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Volume: 7
Article: 8
Page(s): 1-9
Published Date: 01/08/2017
PermaLink:
http://www.palaeontologyonline.com/articles/2017/fossil-focus-archosaur-respiratory-system-breathing-life-dinosaurs/

CITATION OF ARTICLE

Please cite the following published work as:

Brocklehurst, Robert. 2017. Fossil Focus: The Archosaur Respiratory System - Or - Breathing Life into Dinosaurs. Palaeontology Online, Volume 7, Article 8, 1-9.

Published by: Palaeontology [online]

Fossil Focus: The Archosaur Respiratory System — Or — Breathing Life into Dinosaurs

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by Robert Brocklehurst*[1]

Introduction and background

Dinosaurs fascinate people more than almost any other group of fossil animals, and the general public is interested in many open questions on dinosaur biology. How fast could dinosaurs run? Were they warm blooded? If they had feathers, does that mean they could fly? These questions focus on dinosaur metabolism and movement, both of which are intimately linked with the respiratory system, because breathing — the ability to take in air, extract oxygen from it and then expel it from the body along with waste carbon dioxide— sets a fundamental upper limit on how much activity an organism is capable of.

How did dinosaurs breathe? That’s probably not a question palaeontologists get asked as often as the others. Breathing is something we all do all day, every day. You’re probably (hopefully!) doing it right now. However, for something so seemingly ordinary, we still have very little idea how the process works. This is even truer in non-mammals, and especially in animals such as dinosaurs, which seem so different from anything alive today. Technically, dinosaurs *are* alive today, as their direct descendants — birds. The next closest living relatives to dinosaurs are crocodilians, and by studying these living groups we can gain insights into the links between form and function in the respiratory system, which we can then apply back to the fossils.

What we know for sure: Similarities between birds and crocodilians

The internal structures of the lungs of birds and crocodiles are surprisingly similar: a single primary bronchus (or air chamber) with multiple secondary bronchi, all interconnected by a network of smaller tubes called parabronchi. It’s in these parabronchi (and even smaller air capillaries in birds) that most gas exchange occurs. The pattern of airflow in bird and crocodile lungs is also very similar — during both inhalation and exhalation, air flows towards the rear in the bronchi on the lower, or stomach, side of the body, and forward in the bronchi on the upper side, nearest the animal’s back. Unidirectional flow like this was once thought to be characteristic of birds, but is now also known in crocodilians and some other reptiles.

Given that the closest living relatives of dinosaurs both have parabronchial lungs with unidirectional airflow, we can be pretty certain that dinosaurs did too. After that, however, things get a little more complicated ...

The first amendment: Separation of ventilator and exchanger

The main function of the lungs is gas exchange: getting oxygen from the air to the bloodstream (and carbon dioxide from the bloodstream to the air). However, during breathing, the lungs of most animals expand and contract to move fresh air into the lung and expel stale air. This process is known as ventilation. ‘Breathing’ includes both ventilation and gas exchange; in a breath, air enters the lungs, gas exchange occurs, and then the air is removed from the lungs.

Crocodilians have ‘compliant’ lungs, which expand and contract during breathing for ventilation — much like all other amniotes (animals which don’t need to lay their eggs in water: lizards, snakes, turtles, mammals) apart from birds. However, the upper parts of the lung, where the majority of gas-exchange tissue is located, are less mobile than the lower portions, so there is some variation in lung structure in crocodilians. Birds are unique among air-breathing vertebrates in that the lungs, at the top of the ribcage, are rigid and do not expand or contract: they are devoted entirely to gas exchange. Ventilation is achieved through a system of air sacs, which expand and contract (driven by motion of the ribs and the sternum, or breastbone) to create air flow through the lungs. The question is whether dinosaurs also had such a lung–air sac system, and whether they had the same high capacity for gas exchange.

