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Contributions to the Biomechanics of the Vertebral Column II. Rotatory System Induced in the Thoraco-Lumbar Curvature by the Epaxial Musculature

Badania nad mechaniką kręgosłupa II. Ruchy obrotowe krzywizny piersiowo-lędźwiowej wywołane przez umięśnienie nadosiowe

[With 24 Figs.]

I. INTRODUCTION

The vertebral column of terrestrial mammals is constantly subjected to rotatory and transverse forces (Tucker, 1964), so that bending and stretching of the thoraco-lumbar curvature are always performed within this general biomechanical framework. Slijper (1946) assumed that vertebral bodies rotate around an axis situated at the level of the intervertebral discs. However, while rotation of this type is possible for terminal vertebrae, it is not possible when a metamer is attached at both its ends. It is obvious that in the normal condition of the vertebral column, posterior rotation must exert dorsally directed forces at its anterior end and ventrally directed forces at its posterior end. This is illustrated in Fig. 1 where force *d* indicates the direction of rotation and induces vectors *f* and *g* in the body of the vertebra (b). The reacting forces from the rest of the vertebral column (a) are in the opposite direction and are shown as forces *h* and *j*. The effect of rotation will then be the sum of all the forces it induces.

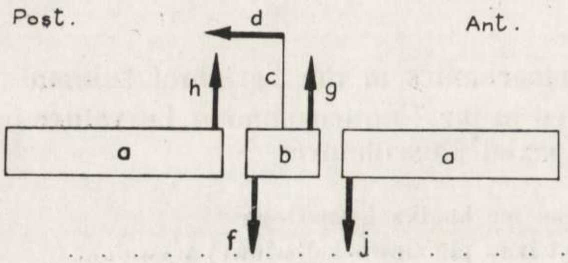

Fig. 1. Distribution of forces in the posterior rotation of a single vertebra.

The main rotatory complex is the epaxial musculature. This is illustrated by comparison between this musculature and the rectus system. Vertebral bending results from the action of the rectus system (Slijper, 1946; Tucker, 1955) which acts primarily at both ends of the curvature and therefore simultaneously on all metameres. Consequently, this action markedly affects the inclination of the vertebrae and has little effect on their rotation. In contrast to the rectus system, the epaxial musculature which effects strainghtening, acts on single metameres along the vertebral column, resulting in a more regional and less simultaneous action and exerts considerable rotational force on all metameres.

The reacting forces *h* and *j* indicated on Fig 1 must change the axis of rotation from the level of the intervertebral discs, as supposed by Slijper, towards the centre of the body of the vertebrae. Thus the object of this paper is to investigate the details of the rotation of a single vertebra and the effect of such rotation on other vertebrae. There are, of course, a large number of variations possible, but it is sufficient to outline the effects of rotation on an individual vertebra in three general situations:

(a) when it is more or less horizontal;
(b) when it is in the thoracic part of the curvature;
(c) when it is in the lumbar part of the curvature.

II. METHODS

The methods used are the same as those described in a previous paper (Tucker, 1964).

III. RESULTS

1. Anterior Rotation of Metameres in the Lumbar Part of the Curvature

A vertebra rotating anteriorly in the lumbar part of the curvature, if it is not opposed by forces from neighbouring vertebrae, would cause the type of deformity shown in Fig. 2. However, forces C^{1} and C^{11} are normal-

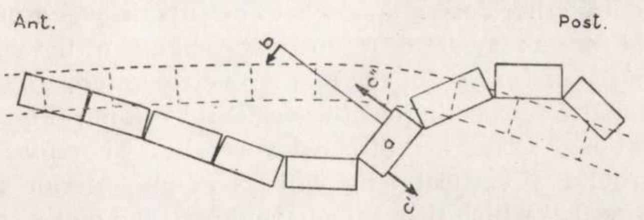

Fig. 2. Deformation in the lumbar part of the vertebral column induced by unopposed anterior rotation of a single vertebra.

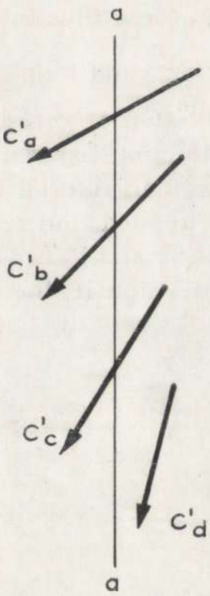

Fig. 3. The different positions (a, b, c, d) of force c′ induced by rotation of a single vertebra relative to the perpendicular a—a.

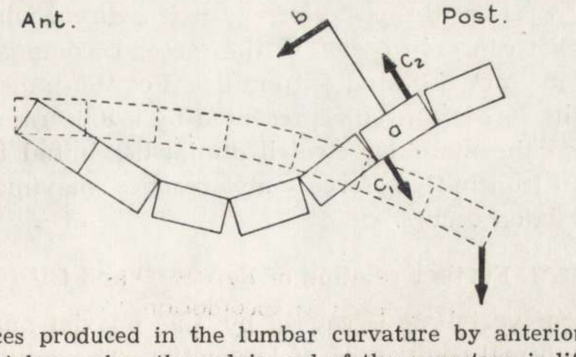

Fig. 4. Forces produced in the lumbar curvature by anterior rotation of vertebrae when the pelvic end of the curvature is lifted.

ly influenced by other forces opposed to or superimposed on them. The same external forces may act differently at each end of the vertebra. This can be shown by an analysis of the relation between forces C^{1} and C^{11} and the gravitational forces acting on the vertebral column (Fig. 3).

All gravitational forces are directed ventrally. Therefore rotation of a vertebra around a vertical axis will exert an anterior force C^{1} and a posterior force C^{11} which respectively reinforce and oppose gravitational vertical force, illustrating the changing relations to gravitational force according to the extent of rotation.

In the unsupported phase of locomotion when the pelvis is lifted, conditions of rotation change to those illustrated in Fig. 4.

