

## Origin of avian flapping flight

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### Abstract

The idea that birds' ancestors are bipedal theropod dinosaurs is now accepted. But there have been various theories about the origin of avian flapping flight for more than a century, and there is still no theory that convinces everyone. The basis of the conventional theories is critically examined here, and a new rationale is presented. Therefore, the method of vertebrate paleobiology for the purpose of restoration and elucidation of evolution is used. Actually, the most plausible hypothesis was already presented long ago, and the evidence of fossils needed to support it has been found. There has been no reasonable basis to maintain otherwise. Animal locomotion is the movement of the center of gravity of the body. The center of gravity of the body is on the legs of bipedal dinosaurs and at the base of the wings that produce lift in flying animals. In the evolution from dinosaurs to birds, the center of gravity of the body must shift from the pelvis to the chest. In conclusion, the tetrapteryx theory of Beebe makes the most sense, and now *Anchiornis* from the Jurassic of Liaoning Province, China is the most informative fossil.

Key words: *Archaeopteryx*, avian flight, flight theory, tetrapteryx

### Previous theories and critical review

The origin of avian flight is one of the most important turning points of vertebrate evolution, along with the landing of fish. This is because changes in the habitat are involved in the transformation of locomotion patterns and evolve a completely new body shape. There have been many different theories for the origin of avian flapping flight. Generally, many hypotheses arise when a problem does not have a generally-accepted solution, because the previous theories cannot be supported. Hence it would be enough to deny the basis of the latest theory, to propose a hypothesis. It is sometimes necessary, however, to consider other theories, for example, when a certain theory is too old and is accordingly overlooked, or the basis of a theory is not appreciated correctly.

Since the discovery of *Archaeopteryx*, there has

been debate about the origin of birds and the origin of flight. Williston (1879) first advocated the cursorial (ground-up) theory. Initially it was thought that the ancestor-descendant relationships between dinosaurs and birds were unlikely (Heilmann 1926; Feduccia 1980). At this stage, Nopsca (1907, 1923) stated that the bird must have been a bipedal running animal before it flew, as the hindlimbs had developed as a running functional complex before the forelimbs evolved into wings (Fig. 1), and that birds must have evolved from a bipedal cursorial ancestor. As a likely consequence, powered flight arose first, while gliding developed as a secondary achievement (Weishampel and Reif 1984). It is correct to presume that it is a bipedal running animal without knowing whether the ancestor of the bird is a dinosaur, but it is wrong to say that powered flight comes first, and gliding is secondary, that is,

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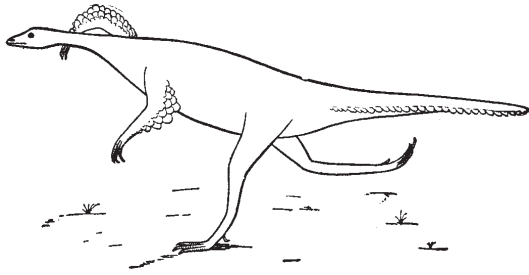


Fig. 1 The cursorial ground-up theory by Nopsca (Lull, 1921).

cursorial (ground-up) theory for the reasons described later.

Abel (1912), the founder of paleobiology, said that the following speaks for the insufficient training of *Archaeopteryx*' ability to fly: the shape of the wings; the size of the wings; the loose connection of the flight feathers with the fingers and the small number of metacarpodigitales; the lack of adjustments in the fingers to attach the primaries; the two-line fletching of the lower legs = the two-line fletching of the lower legs; the long tail with two rows of feathers.

On the other hand, Marsh (1880) was the first to advocate the arboreal gliding theory. The arboreal gliding theories once had the idea of the tetrapteryx theory by Beebe (1915). In Beebe's figure (Fig. 2, see Fig. 13), the transition from four-wing to two-wing animals is depicted in four stages. The feathers of the hind limbs progressively shrink and the feathers of the forelimbs are not only enlarged, but the caudal vertebrae are reduced in number and shortened, while the tail feathers are elongated, and the hip and knee joints are highly flexed. These features are based on observation of the skeletons of the living birds and reptiles. Beebe's theory of the origin of flight in birds is novel and is based upon the presence of series of



Fig. 2 Imaginary figure of the tetrapteryx by Beebe (1915).

sprouting quills (not clothing feathers), found in newly hatched birds, running from the outer, upper part of the hind leg just below the knee nearly to the base of the tail (Beebe 1915). This view correctly understands the recapitulation theory; traces of ancestral adult appear in offspring embryo or at an early age. According to Lull (1921), Beebe was a curator well acquainted with birds. When many paleontologists were discussing the cursorial or arboreal theory based on *Archaeopteryx*, he had advocated that the two-wing stage of the proavis would occur through the four-wing stage.