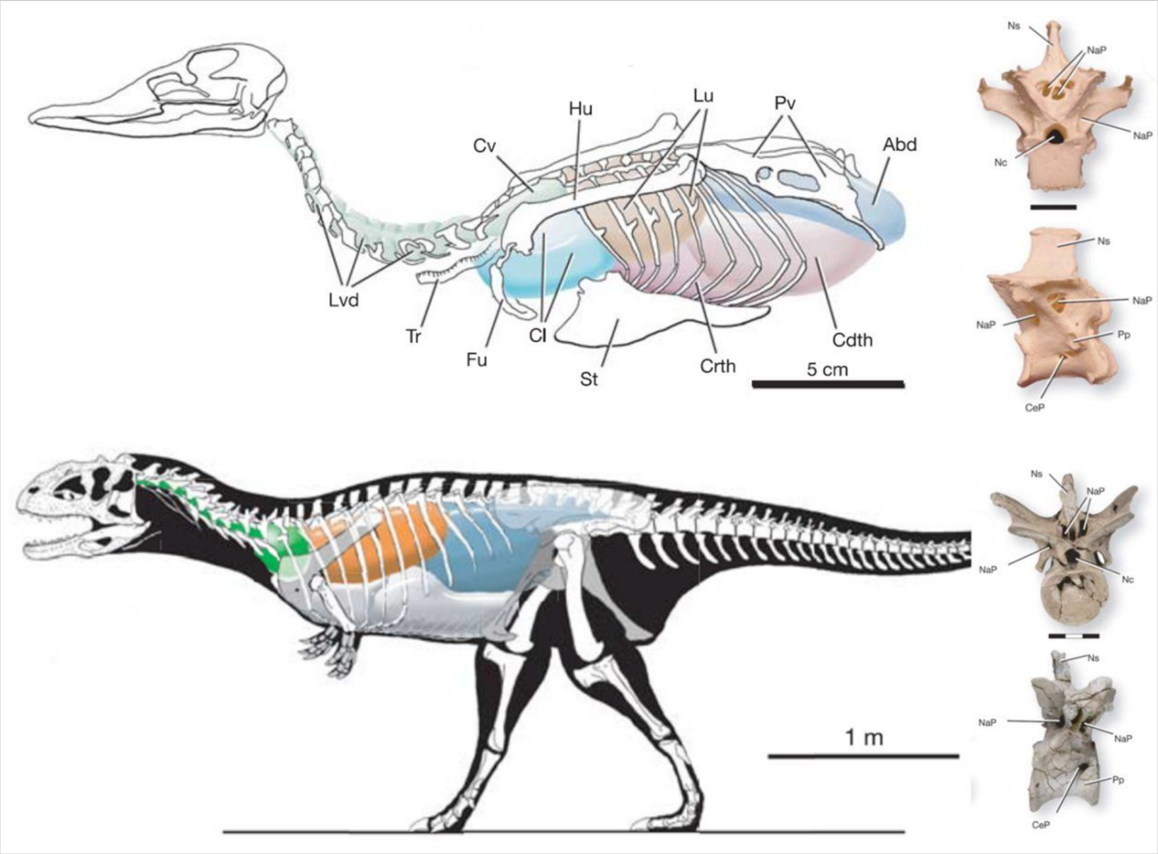

Figure 1 — Top, Air sacs of a duck, and pneumatic features (including pneumatic foramina) of duck vertebrae. Bottom, Reconstructed air sacs of the theropod dinosaur *Majungsaurus*, based on pneumatic features preserved in the fossil bones. Abbreviations: Abd, abdominal air sac; Cdth, caudal thoracic air sac, CeP, central pneumatic foramen; Cl, clavicular air sac; Crth, cranial thoracic air sac; Cv, cervical air sac; Fu, furcula; Hu, humerus; Lu, lung; Lvd, lateral vertebral diverticula; NaP, neural arch pneumatic foramen; Nc, neural canal; Ns, neural spine; Pp, parapophysis. Pv, pelvis; Tr, trachea. From O’Connor and Claessens (2005).

Air-headed: The rise and fall (and rise) of pneumaticity

In the bird lung–air sac system, the presence of air sacs is associated with the skeleton becoming hollowed out and filled with air (pneumatized). Pockets of the respiratory system called diverticulae appear in the bones. This leaves tell-tale marks called pneumatic foramina — holes in the bone that connect to the air-filled inner chambers. These pneumatic foramina have also been found in the fossilized bones of theropods (bipedal meat eaters e.g. *T Rex*, *Velociraptor,* see Fig. 1) and sauropod dinosaurs (long necked herbivores, e.g. *Diplodocus, Brachiosaurus*), so this provides strong evidence for the presence of air sacs in these groups. Additionally, in living birds, specific bones tend to be pneumatized by specific air sacs. This means that patterns of skeletal pneumaticity and which bones were pneumatic can tell us about which air sacs dinosaurs possessed. It turns out that dinosaurs probably had air sacs both in front of and behind the lungs, which could be used to generate unidirectional flow (Fig. 1).

