REVIEW ARTICLE

The Evolution of the Human Species: A Long Journey for the Respiratory System

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Evolution has involved important changes in hominids, particularly in relation to the process of encephalization and the transition to bipedalism. Some of these changes involved structures related to the respiratory system and altered its functional behavior. Changes affecting the relationship between the skull and the spinal column, together with an improved laryngeal structure (allowing vocalization), resulted in a soft and elongated oropharynx, with part of the tongue integrated into its anterior wall, and thus in an increased tendency towards upper airway collapse during sleep. Vertebral bodies moved inwards into the thorax, which became slightly shorter and went from a bell-shaped appearance to that of a flatter barrel-shaped one. This resulted in respiratory muscle mechanics that were more efficient for upright posture. The pulmonary ventilation and perfusion gradients moved from a dorsoventral to a craniocaudal axis, while the structural organization of the respiratory muscles underwent only minor changes.

Key words: *Hominids. Upper airways. Thorax. Respiratory muscles.*

La especie humana: un largo camino para el sistema respiratorio

La evolución ha implicado importantes cambios en los homínidos, sobre todo por el proceso de encefalización y la bipedestación. Algunas modificaciones afectaron a estructuras relacionadas con el aparato respiratorio y cambiaron su comportamiento funcional. Así, los cambios experimentados en las relaciones entre cráneo y columna vertebral, junto con una mejor estructura laríngea (fonación), dieron lugar a una orofaringe blanda y alargada, con parte de la lengua integrada en su pared anterior, lo que facilita el colapso durante el sueño. La caja torácica disminuyó ligeramente su altura, interiorizó las vértebras y pasó además de una forma campaniforme a otra de tipo tonel, más aplanada, lo que dio como resultado una mecánica muscular respiratoria más eficiente para la bipedestación. Los clásicos gradientes ventilatorio y circulatorio pulmonares pasaron de un eje dorsoventral a uno de tipo apicobasal, mientras que los músculos respiratorios apenas modificaron su disposición estructural.

Palabras clave: *Homínidos. Vía aérea superior. Tórax. Músculos respiratorios.*

Most treatises on the evolution of hominids give special emphasis to the elements that differentiate them from other large primates. Thus, whole chapters are dedicated to the evolution of the skull, to the encephalization process, to the prehensile ability of the hands, to changes in dentition, and to changes in the skeletal system required for bipedalism. However, the upright position also posed an important challenge to the respiratory system. The aim of this review is to examine this challenge and the way evolution responded to it. It is a response full of original features that are unique in the animal world, even if today we simply call it "human respiratory physiology," which is to say respiratory function that is normal for *Homo sapiens* —"normal" because it is shared by the great majority of our species. From a phylogenetic perspective, however, it is extraordinary. The classic understanding of the evolution of hominids has been based both on comparison with modern great apes (chimpanzees, bonobos, gorillas, and orangutans) and on paleontological findings of the various species of the genus *Homo* and the genii *Paranthropus* and *Australopithecus*, among others. The analysis of these remains has traditionally been carried out from an anatomical perspective, with more or less speculative deductions about their possible physiology. In recent years, however, genetic analysis has made important contributions to our understanding of the road that has led to the anatomy and physiology of the human being of today.[1]

Modern humans belong to the species *H sapiens*, which developed from a relatively small population of individuals (approximately 3000). Members of this species, phenotypically similar to modern humans as early as 250 000 years ago, left the African continent some 50 000 years ago. Their descendants arrived in Europe a few thousand years later.[2] There they met a close relative, *Homo neanderthalensis*, who, having arrived on the continent 300 000 years earlier, had evolved under the extremely adverse conditions of the last ice age. Both species of the