Gregory (1916) presents an eclectic theory (Lull 1921). In other words, flying birds occur by gliding theory, and the ancestors of ratites have never flown. As will be described later, this is an error looking at the skeleton of an ostrich, which is representative of ratites; ostriches have volant features common with birds throughout their bodies.

Heilmann (1926) thought that bipedality was an essential avian feature and a tetrapteryx stage almost unimaginable. "He also rejected the main line of evidence presented by Beebe, a developmental comparison between developing feathers on the femoral feather tract and those of the wing in the young pigeon (Martin 2008)."

If all other examples of flight in terrestrial vertebrates are rooted in arboreal quadrupedal forms, should bipedality be an expected precursor to avian flight? It wouldn't seem likely, if flight originated in an arboreal glider as is nearly certain with bats and pterosaurs. Such animals place aerodynamic lift above the body mass and distribute it down the length of the body to ensure stability. It is hard to see how the legs could avoid being involved in the early gliding phases (Martin 2008).

De Beer (1954) has described the London specimen of *Archaeopteryx* and noted the origin of flight. There are only three theories which have been advocated to explain the origin of flight in birds, with serious consideration: arboreal "pro-avis" (hypothetical ancestor animal of bird) theory associated with the names of Marsh etc.; cursorial "pro-avis" advanced by Nopsca; and "tetrapteryx" advanced by Beebe. Among them, he supported the arboreal "pro-avis" theory, based on the opposable Ist digit of foot, separate condition of the metatarsals, length of the forelimb equivalent to that of the hind limb, the presence of the clavicle forming furcula, and the presence of claws at the end

of all the three long digits of the hand. And he rejected the compromise theory based on the presence of pygostyle, pneumatic bone, and arrangement of the feathers of living ratites.

According to the cursorial (ground-up) theory, it was initially assumed that the wing became enlarged in order to extend the jumping distance, which would be teleological. Alternatively, the “butterfly net” theory (Fig. 3) would have the wing enlargement arise from that behavior rather than for flight. Ostrom (1973) is a star of “dinosaur renaissance” who revived the argument for the origin of avian flapping flight after half a century. But it seems that he overlooked or could not support the previous views of Abel (1912) and De Beer (1954). Recently, to overcome the weaknesses of these cursorial theories, the eclectic theory, “pouncing proavis” theory (Garner et al. 1999), and the wing-assisted incline running (WAIR) theory (Dial 2003) were proposed, but there are some problems even with these revisions.

The “pouncing proavis” theory attempts to find the origin of flight by plotting on a cladogram the order of acquisition of traits useful for flight: for example, asymmetric flight feathers, backward first toes, thick coracoid bone, pygostyle and so on (Garner et al. 1999). But all these traits are not necessarily indispensable for flight. Even a bat without the flight feathers can flap its wings. The backward first toe is for perching in trees. Therefore, it is incorrect to conclude that the arboreal or the cursorial theories are wrong just because the order of acquisition of these traits is incorrect.

In WAIR a particular behavior of the chick of a species, the Chukar partridge, is assumed to be a model of the origin of avian flapping flight (Dial 2003). However, this behavior in chicks cannot be associated with the origin of a flapping flight in birds; features that are common to general birds should have been reflected in the timing of the embryonic development, and the chick skeleton is basically same shape as the

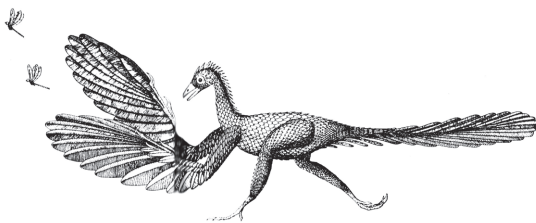


Fig. 3 The “butterfly net” theory by Ostrom (1980).

adult one.

Most of these theories have assumed that Late Jurassic *Archaeopteryx* was ancestral to all other birds. The arboreal gliding theory was considered to have a weak point in that the first toe of *Archaeopteryx* is not turned backward, so that the animal could not climb a tree (Padian 1985). Moreover, it was assumed that there were no tall trees around the former lagoon of Solnhofen, the fossil locality where *Archaeopteryx* was found. Mayr et al. (2005) reported an almost complete skeletal specimen of *Archaeopteryx*. The first toe was not completely inverted and the second toe was hyperextended. But gliding is not limited to starting from a tree; it can also be done from the top of a cliff or a hill. Also, if the ancestor of birds is not *Archaeopteryx*, these points do not matter.

In 2003 very well preserved feathered dinosaur fossils have been collected from Liaoning Province, China. Among them *Microraptor gui* is noted for having long feathers on the hind limb (Xu et al. 2003); it is very similar to the ancestral type which Beebe once assumed and named tetrapteryx (Beebe 1915). Unfortunately, *Microraptor* from the Lower Cretaceous is too late to provide an origin of birds.