Among the dinosaurs, ornithischians (all other herbivores e.g. *Iguanadon*, *Stegosaurus*, *Ankylosaurus*, *Triceratops*) are the odd ones out for not having skeletal pneumaticity. Does this mean they did not have air sacs like sauropods, theropods and birds? Perhaps, although it is also possible that they had a lung–air sac system, but that the air sacs simply didn't invade the bones as they did in other groups. The presence of pneumaticity in pterosaurs, which are close relatives of dinosaurs, complicates things further. Did the ancestors of dinosaurs and pterosaurs have air sacs which were lost in Ornithischians, or did pterosaurs and non-Ornithischian dinosaurs evolve air-sacs independently? Who knows? Only time (and more research) will tell.

The focus on pneumaticity has attracted some critics. Skeletal pneumaticity and air sacs aren't always found together; for example, some aquatic birds, such as penguins, have solid bones to help buoyancy under water, but they still have a lung–air sac system. Also problematic is that the lung itself can also pneumatize bones. If this is a trait found in the ancestors of birds and dinosaurs, then pneumatic features may not indicate the presence of air sacs at all. However, one particular feature remains a dead giveaway and that is a pneumatic hiatus: a gap in the pneumatization of the vertebral column, which indicates diverticulae have come from different places. This has been reported in some dinosaur specimens, such as the sauropod *Haplocanthus*, and provides extra support for the presence of air sacs.

A swinging joint: Costovertebral articulation and lung structure

Birds and crocodilians both have bicapitate (two-headed) ribs, which join the vertebrae in two different places- a lower joint on the vertebral body, and an upper joint on the transverse processes (wing-like projections sticking out from the vertebra) (Fig. 2). In birds, these two joints are vertically aligned - with one higher than the other - and are very well separated. In crocodilians, the first two rib-bearing vertebrae are similar to birds, but in the succeeding vertebrae the lower of the two joints starts to migrate upwards and outwards, away from its position on the vertebral body and towards the upper joint at the end of the transverse process (Fig. 2).

In archosaurs (and other reptiles) the lung is physically attached to the vertebrae and rib heads, so the anatomy of the costovertebral joint (where the ribs meet the vertebrae) directly affects the structure of the lungs. The vertical distance between the two rib joints in birds, combined with generally short transverse processes, results in a grooved 'thoracic ceiling' (the top of the inside of the ribcage), where the rib heads actually cut into the lung tissue (Fig. 2). This helps to provide structural support for the rigid bird lung. In crocodilians, following the movement of the lower joint, the two rib joints lie on a flat horizontal plane. Combined with the long transverse processes, this creates a smooth thoracic ceiling, which allows the lungs to expand and contract during ventilation (Fig. 2).

