

Appendix 2

DESCRIPTION OF SCIENTIFIC ACHIEVEMENTS

Dr. Piotr Jadwiszczak

Department of Genetics and Evolution

Institute of Biology, Faculty of Biology and Chemistry

University of Białystok

Contents

Basic CV information	2
Indication (and description) of a selected scientific achievement	3
Course of education and professional activity	21
Description of scientific achievements	26

NAME: Piotr Jadwiszczak

DATE AND PLACE OF BIRTH: 19th September 1970, Białystok

ADDRESS: Institute of Biology, Faculty of Biology and Chemistry, University of Białystok, Świerkowa 20B, 15-950 Białystok; phone +48 85 745 74 27; fax +48 85 745 73 01; e-mail: piotrj@uwb.edu.pl

EDUCATION AND SCIENTIFIC DEGREES:

2005: Ph.D.; Institute of Biology, Faculty of Biology and Chemistry, University of Białystok; dissertation title: „Fossil penguins of Seymour Island: systematics, evolution and their role in the Eocene ecosystem of the Antarctic” (supervisor: Prof. Andrzej Gaździcki).

2001–2003: Białystok University of Technology, Faculty of Computer Science, three-semester postgraduate studies (computer science for non-computer-science graduates).

1994: M.Sc.; Institute of Biology, Warsaw University Branch in Białystok; M.Sc. thesis „Diversity of the fossil penguin fauna of the Antarctic Seymour Island based on the analysis of tarsometatarsi from the collection of the Institute of Biology, Warsaw University, Branch in Białystok” (supervisor: Prof. Andrzej Myrcha).

1989–1994: Warsaw University Branch in Białystok, Faculty of Mathematics and Natural Sciences, Institute of Biology.

1985–1989: Adam Mickiewicz High School (High School no 1) in Białystok.

SCIENTIFIC WORK:

Since 1 October 2013: Department of Genetics and Evolution, Institute of Biology, Faculty of Biology and Chemistry, University of Białystok; assistant professor.

1 March 1999 – 30 September 2013: Professor Andrzej Myrcha Museum of Nature, Institute of Biology, Faculty of Biology and Chemistry, University of Białystok (since 1 September 2004: the Professor Andrzej Myrcha University Museum of Nature, since 17 April 2013: the Professor Andrzej Myrcha University Center of Nature); research assistant/junior scientist, assistant professor (since 1 December 2007).

1 October 1994 – 14 April 1996: Department of Antarctic Biology of Polish Academy of Sciences in Warsaw; interim agreement associated with participation in the 19th Antarctic Expedition of the Polish Academy of Sciences to the H. Arctowski Station (King George Island, West Antarctica); research assistant/junior scientist.

1 January 1994 – 16 February 1997: Department of Animal Ecology, Institute of Biology, Faculty of Mathematics and Natural Sciences, Warsaw University Branch in Białystok; technician, research assistant/junior scientist (since 15 September 1994).

INDICATION OF A SCIENTIFIC ACHIEVEMENT

[resulting from the article 16 paragraph 2 of the act from 14 March 2003, on the scientific degrees and scientific title, and degrees and title in the arts (Journal of Laws no 65, heading 595 with later changes, like in JoL 2005 no 164, heading 1365, article 251; JoL 2011 no 84, heading 455)]

The scientific achievement is a monothematic set of scientific papers entitled:

Evolutionary history of the Paleogene and Neogene Antarctic penguins

PUBLICATIONS THAT MAKE UP THE SELECTED SCIENTIFIC ACHIEVEMENT:

[1]¹ **Jadwiszczak P.**, Mörs T. 2011. Aspects of diversity in early Antarctic penguins. *Acta Palaeontologica Polonica* 56(2): 269–277. [MSHE²: 30, IF: 1.488](#)

[2] **Jadwiszczak P.** 2013. Taxonomic diversity of Eocene Antarctic penguins: a changing picture. In: Hambrey M.J., Barker P.F., Barrett P.J., Bowman V., Davies B., Smellie J.L. Tranter M. (ed.), *Antarctic Palaeoenvironments and Earth-Surface Processes*. Geological Society, London, Special Publications 381: 129–138 (*chapter in a reviewed monograph*). [MSHE: 5](#)

[3] **Jadwiszczak P.**, Acosta Hospitaleche C. 2013. Distinguishing between two Antarctic species of Eocene *Palaeudyptes* penguins: a statistical approach using tarsometatarsi. *Polish Polar Research* 34(3): 237–252. [MSHE: 20, IF: 0.788](#)

[4] **Jadwiszczak P.**, Acosta Hospitaleche C., Reguero M. 2013. Redescription of *Crossvallia unienwillia*: the only Paleocene Antarctic Penguin. *Ameghiniana* 50(6): 545–553. [MSHE: 25, IF: 1.169](#)

[5] **Jadwiszczak P.**, Krajewski K.P., Pushina Z., Tatur A., Zieliński G. 2013. The first record of fossil penguins from East Antarctica. *Antarctic Science* 25(3): 397-408. [MSHE: 20, IF: 1.417](#)

¹ The numbering in accordance with Appendix 3.

² According to the Communication from the *Minister of Science and Higher Education (MSHE) on the list of scientific journals* (31 December 2014).

[6] Jadwiszczak P. 2014. Synsacra of the Eocene Antarctic penguins: new data on spinal maturation and an insight into their role in the control of walking. *Polish Polar Research* 35(1): 27–39. [MSHE: 20, IF: 0.788](#)

[7] Jadwiszczak P. 2014. At the root of the early penguin neck: a study of the only two cervicodorsal spines recovered from the Eocene of Antarctica. *Polar Research* 33: 23861, <http://dx.doi.org/10.3402/polar.v33.23861>. [MSHE: 25, IF: 1.686](#)

- Total Impact Factor for papers that make up the selected scientific achievement: **7.336**.
- Total MSHE points calculated for these publications: **145**.

INTRODUCTION

Penguins (Aves: Sphenisciformes) are extremely specialized seabirds with breeding grounds scattered between the shores of Antarctica and Galapagos Islands. The oldest fossil record of these birds comes from New Zealand and is dated to ca. 61.5 million years ago (Ma; close to the Early/Middle Paleocene transition; Slack *et al.* 2006, *Mol. Biol. Evol.* 23). Although the breeding ranges of most present-day species do not include the Antarctic, in this very region, within the Eocene La Meseta Formation on Seymour Island (Antarctic Peninsula), the most numerous (thousands of bones, rarely larger fragments of skeletons) and diverse (at least 6 genera and 10 species present) assemblage of fossil Sphenisciformes has been found (e.g., Jadwiszczak 2009 **[16]**). Rare remains of older (Late Paleocene) Antarctic penguins (several dozens of bone fragments) were found in 2000 within the Cross Valley Formation on Seymour Island and preliminarily described five years later (Tambussi *et al.* 2005, *Geobios* 38). The Neogene fossils (two bones) were collected as recently as in 2008, within the Fisher Bench Formation (Prince Charles Mountains, East Antarctica).

The objectives of my studies included into the selected scientific achievement were (among others):

- to analyze the fossil record of *Crossvallia unienwillia* Tambussi, Reguero, Marensi & Santillana, 2005, the earliest Antarctic penguin;
- to clarify the systematics and phylogenetic relationships within a diverse assemblage of the Eocene Antarctic penguins, develop the statistical methodology for estimating the species-level assignment of bones, based on quantitative traits (case of two species from the genus *Palaeudyptes* Huxley, 1859 from the La Meseta Formation), and determine the lower limit of the stratigraphic range of the genus *Anthropornis* Wiman, 1905 – the largest Antarctic penguins;
- to analyze the “form and function” of an intermediate unit of the cervicodorsal spine, and maturation of the synsacrum as well as to assess a degree of development of

the, located within the synsacral canal, alleged additional sense organ for control of balance, in early Sphenisciformes;

- to identify a taxonomic position, determine age as well as to report a comprehensive description and interpretation, also in the evolutionary context, of the remains of the only known fossil penguin from East Antarctica, collected in 2008.

The analyzed specimens came from the four largest collections of the Antarctic fossil penguins. These sets of bones are housed at the University of Białystok (Poland)³, Museo de La Plata (Universidad Nacional de La Plata, La Plata, Argentina), Natural History Museum (London, UK) and Naturhistoriska riksmuseet (Stockholm, Sweden), hereinafter referred to as the Białystok, Argentine, London and Stockholm collections.

➤ ***The Paleogene (66.0 – 23.0 Ma)⁴: the Paleocene (66.0 – 56.0 Ma) – the oldest fossil record of Antarctic penguins***

[4] Jadwiszczak P., Acosta Hospitaleche C., Reguero M. 2013. Redescription of *Crossvallia unienwillia*: the only Paleocene Antarctic Penguin. *Ameghiniana* 50(6): 545–553.

The aim of this work was to conduct a critical analysis of the fossil record from the Cross Valley Formation on Seymour Island, on the basis of which the oldest species of Antarctic penguins, *Crossvallia unienwillia*, had been described. The starting point for us were the preliminary results indicating the existence of bone fragments not included in the original reconstruction (Tambussi *et al.* 2005, *Geobios* 38), the fact that had affected the content of the published descriptions and interpretations. We also wanted to show for the first time the photographic documentation of these bones, indicate the exact locality of the bone collecting site (a map, photos, GPS coordinates) and present more detailed stratigraphic data, among others, a stratigraphic column with the marked position of penguin bones.

The incomplete skeleton of the studied penguin, MLP 00-I-10-1, belongs in the Argentine collection. *C. unienwillia* was found in the upper part (Late Paleocene – Thanetian) of the formation, within the unit Cross Valley C Allomember. Sedimentation had probably occurred in a deltaic environment (Elliot and Trautman 1982, in: Craddock C. (ed.), *Antarctic Geoscience*, University of Wisconsin Press).

We have found that the humeral shaft was actually considerably longer than suggested by the graphical reconstruction shown by Tambussi *et al.* (2005). After identifying

³ For more information on this collection, see the *Course of education and professional activity* section.

⁴ According to the International Chronostratigraphic Chart v. 2014/10.

and filling in the missing fragments, it turned out that the total bone-length difference was 18%. The comparative analysis revealed that, in terms of size, this humerus was smaller than its counterparts in some Eocene penguin species, but it was markedly larger than those assignable to other Paleocene species: *Waimanu manneringi* Jones, Ando & Fordyce, 2006 i *W. tuatahi* Ando, Jones & Fordyce, 2006 z Nowej Zelandii. Size comparison of humeri assigned to *C. unienwillia* and the Emperor Penguin (*Aptenodytes forsteri* G.R. Gray, 1844), the largest representative of modern Sphenisciformes, also came out strongly in favor of the first of these specimens. These results constituted the first undisputed evidence that achieving an extremely large body size (so-called gigantism), the phenomenon typical of many of the younger (i.e., Eocene and Oligocene) species of Sphenisciformes, for the first time had occurred in the Paleocene. The earlier estimate of the body total length of *C. unienwillia* (1.35 m; Tambussi *et al.* 2005) was similar to that attainable by the largest Emperor Penguins (e.g., Williams 1995, *Penguins*, Oxford University Press).

The femur of *C. unienwillia*, originally described on the basis of two distal fragments, was almost completely reconstructed by us. The analysis of the femoral head (*caput femoris*) showed unprecedented in other penguins, both modern and fossil, feature. We noticed that a pit that accommodates the round ligament (*ligamentum teres*) is located medially. In all other Sphenisciformes and their closest living relatives (tubenoses, Procellariiformes) this pit is located either clearly more proximally or its position is intermediate. Detailed analyses ruled out the possibility of confusion resulting from the misinterpretation of destructive effects of external factors (e.g., mechanical destruction). The reasons for such a surprising location of the aforementioned attachment place, due to the apparent lack of most skeletal elements and damage to the bone available, remain obscure.

