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► **To cite this version:**

Pauline Provini. Study on the pelvic system of birds and on the origin of flight. *Revue de Paléobiologie*, 2013. hal-02341363

HAL Id: hal-02341363

<https://hal.science/hal-02341363>

Submitted on 31 Oct 2019

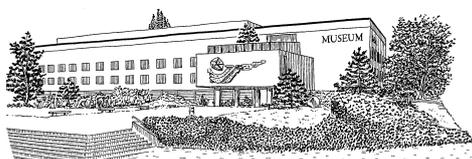
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R E V U E D E PALÉOBIOLOGIE

ISSN 1661-5468

VOL. 32, N° 2, 2013



Muséum d'Histoire Naturelle • Ville de Genève • Suisse

Study on the pelvic system of birds and on the origin of flight

Pauline PROVINI^{1,2}

Abstract

Among the main hypotheses proposed to explain the acquisition of flight, two theories have been the subject of an animated debate for several decades, the terrestrial theory and the arboreal theory. According to the first hypothesis, small cursorial feathered theropods would have used their hindlimbs and their proto-wings to jump higher, leading to the apparition of flapping flight. This idea is supported by the discovery of *Sinosauropteryx*, a small cursorial dinosaur with feathers. The second hypothesis – the arboreal theory – supposes that theropod dinosaurs started flying after an arboreal stage. The development of feathers and wings would have helped to glide until the apparition of flapping flight. The discovery of another fossil, *Microraptor gui* with a large air foil (impressions of feathers are visible on all four limbs and tail) supports this process. The recent discovery of fossils of theropod dinosaurs, marking the transition from strictly terrestrial animals to animals potentially able to fly, has revived the debate about the origin of bird flight. However, despite the remarkable preservation of recently discovered fossils, it seems that paleontological studies alone will not answer all the questions about the origin of flight. Thus, other tools are important to consider, as the study of structure/function relationships among modern birds, which will provide new functional hypotheses on the fossil record. It is interesting to note that the two main hypotheses regarding the origin of flight are based on different interpretations of the pelvic system functions (*i.e.* the pelvis and hindlimbs): In the terrestrial hypothesis, propulsion during take-off is fundamental whereas in the arboreal theory, absorbing impact when landing is the main constraint. Despite the fundamental role of the pelvic system in the locomotion of modern birds, very few studies have focused on this locomotor module and even less in the context of the origin of flight. In this review work, we attempt to demonstrate how the study of the pelvic system of modern birds is essential to provide new evidence on the origin of flight.

Keywords

Birds, theropod dinosaurs, origin of flight, hindlimbs, pelvic system.

Résumé

Etude du système pelvien des oiseaux et l'origine du vol.– Parmi les hypothèses principales proposées pour expliquer l'acquisition du vol, deux théories font l'objet d'un débat animé depuis plusieurs décennies, la théorie terrestre et la théorie arboricole. Selon la première hypothèse, un petit dinosaure théropode bipède et à plumes aurait utilisé ses pattes postérieures et ses proto-ailes pour sauter, ce qui aurait entraîné l'apparition du vol battu. Cette théorie a notamment été corroborée par la découverte de *Sinosauropteryx*, un petit dinosaure terrestre avec des plumes. La seconde hypothèse propose que les dinosaures théropodes aient commencé à voler après un stade arboricole. Le développement des plumes et des ailes les aurait aidés à planer, jusqu'à l'apparition du vol battu. La découverte d'un autre fossile, *Microraptor gui* avec des empreintes de plumes visibles sur les pattes antérieures, postérieures et la queue est favorable à cette hypothèse. La découverte récente de fossiles de dinosaures théropodes, marquant la transition entre des animaux strictement terrestres et des animaux potentiellement capables de voler, a relancé le débat sur l'origine du vol des oiseaux. Cependant, malgré la préservation remarquable des fossiles récemment découverts, il semble que les études paléontologiques seules ne permettront pas de répondre à toutes les interrogations concernant l'origine du vol. Ainsi, d'autres outils sont importants à prendre en compte, comme l'étude des relations structure/fonction chez les oiseaux actuels, qui permettront de proposer de nouvelles hypothèses fonctionnelles chez les fossiles. Il est intéressant de constater que les deux hypothèses principales concernant l'origine du vol se basent sur des interprétations différentes des fonctions du système pelvien (*i.e.* le bassin et les membres postérieurs): dans la théorie terrestre, la propulsion pendant le décollage est fondamentale, alors que dans la théorie arboricole, absorber l'impact lors de l'atterrissage est la principale contrainte. En dépit du rôle fondamental du système pelvien dans la locomotion des oiseaux actuels, très peu d'études se sont focalisées sur ce module locomoteur et encore moins dans le contexte de l'origine du vol. Dans ce travail de revue, nous nous efforçons de démontrer en quoi l'étude du système pelvien des oiseaux actuels est fondamentale pour proposer de nouveaux éléments sur l'origine du vol.