2. Effects of Rotation on Thoracic and Lumbar Ends of the Curvature

It is obvious that anterior rotation of vertebrae in the lumbar part of the curvature will cause flattening, especially where the inclination is marked, and this in turn results in an anterior shift of the thoraco-lumbar curvature. If small forces are applied the scapular end of the thoraco--lumbar curvature shifts anteriorly and if larger forces are applied a shift occurs in two stages, first at the scapular, then at the pelvic end (Fig. 5).

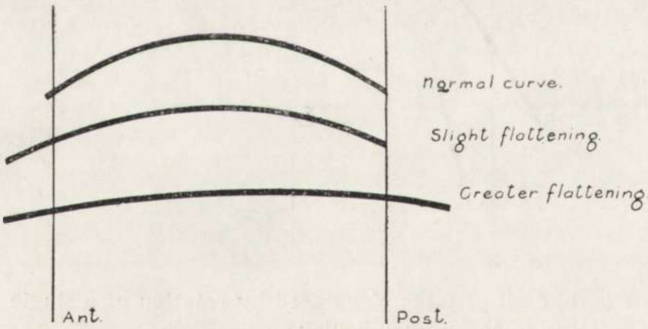

Fig. 5. Two stages of flattening of the normal thoraco-lumbar curvature.

This shift is due to differences in the morphological connections at the two ends of the curvature. At the anterior end, the connection is a loose, muscular type, while at the posterior end it is a direct joint between the bones, and a shift can only occur if the forces become great enough to counteract the mass of the hind extremities. For the same reason, at the posterior end the forces can be represented by a uniform scalar while at the anterior end the muscular stretch diminishes initial transmission of force, and the transmitted force only reaches maximal value after muscular contraction occurs.

3. Further relation of Forces C^{1} and C^{11}

The rotation of vertebrae is caused by the epaxial musculature and, therefore, is a normal component of locomotion. The result of the action of forces C^1 and C^{11} depends on the magnitude of these forces and the presence of external forces. In general, forces C^1 and C^{11} in a single vertebra will tend to change the relation between horizontal and vertical forces by (1) changing the inclinations in the lumbar and thoracic parts of the curvature (flattening); (2) causing a slight change in the position of the whole curvature.

4. Posterior Rotation of Metameres in the Lumbar Part of the Curvature

In posterior rotation, forces C^1 and C^{11} reverse their direction; C^1 now opposes the ventrally directed gravitational forces and C^{11} is now super-

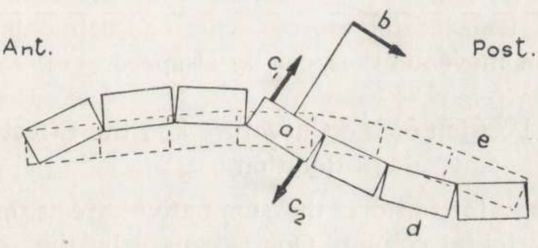

Fig. 6. Deformation in the thoracic part of the vertebral column induced by unopposed posterior rotation of a single vertebra.

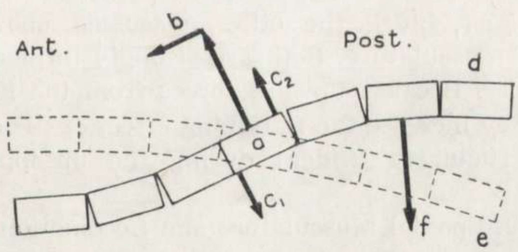

Fig. 7. Forces produced in the thoracic curvature by anterior rotation of a vertebra when the pelvic end of the curvature is lifted

imposed on existing gravitational forces. Posterior rotation of a given metamere, if not opposed by external forces, will result in deformity of the vertebral column as in Fig. 6.

5. Anterior Rotation of Metameres in the Thoracic Part of the Curvature

Anterior rotation in the thoracic part of the curvature, when the pelvic end of the curvature is lifted is shown in Fig. 7. As was seen in Fig. 3, force C^1 is the only effective force and acts to flatten the curvature.

In posterior rotation, the action of forces is the reverse of Fig. 7. Force C^1 now opposes gravitational force, while C^{11} is superimposed on them. Thus C^{11} now acts to flatten the curvature.

6. Rotation of Horizontally Situated Metameres

The general conditions of rotation of these metameres are similar to those discussed previously, and the only effective force is that which reinforces the gravitational force.

7. Straightening of the Curvature

From the above analysis it will be seen that shifting of the curvature and consequent increased length of the vertebral column are important results of any rotation of metameres (Fig. 5). Consequently, they are an important factor in locomotion. T u c k e r (1964) showed that lengthening increases the anterior shift of the forelimb and reinforces the horizontal components of the translocatory forces. These adjustments are related to the effectiveness of movement, especially at speed.

8. Changes in the Position of the Curvature and the Effect on Metameric Rotation

It is now possible to consider the summative effects of two types of rotation on the vertebral column. One is caused by the action of torque which is especially pronounced during the unsupported phases of locomotion and can be expressed by the moment of the field and similar equations (T u c k e r, 1964); the other, discussed above, is due to the action of epaxial musculature. Both are strongly influenced by constant gravitational forces. Because upward forces from the limbs oppose gravitational pull, they increase the flattening effect of the epaxial musculature. This is particularly evident during the unsepported phases of locomotion.

9. Epaxial Musculature and Locomotion

The system of rotatory forces illustrated in Fig. 1, 2, 4, 6, & 7 is multiplied when a number of vertebrae are involved. This will also be infuenced by he morphology of the participating vertebrae.

The following factors will influence rotation:

(a) the shape of the spinous processes;
(b) the number of rotating vertebrae;
(c) the number of muscular insertions on the vertebrae;
(d) morphology of the epaxial musculature;
(e) the function of the epaxial musculature in relation to other structures, e.g. the head.

Some aspects of these points are referred to in paper by S l i j p e r (1946), R i n k e r (1954), and T u c k e r (1955). S l i j p e r considers that the spinous processes transmit the rotatory forces from the musculature to the vertebrae.

