THE COMPARATIVE MORPHOLOGY OF THE VERTEBRATE SPINAL COLUMN. ITS FORM AS RELATED TO FUNCTION

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NINE FIGURES

AUTHORS' ABSTRACT

The form of the vertebral column is definitely related to its function as a supporting rod, a base for attachment of body and limb muscles, and a protection of the spinal cord and nerves. Primitively composed of a series of simple undifferentiated blocks, it progressively becomes complicated through development of articular processes giving added strength and greater mobility. Simultaneously, the centrum and the neural arch become adapted to withstand tension and compression stresses which vary with the movements possible in different regions of the column. These movements are partially determined by the plane of the zygapophyses and the nature of the intercentral articulation, together with the action of the axial muscles and ligaments.

In fish and primitive tetrapods the axial musculature serves as the chief locomotor organ and consists of a series of myomeres extending with little interruption from the head to the tail. In tetrapods the locomotor function is taken over by the limbs and the axial muscles become progressively differentiated into long flexors and extensors of the column and gradually lose their external segmentation.

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INTRODUCTION

A great deal of work has already been done on the vertebral column, but nearly all of it is of a purely descriptive nature. Few, if any, authors have viewed it from a functional standpoint and, except in man, there has been almost no attempt to consider the mechanics of the spine.

The object of this paper, which was undertaken at the suggestion and with the help of Dr. William K. Gregory, is to present the evolution of the vertebral column from a functional viewpoint. We have attempted to analyze the spines of various animals from fish to man, considering each as a functioning structure, trying to show what types of movement were possible and how the vertebral column adapted itself to withstand the various mechanical forces to which it was subjected in the living animal.

For many years past there have been two sets of terms for the parts of the complex vertebrae of fishes and tetrapods. These systems, devised on the one hand chiefly from embryological evidence by Gadow ('33) and on the other from palaeontological evidence by Cope (1888) and his successors, may be equated as follows:

Gadow	*Cope and other workers*
Basidorsals = neural arch (dorsal extension of first ring)	Neurocentrum (fused in midline)
Interdorsals = postero-dorsal half of second ring	Pleurocentra
Basiventrals = antero-ventral half of first ring	Intercentra (hypocentra = haemal arches in caudal region)
Interventrals = postero-ventral half of second ring	Hypocentra pleuralia

In general, Gadow's interpretation of the presence of four pairs of primitive elements in the ideally complete vertebra has now become the most familiar, although in fossil forms this scheme is sometimes difficult to apply.

According to Romer ('30), at a very early period the intercentrum was apparently the dominant element, and from this primitive type of vertebra that of modern amphibians evolved on the one hand and that of higher tetrapods on the other. In the Embolomeri the pleurocentrum was dominant, but in the Rhachitomi and Stereospondyli stress was placed on the intercentrum. Romer also states that, "the main line of vertebral evolution [toward the amniotes] in the early amphibians was the development of the pleurocentrum at the expense of

the intercentrum.'' In the 'gastrocentrous' type of Gadow (ancestral to all amniotes) the posteroventral element (interventral) became dominant. According to Williston ('25) and other palaeontologists, the main centrum of each vertebra in amniotes represents not the interventrals but the interdorsals (pleurocentra).

THE AXIAL SKELETON OF FISH

Living in a medium dense enough to buoy it up and having no direct contact with the ground through limbs, the fish does not have to contend with complicated mechanical stresses. The axial skeleton serves principally as a support and firm base for attachment of the great lateral muscles which are the principal elements of locomotion. It is firm enough to prevent squeezing of the nervous system during extreme muscular contraction and at the same time flexible enough to permit considerable lateral swing in the tail.

Considered from a purely developmental standpoint, the embryologist tells us that the typical vertebral column passes through three stages: the notochordal, the cartilaginous and the osseous. Among fish we find examples of two of these stages in the adult individual. The notochord, around which the elements of the vertebral axis are built, is in itself insufficient as a supporting structure. Palaeontological evidence indicates that bone cells were present in the earliest known fish, so even though the notochord remained unconstricted, it was strengthened by tough sheaths and bony pieces. The fact that a great number of our modern genera have a calcified cartilaginous skeleton shows, however, that in water-living forms bone is not necessarily the only efficient supporting material. Indeed some of our great sharks are very active, fast-swimming fish, capable of twisting and diving with remarkable alacrity. Nevertheless a bony vertebral axis has been retained in a great majority of our modern fish and since it was the ossified column which finally coped with the mechanical stresses of life on land, it is of particular interest in the present study.

With the exception of the two major regions which may be designated as precaudal and caudal, there is little regional differentiation in the fish vertebral column. The vertebral axis is composed of a great number of segments. The precaudal region is marked by one or more pairs of ribs to each segment; in the caudal region the ventral pair of ribs is replaced by a haemal arch which encloses the large ventral blood vessels.

In all fish, with the exception of Lepidosteus, the vertebrae are of the amphicoelous type, i.e., biconcave. The intervertebral space between successive centra is filled by the notochord, which becomes greatly constricted vertebrally. The centra of a generalized fish such as the Tarpon are box-like without any bony intervertebral articulations. They are held together by intervertebral ligaments. Above the centra and within the neural arches there is also a strong 'dorsal longitudinal ligament' which runs the entire length of the column; it serves to bind the vertebrae together and to prevent flexion of the column. Movement between successive vertebrae is probably very restricted but the system as a whole is flexible enough to allow considerable lateral swing of the caudal region.

The primary units of locomotion are the myomeres. The number of these muscle segments equals that of the vertebral segments. Each myomere consists of horizontally arranged muscle fibers bounded anteriorly and posteriorly by myocommata or intermuscular septa. Embryologically they arise as simple vertical bands with a fairly regular external outline. That this arrangement is probably also a primitive one can be seen from a restoration of a cephalaspid. However, they early, both embryologically and palaeontologically, become bent on one another, forming the typical zigzag outline. The whole lateral muscle mass, and therefore the intermuscular septa, are separated by a horizontal septum into a dorsal or epaxial portion and a ventral or hypaxial portion. Viewed in their entirety (fig. 1), we see that the intermuscular septa are folded into cones. On each side of the horizontal septum the cones lie with their apices directed anteriorly; dorsally and

ventrally to these cones, at about the level of the tips of the neural spines in the epaxial portion and the ends of the ventral ribs and haemal spines in the hypaxial portion, the cones lie with their apices directed posteriorly.