We were unable to identify the missing pieces of the shaft of the last one of bones described by Tambussi *et al.* (2005), the tibiotarsus. The analysis of the remaining bone fragments brought a valuable discovery - one of them, after removing the residual bedrock, was recognized as the opisthocoelous thoracic vertebra.

The above-mentioned results enabled us to supplement the descriptions and measurements of the holotype skeleton of *C. unienwillia* and to prepare a revised version of the diagnosis of the species. Using data from the recently published papers devoted to the geologically younger Paleogene penguins, we made the diagnosis much more differentiating. The only known skeleton of the Paleocene Antarctic penguin represented the interesting mix of features found in other Paleocene Sphenisciformes, traits present in geologically younger penguins and unique attributes.

➤ **The Paleogene (66.0 – 23.0 Ma): the Eocene (56.0 – 33.9 Ma) – the most abundant fossil record of Antarctic penguins**

[1] Jadwiszczak P., Mörs T. 2011. Aspects of diversity in early Antarctic penguins. *Acta Palaeontologica Polonica* 56(2): 269–277.

Our studies focused on taxonomic and morphological, in terms of body size, diversity of the Eocene penguin assemblage from the La Meseta Formation on Seymour Island, representing environments related to the near-shore, estuarine and deltaic accumulation. The objective of our work was: (1) to determine the taxonomic position of two species described by Wiman (1905, *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903* 3), *Orthopteryx gigas* and *Ichtyopteryx gracilis*, whose status (due to the choice of the type specimens) was widely questioned (e.g., Simpson 1971, *Proc. R. Soc. Lond. B* 178; Myrcha *et al.* 2002 [10]); (2) to analyze the merits of the separation of two Antarctic species within the genus *Palaeudyptes* (belonging to the so-called giant penguins), in the light of a possible alternative – the existence of a well-marked, in terms of body size, sexual dimorphism; and (3) to assess the usefulness, in terms of estimating body size of fossil penguins, not used before in relation to these birds, generalized (swimmers, non-volant birds) models showing the relationship between body mass and selected measures of the femoral size.

In the analyses, we used the tarsometatarsi, femora and synsacra from the Bialystok, Stockholm and Argentine collections. Some specimens were studied directly, but we also used measurements compiled in earlier studies (Myrcha *et al.* 2002 [10]; Jadwiszczak 2006 [12]). The techniques we utilized comprised standard methods of the exploratory data analysis based on the studies of measures and graphical presentations of a distribution as well as predictive methods proposed by Campbell and Marcus (1992, *Nat. Hist. Mus. Los Angeles Sci. Ser.* 36), and Cubo and Casinos (1997, *Neth. J. Zool.* 47).

The results of a direct analysis of the holotype of *Ichtyopteryx gracilis* Wiman, 1905, a very incomplete tarsometatarsus from the Stockholm collection and tarsometatarsi (including type specimens) of other species of the small Eocene penguins, did not confirm the morphological uniqueness of the former specimen. It should be noted that in the case of *I. gracilis*, its holotype is also the whole hypodigm of this species. Since comparative studies indicated its striking resemblance to the holotype of *Delphinornis gracilis* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002, we have decided to synonymize both Late Eocene species. Our decision led to an interesting, from the nomenclatorial point of view, situation: the generic name *Delphinornis* Wiman, 1905 took precedence over *Ichtyopteryx* Wiman, 1905 (in the original publication appeared prior to the

latter), wherein *I. gracilis* had been erected much earlier than *D. gracilis*. At the same time, both species share the specific epithet (*gracilis*), and therefore, there appeared the secondary homonymy (ICZN 1999: Art. 53.3 and 57.3). The necessary modification to the name, *Delphinornis gracilis* (Wiman, 1905), was accompanied by updating the diagnosis of the species.

Orthopteryx gigas Wiman, 1905 was erected on the basis of a very large synsacrum. All other penguin species proposed by Wiman (1905) were erected on the basis of tarsometatarsal characters (type specimens belong in the Stockholm collection). According to Wiman (1905), this partly damaged specimen was too large to assign it to *Anthropornis nordenskjoldi* Wiman, 1905, and perhaps it should not even be considered as a part of the penguin skeleton. The results of our studies contradicted the theses. Both the length of the specimen and the number of vertebrae forming it (the second Wiman's argument), did not rule out its attribution to Sphenisciformes and its specific identification as *A. nordenskjoldi* (the largest Antarctic penguin ever). Also the postulated non-existence of a "dorsal keel" was not true, and the lack of a „ventral keel”, the feature recognized by Simpson (1946, *Bull. Am. Mus. Nat. Hist.* 87) for actually distinguishing this specimen, in the light of our observations was nothing exceptional. Another argument in favor of, proposed by us, formal synonymization of the genera *Anthropornis* (a name having priority) and *Orthopteryx*, was the presence of a clear swelling within the cranial part of the synsacral body of the discussed specimen. In our opinion, such a structure was related to the need to strengthen the axial skeleton, to compensate for the extremely large body mass (see Jadwiszczak 2001 [9]). Similar supportive structures were present in the tarsometatarsi assignable to some large-bodied Eocene penguins – they constituted a diagnostic feature of the genus *Anthropornis* (Myrcha *et al.* 2002 [10]).

Birds included in the genus *Palaeudyptes* are among the largest Eocene Antarctic penguins (Jadwiszczak 2001 [9]). The main criterion (in practice - the only one), under which two species described from Seymour Island (e.g., Simpson, 1971, *Proc. R. Soc. Lond. B* 178) have been discriminated one from another, was the tarsometatarsal length, wherein the separating value was determined arbitrarily (Myrcha *et al.* 2002 [10]). Our observations showed that the empirical distribution of the discussed feature was marked by intriguing, not perceived before, shape. The distribution of values ($n=32$) from pooled samples did not reveal any discordance with the fitted normal curve (Shapiro-Wilk W test, $W=0.977$, $P=0.71$). The analysis of published works as well as unpublished data suggested that the studied trait obeyed the laws of the normal distribution in many birds. The results obtained for the separated samples (*P. gunnari* Wiman, 1905 – small specimens, *P. klekowskii* Myrcha, Tatur & del Valle, 1990 – large specimens; see Myrcha *et al.* 2002 [10]), in both cases indicated the presence of asymmetry. The negative skew, which appeared in *P. gunnari* ($n=11$), was

not statistically significant (perhaps it resulted from the small sample size). The positive skew was observed among larger specimens (*P. klekowskii*, $n=21$) and was statistically significant (Student t test, $t=2.290$, $P=0.03$).

The results, assuming the existence of a dichotomous grouping variable, clearly indicated the presence of overlapping, differing in the central tendency values, distributions. We suggested that this heterogeneity could have been considered in terms of sexual dimorphism. In the absence of distinct predictors (in a form of nominal variables), the existence of a well-marked differences between the mean/expected body size of males and females (sexual size dimorphism, SSD), was in our opinion, the most likely explanation.

We found, by comparing the measures of relative variability (similar sample sizes), that the variation in tarsometatarsal length in the Antarctic *Palaeudyptes* (pooled species data) was by 22% greater than the variance of the most diverse, in this regard, modern species of penguins - *Eudyptula minor* (J.R. Forster, 1781). On the other hand, this difference was below the value of 55% obtained by comparing *E. minor* and *Megadyptes antipodes* (Hombron & Jacquinet, 1841), the least variable representative of the present-day Sphenisciformes (Livezey 1989, *J. Zool.* 219). Modern Sphenisciformes are characterized by small, but statistically significant SSD (males are slightly larger than females; Livezey 1989). The trend (not statistically significant) of intensification of the SSD with increasing body size is observable in seabirds (Serrano-Meneses and Szekely 2006, *Oikos* 113). Thus, the presented data did not exclude the possibility of the existence of strongly marked SSD among the very large Eocene *Palaeudyptes* penguins. In the case of *Anthropornis*, another genus of the so-called giant penguins from Seymour Island, samples were too small to justify such analyzes.

We also examined the usefulness, for the purpose of body mass prediction in fossil penguins, of the allometric equations proposed by Campbell and Marcus (1992), and Cubo and Casinos (1997). These equations had been developed based on the data (circumference and diameter of the femoral shaft, body mass) for taxonomically heterogeneous groups of modern birds (swimmers, non-volant birds). We noted that the obtained estimates were unrealistically low, especially for large specimens. Despite this, the observed range of variation of these values testified to a significant variation of body size among the representatives of the studied assemblage.

[2] Jadwiszczak P. 2013. Taxonomic diversity of Eocene Antarctic penguins: a changing picture. In: Hambrey M.J., Barker P.F., Barrett P.J., Bowman V., Davies B., Smellie J.L., Tranter M. (ed.), Antarctic Palaeoenvironments and Earth-Surface Processes. Geological Society, London, Special Publications 381: 129–138 (chapter in a reviewed monograph).

The aim of this study was: (1) to identify the oldest fossil record of the largest Antarctic penguins – representatives of the Eocene genus *Anthropornis*, (2) to conduct a critical analysis of species diversity within the smaller representatives of *Palaeudyptes* – another genus of the so-called giant penguins and (3) to clarify the phylogenetic relationships between *Archaeospheniscus wimani* (Marples, 1953) and the species from the genus *Delphinornis*. The studied specimens came from the Białystok and London collections, and the comparative material – also from the Stockholm and Argentine collections.

Analyses of the new (not analyzed) fossil material from the London collection, allowed the identification of the oldest credible fossil record of *Anthropornis*, which comprised two incomplete tarsometatarsi and a fragment of the humerus. The analysis of the available documentation of field work and consultation with Dr. M. Richter, who had possessed extensive knowledge about the location of discoveries made by the British Antarctic Survey in 1989, made it possible to precisely determine the stratigraphic position of these specimens. They came from the probably Early Eocene unit T_{elm}3 of the La Meseta Formation on Seymour Island. So far the known stratigraphic range of *Anthropornis* encompassed the geologically younger units T_{elm}4 – T_{elm}7, and was the most abundant within T_{elm}7 (Myrcha *et al.* 2002 [10]; Jadwiszczak 2006 [12]). I would like to note that the oldest fossil record of *Palaeudyptes gunnari* (giant penguins; Myrcha *et al.* 2002 [10]) and another, undetermined, species and genus – the earliest medium-sized penguins, were collected within T_{elm}3 as well (Jadwiszczak and Chapman 2011 [19]). The sediments that made up this unit, had been accumulated probably at the end of the so-called Early Eocene Climatic Optimum, or shortly thereafter (Ivany *et al.* 2008, *Geol. Soc. Am. Bull.* 120).

The results of the examination of the incomplete tarsometatarsus IB/P/B-0967, one of the specimens recently included into the Białystok collection, suggested the presence of a previously unknown morphotype among smaller tarsometatarsi belonging to the adult Antarctic representatives of *Palaeudyptes*. Of particular interest was a significant degree of elongation of this relatively small specimen, EI > 2.56 (see Myrcha *et al.* 2002: table 1 [10]). Moreover, I found other, poorly preserved, bones (from the Białystok collection) and a cast (London collection), presumably representing the morphotype just mentioned. The explanation for the observed heterogeneity could have been the existence of a third (the smallest) species of Antarctic *Palaeudyptes*.

