NEUROMUSCULAR ACTIVITY AND RESPIRATORY DYNAMICS IN THE CAT

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by

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ABSTRACT

The movements of the external respiratory apparatus of the cat in quiet breathing and under light anaesthesia were recorded by X-ray photography and by a method of stereo cinephotography. This method was specially developed for this purpose and made possible the characterisation in three dimensions of the respiratory movements. The experimental results were extensively analysed in order to identify and characterise the participation of each of the component structures of the respiratory apparatus in its overall movement.

Based on this analysis, models for the mechanical properties of those structures were proposed. It was found that the rib cage behaves in a shell-like manner whereas the diaphragm and the abdominal walls behave as tensile membrane structures. An approach to the study of these models based on the methods of Structural Analysis is suggested. The mechanical properties of the external respiratory apparatus were found to be strongly conditioned by the nervous control of their muscles; for this reason, it is suggested that they resemble closely those of a process-control mechanical plant in which the peripheral effectors are controlled by the commands generated at a central processor which is subserved by the afferent data produced by the monitoring mechanosensors. These findings and conclusions were incorporated into a proposal in which a new method of tackling the study of the mechanics of breathing is outlined. Also outlined are the potentialities of the study of peripheral systems like the respiratory apparatus in the elucidation of the properties of the nervous centres which are responsible for their performance.

CONTENTS

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CHAPTER 1.0

INTRODUCTION

In all but the simplest forms of animal life the Nervous System is the agency through which the activities of all the other systems in the body are regulated and brought into the harmonious cooperation which makes a viable and efficient living being possible. These coordinating and controlling functions of the Central Nervous System are, however, very difficult to interpret in terms of its actual nervous circuitry, not only because of the high density levels of cell packing and interconnecting which characterise it, but also because the nerve cell is a very complex circuit element whose operational properties are anything but well understood. The study of peripheral body functions, in which reasonable access to the controlling nervous signals exists, could constitute a source of valuable information on the way in which the Nervous System operates. Although these functions are themselves far from simple, their study should nonetheless prove to be much more amenable to treatment by the available methods of analysis; and the functional relationships between its component parts which would thus be revealed could then be traced back to the centres where their nervous control originates. In the sense that the performance of the peripheral system is closely dependent on its nervous control, we may conceive the nervous areas where this control is originated as constituting an 'analog' representation, in terms of nervous circuitry, of the function which the peripheral system implements and, therefore, by learning what is happening at the periphery it should be possible to outline the basic principles, functional boundaries and compatibility conditions which characterise the integrated activity of those nervous areas.

The mechanical performance of the respiratory apparatus represents a typical example of a peripheral function whose study satisfies the conditions mentioned above: (1) it is a sufficiently complex function to present a major problem of analysis but which, by the same token, is likely to lead to a large yield of functional relationships; (2) it involves a great number of muscles which, in the majority, are placed near the surface of the body and present extensive access areas; (3) finally, it persists in the state of anaesthesia demanded by most of the experimental procedures.

Inevitably these introductory remarks to some extent draw on the conclusions and insight which has resulted from the detailed study of our subject, but this fact has seemed to us to be helpful in putting over the basic features of the present work.

Muscles generate mechanical actions because, when excited, their fibres tend to contract and thus to move their respective attachment points towards each other or, if this movement is opposed, to apply a tensile force between them. Furthermore, the amount of contraction of the muscle is directly related to the amount of nervous excitation it receives and this, in turn, is subjected to feedback control adjustments which keep the muscle contraction within convenient physiological bounds (Merton, 1964). One of the aims of the present study is to establish a basis on which this neuromuscular activity in the respiratory apparatus can be related in a significant manner to the mechanical performance to which it leads.

The electrical activity in both the nerve and the muscle fibres can be recorded directly and, at least in the effector pathways, be easily related to each other; but the direct survey of neuromuscular activity throughout the system does not in itself satisfy the requirements we have formulated above because it will not, in general, reveal the underlying phenomenon which is responsible for the recorded values. In order to discover this functional architecture, the respiratory apparatus will have to be studied as a machine and this machine defined in such a way that the levels of mechanical activity - which must occur throughout it in order to bring about the desired movements and load responses - can be deduced by direct application of the principles of Mechanics.

The movements which occur in the respiratory apparatus are, however, anything but easy to model. To begin with, its structures possess a great deal of flexibility as illustrated, for instance, by its capability to respond to postural demands and its possession of large contractile membranes, such as the diaphragm and the abdominal walls, which can easily accommodate appreciable amounts of deformation. This relatively large freedom of movement makes it impossible to predict, from purely geometrical considerations, the changes in their configuration which take place as the respiration proceeds. Furthermore, in a healthy animal, the movements of the individual structures tend to be closely controlled by the concerted contraction of the respective muscles and are generally kept to a limited amplitude well within its range of free passive movements; this is strikingly illustrated when, for instance, one of the intercostal nerves is severed and causes the width of the respective intercostal space to increase to its full passive value under the stretching action of the remaining active spaces. In any description of the kinematics of the respiratory apparatus, therefore, the muscular control of the movements must be taken into account alongside constraints of anatomical or of any other nature; this fact means that, whatever the mechanical actions the respiratory apparatus is performing, the muscles are controlled by the nervous system in a manner which is relevant to that very performance.

The mechanical actions performed by the respiratory apparatus are far from trivial. To take again the example of the rib cage, Alexander (1929) showed in dogs that if intercostal nerves on one side of the body were cut, the parasternal region of the same side of the chest was sucked in by the transmural pressure. This fact reflects the shell-like properties of the rib cage which enables it to resist much higher loads than would be possible simply on the basis of its thickness and, at the same time, keep it light and capable of performing the respiratory movements. In terms of the internal stress distribution, a shell-like structure is a very complex phenomenon and, if the cage muscles take active part in bringing about this effect, a great deal can be expected to be learned about the properties of the nervous control of its muscles by a close study of the mechanical performance of the rib cage. The same can, of course, be said about the remaining structures in the respiratory apparatus.

The aim of the present work is to contribute to the establishment of the basic groundwork on which the study of this generalised mechanical performance of the respiratory apparatus can be based.

The first contribution in this area consists of the development of a method of stereorecording of film sequences, which makes possible the three-dimensional characterisation of the movements of the trunk walls. This method, together with X-ray photography, defines in great detail the movements performed by the different structures which constitute the external respiratory apparatus; and, because these movements are so dependent on the activity of the respective muscles, their detailed description is fundamental to the understanding of mechanics of breathing. The kinematic data are then used in conjunction with anatomical facts to interpret the extent and character of the participation of each structure in the overall movements of the external respiratory apparatus; from this analysis, the basic features of models capable of representing the mechanical properties of each structure are developed.

CHAPTER 2.0

SURVEY OF THE MECHANICS OF THE EXTERNAL RESPIRATORY APPARATUS

2.1 - INTRODUCTION

This chapter is dedicated to the review of the main aspects of the work done up to now in the field of the mechanical characterization of the external respiratory apparatus, work which has taken place for the most part within the framework of the pressure-volume analysis approach.

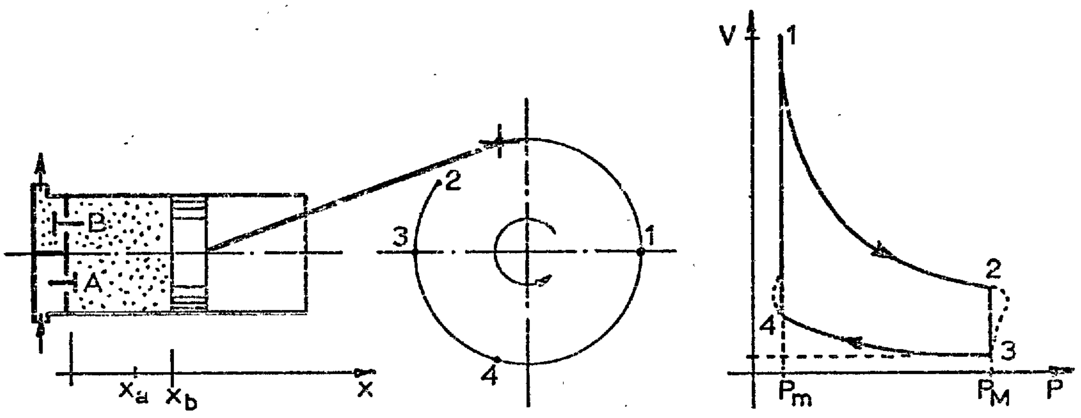
This pressure-volume approach is a natural consequence of the historical evolution followed by the study of the respiratory function: air is the central vehicle in the respiratory process and, naturally, this fact led to an early interest in the study of the associated fluid mechanics, an area of the science of respiration which has been thoroughly investigated. Other aspects of the external respiratory mechanics, such as the movement of the rib cage and of the abdominal walls, the distribution of muscle tensions, the coordination and control of the action of the different muscles, etc., constitute problems which are too complex to be tackled with the tools which have so far been available to the researchers in this field. The pressure-volume analysis, reformulated just after the second world war (Rahn et al., 1946) and consisting of an extension of the concepts of fluid mechanics to the study of the respiratory apparatus, supplied a much needed means of characterization of the mechanical behaviour of this system and made possible a rapid expansion of its quantitative study. The key to this form of analysis is the experimental fact that the respiratory system, when in a passive or relaxed condition and in spite of its structural flexibility, behaves in a reasonably consistent manner for displacements around its equilibrium point; it is this circumstance that confers the pressure-volume analysis the meaning and power it possesses. In spite of its achievements, however, the pressure-volume approach is still severely limited in the range of problems concerning the mechanics of the external respiratory apparatus which it can handle. In particular, this analysis is based on the integral concepts of pressure and volume and does not possess the means to relate quantitatively those concepts with the geometric definition of the structures which materialize them. This point will be raised again in the next section of this chapter, where it will be shown that there is no one-to-one relationship between a given pressure-volume contour diagram and the geometry of the 'chamber' which produces it. In this sense, therefore, the pressure-volume analysis is seriously handicapped, thus explaining why the mechanics of respiration based on this type of analysis has been unable to establish a link between the nervous control of the muscles and the mechanical actions which such control causes them to take.

New approaches are therefore needed and they will have to be based on a detailed study of the machine components themselves. For this reason we have included in this chapter a section devoted to the work done on the kinematic and kinetic characterization of the breathing apparatus and another section dealing with the nervous control of the respiratory muscles, both of which are essential to the development of these new approaches.

2.2 - THE PRESSURE-VOLUME ANALYSIS

2.2.1 - Introduction

The use of pressure-volume or indicator diagrams to assess the overall performance of thermodynamical machines is a long established practice. Figure 2.1 represents the thermodynamical cycle of a reciprocating gas-compressing machine which we have chosen because its operation bears a reasonable resemblance to that of the respiratory machine; the axes of the pressure-volume diagram in figure 2.1 are orientated in accordance with what is usually the practice in respiratory mechanics.



(a) (b)

Fig. 2.1 - Thermodynamical cycle of a reciprocating compressor: (a) diagrammatic representation of the machine cylinder; (b) corresponding pressure-volume indicator diagram.

The diagram of figure 2.1(b) represents the theoretical path followed in the P-V plane by the point representing the state of the machine throughout its basic cycle of operation. Starting with the piston in its outermost position (1) - and the cylinder full of gas let in by the admission valve (A) - we drive it towards its innermost position (3), therefore tracing out the segment 1-2 of the diagram which represents the gas being compressed in the decreasing volume. When the piston reaches point 2, the built up pressure is sufficient to open the exhaust valve (B) and no more compression takes place for the rest of the forward excursion of the piston which ends at point (3). During the phase 2-3 a volume of gas equal to (V_2-V_3), at a pressure P_M, is delivered out of the machine. The reverse journey of the piston, 3-4, first closes the exhaust valve (B) and then proceeds to decompress the remaining gas until a volume P_m is reached and the admission valve is opened; phase 4-1, corresponding to the admission of gas, is then initiated and ends again at position 2. The values P_m and P_M, the limit pressures are determined by conveniently spring loading the admission and exhaust valves. The work done on the fluid by the piston when it moves from x_a to x_b against a varying pressure $P(x)$ is given by:

$$W_{1-2} = \int_{x_a}^{x_b} P(x).A.dx = \int_{V(x_a)}^{V(x_b)} P(V).dV \qquad (2\text{-}1)$$

where A represents the constant area of the cylinder. Hence, by applying this definition to the entire cycle or parts of it, it is possible to work out all the power and energy relationships pertaining to this machine.

When the machine is relatively simple, the pressure-volume diagram can provide some further information, mostly of qualitative nature, regarding particular aspects of the machine performance. The dotted lines between points 2 and 3 and points 4 and 1 in figure 2.1(b), for instance, represent a type of distortion which is identified as 'throttling' and is caused by the reduction of the fluid pressure in the connecting ducts once flow is started by the opening of the respective valve; this effect depends, in extent and signal, on the velocity of the fluid flow and, therefore, on the speed of the piston movement. And it is also quite often possible to use the distortions of the pressure-volume diagram to diagnose minor faults in the performance of the machine which are not visibly shown up in any other way. However, the scope of the pressure-volume diagram as a tool for the characterization of the global performance of a machine is restricted to single chamber systems. If we consider, for instance, a simple machine comprising two cylinders similar to that of figure 2.1, it is easy to see that the individual diagrams, while preserving their usefulness as means of characterizing each cylinder as a component part, cannot be blended together into something which would meaningfully represent the overall performance of the complete machine. Finally, even in single chamber systems, the possibility of interpreting the fine detail of the diagram in terms of the behaviour of individual components in the machine quickly vanishes when the complexity of the machine increases.

2.2.2 - Passive pressure-volume relationships in the external respiratory system

The diagram of figure 2.2(b) represents (Agostoni and Mead, 1964; Rahn et al., 1946) the typical static pressure-volume characteristic of a human subject obtained under conditions of muscular relaxation. It relates the volume of the air space, expressed in percentage of the vital capacity (VC), to the air pressures which must be created in that space in order to force, passively, the walls of the respiratory pump to encompass that volume; the pressures are measured with respect to the pressure at the body surface which is taken thus as zero pressure. As the diagram shows, there is a mid-point position of equilibrium, defined by zero relative air pressure and V_0 relative volume, in which the system tends to stay if undisturbed. The existence of such an equilibrium position is essentially the result of the structural make up of the rib cage. The two sets of intercostal muscles, placed at approximately 100° to each other, will be simultaneously at their rest length only for a particular configuration of the rib cage; if the cage moves away from this position in either direction, the length of the set of intercostal muscles which are antagonistic to that movement will be increased, a change which will be resisted by the elastic stretching of the muscle fibres. Similarly, the rib cartilages, taken as a whole, will only be in an unbent state for a single configuration of the rib cage and will be subjected to bending stresses whenever the latter moves away from that configuration. The combination of all these tendencies results in an overall relaxation point (V_0) which, obviously, is different from that corresponding to the overall system (V_R) and is located at a higher air-volume. At extreme volumes, both above and below the relaxation point, other structural elements such as the ribs proper and the aponeurotic costal linings are also brought in to resist the deforming stresses.

The lowering of the relaxation volume of the rib cage is the result of the combined action of the lungs and the diaphragm. The lungs, as described later in chapter 3.0, are permanently stretched between the peripheral end branches of the respiratory tree and the thorax walls on which, therefore, they exert an inward recoil tension directly proportional to the air space volume. The influence of the diaphragm on the rib cage is a much more difficult matter because of its association with the abdominal muscles and viscerae with which it creates a very complex pneumatic system; this system will be considered again in chapters 4.0 and 5.0 and, for the time being, we will more or less ignore its existence.

The one chamber piston-cylinder system of figure 2.2 represents an imaginary machine which, from the point of view of volume-pressure analysis, is perfectly equivalent to the respiratory apparatus. The free piston on the left together with its respective spring represents the elastic tissue of the lungs; the compound piston on the right is designed in such a way that, when equipped with the set of antagonistic springs shown, it behaves in the very same sense, pressure-volumewise, as the compound walls of the respiratory system. The coupling between the two pistons is achieved, as in the real case, by

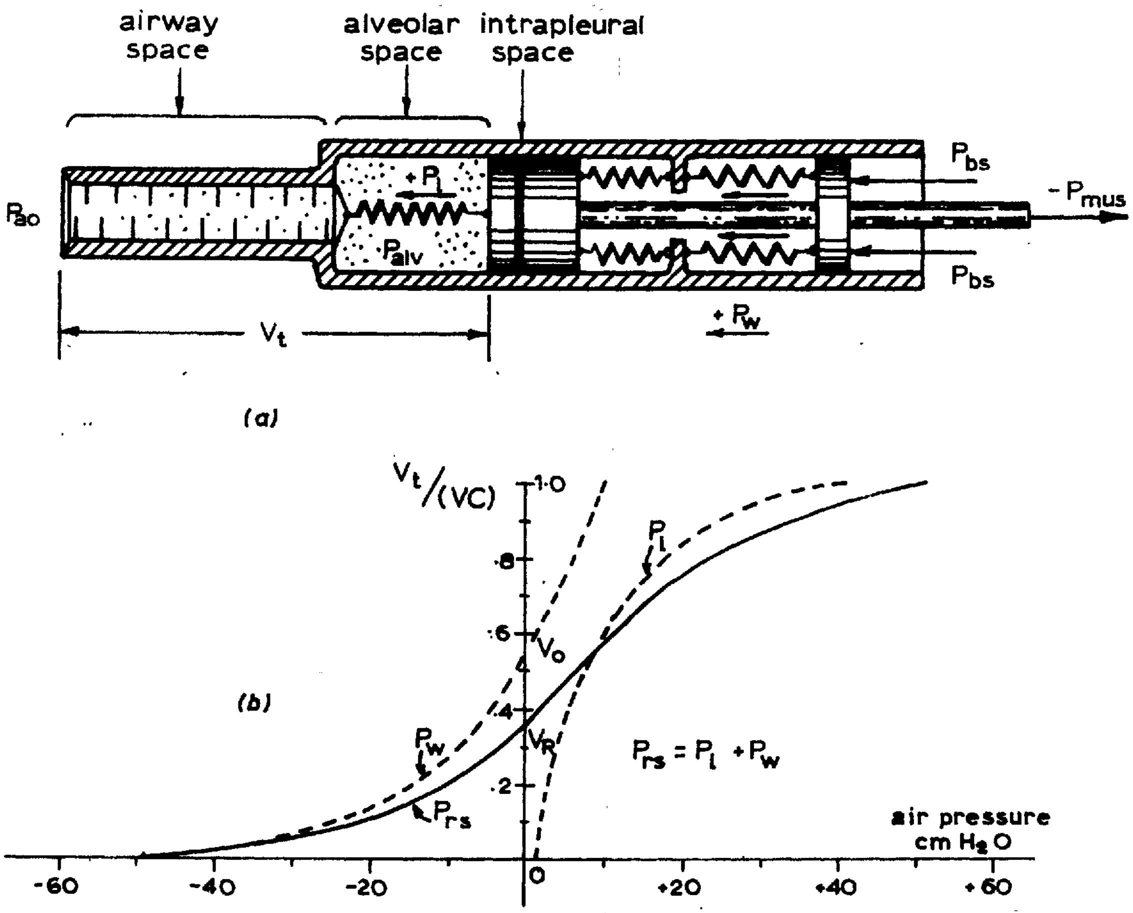


Fig. 2·2 Model of the respiritory system. (a) spring loaded compound piston and cylinder model; (b) corresponding overall passive volume-pressure diagram P_{rs} (V) and its components (in dotted lines).

P_{alv} – air pressure in the alveolar space; P_{ao}–air pressure at the airway opening; P_{bs}–pressure at the body wall; P_l –static tension developed by the lung tissue; P_{mus}–equivalent tension due to the muscle contraction; P_{rs} – static tension developed by the total respiratory system; P_w – idem for the airspace walls; V_0 –equivalent relaxation volume of the rib cage walls; V_R –relaxation volume for the total system.

means of an air-tight, fluid-filled, 'intrapleural space'. The left part of the chamber represents the alveolar space which corresponds to something like 60% of the total air space; this space is followed by an air duct equipped with transverse brakes to produce the same fluid flow resistance as that taking place in the respiratory airways. It is worth noting that the model of figure 2.2 has no particular merit other than allowing us to tie up the properties of the respiratory apparatus - taken in the context of the present analysis - with a physical system which is sufficiently simple to be understood; indeed, there is no limit to the number of models which can be built by changing the geometry, number and characteristics of the individual components and by changing the working principle, and which still display the same pressure-volume diagram. We have considered in our model pressures of two kinds: fluid pressures - P_{alv}, P_{ao} and P_{bs} - which are measured with respect to the atmospheric pressure, and pressures due to mechanical deformation - P_l, P_w and P_{mus}-.

The first group has a straightforward interpretation and only P_{alv} needs a minor clarification: as we will see later, the air in the alveoli is kept still throughout the respiration cycle and, therefore, all the pressure losses which make up the difference between P_{alv} and P_{ao} take place in the conductive part of the respiratory tree. The second group of pressures, represented simply by spring tensions in figure 2.2(a), has a more difficult interpretation in the real respiratory system. These pressures are the scalar (*) equivalents of tensions developed in complex structures which are very hard to visualise.

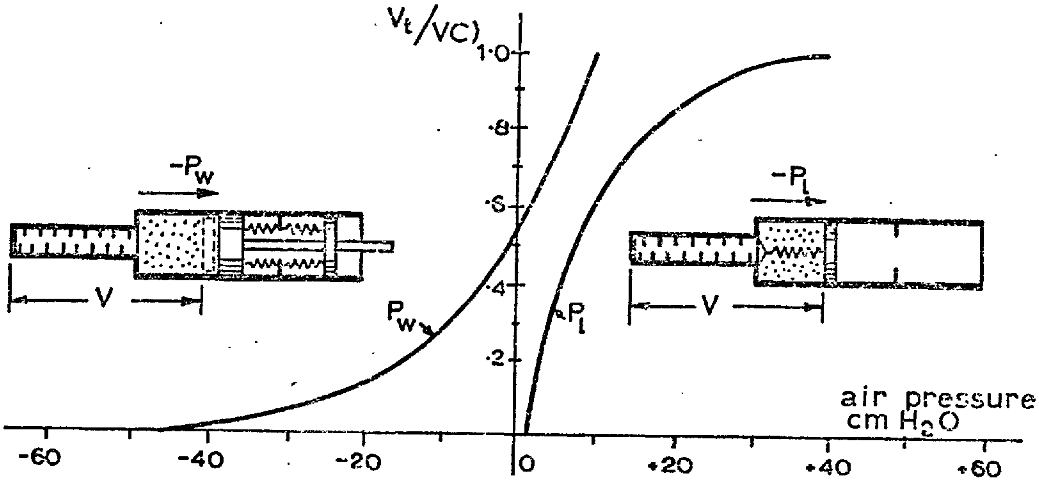


Fig. 2.3 - Measurement of the passive characteristics of the basic components of the model of figure 2.3.

P_{mus} in particular results from the overall action of the muscles, like the intercostal, the abdominal and the bronchial muscles, whose insertions and functions differ enormously; it will be shown in section 2.5.0 that in fact this entity has very little or no physical meaning. Finally, P_l, P_W and P_{rs} represent static pressures and characterise passive properties of the respiratory system, whereas P_{mus} and the air pressures represent both static and dynamic pressures according to the particular conditions of each situation.

The diagram of figure 2.3 illustrates a possible method for the measurement of the component characteristics in the

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(*) In order to be capable of algebraic summation with the air pressures.

idealized model of figure 2.2; we are now going to establish a parallel with similar characterization for the respiratory system. The lungs may be characterized in the manner represented on the right side of figure 2.3: they are excised and inflated and the lung volume together with the air pressure are recorded simultaneously; figure 2.4, represents the pressure-volume characteristic of the excised lung of a cat (Radford Jr., 1964).

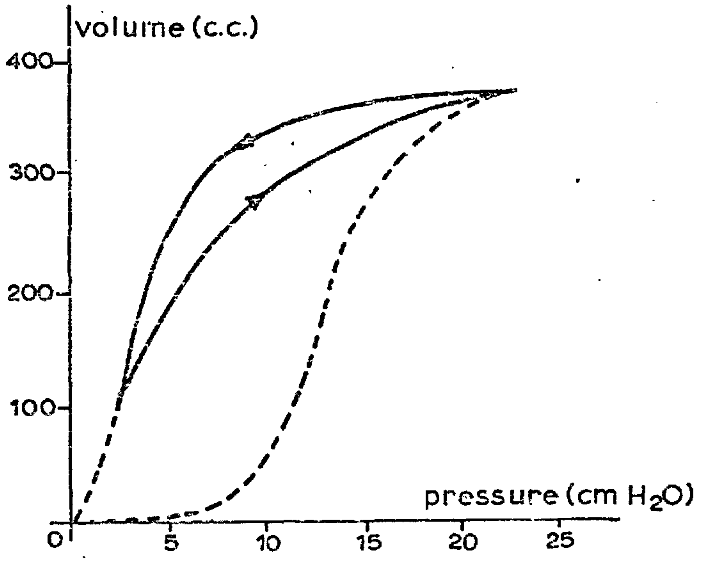

Fig. 2.4 - Volume-pressure characteristics of the excised lung of a cat. Adapted from Radford, 1964.

The lungs are, however, the only component which can be studied in such a direct manner. In fact, to duplicate the procedure suggested on the left hand side of figure 2.3 we would need to replace the lungs in the animal recently killed by a lining which would make the thoracic cavity airtight; this is extremely difficult to do and has not been done to the best of our knowledge. Instead, the physiologists have found a way round this difficulty by measuring the compliance characteristics of the whole respiratory system $P_{rs} = f(V_t)$. The first method used for this purpose, the method of the 'relaxation pressure' (Rahn et al., 1946) relies on the subject's ability to relax completely his respiratory muscles and, therefore, can only be applied to man. Other methods using external pressures to produce thoracic volume changes, are either based on the assumption that the respiratory muscles are relaxed at the end of expiration or, again, on the voluntary muscle relaxation. Finally, the measurement of the static overall characteristics can also be performed under anaesthesia (Butler, 1957; Howell and Peckett, 1957) a method which can be easily applied to animals.

2.2.3 - The pressure-volume plane and the dynamic respiratory cycle

The respiratory apparatus is a single chamber alternating machine and, therefore, the pressure-volume plane can be used, as in section 2.2.1, to represent the state of the system throughout the breathing cycle. We must, however, specify more precisely which values of pressure and volume we are to choose to define the state of the system. Referring to figure 2.2 it is easy to see, if we neglect inertia forces and take the pressures in an algebraic sense, that we may write the following instantaneous equilibrium relationship:

$$- P_{alv} + P_l = (- P_{mus}) - P_w - P_{bs} \tag{2.2}$$

where:

P_{alv} = air pressure in the alveolar space relative to the air pressure in the airway opening;

P_l = tension (pressure) due to passive lung recoil;

P_{bs} = air pressure at the body surface relative to that at the airway opening;

P_{mus} = equivalent tension (pressure) due to the active contraction of the muscles in the air space walls;

P_w = tension (pressure) due to the passive elasticity of the air space walls.

The reason why P_{alv} is affected by a negative sign is because this pressure is measured with respect to the atmospheric pressure and, therefore, it will be assisting P_l when its value is negative and opposing it when positive; a similar relation exists between P_{bs} and P_{mus}, the latter being positive in the direction shown. P_w and P_{mus}, on the other hand, have the same character as P_l and thus are also considered positive when directed inwards, as represented; as we have already seen, it is customary to lump together P_l and P_w to represent the static equivalent passive pressure (P_{rs}) for the total respiratory system:

$$P_{rs} = P_l + P_w \tag{2.3}$$

Equation 2.2 is not correct in so far as we have omitted the inertia forces due to the masses in movement; however, these are (section 4.3.7) sufficiently small to be neglected and we will henceforth treat equation 2.2 as expressing exactly the equilibrium of the forces at play.

It is usual to adopt the volume of the total air space as the corresponding variable in the pressure-volume plane because that is what we can measure directly. Nevertheless, in dynamical conditions and as a result of flow resistance in the airways, the air pressure is not constant throughout the entire air space; furthermore, we have to take into account that we are interested not only in the air pressures but also in the equivalent pressure (tension) of those structural elements, like the lungs, the thoracic walls, etc., which intervene in the respiratory process. For these reasons some authors (Heaf and Prime, 1954; Campbell, 1958) adopted the pleural pressures (P_{pl}) as the pressure variable in the pressure-volume plane, a variable which can either be measured directly (Agostoni et al., 1969; Farhi et al., 1957) or deduced from oesophageal pressure recordings (Fry et al., 1952; Cherniack et al., 1955; Mead et al., 1955; Milic-Emili et al., 1964b).

Referring again to figure 2.2, we see that the pressure to which the pleural fluid is subjected, i.e. the pleural pressure, is given in absolute value and under the same conditions for which the equation 2.2 is valid by either member of that equation; and if we take into account that P_{pl} is measured with respect to the atmospheric pressure and, therefore, has the same sign as P_{alv}, we may write:

$$P_{pl} = P_{alv} - P_l = P_w + P_{bs} + P_{mus} \qquad (2.4)$$

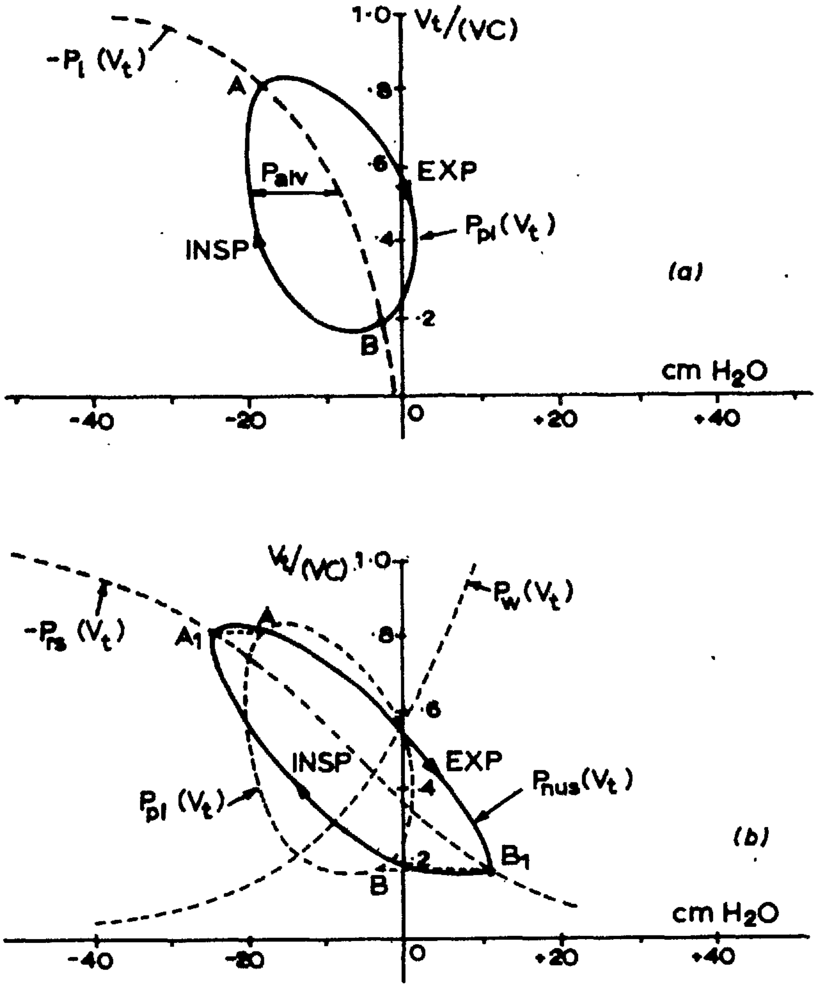

Fig. 2·5 Breathing cycle in the pressure - volume plane.
(a) Campbell representation in terms of the pleural pressure;
(b) Rahn representation in terms of P_{mus}.

The closed pathway shown in figure 2.5(a) represents one breathing cycle in terms of the two variables V_t and P_{pl} (Heaf and Prime, 1954; Campbell, 1958).

It should be pointed out that the closed loops in figure 2.5(a) as well as that in figure 2.6 have shapes which were chosen for convenience of illustration; in practice, their shapes vary from animal to animal and with the conditions of breathing.

The two points A and B where the dotted line $- P_l(V_t)$ crosses the closed loop, and thus where $P_{pl} = - P_l$, correspond, according to equation (2.4), to conditions of zero alveolar pressure, i.e., of no pressure drop or airflow in the airway. Also from the same equation (2.4) we see that the horizontal distance between the $- P_l(V_t)$ curve and the breathing cycle diagram gives, for each point, the respective flow pressure-drop in the lung airways.

From equation (2.4) we can derive a relationship between the tension developed by the thoracic wall muscles and the values measured for the pleural pressure:

$$P_{mus} = + P_{pl} - P_w - P_{bs} \qquad (2.5)$$

Applying this relationship to the figure 2.5(a) where P_{pl} and P_w are supposed to be known as a function of the total air space volume, V_t, and P_{bs} is considered equal to zero, we obtain the loop shown in figure 2.5(b) which constitutes the Rahn representation of the breathing cycle and expresses the equivalent tensions of the thoracic wall muscles as a function of the total volume V_t throughout the entire cycle. In figure 2.5(b) we represent both cycles and the line $P_W = f(V_t)$ which relates the two of them when $P_{bs} = 0$; the points A_1 and B_1 correspond, respectively, to the points A and B in the Campbell representation.

From the equations (2.4) we can write the alveolar pressure in the following two ways:

$$P_{alv} = P_{pl} + P_l \tag{2.6}$$

and:

$$\begin{aligned} P_{alv} &= P_{mus} + (P_l + P_W) + P_{bs} \\ &= P_{mus} + P_{rs} + P_{bs} \end{aligned} \tag{2.7}$$

Therefore, P_{alv} is zero, and no air flow takes place, whenever:

$$P_{pl} = - P_l \tag{2.8}$$

or:

$$P_{mus} = - (P_{rs} - P_{bs}) \tag{2.9}$$

two expressions which are completely equivalent. In the figure 2.5(b), where we consider $P_{bs} = 0$, the line $- P_{rs} = f(V_t)$ represents therefore the set of points of the pressure-volume plane for which there is no air flow in the respiratory airways; muscle pressures to the right of this line produce expiratory flows ($P_{alv} > 0$) and pressures to the left produce inspiratory flows ($P_{alv} < 0$).

2.2.4 - Airways fluid mechanics

We have already seen that P_{alv}, the air pressure in the alveoli, differs from the value of the air pressure at the airway opening, P_{ao}, by an amount which represents the pressure drops in the respiratory tree due to the air flow. The air in the alveoli can be considered perfectly still with the gas exchanges taking place by diffusion and not by mass transport; therefore, the fall in pressure associated with the air flow will occur exclusively in the tracheo-bronchial tree. For the most part of this tree the flow is laminar and the pressure losses are simply proportional to the air velocity measured in units of volume per second (flow); in the upper airways and in the initial generations of bronchi the flow becomes turbulent above a certain air velocity and thus introduces an extra loss component proportional to the square of the fluid velocity. The relationship between these variables is in general determined experimentally and produces results of the form shown in equation (2.10)- which was computed (Mead, 1960) for the human respiratory system:

$$\Delta P = 2.5 \left(\frac{dV}{dt}\right) + 3.3 \left(\frac{dV}{dt}\right)^2 \qquad (2.10)$$

In this equation V is expressed in litres, t in seconds, ΔP in centimetres of water and the two coefficients are adequately dimensioned to guarantee the consistency of the equation. The pressure loss ΔP relates the alveolar pressure, P_{alv}, and the pressure at the airway opening, P_{ao}, in the following manner:

$$P_{alv} = P_{ao} - \Delta P \qquad (2.11)$$

This pressure loss has the sign of the fluid flow and, therefore, is negative in inspiration ($P_{alv} < P_{ao}$) and positive in expiration.

The lungs are stretched between the thoracic walls and the peripheral branches (bronchioles) of the respiratory tree, stretching which gives rise to P_l the passive lung recoil tension. This same tension is of course also felt by the tracheobronchial tree and causes it to undergo a certain increase in its radial dimension as measured with respect to the base of the trachea; this stretching is resisted by the smooth bronchial musculature.- On the other hand the pressure losses ΔP are transmitted to the walls of the respiratory ducts as longitudinal friction forces which, therefore, alternately help and oppose the stretching action due to P_l.

It is common practice in respiratory mechanics to consider a phase plane relating the air volume (V_t) and its derivative ($\frac{dV}{dt}t$), or flow, and to represent in such plane the path followed by the system through the full breathing cycle, as exemplified in figure 2.6.

The principal merit of such a diagram resides in its ability to relate in a very suggestive manner the changes in air volume and in airflow which occur during the breathing cycle; this idea can be extended a step further (Fry and Hyatt, 1960) by associating the three variables, volume, pressure and flow in a three-dimensional diagram. We should, however, keep in mind that the diagram of figure 2.6, as well as the data from which it was deduced, refer almost exclusively to the dynamics of the air flow

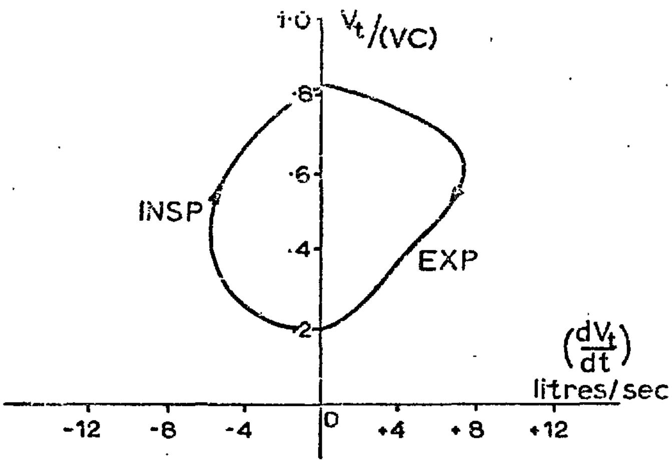

Fig. 2.6 - Air flow phase plane and corresponding cycle for the system whose pressure-volume diagram is represented in figure 2.5. The air flow $V_t = \frac{dV}{dt}t$ is measured at the airway opening and is considered positive in expiration.

in the respiratory tree and has a very limited bearing on the mechanical behaviour of the rest of the breathing apparatus.

2.2.5 - Abdominal pressure distribution

The abdominal viscerae, together with the peritoneal liquid in which they are floating, consitute a sort of compressible fluid (Duomarco and Rimini, 1947) which fills completely the abdominal cavity and has a marked influence on the distribution of pressure throughout that cavity. In order to clarify the influence of the gravitational forces developed in the mass of this 'fluid' on the pattern of pressure distribution inside the abdomen, we organized the diagrams of figure 2.7 which illustrate, for static conditions, the genesis of those patterns. In phase (a) a simple column of fluid is shown in order to represent the fact that the difference in hydrostatic pressure between its top and bottom is constant and equal to the height of the column times the specific gravity of the fluid. In phase (b) the same column of fluid is placed inside a container opened at the bottom end; at this end the absolute pressure is p_{atm}, the atmospheric pressure, and therefore the pressure at the top of the column is $(p_{atm} - p_{fluid})$. In phase (c) the column of fluid is inside a container which is closed with an elastic membrane at the bottom end and opened at the top end where the absolute pressure is therefore p_{atm}; at the membrane end the fluid is in equilibrium under the combined action of its own weight, the tension developed by the membrane and the atmospheric pressure acting on both ends of the column. In order to give an approximated idea of how these forces combine(*), we have drawn the additional diagram where the membrane is represented by two stretched strings joining together at the centre and developing a tensile force, p_m, whose vertical component balances the other forces:

$$2\,p_m \cos\alpha = (p_{fluid} + p_{atm}) - p_{atm} \qquad (2.11)$$

The pressure exerted on the bottom surface of the fluid at this centre point is obtained by adding up the atmospheric pressure and the membrane tension:

$$\begin{aligned} p_{bottom} &= p_{atm} + 2\,p_m \cos\alpha \\ &= p_{fluid} + p_{atm} \end{aligned} \qquad (2.12)$$

The pressure distribution along the length of the

(*) A more accurate description of how these membranes stresses are generated is given in Appendix A.5. See also section 5.4.4.

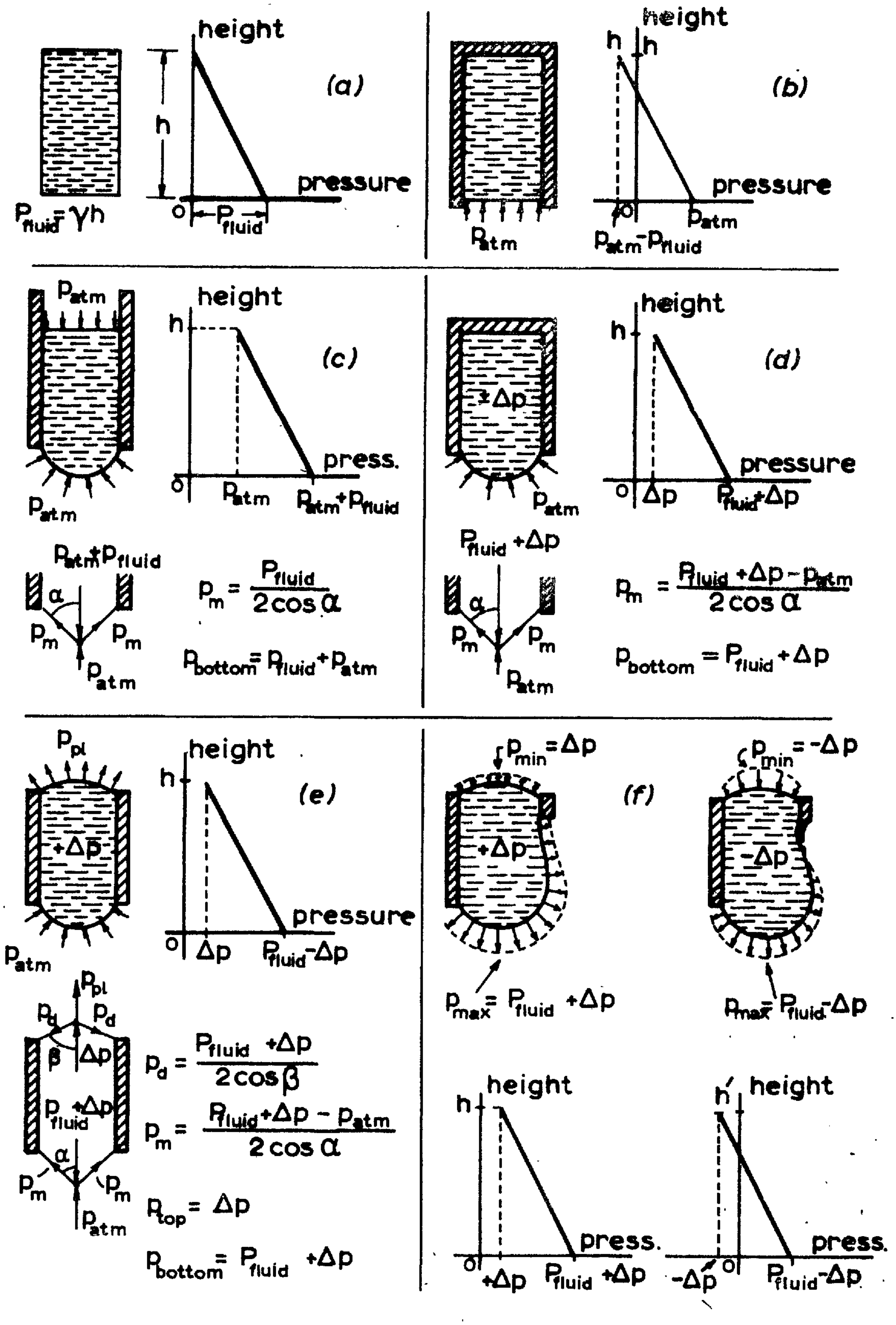

Fig. 2·7 Genesis of the pattern of static abdominal pressure distribution.

column is shown in the accompanying graph. In phase (d) a

Fig. 2.7 - Genesis of the pattern of static abdominal pressure distribution: (a) free column of fluid; (b) fluid in a container opened at the bottom; (c) fluid in a container opened at the top and covered by a membrane at the bottom; (d) closed container with membrane cover at the bottom; (e) container closed at both ends by a membrane, the top one of which is subjected to negative pleural pressure; (f) container with a cross-section similar to that of the abdomen. Explanation in the text.

h- fluid column height; p_{atm}- atmospheric pressure; p_{bottom}- resulting pressure acting on the bottom surface of the fluid; p_d- tension developed by the top (diaphragmatic) membrane cover; p_m- idem for the bottom membrane; p_{pl}- negative pleural pressure; p_{top}- resulting pressure acting on the top surface of the fluid; P_{fluid}- weight of the total fluid column; α,β- angles made with the vertical by the vectors which represent the internal membrane tensions; γ - specific weight of abdominal fluid; Δp- residual fluid pressure at the top of the column.

similar procedure is followed to find the absolute reference of the pressure at the bottom of the column. We see that, this time, the tension developed by the membrane can be greater or smaller than the value needed to balance the weight of the fluid column. If the membrane tension is greater than this balance value, the fluid will be subjected to a bias compression stress, Δp, which adds to the hydrostatic pressure component throughout the fluid mass; when, on the other hand, the membrane tension is smaller than that value, Δp is negative and its absolute value may be anywhere between zero and the maximum $(p_{atm}-P_{fluid})$ which occurs for zero membrane tension. We, therefore, see that by controlling the state of internal tension of the membrane the value of Δp, and with it the location of the pressure diagram along the pressure axis, can also be controlled. In figure 2.7(e) the top of the container is now replaced by a membrane subjected to a negative pressure p_{pl}. The pressure distribution is identical to that of the previous phase with the single difference that the value of Δp is now conditioned by both top and bottom membranes. Finally, in figure 2.7(f), left and right, we represent a sagittal cross-section of the abdominal compartment with the pressure reaction of the fluid on the walls represented by inward and outward going arrows according to its direction. In the diagram of the left, Δp is positive and the fluid reaction is also positive everywhere with a minimum value Δp at the top and a maximum $(p_{fluid} + \Delta p)$ at the bottom, both of which are not directly dependent on the external pressures p_{atm} or p_{pl}. The diagram of figure 2.7(f), right, shows the case when the bias pressure Δp is negative, a situation which occurs when the bottom membrane tension is not able to withstand the pressure $(p_{fluid} - p_{atm})$ and gives in; in these conditions, the abdominal fluid lowers in the compartment enough to build up, at its top surface, a negative bias pressure which is in equilibrium with p_{pl} and p_d. Because Δp depends on p_m and on p_d it cannot be computed without the knowledge of the shape and properties of the membrane or membranes which constitute the boundaries of the abdominal compartment; this computation as it will be shown in chapter 5.0 constitutes quite a difficult task. It is, however. possible to measure Δp experimentally and, once this is known, the distribution of static pressures throughout the abdomen can be deduced from it and the knowledge of the shape of the abdominal cavity and the density of its filling fluid. In practice the gastric pressure is the quantity which is measured and from it the value of Δp - considered as the value of the abdominal pressure at the caudal surface of the diaphragm - can be computed if we neglect the tonus of the stomach and changes in the difference of the hydrostatic levels of the two organs throughout the respiratory cycle. And, finally, if Δp is known and if the pleural pressure is also known, the value of the transdiaphragmatic pressure, given by their algebraic sum, can be computed.

The distribution of the fluid pressure in the abdominal cavity is strongly influenced by the animal posture (Duomarco and Rimini, 1944 and 1947; Agostoni and Mead, 1964) but the diagrammatic analysis of the figure 2.7 is always applicable with minor adjustments. Also, under dynamic conditions due not only to the respiratory movements but to displacements of any other origin, inertia forces will be developed which have to be taken into account together with those of hydrostatic origin. It has been established (Agostoni and Rahn, 1960) that, for a given posture of the body, the gastric pressure varies with respiratory air volume in an acceptably consistent manner; also, as a result of the small range of absolute values covered by the abdominal pressures throughout the respiratory cycle, the volume encompassed by the abdomen can be treated as being approximately constant. These two facts have been taken advantage of (Agostoni, 1961; Milic-Emili et al., 1964a) to characterize the abdominal compartment, in a pressure-volume sense, in the same plane as the thoracic compartment.

2.2.6 - The pressure-volume analysis and the work of breathing

The fact that areas in the pressure-volume plane have the dimensions of work, has suggested the possibility of deducing, from the area delimited by the breathing cycle contour, the amount of work involved in the respiratory act (Fenn, 1951, 1963; Otis, 1964; Otis et al., 1959). However, the relationship between these two entities is not as simple as it may seem. The first point which has to be considered refers to the fact that the pressure and volume represented in the diagram must be consistent, i.e., must apply to the same physical entity, in order to produce meaningful results. In the case of the Campbell and of the Rahn representations of figure 2.6, for instance, this condition is not satisfied in so far as they relate the volume of the total air space with, respectively, the pressure in the pleural space and the fictitious muscular pressure P_{mus}, both of which are external to the air space; the pressure in the air space ranges from P_{ao} to P_{alv} (equation 2.11) while, on the other hand, the volume changes undergone during the breathing cycle by the pleural space are negligible and those undergone by the entity to which the pressure P_{mus} refers are too obscure to be worked out. Indeed, it is not possible to obtain any really meaningful measure of the work done in the breathing act from either of those representations of the phase plane. The only fraction of the work done by the respiratory musculature which could possibly be deduced from pressure and volume considerations is that which refers to the flow of air in the airways: by a detailed study of this airflow in the upper airways and respiratory tree, to which it is confined, it would be possible to obtain the information necessary for the computation of the energy spent in promoting such flow.

The authors we have quoted above used the Rahn representation of the pressure-volume diagram to perform their calculations and, therefore, they obtain the amount of work which would have been done on the inhaled air if this air had been subjected to a uniform pressure equal to P_{mus}. The value thus obtained is obviously larger than that which would be obtained from the computations we have just suggested but, even so, it is only a minor fraction of the values deduced from measurements of oxygen consumption (Campbell et al., 1958; Fritts et al., 1959; Millic-Emili and Petit, 1960). The reasons for this discrepancy stem from the fact that the pressure-volume diagram can, at the most, account only for the energy expenditure involved in overcoming the resistance to the air flow in the airways and the passive elastic forces by which the respiratory apparatus resists movement. The fact that, for instance, the respiratory muscles are responsible for the structural integrity of the rib cage - a task which creates much larger demands on power - is not considered at all. This problem which will be dealt with in later chapters can be briefly considered in the following manner: in the cylinder of figure 2.1 we take for granted the physical stability of its walls and, therefore, do not need to consider the energy necessary for keeping them from collapsing, buckling or bursting; the pressure-volume relationships to which the fluid is subjected thus describe completely all the energy exchanges which take place. In the case of the chest wall 'cylinder', on the other hand, energy must be spent in keeping the walls from collapsing under the action of the negative transthoracic pressure and the abdominal and other muscles; therefore, the respiratory musculature must not only supply the energy absorbed via the air in the airspace as described by a pressure-volume diagram, but also the energy involved in the stabilization of the walls. By 'collapse' of the cage walls we understand the fact that the ribs would not be able to maintain their elevated inspiratory position and would rotate towards the column with the consequent reduction of the total volume encompassed by the cage. This effect is neatly shown in the experiments described in chapter 4.C and relating to the application of Flaxedil. It has also been shown (Alexander, 1929) that when the intercostal muscles are sectioned in anesthetized dogs, the parasternal region of the chest actually sinks in under the load represented by the negative pressure produced by the movements of the diaphragm.

The parallel of the situation described for the rib cage can be illustrated with respect to the device of figure 2.8; in this case the walls of the cylinder would be made semi-flexible and extra work would have to be done to prevent them from deforming under the pressure developed inside it.

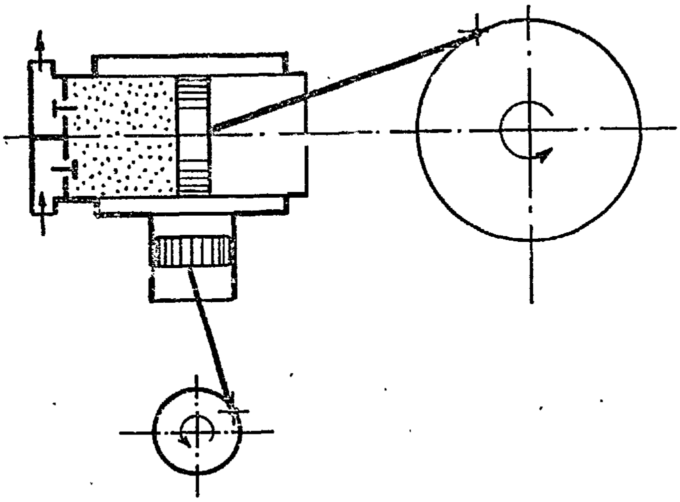

Fig. 2.8 - Reciprocating compressor of figure 2.1 built with a thin walled cylinder.

Finally, we could further illustrate the complexity of the relationship which exists between the fluid pressure-volume diagram and the activity of the muscles which power the breathing act, by noticing that where the diagram of figure 2.5(b) is horizontal - and, therefore, the change of pressure takes place at constant volume - the work done on the fluid is nil, whereas the chest wall muscles will have to alter the number of contracted muscle fibres in order to meet the varying stress produced by the transthoracic pressure. There are, then, changes in the work done by the muscles which are not accounted for in the diagram and, as the energy spent by the muscles is converted into heat and is not recoverable, a large energy expenditure can take place all round the Rahn respiratory cycle without leaving any trace in it. The structural duties performed by the respiratory muscles are not limited to maintaining firm the respiratory 'cylinder' and include those which result from postural demands, locomotion, inertia forces due to mass accelerations, etc. ; none of these duties are taken into account in the pressure-volume diagram.

2.3 - THE MECHANISMS APPROACH

2.3.1 - Introduction

The recording and study of the movements of the external respiratory apparatus has so far deserved a limited attention in respiratory mechanics. The generalized acceptance of the pressure-volume approach, which does not create a serious demand for the kind of information such studies could provide, and the non existence of an alternative mechanisms-minded approach which would depend on such information, are the main reasons for this lack of interest. Some work has been done, however, mostly in connection with the three basic constituents of the external respiratory apparatus - the rib cage, the diaphragm and the abdomen -, and the purpose of this section is to describe it briefly.

2.3.2 - Mechanics of the rib cage

The first attempt to interpret the action of the intercostal muscles, responsible for the movements of the rib cage, is due to Hamberger (Agostoni, 1964) and dates from as far back as 1748. In Hamberger's analysis, the ribs, articulated at the costovertebral joints and at the sternochondral joints, are acted on by the intercostal muscles as shown in figure 2.9 for the case of the external intercostal muscles. The force of contraction Q acting at B on the rib $\overline{AC}$ can be replaced by a

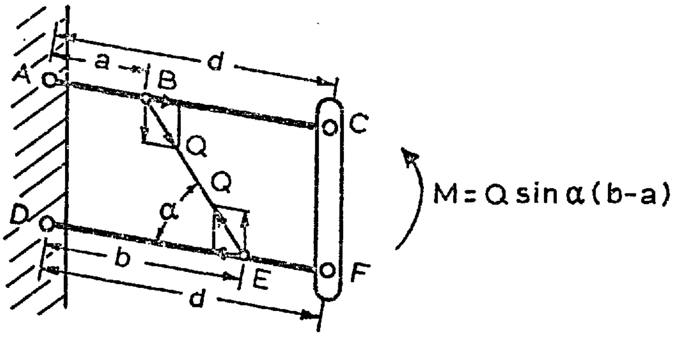

Fig. 2.9 - Action of the external intercostal muscles.

force $Q_1 = \frac{Q.\sin\alpha.a}{d}$ acting at C which produces the same torque at A if the rib is assumed rigid; similarly, the tension Q acting at E can be replaced by a force $Q_2 = \frac{Q.\sin\alpha.b}{d}$ acting at F. The total force acting on the segment of sternum $\overline{CF}$, also supposed rigid, is therefore the difference (Q_2-Q_1) which produces a torque $M = Q.\ \sin\alpha.\ (b-a)$ acting as shown in figure 2.9, i.e., tending to rotate the rib in a counterclockwise direction. In an identical manner the internal intercostal muscles produce a clockwise acting torque.

Hamberger's analysis, correct as it is, is too limited to take into account the fact that the rib cage is neither a planar structure nor is it limited to a single intercostal space. Indeed, the tackling of the global problem posed by the multi-element three-dimensional structure, which the rib cage is, can only be done by the methods of the modern analysis of structures. These are the reasons why this subject has been practically ignored by the researchers in the mechanics of breathing; only few isolated efforts have been made to record the movements of the rib cage (Agostoni et al., 1965; Agostoni and Mognoni, 1966; Jordanaglou, 1970; Konno and Mead, 1967; Polgar, 1949; Wade,

1954) but even these consist of limited observations of basic kinematic relationships and represent no attempt to tackle quantitatively the global phenomenon of the rib cage movement.

2.3.3 - Mechanics of the diaphragm and the abdomen

The diaphragm is a musculo-tendinous dome inserted around the lower margin of the rib cage and subjected to the negative pleural pressure on its cranial side and to the pressure exerted by the abdominal viscerae on its caudal side. To the best of our knowledge no theoretical analysis of the elastic membrane behaviour of the diaphragm has been made so far and only plain X-ray kinematic recordings have been done (Dally, 1908; Herxheimer, 1949; Keith, 1907; Wade, 1954; Wade and Gilson, 1951).

The abdomen constitutes an inflatable structure limited by its lateral muscular walls, the vertebral column and the diaphragm and filled by the abdominal viscerae; this inflatable structure acts as a stabilizer of the lower circumference of the rib cage and its wall muscles are antagonistic of the diaphragm in the respiratory movements. The references given above contain also most of the work done in this area.

2.4 - THE NEURAL CONTROL OF THE RESPIRATORY MUSCLES

2.4.1 - Introduction

The fact that the muscle fibres have to be triggered into contraction by nerve action potentials makes the neurophysiology of the respiratory apparatus in general, and of the external respiratory apparatus in particular, a very central issue of the mechanics of respiration. In fact and contrary to what happens in conventional man-made machines where the movements of the different component parts are geometrically determined, the movements in the respiratory apparatus seem to be determined by the way in which the different muscles are programmed to contract and only secondarily by the existence of geometrical constraints. When such geometrical constraints exist, as for instance in the case of the costovertebral joints, they are not allowed, within the physiological range of their action, to interfere directly in the movements but are, instead, equipped with stretch transducers which participate, via compensatory nervous loops, in the elaboration of the commands issued to the associated muscles.

In spite of its vital role as mediator of the muscular action and, therefore, of the movements occurring in the respiratory process, the study of the nervous control of the respiratory muscles has developed quite outside the field of respiratory mechanics and its major contributions have in fact been concerned with the problems of determining the participation of the different muscles in the respiratory process and of investigating the existence and nature of central and peripheral reflex loops. The task of integrating this nervous control and the kinematic and kinetic detail of the movements executed by the structures which constitute the respiratory machine has not been tackled yet. It is our purpose to try to contribute towards this end through our present work and we have included this section in order to stress the need for considering the neurophysiology of the external respiratory apparatus as an integral part of its mechanical characterization.

2.4.2 - Identification of the respiratory role played by the different muscles

The methods employed to characterize the respiratory role of the different muscles of the external respiratory apparatus include the histological investigation of their nerve fibre supply, the recording of action potential spike trains on nerve filaments which innervate them and the recording of their electromyograms. Using these methods, the participation of the diaphragm (Agostoni et al., 1960; Boyd et al., 1965; Delhez et al., 1965; Koepke et al., 1958; Murphy et al., 1959; Petit et al., 1960; Sant'Ambrogio et al., 1963), of the intercostal muscles (Bronk and Ferguson, 1935; Chennels, 1957; Gesell et al., 1940a, b; Gesell, 1959; Hoshiko, 1962; Koepke et al., 1955, 1958; Murphy et al., 1959; Taylor, 1960), of the abdominal muscles (Bishop, 1964, 1967, 1968; Campbell, 1952, 1957, 1958; Campbell and Green, 1953a, 1953b, 1955; Jones and Pauly, 1957; Tokizane et al., 1952) and other respiratory muscles (Bishop, 1964, 1967, 1968; Campbell, 1955a, b, c, 1958; Jones et al., 1953; Jones and Pauly, 1957; La Ban et al., 1965; Portnoy and Morin, 1956; Raper et al., 1966) in the respiratory process has been reasonably well established.

2.4.3 - Integration of the peripheral structures in the nervous control loops which activate the external respiratory muscles

It has been explained, both in the present and in the previous chapter, that it is only through their nervous integration and control that the mechanical structures which make up the external respiratory apparatus are brought to perform as a proper breathing machine. In what follows we review very briefly the information available to date on the proprioceptive control of the respiratory muscles and analyse the two most important peripheral control assemblages, viz., the 'stretch-reflex servo assemblage' and the control assemblage of the costovertebral articulation.

The rib cage is by far the most complex moving component in the external respiratory apparatus. Its muscles are attached to the skeletal framework made up by the column and by the ribs, the cartilages and their articulations and, therefore, they have to be tightly controlled in order to bring about the harmonious movement of the whole structure. Furthermore, the rib cage also plays a major role in the structural stability of the trunk, a role which depends on the active contraction of its associated muscles and which, therefore, must be taken into account by the centre responsible for the motor control.

There is a great deal of evidence regarding the local proprioceptive control of the external respiratory muscles such as, for instance, the intercostal paralysis produced by the section of the dorsal roots of the intercostal nerves (Coombs, 1918; Nathan and Sears, 1960), the finding of stretch reflexes associated with the intercostal muscles (Euler and Fritts, 1963; Ramos, 1959; Ramos and Mendoza, 1959; Sears, 1958, 1963, 1964a, b) and the existence of fast spinal reflex responses to sudden mechanical loads (Fleish, 1944; Dolivo, 1953). Most of this evidence is related to the intercostal muscles on which the structural integrity of the rib cage itself mostly depends and which are richly supplied with mechanoreceptors (Barker, 1967; Cooper, 1960; Siebens and Puletti, 1961). The diaphragm, although associated also with the rib cage and strongly involved in the movements of respiration, is a much simpler structure and does not seem to possess such an elaborate local control; instead, and in agreement with the fact that its action is mainly concerned with the stretching of the lung tissue, there is evidence (Campbell et al., 1961; Head, 1889) of a proprioceptive control emanating from higher centres in which the output of the lung receptors play a very important part. It is not surprising, therefore, to find that the motor innervation of the diaphragm is supplied from the cervical area of the spinal cord and that the number of mechanoreceptors which have been reported in this muscle (Barker, 1967; Cardin, 1944; Cuénod, 1961; Winckler and Delaloye, 1957; Yasargil, 1962) is considerably smaller than in the intercostal muscles. The section of the dorsal roots of the phrenic nerves causes paralysis of the diaphragm in man (Nathan and Sears, 1960) but not in the cat (Sant'Ambrogio et al., 1962); the hemisection of the spinal cord at the basis of the brain causes the paralysis of the hemi-diaphragm on the same side, an effect which is removed immediately after the opposite phrenic nerve is also sectioned. This effect constitutes the 'crossed phrenic phenomenon' (Chatfield and Mead, 1948; Dolivo, 1953) and, although it does not have a simple explanation, it seems to indicate that the afferent activity of each half of the diaphragm tends to be inhibitory of the motor innervation of the other side (Fleish et al., 1946).

The information regarding the reflex control of the abdominal muscles has been gathered through the study of the reflexes elicited by local distension of the abdominal wall (Pike and Coombs, 1917; Rijnbeck, 1937; Kugelberg and Hagbarth, 1958) or by the compression of the chest wall (Ramos, 1959) and by positive pressure breathing experiments (Bishop, 1964, 1967). In this latter case, it was shown that the reflex expiratory activity of the abdominal muscles is abolished completely if both cervical vagal nerves are cut, or if the spinal cord is sectioned at low cervical or thoracic level or, finally, if the dorsal roots from T8 to L3 are interrupted on both sides. These three means of abdominal muscle paralysis suggest that the abdominal muscles, like the diaphragm, are controlled from a higher centre to which afferent proprioceptive information is brought via the vagi and the spinal afferent pathways. The same experiments (Bishop, 1964) also showed that the evisceration of the abdominal cavity did not interrupt the abdominal reflexes, a fact which suggests that the mediation of the abdominal 'fluid' is not necessary for the establishment of the control reflex.

The mechanoreceptors on which the control of the respiratory muscles is based consist essentially (Barker, 1967) of muscle spindles, Golgi tendon organs, Pacinian corpuscles and Ruffini endings, both isolated and as components of peripheral control assemblages. In this chapter we shall only describe summarily the two most important of these assemblages, namely the 'stretch-reflex servo assemblage' and the 'control assemblage of the costovertebral joint', the latter being here presented in a simplified two-dimension version.

The concept of a feedback or servo system to control the length of muscles was first proposed by Wiener (1948) and Merton (1951) and a great deal of information on the performance of these mechanisms has since accumulated (Granit, 1955; Hammond et al., 1956; Matthews, 1964). The evidence for the existence of such mechanisms in the intercostal muscles, first pointed out by Sears (1958), has been abundantly investigated (Corda et al., 1965; Critchlow and von Euler, 1965; Eklund et al., 1964; Euler and Fritts, 1963; Ramos and Mendoza, 1959; Sears, 1963, 1964a, b).

The 'stretch-reflex servo assemblage', represented in the diagram of figure 2.10(a), consists basically (Bayliss, 1966; Buller, 1966; Euler, 1966; Granit, 1955) of a muscle-spindle stretch-receptor (2), the muscular motor unit or units (1) which the spindle controls, the tendon organ receptor (6) associated with these motor units and, finally, the neural circuitry (7) which supplies the servo system of control. The muscle-spindle (2) consists of a few muscle fibres, in parallel with the muscle units they control, and which possess a differentiated central zone equipped with stretch receptors and contained in a capsule of connective tissue; the rate of firing of the spindle receptors is proportional to the degree of stretching of the central zone, a stretching which can result either from the increasing of the distance between the points of attachment of the fibres or from contraction of these fibres or both. The Golgi tendon organs are also stretch-receptors located in series with the muscles fibres whose stretching tension they control by inhibiting the corresponding nervous input (Granit, 1955).

