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THE RUDIMENTARY HIND LIMBS OF THE SPERMWHALE (PHYSETER MACROCEPHALUS), ITS VARIABILITY AND ALLOMETRY OF GROWTH

by

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Introduction

Since Darwin (1872) it has been known that degenerative characteristics are marked by a high variability. Hitherto existing results indicate that the rudimentary hind limbs of whales seem to be variable as well.

After a phase of rapid retrogression during the eocene the hind limbs hardly underwent any changes since the oligocene, i. e. for about 30 - 40 mill. years. The question arises whether the process of reduction has come to a standstill, while the variability in both size and configuration of the rudimentary pelvic bones continues.

Among the Odontoceti a larger number of pelvic bones has been described more or less completely only in the case of spermwhales (Abel, 1907; van Deinse, 1954; Omura, Nishiwaki, Ichihara and Kasuya, 1962; Berzin, 1972 , Flower, 1869; Pouchet et Beauregard, 1889). These investigations were supplemented using self collected material in order to contribute to the clarification of the mechanism of reduction. From October 1973 to August 1974, 82 pelvic bones of 41 spermwhales (25 males, 16 females) were recovered at the Madeira whaling station.

Results

The shape is unusually variable. Although principally stick-shaped, this variability is conditioned particularly by the different diameters and the multifarious bends or distortions. In general it can be said that the posterior part is wider or more massive than the anterior part, i. e. the bone tapers towards the fore-end. Accordingly the bones are claviform, spatular or drumstick- shaped. However, the rudiment sometimes shows a form which is similar to the apparently not so far reduced finwhale pelvic bone, which Abel (1907) explains in comparison with the reduction of the hind limbs of fossil and recent sirenians as a merged product of ilium, ischium and pubicum. This configuration allows for a classification: the anterior slender part is the ilium, the posterior wider one is the ischium, and just a lateral protuberance is the pubicum (Fig. 1). In many cases the pubicum can be seen clearly (as in Mystacoceti) but it is always the most reduced one of the three elements, ranging from a hardly distinguishable protuberance to complete disappearance.

In the reference bone material there is no trace of an acetabulum although sometimes femor rudiments are found, mostly near the hind end, which are porously ossified or just cartilaginous (Fig. 1). These femors usually occur when the pubicum has disappeared completely.

When comparing the pelvic bones of males and females no sexual differences are evident with regards to configuration. This does not exclude that small differences may exist, as they are supposed to occur in Mystacoceti (Hosokawa, 1951; Omura, Nishiwaki and Kasuya, 1971; Heyerdahl, 1973).

Variability of Growth

The length of the bones can be easily related to the length of the animals (Fig. 2, Fig. 3). Both the body (x) and the pelvic bones (y) are growing in nearly constant proportion and thus they can be described by the equation of allometry :
$y = b \cdot x^a$ or $\log y = \log b + a \cdot \log x$;
a is the ascent of the line representing the relative rapidity of growth ; b determines y when x = 1.
Regression lines (allometry lines) were computed by the following formula :

$$b = \frac{\Sigma y - a \Sigma x}{n} \quad ; \quad a = \frac{n \Sigma xy - (\Sigma x)(\Sigma y)}{n \Sigma x^2 - (\Sigma x)^2}$$

1.) Male, right rudiment ; male, left rudiment (Fig. 2)
2.) Female, right rudiment ; female, left rudiment (Fig. 3)
3.) Male, both rudiments ; female, both rudiments (Fig. 4)

In all these cases there is a significant correlation between the size of the pelvic bones and the body lengths (Tab. 1 , 2) There seems to be no difference between the right and the left bones either in males or in females. ($p > 0,5$).

A sexual difference may be supposed, because the bones of males grow negatively allometric or nearly isometrically ($a = 0,95$). The bones of the females seem to increase more quickly, as they grow positivly allometric ($a = 1,36$). The pelvic bones of an 11 m long female thus are ca. 10 % longer than those of a male of the same size. It must be said that the regression lines do not significantly differ ($p > 0,5$) , but this may be attributed to the relatvely small volume of material.