Ksepka and Clarke (2010, *Bull. Am. Mus. Nat. Hist.* 337), also Ksepka and Thomas (2012, *Proc. R. Soc. Lond. B* 279, *Supplementary Information*), on the basis of results from the phylogenetic analysis of the Sphenisciformes, proposed the inclusion of *Archaeospheniscus wimani* (Marples, 1953) into the genus *Delphinornis* Wiman, 1905. In an attempt to assess the merits of this controversial solution, I used the tarsometatarsal features

from bones representing all Eocene species of Antarctic Sphenisciformes and the Giant Petrel, *Macronectes giganteus* (Gmelin, 1789) – a species closely related to penguins, as an outgroup. The above-mentioned bones constituted the most reliable carriers for the relevant traits under the highly incomplete fossil record of these penguins. Of course, I was aware of the limitations imposed by the short data sequences available and in consequence – a probable appearance of polytomies.

I conducted two phylogenetic analyses based on the maximum parsimony (MP) method. The first analyzed dataset comprised the matrix of tarsometatarsal character states used (as a part of the larger set) by Ksepka and Thomas (2012). The topology of the consensus tree, resulting from two MP trees, suggested the presence of a 'clade' encompassing species from the genus *Delphinornis* and *A. wimani*. In this regard, my results were in line with those reported by the aforementioned researchers. The second analysis was performed based on a modified dataset; among others, I corrected some character states. The length of data sequences did not change, but I reduced a proportion of the non-informative, for a parsimony-based techniques, characters. The topology of the consensus tree, resulting from two MP trees, differed from the previous one – *A. wimani*, *Delphinornis* (three species) and *Marambiornis*+*Mesetaornis* formed a trichotomy (also in the MP trees). The values of the measures of topologic congruence between hierarchical classifications, were either the same or higher than those in the first analysis. Furthermore, the results of both analyses revealed the partially resolved polytomy, but in the case of the corrected character-state matrix, the polytomy was more resolved. The lack of justification for incorporation of *A. wimani* into *Delphinornis* (according to my results), has been recently supported by an output from the studies based on the considerably larger matrices (Chávez Hoffmeister 2014, *Pol. Polar Res.* 35).

[3] Jadwiszczak P., Acosta Hospitaleche C. 2013. Distinguishing between two Antarctic species of Eocene *Palaeudyptes* penguins: a statistical approach using tarsometatarsi. *Polish Polar Research* 34(3): 237–252.

The objective of the study was twofold: to analyse tarsometatarsi representing two extinct, closely related species of Antarctic penguins, *Palaeudyptes gunnari* and *P. klekowskii*, in terms of a quantifiable degree of morphological homogeneity of the genus, and to develop a relatively convenient and reliable method of allocating these bones between the species. The specimens assignable to representatives of *Palaeudyptes* are the most numerous skeletal elements within the fossil record of the Eocene Sphenisciformes from Seymour Island. My former studies (Jadwiszczak and Mörs 2011 **[1]**) had revealed that the diagnostic criteria used to date were too arbitrary and did not take into account the shape of

the empirical distribution of values of the important quantitative traits. In contrast to these studies (Jadwiszczak and Mörs 2011 [1]), highlighting the probable presence of a well-marked SSD (sexual size dimorphism), here we assumed the taxonomic background of the observed heterogeneity. With the current state of knowledge, we cannot completely rule out either of these two explanations.

For the analysis, we used the fossil material from the four largest, studied by me directly, collections of early penguins: the Bialystok, Stockholm, London and Argentine sets of bones. To accomplish the first objective, we chose 16 of the best-preserved tarsometatarsi possessing the diagnostic features of *Palaeudyptes* and, as a point of reference, a holotype of the type species (*P. antarcticus*, Early Oligocene, New Zealand). Other taxa described from the La Meseta Formation were represented by 11 specimens. For the multivariate statistical analysis, we used a novel combination of sophisticated forms of two classical methods of cluster analysis. The hierarchical technique (we used Ward's method) has been enhanced with the calculation of uncertainty measures (and their standard errors) based on multiscale bootstrap resampling. In order to further validate the results, we used the method of the minimum spanning tree. Instead of the classical (non-hierarchical) *k*-means technique, we chose a related (and robust) *k*-medoids method, complemented by a silhouette plot. That diagram allowed, among others, determine the goodness-of-fit of objects to the clusters they were placed by the algorithm, and the goodness-of-fit of the entire model. To determine the optimal number of groups, among which were to be distributed objects, we used the fuzzy cluster analysis, and the stability of the resulting models was assessed by observing changes in the values of Dunn's and silhouette coefficients.

To accomplish the second objective we used the finite mixture model analysis, using the EM (expectation-maximization) algorithm. It was based on a selected quantitative trait of 71 tarsometatarsi from the La Meseta Formation, assignable to the genus *Palaeudyptes*. The criterion of variable selection was, in addition to the size of the available sample, well marked bimodal shape of the empirical distribution of the values (see also Jadwiszczak and Mörs 2011 [1]). The analyzed distributions were represented by the curves obtained by the use of the non-parametric kernel density estimation (KDE) technique. During the study, we also used the PED (penalized expected deviance) – a measure of complexity and fit of the model to empirical data, and Ashman's *D* – a measure of meaningfulness of the separation of two components of a finite mixture of Gaussian distributions.

The results of the conducted analyses suggested that the studied set of specimens had a relatively well marked morphological heterogeneity, according to both the uni- and multivariate approach. Our studies revealed that the diversity of tarsometatarsi assignable to the Antarctic representatives of *Palaeudyptes* indicated that they belonged to two morphotypes, or (most likely) species, differing, among others, in body size. For two clusters

of specimens representing the above-mentioned taxon, the corresponding support values from the hierarchical analysis amounted to 82%. Interestingly, the minimum-spanning-tree topology for the data points obtained from the principal coordinates analysis (PCoA), although did not contradict the above results, it also suggested the existence of a fuzzy boundary between these clusters. The algorithm from the non-hierarchical analysis grouped all the observations in exactly the same way as its counterpart in the hierarchical technique. The values of the silhouette coefficient for two clusters of specimens representing *Palaeudyptes* exceeded 0.50 - the threshold value for the well-supported clusters. In both clusters, there were isolated objects characterized by a relatively weaker fit than others. The cluster representing the larger individuals was dominated by specimens classified as *P. klekowskii*, while the second cluster – by bones assignable to *P. gunnari* (Myrcha *et al.* 2002 [10]). It appeared to be symptomatic that the remaining specimens from these clusters were identified, in former studies, as *Palaeudyptes* sp. In the case of the first of these clusters, the medoid was represented by a bone not identifiable to the species level. The results of the analysis of the Dunn's and silhouette coefficient values, calculated for different sets of parameters of the fuzzy cluster analysis, revealed that the model assuming the presence of four groups of specimens (including two assignable to *Palaeudyptes*) was characterized by the highest stability.

These results have confirmed the validity of the use of signs of bimodality as a selection criterion for the most appropriate feature allowing to accomplish the second purpose of our work. The analysis of sizes of the available samples (differences resulted from the non-uniform distribution of damages) and the shape of the curves obtained using KDE (we had utilized three different selectors) led us to choose the dorsoplantar width of the third tarsometatarsal trochlea of penguins from the genus *Palaeudyptes*, a measurement relatively resistant to errors due to the impact of the mechanical destruction factors. Moreover, the *a posteriori* estimates of the number of components within a mixture of univariate distributions of the variable (using Markov Chain Monte Carlo) showed the lowest ("best") PED value for the two-component model. The finite normal-mixture model analysis allowed the determination of the parameters of the two components (μ and σ) and local estimates of the mixing proportions (λ). The difference between population means (μ_1, μ_2) amounted to 2.7 mm (standard deviation $\sigma_1=\sigma_2=1.2$ mm), under $\lambda_1=0.484$ and $\lambda_2=0.516$. The value of Ashman's D exceeded 2, which indicated the meaningfulness of such a distribution partitioning. The consecutive finite mixture model analysis produced, calculated for each of the 71 observations, two posterior probabilities. They could have been used for a given specimen to assess the uncertainty associated with its mixture-component membership. The uncertainty associated with the assignment of the holotype of *P. gunnari* to Component 1 was slightly smaller than the estimate for the only possible alternative ($P_1=0.5548$,

$P_2=0.4452$). In the case of the considerably larger holotype of *P. klekowskii* – posterior probabilities were decidedly in favour of the Component 2 ($P_1=0.0002$, $P_2=0.9998$). I want to note that the linear correlation between the analyzed feature and bone length (the basic determinant of specimen size) was strong ($r=0.87$) and statistically significant (randomization test⁵; $n=40$, 10000 randomizations, $P=0.0001$). It should be borne in mind that the studied specimens most probably came from populations with overlapping distributions of the analyzed trait, and presumably – most other variables as well. It seems justifiable, however, to indentify the Component 1 as *P. gunnari*, and Component 2 as *P. klekowskii*. Anyway, in the case of a particular specimen, its component membership must be viewed in terms of the probability theory.

Such a probabilistic approach, based on the finite mixture model analysis, represents a novelty in the field of paleontology of penguins (and other birds). Importantly, the proposed statistical method is very flexible (taking into account new specimens updates estimates) and can be used for the analysis of sexual dimorphism and other groups of organisms⁶.

[6] Jadwiszczak P. 2014. Synsacra of the Eocene Antarctic penguins: new data on spinal maturation and an insight into their role in the control of walking. *Polish Polar Research* 35(1): 27–39.

The objective of this work was: (1) to analyze the unique synsacrum (os *lumbosacrale*) of a juvenile representative of the Eocene Antarctic penguins and (2) to assess the condition and importance, for the early Sphenisciformes, of the alleged accessory sense organ for control of balance, localized within the synsacral canal. During my investigations, I used mainly new material, i.e., specimens included recently into the Białystok collection of fossil penguins from the Eocene La Meseta Formation on Seymour Island.

The synsacrum, an important component of the axial skeleton of birds, is made up by ankylosed vertebrae from the lumbar, sacral series as well as the cranialmost elements of the caudal series. Sometimes it is supplemented by the caudalmost thoracic vertebrae. The analysis of an intriguing late Eocene synsacrum IB/P/B-0319 revealed the presence of nine vertebrae representing all of the above-mentioned four segments of the vertebral column. This specimen belonged to a relatively large, though not larger than modern

⁵ I would like to note that this test was performed using Rndom Pro 3.14 (<http://pjadw.tripod.com>), a computer program that I created for statistical data analysis.

⁶ This method has been already recognized by researchers studying dinosaurs, see <http://t102130.science-dinosaurs-general.sciencetalk.info/new-deinocheirus-specimens-found-indicating-basal-ornithomimosaur-t102130-20.html>.

Sphenisciformes, juvenile individual. Most probably this bird had already attained at least partial independence from their parents or even hunted on its own. This was suggested, in addition to the nearshore origin of the Late Eocene sediments, by the results of a comparative analysis of the synsacrum of a juvenile Emperor Penguin. The location of a collecting site of the latter specimen testified to the fact that an individual had already been probably able to leave the breeding colony area.

In terms of morphology, the studied fossil specimen was characterized by an interesting combination of features undoubtedly juvenile (e.g., well-marked boundaries between some vertebrae, including the discontinuous nature of the median (spinous) crest and features more difficult to interpret. The latter category included the presence of a pronounced ventral sulcus (*sulcus ventralis*). Many of the known Eocene adult penguins had not possess such a sulcus, but in modern Sphenisciformes its developmental condition depended on the systematic position and sometimes also on the individual age. For example, it was conspicuous in adult representatives of the genus *Pygoscelis*, but weakly marked in both juvenile and mature *Aptenodytes*. In my opinion, all indications were that the analyzed specimen was the youngest (in terms of ontogeny) known synsacrum assignable to early penguins.

