# COMPARATIVE BIOLOGIC-ANATOMICAL INVESTIGATIONS ON THE VERTEBRAL COLUMN AND SPINAL MUSCULATURE OF MAMMALS

BY

E. J. SLIJPER

FROM THE INSTITUTE OF VETERINARY ANATOMY OF THE STATE-UNIVERSITY, UTRECHT, HOLLAND, DIRECTOR Prof. Dr G. KREDIET

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# I

## INTRODUCTION; HISTORICAL SURVEY

The object of this investigation was to get a better insight into the various factors that are responsible for the structure of the vertebral column and spinal musculature of mammals, and especially into those factors that are responsible for the differences in structure between the various types of animals belonging to this class. Although numerous authors have dealt with this subject, new and accurate comparative anatomical researches were very necessary indeed. Among other things this may be evident now from the fact that in none of our text-books of human anatomy one can find an explanation why the neural spines of the thoracic vertebrae are inclined caudally, while those of the lumbar vertebrae show a direction perpendicular to the vertebral bodies. Nevertheles, this remarkable characteristic in which man and the great apes differ from all other Primates has already been described by VESALIUS, who used it to demonstrate that the description of the human vertebral column given by GALENUS was based on that of a quadrupedal monkey [BROCA (1869)]. In the veterinary-anatomical literature are given some explanations of the direction of the neural spines of the horse, but not a single author explains why the lumbar spines of horse and dog are directed cranially, while those of the goat and sheep stand upright and those of the cow even show a backward inclination (fig. 1).

Comparative anatomical researches on this subject were all the more desired, since technical difficulties make it almost impossible to solve the problem in an experimental way. The attempts of MORITA (1912, 1913) had no success, as will be shown in detail in the 6th part of this paper. Fortunately, however, I have been able to test the results of my work by studying the changes that had taken place in the vertebral column of a little goat, born without fore-legs. This animal lived about one year and moved forward by jumps on its hindlegs in a semi-upright posture, just like a kangaroo or a jumping-mouse [see SLIJPER (1942) and p. 41, 115].

The investigation comprised the study of nearly 90 skeletons and of the spinal musculature of 61 mammals. The latter material was completed by the descriptions given in the literature of the back-musculature of 19 other mammals, so that the data of 80 different species could be compared.

In the first place I wish to express my most heartfelt thanks to Prof. Dr H. BOSCHMA (Leiden), Prof. Dr CHR. P. RAVEN (Utrecht) and Prof. Dr. L. F. DE BEAUFORT (Amsterdam) for the kind and obliging way in which they placed the material of their collections at my disposal. They made it possible to dissect animals that are very difficult to obtain for this purpose.

For furnishing material grateful acknowledgement is also due to Prof. Dr V. VAN STRAELEN (Brussel), Dr P. WAGENAAR HUMMELINCK (Utrecht), Dr G. C. A. JUNGE (Leiden), Dr K. KUIPER (Rotterdam), Mr OUWEHAND

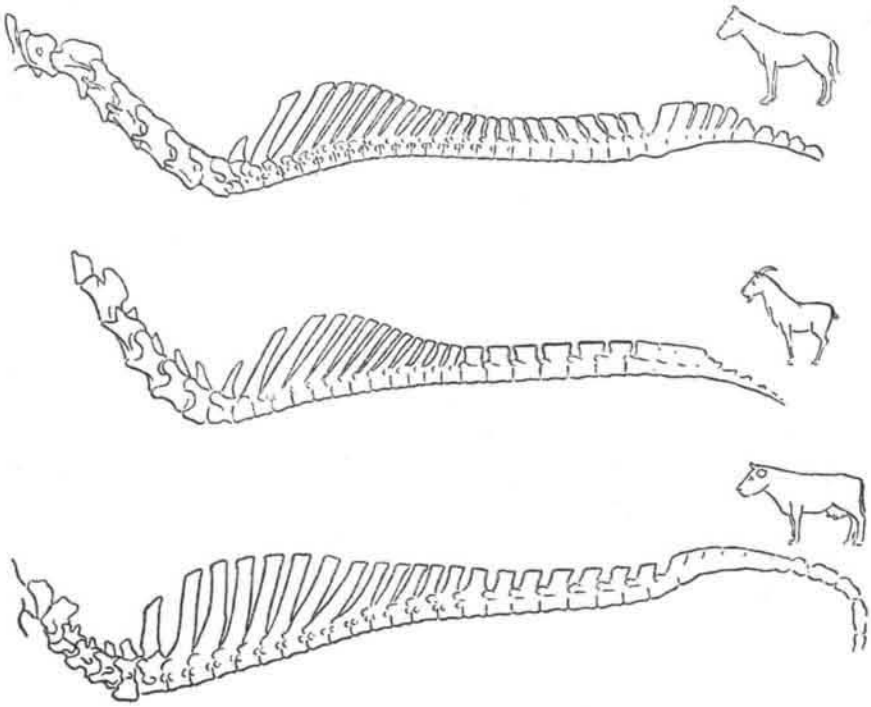

Fig. 1.
Vertebral column of the horse [*Equus caballus* L. (dom.)], the goat [*Capra hircus* L. (dom.)] and the cow [*Bos taurus* L. (dom.)], to show the differences in the direction of the neural spines.

(Rhenen) and Mr J. H. TEN THYE (Utrecht), as well as to Mr W. WIJGA (Utrecht) for the correction of the manuscript and to Dr L. D. BRONGERSMA (Leiden) for the revision of the nomenclature. The investigation of the various factors acting on the vertebral column demanded a certain knowledge of technical problems, especially in the domain of general statics and of bridge-constructions. Without the kindly given collaboration of Mr W. VAN DER HOUT (Bilthoven) and Ir G. J. JANSSONIUS (Amsterdam) I should never have been able to arrive at any result in this subject. I take this opportunity to thank them very cordially.

One of the most striking and at the same time one of the most varying characteristics of the mammalian vertebral column, is the direction of the neural spines. GALENUS has already pointed out, that in a great many of mammals the neural spines of the anterior thoracic vertebrae show a caudal inclination, while those of the posterior thoracic and lumbar vertebrae are directed cranially or perpendicular to the vertebral bodies (fig. 1). ZIEMANN (1838) wrote a dissertation dealing with this phenomenon of anticliny

and BURMEISTER was the first to give the name of anticlinal vertebra to the vertebra whose neural spine has a direction intermediate between that of the anterior and posterior vertebrae. This anticlinal spine always stands upright and in several mammals (especially in a number of Rodentia and Carnivora and in *Thylacinus*) it is markedly shorter than the neighbouring spines (fig. 2). For this vertebra GIEBEL (1853, 1900) used the name "diaphragmatischer Wirbel". This name has occasionally been used in veterinary-anatomical literature too [see for example ELLENBERGER and BAUM (1943)]. VIRCHOW (1913) speaks of the "Grenzwirbel". Since the anticlinal vertebra, however, does not occur in all the species of mammals, LUCAE (1876) proposed to consider the position of the prae- and postzygapophysial articular facets as a criterion for distinguishing two different regions in the vertebral column. In the cranial region the articular facets are nearly horizontal, looking upwards [tangential facets, "Kreisbogentypus"; see KRÜGER (1927) and SLIJPER (1941)], in the caudal region they have an oblique or sometimes a nearly vertical direction, looking inwards (radial facets, "Radiustypus"; fig. 2).

The vertebra of which the praezygapophysial facets are of the tangential, the postzygapophysial of the radial type, bears the name of "vertebra intermedia" [LUCAE (1876)], "Wechselwirbel" [VIRCHOW (1907)], "vertebra thoracalis intermedia" [STROMER (1902)] or "diaphragmatic vertebra" (several different authors; fig. 2). VIRCHOW (1913), however, has already pointed out, that this diaphragmatic vertebra is not always the same as the anticlinal vertebra [see also GOTTLIEB (1915) and REMANE (1936)]. Moreover in some mammals there may be no change at all in the position of the articular facets (see table 7).

In this paper I shall use the name anticlinal vertebra for the vertebra that shows an intermediate position with regard to its neural spine, and the name diaphragmatic vertebra for the vertebra that is intermediate with regard to its articular facets.

There are several theories to explain the length, the inclination and other characteristics of the neural spines of mammals [see also SLIJPER (1936, p. 399)]. These theories may be divided into two important groups. In the first of these groups the vertebral column is considered as an architectonic construction or a part of such a construction. Length and inclination of the neural spines would be determined by the demands of this special construction. In the second group the characteristics of the neural spines are explained by the demands of the spinal musculature.

A. The vertebral column considered as an architectonic construction.

1. *An arched roof.*

This is the oldest opinion. We find it already in GALENUS but also in BERGMANN and LEUCKART (1855), MEYER (1873) and VALLOIS (1922, 1928). They give, however, no explanation about the task of the neural spines. WINSLOW (1732), LUCAE (1876) and GOTTLIEB (1915) believe that the neural spines might be able to prevent sagging of this

arched roof in a ventral direction. This opinion, however, cannot be exact, because in a great many mammals the neural spines do not yet touch one another at the moment that the vertebral column is maximally overstretched in the dorsal direction (dorsal concave). Among others I made this experiment with a monkey (*Cercopithecus* spec.). VALLOIS (1922, 1928) believes that the dorsal musculature would be able to prevent sagging of the arched roof. This, however, is quite incomprehensible.

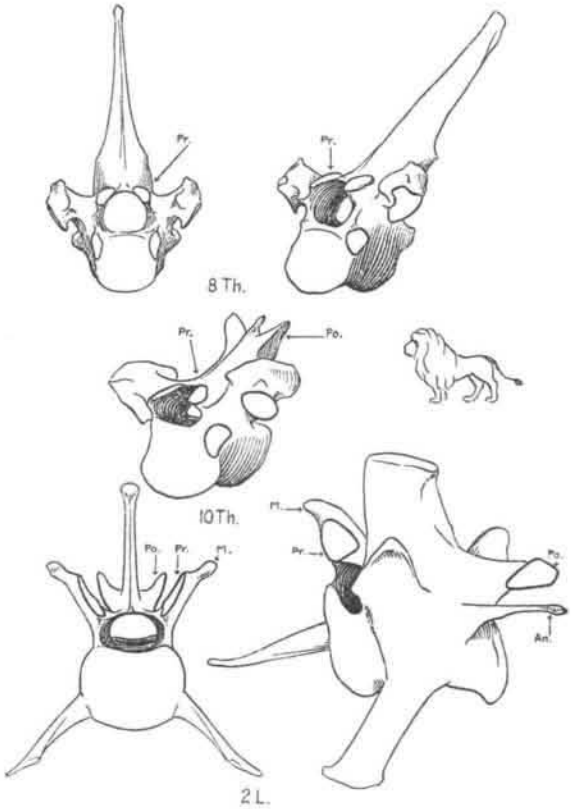


Fig. 2.

Vertebrae of the lion [*Panthera leo* (L.)], to show the position of the zygapophysial articular facets. *Above:* 8th thoracic vertebra (cranial and left side) with tangential facets. *Middle:* 10th thoracic vertebra, the diaphragmatic and anticlinal vertebra (cranial and left side); the praezygapophyses have tangential, the postzygapophyses radial facets. *Below:* 2d lumbar vertebra (cranial and left side) with radial facets. *Pr* = praezygapophysis, *Po* = postzygapophysis, *M* = metapophysis (mammillary process), *An* = anapophysis.

2. *A bridge with parallel girders.*

The opinion, that the vertebral column could be compared to a bridge of this type, has first been published by BERGMANN (1847, p. 694), LUCAE (1876) and EICHBAUM (1890). It has been worked out, however, in detail by ZSCHOKKE (1892). He compared the supraspinous ligament to the upper girder, which he considered as a tension-element. The vertebral bodies were compared to the lower girder (pressure-element), the neural spines to the diagonal braces (pressure-element) and the interspinous ligaments to the vertical braces of the bridge (tension-element) (fig. 3). Especially in veterinary circles this theory has achieved a great success. Its principal followers were WENGER (1915), SIMON (1924, 1926), SCHMALTZ (1928), ZIETZSCHMANN (1925), BRUHNKE (1929) and KRÜGER (1939,

1939a). And even in the most recent text-books of veterinary anatomy and physiology [ELLENBERGER and BAUM (1943), SCHEUNERT, TRAUTMANN and KRZYWANEK (1939)] the opinion of ZSCHOKKE is reproduced without a word of criticism. Only BROWAR (1935, 1940) rejects the theory and WENGER (1915) has already pointed out, that neither

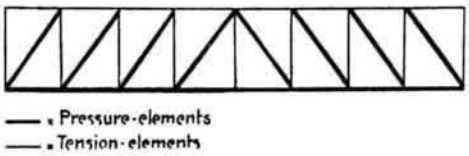


Fig. 3.
Bridge with parallel girders after the wrong opinion of ZSCHOKKE (1892); compare fig. 4.

the direction of the fibres of the interspinous ligaments nor the structure of the compacta of the neural spines is in accordance with this theory, and that the influence of the head and neck has been entirely neglected.

The principal reason, however, to reject this theory is, that in a bridge of this type the upper girder is not a tension-, but on the contrary a pressure-element, while the lower girder represents a tension-element [see FIDLER (1909), JANSEN and fig. 4)]. This has already been demonstrated by BARDELEBEN (1874), who has also shown, that the vertical braces do not represent tension- but pressure-elements.

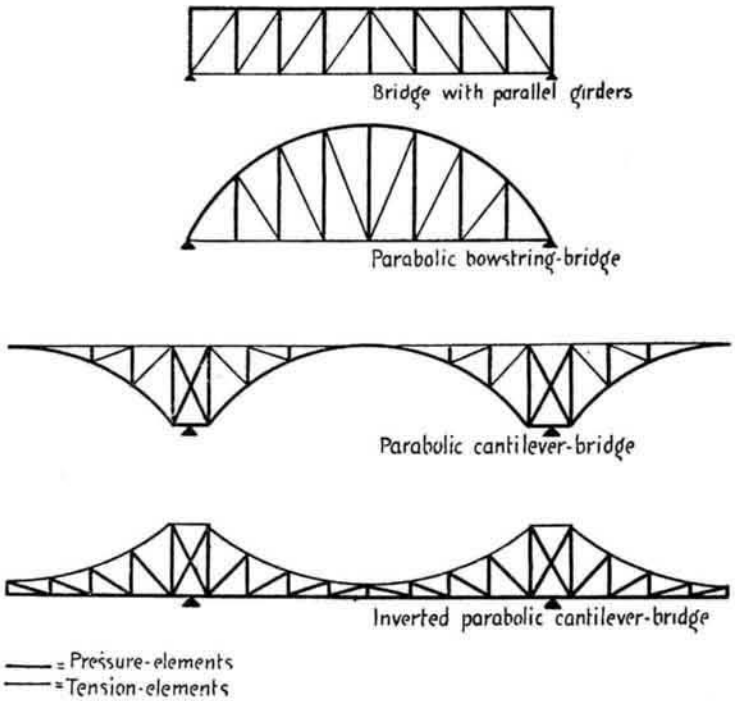


Fig. 4.
Different types of bridges after FIDLER (1909).

3. *A cantilever-bridge.*

Although after SIMON (1926) SEEGER is believed to have compared the vertebral

column already to a bridge of this type. THOMPSON (1917, 1942) has been the first to work out this theory in detail. He considered the vertebral column as a beam strained over two supports or with an inverted parabolic cantilever-bridge (fig. 4 and 5), as for example the Forth-bridge. The ligamentum nuchae and the supraspinous ligament (fig. 20) are said


Fig. 5.
Inverted parabolic cantilever-bridge (Forth-bridge) which, after the opinion of THOMPSON (1917, 1942), might be compared to the vertebral column of mammals.

to represent the upper girder, which in bridges of this type is a tension-element indeed. The vertebral bodies would then represent the lower girder (pressure-element), the converging neural spines of the trunk the converging diagonals of the bridge (pressure-elements) and the interspinous ligaments the diverging diagonals (tension-elements). Followers of THOMPSON are among others MUTEL (1922), ROCKWELL, EVANS and PHEASANT (1938) and GREGORY (1937) [see also SLIJPER (1941)]. GREGORY (1937), however, compared the vertebral column to a common parabolic cantilever-bridge (fig. 4), an opinion that can be rejected at once, since in a bridge of this type the diagonal pressure-elements are converging in the direction of the piers.

At first sight the theory of THOMPSON seems to be very attractive, but if one enters into the details of this comparison it does not hold good. In the first place there are objections concerning the caudal part of the vertebral column. In nearly all mammals the short or light tail does not represent a counterweight to the lumbar region and so we get a stress-diagram as has been given by ROCKWELL, EVANS and PHEASANT (1938) in their fig. 6 c and d (see also my fig. 6). This figure shows, that in such a construction the

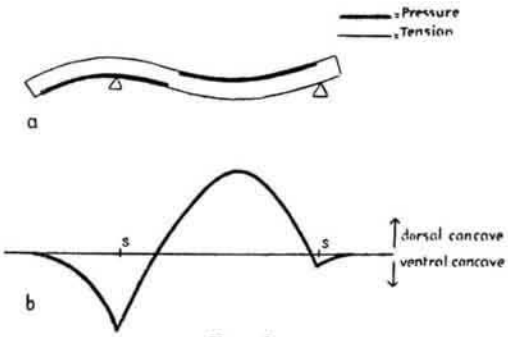


Fig. 6.
a. Deformation of a beam, loaded and supported in a manner similar to the vertebral column of a horse (neck at left side). The deformation has been exaggerated. b. Bending-moment diagram of this beam. After ROCKWELL, EVANS, PHEASANT (1938) (a little altered). $S$ = support.

vertebral bodies of the posterior thoracic and the lumbar vertebrae had to be built as tension-elements and the supraspinous ligament of this region as a pressure-element. Since in reality the contrary is true, a comparison to a bridge of this type cannot hold good with regard to the caudal part of the vertebral column.

Other arguments for rejecting this theory are the fact that the length of the neural

spines would have to increase in the direction of the sacrum, while in reality in almost every mammal the length decreases in the caudal part of the lumbar region [see also MUTEL (1922)]. The fibres of the interspinous ligaments in the lumbar region are not directed from caudo-dorsal to cranio-ventral as THOMPSON supposes, but on the contrary from cranio-dorsal to caudo-ventral (fig. 19). The theory of the cantilever-bridge requires a strong upper girder in the caudal part of the lumbar region. In reality, however, the so-called supraspinous ligament is often very weak or even lacking between the last lumbar and the first caudal vertebra (see p. 28). Moreover the theory does not take into account the differences in the construction of the vertebral column between the various types of mammals. THOMPSON gives an explanation of the fact that in the elephant and the rhinoceros there is no anticliny, but why is there a very distinct anticliny in the hippopotamus, which has nearly the same stature? Why is there anticliny in the horse and not in the cow (fig. 1), why in a tiger but not in a bear? According to the theory of THOMPSON one would expect, that the neural spines in the trunk of a kangaroo or a jumping-mouse would be inclined altogether in a cranial direction, but in reality the vertebral column of these animals does not differ from that of other mammals with a distinct anticliny (fig. 7).

With regard to the cranial part of the vertebral column the comparison with a cantilever-bridge would hold good entirely, if the vertebral column was supported by the fore-leg at the cervico-thoracic border only. In reality, however, the trunk is suspended

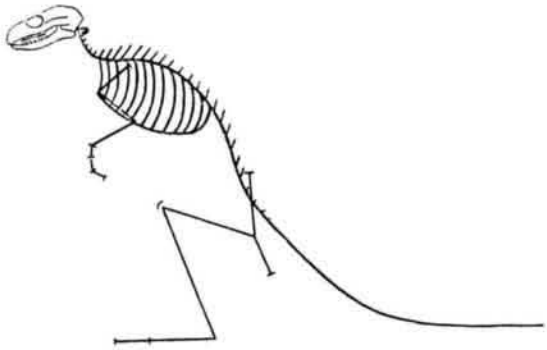

Fig. 7.
Schematic drawing of the skeleton of a kangaroo to show the direction of the neural spines.

on the fore-leg by means of the m. serratus ventralis and the m. pectoralis profundus (see page 18, fig. 11 and table 1). Thus the fore-leg supports the vertebral column in a more or less efficient way from the 3d cervical up to the 8th thoracic vertebra. For this reason the vertebral column in this region acts as a cantilever only to a very limited extent (see further page 95). Moreover THOMPSON does not take account of the fact that the vertebral column is not a separate element but that it is a part of the construction, represented by the whole trunk and neck. It is even very remarkable that he does not consider the work of STRASSER (1913), although he discusses the principle of this work on page 703.

In a quite recent and very detailed publication on the statics and mechanics of the Tetrapod skeleton, GRAY (1944) also rejects the theory of THOMPSON. He has pointed out that the cantilever-principle would be only valid in a very specialized and possibly quite theoretical case of a much more generalized proposition.

### B. The characteristics of the neural spines explained by the demands of the spinal musculature.

Several authors [see for example VON KROGH (1943)] have expressed the opinion that

the influence of the spinal musculature might be held responsible for the direction and other characteristics of the neural spines, without any further explanation. The majority of the authors, however, suppose that the neural spines are inclined into the same direction as the muscular force acting on them. So the thoracic spines would be directed caudally by the influence of the m. spinalis dorsi and the lumbar spines cranially by the influence of the mm. spinalis and longissimus dorsi. This opinion has been given first by BROCA (1869) and further in several different modifications by BARDELEBEN (1874), EICHBAUM (1890), VIRCHOW (1913, 1925, 1929) and LE DOUBLE (1912). It is highly probable that VON STROMER (1902) and DOMBROVSKI (1935) have been thinking of a corresponding explanation.

The untenability of this theory, however, is immediately evident from the fact that the spinal muscles are not inserted into the neural spines in the direction of these spines, but on the contrary nearly perpendicular to it (see part VI). Moreover the direction of the lumbar spines in those mammals that have no anticliny would be quite in contradiction to this theory. Several years ago I proposed another theory, explaining the inclination of the neural spines by the action of the spinal musculature [SLIJPER (1936, p. 402)]. But also the picket-principle proposed in this publication cannot hold good, since the neural spines are attached to the vertebral bodies in a way quite different from that of the picket to the soil.

VALLOIS (1921, 1922) supposes, that the direction of the neural spines might be opposite to that of the muscles inserted into them. In connection with the course of the spinal muscles in mammals, this opinion, however, is quite incomprehensible.

## II

# GENERAL CONSIDERATIONS ON THE STATIC AND DYNAMIC FORCES ACTING ON THE BODY-AXIS (VERTEBRAL COLUMN AND SPINAL MUSCULATURE)

In the foregoing pages I have tried to show that none of the theories published up to the present, is able to explain in a satisfactory way the most remarkable characteristics of the vertebral column of mammals. The starting point of my own considerations on this subject will be the following two facts: In the first place it is not the vertebral column alone that carries the body-weight, but this weight is carried by he whole skeleton of the trunk with its musculature and ligaments. The body-axis (vertebral column and spinal musculature) is only a part of this construction. In the second place the task of the body-axis is not only to carry the body-weight with the aid of the other parts of the skeleton, but also to enable the locomotion of the animal. It has to transmit the locomotive-power from the hind-quarters to the forehand and it has to bend and extend the back while the animal is moving forward, especially when it is galloping.

### 1. *The construction of the trunk-skeleton and the forces acting on its different parts in the mammal standing on all four legs.*

The starting-point of these considerations will be the theory which in principle, has already been pointed out by BARTHEZ (1798), but which has been worked out in detail by STRASSER (1913). The theory has proved to be almost entirely unknown in literature. I have found it only in the work of GMELIN (1925), but this author explains further the construction of the vertebral column in the way of ZSCHOKKE (p. 8).

According to the opinion of STRASSER, the trunk-skeleton must be considered as a bow (the vertebral column and the pelvis with their muscles), bent in the dorsal direction (ventral concave) by a string (the sternum, the abdominal muscles, especially the rectus abdominis, and the connective-tissue of the linea alba; see fig. 8). The bow and its string are connected by the ribs and by the oblique and transverse abdominal muscles, which transmit part of the weight of the intestines directly to the body-axis. This part of the weight tries to extend the bow, but this extension is prevented by the stress [1]) of the string. The other part of the weight rests on the string and so tries to bend the bow. The elasticity of the bow, however, resists this bending-force. It is very difficult to decide, which of these two forces prevails in the living animal; the principal thing, however, is the

[1]) See foot-note on page 32.

fact, that these forces are evenly balanced. One of the most important advantages of this construction is the fact, that it does not exercise a force in cranio-caudal direction on the two supporting piers (the fore- and hind

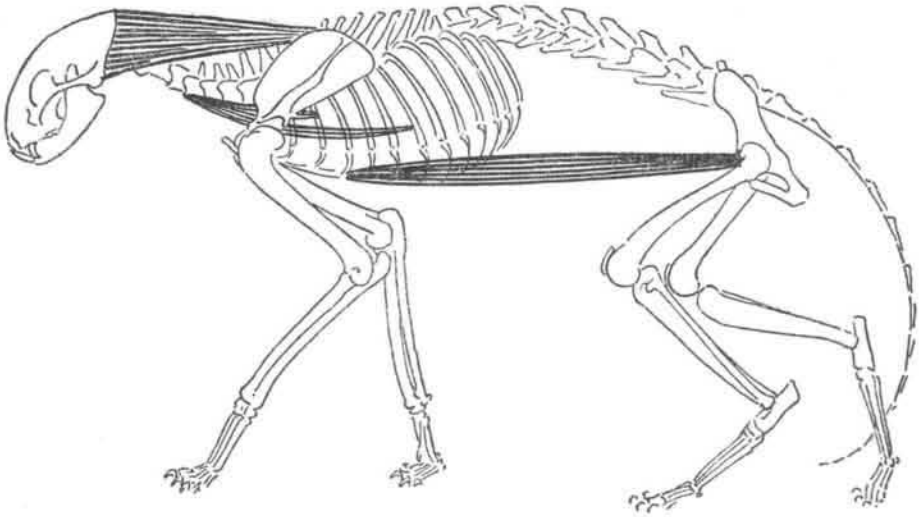

Fig. 8.
Skeleton of a cat (*Felis catus* L.) with the mm splenius, scalenus and rectus abdominis, to show the bow-and-string-construction of the trunk of mammals and the attachment of the head and neck to this construction. Skeleton after ELLENBERGER and BAUM (1943).

leg). GRAY (1944) has shown that the extrinsic musculature of the legs also assumes a certain part in the bow-and-string-construction. The protractors of the foreleg and the retractors of the hind leg try to bend the bow just as the abdominal muscles. The retractors of the foreleg and the protractors of the hind leg try to stretch it just as the epaxial musculature of the back. Unfortunately GRAY has laid too much stress upon the extrinsic muscles and he has paid only very little attention to the abdominal muscles. The importance of these muscles, however, is clearly shown by the fact that in the dead body the vertebral column stretches itself only if the abdominal muscles are cut.

