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GROWTH OF THE SKULL OF THE HARBOUR PORPOISE, *PHOCOENA PHOCOENA* (LINNAEUS, 1758), IN THE NORTH SEA, AFTER AGE DETERMINATION BASED ON DENTINAL GROWTH LAYER GROUPS

by

L. P. J. J. NOLDUS

and

R. J. J. DE KLERK

Noldus, L. P. J. J. & R. J. J. de Klerk: Growth of the skull of the Harbour Porpoise *Phocoena phocoena* (Linnaeus, 1758) in the North Sea, after age determination based on dentinal growth layer groups.

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Key words: Mammalia; Cetacea; Phocoenidae; *Phocoena phocoena*; North Sea; skull; growth; teeth; age determination.

This study of the Harbour Porpoise *Phocoena phocoena* (Linnaeus, 1758) has been undertaken in order to find out whether differences in size and growth rate between the skulls of males and females could be demonstrated. Stuart & Morejohn (1980) have established this phenomenon in the population of the north-eastern Pacific. The material on which this study is based, consists of 76 skulls present in the collection of the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden. They all belong to specimens stranded on the Dutch coast.

In order to determine the age, of all these specimens the number of dentinal growth layer groups (GLG) in the teeth was counted. Thereupon 32 cranial characters were measured of each skull; these measurements were plotted against the number of growth layer groups.

Twenty-nine of the 32 characters showed a significant relationship with the number of growth layer groups. In all cases the female specimens were larger than the male specimens of the same age. After statistical analysis of the results, it turned out that there was no significant difference in growth rate of the skull parts measured. So in this respect there is no distinct sexual difference.

This is in contrast to the results of Stuart & Morejohn (1980) for the population of the north-eastern Pacific: initially smaller sizes but a significantly higher growth rate in females. The difference between the northern Atlantic population and the one from the north-eastern Pacific might support the distinction of the subspecies *P. p. phocoena* and *P. p. vomerina*.

L. P. J. J. Noldus & R. J. J. de Klerk, Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, 2300 RA Leiden, The Netherlands.

INTRODUCTION

The Common or Harbour Porpoise, *Phocoena phocoena* (Linnaeus, 1758), is one of the four species of the genus *Phocoena* Cuvier, 1817. Table 1 gives a survey of the family Phocoenidae. The distribution area of *P. phocoena* is shown in fig. 1, in which the geographical separation of the populations in the north-eastern Pacific and the Atlantic Ocean is apparent.

P. phocoena is the most common representative of the Cetacea in the North Sea and strandings of Harbour Porpoises have always been common. In the past the scientific interest for *P. phocoena* was virtually restricted to its anatomy. The oldest known monography (Tyson, 1680) is worth mentioning in this

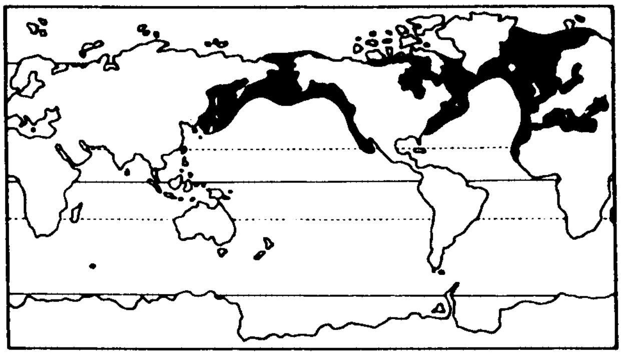


Fig. 1. Distribution area of *Phocoena phocoena* (Linnaeus, 1758), the Common or Harbour Porpoise (after Watson, 1981).

Genus	Species	Subspecies	Distribution area
Phocoena G. Cuvier, 1817	*phocoena* (L., 1758)	*phocoena*	Northern Atlantic Ocean, Mediterranean Sea, Baltic Sea
		vomerina Gill, 1865	Northern Pacific
		relicta Abel, 1905	Black Sea
	spinnipinnis Burmeister, 1865		Eastern and western coast of South America
	dioptrica Lahille, 1912		Patagonia, South Georgia
	sinus Norris & McFarland, 1958		Gulf of California
Neophocaena Palmer, 1899	*phocaenoides* (G. Cuvier, 1828)		South Asia
Phocoenoides Andrews, 1911	*dalli* (True, 1885)		Northern Pacific south to Japan and California

Table 1. Survey of the family Phocoenidae.

respect. Little attention, however, has been paid to growth and development of external features and skull, and to possible differences between males and females in this respect. This is mainly due to the fact that a reliable method of age determination was not known.

The conception that layered structures in teeth could be important in determining the age of Odontoceti arose at about 1940, but was not widely used until about 1960 (Keil, 1966; Kevezal' & Kleinenberg, 1967; Klevezal', 1980). Since then a number of publications on the growth of Cetacea have appeared. These studies have become more and more desirable because, if an efficient protection of Cetacea is to be carried out, reliable information on the structure of populations is necessary. A review of the studies in this respect, published until 1970, is given by Scheffer & Myrick (1980). Most research of *P. phocoena* has been restricted to external characters (Kasuya, 1972, 1976; Van Utrecht, 1978). Other investigators use internal characters, but instead of the teeth as a reference for the age, body length is used (Van Bree, 1973a, 1973b).

There are two recent publications concerning the skull and other bony structures of smaller Odontoceti using dentinal layers as a reference for the age, namely Perrin (1975) in a study of *Stenella* (two species) and Stuart & Morejohn (1980) in a study of *P. phocoena*. The latter authors studied growth and development of mainly the skull for the population of *P. phocoena* in the north-eastern part of the Pacific, which is often considered a distinct subspecies *P. p. vomerina* Gill, 1865. They noticed a distinct sexual difference in growth rates between the skulls of males and females.

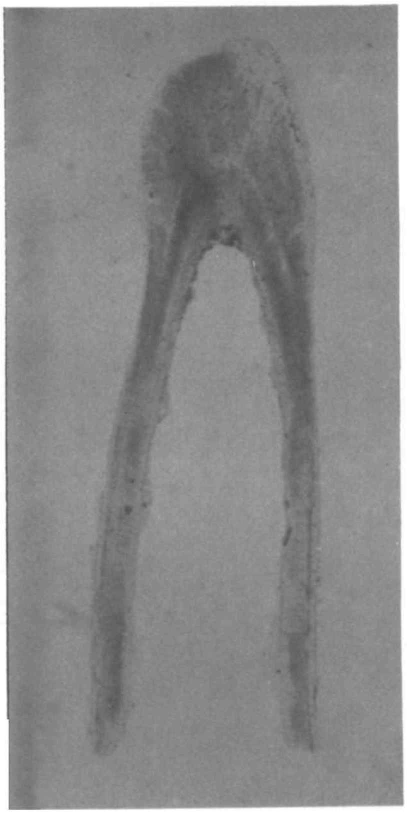
The aim of this study is to investigate whether such a sexual difference can be demonstrated for the northern Atlantic population too. The study had to be restricted to Harbour Porpoises from the North Sea, because material was available from this area only; all the material studied belongs to animals stranded on the Dutch coast.

DETERMINATION OF AGE

Odontoceti usually possess a large set of more or less similar teeth (Keil, 1966). In contrast to other Odontoceti having conical teeth, the teeth of Phocoenidae are spatulate. Counting the number of dentinal layers deposited in the teeth is the most reliable method for the determination of the age of Odontoceti (Klevezal' & Kleinenberg, 1967; Nielsen, 1972; Kasuya, 1972, 1976; Gaskin & Blair, 1977; Van Utrecht, 1978; Scheffer & Myrick, 1980).

On a longitudinal section of a tooth of *P. phocoena* the following parts can

be seen, going from the outside to the inside (figs. 2-5):
– a thin layer of enamel covering the crown; the root of the tooth is covered by a thin layer of cementum;
– the prenatal dentine, which usually has a globular structure;
– the neo-natal line, the borderline between prenatal and postnatal dentine; this is a very thin, light-coloured layer, only visible with a microscope;
– the postnatal dentine; this forms the remaining part of the tooth. It consists of layers which are called growth layer groups (GLG) after Stuart & Morejohn (1980). Each growth layer group consists of a thin, light-coloured zone and a thick, dark zone. According to Gaskin & Blair (1977), the light-



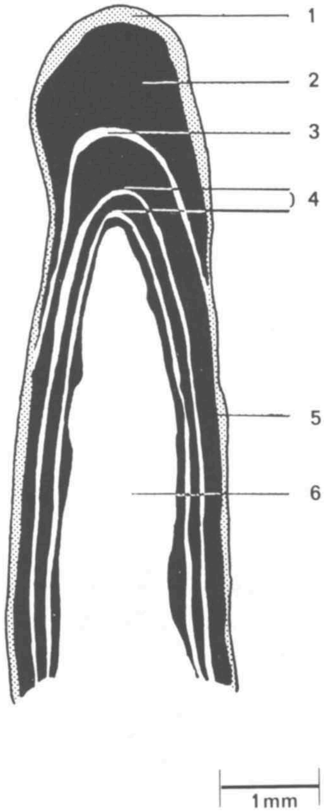
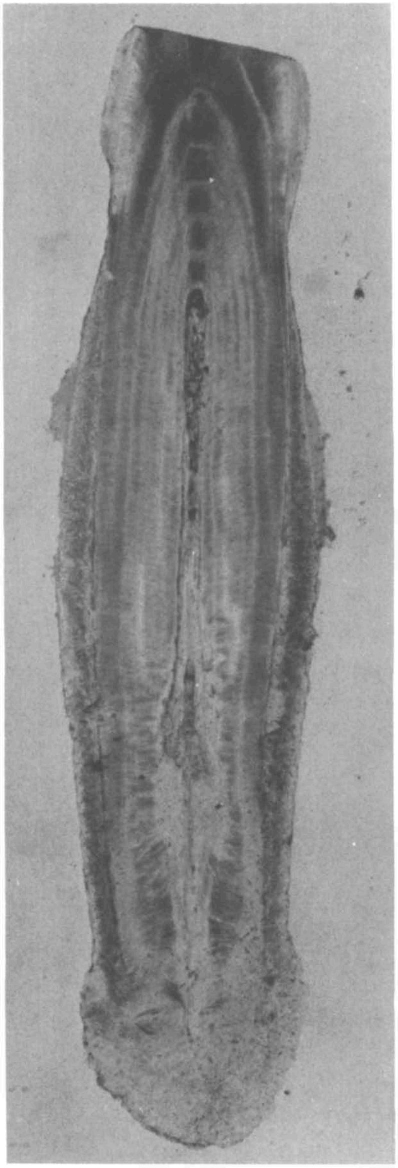


