

Variation in the vertebrae of the common porpoise *Phocoena phocoena* (Linnaeus, 1758) from the North Sea and N.E.Atlantic.

by KOEN VAN WAEREBEEK

1. HISTORICAL REVIEW AND INTRODUCTION

Whale taxonomy in the 19 th century, as is true for other animal groups, is characterized by an enormous proliferation of described species (see e.g. VAN BENEDEN, 1889 ; VAN BENEDEN & GERVAIS, 1880).This is mainly due to an underestimation of intraspecific variability.
However, in the 20th century and especially the last decades, cetologists such as ABEL (1931), NISHIWAKI (1963), MITCHELL et al.(1975), RICE (1977) and others, prefer to distinguish only a minimal number of whale-species, as long as the need of taxonomic separation is not clearly demonstrated. Many articles have now to be published in order to demonstrate the invalidity of several nominal species. For instance, while in the past cetologists distinguished at least 8-10 species of bottlenose dolphins, genus *Tursiops*, today most whale-specialists recognize only 2-3 or even one cosmopolitic species *Tursiops truncatus* (Montagu, 1821) with 2-3 subspecies (WATSON, 1981).

ABEL (1931) probably was the first to realize the untenable situation in the taxonomy of fossil whales : "Wurden in früherer Zeit Untersuchungen über die Variationsbreite gewisser Merkmale wie der Grosse und Richtung der Neurapophysen, etc. bei rezenten Formen angestellt worden sein, so würde vielleicht die Literatur über fossile Cetaceen nicht mit dem unnützen Ballast zahlloser Speciesnamen beschwert worden sein, wie das leider tatsächlich der Fall ist."

PERRIN (1975) concluded that the knowledge of the range and nature of individual osteological variation in an inbreeding unit proved to be of prime importance before any taxonomic consideration could be made.

Forty-five years after ABEL (1931) had stated : "Allerdings liegen bis jetzt kaum irgendwelche brauchbare Studien über den Umfang der Variationsbreite bei rezenten Cetaceen vor.", PERRIN had to admit (1975) that with very few exceptions this necessary basic knowledge did not yet exist for delphinid species.
Although the osteological studies by SLIJPER (1936), discussing i.a. cetacean anatomical diversity, have to be regarded with much respect, the concept of intraspecific variability played only a minor role in his findings. YAMADA (1956) examined the skeletons of 124 of the 150 *Pseudorca crassidens* Owen, 1846 which stranded in Dornoch Firth, Scotland, in

October 1927. Although this author did not give any measurements nor statistic data, he claimed that considerable variation could be observed, especially in the "feeding apparatus" of the skull.
Since 1957 Japanese cetologists, e.g. OMURA, NISHIWAKI, TADAYOSHI, KASUYA and others have been publishing an important amount of original measurements of whale-vertebrae (review see VAN WAEREBEEK, 1982). However ,until now an integrated statistical analysis of these data is lacking.

KLEINENBERG (1956) provided morphological data, including osteological measurements of Tursiops, Delphinus and Phocoena specimens from the Black Sea. Unfortunately he gave no indication of the age nor state of maturity, so that the individual variation is difficult to appreciate, if at all.
CADENAT (1959; in PERRIN,1975) reported on several series of Delphinus delphis Linnaeus, 1758 caught on Africa's east coast and documented the noteworthy individual variation in skull characteristics.
The study by PERRIN (1975) was revolutionary in that the author recognized that in delphinids a considerable osteological variation within the species is the rule rather than the exception. He stated that before progress can be made in the revision of any delphinid group (species, superspecies, genus), thorough studies are to be made of the morphological variation as a result of ontogeny, sexual dimorphism and individual variability in that particular group. Dealing successfully with some of the numerous taxonomic problems in the genus Stenella, PERRIN showed that his analyzing methods based on large samples are the most effective. His work stands as an example for all further osteological research in cetaceans. It requires, however, an enormous amount of material, time, high-level computer facilities and financial means.

It is in many ways a pity that the value of most recent studies on interspecific diversity in cetacean vertebrae tends to be restricted because the authors payed either too little attention (CROVETTO, 1982) or none at all (COZZI, 1981) to the individual and growth-related, intraspecific variability.

2. OBJECTIVE OF THE STUDY

The present study aimed primarely to obtain an idea of the variation in the dimensions of the vertebrae of the common porpoise Phocoena phocoena (Linnaeus, 1758) and to determine the relative importance of the different types of this intraspecific variability.
Because an earlier univariate character-analysis (VAN WAEREBEEK, 1982)

of the five metrical parameters used (see 3.1.) and of several non-metrical backbone parameters in 31 specimens of Phocoena phocoena could not demonstrate any significant sexual dimorphism, I did not discriminate between sexes here.
In order to form an adequate idea of purely individual variation on one side and age-dependent variability on the other side, three different age categories (see 3.2.), based on osteological characteristics, were distinguished and are treated separately.

For all other information on osteological growth-data in the common porpoise, I refer to STUART & MOREJOHN (1980) and VAN WAEREBEEK (1982).

3. METHODS

3.1. Vertebral parameters

The metrical parameters used in this study are those introduced by ABEL (1931) and SLIJPER (1936), which are still used by most present investigators of cetacean osteology.
However, clear definitions of those variables are seldomly given. It is a pity that most authors who publish metrical data on whale vertebrae, neglect to define exactly what they have measured. Comparing such data with those of other authors can thus lead to dubious conclusions. To quote VON DEN DRIESCH (1976) : "... from the point of view of universal validity, to achieve comparable results, the use of the same measurements is of the greatest importance in original research. ".

The following definitions will clarify the variables of use in this study (fig. 1-3) and can be applied to all cetacean vertebrae.

L = length of corpus vertebrae : length in mm of the mediosagittal perpendicular, between the facies terminalis cranialis and the facies terminalis caudalis, at the ventral side of the vertebra. This line includes both vertebral epiphyses, irrespective whether these are fused with their corresponding diaphyses or not.

B = breadth of corpus vertebrae : length in mm of the greatest transverse diameter of the facies terminalis cranialis of the centrum vertebrae, measured perpendicularly on the mediosagittal plane.

H = height of corpus vertebrae : length in mm of the mediosagittal diameter of the vertebral facies terminalis cranialis.

GB = greatest breadth : length in mm between the two outermost tips (apices) of the processus transversi, measured perpendicularly on the mediosagittal plane of the vertebral body.

GH = greatest height : length in mm between the top of the processus spinosus (neurapophyse) and the outermost ventral crest of the vertebral body, measured parallel to the plane of the facies terminalis cranialis.

All measurements were made by means of Vernier-callipers. A precision of 0.05 mm or 0.10 mm proved technically possible and was used in most cases. However, partly because of the considerable individual variation , it afterwards seemed to me that an error-limit of 0.5 mm or even 1 mm is more appropriate for this kind of research (VAN WAEREBEEK,1982). As a rule two measurements, one after the other, were taken ; the mean of the resulting values was used.

3.2. Growth stages

As mentioned before, in order to avoid the picture of individual variability to be distorded by the important variability due to growth, three growth stages are distinguished here. These are defined by a certain degree of fusion of the vertebral epiphyses and can therefore easily been established, even on skeletons with missing teeth or skull. Although this age criterium is much less accurate than the commonly used "dentinal growth layer groups, or GLG" -method (see NIELSEN,1972 ; VAN BREE, 1973b ; GASKIN & BLAIR, 1977), it proved much more practical and possibly even more appropriate for this kind of research.

The definitions of the three main growth stages distinguished here are given below. Two others, i.e. "very juvenile" and "neonatus" (VAN WAEREBEEK, 1982) have not been included here.
Correlations with classical definitions are also given.

1) ADULT :

- growth stage concurring with full sexual and physical maturity.
- all vertebral epiphyses are completely fused with their corresponding diaphyses. The growth-discs have totally disappeared and the epiphyse-diaphyse sutures (lineae epiphyseae) have become invisible or at least very indistinct. Any further length growth has become impossible.
- this growth stage corresponds with SLIJPER 's definition (1936, p.63) : "...K.E.,Körperlich erwachsen. Alle epiphysen sind ankylosiert" ; also with FLOWER's (1864) : "Perfectly adult".

