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Body size of Eocene Antarctic penguins

ABSTRACT: Body size is an important measure in biology and especially in paleobiology. With respect to fossil penguins from the Eocene La Meseta Formation of Seymour Island (West Antarctica) the overall size has to be judged from the dimensions of single bones. The analysis based on selected measurements of hind limb bones from the Polish collection of Eocene Antarctic penguins yielded results supporting predictions published formerly. Estimated body masses and lengths indicate that mean interspecific body size of extinct Antarctic Spheniscidae exceeded that of Recent species.

Key words: Antarctica, Seymour Island, Eocene, penguins, allometry.

Introduction

Body size is an important measure in various biological studies. It influences the structure and functions of an organism and its interactions with environmental factors (see Peters 1983, Schmidt-Nielsen 1984).

The issue of animal size is of particular interest in paleontology, and especially in paleoecology, because skeletal structure and dimensions are often the only sources of information on biology of extinct forms and environmental conditions with which they had to cope. Additional difficulty comes from the quality of the fossil record. Complete skeletons are rarely available for research.

The Eocene penguin fauna from the La Meseta Formation of Seymour Island, Antarctic Peninsula (Fig. 1), represents the only fossil record of Antarctic Spheniscidae (Simpson 1975, 1976; Fordyce and Jones 1990, Jadwiszczak 2000, Myrcha *et al.* 2001). The remains collected on Seymour Island may be the most extensive extinct penguin collections currently known (Fordyce and Jones 1990). Recently, the joined effort of Argentine and Polish scientists resulted in preparation of the

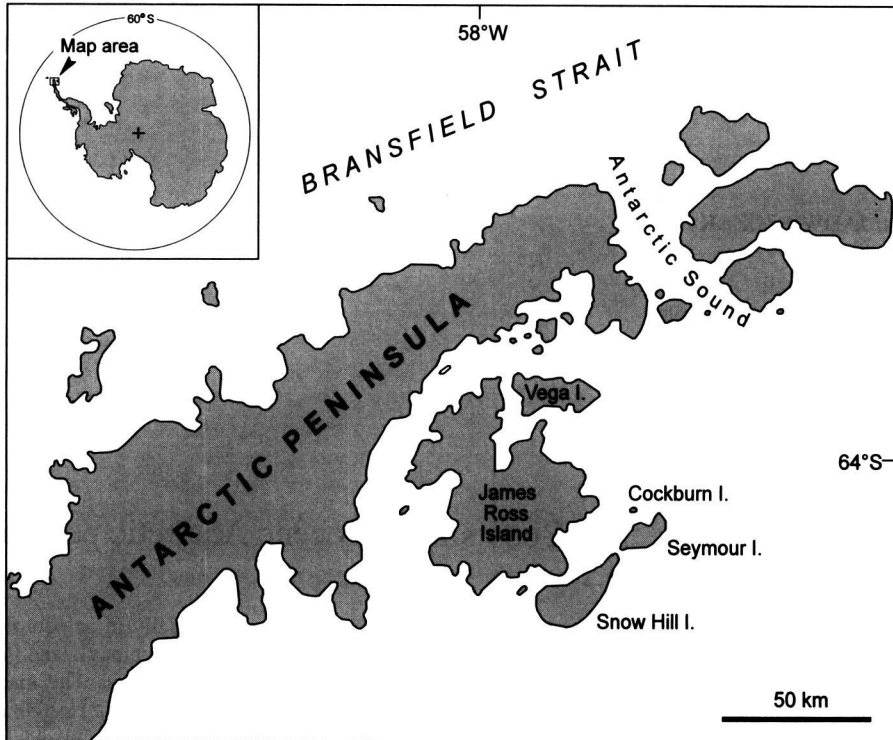


Fig. 1. Map showing the location of Seymour Island in Antarctica.

taxonomic revision of the Eocene Antarctic Spheniscidae based on tarsometatarsal morphology: the number of penguin species from the La Meseta Formation reached ten (Myrcha *et al.* 2001).