Fig. 2 (left). Longitudinal section of a tooth of *Phocoena phocoena* with two dentinal growth layer groups (RMNH 7898); transmitted light. Fig. 3 (right). Diagram of a longitudinal section of a tooth of *Phocoena phocoena* with two dentinal growth layer groups (1 = enamel, 2 = prenatal dentine, 3 = neo-natal line, 4 = one complete growth layer group, 5 = cementum, 6 = pulp cavity).



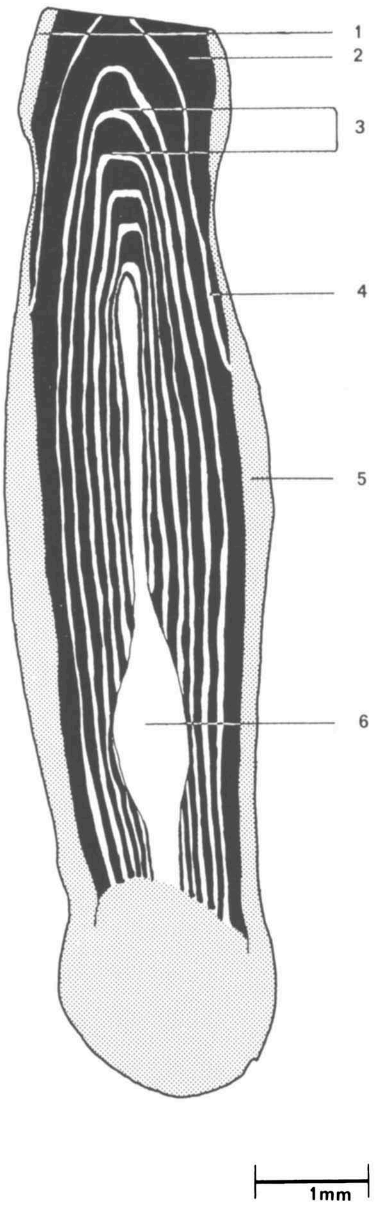


Fig. 4 (left). Longitudinal section of a tooth of *Phocoena phocoena* with six dentinal growth layer groups (RMNH 1696); transmitted light. Fig. 5 (right). Diagram of a longitudinal section of a tooth of *Phocoena phocoena* with six dentinal growth layer groups (1 = enamel, 2 = prenatal dentine, 3 = one complete growth layer group, 4 = neo-natal line, 5 = cementum, 6 = pulp cavity).

coloured zone is deposited between January and August, while the dark zone is formed in the period between June and February. Reasons for this overlap are mentioned by them and will not be discussed here. Towards the centre of the tooth the growth layer groups become thinner; the larger the number of growth layer groups, the smaller the difference in thickness between the light-coloured and dark zones; this is clearly demonstrated in fig. 4.

The postnatal dentine in the root is deposited parallel to the longitudinal axis of the tooth. As the number of growth layer groups increases, the pulpal cavity is filled up gradually. This cavity never closes completely, even at an older age. The growth layer groups can best be counted in the crown part, where they are broader because of the spatulate shape of the tooth.

The maximum number of growth layer groups shows a variation for different geographical areas and, perhaps, examiners. Nielsen (1972) found a maximum of eight growth layer groups for specimens from the north-eastern Atlantic Ocean; Stuart & Morejohn (1980) established a maximum of ten growth layer groups for specimens from the north-eastern Pacific. Van Utrecht (1978) found among his specimens from the North Sea a male with 11 layers and a female with 12 layers, while Gaskin & Blair (1977) once counted a number of 13 growth layer groups in a specimen from the north-western part of the Atlantic Ocean. Nielsen (1972) assumes that after the formation of eight growth layer groups the dentine is deposited in the form of osteodentine, in which no growth layer groups can be distinguished. Gaskin & Blair (1977) do not agree with her, because they have counted up to 13 growth layer groups. Sheldrick (1980) also assumes the formation of osteodentine without visible growth layer groups.

In the cementum growth layers are also present, but these are irregularly shaped and much thinner than those in the dentine, and more difficult to distinguish (Van Utrecht, 1981). Besides, no definite correlation has been found between the number of growth layer groups in dentine and cementum (Sheldrick, 1980). It is therefore not recommendable to carry out countings on these layers in the first place. It must be remarked, however, that the formation of cemental layers continues longer than that of dentinal layers. In order to classify very old specimens, it might therefore be useful to subject them to counting of cemental layers. This has not been done in this study.

Although the number of dentinal growth layer groups as a reference for age has increasingly been used, there is still no certainty whether one complete growth layer group is deposited per annum and whether the age in years coincides with the number of growth layer groups of a specimen. Nielsen (1972) draws conclusions on this subject on the basis of examination of one specimen of *P. phocoena*, held in captivity, of which the dentinal layers had been marked by injections of tetracycline at known intervals of time. Myrick (1980) doubts whether a physiological process like the deposition of dentine proceeds the same way in captivity as under natural circumstances.

MATERIALS AND METHODS

The study is based on material in the collection of the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden, consisting of specimens stranded on the Dutch coast between 1847 and the present day. Only skulls possessing teeth and lacking serious damage were used for examination. Seventy-six skulls met these requirements; 32 of these were males, 29 were females and of 15 skulls the sex could not be traced. Table 2 gives the RMNH collection numbers of the specimens examined. Further data concerning these specimens, such as date and place of stranding, can be found in Broekema (1983).

The age of the skulls has been determined by counting the number of dentinal growth layer groups in the teeth. Next, 32 characters were measured on each skull. These methods are explained below.

98	3112	7895	12752	23586	26130	28017	31224
1446	3519	7898	16163	23588	26261	28482	31225
1606	4254	7899	19884	24171	26326	28588	31227
1636	5082	10640	19886	24994	27126	28589	31228
1696	5651	10759	20637	25106	27225	29138	31229
2124	5830	10817	21647	25527	27278	29139	31230
2458	7396	10951	22214	25605	27282	29316	
2510	7401	11686	23436	25690	27283	29779	
2568	7761	11944	23437	25754	27551	31222	
2608	7892	11949	23584	25969	27552	31223	

Table 2. RMNH collection numbers of specimens examined in this study.

Counting of dentinal growth layer groups

Of each specimen two teeth were removed from the middle of the left lower mandible. Each tooth was glued to a petrographical slide with Lakeside resin. Next, the tooth was manually ground down to half its thickness parallel to the longitudinal axis, on a rotating grinding-wheel with carborundum powder 220 and 250 as abrasive. Hereafter the slide with the tooth attached to it was heated on a stove so that, as the resin became soft, the tooth could be turned. As soon as the resin had hardened again, the tooth was further ground down to a thickness of 100-200 μm. The process was mainly carried out on a grinding-wheel; if necessary, the preparation was finished off with Carbimed waterproof sand-paper grit 600.

Finally, the tooth was embedded in malinol on a microscopical slide and examined through a microscope with transmitted light. Each preparation was examined twice by each researcher, independent of each other, so that eight values of the number of growth layer groups were available for each specimen (see Perrin, 1975). Of these eight values the average was determined and rounded off to whole numbers.

Measuring of characters and processing of data

Of each skull 32 characters were measured by means of marking gauges, by which an accuracy of 1 mm could be reached. The characters and the abbreviations used in this paper are listed in table 3. Figs. 6-15 indicate how the measurements have been carried out. Furthermore, the skull parts mentioned in this paper have been indicated in these figures.

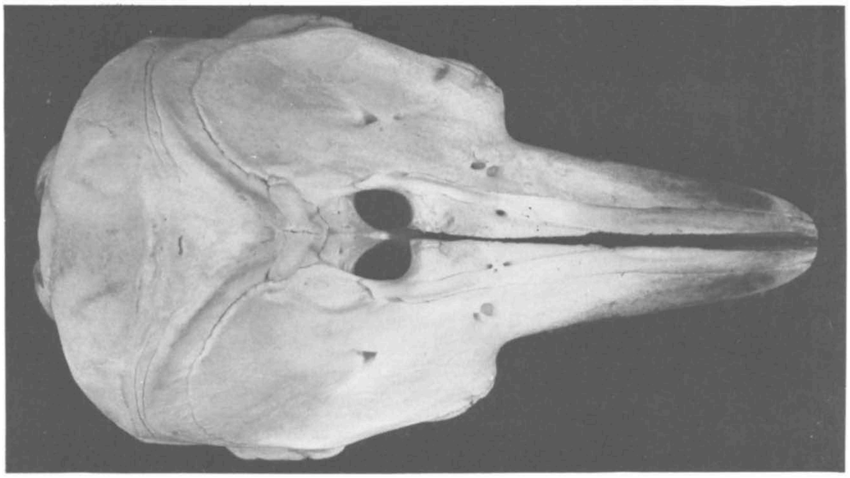
Table 3. List of cranial characters measured.

