LIGHTENING THE GIANTS: PNEUMATIC BONES IN SAUROPOD DINOSAURS AND THEIR IMPLICATIONS FOR MASS ESTIMATES

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Dear Reader,

In December, 2006, the Fundación Conjunto Paleontológico de Teruel – Dinópolis awarded me the Fourth International Award in Palaeontology Research for my 2005 paper on skeletal pneumaticity (air-filled bones) in sauropod dinosaurs. Like previous awardees, I was invited to rewrite the paper for a general audience. In the process of rewriting I deleted some of the technical asides from the original paper, added more introductory and explanatory material—and 11 new figures—and appended a glossary of some of the more technical terms. The result is an almost completely new paper, which was published in December, 2008, as the twelfth entry in the ¡Fundamental! series of paleontological booklets published by Dinópolis. Original reprints are available for sale through Dinópolis. I am making this final manuscript draft freely available to all who are interested. The pagination is not the same as in the official publication, and there may be minor differences of word choice and placement as well. If you need to cite this paper, the correct reference is:

Wedel, M.J. 2007. Aligerando a los gigantes (Lightening the giants). ¡Fundamental! 12:1-84. [in Spanish, with English translation]

Thank you for your interest.

Best,

Matt

INTRODUCTION

Sauropods—giant, long-necked and long-tailed dinosaurs such as *Apatosaurus* and *Brachiosaurus*—were the largest animals to ever walk on land. They were marvels of biological engineering, and that efficiency of design is especially evident in their **vertebrae**, the bones that make up the backbone. The vertebrae of most animals are basically cylinders, with an arch of bone to protect the spinal cord and a few odd bumps that connect to muscles, ribs, or other vertebrae. The **morphology**, or form, of the vertebrae of sauropods follows the same basic plan (Figure 1), but the usual cylinders and arches of the vertebrae are broken down into more complex shapes. The points and edges of the vertebrae are connected by ridges and plates of bone, which are called vertebral **laminae** (Figure 2). In addition, the **centra** or "bodies" of the vertebrae may have deep pits or large holes that open into internal chambers. These laminae and cavities are often considered to be adaptations to lighten the animal by reducing its mass (Osborn, 1899; Hatcher, 1901; Gilmore, 1925). Furthermore, the complex arrangement of laminae and cavities in the vertebrae varies from one species to the next, and so they have been useful in reconstructing the evolution of sauropods (McIntosh, 1990; Wilson, 1999).

The light construction of sauropod vertebrae and the hollow spaces inside them are not unique among animals. Similar vertebrae are present in animals that we see every day: birds. The vertebrae of most birds are hollow and filled with air. The bones are filled with air because they are connected to the lungs by a series of air-filled tubes and sacks. Things that have air inside them—like the tires of an automobile—are said to be **pneumatic**. In most birds, at least part of the skeleton is pneumatic. The complex vertebrae of sauropod dinosaurs resemble those of birds, only they are much larger. But they have features that are only found in pneumatic bones, so paleontologists infer that when the sauropods were alive their vertebrae were also filled with air.

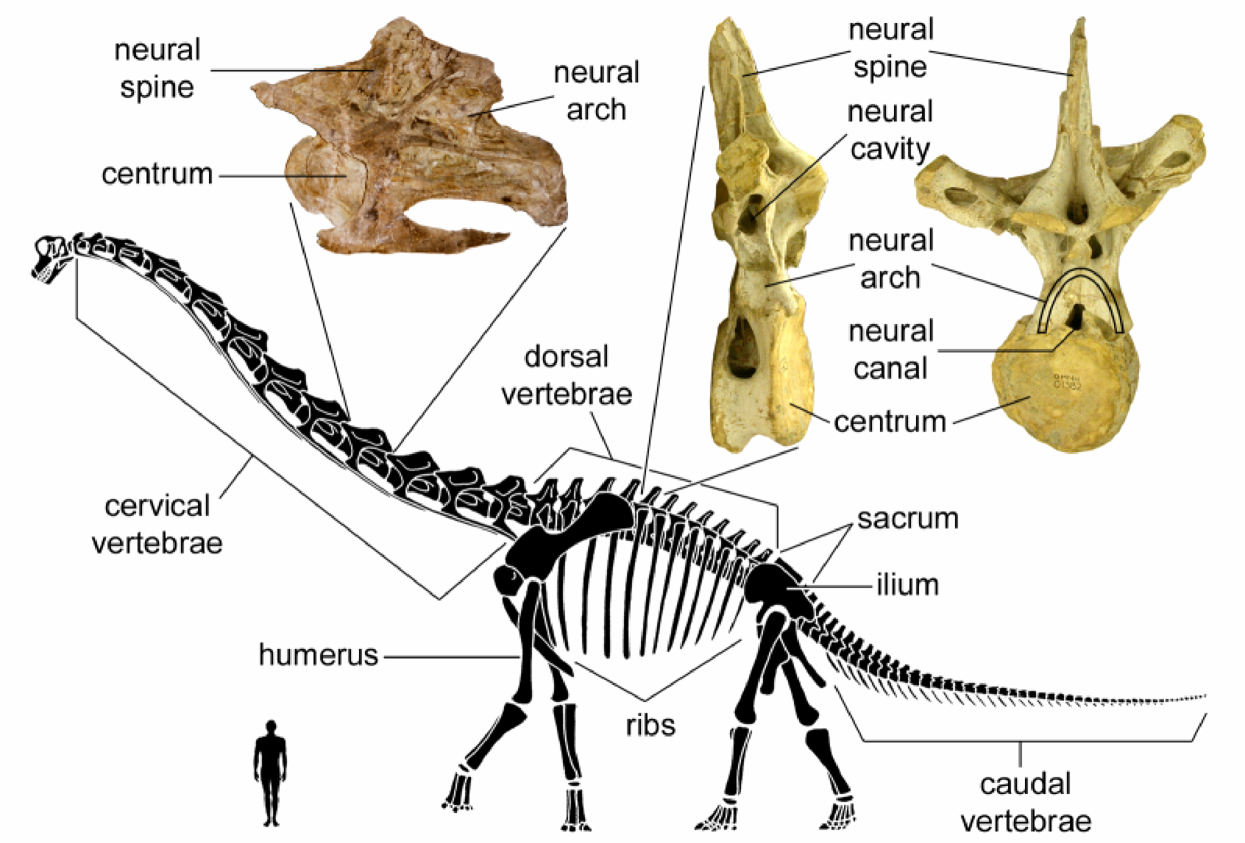

Figure 1. Anatomical terms used in this paper. Cervical vertebrae are neck vertebrae. Dorsal vertebrae are the vertebrae of the trunk, and they support the ribs. The sacrum consists of fused sacral vertebrae, and it is the point of attachment of the pelvis to the vertebral column. The ilium is the bone of the pelvis that attaches to the sacrum. Caudal vertebrae are tail vertebrae. All vertebrae have a centrum, or body, which connect to the vertebrae ahead of and behind them. Above the centrum is the neural canal, the opening through which the spinal cord passes. The neural canal is surrounded and protected by the neural arch. Above the neural arch is the neural spine, which is the point of attachment of ligaments and muscles that help support the body. The bone in the upper part of the forelimb is the humerus. The skeleton shown here is *Brachiosaurus*. The cervical vertebra, BYU 12867, is also from *Brachiosaurus*, and it is 94 cm long. The dorsal vertebra, OMNH 1382, is from *Apatosaurus*, and it is 93 cm tall.

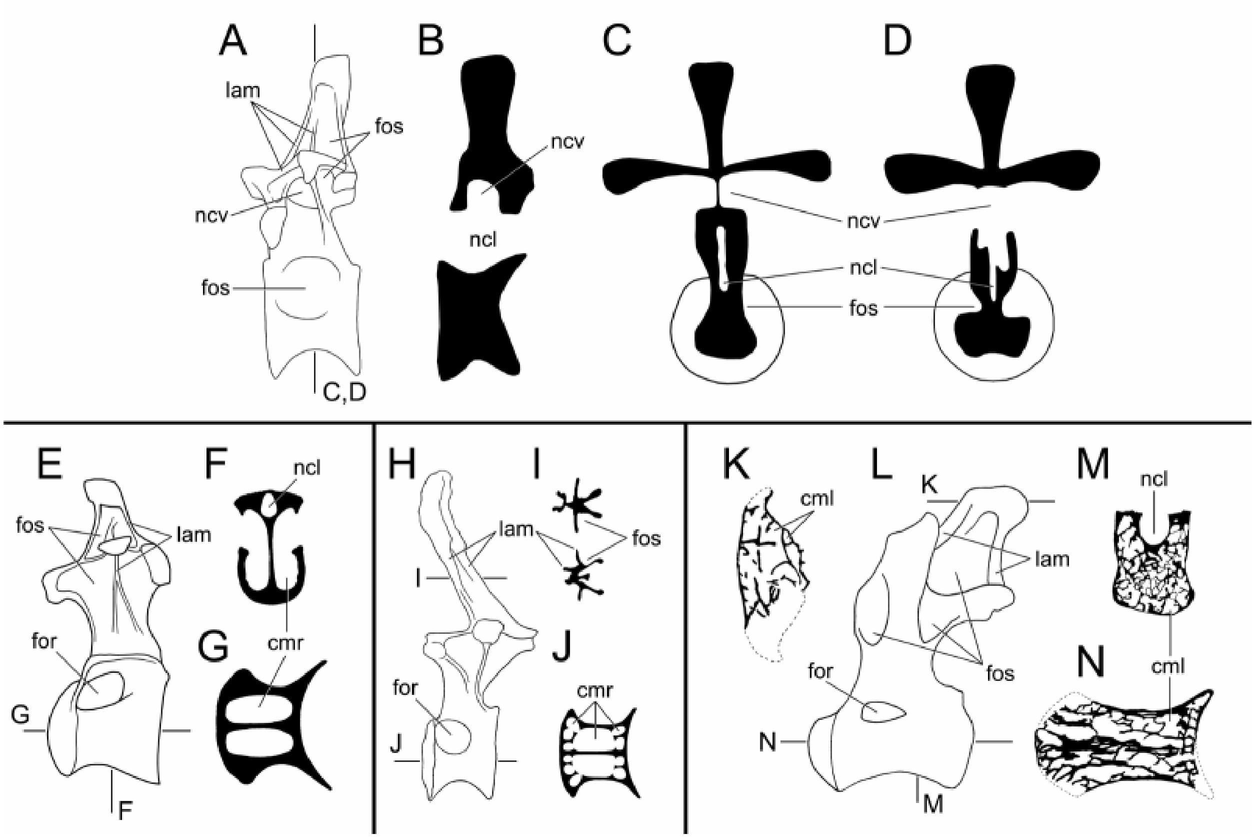

Figure 2. Pneumatic features in dorsal vertebrae of *Barapasaurus* (**A**-**D**), *Camarasaurus* (**E**-**G**), *Diplodocus* (**H**-**J**), and *Saltasaurus* (**K**-**N**). The vertebrae are facing to the left, and are not to scale. **A**, *Barapasaurus* (a primitive sauropod). **B**, a sagittal (front-to-back) section through a mid-dorsal vertebra of *Barapasaurus* showing the neural cavity above the neural canal. **C**, a transverse (side-to-side) section through the vertebra shown in A. In this vertebra, the neural cavities on either side are separated by a narrow median septum and do not connect to the neural canal. The centrum has large, shallow fossae. **D**, a transverse section through the dorsal vertebra shown in B. No bony structures separate the neural cavity from the neural canal. The fossae on the centrum are smaller and deeper than in C. A-D redrawn from Jain *et al*. (1979: pls. 101 and 102). **E**, *Camarasaurus*. **F**, a transverse section through the centrum showing the large camerae that occupy most of the volume of the centrum. **G**, a horizontal section. E-G redrawn from Ostrom and McIntosh (1966: pl. 24). **H**, *Diplodocus*. Modified from Gilmore (1932: fig. 2). **I**, transverse sections through the neural spines of other *Diplodocus* vertebrae (similar to H). The neural spine has no central body of bone for most of its length. Instead it is composed of intersecting bony laminae. This form of construction is typical for neural spines of many sauropods. Modified from Osborn (1899: fig. 4). **J**, a horizontal section, based on several broken vertebrae. The large camerae in the mid-centrum connect to several smaller chambers at either end. **K**, a transverse section through the top of the neural spine of a dorsal vertebra of *Saltasaurus*. Compare the internal pneumatic chambers in the neural spine of *Saltasaurus* with the fossae in the neural spine of *Diplodocus* shown in J. **L**, *Saltasaurus*. **M**, a transverse section through the centrum. **N**, a horizontal section. In most titanosaurs the neural spines and centra are filled with small camellae. K-N modified from Powell (1992: fig. 16).

The possibility that sauropods had pneumatic bones has been recognized for more than a century (Seeley, 1870; Janensch, 1947). However, it was not studied very much before the last decade (Britt, 1997; Wilson, 1999; Wedel, 2003a, b).

The goals of this paper are to review the evidence for **skeletal pneumaticity** (pneumatic bones) in sauropods, and to discuss some new areas of research and to outline possible directions for future studies. The paper is organized around three questions:

1. What lines of evidence do we use to infer that sauropod bones were pneumatic?
2. What aspects or characteristics of these pneumatic bones can we describe?
3. How does the presence of pneumatic bones in sauropods affect our estimates of how much they weighed?

Before attempting to answer these questions, it will be necessary to examine pneumatic bones in living animals. It is often said that "The present is the key to the past." In this case, we can use evidence from animals that are alive today to figure out how animals lived in the past.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York City, USA; **BYU**, Earth Sciences Museum, Brigham Young University, Provo, USA; **CM**, Carnegie Museum, Pittsburgh, USA; **OMNH**, Oklahoma Museum of Natural History, Norman, USA; **YPM**, Yale Peabody Museum, New Haven, USA.

PNEUMATIC BONES IN LIVING ANIMALS

Birds and dinosaurs are not the only animals with pneumaticity (Figure 3). In fact, everyone who reads this paper has some air-filled bones. They are in the front and sides of your head, and we call them **sinuses**. Sinuses are a useful example because they help us understand a strange phenomenon: pneumatic bones.

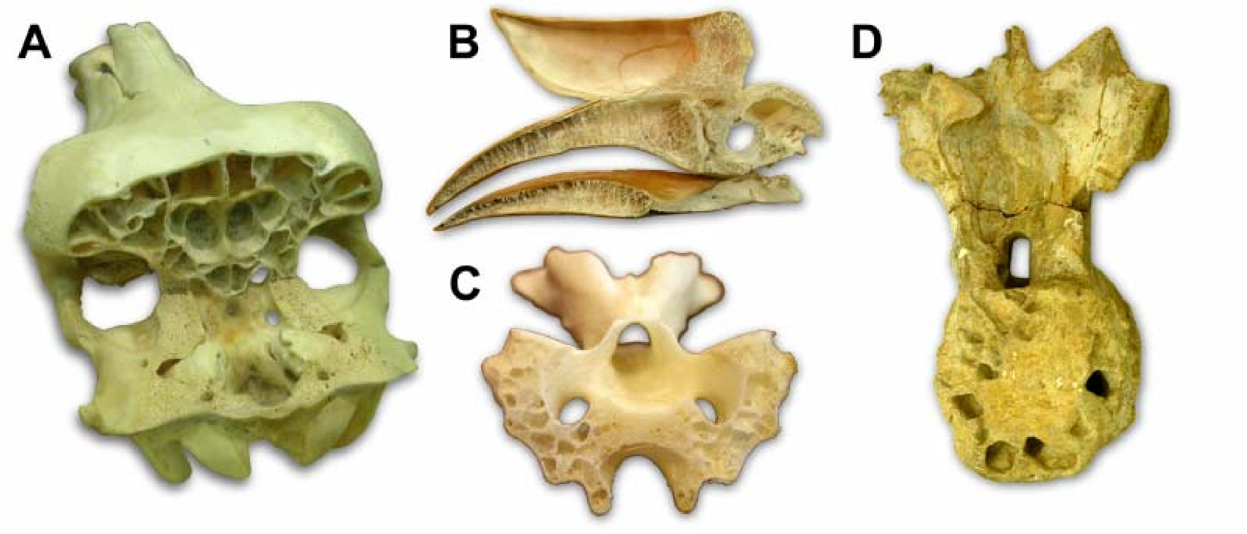

Figure 3. These specimens illustrate the diversity of pneumatic bones. **A**, the skull of a cow with most of the braincase removed. The brain is protected by a honeycomb of pneumatic spaces that develop from the nasal passages. **B**, the skull of a hornbill, a type of bird. Almost all of the bones of the skull are pneumatic. This very lightweight construction is typical of birds. **C**, a vertebra of a turkey. The front of the vertebra has been worn down with sandpaper to reveal the pneumatic chambers inside. It is easy to do this at home with leftover bones from the kitchen. **D**, a vertebra of *Apatosaurus*, OMNH 1312. Like the turkey vertebra shown in C, the front of this vertebra has been worn away by wind and water to reveal the internal chambers. Although this vertebra is many times bigger than the turkey vertebra—53 cm tall, compared to 1.5 cm tall—the internal structure is very similar.