The fossil penguin remains were used in several works to estimate the Eocene penguin body sizes: total length, standing height or weight. The estimates were either based on tarsometatarsal, femoral and humeral lengths (Simpson 1946, 1971a, 1975, 1976) or on regressions of mean body masses of Recent species on principal components of available mean skeletal measurements (Livezey 1989). All these researchers concluded that some of the Tertiary penguins had been probably larger than emperor penguin (*Aptenodytes forsteri*), the largest Recent species of Spheniscidae. Furthermore, other good predictors of avian body size were proposed, *e.g.* long-bone circumference (Anderson, Hall-Martin and Russell 1985), tibiotarsal length (Rising and Somers 1989) and keel length (Senar and Pascual 1997). Usefulness of tarsometatarsal and femoral measurements was also confirmed (Kirkwood *et al.* 1989, Rising and Somers 1989, Senar and Pascual 1997).

The purpose of this work is to assess the scope of interspecific body-size variability in penguins from the Eocene of Seymour Island utilizing diversified fossil material. Studied penguin bones are housed at the Institute of Biology, University of Białystok (abbreviated IB/P/B).

Material and methods

Almost all penguin fossils are isolated bones (Simpson 1975, 1981) and this is particularly the case for extinct Spheniscidae from the La Meseta Formation of Seymour Island (Marples 1953, Jadwiszczak 2000, Myrcha *et al.* 2001). The majority of Tertiary species have been described on the basis of one bone – the tarsometatarsus (Wiman 1905a, 1905b; Marples 1953, Simpson 1971b, Myrcha, Tatur and del Valle 1990, Myrcha *et al.* 2001). Unfortunately tarsometatarsi of fossil and Recent taxa from the same size category often differ in their proportions (Fig. 2). This is paralleled by differences in morphological details (Myrcha *et al.* 2001). Furthermore, some fossil bone measurements exceed the range of Recent ones (Figs 2, 3), and it is assumed that the described function holds for values outside the range of those observed. These factors set important constraints on body-size estimations by extrapolation from measurements of single non-fossil bones.

The body-size estimates were entirely based on hind limb bones from the Polish collection of fossil penguins from the La Meseta Formation (Myrcha and Tatur 1988, Myrcha, Tatur and del Valle 1990, Jadwiszczak 2000) and included taxa established recently (Myrcha *et al.* 2001). Lengths and diameters of fossil femora and tibiotarsi were measured for this study, and tarsometatarsal data were taken from Myrcha *et al.* (2001). All skeletal lengths and diameters were measured with the electronic slide calliper with an accuracy of 0.1 mm. Measurement categories followed those of Stephan (1979, numbers in parentheses, see Table 1 for descriptions of measurement categories): femoral (102, 106, 107), tibiotarsal (110, 113, 114), and tarsometatarsal (120, 123, 124). Data for Recent taxa were taken from the following sources: Stephan (1979, skeletal measurements), Livezey (1989, skeletal measurements), Croxall (1984, body mass), Marchant and Higgins (1990, body mass) and Harrison (1989, body length – the distance measured from the tip of the bill to the tip of the tail). Bivariate logarithmic (base 10) plots of skeletal measurements were used to show differences in intra-bone proportions between skeletal elements of extinct and Recent species (Figs 2, 3).

An allometric relationship between skeletal measurements (Y) and body size (X) was expressed as a standard power function $Y = aX^b$. Slopes (exponents, b) and factors (a) of the allometric equations were estimated using Model II regression method (reduced major axis, RMA) of log-transformed (base 10) data (Table 1). The Model II regression was employed, because both X and Y values were subject to natural variation and measurement error. Furthermore, the variable X was not under control of the investigator. Because of the difference in measurement units of the two variables, determining the slope of the major axis (MA) would be inappropriate in this case (see Sokal and Rohlf 1995). However, controversy over Model II regression continues, and if the regression line is being fitted mainly for purposes of prediction, then the Model I regression techniques are generally applied (Sokal and Rohlf 1995). Thus, the linear regression lines were also fitted to