This zigzag arrangement of the myomeres is of great mechanical importance. The muscle fibers run more or less parallel to the vertebral column. If the intermuscular septa lay at right angles to the column, very little of the force from the contraction of the muscle fibers would be transmitted on to the column. Rather, the pull would be only against the next myomere; it would, therefore, be necessary for all the myomeres on one side of the fish to contract to bring about any

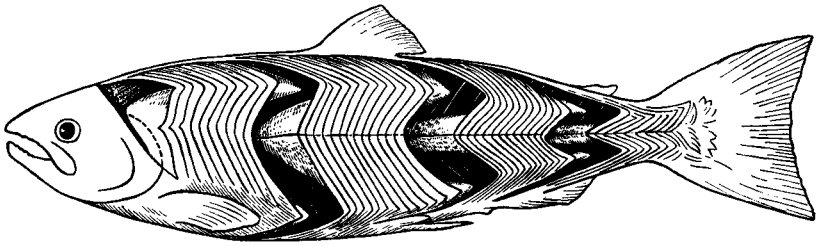

Fig. 1 Typical arrangement of myocommata. (After C. W. Greene and C. H. Greene, The skeletal musculature of the king salmon.)

appreciable lateral bending of the vertebral column. Locomotion would be slowed down and the fish would quickly use up its supply of energy.

Due to the zigzag arrangement of the intermuscular septa, the muscle fibers insert obliquely on to the septa. The direction of the pull exerted by the contracting muscle fibers is very nearly in line with the septa. Therefore the force of the contraction is transmitted directly to the vertebral column. The intermuscular septa insert on the vertebrae at about the middle of each centrum. Thus a myomere is connected with two vertebrae and is said to be intervertebrally situated. Contraction of a single myomere will result in some degree of lateral bending in the column. Violent contraction in only a few of the total number of muscle segments is sufficient to

bring about a strong lateral swing with comparatively little expenditure of energy.

From figure 1 we can see that the angles of the zigzag become increasingly acute from anterior to posterior. In relation to the discussion above, this indicates greater quickness and flexibility of movement in the caudal region than in the precaudal region.

Comparison between a fast-swimming and a very sluggish fish brings out another significant point. Kishinouye ('23), in describing the musculature in the Scombridae, which includes some of our fastest swimming fish, points out that the apices of the forwardly directed cones are stretched out and united into a tendon which extends almost the entire length of the lateral muscle mass. The caudal region is marked by the presence of bony processes on the sides of the centra in the form of a keel. The myomeres in this region are elongated into strong tendons that find firm attachment on to the keel. On the other hand, dissection of the musculature of Amia calva fails to show any fibrous attachment between the apices of the cones, although the septa show a tendency to be pulled out into short bands that could easily join together into a tendon. The caudal myomeres are unspecialized. In the scombrids the formation of these tendons, which lie parallel or at a slight angle to the vertebral column, enables these fish to make the extremely quick and powerful movements for which they are famous.

The ribs of fish develop in response to muscle pull. The ventral pair are always present in teleosts and they usually articulate with a transverse process borne on the centrum. The so-called dorsal ribs, or epipleurals, are highly variable; when present they may have a tendinous attachment on to the centrum, the transverse process, the neural arch, or even on the ventral ribs. Sometimes there are additional ossifications which have no direct connection with the column, merely lying free in the intermuscular septa. They all serve to strengthen and support the muscles.

In many of the higher teleosts we find the beginning of bony intervertebral articulations. These 'zygapophyses' develop either on the centra or on the arches. Sometimes they are only small triangular braces but when they actually overlap, the articulation is always in a vertical plane. While their presence may increase the flexibility of the column to some extent, in extreme cases (e.g., sailfishes) they serve the more important function of locking the vertebrae together to form a stiff axis which must act as a sort of spring. In this way the vertebral column is made to take over one part of the work of the muscles. When the myomeres on one side of the body contract, the rigid column is bent as a bar of spring steel might be bent, so that when the myomeres relax the column springs back into line without contraction of the myomeres of the other side. Thus the speed and strength of the stroke is increased.

The caudal region of Amia presents a curious parallel to the two-ringed condition of the early amphibians, as there are intercalated, non-arch-bearing centra. It is likely, however, that this two-ringed condition arose in an entirely different manner in Amia than in the embolomeres and that the elements are not homologous. The myocommata insert only on the arch-bearing centra, so that the intercalated elements are entirely intramuscular. Since the number of joints is doubled, one would expect greater flexibility in such a vertebral column, but as Amia is noted for its sluggish habits, the presence of these intercalated elements can be explained only as a genetic character inherited from some earlier amioid such as Caturus or Eurycormus, where the two-ringed condition was well started. The fact that is of greatest interest in relation to the present study is that, in spite of the remarkable modification of the bony elements, there has been no appreciable change in the arrangement of the myomeres.

THE AXIAL SKELETON OF TETRAPODS

With the emergence of the tetrapods in the Devonian and Carboniferous, the vertebral column assumed new functions and was subjected to many stresses and strains which were

not present in a completely aquatic environment. Although the primary function of the vertebral column was still protection of the spinal cord, it now also served as a sort of beam supporting the weight of the head, ribs, viscera, etc., which had formerly been carried by the water. The paired limbs took over a large share of the locomotor function, consequently reducing the size of the axial musculature.

Early amphibian types

In the primitive amphibians, the Embolomeri, the vertebrae were made up of three pieces, one neural arch and two checker-like blocks, the intercentrum and the pleurocentrum, the latter being the larger. The relatively great distance between the pectoral and pelvic limbs, plus their sprawling position, placed most of the body weight on the trunk vertebrae. In supporting this weight the spinal column was subjected to tension and compression stresses which, in the trunk region, were taken over by the centra and neural arches respectively. Judging from the massive, closely spaced spinous processes and neural arches as compared with the relatively smaller centra, the neural arch mass of the embolomere was subjected to predominant compression forces.

Terrestrial life required a stronger spine than that of fish, so articular processes, restricting the flexibility of the column, became increasingly important. In the Palaeozoic crossopterygians the neural arches of adjacent vertebrae inclined backward and certain specimens of Eusthenopteron show clearly a bowing backward of the posterior contour of the neural arch just above the exit of the spinal nerve. This outwardly flaring part may have merely overlapped without touching the anterior border of the following neural arch. Definite zygapophysial articulations arose when the neural arches became spaced from each other, the zygapophysial articulations above the nerve exit thus becoming supported on definite flanges or processes. According to the palaeontological evidence, the various zygapophyses, zygosphenes, etc., are direct outgrowths of the neural arches. According to

Mookerjee ('36), however, in modern genera these zygapophyses form from migratory connective tissue cells that become attached to the neural arches, forming processes. To us, however, the present source in embryology of any particular bony part is not necessarily a sure guide to its remote phylogenetic origin. Therefore, the hypothesis that articular processes developed through hypertrophy of those parts of the neural arch which were exposed to functional stresses seems more in keeping with the fossil evidence.

