

Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part two, skull

C. L. Stewardson, T. Prvan and M. A. Mejer

© Journal of Anatomy (Cambridge)

Manuscript submitted 2001.

ABSTRACT

Morphology, relative size and growth of the skull in 83 Cape fur seals, *Arctocephalus pusillus pusillus*, from the coast of southern Africa are described. Skull measurements ($n = 32$ variables) were examined in relation to standard body length (SBL), condylobasal length (CBL) and chronological age (y) using linear regression. Animals ranged from 10 mo to ≥ 12 y. Twenty four animals were of known-age, while 39 were aged from counts of incremental lines observed in the dentine of tooth sections. Morphological observations were generally consistent with earlier studies by Rand (1949b, 1950, 1956) and Repenning *et al.*, (1971). Condylobasal length was highly, positively correlated with SBL and age. Overall, skull variables grew at a slower rate than SBL, apart from height of mandible at meatus and angularis to coronoideus, which expressed isometry relative to SBL. Condylobasal length continued to increase until at least 12 y, with no obvious growth spurt between 8–10 y, when social maturity (full reproductive capacity) is attained. Mean CBL was 19.4% of SBL in yearlings; 15.5% in subadults, and 13.7% in adults. Apart from the dentition, all variables of the facial skeleton followed a somatic growth trajectory. Most of these variables expressed positive allometry relative to CBL, with greatest growth occurring in the vertical part of the mandible. Mastoid breadth, and gnathion to middle of occipital crest, expressed a strong secondary growth spurt at 10 y. Breadth of brain case, and basion to bend of pterygoid, followed a neural growth trajectory, scaling with negative slope relative to CBL. Sutures of the brain case (i.e., basioccipito-basisphenoid, occipito-parietal, interparietal and coronal) closed before those of the facial skeleton. Condylobasal length was found to be a 'rough indicator' of SBL and age group (adult, subadult), but not of absolute age. Suture age was not considered to be a good indicator of absolute age or age group.

Key words: Pinnipeds, skull morphology, skull growth, allometry

INTRODUCTION

Earlier cranial growth studies in pinnipeds were based on unreliable age determination techniques, including: (i) the extent of closure of cranial sutures; (ii) body length, colour of vibrissae, pelage and general appearance; (iii) ovarian structure; and (iv) baculum development (e.g., Hamilton, 1934, 1939; Lindsey, 1937, 1938; Bertram, 1940; Douth, 1942; Rand, 1949*a, b*, 1950, 1956; Sivertsen, 1954; Burns & Fay, 1970). Therefore, observed growth patterns could not be quantified with any real meaning (King, 1972). It was not until the 1950s that a reasonably precise method of age determination was established, i.e., age inferred from incremental lines on or in teeth (Scheffer, 1950; Laws, 1953; McCann, 1993).

Within the Otariidae, information on cranial and mandibular growth based on animals aged from tooth structure, or on animals of known-age (i.e., animals tagged or branded as pups), is only available for a small number of species including *Callorhinus ursinus*, northern fur seal (Scheffer & Wilke, 1953); *Zalophus californianus*, California sea lion (Orr *et al.*, 1970); and *Eumetopias jubatus*, northern (Steller) sea lion (Fiscus, 1961), and very few skull variables have been examined. Currently, there is no detailed information on cranial growth according to age (y) in southern fur seals.

In the mammalian skull, there are two growth models, neural and somatic, each with two types of growth, monophasic and biphasic (Todd & Schweiter, 1933; Scott, 1951; Moore, 1981; Sirianni & Swindler, 1985). In neural growth, skull components associated with the nervous system (i.e., braincase, orbital and otic capsules) grow rapidly during prenatal and early postnatal life, completing most of their growth well before the rest of the body (Moore, 1981). In somatic growth, all other skull components (i.e., facial skeleton) follow a more protracted growth course (Moore, 1981). After the initial growth spurt experienced during early development, growth may be reasonably constant (monophasic growth), or there may be a secondary growth spurt in older animals (biphasic growth).

Here we examine the skulls of 83 male Cape fur seals, *Arctocephalus pusillus pusillus*, from southern Africa. Specific objectives were to: (i) describe the general morphology of the skull; (ii) quantify growth of skull measurements ($n = 32$ variables) relative to standard body length ($n = 74$ animals), condylobasal length ($n = 83$ animals) and chronological age ($n = 63$ animals); and (ii) determine if condylobasal length and suture closure are useful indicators of age and/or standard body length. This study is the second in a series of papers initiated to develop baseline descriptions of Cape fur seal morphology and to examine growth patterns.

MATERIALS AND METHODS

Collection of specimens

Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). From this collection¹, skulls from 59 males were selected for examination (Appendix 4.1). Apart from specimens collected before May 1992 ($n = 16$), all specimens were collected by the first author. One animal (PEM2238) was collected NE of the study area, at Durban.

The sample was supplemented with measurements from 24 skulls from Marine and Coastal Management (MCM), Cape Town. These skulls were from males that had been tagged as pups, and were therefore of known-age (1–12 y). MCM seal specimens are accessioned as AP followed by a number.

East coast and west coast animals

Additional skulls from Sinclair Island (West coast of southern Africa, 27° 40'S, 15° 31'E) were measured (condylobasal length only) to determine if Eastern Cape seals ($n = 28$ males) were of similar size to those inhabiting west coast waters ($n = 12$ males). PEM animals were adults 7–12+ y. West coast animals were adults of unknown-age. West coast animals were collected by Dr R. W. Rand in the 1940s and housed in the South African Museum, Cape Town.

Preparation and measurement of skulls

Skulls were defleshed and macerated in water for 2–3 mo. Water was changed regularly. Skulls were then gently washed in mild detergent (or brushed with water), and air dried at room temperature. A small number of skulls were defleshed and gently boiled. Dry specimens were measured ($n = 32$ linear measurements) to the nearest 0.5 mm using a vernier calliper (Table 4.1, Fig. 4.1).

Variables used correspond to those reported in earlier otariid studies (Sivertsen, 1954; Orr *et al.*, 1970; Repping *et al.*, 1971; Kerley & Robinson, 1987). Variables were grouped by region in an attempt to reflect a functional cranial analysis and to assess overall skull size (Hartwig, 1993, modified) (Table 4.1).

All PEM measurements (and measurements taken from Sinclair Island skulls) were recorded by the first author. The majority of MCM measurements were recorded by the third author.

¹Skull measurements recorded by the first author, from 103 of these animals, were previously made available to S. Brunner for her honours project and subsequently published in a comparative growth study, i.e., Brunner (1998).

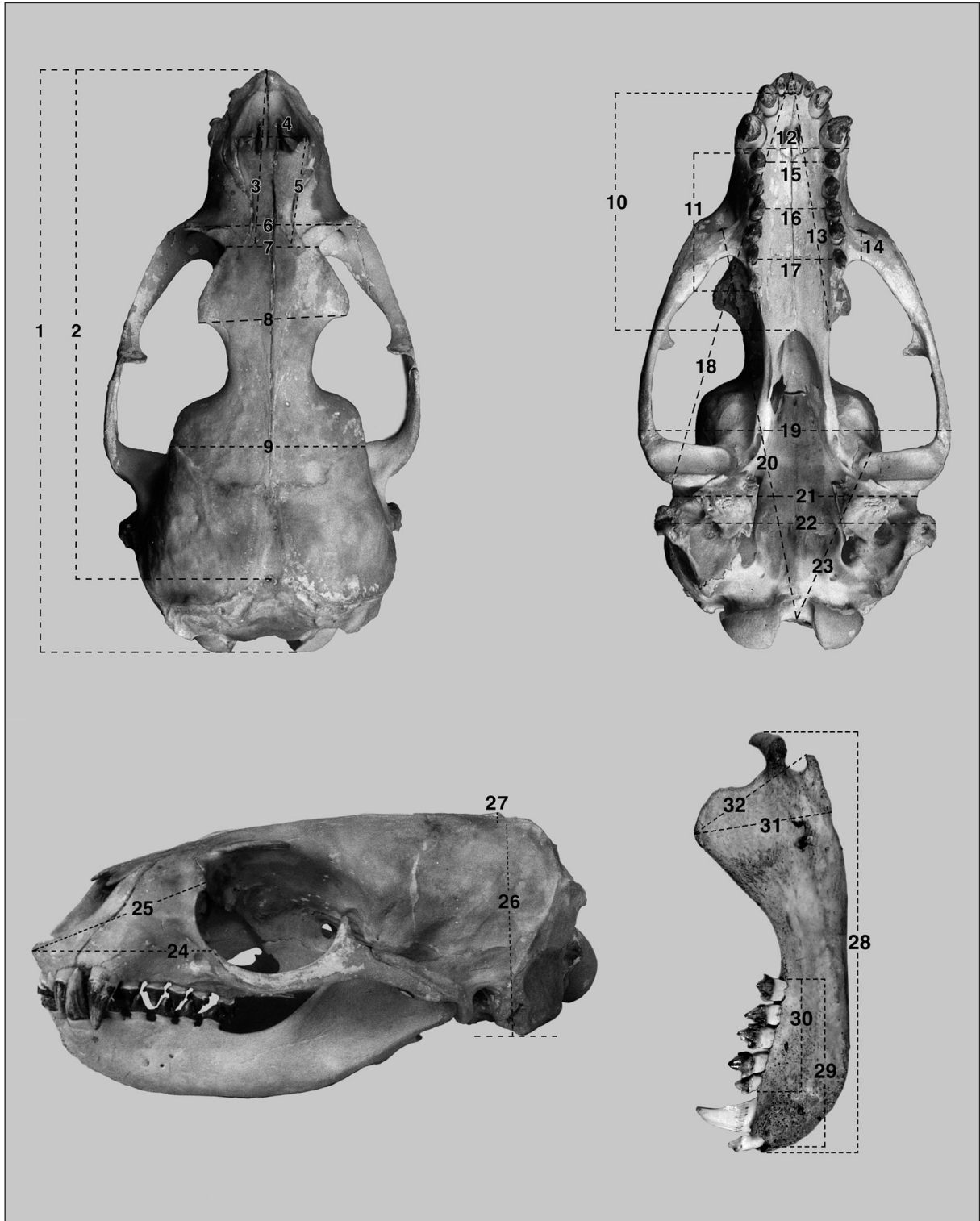


Fig. 4.1 Diagram of a Cape fur seal skull (PEM554) indicating individual measurements taken. Measurements defined in Table 4.1

Suture index

Eleven cranial sutures from 48 skulls were examined and assigned a value of 1–4, according to the degree of closure (1 = suture fully open; 2 = suture less than half-closed; 3 = suture more than half-closed; and 4 = suture completely closed)

(Fig. 4.2). These values were added to give a total suture index (SI), ranging from 11 (all sutures open) to 44 (all sutures closed).

Table 4.1 *Linear skull measurements (n = 32) taken from male Cape fur seals in this study. Measurements illustrated in Fig. 4.1*

Code	Variable	Region	Function
Dorsal			
D1	Condylbasal length (posterior point on the occipital condyles to the most anterior point on the premaxilla)	–	–
D2	Gnathion to middle of occipital crest	–	R/V
D3	Gnathion to posterior end of nasals	splanchnocranium	R/V
D4	Greatest width of anterior nares (distance between the anterior margins of the nares)	nasal	R/V
D5	Greatest length of nasals (distance between the anterior and posterior margins of nasals)	nasal	R/V
D6	Breadth at preorbital processes	–	–
D7	Least interorbital constriction	frontal	–
D8	Greatest breadth at supraorbital processes	frontal	F
D9	Breadth of brain case (at the coronal suture, anterior to the zygomatic arches)	neurocranium	BC
Palatal			
P10	Palatal notch to incisors (posterior margin of first incisor alveolus to palatal notch, excluding cleft)	palate	R/V, F
P11	Length of upper postcanine row (anterior margin of postcanine one alveolus to the most posterior margin of postcanine six alveolus)	palate (dentition)	F
P12	Greatest bicanine breadth	palate	R/V, F
P13	Gnathion to posterior end of maxilla (palatal)	palate	R/V, F
P14	Breadth of zygomatic root of maxilla	zygomatic arch	F
P15	Breadth of palate at postcanine 1 (excluding the alveoli)	palate	F
P16	Breadth of palate at postcanine 3 (excluding the alveoli)	palate	F
P17	Breadth of palate at postcanine 5 (excluding the alveoli)	palate	F
P18	Gnathion to posterior border of postglenoid process	–	R/V, F
P19	Bizygomatic breadth (maximum distance between the lateral surfaces of the zygomatic arches)	zygomatic arch	F
P20	Basion to zygomatic root (anterior)	–	–
P21	Calvarial breadth (greatest transverse width across of the skull base, anterior to the mastoid)	basicranium	A
P22	Mastoid breadth (width across the processes)	basicranium	A, F
P23	Basion to bend of pterygoid (anterior of basion to anterior of pterygoid)	basicranium	BC, A, F
Lateral			
L24	Gnathion to anterior of foramen infraorbital (= lateral face length)	splanchnocranium	R/V
L25	Gnathion to posterior border of preorbital process	splanchnocranium	R/V
L26	Height of skull at base of mastoid (excluding crest)	–	–
L27	Height of sagittal crest	neurocranium	BC, F
Mandibular			
M28	Length of mandible (posterior margin of condyle to anterior margin of the first incisor alveolus)	mandible	F
M29	Length of mandibular tooth row (anterior margin of the first incisor alveolus to the most posterior margin of postcanine five alveolus)	mandible (dentition)	F
M30	Length of lower postcanine row (anterior margin of postcanine one alveolus to the most posterior margin of postcanine five alveolus)	mandible (dentition)	F
M31	Height of mandible at meatus (dorsal margin of coronoid process to the base of the angularis)	mandible	A, F
M32	Angularis to coronoideus (dorsal margin of coronoid process to the top of the angularis)	mandible	F

Function: A, auditory; BC, braincase; F, feeding; R/V, respiration /vocalisation.

(measurements taken from other otariid studies - Sivertsen, 1954; Orr *et al.*, 1970; Repenning *et al.*, 1971; Kerley & Robinson, 1987; Hartwig, 1993).



Fig. 4.2 Diagram of a Cape fur seal skull (PEM554) showing the position of sutures examined in this study. 1. occipito-parietal; 2. interparietal; 3. coronal; 4. interfrontal; 5. internasal; 6. premaxillary-maxillary; 7. basioccipito-basisphenoid; 8. basisphenoid-presphenoid; 9. squamosal-parietal; 10. squamosal-jugal; 11. maxillary.

Age determination

The total number of aged animals (known-age animals and canine aged animals) was 63. All MCM skulls ($n = 24$) were of known-age. Of the 59 PEM animals in the study: (i) 28 were aged from counts of incremental lines observed in the dentine of upper canines as described in Stewardson *et al.*, (200Xa), i.e., range 1–10 y; (ii) 11 were identified as adults > 12 y² (i.e., pulp cavity of the upper canine closed); and (iii) 20 y were not aged.

For this study, the following age groups were used: yearling (10 mo to 1 y 6 mo); subadult (1 y 7 mo to 7 y 6 mo); and adult (≥ 7 y 7 mo) (Table 4.2). Very old animals of known-age were not available for examination (estimated longevity is c. 20 y).

Currently, examination of tooth structure is the most precise method of age determination in pinnipeds; however, counts are not without error. For information of the reliability of this method see Oosthuizen (1997).

Classification of growth patterns

In the present study, neural and somatic growth patterns were distinguished as follows: [(mean skull measurement for adults ≥ 12 y – mean skull measurement for subadults at 7 y) $\times 100\%$]/mean skull measurement for subadults at 7 y. Where the percent increase in variable size was $< 6\%$, growth was classified as neural, i.e., most growth was completed as subadults. Where percent increase was $\geq 6\%$, growth was classified as somatic, i.e., growth continued to increase in adults. Percentage increase for each variable is given in Table 4.3.

Statistical analyses

Skull measurement error

For most PEM skulls, duplicate measurements were taken of 7 randomly selected variables to assess measurement error. The 1-sample sign test was used to test the null hypothesis that the true median was equal to the hypothesised median. The Wilcoxon

² In Cape fur seals, animals > 13 y can not be aged from counts of growth layer groups in the dentine of upper canines because the pulp cavity closes which terminates tooth growth, hence the age group ' ≥ 12 y'.

sign-rank test requires the assumption that the parent population is symmetric (Gibbons & Chakraborti, 1992, p. 155). However, the distribution of data was not symmetric for all variables, thus the less powerful sign test was used. Interobserver error was not assessed.

Condylbasal length expressed in relation to standard body length

Growth in condylbasal length (CBL), relative to standard body length (SBL), was calculated as follows, using paired samples only:

$$\text{CBL (mm)/SBL (mm)} \times 100\%$$

As the approximate variance of the ratio estimate is difficult to calculate, percentages must be interpreted with caution (Cochran, 1977, p. 153).

Condylbasal length as an indicator of SBL and age

The degree of linear relationship between log CBL, log SBL and age (y) was calculated using the Spearman rank-order correlation coefficient. Linear discriminant function analysis (Mahalanobis squared distance) was used to predict the likelihood that an individual seal will belong to a particular age group (subadult, adult) using one independent variable, skull length (see Stewardson *et al.*, 200Xa for further details). Yearlings were not examined because of small sample size, i.e., $n = 2$ yearlings.