1. CBL	Condylobasal length: distance along the midline of the skull from a line connecting the anterior margins of the rostrum to a line connecting the posterior margins of the condyles (fig. 7).
2. CH	Cranial height: height of cranium from the most ventral point of the basioccipital to the posterior margin of the supraoccipital (figs. 9, 11).
3. SW	Squamosal width: greatest width of the skull across the zygomatic processes of the squamosals (figs. 7, 11).
4. RL	Rostral length: distance along the midline of the skull from a line connecting the anterior margins of the rostrum to a line across the posterior limits of the anteorbital notches (fig. 7).
5. RW	Rostral width: width of the rostrum along a line connecting the posterior limits of the anteorbital notches (fig. 7).
6. RWH	Rostral width halfway: width of the rostrum taken as a perpendicular to the midline of the skull halfway the rostral length (fig. 7).
7. LRAL	Length rostrum – left anteorbital notch: distance from the intersection of the line connecting the anterior margins of the rostrum and the midline of the skull, to the posterior limit of the left anteorbital notch (fig. 7)
8. LRAR	Length rostrum – right anteorbital notch: as above, right.
9. PLL	Praemaxillar length, left: distance, parallel to the midline of the skull, from the left anterior margin of the rostrum to the posterior limit of the left praemaxilla (fig. 7).
10. PLR	Praemaxillar length, right: as above, right.
11. PW	Praemaxillar width: greatest width of the praemaxillae taken as a perpendicular to the midline of the skull (fig. 7).

12. PWH	Praemaxillar width halfway: width of the praemaxillae taken as a perpendicular to the midline of the skull, halfway the rostral length (fig. 7).
13. MLL	Maxillar length, left: distance, parallel to the midline of the skull, from the left anterior margin of the rostrum to the posterior limit of the left maxilla (fig. 7).
14. MLR	Maxillar length, right: as above, right.
15. LRN	Length rostrum – nare: distance, parallel to the midline of the skull, from a line connecting the anterior margins of the rostrum to the anterior point of the left nare (fig. 7).
16. NWL	Nare width, left: greatest width of the left external nare (fig. 7).
17. NWR	Nare width, right: as above, right.
18. NW	Nasal width: greatest width of the nasals (fig. 7).
19. TL	Temporal length: greatest distance from the midpoint in the space between the zygomatic process and the frontal process to the posterior margin of the raised suture around the temporal area (fig. 9).
20. TH	Temporal height: greatest height of the temporal area measured at right angles to the temporal length (fig. 9).
21. CW	Condyle width: greatest distance from the left to the right edge of the occipital condyles (fig. 11).
22. FW	Width of foramen magnum: greatest width of foramen magnum (fig. 11).
23. LAP	Length of anteorbital process: greatest length of the left anteorbital process (fig. 9).
24. LML	Mandibular length, left: distance from the anterior to the posterior tip of the left mandible taken parallel to its longitudinal axis (fig. 15).
25. LMR	Mandibular length, right: as above, right.
26. HML	Mandibular height, left: greatest height of the left mandible taken as a perpendicular to the ventral margin of the mandible at the coronoid process (fig. 15).
27. HMR	Mandibular height, right: as above, right.
28. LDF	Length of dental foramen: distance from the anterior point of the left dental foramen to the mesal rim of the internal surface of the mandibular condyle (fig. 15).
29. LMxGL	Length of maxillar groove, left: distance from the anterior tip of the left maxilla to the posterior limit of the groove in which the alveoli are situated (fig. 13).
30. LMxGR	Length of maxillar groove, right: as above, right.
31. LMdGL	Length of mandibular groove, left: distance from the anterior tip of the left mandible to the posterior limit of the groove in which the alveoli are situated.
32. LMdGR	Length of mandibular groove, right: as above, right.

After the procedure mentioned above, a dataset became available containing the values of 32 characters for 76 specimens.* Further calculations were only carried out with the data of the 61 specimens of known sex. For all characters a number of statistical values were determined first, separately for males and females: minimum, maximum, avarage and standard deviation. Next, the values of all characters were plotted against the number of growth layer groups. If the values are plotted directly against the numbers of dentinal layers, one obtains curves. Comparing such curves is very difficult, as is shown by Stuart & Morejohn (1980). Plotting the values against the natural logarithms of the numbers of dentinal layers yields clearer results. In that case one

* This dataset is present at the Rijksmuseum van Natuurlijke Historie, Leiden.



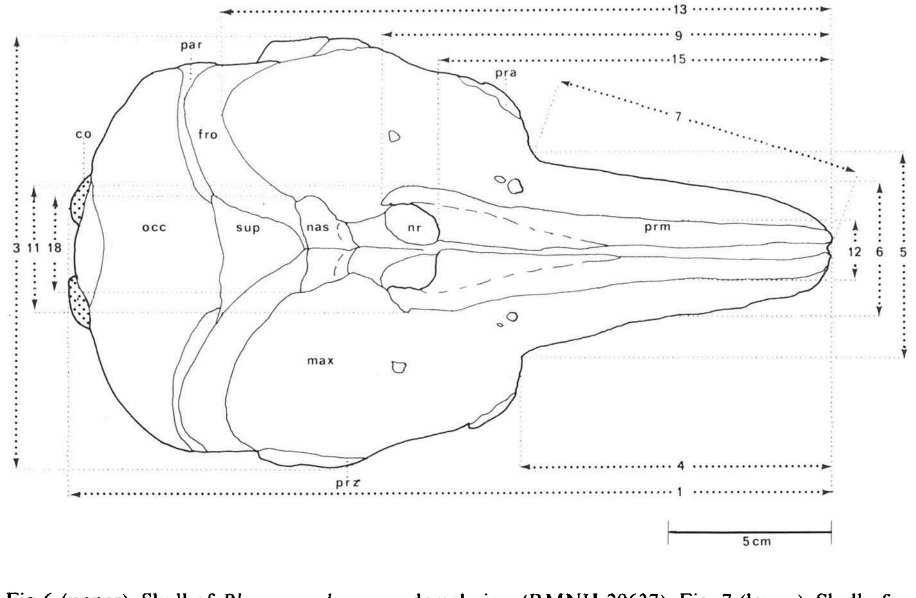
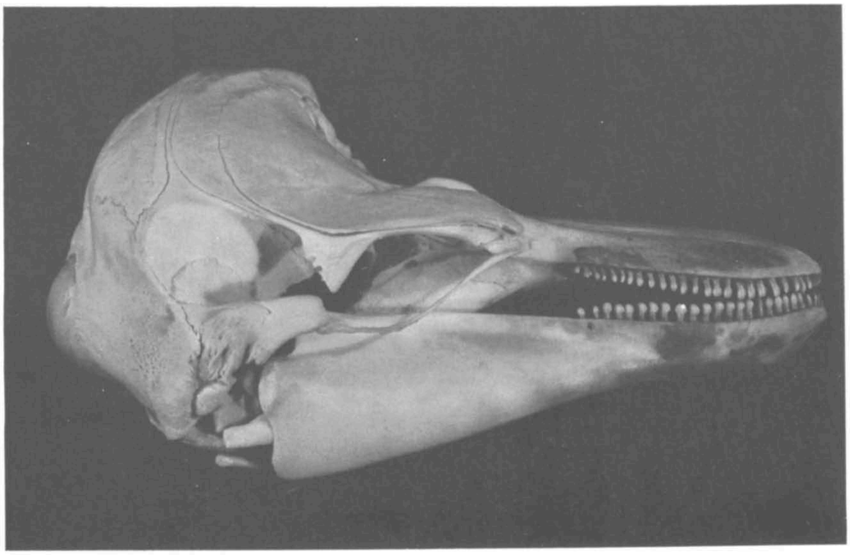


Fig 6 (upper). Skull of *Phocoena phocoena*, dorsal view (RMNH 20637). Fig. 7 (lower). Skull of *Phocoena phocoena* in dorsal view, with the characters described in table 3 (numbers: see table 3). Legend of abbreviations used in figs. 7-15. bao = basioccipitale; bas = basisphenoid; co = condylus occipitalis; dent = dentale; fd = foramen dentale; fm = foramen magnum; fro = frontale; jug = jugale; lac = lacrimale; max = maxillare; nas = nasale; nr = nare; occ = occipitale; pal = palatinum; pam = processus articularis mandibulae; pcm = processus coronoideus mandibulae; par = parietale; pra = processus anteorbitalis (frontale); prm = praemaxillare; prz = processus zygomaticus (squamosum); pte = pterygoid; squ = squamosum; sup = supraoccipitale; sym = symphisis mandibulae; temp = temporale.