Mots-clés

Oiseaux actuels, dinosaures théropodes, origine du vol, système pelvien.

¹ Muséum National d'Histoire Naturelle, EGB, UMR 7179, 55 rue Buffon, F-75005 Paris, France. E-mail: pauline.provini@gmail.com

² Université Paris Descartes, 12 rue de l'Ecole de Médecine, F-75270 Paris, France

MOVING THROUGH THE AIR

There are many different ways to move through the air, more or less efficient in producing aerodynamic forces. If we use a recently proposed definition (Dudley & Yanoviak, 2011), flight includes every controlled aerial behavior, comprising aerodynamic structures (the wings), or not. With this definition, falling is not really a type of flight since it does not involve any particular adaptation to control the trajectory of the fall, to reorient the body or to regulate lift or drag in order to decrease the rate of descent.

Usually, four types of flight are defined in living vertebrates: parachuting, gliding, soaring and flapping (Lull, 1906; Oliver, 1951; Savile, 1962; Padian, 1985). Of course, as only an arbitrary angle, of less than 45 degrees with the horizontal for parachuting or greater than 45 degrees for gliding, marks the frontier between two of these types of flight, we can assume that those definitions are artificial, hence the idea of “descending flight” to describe the continuum between parachuting and gliding (Dudley *et al.*, 2007).

In gliders, lift forces are produced by a membrane and drag is reduced by a streamlined airfoil. Often, some maneuverability in air is possible, especially to reorient the body during the fall, as in some lizards (Johnsonmurray, 1987; Emerson & Koehl, 1990; Emerson *et al.*, 1990; McCay, 2001; Dudley, 2002; Socha & LaBarbera, 2005; Socha *et al.*, 2005; Wilkinson *et al.*, 2006). Following the same continuum, soaring is essentially a form of gliding that requires specific adaptations to sustain the animal in the air without flapping its wings. The rising is due to thermals or other meteorological features, such as wind speed changing with altitude (Pennycuik, 1972). Only large animals can be efficient soarers and thus, only a few animals are known or thought to have specialized in soaring: the larger of the extinct pterosaurs (Brower, 1983), and some large birds.

In all the previous types of flight, the animals make passive use of lift and drag forces to fly. The aerodynamic surfaces around the body or the limbs are sufficient to move through the air, as opposed to flying animals that actively flap their wings to produce thrust. The physical constraints that surround flight are strong enough to shape animal structure during evolution and therefore, those flying taxa share many similarities: A wing is formed by extended forelimbs, with pectoral girdle bones and muscles enlarged and stiffened, there is also an adaptation to save mass in order to decrease the energetic demand of flight (Rayner, 1988). As far as we know, true flapping flight has evolved in only three groups of vertebrates, pterosaurs, chiropterans and theropods. It is the origin of this particular behavior that we are interested in understanding here, among theropods (including birds).

DIFFERENT THEORIES ON THE ORIGIN OF FLIGHT

Several hypotheses are competing to explain the origin of avian flight, and the controversy still exists even nowadays. Historically, two evolutionary mechanisms have been proposed for the origin of powered flight in birds, the arboreal (“trees-down”) theory and the cursorial (“ground-up”) theory.

