FLIGHTLESSNESS AND LONG BONE ALLOMETRY IN PALAEOGNATHIFORMES AND SPHENISCIFORMES

by

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ABSTRACT

Palaeognathiformes and Sphenisciformes are the only two major taxa that have lost the capacity for flying. Nevertheless, the consequences of this flightlessness are completely different. While Palaeognathiformes are all running birds, Sphenisciformes are adapted to swimming. To study the morphology of leg and wing bones, length, sagittal and transverse diameters and second moment of area of humerus, ulna, radius, femur, tibiotarsus and tarsometatarsus were measured. Thirty-three specimens from fourteen species of Palaeognathiformes and eleven specimens from seven species of Sphenisciformes were studied. Several non-flying species from other avian orders were also considered. Regressions of all these parameters were calculated with body mass as the independent variable. For each bone, the ratio sagittal diameter/transverse diameter was also calculated. Most of the correlations are significantly different from the isometric condition. From a mechanical point of view, the most interesting result is that the second moment of area of the leg long bones always scales with strong positive allometry, whereas in the case of the wing long bones, the scaling shows high negative allometry. Biometrically, Sphenisciformes display a constant wing long bone morphology, with transverse diameters much larger than sagittal. In contrast, Palaeognathiformes present a highly variable morphology of the wing bones, affecting length and diameters.

KEY WORDS: birds, flightlessness, long bones, scaling, cross-section, swimming, running, Sphenisciformes, Palaeognathiformes, evolution.

INTRODUCTION

The inability to fly is a condition that has been acquired in a more or less independent way for a large number of avian species, inhabiting either aquatic or terrestrial environments (FEDUCCIA, 1985). Frequently, the flightless condition developed in an aquatic environment implies the modification

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of wings for swimming propulsion, while in a terrestrial environment the most typical flightless birds are clearly runners, showing a tendency towards large size and strong legs (CRACRAFT, 1974). Various adaptative pressures have been postulated to act in either terrestrial or aquatic environments. These ideas also involved the consideration of a particular evolutionary mechanism (heterochrony) (LIVEZEY, 1995). See also DE BEER (1954) for an early formulation and DAWSON et al. (1994) for recent experimental evidence in favour of the heterochronic hypothesis in Palaeognathiformes.

A brief general overview of the occurrence of flightlessness in birds shows that only two high-level taxa (orders) have lost the ability to fly, namely Palaeognathiformes and Sphenisciformes, but while the former order is a classic example of running adaptation, the species of the latter order are typical swimmers. Here we present the results of a study on the scaling of the long bones, both in Palaeognathiformes and Sphenisciformes, in comparison with other examples with different degrees of flightlessness. In mammals, especially insectivores and rodents, it has been shown that aquatic life leads to mechanical constraints that differ from those acting on standard terrestrial locomotion (BOU et al., 1987, 1990; CASINOS, 1994; CASTIELLA & CASINOS, 1990). Here we attempt to identify differences and/or parallelisms in the pattern of flightlessness in the two orders, Palaeognathiformes and Sphenisciformes, involving running and swimming adaptation, respectively. As a working hypothesis we assume that while a selective pressure due to swimming has acted either on wings or wings and legs in Sphenisciformes, in running Palaeognathiformes the different degree of wing reduction is a consequence of the absence of a specific selective pressure related to locomotion.

MATERIAL AND METHODS

Sixty-two specimens from 33 species of birds were used in the present study. They are the following:

Order Sphenisciformes

Family Spheniscidae

Aptenodytes patagonicus (Miller, 1778) (1)
Eudyptes chrysocome (Forster, 1781) (3)
Eudyptes chrysolophus (Brandt, 1837) (2)
Pygoscelis adeliae (Hombron and Jacquinot, 1841) (1)
Pygoscelis antarctica (Forster, 1781) (1)
Pygoscelis papua (Forster, 1781) (2)
Spheniscus magellanicus (Forster, 1781) (1)