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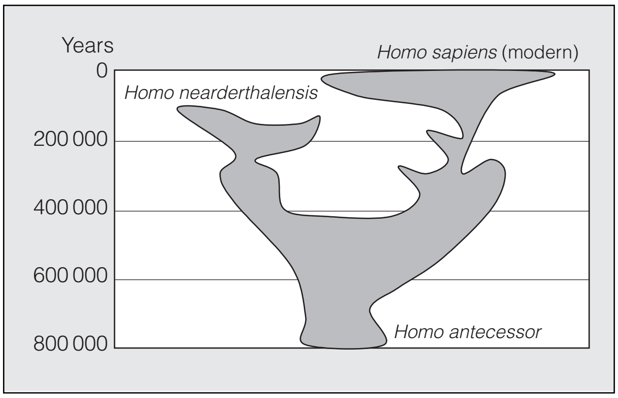


Figure 1. Evolution of the most recent hominids on the European continent, showing the coexistence of *Homo neanderthalensis and Homo sapiens.*

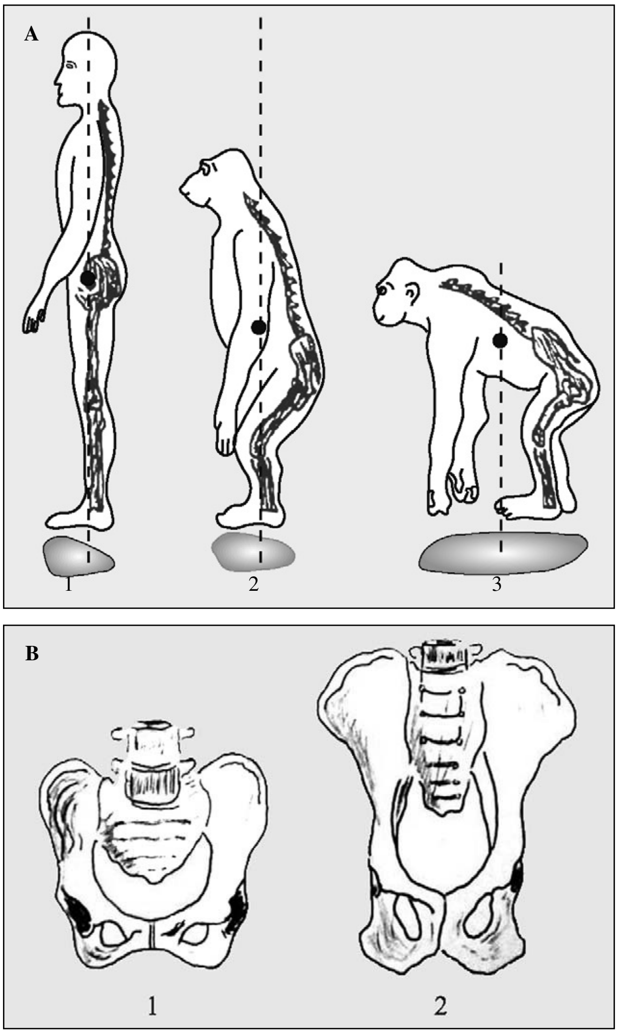


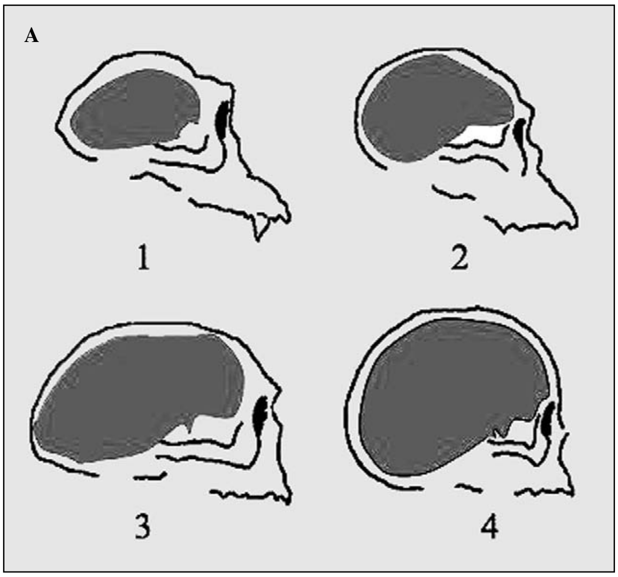
Figure 2. A: bipedalism in the human being *(1)* and in the chimpanzee *(2)*. Drawing 3 shows the customary position of the chimpanzee, with 4 points of support. We can see the centers of gravity and their projections onto the base of support. In drawings 1 and 3 the position is anatomically appropriate. In drawing 2, however, the position is unstable. Bipedalism and erect gait are possible at the cost of considerable muscular effort. B: representation of the pelvis in the modern human (1) and in the adult chimpanzee *(2)*.