The primary function of this bone in birds is probably shortening and stiffening of the axial skeleton in order to improve the flight performance (Kaiser 2007, *The Inner Bird: Anatomy and Evolution*, University of British Columbia Press). The lumbosacral part of the spinal cord emanates the, complex and paired, lumbosacral plexus (innervating hind limbs, among others) and forms a characteristic enlargement. This intumescence is reflected in the shape of the middle portion of the synsacrum, including the synsacral canal. Moreover, it encompasses the spinal sinus housing an enigmatic glycogen body. The dorsal wall of the synsacral canal is characterized by the presence paired transverse grooves, which are best developed along the above-mentioned intumescence and demarcate individual vertebrae included into the synsacrum. These grooves are lined by membranes made of connective tissue (i.e., meninges) forming the semicircular canals filled with fluid. According to the results obtained by Necker (1999, *Eur. J. Morphol.* 37; 2005, *Anat. Embryol.* 210; 2006, *J. Comp. Physiol. A* 192), this fluid bathes and mechanically stimulates the lateral accessory lobes (also known as the lobes of Lachi) made of the nervous tissue, which are the evaginations of the spinal cord. The whole system resembles the functioning of the semicircular canals of the inner ear and, according to Necker, presumably acts as a specific sense organ of balance associated with walking. In modern penguins and other birds, in which the role of the feet in this respect is very limited (e.g., swifts and cormorants), the discussed structure is relatively poorly developed.

The studies of the shape of the synsacral canal in three Late Eocene specimens, allowing its direct analysis and creating casts, indicated the presence of the characteristic enlargement testifying to the existence of the lumbosacral intumescence of the spinal cord. These specimens had belonged in the skeletons of the large-sized adult Eocene Antarctic penguins. The system of transverse grooves was conspicuous – depressions shaping the semicircular canals were best developed within the lumbar segment. The results of the comparative analysis of casts showing the surface shape of the synsacral-canal walls in the fossil penguins and those published for other birds (Jelgersma 1951, *Zool. Meded.* 31; Necker 2006) were unequivocal. The alleged sense organ, in the case of the large-sized Eocene Sphenisciformes, was at most slightly more developed than its counterpart in modern swifts, hence – also present-day penguins (see above), whereas it was clearly inferior in this respect to the corresponding structure in birds intensively using their legs, such as ostriches and pigeons. My results suggested that the importance of this organ to the Eocene and modern penguins, undoubtedly specialized seabirds, was comparable and relatively small.

[7] Jadwiszczak P. 2014. At the root of the early penguin neck: a study of the only two cervicodorsal spines recovered from the Eocene of Antarctica. *Polar Research* 33: 23861, <http://dx.doi.org/10.3402/polar.v33.23861>.

The work focused on the transitional, in terms morphology of vertebrae, located at the root of the neck, segment of the vertebral column⁷ of the Eocene Antarctic penguins. So far, this important from the functional point of view segment of the axial skeleton of the early Sphenisciformes from Seymour Island, due to the lack of identified fossils, has not been studied. The task that I have set myself in this work was to identify, within the available material, the fossil specimens that meet the aforementioned criterion of location and to analyze them in terms of comparative and functional morphology, also in an evolutionary context.

Only two Late Eocene fossils were represented by articulated vertebrae forming the relevant segment, encompassing the transition between the cervical and thoracic spine. These specimens came from the Late Eocene unit Tem7 of the La Meseta Formation on Seymour Island. In both cases, I found the presence of three vertebrae (14 – 16): two elements forming a transitional cervicothoracic (or cervicodorsal) series and the first “true” thoracic vertebra.

⁷ Cervicothoracic transitional vertebrae *sensu* Baumel i Witmer (1993, w: Baumel i in., *Handbook of Avian Anatomy: Nomina Anatomica Avium, Nuttall Ornithological Club*).

The first specimen, IB/P/B-0981, was one of the bones recently included into the Białystok collection of fossil penguins. It had belonged in the skeleton of the individual presumably larger than the modern Gentoo Penguins (*Pygoscelis papua*), but smaller than King Penguins (*Aptenodytes patagonicus*). The second specimen, MLP 96-I-6-13, belonged to the Argentine collection and was described by Acosta Hospitaleche and Reguero (2010, *Antarct. Sci.* 22) as „thoracic vertebrae still joined”. It was a fragment of the incomplete skeleton assigned by the above-cited researchers to *Palaeudyptes gunnari*, a representative of the so-called giant penguins.

In 2012, I directly examined this skeleton and came to the same conclusion - the bones had belonged to a representative of *Palaeudyptes*. In the current paper, I confirmed, based on the results of my previous statistical analysis (Jadwiszczak and Acosta Hospitaleche 2013 [3]) and a very high value of the Bayes factor (343.8 for the choice between *P. gunnari* and *P. klekowskii*), the correctness of the above assignment at the species level.

The short portion of the spine located at the base of the neck is the caudalmost segment of the axial skeleton of the anterior part of the body of modern penguins, within which some degree of median-plane mobility is still possible (Stephan 1979, *Mitt. Zool. Mus. Berlin* 55, *Suppl.: Ann. Orn.* 3). The results of the analyses of both specimens suggested that the Eocene representatives of Antarctic penguins did not differ considerably, in terms of the above-mentioned biomechanical properties, from the living birds from this order. It was indicated by the shape and spatial orientation of the articular surfaces (of the shaft and articular processes), cranioventral foveae, which accomodates (during the neck bending) the ventral edge of the articular surface from the preceding vertebra, and the attachment surfaces for the elastic ligaments connecting individual vertebrae.

I also spotted the presence of traits not found so far in the present-day penguins. The specimen IB/P/B-0981 was characterized by unusual distinctness (depth, sharp edges) lateral concavities of the shaft in the first (caudalmost) transitional (cervicodorsal) vertebra. Perhaps, the feature discussed here reflected the shape of the diverticula of air sacks (*sacci pneumatici*), which in birds can reach as far as the cranialmost thoracic vertebrae. Such a possibility was suggested by the clearly dull surface of these depressions (see Wedel 2005, in: Rogers and Wilson (eds.), *The sauropods: evolution and biology*, University of California Press). The larger specimen (MLP 96-I-6-13) probably was similar in this regard. The unique feature of IB/P/B-0981 was the relatively small size of the intervertebral foramina located between the second cervicodorsal vertebra and the first “true” thoracic element. The significance of this was unclear, but it should be noted that it could have been associated with the configuration of the nervous brachial plexus.

➤ ***The Neogene (23.0 – 2.6 Ma): the Miocene (23.0 – 5.3 Ma) – the only fossil record of penguins from East Antarctica***

[5] **Jadwiszczak P.**, Krajewski K.P., Pushina Z., Tatur A., Zieliński G. 2013. The first record of fossil penguins from East Antarctica. *Antarctic Science* 25(3): 397–408.

The aim of this work was a comprehensive analysis of the only known skeleton elements of fossil penguins from East Antarctica. The results of the study were to answer the questions about the taxonomic position and its evolutionary context, age (including geological one) and the environment of these birds. The fossils discussed here were found in 2008 by the Russian-Polish Field Party working under the 53rd Russian Antarctic Expedition. The material came from the Miocene Fisher Bench Formation located within the Fisher Massif (Prince Charles Mountains, East Antarctica). These were not only the first such findings from the east part of the continent and south of the Antarctic Circle, but also, the only Antarctic penguin remains known from the Neogene. Both unique specimens were incorporated into the Białystok collection of fossil penguins.

We identified these fossils as two well-preserved elements of the wing skeleton: the right humerus (IB/P/B-0965) and left radius (IB/P/B-0966). Since the specimens had been found at a distance of not more than 2 cm apart, resembled each other in terms of color, had a similar state of preservation and matching size, we assumed that they belonged to the same individual.

As we had the humerus, the most characteristic (except for the tarsometatarsus) skeletal element of Sphenisciformes, it was possible to determine taxonomic position of the penguin from the Prince Charles Mountains. The analyzed humerus possessed a feature that was diagnostic for the crown-group penguins (Ksepka and Thomas 2012, *Proc. R. Soc. Lond. B* 279) – a pit located between the *sulcus transversus* and *tuberculus dorsalis* representing the ligamental attachment surface. This bone resembled, in terms of shape of the above-mentioned pit, the humerus of the modern *Spheniscus magellanicus* (J.R. Forster, 1781) from South America. Furthermore, the good preservation of the analyzed specimen allowed to detect the indisputable presence of three of the five reported by Göhlich (2007, *Acta Palaeontol. Pol.* 52) diagnostic features of the genus *Spheniscus* Moehring, 1758. The next (fourth) feature, in our opinion, probably was also present, and the last one was not, in fact, of diagnostic importance (the above-cited researcher had some doubts as well). We also noticed that the similar length of the two most distal trochlear processes of the distal epiphysis was probably another autapomorphy.

These bones probably belonged in the skeleton of the adult representative of the medium-sized penguins, taking modern Sphenisciformes as a reference point. It resembled

in this regard Antarctic and Subantarctic Gentoo Penguins, *Pygoscelis papua* (J.R. Forster, 1781). The individual from the Prince Charles Mountains was undoubtedly larger than all modern penguins from the genus *Spheniscus* and the earliest representative of this clade, the Miocene *S. muizoni* Göhlich, 2007, but in terms of body size, was inferior to the Mio-Pliocene *S. urbinai* Stucchi, 2002 (both species have been known solely from South America). Most likely, the penguin from the Prince Charles Mountains represented a new species within *Spheniscus*, a genus so far unknown from the coast of Antarctica, but the modest fossil record did not allow for the formal erection of a new species.

The results of the analysis of the stable strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) for three independent samples of the low-Mg calcite shell of a pectenoid bivalve cf. *Adamussium colbecki* (Smith, 1902), found together with the penguin bones, indicated the Late Miocene (Tortonian) age of these specimens (10.2 Ma; 9.5 – 11.45 ± 0.4 Ma). This estimate was in line with the results of the biostratigraphic studies based on diatoms. This meant that the studied specimens were among the oldest known remains attributable to the genus *Spheniscus*. The results of mineralogical studies and assessments of the diagenetic modification suggested the moderate bioapatite (the main mineral of a bone) alteration, reflecting the alteration in a marine environment. The sediments containing discussed bones, which are currently at a height of ca. 330 m above sea level, represented, uplifted in the later epochs, floor of a Miocene fjord. The presence of numerous fragments of pectenoid shells and the nearshore diatom species indicated a pronounced retreat of the ice sheet in the Lambert embayment and a marine incursion. Currently, the nearby Prydz Bay region is a breeding place and "hunting ground" for many species of birds (Woehler 1997, *Polar Biol.* 17), and there is no indication that at the end of the Miocene, the situation was radically different. The presence of a representative of Sphenisciformes in the coastal waters of East Antarctica did not necessarily testify to the existence of nearby breeding colonies of these birds, although such a possibility was highly probable.

The breeding ranges of penguins from the genus *Spheniscus* are constrained to South America and, in the case of a sole species, southern Africa. So far, the fossil record of these birds did not contradict the above statement (Jadwiszczak 2009 [16]). Given the dominant pattern of ocean currents and the fact that the Miocene penguin from the Prince Charles Mountains was geologically older than the earliest representatives of the genus *Spheniscus* from Africa, it appears that East Antarctica had been likely to play an important role in the evolution of the Neogene penguins. Presumably, it had been a natural bridge that allowed for the colonization of the coast of Africa.

SUMMARY

The conducted studies revealed that the oldest, dated to the Late Paleocene, fossil record of Antarctic penguins possessed a largely untapped potential, in terms of information content, and, in addition to limb bones, a single thoracic vertebra. These fossils, found within the Cross Valley Formation on Seymour Island and representing the type specimen of *Crossvallia unienwillia*, constituted the first evidence that some early Sphenisciformes had attained unusually large body size. The most intriguing osteological feature of this bird was, unique within the Sphenisciformes, morphology of the femoral head.