The working principle of the stretch-reflex servo assemblage is illustrated in figure 2.10(a). In phase (a1) the muscle unit is contracted to balance the load (9) and the system is in equilibrium. In phase (a2) the electrical input is increased causing an immediate increase in the excitation of the muscle spindle fibres (intrafusal fibres) which contract further and force the rate of firing of its stretch-receptors to go up; this higher electrical output from the muscle spindle is fed to the '$\alpha-\gamma$ linkage processor' and determines an increase in the contraction of the muscle-unit which thus takes up a further load. In phase (a3) a new equilibrium has been reached, in which the contraction of the intrafusal fibres is still identical to that of phase (a2) but, because the muscle has shortened, the firing of the muscle spindle stretch-receptors has been reduced to a rate somewhere between those of phases (a1) and (a2). The tendon receptors are not shown active in this diagram in order to

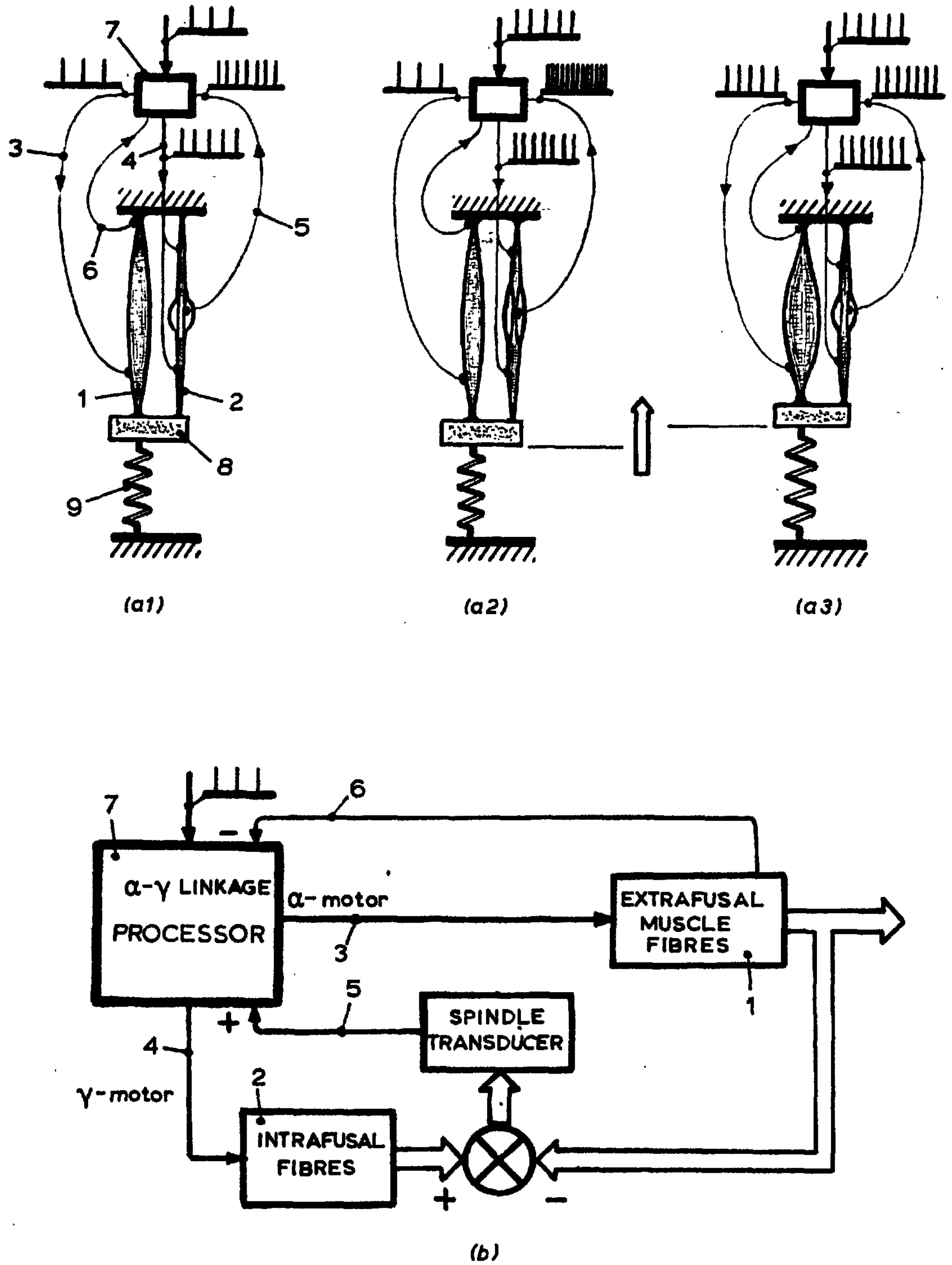

Fig. 2·10 Stretch-reflex-servo assemblage : (a) operation of the servo system : 1-initial state; 2-arrival of command for increased muscle contraction; 3-final position. (b) Block diagram of the system. 1-extrafusal muscle fibres; 2-intrafusal muscle fibres; 3-α-motor fibres; 4-γ-motor fibres; 5-muscle spindle afferent fibres; 6-muscle tendon organ afferent fibres; 7-(α-γ) linkage processor; 8- moving bone; 9-load.

keep it reasonably simple, although they are an integral part of the assemblage. The block diagram of the stretch-reflex-servo assemblage is shown in figure 2.10(b) where the thin arrows represent electrical signal flows and the wide arrows represent mechanical transduction flows.

A two-dimensional version of the joint-control assemblage is represented in figure 2.11, which shows the two antagonistic motor units (2), the synovial joint (4) and the lateral ligaments (3). The stability of the joint is primarily guaranteed by the lateral ligaments and the capsular ligaments of the synovial joint; the movements of the joint are guided by the synovial joint but conditioned by the ligaments, both the lateral ones and the capsular ligaments of the synovial joint. These ligaments which are very flexible, very strong and inelastic allow a very smooth movement of the joint within its physiological range and obstruct completely the movement outside this range. There is good reason to believe (Gray's Anatomy, 1954) that, in life, the joint muscles are controlled in such a way that the amplitude of the joint movements is determined by them and not by the stretching of the ligaments which, indeed, tends to cause a sensation of pain whenever it occurs; it is of advantage to think of the joint as a floating hinging device which is kept centred through the action of its own positioning servo system. This servo is fed with the afferent data, originating in the receptors of the ligaments, and which is processed by the joint control system in such a way that the coordination of the muscles is properly achieved. When a movement command reaches the processor, this organ excites the antagonistic muscles in accordance with the desired movement, the load on the system and the constraints represented by the geometrical arrangement of the ligaments.

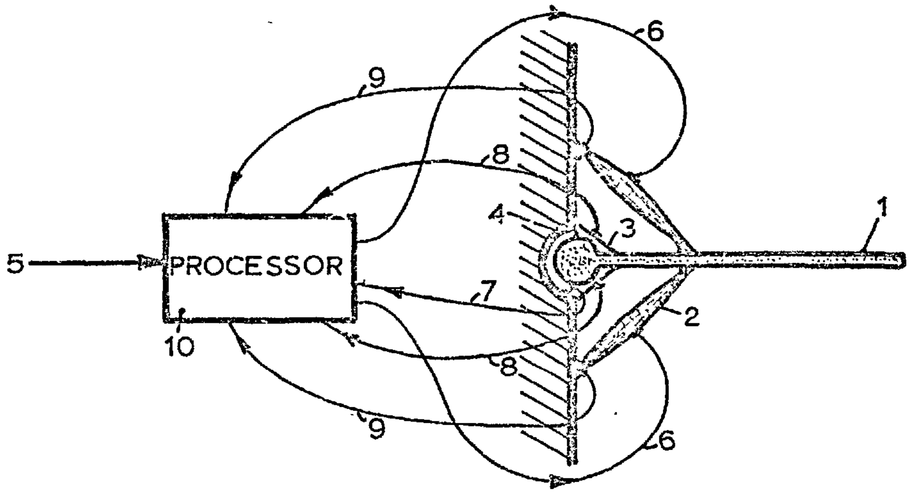

Fig. 2.11 - Two-dimension joint-control assemblage.

1- moving bone; 2- muscles; 3- lateral ligaments; 4- synovial joint; 5- input to the joint processor; 6- motor fibres to the muscles; 7- afferent from the synovial joint; 8- afferents from the lateral ligaments; 9- afferents from the tendon organs; 10- control processor.

The mechanoreceptors have been studied in the costo-vertebral joints (Godwin-Austin, 1967, 1969, 1969a) and in the knee joint (Andrew and Dodt, 1953; Boyd and Roberts, 1953; Eklund and Skoglund, 1960; Gardner, 1944, 1948; Skolund, 1956) of the cat and found to be essentially of two types: the Ruffini-like receptors of the slow adapting type and fast adapting receptors sensitive only to the rate of change of their stretching. These receptors are located in the ligaments and monitor all the parameters which define the degrees of freedom of the joint: angular or gliding movements of the joint, pulling away of the articular surfaces, etc., are monitored by receptors in the ligaments which tend to be stretched by the movement; compression stresses on the joint are monitored by the receptors in the capsular ligaments of the synovial joint, ligaments which tend to be stretched by the increase of the pressure on the synovial fluid.

It has been suggested (Hammond et al., 1956) that the functional role of the stretch-reflex-servo, both in the control of posture and in the dynamic control of the respiratory movements (Corda et al., 1965) consists in supplying a length follow up servo loop which compensates for the loading of the system. According to this concept, the centre which commands the stretch-reflex assemblage feeds simultaneously the intrafusal fibres with a conveniently scaled version of the excitation applied to the associated motor units; if, because of loading effects, the shortening which results for both intra and extra fusal fibres is not the same, the muscle spindle receptor firing rhythm will alter accordingly and cause the '$\alpha-\gamma$ linkage processor' to introduce an extra component to adjust the muscle tension developed by the motor unit.

We see, therefore, that the information passed on by the controlling centre to the assemblage expressed length changes of the distance between attachment points of the motor units and not muscle tension, an entity which plays a role of a dependent variable(*). The same conclusion is, of course, perfectly correct

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(*) Muscle tension is directly monitored by the tendon organs in series with the muscle fibres and whose output plays a role of negative feedback to avoid excessive muscle contraction.

for the joint-control assemblage of figure 2.11, where the role of the linear length is played by the angular length of rotation.

2.5 - SUMMARY AND DISCUSSION

In the present chapter the pressure-volume approach to the study of the respiratory mechanics and the data available on the proprioceptive control of respiration are reviewed very briefly.

The pressure-volume approach is presented in such a way as to emphasize its inadequacy for the mechanical analysis of the mechanics of the external respiratory apparatus. Thus, the simple device of figure 2.1(a) is introduced as an example of a system with only two degrees of freedom: the pressure, which is constant everywhere in the chamber of the cylinder, and the volume of this same chamber which, because the cross-sectional area of the cylinder is constant, is proportional to the displacement of the piston and, therefore, defines in a unique way the position of all the moving parts which drive the piston or are driven by it. Provided, then, that the kinematics of the mechanisms associated with the piston are known, the specification of the values of the pressure and volume of the gas inside the chamber is enough to define completely the state of such a machine from both the thermodynamical and mechanical points of view.

The situation with regard to the external respiratory apparatus is, of course, quite different: the pressure inside the 'chamber' varies from point to point and the volume does not correspond to a unique configuration or shape of that 'chamber'. The simple kinematic relationships which can be postulated for the machine of figure 2.1(a) and with which the instantaneous positions of all the component parts can be deduced from that of the piston, have absolutely no counterpart in the mechanics of the external respiratory apparatus. Thus, the movements of the component structures of this apparatus, the distribution and control of the muscular tensions throughout them are, amongst others, questions with a fundamental bearing on the mechanical definition of the respiratory act which are beyond the scope of the conceptual package embodied in the pressure-volume analysis. The introduction of the concept of a unique passive or relaxed characteristic (Rahn et al., 1946) represents a tentative to complement this type of analysis with a perfectly well defined kinematic framework similar to that described above in connection with figure 2.1(a). The movements of the respiratory structure, however, are not uniquely determined but are a result of the nervous control of their respective muscles, control which integrates requirements of postural and other natures and which can, therefore, present large variations. That this is so is borne out by the dependence of the relaxation pressure characteristic on posture (Rahn et al., 1946), the variability of the muscular contraction patterns producing the same relaxation characteristic (Delhez et al., 1963), the variability of the dynamic contour produced in successive breathing cycles (Petit et al., 1960; Agostoni and Torri, 1967) and, finally, by the fact that the rib cage cannot maintain an elevated position or its completely convex shape, under the transthoracic pressure, without the intercostal muscles being active (Alexander, 1929). Thus, by postulating a 'passive' relaxation characteristic, the pressure-volume analysis ignores the sophisticated control mechanisms of which this characteristic, as well as the apparatus dynamical behaviour, are the end product. This fact constitutes the single most important reason why this type of approach has been incapable of supplying the framework on which the neurophysiological study of the respiratory apparatus could be integrated and interpreted. New approaches, capable of tackling simultaneously the kinematic, kinetic, structural and control facets of the overall problem have to be introduced.

Finally, it should be pointed out that although the pressure-volume analysis cannot be successfully used for the study of the mechanics of the external respiratory apparatus, its role in the clinical applications of respiratory mechanics, where after all it originated, will continue to be of crucial importance.

CHAPTER 3.0

ELEMENTS OF THE DESCRIPTIVE ANATOMY OF THE RESPIRATORY APPARATUS

3.1 - INTRODUCTION

In the previous chapters it was explained why it has been decided to approach the study of the mechanics of respiration from a mechanisms point of view and how, therefore, we need a detailed characterization of the functional elements involved in the breathing process; this chapter is intended to provide the minimum of anatomical data which is necessary to define with reasonable clarity the 'machine' we pretend to model. The information here presented is based on the available literature(*) and has been organized by articulating together those aspects which are relevant to our work; the results obtained not only are not easily accessible in the referred sources but also represent the foundations on which a complete quantitative specification, similar to what is done in machine design, could eventually be built for the respiratory machine. Drawings and diagrams, which represent already a measure of quantification, were used whenever possible; with few exceptions, duly acknowledged, these diagrams

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(*) Booth, 1948; Bourdelle and Bressou, 1953; Bourdell, Bressou and Florentin, 1947; Boyd et al., 1956; Bradley, 1967; Chaveau et al., 1903; Cook, 1965; Davison, 1947; Foust and Getty, 1947; Gamgee and Law, 1862; Gray's Anatomy, 1954; Greenblatt, 1954; Harrison, 1952; Hyman, 1942; Jayne, 1898; Jouffroy et al., 1968; Leach, 1961; Miller, 1952; Reichard et al., 1934; Romer, 1955; Sisson and Grossman, 1945; Taylor, 1959; Taylor and Weber, 1951.

are original and have been checked as well as possible on animals kindly made available to us by Dr. T.A. Sears at the Institute of Neurology, Queen's Square, London, W.C.1. The reason for our involvement in this type of effort resides precisely in the nonexistence in the published literature of the kind of detailed illustration we considered necessary for the mechanical characterization of the respiratory machine.

From a mechanisms point of view the respiratory apparatus represents a reciprocating air pump with a bellows-like action. This pump, illustrated in figure 3.2, consists of a chamber, the thoracic cavity, limited by the vertebral column, the anterior part of the rib cage and the diaphragm. Inside the chamber the air is contained in two bag-like organs, the lungs, connected in parallel and in communication with the atmosphere through the trachea and the upper airways. The motive power is applied to the walls of the chamber and causes their geometry, and therefore the volume they encompass, to change in order to produce the desired air flow. For purposes of anatomical characterization the respiratory apparatus is here considered as being divided into Internal Apparatus and External Apparatus. The first of these divisions consists of all the respiratory contents of the thoracic cavity and the upper airways and is dealt with in the first section; the second corresponds to the thoracic and diaphragmatic-abdominal walls which are described in section two in terms of their musculature. Finally, section three summarises the basic information relative to the innervation of the total respiratory apparatus.

3.2 - THE INTERNAL RESPIRATORY APPARATUS

3.2.1 - Introduction

This section defines the main anatomical features of the organs which form what we have called the Internal Respiratory Apparatus and whose function is to perform the oxygenation of the blood. From a purely mechanical point of view, however, this system interests us only in so far as it represents the main load the respiratory musculature has to overcome and this fact is therefore reflected in the material presented in this section.

3.2.2 - The mediastinum

The thoracic cavity is divided along its sagittal plane into two sub-chambers, one for each lung; the septum between these sub-chambers, called the mediastinum, lodges the oesophagus, the trachea, the heart and its associated great vessels, some nerve and lymphatic filaments and plexuses and, also loose fibrous-connective tissue. The lateral surface of the mediastinum is defined on both sides by a serous membrane which extends from the sternum to the costovertebral joints and from the diaphragm to the apex of the chambers; these membranes constitute the mediastinal part of the left and right parietal pleurae which line completely the inner surface of the respective thoracic sub-chambers. At the vertex of the thorax the mediastinum is continuous with the deep cervical fascia - a fibro-areolar tissue which embeds the viscerac, muscles and vessels of the neck - and forms the two apexes in which the chambers end cranially. This region of the mediastinum is strengthened by the inclusion of the roots of some muscles, e.g., the sternohyoideus, the sternothyreoideus, the longus colli and the scaleni and by a local hardening of the cervical fasciae in order to withstand the pressures which are developed inside the chambers. The other boundaries of the mediastinum are the sternum, the vertebral column and the central area of the diaphragm.

The mediastinum is widest in its centre-caudal region where the heart is located. The heart itself is contained in a double walled bag, the pericardium, whose fibrous external wall is so related to the other structures in the mediastinum and the sternum that it enjoys a firm suspension inside the thoracic cavity. Firstly, the fibrous pericardium is continued cranially in the outer coating of the great vessels with which it therefore forms a common sleeving system; secondly, it is attached to the fleshy part of the diaphragm, the strong coronary and triangular ligaments and to the sternum by the two sternopericardial ligaments, looser fibrous structures which are connected one (the superior) near the sternochondral articulation of the first ribs and the other (the inferior) near the sternal insertion of the diaphragm; and, finally, the pericardium is continuous with the general fibrous tissue in the mediastinum to whose structures and boundaries it is thereby related.

3.2.3 - The pleurae

The pleurae are serous membranes which line the inner surface of the thoracic cavities and the outer surface of the lungs; in each cavity the pleura which lines the inner surface of the cavity - parietal pleura - is continuous with the pleura - the visceral or pulmonary pleura - which covers the respective lung. It is normal practice to consider the parietal pleura as made up of three parts named according to the area of the chamber they cover: the mediastinal pleura limits the lateral surface of the mediastinum, the costal pleura placed over the rib cage and the diaphragmatic pleura over the hemidiaphragm which forms the caudal wall of the chamber. Approximately at the level of the atria of the heart the mediastinal pleura of either chamber develops a lateral expansion which ensleeves the root of the lung and continues to become the visceral pleura of the lung inside the cavity. Both parietal and visceral pleurae originate from the same mesothelial membrane which, in the embryo, lines the primordial pleural cavity; the lungs, sprouting from its root on the medial or mediastinal wall of this cavity, grow to fill completely the pleural cavity pushing its outer surface into intimate contact with the inner lining of the original cavity. Once in contact, the two pleurae become an active-membrane system filled with a very thin layer of gas-free pleural liquid; this system constitutes a perfect mechanical transmission between the chamber walls and the lung surface because, not only does it provide a tight non-elastic coupling, but it also allows the surface-sliding, demanded by the lung as it adapts to the changes in the geometry of the chamber, to take place in frictionless

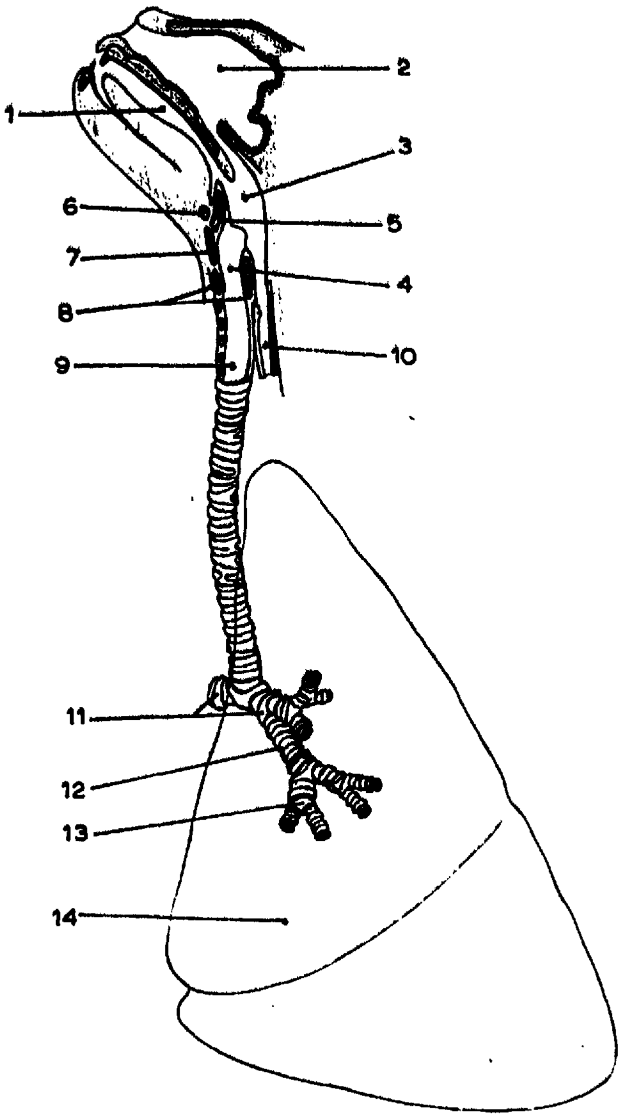


Fig. 3·1 Respiratory airways of the cat.

1 - mouth cavity; 2-nasal cavity; 3-pharynx; 4-larynx; 5-epiglottis; 6-hyoid bone; 7-thyroid cartilage; 8-cricoid cartilage; 9-trachea; 10-oesophagus; 11-primary bronchi; 12-secondary bronchi; 13-tertiary bronchi; 14-left lung.

conditions. This intimate relationship between the parietal and the visceral pleurae is interrupted in a few regions of the thoracic cavity, where one of them folds together with exclusion of the other: the fissures between pulmonary lobes, for instance, are lined by folds in the visceral pleura, in which the opposite surfaces of contiguous lobes create the mechanical coupling described above. Another example occurs at the line of reflection between the costal and diaphragmatic parts of the parietal pleura: this line is located so far back with respect to the rim of the lung (figure 3.2) that those two parts of the pleura come into contact for an appreciable extent all around the costal wall. This contact area, called the 'diaphragmatic recess', provides the room into which the rim of the lung moves when higher inspiratory volumes are needed, i.e., when the diaphragm moves back. Finally, a similar situation occurs along the line of reflection between the costal and the mediastinal parts of the parietal pleura, giving rise to the 'costo-mediastinal recess'.

3.2.4 - The airways

The lungs are in communication with the outside atmosphere via a system of chambers and airducts which, not only carry the air to and from the alveoli, where the oxygen-carbon dioxide gas exchange takes place, but also participate in the mechanical performance of the respiratory pump, both directly and through auxiliary functions. The main components of this airway system, as represented diagrammatically in figure 3.2, are the mouth and nasal cavities, the pharynx, the larynx, the bronchi and the bronchioles; the last two designations refer to groups of similar elements which, together with the trachea and the larynx constitute the conductive zone of what is known as the respiratory tree (Weibel, 1964); the bronchioles are followed peripherally by the alveolar ducts and sacs which are already part of the lung parenchyma.

The air may be taken in either through the mouth or through the nostrils because their respective cavities constitute parallel pathways with respect to the pharynx. However, the nasal cavities are specifically designed for this role: their shape is such that the air flow is disturbed and eddies are generated which force the air against the walls where a mucous membrane lining promotes its purification and corrects its temperature and humidity. The pharynx is common to the respiratory tract and to the digestive tube and constitutes the area where the food and air pathways cross: from the mouth to the oesophagus and from the nasal cavities to the larynx. The larynx is the entrance to the tracheo - bronchial tree, which it supplies with both an anchoring point and an isolating valve system, and consists of a framework of articulated cartilages and the associated musculature for its attachment to the structures of the neck and head. The main structural element of the larynx is the cricoid cartilage, a strong ring on whose caudal border the trachea is attached and which provides an articulated support for the thyroid cartilage and the two arytenoid cartilages (Taylor and Weber, 1951); the thyroid and the arytenoid cartilages supply a basis for the attachment of the thyroarythenoid muscles (the true and false vocal cords), the ventricular and vocal mucous membrane folds with which they form the glottis or larynx opening. Thanks to its muscles, the glottis can be shut completely and thus block the airflow through the larynx; this action is necessary whenever the intrathoracic or intra- abdominal pressures have to be raised as in defecation, vomiting, coughing, etc. The arythenoid cartilages constitutes also the point of articulation for the epiglottis cartilage, the organ whose function is to shield the glottis during swallowing.

The muscles which relate the larynx to the surrounding structures are relayed to it via a bone- the hyoid bone- itself connected to the larynx cartilages by muscles and ligaments. The larynx muscles originate as follows: the mylohyoideus and the geniohyoideus muscles from the mandible, the digastric muscle from the mandible and the occipital bone and, finally, the sternohyoideus muscle from the first costal cartilage. An exception to the above rule is the sternothyroideus muscle which connects the thyroid cartilage and the first costal cartilage.

The trachea is a thin-walled fibromuscular tube which connects the larynx to the lungs; at the approximate level of the atria of the heart, the trachea bifurcates into the two primary bronchi, one for each of the two lungs. Once inside the lungs, the primary bronchi generate the secondary or lobar bronchi (figure 3.1), one for each lung lobe, which in turn divide again into the third generation bronchi and so on, for something like fifteen generations. This division process, in which each branch generates two or more daughter branches of smaller size (in diameter and length), is accompanied by a gradual change in the structure of the walls of the branches which eventually leads to the terminal elements or bronchioles. The walls of the trachea and of the primary bronchi consist of three concentric sleeves which are, starting from the outside, the fibrous-cartilagenous membrane, the sub- mucous membrane and the mucous membrane, in this order. The mucous membrane or mucosa consists of a mucus-secreting epithelium supported by the respective basement- membrane which, in turn, is further strengthened by a highly irrigated fibrous membrane called the 'tunica propria'. The mucous membrane is continuous all the way from the larynx right up to the bronchioles. The fibro- cartilageneous membrane, on the outside of the wall, is made of longitudinal bundles of elastic and collageneous fibres in which cartilageneous elements and transverse bands of smooth muscle fibres are embedded. Finally, the mucous membrane, made of loose elastic fibres, constitutes a mechanical isolator between the two previous layers.

If we follow the respiratory tree from the trachea towards its periphery we will witness the following changes in the elements of the fibro- cartilagenous membrane: the cartilage, which up to the level of the primary bronchi have the shape of incomplete circular rings disposed parallel to each other along the ventral face, gradually change their shape and become smaller, disappearing completely by the time the bronchioles are reached. The muscle bundles, initially located between and attached to the tips of the cartilages, become progressively more independent of the cartilages and revealing more clearly their organization in helical bands of increasing pitch. The fibrous tissue itself changes by becoming increasingly thinner and by developing a growing number of fibrous connections with the innerlying mucous- membrane; when the primary bronchioles are reached, these connections rapidly grow stronger and extend to the entire cross- section of the fibrous cartilagenous membrane whose end is thus brought about by its fusion into the mucous membrane of the bronchioles.

The bronchioles, which carry the branching process for a few generations more, represent the stage in the peripheral evolution of the bronchial airways at which the fibro-cartilagenous membrane ceases to be present in the wall of the airducts. Another very important change also takes place at this level: the bronchi are mechanically isolated by a sheath of loose connective tissue - the peribronchium - inside which they are free to alter their dimensions, both diameter and lengthwise, without disturbing the surrounding lung tissue; the peribronchium, however, does not extend to the bronchioles, whose walls are, instead, firmly anchored in the pulmonary parenchyma. It is therefore reasonable to adopt, as we have done in this section, a mechanical point of view and consider the bronchi as being external to the lungs and the bronchioles as the peripheral attachment zone for the conductive respiratory tree; the attachment at the other end is provided by the trachea through its connections to the larynx, the mediastinum and the pericardium.

The conductive respiratory tree is subjected to longitudinal traction forces which arise from the elastic recoil of the lung tissue and, in dynamic conditions, from fluid friction losses along its length. These forces, which are more pronounced

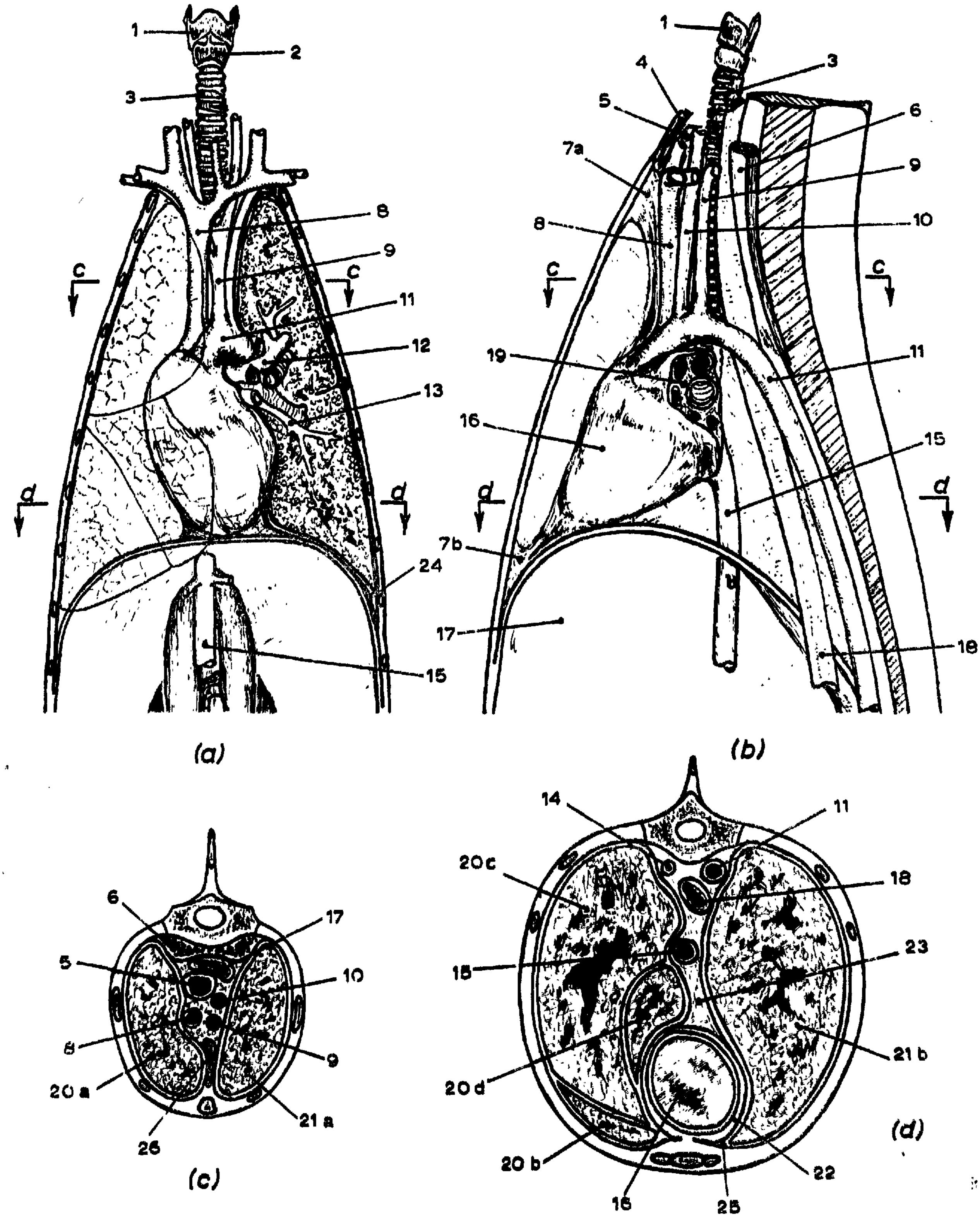


Fig. 3·2 Respiratory apparatus of the cat.

at the base and lower costal surfaces of the lungs, tend to draw the respiratory tree in a ventro-caudal direction (Mescham, 1951) and to pull it out of the apical lobes, thus helping to equalise the degree of inflation throughout the lung; the bronchial musculature, thanks to its helical configuration, is also able to reinforce this effect by contracting selectively throughout the respiratory tree.

Fig. 3.2 Respiratory apparatus of the cat.

Cross-sections: (a) through a frontal plane; (b) in a sagittal plane and in vertical planes at the level (c) of the fourth thoracic vertebra and (d) the ninth thoracic vertebra.

1- thyroid cartilage; 2- cricoid cartilage; 3- trachea; 4- sternomastoideus m.; 5- sternohyoideus and sternothyreoideus m.; 6- logus colli m.; 7(a)- anterior sternopericardial ligament; 7(b)- posterior sternopericardial ligaments; 8- superior vena cava; 9- subclavian artery; 10- innominate artery; 11- aorta vein; 12- pulmonary artery; 13- pulmonary veins; 14- azygos vein; 15- vena cava caudalis; 16- heart; 17- diaphragm; 18- oesophagus; 19- root of the left lung; 20(a,b,c,d)- right lung: apical, cardiac, diaphragmatic and intermediate lobes, respectively; 21(a,b)- left lung: apical and diaphragmatic lobes; 22- pericardium; 23- mediastinum; 24- costomediastinal recess; 25- costodiaphragmatic recess; 26- thymus gland.

3.2.5 - The lungs

The lungs have already been referred to as the two large organs which fill the respiratory cavities. When inflated, both lungs are roughly conical in shape with a rounded vertex or apex at the cranial end and a concave, semilunar basis which fits the dome of the respective hemi- diaphragm. The lungs are divided by deep fissures into lobes, three in the left lung and four in the right lung which are called, according to their relative position, and respectively, the apical, the cardiac, the diaphragmatic and the intermediate lobes; the last one, which only exists in the right lung, is located between the diaphragmatic lobes of the two lungs, the heart and the diaphragm. The lungs are related to the inner surface of the respective respiratory cavity through the hydraulic coupling described in the previous section which, not only keeps them from collapsing under the elastic stresses developed in their own tissue, but allows the tangential sliding of their surface with respect to that of the cavities to take place. This freedom of movement is particularly important on the costal and diaphragmatic surfaces of the lung where the walls of the cavity undergo the greatest geometric changes during respiration; together with the division in lobes, it confers to the lung a great fluidity of movement in filling the respective cavity. The mediastinal surface of the lung is connected to the heart and the trachea by a short, roughly triangular bridge called the root of the lung; the roots of the two lungs are approximately aligned with each other, one on each side of the heart at the level of the respective atrium. The root of the lung contains the structures by which each lung communicates with the rest of the body: the bronchus for the inlet and outlet of air, the pulmonary artery which brings in the blood to be aerated; the pulmonary veins to carry the venous blood back to the heart and the bronchial artery for the **perfusion** of the lung tissues: it also contains lymph vessels and glands, nerve plexuses and areolar tissue.

The air and blood conduits entering through the root of the lung, branch out in the manner described for the bronchial tree and end up in the alveoli and in the capillaries, respectively The bronchioles undergo a few generations of branching until they gradually fuse with the surrounding lung tissue and some alveoli start appearing on their walls, a stage in which they are called respiratory bronchioles. Then, they branch out into several ramifications, each terminated by a small chamber, which are called alveolar ducts and alveolar sacs , respectively, and which consititute the true respiratory zone of the respiratory tree. The walls of the alveolar ducts and sacs are completely made up of small pocket-like chambers - the alveoli - stacked together side by side and opening into the common air space. The number of alveoli reaches a few tens of millions and they account for about fifty per cent of the total lung volume (Weibel, 1963); their distribution around the respiratory tree is such that their distances to the root of the lung show a well peaked unimodal distribution (Ross, 1953). The walls of the alveoili are an integral part of the pulmonary parenchyma whose elaborate fibrous framework is responsible for keeping them open and inflated, as well as providing support for the profuse capillary network embedded in them. The alveolar mass is kept from collapsing by the combined action of the visceral pleura, which is adherent to the cavity walls, and the tracheo- bronchial tree, which is anchored along the mediastinum and through its attachment to the larynx. The vascular system of the lungs, i.e., the pulmonary veins and arteries and the bronchial arteries, undergoes a similar branching process following very closely the bronchial ramifications. Like the bronchi, they are mechanically isolated from the lung parenchyma by a sheath of loose connective tissue which is continuous with the peribronchium but which, in this case, is present right up to the arterioles feeding the capillaries in the **alveolar walls.** The vascular network is under the same stretching forces as the respiratory tree and contributes a parallel elastic component towards the equilibrium with those forces.

3.3 - THE RESPIRATORY MUSCULATURE

3.3.1 - Introduction

The purpose of this section is to characterize the anatomical elements which provide the mechanical power required by the respiratory machine and which constitute the respiratory musculature. This musculature is organised into two systems, one made up by the muscles of the air passages and the other by the external respiratory musculature, both of which are in turn divided into two further groups: the tracheo-bronchial system and the upper airway system in the first case and the primary and secondary respiratory muscle system in the latter case.

The tracheo-bronchial system consists of the smooth involuntary muscles of the tracheal and bronchial walls which have been briefly described in the previous section and which are responsible for the active constriction and patency of the respiratory tree; the upper airway system comprises the striated voluntary muscles of the larynx which have also been referred to in section 3.2. These two groups of muscles play a very limited role in our model of the respiratory system and, for that reason, no further effort is made to characterize them in greater detail.

The external primary respiratory muscles, all of the striated voluntary type, are characterized by being primarily involved in the movements of respiration and they constitute the main subject of this section. Other muscles, such as for instance the superficial muscles of the trunk and the neck and the muscles responsible for the attachment of the front limbs, also affect the performance of the respiratory apparatus by conditioning its

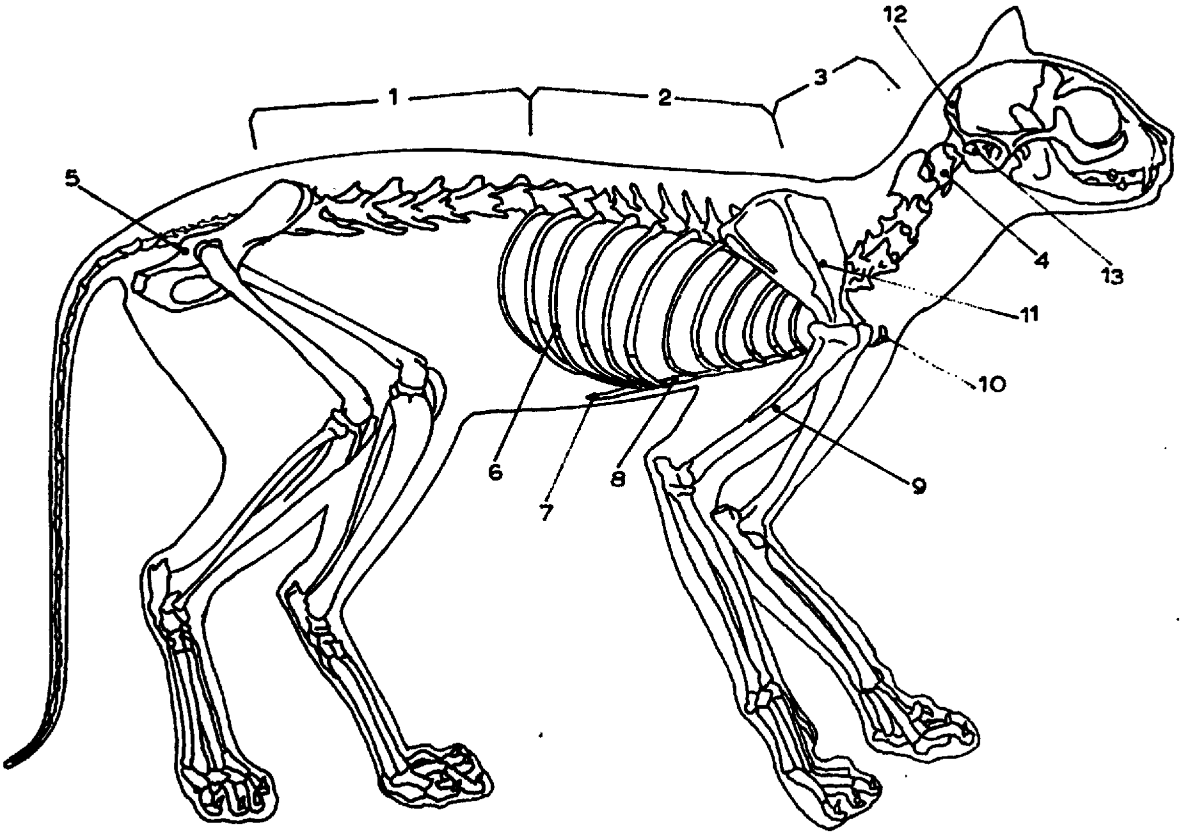


Fig. 3·3

Skeleton of the cat

1- Lumbar vertebrae; 2-thoracic vertebrae; 3-cervical vertebrae; 4-atlas vertebra; 5-coxal bones; 6-ribs; 7-xiphoid process of the sternum; 8-sternum; 9-humerus; 10-clavicle; 11-scapula; 12-lamboidal crest; 13-basioccipital bone boundary load conditions and by participating more or less pronouncedly in the powering of the breathing movements in forced or impaired respiration. These muscles, the secondary external respiratory muscles, have however a limited role in quiet respiration and for that reason are not taken into account in our model of the respiratory machine; they will be briefly considered in chapter 5. in connection with the analysis of the structural functions they are mainly concerned with.

The body of the animal is built around a framework of bone and cartilageneous structure, the skeleton, on which the muscles are attached. The central structure element in this framework is, as figure 3.3 shows, the vertebral column which extends all the way from the base of the skull to the pelvic bones and the tip of the tail and consists of the caudal, sacral (sacrum), lumbar, thoracic and cervical vertebrae. The vertebral column dominates the two parts of the body which interest our model of the respiratory ventilator: the thoracic and the abdominal cavities. The first of the two is entirely delimited by the rib cage formed by the column, the ribs, their cartilages and the sternum. The ribs, thirteen in number on either side, are thin arched bones which articulate dorsally with the vertebral column and are connected by rounded bars of hyaline cartilage to the sternum. The abdominal cavity is defined by the abdominal muscles stretching from the caudal border of the rib cage to the coxal bones (figures 3.3 and 3.5) and the vertebral column. The two cavities, thoracic and abdominal, are contiguous with each other and form an overall body cavity which resembles an ellipsoid of revolution.

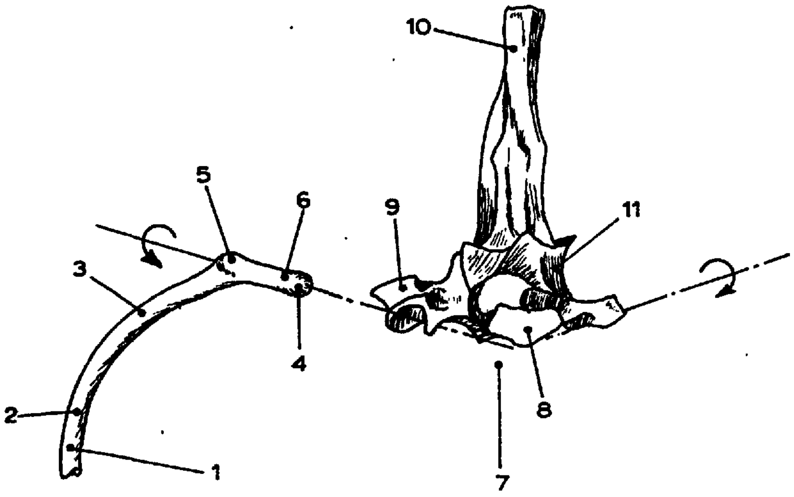


Fig. 3·4

Exploded view of a costo-vertebral articulation

1-Rib; 2-shaft of the rib; 3-angle; 4-head; 5-tubercle; 6-neck; 7-thoracic vertebra; 8-centrum; 9-transverse process; 10-spinous process; 11-posterior articular process.

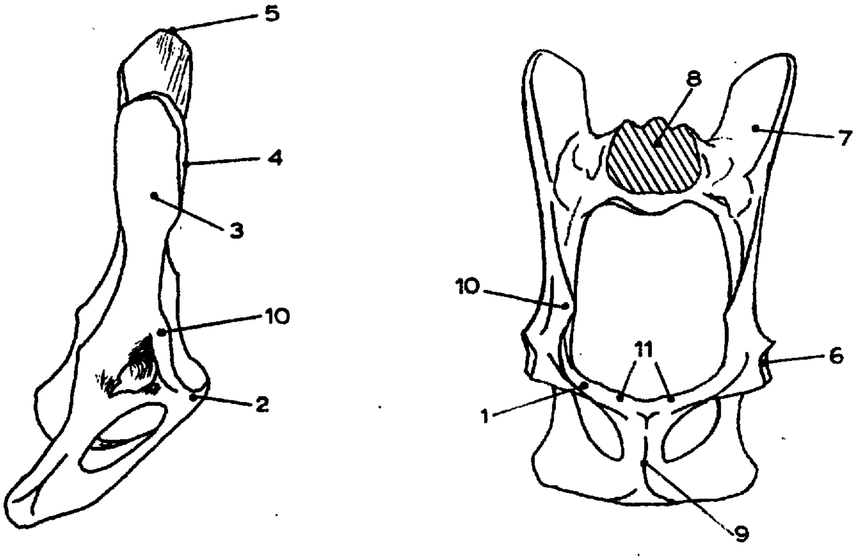


Fig.3·5

Coxal bones

1-Body of the pubis; 2-spine of pubis; 3-ilium; 4-anterior superior spine; 5-crest of ilium; 6-acetabulum; 7-surface for attachment of spinal muscles; 8-cross-section of the sacrum.; 9-symphysis pubis; 10-pectineal line; 11-pubic tubercle

The diagram of figure 3.6 shows some cross- sections through the walls of the body cavity at four different levels; the numbers indicate the bony, aponeurotic and muscular elements in the wall which are crossed, in the same order, by the line where the numbers are attached. These cross- sections show clearly how the vertebral column is associated with a powerful muscular mass which makes it the foundation of the structural stability of the animal's body. Cross-sections (d) and (e) through the thoracic end of the body cavity, show the rib cage surrounded by a complex system of muscles most of which, as we shall be showing later, are concerned with the attachment of the upper limbs; cross-sections (b) and (c) make clear the absence of bone structures, other than the vertebral column, in the walls of the abdominal cavity whose shape is therefore determined by the reaction to the muscular constraint of the abdominal viscerae.

The muscles of the rib cage are inserted between ribs or between the ribs and the column or the sternum, and tend to be short; the muscles of the abdominal wall, having to cover larger spans, are related to their boundaries by several fibro- tendinous structures, the most important of which are the following (Gray's Anatomy, 1954):

1. The lumbodorsalis fascia, shown in figure 3.6(23), is a dense fibrous membrane stretching from the back of the neck to the sacrum and the iliac crest and covering the deep muscles of the back of the trunk. In the thoracic region, it consists of a thin fibrous sheet extending from the spines of the thoracic vertebrae to the angles of the ribs and covering the deep muscles of the column. In the lumbar region, the lumbodorsalis fascia

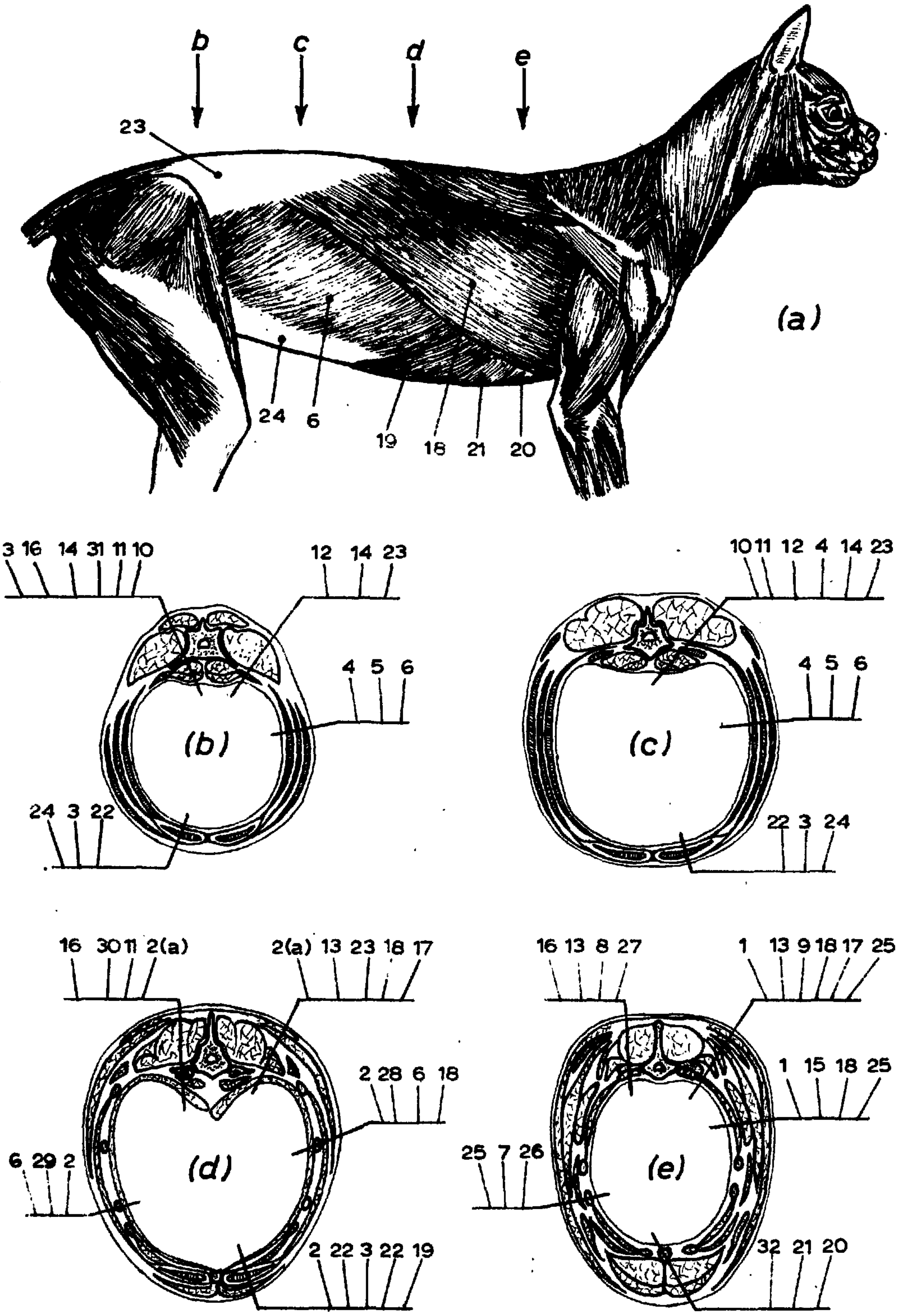


***Fig.3-6** Superficial muscles of the cat (a) and wall cross sections at the level of : (b) fifth lumbar, (c) second lumbar, (d) thirteenth thoracic and (e) sixth thoracic vertebrae.*

1- Intercostals (intimi, internus and externus) muscles; 2-diaphragm m.;2a-crura; 3-rectus abdominis m.; 4-transversus abdominis m.; 5-obliquus abdominis internus m.; 6-obliquus abd. externus m.; 7-scalenus m.; 8-levator costae m.; 9-serratus posterior superior m.; 10-psoas minor m.; 11-psoas major m.; 12-quodratus lumborum m.; 13-iliocostalis muscle; 14-erector spinae m.; 15-serratus anterior m.; 16-longissimus dorsi m.; 17-spinotrapezius m.; 18-latissimus dorsi m.; 19-xiphihumeralis m.; 20-pectoralis major m.; 21-pectoralis minor m.; 22-sheath of the transversus abdominis m.; 23-lumbodorsalis fascia; 24-aponeurosis of the obliquus abdominis externus m.; 25-panniculus dorsi; 26-fifth rib; 27-sixth rib; 28-eleventh rib 29-twelth rib; 30-thirteenth rib; 31-fifth lumbar vertebra; 32-sternum.

(Partially adapted from Bourdelle and Bressou 1953)

splits medially into three parallel layers which cover separately the quadratus lumborum and the sacrospinalis muscles and which are reunited along the ventral border of the fascia to constitute the aponeurotic insertion of the flat muscles of the abdomen; these layers of the lumbodorsal fascia have separate insertions on the spinous and transverse processes of the lumbar and sacral vertebrae, the iliac crest and the caudal border of the thirteenth rib.

2. The inguinal ligament is a thick ligamentous band which stretches from the anterior superior iliac spine to the pubic tubercle pectineal line - figure 3.7 - and is formed conjointly by the aponeurosis of the three abdominal muscles and the psoas-iliacus muscular complex.

3. The linea alba is a tendinous band which stretches from the xiphoid process of the sternum to the symphisis pubis in the pelvic bones and represents the result of the fusion of the ventral aponeurosis of the three abdominal muscles.

3.3.2 - Anatomical characterization of the primary respiratory muscles

The primary respiratory muscles not only supply the breathing apparatus with the mechanical power it needs but actually constitute one of the main components of its walls. These muscles, as shown in table 3.1 and figures 3.7 and 3.8, are organized in three layers, which are common to both the thoracic and the abdominal compartments, and will be described according to this layout; the vertebral column, which is not a

TABLE 3.2: PRIMARY RESPIRATORY MUSCLES

Region	Inner Layer	Intermediate Layer	Outer Layer
Thorax	Transversus thoracis: 1. Intercostales intimi 2. Subcostales 3. Sternocostales Diaphragm	Intercostales interni Intercostales externi Transversus costarum Levatores costarum	Scaleni Serratus posterior inferior Serratus posterior superior
Abdomen	Transversus abdominis Retractor costae ultimae Quadratus lumborum	Rectus abdominis Obliquus abdominis internus	Obliquus abdominis externus
Vertebral Column			Iliocostalis lumborum Iliocostalis thoracis Longissimus thoracis

compartment, is also included in table 3.1 because some of its associated muscles are attached to the ribs and therefore affect directly the movements of the rib cage. We will now summarize the main anatomical features of the muscles in each layer; the numbers in brackets after the name of a muscle refer, respectively, to figure 3.7 for the muscles of the inner layer and to figure 3.8 for those of the intermediate and outer layers.

The muscles in the inner layer are the following (figure 3.7):

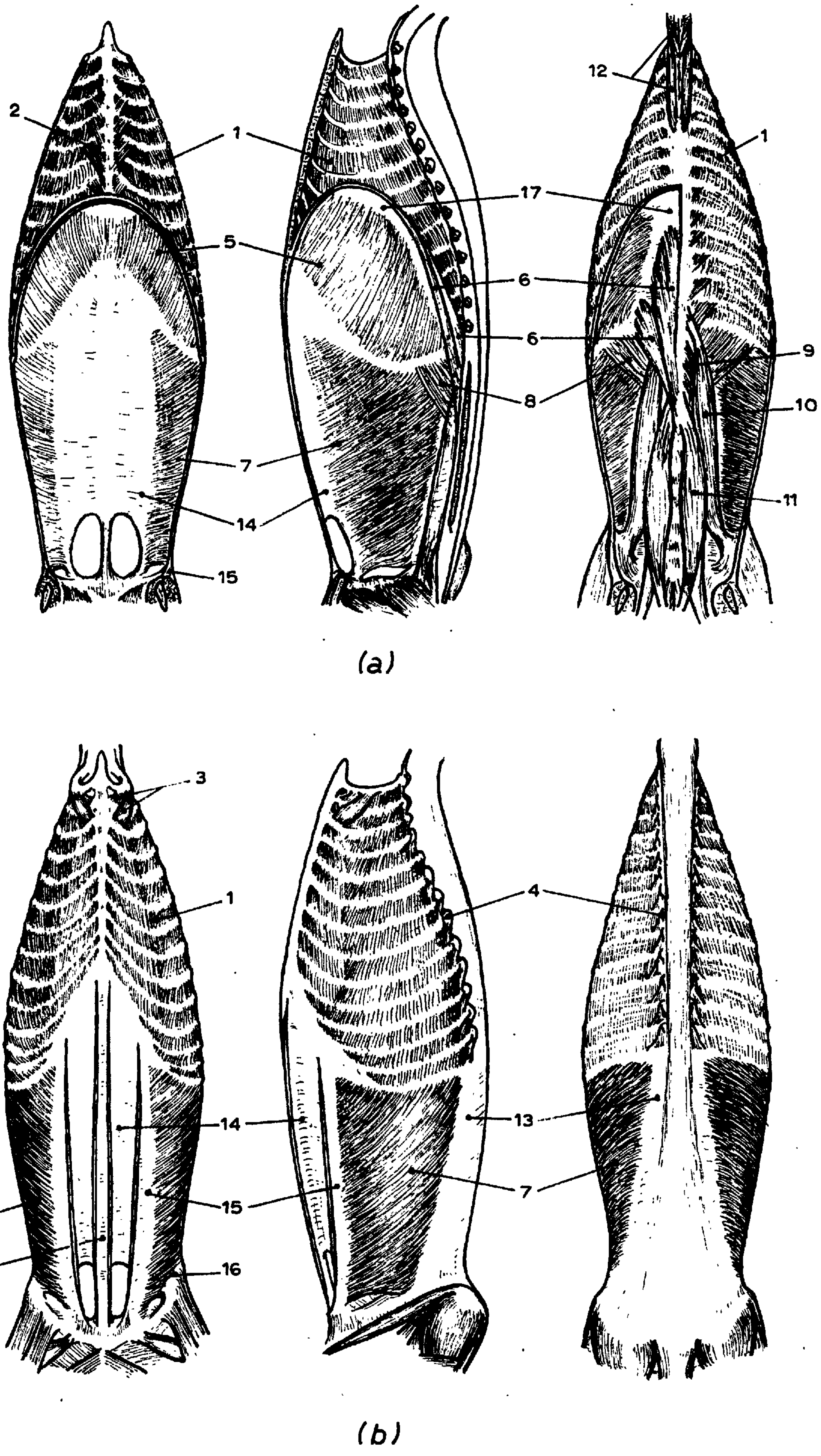
Transversus Thoracis(2): this is the collective designation of three groups of muscles which are attached to the inner surface of the thoracic cavity, one on the ventral side- the sternocostales- and two on the dorsal side - the intercostales intimi and the subcostales-. The intercostales intimi muscles are located in the intercostal spaces midway between the column and the sternum, ventrally to the angle of the rib and continuous to the corresponding subcostales muscles. The muscle fibres are attached to the facing borders of contiguous ribs and are parallel to the fibres of the internal intercostal muscle, i.e., moving away from the sternum in the cranio- caudal direction; the fibres of these muscles predominate mostly in the last intercostal spaces. The subcostales muscles are usually reduced to a few fasciculi mostly in the posterior part of the thorax. Their fibres originate in the inner surface of the angle of the ribs and have the same direction as those of the intercostales interni from which they are only distinguishable for the fact that they can bridge two or more intercostal spaces. The sternocostales muscles form a roughly triangular plane of muscular and tendinous fibres which originate from the aponeurosis covering the inner surface of the sternum, the xiphoid process and the sternal end of the last costal cartilages and which insets in the inner surface of the costal cartilage by five or six diverging digitations up to the level of the costochondral joints; at the caudal end and on both sides of the xiphoid process, the posterior fibres of the sternocostales interdigitate with the transversus abdominis muscles which, in that region, penetrates inside the thoracic cavity.

The Diaphragm(5) is a thin musculo-tendinous membrane which separates the thoracic and the abdominal compartments one from the other. It possesses in the central region a strong aponeurotic structure, called the 'central tendon', which has a roughly circular centre area continued into a narrower strip up to the vertical column. The muscle fibres radiate peripherally from the central tendon and terminate, first, by two short fleshy strips on the inner surface of the xiphoid process and then, following on either side, by a series of digitations which insert, all around the abdomen and up to the edges of the dorsal portion of the central tendon, on the inner surface of the cartilages and shafts of the last five ribs. In the lumbar region the diaphragm is constituted by four thick bundles of fibres originating medially from the lower surface of the central tendon; the two central and bigger ones converge into two tendinous pillars, or crurae, for the attachment to the longitudinal ligaments of the vertebral column at the level of the second to the fourth lumbar vertebrae; the two smaller bundles are located one on each side of the previous ones and are attached laterally to the same ligament by a smaller pillar.

The <u>Transversus Abdominis</u> muscle (7) is a thin flat muscle whose fibres run transversely across the side walls of the abdomen from the inguinal and the lumbodorsalis fascia to a ventral aponeurosis which is continuous with the linea alba. This ventral aponeurosis starts at the pubis via the conjoint tendon, formed together with the aponeurosis of the obliquus internus and then blends longitudinally with the sheath of the rectus abdominis muscle on the same side. The lumbodorsalis fascia, on the dorsal side, relates the transversus abdominis successively to the iliac crest, the transverse processes of the lumbar vertebrae and to the inner surface of the thirteenth rib and of the last six rib-cartilages, where the transversus abdominis interdigitates with the diaphragm and the sternocostales.

The <u>Retractor Costae Ultima</u> muscle(8) originates in the transverse processes of the first four lumbar vertebrae and inserts in the caudal border of the last rib lying internally to the transversus abdominis muscle (Jouffroy et al., 1968).

The <u>Quadratus Lumborum</u> muscle(9) starts caudally from the anterior inferior spine of the ilium and the iliolumbar ligament and its fibres, placed longitudinally along the column, insert in the successive lumbar transverse processes and in the head of the last rib or ribs.



(a)

(b)

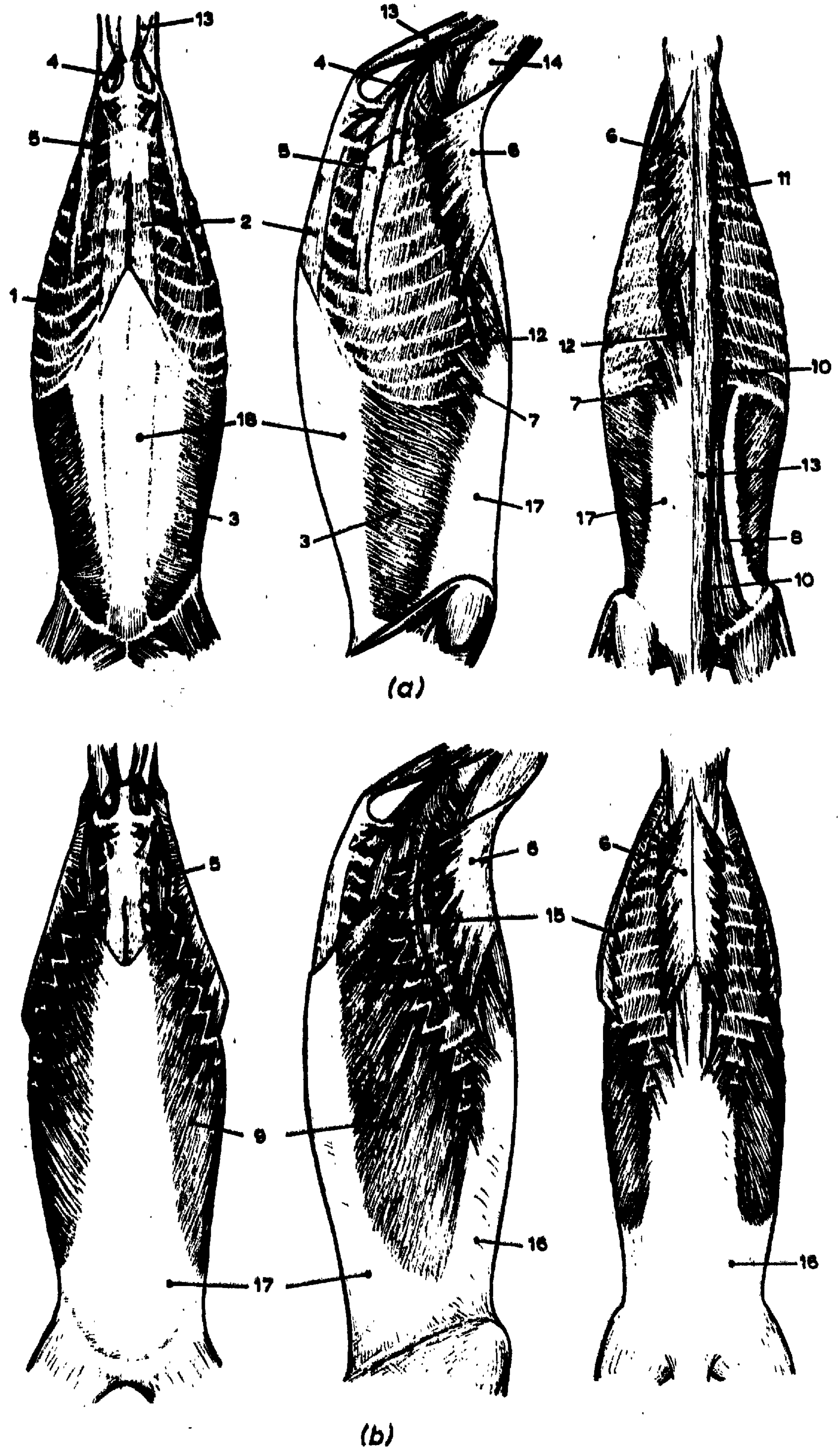
Fig. 3·7

Fig. 3.7 - Muscles of the trunk: (a) inside and (b) outside surfaces of the inner layer of the trunk muscles. In both cases, the ventral, lateral and dorsal walls are shown, respectively, at the left, centre and right of the page.

1- intercostales interni m.; 2- transversus thoracis m.; 3- transversus costarum m.; 4- levatores costarum m.; 5- diaphragm m.; 6- crurae of the diaphragm; 7- transversus abdominis m.; 8- retractor costae ultima m.; 9- quadratus lumborum m.; 10- psoas minor m.; 11- psoas major m.; 12- longus colli m.; 13- lumbodorsalis fascia; 14- aponeurosis of the rectus abdominis muscle; 15- fascia of the transversus abdominis muscle; 16- inguinal ligament; 17- tendon of the diaphragm; 18- linea alba.

Fig. 3.8 - Muscles of the trunk: (a) intermediate and (b) outer layer of the trunk muscles. In both cases, the ventral, lateral and dorsal walls are shown, respectively, at the left, centre and right of the page.

1- intercostales m.; 2- rectus abdominis m.; 3- obliquus abdominis; internus m.; 4- scalenus primae costae m.; 5- scaleni transcostalis m.; 6-serratus posterior superior m.; 7- serratus posterior inferior m.; 8- quadratus lumborum m.; 9- obliquus abdominis externus m.; 10- iliocostalis lumborum m.; 11- iliocostalis thoracis m.; 12- longissimus thoracis m.; 13- sternomastoideus m.; 14- splenius m.; 15- serratus anterior m.; 16- lumbodorsalis fascia; 17- aponeurosis of the rectus abdominis muscle; 18- linea alba.



(a)

(b)

Fig. 3·8

The muscles of the intermediate layer are the following (Figure 3.8):

The Intercostales muscles(1) constitute the main motor element of the rib cage and are organised in two parallel layers which lodge in the twelve intercostal spaces. In each layer, the muscle fibres, strongly intermingled with tendinous fibres, are attached to the facing borders of contiguous ribs with which they make approximately the same angle throughout the rib cage. These two layers are identified according to their position relatively to the ribs as two different muscles:

The Intercostales Interni, which constitute the inner layer, cover each intercostal space from the sternum to the angle of the ribs; from there onwards and up to the costotransverse ligament, they are replaced by an aponeurotic layer called the posterior intercostal membrane. The fibres in this layer originate from the floor of the costal groove of each rib and its corresponding cartilage, and stretch obliquely in a dorso-caudal direction towards its insertion in the upper border of the next rib.

The Intercostales Externi muscles constitute the outer layer and cover the intercostal space from the tubercle of the rib to the costo-chondral joint, where they are continued up to the sternum by an aponeurotic layer called the anterior intercostal membrane. The fibres of these muscles make an angle of about 100° with the corresponding fibres in the intercostal interni and are stretched between the lower border of one rib and the upper border of the rib which follows it caudally.

The <u>Transversus Costarum</u> muscles (figure 3.7(3)) constituted by a pair of short superficial digitations, originates in the first rib near the insertion of the scalenus primae costae muscle and inserts in the cartilages of the two following ribs and the fascia of the rectus abdominis on the cranial end of the sternum.

The <u>Levatores Costarum</u> muscles (figure 2.7(4)), one per each intercostal space, are strong musculo-tendinous bundles which originate in the transverse processes from the last cervical up to the thirteenth thoracic vertebrae and stretch down and obliquely to reach the nearest rib at the rear. The insertion takes place along the front edge and outer surface of this rib between the tubercle and the angle, and covers a length which increases cranio-caudally. The fibres of these muscles have the same orientation as those of the intercostales externi.

