
0.0688500	228.5000	3444.500	2
0.4535000	205.4750	198.005	2
1.2935000	595.5388	191487.404	4
2.1970000	1044.5833	442006.250	4
3.0940000	1110.8333	581102.083	3
4.4660000	1159.0000	439728.667	4
6.2890000	1092.2500	788605.188	3
9.4270000	800.0508	263434.389	6
12.7140000	653.9625	351634.528	5
14.8950000	772.0000	223154.375	5
19.5000000	513.8533	162399.349	5

Table 17: Model-fitting results for testudinidae, genera, Eurasia, continental

	logL	K	AICc	Akaike.wt
GRW	-82.20698	2	169.7473	0.222
URW	-82.42344	1	167.2469	0.776
Stasis	-87.19538	2	179.7241	0.002

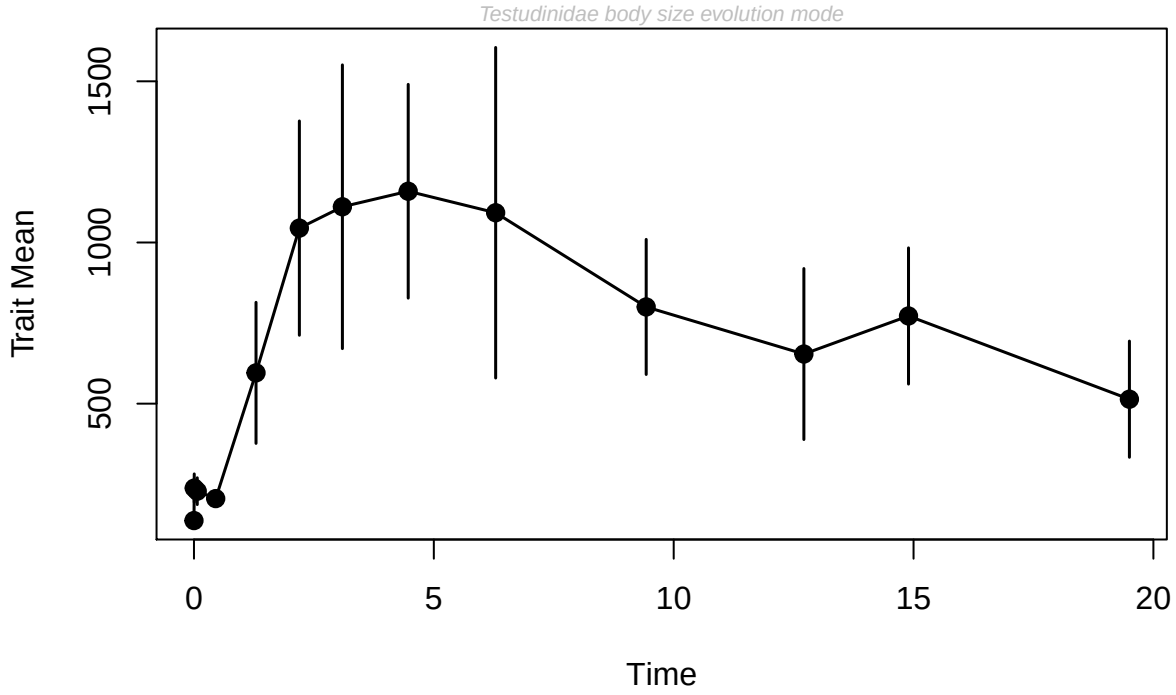


Figure 14: paleoTS, genera, Eurasia, continental

4.4.4. Eurasia, genera, insular

Table 18: paleoTS object, Eurasia, insular

tt	mm	vv	nn
0.0000005	137.2637	0.000	1
0.0058500	271.4596	5668.485	4
0.0688500	644.3333	105436.333	3
0.4535000	722.5000	0.000	1
1.2935000	882.0356	105684.077	6
2.1970000	953.6667	652233.889	5
3.0940000	891.0000	383430.000	5
4.4660000	620.4444	134562.926	3
6.2890000	1900.0000	5000.000	2
19.5000000	800.0000	0.000	1

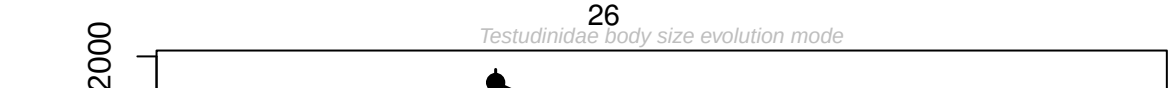
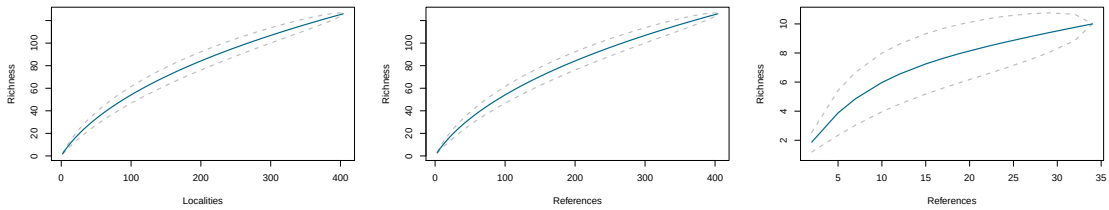


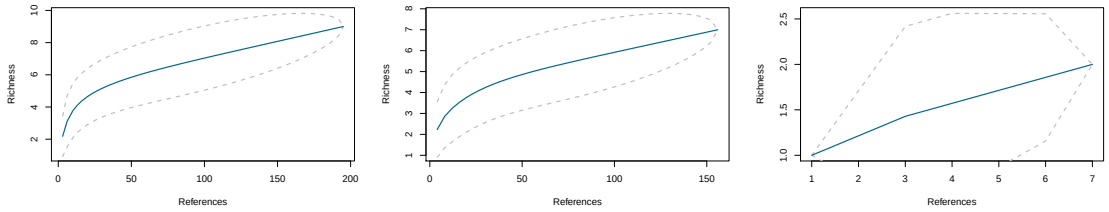
Table 19: Model-fitting results for testudinidae, genera, Eurasia, insular

	logL	K	AICc	Akaike.wt
GRW	-69.56419	2	145.1284	0.193
URW	-71.67437	1	145.9202	0.130
Stasis	-68.31026	2	142.6205	0.677

