

XVII.—**Scottish National Antarctic Expedition: Observations on the Anatomy of the Weddell Seal (*Leptonychotes Weddelli*).** By **David Hepburn, M.D., C.M.,** Professor of Anatomy, University College, Cardiff (University of Wales). Part III.

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**THE RESPIRATORY SYSTEM, AND THE MECHANISM OF RESPIRATION.**

In the specimen under consideration there were fifteen pairs of ribs, of which nine pairs were vertebro-sternal. The costal cartilage associated with each of these was long and very flexible. The articulation of the first pair of costal cartilages with the sternum was effected by means of a short but strong band of fibrous tissue, which permitted considerable freedom of movement and did not form a junction of the more or less rigid character seen in man.

The chondro-sternal joints of the second, third, and fourth costal arches were of the diarthrodial variety, each joint being divided into two separate cavities by an inter-articular ligament. The fifth, sixth, seventh, eighth, and ninth chondro-sternal joints presented diarthrodial joints without interarticular ligaments.

The sternum was long, narrow, somewhat like a four-sided rod, and divided into segments (suggestive of vertebral centra) by amphiarthrodial joints which were placed opposite the chondro-sternal joints from the second to the ninth. A suprasternal tapering cartilage extended towards the head for a distance of two inches, while the ensiform cartilage extended backwards to a similar distance and ended in a broad semi-lunar expansion.

The intercostal muscles were well developed, being thick and fleshy, presenting little or no fibrous intersection. They were arranged so as to present an external and an internal muscle in each intercostal space, and the direction of their fibres was similar to that seen in man; but the fibres of the external muscle were continued between the costal cartilages close up to the margin of the sternum without the intervention of an intercostal membrane.

The triangularis sterni muscle arose from the deep surface of the sternum on its own side of the mesial plane. It consisted of a number of slips, which were wide enough to give the appearance of a complete sheet of muscle. These were attached to the sternum from the level of the third costal cartilage backwards to the level of the ninth. The fibres ran forward and outwards to be inserted into the deep surfaces of the costal cartilages from the second to the ninth inclusive, and into fibrous bands which passed from one cartilage to the other. The general line of insertion into the costal cartilages was near to the series of costo-chondral joints, each of which, except that of the first rib,

formed a diarthrodial joint. On the ninth costal cartilage this muscle interdigitated with the attachment of the diaphragm. This large, well-developed muscle was supplied by a series of twigs derived from the intercostal nerves in relation to which it was attached.

The sterno-mastoid muscle extended from the anterior end of the sternum and from the side of its pointed suprasternal cartilage to the mastoid process. There being no clavicle, this muscle appeared narrow.

The sterno-hyoid and sterno-thyroid muscles arose from the sternum under cover of the previous muscle. They formed a thin continuous sheet which probably included the omo-hyoid muscle along its lateral border in the vicinity of the hyoid bone. The entire sheet was innervated from the hypoglossal nerve, and the insertion of fibres into the thyroid cartilage and into the hyoid bone suggested the character of its constituent parts. A thin band of muscle fibres occupying their usual position formed the thyro-hyoid muscle.

There were two well-defined scalene muscles, both of which were situated on the dorsal side of the subclavian vessels and cervical nerves, and may therefore be regarded as the representatives of the scalenus medius and scalenus posticus muscles.

The musculus scalenus medius was inserted into the costal cartilage of the first rib close to the costo-chondral articulation.

The musculus scalenus posticus was inserted into the lateral aspects of the third, fourth, fifth, and sixth costal cartilages close to the costo-chondral articulations. At each insertion the pointed attachment interdigitated with similar attachments of the musculus obliquus externus abdominis, whose digitations extended to the cartilage of the first rib.

Regarding the skull and the cervical column as providing the more fixed or rigid attachment for the scalene and sterno-mastoid muscles, it is fairly evident that these muscles may act as elevators of the ribs and sternum by drawing them towards the head.

The diaphragm was well defined in all its parts, but its dorso-lateral portions were very thin, and in the absence of a central tendon of the trefoil type it presented appearances deserving detailed description, more especially in regard to the important position occupied by this muscle in the mechanism of respiration. Its strongest part was the mesial or vertebro-sternal element, which presented two well-marked, pointed crura attached to the lumbar vertebræ. From this origin the muscular fibres passed in a ventral direction on either side of the abdominal aorta until they reached the ventral aspect of this vessel, where to a small extent their fibres intermingled; but for the most part the fibres of the right crus were on the ventral side of those of the left crus.