Inuzuka (2006) introduced the occurrence of a four-winged feathered dinosaur called *Microraptor* and Beebe’s tetrapteryx theory in a column of a textbook on vertebrate paleobiology called “Dinosaur osteology”. Chatterjee and Templin (2007) proposed a biplane theory with ventral wings on the hind limbs of *Microraptor*. Martin (2008) introduced the Beebe’s theory in the most detailed review of avian flight. However, it is an error by the model method of restoration (Inuzuka 1984) that the specific species of *Longisquama* was taken up, as is the case with Hoatzin and Chukar partridge. Ruben (2010) also summarized the review and introduced the Beebe’s theory and *Microraptor*, but he has a slightly skeptical impression of the gliding theory. Alexander et al. (2010) attempted to restore the body of *Microraptor*.

In 2009, another four-winged dinosaur which named *Anchiornis* was found in the Late Jurassic deposit in China (Xu et al. 2009; Hu et al. 2009). And the depositional age was slightly older than *Archaeopteryx* age. With the discovery of the four-winged feathered dinosaur *Microraptor* and *Anchiornis* (Xu et al. 2014) in this century, Beebe’s tetrapteryx theory was reviewed and no running or eclectic theory was found. However,

it seems that the essence of the locomotion of flight is not understood from the fact that there are discussions about the orientation of the hind limbs and the distribution of the flying feather of the hind wings. Since this is a matter of evolution from bipedal dinosaurs to flying birds, we have to refer to all types of vertebrate locomotion, not just the bird's ancestors, to investigate the origin of flapping flight.

#### Vertebrate body shape, habitat and mode of locomotion

It is extremely difficult to reconstruct mode of locomotion of extinct animals. It is because there is no paleontological proof of swimming and flying, except for fossil footprints of ground walking. To reconstruct the body shape and locomotor function of extinct animals, comparison with living animals is essential. As the restoration method basically proceeds from form to function, it is firstly necessary to compare animal skeletal morphology.

The shape of a vertebrate depends on the medium of the habitat and mode of locomotion (Inuzuka 2006). Habitat is divided into three large categories, water, land, and sky, and the corresponding body forms are typically the piscoid (fish type), the theroid (beast type), and the avioid (bird type) (Fig. 4).

Since the density of water is high, the gravity and buoyancy are almost balanced in the piscoid form.

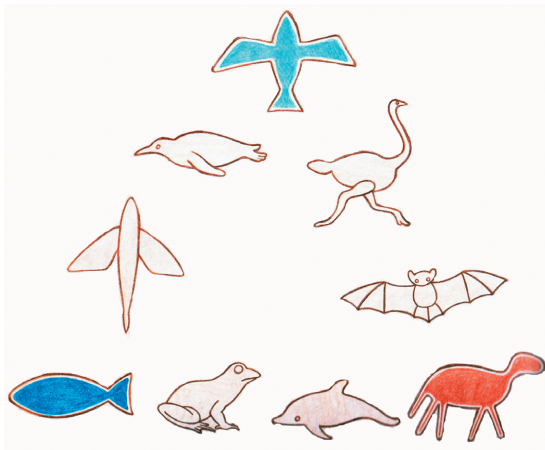


Fig. 4 Triangular diagram of animal body shape and habitat (Inuzuka and Oshima, 2015).

Place the majority of animals living in the habitats of water, land and sky at the top of the triangle diagram with symbols of a typical swimming piscoid in the sea, a walking theroid on the ground, and a flying avioid in the sky. Symbol colors of habitats are marine blue, terrestrial red, sky blue. The contours of converging animal on each side resemble the typical of a new environment.

The vertebral column passes through the center of the body, which becomes relatively symmetrical not only bilaterally but also dorsoventrally. A mouth opens at the cranial end of the body and, along with a brain and special sensory organs, constitutes a head. Fishes living in the water basically swim. To get thrust, the body pushes the water backwards and experiences the reaction. In typical fish the caudal body and the tail fin play this role. Loss of energy is small because the head, the trunk with the center of gravity, and the propeller, the tail fin, are in a straight line. Thus the piscoid form, tapering at each end, is typical of aquatic animals (Inuzuka 2006).

Because an animal hardly receives buoyant force on land, it first needs countermeasures to gravity. The tetrapod vertebral column is situated dorsally in the trunk, convexly curved, and has a structure that hangs the internal organs from above. To walk, an animal must lift the body from the ground. For this reason, the theroid has the shape of a bridge supporting the torso with fore- and hind limbs. Since the mouth, the nutrition-intake device, cannot be rapidly brought to an arbitrary space integrally with the trunk which must stand on the ground, the opercula are removed to be the independent neck and the degree of freedom of the position and orientation of the head is increased. As a result, the basic design of the theroid, with the head and narrow neck in front of the trunk and the lengthened limbs below, is dictated by the lifestyle of terrestrial walking (Inuzuka 2006).

