Сборник трудов Зоологического музея МГУ им. М.В. Ломоносова
Archives of Zoological Museum of Lomonosov Moscow State University
Том / Vol. 54 Стр. / Pp. 350–355

AVIAN FLIGHT AND STABILITY

Walter J. Bock

Department of Biological Sciences, Columbia University; wb4@columbia.edu

The discovery of the fossil genus *Microraptor* in China with elongated flight feathers attached to its hind legs led to considerable analysis of its flying ability and much speculation on for adaptive significance of this tetrapteryx pattern (W. Beebe). The pelvic wings definitely provided additional lift in these early birds, but their essential function and adaptiveness appears to be placing the center of lift posterior to the center of mass in these first flying birds for proper longitudinal stability. Once large pectoral flight muscles evolved in connection with flapping flight, the pelvic wings and the elongated tail were no longer needed for longitudinal stability with the results that the pelvic wings disappeared and the *Archaeopteryx*-like tail could be shortened with all of the tail feathers attaching to the plate-like pygostyle. Hence strong support is provided for Beebe's tetrapteryx hypothesis as well as for the theory that the origin of avian flight was from the trees down, not from the ground up.

ПОЛЁТ И СТАБИЛЬНОСТЬ У ПТИЦ

Уолтер Дж. Бок

Открытие в Китае ископаемого рода *Microraptor* с удлинёнными маховыми перьями на задних конечностях побудило к детальному исследованию способности к полёту и масштабным рассуждениям о тетраптерности (У. Биб). У этих ранних птиц задние крылья несомненно добавляли подъёмную силу, однако их основная функция и приспособительное значение состояли в размещении центра подъёмной силы в центре масс тела птицы для обеспечения нужной продольной устойчивости. При появлении увеличенных грудных мышц в связи с развитием машущего полёта задние крылья и удлинённый хвост оказались ненужными, в результате хвост *Archaeopteryx*-типа смог укоротиться, а его перья прикрепиться к небольшому пигостилю. Эта схема служит важным подтверждением третраптерной гипотезы Биба, а также гипотезы происхождения полёта птиц «сверху вниз» (с деревьев на землю), а не «снизу вверх» (с земли на дерево).

Discovery of the Mesozoic fossil bird, *Microraptor* (Zu et al., 2000, 2003; Wikipedia, 2015a) provided the first clear indication that early birds possessed flight feathers on the hind limb. Subsequent work suggested most strongly that *Archaeopteryx* also possessed such flight feathers which may have been unknowingly removed during the early preparation of these specimens. Almost a century earlier (Beebe, 1915) based on observations of the development of feathers on the hind limb of pigeons and interpretation of full-sized photographs of the Berlin specimen of *Archaeopteryx* concluded that this earliest-known fossil bird possessed flight feathers on the hind limbs. He concluded that birds has an initial tetrapteryx stage in their evolution. To my knowledge, Beebe did not pursue this idea further and while his paper was known to many workers, no further thought was given to the possibility of a four-winged condition in early avian evolution until 2000 and the discovery of *Microraptor*. Subsequent observations strongly suggest that Archaeopteryx possessed flight feathers on its hind limbs (Feduccia, 2012, p. 68). Several additional, excellent specimens of *Microraptor* were discovered and a few other early avian taxa, such as *Anchiornis* as well as *Pedopenna* and an unnamed basal enantiornithine, have been described (Feduccia, 2012).

1. Why four wings

As soon as the four winged structure in *Microraptor* was described, a number of ornithologists, paleontologists and morphologists inquired into the functional and adaptational explanations for this newly realized flight structure in these early birds. In his early paper, Beebe made no attempt to provide these explanations which was not surprising because powered airplanes were in their infancy and knowledge of aerodynamic engineering has scarcely trickled down to biologists interested in avian flight.