There is a large group of animals (e.g. *Phenacodus primaevus*, *Bos taurus*, *Mastodon*, *Arsinoitherium*, *Sus scrofa*, *Dolichorhinus*, *Enteledon*, *Brontops*, and *Bison*) (see illustrations, Tucker, 1964) in which the thoracic spinous processes are the longest and consequently rotatory forces are maximal in them. In others the vertebrae have spines of more or less equal size along the whole curvature (e.g. *Scelidotherium*, *Mesopithecus*, *Astropotherium*) or the thoracic spinous processes themselves may be of various lengths with consequent variation of rotatory force within the one area (e.g. *Cricetinae*). In addition, the effect of the length of the lever is influenced by the position of insertion of the various parts of the epaxial musculature on the spinous processes, and this may occur at various levels as illustrated in the case of *Sigmodon* (Fig. 8).

The other factors listed will not be discussed further in this paper.

10. Formation of the Rotatory Systems.

The simultaneous rotatory action of a number of vertebrae will create a rotatory system whose action will depend on the epaxial musculature. The following systems are possible in the thoraco-lumbar curvature:

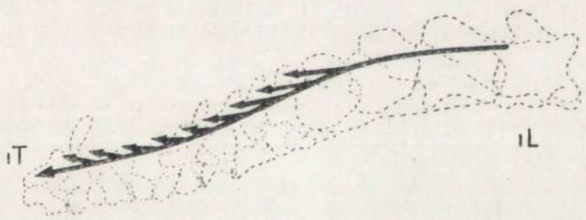

Fig. 8. Insertions of *M. semispinalis dorsi* in *Sigmodon* (after Rinker). (According to May, 1964, the correct name for this muscle in the thoraco-lumbar region is *M. spinalis dorsi*).

A. Internal Rotatory Systems:

(1) A simple rotatory system: — When the vertebrae comprising the system have roughly the same angle of inclination, i.e. they must all lie on one side of the curvature.

(2) A compound rotatory system: — When the vertebrae comprising the system have different angles of inclination, i.e. they lie on both sides of the curvature.

B. External Rotatory Systems:

An external rotatory system exists when the rotating system is conected with and influenced by structures outside the thoraco-lumbar curvature. Such a system may be: —

(1) An external anterior rotatory system which is connected with cervical musculature and the head.

(2) An external posterior rotatory system which is connected with the pelvic musculature.

The rotatory system can be conveniently illustrated on the thoraco--lumbar curvature of *Sigmodon* (*Cricetinae*) (Fig. 8). It can be seen that in dissected specimens, the insertions of *m. spinalis dorsi* are situated between T_1 and L_1, resulting in posterior rotation of thoracic vertebrae, while rotation in the lumbar vertebrae is slight and in the opposite direction. This example also illustrates the importance to the rotatory system of the level of insertion of the musculature. The vertebrae T_1, T_2, T_3, T_4 have similar inclinations, and muscular insertions roughly at the same level. However, the spinous process of T_5—T_8 have a different and more pronounced inclination.

As this example introduces us to the application of biomechanical principles to living structure, it may be as well to elaborate at this point. In the case discussed, the effect of rotation is an outcome of a number of factors illustrated in Fig. 9 which shows: (1) inclination of vertebral

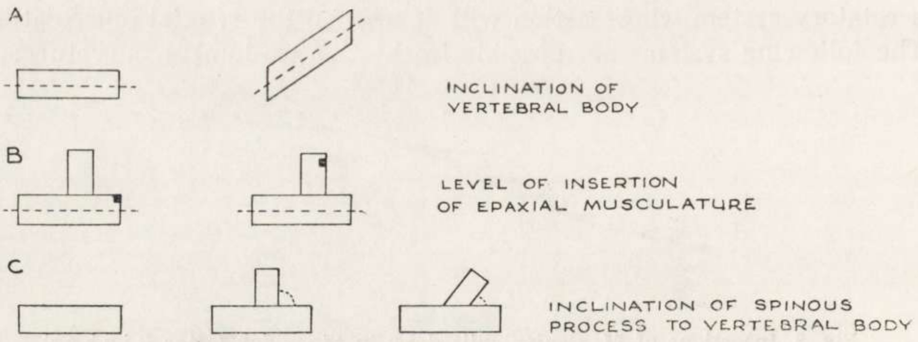

Fig. 9. The factors included in the rotation effect: (A) inclination of vertebral body; (B) level of insertion of epaxial musculature; (C) inclination of spinous processes to vertebral body.

bodies: (2) the level of insertion of epaxial musculature; and (3) the inclination of the spinous process of the vertebral body. Consequently, the effective rotation of e.g. T_6 (Fig. 8) can be expressed as the effect of rotation of T_1 plus the increased leverage due to its higher muscular insertion, minus the loss due to the posterior inclination of its spinous process. The whole rotatory effect will be modified as a result of the inclination of the vertebrae illustrated in Fig. 9. The complete rotatory effect must, of course, be considered within the framework of gravitational forces (Tucker, 1964).

The function of a simple system is easily understood. Some problems involved in the functioning of compound rotatory systems are illustrated in Fig 10, drawn after Rinker (1954), showing the insertions of *M. lon-*

gissimus dorsi in *Sigmodon*. This muscle extends from the last cervical vertebra to the sacrum and has insertions at different levels on the vertebrae which have different inclinations and heights of their spinous processes. In a similar manner, the external rotatory systems are exemplified in the morphology of *M. longissimus cervicis* (Fig. 11) and in *M. longissimus capitis* and *M. semispinalis capitis* (Fig. 12) in *Sigmodon* (after Rinker, 1954). The topography of these muscle, if compared with *M. longissimus dorsi*, explains the opposite rotatory actions on the thoracic vertebrae.

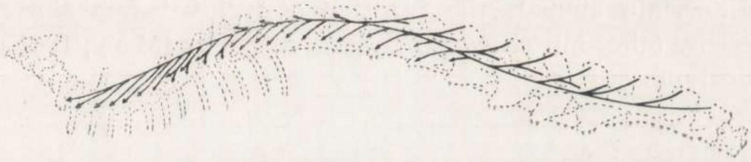

Fig. 10. Insertions of *M. longissimus dorsi* (after Rinker).