The <u>Recti Abdominis</u> muscles(2) are two long and narrow strips of muscular fibres, one on each side of the linea alba and divided transversally into three or four segments by tendinous bands, which originate by two large and flat tendons from the tubercle of the pubis and are inserted by an aponeurotic strip in the first and second costal cartilage and the sternum, and are inserted in the first costal cartilage by a thin aponeurotic strip and in the sternal end of the second to the seventh rib cartilages. These muscles are enclosed in a sheath which blends with the linea alba and is formed from the aponeurosis of the three lateral abdominal muscles: the external wall of this sheath, continuous from the pubis to the thorax, is formed primarily from the aponeurosis of the obliquus externus muscle while its internal wall derives basically from the aponeurosis of the transversus abdominis muscle: the aponeurosis of the obliquus abdominis internus muscle contributes to the external wall over a third of the length of the sheath at its caudal end and contributes to the internal wall over the rest of the length of the sheath.

The Obliquus Abdominus Internus muscle(3) is a thin layer of muscular fibres strongly mixed with tendinous elements, which lie obliquely almost at right angles to the fibres of the transversus abdominis muscle. The fibres of this muscle originate in the lumbodorsalis fascia, the iliac crest, the inguinal ligament and, via the conjoint tendon, from the pubis; from these origins the fibres move ventro-cranially to blend with the sheath of the rectus abdominis muscle via an aponeurosis which becomes broader as it progresses towards its area of attachment in the last rib-cartilages which still insert in the sternum. The muscle fibres originating from the cranial end of the lumbodorsalis fascia, on the other hand, go to insert by semitendinous digitations in the external surface of the posterior border of the last ribs in close continuity with the fibres of the serratus posterior inferior muscle.

The muscles of the outer layer are the following (figure 3.8):

The Scaleni muscles consist of the following two groups: the scalenus primae costae(4) arises from the transverse processes of the last three or four cervical vertebrae in the form of a few digitations which are then inserted in the front edge of the first rib. The second group, the scalenus transcostalis originates from the transverse processes of all cervical vertebrae and then divides into two branches, one which is inserted near the angle of the second and the third rib, and another which is inserted in the last four ribs from the fourth to the ninth.

The Serratus Posterior Inferior muscle(7) consists of four quadrilateral digitations originating from the spines of the first lumbar vertebrae and their interspinous ligaments and inserting slightly beyond the angles of the last four ribs on their posterior and dorsal surfaces.

The Serratus Posterior Superior muscle(6) is a thin quadrilateral muscle originating from the median raphe which extends from the spinous processes of the second cervical vertebra to that of the tenth thoracic vertebrae and inserting by fleshy digitations on the cranial and dorsal surfaces of the first nine ribs ventrad of their angles.

The Obliquus Abdominis Externus(9) is the strongest of all the three flat abdominal muscles and its fibres run in a direction approximately perpendicular to those of the obliquus internus muscle. It originates from the last ten ribs by as many fleshy digitations which are aligned obliquely in the dorsocaudal direction and alternate with the similar digitations of of the rib where it originated; the last four bundles insert on the transverse process of the seventh cervical vertebra.

The Longissimus Thoracis muscle(13) separates (Jouffroy et al.,; 1968) from the Erector Spinae just before the thoracic region and continues up to the base of the neck, gradually becoming thinner as it progresses. It is possible to distinguish two types of fibres in this muscle: the fibres in the outside layer originate mostly from the common tendon and insert into the cranial edge of the region between the tubercle and the angle of all the ribs - with the exception of the last - and the transverse process of the seventh cervical vertebra; the other group of fibres, placed medially with respect to the previous ones, are attached in the lumbar region to the transverse and accessory processes of the lumbar vertebrae and the middle layer of the lumbar fascia, and are inserted cranially by rounded tendons in the transverse processes of all the thoracic vertebrae. The longissimus thoracis is the principal extensor of the column and forms, together with the longissimus cervicis and the longissimus capitis muscles, the intermediate and the largest of the three columns in which the sacro-spinalis muscle can be divided.

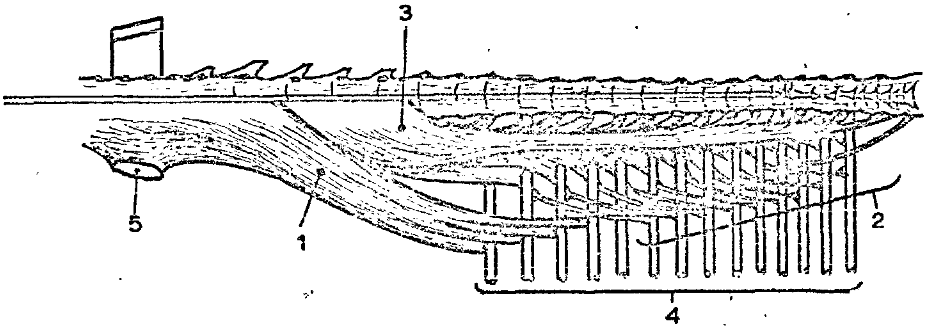


Fig. 3.9-Diagrammatic representation of the muscles of the vertebral column which have costal insertions.
1- Iliocostalis lumborum m.; 2- iliocostalis thoracis m.; 3- longissimus thoracis m.; 4- ribs; 5- ilium.

3.4 - INNERVATION OF THE RESPIRATORY APPARATUS

3.4.1 - Introduction

This section deals with the main features of the nervous circuitry associated with the respiratory apparatus.

The vertebrate nervous system is divided into central nervous system and peripheral nervous system. The central nervous system is constituted (figure 3.10) by the spinal cord or medulla spinalis (6) lodged in the vertebral column and the brain, located in the cranial cavity, which includes the medulla oblongata (4), the pons Varolii (2), the midbrain, the diencephalon, the cerebellum (5) and the cerebral hemispheres (1). The peripheral nervous system consists of the cerebro-spinal and of the autonomic nervous systems. The first of these systems is made up by the twelve pairs of cranial nerves arising from the brain and by the spinal nerves which originate in the spinal cord and are organised in eight cervical, thirteen thoracic, seven lumbar and seven or eight caudal nerve pairs; each pair of the spinal nerves arises from the respective segment of the spinal cord and leaves the vertebral canal through the corresponding pair of intervertebral foramina(figure 3.10(b)). The cranial nerves are named as follows: olfactory, optic, oculomotor, trochlear, trigeminal, abducens, facial, acoustic, glossopharyngeal, vagus, accessory and hypoglossal. The first of these nerves arises from the olfactory bulb; the second, third and fourth, which innervate the eye and its musculature, from the diencephalon and the mid brain; the fifth from the pons, the seventh from the trapezoidal body which connects the pons to the medulla oblongata and the sixth, eighth, ninth, tenth, eleventh and twelfth from the medulla oblongata.

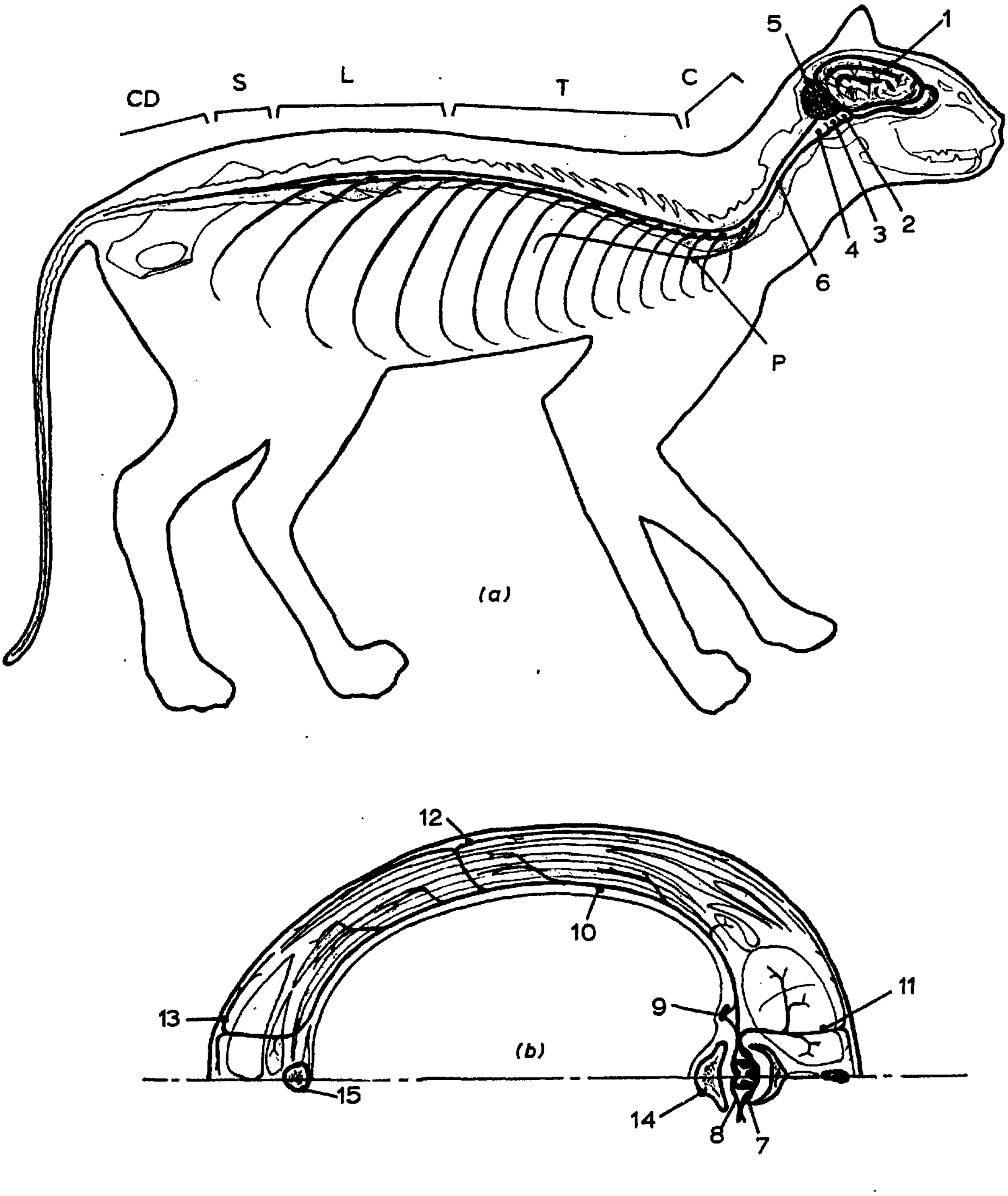


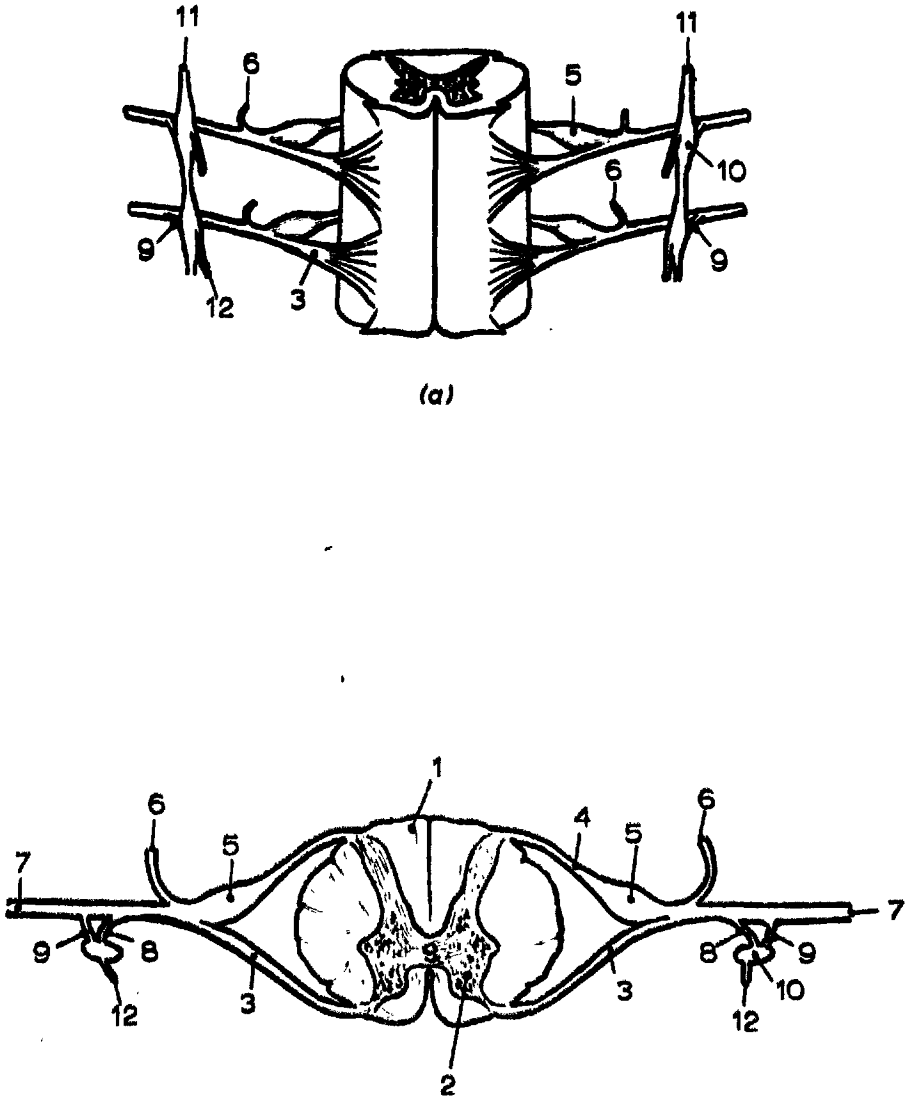
Fig. 3·10 Effent innervation of the respiratory muscles : (a) spinal nerves, (b) typical distribution of the terminations of a thoracic nerve.

Spinal nerves : C - cervical ; CD- caudal ; T - thoracic ; L - lumbar ; P - phrenic ; S - sacral.

1 - cerebral hemisphere ; 2 - pons ; 3 - trapezium ; 4 - medulla oblongata ; 5 - cerebellum ; 6 - spinal cord ; 7 - posterior root ; 8 - anterior root ; 9 - sympathetic ganglion ; 10 - anterior primary ramus ; 11 - posterior primary ramus ; 12 - lateral cutaneous branch ; 13 - ventral cutaneous branch ; 14 - vertebra ; 15 - sternum.

Figure 3.11 represents a diagrammatic view of the cross section through one of the segments of the spinal cord showing the ventral and the dorsal roots of the respective spinal nerve. The ventral root contains mainly efferent or motor fibres which are the axons of the nerve cells whose bodies are located in the anterior column of grey matter on the same side of the cord; the dorsal root contains afferent nerve fibres connecting the receptors in the muscles to the spinal cord and whose bodies are located in the dorsal ganglion.

The autonomic peripheral system consists of the nerve pathways which supply the involuntary effectors (smooth muscles and glands) in the viscerae and blood vessels, which are responsible for the autonomic maintenance of the internal body environment (homeostasis). In these pathways the fibres which innervate the automatic effectors are generally unmyelinated and have their cell bodies located outside the central nervous system in special ganglia; the nervous motor discharges are relayed to them by myelinated (preganglionic) fibres, which originated from cell bodies situated in the central nervous system. This arrangement contrasts with that of the skeletal muscle innervation where the latter type of cells go all the way from the central nervous system to the motor-junctions in the muscles. The autonomic system can be further divided in sympathetic and parasympathetic systems whose action on the muscles is of antagonistic character. The preganglionic fibres of the sympathetic system come out of the spinal cord in the anterior primary roots of the thoracic and upper lumbar spinal nerves and enter the ganglia of the two sympathetic ganglionar chains or trunks (figure 3.11(11)), one on either



(a)

(b)

Fig. 3·11 Insertion of the spinal nerves : (a) segmental organization of the spinal cord; (b) diagrammatic cross-section through a cord segment.

1-white nervous matter; 2-grey matter ; 3-ventral nerve root; 4-dorsal nerve root; 5-dorsal ganglion; 6-posterior spinal nerve ramus; 7-anterior spinal nerve ramus ; 8-white ramus communicantes; 9-grey ramus communicantes ; 10-sympathetic ganglion ; 11-sympathetic chain or trunk; 12-visceral nerve ramus.

side of the vertebral column, by the white rami communicantes (figure 3.11(8)); the post ganglionic fibres return to the spinal nerves by the grey rami communicantes and also form nerve filaments which travel to the thoracic and abdominal viscerae and blood vessels (figure 3.11(12)). Generally speaking, each preganglionic fibre is related to a large number of postganglionic cells and, as a result, the discharges of the sympathetic system tend to be diffusely distributed. The parasympathetic preganglionic fibres leave the central nervous system as part of the third (oculomotor), the seventh (facial), the ninth (glossopharyngeal), the tenth (vagus) and the eleventh (accessory) cranial nerves and of the second, third and fourth sacral nerves; the corresponding ganglia, unlike their sympathetic counterparts, are located in or are very close to the structures they innervate.

3.4.2 - Innervation of the primary respiratory muscles

The primary respiratory muscles are innervated by the anterior primary rami of the spinal nerves. As table 3.2 shows, the intercostales, the transversus thoracis and the transversus costarum muscles are innervated exclusively by the thoracic nerves. Also with exclusive thoracic innervation are the levatores costarum and the serrati posterior muscles which will be shown in a later chapter to be closely related to the costovertebral joints and therefore to the movements of the rib cage. The three abdominal muscles have mixed thoraco-lumbar innervation which in the case of the obliquus abdominis externus has still a very extensive thoracic component. The retractor costae ultimae and the quadratus

TABLE 3.2: INNERVATION OF THE PRIMARY RESPIRATORY MUSCLES BY THE SPINAL NERVES

MUSCLES	ANTERIOR PRIMARY RAMI																											
	Cervical								Thoracic														Lumbar						
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7
Transversus Thoracis										•	•	•	•	•	•	•	•	•	•	•								
Diaphragm				•	•	•										•	•	•	•	•	•							
Transversus Abdominis																	•	•	•	•	•	•						
Retractor Costae Ultimae																						•	•					
Quadratus Lumborum																							•	•				
Intercostales									•	•	•	•	•	•	•	•	•	•	•	•	•							
Transversus Costarum									•																			
Levatores Costarum									•	•	•	•	•	•	•	•	•	•	•	•	•							
Rectus Abdominis																	•	•	•	•	•	•	•	•				
Obliquus Abdominis Internus																				•	•	•	•	•				
Scaleni	•	•	•	•	•	•																						
Serratus Posterior Inferior									•	•	•	•	•	•	•	•	•											
Serratus Posterior Superior																		•	•	•	•							
Obliquus Abdominis Externus											•	•	•	•	•	•	•	•	•	•	•	•	•	•				

lumborum muscles are innervated by the first lumbar nerves. The scaleni and the diaphragm have cervical innervation; the latter is fed by the left and right phrenic nerves, each of which result from the confluence of three small nerve branches derived respectively from the fifth, sixth and seventh primary rami of the cervical nerves. [redacted]

The iliocostalis lumborum, the iliocostalis thoracis and the longissimus thoracis muscles, like all the deep muscles of the back are innervated by the posterior rami (figure 3.10(11)) of the primary spinal nerves; the same is also true with respect to the levatores costarum (Fujita, 1965; Morrison, 1954) which, therefore, also belong to the dorsal musculature of the trunk.

It is also of interest to consider the innervation of the secondary respiratory muscles. The sternomastoideus, a flat muscle placed obliquely on the side of the neck between the anterior surface of the manubrium sterni and the posterior surface of the occipital and temporal bones and which assists the action of the scaleni muscles in forced respiration, is innervated by the anterior ramus of the first cervical nerve and by the eleventh cranial nerve (spinal accessory nerve) which is formed by the confluence of a nerve root from the lateral surface of the medulla oblongata with rootlets derived from the first five or six segments of the spinal cord.

The muscles responsible for the attachment of the front limbs (section 5.2.3) are innervated as follows: the serratus anterior muscle by the posterior thoracic nerve which originates from the ventral ramus of the seventh cervical spinal nerve; the latissimus dorsi, the xiphihumeralis, the pectoralis major, the pectoralis minor and the pectoantibrachialis muscle by the anterior thoracic nerve and, for the first muscle, the caudal subscapular nerve, both of which belong to the brachial plexus of nerves formed from the ventral rami of the fifth, sixth, seventh and eighth cervical and first thoracic spinal nerves; the occipitoscapularis and the levator scapulae ventralis by the ventral rami of the third and fourth cervical spinal nerves; finally, the clavotrapezius, the acromiotrapezius and the spirotrapezius muscles are innervated by the spinal accessory nerve and by the anterior rami of the first four cervical spinal nerves and the rhomboideus muscle by the anterior rami of the first four thoracic spinal nerves.

3.4.3 - Innervation of the lungs and respiratory airways

The lungs are innervated both by sympathetic fibres originating in the upper thoracic ganglia and by vagal parasympathetic fibres which feed ganglia in the anterior and posterior pulmonary plexuses situated at the root of the lung. From these plexuses both types of postganglionic fibres are distributed to the smooth muscles of the blood vessels and the bronchi throughout the lungs. In the bronchi, the parasympathetic innervation promotes the contraction of the muscles and produces bronchial constriction and shortening, whereas the sympathetic innervation has the opposite effect and results in bronchial dilation. The trachea is innervated by the vagi and its recurrent laryngeal nerve branches and by fibres from the sympathetic trunks and a similar control of the tracheal musculature is achieved. The sensory receptors in the lungs and the tracheo-bronchial tree include (Widdicombe, 1964) subepithelial receptors responsible for the cough reflex, stretch receptors in the smooth musculature and in the walls of the alveolar ducts, atria and alveoli, chemoreceptors etc. and their afferent nerve fibres run in the vagi nerves. The reflexes mediated by these receptors together with the reflexes from the heart and the systemic circulation are the chief determinants (Aviado et al., 1955) of the mode in which the respiratory act takes place.

3.5 - SUMMARY AND DISCUSSION

In this chapter the anatomy of the main structures in the respiratory apparatus has been briefly reviewed. Only structures which have a direct bearing on its mechanical performance have been considered.

The information presented here is essentially qualitative in nature and constitutes the bare minimum necessary to the understanding of the movements and force relationships which occur during respiration. These data would, however, be insufficient for the development of rigorous models of the structures in the respiratory apparatus. Such models need accurate quantitative information which to the best of our knowledge is still not available; they also need a higher degree of detail particularly with respect to muscle innervation and this, again, is still not available. We must conclude, therefore, that a large amount of work has to be done in this area before truly realistic models of the respiratory apparatus can be devised. In the following chapter a contribution is made to the quantitative characterization of these structures, namely the ribs and rib cage, the diaphragm and the abdomen.

CHAPTER 4.0

EXPERIMENTAL CHARACTERIZATION OF THE KINEMATICS OF THE EXTERNAL RESPIRATORY APPARATUS

4.1 - INTRODUCTION

The movements performed by the external respiratory apparatus during the breathing process are, like all biological phenomena, of a very complex nature and very difficult to quantify. In particular, these movements are not completely determined by geometric or kinematic constraints and, therefore, their study will have to resort to more evolved concepts such as those developed for the design of complex man-made structures and systems. Nevertheless, the detailed knowledge of the displacements undertaken by the structures which constitute the external respiratory apparatus during the respiratory act, is still essential to any realistic analysis of the mechanics of breathing. The material presented in this chapter is intended as a contribution towards this end.

The central problem of an experimental study of this nature consists in defining with adequate accuracy the movements of three-dimensional structures, most of which are hidden underneath the skin of the animal. The final solution for such problem may prove to be some form of X-ray stereo cinephotography capable of satisfying the requirements outlined above. As shall be described in chapter 6.0, however, we made use of a different method which, although not as accurate as some modern methods of stereophotogrammetry, produced results of quite sufficient quality to enable us to quantify the movements of the respiratory apparatus. In this technique the skin over the thorax and most of the abdomen on one side of the body of the animal is removed and small reflective markers are glued to the exposed structures. The animal is fixed to a surgical table in a prone position with its vertebral column firmly maintained in an almost horizontal configuration; this table is equipped with two mirrors, one above the animal and the other below, which provide two lateral images of the body. A 16 mm cine-camera, previously aligned with the perpendicular to the centre of the frame on which the mirrors are mounted, is used to photograph the breathing movements, the film thus produced being processed frame by frame; for each frame, the three space coordinates of each individual marker are obtained by combining the frontal and mirror images of that marker according to the basic laws of geometric optics. Once the coordinates of the markers are known, three orthogonal projections of the complete set of markers in the frame are produced, and in them, the rib cage and the exposed abdominal surface are 'fitted' with the help of the additional information supplied by X-rays and measurements on the animal and its dead carcass. We have found that the positions of the individual markers can be defined within a sphere 0.5 mm in diameter centred at the base of the marker. This precision is consistent with the fact that the localization of the ribs with respect to the markers has to be done by approximate interpolation.

The data presented in this chapter are based on results obtained from experiments performed on four cats and spread over a period of almost two years during which both the experimental technique and the numerical processing of the photographic data were developed and brought to an acceptable level of accuracy and efficiency. A total of over sixty film frames, chosen on an average basis of three 'spontaneous respiration' and two 'artificial respiration' breathing cycles per film and five frames in each breathing cycle, were fully processed in the last three films made. In order to give an idea of the amount of effort that such a task represents, we point out that there are about 300 marker positions in each frame which are digitized and processed to provide the basic framework for the three orthogonal projections on which the ribs and abdominal surface are to be 'fitted' (cf. section 6.3.3); this operation, performed on a drawing board and by working simultaneously with the three projections of the markers and of the structures which are being 'fitted', is extremely time consuming. Once the desired structures of the trunk are drawn, a collection of 15 points is implanted on each of the three projections of all the thirteen ribs and of five abdominal transversal cross-sections; the coordinates of these points are digitized - again, manually - to supply the data with which certain lengths and distances are computed and checked against their values measured on the living animal and on its dead carcass. If the errors found in these checks are larger than the accepted maximum value, the shapes of the 'fitted' structures are retouched accordingly and new marker points implanted on them, digitized and rechecked. The need for these checks and consequent corrections comes from the fact that there is no automatic way of locating the structures of the trunk with respect to the markers and only by simultaneous interpolation on the three orthogonal projections can this work be done.

The checking procedure outlined above reduces the errors due to the interpolation and tends to uniformise them for all the frames of the same film sequence.

There are at least two reasons why so many frames had to be processed during the course of our investigations. First of all, it was our purpose to characterize the respiratory movements of the anaesthetized cat in terms of changes in the shape and configuration of the respiratory structures which, although apparently not very large, have a great significance in the distribution of stresses throughout those structures. And, as it is very difficult to assess the amount by which three-dimensional bodies differ in shape unless their three-orthogonal projections are drawn, it became necessary to process as many frames in as many breathing cycles as the means at our disposal permitted. Secondly, the development of our method of stereophotography involved the processing of an appreciable number of film frames, many of which turned out to be of inferior quality; indeed, only the last two films were considered good enough and our results are based on them. We must emphasise, once again, that it was our aim to characterize the changes in the shape of the respiratory structures with the maximum accuracy allowed by our experimental method. This is the kind of information which is necessary for the study of the respiratory movements in terms of stress analysis. However, when faced with the problem of reporting these results in this thesis, we came to the conclusion that the most sensible way of concentrating these data was to draw composite diagrams in which the extreme configurations and a few of the intermediate configurations taken by the main structures during the respiratory cycle, are shown together. In this way the character and amplitude of the shape changes which occur during the respiratory cycle are presented in the most suggestive way; we also found that it would be purposeless to try to show the evolution of the movements over several periods because the changes which take place are very small in comparison with those which occur within a single cycle.

It should in principle have been possible to apply our technique of photogrammetry to a greater variety of experimental conditions but, unfortunately, we were unable to do that because of time limitations. Indeed, in its present form our technique is extremely time consuming and, consequently, its application will not become a fully practical proposition unless computer controlled methods of three-dimensional interpolation, similar to those used in conventional stereophotogrammetry, are introduced. For the numerical processing and curve drawing we used the London University CDC 6600 computer in conjunction with a Calcomp incremental plotter and the IBM 1800 computer in the Engineering in Medicine Laboratory of Imperial College together with an analog XY recorder.

Finally we point out that, due to technical difficulties, only half of the animal is photographed. This implies that the animal must be placed in a straight position and that the symmetry of the movements must be guaranteed. We did our best to satisfy these conditions but had no means of making absolutely sure that they were fully observed. We may, however, accept that they were achieved in so far as the general kinematic behaviour is concerned, but position errors of this nature will influence adversely the computation of the absolute chest and abdominal volumes.

4.2 - KINEMATICS OF THE BREATHING PROCESS

4.2.1 - Introduction

The structures in whose movements we are interested are the rib cage, the abdominal walls and the abdominal contents. Unfortunately only the walls of the rib cage and abdomen are shown in the films and, therefore, we have to deduce the movements of the other structures by indirect means. The movements of the rib cage are obtained by drawing the ribs with respect to markers on them as described in the introduction. The movements of the diaphragm and abdominal contents are analysed from still X-ray photographs taken in a position which is perpendicular to the side of the animal and to its backbone along the sagittal plane at different instants in the respiratory cycle. The data thus obtained are insufficient to define accurately the movements of these organs because the X-rays were not taken simultaneously and, therefore, do not provide the two projections which are needed for their exact location in space; nevertheless, the X-rays give a very good idea of the displacements which take place and allow an approximate estimation of their magnitude.

Figure 4.1 represents variations in the œsophageal pressure and in the tidal volume which took place during the filming of the spontaneous breathing movements. The film of this sequence was processed at every sixth frame for several of the respiratory cycles including the third one which represents a deeper breath. The breathing period corresponds approximately to 33 film frames, i.e., to 33/16 seconds. In figure 4.2 the volume encompassed by the rib cage is represented together with

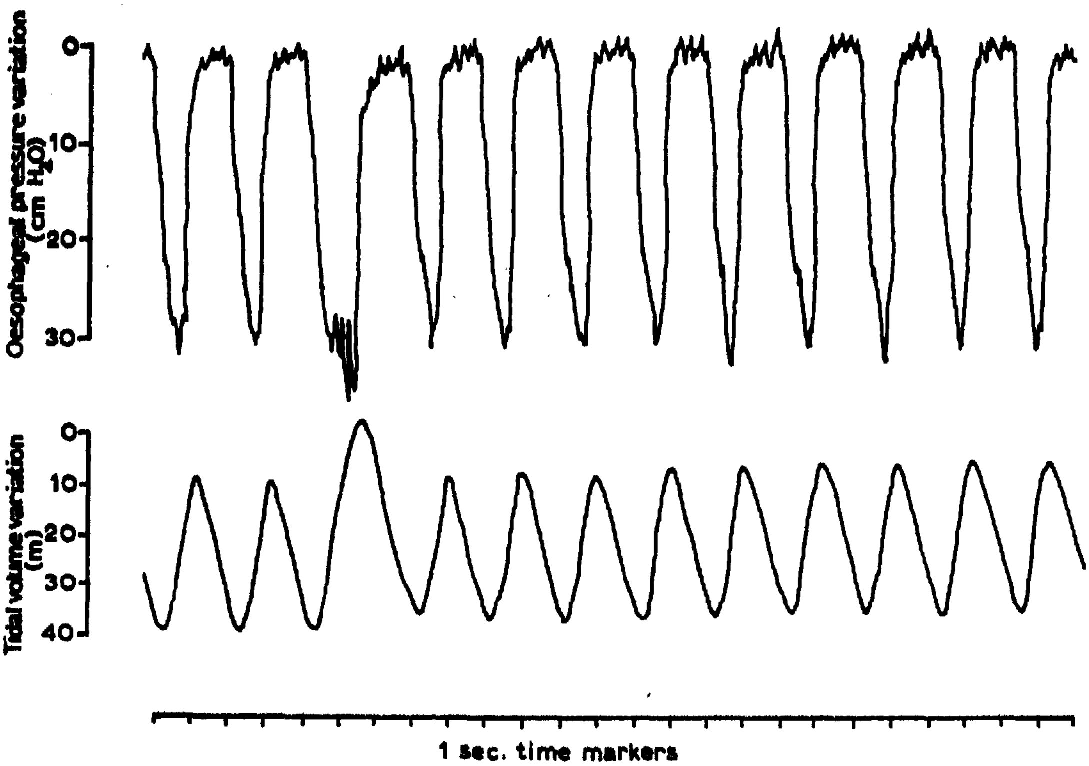


Fig. 4·1

Time course of the esophageal pressure and the tidal volume during the filming of the spontaneous breathing movements in the anesthetized animal.

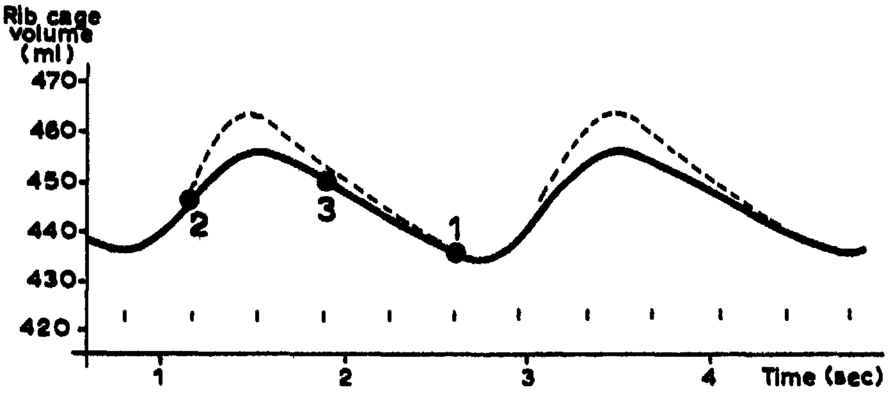


Fig. 4·2

Time evolution of the volume limited by the rib cage, as computed from successive film frames, and its approximate relationship to the tidal volume (broken line). The markers above the time axis indicate the relative location of the frames of the film which were processed for this computation and the three circles represent the frames used in Figs. 4·4 and 4·5 to illustrate the spontaneous respiratory movements.

the total tidal volume and thus allowing the assessment of the approximate contribution of the diaphragm; this contribution seems to be about half that of the rib cage and displays faster time constants. Unfortunately, we are not able to compute the volume of the rib cage with sufficient accuracy to make the results above something more than a rough estimate of the volume changes which take place. We would like to point out, however, that apart from being a convenient way of specifying the overall performance of the breathing process, the rib cage volume has a very limited kinematic significance, because it is not related in a unique manner to the displacements of the structures to which it corresponds.

All the drawings in this section, with the exception of the X-ray tracings, are represented in a 1/1-scale.

4.2.2 - The spontaneous respiratory cycle

In order to characterize kinematically the spontaneous respiratory process in the anaesthetized animal we make use of the data, obtained from a 16 mm cine-film and still X-ray photographs, which are summarized in figures 4.3 to 4.6. Figures 4.3 and 4.4 compare the views of the lateral and ventral surfaces of the thorax and abdomen in the extreme positions of peak inflation and deflation as they occur in the third breathing cycle of figure 4.1; this cycle represents a 'deep breath' and therefore enhances the relative displacements of the structures of the respiratory apparatus. The study of these drawings leads to the following conclusions:

1- The rib movement responsible for the inflation of the cage consists of a rotation upwards and forwards which increases the transverse dimension of the chest all along its length. This movement of the ribs is accompanied by a displacement of the sternum in a caudal direction and an opening of the 'elbow' angles of the rib cartilages. This behaviour of the rib cage elements is certainly not an artifact due to the mutilations to which the animal has been subjected because the same movements are just as pronounced in an intact, although anaesthetized, animal we examined.

2- The inspiratory movements have greatest amplitude in the region of the rib cage limited by the 4th and 10th ribs, diminishing gradually on both sides towards its cranial and caudal ends.

3- In this respiratory mode, inflation seems to be an essentially thoracic phenomenon with the abdomen playing a part of a driven compartment. When the cage inflates, the abdomen is also inflated at its lower cranial end region as a result of both the slight rise of the rib-cartilages in the area and, also, of the pressure exerted on the viscerae by the diaphragm (cf. figure 4.9). In its central region, however, the abdomen moves in an opposite direction as shown clearly by the 25 and 30 mm level contours in figure 4.3, which in peak inflation advance into the chest region and drop downwards in the dorsal region of the abdomen.

Figures 4.5 and 4.6 consist, respectively, of vertical and horizontal cross-sections along planes which, as shown in figure 4.2, are perpendicular to the median plane of the body. These cross-sections refer to three film frames 1, 2 and 3, equally spaced in the respiratory cycle, whose relative position is shown in figure 4.2 by the three numbered circles. The cross-section of figure 4.5 shows that the dorsal and ventral regions of the walls of both the thorax and abdomen undergo displacements in the same direction throughout the respiratory cycle; the lateral region of these walls, however, displays movements in the opposite direction so that when the cage inflates the abdomen deflates and vice-versa. This effect, which has already been described in connection with figure 4.3, suggests the possibility that the volume encompassed by the abdomen will tend to stay approximately constant throughout the entire breathing period. Indeed, the shape of the abdominal cross-section (cf. figure 4.5- D,E,F) is such that the abdominal walls are practically unable to resist inward transverse forces acting normally to their lateral surfaces. In these conditions, therefore, they will be sucked in whenever the abdominal pressure in their immediate neighbourhood decreases as a result of, for instance, the movements forced on the viscerae by the rib cage and the diaphragm. This response of the lateral abdominal walls could, thus, supply a mechanism capable of keeping the abdominal pressure - and with it the abdominal volume - approximately constant. We have, in fact, been unable to detect any significant departure from the figure of 360 cc we computed for the volume of that part of the abdomen considered in the film frames we digitized(*). Our result must be taken with caution both because we only have access to about 2/3 of the total abdominal volume and because of the limited precision of our method for evaluation of that volume.

Figures 4.7 to 4.10 are tracings of X-ray plates of the

(*) The abdominal volume we computed is that of the cylinder limited cranially by the edge of the rib cage and by the most caudad markers in the photographs.

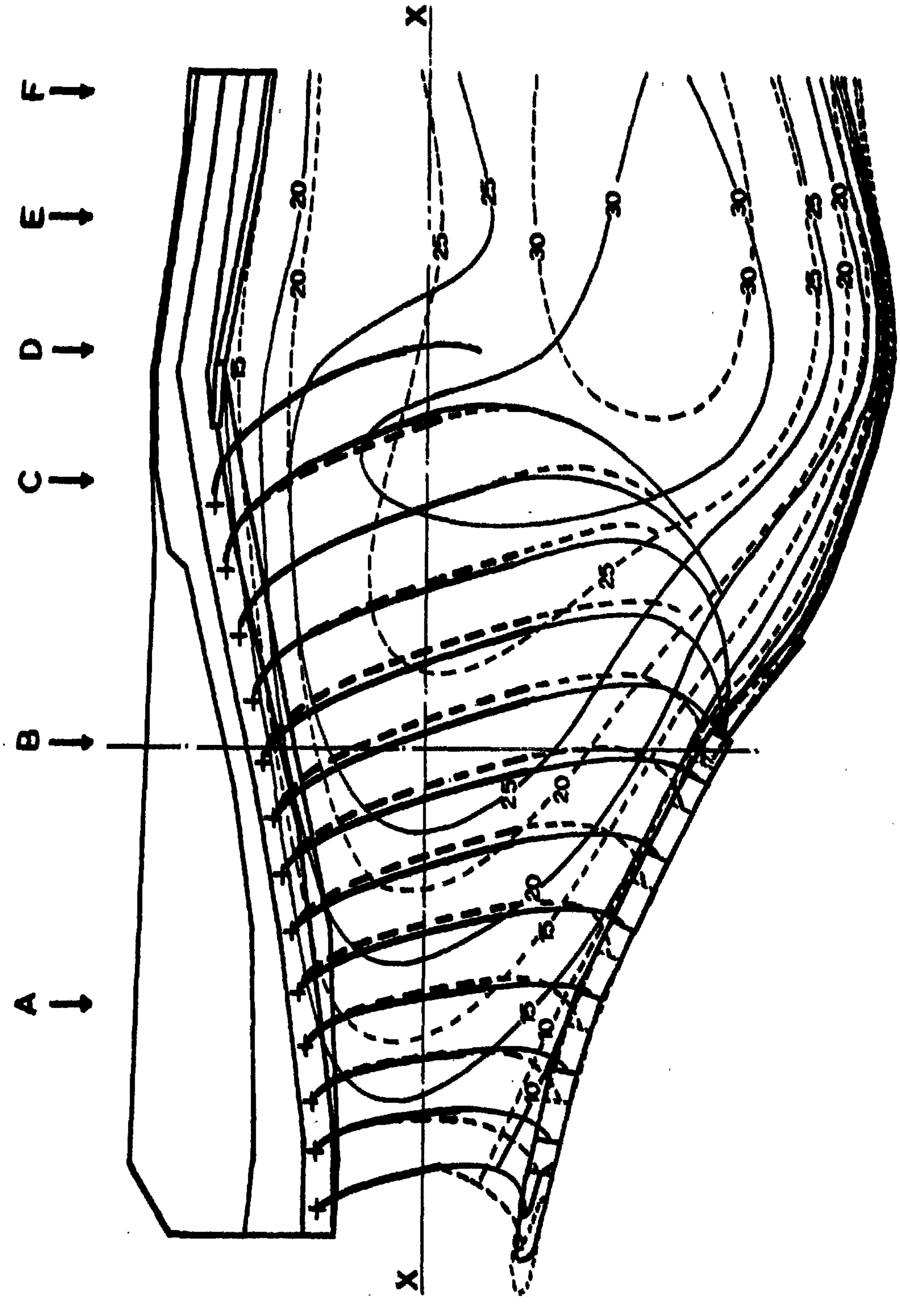


Fig. 4·3

Spontaneous breathing: comparison between the lateral views of the positions of peak inflation (solid line) and peak deflation (broken line). A,B,C,D,E and F represent the levels at which the vertical cross-sections of Fig.4·5 are taken.

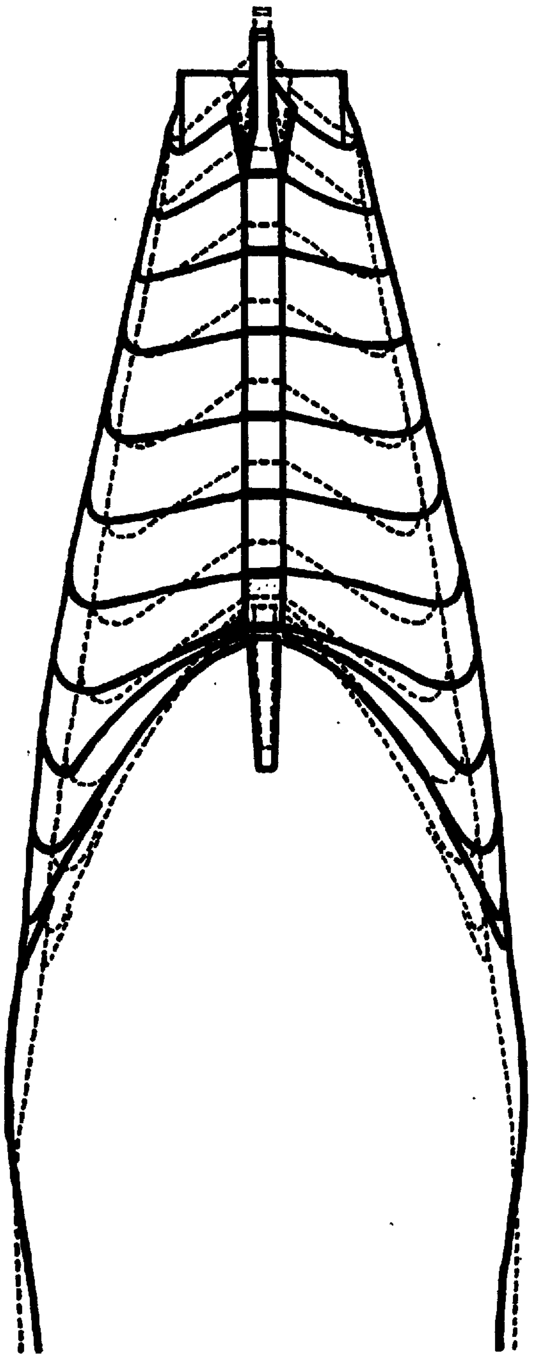


Fig. 4·4

Spontaneous breathing: comparison between the ventral views of the positions of peak inflation (solid line) and peak deflation (broken line).

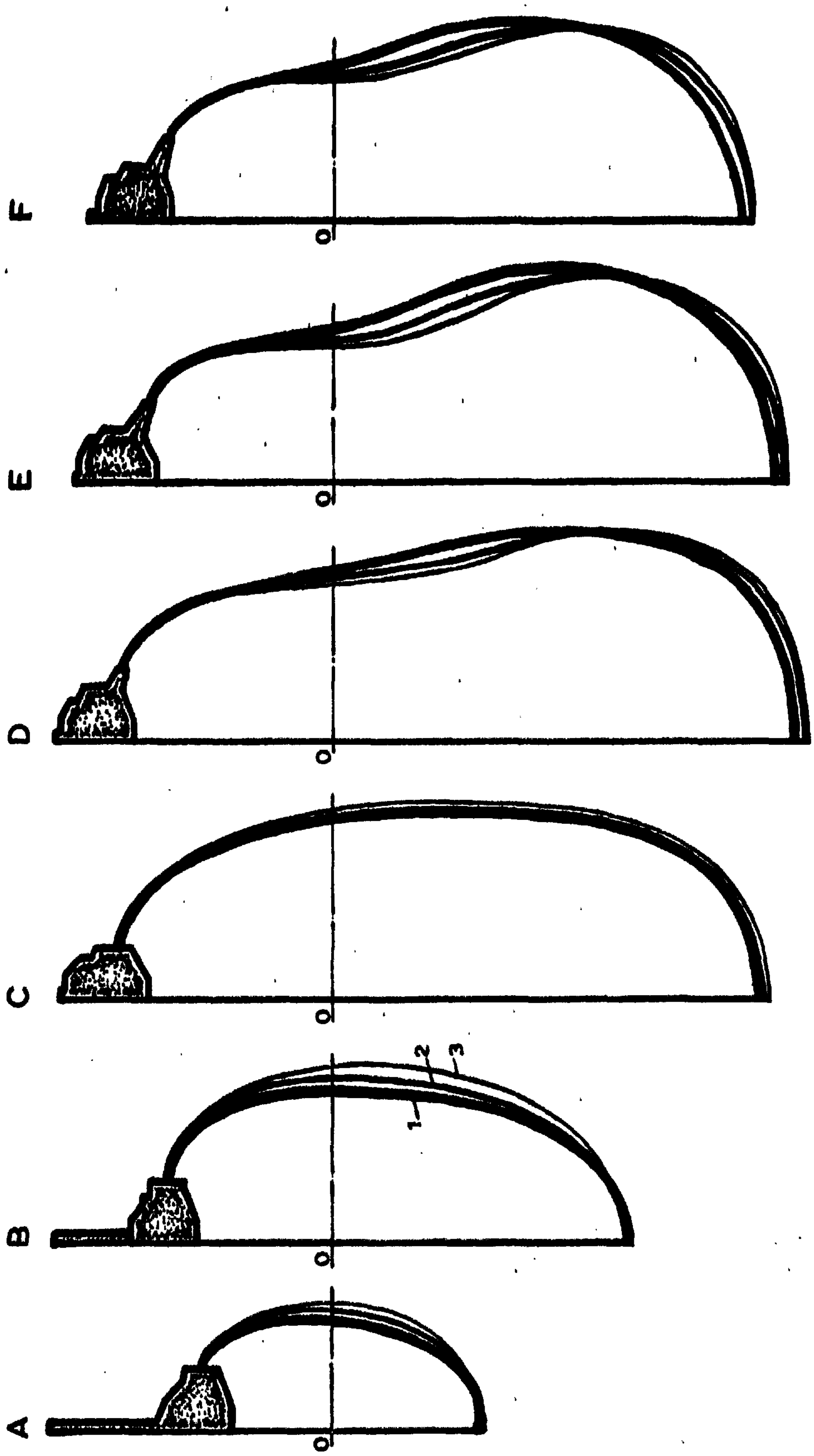


Fig. 4·5

Spontaneous breathing cycle: vertical cross-sections taken at the levels A,B,C, D,E and F (Fig.4·3). The three lines of different thickness in each cross-section represents one of the three equidistant instants in the breathing cycle illustrated by the circles in Fig. 4·2; the thickest line corresponds to frame 1, the next to frame 2 and the thinnest line to frame 3.

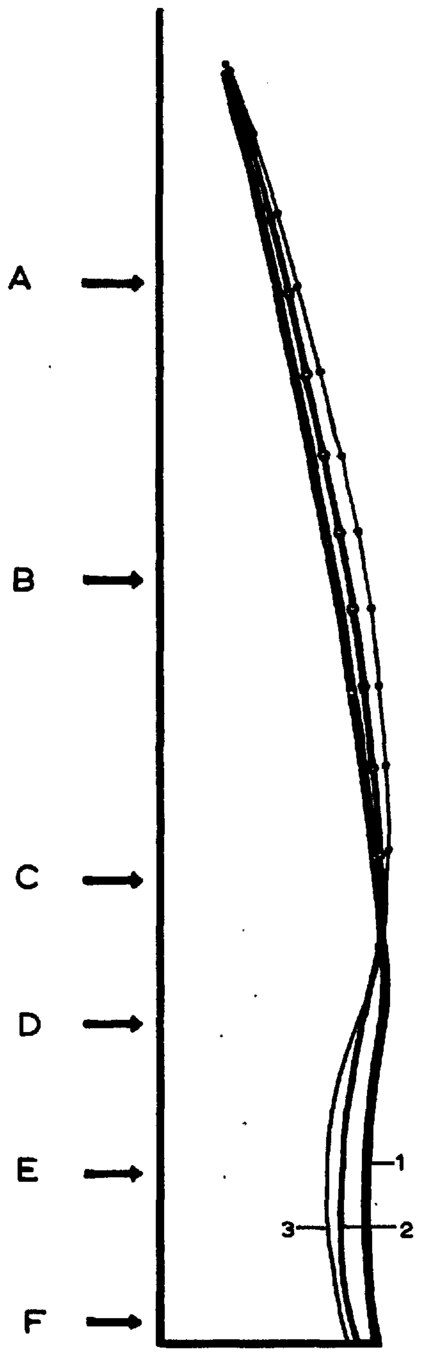


Fig. 4·6

Spontaneous breathing cycle: horizontal half cross-section by a plane normal to the sagittal plane of the animal and located 10 mm below the X-X axis shown in Fig. 4·2. The three sections, designated 1,2 and 3 refer to the same frames as those in Fig. 4·5.

peak inflation and deflation positions taken looking at the side and the top of the animal along directions which are approximately orthogonal. These drawings show quite clearly the movements performed by the internal organs during the breathing process, movements for which the diaphragm bears most of the responsibility. The main muscular masses of the diaphragm are the crurae, which connect the central tendon to the vertebral column; their powerful contraction displaces (cf. figure 4.9) in the caudal direction both the pleura and the viscerae on their abdominal side, an action in which they of course are seconded by the contraction of the remaining peripheral fibres (cf. figure 4.10). This contraction of the diaphragm forces the viscerae in a caudo-ventral direction and in this way causes the bulging in the lower cranial region of the abdomen; at the same time, the downward movement of the viscerae would tend to cause a depression in the central region of the abdomen and brings about an inward movement of the lateral abdominal walls in this area.

The considerations just made seem therefore to indicate that the distribution of abdominal pressures as well as the abdominal volume are both kept essentially constant throughout the cycle. We would like to point out in this connection that the volume of the abdomen is appreciably larger than that of the thorax, and consequently, the changes which the rib cage and the diaphragm force upon it represent a much smaller fraction of the total volume; this means therefore that, although the abdomen experiences quite large changes in shape during the respiratory cycle, the actual alterations in its volume needed to accommodate

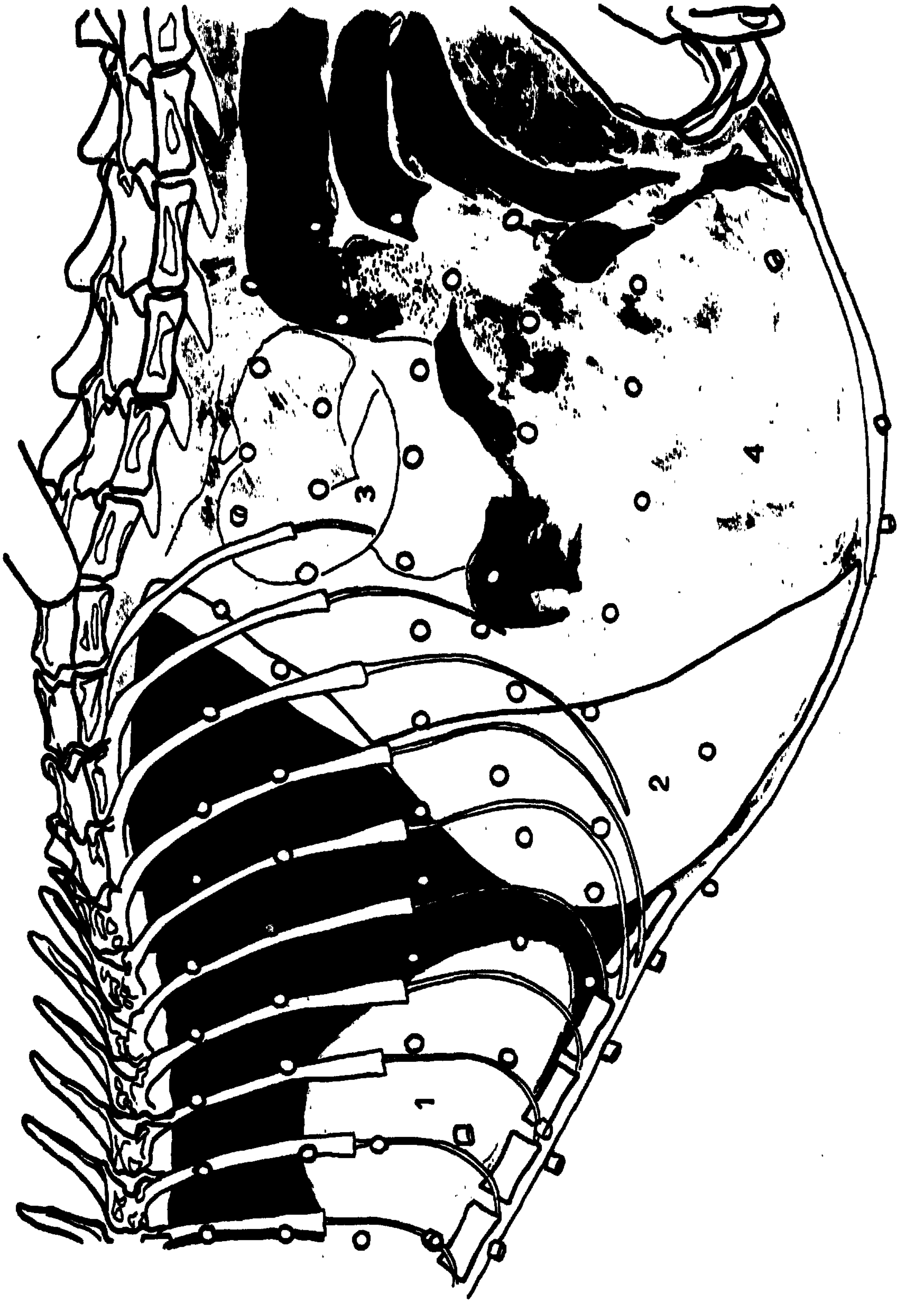


Fig. 4·7

Spontaneous breathing cycle: tracing taken from the X-ray representing a side view of the position of the trunk in peak inflation (inspiration). Only the ribs on the frontal side of the animal have been drawn.

1. Heart; 2. Liver; 3. Kidneys; 4. Intestines.

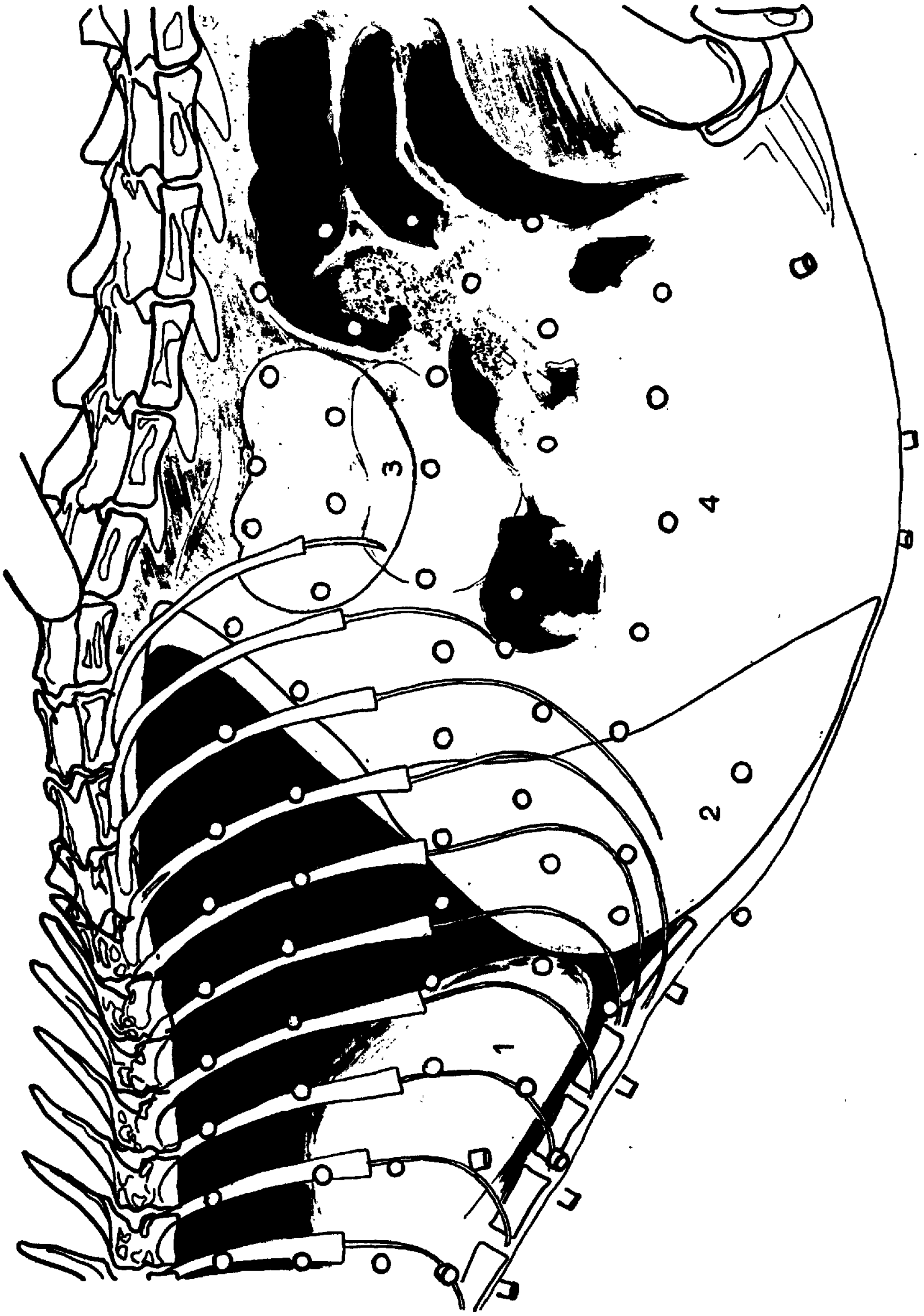


Fig. 4·8

Spontaneous breathing cycle: tracing taken from the X-ray plate representing a side view of the position of the trunk in peak deflation (expiration).
1. Heart; 2. Liver; 3. Kidneys; 4. Intestines.

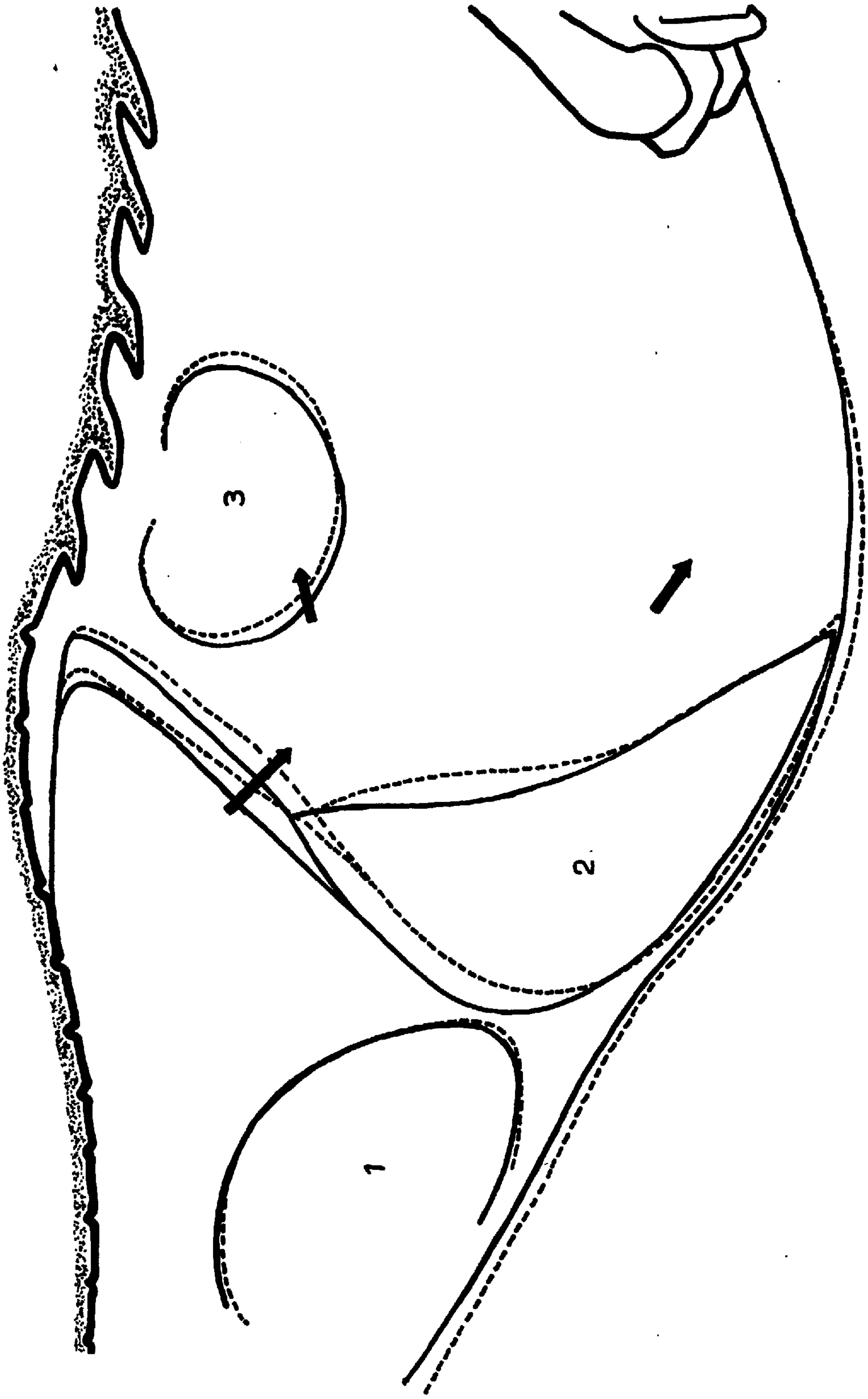
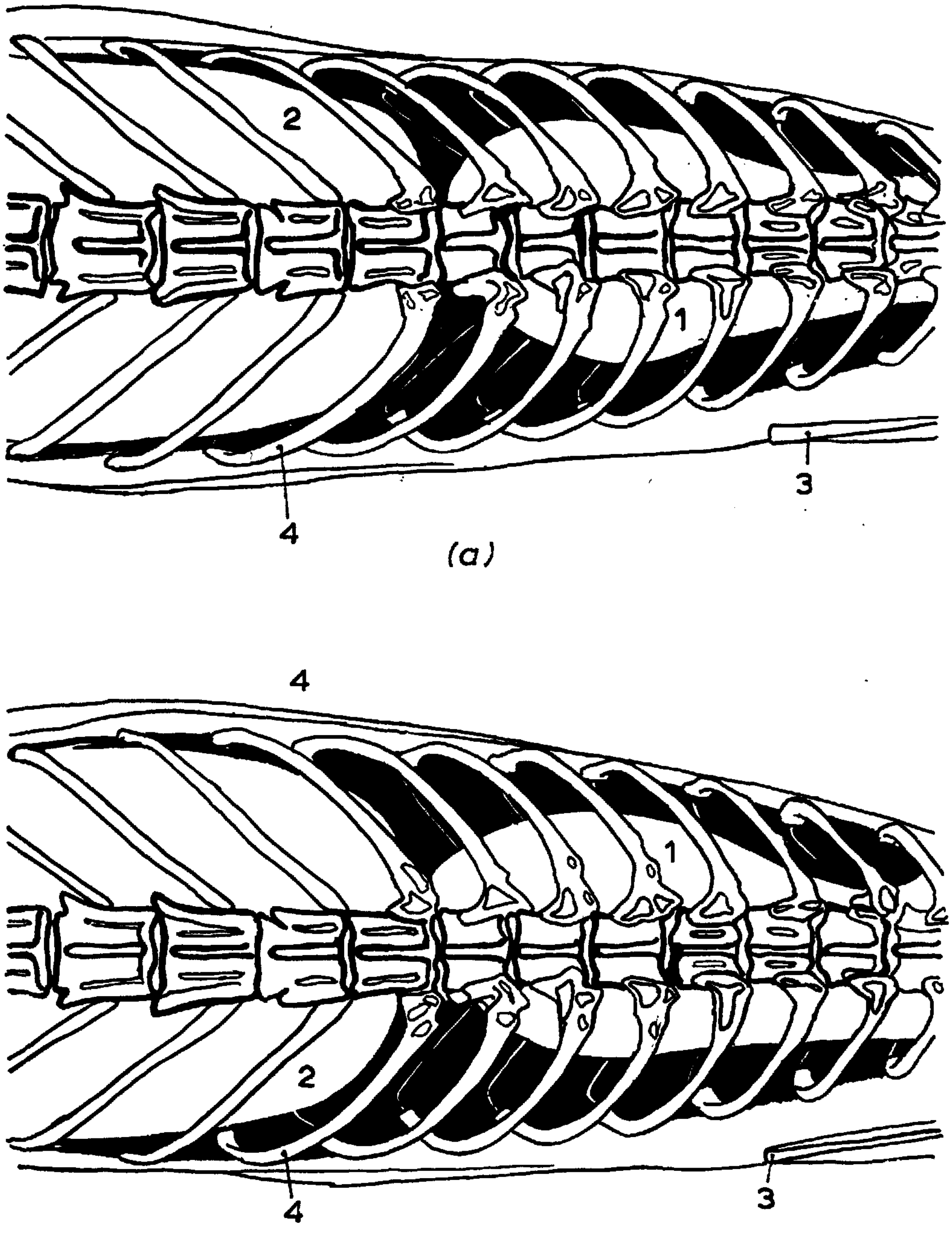


Fig. 4·9

Spontaneous breathing cycle : comparison between the main features of the side X-ray views of the positions of the trunk in peak inflation (-----) and peak deflation (——).

1. Heart; 2. Liver; 3. Kidneys.



(a)

(b)

Fig. 4.10

Spontaneous breathing cycle: tracings of the X-ray plates representing the top views of the positions of (a) peak deflation and (b) peak inflation.