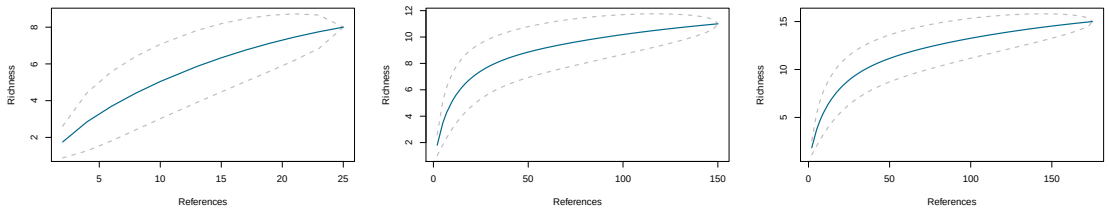
Appendix A Sampling Accumulation Curves



(a) Species per locality (b) Species per reference (c) Africa



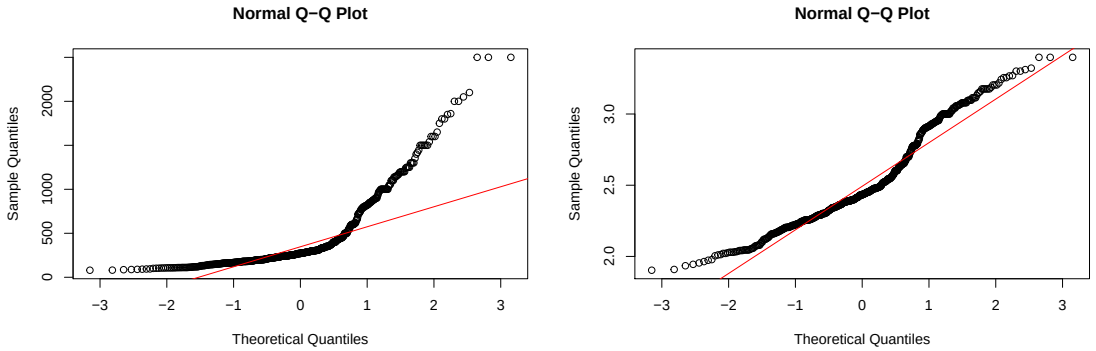
(d) America (e) North America (f) South America



(g) Asia (h) Europe (i) Eurasia

Figure 16: 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.

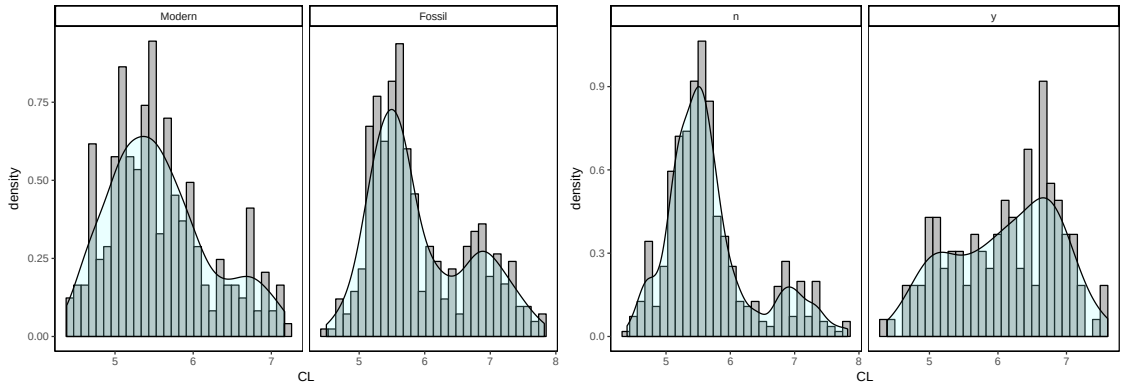
Appendix B Histograms



(a) Raw data

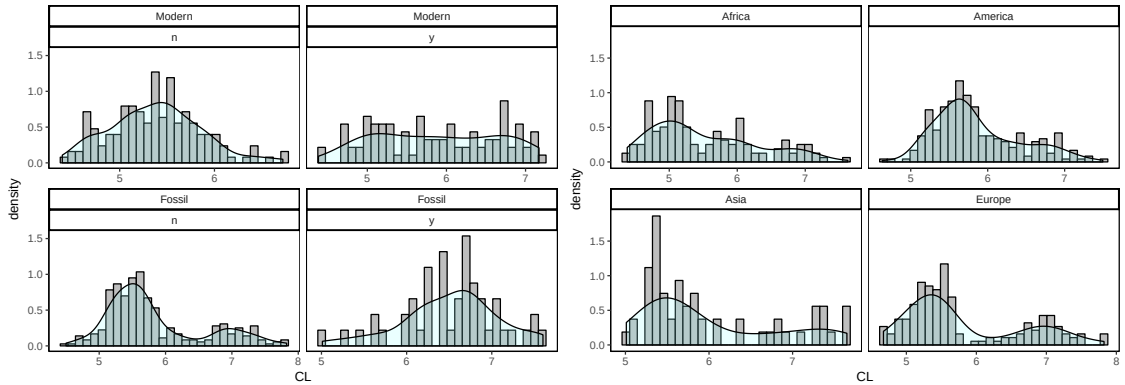
(b) Logtransformed data

Figure 17: Visual test for normal distribution. In case of normally distributed data, the black circles should follow the red line, which is not the case for either raw data nor log-transformed data. Therefore, data is not normally distributed.



(a) Fossil vs. modern

(b) Continental vs. insular



(c) Fossil vs. modern, continental vs. insular

(d) Per continent

Figure 18: Histograms for several subgroups of the dataset.