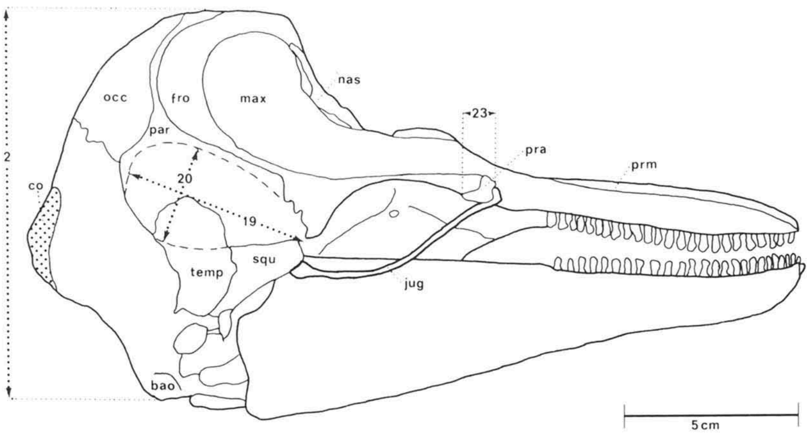
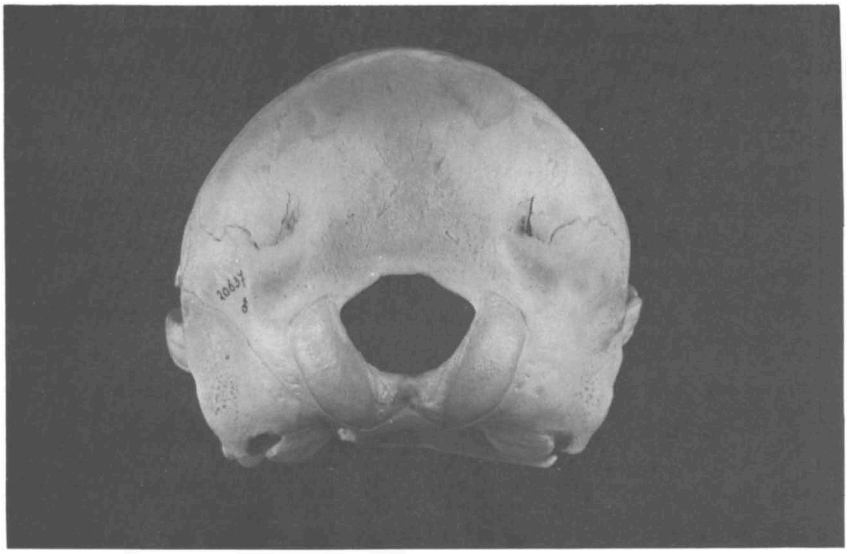


Fig. 8 (upper). Skull of *Phocoena phocoena*, lateral view (RMNH 20637). Fig. 9 (lower). Skull of *Phocoena phocoena* in lateral view, with the characters described in table 3 (abbreviations: see fig. 7; numbers: see table 3).

can draw straight lines through the scatter diagrams, which can be compared on the basis of their slope and intercept.

Before the natural logarithms of the number of dentinal growth layer groups were calculated, the value one was added to all numbers, in order to



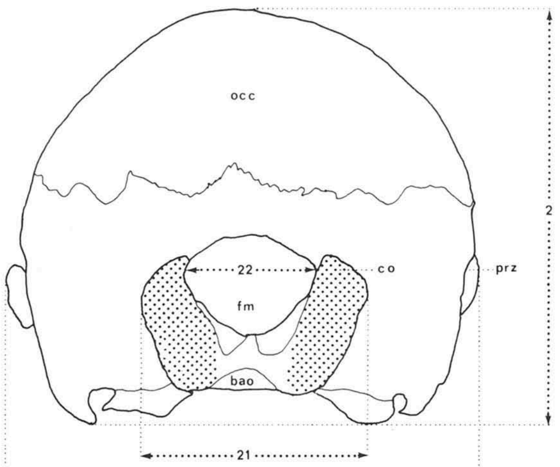
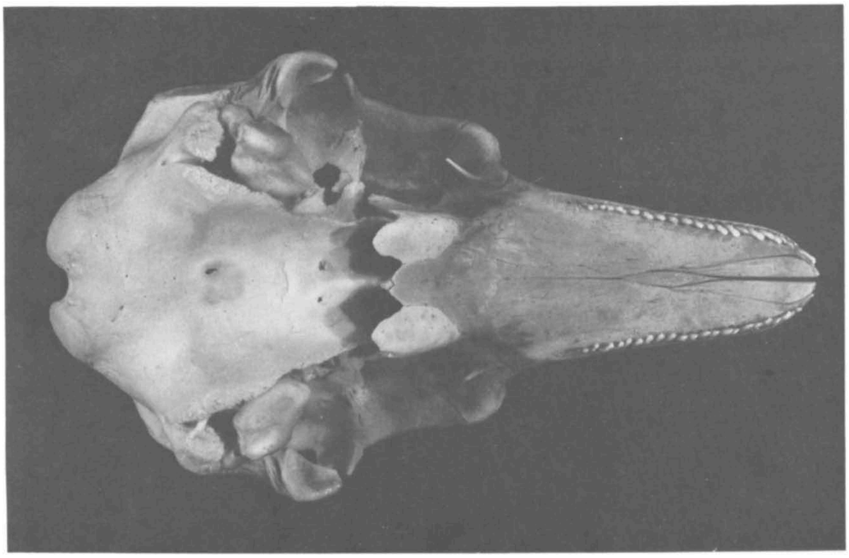


Fig. 10 (upper). Skull of *Phocoena phocoena*, caudal view (RMNH 20637). Fig. 11 (lower). Skull of *Phocoena phocoena* in caudal view, with the characters described in table 3 (abbreviations: see fig. 7; numbers: see table 3).



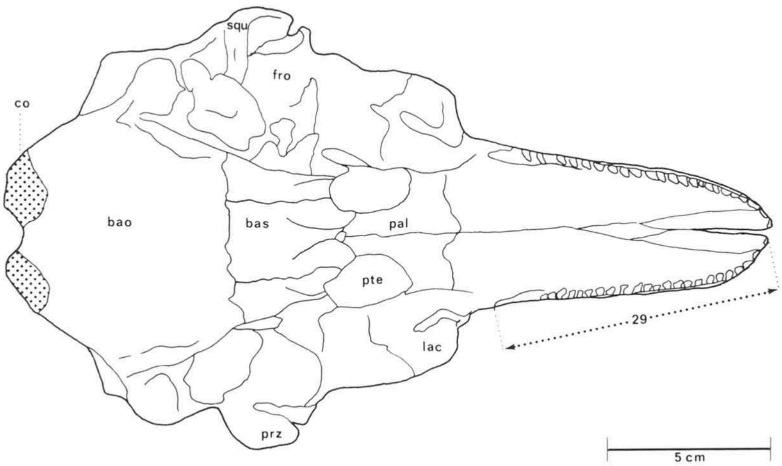
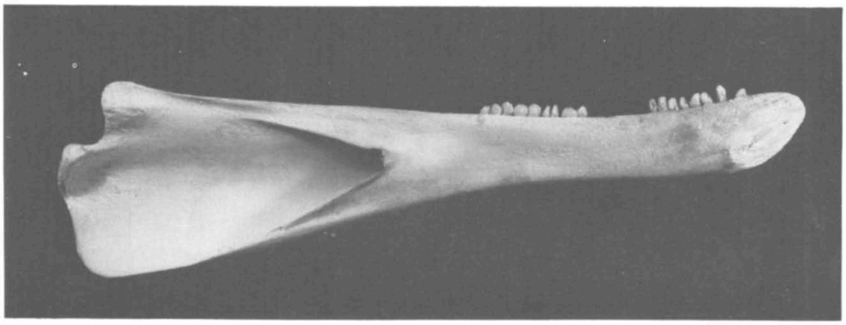


Fig. 12 (upper). Skull of *Phocoena phocoena*, ventral view (RMNH 22214). Fig. 13 (lower). Skull of *Phocoena phocoena* in ventral view, with the characters described in table 3 (abbreviations: see fig. 7; numbers: see table 3).

allow incorporation of specimens with zero growth layer groups into the plots. This has no consequences for the course of the regression lines. After this, for each of the 32 characters the values of the male and female specimens could be plotted against ln(GLG + 1).

Subsequently, for each scatter diagram the slope and intercept of the



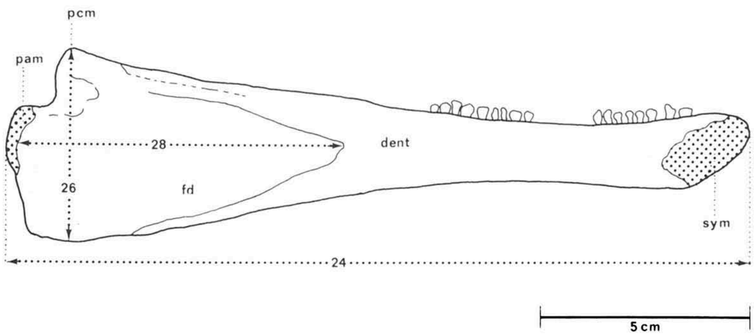


Fig. 14 (upper). Left mandible of *Phocoena phocoena*, lingual view (RMNH 27278). Fig. 15 (lower). Left mandible of *Phocoena phocoena* in lingual view, with the characters described in table 3 (abbreviations: see fig. 7; numbers: see table 3).

matching regression line were determined by means of linear regression. Besides, the correlation coefficient and the sum of squares were calculated. If the correlation coefficient was significant at the 0.05 level for a normal distribution, a regression line was added to the scatter diagram. The reason for this is that only diagrams that show a significant relationship between the character and the number of growth layer groups, may be compared to each other (Stuart & Morejohn, 1980).