genus *Homo* coexisted or competed in Europe for a long period (some 150 000 years) (Figure 1),[3] although it is not entirely clear whether they exchanged genetic material.[4,5] Some recent studies have suggested that they may have, although the percentage contribution of *H neanderthalensis* to our genome must have been small. The possible qualitative importance of such an exchange might be greater, however, as it may have facilitated the development of our brain.[6] Various paleontological findings further show that there was also enriching cultural exchange between the 2 hominid species.[7]

Let us review briefly the possible causes of the transition to the upright position and its main consequences for our anatomy and physiology. While it is true that some great apes can also walk upright, this is at the expense of a considerable expenditure of energy. They are not anatomical but postural bipeds in that their pelvis and lower limbs are not designed for walking on 2 limbs (Figure 2).[8,9] As a consequence, their center of gravity does not run in a perpendicular line from the pelvis to the ground, but somewhat more forward. This makes it difficult to maintain an upright posture. Bipedalism gave hominids important competitive advantages. It meant improved ability to survey the surroundings, allowing them to detect dangers at a greater distance and better identify feeding opportunities. It also freed the upper limbs from having to participate in walking.[9] This made it progressively easier to handle instruments, thus allowing first more effective defense and a greater ability to obtain food, and finally the development of culture.

Parallel to these changes, which were so important for the later development of our species, there occurred other changes that were facilitated by an upright posture. The skull, for example, underwent a series of very important modifications. One of them, the change in position of the opening between the base of the skull and the spinal column (foramen magnum), has proved especially useful in paleontology, as it allows a primate to be classified in a species in the genus *Homo*. This opening, located at the back of the skull in quadrupeds, shifted to the bottom of the skull in bipeds (Figure 3A).[10] This particular placement of the point of conjunction between the skull and the spinal column made it possible to keep the head erect without difficulty. This facilitated a broader view of the environment that was doubtless extremely useful to our ancestors. It must be remembered that bipedalism is believed to have developed in the context of the transition from a heavily wooded terrain to a more savanna-like landscape. The deforestation of the easternmost part of the African continent was probably due to the appearance of the East African Rift System some 18 000 000 years ago.[11] It modified the climatic conditions to the east of this great orographic feature, making it difficult for rains to reach the region, and divided the great ape population into those whose surroundings remained great tropical forests (Western Africa) and those whose surroundings became increasingly arid, with greater distances between protective wooded areas (Eastern Africa). In this savanna-like environment, the broader view of the surroundings that bipedalism allowed (about 7 000 000 years ago) was no doubt very useful for catching sight of predators. While the point of conjunction between the skull and the spinal column shifted, the skull itself was also undergoing important changes. The size of the skull in primates is generally proportional to that of the whole body. Hominids, however, constitute a clear exception to this rule, as their skulls need to house a proportionally much larger brain. Furthermore, certain areas of the brain (such as the associative parietal area) have increased in relative size.[12] Through a process occurring inside the skull known as encephalization, brain weight increased in relation to total body weight (Figure 3B).[12-14] It is believed that increased intake of meat[15] (a consequence of anatomical improvements), and the resulting spare time (unimaginable in a herbivore) were essential to this process. It is well known that in the various species of mammals the size of the digestive tract is inversely proportional to that of the brain,[15] but this means that calories must be used very efficiently to feed a large brain.[12] The introduction of meat into the diet is believed to have also represented a competitive advantage over a strictly herbivorous diet, which is highly dependent on seasonal and climatic factors.