Appendix C Boxplots

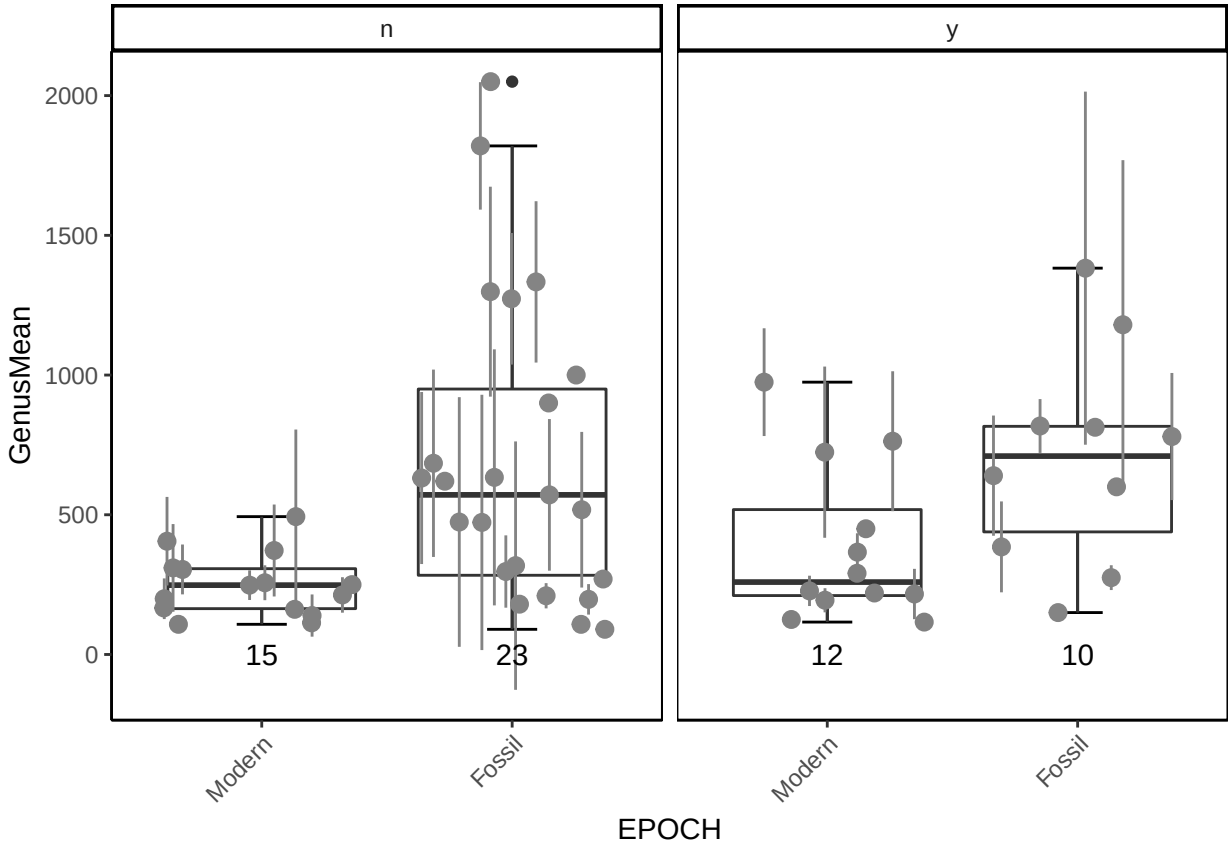


Figure 19: Boxplots fossil vs. modern, continental vs. insular species.

Wilcoxon Rank Sum Test (unpaired data):

modern continental < fossil continental (P = 4.8532266×10^{-8})

modern insular < fossil insular (P = 0.0018564)

Kruskal-Wallis-Test:

Continent means differ (P = 1.0833256×10^{-6}) (still have to look into the details. . .)