The youngest fossil record of penguins came from the Fisher Massif (Prince Charles Mountains). Its age was dated to ca. 10.2 Ma (Late Miocene). These have been the only such fossils attributable to the Sphenisciformes found in East Antarctica and also south of the Antarctic Circle. I have shown that the well-preserved humerus and radius belonged in the skeleton of the extinct representative of the modern genus *Spheniscus*. The location and age of this finding as well as the pattern of dominant sea currents, suggest that East Antarctica could have played an important bridge role during the geographical and evolutionary expansion of the *Spheniscus* lineage.

The most abundant and diverse fossil record of Sphenisciformes was found within the Eocene La Meseta Formation on Seymour Island. The evaluation of the paleontological material indicated the validity of the formal synonymization of the genera *Orthopteryx* and *Anthropornis*, *Ichtyopteryx* and *Delphinornis*, and also – the lack of justification for the inclusion of *Archaeospheniscus wimani* into *Delphinornis*. I found that the largest Antarctic penguins (*Anthropornis*) had a wider stratigraphic range than previously thought, encompassing also the presumably Early Eocene unit Teln3. I suggested that, currently, the best method of species-level classification for bones attributable to the Antarctic *Palaeudyptes*, traditionally allocated between two species, is a probabilistic approach, and proposed the appropriate statistical technique. I pointed out an alternative explanation for the existence of the wide range of variability among these specimens – the presence of the strongly marked sexual dimorphism (sexual size dimorphism, SSD). Moreover, I noticed the possible existence of the third (small) species of the Antarctic *Palaeudyptes*.

I drew attention to the fact that two characteristic segments of the vertebral column of the Eocene penguins, the base of the neck and synsacrum, in terms of the functional morphology, are very similar to their modern counterparts. This statement concerned both the mobility of the cervicodorsal spine and condition of the alleged accessory sense organ of balance located within the synsacral canal. Moreover, I described the youngest (in terms of ontogeny) known synsacrum assignable to the early Sphenisciformes.

The conducted studies involved a wide range of specimens representing extinct Antarctic penguins and the results significantly expanded knowledge on the evolutionary

history of the order Sphenisciformes. It should be noted that the known Paleogene fossil record of these birds ends up on the Eocene/Oligocene transition and the Neogene fossils are extremely rare and relatively young (Late Miocene). This means that we know almost nothing about 24 million years of the presence of penguins in the Antarctic. It is to be hoped that further geological and paleontological exploration of the region will bring new discoveries that help to fill the gap.

COURSE OF EDUCATION AND PROFESSIONAL ACTIVITY

I was born in 1970 in Białystok. Between 1985 and 1989, I attended the Adam Mickiewicz High School (High School no 1) in Białystok (UNESCO Associated School). According to my interests, I was in a class with a specialization in biology and chemistry. In 1989, I passed the exams and was admitted to study biology (a specialization in teaching) at the Institute of Biology, Warsaw University, Branch in Białystok (IB WU-BB).

M.Sc. IN BIOLOGY STUDIES. Being a third-year student, I have learned about the opportunity to participate in the studies of a large, amounting to over a thousand specimens, collection of the early (Eocene) Antarctic penguins. The aforementioned set of fossils remained under curation of Prof. Andrzej Myrcha, one of its creators, a well-liked by students, charismatic lecturer and researcher, head of the Department of Animal Ecology and director of IB WU-BB. My fascination with his personality, achievements of the potential promoter and the prospect of gaining access to unique specimens and conducting paleontological studies, prompted me to apply for joining the team. This step determined the direction of my professional life. Prof. A. Myrcha accepted my candidature for a position as his master's student.

For two years I have prepared and reconstructed the specimens as well as dealt with their morphological and taxonomic analysis, and preliminarily cataloged the collection. I paid special attention to tarsometatarsi, the most important, from the taxonomic point of view, bones of the fossil penguins. I was able to clean up the remnants of the matrix for a significant portion of these specimens and to determine their taxonomic position at the species level. During analyses, it appeared that some of the bones belonged to the representatives of yet undescribed genera and/or species. I understood what the so-called emotion of discovery, crowning months (or even years) of painstaking research, is, and eventually became convinced of outstanding beauty of scientific work.

By mid-1994, I prepared a comprehensive documentation containing, among others, detailed descriptions of morphological characters with the indication of features of the

presumed diagnostic importance, and numerous measurements. This was supplemented by a comprehensive discussion. I defended my master thesis, entitled "Diversity of the fossil penguin fauna of the Antarctic Seymour Island based on the analysis of tarsometatarsi from the collection of the Institute of Biology, Warsaw University, Branch in Białystok", on 15 July 1994.

On 15 September 1994, I was employed as a research assistant/junior scientist. As an assistant, under the scientific supervision of Prof. Marek Konarzewski, I was to do research on ecophysiology of birds, i.e., in line with the mainstream activity of the Department of Animal Ecology of IB WU-BB.

ANTARCTIC EXPEDITION. Following the earlier arrangements, on the fall of 1994, I became a member of the research team of the 19th Antarctic Expedition of the Polish Academy of Sciences to the H. Arctowski Station (King George Island, West Antarctica). Because of that, between 1 October 1994 and 14 April 1996, I was employed as a research assistant at the Department of Antarctic Biology, Polish Academy of Sciences (DAB PAS), based in Warsaw, the unit responsible for the organization of Antarctic expeditions. Such a periodic change of employer was the standard way of dealing with persons qualified to participate in an Antarctic expedition. My scientific duties, while on King George Island, included several independent spheres of activity.

Decidedly, the biggest challenge was the field work related to the study of ecological and ecophysiological aspects of the development of the Wilson's Storm Petrel, *Oceanites oceanicus* (Kuhl, 1820), chicks. These very interesting seabirds, nesting mainly in the rock crevices, are regarded as the the smallest endotherms of the Antarctic.

The next task was to collect samples of the winter food of the Gentoo Penguins, *Pygoscelis papua* (J.R. Forster, 1781). We used the method based on the stomach lavage under the quasi-laboratory conditions. The collected and preserved samples, after returning to Poland, were transferred to researchers from the Lodz University, as required by prof. Andrzej Myrcha.

My other duties included providing technical assistance during the work related to the projects implemented by Piotr Kosiorek (DAB PAS). During this activity, I participated in the collection of blood samples from a wing vein of penguins from the genus *Pygoscelis* and anchoring of data loggers (environmental-data recorders) to the backs of the selected pygoscelids as well as their recovery in the next breeding season. I took part in the, run for many years, monitoring of birds and marine mammals (pinnipeds) in the Admiralty Bay area. The few free moments of the summer season I devoted to the collection of skeletal fragments of seabirds, predominantly limb bones, the remains of victims of land and marine

predators. This set was later included into the collection of the comparative material created by Prof. Andrzej Myrcha at the IB WU-BB, primarily for studies of extinct penguins.

RETURN TO SCIENTIFIC WORK AT THE WU-BB. In the mid-April of 1996, after returning from the expedition, I resumed my work in the Department of Animal Ecology (IB WU-BB). I led classes, participated in studies of the developmental ecophysiology of chicks of some domestic birds. I conducted the laboratory analyses of corpses of Wilson's Storm Petrel chicks (brought from the Antarctic). They involved, among others, determination of fat content using the Soxhlet extraction method. Unfortunately, issues of the research conducted in the Department of Animal Ecology and planned doctorate subject strongly contrasted with my real, aroused during my master's studies, interests – palaeontology of penguins. In 1997, not seeing any possibility (also in the longer term) of studying the topics that I was passionate about, I decided to quit my job at the university.

EMPLOYMENT AT THE UNIVERSITY OF BIALYSTOK. Between 1998 and 1999, I worked as a sales representative for the trading company associated with the laboratory diagnostics industry. In 1999, I was proposed a research-assistant position at University of Bialystok and to take responsibility (technical and scientific) for the unique set of fossil penguins included into collections of the emerging Museum of Nature of the Institute of Biology. I started my new job on 1 March 1999.

Between 1999 and 2013, I co-created the above mentioned museum, which subsequently modified its name twice (the Professor Andrzej Myrcha University Museum/Center of Nature), led classes at the Institute of Biology, and analyzed and cataloged the, entrusted to my care, collection. I renewed a co-operation with Prof. Andrzej Gaździcki (Institute of Paleobiology, Polish Academy of Sciences) and Prof. Andrzej Tatur (Institute of Ecology PAS), who together with, deceased in 1997, Prof. Andrzej Myrcha created the studied collection. I made professional contact with two Argentine researchers studying the fossil penguins – Dr. Claudia Tambussi and her graduate student, Jorge Noriega, from the Museo de La Plata. Within four years, I became an author or co-author of six scientific papers (two neontological and four paleontological works) devoted to birds **[Appendix 3]**. I would like to notice that my first paper (Gębczyński and Jadwiszczak 2000 **[8]**) was devoted to the Wilson's Storm Petrels and was partly based on results from the analyses of the material I collected during the Antarctic expedition.

In 2001, I participated the postgraduate program in computer science at the Faculty of Computer Science, Bialystok University of Technology. I graduated in 2003 with the highest grade. Since 2004, I have been a webmaster of the Institute of Biology (Faculty of Biology and Chemistry, University of Bialystok; <http://biologia.uwb.edu.pl>).

Ph.D. THESIS AND THE SUBSEQUENT PROFESSIONAL ACTIVITY. On 5 July 2005, I defended my doctoral dissertation entitled „Fossil penguins of Seymour Island: systematics, evolution and their role in the Eocene ecosystem of the Antarctic”. The main purpose of the work was the taxonomic analysis of the Białystok collection of bones of the Eocene Antarctic penguins, with the exception of tarsometatarsi – studied for the M.Sc. thesis, treated as a reference point. I also took into consideration some aspects of evolution, by comparison with younger (in terms of geologic time) specimens, and paleoecology of these birds. The promoter of my thesis was Prof. Andrzej Gaździcki from the Institute of Paleobiology (Polish Academy of Sciences), and the defense of the dissertation took place at the Institute of Biology, Faculty of Biology and Chemistry, University of Białystok (IB UofB).

In December of 2007, I moved from the research assistant to assistant professor position. Between 2008 and 2012, I was Dean’s plenipotentiary for information and promotion. At the beginning of 2011, I was elected as a member of the Committee on Polar Research of the Polish Academy of Sciences (CPR PAS; term of office: 2011–2014). Since 2012, I have been a member of the Board of the Institute of Biology as well as the Board of the Faculty of Biology and Chemistry. In 2013, I was nominated by the Scientific Committee on Antarctic Research National Committee of Poland, together with two other Polish researchers, for a candidate to the *1st SCAR Antarctic and Southern Ocean Science Horizon Scan*. Since 1 October 2013, I have been an assistant professor at the Department of Genetics and Evolution IB UofB. In 2014, I was invited by the chair of the of the CPR PAS to join the editorial board (as an Associate Editor) of *Polish Polar Research*, a scientific journal of international reach, the official quarterly publication of the CPR PAS. On 28 January 2015, I was informed about my re-election as a member of the Committee (term of office: 2015-2018).

In the course of my work I led lectures, lab. classes and specialization lab for students of a five-year master’s program as well as three-year bachelor’s and two-year master’s programs of two degree courses – biology and environment protection, and for the ERASMUS program students (after a doctoral degree: 12 different classes). I was a consultant (in terms of biostatistics) of several master’s theses of students from the Institute of Biology, University of Białystok and creator of a computer program for the statistical data analysis (Rundom Pro), available from my web site. I prepared and conducted a five-day workshop "Basics of Bioinformatics" for the employees of the Wrocław University of Life Sciences (2010). As a staff member of the Professor Andrzej Myrcha Museum (later also University Museum and University Center) of Nature, I acquainted elementary, junior high and high school students, and all other visitors (including foreign visitors) with exhibitions organized as a part of the activity of this unit, including exhibitions organized during the

Podlasie Festival of Arts and Sciences and Academic Day. I am the author of a book entitled „Understanding statistics/Zrozumieć statystykę” (My Book, Szczecin, 2010) and two paleozoological entries in the Polish edition of Wikipedia.