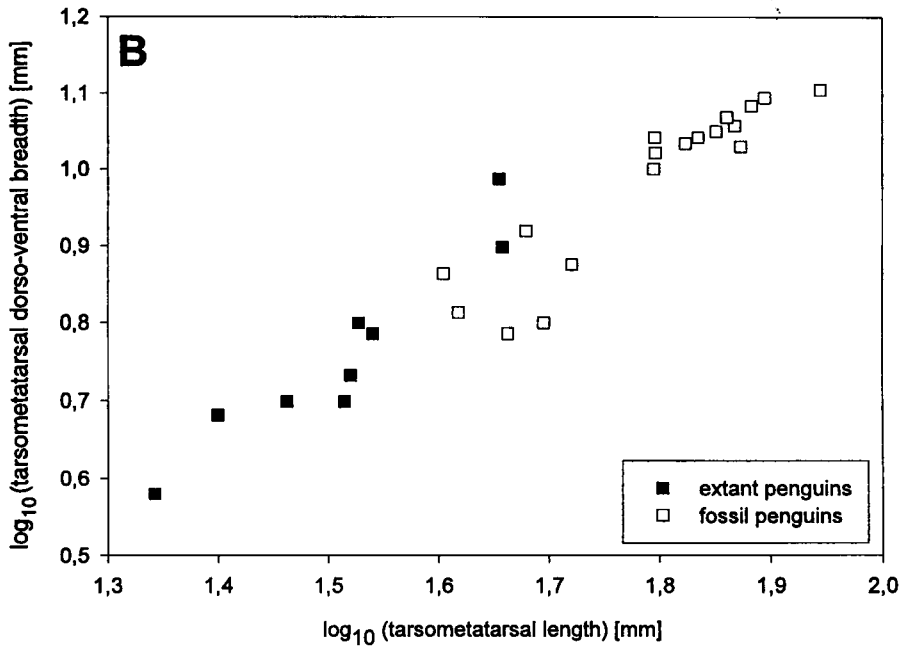
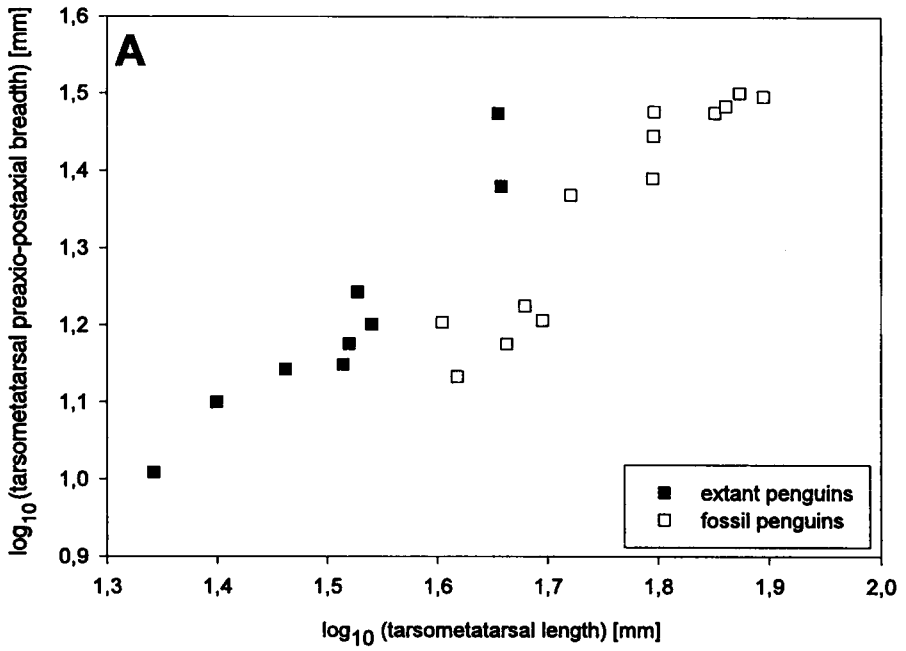


Fig. 2. Logarithmic plots of tarsometatarsal lengths and preaxio-postaxial (A) as well as dorso-ventral (B) breadths for Recent (mean values) and Eocene penguins.