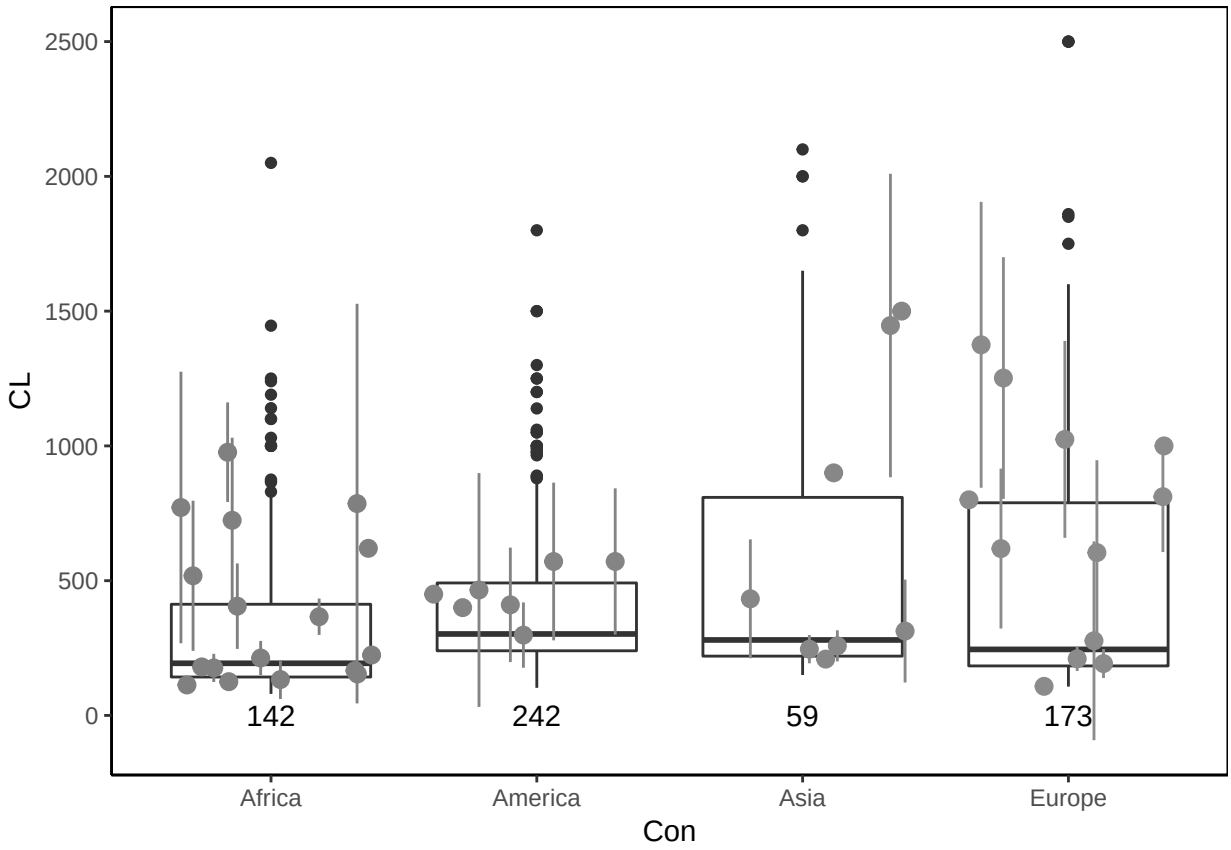
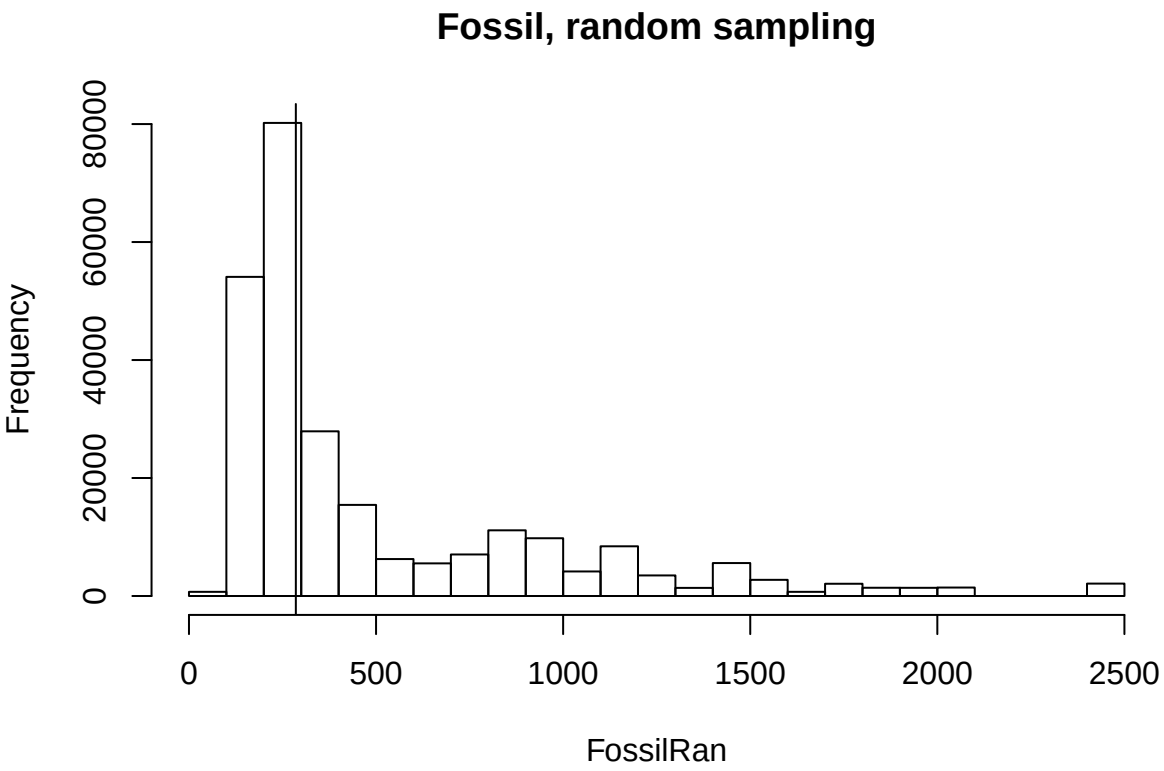
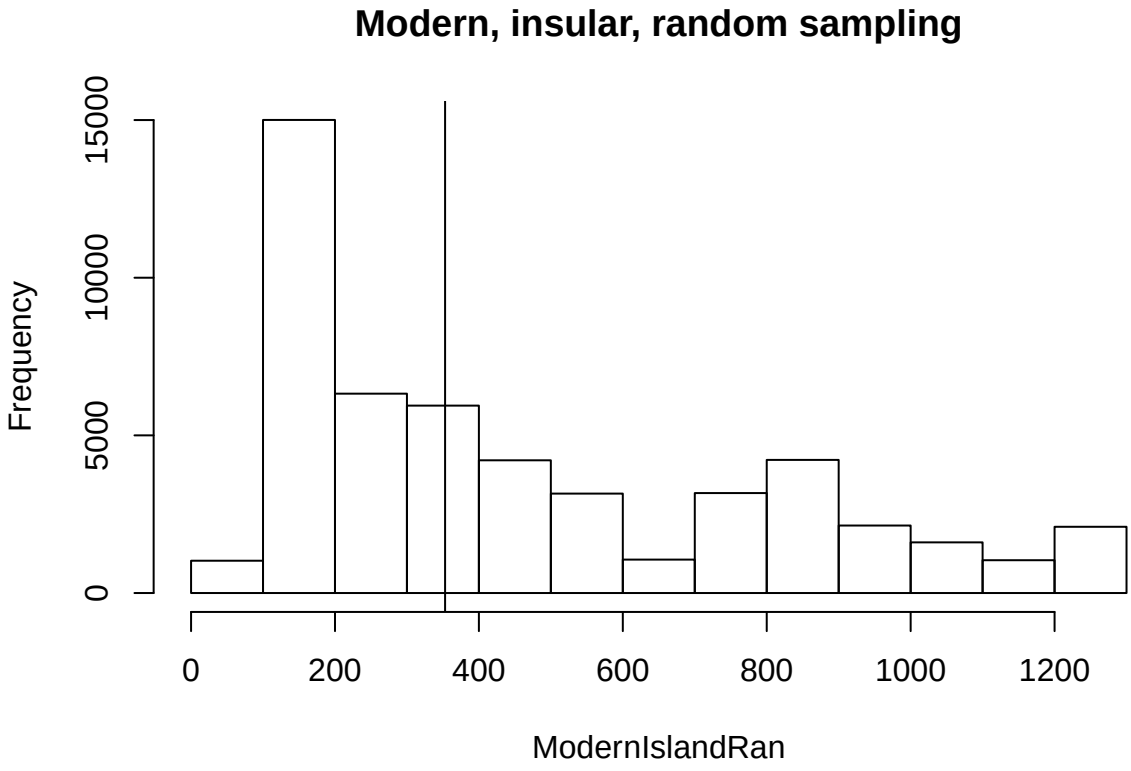
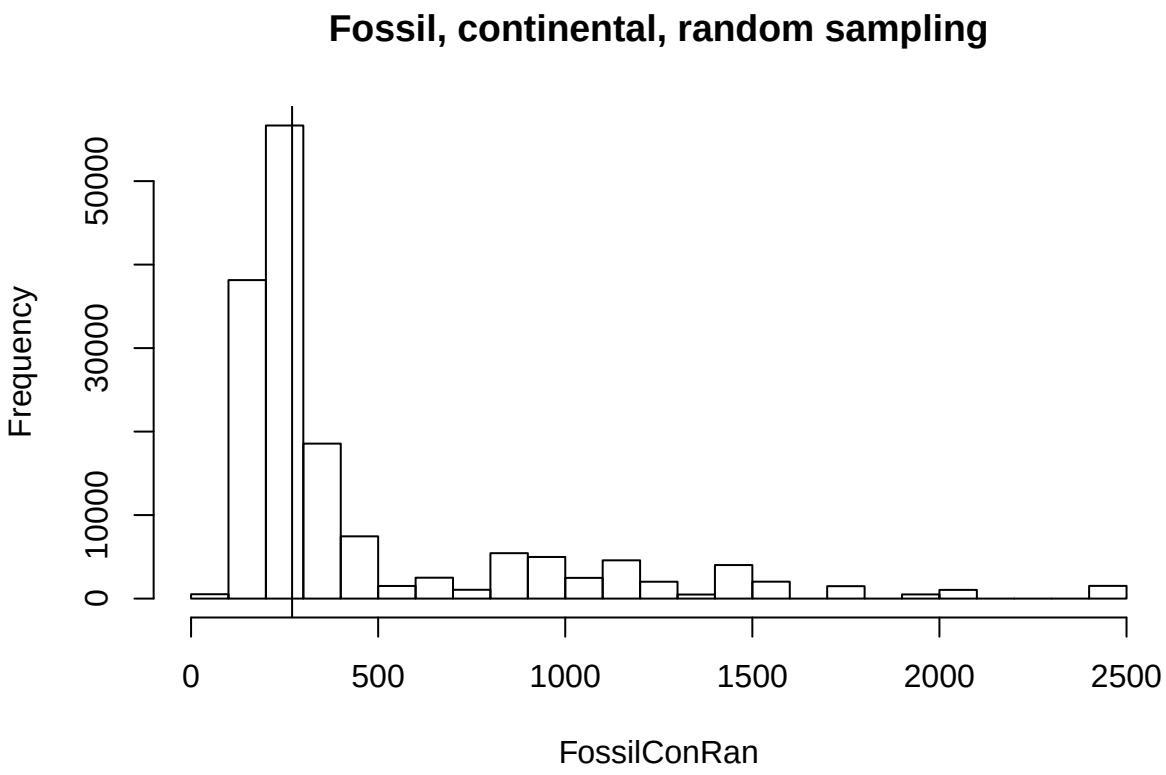