The arboreal theory suggests that active flight originated from a gliding type of animal able to climb trees or cliffs. The discovery of fossils, such as *Microraptor gui* (Xu *et al.*, 2003) with a wide airfoil seems to suggest this process. Darwin was probably the first to suggest the arboreal theory for the origin of flight in bats (Darwin, 1859), Marsh (Marsh, 1880) applied it to birds and Bock (Bock & Vonwahlert, 1965) developed this concept.

On the other hand, several other scientists (Williston, 1879; Nopcsa, 1907, 1923), proposed the cursorial theory, which states that a ground-running biped evolved into an active flier. This theory was later supported by, for example, the discovery of *Sinosauroptryx*, a small cursorial dinosaur with “protofeathers” (Ji & Ji, 1996). A lot of recent studies are consistent with the arboreal theory, supporting the existence of a gliding stage for flapping flight in birds (Geist & Feduccia, 2000; Long *et al.*, 2003; Zhou, 2004; Longrich, 2006; Chatterjee & Templin, 2007). However, one study inferred that a theoretical model of *Archaeopteryx* would run at a sufficient speed to generate aerodynamic forces to take-off (Burgers & Chiappe, 1999).

This artificial dichotomy is somehow linked to the debate on the origin of birds (Zhou, 2004). Indeed, the arboreal theory was associated with the thecodont origin of birds (Bock, 1985; Feduccia, 1999), whereas the cursorial theory was coupled with a theropod origin of birds (Ostrom, 1986; Padian & Chiappe, 1998; Padian, 2001). The origin of birds has attracted wide scientific interest through the last centuries (Witmer, 1991), and this topic has recently become a relative consensus (Gauthier, 1986; Chatterjee, 1997; Sereno, 1999; Xu *et al.*, 2000; Prum, 2002; Xu *et al.*, 2003; Zhou, 2004; Mayr *et al.*, 2005; Chiappe, 2007; Senter, 2007; Xu *et al.*, 2007). We can now safely state that birds have a theropod origin. Therefore the Manichean vision on the origin of flight has been partly shattered over the last decades with the new elements on the origin of birds (Padian, 2001), and alternative hypotheses have been proposed for the origin of flight (Caple *et al.*, 1983; Garner *et al.*, 1999; Dial, 2003).

HOW TO SOLVE THE QUESTION OF THE ORIGIN OF FLIGHT?

Over the last ten years, many fossils of theropods and birds have been discovered in Lower Cretaceous

sediments (Buffetaut *et al.*, 1995; Zhou & Zhang, 2003; Buffetaut *et al.*, 2005; Walker *et al.*, 2007). With their abundance and their exceptional preservation (even if often flattened) they provide exceptional evidence for understanding the origin(s) of flight. A mosaic of shapes is visible among the dozens of species recently discovered (Clarke & Middleton, 2008), which allows one to retrace the evolution of theropods morphospace. In spite of the remarkable aspects of the Chinese fossils, it remains difficult to propose functional hypotheses for those fossils, and their ability to fly is usually unclear and controversial (Chatterjee & Templin, 2007). It is often accompanied by doubtful interpretations of the ability to move, especially to fly. It is indeed perilous to propose functional interpretations only based on fossils with morphology of the feathers, hindlimbs, and forelimbs sometimes very different from those of living birds (Gee, 1998; Heers & Dial, 2012).

As the skeleton is one of the main clues available for fossils, we have to link morphological features on the skeleton with a specific function. To do so, we can use the closest animals for which we can analyze both the function and the morphology, *i.e.* modern birds. Of course living birds are derived forms of an ancestral state, possibly found among the available fossils. But, it is more likely that the fossils we have found by now are not the direct ancestors of the birds we are living with. Truthfully, it does not really matter! Indeed, the concept consists of using extant birds as a tool, with a given morphology, a given musculature and skeleton, and a given behavior that would allow the study of a given function (Hutchinson & Allen, 2009; Hutchinson *et al.*, 2011). Such studies would provide evidence of the required morphological features needed to realize the function. If a fossil with similar skeletal features were found, we could then hypothesize that it was able to achieve the same kind of function as the modern bird.