It would be very tempting indeed to compare this construction to a parabolic bowstring bridge (fig. 4), and especially to that type of bowstring bridges in which the bow is not constructed as a single bar but as a web, as for example the bridge at Katerveer, the railway-bridge at Nijmegen or the Birchenough bridge in Rhodesia (Ill. London News 21–12–35) (fig. 9). A bridge of this type may be compared to an arched roof. But the shoving-away of the ends of the bridge is not prevented by the piers, as it happens in an arched roof, but by the string (the carriage-road of the bridge). The fundamental difference between the bowstring-bridge and the trunk-skeleton, however, is the fact, that the bow of the bridge is not an elastic construction as is the bow of a common bow-and-string, but that

it is a simple pressure-element, which does not try to assume a stretched shape again. Thus in the bridge the upper girder of the bow must always be constructed as a pressure-element, while in the elastic bow of a common

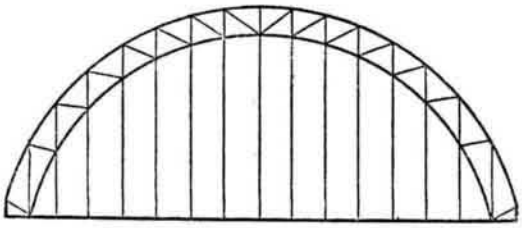

Fig. 9.
Schematic drawing of a parabolic bowstring-bridge with a bow constructed as a web (bridge at Katerveer).

bow-and-string the upper girder may be constructed as a tension-element. And this is the case in the body-axis of mammals.

The elasticity of the body-axis is caused by the elasticity of the intervertebral discs, the interspinous and other intervertebral ligaments and by the ligamentum nuchae of those mammals that possess this ligament (p. 28, fig. 20). For the greater part the elasticity, however, is caused by the tonus of the epaxial spinal musculature. This construction is very advantageous, as it is not a fixed one. For the stress of the bow and its string can thus be adapted to any given posture of the standing body and to any locomotory phase. This could never be attained by the mere action of the ligaments.

That the trunk of a mammal may indeed be compared to the construction of a common bow-and-string, is clearly demonstrated by the fact that in those mammals, in which the elasticity of the body-axis is partly caused by the ligaments, the vertebral column stretches oneself if we cut the abdominal musculature (the string) in the dead animal. In consequence of the action of the ligamentum nuchae this phenomenon may be clearly seen in almost every Ungulate, especially in the goats and antelopes. But it was very obvious too in a monkey (*Cercopithecus* spec.), whose interspinous ligaments were very elastic. The exactness of the above-made comparison may also be demonstrated by the fact that the back of a horse does not sag in a ventral direction under the load of a mounting rider (as to a certain degree the bow of a bridge would do), but on the contrary that in this situation the back is curved in a dorsal direction to increase the elastic stress of the body-axis. In order to get a better insight into the different muscular forces that play an important part in the construction of the trunk of mammals, I have planned out researches about the tonus of the body-musculature in the standing mammal.

That in a mammal, standing on all four legs, the vertebral column of the trunk has the shape of a bow, has already been demonstrated by several different authors. Some

mammals really show a beautiful bow between the first thoracic vertebra and the acetabulum, as for example can be seen in *Hydrochoerus hydrochaerus* (L.) [VIRCHOW (1910a)], *Cavia porcellus* (L.) [SPUHLER (1938)], *Erinaceus europaeus* (L.) [HERTER (1938), FRASER (1939)], *Solenodon paradoxus* Brandt [MOHR 1938)] and the *Ursidae* [VIRCHOW (1910, 1913)] (fig. 10 b). In other mammals the vertebral column in general

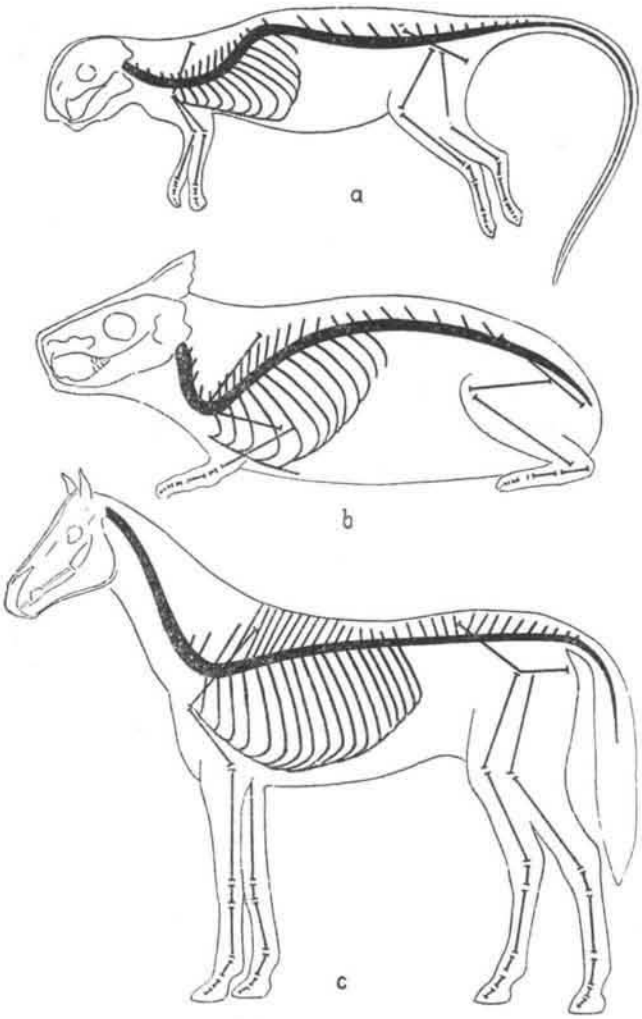


Fig. 10.
Schematic drawings of the skeletons of: a. the black rat (*Rattus rattus* L.) after an X-ray photograph of DOHMANN (1931); b. The Guinea-pig [*Cavia porcellus* (L.)] after an X-ray photograph of SPUHLER (1937); c. The horse [*Equus caballus* L. (dom.)] after ELLENBERGER and BAUM (1943), to show the shape of the vertebral column and the direction of the neural spines.

has also the shape of a bow, but the middle region of this bow is extremely bent in a dorsal direction and has the shape of a hump. The cranial and caudal part of the column may even be slightly concave in a dorsal direction (fig. 10 a). This type of vertebral column has been described of *Didelphis virginiana* Kerr [COUES (1872)] *Rattus*

*norvegicus* (Berkenhout) [DOHMANN (1931)], *Spermophilopsis leptodactylus* (Lichtenstein) [FRASER (1939)], *Allactaga maior* (Kerr) [FRASER (1939)], *Felis catus* (L.) [AUER (1914)], *Panthera tigris* (L.) and other *Felidae* [VIRCHOW (1925)]. In the *Canidae* and especially in the dog (*Canis familiaris* L.) the shape of the vertebral column is intermediate between the first and second type [REUTER (1933)]. In some races the bow even may be very flat [HEILIGTAG (1938)] as will be described below (3d type). The third type of mammalian vertebral column has the shape of a very flat bow. It is a little bit curved in the thoracic region, but the lumbar part of the column is straight. This is the characteristic vertebral column of the majority of the Ungulates, especially of the *Equidae, Bovidae, Capridae, Ovidae, Cervidae* and *Antilopidae* [fig. 10 c; VIRCHOW (1917), WENGER (1915), SCHMALTZ (1924, 1928), SISSON and GROSSMAN (1938), ELLENBERGER and BAUM (1943)]. The vertebral column of the trunk is an almost straight bar to its whole extent in the *Rhinocerotidae* and the *Proboscidea* [VIRCHOW (1910 b)].

According to KRÜGER (1939, 1939 a) the vertebral column of the living horse should be slightly convex in a ventral direction. I believe, however, that with regard to a horse with a good muscular tonus this opinion does not hold good. VIRCHOW (1925) supposes that the "Eigenform" of the vertebral column (that is the shape of the separate column with its ligaments but without muscles and tendons) resembles the profile of the back. Since in most mammals, however, the shoulder-blades rise above the neural spines of the first thoracic vertebrae, the vertebral column of the living animal must show a greater curvature than the "Eigenform" of the column in the dead one. The difference may probably be caused by the failing of the action of the abdominal musculature (the string of the bow).

If the body-axis may be compared to an elastic bow, the upper part of this axis (the neural spines with their muscles and ligaments) will be extended, while the lower part (the vertebral bodies) will be compressed. This is quite in accordance with the structure of the bones, muscles and ligaments (see also p. 31). An overstretching of the body-axis will be prevented by the abdominal musculature (the string) and to a small degree by the ventral longitudinal ligament of the vertebral column. The neural spines with their ligaments and muscles prevent the body-axis from being bent too far in a dorsal direction (ventral concave). When the vertebral column is dorsally bent, the ligaments and muscles are extended because the distance between the neural spines is increasing. This increase of the distance always takes place, no matter how the direction of these spines may be. So the inclination of the neural spines will in no respect depend on the demands of the bow-and-string construction. If the height of the spines should be affected by the demands of this construction, it could be expected that the height would increase towards the middle of the trunk. Since, on the contrary, the height decreases towards this point, we may conclude that neither the height, nor the inclination of the neural spines depend on the demands of the construction of the trunk in its entirety, but that these characteristics must be affected only by the demands of the muscles and ligaments, attached to them.

An unfavourably constructed part of the trunk is the attachment of the string to the cranial end of the bow. The transmission of forces from the

sternum to the vertebral column by the first rib is very unfavourable. In connection with the anatomy of the internal organs, however, this manner of attachment was inevitable. The disadvantage of this construction is made as small as possible by the fact that the first rib is always relatively short, that the mobility of its costo-vertebral articulation is very limited and that it is fixed firmly to the cervical vertebral column by the m. scalenus (fig. 8). The attachment of the string to the caudal end of the bow is much less disadvantageous, since the direction of the axis of the pelvis in a great many mammals is the same as that of the caudal part of the vertebral column [SLIJPER (1942)] and since the sacro-iliac joint is an almost immovable connection.

As is shown in fig. 8 the bow-and-string construction of the trunk at the hip-joint is supported by the hind leg, while at the cervico-thoracic border it is suspended on the foreleg by the m. serratus ventralis and the m. pectoralis profundus (fig. 11). Although BAUM and ZIETZSCHMANN

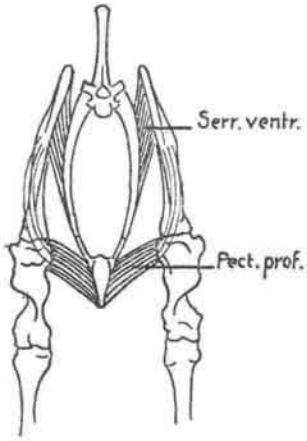


Fig. 11.
Schematic drawing to show the manner of attachment of the trunk of a horse to the supporting foreleg by the m. serratus ventralis and the m. pectoralis profundus.

(1936) in their anatomy of the dog do not mention this function of the pectoralis profundus, undoubtedly the muscle represents one of the most important supports of the trunk, because the tuberculum humeri minus (chief point of insertion) lies above the level of the sternum (chief point of origin). Just as the m. serratus ventralis (4200 g) it is one of the heaviest muscles of the horse [4000 g; SCHMALTZ (1928)]. The task of these two muscles in some mammals is supported by the clavicula and especially in Ungulates by the fascia serrata, the tunica flava (fig. 20), the m. rhomboideus and trapezius thoracis and the inner dorso-scapular ligament (horse).

The head and neck of the mammal may be considered as a loaded beam, supported at one end only by being attached to the cranial end of the trunk skeleton, just like a beam that is built into a wall (fig. 12).

The load of the head and neck, however, is not carried by the cervical vertebrae only, but this beam is supported by a certain number of stretched cords. Technicists use such a construction very often, as we can see every

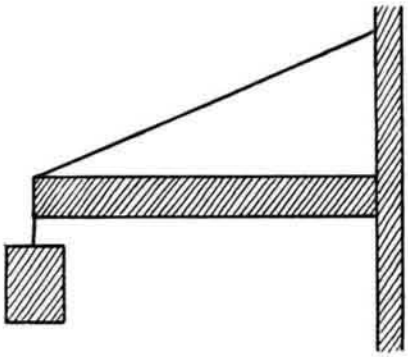

Fig. 12.
Beam supported at one end only by being built into a wall and receiving additional support by a stretched cord.

day for example by sign-bords or by the gate-bars of a level-crossing. In the mammal these cords are represented by the pars cervicis of the m. serratus ventralis [Origin: transverse processes of 3d—7th cervical vertebra; (see table 1); Insertion: dorsal area of inner surface of scapula, that is the highest point of the supporting fore-leg], by the m. trapezius and rhomboideus cervicis et capitis (Origin: medio-dorsal connective-tissue of the neck; Insertion: highest point of scapula), but certainly for the greater part by the m. splenius.

The origin of this muscle lies at the fascia lumbo-dorsalis in the region of the withers, at the summits of the anterior (mostly the 2d and 3d) thoracic neural spines and at the medio-dorsal connective-tissue of the neck (see p. 29 and fig. 8). The muscle is inserted into the linea nuchalis sup. of the skull and in several different mammals also into the first cervical vertebrae. In Ungulates the area of insertion even may be extended up to the 6th cervical vertebra (see table 1). The m. spinalis cervicis too plays a certain part in supporting the head and neck. This muscle originates at the neural spines of the first or the first two thoracic verebrae and is inserted into the neural spines of the 2d—7th cervical vertebra. Moreover it contains a great deal of short interspinous fibres [STIMPEL (1934): medialer Strang des Spinalis]. The direction of the m. semispinalis capitis [Origin: by means of the fascia lumbo-dorsalis at the neural spines and metapophyses (mammillary processes) of the first 3—8 thoracic vertebrae (table 1), articular processes of the caudal cervical vertebrae; Insertion: occipital bone of skull] is not a very favourable one to support the head and neck. Nevertheless it may perform a certain part of this task. In some mammals the support of the head and neck is partly taken over by the connective-tissue of the neck and especially by the ligamentum nuchae (fig. 20). On page 29 these elements will be dealt with in detail.

Thus in the quadrupedal land-mammal the trunk-skeleton with its muscles and ligaments may be considered as a bow-and-string construction. At the cranial end of this costruction a beam, supported at one end only, is

attached. This beam receives additional support from the above-mentioned muscles and ligaments, especially from the m. splenius and the lig. nuchae (fig. 8).

The tail represents a similar beam but is of very small importance, so that it will not be discussed further in this paper.

## 2. *The forces, acting on the vertebral column in the mammal that moves forward or that stands on its hindlegs.*

Although in a great many mammals the manner of locomotion has not yet been studied in detail, there are several publications that may give us an impression of the most important movements of mammals in their different natural paces. In the nature of the case these investigations in the first place concerned the domestic animals and especially the horse.

The most important work about the locomotion of this mammal has been done by BÖHM (1887), STILLMAN (1882), MUYBRIDGE (1899), LE HELLO (1914), WALTER (1926), SCHMALTZ (1928), KRÜGER and THUR (1928), RICHTER (1930, 1932), KADLETZ (1935) and KRÜGER (1939, 1939 a, 1940, 1940 a, 1940 b). Data about the locomotion of the dog we can find in the work of SCHÄME (1932), about the cat in that of MANTER (1938) and about the mammals in general in the publications of MAREY (1901), GREGORY (1912), BÖKER and PFAFF (1931), MAGNE DE LA CROIX (1936), GRAY (1944), but especially in the beautiful and never equalled work of MUYBRIDGE (1899). The descriptions of the foot-marks of mammals may also give us valuable information about their manner of locomotion [see for example BRANDT-EISERHARDT (1939)].

From all these investigations it may be concluded that the mammals principally show five different natural paces: the walk, the trot, the amble, the leaping-gallop and the horse-gallop [see fig. 13 and SLIJPER (1941)].

The walk is a pace common to all mammals. As can be seen in fig. 13, in the walk on the branches of the trees and in the very slow walk on the ground, the body is always supported by three legs. If the speed of the walk increases, the body alternately may be supported by three or two, lateral or diagonal legs. The sequence of the limb movements and consequently that of the foot impacts shows a diagonal pattern, for example: right fore foot, left hind foot, left fore foot, right hind foot, etc. GRAY (1944) has shown that the slow walk in which the body is always supported by three legs, is the most stable pace, since in this case the projection of the centre of gravity always lies inside the triangle of support. In the more rapid paces a stable locomotion is only guaranteed if the sequence of limb movements conforms to the diagonal pattern. GRAY has also shown that in Tetrapods this diagonal pattern phylogenetically is already a very old one and that it is founded on a clearly defined reflex pattern. The chief locomotory propulsion is given by the hind leg. It presses forward the vertebral column, which is suspended by muscles and ligaments (see page 18) on one of the fore-legs, while at the same time the other fore-leg is moved forward. In consequence of these propulsive and brake forces the vertebral column

will have to resist a bending strain, acting as well in the dorso-ventral as in the lateral direction [see also MATTHEW and CHUBB (1927, p. 42, fig. 28)].

The slow t r o t may be considered as an accelerated walk. It shows also the diagonal sequence of limb movements and the body is alternately

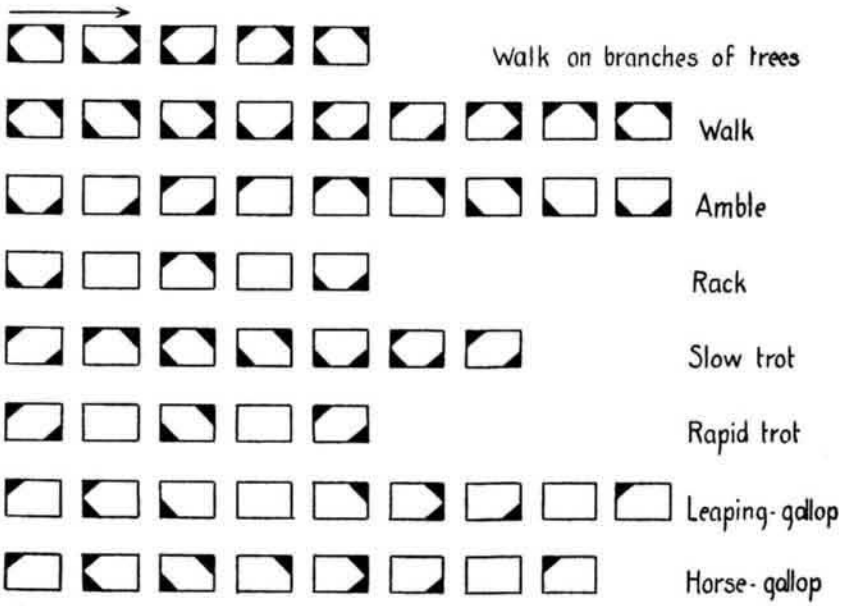


Fig. 13.
Diagram of the different paces of mammals. Every series of rectangles represents from left to right a film of a moving animal. Every rectangle represents a phase of the pace in question. The legs that are in contact with the ground are marked by the filling up of the corresponding edge of the rectangle. After SLIJPER (1941).

supported by two or three legs. If the speed increases, however, the animal alternately floats in the air or is supported by two diagonal legs. The trot is found in almost every mammal, with the exception of the amblers. The forces acting on the body in the trot will practically be the same as in the walk.

Practically the a m b l e is also an accelerated walk, in the slow amble the body is alternately supported by two or three diagonal or lateral legs. The swifter the animal moves forward in this pace, however, the more the diagonal pattern is substituted by a lateral one, for example: right fore foot, right hind foot, left fore foot, left hind foot etc. Of course this manner of locomotion will be less stable than the walk or trot. The centre of gravity is moved in the transversal direction and the vertebral column will be submitted to rotatory forces. The amble is the chief manner of rapid locomotion of the *Camelidae, Giraffidae, Proboscidea, Hippopotamidae* and big *Ursidae*. Horses, dogs and probably *Bison* and *Connochaetes* too now and then may show this pace. It may be doubted, however, if for the horse and

dog it is a natural pace. If the speed of the animal increases, the amble may change into the r a c k. For nearly half the time the animal then floats in the air and for the other half the body is supported by one or two lateral legs. A natural pace is the rack in camels and giraffes, but occasionally it may be seen in some domesticated horses and dogs too.

The g a l l o p is characterized by the fact, that there are one or two phases in which the body floats in the air and by the fact that in the remaining time the body-weight is alternately supported by the fore- and the hind legs. There are two different types of gallop: the leaping-gallop and the horse-gallop.

The different phases of the l e a p i n g - g a l l o p are (fig. 13, 14, 16): hind legs placed on the ground — hind legs make one step — the body is

Fig. 14.
Dog moving forward in a leaping-gallop. After a film of MUYBRIDGE (1899).

pushed forward by the hind legs, the back is stretched maximally — floating phase — the animal comes down on its fore-legs — the fore-legs make one step — the body is pushed forward by the fore-legs, the back is maximally bent, the hind legs are brought forward under the body — the animal comes down on the hind legs — and so on. The most important characteristic of this type of gallop is the fact that the body-axis is alternately stretched and bent to its maximum degree (fig. 15). This requires a great mobility of the vertebral column of the trunk and especially of the middle part of this column. In the nature of the case, the spinal musculature of the animals that can move forward in a leaping-gallop must be much better developed than that of the mammals that walk or trot only. The leaping-gallop is the rapid type of locomotion of some *Marsupialia* and *Insectivora*, nearly all *Rodentia* and *Carnivora* (fig. 16; the *Ursidae* included; only *Acinonyx* probably shows a kind of horse-gallop) and of the *Suidae* (fig. 16) and *Tragulidae*. The smaller Ungulates, as for example some species of deer and antelopes, show a transitional type of locomotion between this gallop and the horse-gallop. In general it may be said that with an increasing size of the animals the mobility of the centre of the back decreases, so that the leaping-gallop changes into a horse-gallop. In his comparison between the locomotion of the red deer and the roe, DARLING (1937) has shown that the environment in which the animal usually lives, may excercise a distinct influence on the type of locomotion.

The h o r s e - g a l l o p is characterized by the fact that after the floating phase the legs are placed on the ground and lifted up again in the following order of succession (fig. 13): left hind leg — right hind leg and left fore-leg — right fore-leg (right-hand gallop). The principal pushing-

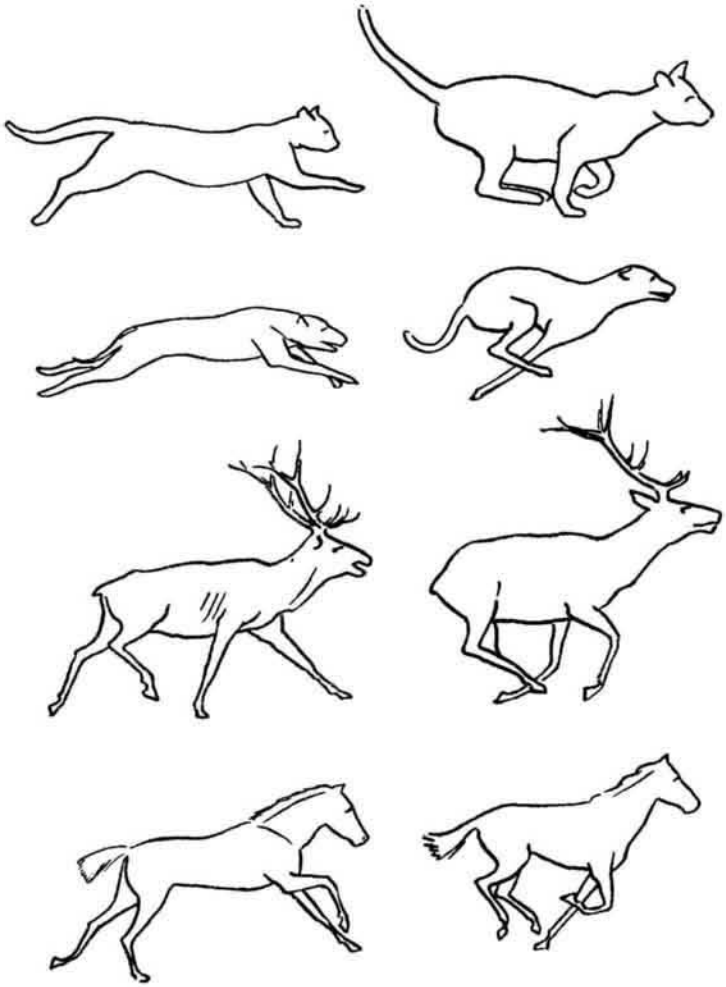

Fig. 15.

Two different phases of the leaping-gallop (cat, dog) and the horse-gallop (deer, horse) to show the movements of the back in these paces. Left: phase in which the back is maximally stretched. Richt: phase in which it is maximally bent. After a film of MUYBRIDGE (1899).

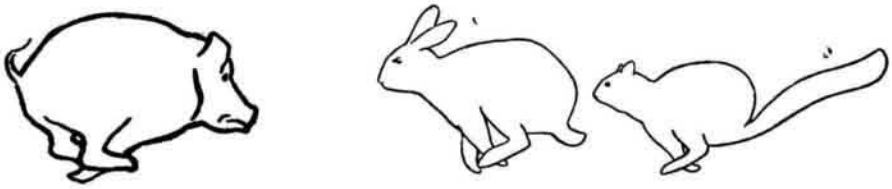

Fig. 16.

Leaping-gallop of a wild boar (*Sus scrofa* L.), a rabbit [*Oryctolagus cuniculus* (L.)] and a squirrel (*Sciurus vulgaris* L.) after photographs of BERGER (1928) and JAEGER (1939).

power is given by the hind legs, but it appears that a part of this power also is given by the right fore-leg (in the left-hand gallop by the left fore-leg). The horse-gallop is further characterized by the fact that there are practically no movements of the back (fig. 15, 17). The small movements that

Fig. 17.
Horse moving forward in a right-hand horse-gallop. After a film of MUYBRIDGE (1899).

may be seen take place in the lumbo-sacral joint. The horse-gallop is the rapid type of locomotion of the *Equidae*, the big *Ruminantia* (buffalo, cow, goat, sheep, some deer and antelopes) and probably also of the *Rhinocerotidae*. Some camels and giraffes may apparently show this type of locomotion too. In contrast with the leaping-gallop the horse-gallop requires a very immovable vertebral column.

At first sight one might be inclined to suppose that especially in the leaping-gallop during the phases, that the body is supported by the fore- or hind legs only, the body-axis might be compared to a beam supported at one end only. The forces acting on a moving construction, however, may differ considerably from that acting on the same construction at rest. The greater the frequency of the different phases with regard to the mass of the animal, the more the phases in which the body is supported by one pair of legs only may be neglected —and the more the moving body may be compared to a body standing on all four supports.

On the other hand, the body-axis of a quadrupedal mammal that rises on its hind legs and remains for a shorter or longer time in this erect or semi-erect posture, may indeed be compared to a beam supported at one end only. The more the body-axis is inclined, the greater the bending-moment of this beam will be. This erect or semi-erect posture will appear to be one of the most important postures to take into consideration if we want to discuss the different forces that are responsible for the structure of the column.

Almost every quadrupedal mammal now and then stands or sits on its hind legs only. The horse may show this posture with a rider mounted ("Levade"; fig. 18a) but also in its natural life (for example when horses are fighting). We know it from goats, dogs, hares and from many other Rodents (think for example of an eating squirrel; fig. 18f). Among the Carnivores it is especially the bear that may rest during a comparatively long time on its hind legs only and it does so not only in the zoological garden, but in its natural life too (fig. 18c). The upright posture, however,

is also known from many other Carnivores as for example from the marten [SCHMIDT (1943, plate 12)].