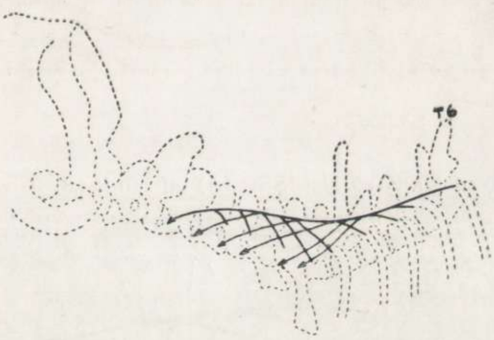

Fig. 11. Insertions of *M. longissimus cervicis* (after Rinker).

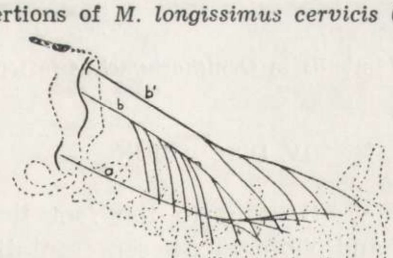

Fig. 12. Insertions of *Mm. longissimus capitis* (a) and *semispinalis capitis* (b, b′) (after Rinker).

The importance of rotatory systems is especially accentuated in animals of semi-aquatic habit. In animals which use two different means of locomotion (e.g. *Ondatra zibethica*), the rotatory system is important in adopting a suitable position of the vertebral column (Fig. 13).

The main rotatory muscle in mammals is *M. longissimus dorsi*. It extends over the whole thoraco-lumbar curvature with the sole exception of *Ornithorhynchus (*Fig. 14) in which animal it persists only as *M. ilio-lumbalis*. In the course of evolution this muscle changes considerably. Initially having insertions on all thoracic and lumbar metapophyses (Fig. 15) as thoraco-lumbar curvatures develop with increasing specialisation of locomotion, this muscle increases the number of insertions, extends towards the sacrum (Fig. 16) and attaches itself to aponeuroses (Figs. 14 and 16 — after Slijper, 1946; Fig. 15 modified from Slijper, 1946). The increased number of insertions need not be paralleled by an increase in volume of the muscle, which is related to a number of mechanical factors. In certain animals the function of *M. longissimus dorsi* may be taken over by other muscles e.g. *M. glutei* in the ox (May, 1964 personal communication).

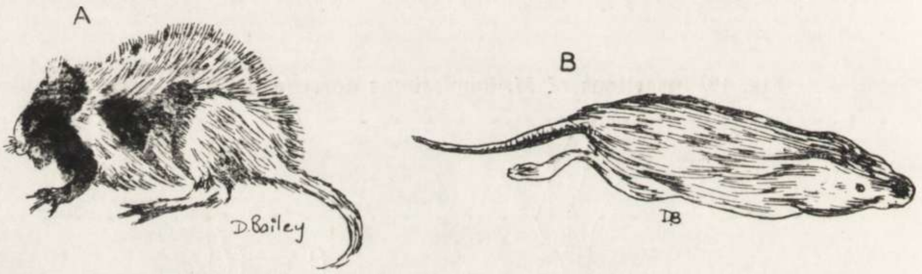

Fig. 13. Posture of *Ondatra zibethica* (A) on land; (B) in water (after Müller).

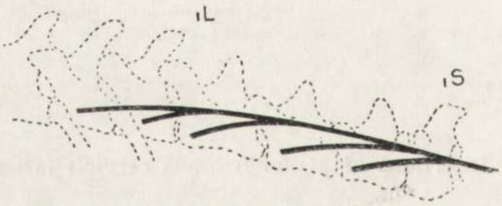

Fig. 14. *M. iliolumbalis* in *Ornithorhynchus* (after Slijper).

IV. DISCUSSION

Ottaway (1962) drew attention to the fact that an impression of motion can be achieved and photographic representation of various phases of motion can be done without any knowledge of anatomy and the details of function, but the situation is completely different when it comes to an understanding of the mechanisms involved. This can only be done through careful analysis based on morphology, physics and physiology. Each of these branches contributes to the concepts of biomechanics, an essential part of which is the relation of structures to each other which determines the distribution of forces and consequent actions.

Since the formation of the thoraco-lumbar curvature depends on the action of gravitational forces and of forces derived from the limbs, any variation in locomotion should affect it greatly. A number of morphological and functional adaptations in mammals were discussed in a previous paper (T u c k e r, 1964). One of the main evolutionary changes among vertebrates is reflected in the connection of the limbs with the vertebral column. In fish, and primitive aquatic reptiles neither the scapula nor the pelvic girdle are connected with the vertebral column. The main changes due to terrestrial locomotion are (1) direct contact between pelvic girdle and vertebral column; (2) a definite trend to move the scapula from an infra-vertebral to a supravertebral position. This tendency reaches its height in primates where the scapula has acquired a more or less horizontal position (Fig. 17). It is of interest to note in passing

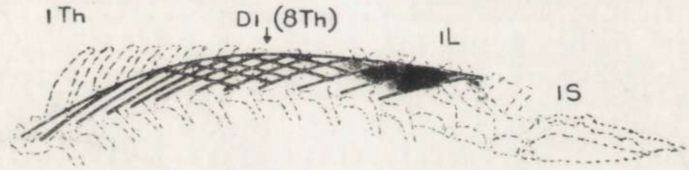

Fig. 15. *M. longissimus dorsi* in *Dasypus novemcinctus* (after S l i j p e r).

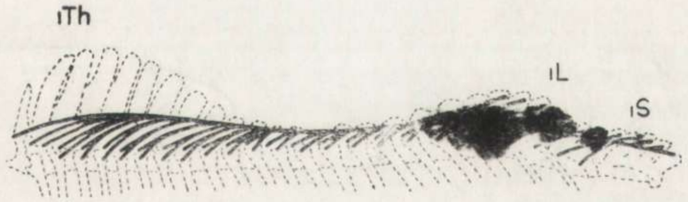

Fig. 16. Epaxial musculature in *Diceros bicornis* (after S l i j p e r).

that this figure shows that a dorsal transposition of the scapula is accompanied by a simultaneous ventral transposition of the pelvis.