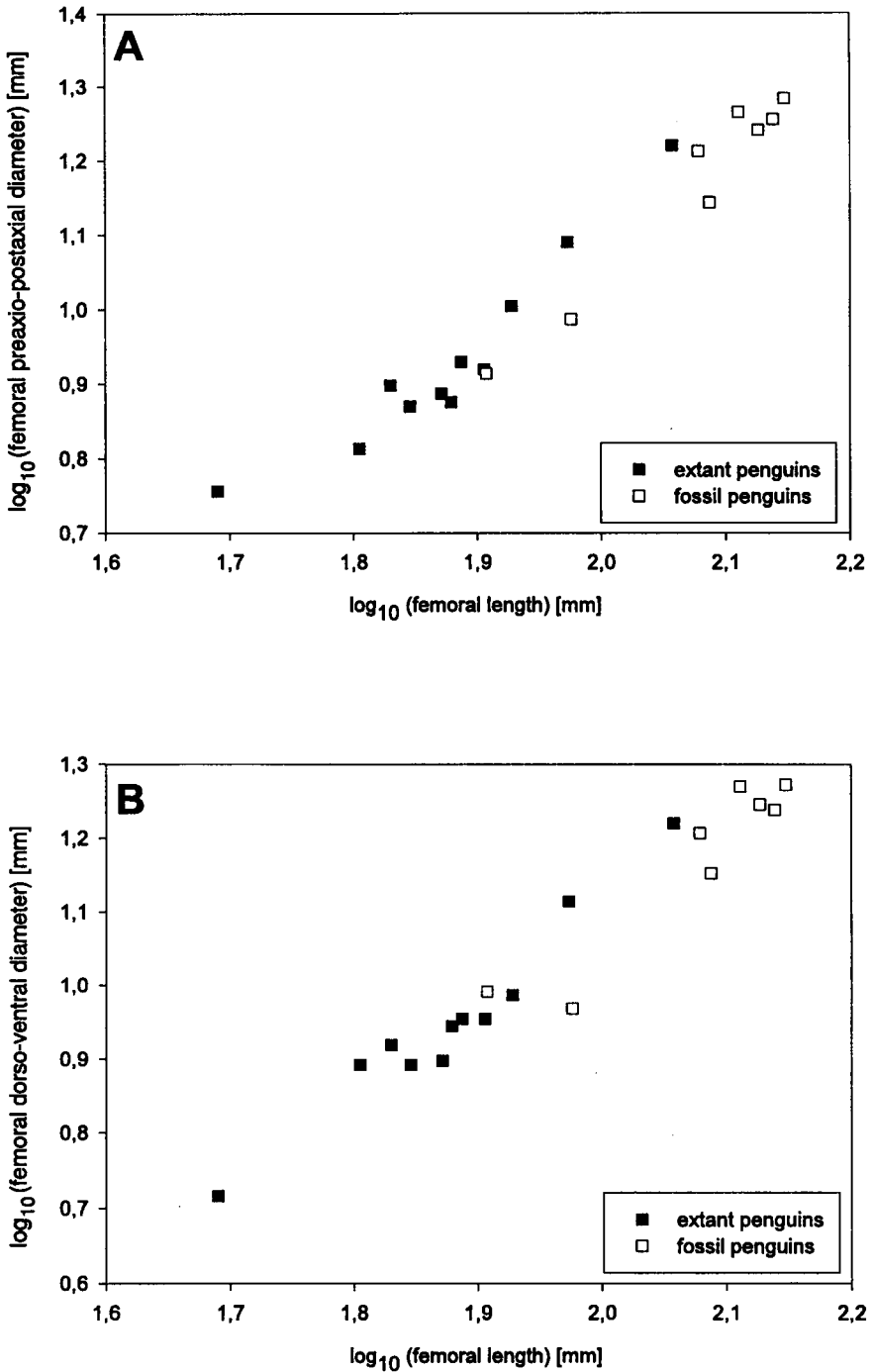


Fig. 3. Logarithmic plots of femoral lengths and preaxio-postaxial (A) as well as dorso-ventral (B) diameters for Recent (mean values) and Eocene penguins.

Table 1

Allometric equations of form $Y = aX^b$ relating mean body masses and lengths (X) of Recent penguin species with selected measurements of their hind limb bones (Y; lengths in mm, masses in kg). The equations were obtained by Model II regression method (reduced major axis, RMA) after transformation to logarithms. Abbreviations: n – number of Recent species, m – number of fossil bones, r – Pearson's product-moment correlation coefficient, BM – body mass, BL – body length, CI – confidence interval.