1. Heart ; 2. Diaphragm; 3. Scapula; 4. 10th rib.

the tidal volume changes, are most likely of quite secondary importance.

4.2.3 - Comparison between spontaneous and artificial ventilation

In order to increase our understanding of the mechanical properties of the external respiratory apparatus and, in particular, to relate them to the concepts of the pressure-volume analysis we performed experiments in which the animal was paralysed by Flaxedil and artificially ventilated according to the regime shown in figure 4.11.

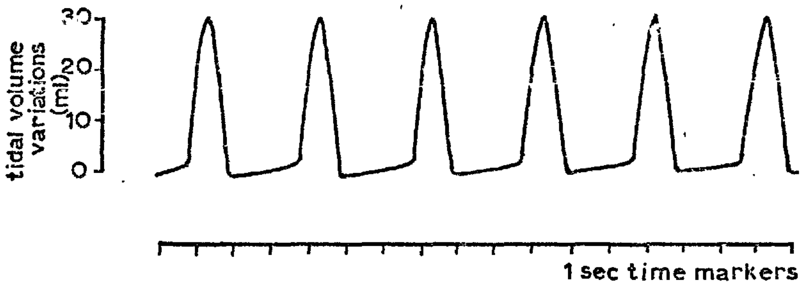


Fig. 4.11 - Tidal volume waveform in the experiment of artificial ventilation.

The most important conclusions to be drawn from these experiments seems to be the recognition that the artificial ventilation corresponds to a quite distinct respiratory mode. This result is understandable if we consider the mechanical complexity of the structures which take part in the respiratory act, and most important of all, that their movements result not only from geometrical and structural constraints but also from

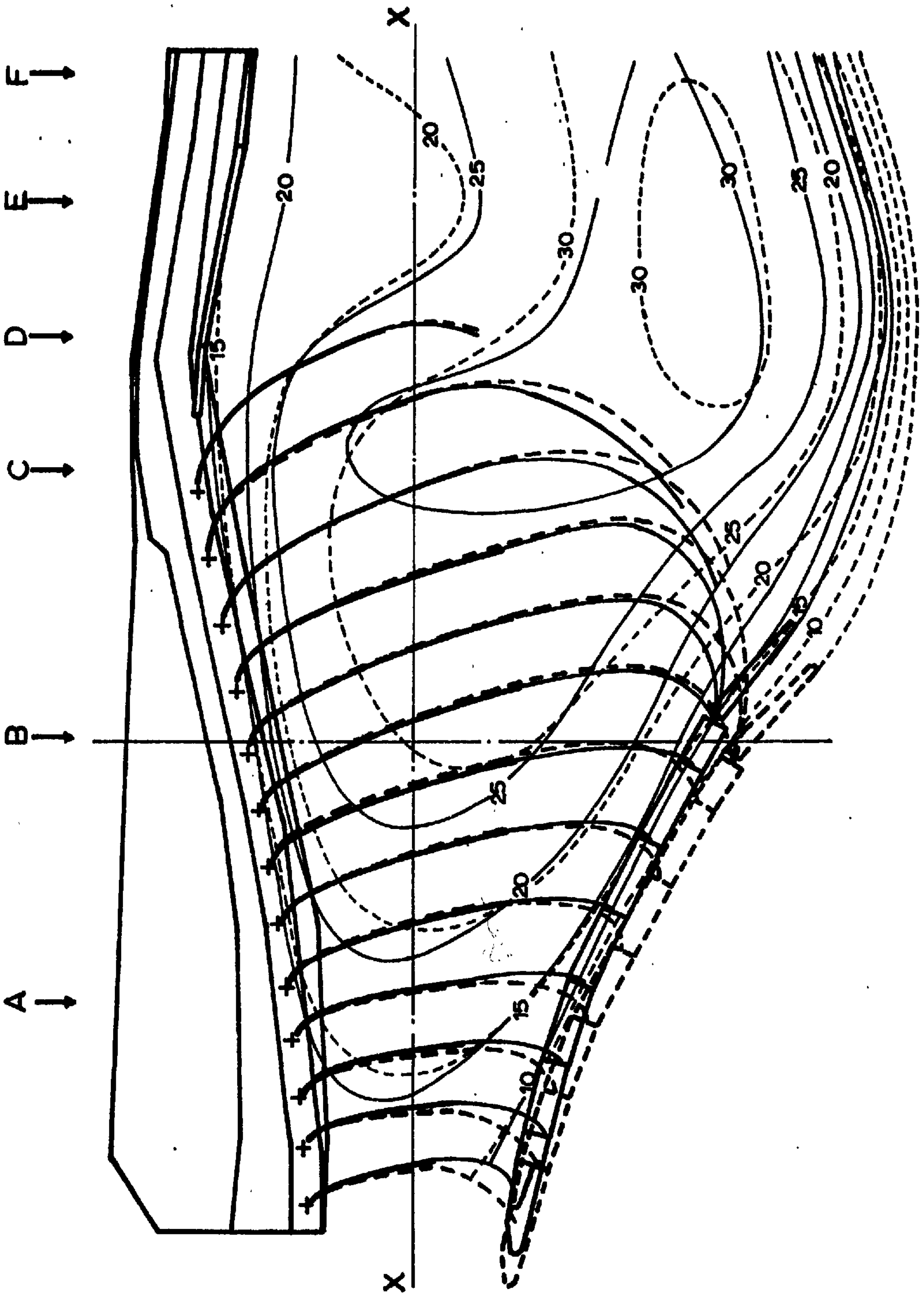


Fig. 4·12

Comparison between spontaneous and artificial ventilation: lateral views of the positions of peak inflation for natural (solid lines) and artificial (broken lines) respiration. A B C D E and F represent the levels at which the vertical cross-sections of Fig. 4·13 are taken.

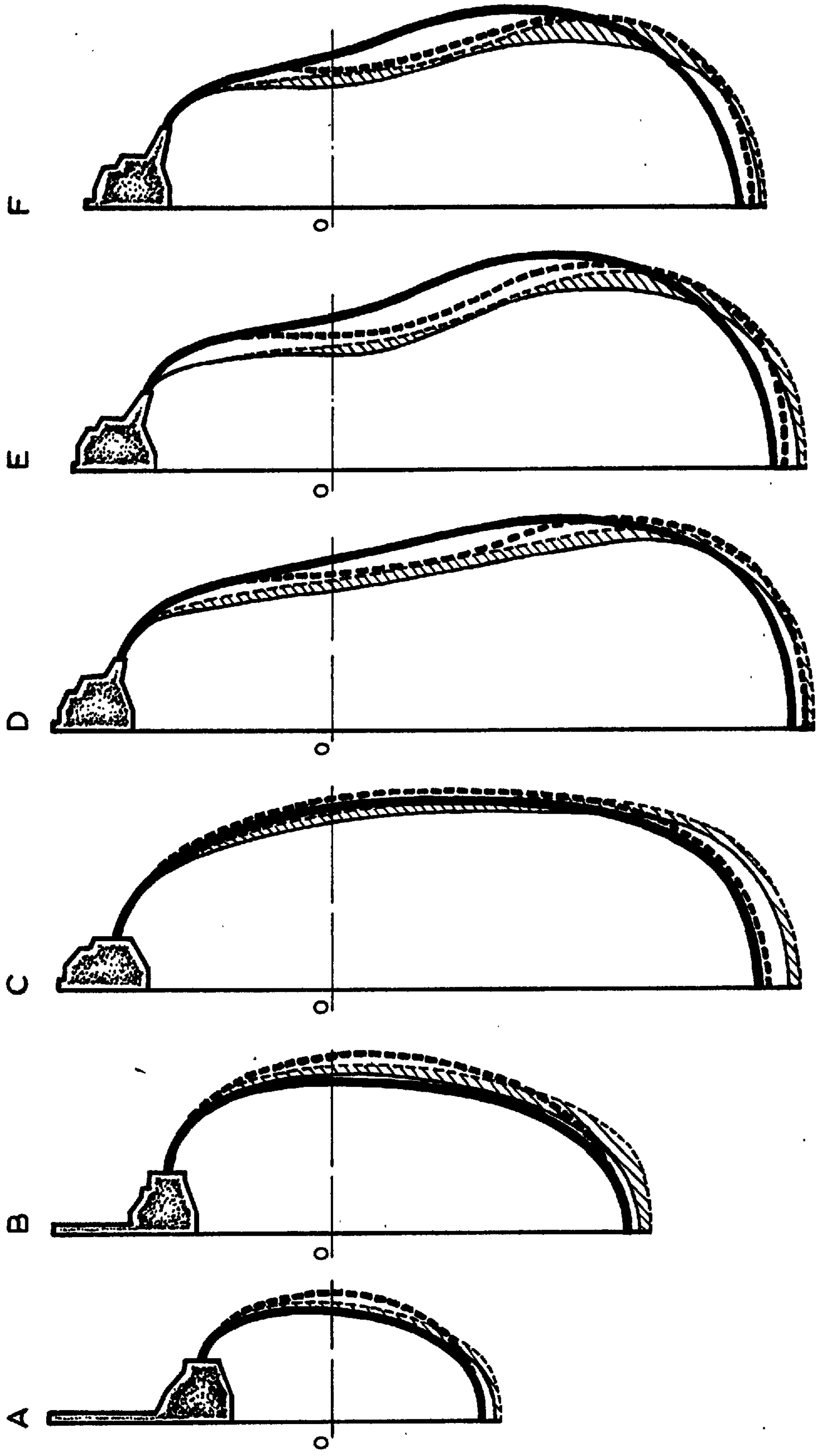


Fig. 4·13

Comparison between spontaneous and artifial ventilation: vertical cross-sections at the levels A, B, C, D, E and F shown in Fig. 4·12: The cross-sections which are represented are those which correspond to spontaneous peak inflation (━ ━ ━ ━) and peak deflation (━━━) and to artificial respiration both in peak inflation (- - - - -) and deflation (———).

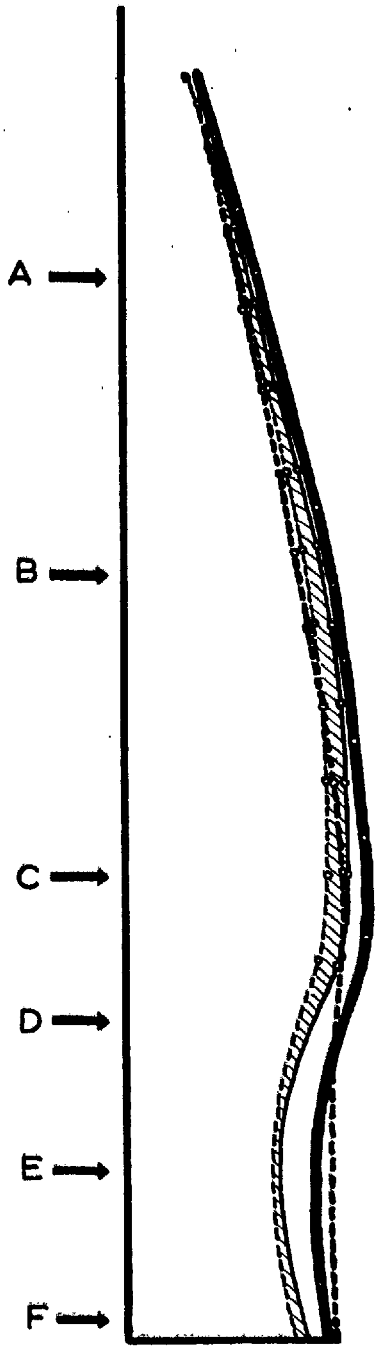


Fig. 4·14

Comparison between spontaneous and artificial ventilation: horizontal cross-section by a plane normal to the sagittal plane of the animal and located 10 mm below the X–X axis shown in Fig. 4·12. The cross-sections shown here obey the same convention as in Fig. 4·13.

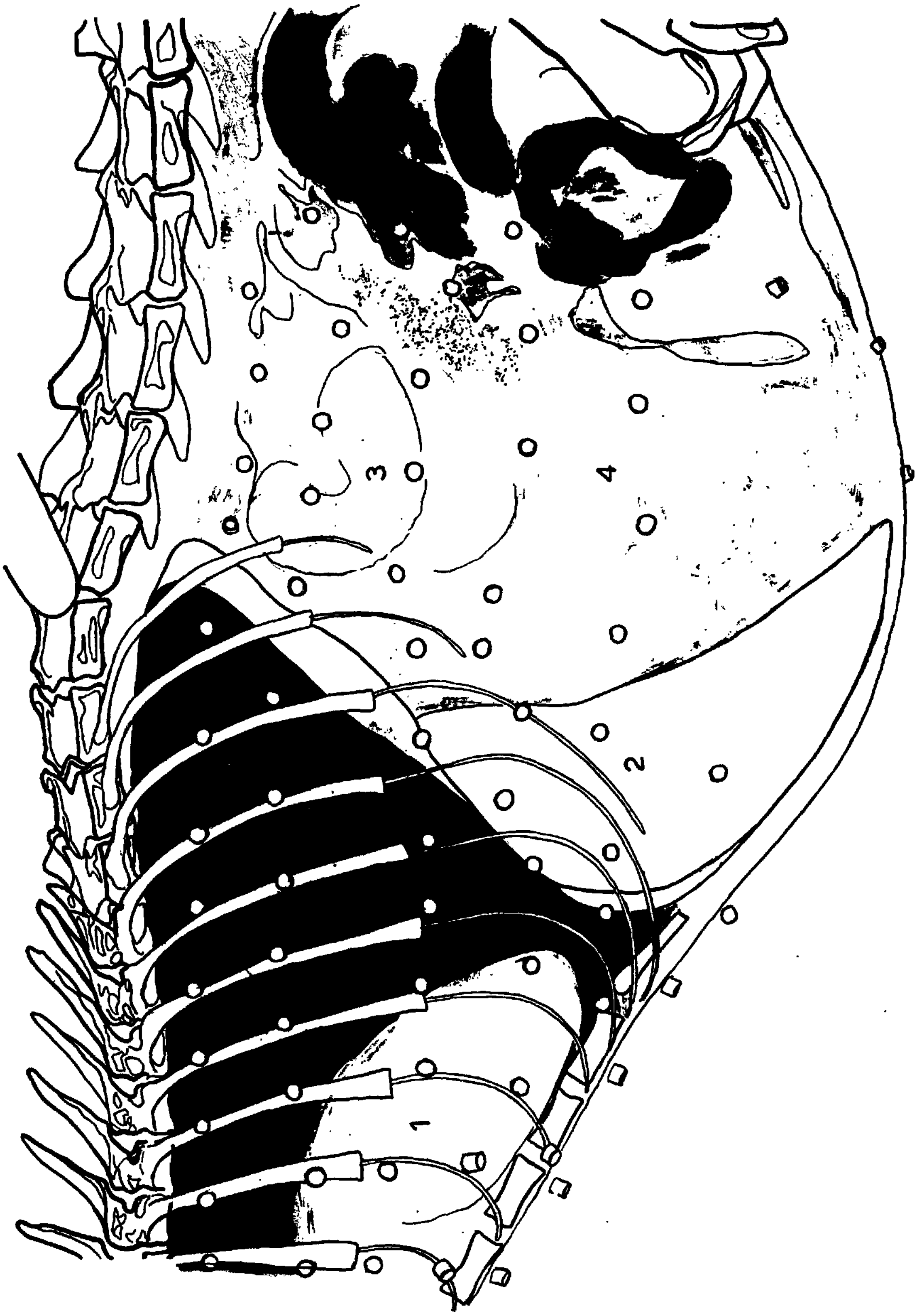


Fig. 4·15

Artificial respiration; tracing taken from an X-ray plate which represents a side view of the trunk position in peak inflation (inspiration).

1. Heart; 2. Liver; 3. Kidneys; 4. Intestines.

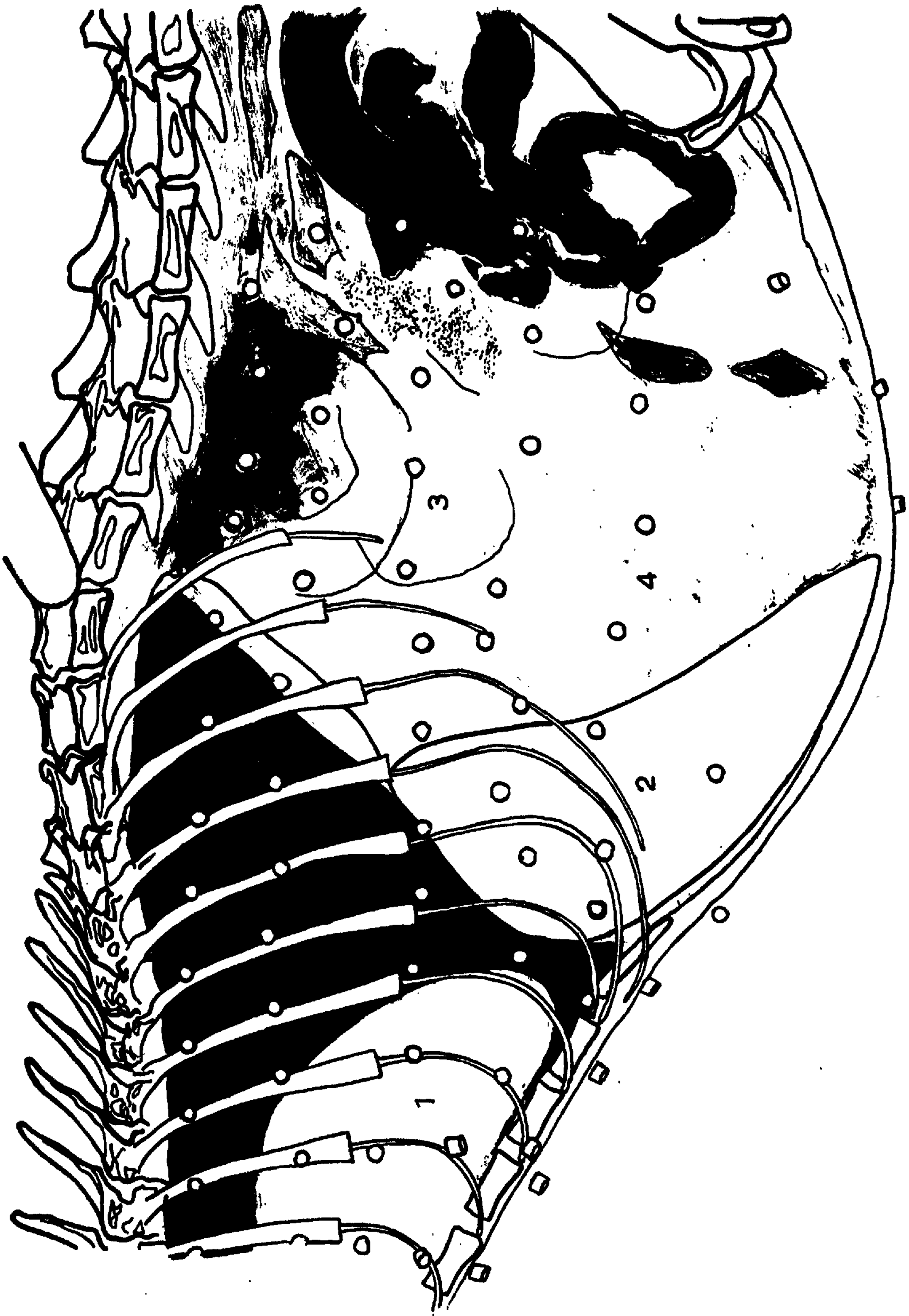


Fig. 4·16

Artificial respiration: tracing from an X-ray plate of the side view of the trunk position in peak deflation (expiration).
1. Heart; 2. Liver; 3. Kidneys; 4. Intestines.

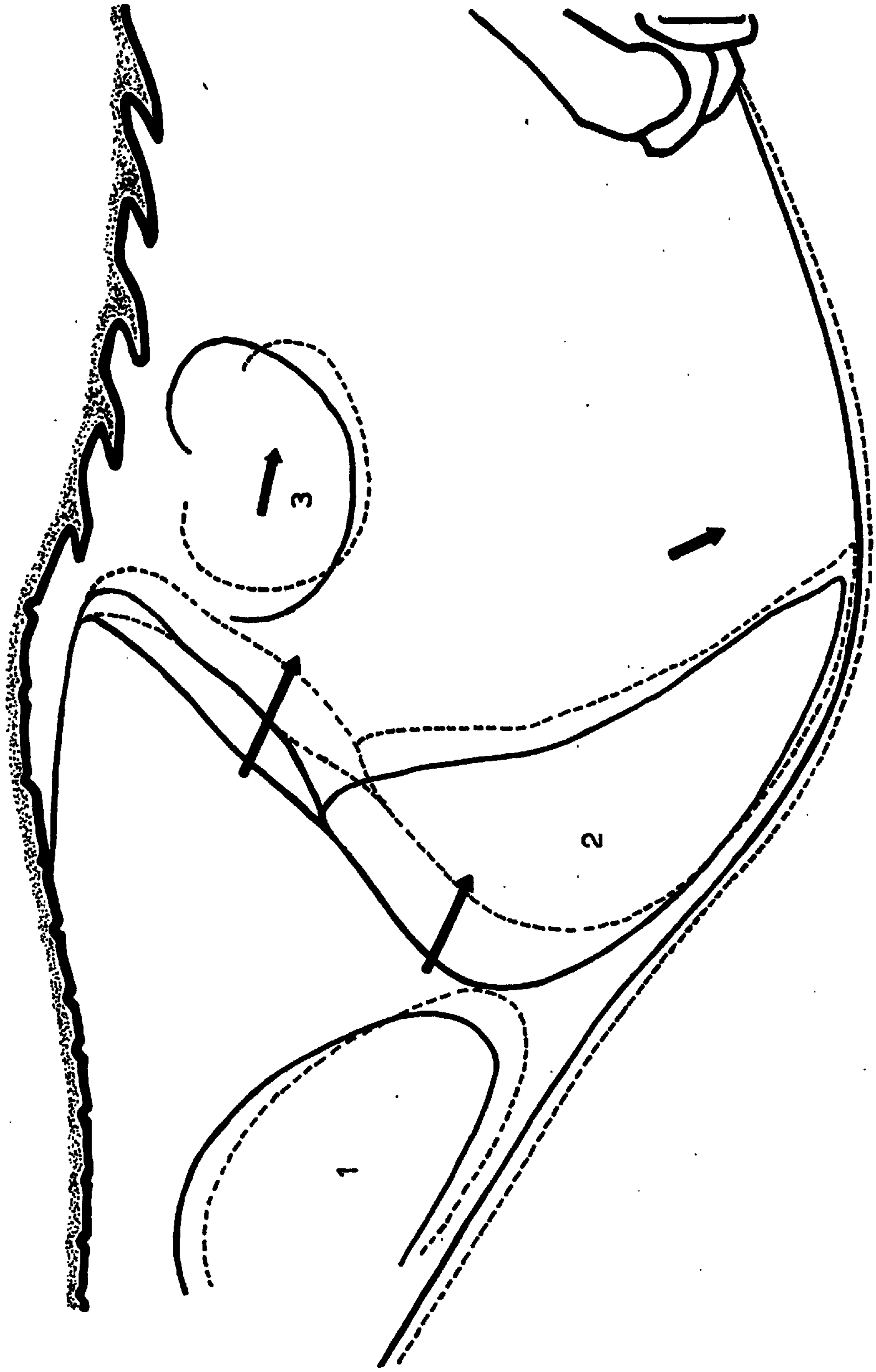


Fig. 4·17

Artificial respiration: comparison between the positions of peak deflation (———) and inflation (- - - -) as shown in side views of the trunk.

1. Heart; 2. Liver; 3. Kidneys.

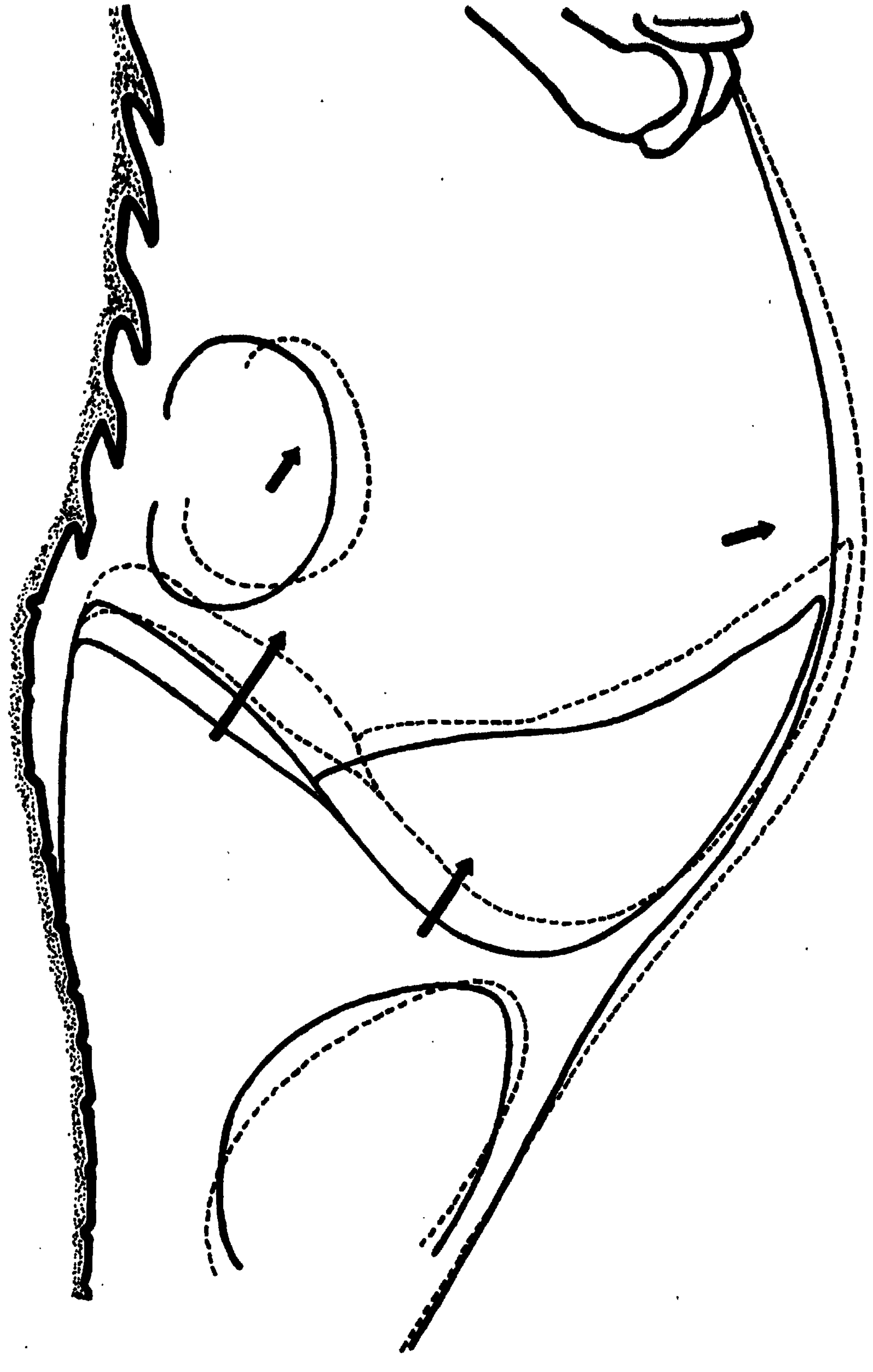


Fig. 4·18

Comparison between spontaneous and artifial ventilation : tracing of the X-ray plates of the side views of the trunk for the position of peak inflation in spontaneous (——) and forced (- - - -) ventilation.

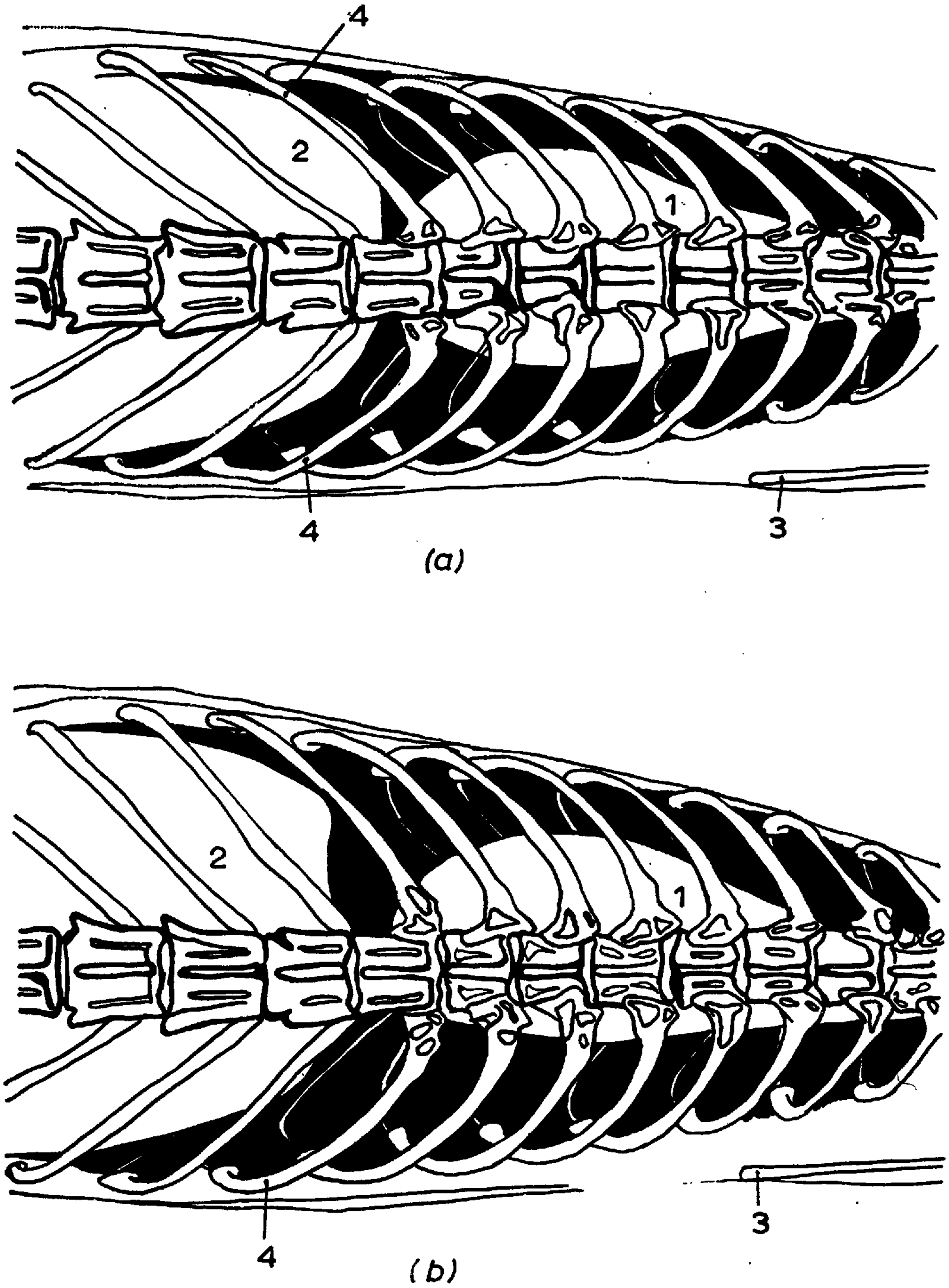


Fig. 4·19

Artificial respiration: tracings taken from X-ray plates representing the top views of the trunk positions in (a) peak inflation and (b) peak deflation.

1. Heart ; 2. Diaphragm ; 3. Scapula ; 4. 10th rib.

the way in which the active contraction of the muscular masses takes place. The drawings of figures 4.12 to 4.14 show side views and cross-sections of the trunk for its peak inspiratory and expiratory positions. These drawings illustrate how the blockage of the so-called 'tonic' muscular activity in the muscles of the trunk allows the weight of the viscerae to deform the rib cage and the abdomen, increasing their antero-posterior dimensions and decreasing their transverse dimensions; this effect forces the trunk into a configuration which is completely dintinct from those occurring in spontaneous breathing.

As far as our computation of the thoracic and abdominal volumes could reveal, no detectable difference exists in their values for the position of peak expiration in spontaneous and artificial respiration. However, when the lungs are artificially inflated with an increment in the volume of air of similar magnitude to the natural tidal volume, the increase of the thoracic volume is only slightly above one half of that which takes place in spontaneous respiration. This finding seems to be in agreement with the information contained in figures 4.17, 4.18 and 4.19 which show a much more pronounced displacement of the diaphragm during artificial inspiration; naturally, the larger surface area of the abdomen combined possibly with a larger passive compliance of its wall and a certain degree of compression of the air contained inside its viscerae, makes the diaphragm easier to move under the pressure of the incoming air than the walls of the rib cage whose structures are harder to deform. Figure 4.19(a) shows that even in expiration the position of the diaphragm is already more receded in artificial than in natural respiration; this is due to the lowering of the position of the abdominal contents which pull the diaphragm down. A further feature of the artificial ventilation is the irregular shape the diaphragm takes as a result of the irregular distribution of resistance presented by the abdominal viscerae (cf. figure 4.19(b)).

It should be emphasized that although the changes in the trunk configuration which occur as a result of the blockage of the 'tonic' muscular activity (cf. figures 4.12 to 4.14) are not large in absolute terms, they are enormous compared with the length changes - of the order of tenths of a millimetre - on which the mechanoreceptors operate. This is particularly true in the region of the costalcartilages where, apparently, the intercostal spacing widens to the full extent allowed by the connective tissue in parallel with the passive muscle fibres. It should further be noticed that the loads applied to the respiratory apparatus in our experiments are not likely to cause particularly large deformations, as they consist of the reasonably light weight of the viscerae and the ballooning effect of the pumped air; if, for instance, a negative pressure had been produced in the lungs, it is quite likely that the parasternal region of the cage would have been sucked in (Alexander, 1929; Cetrángolo, 1930; Joly and Vincent, 1937) and the overall distortion of the trunk shape would be much more spectacular.

4.3 - ADDITIONAL CHARACTERIZATION OF THE RIB CAGE

4.3.1 - Introduction

In this section we present further data on those characteristics of the rib cage components which affect their mechanical performance. We start by listing typical values of the length of the ribs and associated cartilages, information which is necessary in the procedure for 'fitting' the rib cage to the set of experimental markers; we, next, give values of the direction cosines of the ideal axes of rotation of the costovertebral joints and show the approximate trajectories described by the tips of the ribs in a breathing cycle, together with those which they would describe if the costovertebral joints were purely rotational around the axes defined above. This is followed by the planifications or rectifications of the lateral walls of the rib cage and the implant in them of the direction of a set of intercostal muscle fibres, the measurement of their approximate lengths and length variations and, also, the areas of the intercostal spaces. Finally, we make an estimation of the relative value of the inertia forces which are developed in the structures of the rib cage and enquire if they can be neglected by comparison with those due to the transmural pressure.

4.3.2 - Length of the ribs and rib-cartilages

Table 4.1 and figure 4.20 give the average values of the lengths of the ribs and associated cartilages as measured in four cats. The ribs are here considered as beginning at the point where the imaginary axis of rotation of the costovertebral joint intercepts the surface of the rib tubercle (cf. figure 3.4) and as ending at the costochondral joint; the rib-cartilage starts at this joint and ends at the sterno-chondral joint. The precision with which the lengths of the ribs and cartilages can be measured is greatly impaired by the curvature of these elements and by the difficulty of defining accurately their extremities; as a result, the values given in table 4.1 are defined with an accuracy not greater than plus or minus 1 mm. Within these limitations, however, the lengths given here apply closely to all four animals in which measurements were made; the individual deviations from the average values is greatest for the last ribs but even there only of the order of ± 1.5 to 2.0 mm and so, comparable to the precision with which the lengths are defined.

Table 4.1 - Typical length of the ribs and rib-cartilages in adult cats.

Rib n^{o}	Rib length (mm)	Cartilage length (mm)	Total rib and cartilage length (mm)
1	22	19	41
2	26	21	47
3	31	24	55
4	37	28	65
5	44	33	77
6	50	39	89
7	56	45	101
8	60	53	113
9	63	61	124
10	62	70	132
11	59	57	116
12	53	42	95
13	46	26	72

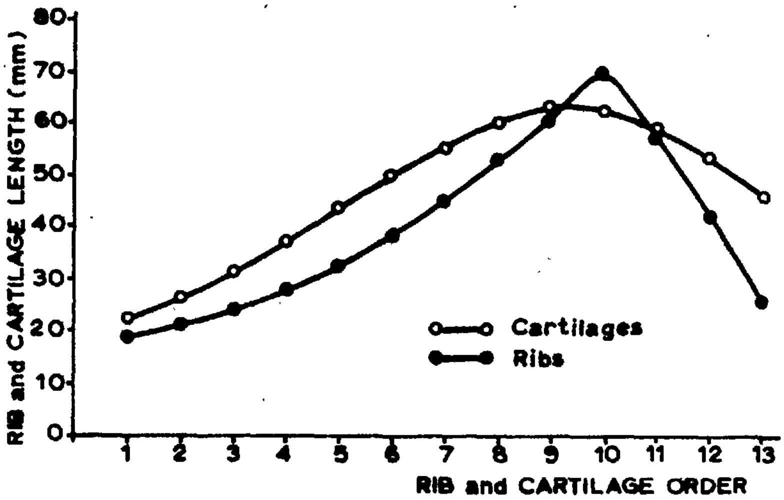


Fig. 4·20

Typical lengths of the ribs (o—o) and of the rib-cartilages (●—●) in adult cats.

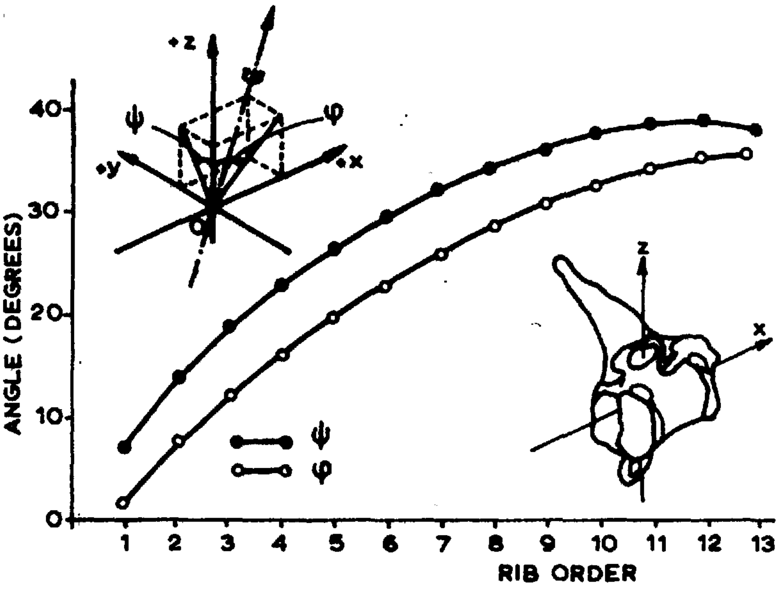


Fig. 4·21

Typical values of the angles φ (o——o) and ψ (●——●) which define the ideal axes of rotation of the costo-vertebral joints, expressed in the intrinsic axes of the vertebrae. The axes 0-x and 0-y are chosen so as to make acute angle with the corresponding axes in Fig. 4·3 and with 0-x, as the diagram shows, lying along the axis of longitudinal symmetry of the vertebra.

4.3.3 - The movements of the ribs

The angle values given in table 4.2, which have the same meaning as in figure 4.21, define the direction of the ideal axes of rotation around which the costovertebral joints would articulate if they had the nature of pure axial rotations; once the angles φ and ψ are known, the direction cosines are obtained by the following formulae:

$$\begin{aligned} l &= n \cdot \tan\varphi \\ m &= n \cdot \tan\psi \\ n &= (1 + \tan^2\varphi + \tan^2\psi)^{-\frac{1}{2}} \end{aligned} \qquad (4.1)$$

where the direction cosines l, m and n refer to the angles made by the axes with OX, OY and OZ, respectively. These angles, measured according to the method described in chapter 6.0, are expressed in the intrinsic reference frame of axes, shown in figure 4.21, in which the X-axis is the longitudinal axis of symmetry of the vertebra and the Z-axis is defined by the

Table 4.2 - Definition of the angles φ_i and ψ_i, expressed in the intrinsic system of reference axes, of the ideal axes of rotation of the costo-vertebral joints.

Rib n°	(°)	(°)	Rib n°	(°)	(°)
1	2.0	7.0	8	28.5	34.0
2	8.0	14.0	9	30.5	36.0
3	12.0	19.0	10	32.5	37.5
4	16.0	23.0	11	34.0	38.5
5	19.5	26.5	12	35.0	39.0
6	22.5	29.5	13	35.5	38.0
7	26.0	32.0			

centres of the two costovertebral joints. The knowledge of the values of these angles together with the knowledge of the orientation of each vertebra with respect to an overall system of reference axes (cf. figure 4.3), makes possible the computation of the trajectories which the tips of the ribs would describe if the costovertebral joints were purely rotational around the axes described above. The method for such computation is described in Appendix A.3 and it was used to obtain the circular trajectories shown in figure 4.22 which correspond to an orientation of the individual vertebrae with respect to the overall X- and Y-axes (figure 4.22) as defined in table 4.3.

Table 4.3 - Angles, measured in the clockwise direction, the X- and Y-axes of the intrinsic system of reference of each vertebra have to rotate in order to become parallel to their counterparts in the overall system of reference of figure 4.22; the Z-axis is parallel in all the systems of axes.

Costo--vertebral joint	Orientation angle (°)	Costo--vertebral joint	Orientation angle (°)
1	29.0	8	5.0
2	25.5	9	7.5
3	20.5	10	12.0
4	15.5	11	20.0
5	11.0	12	27.0
6	7.0	13	30.0
7	5.0		

The first costovertebral joint is the only one which can be reasonably described by the simple axial rotation model; in all the other double jointed ribs, from the 2nd to the 10th, the

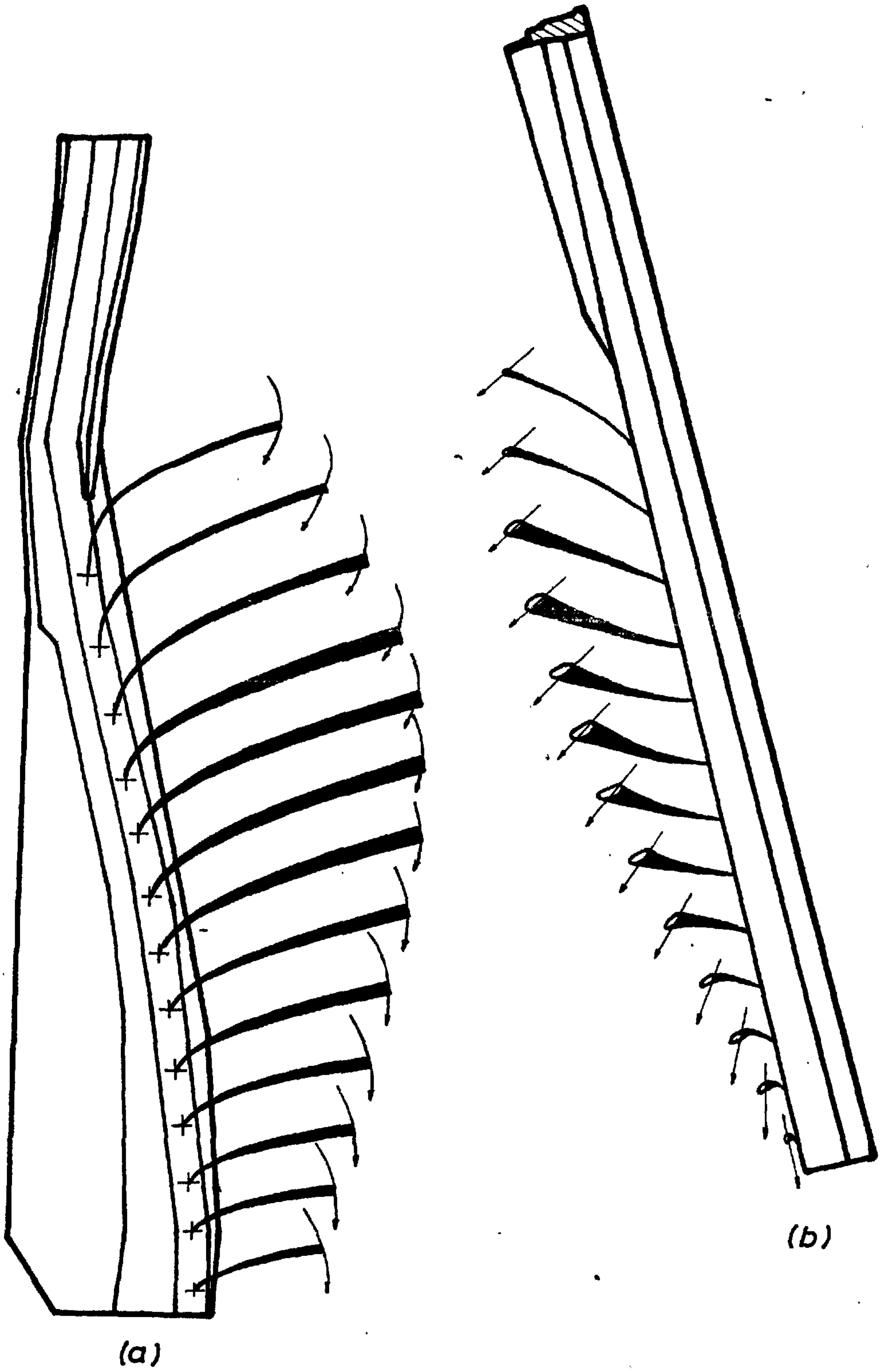


Fig. 4·22

Movement of the tips of the ribs in spontaneous breathing:
(a) lateral view and (b) view from underneath in the direction which corresponds to maximum lateral dimensions of the loops described by the tip of the ribs.
The arrows in both views indicate the trajectories which the tips would describe, starting at the peak deflation position, if the movement of the ribs was one of pure rotation around the axes defined in Table 4·2.

articulation between the tubercle of the rib and the vertebral transverse process becomes gradually more opened, or flattened, to allow an increasing amount of sliding of the surfaces in contact; in the last three ribs, the articulation with the transverse process is completely absent giving the joint a much greater freedom of movement. However, in spite of these departures from a simple axial- rotation model shown by the costo-vertebral joints, the movement of the ribs does not, for small amplitudes, differ exaggeratedly from what it would be in the ideal case, as figure 4.22 shows; the agreement between the two types of trajectories means that the analysis of the kinematic properties of the rib cage may be based, at least in a preliminary phase, on the model of purely axial costo-vertebral articulations.

4.3.4 - Rectification of the rib cage surface

The rib cage is a hollow structure whose thickness is small compared with its other dimensions and, therefore, which responds to applied loads in a shell-like manner, i.e., by means of a stress-strain field which can be considered, in a first approximation, as independent of the thickness of the cage walls; this field can therefore be described as a function only of two co-ordinates defined over the rib cage surface, in which it exists. A very convenient way of presenting data on this stress-strain field will therefore be to map it on the rectified surface of the rib cage. The rectification of the rib cage is also a very useful tool for the study of the geometric changes which the applied forces cause in the wall structures; these deformations are very difficult to analyse by other methods and are essential to the computation of the stress distribution. We understand by rectification or planification of a three-dimensional surface the plane area which is obtained when the surface is cut open and forced to adapt to a plane surface. This operation is straightforward for single-curvature surfaces, such as cylinders and cones, but for surfaces of double curvature it involves its breaking-up into sectors small enough to be treated approximately as a single curvature surface element. To perform the rectification of the rib cage surface we utilise the method described in Appendix A.2 which deals separately with each intercostal space in order to allow for the double curvature of their surface; figures 4.23 to 4.25 were obtained by this method. As we see, the rectified intercostal segments fit each other very nicely indicating that the cage is almost a ruled surface as a result of the predominance of the curvature around its longitudinal axis. Figure 4.23 compares the rectified cage surface in peak inflation and deflation and reveals clearly the changes which occur in the shapes of the cartilages and intercostal spaces. Figures 4.24 and 4.25 show the orientation of the fibres in both sets of intercostal muscles for the end positions of inspiration and expiration, respectively, in the spontaneous respiratory cycle. The orientation of the muscle fibres in the intercostal spaces was obtained by the method described in section 6.2.4 for a set of approximately equidistant fibres; once the attachment points of these fibres on the ribs and rib-cartilages are known for one position of the cage, their position for other configurations of the cage is easily obtained by locating the attachment points on the ribs of the corresponding rectified surface. This

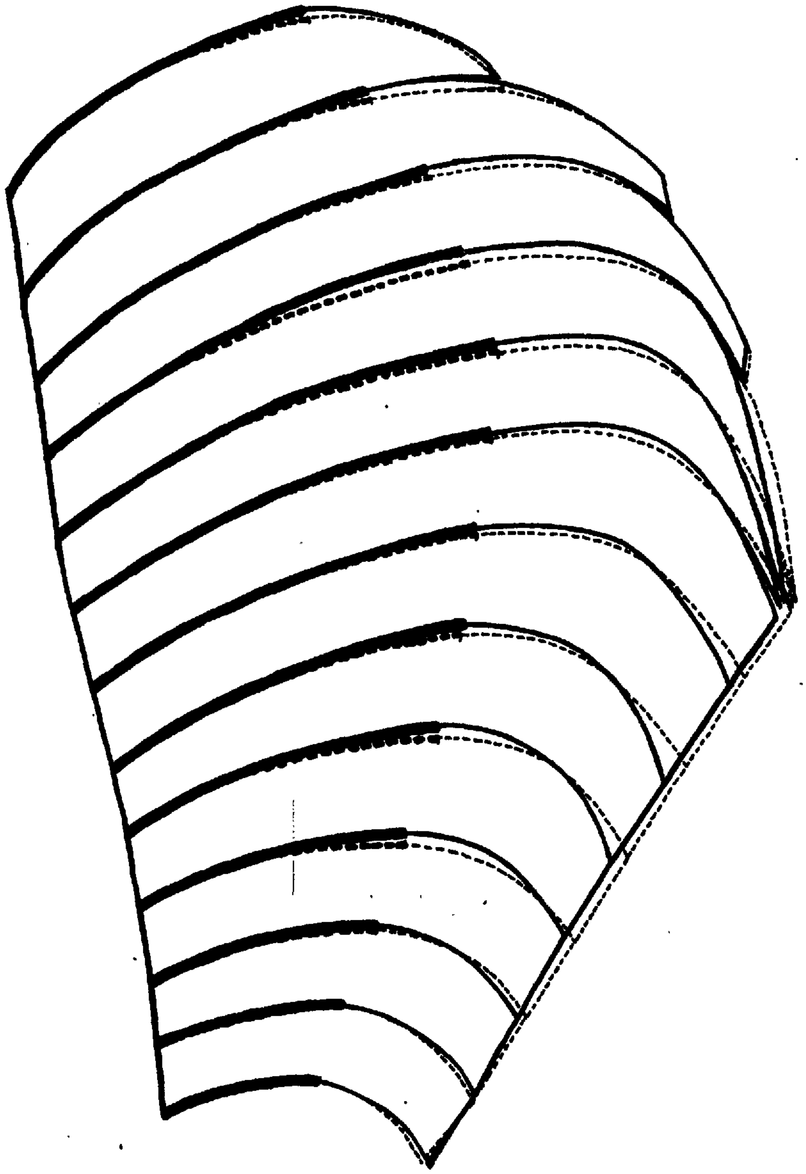


Fig. 4·23

Spontaneous breathing: comparison of the rectified surface of the rib cage in peak deflation (——) and peak inflation (– – – –).

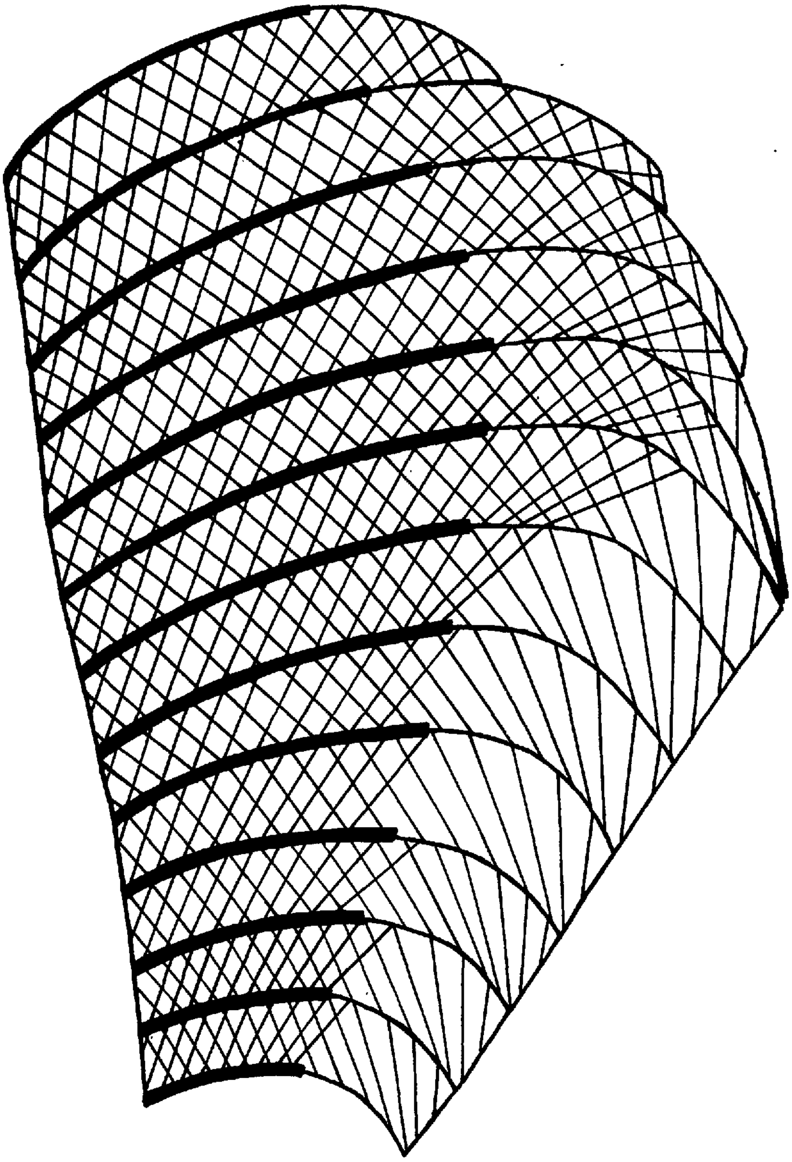


Fig. 4·24

Spontaneous breathing (peak inflation): orientation of the fibres in the intercostal muscles on the rectified surface of the rib cage.

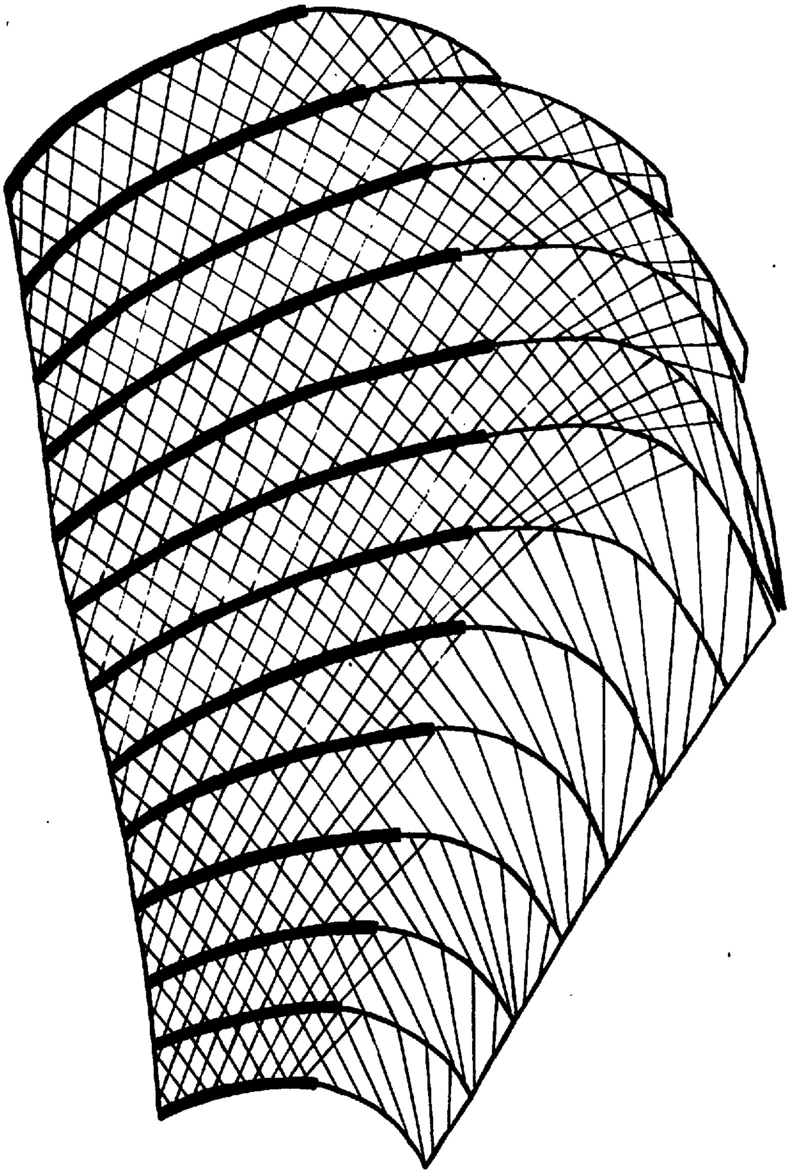


Fig. 4·25

Spontaneous breathing (peak deflation): orientation of the fibres in the intercostal muscles on the rectified surface of the rib cage.

is the way in which the fibres drawn in figures 4.24 and 5.25 are related. The length of these fibres was then read from the drawings and plotted in figures 4.26 and 4.27, for the internal and external intercostal muscles, respectively; these data are organised in twelve graphs, one per each intercostal space, each including the lengths of the corresponding set of fibres for the positions of end inflation and end deflation.

As can be seen in figure 4.26, the fibres of the internal intercostal muscles present a peak in the length value in the region of the 'elbow' of the costalcartilage; also, only the muscle fibres in this region show a measurable difference in length at the two extreme inflation and deflation configurations of the spontaneous respiratory cycle. The length of the fibres of the external intercostal muscles, on the other hand and as shown in figure 4.27, show a much less pronounced 'elbow' peak and seem to suffer no changes in length throughout the respiratory cycle.

This is a very surprising result as one would expect the stretch-reflex servo assemblages to be operative everywhere in the rib cage and their operation depends on changes in the lengths of the intercostal fibres. The first explanation for this unexpected finding to occur to us is the possibility that the length changes which take place are just too small to be detected within the accuracy of our method. We must, however, realise that the lines drawn in figures 4.24 and 4.25 represent the projection of the chosen muscle fibres on the external surface of the rib cage and, for that reason, the above results refer strictly to distances between points on adjacent ribs and not necessarily to the length of the fibres inserted between those points. In order to check what happens to the fibre length, account must be taken

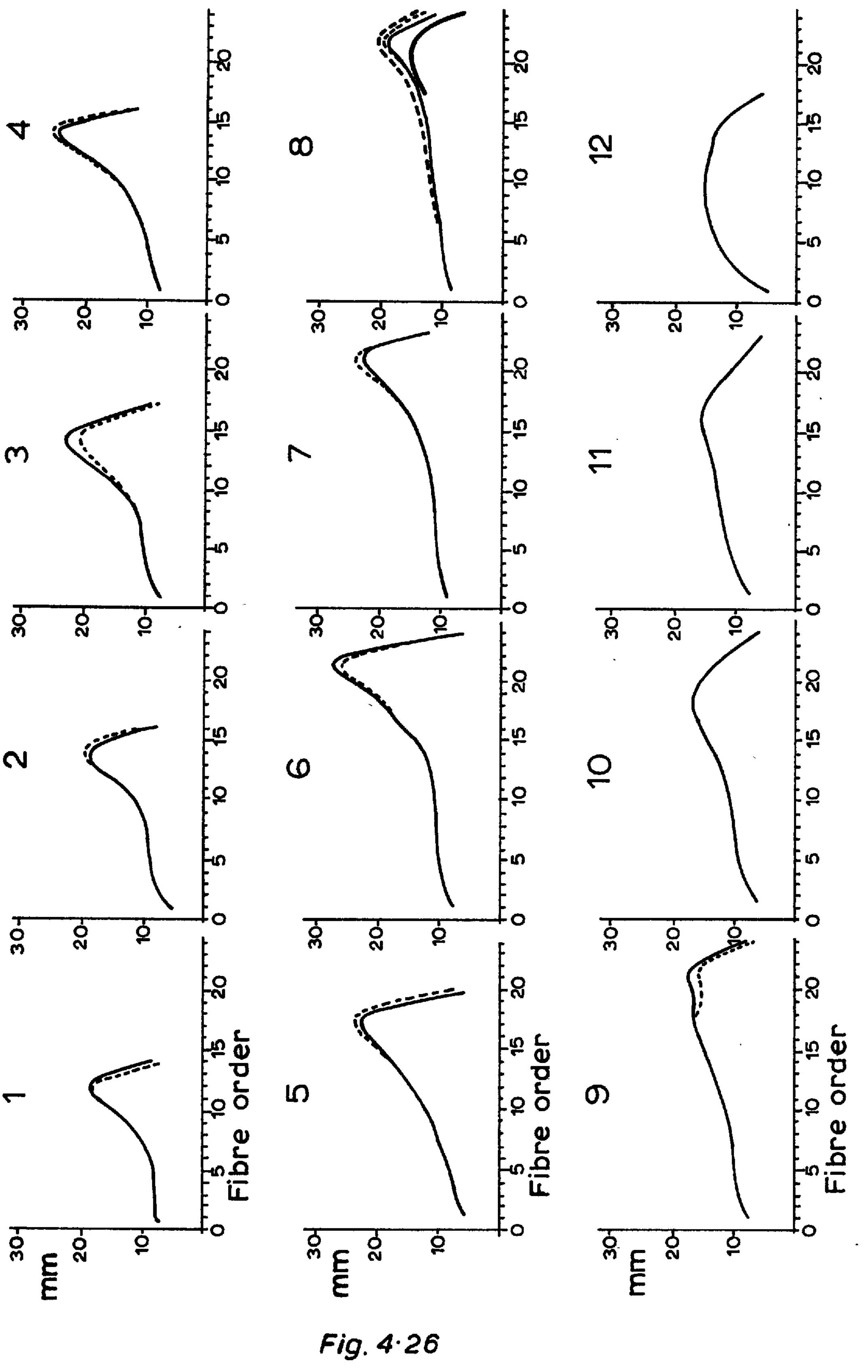


Fig. 4·26

Length of the internal intercostal muscle fibres in peak deflation (———) and inflation (- - - - - -). Abcissae: order numbers which designate the position of the respective fibres as represented in Figs. 4·24 and 4·25 from whose top the numbering starts. Ordinates: length of the fibres in millimetres. The numbers inside the graphs designate the intercostal space to which it refers. In graph number 8, the length of the fibres in artificial respiration, for both peaks of inflation (- - - - -) and deflation (———), is also shown for comparison.

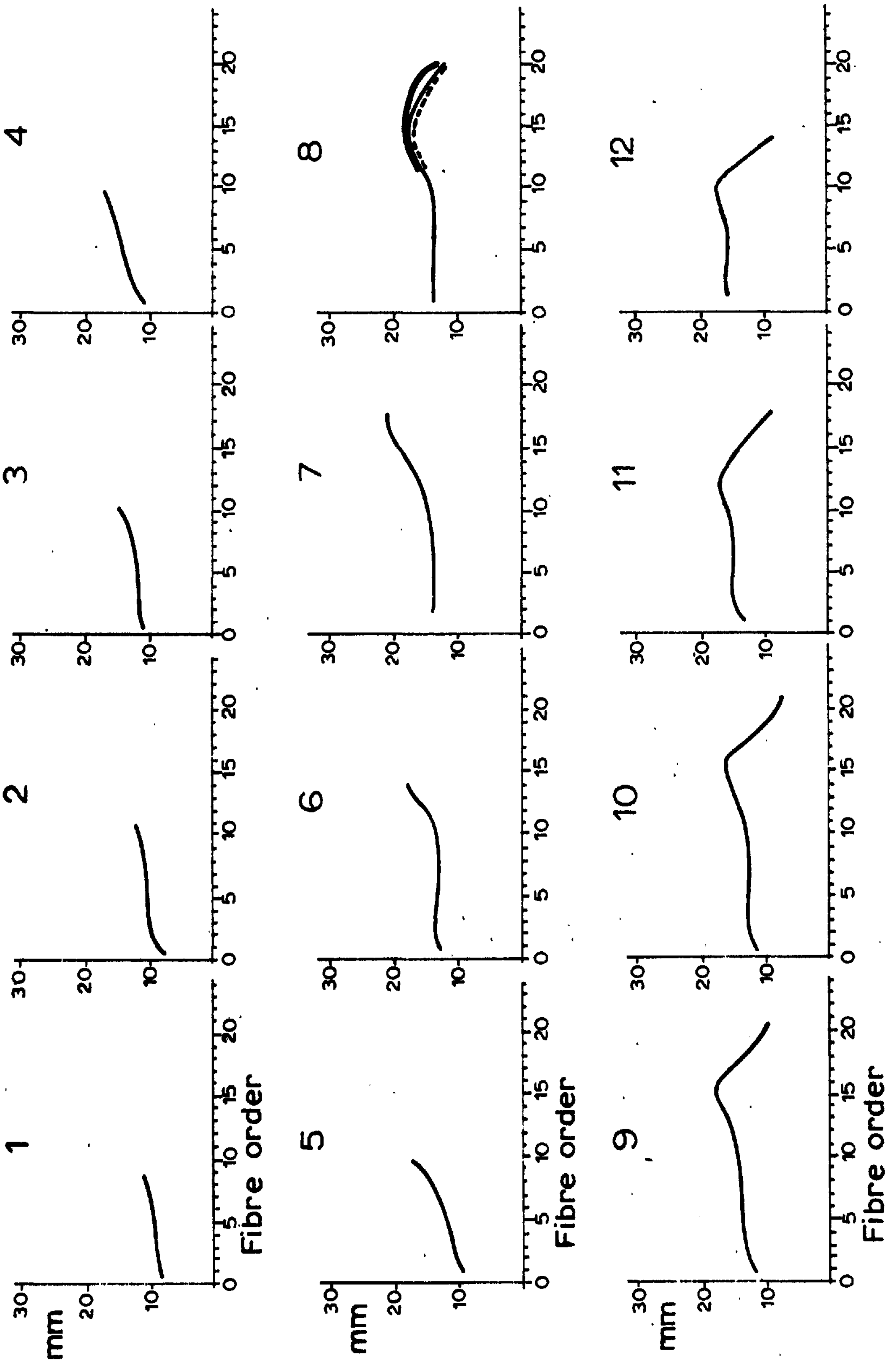


Fig. 4·27

Length of the external intercostal muscle fibres in peak deflation (———) and inflation (-----). Abcissae and ordinates as in Fig. 4·26. Also, in graph 8 the length of the last fibres for peak deflation (▬▬) and inflation (▬ ▬ ▬) in artificial respiration is shown for comparison.

of the 'sagging' which the transmural pressure may induce on the intercostal spaces, a matter which will be taken up in section 4.3.5.

The fact that the changes in the length of the fibres due to the spontaneous breathing movements, if they occur, are for the most part too small to be detected in our data, does not also mean that large changes cannot be forced on them without disturbing unduly the shape of the rib cage. To illustrate this point we have drawn in graph number eight of both figures 4.26 and 4.27 the length distribution of the same fibres under conditions of artificial ventilation; only the last fibres are considered because only they show appreciable departures from their lengths in spontaneous breathing, but these length changes must be considered as quite significant.