Within the thoraco-lumbar curvature the existence of anticliny constitutes a general problem. S l i j p e r's (1946) comparative research in this subject dealt with the relationship between direction of the vertebral processes and morphology of the epaxial musculature. However, another aspect exists, arising from the material presented in this and a previous paper, namely that the anticlinal vertebra varies in its position on the thoraco-lumbar curvature in different species. Further, the significance of the inclination of the spinous process cannot be assessed without taking into consideration its relation to variations in the shape of the curvature. Details of this relationship are, at present, relatively little known. However, anticliny may be better interpreted in terms of the interaction between anterior and posterior rotatory forces to be referred to later in the discussion.

So far discussion of the vertebral column has dealt with the straight column of aquatic animals and the curved vertebral column of terrestrial quadrupeds. The bipedal variation of terrestrial locomotion is a very characteristic one, and it causes a fundamental change between rotatory forces and locomotion. For instance, the straightening of the thoraco-lumbar curvature, while helpful in the locomotion of quadrupeds, will

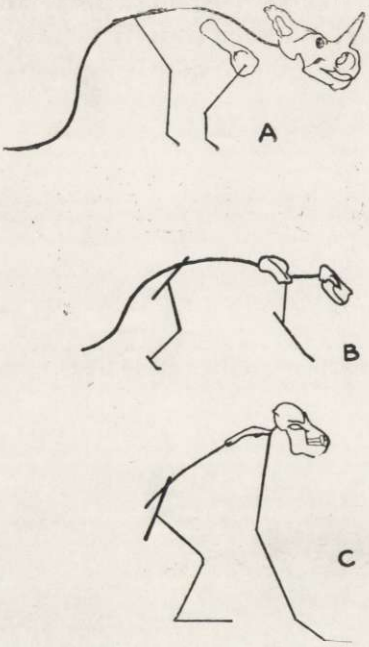

Fig. 17. The evolution of scapular / vertebral relations in a terrestrial environment: (A) infra-vertebral scapula (*Monoclonius*); (B) scapula on the vertebral level (*Barylambda*); (C) supra-vertebral scapula (*Pongo*).

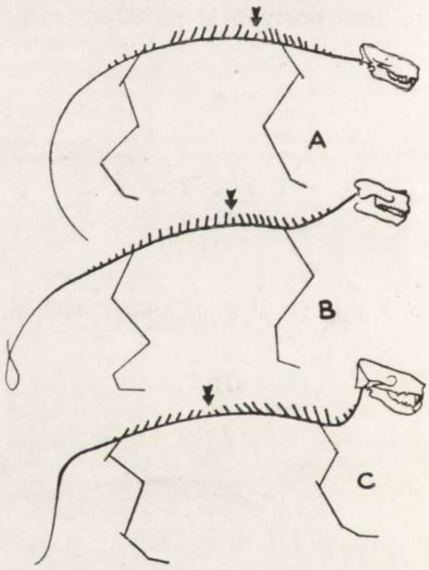

Fig. 18. The position of the anticlinal vertebra: (A) *Sinopa rapax*; (B) *Patriofelis*; (C) *Hyaenodon*.

hinder movement in man by shifting the centre of gravity posteriorly. Similarly, in man rotatory forces of a gravitational nature are only present in the thoracic part of the curvature and are seldom great. They can be reduced or changed by the action of rotatory systems of epaxial origin. Consequently, the position of the centre of gravity is influenced by epaxial rotatory systems to a much greater extent in man than in quadrupeds.

Due to the change of posture, the translocatory forces in locomotion change their direction in relation to the vertebral column from parallel in most mammals to transverse in man. This is accompanied by a shift of the main curvature towards the thoracic part.

It seems then, that the epaxial musculature functions in relation to locomotion in three different ways —

(1) In aquatic mammals, the permanent stretching of the thoraco-lumbar curvature has a locomotory value;

(2) In quadruped mammals straightening of the curvature is important at certain phases of locomotion;

(3) In man, its contribution to locomotion lies in maintenance of the centre of gravity. In all three cases, it forms an important biomechanical element.

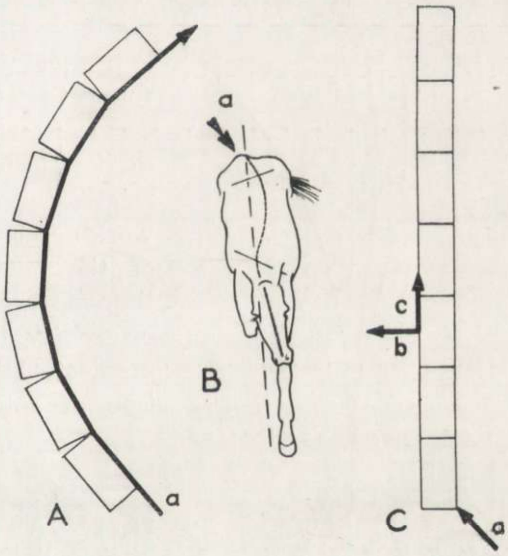

Fig. 19. Lateral bending of the vertebral column during locomotion. (A) Marginal transmission of stress in the vertebral column. (B) Lateral bending in the vertebral column of a horse. (C) Diagram of the distribution of forces causing lateral bending in the unilateral thrust.

The transmission of forces along the vertebral column is complicated by development of functional scoliosis due to the alternate use of left and right limbs. The locomotory push from one limb causes a lateral vector (Fig. 19C) which results in the scoliosis illustrated in Fig. 19B. Consequently the locomotory force is transmitted from one metamer to the next, not through the central part of the vertebral articular facet, but through its lateral margin (Fig. 19A). This shift may be partially corrected by *M. longissimus dorsi*. Superficially, this bending resembles the undulatory movement of *Ophidia* (G r a y, 1953) however it does not have a wave-like character and always occurs without the interference of external forces.

