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On the eggs of Brazilian *Podocnemis* (Testudines, Podocnemididae)

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INTRODUCTION

Four species of *Podocnemis* occur in the rivers and lakes of Brazilian Amazonia: *P. erythrocephala* (Spix, 1824), *P. expansa* (Schweigger, 1812), *P. sextuberculata* Cornalia, 1849, and *P. unifilis* Troschel, 1848. There are two extra-limital species of the genus, *P. lewyana* A. Duméril, 1852, which occurs principally in the valley of Magdalena in Colombia, and *P. vogli* Müller, 1935, in the Orinoco drainage of Venezuela. Another species of the family, *Peltocephalus dumerilianus* (Schweigger, 1812) is also widespread in Amazonia.

Among the Brazilian species, *P. erythrocephala* is limited to the Rio Negro drainage, in itself a large area; the others have exceedingly broad distributions, essentially pan-Amazonian. They are all subject to heavy human predation, as the meat is a real delicacy and the eggs regionally much appreciated.

The degree of pressure is not the same on all forms. Formerly, *P. expansa*, “tartaruga” par excellence (the most prestigious animal in Amazonia), which is very visible during reproduction, as it lays in large bands on traditional beaches, and is a large animal, magnificent as food, used to be under heavy pressure. Besides the demand for the meat, the eggs were harvested as a source of fat, especially lamp oil. It is now protected in the traditional beaches, and the pressure has been relieved.

P. unifilis, “tracajá” is the second in size and esteem. The meat is very good and the eggs are eagerly sought, being widely credited with aphrodisiac virtues. Tracajá is not hard to catch with appropriate gear, but are protected during reproduction by laying individually on any type of ground, and thus frequently passing unnoticed. The nests are reasonably well disguised; trained dogs and horses are used to look for them.

P. sextuberculata, “pitiú” or “iaçá” (Vanzolini & Gomes, 1979), and *P. erythrocephala*, “irapuca” (Mittermeier & Wilson, 1974), are small species, that lay in small groups on sand beaches of any description. They do not get special attention, but, on being stumbled upon, are not spared.

P. dumerilianus (“cabeçudo”), is the least frequent species and a secretive breeder, which lays individually in leaf litter and rotten wood. It is not particularly persecuted. I have never been able to obtain a clutch.

The Brazilian government has been in recent years making a genuine effort to protect the fauna in general, and especially those species whose preservation results in improved living conditions for local populations, including the persistence of traditional ways of life — in the case the use of turtles as a food supply of extended cultural significance. To these efforts at conservation I feel a certain lack of basic scientific information. It has long been the practice of this Museum in field excursions to supplement materials important to systematics (our primary business) with materials and data relevant to ecology, and especially to conservation. We have assembled some amount of information on turtles, and here I present data, thus far not available, on egg shape and volume in *Podocnemis*.

MATERIALS

I have used in this work 17 samples with a total 248 eggs, all catalogued in our collection. With the exception of a sample of *unifilis* eggs, mentioned below, all were collected by Museum field parties; the circumstances of collection were routinely recorded in the field, and are usually available, of course at different levels of detail and clarity.

In the context of the present investigation, i.e. shape and volume of eggs, two aspects are all-important: (i) have the eggs reached definitive size and shape and (ii) are they traceable to single clutches or to (commercial) pools of eggs. The latter are common in Amazonia, especially in the case of *P. unifilis*.

The samples used in the present work are:

P. erythrocephala. Two sets of 8 eggs each (MZUSP 2886, 2887) obtained by autopsy, at the Rio Cuieiras, which enters the Rio Negro from the left (east) some 60 km upriver from Manaus; collected on October 26-27, 1973. No further details in the field notes.

P. expansa. Three samples (MZUSP 2870, 2871 and 2893, respectively 5, 4 and 6 eggs). The first two

samples were collected by myself on the well-known Taboleiro Leonardo, Rio Trombetas. This seasonal beach was brought into the literature by myself (Vanzolini, 1967); it is a traditional laying site, now very efficiently protected by the government. *P. expansa* and *P. unifilis* abound there and *P. sextuberculata* is not hard to find. My specimens were collected on October 8 and 9, 1965. The third sample, from the same locality, is not accompanied by field notes. (This sample was eventually proved not to belong to *P. expansa*, as will be discussed below).

The eggs I obtained at the Taboleiro had already been laid and buried but had been dug out by other females nesting in the same sites. The eggs of each sample were close together, and I do not doubt that they belonged to single clutches. Of course, having been laid, they were mature.

P. sextuberculata. I have 5 samples of this little-known species: MZUSP 2872 (6 eggs) from autopsy of a female at Taboleiro Leonardo; MZUSP 2875 (18) and 2888 (30) from the Rio Solimões near the mouth of the Rio Juruá; 2878 (16) from Jacaré, a village on the left bank of the Rio Solimões; 12884 (12), from Lake Miuá, also on the Solimões. These Solimões samples are not accompanied by field notes, but it is certain that they were bought from egg pools - collected from nests and thus mature.

