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Contributions to the Biomechanics of the Vertebral Column**I. Biomechanical Characteristics of the Thoraco-Lumbar Curvature****Badania nad biomechaniką kręgosłupa****I. Biomechaniczna charakterystyka krzywizny piersiowo-lędźwiowej**

[With 2 Tables, 22 Figs & 7 Pls.]

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I. INTRODUCTION

The importance of the vertebral column is emphasised by the division of animals into invertebrate and vertebrate groups (L a m a r c k). The "backbone" forms the basis of all body movements, hence the study of its biomechanical properties contributes to our knowledge of the essential relationship between morphology and function.

The mechanics of the vertebral column have been studied in various ways, for example: by studying the morphology of the vertebral processes and their changes with reference to the function of epaxial musculature (Slijper, 1946); by analysing lateral bending of the vertebral column as a factor in locomotion (Gray, 1953); or by submitting the human vertebral column to various kinds of stress (Wyss & Ulrich, 1954). Before a meaningful experimental approach to a complex functional system can be attempted, an extensive mechanical analysis of the system must be made. A general analysis of the mechanics of the tetrapod skeleton including some conclusions concerning the vertebral column was published by Gray (1944). He considered that the vertebral column consists of "a flexible overhung beam supported by four elastic legs". The hypotheses comparing the function of the vertebral column to an "arched roof", "a bridge with parallel girders" and to a "cantilever bridge" were discussed, together with the relevant literature by Slijper (1946). He draws attention to the importance of the vertebral processes but does not give full consideration to the spinal curvature and the vertebral bodies themselves. Since these hypotheses do not cover the whole range of functional significance of the vertebral column, an investigation of the properties of spinal curvature is the main purpose of the following study.

The spinal curvature consists of a number of articulations, hence the properties of angular relations are basic to its analysis. In so far as all relations can be expressed as ratios, they are non-dimensional. Consequently, biomechanical investigations may reveal general and non-dimensional properties in structures which are themselves particular and dimensional. Thus the significance of any structure is the sum of its dimensional and non-dimensional properties, the point at which abstraction and reality meet.

The discussion which follows is divided into three parts. The first deals with analytical definitions and concepts related to angular relations and with the distribution of forces and induction of torque. In the second section, biomechanical data from a variety of vertebral columns are tabulated and examples of their analyses discussed in some detail. The final section of the work deals with the biological implications of conclusions drawn from the analytical treatment and exemplifies these by relating them to representative types of animals.

The method used throughout this study is biomechanical analysis. Its advantages and disadvantages are discussed by Gray (1944). For estimation of basic relations, the position of relevant parts in mounted skeletons is outlined. The shape of the thoraco-lumbar curvature is reproduced by a line drawn along the dorsal margin of the vertebral bodies; the position of the *spina scapulae* is taken as the axis of the scapula, and the axis of the coxal bone estimated as in Fig. 1.

II. ANALYTICAL DEFINITIONS AND CONCEPTS

1. The thoraco-lumbar curvature

The mammalian vertebral column bends dorsally between its sacral and cervical parts forming the thoraco-lumbar curvature. This curvature defines the angular relations between the vertebral column and coxal bone and between the vertebral column and scapula. The intervertebral articulations lying between the scapular and coxal regions include



Fig. 1. The axis (WB) of the coxal bone of a cow.

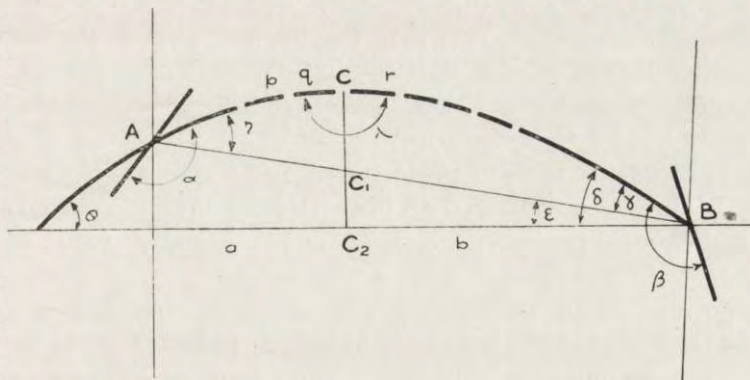


Fig. 2. Angles defining the thoraco-lumbar curvature (see explanation in text)

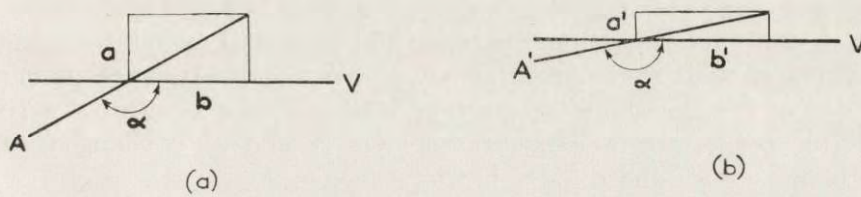


Fig. 3. Explanation in text.



Fig. 4. Explanation in text.

a number of angles which affect the mechanical properties of the column itself. Fig. 2 illustrates the basic angular relations in the thoraco-lumbar curvature and defines the terms used in this analysis.

It can be seen that the angles used in defining the thoraco-lumbar curvature are as follows:

Thoraco-scapular angle (α); sacro-coxal angle (β); intervertebral angle (λ) between vertebrae q and r ; the inclination of the lumbar part of the curvature is shown by the angle (γ) between the chord (C_1) and the lumbar portion of the curvature; inclination of the thoracic part is shown by the angle (η) between the chord and the thoracic portion. Supplementary data can be obtained by the angle (ϵ) formed between the chord and the horizontal component of thrust from the hind limb; from the angle (δ) between the horizontal component and the lumbar part of the curvature and the corresponding angle (θ), with the thoracic part of the curvature.

The values of these angles will define in turn the length of a and b . The height of the curvature at its apex is the distance $C - C_1$ which enables the transposition of force from point C_2 to C .

The angle ϵ and the ratio of projection a and b indicate the position of the thoraco-lumbar curvature. The properties of the curvature can thus be described by: its position; value of angles α and β ; value of angles $\lambda_1 \lambda_2 \lambda_3$ etc.

The magnitude of angles α and β governs the distribution of vertical and horizontal components of forces originating from the limbs as well as those from the vertebral column itself. The influence of these angles on the distribution of forces is shown in Figs. 3 and 4.

In Fig. 3 the position of the axis of the scapula A is changed, while the position of the corresponding part of the vertebral column V remains fixed. The shift of A to A' results in $\alpha' > \alpha$ and this in turn results in $a > a'$ but $b' > b$. In Fig. 4 the position of the scapular element A is fixed while the position of the vertebral element (V and V') is changed. This results in $\alpha'' > \alpha'''$ and $a''' > a''$ but $b'' > b'''$.

2. Translocatory and gravitational forces

The interaction of gravitational and translocatory forces creates a biomechanical background for all movements of terrestrial mammals. These interactions depend on the angular relations between the vertebral column and the scapula and pelvis and also on the biomechanical properties of the thoracolumbar parts of the curvature, i.e. its position, height and length of thoracic and lumbar parts. Gravitational and translocatory forces reach an equilibrium by developing passive and active stresses in the thoraco-lumbar curvature and in the muscular systems associated

with it. These stresses in the vertebral column have different magnitudes of changeable duration. Gravitational forces have three properties:

1. They are mainly passive forces which must be held in equilibrium by active muscular forces.
2. They are variable in magnitude, due to variation in distribution of stress in the body.
3. They show relative stability of vectors.

This stability of vectors is also characteristic of translocatory forces, mainly because of the relative stability of the angles α and β . In contradistinction to the stability of vectors, the scalars (magnitude) and duration of stress are very variable. The motionless animal is usually in a relatively stable equilibrium. However, when the animal is in motion, this state is replaced by an unstable equilibrium created by translocatory forces from the limbs and variable forces from the mass of the horizontally moving body.

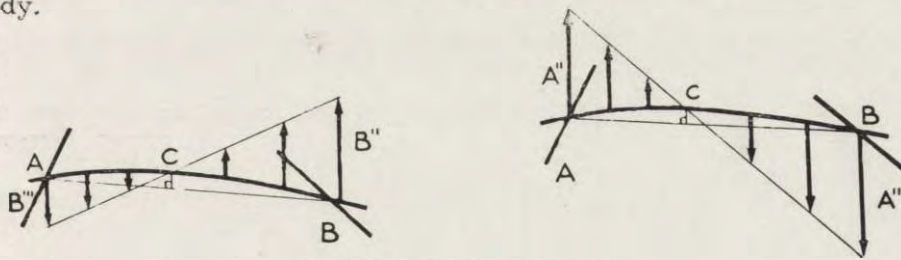


Fig. 5. Explanation in text.

Fig. 5(a) represents a state of equilibrium in a motionless animal. When, however, this equilibrium is destroyed by a force B'' from the hind limbs applied at B , it results in a change of position of the vertebral column and consequent increase in the force B''' on the opposite end of the curvature by increasing its inertia or by shifting the centre of gravity.

When in the final stage of movement a force A'' is applied from the forelimbs at point A , the torque is reversed and in consequence a downward force A''' will be exerted on the sacral end of the curvature (Fig. 5b). The nature of the vertebral curvature influences transmission of the torque usually by increasing the downward inclination of the vector and the thrust downwards at the opposite end of the curvature, adding to the gravitational forces already operative at this point. The importance of these forces in the locomotion of animals is revealed by subsequent analysis.