How does the air get into the bones? In all cases that we know of, including both humans and animals, bones can only become filled with air if they are somehow connected to the respiratory system, whether it is the airways in the head, the windpipe or **trachea**, or the lungs themselves. Humans and other mammals have two kinds of pneumaticity. The first kind is **paranasal pneumaticity**, in which some of the bones of the skull can become filled with air because they are connected to the nasal passages. The sinuses in your cheeks and forehead are an example of paranasal pneumaticity. The second kind is **paratympanic pneumaticity**, in which some of the bones at the bottom and sides of the skull can become filled with air because they are connected to the air-filled spaces in the ears. In humans, paratympanic pneumaticity is usually only present in the temporal bone on the side of the skull. If you press against the side of your head behind your ear, you will feel a small bump of bone, about the same size and shape as your thumb. This bump is part of the temporal bone, and it is connected to the air-filled spaces of your middle ear. In other mammals, the base of the skull is often pneumatic, but this happens only rarely in humans.

The pneumatic bones in your head are connected to your nasal airways or to your ears—but connected by what? These connections are made and maintained by **diverticula**, which are pouches of **epithelium** (tissue that lines your internal surfaces) that grow out into the surrounding bones. For example, when you were a baby, pouches of epithelial tissue in your nose pushed up into the bones of your forehead. The spaces enlarged as you grew up, and today they form your frontal sinuses. But those sinuses are still lined with epithelium that is much like the inner lining of your nose, and the sinuses are still connected to your nasal passages, as you may discover when you have a cold. The air-filled pouches of epithelium that fill your sinuses are called pneumatic diverticula. The growth of the diverticula into the bones produces the pneumatic cavities, or holes in the bone, that house the diverticula.

Paranasal and paraympanic pneumaticity are both examples of cranial pneumaticity, or pneumaticity in the bones of the skull. Cranial pneumaticity is found in mammals and also in **archosaurs**, the “ruling reptiles” (Witmer, 1997, 1999). The only groups of archosaurs that are alive today are crocodilians and birds, but there are many extinct groups—including sauropods (Figure 4). In all of these cases, the diverticula that **pneumatize** (bring air into) the bones of the skull develop from the nasal passages or the air-filled spaces in the middle ear.

Other parts of the respiratory system may produce diverticula as well. Diverticula of the upper airways and trachea are present in at least some species from most groups of **tetrapods** (animals with four legs or whose ancestors had four legs, including snakes). Examples include throat sacs in frogs (Duellman and Trueb, 1986), the inflatable hoods of cobras and other snakes (Young, 1991, 1992), and a variety of inflatable sacs and pouches in birds (King, 1966; McClelland, 1989a) and primates (Janensch, 1947). Most of these diverticula are used to inflate special structures that alter the animal’s call, or make a visual display, or both. However, these diverticula do not invade the skeleton except in one case. The hyoid bone, a small arch of bone in the throat that supports some of the muscles of the neck and tongue, is pneumatized by a diverticulum of the trachea in the howler monkey, *Alouatta* (Janensch, 1947). In some birds, diverticula of the paranasal and paratympanic air spaces grow out of the skull and pass down the neck, either under the skin or between the bodies of the neck muscles (King, 1966). These diverticula do not invade any bones. In extremely rare cases in humans, diverticula from the skull can grow into the first vertebra of the neck (Sadler *et al*., 1996). This can only happen if the first vertebrae has already fused to the skull, so all of these cases are **pathologies** (unhealthy variations). Among living animals, only birds have extensive pneumatization of the **postcranial**

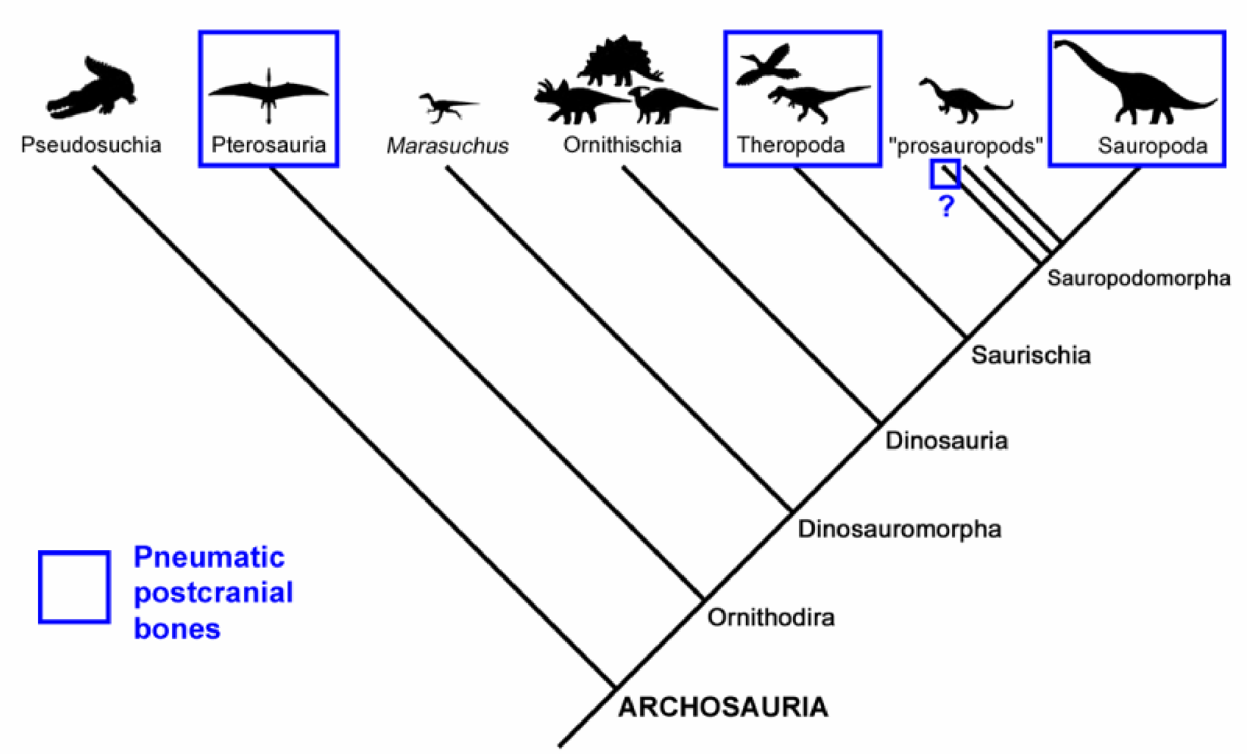

Figure 4. The evolutionary relationships of the archosaurs, or “ruling reptiles”. The only surviving branches of this group are crocodilians (members of Pseudosuchia) and birds (members of Theropoda). Pneumatic postcranial bones are found in pterosaurs, sauropods, and theropods (including birds). “Prosauropods” are a group of sauropod relatives whose relationships are not well understood. There is some evidence for pneumaticity in “prosauropods”, but it was not obvious or widespread as in the other groups. Postcranial pneumaticity may have evolved once, in Ornithodira (the group that includes pterosaurs and dinosaurs), and been lost in Ornithischia. Alternatively, it may have evolved independently several times.

skeleton (the rest of the skeleton other than the skull).

The lungs of birds are very different from our lungs. In fact, they are unique in the animal kingdom (Figure 5). The lungs themselves are small and not very flexible, but they are attached to a system of large **air sacs** in the **thorax** and **abdomen** (King, 1966; Duncker, 1971; McClelland, 1989b). These air sacs are empty—in other words, they contain no tissue except a thin lining of epithelium. Like us, birds breathe by movements of muscles and bones, but instead of expanding and compressing the lungs as we do, the breathing movements of birds expand and compress the air sacs, and the air sacs blow air through the lung. The air sacs are connected in such a way that birds get fresh air blown through their lungs when they inhale, and then again when they exhale (fresh air is stored in some of the air sacs between inhalation and exhalation). This constant flow of fresh air through the lungs means that birds can pull much more oxygen out of the air than mammals can, and that allows birds to perform feats that are impossible for most mammals, such as flying at an altitude of 9 kilometers where the air is very thin. By comparison, human climbers on high mountains usually need bottled oxygen once they get higher than 7 kilometers above sea level.

In addition to providing large amounts of oxygen, the air sacs give rise to a network of diverticula (Figure 6). These diverticula may spread throughout the body: in between the internal organs, between the bodies of the muscles, and even under the skin (Richardson, 1939; King, 1966; Duncker, 1971). If one of these diverticula comes into contact with a bone, it may press into the bone in the same way that the diverticula of your nasal cavities pressed into the bones of your forehead when you were young. But how, exactly, does this happen?

One of the best descriptions of the process of pneumatization was published by Bremer (1940), on the **humerus** (upper arm bone) of the chicken (*Gallus*). When the diverticulum comes

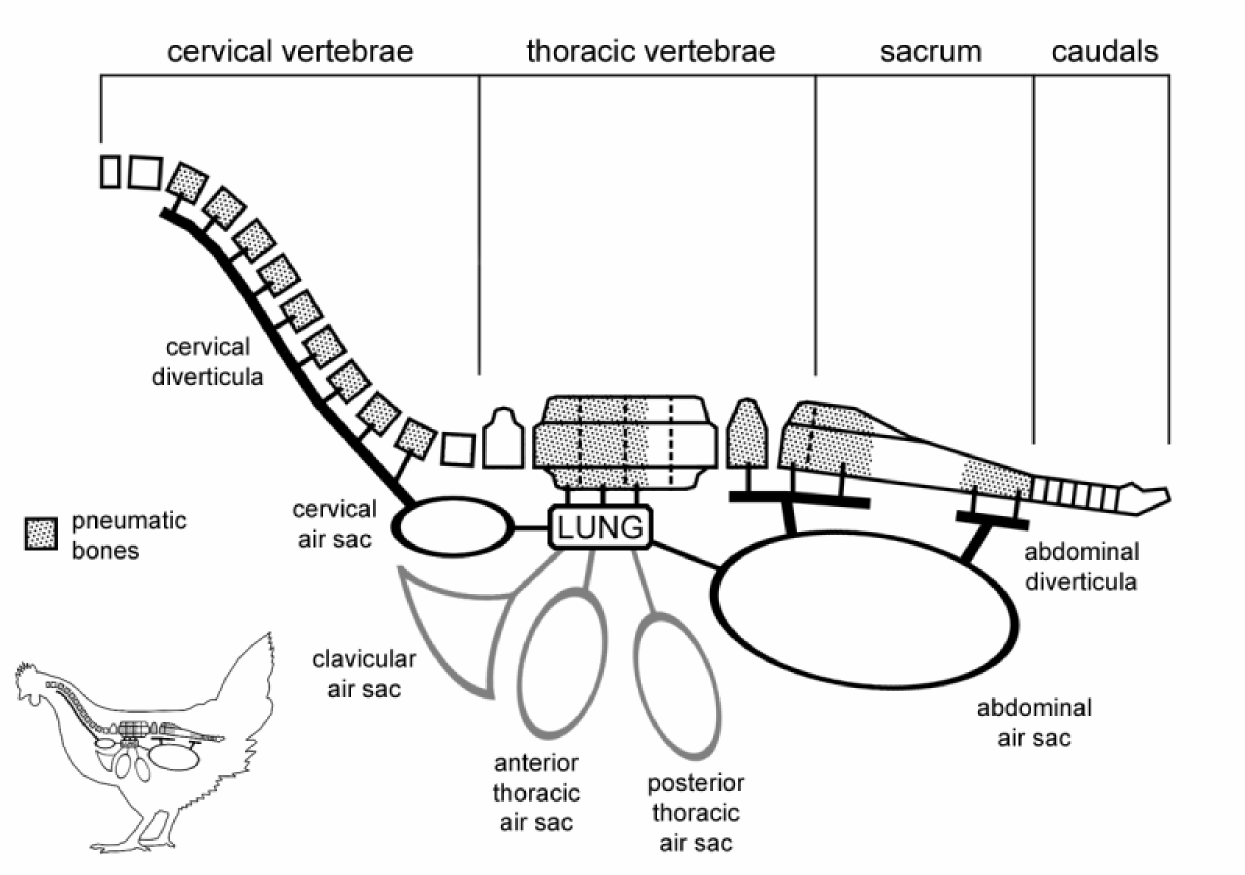

Figure 5. The lungs and air sacs of the chicken and their relationship to the vertebral column. In addition to blowing air through the lungs during breathing, the air sacs also send out diverticula which pneumatize much of the skeleton (only the pneumatic vertebrae are shown here). The lungs themselves send diverticula into the vertebrae next to them. Because diverticula can develop from so many sources, almost the entire postcranial skeleton can become pneumatized.

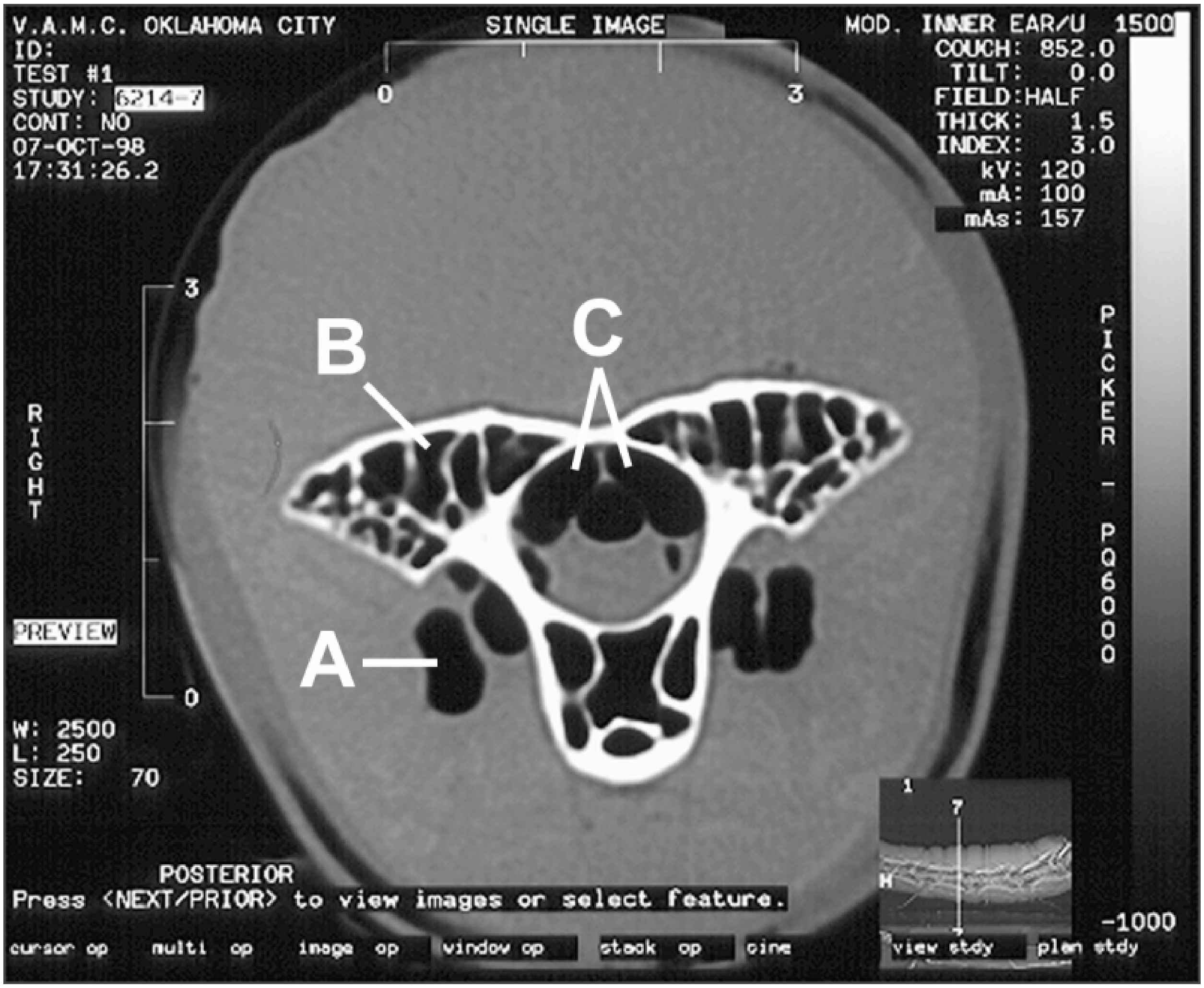

Figure 6. A CT cross-section of an ostrich neck. In this view, bone is white, muscles and other soft tissues are gray, and air spaces are black. **A**, diverticula of the cervical air sac that grow alongside the bones of the neck (compare to Figure 5). **B**, air spaces inside the bone that result from pneumatization. **C**, other diverticula actually grow into the neural canal and lie on top of the spinal cord.

into contact with the bone, special cells called **osteoclasts** start to break down the bone ahead of the diverticulum. As the bone breaks down, it is replaced with softer tissue which degenerates or is absorbed into the body, and the diverticulum expands to fill the newly-created space. As the diverticulum “drills” through the outside of the bone, it produces a hole, or pneumatic **foramen**. Once the diverticulum penetrates into the space inside the bone, the bone **marrow** is also absorbed and the diverticulum spreads until it fills most or all of the internal volume of the bone. The bony struts inside the bone become smaller and less numerous, and the inner layers of the outer wall of the bone are absorbed. When pneumatization is complete, the bone may still look essentially the same on the outside (except that there will be a pneumatic foramen present somewhere). But the internal structure of the bone is very different. The bony struts are reduced, the chambers are larger, the walls are thinner, and the entire bone is lighter than it was before (Figure 7).