Figures 4.28 and 4.29 compare the rectifications of the cage for the peak inflation and deflation positions in artificial respiration with, respectively, the configurations of the peak inflation and deflation in spontaneous breathing. These drawings show that in artificial ventilation the ribs are more rotated towards the vertebral column than in spontaneous breathing and that the elbows of the cartilages are more pronounced. This effect, as has already been said, is caused by the weight of the abdominal viscerae and the absence of tonic musuclar activity. Figures 4.28 and 4.29 show also that the configurations taken up by the cage in artificial respiration are quite different from those which occur in spontaneous breathing. It may, of course, be possible to achieve greater agreement between the two types of ventilation by generating the desired tidal volume at higher

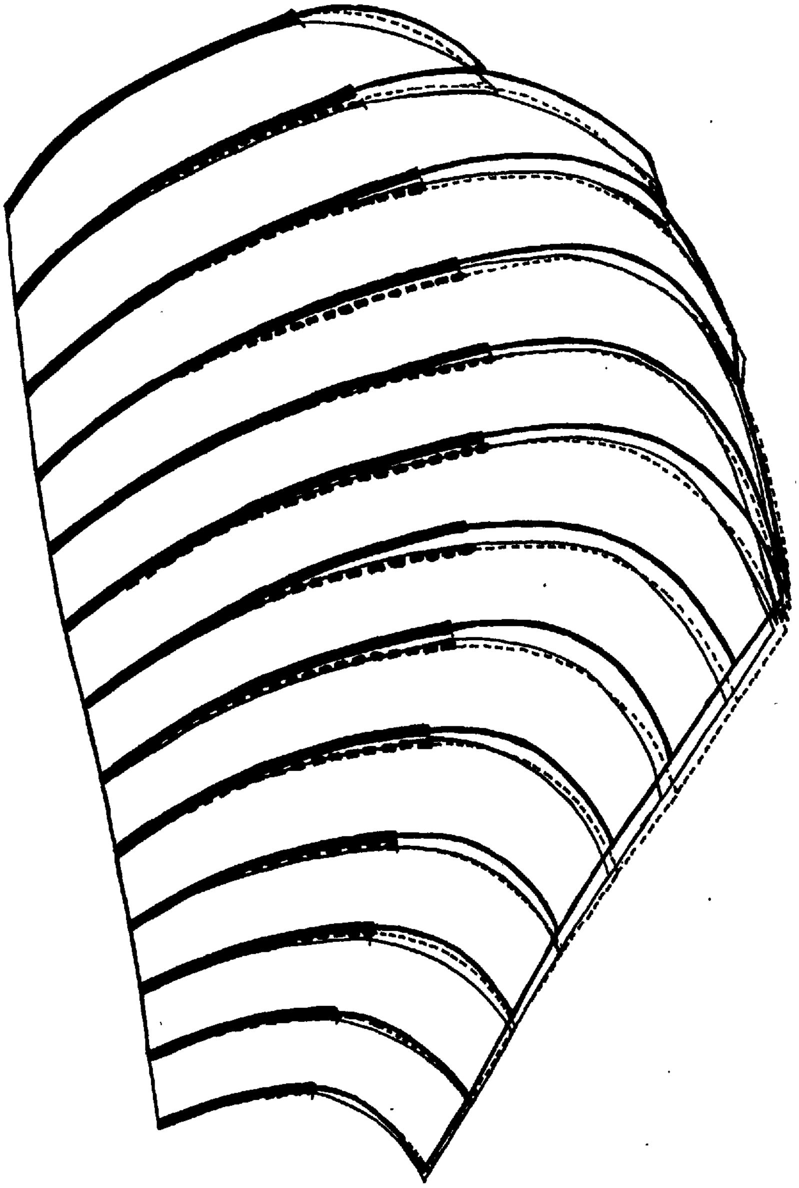


Fig. 4·28

Rectified rib cage surface: comparison between peak deflation in spontaneous respiration (———) and peak inflation (▬▬▬) and peak deflation (-------) in artificial respiration.

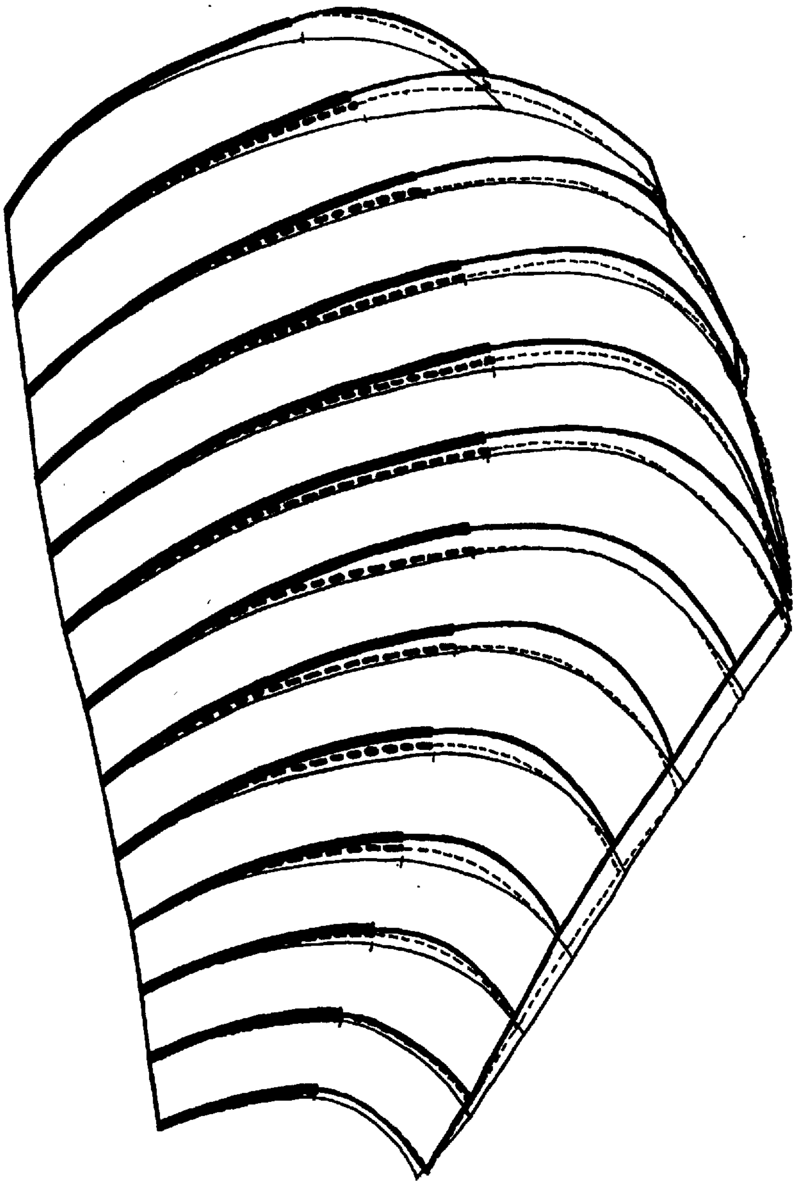


Fig. 4·29

Rectified rib cage surface: comparison between peak inflation in spontaneous respiration (———) and peak inflation (▬▬▬) and peak deflation (------) in artificial respiration.

air pressures; this method, however, would certainly bring about an even greater disturbance of the configurations of the diaphragm and the other abdominal walls.

Finally, figures 4.28 and 4.29 show that changes in shape and dimensions of the intercostal spaces between the peaks of inspiration and of expiration are larger than in spontaneous respiration. It also shows again the fact, pointed out in section 4.3.2, that the changes in the configuration of the rib cage brought about by the application of Flaxedil are very large when measured in terms of the length changes which the respective mechanoreceptors need to operate on.

4.3.5 - The sagging of the surface of the intercostal spaces

So far we have not taken into account the sagging which the transmural pressure may tend to cause on the surface of the intercostal spaces and, therefore, we considered not the true surface of the rib cage but the envelope surface which can be defined as resting on, and tangent to, the external face of the ribs and rib-cartilages. As a consequence of this fact, the area of the rectified surface is smaller than the surface of the cage and smaller are also the lengths of the muscle fibres measured on the rectified surface. Unfortunately, the surface of the intercostal muscles is only visible in the animal preparation utilized in our experiments over a narrow strip of the cage surface above the insertion of the obliquus abdominis externus; in this region, the sagging of the intercostal surfaces in phase with the transmural pressure is well marked and, although no exact measurement of its magnitude was attempted, we estimate its value at a few tenths of a millimetre. The diagram of figure 4.30 represents an intercostal muscle fibre and the cross-section of the ribs at the attachment points; for small values of the sag, the shape of the fibre may be approximated by a parabola (Rektorys, 1969) whose equation, referred to its lowest

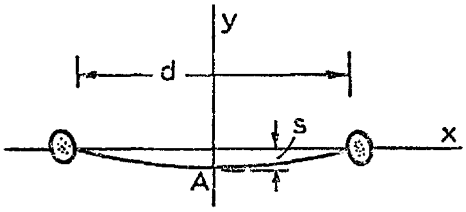


Fig. 4.30 - The effect of sagging on the total length of an intercostal muscle fibre: d- distance between attachment points on the ribs; s- fibre sag at its centre.

point A, is:

$$y = 4.s.(x/d)^2 \tag{4.2}$$

where s is the value of the sag at the centre of the fibre and d the straightline distance between the two attachment points. The actual length of the fibre, d_a, is computed from (4.2) to be:

$$d_a = 4.s.\sqrt{1+(d/4s)^2} + (d/8s)^2.\mathrm{arsinh}\,(4s/d) \tag{4.3}$$

and from this expression we deduce that, for a typical fibre length of 10 mm, a sag of 0.3 mm results in a length increase of 0.48 mm.

The importance of this effect becomes clear when we consider the results of the previous section in which, apparently, no change in the length of the muscle fibres was detected in the costal regions during respiration.

It was then pointed out that, strictly speaking, the observations only indicated that the distances between fixed points on adjacent ribs remained essentially constant and that changes in the length of the muscle fibres could still occur, in particular as a result of sagging in the intercostal space surfaces under the transmural pressure. This fact raises a most interesting possibility, namely, that the length changes due to this sagging may constitute the very way in which the transmural pressure, and with it the load it represents for the cage structures, may be monitored and compensated for. The principle of such a mechanism would then be as follows: when the sagging increases the length of the muscle spindles in the intercostal muscles, the associated position control system reacts and contracts the muscles it subserves, building the tension in them to the level necessary to resist the load. This mechanism would obviously apply to all the intercostal spaces and would be integrated in such a way as to avoid excessive local responses; such over-responses would be felt as an additional load by the other structures in the cage and eventually bring into operation some form of inhibitory action. A mechanism of the type just outlined would operate perfectly under normal physiological conditions when the load on the rib is essentially associated with negative transmural pressures; it would also operate well when positive transmural pressures caused ballooning of the cage walls, although this situation would tend to bring about the contraction of the muscles which are wrapped around the cage, namely those concerned with the suspension of the front limbs, the rectus and oblique abdominal muscles and the serrati muscles.

4.3.6 - Area of the rib cage surface

Table 4.4 contains the areas of the intercostal spaces for the two configurations shown in figure 4.23. These areas are computed by adding up the areas of the plane triangular facets which are used to approximate the surface of the intercostal spaces (cf. figures A2.1 and A2.2). The values of the areas thus calculated, are smaller than those which correspond to the real envelope surface (i.e., with no sagging taken into account) of the rib cage, but the error can be always made sufficiently small by increasing the number of facets used to approximate the surface.

Table 4.4 - Approximate value, in square centimetres, of the areas of the intercostal spaces in spontaneous respiration

Space nº	Phase		Space nº	Phase	
	Expiration	Inspiration		Expiration	Inspiration
1	4.63	4.56	7	11.07	11.20
2	5.15	5.11	8	10.95	11.07
3	6.39	6.37	9	10.77	10.82
4	7.84	8.13	10	8.63	8.70
5	8.08	8.39	11	7.34	7.35
6	10.89	11.09	12	6.35	6.33

As can be seen in table 4.4, the changes in the values of the intercostal space areas during the respiratory cycle are very small when measured on their projections on the cage envelope surface.

The total projected area of the cage as given above varies between 196 and 198 cm^2, respectively in peak expiration and peak inspiration, and therefore remains approximately constant throughout the respiratory cycle as one would expect from the near constancy of the width of the intercostal spaces. The configuration of the cage, on the other hand, alters noticeably as shown in figure 4.3 and 4.4; these changes are, however, produced mainly by changes in the shape of the costalcartilages - where, as we have seen, the largest changes in the fibre length take place - and without appreciable alteration of the total area of each intercostal space.

It is of some interest to notice that at the peak inspiratory transmural pressure of 30g/cm^2 this area corresponds to a total compression force on the cage of 5.94 kg, definitely larger than the total weight of animal.

4.3.7 - Inertia forces developed in the rib cage movements

Figure 4.31 represents the displacements and the accelerations in the movement of the tip of the 8th rib referred, as in figure 4.22, to its position in peak deflation. This point is situated in the region of the cage where the largest respiratory movements occur and it may, therefore, be used for the estimation of the inertia forces which are developed in the rib cage. For this purpose, we assume that the vectorial acceleration $\ddot{a}$ applies to all the points of the rib and we consider it loaded by a weight of 30 g of bone, muscle and other tissues; in this way we make sure that the calculated value of the inertia forces exceeds its real value. The peak inertia force of the loaded rib is thus obtained by multiplying the mass which corresponds to the 30g weight by the value of the acceleration $\ddot{a} = 3$ cm/sec^2:

$$I.F. = 30 \cdot 3 / 980 = 0.09g \qquad (4.4)$$

where 980 cm/sec^2 is the acceleration of gravity.

In order to acquire an idea of the relative importance of these forces we compute the value of the transverse forces developed by the peak transmural pressure over an area of the same order of magnitude as that of the intercostal spaces on either side of the rib (11 cm^2). Thus, if we use the value of 30 g/cm^2 given in figure 4.1, we obtain the following total transverse force on the rib:

$$T.F. = 30 \cdot 11 = 330 \text{ g} \qquad (4.5)$$

which is four orders of magnitude larger than (4.4). It should also be noted that the largest values of the acceleration $\ddot{a}$ occur during the inspiratory phase, i.e., they coincide with the pressure pulse of figure 4.1. Similar results can be shown to hold for the structures of the abdominal compartment. It is therefore legitimate to conclude that we can neglect the contribution of the inertia forces in the study of the dynamics of the external respiratory apparatus and can treat the corresponding movements as a succession of conveniently spaced still frames, each of which is studied as a static problem in structural analysis.

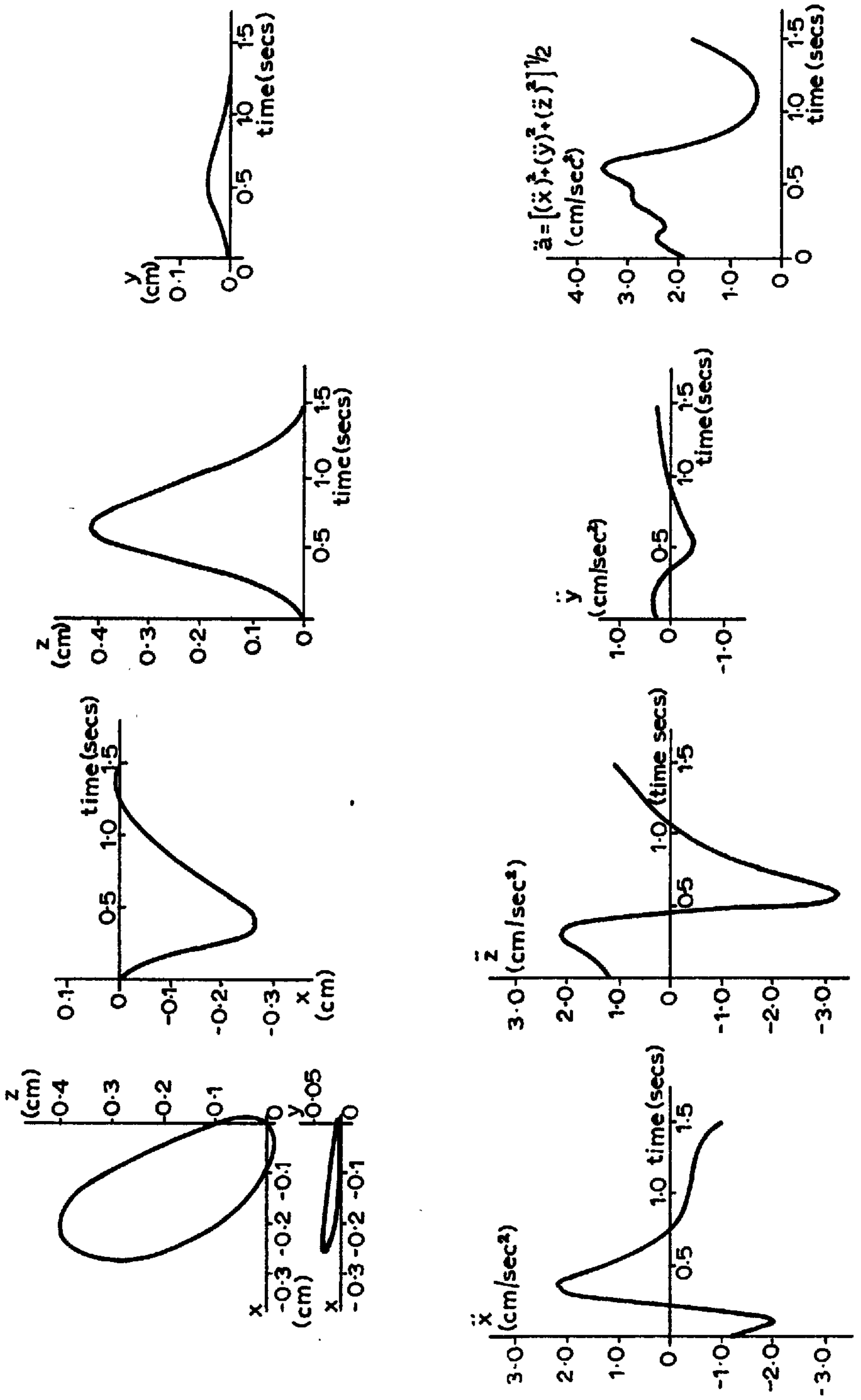


Fig. 4·31

Displacements and accelerations in a full period of the movement of the tip of the 8th rib referred to its position in peak deflation. x, y, z, $\ddot{x}$, $\ddot{y}$, and $\ddot{z}$ represent the components of the displacements and accelerations, respectively, expressed in the reference frame of axes of Fig. 4·22; $\ddot{a} = \sqrt{(\ddot{x})^2+(\ddot{y})^2+(\ddot{z})^2}$ is the amplitude of the instantaneous vectorial acceleration.

4.4 - SUMMARY AND DISCUSSION

The experimental work reported in this chapter was undertaken as an attempt to clarify the nature of the movements performed by the various structures of the external respiratory apparatus during the breathing process, and it led to the following main results:

1- The rib cage and the diaphragm are the basic driving components in the inspiratory movements of spontaneous breathing for the animal posture and conditions of the experiment. The abdomen seems to behave as a driven compartment whose much larger volume remains comparatively unchanged throughout the respiratory cycle. However, the fact that the abdomen appears to follow passively the shape changes imposed on it by the rib cage and the diaphragm could be misleading because the abdominal muscles may be contributing to the respiratory drive by becoming more active during the expiratory phase, a possibility that we did not check.

2- The application of Flaxedil brings about a change in the shape of the trunk. This change is due to the fact that the ribs and the rib cartilages can no longer maintain an elevated position under the weight of the abdominal viscerae, weight which is transmitted to them by the abdominal muscles. This, therefore, shows the functional importance of the 'tonic' or non-phasic activity of the muscles responsible for the structural stability of the thorax.

3- For small amplitudes, the movement of the ribs may be treated as simple axial rotations around the costo-vertebral joints. The corresponding axes of rotation are such that, in inspiration, the ribs move simultaneously forward and upwards and, consequently, the cartilages have to open their elbow angle in order to increase the length of the new cross-sectional perimeter. Another important consequence of this opening of the elbow angle is the fact that the cartilages assume a shape better suited to resist the transmural pressure which should act on them as a compression along their longitudinal axes.

4- The changes in length of the intercostal muscle fibres in the costal region are, when measured on their projections on the envelope surface of the rib cage, generally too small to be noticeable in the data we have. Those fibres do, however, undergo a certain amount of sagging under the action of the transmural pressure and, thus, suffer increases in length of the order of a few tenths of a millimetre. This sagging effect could therefore be the vehicle for the control system which is responsible for the grading of the muscle tension distribution throughout the rib cage surface under load.

5- The length changes in the intercostal muscles are very small compared with their total lengths; the same is also true for the other muscles associated with the rib cage such as the levatores costarum and the serratus anterior posterior. This means, therefore, that in the modelling of the mechanics of the rib cage we may treat the muscles as constant-length devices, a characteristic which considerably simplifies their transfer function. Insofar as the muscle spindles are concerned, these findings regarding length changes are in agreement with data obtained elsewhere (Matthews and Stein, 1969) which showed that in the range of frequencies occurring in quiet respiration, the primary endings have a linear response and their maximum sensitivity for length changes up to about a tenth of a millimetre.

6- The costalcartilages in the parasternal region are supported by the internal intercostal muscle fibres radiating from the chondrosternal joint and this accounts for the respiratory activity of these fibres. Elsewhere in the cage, their contribution to inspiration may be thought of as resulting from existence of stresses whose direction does not coincide with that of the external intercostal muscles and, therefore, have to be balanced by vectorial composition of forces; the occurrence of such non-aligned stresses is extremely likely in a structure like the rib cage when performing such heavy work - for instance, the total compression on the cage surface is, using the values of peak pressure and area given in the previous sections, of the order of 6 kg, i.e., about two times the full weight of the animal. Experience has, indeed, shown that the internal intercostal muscles have an important inspiratory participation (Gesell, 1936).

7- The action of the diaphragm is primarily determined (cf. figure 4.9) by the contraction of the muscles which connect the central tendon to the vertebral column - the crurae - and to which they transmit most of the load represented by the displacement of the abdominal viscerae; the contraction of the peripheral muscle fibres contributes also to the performance of this function which includes the overcoming of the transdiaphragmatic pressure. An interesting particular of the peripheral regions of the diaphragmatic dome is that they contract into a shape which, in cross section (cf. figure 4.10), resembles very closely that of a 'catenary of constant strength' (Rektorys, 1969) which is the shape taken, under its own weight, by a perfectly flexible and inelastic cable, when suspended freely in the air, if its cross-section is made to vary along its length so as to guarantee a constant value of stress everywhere. The implications of this analogy are that the cross-section and the relative extension of the muscular and aponeurotic components in the diaphragm have evolved to a solution of approximate equal stress at every point under load.

8- The contents of the abdominal compartment constitute a sort of 'fluid' because of their capability to undergo mass movements. However, the density, viscosity and character of this 'fluid' vary from region to region, conferring it an essentially heterogeneous and anisotropic nature. The viscerae in contact with the diaphragm in particular, have limited mobility and therefore tend to be deformed by movements of the diaphragm (cf. figure 4.18)and to influence very markedly the shape changes in the cranial region of the abdomen.

9- The inertia forces which develop in the structures of the external respiratory apparatus can be ignored because they are very much smaller than the normal loads which are applied to it(*). The kinetic study of the movements of the external respiratory apparatus can thus be performed through the analysis of a succession of still configurations for which the equilibrium of the applied forces and internal stresses can be studied by the methods of Structural Analysis. Once these forces are computed for each configuration, their evolution in time is obtained by a suitable 'animation' of the individual results, in the same way in which the animation of the geometrical configurations

(*) **The forces due to the viscous dumping in the muscles have not been considered here because we have only dealt with the forces acting on the ribs.**

reconstitutes the movements of the respiratory apparatus.

10- Although we have not actually measured the time constants of the response of the 'stretch-reflex servo assemblage' of the respiratory muscles to changes in muscle length, we can in view of the contraction times of these muscles (Andersen and Sears, 1964) and the time constants of the primary afferent fibres in the muscle spindles (Crowe and Matthews, 1964) assume with confidence that it is smaller than one tenth of a second. But, if this is so, it follows that the neuro-muscular system which is responsible for the structural stability of the respiratory apparatus is able to correct for variations in the load which are at least ten times faster than the respiratory frequency. We may therefore conclude that, although the respiratory slow modulation of the neuromuscular activity in the respiratory apparatus is the most obvious and apparently all-dominant, in true fact the most significant component of that activity - the one which reflects the response to structural requirements - will have to be found in the fast changing signals which accompany that modulation.

11- As it has been pointed out in section 4.3.2 and 4.3.4, the silencing of the respiratory muscles leads to shape changes in the structures of the respiratory apparatus which are, generally speaking, very large in comparison with the length changes for which the stretchreceptors are most sensitive (Matthews and Stein, 1969). This fact is very important in so far as it strongly suggests that the control of the respiratory muscles is such that they tend to keep the structures in the system stabilized in the central region of the range of displacements which their passive constraints allow them. In other words, it seems reasonable to think that these muscles are integrated in a position control servo system in which the crossed feedback between antagonistic muscle units brings in the necessary power to keep the subserved structure in a stabilized position. Furthermore, the respiratory muscles are able to perform in this manner even under the influence of very large loads. As we have pointed out already in section 4.3.2, the loads applied to the respiratory apparatus in our experiments were not very adequate to show the extent in which the stability of its shape depends on the coordinated contraction of the respiratory muscles. Indeed, the weight of the viscerae - typically 0.3 kg. - represents a quite small load as compared for instance to that due to the inspiratory transmural pressure (cf. section 4.5.3); also, the method of artificial positive pressure respiration which was used tends to balloon the chest wall against the resistance of its passive connective and muscular tissues and, thus, preserves the stability of the shape. The situation would change radically if negative pressure was created in the lungs as illustrated by experiments of multiple intercostal neurectomy (Alexander, 1929; Cetrángolo, 1930; Joly and Vincent, 1937) in which the anterior parasternal region of the paralysed side of the cage sinks in paradoxically. These more radical changes point out the fact that, apparently, the mechanism which keeps the structures 'centred' at their middle passive position, is also quite adequate to assist those structures in resisting the loads applied to them. This conclusion, however, implies that the nervous system which controls these muscles has means of distributing the muscular activity throughout the entire system in such a way as to avoid the occurrence anywhere of unduly large stresses or bending or twisting moments which would very easily tend to occur in such complex structures; in other words, one is led to imagine that if excessive work is demanded from the muscles anywhere in the system, this excessive demand is capable of influencing the muscular activity in other parts of the system and that this influence is consistent with the proper load response of the same system. Finally, the respiratory apparatus must accommodate large deflections, such as those associated with trunk rotation or flexions, which bring about large departures from the above mentioned 'centred' positions without impairing the load response of the system.

The facts listed above, therefore, suggest that the nervous system control of the muscle activity in the respiratory apparatus resembles closely the way in which industrial process-control plants are integrated by their central computer; this computer works out, according to a certain strategy and the data produced by the sensors distributed in the plant, the commands which are issued to the effector units and thus creates a harmonious and efficient overall system.

CHAPTER 5.0

FUNCTIONAL ELEMENTS FOR THE MODELLING OF THE MECHANICAL PROPERTIES OF EXTERNAL RESPIRATORY APPARATUS

5.1- INTRODUCTION

The purpose of this chapter is to proceed further with the qualitative or semi-quantitative analysis of the mechanical properties of the structures which constitute the respiratory apparatus; the results of the previous chapter are now combined with other anatomical data and interpreted in terms of their implications on the functional integration of the different structures in the respiratory apparatus. The conclusions which are thus reached, not only clarify many details of the performance of the external respiratory apparatus, but also constitute a reasonably complete framework in which its realistic modelling can be achieved. We shall continue to assume the vertebral column and the coccyx as fixed in space and constituting the basic reference framework for the movements of the respiratory apparatus; this of course means that no flexion or bending of the column is considered. Also, only small deformations of the other structures, in particular of the abdominal walls, will be taken into consideration.

This chapter is organised as follows: the rib cage is analysed in connection with its participation in the maintenance of the postural stability of the trunk and the suspension of the front limbs; the role played by the articulations in the cage both in conditioning the relative movements of the supporting elements and as an integral part of the control mechanism which supervises the movements and configuration of the cage is considered next. We then analyse the participation of the intercostal muscles in the response of the cage to loads and in preventing bending of the costalcartilages and ribs, and follow it with the study of the mode of action of the structures which constitute the boundaries of the rib cage. The participation of the abdominal compartment in the mechanics of respiration is considered in terms of the mechanisms involved in the stabilization of the caudal rim and of the overall configuration of the rib cage and in terms of the role played by the abdominal viscerae as mediators of the action of the abdominal muscles and the diaphragm.

We end this chapter with the analysis of the fundamental principles on which the modelling of the mechanical properties of the external respiratory apparatus could be performed.

5.2 - STRUCTURAL ORGANIZATION OF THE RIB CAGE

5.2.1 - Introduction

The rib cage is an integral part of the axial skeleton and, therefore, directly involved in the structural integration and stability of the body. Also, and like the vertebral column, it must be so articulated as to allow the flexion and rotation movements of the trunk and, finally, it must be capable of permitting the breathing manœuvres which depend on changes of the chest volume. Although we do not intend to tackle the problem of the mechanical performance of the rib cage in such general terms, and are only concerned with its respiratory function, the requirements outlined above still have to be considered because of the extent in which they condition the rib cage design. In this section we will try to bring together some facts and relationships which are essential for the analysis of the mechanical properties of the rib cage. We start by considering the general problem of the structural integration of the animal's body and the contribution of the rib cage to this function and continue with a brief account of the system by which the front limbs are attached to the thorax. Both of these functions give rise to loading of the rib cage and, therefore, exert a strong influence on the size and organization of its structures. We consider next the articulation between the bone and cartilageneous structures which make up the cage; these articulations constitute functional assemblages which perform the double role of connecting together the supporting structures and of providing a system of displacement monitors which, together with the muscle's own mechanoreceptors generate the afferent data on which the integrative muscular control is based. The osseous-cartilagenous framework of the rib cage consists of four types of structures, namely, the thoracic part of the vertebral column, the ribs, the costalcartilages and the sternum, itself made up by the sternebrae, the manubrium and the xiphoid process; consequently, five different types of joints, respectively called vertebral, costovertebral, costochondral, chondrosternal and sternal, are involved in the assemblage of this framework. The vertebral joints, comprising the cartilagenous joint between the vertebral bodies and the synovial joints between the vertebral arches, will not be considered in detail because in our model of the respiratory system the vertebral column is assumed fixed and rigid. The costovertebral joints include the costotransverse and the costocapitular joints and will be analysed in some detail to illustrate the main features of the joint control assemblage. The remaining types of joint, which are simpler than the previous ones, will be described summarily.

5.2.2 - The postural stability of the trunk

The postural stability of the vertebral column, the main structural element of the trunk, is achieved by means of a system of short and long muscles which connect the vertebrae with each other and the bone structures such as the coxal bones and the ribs (Gray's Anatomy, 1954). The short muscles of the column, although they help in its movements and in stabilizing it against buckling, have as their main function to guarantee the cohesion of the vertebrae. The most important short muscles are the following:

the interspinalis - stretching between the spines of contiguous vertebrae - , intertransversii - between the transverse processes - and the rotatores - connected between the transverse process of a vertebra and the laminae of the vertebra which preceeds it cranially - .

The long muscles of the column are the ones responsible for the bending of the column laterally (flexion), for rotating it and for extending it (as a result of increasing its radius of curvature). Besides the iliocostalis and longissimus thoracis described in section 3.3.2, the most important of these long muscles are the following: the longissimus cervicis and the longissimus capitas - between the transverse processes of the anterior thoracic and the posterior cervical vertebrae - , the spinalis and the semispinalis - from the spines and from the transverse process, respectively, of one vertebra to the spine of another vertebra situated several vertebral spaces away cranially - and the multifidus - a system of independent muscular fasciculi, varying in length from one to five intervertebral spaces, and attached to the mammillary processes of the vertebrae in the lumbar region and to the transverse processes in the cervical region.

All the long muscles, however, lie on the dorsal side of the vertebral column and their contraction tends, as figure 5.1(a) shows, to open the dorsal angle; they are, therefore, very effective in resisting all dorso-ventral bending stresses which tend to reduce that angle but are most ineffectual for stresses in the opposite direction. The latter stresses are resisted by the combined action of the thoracic cage, the scaleni,

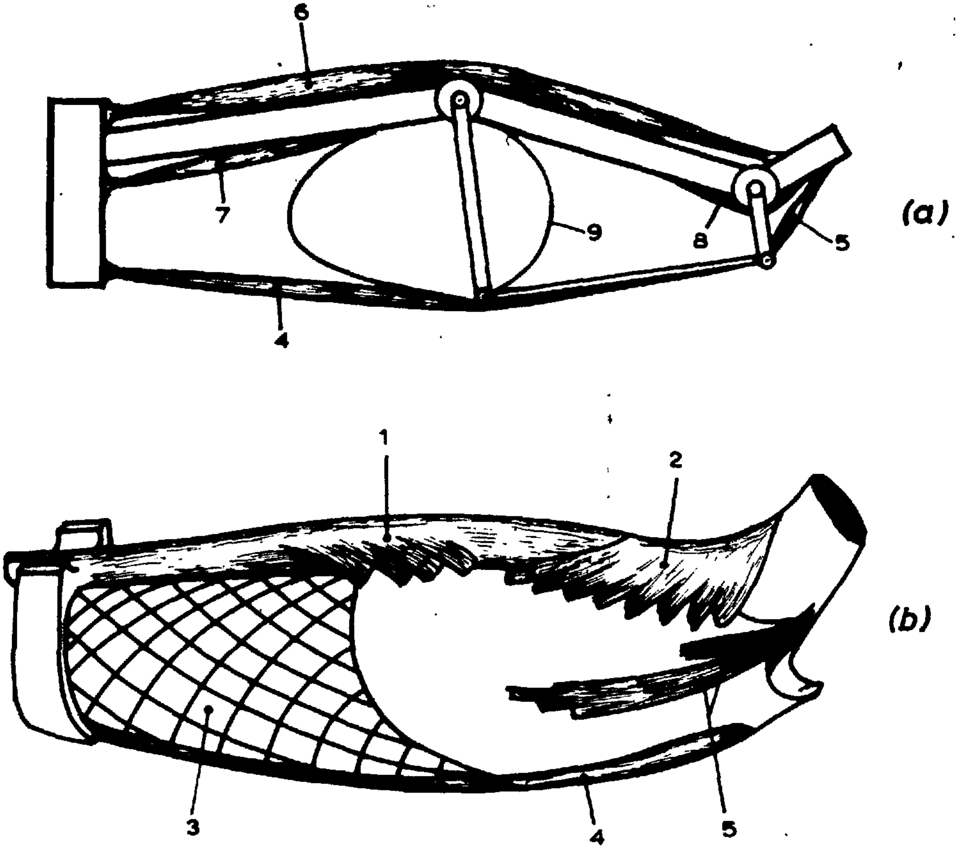


Fig. 5·1 Diagrammatic representation of: (a) the muscles of the trunk which act in the sagittal plane and (b) main muscles responsible for the stability of the trunk.

1 - Serratus posterior inferior m.; 2-serratus posterior superior m.; 3—transversus abdominis and obliquus abdominis muscles; 4-rectus abdominis m.; 5-scalenus m.; 6- muscles of the column; 7-psoas minor and quadratus lumborum muscles; 8-longus colli muscle; 9-abdominal viscerae.

the sternomastoideus and the rectus abdominis muscles and the pelvic bones (Gray, 1944; Slipjer, 1946). The pelvis itself is joined to the vertebral column through the sacroiliac joint, a very powerful coupling which virtually locks the two structures to each other.

The trunk is a three dimensional structure and therefore has to be stabilized also with regard to the lateral bending. Again, the rib cage together with the abdominal muscles - the transversus, the obliqui, the retractor costae ultimae and the quadratus lumborum - constitute a well levered and potent postural stabilizer; the forward attachment of the obliquus externus muscle on the shafts of the anterior ribs, as shown in figure 3.8(b), reflects the very adaptation of this muscle to such a role. The diagram of figure 5.1(b) highlights the important part played by the thoracic cage in the structural stability of the trunk and, indeed, it is only in so far as the rib cage itself is sufficiently stable and firm that the abdominal muscles are at all able to perform a useful role.(*)

The rib cage is the second largest bone structure in the body and the achievement of its proper functioning constitutes a feat of engineering just as remarkable as that which the vertebral column represents. The rib cage is held firm by the combined powerful action of the intercostal muscles, abdominal muscles and

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(*) The external obliquus is not represented explicitly in figure 5.1(b) in order to avoid complicating this diagram excessively.

the shell effect produced by its shape; in normal conditions, this mechanism is quite enough to guarantee the adequate performance of the rib cage functions. When the demands on the contribution of the cage to the stability of the body increase, the animal is able to resort to the following measures:

1- the compression of the abdominal viscerae in order to stabilize the caudal boundary of the cage as shown in figure 5.1(a);

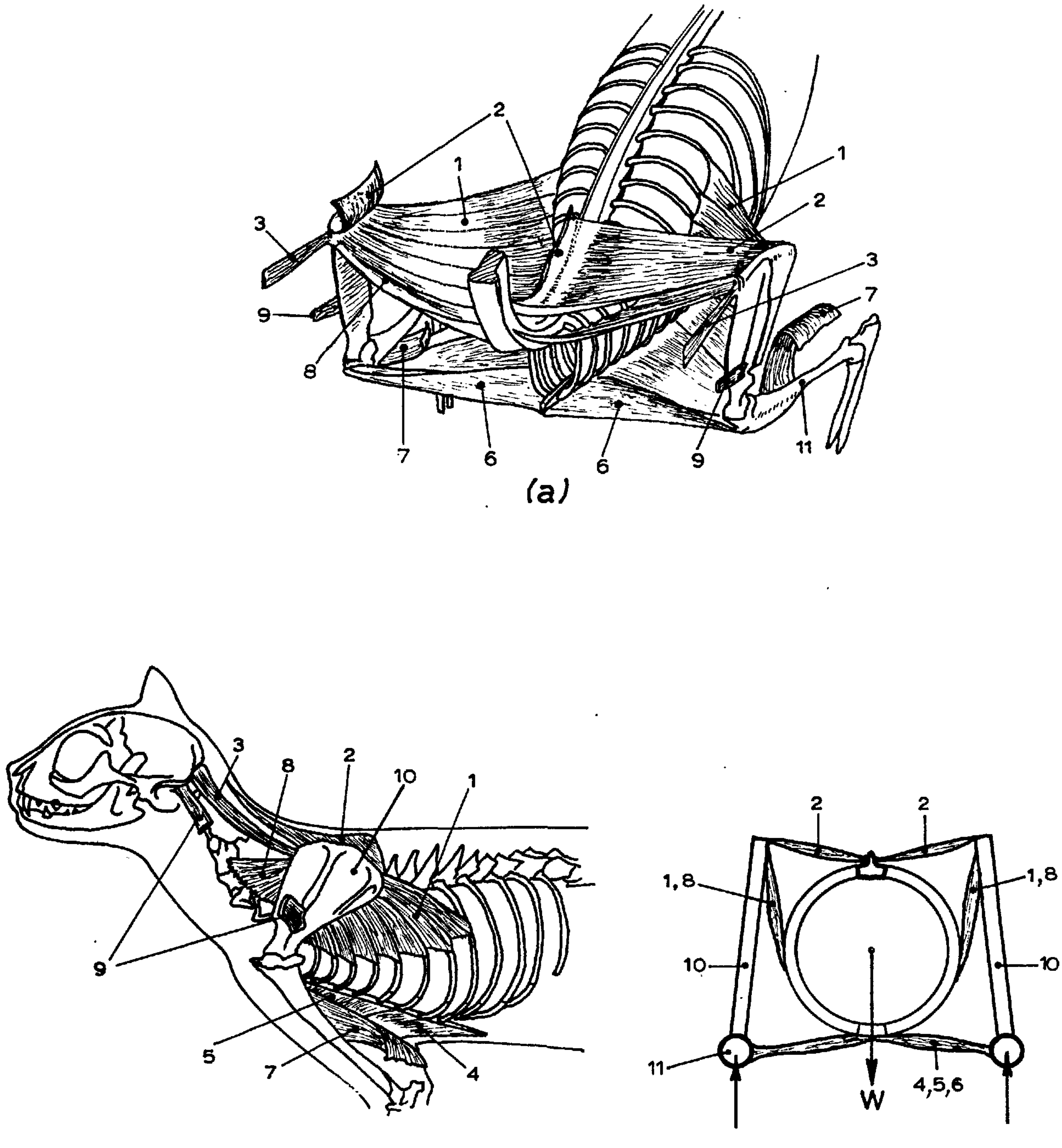
2- the mobilization of the muscles overlaying the rib cage such as the serrati posterior muscles and the muscles which connect the front limbs to the trunk, in order to guarantee that the shape of the rib is not disturbed by the extra load;

3- the contraction of the scaleni and the sternomastoideus muscles, in conjunction with the abdominal muscles, to neutralize the asymmetrical loads which would bend the vertebral column laterally.

Finally, the attachment of the rib cage to the vertebral column must, of course, be such that the two structures are firmly connected together and behave as a single body, a result which is achieved by the combined action of the deep muscles of the back, the levatores costarum, the serrati posterior and the obliquus abdominis externus muscles. This point will be further analysed in section 5.2.4.

5.2.3 - The attachment of the front limbs to the trunk walls

The diagrams of figure 5.2 and 5.3 illustrate the organisation of the muscles responsible for the attachment of

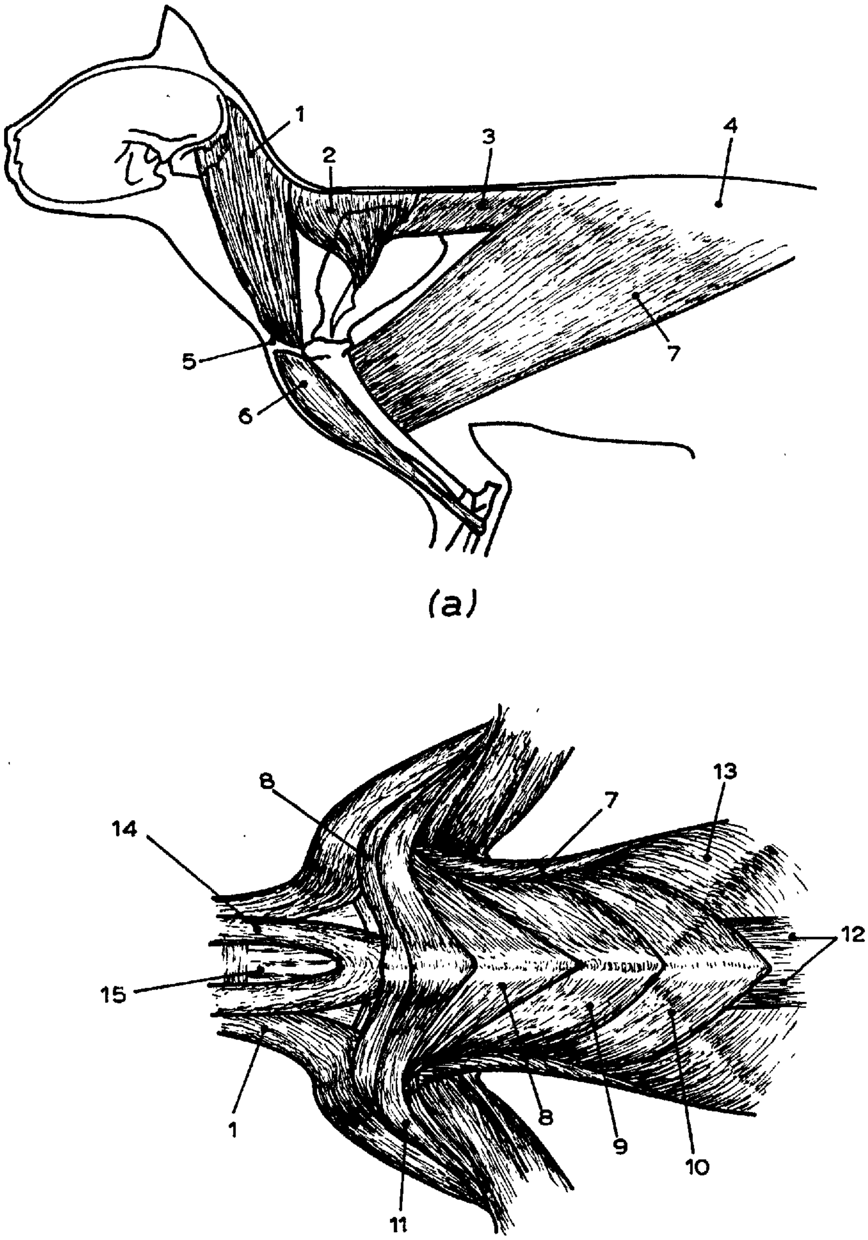


(b)

(c)

Fig. 5·2 Deep muscles involved in the attachment of the front limbs to the trunk wall: (a) perspective view, (b) side view and (c) model of the insertion of these muscles.

1.-Serratus anterior m.; 2-rhomboideus m.; 3- occipitoscapularis m.; 4-xiphihumeralis m.; 5-pectoralis minor m.; 6-pectoralis major m.; 7-latissimus dorsi m.; 8-levator scapulae dorsalis m.; 9-levator scapulae ventralis m.; 10-scapula; 11-humerus



(a)

(b)

Fig. 5·3 Superficial muscles involved in the attatchment of the front limbs to the trunk wall : (a) side view and (b) ventral view.

1 – Clavotrapezius m. ; 2 – acromiotrapezius m. ; 3 – spinotrapezius m. ; 4 – lumbodorsalis fascia ; 5 – clavicle ; 6 – triceps brachi m. ; 7 – latissimus dorsi m. ; 8 – pectoralis major m. ; 9 – pectoralis minor m. ; 10 – xiphihumeralis m. ; 11 – pectoantibrachialis m. ; 12 – rectus abdominis m. ; 13 – obliquus abdominis externus m. ; 14 – sternomastoideus ; 15 – sternohyoideus.

(Partly adapted from Davison, 1947)

the front limbs to the thorax. The diagrams (b) and (c) in figure 5.2 show how the cranial end of the thorax can be thought of as being suspended from the scapulae (10) by the levator scapulae dorsalis muscle (8), which is attached to the last cervical vertebrae, and the serratus anterior muscle (1) which originates from the sides of the first ten ribs. In order to make this suspension stable, the scapulae are drawn towards the median saggital plane of the body by two sets of muscles: the rhomboideus (2) and, operating via the humerus (11), the xiphihumeralis (4) and the pectorales (5,6) muscles; the effects of the contraction of these muscles is a compression of the cranial end of the thorax. The main load applied by the front limbs to the rib cage consists of the tangential reactions at the point where the serratus anterior muscle attaches on the rib shaft and thus, as these attachments are directly opposed by those of the obliquus externus muscle, the weight of the animal on its front legs is converted into a compression of the abdominal and thoracic compartments.

5.2.4 - The costovertebral articulations

The costovertebral articulation contains two separate components, namely, the costocapitular articulation and the costotransverse articulation. The thirteen costovertebral articulations on the left side of the vertebral column are shown in figure 5.4 in order to clarify the relative position of the ribs and the articular surfaces; figure 5.4 also shows that the last three ribs only have the costocapitular component which articulates the head of the rib

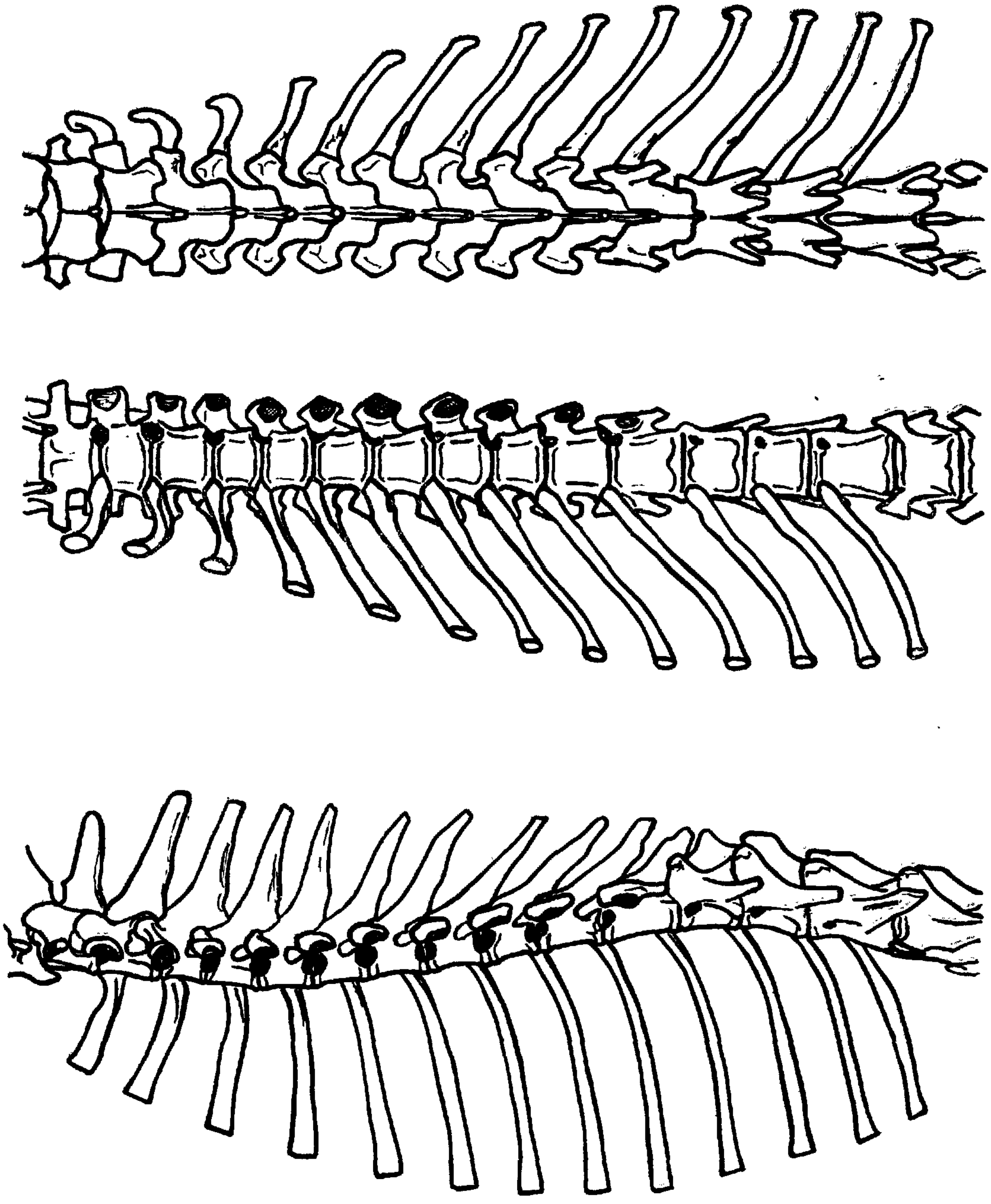
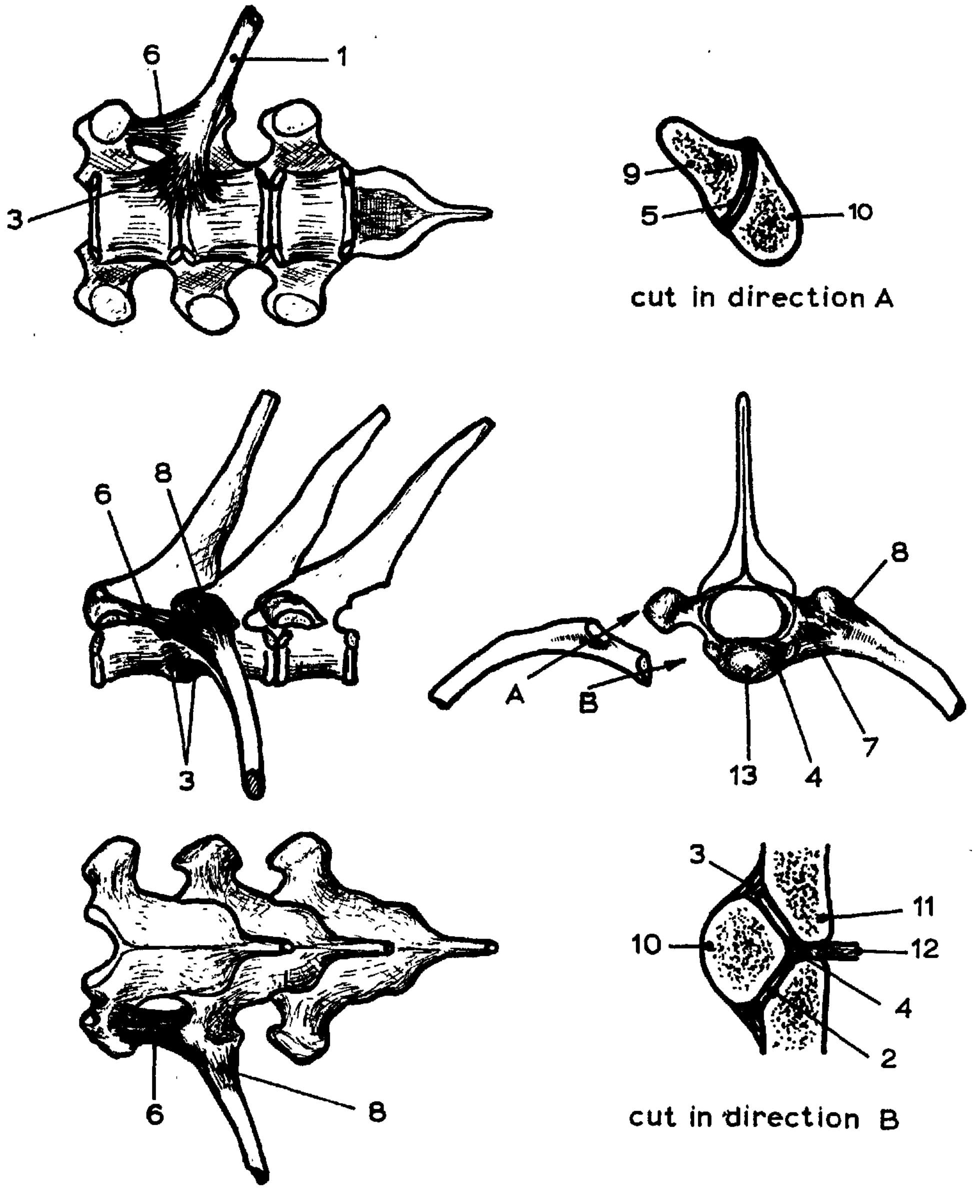


Fig. 5·4 Three projections of the vertebral column showing the costovertebral articulations and the relative positions of the articular surfaces and the ribs.



cut in direction A

cut in direction B

Fig. 5·5 Diagrammatic representation of the articular surfaces and ligaments of the 5th. costovertebral joint.

1-rib; 2-capsular ligament of the capsular joint; 3-radiate ligament; 4-intra-articular ligament; 5-capsular ligament of the costo-transverse joint; 6-superior costotransverse ligament; 7-inferior costotransverse ligament; 8-lateral costotransverse ligament; cross-section along the direction A of:- 9-rib tubercle; 10-transverse process of the vertebra; cross-section along the direction B of:- 11-head of the rib; 12-vertebral body.

with the body of a single vertebra instead of two which is the case for the first ten ribs.

In figure 5.5 the fifth costovertebral articulation is represented in more detail by means of several diagrams; the structures represented in these diagrams will be referred to, in the description which follows, by the same numbers used to designate them in figure 5.5.

The costocapitular articulation has a rotatory character and consists of two synovial joints, one on each side of the head of the rib and connecting it to the bodies of the adjacent vertebrae; the ligaments associated with this articulation are the capsular ligament (2) of each synovial joint, the intra-articular ligament (4), which connects the head of the rib (11) to the intervertebral disc (13) and separates the two synovial joints, and the radiate ligament (3) connecting the head to the bodies (12) of the two vertebrae and the intervertebral disc.

The costotransverse articulation, between the tubercle of the rib and the transverse process of the vertebra, is of the gliding type. Its ligaments are the capsular ligaments (5), the superior costotransverse ligament (6) connecting the neck of the rib to the transverse process of the vertebra immediately cranial to the rib, the inferior costotransverse ligament (7) which connects the back of the neck of the rib with the transverse process of the vertebra with which the rib articulates and, finally, the lateral costotransverse ligament (8) between the tubercle of the rib and the transverse process of the vertebra.

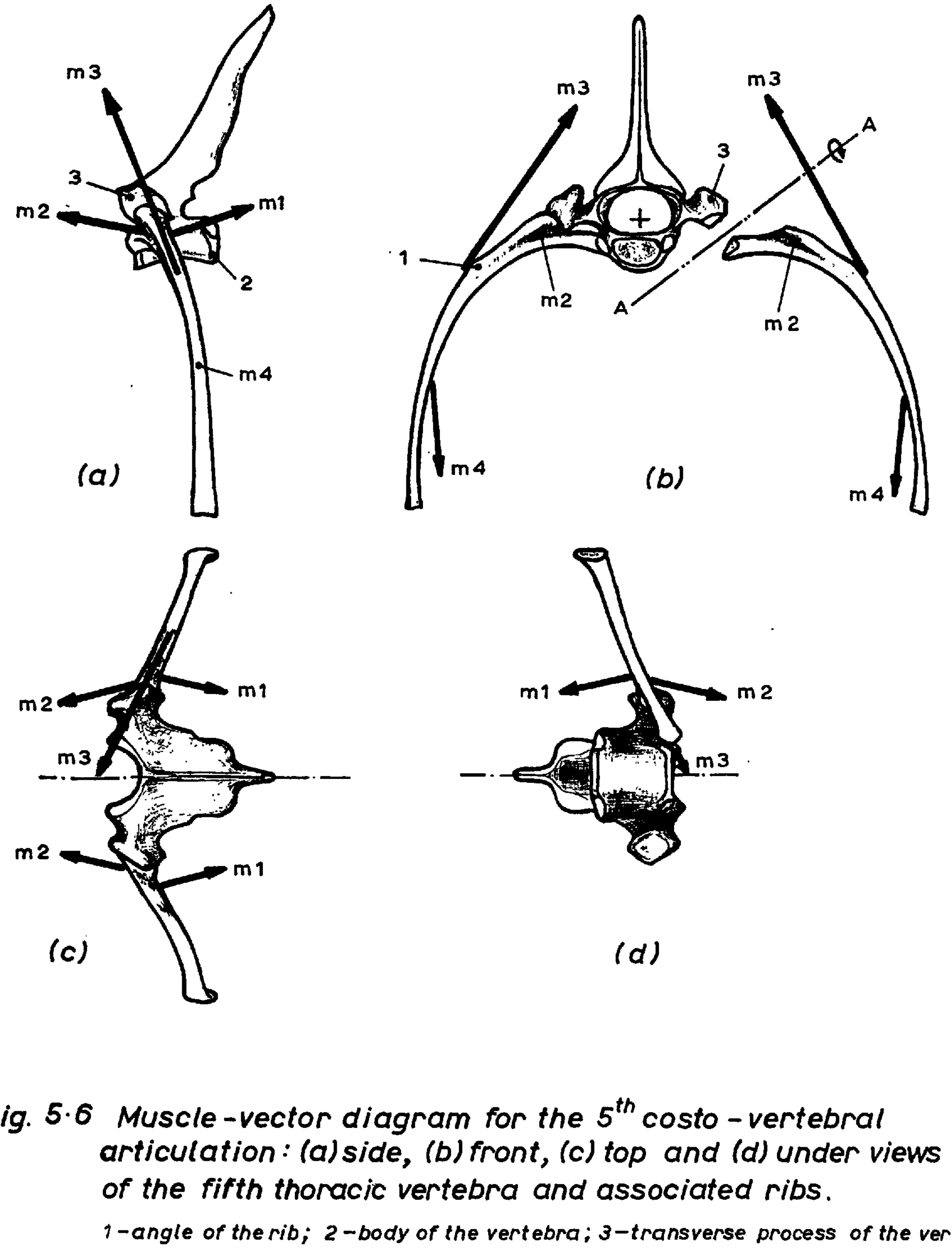


Fig. 5·6 *Muscle-vector diagram for the 5th costo-vertebral articulation: (a) side, (b) front, (c) top and (d) under views of the fifth thoracic vertebra and associated ribs.*

1-angle of the rib; 2-body of the vertebra; 3-transverse process of the vertebra; m1-iliocostalis lumborum, iliocostalis thoracis and longissimus thoracis muscles; m2-levatores costae m.; m3-serratus posterior superior m.; m4-obliquus abdominis externus m.

With the exception of the last three ribs, the movements of these articulations are limited and can be approximated to a rotation around an axis passing through the head and tubercle of the rib, as was shown in section 4.3.3.

The nature of the movements which an articulation is capable of performing as well as its capability to handle loads is determined mainly by the shape of its articular surfaces and the ligaments and muscles associated with it (Clark, 1958). The ligaments are band-like structures composed essentially of collageneous fibres and, therefore, they are pliable and flexible while at the same time having a high Young's modulus; with these characteristics, the ligaments do not interfere with the movements of the joint unless they are stretched to their full length in which case they effectively resist any further movement; the ligaments, however, are not intended to work under prolonged tensional stress and are equipped with mechanoreceptors which bring about the action of the muscles which antagonise the source of tension. This mechanism, already described in section 2.4.3, plays a crucial role in the stabilization of the joint.

Articulations are fundamentally designed to resist compressive forces and, therefore, they have to be assisted by a set of muscles which introduce compensatory forces and transform the loading regime into one of a compressive character. In the case of the costovertebral articulation this muscular system, illustrated in figure 5.6, consists of four groups of muscles: m_1- the iliocostalis lumborum, iliocostalis thoracis and the longissimus thoracis muscles; m_2- the levatores costarum muscles; m_3- the serratus posterior muscle; m_4- the obliquus abdominis externus muscle. The first two groups of muscles react to loads directed tangentially to the rib cage in either direction, whereas the serratus muscle, in conjunction with the obliquus, takes care of loads which tend to pull apart the two surfaces of the joint. These four lines of muscular contraction together with the reaction of the articular surfaces, are able to accommodate all the loads which the articulation is likely to be subjected to during the animal's life. Figure 5.6 also shows that the system constituted by m_1, m_2 and m_3 would not be able, alone, to compensate for loads operating along the action line of the serratus muscle and tending to rotate the ribs around an axis normal to the plane of the rib and passing through the costrotransverse joint; this is, indeed, an effect that the serratus muscle itself tends to create when it contracts. The stability of the articulation with regard to these dislocating moments is obtained through the action of the obliquus externus muscle whose contraction forces the tip of the rib to rotate inwards thus introducing a compensatory moment.

The diagram of the figure 5.7 represents an idealised version of that of the figure 5.6 in which the joints have been replaced by spherical rotulae with darkened sectors corresponding to the surfaces of contact with the transverse process and the bodies of the two ribs; the conical surfaces represent the ligamentous structures which hold the joints together. This diagram shows more clearly the role played by the obliquus muscle in stabilising the costovertebral articulation which can then be firmly pushed against its articular surfaces by the serratus muscle. It should be noted that the moment of each of the muscles

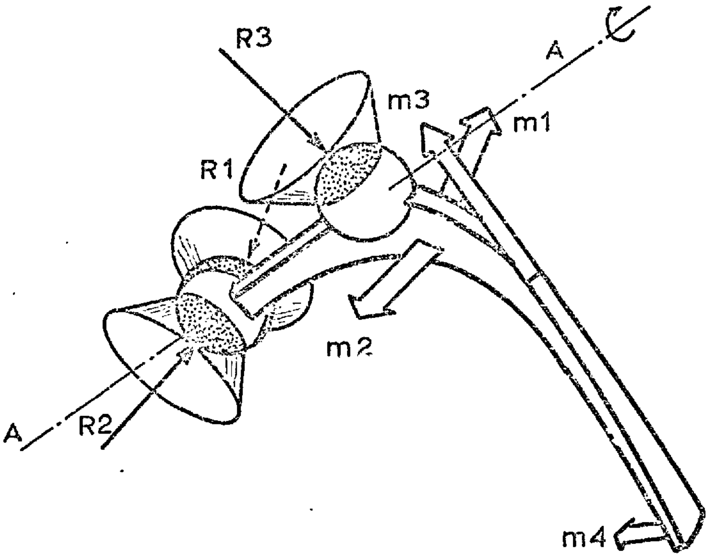


Fig. 5.7 - The costo-vertebral articulation. R1, R2 and R3- reactive forces due to the surfaces of the vertebral joints. Lines of action of the muscles: m_1- iliocostalis lumborum, iliocostalis thoracis and longissimus thoracis muscles; m2- levatores costarum muscles; m3- serratus posterior muscle; m4- obliquus obdominis externus muscle.

represented in figures 5.6 and 5.7 with respect to the main rotation axis $\overline{AA}$ of the articulation is so small, because the muscle acts either too close to the axis or parallel to it, that it can be neglected in comparison with the powerful driving moments developed by the intercostal muscles.

The model of articulation we have described depends so much on the rigorous equilibrium of the muscular actions that it would not be able to work at all without the coordinating action of an elaborated control system similar to that described in section 2.4.3. It is reasonable to assume that the basic task of this control system is to maintain all the ligaments of the joint relatively free of tensile stresses; if this is so, then the system reacts similarly to slight movements of the joint whichever their direction and it is only for geometrical reasons that a much greater amplitude is possible for angular displacements around the main axis of rotation.

Finally, we remark that a similar mechanism of load compensation must operate for the articulation of the last three rib pairs. This articulation differs from that of the first rib in that the head of the rib only articulates with one vertebra, the costotransverse joint is much looser and the serratus posterior inferior replaces the serratus posterior superior and draws the rib in a caudal direction towards the column; this type of joint articulation allows the rib a much greater freedom of movement which makes the rib a sort of mechanical adaptor between the rib cage and the abdomen and at the same time reduces its importance as element in coupling between the rib cage and the vertebral column.

5.2.5.- The other articulations of the rib cage

In this section all the other types of articulations of the rib cage are described briefly; all these types, although they range from synarthroses to diarthroses, can be shown to participate of a dynamic muscular control along similar lines to those described for the costovertebral joints.

The costochondral joints are synarthroses or fixed joints made up by the ends of the rib and associated cartilage, ends which fit together and are maintained in position by the continuity of the periosteum and the perichondrium. In the case of these joints, as in the case of the joints which follow, only the intercostal muscles are directly attached to the members of the joint; the other muscles necessary for their stability are attached elsewhere in the rib cage and act indirectly on the joint.

The first nine costalcartilages articulate with the sternum by the diarthrodial or synovial chondrosternal joints. The first pair of these joints is located on the dorsal side of the manubrium and have a common capsule. The remaining pairs are located on the sides of the sternum, between the sternebrae, and their axis of rotation is approximately perpendicular to the longitudinal axis of the sternum. The ninth cartilage is also firmly united to the xiphoid process by the chondro-xiphoid ligament. The cartilages of the last four ribs, on the other hand, do not articulate with the sternum; instead, each of them, with the exception of the thirteenth, is loosely bound by fibrous tissue to the cartilage which precedes it in the cranial direction.

Finally, the sternebrae articulate with each other by means of cartilage, forming a synchondrosis which is kept together by an envelope of fibrous tissue.