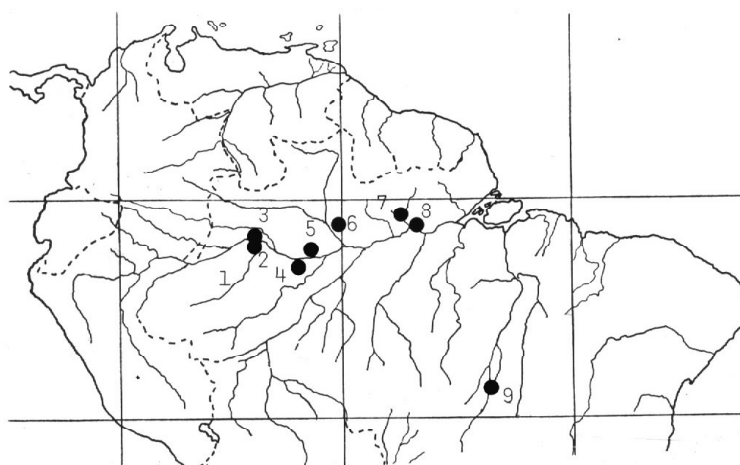
P. unifilis. There were 6 samples in the collection, all bought from pools offered for sale: MZUSP 2880 (18 eggs) and 2881 (6) from Coarí, on the right bank of

the Rio Solimões; 2890 (36) from Fonteboa, also on the right bank of the Solimões; 2874 (10), Taboleiro Leonardo, Rio Trombetas; 2891 (13) and 2892 (19), from Oriximiná, near the mouth of the Trombetas.

Thus with the exception of the eggs of *P. erythrocephala*, I am fairly secure that all our samples are constituted by mature eggs, having reached full size and shape. It may be added that all *P. unifilis* eggs have a perfect calcareous shell.

Well after this work was started I realized that direct measurement of the volume of at least some eggs was indispensable to constrain the results of geometrical methods. The few apparatus described in the literature for the direct measurement of turtle egg volume are difficult to build and to operate. I decided to measure volumes by filling empty egg shells with water and weighing them before and after (I thank Isaias Raw for the suggestion). The only species of *Podocnemis* amenable to this treatment is *P. unifilis*, the only one with a calcareous shell. I applied to IBAMA, the Brazilian fish and wildlife agency, for fresh eggs, and was promptly supplied with 23 eggs (MZUSP 4014) from Praia do Arí, Rio Araguaia.

Comment. I find it important to stress that this is an opportunistic investigation, not a properly designed one. There is justification, though. Some ground has been broken, and a first frame of reference is available



Map 1. 1, Rio Juruá (mouth at 02° 37' S, 65° 50' W). 2, Fonteboa (0232, 6602). 3, Jacaré (0224, 6608). 4, Coarí (0406, 6309). 5, Lago Miuá (0346, 6213). 6, Rio Cuieiras (mouth at 0250, 6030). 7, Taboleiro Leonardo (0120, 5645). 8, Oriximiná (0146, 5551). 9, Praia do Arí (1255, 5031).

for further research, by necessity logistically difficult: vast areas and precise seasons are involved. Progress has been made in some methodological aspects, especially in the estimation of egg volume. Goes without saying that this type of work is very rewarding to the professional systematist, always preoccupied with his unrequitable indebtedness to the fauna, and with the hard relationships between collecting and conserving.

METHODS

The eggs of freshwater turtles vary around the shape of an ellipsoid of revolution, characterized by one major (“length”) and one minor (“width”) orthogonal diameters. How much individual eggs differ from an ellipsoid with the same diameters is estimated through a dimensionless parameter first proposed by Preston (1953) as the “bicone” of bird eggs, and later applied, very didactically, by Maritz & Douglas (1994) to reptilian eggs.

In the present work the direct measurement of volume was done as follows: (i) the egg was blown empty, washed and dried; (ii) one of the holes bored to empty the egg was plugged with plasticine, and the egg weighed in a Pesola dynamometer; (iii) it was next filled with tap water and weighed again. The difference in grams between the two weights was taken as the volume of the egg in cubic centimeters.

As to the indirect (geometrical) estimates of egg volume, the procedure, following Maritz & Douglas (1994) was:

1. The eggs were photographed next to a scale (Plate 1), the photographs enlarged a little over twice and xerox copies made of the enlargements. On the xerox copies were measured: (i) the major (L) and (ii) the minor (W) diameters, and (iii) the length of a secant (D) inclined 30° over the major diameter and passing through the interception of the diameters.