Discussion

Embryological examinations indicate that in the earliest state of developement fore and hind limbs are in principle extant in a like manner (Hosokawa, 1951 ; Ogawa, 1953 ; Hosokawa, 1955 ; Sinclair, 1962 ; own material). But even in a 15 mm long spermwhale embryo the hind limbs are smaller than the fore limbs and they have disappeared at a length of 25 mm. Hence it may be inferred that, after the first anlage of the hind limbs, there is an early rudimentation because of an obviously negative allometric growth, and there must be an allometric angle during the late embryonic or postembryonic phase into positive direction. Because of the positive allometric growth of the pelvic bones of whales during later phases of development it might be concluded that the rudiments are not without any functions.

These elements are connected especially with the musculus ischiocavernosus (= erector penis) of the males and with the musculus erector clitoridis of the females (Abel, 1907,; Slijper, 1962 ; Harrison, 1969 ; Green, 1972 ; own observations). These corresponding muscles may be well developed, especially in females, as a result of adaptation to life in water (for instance with regard to mating) . It may be assumed that this development took place later than the rudimentation of the hind limbs and regarding the Thesis of Haeckel it is understandable that the retention of the pelvic rudiments is guaranteed by a positiv or isometric allometric growth only during the later phases of development. In this case the size of the bones seems to be much more important than a fixed configuration.

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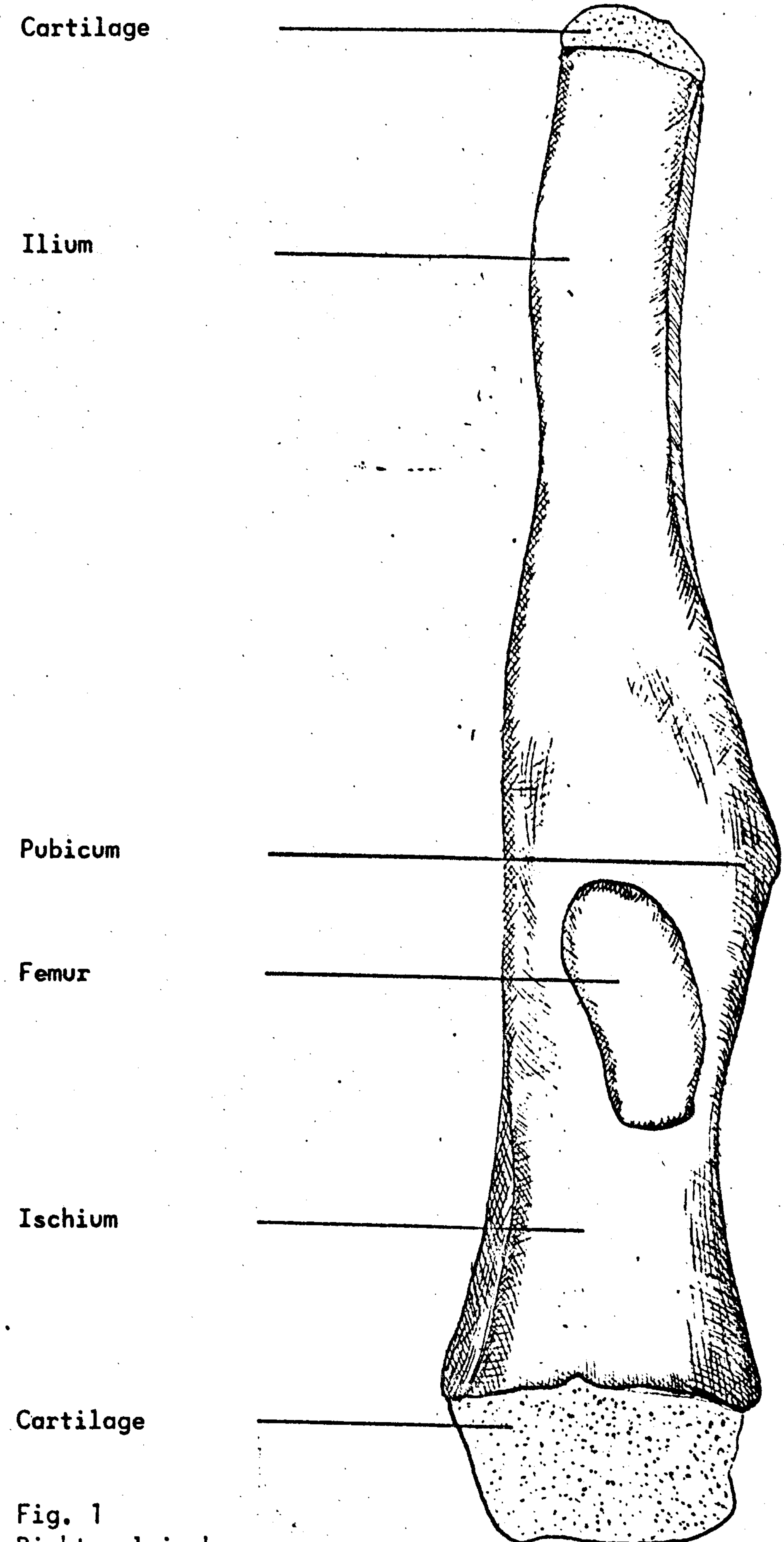