Suture index as an indicator of age

The degree of linear relationship between suture age and canine age (y) was calculated using the Spearman rank-order correlation coefficient. Linear discriminant function analysis was used to differentiate between subadult and adult skulls using one independent variable, suture age.

Bivariate allometric regression

The relationship between value of skull measurement and: (i) SBL, (ii) CBL, (iii) age (y), was investigated using the logarithmic (base e) transformation of the allometric equation, $y = ax^b$ which may equivalently be written as $\log y = \log a + b \log x$. 'Robust' regression (Huber M-Regression) was used to fit straight lines to the transformed data. The degree of linear relationship between the transformed variables was calculated using the Spearman rank-order correlation coefficient, r (Gibbons & Chakraborti, 1992). Testing of model assumptions, and hypotheses about the slope of the line, followed methods described by Stewardson *et al.*, (200Xa).

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23); Microsoft © Excel 97 (Microsoft Corp., Seattle, 1997) and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

RESULTS

Skull measurement error

Of the 7 variables that were measured twice, measurements were reproducible at the 5% significance level (range for p -values: 1.0–0.08). Height of sagittal crest (L27), and height of skull at base of mastoid (L26), were difficult to measure accurately, thus must be interpreted with caution.

Skull morphology

The youngest animals in the sample were 10 mo of age (Fig. 4.3a; Table 4.3). In these individuals, the skull was *c.* 160 mm in length (D1) and 87 mm wide (P19). The brain case was relatively large, measuring 120 mm (75% of CBL) from the most posterior end of nasals to the most posteriorly projecting point on the occipital bone, in the mid-sagittal plane. There were no signs of bony ridges or prominences. Relative to CBL, the face and mandible were short. Milk dentition had not been completely replaced by permanent teeth in animal AP4999. It was clear that the deciduous canines persist in some animals until their tenth month.

In adults 10 y of age, the skull was rugose, with heavy bony deposits (Fig. 4.3b; Table 4.3). Mean length (D1) and breadth (P19) was 248 mm and 142 mm, respectively. The braincase was 157 mm in length (63% of CBL), and a sagittal crest was present (4.4–12.0 mm in height, $n = 5$). The forehead was convex at the supraorbital region. Relative to CBL, the face was long, with long nasals that flared anteriorly. The ratio of nasal breadth to length was 1 : 1.5. The palate was long, moderately broad and arched. The ratio of palatal breadth (P15–17) to palatal length (P10) was 1 : 3–4. The maxillary shelf at the root of the zygomatic process (P14) was very short in an antero-posterior direction (16 mm; 6% of CBL). The mandible was long with a broad coronoid process. The tooth rows were parallel, with enlarged third incisor; large canines; robust, tricuspid postcanines (PC); and a slight diastema between upper PC 5 and 6 (Repenning *et al.*, 1971; present study). Dental formula was $(I^{3/2} C^{1/1} PC^{6/5})$.

East coast and west coast animals

Available data suggested that skulls from adult males, 7–12+ y, from Eastern Cape fur seals (mean 246.6 ± 2.5 mm; range 213.7–266.8 mm; $n = 28$) were significantly smaller than skulls from adult animals inhabiting west coast waters (mean 259.4 ± 4.5 mm; range 225.6–282.1 mm; $n = 12$) (at the 5% significance level two sample t -test²: $t = -2.48$; $P = 0.024$; $df = 17$).

However, skulls from adult males, > 12 y, from the Eastern Cape (mean 255.7 ± 2.6 mm; range 239.9–266.6 mm; $n = 11$) were not significantly smaller than skulls from adult animals inhabiting west coast waters (mean 259.4 ± 4.5 mm; range 225.6–282.1 mm; $n = 12$) (at the 5% significance level two sample t -test²: $t = -0.71$; $P = 0.49$; $df = 17$).

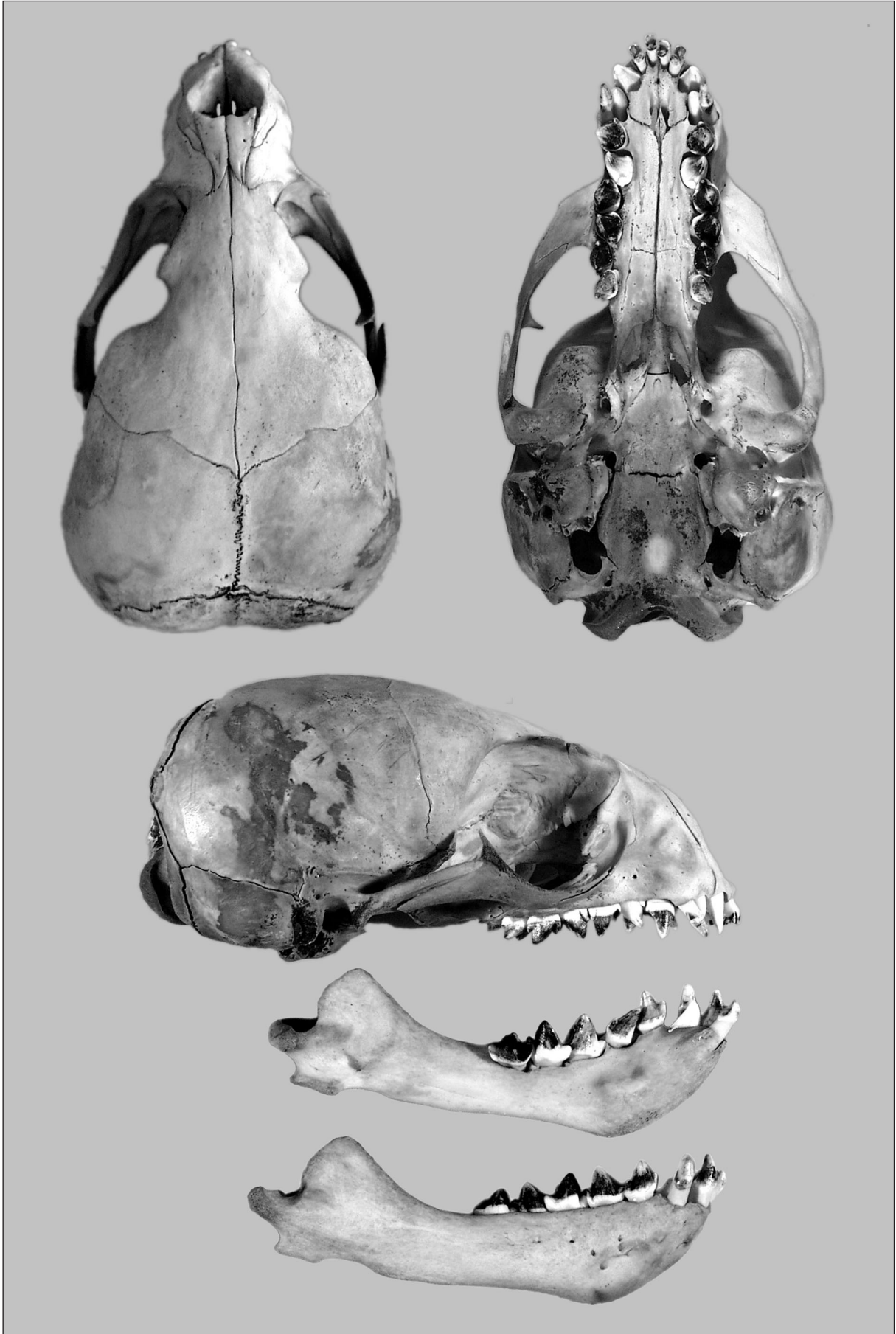


Fig. 4.3a Size and shape of the Cape fur seal skull: juvenile 10 mo (AP4999).

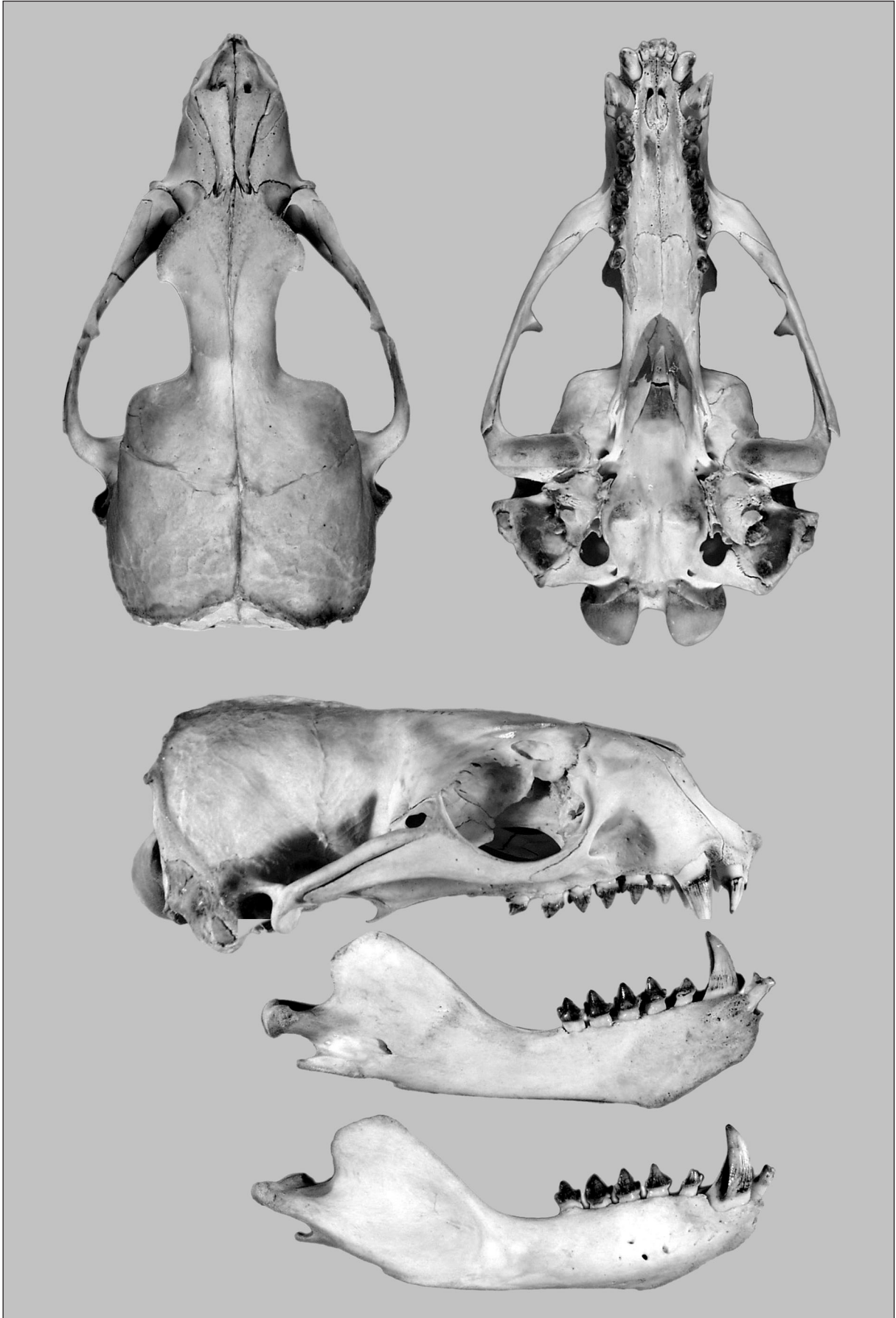


Fig. 4.3b Size and shape of the Cape fur seal skull: adult 10 y (AP4992).

Table 4.2 The age distribution of Cape fur seals

Age group	Age ^a (y)	Frequency	Percentage
Yearling	1	2	3.2
Subadult	2	2	3.2
	3	2	3.2
	4	8	12.7
	5	4	6.3
	6	4	6.3
	7	12	19.0
Adult	8	7	11.1
	9	5	7.9
	10	5	7.9
	≥ 12	12	19.0
Total		63	100

^a **Animals 1–10 y:** 23 MCM animals were of known-age; 28 PEM animals were aged from counts of incremental lines observed in the dentine of upper canine.
Animals ≥ 12 y: one MCM animals was 12 y; 11 PEM males were > 12 y, i.e., the pulp cavity of the upper canine was closed.

Condylbasal length expressed in relation to SBL

Relative to SBL, condylbasal length decreased with increasing SBL, i.e., 19.4% (yearlings), 15.5% (subadults), 13.8% (adults, 8–10 y) and 13.6% (adults ≥ 12 y) (Table 4.4).

Condylbasal length as an indicator of age

Condylbasal length continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). In animals 1–10 y, growth in skull length was highly positively correlated with age (y) ($r = 0.89$, $n = 51$) (Fig. 4.4b). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate (the residuals were not scattered randomly about zero, see Weisberg, 1985, p. 23). Thus, CBL could not be used as a reliable indicator of absolute age. The coefficient of variation in skull length for young males 1–5 y (12.3%) was considerably higher than in older males (8–10 y, 4.3%; ≥ 12 y, 5.7%) (Table 4.3).

Although CBL was not a useful indicator of absolute age, it was a 'rough indicator' of age group. When skull length is known, the following linear discriminant functions can be used to categorise each observation into one of two age groups—adult or subadult:

$$y_1 = -98.43 + 0.91x$$

$$y_2 = -129.06 + 1.05x$$

where x = skull length (mm); subscript 1 = subadult; and subscript 2 = adult. The seal is classified into the age group associated with the

linear discriminant function which results in the minimum value. Of the 61 observations in this study 85% were correctly classified using this method (Table 4.5).

Condylbasal length as an indicator of SBL

Skull length was highly, positively correlated with SBL ($r = 0.93$, $n = 74$; Fig. 4.4a). When CBL is known, the following equation (linear least squares fit; untransformed data) can be used as a 'rough indicator' of SBL:

$$y = -4.11 + 1.69x$$

which may equivalently be written as $SBL = e^{-4.11} \times CBL^{1.69}$, where the S.E. of the intercept is 0.28 and the S.E. of the slope is 0.05 ($n = 74$).

Suture index as an indicator of age

The sequence of suture closure according to age (y) and age group is depicted in Table 4.6. Sutures $i-xi$ showed signs of partial closure at different times, and the time taken to reach full closure was different for each suture. The cranial sutures (basioccipito-basisphenoid, coronal, occipito-parietal and interparietal) were the first to partially close. The squamosal-jugal, squamosal-parietal, maxillary, premaxillary-maxillary, and interfrontal were the last to show signs of partial closure (order of partial closure unknown), with the basisphenoid-presphenoid and internasal remaining fully open in all specimens examined.

The exact sequence of full closure for all 11 sutures could not be established because animals of known-age, > 12 y, were not available for analysis. However, the basioccipito-basisphenoid and occipito-parietal were the first sutures to fully close in animals 3 and 4 y, respectively; followed by the interparietal in some animals ≥ 7 y; and then the coronal or squamosal-jugal in animals ≥ 12 y.

In animals 1–10 y, suture age was highly positively correlated with age ($r = 0.81$, $p = 0.000$, $n = 38$) (Fig. 4.5c). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate.

Furthermore, linear discriminant function could not be used satisfactorily to categorise each observation into age groups, i.e., of the 46 animals examined, all subadults ($n = 26$) were correctly classified; however, seven (35%) of the 20 adults were incorrectly classified as subadults.

Suture age was highly positively correlated with SBL ($r = 0.89$, $p = 0.000$, $n = 63$) (Fig. 4.5a). Information on suture age as an indicator of physiological maturity is presented elsewhere (Stewardson *et al.*, 200Y).

Bivariate allometric regression

Regression statistics for skull measurements (D1–M32) on SBL, CBL and age (y) are given in Appendix 4.2–4.4. Overall, correlation coefficients

² The two sample t-test used in the above analysis does not use the assumption of equal variance and D.F. ≠ $n - 1$.

Table 4.3 Summary statistics for dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull variables according to age (y) and age group. Data presented as mean skull variable in mm ± S.E., followed by coefficient of variation in round brackets, and skull variable expressed as a percentage of skull length. Maximum value of each variable (males of unknown-age), and classification of growth pattern, are also presented.