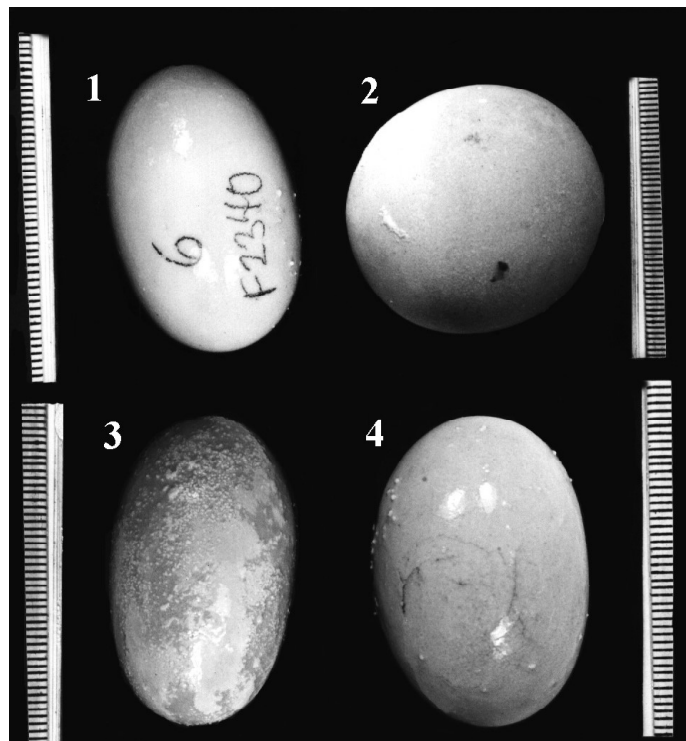


Plate 1. *Podocnemis* eggs.

1. *P. erythrocephala* 2886 (egg 6), Rio Cuieiras. L: 40 mm; W: 24; D: 33; c (bicone): -0.034; e (excentricity): 3.58; V (2): 12 cm³.
2. *P. expansa* 2870 (1), Taboleiro Leonardo. L: 44 mm; W: 43; D: 43; c: -0.086; e: 0.99; V (2): 43 cm³.
3. *P. sextuberculata* 2875 (16), Boca do Juruá. L: 42 mm; W: 24; D: 36; c: 0.217; e: 3.76; V (2): 13 cm³.
4. *P. unifilis* 2890 (31), Fonteboa. L: 38 mm; W: 27; D: 35; c: 0.117; e: 3.07; V (2): 15 cm³.

As will be discussed below, I tested the congruence of the measurements on photos by measuring the same eggs with calipers, in replicate. No differences were found, and so in what follows only the photo measurements are used, since this introduced no bias and especially since there is no direct very of measuring the secant.

2. The three measures (L, W and D) were applied to Maritz & Douglas's formulas for the bicone c and the volume $V(1)$ of the eggs:

$$c = \frac{4L^2}{3D^2} * \left(\frac{LD}{W * SQR(4L^2 - 3D^2)} - 1 \right)$$

$$V(1) = \pi / 6000 * \left(\frac{3c^2 + 14c + 35}{35} \right) * LW^2$$

The measurements are taken in millimeters and the resulting volumes in cubic centimeters.

3. Finally, the excentricity and volume were estimated by the formula for the ellipsoid of revolution.

$$e = (SQR(a^2 - b^2)) / a$$

where $a = L/2$ and $b = W/2$,

$$V(2) = \pi / 6000 * LW^2$$

The units are the same as before.

Statistical methods

Only very simple statistical methods were used, following Dixon & Massey (1983), Zar (1999), Vanzolini (1993) and Siegel (1956, 1975).

In the text and tables the following conventions are followed:

N, specimens in sample

R, range of the variable

m, mean \pm its standard deviation

s, sample standard deviation

V, coefficient of variation

V (d), volume directly measured

V (1), volume estimated by the bicone

V (2), volume estimated by the ellipsoid

Levels of significance are indicated as

* significant at the 5% level,

** at the 1%,

*** at the 0.1%,

ns not significant at the 5% level.

In the tables of Tukey's test, vertical lines to the left of the table encompass samples that do not differ at the 5% level.

Podocnemis unifilis

Of this species we have 7 samples, spanning some 1,100 km of Amazon; to it belongs the sample whose volumes were directly measured. Analysis of the traçajá data, especially in what concerns matters of method, may well serve as background to the other species.

MZUSP 4014

We start with the questions directly related to measurement. Sample 4014 comprises 23 eggs, of which all measurements could be reliably taken. Besides being measured on the photograph, each egg was submitted to two replicate measurements with calipers. Analysis of variance reveals ($F = 0.103$ ns) that, in the case of the major diameter (L), the mean of the photographic measurement (45.9 mm) does not differ significantly from those of the caliper replicates (46.1 and 46.2 mm). The data for the minor diameter (W) also closely agree. I thus consider valid the measurements taken on xerox copies of photographs.

The means of the 3 estimates of the volume (Tables 1 and 2) closely agree among themselves; in the analysis of variance $F = 1.207$ ns.

This, however, refers to averages, not to indivi-

dual measurements. These must be addressed by regression analysis, egg by egg, taking as independent variables the two geometrical estimates and as dependent variable, to be predicted, the direct measurement. In neither case was the regression significant: in the estimate by the bicone $F = 0.050$ ns, in that by the ellipsoid $F = 0.129$ ns.

Complementarily, it must be noted that the mean of the bicone for this sample, 0.033 ± 0.0371 , does not differ significantly from zero. This confirms the applicability of the ellipsoid formula, which is simple and depends on only two measurements easily taken and current in the literature. I rather like this conclusion.

Table 1. Sample 4014, *P.unifilis*. V(d), volume determined directly . V(1), by means of the bicone. V(2), by the ellipsoid.

Egg	V(d)	V(1)	V(2)
1	22	20	19
2	22	19	22
3	22	18	20
5	22	22	22
8	19	20	19
9	21	22	21
10	20	23	23
11	21	22	23
12	21	21	21
13	20	23	21
14	22	22	22
15	22	21	20
16	22	22	21
17	21	22	22
18	22	20	21
19	23	22	22
20	23	22	21
21	23	21	21
23	23	21	20

Table 2. Sample 4014, *P. unifilis*, estimates of egg volume.