In the bipedal mammals the posture of the body-axis entirely

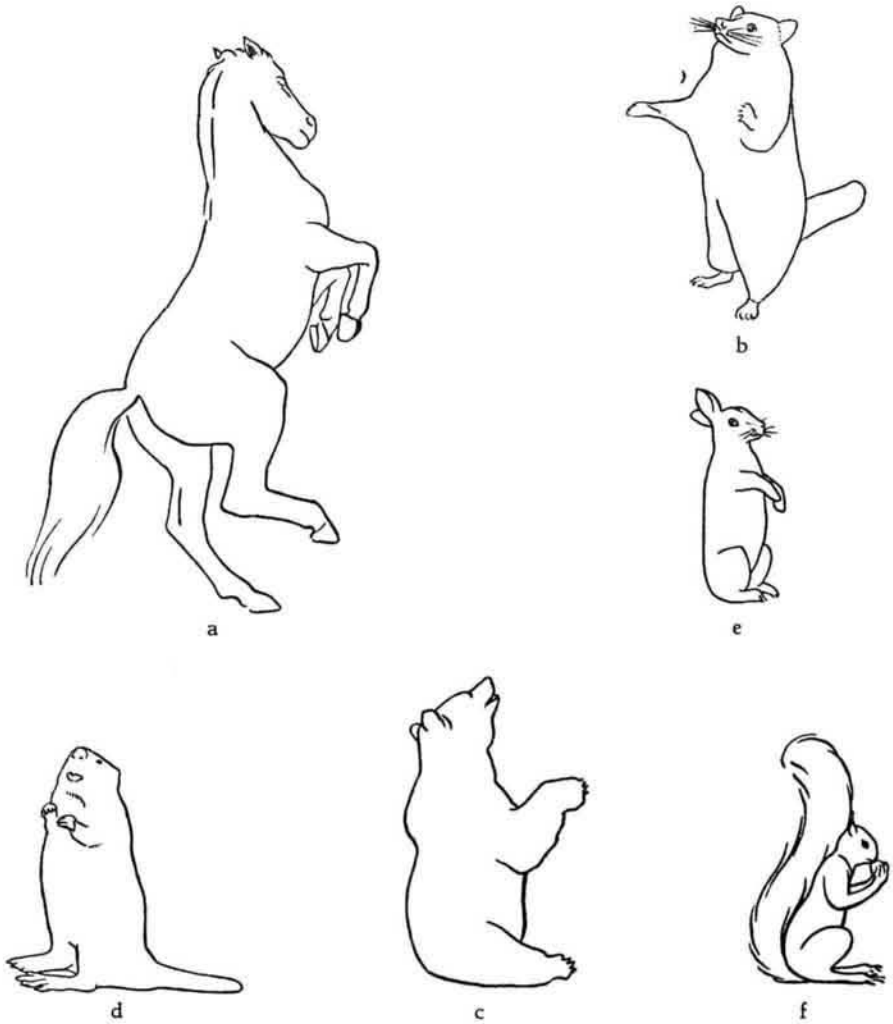


Fig. 18.
Several different mammals that may show an erect or semi-erect posture during a shorter or longer time. a. Horse [*Equus caballus* L. (dom.); "levade"]; b. Raccoon [*Procyon lotor* L.; after PICKWELL (1940)]; c. Bear (*Ursus arctos* L.; after CORNISH); d. Beaver [*Castor canadensis* Kuhl; after CARR (1938)]; e. Rabbit [*Oryctolagus cuniculus* (L.); after IJSSELING and SCHEYGROND (1943)]; f. Squirrel (*Sciurus vulgaris* L.).

agrees with that of erected quadrupedal mammals. BRAUS (1921) has already shown, that in the human trunk there is a certain equilibrium between the action (tonus) of the spinal and the abdominal musculature. Thus to a certain degree the trunk of bipedal mammals may be compared to a bow-and-string construction. Since this construction, however, is sup-

ported only by the hind legs, especially the body-axis may be considered as a beam supported at one end only. The more the body-axis is inclined (as for example in kangaroos and jumping-mice; fig. 7) the greater the bending-moment of this beam will be. In the moving bipedal mammal the body-axis will be exposed to nearly the same forces as in the standing one.

The same situation is found in the flying mammals, the bats. Here the body is alternately supported by the fore-legs (when flying) and by the hind legs (when hanging). The vertebral column of the bats is movable only to a very small degree and the spinal musculature shows a comparatively weak development [VALLOIS (1922)].

In the nature of the case the structure of the body-axis of aquatic mammals will in no way be influenced by the body-weight, if at least the animals never leave the water (*Cetacea, Sirenia*). The abdominal muscles and the body-axis are only in the service of the locomotion of the animals. This locomotion will be discussed at length on page 70.

## III

# THE LIGAMENTS OF THE BODY-AXIS

Since the ligaments of the vertebral column are responsible for a certain part of the stress and elasticity of the body-axis I have paid special attention to these elements, which usually are almost completely neglected in literature.

### 1. *Ligamenta interspinalia.*

With the exception of the Ungulates, in nearly all mammals these ligaments are very poorly developed, because the development of the mm interspinales is usually comparatively good or even strong. In a specimen of *Echinosorex* spec., however, I found that the ligaments were very well developed in the lumbar region and in some monkeys they may be strong and even very elastic throughout the whole vertebral column. In the gorilla they were practically wanting in the thorax, but in the lumbar region the ligaments were present, although short, fibrous and not very strong. The same may be said of the human vertebral column [FICK (1911, Bd. 1, p. 75), STRASSER (1913), BRAUS (1921), VAN DEN BROEK, BOEKE and BARGE (1922)]. In the lumbar region the ligaments, however, are better developed than in the gorilla. Between the vertebral arches they even consist of elastic fibres.

In nearly all Ungulates the interspinous ligaments are strongly developed. With the naked eye they usually do not give the impression, that they consist of elastic fibres. Only the anterior thoracic (± 1—8 Th) ligaments of the goat and camel and the posterior thoracic and lumbar ligaments of an adult elephant showed a distinct yellow colour. By microscopic examination, however, a great many interspinous ligaments of the other domestic animals prove to contain numerous strong elastic fibres too.

The direction of the fibres varies, especially in the thoracic region. In the cranial part of the thorax of the dog and goat the direction is oblique from caudo-dorsal to cranio-ventral. In the caudal part of the thorax of the goat and in the whole thorax of the horse and lama they show quite the opposite direction (from cranio-dorsal to caudo-ventral; fig. 19). In the cow the direction of the fibres is nearly vertical, in *Cercopithecus* on the contrary nearly horizontal. The angle of insertion into the neural spines too shows a considerable variation. In all the above-mentioned mammals, however, as well as in man and the gorilla, the direction of the posterior thoracic and lumbar ligaments was always from cranio-dorsal to caudo-ventral, irrespective of the direction of the neural spines.

It is a matter of course that the interspinous ligaments will always be stretched, if the vertebral column is bent in the dorsal direction (ventral concave) and that they are able to prevent too far bending. Why the direction of the fibres, however, varies to such a marked degree, still remains a subject for further researches (see also p. 17).

### 2. *Ligamentum supraspinale.*

In nearly all text-books of veterinary anatomy a supraspinous ligament is described. It is said to represent a continuation of the ligamentum nuchae and extend over the summits of the neural spines from the withers to the sacrum [ELLENBERGER and BAUM (1943), SISSON and GROSSMAN (1938), KADLETZ (1932, taf. 20, fig. 114), SCHMALTZ (1924; Bd. 1, Taf. 22a, 24; 1928, p. 37), KRÜGER (1939, 1939a), DEMETER (1916),

MOSKOFF (1933); see also the description of the giraffe from OWEN (1838) and VALLOIS (1926, p. 196)]. My own researches on this ligament were chiefly made on the horse, the cow, the goat, the camel, the lama, the gazel, the elephant and the dog.

All these animals had a very well developed ligamentum nuchae (fig. 20), which extended over the summits of the thoracic neural spines up to the posterior thoracic vertebrae. In the region caudal of the withers, however, the ligament very rapidly decreased in size and the elastic fibres by degrees were replaced by fibrous ones. In the posterior thoracic region (in the elephant already in the middle of the thorax) the ligament was fused with the fascia lumbo-dorsalis and the tendons of the m. spinalis dorsi [see also SJOMUSCHKIN (1934)].

Into the summits of the last thoracic and the lumbar vertebrae the tendons of the mm spinalis and longissimus dorsi are inserted. As will be described in detail on p. 90 (see fig. 19), these tendons are attached to the periosteum of the summit of two or three neural

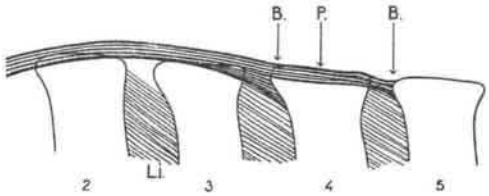


Fig. 19.
Very schematic drawing of the 2d—5th lumbar neural spine of the horse [*Equus caballus* L. (dom.)] (left side) with the insertion of one single tendon of the m. longissimus dorsi. This tendon is only very loosely connected with the 2d lumbar spine. It is attached very firmly by connective tissue at the 3d and completely interwoven with the periosteum of the 4th lumbar spine (P.). Moreover the tendon is inserted directly into the bone of the 4th and 5th lumbar spine (*B*). *Li* = ligamentum interspinale.

spines cranial of the spine into which they are inserted by means of their fusion with the interspinous ligaments. Here and there I found some weakly developed interspinous fibres between the summits of two successive neural spines, but between the last lumbar and the first sacral spine these fibres were entirely wanting.

Thus a real continuous, supraspinous ligament anatomically does not exist in this region of the vertebral column. The so-called supraspinous ligament of the veterinary anatomists proves to consist of the coalesced tendons of the mm longissimus and spinalis. Although morphologically there is no supraspinous ligament at all, functionally it is represented by the above-mentioned tendons. The supraspinous connection, however, even functionally is very weak or nearly entirely wanting between the last lumbar and the first sacral vertebra.

In the gorilla I did not find a trace of a supraspinous ligament. In man it has been described by STRASSER (1913), FICK (1911) and other human anatomists. In connection with the above-mentioned facts, however, new researches about this ligament in man might be made.

## 3. *Ligamentum nuchae.*

A distinct ligamentum nuchae is wanting in all *Monotremata, Marsupialia, Insectivora, Edentata, Rodentia, Tubulidentata, Chiroptera, Cetacea, Sirenia, Primates* and *Carnivora* with the exception of the *Canidae*. Some representatives of these orders, however, have a more or less well developed, fibrous, median septum between the right and left dorsal muscles of the neck (*Erinaceus, Cavia,* several *Primates* [VON EGGELING (1922] and man [VIRCHOW (1909)]. In some mammals the dorsal margin of this septum may be developed as a separate fibrous cord between the occipital bone and the anterior thoracic

vertebrae [the dorso-medial connective-tissue; *Macropodidae, Ursidae* (see also VIRCHOW; 1909), *Canidae, Panthera leo* (L.)].

A distinct elastic ligamentum nuchae has only been found in the *Canidae* and the *Ungulata*. In the *Canidae* it is an elastic cord between the neural spine of the 2d cervical vertebra and the summits of the spines of the thoracic vertebrae (see also p. 94). The pig only possesses a few elastic fibres in the median nuchal septum. The other Ungulates, however, are all in the possession of a very well developed ligamentum nuchae that consists of a funicular and a lamellar part (fig. 20). The funicular part (pars occipitalis)

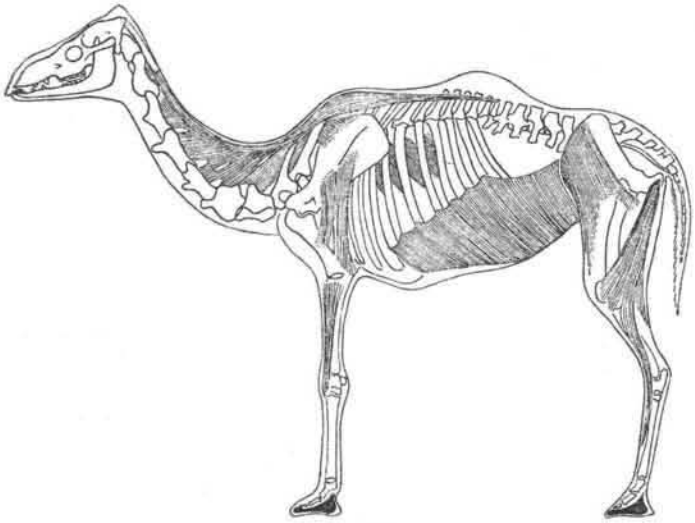

Fig. 20.
Skeleton of a camel (*Camelus bactrianus* L.) with the elastic ligaments (lig. nuchae, lig. intercostalia) and the elastic areas of the great fasciae. After SLIJPER (1941).

is a very strong elastic cord between the protuberantia occipitalis externa and the thoracic spines, to which it is attached by means of the cartilagineous summits of these spines (see also p. 86). In several animals it is not attached to the first or the first two thoracic vertebrae. The lamellar part originates in the neural spines of the cervical vertebrae. In some species of Ungulates (*Tragulus, Lama, Tapirus, Equus, Hippopotamus, Elephas*) its fibres are attached separately to the first three thoracic spines. In other animals they fuse with the funicular part and insert together with it (*Gazella, Odocoileus, Rhinoceros*). Sometimes the fibres originating in the 6th and 7th cervical spine are attached separately to the first two thoracic spines [*Bos, Capra, Camelus*; see also the publications of MOSKOFF (1933), DEMETER (1916) and SJOMUSCHKIN (1934)].

It is a very remarkable fact that the m. splenius of the Ungulates (with the exception of the *Camelidae*, where it is wanting) is very well developed, although the ligamentum nuchae supports the head and neck too. The muscle inserts not only into the occipital bone but also into the transverse processes of the first 4—6 cervical vertebrae (see table 1).

Now one may ask oneself what factors might be responsible for the development of the ligamentum nuchae and the strong development of the m. splenius in the Carnivores and Ungulates. Naturally in the first place we may think of the size of the head and the length of the neck. From the data given in table 7, it follows that the length of the neck in % of the length of the trunk is in *Marsupialia* 14—32, *Edentata* 25—54,

*Rodentia* 10—23, *Insectivora* 20—26, *Primates* 15—30, small *Carnivora* 24—48, *Ursidae* 40, *Felidae* 32, *Suidae* 25. In the *Canidae* this percentage is 46 and in the Ungulata provided with a distinct lig. nuchae and a comparatively light head 32—129. Thus the development of the ligamentum nuchae may partly be connected with the length of the neck and the size of the head.

I believe, however, that there is still an other important factor that may be responsible for the development of this ligament: the absolute size of the animal. Although BORELLUS (1685) had already pointed out that the achievements of a small animal are proportionally greater than of a big one, STRAUS–DURCKHEIM (1828, p. 189) has been the first to show that this phenomenon may be ascribed to the fact that with increasing body-size the muscular strength increases in the square, while the body-weight increases in the cube. For the muscular strength is directly proportional to the surface of the tranverse section of the muscle [see also BERGMANN (1847), BERGMANN and LEUCKART (1855) and the work of KLATT (1913), who applied this principle to explain several characteristics of the mammalian skull].

The moment of the force that must be resisted by the cervical vertebrae, the m. splenius and the other muscles of the neck, is the weight of the head multiplied by the length of the neck. Hence, with increasing body-size the moment of the force acting on the neck-muscles increases in the 4th power, while the muscular strength only increases in the square. Thus we may understand, that in mammals with a comparatively great body-size, not only the area of insertion of the m. splenius is enlarged but that this muscle also receives additional support from the ligaments of the neck.

In several big animals this phenomenon is not limited to the support of the neck, but we may find it in other parts of the body too. It is a very striking fact that in the horse the fasciae of the trunk and limbs are not only very well developed, but that in several places they are very elastic too [see also KRÜGER (1931)]. The same may be said of the elephant, the rhinoceros and the camel (fig. 20). The dissection of an adult elephant showed that especially the fascia spino-transversaria and the aponeuroses of the mm serratus dorsalis and latissimus dorsi were very thick elastic sheets. In an adult rhinoceros all the fasciae of the neck, the external dorso-scapular ligament, the tunica flava and in several different places the fasciae of the limbs too, showed a very elastic development. Fig. 20 shows that in the camel especially the tunica flava, the fasciae of the limbs and some intercostal ligaments were very elastic. On the other hand it must be said, that the very small Ungulate *Tragulus* possesses a distinct ligamentum nuchae, although the lamellar part is very poorly developed. So it is not the absolute size of the animal alone that is responsible for the development of the elastic fasciae and ligaments.

## IV

## THE VERTEBRAL BODIES

### A. General considerations.

In the second part of this paper I tried to demonstrate that the vertebral column of the mammal, standing on all four legs, may be compared to the bow of a bow-and-string-construction. To the cranial end of this construction the neck is attached, which may be compared to a beam supported at one end only and receiving additional support from some cords. The vertebral column of the bipedal mammal and the quadrupedal mammal erected on its hind legs, may chiefly be compared to a beam supported at one end only. Hence the principal static function of the body-axis will be to resist bending in the dorsal direction (ventral concave). Bending in the ventral direction (dorsal concave) is chiefly resisted by the abdominal muscles.

Experiments of MEYER (man; 1873) and WENGER (horse; 1915) have shown that the neutral axis of the adult vertebral column lies in the centre of the vertebral bodies, and not on the level of the spinal cord, as SCHWANKE (1937) believes. In the fetus of the horse, however, the neutral axis indeed lies on this level. So the structure of the bone of the vertebral bodies and the cartilage of the intervertebral discs must not only be adapted to resist pressure, as MUTEL (1921), GALLOIS et JAPIOT (1925) and especially FALK (1940) believe, but also to resist tension. BARDELEBEN (1874), MUTEL (1921, 1922) and GALLOIS and JAPIOT (1925) have shown that the ventral part of the vertebral column, consisting of the bodies, the neural arches and the zygapophyses, is constructed just like a web (fig. 81, p. 80).

It is without doubt that the size and shape of the vertebral bodies and the intervertebral discs will depend on the different forces, acting on them in the different regions of the vertebral column. Among others this may be demonstrated by the fact, that in the new-born child the vertebral bodies have altogether the same shape, while in adult men the shape of the thoracic bodies is quite different from that of the cervical or lumbar ones [MOSER (1889), NAUCK (1939)]. In general, the same phenomenon may be met with in the horse, although after WENGER (1915) already in the fetal horse there may be a slight difference in shape of the vertebral bodies in the different regions of the column. These differences, however, do not correspond exactly with those of the adult animal.

However, it is also without doubt that the size and shape of the vertebral bodies and intervertebral discs will depend to a certain degree on the development of the other parts of the vertebrae: the neural arches, the zygapophyses, and especially the neural spines with their muscles and ligaments. If the neural spines are high and strong or if the zygapophysial

joints attach the vertebrae to another very firmly, the stress [1]) of the vertebral bodies may be comparatively less than if the spines are low and the zygapophysial joints are very movable.

Several authors have tried to explain the above-mentioned differences in size and shape of the vertebral bodies by studying their linear dimensions [WENGER (1915), GOTTLIEB (1915], the surface of their transverse-section [ZSCHOKKE (1892)], their weight [KRÜGER (1927a)] or their specific weight [BRUHNKE (1929)]. NAUCK (1932) tried to solve the problem by studying the ratio of the sagittal and transversal dimensions of the bodies. His conclusions, however, are founded on a few number of mammals only. If NAUCK had studied a greater material, he would have seen that with this method one no more arrives at a result than with the other ones.

The principal fault, hitherto made by all the different authors, is the fact that none of these dimensions may be considered as a criterion for the stress of the vertebral column. Since the principal static function of this column is to resist bending, only the moment of resistance against bending may be considered as a criterion for this stress. This moment of resistance is represented by the product of the breadth (the transverse diameter) and the square of the height (the sagittal diameter) of a beam ($bh^2$). In consequence I have calculated this moment of resistance in the different regions of the vertebral column.

Since the strength of a construction is defined by the strength of its weakest part, with regard to the vertebral column, the moment of resistance of each intervertebral disc really ought to be determined. Since in dried skeletons, however, this is impossible, I determined the dimensions of that part of the caudal surface of the vertebral bodies to which the intervertebral disc is attached. These dimensions will not differ very much from those of the discs.

Since the formula $W = 1/6\ bh^2$ ($W$ = moment of resistance; $b$ = breadth; $h$ = height) is only valid with regard to a rectangular beam, in the case of the vertebral column the formula $W = \frac{I}{e}$ ($I$ = moment of inertia; $e$ = distance between centre of gravity and highest point of a non-rectangular cross-section) should be used. The determination of the moment of inertia, however, takes up much time and it is only possible in unmounted skeletons. Since the shape of the intervertebral discs does not differ very much from a rectangular beam, in my opinion the determination of the moment of resistance was quite sufficient to give an impression of the stress of the vertebral column in its different regions. Besides in some mammals (as for example in the lion) I have determined the moment of inertia as well as the moment of resistance of all vertebrae. As is shown in fig. 21, the course of the two curves is always almost completely parallel.

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[1]) In accordance with the terminology of FIDLER (1909), in this paper I shall use the following terms: Strain = the force (tension or pressure) that tries to deform a certain beam. Stress = the inner forces of the beam (dependent on the nature of the material) that offer resistance to the above-mentioned deforming forces.

So in the skeletons of 40 different species of mammals I have made a curve of the height, the breadth and the moment of resistance ($bh^2$) of

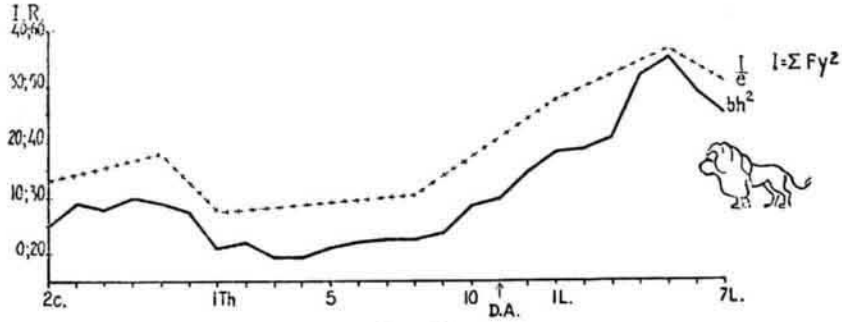


Fig. 21.

Diagram of the moments of resistance ($bh^2$) and the moments of inertia ($\frac{I}{e}$) of the vertebral bodies in the different regions of the vertebral column of the lion [*Panthera leo* (L.)].

the caudal surfaces of the cervical, thoracic and lumbar vertebral bodies (see fig. 22—27; 31—35). With regard to the lateral bending-stress of the vertebral column, the lateral moment of resistance ($hb^2$) ought also to have been considered. Since this lateral bending (in the moving animal; see page 20), however, is of minor importance as the sagittal bending, the lateral moment of resistance has been neglected. Some phenomena, concerning lateral bending, may be explained sufficiently by the linear diagram of the breadth of the vertebral bodies.

B. Quadrupedal terrestrial mammals.

In table 2 a survey is given of the shape of the diagram of moments ($bh^2$) of the vertebral column in a number of different types of quadrupedal terrestrial mammals. According to this survey and to the figures 22—27, in these mammals three different types of diagrams can principally be distinguished:

In the first type the curve is practically horizontal (I a) or rises only to a very small degree (I b) from the 2d cervical vertebra up to one of the posterior thoracic vertebrae. In the region caudal of this point, the curve rises very markedly, but in the posterior lumbar region there may be a distinct decline again (I b). The second type is characterized by a slight rising of the curve in the neck, followed by a corresponding decline in the anterior thoracic region. The curve then remains horizontal up to one of the posterior thoracic vertebrae. Then it rises in the same way as the curves of the first type. Only in the lion is this rising followed by a decline in the posterior lumbar region. All the representatives of the third type show a very high summit of the curve in the caudal part of the neck. In their further course the curves may quite well resemble that of the

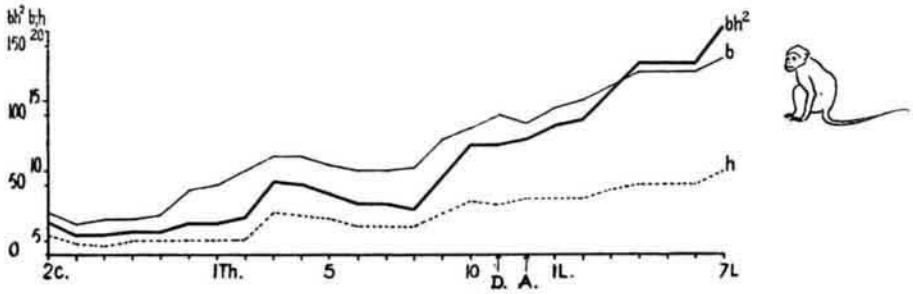


Fig. 22.
Monkey; *Macaca irus fascicularis* (Raffl.) (Type Ia).

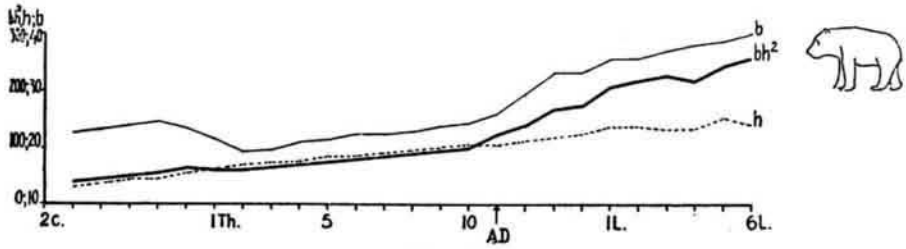


Fig. 23.
American black bear; *Euarctos americanus* (Pall.) (Type Ib).

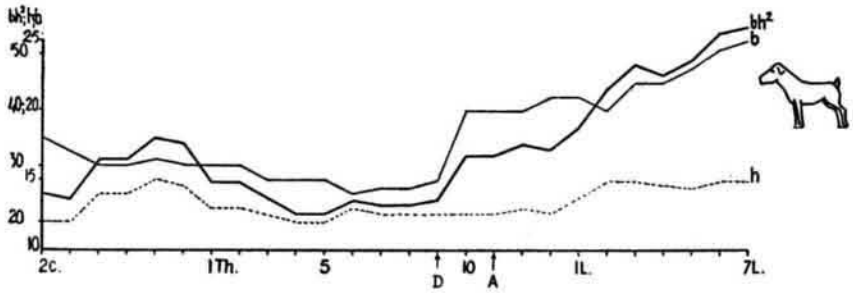


Fig. 24.
Dog; *Canis familiaris* L. (dom.) (Type II).