Age group	Age (y)	n ^a	D1	D2	D3	D4	D5	D6	D7
Yearling	1	2	159.7 ± 2.6 (2.3)	144.8 ± 2.4 (2.3) 90.7%	54.1 ± 1.0 (2.6) 33.9%	20.3 ± 0.1 (0.7) 12.7%	25.1 ± 1.6 (8.8) 15.7%	40.8 ± 0.1 (0.3) 25.6%	21.6 ± 0.3 (1.6) 13.5%
Subadult	2	2	174.5 ± 7.2 (5.8)	148.7 ± 2.1 (2.0) 85.2%	56.3 ± 2.6 (6.4) 32.2%	17.9 ± 0.4 (3.2) 10.3%	25.7 ± 0.7 (3.9) 14.7%	45.0 ± 3.8 (11.8) 25.8%	22.1 ± 1.3 (8.0) 12.6%
	3	2	196.2 ± 1.8 (1.3)	162.8 ± 1.9 (1.7) 83.0%	64.9 ± 1.9 (4.1) 33.1%	21.5 ± 1.0 (6.6) 11.0%	33.1 ± 1.9 (8.1) 16.9%	48.6 ± 0.3 (0.7) 24.8%	24.7 ± 0.9 (5.1) 12.6%
	4	8	205.2 ± 4.7 (6.4)	173.6 ± 4.0 (6.6) 84.6%	71.1 ± 1.8 (7.1) 34.7%	22.8 ± 0.3 (4.2) 11.1%	34.1 ± 1.3 [6] (9.4) 16.8%	54.6 ± 1.3 (6.7) 26.6%	29.5 ± 0.8 (8.0) 14.4%
	5	4	217.0 ± 4.3 (4.0)	183.5 ± 3.4 (3.7) 84.6%	75.7 ± 1.8 (4.8) 34.9%	24.2 ± 0.5 (4.4) 11.1%	37.2 ± 0.8 (4.5) 17.1%	57.3 ± 2.3 (8.0) 26.4%	31.0 ± 1.1 (7.1) 14.3%
	6	4	220.6 ± 3.4 (3.1)	187.6 ± 4.4 (4.7) 85.0%	76.1 ± 0.7 [3] (1.6) 35.0%	23.6 ± 1.5 (12.9) 10.7%	39.0 ± 2.7 (13.9) 17.7%	59.9 ± 0.5 (1.6) 27.1%	31.2 ± 0.7 (4.6) 14.1%
	7	12	230.6 ± 2.1 (3.2)	197.8 ± 1.9 [11] (3.2) 85.5%	81.3 ± 1.5 (6.5) 35.3%	25.0 ± 0.6 [11] (7.8) 10.8%	40.1 ± 0.6 (5.1) 17.4%	63.6 ± 1.0 (5.6) 27.6%	33.9 ± 0.7 (6.9) 14.7%
	2–7	32	215.7 ± 3.2 (8.3)	183.0 ± 2.9 [31] (9.0) 90.9%	74.8 ± 1.5 [31] (11.1) 34.7%	23.4 ± 0.4 [31] (10.4) 10.9%	37.0 ± 0.9 [30] (13.0) 17.1%	58.0 ± 1.2 (11.3) 26.9%	30.8 ± 0.7 (12.8) 14.3%
Adult	8	7	236.8 ± 4.5 (5.0)	206.9 ± 5.6 (7.1) 87.4%	83.6 ± 2.3 (7.2) 35.3%	26.5 ± 0.9 [6] (8.7) 11.2%	41.6 ± 1.7 [6] (9.9) 17.6%	66.0 ± 1.5 (6.0) 27.9%	36.5 ± 1.2 (8.5) 15.4%
	9	5	242.2 ± 1.6 (1.5)	206.5 ± 5.3 [4] (5.1) 85.1%	84.3 ± 1.9 [4] (4.6) 34.8	28.2 ± 1.2 (9.4) 11.6%	40.5 ± 2.0 [4] (9.9) 16.7%	67.2 ± 1.5 [4] (4.3) 27.7%	38.4 ± 1.9 [4] (9.9) 15.8%
	10	5	248.2 ± 4.7 (4.2)	220.1 ± 6.1 (6.1) 88.7%	89.9 ± 2.5 (6.3) 36.2%	29.0 ± 1.0 (8.1) 11.7%	44.3 ± 2.1 (10.7) 17.9%	68.7 ± 3.2 (10.3) 27.7%	38.6 ± 0.7 [4] (3.6) 15.3%
	8–10	17	241.7 ± 2.5 (4.3)	210.9 ± 3.5 [16] (6.7) 87.2%	85.7 ± 1.4 [16] (6.9) 35.5%	27.8 ± 0.6 [16] (9.1) 11.5	42.2 ± 1.1 [15] (10.2) 17.5%	67.2 ± 1.2 [16] (7.1) 27.8%	37.6 ± 0.8 [15] (7.8) 15.5%
	≥ 12	12	249.9 ± 4.1 (5.7)	225.3 ± 5.0 [11] (7.3) 90.1%	92.4 ± 2.2 (8.1) 37.0%	29.6 ± 0.8 (9.0) 11.9%	47.0 ± 1.4 (10.1) 18.8%	69.1 ± 1.8 [10] (8.4) 27.9%	38.0 ± 1.2 [10] (9.6) 15.2%
Total		63		60	61	61	59	60	59
Mean for males ≥ 200 cm [max. value in brackets] ^b			259.2 ± 7.0 [275.4]	234.8 ± 9.4 [254.4]	97.4 ± 4.7 [108.9]	30.6 ± 1.1 [33.8]	50.2 ± 2.9 [57.6]	72.3 ± 4.0 [3] [77.0]	38.4 ± 0.5 [42.8]
Growth pattern, Evidence of a SGSC ^c			Somatic, 8% No	Somatic, 14% 10 y (strong)	Somatic, 14% 10 y (weak)	Somatic, 18% No	Somatic, 17% (see text)	Somatic, 9% No	Somatic, 12% No

Variables: D1 condylobasal length; D2 gnathion to middle of occipital crest; D3 gnathion to posterior end of nasals; D4 greatest width of anterior nares; D5 greatest length of nasals; D6 breadth at preorbital processes; D7 least interorbital constriction.

continued next page

were moderately to strongly positive, i.e., most points on the scatter plot approximate a straight line with positive slope, $r \geq 0.70$. Exceptions included breadth of brain case on SBL, CBL and age (y) ($r = 0.3$ – 0.4); length of upper PC row on age (y) ($r = 0.59$), and breadth of zygomatic root of maxilla on age (y) ($r = 0.57$). SBL was strongly positively correlated with age (y) ($r = 0.87$). Although correlation coefficients indicate that linearity was reasonably well approximated for most variables by log-log transformations, a linear relation did not necessarily best describe the relationship.

Growth of skull variables according to region

Most variables within a given region were significantly positively correlated with each other, $r \geq 0.70$ (Appendix 4.5). Exceptions were: (i) breadth of

palate at PC 5 (P17) with length of upper PC row (P11) ($r < 0.7$; significant at 0.01); and (ii) breadth of brain case (D9) with height of sagittal crest (L27) ($r = 0.25$; not significant).

Neurocranium region (D9, L27)

Breadth of brain case (D9) followed a neural growth pattern, with most growth completed by 6 y (84 mm) (Fig. 4.6). Overall growth scaled with negative slope ($b = 0.17$) relative to CBL. In yearlings, the brain case was proportionally long, i.e., 75% of CBL in yearlings, and 63% of CBL at 10 y. Growth in length of the brain case (31% at 10 y relative to yearlings, RTY) was much greater than growth in breadth (8% at 10 y, RTY). The ratio of breadth to length increased from 1 : 1.5 (yearlings) to 1 : 1.9 y (10 y).

Height of sagittal crest (L27) appeared to follow a somatic growth pattern; however, there was great variation among individuals of similar age. The crest

continued from previous page

Age group	Age (y)	<i>n</i> ^a	D8	D9	P10	P11	P12	P13	P14
Yearling	1	2	38.2 ± 0.4 (1.5) 23.9%	78.0 ± 0.4 (0.6) 48.8%	64.3 ± 0.7 (1.4) 40.2%	40.5 [1*] (-) 25.0%	33.8 ± 1.2 (4.8) 21.1%	73.0 ± 0.5 (1.0) 45.7%	12.9 ± 0.5 (5.5) 8.1%
Subadult	2	2	37.8 ± 1.9 (7.1) 21.7%	78.7 ± 1.3 (2.2) 45.1%	66.2 ± 3.0 (6.4) 37.9%	43.2 ± 0.3 (0.8) 24.7%	32.5 ± 1.6 (6.8) 18.6%	77.7 ± 1.2 (2.1) 44.5%	11.3 ± 0.3 (3.8) 6.5%
	3	2	39.5 [1*] (-) 20.3%	81.7 ± 4.0 (6.8) 41.6%	82.3 ± 2.8 (4.8) 42.0%	62.1 ± 0.7 (1.5) 31.6%	35.2 ± 0.8 (3.0) 17.9%	89.3 ± 0.1 (0.2) 45.5%	12.4 ± 0.3 (3.4) 6.3%
	4	8	45.6 ± 1.6 (10.2) 22.2%	81.7 ± 1.1 (3.7) 39.8%	87.9 ± 2.5 (8.1) 42.8%	49.8 ± 0.4 (2.5) 24.3%	39.6 ± 0.8 (5.5) 19.3%	94.2 ± 2.7 (8.1) 45.9%	12.7 ± 0.3 (7.0) 6.2%
	5	4	46.7 ± 2.0 (8.4) 21.5%	82.2 ± 1.6 (3.9) 37.9%	88.6 ± 2.3 [3] (4.4) 41.6%	54.2 ± 2.4 (9.0) 25.0%	42.5 ± 1.3 (6.1) 19.6%	101.9 ± 3.2 (6.2) 47.0%	14.5 ± 0.7 (9.5) 6.7%
	6	4	46.3 ± 1.3 (5.6) 21.0%	83.7 ± 1.7 (4.0) 37.9%	94.1 ± 1.1 (2.7) 42.3%	54.9 ± 0.8 (3.3) 24.7%	43.0 ± 0.7 (3.4) 19.6%	103.9 ± 1.4 (3.0) 47.0%	14.1 ± 0.6 (8.8) 6.4%
	7	12	52.5 ± 1.2 [11] (7.7) 22.7%	84.1 ± 0.8 (3.3) 36.4%	97.8 ± 1.7 (6.0) 42.4%	57.2 ± 0.8 (4.8) 24.8%	45.9 ± 0.5 [11] (3.3) 19.8%	110.6 ± 1.3 (4.0) 48.0%	13.8 ± 0.4 (10.4) 6.0%
	2-7	32	47.6 ± 1.0 [30] (12.0) 22.1%	82.7 ± 0.6 (3.9) 38.3%	90.9 ± 1.7 [31] (10.6) 42.2%	54.2 ± 0.9 (9.3) 25.1%	41.9 ± 0.8 [31] (10.3) 19.5%	101.3 ± 1.9 (10.6) 46.9	13.4 ± 0.3 (10.6) 6.2%
Adult	8	7	53.6 ± 0.4 [5] (1.8) 22.8%	84.6 ± 2.0 (6.3) 35.7%	99.6 ± 2.5 (6.6) 42.1%	57.7 ± 1.8 (8.4) 24.4%	47.9 ± 1.3 (7.2) 20.2%	112.0 ± 2.6 (6.0) 47.3%	14.4 ± 0.5 (9.7) 6.1%
	9	5	56.5 ± 2.8 [3] (8.6) 23.2%	83.1 ± 1.3 (3.0) 34.3%	105.6 ± 0.7 (1.5) 43.6%	60.2 ± 1.2 (4.4) 24.9%	46.6 ± 0.8 (3.7) 19.2%	115.0 ± 0.9 [4] (1.5) 47.3%	14.4 ± 0.7 (11.0) 5.9%
	10	5	57.3 ± 1.9 (7.5) 23.1%	84.2 ± 0.9 (2.3) 33.9%	109.3 ± 3.7 (7.6) 44.0%	59.3 ± 1.2 (4.7) 23.9%	51.1 ± 2.8 (12.2) 20.6%	117.2 ± 1.9 (3.6) 47.2%	16.0 ± 1.1 (14.9) 6.4%
	8-10	17	55.7 ± 1.0 [13] (6.6) 23.0%	84.0 ± 0.9 (4.5) 34.8%	104.2 ± 1.8 (6.9) 43.1%	58.9 ± 0.9 (6.3) 24.4%	48.4 ± 1.0 (8.9) 20.0%	114.4 ± 1.3 [16] (4.7) 47.3%	14.8 ± 0.4 (12.3) 6.1%
	≥ 12	12	58.0 ± 2.1 (12.4) 23.2%	84.0 ± 1.3 (5.2) 33.6%	106.3 ± 2.0 (6.3) 42.0%	62.0 ± 1.6 (8.6) 24.5%	54.1 ± 1.1 (6.8) 21.4%	118.4 ± 2.4 (6.8) 46.7%	17.2 ± 0.4 (7.7) 6.8%
Total		63	57	63	62	62	62	62	63
Mean for males ≥ 200 cm [max. value in brackets] ^b			62.8 ± 2.3 [69.1]	85.2 ± 0.9 [3] [90.0]	112.8 ± 4.4 [123.0]	60.5 ± 2.1 [70.5]	53.7 ± 3.3 [62.2]	123.7 ± 4.1 [134.6]	17.4 ± 1.0 [20.0]
Growth pattern, Evidence of a SGS ^c			Somatic, 10% 7 y (weak)	Neural, 0% No	Somatic, 9% No	Somatic, 8% No	Somatic, 18% (see text)	Somatic, 7% No	Somatic, 25% No

Variables: D8 greatest breadth at supraorbital processes; D9 breadth of brain case; P10 palatal notch to incisors; P11 length of upper postcanine row; P12 greatest bicanine breadth; P13 gnathion to posterior end of maxilla; P14 breadth of zygomatic root of maxilla.

continued next page

was absent in juveniles and young subadults. Evidence of crest formation was apparent in one 4 y old ($n = 7$), two 6 y olds ($n = 4$), eight 7 y olds ($n = 8$), and all males ≥ 8 y. Maximum crest height was 11–12 mm ($n = 4$). There was some evidence of a very slight secondary growth spurt in some males at *c.* 10 y, but sample size was too small to confirm this observation.

Basicranium region (P21, P22, P23)

Calvarial breadth (P21) followed a somatic, monophasic growth pattern. Overall growth in variable size increased in proportion ($b = 1$) to skull size, increasing by 49% at 10 y (RTY).

Mastoid breadth (P22) followed a somatic growth pattern. Overall growth scaled with positive slope ($b = 1.29$) relative to CBL, increasing by 80% at 10 y (RTY). A prominent secondary growth spurt was apparent at 10 y (Fig. 4.7).

Basion to bend of pterygoid (P23) followed a neural growth pattern, with most growth completed

by 7 y (76 mm). Overall growth in variable size was negatively allometric relative to CBL.

Frontal region (D7, D8)

Least interorbital constriction (D7) followed a somatic, monophasic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 79% at 10 y (RTY). Most growth was completed by 9 y.

Greatest breadth at supraorbital processes (D8) followed a somatic growth pattern. Overall growth scaled with a very slight positive slope ($b = 1.03$) relative to CBL, increasing by 50% at 10 y (RTY). A weak secondary growth spurt was apparent at 7 y.

Zygomatic arch (P14, P19)

Breadth of zygomatic root at maxilla (P14) followed a somatic, monophasic growth pattern. Overall growth was isometric relative to CBL, increasing by 24% at 10 y (RTY).