Large animals need wings to float in the air. Birds can float in the air and go forward by lift of wings balancing with gravity. Birds moving at high speed in the air are streamlined. The fuselage progresses with fusion of thoracolumbar and sacral vertebrae to form a synsacrum and becomes compact with a large sternum, reducing drag. The wing surfaces are orthogonal to the traveling direction, the leading edge of the wing is rigid and the rear part flexible, so that thrust can be generated on both upstroke and downstroke. The tail is degenerate, with the caudal vertebrae shortened and fused into a pygostyle; tail feathers grow, and work as a brake and a rudder essential for a rapidly-moving body. Because the forelimbs are converted to wings, the body has to be supported on the ground only by the hind limbs. Since they are not the main propellers, they are small like the wheels of an airplane. Since the hind limbs lie behind the centroid of the

body, when landing, the body is tilted backward for balance, and the hind legs are flexed deeply at the hip and knee joints. In this way, it is possible to understand the aviooid design and attitude as being dictated by the demands of both flight and terrestrial walking (Inuzuka 2006).

When each basic design, piscooid, theroid, and aviooid, is placed at an apex of a triangle, animals with intermediate habitats and modes of locomotion are situated at some intermediate points (Fig. 4). Although frogs and geckos are taxonomically members of amphibians and reptiles, respectively, their body shapes can be regarded as intermediate between piscooid and theroid types. So to speak, what are called terrestrial tetrapods are specializations of sarcopterygian fish for land locomotion. Among mammals, the cetaceans and sirenians have returned to the piscooid type, and the bats have shifted to the aviooid. Among birds, ratites have approached the theroid type, while natatorial birds such as penguins have approached the piscooid type. As a result, the minority of animals located at the vertices of the middle triangle are similar in shape to the representatives of the majority at the apices. These transitional animals are good materials for exploring the relationship between the body form and the environment (Inuzuka 2006).

#### Comparison of flying and gliding animals

The greatest difference between the arboreal gliding and terrestrial cursorial theories is whether or not the avian ancestor went through a gliding stage, when it started to take off from the ground. Hence, the form of extant gliders is compared with that of the fliers. The common point of the flapping wings of the flying birds and bats should be compared with a variety of patagia of gliders, in order to find the differences between the flapping flight and gliding. The flapping fliers only include bats and the majority of birds. All flapping fliers are paired-wing animals with forelimbs as wings and cannot walk or climb with their forelimbs. On the other hand, the gliders include flying fish, amphibian parachute frogs, reptiles of flying lizards and snakes, and mammals such as sugar gliders, flying squirrels, flying lemurs, and so on. In gliders the area of any part of the body may be expanded, such as pectoral fins, toe webs, patagia on the flanks, etc., if it increases drag. Their manus of forelimbs can also be used for walking or climbing.

Biomechanically, animal locomotion can be said

to be a movement of the centroid of the body (Inuzuka 2006). The centroid line of any body in bipedal standing posture passes through the foot. The main locomotor organs occupy a large proportion of the body. For example, the brachiating apes such as gibbons have the upper limb longer than the lower limb, the reverse of bipedal-walking humans (Inuzuka 2010). As described above, the main locomotor organs occupy a large area in the body in modern animals, so even in extinct animals, if outline of the body is known, the main locomotor organs can be estimated.

#### Posture and center of gravity of modern birds

Animals must stand stably when resting and move efficiently when moving. In other words, it is necessary to combine the contradictory functions of body stability and motility. Vertebrates such as dinosaurs, birds, and mammals are designed for motility. Lateral limb-typed reptiles have the same posture as when they are alive, even if they die. In other words, the position of the centroid is low for the area occupied by the grounding point.

Schemata of the standing postures of bipedal vertebrates include the cursorial ostrich and the underwater-swimming penguins (Fig. 5). Both penguins and ostriches share common points with flying birds, such as short femurs for pelvis, shortened caudal vertebrae, and flexed hip and knee joints, despite differences in their habitats and modes of locomotion, so these are characteristics peculiar to birds in general (Fig. 6).

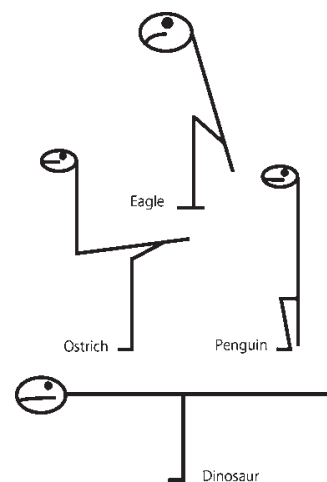


Fig. 5 Comparison of standing postures of bipedal vertebrates (Inuzuka, 1993 modified).



