

Chapter 14

Pectoral Girdle Morphology in Early-Diverging Paravians and Living Ratites: Implications for the Origin of Flight

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ABSTRACT

Discussions about the origin of flight almost unanimously assume that early birds positioned (and moved) their wings in the same basic manner as living flying birds, with reconstructed wings extended with the airfoil surface parallel to the ground and forelimbs moving in a dorsoventral arc. Such reconstructions of wing posture and movements for extinct avialans are based on highly specialized flying neognaths, in which the glenoid cavity is horizontally extended and laterodorsally faced, thus allowing wide humeral rotation and increased upward excursion. However, living ratites exhibit a sharply different pattern of pectoral girdle (or shoulder girdle) morphology and associated wing movements: in both *Rhea* and *Struthio* the glenoid cavity faces laterally, but its major axis is almost vertical. In consequence, wings predominantly move following an anterolateral to postero-medial abduction-adduction arc. Initial experimental results with *Rhea americana* demonstrate their inability to perform WAIR (wing-assisted incline running), suggesting a causal relationship between the inability to flap the wings vigorously and its pectoral girdle morphology (with glenoid cavity subvertically oriented, poorly developed acrocoracoid process, and m. supracoracoideus playing a protractor rather than elevator function). Early-diverging paravians (e.g., *Saurornitholestes*, *Buitreraptor*, *Microraptor*) and early-diverging birds (e.g., *Archaeopteryx*, *Anchiornis*) share a closely similar morphology of scapula and coracoid, with a glenoid cavity facing laterally and with its greater axis oriented subvertically. This condition of the glenoid resembles that of ratites, allowing one to infer that fully extended wings of early-diverging paravians (including *Archaeopteryx*) oriented their surface obliquely to the ground. Experimental results, in conjunction with anatomical observations in both flying and flightless living birds, warn about the purported generalized ability of early-diverging paravians to perform WAIR. Even if they were capable of symmetrical flapping, their wing movements were different from those of living neognaths, because the glenoid retained both a plesiomorphic morphology and orientation. Wing strokes as hypothesized here for early-diverging paravians may have generated thrust with little or no lift. WAIR behavior was present in the common ancestor of Neognathae, and also probably present in early-diverging ornithothoracines. However, WAIR performance among early-diverging paravians and early birds remains uncertain. In agreement with

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recent contributions, we conclude that the origin of flapping flight (and eventually WAIR) emerged in birds that diverged later than *Archaeopteryx*, with the acquisition of a horizontally placed major glenoid axis, which allowed wider dorsoventral forelimb excursions.

INTRODUCTION

Living neognaths are the main source of information used for reconstructing muscles, wing movements, and running behavior of early birds. In particular, WAIR, a form of terrestrial locomotion in steeply inclined surfaces, involving flapping and running behavior, has been considered as an evolutionary stage previous to the acquisition of flying capabilities (e.g., Dial, 2003; Bundle and Dial, 2003; Dial et al., 2008; Heers and Dial, 2012; Heers et al., 2014; Dudley et al., 2007; but see Evangelista et al., 2014). These authors used the developing wings of the ground birds (in particular, chukar partridges) as possible analogs/homologs of historical wing forms to provide empirical evaluation of aerodynamic potential in flapping theropod “protowings.”

This behavior has been documented in several orders of neognathan birds (see Dial, 2003; Jackson et al., 2011), performed by both juvenile and adult individuals (Heers et al., 2018). To perform this behaviour the wings adopt a characteristic oblique posture and undergo strong anteroposterior symmetrical flapping. Notably, ratites exhibit a sharply different posture and range of movements of their wings, compared with those of neognaths. Such peculiar anatomical and behavioral features of ratites remain poorly studied and, most importantly, were virtually ignored in discussions on the origin of flight stroke, with the exception of the Ph.D. dissertation of H. Davis (2005) in which some aspects of WAIR capabilities on ratites were analyzed in detail.