Fig. 22—24.
Diagram of the height ($h$), breadth ($b$) and moment of resistance ($bh^2$) of the vertebral bodies in the different regions of the vertebral column (Type Ia, Ib, II). $D$ = diaphragmatic vertebra; $A$ = anticlinal vertebra; C = cervical; $Th$ = thoracic; $L$ = lumbar vertebra.

second type [without (III a) or with (III b) a decline in the lumbar region], or there may be no rising at all in the posterior thoracic region, so that the curve is almost horizontal from the anterior thoracic region up to the last lumbar vertebra (III c).

At first sight this seems to be a very remarkable and unexpected result. For if the vertebral column may be compared to a bent bow and a beam supported at one end only, one might expect that the diagram of moments should have a shape as is shown in fig. 28. In the first place, however,

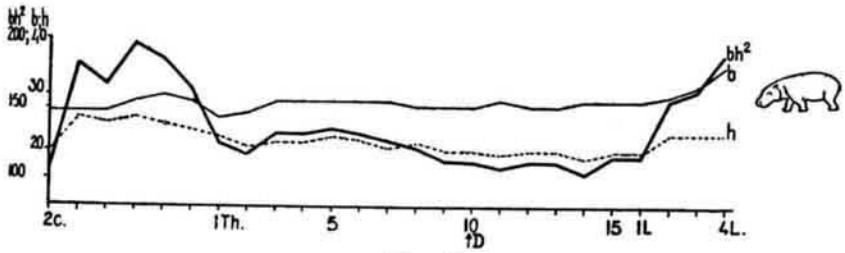


Fig. 25.
Pigmy Hippopotamus; *Choeropsis liberiensis* (Mort.) (Type IIIa).

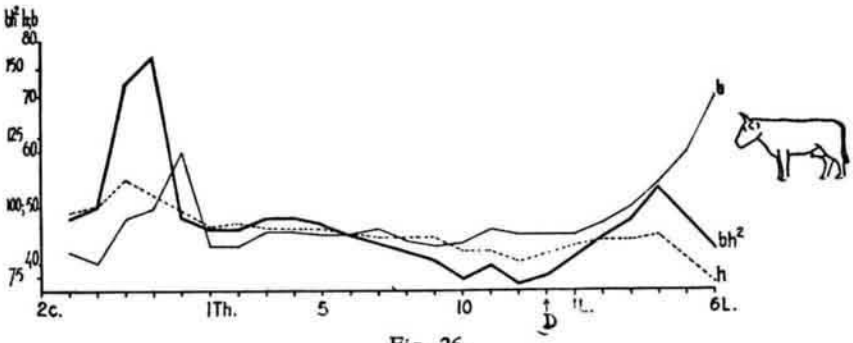


Fig. 26.
Cow; *Bos taurus* L. (dom.) (Type IIIb).

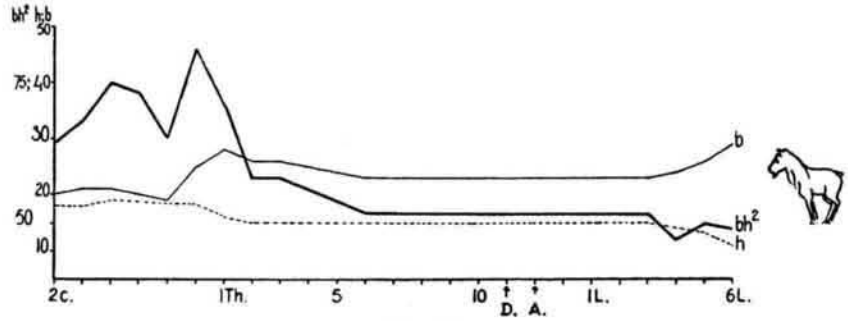


Fig. 27.
Goat; *Capra hircus* L. (dom.) (Type IIIc).

Fig. 25—27.
Diagram of the height, breadth and moment of resistance of the vertebral bodies in the vertebral column (Type III). For further explanation see fig. 22—24.

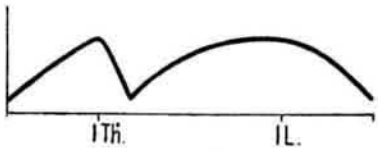


Fig. 28.
Diagram of moments of the vertebral column in quadrupedal mammals that might be expected if the vertebral column is compared to a bow with a beam supported at one end only, attached to the cranial side of this bow.

we must take into account that the stress of a beam or any other architectural construction must always be adapted to that situation in which the maximal forces act on it. With regard to the vertebral column this is the erect or semi-erect posture of the body, when the animal stands or sits on its hind legs only (p. 24, fig. 18). Thus, if there were no other factors, it might be expected that the stress-diagram should have the shape of a straight line, rising in the caudal direction (fig. 29).

In the second place, however, we must take into account that the stress

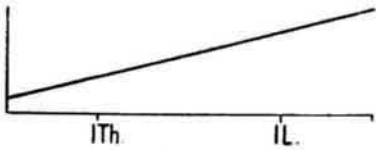


Fig. 29.
Diagram of moments of the vertebral column in quadrupedal mammals that might be expected if the vertebral column is compared to a beam supported at one end only (erect or semi-erect posture).

of the body-axis does not depend on the vertebral bodies only, but also on the other elements of this axis, the neural spines, the transverse processes, the zygapophyses, the muscles and the ligaments. If in a certain region of the vertebral column one or more of these elements are better developed than in the other regions, the vertebral bodies may proportionally show a minor development and consequently a minor moment of resistance. This state of things may principally occur in three different regions of the vertebral column:

1. *In the neck.*

The weight of the head and neck is supported not only by the vertebral column but also by the muscles and ligaments, described on page 19 (chiefly the m. splenius, the ligamentum nuchae and in the mammal standing on all four legs also the m. serratus ventralis pars cervicis). The better these elements are developed, the less the bending-stress of the vertebral bodies can be. In that case, instead of the bending-stress we must take into account a longitudinal pressure-stress of the vertebral bodies. This stress may be calculated with the formula $D = \frac{px}{y}$ [$p$ = weight of the head; $x$ = perpendicular distance between vertebral body and head; $y$ = distance between vertebral body and stretching-cord (for example the lig. nuchae)] if we want to neglect the weight of the neck, or with the formula $D = \frac{1}{2} q \frac{x^2}{y}$ if we do not want to neglect this weight. I have plotted out the functions $\frac{x^2}{y}$ and $\frac{x}{y}$ of some domestic animals (cow, horse, dog). The curve $\frac{x}{y}$ was nearly horizontal, the curve $\frac{x^2}{y}$ showed a slight rising in the

caudal direction. Since moreover the pressure-strain is much smaller than the bending-strain, it may be neglected in our considerations about the shape and size of the vertebral bodies.

Thus the shape of the diagram of moments in the neck will principally depend on the strength of the stretching-cords, that is in the first place the strength of the m. splenius and the other muscles. And since the relative strength of these muscles is inversely proportionate to the absolute size of the animals (see page 30), it will be evident that with increasing size of the animals the stress of the cervical vertebral column must increase, because the stress of the muscles decreases.

So in small mammals the curve of the moments of resistance in the neck is almost horizontal, since the stress of the cervical part of the body-axis chiefly depends on the muscles (type I). The animals, belonging to the second type, show already a slight rising of the curve in the cervical region; they are of intermediate size. In the big mammals at least, the curve represents in the neck the characteristic diagram of a beam, supported at one end only. In spite of the additional support of the ligaments [1]), the stress of the cervical part of the body-axis here depends to a much greater degree on the vertebral bodies than in the small mammals (type III).

2. *In the thorax.*

It might well be expected, that there would be a uniform rising of the curve from the first up to the last thoracic vertebra. But in reality, in all mammals after the summit in the neck, there is a marked decline of the curve. After this decline it remains horizontal or nearly horizontal up to the 8th—12th thoracic vertebra. This phenomenon may be explained by the supposition that the stress of the body-axis in this region to a greater or lesser part depends on other elements than on the vertebral bodies. As such in the first place we may think of the neural spines with their muscles and ligaments. Since in the moment of resistance the height of the neural spines also figures as a square, every increase of this height may be followed by a decrease of the height of the vertebral bodies and consequently by a decrease of their moment of resistance. As figs 1, 46, 50, 101, 102, 109 show, in nearly every mammal the anterior thoracic spines are much higher than the posterior thoracic and lumbar ones. Especially in the Ungulates this difference in height is very striking (withers).

A second factor that may be taken into account is the fact that also the ribs, and especially the true ribs, may be responsible for the stress of the body-axis. In general, the mammals possess 7—9 true ribs, a number that corresponds in a measure with the point at which the rising of the curve begins.

From the facts, however, that on an average there are 8 true ribs and

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1) The strength of the ligaments is also directly proportionate to the surface of their cross-section, that is inversely proportionate to the size of the animal.

that the neural spines of the 8th—12th thoracic vertebrae are already comparatively low, one would draw the conclusion that the rising of the curve as a matter of fact should begin at the 6th—8th, instead of at the 8th—12th thoracic vertebra. It is highly probable, however, that this phenomenon is caused by the fact that the mobility of the vertebral column does not allow the vertebral bodies to be as high as should be required for the strength of the body-axis. On page 58 it will be discussed at length that exactly in this diaphragmatic region the mobility of the mammalian vertebral column is maximal.

If these considerations are exact, then in this region the vertebral column must show its weakest spot. Although more researches on this subject are still required, from the data given in literature we may conclude that in mammals the weakest spot of the body-axis is found indeed in the posterior thoracic region. This follows from the date given by BARTHEZ (1798; wolf), SIMON (1926; horse, 13 Th.), BITTNER (1927; horse, 10—15 Th.), GALLOIS et JAPIOT (1925; man, 12 Th.).

3. *In the lumbar region.*

The rising of the curve in the posterior thoracic and lumbar region may evidently be explained by the fact that here the stress of the body-axis chiefly depends on the structure and dimensions of the vertebral bodies and the intervertebral discs. The remarkable decline of the curve of some mammals (Type I b, *Panthera leo* L.; type III b) in the posterior lumbar region, however, as well as the horizontal course of type III c, still require a special explanation.

It may be expected that in this region too there will be other elements that cause the stress of the vertebral column to a greater or less degree. These elements are: 1st. The ligamentum ilio-lumbale, a remarkable strong fibrous connection between the transverse processes of the last or the last two lumbar vertebrae and the ilium. In several mammals these transverse processes even lie between the alae ilii. The development of the ligamentum is especially strong in a great many Ungulates and in man and the great apes. 2d. The accessory articulations or even synostoses between the transverse processes of the last lumbar vertebra and the sacrum and between the last and last but one lumbar vertebrae. These accessory joints are especially well developed in the *Equidae* and *Rhinocerotidae*. 3d. The increase of the transverse diameter between the zygapophysial joints in the lumbar region and especially at the articulatio lumbo-sacralis. Between the 3d and the last lumbar vertebra this distance increases in the lion from 33—58, in the cow from 58—75 and in the horse from 28—42 mm. 4th. The embracing zygapophyses of the postdiaphragmatic region. This characteristic has only been found in the *Artiodactyla*. In all representatives of this order the praezygapophyses embrace the articulating postzygapophyses in such a manner that the joints are practically immovable (fig. 30).

I believe that the factors mentioned sub 1—3 are chiefly responsible for the decline of the curve of the types I b and III b. The decline of the curve is caused by a decrease of the height and breadth of the vertebral bodies

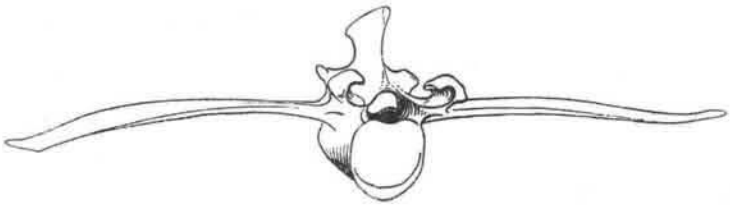

Fig. 30.
Cranial view of a lumbar vertebra of the cow [*Bos taurus* L. (dom.)] with embracing praezygapophyses.

or of their height only (fig. 23 and 26). Thus one might expect that in the first place this decrease would be compensated by a strengthening of the vertebral column in the sagittal direction. In reality, however, the posterior lumbar vertebral column is chiefly strengthened in the transverse direction. This phenomenon may be explained by the fact that in this region there is required practically no lateral mobility of the body-axis, while especially at the lumbo-sacral joint the dorso-ventral mobility is even comparatively great (see page 24).

The horizontal course of the curves of type III c may chiefly be caused by the embracing zygapophyses (fig. 30). It is a very striking fact that these horizontal curves are only shown by the Artiodactyls of moderate size (*Capridae, Ovidae,* comparatively small *Cervidae* and *Antilopinae*; *Taurotragus* shows an intermediate position between III b and III c). This may be explained by the supposition that in the big Artiodactyls even this additional strengthening of the body-axis is not sufficient to permit a weakening of the vertebral bodies. It does not explain, however, why the pig does not belong to type III c.

In the foregoing pages I have tried to explain the general shape of the diagram of moments in several different types of quadrupedal mammals. Now, only the fact that everywhere in the vertebral column (with the exception of some Ungulates: *Equidae, Bos, Rhinoceros*) the vertebral bodies are always more broad than high, still needs further explanation. On page 33 we have seen that, although the sagittal bending of the vertebral column is of greater importance than the lateral bending, yet the lateral bending may by no means be neglected. Now the additional strengthening of the vertebral column in the sagittal direction, by means of the neural spines with their muscles and ligaments, is of much more importance than the transverse additional strengthening by means of the transverse processes and their ligaments. For the ligamenta intertransversaria always show a comparatively weak development. This may explain, why the transverse diameter of the vertebral bodies is always greater than the sagittal one and

also why in so many big mammals the rising of the curve in the posterior thoracic and lumbar region is almost exclusively caused by an increase of the breadth (fig. 24—26; *Equidae, Hippopotamidae, Bovidae, Camelidae, Canidae, Felidae*), while in the smaller mammals this rising is chiefly caused by an increase of breadth and height (fig. 22—23; *Didelphis, Sciurus, Loris, Macaca, Manis, Castor, Euarctos, Sus, Hydrochoerus*; also, however, *Elephas*).

The shape of the cervical vertebral bodies of some Ungulates (more high than broad) may perhaps be explained by the supposition, that in these big animals the additional support of the stretching-cords (chiefly the lig. nuchae) is not quite sufficient. Since in the Elephant, however, the vertebral bodies are more broad than high, it will be evident that other factors must be taken into account. Further researches on this subject are still wanted.

## C. Bipedal terrestrial mammals.

Among the bipedal terrestrial mammals data about the shape and size of the vertebral bodies were available from *Macropus giganteus* Zimm., *Macropus robustus cervinus* Thomas, [after NAUCK (1932)], *Pongo pygmaeus* (Hoppius), *Gorilla gorilla* (Sav. et Wym.) [after NAUCK (1932)] and *Homo sapiens* L.

In order to explain the shape of the diagram of moments in quadrupedal mammals, we have compared the body-axis of these mammals to a beam supported at one end only, because the forces acting on this axis are maximal when the animal stands on its hind legs only. Since in bipedal terrestrial mammals the highest neural spines of the trunk are found in the anterior thoracic region, exactly as in their quadrupedal relatives, it might be expected that the curves of the bipedal mammals would show the same decline in the anterior thoracic region, as in the quadrupedal ones. The figures 31—32, however, show that in all bipedal mammals the curve

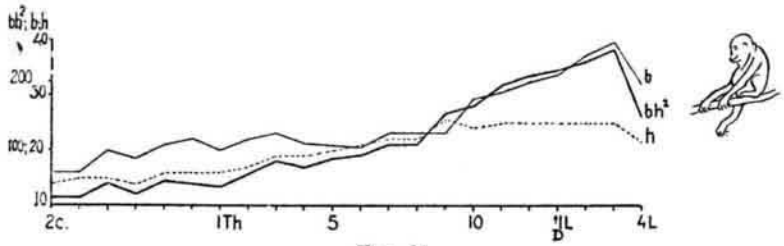


Fig. 31.
Orang-utan; *Pongo pygmaeus* (Hoppius).

rises almost uniformly from the third cervical up to the last lumbar vertebra, exactly as in a beam supported at one end only without additional strengthening.

In my opinion the explanation of this phenomenon must be found in the fact that these bipedal mammals stand and move on their hind legs for a considerably longer time than the erected quadrupedal mammals. On

page 37 it has been shown that the additional strengthening of the body-axis, that is caused by the anterior thoracic neural spines, is based in the last instance on the strength of the spinal musculature attached to these

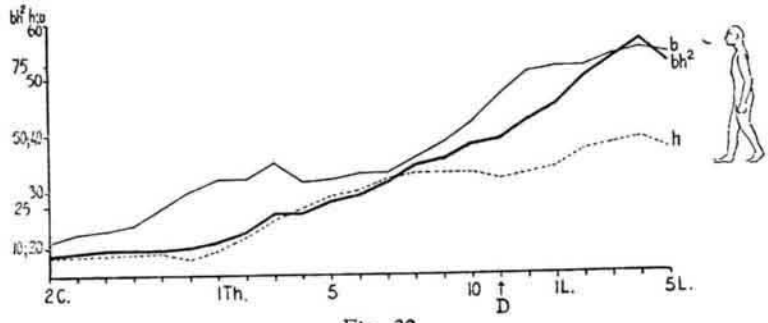


Fig. 32.
Man: *Homo sapiens* L.

spines. If an animal, however, stands on its hind legs for a comparatively long time, these muscles get tired and with this tiredness the additional strength caused by the neural spines gets lost. Thus in the bipedal mammals the stress of the body-axis almost entirely must depend on the stress of the vertebral bodies, and consequently the diagram of moments of these

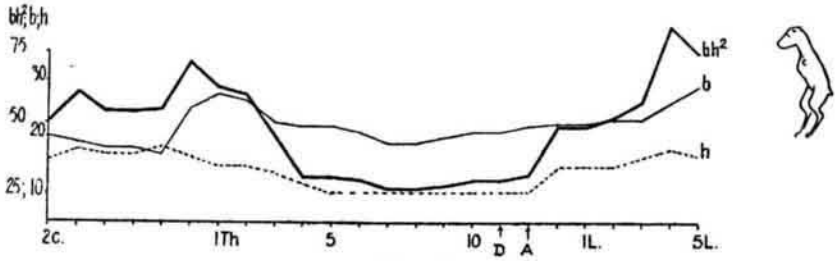


Fig. 33.
Bipedal goat (see page 5).

Fig. 31—33.
Diagram of the height, breadth and moment of resistance of the vertebral bodies in the different regions of the vertebral column in bipedal mammals. For further explanation see fig. 22—24.

bodies must resemble that of a common beam supported at one end only.

The bears are comparatively big quadrupedal mammals that stand or sit now and then for a comparatively long time on their hind legs. So it is quite in accordance with the foregoing considerations that the stress-diagram of these animals shows an intermediate shape between that of the quadrupedal and that of the bipedal terrestrial mammals (fig. 23).

## D. The bipedal goat.

Fig. 27 shows the stress-diagram of a normal goat and fig. 33 that of the little goat without fore-legs that lived about one year and moved

foreward on its hind legs in a semi-upright posture [p. 5 and SLIJPER (1942)]. The foregoing considerations explain quite evidently, that the curve of the bipedal goat rises in the lumbar region instead of being horizontal as in the normal animal. But why is there a marked decline of the curve in the anterior thoracic region? Why does not the diagram resemble that of the bipedal terrestrial mammals? The explanation of this phenomenon is given by the fact that the goat is an Ungulate. Thus its thoracic spines are not only connected by muscles, but also by interspinous ligaments and especially by the strongly developed ligamentum nuchae. These ligaments do not get tired. Moreover the anterior seven thoracic spines were markedly higher than in the normal goat (p. 115 and fig. 122). Thus there is an additional strengthening of the anterior thoracic vertebrae and thus there may be a correspondingly weaker development of the vertebral bodies in this region.

## E. The aquatic mammals.

Among the aquatic mammals I have studied the size and shape of the vertebral bodies of *Phocaena phocaena* (L.), *Trichechus inunguis* (Natt.) and *Phoca vitulina* L. Data were also available of *Mirounga leonina* (L.) [NAUCK (1932)].

With regard to the permanent aquatic mammals, the influence of the body-weight (gravitation) on the vertebral column may be neglected. Only the locomotive power and the resistance of the water must be taken into consideration. In the 5th part of this paper it will be pointed out in detail that in general the centre of the locomotive movements of these animals lies at the basis of the tail. Thus the body-axis may be compared to a beam supported in its middle, or with two beams supported at one end only. The resistance of the water tries to bend each of these beams.

Thus the curve of the moments of resistance of the vertebral bodies must show a uniform rising from the first cervical up to the last lumbar vertebra, followed by a uniform decline in the caudal region. As is shown in fig. 34,

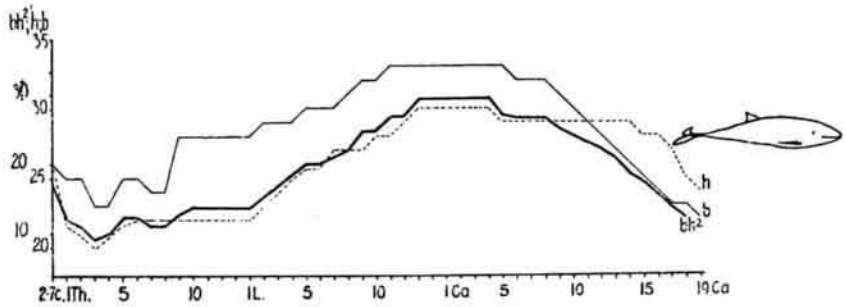


Fig. 34.
Common porpoise: *Phocaena phocaena* (L.).

the curve really has this shape. That there is no decline in the anterior thoracic region may be explained by the fact that in *Cetacea* and *Sirenia*

the anterior thoracic spines are not higher than the posterior thoracic and lumbar ones, as in ordinary land-mammals, but that on the contrary they are lower [SLIJPER (1936)].

In the temporary aquatic mammals the centre of the locomotive movements (they chiefly move forward by alternate strokes of their hind legs;

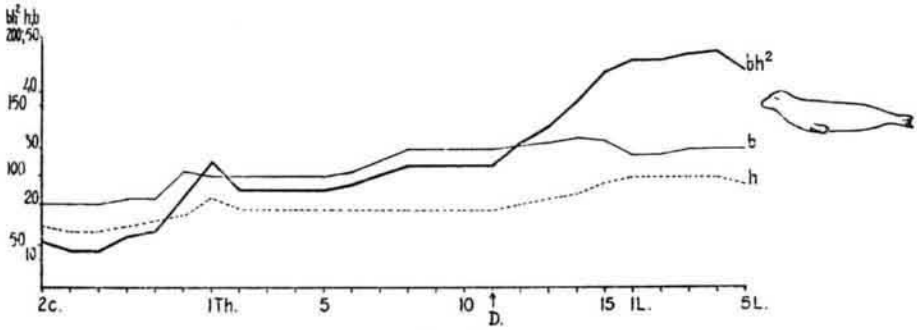


Fig. 35.
Common seal; *Phoca vitulina* (L.).

Fig. 34—35.
Diagram of the height, breadth and moment of resistance of the vertebral bodies in the different regions of the vertebral column in aquatic mammals. For further explanation see fig. 22—24. *Ca* = caudal vertebra.

see page 70) lies nearly at the ilio-sacral joint. Since the animals practically have no tail, a uniform rising of the curve from the first cervical up to the last lumbar vertebra might be expected, if the height of the neural spines in the different regions was the same as in the permanent aquatic mammals. In reality, however, in the *Pinnipedia* the anterior thoracic spines are higher than the posterior thoracic and lumbar ones, just as in ordinary quadrupedal land-mammals. Thus the shape of the curve is intermediate between that of the terrestrial Carnivores and that of the *Cetacea* (fig. 35).

# V

# THE EPAXIAL SPINAL MUSCLES AND THE MOBILITY OF THE VERTEBRAL COLUMN

On page 17 the conclusion has been drawn that the height and inclination of the neural spines in mammals depend on the demands of the muscles and ligaments, attached to them. In consequence, it was necessary to make careful investigations about the structure of the epaxial spinal musculature in a great number of different species of mammals. In studying the literature on this subject, it was rather astonishing to observe that only of 19 different mammals usable descriptions of these muscles could be found. With the exception of the authors, dealing with man and the domestic animals, accurate descriptions have practically only been given by VALLOIS, VIRCHOW and WINCKLER. To get a material of 80 different species of mammals, I was obliged to dissect the spinal musculature of 61 mammals myself (see table 3).

## A. General morphology of the epaxial spinal musculature.

VALLOIS (1922) has shown that among the epaxial spinal muscles of Reptiles three different systems may be distinguished: 1st The lateral system: m. ilio-costalis. In connection with the movements of the body-axis, which chiefly take place in the lateral direction [creeping locomotion; see SLIJPER (1941)], this muscle is very strongly developed; the ribs serve as levers. The structure of the muscle is entirely metameric, the different muscular fascicles originate at and insert into the myosepta and the ribs. 2d The intermediate system: m. longissimus. This muscle shows a moderate and likewise entirely metameric development, although the fascicles are longer than those of the m. ilio-costalis. They originate [1]) at the myosepta and the intermuscular septa of the fasciae and insert, 5—6 vertebrae caudal of this point, into the praezygapophyses and the transverse processes (fig. 36). Moreover there are short mm. intertransversarii. 3d The medial system: m. transverso-spinalis. This generally very well developed muscle consists of a number of different systems of fascicles. Some of them are very weakly developed and besides they do not occur in all Reptiles (m. tendino-articularis, m. neuro-spinalis, m. interarticularis). The three important systems of fascicles are (fig. 36): a. m. articulo-spinalis, short metameric fasciculi originating at the neural spines and inserted into the prae-

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[1]) In all further descriptions the cranial attachment of the muscle is called origin, the caudal attachment insertion.

zygapophyses of the 3d vertebra caudal of their point of origin. b. M. spino-articularis, short metameric fasciculi originating at the praezygapophyses and inserted into the neural spine of the 3d vertebra caudal of their point of origin. c. M. interspinales between the neural spines of two consecutive

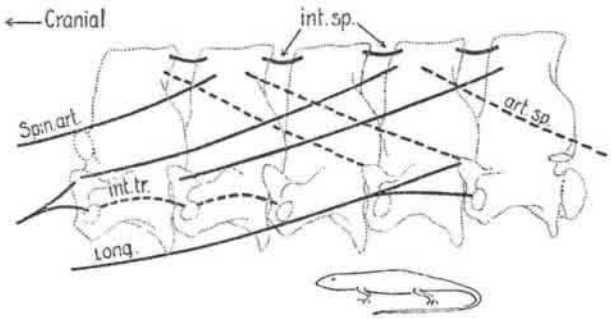


Fig. 36.
Schematic drawing of the structure of the m. transverso-spinalis in Reptiles. int. sp. = m. interspinales; art. sp. = m. articulo-spinalis; spin. art. = m. spino-articularis; intr. tr. = m. intertransversarii; long. = m. longissimus dorsi.

vertebrae. OLSON (1936) has shown that in Reptiles there is a certain tendency to a shifting of the attachment of the muscles from the myosepta into the skeleton and to a development of longer fasciculi.