The development of intervertebral discs was another important land adaptation. They prevented the adjacent surfaces of the vertebrae from breaking down under the constant minute traumata to which land locomotion subjected them. These discs appear to have arisen as ossifications in the notochordal sheath of the intervertebral spaces. In various fish which we examined the edges of the vertebrae are sharp and the intervertebral rings slight or absent. In Eusthenopteron the central rings in the neck have very rounded edges, implying rather large intervertebral rings. The roundness of the ends of the rings increases in pelycosaurs and in Cynognathus, implying well-developed intervertebral discs. In the tail region of geckos the intervertebral half-rings appear to be true intercentra and are so named by Camp ('23); they likewise support the haemapophyses. In most mammals the intervertebral discs become secondarily fibro-cartilaginous, except in a few cases. In the moles (Scalops, Myogale) we find well-developed intervertebral nodules in the lumbar region representing the ventral part of the intervertebral discs. In a young Solenodon we find remarkably large intervertebral discs, suturally attached to the front ends of the lumbar vertebrae, almost suggesting the embolomerous condition. Among Cetacea the intervertebral discs often remain separate even in the adult.

In short, present evidence indicates that intervertebral discs in general are homologous with intercentra and like the latter have been derived from the intercentral portion of the perichordal sheath.

Eryops represents a late Palaeozoic side branch from the line leading to the higher tetrapods. In it each vertebral segment consisted of four pieces, one neural spine and arch, two wedge-shaped pleurocentra and one wedge-shaped intercentrum, the latter making up the body of the centrum (fig. 2). The neural arch and attached zygapophyses were well developed. The prezygapophyses faced obliquely upward and inward, and the postzygapophyses faced downward and outward. While greatly limiting dorsal flexure, this permitted considerable lateral bending. Even though the neural arch and the intercentrum were firmly bound to one another and to the paired pleurocentra with ligaments and articular capsules, their articular surfaces were covered with cartilage. It is conceivable that disruption of vertebral elements would have occurred if the slippery, cartilage-coated surfaces of the wedge-shaped elements had been subjected to great extension or flexion motions. There was no danger of this with lateral motions. The spinous processes were much higher and more slender than in the embolomeres, indicating a more massive dorsal musculature which was in keeping with the greater size of the beasts.

Olson's ('36) restoration of the dorsal axial musculature of Eryops shows the myosepta attached on the side of the neural spine and arch of each vertebra and on the rib connected with it, thus dividing the muscle mass into the same number of segments as vertebrae. This was also probably the condition in the embolomeres. Since this distinctly metameric character of the axial muscles of the early amphibians was very like that of fish, it is probable that the axial muscles still played an important role in locomotion.

The ribs of these early tetrapods were large, curved and two-headed. The origin of the two-headed rib from the single-headed fish rib is a perplexing problem tied up with other terrestrial modifications and adaptations. With the gradual reduction in the size and importance of the dorsal axial musculature in the tetrapods, the importance of the 'dorsal' ribs as an anchor for the locomotor muscles increased. Consequently

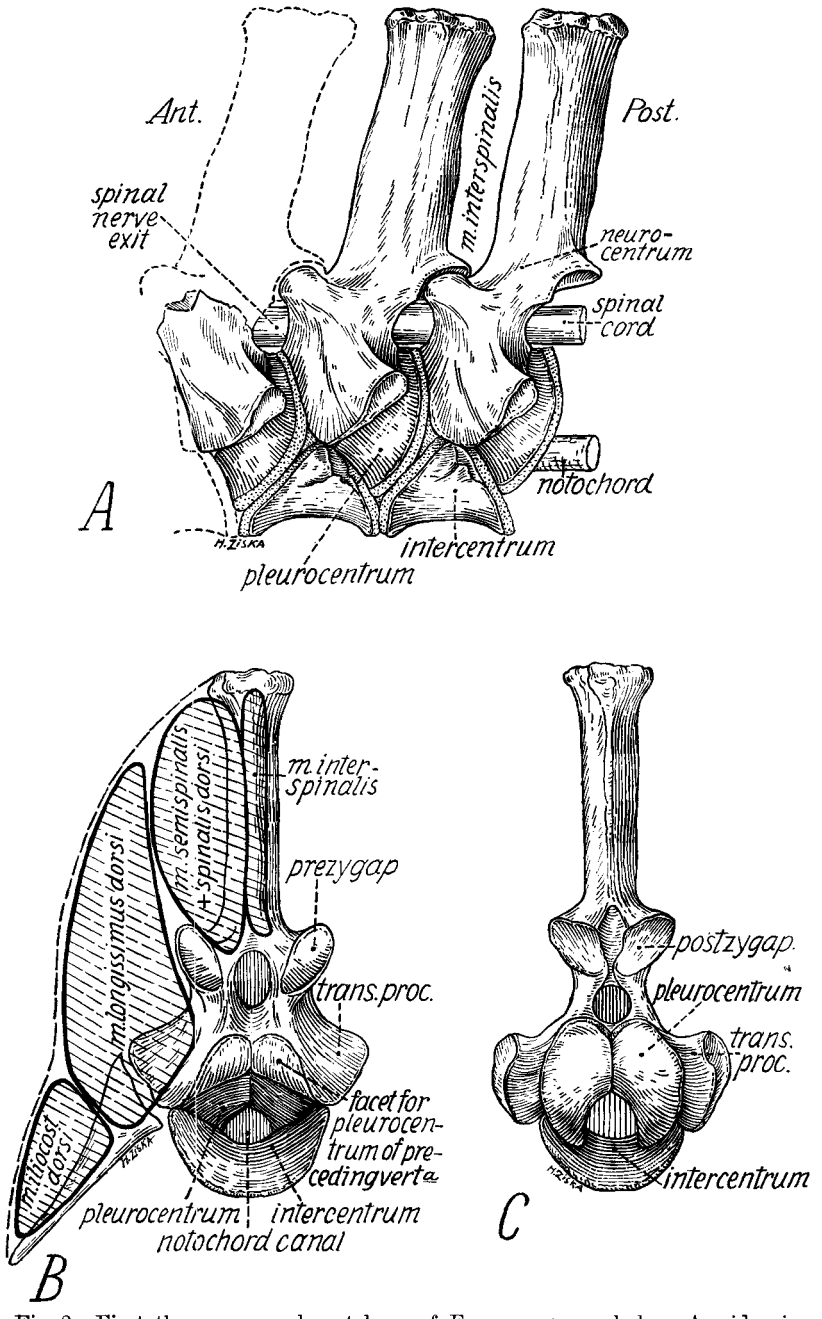

Fig. 2 First three presacral vertebrae of Eryops megacephalus; A, side view; B, front view—muscles restored after Olson; C, rear view.