3. Transmission of forces along the vertebral column

Basic mechanical conditions are imposed on the vertebral column by its segmentation. Vertebrae are bound together by muscles and ligaments.

The biomechanical effect of the ligaments is a function of their position on the concave or convex side of the curvature and the magnitude of stresses induced in the ligaments is proportional to movement of their vertebral insertions (Fig. 6).

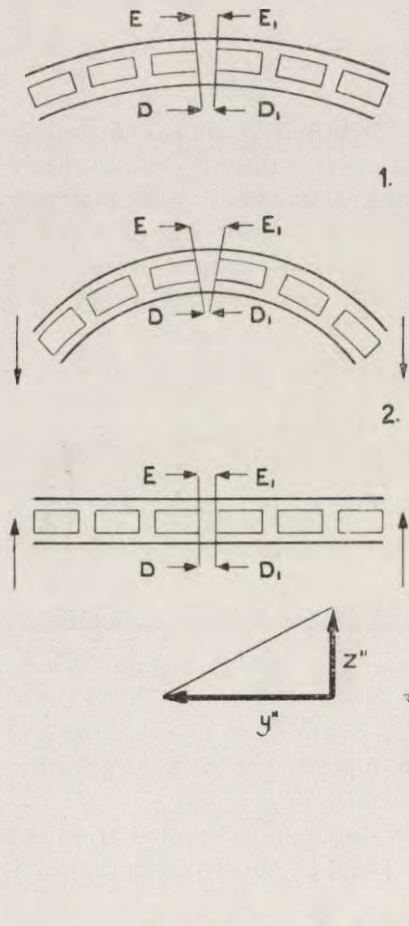


Fig. 6. Forces induced between vertebrae in the straight and curved vertebral column. No. 1 represents the usual position of the curvature. Arrow indicates direction of main force; E and D are the induced forces between vertebrae.

Fig. 7. Horizontal and vertical forces in successive vertebrae.

The metameric structure of the vertebral column is responsible for three fundamental properties: (1) elasticity; (2) a system of intervertebral buffers (intervertebral discs); (3) the ability to disperse and diminish vectors transmitted along the thoraco-lumbar curvature. These vectorial changes strongly influence the interaction between gravitational and translocatory forces by separating a force into two components — one is the true locomotory force, situated in a horizontal plane, while the other is a vertical force (Fig. 7).

An initial thrust on the column is translated into a series of predominantly vertical Z, Z', Z'' , and horizontal Y, Y', Y'' forces which diminish progressively as they pass from one vertebra to the next. The resultant X depends on Z and Y , hence the parallelogram of forces is specific for each vertebra. Both translocatory and antigravitational components of the force diminish progressively towards the anterior end of the column and change their direction according to the inclination of successive vertebrae. Transformation of the locomotory thrust at the thoracic end of the curvature is shown in Fig. 8.

In this diagram, force H is the locomotory force proper and force N is a gravitational force. Such a system once set in motion reverts to stable equilibrium if a force of equal magnitude is applied to oppose force S . This

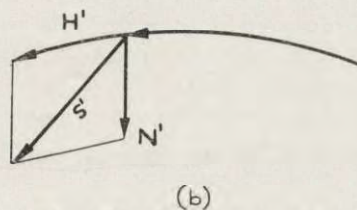
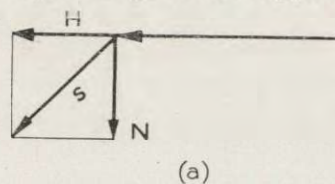


Fig. 8. Explanation in text.

force is usually produced in quadrupeds by moving the forelimbs anteriorly. Because of the shape of the thoraco-lumbar curvature, locomotory force H (Fig. 8a) acquires a different vector H' (Fig. 8b), consequently force S' also changes direction. As vector S' forms a sharper angle with the ground it is more effective in stopping the body by a sudden anterior movement of the forelimbs than is the case with vector S . Furthermore additional complications occur, since force H' is a compound force consisting of two elements F and G (Fig. 9).

Force F is a true locomotory force, force G results from the change of horizontal vector H to vector H' and adds to the existing force N , causing still further elongation of the parallelogram of forces and a new position of force S at S'' .

The definition of horizontally and vertically directed forces in the vertebral column enables us to consider their biological importance. There is little doubt that changes in position of force S result in the creation of optimal conditions for the sudden production of stable equilibrium. Mammals which can rapidly increase the bending of the thoraco-lumbar curvature can stop suddenly and turn suddenly, as shown by rabbits and hares, goats, mountain sheep, cats, viverids and mustelids. By contrast, mammals with a flat thoraco-lumbar curvature and a limited capacity to change vector S are unable to turn quickly in the above manner. Rather,

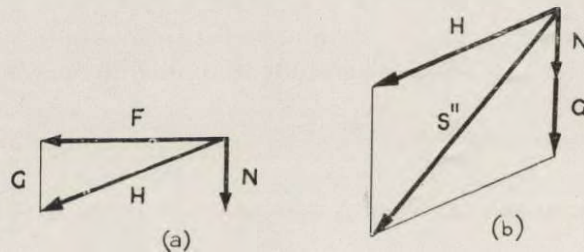


Fig. 9. Explanation in text.

the mechanism used depends on the diminution of angle β . Thus two different types of biomechanical adjustment have developed to counteract the rectilinear movement of the body at the two ends of the thoraco-lumbar curvature. These mechanisms divide animals into those which turn suddenly after jumping e.g. *Leporidae* and those which turn before they jump e.g. *Equidae*. The first of these groups can be called antero-torsial and the second postero-torsial.

4. Buckling of the Vertebral Column

The importance of the thoraco-lumbar curvature is also shown in its resistance to ventral buckling. Since gravitational vectors always have a ventral direction, a completely straight vertebral column would buckle easily; indeed, the ventral deformity lordosis, is not rare in *Equidae*, which

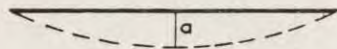


Fig. 10. Explanation in text.

have a relatively straight vertebral column. Temporary or permanent lordosis causes a redistribution of forces similar to the simple deflection of a beam, changing the transmission of stresses along the vertebral column by introducing a new moment of force (Fig. 10).

So far, discussion has been focussed on the horizontally and ventrally directed forces present in the vertebral column. Turning now to the dorsally directed vectors, it seems clear that this component of the loco-

motory force is an important factor in changing a stable equilibrium into an unstable one and thus facilitating various phases of movement. Figures 11 (a), (b) and (c) illustrate this effect.

In Fig. 11(a) initially dorsally directed vectors P change their direction at C due to change in the inclination of vertebrae. The effect of these dorsally directed forces shifts the mass of the whole body (Fig 11(b), from O to O' , the axis of the body is translocated on angle g , causing a shift of the centre of gravity of the body from S to S' which places it further above the front limbs than previously. Fig. 11(c) represents diagram-

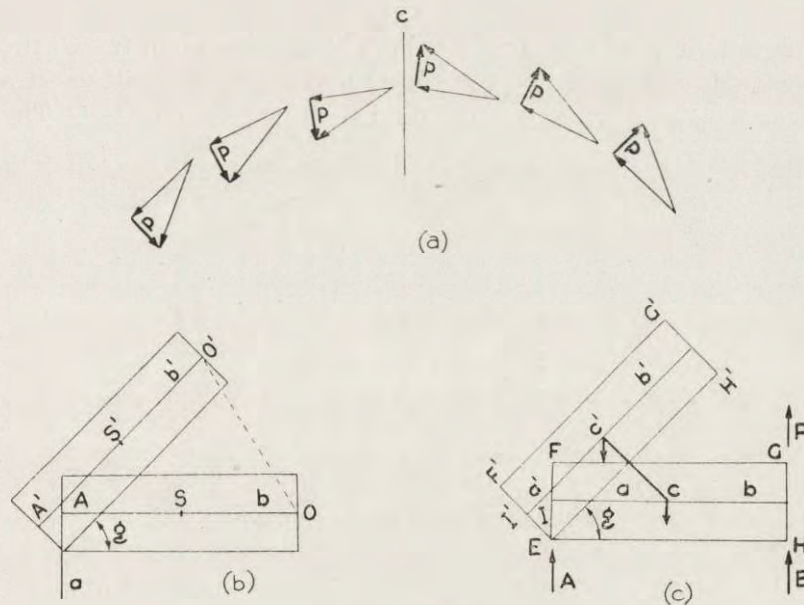


Fig. 11. Explanation in text.

matically the vectors acting on the trunk and their effect on change of equilibrium. Block $EFGH$ is supported at points E and H by the dorsally directed forces A & B . C represents the centre of gravity and at this point the resultant of all gravitational forces acts on the structure. a & b are the distances between the gravitational resultant and supports A and B respectively. If a force P is induced in the block, the whole system will turn through angle g at point E and take up position $E'F'G'H'$. The centre of gravity moves from C to C' , the distance $C-C'$ being related to angle g and the distance from the new centre of gravity to the point I . The axis of rotation passes through the line CC' .

5. Bending moment and transverse forces of the vertebral column

So far gravitational forces have been considered in relation to the supported body. However, these forces acquire special importance during the unsupported phases of locomotion. They act at either end of the thoraco-lumbar curvature and can be defined by means of (1) the static moment of the field, (2) by the bending moment and (3) by the transverse forces.