This distinction between the fibres of the two crura was maintained as they continued towards the œsophagus, along the lateral aspects of which they passed, thereby forming the œsophageal opening, which was practically in the mesial plane. A short distance on the ventral side of the œsophageal opening the muscular fibres were inserted into a circular tendinous ring placed slightly to the right of the mesial plane, and through this

ring the inferior vena cava passed. From the ventral face of this tendinous ring strong muscular bands extended to the deep face of the broad ensiform cartilage.

From each side of the dorsal segment of the fibrous ring surrounding the inferior vena cava there extended a narrow tendinous septum in the dorso-lateral direction. Neither of these septa reached the ribs, although the one on the right side was more strongly marked than that on the left side. Into the dorsal faces of these septa there were inserted muscular fibres derived from the lateral aspects of their respective crura, as well as a small, feeble muscular slip from the ventral surface of the second last rib (the 14th) near its head.

From the ventral aspects of the tendinous septa under consideration, a sheet of muscular fibres passed outwards to be attached by slips or digitations into the ribs close to their junction with cartilages from the 8th to the 13th inclusive. The digitation belonging to the 13th rib was attached just in front of the angle of the rib. This ventro-lateral part of the diaphragm was very thin. Areolar tissue occupied the intervals between digitations attached to the 13th and 14th ribs, and also between the 14th rib and the lateral margin of the crus. The association of the diaphragm with the 15th rib was so feeble as to be doubtful. Probably these weak places may be regarded as corresponding to arcuate ligaments, although in the human sense these structures were undefined. At any rate, these arched ligaments had no other representation, neither could the slight intermingling of crural fibres on the ventral aspect of the aorta be regarded as other than a very feeble median arched ligament. Altogether the dorso-lateral development of the diaphragm was extremely feeble. Those muscular fibres attached to the 8th rib were in close contact with the mesial part of the diaphragm between the sternum and the fibrous ring enclosing the inferior vena cava.

From what has been described it will be evident that there was no central tendon of the trefoil pattern, but in its place a vena caval ring, from which there extended two dorsal-lateral septa, of which the right was the stronger marked. The shortness of the left septum permitted a greater mingling of the fibres belonging to the left crus with those forming the rest of the left half of the diaphragm.

The general arrangements within the chest cavity do not call for special discussion. The two pleural sacs and the mediastinal interval followed the customary disposition. It may, however, be noted that the mediastinal layers of pleural membrane were in close apposition from the second segment of the sternum backwards to the hinder end of the sternum, and that consequently the ventral or anterior section of the mediastinum was a mere chink, in its sternal relations.

The lungs were extremely dark in colour, brown almost to black. They were quite soft, but yielded no feeling of crepitation on pressure, so that they suggested a complete absence of air.

When they were removed each was placed in water, and they sank as if solid. A small portion cut from the lung also sank in water, so that this tissue had entirely lost its buoyancy. It is not quite easy to account for such a complete absence of air from

the substance of the lung. The animal is known to have lived for some days, because it was killed by poisoning with hydrocyanic acid after an attempt had been made to rear it by artificial feeding. The carcass was preserved by injecting an arsenical solution. Neither of these processes would account for the absence of air from the lung tissue. We must therefore assume that either the natural elasticity of the lung tissue has produced the condition noted, so that the expiratory apparatus of the animal is able to produce a practical deflation of the lungs, which is doubtful; or that, partly owing to the length of time they have been preserved and partly owing to the preservative solutions, the air has practically all passed into solution and disappeared.

A portion of the lung was prepared for microscopic examination, and, notwithstanding the number of years that have elapsed since the animal was embalmed, the different tissues were easily recognisable, but to staining agents such as hæmatoxylin and eosin they reacted very slowly and not very satisfactorily.

The hyaline cartilage of the bronchioles was cellular, and very similar to the cartilage in the ear of the mouse.

The lobules of the lung were very clearly defined by interlobular tissue, which was continuous with the sub-pleural tissue, and throughout this tissue there was a well-marked amount of elastic fibres.