Ratites have been considered as the best living analogs of extinct paravians (Feduccia, 1986). We are aware, however, that these birds are secondarily flightless, being descendants of flying avian ancestors (Faux and Field, 2017). Moreover, ratites are sharply distinguished from the remaining avians (as well as from extinct early-

diverging paravians), in the absence of furcula, rectricial feathers symmetrical and with poorly cohesive vanes, acrocoracoid process (= biceps tubercle) reduced, and humerus with a pronounced exaggerated medial torsion of its distal end, thus producing the distinctive hanging of the forearms (Raikow, 1968). We will pay attention, however, to those morphological traits of ratites that, interestingly, look closer to early-diverging paravians than to flying avians.

The aim of the present paper is to explore how ratites behave when climbing slopes, and particularly how they move their wings. We will also compare the pectoral girdle anatomy of these flightless birds with that of early-diverging paravians (i.e., *Archaeopteryx*, *Buitreraptor*), considering the notable morphological similarities they share.

MATERIALS AND METHODS

Reconstruction of scapular position on thorax: available theropod specimens three-dimensionally or two-dimensionally preserving the pectoral (or shoulder) girdle support the view that the location of the scapula on the thorax is still a matter of discussion among of early-diverging paravians (e.g., Senter, 2006) with a high degree of uncertainty. Reconstructions presented here assume a scapular blade in an almost horizontal position, with a slight ventral inclination of the anterior extremity of the scapula, similar to that seen in living flying avians. Even assuming this derived position of the scapular blade for *Archaeopteryx* and *Buitreraptor*, the major axis of their glenoid cavities is more anteroventrally inclined than the subhorizontal major axis seen in living flying avians.

Experiments and observations carried out on living American ostriches (*Rhea americana*) were made in the Estación de Cría de Animales Silvestres (ECAS, Universidad Nacional de La Plata, Buenos Aires, Argentina) (see videos in online Supplement, at doi.org/10.5531/sd.sp.44).



FIG. 1. Wing posture of American ostrich (*Rhea americana*) with the humerus totally abducted. Photograph taken by Ramón Moller Jensen.

We follow the phylogenetic hypothesis of Agnolín and Novas (2013) and Agnolín, et al. (2019) depicting *Anchiornis* as an early-diverging avialan (see Pittman et al., chapter 1). We use the following phylogenetic definitions: Avialae (avialans) refers to all birds including early fossil ones. Aves (avians) refers to the avian crown group only.

COMPARATIVE ANATOMY

Osteological and muscular characteristics of most living avians have been fairly well described in dozens of excellent papers (e.g., Ostrom, 1976). Thus, we will address selected features to compare ratite birds with early-diverging paravians.

Living flying avians exhibit the glenoid cavity with the long axis roughly parallel to the vertebral column. The coracoidal portion of the glenoid is horizontally extended, laterodorsally faced, with the external margin projected outward; the scapu-

lar portion of the glenoid, instead, is much smaller in size than the coracoidal portion, is vertically oriented, and faces laterally. This kind of glenoid allows wide forelimb movements, especially humeral longitudinal rotation (Poore et al., 1997). The avian humerus can adopt a position through which its flexor surface fully orientates anteriorly, thus to prepare for the downstroke, and orienting the articulation plane of both elbow and wrist perpendicular to the downstroke direction. In flying Aves the horizontal position and anterior extension of the glenoid cavity is accompanied by the anterodorsal growing of the acrocoracoidal process, which receives the attachment of *m. biceps brachii* (which acts to flex the forearm and to protract the humerus to a small degree) and *m. coracobrachialis cranialis* (one of the main protractors of the humerus), as well as different ligaments, including the *ligamentum acrocoracohumerale* (one of the main maintainers of the integrity of