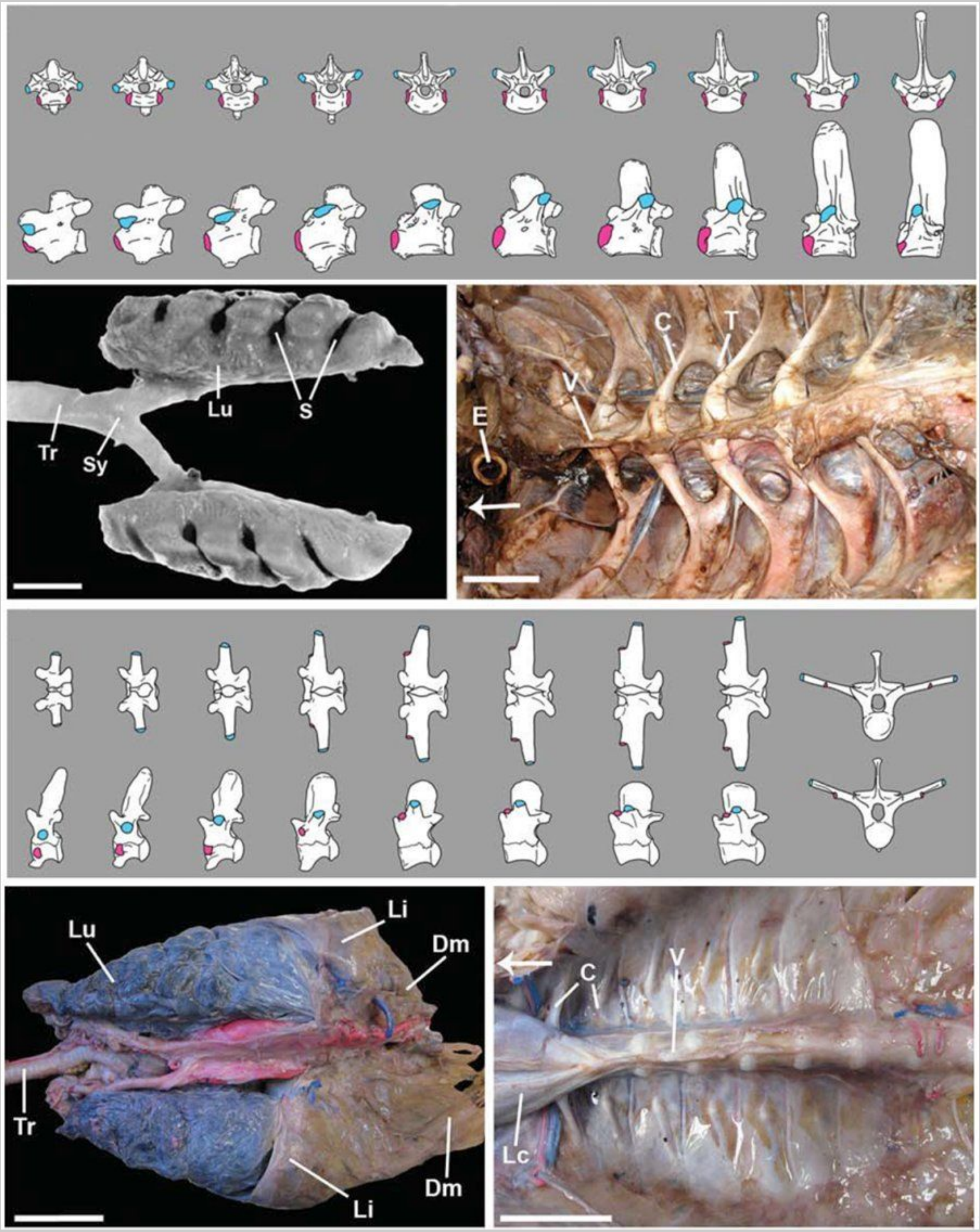

Figure 2 — Upper three panels, Ostrich. Top, Diagrams of the vertebrae shown from the front and from the side, two joints marked in pink & blue. Left; View of the lungs (Lu), trachea (Tr) and sulci (S - grooves where the ribs cut into the lung). Right- Interior of the ribcage with internal organs removed, showing vertebrae (V) and rib heads (C, capitulum; T, tuberculum). Lower three panels, Alligator. Top, Diagrams of the vertebrae shown from the top, side and front (last two only). Left, View of the lungs (Lu), trachea (Tr), liver (Li) and diaphragmaticus muscle (Dm, cut). Right, Interior of the ribcage with internal organs removed showing vertebrae (V) and rib heads (C, capitulum). Arrow points towards the head. Modified from Schachner et al. (2011).

Dinosaurs show a variety of shapes in their costovertebral joints, but all are more like those of birds than of crocodilians. Close fossil relatives of the dinosaurs, such as *Silesaurus*, show that the two joint facets remain separated for most of the vertebral column. The most crocodilian-like vertebrae are seen in early ornithischian dinosaurs: the lower joint does migrate upwards, but much more slowly than in crocodilian. Later members of this group are more like birds in that all the joints remain separated. Both sauropods and theropods have birdlike vertebrae and ribs. Combined with the data from pneumaticity in these groups, this suggests that they had a birdlike respiratory system with an immobile lung ventilated by air sacs.