X	Y	n	m	a	b ± 95%CI	r p < 0.01
BM	Femoral length	12	8	51.41	0.247±0.064	0.93
BM	Femoral preaxio-postaxial diameter	11	21	4.993	0.338±0.095	0.93
BM	Femoral dorso-ventral diameter	11	21	5.263	0.335±0.067	0.96
BM	Tibiotarsal length	10	3	72.39	0.298±0.063	0.97
BM	Tibiotarsal preaxio-postaxial diameter	9	17	5.163	0.303±0.067	0.97
BM	Tibiotarsal dorso-ventral diameter	9	17	4.766	0.305±0.074	0.96
BM	Tarsometatarsal length	9	23	21.95	0.243±0.104	0.88
BM	Tarsometatarsal preaxio-postaxial breadth	9	25	9.412	0.332±0.084	0.96
BM	Tarsometatarsal dorso-ventral breadth	9	34	3.636	0.285±0.071	0.96
BL	Femoral length	12	8	0.393	0.804±0.218	0.92
BL	Femoral preaxio-postaxial diameter	11	21	0.006	1.101±0.398	0.88
BL	Femoral dorso-ventral diameter	11	21	0.007	1.093±0.292	0.93
BL	Tibiotarsal length	10	3	0.201	0.971±0.272	0.94
BL	Tibiotarsal preaxio-postaxial diameter	9	17	0.013	0.986±0.319	0.93
BL	Tibiotarsal dorso-ventral diameter	9	17	0.012	0.992±0.345	0.92
BL	Tarsometatarsal length	9	23	0.183	0.790±0.333	0.88
BL	Tarsometatarsal preaxio-postaxial breadth	9	25	0.014	1.079±0.378	0.92
BL	Tarsometatarsal dorso-ventral breadth	9	34	0.013	0.927±0.319	0.92

the data by means of least squares regression analysis (Table 2). In order to meet the model assumptions the body size was arbitrarily identified as the independent variable. As the standard error of the slope in the RMA analysis can be approximated by the standard error of the least squares slope (Sokal and Rohlf 1995), the latter was used to assign confidence limits to the RMA regression coefficient. Pearson's product-moment correlation coefficients (r) were computed for the samples (Tables 1 and 2). The randomization tests for $r = 0$ were carried out comparing the observed value of a correlation coefficient with the distribution of values that was obtained by pairing the X and Y values at random (10000 randomizations, Manly 1997).

Results and discussion

The results are shown in Tables 1–3. Estimates obtained from Model I regression equations are larger than those calculated from RMA equations (Table 3). However, these differences do not affect the pattern described by means of Model II regression analysis and they are not discussed here.

Table 2

Allometric equations of form $Y = aX^b$ relating mean body masses and lengths (X) of Recent penguin species with selected measurements of their hind limb bones (Y; lengths in mm, masses in kg). The equations were obtained by Model I regression method (least squares regression) after transformation to logarithms. Recent species (n) and fossil bone (m) numbers as in Table 1. Abbreviations: r – Pearson's product-moment correlation coefficient, BM – body mass, BL – body length, CI – confidence interval, SEE – standard error of the estimate, PE – prediction error.

