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MASS-LENGTH RELATIONSHIPS IN MACROTEIID AND OTHER LIZARDS ARE INSENSITIVE TO ECOLOGY AND GEOGRAPHY (SAURIA, TEIIDAE)

P.E. VANZOLINI

ABSTRACT

No differences were found among regressions of body mass on length for 8 species of macroteiid lizards (5 genera, 18 geographical samples, 11 localities), encompassing marked ecological contrasts and modes of locomotion. The same results were obtained for all cases available in the literature, including in all 19 species of 3 families, from 4 continents, and additionally one species of salamander. It is suggested that this uniformity can only be explained by general mechanical constraints.

INTRODUCTION

The lizard family Teiidae is divided in two groups of genera, recognized informally (''macroteiids'' and ''microteiids'') or even given formal family (Teiidae, Gymnophthalmidae) or subfamily status (Presch, 1988). The macroteiids comprise seven genera; for five of these I have, along the years, collected measurements and weights taken in the field in diverse areas of Brasil. The amount of data presently available is sufficient for a first statistical analysis, aiming at discerning the importance of geographical distribution and of ecological features on the body mass/length relationships. The present result is an unmistakable and surprising homogeneity of these relationships. One species of salamander, introduced as a control, also closely agreed with the lizards.

MATERIALS

The seven genera of macroteiids are *Ameiva, Cnemidophorus, Crocodilurus, Dicrodon, Kentropyx, Teius* and *Tupinambis*. Systematics at the species level of the larger genera is still quite unsatisfactory; I personally tally about 24 species for the group in South America.

The materials includes 18 samples of 8 species belonging to 5 genera and comprising 222 specimens from 11 localities (Map 1):

Ameiva ameiva (L., 1758): Santa Maria do Boiaçu, Roraima, 1991, 37 specimens; Roraima, several locatities, 1990, 8; Barreira, Pará, 1970, 44; Santa Cruz da Serra, Rondônia, 1984, 27.

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Kentropyx pelviceps Cope, 1868: Santa Maria do Boiaçu, 1991, 12; Roraima, 1990, 10; Santa Cruz da Serra, 1984, 7.
Kentropyx calcarata Spix, 1825: Monte Cristo, Pará, 1970, 20; Santa Cruz da Serra, Rondônia, 1984, 11; Itamaracá, Pernambuco, 1971, 2.
Cnemidophorus lemniscatus (L., 1758): Santarém, Pará, 1970, 15; Alter do Chão, Pará, 1970, 18.
Crocodilurus lacertinus (Daudin, 1802), Santa Maria do Boiaçu. Roraima, 1991, 3.
Tupinambis sp.: Santa Maria do Boiaçu, Roraima, 1990-1991, 3 (the status of Roraima *Tupinambis* is not yet settled; it is, however, safe to say it differs from general Amazonian *Tupinambis teguixin*).
Tupinambis teguixin (L., 1758): two localities on the Rio Japurá, Amazonas, 1977, 5.

LOCALITIES

The localities sampled involve a broad geographical area (ca. 1.5 million km²) and a wide range of ecological features.

Santa Maria do Boiaçu is a riverside locality on the lower Rio Branco (00°32'S, 61°50'W); the general ecology is terra firme forest, and that is where the lizards were collected, with the exception of aquatic *Crocodilurus lacertinus*, caught in a neighboring lake. The other two Roraima localities sampled, São Luís do Anauá (00°57'N, 59°59'W) and Maloca Sorocaima (04°20'N, 61°08'W) are in isolated patches of forest in the middle of open formations (Vanzolini and Carvalho, 1991).

The Amazonas localities on the Rio Japurá are Costa da Saracura (01°46'S, 66°45'W) and Ilha do Mojuí (02°10'S, 65°13'W). Both consist of varzea (seasonally flooded) forest.

Four localities are in Pará. Barreira and Monte Cristo are across from each other on the Rio Tapajós at 04°04'S, 50°45'W, in terra firme forest. Santarém (02°25'S, 54°48'W), at the mouth of the Tapajós, is in second growth open formations; the lizards collected there *(Cnemidophorus lemniscatus)* are strictly perianthropic. They belong to a bisexual population of a species with a regional preponderance of parthenogenetic clones (Vyas et al., 1990).

The Rondonia locality, Santa Cruz da Serra (10°40'S, 62°34'W) was formerly in dry terra firme forest (Vanzolini, 1986); at the time of collecting it was already an agricultural area.

Itamaracá (07°45'S, 34°50'W), in Pernambuco, is in the Atlantic forest (Vanzolini, 1974). The specimens were collected in small (a few hectares) remains of forest.