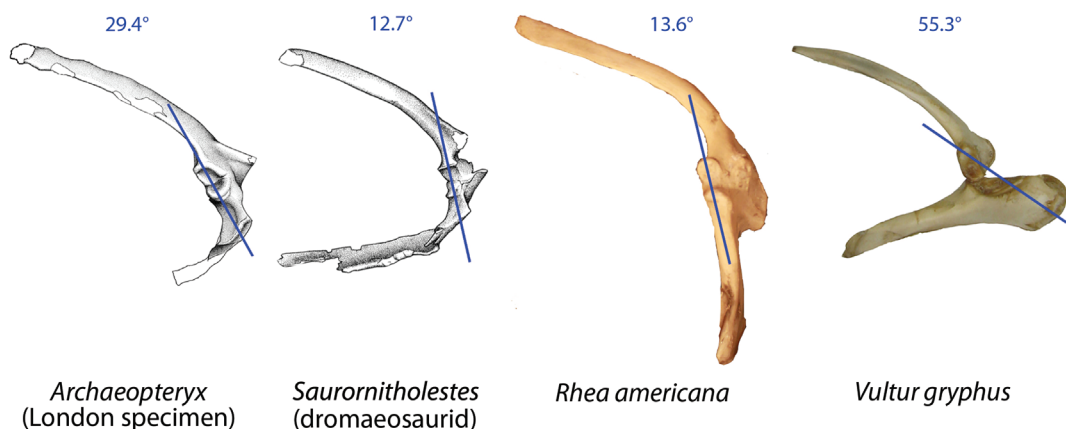


FIG. 2. Angle formed between the main axis of the scapulocoracoid glenoid and main vertebral column axis in selected paravians. Pectoral girdle of the London specimen of *Archaeopteryx*, *Saurornitholestes*, *Rhea americana*, and *Vultur gryphus*, in right lateral view. Not to scale.

the shoulder joint during aerial locomotion; Baier et al. 2007; 2013). The energetic and sustained wing flapping performed by living avians (mainly during takeoff and WAIR behavior) is congruent with the morphology described above for the glenoid cavity, as well as the development of m. supracoracoideus, which rotates and pulls the humerus upward (see Ostrom, 1976).

Extant flightless ratites exhibit a sharply different wing posture to that of the remaining living birds: their forearms hang ventrally when the humerus is in maximum horizontal abduction (fig. 1). Consequently, wing movements differ from those of flying living birds in that the adduction-abduction arc is predominantly anteroposterior, instead of dorsoventral. Such distinction in wing posture and movements ultimately relays in the different shape and position of the glenoid cavity, with both scapular and coracoidal portions subequal in size and occupying the same dorsoventral plane; in *Rhea* the long axis of the glenoid cavity forms an angle of approximately 13.5° with respect to the vertebral column (fig. 2).

Archaeopteryx and the remaining early-diverging paravian theropods (e.g., *Buitreraptor*, *Microraptor*, *Sinornithosaurus*, *Anchiornis*; Xu, 2002; Pei et al., 2017; Novas et al., 2018; Agnolín et al., 2019) share with *Rhea* a closely similar morphology of the pectoral girdle (fig. 2), with

glenoids laterally oriented and with the major axis subvertical. In early-diverging birds (e.g., *Archaeopteryx*, *Anchiornis*) the glenoid facet retained the lateral orientation seen in other early-diverging paravians (e.g., *Buitreraptor*), and with both sections (scapular and coracoidal) subequal in size and aligned on the same dorsoventral plane (see Jenkins, 1993; Baier et al., 2007; Novas et al., 2018; Agnolín et al., 2019). Manipulation of bones of early-diverging paravians (e.g., *Buitreraptor*) depict movements that are predominantly anterodorsal to posteroventral, similar to those described above for *Rhea* and *Struthio*. General resemblance of pectoral girdle and humerus of early-diverging paravians (e.g., *Buitreraptor*, *Bambiraptor*, *Deinonychus*; Ostrom, 1969; Burnham, 2004) preserved three-dimensionally and early-diverging birds (e.g., *Archaeopteryx*, *Anchiornis*) preserved two-dimensionally on slabs suggest that the latter ones retained almost the same basic forelimb posture and range of movements as in other early-diverging paravians. Aside from glenoid orientation, early-diverging paravians (e.g., *Microraptor*, *Saurornitholestes*, *Archaeopteryx*) resemble living ratites in the presence of a nonkeeled sternum, coracoid with biceps tubercle (= acrocoracoidal process) much less developed than in neognaths, and lack of trios-