If a bone is pneumatic, the air has to get into the bone through a diverticulum, and the diverticulum has to get into the bone through a hole. So almost all pneumatic bones have one or more large holes on the outside, which are the pneumatic foramina. Human medical histories and experiments on birds have shown that these pneumatic foramina must remain open for a pneumatic bone to develop properly and be maintained. If the foramen is closed—for example, by a disease or injury—the air space inside the bone will eventually be replaced by new bone growth (Ojala, 1957). So, in general pneumatic bones can be easily recognized by the presence of large foramina. There is only one exception to this rule. If a bone is in contact with another bone that is pneumatic—for example, two skull bones that come together at a joint or suture—the diverticulum from the pneumatic bone can sometimes cross the suture to invade another bone. A bone that is pneumatized in this fashion may not have a large, obvious foramen on the

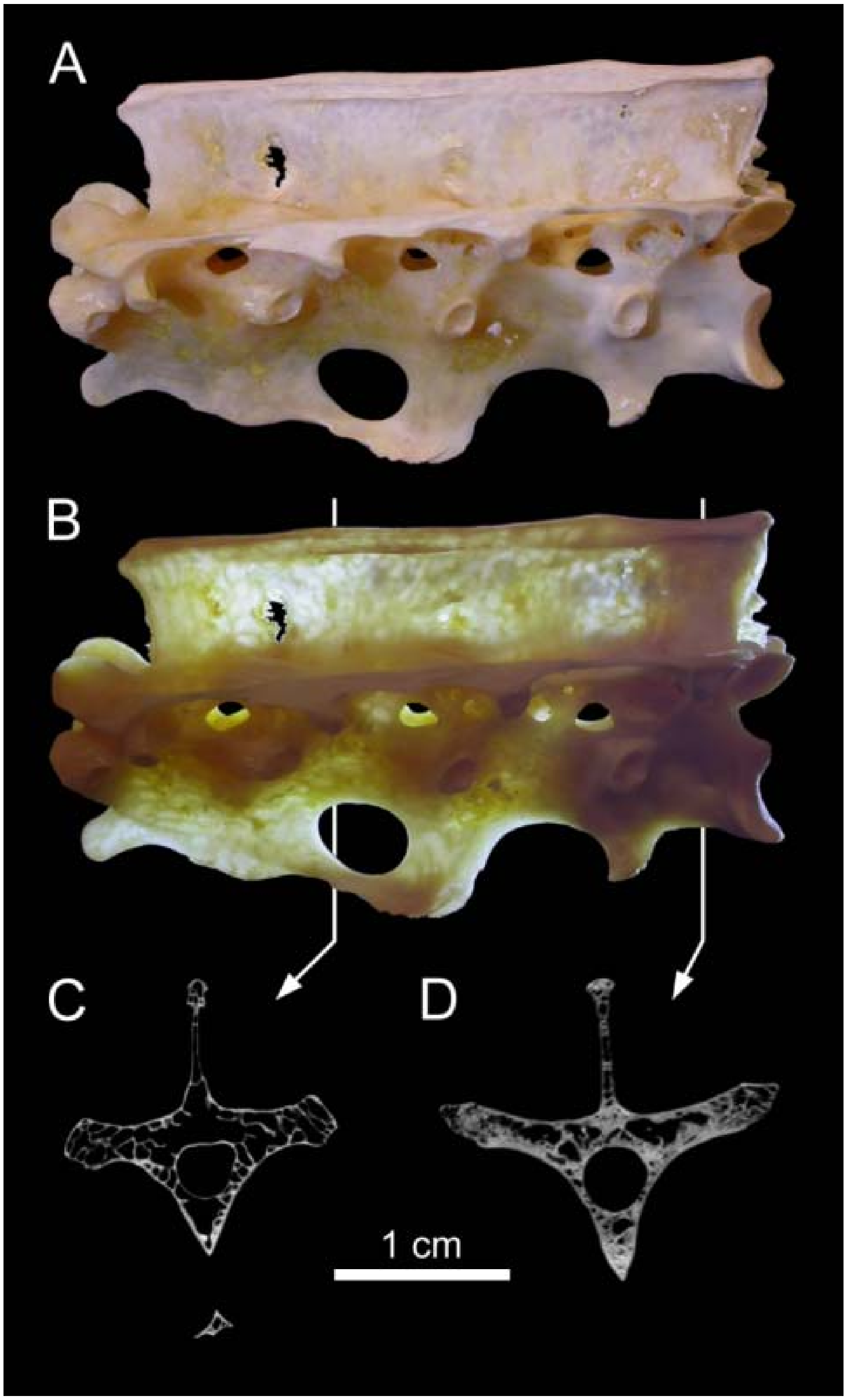

Figure 7. A block of fused dorsal vertebrae from a chicken (compare to Figure 5). This block contains four vertebrae. The three on the left have been pneumatized, but the fourth has not. **A**, the vertebrae under normal light. **B**, shining a light through the vertebrae from behind reveals the light construction of the first three compared to the dense construction of the fourth. **C**, a CT section through one of the pneumatized vertebrae shows its thin walls, large chambers, and small internal struts. **D**, a CT section through the apneumatic vertebra shows thicker walls, smaller chambers, and larger internal struts. The fused block of vertebrae is 4 cm long.

outside. This second kind of pneumatization was recognized by Witmer (1990), who called it **extramural pneumatization**. This is in contrast to the typical development, in which a diverticulum invades a bone directly and produces a pneumatic foramen, which is called **intramural pneumatization**. Extramural (bone to bone) pneumatization happens in the skulls of mammals and birds, and it can also happen in the postcranial skeleton, for example, between fused vertebrae in the chicken (King, 1957; Hogg, 1984a; see Figure 7).

WHAT EVIDENCE DO WE USE TO INFER PNEUMATICITY IN FOSSILS?

How do we recognize skeletal pneumaticity? Compared to **apneumatic** bones—that is, normal, marrow-filled bones—pneumatic bones are lighter, thinner-walled, and have larger spaces and fewer supporting struts inside. They also have pneumatic foramina, except in a few cases of extramural pneumatization. These changes make it possible to deduce that bone was pneumatic even if the diverticula have rotted away and the air spaces are filled with soil or rock, as is the case with fossils. But diverticula may also leave more subtle traces on the bones that they contact, including **fossae** (shallow depressions), tracks or grooves on the surface of the bone, and differences in the surface texture of the bone tissue. All of these traces are potential evidence of pneumaticity.

However, many other soft tissues interact with bones, including muscles, blood vessels, nerves, cartilage, and fat deposits. Like diverticula, all of these tissues can influence the morphology and appearance of adjacent bones. If we are trying to determine whether a fossilized bone was pneumatic or not, it may not be enough to show that it has foramina and fossae. We also need a set of criteria to distinguish the traces of pneumatic diverticula from the traces left by other soft tissues.

Several authors, including Hunter (1774) and Müller (1907), list differences between pneumatic and apneumatic bones. These authors focused on recognizing pneumaticity in the bones of living birds. Their lists include characteristics that are not usually preserved in fossils, such as vascularity (number of blood vessels), fat content, and color. The most comprehensive list of pneumatic features in fossil bones was provided by Britt (1993, 1997). He listed five features: internal chambers connected to foramina, fossae with crenulate (wrinkled) texture, smooth or crenulate tracks (grooves), bones with thin outer walls, and large foramina. I discuss each of these in turn.

Internal Chambers With Foramina

The most obvious characteristic of pneumaticity is the presence of foramina that lead to large internal chambers. Large chambers are present in the **presacral vertebrae** (the vertebrae of the neck and trunk) of most sauropods. They may also be present in the **sacral vertebrae** (which connect to the pelvis) and **caudal vertebrae** (or tail vertebrae), as in *Apatosaurus* and *Diplodocus* (Figure 8). In birds, such chambers are always produced by pneumatic diverticula (Britt, 1993). The presence of similar chambers in the bones of sauropods, **theropods**, and **pterosaurs** has been accepted by most authors as unequivocal evidence of pneumaticity (Seeley, 1870; Cope, 1877; Marsh, 1877; Janensch, 1947; Romer, 1966; Britt, 1993, 1997; O'Connor, 2002). There is simply no alternative explanation, because no other process other than pneumatization produces large foramina that lead to internal chambers. As Janensch (1947: 10, translated from the German by G. Maier) said, "There is no basis to consider the [pneumatic] cavities in sauropod vertebrae as different from similar structures in the vertebrae of birds" (Figure 9).

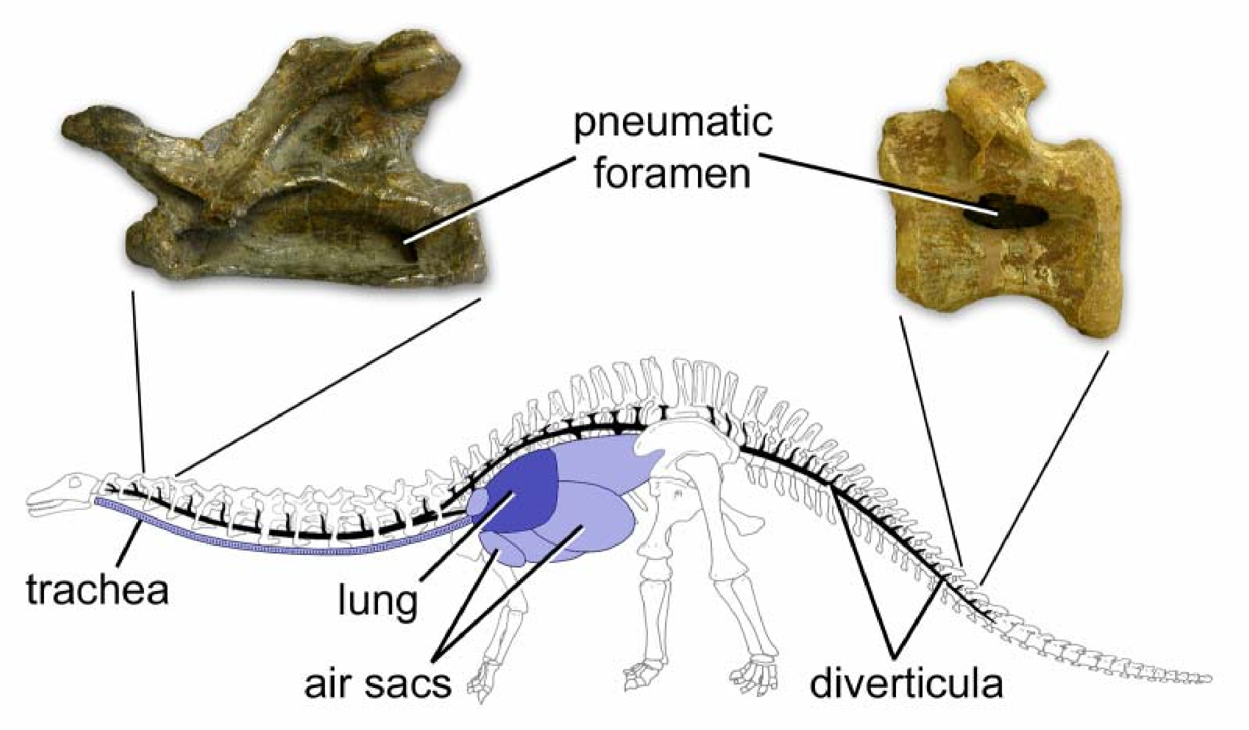

Figure 8. Hypothetical reconstruction of the respiratory system of a diplodocid sauropod. The left forelimb, shoulder, and ribs have been removed for clarity. The lung is shown in dark blue, air sacs are light blue, and pneumatic diverticula are black. The length of the diverticula is shown by the presence of pneumatic features on all of the vertebrae from the front of the neck to the middle of the tail. The rest of the respiratory system has been restored based on that of birds. The skeleton is redrawn from Norman (1985: 83). The cervical vertebra is AMNH 7535, and the caudal vertebra is OMNH 2055.

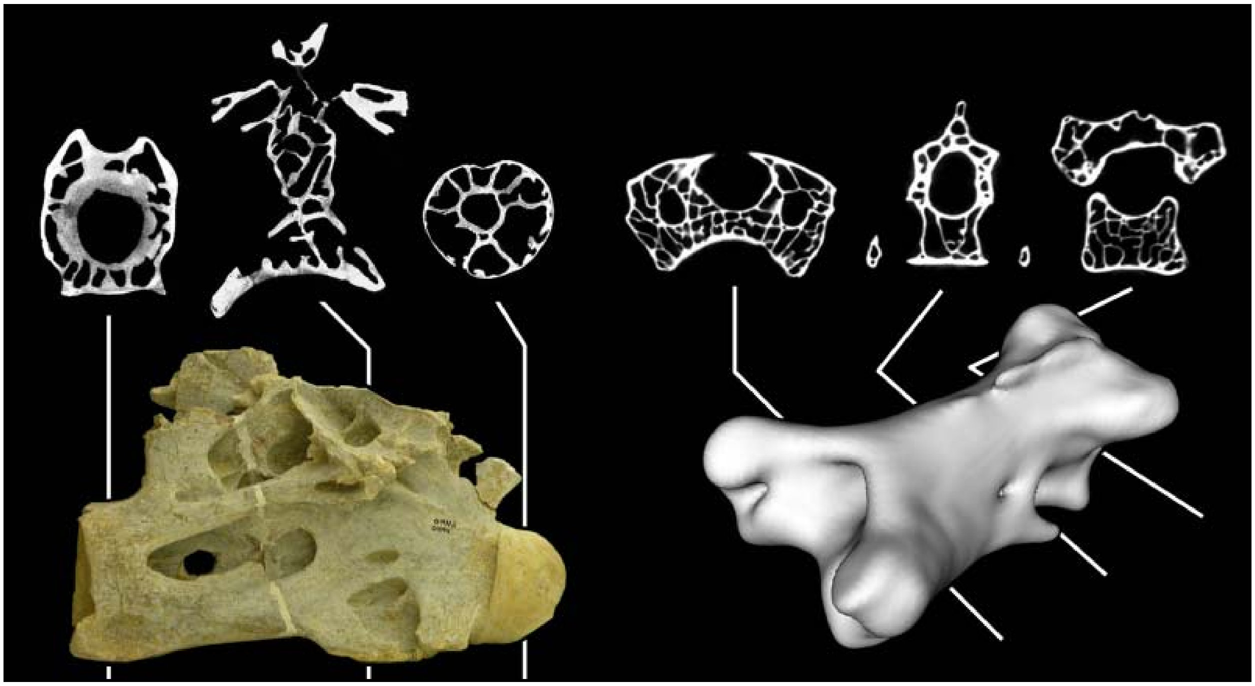

Figure 9. CT slices through cervical vertebrae of *Apatosaurus* (left) and a swan (right) show that although the two animals are very different in size, the construction of their vertebrae is very similar. The *Apatosaurus* vertebra is OMNH 1094, and it is 51 cm long. The swan vertebra is 2.5 cm long (1/20 as large).

One of the main differences between the pneumatic vertebrae of different sauropod **taxa** (species or groups of species) is the subdivision of the internal chambers (Figure 10). In some taxa, such as *Camarasaurus*, the vertebrae have only a few large chambers, whereas in others, such as *Saltasaurus*, the vertebrae have many small chambers (Figure 2). Vertebrae with many small chambers have been described as ‘complex’ (Britt, 1993; Wedel, 2003b), in contrast to ‘simple’ vertebrae with few chambers. The idea of ‘biological complexity’ has several potential meanings (McShea, 1996). In this paper, complexity only means the level of internal subdivision of pneumatic bones; complex bones have more chambers than simple ones.