A very important Brasilian locality cited in the literature (Exu: Anderson and Vitt, 1990) is in the core area of the northeastern caatingas (Ab'Saber, 1977; Vanzolini et al., 1980).

LIZARD ECOLOGY

Of the seven species studied, one *(Crocodilurus lacertinus)* is fully aquatic: it lives on the muddy banks of Amazonian lakes. Two species *(Kentropyx calcarata* and *pelviceps)* climb on fallen tangles and assorted low vegetation on the edge of the forest or in small clearings penetrated by the sun. *K. pelviceps* is strictly Amazonian, but *K. calcarata* has a disjunct distribution, occurring both in Amazonia and in the northern Atlantic forest. *Cnemidophorus lemniscatus* is a grass-inhabiting ground-dweller in open formations; although it is strictly Amazonian in distribution, it does not enter the forest. The ecology of Amazonian *Tupinambis* is poorly known; it equally frequents terra firme and varzea forest as well as perianthropic localities (it is a great chicken coop thief). *Ameiva ameiva* is certainly the most euryoecic lizard in South America. It is equally abundant in the Amazonian forest, which it enters along trails and clearings (being a heliophil), in the Central Brasilian cerrados and in the northeastern caatingas (Vanzolini et al., 1980). It is a strict ground dweller.

All the species, with the possible exception of *Crocodilurus lacertinus*, are heliophils that function at high body temperatures. It seems safe to say, however, that there are enough contrasting habits and habitats, as well as geographic distance among the samples, to verify the influences of these factors on weight/length relationships.

Methods

Initially (starting 1970), specimens were weighed in the field, measured and sexed in the laboratory. In the eighties I changed to measuring in the field, and from 1990 on additionally to immediate sexing, by expression of the hemipenes. Data were taken only on specimens with complete tails. Measurements (snout to vent length) were taken with a metal tape to the nearest millimeter. Weights were taken with Pesola scales to the nearest gram (in the case of weights smaller than 5 g to the nearest tenth of a gram, rounded to whole g in the laboratory).

The basic tool of statistical analysis is ordinary regression analysis. There has been a trend in the literature towards methods that take into consideration error in the independent variable, but it seems that this does not apply to our type of data, in which there is no proper "major axis", and especially since the coefficients of correlation are unvaryingly very high (McArdle, 1988). In the statistical analysis I started with homogeneous (one species, one locality, one collection, one sex) samples with more than 5 specimens. In preference to analysis of covariance, which in the context would have little, if any, biological meaning, I preferred (Hemmingsen, 1960) to successively pool the samples to be compared, taking the resulting coefficients of determination as the criterion of homogeneity. Then I added the small samples, resulting into a final equation for all the macroteiid specimens available.

Results

The relevant data are shown on Tables 1 and 2.

The two anamorphoses adopted, log-log (power function) and cubic root of body mass, are in excellent agreement: Spearman's coefficient of rank correlation between the respective coefficients of determination is 0.95. This is only to be expected, since the regression coefficient of the power functions varies around 3, that of the general joint regression for all macroteiids being 2.9. It is thus unnecessary, in what follows, to consider separately the two anamorphoses. All graphs will refer to the log-log transformation.

All the coefficients of determination, as could expected from past experience and from the literature, are extremely high: more than one half of them are above 0.97, only one being a little below 0.90.

It is also striking that the joint macroteiid regression, resulting from the fusion of 18 samples of 8 species ranging in body length from 30 to 300 milimeters, in weight from a few grams to over half a kilogram, covering about 1.5 million square kilometers, has a coefficient of determination of 0.99.

Some of the contrasts whose study is allowed by the materials at hand and by data from Anderson and Vitt (1990), who reported on lizards from the semi-arid northeast of Brazil, can be profitably illustrated.

Mode of locomotion varies. *Ameiva ameiva* is a ground dweller, *Kentropyx pelviceps* climbs fallen tangles and low vegetation, *Crocodilurus lacertinus* is a compressed-tailed swimmer. Graph 1 shows the close agreement among the three species.

As to geographical distance, Itamaracá in Pernambuco and Santa Cruz da Serra in Rondonia are more than 3,000 km apart. Graph 2 shows the individual points for *Kentropyx calcarata* from the two locatilies, and the computed line for the Rondonia sample.

A still more extreme comparison, involving both distance and ecology, can be made among *Cnemidophorus lemniscatus*, Amazonian, *C. ocellifer*, from the semi-arid Northeastern and *C. tigris*, from the United States (Graph 3). The lines do not exactly coincide, but are very close.

Ameiva ameiva occurs in all sorts of habitats in South America. A comparison of northeastern (semi-arid) and Amazonian (super-humid) samples (Graph 4) shows complete agreement.

