

UDC 591.174:598.2

PREADAPTIVE STAGE FOR FLIGHT ORIGIN

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Preadaptive Stage for Flight Origin. Bogdanovich, I. A. — Bipedalism as a preadaptive stage for bird's flight is considered. We attribute the formation of full bipedalism in bird ancestors with pelvic limbs transition from segmental to parasagittal position. This transition was fast enough. We can assume that the pectoral limbs freed from the support remained while laterally spaced and gave set of transformations with different degrees of reduction. Thus morphologically “winglike” version of the thoracic limbs could appear. Parasagittal pelvic limbs allowed birds ancestors fast and maneuverable running, while the movements of free and highly movable thoracic limbs (feathered unrelated to flight) provided dynamic stability of the animal. In addition, their fluttering movements facilitate hopping from one branch to another and the descent from the trees. On the bottom branches protobirds could jump with perching just by the pelvic anisodactyl limbs, not by thoracic as had supposed earlier. Active interaction of the primary simple feathers with air as well as its protective function could become an impetus for their transformation into differentiated structures. Unlike gliding (as preadaptive stage for active flight) bipedalism with free feathered forelimbs provides per se parallel development of two autonomous enough locomotor systems of birds (flight and terrestrial locomotion) and extensive adaptive radiation of representatives of the class.

Key words: bipedalism, flight, birds.

Despite the long history of the study of the origin of birds and flight, the origin and subsequent evolution of feathered wings remains one of the most controversial topics in the vertebrate paleontology (Kaiser, Dyke, 2014). For example, the question of preadaptive stage preceding the flight is not entirely unambiguous. As such the terrestrial, through the running and jumping (Dececchi et al., 2016), and arboreal, through gliding (Czercas, Feduccia, 2014) hypotheses are still being discussed.

Up to a certain time it was common belief that the way of becoming the birds as a taxon, the transformation of thoracic limbs into wings led to bipedalism (Du Brul, 1962; Ilichyov et al., 1982). Today, the transition to bipedal locomotion with full exemption of thoracic limbs from the support function is considered as a stage that preceded the origin of flapping flight of birds (Long et al., 2003; Kurochkin, Bogdanovich, 2008, 2010). In another point of view the gliding (when in process of air locomotion both fore and hind limbs are involved) is much better suited as a transitional stage to flapping flight than bipedalism, which only leads to reduction of muscles and thoracic limbs as whole (Panyutina et al., 2015). It is impossible not to admit that the exemption of the thoracic limbs from the support-locomotor function was followed by their partial reduction. It is known that reduced organs demonstrate a very large and diverse variability of their parts due to the termination or weakening of natural selection and preservation of independent variations of these parts (Schmalhausen, 1947). Thus after removal of the support function of thoracic limbs ancestors of birds could give a “bouquet” of transformations with varying degrees of reduction. We have previously noted the probable relationships of the transition to bipedal locomotion with the transition of the pelvic limb in parasagittal position (Bogdanovich, 2014). The known papers on the specified transition of limbs are focused precisely on the pelvic limbs (Parrish, 1986; Sennikov, 1989; Kuznetsov, Sennikov, 2000). We can assume that exempt from support forelimbs remained laterally spaced. Such thoracic limbs (not placed under the body) are more likely candidates for conversion to wings in phyletic lineage of birds. Acquisition of parasagittal position by free thoracic limbs occurred later due to restructuring of the shoulder joint with increasing of degrees of freedom (Jenkins, 1993). Transition of pelvic limbs in parasagittal position in archosaurs was fast enough, and a very decisive step (Kuznetsov, 1999; Kuznetsov, Sennikov, 2000), it had a revolutionary character (Sennikov, Makarov, 2009) and becoming a true breakthrough in the evolution of terrestrial locomotion (Zinoviev, 2010). Agreeing with the authors mentioned above, we also believe that the transition to the parasagittal position was fast enough, perhaps, closest to the saltation. Adopted today postural grades, for example (sprawling, semierect, fully erect) have been marked subjectively and the difference between them is so great that it seems evaluated through saltations between stable and discrete functional mechanisms (Gatesy, 1991). Thulborn (1984) also consider saltation from reptiles (segmental limbs) to the birds (parasagittal limbs) with the occasional (seemingly) appearance of a coordinated set of adaptations for flight.

We attribute the specified pelvic limbs transition (segmental–parasagittal) to the formation of full bipedalism and exemption of vertebral column from the obligatory lateral bending of body (Bogdanovich, 2014). After removal of the support function the emergence of morphologically “winglike” version of partially reduced thoracic limbs seems probable. Thus, it seems quite fair the conclusion of the one of first consistent Darwin’s unfollowers — G. Mivart: “It is difficult to believe that the avian limb was developed in any other way than by a comparatively sudden modification of a marked and important kind” (Mivart, 1871, p. 121).

According to Sennikov (1989) in progressive groups of archosaurs bipedalism was the main way of realization of high-speed locomotion. The advantage in speed of biped over the four-legged confirmed by recent studies (Kubo, T., Kubo, M., 2012). The specified advantage could be achieved under condition of parasagittal pelvic limbs. Any movement of the limbs out of a parasagittal plane reduces the speed of forward movement (Coombs, 1978). Thus, pelvic limbs transition in parasagittal position can be considered as one (if not the only) of reasons for bipedalism becoming among the archosaurs. Other reasons virtually are not studied (Kubo, T., Kubo, M., 2012). Attempts to achieve of parasagittal limbs are known also for four-legged representatives of archosaurs (Sennikov, 1989, 1999), but full parasagittal condition in dinosaur-bird line is noted in connection with full bipedalism.