Lily-livered dinosaurs: The curious case of the dinosaurian diaphragm

The How, precisely, dinosaurs ventilated their lungs has been the subject of much debate because it correlates with lung structure and gas-exchange potential. Over the years, several scientists have gone against the grain, challenging the mainstream scientific consensus to propose that dinosaurs were cold-blooded (ectotherms), incapable of sustaining birdlike metabolic rates or activity levels. Many of these suggestions were based on the idea that dinosaurs had crocodilian-like lungs and a particularly crocodilian way of ventilating them.

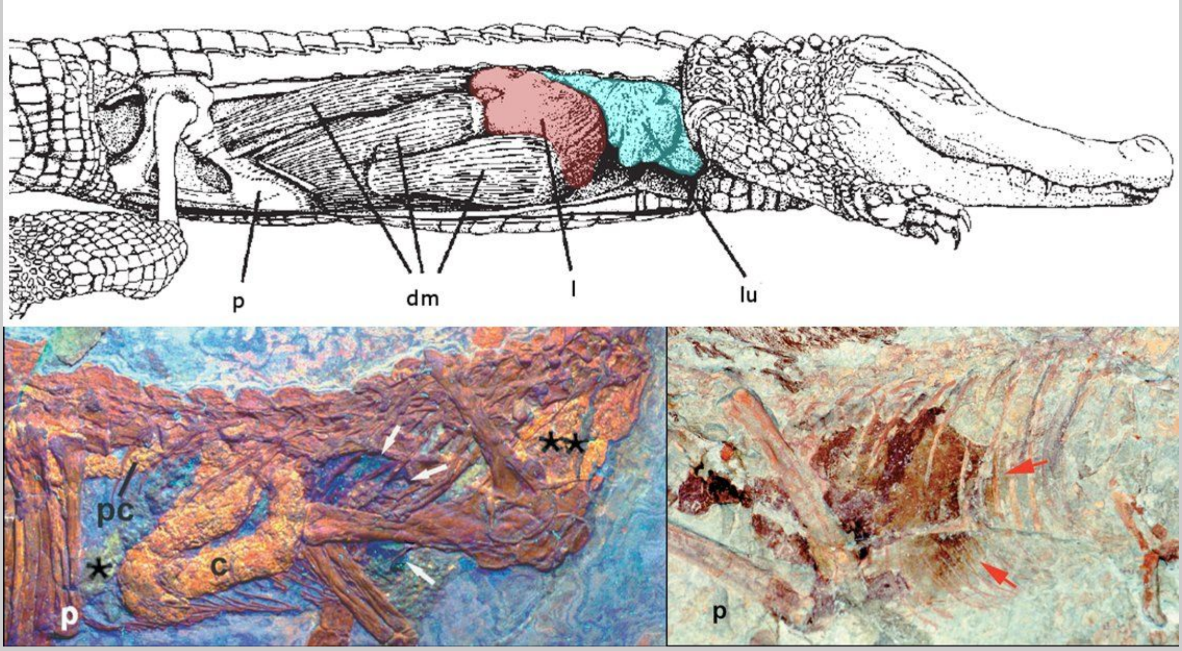

Figure 3 — Top, the anatomy of the diaphragmaticus (dm), liver (l), lungs (lu) and pubic bone (p) in living crocodilians. Bottom, fossil dinosaurs purported to show remains of the liver (marked with arrows), soft tissues (pc, posterior colon, c, colon) and other adaptations to a crocodilian 'hepatic piston' ventilation mechanism (single asterisk marks "diaphragmatic muscles") in *Scipionyx* (left) and *Sinosauropteryx* (right). From Ruben et al., (1997, 1999).

In living crocodilians, motion of the ribcage isn't the only way to expand the lungs. They also have a 'hepatic piston' diaphragm for ventilation. This is driven by the contraction of the diapraghmaticus: a long, straplike muscle that runs from the pelvis to the liver. When the diaphragmaticus contracts, the liver and other internal organs are pulled backwards, increasing the volume of the lung cavity and causing breath to be drawn in (Fig. 3). This is associated with other crocodilian features such as a lack of ribs attached to the lower spine — similar to that of mammals, which also possess a diaphragm (evolved independently) — and the smooth thoracic ceiling that allows the lungs to expand and contract from back to front.