The body-axis of the Reptiles is chiefly an organ of locomotion, especially adapted to movements in the lateral direction. It carries the body-weight only to a very limited extent, since the belly of the animals nearly always rests on the ground [creeping; see SLIJPER (1941)]. On the contrary, the body-axis of mammals carries an important part of the body-weight, since it serves as the bow of the bow-and-string-construction of the trunk (p. 13). The muscles chiefly have to prevent movements in the sagittal direction. Moreover the body-axis of mammals is also an organ of locomotion, especially in those animals that show a leaping-gallop (p. 22). But also these movements take place in the sagittal plane. From the nature of the case the musculature of the body-axis of mammals shows a tendency to adapt itself to these tasks. In the following pages the different ranks of adaptation of the three systems of epaxial musculature will be dealt with separately.

1. *M. ilio-costalis.*

WINCKLER (1936) supposes that the m. ilio-costalis of mammals shows a tendency to emancipate itself from the m. longissimus. This opinion, however, is founded on the erroneous supposition that the structure of the musculature of Insectivores must in every way be considered as primitive. From my own investigations it follows that three principal tendencies may be distinguished in the phylogenetic development of this muscle in mammals.

In the first place there is a tendency to a narrowing of the muscle, that

may be explained by the fact that the lateral movements of the body-axis for the greater part are replaced by sagittal ones. Thus the thoracic part of the muscle is always comparatively narrow (fig. 37). In a few orders of

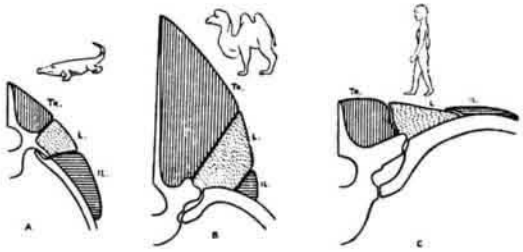

Fig. 37.
Schematic transverse sections of the 7th thoracic vertebra and the epaxial musculature of a Reptile (a), a quadrupedal mammal (b) and man (c), to show the mutual differences in position and development of the three muscular systems. a. *Crocodilus palustris* after VALLOIS (1922); b. *Camelus bactrianus* L.; c. *Homo sapiens* L.

mammals, however, the m. ilio-costalis thoracis shows a marked enlargement, which may be considered as a highly specialised characteristic (p. 47). A moderate broadening is met with in man and the anthropoid apes and in some heavy Ungulates (*Hippopotamus, Elephas, Loxodonta, Rhinoceros*; fig. 42, 52, 70). In man and the great apes this phenomenon may be connected with the great increase of the transverse diameter of the trunk (fig. 37, p. 64). In the heavy Ungulates it is perhaps connected with the respiratory movements (expiration). In the aquatic mammals the enlargement of the muscle is certainly connected with these respiratory movements, as well as with the increased lateral movements of the body (p. 73). The *Sirenia* and *Mystacoceti* possess a narrow ilio-costalis thoracis, just as the terrestrial mammals (fig. 79). But in *Ornithorhynchus*, the *Pinnipedia*, the *Delphinapteridae*, *Delphinidae* and *Phocaenidae* it is a very large muscle, which covers the greater part of the lateral surface of the thorax [see SLIJPER (1936, 1939, fig. 80 and p. 73). A very broad and thick ilio-costalis lumborum was found in *Dasypus* (fig. 38), but not in the other Edentates.

In the second place, there is a tendency to the development of long muscular fascicles, although in most mammals the thoracic part of the muscle retains the primitive metameric structure quite well.

In the third place, the m. ilio-costalis lumborum (origin: last ribs, transverse processes of lumbar vertebrae; insertion: transverse processes of lumbar vertebrae but chiefly ilium) shows a marked tendency to a fusion of its fascicles with those of the m. longissimus dorsi and to a fusion with the fascia spino-transversaria. The fused muscles are called m. erector spinae (fig. 40—42). In consequence of these fusions the muscle acquires an attachment to the metapophyses and especially to the neural spines of the lumbar and sacral vertebrae and thus it is able to move the vertebral column in the sagittal plane.

The m. ilio-costalis lumborum is perfectly free from the m. longissimus in *Ornithorhynchus*, the *Edentata* (fig. 38) and some *Insectivora* (*Ptilocercus;* see table 3). It is also perfectly free in the majority of the aquatic mammals (*Lutra, Phoca, Trichechus, Cetacea;* fig. 77, 79, 80), but in these animals this is not a primitive characteristic but on the contrary a

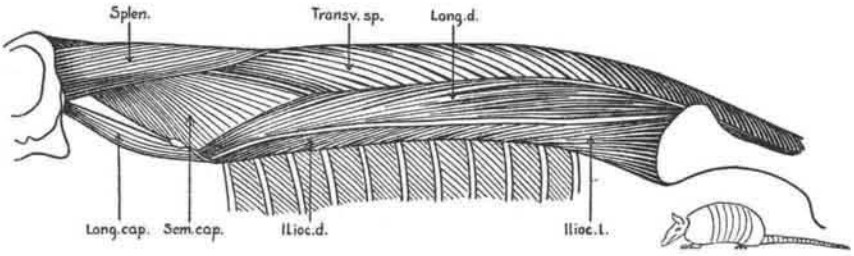


Fig. 38.
Epaxial musculature of the Peba-armadillo, *Dasypus novemcinctus* L. Undifferentiated transverso-spinalis. Longissimus only inserted into metapophyses. Perfectly separate ilio-costalis.

very specialised one, since in *Dugong* and *Zalophus* the muscle is still a little bit fused with the m. longissimus. The aquatic mammals have lost the insertion into the metapophyses and the neural spines again, in adaptation to their increased mobility in the horizontal plane. Man and the anthropoid apes also show a secondary tendency to a separation of the ilio-costalis and the longissimus as an adaptation to the broadening of the trunk [fig. 70; see also VALLOIS (1928)]. In a number of *Marsupialia* and *Insectivora* the m. ilio-costalis lumborum is only connected with the pars ilio-lumbalis of the m. longissimus (see p. 49), so that it is not yet inserted into the metapophyses and the neural spines (fig. 39). The majority of the land-mammals, however, possess an ilio-costalis lumborum

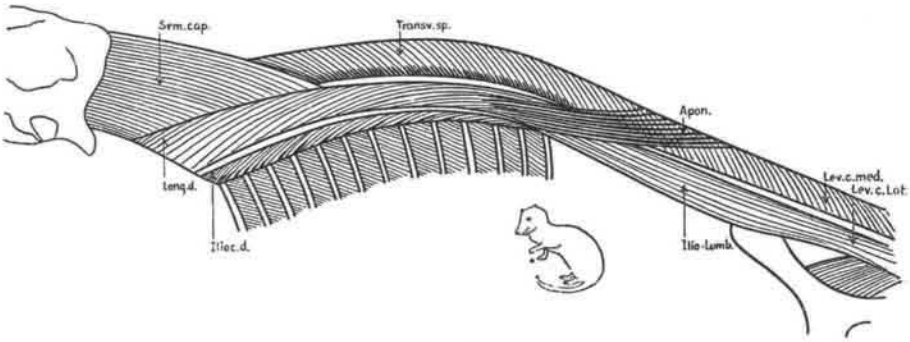


Fig. 39.
Epaxial musculature of an opossum, *Metachirus nudicaudatus* (E. Geoffr.). Undifferentiated transverso-spinalis with semispinalis. Longissimus chiefly inserted into metapophyses, only a few aponeurotic fibres run into the neural spines. Very strongly developed and almost separate ilio-lumbalis. Ilio-costalis lumb. completely fused with ilio-lumbalis.

that is not only fused with the m. ilio-lumbalis but with the aponeurosis of the m. longissimus, with the metapophysial tendons and with the fascia spino-transversaria. Thus the fascicles of the ilio-costalis are also inserted into the metapophyses but especially into the lumbar and sacral neural spines (fig. 40). The most complete fusion is met with in the Ungulates. Here the m. ilio-costalis dorsi terminates about the middle of the lumbar region

or even at the ilium (heavy animals), the ilio-costalis lumborum can in no way be separated from the erector-spinae-complex (fig. 41, 42, 52).

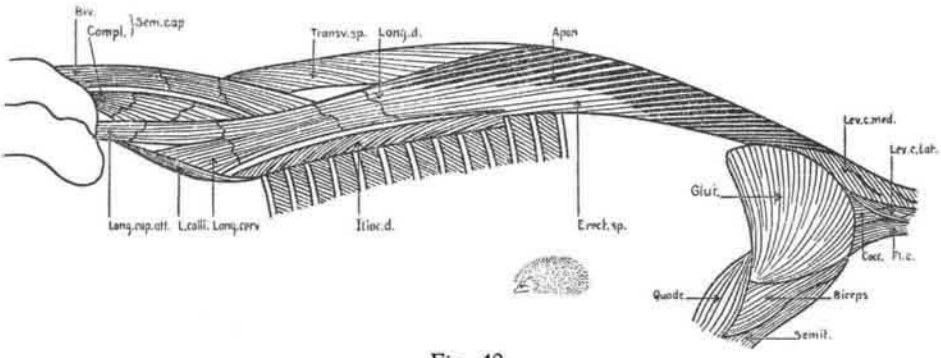


Fig. 40.

Epaxial musculature of the hedgehog, *Erinaceus europaeus* L. Undifferentiated transverso-spinalis. Longissimus chiefly inserted into neural spines with strong aponeurosis. Ilio-costalis lumb. completely fused with longissimus (erector spinae).

## 2. *M. longissimus dorsi.*

In opposition to the Reptiles, the fascicles of the m. longissimus dorsi of the mammals are attached only to the skeleton. They originate at the proximal parts of the ribs and at the transverse processes. In some mammals the muscle consists of comparatively short metameric fascicles that are inserted into the metapophyses. This primitive structure of the muscle is very well developed in the *Edentata*, especially in *Dasypus* and *Choloepus* (fig. 44), but in several other mammals the fasciculi of the m. longissimus

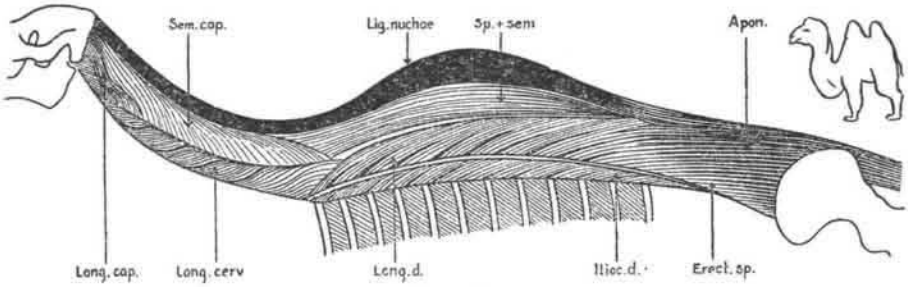


Fig. 41.

Epaxial musculature of the camel, *Camelus bactrianus* L. Spinalis and semispinalis inserted together with longissimus into the lumbar and sacral vertebrae. Ilio-costalis lumb. completely fused with longissimus (erector spinae). Ilio-costalis dorsi terminating at 3d lumbar vertebra. Remark the expansion of the ligamentum nuchae at the withers.

likewise are inserted into all the thoracic and lumbar metapophyses (*Erinaceus, Jaculus, Allactaga, Dipodomys, Mydaus, Phoca, Elephas, Balaenoptera*). In other mammals, however, the fasciculi inserted into the thoracic metapophyses have but a rudimentary character [as for instance in man and the Primates; see also NISHI (1938)].

In connection with the special movements of the mammalian body-axis in the sagittal plane, the m. longissimus dorsi shows a marked tendency to the development of long fascicles with long tendons that originate at the prae- and are inserted into the postdiaphragmatic vertebrae. There is also a marked tendency to a shifting of the insertion from the metapophyses into the summits of the postdiaphragmatic neural spines. So the muscle acquires a considerably longer lever to move these vertebrae. The attachment to the summits of the neural spines may be brought about by the insertion of the muscular fasciculi into the fascia spino-transversaria (*Manis, Perameles, Phalanger, Tupaia, Macroscelides, Talpa*). This primitive

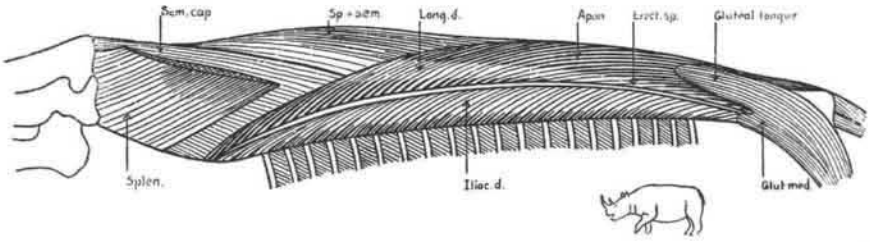


Fig. 42.
Epaxial musculature of the common African rhinoceros, *Diceros bicornis* (L.). Aponeurosis of splenius transversely cut. Spinalis et semispinalis. Longissimus only inserted into neural spines. Ilio-costalis lumb. completely fused with longissimus (erector spinae). Ilio-costalis dorsi terminating at ilium. Well developed gluteal tongue.

manner of insertion into the spines in the majority of the mammals, however, is replaced by an insertion by means of a superficial aponeurosis, consisting of flat, but usually quite well developed tendons (fig. 39—42). A m. longissimus which, apart from the attachment to the ilium, is only inserted into the metapophyses, does not occur in many species of mammals. I found it only in *Dasypus* and *Choloepus* (fig. 38, 44). In *Manis* and in several *Marsupialia* and *Insectivora* the metapophysial tendons are still of more importance than the spinal ones (fig. 39), but in the majority of mammals the spinal tendons are better developed (fig. 40, 41, 42, 45). In some Ungulates and Primates the metapophysial tendons may even be completely absent (fig. 46).

The mammalian m. longissimus dorsi differs also very markedly from that of the Reptiles by the presence of its insertion into the ilium. This connection with the ilium is brought about by a new muscular element originating at the last rib, the transverse processes, neural arches and lateral sides of metapophyses of the last thoracic and all lumbar vertebrae and at the anapophyses of these vertebrae (frequently by means of very distinct tendons). The muscle is inserted into the inner side of the ala ilii and it is often fused with the m. ilio-costalis (see p. 47). VIRCHOW (1929) gave it the name of m. ilio-lumbalis, WINCKLER (1938) called it pars lumborum m. longiss. dorsi, EISLER (1912) m. longissimus lumborum.

In the *Monotremata* the m. ilio-lumbalis is the only part of the m. longissimus that is present (fig. 43). The absence of the other parts, however, must be considered as a very specialised characteristic, although up to the present no researches have been made about the signification of this phenomenon. A free m. ilio-lumbalis has been met with in

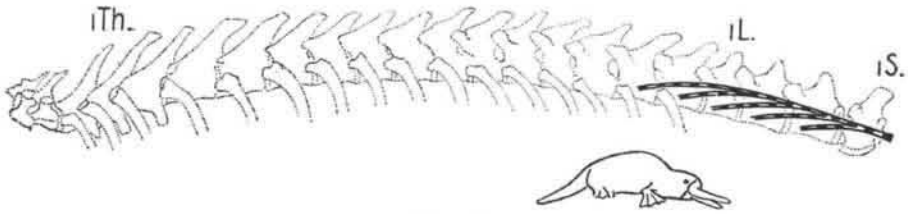


Fig. 43.
Schematic drawing of the structure of the m. longissimus dorsi in the platypus, *Ornithorhynchus anatinus* (Shaw). Only a m. ilio-lumbalis present.

*Choloepus, Erinaceus, Tupaia, Psammomys, Orycteropus, Tapirus* and *Hippopotamus*. It is partly fused with the other parts of the longissimus in *Didelphis* (fig. 39), *Macroscelides*, the majority of the *Carnivora* and a great number of *Primates* (*Cercopithecus*,

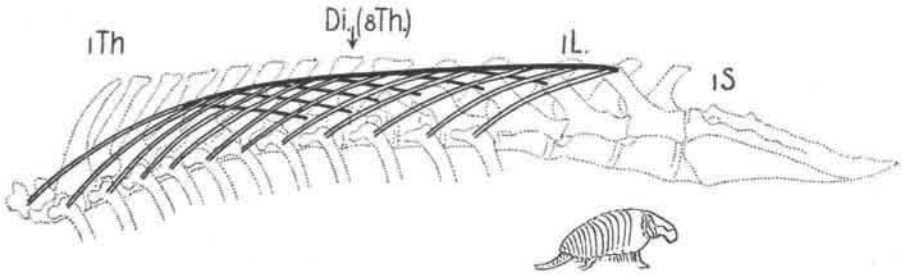


Fig. 44.
Schematic drawing of the structure of the m. longissimus dorsi in the Peba-armadillo, *Dasypus novemcinctus* L. Origin white, insertion black. *Di* = diaphragmatic vertebra. Longissimus only inserted into metapophyses.

*Saimiri, Papio, Erythrocebus, Gorilla*). In the other mammals, and especially in the *Ungulata* and *Rodentia*, the fusion is complete (fig. 45). The m. ilio-lumbalis is secondarily wanting in *Lutra*, the *Sirenia* and *Cetacea* and in *Rhinoceros* (fig. 46). In the

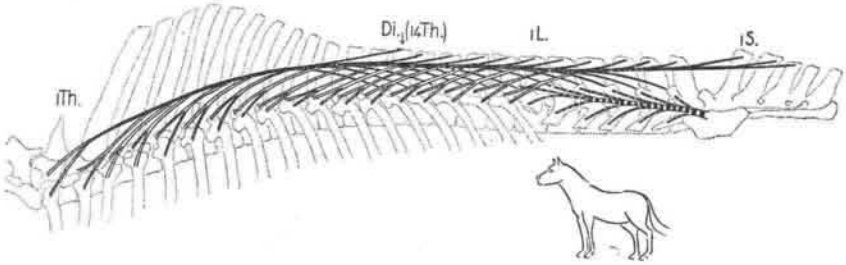


Fig. 45.
Schematic drawing of the structure of the m. longissimus dorsi in the horse, *Equus caballus* L. (dom.). M. ilio-lumbalis black and white. See also fig. 44. Longissimus inserted into ilium, metapophyses and neural spines, chiefly of postdiaphragmatic region.

aquatic mammals this phenomenon is caused by the intimate fusion of the m. longissimus dorsi and the m. levator caudae lateralis; it is a very distinct adaptation to aquatic life (see p. 76). In *Rhinoceros* (see table 3, note 23 and 24) the fascicles of the longissimus are only inserted into the neural spines (fig. 42, 46). Further researches about the signification of this character are wanted.

The most cranial point of origin of the m. longissimus dorsi in the majority of mammals is found at the 6th or 7th cervical or at the 1st thoracic vertebra. In some mammals,

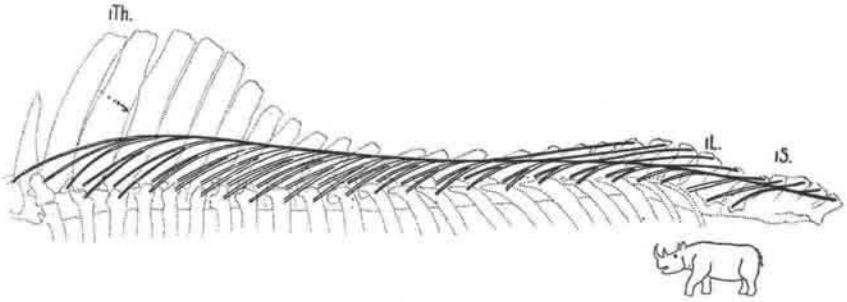


Fig. 46.
Schematic drawing of the structure of the m. longissimus dorsi in the common African rhinoceros, *Diceros bicornis* (L.). See also fig. 44. Longissimus only inserted into neural spines.

however, there is an intimate fusion between the m. longissimus dorsi and the m. longissimus cervicis and capitis (*Macropus, Dorcopsis, Phalanger, Cuniculus, Cricetus, Sciurus, Orycteropus, Nycticebus, Saimiri, Ateles, Cetacea, Rhinoceros, Loxodonta*, not, however, in *Elephas*).

According to VALLOIS (1922) all mammals possess mm. mammillo-styloidei, short fascicles of the longissimus-system, originating at the transverse processes and inserted into the metapophyses (fig. 47). I found them

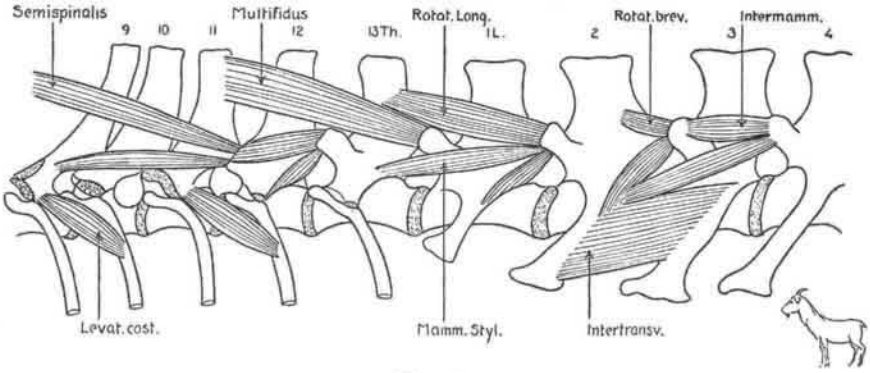


Fig. 47.
Schematic drawing of the short muscles of the body-axis in the goat, *Capra hircus* L. (dom.). In every segment only a part of these muscles has been reproduced.

very distinctly developed in *Capra, Gazella* and *Odocoileus*, but only in the post-diaphragmatic region.

3. *M. transverso-spinalis.*

The name m. transverso-spinalis is given to all muscles, lying medial of the zygapophyses (fig. 37). The m. spino-articularis of the Reptiles does not occur in mammals. The m. articulo-spinalis, on the contrary, may be quite well developed and it may be differentiated into a number of more or less separate muscular systems. Since in the different authors the nomenclature of these systems is not always the same, it will first be stated that in this paper the following names will be used (fig. 47):

Semispinalis: Fascicles originating at the neural spines and inserted into the metapophyses belonging to a vertebra, 4 or usually more vertebrae caudal of the vertebra at which they originate.

Multifidus: Corresponding fascicles, inserted into the 3d (sometimes into the 4th) vertebra caudal of the vertebra at which they originate.

Submultifidus:

Rotatores longi: Corresponding fascicles, inserted into the the 2d vertebra caudal of their vertebra of origin.

Rotatores breves: Corresponding fascicles inserted into the metapophysis of the 1st vertebra caudal of their vertebra of origin.

Interspinales: Fascicles between the neural spines of two consecutive vertebrae.

Spinalis: Fascicles between the neural spines. The insertion lies at least two, usually however a great number of vertebrae caudal of the vertebrae at which they originate. WINCKLER (1939) gave the name m. spinalis also to fascicles between the neural spines and the metapophyses. This, however, should not be done [VIRCHOW (1916), PLATTNER (1922) and others].

Intermammillares: Fascicles between the metapophyses (or in the thorax, where these apophyses are wanting, between the neural arches) of two consecutive vertebrae. Sometimes they are inserted into the 2d vertebra caudal of their vertebra of origin.

It is highly probably that the most primitive structure of the mammalian transverso-spinalis is met with in those cases in which there are only a m. multifidus and shorter fascicles (submultifidus, interspinales, intermammillares). I found this structure of the muscle in the trunk of *Choloepus* and *Dugong*. As a rule, however, we may suppose that the muscle shows a primitive structure in those mammals that possess an undifferentiated transverso-spinalis. This undifferentiated muscle is composed of semispinalis-, multifidus-, submultifidus-, interspinalis- and intermammillaris-fascicles, fused to a solid mass, in which the separate elements cannot

clearly be distinguished. The semispinalis-fascicles are usually comparatively short. They are inserted into vertebrae 5—6 vertebrae caudal

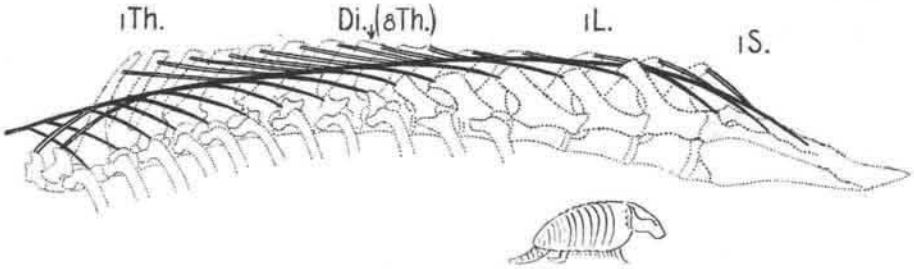


Fig. 48.
Schematic drawing of the structure of the m. transverso-spinalis of the Peba-armadillo, *Dasypus novemcinctus* L. See also fig. 44. Undifferentiated transverso-spinalis only inserted into all metapophyses. Origin at all neural spines.

of those at which they originate (fig. 48). An undifferentiated transverso-spinalis that is present throughout the whole trunk, has been found in *Tachyglossus, Dasypus, Erinaceus,* some *Rodentia, Chiroptera, Trichechus* and the majority of the *Cetacea* (fig. 38, 39, 48, 79, 80). In the aquatic mammals, however, the presence of this undifferentiated transverso-spinalis must not be considered as a primitive, but, on the contrary, as a highly specialised character (see p. 77).