The results of my studies were presented by me in a form of oral presentations (nine speeches) and posters during national and international conferences and workshops. My participation in the 9th International Symposium on Antarctic Earth Sciences in Potsdam (Germany) in 2003 was possible owing to a conference scholarship sponsored by Deutsche Forschungsgemeinschaft (DFG, German Research Foundation). In 2008, I got a “covering the costs of participation” – a conference scholarship sponsored by the National Geographic Polska, allowing me to participate in the 9th Czech-Polish-Slovak Paleontological Conference in Warsaw.

Appreciating the importance of the peer-reviewing for the progress of science, I prepared 22 reviews of manuscripts submitted to the editors of 15 journals, in the vast majority included in the so-called Philadelphia list, and one project of a foreign research grant (USA). I am a member of two international scientific societies, the *Society of Avian Paleontology and Evolution* (SAPE; since 2009) and *Asociación Paleontológica Argentina* (APA; since 2013) as well as a scientific and educational organisation – the *National Geographic Society* (since 1999). The full list of my teaching, popularization and organizational achievements is available in **Appendix 3**.

I am the author, or co-author, of 26 scientific papers: 16 articles published in the journals included in the so-called Philadelphia list, six reviewed papers (in English) in journals not included in this list (in a year of article publication), four chapters (in English) in reviewed monographs, two popularizing works (in Polish) and a book [Appendix 3]. They were cited 96 times, without self-citations – 63 times (according to Web of Science); according to Scopus Scopus, respectively: 255 and 170 times. The Hirsch Index amounted to 6 (according to Web of Science; Scopus – 7), and the Total Impact Factor – 18.132. A total of my work gained 482 MSHE points (according to the Communication from the Minister of Science and Higher Education [MSHE] on the list of scientific journals [31 December 2014]). I am the only, first or corresponding author of the vast majority of these works [Appendix 3].

A large part of these publications resulted from my two foreign grants (EU program SYNTHESYS) and a visit to the Museo de la Plata (La Plata, Argentina) – at the invitation of Dr. Marcelo Reguero (a curator of the fossil vertebrate collection). The implementation of the the above grants, in which I served the role of a project leader and only investigator, was also associated with short-term research visits to foreign institutions (the Natural History Museum in London and Naturhistoriska riksmuseet in Stockholm). The scientific co-operation with a team of paleontologists from the Museo de La Plata (namely Dr. Carolina Acosta

Hospitaleche and Dr. Marcelo Reguero) is still continued. I also keep in contact with my former hosts (Dr. Sandra Chapman and Dr. Thomas Mörs) from the institutions in which I implemented my grants. In December 2014, I got my third grant under the program SYNTHESYS (to be implemented at the Natural History Museum at Tring, UK, in 2015).

A source of great satisfaction for me is the opportunity to participate in genetic studies of endangered birch species, run by my wife, Dr. Katarzyna Jadwiszczak from the Institute of Biology, University of Białystok. Due to my commitment to this research, I was a co-author of two publications in the field of population genetics of the dwarf birch (*Betula nana* L.; Jadwiszczak *et al.* 2012 [29], Jadwiszczak and Jadwiszczak 2014 [21]).

DESCRIPTION OF SCIENTIFIC ACHIEVEMENTS

My documented (in a form of publications) scientific activity focused on two issues – the ecological and ecophysiological aspects of breeding in present-day birds associated with aquatic ecosystems, and paleontology of Antarctic penguins. The former issue concerned two species: Wilson's Storm Petrel, *Oceanites oceanicus* (Kuhl), a small Antarctic seabird from the order Procellariiformes, and Black-headed Gull, *Chroicocephalus (Larus) ridibundus* (L.) (Charadriiformes), the most common species of gulls in Poland.

ECOLOGY AND ECOPHYSIOLOGY OF BREEDING IN MODERN BIRDS.

Antarctic birds. – Wilson's Storm Petrels are colonial birds, which lay a single egg. It usually takes ca. 3.5 months from laying to offspring fledging (Beck and Brown 1972, *Brit. Antarct. Surv. Scien. Rep.* 69; Wasilewski 1986, *Pol. Polar Res.* 7).

Wilson's Storm Petrel chicks accumulate very large stores of fat, which can represent up to 80% of their dry body mass. The better part of these stocks is metabolized just prior to fledging (Obst and Nagy 1993, *Condor* 95). The aim of the study, carried out in co-operation with Dr. Andrzej Gębczyński from the Department of Animal Ecology (Institute of Biology, University of Białystok), was to clarify the role the fat stores for growth of the above-mentioned chicks based on the material and data collected by us during two Antarctic expeditions (1990–1991 and 1994–1996), in the Admiralty Bay area (King George Island, West Antarctica). We measured length of the tarsometatarsus, wing and head, determined body mass as well as lipid and water indices in growing chicks.

We found that relatively stable growth of chicks during the first three weeks of life, did not indicate substantial fluctuations in the availability of food resources of the marine environment. The comparison of values of lipid and water indices (calculated also for the birds found dead) allowed us to demonstrate that in the second half of the period of stay in the nest, changes in body mass of young storm petrels depended primarily on the variable

amount of accumulated fat. The stable level of the lean dry mass (LDM) and lack of association between body mass and linear measurements suggested that the food provided by the parents ensured a surplus of biogenic elements necessary for the development of the skeleton and feathers. Our results indicated that the proximate cause of the build-up of large fat stores in chicks was overfeeding by parents. The ultimate reason for this was presumably protecting offspring against death during periods of starvation caused by blocking access to the nest (crevices, burrows) during heavy snowfall (Gębczyński and Jadwiszczak 2000 [8]).

Domestic birds. – Another research project, carried out under the supervision of Dr. Norbert Duda and in collaboration with Dr. Włodzimierz Chętnicki (both from the Department of Vertebrate Zoology, Institute of Biology, University of Białystok), focused on the intraspecific parasitism in a domestic bird species – Black-headed Gulls. The representatives of this species are characterized by a strong fidelity to the breeding sites and their normal clutch contains three eggs.

The studied reproductive strategy, found among others in three other species from the genus *Larus* (Yom-Tov 2001, *Ibis* 143), is based on the use of certain birds parental behavior of individuals belonging to the same species by tossing their own eggs. The persistence of this phenomenon in the population could possibly be explained on the basis of either the theory of kin selection or reciprocal altruism. Some birds remove tossed eggs, damage them or even abandon their nests (Payne 1997, in: Clayton and More (eds.), *Host-parasite evolution: General principles and avian models*, Oxford University Press). However, most instances of such parasitism are difficult to determine by direct observation, hence other methods are used - field or molecular ones. For the analysis, we chose the breeding colony of Black-headed Gulls from the Dojlidy Ponds (Białystok).

The direct observation of nests showed no cases of intraspecific nest parasitism in breeding gulls, but we received several strong premises and some indirect evidence indicating the presence of this phenomenon among the representatives of the studies species. Almost 7% of the analyzed clutches contained more than three eggs, in the case of almost 6% of them, we detected signs of behavior of adult birds that might have indicated defense against parasitism - abandoned clutches, damaging or removal of eggs. In the case of other 3.6% of clutches we noted probable signs of acceptance of a tossed egg: the irregular rate of appearance of successive eggs in the nest and the presence of chicks and so-called late eggs (one or two) in the same nest. Especially valuable evidence was provided by three cases of egg transfer between adjacent nests, identified owing to their labeling with a marker. In addition, we analyzed the differences in size between successive three eggs in the clutch. The first egg was the largest one, whereas the last egg – the smallest within the whole clutch; differences were statistically significant ($P < 0.001$). In the case of clutches that had also the fourth egg, it was significantly larger than the third one ($P = 0.02$). Interestingly, in

as many as 66% of the 32 photographed clutches, the third egg differed in color from remaining eggs. Such cases of asymmetry (in size and color) have been interpreted by us as part of the protective mechanism against intraspecific nest parasitism in Black-headed Gulls, e.g. by sending a clear warning to other birds that the egg laying has already ended in this nest (Duda *et al.* 2003 [11]).

PENGUIN PALEONTOLOGY. The main area of my interest remains, since my master's studies, paleontology and evolution of the penguins (order Sphenisciformes), especially those from the Antarctic region. In this context, it seems worth a reminder the fact of my participation in the study of modern penguins and tubenoses (Procellariiformes) from the Antarctic King George Island. The representatives of the latter order of birds are considered to be the closest living relatives of the modern Sphenisciformes (Hackett *et al.* 2008, *Science* 320).

Systematics and phylogenetic relationships. – The basic problem, which one ought to deal with when studying the extinct Antarctic penguins, was the issue of clarification of systematics of these birds. Until 2005, the known fossil record of Sphenisciformes came exclusively from the Eocene (56 – 34 Ma) La Meseta Formation, located on Seymour (Marambio) Island, West Antarctic. The fossils were almost solely represented by isolated bones. The first published systematics of early penguins from Seymour Island (Wiman 1905, *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903* 3) was based, with one exception, on the morphological features and dimensions of the tarsometatarsi. The last twentieth-century comprehensive review of the systematics of these birds was presented by Simpson (1971, *Proc. R. Soc. Lond. B* 178), a co-founder of the „synthetic theory of evolution”. According to this researcher, the analyzed assemblage of the Eocene Sphenisciformes was represented by five genera and six species: *Anthropornis nordenskjoldi* Wiman, 1905, *Anthropornis grandis* (Wiman, 1905), *Archaeospheniscus wimani* (Marples, 1953), *Delphinornis larseni* Wiman, 1905, *Palaeudyptes gunnari* (Wiman, 1905) and *Wimanornis seymourensis* Simpson, 1971. Only in the case of the last of above taxa the type specimen (holotype) was a bone other than the tarsometatarsus – the humerus. Over the last two decades of the twentieth century, the fossil record of the Eocene Antarctic penguins expanded by thousands of new specimens. Decidedly, the largest, and still growing, collections of this paleontological material are two sets – the Argentine and Białystok⁸ collections. Based on the material from the latter collection Myrcha *et al.* (1990,

⁸ The Białystok collection owes its origin to the aforementioned Professors: Andrzej Myrcha, Andrzej Tatur and Andrzej Gaździcki.

Alcheringa 14) described a new species of early penguins – *Palaeudyptes klekowskii* Myrcha, Tatur & del Valle, 1990.

In a close co-operation with A. Tatur and A. Gaździcki as well as Argentine researchers, Claudia Tambussi, Jorge Noriega and Rodolfo del Valle, I updated the results presented in my master's thesis and extended the scope of the material studied using specimens from the Argentine collection. The direct analysis of 126 tarsometatarsi, the most characteristic skeletal elements of penguins, and published photographs and descriptions of the comparative material, allowed our team to assess the minimum taxonomic diversity of the fossil Sphenisciformes from Seymour Island (Myrcha *et al.* 2002 [10]). We positively verified the presence of four genera and six species: *Anthropornis nordenskjoldi*, *A. grandis*, *Archaeospheniscus wimani*, *Delphinornis larseni*, *Palaeudyptes gunnari* and *P. klekowskii*. The taxonomic diagnoses, i.e., sets of unique, compared to closely related taxa, traits or combinations thereof, in all of the studied genera and species required modification. Moreover, we erected two new genera (*Marambiornis* and *Mesetaornis*) and four species of relatively small penguins from the youngest unit of the La Meseta Formation (Telm7, Late Eocene, e.g., Marensi 2006, in: Francis *et al.* (eds.), Cretaceous-Tertiary high-latitude palaeoenvironments, James Ross Basin, *Geol. Soc. London Spec. Publ.* 258):

- *Delphinornis arctowskii* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002,
- *Delphinornis gracilis* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002,
- *Marambiornis exilis* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002,
- *Mesetaornis polaris* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur & del Valle, 2002.