All the air spaces were shrunken, *i.e.* collapsed, almost to the point of obliteration, but they were free from exudation. The capillary blood-vessels in the walls of the air spaces were crowded with blood corpuscles, which may have been the result of the preservative injection.

There is some reason, therefore, for considering that the normal elasticity of the lung in this seal was much greater than that of man, and that, consequently, the air would be much more effectively expelled from the lungs of the seal during expiratory movements.

Attention may be drawn to certain of the body muscles whose attachments and disposition were such as to add to their expiratory value. The panniculus carnosus muscle was a thin sheet enveloping the trunk from the hinder end of the abdomen to the face, and on the face and head forming a cowl modified for facial or expression muscles in relation to the various apertures in that region. The fore limbs were in effect pushed through this axial sheet. The disposition of its fibres showed dorso-lateral and ventro-lateral directions, separated from each other by a lateral aponeurosis, and attached by aponeurotic fibres to the dorsal and ventral mesial lines such as may be seen in the porpoise, but less distinct. The direction of the muscle fibres in the dorso-lateral section was obliquely from before (cephalic) backwards (caudal), whereas in the ventro-lateral section their direction was obliquely from behind forwards. The general effect of the contraction of this sheet would be to expel the air from the very elastic and flexible thorax, as well as to compress the abdomen.

The musculus obliquus abdominis externus showed no attachment to the ilium. By one end it was attached through digitations to the entire series of costal arches from

the first to the fifteenth. Its fibres were directed obliquely backwards towards the ventral mesial line, and, having given place to a thin aponeurotic sheet, many of these fibres interlaced with those from the opposite side to form the linea alba.

The hinder part of the muscle, however, did not form any attachment to the ilium, but as a muscular arch, equivalent to the ligament of Poupart, they were attached to the ventral aspect of the body of the pubis. Near to the pubis a slit in the muscle sheet served the purpose of an external inguinal ring, in which the spermatic cord was situated. A muscle so attached could clearly act as a very powerful expiratory muscle provided the glottis were open.

The *musculus obliquus abdominis internus* was attached dorsally to the lumbar aponeurosis and to the crest of the ilium, while ventrally it was inserted into the hinder borders of the last four ribs and also through its aponeurosis into the linea alba. The greater proportion of its aponeurotic fibres passed ventrally to the *rectus abdominis* muscle along with those of the external oblique, but a few of them blended feebly with the aponeurosis of the *transversalis abdominis* muscle. This muscle (*transversalis*) presented lumbar and iliac attachments as well as a series of digitations on the hinder seven or eight ribs. Its mesial attachment to the linea alba was by an aponeurotic sheet placed on the deep side of the *rectus abdominis* muscle. The hinder or inguinal margins of these two last muscles were very closely, almost inseparably, blended together, and both were much thinner than the external oblique muscle.

The *rectus abdominis* muscle occupied an abdominal sheath whose composition has already been indicated. It was attached posteriorly to the body of the pubis, and extended anteriorly to the first costal cartilage, to which, as well as to all the other sternal cartilages, it was attached by tendinous slips. Here again we can see that this muscle, acting from a rigid attachment to the pubis, may act as a powerful expiratory muscle in association with an open glottis.

The lungs, beyond what has already been said, do not call for detailed description. Each presented a great oblique fissure, and thereby an apical and a basal lobe. In addition the right lung possessed a transverse fissure, and therefore a middle or ventral lobe. Furthermore, the right lung had an azygos lobe on its mediastinal aspect in relation to the margin between diaphragm and pericardium.

On several occasions I have had the opportunity of making a detailed examination of the respiratory mechanism of mammals whose habitat is either partly or entirely marine, and on each occasion I have been impressed by the remarkable flexibility of their thoracic wall, with the associated peculiarities in the attachments of certain of the muscles. Attention has already been drawn to some of these peculiarities in the descriptions given above, and it is almost impossible to avoid the conclusion that respiration necessitates a more flexible chest-wall in the case of mammals surrounded by water than in those which are surrounded by air, apart from the fact that the normal attitude of the latter may be horizontal, as in the case of quadrupeds, or vertical, *i.e.* erect, as in the case of man.