Attention to the functional properties of the four wings as present in *Microraptor* was almost completely limited to the added lift provided by the hind limb wings in comparison to the early biplanes as were common up into the 1930's. Several groups constructed models of the four-winged *Microraptor* and tested them in wind tunnels (Alexander et al., 2010; Feduccia, 2012). A difficult problem was the orientation of the hind limbs relative to the body and of the several segments of the limb relative to each other. These problems resulted from an incomplete knowledge of the articular surfaces and the absence of any knowledge of the articular ligaments of the hip joint and of the several segments of the hind limb. The articular ligaments have the major role in determining the type and range of movement of skeletal elements at their articulations. The model constructed by Alexander et al. (2010) preformed well (see also Rubin, 2010; Feduccia, 2012) and demonstrated that the elongated feathers on the hind limb could provide lift. The Alexander's model and one constructed by a group at the American Museum of Natural History were featured in a Nova television program in the United States (Feduccia, 2012; I have not watched this Nova program). And several other groups discussed the ability of *Microraptor* to use the hind limb wing to move through the air (Chatterjee, Templin, 2007; see also Feduccia, 2012). Two important factors that was not mentioned about these models were the distribution of mass in these models and whether this distribution was reasonably related to the presumed distribution of mass of *Microraptor*.

The conclusion of the tests of the flying ability of the model, especially that of the Kansas group (Alexander et al., 2010), was that it flew well. Its performance in the wind tunnel tests was superior to its rival and the MIT aerodynamic engineers were enthusiastic about it, saying that it "climbed steadily and more predictably than anything they had seen so far" (Feduccia, 2012, p. 183).

These tests, as well as the conclusions reached by other workers on the function of the four wings of *Microraptor*, demonstrated that this configuration of wings resembling that of an avian biplane worked perfectly well in producing lift. To my knowledge, no comparisons were made between the four-winged model and a similar two-winged model lacking only the ventro-posterior set of wings on the hind limbs.

Moreover none of these analyses and discussions of the functional properties of the four-winged configuration seen in *Microraptor* and presumably present in *Archaeopteryx* and other early birds such as *Archiornis*, *Cryptovolans*, and possibly *Sinornithosaurus* (Feduccia, 2012). No ideas were presented as to the functional and adaptive significances of the second wing in these early birds and why the second wing disappeared quickly in the further evolution of birds? Is there any foundation to the strong suggestion by Beebe (1915) that a tetrapteryx stage existed and even had to exist in the evolution of flight in the earliest steps in avian evolution of birds?

Before turning to what seems to be the solution to these two questions, mention should be made to the tail of these early birds as well documented by the tail processed by *Archaeopteryx* and known ever since this basal bird was described in the early years of the 1860s. As is well known to anyone concerned with the origin of birds, the tail of *Archaeopteryx* consists of a long series of caudal vertebrae with a pair of stiff feathers attached to the lateral side of each vertebrae. This is strikingly different from the tail of later birds in which the caudal vertebrae are fused into a plate-like pygostyle to which all of the tail feathers (remiges) attach. Most studies of the tail in avian flight have concentrated on other functions, such as steering, directing the flow of air after it passes the wing, and etc. but this does have a role in providing some lift, especially at very low speeds (Pennycuick, 1975, 2008), although not in all birds. The lift provided by the avian tail was measured experimentally in *Sturnus vulgaris* (Maybury et al., 2001). In *Archaeopteryx* and other basal birds, the tail seems to function mainly, or entirely, to provide additional lift during flight; it appears poorly suited to assist steering during flight.

2. Stability

Solutions exist to the two questions posed above and indeed well before the flight feathers were discovered on the hind legs of *Microraptor* and other very early birds. This solution is based on the concept of stability as applied to flying objects such as airplanes and animals. Stability, or stable equilibrium, is a property of objects in which the object will return to its original position after being acted upon by an external force. Objects on a flat, horizontal plane are stabile until their center of gravity moves outside of its base (Wikipedia, 2015b). Stability increases if the base of the object becomes broader or if the center of gravity is closer to its base. Unstable objects will continue to move further from their original position if acted on by an external force. A come standing on its base if stabile, but is unstable if standing on its pointed tip.