Finally, a curious case is that of *Tupinambis*. The Amazonian sample (two species and sexes combined) closely agrees with northeastern females (Graph 5).

Table 1. Regression of the logarithm of mass on the logarithm of snout to vent length

	N	R(x)	R(y)	b		a		F	r^2
Ameiva ameiva									
Boiaçu	37	50 - 156	3 - 110	3.1156 ±	.04214	-4.7735 ±	.08318	5466.371	.9936
Roraima 1990	8	58 - 155	6 - 100	2.7925	.11813	-4.1343	.024017	558.792	.9894
Barreira	44	49 - 146	3 - 101	3.1801	.05469	-4.9098	.10864	3377.770	.9877
Rondônia	27	46 - 130	4 - 84	2.9585	.07451	-4.4391	.14507	1576.571	.9844
General	116	46 - 156	3 - 110	3.0410	.03278	-4.6230	.06477	8607.422	.9869
Kentropyx pelviceps									
Boiaçu	12	40 - 100	2 - 30	3.0088	.05237	-4.5378	1.14414	3201.258	.9970
Roraima 1990	10	35 - 75	2 - 15	2.9766	.38424	-4.4228	.62956	60.014	.8824
Rondônia	7	55 - 98	4 - 26	3.1468	.15442	-4.8475	.29255	415.166	.9881
General	29	35 - 100	2 - 30	2.7367	.13312	-4.0453	.23710	777.547	.9664
Kentropyx calcarata									
Monte Cristo	20	58 - 105	6 - 31	2.7838	.10395	-4.1192	.16948	717.196	.9755
Rondônia	11	52 - 100	5 - 29	2.6811	.11636	-3.9055	.22157	530.878	.9833
General	33	52 - 105	5 - 31	2.7545	.07651	-4.0588	.14666	1296.010	.9766
Tupinambis	8	120 - 316	45 - 1050	3.3200	.06590	-5.2644	.14866	1069.964	.9976
Cnemidophorus lemniscatus									
Santarém	15	40 - 73	2 - 12	3.0367	.18156	-4.5728	.32370	279.734	.9566
Alter do Chão	18	32 - 56	1 - 6	2.7481	.22378	-4.0476	.26880	150.811	.9041
General	33	32 - 73	1 - 12	2.7857	.11220	-4.1168	.19194	616.413	.9521
Macroteiids, general	222	32 - 316	1 - 1050	2.8984	.02144	-4.3347	.04114	18275.515	.9881
Ambystoma maculatum	92	29 - 97	8 - 24	2.7023	.02498	-4.0382	.04577	11702.310	.9924

N individuals in sample. R(x), R(y), ranges of the variables. b, slope (regression coefficient) and its standard deviation. a, intercept (regression constant) and its standard deviation. F, quotient of variances (significance of the regressions — all significant at the 0.1% level). r^2, coefficient of determination.

Table 2. Regression of the cubic root of mass on snout to vent length

	N	R(x)	R(y)	b		a		F	r^2
Ameiva ameiva									
Boiaçu	37	50 - 156	3 - 110	.032 ±	.0004	-.086 ±	.0424	1747.481	.9939
Roraima 1990	8	58 - 155	6 - 100	.028	.0016	.279	.1884	291.749	.9799
Barreira	44	49 - 146	3 - 101	.032	.0006	-.191	.0583	3120.540	.9867
Rondonia	27	46 - 130	4 - 84	.032	.0009	-.048	.0868	1214.625	.9798
General	116	46 - 156	3 - 110	.031	.0004	-.055	.0365	7441.207	.9849
Kentropyx pelviceps									
Boiaçu	12	40 - 100	2 - 30	.031	.0008	.002	.0585	1482.647	.9933
Roraima 1990	10	35 - 75	2 - 15	.033	.0031	-.002	.1421	111.491	.9330
Rondonia	7	55 - 98	4 - 26	.031	.0017	-.083	.1382	333.666	.9852
General	29	35 - 100	2 - 30	.030	.0011	.098	.0712	777.547	.9664
Kentropyx calcarata									
Monte Cristo	20	58 - 105	6 - 31	.028	.0012	.206	.1001	593.034	.9705
Rondonia	11	52 - 100	5 - 29	.029	.0013	.205	.1091	477.323	.9815
General	33	52 - 105	5 - 31	.029	.0008	.178	.0675	1306.135	.9749
Cnemidophorus lemniscatus									
Santarém	15	40 - 73	2 - 12	.032	.0021	-.026	.1307	229.756	.9464
Alter do Chão	18	32 - 56	1 - 6	.030	.0022	.119	.1022	178.341	.9177
General	33	32 - 73	1 - 12	.030	.0011	.108	.0600	717.609	.9586
Tupinambis	8	120 - 316	45 - 1050	.034	.0008	-.645	.1650	1854.261	.9969
Macroteiids, general	222	32 - 316	1 - 1050	.031	.0002	-.001	.0210	20210.912	.9892
Ambystoma maculatum	92	28 - 97	.8 - 22	.027	.0003	.164	.0238	7240.558	.9877