The increase in the size of the brain was accompanied by an increase in neuronal density (which may be as much as 50% greater in modern humans than in great apes)[16] as well as in the number of neural connections.[17] This does not always indicate greater capacity, but it does indicate greater structural complexity. Unfortunately, we do not have samples of cerebral tissue, which is highly perishable, from primitive hominids. Some of the sense organs were also modified in the course of evolution. In fact, somewhat earlier, when differentiation among primates first began, vision became frontal and, consequently, stereoscopic.[8,12] This change, which proved fundamental for survival in trees as it made it easier to calculate distances, was probably very important in the later colonization of the savanna and other ecosystems by hominids. Together with the upright position and the erect carriage of the head, it meant a greater and much improved field of vision. Consequently, other senses that had hitherto been essential to survival, such as smell and hearing, lost relative importance in hominids. Certain changes in dentition derived from their feeding habits occurred as well, although the general dentition pattern of hominids is similar to that of great apes.[8,18] Both have 2 generations of teeth (deciduous and



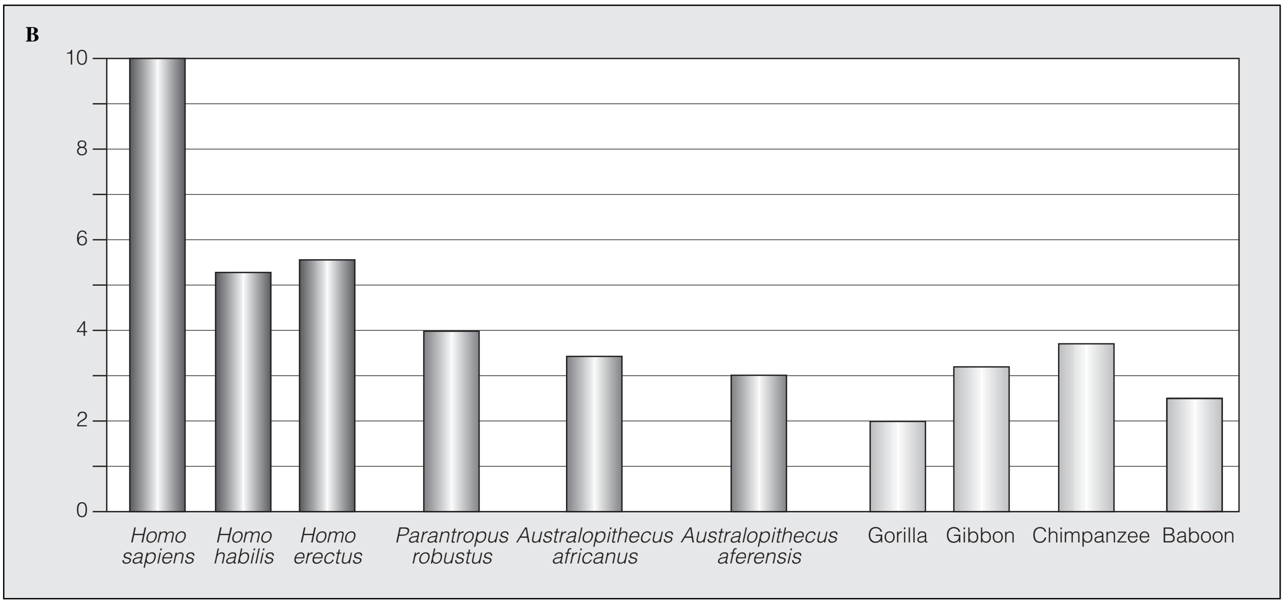


Figure 3. A: schematic representation of the skull and brain of various primates: chimpanzee (*1*), *Australopithecus* (*2*), *Homo erectus* (*3*) and modern *Homo sapiens* (*4*). B: relative encephalization in various species of apes and hominids compared to the modern human (for details, consult text and references).