5.3 - FUNCTIONAL PROPERTIES OF THE RIB CAGE STRUCTURES

5.3.1 - Introduction

From a structural point of view, the importance of the rib cage is only second to that of the vertebral column with which it shares many of its functional characteristics. In both cases bone and cartilageneous structures are integrated by muscular and aponeurotic masses which both constrain and power their relative movements; this system, in which huge reserves of muscular power are connected to supporting structures characterised by very limited freedom of movement and a low breaking strength, is only possible thanks to a complex control apparatus. The freedom of movement of the supporting structures is limited both by their own geometry and that of the common joints. In figure 5.8, two planar kinematic chains, one resulting from the other by adding to it three more of the basic three-linkage elements, illustrate how the increase in the complexity of a mechanism reduces the amount of its free movements. Although the rib cage is a three-dimensional structure, the fact that it possesses thirteen ribs together with

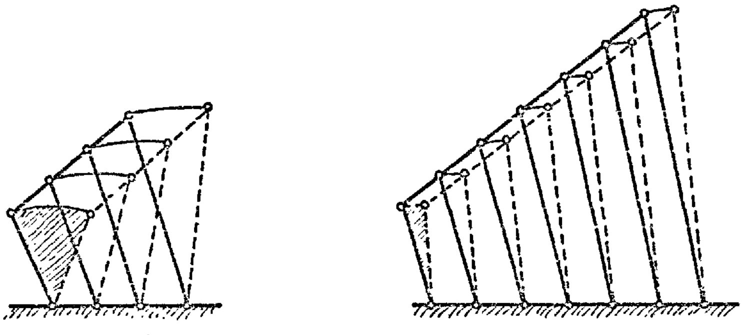

(a) (b)

Fig. 5.8 - Freedom of movement in planar kinematic chains made up of 3-bar linkage elements connected together: (a) four element chain; (b) seven element chain formed by adding three more elements to the previous chain. The two positions of the chains shown are the extreme positions which they can take.

the interconnecting tissues means that almost any amount of movement from the rest or centre position will cause the cartilages to bend; this is a delicate situation in view of the amount of muscular power potentially available in the cage musculature. Indeed, when properly functioning the cat's rib cage is a remarkably strong device as can be appreciated from the fact that the total muscle peak force associated with it amounts to something like 78kg, a figure computed on the basis of an average 3 kg intercostal muscles peak force (cf. section 5.3.2). Granted that the muscles are not supposed to tetanize simultaneously and that the muscle force is deployed over a large area of bone and cartilage, the possibility still exists of bending stresses being produced which are dangerously close to the breaking point of the material the structures in the cage are made of.

The nature of the stresses to which the ribs and costal cartilages are subjected may be appreciated by taking advantage of the fact that, in result of the direct adaptive response of the cancellous tissue to tensile and compressive stimulus (Laux, 1930; Clark, 1958), the muscles and ligaments exert a plastic action on

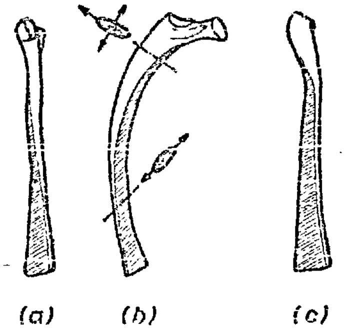


Fig. 5.9 - Three orthogonal views of the fourth left rib: (a) front (b) side and (c) back views.

the shape of the supporting structures to which they are attached; the amplitude of the stresses may also be assessed by assuming that the bone or cartilagenous tissue tends to develop in such a way as to achieve, for the predominant loads it resists, a state of approximately constant stress throughout the entire mass of the structure. The shape of the typical rib shown in figure 5.9 can thus be interpreted as follows: the cross-section of the rib above its neck is widest in a direction perpendicular to the longitudinal axis of the thorax, creating a shape which guarantees a large contact area in the costovertebral joint and at the same time allows it to rotate easily; the lateral surfaces in the neck of the rib provide the room needed for the attachment of the levatores costarum, iliocostalis lumborum, iliocostalis thoracis and longissimus thoracis muscles. Below its angle, the rib twists in order to align with the surface of the cage the largest axis of its elliptical cross-section; this orientation, which is also shared by the costal cartilage, means that in this area the stresses due to the wall muscles are far larger than those due to transmural forces. This point is of great importance and means that the ribs and cartilages work fundamentally as struts, i.e., in compression; the bending moments which necessarily tend to arise are eliminated by the combined action of the intercostal muscles, the muscles overlying the cage and the 'shell' effect which the convexity of the cage shape creates.

In this section we analyse the conditions in which the supporting structures in the cage are loaded, the role played by the intercostal muscles in compensating for the in-plane components of the bending moments and the mechanisms which power the respiratory rib movements. We follow this analysis with the study of the boundaries of the rib cage in order to establish the principles on which the modelling of the functional properties of the rib cage will be attempted.

5.3.2 - Loading regime of the rib- costalcartilage elements

We have referred in section 2.3.2 to the linkage mechanism devised by Hamberger to explain the action of the intercostal muscles in powering the respiratory movements of the rib cage; we also described summarily how the diagonal orientation of the muscle fibres creates a net moment which forces the system to rotate in the desired direction. We are now going to analyse the application of this principle to the real rib cage structures. In figure 5.10 we show an intercostal space and two linkage systems, one with rigid bars and the other with half rigid, half flexible bars in order to approximate more closely the real situation. The purpose of this diagram is to highlight the fact that the Hamberger's model implies the rigidity of all the links in the respective mechanism. Indeed, if some of the bars in the linkage do not withstand the bending moments created by the contraction of the muscle fibres, the structure will deform and no consistent net rotation will take place. This situation is illustrated in the diagram of figure 5.10(b) where the thin rods correspond to the costalcartilages of figure 5.10(a).

The mechanical characteristics of the material which constitutes the ribs and the cartilages can be obtained from tables

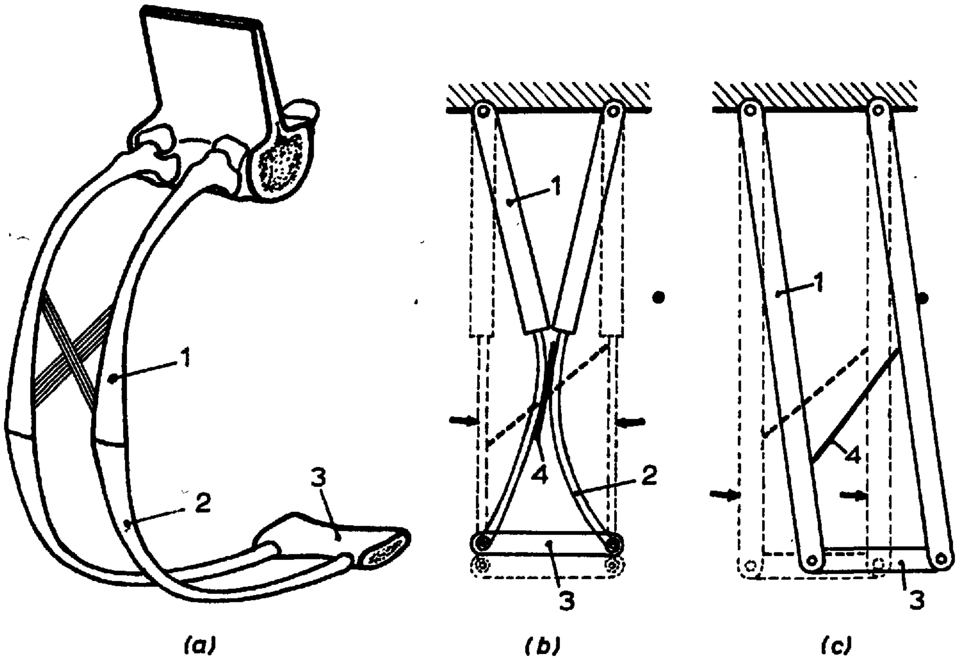


Fig. 5·10 Application of the Hamberger's model to the intercostal space structural system; (a) real intercostal space; (b) flexible-bar linkage mechanism; (c) Hamberger's rigid bar model. The solid lines represent the final position of the linkage after contraction of the muscles and the broken lines represent its initial position. 1-rib or rigid bar; 2-cartilage or flexible bar; 3-sternum; 4-internal intercostal muscle fibre.

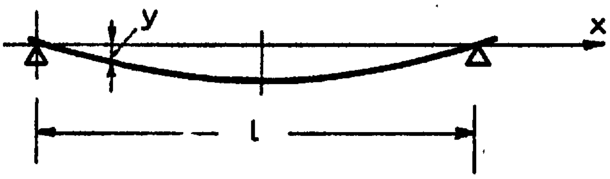


Fig. 5·11 Bending of a simply supported uniform beam under a uniformly distributed load. x - distance measured from the origin at the left support
y - beam deflection.

5.1 and 5.2. In table 5.1 the values of the ultimate strength, i.e., the value of the load at which the rupture of the material occurs, is given for bone, tendon and costal cartilage in a wet and unembalmed state and for three types of stress. Table 5.2 gives the elastic coefficient or Young's modulus of the same materials under compressive and tensile stresses.

In order to use these tables to characterise the ribs, we have to take into account that they consist of an external layer of compact bone a few tenths of a millimetre thick, surrounding a core of spongy substance whose contribution to the strength of the rib is negligible. We may now compare the mechanical properties of the ribs and cartilages by considering the idealized experiment of figure 5.11 in which a rod of uniform cross-section, and resting on simple supports at its end, is subjected to a uniformly distributed load; in the case of the cartilagenous material, the cross-section is a circle whereas in the case of the rib the cross-section is an annulus with the same outer diameter and about 0.3 mm thick. The maximum deflection of the rod, at its centre, is given by **(Prescott, 1961):**

$$y_{max} = \frac{5.w.l^4}{384} \cdot \frac{1}{E\ I} \qquad (5.1)$$

where E is the Young's modulus of the material, I is the polar moment of inertia of the cross-section of the rod, w the load density and l the length of the rod, all expressed in the same system of units. Expression 5.1 applies to both cases provided that E has the corresponding value from the table 5.2 and I is taken as being (Meriam, 1959):

Table 5.1: Ultimate strength for compressive, tensile and shear stresses of wet bone, cartilage and tendon.

Material	Origin	Stress	Strength (kg/mm^2)	Author
compact BONE	Human	Compression Tension Shear	18 10 6	Evans,1957; Ibuki,1964a
costal CARTILAGE	Pig	Compression Tension Shear	1.0 0.5 0.6	Endo and Takigawa,1953 Ibuki,1964b
limb TENDON	Human	Tension	9	Benedict et al.,1969

Table 5.2: Young's modulus for compressive and tensile stresses of wet bone, cartilage and tendon.

Material	Origin	Stress	Young's Modulus (kg/mm^2)	Author
compact BONE	Human	Compression Tension	1600 1000	Dempster and Liddicoat,1952
costal CARTILAGE	Pig	Compression Tension	8 2	Endo and Takigawa,1953
limb TENDON	Human	Tension	105	Benedict et al.,1969

$$I_{cart.} = (\pi/2).\ R^4 \tag{5.2}$$

and

$$I_{rib} = (\pi/2).(R^4 - r^4) \tag{5.3}$$

with R and r representing respectively the outer and inner radius of the cross-sections. In these conditions, and taking R = 0.75 mm, the ratio of the maximum deflection in the two cases is:

$$(y_{max})_{cart}/(y_{max})_{rib} = \frac{1000.(0.32-0.04)}{8\ .\ 0.32} = 109 \tag{5.4}$$

In practice, the external dimensions of the average cross-section of a rib are larger than those of the respective costal-cartilage and, therefore, the ratio given in 5.4 means that the rib may be treated, in comparison with the cartilage, as being perfectly rigid thus making the model of figure 5.10(b) a good approximation to the structures of the intercostal space.

It is difficult to determine exactly the deflection which the cartilages in figure 5.10(a) suffer under the loading produced by the contraction of the intercostal muscles because of the complex structure formed by the combination of the rib and the cartilage, but a rough estimation may be obtained by the following considerations: if we assume that the intercostales are able to develop a maximum tension of 0.1 kg/mm^2 of physiological cross-section (Fenn, 1963) and that the effective(*) thickness of the internal and external layers is 0.5 mm, and the length of the intercostal space is 90 mm, then the total load in the intercostal space will have an absolute maximum of about:

(*) The tension due to the two intercostal layers has to be combined vectorially.

$$P_{MAX} = 0.1 \cdot 0.5 \cdot 90 = 4.5 \text{ kg} \qquad (5.5)$$

which is larger than the total weight of the animal. If this type of loading was allowed, the intercostal space would collapse as shown in figure 5.10(b). In fact, even a load density as small as one thousandth of that which produces P_{MAX} would cause a peak deflection, y_{max}, of about 4 mm in the 40 mm length of the costal-cartilage defined in figure 5.11; this deflection would already bring the two ribs into contact and higher load would increase the deformation of the structure and soon lead to the rupture of the cartilages.

The consideration above lead us to consider the possibility that the intercostal muscle fibres behave as 'stays' with the main role of guaranteeing the rib- costalcartilage elements are maintaine free from bending moments and resist the loading by pure compression. This cooperation between the muscles and the supporting structures in the body corresponds to a general principle (Pauwels, 1948) whereby the latter are made to work essentially in compression, flexure being carefully avoided by the introduction of balancing loads by the associated muscles. The need for this functional policy stems from the fact that bending of the structures tends to create high local values of stress which could easily reach the rupture level. In order to illustrate this amplifying effect of bending, we consider again the uniform beam of cartilagenous material and of circular cross-section defined in connection with figure 5.11. The maximum bending moment occurs at the centre and its value is given by (Prescott, 1961):

$$M_{1/2} = \frac{w.l^2}{8} \qquad (5.6)$$

The bending of the beam stretches its lower part and compresses the upper part. If we assume that the shape of the beam in the region of maximum bending moment can be approximated by an arc of circle, the maximum stress on the outermost fibres of the material and on both sides will be given by (Wang, 1953):

$$T = \frac{M.R}{I} \tag{5.7}$$

where, as before, R is the radius of the cross-section and I its moment of inertia. Combining relationships 5.6 and 5.2, we get for the maximum stress the following value:

$$T = (w.l) \cdot \frac{1}{12.56\ R^3} \tag{5.8}$$

The first factor in the above expression, wl, represents the total load applied to the beam and T the tension, compressive above and tensile below, which it produces in the outermost fibres of the beam in the half length cross section. We see, therefore, that the rupture value of T will be reached for a load wl which is $1/12.56\ R^3$ times smaller than it would be if the same load was a straight compression or tension;in the case of our example this factor has a value of 12.

The ratio between the maximum allowable load in pure compression (or tension) and the maximum allowable load in bending depends on the geometry of the cross-section and the exact conditions of loading but, in general, it is sufficiently high to represent a serious deterioration in the performance of the structures subjected to bending.

5.3.3 - The intercostal muscles integration of the supporting structures of the cage

The basic conclusion of the previous section is that the supporting elements in the cage must work in an essentially compressive mode which is achieved and maintained by the action of the intercostal muscles. This conclusion, reached by considering the very low resistance to bending of the costalcartilages, poses three questions which we will now try to clarify. The first of these questions refers to the ability of the intercostal muscles to remove the bending moments which may arise. Figure 5.12 illustrates the planar version of a costalcartilage segment 'hanging' from the adjacent cartilages by the intercostal muscle fibres. For the sake of argument, we assume that the outside cartilages are held firmly in position. Due to the curved shape of the cartilage segment, the compression load P applied at its end will tend to increase the bending angle and, consequently, to stretch the muscle fibres in the intercostal space 2 and to relax those in space 1; however, if we assume that the mechanoreceptor control loop has sufficient gain, the muscle spindles on side 2 will bring the degree of activity of the respective muscle fibres to the level required to produce the component F_m, shown in the diagram, which brings the cartilage back to its original position. We may therefore postulate the formal existence of a servo system(*) which keeps the cartilage 'floating' on the border of the inter-

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(*) The existence of such servo system has been deduced already from neurophysiological considerations as pointed out in section 2.4.3.

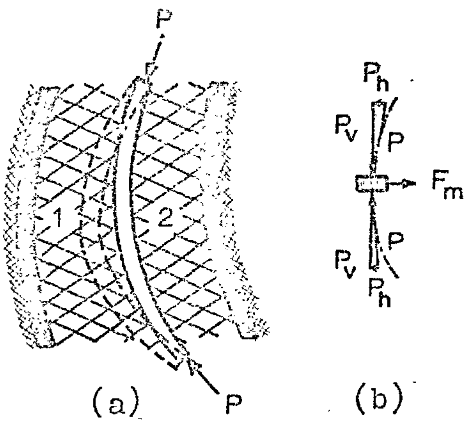

Fig. 5.12 - Action of the intercostal muscles: (a) planar representation of a length of costal cartilage supported from the adjacent costalcartilages by the intercostal muscles. The segment is represented in two positions, before (solid lines) and after (interrupted lines) the application of a compression force P to its end. (b) free-body diagram defining the equilibrium of forces in an elementary sector of the cartilage. P- compression force; P_v and P_h- vertical and horizontal components of P; F_m- equilibrium tension developed by the muscles.

costal spaces. This servo system will contain at least **twelve** basic units - one for each intercostal space - subjected to an overall control which avoids the possibility of the system becoming unstable. This instability would arise if, for any reason, one of the intercostal spaces became too active, in which case the other spaces would also have to increase their activity in order to try to balance the loads transmitted to them; this reaction would then force the first space to increase further its activity and the process would grow until the system had run completely away to an extreme position of some kind. Obviously this type of behaviour would be completely unsatisfactory and must be prevented by the introduction of a dominating central control which compares the responses of all the intercostal spaces and avoids the kind of 'competitive' reaction outlined above.

The application of the model of figure 5.12 to the first and last intercostal spaces leads to the following conclusions:

1- the last rib and costalcartilages which form the caudal boundary of the cage will depend on the abdominal muscles to supply the counterpart for the action of the intercostal muscles in the twelfth space. Indeed, without this abdominal firm support, the lower end of the rib cage, right up to the ninth rib, would collapse, i.e., the ribs would come close together;

2- the first rib and cartilage are sufficiently short and thick to withstand the tension developed by the muscles in all the intercostal spaces, which are connected in **cascade** to them, and to which they constitute the anchorage; the first rib and cartilage can be helped in this role by the scalenus primae costae and the sternomastoideus muscles but these muscles are not generally very active in quiet respiration (Raper et al., 1966);

3- if the rib-costalcartilage elements are essentially subjected to compression then their shape will make them transmit to the sternum a system of reactions whose net resultant will tend to force it forward and outwards, a thrust which is balanced by the rectus abdominis muscle as shown in figure 5.13. The other abdominal muscles, the retractor costae ultimae and the serratus posterior inferior, acting on the ribs, also contribute to this action.

4- This system of muscle tensions and reactions means that the entire trunk wall is in a state of stress whose intensity

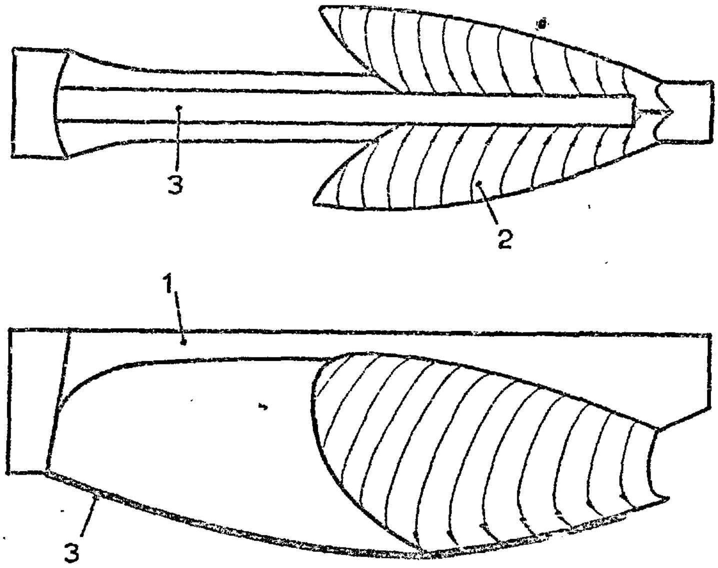

Fig. 5.13 - Reaction of the ribs on the sternum and their compensation by the rectus abdominis muscle.
1- vertebral column; 2- rib cage; 3- rectus abdominis muscle.

varies from a minimum guaranteed by the 'tonic' muscular activity, to peaks, such as those occurring in inspiration; it also means that this 'tonic' activity, instead of being just the result of spontaneous random stimulation of the muscles, does in fact correspond to the nervous control solution of a sophisticated structural problem, a fact which is borne out by the large deformation suffered under Flaxedil by the animals in our experiments.

A second question we want to answer refers to the possibility of the intercostal muscles being able to, alone, prevent the bending of the rib-costalcartilage elements of the rib cage. The answer to this question is that, for small deformations, they certainly are. Although figure 5.12 shows only what happens when the rib-cartilagenous element stays in the surface defined by the two adjacent intercostal spaces, it is not difficult to see that if the deformation causes the element to bulge away from that surface over a short length, the increased activity of the fibres from both intercostal spaces in that area will tend to eliminate the bulge. This mechanism, however, becomes inadequate for large deformations which affect extensive areas of the cage; in this case, the animal resorts to the muscles which overlie the cage, a point which we will take up again in section 5.3.4.

Finally, the third question associated with the conclusions of the previous section refers to mechanism which is responsible for the compressive end loads on the rib elements. The most important physiological loads, such as those due to the inspiratory transmural pressure and those transmitted by the front limbs, are applied to the cage as an approximately uniform compressive pressure normal to the surface of the cage; these pressures are represented in figure 5.14(a) as acting on the cross-section of the thorax. In figure 5.14(b) a sector of the cross-section is isolated to show the 'wedge' effect which it produces under the action of the external pressure; this effect results from the decreasing perimetral dimensions of the cross-section as seen in the inward direction. Finally, figure 5.14(c) shows the free-body diagram which describes the equilibrium of the forces to which the sector of the cross-section is subjected, again illustrating how stresses along a direction normal to the cross-section of the cage are generated from pressures which are normal to the surface of the cage.

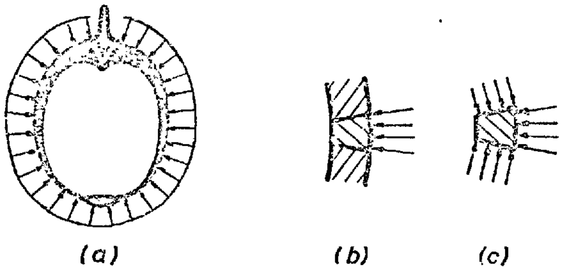

Fig. 5.14 - Genesis of the compressive force in the supporting structures of the rib cage: (a) cross-section (b) 'wedge' effect which transforms normal pressures into compression, illustrated by isolating an element of the cross-section.

5.3.4 - The inspiratory elevation of the ribs

The movements of the rib cage described in chapter 4.0 consist of a displacement forward and upwards of the shaft of the ribs and of the costalcartilages. We are now going to investigate how this movement is produced in terms of the muscles which power them. The first point which we will try to clarify is whether the driving mechanism in figure 5.10(c) could be responsible for this movement of the ribs. As we have seen, the intercostal muscles(*) are perfectly capable of maintaining the costal cartilages free from bending moments and therefore behaving as perfectly rigid struts; in so far as this assessment is correct, then, the mechanism of figure 5.10(c) is a correct description of the way in

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(*) In the parasternal region of the first seven intercostal spaces the external intercostal muscles are absent and their role is largely performed by the sternocostales muscles.

which the intercostal muscles operate. The fact that the intercostal spaces are three-dimensional rather than planar structures, leads of course to more complex movements than those implied in figure 5.10(c), as we have seen for instance in section 4.2.2 where it was shown that, when the ribs elevate in inspiration, the sternum moves caudally instead of cranially. This movement is apparently in contradiction with the principle of Hamberger's model, but this contradiction is removed by noticing that the rotation axes of the sternal joints, which in figure 5.10(c) are perpendicular to the median plane of the mechanism, are parallel to this plane in figure 5.10(a). In this way, therefore, the backward movement of the sternum is perfectly compatible with the forward movement of the rib; furthermore, the action of the intercostales does not preclude a certain amount of deformation of costalcartilages as necessary to adjust to the deformed geometry of the cage.

Other muscles of the trunk also have fibres orientated in the right direction; these muscles are, for instance, the levatores costarum, the serratus posterior superior, the sternomastoideus and the scaleni. The levatores costarum are very closely related to the external intercostal muscles and share some of their driving function; however, the fact that they contribute with an off-plane component in the direction of the costotransverse joints suggests, as we already pointed out in section 5.2.4, that they play an important role in the stabilization of these joints. The serratus muscles act at an angle with respect to the cage surface so that their contraction tends to lift the ribs; and they are antagonistic (cf. figure 3.8) of the serratus posterior inferior, the obliquus abdominis externus, the iliocostalis lumborum and longissimus thoracis. We may therefore conclude that, apart from any contribution to the forward drive of the ribs, they participate in two very important functions: the stabilization of the costovertebral joints and the protection of the cage against deformation under excessive loads. Both of these functions will be analysed in the next section. The scaleni and the sternomastoideus do not usually participate, in any substantial measure, in the inspiratory activity.

The reverse movement of the rib cage, corresponding to the displacement of the ribs down and backwards, is performed by the contraction of the internal intercostal muscles assisted by the abdominal muscles, the retractor costae ultimae and the serratus posterior inferior.

5.3.5 - Boundaries of the rib cage: cranial edge

The muscles attached to the cranial edge of the rib cage are the rectus, the transversus costarum, the scaleni and the sternomastoideus. The rectus plays the very important function of compensating for the combined thrust of the costal cartilages in order to define firmly the position of the first rib. The transversus is attached to the first rib and to the sternum to which it transfers the pulls due to the insertion of the neck muscles; it also shares the respiratory function of the external intercostal muscles in the first two spaces. The scaleni and the sternomastoideus muscles are disposed in such a way that their contraction will tend to raise the frontal end of the rib cage and, therefore, to contribute to the inspiratory process; except in hyperpnea, however, the activity of these muscles is usually very moderate (Campbell, 1958; Campbell et al., 1970; Raper et al., 1966).

5.3.6 - Boundaries of the rib cage: caudal edge

The caudal edge of the rib cage is formed by the thirteenth rib, the tenth to thirteenth costal cartilages and the xiphoid process. On this boundary the following structures are attached:

1- The transversus abdominis muscle: on the inner surfaces of the thirteenth rib and of the tenth to thirteenth cartilages (cf. figure 5.15).

2- The diaphragm: with the same insertions as the previous muscle and, in addition, a median attachment to the inner surface of the xiphoid process.

3- The obliquus abdominis internus muscle: attached to the posterior border of the last rib and the penultimate costal-cartilage.

4- The retractor costae ultimae: attached to the inferior border of the last rib (cf. figure 5.15).

5- The last digitation of the serratus posterior inferior: also related to the last rib on whose posterior border and outer surface it inserts.

6- The linea alba which connects the xiphoid process to the symphisis pubis.

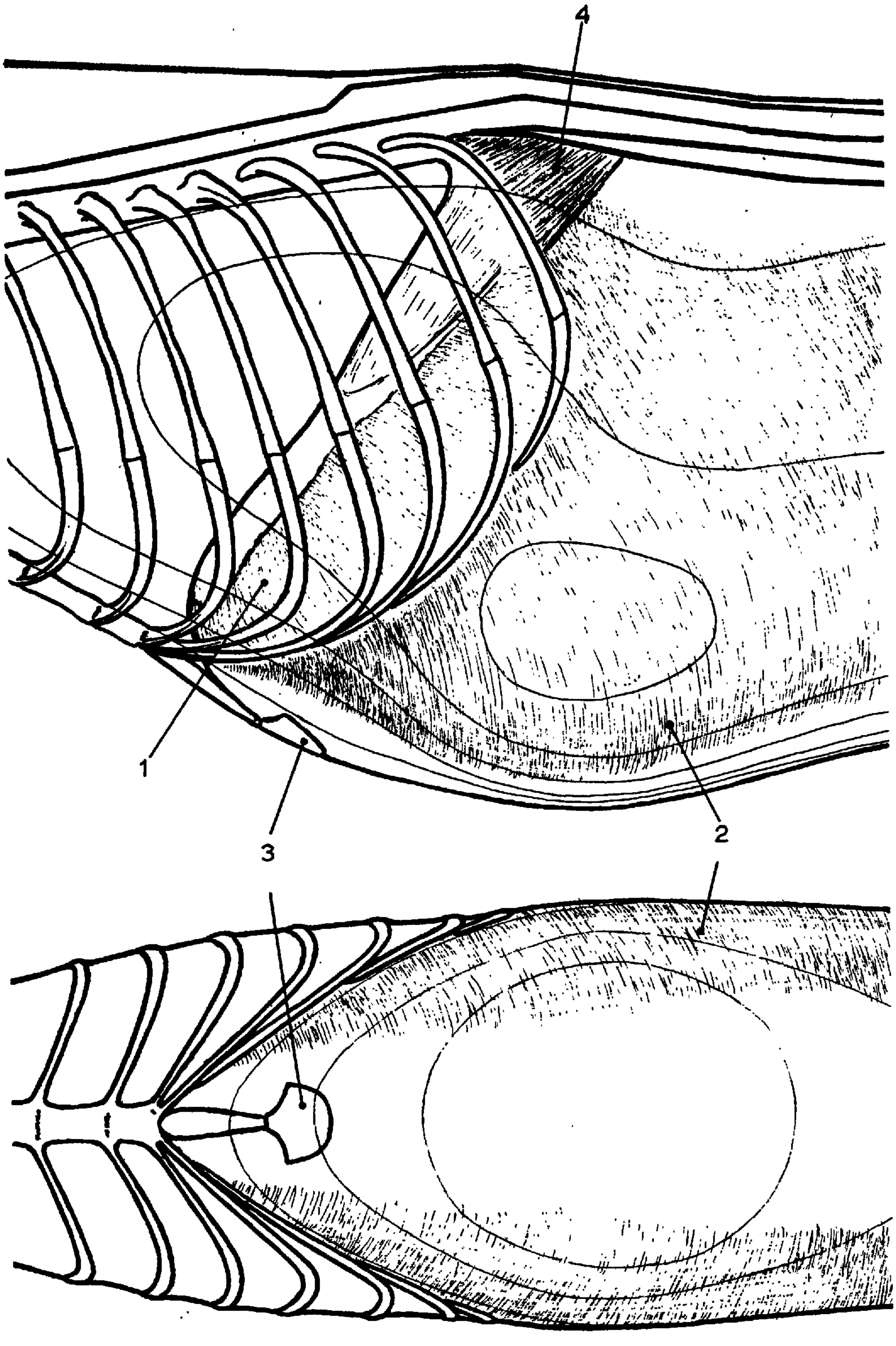

Fig. 5·15 Diagrammatic view of the central region of the trunk showing the inner abdominal muscular layer and level contours referred to the median plane of the body. 1-diaphragm; 2-transversus abdominis muscle; 3-xiphoid process; 4-retractor costae ultimae muscle.

7- The aponeurosis of the transversus abdominis muscle: in continuity with the xiphoid process, the linea alba and the sternal end of the tenth costal cartilage.

With the exception of the diaphragm, all the muscles listed above should have a similar action, namely, to contribute to the creation, all around the edge of the rib cage, of a pull in a cranio-caudal direction which would stabilise the lower intercostal spaces by preventing the respective costalcartilages from bending under the tensions developed by the intercostal muscles. The contraction of the diaphragm, on the other hand, produces a pull which is also tangent to the boundary surface all around its periphery but which tends to pull it in a cranial rather than caudal, direction. The first family of boundary muscles would then have to develop forces of sufficient magnitude to immobilize the caudal rim of the cage against the combined action of the diaphragm and the intercostal muscles. This response of the boundary muscles should achieve equilibrium for the tangential forces along the caudal edge of the rib cage; the stabilisation of this edge against transverse forces is very likely to be achieved thanks to the support provided by the abdominal viscerae in particular the liver against which both the abdominal wall and the lower edge of the cage rest (cf. figure 4.15 and 4.16).

The retractor costae ultimae and the serratus posterior muscles are inserted on the first two or three lumbar vertebrae, the first muscle inserting on their transverse process and the second on their spines and on the associated supra-spinous ligament. Consequently, the action of these two muscles is that of drawing the last rib back and upwards, tending to bring it closer to the vertebral column. The abdominal components of the boundary muscles, on the other hand, do not have such firm points of attachment and their contraction simply tends to reduce the abdominal volume and, consequently, the compression of the abdominal viscerae is the essential vehicle for the action of these muscles on the caudal boundary of the rib cage. Under normal conditions, the amount of compression of the abdominal contents is very small but, because of the shape and firmness of these contents, in particular of the liver, this level of compression is quite enough to allow the abdominal muscles to perform their part in the stabilisation of the trunk.

If the boundary muscles have such an important role in the stabilisation of the caudal periphery of the rib cage, a close control linkage must exist between the sensory receptors in this region and the contraction of the associated boundary muscles. The existence of this linkage has been established by means of positive pressure breathing experiments (Bishop, 1964) which showed that the expiratory response of the abdominal muscles was elicited only when the cervical vagal nerve, the spinal cord above the L1 segment and the dorsal roots on either side of the T8 to the L3 segments were simultaneously intact; the coexistence of these two pathways suggests that this type of control of the abdominal muscles is issued at higher level but takes into account the efferent flow of both vagal origin and costal origin. To the best of our knowledge, the way in which the sensory information is originated in the boundary intercostal spaces has not, so far, been investigated; the foregoing remarks, however, suggest that it could be taken from the output of the stretch receptors in these spaces. Indeed, a deficiency in the response of the boundary muscles would allow the last ribs and costalcartilages to move forward under the combined action of the diaphragm and the intercostal muscles, a movement which would bring about a narrowing and eventual collapse of the respective intercostal spaces; this situation can therefore be monitored by the associated mechanoreceptors. Simultaneously, the failure of the caudal edge of the cage to provide the firm support needed by the diaphragm, would impair the ability of this muscle to oppose the lung recoil and the transmural pressure and would, therefore, be revealed in the output of the lung sensory receptors which participate in the control of the contraction of the boundary muscles.

The positive pressure breathing experiment is well suited for the analysis of this type of interplay between the boundary structures because it exaggerates the movements which take place in normal expiratory conditions: the rib cage is forced to come further down than it normally does in order to squeeze the air out of the pressurised lungs and this movement will tend to compress the peripheral intercostal spaces; this effect must then be opposed by a more vigorous pull on the boundary periphery.

In conclusion, the caudal boundary of the rib cage will be considered as being subjected to purely tangential reactions which are largely parallel to the longitudinal axis of the animal and whose amplitude is continually adjusted to the level of overall load on the rib cage by a control system mediated by the stretch receptors located in the last intercostal spaces and in the lungs.

5.3.7 - Boundaries of the rib cage: dorsal edges

The rib cage terminates dorsally on either side of the vertebral column and is joined to it by the costovertebral articulations, their associated musculature and by aponeurotic structures such as the posterior intercostal membrane and the lumbodorsal fascia. The loads the rib cage sees along these boundaries are, of course, the reactions of the vertebral column and of the dorsal muscles which insert on the ribs. It has been pointed out in section 5.2.4 that the muscles which subserve the costovertebral articulations are controlled in such a way as to make sure that the loads on the opposing surfaces of the costovertebral articulations are normal to them and of purely compressive nature; this fact means, therefore, that at the level of these articulations the ribs are free from transverse forces and bending or rotating moments which, when they tend to occur, are compensated for by the muscles associated with the articulations (cf. figures 5.6 and 5.7).

These muscles, however, introduce additional reactions somewhere along the vertebral end of the ribs. Thus, the iliocostales, the longissimus thoracis and the levatores muscles, acting close to the column boundary, contribute directly to the reactions although the contribution of the levatores costarum is predominant over that of the other muscles. In fact, the levatores costarum supply a component which helps to compensate for the moment which tends to rotate the rib cage in a caudal direction and which is due to the action of the ensemble of the abdominal muscles. The levatores costarum are backed in this function by the serratus posterior muscle which, besides this action, also pulls the angles of the ribs towards the vertebral column, an action which is essential to the stability of the costovertebral articulations. The serratus posterior inferior acts in a different manner and pulls the last four ribs in a caudal direction as it is necessary to stabilise the rib cage periphery against both the action of the diaphragm and that of the transmural pressure.

We may, therefore, summarise the boundary conditions at the dorsal edge of the rib cage as follows: (1) a purely compressive, transverse force free and moment free reaction at the costovertebral joints; (2) a transverse reaction directed from the transverse process of each vertebra to the rib immediately caudad to it in the direction of the respective levator costarum bundle; (3) the action of the scratti muscles which pull the ribs firmly against their articulations.

5.3.8 - Boundaries of the rib cage: overlaying muscular layer

Powerful as they are the intercostal muscles are located in the surface of the rib cage and therefore unable to oppose effectively any asymmetrical or excessive loads which will tend to cause large deformations of the rib cage. In order to protect itself against such loads, it would clearly be possible for the animal to make use of the muscles which lie over the cage surface; these muscles are diagrammatically shown in figure 5.16 together with some of the deformation modes which may occur. The most important of these muscles are the serratus posterior superior, the obliquus abdominis externus, the rectus abdominis and those responsible for the suspension of the front limbs.

In the absence of large loads, the cage has the regular, approximately elliptical, cross-section illustrated in figure 5.16(a); this condition corresponds with a shell-like mode of load response in which the bending moments are everywhere negligible. Figure 5.16(b) depicts the case of an excessive load applied laterally; in this case large bending moments would occur at all the three joints of the rib-costal cartilage elements. The animal could react against this condition by contracting the serratus posterior superior, which would raise the ribs back to their normal position, and the externus obliquus and the rectus abdominis which would lift the ventral surface of the thorax. In general, of course, the load will not be as simple as we have portrayed and other muscles are certainly called upon to produce the correct pattern of muscular response; nevertheless, the description above illustrates a likely mechanism of the animal response to a forced reduction in the transverse dimensions of the thorax.

In figure 5.16(c) the case of a dorso-ventral compression is illustrated. In this case, the response would consist of breathing in, so as to create a negative pressure in the thorax, at the same time as the muscles which suspend the front limbs and the externus obliquus were contracted.

During its life, the animal experiences violent loads of a great variety, such as localised blows, large area squeezes, etc., most of which are far more complex than the loading regimes described above. Moreover, the responses which we have prescribed

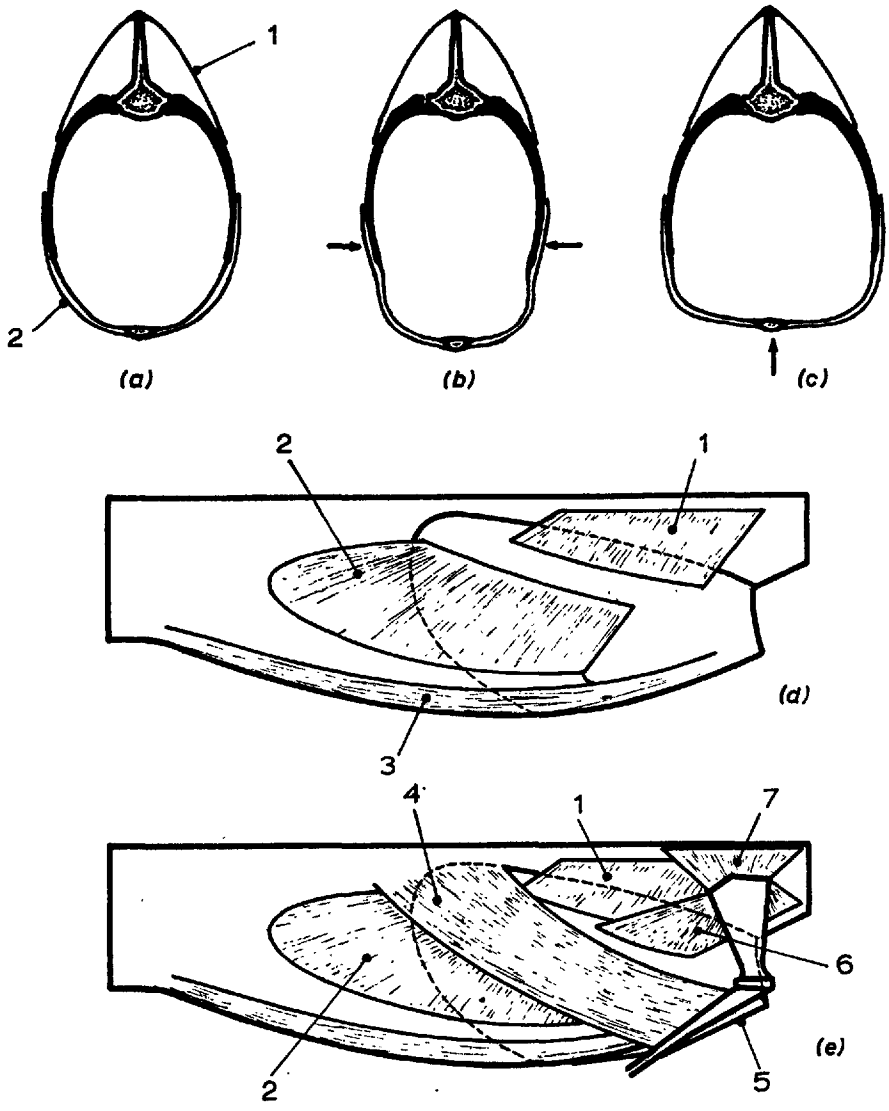

Fig. 5·16 - Large scale deformations of the rib cage : (a) diagrammatic representation of the normal cross-section at the level of the eighth thoracic vertebra; (b) idem under lateral compression; (c) idem under ventro-dorsal compression; (d) trunk muscles responsible for the rib cage reaction; (e) muscles for the attachment of the front limbs.

1- serratus posterior superior m.; 2-obliquus externus abdominis m.; 3- rectus abdominis m.; 4-longissimus dorsi m.; 5-pectorales and xiphihumeralis m. 6-serratus anterior m.; 7-rhomboideus, acromiotrapezius and spinotrapezius m.

represent only a broad outline of what may be envisaged to happen with no attempt made to define the time sequence, the amplitude and the nature of the movements of the muscles involved. Sketchy as it is, however, the analysis on this basis suggests that the essential feature of the animal's response is the correct recruitment of the muscular masses whose contraction would oppose the deformation caused by the load and restitute the cage to its normal configuration in which the action of the intercostal muscles is most effective. We conclude, therefore, by postulating an independent control system, which integrates the muscles defined in figure 5.16 and which would be responsible for the maintenance of the overall rib cage shape.

5.4 - FUNCTIONAL PROPERTIES OF THE ABDOMINAL COMPARTMENT

5.4.1 - Introduction

In this section we review the functional properties of the abdominal compartment in order to define its participation in the overall model of the respiratory apparatus. The abdominal compartment is functionally made up by the vertebral column, the abdominal walls, the viscerae and the diaphragm. As we have already said, the column and the pelvic bones constitute the structural reference system, considered fixed in space and undeformable, on which the model is based. The abdominal viscerae constitute the medium through which the synergistic action of the abdominal muscles and the diaphragm is made possible; from anatomical relationships and from observation of the visceral movements in our records it seems clear that the viscerae also plays a crucial role in ensuring that the mechanical coupling between the caudal edge of the rib cage and the diaphragm and abdominal muscles takes place in such a way that a balance of forces is possible. The crurae are the main muscular components of the diaphragm and from their attachment on the vertebral column they pull the viscerae into the abdominal compartment; the peripheral fibres are shaped by the viscerae so that their reaction on the rib cage is tangent to it. The abdominal muscles are shown to be separable into two functional groups, one which is essentially concerned with the balancing of the thrust of the diaphragm on the rib cage and another which is more involved in the overall stability of the trunk. The concept of compression bias is introduced in order to define the pressure distribution in the abdominal compartment in a way which makes the phenomenon easier to understand and, simultaneously, is best suited for the eventual analysis of the membrane problem which the diaphragmatic and abdominal walls constitute.

5.4.2 - Mechanical role of the abdominal viscerae

The coupling of the actions of the diaphragm and abdominal muscles is achieved via the compression of the abdominal viscerae diagrammatically represented in figure 5.17 and whose participation in the respiratory movements deserves some attention.

The main organs housed in the abdomen are the liver, the stomach, the kidneys, the intestines, the pancreas, the spleen, the adrenal glands, the reproductive organs and the bladder; these organs are connected, subserved or related by structures which include the blood and lymphatic vessels, nervous plexuses and fibres, deferent ducts, connective and fatty tissue and the peritoneum. The dynamical behaviour of the abdominal viscerae has been likened, in terms of respiratory mechanics, to that of an incompressible fluid (Agostoni and Rahn, 1960), an analogy which results from their relative facility to undergo mass displacements and from the consideration that only limited pressure variations occur in the abdomen during quiet breathing. The intestines, particularly the jejunum and the ileum, are very good examples of organs capable of this fluid-like mobility and, indeed, they make up most of the abdominal volume. The other viscerae, however, are not in such a good agreement with this model as, generally speaking, they tend to be smaller and more compact and are in much closer relationship with the framework which the structures referred to above constitute; this framework constraints their movements to a very considerable degree and changes the character of their collective mechanical behaviour.

The transpyloric cavity, delimited at the cranial end of the abdomen by the diaphragm and the costal walls, is occupied almost entirely by the liver, an organ which, because of its position, size, shape and firmness, plays a leading role in the respiratory function of the abdominal compartment. The liver is closely related to the diaphragm via the coronary, the falciform and the triangular ligaments and to the anterior abdominal wall by the coronary ligament and the ligamentum teres; the liver is also connected to the gall bladder, the stomach, the duodenum, the right kidney and suprarenal gland, the inferior vena cava and the portal and hepatic blood vessel systems. These relations determine both the shape or the organ and the nature of its movements; thus, the cranial surface of the liver, moulded on those of the diaphragm and ventral abdominal wall, is convex and wedge-like whereas its caudal surface bears the rough imprints of the adjacent viscerae, namely, the stomach, the intestines, pancreas and right kidney. The mechanical coupling between the diaphragm and the liver creates a piston-like effect by which the movements of the diaphragm are forced on the remaining abdominal contents or, vice-versa, the movements of the latter are forced on the former. The concavity of the base of the liver is a very convenient feature of its shape because, whenever the organ is compressed, this base tends to 'open' and to force out the rim of the rib cage which is thus held firmly in position against the pull

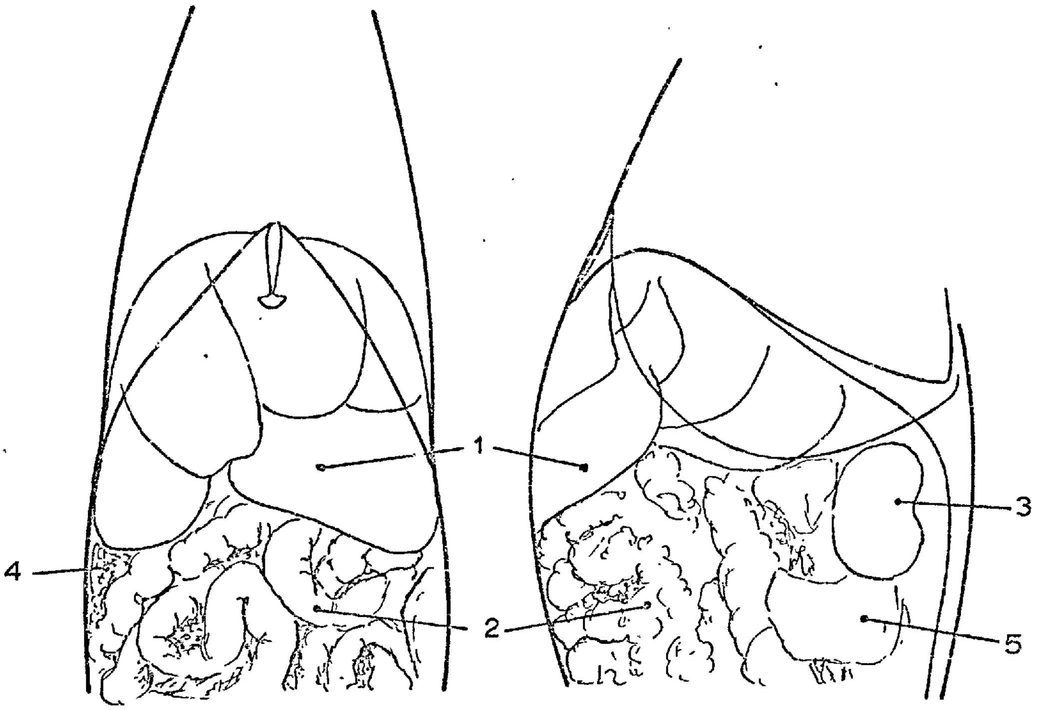

Fig. 5.17 - Layout of the abdominal compartment in the cat. 1- Liver; 2- intestines; 3- kidney; 4- pancreas; 5- spleen.

exerted by the abdominal muscles; this effect is indeed the main mechanism responsible for the stability of the caudal boundary of the rib cage. Finally, the liver is divided into three main lobes which, like those in the lungs, compatibilise its large size with the degree of mobility or fluidity demanded by its mechanical role.

The consistency of the other organs and structures which are partially or totally inside the transpyloric cavity ranges from the firmness of the kidneys to the collapsible character of the stomach and the abdominal blood vessels. However, their sizes are small in comparison with that of the liver which is unquestionably the dominant mechanical component in this region of the abdomen. The contraction of the abdominal muscles not only compresses the viscerae but also forces them to move inside the abdomen. Indeed, the orientation of the muscle fibres in the abdominal wall is such that the degree of compression is maximum in the umbilical or equatorial region of the abdomen and, consequently, the viscerae are forced to move into both the diaphragmatic and pelvic cavities. These displacements of the viscerae are, of course, the most convenient for the build up of pressure required in expulsive tasks such as those which occur in association with respiration and defecation.

5.4.3 - The diaphragm

The diagrams of figure 5.18 represent two views of the diaphragm and show the structures already referred to in section 3.3.2, namely, the two crurae, the central tendon and the radial muscle fibres. Figure 5.19 represents two longitudinal cross-sections of the abdominal walls and the diaphragm.

We want now to consider the relations of the diaphragm to the adjacent organs in both the thoracic and the abdominal compartments in order to assess how these relations affect their respective mechanical performance.

The diaphragm possesses three large openings, or hiati, through which a few structures are passed into the abdominal cavity. The most dorsal of these openings, essentially of aponeurotic character, is situated medially between the two crurae and the vertebral column; this opening is called the

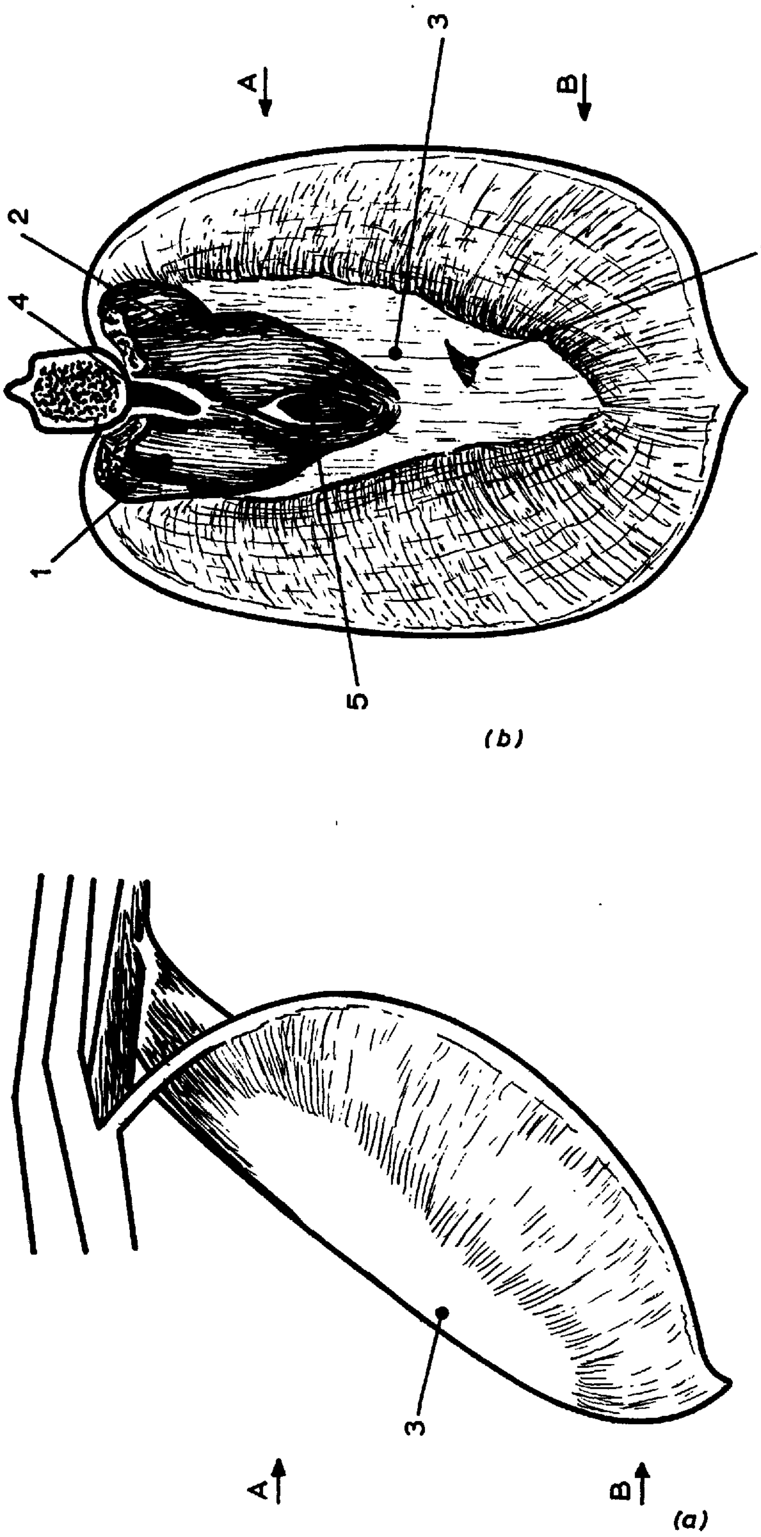

Fig. 5·18 - Diagrammatic representation of the diaphragm: (a) lateral view; (b) view of the caudal surface.
1 - left crura; 2 - right crura; 3 - central tendon; 4 - aortic hiatus; 5 - oesophageal hiatus; 6 - caval foramen.

aortic hiatus and through it pass the aorta, the thoracic duct and sometimes the azygos vein. The second opening, called the oesophagus hiatus, is situated between the muscular fibres of the two crurae and transmits the oesophagus and the oesophageal trunks of the vagus nerves; a third opening, the caval foramen, on the right of the central tendon passes the inferior vena cava. The effect the movements of the diaphragm have on these structures which pass through it varies with the opening. In the case

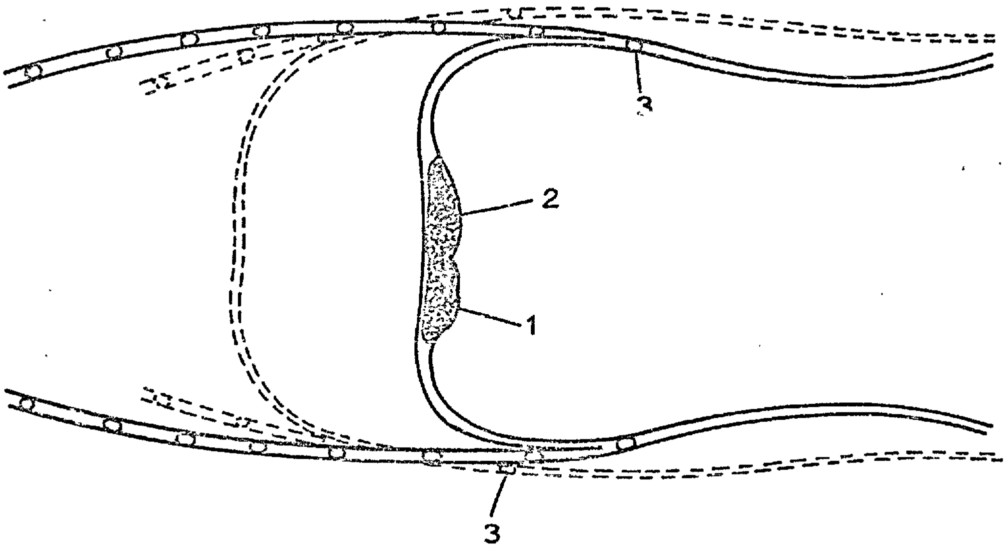

Fig. 5.19 - Longitudinal cross-sections through the abdominal walls and diaphragm respectively at the levels A (solid lines) and B (broken lines) in figure 5.16.

1- left crura; 2- right crura; 3- thirteenth rib.

of the vena cava, the tendinous nature of the tissue in which the opening occurs and the fact that there is continuity between the walls of the vessel and the margin of the opening, imply that the inferior vena cava is forced to follow the movements of the diaphragm in a region where they have maximum amplitude but at the same time its cross-section there is held firmly constant.

The oesophageal opening, on the other hand, is defined by muscular masses which tend to compress or strangle the oesophagus when they contract, forcing it to close and to move with the diaphragm; finally, the position of the aortic opening guarantees that the structures which pass through it are not appreciably disturbed by the diaphragmatic movements. Other minor apertures exist in the diaphragm to let into the abdomen thin nerves and small veins which are also forced to follow the movements of the diaphragm; however, these two types of structures only constitute a minor part of the load which the diaphragm, as one of the main sources of mechanical power in the respiratory process, has to drive. The most important loads for which the action of the diaphragm is intended would seem to be the result of the following causes:

1- The elastic recoil of the lung tissue; 2- the negative pressure developed by the air flow in the airways; 3- the resistance to movement presented by the abdominal viscerae; 4- the forces developed along the caudal edge of the rib cage by all the other muscles with costal insertion.

The way in which the diaphragm copes with these loads must be strongly influenced by its intimate mechanical relationship with the lungs and the liver. The coupling with the lungs is, of course, the vehicle through which the diaphragm performs the most important of its respiratory work; it also has a strong bearing on the shape of the muscular fibres in the pars costalis and, therefore, on the conditions in which that work is performed. The shape of the diaphragm is also dependent on its coupling with the liver because of the convexity and firmness of the cranial surface of this organ and, as we have already pointed out in section 4.5.0, the horizontal cross-sections of the diaphragm resemble (cf. figure 5.19) catenaries of constant strength, a fact for which the lungs and the liver have a major responsibility. The compression of the liver, caused either by the diaphragm or the abdominal muscles or both, forces its base to open and to push against the caudal edge of the rib cage which, being simultaneously pulled caudally by the transversus and internus obliquus muscles, is thus firmly held in position. We have found in our experiments (cf. section 4.3.2) evidence of a sizeable tonic activity in the external trunk muscles, a finding which is in agreement with the experimental evidence (Boyd and Basmajian, 1963) that the diaphragm tends to be active throughout the respiratory cycle; thus, although the variations of the abdominal pressure during quiet breathing are comparatively small (Campbell and Green, 1953a,b; Lewis, 1908), the tonic activity may well provide a pressure 'pedestal' of sufficient magnitude to keep the liver in contact with the diaphragm and thus to guarantee the proper performance of the roles ascribed above to the liver.

The inspiratory movements of the diaphragm are dominated (cf. figure 4.9) by the contraction of the crurae which, thanks to the close relation between the liver and the diaphragm, firmly pushes the abdominal viscerae into the abdomen; this 'scoop' action, therefore, transfers to the vertebral column most of the load handled by the diaphragm. The fibres in the pars sternalis and pars costalis constitute a muscular band stretched between the periphery of the central tendon and that of the caudal border of the rib cage; the load which the fibres in this band take from the lung and the abdominal viscerae is transmitted to the vertebral column via the central tendon and to the costal and sternal insertion of the fibres.

We have so far represented the diaphragm as an essentially symmetrical bi-domed structure; this description applies to the shape assumed by this organ in the prone position adopted in our experiments and as long as we ignore the asymmetry which the attachment of the pericardium introduces. In real life, however, the shape of the diaphragm like that of the abdominal walls changes with posture as a result of the weight and 'fluidity' of the abdominal viscerae.

5.4.4 - The abdominal muscles

The obvious functions of the abdominal muscles are to contain and support the abdominal viscerae, to integrate the structural unity of the trunk and to assist the respiratory and expulsive processes, all of which are intimately related to the build up of pressure in the abdominal compartment. We have referred above to the evidence regarding the tonic activity of the trunk muscles and pointed out that it creates a pedestal or bias state of compression of the viscerae in the abdomen. In order to elucidate the role of this bias compression, Δp, in the distribution of the abdominal pressures, we apply the analysis of section 2.2.5 to the two-dimensional cat in the prone position of figure 5.20.

The three fundamental types of body forces acting on the abdominal fluid are the compression Δp created by the contraction of the wall muscles, the hydrostatic gravity forces which we

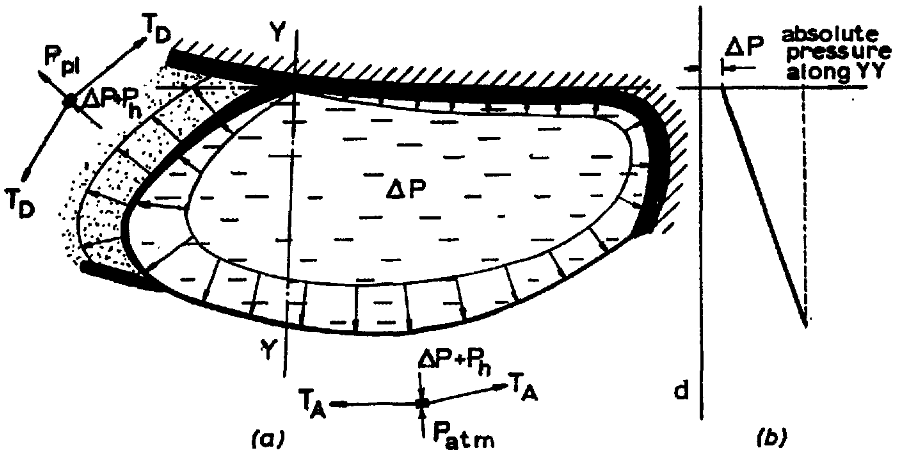

Fig. 5·20 Distribution of the pressure in the abdomen of a cat in the prone position: (a) sagittal cross-section through the median plane; (b) distribution of the pressure along the vertical Y for illustration. ΔP–compression bias due to the tonic activity of the wall muscles; P_h -hydrostatic pressure; P_{pl} - intrapleural pressure; P_{atm}-atmospheric pressure; T_A -stretch tension in the abdominal wall; T_D-stretch tension in the diaphragm; d-vertical distance measured from the highest point inside the abdomen.

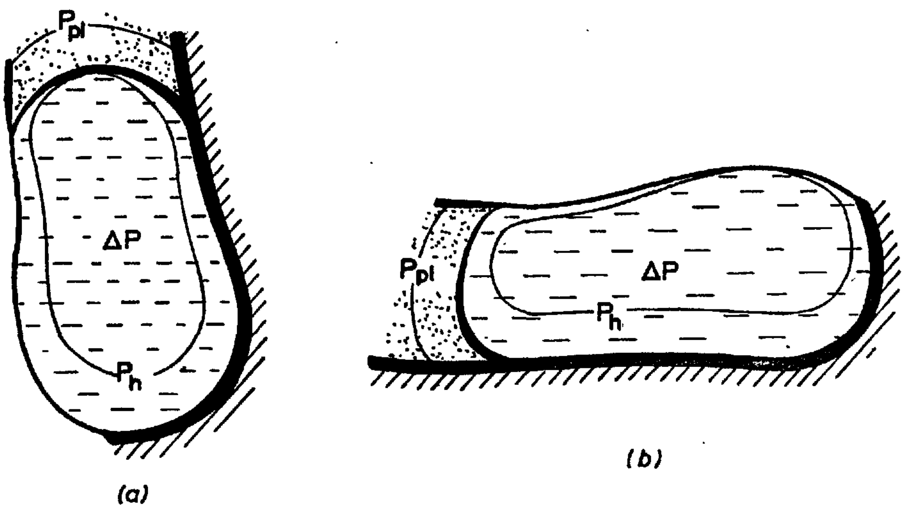

Fig. 5·21- Distribution of the hydrostatic and intrapleural pressures in the cross-section of the abdomen of a cat for two different postures: (a) standing and (b) lying on one side. P_h -hydrostatic pressure; P_{pl} - intrapleural pressure.

denote by P_h and the inertia forces created by the movements of the animal or of the abdominal walls but which we do not consider here; the magnitude of the hydrostatic pressure is represented by the scaled diagram shown all around the walls in the diagram of figure 5.20. The pressure anywhere inside the mass of the fluid is given by the sum of Δp and the local value of P_h and this pressure is in equilibrium, at the walls, with the tension T_A developed by the abdominal muscles. These muscles, whose fibres are organised into two sets orientated at approximately 100^o to each other (cf. figures 3.7 and 3.8) confer to the abdominal walls the characteristics of a contractile membrane which is able to resist an inflating transverse pressure thanks to the stress mechanism outlined for shell membranes in Appendix A.5. In figure 5.20 these membrane stresses are represented by the vector T_A in order to give an intuitive idea of how the membrane operates; this tension varies, in general, from point to point throughout the membrane because of changes in the value of not only the internal pressure but also of the geometry of the walls themselves. The foregoing considerations apply also entirely to the diaphragmatic wall of the abdomen, with the only difference that P_{atm} is replaced by $-P_{pl}$, the intrapleural pressure. We can now see the meaning of the compression bias Δp: the static pressure distribution in the abdominal 'fluid' is uniquely determined by the value of Δp and by the distribution of the hydrostatic pressure differences referred to the highest point in the abdomen; once the values of both these entities are known, the absolute values of the pressure anywhere in the abdomen are also known. No reference is made in the last statement to the pressures on the external surface of the walls; this is so because of the way in which the walls work: the wall adapts its shape and state of stress to balance the pressure differences across it and, thus, as long as the wall and its end supports are able to withstand the stresses, the same distribution of absolute values of pressure can be maintained inside the abdomen irrespective of the pressures outside the walls. This fact also shows why it is not possible to deduce the values of the abdominal pressures from measurements of the lung pressure, unless the component of the tension T_D along the normal to the surface is also known. The compression bias Δp may, in principle, have any value compatible with the physiology of the abdominal components. If Δp is positive, the viscerae will be compressed everywhere in the abdomen by an amount equal to $\Delta p + P_h$; if p is negative, the viscerae in those regions where P_h is smaller than Δp will be subjected to depression and will tend to stretch. In normal conditions the animal will vary the value of Δp according to the different requirements, such as those of postural nature, it may have to satisfy; these variations in Δp will of course have the same value everywhere in the abdomen.

Figure 5.21 shows the two dimensional cat from two different positions, namely standing and lying on its side, in order to illustrate the influence of posture on the distribution of the hydrostatic pressure.