N individuals in sample. R(x), R(y), ranges of the variables. b, slope (regression coefficient) and its standard deviation. a, intercept (regression constant) and its standard deviation. F, quotient of variances (significance of the regressions — all significant at the 0.1% level). r^2, coefficient of determination.

Table 3. Regression of the logarithm of mass on the logarithm of snout to vent length. Data from the literature

	N	R(x)	R(y)	b	a	F	r^2
Gennaro, 1974, New Mexico							
Holbrookia m. maculata	9	20 - 60	.25 - 6.00	2.9331	-4.3974		.9981
Case, 1976, California							
Sauromalus obesus							
Little Lake	8	80 - 220	20 - 396	2.8984	-4.1864		.9970
Amboy	6	80 - 180	20 - 172	2.5808	-3.6209		.9968
Van Devender, 1982, Costa Rica							
Ctenosaura similis	402	50 - 280	(x) - 707	3.07	-4.65		.983
Iguana iguana	441	80 - 360	(x) - 1837	3.15	-4.78		.972
Lewis, 1986, Puerto Rico							
*Ameiva exsul**	22	67 - 154	11 - 133	3.4043	-5.2876		.9634
Busack, 1987 (Morocco)							
Lacerta andreanszkyi	29	24 - 54	.30 - 3.00	2.8797 ± .13172	-4.4985 ± .21292	477.928	.9465
Perry, 1989, Israel							
Acanthodactylus boskianus **	6	30 - 75	.5 - 13.3	3.5040	-5.5005		.9951
*A. schreiberi***	7	30 - 90	.5 - 18.2	3.2654	-5.1550		.9995
*A. scutellatus***	9	30 - 70	.4 - 8.4	3.4491	-5.4119		.9915
Lacerta laevis	6	30 - 75	.5 - 13.3	3.5049	-5.5007		.9956
*Mesalina guttulata***	10	25 - 70	.3 - 6.9	3.0681	-4.8297		.9983
Anderson & Vitt, 1990, Northeastern Brasil							
Ameiva ameiva ♂	171			3.20 ± .04	-4.96		.97
♀	143			3.09 .07	-4.75		.92
Cnemidophorus ocellifer ♂	258			2.90 .05	-4.40		.93
♀	204			2.89 .08	-4.41		.88
Tupinambis teguixin ♂	11			3.03 .09	-4.34		.99
♀	19			3.49 .20	-5.68		.94

N individuals in sample. R(x), R(y), ranges of the variables. b, slope (regression coefficient) and its standard deviation. a, intercept (regression constant) and its standard deviation. F, quotient of variances (significance of the regressions — all significant at the .01% level). r^2, coefficient of determination. *, recalculated from individual data on a published graph. **, recalculated from a hand-drawn curve through a published graph.

Table 4. Regression of the cubic root of mass on snout to vent length. Data from the literature

	N	R(x)	R(y)	b	a	F	r^2
Gennaro, 1974							
Holbrookia m. maculata							
New Mexico	9	20 - 60	.25 - 6.00	.030	.046		.9964
Case, 1976							
Sauromalus obesus							
Little Lake, California	8	80 - 220	20 - 396	.028	.471		.9948
Van Devender, 1982							
Ctenosaura similis	10	75 - 300	9 - 707	.032	-.633		.9790
Iguana iguana	6	100 - 350	33 - 1837	.035	-.502		.9947
Costa Rica							
Lewis, 1986							
Ameiva exsul							
Puerto Rico	22	67 - 149	11 - 133	.038	-.573		.9637
Busack, 1987							
Lacerta andreanszkyi	29	24 - 54	.30 - 3.00	.026 ± .0013	.060 ± .057	373.660	.9326
Morocco							
Perry, 1989							
Acanthodactylus boskianus	6	30 - 75	.79 - 2.37	.0343	-.286		.9922
A. schreiberi	7	30 - 90	.79 - 2.63	.0304	-.141		.9988
A.scutellatus	9	30 - 70	.74 - 2.03	.0309	-.118		.9923
Lacerta laevis	6	30 - 75	.79 - 2.37	.0344	-.292		.9902
Mesalina guttulata	10	25 - 70	.67 - 1.90	.0275	-.0303		.9980

N individuals in sample. R(x), R(y), ranges of the variables. b, slope (regression coefficient) and its standard deviation. a, intercept (regression constant) and its standard deviation. F, quotient of variances (only value computed significant at the .01% level), r^2, coefficient of determination. All data read from hand-drawn curves through published graphs.