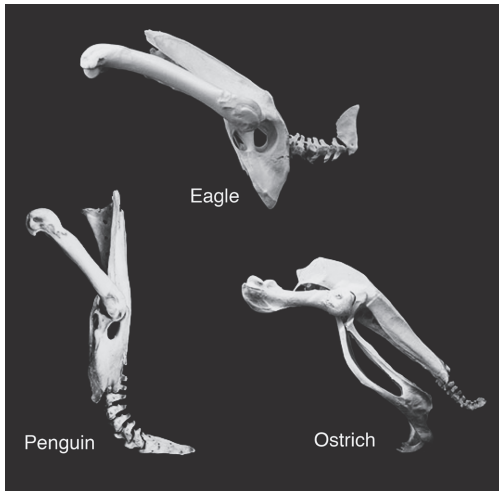


Fig. 6 Comparison of left side views of bird pelvis, caudal vertebrae, and femur. Above: eagle, typical flying bird; left: penguin, secondarily adapted for aquatic life; right: ostrich, secondarily adapted for cursorial life.

It is difficult to accurately measure the position of the center of gravity of the body even in modern animals (Lessertisseur and Saban 1967). Therefore, it is inferred from the change in posture under different environments. Waterfowl of the Anatidae, such as swans, can swim on the surface of the water, walk on the ground, and fly in the sky. As mentioned above, the balance of the body during flight is the most difficult among swimming, walking and flying. Therefore, the center of gravity of the body must be situated on the winged chest in Aves (Fig. 7). If the fuselage is level during flight and there is no center of gravity in the position of the wings that generate lift, a stable attitude can never be maintained in the air.

When standing on the ground with this body, the centroid line must be placed on the feet, so the trunk is tilted backward and the neck position is raised (Fig. 8). Since the hip joint bends and the knees come to the side of the abdomen, the width of the left and right legs widens. It follows that a bird walks with the toes pointed inward so that they are as close to the centroid of the body as possible, and toddles step by step tilting the body.

On the water surface, the posture is stable if the buoyancy center overlaps the centroid line. Rather, the head is kept as close to the center of gravity as possible so that it can be easily turned. This is why the swan's neck has a unique 2-shaped. The long neck helps with these changes in posture.

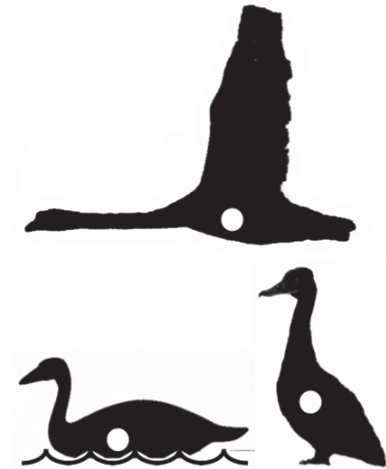


Fig. 7 Posture of waterfowls. Top: Flying posture, Left: Swimming posture, Right: Standing on the ground. ○: Position of the center of gravity of the body

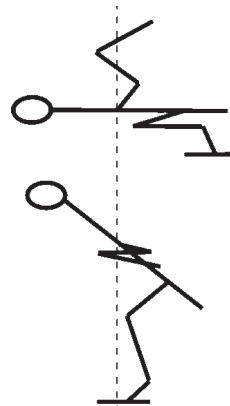


Fig. 8 Bird skeleton. Top: Flight attitude, Bottom: Standing. The dotted line is the centroid line.

Large raptors with large head are almost vertical when they perch on a tree branch (Fig. 5). Nocturnal and carnivorous owls are even more vertical. When measuring the distance to the prey with stereoscopic eyes, the axis of rotation of the neck does not shift. Furthermore, the branch is grasped with a unique anti-toe foot so that the posture is stable. The above observations suggest that the center of gravity of the bird's body must be at the chest.

#### Comparison of skeletons of bipedal dinosaurs with birds

Once, before a characteristically avian furcula was discovered in any reptile, it was contested whether the ancestors of birds were eoschians or dinosaurs. When this bone was found in dromaeosaurids, whose

skeleton is similar to that of *Archaeopteryx*, these bipedal theropods were concluded to be the avian ancestors (Norell et al. 1997).

Lots of reconstruction figures of *Archaeopteryx* have been drawn, but their postures differ depending on authors. The reconstruction figure of *Archaeopteryx* by Heilmann is drawn side by side with the pigeon (Fig. 9). Judging from the viewpoint mentioned above, this posture is clearly an error making a modern bird the model. Among the bipedal theropods referred to be the avian ancestor, skeleton of *Compsognathus* had been supposed to be most similar to that of *Archaeopteryx* in size and shape. But previous figure of *Compsognathus* by Heilmann was assumed to be more flexible spine like a modern lizard. The recent reconstructed posture of bipedal dinosaurs has a seesaw structure balanced stiffer horizontal spine (Fig. 10). Therefore, the skeleton of *Archaeopteryx* with similar elements in size and shape is to have been in the same posture as that of *Compsognathus*.