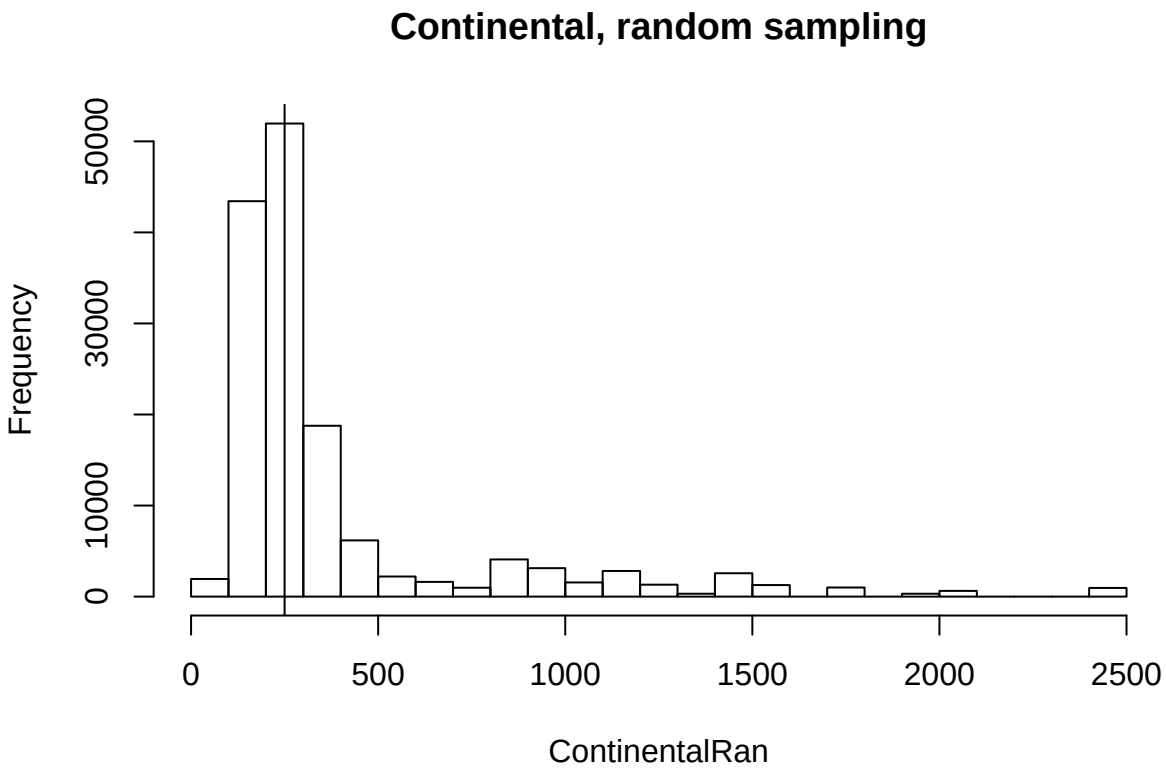
Figure 20: Boxplot: body size on different continents, genera summarised