Literature

Besides the paper by Anderson and Vitt (1990) mentioned above, which is especially important, as it deals with Brazilian teiids from a semi-arid region, I found in the literature six papers relevant to the present discussion (Tables 3 and 4).

Gennaro (1974) studied the growth of the small iguanid *Holbrookia m. maculata* in New Mexico. He published a scatter diagram, in natural units, of mass on body length, with different symbols for males and females. Inspection indicating no evidence of sexual dimorphism, I enlarged the graph, drew a free hand curve through the points and read the weights corresponding to nine equally spaced body lengths; on these I computed the log-log and cubic root regressions. The slopes and intercepts are strikingly similar to my results for macroteiids. It should be noted that the values of the coefficient of determination shown on Tables 3 and 4 for this and for similar cases are presented of course only as an indication of the quality of the hand-drawn curve, not for statistical testing.

Case (1976) published similar data for two populations of the large iguanid *Sauromalus obesus* from California. Using the same approach as for Gennaro's data, I again obtained regressions with coefficients in the same range as those for macroteiids.

Van Devender (1982) published data on two maximum-sized iguanids, *Ctenosaura similis* and *Iguana iguana*, from Costa Rica. He computed log-log regression (using natural logarithms) of mass on body length. Applying again, as a check, the hand-drawn curve method to these data, I obtained estimates of the parameters varying from coincident to differing from his by 4%, which obviously validates the method. Van Devender's statistics, transformed to common logarithms, again closely agree with mine.

Lewis (1986) published a log-log graph of mass against body length for *Ameiva exsul* from Puerto Rico. I enlarged his graph and read from it the actual values, separately for males and females. Taking every third value of each list I computed the regressions for both sexes and, finding no sexual differences, for the ensemble. Agreement with the foregoing analyses is again very good.

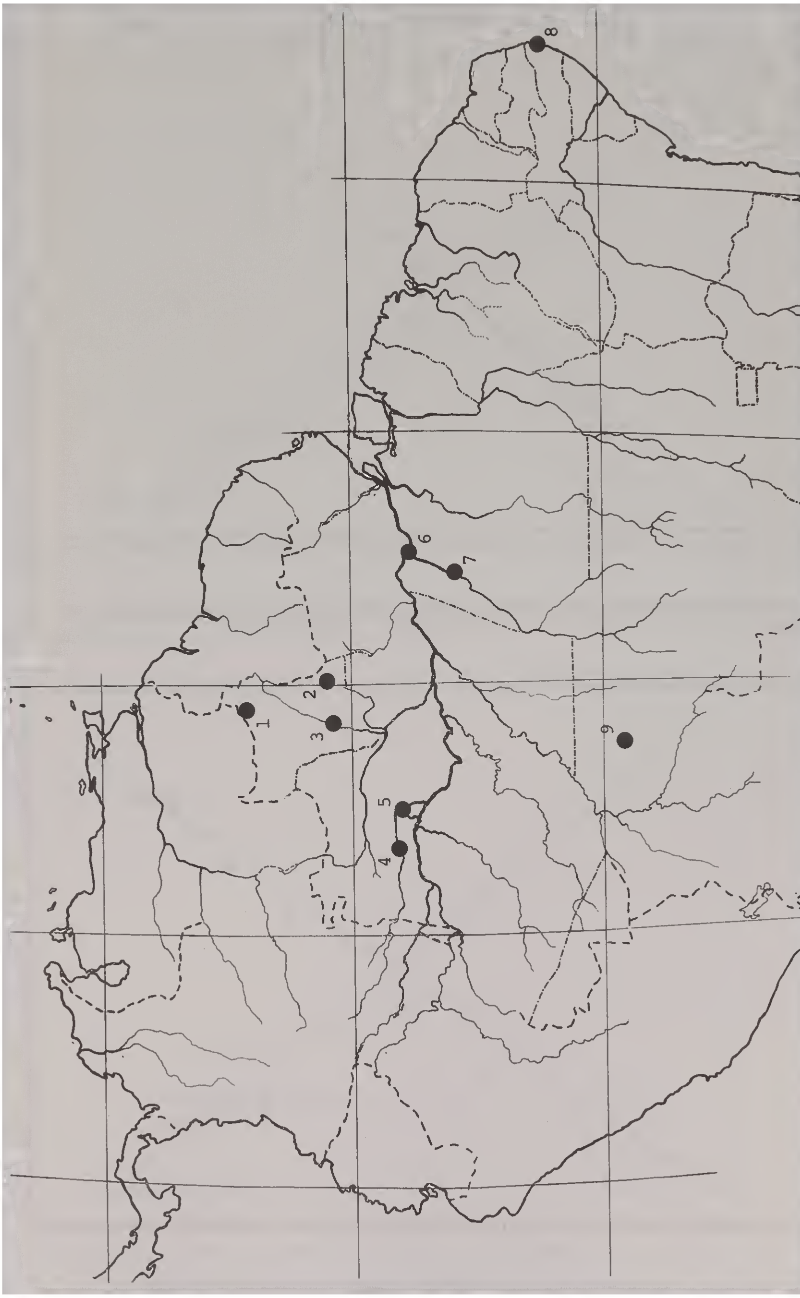
Busack (1987) studied the very small *Lacerta andreanszkyi* in Morocco. He computed the regression of cubic root of mass on body length. (There is a typographical mistake in the legend of his Fig. 1: he cites the slope as 0.07 and the intercept as 0.03; it is the reverse). I read the actual values from the graph and, taking again every third value, computed the regressions, for the sexes separately and together. Once more agreement with macroteiid data and with the data from the literature is striking.