Fig. 1
Right pelvic bone
of a male , with cartilaginous
ends and femur rudiments in ca. original length.

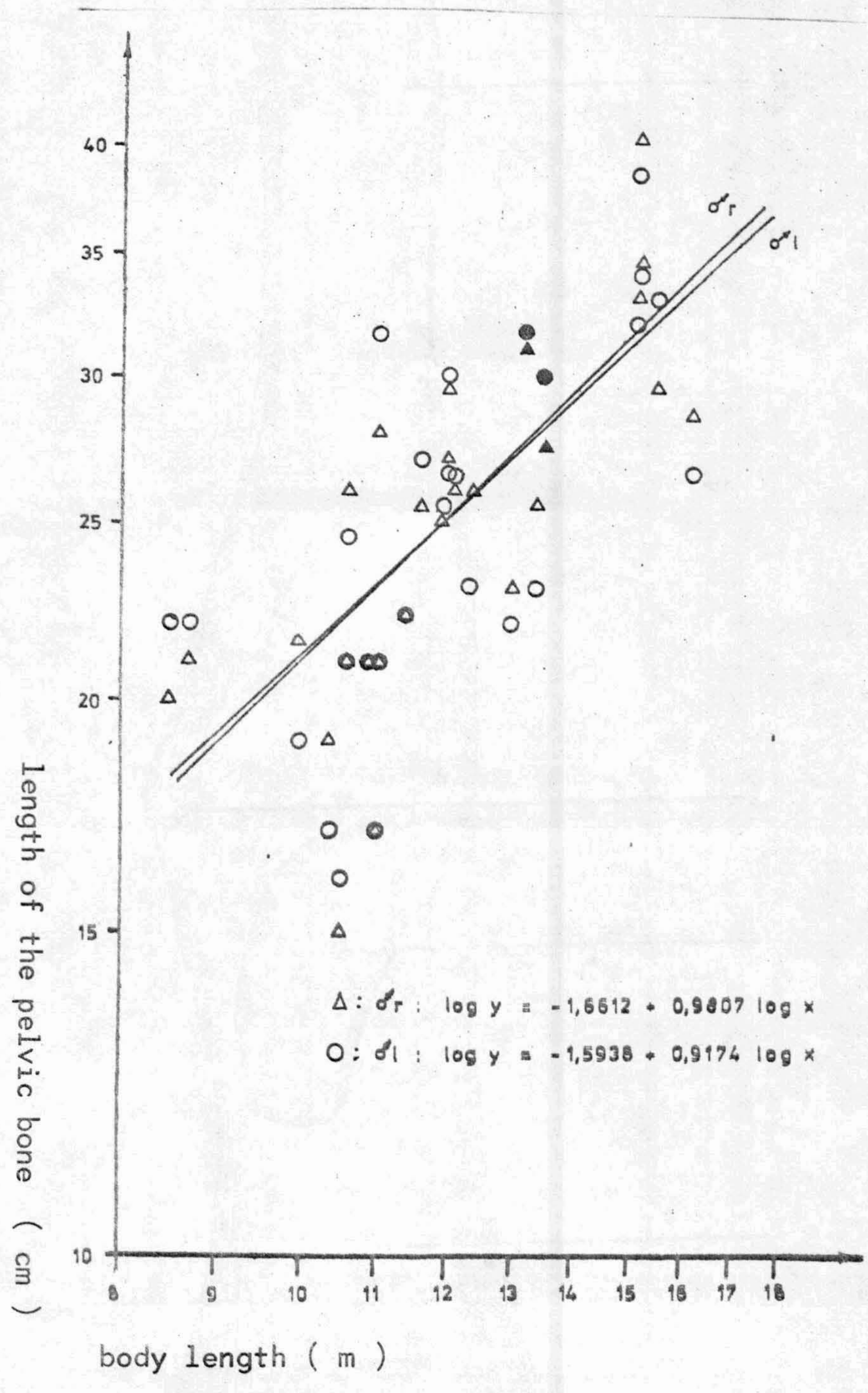

Fig. 2
Allometry lines for right (r) and left (l) lengths of the pelvic bones of males in relation to body lengths.
The ascents of the lines are not significantly different ($p > 0,5$).