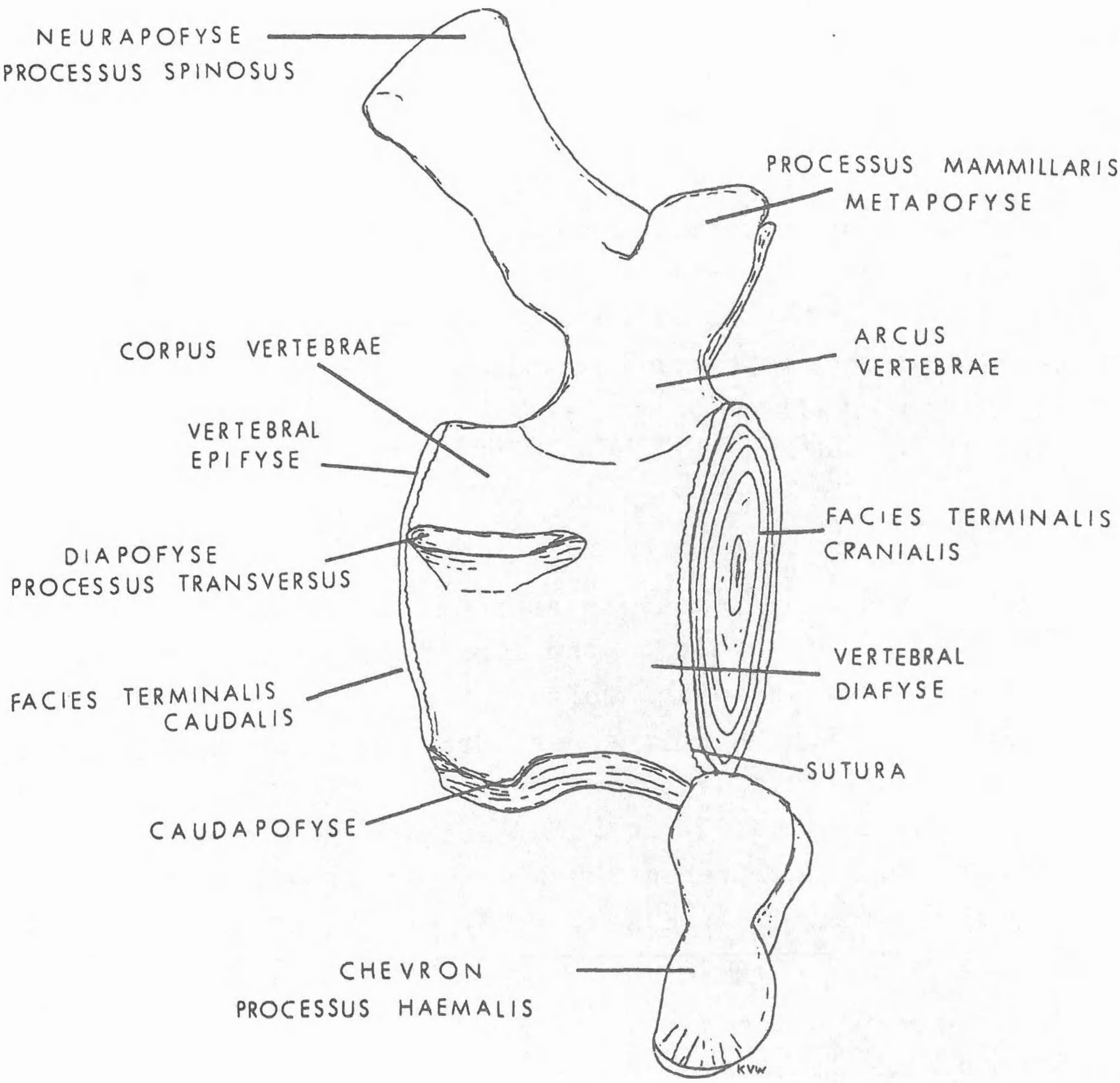

Fig.1. General morphology of cetacean vertebra, in right lateral view. Here typical " Y-vertebra ", i.e. caudal vertebra with corresponding preceding chevron bone. In Phocoena phocoena the processus mammillaris are relatively smaller and somewhat higher positioned.

2) SUBADULT :

- physically not yet full-grown ; mostly, perhaps always, sexually mature.
- at least part of the vertebral epiphyses but not all of them, are more or less fused with their corresponding vertebral diaphyses. Vertebral suture-lines are still visible in each regio of the vertebral column. Limited length growth is therefore still possible. Growth-discs of the caudals are the first ones to disappear, the anterior lumbar vertebrae and posterior thoracal vertebrae are the last to lose their growth ability.
- this growth stage corresponds with SLIJPER's definition (1936, p.63) : "... G.E., Geschlechtlich erwachsen.Epiphysen noch nicht ankylosiert" ; FLOWER (1864) speaks about "Adolescent".

3) JUVENILE :

- physically in full growth. May or may not be sexually mature.
- none of the vertebral epiphyses are fused with their corresponding diaphyses (except, sometimes the very last caudals). In preparing such skeletons for conservation, the epiphyses often detach from their vertebral centra.
- except for the growth-discs, intervertebral discs (disci intervertebrales) and articulation heads (with ribs), there is no cartilaginous substance : the ossification centra of the vertebrae are completely ossified, in contrast with the earlier mentioned "very juvenile" and "neonatus" growth stages.
- corresponds with SLIJPER's (1936, p.63) "J, Jung" and FLOWER's "Young".

3.3. Interpretation

When comparing and statistically treating measurements of homologous vertebrae, the backbone can be described in two different ways, either absolutely, using the absolute serial number (e.g. vertebra 47) of a particular vertebra, or relatively, if one considers the position of the given vertebra within the appropriate backbone region (e.g. caudal 6).

It has been shown (VAN WAEREBEEK, 1982) that, even intraspecifically, the exact vertebral homology is very difficult to demonstrate, except for the cervical region. The "absolute method" of counting therefore is preferred.

For each growth stage and each vertebral parameter (not for GH and GB in juveniles), statistical data are available, based on the corresponding sample of each vertebra.

The calculations were carried out by the IBM computer of the Centraal Rekeninstituut (CRI) at the State University of Leiden.
Three successive APL programmes were used, i.e. SAMSTAT, MALLVAR and DICE (ZANDEE, 1975, 1976, 1977).
The SAMSTAT or sample statistics programme calculated 18 distribution parameters of each series sample, a.o. mean, standard deviation, variance, coefficient of variation, standard error of means, chi-square cumulant, Fisher test on total normality, etc.
The MALLVAR programme directed the printing and arrangement of these parameters in a series of character arrays. For reasons of economy I do not reproduce these matrices here.

Finally the DICE programme produced dicegrams (fig. 4-16) for each age category as graphic illustrations of the mean values of each of the five vertebral parameters as a function of the absolute vertebral number.
Because of the absence of measurements for all but one (the atlas) cervical vertebrae, i.e. V2 - V7, the abscissa does not in fact indicate the absolute serial number (atlas excepted), but this number minus six. For instance, co-ordinate point 60 on the dicegram corresponds with the last caudal V66 ; co-ordinate point 2 with the first thoracal vertebra V8.
The normality tests proved positive for all samples taken and for each growth stage, with the exception of some posterior caudals on which no statement could be made because they were missing in several specimens.
The dipersion measure of use in the dicegrams is the standard error of means, i.e. the standard deviation of the sampling distribution of means (SPIEGEL, 1972). The length of the dotted line above and below each plotsymbol is the mean plus or minus two times the standard error. This creates a 95.45 % probability range in which the measuring mean of each other sample of Phocoena phocoena, collected in the same area, is expected to fall.

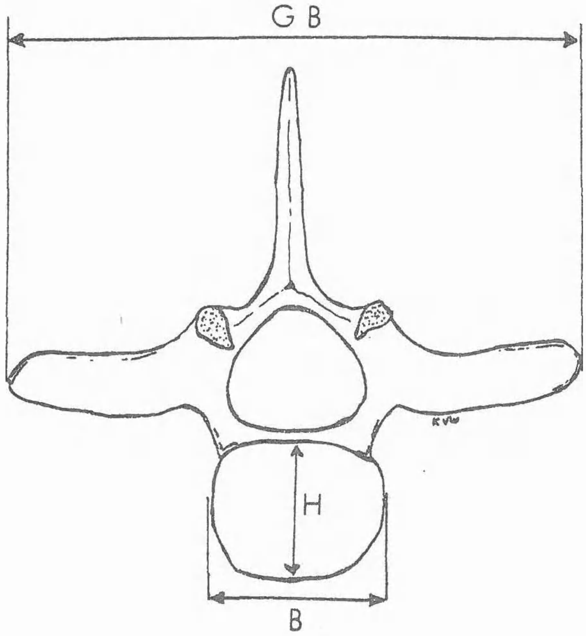

Fig.2. Frontal view of general cetacean thoracic vertebra. Although applicable to Phocoena phocoena, it is not typical for it. Vertebral parameters : GB = greatest breadth ; B = breadth of corpus vertebra ; H = height of corpus vertebra.

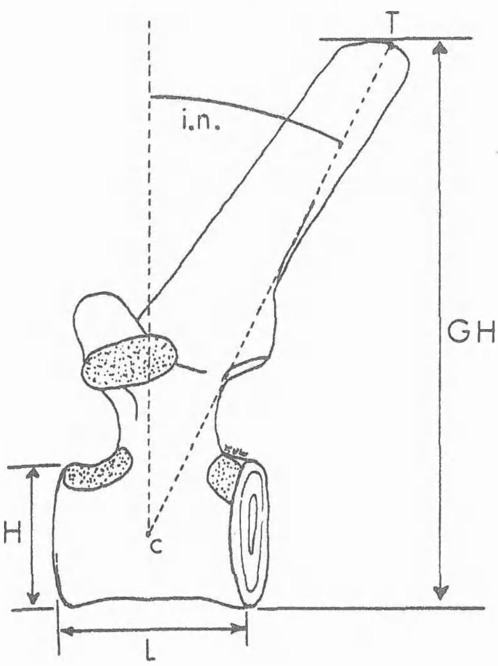

Fig.3. Left lateral view of general cetacean thoracic vertebra. Applicable to but not typical for Phocoena phocoena. Vertebral parameters : GH = greatest height ; L = length of corpus vertebrae; H = height ; c = centrum ; T = middle of top ; i.n. = inclination of neurapophyse.

4. MATERIAL

Phocoena phocoena is the most common cetacean of the North Sea and is therefore rather abundant in the collections of western European natural history musea. My need of several complete and undamaged skeletons of the common porpoise and some other delphinids made me visit four scientific institutions in Belgium and the Netherlands.
The following abbreviations are used in the text.

- KBIN : Koninklijk Belgisch Instituut voor Natuurwetenschappen, i.e. Brussels Natural History Museum.
- RUG : Zoological Museum, Rijksuniversiteit Gent.
- RMNH : Rijksmuseum van Natuurlijke Historie, i.e. Leiden Natural History Museum.
- ZMA : Zoölogisch Museum Amsterdam, i.e. Institute for Taxonomic Zoology, University of Amsterdam.

