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Studies in the Mechanics of the Tetrapod Skeleton

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1. From a mechanical point of view the organization of a tetrapod's body is essentially that of a segmented, flexible and overhung beam supported by four limbs; each limb can operate both as a strut and as a lever. A substantial number of physiological and morphological facts receive rational explanations when subjected to mechanical considerations imposed by the animal's own weight.

2. The general conditions under which a tetrapod can use any particular limb for purposes other than the support or propulsion of the body depends on the positions of the four feet relative to the centre of gravity of the body.

When a cursorial tetrapod is standing on four legs, the contribution which any one limb makes towards the support of the body can vary within limits which can be defined in terms of (1) the weight of the body, (ii) the positions of the centres of pressure of the four feet relative to the centre of gravity of the body. If the thrust of one limb is known that of each of the other three can be calculated.

3. If the vertical thrust of any one limb be increased, there must be a simultaneous increase in the thrust of the diagonally situated limb and a decrease in the thrusts of both feet situated on the other diagonal. The reflex myotactic response of mammalian extensor muscles to mechanical stretch provides an adequate mechanism for ensuring effective co-ordination between the vertical thrusts exerted by each of the four limbs. The physiological response of all the limbs to flexor stimulation of any one of them conforms to the mechanical requirements for stability ; it probably represents an extreme instance of readjustment of limb thrusts.

4. In bipedal forms a quadrilateral of support is provided by the heel and toes of the two feet: the conditions of stability are essentially the same as in tetrapods.

5. If a tetrapod stands on an inclined slope (in a posture similar to that normally adopted on a horizontal surface) the extent of the resultant redistribution of weight between front and hind feet is inversely proportional to the relative length of body and limbs. A long low body is a mechanical adaptation to a scansorial habit. The typical postures adopted by tetrapods when standing on steep slopes (viz. either with the axes of the limbs retracted or the back horizontal and the hind limbs flexed) conform to the principle that the distribution of the total weight of the body between the various limbs should approximate closely to that characteristic of the animal standing in a normal posture on a horizontal surface. The same principle applies to the posture adopted by an animal when exposed to restraint by an extraneous horizontal force.

6. The limbs of a tetrapod can contribute towards the support of the body either in the capacity of struts or in the combined capacity of struts and levers. When acting as a strut a limb exerts forces along its own mechanical axis only, the moment of the muscular tensions operating about the hip or shoulder joint being zero. When a limb is acting as a lever the limb exerts both against the body and

against the ground forces at right angles to its mechanical axis; it is able to do so by means of the muscles whereby the limb is attached to the body.

7. When a limb is acting as an inclined strut the couple which is exerted on it by the weight of the body must be compensated by a couple due to (1) a horizontal force exerted on its proximal end by the body, and (ii) friction or other horizontal force acting at the foot. The horizontal force acting on the proximal end of the limb represents the resultant horizontal force exerted on the body by the three other limbs. Instances are described of two or more limbs co-operating, either as longitudinal or transverse struts, for the support of the body.

8. When subjected to tension from a muscle originating on the body, a limb operates as a lever and exerts equal but opposite horizontal forces against the ground and against the body. At the same time it exposes the body to a turning couple whose moment is equal to that of the muscle's tension about the centre of rotation of the joint.

By means of the muscles which operate between the body and the limb an animal can control the horizontal forces exerted by a limb against the body and against the ground.

9. The muscular co-ordination between two or more limbs, acting as levers, is described. For any given position of the feet relative to the centre of gravity of the body, the minimum total muscular effort required to maintain equilibrium is always the same. The distribution of this effort between the muscles of the various limbs can, however, be varied between relatively wide limits, either by changing the tension of one or more extrinsic muscles or by changing the distribution of weight between the feet by a change in the axial thrust of the limb. The whole of the limb musculature of the animal must be regarded collectively as one functional unit.

10. The particular pattern of muscular activity adopted for any given posture and loading of the limbs is probably such that the strain is distributed between the relevant muscles in proportion to their ability to develop and sustain tension.

11. The quantitative muscular effort required for the stabilization of any limb joint depends on the magnitude and direction of the reaction of the ground against the foot and on the distance of the centre of rotation of the joint from the line of action of this force. Since the reaction of the ground against the foot is under the control of the animal, the latter can continue to stand whilst varying the strain falling on any one intrinsic or extrinsic muscle provided it readjusts the activity of all the others not only in the same but also in all the other limbs. Instances are given of the co-ordination of the musculature in the four limbs of an animal standing at rest.

12. The digitigrade habit is associated with a posture of limbs in which the line of action of the body weight passes anteriorly to the distal metacarpal or metatarsal joints.

13. The forces exerted on joints by curvilinear muscles are discussed. In general the centripetal pressure exerted by the muscle is equal and opposite to the resultant longitudinal thrusts exerted by the two main bones composing the joint. Brief reference is made to multi-joint muscles.

14. The nature of the strains imposed on the vertebral column by the weight of the body and by the forces exerted by the ground against the feet of a tetrapod are discussed.

15. The mechanical picture presented by a tetrapod is essentially that of a flexible overhung beam supported by four elastic legs; only under very special circumstances can the body be compared to two balanced centilevers.

16. By means of the muscles of its limbs an animal can increase or decrease the strain falling on its vertebral musculature or vice versa.

17. As a propulsive mechanism, the limb of a tetrapod functions as an extensible strut and as a lever. In so far as it acts as a propulsive strut, the limb is extended by its own intrinsic musculature and the mechanism of locomotion is essentially that of a punt when propelled by a pole. In so far as the limb functions as a lever, it is operated by its extrinsic musculature and the mechanism is essentially similar to that of a canoe propelled by a two-handed paddle, the distal end of which remains fixed.

18. In so far as it operates as a strut any limb in a retracted posture exerts a propulsive action; a similar limb in a protracted posture exerts a braking action. In both cases the horizontal force acting on the body depends on the axial thrust of the limb's musculature and on the angle of inclination of the limb. The propulsive or braking action of a limb operating as a strut can be increased or decreased by the operation of the limb as a lever. During each cycle of movement a limb alternately acts as a brake or as a propulsive element; over the whole cycle the fore limbs of a cursorial mammal probably exert a resultant braking action whereas the hind limbs have a resultant propulsive action.

19. The diagonal co-ordination of limb movements seen in nearly all tetrapods enables the limbs to propel the body forwards with a minimum of uncompensated pitching or rolling couples. It is in fact the only pattern of movement which enables the body to be in static equilibrium with its own weight at all phases of the movement; the animal can therefore come to rest at any point without falling over.

20. The forces acting on the body and at the feet of a moving animal are discussed, and brief reference made to the relative importance of front and hind limbs as organs of propulsion.

21. The locomotory significance of the axial musculature of the vertebral column is described.

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