Stability also applies to flying objects of which the important type for this analysis is longitudinal stability (Wikipedia, 2009, 2015b) which is stability around the longitudinal axis of the airplane. Longitudinal stability depends on the position of the center of mass relative to the center of lift. If the center of mass lies behind the center of lift, the flying object is unstable; if the center of mass is too far in front of the center of lift, the flying object is too nose heavy. Hence the position of these two centers has to be located carefully to insure the proper degree of longitudinal stability. Various treatments of avian flight mention stability of the bird in flight but do not specify how the avian construction results or does not result in longitudinal stability.

Peters and Gutmann (1985, fig. 4, p. 238) clearly emphasize that for stabile flight, especially in the initial gliding stage in the evolution of avian flight, a large feathered tail was needed to provide lift in addition to that provided by the wings. They excluded consideration of lifting planes formed flight feathers on the hind limbs because their analysis was well before the discovery of *Microraptor*. They pointed out that in these earliest, gliding birds, the largest mass of muscles were concentrated in the hind limbs (see also Bock, 2013) which would result in the center of gravity (= center of mass) being located posterior to the center of lift if the only lift was generated by the airfoils of the forelimb (= avian wings).

Archaeopteryx, and almost certainly *Microraptor* and other early birds, had well developed wings but small pectoral flight muscles. They were gliders, climbing up trees and gliding to other trees and back to the ground. Their pelvic limb musculature was well developed. Consequently their center of mass was much further posterior than in later birds which possessed large flight muscles in their pectoral region. The result of being gliding fliers with their center of mass located further posterior in their body meant that these earliest birds were longitudinally stabile. The hind limb wings added to the lift generated by the tail and positioned the center of lift posterior to the center of mass and restored the longitudinal stability in these animals which was essential for successful gliding.

With the development of active flapping flight made possible by the great increase in the size of the pectoral muscles, the center of mass of birds shifted forward and lay anterior to the center of lift of the wings. The lift of the hind limb wings was not needed nor was the lift of the *Archaeopteryx*-like tail. Hence two further changes could occur in avian evolution. The hind limb wings could be lost as these secondary wings were awkward and interfered with the use of the hind limbs for terrestrial locomotion. The elongated *Archaeopteryx*-like tail could evolve into the typical avian tail with the decrease in the number of caudal vertebrae and the subsequent fusion of these vertebrae into the plate-like pygostyle to which all of the tail feathers attached. This allowed the evolution of a tail that was suitable for the different functions and biological roles possessed by the tail in modern birds but would not have been possible in the elongated *Archaeopteryx*-like tail such as greater steering, additional control of the air flow from the wings, etc. (Pennycuick, 1975, 2008; Norberg, 1990; Maybury et al., 2001).

Most interesting is that Beebe (1915) proved to be completely correct in his prophecy that a tetrapteryx stage existed in the early evolution of birds.

3. Evolutionary steps in avian flight

After his detailed redescription of the London specimen of *Archaeopteryx* (De Beer, 1954a), De Beer formulated the important concept of mosaic evolution (de Beer, 1954b) in which he argued that evolutionary changes occur in a series of steps that must be understood in the sequence in which they took place. The evolution of avian flight certainly illustrates the pattern of mosaic evolution as follows:

1) Evolution of feathers, orientation in a three dimensional world for a partial life within trees.

2) Flattened and spread-out body to provide a maximum surface area for parachuting from trees.

3) Development of greater surface area with longer feathers on both limbs and on the elongated tail for better parachuting and then gliding a greater distance when descending from trees.

4) Aerodynamic surfaces of the hind limbs (Beebe's tetrapteryx stage; *Archaeopteryx* stage) and tail to place the center of lift posterior to the center of mass for longitudinal stability and better flying abilities, both gliding and later active flapping flight.

5) Development of larger pectoral muscles and a stronger pectoral girdle for flapping flight (post-*Archaeopteryx* stage) placing the center of mass anterior to the center of lift provided by the pectoral wings.

6) Loss of the pelvic wings, no longer needed, and shorting the caudal vertebrae which fused into the pygostyle for the attachment of all tail feathers.