X	Y	a	b ± 95%CI	r p < 0.01	SEE	PE
BM	Femoral length	52.88	0.230±0.064	0.93	0.035	0.018
BM	Femoral preaxio-postaxial diameter	5.192	0.313±0.095	0.93	0.051	0.034
BM	Femoral dorso-ventral diameter	5.364	0.323±0.067	0.96	0.036	0.016
BM	Tibiotarsal length	73.60	0.288±0.063	0.97	0.033	0.014
BM	Tibiotarsal preaxio-postaxial diameter	5.243	0.294±0.067	0.97	0.035	0.011
BM	Tibiotarsal dorso-ventral diameter	4.854	0.294±0.074	0.96	0.038	0.014
BM	Tarsometatarsal length	23.05	0.213±0.104	0.88	0.054	0.032
BM	Tarsometatarsal preaxio-postaxial breadth	9.620	0.318±0.084	0.96	0.043	0.017
BM	Tarsometatarsal dorso-ventral breadth	3.703	0.274±0.071	0.96	0.036	0.012
BL	Femoral length	0.592	0.742±0.218	0.92	0.037	0.017
BL	Femoral preaxio-postaxial diameter	0.015	0.967±0.398	0.88	0.066	0.072
BL	Femoral dorso-ventral diameter	0.011	1.021±0.292	0.93	0.048	0.032
BL	Tibiotarsal length	0.295	0.912±0.272	0.94	0.044	0.023
BL	Tibiotarsal preaxio-postaxial diameter	0.020	0.919±0.319	0.93	0.050	0.029
BL	Tibiotarsal dorso-ventral diameter	0.020	0.913±0.345	0.92	0.055	0.040
BL	Tarsometatarsal length	0.341	0.695±0.333	0.88	0.053	0.026
BL	Tarsometatarsal preaxio-postaxial breadth	0.024	0.992±0.378	0.92	0.060	0.046
BL	Tarsometatarsal dorso-ventral breadth	0.021	0.855±0.319	0.92	0.050	0.029

The dorso-ventral breadth seems to be most appropriate tarsometatarsal measurement for predicting the body mass of both, Tertiary and Recent species (see Fig. 2, Table 1). Predicted values are very similar to those published by Livezey (1989) for five extinct species from Seymour Island, however, this researcher mistakenly dealt with *Anthropornis grandis* as the largest species. When this mistake is corrected the only difference is the estimate for *A. grandis* – the value presented in Table 3 is 15% lower than that reported by Livezey (1989). Surprisingly, some individuals could be even heavier – the extrapolated body mass for the specimen IB/P/B-0293 described as *Anthropornis* sp. (Myrcha *et al.* 2001) was 89.9 kg. Mean body masses of extant species range from 1.1 kg for *Eudyptula minor* to 32.5 kg for *Aptenodytes forsteri* (Croxall 1984). Birds from the former taxon are probably c. 80% lighter than *Marambiornis exilis*, the smallest species from the Eocene of Seymour Island. The body mass of the largest extinct Spheniscidae (*Anthropornis*) could be 277% of the mean value reported for *Aptenodytes forsteri* (Croxall 1984).

All estimated values are, of course, nothing more than just rough predictions based on the assumption that a given bone measure correlates well with and is a

good predictor of body mass. However, they seem quite reasonable. The considerable variability of estimates obtained for species represented by numerous specimens, *Palaeudyptes klekowskii* and *P. gunnari* (Table 3), can be explained in several ways. One of them is that the range of variation for body size increases with mean body size in birds (Hallgrímsson and Maiorana 2000) and these taxa were large ones. However, it ought to be stressed that there are considerable changes in body mass of Recent penguins which fast during incubation, as well as weight changes due to egg formation and laying (Calder 1985). In unsexed emperor penguins at Cape Crozier weights ranged from 26.5 to 41.0 kg ($n = 33$) during chick-rearing period (Wilson 1907), and in adult yellow-eyed penguins (*Megadyptes antipodes*) from Otago Peninsula weights attained values from 4.3 to 6.4 kg ($n = 160$) during late incubation period (Richdale 1951).

Estimates obtained from other hind limb bones are not explicit. The dorsoventral diameter of the femur most strongly correlates with body mass in Recent species (Table 1). The range of values predicted for Eocene penguins is narrower than that calculated from tarsometatarsal measurements. It is also markedly shifted downwards. However, this could be explained by the degree of preservation of the fossil material. There are specimens excluded from considerations because of their poor preservation (e.g. IB/P/B-0342), but testifying to existence of Eocene penguins much heavier than 44 kg, the largest estimate obtained from femoral data. Extrapolations from tibiotarsal measurements are even more hazardous – only three specimens are nearly complete and allow more complex comparisons with bones of extant taxa. Values obtained from different measurements of the same bone differ considerably which suggests discrepancy of proportions between extinct and extant species.

The total length estimations based on tarsometatarsal data indicate that fossil penguins were medium- or large-sized birds. Mean values for Recent penguins range from 40.0 cm for *Eudyptula minor* to 115.0 cm for *Aptenodytes forsteri* (Harrison 1989), whereas estimates for fossil taxa range between 74.7 and 170.5 cm.