Extramural Pneumatization— The only obvious opportunities for extramural pneumatization in the postcranial skeletons of sauropods are between fused sacral and caudal vertebrae and between the sacral vertebrae and the **ilium** (one of the bones of the pelvis). Sacral vertebrae of baby sauropods have deep fossae (Wedel *et al*., 2000: fig. 14), and, at least in *Apatosaurus*, internal chambers are present before the sacral vertebrae fuse together in development (Ostrom and McIntosh, 1966: plate 30). The blocks of fused caudal vertebrae in *Diplodocus* often include vertebrae with large pneumatic foramina (Gilmore, 1932: fig. 3). It is possible that fused vertebrae that lack foramina could be pneumatized by adjacent pneumatic vertebrae, but this has not been demonstrated.

Sanz *et al*. (1999) reported that ‘**cancellous** tissue’ is present in the presacral vertebrae, ribs, and ilium of the titanosaurs *Epachthosaurus* and *Saltasaurus*. The presacral vertebrae of *Saltasaurus* are pneumatic and have **camellate** internal structure (Figure 2), and pneumatic ribs are known in several titanosaurs (Wilson and Sereno, 1998). Further, **spongiosa** (as defined by Francillon-Vieillot *et al*., 1990), or marrow-spaces, are present in the unpneumatized vertebrae of many—possibly all—sauropods (see the section on mass estimates below), so cancellous bone is

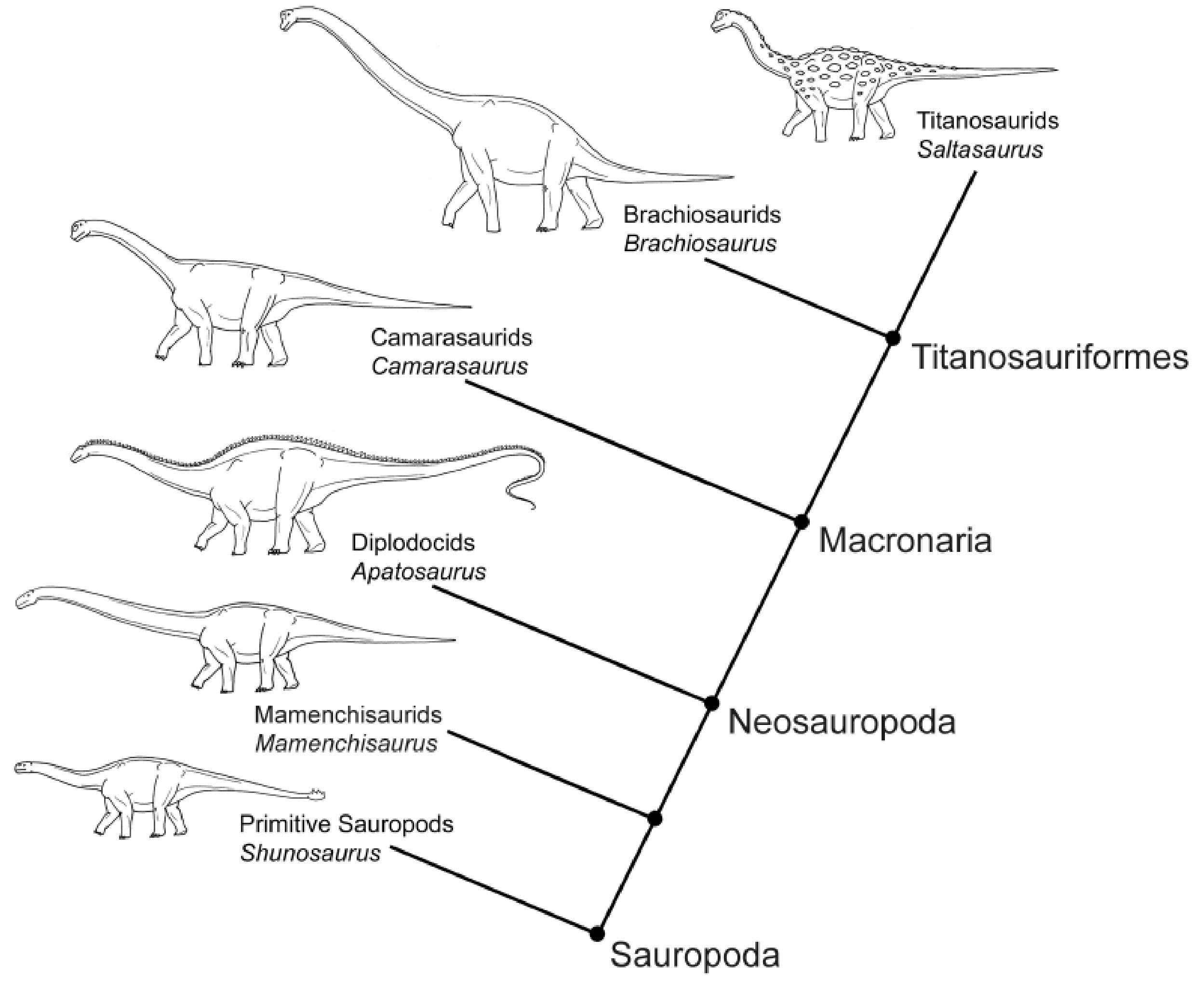

Figure 10. A simplified evolutionary tree of sauropods. In the most primitive sauropods the evidence for pneumaticity is equivocal, but pneumaticity is well-developed in the mamenchisaurids and in all the members of Neosauropoda. Complex internal structures are present in the vertebrae of at least some mamenchisaurids, diplodocids, brachiosaurids, and titanosaurids, but the evolution of this character is still not well understood. This tree is highly simplified; please see Wilson (2002) and Upchurch *et al*. (2004) for more details.

not limited to titanosaurs. For these reasons, it seems that the 'cancellous tissue' of Sanz *et al*. (1999) is pneumatic bone with many small chambers. If so, then the ilia of some titanosaurs may have been pneumatic. If so, the ilium may have been pneumatized by diverticula of air sacs in the abdomen, or by extramural pneumatization from the sacral vertebrae. However, the possibility of ilial pneumatization must remain speculative until better evidence for it is presented.

Neural Cavities— In many sauropods, the **neural spines** of the **dorsal vertebrae** contain large chambers. These chambers are connected to the outside by way of large foramina on the sides of the **neural arches**. Upchurch and Martin (2003) called such chambers "**neural cavities**" and discussed their appearance in *Cetiosaurus*, *Barapasaurus*, and *Patagosaurus* (Figures 1 and 2). In some dorsal vertebrae of *Barapasaurus*, the **neural canal** (the tube of bone through which the **spinal cord** passes) is open at the top and shares a connection with the neural cavity (Jain *et al*., 1979). Upchurch and Martin (2003) mentioned that similar cavities are present in some more advanced sauropods, and Bonaparte (1986: fig. 19.7) illustrated neural cavities in Camarasaurus and Diplodocus. Jain *et al*. (1979) and Upchurch and Martin (2003) also described a second form of neural cavity which is divided into two halves by a **median septum** (a thin, vertical plate of bone) and does not share a connection with the neural canal. Neural cavities are thought to be pneumatic for the same reason as the more familiar cavities in the centra of the vertebrae: they are large internal chambers connected to the outside through large foramina (Britt, 1993).

Pneumatic Ribs— The ribs of some sauropods have large foramina that lead to internal chambers. The best known examples of pneumatic ribs in sauropods are in *Brachiosaurus* (Riggs, 1904; Janensch, 1950). Pneumatic ribs are also present in *Euhelopus* and some titanosaurs (Wilson and Sereno, 1998). Gilmore (1936) described a foramen that leads to an internal cavity in a rib of *Apatosaurus*, and pneumatic ribs have also been reported in the diplodocid *Supersaurus* (Lovelace *et al*., 2003). Pneumatic ribs have not been found in *Haplocanthosaurus*, *Camarasaurus*, or any basal diplodocoids. The character evidently evolved independently in diplodocids and titanosauriforms. along with other pneumatic characters, including complex vertebral chambers and pneumatic caudal vertebrae (see below).

Fossae and Laminae

Pneumatic Fossae— Fossae are present in the vertebrae of most sauropods (Figure 11), and these fossae are often the only evidence of pneumaticity. For example, the vertebrae of *Barapasaurus* have shallow fossae on the centra and neural spines, but they lack the large internal chambers typical of later sauropods (Figure 2). Are these fossae pneumatic? The simple assumption that all fossae are pneumatic is naïve; as discussed above, other soft tissues can also produce fossae on the surfaces of bones. On the other hand, to deny that any fossae are pneumatic unless they contain foramina that lead to large internal chambers is equally false. We need criteria to distinguish pneumatic fossae from non-pneumatic fossae.

The best case for a pneumatic fossa is a fossa that contains pneumatic foramina within its boundaries. The *Brachiosaurus* vertebra shown in Figure 12 has large foramina in most of the fossae on the lateral sides of the centrum and neural spine (see also Janensch, 1950, and Wilson, 1999). Similar foramina-within-fossae are present in the vertebrae of many other sauropods, including *Diplodocus* (Hatcher, 1901: plates 3 and 7), *Tendaguria* (Bonaparte *et al*., 2000: fig. 17 and plate 8), and *Sauroposeidon* (Wedel *et al*., 2000: fig. 8b). The inference that these fossae are pneumatic relies on the presence of obviously pneumatic features within the fossae. The

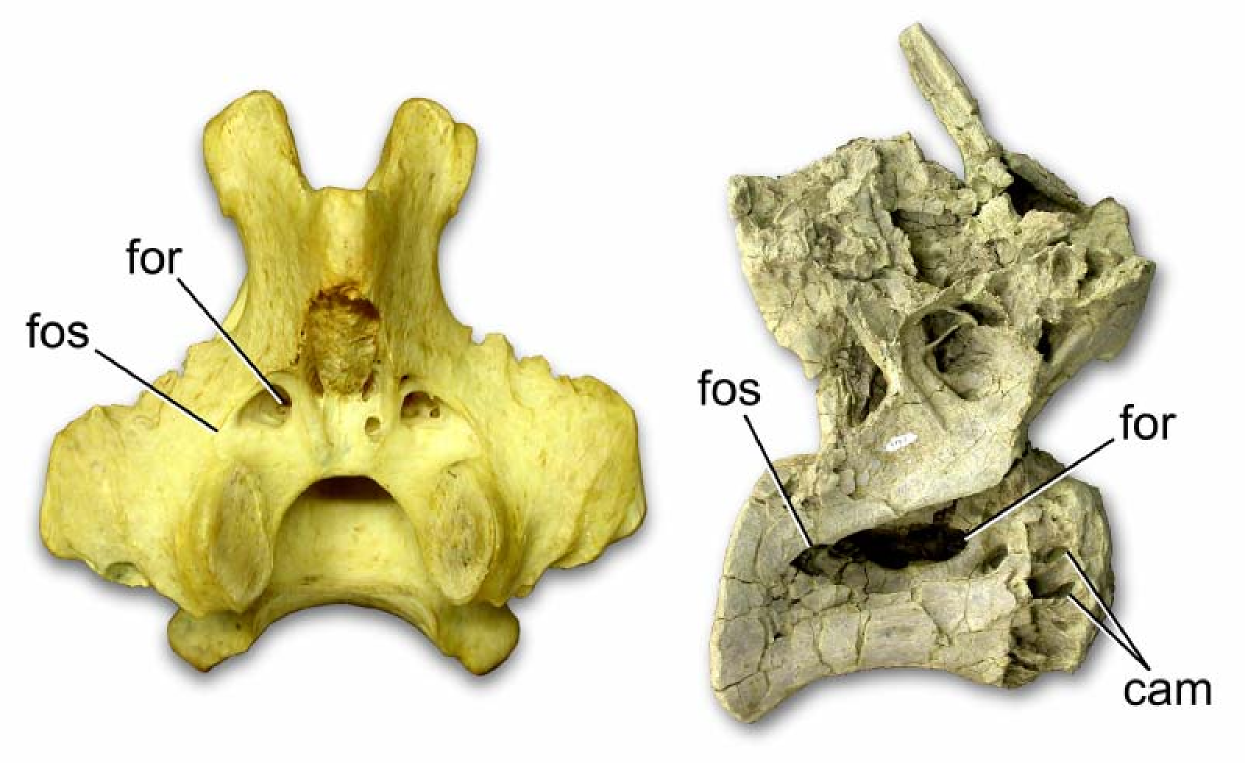

Figure 11. Pneumatic fossae and foramina in dorsal vertebrae of an emu (a large flightless bird) and an undescribed sauropod from Montana. In both cases, the foramen sits inside a larger depression or fossa. The front of the sauropod vertebra is worn away, and some of the small internal chambers or camellae can be seen. The sauropod vertebra is YPM 5147, and it is 49 cm tall. The emu vertebra is 7.5 cm wide. **Abbreviations:** for, foramen; fos, fossa; cam, camellae.

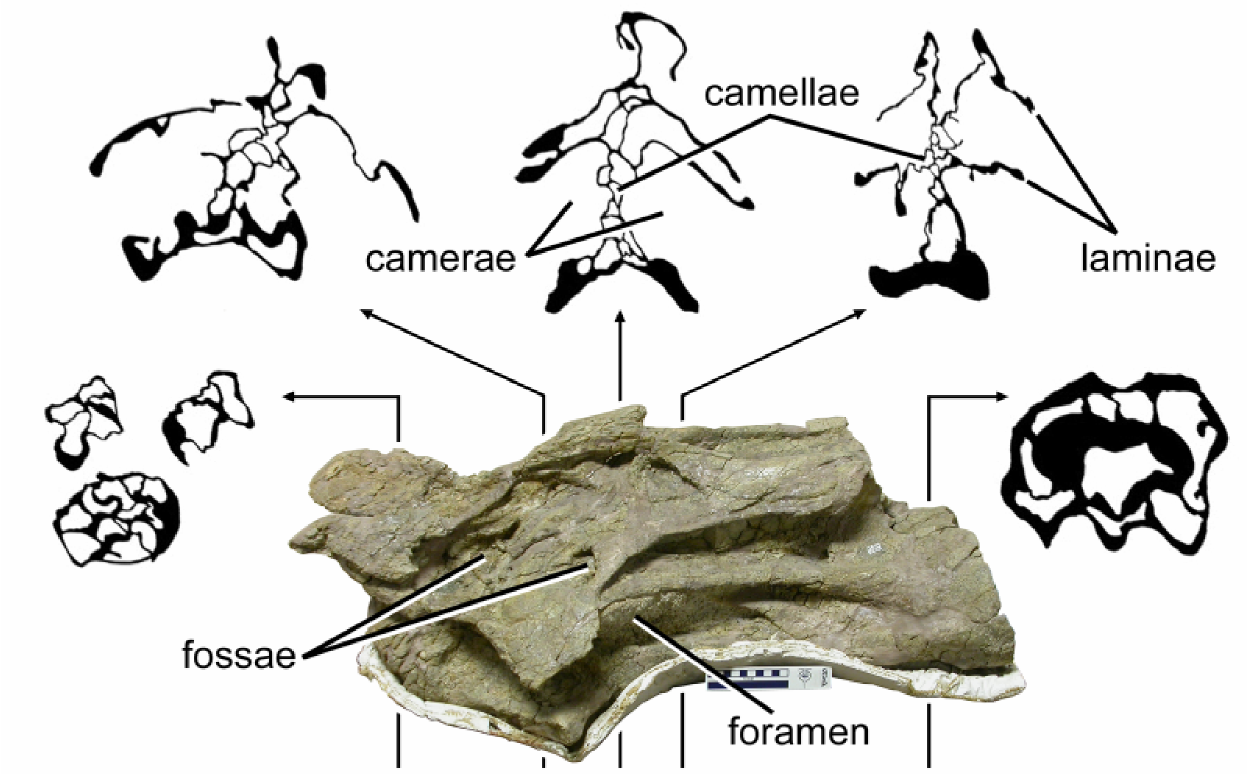

Figure 12. CT sections through a cervical vertebra of *Brachiosaurus*, BYU 12866. The volume of air in the neural arch and spine is unknown, but it may have equaled or exceeded the volume of air in the centrum. The vertebra is 82 cm long.

inference of pneumaticity is less supported in the case of “blind” (or dead end) fossae that contain no foramina, such as the large fossae on the centra of the dorsal vertebrae in *Barapasaurus* (Figure 2).