On the other hand, this flexibility of the chest becomes not only a drawback, but may be an actual source of danger when the marine mammal comes on shore either by intention or as the result of accident. Thus it is well known that a cetacean dies when it runs aground, not necessarily by starvation, but because it is suffocated, since the flexibility of its chest-wall renders respiratory movements impossible under the superincumbent weight of its body.

The leader of the Scottish National Antarctic Expedition made very careful observations on the attitude of seals when they left the water and resorted to the ice, and he noted that they do not assume positions which would hamper their chest movements. Thus they recline on the side when asleep so as to leave the movements of one side of the chest unimpeded, while at other times their common attitude is to lie prone with the chest raised off the ground by the short fore limbs. Considerations of this kind lead to the conclusion that respiration, but more especially the act of inspiration, can be seriously impeded or even rendered impossible by the weight of the animal's own body. That free inspiratory movement of the chest-wall in man may be hampered by the weight of his body may be readily observed in the case of an operatic singer who, by the exigencies of his performance, is called upon to sing in the supine position; for although in this position he can fill his lungs sufficiently for ordinary respiration, yet he cannot inspire deep enough for effective vocalisation. Clearly, therefore, the respiratory mechanism is affected by the attitude of the individual as well as by the surrounding medium, air or water, in which the animal performs the necessary respiratory movements.

There can be no doubt that, whatever the natural attitude of the mammal may be, or whatever its habitat, the ordinary movements of inspiration and expiration are carried out with the minimum expenditure of effort consistent with the amount of air required for each respiratory act. On the other hand, special circumstances may call for additional or extraordinary efforts both as regards inspiration and expiration. The discussion of respiratory movements is usually left, and by many observers considered properly left, to the physiologist; but as these movements are entirely dependent upon a definite mechanism in which the muscular arrangements play an important part, they cannot fairly be excluded from the province of the anatomist, and it is from the standpoint of structure that I propose to offer some observations which seem warranted by the conditions I have seen in the seal under consideration, as well as in the porpoise.

It may be well in the first instance to deal with the lungs themselves; and, as the condition in which I found them has already been stated, it will only be necessary to add that, except for the presence of the azygos lobe on the right side, they corresponded with the human lungs so far as the number and arrangement of fissures and lobes was concerned. There is no reason to suppose that during the act of inspiration they would inflate in a manner different from the lungs of man. Now, among the many interesting, elaborate, and ingenious attempts to explain the respiratory act, none is more suggestive

than that of KEITH,\* who approaches the discussion of the subject more as an anatomist than as a physiologist.

It is not my intention to follow Professor KEITH in detail and offer a criticism of the conclusions arrived at by him. At the same time, some of his statements appear to me to overlook certain of the anatomical facts. Perhaps the most important fundamental statement made by KEITH is in reference to the lungs when he says "the upper lobe is normally expanded by one mechanism, the lower by another," and as a consequence he insists that "the great fissure, which divides the upper from the lower lobe, is functional in its significance." Supposing this view to be correct, it would follow that since there is a third lobe in the right lung of man and a fourth or azygos lobe in the right lung of a quadruped, with the fissures required for their delimitation, the mechanism for expanding the right lung must differ from that required for the left lung. Further, as regards the apical or upper lobe, KEITH maintains that because of the impressions of certain ribs upon the lateral and anterior aspects of the upper lobe, but not upon "the dorsal surface of the upper lobe," there is "a constant relationship between ribs and spaces" for that part of the lobe which presents impressions, but a "downward and upward" movement of the dorsal unmarked part, in which it follows the movement of the lower lobe, because "the lower lobe and the dorsal part of the upper lobe are chiefly expanded by a diaphragmatic mechanism." The argument for a functional significance for the great oblique fissure seems to me unnecessary if the substance of the apical lobe is to expand in two different ways simultaneously, for, at least as far as the dorsal part is concerned, the presence of the fissure does not seem to confer any advantage.