The 21 specimens of Phocoena phocoena discussed in the present paper have been randomly collected at different localities and at different times. However, all of them originate from the North Sea or N.E. Atlantic which can be regarded as a single stock consisting of an unknown number of natural populations.
Each of the three age categories distinguished has material of both sexes ; one specimen is of undetermined sex.
For each skeleton only the following,most essential, data are given besides the registration number : museum, sex, origin and collecting date. More information on the specimens studied, and tables with the original vertebral measurements have been given in author's thesis (VAN WAEREBEEK, 1982).

ADULTS (sample size = 6)

Reg.1530 : KBIN ; male ; in river Nete ; Lier (Belgium) ; 28-08-1931
Reg.1529 : KBIN ; female ; Brittany (France) ; date unknown
Reg.1529 : KBIN ; female ; near Antwerp, Westerschelde ; 1868
14517 : ZMA ; male ; Schiermonnikoog, Wadden Sea ; 10-07-1971
4794 : ZMA ; female ; south of Doggersbank ; 19-06-1961
RN 2606 : RUG ; sex unknown ; origin and date unknown (probably Belgian coast)

SUBADULTS (sample size = 8)

Reg.1529 : KBIN ; female ; between Mariakerke and Oostende (Belgium) ; 30-07-1933

Reg.16233 : KBIN ; female ; origin and date unknown (Belgian coast ?)
Reg.16983 : KBIN ; female ; Blankenberge (Belgium) ; 7-12-1970
Reg.1528 : KBIN ; sex unknown ; near Nieuwpoort (Belgium) ; 4-08-1875
Reg.1529 : KBIN ; male ; near Antwerp, Westerschelde ; 2-09-1869
2644 : ZMA ; female ; Doggersbank ; 19-02-1959
7623 : ZMA ; male ; 10 miles N.E. of buoy B1, North Sea ; date unknown

JUVENILES (sample size = 8)

Reg.1528 : KBIN ; female ; near Antwerp, Westerschelde ; 22-07-1867
Reg.16982 : KBIN ; female ; Raversijde-Oostende (Belgium) ; 10-11-1970
Reg.1528 : KBIN ; male ; river Elbe (West-Germany) ; date unknown
Reg.17691 : KBIN ; male ; Middelkerke (Belgium) ; 19-03-1973
Unregistered : KBIN ; female ; Blankenberge (Belgium) ; 13-11-1981
21647 : RMNH ; female ; Katwijk-Noordwijk (the Netherlands) ; 1970
13836 : ZMA ; male ; Den Helder (the Netherlands) ; 13-11-1970
OD.2 : author's collection ; sex unknown ; 3 km north of Brora (Scotland) ; 25-07-1981

5. RESULTS AND DISCUSSION

Although we find a relatively stable overall shape for the curves of each vertebral parameter (fig.4 - 16), scrutinizing smaller sections of the curves of different growth stages reveals some obvious differences. For instance, the absolute serial positions where each parameter reaches its maximum value are subject to certain, however small, changes related to the growth stage (see table 1). These shifts probably are due to allometric growth along the backbone.
Indeed, OMURA (1971) stated earlier, when treating osteology in baleen whales that "... it is desirable to use fully grown or physically mature specimens, because it is well established that the proportions of the whale body are changeable during the course of growth in almost all species."
Because of the natural continuity in all growth-processes and an important individual variability most probability-ranges of each growth stage overlap with those of their neighbouring stage(s).
Overlap between adults and subadults appears more extensive than between subadults and juveniles. This last phenomenon can be explained by the explosive growth in juvenile animals and a much slower growth-rate in subadults, as described by STUART & MOREJOHN (1980).

	ADULTS	SUBADULTS	JUVENILES
GH	24	25	no dicegram
GB	22	22	no dicegram
L	19	16	14 - 15
B	35	36	38
H	46	46	42

Table 1. Absolute vertebral positions (i.e. abscissa number +6 , see fig.4 - 16) of mean peak values of respective parameters.
Note the shifts in position due to allometric growth.

Obviously, in absolute terms, variability is unequal along the backbone (except for parameter "centrum breadth"). It is high in some parts, e.g. in the anterior vertebrae for parameters"greatest height"(fig. 4 - 5) and "centrum length" (fig. 8 - 10) and low in other parts, e.g. in the posterior vertebrae for the same parameters. This pattern however appears to be rather independent from the age category.
The peak in absolute variability always occurs in the anterior half of the backbone ("centrum breadth" shows no peak).
Relatively spoken, because this is also the region with by far the largest vertebrae, there is a strong compensating effect that at the same time attenuates the differences in variability and creates an inverse situation. Indeed the first half of the backbone, up to vertebra 30 - 35, shows the lowest relative variation. It therefore will be the most useful part in comparative studies with other species' backbones. The caudal vertebrae with their higher individual variation would be less apt to that purpose.
It has indeed been demonstrated (VAN WAEREBEEK, 1982) that comparative morphology of delphinid backbones can be useful in establishing taxonomic and thus evolutive relationships between different species.
One prerequisite for developing this new technique in cetacean taxonomy is that large amounts of vertebral metrical data of many odontocetes would become available.

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SUMMARY

Morphological variability is examined in the vertebrae of 21 specimens of the common porpoise Phocoena phocoena (Linnaeus, 1758) from the North Sea and N.E.Atlantic waters.
To avoid interference growth-dependent variability with individual variability, three osteologically defined growth stages, namely adults, subadults and juveniles have been treated separately.
Five size-parameters, i.e. greatest height (GH), greatest breadth (GB), centrum height (H), centrum breadth (B) and centrum length (L) were measured on each vertebra. A statistical analysis produced dicegrams with means and 95 % probability ranges for each parameter and each growth stage.

RESUMEN

Se examina la variabilidad morfológica en las vértebras de 21 ejemplares del delfín común Phocoena phocoena (Linnaeus, 1758) de las aguas del Mar del Norte y del Atlantico Noreste. Han sido tratados separadamente tres estados de crecimiento, osteologicamente definidos : adultos, subadultos y juveniles ; con la finalidad de eliminar interferencias de variabilidades dependientes del crecimiento con variabilidades individuales. En cada vértebra fuerou tomadas 5 mechidas : altura total (GH), ancho total (GB), altura central (H), ancho central (B) y longitud central (L). En anális esta distigo produjo diagramas con medias y rangos con 95 % de probabilidad para cada parametro y para cada estado de crecimiento.

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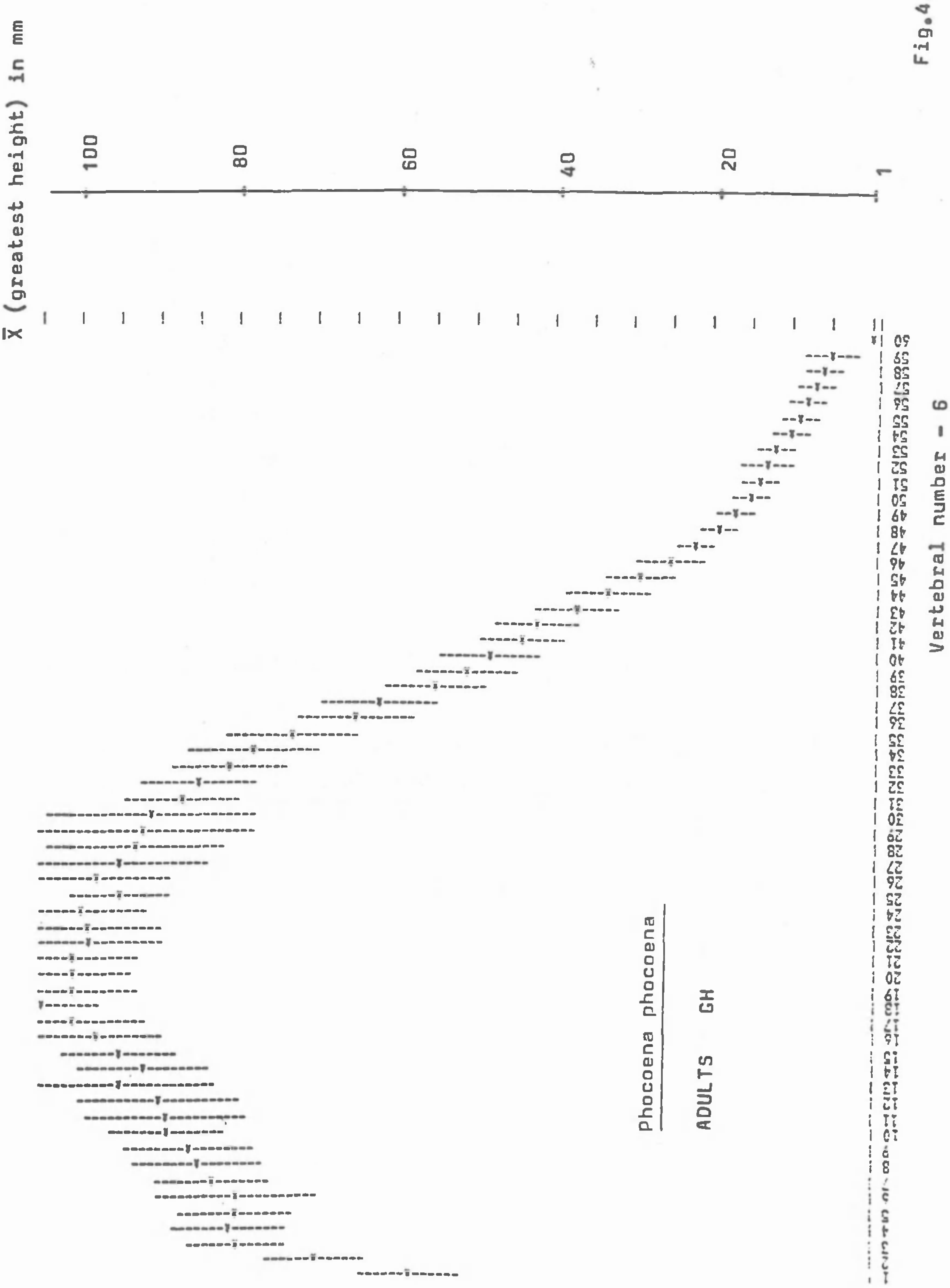
X̄ (greatest height) in mm
100
80
60
40
20
1
Phocoena phocoena
ADULTS GH
Vertebral number - 6

Fig.4.