1. The static moment of the field can be outlined in the following manner: Consider a block with a certain specific weight. The forces acting in such a block are related to its specific weight and the magnitude of the field in question (Fig. 12).

The magnitude of the field is a factor defining the number of specific units of weight which act in a block. At a given section $O-O$, the parts on either side of the section ($O-A-O$ and $O-B-O$) will exert a force known as the static moment of the field about the section $O-O$. The plane

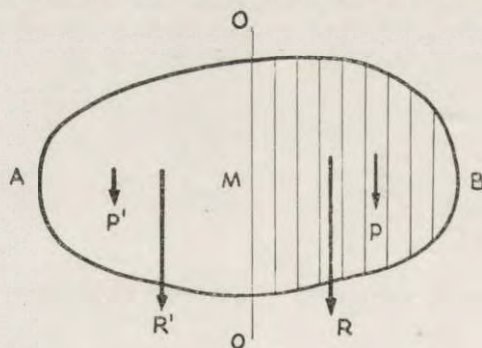


Fig. 12. Explanation in text.

$O-B-O$ may be considered to consist of a great number of small fields each of which exerts a certain force P which, in the case of a block of even thickness, is defined by the size of the field discussed. These small fields are bounded by lines parallel to $O-O$ and are, in fact, small trapeziums with sides small enough to be considered straight lines. Each force P is exerted at the centre of gravity of its trapezium. The force acting on the section $O-O$ is thus the resultant R of all forces P . The same situation applies on the other side i.e. the force R' is the resultant of all forces P' . Consequently, on both sides we have forces R and R' which exert moments (forces \times distance) equal to the algebraic sum of their components. The moment of inertia (I_s) of a number of parallel forces in relation to a given section is the sum of the active forces multiplied by the square of the distance ($I_s = Py^2$).

It is clear from this that gravitational forces acting on the vertebral column may be measured as static moments of the field. Translating this

to terms of the animal body, these static equations must be applied to the arch of the thoraco-lumbar curvature since the vertebral column forms the only rigid support of the trunk.

2. The bending moment (MQ) of a beam in a given section $Q-Q$ is the sum of moments of all forces on one side of the section which exert an action in relation to the centre of the section. By definition, a body in equilibrium must have the sum of projection of forces onto abscissa and ordinate equalling 0 ($\Sigma M = 0$; $\Sigma y = 0$; $\Sigma x = 0$). In the animal body moment M_1 which acts on one side of the vertebral column together with moment M_2 acting on the other side must equal 0 ($M_1 + M_2 = 0$). To express this in biological terms, since all moments have a rotatory action (positive or negative) the vertebral column is thus constantly subjected to rotatory forces. These are applied to each of the vertebral components of the column and it is the constant task of the epaxial musculature to counteract the effect of these rotational forces.

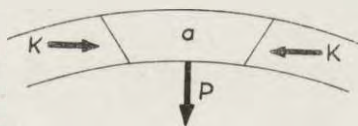


Fig. 13. Explanation in text.

3. Transverse forces. Rotatory forces are always complicated by the existence of transverse forces which result in a downward thrust on any particle situated on one side of the section and in an upward thrust on particles situated on the other side. Consequently, the transverse force in a given section is always the sum of forces which act on one side of the section. However, the moment of section $Q-Q$ is equal to the reaction of the supporting limb multiplied by its distance from the given section, minus the product of the gravitational force and the distance from the point of application of the force to the section. In curvatures, the moment of any given section is defined as the sum of moments on one side of the section in relation to its centre.

Transverse forces, like the rotatory forces discussed above, are permanent components of the work of the vertebral column and are resisted by the strong development of the articular processes of the vertebrae. For this reason they are strongly developed in terrestrial mammals but reduced or absent in fish where gravitational forces are unimportant.

6. The single vertebra as a wedge

The development of articular processes enables us to treat vertebrae, at least in some cases, as a number of wedges in equilibrium. At least two forces P and K act on every wedge (Fig. 13). Force K is a reaction from the limbs and force P is the sum of the gravitational forces from the trunk acting on the vertebra and the weight of the vertebra itself.

III. AN ANALYSIS OF THE BIOMECHANICAL CHARACTERISTICS
OF SOME VERTEBRAL COLUMNS

All terrestrial mammals must contend with the various forces described above but further enquiry is needed to show the specific role they play in various forms of animal locomotion. Because of the large scope of the total problem, investigations in this paper have been limited to a study of the angles α and β and the position of the thoraco-lumbar curvature.

As the purpose of this study is not a statistical one and is not concerned with actual measurement of the values of the forces but rather with their

Table 1.
Relations of angles α and β in various mammals.

Name	Graph No.	α°	β°	$(\beta - \alpha)^\circ$	$(\alpha + \beta)^\circ$	a/b
<i>Coryphodon radians</i>	1	128	149	+21	277	$\frac{9}{10}$
<i>Brontops robustus</i>	2	139	139	0	278	1
<i>Procavia</i>	3	162	126	-36	288	$\frac{3}{2}$
<i>Bos taurus</i>	4	137	143	+6	280	$\frac{5}{7}$
<i>Falacotherium</i>	5	138	133	-5	271	$\frac{2}{3}$
<i>Toxodon</i>	6	150	137	-13	287	$\frac{5}{3}$
<i>Sinopa rapax</i>	7	143	143	0	286	$\frac{12}{17}$
<i>Felis domestica</i>	8	130	137	+7	267	1
<i>Astrapotherium</i>	9	135	160	+25	295	$\frac{6}{7}$
<i>Mastodon augustiæns</i>	10	117	125	+8	242	1
<i>Camelus</i>	11	132	119	-13	251	$\frac{12}{23}$
<i>Entelodon</i>	12	137	161	+24	298	$\frac{1}{2}$
<i>Dolichorhinus hyognathus</i>	13	139	148	+9	287	$\frac{7}{6}$
<i>Arsinoitherium zitteli</i>	14	138	138	0	276	1
<i>Sus scrofa</i>	15	132	164	+32	296	1
<i>Equus caballus</i>	16	140	147	+7	287	$\frac{1}{2}$
<i>Diprotodon australis</i>	17	106	149	+43	255	$\frac{10}{7}$
<i>Homalotherium</i>	18	133	138	+5	271	$\frac{17}{27}$
<i>Chalicotherium</i>	19	110	149	+39	259	$\frac{15}{17}$
<i>Bison occidentalis</i>	20	128	143	+15	271	$\frac{1}{3}$
<i>Scelidotherium</i>	21	159	151	-8	310	$\frac{5}{4}$
<i>Mesopithecus pentelicus</i>	22	153	171	+18	324	$\frac{1}{3}$
<i>Phenacodus primaevus</i>	23	133	153	+20	286	$\frac{7}{8}$
<i>Hyracotherium</i>	24	137	143	+6	280	1
<i>Uintatherium</i>	25	135	145	+10	280	$\frac{13}{13}$
<i>Smilodon neogens</i>	26	127	152	+25	279	$\frac{5}{7}$
<i>Helladotherium duvernoyi</i>	27	143	143	0	286	$\frac{2}{3}$

relevance to a variety of methods of locomotion, it was considered sufficient to select representative specimens of various mammalian types, relying on the published works of many authors (see Acknowledgements).

1. The importance of angles α and β

In order to establish the importance of these angles they were measured and compared in a number of animals. The values obtained are tabulated in Table 1 and expressed graphically in Fig. 14.

The thoraco-lumbar curvature would be most regular when angles α and β are each about 135° (Fig. 15).

These conditions result in the most regular distribution of horizontal and vertical forces in WA and WB , and will result in angles $\alpha + \beta =$ approx. 270° . Of all the species investigated, only *Homalodotherium*,

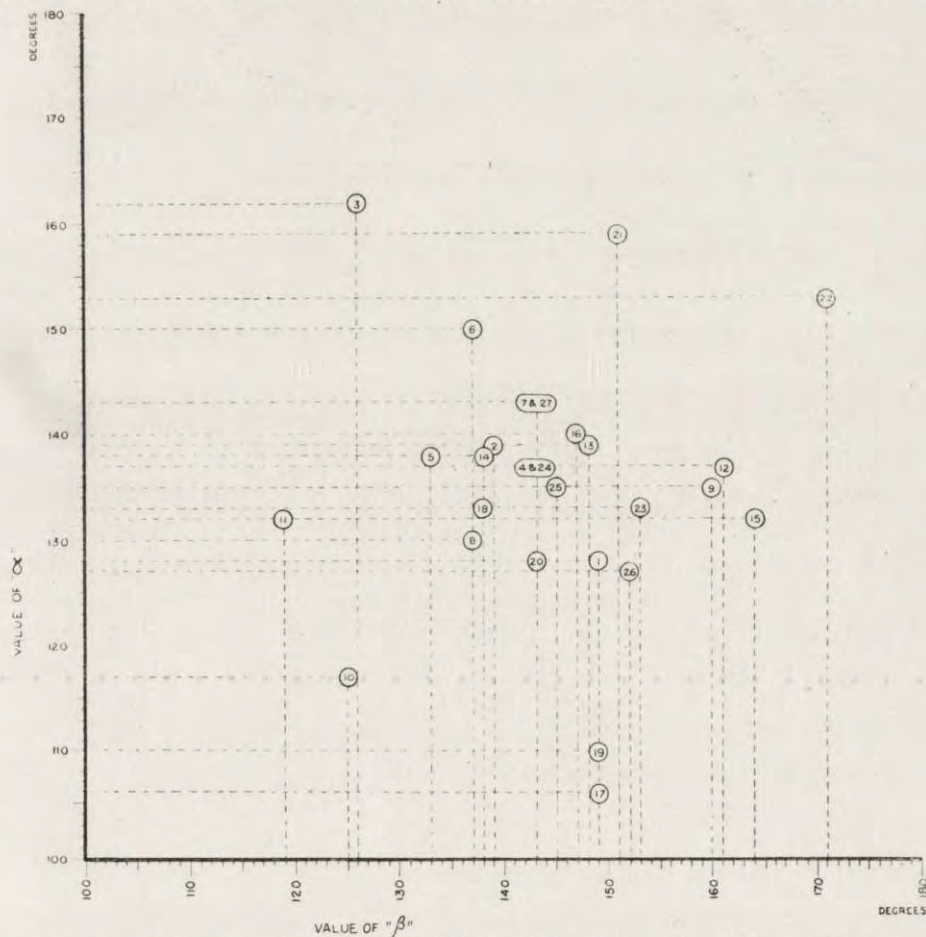


Fig. 14. The magnitude of angles α and β in various mammals. The numbers correspond to those in Table I.