permanent), although their appearance is somewhat different, especially that of the canines. These stand out because of their size in the great apes, especially in male gorillas. The canines of the genus *Australopithecus* were also somewhat larger than ours and those of other species of the genus *Homo*. The dental arches, determined by the width of the skull, the length of the jaw, the surrounding soft tissues, and the size and angle of the teeth, are somewhat different among the various species. For example, the shape of the mandibular dental arch in modern humans and in hominid fossils is generally parabolic or rounded, while it is V-shaped in some species of *Australopithecus* and U-shaped in modern great apes.[19] The upper dental arch, important in ventilation because of its connection to the palate, is also wider in the genus *Homo* than in *Australopithecus* or the great apes.[19] An equally interesting consideration from the point of view of respiration is the relative prognathism of some species, such as the various *Australopithecus*, *H neanderthalensis*, and *H antecessor*.[20] The absence of a chin, however, does not necessarily mean an effective reduction of oral space or competition among the various components for available space. .

As we continue down the skeletal system, we come to 2 other structures that underwent significant change during the evolution of bipedalism: the shoulder and pelvic girdles. In the case of the shoulder girdle, the modifications resulted from the freedom acquired by the upper limbs. As mentioned, these limbs lost their function of supporting walking and, with the development of various features of the hand,[9] it became possible for them to handle tools,[21] a function believed to be intimately connected with the development of higher functions such as abstraction and planning. In the pelvic girdle the changes had both functional and structural repercussions, as the new positioning of the lines of gravity required a less robust pelvis and a bony birth canal that was less straight and less wide.[22] This characteristic, already present in members of the genus *Australopithecus*,[8] coincided with the development of a larger skull. This made birth somewhat difficult and made it necessary for part of the skull's development to continue into childhood.[8,12] Fortunately, the social circumstances of hominids made it possible for them to take good care of their young during this period, thereby contributing to their learning. Thus, we humans, from the very beginning of our lives, are conditioned by our bipedalism.

How did bipedalism affect the modern position of the airways, the thorax, and their various elements? With regard to the upper airways, and thus to a considerable part of our anatomical dead space, it should be noted that these structures vary widely from species to species. Thus, a swan or a giraffe has a considerable volume of air that is not involved in gas exchange.[23] While the differences between the great apes and our distant ancestors on the one hand and *H sapiens* on the other are fewer, they are nonetheless interesting from the point of view of pneumology and respiratory physiology.

The upper airways are among the parts of the body that have undergone the greatest change over time. The available information concerning these changes is fragmentary, although it has been possible to get some picture on the basis of chance discoveries of bones associated with the pharynx, larynx, and tongue. In modern great apes the pharynx is closely connected to the bones of the skull, while in modern humans only a small portion is in contact.[24] This, together with the different configuration of the lower part of the skull, gives us a wider and higher nasopharynx.[25] While more primitive hominids such as the *Australopithecus* seem to have had a nasopharynx similar to that of modern great apes,[25] the nasopharynx of primitive members of the genus *Homo* was already quite similar to our own.[8]

The larynx in chimpanzees, gorillas, and orangutans is located higher up (near the base of the tongue) and is tilted back more than in the modern human and this makes vocalization enormously difficult for these animals. In addition, humans can close off the entrance to the larynx completely, giving a cough considerable explosive force. This has a clear adaptive advantage if we consider that this expulsive effort is exerted against gravity. The epiglottis plays an important protective role in aspiration in modern great apes, while this role is relatively unimportant in modern humans. Some believe that the airway configuration in our hominid ancestors, with a small pharynx, forced them to breathe predominantly through the nose,[26] thus limiting their ability to vocalize.[27] Others, however, believe that some primitive hominids, such as the Neanderthals, had an even larger pharynx than modern humans. An interesting and unexplored question concerns the consequences that the special airway configuration of early hominids had on respiratory diseases, specifically on those related to sleep-disordered breathing. Modern great apes snore,[28] but appear not to present a significant number of sleep apneas.[29] However, as we have noted, the larynx in adult humans is much lower than that of great apes. Although this position facilitates vocalization, it also entailed the development of a soft oropharynx, making it much easier for the larynx to collapse during sleep. Some hominids (such as ourselves) have tongues with certain characteristics and positions that make it difficult to keep the airway free in decubitus position. The tongue in these hominids lies in a smaller oral cavity, as a result of changes in the configuration of skull and face, yet it is relatively wide but just as long as those of the great apes.[29] As a result, the human tongue has a pharyngeal portion (Figure 4A). Unfortunately, humans have not developed specific upper airway muscles to overcome these difficulties, although it has been suggested that one of our more robust ancestors may have had such a set of muscles. We can only speculate about the selective pressure that an excessive tendency for the upper airway to collapse during sleep exerted on our distant ancestors, as it must have been a disadvantage for day-to-day survival in the savanna. This is one of the secrets of our history.