the ribs were forced to acquire a more stable connection with the vertebrae. This was accomplished either by the development of a second head, the tuberculum, or by the subdivision of the wide proximal head into two branches, namely, a capitulum articulating with the intercentral discs or intercentra and a tubercle articulating at first with the side of the neural arch, later with a diapophysis or dorsal transverse process. These strongly attached ribs furnished an excellent anchoring place for the anterior serrati, and perhaps other muscles which supported the pectoral girdle and limbs.

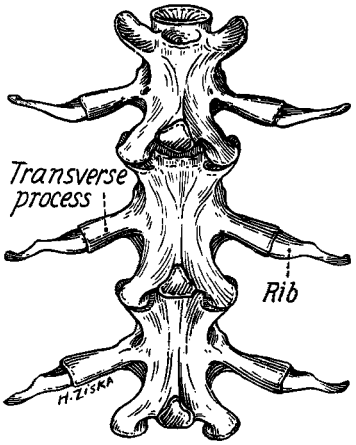

Fig. 3 Cryptobranchus. Three dorsal vertebrae, dorsal view.

This base for muscular attachment was not important in sprawling forms, but in the later reptiles and mammals, where the limbs were brought in under the body, raising it off the ground, the supporting function of the muscles became of primary importance. This firmer, two-headed attachment naturally eliminated dorsoventral movement of the ribs but still permitted cephalo-caudad movement, a feature of particular significance when costal breathing appeared in the reptilian stage of evolution.

On the other hand, in a modern urodele such as Cryptobranchus (fig. 3), which has become secondarily aquatic, the ribs are reduced to short rods on the ends of well-developed

transverse processes. The axial muscles are also somewhat specialized. Although still definitely divided into epaxial and hypaxial portions, they are no longer of approximately equal volume, as the horizontal septum has moved fairly high up on the side of the body, reducing the size of the epaxial muscle mass. The latter is conspicuously metameric and presents a band-like appearance. In contrast to the relatively simple condition of the epaxial muscles is the specialization in the hypaxial muscle mass, which is divided into external oblique, internal oblique, transversus and rectus abdominus.

Although the short ribs of Cryptobranchus are a characteristic inherited from its branchiosaurian ancestors, it is possible to correlate their reduction with the habitat that the animal has adopted. Since it is entirely aquatic, most of the body weight is supported by the water, and as it is not very active, swimming mostly by means of its tail, the viscera are not subjected to the pressure of sudden, violent contractions of the somatic muscles. The needed support, which in a fish is furnished by the long curved ribs, is in the urodele taken over by the specialized hypaxial muscle layers.

Fixation of the holocentrous type among amniotes

In the most primitive reptiles, the cotylosaurs, the neural arch mass was still heavy as compared with the centra, again indicating that the neural arches were subjected to greater compression than tension stresses. The plane of the articular processes remained in the oblique position facilitating the lateral bending of the spine necessary in these still sprawling forms. The intercentra were already beginning to be reduced in size. In Seymouria the capitulum of the rib still attached on them, but in Diadectes the intercentra were quite small and the body of the vertebrae was composed of the pleurocentrum to which the neural arch was suturally connected. The latter arrangement is that found in the majority of the higher reptiles except for the Squamata, where the neuro-central suture has entirely disappeared. This solid mechanical unit was more efficient for the transmission of stresses and was thus a stronger and more stable protection for the nervous system.

In direct contrast to the simplicity of the vertebral body was the extensive and complicated development of accessory articular processes on the neural arches (hyposphenes, hypantra; zygosphenes, zygantra). This occurred in many different groups of reptiles as a method of strengthening and restricting the torsion of the column.

With the appearance of the reptiles, the dorsal axial muscles began to lose the band-like appearance which was characteristic of amphibians and were reduced in volume. According to Olson ('36), the dorsal axial musculature of Diadectes was more advanced than that of Eryops, in that the erector spinae group was becoming differentiated from the rest of the muscle mass. The medial epaxial muscles were also beginning to lose their definite metameric character, now bridging several vertebral segments and attaching by tendinous slips on to the neural arches and spines. The lateral epaxial muscles remained metameric and attached by myocommata to the ribs.

In the mammal-like reptiles as the legs were gradually pulled in under the body, raising it off the ground, the center of gravity was shifted forward, placing most of the body weight over the fore limbs and freeing the hind limbs for propulsion. This change in the distribution of body weight brought about other modifications, such as rotation of the articular processes, alteration of vertebral architecture and further refinements in the axial muscles and their attachments, which will be discussed in more detail in the section dealing with advanced quadrupedal locomotion.

Marked regional differentiation was apparent through reduction in the size of the ribs in the cervical region and their shortening in the lumbar region. The centra and neural arch mass had become more nearly equal in size, indicating that tension and compression stresses above and below the spinal cord were also of nearly equal force. Well-developed intervertebral discs absorbed the ever increasing intensity of the shocks resulting from the relatively greater speed made possible by the position of the limbs.

In Cynognathus the posterior dorsal and lumbar regions were greatly strengthened by a unique development of flat uncinate-like processes on the ribs (fig. 4). These overlapping processes were, according to Gregory and Camp ('18), due to the great development of the ilio-costalis muscle. Their presence made a strong supporting shelf for the axial musculature but did not restrict the mobility in this region, which was probably quite free in all directions except extension.