Palaeotherium and *Bison* approach this figure; *Mastodon* has the smallest value, while the highest values (greater than 300°) are found in *Mesopithecus* and *Scelidotherium*. In most animals β is greater than a [Table 1, $(\beta - a)^\circ$]. a and β together with the height of the curvature influence the inclination of vertebrae, while the lengths of a and b determine the number of metamers of similarly orientated inclinations.

From the previous discussion, it is seen that the magnitude of forces A at the anterior part of the thoraco-lumbar curvature and force B at the posterior end are closely related to angles a and β . Both forces translocate the centre of gravity of the body during locomotory movements, influence

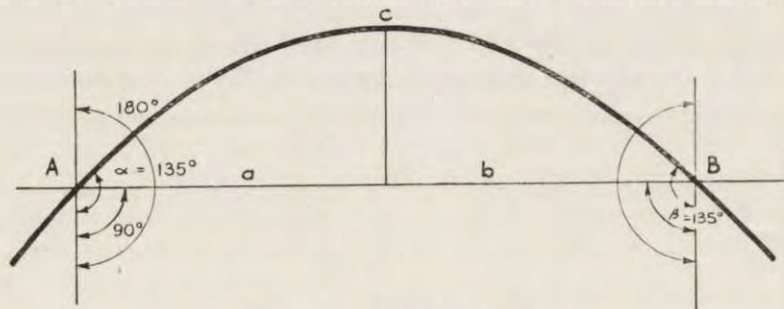


Fig. 15. Explanation in text.

an unstable equilibrium (Figs. 3 and 4) and induce forces A' , A'' , A''' and B' , B'' and B''' . These forces are illustrated in various types of vertebral columns in Plates I—VII.

When the thoraco-lumbar curvature acts as a rigid structure every exertion of force A induces not only the set of forces A'' but also a corresponding set of forces A''' (of opposite direction) so that A'' is mapped into the set A''' (see Plate I). Similarly, force B induces the sets B'' and B''' . Since force B''' must necessarily induce force A and thus in turn A'' and A''' , therefore forces A and B are in constant and close relationship. The set of forces B'' induces in the first locomotory phase the set B''' which under normal conditions induces A'' and this in turn induces the set A''' . If n denotes the number of forces in set B in a full locomotory cycle, then the relationship of forces (R) may be expressed algebraically as:

$$\begin{array}{ccccccc} n & & n & & n & & n & & n & & n \\ B'' & R & B''' & \text{and } B''' & R & A'' & \text{and } A'' & R & A''' \\ 1 & & 1 & & 1 & & 1 & & 1 \end{array}$$

and if the phases of motion are repeated —

$$\begin{array}{ccc} n & & n \\ A''' & R & B'' \text{ etc.} \\ 1 & & 1 \end{array}$$

It can be seen from this that forces A and B possess reflexive (ARA) and symmetrical (ARB and BRA) properties.

The biological consequence of this relationship is that the concept of the vertebral curvature as a "bridge" cannot be applied to the unsupported body. While this concept may be applicable to the "standing" animal, during locomotion the principle of displaced torque must be applied. The thoracic and lumbar parts of the curvature will each perform similar work during a complete cycle of locomotion but due to the reflexive and symmetrical properties of the forces concerned, at any particular moment of locomotion they act differently.

2. The relation of the magnitude of forces induced at the thoracic and lumbar ends of the curvature

A more detailed analysis of the relationship of forces A and B can be achieved by examining their magnitude. As expressed by scalars, the magnitude of each is interdependent. Since the number of variations is indefinitely great, it is sufficient to show this interdependence under three basic conditions, which are:

1. where all forces at $A =$ forces at B ($WA = WB$).
2. where all forces at A are greater than forces at B ($WA > WB$).
3. where all forces at A are less than forces at B ($WA < WB$).

If $WA = WB$ and no other forces apply, the factor which affects the parallelogram of forces is the magnitude of angles α and β . In other words, the angles α and β will determine forces A'' , A''' , and B'' and B''' . In the case of *Smilodon* (Plate I) where $\alpha < \beta$, the vertical component A is greater than vertical component B . This has a decisive effect on the work of the vertebral column and thus on the agility of the animal. The relationship of angles α and β is modified by the relation of projections a and b . In the case of *Smilodon* β is greater than α , with the result that the posterior lever of the torque is greater than the anterior. The induced forces B''' are increased by the anterior shift of the centre of gravity but in the following phase of locomotion they are reduced by the shorter lever a . Where α is small, if $b > a$ the induced forces B''' are relatively small.

The algebraic relationship will be:

$$\begin{array}{rcl}
 \beta & R & b \\
 b & R & a \\
 \beta & R & B''' \\
 B'' & R & B''' \\
 B''' & R & a
 \end{array}
 \qquad
 \begin{array}{rcl}
 \alpha & R & A'' \\
 A'' & R & A''' \\
 A''' & R & B'' \\
 B'' & R & B'''
 \end{array}$$

Position of Scapular Margin	Inclinations of Thoraco-Lumbar Curvature	Articular Angles in Hind Limbs
Above spinous processes	marked difference	small
On level of vertebral bodies	uniform	large
Above vertebral bodies	uniform	small
Slightly above vertebral bodies	irregular	large
On level of vertebral bodies	regular	moderate
On level of spinous processes	regular	moderate
Above spinous processes	regular	large
On level of spinous processes	regular	large
Above vertebral bodies	regular	very large
On level of vertebral bodies	nearly regular	very large
Above level of vertebral bodies	regular	large
Above level of vertebral bodies	regular	moderate

$A''' > B'''$	Above level of vertebral bodies	irregular	moderate
$A''' > B'''$	Level of vertebral bodies	irregular	large
$A''' = B'''$	Above level of vertebral bodies	regular	very large
$A''' > B'''$	On level of spinous processes	regular	moderate to small
$A''' > B'''$	On level of spinous processes	regular	very large
$A''' > B'''$	Above vertebral bodies	regular	large to moderate
$A''' > B'''$	Slightly above vertebral bodies	irregular	small
$A''' > B'''$	Above vertebral bodies	irregular	large
$A''' > B'''$ (slightly)	Above vertebral bodies	irregular	large
$A''' = B'''$	On level of vertebral bodies	regular	large to moderate
$A''' > B'''$	Above vertebral bodies	regular	large to moderate
$A''' > B'''$	Above spinous processes	regular	moderate
$A''' < B'''$	Below vertebral bodies	regular	small
$A''' < B'''$	Above spinous processes	irregular	large
$A''' > B'''$	On level of vertebral bodies	regular	large

In contrast to *Smilodon*, the thoraco-lumbar curvature of *Procavia* (*Hyrax*) (Plate I) is characterised by $a > \beta$ and projection $a > \text{projection } b$. To achieve unstable equilibrium (i.e. to shift the centre of gravity forward) *Procavia* requires an intensive movement of the lumbar end of the curvature, to compensate for the comparatively short length of b . This can only be achieved by the presence of relatively small angles of articulation between the long bones of the hind limbs, producing a characteristic accordion-like bending. This is always accompanied by a large value of a , resulting in a column in which the posterior torque is very small, i.e. force A'' is comparatively small and induced force A''' even smaller. This indicates that when a is large the forces which directly oppose the horizontal component of thrust throw a heavy strain on the musculature of the thorax and anterior limbs.

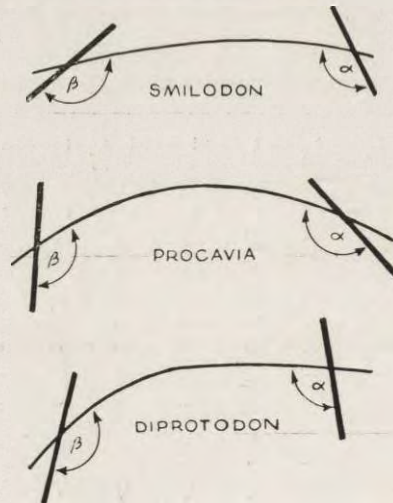


Fig. 16. Comparison of the thoraco-lumbar curvature of *Smilodon*, *Diprotodon* and *Procavia*.