Anderson and Vitt (1990) reported on three macroteiids from Exu, in the caatingas of Pernambuco, Brasil and on *Cnemidophorus tigris*, from the United States. They fitted log-log (natural logarithms) regressions to the sexes separately and found no sexual differences. Transforming their data into common logarithms one sees again very good agreement with the previously mentioned data. The comparisons between their lines and ours, emphasizing the ecological difference between the super humid hylaea and the caatingas — a difference not reflected in the regressions of mass on body length — has already been commented upon.

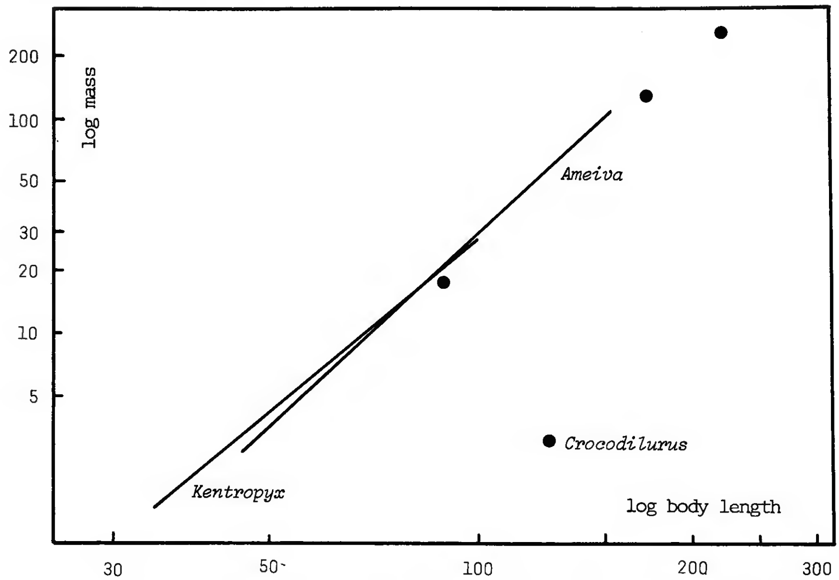
Finally Perry (1989) published graphs and statistical data on the mass-length relationships of five species of small lacertids in Israel. Taking data from hand drawn curves permitted fitting equations as previously done. My calculations do not fully agree with Perry's (they did with van Devender's), but they closely agree with the other cases I analyzed.