Total length is naturally more than the standing height of the bird. Simpson (1946) noted that the difference seemed usually to be between 5 and 10 per cent. Given this, the results of this study support the broadly accepted view that many of the fossil penguins were indeed larger than the largest extant species (Simpson 1975, 1976). In Simpson's (1946) opinion it is probable that the largest extinct species were heavier than an average man, although they were not so tall. Estimates presented in Table 3 support that suggestion – predicted body lengths do not exceed 172 cm. Standing heights of fossil penguins from Seymour Island estimated from tarsometatarsal data range between 67.0–71.0 (*Marambiornis exilis*) and 153.5–162.0 cm (*Anthropornis* sp.). Values discussed in this study are similar to those presented by Simpson (1976).

The interspecific average of the body sizes of fossil penguins is larger than that of Recent Spheniscidae. Since this study includes the largest sample of Eocene taxa so far, the result is robust, even if the values obtained are crude estimates. Fos-

Table 3

Predicted body masses (PBM) and lengths (PBL) for fossil penguins from Seymour Island (masses in kg, lengths in cm). Values were calculated by means of Model II regression method from the selected bone dimensions (values in parentheses were calculated by means of Model I regression method); n – number of specimens.

Species	Measurement	n	PBM		PBL	
			Mean	Range	Mean	Range
<i>Anthropornis nordenskjoldi</i> Wiman, 1905	Tarsometatarsal dorso-ventral breadth	2	81.7 (97.8)	80.6–82.8 (96.3–99.2)	165.6 (199.2)	164.9–166.3 (198.3–200.2)
<i>Anthropornis grandis</i> (Wiman, 1905)	Tarsometatarsal dorso-ventral breadth	1	–	44.2 (51.1)	–	137.0 (162.1)
<i>Anthropornis</i> sp.	Tarsometatarsal dorso-ventral breadth	1	–	89.9 (108.0)	–	170.5 (205.7)
<i>Palaeudyptes klekowskii</i> Myrcha <i>et al.</i> , 1990	Tarsometatarsal dorso-ventral breadth	12	56.0 (65.7)	41.3–74.1 (47.6–88.2)	147.0 (175.0)	134.3–160.7 (158.6–192.8)
<i>Palaeudyptes gunnari</i> (Wiman, 1905)	Tarsometatarsal dorso-ventral breadth	7	41.1 (47.4)	32.5–50.2 (36.9–58.5)	133.7 (157.8)	124.6–142.6 (146.2–169.3)
<i>Archaeospheniscus wimani</i> (Marples, 1953)	Tarsometatarsal dorso-ventral breadth	2	13.0 (14.0)	12.7–13.3 (13.7–14.4)	94.1 (107.6)	93.4–94.7 (106.7–108.4)
<i>Delphinornis larseni</i> Wiman, 1905	Tarsometatarsal dorso-ventral breadth	4	14.1 (15.3)	10.5–18.1 (11.2–19.9)	95.8 (109.7)	88.0–104.2 (100.1–120.2)
<i>Delphinornis gracilis</i> Myrcha <i>et al.</i> , 2001	Tarsometatarsal dorso-ventral breadth	2	8.1 (8.5)	7.7–8.5 (8.1–9.0)	81.4 (91.8)	80.0–82.7 (90.2–93.5)
<i>Delphinornis arctowskii</i> Myrcha <i>et al.</i> , 2001	Tarsometatarsal dorso-ventral breadth	1	–	11.5 (12.4)	–	90.7 (103.4)
<i>Mesetaornis polaris</i> Myrcha <i>et al.</i> , 2001	Tarsometatarsal dorso-ventral breadth	1	–	6.9 (7.2)	–	77.4 (86.9)
<i>Marambiornis exilis</i> Myrcha <i>et al.</i> , 2001	Tarsometatarsal dorso-ventral breadth	1	–	6.1 (6.4)	–	74.7 (83.7)
–	Femoral dorso-ventral diameter	21	21.3 (23.5)	3.6–44.0 (3.6–49.6)	103.9 (119.7)	64.0–137.6 (71.0–161.3)
–	Tibiotarsal preaxio-postaxial diameter	17	40.1 (45.8)	2.7–91.3 (2.7–106.7)	121.1 (128.3)	58.2–171.3 (58.3–185.3)

sil Spheniscidae from the La Meseta Formation had also a wider absolute range of interspecific size variability, expressed as the difference between extreme values.