I am not disposed to maintain that the fissures of the lungs have no significance, although to my mind it is rather structural than functional. Even "the obliteration of the pleural cavity by adhesions has so little apparent effect on the respiratory movements that their presence cannot be detected during life," any more than the obliteration of the lobulated character of the kidneys interferes with their functions. After all, the outstanding requirement is that the lungs shall expand to the capacity corresponding to the immediate muscular effort that is being performed, and naturally, therefore, the capacity undergoes constant variation. With this end in view, I cannot but think it is best to consider the muscular mechanism of inspiration *as a whole*, and the muscular mechanism of expiration *as a whole*, since it is their co-ordinated and not their individual action that we depend upon. Probably, in quiet ordinary breathing, no animal, any more than the human individual, employs the full scope of its inspiratory mechanism, and hence in man it has become customary to employ such terms as "thoracic" and "abdominal" to indicate the character of the inspiratory effort which is most noticeable in the female and in the male respectively. At the same time, there is no record of this distinction in the inspiratory act among the sexes of the lower animals, nor between the human sexes during infancy and early adolescence. It

\* "The Mechanism of Respiration in Man," by ARTHUR KEITH, pp. 182-207, in *Further Advances in Physiology*, edited by LEONARD HILL, published by Edward Arnold, London, 1909.

appears to me, therefore, that the double mechanism which KEITH supports for the expansion of the apical and basal lobes of the lung is more apparent than real, and that the so-called *types* of breathing in man are rather the result of the erect attitude whereby, from the natural configuration and diameters of the diaphragmatic section of the thoracic cavity in the two sexes, it is with less muscular effort that the male expands the lower part of his chest and the female expands the upper part of her chest in order that each may obtain the amount of air necessary for ordinary quiet breathing. When additional efforts call for more air, or when, as in the supine position, the easy movement of the chest is impeded, then there is an immediate departure from the characteristic method; but I do not think that we must postulate a double inspiratory mechanism.

The key to the whole mechanism of inspiration is undoubtedly the part performed by the contraction of the diaphragm. We cannot, therefore, overestimate the importance of its attachments and structure; nor must we forget that, like any other muscle, its action is the result of the contraction of its fibres, whereby its attached ends are brought more or less near to each other. The most favourable method of examining the diaphragm is to consider the adult structure from the point of view of its development.

The first part of the diaphragm to appear in the embryo, and the part which may be considered the most powerful in the adult, is its mesial or vertebro-sternal portion, whose vertebral ends or crura arise from the lumbar vertebræ and constitute its axial or fixed end. These muscular fibres having adapted themselves to the positions of the abdominal aorta and the œsophagus, by a certain amount of intermingling of the fibres from opposite sides of the mesial plane, become inserted into the central tendon, whose shape varies from the trefoil tendon of man to the vena caval ring with its lateral septa as seen in the Weddell seal. From the ventral aspect of these tendinous structures a second set of muscular fibres extends to the deep surface of the lower or hinder end of the sternum. The mesial part of the diaphragm is therefore in reality a digastric muscle pursuing an arched course from the vertebral column to the sternum. The arched character of its course is more pronounced in its dorsal segment, while in its ventral or sternal segment the arched character is lost, being replaced by a straight or flat course. This change in the curve of the two segments is due partly to the disposition of the abdominal viscera and partly because the vertebral attachments are some distance farther tailwards than a point which would correspond with the hinder end of the sternum.

By its contraction two results may follow:—(1) the lower (hinder) end of the sternum is either drawn closer to the vertebral column or else prevented from being projected ventrally (forwards) by other influences; (2) the arched dorsal segment between the vertebral column and the central tendon becomes more or less flattened, and in consequence the adjacent abdominal viscera are pushed towards the ventral abdominal wall. At the same time its restraining or bracing action upon the hinder end of the sternum becomes correlated to the restraining action of the first costal arches upon the manubrium sterni, whereby the manubrium sterni is maintained at a relatively fixed distance from



the vertebral column. By reason of the somewhat rigid character of the first costal cartilages in man, as well as from the fact that they are frequently encased in an ossified shell, the restraining nature of the connection between the first pair of ribs and the sternum is very well marked; but even in the Weddell seal, where a short and powerful fibrous ligament takes the place of the first costal cartilage, the manubrium is very firmly retained in its relation to the backbone.

The next part to be added to the diaphragm developmentally constitutes its ventro-lateral segments. In the adult these are composed of muscular fibres which arise from the ventral and lateral aspects of the central tendon. From this position they extend in a fan-shaped manner to be inserted into the deep surfaces of the costal arches by digitations which correspond very closely in number with those ribs that do not reach the sternum directly through their costal cartilages—that is to say, the false or vertebro-abdominal series of ribs.