The suggestion that theropods breathed in this way is mostly based on the interpretation of a few exceptionally preserved specimens. *Sinosaruopteryx* and *Scipionyx* show possible traces of the liver, which seems to divide the body cavity vertically into a thorax (containing the heart and lungs) and abdomen (containing the other internal organs), much like crocodilians. *Scipionyx* also preserved structures that were originally interpreted as strands of diaphragmatic musculature (Fig. 3).

However, what some researchers called the clear outline of the liver in *Sinosauropteryx* others saw as the result of damage and subsequent repairs to a specimen. The *Scipionyx* 'muscle traces' have also been reinterpreted as features of the rock the fossil was found in, not the animal's biology, and so did not represent the remains of a croc-like diaphragm. Additionally, dinosaurs lack other crocodilian features associated with hepatic-piston breathing, such as a rib-free lower spine. As a result, the idea that dinosaurs ventilated their lungs using a croc-like diaphragmaticus arrangement has been rejected by most researchers. Like birds, dinosaurs almost certainly ventilated their lungs using motion of the ribs and sternum.

Belly laughs and belly ribs: Gastralia and cuirassial breathing

Gastralia, or 'belly ribs' are bones which form in the belly wall of modern crocodiles and many fossil groups, including theropods and sauropods. Ornithisichians are once again the odd ones out, because they don't have gastralia. In modern crocs, belly ribs stiffen the belly wall and help to prevent abdominal collapse — inward movement of the internal organs and belly wall during breathing, which reduces the available volume for the lungs.

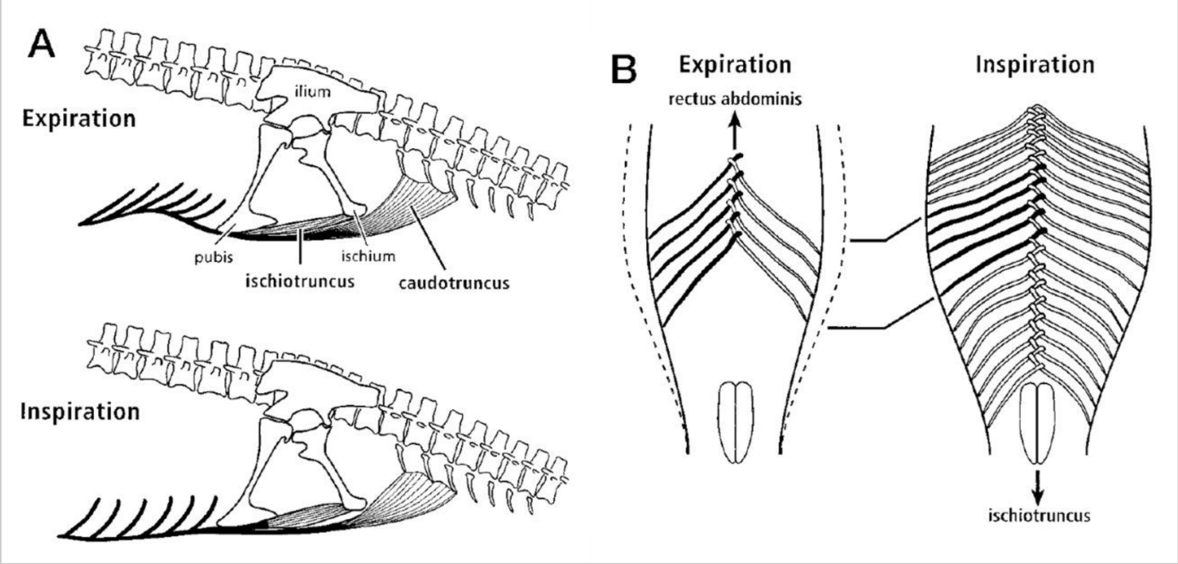

Figure 4 — Diagram of the cuirassial breathing system in theropod dinosaurs. When breathing out (expiration), the rectus abdominis muscle pulls the gastralia forwards, swinging the ends of the gastralia inwards and compressing the belly wall. When breathing in, contraction of the pelvic muscles (such as the ischiotruncus) pulls the gastralia to the back, causing them to swing out and expand the body cavity. Diagrams also show the bones of the pelvis (ilium, ischium and pubis) and other musculature (e.g. caudotruncus). From Carrier and Farmer, (2000).