Finally, an F-test was carried out in order to determine whether the differences in growth rates between male and female specimens, represented by the slopes of the regression lines, were significant (see Gilbert, 1973). The F-value is defined as follows:

$$F = \frac{n + m - 4}{2} \times \frac{SS_{total} - SS\,♂ - SS\,♀}{SS\,♂ + SS\,♀},$$

in which: n = number of male specimens;
m = number of female specimens;
SS = sum of squares.

The critical value stood at 3.15 for all characters, with a normal distribution and an 0.05 level of significance.

RESULTS

Among the specimens studied, the largest number of growth layer groups is nine for the males and ten for the females. Table 4 gives minimum, maxi-

Character	Average		S.D.		Minimum		Maximum	
	♂	♀	♂	♀	♂	♀	♂	♀
CBL	24.27	25.47	2.29	1.79	18.20	20.70	28.00	28.30
CH	11.51	12.05	1.13	0.85	8.60	9.80	14.70	13.30
SW	13.98	14.73	1.55	1.36	9.60	11.80	16.90	17.10
RL	10.02	10.58	1.21	1.03	6.70	8.30	11.50	12.60
RW	6.42	6.92	0.88	0.86	3.80	5.10	7.90	8.30
RWH	4.37	4.63	0.51	0.55	2.80	3.60	5.20	5.50
LRAL	10.31	10.93	1.23	1.05	7.20	8.70	12.00	12.70
LRAR	10.51	11.08	1.28	1.08	7.10	8.60	12.20	12.90
PLL	14.57	15.37	1.54	1.33	10.80	11.90	17.00	17.60
PLR	14.49	15.18	1.48	1.25	10.70	12.40	16.70	17.30
PW	3.48	3.71	0.35	0.37	2.60	2.80	4.00	4.30
PWH	2.03	2.30	0.24	0.35	1.20	1.60	2.40	3.00
MLL	19.43	20.61	2.41	1.65	11.30	16.50	22.40	24.00
MLR	19.48	20.60	2.37	1.57	11.60	16.70	22.40	23.50
LRN	13.03	14.00	1.58	1.28	8.70	11.10	15.10	16.30
NWL	1.23	1.28	0.18	0.17	0.80	1.00	1.60	1.60
NWR	1.24	1.31	0.19	0.17	0.80	1.00	1.50	1.70
NW	2.88	3.05	0.38	0.37	1.90	2.00	3.50	3.50
TL	5.19	5.52	0.69	0.55	3.40	4.30	6.50	6.70
TH	3.64	3.78	0.47	0.35	2.60	3.00	4.50	4.40
CW	5.94	6.14	0.63	0.86	4.00	3.10	6.80	7.20
FW	2.94	3.06	0.31	0.76	2.30	2.50	3.60	6.60
LAP	2.25	2.39	0.35	0.34	1.70	1.80	3.30	3.30
LML	18.22	19.36	1.87	1.52	13.30	15.90	20.80	22.20
LMR	18.34	19.43	1.85	1.53	13.40	15.90	21.30	22.10
HML	4.90	5.31	0.62	0.50	3.40	4.20	6.40	6.20
HMR	4.89	5.30	0.66	0.50	3.00	4.20	6.40	6.20
LDF	7.38	7.93	0.79	0.73	5.20	6.20	8.60	9.20
LMxGL	8.93	9.61	1.19	0.94	5.90	7.60	10.50	11.30
LMxGR	9.02	9.65	1.19	0.90	6.30	7.60	10.60	11.30
LMdGL	9.91	10.47	1.34	1.09	6.80	8.70	11.80	12.50
LMdGR	10.00	10.52	1.38	1.17	6.80	8.70	12.10	12.90

Table 4. Minima, maxima, averages and standard deviations of the characters measured (cm).

mum, average and standard deviation of all measurements. These data clearly show that minima, maxima and averages are larger in females than in males.

Slope and intercept of the calculated regression lines, as well as the correlation coefficient and the degree of significance of the relationship between measurements and ln(GLG + 1) are given in table 5. From this can be gathered that 29 of the 32 characters show a significant relationship with ln(GLG + 1) for males as well as for females, at the 0.05 level of significance. The following characters did not show a significant relationship with age: width of foramen magnum (FW, ♂ and ♀), length of anteorbital process (LAP, ♂) and nasal width (NW, ♀). The left nare width (NWL, ♀) shows

Character	Equation of the regression line ♂	Equation of the regression line ♀	r ♂	sign.	r ♀	sign.
CBL	y = 2.68x + 20.51	y = 2.14x + 22.36	0.746	+ + + +	0.574	+ + + +
CH	y = 1.12x + 9.93	y = 0.93x + 10.70	0.634	+ + + +	0.527	+ + + +
SW	y = 1.78x + 11.48	y = 1.96x + 11.89	0.733	+ + + +	0.704	+ + + +
RL	y = 1.39x + 8.07	y = 1.11x + 8.98	0.734	+ + + +	0.516	+ + + +
RW	y = 0.95x + 5.10	y = 1.00x + 5.47	0.687	+ + + +	0.562	+ + + +
RWH	y = 0.53x + 3.62	y = 0.56x + 3.80	0.665	+ + + +	0.496	+ + + +
LRAL	y = 1.43x + 8.30	y = 1.29x + 9.06	0.743	+ + + +	0.590	+ + + +
LRAR	y = 1.51x + 8.38	y = 1.23x + 9.29	0.751	+ + + +	0.548	+ + + +
PLL	y = 1.81x + 12.03	y = 1.20x + 13.62	0.752	+ + + +	0.434	+ + +
PLR	y = 1.79x + 11.98	y = 1.06x + 13.64	0.774	+ + + +	0.407	+ + +
PW	y = 0.38x + 2.94	y = 0.36x + 3.19	0.703	+ + + +	0.469	+ + + +
PWH	y = 0.24x + 1.70	y = 0.38x + 1.74	0.639	+ + + +	0.521	+ + + +
MLL	y = 2.92x + 15.33	y = 1.84x + 17.94	0.774	+ + + +	0.536	+ + + +
MLR	y = 2.81x + 15.53	y = 1.66x + 18.19	0.757	+ + + +	0.510	+ + + +
LRN	y = 1.88x + 10.40	y = 1.35x + 12.03	0.760	+ + + +	0.508	+ + + +
NWL	y = 0.19x + 0.95	y = 0.12 + 1.11	0.697	+ + + +	0.329	+
NWR	y = 0.21x + 0.94	y = 0.18x + 1.05	0.714	+ + + +	0.502	+ + + +
NW	y = 0.37x + 2.35	y = 0.11x + 2.89	0.628	+ + + +	0.145	n.s.
TL	y = 0.65x + 4.28	y = 0.77x + 4.41	0.602	+ + + +	0.676	+ + + +
TH	y = 0.40x + 3.08	y = 0.27x + 3.39	0.544	+ + + +	0.379	+ +
CW	y = 0.62x + 5.06	y = 0.68x + 5.28	0.630	+ + + +	0.519	+ + + +
FW	y = 0.10x + 2.80	y = 0.19x + 2.66	0.207	n.s.	0.273	n.s.
LAP	y = 0.13x + 2.07	y = 0.39x + 1.82	0.244	n.s.	0.555	+ + + +
LML	y = 2.14x + 15.28	y = 1.89x + 16.61	0.742	+ + + +	0.598	+ + + +
LMR	y = 2.09x + 15.39	y = 1.81x + 16.81	0.722	+ + + +	0.568	+ + + +
HML	y = 0.68x + 3.96	y = 0.64x + 4.38	0.719	+ + + +	0.623	+ + + +
HMR	y = 0.72x + 3.89	y = 0.70x + 4.28	0.700	+ + + +	0.674	+ + + +
LDF	y = 0.81x + 6.25	y = 0.79x + 7.78	0.670	+ + + +	0.519	+ + + +
LMxGL	y = 1.30x + 7.10	y = 0.88x + 8.34	0.697	+ + + +	0.448	+ + + +
LMxGR	y = 1.31x + 7.18	y = 1.04x + 8.13	0.705	+ + + +	0.556	+ + + +
LMdGL	y = 1.20x + 8.22	y = 0.96x + 9.05	0.573	+ + + +	0.410	+ + +
LMdGR	y = 1.19x + 8.32	y = 1.32x + 8.69	0.500	+ + + +	0.491	+ + + +

Table 5. Regression lines, correlation coefficients (r) and degrees of significance of the relationship between the characters measured and ln(GLG + 1) (levels of significance: + + + + = 0.005; + + + = 0.01; + + = 0.025; + = 0.05; n.s. = not significant).

a significance with p = 0.05; the temporal height (TH, ♀) shows a significance with p = 0.025; the left praemaxillar length (PLL, ♀), the right praemaxillar length (PLR, ♀) and the length of the left mandibular groove (LMdGL, ♀) show a significance with p = 0.01. All remaining 55 regression lines are significant at the 0.005 level.