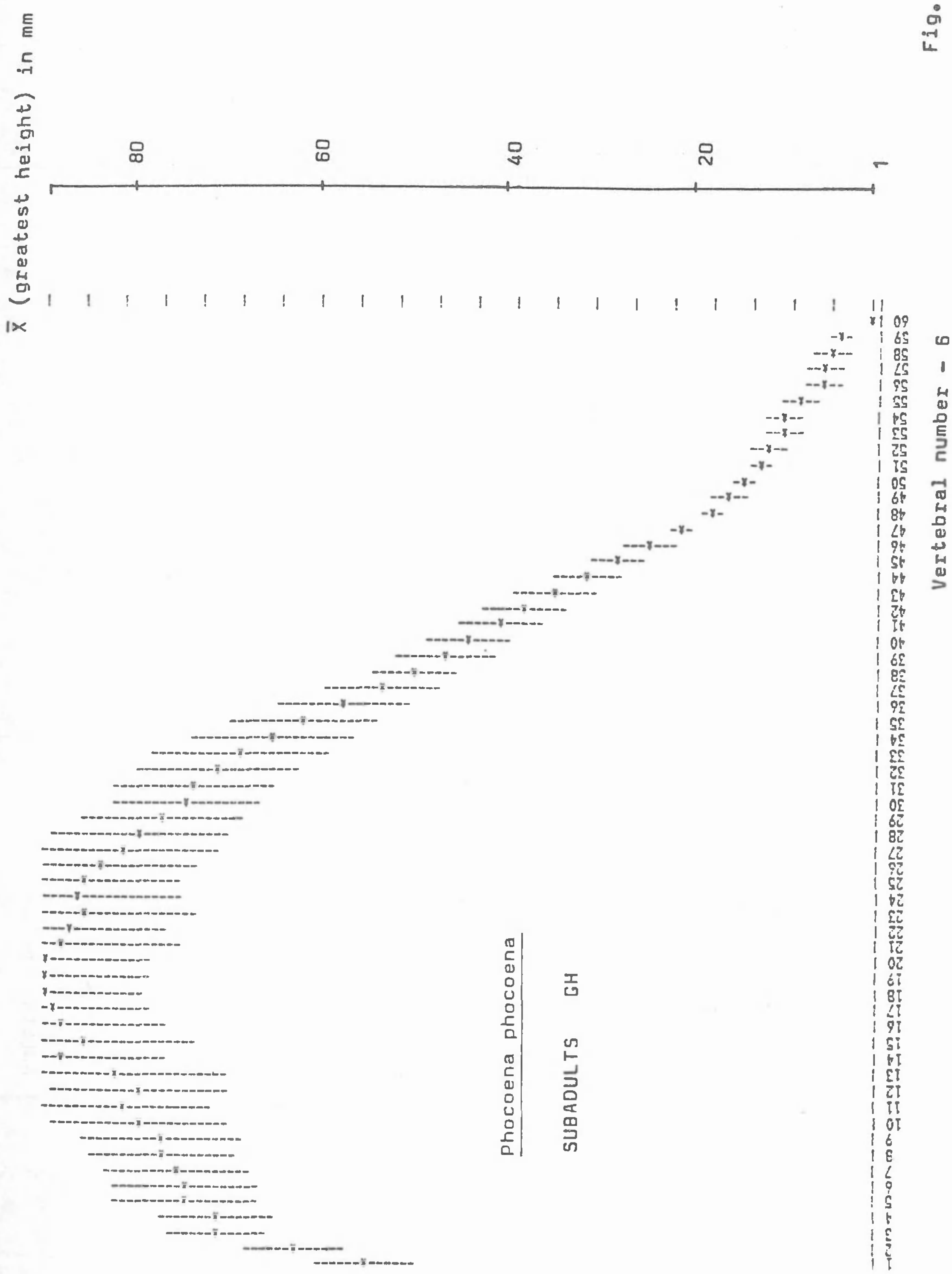
X̄ (greatest height) in mm
80
60
40
20
1
Phocoena phocoena
SUBADULTS GH
Vertebral number - 6
1 2 3 4 5-6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60

Fig.5.

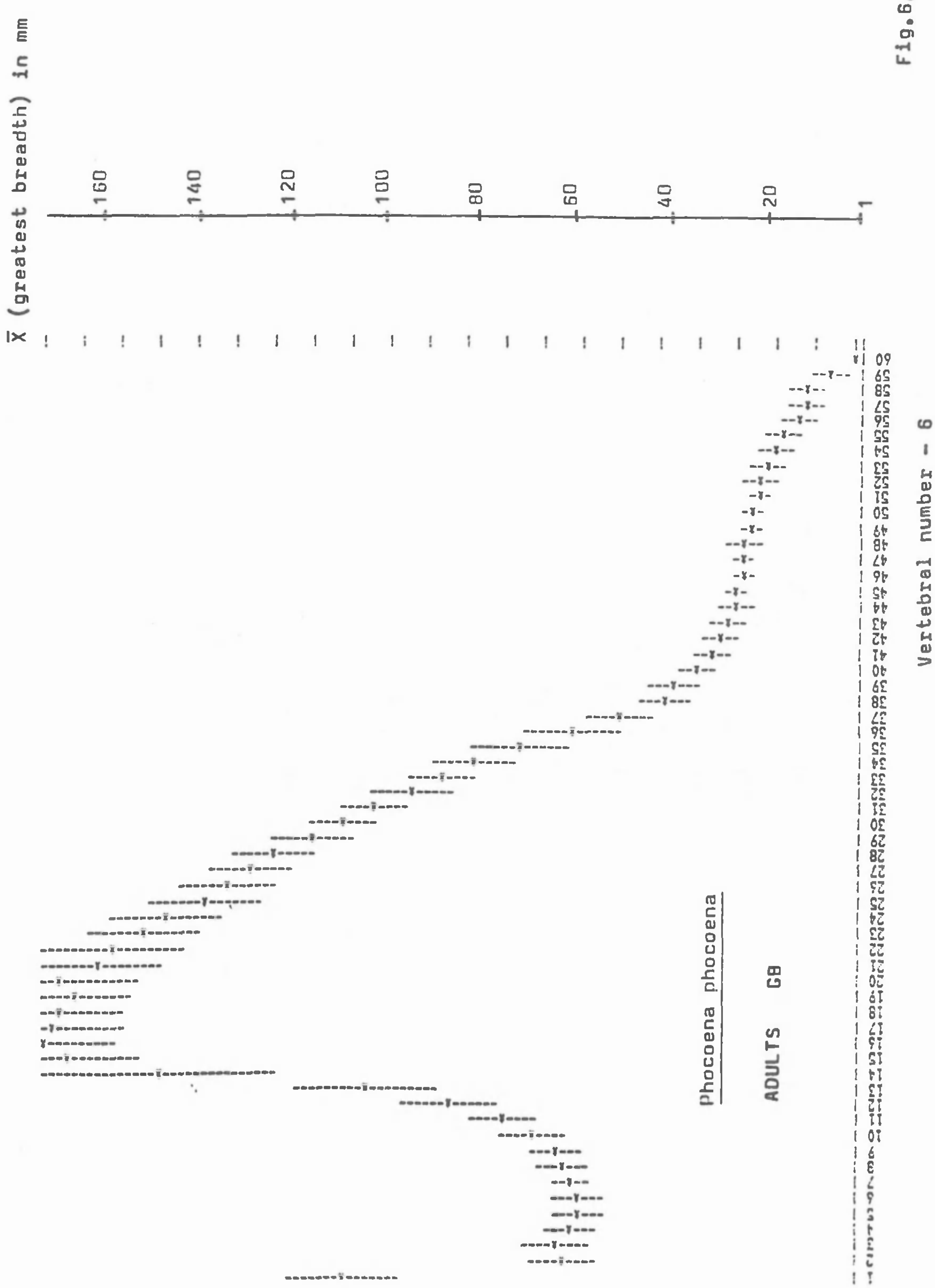
X̄ (greatest breadth) in mm
160
140
120
100
80
60
40
20
1
Phocoena phocoena
ADULTS GB
Vertebral number - 6

Fig.6.