Method	N	R	m	s	V
V(d)	19	19-23	21.7 ± 0.25	1.1	5.1
V(1)	19	18-23	21.1 ± 0.31	1.3	6.3
V(2)	19	19-24	21.1 ± 0.28	1.2	5.8

Another way of arguing for the equivalence of the two geometrical methods of estimating the volume of *P. unifilis* eggs consists in regressing the two estimates for a number of samples. In the case of the 7 *unifilis* samples at hand, the coefficient of regression $b = 1.051 \pm 0.0362$, not significantly different from 1, and the intercept $a = -1.144 \pm 1.2283$, not significantly different from zero; that is to say, to convert one estimate into the other, multiply by one and add nothing. The relationship is practically perfect: the coefficient of determination $r^2 = 0.9941$.

Volume. Table 3 shows the statistics of the distributions of frequencies of egg volume, V (2), of the 7 samples of *P. unifilis*. Analysis of variance affords $F = 41.730$ ***, which leads to Tukey's test - its results are shown on Table 4. It becomes clear that it is not possible to adopt an average or a modal value of egg volume for the species. Even a geographical common denominator is not possible: the two Coarí samples differ significantly.

As a matter of caution I repeated the analysis for egg volume as determined by the bicone, V (1) (this was done for all species); the results were always in exact agreement, in all details.

Table 3. *P. unifilis*, statistics of the distributions of frequencies of V(2).

Sample	N	R	m	s	V
4014 Araguaia	23	19 - 24	21.3 ± 0.25	1.2	5.6
2874 Leonardo	10	15 - 19	16.1 ± 0.44	1.4	8.7
2891 Oriximiná	13	14 - 18	14.9 ± 0.30	1.1	7.1
2892 Oriximiná	19	15 - 19	16.4 ± 0.27	1.2	7.2
2880 Coarí	18	14 - 21	15.9 ± 0.35	1.5	9.3
2881 Coarí	6	10 - 12	11.7 ± 0.32	0.7	6.3
2890 Fonteboa	35	10 - 20	14.9 ± 0.38	2.3	15.1

Table 4. *P. unifilis*, V(2), Tukey's test.

Sample	m	N
2881 Coarí	11.7	6
2891 Oriximiná	14.9	13
2890 Fonteboa	14.9	35
2880 Coarí	15.9	18
2874 Leonardo	16.1	10
2892 Oriximiná	16.4	19
4014 Araguaia	21.3	23

Parameters of shape. The statistics concerning the bicone are shown on Table 5. Although some values of the bicone differ significantly from zero, while others do not, analysis of variance showed homogeneity of the samples ($F = 1.877$ ns); it was thus possible to compute the last row of Table 5, with average values of all samples. Thus, although the values of the volume of *P. unifilis* eggs vary widely between and within localities, shape, in what concerns departure from the ellipsoid, is constant over all.

The excentricity of the generating ellipsis is

analyzed in Tables 6 and 7. Analysis of variance shows heterogeneity ($F = 19.380$ ***), and Tukey's test shows a situation less simple than that for the bicone. Three groups can be discerned: (i) Leonardo, (ii) Araguaia and (iii) the remainder. The fact that Araguaia is in a solitary position might have been expected: these are eggs laid in the core of the cerrados, while all others were laid in Amazonian forest. However, the fact that Leonardo differs significantly from Oriximiná, on the same river, precludes acceptance of a geographical factor in Amazonia.

Table 5. *P. unifilis*, statistics of the distributions of frequencies of the bicone.

Sample	N	R	m	t	s
2874 Leonardo	10	- 0.086 - 0.226	0.0971 ± 0.03659	2.654*	0.1157
2880 Coarí	18	- 0.131 - 0.173	$- 0.0168 \pm 0.01984$	0.848 ns	0.0842
2881 Coarí	6	- 0.248 - 0.194	0.0018 ± 0.05920	0.031 ns	0.1450
2890 Fonteboa	35	- 0.724 - 0.467	0.0161 ± 0.03000	0.537 ns	0.1775
2891 Oriximiná	13	- 0.017 - 0.238	0.0765 ± 0.01812	4.223**	0.0653
2892 Oriximiná	19	- 0.077 - 0.214	0.0566 ± 0.01814	3.120**	0.0791
4014 Araguaia	23	- 0.450 - 0.241	0.0075 ± 0.03096	0.149 ns	0.0234
General	124	- 0.724 - 0.467	0.0280 ± 0.01250	2.319*	0.1342

Table 6. *P. unifilis*, statistics of the distributions of frequencies of the excentricity.

Sample	N	R	m	s	V
2874 Leonardo	10	3.60 - 4.11	$3.90 + 0.049$	0.16	4.0
2880 Coari	18	3.30 - 3.60	$3.42 + 0.025$	0.11	3.2
2881 Coari	6	2.93 - 3.37	$3.19 + 0.062$	0.15	4.7
2890 Fonteboa	35	1.93 - 3.59	$3.12 + 0.061$	0.36	11.5
2891 Oriximiná	13	3.19 - 3.68	$3.41 + 0.040$	0.15	4.3
2892 Oriximiná	19	3.19 - 3.60	$3.37 + 0.028$	0.15	3.6
4014 Araguaia	23	3.21 - 4.06	$3.61 + 0.053$	0.25	7.0

Table 7. *P. unifilis*, excentricity, Tukey's test.