In figs. 16-23 the regression lines have been drawn for those characters of which the values show a significant relationship with ln(GLG + 1) for the males as well as the females. From table 5 and figs. 16-23 the following is apparent:

In all cases the regression line for female specimens lies above that for male specimens. In the few figures with a point of intersection, the main part of the

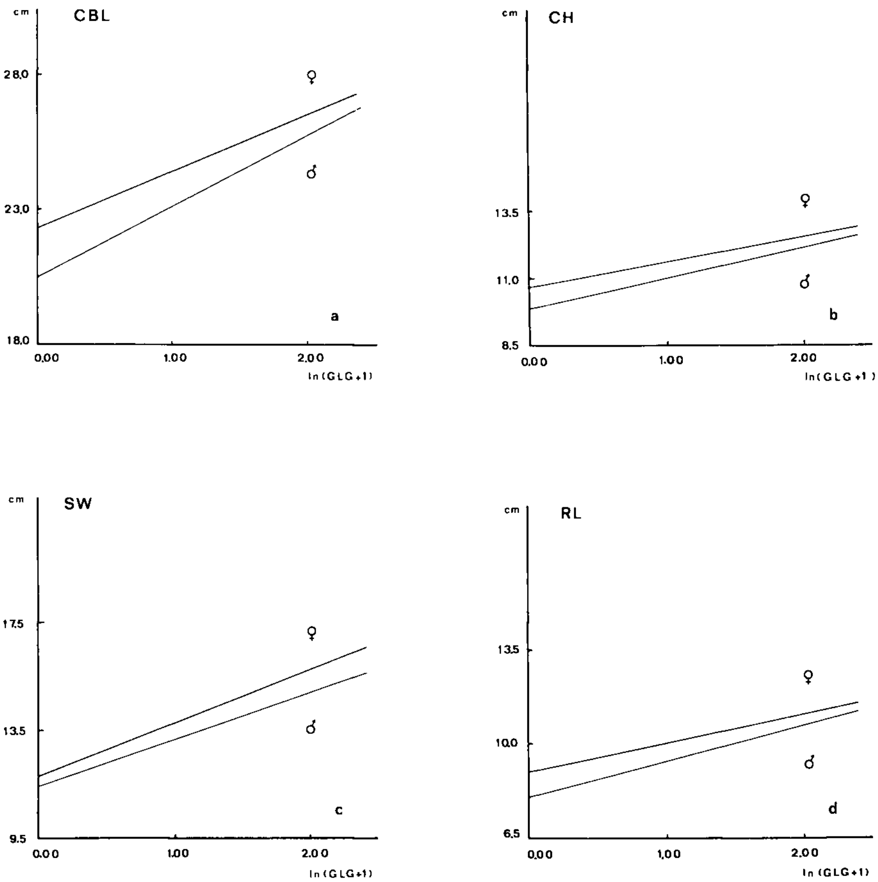


Fig. 16. Relationship to ln(GLG + 1) of: a, condylobasal length (CBL); b, cranial height (CH); c, squamosal width (SW); d, rostral length (RL).

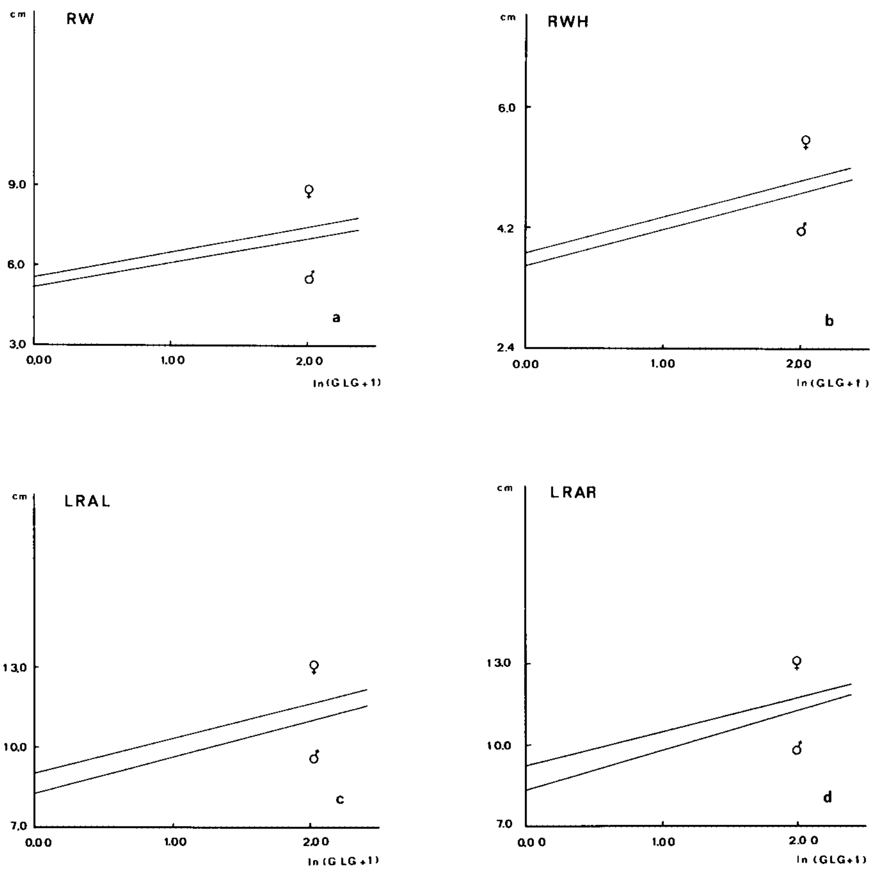


Fig. 17. Relationship to ln(GLG + 1) of: a, rostral width (RW); b, rostral width halfway (RWH); c, length rostrum — left anteorbital notch (LRAL); d, length rostrum — right anteorbital notch (LRAR).

female regression line lies above the male line. This already follows from table 4, because for all measurements the females yielded higher values than the males.

In most diagrams there is a more or less distinct convergence of the regression lines, which means a larger slope for males than for females. This indicates a higher growth rate for males than for females, in some cases leading to an intersection of the regression lines. In some diagrams the lines are almost parallel, in a few cases they slightly diverge.

On the basis of these results, one may conclude that female specimens are

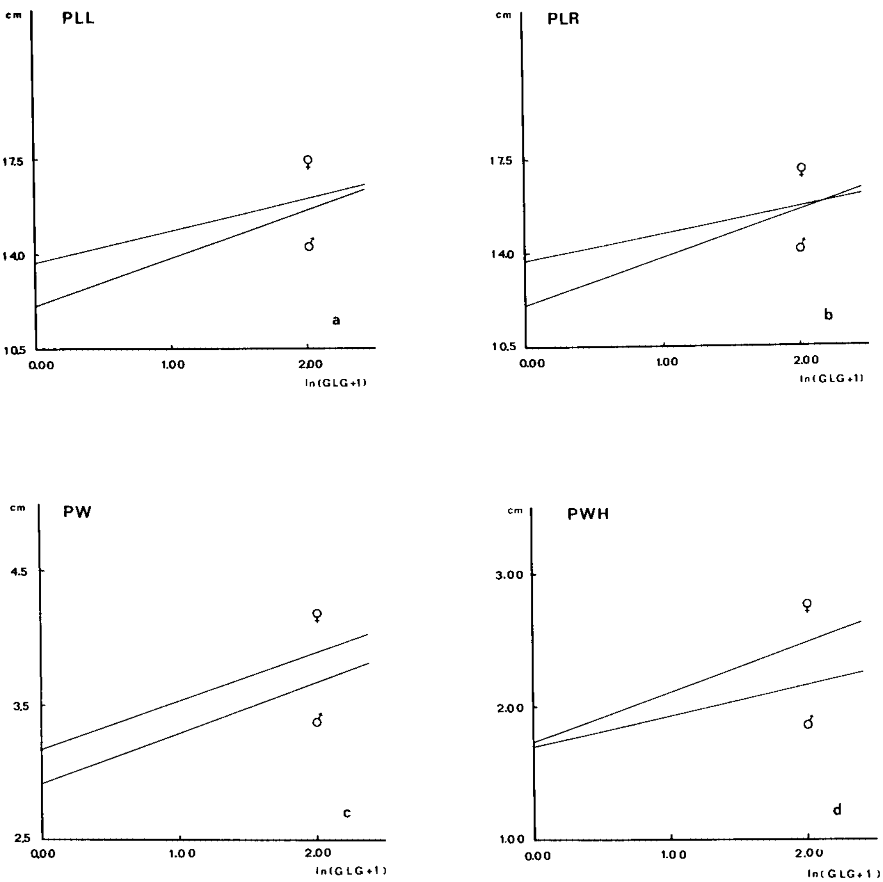


Fig. 18. Relationship to ln(GLG + 1) of: a, praemaxillar length, left (PLL); b, praemaxillar length, right (PLR); c, praemaxillar width (PW); d, praemaxillar width halfway (PWH).

larger than male specimens, but males usually have a higher growth rate, so that the differences in size for most characters decrease as age increases.

One thing, however, should be kept in mind while examining the diagrams. Direct comparison is made difficult because the units into which the Y-scale has been divided, are not always the same. For some characters these units are 0.05 cm, for others 0.5 cm. Since the sizes of the examined skull elements vary widely, it is possible that two diagrams which apparently show a similar degree of convergence, are in fact quite different.