As we continue down the upper airways, we come to the trachea and the large airways. There are no major differences between those of the great apes and those of humans.[30,31] While no remains of the trachea and large

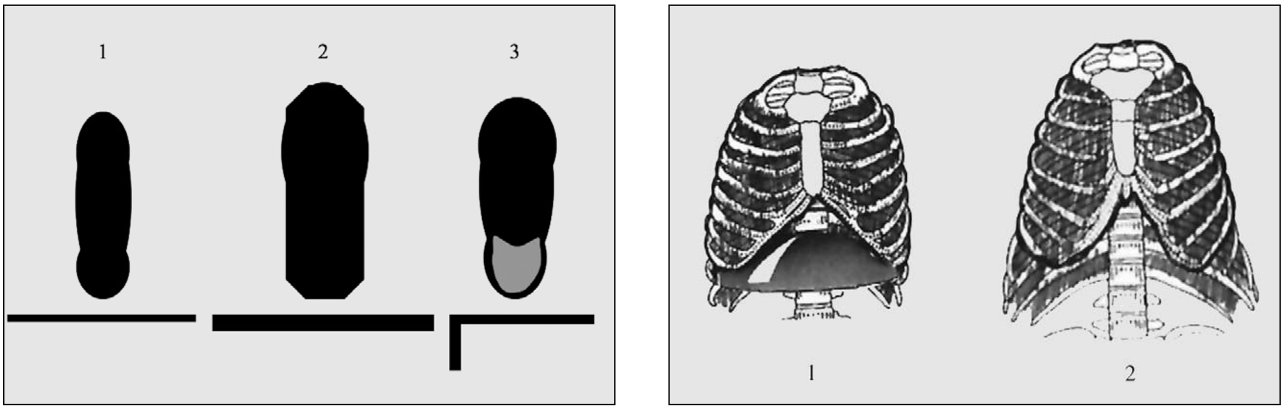


Figure 4. A: schematic representation of the tongue. The upper part shows its flat projection in great apes (*1*), in Neanderthal man (*2*), and in modern *Homo sapiens* (*3*). The vertical gray portion forms part of the anterior wall of the oropharynx. The tongue of *Homo erectus* (not shown) was similar to that of the modern human. The lower part shows a lateral view of the topographical position of the tongue in relation to the oral cavity and oropharynx: completely oral in 1 and 2, and partially oropharyngeal is modern humans (*3*). B: representation of the human thorax (*1*), with its external and parasternal intercostal muscles and diaphragm, and of an adult chimpanzee (*2*), with its bell-shaped thorax.

airways of other hominids are available, there is every indication that their distribution and morphology must have been similar to ours, with small differences due to size.