If we decided to use this framework to try to make inferences about the origin of flight, would other flying animals be relevant to our study? As noted above, the fundamental morphological features required to fly are similar among extant and extinct flying vertebrates (Hildebrand, 1974; Rayner, 1988). However, the basic design of a pterosaur (Hildebrand, 1974; Norberg, 1985; Rayner, 1988) or a bat (Rayner, 1986) is radically different from the basic design of a theropod, especially if we consider limb morphology. Therefore, we can assume that the mechanisms involved in the origin of flight in those forms of animals would be different from the origin of avian flight.

Therefore, birds themselves are the most relevant model to study the origin of avian flight. Of course, modern birds are derived forms and are adapted to diverse environments, thus, phylogeny and adaptations to the mechanical constraints of a given environment influence the morphology we can observe today. However, those biases are partly compensated by the fact that a

diversity of methodological tools are available nowadays (Felsenstein, 1985) to take into account the phylogenetic relationships in comparative analyses and by the fact that birds present a relatively conservative and homogenous overall design (Abourachid & Höfling, 2012). Indeed, modern birds all have a rigid trunk, forelimbs designed as wings, hindlimbs with three long segments and digits, a short tail reduced to a pygostyle, a mobile neck and beaked jaws.

When thinking about the origin of flight, the first function we would be tempted to consider is flight itself. Flight in extant birds has been abundantly studied and is still an active topic of research. Yet it does not provide much information on the abilities of the fossils to fly. Indeed, studies on the biomechanics of flight have mostly focused on muscles (e.g. Biewener *et al.*, 1992; Dial, 1992; Dial & Biewener, 1993; Gatesy & Dial, 1993; Dial *et al.*, 1997; Biewener *et al.*, 1998; Williamson *et al.*, 2001; Tobalske *et al.*, 2005; Askew & Ellerby, 2007; Tobalske & Biewener, 2008), which are not directly available on fossils. When the skeleton is studied, most authors have centered their research on the pectoral girdle, for example on the furcula (Jenkins *et al.*, 1988; Baier *et al.*, 2007), which is usually very different in fossils. Indeed, the diversity of pectoral girdle morphology among fossils of birds (e.g. Ostrom, 1974; Zhou & Hou, 1998; Zhou & Zhang, 2002, 2003) makes it very difficult to directly link the motion of modern birds to a specific morphology that could be visible on fossils (Heers & Dial, 2012).

Another motion associated with flight and observed in a great diversity of bird families is Wing Assisted Inclined Running (WAIR) (Dial, 2003; Dial *et al.*, 2006). It involves a flapping motion of the wings to climb on trees or inclined substrates. The mechanics of this behavior are well known (Bundle & Dial, 2003), especially for juveniles with dramatically reduced wing area compared to the adults (Jackson *et al.*, 2009), and demonstrates the exaptation of the wing for flight. WAIR is of interest to investigate the origin of flight, for example from an ontogenetic point of view (Dial *et al.*, 2008; Heers & Dial, 2012).

Take-off and landing are also intimately linked to flight. Whether becoming airborne from the trees or from the ground, a transition between the substrate and the air is necessary before and after any kind of flight, regardless of the substrate. Thus, the debate about the origin of flight is closely linked to the ability to take-off and land, especially in the presence of not fully functional wings in fossils. Moreover, those phases of flight are energetically costly and are to be linked to strong adaptive constraints (Dial, 1992; Tobalske & Dial, 2007). In spite of the studies which have focused on take-off and landing in flight and in its origin (Norberg & Norberg, 1971; Simpson, 1983; Heppner & Anderson, 1985; Gatesy & Dial, 1993; Bonser & Rayner, 1996; Earls, 2000; Tobalske & Dial, 2000; Askew *et al.*, 2001; Dial *et al.*, 2008; Berg & Biewener, 2010; Provini *et al.*, 2012b), the mechanics of