continued from previous page

Age group	Age (y)	n ^a	P15	P16	P17	P18	P19	P20	P21
Yearling	1	2	14.1 ± 0.7 (6.5) 8.8%	18.4 ± 0.5 (3.8) 11.5%	20.8 ± 0.1 (0.3) 13.0%	111.1 ± 0.3 (0.3) 69.6%	86.6 ± 0.5 (0.8) 54.2%	109.3 ± 2.2 (2.8) 68.5%	77.3 ± 2.0 (3.7) 48.4%
Subadult	2	2	13.0 ± 0.4 (3.8) 7.4%	16.7 ± 0.3 (2.5) 9.6%	20.7 ± 0.7 (4.8) 11.9%	122.4 ± 3.4 (3.9) 70.2%	92.6 ± 3.0 (4.5) 53.1%	120.0 ± 5.7 (6.7) 68.9%	77.8 ± 1.5 (2.6) 44.6%
	3	2	16.3 ± 0.2 (1.7) 8.3%	19.6 [1*] (-) 10.1%	25.0 ± 1.6 (8.8) 12.7%	141.0 ± 1.3 (1.3) 71.9%	103.8 ± 1.7 (2.2) 52.9%	133.0 ± 0.4 (0.4) 67.8%	87.3 ± 0.7 (1.0) 44.5%
	4	8	17.2 ± 0.5 (7.7) 8.4%	21.9 ± 0.6 (7.2) 10.6%	26.0 ± 1.1 (12.3) 12.7%	150.0 ± 4.1 (7.8) 73.1%	111.0 ± 2.7 (6.8) 54.1%	139.8 ± 3.2 (6.5) 68.1%	93.6 ± 2.4 (7.4) 45.6%
	5	4	20.7 ± 1.2 [3] (9.8) 9.4%	23.8 ± 1.1 [3] (7.9) 10.8%	30.1 ± 1.7 (11.2) 13.9%	162.4 ± 4.7 [3] (5.0) 74.1%	121.9 ± 3.6 (5.9) 56.2%	148.3 ± 2.6 (3.5) 68.4%	104.0 ± 2.3 (4.4) 47.9%
	6	4	19.6 ± 0.4 (4.2) 8.9%	23.4 ± 0.6 (6.1) 10.5%	29.2 ± 1.2 (9.1) 12.9%	162.1 ± 1.7 [4] (2.1) 74.2%	121.0 ± 3.2 (6.0) 54.5%	150.2 ± 1.3 (1.9) 68.0%	102.6 ± 0.4 (0.8) 46.5%
	7	12	20.7 ± 1.2 [8] (16.0) 8.9%	25.0 ± 0.4 [8] (4.5) 10.7%	30.5 ± 0.7 [11] (7.6) 13.2%	173.2 ± 1.8 [10] (3.3) 74.9%	125.7 ± 2.1 (5.7) 54.5%	157.5 ± 1.4 (3.0) 68.3%	107.5 ± 1.3 (4.3) 46.6%
	2-7	32	18.6 ± 0.6 [27] (16.2) 8.7%	22.8 ± 0.5 [26] (11.5) 10.6%	28.2 ± 0.7 [31] (13.4) 13.0%	158.4 ± 3.0 [28] (10.3) 73.8%	117.6 ± 2.0 (9.8) 54.5%	147.2 ± 2.1 (8.2) 68.2%	99.9 ± 1.7 (9.8) 46.3%
Adult	8	7	23.4 ± 0.8 [6] (8.8) 9.9%	26.3 ± 0.9 [6] (8.3) 11.1%	32.6 ± 0.9 (7.3) 13.8%	178.5 ± 4.2 (6.3) 75.4%	135.1 ± 3.3 (6.4) 57.1%	161.0 ± 3.4 [6] (5.6) 68.0%	111.8 ± 2.5 (5.4) 47.4%
	9	5	22.6 ± 0.7 [4] (6.5) 9.3%	25.0 ± 0.9 [4] (7.1) 10.3%	29.8 ± 1.1 (8.1) 12.3%	184.3 ± 2.0 [4] (2.1) 75.9%	137.1 ± 1.8 (2.9) 56.6%	164.6 ± 0.7 (1.0) 68.0%	112.0 ± 1.5 (3.0) 46.3%
	10	5	26.7 ± 1.1 [4] (8.1) 10.6%	27.0 ± 1.8 (14.8) 10.9%	35.7 ± 0.3 [4] (1.9) 14.1%	189.0 ± 3.4 (4.1) 76.2%	141.8 ± 2.9 (4.6) 57.1%	173.3 ± 2.7 [4] (3.1) 68.7%	115.5 ± 2.9 (5.7) 46.6%
	8-10	17	24.1 ± 0.7 [14] (10.3) 9.9%	26.2 ± 0.7 [15] (10.6) 10.8%	32.5 ± 0.8 [16] (9.3) 13.4%	183.2 ± 2.4 [16] (5.2) 75.8%	137.7 ± 1.7 (5.2) 57.0%	165.2 ± 2.0 [15] (4.8) 68.2%	113.0 ± 1.4 (4.8) 46.8%
	≥ 12	12	28.0 ± 0.8 [11] (11.3) 11.0%	30.0 ± 0.8 [11] (8.5) 11.8%	35.8 ± 0.6 (6.5) 14.1%	195.3 ± 2.1 [11] (3.4) 76.0%	150.6 ± 2.1 (4.7) 59.5%	173.6 ± 1.8 (3.7) 68.5%	121.0 ± 1.6 (4.3) 47.8%
Total		63	54	54	61	57	63	61	63
Mean for males ≥ 200 cm [max. value in brackets] ^b			28.7 ± 2.5 [35.4]	28.9 ± 1.4 [32.7]	36.5 ± 1.6 [40.9]	197.0 ± 6.3 [211.6]	140.0 ± 2.0 [158.9]	174.8 ± 4.9 [183.4]	120.2 ± 2.7 [126.1]
Growth pattern, Evidence of a SGSC ^c			Somatic, 35% No	Somatic, 20% No	Somatic, 17% (see text)	Somatic, 13% No	Somatic, 20% No	Somatic, 10% No	Somatic, 13% No

Variables: P15 breadth of palate at postcanine 1; P16 breadth of palate at postcanine 3; P17 breadth of palate at postcanine 5; P18 gnathion to hind border of postglenoid process; P19 bizygomatic breadth; P20 basion to zygomatic root; P21 calvarial breadth.

continued next page

Bizygomatic breadth (P19) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope ($b = 1.12$) relative to CBL, increasing by 64% at 10 y (RTY). The ratio of bizygomatic breadth to CBL was 1 : 1.8 in yearlings and adults. Bizygomatic breadth was generally the widest part of the skull; however, mastoid breadth exceeded bizygomatic breadth in 10 animals (7 subadults; 3 adults).

Splanchnocranium region (D3, L24, L25)

Gnathion to posterior end of nasals (D3) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 66% at 10 y (RTY). A weak secondary growth spurt was apparent at 10 y.

Gnathion to foramen infraorbital (L24) and gnathion to posterior border of preorbital process (L25) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope ($b =$

1.26, 1.25) relative to CBL, increasing by 62% and 70% at 10 y (RTY), respectively.

Nasal region (D4, D5)

Width of anterior nares (D4) followed a somatic, monophasic growth pattern. Overall growth was isometric relative to CBL (Fig. 4.8), increasing by 43% at 10 y (RTY).

Greatest length of nasals (D5) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 76% at 10 y (RTY). There was some evidence of a very slight secondary growth spurt at 10 y, but this may have been an effect of sampling. The ratio of nasal breadth to length increased from 1 : 1.2 (yearlings) to 1 : 1.5 y (10 y).

Palatal region (P10, P11, P12, P13, P15, P16, P17)

Palatal notch to incisor (P10) and gnathion to posterior end of maxilla (P13), followed a somatic

continued from previous page

Age group	Age (y)	n ^a	P22	P23	L24	L25	L26**	L27**	M28
Yearling	1	2	74.8 ± 2.1 (4.0) 46.9%	59.6 ± 0.9 (2.0) 37.3%	45.7 ± 2.5 (7.6) 28.6%	48.3 ± 0.4 (1.2) 30.3%	73.1 [1*]	0.0	98.9 ± 0.1 (0.1) 62.9%
Subadult	2	2	82.0 ± 3.2 (5.4) 47.0%	62.6 ± 4.1 (9.2) 35.9%	42.2 ± 2.7 (9.0) 24.2%	52.2 ± 1.7 (4.5) 29.9%	72.3 ± 0.9	0.0 [1]	114.8 ± 9.1 (11.2) 65.8%
	3	2	93.9 ± 0.7 (1.0) 47.8%	66.5 ± 0.7 (1.4) 33.9%	57.1 ± 3.6 (8.9) 29.1%	59.1 ± 0.3 (6.7) 30.1%	– [0]	0.0	126.0 ± 1.2 (1.3) 64.2%
	4	8	100.9 ± 2.8 (7.9) 49.2%	69.8 ± 1.2 (5.0) 34.0%	61.4 ± 2.7 (12.4) 29.9%	64.3 ± 2.5 (11.2) 31.3%	77.6 ± 0.6 [4]	0.07 ± 0.07 [7]	136.5 ± 3.8 (7.9) 66.5%
	5	4	109.8 ± 3.5 (6.3) 50.6%	74.6 ± 0.9 (2.5) 34.4%	63.1 ± 1.2 (3.9) 29.1%	69.3 ± 1.8 (5.2) 31.9%	86.0 ± 2.1 [3]	0 [2]	147.2 ± 4.8 (6.5) 67.8%
	6	4	111.5 ± 1.6 (3.2) 50.3%	73.8 ± 0.4 (1.2) 33.6%	64.5 ± 1.8 (6.2) 29.8%	71.9 ± 1.4 (4.3) 32.5%	86.5 ± 0.8 [3]	0.7 ± 0.5 [4]	149.7 ± 1.9 (2.9) 68.0%
	7	12	119.3 ± 1.8 (5.1) 51.7%	76.2 ± 0.7 (3.2) 33.0%	69.4 ± 1.1 (5.5) 30.1%	75.0 ± 1.0 (4.8) 32.5%	94.2 ± 1.5 [9]	4.5 ± 1.2 [8]	159.6 ± 1.7 (3.7) 68.7%
	2–7	32	108.7 ± 2.1 (11.3) 50.3%	72.7 ± 0.8 (6.5) 33.7%	63.6 ± 1.4 (12.8) 29.5%	68.9 ± 1.4 (11.5) 31.9%	86.7 ± 1.8 [21]	1.6 ± 0.6 [24]	146.3 ± 2.7 (10.5) 67.6%
Adult	8	7	124.4 ± 2.7 (5.8) 52.5%	77.4 ± 1.2 (4.1) 32.7%	71.6 ± 1.4 (5.2) 30.3%	77.9 ± 1.5 (5.0) 32.9%	100.1 ± 3.3	5.4 ± 0.7 [4]	168.1 ± 3.5 [6] (5.1) 70.5%
	9	5	125.0 ± 3.5 [4] (5.5) 51.9%	76.7 ± 1.0 [4] (2.5) 31.9%	71.8 ± 0.7 (2.2) 29.6%	78.8 ± 1.3 [4] (3.3) 32.5%	101.8 ± 5.3	6.0 ± 1.6 [3]	168.8 ± 1.1 (1.4) 69.7%
	10	5	134.3 ± 4.4 (7.4) 54.1%	78.6 ± 2.6 (7.3) 31.7%	74.0 ± 1.7 (5.3) 29.8%	82.1 ± 2.0 (5.5) 33.1%	108.0 ± 6.8	9.2 ± 1.3	177.0 ± 6.0 (7.6) 71.3%
	8–10	17	127.6 ± 2.2 [16] (6.9) 52.9%	77.6 ± 0.9 [16] (4.8) 32.0%	72.4 ± 0.8 (4.5) 29.9%	79.4 ± 1.0 [16] (5.1) 32.9%	103.5 ± 2.8	7.1 ± 0.8 [12]	171.1 ± 2.4 [16] (5.6) 70.5%
	≥ 12	12	139.4 ± 2.2 [11] (5.0) 55.3%	80.4 ± 0.9 [11] (3.5) 31.8%	78.2 ± 1.1 (4.6) 30.9%	85.6 ± 1.1 (4.4) 33.8%	115.5 ± 1.0 [11]	8.2 ± 0.8 [9]	175.1 ± 3.9 (7.7) 70.2%
Total		63	61	61	63	62	50	47	62
Mean for males ≥ 200 cm [max. value in brackets] ^b			139.7 ± 4.5 [149.7]	84.2 ± 1.8 [87.4]	80.8 ± 2.9 [88.3]	89.0 ± 3.2 [96.6]	116.4 ± 4.8 [126.2]	6.5 ± 1.2 [12.0]	184.1 ± 6.1 [194.1]
Growth pattern, Evidence of a SGSC ^c			Somatic, 17% 10 y (strong)	Neural, 5% No	Somatic, 13% No	Somatic, 19% No	Somatic, 23% 10 y (weak)	Somatic, 82% (see text)	Somatic, 10% No

Variables: P22 mastoid breadth; P23 basion to bend of pterygoid; L24 gnathion to anterior of foramen infraorbital; L25 gnathion to hind border of preorbital process; L26 height of skull at bottom of mastoid; L27 height of sagittal crest; M28 length of mandible.

continued next page

growth pattern. Overall growth scaled with a very weak positive slope ($b = 1.07, 1.06$) relative to CBL, increasing by 70% and 61% at 10 y (RTY), respectively.

Length of upper PC tooth row (P11) followed a somatic, monophasic growth pattern. Overall growth scaled with negative slope ($b = 0.84$) relative to CBL, increasing by 46% at 10 y (RTY).

Greatest bicanine breadth (P12) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 51% at 10 y (RTY). There was some evidence of a very slight secondary growth spurt at 10 y, but this may have been an effect of sampling.

Breadth of palate at PC 1 (P15), 3 (P16) and 5 (P17) followed a somatic growth pattern, increasing by 89%, 47% and 72% at 10 y (RTY), respectively. Overall

growth expressed strong positive allometry for breadth at PC1; positive allometry for PC5; and isometry for breadth at PC3, relative to CBL. There was some evidence of a very slight secondary growth spurt in breadth at PC5 at 10 y, but this may have been an effect of sampling. The ratio of palatal breadth at PC5 (P17) to palatal length (P10) was 1 : 3 in both yearlings and adults (10 y).

Mandible (M28, M29, M30, M31, M32)

Length of mandible (M28) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope ($b = 1.22$) relative to CBL, increasing by 79% at 10 y (RTY).

Length of mandibular tooth row (M29) and length of lower post-canine row (M30) followed a neural

continued from previous page

Age group	Age (y)	n ^a	M29	M30	M31	M32
Yearling	1	2	46.8 ± 1.5 (4.5) 28.8%	37.4 [1*] (-) 23.8%	25.9 [1*] (-) 16.5%	28.3 [1*] (-) 18.0%
Subadult	2	2	50.9 ± 1.0 (2.8) 29.2%	35.9 ± 0.1 (0.4) 20.6%	29.1 ± 3.3 (15.8) 16.7%	32.0 ± 1.4 (6.0) 18.3%
	3	2	54.3 ± 1.2 (3.1) 28.5%	39.4 ± 0.8 (2.7) 20.6%	35.6 ± 2.4 (9.3) 17.1%	38.4 ± 1.8 (6.6) 18.8%
	4	8	59.3 ± 2.4 (11.6) 28.9%	39.4 ± 1.1 [6] (6.7) 19.5%	38.4 ± 1.9 [7] (12.8) 18.7%	40.5 ± 2.1 [7] (13.9) 18.7%
	5	4	61.3 ± 1.0 [3] (2.9) 28.8%	42.5 ± 0.8 (4.0) 19.6%	41.7 ± 2.1 (9.9) 19.2%	45.7 ± 1.4 (6.1) 21.1%
	6	4	61.3 ± 1.4 [3] (4.6) 27.6%	43.5 ± 0.7 (3.9) 19.6%	44.2 ± 1.5 (7.7) 20.4%	46.2 ± 1.3 (6.5) 21.2%
	7	12	67.5 ± 0.6 (3.2) 29.0%	45.4 ± 0.4 (2.9) 19.5%	48.2 ± 0.9 (6.5) 20.8%	49.3 ± 0.9 (6.3) 21.3%
	2-7	32	62.1 ± 1.1 [30] (10.2) 28.9%	42.5 ± 0.6 [30] (8.0) 19.6%	42.6 ± 1.2 [31] (15.6) 19.7%	44.7 ± 1.1 [31] (13.7) 20.7%
Adult	8	7	70.0 ± 1.0 (3.7) 29.6%	46.7 ± 0.8 (4.3) 19.7%	54.2 ± 1.9 (9.5) 22.9%	54.4 ± 1.9 (9.2) 23.0%
	9	5	67.4 ± 0.6 (1.9) 27.8%	46.6 ± 0.7 (3.3) 19.3%	53.7 ± 2.1 (8.8) 22.2%	53.2 ± 1.4 (5.8) 22.0%
	10	5	69.7 ± 1.8 [4] (5.1) 28.4%	46.3 ± 1.2 (5.7) 18.6%	59.5 ± 3.8 (14.2) 24.0%	58.0 ± 3.8 [4] (13.0) 23.4%
	8-10	17	69.1 ± 0.7 [16] (3.9) 28.7%	46.6 ± 0.5 (4.2) 19.3%	55.6 ± 1.5 (11.4) 23.0%	54.9 ± 1.3 [16] (9.5) 22.8%
	≥ 12	12	67.9 ± 2.0 [8] (8.4) 27.8%	46.6 ± 1.1 [11] (7.9) 18.6%	61.7 ± 2.4 (13.4) 25.0%	61.7 ± 1.9 (10.6) 24.6%
Total		63	56	59	61	60
Mean for males ≥ 200 cm [max. value in brackets] ^b			75.4 ± 8.1 [83.5]	47.0 ± 1.3 [52.5]	62.2 ± 3.5 [68.8]	65.8 ± 1.6 [69.0]
Growth pattern, Evidence of a SGS ^c			Neural, 0.6% No	Neural, 3% No	Somatic, 28% 10 y (weak)	Somatic, 25% 10 y (weak)

Variables: M29 length of mandibular tooth row; M30 length of lower postcanine row; M31 height of mandible at meatus; M32 angularis to coronoides.

Skull variable expressed as a percentage of skull length = skull measurement (mm)/CBL(mm) × 100% (only paired samples analysed).

^a Number of skulls for canine aged and known-aged animals. Sample size given in square brackets where this does not equal total sample size.

^b Mean value of variable ± S.E. for the 4 largest males (≥ 200 cm) of unknown-age; maximum value in brackets.

^c For classification of growth patterns (somatic or neural) see materials and methods; SGS, secondary growth spurt.

* S.E. of one measurement can not be measured.

** L26 and L27 were difficult to measure accurately.

Table 4.4 Growth in mean condylobasal length relative to mean standard body length

Age group	Age (y)	n ^a	Mean CBL ^b (mm)	Mean SBL ^c (cm)	CBL rel. to SBL ^d
Yearling	1	2	159.7 ± 2.6	82.5 ± 2.5	19.4%
Subadult	2	2	174.5 ± 7.2	94.5 ± 4.5	18.5%
	3	2	196.2 ± 1.8	121.0 ± 3.0	16.2%
	4	8	205.2 ± 4.7	126.0 ± 5.2	16.3%
	5	4	219.3 ± 5.1 [3]	141.0 ± 3.8 [3]	15.6% [3]
	6	4	220.6 ± 3.4	149.0 ± 1.7	14.8%
	7	12	232.0 ± 2.5 [9]	159.0 ± 3.4 [9]	14.6% [9]
	2-7	32	214.7 ± 3.6 [28]	138.9 ± 4.1 [28]	15.5% [28]
Adult	8	7	238.8 ± 6.0 [5]	170.4 ± 7.6 [5]	14.0% [5]
	9	5	242.7 ± 2.0 [4]	170.8 ± 2.3 [4]	14.2% [4]
	10	5	248.2 ± 4.7	187.4 ± 6.5	13.2%
	8-10	17	243.3 ± 2.8 [14]	176.6 ± 4.0 [14]	13.8% [14]
	≥ 12	12	250.4 ± 4.5 [11]	183.7 ± 5.8 [11]	13.6% [11]
Total		63	55	55	55

^a Number of skulls from canine aged and known-age animals with both CBL and SBL recorded. Of the 63 aged animals, SBL was not recorded for 8 animals, i.e., n = 55. Sample size given in square brackets where this does not equal total sample size.