The lung of vertebrates is in reality a diverticulum of the digestive tract,[23] and is structurally highly complex. In mammals, this complexity involves the presence of a respiratory tree with multiple branches ending in millions of alveoli.[23] It is there that pulmonary gas exchange between gaseous (alveolar) and liquid (capillary) phases occurs. For this exchange to take place properly it is important that ventilation and perfusion be well matched and that there be no limitation to the passage of gases through the alveolar-capillary interface.[32] An interesting point from the perspective of comparative anatomy and physiology is that smaller mammals have a greater capacity for gas exchange than larger ones due to the proportionally larger surface of the alveolar-capillary interface.[23] However, we must remember that much of our accepted knowledge about respiratory mechanics and the distribution of ventilated air and pulmonary circulation has been obtained from animal species that are not natural bipeds. This suggests that some of the principles that we apply routinely cannot really be extrapolated to humans. It must also be remembered that age is important, as in great apes and in humans the number of alveoli continues to increase after birth, reaching its maximum during childhood.[33] With age as well, changes occur in the lung parenchyma that slightly mimic those observed in emphysema. Unfortunately, as the lung consists of soft tissue, we have no information about what it was like in other species of the genus *Homo*. However, given that the lungs of modern great apes are structurally similar to ours, we can deduce that the lung of earlier *Homo* species was not very different from our own. Another question is the distribution of ventilation and perfusion in the lung, as both have a vertical gradient that depends on gravity and respiratory pressures.[32] In the case of perfusion, the gradient is particularly dependent on the force of gravity, although it can be modified locally by intraalveolar pressure (which can collapse the vessels continuously or intermittently if it is too high) or by local vascular resistance. In the case of ventilation, regional differences in pleural pressure cause greater changes in volume in the lower alveoli, which thus receive a larger volume of gas. In the human being, the upright posture has meant the shift of the ventilation and perfusion gradient to a craniocaudal axis, while in other mammals this gradient is mainly dorsoventral.[34,35] The great apes probably present an intermediate situation, although studies on this are lacking.

The rib cage also changed with bipedalism. Modern humans have 7 cervical vertebrae, 12 thoracic vertebrae, 5 lumbar vertebrae, 5 sacral vertebrae, and 4 coccygeal vertebrae.

If we compare this distribution to that of modern great apes, we see that while the number of cervical vertebrae is the same, gorillas and chimpanzees have more dorsal vertebrae.[36] This means that they have a greater proportion of vertebrae in the thorax. It must be remembered that the dorsal vertebrae have articular facets for the ribs, and this means that the great apes have an extra rib and a proportionally longer rib cage than humans. However, the number of true ribs (connected to the sternum by their own chondrocostal cartilages) and floating ribs (articulated on only 1 facet of the vertebrae and without anterior contact) is similar in humans and modern great apes. Both also possess an extra so-called false rib (connected to the sternum by the cartilages of the upper ribs). However, modern humans have the so-called cervical rib[37,38] and this has led some authors to speculate that this rib might really be a modification of the first dorsal rib[8] secondary to the new use of the upper limbs (once again, we see the relevance of bipedalism). The effect of this characteristic, which humans share with *Australopithecus* and *H neanderthalensis*, is that the number of ribs is the same in humans and in apes. The

Australopithecus had very robust thoracic vertebrae and ribs, and this, together with a powerful thoracic musculature, must have been very useful for climbing trees and performing heavy tasks.[39] These characteristics remained present to some degree in the later Neanderthals,[40] although their dorsal vertebrae were already more similar to ours. Another interesting aspect from an evolutionary standpoint is that the spinal column of the great apes, including that of the genus *Homo*, moved inwards into the thorax (thereby moving the center of gravity forward, providing important advantages for bipedalism), while in the other mammals it remained outside the thorax.[8] The sternum, the final component of the bony thorax that closes it in front, is wider in humans and in great apes than in other, phylogenetically more distant, apes.

In general, the rib cages of modern humans and the great apes are similar, with a wide transverse diameter contrasting with a smaller ventrodorsal diameter. This gives rise to a flattened section in the anteroposterior direction. The rib cage of the other primates, on the other hand, is elongated in the anteroposterior direction, and this affects respiratory mechanics in specific ways.[36] This point is often underestimated when animal models of respiratory diseases are designed using common laboratory primates such as baboons or spider monkeys. It is interesting to note that the varying thorax shapes develop after birth, as the anteroposterior and transverse diameters are similar in the fetuses of humans and other primates. However, despite the similarities in the configuration of its cross-section area, there are differences between the thorax of humans and those of great apes. The human thorax has a characteristic barrel-shaped appearance, while that of the great apes has a more bell-shaped or inverted funnel appearance (Figure 4B).[36,41,42] This implies a different configuration of rib cage muscle components, especially in the lower intercostal muscles and the diaphragm itself.