In dinosaurs, the center of gravity of the body is at the base of the hind limbs, whether bipedal or quadruped. Facultatively-bipedal dinosaurs ran bipedally; the body weight of the cranial half and the long tail are balanced with the hip joint as a fulcrum (Fig. 11). In the bird's skeleton, the center of gravity is at the base of the wings of the forelimbs. In order for a dinosaur to evolve to a bird, the position of the center of gravity of the body must be displaced from the hind limbs to the forelimbs. In fact, all the characteristics of the bird skeleton are related to this point. The

shortening of the caudal vertebra, the shortened femur for the pelvis, the hip and knee joints in the flexed position, and the shortened fuselage all contribute to the anterior displacement of the centroid of the body.

*Struthiomimus* means "an ostrich mimic", but Osborn, who gave this dinosaur its name, only reconstructed the skeleton using an ostrich as a model (Fig. 12). Indeed, the ostrich has many features that are essential for birds to fly as opposed to dinosaurs, such as a median flat plate-like sternum, a strong coracoid bone that supports the position of the shoulder joint during flight, a large pelvis including a synsacrum that compacts the fuselage, a light and short femur, and

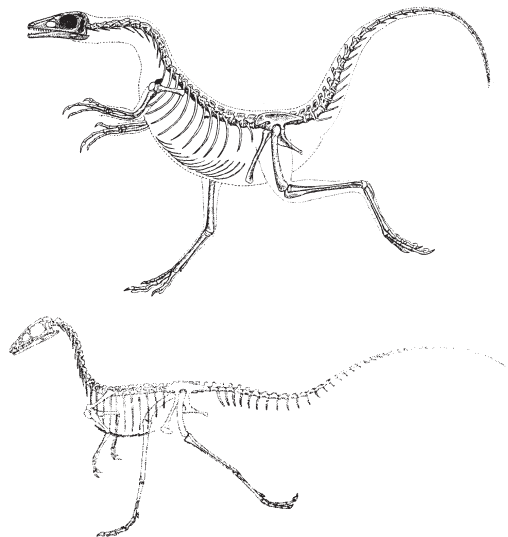


Fig. 10 Skeletal reconstruction of *Compsognathus*. Top: Reconstruction by Heilmann (Feduccia, 1980), Bottom: Reconstruction by Ostrom (Feduccia, 1999).



Fig. 9 Skeletal reconstruction of *Archaeopteryx* by Heilmann (Vandebroek, 1969).

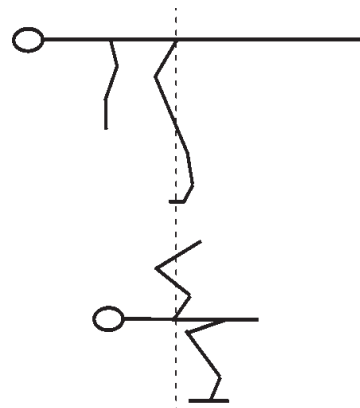


Fig. 11 Dinosaur and bird skeletons. Top: Dinosaurs, Bottom: Birds. The dotted line is the centroid line.

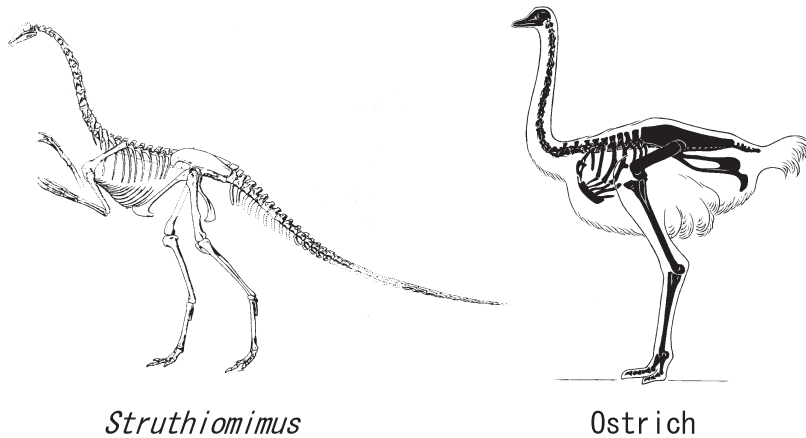


Fig. 12 Comparison of skeletons between *Struthiomimus* and ostrich. Both skeletons are completely different in length of pelvis, length of caudal vertebrae, and length and direction of femur.

short caudal vertebrae ending in a pygostyle, so there is no doubt that the ancestors of ratites once flew.