Procavia has an infravertebral position of the scapula, usually associated with a large a , while a small a often results in the supravertebral position of the scapula.

Diprotodon (Plate I) provides an example of a thoraco-lumbar curvature where the difference in magnitude of a and β is very great, nearly twice that of *Smilodon*. *Diprotodon* has anterior inclinations similar to *Procavia* and *Smilodon* and posterior inclinations similar to *Procavia* (Fig. 16).

In spite of the similarity of inclinations, a highly significant difference exists between the curvature in *Diprotodon* and *Procavia* in the magnitude of angle a . A small magnitude of a results in translocation of most forces

WA into A'' . Consequently, the vertical component A''' in *Diprotodon* and the horizontal component are much greater than in the other two examples given. Where the magnitude of a is large (*Procavia*), the angles of articulation in the hind limb are small; where a is small (*Diprotodon*), angles of hind limb articulation are relatively large. This indicates that in animals with a thoraco-lumbar curvature of relatively short b and relatively large β the angles of the long bones of the hind limbs are influenced by the magnitude of a .

It is easy to see that *Diprotodon*, having a small horizontal component of force A and large angles of articulation in the hind limbs, is poorly adapted to sudden stopping or turning. The very stable equilibrium of this animal is a result of $b < a$ and the considerable magnitude of forces B''' induced by B'' . Since B''' is related to A'' and a is related to A'' , conditions favour an increased magnitude of A'' , making sudden starts or rapid reduction of speed very difficult.

From the above examples it is easy to see that in mammals with short b the centre of gravity can be translocated in one of the following ways —

1. Where a relatively small β is connected with low magnitude of the angles of articulation in the hindlimbs (*Procavia*) this gives quick translocatory effect but demands considerable energy and is difficult to maintain in animals of large body weight.

2. Where there is considerable inclination in the lumbar part of the curvature, but β is large and the angles of articulation of the lower limbs are large (*Diprotodon*), change in position of the thoraco-lumbar curvature is difficult and when connected with a small value of a hinders the animal's agility considerably.

3. Where the metameric inclination in both parts of the curvature is similar and β is of a magnitude (about 133°) which gives approximately equal distribution of forces WB , this results in the moderate magnitude of the angles of articulation of the hind limbs. This is exemplified in *Uintatherium* (Plate I).

The above examples should be sufficient to show how the thoraco-lumbar curvature of any animal can be analysed. Data related to other species are tabulated in Table 2 and illustrated in Plates II—VII.

IV. DISCUSSION AND BIOLOGICAL IMPLICATIONS

The material presented in this paper can be conveniently discussed in relation to the mathematical definition of physical forces, to the result of this study on the general biological outlook and finally, in relation to the function of the thoraco-lumbar curvature itself.

1. The mathematical definition of physical forces

Today the importance of physical laws for biological structure is clearly acknowledged and the problem remains only in the choice of methods of investigation. Specific methods and approaches used in this paper are an enlargement of certain aspects of general biomechanical methods whose validity has been discussed by other authors (e.g. Gray, 1944). The methods used of necessity introduce a specific algebraic nomenclature and method of operation. In contradistinction to the belief of the 18th century mathematician, Condorcet (Ackerknecht, 1953), who thought that the study of morphology was already complete, mathematical and physical concepts are emphasised here to further the study of morphology and increase its content.

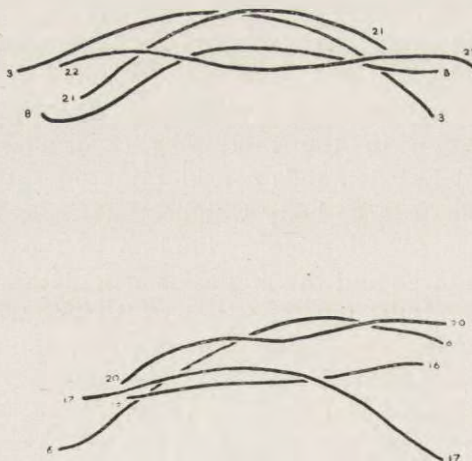


Fig. 17. Variation in shape of thoraco-lumbar curvature. Numbers correspond to those in Table 1.

2. General biological outlook

Three main points appear to emerge from this study:

1. that the relations within the locomotory system at a given moment (connections) (Tucker, 1953) are always supplemented by a sequence of relations in time (consecution). This emphasises the importance of position in anatomy instead of the customary treatment of structure as a static entity.
2. Biomechanical reflexes are the outcome of the necessary sequence of events in locomotion. These biomechanical reflexes take precedence

over all other activities, despite the circumstances which initiated them — e.g. whatever impulse may make an animal jump, biomechanical reflexes preclude all others till equilibrium is regained. The relationships stated earlier are in fact algebraic statements of these biomechanical reflexes.

3. The character of locomotory movements: the constant presence of torque is an important element in the locomotion of animals i.e. there is always a posterior or anterior rotation cut short by opposing forces as seen in simple form in the movement of a rocking horse. This is as characteristic of mammalian tetrapod movement as "wave" motion is for snakes and ameboid movement for protozoa. It is on this point that the present analysis differs from previous studies based on the similarity of the thoraco-lumbar curvature to various types of bridges. The similarity to a bridge vanishes when the body is unsupported, or supported at one end only, as happens in the normal sequence of mammalian locomotion.

3. Function of the thoraco-lumbar curvature

Variations in the shape of the thoraco-lumbar curvature in a number of animals are shown in Fig. 17.

Maximal height of the curvature usually occurs in the anterior part of the curve. The majority of animals have a curvature of regular shape and the inclinations are usually greater in the lumbar part. The torque induced in the curvature is influenced by the shape of the vertebral column and the length of projections a and b , which may favour anterior or posterior rotation, or be in approximately neutral position. This together with the inclinations and the relative height of points A and B defines the position of the centre of gravity in the standing animal.

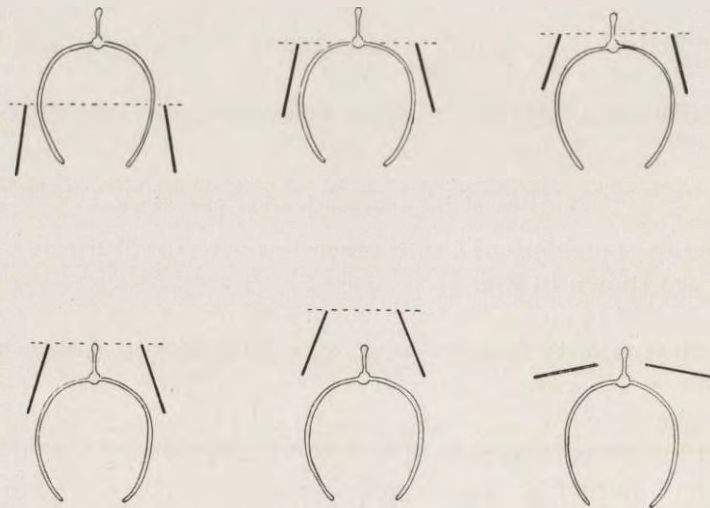
4. Conditions at the scapular and coxal ends of the curvature

Discussion of the forces at the scapular end of the curvature must involve the magnitude of α and the position of the scapular margin with relation to the vertebral column. The latter point must be taken into consideration together with limb length in determining the height of the centre of gravity (Fig. 18).

The difference in the position of the scapula in relation to the vertebral column is reflected in variations in biomechanical conditions within the ventral serrate muscle which is particularly important in the transmission of forces from the scapula to the vertebral column. Unfortunately no detailed comparative study of the structure of this muscle as related to the position of the scapula and the costal joints is at present available.

Magnitude of α : The importance of this angle is twofold: it contributes to the division of forces provoking a posterior torque and it

assists in stopping forward movement. As already discussed and illustrated in Fig. 15, the torque provoked is maximal when α is 90° , the effect on forward movement is maximal when $\alpha=180^\circ$. Since either of these conditions is not biologically feasible, the values of α must lie somewhere between 90° - 180° . The ideal balance between the forces is achieved where $\alpha = 135^\circ$. Reference to Table 1 shows that the lowest value is for *Diprotodon* ($\alpha = 106^\circ$) and the highest for *Procavia* ($\alpha = 162^\circ$). The table also shows that many animals have a value for α close to 135° : *Brontops*, *Bos taurus*, *Palaeotherium*, *Astrapotherium*, *Camelus*, *Entelodon*, *Doli-*



SIX POSITIONS OF THE SCAPULA
IN RELATION TO THE VERTEBRAE.

Fig. 18. Explanation in text.

chorhinus, *Arsinoitherium*, *Sus scrofa*, *Equus caballus*, *Homalodotherium*, *Phenacodus*, *Hyracotherium* and *Uintatherium*. This list includes a number of mammals which are now extinct, in which other properties of the thoraco-umbar curvature proved ill adapted for a number of reasons. The contemporary species on this list share a general "all round" character of locomotive abilities, they move reasonably well and are fairly efficient in both starting and stopping.

Magnitude of β : At the posterior end of the curvature, the general conditions affecting torque are comparable to those discussed for α . Table 1 indicates that the smallest value of β is 119° for *Camelus* and the greatest for *Mesopithecus pentelicus* (171°). The mammals where

$\beta = \text{approx. } 135^\circ$ include the extinct species *Arsinoitherium*, *Homalodotherium*, *Brontops*, *Palaeotherium* and *Toxodon* and also *Felis domestica*.