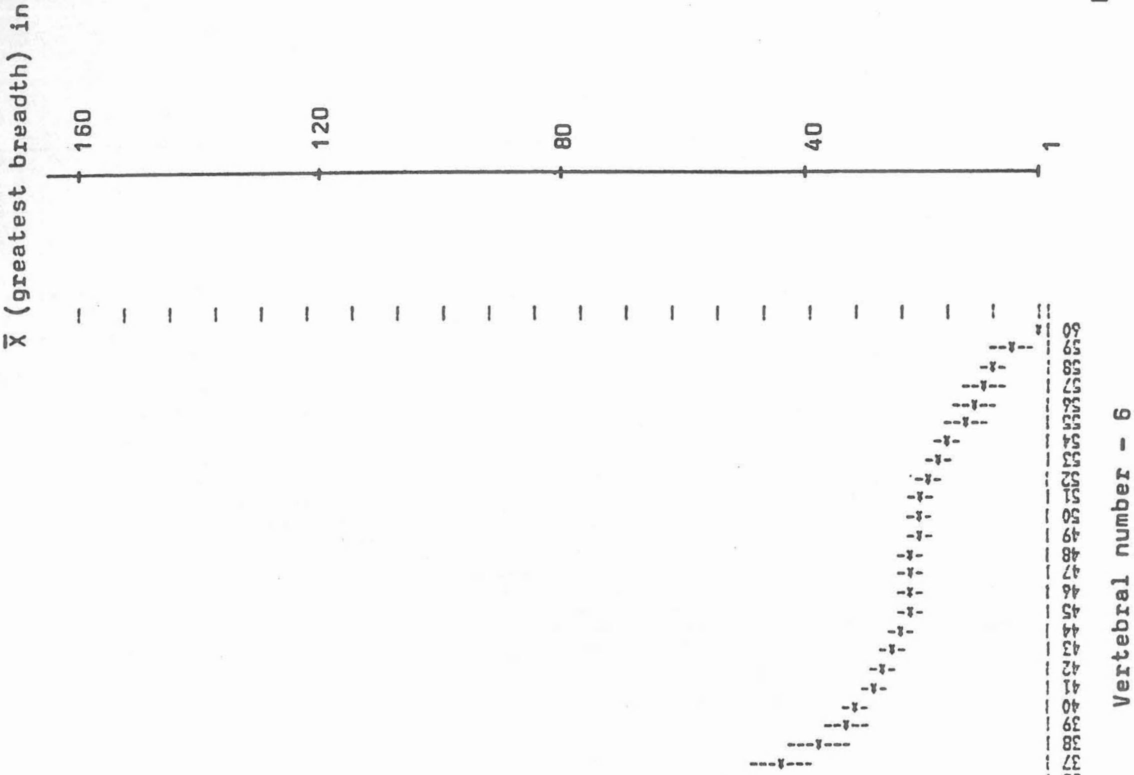
X̄ (greatest breadth) in mm
160
120
80
40
1
Phocoena phocoena
SUBADULTS GB
Vertebral number - 6

Fig.7.

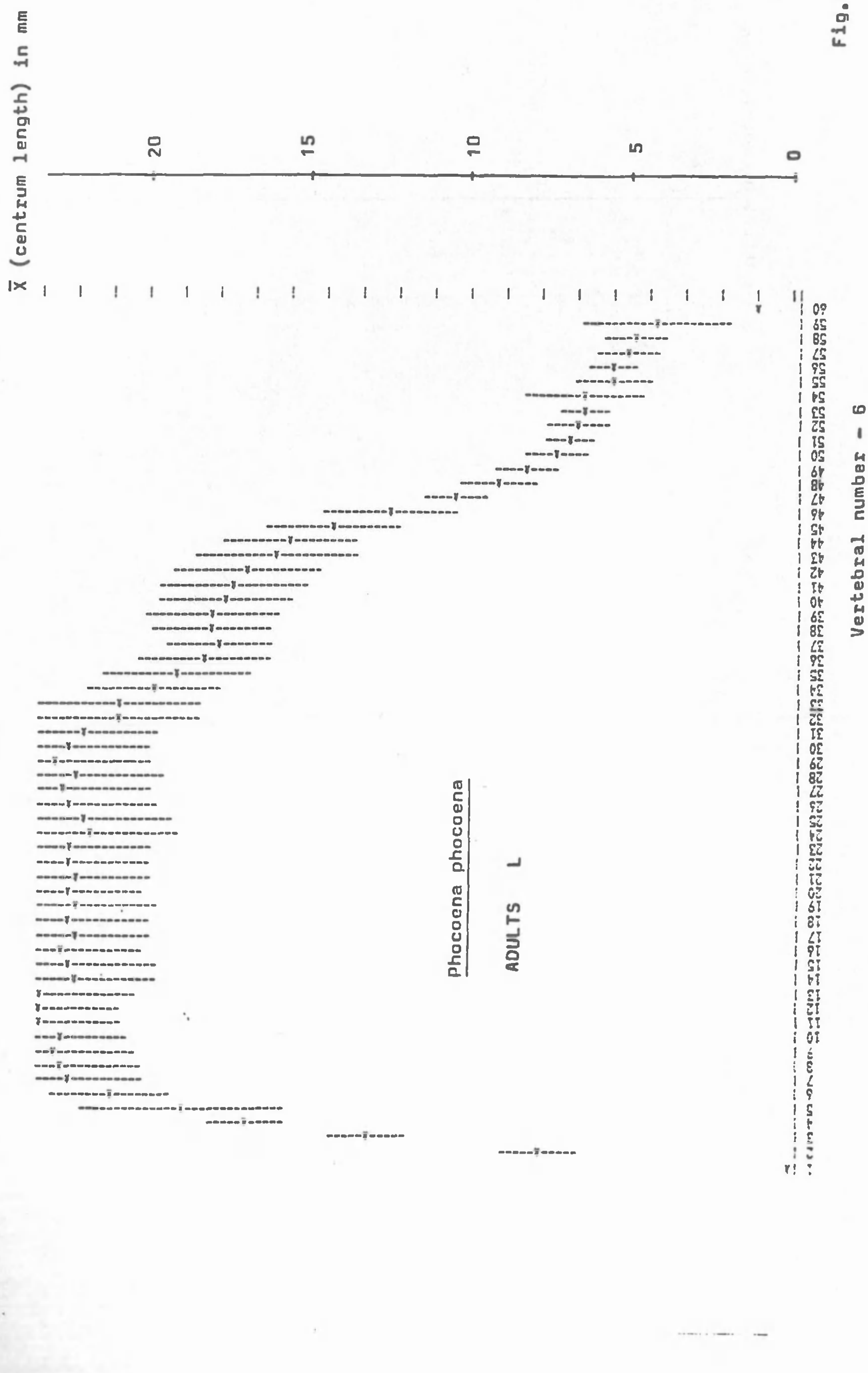
X̄ (centrum length) in mm
20
15
10
5
0
Phocoena phocoena
ADULTS L
Vertebral number - 6

Fig.8.

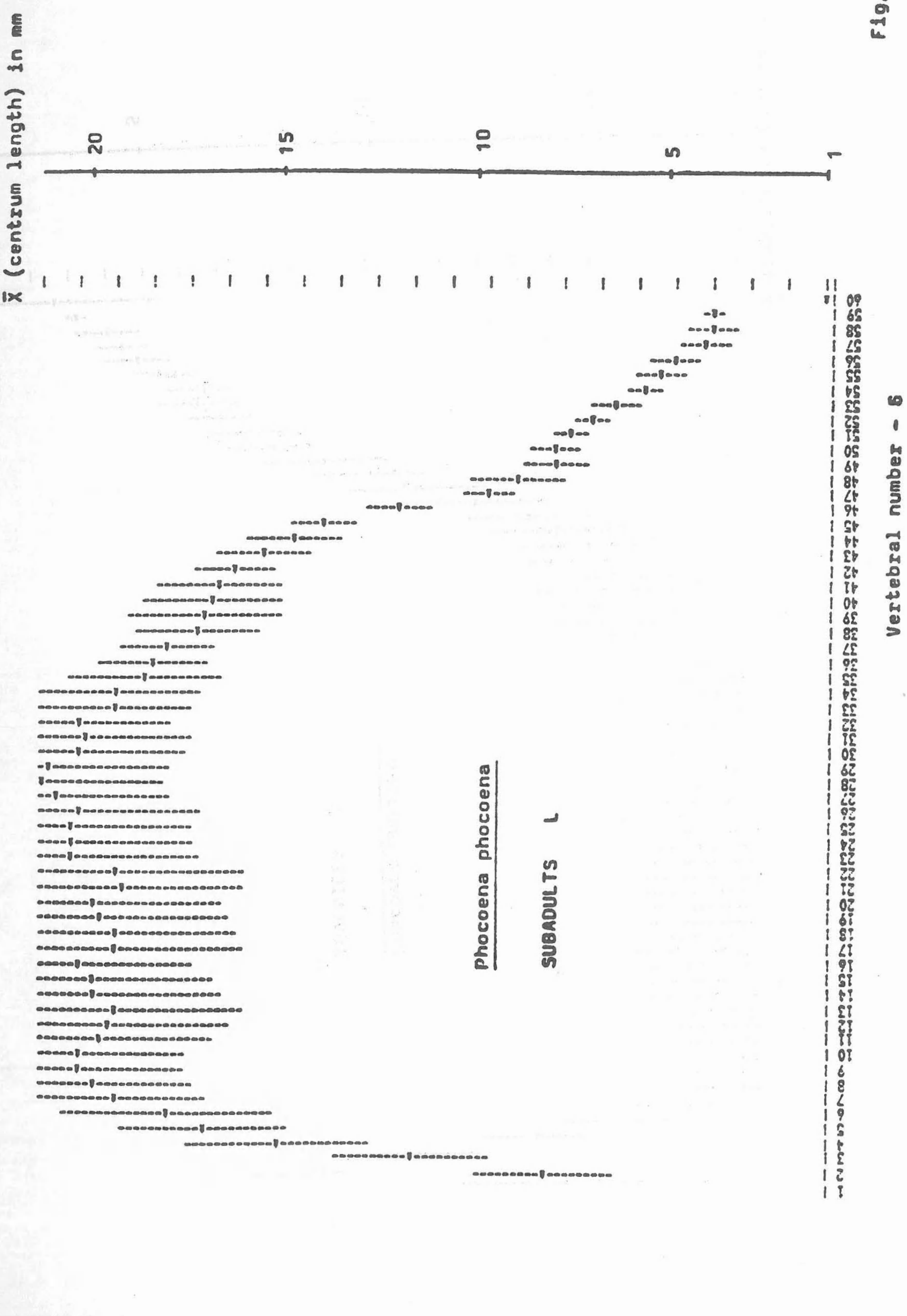
X̄ (centrum length) in mm
20
15
10
5
1
Phocoena phocoena
SUBADULTS L
Vertebral number - 6

Fig.9.