Wilson (1999) proposed that ‘subfossae,’ or fossae-within-fossae, are also evidence of pneumaticity. This hypothesis is supported by the complex morphology of some pneumatic diverticula in birds. In the ostrich, the large diverticula that lay alongside the cervical vertebrae consist of bundles of smaller diverticula (Figure 6). If a bundle of diverticula comes into contact with a bone, the entire bundle might produce a large fossa, and within that large fossae each smaller diverticulum in the bundle might produce a subfossa. This hypothesis can and should be tested in future computed tomography (CT) studies.

Britt (1993) proposed that crenulate (or finely wrinkled) texture of the external bone is evidence that some fossae are pneumatic. In the vertebrae of *Sauroposeidon* the difference in texture between the pneumatic fossae and the adjacent bone is striking, and this allows the boundaries of the fossae to be precisely determined (Wedel *et al*., 2000: fig. 7). However, there is little doubt that the fossae of *Sauroposeidon* are pneumatic, because they contain pneumatic foramina. The inference that a blind fossa is pneumatic based only on its texture is not as well supported. Blind fossae can also contain muscles or **adipose** (fatty) tissue (O’Connor, 2006). No one knows yet if these three kinds of fossae can be distinguished on the basis of bone texture. Until this is tested, bone texture by itself should not be used as evidence of pneumaticity. One way to test One possibility would be to compare thin slices of bone from each kind of fossa—pneumatic, muscular, and adipose—and see if there are differences at the microscopic level. No one has performed this study yet, and there are many opportunities for further research.

To determine if a fossa is pneumatic or not, it is worthwhile to look at other pneumatic features on or in the same bone. Consider the fossa on the side of the neural spine in a vertebra of *Haplocanthosaurus* (Figure 13). This fossa does not contain any pneumatic foramina or subfossae and the bone texture is smooth rather than wrinkled. In other words, nothing about the fossa itself shows that it was pneumatic (as opposed to containing fat or other soft tissues). However, the centrum of the same vertebra contains deep, sharp-lipped cavities that are clearly pneumatic. The presence of these cavities shows that the vertebra was in contact with pneumatic diverticula. Because we already know that pneumatic diverticula reached this vertebra, it seems safe to infer that the fossa on the neural spine is also pneumatic. At least, the inference of pneumaticity is better supported than it would be based on the neural spine fossa alone.

It is tempting to assume that the fossae of basal sauropods are pneumatic because later sauropods have pneumatic cavities in the same places. For example, in *Brachiosaurus* the fossa on the side of the neural spine is clearly pneumatic because it contains pneumatic foramina (Figure 12). Does this mean that the same fossa in *Barapasaurus* is also pneumatic? The answer seems to be that the fossae may be in the same places, but that does not mean that they were produced by the same developmental processes. The shallow fossae of basal sauropods may have contained deposits of fat such as those identified in birds by O'Connor (2006). It is possible that fat deposits were replaced by pneumatic diverticula later in sauropod evolution. In that case, the position of the fossae would have remained the same, but the tissue that filled the fossae would have changed.

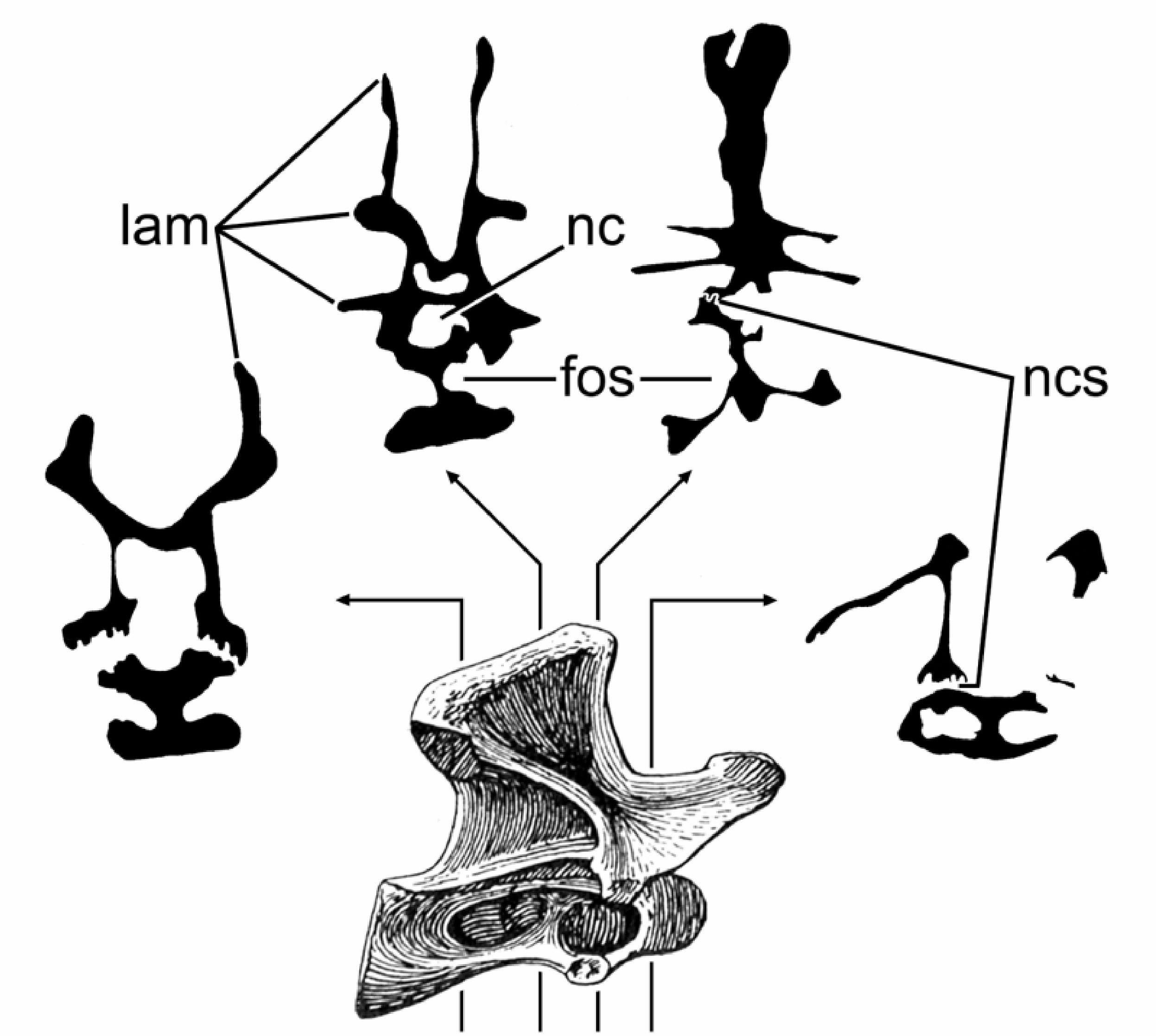

Figure 13. CT sections through a cervical vertebra of *Haplocanthosaurus*, CM 879-7. This animal was not fully grown when it died, and the neural spine of this vertebra is not completely fused with the centrum. If the animal had lived, the neural spine and centrum would have fused along the neurocentral suture. The vertebra is 22 cm long. Modified from Hatcher (1903: pl. 2). **Abbreviations:** fos, fossae; lam, laminae; nc, neural canal; ncs, neurocentral sutures.

Other Characteristics of Pneumaticity

Pneumatic tracks, thin outer walls, and large foramina are not likely to be falsely interpreted as pneumatic features in sauropods. External tracks are only rarely identified in sauropods. Wedel *et al*. (2000: fig. 7) illustrated a pneumatic track in *Sauroposeidon*, but the inference of pneumaticity was not based on the track by itself. Rather, the track was identified as pneumatic because it is connected to a deep pneumatic chamber. Many sauropod vertebrae have thin outer walls, especially those of the aforementioned *Sauroposeidon* (Figure 14). However, the thin outer walls of sauropod vertebrae always contain large internal chambers that are clearly pneumatic, so, again, the inference of pneumaticity does not rest on the questionable feature. Finally, there is the question of foramina that are not pneumatic. Bone is living tissue and bones must have many small holes for the passage of blood vessels and nerves. Britt *et al*. (1998) proposed that pneumatic foramina could be distinguished from blood vessel and nerve foramina on the basis of relative size. Pneumatic foramina are typically much larger. The two kinds of foramina could also be distinguished based on the internal structure of the vertebrae. Pneumatic vertebrae typically lack spongiosa (Bremer, 1940; Schepelmann, 1990). Instead, their outer walls and inner chambers are composed of **compact bone** (Reid, 1996). The presence of spongiosa inside a vertebra is evidence that it is either apneumatic, or at least incompletely pneumatized (King, 1957). Distinguishing pneumatic foramina from blood vessel and nerve foramina is a potential problem in studies of birds and other small theropods, but most sauropods are simply so large that the different kinds of foramina are not likely to be confused. Even baby sauropods tend to have large pneumatic fossae rather than small foramina (see Wedel *et al*., 2000: fig. 14).

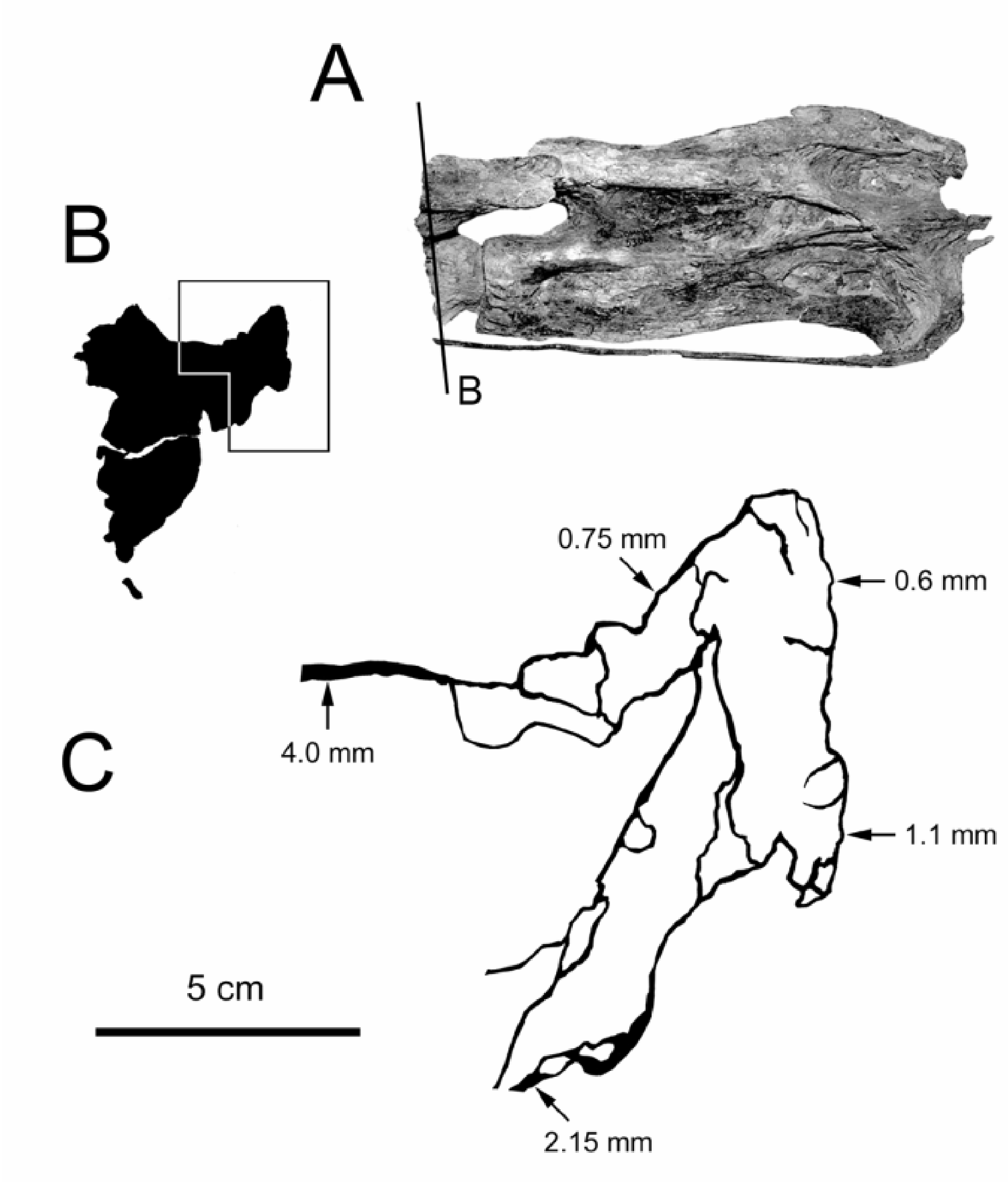

Figure 14. Internal structure of a cervical vertebra of *Sauroposeidon*, OMNH 53062. **A**, parts of two vertebrae from the middle of the neck. The field crew that dug up the bones cut though one of them to divide the specimen into manageable pieces. **B**, cross section of C6 at the level of the break, traced from a CT image and photographs of the broken end. The left side of the specimen was facing up in the field and the bone on that side is badly weathered. Over most of the broken surface the internal structure is covered by plaster or too damaged to trace, but it is cleanly exposed on the upper right side (outlined). **C**, the internal structure of that part of the vertebra, traced from a photograph. The arrows indicate the thickness of the bone at several points, as measured with a pair of digital calipers. The camellae are filled with sandstone.

DESCRIPTION OF PNEUMATIC BONES

At least four aspects of pneumatic bones can be described: traces of pneumaticity on the outside of the bones (discussed above); the complexity of the internal chambers; the ratio of bone to air space within a bone; and the distribution of pneumatic bones in the body.

Internal Complexity of Pneumatic Bones

Longman (1933) recognized two broad types of sauropod vertebrae: those with a few large chambers and those with many small chambers. However, he limited his comments to the structure of the bones, and did not discuss pneumatization or any other mechanism that might explain how the chambers were formed. Britt (1993, 1997) independently made the same observation. He called the large chambers "**camerae**" (literally, cavities) and the small chambers "**camellae**" (literally, small cavities). Vertebrae with large chambers are described as "**camerate**" and those with small chambers are described as "camellate". Wedel *et al*. (2000) and Wedel (2003b) discussed the evolution of different internal structure types. In general, the vertebrae of primitive sauropods such as *Shunosaurus* and *Barapasaurus* have fossae but lack internal chambers. Camerae are present in the vertebrae of diplodocids and *Camarasaurus*. *Brachiosaurus* has a combination of both camerae and camellae. The vertebrae of *Sauroposeidon* and most titanosaurs lack camerae and are entirely filled with camellae, although some titanosaurs may have camerae. From published descriptions (Young and Zhao, 1972; Russell and Zheng, 1994), the vertebrae of *Mamenchisaurus* appear to be camellate.

With all of this information available, it might seem that the internal structures of sauropod vertebrae and their evolutionary history are well understood. In fact, the internal structure of the vertebrae is only known for a small minority of sauropods. Even in those taxa for which the internal structure is known, this knowledge is usually limited to a handful of vertebrae or even a single vertebra. This limited information makes it very hard to separate meaningful differences from the variation that is found in most traits in most living things. But in spite of these limitations, three broad generalizations can be made. First, the vertebrae of very young sauropods tend to have a simple I-beam shape in cross section, with large lateral fossae separated by a median septum (Wedel, 2003b). This is true even for taxa which have highly subdivided vertebrae as adults, such as *Apatosaurus*. In these taxa the internal complexity of the vertebrae increased during development. The second generalization is that complex internal structures evolved several times, in *Mamenchisaurus*, diplodocids, and one or more times in Titanosauriformes (Wedel, 2003b). This suggests a general evolutionary trend toward increasing complexity of vertebral internal structure in sauropods. Finally, the largest and longest necked sauropods, such as *Mamenchisaurus*, the diplodocines, brachiosaurids, *Euhelopus*, and giant titanosaurs, all have complex internal structures. The presence of complex internal structures in the vertebrae of the largest and longest necked sauropods suggests that size, neck length, and internal structure are related (Figure 15).

Volume of Air Within a Pneumatic Bone

The aspect of pneumaticity that has received the least attention until now is the ratio of bone tissue to empty space inside a pneumatic bone. Although many authors have noted the weight-saving design of sauropod vertebrae (Osborn, 1899; Hatcher, 1901; Gilmore, 1925), no one has estimated just how much mass was saved. The savings in mass could have important implications for the study of sauropods.