The holotypes of newly-erected species came solely from the Białystok collection. Their binomial names were indexed in the 141st volume of the Zoological Record and registered in the ZooBank (<http://zoobank.org>).

The next stage of research on the taxonomy of the Eocene Antarctic penguins was an attempt to assign the remaining skeletal elements to the species described on the basis of the tarsometatarsi. I devoted the essential part of my doctoral dissertation to these issues. The results, that I obtained, have been published (Jadwiszczak 2006 [12]). The analyses involved almost 700 bones from the collection remaining under my curation. I utilized indirect reasoning, based, among others, on the size and shape differences between specimens, and frequencies of morphotypes. I confirmed the reliability of the estimate of diversity within the studied assemblage of the Sphenisciformes, proposed in my earlier work, which I think was composed of at least six genera and ten species. Not all bones, because of their condition, could have been taken into consideration, but large morphological heterogeneity, for example, among the incomplete small-sized humeri, suggested the possibility of the existence of other, still undescribed, penguin species. The representatives of all the described species most probably co-existed (in terms of ecological time) when the sediments

of the youngest unit of the La Meseta Formation were formed. The fossils attributed to four species of the smallest penguins from Seymour Island, *Delphinornis arctowskii*, *D. gracilis*, *Mesetaornis polaris* i *Marambiornis exilis*, came exclusively from the above-mentioned unit. Some of the presented in the publication skeletal elements of the early Antarctic penguins (the neurocranium, pygostyle, furcula, pelvic bone, ungual phalanx) were not known so far.

The oldest specimens from the analyzed Białystok collection were found within two, presumably Early Eocene in age (Marensi 2006, in: Francis *et al.*, Cretaceous-Tertiary high-latitude palaeoenvironments, James Ross Basin, *Geol. Soc. London Spec. Publ.*

258; Ivany *et al.* 2008, *Geol. Soc. Am. Bulletin* 120), units of the La Meseta Formation – Telm1 and Telm2. I described them in my next work (Jadwiszczak 2006 [13]). I concluded that among 18 studied specimens, 14 bones from Telm2s were found *in situ*, the remaining four (from Telm1 i Telm2) most probably were also not allochthonous. The identified bones comprised the humeri, tibiotarsi, phalanges from the foot skeleton, one femur, carpometacarpus and incomplete upper jaw. All the specimens, because of their size, certainly did not belong in the skeletons of penguins from any of the aforementioned four species of the smallest Sphenisciformes of Seymour Island.

I challenged the validity of describing new species of the Eocene Antarctic penguins based on isolated bones other than the tarsometatarsi, the case of *Tonniornis mesetaensis* and *T. minimum* (Tambussi *et al.* 2006, in: Francis *et al.* (eds.), *Cretaceous-Tertiary high-latitude palaeoenvironments, James Ross Basin, Geol. Soc. London Spec. Publ.* 258), for these skeletal elements, because of the nature of the fossil record (lack of the well-preserved larger parts of the skeleton), constituted too weak a basis for such decisions. My view has been accepted by a majority of students of the extinct penguins. Moreover, I proposed to replace the name of the biostratigraphical unit *Anthropornis nordenskjoeldi* biozone (Tambussi *et al.* 2006) with the term *Palaeudyptes klekowskii* biozone. *P. klekowskii* was a species decidedly more characteristic of the unit Telm7 than *A. nordenskjoeldi* – it was more abundant in terms of the specimen count than *A. nordenskjoeldi* (and representatives of other genera), this was its so-called abundance biozone, and also it had much more constricted stratigraphic range than *P. gunnari*, found also within much older sediments (Telm3; see Jadwiszczak 2006 [12]).

The proximal fragment of a small-sized tarsometatarsus (from the Białystok collection), I studied in 2008 (Jadwiszczak 2008 [14]), provided another strong premise suggesting that the previously estimated taxonomic diversity of fossil penguins from the La Meseta Formation was actually higher. The aforementioned specimen, which was found within Telm7, after a thorough cleaning of the remains of the matrix, was so clearly different from other tarsometatarsi that, in my opinion, represented yet undescribed genus and

species. Eventually, I decided that the material analyzed is too modest, so that I could designate it as the holotype.

The analysis of a rarefaction curve based on 104 tarsometatarsi assigned to six genera (Wiman 1905; Marples 1953, *Falkland Islands Dependencies Survey Scientific Reports 5*; Myrcha *et al.* 2002 [10]) and the above specimen, revealed that the probability of the existence of yet undescribed penguin genera from the La Meseta Formation is rather small. It was suggested by the rarefaction-curve shape, showing an expected number of taxa as a function of a specimen count (n). For the large n -s, the aforementioned curve began to flatten or, in other words, the acute angle between the tangent to the curve and the abscissa for n close to 105 was small (Jadwiszczak 2010 [26]). The sensitivity of the method, due to the large differences in the genera sizes (in terms of specimen counts) was limited, but symptomatic is the fact that, until now, despite intensive field work conducted by the Argentine paleontologists on Seymour Island, no new species has not been formally described.

The detailed analyses of bones attributable to *Anthropornis* from the Argentine, Bialystok and Stockholm collections revealed the presence of the intriguing heterogeneity of the hypotarsal morphology. We observed that some specimens were characterized by the bipartite medial crest, while in others the crest was undivided (Acosta Hospitaleche and Jadwiszczak 2011 [17]). Interestingly such a dichotomy was not related to either the bone size or stratigraphic position (age). Our finding suggested that the current main criterion for the division of the genus *Anthropornis* into two species, the specimen-size criterion (Wiman 1905, Simpson 1971, Myrcha *et al.* 2002 [10]), was not justified (Acosta Hospitaleche and Jadwiszczak 2011 [17]).

The analysis of the shape of medial margins of two, not fully formed tarsometatarsi, assignable to *Anthropornis* and *Palaeedyptes*, pointed to their surprising similarity. Both specimens possessed a characteristic (sharp) tuberosity. Such a tuberosity, in adults in a form of a mild convexity of the middle portion of the margin, had been considered as a diagnostic feature of the former of the aforementioned genera. That similarity, if not a coincidence (e.g., resulting from an injury suffered by a very immature representative of the *Palaeedyptes* penguins), might have testified to the close affinity between these genera. The results of the phylogenetic analysis presented in my later work, included into my selected scientific achievement (Jadwiszczak 2013 [2]), suggested such a possibility. Considering the probable phylogenetic affinities of *Palaeedyptes* relative to the Eocene penguins from lower latitudes, I noticed that the postulated relationship with Peruvian *Inkayacu paracasensis* Clarke, Ksepka, Salas-Gismondi *et al.*, 2010 (Clarke *et al.* 2010, *Science* 330) was even more likely than previously thought. Two of the five diagnostic features of *I. paracasensis* (Clarke *et al.* 2010), were not differentiating, for their states

coincided with the states identified by me in specimens (the jaw and femur from the Białystok collection) attributable to *Palaeudyptes* (Jadwiszczak 2011 [18]).

The issues of the interspecific diversity among the Antarctic representatives of *Palaeudyptes*, were considered in three publications included into my selected scientific achievement (Jadwiszczak and Mörs 2011 [1], Jadwiszczak 2013 [2], Jadwiszczak and Acosta Hospitaleche [3]). In turn, the analysis of the earliest Paleogene penguins and the only Neogene fossils were presented in two subsequent works included into my selected scientific achievement (Jadwiszczak *et al.* 2013 [4]; Jadwiszczak *et al.* 2013 [5]).

Body size. – The assemblage diversity can be considered at different levels and in different contexts. In the case of the Eocene penguins from the La Meseta Formation, the strongest emotions, apart from considerations about their systematics, have been raised by their body size estimations (e.g., Simpson 1976, *Penguins: past and present, here and there*, Yale University Press). Since the nineteenth century, thanks to the work of Huxley (1859, *Q. J. Geol. Soc. Lond.* 15), there was a well-known fact that at least some penguins living in the past geological epochs attained the unusually large body size. In the case of studies of the Antarctic Sphenisciformes, that thesis also proved to be true (Wiman 1905). The body size is a very important measure in biological research (including paleobiology), for it affects the structure and function of the body and its interaction with the environment (e.g., Schmidt-Nielsen 1984, *Scaling, why is animal size so important*, Cambridge University Press).

The analysis of specimens from the Białystok collection of fossil penguins from Seymour Island revealed that, at least four species of these birds, *Anthropornis nordenskjöldi*, *A. grandis*, *Palaeudyptes klekowskii* and *P. gunnari*, had exceeded, in terms of size, the largest modern penguins (Jadwiszczak 2001 [9]). Taking into account the obvious shape (proportions) differences among the studied bones attributable to both the early and modern representatives of the Sphenisciformes, I conducted the measurement selection, and the chosen variables were then used in the statistical analyses. The starting point was the determination of allometric equations showing the relationship between the logarithms of the values of selected linear measurements and the logarithms of the length and weight of modern penguins. I utilized two models of the simple linear regression analysis, in the case of the model II regression I chose the reduced major axis (RMA) approach. The results I obtained suggested that the body mass could have theoretically varied between 6 kg (*M. exilis*) and 108 kg (*Anthropornis* sp.), whereas the body length could have been (respectively) from 75 to 206 cm. Obviously, the above values were nothing more than just a rough estimates, most probably they were overestimated. The mean body length of the largest modern penguins, the Emperor Penguins, is 115 cm, and the body mass – 32.5 kg. The smallest representatives of the four so-called giant Sphenisciformes from Seymour Island, *P. gunnari*, weighed on average above 35 kg, reaching a body length exceeding

(sometimes significantly) 130 cm. The range of size variability was, in the case of the Sphenisciformes, undoubtedly wider in the first half of the Cenozoic era than nowadays. (Jadwiszczak 2001 [9]).

In my later work (Jadwiszczak and Mörs 2011 [1]), I drew attention to the risk associated with the use, for the prediction of body size parameters of the Eocene penguins, the allometric equations developed on the basis of data for taxonomically heterogeneous groups of modern birds (swimmers, non-volant etc.). The article, of which I was the first author, has been discussed in the section dedicated to my selected scientific achievement.

Analysing the London collection of the Eocene penguins, I found the oldest known bones representing the medium-sized Sphenisciformes, i.e., individuals larger than the Little Penguins, but smaller than the Emperor Penguins. The incomplete humerus NHMUK BAS A2481, not assignable to any species or genus, came from the presumably Early Eocene unit Telm3 of the La Meseta Formation (Jadwiszczak and Chapman 2011 [19]). To date, the fossil record of such penguins has been collected exclusively within younger units, Telm4 – Telm7 (e.g., Myrcha *et al.* 2002 [10]). A few years later, studying the remains of the oldest Antarctic penguin (*Crossvallia unienwillia*) from the Paleocene Cross Valley Formation on Seymour Island, I found that this individual was undoubtedly the earliest known bird from the group of the so-called giant penguins. The paper, of which I was the first author, has been discussed in detail in the section devoted to my selected scientific achievement (Jadwiszczak *et al.* 2013 [4]).