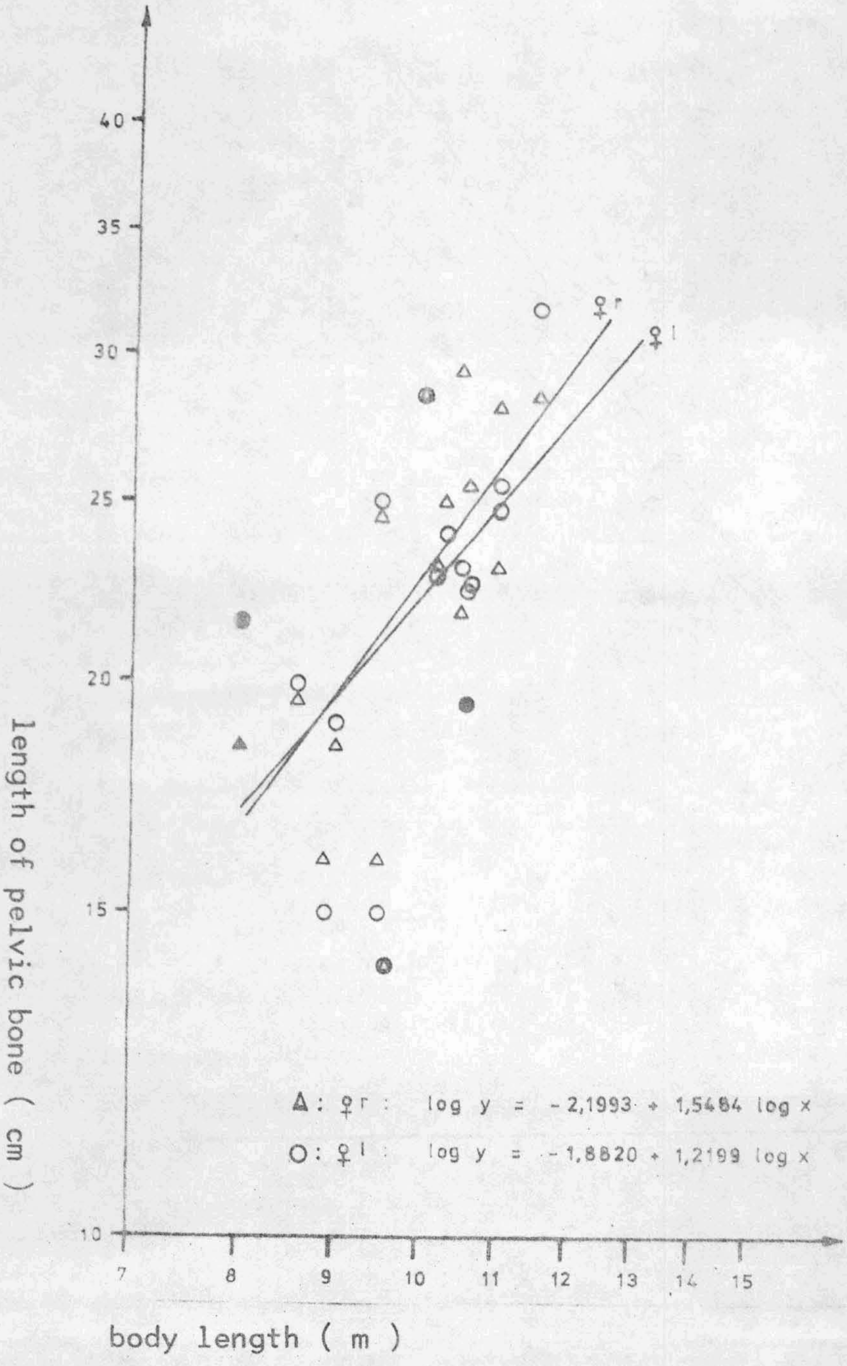

Fig. 3
Allometry lines for right (r) and left (l) lengths of the pelvic bones of females in relation to body lengths .
The ascents of the lines are not significantly different ($p > 0,5$).