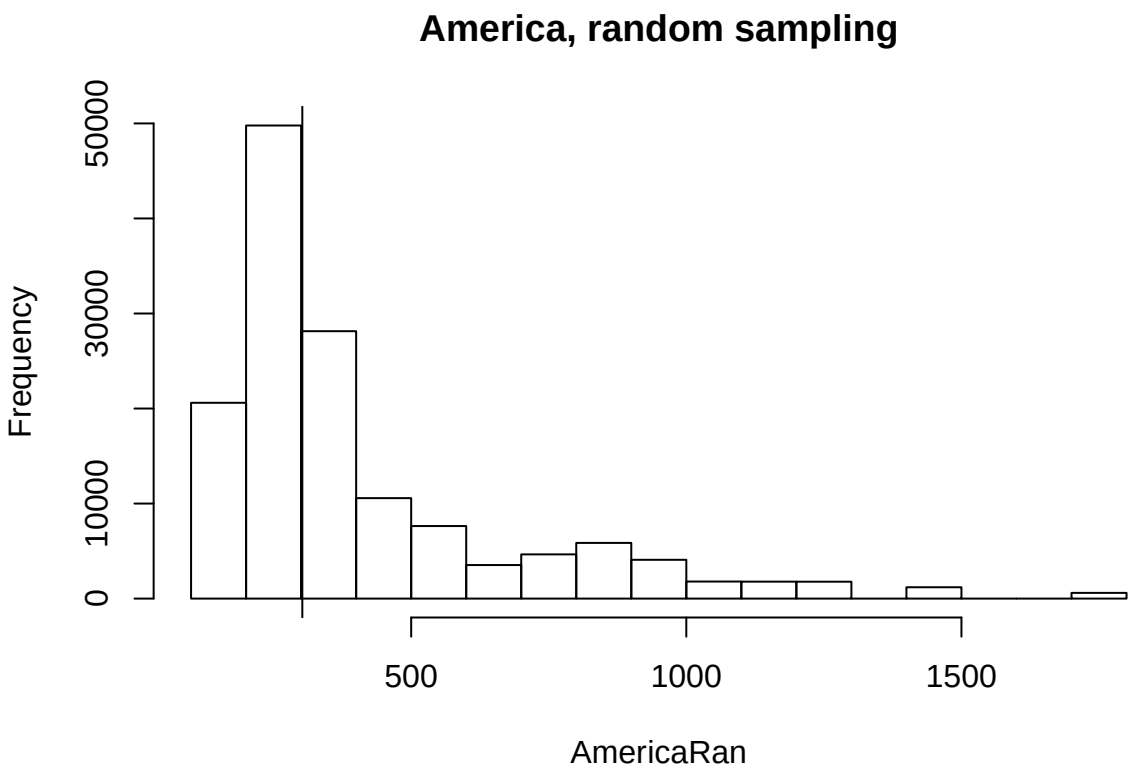
Appendix D Random Sampling

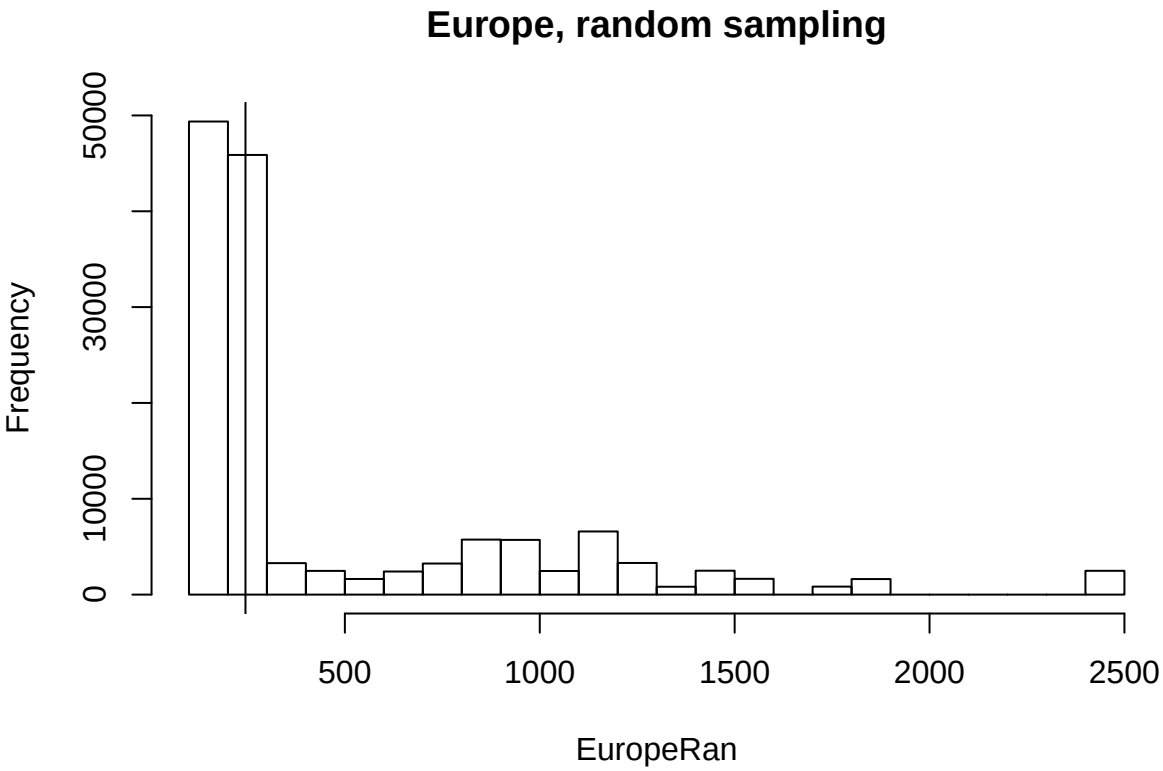


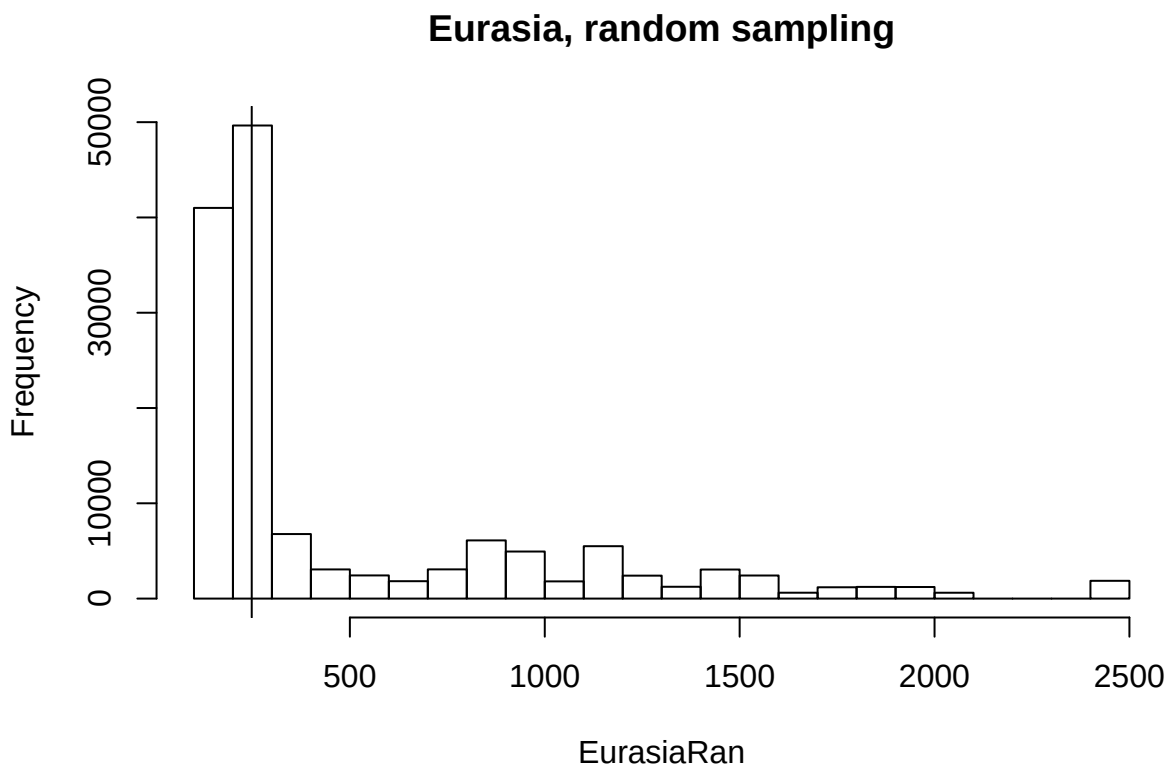



Fossil, continental, random sampling
Frequency
0
10000
30000
50000
0
500
1000
1500
2000
2500
FossilConRan