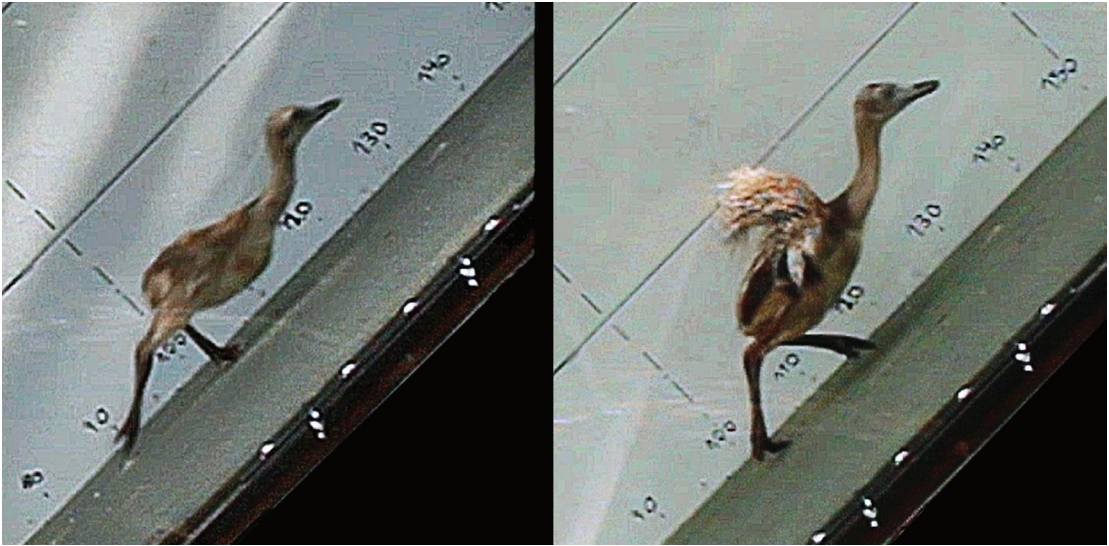


FIG. 3. *Rhea americana* siblings climbing a 45° ramp without performing WAIR. Individual on the left has its wings folded to the body, individual on the right has its wings extended.

seal canal, suggesting a feeble development of muscle mass of both *m. pectoralis* and *m. supracoracoideus*. Regarding the latter muscle, the less-developed acrocoracoidal process seen in living ratites does not modify its course. Thus, contraction of this muscle produces the forward (not upward) movement of the humerus, a function that was envisaged by Ostrom (1976) for *Archaeopteryx*.

The lack of a “twisted” glenoid (that is, without a large coracoidal surface dorsally faced) suggests that early-diverging birds (e.g., *Archaeopteryx*, *Anchiornis*) did not attain the amplitude of forelimb movements, nor the humeral trajectory over the glenoid, as characteristically occurs in living flying avians (Ostrom, 1976; Poore et al., 1997). But probably the most important consequence of humeral articulation over the glenoid is the wing orientation: in both early-diverging paravians (e.g., *Deinonychus*, *Bambiraptor*) and flying avians (e.g., *Vultur*) the longest axis of the humeral head is parallel to the major distal axis; thus, the main controller of wing-surface inclination with respect to the ground is the inclination of the major axis of the glenoid cavity.

WAIR PERFORMANCE AMONG LIVING BIRDS

Although WAIR has been hypothesized to be plesiomorphically present for paleognaths, the hypothesis was based on observations of tinamids (Dial, 2003; Dial et al., 2008; Heers et al., 2014) and experiments on their sister group (ratites) are still poorly explored (but see Davis, 2005). We offer experimental results of the running behavior of a flightless bird climbing a slope, substantiating that, among living birds, WAIR is exclusive of flying forms.