This thin sheet of muscle becomes more and more arched as its slips sink lower on the series of ribs. When therefore it contracts, each digitation will either draw its own particular rib nearer to the central tendon or else maintain the ventral end of its rib at a more or less definite distance from the central tendon.

In this way the ventral ends of the false ribs are provided with temporary or intermittent fixed points, fixation by the contraction of the diaphragm being substituted for fixation by the sternum, as is the case with vertebro-sternal ribs. In fact, the series of ribs could with effect be classified as vertebro-sternal and vertebro-diaphragmatic.

The flattening of the arched surfaces of the diaphragm must increase the available thoracic space, but under ordinary conditions the addition so provided cannot of itself be very great, and only becomes important as the central feature of a larger movement.

Developmentally, the last part to be added to the diaphragm is also its weakest part both in man and in the Weddell seal. This is the dorso-lateral segment, which consists of muscular fibres forming a delicate sheet extending between the dorso-lateral aspects of the central tendon and the ligamenta arcuata externa and interna, and through these with the vertebral column on the one hand and the last rib on the other. The arched course of these fibres in man must enable them to aid the flattening of the dorsal parts of the diaphragm and thereby again assist in pushing the abdominal contents in a ventral direction, but in the seal they are so feebly developed that the effect of their contraction must be practically negligible. I do not doubt that contraction of the diaphragm may produce some depression of the central tendon, more especially at its dorsal side, but I doubt whether the depression of the central tendon can take place on its sternal side or be so pronounced as a whole as to give the "piston action" described by some observers. My reasons for holding this view may be shortly summarised. The pericardial bag rests by its base upon the diaphragm, and, when a central tendon of the trefoil pattern is present, the fibrous bag and the central tendon are intimately united to each other, but the ventral surface of the pericardium is attached to the manubrium sterni by a sterno-pericardial ligament which is described

by MACALISTER\* as strong and rounded. A similar ligament of weaker character attaches the pericardium to the ensiform cartilage. These ligaments, especially the former, would resist the traction of the pericardium in the abdominal direction, and so resist the depression of the central tendon. Again, the normal liver presents indented grooves corresponding to, and resulting from apposition with, the ribs which cover it, and these grooves indicate a fairly constant relation between the liver and the ribs, since they could not be formed by any plunging or piston action communicated to the liver from the diaphragm. If, on the other hand, the flattening of the dorsal portion of the diaphragm pushed the liver ventrally towards the ribs, and at the same time the contraction of the ventro-lateral portions of the diaphragm drew the lower ribs towards the liver or even maintained them in a position to resist the liver, then the liver markings would be at once accounted for. Further, STARLING† states that during ordinary respiration the central tendon of the diaphragm is practically motionless, but that as soon as respiration becomes laboured there is an actual downward movement of the diaphragm, and that during laboured inspiration the breathing is mainly thoracic in both sexes, "and the abdomen recedes with each inspiration." Apparently, therefore, according to this observer, it is fair to conclude that a laboured inspiration, by calling for more powerful action of the diaphragm, results not only in greater flattening and depression of the dorsal segment of the arched diaphragm, but also in the lower ribs being drawn closer to its central tendon than during ordinary breathing, which is just what an examination of the muscular attachments would lead one to expect. I therefore arrive at the general conclusion that the diaphragm is the keystone in the inspiratory mechanism, and that its chief action consists in resisting the ventral (forward) movement of the hinder (lower) end of the sternum and of those ribs which are not directly articulated to the sternum. As a result of this controlling action the whole series of ribs may participate uniformly in a general lifting or elevating movement which characterises their position at the end of inspiration as contrasted with their sunken or depressed position at the end of expiration. Such an elevation of the ribs does not call for any rotation of their shafts, and indeed, from the nature of their capitular and tubercular articulations with the vertebral column, rotation of the shaft would be impossible. But the chondro-sternal as well as the articulations just mentioned are from the nature of their ligaments adapted to the movements of elevation and depression of the rib as a whole, and even a small amount of such movement at the vertebral end of a rib would tend to be magnified by the length and obliquity of its shaft. In fact, the capsules of the costo-transverse articulations are sufficiently long to permit of the gliding action necessarily associated with such elevation and depression.