The gastralia of sauropods and particularly theropods differ from those of modern crocodilians, in that they are jointed. This turned the ribcage and gastralia into a 'cuirassal basket', which could have been widened or narrowed through the combined action of the intercostal muscle moving the ribs and the pelvic muscle moving the gastralia. Movement of the gastralia would have increased total volume of air flow, and ventilation of the rear air sacs (see Fig. 4). Early fossil birds such as

Archaeopteryx still have gastralia, but in more advanced fossil birds these have been lost. This coincides with the rearward expansion of the sternum, which has replaced the gastralia in modern birds as the ventilator of the rear air sacs.

Due (uncinate) process: Leveraging the avian ribcage

Almost all modern birds have backwards-projecting processes on their ribs, called uncinates. These act as skeletal levers, making the breathing musculature more efficient. The length of these processes in birds is correlated with how the birds move — short in running birds, intermediate in flying birds and long in diving birds — and with metabolic rate (Fig. 5).

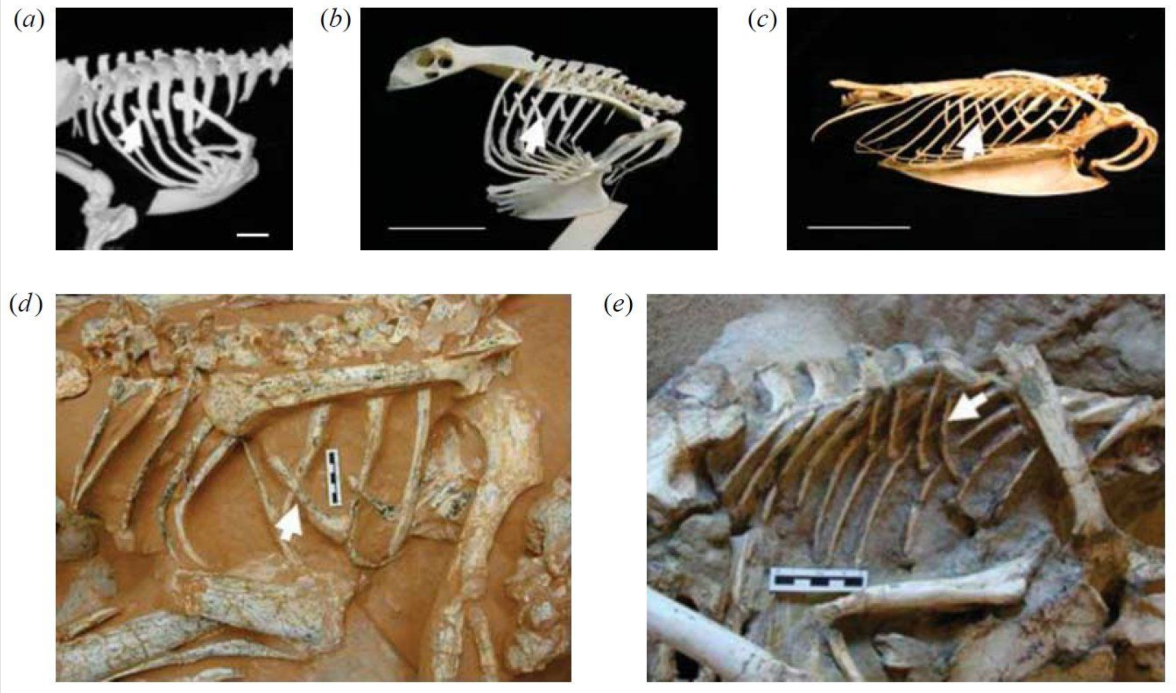

Figure 5 — Uncinate processes (marked by the arrows) in (a) a running cassowary, (b) a flying eagle owl and (c) a diving razor bill. (d) and (e) show uncinates in fossils; an ovripatrid (d) and velociraptor (e). From Codd et al., (2008).

Uncinates are also known from some theropods, such as *Velociraptor* and *Oviraptor*, as well as from fossil birds (Fig. 5). One puzzling thing about dinosaur uncinates is that they're very long, much closer in length to those of modern diving birds than those of running birds. This is possibly the result of how the processes attach to the ribs; whereas in birds they're solidly fused to the bony rib, in dinosaurs it's possible that they were joined by cartilage. This would have reduced the efficiency of the force transfer from the breathing muscles to the rest of the ribcage, and so to get the same effect you'd need a longer lever (and so a longer uncinate).