In adaptation to the special mobility of the vertebral column (p. 58), in all other mammals a marked tendency can be determined to the

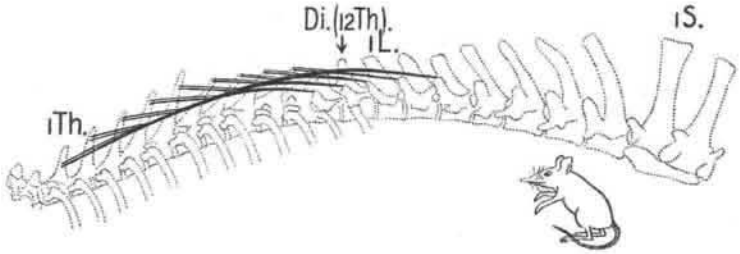


Fig. 49.
Schematic drawing of the structure of the m. transverso-spinalis in the jumping-shrew, *Macroscelides* spec. See also fig. 44. Undifferentiated transverso-spinalis and semispinalis inserted only into metapophyses, chiefly of postdiaphragmatic region. Origin only at praediaphragmatic spines.

following transformations of this primitive transverso-spinalis: 1st. The separation of the muscle in its different components. As can be seen in table 3, this process has taken place first in the praediaphragmatic region. There are a number of mammals that show in this region a highly differentiated transverso-spinalis, while in the postdiaphragmatic region the muscle shows still the undifferentiated structure (*Metachirus, Echinosorex, Macroscelides, Ptilocercus, Psammomys*; fig. 39). 2d. The development of long

semispinalis-fascicles, originating at the prae- and inserted into the postdiaphragmatic vertebrae (fig. 49, 50). 3d. The development of a m. spinalis whose fascicles also originate at the prae- and insert into the postdia-

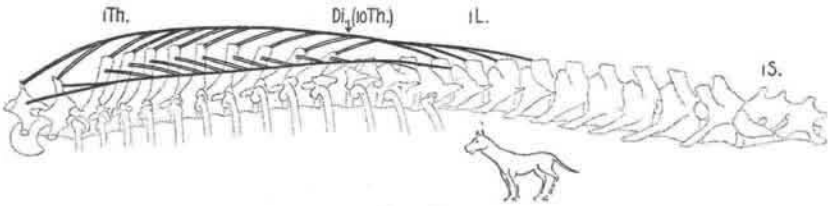


Fig. 50.
Schematic drawing of the structure of the m. transverso-spinalis of the dog, *Canis familiaris* L. See also fig. 44. Semispinalis and spinalis (shorter elements not reproduced). Origin at prae-, insertion at postdiaphragmatic neural spines and metapophyses.

phragmatic vertebrae [see also WINCKLER (1939)]. In a great many mammals the spinalis is still comparatively weakly developed. It is very well developed, however, in a number of *Carnivora*, *Rodentia* and *Primates* and especially in all *Ungulates* (fig. 40, 41, 42, 50, 51, 52, 53). In some

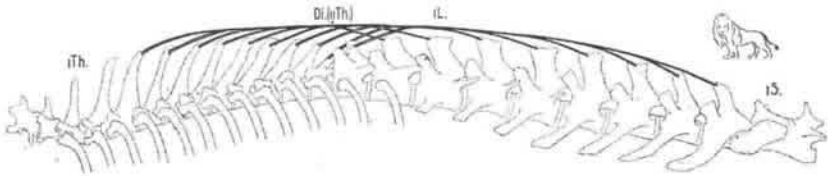


Fig. 51.
Schematic drawing of the structure of the m. transverso-spinalis in the lion, *Panthera leo* (L.). See also fig. 44. No semispinalis (shorter elements not reproduced). Origin of spinalis at prae-, insertion at postdiaphragmatic neural spines.

representatives of these orders (for example the lion, the horse and the pig) the m. semispinalis may even be completely replaced by the spinalis (fig. 51). It is quite evident that, the better the m. spinalis is developed, the longer the levers by means of which the vertebrae are moved will be.

With regard to the short fascicles of the transverso-spinalis (fig. 47) it may be stated that the m. submultifidus is not always limited to the praediaphragmatic region, as VIRCHOW (1913) supposed. This is only the case in the *Carnivora*, but in the *Ungulata* and *Primates* the fascicles have also been found in the postdiaphragmatic region, although it must be admitted that generally the praediaphragmatic part of the muscle is better developed [see also KRÜGER (1927) and SJOMUSCHKIN (1934)]. The mm intermammillares are chiefly found in the postdiaphragmatic region, as has also been stated by VALLOIS (1922) and SJOMUSCHKIN (1934). Only in *Choloepus* and *Psammomys* they were also present in the praediaphragmatic region.

In *Manis* and some *Cetacea* (see p. 77 and fig. 80) there is an undifferentiated transverso-spinalis from the back part of the skull up to the point of the tail. But the

other mammals generally possess a distinct m. semispinalis cervicis and always a distinct semispinalis capitis (fig. 38—41, 52). As can be seen in table 1, the development of the m. semispinalis capitis and the length of its area of insertion are sometimes correlated with the weight of the head and the length of the neck [*Hippopotamus, Elephas, Rhinoceros*; see also VALLOIS (1922)]. This correlation, however, is not always very distinct, as can be seen by the comparison of the two digging mammals *Dasypus* and *Talpa*.

A distinct accessory semispinalis has been found in the lumbar region of *Macropus* and *Dorcopsis* (see table 3, note 16 and 17). In *Macropus giganteus* Zimm., however, this element was completely fused with the other parts of the transverso-spinalis. The development of this element may be connected with the upright posture (see also p. 70).

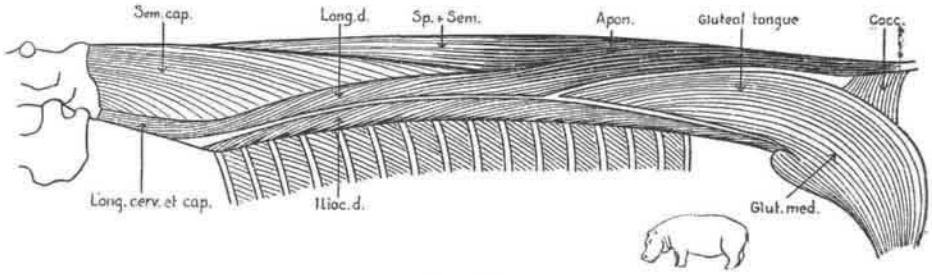


Fig. 52.
Epaxial musculature of the hippopotamus, *Hippopotamus amphibius* L. M glutaeo-biceps removed. Inserting tendons of spinalis and semispinalis partly fused with aponeurosis of longissimus. Longissimus chiefly inserted into neural spines with strong aponeurosis. Ilio-costalis lumb. completely fused with longissimus (erector spinae). Ilio-costalis dorsi terminating at ilium. Strongly developed gluteal tongue.

## 4. *The gluteal tongue.*

In the lumbar region of a great number of Ungulates, a special element is added to the epaxial spinal musculature, viz. the gluteal tongue (fig. 42, 52, 53). For in these mammals the m. glutaeus medius originates not only

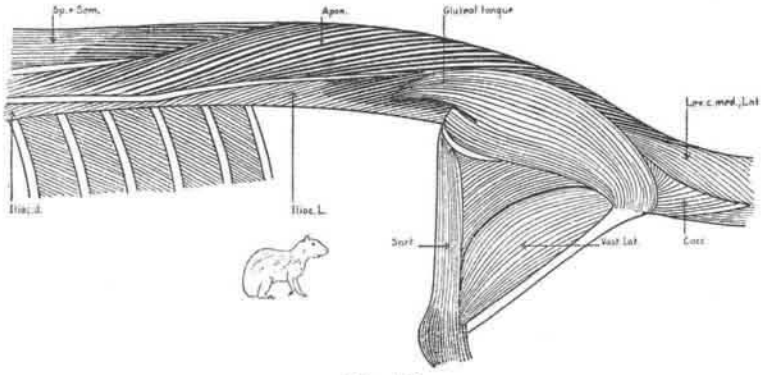


Fig. 53.
Caudal part of the epaxial musculature of the paca, *Cuniculus paca* (L.). Inserting tendons of spinalis and semispinalis partly fused with aponeurosis of longissimus. Longissimus chiefly inserted into neural spines with strong aponeurosis. Ilio-costalis lumb. chiefly inserted into neural spines by means of the aponeurosis of the longissimus. Glutaeus medius with very distinct gluteal tongue.

at the ilium, but also by means of this muscular tongue at the aponeurosis of the m. longissimus dorsi (the superficial tendons of this muscle or of the m. erector spinae).

The gluteal tongue does not occur in the *Camelidae* and *Proboscidea*. It is comparatively short in *Tragulus, Sus, Rhinoceros* (in the fetus of *Rh. sondaicus* Desm. it was even completely absent), *Gazella, Odocoileus, Cervus, Capra* and *Bos* (fig. 42). The horse (*Equus*) possesses a long gluteal tongue, but the strongest development was found in *Hippopotamus* and *Tapirus* (fig. 52). In these two species the tongue is completely fused with the m. ilio-lumbalis. Its cranial point lies at the 12th (*Hippopotamus*) or 17th (*Tapirus*) rib. The gluteal tongue is a special characteristic of the Ungulates, it has not been found in the representatives of any other order of mammals, with the exception of *Cuniculus paca* (L.) (fig. 53). This comparatively big Rodent possesses a gluteal tongue whose cranial point lies on the level of the 4th lumbar vertebra.

KOLESNIKOW (1928) believed that there was a certain correlation between the development of the m. ilio-costalis lumborum and the gluteal tongue. As table 3 shows, however, this conclusion has been based on too small a material; the correlation does not exist. As will be shown on p. 62, the development of the tongue might be connected with the size of the animals and the special mobility of their body-axis.

## B. The body-axis of the quadrupedal terrestrial mammals.

From the nature of the case, the general structure of the epaxial spinal musculature will depend on the mobility of the vertebral column. And this mobility again will be correlated with the general manner of locomotion of the animals (see p. 20). The mobility of the vertebral column can be studied by means of flexion-experiments (fig. 55—57, 60, 61, 64, 73, 76). Unfortunately up to the present only a small number of these experiments have been made with very different methods. Thus the exact outcomes of these experiments (the numbers) cannot always be compared and for the present we ought to be satisfied with some general terms as highly mobile, small mobility etc. (see table 4).

### 1. *The neck.*

In most mammals the neck is very mobile in the lateral direction, especially in its caudal part. In the horse, for example, the neck shows a special lateral mobility between the 4th and 7th cervical vertebra. In monkeys [*Saimiri, Cercopithecus, Cebus;* see also LUCAE (1876)] and in the kangaroo (*Macropus giganteus* Zimm.), however, the lateral mobility is comparatively small. REUTER (1933) says that the mobility of the cervical vertebral column of the dog in the ventral direction (dorsal concave) is comparatively small. My own experiments, however, have shown that this statement is not exact (fig. 55). As in nearly all other mammals, the neck of the dog is very mobile in the ventral direction. The mobility is especially localized in the caudal part; in the horse, for example, especially in the joints between the 6th and 7th cervical and between the 7th cervical and 1st thoracic vertebrae [fig. 61; see also WENGER (1915)]. In most mammals the neck may be bent so far in the ventral direction (dorsal concave) that the back part of the head touches the dorsal surface of the back (fig. 55, 57, 73). In some other mammals, however, the mobility in this direction is comparatively small (fig. 64).

VIRCHOW [1915; *Oryctolagus cuniculus* (L.), *Euarctos americanus* (Pall.), *Panthera leo* (L.)] has already pointed out that in the dorsal direction (ventral concave) the cervical vertebral column can be stretched only so far, that the vertebrae are lying in a straight line. I made the same observation with regard to the dog, the horse, the kangaroo and several monkeys (fig. 55, 57, 61, 64). A further dorsal flexion (ventral concave) is chiefly prevented by the ligaments. Thus the fact that even the Ungulates with their long necks

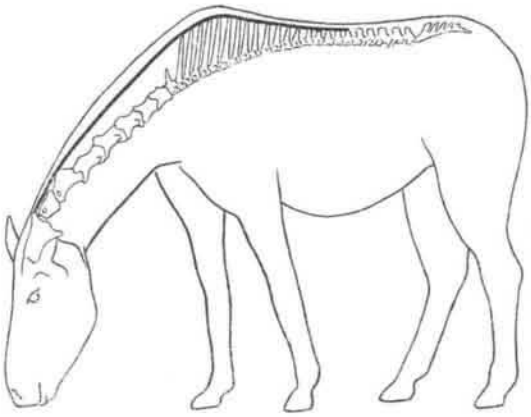

Fig. 54.
Schematic drawing of a grazing horse, *Equus caballus* L. (dom.), to demonstrate the straight cervical vertebral column and the flexure of the thoracic part of this column. Remark the position of the fore-legs.

can reach the ground with their mouth, is not based on the mobility of the neck. It is made possible by the mobility of the thoracic vertebrae, just cranial of the diaphragmatic vertebra, by the mobility of the atlanto-occipital joint and by the posture of the fore-legs (fig. 54). In the kangaroo the first thoracic vertebrae were also very mobile (fig. 57, 73).

## 2. *The trunk.*

A survey of the mobility of the vertebral column in the trunk of mammals is given in table 4.

### a. *Primitive mammals.*

Unfortunately only very few data are available of mammals with a primitive manner of locomotion (mammals that do not move in a gallop or amble). There is, however, a certain probability that these mammals possess a vertebral column that shows almost the same degree of mobility in every region of the trunk. This is quite in accordance with the development of the epaxial muscles. On p. 52 we have seen that in primitive mammals these muscles show an almost metamerical arrangement, that the long spinal tendons of the m. longissimus are wanting or weakly developed and that generally there is an undifferentiated transverso-spinalis without spinalis-fascicles.

### b. *Mammals with leaping-gallop.*

In the mammals that move forward in a leaping-gallop the praediaphragmatic region is very mobile in the dorsal (ventral concave) and fairly well mobile in the ventral direction (dorsal concave; fig. 55, 57). The mobility is especially large in the diaphragmatic region (fig. 58). The postdiaphragmatic region is much less mobile in the dorsal (ventral concave) and

almost or absolutely immobile in the ventral direction. The region immediately caudal of the diaphragmatic vertebra is more mobile than the other

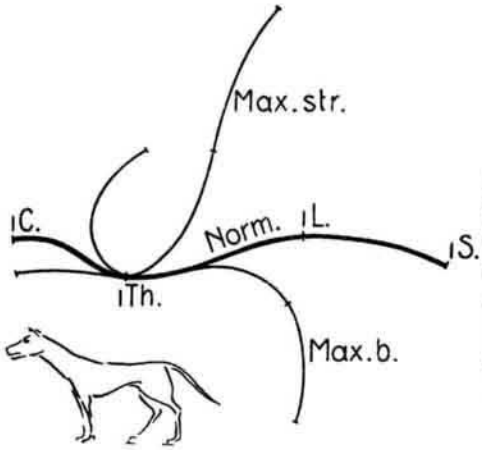


Fig. 55.
Experiments on the dorso-ventral flexibility of the vertebral column (with its ligaments) of the dog, *Canis familiaris* L. Norm. = normal shape of vertebral column. Max. str. = maximally stretched (maximal flexibility in the dorsal direction). Max. b. = maximally bent (maximal flexibility in the ventral direction).

parts of the postdiaphragmatic region. The mobility of the lumbo-sacral joint is always comparatively large in both directions.

The mobility of the vertebral column in the dorsal direction (ventral

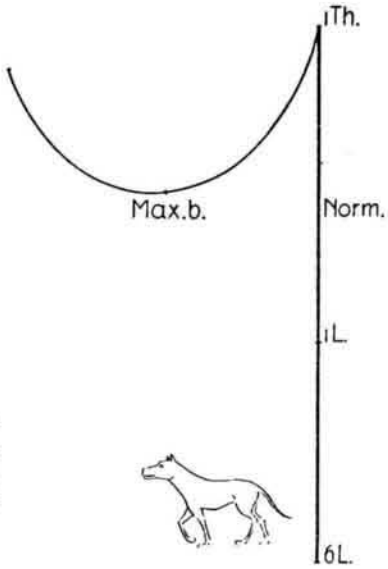


Fig. 56.
Experiments on the lateral flexibility of the vertebral column (with its ligaments) of the dog, *Canis familiaris* L. Norm. = normal shape of vertebral column. Max. b. = maximally bent in the lateral direction.

concave) and especially the mobility of its diaphragmatic region may be very beautifully observed, when the animals are sitting (fig. 59). The majority of these animals is able to sit on the tarsus and metatarsus of the hindlegs and the phalanges of the fore-legs. In this posture the vertebral column is bent to a comparatively high degree in the dorsal direction (ventral concave) and it shows a very characteristic hump in the diaphrag-

matic region. Among others this may be seen very beautifully in the cat, in some Rodents and in monkeys.

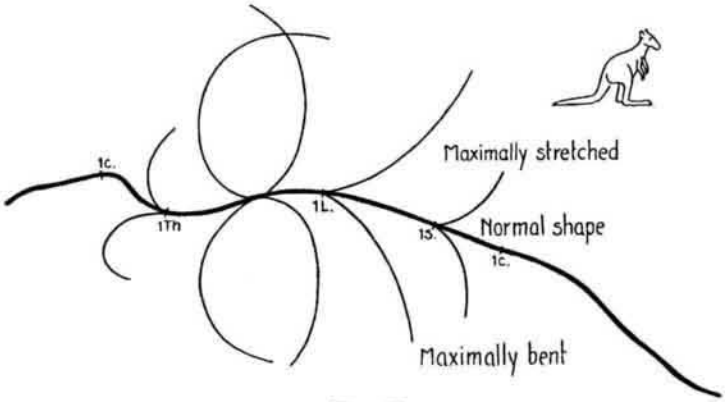


Fig. 57.
Experiments on the dorso-ventral flexibility of the vertebral column (with its ligaments) of the common gray kangaroo, *Macropus giganteus* Zimm. (see also fig. 55).

Very little is known about the factors that limit the mobility of some parts of the vertebral column. As follows from the data of table 4, a general rule about this question up to the present cannot be given. Neither the position of the zygapophysial articular surfaces, nor the absence or presence of anapophyses gives a satisfactory explanation.

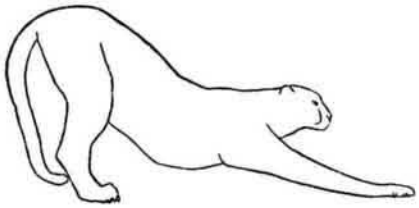

Fig. 58.
Drawing of a stretching cheeta or hunting-leopard (*Acinonyx jubatus* Erxleb.), to demonstrate the flexibility of its back in the dorsal direction (dorsal concave).

The anapophyses indeed are able to limit the mobility to a very high degree (especially, however, in the lateral direction; fig. 2, 107), but there are also mammals that show a comparatively large mobility in the region provided with these apophyses (fig. 56). In the first place the anapophyses serve as muscular attachments.

As follows from the descriptions given on page 53, the epaxial musculature of mammals moving in a leaping-gallop is highly adapted to the above described mobility of the vertebral column. In all three systems of muscles a distinct tendency is found to the development of long muscular fascicles originating at the prae- and inserted into the postdiaphragmatic vertebrae. Thus the vertebral column especially may be bent and stretched with the highly mobile diaphragmatic region serving as the centre of these movements (fig. 57, 58). Further a distinct tendency has been found to a shifting of the insertion of all three systems from the transverse processes and the metapophyses into the summits of the neural spines, in order to get a longer lever for the movements of the vertebrae. This tendency caused the fusion of the m. ilio-costalis and longissimus (erector spinae),

the development of the superficial tendons of the m. longissimus and the development of the m. spinalis.

Generally it may be said that primitive conditions have been found in

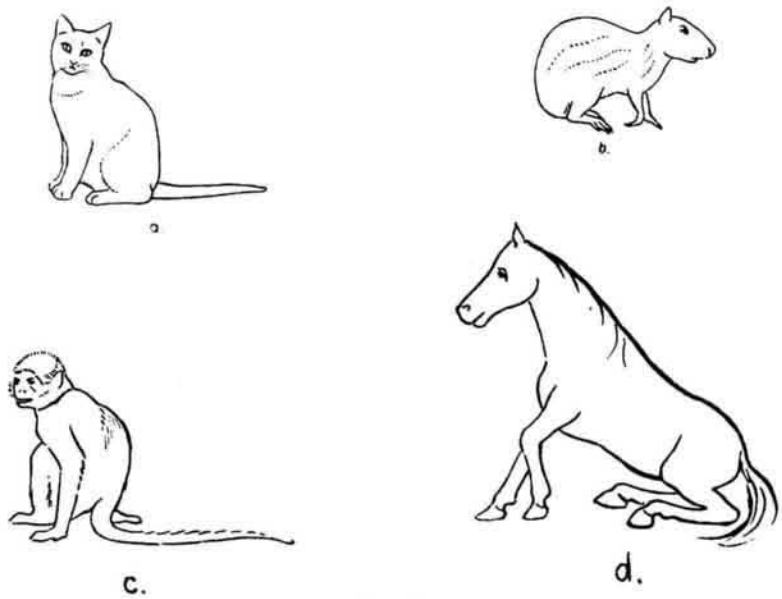


Fig. 59.
Four different sitting mammals to demonstrate the curved profile of the back (characteristic hump in the diaphragmatic region) in sitting Carnivores, Rodents and Monkeys and the straight profile in sitting Ungulates. a. Cat, *Felis catus* L.; b. Paca, *Cuniculus paca* (L.); c. Mangabey, *Cercocebus fuliginosus* E. Geoffr.; d. Horse, *Equus caballus* L. (dom.). After CORNISH.

the *Monotremata* and *Edentata*. A beginning of specialisation is shown by some *Marsupialia* and *Insectivora*, other representatives of these orders, however, are already highly specialised. A high degree of specialisation further is met with in *Rodentia*, *Carnivora* and the non-anthropoid *Primates* (see table 3).

c. *The Ungulates.*

On page 22 it has been shown that some primitive Ungulates (for example the *Suidae*) still move in a leaping-gallop. The specialised representatives of this order, however, show either a horse-gallop or an amble (some species also a rack) when they are moving forward swiftly. The horse-gallop and the amble are characterised by a very small mobility of the back in the sagittal plane. As is shown in table 4 and fig. 60, the vertebral column of these animals cannot be bent in the ventral direction (dorsal concave). The mobility in the dorsal direction (ventral concave) is comparatively small and limited to the region immediately cranial of the diaphragmatic vertebra. This mobility is necessary with regard to the ventral movement of the neck in grazing animals (see p. 57 and fig. 54).

The lumbo-sacral joint shows also a certain degree of mobility in the dorsal direction (ventral concave) in connection with the movements of the horse-gallop (see p. 22 and fig. 15—17). The small degree of mobility of

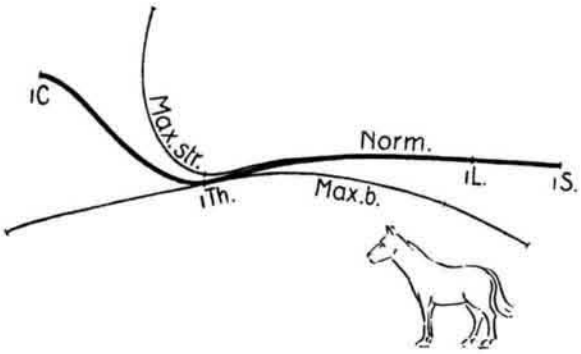


Fig. 60.
Experiments on the dorso-ventral flexibility of the vertebral column (with ligaments) of the horse, *Equus caballus* L. (dom.). See fig. 55.

the vertebral column in the dorsal direction (ventral concave) is demonstrated very beautifully when the animals are sitting. Fig. 59 shows that there is a very marked difference in shape between the back of a sitting cat or monkey and a sitting horse. Apart from that, it must be pointed out that the sitting posture is very rarely seen in Ungulates. The vertebral

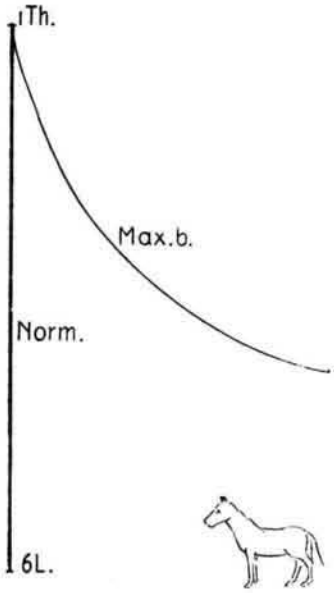


Fig. 61.
Experiments on the lateral flexibility of the vertebral column (with ligaments) of the horse, *Equus caballus* L. (dom.). See fig. 55.

column of the small Ungulates (some antelopes, goats, sheep, deer) generally is a little more mobile than that of their big relatives, especially in the diaphragmatic region. They may show a transitional type of locomotion between the leaping-gallop and the horse-gallop.

The mobility of the praediaphragmatic region is chiefly limited by the very high neural spines and their ligaments. In the postdiaphragmatic region the limitation in the first place is caused by the embracing zygapophyses that are found in every Ungulate with the exception of the *Tragulidae, Tapiridae, Rhinocerotidae* and *Proboscidea* (see p. 39 and fig. 30). In the *Equidae* they are only present from the 18th thoracic up to 4th lumbar vertebra. Besides the mobility is limited by the accessory articulations between the transverse processes of the last lumbar vertebrae and the first sacral vertebra (*Equidae, Rhinocerotidae, Proboscidea,* many big *Artiodactyla*), although these articulations in the first place limit the mobility in the lateral direction. In the *Rhinocerotidae* and *Proboscidea* there is no diaphragmatic vertebra, all vertebrae possess zygapophyses of the tangential type; moreover the lumbar region of these animals is very short (fig. 109).

From the data given in table 3 it follows that the epaxial musculature of the Ungulates in the first place shows the general tendencies characteristing this musculature in all terrestrial mammals, viz.: the development of long fascicles and the shifting of the insertion into the neural spines. The musculature of the Ungulates, however, is especially characterised by the tendency to a shifting of the insertion of the tendons of the m. longissimus dorsi from the neural spines of the lumbar into those of the sacral vertebrae. In *Tragulus* and *Hippopotamus* the tendons of the longissimus inserted into the lumbar spines show already a weaker development than those inserted into the sacral vertebrae. In *Cervus, Odocoileus, Gazella* and *Capra* this difference in the development is very striking and in *Bos* and the *Proboscidea* the muscle is only inserted into the sacral spines (fig. 62).

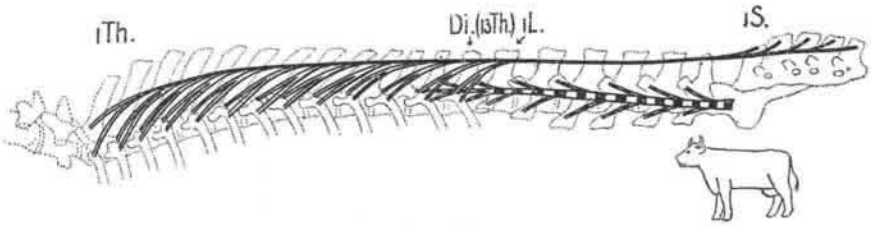


Fig. 62.
Schematic drawing of the structure of the m. longissimus dorsi in the cow, *Bos taurus* L. (dom.). Origin white, insertion black. M. ilio-lumbalis black and white. The muscle is only inserted into the ilium and the sacral spines.

At the same time the insertion of the m. spinalis is extended into the sacral vertebrae (fig. 52).

It will be quite evident now, that this phenomenon is connected with the limitation of the mobility of the body-axis to the lumbo-sacral joint. It is highly probably that this limitation, as well as the fact that many Ungulates are very heavy animals, may also be connected with the development of the gluteal tongue (see p. 55). For this gluteal tongue too is able to stretch the lumbo-sacral joint. This opinion is supported by the fact that in the bipedal goat the gluteal tongue was twice as long and much thicker than in the normal one [see SLIJPER (1942)].

In connection with the limitation of the mobility of the body-axis the

epaxial musculature of the Ungulates also shows a marked tendency to a reduction of the fleshy and a better development of the tendinous elements of these muscles. More and more they get the character of a tension-musculature. In the heaviest Ungulates that have the most immovable body-axis, the epaxial musculature even may show a very marked reduction. The animals move forward practically entirely with their legs. So CRILE (1941), who dissected a great many mammals, was especially struck by the fact that in the elephant and the rhinoceros the masses of muscle were concentrated in five areas of the body — the head and the four legs —, while only a narrow strip of muscle extended along the length of the spine.