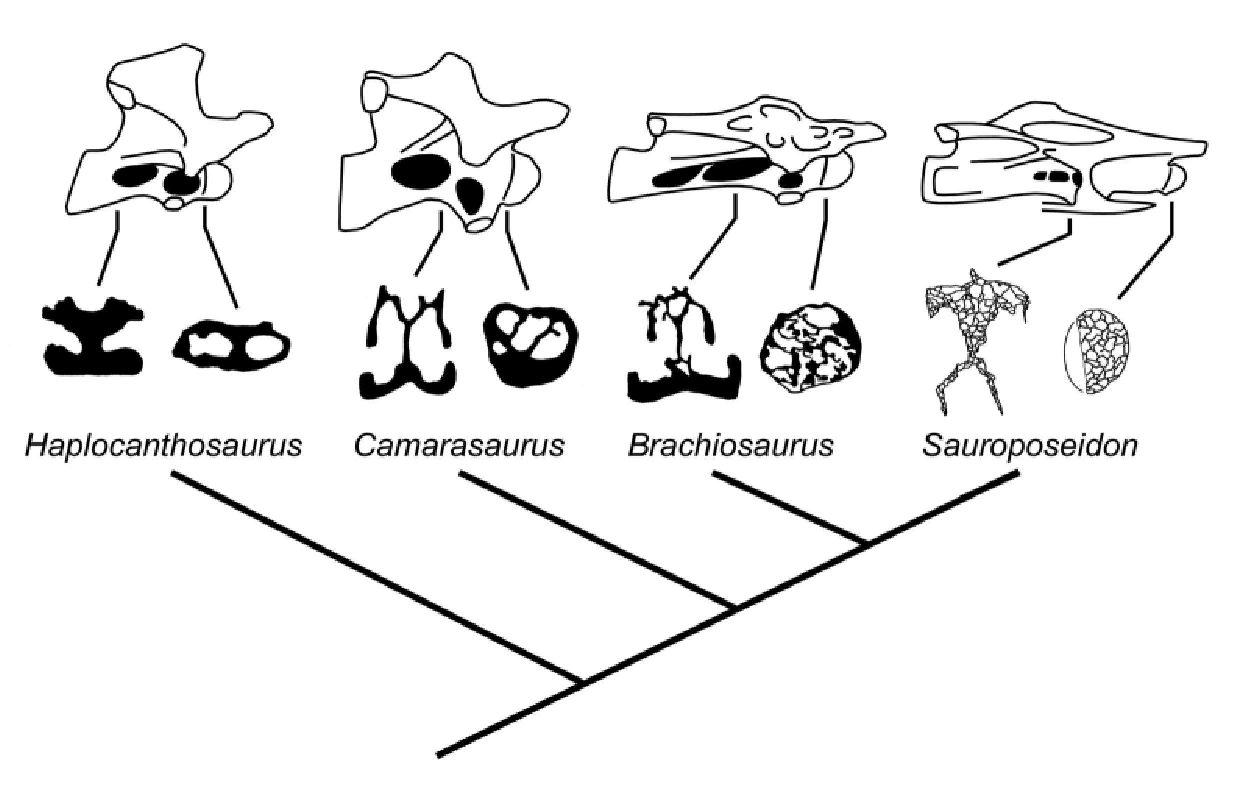

Figure 15. Evolution of neck vertebrae in the lineage leading to *Sauroposeidon*. In general, sauropods with longer necks have longer vertebrae and more complex internal structures. The evolution of very long necks in sauropods—up to 9 meters in *Brachiosaurus* and 11.5 meters in *Sauroposeidon*—was probably aided by the mass reduction produced by pneumatization.

Currey and Alexander (1985) and Cubo and Casinos (2000) reported data on the construction of the limb bones of birds, which are tubular and may be filled with marrow or air. In both studies, the variable of interest was *K*, the inner diameter of the bone divided by its outer diameter. A bone with very thick walls will have a low value of *K*, and a bone with thin walls will have a high value of *K*, but *K* is always a number between zero and one. (If *K* was zero, the bone would have no internal diameter—in other words, it would be solid. If *K* was greater than one, the inside diameter would be larger than the outside diameter, which is impossible.) Both studies found average values of *K* between 0.77 and 0.80 for pneumatic bones. The average for marrow-filled bird bones is 0.65 (Cubo and Casinos, 2000), and the average for land mammals is 0.53 (calculated from Currey and Alexander, 1985: table 1).

The *K* value can only be calculated for tubular bones; it is meaningless when applied to bones with more complex shapes or internal structures, such as sauropod vertebrae. I propose the Air Space Proportion (ASP), or the proportion of the volume of a bone (or the area of a bone cross section) that is occupied by air spaces, as a variable that can be calculated for both tubular and non-tubular bones. One problem is that measuring the volumes of objects is difficult and often imprecise. It is usually easier to measure the relevant surface areas of a cross section. This method is not perfect, because any one cross section probably will not accurately represent the entire bone. Nevertheless, it may be easier to take the average of several cross sections as an approximation of the volume than to directly measure the volume, especially in the case of large, fragile sauropod vertebrae.

For the bird bones described above, measurements were only taken on a single cross section located at middle of the shaft of the bone. Therefore, the ASP values I am about to discuss may not be representative of the entire bones, but they are probably at least close to the volumes (total volume and air volume) of the bone shafts. For tubular bones, ASP may be found by taking the square of K. If r is the inner diameter and R the outer, then K is r/R, ASP is $\pi r^2/\pi R^2$ or simply r^2/R^2, and ASP=K^2. For the K of pneumatic bones, Currey and Alexander (1985) report lower and upper bounds of 0.69 and 0.86, and I calculate an average of 0.80 from the data presented in their table 1. If these values of K are converted to ASP, as described above, the resulting lower and upper bounds are 0.48 and 0.74, with an average of 0.64. Using a larger sample size, Cubo and Casinos (2000) found a slightly lower average K of 0.77 which gives an ASP of 0.59. The average ASP values of 0.59 (based on Cubo and Casinos, 2000) and 0.64 (based on Currey and Alexander, 1985) imply that, on average, the shafts of pneumatic limb bones in birds are 59-64% air by volume.

How do these numbers compare with the ASPs of sauropod vertebrae? To find out, I measured the area of bone and the total area for several cross-sections of sauropod vertebrae (Figure 16). The cross sections are taken from **CT** scans, published papers, and photographs of broken or cut vertebrae. I used Image J to analyze the images; Image J is a free program available online from the National Institutes of Health (Rasband, 2003). The results are presented in Table 1. The results are tentative: I have only analyzed a few vertebrae from a handful of taxa, and only one or a few cross sections are available for each bone, so the results may not be representative of either the vertebrae, the regions of the vertebral column, or the taxa to which they belong. The sample includes mostly cervical vertebrae simply because cervical vertebrae are long and low and therefore they fit through CT scanners better than dorsal or sacral vertebrae. In spite of these limitations, it is possible to make some tentative conclusions.

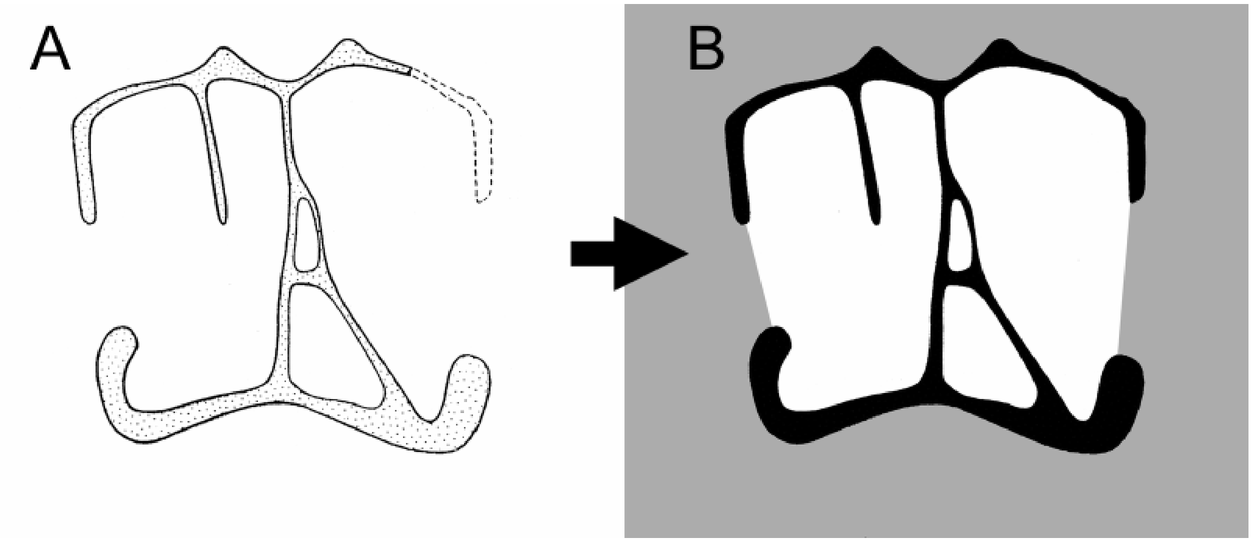

Figure 16. How to determine the air space proportion (ASP) of a bone section. **A**, a section is traced from a photograph, CT image, or published illustration; in this case, a transverse section of a *Tornieria africana* cervical vertebra from Janensch (1947: fig. 3). **B**, imaging software is used to fill the bone, air space, and background with different colors. The number of pixels of each color can then be counted using Image J (or any program with a pixel count function) and used to compute the ASP. In this case, bone is black and air is white, so the ASP is (white pixels) / (black pixels + white pixels).

Table 1. The air space proportion (ASP) of transverse sections through vertebrae of sauropods and other saurischians. Only values for published sections are presented. Much more work will be required to determine norms for different taxa and different regions of the vertebral column, and the values presented here may not be representative of either. Nevertheless, these values suggest that pneumatic sauropod vertebrae were often 50-60% air by volume.

Taxon	Region	ASP	Source
Apatosaurus	Cervical condyle	0.69	Wedel (2003b: fig. 6b)
	Cervical mid-centrum	0.52	Wedel (2003b: fig. 6c)
	Cervical cotyle	0.32	Wedel (2003b: fig. 6d)
Barosaurus	Cervical mid-centrum	0.56	Janensch (1947: fig. 8)
	Cervical, near cotyle	0.77	Janensch (1947: fig. 3)
	Caudal mid-centrum	0.47	Janensch (1947: fig. 9)
Brachiosaurus	Cervical condyle	0.73	Janensch (1950: fig. 70)
	Cervical mid-centrum	0.67	Wedel *et al*. (2000: fig. 12c)
	Cervical cotyle	0.39	Wedel *et al*. (2000: fig. 12d)
	Dorsal mid-centrum	0.59	Janensch (1947: fig. 2)
Camarasaurus	Cervical condyle	0.49	Wedel (2003b: fig. 9b)
	Cervical mid-centrum	0.52	Wedel (2003b: fig. 9c)
	Cervical, near cotyle	0.50	Wedel (2003b: fig. 9d)
	Dorsal mid-centrum	0.63	Ostrom & MacIntosh (1966: pl. 23)
	Dorsal mid-centrum	0.58	Ostrom & MacIntosh (1966: pl. 24)
	Dorsal mid-centrum	0.71	Ostrom & MacIntosh (1966: pl. 25)
Pleurocoelus	Cervical mid-centrum	0.55	Lull (1911: pl. 15)
Phuwiangosaurus	Cervical mid-centrum	0.55	Martin (1994: fig. 2)
Saltasaurus	Dorsal mid-centrum	0.55	Powell (1992: fig. 16)
Sauroposeidon	Cervical prezyg. ramus	0.89	Figure 4
	Cervical mid-centrum	0.74	Wedel *et al*. (2000: fig. 12g)
	Cervical postzygapophysis	0.75	Wedel *et al*. (2000: fig. 12h)
Theropoda	Cervical prezygapophysis	0.48	Janensch (1947: fig. 16)
	Dorsal mid-centrum	0.50	Janensch (1947: fig. 15)
Mean of sauropod measurements (13.17/22)		0.60	

First, the ASP values range from 0.32 to 0.89, with an average of 0.60. Therefore it seems that most sauropod vertebrae contained at least 50% air by volume, and probably a little more. This assumes that the cavities in sauropod vertebrae were entirely filled with air and that the amount of soft tissue was negligible. Chandra Pal and Bharadwaj (1971) found that the air spaces in pneumatic bird bones are lined by a very thin layer of simple epithelial tissue, so the assumption is probably valid. The ASP values found here for sauropod vertebrae are similar to the range and average found for pneumatic limb bones of birds. In other words, despite being much larger the pneumatic vertebrae of sauropods were as lightly built as the pneumatic bones of birds!

Second, even from this limited data it is clear that ASP can vary widely from slice to slice within a single vertebra and probably also between vertebrae of different regions of the skeleton, and between individuals of the same species. As we collect more data we may find more predictable relationships. On the other hand, the system may have so much variation that such relationships will not be found. Most pneumatic systems (for example, sinuses) have very high levels of variation (e.g., King, 1957; Cranford *et al*., 1996; Weiglein, 1999), and it would be surprising if ASP were not also highly variable.

Third, the lowest values of ASP—0.32 in *Apatosaurus* and 0.39 in *Brachiosaurus*—are for slices through the **cotyle**, or bony cup, at the back end of the centrum. Here the walls of the vertebrae are doubled back on themselves to form the cup, and the wall of the cotyle itself is at an angle to the slice so it looks thicker in cross section. The cotyle is surrounded by pneumatic chambers in both *Apatosaurus* and *Brachiosaurus*, but these become smaller and eventually disappear toward the end of the vertebra. For these reasons, the cotyle will naturally have a lower ASP than the rest of the vertebra.

Fourth, *Sauroposeidon* has the highest values of ASP, up to a remarkable 0.89. The values for *Sauroposeidon* are even higher than those for the closely related *Brachiosaurus*. The very high ASP of *Sauroposeidon* probably evolved to help lighten its extremely long (~12 meter) neck.

Finally, ASP appears to be unrelated to the internal complexity of the vertebrae. The *Saltasaurus* vertebra is the most highly subdivided of the sample. The I-beam-like vertebrae of the juvenile *Pleurocoelus* and *Phuwiangosaurus* are the least subdivided; the other examples fall somewhere in the middle. Nevertheless, most values in the table, including those for *Saltasaurus*, *Pleurocoelus*, and *Phuwiangosaurus*, fall between 0.50 and 0.60. The averages for all taxa other than *Sauroposeidon* also fall within the same range, so ASP does not seem to be related to internal complexity.

These results are preliminary, and much work remains to be done. We need more data from living animals for comparison. Also, the importance of pneumaticity for sauropod **biomechanics** is only starting to be explored.

Distribution of Pneumaticity Along the Vertebral Column

The two previous sections dealt with the characteristics of a single pneumatic bone. We must also consider the location of pneumatic features in the skeleton. As discussed above, if a pneumatic cavity is to develop and persist, it must maintain a constant connection to the respiratory system by way of the diverticula. That means that if we find a pneumatic vertebra halfway down the tail of a sauropod, we know the diverticula must have extended at least that far. The diverticula themselves do not fossilize, but their traces on the skeleton do, and we can use those traces to learn about how widespread the diverticula were in a particular animal. For example, in *Diplodocus* pneumatic foramina are present on every vertebra between the second vertebrae of the neck and the nineteenth vertebra of the tail (Gilmore, 1932, and personal observations). This means that in life the pneumatic diverticula reached at least as far forward as the second cervical vertebra and at least as far back as the nineteenth caudal vertebra (Figure 8). Possibly the diverticula were even more widespread and but failed to pneumatize any more bones, but they could not have been any less widespread.

In general, more advanced sauropods tended to pneumatize more of the vertebral column. Except for the first cervical vertebra, which is always apneumatic, pneumatic chambers (or at least large fossae) are present in the cervical vertebrae of *Shunosaurus*; in the cervical vertebrae and some of the dorsal vertebrae of *Jobaria*; in all of the presacral vertebrae of *Cetiosaurus*; in the presacral and sacral vertebrae of most neosauropods; and in the presacral, sacral, and caudal vertebrae of diplodocids and saltasaurids (Figure 17). This progression of vertebral pneumaticity toward the back of the animal also occurred in the evolution of theropod dinosaurs (Britt, 1993), and it occurs during the development of living birds (Cover, 1953; Hogg, 1984b). The similarity of these patterns is another line of evidence that sauropods had lungs and air sacs like those of birds.

A PALEOBIOLOGICAL PROBLEM: MASS ESTIMATES

The implications of pneumaticity for sauropod **paleobiology**—the study of the lives of fossil organisms—are only beginning to be explored. In particular, pneumaticity may be an important factor in future studies of the biomechanics and **physiology** of sauropods. The most obvious implication of pneumaticity is that sauropods may have weighed less than is commonly thought. The problem of estimating the masses of sauropods is addressed in this section.