^b Condylobasal length (mean ± S.E.).

^c Standard body length (mean ± S.E.). SBL is defined as the length from the nose to the tail in a straight line with the animal on its back.

^d CBL (mm)/SBL (mm) × 100%.

growth pattern, with most growth completed by 7 y (68 mm; 45 mm). Growth was negatively allometric relative to CBL (Fig. 4.9). The ratio of the length of the lower PC row (M30) to upper PC row (P11) was 1 : 1.1 (yearlings) and 1 : 1.3 (10 y).

Height of mandible at meatus (M31), and angularis to coronoideus (M32), followed a somatic growth pattern, with a weak secondary growth spurt at 10 y. Overall growth expressed strong positive allometry relative to CBL (Fig. 4.10), with variables increasing by 130% and 105% at 10 y (RTY), respectively. Growth in vertical height of the mandible was considerably greater than that of length.

Abnormalities

Of the 60 PEM skulls examined, 14 (23%) had a cleft palate varying in severity from slight clefts to moderate deformity (PEM: 951, 958, 1453, 1560, 1882, 2050, 2051, 2052, 2053, 2132, 2137, 2141, 2197, 2253), and abnormal bony deposits were observed on the occipital bone, at the base of the parietal in PEM2049. In addition, it was clear that the deciduous canines persist in some animals until their tenth month (i.e.,

Table 4.5 Discriminant analysis for seal age group (sub-adult, adult) inferred from skull length

Known age group	<i>n</i> ^a	Classification into age group	
		1	2
		Subadult (1 y 7 mo to 7 y 6 mo)	Adult ^b (≥ 7 y 7 mo)
1	32	26 (81%)	3
2	29	6	26 (90%)
Total	61	32	29

^a Number of seals of known-age (MCM animals tagged as pups), and aged from counts of incremental lines observed in the dentine of upper canines (PEM animals). Yearlings excluded, i.e., *n* = 61. Percentage of animals correctly classified into age group is given in brackets.

^b Included animals ≥ 12 y.

AP4999). According to Rand (1950): (i) deciduous canines are lost by the end of March; (ii) permanent canines do not erupt from the gums before 4 mo of age and are well developed by 8 mo (end of July).

Table 4.6 Suture index for male Cape fur seals according to age (y) and age group

No ^a	Suture ^b	Yearling		Subadults				Adults				
		10 mo	2 y	3 y	4 y	5 y	6 y	7 y	8 y	9 y	10 y	≥12 y
viii	Basioccipito-basisphenoid (brain case)	1	1	4	1*–4	4	4	4	4	4	4	4
i	Occipito-parietal (brain case)	1	1	3	2–4	4	3–4	4	3–4	4	4	4
ii	Interparietal (brain case)	1	1	1	1–2	1–2	1–3	1–4	1–4	2–4	3	3–4
iii	Coronal (brain case)	1	1–2	2	1–3	1–2	2–3	1–3	1–3	1–3	3	3–4
x	Squamosal-jugal (face-zygomatic)	1	1	1	1	1	1	1	1–2	1	2	3–4
vi	Premaxillary-maxillary (face-maxilla)	1	1	1	1	1	1	1	1	1	1	1–3
xi	Maxillary (face-maxilla)	1	1	1	1	1	1	1	1	1	1	1–3
ix	Squamosal-parietal (brain case)	1	1	1	1	1	1	1	1	1	1	1–3
iv	Interfrontal (brain case)	1	1	1	1	1	1	1	1	1	1	1–2
viii	Basisphenoid-presphenoid (brain case)	1	1	1	1	1	1	1	1	1	1	1
v	Internasal (face-nasal)	1	1	1	1	1	1	1	1	1	1	1
	Suture index ^c	11	11–12	17	13–19	17–19	18–21	18–21	19–22	18–23	22	27–33
	Total no. skulls = 48	2	2	2	7	3	4	8	6	3	1	10

^a Suture numbers i–xi correspond to Fig. 2.

^b Sutures arranged in order of closure (1, suture fully open; 2, suture less than half-closed; 3, suture more than half-closed; 4, suture completely closed).

^c Total value of the 11 cranial sutures (minimum and maximum). Note that the suture index is not necessarily the total value of each column.

Age inferred from counts of incremental lines observed in the dentine of upper canine, and from animals tagged as pups.

*The basioccipito-basisphenoid was fully open in one 4-y-old (AP4496).

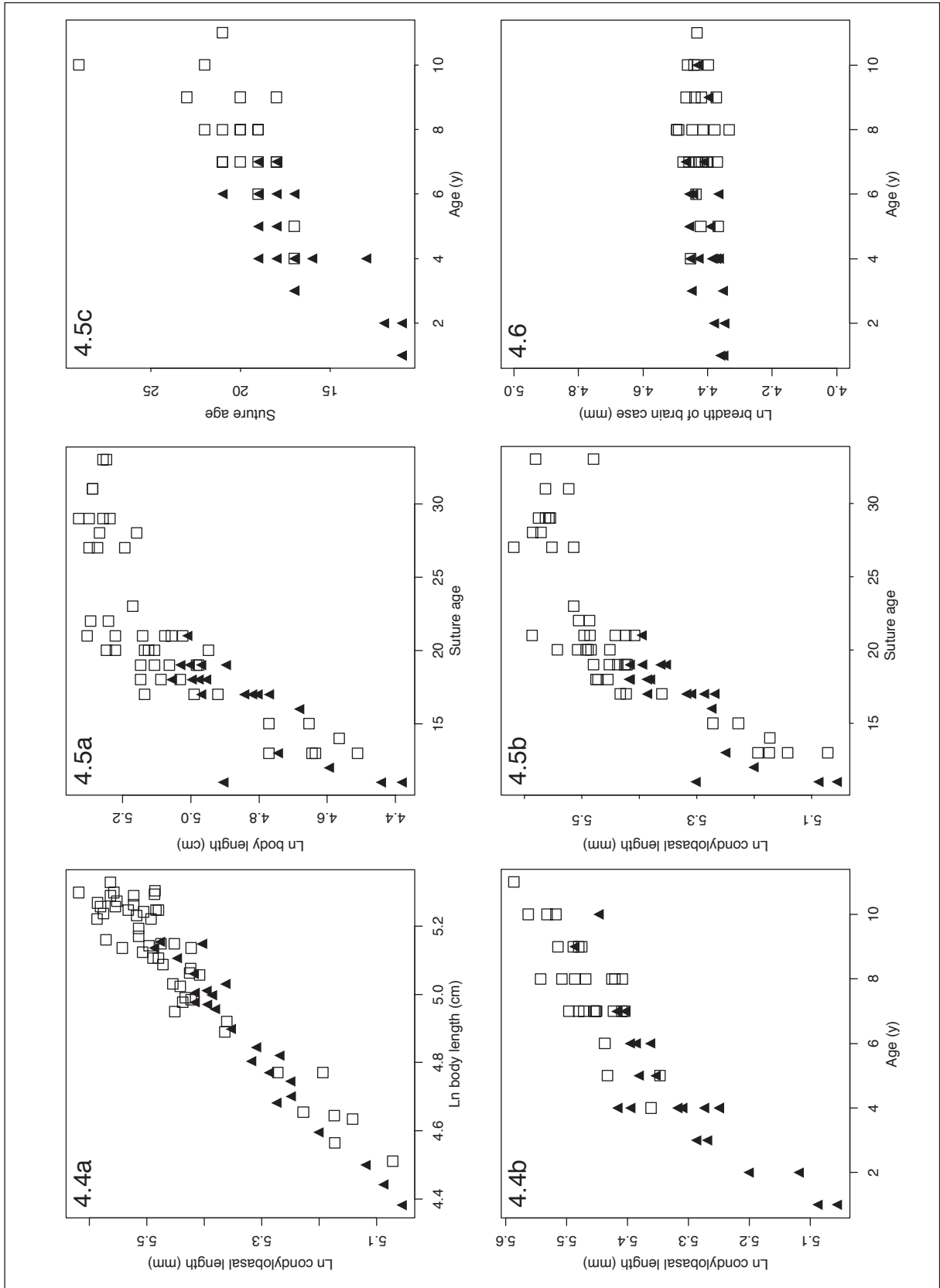


Fig. 4.4a, 4.4b Bivariate plot of log condylobasal length (mm) on: (a) log body length (cm) and (b) age (y).

Fig. 4.5a, 4.5b, 4.5c Bivariate plots of: (a) log body length (cm) on suture age; (b) log condylobasal length (mm) on suture age; (c) suture age on age (y).

Fig. 4.6 Example of neural growth. Log breadth of brain case (mm) on age (y).
Solid triangles, known-age animals (MCM). Squares, canine aged animals (PEM).

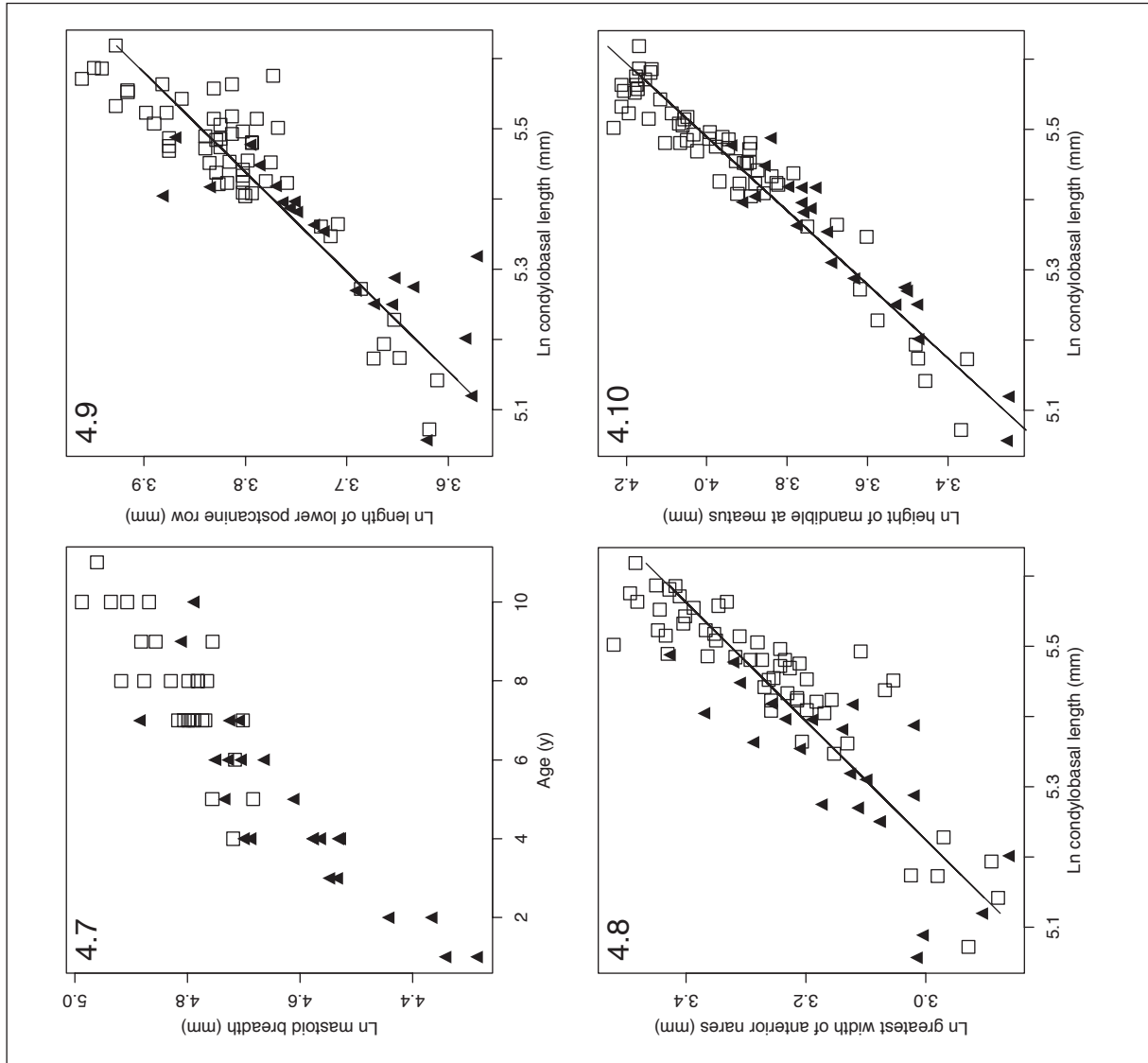


Fig. 4.7 Example of somatic, biphasic growth. Log mastoid breadth (mm) on age (y).

Fig. 4.8 Example of isometric growth. Log greatest width of anterior nares on log condylobasal length (mm).

Fig. 4.9 Example of negative allometry. Log length of lower postcanine row (mm) on log condylobasal length (mm).

Fig. 4.10 Example of strong positive allometry. Log height of mandible at meatus (mm) on log condylobasal length (mm).

Solid triangles, known-age animals (MCM). Squares, canine aged animals (PEM).

DISCUSSION

Skull size

Arctocephalus pusillus is the largest of the fur seals, therefore the skull is correspondingly large. In the present study, the maximum CBL was 275.4 mm (PEM898); however, skulls up to 307 mm (Australian fur seal, *A. p. doriferus*) have been reported (Cruwys & Friday, 1995). As with all southern fur seals, the skull is considerably larger in males than in females, reflecting pronounced sexual dimorphism (see Stewardson *et al.*, 200Xb).

East coast and west coast animals

It has been suggested that marine mammal species inhabiting warmer waters may be smaller in body

size than marine mammal species inhabiting cooler waters (Ross & Cockcroft, 1990). Long-term climatic data in Algoa Bay, based on daily measurements, indicate that the mean water temperature is 16–17° C in winter and 21–22° C in summer. For Luderitz (near Sinclair Island), mean water temperature is 12–13° C in winter and 14–15° C in summer, considerably cooler than Eastern Cape waters (Dr M. Grundlingh, pers. comm.). When comparing CBL from adult Cape fur seals from these two geographic locations, we did not find sufficient reason to reject the hypothesis that the population means for skull length were equal using PEM animals > 12 y. However, it is not clear if this result was influenced by a larger number of older adults in the PEM sample. When younger PEM animals were included in the adult sample (7–12+ y), Eastern Cape seals were found to be significantly smaller than west coast seals. Further testing using a larger sample of aged animals is required.

Skull shape

Morphological observations of the skull were generally consistent with earlier studies by Rand (1949b, 1950, 1956) and Repenning *et al.*, (1971). As for all otariids, the frontal bones project anteriorly between the nasal bones; supraorbital processes are present; the tympanic bulla are small and flat, comprised primarily of the ectotympanic; the alisphenoid canal is present; the mastoid processes are massive; the jugal-squamosal joint of the zygomatic arch overlap; and deep transverse grooves occur on the occlusal surface of the upper incisors (Burns & Fay, 1970; King, 1983; present study).

Within the species, the forehead is convex at the supraorbital region; the snout is long; the nasals are long and flared anteriorly; the palate is moderately broad and arched; the maxillary shelf at the root of the zygomatic process is very short in an anterior-posterior direction; the tooth rows are parallel, with robust, tricuspid PC, and a slight diastema between upper PC 5 and 6 (Repenning *et al.*, 1971; present study).

As with other species of this genus, the interorbital region (D7) was less than 20% of CBL in adults (i.e., 15%); palatal notch to the incisors (P10) was more than 37% of CBL (i.e., 43%); and nasal length (D5) fell within 14% (smallest fur seal, *A. galapagoensis*) and 18% (largest fur seal, *A. pusillus*) of CBL (i.e., 18%) (Scheffer, 1958; Cruwys & Friday, 1995; present study).

Condylbasal length as an indicator of SBL and age

In male Cape fur seals, CBL continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). The absence of very old skulls of known-age (18–20 y), made it difficult to determine overall growth in CBL. In contrast CBL continues to increase until at least 13 y in male *C. ursinus* (Scheffer & Wilke, 1953, but see Scheffer & Kraus, 1964) and slows at 10 y in male *E. jubatus* (Fiscus, 1961).

Condylbasal length was found to be a reasonable indicator of SBL and age group, but not of absolute age. The classification criteria for SBL developed in this study will be particularly useful when a seal is decomposed/scavenged (total SBL can not be measured), and/or the skull is incomplete /absent (total SBL can not be extrapolated from skull length). The classification criteria for age group will be particularly useful when canines are not available for age determination; or museum records have been misplaced or destroyed. As more specimens become available, the classification criteria will be more precise.