Recently M i l e s & S u l l i v a n (1961) reviewed the earlier literature on this lateral movement in man and considered that there is always a combination of abduction and torsion. They found that bending of the human vertebral column to the right is accompanied in many subjects by translocation of the lumbar region to the left and vice versa (Fig. 20). In their earlier study (1959) they found great variation in the shape of the vertebral column of the human. The direct influence of *m. quadratus lumborum* and its double innervation may offer some explanation of the variation in lateral movement. However, it is interesting to point out that this movement is similar in certain aspects to the locomotary bending of one phase of wave movement in ophidians, especially if the human vertebral column is considered as representing a segment of the longer column of snakes.

Joseph & McCall (1961) investigated the differences in muscular activity at various levels of the human vertebral column, and found that there is little or no activity in the cervical and lumbar regions and moderate or marked activity in the lower thoracic. They related this finding to the amount of muscular work necessary to maintain the normal position of the vertebral column. Since the lower thoracic region deviates most from the centre of gravity, the muscular work required here is greatest. Although the authors make no mention of rotatory forces in vertebrae, their findings corroborate the results discussed above that in man rotatory forces of a gravitational nature are present only in the thoracic part of the curvature.

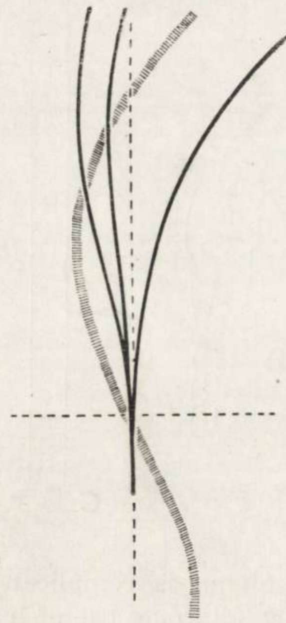

Fig. 20. Various degrees of translocation to the left in bending the human vertebral column to the right (black lines). For comparison the cross-hatched line represents a segment of the vertebral column of a snake during locomotory movement.

The importance of musculature in maintaining the curvature in the various locomotory phases is emphasised by Freye (1954) who discusses the vertebral column of the beaver and shows that the curvature in the live animal may differ from that estimated from the articulated skeleton.

The comparatively low level of muscular activity in the lumbar part of the curvature does not indicate an absence of vectors other than perpendicular, but rather, than these forces are opposed by non-muscular structures. Davis (1961) indicates that in the lumbar region of the human vertebral column, gravitational forces on the vertebral bodies are resolved into two components, one acting obliquely downward and backwards, the other acting forwards; this forward component is counteracted by the processes of the lumbar neural arches.

There are a number of observations regarding the variation of vertebrae in various mammals, mostly of a purely morphological and statistical character, but their evaluation in relation to movements is still lacking. (Stecher, 1959, 1961, 1962a, b; Stecher & Goss, 1961; Pilarski & Roskosz, 1959). Stecher (1962a) indicates that, as a result of his study of the lumbar vertebral column of the horse, increase in size of an animal imposes great muscular disadvantages for locomotion. He concludes that the stride varies directly with the length of the animal, and muscle pull with the square of the length, while the weight varies with the cube of the length. Momentum is increased inordinately since it is a product of speed and mass. In animals such as the horse, ox, camel, and elephant this is compensated for by a relative stiffness of the caudal portion of the column. The horse develops special lateral joints in the caudal lumbar region, unique to this species and found in all horses, domestic, wild and prehistoric. In all probability, these lateral joints enable horses to stabilise the vertebral column during rearing (May, 1964 personal communication).

The relation of the vertebral column to the movement of the sacrum was discussed by Weisl (1954) who concentrated on the articular surfaces. On a more comparative basis, the relation of the morphology of the limbs and vertebral column to movement was discussed by Stapley (1912), Snyder (1954, 1961, 1962) and Slijper (1946). Stapley concentrated on the cervical region, Snyder studied the morphology of bipedal lizards from a functional point of view and Slijper studied in detail the vertebral column and spinal musculature in mammals. From Snyder's studies it is obvious that changes which lead to manipulation of the centre of gravity are most important in transition from quadruped to bipedal locomotion, which in lizards has been achieved without fundamental modification of the morphology of the pelvic appendage.

Manipulation of the centre of gravity primarily depends on (1) the interaction between translocatory and horizontal forces (Tucker, 1964) and (2) the exertion of other forces on the vertebral column — hence in the column the functional meeting of two types of force is produced. The magnitude of both forces depends on the translocatory mechanism. As shown in Fig. 21, if the pelvis is raised, horizontal forces are diminished, but gravitational forces are doubly increased since (1) raising the pelvis increases weight exerted at the anterior end and (2) the "pushing" force (upper arrows, Fig. 21B) is added to the gravitational forces at the anterior end. At any given point of meeting, the two given sets of forces are reciprocally proportional. Furthermore, these forces always act together, i.e., they cannot be considered independently in locomotion. Algebraically, both sets of forces are equivalent.