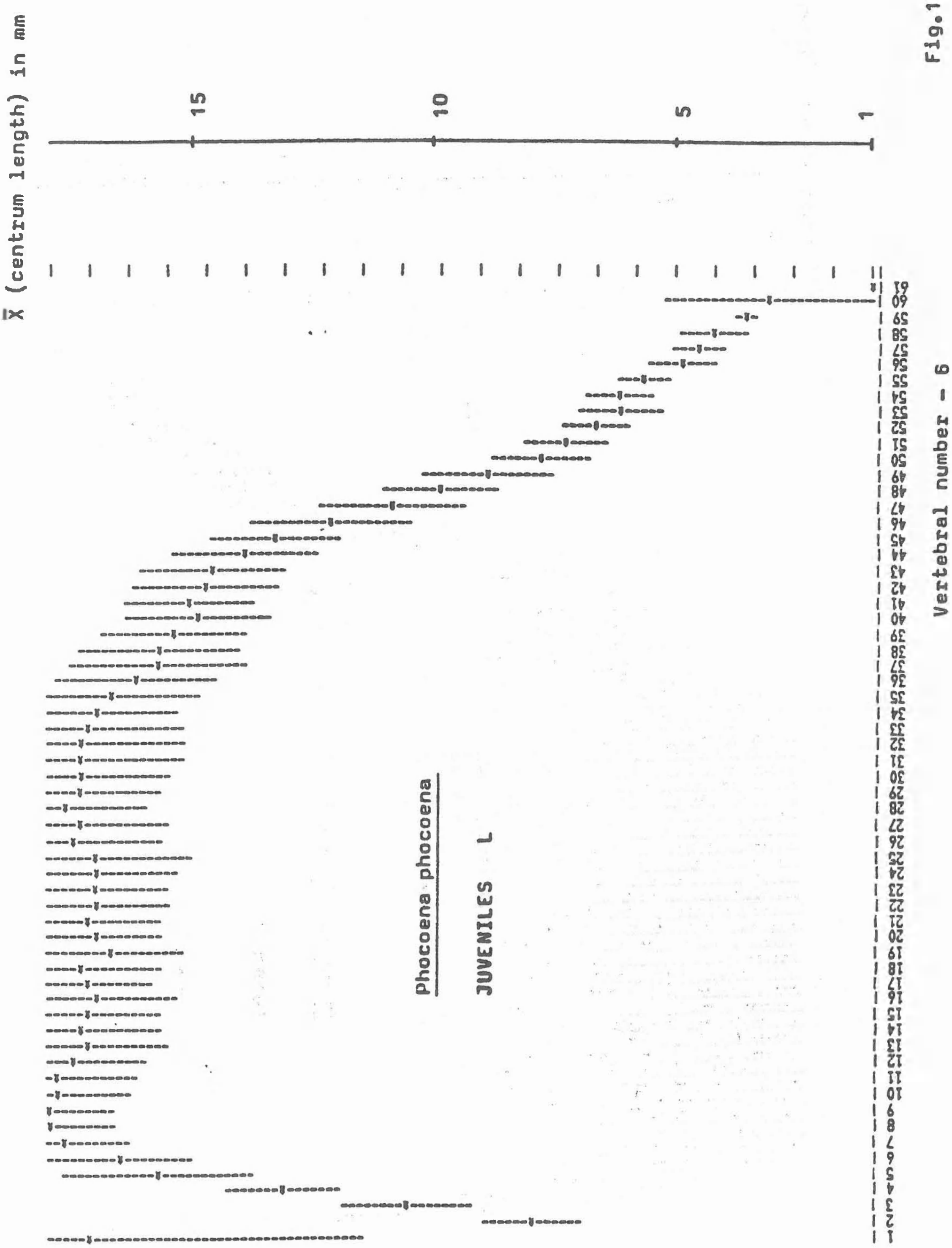
X̄ (centrum length) in mm
15
10
5
1
Phocoena phocoena
JUVENILES L
Vertebral number - 6

Fig.10.

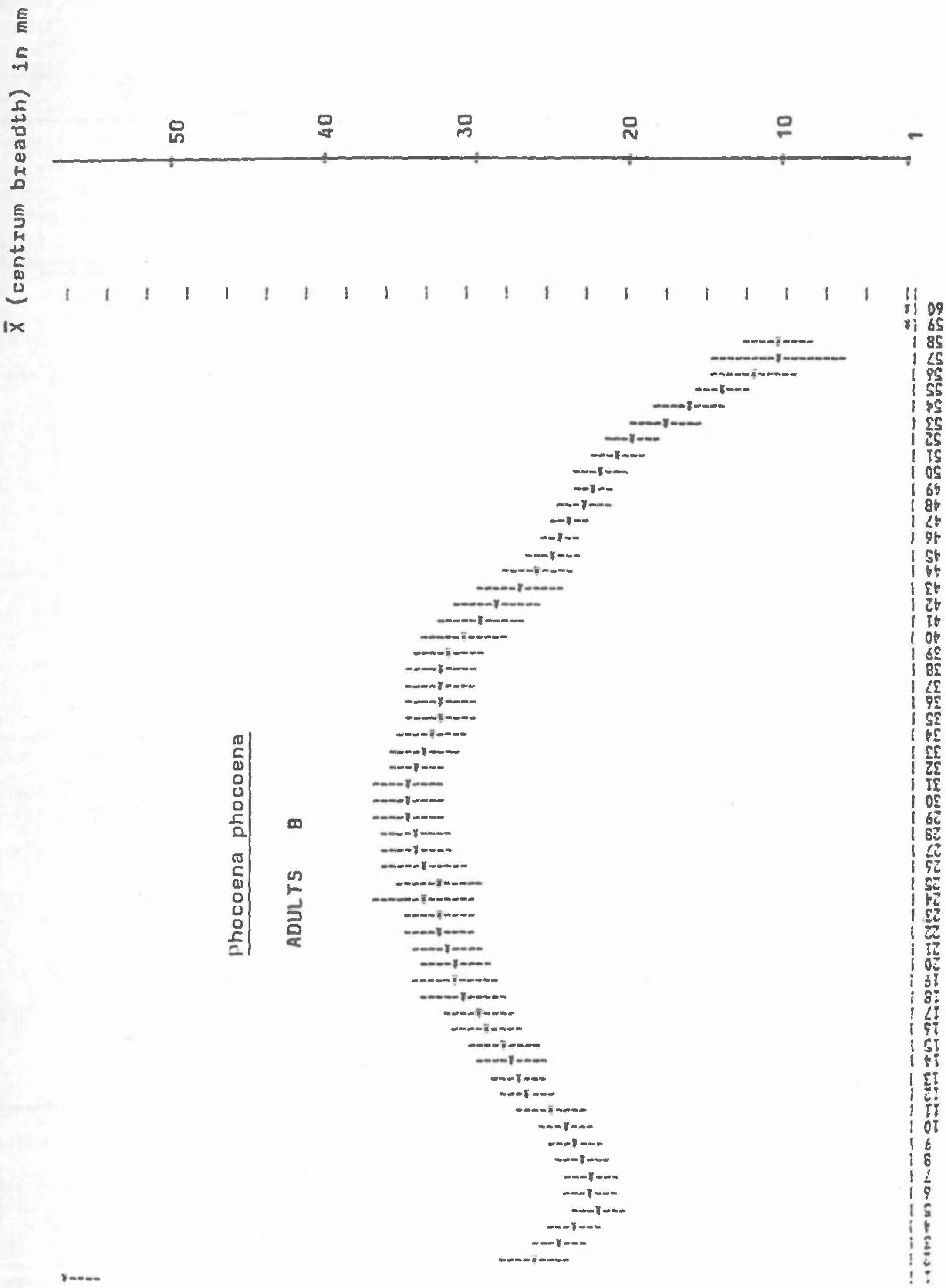
X̄ (centrum breadth) in mm
50
40
30
20
10
1
Phocoena phocoena
ADULTS B
Vertebral number - 6

Fig.11.