We made repeated observations on 7 juvenile specimens, 1 week old, of *Rhea americana* climbing a slope at angles of 10°, 20°, 30°, 40°, and 45°. Juveniles climbed slopes with difficulty (fig. 3; see also videos online in the Supplementary data at doi.org/10.5531/sd.sp.44), including arrests of the march, backward steps, and sometimes forward jumps. The difficulty in climbing, not surprisingly, was augmented with steeper slopes. Two types of behavior were observed: (1) climbing without extending the wings; or (2) climbing extending separately each wing to stabilize the body. In all cases, the individuals

inclined their bodies forward, to avoid falling back. In sum, rhea's wings do not cooperate aerodynamically with the hind limbs to climb a slope. In conclusion, none of the studied specimens performed WAIR (videos available online at doi.org/10.5531/sd.sp.44), in agreement with previous work by Davis (2005) carried out on rheas, ostriches, and emus. Experimental results are in agreement with observations noted by early naturalists (e.g., Darwin, 1839; Muñiz, 1885), that wings of ratites do not perform symmetrical movements even when these birds are engaged in running and fighting. Recently, Schaller (2008) recorded a similar behavior for the African Ostrich, *Struthio camelus*.

DISCUSSION

The WAIR hypothesis assumes that early birds positioned (and moved) their wings in the same basic manner as in living flying birds. WAIR-based reconstructions of wing posture and movements for extinct avialans are based on the highly specialized flying neognaths, in which the glenoid cavity is laterodorsally faced and horizontally oriented, thus allowing upward and downward wing excursions.

We do not dismiss the explanatory power of the WAIR in the understanding of bird flight evolution, since this behavior might have been present in the common ancestor of Aves, and there exist anatomical reasons to suspect its presence among early-diverging ornithothoracines (Dial et al., 2008; Heers and Dial, 2012). Discussions, in fact, center on whether earlier birds (e.g., *Archaeopteryx*) already had the ability to perform WAIR. Heers and Dial (2012) claim this behavior was already present in early-diverging coelurosaurians. However, as analyzed previously, two lines of evidence weaken this WAIR interpretation: the inability of the ratites to perform WAIR (Davis, 2005, and this study), and the wing beat inferred for *Archaeopteryx* (based on general morphology of pectoral girdle, muscle pattern, and orientation and shape of the glenoid cavity).

It is remarkable that ratites, which are devoid of a derived morphology of the pectoral girdle, do not perform WAIR (both hatchlings and adults). This suggests that a causal relationship may exist between archaic pectoral girdle morphology and the inability to perform symmetrical strong flapping. In other words, their wings generate neither thrust nor lift. The weak and occasional symmetrical flapping performed by ratites may also mirror the fact that both *m. supracoracoideus* and *m. pectoralis* had postural rather than locomotor functions (Rosser and George, 1985).

As Heers, et al. (2014) pointed out, muscles of hatchling avians are less voluminous than in adults, thus lending support to the idea that early paravians were able to flap and perform WAIR, in spite of their less-developed pectoral and supracoracoidal muscle masses. Nevertheless, we concur with Dececchi, et al. (2016) in that juvenile avians already have adult pectoral attributes, including a dorsally oriented glenoid fossa and path of the tendon of *m. supracoracoideus* through the triosseal foramen (thus allowing the elevator action of *m. supracoracoideus*). These anatomical and functional characteristics described for flying avians sharply differ from ratite birds, in which the *m. supracoracoideus* plays a humeral protractor role, a function also inferred for early-diverging avialans (Ostrom, 1976). Wing stroke in early-diverging avialans probably lacked the upward humeral excursion and longitudinal twisting (during upstroke) of the kind occurring in living flying avians (Ostrom, 1976; Poore et al., 1997).