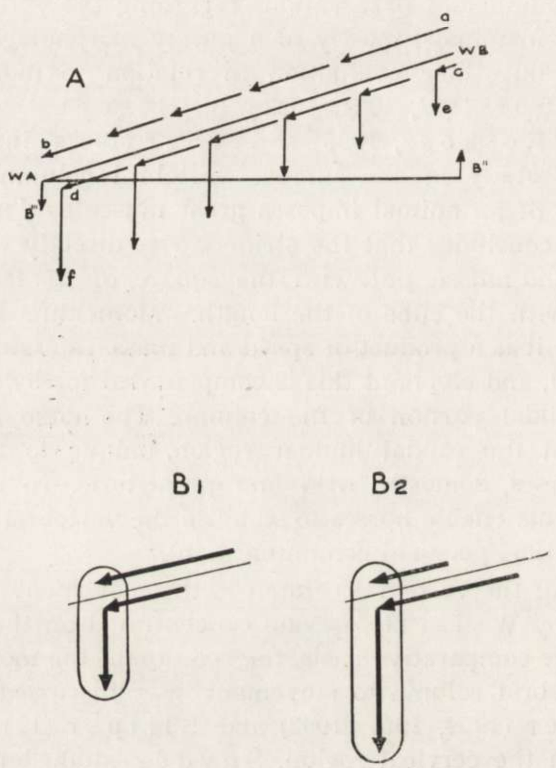

Fig. 21. The mutual interrelationship of gravitational and translocatory forces in the vertebral column: (A) $B'' - B'''$ represents the horizontal position of the vertebral column, where B'' is a perpendicular component of the translocatory force, and B''' is the related, ventrally directed vector (T u c k e r, 1964). The change in position of the vertebral column from B''—B''' to WB—WA will result in progressive diminution of the effective translocatory force from a to b, and simultaneous increase (Ge to df) in gravitational forces resulting from translocatory thrust. B_1 and B_2 illustrate conditions at the posterior and anterior ends of the curvature showing that gravitational and translocatory forces are mutually interrelated.

This interaction between translocatory and gravitational forces is less complicated in reptiles as exemplified by the goanna (*Varanus varius*). From Fig. 22 it is seen that unstable equilibrium is achieved by raising the centre of gravity only and force g in Fig. 21 (B) is not increased at the anterior end of this column. This is a simpler and less effective means of initiating locomotion than in mammals and is due to the fact that in reptiles, the limb is held out at an angle to the body, whereas mammals have rotated the limb until it is placed under the body and parallel to its long axis.

A basic point to be seen, then, from the above discussion is that *m. longissimus dorsi* which stretches the vertebral column is one of the important muscles in locomotion. Its action is built on the preparatory arching of the column by the rectus musculature (T u c k e r, 1955).

An important conclusion from S l i j p e r's (1946) investigation was that the epaxial musculature functions to prevent deviations of the verte-

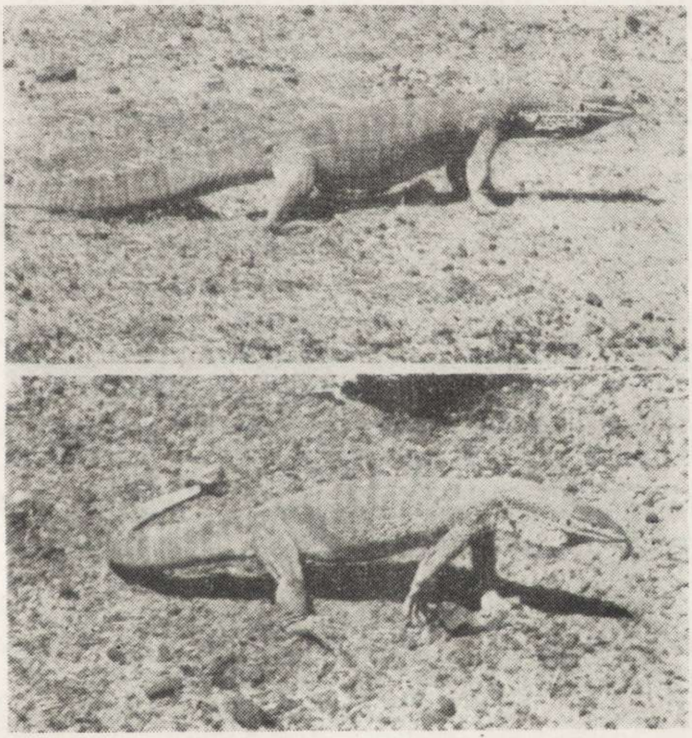

Fig. 22. The acquisition of unstable equilibrium in reptiles (*Varanus varius*). Note that the centre of gravity is raised, but the lateral position of the hind limbs does not raise the posterior end of the thoraco / lumbar curvature. (Photographs by courtesy of Mr. Ian S m i t h).

bral column from the sagittal direction, a feature which he considers of evolutionary significance. This, of course, can only be achieved with bilateral muscular action. Although he considers in detail the relation of the muscles to the spinous processes, he does not extend his analysis to the forces present in the vertebral column itself. From the present analysis, it is clear that the stabilising anteriorly directed vector in the vertebral column is the result of multiple rotations within the column. Consequently, in the vertebral column, at least two parallel anteriorly directed vectors are present, one resulting from the translocatory force from the limbs (b), the other from the rotatory action of the epaxial musculature (*a*, *a′*) (Fig. 23).

A third parallel vector (c) is also present due to the meeting of gravitational and translocatory forces which have already been illustrated in Fig. 21. It is interesting to consider the relation between these three parallel vectors: it is clear that maximal danger of lateral deviation occurs at the beginning of translocatory thrust (i.e. the two vectors from the limbs), and consequently, the maximal protective value of the anterior vector from the epaxial musculature must be applied just before the

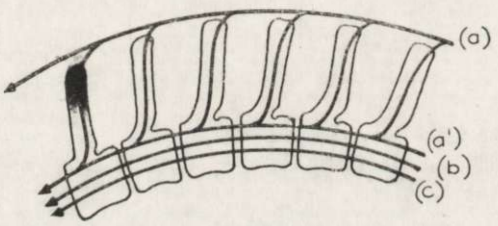

Fig. 23. Parallel vectors in the thoraco-lumbar curvature (see explanation in text).

thrust from the limbs. This leads to an important sequence of locomotory movements which may be as follows:

(1) a "fixing" action of the epaxial musculature producing a moderate rotation;

(2) the anterior vector due to elevation of the pelvic end of the column;

(3) the translocatory force from the hind limbs;

(4) a "stretching" action of the epaxial musculature.

In the first phase, the epaxial musculature acts to stabilise the column and prevent the dissipation of forces.