Suture index as an indicator of age

Although cranial sutures close progressively with age, suture age was not considered to be good indicator of chronological age (y) or age group (present study). Similar observations have been made in other male

otariids, e.g., in *C. ursinus*, the rate of suture closure is highly variable, and like SBL and CBL, is a poor indicator of chronological age (Scheffer & Wilke, 1953). Suture age is examined in more detail elsewhere (Stewardson *et al.*, 200X)

Function and growth

Neurocranium region

In mammals, growth of the protective brain case corresponds closely to that of the enclosed brain (Moore, 1981). The brain/brain case grows rapidly during prenatal and postnatal life; attains full size early in development before that of the basicranium or face; and scales with negative slope relative to skull size (Moore, 1966, 1981; Bryden, 1972; King, 1972; Gould, 1975; Moore & Lavelle, 1975; Enlow, 1982; Shea, 1985; Wayne, 1986; Hartwig, 1993; Morey, 1990; present study). Early maturation of the brain /brain case is essential for nervous control of the body.

The sagittal crest strengthens the skull, and provides an increased surface area for muscle attachment. In adults, large crest size is advantageous in combat behaviour between breeding bulls, and in feeding (increases bite force). Sagittal crest height begins to increase in size at 4–7 y (highly variable), reaching at least 12 mm in some adult males. In male *Z. californianus*, the sagittal crest begins to develop at 5 y, with height ranging from 11–36.5 mm in adults (Orr *et al.*, 1970). In male *E. jubatus*, sagittal crest height ranged from 7–37 mm in adults (Fiscus, 1961). Variation in crest height in older males presumably reflects differences between breeding and non-breeding bulls.

Basicranium region

The basicranium accommodates the hearing apparatus (Enlow, 1982). As with other mammals, growth of the otic capsule (and associated structures) appears to follow a neural growth pattern (Bast & Anson, 1949; Hoyte, 1961; Moore, 1981). Early development of the otic capsule enables juveniles to recognise the ‘pup-attraction call’ of their mothers. Mother-pup recognition is critical for pinnipeds living within a colony where separation is frequent, and mother-pup pairs are numerous (see Rand, 1967; Trillminch, 1981; Oftedal *et al.*, 1987; Bowen, 1991).

Unlike the otic capsule, calvarial breadth and mastoid breadth mature much later in life (present study). In adults, enlarged mastoids are advantageous in combat behaviour between breeding bulls, and in feeding (large head size/increases bite force); and facilitate directional hearing (provides a greater surface area of specific orientation for selective reflection of sound) (Repenning, 1972).

Frontal region

The interorbital region provides the structural base for the snout (Enlow, 1982). The dimensions of this region increase with age to accommodate the development of the proportionally large snout.

The supraorbital processes strengthen the skull (very thick in adults), protects the orbital region, and increases bite force. In adults seals, this enlarged structure is advantageous in feeding, and in combat behaviour between breeding bulls.

Zygomatic arch

The zygomatic arch protects the eye, provides a base for the masseter and part of the temporal muscle, accommodates conductive hearing (squamous root) and is the point of articulation for the mandible (Evans, 1993; Reppenning, 1972). As with other mammals, the zygomatic arch enlarges laterally and inferiorly to accommodate enlargement of the head, and a correspondingly greater temporal muscle mass (Moore, 1981; present study).

The orbital border of the zygomatic bone forms the ventral margin of the eye socket. As with other pinnipeds, the orbits were large to accommodate large eyes (King, 1972). In Cape fur seals, the horizontal diameter of the eye is *c.* 40 mm (e.g., animals AP5215, 2 y 4 mo; AP5210, 3 y). Although large eyes are potentially advantageous in the detection of benthic and/or fast moving pelagic prey (David, 1987), vision is not necessary to locate/capture prey (see King, 1983).

Splanchnocranium region

In Cape fur seals, lateral face length and width of snout at the canines, scaled with positive slope relative to CBL, similar to that of wild canids (Lumer, 1940; Morey, 1990). As the face and snout increased in length, the brain case and orbits became proportionally smaller.

In mammals, the size and shape of the brain establishes boundaries that determine the amount of facial growth; and special sense organs housed within the face influence the direction of growth (Enlow, 1982). In adult Cape fur seals, the brain is relatively large and more spherical than in terrestrial carnivores (Harrison & Kooyman, 1968; King, 1983), yet long and narrow compared to humans (i.e., small cerebrum). Therefore, the snout is correspondingly long and narrow. The wide nasal openings were aligned in a horizontal plane with the nerves of the olfactory bulb; and the orbital axis is pointed straight forward in the direction of body movement (Enlow, 1982; present study).

Nasal and palatal region

The naso-maxillary complex is the facial part of the respiratory (nasal cavity) and alimentary (oral cavity) tracts, which also facilitates sound production and the sense of smell. The floor of the nasal cavity forms the roof of the oral cavity, thus growth of the two cavities was highly coordinated. Growth was predominantly somatic, with similar allometric trends to those of wild canids (Lumer, 1940; Wayne, 1986; Morey, 1990). Progressive growth of this region is needed to accommodate the large dental battery.

Growth of dentition has been described by Rand (1950, 1956). At 6 to 12 mo, Cape fur seals gradually transfer from milk to solids (fish, crustacean and cephalopod) (Warneke & Shaughnessy, 1985). Although the small, deciduous teeth are usually lost by the end of the first 5 mo (Rand, 1956), deciduous canines may persist for 10 mo (present study). The permanent teeth are used to hold slippery prey (gripping), and to reduce prey size (biting and shearing). Growth of the permanent teeth is a gradual process, with diet becoming more varied with age and experience (Rand, 1959). In the upper jaw, the canines protrude beyond the tip of the 3rd upper incisor only in the 2nd y (Rand, 1956).

In male Cape fur seals, the ability to produce sound is evident at birth, with vocal skills broadening with increased age (Rand, 1967). In otariids, the production of sound is important in mother-pup recognition; communicating within a colony; and affirmation of territorial boundaries and social status (e.g., Stirling & Warneke, 1971).

Although the olfactory area is reduced when compared to terrestrial carnivores, the sense of smell appears to be well developed, and plays an important role in the detection of sexually receptive females, and land predators (Harrison & Kooyman, 1968; Peterson, 1968; King, 1983; Renouf, 1991; Wartzok, 1991).

Mandible

Using human anatomy as a model, the horizontal part of the mandible (corpus) provides the structural basis for tooth formation, and the vertical part (ramus = condyle, angular process, coronoid process, masseteric fossa) provides areas for articulation and muscle attachment.

As with other carnivores, the ramus increased substantially in height to accommodate implantation of the teeth, and expansion of the nasal region (Evans, 1993; Enlow, 1982; present study). The coronoid process grew upwards and backwards increasing in thickness on the anterior borders; the condyles grew backwards, beyond the level of the coronoid process; and the masseteric fossa formed a large, deep depression for jaw muscle (masseter and temporalis) attachment. Large jaws and jaw muscles are advantageous in feeding and in combat behaviour between breeding bulls (increases bite force/increases gape).

In mammals, the mandible of newborns is proportionally smaller than the upper jaw, and therefore must grow at a slightly faster rate to provide anatomical balance (Enlow, 1982). In order to achieve correct occlusal relationships between upper and lower dentition, the rate of growth between the mandible and maxilla needs to be highly coordinated (Moore, 1981). In Cape fur seals, the PC teeth are robust, therefore the tooth row is long.

Growth rate of the lower PC row ($b = 0.7$) was similar to that of the upper PC row ($b = 0.8$), relative

to CBL. Overall percent increase in growth was greater in the upper jaw because there are 6 PC in the upper jaw and only 5 in the lower jaw. The ratio of length of the lower PC row to upper PC row was 1 : 1.1 in yearlings, and increased to 1 : 1.3 in adults (at 10 y). Growth of the anterior dentition was considerably greater than that of the PC, due to development of the large canines.

CONCLUSION

Information presented in this study confirms earlier descriptions of the Cape fur seal skull (Rand, 1949*b*, 1950, 1956; Repenning *et al.*, 1971), and provides new information on skull growth according to age (y). In male Cape fur seals, CBL continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). Growth of the skull was a differential process and not simply an enlargement of overall size. Components within each region matured at different rates and grew in different directions. Apart from the dentition, all variables of the facial skeleton followed a somatic growth trajectory, and most variables were positively allometric with CBL. Breadth of braincase and basion to bend of pterygoid followed a neural growth trajectory and scaled with negative slope relative to CBL. Condylbasal length and suture age were found to be poor indicators of absolute age. However, CBL was a reasonable indicator of SBL and age group.

Further information is needed on cranial capacity; orbital size; tooth eruption; and the development of the sagittal crest in relation to chronological age and social status. Meaningful biological, evolutionary and functional inferences on skull growth can only be made when similar data is available for other pinniped species of known-age. Multivariate statistical procedures can then be employed to summarise morphometric relationships within and among populations.

ACKNOWLEDGEMENTS

We wish to express our sincere appreciation to the following persons and organisations for assistance with this study: Dr V. Cockcroft (Port Elizabeth Museum), Dr J. Hanks (WWF-South Africa) and Prof. A. Cockburn (Australian National University) for financial and logistic support; Mr B. Rose (Oosterlig Visserye, Port Elizabeth) who enabled us to collect seals from his commercial fishing vessels; Dr G. Ross (formerly Port Elizabeth Museum) and Dr V. Cockcroft for the use of PEM skulls collected before April 1992 ($n = 16$ skulls); Dr J.H.M. David (MCM) for the use of MCM skulls of known-age; Mr H. Oosthuizen for assistance with aging techniques; Mr S. Swanson (MCM) for assistance with data extraction and measurement of MCM specimens; Mr N. Minch (Australian National University) for photographic editing; Dr C. Groves and Dr A. Thorne (Australian National University), and Dr J.H.M. David (MCM) for their constructive comments on an earlier

draft of this manuscript. This paper is part of a larger study compiled on behalf of the World Wild Fund For Nature – South Africa (project ZA-348, part 1b).

REFERENCES

- BAST TH, ANSON BJ (1949) *The temporal bone and the ear*. Springfield: Charles C. Thomas.
- BERTRAM GCL (1940) The biology of the Weddell and crabeater seals, with a study of the comparative behaviour of the Pinnipedia. British Museum (Nat. Hist.) British Graham Land Expedition 1934–37, vol. 1, pp. 1–139. London.
- BOWEN WD (1991) Behavioural ecology of pinniped neonates. In *Behaviour of pinnipeds*, (ed. Renouf D), pp. 66–127. London: Chapman and Hall.
- BRUNNER S (1998) Cranial morphometrics of the southern fur seals *Arctocephalus forsteri* and *A. pusillus* (Carnivora: Otariidae). *Australian Journal of Zoology* **46**, 67–108.
- BRYDEN MM (1972) Growth and development of marine mammals. In *Functional anatomy of marine mammals*, (ed. Harrison RJ), vol. 1, pp. 58–60. London, New York: Academic Press.
- BURNS JJ, FAY FH (1970) Comparative morphology of the skull of the Ribbon seal, *Histiophoca fasciata*, with remarks on systematics of Phocidae. *Journal of Zoology (London)* **161**, 363–394.
- COCHRAN WG (1977) *Sampling techniques*, 3rd edn, New York: John Wiley and Sons.
- CRUWYS E, FRIDAY AE (1995) A comparative review of condylbasal lengths and other craniometric characters in 30 species of pinniped. *Polar Record* **31**, 45–62.
- DAVID JHM (1987) Diet of the South African fur seal (1974–1985) and an assessment of competition with fisheries in southern Africa. In *The Benguela and comparable ecosystems*, (ed. Payne AIL, Gulland JA, Brink K H). *South African Journal of Marine Science* **5**, 693–713.
- DOUTT KJ (1942) A review of the genus *Phoca*. *Annals of the Carnegie Museum* **29**, 61–125.
- ENLOW DH (1982) *Handbook of facial growth*, 2nd edn, Philadelphia: W. B. Saunders.
- EVANS HE (1993) *Miller's anatomy of the dog*, 3rd edn, Philadelphia: W. B. Saunders Company.
- FISCUS CH (1961) Growth in the Steller sea lion. *Journal of Mammalogy* **42**, 218–223.
- GIBBONS JD, CHAKRABORTI S (1992) *Nonparametric statistical inference*, 3rd edn, New York: Marcel Dekker, Inc.

- GOULD SJ (1975) Allometry in primates, with emphasis on scaling and the evolution of the brain. In *Approaches to primate paleobiology*, (ed. Szalay F), pp. 244–292. Basel: Krager.
- HAMILTON JE (1934) The southern sea lion, *Otaria byronia* (de Blainville). *'Discovery' Report* **8**, 269–318.
- HAMILTON JE (1939) A second report on the southern sea lion, *Otaria byronia* (de Blainville). *'Discovery' Report* **19**, 121–164.
- HARTWIG WC (1993) *Comparative morphology, ontogeny and phylogenetic analysis of the Platyrrhine cranium*. PhD thesis, University of California, Berkeley. Published in 1995 by the UMI Dissertation Services, A Bell & Howell Company, Michigan. pp. 628.
- HARRISON RJ, KOOYMAN GL (1968) General physiology of the Pinnipedia. In *The behaviour and physiology of pinnipeds*, (ed. Harrison RJ, Hubbard RC, Peterson RS, Rice CE, Schusterman RJ), pp. 211–296. New York: Appleton-Century-Crofts.
- HOYTE DAN (1961) The postnatal growth of the ear capsule in the rabbit. *American Journal of Anatomy* **108**, 1–16.
- KERLEY GIH, ROBINSON TJ (1987) Skull morphometrics of male Antarctic and subantarctic fur seals, *Arctocephalus gazella* and *A. tropicalis*, and their interspecific hybrids. In *Status, biology, and ecology of fur seals: Proceedings of an international symposium and workshop*, Cambridge, England, 23–27 April. (ed. Croxall JP, Gentry RL), *NOAA Technical Report NMFS* **51**, 121–131.
- KING JE (1972) Observations on phocid skulls. In *Functional Anatomy of Marine Mammals*, (ed. Harrison RJ), vol. 1, pp. 81–115. London, New York: Academic Press.
- KING JE (1983) *Seals of the world*, 2nd edn, London: British Museum (Nat. Hist.), Oxford University Press.
- LAWS RM (1953) The elephant seal (*Mirounga leonina* Linn.). 1. Growth and age. *Falkland Islands Dependencies Survey Scientific Reports* **8**, 1–62.
- LINDSEY AA (1937) The Weddell seal in the Bay of Whales, Antarctica. *Journal of Mammalogy* **18**, 127–144.
- LINDSEY AA (1938) Notes on the crab-eater seal. *Journal of Mammalogy* **19**, 456–461.
- LUMER H (1940) Evolutionary allometry in the skeleton of the domesticated dog. *American Naturalist* **74**, 439–467.
- MCCANN TS (1993) Age determination. In *Antarctic seals, research methods and techniques*, (ed. Laws RM), pp. 199–227. Great Britain: Cambridge University Press.
- MOORE WJ (1966) Skull growth in the albino rat (*Rattus norvegicus*). *Journal of Zoology (London)* **149**, 137–144.
- MOORE WJ (1981) *The mammalian skull*. London: Cambridge University Press.
- MOORE WJ, LAVELLE CLB (1975) *Growth of the facial skeleton in the Hominoidea*. London: Academic Press.
- MOREY DF (1990) *Cranial allometry and the evolution of the domestic dog*. PhD thesis, University of Tennessee, Knoxville. Published in 1994 by the UMI Dissertation Services, A Bell & Howell Company, Michigan. pp. 306.
- OFTEDAL OT, BONESS DJ, TEDMAN RA (1987) The behaviour, physiology and anatomy of lactation in the Pinnipedia. *Current Mammalogy* **1**, 401–441.
- OOSTHUIZEN WH (1997) Evaluation of an effective method to estimate age of Cape fur seals using ground tooth sections. *Marine Mammal Science* **13**, 683–693.
- ORR RT, SCHONEWALD J, KENYON KW (1970) The Californian sealion: skull growth and a comparison of two populations. *Proceedings of the Californian Academy of Sciences* **37**, 381–394.
- PETERSON RS (1968) Social behaviour in pinnipeds with particular reference to the northern fur seal. In *The behaviour and physiology of pinnipeds*, (ed. Harrison RJ, Hubbard RC, Peterson RS, Rice CE, Schusterman RJ), pp. 3–53. New York: Appleton-Century-Crofts.
- RAND RW (1949a) Studies on the Cape fur seal *Arctocephalus pusillus pusillus* 1. Age grouping in the female. Progress report submitted June 1949.
- RAND RW (1949b) Studies on the Cape fur seal *Arctocephalus pusillus pusillus* 3. Age grouping in the male. Progress report submitted November 1949.
- RAND RW (1950) On the milk dentition of the Cape fur seal. *Journal of the Dental Association of South Africa* **5**, 462–477.
- RAND RW (1956) The Cape fur seal *Arctocephalus pusillus pusillus* (Schreber): its general characteristics and moult. *Sea Fisheries Research Institute Investigational Report, South Africa* **21**, 1–52.
- RAND RW (1959) The Cape fur seal *Arctocephalus pusillus pusillus*. Distribution, abundance and feeding habits off the South Western Coast of the Cape Province. *Sea Fisheries Research Institute Investigational Report, South Africa* **34**, 1–75.
- RAND RW (1967) The Cape fur seal *Arctocephalus pusillus pusillus* 3. General behaviour on land and at sea. *Sea Fisheries Research Institute Investigational Report, South Africa* **60**, 1–39.