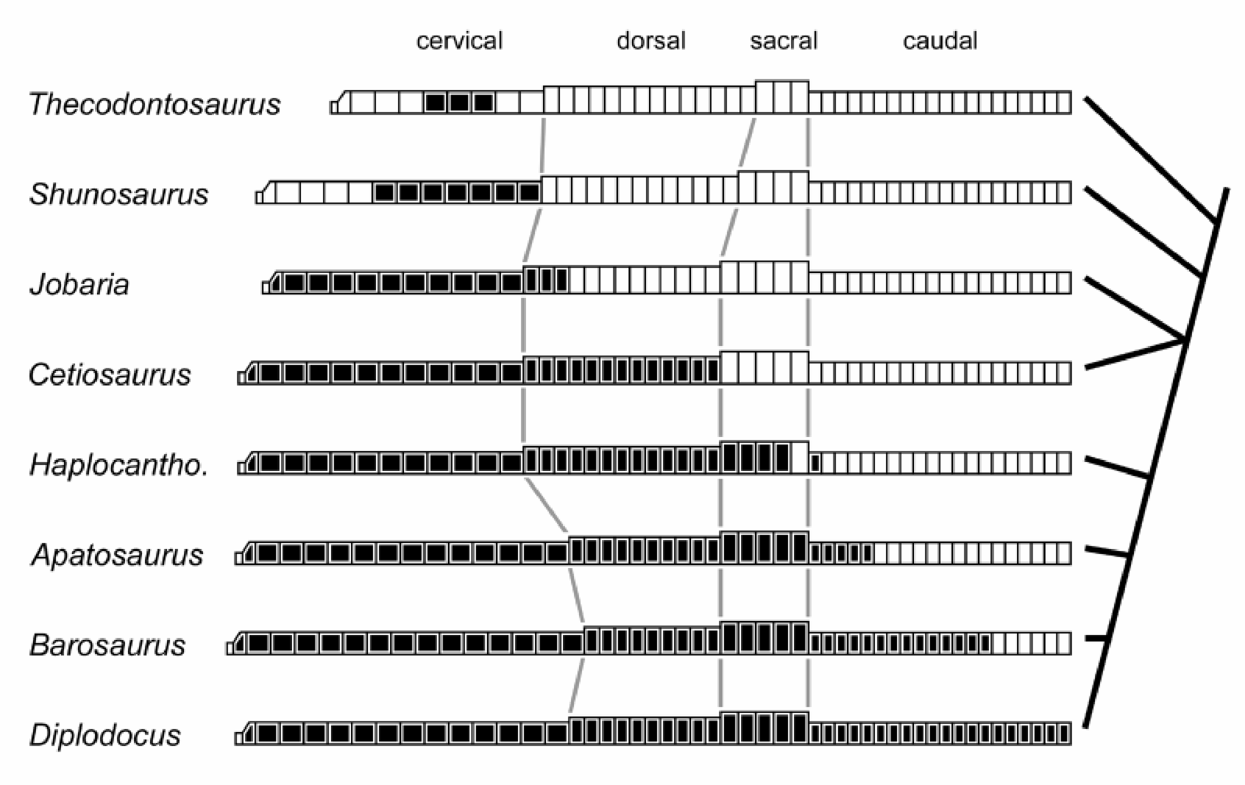

Figure 17. A diagram showing the distribution of pneumatic features (black boxes) along the vertebral column in sauropods. Only the evolutionary line leading to diplodocids is shown here. The same extension of pneumatic features down the spine also occurred independently in macronarian sauropods and several times in theropods, and it happens today during the development of birds.

The observation that most sauropod skeletons were highly pneumatic raises two separate questions. The first is about the methods we use to study sauropods: how can we take pneumaticity into account in estimating the masses of sauropods? The second is a paleobiological question about the animals themselves: if pneumaticity made sauropods significantly lighter, how does that affect our understanding of sauropods as living animals? If pneumaticity did not make sauropods significantly lighter, then the second question is moot, so we should first consider the question about methods.

Methods

Mass is one of the most important characteristics of living things, because so many other variables depend on mass. How fast did an animal grow? How fast could it move? How much did it need to eat? How much oxygen did it need? How many offspring could it produce? All of these paleobiological questions require that we know something about the mass of the animals in question.

The masses of dinosaurs are estimated using two different methods. The first method is limb bone **allometry**. Large animals are not simply scaled up versions of smaller animals. The bones of large animals have to be proportionally thicker to safely support their bodies. Rabbits have long, thin leg bones. The leg bones of horses are much thicker, proportionally, even though horses are still fast-moving animals. And the leg bones of rhinoceroses and elephants are very thick compared to their lengths, even though these large animals are capable of moving rapidly. When large numbers of species of different sizes are studies, it is found that the proportional thickness of the limb bones increases as the animals increase in mass. Once the average relationship between mass and limb bone proportions has been found, that relationship can be used to estimate the mass of an animal based only on the thickness of its limb bones (Russell *et al*., 1980; Anderson *et al*., 1985).

One problem with these methods is that different groups of animals have different relationships between mass and limb bone thickness. An equation that works for mammals will not work on birds, for example. This problem is very serious for groups that are entirely extinct, such as sauropods, because there are no living members that can be used to develop the method in the first place! Another problem with this method is that it is not very precise. Animals with the same limb bone proportions may vary in mass by a factor of two or more. It is not very satisfactory to learn that *Apatosaurus* might have weighed anywhere from 15 to 30 tons; we could have figured that much out without using limb bone allometry.

If limb bone allometry is used to estimate mass, then there is no need to account for pneumaticity. The animal’s limb bones were as thick as they needed to be to support the animal’s mass, regardless of how the body was constituted (with air spaces or without). If an animal with a pneumatic skeleton was lighter than it would have been otherwise, this should already be reflected in the form of its limb bones, and no correction is necessary.

The other method of estimating the masses of dinosaurs and other extinct animals is the **volumetric** method (Colbert, 1962; Paul, 1988, 1997; Henderson, 1999). This method requires four steps. First, a scale model of the animal is constructed. The model may be a physical object made of clay or plastic, or it may be a 3D digital model constructed inside a computer program. In either case, it is important that the model be as accurate as possible. Second, the volume of the scale model is measured. This can be done by volumetric displacement, in which the model is placed in a container of water or a sandbox and the amount of water or sand that it displaces is measured. The volume can also be measured mathematically, by slicing the model (usually a 3D computer model) into many thin slices, measuring the volume of each slice by itself, and then adding the results for all of the slices. A simple version of this, called graphic double integration, only requires accurate photographs or drawings of the model and it can be performed quickly by one person using a ruler and a calculator (see Hurlburt 1999 and Murry and Vickers-Rich 2004 for instructions).

Next, the volume of the model is multiplied by the scale factor to obtain the volume of the organism in life. For example, *Brachiosaurus* was 5.6 meters tall at the shoulder. If the model of *Brachiosaurus* used in the study is 14 cm tall at the shoulder, the scale factor is 560 ÷ 14 = 40. In other words, a live *Brachiosaurus* would be 40 times taller than the model. It would also be 40 times longer and 40 times wider. Because we are scaling up a volume, which exists in all three dimensions of space, we must multiply the volume of the model by the scale factor three times (once for each dimension). So although the live *Brachiosaurus* would be 40 times larger than the model in any one dimension, such as height, its volume was 64,000 times greater (40 x 40 x 40). A model *Brachiosaurus* with a shoulder height of 14 cm might have a volume of 0.5 liters, which would imply that a live *Brachiosaurus* would have a volume of 32,000 liters.

Finally, the volume of the organism is multiplied by the estimated density to obtain its mass. The density of water is 1 kilogram per liter, and the density of living tissue is very close to that of water, so if we did not take any other factors into account, the *Brachiosaurus* in the example above would have an estimated mass of 32,000 kilograms, or 32 metric tons.

However, there are other factors to take into account. The lungs of animals are filled with air and have a much lower density than the rest of the body, so the density of most animals is somewhat less than 1 kilogram per liter. And in the case of sauropods, the air in the diverticula and the spaces inside the skeleton should also be considered. If these additional air spaces are not accounted for, the resulting mass estimates could be too high.

The presence of air in the respiratory system and pneumatic diverticula can be accounted for in the first step, by reducing the volume of the model, or in the last step, by adjusting the density used in the mass calculation. Both methods have been used in previous mass estimates of dinosaurs. Alexander (1989) used plastic models in his volumetric study, and he drilled holes to represent the lungs. Henderson (1999) included lung spaces in digital models that he used estimating mass, and he included air sacs and diverticula in a later study on the **buoyancy** of swimming sauropods (Henderson, 2004). Paul (1988, 1997) used the alternative method of adjusting the density values for the mass calculations. He assigned the trunk a density of 0.9 kg/L to account for lungs and air sacs, and in the neck he used a density of 0.6 kg/L to account for pneumatization of the vertebrae.

Before attempting to estimate the volume of air in a sauropod, it is important to recognize that the air was distributed among four separate regions: (1) the trachea, (2) the ‘core’ respiratory system of lungs and air sacs, (3) the diverticula that lay outside the skeleton (i.e., among the viscera and muscles and under the skin), and (4) the pneumatic bones. These divisions are important for two reasons. First, the volumes of each region can be estimated with different degrees of confidence. The volume of air in the skeleton can be estimated with a high degree of confidence, because the sizes of the air spaces can be measured from fossils. In contrast, the trachea is outside of the skeleton and is not usually preserved in fossils, so its volume must be estimated by comparison to living animals. This leads to the second point, which is that estimates of all four regions can be made independently, so that skeletal pneumaticity can be taken into account regardless of what is known or assumed about the other three regions.

An Example Using *Diplodocus*

Consider the volume of air present inside a living *Diplodocus*. Most published mass estimates for *Diplodocus* (Colbert, 1962; Alexander, 1985; Paul, 1997; Henderson, 1999) are based on CM 84, the nearly complete skeleton described by Hatcher (1901). Uncorrected volumetric mass estimates—i.e, those that do not include lungs, air sacs, or diverticula—for this individual range from 11,700 kg (Colbert, 1962, as modified by Alexander, 1989: table 2.2) to 18,500 kg (Alexander, 1985). Paul (1997) calculated a mass of 11,400 kg using the corrected densities cited above, and Henderson (1999) estimated 14,912 kg, or 13,421 kg after subtracting 10% to represent the lungs. For the purposes of this example, the volume of the animal is assumed to have been 15,000 liters. The estimated volumes of various air reservoirs and their effects on body mass are shown in Table 2.

Estimating the volume of air in the vertebral centra is the most straightforward. I used published measurements of centrum length and diameter from Hatcher (1901) and Gilmore (1932) and treated the centra as cylinders. I multiplied these volumes by 0.60, the mean ASP of the sauropod vertebrae listed in Table 1, to determine the total volume of air in the centra.

The volume of air in the neural spines is harder to calculate. The neural spines are complex shapes, and they can not be replicated with simple geometric models. Based on the size of the neural spine relative to the centrum in most sauropods (see Figure 12), it seems reasonable to assume that in the cervical vertebrae, at least as much air was present in the arch and spine as in the centrum, if not more. In the high-spined dorsal and sacral vertebrae (see Figures 1 and 2), the volume of air in the neural arch and spine may have been twice that in the centrum. Finally, the vertebrae at the base of the tail have large neural spines but the size of the spines decreases

Table 2. The volume of air in *Diplodocus*. See the text for methods of estimation.

System	Total Volume (L)	Air Volume (L)	Mass Savings (kg)
Trachea		104	104
Lungs and air sacs		1500	1500
Extraskeletal diverticula		?	?
Pneumatic vertebrae			
Centra			
Cervicals 2-15	136	82	
Dorsals 1-10	208	125	
Sacrals 1-5	75	45	
Caudals 1-19	329	198	
Subtotal for centra	748	450	
Neural spines			
Cervicals 2-15	136	82	
Dorsals 1-10	416	250	
Sacrals 1-5	150	90	
Caudals 1-19	165	99	
Subtotal for spines	867	520	
Subtotal for vertebrae	1615	970	1455
Total volume of air spaces		2574	
Total mass replaced by air spaces			3059

rapidly down the length of the tail. On average, the caudal neural spines of *Diplodocus* may have contained only half as much air as the centra. These estimates are admittedly rough, but they are probably conservative (too low rather than too high) and so they are good enough for this example.

During pneumatization of the skeleton, bony tissue and bone marrow are replaced by air-filled diverticula. The density of the bone and marrow that is removed must be taken into account to estimate how much mass was saved by pneumatization. In apneumatic sauropod vertebrae the internal structure is filled with spongiosa, which contains red bone marrow in life (Figure 18). In birds, the pneumatic diverticula erode the inner surfaces of the bone in addition to replacing the spongiosa (Bremer, 1940), so pneumatic bones tend to have thinner walls than apneumatic bones (Currey and Alexander, 1985; Cubo and Casinos, 2000). The tissues that may have been replaced by diverticula have densities that range from 0.9 kg/L for some fats and oils to 3.2 for apatite, the dense mineral that gives bones their strength (Schmidt-Nielsen, 1983: 451 and table 11.5). For this example, I estimated that the tissue replaced by the diverticula had an average density of 1.5 kg/L (calculated from data in Cubo and Casinos, 2000), so air cavities that total 970 liters replace 1455 kg of tissue. The trachea, lungs, air sacs, and diverticula outside the skeleton did not replace bony tissue in the body. They are assumed to replace soft tissues with a density of 1 kg/L in the solid model.

Outside of the skeleton, pneumatic diverticula may pass among the viscera and muscles and under the skin. None of these leave traces that are likely to be fossilized. The most that we can infer is that these **extraskeletal** diverticula must have been at least as widespread in the body as the pneumatic bones. In the example of *Diplodocus* used above, we can infer that the diverticula associated with the vertebrae must have extended from the front of the neck to the

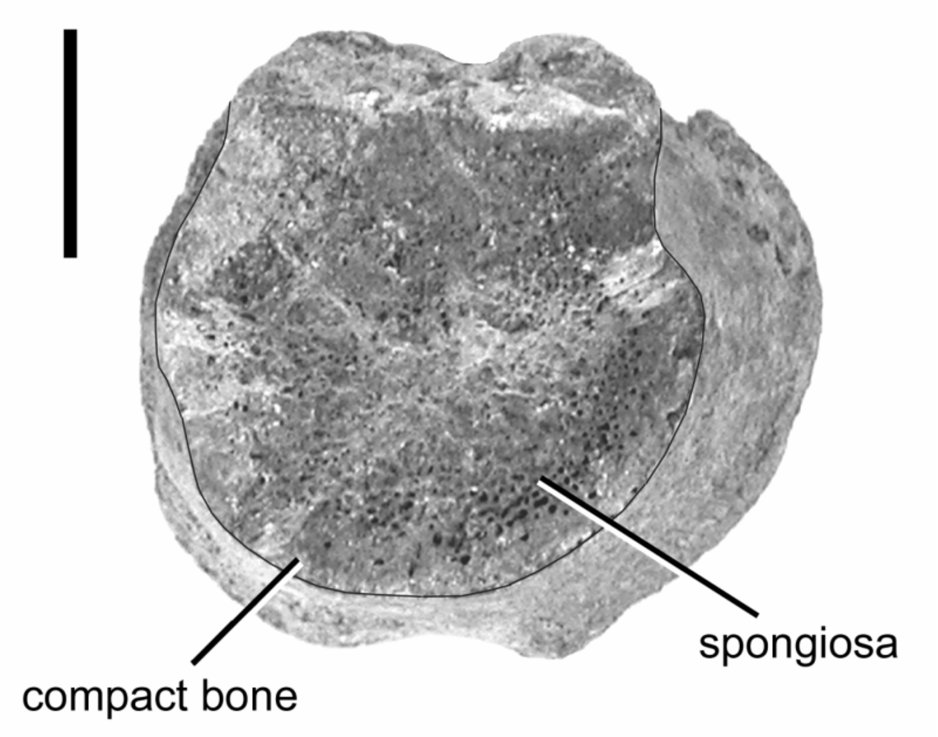

Figure 18. Internal structure of a caudal vertebra of an unidentified sauropod from Montana, OMNH 27794. The internal structure is composed of apneumatic spongiosa. In life, it would have been filled with bone marrow. Compare the dense spongiosa inside this vertebra with the open chambers of the pneumatic vertebrae shown in other figures. Scale bar is 1 cm.

middle of the tail. Still, the size of the diverticula and their precise courses through the body are unknown. No one has ever determined the volume of air in the diverticula of a living bird. For this reason, Table 2 does not include a volume estimate for the extraskeletal diverticula.

To estimate the volume of the trachea, I used the allometric equations presented by Hinds and Calder (1971) for birds. The length equation, $L = 16.77M^{0.394}$, where L is the length of the trachea in cm and M is the mass of the animal in kg, gives a predicted tracheal length of 6.8 meters for a 12-ton animal. The neck of *Diplodocus* is 6.7 meters long and the trachea may have been somewhat longer, which is close enough to justify using the equations, especially for the low level of detail needed in this example. The volume equation, $V = 3.724M^{1.090}$, gives a volume of 104 liters.