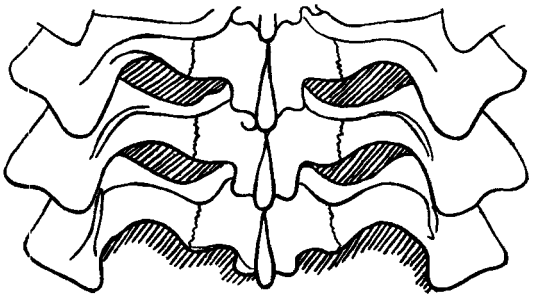

Fig. 4 Cynognathus. Posterior dorsal vertebrae, dorsal view. (From S. W. Williston, The osteology of the reptiles, after Seeley.)

Further evolution of the column in quadrupedal mammals

With the appearance of mammals and their subsequent development to a major position in the vertebrate world, proficiency in land locomotion reached its zenith. Again, as in the earlier vertebrates, it was modifications in the appendicular skeleton that initiated the changes in the vertebral column.

Whereas in lower vertebrates lateral flexure of the column was predominant, most mammals have a characteristic method of running in which their body alternately doubles up and straightens out in the vertical plane (Gregory, '12). Two changes occurred in the lumbar vertebrae that facilitated this extensive vertical flexion and extension, which in many forms is centered in the anticlinal vertebra: the lumbar region lengthened out by reduction of the dorsal region; and the articular processes rotated to a nearly vertical plane.

There was a corresponding modification in the axial muscles. The consolidation of the primitively metameric musculature into long spinal flexors and extensors, already started in the mammal-like reptiles, was carried out to a greater degree through the differentiation of the erector spinae group into longissimus dorsi, multifidus, ilio-costalis, spinalis dorsi, etc.

These new muscle layers in turn affected the body structure through their need for firmer attachments on the vertebrae. The areas of attachment became prolonged as the metapophyses, or mammillary processes, and the anapophyses, or accessory processes. The former, to which the multifidus attached, extended cephalad from their bases on the superior articular processes; the latter, to which the longissimus dorsi attached, extended caudad from their bases on the transverse processes. In addition, the tips of the transverse processes, on which the quadratus lumborum inserted, were in many mammals deformed and extended caudally.

The application of mechanical principles to an analysis of vertebral function has interested many workers. The common analogy they present is that of a bridge, usually of a cantilever type (Thompson, '17). That there is such a resemblance cannot be denied, but a bridge is a relatively solid structure and the spine is made up of a series of multi-articulated blocks that are poised on two movable pillars in a fashion only somewhat analogous to the manner in which a bridge is supported by its piers.

Because the spine is constructed of a series of separate units, the interplay of forces in such a fabrication is rather complex. It does not lend itself to analysis as readily as the solid structure of a bridge or beam. There must be a center or fulcrum of rotation between vertebral segments, and through such an area or point the sum of all forces concerned in maintaining the integrity of the spine under given conditions of weight support or motion will be concentrated.

The center of vertebral motion is the nucleus pulposus of the intervertebral disc. This very versatile structure has yet another action, that of serving as a 'hydraulic shock-absorber'

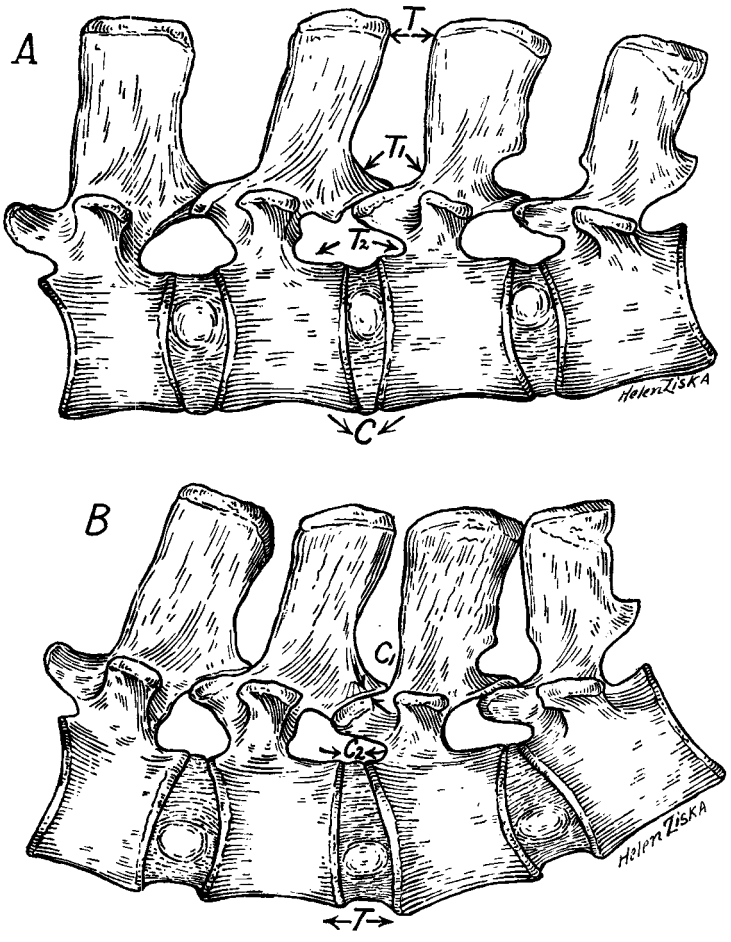

Fig. 5 Diagrammatic representation of vertebrae in flexion and extension showing reversal of forces transmitted by the centra and the neural arch mass. The play of the nucleus pulposus is slightly exaggerated. In life the nucleus pulposus is covered by the annulus fibrosus.

In A, the interspinous (T), subflavian and interarticular (T_1) ligaments and the posterior longitudinal ligament (T_2) resist tension while the ventral margins of the centra (C) resist compression. $X = T + T_1 + T_2 + C$.

In B, it is the reverse of A. The ligaments are lax or contracted and the articular processes (C_1) and the dorsal margins of the centra (C_2) resist compression. The anterior longitudinal ligament (T) is under tension. $Y = C_1 + C_2 + T$.

X and Y in the above formulae represent the combined tension and compression forces resisted by the nucleus pulposus under the conditions depicted.

to aid in dissipating the shocks of locomotion. The nucleus pulposus is the central semi-fluid, gelatinous substance that is enclosed by the annulus fibrosus, the peripheral fibro-cartilage of the intervertebral discs. It is not completely fixed in a single location on the articular surface of the vertebral bodies but enjoys a small latitude of motion. It moves ventrally with extension, dorsally with flexion, and to the opposite side with lateral motions of the spine. This is illustrated in figure 5. It is normally located slightly dorsal to the center of a vertebral body.