β is usually larger than α , the difference in value of $(\beta - \alpha)^\circ$ ranging from $+43^\circ$ in *Diprotodon* to -36° in *Procavia*. The sum of $(\alpha + \beta)^\circ$ is relatively stable i.e. where one deviates from the middle value of 135° , the other tends to compensate, so that the sum of the two remains fairly constant at about 270° , the only marked deviation in the examples chosen is *Mesopithecus* (324°). Here the difference is due to a large value of β (171°), a characteristic of primates which approach an erect posture.

5. Force A''' and B''' in relation to gravitation

In the motionless animal, gravitational forces are static. During locomotion torque is induced in the thoraco-lumbar curvature by applying muscular thrust and by transforming static energy into kinetic energy at the other end of the curvature. This is done by shifting the centre of gravity as one end of the thoraco-lumbar curve is lifted. As speed increases, inertia (gravitational forces) increases in value and correspondingly causes increased torque reaction.

The resultant transmission of forces along the vertebral column is influenced by the inclination, height, position of the curvature and the length of projection a and b . In Table 2, relation of forces B''' and A''' denotes the relative proportion of forces induced at opposite ends of the curvature, i.e. where $B''' > A'''$, forces at B are more efficiently transposed in the torque than forces at A .

In most animals the perpendicular component of force (A'') is greater at the thoracic end of the curvature, indicating that the major force in stopping is achieved by shifting the centre of gravity and inducing the posterior torque rather than by direct opposition to the horizontal translocatory force. The perpendicular component is emphasised whenever there is a marked inclination in curvature, while the horizontal component is best transmitted in relatively straight vertebral columns. The latter type is exemplified by the horse, pig and ox. In contradistinction, the anterior torque depends largely on the magnitude of the articular angles of the hind limbs. When the angles are small, translocation of the lumbar end of the curvature is readily achieved and production of torque is more efficient. When the angles are large, little translocation is possible. There are three main functions of the hind limbs — (a) reaction to the body weight, (b) inducement of torque and (c) induction of translocatory force. Each of these functions may be more or less stressed in various mammalian types.

Functional relations between the magnitude of the angles in the hind limb and the shape of the thoraco-lumbar curvature are very close. A range of angles from very small to very large is shown in Fig. 19. This indicates a general biomechanical rule relating to the size of angles of the hind limb, body weight and the nature of the thoraco-lumbar curvature:

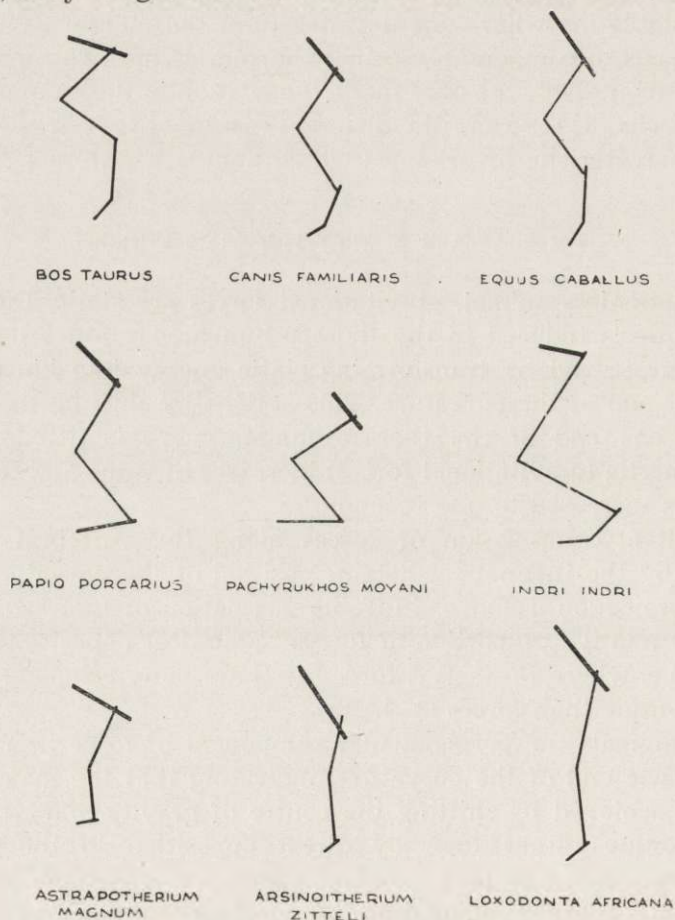


Fig. 19. Explanation in text.

(a) Where body weight is heavy, (Fig. 19, bottom row) articular angles of the hind limb are always large, the animal is a slow starter and its ability to stop depends on the type of curvature and angles α and β .

(b) Where body weight is small, (Fig. 19, middle row) the articular angles of the hind limbs are often small. Such animals start quickly and may run only in short bursts or persistently change direction (antero-torsial animals) depending on the characteristics of the thoraco-lumbar curvature.

(c) Where body weight is moderate, (Fig. 19, top row) as exemplified in a wide range including dogs, horses and ruminants, the angles of articulation may be moderate, giving the animal a basic ability for well sustained effort.

It is the perpendicular forces which are responsible for the thoraco-lumbar curvature and its specific shape. In mammals where perpendicular forces are reduced or absent the curvature vanishes. This is

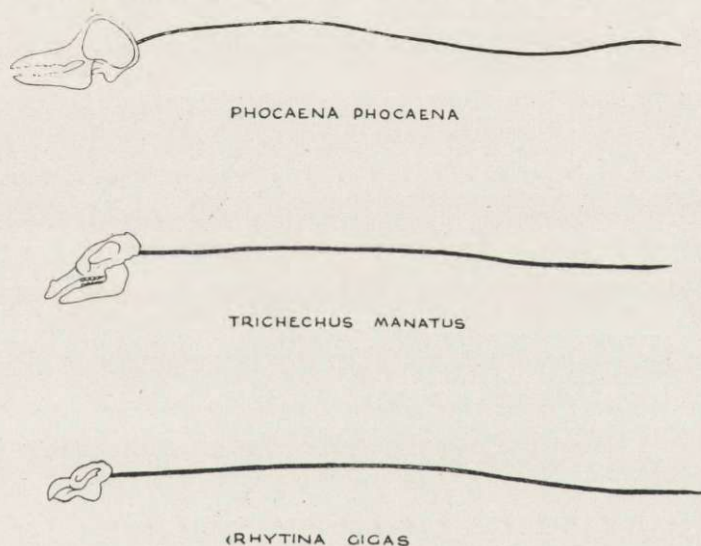


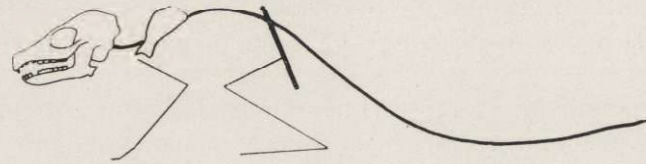
Fig. 20. Explanation in text.



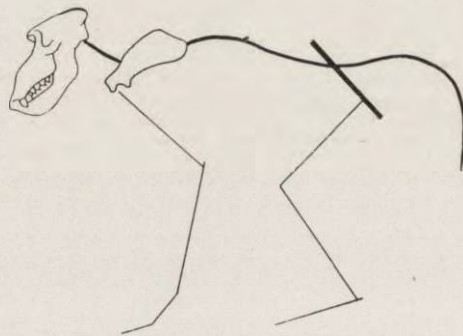
Fig. 21. Explanation in text.

characteristic of marine animals (see Fig. 20). In aquatic animals which still maintain functional hind limbs, the curvature is slight but distinct (Fig. 21).

The curvature is also characteristically moulded when the perpendicular forces are attached predominantly at one end only. The curvatures of primates are all irregular and flat at the lumbar end e.g. *Mesopithecus pentelicus* (Plate VI). To reduce the action of perpendicular forces on the thoracic part of the vertebral column, many mammals show a tendency

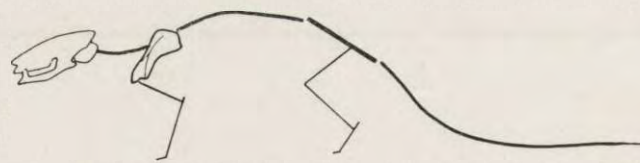


ELEPHANTULUS ROZETI



PAPIO PORCARIUS

a.



METACHEIROMYS TATUSIA

PROPALAEOHOPLOPHORUS
AUSTRALIS

b.

Fig. 22 a & b. Various degrees of alignment of the scapula with the thoracic part of the thoraco-lumbar curvature.

to align the scapula in parallel with the thoracic part of the curvature. An extreme example of this is shown in the extinct *Propalaeohoplophorus australis* (Fig. 22b). Where this is associated with a supra-spinous position of the scapula it leads to new biomechanical horizons as exemplified by the primates.

V. SUMMARY

1. The existence of a thoraco-lumbar curvature is the dominant biomechanical feature of mammalian vertebral columns. A number of vertebral columns are analysed according to biomechanical concepts outlined in the text and the biological implications which result are discussed.

2. The thoraco-lumbar curvature is functionally important in resistance to buckling and in determining mechanical ability and agility.