Continental, random sampling
Frequency
0
10000
30000
50000
0
500
1000
1500
2000
2500
ContinentalRan


America, random sampling
Frequency
0
10000
30000
50000
500
1000
1500
AmericaRan


Europe, random sampling
Frequency
0
10000
30000
50000
500
1000
1500
2000
2500
EuropeRan



Appendix E Tables

Table 20: 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 sombrerensis	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

EpochBins	Taxon	n	meanCL
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
Middle Pleistocene	Geochelone sp.	1	170.0000
Middle Pleistocene	Gopherus agassizi	1	445.0000
Middle Pleistocene	Gopherus laticaudatus	1	375.0000
Middle Pleistocene	Gopherus polyphemus	31	300.4316
Middle Pleistocene	Hesperotestudo bermudae	2	385.0000
Middle Pleistocene	Hesperotestudo equicomes	1	340.0000
Middle Pleistocene	Hesperotestudo sp.	2	1650.0000
Middle Pleistocene	Testudo kenitrensis	1	132.0000
Middle Pleistocene	Testudo lunellensis	4	215.4250
Lower Pleistocene	Centrochelys atlantica	1	400.0000
Lower Pleistocene	Centrochelys robusta	3	883.3333
Lower Pleistocene	Cheirogaster cf. gymnesica	1	789.0000
Lower Pleistocene	Cheirogaster sp.	1	925.0000
Lower Pleistocene	Chelonoidis sp.	3	716.6667
Lower Pleistocene	Eurotestudo globosa	1	263.0000
Lower Pleistocene	Eurotestudo hermanni	2	205.0000
Lower Pleistocene	gen. indet.	1	900.0000
Lower Pleistocene	Geochelone sp.	1	340.0000

EpochBins	Taxon	n	meanCL
Lower Pleistocene	Gopherus berlandieri	2	225.6500
Lower Pleistocene	Gopherus flavomarginatus	1	450.0000
Lower Pleistocene	Gopherus pertenuis	1	1050.0000
Lower Pleistocene	Gopherus polyphemus	3	254.4667
Lower Pleistocene	Gopherus sp.	6	233.9667
Lower Pleistocene	Hesperotestudo crassiscutata	5	285.6000
Lower Pleistocene	Hesperotestudo incisa	7	234.6286
Lower Pleistocene	Hesperotestudo mlynarskii	2	184.2500
Lower Pleistocene	Hesperotestudo sp.	1	1500.0000
Lower Pleistocene	Hesperotestudo turgida	1	230.0000
Lower Pleistocene	Megalochelys sondaari	2	909.0000
Lower Pleistocene	Megalochelys sp.	3	1130.4667
Lower Pleistocene	Psammobates antiquorum	1	107.8000
Lower Pleistocene	Testudo changshanesis	1	330.0000
Lower Pleistocene	Testudo graeca	1	195.0000
Lower Pleistocene	Testudo hermanni	2	176.5500
Lower Pleistocene	Testudo marginata	3	270.0000
Lower Pleistocene	Titanochelon gymnesica	1	1300.0000
Gelasian	Centrochelys marocana	1	2050.0000
Gelasian	Eurotestudo cf. hermanni	1	150.0000
Gelasian	Gopherus sp.	15	185.7467
Gelasian	Hesperotestudo campester	1	1000.0000
Gelasian	Hesperotestudo sp.	1	1000.0000
Gelasian	Manouria punjabiensis	1	900.0000
Gelasian	Megalochelys atlas	3	1683.3333
Gelasian	Testudo aff. kenitrensis	1	142.0000
Gelasian	Testudo oughlamensis	1	120.0000
Gelasian	Testudo ranovi	1	200.0000
Gelasian	Testudo sp.	2	192.0000
Gelasian	Testudo transcaucasia	1	150.0000

EpochBins	Taxon	n	meanCL
Gelasian	Titanochelon aff. schafferi	1	1860.0000
Gelasian	Titanochelon sp.	1	1420.0000
Piacencian	“Aldabrachelys” laetoliensis	1	1000.0000
Piacencian	Aldabrachelys ? sp.	2	1500.0000
Piacencian	Centrochelys vulcanica	1	610.0000
Piacencian	Chelonoidis alburyorum	4	442.7500
Piacencian	Gopherus canyonensis	1	885.5000
Piacencian	Hesperotestudo johnstoni	1	235.0000
Piacencian	Hesperotestudo oelrichi	1	283.8000
Piacencian	Hesperotestudo riggsi	2	180.5000
Piacencian	Hesperotestudo sp.	1	176.0000
Piacencian	Homopus fenestratus	1	90.0000
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

EpochBins	Taxon	n	meanCL
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
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

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

Table 21: 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 ducateli	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
Centrochelys vulcanica	1	610.0000
Cheirogaster cf. gymnesica	1	789.0000
Cheirogaster gymnesica	1	739.0000
Cheirogaster richardi	1	1155.0000
Cheirogaster sp.	5	1227.0000
Chelonoidis alburyorum	4	442.7500
Chelonoidis cubensis	1	1139.0000
Chelonoidis denticulata	1	616.0000
Chelonoidis lutzae	1	830.0000
Chelonoidis marcanoi	4	672.2500
Chelonoidis monensis	1	500.0000
Chelonoidis sombrerensis	1	990.0000
Chelonoidis sp.	9	645.5556
Ergilemys oskarkuhni	2	209.0000
Ergilemys sp.	1	1000.0000
Eurotestudo aff. hermanni	2	187.0000
Eurotestudo cf. hermanni	1	150.0000
Eurotestudo globosa	1	263.0000
Eurotestudo hermanni	5	201.0200