Even assuming that *Archaeopteryx* was able to symmetrically flap its wings in a gravitational frame as in living birds, the flapping probably did not attain the frequency and endurance as those living neognaths performing WAIR. Most recent studies on pectoral girdle anatomy and function in early-diverging paravians (Jenkins, 1993; Senter, 2006; Turner et al., 2012; Dececchi et al. 2016) agree that *Archaeopteryx* was not capable of strenuous flapping ability.

As important as frequency and endurance of flapping activity is the wing position in respect to

both vertebral column and ground. Dial (2003) already interpreted the glenoid orientation of *Archaeopteryx* as an intermediate condition between early-diverging theropods and living birds (Jenkins, 1993), which allowed anteroposterior limb excursions resembling those employed by juvenile and adult ground birds during WAIR. As said before, early-diverging paravians and early birds probably had a posture of wings different from neognaths, being more similar to that of ratites, with an arc of movement anterodorsal to posteroventral, and main wing surface posteroventrally oriented in maximum abduction (Novas and Agnolín, 2014). In the same line of thought, Voeten, et al. (2018) hypothesized that *Archaeopteryx* oriented its wing surface posteroventrally (that is, oblique to the ground). Flapping wings, which moved anterodorsally to posteroventrally, may have predominantly produced thrust, but a small lift force.

This alternative reconstruction of the wing posture and movements of early-diverging avialans gives rise to the following question: could this “oblique” wing surface have generated enough lift to allow *Archaeopteryx* to become airborne? Could this kind of primitive wing have produced enough thrust to help the hind limbs in climbing pronounced slopes? The “inclined” wing surface inferred for early-diverging avialans apparently did not constitute optimal conditions to sustain gliding, but feeble development of wing muscles does not support ability for WAIR.

The oblique posture of wing surface in maximum abduction, as inferred for early-diverging paravians, invites review of aerodynamic experiments, both physically and mathematically based (e.g., Alexander et al., 2010; Evangelista et al., 2014), which assume a priori a flying avian wing posture for *Archaeopteryx* and *Microraptor*.

SUMMARY

Flying avians have been used as the best (and sole) living birds to study flight ability in early avialans. Nevertheless, living ratites constitute a

source of information that cannot be neglected at this time to interpret muscle function, forelimb movements, and running-flapping behavior in early-diverging paravians. After all, the portion of the theropod phylogenetic tree comprising oviraptorosaurians, dromaeosaurids, troodontids, microraptorines, unenlagines, anchiornithines, archaeopterygids, jeholornithids, saepeornithids, and confuciusornithids saw a locomotory transition(s) from fully terrestrial to aerial animals. How to determine the ability for flight (either flapping or gliding) of some of these groups (principally microraptorines, anchiornithines, and archaeopterygids) is a matter of debate (Sullivan et al., 2016; see Pittman et al., chapter 10).

The experimental information on ratite behavior, in conjunction with the morphological resemblance among early-diverging paravians and living ratites, lends support to the interpretation that early-diverging paravians were unable to perform WAIR.

Available information suggests that the glenoid frame was still operating a “shift” among early-diverging paravians, and that it did not acquire a modern (i.e., avianlike) position and shape until much later, in the evolution of birds (e.g., probably at the level of Ornithothoraces or more likely Ornithuromorpha; Mayr, 2017). This means that early-diverging avialans must have exhibited a flight style different from that attained in ornithuromorphs. In this regard, recent studies recognize that early-diverging birds had wing-folding capacity (Serenó and Rao, 1992), remige geometry (Feo et al., 2015), feather arrangement/rachis (Nudds and Dyke, 2010; Longrich et al., 2012), and supracoracoidal muscle development (Ostrom, 1976; Mayr, 2017) that were different from ornithuromorph birds.

Moreover, the generalized presence of well-developed hind wings among early-diverging paravians and early avialans clearly shows that unusual anatomical, functional and behavioral patterns prospered during the early stages of bird evolution (Sullivan et al., 2016; Agnolín et al., 2019). The view that flying styles among early-diverging birds have no analogs among living birds is gaining ground.