So, how did dinosaurs breathe exactly?

In summary, dinosaurs breathed using partitioned lungs. In some dinosaurs, these were fully split into a gas-exchanging lung and ventilatory air sacs. Evidence for air sacs comes from pneumatic features preserved in bones, and the patterns of pneumaticity (such as pneumatic hiatuses). Evidence for a rigid lung — or at least one with certain rigid regions specialized for gas exchange — also comes from the anatomy of the costovertebral joints, which are generally vertically oriented and are more like those of birds than those of crocodilians. It's also fairly clear how they ventilated their lungs: not with a crocodilian-style diaphragm, but through the motion of the ribs and sternum. Some theropods even had very birdlike modifications to their ribcage in the form of uncinate processes. The respiratory system of dinosaurs was probably capable of sustaining fairly high levels of activity and high metabolic rates, consistent with evidence from bone and other sources, that dinosaurs did not simply have 'reptilian' cold-blooded lifestyles.

Suggestions for further reading

Claessens, L. P. A. M. Anatomical transformations and respiratory innovations of the archosaur trunk. In: *Great Transformations in Vertebrate Evolution* (eds Dial, K. P., Shubin, N. & Brainerd, E. L.) 91–106 (University of Chicago Press, 2015) — *A great review and summary of breathing in dinosaurs, birds, crocs and pterosaurs (recommended you read this first before delving into the more specialised sources below).*

Farmer, C. G. Similarity of crocodilian and avian lungs indicates unidirectional flow is ancestral for archosaurs. *Integrative & Comparative Biology* **55,** 962–971 (2015). DOI: 10.1093/icb/icv078

O'Connor, P. M. & Claessens, L. P. A. M. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* **436,** 253–256 (2005). DOI: 10.1038/nature03716

Farmer, C. G. On the origin of avian air sacs. *Respiratory Physiology & Neurobiology* **154,** 89–106 (2006). DOI: 10.1016/j.resp.2006.04.014

Wedel, M. J. Evidence for bird-like air sacs in saurischian dinosaurs. *Journal of Experimental Zoology* **311A,** 611–628 (2009). DOI: 10.1002/jez.513

Benson, R. B. J., Butler, R. J., Carrano, M. T. & O'Connor, P. M. Air-filled postcranial bones in theropod dinosaurs: physiological implications and the 'reptile'–bird transition. *Biological Reviews* **87,** 168–193 (2012). DOI: 10.1111/j.1469-185X.2011.00190.x

Schachner, E. R., Lyson, T. R. & Dodson, P. Evolution of the respiratory system in nonavian theropods: Evidence from rib and vertebral morphology. *The Anatomical Record* **292,** 1501–1513 (2009). DOI: 10.1002/ar.20989

Schachner, E. R., Farmer, C. G., McDonald, A. T. & Dodson, P. Evolution of the dinosauriform respiratory apparatus: New evidence from the postcranial axial skeleton. *The Anatomical Record* **294,** 1532–1547 (2011). DOI: 10.1002/ar.21439

Ruben, J. A. *et al*. Pulmonary function and metabolic physiology of theropod dinosaurs. *Science* **283,** 514–516 (1999). DOI: 10.1126/science.283.5401.514

Currie, P. J. & Chen, P. Anatomy of Sinosauropteryx prima from Liaoning, northeastern China. *Canadian Journal of Earth Sciences* **38,** 1705–1727 (2001). DOI: 10.1139/e01-050

Carrier, D. R. & Farmer, C. G. The evolution of pelvic aspiration in archosaurs. *Paleobiology* **26,** 271–293 (2000). DOI: 10.1666/0094-8373(2000)026<0271:TEOPAI>2.0.CO;2

Codd, J. R., Manning, P. L., Norell, M. A. & Perry, S. F. Avian-like breathing mechanics in maniraptoran dinosaurs. *Proceedings of the Royal Society of London B: Biological Sciences* **275,** 157–161 (2008). DOI: 10.1098/rspb.2007.1233

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