One salamander included, and conclusion

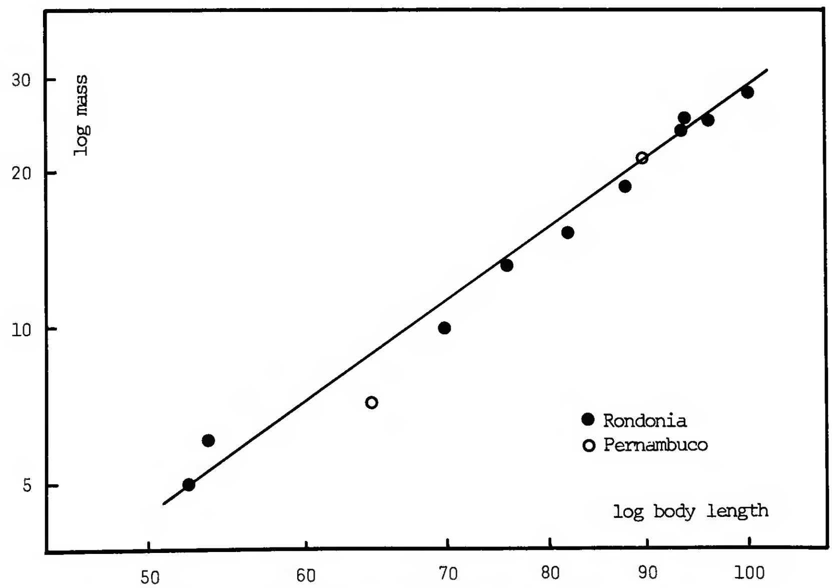
In a first version of this paper I concluded that the probable cause of the homogeneity of the regressions would be linked to thermoregulation, since all species involved, with the possible exception of *Crocodilurus lacertinus*, were heliophils and agreed in no other respect. I regretted then not having an adequate sample of umbrophil lizards. Richard G. Zweifel, who received the ms for criticism, offered me the next best thing: a sample of 92 specimens, juveniles and adult males, of *Ambystoma maculatum*. This sample closely agrees with the lizards, which removes the phenomenon from physiology directly into broad mechanics, which is where I must leave it for now.



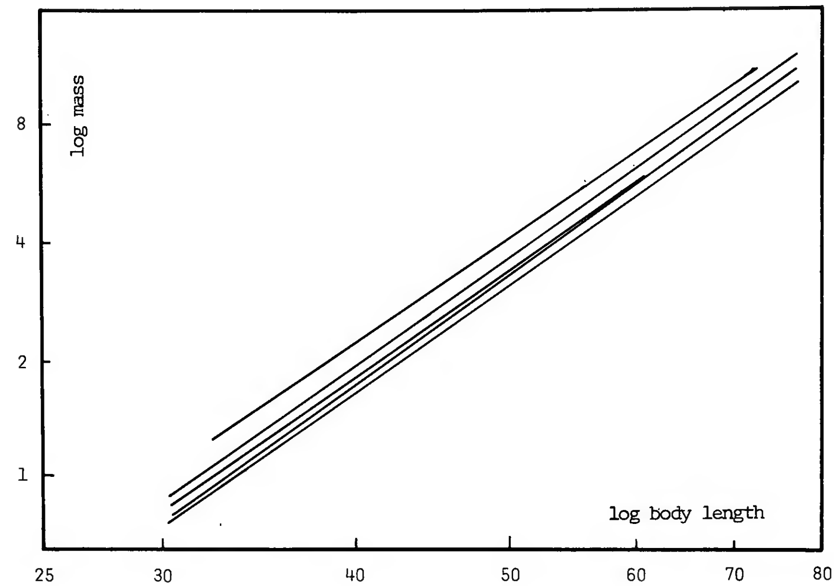
Localities of macroteiid samples: 1, Maloca Sorocaima. 2, São Luís do Anauá. 3, Santa Maria do Boiaçu. 4, Costa da Saracura. 5, Ilha do Mojuí. 6, Santarém and Alter do Chão. 7, Monte Cristo and Barreira. 8, Itamaracá. 9, Santa Cruz da Serra.



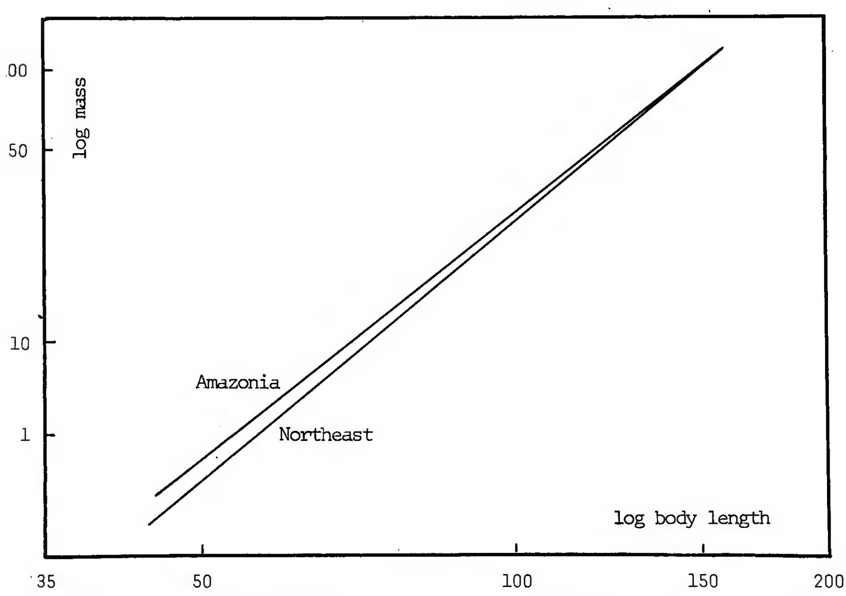
Graph 1, *Ameiva ameiva, Kentropyx (calcarata + pelviceps), Crocodilurus lacertinus*: regression of mass on body length.