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REFERENCES

- Agnolín, F. and F.E. Novas. 2013. Avian ancestors: a review of the phylogenetic relationships of the theropods Unenlagiidae, Microraptoria, *Anchiornis* and Scansoriopterygidae. Dordrecht: Springer Science & Business Media.
- Agnolín, F., M. J. Motta, F. Brissón Egli, G. Lo Coco, and F. E. Novas. 2019. Paravian phylogeny and the dinosaur-bird transition: an overview. *Frontiers in Earth Science* 6: 252.
- Alexander, D.E., E. Gong, L.D. Martin, D.A. Burnham, and A.R. Falk. 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: 2972–2976.
- Baier, D.B., S.M. Gatesy, and F.A. Jenkins. 2007. A critical ligamentous mechanism in the evolution of avian flight. *Nature* 445: 307–310.
- Baier, D.B., S.M. Gatesy, and K.P. Dial. 2013. Three-dimensional, high-resolution skeletal kinematics of the avian wing and shoulder during ascending flapping flight and uphill flap-running. *PLoS One* 8: e63982.
- Bundle, M.W. and K.P. Dial. 2003. Mechanics of wing-assisted incline running (WAIR). *Journal of Experimental Biology* 206: 4553–4564.
- Burnham, D.A. 2004. New information on *Bambiraptor feinbergi* from the Late Cretaceous of Montana. In P.J. Currie, E.B. Koppelhus, M.A. Shugar, and J.L. Wright (editors), *Feathered dragons: studies on the transition from dinosaurs to birds*: 67–111. Indianapolis: Indiana University Press.
- Darwin, C. 1839. Narrative of the surveying voyages of his majesty's ships *Adventure* and *Beagle* between the years 1826 and 1836, describing their examination of the southern shores of South America, and the *Beagle's* circumnavigation of the globe. Journal and remarks. 1832–1836. London: Henry Colburn.
- Davis, H.D. 2005. Negotiating a three-dimensional environment: limb kinematics of terrestrial birds during sloped ascents. M.S. thesis, Missoula, University of Montana.
- Dececchi, T.A., H.C.E. Larsson, and M.B. Habib. 2016. The wings before the bird: an evaluation of flapping-based locomotory hypotheses in bird antecedents. *Peer J* 4: e2159.
- Dial, K.P. 2003. Wing-assisted incline running and the evolution of flight. *Science* 299: 402–404.
- Dial, K.P., B. Jackson, and P. Segre. 2008. A fundamental avian wing-stroke provides new perspective on the evolution of flight. *Nature* 451: 1–6.
- Dudley, R., et al. 2007. Gliding and the functional origins of flight: biomechanical novelty or necessity? *Annual Review of Ecology, Evolution, and Systematics* 38: 179–201.
- Evangelista, D., S. Cam, T. Huynh, I. Krivitskiy, and R. Dudley. 2014. Ontogeny of aerial righting and wing flapping in juvenile birds. *Biology Letters* 10: 20140497.
- Faux, C. and D.J. Field. 2017. Distinct developmental pathways underlie independent losses of flight in ratites. *Biology Letters* 13: 20170234.
- Feo, T.J., D.J. Field, and R.O. Prum. 2015. Barb geometry of asymmetrical feathers reveals a transitional morphology in the evolution of avian flight. *Proceedings of the Royal Society B, Biological Sciences* 282: 20142864.
- Heers, A.M., and K.P. Dial. 2012. From extant to extinct: locomotor ontogeny and the evolution of avian flight. *Trends in Ecology and Evolution* 27: 296–305.
- Heers, A.M., K.P. Dial, and B.W. Tobalske. 2014. From baby birds to feathered dinosaurs: incipient wings and the evolution of flight. *Paleobiology* 40: 459–476.
- Heers, A.M., J.W. Rankin, J.R. Hutchinson. 2018. Building a bird: musculoskeletal modeling and simula-