At high speed and maneuverability of terrestrial locomotion movements of highly mobile laterally spaced thoracic limbs in bipedal birds ancestors, feathered without relation to flight (Cowen, Lipps, 1982; Kurochkin, 2006 and others) provided a dynamic stability of the animal. In addition, the fluttering movement of feathered thoracic limbs facilitated moving from one tree branch to another and descending from trees (Kurochkin, Bogdanovich, 2010). On the bottom branches a probirds could jump with perching just by the pelvic limbs (Bogdanovich, 2007) not by thoracic limbs as had supposed earlier (Martin, 1983). We assume that both interaction of initially simple feathers with air and their protective function could be stimuli for their transformation into differentiated structures (see review in Kaiser, Dyke, 2014). Perhaps the lack of arboreal stage in the last models of the formation of wings for flapping flight (Deccechi et al., 2016) has not allowed confirming the effect of locomotion on this process. Thus it does not seem unlikely to us that the locomotion played a role in the evolution of the feather before the elongated feathers on the forelimbs have formed the original wing (Kaiser, Dyke, 2014).

Development of flapping wing determined the emergence of a new phyletic lineage leading to modern birds. At another phyletic line pectoral limbs got back to the support function (but in parasagittal position) in the representatives of secondary four-legged dinosaurs, who were initially bipedal (Orlov, 1989; Sennikov, 1989).

The remained bipedal theropods show a wide variety of thoracic limbs models (Middleton, Gatesy, 2000) with not quite clear functions. Manipulative function of thoracic limbs (Osborn, 1916) in conjunction with a partial reduction of the fingers and the tight abutment of remaining fingers to each other is unlikely to be sufficiently effective (Bogdanovich, 2000); hypothesis about the use of thoracic limbs as an “insect nets” (Ostrom, 1976, 1979) received quite justified criticism (Martin, 1983). More recent studies of the joints and its biomechanics suggest that the possible movements of theropod thoracic limbs are much smaller than indicated a hypothetical models; manipulative function (grasping and prey keeping, digging and others) were not possible at the basal theropods (Carpenter, 2002; Senter, 2006 a, b). It could also indicate a quite rapid transition to bipedalism, not related to the emergence of new functions of thoracic limbs.

At the different lines of reptiles (including dinosaurs) thoracic limbs were used for gliding flight (Kurochkin, 2001, 2007). In passive flying animals (gliders) common center of flying membrane must coincide with the center of gravity (Beebe, 1915). To satisfy this condition, the feathers should be located not only on the hands and tail, but also at the pelvic limbs. The existence of such a hypothetical form called *Tetrapteryx* (Beebe, 1915), was remarkably confirmed by modern discoveries of “four-winged” dinosaurs and some enantiornithines with feathers on all the limbs (Xu et al., 2003; Kurochkin, 2004; Xu, Zhang, 2005) and more ancient archosaurs (Czercas, Feduccia, 2014). Obviously, such form as one of the attempts air conquering was deadlock. Morphologically the gliding is provided absolutely differently compared to the active flight (Padian, 1983). Thus the gliding is incompatible with the further

forming of flapping flight (Caple et al., 1983). It is not known any one group of tetrapods, where the transition from gliding to flapping flight occurred, and where the primitive form would be gliding, and advanced — flapping fliers (Long et al., 2003). In contrast to the active flight the gliding does not require the full transition to bipedalism.

For mammals, however, a scenario in which the gliding stage (colugo stage) preceded the formation of flapping flight (bats stage) was proposed (Panyutina et al., 2015). It is assumed that transition from the first stage (with a well-developed membrane between the fore- and between the hind limbs) to the last is predetermined by increasing of anterior (interdigits) part of the membrane initially for better gliding control (Panyutina et al., 2015). Although for such control the posterior part of the membrane seems to be more effective. Development of the distal (anterior) aerodynamic plane since digits, is more logical to expect at development of flapping wings, because at flapping just a distal end of limb moves most rapidly and better interact with air. At development of planning such difference in speed are not present and plane of wing will form from the body more likely. Such design is stronger and aerodynamically advantageous as does not create a gap between the flying surface and the body (Kurochkin, Bogdanovich, 2010). In birds ancestors exactly on the most distal segments of the forelimbs first simple feathers appeared, initially as a demonstration structures (Cowen, Lipps, 1982; Kurochkin, Bogdanovich, 2008). As mentioned above, the appearance of feathers (regardless of reasons), could have been useful both for terrestrial bipedal locomotion and for the movement on tree branches or bushes (Kurochkin, Bogdanovich, 2008).

Flapping flight with a continuous (solid) flying membrane was realized in two groups — pterosaurs and bats. But in both cases a significant reduction of terrestrial locomotion apparatus was “paid” for it. Appearance of featherlike structures (and later — true feathers) could determine another strategy of the locomotor apparatus development in the ancestors of birds. Multi-slit (in this case feathered) wing has markedly greater coefficient of lifting force as compared with a continuous (solid) one (Alexander, 1968). Therefore, the active flight arising from the fluttering movements of feathered thoracic limbs, perhaps not so much “drew off” muscular mass from an alternative system of pelvic limbs, and was not correlated with the growth of the flying membrane. Both favored subsequently per se parallel development of both systems (Bogdanovich, 2000; Kurochkin, Bogdanovich, 2008, 2010). In turn, the same high specialization of two autonomous enough locomotor systems of birds (flight and terrestrial locomotion), has provided an extensive adaptive radiation of representatives of the class.

I am grateful to N. V. Zelenkov and A. G. Sennikov (Paleontological Institute, Russian Academy of Sciences) for their helpful comments in improving the manuscript.

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Received 18 October 2016

Accepted 23 May 2017