A primary principle of physics is that any force that is applied to a body will produce deformation. If a double overhang beam is loaded so that one of its supports carries two-thirds of the load and the other support one-third of the load, the resultant deformation will resemble figure 6, C. (The drawing exaggerates the deformation.) In a beam there is a central neutral zone, an area that carries neither compression nor tension stresses. This is represented by the dotted line in the figure. There is no analogous neutral zone in the spine. The part of the vertebral body that would be expected to represent a neutral area here serves as the center or fulcrum of motion. Hence it must resist the sum of all tension and compression forces conveyed to it (fig. 5).

We may note that the structure of a vertebral body at this area indicates the rather considerable stresses it must withstand (fig. 7, A). There is an analogy, however, between the forces that the concave and convex sides of a loaded beam convey and the forces carried by the neural arch mass and the ventral margins of the vertebral centra of the column. In figure 6, C, the shading on the concavity of the curves represents the area under compression stress; the other half of that section of the beam is under tension.

The weight of the head and neck of a quadruped tends to produce flexion of the cervical vertebrae (fig. 5, A). The neural arch mass therefore transmits tension stresses and the vertebral centra resists compression stresses. Both types of stresses become increasingly heavy as the dorsal region is

approached. A reversal of the deformation, and hence a reversal of stresses, occurs somewhere in the dorsal region (fig. 6, C, D). The heavier the head and neck in proportion to the rest of the body, the more caudally situated is this point. The vertebrae caudad to this point tend to be extended and their neural arches therefore carry a compression load, while the ventral margins of the vertebral bodies and the anterior longitudinal ligament transmit tension stresses (fig. 5, B).

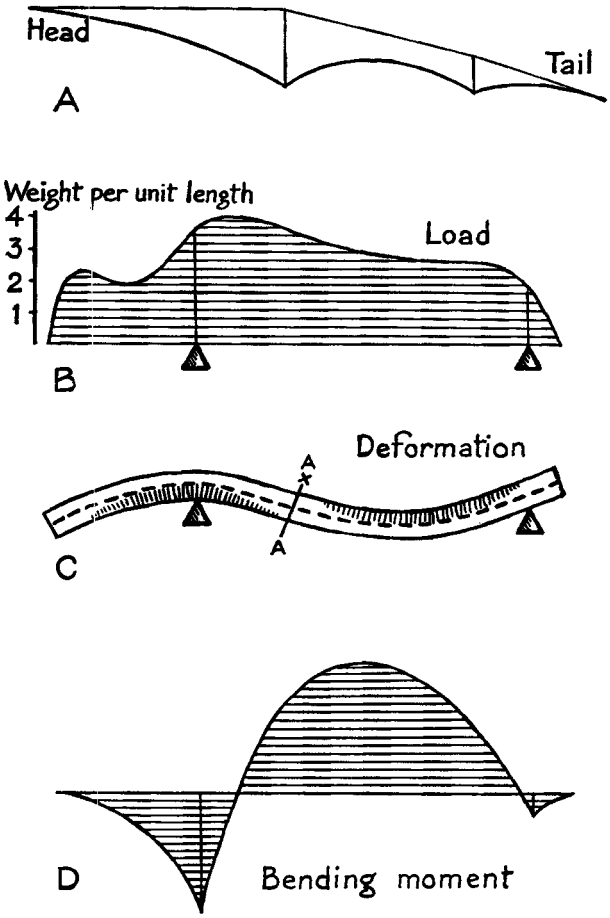

Fig. 6 A, diagram after D'Arcy Thompson depicting stress relationships in the vertebrae of a horse, B, load, and D, bending moment diagrams of a beam, loaded and supported in a manner similar to the column of a horse. C, deformation of the beam under the load (exaggerated).

The massive bodies of the cervical vertebrae of many quadrupeds are in decided contrast to the more weakly constructed centra in the dorsal and even in the lumbar region; whereas the neural arches of the cervical vertebrae, while frequently possessing elongated spinous processes, are often lightly constructed in comparison to those in the dorsal and lumbar regions.

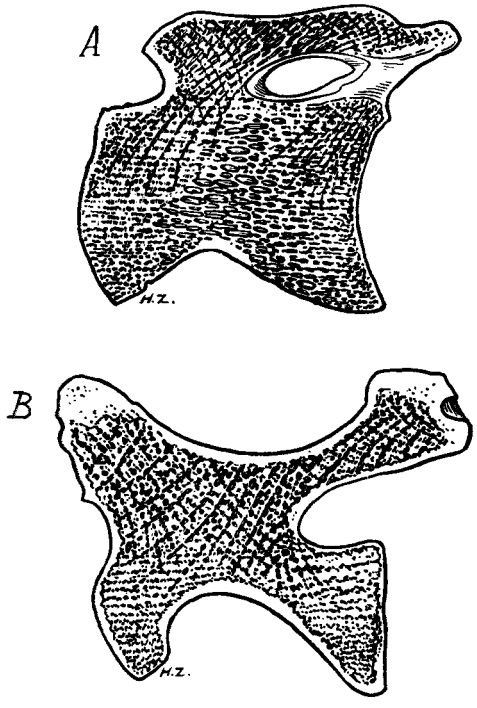

Fig. 7 'Trajectories' of A, a dorsal vertebra of an ox, B, a lumbar vertebra of an ox, plotted from photographs of sagittal section in K. Bardeleben, Beitraege zur Anatomie der Wirbelsäule.

The ox is a heavy-headed, long-necked animal. In figure 7 one of the first dorsal vertebrae and a lumbar vertebra are shown. The centra of the dorsal vertebrae are better constructed to withstand compression stresses than those of the lumbar vertebrae, the reverse being true of their neural arches, those in the lumbar region being stronger than the neural arches of the dorsal vertebrae.

The deductions that may be made from these observations appear fairly straightforward. In keeping with what has already been said about the transmission of forces in a beam and in the spine, one can interpret the presence of a relatively (in contrast to other regions of the spine) sturdy and large vertebral centrum in a particular region only as indication that these elements at this point must carry a compression load. A relative increase in the strength and size of the neural arch mass in another region indicates that these elements here carry a compression load. The elongated spinous processes over the withers of many quadrupeds are admirably situated and directed to transmit tension stresses to the dorsal and lumbar regions, and to dissipate them as compression stresses in the vertebrae to which they are affixed.

Bones do not resist tension as well as ligaments, hence it is entirely in keeping with what is known of the physiology of bone that in those regions where ligaments can more efficiently handle tension stresses, there is a relative reduction in the mass of bone present.