Sample	m	N
2890 Fonteboa	3.12	35
2881 Coari	3.19	6
2892 Oriximiná	3.37	19
2891 Oriximiná	3.41	13
2880 Coari	3.42	18
4014 Araguaia	3.63	17
2874 Leonardo	3.90	10

Comment. The following conclusions seem reasonable:

1. The two methods (bicone and ellipsoid) of estimating volume are equivalent, in what concerns averages, and agree with direct measurement.

2. Individual (inter-sample), as against geographical variation seems to be the rule for volume and for excentricity; the bicone is homogeneous throughout the sample space.

Against this background we may place the other Brazilian species of the genus, for which we have the same measurements as for *unifilis*, except of course direct measurement of volume.

Podocnemis sextuberculata

This species ranks second in the number, 5, of available samples.

The congruence of the two methods of volume estimation was verified, as previously, both by comparison of means and by regression of V (1) on V (2). The comparisons of means yielded values of *t*

between 0.075 and 1.289, not significant at any number of degrees of freedom. The coefficient of regression was 1.005 ± 0.0223 , not significantly different from 1; the intercept was -0.252 ± 1.642 , not significantly different from zero. Thus, in what follows, we'll deal again only with V (2), the volume estimated through the ellipsoid.

The data on volume are shown on Table 8. The analysis of variance indicates heterogeneity (F = 52.319 ***). Tukey's test (Table 9) shows extreme variability; two samples from Boca do Juruá are in agreement, but the third sample from the same locality disagrees with them.

Turning to the shape of the eggs, there is no variability in the bicone (Table 10; analysis of variance, F = 0.925 ns). Thus an over-all bicone was computed and can provisionally be used to characterize the species. With regard to the excentricity (Table 11), analysis of variance indicated heterogeneity (F = 13.922), although the multiple comparison tests failed to identify units; no over-all excentricity was computed.

TABLE 8. *P. sextuberculata*, statistics of the distributions of frequencies of V(2).

Sample	N	R	m	s	V
2872 Leonardo	6	16 - 23	19.2 ± 0.89	2.2	11.7
2884 Lago Miuá	12	18 - 27	21.9 ± 0.65	2.3	10.4
2875 Boca Juruá	17	11 - 14	13.0 ± 0.16	0.7	5.1
2876 Boca Juruá	18	10 - 20	13.4 ± 0.51	2.2	16.2

TABLE 9. *P. sextuberculata*, V(2), Tukey's test.

Sample	m	N
2872 Leonardo	19.2	6
2884 Lago Miuá	21.9	12
2875 Boca Juruá	13.0	17
2876 Boca Juruá	13.4	18
2888 Boca Juruá	16.9	30

TABLE 10. *P. sextuberculata*, statistics of the distributions of frequencies of the bicone.

Sample	N	R	m	t	s
2872 Leonardo	6	- 0.074 - 0.096	- 0.140 ± 0.04447	0.315 ns	0.1089
2884 Lago Miuá	12	- 0.115 - 0.092	0.0253 ± 0.02601	0.973 ns	0.0901
2875 Boca Juruá	17	-0.094 - 0.281	0.0625 ± 0.02549	2.452*	0.1051
2876 Boca Juruá	18	- 0.228 - 0.214	0.0229 ± 0.03503	0.654 ns	0.1486
2888 Boca Juruá	30	- 0.122 - 0.217	0.0626 ± 0.01712	3.657**	0.0937
2878 Jacaré	16	- 0.048 - 0.086	0.0388 ± 0.01073	3.616**	0.0411
General	99	- 0.228 - 0.281	0.0424 ± 0.01030	4.113***	0.1025

TABLE 11. *P. sextuberculata*, statistics of the distributions of frequencies of the excentricity.

Sample	N	R	m	s	V
2872 Leonardo	6	3.19 - 3.71	3.469 ± 0.0786	0.192	5.6
2884 Lago Miuá	12	3.62 - 4.06	3.854 ± 0.0381	0.132	3.4
2875 Boca Juruá	17	3.39 - 3.93	3.755 ± 0.0301	0.124	3.3
2876 Boca Juruá	18	3.31 - 4.01	3.777 ± 0.0411	0.175	4.6
2888 Boca Juruá	30	3.32 - 4.06	3.668 ± 0.0343	0.188	5.1
2878 Jacaré	16	3.16 - 3.67	3.446 ± 0.0288	0.115	3.3

Podocnemis expansa

Of this, the most neuralgic of Amazonian turtles, we had at the beginning three samples (later reduced to two), from a single locality, Taboleiro Leonardo. It is actually a very important locality; it unfailingly receives every year a large number of breeding turtles (Padua & Alho, 1982), which enjoy full protection. In fact, it is an ideal place to do research on *Podocnemis* reproduction, as three of the four Brazilian species are common there.