## C. The body-axis of the hanging-climbing and the bipedal walking Primates.

### 1. *Locomotion, posture.*

BÖKER (1935), PRIEMEL (1937), SLIJPER (1941) and other authors have shown that among the climbing Primates two types of locomotion may be distinguished: the walking-climbing and the hanging-climbing. Walking-climbing monkeys chiefly move forward in the direction of the branches of the trees by a manner of locomotion that is shown in fig. 63. The body is supported alternately by 4, 3 or 2 (diagonal) legs that grasp the

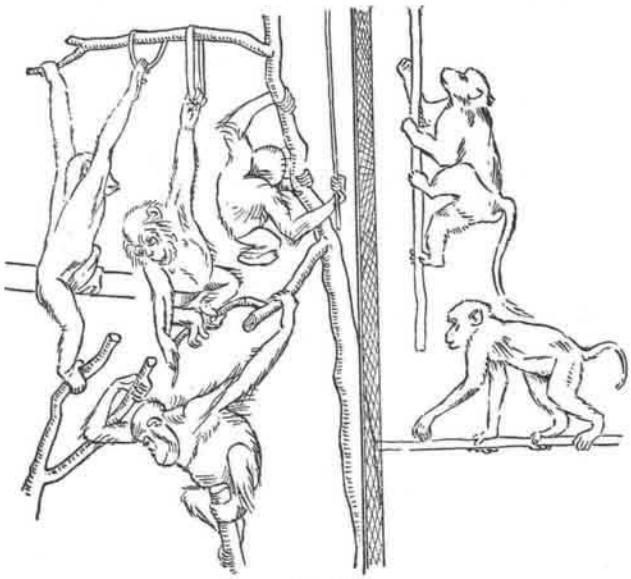

Fig. 63.
Left: hanging-climbing apes; motion-studies of orang-utan, *Pongo pygmaeus* (Hoppius) and chimpanzee, *Pan paniscus* Schwartz. Right: walking-climbing monkeys; motion-studies of macaque, *Nemestrinus nemestrinus* (L.) and baboon, *Papio cynocephalus* (L.). After BREHM (1891), CORNISH and MUYBRIDGE (1899).

branches by means of their prehensile hands and feet. A great many of these animals is digitigrade, not only when they are moving forward swiftly, but also when they are standing. This type of locomotion is shown by all Primates with the exception of *Ateles*, the *Hylobatidae*, the *Pongidae* (anthropoid apes) and man.

*Ateles*, the *Hylobatidae* and the *Pongidae* are hanging-climbing animals. They move

forward chiefly perpendicular to the direction of the branches, either by means of all four extremities or only by means of the upper ones. The animals that move chiefly by means of all four extremities (chimpanzee, gorilla; also some big *Cercopithecidae*) push off with their hind legs and then grasp the branches and pull themselves up with their arms (fig. 63). The gibbon, the orang utan and *Ateles* hang from the branches of the trees by means of their arms only. When moving forward they swing themselves from branch to branch almost without the aid of the hind legs. There is, however, no distinct limit between these two types of hanging-climbing locomotion. For the chimpanzee uses the swinging type of climbing when he is moving from tree to tree in stead of the pushing off with the hind legs as all leaping monkeys do [see NISSEN (1932)].

All hanging-climbing Primates are characterised by the upright posture of the body during this locomotion. Adaptations in their structure to this upright posture are chiefly a shortening, broadening and dorso-ventral flattening of the trunk and a special shortening of the lumbar region [position of the centre of gravity; see VAN DEN BROEK (1908), KEITH (1923, 1940), PRIEMEL (1937), SLIJPER (1941) and fig. 115, 116]. Besides the anthropoid apes are characterised by their prehensile hands.

Man is the only mammal that walks on its hind legs with a trunk evenly balanced in a vertical position on these legs. The same adaptations to the upright posture that have been described above are also found in man.

## 2. *Mobility of the vertebral column.*

From experiments with the vertebral column (see table 4) and from observations about the manner of locomotion of different species of monkeys, made in zoological gardens, it appeared that the mobility of the back of walking-climbing monkeys is principally the same as that of the quadrupedal terrestrial mammals that can move forward in a leaping-gallop (compare fig. 64 with fig. 55 and 57). The ordinary manner of locomotion of these monkeys on the ground is a kind of trot. In this pace the back practically shows no movements. When the animals climb or leap on the rocks or in the trees, they use also in the first place their arms and legs. Besides, however, very distinct movements of the back may be observed. Some species [for example *Cebus capucinus* (L.)] are able to stretch their back so far that it shows a distinct dorsal-concave shape. In *Comopithecus hamadryas* (L.) the concavity was very small and in *Cercopithecus aethiops sabaeus* (L.) the back was quite straight when it was maximally stretched (fig. 64). Generally it may be said, however, that all these animals show a very striking mobility of the back in the diaphragmatic (usually also the anticlinal) region, just as the terrestrial mammals that move forward in a

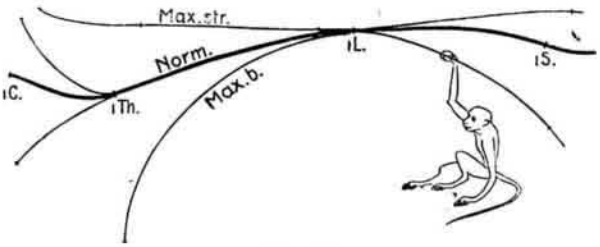


Fig. 64.
Experiments on the dorso-ventral flexibility of the vertebral column (with ligaments) of a monkey, *Cercopithecus* spec. See fig. 55.

leaping-gallop (fig. 55). When sitting the animals also show the characteristic hump in the anticlinal region (see p. 58 and fig. 59, 65).

Every one who is able to observe a climbing, walking or sitting anthro-

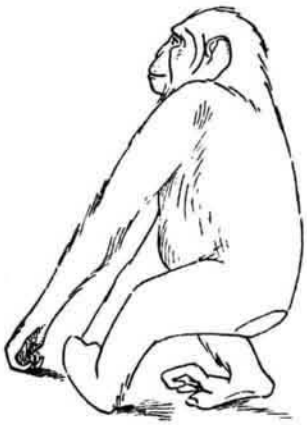

Fig. 65.
Upright walking chimpanzee, *Pan paniscus* Schwartz. After BREHM (1891).

poid ape, will immediately see that the mobility of their back differs in a very striking way from that of the walking-climbing monkeys [see VIRCHOW (1925) and the figures of BREHM (1914) or GIESELER (1936)].

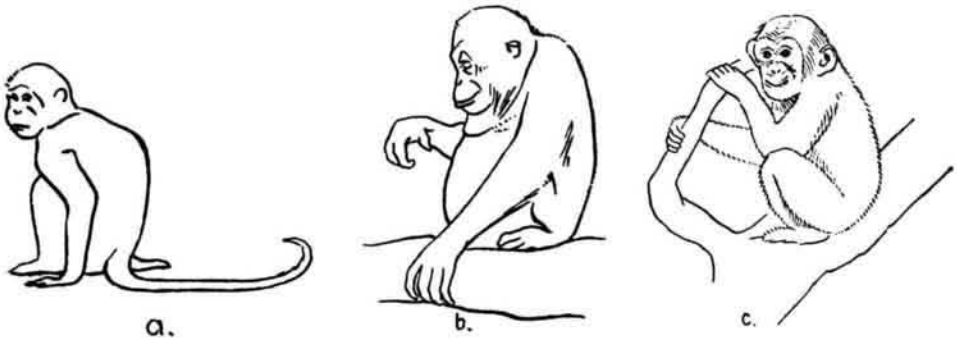


Fig. 66.
a. Mangabey, *Cercocebus fuliginosus* E. Geoffr.; b. orang utan, *Pongo pygmaeus* (Hoppius); c. chimpanzee, *Pan paniscus* Schwartz. The figure demonstrates the curved profile of the back in sitting monkeys and the straight back of sitting apes. After CORNISH and FLOWER (1891).

As it has also been shown by experiments with the vertebral column [see table 4 and VIRCHOW (1925)], the back shows only a very small mobility (fig. 67). When the animals are climbing, leaping or walking the back is almost perfectly straight (fig. 63, 65). The manner of sitting is quite different from that of the monkeys and the majority of the terrestrial mammals; they sit almost in the same way as man does, with their hands resting on the ground or on a branch. When sitting the back of the chimpanzee is perfectly straight, that of the orang utan is slightly bent, just as

the back of a man sitting at his writing-table (fig. 66). Even when the animals put their head between their hind legs, only a very slight curvature

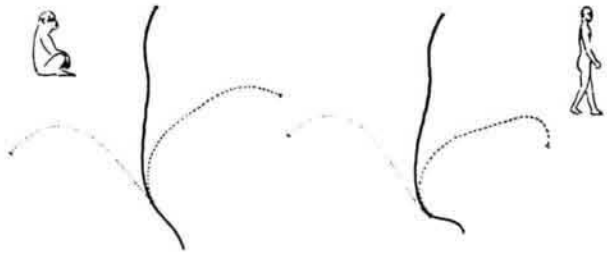

Fig. 67.
Experiments on the dorso-ventral flexibility of the vertebral column (with ligaments) of the chimpanzee, *Pan paniscus* Schwartz and man, *Homo sapiens* L. Black line: normal shape (in man "Eigenform"). Dotted lines: maximal flexibility in ventral (dorsal) direction. After BLUNTSCHLI (1912) and VIRCHOW (1911).

of the back can be seen. Practically all movements take place in the neck and the hip-joint.

As can be seen from the figures of FICK (1911; III, fig. 52—54, 60)

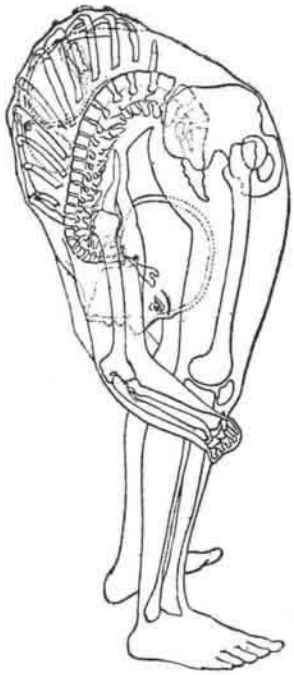

Fig. 68.
Skeleton and outline of the body of a contortionist, to demonstrate the small flexibility of the human thoracic vertebral column in the dorsal direction.
After FICK (1911).

and BLUNTSCHLI (1912), the mobility of the body-axis of the hanging-climbing mammals agrees quite well with that of man (fig. 67). Both show not only a very small mobility but also the very characteristic pheno-

menon that exactly the diaphragmatic region is almost the least mobile of the whole vertebral column (fig. 68, 69).

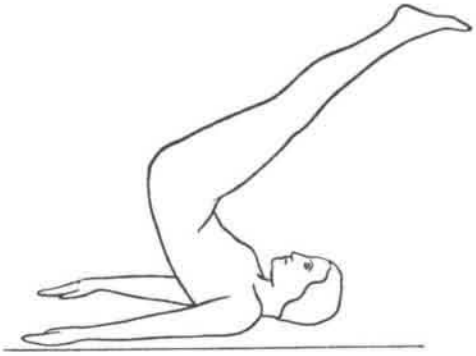

Fig. 69.
Outline of the body of a woman doing gymnastics, to demonstrate the small flexibility of the human thoracic vertebral column in the ventral direction.

3. *Epaxial muscles.*

The epaxial musculature of man and the anthropoid apes especially has been studied by EISLER (1912), VIRCHOW (1916), BRAUS (1921), PLATTNER (1922), FICK (1925), VALLOIS (1928), STEWART (1936), WINCKLER

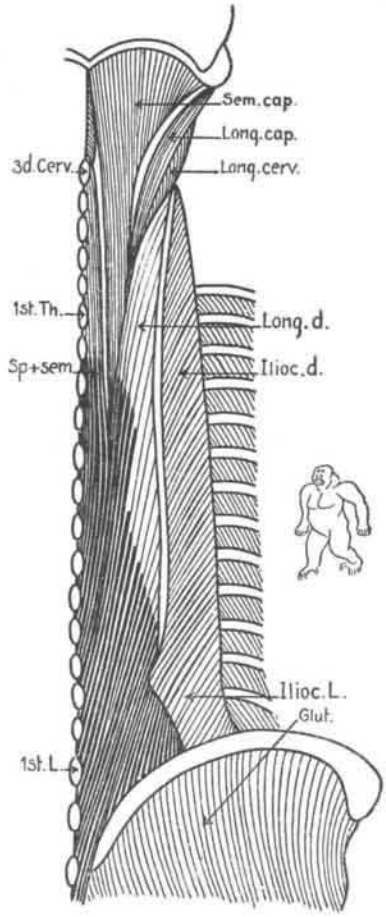


Fig. 70.
Epaxial musculature of a gorilla, *Gorilla gorilla* (Sav. et Wym.). Spinalis et semispinalis. Longissimus dorsi inserted into ilium and neural spines with very strong aponeurosis. Broad ilio-costalis dorsi. Broad ilio-costalis lumb. inserted into ilium, partly separately and partly by means of the aponeurosis of the longissimus.

(1937, 1938, 1939), NISHI (1938) and KEITH (1940). I completed these researches by the dissection of a 9½ years old male of the gorilla (fig. 70). These investigations have shown that, in adaptation to the upright posture of the animals and the very small mobility of their back, the epaxial musculature shows the following characteristic differences from that of the walking-climbing monkeys [1]):

1st. An increase in strength of the m. erector spinae, since in these upright going and comparatively heavy animals the muscles of the back will sooner get tired than in their quadrupedal relatives (see p. 41). 2d. A marked tendency to a separation of the m. ilio-costalis from the m. longissimus and to a broadening and strengthening of the m. ilio-costalis. In the gorilla, for example, almost all tendons of this muscle are inserted into the ilium and almost none into the neural spines. This may be connected with the general broadening of the body. 3d. A very striking tendency to the extension of the area of insertion of the m. longissimus dorsi from the postdiaphragmatic into the praediaphragmatic region. The same characteristic may be observed with regard to the m. semispinalis (fig. 71, 72).

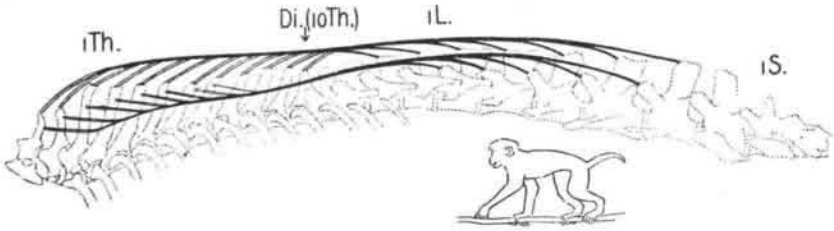


Fig. 71.
Schematic drawing of the structure of the m. transverso-spinalis in the macaque, *Nemestrinus nemestrinus* (L.). See fig. 55. Spinalis and semispinalis originating at prae- and inserted into postdiaphragmatic vertebrae. See also fig. 72.

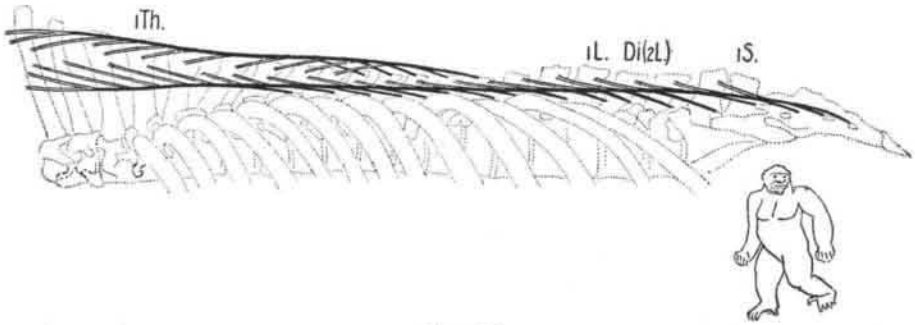


Fig. 72.
Schematic drawing of the structure of the m transverso-spinalis in a gorilla, *Gorilla gorilla* (Sav. et Wym.). See fig. 55. Origin and insertion of spinalis and semispinalis completely independent of diaphragmatic vertebra. See also fig. 71.

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1) The epaxial musculature of these monkeys practically shows the same characteristics as that of the terrestrial mammals, moving forward in a leaping-gallop (see p. 56).

This is evidently connected with the decrease of mobility in the diaphragmatic region. 4th. The same may be said of the very marked reduction of the m. spinalis, since this muscle especially causes the movements on the diaphragmatic region (fig. 71, 72). 5th. A very marked increase in size of the m. semispinalis and the m. multifidus, especially in proportion to the m. longissimus. Especially in the lumbar region these muscles are very strongly developed, but in the neck and the anterior thoracic region their development is also stronger than in the quadrupedal monkeys. The m. spinalis cervicis, on the contrary, is usually only weakly developed and may even be completely absent [gorilla; see also VON EGGELING (1922)]. Thus, with decreasing mobility of the back, a decrease of the long motion-musculature and an increase of the tension-musculature may be observed (see also p. 63).

D. The body-axis of the bipedal jumping mammals.

The kangaroos (*Macropodidae*), the elephant-shrews (*Macroscelides*), the jumping-hares (*Pedetidae*) and the jumping-mice (*Dipodidae*) are characterised by the fact that they move forward on their hind legs in a jumping manner. The body-axis shows a semi-upright position, the fore-legs are usually very short and the body is counterbalanced to a certain degree by the long tail. In opposition to the hanging-climbing and the upright walking mammals the body-axis of these animals shows the same kind and degree of mobility that has been described on page 58 for the quadrupedal terrestrial mammals moving forward in a leaping-gallop (fig. 55, 57). As can be seen in fig. 73, the mobility of the vertebral column of

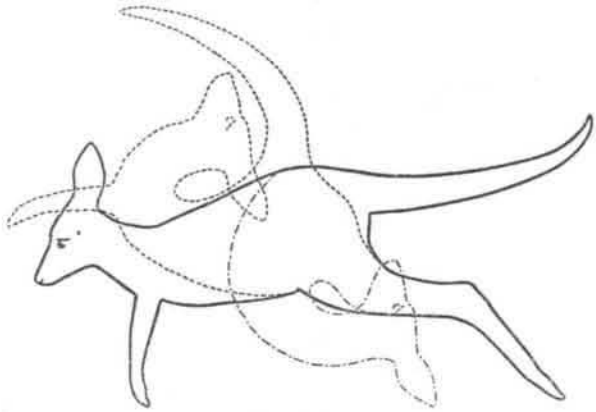

Fig. 73.
Experiments on the flexibility of the body of the common gray kangaroo, *Macropus giganteus* Zimm. See also fig. 57. Black line: normal shape. Dotted lines: maximal dorsal and ventral flexibility.

the kangaroo (*Macropus giganteus* Zimm.) was even very large, especially in the diaphragmatic region. Also the epaxial musculature does not show any characteristic differences from that of the quadrupedal mammals, with

the exception of the accessory m. semispinalis in the lumbar region of the kangaroo (p. 55).

## E. The body-axis of the flying mammals.

Experiments about the mobility of the vertebral column of the *Chiroptera* up to this day have not been made. In general, however, it may be said that the mobility of the back of bats is very small, just as in birds [SLIJPER (1941)]. This phenomenon is evidently connected with the very striking reduction of the epaxial musculature. After VALLOIS (1923) the m. spinalis, semispinalis and ilio-costalis dorsi are completely absent, the m. longissimus dorsi and the m. ilio-costalis lumborum are only poorly developed. The musculature of the neck, however, shows a very strong development.

## F. The body-axis of the aquatic mammals.

### 1. *Locomotion.*

With the exception of man, and probably also of the anthropoid apes, the centre of gravity of all mammals is situated at such a point of the body that, if the animals are going into the water, their nostrils are always just above the surface of the water [KRÜGER 1940 c)]. This enables them to swim by means of the normal walking-movements of their limbs. This manner of walking-swimming with all four limbs can also be observed in a great number of semi-aquatic mammals, as for example in the polar bear, the capybara, the hippopotamus, the platypus and especially in a number of Marsupials, Rodents and Insectivores [see BÖKER (1935), HOWELL (1930), KNESE (1936)]. Some of these animals swim chiefly with their fore-legs (*Thalarctos, Ornithorhynchus*), but the majority of them chiefly use the hind legs and support the movements of these legs by different movements of the tail, as for example *Latax lutris* (L.), *Castor canadensis* Kuhl [BOHMANN (1939)], *Ondatra zibethica* (L.) [KÖRTLER (1928), MIZELLE (1935)] and many aquatic Rodents, Insectivores and Marsupials [KNESE (1936), HOWELL (1930), BÖKER (1935)]. Since all these mammals show a perfect terrestrial locomotion too, their trunk and their vertebral column do not show very characteristic adaptations to the aquatic locomotion [see for example BOHMANN (1939)].

These adaptations, however, may be observed indeed in those semi-aquatic mammals that swim almost or perfectly without the aid of their limbs but only or chiefly by means of undulating movements of their body and tail. Some of these mammals also move forward on the land quite well, as for example *Lutra* and the other *Lutrinae* [aquatic locomotion by means of undulating movements in a vertical plane; HOWELL 1930)], or the Insectivores *Potamogale, Limnogale* and *Desmana* [aquatic locomotion by means of undulating movements in a horizontal plane; ABEL (1912)].

The *Pinnipedia,* however, move forward on the land only in a very helpless manner since their limbs are transformed into flippers. Among these semi-aquatic mammals the sea-lions (*Otariidae*) are better adapted to the terrestrial locomotion than the seals (*Phocidae*). In different zoological gardens I made observations about the swimming-movements of these animals; very beautiful records, however, could be obtained by studying the film, made in the Royal Zoological Garden "Artis" at Amsterdam by mrss PORTIELJE and VERKRUYSEN. When swimming, the Pinnipeds stretch their fin-like hind limbs in a backward direction as far as possible and then put the soles of their feet together in the median plane (fig. 74). So these hind limbs may serve as a kind of vertical tail-fin. The flippers (fin-like fore-limbs) are practically only used in steering. When swimming slowly, the sea-lions move forward by means of undulating movements of their whole body in a vertical plane. When swimming swiftly, however, one can observe practically only undulating movements of the hind part of the body and the hind limbs

in a horizontal plane. This is also the manner of swimming of the seals. The direction of the feet is not quite vertical but somewhat inclined, so that they cause a kind of sculling-movement [see also LANGWORTHY, HESSER and KOLB (1938)].

The purely aquatic mammals (*Cetacea* and *Sirenia*) have a snake- (some *Archaeoceti*)

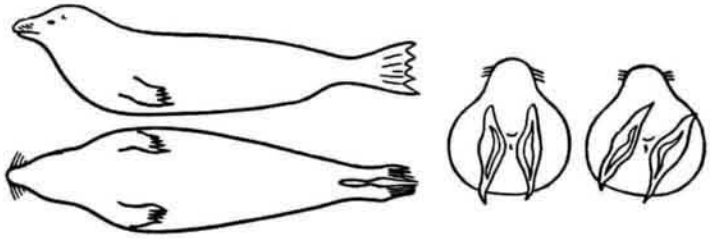

Fig. 74.
Lateral, ventral and caudal view of the body of the common seal, *Phoca vitulina* L., to demonstrate the position of the hind legs. After LANGWORTHY, HESSER, KOLB (1938).

or torpedo-like body with a long tail, provided with a horizontal tail-fin. This fin is an outgrowth of the skin and the underlying, very strong and fibrous connective-tissue. The fibres of this tissue are intimately connected with the tendons of the tail-musculature, so that these muscles are able to place the fin in every desired position [ROUX (1883) and fig. 79, 80]. The flippers are only used in steering [DRUZHININ (1924)]. Observations of swimming porpoises and dolphins [SLIJPER (1936)] and especially the experiments of SHOULEJKIN, NARKHOV (1939) and STASS (1939) with *Delphinus* and *Tursiops* have shown that these animals make only very little movements with their body (fig. 76). The principal manner of locomotion is a kind of sculling-movement with the tail, in a vertical as well as in a horizontal plane [see also KELLOGG (1928): "the flukes cut the water laterally and obliquely downward].

## 2. *Mobility of the vertebral column.*

Experiments about the mobility of the vertebral column of aquatic mammals up to this day have only been made with the common porpoise [*Phocaena phocaena* (L.), see SLIJPER (1936; p. 251, fig. 116—117) and fig. 76]. A certain impression about this mobility, however, may be obtained by studying the factors limiting it, viz.: the zygapophyses, the metapophyses and the neural spines (fig. 119, 120). A survey of these factors is given in table 5. I must, however, admit at once that these characteristics only may give a very rough impression about the mobility; several other factors, that are yet unknown, may influence it to a comparatively high degree (see also p. 112).

From table 5 it may be seen that in the *Lutrinae* and the *Pinnipedia* these characteristics do not differ from that of the terrestrial mammals. Nevertheless the mobility of the vertebral column of the *Otariidae* in the ventral direction (dorsal concave) is much higher than in the land-mammals. This may be illustrated by the photographs published by VIRCHOW [1925; fig. 2; *Zalophus californianus* (Lesson)] and especially by KRUMBIEGEL (1933; *Macrorhinus angustirostris* Gill, *Macrorhinus leoninus* L.; see also fig. 75). These photographs show that the prae- and postdiaphragmatic

regions of the vertebral column are not bent very much, but that an extremely high bending of the back is possible in the diaphragmatic region.

The history of the *Cetacea* and *Sirenia* shows that in these orders of

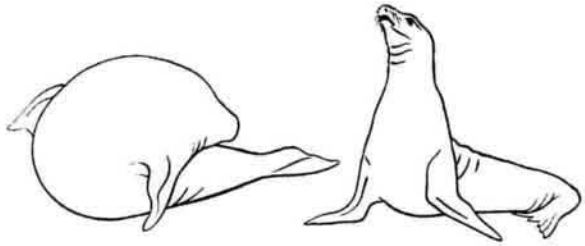

Fig. 75.
Left: sea-elephant, *Macrorhinus leoninus* (L.), curving its back very strongly in the dorsal direction (dorsal concave) to catch a fish lead down on its crupper. After KRUMBIEGEL (1933). Right: rising sea-lion, *Zalophus californianus* (Lesson), to demonstrate the flexibility of the back in the dorsal direction (dorsal concave).

mammals, with progressive adaptation to the life in the water, either the sudden change in the position of the zygapophysial articular facets has disappeared, or even that the number of the zygapophysial joints themselves has been reduced. The number of vertebrae provided with these joints, becomes smaller and smaller and in the *Mystacoceti* only the 4 or 5 first thoracic vertebrae are connected by articulating zygapophyses or even only by syndesmoses. In the *Ziphiidae* the number of articulating vertebrae is also very small and in the *Physeteridae* the zygapophysial joints may be completely absent. It is highly probably that the reduction of the zygapophyses causes a greater mobility of the vertebral column. But it is equally probably that, especially in the *Platanistidae, Delphinidae* and *Phocaenidae,* this mobility, at least in the sagittal direction, is reduced again. This reduction is not only caused by the increase of the number of articulating vertebrae, but also by the high neural spines that are placed so closely together that they touch one another when the back is slightly overstretched (dorsal concave). In some species the metapophyses embrace the foregoing neural spines. This reduces the mobility in the lateral direction.