In order to examine whether significant differences in growth rate exist, an

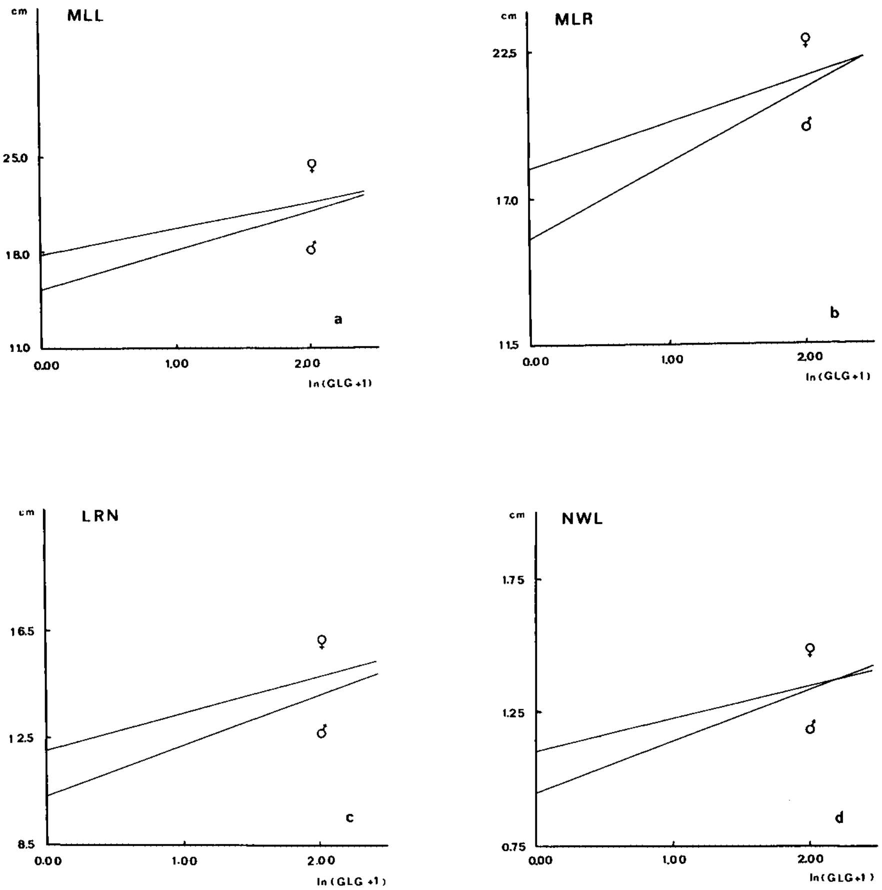


Fig. 19. Relationship to ln(GLG + 1) of: a, maxillar length, left (MLL); b, maxillar length, right (MLR); c, length rostrum – nare (LRN); d, nare width, left (NWL).

F-test was carried out. The results are given in table 6. From the fact that none of the F-values exceeds the critical value of 3.15, belonging to the 0.05 level of significance, one may conclude that none of the diffences in slope between male and female graphs is significant.

CONCLUSIONS AND DISCUSSION

The results of this study have shown that differences exist between males

Character	SS ♂	SS ♀	SS_{total}	F
CBL	90.24	29.53	122.85	0.74
CH	15.83	5.57	22.07	0.90
SW	39.98	24.74	66.32	0.70
RL	24.36	7.89	32.95	0.62
RW	11.25	6.47	18.41	1.11
RWH	3.54	2.05	5.78	1.01
LRAL	25.70	10.72	37.57	0.90
LRAR	28.90	9.80	39.49	0.59
PLL	41.42	9.35	51.04	0.14
PLR	40.39	7.20	46.80	−0.47
PW	1.84	0.83	2.79	1.34
PWH	0.72	0.94	1.68	0.45
MLL	107.71	21.81	128.84	−0.15
MLR	99.56	17.83	115.69	−0.41
LRN	44.49	11.86	57.59	0.63
NWL	0.50	0.09	0.56	−0.79
NWR	0.58	0.21	0.81	0.61
TL	5.27	3.80	9.28	0.70
TH	2.02	0.47	2.47	−0.13
CW	4.90	2.99	8.18	1.04
LML	55.83	23.14	83.58	1.32
LMR	51.68	21.08	75.17	0.72
HML	5.67	2.67	8.92	1.97
HMR	6.40	3.18	10.13	1.66
LDF	8.18	4.06	13.18	2.21
LMxGL	21.40	4.40	26.70	0.39
LMxGR	21.81	7.02	29.63	0.78
LMdGL	18.30	5.39	24.81	1.34
LMdGR	16.64	8.51	24.74	−0.46

Table 6. Sum of squares (SS) and F-values of the characters measured.

and females of *P. phocoena* in the average length of the different parts of the skull. For all characters showing a significant relationship with the number of growth layer groups in the dentine, it turned out that the sizes of females are distinctly larger than those of males.

This dimorphism, however, has no connection with a difference in growth rate between males and females. On the other hand, the 29 graphs presented in this paper give the impression that such a difference does exist: in 22 of the 29 diagrams a more or less distinct convergence could be detected. This means that in these cases the skull parts of male specimens increase faster in size than those of females, although the diffences in slope of the regression lines, according to the F-test, are not significant.

These results do not correspond with what Stuart & Morejohn (1980) found for the population of the north-eastern part of the Pacific. These authors carried out a similar study; seven of their characters have been incorporated in

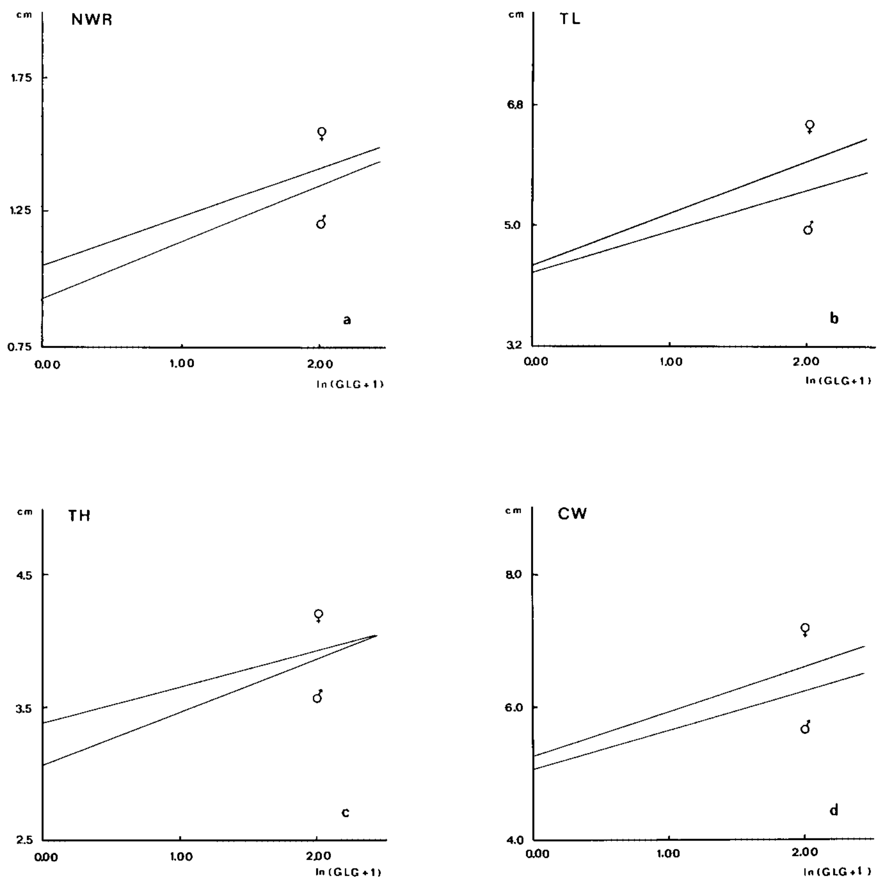


Fig. 20. Relationship to ln(GLG + 1) of: a, nare width, right (NWR); b, temporal length (TL); c, temporal height (TH); d, condyle width (CW).

the underlying study. These are: condylobasal length (CBL), squamosal width (SW), rostral length (RL), rostral width (RW), mandibular length (ML), mandibular height (MH) and length of dental foramen (LDF). For all their characters they not only found lower initial values — of zero-aged specimens — for females than for males, but also a significantly higher growth rate for males. The difference between the diagrams of Stuart & Morejohn (1980) and those presented in this paper has been reflected in a simplified form in fig. 24.

Gill (1865), who first described the population of the northern Pacific as *P. vomerina*, distinguished it from *P. phocoena* of the North Atlantic on the basis of the larger vomerine bone and the greater number of teeth. Norris &

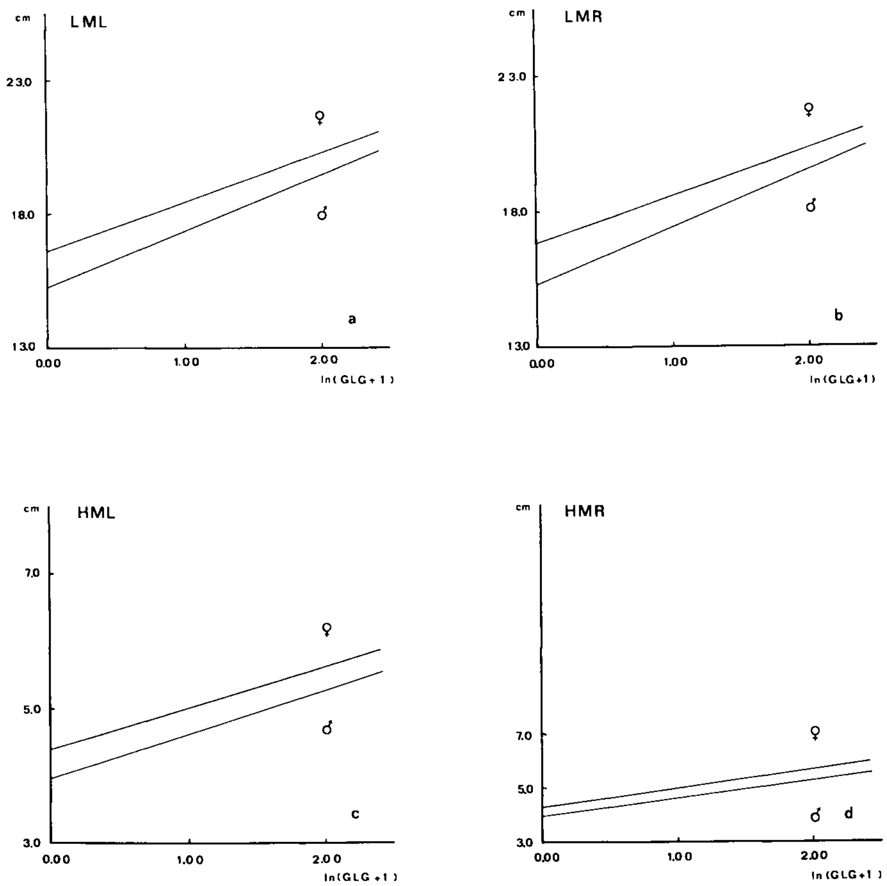


Fig. 21. Relationship to ln(GLG + 1) of: a, mandibular length, left (LML); b, mandibular length, right (LMR); c, mandibular height, left (HML); d, mandibular height, right (HMR).

