Foreword

This monograph is devoted to a particularly interesting scientific problem of the origin of flight in mammals. The first gliding mammal, known as *Volaticotherium*, appeared as early as the Jurassic, approximately 150 Ma. Subsequently, gliding flight emerged independently several times among marsupials, rodents, and colugos. On the contrary, flapping flight in mammals was only developed in chiropterans and became as perfect as in birds and extinct pterosaurs. The acquisition of this ability was a key adaptation, allowing a wide adaptive radiation of chiropterans; in the modern mammalian fauna, they display the second greatest species diversity just after rodents.

Bats appeared in the fossil record in the Eocene on all continents except for Antarctica and South America. North America has yielded complete skeletons of Early Eocene bats. These first reliable representatives of the order Chiroptera already had completely formed adaptations for flapping flight. Therefore, they provide very little information for understanding the initial causes of the appearance of this key adaptation. It is only possible to reconstruct them based on indirect characters provided by analysis of flying adaptations of living forms. This monograph is just devoted to this question.

Flapping flight in the atmosphere of the Earth imposes heavy demands on the flight apparatus of vertebrates. Great mechanical forces, work, and power produced in the shoulder girdle combined with fine adjustment of the angle of attack of the flapping wing pose stringent requirements upon the flight apparatus. The convergence of bats and birds in this respect is evident. It is not a gross exaggeration to assume that Chiroptera approach Aves in diversity. Against a background of general convergence of the two groups, it is particularly interesting how the same external requirements resulted in the appearance of peculiar general design of the flight apparatus in chiropterans. This is undoubtedly associated with ancestral morphological features; it is evident that ancestors of chiropterans already had parasagittal limbs and a perfect terrestrial locomotion, which was thoroughly investigated experimentally in many marsupials and placentals.

The study of the locomotor apparatus is of interest, since its adaptations form the general appearance of animals and directly reflect requirements of environments. At the same time, while running, digging, swimming, and climbing of mammals are

considered in many studies, flight of chiropterans has undeservedly received little attention. As compared with other locomotion patterns, flapping flight is more difficult to study experimentally and analyze, since it does not produce visible tracks, rapid wing movements escape video recording at a standard frame rate, and the distribution of external forces over the wing surface at natural interaction with air is difficult to model. As for morphological studies of bats, they have usually been restricted to this order itself without consideration of the most interesting points concerning evolutionary transition from non-flying to flying forms. As a result, the origin of flapping flight in mammals is discussed in much fewer publications than that of birds. A more or less detailed hypothesis for the origin of flight in mammals has not yet been proposed.

The present book prepared by employees of the Vertebrate Zoology Department of the Biological Faculty of Moscow State University, which is well-known for the old traditions of studies in the field of comparative anatomy and functional morphology, bridges this gap and opens a new page in the analysis of flight in mammals. The approach implemented by the authors combines the complex morphobiological method of K. A. Yudin and the method of the force–balance analysis of the musculoskeletal mechanisms developed by F. Ya. Dzerzhinsky, a teacher of all authors of this book. The purpose and problems posed in this work expand far beyond the framework of the study of chiropteran flight, which was developed by predecessors. Even the primary description of the morphological material discloses purposeful interest of the authors in the evolutionary development of flapping flight in mammals.

A particularly inspiring point is the fact that the topic chosen is rather new for the authors, so that they are not constrained by routine technique for studying the flight and bravely introduce approaches that were developed in neighboring fields of functional morphology. The flight apparatus seems as beneficial as the jaw apparatus of birds or limbs of cursorial mammals for the revelation of remarkable adaptations by the methods familiar to the authors. For example, the authors successfully apply graphic analysis of the static equilibrium, which was of great importance in the treatment of adaptive sense of a number of other musculoskeletal mechanisms, and corroborate that, in this case, it is also heuristic and fruitful. They show that the shoulder girdle of bats is enormously loaded, with forces being of an order of magnitude greater than the animal's weight; among mammals such heavy loading probably occurs in specialized diggers only. This results in prominent adaptations of chiropteran shoulder girdle, which the authors successfully treat by the analysis of general distribution of forces. There is no doubt that, in the future, detailed analysis of forces will provide a precise treatment of adaptive sense of particular differences between various bats in the elements of the shoulder girdle.

The ideas of the authors about the formation of flight in mammals are presented as an evolutionary scenario. In their opinion, the basic structural changes in the course of transition from terrestrial quadrupedal locomotion to flapping flight were associated with the change of the limb action plane from parasagittal to frontal. The authors have shown convincingly that this change was only possible through an intermediate stage of running along the vertical tree trunks; to grasp it animals had to sprawl forelimbs laterally as far as possible. The next step involved the development

of a wing membrane between the fore and hindlimbs on each body side for gliding from tree to tree. Subsequently, the formation of a membrane between fingers allowed movements of the manus to be used for more efficient manoeuvring during gliding. Apparently, the membranous manus has become extremely prospective, so further development resulted in the acquisition of flapping flight and, hence, appearance of a new mammalian order, Chiroptera. This elegant evolutionary scenario is attractive due to its simplicity and is supported by extensive factual evidence and observations provided in the monograph. This completely novel hypothesis can be tested by future paleontological findings, although they are extremely rare for tropical arboreal animals.

Thus, it is possible to state with confidence that the authors are highly qualified specialists and their hypothesis is a great scientific achievement – a real boon for future researchers in the field of mammal and vertebrate evolutionary morphology. Such hypotheses are necessary for a better understanding of the mechanisms of the evolutionary process and the development of key morphobiological adaptations. Therefore, this monograph is a great event not only for zoology, but also for general biology and evolutionary theory.

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