Reconstructions and functional morphology. – The analysis of the four most proximal wing bones of the medium-sized Eocene penguin, presumably not larger than *Delphinornis larseni*, revealed that most likely they belonged in the limb skeleton of a single individual. The specimens from the Białystok collection came from the same locality (within Telm7 of the La Meseta Formation), possessed the matching sizes, same color and surface texture. Presumably, they had been mistakenly separated during transport or preparation. In terms of size proportions of member elements, the studied skeleton resembled its counterparts in modern penguins, but differed from them with regard to the angle formed by the humerus and ulna (Jadwiszczak 2010 [26]). Interestingly, the above-mentioned humerus, like other “small-sized” humeri, was characterized by a weakly marked bipartition of the pneumatic fossa (*fossa pneumatica*) of the humeral head. Such a feature is not observable in large Eocene penguins, but is present in the present-day Sphenisciformes (Jadwiszczak 2006 [13]).

I also made an attempt to create an accurate reconstruction of the limb skeleton of the largest Eocene penguins from Seymour Island (Jadwiszczak 2012 [20]). Based on the material from all the aforementioned collections, I recreated the size, shape and arrangement of the bones forming the wing and a large part of the hind limb skeleton of an individual

belonging to the genus *Anthropornis*. This was a development of the concept presented by Marples (1953, *Falkland Islands Dependencies Survey Scientific Reports* 5). Moreover, I presented the reconstruction of the incomplete wing skeleton of *Palaeudyptes gunnari* (individual bones had been already described by Acosta Hospitaleche and Reguero [2010, *Antarc. Sci* 22]) and a fragment of the hind limb assignable to *P. klekowskii* (matching on the basis of sizes of the articular surfaces). I noted, among others, the very “modern” morphology of the distal epiphysis of the carpometacarpus attributable to *Anthropornis*, not present in other Eocene Antarctic penguins as well as the presumably differentiating, with regard to the genera *Anthropornis* and *Palaeudyptes*, details of morphology of both tibiotarsal epiphyses.

One of my most recent works (Jadwiszczak and Gaździcki 2014 [22]) was devoted to the heterogeneity in the condition of the first/hind toe (the smallest one) in the Eocene penguins from Seymour Island. We used the indirect reasoning, for the above skeletal element of the early Sphenisciformes was not known. We observed a large heterogeneity in the relative size of the contact area of the first (free) metatarsal (*os metatarsale* I, bestead at the base of the toe) with the tarsometatarsus, not always related to the size of the specimen. A vast majority of large tarsometatarsi from the Białystok collection (e.g., bones from the genus *Palaeudyptes*) did not possess any traces of attachment surface. In this respect, the most interesting bone appeared to be the specimen IB/P/B-970 characterized by a clearly marked bony crest, interpreted by us as the first metatarsal, a remnant of the strongly reduced toe. Our observations suggested the presumably large evolutionary plasticity in the foot skeleton of the studied birds.

Two publications devoted to the axial skeleton, namely, to the segment of the vertebral column located at the root of the neck (Jadwiszczak 2014 [7]) as well as the synsacrum and (located within it) alleged sense organ of balance (Jadwiszczak 2014 [6]), were discussed in the section dedicated to my selected scientific achievement.

Causes of diversity of the studied assemblage. – The obvious question that arised during the analysis of this unusually diversified, in terms of both the morphology and systematics, assemblage of early Antarctic penguins, was related to the reasons of such variability. One of my attempts to explain the origin of this phenomenon was based on Reichholf’s considerations (Reichholf 1996, *Twórczy impuls, nowe spojrzenie na ewolucję/The creative impulse, a new insight into evolution, PWN*) (Jadwiszczak 2000 [23]; Jadwiszczak 2003 [24]).

I suggested that the formation of such an assemblage was made possible through adaptive radiation under the periodic food shortage in the environment. My suggestion corresponded with the Reichholf’s thesis (based on the observation of contemporary biomes), which stated that the diversification of organisms resulted mainly from the long-term

resource shortages, and the preceding evolutionary breakthroughs were made possible by the emergence of excess, for example the availability of new ecological niches. A deficiency forces specialization, and indirectly may intensify speciation. Probably, only some species could have evolved due to such an *in situ* evolution, because penguins are highly mobile animals – representatives of certain species could have occurred only periodically. It is worth noting that the importance of the Antarctic Peninsula, and nearby Seymour Island, for the evolution of penguins (also modern ones) has been repeatedly highlighted (Baker *et al.* 2006, *Proc. R. Soc. Lond. B* 273; Ksepka *et al.* 2006, *Cladistics* 22; Ksepka and Thomas 2012, *Proc. R. Soc. Lond. B* 279). The results of studies of the Late Eocene assemblages of molluscs (Stilwell and Zinsmeister 1992, *Ant. Res. Ser.* 55) and echinoderms (indirectly – also fish and crustaceans; Aronson *et al.* 1997, *Geology* 25) suggested that such deficiency conditions most likely had periodically occurred in the area of the current Seymour Island. The fact is that the greatest diversity (the presence of all the described taxa) the studied fossil penguin assemblage attained within the youngest strata of the La Meseta Formation (Telm7), traditionally connected with a pronounced climate cooling just prior to the expansion of the continental ice-sheet close to the Late Eocene/Oligocene transition (ca. 34 Ma) (see fig. 2 in: Jadwiszczak 2010 [25]).

I would like to note that the results of the analyses of the partial penguin skulls from the La Meseta Formation, recently reported by Haidr and Acosta Hospitaleche (2012, *N. Jb. Geol. Paläont. Abh.* 263/2), testified to the presence of the clear trophic specialization among Late Eocene Antarctic penguins. The above authors suggested the existence of the medium-sized fossil penguins that had fed on the diversified prey as well as piscivorous species (small- and large-sized penguins) and large-sized sphenisciforms fed on small crustaceans. The postulated by those researchers diversity of food preferences was significantly lower in the older units of the formation. The skulls of birds have a relatively low fossilization potential, hence the specimens representing the beak, braincase etc. are very rare. One of the best-preserved of such specimens is a dagger-like upper jaw from the Białystok collection (IB/P/B-0167), assignable to the skeleton of a very large penguin (?*P. klekowskii*), frequently presented in publications as an example of a specialization for hunting larger fish or squids (Myrcha *et al.* 1990, *Alcheringa* 14; Jadwiszczak 2000 [23], 2003 [24], 2010 [25]). The less elongated and clearly smaller mandible (IB/P/B-0653), presumably assignable to *A. wimani* or *P. gunnari*, indicated a shorter, though “shallow”, beak – an organ not suitable for hunting small shoaling crustaceans (Jadwiszczak 2006 [12], 2010 [25]).

I, together with my collaborators, also addressed other, resulting from a change in emphases, possible explanations for a large diversity of fossil penguins from the unit Telm7 of the La Meseta Formation. The changes of climate conditions and the associated alterations in other abiotic components of the environment as well as the remodeling of the

trophic structure of the ecosystem had to affect the least numerous constituent of the food web, large predators. The sharks disappeared from the fossil record, but (for example) the toothed whales, potential competitors for food resources, and the gadiform fishes became more abundant. Perhaps such a change of "game rules" was an incentive for the processes of speciation (and/or specialization) in the Late Eocene Sphenisciformes (Myrcha *et al.* 2002 [10]; Jadwiszczak 2010 [25])

Review papers. – I have always been deeply convinced of the great importance of the review and popularizing articles, especially for novice researchers and those interested in the progress of science. I wrote two such publications on the evolutionary history of the Sphenisciformes.

The main goal of one of the above-mentioned works (Jadwiszczak 2009 [16]) was to summarize the current state of knowledge on penguin evolution in the 150th anniversary of erecting the first extinct species of these fascinating birds – *Palaeudyptes antarcticus* Huxley, 1859. My intent was to prepare the first, after 20 years (Fordyce and Jones 1990, in: Davis i Darby (eds.), *Penguin Biology*, Academic Press), compilation of the most important achievements of the penguin paleontology. It was all the more important, for the 21st century had brought a number of breakthroughs and as a result – a marked increase in interest in the issues of evolutionary past of the order Sphenisciformes. The discussed work focused mainly on paleontological studies, but I also included the available results from the molecular studies based on the present-day material.

The second publication (Jadwiszczak 2013 [28]) became a part of the thematic issue of the *Kosmos* journal devoted to studies of polar ecosystems. The issues raised in this work concerned the results of studies devoted to the oldest (i.e., Paleocene and Eocene) fossil record of penguins. The scope of both papers was not limited to the Antarctic penguins though.

PALEONTOLOGY OF OTHER GROUPS OF BIRDS. Discovered remains of Eocene Antarctic penguins are often accompanied by fossils representing other groups of organisms. Some of these specimens are sometimes included, as "accompanying material", into collections of fossil Sphenisciformes. The specimen IB/P/B-0698 from the unit Telm6 of the La Meseta Formation (Seymour Island) fitted in this category. This fossil was found in 1992 by Prof. A. Gaździcki and Prof. A. Tatur (both from the Polish Academy of Sciences), and whereupon was included into the Białystok collection. A more detailed analysis of the specimen was conducted several years later, and our findings were consulted with researchers abroad. This fossil resembled an incomplete jaw (an upper part of the beak) of the representative of the family Threskiornithidae (ibises). If our taxonomic identification was correct, it represented

the oldest known fossil record of this family from the Southern Hemisphere (Jadwiszczak *et al.* 2008 [15]).

GENETIC STRUCTURE OF RELICT POPULATIONS OF BIRCHES. A valuable diversion from my, focusing on birds, scientific activity was, as already mentioned, participation in projects carried out by Dr. Katarzyna Jadwiszczak. These studies concerned the genetic structure of populations of relict birch species, the shrub birch, *Betula humilis*, Schrk. and dwarf birch *B. nana* L. Among others, we assessed the genetic variation resources in the Polish populations of the dwarf birch. The values of the studied parameters were found to be lower than those in the shrub birch, which is more abundant in Poland; the lowest values were found in two populations from the Sudety Mountains. We indicated, based on results of our analyses, the most probable factors responsible for such a situation: significant reductions of population sizes (during the ice-sheet expansion and also more recently), the genetic drift (strongly marked in small populations), natural selection (the impact of competitive species) and geographic isolation (Jadwiszczak *et al.* 2012 [21]). Moreover, we showed that in Polish populations of the studied species, there were only two haplotypes of the chloroplast DNA. Interestingly, the populations from the Sudety Mountains represented two different phylogeographic lineages. The most probable explanation of such a distribution appears to be the recolonisation of the Central Europe from the area of two (east and west) glacial refugia. The issues of the studies and conservation the dwarf birch, we presented in a popularizing article published in the *Chrońmy Przyrodę Ojczystą* journal (Jadwiszczak and Jadwiszczak 2014 [29]).

OTHER TOPICS. In 2010, I wrote a book (Jadwiszczak 2010 [27]) that familiarize the B.Sc., M.Sc. and Ph.D. students as well as researchers with the issues of the statistical data analysis, especially in biology and related branches of science. Statistics proved to be a very useful tool in the study of fossil penguins (e.g., Jadwiszczak and Mörs 2011 [1], and Jadwiszczak and Acosta Hospitaleche 2013 [3]).

PROSPECTS. The dynamic development of the paleontology of penguins (growing collections of fossils, recent discoveries of better-preserved specimens, the intensification of contacts between researchers) allows an optimistic approach to the further research in this field. In the near future, I would like to give special attention to the functional morphology of Sphenisciformes. I plan to acquire a 3D scanner, a tool that would help to facilitate reconstruction work (in co-operation with the appropriate graphics software) and to create realistic 3D models. I have been constantly improving my skills in the three-dimensional computer graphics (using the Blender, Mudbox, Sculptris and other computer programs) and

statistical data analysis (especially based on the R environment). The EC-funded grant (under the SYNTHESYS program), which I gained in December 2014, will allow me to deepen my knowledge of the anatomy of the present-day representatives of Sphenisciformes (owing to examination of the collection housed at the Natural History Museum at Tring, UK).

Białystok, 3.02.2015 r.

Piotr Jadwiszczak