- tion of wing-assisted incline running during avian ontogeny. *Frontiers in Bioengineering and Biotechnology* 6:140.
- Jackson, B.E., B.W. Tobalske, and K.P. Dial. 2011. The broad range of contractile behaviour of the avian pectoralis: functional and evolutionary implications. *Journal of Experimental Biology* 214: 2354–2361.
- Jenkins, F.A. 1993. The evolution of the avian shoulder joint. *American Journal of Science* 293: 253–253.
- Longrich, N.R., J. Vinther, Q. Meng, Q. Li, and A.P. Russell. 2012. Primitive wing feather arrangement in *Archaeopteryx lithographica* and *Anchiornis huxleyi*. *Current Biology* 1094: 2262–2267.
- Mayr, G. 2017. Pectoral girdle morphology of Mesozoic birds and the evolution of the avian supracoracoideus muscle. *Journal of Ornithology* 158: 859–867.
- Muñiz, F.J. 1885. Historia natural: el ñandú o avestruz pampeano. In D.F. Sarmiento (editor), *Vida y escritos del coronel Francisco J. Muñiz*: 84–90. Buenos Aires: F. Lajouane.
- Novas F.E., and F.L. Agnolín. 2014. Scapular girdle morphology in paravians and implications for the origin of flight. Fourth International Palaeontological Congress, Abstract Vol. A145. September 2014. Mendoza. Argentina: CCT-CONICET.
- Novas, F.E., F. Brissón Egli, F.L. Agnolín, F.A. Gianechini, and I.A. Cerda. 2018. Postcranial osteology of a new specimen of *Buitreraptor gonzalezorum* (Theropoda, Unenlagiidae). *Cretaceous Research* 83: 127–167.
- Nudds, R.L., and G.J. Dyke. 2010. Narrow primary feather rachises in *Confuciusornis* and *Archaeopteryx* suggest poor flight ability. *Science* 328: 886–889.
- Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History Bulletin* 30: 1–165.
- Ostrom, J.H. 1976. Some hypothetical anatomical stages in the evolution of avian flight. *Smithsonian Contributions to Paleobiology*: 1–21.
- Pei, R., Q. Li, Q. Meng, M. Norell, and K. Gao. 2017. New specimens of *Anchiornis huxleyi* (Theropoda, Paraves) from the late Jurassic of northeastern China. *Bulletin of the American Museum of Natural History* 411: 1–67.
- Poore, S.O., A. Sanchez-Haiman, and G.E. Goslow. 1997. Wing upstroke and the evolution of flapping flight. *Nature* 387: 799–802.
- Raikow, R.J. 1968. Maintenance behavior of the Common Rhea. *The Wilson Bulletin* 80(3): 312–319.
- Rosser, B.W.C., and J.C. George. 1985. Histochemical characterization and distribution of fiber types in the pectoralis muscle of the ostrich (*Struthio camelus*) and emu (*Dromaius novaehollandiae*). *Acta Zoologica* 66: 191–198.
- Schaller, N.U. 2008. Structural attributes contributing to locomotor performance in the ostrich (*Struthio camelus*). Ph.D. dissertation, University of Heidelberg, Heidelberg, Germany.
- Senter, P. 2006. Scapular orientation in theropods and basal birds, and the origin of flapping flight. *Acta Palaeontologica Polonica*, 51: 305–313.
- Sereno, P.C., and C. Rao. 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. *Science* 255: 845–848.
- Sullivan, C., X. Xu, J.K. O'Connor. 2016. Complexities and novelties in the early evolution of avian flight, as seen in the Mesozoic Yanliao and Jehol biotas of Northeast China. *Palaeoworld* 26: 212–229.
- Turner, A.H., P.J. Makovicky, and M.A. Norell. 2012. A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History* 371: 1–206.
- Voeten, D.F.A.E., et al. 2018. Wing bone geometry reveals active flight in *Archaeopteryx*. *Nature Communications* 9: 923.
- Xu, X. 2002. Deinonychosaurian fossils from the Jehol Group of western Liaoning and the coelurosaurian evolution. Ph.D. dissertation, Chinese Academy of Sciences, Beijing.