Fortunately, we have remains of both the ribs and the vertebrae of early hominids and this gives us an approximate idea of what their thorax and some parts of their respiratory system were like. The remains of *Australopithecus* seem to indicate that the thorax of these hominids had a rounded section, different from ours, and more similar to that of some species of modern apes.[41] In fact, the general appearance of the thorax was actually bell-shaped, like that of modern chimpanzees. However, their first rib was similar to that of modern humans, and this is interpreted as a consequence of an erect thorax[43] and of the freeing of the upper limbs.[38] A more modern species, the Neanderthal man, had an extremely robust thorax, with much sturdier vertebrae and ribs than ours, although the curvature of the last ribs was less pronounced. The result was a larger thorax with great mechanical potential.

Contractions of the respiratory muscles, particularly those responsible for inspiration, generate greater negative pressure in the pleural space. As we know, this greater negative pressure is transmitted to the alveolar space and causes air to enter the lungs. Obviously, the position of the diaphragm, the principal respiratory muscle, is quite different in bipeds and quadrupeds, and in fact, there are positions that we might call intermediate, at least from the ventilatory and cardiovascular standpoint. In such positions—seen in the modern great apes, for example—the rib cage and trunk are generally in a tilted position. Therefore, the transition from a position parallel to the force of gravity to a perpendicular one was probably gradual. It is also interesting to note that our rib cage returns to a parallel position when we sleep. We have seen that the bony thorax underwent changes in its shape and that these modifications were probably accompanied by changes in the muscles as well. In modern humans the diaphragm is roughly circular, originating at the base of the bony thorax and terminating at its tendinous central portion. Its shape is reminiscent of a double cupula (with 2 azimuth points) which flattens and descends as it contracts. In the chimpanzee, although the shape is similar, the muscular portion is wider and the central tendon smaller.[8,44] The opposite is true of the gorilla, whose diaphragm has a large central tendon and a relatively small muscular portion.[45] This probably has functional repercussions on the maximum pressures that each is able to generate, although we are unaware of studies in this area. Information on the diaphragm of early hominids is scant because, as mentioned earlier, muscle tissue is not preserved. However, marks on bones indicate that their diaphragm muscles were powerful (especially those of Neanderthals),[8] and these early humans were probably capable of generating pressures far greater than we can. The similarities between our muscles and those of modern great apes suggest that that the general shape of the diaphragm in early *Homo* species was similar to our own.

A series of muscles assist the human diaphragm in ventilation. These are the so-called accessory muscles of respiration. Among them are the scalene, intercostal, and sternocleidomastoid muscles.[46] Of course, many other muscles, such as the great dorsal (latissimus dorsi), pectorals, serratus, or even the deltoids and biceps, can intervene in breathing when performed under loads.[47,48] The activity of the intercostal muscles has been studied mainly in dogs[49,50] or in laboratory monkeys.[51] From these models it has been deduced, for example, that the upper intercostal muscles show greater inspiratory activity than the lower ones. However, it is probable that some of this knowledge cannot be extrapolated to humans in the upright position, or even to apes with an intermediate trunk position. Obviously the only information on the form and function of the intercostal muscles in early hominids comes from marks of bone insertion. Unfortunately, the ribs themselves are difficult to preserve, and this limits what we can observe. However, as in the case of the diaphragm, the impressive marks on the bones of *H neanderthalensis* suggest that the thoracic muscles were highly developed[8] and had a similar arrangement to that of modern humans and great apes.

In summary, the development of vocalization and the transition to the upright posture characteristic of species of the genus *Homo* involved a series of structural and functional changes in various elements of our respiratory system. To understand these changes, we use both findings from now extinct hominids (classic paleontology and anthropology, recently enhanced by genetic studies) and the similarities and differences with respect to modern great apes (primatology and comparative anatomy and physiology). This allows us to affirm that the upright posture, the consequent freeing of the upper limbs, and vocalization probably led to the development of a thorax that was mechanically more efficient, with lungs adapted to maintaining an adequate ventilation-perfusion ratio in the new situation. Some of the changes, however, also favored the appearance of negative effects, such as sleep apneas.

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