- RENOUF D (1991) Sensory reception and processing in Phocidae and Otariidae. In *Behaviour of pinnipeds*, (ed. Renouf D), pp. 345–394. London: Chapman and Hall.
- REPENNING CA (1972) Underwater hearing in seals: functional morphology. In *Functional Anatomy of Marine Mammals*, (ed. Harrison RJ), vol. 1, pp. 307–331. London, New York: Academic Press.
- REPENNING CA, PETERSON RS, HUBBS CL (1971) Contributions to the systematics of the southern fur seals, with particular reference to the Juan Fernandez and Guadalupe species. *Antarctic Research Series* **18**, 1–34.
- ROSS GJB, COCKCROFT VG (1990) Comments on Australian bottlenose dolphins and the taxonomic status of *Tursiops aduncus* (Ehrenberg, 1832). In *The Bottlenose Dolphin* (ed. Leatherwood SL, Reeves RR), pp. 101–125. London: Academic Press.
- SCHEFFER VB (1950) Growth layers on the teeth of Pinnipedia as indication of age. *Science* **112**, 309–311.
- SCHEFFER VB (1958) *Seals, sea lions, and walruses: a review of the Pinnipedia*. London: Stanford University Press.
- SCHEFFER VB, WILKE F (1953) Relative growth in the northern fur seal. *Growth* **17**, 129–145.
- SCHEFFER VB, KRAUS BS (1964) Dentition of the northern fur seal. *US Fisheries and Wildlife Services, Fishery Bulletin* **63**, 293–315.
- SCOTT JH (1951) The comparative anatomy of jaw and tooth eruption. *Dental Record* **71**, 149–67
- SHEA BT (1985) Ontogenetic allometry and scaling: A discussion based on the growth and form of the skull in African apes. In *Size and scaling in primate biology*, (ed. Jungers WL), pp. 175–205. New York: Plenum Press.
- SIRIANNI JE, SWINDLER DR (1985) *Growth and development of the pigtailed macaque*. Boca Raton, Florida: CRC Press.
- SIVERTSEN E (1954) A survey of the eared seals (family Otariidae) with remarks on the antarctic seals collected by M/K 'Norvegia' in 1928–1929. *Det Norske Videnskaps – Akademii Oslo, Scientific results of the Norwegian Antarctic expeditions 1927–1928 et sqq.* **76 pp.**
- STEWARDSON CL, PRVAN T, MEYER M (200Xa) Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part one, external body. *Journal of Anatomy (Cambridge)* (submitted 2001).
- STEWARDSON CL, PRVAN T, MEYER M (200Xb) Sexual dimorphism in the adult Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): standard body length and skull morphology. *Zoological Journal of the Linnean Society* (submitted 2001).
- STEWARDSON CL, PRVAN T, MEYER M, SWANSON S (200Y) Suture age as an indicator of physiological age in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae). *Zoological Journal of the Linnean Society* (submitted 2001).
- STIRLING I, WARNEKE RM (1971) Implications of a comparison of the airborne vocalisations and some aspects of the behaviour of the two Australian fur seals, *Arctocephalus* spp., on the evolution and present taxonomy of the genus. *Australian Journal of Zoology* **19**, 227–241.
- TODD TW, SCHWEITER FP (1933) The later stages of developmental growth in the hyena skull. *American Journal of Anatomy* **52**, 81–123.
- TRILLMINCH F (1981) Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. *Behaviour* **78**, 21–42.
- WARNEKE RM, SHAUGHNESSY PD (1985) *Arctocephalus pusillus pusillus*, the South African and Australian fur seal: taxonomy, evolution, biogeography, and life history. In *Studies of Sea Mammals in South Latitudes*, (ed. Ling JK, Bryden MM), pp. 53–77. Proceedings of a symposium of the 52nd ANZAAS Congress in Sydney, May 1982. South Australian Museum.
- WARTZOK D (1991) Physiology of behaviour in pinnipeds. In *Behaviour of pinnipeds*, (ed. Renouf D), pp. 236–299. London: Chapman and Hall.
- WAYNE RK (1986) Cranial morphology of domestic and wild canids: the influence of developmental and morphological change *Evolution* **40**, 243–261.
- WEISBERG S (1985) *Applied linear regression*, 2nd edn, New York: John Wiley and Sons.

Appendix 4.1 *Cape fur seals (n = 83) examined in this study. Animals were collected from the coast of southern Africa between December 1982 and July 1997.*

ID No.	Date of collection	Approximate location ^a	Region ^b	Method of collection ^c	SBL (cm)	
1.	PEM898	22 Dec 82	1 km E of Van Starden's River Mouth, St. Francis Bay (FB)	ECP	stranding	200
2.	PEM916	Jan 1983	Willows, Port Elizabeth (PE) (34° 03'S, 25° 35'E)	ECP	stranding	91
3.	PEM917	11 Jan 83	2 km W of Maitland River Mouth, FB	ECP	stranding	104
4.	PEM951	16 May 83	35 km E of Sundays River Mouth, Woody Cape (WC)	ECP	stranding	170
5.	PEM958	13 Dec 83	Humewood, PE (33° 59'S, 25° 40'E)	ECP	other	190
6.	PEM975	7 Oct 83	40 km E of Sundays River Mouth, WC	ECP	stranding	172
7.	PEM1073	12 Sep 84	Oyster Bay (34° 10'S, 24° 39'E)	ECP	stranding	133
8.	PEM1453	30 Jan 88	3 km E Kabeljous River Mouth, Jeffreys Bay	ECP	stranding	193
9.	PEM1507	5 Feb 88	Kings Beach, PE (33° 58'S, 25° 39'E)	ECP	stranding	198
10.	PEM1560	26 Oct 88	Seaview (34° 01'E, 25° 17'S)	ECP	stranding	201
11.	PEM1587	18 May 89	Amsterdamhoek (33° 52'S, 25° 38'E)	ECP	stranding	192
12.	PEM1698	12 Apr 90	25 km E of Sundays River Mouth (WC)	ECP	stranding	190
13.	PEM1704	19 June 90	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	NR	147
14.	PEM1868	24 Sep 91	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	199
15.	PEM1877	2 Apr 92	Lauries Park, PE (34° 02'S, 25° 23'E)	ECP	stranding	185
16.	PEM1879	13 Apr 92	Flat Rocks, PE (34° 00'S, 25° 42'E)	ECP	stranding	200
17.	PEM1882	6 May 92	King's Beach, PE (33° 58'S, 25° 39'E)	ECP	stranding	180
18.	PEM1890	13 July 92	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	192
19.	PEM1891	18 July 92	Hobie Beach, SE of King's Beach (33° 58'S, 25° 39'E)	ECP	rehab. (D)	137
20.	PEM1892	27 July 92	Sardinia Bay (34° 02'S, 25° 29'E), 800 m E of boat shed	ECP	stranding	185
21.	PEM1895	29 July 92	Cape Recife, PE (34° 02'S, 25° 42'E), 2 km E of lighthouse	ECP	stranding	188
22.	PEM2004	25 July 92	EC trawl grounds (34° 45'S, 24° 18'E–34° 48'S, 24° 00'E)	ECP	by-catch	–
23.	PEM2006	13 Aug 92	EC trawl grounds (34° 45'S, 24° 25'E–34° 42'S, 24° 40'E)	ECP	by-catch	–
24.	PEM2007	14 Aug 92	EC trawl grounds (34° 42'S, 24° 51'E–34° 42'S, 24° 42'E)	ECP	by-catch	–
25.	PEM2008	14 Aug 92	EC trawl grounds (34° 41'S, 24° 42'E–34° 38'S, 24° 54'E)	ECP	by-catch	–
26.	PEM2009	22 Aug 92	EC trawl grounds (34° 41'S, 24° 45'E–34° 37'S, 24° 59'E)	ECP	by-catch	–
27.	PEM2010	22 Aug 92	EC trawl grounds (34° 47'S, 24° 11'E–34° 46'S, 24° 25'E)	ECP	by-catch	–
28.	PEM2013	14 Sep 92	EC trawl grounds (34° 24'S, 25° 50'E–34° 25'S, 26° 02'E)	ECP	by-catch	–
29.	PEM2014	25 Sep 92	EC trawl grounds (34° 23'S, 26° 04'E–34° 23'S, 25° 58'E)	ECP	by-catch	–
30.	PEM2035	11 Mar 93	The Pipes, SE of Pollock Beach (33° 59'20"S, 25° 40' 30"E)	ECP	stranding	118
31.	PEM2036	19 Mar 93	Black Rocks, Algoa Bay (AB) (33° 50'S, 26° 15'E)	ECP	stranding	–
32.	PEM2044	28 May 93	Seaview (34° 01'S, 25° 17'E), Otter Pools	ECP	stranding	206
33.	PEM2045	30 May 93	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	145
34.	PEM2046	19 May 93	EC trawl grounds (35° 09'S, 21° 28'E)	ECP	by-catch	141
35.	PEM2048	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E–34° 50'S, 23° 40'E)	ECP	by-catch	157
36.	PEM2049	7 June 93	Kini Bay, Western Beach (34° 01'S, 25° 26'E)	ECP	stranding	174
37.	PEM2050	8 June 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	ECP	stranding	165
38.	PEM2051	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	ECP	by-catch	168
39.	PEM2052	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	ECP	by-catch	171
40.	PEM2053	28 June 93	EC trawl grounds (34° 46'S, 24° 21'E–34° 44'S, 24° 32'E)	ECP	by-catch	153
41.	PEM2054	29 June 93	EC trawl grounds (34° 45'S, 24° 28'E–34° 47'S, 24° 18'E)	ECP	by-catch	165
42.	PEM2081	19 July 93	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	162
43.	PEM2082	July 93	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	176
44.	PEM2087	17 Aug 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	ECP	stranding	190
45.	PEM2132	20 Dec 93	Woody Cape, AB (33° 46'S, 26° 19'E)	ECP	stranding	195
46.	PEM2137	5 Jan 94	Summerstrand, PE (34° 00'S, 25° 42'E)	ECP	rehab. (D)	118
47.	PEM2140	17 Jan 94	40 km E of Sundays River Mouth, WC	ECP	stranding	187
48.	PEM2141	17 Jan 94	39 km E of Sundays River Mouth, WC	ECP	stranding	198
49.	PEM2143	21 Jan 94	Seaview (34° 01'S, 25° 17'E)	ECP	stranding	189
50.	PEM2151	3 Feb 94	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	194
51.	PEM2197	12 July 94	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	160
52.	PEM2198	July 94	Plettenberg Bay (34° 03'S, 23° 24'E)	ECP	stranding	105
53.	PEM2201	5 July 94	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	103
54.	PEM2238	July 1994	Durban (29° 50'S, 31° 00'E)	– ^d	rehab. (D)	96
55.	PEM2248	12 Aug 94	Seaview (34° 01'S, 25° 27'E)	ECP	stranding	158
56.	PEM2252	22 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	172
57.	PEM2253	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	152
58.	PEM2254	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	146
59.	PEM2257B	8 Oct 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	170
60.	MCM1565	25 Sep 84	2 miles offshore the Vondeling area (33° 18'S, 18° 06'E)	WC	sci. permit	118

continued on next page

continued from previous page

ID No.	Date of collection	Approximate location ^a	Region ^b	Method of collection ^c	SBL (cm)	
61.	MCM1786	30 Sep 94	St Helena Bay	WC	stranding	85
62.	MCM1809	14 Nov 84	Kleinzee	WC	sci. permit	173
63.	MCM1810	12 Feb 84	Kleinzee	WC	sci. permit	172
64.	MCM2763	10 Feb 85	Doringbaai area (31° 30'S, 16° 30'E)	WC	by-catch	127
65.	MCM2795	27 July 88	Demersal fishing grid 502	SWC	by-catch	158
66.	MCM3582	6 June 86	Offshore Dassen Island (33° 21'S, 17° 40'E)	WC	by-catch	142
67.	MCM3586	22 Apr 86	8 miles off Wilderness	SC	by-catch	144
68.	MCM3587	5 June 86	25 nm west of Mossel Bay	SC	by-catch	145
69.	MCM3636	17 July 87	West of Dassen Island (37° 45'S, 17° 35'E)	WC	by-catch	148
70.	MCM4365	13 Mar 90	3.5 nm off Gouritz River Mouth (34° 23'S, 21° 51'E)	SC	by-catch	124
71.	MCM4388	23 Oct 90	20 nm south of Gouritz River Mouth (34° 26'S, 21° 53'E)	SC	by-catch	122
72.	MCM4577	17 Jan 94	Cape Town Harbour	WC	stranding	150
73.	MCM4595	17 Oct 95	Off Cape Point (34° 45'S, 21° 49'E)	SW	by-catch	134
74.	MCM4597	15 Sep 95	South of Dassen Island (33° 30'S, 17° 40'E)	WC	by-catch	170
75.	MCM4989	14 Aug 96	St Helena	WC	by-catch	99
76.	MCM4992	13 Sep 96	Demersal fishing grid 493 (35° 30'S, 18° 56'E)	SW	by-catch	165
77.	MCM4996	28 Sep 96	Offshore Saldahna Bay (33° 10'S, 17° 14'E)	WC	by-catch	115
78.	MCM4999	10 July 96	Seal Island, St Helena Bay	WC	by-catch	80
79.	MCM5002	10 Jun 96	Offshore Saldahna Bay (33° 16'S, 17° 07'E)	WC	by-catch	108
80.	MCM5133	14 Jan 97	Offshore Plettenberg Bay (34° 30'S, 23° 30'E)	ECP	by-catch	153
81.	MCM5135	23 July 97	Offshore Stompneus Lighthouse	WC	stranding	110
82.	MCM5136	15 July 97	Offshore St Helena Bay (32° 27'S, 17° 38'E)	WC	by-catch	149
83.	MCM5145	Nov 94	St Helena Bay	WC	by-catch	90

^a Kabeljous River Mouth (34° 00'S, 24° 56'E); Maitland River Mouth (33° 59'S, 25° 18'E); Sundays River Mouth (33° 43'S, 25° 51'E); and Van Starden's River Mouth (33° 58'S, 25° 13'E).

^bWC (west coast), north of Cape Point Lighthouse (34° 21'S, 18° 29'E); SWC (south west coast), south of Cape Point Lighthouse to Cape Agulhas (34° 50'S, 20° 00'E); SC (south coast), east of Cape Agulhas, but excluding the Eastern Cape; and ECP (Eastern Cape Province), Plettenberg Bay (34° 03'S, 23° 24'E) to East London (33° 03'S, 27° 54'E).

^cStranding, animal washed up dead on beach ($n = 38$). By-catch, animal incidentally caught in a commercial trawl net during fishing operations ($n = 37$). Sci. permit, animal collected under scientific permit or harvested ($n = 3$). Rehab. (D), animal died during rehabilitation at the Port Elizabeth Oceanarium ($n = 3$). Other, animal died from other causes ($n = 1$, PEM958 found floating in the ocean off Humewood beach).

^dAnimal PEM2238 collected NE of the Eastern Cape, i.e., Durban (29° 50'S, 31° 00'E).

NR. not recorded.