Case (1992) compared fossil penguin diversity in the La Meseta Formation with Recent penguin diversity at different geographic localities through the number of sympatric species and size classes present. Obtained numbers were higher than those reported for Recent Spheniscidae. The northern Antarctic Peninsula (Fig. 1) experienced a climatic deterioration from very warm, wet conditions (early Middle Eocene c. 47 Ma) to a cold and relatively dry regime during latest Eocene (post c. 34 Ma). However, there is no evidence for glaciation on Seymour Island during that period (Dingle, Marensi and Lavelle 1998). The largest Recent Spheniscidae inhabit cold and the smallest ones – warm waters, but there is no correlation between environmental temperature and body size throughout the family (Stonehouse 1969). Furthermore, Simpson (1971b) noted that there were adapta-

tions to climate other than body size and these might be more crucial. Fordyce and Jones (1990) suggested that the large size of some fossil penguins may have evolved for several other reasons, *e.g.* hydrodynamics, adaptation against predators, or acquisition of some determinant of K strategies. Jadwiszczak (2000) explained the abundance and diversity of Eocene Antarctic species in terms of adaptive radiation during periods of adverse trophic conditions.

The pattern of interspecific body-size distribution in fossil penguins is possibly affected by taphonomic processes during sedimentation of the La Meseta Formation (Feldmann and Woodburne 1988, Porębski 1995, 2000; Gaździcki 1996, Marensi, Santillana and Rinaldi 1998). Bones of birds from small species are probably underrepresented in the studied collection. However, at least two additional observations support my conclusions. First, any increase in the number of small taxa would only increase the interspecific body-size variability. Second, a large number of small species were described, and small tarsometatarsi from the Polish collection, *e.g.* four holotypes (Myrcha *et al.* 2001), often show better preservation than the larger ones. The ratio of large to small species numbers seems to indicate a high probability of small taxa being preserved. Thus, the data may reflect accurately the distribution of sizes in Eocene penguins.

Conclusions

The analysis of hind limb bones from the rich and diversified collection of Eocene Antarctic Spheniscidae yielded results testifying to larger mean interspecific body size relative to Recent taxa. Estimated values were similar to those published formerly (Simpson 1975, 1976; Livezey 1989) and gave an indication of the wide range of fossil penguin sizes. However, some differences in intra-bone proportions between Eocene and Recent elements of penguin skeletons as well as methodological intricacies preclude precise predictions of body mass and length. Provided that known fossil taxa are representative of the Eocene penguin avifauna, this pattern suggests the paleoenvironmental conditions promoting large-bodied birds.

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Streszczenie

Wielkość organizmów jest istotnym czynnikiem w wielu badaniach biologicznych. W przypadku dużej części wymarłych kręgowców masa i długość ciała są oszacowywane w oparciu o pomiary zachowanych elementów szkieletu. Takie wyzwanie stanowią również szczątki eoceniskich pingwinów z antarktycznej Wyspy Seymour (fig.1). Zbiór ten jest przechowywany w Instytucie Biologii Uniwersytetu w Białymstoku.

Analiza materiału kopalnego (kości kończyny tylnej) została przeprowadzona przy pomocy równań allometrycznych (w postaci standardowej funkcji potęgowej) uzyskanych po zbadaniu zależności występujących u współczesnych przedstawicieli rodziny Spheniscidae (tab. 1–2). Ponieważ niektóre kości ptaków eoceniskich i współczesnych różnią się pod względem proporcji (fig. 2–3) dokonana została selekcja pomiarów, zaś wyniki traktowane były jako wartości przybliżone.

Uzyskane dane świadczą o bardzo dużym zakresie międzygatunkowej zmienności masy i rozmiarów liniowych ciała wśród kopalnych pingwinów z Wyspy Seymour (tab. 3). Średnie wartości wspomnianych parametrów były prawdopodobnie wyższe niż ich odpowiedniki u współczesnych Spheniscidae.