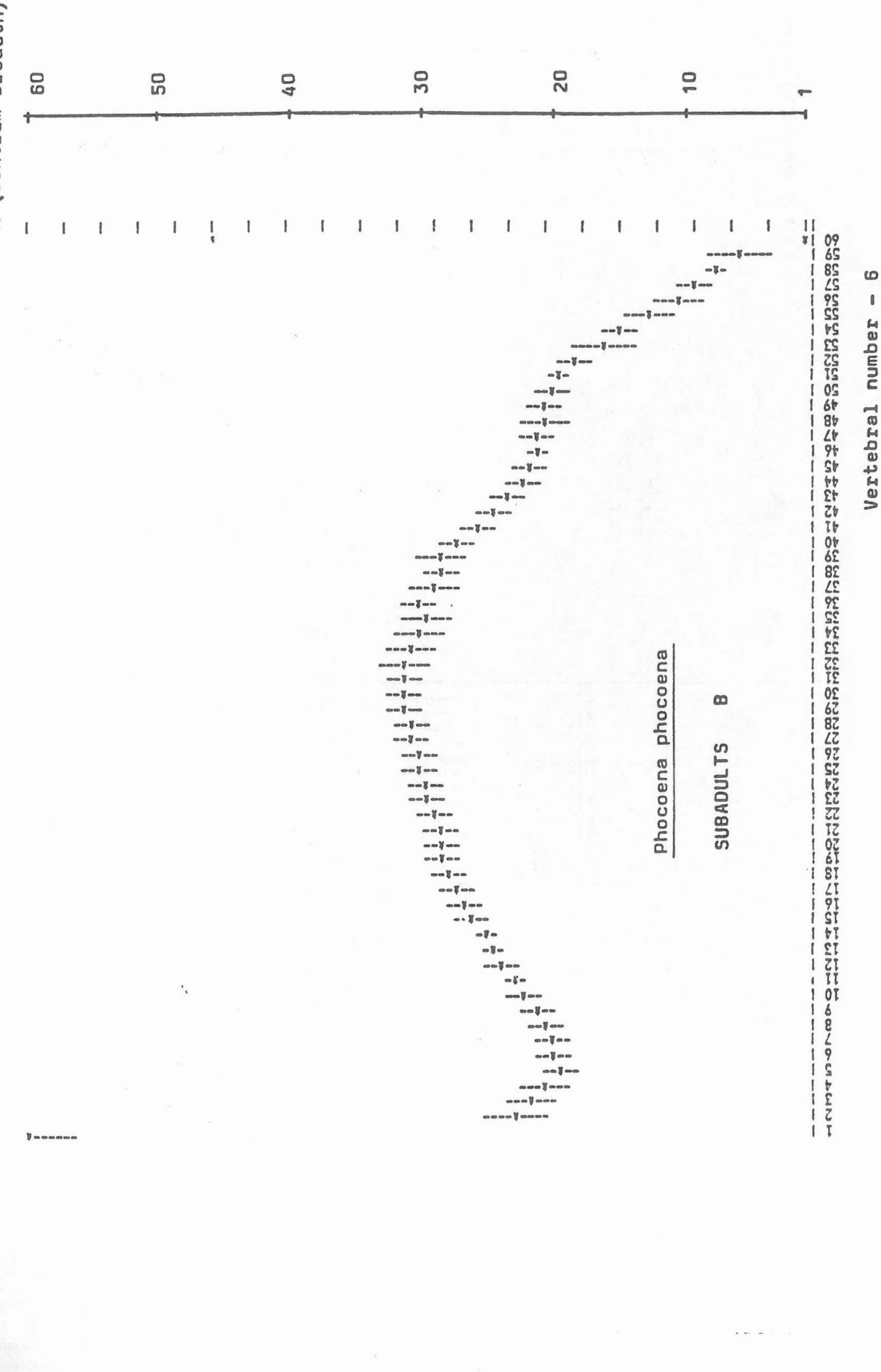
X̄ (centrum breadth) in mm
60
50
40
30
20
10
1
Phocoena phocoena
SUBADULTS B
Vertebral number - 6

Fig.12.

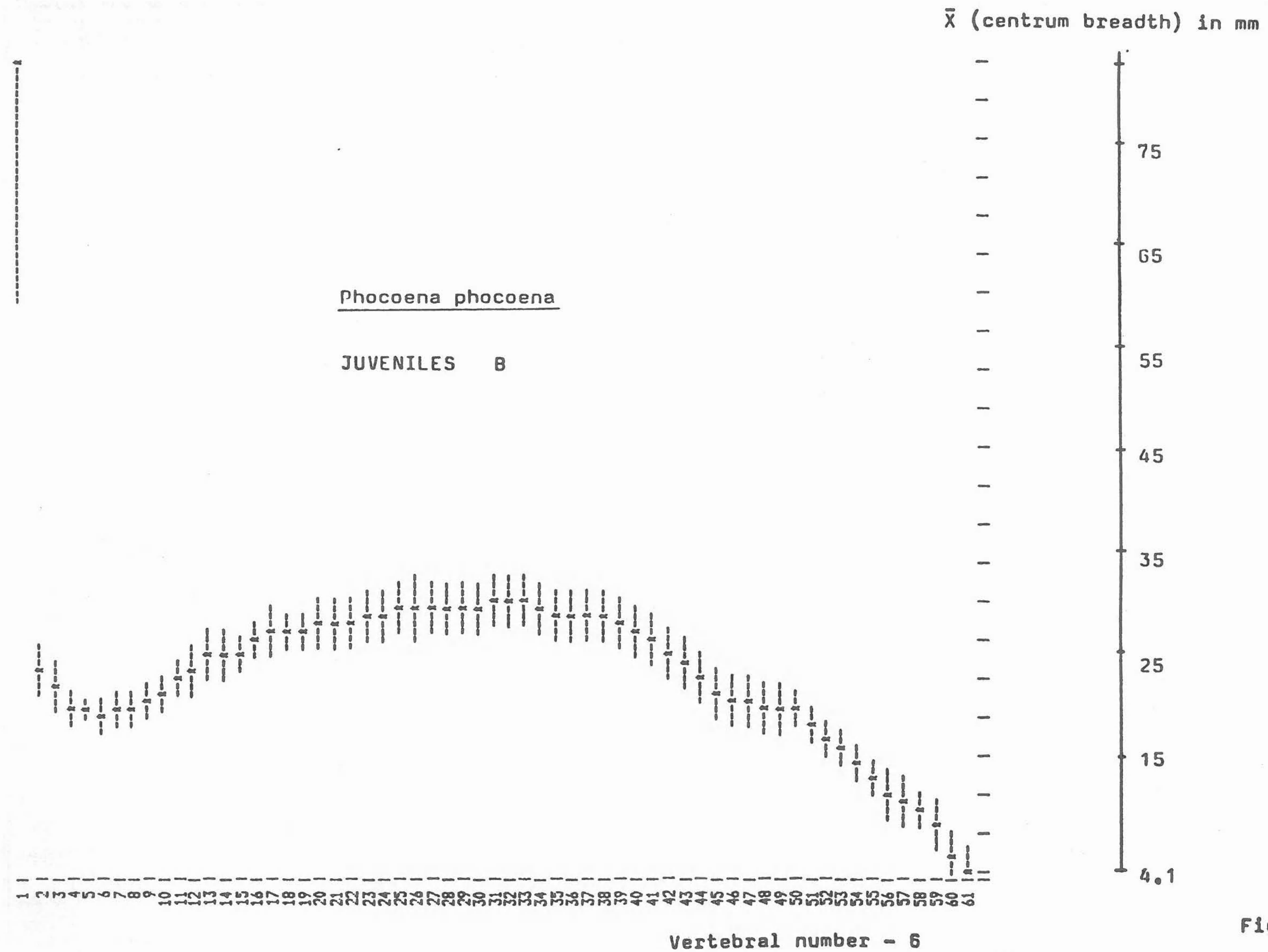
X̄ (centrum breadth) in mm
75
65
55
45
35
25
15
4.1
Phocoena phocoena
JUVENILES B
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61
Vertebral number - 6

Fig.13.

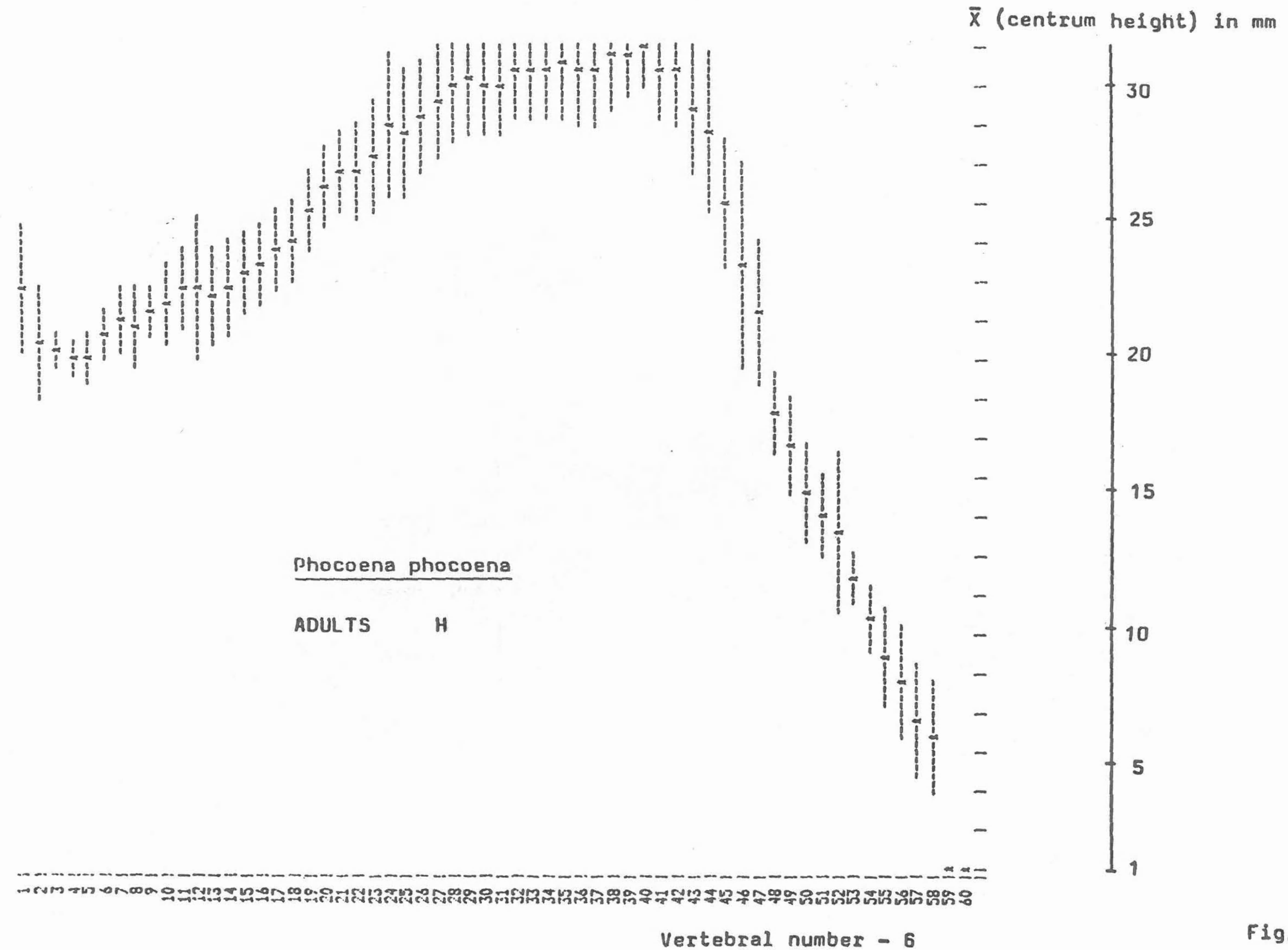
X̄ (centrum height) in mm
30
25
20
15
10
5
1
Phocoena phocoena
ADULTS H
Vertebral number - 6