Appendix 4.2 'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on log length of seal

Dependent variable	Linear regression				Allometry		
	<i>n</i> ^a	Intercept ± S.E.	Slope ± S.E.	<i>r</i> (<i>p</i>)	Alternative hypothesis	<i>d.f.</i>	<i>p</i>
Dorsal							
D1 Condylbasal length	74	2.65 ± 0.08	0.55 ± 0.02	0.93 (0.00)	H ₁ : $\hat{\beta} < 1$	72	0.00
D2 Gnathion to middle of occipital crest	73	2.51 ± 0.11	0.55 ± 0.02	0.93 (0.00)	NA	NA	NA
D3 Gnathion to posterior end of nasals	71	1.12 ± 0.12	0.65 ± 0.02	0.92 (0.00)	NA	NA	NA
D4 Greatest width of anterior nares	71	0.16 ± 0.19	0.61 ± 0.04	0.88 (0.00)	H ₁ : $\hat{\beta} < 1$	69	0.00
D5 Greatest length of nasals	70	0.19 ± 0.20	0.69 ± 0.04	0.85 (0.00)	H ₁ : $\hat{\beta} < 1$	69	0.00
D6 Breadth at preorbital processes	69	0.85 ± 0.13	0.65 ± 0.03	0.90 (0.00)	NA	NA	NA
D7 Least interorbital constriction	69	-0.04 ± 0.16	0.70 ± 0.03	0.88 (0.00)	H ₁ : $\hat{\beta} < 1$	67	0.00
D8 Breadth at supraorbital processes	65	1.07 ± 0.18	0.57 ± 0.04	0.86 (0.00)	H ₁ : $\hat{\beta} < 1$	63	0.00
D9 Breadth of brain case	71	3.95 ± 0.09	0.10 ± 0.02	0.40 (0.00)	NA	NA	NA
Palatal							
P10 Palatal notch to incisors	73	1.56 ± 0.15	0.60 ± 0.03	0.86 (0.00)	H ₁ : $\hat{\beta} < 1$	71	0.00
P11 Length of upper postcanine row	73	1.70 ± 0.15	0.46 ± 0.03	0.77 (0.00)	NA	NA	NA
P12 Greatest bicanine breadth	73	0.58 ± 0.16	0.64 ± 0.03	0.92 (0.00)	H ₁ : $\hat{\beta} < 1$	71	0.00
P13 Gnathion to posterior end of maxilla	73	1.74 ± 0.10	0.58 ± 0.02	0.91 (0.00)	H ₁ : $\hat{\beta} < 1$	71	0.00
P14 Breadth of zygomatic root of maxilla	74	0.45 ± 0.27	0.44 ± 0.05	0.74 (0.00)	H ₁ : $\hat{\beta} < 1$	72	0.00
P15 Breadth of palate at postcanine 1	72	-1.16 ± 0.25	0.84 ± 0.05	0.89 (0.00)	H ₁ : $\hat{\beta} < 1$	70	0.001
P16 Breadth of palate at postcanine 3	72	0.21 ± 0.19	0.60 ± 0.04	0.87 (0.00)	H ₁ : $\hat{\beta} < 1$	70	0.00
P17 Breadth of palate at postcanine 5	71	-0.02 ± 0.18	0.68 ± 0.04	0.87 (0.00)	H ₁ : $\hat{\beta} < 1$	69	0.00
P18 Gnathion to hind border of postglenoid process	72	1.88 ± 0.08	0.65 ± 0.02	0.93 (0.00)	NA	NA	NA
P19 Bizygomatic breadth	74	1.69 ± 0.12	0.62 ± 0.02	0.91 (0.00)	NA	NA	NA
P20 Basion to zygomatic root (anterior)	72	2.36 ± 0.07	0.53 ± 0.01	0.93 (0.00)	NA	NA	NA
P21 Calvarial breadth	72	1.76 ± 0.09	0.58 ± 0.02	0.94 (0.00)	NA	NA	NA
P22 Mastoid breadth	72	1.15 ± 0.11	0.72 ± 0.02	0.93 (0.00)	NA	NA	NA
P23 Basion to bend of pterygoid	72	2.52 ± 0.08	0.36 ± 0.02	0.91 (0.00)	H ₁ : $\hat{\beta} < 1$	70	0.00
Lateral							
L24 Gnathion to foramen infraorbital	73	0.85 ± 0.14	0.67 ± 0.03	0.91 (0.00)	H ₁ : $\hat{\beta} < 1$	71	0.00
L25 Gnathion to hind border of preorbital process	73	0.89 ± 0.11	0.68 ± 0.02	0.92 (0.00)	NA	NA	NA
L26 Height of skull at bottom of mastoid	61	1.40 ± 0.20	0.63 ± 0.04	0.90 (0.00)	NA	NA	NA
L27 Height of sagittal crest	55	–	–	0.73 (0.00)	–	–	–
Mandibular							
M28 Length of mandible	74	1.58 ± 0.09	0.69 ± 0.02	0.94 (0.00)	H ₁ : $\hat{\beta} < 1$	72	0.00
M29 Length of mandibular tooth row	64	1.70 ± 0.12	0.49 ± 0.02	0.85 (0.00)	H ₁ : $\hat{\beta} < 1$	62	0.00
M30 Length of lower postcanine row	69	1.96 ± 0.11	0.36 ± 0.02	0.83 (0.00)	H ₁ : $\hat{\beta} < 1$	67	0.00
M31 Height of mandible at meatus	72	-1.45 ± 0.19	1.06 ± 0.04	0.93 (0.00)	H ₁ : $\hat{\beta} \neq 1^{**}$	70	0.26
M32 Angularis to coronoideus	70	-0.89 ± 0.17	0.95 ± 0.03	0.94 (0.00)	H ₁ : $\hat{\beta} \neq 1^{**}$	68	0.28

^a Number of skulls from aged and unaged animals with both skull variable and SBL recorded. Of the 83 aged and unaged animals, SBL was not recorded for 9 animals, i.e., *n* = 74.

r, Spearman rank-order correlation coefficient.

NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.

** Since the *p*-value was > 0.05 then we cannot reject H₀ in favour of H₁ at the 5% significance level; therefore growth is isometric.

Appendix 4.3 'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on log condylobasal length

Dependent variable	Linear regression				Allometry		
	<i>n</i> ^a	Intercept ± S.E.	Slope ± S.E.	<i>r</i> (<i>p</i>)	Alternative hypothesis	<i>d.f.</i>	<i>p</i>
Dorsal							
D2 Gnathion to middle of occipital crest	79	-0.22 ± 0.17	1.01 ± 0.03	0.97 (0.00)	NA	NA	NA
D3 Gnathion to posterior end of nasals	80	-2.01 ± 0.19	1.18 ± 0.04	0.95 (0.00)	H ₁ : $\hat{\beta} > 1$	78	0.00
D4 Greatest width of anterior nares	79	-2.62 ± 0.32	1.08 ± 0.06	0.87 (0.00)	H ₁ : $\hat{\beta} \neq 1^{**}$	77	0.18
D5 Greatest length of nasals	78	-3.21 ± 0.31	1.27 ± 0.06	0.88 (0.00)	H ₁ : $\hat{\beta} > 1$	76	0.00
D6 Breadth at preorbital processes	78	-2.19 ± 0.21	1.16 ± 0.04	0.92 (0.00)	H ₁ : $\hat{\beta} > 1$	76	0.00
D7 Least interorbital constriction	78	-3.36 ± 0.30	1.27 ± 0.06	0.89 (0.00)	H ₁ : $\hat{\beta} > 1$	76	0.00
D8 Breadth at supraorbital processes	74	-1.66 ± 0.34	1.03 ± 0.06	0.83 (0.00)	NA	NA	NA
D9 Breadth of brain case	80	3.48 ± 0.19	0.17 ± 0.03	0.39 (0.00)	NA	NA	NA
Palatal							
P10 Palatal notch to incisors	82	-1.22 ± 0.20	1.07 ± 0.04	0.89 (0.00)	NA	NA	NA
P11 Length of upper postcanine row	82	-0.54 ± 0.23	0.84 ± 0.04	0.77 (0.00)	NA	NA	NA
P12 Greatest bicanine breadth	82	-2.38 ± 0.26	1.14 ± 0.05	0.93 (0.00)	H ₁ : $\hat{\beta} > 1$	80	0.00
P13 Gnathion to posterior end of maxilla	82	-1.06 ± 0.11	1.06 ± 0.02	0.96 (0.00)	NA	NA	NA
P14 Breadth of zygomatic root of maxilla	83	-1.97 ± 0.48	0.85 ± 0.09	0.75 (0.00)	H ₁ : $\hat{\beta} \neq 1^{**}$	81	0.17
P15 Breadth of palate at postcanine 1	73	-4.89 ± 0.48	1.47 ± 0.09	0.89 (0.00)	H ₁ : $\hat{\beta} > 1$	71	0.00
P16 Breadth of palate at postcanine 3	73	-2.42 ± 0.35	1.04 ± 0.06	0.87 (0.00)	H ₁ : $\hat{\beta} \neq 1^{**}$	71	0.56
P17 Breadth of palate at postcanine 5	80	-3.11 ± 0.34	1.20 ± 0.06	0.85 (0.00)	H ₁ : $\hat{\beta} > 1$	78	0.001
P18 Gnathion to hind border of postglenoid process	77	-1.18 ± 0.12	1.16 ± 0.02	0.96 (0.00)	NA	NA	NA
P19 Bizygomatic breadth	83	-1.25 ± 0.21	1.12 ± 0.04	0.89 (0.00)	NA	NA	NA
P20 Basion to zygomatic root (anterior)	81	-0.16 ± 0.08	0.96 ± 0.02	0.97 (0.00)	NA	NA	NA
P21 Calvarial breadth	81	-0.76 ± 0.16	1.00 ± 0.03	0.94 (0.00)	NA	NA	NA
P22 Mastoid breadth	81	-2.22 ± 0.17	1.29 ± 0.03	0.95 (0.00)	NA	NA	NA
P23 Basion to bend of pterygoid	81	0.89 ± 0.12	0.63 ± 0.02	0.90 (0.00)	H ₁ : $\hat{\beta} < 1$	79	0.00
Lateral							
L24 Gnathion to foramen infraorbital	82	-2.61 ± 0.17	1.26 ± 0.03	0.94 (0.00)	NA	NA	NA
L25 Gnathion to hind border of preorbital process	82	-2.49 ± 0.14	1.25 ± 0.03	0.97 (0.00)	NA	NA	NA
L26 Height of skull at bottom of mastoid	70	-1.90 ± 0.32	1.19 ± 0.06	0.94 (0.00)	NA	NA	NA
L27 Height of sagittal crest	60	–	–	0.80 (0.00)	–	–	–
Mandibular							
M28 Length of mandible	82	-1.58 ± 0.10	1.22 ± 0.02	0.98 (0.00)	NA	NA	NA
M29 Length of mandibular tooth row	73	-0.61 ± 0.19	0.88 ± 0.04	0.85 (0.00)	H ₁ : $\hat{\beta} < 1$	71	0.002
M30 Length of lower postcanine row	78	0.22 ± 0.18	0.66 ± 0.03	0.84 (0.00)	H ₁ : $\hat{\beta} < 1$	76	0.00
M31 Height of mandible at meatus	81	-6.31 ± 0.32	1.88 ± 0.06	0.95 (0.00)	H ₁ : $\hat{\beta} > 1$	79	0.00
M32 Angularis to coronoideus	79	-5.11 ± 0.28	1.66 ± 0.05	0.95 (0.00)	H ₁ : $\hat{\beta} > 1$	77	0.00

^a Number of skulls from aged and unaged animals with both skull variable and CBL recorded. CBL was recorded for all animals, *n* = 83.

r, Spearman rank-order correlation coefficient.

NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.

** Since the *p*-value was > 0.05 then we cannot reject H₀ in favour of H₁ at the 5% significance level; therefore growth is isometric.

Appendix 4.4 'Robust' least squares straight line equations and Spearman rank-order correlation coefficients for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on age (y)

Dependent variable	Linear regression			
	<i>n</i> ^a	Intercept ± S.E.	Slope ± S.E.	<i>r</i> (<i>p</i>)
Dorsal				
D1 Condylbasal length	51	5.15 ± 0.02	0.04 ± 0.00	0.89 (0.00)
D2 Gnathion to middle of occipital crest	49	4.97 ± 0.02	0.04 ± 0.00	0.92 (0.00)
D3 Gnathion to posterior end of nasals	49	4.04 ± 0.02	0.05 ± 0.00	0.87 (0.00)
D4 Greatest width of anterior nares	49	2.95 ± 0.03	0.04 ± 0.00	0.81 (0.00)
D5 Greatest length of nasals	47	3.30 ± 0.03	0.05 ± 0.00	0.76 (0.00)
D6 Breadth at preorbital processes	50	3.77 ± 0.02	0.05 ± 0.00	0.87 (0.00)
D7 Least interorbital constriction	49	3.09 ± 0.03	0.06 ± 0.00	0.89 (0.00)
D8 Breadth at supraorbital processes	45	3.60 ± 0.03	0.05 ± 0.00	0.85 (0.00)
D9 Breadth of brain case	51	4.38 ± 0.01	0.01 ± 0.00	0.31 (0.00)
Palatal				
P10 Palatal notch to incisors	50	4.24 ± 0.03	0.05 ± 0.00	0.84 (0.00)
P11 Length of upper postcanine row	50	3.78 ± 0.03	0.03 ± 0.00	0.59 (0.00)
P12 Greatest bicanine breadth	50	3.48 ± 0.02	0.05 ± 0.00	0.87 (0.00)
P13 Gnathion to posterior end of maxilla	50	4.36 ± 0.02	0.04 ± 0.00	0.83 (0.00)
P14 Breadth of zygomatic root of maxilla	52	2.45 ± 0.03	0.03 ± 0.00	0.57 (0.00)
P15 Breadth of palate at postcanine 1	43	2.57 ± 0.03	0.07 ± 0.00	0.89 (0.00)
P16 Breadth of palate at postcanine 3	43	2.89 ± 0.03	0.04 ± 0.00	0.77 (0.00)
P17 Breadth of palate at postcanine 5	49	3.05 ± 0.03	0.05 ± 0.00	0.74 (0.00)
P18 Gnathion to hind border of postglenoid process	46	4.79 ± 0.02	0.05 ± 0.00	0.92 (0.00)
P19 Bizygomatic breadth	51	4.50 ± 0.02	0.05 ± 0.00	0.89 (0.00)
P20 Basion to zygomatic root (anterior)	49	4.77 ± 0.02	0.04 ± 0.00	0.90 (0.00)
P21 Calvarial breadth	51	4.36 ± 0.02	0.04 ± 0.00	0.89 (0.00)
P22 Mastoid breadth	50	4.37 ± 0.02	0.06 ± 0.00	0.91 (0.00)
P23 Basion to bend of pterygoid	50	4.14 ± 0.02	0.02 ± 0.00	0.75 (0.00)
Lateral				
L24 Gnathion to foramen infraorbital	51	3.88 ± 0.03	0.05 ± 0.005	0.81 (0.00)
L25 Gnathion to hind border of preorbital process	50	3.92 ± 0.03	0.05 ± 0.00	0.87 (0.00)
L26 Height of skull at bottom of mastoid	39	4.17 ± 0.03	0.05 ± 0.005	0.79 (0.00)
L27 Height of sagittal crest	38	–	–	0.86 (0.00)
Mandibular				
M28 Length of mandible	50	4.70 ± 0.02	0.05 ± 0.00	0.91 (0.00)
M29 Length of mandibular tooth row	48	3.89 ± 0.02	0.04 ± 0.00	0.75 (0.00)
M30 Length of lower postcanine row	47	3.59 ± 0.02	0.03 ± 0.00	0.76 (0.00)
M31 Height of mandible at meatus	49	3.31 ± 0.04	0.08 ± 0.01	0.90 (0.00)
M32 Angularis to coronoideus	48	3.42 ± 0.03	0.07 ± 0.00	0.88 (0.00)
Log body length	44	4.53 ± 0.03	0.07 ± 0.00	0.87 (0.00)

^a Number of skulls with skull variable and age recorded (only animals 1–10 y were included in analysis, i.e., *n* = 51).

r, Spearman rank-order correlation coefficient.

[Model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test for allometry not applicable].

Appendix 4.5 Spearman rank-order correlation coefficients for log skull variables according to region

Frontal							
	Var (D7)	Var (D8)					
Var (D7)	1.00 (79)	0.93 (71)					
Var (D8)	0.93 (71)	1.00 (75)					
Nasal							
	Var (D4)	Var (D5)					
Var (D4)	1.00 (79)	0.81* (76)					
Var (D5)	0.81* (79)	1.00 (78)					
Neurocranium							
	Var (D9)	Var (L27)					
Var (D9)	1.00 (80)	0.25 (59)					
Var (L27)	0.25 (59)	1.00 (60)					
Zygomatic arch							
	Var (P14)	Var (P19)					
Var (P14)	1.00 (83)	0.71* (83)					
Var (P19)	0.71* (83)	1.00 (83)					
Basicranium							
	Var (P21)	Var (P22)	Var (P23)				
Var (P21)	1.00 (82)	0.97 (80)	0.88 (80)				
Var (P22)	0.97 (80)	1.00 (82)	0.85 (81)				
Var (P23)	0.88 (80)	0.85 (81)	1.00 (82)				
Splanchnocranium							
	Var (D3)	Var (L24)	Var (L25)				
Var (D3)	1.00 (80)	0.94* (79)	0.96* (80)				
Var (L24)	0.94* (79)	1.00 (82)	0.98* (81)				
Var (L25)	0.96* (80)	0.98* (81)	1.00 (82)				
Mandible							
	Var (M28)	Var (M29)	Var (M30)	Var (M31)	Var (M32)		
Var (M28)	1.00 (83)	0.83 (73)	0.79 (78)	0.88 (81)	0.88 (79)		
Var (M29)	0.83 (73)	1.00 (74)	0.92 (69)	0.82 (72)	0.80 (71)		
Var (M30)	0.79 (78)	0.92 (69)	1.00 (79)	0.78 (78)	0.80 (76)		
Var (M31)	0.88 (81)	0.82 (72)	0.78 (78)	1.00 (82)	0.97 (80)		
Var (M32)	0.88 (79)	0.80 (71)	0.80 (76)	0.97 (80)	1.00 (80)		
Palate							
	Var (P10)	Var (P11)	Var (P12)	Var (P13)	Var (P15)	Var (P16)	Var (P17)
Var (P10)	1.00 (82)	0.76* (81)	0.84* (81)	0.91* (81)	0.78* (72)	0.78* (72)	0.75* (79)
Var (P11)	0.76* (81)	1.00 (82)	0.76* (81)	0.79* (81)	0.76* (72)	0.76* (72)	0.64* (79)
Var (P12)	0.84* (81)	0.76* (81)	1.00 (82)	0.90* (81)	0.93* (73)	0.95* (73)	0.91* (80)
Var (P13)	0.91* (81)	0.79* (81)	0.90* (81)	1.00 (82)	0.84* (72)	0.84* (72)	0.83* (79)
Var (P15)	0.79* (72)	0.76* (72)	0.93* (73)	0.84* (72)	1.00 (73)	0.93* (72)	0.93* (72)
Var (P16)	0.78* (72)	0.76* (72)	0.95* (73)	0.84* (72)	0.93* (72)	1.00 (73)	0.95* (71)
Var (P17)	0.75* (79)	0.64* (79)	0.91* (80)	0.83* (79)	0.93* (72)	0.95* (71)	1.00 (80)

$p = 0.62$ for D4 and D5; $p = 0.00$ for all other variables.

* Significant at the 1% level (2-tailed).

Sample size in brackets.