3. The vertebral column is constantly subjected to rotatory and transverse forces.

4. The concept of the vertebral column as a bridge cannot be applied to the unsupported body. During locomotion, the principle of displaced torque must be applied.

5. The concept of biomechanical reflexes is stated and their place in the sequence of events in locomotion is discussed.

6. Formation of the thoraco-lumbar curvature depends on perpendicular forces, which are mainly derived from the hind limbs. In aquatic mammals, loss of the hind limbs is correlated with disappearance of the curvature.

7. The relation between type of thoraco-lumbar curvature and articular angles of the long bones of the hind limb is discussed and illustrated.

8. The scapula is discussed in relation to the vertebrae and inclination of the thoracic end of the curvature.

9. Comparative biomechanical data for a number of mammalian species are presented in table form.

Acknowledgements: My thanks are due to Professor Ottaway, University of Bristol, for his helpful suggestions and to Mrs. Jean Kratzing for help in preparing the manuscript. Mr. N. D. S. May kindly read the manuscript. I would also like to thank the following for their permission to publish figures used in this study:

MacMillan and Co., London for figures of *Diprotodon australis*, *Homalodotherium* and *Chalicotherium* from Parker and Haswell, "Zoology"; the Clarendon Press, Oxford and Professor J. Z. Young for figures of *Proavia*, *Uintatherium*, *Felis domestica*, *Coryphodon*, *Hyracotherium*, *Scelidotherium*, *Bos taurus*, *Sus scrofa*, *Entelodon*, *Palaeotherium*, *Toxodon*, *Astrapotherium*, *Brontops robustus*, *Equus caballus*, *Camelus dromedarius*, from Young's "The Life of the Vertebrates"; Gustav Fischer, Verlag, Jena for figures of *Smilodon*, *Bison occidentalis*, *Phenacodus primaevus*, *Mastodon*, *Arsinoitherium*, *Dolichorhinus hyognathus*, *Sinopa rapax*. *Mesopithecus pentelicus*, from Abel's "Lebensbilder".

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STRESZCZENIE

1. Zasadniczą biomechaniczną właściwością kręgosłupa ssaków jest istnienie krzywizny piersiowo-lędźwiowej. Przeprowadzono analizę biomechaniczną kręgosłupów 27 gatunków ssaków i przedyskutowano znaczenie biologiczne uzyskanych wyników.

2. Krzywizna piersiowo-lędźwiowa jest funkcjonalnie ważna jako przeciwstawienie wyginaniu się kręgosłupa i czynnik determinujący jego mechaniczne możliwości i sprężystość.

3. Kręgosłup stale podlega działaniu sił obrotowych i poprzecznych.

4. Koncepcja kręgosłupa jako mostu nie może być zastosowana do ciała niepodpartego. Podczas ruchu powinna być przyjęta zasada przemieszczającego się momentu skręcającego.

5. Wprowadzono pojęcie refleksu biomechanicznego (biomechanical reflex) i dyskutowano jego rolę w lokomocji.

6. Kształtowanie się krzywizny piersiowo-lędźwiowej zależy od sił prostopadłych, pochodzących od kończyn tylnych. U ssaków wodnych utrata kończyn tylnych jest skorelowana z zanikiem krzywizny kręgosłupa.

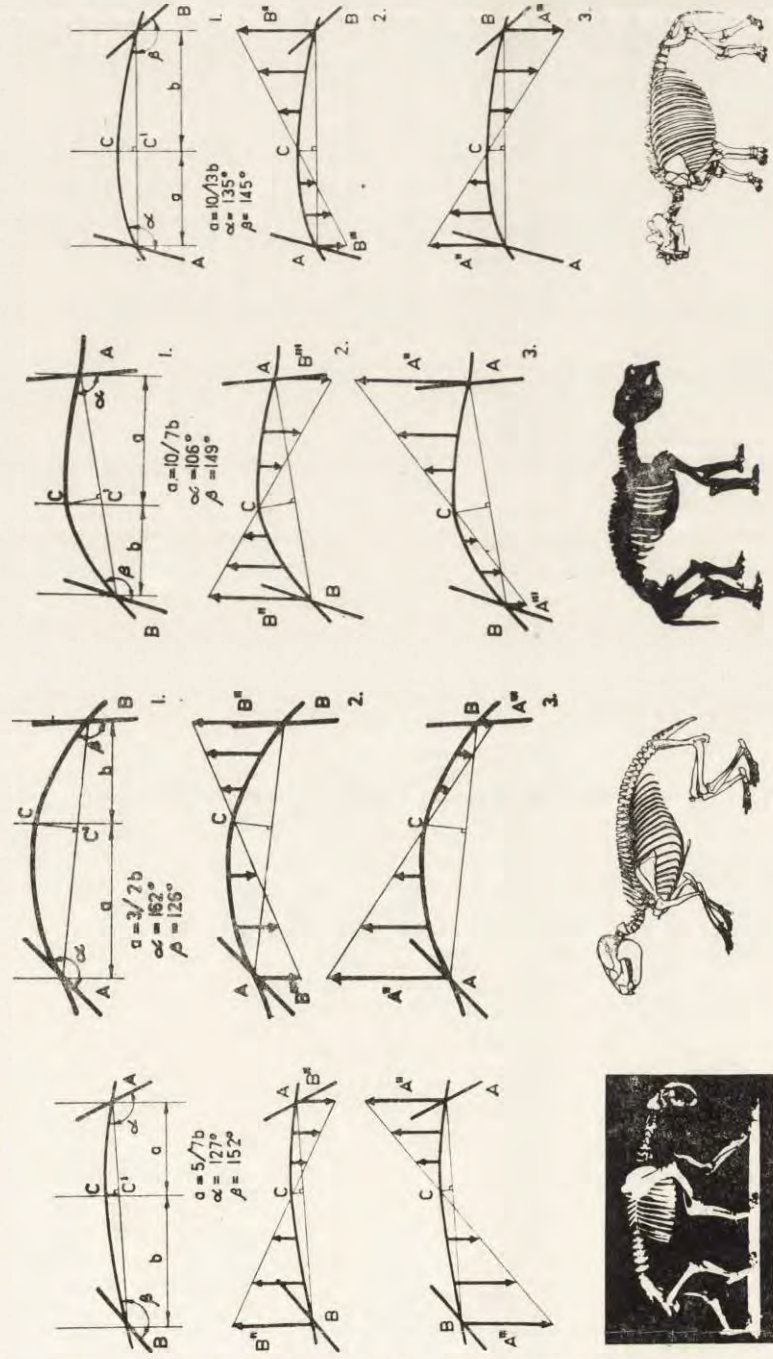
7. Na rycinach i w dyskusji przedstawiono związek między typem krzywizny piersiowo-lędźwiowej i kątami stawowymi kości długich kończyny tylnej.

8. Łopatka jest rozpatrywana w związku z kręgami i z nachyleniem piersiowego odcinka krzywizny.

9. Porównawcze dane biomechaniczne dla 27 gatunków ssaków są przedstawione w postaci tabel (Tabele 1, 2) i Tablic (I—VII).

PLATES I—VII.

Biomechanical characteristics of various mammalian thoraco-lumbar curvatures.