The participation of the abdominal muscles in the respiratory process involves two complementary aspects, namely, the creation of an expiratory drive and the stabilisation of the caudal boundary of the rib cage, both of which are mediated by the raising of the abdominal bias compression Δp. According to their cranial insertion the abdominal muscles may be divided into two groups: one constituted by the transversus and the internus obliquus which are attached to the caudal edge of the rib cage and another, formed by the recti and the externus obliquus muscles, whose insertions are beyond the edge of the rib cage and on its external surface. The action of the first of these groups is to provide the boundary reactions which balance the forward thrust due to the contraction of the diaphragm. In order to analyse the pattern of activity of these muscles, we consider the reactions transmitted by the diaphragm to its sternocostal insertions. First of all, the abdominal viscerae push the diaphragm against the cage walls and thus the two structures are tangential to each other all around the length of their common boundary. The diaphragm fibres are stretched under the tension due to the abdominal pressure and to the recoil of the lung tissue; if we assume linear elastic properties for the lung tissue, then the loading its stretching produces on the diaphragm will increase in inspiration when the degree of stretching is maximum. It is also during inspiration that the pressure drop due to the air flow has the same direction as the resistive forces due to the lung recoil. In expiration, the air flow pressure opposes the tensions due to the lung recoil and the reactions on the rim of the rib cage are reduced. We are, therefore, led to the conclusion that the activity of the abdominal muscles which are antagonistic of the diaphragmatic pull must be maximum in inspiration and consist of a continuous 'tonic' pedestal on which the inspiratory peak is superimposed. The same pattern of activity must also be found in the other boundary muscles such as the retractor costae ultimae and the serratus posterior inferior.

The second group of the more powerful external abdominal muscles is mainly concerned with the structural stability of the trunk. The externus obliquus, however, is very effective in assisting the compression of the viscerae because of its insertion high on the shafts of the ribs; its contraction raises the abdominal pressure and simultaneously forces the rib cage border firmly down against the pressurised abdomen.

Although both these groups of muscles participate in the mechanism of abdominal compression, we must bear in mind the fact that only those in the first group are truly antagonistic of the diaphragm; the external muscles, on the other hand, are more concerned with direct abdominal compression and their activity will tend to show a predominant expiratory component. In the general case the combined pattern of abdominal activity is either of uniform intensity or shows a peak at the beginning of expiration (Gesell, 1940).

We have seen how the experiment of positive pressure breathing could be interpreted as evidence of the existence of a local control mechanism opposed to the collapse of the last intercostal spaces. We will therefore consider that the nervous control of the abdominal muscles consists of a rhythmic component originated in the respiratory centre plus two groups of local control systems subserved one by the lung mechanoreceptors and the other by the receptors in the caudal boundary of the rib cage; the first two components of this nervous control are, of course, also common to the diaphragm.

5.5 - MODELLING OF THE MECHANICAL BEHAVIOUR OF THE STRUCTURES IN THE RESPIRATORY APPARATUS

5.5.1 - Introduction

We end this chapter with an outline of the basic principles along which the component structures and the whole of the external respiratory apparatus could be modelled. Indeed, we invested a great deal of our time in trying to locate the tools which would make possible such a modelling and, as they are not familiar to the researcher in the field of mechanics of breathing it seems of interest to report them here in order to spare future workers in this field the need for a similar search.

The structures which constitute the external respiratory apparatus include the vertebral column which can be treated as a kinematically determined mechanism, the rib cage which behaves as a ribbed shell, the diaphragm and the abdominal walls which constitute tensile membranes and the abdominal viscerae whose behaviour can be likened to that of a fluid. The study of these structures must be performed within the framework of the Structural Analysis as developed for civil and aeronautical engineering applications (Flügge, 1960; Gennaro, 1965; Goldenveizer, 1961; Novozhilov, 1959; Rivello, 1969; Rubinstein, 1966; Schleyer, 1967; Sokolnikoff, 1956; Timoshenko and Woinowsky-Krieger, 1959; Trostel, 1967; Willems and Lucas Jr., 1968; Zienkiewicz and Chang, 1967).

The implementation of any of the models we are about to outline is a major undertaking and, unfortunately, that is beyond the scope of the present work of which, nevertheless, they constitute the natural sequence.

5.5.2 - Vertebral column

Although we have so far treated the vertebral column as a rigid beam, the complete model of the external respiratory **apparatus will include** that of the vertebral column. This structure is, perhaps, the easiest one to model in so far as the vertebrae have movements which can, with reasonable accuracy, be treated as geometrically and kinematically determined; in these circumstances, the deformations of the column, the length and tension of its muscles and, therefore, the nervous control of these muscles can be related to each other as long as the loads on the vertebrae are known. These loads are those transmitted to them by the rib cage, the abdominal walls and the viscerae directly attached to the column. The vertebral column can thus be modelled as a complex beam consisting of a collection of vertebrae interrelated by short and long muscles which are controlled locally and globally by reflex control loops.

5.5.3 - Rib cage

The function of the rib cage, as a structure, is fundamentally that of resisting compressive transmural forces as described in section 5.3.3. The only components in the rib cage which are able to resist compressive stresses are, however, the ribs and the costalcartilages, as the muscle fibres are only able to resist tensile forces. We can, therefore, assume that the intercostal muscles perform the double role of (1) guarantee-

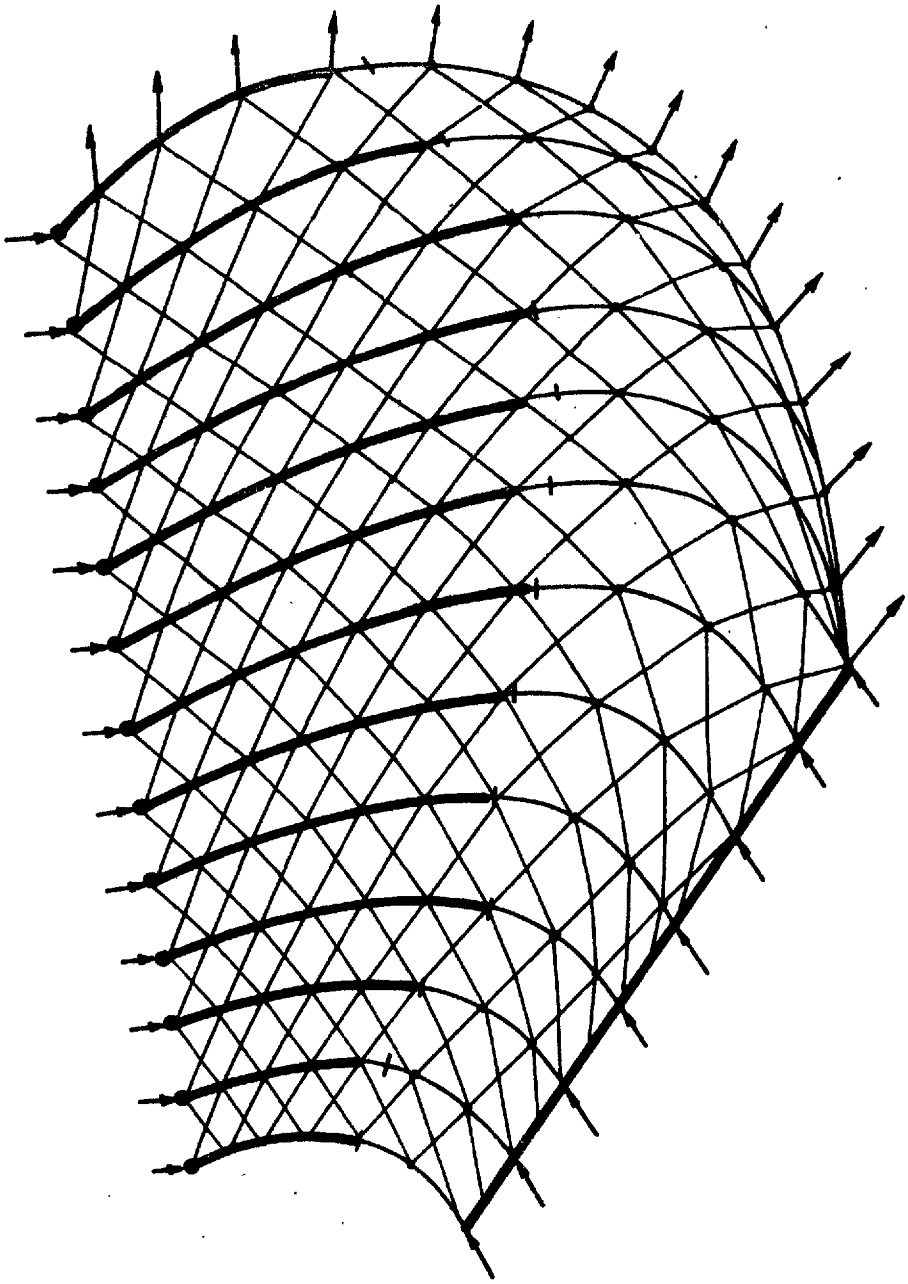

Fig. 5-22 Median plane projection of the idealization of the rib cage as should be used for the analysis of its stress and strain distribution under load.

ing that ribs and cartilages are constantly free from bending moments and (2) keeping the structural stability of the cage by taking care of the tensile stresses which develop between the ribs.

In these conditions, the rib cage must be modelled as a collection of thirteen beams connected between the vertebral column and the sternum and stayed by the intercostal and abdominal muscles. This system is subjected to the boundary conditions described above and to the transmural pressure and to the load transmitted to it by the front limbs. In order to model the rib cage structure, a number of similarly spaced nodes are chosen on the ribs and costalcartilages as shown in figure 5.22 which represents the projection of the rib cage structure on the median plane of the animal's body; the muscle fibres are connected between these nodes in adjacent ribs. These muscle fibres and the segments of the ribs and costalcartilages between the nodes are replaced by their 'finite element' representation (Gennaro, 1965; Martin, 1966; Willems and Lucas Jr., 1968) and the system of stresses and moments deduced by matricial methods once the boundary forces are known or postulated.

We have said before that, because of the ratio of the thickness of the rib cage walls to its transverse dimensions, this structure must respond to loads in a way which closely resembles that of an homogeneous shell of similar form and dimensions and of suitable material and thickness. This principle is actually taken advantage of in practical applications such as the study of complex braced domes of simple geometrical forms for which the solution of the shell problem is simpler than that of

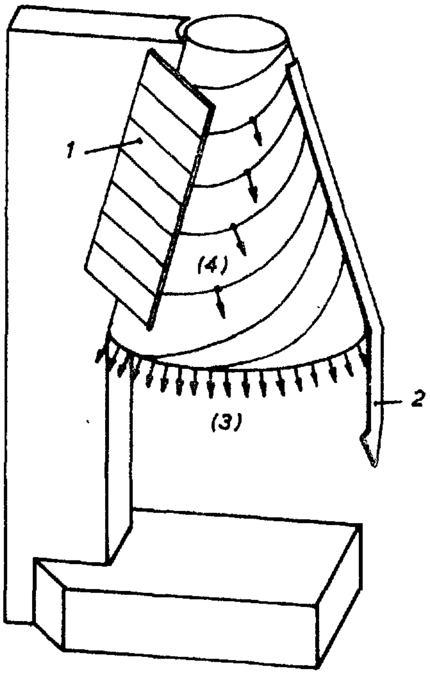

Fig. 5-23 Simplified shell representation of the rib cage.
1-serrati posterior muscles; 2-rectus abdominis muscles; 3-obliquus internus, transverse abdominal and retractor costae ultimae muscles; 4-obliquus abdominis externus muscle.

the real structure (Benjamin, 1963). In our case, this analogy allows us to use the simpler mathematical formulation of the stress-strain shell problem as expressed in Appendix A.5, and deduce from it conclusions of some interest. First of all, the state of stress at every point in the shell can be characterised by two principal directions at right angles to each other and along which the stress is purely tensile or purely compressive (Flügge, 1960). It is also possible for each of the principal directions to define a family of trajectories which are tangent at each point to the respective principal direction at that point. If we recall what we said above about the load carrying characteristics of the rib cage components we see that it is legitimate to assume that the rib-costalcartilage elements are most likely placed along trajectories of purely compressive principal directions as they occur for the dominant load regimes that the rib cage has to withstand. This is illustrated in figure 5.23 where the equivalent shell representation of the rib cage is 'cantilevered' to a stronger column representation of the vertebral column by the serrati posterior, the levatores and other dorsal muscles; this shell is loaded by the normal pressure - not shown - due to the lungs and to the muscles which connect the front limbs and by the tangential forces due to the four abdominal muscles. On the surface of the shell we have drawn the contours of a few principal compressive stress trajectories based on the shape of the ribs but which are very much in agreement with the way in which we believe this structure must respond to its load.

5.5.4 - Diaphragm and abdominal walls

The diaphragm and the abdominal walls have in common the characteristic that they can only withstand tensile stresses and they, therefore, tend to respond to loads in a membrane-like manner. The diaphragm differs from the abdominal walls in the fact that it is formed by two quite distinct types of components, the crurae and the radial fibres both inserted in the central tendon but with characteristics which demand an independent model for each of them. Abdominal walls can be thought of as a much more uniform membrane in which the fibres of the internus obliquus and the transverus muscles are orientated at almost 90° to each other in order to take up stresses over a wide range of directions; they form a cylinder of flexible musculo-aponeurotic tissue attached dorsally to the column through the lumbodorsalis fascia, to the coccyx and to the caudal edge of the rib cage. In both cases these membranes undergo large deformations which are of nonlinear nature and can only be studied by variational methods based on the principle of minimum deformation energy (Sokolnikoff, 1956; Trostel, 1967).

The boundary conditions for the diaphragm are the edge forces around the periphery of the pars sternalis and pars costalis, and the loads due to the lung recoil, the dynamic air pressure drop in the airways and the load due to the adjacent abdominal viscerae. The abdominal walls have as boundary the same caudal edge of the rib cage and as load the reaction of the abdominal viscerae.

The proprioceptive control of both the diaphragm and the muscles of the abdominal walls is, as reported in section 2.4.3, much simpler than that of the intercostal muscles.

The abdominal viscerae must be divided into two groups, one which includes all the viscerae with attachments to the abdominal boundaries and another, formed basically by the intestines, which is fluid-like in its movements.

5.5.5 - Integration of the individual models into an overall system

The creation of a system capable of replicating the mechanical behaviour of the respiratory apparatus implies the integration of the models described above through an adequate interfacing. In fact, the boundary conditions to which each of the individual models is subjected are determined by the response of the other structures it contacts and, therefore, a great deal of interplay takes place between the different structures. If the individual models are implemented in numerical form, this interplay implies iterative methods of solution in which the response of each model is fed back to the other models thus altering the boundary conditions to which the latter are subjected and causing a further readjustment of their responses, and so on until the system converges into a common stable solution. The interfacing between the various models is actually much more complex than just simple boundary conditions. Indeed, as the movements and the internal stresses which the muscle contractions cause are ultimately originated in the nervous system, we will need to have a previous knowledge of the 'strategies' which are adopted in the production of the patterns of muscular activity so as to predict the flow of activity in the external respiratory apparatus; these 'strategies' must therefore be incorporated in the overall model as a 'dictionary' of contraction patterns through which the responses to the loads are achieved. In general these strategies will not be all obvious and will have to be tentatively chosen and corrected until a stable and realistic overall behaviour is achieved.

The basic information which is necessary to put together in order to model the mechanical properties of the respiratory apparatus may, therefore, be summarised in the following items:

1- Individual models must be devised for each of the structures which form the respiratory system, each model characterising the respective structure with respect to (a) its relevant anatomical and structural features, (b) the kinematics of its controlled movements, (c) the relationship between the activity of its muscles and the tensions they develop, (d) the type of mechanical loads to be considered, (e) the influence of the boundary loads created by the other structures and (f) the mechanisms which relate loads and structure configuration and stresses.

2- Models for the mechanical interfaces between the five basic structural units; these models must characterise the way in which the loads, tensions and configuration of each unit are reflected on the neighbouring units.

3- Models for the sensory assemblages which specify how the receptor output is related to changes in configuration and how this output supplies all the information necessary for the control of that configuration.

4- Models for the control systems which integrate each of the individual structures. These models, based on the assumption that at the least formally the individual control systems have an independent existence, must be capable of guaranteeing the proper performance of the corresponding unit under the load and boundary conditions it encounters in practice.

5- A model of the basic functional organisation of the central processor in which are specified the interconnections between the individual control units, the priorities to be respected in their inter-connection and the logical framework on which the patterns of response must be based.

5.6 - SUMMARY AND DISCUSSION

The material collected in this chapter is intended to complement that in the previous chapter in the establishment of the groundwork on which the modelling of the mechanical properties of the external respiratory apparatus will be based. The main points to emerge from the analysis undertaken in this chapter are the following:

1- The rib cage is the most important structural component in the respiratory apparatus and the double need for it to be strong and to be able to move creates severe design problems which are met by the intercostal and overlying musculature under the supervision of a very efficient nervous control system.

2- The costovertebral articulations perform the treble role of connecting the rib cage to the vertebral column, of supplying the rotatory joints for the respiratory movements of the ribs and, finally, of participating in the control system which guarantees the structural stability of the rib cage. Once again, power and finely controlled movements have to coexist in the same structure, a result achieved by the same postural control system. The costovertebral joints may be thought of as 'floating' devices supported by the associated muscles and maintained in a centred position by the servocontrol of these muscles.

3- The remaining articulations of the rib cage are simpler than the costovertebral ones; they perform the double function of making possible, or restricting, the relative movements of the structures in the cage and of participating also in the overall postural control.

4- The bone and cartilage components of the cage are designed to work in compression, as struts, in order to take maximum advantage of their mechanical properties and to guarantee a comfortable margin of load safety. The job of assuring that all the bending moments are removed is performed basically by the intercostal muscles in conjunction with the abdominal muscles and those which overlie the cage surface.

5- The mechanism which allows the intercostal muscles to protect the costalcartilages from bending consists of servo-loops based on the stretchreceptors and muscle fibres in the two intercostal spaces adjacent to each cartilage. These control loops avoid excessive cartilage bending by opposing the stretching of the intrafusal muscle fibres; there is at least one control loop per rib and they are all integrated at a higher level in order to coordinate their response all over the cage.

6- For the costalcartilages which form the caudal edge of the cage, the intercostal muscles are replaced, on one of the sides, by the abdominal muscles which insert at the boundary and whose role is therefore to withstand the forward pull of the intercostales and to maintain taut the last intercostal spaces.

7- Thanks to the small degree of bending allowed to the costalcartilages, the Hamberger's model for the respiratory movements of the ribs is a good approximation to the process which actually takes place.

8- The mechanical loading regime of the rib cage may be defined as consisting of a normal load on its surface due to the lung recoil, airway pressure drop, etc., together with five boundary conditions: one at each of the cranial and caudal edges, one for each of the dorsal edges and a fifth one represented by the muscles which lie on the external surface. The cranial boundary consists of the first rib and cartilage and the frontal end of the sternum. The sternum receives the thrust from all the ribs which, together with the action of the rectus abdominis, keep it firmly held in position; the first rib and cartilage, on the other hand, are sufficiently short and strong to constitute a solid anchoring point for the ensemble of the intercostal muscles.

9- The caudal boundary receives the insertion of the diaphragm and the abdominal muscles and the impulsion from the abdominal viscerae. The diaphragm produces a pull in a cranial direction which, thanks to the action of the viscerae, is tangent to the surface of the cage at the rim and is in equilibrium with the pull due to abdominal and retractor costae ultimae muscles.

10- The dorsal boundary conditions consist of purely compressive reactions on the costovertebral joints, plus a component pulling the neck of the ribs along the direction of the levatores costarum muscles and, finally, a component forcing the ribs against the column and acting along the direction of the serratus posterior.

11- The fifth boundary of the rib cage, constituted by the overlying muscle layer, is concerned with the loads which tend to make the configuration of the cage depart from its normal shell-like shape.

12- The abdominal viscerae, and in particular the liver, play a crucial role in mediating the action of the abdominal muscles and are essential for the stabilisation of the caudal boundary and the overall configuration of the cage.

The contraction of the diaphragm is dominated by the 'scoop' action of the crurae which transmits to the vertebral column the bulk of the load associated with its movements.

The information gathered in this chapter serves the immediate purpose of interpreting the main features of the mechanics of the cat's breathing machine in a much greater detail than has so far been done; it should also provide the foundations on which the modelling of the mechanical performance of this machine may be based. This possibility is made clearer in section 5.5 where the modelling of the structures in the external respiratory apparatus is outlined.

Finally, we recall that in section 5.3.7 we referred to two situations of severe loading of the rib cage and prescribed the responses which, in our opinion, would compensate adequately for the load and return the cage to its normal shape. Independently of whether or not they are precisely correct, the solutions we suggested illustrate, in broad lines, the kind of decisions the nervous system of the animal has to make in order to respond conveniently to each loading situation. These 'decisions', which are taken on the merit of the data produced both by the respiratory centre and the receptors all over the respiratory machine, are manifestations of a veritable process-control set-up in which the input data is processed in order to implement certain policies of action. In other words, the area of the nervous system in charge of the respiratory apparatus should not be envisaged merely as a collection of ohmic interconnections, but as a proper computing system which is able to perform functional operations on the data it receives, to compare results in different levels of processing and to observe priorities and strategies of response. It is indeed of great importance to bear this fact in mind when trying to study the mechanical properties of the respiratory apparatus as the geometry of its movements is fundamentally determined by the associated 'computer'. This principle of a computer control of the machine kinematics is illustrated for a simple machine in Appendix A.4, where it is shown how the dynamic properties of this machine can be profoundly modified by the introduction of computer controlled servo-effectors.

CHAPTER 6.0

METHODS

6.1 - INTRODUCTION

This chapter describes the methods used in obtaining the data presented in the previous chapter; these methods deal with the preparation and handling of the animal, the use of a form of stereophotography to measure the coordinates of marker points on the moving structures, the measurement of the length of the ribs and rib-cartilages, the recording of the relative orientation of the intercostal muscle fibres, the measurement of the direction cosines of the axes of rotation of the costo-vertebral joints and, finally, the numerical processing of data provided by the photographic records.

The second of these methods, developed specially for this experiment, deserves a few comments: the technique of stereophotography we have used consists in obtaining, in a single cine-film, a sequence of stereo-image pairs of a set of small markers conveniently deployed over the chest and abdominal surfaces. The film frames are magnified and the coordinates of the stereo-pairs are read and processed with the help of the formulae (1) and (15) in Appendix A.1 to yield the x,y and z coordinates of the markers; these coordinates are then used to draw, using automatic plotters, the (x,y), (y,z) and (x,z) orthogonal projections of the whole set of markers, based on which the structures of the trunk will be reconstituted. The main reasons why the method just outlined was adopted were the need for a cine record of the movement, the fact that most of the relevant structures were not visible on the surface, the steep inclination of the dorsal and ventral surfaces of the body with respect to its lateral surface, the lack of easy access to conventional equipment for photogrammetry and, finally, the fact that trial runs had shown that it was possible to recover the position of a point in space with a precision better than that given by a sphere of 0.5 mm diameter centred at its exact position. There are many sources of error in the production of a photographic record by such method, the most important being the aberrations in the optics of the camera, the imperfections and lack of flatness on the mirror surfaces, the misalignment of the mirrors with respect to each other and to their base, the misalignment of the camera with respect to the mirrors, the errors in the measurement of the distances L, H_1 and H_2 (cf. Appendix A.1) and, finally, the definition of the film.

In order to reduce these sources of error the mirror system was machined carefully and the distance of the camera to the subject (L = 2845 mm) chosen so as to minimise the angle subtended by photographic field (less than 4^o) and the influence of the errors introduced in the measurement of L, H_1 and H_2. The recovery of the information contained in the cine-photographs introduces further sources of error represented mainly by the deficiencies in the optics of the magnifying system, the relative size of the markers and the limitations of the digitising machine with which the coordinates of the markers are read. Furthermore, the size of the markers implies, of course, that they produce large images on which it is difficult to locate a reference point; it is this feature that represents the greatest contribution to the size of the sphere of imprecision given above. This contribution to the overall error can be reduced by the use of the following precautions: 1. A careful study of the position and orientation of all the markers, both during the experiment and on the photographs, simplifies greatly the task of locating the centre of the base of the marker, which is its reference point; 2. the slowness of the respiratory movements creates a great deal of redundancy on successive frames which may be used collectively to define the position of the marker; 3. quite a number of markers are visible on both mirrors and, thus, their position can be worked out in two ways and averaged. Incidentally, these double images provide a way of checking the precision of the optical system.

Although some of the error sources which were mentioned above can be quantified, the general problem of the overall precision of the method is too complex to be worked out. Instead, we applied it to known solids, mainly cylinders with cross-sections of several shapes and sizes, and were able to reconstitute the positions of the markers well within the sphere of imprecision given above.

6.2 - EXPERIMENTAL METHODS

6.2.1 - Introduction

Under the heading 'experimental methods' we have grouped those methods which have been used in connection with the measurements performed both on live animals or on their dead remains. The most important of these methods is the one described in section 6.2.2 and which was developed at the Institute of Neurology, Queen Square, London, in collaboration with Drs. T.A. Sears and D.T. Stagg. This method involves extensive surgical preparation of the animal in order to expose the main structures in the external respiratory apparatus and represents a bold approach to the problem of recording the movements of those structures and for it I am indebted to Dr. T.A. Sears. The methods of the last two sections represent a modest incursion in the field of quantitative anatomy based on direct measurements using mechanical instruments.

6.2.2 - Animal preparation

The experiments were performed on cats weighing 1.8 to 4.0 kg, anaesthetized with sodium pentobarbitone, at a concentration of 30 mg per kg of body weight, and injected regularly in order to maintain a reasonably constant state of light anaesthesia. The animals were tracheostomized for connection to a **spirometer**. After shaving the fur on the left side of the trunk, the animal's skin is removed over an area delimited approximately as follows:

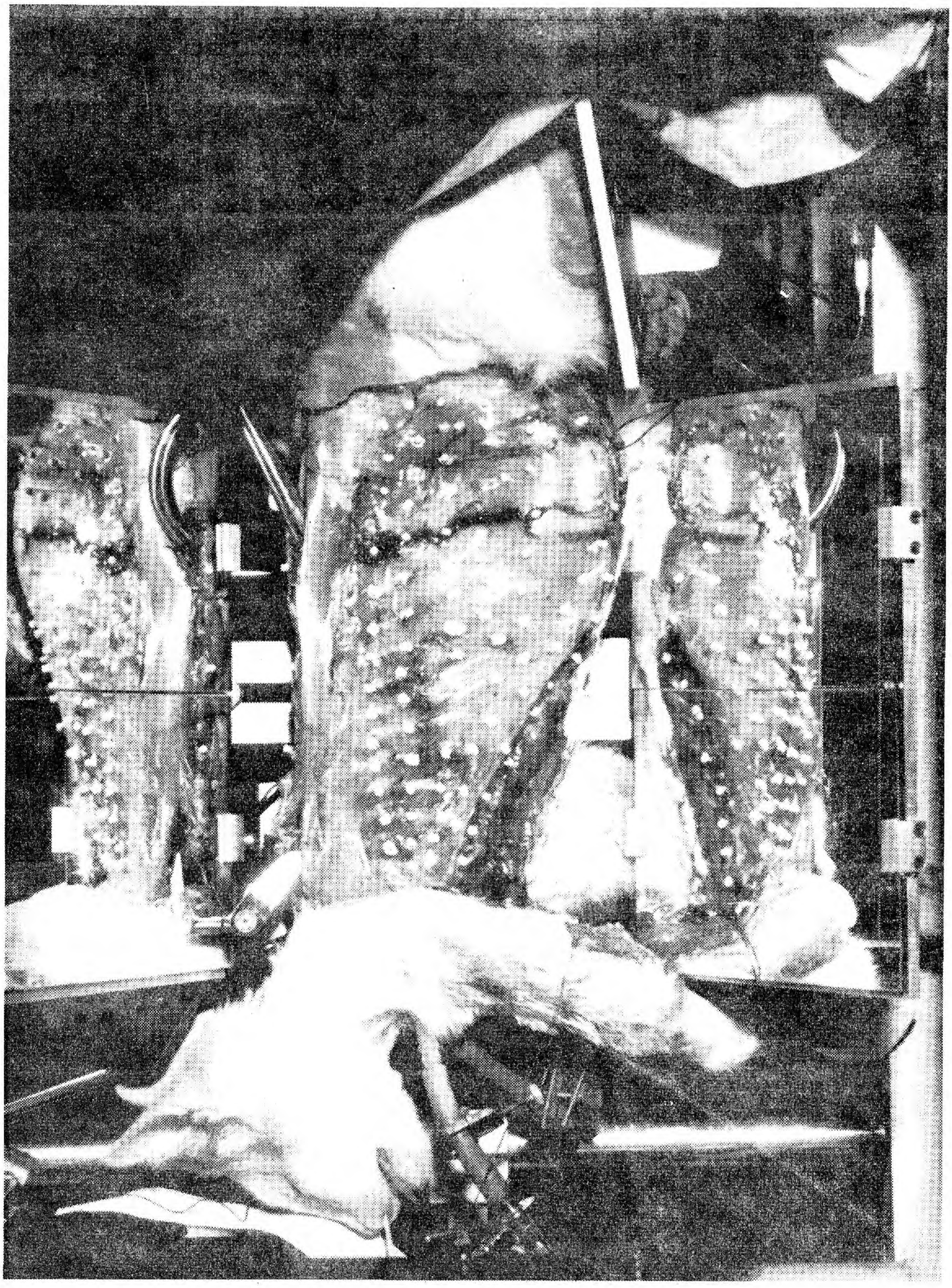

Fig. 6·1 Photograph of the experimental set-up with the animal in position.

(1) along the first rib from the manubrium to the spine of the last cervical vertebra; (2) along the spine-line of the vertebral column from the last cervical vertebra to the sixth lumbar vertebra; (3) along a transversal incision on the side of the abdomen from L6 to a little beyond the umbilical line on the ventral surface of the abdomen; (4) that incision is continued back again to the starting point over the manubrium. Next, the superficial muscles which provide the suspension for the front limb of that side are removed in order to expose the intercostales, the rectus and oblique abdominal muscles and all the muscles of the back from the serrati posterior downwards.

Once this dissection has been performed, the animal is placed prone in an experimental frame (cf. figure 6.2) and immobilized by two clamps which hold the vertebral column firmly; the legs are supported by a rectangular base and the head by a piece of thread from a bar mounted on the frame (cf. figure 6.1). The vertebral column of the animal is placed in an approximately horizontal position and the sagittal plane of the body is made parallel to the base of the system of mirrors (cf. Appendix A.1) used for the photographic recording. Care is taken to ensure that the vertebral column is not bent laterally, that the posture of the animal is correct and that the images on the mirrors show complete views of the top and bottom sides of the animal's body.

The left front limb is then severed from the trunk and pulled aside in order to allow an unhindered view of the cranial end of the rib cage. The ribs and the abdominal surface are outlined with reflective markers applied with surgical glue (cf. section 6.2.3). The tracheostomy cannula is connected to a spirometre in a closed breathing circuit **supplied from a balloon**

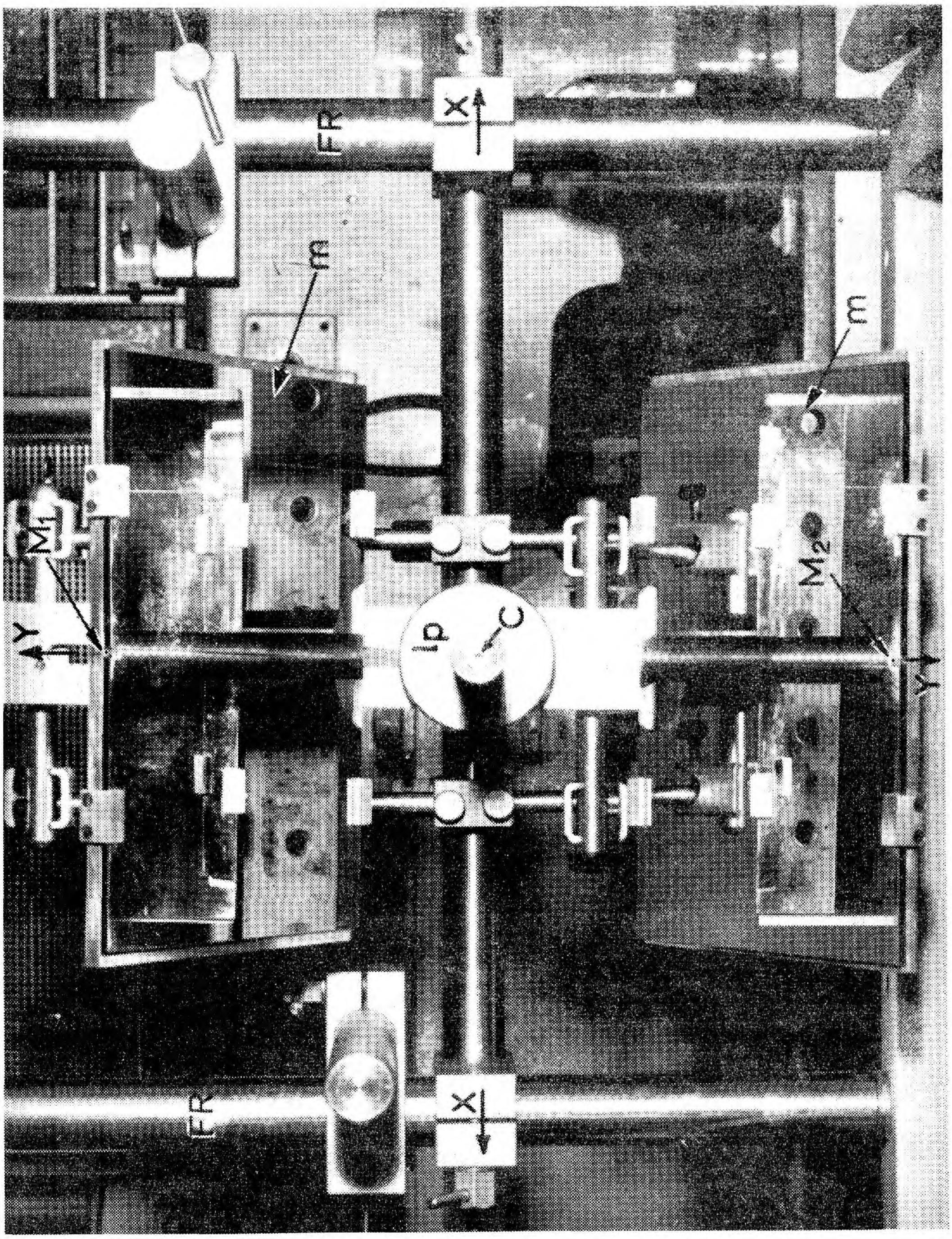

Fig. 6·2 Mirror system used in the experiment

lp – removable "light pencil" for alignment of the camera ; m – plane mirrors ; C – centre of the mirror system ; M1 and M2 – circular markers which define the vertical axis of the mirror system ; FR – frame containing a mixture of 5% CO_2 and 95% O_2 so as to promote a deeper level of breathing. The oesophageal balloon is located in position and connecet to a Greer micromanometer, Mercury Electronics type MM/M3 and the tidal volume is obtained from the calibrated output of a potentiometer driven by the spirometer; both the tidal volume and the oesophageal pressure are tape recorded.

Figure 6.1 shows the animal in position and ready for the experiment.

A first film sequence, lasting for over half a minute and corresponding to spontaneous breathing conditions under anaesthesia, is made while, simultaneously, the tidal volume and the oesophageal pressure are recorded.

The second phase of the experiment is initiated with the intravenous application of 2.3 cc of gallamine triethiodide (Flaxedil) at a concentration of 8 mg/cc. The gradual muscular paralysis caused by the Flaxedil is recorded in film as well as the two other variables, tidal volume and pressure. Next, the animal is artificially ventilated to a tidal volume of the same magnitude as in spontaneous respiration and a similar length of film is made together with the record of pressure and volume.

In a third phase the animal still under the action of the Flaxedil and artificially ventilated, is X-rayed both from the side and from above along directions which make 90° with each other; for each of these positions, X-ray exposures are made at the instants of peak inflation and deflation.

Finally, a fourth phase takes place after the animal has completely recovered from the Flaxedil, as shown by the volume and the pressure recordings. In this phase, the X-ray procedure described above is repeated again.

6.2.3 - Photographic procedure

The photographic recording was made with an Arriflex 16-mm cine-camera, equipped with a zoom lens fitting Som Berthiot 1:3,8, operating at a speed of 16 frames per second and adjusted for an exposure n = 4.5 and a focal distance of 60 mm; the camera was located at 2845 mm from the subject datum plane and the mirror system shown in figure 6.2, and described in Appendix A.1, was used in order to provide the three views which are necessary for the recording of depth information.

An Ektachrome EF 7242 Kodak colour film was used and the subject was illuminated with a 500 Watt spotlight placed immediately underneath the camera and aligned with its optical axis.

The ribs and costal cartilages and the surface of the abdomen are outlined with reflective markers. The markers are made of a small length of PVC sleeving whose lateral surface is covered by a band of red 'Scotchlite' reflecting tape(*) and one of the ends by a disc of the same material; the overall dimensions of the markers are a diameter of 2.5 mm and a length also of 2.5 mm. The markers are stuck to the body with surgical glue(**). The use of highly reflective Scotchlite tape in conjunction with spot-

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(*) Minnesota Mining and Manufacturing Co. Ltd., Code No. 3272

(**) Johnson and Johnson DUO surgical adhesive.

light illumination is necessary so as to get a good contrast against the shining wet muscle surface,a need which also accounts for the colour film and the relatively large size of the markers. Another reason for the large size is the steep gradient on the subject's cross-section profile which would make, on a large proportion of the body, a smaller marker invisible either on the mirror images or on the frontal view.

The camera is first aligned in a direction perpendicular to the base of the mirrors with the help of a 'light pencil', shown in figure 6.2 and also described in Appendix A.1; once the camera is aligned, it must be maintained rigorously in the same position throughout the experiment. The first film sequence records the mirror system and the 'light pencil' in order to establish the centre of the film; two circular marks (M_1 and M_2) located on the vertical through the centre (C) of the mirror system, on which the centre of the 'light pencil' also lies, and placed one on the external edge of each mirror, provide the common ordinate axis (YY) for all the film frames. After it has been photographed, the 'pencil' is removed and a calibration cylinder is placed in the frame and filmed for checking purposes. The photographic set-up is then ready for the experiment which proceeds as described in section 6.2.2.

6.2.4 - Measurement of the length of the ribs and the direction of the intercostal muscle fibres

The measurement of the length of the ribs and rib-cartilages and the determination of the direction of the intercostal muscle fibres are made on tracings of the intercostal spaces. These tracings are produced by bringing into very close contact with the cage, from which the superficial muscles have been removed, narrow strips of thin transparent plastic paper which cover three or four intercostal spaces depending on the curvature of the region to be recorded. After the strip is fixed in place, the desired elements are traced on it; this process is then repeated until all the cage is covered. The direction of the muscle fibres is first recorded for the external intercostal muscles and, after the removal of these muscles, for the internal intercostal; this method could be used to record the fibre direction in the other muscles although, for most of them, there would not be a reference frame comparable to the one provided by the rib cage. The precision afforded by these methods is poor, as already explained in section 4.3.2; its improvement, however, would have implied complex and expensive tools and the effort was not considered justified.

6.2.5 - Measurement of the angles of rotation of the costovertebral joints

The vertebral column, from the first cervical to the fourth lumbar vertebrae, is carefully separated from the ribs and the rest of the cleaned skeleton and firmly mounted, on its side, on a steel rectangular base. The surface of this base constitutes the XOY plane of reference; two axes, one parallel to each side, are drawn on it at right angles and crossing at its centre. The vertebral column is positioned in the direction of the longest or X-axis, with its mid point at the origin and the two sides of the 'S' placed symmetrically to the same axis. The longitudinal axis of the column is made parallel to the surface of the base and the two transverse processes on each vertebra are placed on a normal to that surface. Once the column is set in position, it is carefully drawn and for each vertebra a set of intrinsic X- and Y-axes is defined: the X-axis is parallel to the longitudinal axis of symmetry of vertebra and contains the projection of the centre of its transverse processes; the Y-axis is perpendicular to X-axis at the same point. The angle made by each of these intrinsic set of axes with the main X- and Y-axes is measured for all of them.

Thin steel rods, about 0.8 mm in diameter and 35 mm long, are located so as to pass, as closely as possible, through the centres of the two sets of joints on the free side of the vertebrae which correspond to the head and to the tubercle of the rib; for the last three ribs the rods are approximately aligned with the transverse process of the respective vertebra. The rods are glued in place and allowed time to set.

The direction cosines which define the rotation axes of the costo-vertebral joints are those which correspond to the angles the steel rods make with a frame of reference constituted by the X- and Y-axes drawn on the surface of the base and a Z-axis normal to them at the origin.

The measurement of these angles is processed as follows: the rectangular plate where the column is mounted is placed in a universal vice with the X-axis in a vertical position and carefully aligned with the centre of horizontal rotation of the vice; in this position, the Y-axis on the plate and the Z-axis, normal to it, are both horizontal and parallel to the surface table where the vice rests. To measure the angles (cf. figure 4.21) of each costovertebral joint, the table of the vice is rotated, first around the vertical axis and then around its horizontal axis, until the rod is aligned with a reference direction; the angles φ and ψ are then given directly on the two graduate scales of the universal vice.

The reference direction used for the measurements is created by placing before-hand the universal vice in such a position that the plane defined by its two rotation axes is parallel to that of one of the side faces of the surface table where the vice rests; the plane of this side face is taken as the reference plane and the reference direction is then materialised with a steel rod, similar to those used for the articulations, which is mounted on a surface block in a direction perpendicular to the reference plane. The positioning of this steel rod is achieved with a dial gauge and, once it is set, the rod can be moved parallel to itself thanks to two prongs on the base of the surface block.

Once the angles φ and ψ are measured with respect to the overall system of reference, their values are converted to the intrinsic system of axes by the following formulae:

$$\begin{aligned} \tan\varphi_i &= \tan\varphi \,.\, \cos\theta - \tan\psi \,.\, \sin\theta \\ \tan\psi_i &= -\tan\varphi \,.\, \sin\theta - \tan\psi \,.\, \cos\theta \end{aligned} \qquad (6.1)$$

where φ_i and ψ_i stand for the corresponding intrinsic angle values. Formulae (6.1) represent a simple rotation, by θ degrees in the anti-clockwise direction, of the X- and Y-axes on the XOY plane.

The importance of the φ_i and ψ_i angles resides in the fact that they allow the computation of the direction cosines of the axes of rotation of the costo-vertebral joints expressed in the intrinsic referential of each vertebra. Once these direction cosines are known, their value for any configuration of the vertebral column can be computed as long as the position of each vertebra is fully known with respect to a chosen overall system of reference; from these values of the direction cosines, the complete kinematics of the simple axial rotation of the ribs can be deduced.

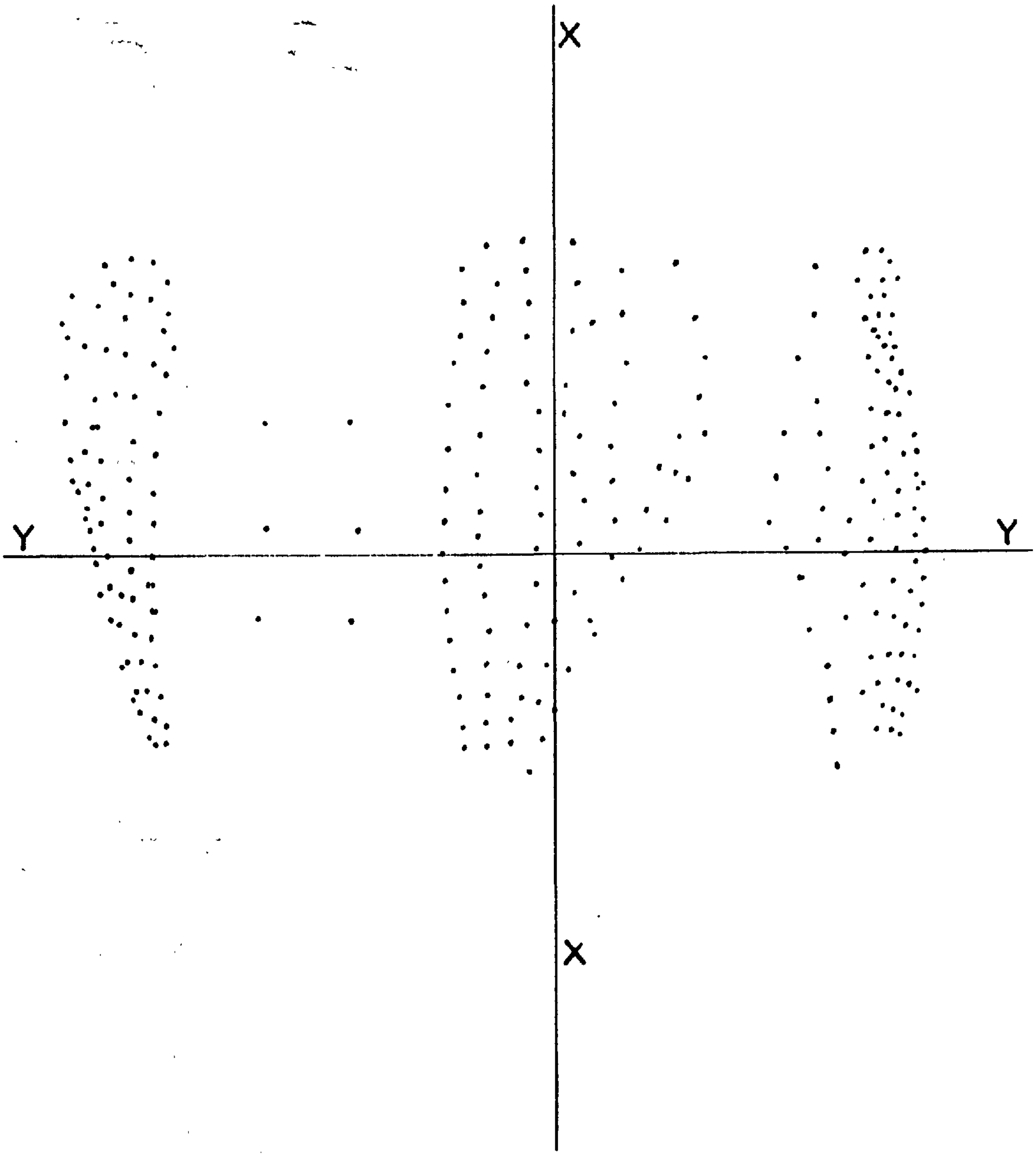

Fig. 6·3 Tracing of the markers from the film frame of Fig. 6·1

6.3 - NUMERICAL METHODS

6.3.1 - Introduction

The methods described below are those which were used to process the cine-film of the respiratory movements of the cat in order to recover the three-dimensional information necessary for the quantitative characterization of these movements. These methods are essentially in the nature of computer graphics and were implemented on the IBM 1800 computer in the Engineering in Medicine Laboratory of Imperial College in conjunction with a Bryans type 26000 A3 XY analog plotter and on the University of London CDC 6600 system in conjunction with a Calcomp incremental plotter.

6.3.2 - Processing of the film frames

In each of the relevant sections of the filmed records obtained by the methods described in sections 6.2.2 and 6.2.3, a set of frames is selected for processing. Typically, this set is made up of every third frame over a period of four or five respiratory cycles. The picture in each of the chosen film frames is magnified to twice the real size dimensions and the markers on it, including those used to locate the ordinate axis and the origin, are transferred to a sheet of plastic tracing paper. The result is illustrated in figure 6.3 obtained by tracing the markers of figure 6.1. Next, the tracings of all the chosen frames are taken to a XY digitizer(*) where the coordinates of the YY-axis, the origin and the marker are read and punched on cards. The cards are then processed on a digital computer which reduces the coordinates read in the digitizer to a system of axes centred at the origin of the tracing of each frame and with the YY-axis as its ordinate axis. After that, the computer programme implements the formulae given in Appendix A-1 by which the three x, y and z orthogonal coordinates of each of the markers are synthetized. Using these coordinates, the computer controls an automatic plotter which produces three orthogonal (x,y), (x,z) and (y,z) projections of the whole set of markers. These projections are illustrated, for the set of markers on the rib cage, by figures 6.4, 6.5 and 6.6. In these projections, the median plane of the animal coincides with the XOY reference plane, a result which is achieved by 'rotating the animal's body' by means of a computer programm. It is, in fact, very difficult to place the animal in the experimental frame in such a way that the sagittal plane of the body coincides exactly with the datum plane at the base of the mirror frame; as a general rule, these two planes are inclined with respect to each other and, also, are not coincidental at the point where the optical axis of the camera intercepts them. The set of markers has, therefore, to be rotated in the computer until the coincidence of the two planes mentioned above is achieved; in this operation we are guided by the knowledge of the position, with respect to the sagittal plane of the animal, of the markers

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(*) Mark I Pencil Follower, D-mac Ltd., London.

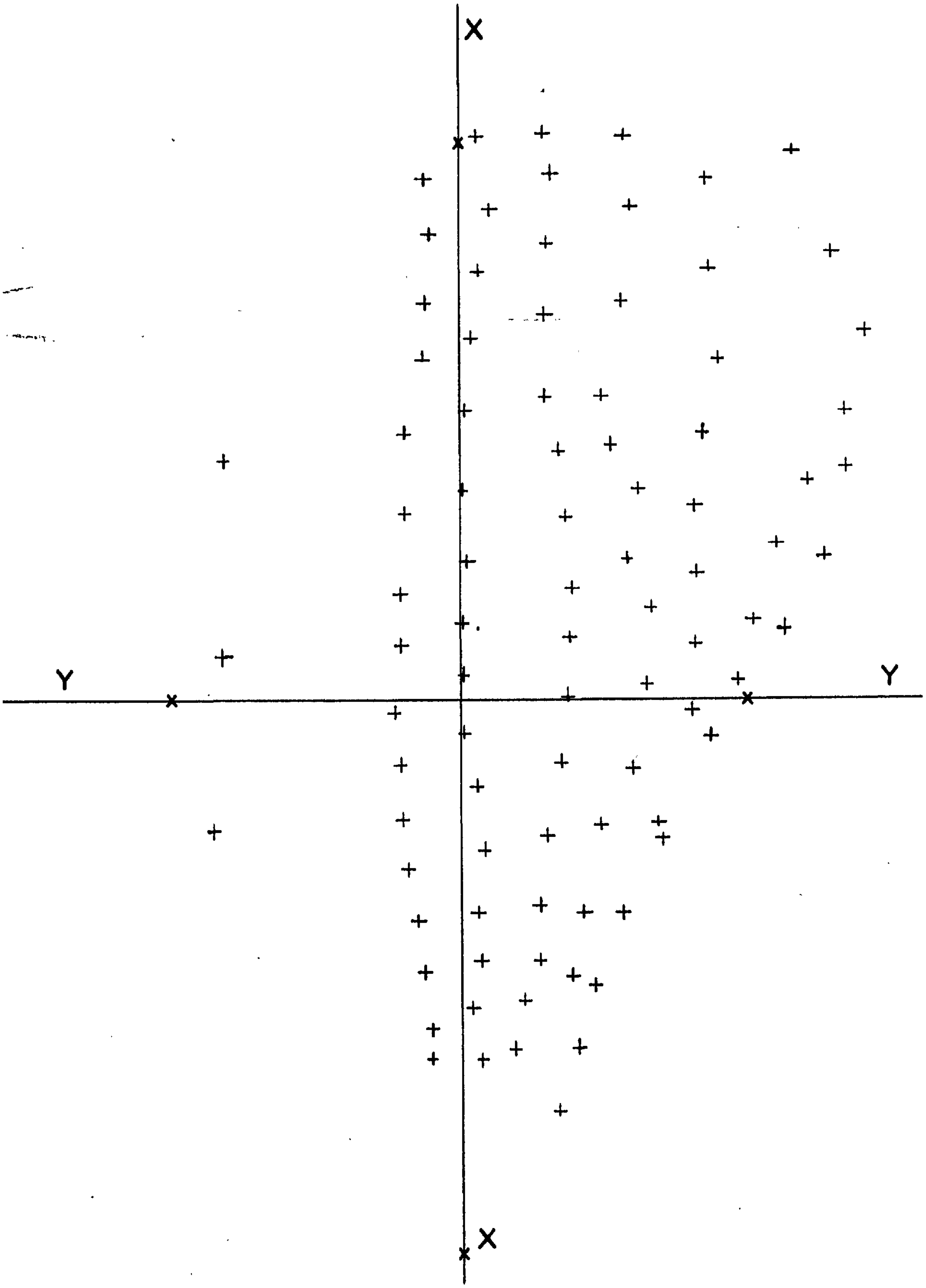

Fig. 6·4 (X,Y) projection of the set of markers on the thorax.

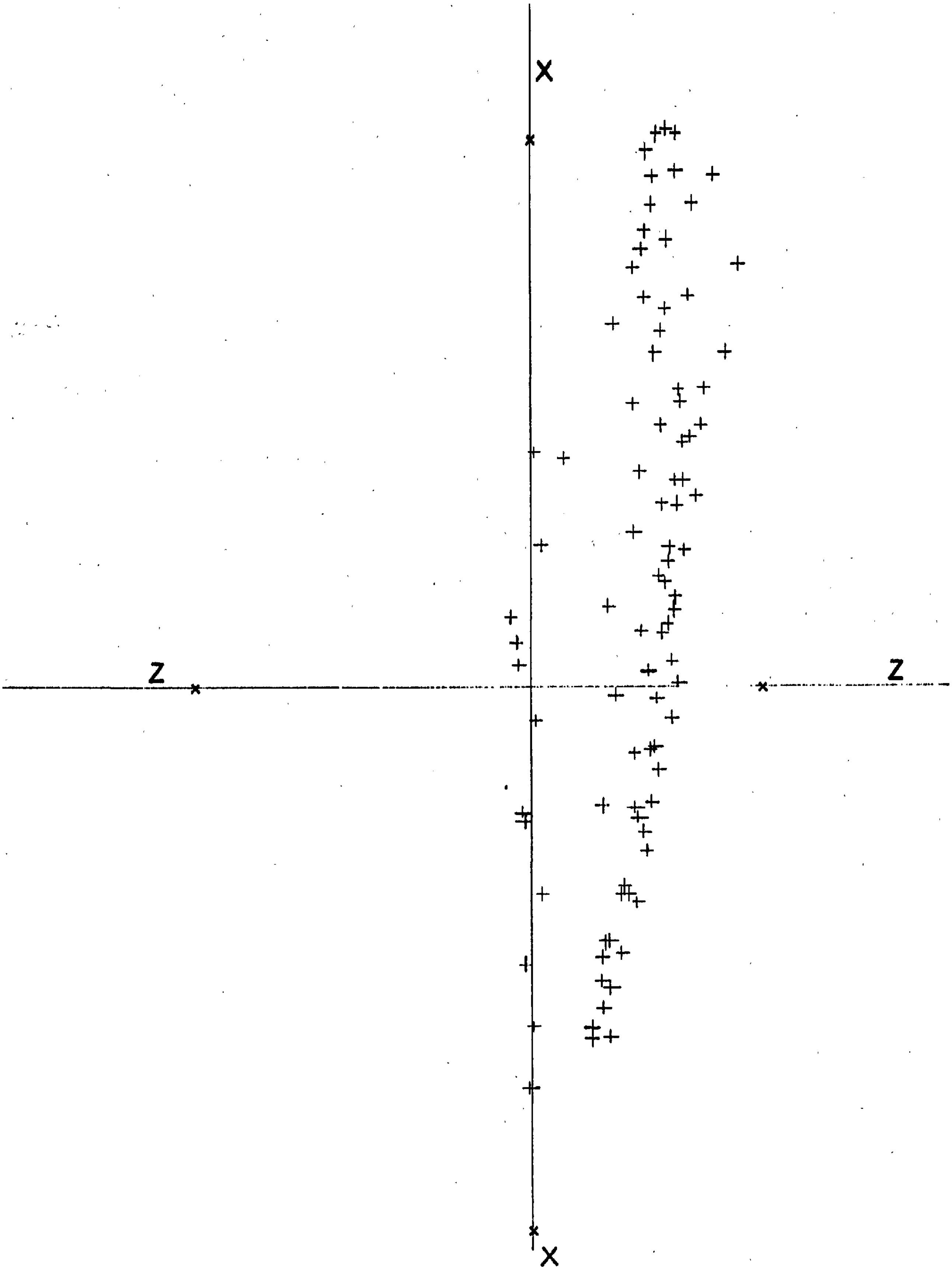

Fig. 6·5 (X,Z) projection of the set of markers on the thorax.

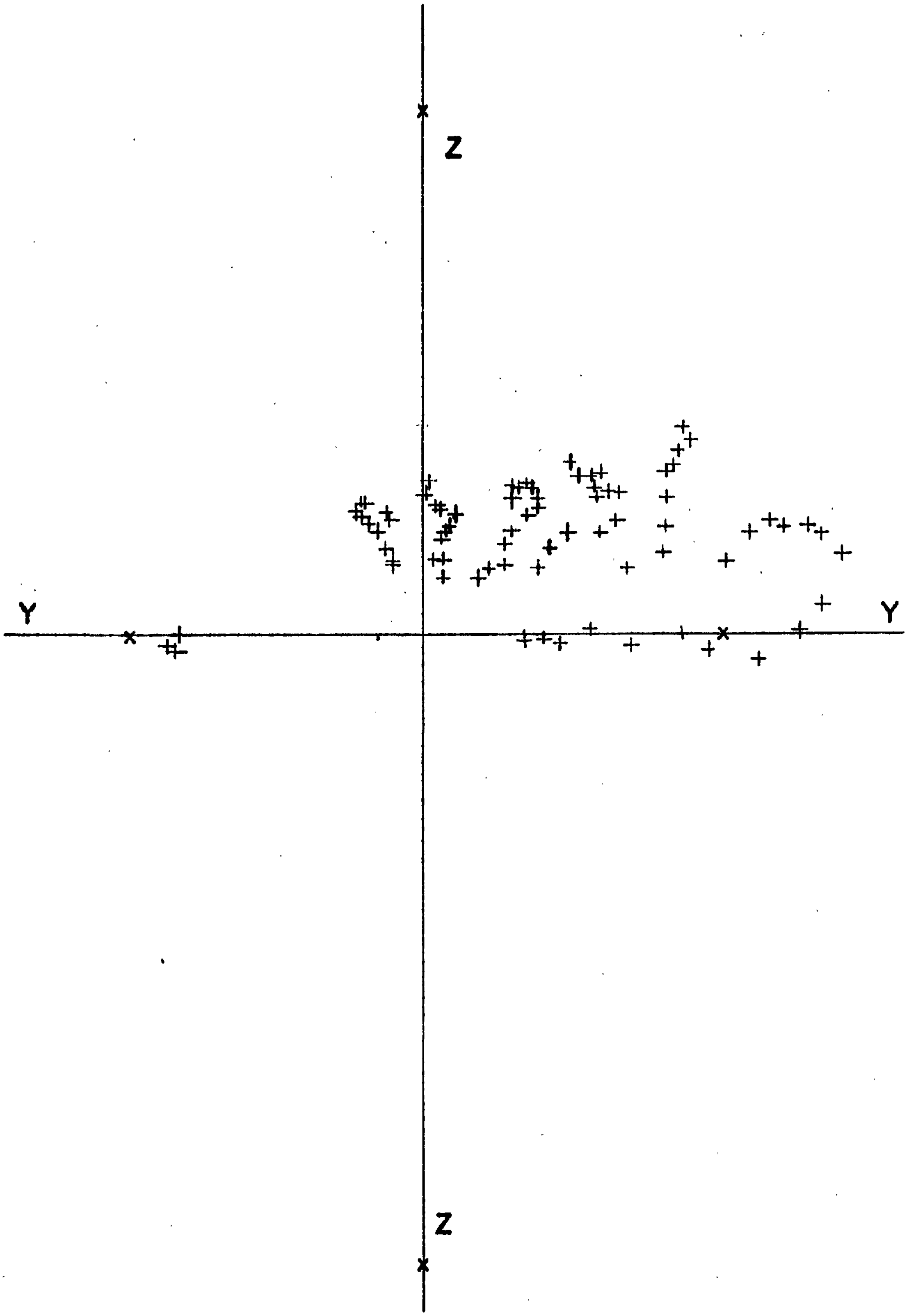

Fig. 6·6 (Y, Z) projection of the set of markers on the thorax.

on the sternum and on the spines of the vertebrae. This correction is necessary because we have to use these projections to locate the structures of the trunk with respect to the markers and it would be almost impossible to do it with the original projections.

6.3.3 - Reconstitution of the structures of the trunk from the three-dimensional set of markers

The corrected orthogonal (x,y), (x,z) and (y,z) projections of the total set of markers represented in figures 6.4 to 6.6 constitute the framework on which the ribs, the vertebral column, the sternum and the level contours on the surfaces of the trunk can be drawn.

The three projections are either drawn directly or mounted with their coordinate axes aligned so that the three projections of each marker are in correspondence. This system of projections is placed on a drawing board and the structures referred to above are drawn by careful interpolation of distances to the markers measured simultaneously on the three projections. In this operation, use is made of the knowledge of the position of the markers with respect to the ribs and the other structures, knowledge which is obtained from measurements on the animal, on its dead carcass and on X-ray photographs. Although the ribs constitute to some extent a best fit for the corresponding set of markers, interpretation errors may be introduced and, therefore, a further check is introduced by computing the length of the ribs and cartilages as they have been drawn and compare these lengths with their real values; corrections are then introduced by retouching the shape of these structural elements according to the differences in value which were found. The type of result which we are able to obtain by this procedure is illustrated in figure 6.7 in which the (x,y) and (y,z) projections of the reconstituted or 'fitted' structures are represented on a 1/1-scale. Finally, once the structures in the film frame are drawn, a number of points - the same for all the frames - is implanted on their three projections in order to make it possible to digitize them in terms of the orthogonal coordinates of those points. These coordinates constitute then the final data with which the computation of the kinematic results, volumes, areas, etc., is performed.

This entire procedure - which is extremely tedius and time consuming - has, of course, to be repeated for each single film frame which is analysed.

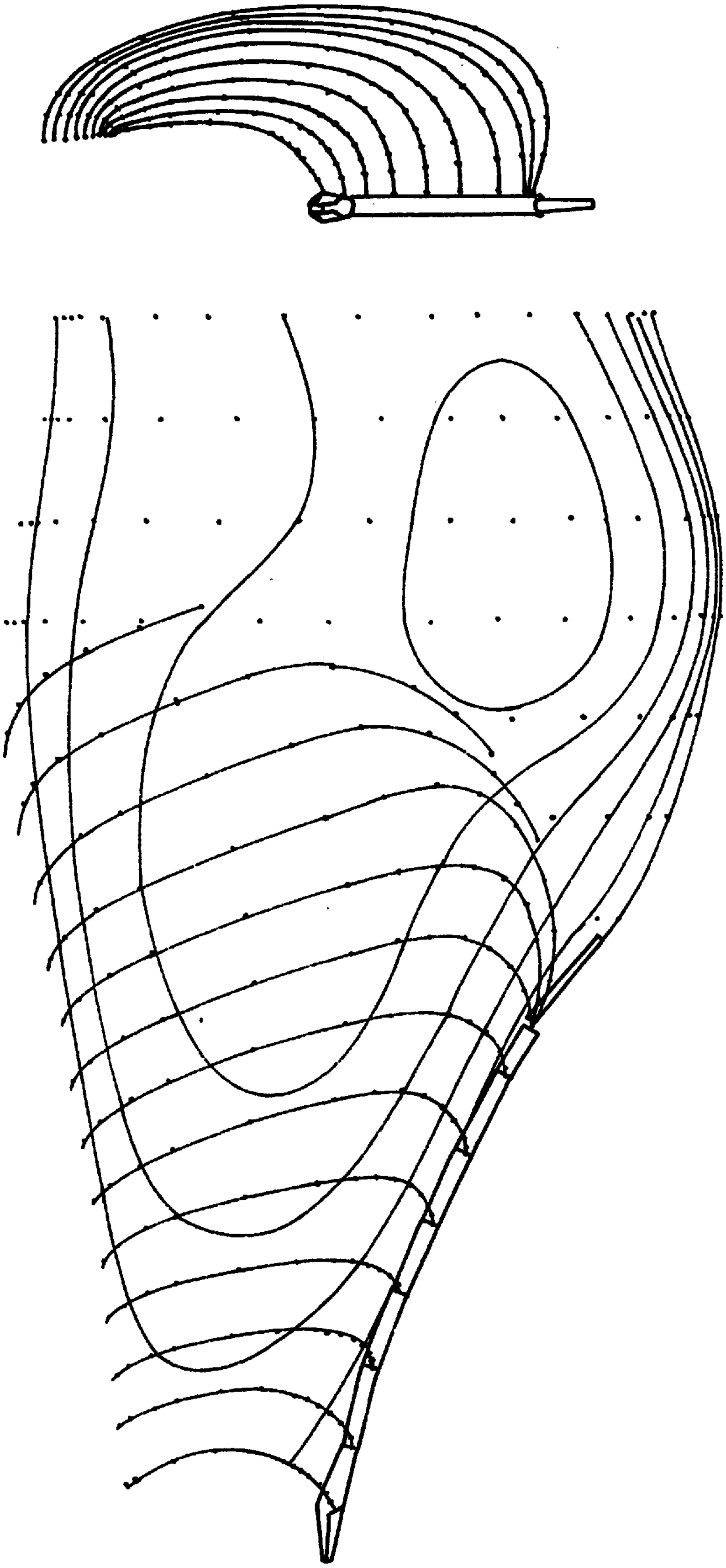

Fig. 6·7

Side and partial front views of the 'fitted' rib cage and abdominal wall showing a set of implanted points for their digitization. The front view only contains the first ten ribs; the other ribs and the cross-sections of the abdomen have to be drawn separately because, in this view, they would fall on top of the represented ribs and so they have been omitted here.

6.4 - SUMMARY AND DISCUSSION

In this chapter we have described briefly the methods which we have used to gather and process the experimental data presented in the previous chapters. These methods include direct measurements on the carcass or skeleton of the animal, indirect measurements of marker coordinates by stereophotography and numerical methods by which these data are handled. The precision which can be achieved in the direct measurement methods is quite poor when compared with that practised in machine engineering. The improvement of this situation, however, would have demanded the construction or acquisition of sophisticated measuring equipment which would constitute a large scale investment only justified for a long term utilization, whereas our aim is simply to provide preliminary results on data which we were unable to obtain anywhere else and, particularly, to show that there is a need for such data. The second type of methods is slightly more accurate and is perfectly adequate for the analysis of the gross changes of configuration which the structures of the external respiratory apparatus undergo in respiration; they are, however, inadequate (cf. section 4.3.4) for assessing detail points, such as the changes in muscle fibre length, for which other methods must be used.

The accuracy of the photographic data can be improved greatly and the procedure for its processing simplified appreciably by the use of more conventional techniques of stereophotogrammetry (Beard, 1967; Beard and Burke, 1967; Miskin, 1956). Another technique of great precision which may prove most valuable in this field is the use of Moire' interference patterns (Takasaki,

1970) to draw contour lines on the experimental subject. It should, however, be pointed out that the data needed for the kinematic characterisation of the respiratory apparatus interests both the position of the surfaces of the body and the structures hidden behind them and not represented on the photographic records by either of these methods; the localisation of these structures with respect to the photographic data would have to be done by a method similar to the one we have used and would therefore bring down the overall accuracy to identical level.

The rhythm of the respiratory process in quiet respiration is sufficiently slow to allow the use of filming speeds of the order of 2 to 4 frames per second without serious loss of kinematic information. These speeds would then make possible the use of other cameras, such as the 35 mm time-lapse camera, with a consequent improvement of the quality of photographic record. Another possibility is the use of purely still cameras in conjunction with a 16 mm cinefilm for control, in the way we have done with the X-ray photographs.

CHAPTER 7.0

SUMMARY AND DISCUSSION OF THE WORK

The present work has been organised into two chapters which review the material available in two fields of Physiology with a direct bearing on the study of the mechanical phenomenon of breathing, one chapter in which the results obtained in laboratory experiments by means of X-ray photography and stereo cinephotography are presented, one chapter in which these results are analysed and interpreted in order to define the foundations for the modelling of the mechanical behaviour of the structures which constitute the external respiratory apparatus and, finally, a chapter which describes the essential features of the methods used for the gathering and processing of the experimental data. We are now going to review and discuss the material of each of these five chapters.