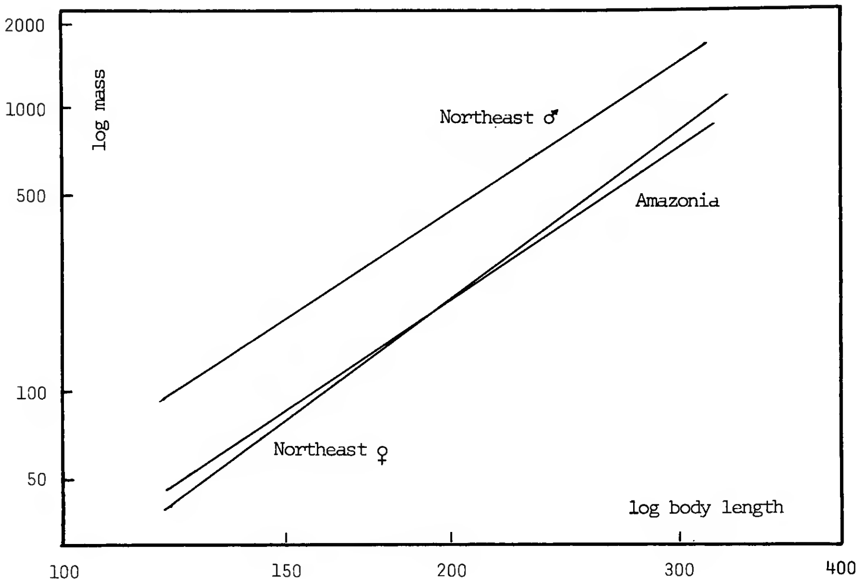
Graph 2, *Kentropyx calcarata*, Rondonia and Pernambuco: regression of mass on body length.



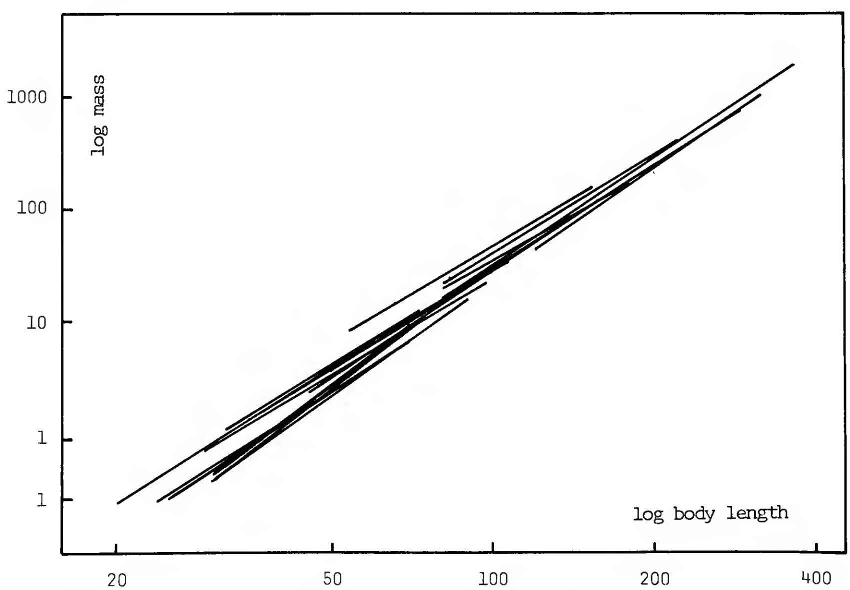
Graph 3, *Cnemidophorus*: regression of mass on body length. At 40 mm body length, from top to bottom: *C. lemniscatus, tigris* ♂, *ocellifer* ♂, *tigris* ♀. *ocellifer* ♀.



Graph 4, *Ameiva ameiva*, Amazonia and northeastern Brasil: regression of mass on body length.



Graph 5, *Tupinambis* spp., Amazonian and northeastern Brasil: regression of mass on body length.



Graph 6, Regression of mass on body length for all samples, from this study and from the literature.

ACKNOWLEDGMENTS

W. Ronald Heyer, C.W. Myers, E.E. Williams and Richard G. Zweifel kindly read the original manuscript. Williams brought to my attention Perry's paper, then unavailable in Brasil. Zweifel contributed his personal data on *Ambystoma maculatum*, which changed the conclusion of this paper. Francisca do Val drew Graph 6.

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