The relevant data are summarized on Table 12. It is immediately apparent that in all characters analyzed samples 2870 and 2871 tend to agree between themselves and to widely disagree with 2893. In fact, analysis of variance, followed by Tukey's test (see, for an example, Table 13) makes that very plain, and I consider sample 2893 as not belonging to *P. expansa*. That such a conclusion can be reached with sureness is to me one

the good points of this work.

Of the two other species that occur in the area, sample 2893 fits very closely *P. sextuberculata*, both in volume and in the shape parameters; although I am morally certain that there is where it belongs, I am not using the sample in the present study.

In *P. expansa* again the two estimate of the volume were congruent, judging from the means, whose differences showed values of *t* below 1. The regressions, however, gave conflicting results: for sample 2870 $b = 0.782 \pm 0.0574$ significantly different from 1. For sample 2871 $b = 1.183 \pm 0.0935$, not significantly different from 1.

Another point to be mentioned is that the two means for the bicone did not differ significantly between themselves, but one differed significantly from zero, while the other did not. All in all, data on this all-important species are few and unsatisfactory.

TABLE 12. *P. expansa*, statistics of the distributions of frequencies of the volume and shape parameters.

Character	Sample	N	R	m	s	V
V(2)	2870	5	25 - 43	32.1 ± 2.88	6.4	20.0
	2871	4	27 - 31	28.7 ± 0.85	1.7	5.9
	2870 + 2871	9	25 - 43	30.6 ± 1.67	5.0	16.4
	"2893"	6	13 - 18	16.0 ± 0.78	1.9	12.0
bicone	2870	5	- 0.193 - 0.0702	- 0.0231 ± 0.04506 ns	0.1008	
	2871	4	-0.228 - 0.0660	0.1561 ± 0.04148 ns	0.0830	
	2870 + 2871	9	- 0.228 - 0.0702	- 0.0822 ± 0.03771 ns	0.0113	
	"2893"	6	- 0.0677 - 0.188	0.413 0 ± 0.04239***	0.1058	
excentricity	2870	5	0.494 - 1.905	1.343 ± 0.2729	0.610	45.4
	2871	4	1.444 - 2.348	1.784 ± 0.2164	0.433	24.3
	2870 + 2871	9	0.494 - 2.348	1.539 ± 0.1857	0.557	36.2
	"2893"	6	2.945 - 3.703	3.480 ± 0.1116	0.2730	7.9
V(1)	2870	5	25 - 39	31.7 ± 2.27	5.07	16.0
	2871	4	26 -31	28.1 ± 1.01	2.02	7.2
	2870 + 2871	9	25 -39	30.1 ± 1.41	4.24	14.1

TABLE 13. *Podocnemis*, Taboleiro Leonardo, V(2), Tukey's test.

Sample	m	N
<i>unifilis</i> 2874	16.1	10
" <i>expansa</i> " 2893	17.2	6
<i>sextuberculata</i> 2872	19.2	6
<i>expansa</i> 2871	28.7	4
<i>expansa</i> 2870	32.2	5

Podocnemis erythrocephala

Two samples, of 8 eggs each, are at hand. They are reportedly from two autopsied females; nothing else is on file.

The data are on Table 14. It is remarkable that the two samples differ significantly in volume and

excentricity but not in bicone; this does nor differ significantly from zero in either case.

The differences between two samples from the same locality, collected at the same time, must be due to different stages of maturation of the eggs; these data must be used with caution.

TABLE 14. *Podocnemis erythrocephala*, statistics of the distributions of frequencies of the volume and shape parameters.

Character	Sample	N	R	m	s	V	t
V(2)	2886	8	12 - 15	13.2 ± 0.28	0.8	6.1	4.772***
	2887	8	11 - 13	11.6 ± 0.19	0.5	4.6	
bicone	2886	8	- 0.164 - 0.127	- 0.0236 ± 0.03048 ns	0.0862		0.713 ns
	2887	8	- 0.056 - 0.138	0.0045 ± 0.02498 ns	0.0707		
excentricity	2886	8	3.49 - 3.76	3.607 ± 0.0326	0.0922	2.6	6.986***
	2887	8	3.27 - 3.39	3.341 ± 0.0198	0.0559	1.7	
V(1)	2886	8	12 - 15	13.1 ± 0.29	0.8	6.4	4.545***
	2887	8	11 - 13	11.5 ± 0.17	0.5	4.2	

DISCUSSION

Volume

The analyses of individual species showed, for three out of the four, very large variation from sample to sample, even within the same locality (*unifilis* at Coarí, Table 4; *sextuberculata* at Boca do Juruá, Table 9; *erythrocephala* at the Rio Cuiciras, Table 14).

This might be attributed to differences in the degree of maturation of the clutches, but not in the case of *P. unifilis*, the calcareous shell of whose eggs, once laid, is not likely to grow. Additionally, eggs bought have usually been plundered from nests.

There is thus no expectation of profitable comparison among the species; none of them can be numerically described in summary. One solid fact, however, is that, where three species occur together (Leonardo, Table 13), the eggs of *expansa* are significantly larger. It is the largest species of the genus, adult females reaching 60+ cm carapace length (*unifilis* reaches close to 50, the other two around 30).