In chapter 2. the pressure-volume approach to the mechanics of respiration is analysed in some length in order to illustrate its scope and its limitations. The pressure-volume analysis represents a first attempt to quantify the mechanical respiratory act and has obvious clinical implications by supplying easily understood indices of respiratory performance. This approach together with the study of the fluid and tissue dynamics of the lungs and respiratory airways, has traditionally constituted the discipline of respiratory mechanics. The study of the properties and dynamical behaviour of those body structures which, although not in direct contact with the air, nevertheless supply the motive power for the respiratory movements has been so far almost completely neglected. This omission in the study of the mechanics of breathing has been accepted on the assumption that the respiratory movements of those structures are well conditioned and, therefore, that they are simply related to the breathing patterns described in the pressure-volume diagram. There has, however, recently been a tendency towards paying greater attention to the kinematics of the respiratory movements (Agostoni et al., 1965; Agostoni and Mognoni, 1966; Jordanaglou, 1970; Konno and Mead, 1967) although the study of the movements of the external respiratory apparatus has still not yet been looked upon as constituting a field of research in its own right. In chapter 2. we also introduce a brief review of the available basic knowledge regarding the neural control of the respiratory muscles, which includes not only the identification of the role played by these muscles but **also the evidence regarding their proprioceptive control.** The work done in this area on the other hand, takes a limited account of the detail of the mechanical actions which result from the nervous data that constitutes its subject. It is indeed one main object of the present work to draw attention to the fact that the study of the mechanics of the respiratory apparatus is potentially capable of bringing together these two fields of the physiology of Respiration. Chapter 2. finishes with a reference to the two principal proprioceptive control assemblages involved in the control of the respiratory movements, namely the 'stretch-reflex servo assemblages' and the 'control assemblage of the costo-vertebral joint' and concludes that in both types of assemblage the respective controlling centres feed the assemblage with demands for the implementation of changes in the distance between attachment points of the components of the assemblages; the muscle tensions which result when these demands are obeyed, are monitored by the output of the tendon organs, output which is in turn integrated in such a way as to keep those tensions within acceptable physiological levels.

Chapter 3. contains the elements of descriptive anatomy which are essential to the understanding of the mechanical performance of the respiratory apparatus. The main components of the internal respiratory apparatus are first described in order to give some insight on the origin of the transmural pressures on the thoracic walls. The notion is advanced that during inspiration the respiratory tree tends to be pulled in a ventroposterior direction away from the apical lobes of the lung, thus resulting in a more uniform degree of inflation throughout the lungs. The principal or primary muscles, responsible for the movements of the external respiratory apparatus, are described in some length with regard to their main anatomical features, their insertions and innervations. Whenever possible, diagrams and drawings are included in order to clarify the description and relative position of the muscles. It should be pointed out that it is impossible to model adequately the mechanical properties of the respiratory apparatus without a detailed quantitative description of the anatomical structures which go to make it up. Although, obviously, the material presented in chapter 3. is far from supplying this exhaustive information, it has been included not only because it already performs that function to a modest extent but specially, in order to make perfectly clear its importance to the study of the mechanics of breathing. It is, indeed, quite reasonable to assume that the reason why the anatomy of the external respiratory apparatus is still essentially of qualitative character is the fact that no serious demand has existed for a different type of results. Thus, not much is known about the exact dimensions and shapes of the muscles, their contents in tendinous fibres, their composition in slow and fast muscle fibres, the specific tension they are able to develop, their innervation ratios, their supply of mechanoreceptors, etc.; and similarly limited is our knowledge of the detailed quantitative anatomy of the remaining structures in the external respiratory apparatus. The exact modelling of this apparatus as a breathing machine, however, will not be possible without this information and we certainly hope that the approach to the mechanics of breathing we are proposing in this work will help to bring about the demand for its acquisition. To a very modest extent, we have already contributed towards this end with the results presented in chapter 4., where we give the length of the ribs, the area of the rib cage surface, the angles of rotation of the costovertebral joints and the dimensions of the rib cage and abdomen.

Chapter 4. describes the main results obtained by the experimental methods used in connection with this work, results which make possible a reasonably accurate characterisation of the breathing movements performed by the animal under the conditions in which they were recorded. The movements which occur in light anaesthesia are described by 1/1-scale diagrams in which the extreme positions of inflation and deflation are shown together.

From such composite drawings and from X-ray tracings it is possible to evaluate the amount of movement which takes place and to conclude that the basic driving structures in inspiration are the rib cage and the diaphragm. The movement of the ribs and costalcartilages are characterised as being a rotation which forces the rib shafts forward and upwards, at the same time as the sternum moves backwards in order to compensate for the increased perimeter of the thoracic cross-section. The movements of the abdomen are also shown in appreciable detail both by depth contours on the side views and by cross-sections. It is thus made clear that in inspiration the abdominal walls are lifted at their cranial end by the elevation of the ribs and compression of the abdominal viscerae by the diaphragm, whereas in their centrolateral regions these walls are sucked in, suggesting a reasonably constant abdominal volume; in expiration, the movements of these organs are reversed and, most possibly, the abdominal muscles take an active part in powering this respiratory phase.

The application of an inhibitor of the neuromuscular transmission (Flaxedil) brings about a marked change in the configuration of the trunk as a result of the elimination of the 'tonic' muscular activity and which allows the trunk to yield to the weight of the abdominal viscerae. This fact highlights the functional significance of the 'non-phasic' activity in the functional integration of the body structures. Indeed, our results seem to indicate that although the rhythmic muscular activity is the most obvious component in the performance of the respiratory muscles, it may well not be the most significant component; this role is more likely to be played by the 'tonic' muscular activity, as can be understood by noticing that the structures of the respiratory apparatus are permanently under some amount of loading which has to be taken care of by the 'non-phasic' muscular activity; the increase in load brought about by inspiration is not essentially different from any other load and can be tackled in a similar, if stronger, manner. This view is also supported by the fact that the response of the stretch-reflex assemblages which mediate the reaction of the structures to loading is appreciably faster than the respiratory rhythm.

The deformation which the ribs and costalcartilages undergo during both spontaneous and artificial respiration is described in the composite drawings of figure 4.23 to 4.29 in which the surface of half the rib cage is rectified. As can be seen, the most important deformations take place, as it is to be expected, in the region of the costalcartilages; the comparison between artificial and natural respiration shows the same shape distortion already visible in the previous views of the trunk.

Finally, the inertia forces were evaluated for a point on the eighth rib and found to be negligible in comparison with the other respiratory loads.

The material presented in chapter 5. is conceived as supplying the basic data for the construction of functional models of the structures which form the external respiratory apparatus. This material is obtained by combining the results reported in chapter 4. with further anatomical data and with an interpretive effort which, it is argued, elucidates to an appreciable degree the mechanical performance of the different structures in the respiratory apparatus. It should be emphasised that a full understanding of the respiratory movements of the different structures cannot be achieved from purely mechanical or anatomical considerations and that such understanding can only be achieved by a laborious process which will include electromyographic probing, nerve activity recording, and gradually improved modelling. However, a great deal of understanding can already be gained by a careful study of the data in our possession and that is amply exemplified in chapter 5.

The participation of the rib cage in the stability of the trunk and in supplying the basis for the attachment of the front limbs is first analysed in the detail which the available anatomical data allows. This analysis gives in qualitative terms a quite clear idea of the functions, other than those of respiratory nature, which the rib cage has to perform. A great deal of quantitative anatomy and electromyography will have to be acquired before a model, in precise machine engineering terms, can be built for these functions. The same is true for the other functions described in this chapter. The articulations of the rib cage, in particular the costovertebral articulations, are analysed both as elements which allow or restrict the relative movement of related bones and cartilages and as integrating assemblages in the proprioceptive control of respiration. The relative flexural rigidity of the ribs and costalcartilages is compared and shown to imply a delicate control of the intercostal muscle fibres in order to prevent bending of those cartilagenous elements. Thus, the need for stretch-reflex servoloops in the intercostal muscles is deduced from purely mechanical considerations; these considerations also show that the Hamberger's model for the action of the intercostal muscles is a correct, albeit simplified, description of this behaviour.

The modelling of the respiratory apparatus will eventually consist of separate models for each of the main structures, models which are then associated together through boundary conditions. The five boundaries of the rib cage are analysed to an appreciable length in order to obtain the basic information which is needed for the modelling not only of the rib cage, but also of the diaphragm and the abdomen.

Chapter 5. also deals with the mechanical characterisation of the abdominal compartment. It analyses the fundamental role played by the abdominal viscerae, in particular the liver, in the stabilisation of the thoraco-abdominal boundary. Also introduced is the notion of a bias abdominal compression Δp, created by the contraction of the abdominal wall muscles and which could be used by the animal to meet physiological requirements(*). Finally, the abdominal wall muscles are considered as divided into two basic groups, those in the inner and intermediate layers which are truely antagonistic of the diaphragm and whose activity must be greater during inspiration, and the external obliquus muscle whose functions include the opposing of the serratus anterior which supports the front limbs, and the compression of the abdominal compartment.

Chapter 6. describes the experimental methods used in gathering and processing of the experimental data involved in this work. The most important of these methods is that of the stereo cinephotographic recording and associated numerical and graphical

(*) It is reasonable to assume that ΔP is the control variable used by the abdominal constritor muscles to optimize the operation of the respiratory stuctures.

processing which, although producing results of satisfactory quality, are still extremely laborious and, for a larger scale programme of photogrammetric study, a more expensive and specialised installation will have to be created in order to make possible its utilization in a routine and speedy fashion. It should be emphasised that these methods are not only invaluable in the study of kinematics of the respiratory movements but also in the anatomical characterisation of the structures in the respiratory apparatus whose shape does not allow simple methods of measurement to be applied.

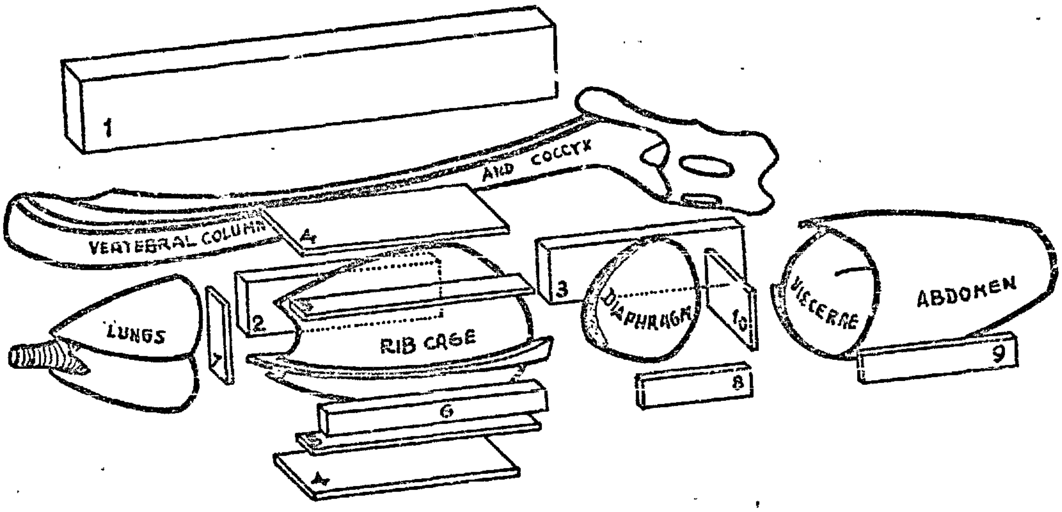

Fig. 7.1 - Functional organisation of the respiratory apparatus of the cat. The main structures are as follows: 1- central 'computor'; 2- costovertebral neural assemblage; 3- external muscles control neural assemblage; 4- intercostal stretchreceptor and tendon organ neural assemblage; 5- costochondral proprioreceptor assemblage; 6- chondrosternal proprioreceptor assemblage; 7- lungs proprioreceptor assemblage; 8- diaphragm proprioreceptor assemblage; 9- abdominal proprioreceptor assemblage; 10- thorax-abdomen interface neural assemblage.

The fundamental contribution of the present work resides in the formulation of a different approach to the study of the mechanics of respiration; the respiratory apparatus is conceived as a process-control mechanical plant, in which the different constituent structures are integrated by a nervous control processor.

Figure 7.1 represents the general layout of the external respiratory system organised so as to emphasise its character of a process control mechanical plant. Three types of components go into its constitution:

1- The physical structures which undergo the movements and perform the mechanical actions the system is designed for. These structures are, essentially, the vertebral column and pelvic bones, the rib cage, the lungs and associated airways, the diaphragm, the abdomen and the abdominal viscerae.

2- The monitoring sensors which we have grouped into assemblages, the most important of which are those of the costovertebral joints, of the stretchreceptors in the intercostal spaces, of the stretchreceptors in the muscles responsible for the postural stability of the trunk, of the receptors in the costochondral and chondrosternal joints, of the receptors in the thorax-abdomen boundary and, finally, those which correspond to the mechanoreceptors in the lungs and airways, in the diaphragm and in the abdomen.

3- The central processor, a general designation for the nervous circuitry, both at segmental and brain level, which integrates all the parts of the system.

The existence of these three types of functionally distinct components is reflected in the different areas of information which must be covered in order to achieve a global characterisation of a mechanical system of this kind. These types of information are the following:

1- The kinematic description of the movements which take place in the physical structures under the control of the integrating nervous system, as distinct from the movements which could take place if only geometrical and structural constraints existed (cf. Appendix A4).

2- The distribution throughout the model of the muscular tension and of the stresses in the other tissues which occur during the controlled movements; this information, together with the previous one, defines completely the structural engineering problem which each physical component constitutes.

3- The distribution of sensory activity in all the receptor assemblages. This information defines the input to the central processor and, together with the nervous efferent traffic to the muscles, constitutes a basis on which the nature of the performance of the central processor may be analysed.

4- The main features of the activity which goes on in the central processor must be related to points of the following kind:

(a) do the main physical structures in the system possess individual local control at segmental level, for instance, or are they all controlled simultaneously?

(b) how is the control of each individual structure related to that of the other structures and how is the overall system organised in terms of priorities and functional hierarchies?

(c) can the strategies implemented by the control system in different situations be quantified and categorised?

(d) how does the processor achieve the structural stability and the proper load response in the different structures and the global system itself?

The items of information described above would, if available, characterise completely the mechanical performance of the system. Unfortunately this information is not easily obtained in the case of the respiratory apparatus. The first and most obvious approach to the problem of acquiring it is of course the use of animals to perform experiments and measurements; this solution, however, is far from being simple or straightforward for the following reasons: 1- the animal's body is organised in layers and only the superficial anatomical structures are easily accessible without appreciable mutilation of the animal; 2- it is practically impossible to monitor, in any really extensive way, the activity of the muscles, nerve fibres and sensory endings not only because of their inaccessibility but also because of the size of the measuring devices; the same difficulties apply to the measurement of the deformations and stresses in the various tissues. As a consequence of these limitations, the information which it is possible to gather by this method is extremely patchy and hardly adequate for the global analysis of the mechanics of the respiratory apparatus.

A different but complementary approach to this problem consists in the building of models based on well defined functional components and whose performance is progressively improved and brought closer to that of the animal. The power of this method resides in the fact that the model represents a much simpler system whose functioning is based on known premises, thus making it susceptible of a satisfactory description; models constitute therefore a potent device for the understanding of the experimental data and are, at the same time, a source of demand for further investigation.

It is in this connection that the material contained in the present work can be of appreciable help. In fact, quite a great deal of information has been gathered on the kinematic characterisation of the respiratory movements thanks to the photographic methods we have used. These results not only go a long way to clarify the nature of the movements undergone by the respiratory structures in quiet breathing but also they make plain the need for such methods and for such data in the characterisation of the mechanics of breathing. The functional interpretation of the experimental data in chapter 5., besides contributing to an increased understanding of the respiratory movements, opens the way to the formulation of realistic models for those structures. The methods and techniques of Structural Analysis are suggested as the proper framework for the formulation of such models and it is our conviction that these will be the broad lines along which this field of Physiology will develop.

Finally, there is a further aspect in the approach to the mechanics of breathing advocated in this work and which may have very promising applications.

We have reproduced in Appendix A.5 the basic ideas involved in the finite difference method of numerical integration of the shell- membrane equations. This method translates into a discrete form the measure in which the value of the solutions to the stress problem of each point is influenced by the values of the functions in the immediate neighbourhood of that point. Also, the method implements the solution by solving simultaneously all the difference equations for the whole grid of points in the structure, thus observing the character of integral solution which the distribution of stress throughout the structure possesses. It is, therefore, very tempting to establish a close parallel between the grid of points and the value of the stress solutions there with the discrete muscle units and mechanoreceptors; and to compare the process of numerical integration and the functional interrelation between the nervous areas to which the afferent and efferent nerve fibres lead to or come from. This is particularly true of the rib cage which not only is the most complex structure in the external respiratory apparatus but, presumably for that very reason, is more richly equipped with mechanosensors. It is true that the proprioceptive assemblages have a functional performance which is appreciably more complex than that implicit in the difference equations of Appendix A.5. However, just as those difference equations represent an approximation, the description of the proprioceptive assemblages can be simplified in order to facilitate the comparison between the two 'methods' of solution and the similarities between them explored to a great length. It should be pointed out that modern numerical methods for the solution of the stress problem in generalised shell and other statically indetermined structures are based on the principle of minimum virtual displacement stress energy and, therefore, produce a discrete numerical procedure which must be quite akin to the principles of tissue and energy economy which are generally observed in biological systems.(*)

The parallel just described suggests a different approach to the study of the nervous areas which control the respiratory apparatus. This approach, which could be applied to other physiological functions, would thus consist of investigating the properties of the respiratory nervous centres via the study of the performance of the peripheral system or systems they control. Generally speaking, when the performance of a system is studied at a level in which the participation of the nervous control has to be taken into account, the phenomenon that performance represents is sufficiently complex to implicate a wealth of elaborate functional relationships; it will also be so close to the basic components - the cells - that it will be possible to pin down such a framework of operational properties to the individual components which actually implement them.

(*) The known adaptive responses of bone tissue to stress stimulus (Laux, 1930; Clark, 1958) and the constant destruction and regeneration of the nerve endings on the muscle fibres (Baker, 1967) which presumably adapts the innervation of the muscles to the functional demands on it.

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APPENDIX A.1

THE OPTICS OF THE PHOTOGRAPHIC SYSTEM

In order to recover the third dimension, or depth, from the photographic records, we created two side views of the subject by means of the mirror system shown in figure A1.1. This system consists essentially of two plane front aluminised mirrors placed parallel to one another and at 30° with respect to their common base; these mirrors are mounted on rectangular plates each attached to a supporting bracket whose position with regard to the base is precisely defined by a slot in the latter. All the metallic parts in this structure are in duraluminium and were machined to within a tolerance of ± 0.001 inch and the angles defined to within ± 0.5'. The plane mirrors were made of rectangular plates, 3 x 160 x 230 mm in size, ground polished and front aluminised and flat to less than ten mercury line wavelengths as measured in a Fizeau interferometre. This system

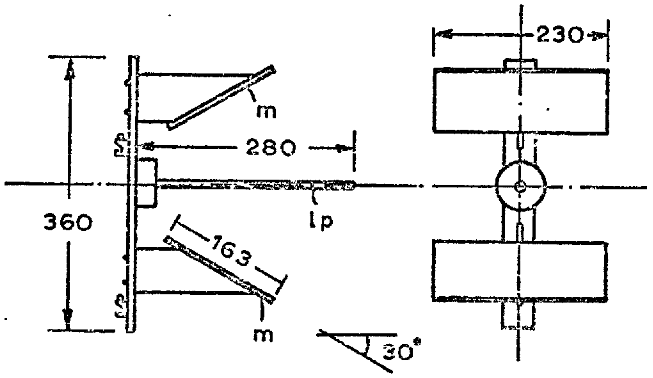


Fig. A1.1 - Mirror system used in the production of multi-projection cine-photographs. lp - removable 'light pencil' for alignment of the camera; m - plane mirrors.

is used in conjunction with an operatory table on which it is mounted with the common base of the mirrors in a vertical position and the animal placed horizontally between the mirrors; both mirrors may be moved along the base in order to facilitate the positioning of the animal.

Figure A1.1 shows also the 'light pencil' which is used for the alignment of the cine-camera in a direction normal to the base of the mirror structure. This device consists of a 280 mm long rod connected at 90° to a cylindrical base by which it is mounted on the mirror structure; the rod is machined to create a longitudinal bore of 0.6 mm effective diameter through which the light of a torch bulb, located inside the cylindrical base, can be seen. The camera is aligned by moving it in its support until this light at the base of the 'light pen' becomes visible against a darkened background; in this way the camera can be aimed along a direction which makes with the normal to the base of the mirrors an angle not greater than 15'.

Figure A1.2 represents the basic geometry of the photographic system under the assumption of perfect perpendicularity between the camera axis and the base of the mirrors and perfect quality of the mirror surface and mounting. In this figure $P_0(x_0,y_0,z_0)$ is a point on the object, $P_2(x_2,y_2,z_2)$ its image as seen from the lens, and $P_1(x_1,y_1,z_1)$ the trace on the mirror surface of the ray $\overline{NP_2}$; Q_0 and Q_1 are the images of P_0 and P_2 (and P_1) respectively, on the image plane of the lens system.

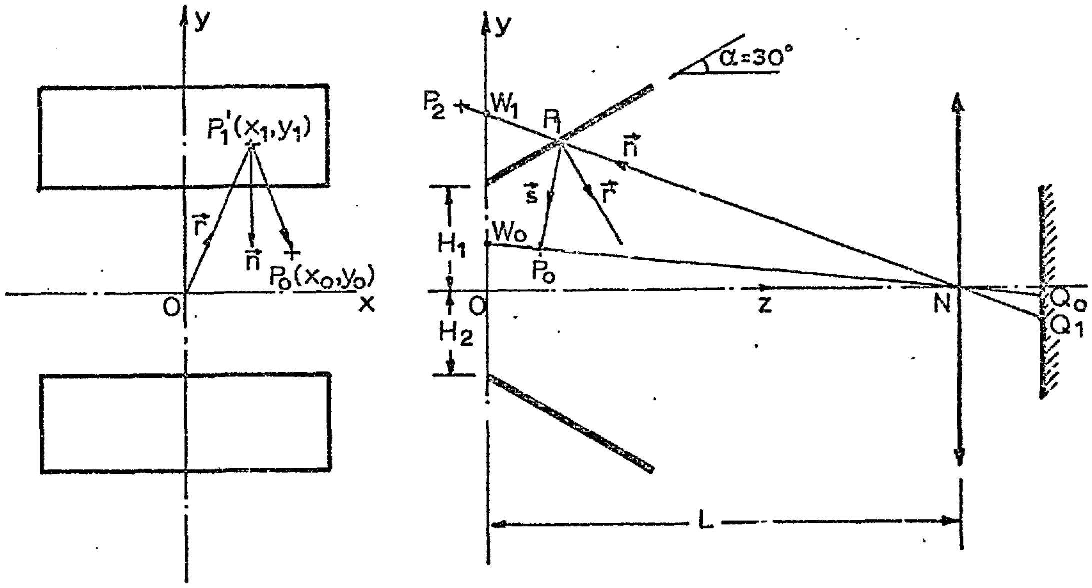


Fig. A1.2 - Geometry of the photographic system: L - distance from the bottom edge of the mirrors to the axis of the lens system; N - nodal point of this system; H_1 and H_2 - distance of the internal edge of each mirror to the axis of the lens system; α - angle made by the plane of the surface of the mirrors with the lens axis; $\vec{r} = \overline{NP_1}$; $\vec{s} = \overline{P_1P_0}$; $\vec{n}$ = normal to the mirror surface at P_1.

From a purely geometrical point of view the images Q_0 and Q_1 are homologous of the traces of the lines $\overline{NP_1 NP_2}$ and $\overline{NP_0}$ on the plane z = o, $W_1(x_3,y_3)$ and $W_0(x_4,y_4)$; therefore, their coordinates are related to those of $P_0(x_0,y_0,z_0)$ and $P_1(x_1,y_1,z_1)$ as follows:

$$x_0 = x_3 \cdot (1 - z_0/L)$$
$$y_0 = y_3 \cdot (1 - z_0/L)$$
$$x_1 = x_4 \cdot (1 - z_1/L)$$
$$y_1 = y_4 \cdot (1 - z_1/L) \qquad (1)$$

The coordinates of the points W_1 and W_0 are read from the photographs and multiplied by a suitable scaling factor. The equation which describes the surface of the mirrors is the following:

$$x = 0$$

$$a \,.\, z = *y - H \qquad (2)$$

where $a = \tan\alpha$, $* = +1$ for the top mirror, $* = -1$ for the bottom mirror and H has the value corresponding to the mirror considered. If we combine this equation, which is satisfied by y_1 and z_1, with the last equation in the system (1), we obtain the result:

$$x_1 = x_4 \,.\, B$$

$$y_1 = y_4 \,.\, B$$

$$z_1 = [(\bar{y}_4 - H)/(a.L - H)] \,.\, B.L \qquad (3)$$

where $\bar{y}_4$ = modulus (y_4) and

$$B = (a.L - H)/(a.L - \bar{y}_4) \qquad (4)$$

The coordinates of $P_0(x_0,y_0,z_0)$ can be obtained from those in equation (3) if the vector $\vec{s}$, which connects the two points P_0 and P_1 is known. This vector lies in the same plane as $\vec{r} = \overline{NP_1}$ and the normal to the mirror surface at P_1, and makes with $\vec{n}$ the same angle as $\vec{r}$; it may, therefore, be determined in the following manner:

The equations of the straight line which connects P_1 with the nodal point of the lens system, N(0,0,L), are as follows:

$$\frac{x-x_1}{-x_1} = \frac{y-y_1}{-y_1} = \frac{z-z_1}{L-z_1} \qquad (5)$$

According to equation (2), the normal $\vec{n}$ at P_1 is given by:

$$\frac{x-x_1}{0} = \frac{y-y_1}{-*} = \frac{z-z_1}{a} \tag{6}$$

and, therefore, the cosine of the angle made by (5) and (6) is equal to:

$$\cos\varphi = \frac{*y_1 + a\ .\ (L - z_1)}{\sqrt{1+a^2}\ .\ \sqrt{x_1^2 + y_1^2 + (L - z_1)^2}} \tag{7}$$

The line $\vec{s}$ which joins P_1 and P_0 lies in a cone with the vertex in P_1, the axis $\vec{n}$ and containing $\vec{r}$ as a generatrix. Any generatrix of this cone satisfies the general equation:

$$\frac{x-x_1}{\beta} = \frac{y-y_1}{\gamma} = \frac{z-z_1}{\delta} \tag{8}$$

where the parameters β, γ and δ satisfy the following relationship:

$$\cos\varphi = \frac{a\ .\ \delta - *\gamma}{\sqrt{1+a^2}\ .\ \sqrt{\beta^2 + \gamma^2 + \delta^2}} \tag{9}$$

Equating the two expressions of $\cos\varphi$ given by (7) and (9) and introducing the values of β, γ and δ from (8), we obtain the equation of the cone defined by $\vec{r}$, $\vec{s}$ and $\vec{n}$:

$$(x-x_1)^2+(1-A^2).(y-y_1)^2+(1-a^2A^2)(z-z_1)^2++*2aA^2(y-y_1)(z-z_1)=0 \tag{10}$$

in which A^2 is given by:

$$A^2 = \frac{x_1^2+y_1^2+(L-z_1)^2}{[a.(L-z_1)++*y_1]^2} \tag{11}$$

The line $\vec{s}$ also lies in the plane defined by the lines $\vec{r}$ and $\vec{n}$ whose equation is:

$$(x-x_1)[a.y_1-\ast(L-z_1)] - (y-y_1).a.x_1-\ast(z-z_1)\ x_1 = 0 \qquad (12)$$

If we introduce the value of $(z-z_1)$ deduced from this equation in equation (10) we obtain the two generatrices along which the plane (12) intersects the cone (10); one of these generatrices is that given by equation (5), already known, and the other, given by the following equations:

$$\frac{x-x_1}{E} = \frac{y-y_1}{F} = \frac{z-z_1}{G} \qquad (13)$$

in which:

$$E = (1-a^2).x_1$$

$$F = -[(1-a^2).y_1+\ast 2a.(L-z_1)]$$

$$G = -[(1-a^2).(L-z_1)-2a.y_1], \qquad (14)$$

is the line $\bar{\bar{s}}$ we wanted to get. To determine z_0, we combine one of the equations (13) with the corresponding equations in (1) and (3) and obtain the following result:

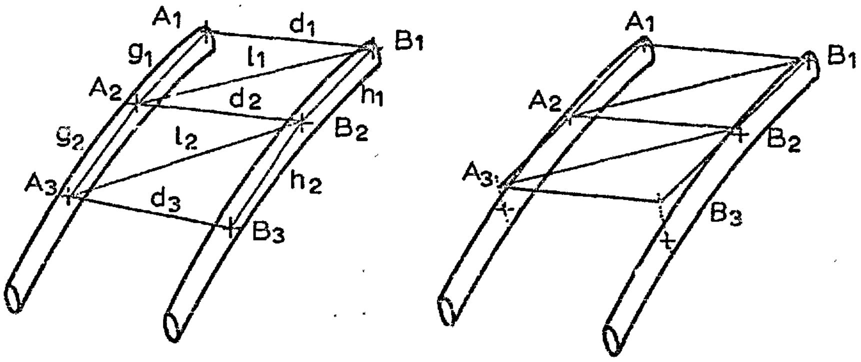
$$z_0 = [z_1-(G/F)(y_3-B.y_4)][(1-(G/F)(y_3/L)]^{-1} \qquad (15)$$

This is the value of the distance of $P_0(x_0,y_0,z_0)$ to the plane $z = 0$; once z_0 is known, formulae (1) gives the values of x_0 and y_0 corrected for the effect of perspective.

APPENDIX A.2

NUMERICAL RECTIFICATION OF THE RIB CAGE SURFACE; COMPUTATION OF AREAS AND VOLUME

The area of the intercostal space limited by the segments of two contiguous ribs, as shown in figure A2.1, between points A1, A3, B1 and B3 is given approximately by the sum of the areas of the triangles (A2, A1, B1), (B1, B2, A2), (A3, A2, B2) and (B2, B3, A3). Within this approximation, this fraction of the intercostal space will be rectified if those triangular facets are made to rotate around their common sides until they all lie in the same plane. This operation will, of course, be performed by drawing successively those triangles using for each one the side in common with the previous one as the base for its construction. Before tackling the problem of the rectification proper, let's consider that of building a triangle given its sides as exemplified for (A3,B3,B2). For this purpose we consider



(a) (b)

$d_1 = \overline{A1B1}$ $g_1 = \overline{A1A2}$ $h_1 = \overline{B1B2}$ $l_1 = \overline{B1A2}$
$d_2 = \overline{A2B2}$ $g_2 = \overline{A2A3}$ $h_2 = \overline{B2B3}$ $l_2 = \overline{B2A3}$

Fig. A2.1 - Plane triangular facet approximation to surface of the intercostal spaces.

a set of intrinsic axes, OX' and OY' (figure A2.2), and mark on the OX' axis two points, M(0,0) and N(l_2,0), separated therefore by a distance equal to the length of the side $\overline{A3B3}$ of the triangle; the third vertex of the rectified triangle, P(x'_p,y'_p), is defined as the intersection of two circumferences centred in M and in N and whose radii are, respectively, d_3 and h_2. These co-ordinates are therefore given by the following formulae:

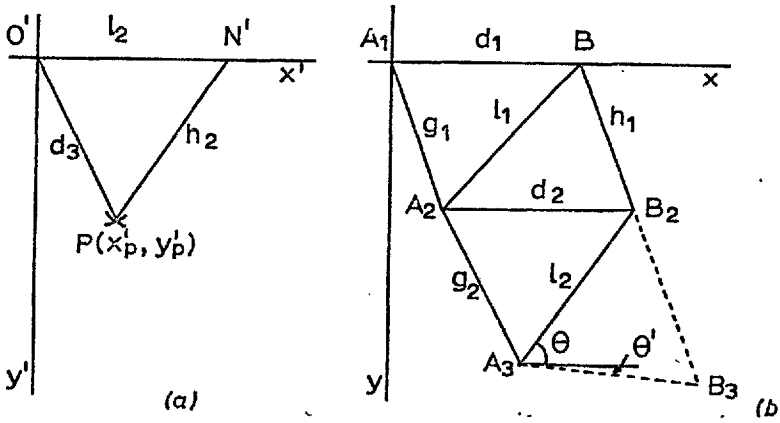


Fig. A2.2 - Rectification of an intercostal space. (a) triangle (A3,B3,B2) drawn in an auxilliary set of intrinsic axes; (b) the same triangle after having been transferred to the rectified construction of the respective intercostal space.

$$x'_p = \frac{l_2^2 + d_3^2 - h_2^2}{2l_2}$$

$$y'_p = \sqrt{d_3^2 - (x'_p)^2} \qquad (1)$$

where d_3, h_2 and l_2 are defined in figure A2.1.

In order to add this triangle to the rectified version of the intercostal space surface (figure A2.1(b)), all we need do is a change of variables which brings O' to coincide with A3 and the axis O'X' with $\overline{A3B2}$. If we assume known the angle θ , measured positively in the clockwise direction, made by $\overline{A3B2}$ with OX and the coordinates of A3 with respect to the new set of axes, then the coordinates of B3 in this system of axes are given by:

$$x_{B3} = x_{A3} + x_P' \cos\theta + y_P' \sin\theta$$

$$y_{B3} = y_{A3} - x_P' \sin\theta + y_P' \cos\theta \qquad (2)$$

In order to add the next triangle to the rectification, it is necessary to know the coordinates of A_3, which we have assumed to be known, and the sine and cosine of the angle θ' , which $\overline{A3B3}$ makes with the OX axis; these values are calculated as follows:

$$\cos\theta' = \frac{x_P' \cdot \cos\theta + y_P' \cdot \sin\theta}{\sqrt{(x_P')^2 + (y_P')^2}}$$

and

$$\sin\theta' = \frac{-x_P' \cdot \sin\theta - y_P' \cdot \cos\theta}{\sqrt{(x_P')^2 + (y_P')^2}} \qquad (3)$$

Thus, as for the first triangle it is $x_{A3}=y_{A3}=0$ and $\theta=0$, we are able to progress from triangle to triangle, each supplying the vertex and the angle necessary for the construction of the next, until all the intercostal space is rectified.

The computation of the areas of the intercostal spaces is done, similarly, by adding up the areas of the rectified triangular facets. The area of each facet may be computed using Heron's formula (Rektorys, 1969):

$$A = \sqrt{s.(s-a).(s-b).(s-c)}$$

$$s = 0.5\ (a+b+c) \qquad (4)$$

where a,b and c are the lengths of the sides.

For the computation of the volume of the rib cage the basic unit is the triangular prism which has a facet and its projection on the XOY plane as bases (figure A2.3). The expression for the volume of such a prism is the following:

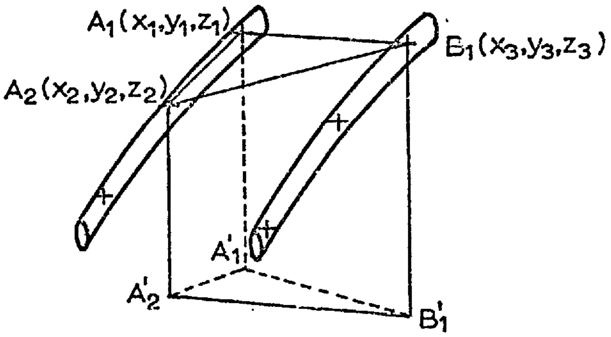


Fig. A2.3 - Elementary prism for the computation of the rib cage volume

$$V = (1/6).(z_1+z_2+z_3).\ \mathrm{mod}(a_1b_2-b_1a_2) \qquad (5)$$

in which:

$$a_1 = x_1-x_2 \qquad a_2 = x_3-x_2$$

$$b_1 = y_1-y_2 \qquad b_2 = y_3-y_2 \qquad (6)$$

APPENDIX A.3

COMPUTATION OF THE THREE-DIMENSIONAL TRAJECTORIES DESCRIBED BY THE TIP OF A RIB ROTATING AROUND A FIXED AXIS.

In the diagram of figure A3.1 which represents a rib and its axis of rotation, we consider known the coordinates of the points $Q(x_q, y_q, z_q)$ and $T(x_t, y_t, z_t)$, respectively the centre of rotation of the tubercle of the rib and the tip of the rib at a given instant in time; also known are the direction cosines (l, m, n) of the axis of rotation O'Z'. With this information, we are able to determine the equation of the plane π which is normal to the axis of rotation O'Z' and contains the point T:

$$l\ (x - x_t) - m\ (y - y_t) - n\ (z - z_t) = 0 \qquad (1)$$

which together with that of the axis of rotation:

$$\frac{x - x_q}{l} = \frac{y - y_q}{m} = \frac{z - z_q}{n} \qquad (2)$$

provides the coordinates of the point O' where they intersect:

$$\begin{aligned} x_{O'} &= x_q + k.l \\ y_{O'} &= y_q + k.m \\ z_{O'} &= z_q + k.n \end{aligned} \qquad (3)$$

with the parameter k being given by:

$$k = l.(x_t - x_q) + m.(y_t - y_q) + n.(z_t - z_q) \qquad (4)$$

We now consider a new system of rectangular axes, associated or intrinsic to the rib, with the origin at the intersection of the axis of rotation O'Z' with the plane π ; the axis O'Z' is the new Z-axis. The new Y-axis is defined by the intersection on π by the plane which contains O'Z', and $O'Z_1$ a parallel to OZ drawn through O'; the positive semi-axis O'Y' is that which makes an acute angle with $O'Z_1$. Finally, the $O'X'$ axis is chosen to be perpendicular to the plane $Z'O'Y'$ and orientated so that the diedral angles (O,X,Y,Z) and (O,X',Y',Z') have the same sign. The new set of reference axes is related to the original set by the matrix of direction cosines given in table I (Bell, 1931).

Table I - Matrix of the direction cosines which relate the two sets of axes defined in the text

	x	y	z
x'	$\frac{-m}{\sqrt{l^2+m^2}}$	$\frac{l}{\sqrt{l^2+m^2}}$	0
y'	$\frac{-m.l}{\sqrt{l^2+m^2}}$	$\frac{-m.n}{\sqrt{l^2+m^2}}$	$\sqrt{l^2+m^2}$
z'	l	m	n

The coordinates of a point P in the new system may therefore be expressed in terms of its coordinates in the OXYZ system as follows:

$$x'_P = -\frac{m}{\sqrt{l^2+m^2}} \cdot (x_P - x_{O'}) + \frac{l}{\sqrt{l^2+m^2}} \cdot (y_P - y_{O'})$$

$$y'_P = -\frac{l.n}{\sqrt{l^2+m^2}} \cdot (x_P - x_{O'}) - \frac{m.n}{\sqrt{l^2+m^2}} \cdot (y_P - y_{O'}) + \sqrt{l^2+m^2} \cdot (z_P - z_{O'})$$

$$z'_P = l \cdot (x_P - x_{O'}) + m \cdot (y_P - y_{O'}) + n \cdot (z_P - z_{O'}) \qquad (5)$$

The movement of the rib we are considering consists of a simple rotation around O'Z' and, therefore, its tip describes a circumference (c) centred at O'. The coordinates, expressed in the intrinsic system of reference, of any two positions T_1 and T_2 of T are related in the following manner:

$$x'_{T_2} = \cos\eta \cdot x'_{T_1} - \sin\eta \cdot y'_{T_1}$$

$$y'_{T_2} = \sin\eta \cdot x'_{T_1} + \cos\eta \cdot y'_{T_1}$$

$$z'_{T_2} = z'_{T_1} \qquad (6)$$

where η is the angle made by the radius O'_{T_1} and O'_{T_2} measured positively in the clockwise direction.

We are now in the position of being able to compute a series of points on the circumference (c) by using the following procedure: using equations (5) the coordinates of the initial position T of the rib tip are converted to the intrinsic system of reference axes; then, choosing a step angle η the equations (6)

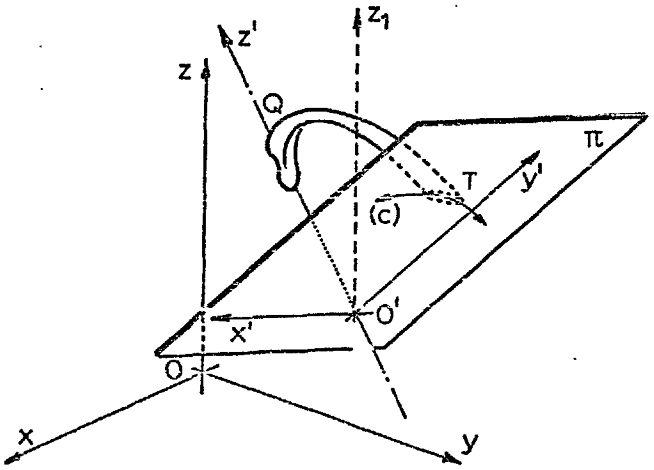


Fig. A3.1 - Movement of a rib about the ideal axis of rotation of its costovertebral joint: c -trajectory of the tip T of the rib; π - plane perpendicular to O'Z' and containing the point T.

are applied repeatedly, each time taking as coordinates of T_1 those computed for T_2 in the previous step. In this manner and using both a positive and a negative step, a collection of points on the circumference described by T are obtained. Finally, the coordinates of these points are converted to the original system of reference axes by means of the following formulae derived from the matrix of table I:

$$\begin{aligned} x &= x_{0'} + \left(-\frac{m}{\sqrt{l^2+m^2}}\right).\ x' + \left(-\frac{l.n}{\sqrt{l^2+m^2}}\right).\ y' + l.\ z' \\ y &= y_{0'} + \left(\frac{l}{\sqrt{l^2+m^2}}\right).\ x' + \left(-\frac{m.n}{\sqrt{l^2+m^2}}\right).\ y' + m.\ z' \\ z &= z_{0'} + \left(\sqrt{l^2+m^2}\right).\ y' + n.\ z' \end{aligned} \qquad (7)$$

APPENDIX A.4

COMPUTER CONTROL OF THE KINEMATICS OF MACHINES

In order to illustrate the dintinction between geometrically determined and computer determined movements consider the very simple machine represented in figure A4.1(a) and made of three coplanar links articulated at the points A_1, A_2 and A_3. In such a simplified form, the machine can be widely deformed by the loads applied to it as the sample trajectory (a) shown in the figure exemplifies for a particular time varying load. If we now install at each of the points A_1, A_2 and A_3 a servomotor capable of controlling the angles α_1, α_2 and α_3 made by the links which join at those points, we will be able to determine rigorously the geometry of the trajectories which the machine is capable of following.

The diagram of the figure A4.1(b) represents the situation in which the point A_4 is forced to move along the OY-axis exclusively and the point A_3 is obliged to keep on a circumference of radius R and centre at the point (c,0). It is easy to show that in these circumstances the angles α_1, α_2 and α_3 satisfy the following two relationships:

$$d_1 . \cos\alpha_1 - d_2 . \cos(\alpha_2 - \alpha_1) - d_3 . \cos(\alpha_3 - \alpha_2 + \alpha_1) - b = 0$$

$$a_1 . \cos\alpha_1 - a_2 . \cos\alpha_2 - a_3 . \cos(\alpha_2 - \alpha_1) - a_4 = 0 \qquad (1)$$

where α_1, α_2, α_3, d_1, d_2, d_3 and b have the same meaning as in figure A4.1(a) and

$$a_1 = 2\, d_1\ (b + c) \qquad a_3 = -\, 2d_2\ (b + c)$$

$$a_2 = 2\, d_1\ d_2 \qquad a_4 = d_1^2 + d_2^2 + (b + c)^2 - R^2 \qquad (2)$$

The first equation in (1) is obtained by making the X-coordinate of point A_4 equal to zero and the second equation (1) represents the condition for A_3 to stay on circumference (c).

The computing set-up shown in figure A4.3 represents a possible solution for the problem of generating the signals which have to be fed to the servomotors in order to guarantee that equations (1) are satisfied. In this system the value of α_3 is checked against two limit values, α_{max} and α_{min}, and a corrected value α_3' is produced and fed to a computer which uses equations (1) to generate corrected values for α_1 and α_2; these

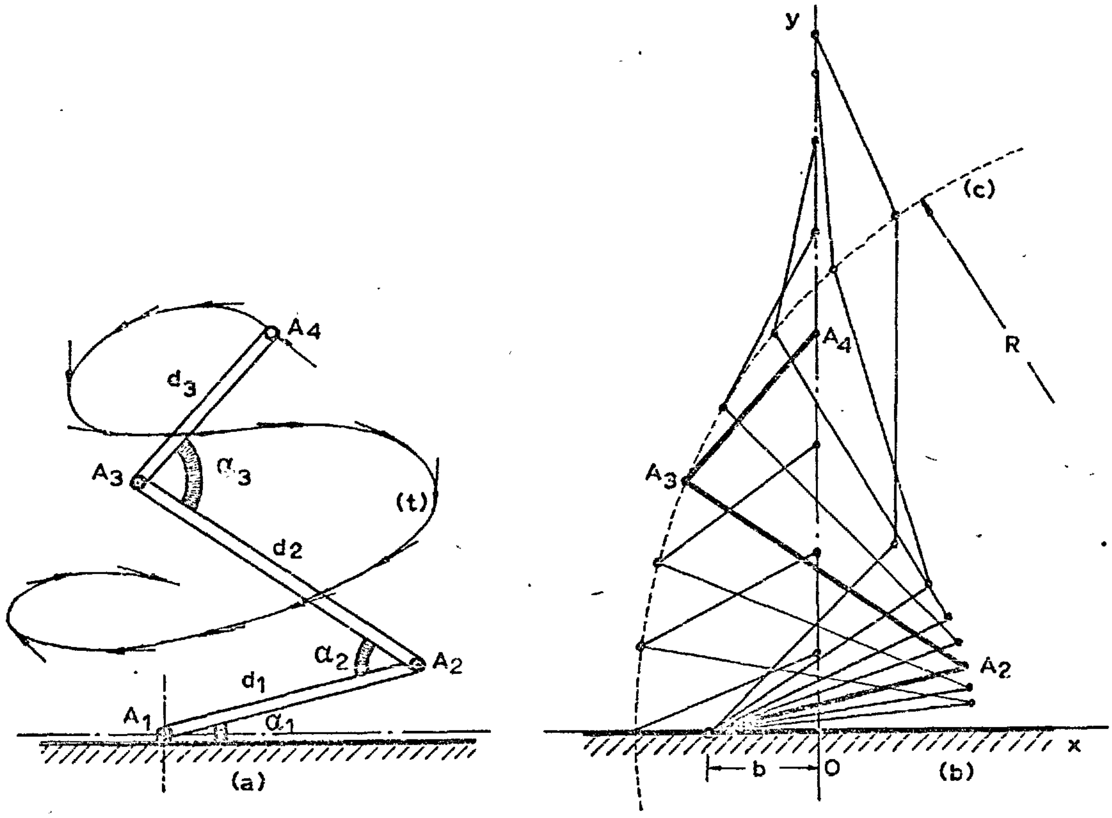


Fig. A4.1 - Limitation of the freedom of movement of a kinematic chain by the servocontrol of the angles of articulation of its links: (a) kinematic chain with simple pinned joints between the links shown together with a sample trajectory, (t); (b) the same chain under the control of servomotors, located at the joints, which adjust continuously the values of the angles α_1, α_2 and α_3 so as to make A_3 to move permanently on the circumference (c) and A_4 on the OY-axis.

new values of the angles are then passed, together with their original values, to difference devices whose output is amplified and fed to the respective servomotor. Thus, if the points A_3 and A_4 are correctly located, the original and primed values of the angles will be equal and the output of the servoamplifiers will be zero; whenever the two sets of angle values are not the same the output of the amplifiers will be such as to make the servomotors bring the points back to the desired loci. Therefore, if we assume servo systems of sufficient power to overcome the applied loads, the machine of figure A4.1(b) will always move along the same trajectories whichever the direction and nature of the loads.

Figure A4.2 represents, in the space of the three dimensions α_1, α_2, α_3, the geometric entities associated with the machine of figure A4.1(b). The surface S corresponds to the first condition in (1), relating the movements of A_4 along the OY-axis; the values of α_1, α_2 and α_3 for any point in this surface define an acceptable configuration of the machine. The cylinder whose axis is parallel to $O\alpha_3$ and whose trace in the plane $(O\alpha_1\alpha_2)$ is the curve (t), represents the surface which corresponds to the condition of A_3 moving along the circumference (c) in figure A4.1(b). The intersection of these two surfaces, γ, therefore represents the locus of the points $(\alpha_1, \alpha_2, \alpha_3)$ for which A_3 and A_4 satisfy simultaneously the conditions imposed on them. If a sudden load throws the point representative of the state of the machine to a position P (cf. figure A4.2), the computing setup will bring it back to the position P' intersected on γ by the horizontal plane which contains P; this correcting

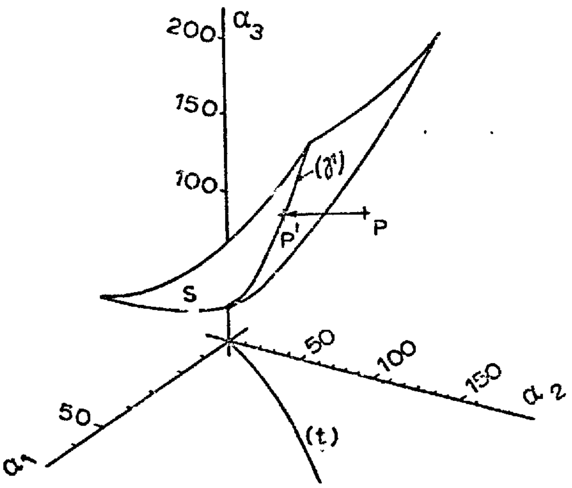


Fig. A4.2 - Geometry of the machine of figure A4.1(b) represented in the three-dimensional space defined by the three joint angles α_1, α_2 and α_3. S- surface which contains the points for which A_4 is constrained to move along the OY-axis; (t)- trace on the $(O\alpha_1\alpha_2)$ plane of the cylinder which corresponds to the condition of A_3 moving permanently on the circumference (c); the intersection of these two surfaces defines the locus γ of the points which satisfy both conditions.

trajectory is determined exclusively by the operational properties of the computing system. We have considered the response of the system as being instantaneous and its gain infinite; in a real system there will be a finite error and the correcting trajectories, in both the (x,y) and $(\alpha_1, \alpha_2, \alpha_3)$ spaces, will be rounded by the response delays of the various components in the system.

The following conclusions can be drawn from the example just considered:

1- A generalised machine may be built by the association of a basic mechanism with a control system constituted by an adequate number of sensors and effectors integrated by a processing set-up. The freedom of movement in the new machine will be necessarily smaller than in the original machine by an extent which is determined by the constraints introduced by the control

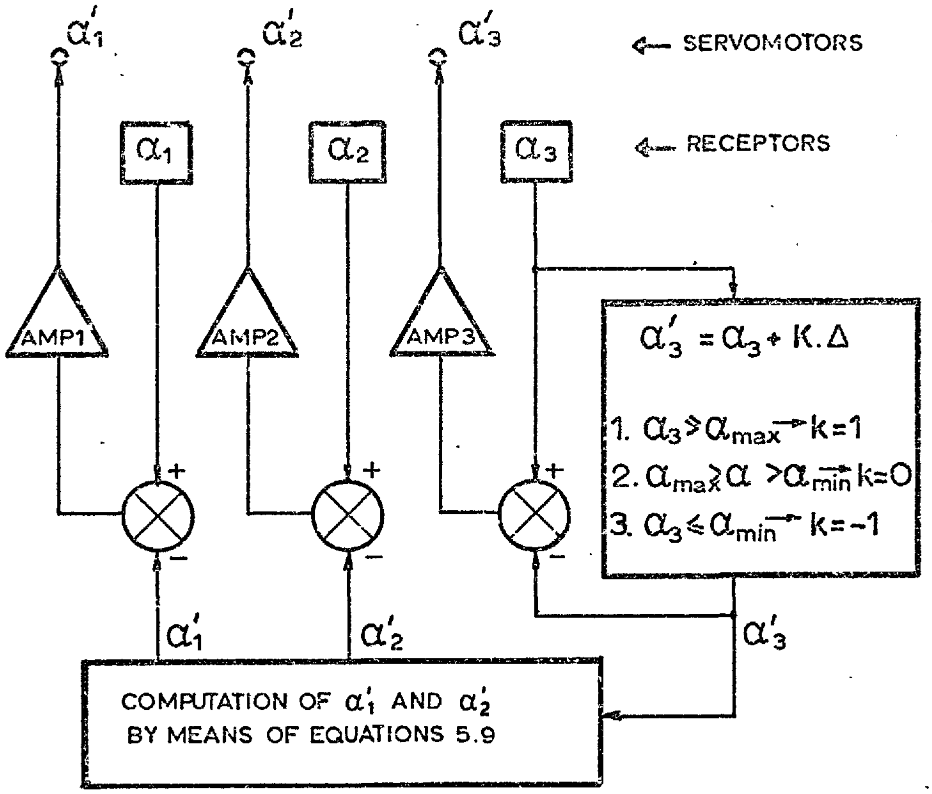


Fig. A4.3 - Block diagram of a servosystem which implements the machine represented in figure A4.1(b).

system. It should be pointed out that this definition of the generalised machine is merely an extension of the normal concept of machine; in this latter case the 'computer' is represented by the physical components of the machine which are, after all, analogic materialisations of the kinematic relationships which they are intended to implement. Therefore, what is novel in the definition given above is the association of different technologies in the same device: the physical machine itself and the computing and interconnecting circuitry which itself does not participate in the actual movements.

2- The kinematic properties of the new machine can only be completely defined when both the geometry of its moving parts and the 'geometry' of its control space are known. Indeed, the geometry of the movements of the physical machine cannot be related in a unique manner to the kind of control system which is responsible for it and, therefore, the latter must be investigated for each individual case.

APPENDIX A.5

ELEMENTS OF THE MEMBRANE THEORY OF SHELLS

By definition a shell is a three-dimensional structure of curved shape whose thickness is very small compared with its other two dimensions. In this appendix we consider only the case in which the ratio of the thickness to the other two dimensions of the shell is so small that bending or twisting moments cannot occur, and therefore the shell behaves as an elastic membrane. Figure A5.1 represents an infinitesimal element cut on a shell by planes respectively perpendicular to the x- and y- axes; the shell has a middle surface described by the equation z=z(x,y) and is subjected to a load whose components per unit area are F_x, F_y and F_z. The static equilibrium of this element can be expressed by the following equations (Flügge, 1960; Timoshenko and Woinowsky-Krieger, 1959):

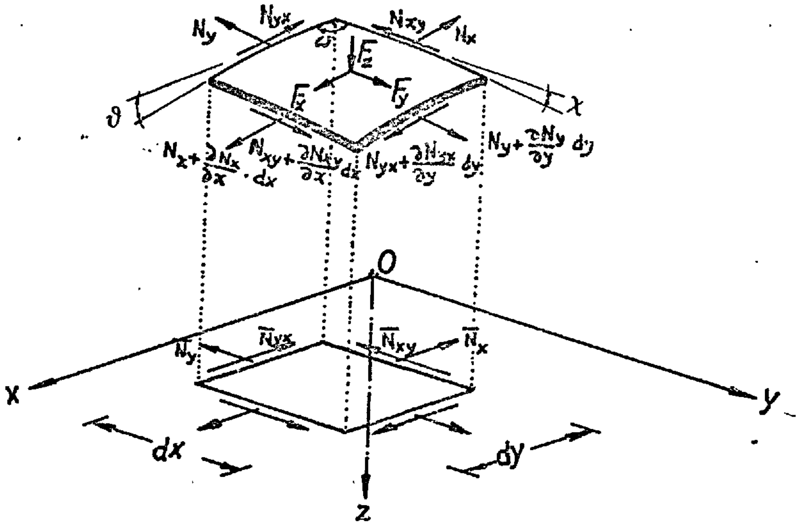


Fig. A5.1 - Equilibrium of a shell element under external force.

$$\frac{\partial \overline{N}_x}{\partial x} + \frac{\partial \overline{N}_{xy}}{\partial y} + \overline{F}_x = 0$$

$$\frac{\partial \overline{N}_{xy}}{\partial x} + \frac{\partial \overline{N}_y}{\partial y} + \overline{F}_y = 0$$

$$r\,\overline{N}_x + 2s\,\overline{N}_{xy} + t\,\overline{N}_y = -\overline{F}_z + p\,\overline{F}_x + q\,\overline{F}_y \qquad (1)$$

in which $\overline{N}_x$, $\overline{N}_y$, $\overline{N}_{xy} = \overline{N}_{yx}$, $\overline{F}_x$, $\overline{F}_y$ and $\overline{F}_z$ are the horizontal components of the stress resultants and the loads and satisfy the following relationships:

$$\frac{N_x}{\overline{N}_x} = \frac{\overline{N}_y}{N_y} = \frac{\cos\chi}{\cos\vartheta}$$

$$N_{xy} = N_{yx} = \overline{N}_{xy} = \overline{N}_{yx}$$

$$\frac{\overline{F}_x}{F_x} = \frac{\overline{F}_y}{F_y} = \frac{\overline{F}_z}{F_z} = \frac{dA}{dx.dy} = \frac{(1-\sin^2\chi\ .\ \sin^2\vartheta)^{\frac{1}{2}}}{\cos\chi\ .\ \cos\vartheta} \qquad (2)$$

where dA is the area of the shell element, and:

$$p = \tan\chi = \frac{\partial z}{\partial x} \qquad q = \tan\vartheta = \frac{\partial z}{\partial y}$$

$$r = \frac{\partial^2 z}{\partial x^2} \qquad s = \frac{\partial^2 z}{\partial x \partial y} \qquad t = \frac{\partial^2 z}{\partial y^2} \qquad (3)$$

are the first and the second derivatives of the middle surface of the shell $z=z(x,y)$. The stress resultants can be expressed in terms of an Airy type stress function $\Phi(x,y)$ in the following way:

$$\overline{N}_x = \frac{\partial^2\Phi}{\partial y^2} - \int_{x_0}^{x} \overline{F}_x\,dx$$

$$\overline{N}_y = \frac{\partial^2\Phi}{\partial x^2} - \int_{y_0}^{y} \overline{F}_y\,dy$$

$$\overline{N}_{xy} = -\frac{\partial^2\Phi}{\partial x \partial y} \qquad (4)$$

in which case the first two equations in (1) are satisfied identically and the third becomes:

$$t \frac{\partial^2\Phi}{\partial x^2} - 2s \frac{\partial^2\Phi}{\partial x \partial y} + r \frac{\partial^2\Phi}{\partial y^2} = P \tag{5}$$

where

$$P = - \overline{F}_z + p \overline{F}_x + q \overline{F}_y + r \int_{x_0}^{x} \overline{F}_x \, dx + t \int_{y_0}^{y} \overline{F}_y dy \tag{6}$$

The lower limits in the integrals of equations (4) and (6), x_0 and y_0, are suitably chosen but fixed initial values of x and y respectively. Equation (5) defines in cartesian coordinates the membrane stress distribution for a shell of arbitrary shape. This equation, together with the conditions at the edges of the shell defines a boundary value problem whose solution gives the values of $\Phi(x,y)$ throughout the shell and from these values and equations (2) and (4) those of N_x, N_y and N_{xy}. Except for a few special cases (Flügge, 1960), the stress problem represented by equation (5) and the associated boundary conditions can only be solved by approximated numerical methods one of which we are going to exemplify in connection with the shells shown in figure A5. 2. This method, based on the replacement of the derivatives in equation (5) by their finite difference representation, makes possible the evaluation of the stress function $\Phi(x,y)$ on a network of discrete points defined on the XOY projection of the shell surface by two families of equidistant parallel lines, one normal to Ox and with the lines spaced by Δx and the other normal to Oy and spaced by Δy. The points of this network are projected vertically on the surface z=z(x,y) of the shell in order to define the corresponding values of p, q, r, s and t which enter into equation (5). Using double indexing, the first index referring to the direction of the Ox axis and the second to the Oy axis direction, the derivatives of the stress function at the (m,n) node of the grid may be written as follows:

$$\left(\frac{\partial^2\Phi}{\partial x^2}\right)_{m,n} \simeq \overline{\Delta x}^{-2} \cdot (\Phi_{m+1,n} - 2\Phi_{m,n} + \Phi_{m-1,n})$$

$$\left(\frac{\partial^2\Phi}{\partial y^2}\right)_{m,n} \simeq \overline{\Delta y}^{-2} \cdot (\Phi_{m,n+1} - 2\,\Phi_{m,n} + \Phi_{m,n-1})$$

$$\left(\frac{\partial^2\Phi}{\partial x\partial y}\right)_{m,n} \simeq (4\,\Delta x\;\Delta y)^{-1} . (\Phi_{m+1,n+1} - \Phi_{m-1,n+1} - \Phi_{m+1,n-1} + \Phi_{m-1,n-1}) \qquad (7)$$

in which $\Phi_{m,n}$ is the value of $\Phi(x,y)$ at the (m,n) node.

If the above expressions are introduced into equation (5) and assuming $\Delta x = \Delta y = d$, the following approximate relationship is obtained:

$$2(r_{m,n}) + t_{m,n}).\ \Phi_{m,n} - t_{m,n}.\ (\Phi_{m+1,n} + \Phi_{m-1,n}) - r_{m,n}.\,(\Phi_{m,n+1} + \Phi_{m,n-1}) +$$

$$+ \frac{s_{m,n}}{2} . \ (\Phi_{m+1,n+1} - \Phi_{m+1,n-1} - \Phi_{m-1,n+1} + \Phi_{m-1,n-1}) - d^2 .\, P_{m,n} = o \qquad (8)$$

in which $P_{m,n}$, $r_{m,n}$, $s_{m,n}$ and $t_{m,n}$ are the corresponding values, at the (m,n) grid node, of P(x,y) and of the second derivatives of the equation z(x,y) of the middle surface of the shell.

Normally, the equation of this middle surface is known - and its

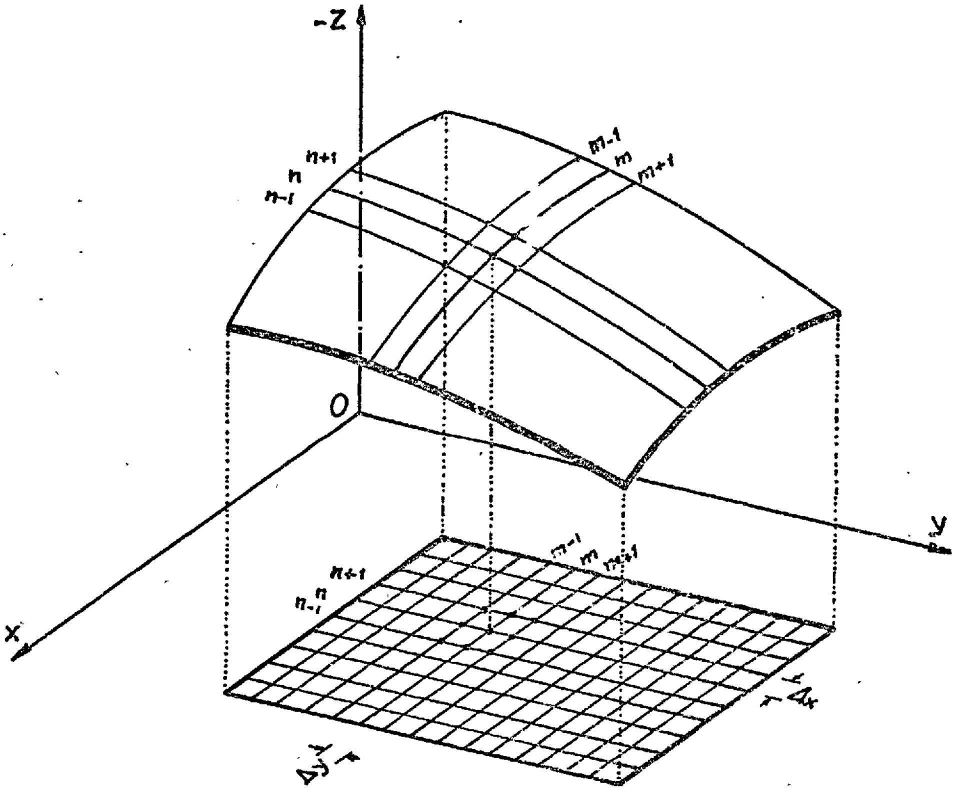


Fig. A5.2 - Finite difference method of integration of the stress equation for a simple shell.

derivatives can therefore be computed - and the components of the load are also known. The integrals in equation (6) are computed for each (m,n) grid node along the grid lines which cross at that node, starting from the initial values x_0 and y_0 which are the same for all the points of the grid. Along the edges of the shell, equation (8) cannot be applied because it would imply the knowledge of the stress function on grid points situated outside the domain of integration; this difficulty is removed by making use of the equations (4) which express the values of the stress function in terms of its values on the boundaries, the integrals of $\overline{F}_x$ and $\overline{F}_y$ and the values of the edge loads $(\overline{N}_x)_{edge}$, $(\overline{N}_y)_{edge}$ and $(\overline{N}_{xy})_{edge}$ at the boundaries.

Equation (8) therefore applies to all the points of the grid, both internal and on the boundaries. It states that the value of the stress function on any grid node and its value on the nodes which surround it (cf. figure A5.3) must be so related that the corresponding functional relationship it expresses for that node is satisfied. Furthermore, if the x and y components of the load are not zero everywhere, the values of the components on distant grid nodes will influence the equilibrium condition (8) via the integrals in $P_{m,n}$.

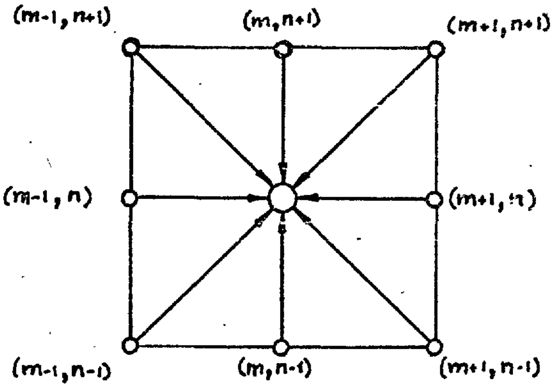


Fig. A5.3 - Dependence of the value of the stress function at the node (m,n) on the influence of the surrounding nodes.

If we apply equation (8) to all the points of the grid, we obtain a system of linear algebraic equations whose unknowns are the values of the stress function on the grid points. These equations in the system must now be solved conjointly in order to yield the values of those unknowns. There are several methods for the numerical solution of these equations, the most important of which (Willems and Lucas Jr.) are the Gauss elimination, the Seidel iterative and the relaxation methods. Whichever the method, however, the point which has most outstanding implications to our work is always the same: that the complete collection of functional relationships derived from (8) for all the nodes of the grid must be satisfied simultaneously and in a consistent manner. The distribution of stresses in a shell is therefore a global problem in which the value of the solution at any point is related and dependent on the values of the loads and of the stresses everywhere else in the shell and its boundaries. The numerical solution of the system of algebraic equations, particularly when using iterative methods, also draws attention to the character of a convergent process which such solution has, as embodied in the successive approximations along a convergent computing algorithm. This aspect of the stress boundary problems could be quite illuminating when considered in connection with the way the animal solves its rib cage boundary problem via the network of intercostal stretch-reflex servo assemblages.