It may be seen then that the vertebral bodies in the cervical region of any animal (excepting the sloth) normally convey compression stresses. There is a reversal in this flow of force at some point in the dorsal region, the exact location of this point depending on two things: the relative weight of the head and neck in comparison to that of the trunk, and the length of the trunk. (The shorter and lighter the head and neck are, the closer the site of stress reversal to the cervical-dorsal junction.) In those segments caudad to this point, the neural arches are under compression stresses, while the tension stresses are transmitted by the ventral margins of the centra and the anterior longitudinal ligament.

With the exception of forms possessing a long and heavy tail, the sacral and caudal, or coccygeal, vertebrae represent an almost negligible 'posterior over-hang' part of the spine.

THE COLUMN IN MAN

One of the most important effects resulting from the assumption of an upright position was the reversal of force transmission in the dorsal and lumbar regions of the spine. Although, as already noted, the spine is not a solid object but a series of connected blocks, the spine of bipedal and orthograde animals may be compared with a pillar that is supporting a weight that lies in front of it. In such a spine there is no reversal of forces at any point as we pass backward. All of the bodies, under normal conditions, resist compression stresses, while the neural arch mass carries the tension stresses. That is, the spine is under a flexion deformity (fig. 5, A). The middle dorsal vertebral bodies are more sturdy and the neural arch mass is more delicate than the corresponding parts of a quadruped (fig. 8, B, C).

Because of their long tails, the center of gravity in many early reptiles was located rather far posteriorly. Under suitable conditions some of these animals could easily have elevated the fore part of their body from the ground and apparently, in certain groups, this presented some advantages over usual methods of quadrupedal locomotion; it was therefore developed as their method of locomotion.

Man has developed bipedal locomotion to its most perfect stage. Consequently, because of the alterations in stress transmission that such a position entailed, extensive changes in vertebral design have occurred. Correspondingly, in all bipeds and in animals such as sloths that live in an inverted position, we find appropriate architectural modifications. No other bipeds, however, are capable of full extension of thigh on trunk in the normal posture, man being the only one to have accomplished this.

The shortening of the vertebral column in higher primates from the mammalian average of 26 to 27 presacral segments to a spine of 23, 24 or 25 segments, served several purposes. The rib cage and pelvis were approximated, giving the abdominal viscera additional protection against trauma and at

the same time alleviating some of the dragging strain on mesenteries that a long loin coupled with an upright position entailed. In addition to this, it enabled orthogrades to more easily maintain their upright position by insuring better lateral stability.

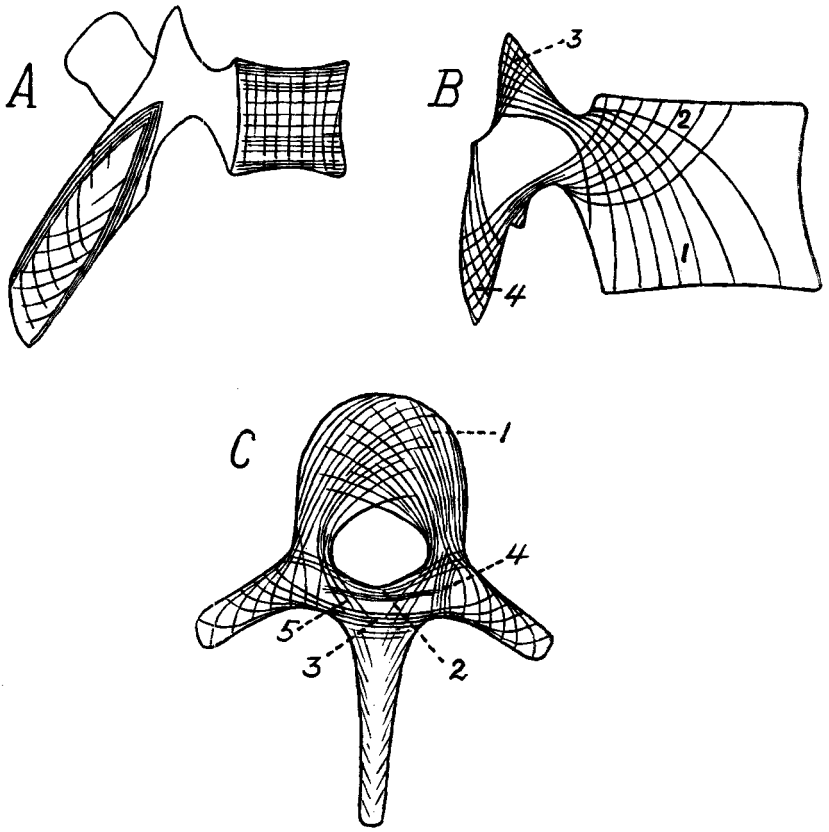

Fig. 8 Schematic drawing of the internal architecture of a human dorsal vertebra. A, median sagittal section. The parallel trabeculae of the centrum designed to resist the predominant compression forces encountered here is well seen. B, lateral sagittal section. 1 and 2, the oblique trabecular system of the zygapophyses; 3 and 4, reinforcing trabeculae of the oblique system. C, horizontal section. 1, 4 and 5, horizontal trabecular system of the accessory (spinous and transverse) processes; 2 and 3, reinforcing (intertransverse) trabeculae of the horizontal system. (From Gallois and Japiot, Architecture intérieure des vertèbres.)

The internal structure of a human vertebra is designed to withstand certain forces. The body has been termed the passive element. It resists the compression stresses of transmitted body weight and also serves as a base for the attachment of the apophyses, the levers by which spinal mobility is effected. These latter are the active elements and are reinforced to resist stresses from all directions (fig. 8). In relation to this compression-resisting function of the vertebral centrum, it is interesting to note that, as we pass from the cervical through the dorsal to the lumbar region, there is a constant uniform increase in the size of the centra, this being in keeping with the progressively heavier load each segment is called upon to bear as the sacrum is approached.

The trabeculae making up the vertebral centra of all bipeds and those centra in quadrupeds which resist compression stresses are arranged with their axes parallel to one another and in line with the flow of force that they must resist (figs. 7, 8, A).