A ranking of all samples available (Table 15) indicates that the three lesser species of the genus do not differ significantly in egg volume. This is indeed confirmed by Kruskal-Wallis's analysis of variance by

ranks (Siegel, 1975), which stops much short of significance ($H= 6.456$ ns).

Shape

Of the two geometrical parameters, I shall limit the discussion of egg shape to the excentricity of the generating ellipsis. The bicone is a much less intuitive character, and varies erratically in our materials.

A ranking of all samples (Table 16) shows that *expansa* has practically round eggs, and in this differs from the other three species (Kruskal-Wallis analysis of variance by ranks, $H= 8.164$ *), which do not differ among themselves (Kruskal-Wallis $H= 4.033$ ns).

Another way of looking at the shape of eggs is through the relationship between the two diameters, i.e., the regression of egg width on egg length. Table 17 shows the respective statistics.

Of the samples studied, only 4 showed significant regressions. Some of negative cases can be attributed to shortness of range of the variables (Vanzolini, 1993: 93). One way of circumventing this difficulty, although with some loss of information, is to combine samples from a locality. This led to

significant regressions only in two cases, *P. erythrocephala* and *P. unifilis* from Coari.

Of all regression analyses, the only meaningful one is that of *P. expansa*. The two individual regressions are significant and do not differ between themselves. The joint regression is highly significant ($r^2 = 0.9416$), which means that the relationship is important to the animal. The coefficient of regression (b) does not differ significantly from 1; the intercept

does not differ significantly from zero: the eggs of *P. expansa* are virtually spherical (as already demonstrated above).

Another comparison that can be made is between Coari (sum) and the Fonteboa *P. unifilis* — both localities are on the Rio Solimões. The coefficients of regression differ significantly ($t = 2.332$, 56 df), which confirms the high heterogeneity of this species.

TABLE 15. *Podocnemis*, $V(2)$ in all samples.

Sample	Locality	N	R	m
1. <i>unifilis</i> 2881	Coari	11	9 - 11	10.3 ± 0.20
2. <i>sextuberculata</i> 2878	Boca Juruá	16	11 - 12	11.6 ± 0.11
3. <i>erythrocephala</i> 2887	Rio Cuieiras	8	11 - 13	11.6 ± 0.19
4. <i>sextuberculata</i> 2875	Boca Juruá	17	11 - 14	13.0 ± 0.16
5. <i>erythrocephala</i> 2886	Rio Cuieiras	8	12 - 15	13.2 ± 0.28
6. <i>sextuberculata</i> 2870	Boca Juruá	18	10 - 20	13.4 ± 0.51
7. <i>unifilis</i> 2890	Fonteboa	35	10 - 20	14.9 ± 0.38
8. <i>unifilis</i> 2891	Oriximiná	13	14 - 18	14.9 ± 0.30
9. <i>unifilis</i> 2880	Coari	18	14 - 21	15.9 ± 0.35
10. <i>unifilis</i> 2874	Leonardo	10	15 - 19	16.1 ± 0.44
11. <i>unifilis</i> 2892	Oriximiná	19	15 - 19	16.4 ± 0.27
12. <i>sextuberculata</i> 2888	Boca Juruá	30	12 - 21	16.9 ± 0.48
13. <i>sextuberculata</i> 2872	Leonardo	6	16 - 23	19.2 ± 0.89
14. <i>unifilis</i> 4014	Araguaia	23	19 - 24	21.3 ± 0.25
15. <i>sextuberculata</i> 2884	Lago Miuá	12	18 - 27	21.9 ± 0.65
16. <i>expansa</i> 2871	Leonardo	4	27 - 31	28.7 ± 0.85
17. <i>expansa</i> 2870	Leonardo	5	25 - 43	32.1 ± 2.88

TABLE 16. *Podocnemis*, excentricity in all samples.

Sample	Locality	N	R	m
1. <i>expansa</i> 2870	Leonardo	5	0.49 - 1.91	1.34 ± 0.273
2. <i>expansa</i> 2871	Leonardo	4	1.44 - 2.35	1.78 ± 0.216
3. <i>unifilis</i> 2890	Fonteboa	35	1.93 - 3.59	3.12 ± 0.061
4. <i>unifilis</i> 2881	Coarí	6	2.93 - 3.37	3.19 ± 0.062
5. <i>erythrocephala</i> 2887	Rio Cueiras	8	3.27 - 3.39	3.34 ± 0.020
6. <i>unifilis</i> 2892	Oriximiná	19	3.19 - 3.60	3.37 ± 0.028
7. <i>unifilis</i> 2891	Oriximiná	13	3.19 - 3.68	3.41 ± 0.040
8. <i>unifilis</i> 2880	Coarí	18	3.30 - 3.60	3.42 ± 0.025
9. <i>sextuberculata</i> 2878	Boca Juruá	16	3.16 - 3.45	3.45 ± 0.029
10. <i>sextuberculata</i> 2872	Leonardo	6	3.19 - 3.71	3.47 ± 0.079
11. <i>unifilis</i> 4014	Araguaia	23	3.21 - 4.06	3.61 ± 0.053
12. <i>erythrocephala</i> 2886	Rio Cueiras	8	3.49 - 3.76	3.61 ± 0.033
13. <i>sextuberculata</i> 2888	Boca Juruá	30	3.31 - 4.06	3.67 ± 0.034
14. <i>sextuberculata</i> 2875	Boca Juruá	17	3.39 - 3.93	3.76 ± 0.030
15. <i>sextuberculata</i> 2876	Boca Juruá	18	3.31 + 4.01	3.78 ± 0.041
16. <i>sextuberculata</i> 2884	Lago Miuá	12	3.62 - 4.06	3.85 ± 0.038
17. <i>unifilis</i> 2874	Leonardo	10	3.60 - 4.11	3.90 ± 0.049

TABLE 17. Statistics of the regression of egg width on egg length.