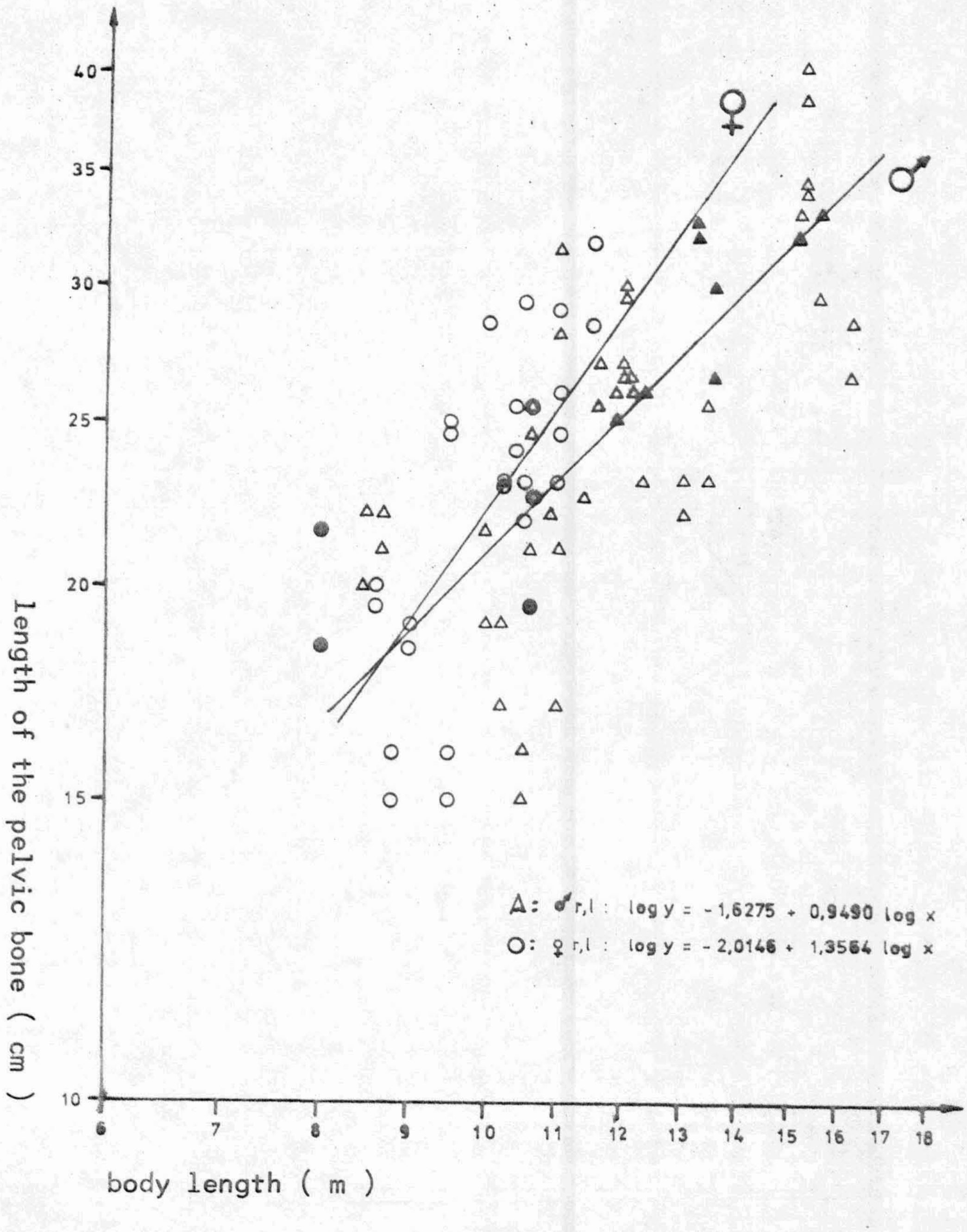

Fig. 4
Allometry lines for both (r + l) lengths of the pelvic bones of males and females in relation to body lengths.
The ascents of the lines are not significantly different ($p > 0,5$).

Tab. 1
Dates of the males

No.	Body length (x) (m)	right pelvic bone (y_1) (cm)	left pelvic bone (y_2) (cm)
1	10,50	15,0	16,0
2	10,60	21,0	21,0
3	11,60	25,5	27,0
4	15,20	34,5	34,0
5	16,20	28,5	26,5
6	12,30	26,0	23,0
7	12,10	26,0	26,5
8	13,00	23,0	22,0
9	13,40	25,5	23,0
10	10,00	21,5	19,0
11	11,00	17,0	17,0
12	10,90	22,0	22,0
13	11,40	22,5	22,5
14	10,40	19,0	17,0
15	11,90	25,0	26,0
16	15,50	29,5	33,0
17	15,20	40,3	38,5
*18	13,20	32,0	32,7
*19	13,50	27,5	30,0
20	11,00	28,0	31,5
21	12,00	27,0	26,5
22	11,00	21,0	21,0
23	10,60	25,5	24,5
24	12,00	29,5	30,0
25	8,50	20,0	22,0
26	8,70	21,0	22,0
27	15,10	33,0	32,0