McFarland (1958), however, consider these differences insufficient and state that a final solution of the validity of the taxon *P. p. vomerina* has yet to be found. In a review of the species, Gaskin et al. (1974) agree with this. Although the study presented in this paper has yielded differences between the two populations of *P. phocoena*, we dare not state at this place whether these form sufficient reason for the subspecific distinction of the populations concerned.

Some factors that may have influenced the results of this study are:

The number of examined specimens. — This study is based on 76 skulls, of 61 of which the sex is known. Is this number representative for the whole

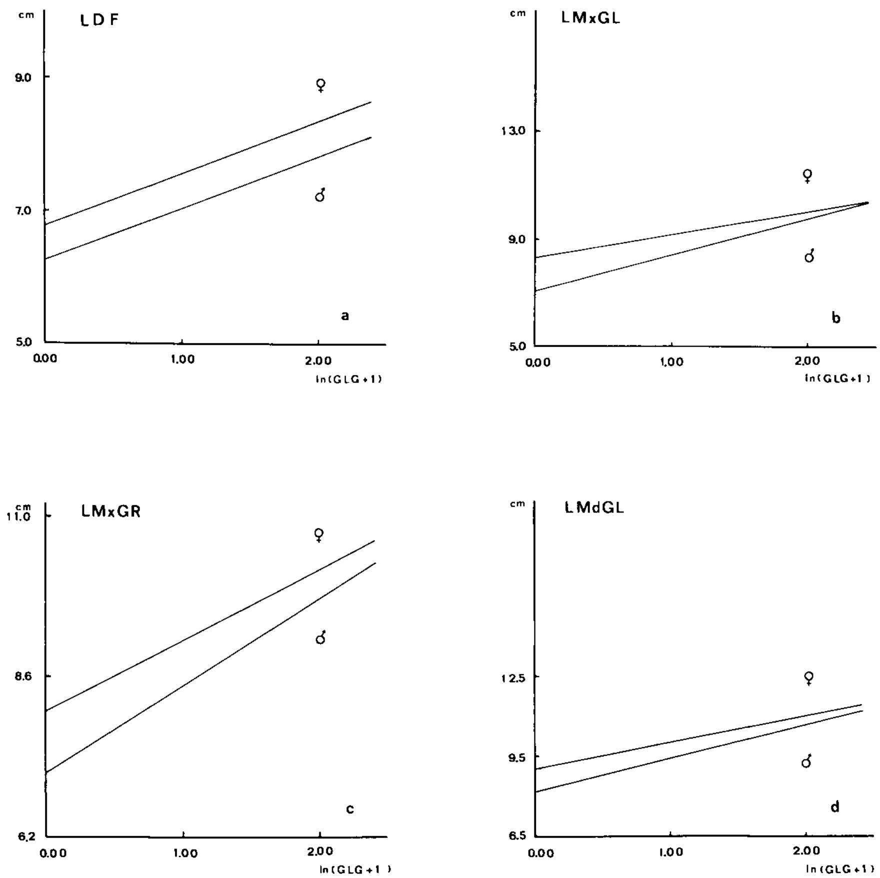


Fig. 22. Relationship to ln(GLG + 1) of: a, length of dental foramen (LDF); b, length of maxillar groove, left (LMxGL); c, length of maxillar groove, right (LMxGR); d, length of mandibular groove, left (LMdGL).

North Sea population? Gaskin & Blair (1977) examined 121 skulls with known sex; on the other hand, Stuart & Morejohn (1980) based their conclusions on 57 skulls of known sex. The fact that in our collection the age class with seven growth layer groups is not present, indicates that our sample may not have been sufficient. In further studies all Dutch material as well as the collections of institutes in other countries situated on the North Sea, should be incorporated.

The method of age determination. — The use of a grinding-wheel yields sections the thickness of which has to be estimated. The use of a slow-rotating

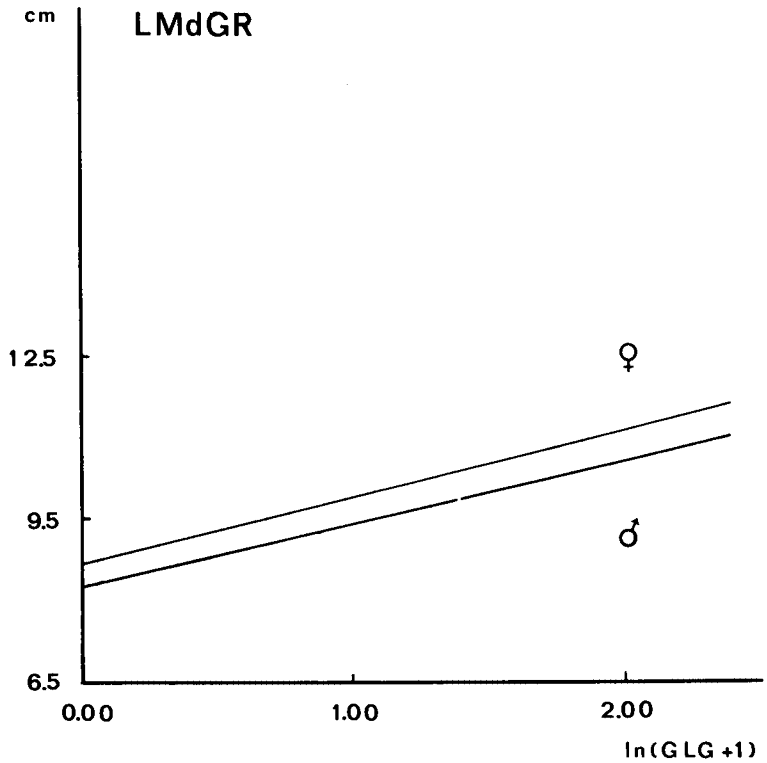


Fig. 23. Relationship to ln(GLG + 1) of: length of mandibular groove, right (LMdGR).

diamond-saw is preferable, by which sections of exact thickness and with a smoother surface can be produced (Van Utrecht, 1978). The latter often left much to be desired, which hampered counting of the growth layer groups.

Specimens with ten dentinal growth layer groups can be ten years old or older (assuming that one group is deposited per annum). As said above, the layered deposition of dentine ends at about the tenth year. All older specimens therefore end up in the same category in the graphs. Although the reliability of the method is still the subject of discussion (Sheldrick, 1980; Van Utrecht, 1981), counting of cemental layers may lead to the distinction of older age classes, so that the growth diagrams would give a more exact reflection of the real situation.

The relation between the number of growth layer groups in the dentine and the age in years certainly deserves further study. Most researchers in this field assume that one dentinal growth layer group is deposited per annum, but this

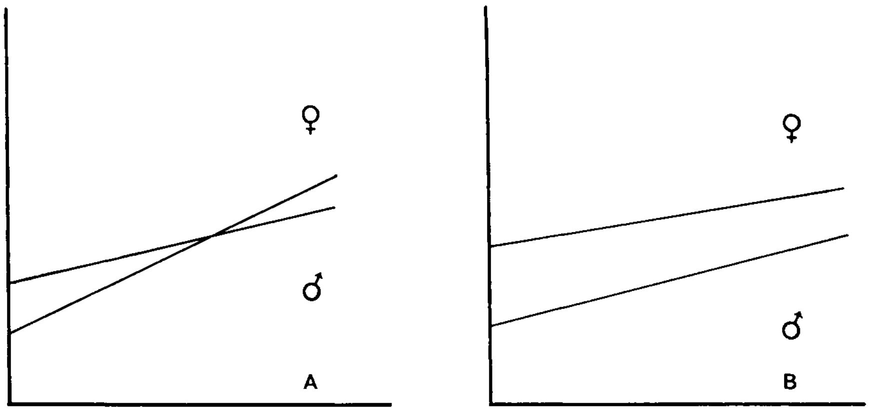


Fig. 24. Simplified representation of the relationship between cranial characters and ln(GLG + 1) as found by Stuart & Morejohn (1980) (a) and in this study (b).

has not been proved sufficiently. The conclusion of Nielsen (1972), based on one specimen in captivity, can hardly be considered sufficient evidence. At present, thorough examinations of the correlation between age and number of dentinal growth layer groups are being undertaken (Myrick, 1980).

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