#### Tetrapteryx theory to centroid approach theory

It is impossible that flapping flight began by leaping from bipedal running without going through a gliding stage. A bipedal dinosaur kicks the ground with its hind limbs to gain thrust, so the thrust drops at the moment both feet lift off the ground. Large waterfowl can glide over the surface of the water and take off because the winged chest has the center of gravity of the body. The reason why an airplane can fly stably is because this point is strictly designed, otherwise it will soon stall like a paper airplane. Similarly, animals with their center of gravity at their hips can never fly, no matter how quickly they are accelerated, no matter how many times they jump. Hind legs with feathers would just be an obstacle to running and the animal will never run fast (Inuzuka 2006). If the wings of the forelimbs were enlarged due to predation, the tail would have to be huge and balanced in order to run on the hindlimbs. Otherwise it wouldn't even be able to stand on two legs. Consequently avian flapping flight can only have begun from the gliding by a bipedal dinosaur with four wings starting from an elevation.

To deduce the origin of the flight, evidence related to the locomotion should be most important. Based on comparison with living animals, a four-winged animal must have been a glider. In the case of a glider, it is convenient that the body surface area increases, wing surface load decreases, and staying time increases, if there are feathers also on the hind legs. It might not

have asymmetric flight feathers. The wings of the hind limbs may be in the sagittal position. The centroid of the body might not be located near the forelimb. The animal should have been able to climb a tree using the forelimb.

Beebe (1915) has already described the process of transition from four-winged to pair-winged animals (Fig. 13). Quoting this Tetrapteryx stage from Beebe, "flight was merely gliding, the fingers were too free,

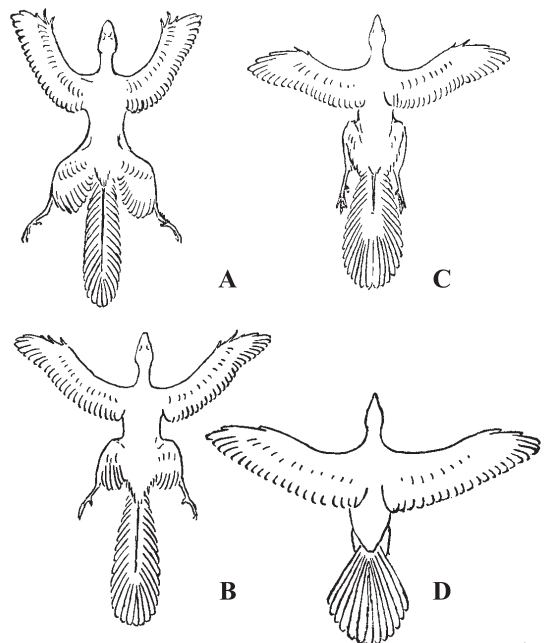


Fig. 13 Stages in the development of flight (Beebe, 1915). A: Tetrapteryx, B: Archaeopteryx, C: hypothetical stages, D: modern bird.



the arm bones too delicate, the sternum small or absent, and these facets, considered in connection with the small, weak pelvis, make it impossible to picture the creature as flying skillfully about. In succeeding generations the pelvic wings would become more and more reduced. ... Yet the function of the pelvic wings had been so passive and negative that no musculing had been necessary, no increase or coalescence of bony tissue. ... Millions of years after they were of use, the feathers of the pelvic wing are still reproduced in embryo and nestling” (Lucas 1929). Thinking about how the flapping bird has evolved from bipedal dinosaurs, it is appreciated that the forward dislocation of the centroid is essential. To advance is to move the center of gravity of the body forward. If four-winged dinosaurs glide from the tree, the gliding distance increased as the wings of the forelimbs expanded and the flying wings were completed, so the femur and caudal vertebrae should have tended to shorten or reduce.

Since *Archaeopteryx* has been discovered, it has been considered to be an intermediate between reptiles and birds in having teeth, feathers, and a long tail. It has been thought that flying became possible for birds by losing heavy teeth and long caudal vertebrae and acquiring feathers. According to the comparative and functional morphological perspective mentioned above, since in *Archaeopteryx* long caudal vertebrae and a long femur as in bipedal theropods are still present, it seems that it was capable of gliding, but not flapping flight (Abel 1912; De Beer 1954). Foth et al. (2014) discuss the distribution of feathers in new specimens of *Archaeopteryx*.

Complete birds had already existed in the Cretaceous, but recently four-winged feathered dinosaurs have been discovered in older strata. This fossil, *Anchiornis* from the Jurassic Period of Liaoning (Xu et al. 2009; Hu et al. 2009), is the most influential evidence at present, and there is a possibility that its morphology may date back even further. As for avian ancestors, as noted above, there were two views. When the ancestor was decided to be a bipedal theropod, it should have been decided to be a four-winged arboreal gliding theory (Inuzuka 2006). This is because, as mentioned above, bipedal dinosaurs can never take off without going through the gliding stage.