Slijper (1946) discussed the forces which cause a posterior rotation of the vertebrae but did not consider the presence of forces causing anterior rotation which exist for the reason that any muscular contraction must exert force at both ends of the muscle. The phenomenon of anticliny referred to earlier may, therefore, at least in part be an expression of this mechanical set-up, thoracic spinal processes having a posterior inclination in an area where posterior rotation is predominant. The spinal processes are straight in the lumbar area where anterior and posterior rotation are both common. Another factor which may influence the position of the anti-clinal vertebra includes the mechanics of the cervical and cranial parts of the skeleton.

There are, of course, many other actions leading to extensive bending of the vertebral column. Slijper (1946) discusses and illustrates this property of flexibility. As, however, they are not directly related to the general locomotion of mammals, they are outside the scope of the present discussion.

Finally, let us consider the mechanical contributions to torque made by the different rotatory systems evoked by the epaxial musculature.

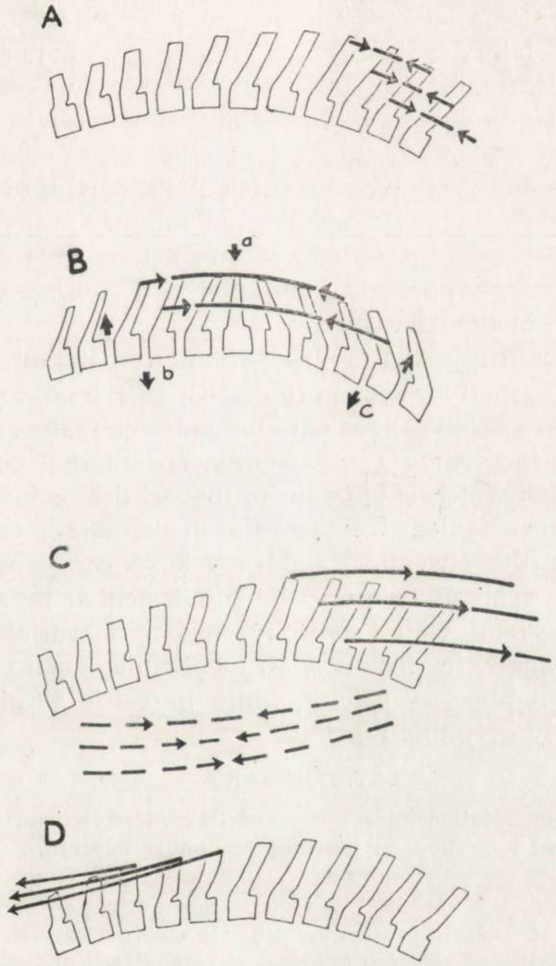

Fig. 24. (A) A simple rotatory system. (B) A compound rotatory system: *a* is the anticlinal vertebrae, *b* illustrates posterior rotation in the thoracic part, and *c* anterior rotation in the lumbar part of the curvature. (C) An external posterior rotatory system and the opposing rectus system (indicated by broken lines). (D) An external anterior rotatory system. Such a system may be opposed by all systems illustrated in (A), (B) and (C).

A simple rotatory system (Fig. 24A) in most cases is limited to the lumbar portion of the thoraco-lumbar curvature. When the inclination of the vertebrae is close to zero as in most of the *Equidae* and *Pecora*, the action of the system supplies an extra stabilising force discussed by Slijper (1946). In curvatures with a marked inclination, the simple rotatory system in the posterior part of the curvature will facilitate translocatory thrust, but only in the initial stages, and does not influence the manner in which the translocatory thrust is opposed by the front limbs.

A compound rotatory system (Fig. 24B) will have a much wider range of functions. Its influence on anticliny has already been discussed; in addition its action on change in vertebral inclination will be much more pronounced with an increased stretching effect. Furthermore, it also influences the manner in which the front limbs oppose the translocatory shift. Both simple and compound internal rotatory systems simultaneously contain anterior and posterior rotatory action. This fact may throw a new light on the morphological variation in vertebrae at the thoracic and lumbar ends of the curvature.

An external rotatory system induces rotation in one direction only. An external posterior rotatory system (Fig. 24C) will tend to diminish the inclination of the curvature; An external anterior system (Fig. 24D) will tend to increase inclination. Consequently, an external posterior system provokes an action which is opposite to that of the rectus system, while an external anterior system increases the inclination of vertebrae in the anterior part of the curvature and provokes a correcting action by an internal rotatory system. This may be supplemented by a posterior external rotatory system, which shows morphological variations in various animals. In the horse, for instance, *M. longissimus dorsi* extends posteriorly over the lumbo-sacral joint, while in cattle *M. glutaeus medius* extends anteriorly over this junction.

V. SUMMARY

The conditions of rotation of a single vertebra, its relation to the vectors in other vertebrae, and its action on the thoraco-lumbar curvature were analysed in detail.

During locomotion, the vertebral column is constantly subjected to two groups of rotatory forces, one due to torque, the other to rotation of vertebrae induced by the epaxial musculature. These latter forces were analysed and their classification suggested.

The role of the epaxial musculature in locomotion was considered with reference to the shape of the curvature, the relation of rotation to lateral bending, and to translocatory forces.

The interaction of vectors within the vertebral column was analysed, and the relation of anticliny to rotational forces was pointed out.

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STRESZCZENIE

Szczegółowo analizowano warunki ruchu pojedynczych kręgów, ich stosunek do wektorów innych kręgów i działania na krzywiznę piersiowo-lędźwiową kręgosłupa.

Podczas poruszania się kręgosłup podlega działaniu dwu grup sił obrotowych: 1. powodowanych momentem skręcającym, 2. wynikających z obrotu kręgów działaniem umięśnienia nadosiowego. Analizowane były te ostatnie siły i zaproponowano ich klasyfikację.

Rola umięśnienia nadosiowego w lokomocji rozpatrywana była w odniesieniu do kształtu krzywizny kręgosłupa, stosunku obracania się do wyginania bocznego i sił przemieszczających.

Analizowano współdziałanie wektorów w obrębie kręgosłupa i wskazano na stosunek jego wygięcia do sił obrotowych.