Taxon	n	meanCL
gen. indet.	8	654.1250
Geochelone crassa	1	865.0000
Geochelone hesterna	1	278.0000
Geochelone s. l.	1	1750.0000
Geochelone sp.	10	626.2000
Geochelone stromeri	2	387.5000
Geochelone tedwhitei	2	405.0000
Gopherus ? sp.	2	500.0000
Gopherus agassizi	2	348.5000
Gopherus berlandieri	2	225.6500
Gopherus canyonensis	1	885.5000
Gopherus flavomarginatus	1	450.0000
Gopherus laticaudatus	1	375.0000
Gopherus mohavetus	5	324.8000
Gopherus pertenuis	1	1050.0000
Gopherus polyphemus	54	295.1144
Gopherus praecedens	1	360.0000
Gopherus sp.	21	199.5238
Hesperotestudo alleni	1	240.9000
Hesperotestudo bermudae	2	385.0000
Hesperotestudo campester	1	1000.0000
Hesperotestudo crassiscutata	11	367.1818
Hesperotestudo equicomes	1	340.0000
Hesperotestudo incisa	8	234.3950
Hesperotestudo johnstoni	1	235.0000
Hesperotestudo mlynarskii	2	184.2500
Hesperotestudo oelrichi	1	283.8000
Hesperotestudo orthopygia	2	941.0000
Hesperotestudo riggsi	5	175.1600
Hesperotestudo sp.	8	1098.6250

Taxon	n	meanCL
Hesperotestudo turgida	1	230.0000
Hesperotestudo wilsoni	1	226.0000
Homopus fenestratus	1	90.0000
Impregnochelys pachytectis	1	620.0000
Indotestudo elongata	1	270.0000
Manouria punjabiensis	1	900.0000
Megalochelys atlas	7	1735.7143
Megalochelys sondaari	2	909.0000
Megalochelys sp.	3	1130.4667
Mesocherus orangeus	5	180.0000
Namibchersus aff. namaquensis	3	696.6667
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

Taxon	n	meanCL
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
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 22: 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

EpochBins	Genus	n	meanCL
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
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

EpochBins	Genus	n	meanCL
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
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

EpochBins	Genus	n	meanCL
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
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/Aquitanian	Caudochelys	1	334.0000

EpochBins	Genus	n	meanCL
Burdigalian/Aquitanian	gen.	1	270.0000
Burdigalian/Aquitanian	Geochelone	4	652.5000
Burdigalian/Aquitanian	Impregnochelys	1	620.0000
Burdigalian/Aquitanian	Mesocherus	5	180.0000
Burdigalian/Aquitanian	Namibchersus	9	518.1111
Burdigalian/Aquitanian	Paleotestudo	2	146.1500
Burdigalian/Aquitanian	Testudo	6	252.1167
Burdigalian/Aquitanian	Titanochelon	1	1001.0000

Table 23: 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

Genus	n	meanCL
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
Titanochelon	20	1315.2000

Table 24: General statistics of body size data: all, per time bin, insular and continental, per continent (all referring to CL: min, max, variance, mean, logmean, median, logmedian, skewness, logskewness, kurosis, logkurtosis

nCL	min	max	var	mean	logm	med	logmed	skew	logsk	kurt	logku	Variable
616	80.00	2500	164537.80	437.2	2.5	270.5	2.4	2.14	0.69	8.00	2.73	all
253	80.00	1300	67485.50	330.3	2.4	242.0	2.4	1.83	0.58	5.87	2.69	Modern
49	102.44	1250	69690.66	445.9	2.6	334.7	2.5	1.20	0.24	3.61	2.56	Upper Pleistocene
53	132.00	1800	97910.83	387.1	2.5	292.9	2.5	3.03	1.52	12.24	5.55	Middle Pleistocene
57	107.80	2000	161948.82	463.5	2.5	263.0	2.4	1.74	0.73	5.76	2.40	Lower Pleistocene
31	118.90	2050	411224.51	555.2	2.5	194.9	2.3	1.31	0.93	3.12	2.11	Gelasian
21	90.00	1600	270535.82	610.6	2.6	428.0	2.6	1.00	0.14	2.50	1.99	Piacencian
26	176.00	2500	476162.71	955.2	2.9	857.5	2.9	1.11	-0.40	3.56	2.30	Zanclean
10	140.00	2100	602611.21	948.9	2.8	916.0	2.9	0.26	-0.22	1.49	1.29	Messinian
45	107.00	1540	175470.12	462.7	2.5	250.0	2.4	1.49	0.81	3.74	2.54	Tortonian
27	111.00	1500	126060.40	337.7	2.4	220.0	2.3	2.49	1.77	7.77	5.30	Serravallian
14	270.00	1600	230451.33	747.9	2.8	700.0	2.8	0.30	0.03	1.55	1.18	Langhian
30	113.00	1100	76288.76	406.8	2.5	302.4	2.5	1.27	0.45	3.45	2.26	Burdigalian/Aquitanian
253	80.00	1300	67485.50	330.3	2.4	242.0	2.4	1.83	0.58	5.87	2.69	Modern
363	90.00	2500	219004.66	511.7	2.6	285.6	2.5	1.83	0.68	6.11	2.42	Fossil
469	81.00	2500	157808.79	392.9	2.5	250.0	2.4	2.65	1.07	10.57	3.74	continental
147	80.00	2000	160834.35	578.5	2.6	500.0	2.7	1.02	-0.27	3.95	2.05	insular

nCL	min	max	var	mean	logm	med	logmed	skew	logsk	kurt	logku	Variable
157	81.00	830	17009.02	244.0	2.3	221.0	2.3	1.92	0.29	8.09	2.98	modern-con
96	80.00	1300	118641.09	471.5	2.6	353.0	2.5	0.82	0.01	2.47	1.77	modern-ins
312	90.00	2500	212116.79	467.9	2.5	270.0	2.4	2.11	0.96	7.25	2.96	fossil-con
51	150.00	2000	180825.40	780.0	2.8	750.0	2.9	1.11	-0.40	4.02	3.18	fossil-ins
142	80.00	2050	112417.26	347.7	2.4	193.5	2.3	2.10	0.68	7.97	2.48	Africa
242	102.44	1800	82209.71	415.0	2.5	302.2	2.5	1.92	0.75	6.79	2.91	America
59	150.00	2100	323123.20	585.5	2.6	280.0	2.4	1.43	0.85	3.61	2.24	Asia
173	107.00	2500	254222.84	491.2	2.5	245.0	2.4	1.86	0.81	6.30	2.34	Europe

Acknowledgements

Declaration of Authorship