		right pelvic bone	left pelvic bone
		n= 27	n= 27
		a=-1,6612	a=-1,5938
		b= 0,9807	b= 0,9174
		t= 5,5628	t= 4,5237
		p< 0,001	p< 0,001

n= 54
a=-1,6275
b= 0,9490
t= 7,1994
p < 0,001

* Literature dates , Abel, 1907

Tab. 2
Dates of the females

No.	Body length (x) (m)	right pelvic bone (y_1) (cm)	left pelvic bone (y_2) (cm)
1	10,00	28,5	28,5
2	10,30	25,0	24,0
3	10,50	21,8	23,0
4	10,50	29,4	-
5	11,50	28,5	31,9
6	10,20	23,1	22,9
7	11,00	29,1	24,6
8	10,60	22,6	22,6
9	9,00	18,4	19,0
*10	8,00	18,5	21,5
11	11,00	23,0	26,0
*12	10,60	-	19,5
13	10,60	25,5	22,5
14	9,60	14,0	14,0
15	9,50	24,5	25,0
16	8,80	16,0	15,0
17	8,60	19,5	20,0
18	9,50	16,0	15,0

	right pelvic bone (y_1)	left pelvic bone (y_2)
	n=17	n=17
	a=-2,1993	a=-1,8820
	b= 1,5484	b= 1,2199
	t= 3,4892	t= 2,4686
	p< 0,005	p< 0,025

n=34
a=-2,0146
b= 1,3564
t= 4,1937
p< 0,001

* Literature dates, Abel, 1907