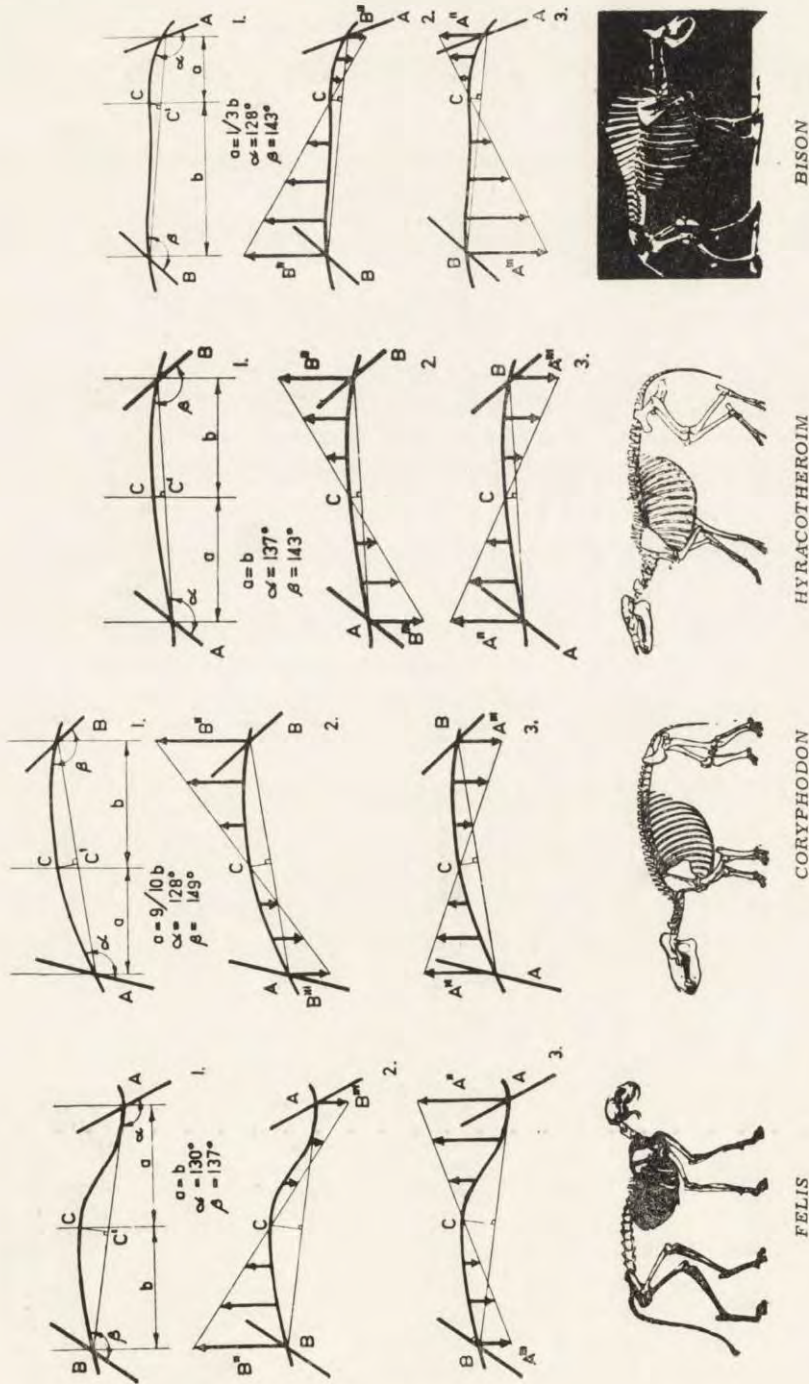
UINATHERIUM

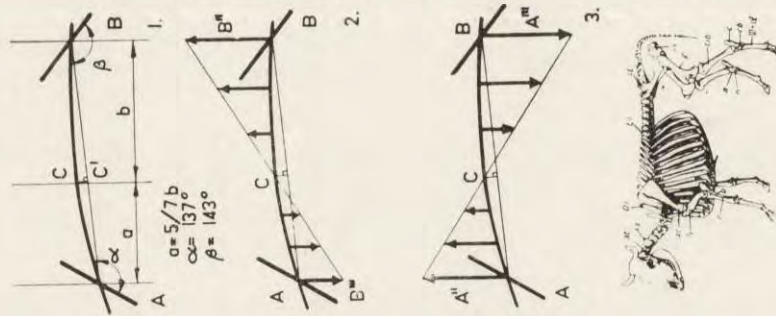
DIPROTODON

PROCAVIA

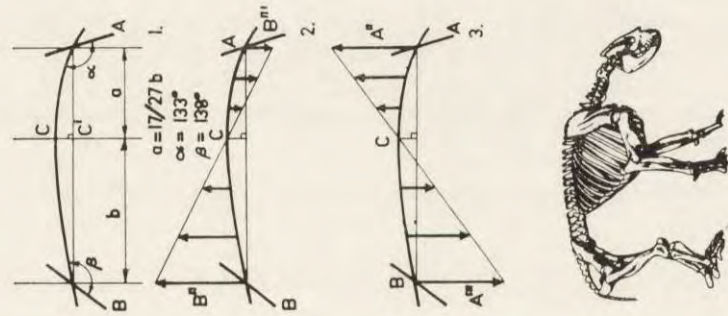
SMILODON

R. Tucker

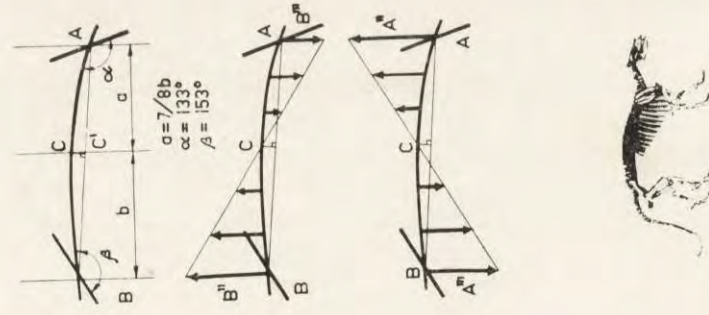




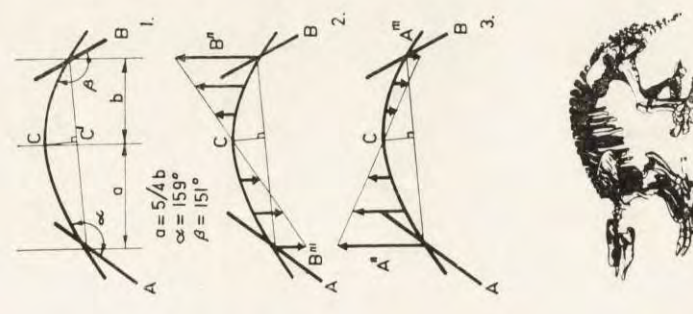
BOS



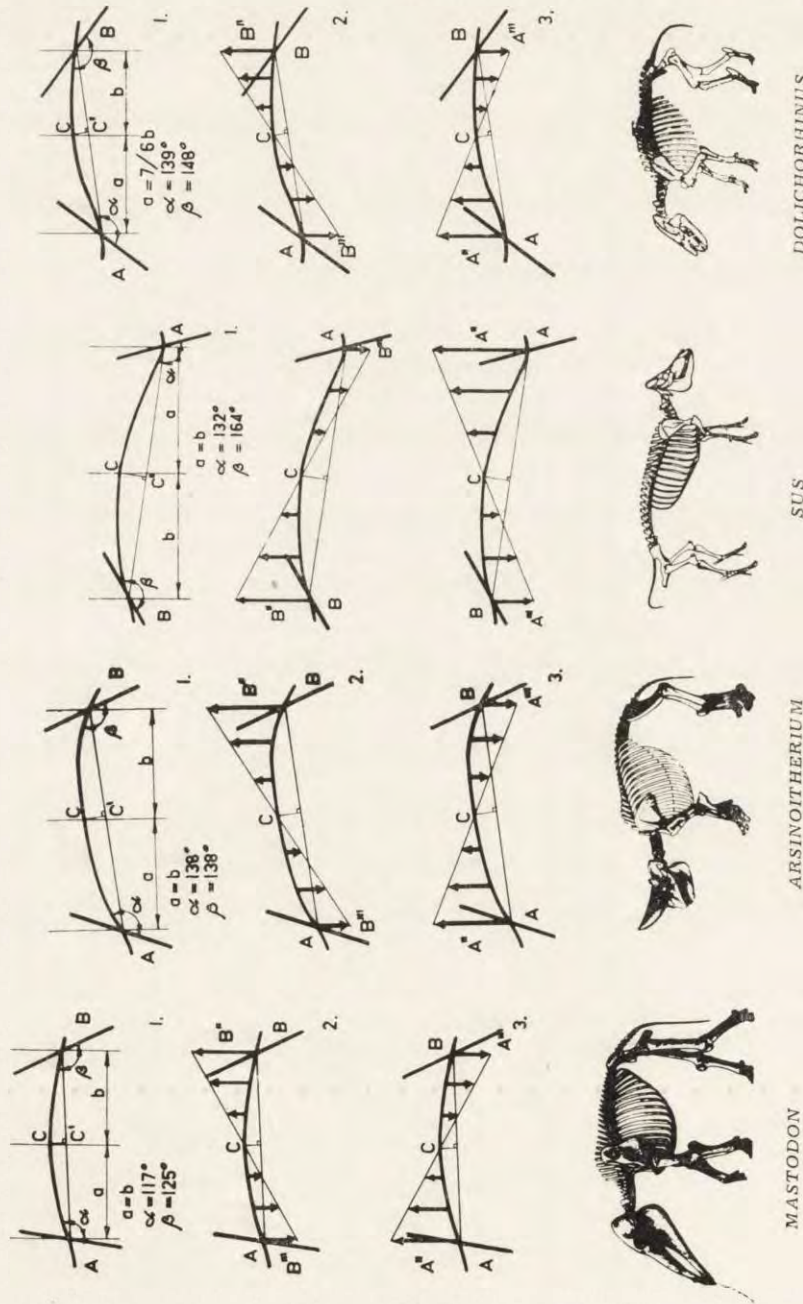
HOMALODOTHEIUM

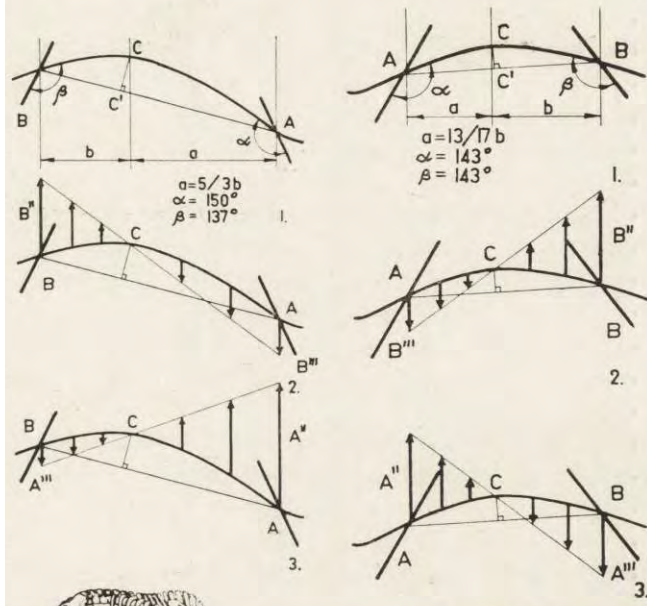


PHENACODUS



SCELIDOTHEIUM





TOXODON



SINOPA