In the seal there are two muscles whose attachments are only readily comprehensible when considered as part of the mechanism for depressing the ribs after they have

\* MACALISTER, *Text-book of Human Anatomy*, 1889.

† E. H. STARLING in Schäfer's *Text-book of Physiology*, vol. ii. pp. 276 and 280.

been elevated. These are the *musculus obliquus externus abdominis* and the *musculus rectus abdominis*. Both of these muscles are attached to the pubis, *i.e.* to the unyielding or rigid pelvis, and between them they provide slips or digitations of insertion into nearly all of the ribs, even extending to the first. Further, the *musculus obliquus abdominis externus* has no attachment to the ilium—in other words, both of these powerful muscles were pubo-costal in their attachments. With a distended chest and a glottis firmly closed so as to render the chest wall fairly rigid, these muscles by their contraction could clearly compress the abdominal contents; but in association with an open glottis, of necessity they must pull their rib attachments towards the pubis—in other words, they must act as depressors of the ribs and thus as powerful expiratory muscles. Such a depressor action compels one to presume and to accept an elevated position of the ribs during inspiration.

There is nothing in the mechanism which seems to require one mode of action for inspiration by the vertebro-sternal ribs and another mode of action by the vertebro-abdominal ribs. Of course, the first costal arch, from the nature of its sternal articulation, is, even in the seal, capable of less elevation than those ribs whose shafts and costal cartilages are longer and whose sternal articulations permit greater freedom of movement; but, in order to secure a uniform method of elevation throughout the series of ribs, it is necessary to provide some more rigid line or *point d'appui* for the start of the movement, and the combination of the first costal arch with the manubrium sterni, together with their powerful scalene and sterno-mastoid muscles, provides such a line. Moreover, in man the clavicle is added to this line by the sterno-mastoid and trapezius muscles as well as by such ligaments as the costo-clavicular and the sterno-clavicular. Again, it will be found that those ribs which elevate most readily are just those whose *heads* are provided with an interarticular ligament passing between the head and the intervertebral disc. Such a powerful structure would be unnecessary unless there were a tendency for the head of the rib to be drawn away from the vertebral column as the dorso-ventral and transverse thoracic diameters increased owing to the elevation of the ribs in full inspiration. There is no ordinary form of inspiration which requires a larger amount of air under regulated control than the inspiratory movement performed by the trained singer, and one of the approved methods of obtaining this result aims at the expansion of the large dorsal surface of the lungs by cultivating the upward movement of the ribs in relation to the dorsal surface of the chest, as being not only easier than, but preferable to, a forced action of the diaphragm. An examination of the mechanism of respiration leads me to the conclusion that, in all forms of respiration, this mechanism acts in the same way, but not, in all its parts, to the same extent, for any particular respiratory act; that ordinary and laboured respiration differ in degree rather than in kind; that the degree of respiration depends upon the amount of air required for any particular form of exertion; that the difference between the respiration of the quadruped and the respiration of man results from differences in their attitude (horizontal and erect), whereby each cultivates that form of chest movement which

requires the minimum of muscular effort. The differences between the adult human male and female types of breathing are adaptations due to the avoidance of severe muscular effort so long as a smaller effort will serve the purpose, and in my opinion they result from the normal differences in the lower or diaphragmatic diameters of the thoracic cavity in the two sexes. To a large extent these differences may be accounted for by the width of the female false pelvis as compared with that of the male. Since the abdomen proper (*i.e.* excluding the true pelvis) contains no organs which are not common to both sexes, it follows that a wide false pelvis, by providing increased accommodation in the lower abdominal regions, is naturally associated with a reduction in the dimensions of the upper or diaphragmatic end of the abdomen. These conditions make elevation of the sternal ribs more necessary in the female than in the male, whose larger diaphragmatic thorax permits of ordinary breathing without the pronounced or visible elevation of his sternal ribs, although their movement may become visible whenever the supply of air required calls for an extension of the elevating movement.

In either sex, a change from the erect attitude to the horizontal (*e.g.* to the supine) position is usually followed by the introduction of more or less of the respiratory features of the opposite sex, owing to the temporary interference with the amount of rib movement in common use when the ribs are unobstructed.