Finally, the volume of the lungs and air sacs must be taken into account. The volume of the lungs and air sacs cannot be determined precisely, but they had to fit inside the ribcage and share space with the viscera. Based on measurements from crocodilians and large mammals, Alexander (1989) subtracted eight percent from the volume of each of his models to account for lungs. Data presented by King (1966: table 3) indicate that the lungs and air sacs of birds may occupy 10-20% of the volume of the body. Hazlehurst and Rayner (1992) found an average density of 0.73 kg/L in birds. On this basis, they concluded that the lungs and air sacs occupy about a quarter of the volume of the body in birds. However, some of the air in their birds was probably contained in extraskeletal diverticula or pneumatic bones, so the volume of the lungs and air sacs was probably somewhat smaller. In order to err on the side of safety, I put the volume of the lungs and air sacs at 10% of the body volume.

The results of these calculations are necessarily tentative. The lungs and air sacs were probably not much smaller than estimated here, but they may have been much larger; the trachea could not have been much shorter but may have been much longer (see McClelland, 1989a for examples of very long or expanded trachea in birds); the neural spines of the vertebrae may have contained much more or somewhat less air; the ASP of *Diplodocus* vertebrae may be higher or lower; and the bone tissue and marrow replaced during pneumatization may have been more or less dense. The extraskeletal diverticula have not been accounted for at all, although they ran most of the length of the animal and probably had a large total volume. But in spite of these uncertainties, it seems likely that the vertebrae of *Diplodocus* contained a large volume of air, possibly 1000 liters or more if the very tall neural spines are taken into account. This air mainly replaced dense bony tissue, so pneumatization may have lightened the animal by up to 10%—and that does not include the extraskeletal diverticula or pulmonary air sacs. In the example presented here, the volume of air in the body of *Diplodocus* is calculated to have replaced about 3000 kg of tissue that would have been present if the animal were solid. If the total volume of the body was 15,000 liters and the density of the remaining tissue was 1 kg/L centimeter, the body mass would have been about 12 metric tons and the density of the entire body would have been 0.8 kg/L. This is lower than the densities of lizards and crocodilians (0.81-0.89 kg/L) found by Colbert (1962), higher than the densities of birds (0.73 kg/L) found by Hazlehurst and Rayner (1992), and about the same as the densities (0.79-0.82 kg/L) used by Henderson (2004) in his study of sauropod buoyancy. Note that the amount of mass saved by skeletal pneumatization is independent of the estimated volume of the body, but the proportion of mass saved is not. So if we start with Alexander's (1985) 18,500 liter estimate for the body volume of *Diplodocus*, the mass saved is still 1455 kg, but this is only eight percent of the solid mass, not ten percent as in the previous example.

It could be argued that reducing the estimated mass of a sauropod by only 8-10% is pointless. The mass of the living animal may have changed by that amount or more from season to season, depending on the amount of fat it carried and how much food it held in its gut (Paul, 1997). Further, the proposed correction is tiny compared to the range of mass estimates produced by different studies, from 11,700 kg (Paul, 1997) to 18,500 kg (Alexander, 1985). However, there are several reasons for taking into account the mass saved by pneumatization. The first is that estimating the mass of extinct animals is filled with uncertainty, but we should account for as many sources of error as possible. Pneumaticity is a particularly large source of error if it is not considered. Also, the range of mass estimates for a given dinosaur may be very wide, but 8-10% of the body mass is still a large fraction of any one estimate. The entire neck and head account for about the same percentage of mass in volumetric studies (Alexander, 1989; Paul, 1997), so failing to account for pneumaticity may be as great an error as omitting the neck and head from the model! These reasons for considering the effect of pneumaticity just affect our methods. There is also the paleobiological impact, which is that the living animal was 8-10% lighter because of pneumaticity than it would have been without. This may explain the presence of extensive pneumaticity in many sauropods.

Paleobiological Implications

The importance of pneumaticity for sauropod paleobiology is not yet well understood. To date, Henderson's (2004) work on the buoyancy of swimming sauropods is the only study of the biomechanical effects of pneumaticity. Henderson included pneumatic diverticula in and around the vertebrae in his computer models of sauropods, and found that floating sauropods were both highly buoyant (they floated high in the water) and highly unstable (they tended to tip over).

Pneumaticity may also be important in future studies of neck support in sauropods. Alexander (1985, 1989) looked into the problem of how *Diplodocus* held up its long neck. His calculations were based on a volumetric estimate of 1340 liters (and, thus, 1340 kg) for the neck and head. Using the values in Table 2, one fifth of that volume, or 268 liters, was occupied by air spaces. If Paul (1997) and Henderson (2004) are correct, the density of the neck may have been as low as 0.6, which would bring the mass of the neck down to about 800 kg (you can get the same result by applying the air volumes in Table 2 to a more slender neck model than the one used by Alexander). As the mass of the neck goes down, the problems with holding it up are alleviated. This was especially important for the largest sauropods, which had necks more than 10 meters long (Wedel and Cifelli, 2005).

PROBLEMS AND PROSPECTS FOR FURTHER RESEARCH

Despite a long history of study, research on pneumaticity is still in its infancy. Anyone who doubts this statement is directed to Hunter (1774). In the first published study of pneumaticity, Hunter developed two **hypotheses** that are still being tested today: pneumaticity may lighten the skeleton, or it may strengthen the skeleton by allowing bones to be larger without being heavier (see Witmer, 1997, for further discussion of these ideas). Although many later authors have documented the pneumaticity of birds (e.g., Crisp, 1857; King, 1957), most have focused on one or a few species (O'Connor, 2004), some have produced conflicting accounts (reviewed by King, 1957), and few have attempted to test functional hypotheses (but see Warncke and Stork, 1977; Currey and Alexander, 1985; Cubo and Casinos, 2000; O'Connor, 2004). The evolution of pneumaticity in birds is not well known because few species have been studied (King, 1966, O’Connor, 2004). Limits of knowledge of pneumaticity in living animals limit what can be inferred from the fossil record.

Another problem for studies of pneumaticity in fossil organisms is small sample sizes. As mentioned above, pneumaticity has only been studied in a few taxa and the importance of variation is unknown. Sample sizes are limited by the inherent characteristics of fossils: fossilized bones are rare, at least compared to the bones of living animals; they may be crushed or distorted; and they are often too large, too heavy, or too fragile to be easily studied. Even if these difficulties are overcome, most of the pneumatic morphology is still invisible because it is locked inside the bones.

Sources of Data

Information on the internal structure of fossil bones comes from three sources: CT scans, bones that have been deliberately cut into sections, and broken bones. Although CT studies of fossils are becoming more common, few people have access to scanners and the scans are often too expensive. Large fossils, such as sauropod vertebrae, cause other problems. Most medical CT scanners have openings 50 cm or less in diameter, and many sauropod vertebrae are simply too big to fit through the scanners. Furthermore, medical scanners are not designed to work on large, dense objects like sauropod bones. The relatively low-energy x-rays employed by medical scanners often do not have enough energy to pass through large bones. Industrial CT scanners designed to test aircraft parts and other mechanical devices have the power to scan denser materials, but the rotating platforms used in many industrial scanners are too small to accept most sauropod vertebrae. Although CT is a promising technology, for the near future it will probably not be widely used.

Cut sections of bones can also provide valuable information about pneumatic internal structures. The cuts may be made in the field to break groups of bones into manageable pieces, as in the cut *Sauroposeidon* vertebra shown in Figure 14. Less commonly, bones may be deliberately cut to expose their cross sections or internal structures, such as the cut specimens illustrated by Janensch (1947: fig. 5) and Martill and Naish (2001: pl. 32). Cutting into specimens is destructive and potentially dangerous for both researchers and fossils. Although cut specimens will continue to appear from time to time, they are unlikely to become a major source of data.

In contrast, broken bones are quite common. The delicate structure of pneumatic bones, even large sauropod vertebrae, may make them more prone to break than apneumatic bones. For these reasons broken bones are an important source of data on pneumaticity, and they could be used even more in the future. Published illustrations of broken sauropod vertebrae are numerous, and include Cope (1878: fig. 5), Hatcher (1901: plate 7), Longman (1933: plate 16 and fig. 3), and Dalla Vecchia (1999: figs. 2 and 19). Examples of cut and broken bones are shown in Figures 3, 11, and 18.

Directions for Future Research

Four characteristics are listed above under ‘Description of pneumatic bones’: (1) pneumatic features on the surfaces of bones, (2) internal structure, (3) ASP, and (4) distribution of pneumaticity in the skeleton. Only the second of those, internal structure, has been systematically surveyed in sauropods (Wedel, 2003b), although aspects of the first are treated by Wilson (1999). Knowledge of the fourth is mainly limited to the observation that some diplodocids and titanosaurs have pneumatic caudal vertebrae and other sauropods do not (Wedel, 2003b). Only limited data on the ASPs of sauropod vertebrae are available, in Table 1 and also in Schwarz and Fritsch (2006) and Woodward (2005). Not only do all four areas need further study, the levels of variation should be determined whenever possible. Similar data on pneumaticity in pterosaurs, extinct theropod dinosaurs, and birds are needed to test evolutionary and functional hypotheses.

The pneumatic diverticula of birds are the bridge between the core respiratory system of lungs and air sacs and the pneumatic bones. Understanding the development, evolution, and possible functions of diverticula is therefore crucial for interpreting pneumaticity in extinct animals. Müller (1907), Richardson (1939), Cover (1953), King (1966), Duncker (1971) and a few others described the form and extent of the diverticula in the few birds for which it is known, but information on many bird species is lacking or has been poorly documented (King, 1966). The development of the diverticula is very poorly understood; most of what we think we know is based on patterns of skeletal pneumatization (Hogg, 1984a; McClelland, 1989b). Such inferences tell us nothing about the development of the many diverticula that do not contact the skeleton or pneumatize any bones. These diverticula could not have evolved to pneumatize the skeleton. Most diverticula that pneumatize the skeleton must grow out from the core respiratory system before they reach their ‘target’ bones, so they probably also evolved for reasons other than pneumatizing the skeleton (Wedel, 2003a). Those reasons are unknown, in part because the functions of diverticula are not clear. Three important questions that could be answered with existing methods are: (1) what volume of air is contained in the diverticula in life; (2) what is the rate of **diffusion** of air into and out of blind-ended diverticula; and (3) in cases where diverticula of different air sacs grow together and fuse, does air circulate through the resulting loops?

Finally, more work is needed on the origins of pneumaticity. Potential areas of study the structure and functions of vertebral laminae (Wilson, 1999), and the early development of pneumaticity in birds. In addition, if we are to accurately interpret potentially pneumatic features in fossils we need better criteria for distinguishing the skeletal traces of adipose tissue, muscles, blood vessels, and pneumatic diverticula. This problem is the subject of ongoing research by O'Connor (2006).

CONCLUSIONS

The best evidence for pneumaticity in a fossil bone is the presence of large foramina that lead to internal chambers. Based on this criterion, pneumatic diverticula were present in the vertebrae of most sauropods and in the ribs of some. Vertebral laminae and fossae were clearly associated with pneumatic diverticula in most advanced sauropods, but it is not clear whether this was the case in more primitive sauropods. Measurements of vertebral cross sections show that, on average, pneumatic sauropod vertebrae were 50-60% air by volume. Taking skeletal pneumaticity into account may reduce mass estimates of sauropods by up to 10%. Although the functions of pneumaticity in sauropods and other archosaurs remain largely unexplored, most of the important questions could be answered with existing methods, and there is great potential for progress in future studies of pneumaticity.

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GLOSSARY

Abdomen—the part of the body between the ribcage and the pelvis, which contains many of the internal organs

Adipose tissue—a special tissue that stores energy in the form of lipids; commonly called 'fat'

Air sacs—in birds, large sacs that are empty (not filled with tissue) and which blow air through the lungs when driven by movements of the ribcage

Allometry—literally, "different measures"; the change in proportion of the different parts of an organism as a result of growth

Apneumatic—not pneumatic, not containing air

Archosaurs—"ruling reptiles", the evolutionary group that includes crocodilians, pterosaurs, extinct dinosaurs, and birds; birds are the only surviving group of dinosaurs

Biomechanics—the mechanical functioning of a living body; the study of organisms as machines

Buoyancy—tendency to float in water

Camellae—literally, "small chambers", the term given to the small, irregular, pneumatic chambers found in the vertebrae of some pterosaurs, sauropods, and theropods (including birds)

Camellate—containing camellae

Camerae—literally, "chambers", the term given to large, usually paired, pneumatic chambers found in the vertebrae of some pterosaurs, sauropods, and theropods

Camerate—containing camerae

Cancellous—having a porous structure with many small cavities; this is an imprecise term when applied to bone because it could refer to either spongiosa or camellae

Caudal vertebrae—tail vertebrae

Centrum—the “body” or cylindrical part of a vertebra, which connects to other vertebrae

Cervical vertebrae—neck vertebrae

Compact bone—bone tissue that lacks holes or spaces; in most bones, the marrow spaces or air spaces on the inside are surrounded by walls of compact bone that form the outside of the bone

Cotyle—the bony cup at one end of a vertebra, which forms the socket for the ball-and-socket joints between vertebrae

CT—short for “computed tomography”, a method of obtaining image slices through objects using X-rays; popular in paleontology because it allows fossils to be “sliced” without destroying them

Diffusion—passage of a material from a region of high concentration to a region of low concentration

Diverticulum (plural: diverticula)—a pouch or sac that branches out from a hollow organ or structure

Dorsal vertebrae—vertebrae of the trunk, from the base of the neck to the top or front of the pelvis

Epithelium—tissue that covers a surface or lines a cavity

Extramural pneumatization—pneumatization of one bone from another, adjacent pneumatic bone; bones that are pneumatized in this way may not have any pneumatic foramina on the surface

Extraskeletal—outside the skeleton

Foramen (plural: foramina)—a hole in a body part, usually in a bone

Fossa (plural: fossae)—a depression in a body part, usually in a bone; differs from a foramen in that it only indents the surface but does not pass through

Humerus—the upper arm bone

Hypothesis—a tentative explanation that is subject to further testing

Ilium—the bone of the pelvis that attaches to the sacral vertebrae; it forms the bony connection of the hindlimb to the vertebral column

Intramural pneumatization—pneumatization of a bone directly by a diverticulum that enters through a pneumatic foramen

Lamina (plural: laminae)—a plate or ridge of bone, such as those found in the vertebrae of most sauropods

Marrow—the soft tissue inside of bones, which may be used for making blood cells or storing fat

Median septum—a thin vertical plate of bone that separates paired chambers within a bone

Morphology—form or structure of an organism or one of its body parts; the study of that form

Neural arch—the arch of bone on top of the centrum that surrounds the neural canal and protects the spinal cord

Neural canal—the tunnel through a vertebra through which the spinal cord passes

Neural cavity—a pneumatic chamber immediately above or beside the neural canal; in some cases the neural cavities have openings into the neural canal

Neural spine—the ridge of bone that sticks up on the top of a vertebra, to which ligaments and muscles attach

Osteoclasts—large cells that break down bone tissue

Paleobiology—the study of fossil organisms as living things

Paranasal pneumaticity—pneumaticity produced by diverticula of the nasal passages

Paratympanic pneumaticity—pneumaticity produced by diverticula of the middle ear

Pathology—a deviation from a healthy or normal condition

Physiology—the functions and activities of living organisms

Pneumatic—containing air or filled with air

Pneumatize—to bring air into something or to fill it with air

Postcranial skeleton—the skeleton behind the head; essentially, the entire skeleton except the skull

Presacral vertebrae—vertebrae forward of the sacrum and pelvis, includes both cervical and dorsal vertebrae

Pterosaur—a flying reptile related to dinosaurs, but not a bird

Sinus (plural: sinuses)—generally, a cavity or passage; usually refers to a pneumatic chamber in one of the bones of the face

Skeletal pneumaticity—the presence of air inside bones

Spinal cord—the large cord of nerve tissue that runs down the vertebral column and conducts information to and from the brain

Spongiosa—part of a bone made up of spongy tissue and filled with marrow in life

Taxon (plural: taxa)—a taxonomic category or group, such as a species or a group of species

Tetrapods—vertebrate animals with four limbs, or whose ancestors had four limbs; tetrapods include amphibians, reptiles, mammals, and birds

Theropod—a dinosaur more closely related to birds than to sauropods; theropods include all known meat-eating dinosaurs, but not all theropods ate meat

Thorax—the part of the body enclosed by the ribcage

Trachea—the windpipe, a tube that connects the lungs to the mouth and nose

Vertebra (plural: vertebrae): a single piece of the backbone

Volumetric—relating to measurement by volume

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