This pattern of evolutionary changes in the origin and perfection of avian flight is consistent with the fossil record and the theory that birds flew from the trees down and not from the ground up.

References

Alexander D.E. 2002. Nature's flyers. Birds, insects and the biomechanics of flight. Baltimore & London: The Johns Hopkins University Press. 384 p.

Alexander D.E., E. Gong L.D. Martin D.A. et al. 2010. Model tests of gliding with different hindwing configurations in the four-winged dromaeosaurid *Microraptor gui*. — Proceedings of the National Academy of Sciences of the United States of America, 107 (7): 2972–2976.

Beebe C.W. 1915. A tetrapteryx stage in the ancestry of birds. — Zoologica, 2 (2): 39–52.

Bock W.J. 2013. The furcula and the evolution of avian flight. — Paleontological Journal, 47 (11): 1236–1244.

Bock W.J. 2015. Review of: Riddle of the Feathered Dragons, by Alan Feduccia. — The Wilson Journal of Ornithology, 127. In Press.

Bock W.J., Bühler P. 1995. Origin of birds: Feathers, flight and homoiothermy. — Archaeopteryx, 13: 5–13.

Chatterjee S., Templin R.J. 2007. Biplane wing planform and flight performance of the feathered dinosaur *Microraptor gui*. — Proceedings of the National Academy of Sciences of the United States of America, 104 (5): 1576–1580.

de Beer G.R. 1954a. *Archaeopteryx lithographica*. A study based on the British Museum specimen. London: British Museum (Natural History). 68 p.

de Beer G.R. 1954b. *Archaeopteryx* and evolution. — The Advancement of Science. D. Zoology, 11: 160–170.

Feduccia A. 2012. Riddle of the feathered dragons. Hidden birds of China. New Haven: Yale University Press. 368 p.

Maybury W.J., Rayner J.M.V., Couldrick L.B. 2001. Lift generation by the avian tail. — Proceedings of the Royal Society, London, ser. B, 268: 1443–1448.

Maynard Smith, J. 1952. The importance of the nervous system in the evolution of animal flight. — Evolution, 6 (1): 127–129.

Norberg U.M. 1990. Vertebrate flight: Mechanics, physiology, morphology, ecology, and evolution. Berlin: Springer Verlag. 291 p.

Pennycuick, C. J., 1975. Mechanics of flight. — Farner D.S., King J.R. (eds). Avian biology, Vol. V. New York: Academic Press. P. 1–75.

Pennycuick C.J. (ed.). 2008. Modelling the flying bird. Theoretical Ecology Series, Vol. 5. Burlington: Academic Press. 480 p,

Peters S.D., Gutmann W. 1985. Constructional and functional preconditions for the transition to powered flight in vertebrates. — Hecht M.K., Ostrom J.H., Viohl G., Wellnhofer P. (eds). The beginnings of birds. Proceedings of the International Archaeopteryx Conference. Eichstätt: Jura Museum. P. 233–242.

Rayner J.M.V. 2001. On the origin and evolution of flapping flight aerodynamics in birds. — Gauthier J., Gall L.F. (eds). New perspectives on the origin and early evolution of birds. New Haven: Peabody Museum Natural History. P. 363–385.

Rubin J. 2010. Paleobiology, arcade games, and the origins of avian flight. — Proceedings of the National Academy of Sciences of the United States of America, 107 (7): 2733–2734.

Wikipedia. 2009. Longitudinal static stability. — https://en.wikipedia.org/wiki/Longitudinal_static_stability.

Wikipedia. 2015a. *Microraptor*. — https://en.wikipedia.org/wiki/Microraptor# References.

Wikipedia, 2015b. Flight dynamics. — https://en.wikipedia.org/wiki/Flight_dynamics.

Xu X., Zhou Z., Wang X. 2000. The smallest known non-avian theropod dinosaur. — Nature, 408: 705–708.

Xu X., Zhou Z., Wang X. et al. 2003. Four-winged dinosaurs from China. — Nature, 421: 335–400.