Liberation from gravity appears to have been a theme of vertebrate evolution as a whole. We consider the habitats in the order of water, land and sky because

the modes of locomotion have evolved in this order; vertebrates have gradually heightened the position of the centroid of the body to counteract the gravity of the earth. In other words, it has increased locomotion efficiency at the price of stability (Inuzuka 2006). In the benthic armored fish, the thrust of the tail produced the lift with the body shape of a hydrofoil, and the osteichthyans evolved the air bladder. As their habitat has changed from water to land, tetrapods reoriented their limbs ventrally against gravity, locomotion has converted from aquatic to terrestrial one. From reptiles to mammals orientation of the limbs was converted from the lateral type to the inferior type (Fig. 14). Dinosaurs quickly adopted bipedalism with inferior-type hind limb posture. This can be seen as a parallelism with mammals. The evolution of avian flight also involved a shift from quadrupedal primitive reptiles, via bipedal dinosaurs, so that the position of the centroid gradually became higher. That the wings of bats have extended back to the hind legs is evidence that their ancestors were gliders.

When considering the origin, acquisition, and degeneration of organs, it is teleological to assume the morphology and function of offspring in advance. For example, in mammals, there is diversity in the fate of the clavicle. When considering the reasons for the degeneration of the clavicle of ungulates, one should look for the disadvantages of having the clavicle rather than the advantages of not having it (Inuzuka 1992).

It is common knowledge that paleontology begins with the production of fossils. However, Inuzuka (1997) proposed predictable paleontology by assuming the shape and trace of fossil footprints from the reconstructed

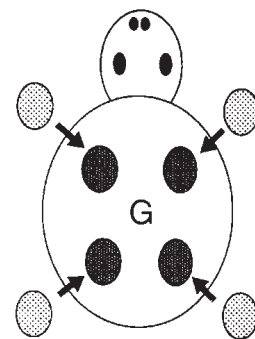


Fig. 14 Centroid approach theory (Inuzuka, 1992). When the limb type transforms from a lateral-type reptile (light color) to an inferior-type mammal (dark color), the forelimb rotates backward and the hindlimb forward, so the grounding points of the foot approach the centroid (G) of the body.

skeleton of desmostylians. In this paper, the classical descriptive study is called “follow-up paleontology”. Beebe (1915), on the other hand, gained insight into the origin and evolution of bird flight from ontogeny of modern birds 100 years before the discovery of fossils. From this point, of the three theories given by De Beer (1954), the tetrapteryx theory is the most reasonable and can be evaluated.

Nevertheless, Beebe’s tetrapteryx theory did not become an established theory. The possible reason is that, like the other theories, he accumulated the facts on which his theory was based, but did not give evidence that the other theories did not hold. At that time, biomechanics and aerodynamics were not used to study the restoration and evolution of extinct animals, so other theories could not be criticized.

From current knowledge, flapping flight must have started with the gliding of a four-winged proavis, but even Beebe’s tetrapteryx theory was unaware of the position of the centroid. Indeed, a figure of the force acting on the wing of a bird is commonly shown in books on biomechanics, but one showing the position of the centroid of the body is very rare. What is indispensable for flight is that lift acts directly above the centroid line of the body.

If the theory based on the above reasoning is distinguished from traditional “arboreal gliding theory” or “tetrapteryx theory”, it is appropriate to say that “centroid approach theory” can support the overlooked part of “tetrapteryx theory”. The position of the centroid of the body is the decisive factor in the evolution of vertebrate posture and locomotion. For example, a crocodile-like posture with elbows and knees protruding to the side of the trunk is called a lateral-limb type. While, the horse-like posture in which the forelimbs and hind limbs are extended under the trunk is an inferior-limb type. During the evolutionary transition from lateral-limb type primitive reptiles to inferior-limb type mammals, the posture was changed by turning the elbows backwards and the knees forwards in lateral view. There were several hypotheses as to why this was the case. “Mammalian locomotion involved a change in limb posture from sprawling to semi-erect,” “This change placed the hands and feet closer to the body’s center of gravity” (Radinsky 1987). This theory can be explained both when the body is viewed cranially and laterally, and is the most rational, so it was named the “center of gravity approach theory” (Fig.14; Inuzuka

1992). Even in avian flapping flight, it is most important for the centroid of the body to approach the wings that produce lift.

In conclusion, if it is only the origin of the avian flapping flight, the Beebe’s tetrapteryx theory is correct. This hypothesis was proved by the discovery of fossils 100 years later. However, as a result of the weak scientific grounds at that time allowing the proposal of other theories, the conflict between the cursorial theory and the gliding theory continued for many years. When considering the evolution of vertebrate locomotion in general, the “centroid approach theory” is more appropriate; this theory is more universal than the tetrapteryx theory and is valid not only for the avian flapping flight from bipedal dinosaurs, but also for the transition from lateral-type quadrupedal primordial reptiles to bipedal dinosaurs and inferior-type mammals.

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