Fig.14.

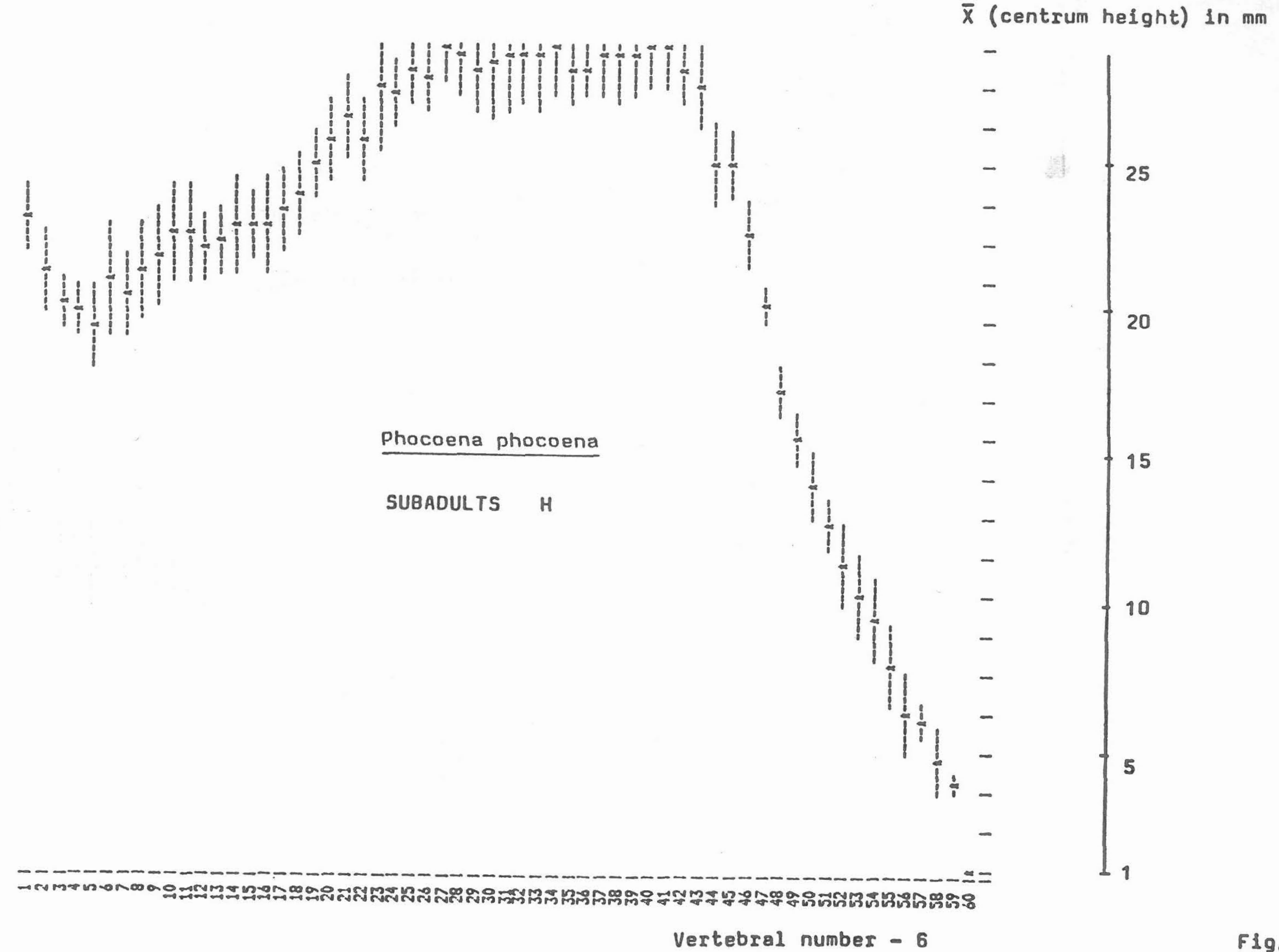
X̄ (centrum height) in mm
25
20
15
10
5
1
Phocoena phocoena
SUBADULTS H
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60
Vertebral number - 6

Fig.15.

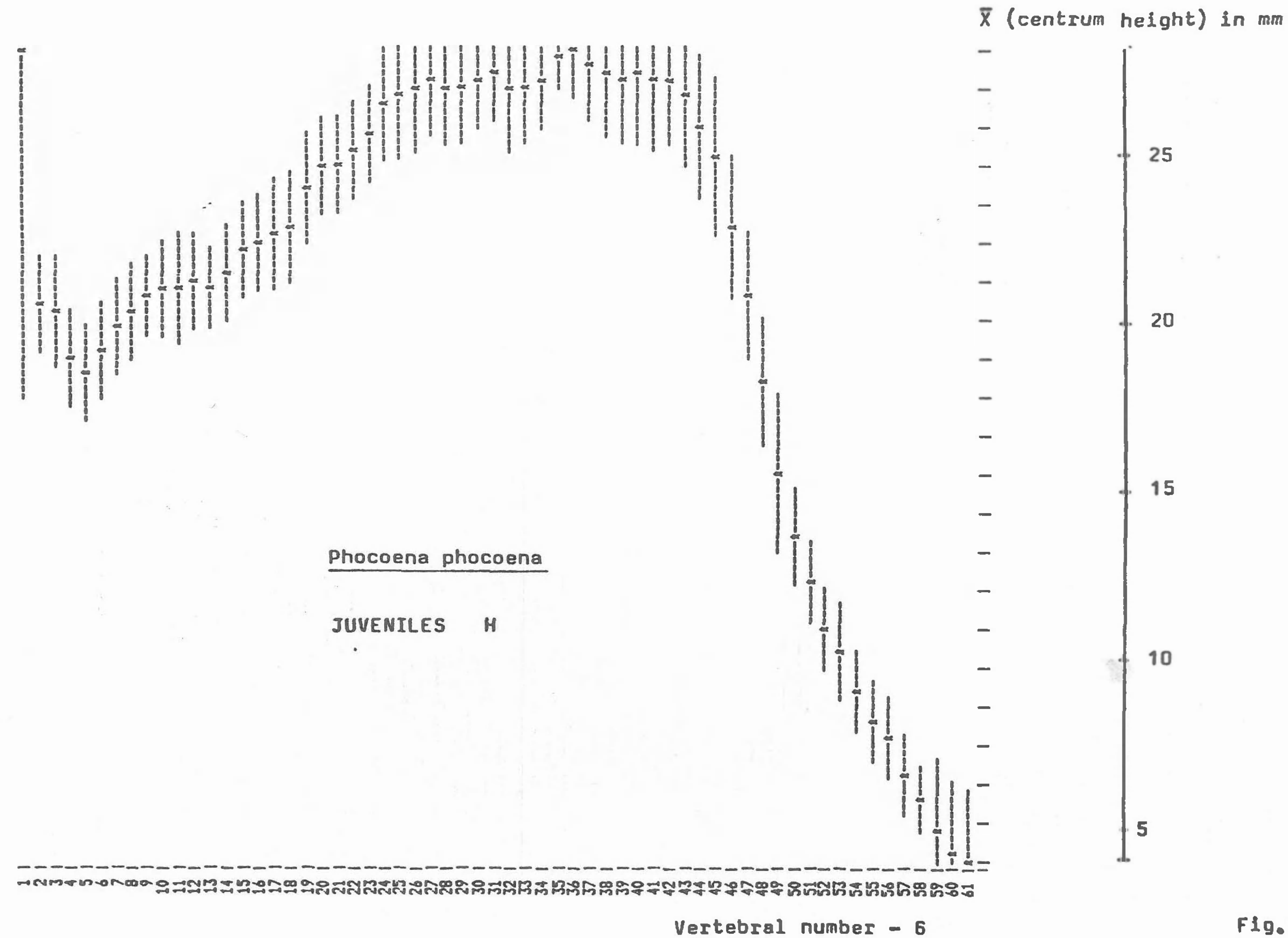
X̄ (centrum height) in mm
25
20
15
10
5
Phocoena phocoena
JUVENILES H
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61
Vertebral number - 6

Fig.16.