these behaviors and their linkages with morphology are still poorly understood. Moreover, even if two locomotor modules are involved during take-off and landing, *i.e.* legs and wings, to date, only three studies have considered both of them during take-off (Earls, 2000; Tobalske *et al.*, 2004; Provini *et al.*, 2012b) and have demonstrated the primary role of the hindlimbs to initiate flight. Although legs are essential in a great variety of locomotor behaviors in modern birds (Abourachid & Höfling, 2012), such as during walking, paddling (Provini *et al.*, 2012a) hopping and during take-off and landing, they are usually less studied than wings. Yet, in both the cursorial theory and in WAIR, leg propulsion during take-off or running is fundamental. For the arboreal theory, the legs are also crucial in dampening the impact during landing, one of the main constraints. Furthermore, in bipedal theropods the hindlimbs are obviously a key part of the animal (Hutchinson & Allen, 2009) and their morphology is less modified than the pectoral girdle, which makes them particularly interesting to investigate in the context of the origin of flight.

Recent work has shown that modern birds, for example zebra finch (*Taeniopygia guttata*) and diamond dove (*Geopelia cuneata*) use a hindlimb-driven take-off and landing (Provini *et al.*, 2012b; Provini *et al.*, in review). Thus, the key role of the legs in all locomotor behaviors has now been assessed: during terrestrial locomotion of course, but also for flight during the initial propulsion of take-off (Provini *et al.*, 2012b) and during the impact phase of landing (Provini *et al.*, in review). The major role of the hindlimbs in these last two phases of flight has been demonstrated in a widespread sample of modern birds, as European starling (*Sturnus vulgaris*), common quail (*Coturnix coturnix*) (Earls, 2000) and even rufous hummingbird (*Selasphorus rufus*) (Tobalske *et al.*, 2004). Even if additional studies must be carried out to test the generality of hindlimb-driven take-off and landing in modern birds, recent work are consistent with the implication of the hindlimbs in a theoretical proto take-off that would initiate flight in theropod dinosaurs even with not fully functional wings. This model was proposed by (Cagle *et al.*, 1983; Garner *et al.*, 1999) and is known as the pouncing or the leaping model. It suggests that flight evolved from bipedal animals that would escape predators by jumping, leading to the origin of flight. Indeed, in cursorial theropod dinosaurs, powerful hindlimbs would have been a useful exaptation to a hindlimb driven take-off and a potential origin of flight. If we add the fact that aerodynamical study of take-off has revealed that an incremental use of the wings during the first wingbeats (Provini *et al.*, 2012b) can modulate leg performance and contribute to weight support, we can propose a relevant model for the evolutionary origin of flapping. Therefore, we could combine two theories for the origin of flight, the leaping and WAIR models (Cagle *et al.*, 1983; Garner *et al.*, 1999; Dial, 2003), by proposing a hindlimb-driven take-off, assisted by a gradual use of the forelimbs

during evolution. It is interesting to note that this new model for the origin of flight is not constrained by the initial substrate. Even if theropod dinosaurs, especially the ancestors of Aves were cursorial, this model could also be applied to arboreal animals. Thus, the dichotomy “ground-up” vs. “trees-down” is not relevant anymore in this context.

To summarize, the study of the pelvic system in modern bird locomotion has proved to be relevant to study the origin of flight, and to propose new hypotheses liberated from the traditional theories. Moreover, the fact that in modern bird locomotion the femur seems systematically kinematically linked to the trunk (Abourachid *et al.*, 2011; Provini *et al.*, 2012a) reinforces the importance of considering the trunk as an additional segment of the locomotor system, instead of focusing only on the hindlimbs. We hypothesize that the functional link between the femur and the trunk should be translated into morphological features, such as the existence of correlations between the different trunk parts and the hindlimb lengths. Moreover, the relative position of the acetabulum on the pelvis could be linked to the role of the trunk in the locomotion of modern birds. The trunk shortening, associated with both tail reduction and a shortening of the pre-acetabular parts of the trunk has implications for this position of the acetabulum and for the position of the center of mass. This change would lead to a more horizontally oriented femur in modern birds than in ancestors of birds.

ACKNOWLEDGMENTS

This research was supported by grants from the UMR 7179, l'Action Transversale du Muséum National d'Histoire Naturelle Formes possibles, formes réalisées and from the Ecole Doctorale Frontières du Vivant and Bettencourt-Schueller foundation fellowships. We would like to thank la ville de Montbéliard for its funding support.

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Accepté janvier 2013