In general, the articular processes in corresponding regions of the spines of bipeds, excepting birds, and quadrupeds are aligned in the same planes, and motions in such corresponding regions are hence of the same type. The accessory processes are well developed, as one might expect from the increased function of the erector spinae muscle, which is now the most important muscle concerned with maintaining an upright position. This exception, however, must be noted. The accessory processes of man are poorly developed, and the articular processes in the lumbar region show a strong tendency to rotate from a vertical to an oblique plane. This is because flexion or extension motions in man are of not nearly the same importance as is stability of his spine. Articular processes which lie in a vertical (sagittal) plane do not resist the displacing forces that man's spine is subject to as well as do more horizontal processes. The incidence of dislocation and spondylolisthesis is somewhat higher in individuals possessing the vertical type of articular processes. Rotation of the zygapophyses to an oblique position (or horizontal in some individuals) adds

a buttress action to the articular function of the processes and therefore contributes to stability. At the lumbo-sacral junction a vertical type of articular plane (known in man as the external-internal type) renders the column especially prone to injury from slight trauma. It does not anchor the spine on

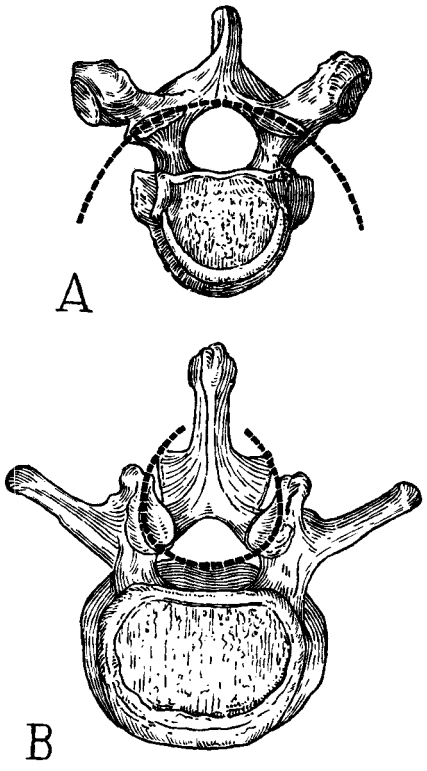

Fig. 9 A, a dorsal and B, a lumbar vertebra of man showing how the planes of the articular processes represent arcs of circles whose centers are located A, in the centrum and B, in the neural arch.

the sacrum as securely as does an oblique or horizontal (anteroposterior type) plane of articulation.

The articular processes of man's spine show another point of interest. Those in the dorsal region represent arcs of a circle whose center is located in the vertebral body. Rotation of one segment on another can therefore easily occur. In the

lumbar region the articular processes represent arcs of a dorsally situated circle. Extensive rotation in this region can only occur if one vertebral body shears upon another (fig. 9). G. S. Huntington, late Professor of Anatomy at Columbia University, was apparently the first to recognize this relationship and point it out in his lectures.

It is also interesting to note that the sacra of almost all bipeds are deepened anteroposteriorly so as to increase their contact surface with the ilium along the line of force transmission.

And finally, the development of a lumbar curve in man, alone of all animals, has enabled him to comfortably maintain his upright posture. Other regions of the spine have altered secondarily: the sacrum has tilted forward at a more oblique angle; the dorsal curve is accentuated; and a cervical curve has been added. The center of body weight has therefore moved directly over the heads of the femurs and closer to the spine, which is the central pillar through which most of the body weight is transmitted.

SUMMARY

In general, anatomists and embryologists have constructed a fairly adequate descriptive background for a study of the vertebral column, and it is now necessary to view this structure as it actually functions in the living animal. A review of an evolutionary series from fish to man serves as a basis for such a study.

The vertebral column of a fish is relatively simple in construction, reflecting its primitive, uncomplicated functions. It serves as a protective mantle for the spinal cord; it acts as the base of muscle attachment and action; and it may, in some species, serve as a stiffening spring whose spontaneous recovery after distortion conserves energy.

There is but little regional differentiation in the spine of fish, except into precaudal and caudal segments. Zygapophyses are usually absent or only weakly developed except in those fish where their presence contributes to the 'spring' action mentioned above.

The primary units of locomotion are the myomeres, which attach on to the middle of the centra by myocommata. They are typically folded into anteriorly and posteriorly directed cones in such a way that the myocommata exert an oblique pull against the vertebral column and contraction of a few myomeres effectually moves several segments.

Since the spine of a fish is equally supported by the buoyant medium that the animal inhabits, it is exposed to no stresses except those associated with motion. On the other hand, the spine of a tetrapod is supported at two points by limbs and hence compression and tension forces are constantly present under simple conditions of weight support. These forces are magnified with locomotion.

Therefore, in amphibians and reptiles we find the beginning of regional differentiation, the development of zygapophyses as efficient articular mechanisms, the introduction of intervertebral discs and differentiation of the primitive metameric muscles into long spinal flexors and extensors.

Regional differentiation was an adaptation designed to facilitate land locomotion and it was associated with certain changes in the planes of the articular processes. These changes resulted in added spinal stability and in restriction of spinal motions to those that best met the requirements of a particular region of the spine. In the dorsal region they restricted motion to lateral bending; in the lumbar region only flexion and extension were permitted.

Although the column and limbs of a quadruped have been considered as analogous to a bridge supported by piers, the weight of the head at the front end and the weight of the viscera in the posterior dorsal and lumbar regions produce a deformation in the column which is more analogous to that of a loaded double-overhang beam, in that there is a variation in vertebral architecture in different regions of the spine and a relationship between this and the forces such parts must resist. In the cervical region of all tetrapods, except the sloth, the centra convey the compression forces and the neural arch mass the tension forces. Somewhere in the dorsal region

there is a reversal in this transmission of forces. Caudad to this point and throughout the lumbar region the centra carry tension forces and the neural arch mass transmits the compression forces.

However, the fact that the column is made up of a series of multi-articulated blocks introduces a factor which has no analogy in a solid beam. The successive centra rotate upon each other, the center of this rotation being located in the nucleus pulposus of the intervertebral discs. In a beam there is a neutral zone which carries neither compression nor tension stresses, but in a segmented column the corresponding portion serves as the center through which all compression and tension forces are concentrated.

On the other hand, in the vertebral column of a bipedal animal there is no reversal in the flow of forces, as the centra are uniformly under a compression load and the neural arches are under a tension load. This is marked by a uniform increase in the relative size and strength of each vertebra from head to sacrum.

In spite of this the articular processes of bipeds remain in much the same plane as in quadrupeds and the range of motion in corresponding regions of the spine is practically the same. In man, however, stability of the column is of more importance than extensive flexion and extension and the more oblique plane of the articular processes helps to strengthen the lumbosacral portion against possible dislocation.

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