	N	R(x)	R(y)	b	a	F	r ²
<i>erythrocephala</i>							
2886 Rio Cueiras	8	40 - 42	24 - 28	0		0	
2887 Rio Cueiras	8	37 - 39	23 - 25	0.452 ± 0.3414		1.750 ns	
Sum	16	37 - 42	23 - 28	0.221 ± 0.0866	15.98 ± 0.571***	6.487*	0.3166
<i>expansa</i>							
2870 Leonardo	5	38 - 43	33 - 42	1.474 ± 0.4133	-22.63 ± 2.996***	12.712*	0.8091
2871 Leonardo	4	39 - 51	36 - 47	0.911 ± 0.0093	0.45 ± 2.534 ns	9159.268***	0.9998
Sum	9	38 - 51	33 - 47	0.970 ± 0.0913	-2.24 ± 1.800 ns	112.818***	0.9416
<i>sextuberculata</i>							
2872 Leonardo	6	40 - 45	28 - 31	0.256 ± 0.2935		0.763 ns	
2875 Boca Juruá	18	39 - 45	23 - 28	0.292 ± 0.1752		2.771 ns	
2876 Boca Juruá	18	39 - 46	22 - 29	0.278 ± 0.2594		1.147 ns	
2878 Boca Juruá	16	36 - 41	23 - 24	0.032 ± 0.0576		0.302 ns	
2888 Boca Juruá	31	39 - 49	24 - 29	0.411 ± 0.0927	9.09 ± 0.681***	19.668***	0.4041
Sum Boca Juruá	83	36 - 49	22 - 29	0.446 ± 0.0677	6.50 ± 0.465***	48.918***	0.3765
<i>unifilis</i>							
2874 Leonardo	10	42 - 47	25 - 27	-0.049 ± 0.2469		0.039 ns	
2880 Coarí	18	40 - 44	26 - 30	0.447 ± 0.2135		4.393 ns	
2881 Coarí	6	34 - 37	23 - 24	0.167 ± 0.1667		1.000 ns	
Sum Coarí	24	34 - 44	23 - 30	0.572 ± 0.0755	3.45 ± 0.591***	57.356***	0.7228
2890 Fonteboa	36	30 - 49	24 - 33	0.302 ± 0.0682	15.44 ± 0.509***	19.621***	0.3659
2891 Oriximiná	13	39 - 43	25 - 28	0.040 ± 0.1845		0.047 ns	
2892 Oriximiná	19	39 - 43	26 - 29	0.203 ± 0.1915		1.127 ns	
Sum Oriximiná	32	39 - 43	25 - 29	0.243 ± 0.1445		2.834 ns	
4014 Araguaia	21	43 - 49	29 - 33	0.244 ± 0.1135		2.263 ns	

Identification of eggs

The eggs of *P. unifilis*, elongate and with a calcareous shell, and of *P. expansa*, spherical, are unmistakable. It is not possible at present to discriminate biometrically between *erythrocephala* and *sextuberculata* eggs.

CONCLUSION

This avowedly opportunistic and preliminary study permits nevertheless some conclusions capable of orienting continuation and amplification of research.

It is clear that much variability exists, and that tracking its cause and circumstances is a first design. This depends essentially on a scheme of sampling. Several areas must be sampled, with replication, and with the collection of as ample a repertoire of data as possible. Each sample must be unequivocally related to one female, herself duly measured and weighed, or at least to one nest. It will be important to note clutch size. In all forms except *P. unifilis*, autopsy should be avoided, as in species with soft-shelled eggs there is no way, besides readiness to lay, of ascertaining maturity of the eggs.

The present data on *P. unifilis* and *P. sextuberculata*, although not yet sufficient, are somewhat better than those on *expansa* and *erythrocephala*, which should deserve priority. There should be no problem in getting *expansa* eggs. The traditional beaches are well known and protected, the numbers of females that frequent them are large, it is possible to follow closely oviposition, and the collection of moderate samples of eggs will not harm the demography. On the contrary, nothing is known about *erythrocephala*; all remains to be done. It is not rare where it occurs (Mittermeier & Wilson, 1974) and with the help of local people it seems there would be no problem.

In the case of *sextuberculata* and *unifilis*, it will take some field work to locate a suitable number of properly distributed nests; this may take time and travel, but not more than that.

As to methods, it seems reasonable to conclude that the estimation of volume by means of the ellipsoid is satisfactory, and that excentricity is a good index of

shape. It would be advisable, however, to execute more direct determinations of the volume of *P. unifilis* eggs.

All in all, a reasonably thorough sampling scheme should afford a deeper look into the reproductive biology of these most attractive animals.

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