These considerations are quite in accordance with the data of BÖKER (1935), NARKHOV (1939) and STASS (1939) and the experiments of SLIJPER (1936) that have shown, that the thoracic and lumbar region of the porpoises and dolphins (*Phocaenidae* and *Delphinidae*) is comparatively stiff and that the swimming movements almost completely are exercised by the tail (fig. 76). It is, however, not improbable that the *Mystacoceti* and *Ziphiidae,* where no limiting factors are present and either the thorax (*Ziphiidae*) or the sternum [*Mystacoceti*; see SLIJPER (1936)] are very short, show a greater mobility of their trunk and that they swim by means of a kind of undulating movements of the whole body and tail. Experiments

and observations on living animals to prove this supposition, however, must still be made.

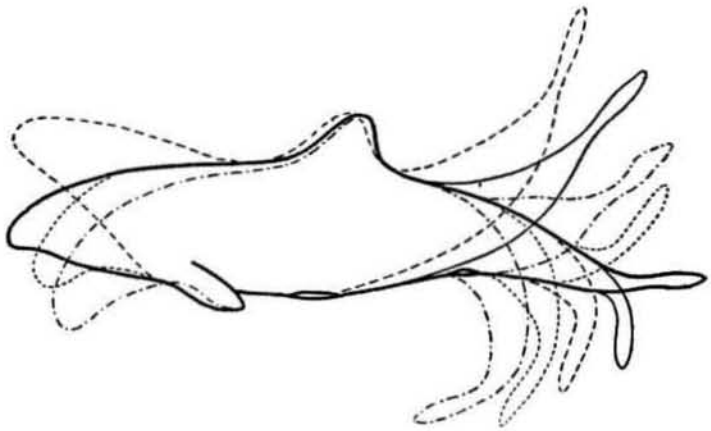

Fig. 76.
Experiments on the dorso-ventral flexibility of the body of the common porpoise, *Phocaena phocaena* (L.). Thick black line = normal shape. Remark the small flexibility of the thoracic region. After SLIJPER (1936).

### 3. *Epaxial muscles.*

To study the musculature of the aquatic mammals, I dissected specimens of *Lutra lutra* (L.), *Zalophus californianus* (Lesson) (fetus), *Phoca vitulina* L., *Dugong australis* (Owen) (fetus), *Trichechus inunguis* (Natt.), *Balaenoptera musculus* L. (fetus), *Balaenoptera acutorostrata* (Lacép.) (fetus), *Delphinapterus leucas* (Pallas) (fetus) and *Phocaena phocaena relicta* Abel (fetus). Previously I had already dissected specimens of *Pseudorca crassidens* (Owen) [see SLIJPER (1939)], *Hyperoodon ampullatus* (Forst.), *Orca orca* L., *Grampidelphis griseus* (Cuv.), *Delphinus delphis* L., *Tursiops truncatus* (Mont.) and *Phocaena phocaena* L. [see SLIJPER (1936)]. Some data were also available of *Balaenoptera borealis* Lesson [SCHULTE (1916)], *Kogia breviceps* Blainv. [SCHULTE and SMITH (1918)], *Monodon monoceros* L. [HOWELL (1930 a)], *Globicephalus melas* Trail [MURIE (1874)], *Lagenorhynchus albirostris* Gray [MURIE (1873)] and *Meomeris phocaenoides* Cuv. [HOWELL (1927)] [see also SLIJPER (1936; table 16)].

All aquatic mammals possess neither a ligamentum nuchae nor a ligamentum supraspinale or ligamenta interspinalia. The mm interspinales are very well developed.

In the majority of the aquatic mammals the m. ilio-costalis is very strongly developed. The ilio-costalis dorsi of *Lutra*, the *Sirenia* and the *Mystacoceti* is as narrow as in the land-mammals (fig. 79). In *Zalophus* it is already distinctly broader and in *Phoca* it is the broadest of the three epaxial muscles and covers a third part of the ribs (fig. 77). In the *Odontoceti* the muscle is expanded as a thin sheet over the whole lateral surface of the ribs and often reaches the sternum with its ventral border [see fig. 80 and SLIJPER (1936)]. The ilio-costalis lumborum is especially well developed in the *Pinnipedia* and the effect of the muscle is still enlarged by the shape of the ala ilii, which projects laterally in a very characteristic way (fig. 78). In the *Cetacea* and *Sirenia* the ilio-costalis lumborum is comparatively narrow (fig. 79, 80), but its effect is highly enlarged by

the very long transverse processes. With the exception of *Trichechus*, the ilio-costalis lumborum of the representatives of these orders is completely

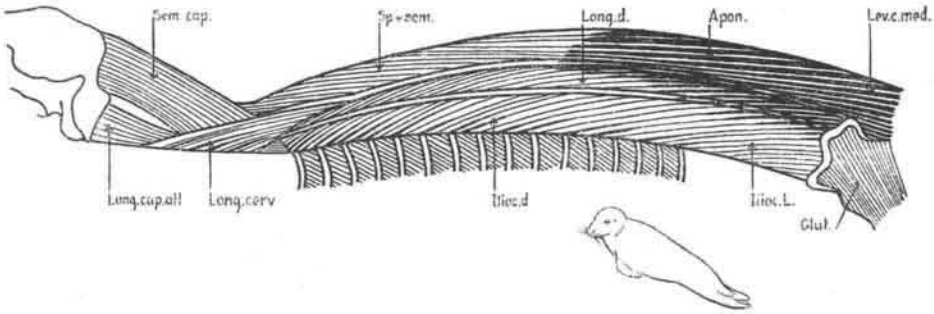


Fig. 77.
Epaxial musculature of the common seal, *Phoca vitulina* L. Spinalis et semispinalis. Spinalis-fibres inserted into neural spines with strong aponeurosis. Longissimus chiefly inserted into metapophyses, some aponeurotic fibres fused with aponeurosis of spinalis. Almost separate and very broad ilio-costalis lumb., inserted into laterally projecting ala ilii. Comparatively broad ilio-costalis dorsi.

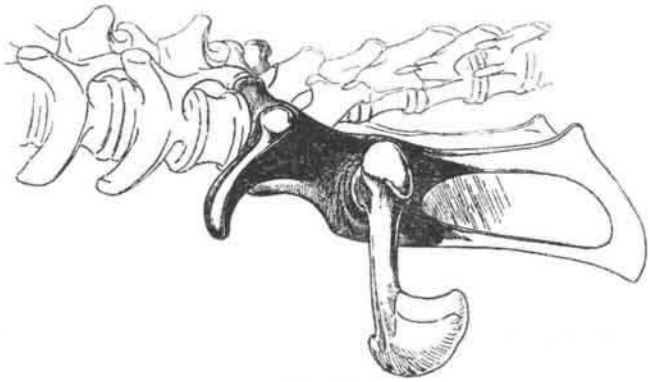

Fig. 78.
Last lumbar vertebrae and pelvis of the common seal, *Phoca vitulina* L., to demonstrate the laterally projecting ala ilii.

fused with the m. intertransversarius caudae dorsalis [see SLIJPER (1936)]. The cranial end of the ilio-costalis dorsi is fused with the m. ilio-costalis cervicis. Thus in these animals there is a continuous ilio-costalis from the atlas up to the tail-fin; *Kogia* even possesses an ilio-costalis capitis. In the *Pinnipedia* and *Dugong* the ilio-costalis lumborum is still a little connected with the m. longissimus, but in *Lutra*, the *Cetacea* and *Trichechus* it is quite a separate muscle that has lost entirely its insertion into the metapophyses and the neural spines. All the above-described characteristics may evidently be considered as adaptations to the lateral mobility of the body, which is much greater than in the terrestrial mammals (see p. 70).

Just as the m. ilio-costalis dorsi, the m. longissimus dorsi of the aquatic

mammals also shows a marked tendency to fuse with the homologous muscles in the neck and tail. A separate longissimus cervicis and capitis has been found in *Lutra*, the *Pinnipedia*, *Dugong*, *Balaenoptera musculus*

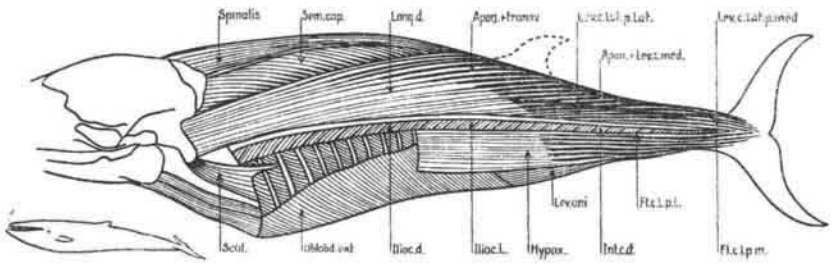


Fig. 79.

Musculature of the trunk and tail of the lesser rorqual, *Balaenoptera acutorostrata* Lacép. Obliquus abd. ext. partly removed to show the m. hypaxialis. Remark the complete fusion of the muscles of the trunk with the correspondant muscles of the tail. Special type of spinalis, originating at the occiput and inserted into the thoracic neural spines. Longissimus dorsi completely fused with long. cerv. et cap. Transverso-spinalis and levator caudae medialis completely covered by the strong aponeurosis of the longissimus. Comparatively narrow ilio-costalis dorsi (compare fig. 80).

L., *Balaenoptera borealis* Lesson, *Delphinapterus*, *Monodon* and *Kogia*. They are completely fused with the longissimus in *Balaenoptera acutorostrata* (Lacép.) [CARTE and MACALISTER (1868), however, found a separate longissimus cerv. et cap.], the *Delphinidae* and *Phocaenidae* (fig. 79, 80). In the *Pinnipedia* the longissimus dorsi is inserted into the ilium, but also partly fused with the extensor caudae lateralis (fig. 77). In these animals the tail-muscles, however, are only poorly developed. In *Lutra* the muscle has no insertion into the ilium, it is completely fused with the extensor caudae lateralis. This is also the case in the *Cetacea* and *Sirenia* (fig. 79, 80). By these fusions a mighty muscular complex has come into existence,

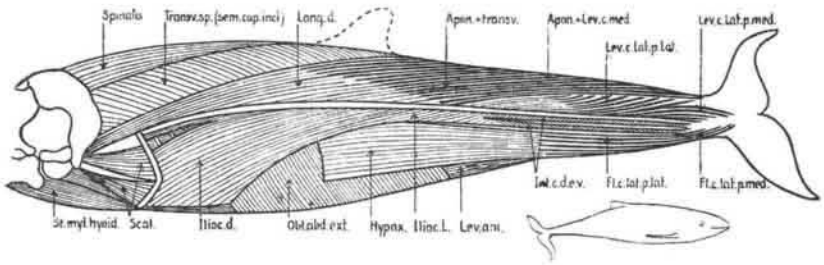


Fig. 80.

Musculature of the trunk and tail of the common porpoise, *Phocaena phocaena* (L.). Obliquus abd. ext. partly removed to show the m. hypaxialis. See also fig. 79. Characteristic differences with the musculature of the lesser rorqual (fig. 79) are: m. ilio-costalis dorsi expanded over the whole lateral surface of the thorax. Both intertransversarii caudae dorsalis and ventralis present.

whose origin reaches from the back part of the skull into the middle of the tail.

In the *Cetacea* there are three systems of enserting tendons, viz. (see also table 3, note 29):

1. Superficial tendons, inserted into the summits of the neural spines. They are homologous with the superficial tendons of the terrestrial mammals. In *Lutra* they are only present at the lumbar, sacral and anterior caudal vertebrae. In the *Cetacea* they reach from the first lumbar vertebra up to a point that lies a little cranial of the tail-fin, and in the *Sirenia* they are even present in this fin.

2. Deep tendons, inserted into the metapophyses, homologous with the corresponding tendons of the m. longissimus and extensor caudae lateralis of the land-mammals [m. extensor caudae lat. pars medialis; SLIJPER (1936)]. In the *Cetacea* these tendons are usually present from the first thoracic vertebra up to the cranial border of the tail-fin. In *Lutra* and *Dugong* the cranial point of insertion lies at one of the last thoracic or at the first lumbar vertebra, but in the *Pinnipedia* and *Trichechus* the insertion begins already at one of the anterior thoracic vertebrae. Thus the aquatic mammals show a distinct shifting forward of their metapophysial inserting tendons. This phenomenon may be connected with the disappearance of the diaphragmatic vertebra and the special mobility that is connected with the existence of this vertebra in the land-mammals (see also p. 72). In *Lutra*, the *Pinnipedia* and the *Sirenia* these tendons are present up to the tip of the tail.

3. But in the *Cetacea* a separate system of long tendons has been differentiated, which inserts only into the vertebrae of the tail-fin [m. extensor caudae lateralis pars lateralis; SLIJPER (1936)]. These tendons may be considered as a continuation of both the superficial and the metapophysial tendons. Their existence is evidently connected with the sculling-movements of the tail, which may be highly influenced by the different inclination of the lobes of the tail-fin.

In the *Pinnipedia* the metapophysial tendons are much better developed than the superficial ones. This is evidently connected with the fact that the neural spines of the lumbar region are very short, the metapophyses, on the contrary, very well developed. Besides, in *Phoca* the metapophyses project very markedly in the lateral direction, a fact that may be considered as an adaptation to the swimming-movements of the body that are chiefly exercised in the horizontal plane, while the sea-lions can also swim by means of vertical movements (see p. 70).

Very strong metapophyses and comparatively low neural spines are found in the posterior lumbar and caudal region of the *Archaeoceti*. This phenomenon may perhaps be considered as an indication that, especially the snake-like species among them, at least partly moved forward by means of undulating movements in the lateral direction. In the *Sirenia* and *Odontoceti* the superficial tendons are usually as strongly developed as the metapophysial ones and in the *Mystacoceti* they are even stronger than the metapophysial tendons. For in the *Cetacea* and *Sirenia* the lateral movements are not of so much importance as in the *Pinnipedia*. The movements chiefly take place in the vertical plane. The lever of the inserting tendons of the m. longissimus of the *Cetacea* and *Sirenia* not only is lengthened by the very distinct lengthening of the lumbar neural spines, but in some families of the *Cetacea* (*Physeteridae, Eurhinodelphidae, Platanistidae, Delphinapteridae, Delphinidae, Phocaenidae*) also by a proces that I have previously described as the shifting-upward of the metapophyses in the lumbar region [SLIJPER (1936, chapter 14, II d., p. 415)]. At present I might give it as my opinion that the significance of this shifting upward is to obtain a longer lever for the metapophysial tendons and not to obtain a greater area of origin for the caudal part of the longissimus-complex.

In all aquatic mammals the m. transverso-spinalis is so intimately fused with the m. extensor caudae medialis that both muscles form one single

muscular complex. Although there is always a separate and well developed m. semispinalis capitis, in some *Cetacea* (*Delphinapteridae, Delphinidae*) the thoracic part of the m. transverso-spinalis reaches up to the skull and originates with comparatively strongly developed muscular fascicles at the occipitale. The dissection and the description of this transverso-spinalis-complex of the *Cetacea* is a very difficult task, since already in older fetusses its fascicles are intimately fused with that of the longissimus-complex. In consequence the descriptions of this muscle in literature are usually very inaccurate.

Dissections of Cetacean fetusses, made in the last five years, have shown that also the descriptions, given in my publications of 1936 and 1939, were not quite satisfactory. It has appeared that the muscular fascicles and tendons, described as extensor caudae lateralis pars medialis do not belong exclusively to the longissimus-complex, but that they contain also the long metapophysial tendons of the transverso-spinalis complex (extensor caudae medialis). This may also be evident from the description of MURIE (1874; p. 277, fig. 6; *Globicephalus melas* Trail), who says that the transverso-spinalis-complex (MURIE: "spinalis") is also inserted into the lumbar and caudal metapophyses, as well by means of short as by long tendons and that it is fused with the caudal continuation of the longissimus (MURIE: "conjoined spinalis dorsi and levator caudae internus"). Further it has appeared that the transverso-spinalis of the *Mystacoceti* in the lumbar region is better developed than one might conclude from the descriptions in literature.

Thus I might give the following new description of the transverso-spinalis complex of the *Cetacea* (see also table 6 and fig. 79, 80):

In all *Cetacea* there is an undifferentiated transverso-spinalis, reaching from the first cervical vertebra (in *Delphinidae* and *Delphinapteridae* even from the skull) up to the cranial border of the tail-fin. In the neck and thorax it consists almost quite or entirely of multifidus- and shorter fascicles; in the caudal part of the thorax the number of semispinalis-fascicles is increasing and in the lumbar and caudal region the muscular fascicles and tendons may even be very long. So into the metapophyses of the lumbar and caudal vertebrae are inserted short as well as long tendons. The long tendons are completely fused with the long metapophysial tendons of the m. longissimus dorsi and its caudal continuation, the m. extensor caudae lateralis (these fused muscles have previously been described under the name extensor caudae lateralis pars medialis).

Compared with that of the terrestrial mammals, the transverso-spinalis of the *Cetacea* is very strongly developed. Compared with the other parts of the muscle, the multifidus-fibres of the cervical and thoracic region of the *Mystacoceti* are only weakly developed, but the long fascicles of the lumbar and caudal region show a very strong development. In the *Odontoceti* already some long fibres have been found in the thorax, but their number is also increasing very distinctly in the lumbar region. Throughout the whole body-axis the muscle is very well developed. In the posterior lumbar region, however, of those *Odontoceti* that show a shifting-upward of their metapophyses [see p. 112 and SLIJPER (1936)], the area of origin of the muscle is diminished and in consequence the muscle in this region is less developed than in the other parts of the vertebral column.

The m. transverso-spinalis of the *Sirenia* is also intimately fused with the m. extensor caudae medialis. It is an undifferentiated transverso-spinalis, which in the dugong almost completely consists of multifidus- and shorter fascicles.

The transverso-spinalis of the aquatic mammals is further characterised by the fact that the semispinalis-fascicles originating at the prae- and inserted into the postdiaphragmatic vertebrae show a distinct tendency to disappear. As can be seen from table 6 they are still present in *Lutra*. In

the *Pinnipedia* a great number of semispinalis-fascicles is already inserted into praediaphragmatic vertebrae and in the *Cetacea* and *Sirenia* there is not the slightest relation to a diaphragmatic vertebra at all. This phenomenon is evidently connected with the kind of mobility of the vertebral column, which is quite different from that of the terrestrial mammals (see p. 58 and 72). The same phenomenon may be observed with regard to the m. spinalis, which in the land-mammals originates at the prae- and is inserted into the postdiaphragmatic vertebrae. In *Lutra* and the *Pinnipedia* this m. spinalis is already very weakly developed and in the *Cetacea* and *Sirenia* it is either entirely wanting, or there is a m. spinalis with a quite different origin (at the occipitale) and insertion (into the anterior thoracic vertebrae). It acts as a kind of fixator of the head. The spinalis of *Dugong* shows an intermediate position between that of the terrestrial mammals and the *Cetacea*.

To sum up, the body-axis of the aquatic mammals is characterised by the following adaptations to the swimming-movements (sculling-movements with the hind part of the body and the tail or with the tail only):

1. Disappearance of the diaphragmatic vertebra and the mutual mobility of the two regions of the vertebral column.

2. Corresponding disappearance of those fascicles of the longissimus, spinalis and semispinalis that originate cranial and are inserted caudal from the diaphragmatic vertebra. Development of a special type of spinalis.

3. Increasing mobility of the vertebral column, but decrease of this mobility again in the *Platanistidae, Delphinidae* and *Phocaenidae*, where the movements are almost limited to the tail.

4. Increase in length of the lumbar spines and transverse processes, shifting upward of the metapophyses in some Cetacean families (longer levers).

5. In all three systems of epaxial muscles there is a tendency to the development of very long fascicles with long tendons. The muscles reach from the skull to the tip of the tail. The m. transverso-spinalis is very strongly developed.

6. Separate m. ilio-costalis in adaptation to lateral movements.

# VI

# THE NEURAL SPINES

## A. General considerations.

On page 17 it has already been demonstrated that the direction of the neural spines only depends on the special demands of the muscles and ligaments inserted into them. The following three suppositions may serve as the starting-point for the considerations given in this chapter:

1st. The neural spines must be considered as levers, transmitting the force, exercised by the muscles and ligaments, to the vertebral bodies.

2d. The direction of the neural spines will be determined by the resultant of the muscular and ligamentous forces acting on them.

3d. The most favourable direction of the neural spines is the direction perpendicular to that of the muscular and ligamentous forces acting on them.

In 1798 this principle was already mentioned by BARTHEZ (1798), although he gave neither an explanation of the principle itself, nor a working-out of it with regard to the spinal musculature. The work of BARTHEZ, however, has attracted very little attention. His opinion has been adopted by STRASSER (1913; p. 24—25) and LE DOUBLE (1912; p. 410—412). The explanation of the principle with regard to the spinal musculature, given by these two authors, however, is quite incomprehensible. Thus is this chapter I shall try in the first place to explain why the above-mentioned suppositions must be true. In the second place the direction of the neural spines in the different species of mammals will be explained with the aid of the above-mentioned principle.

Although the fact that the neural spines serve as levers has not been mentioned very often in literature [EICHBAUM (1890), GMELIN (1925), BRAUS (1921), GRAY (1935)] it is so evident, that it needs no further explanation. The structure of the neural spines, the direction of the stress-lines of the spongiosa ["Spitzbogensystem", as in a beam supported at one end only; see BARDELEBEN (1874), ZSCHOKKE (1892), MURRAY (1936), GALLOIS et JAPIOT (1925) and fig. 81] and compacta [BRUHNKE (1929)] are quite in accordance with this conception.

There are two reasons why the direction of the neural spines perpendicular to that of the muscles and ligaments, is the most favourable. The first of these reasons is the fact that, if the neural spine shows this direction, a maximal effect is attained with a minimal length of the spine. Thus the reason may be called: economising of material. To explain this fact, we have to remember that the effect of a certain force depends on its moment, that is the product of force and arm ($P \times X$, fig. 82). The length of the

arm is represented by the length of the line drawn from the centre of rotation ($R$) perpendicular to the line representing the force ($P$). To

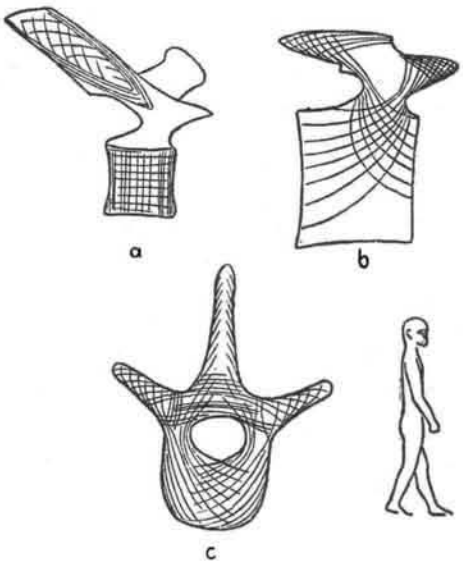


Fig. 81.
Schematic drawing of the direction of the spongiosa-lamellae in a thoracic vertebra of man. a. nearly median, b. sagittal, c. transverse section. After GALLOIS et JAPIOT (1925).

simplify the considerations we shall consider only the movements of one single vertebra, and then we may suppose that the centre of rotation is found somewhere in the intervertebral disc (fig. 82).

Now suppose that, if a certain muscular force $P$ is sufficient to move

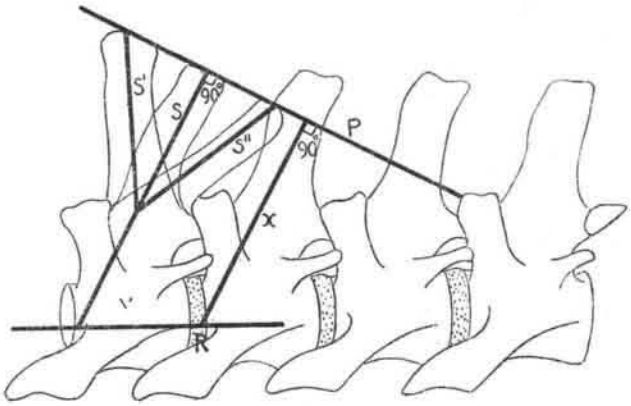


Fig. 82.
Schematic drawing of four lumbar vertebrae of a mammal to demonstrate that if only one muscle (P; in this case the m. multifidus) is attached to the neural spine, the direction of the spine perpendicular to that of the muscle is the most favourable (shortest spine).

the vertebra $V$, the arm must have a length $X$. Then fig. 82 shows without more that an arm $X$ is attained if the length and direction of the neural spine are represented by $S$, $S'$, $S''$. But this figure shows also without more

that the neural spine $S$, that is the spine perpendicular to the muscular force, is the shortest of all possible spines and thus saves most material. The moment of resistance ($^1/_6\, bh^2$) and in consequence the breadth (longitudinal diameter) and thickness (transverse diameter) of the spines are not influenced by the angle of insertion of the muscular force, since the force $P'$ may be resolved into a force that has the same direction as the spine ($b$) and a force ($a$) perpendicular to it (fig. 83). If a muscle is not inserted with

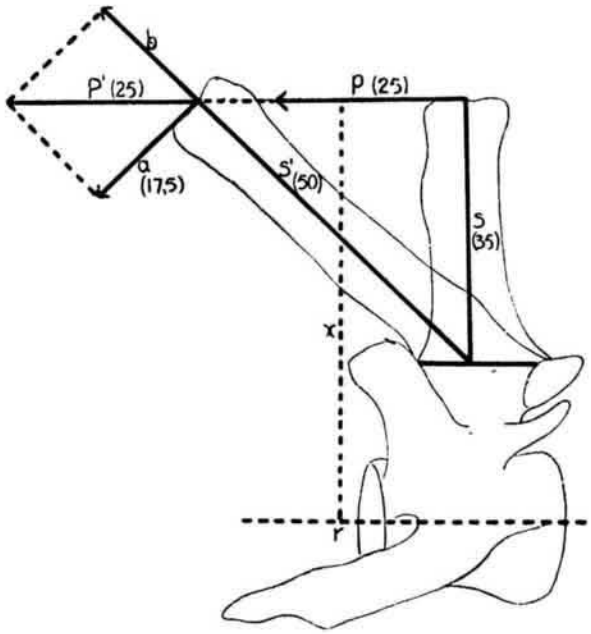


Fig. 83.
Schematic drawing of a lumbar vertebra of a mammal to demonstrate that the moment of resistance of the neural spine and consequently also its height and breadth, are not influenced by the angle between the spine and the muscle attached to it. The spine $S$ has to resist a force $S \times P = 25 \times 35 = 875$. The force $P'$ may be resolved in $a$ and $b$. $S'$ has to resist a force $S' \times a = 17{,}5 \times 50 = 875$.

a narrow tendon, but if it is attached to a comparatively large area of the neural spine, the most favourable direction of the neural spine will be the direction perpendicular to the highest fibre of the muscle, as is shown in fig. 84.

There is, however, no neural spine to which only one single muscle or ligament is attached. There are always two, but usually more muscles and ligaments, and thus we have to take into account several different forces, acting in different directions. In fig. 85 it is shown that, if a muscular force $P$ with an arm $X$ and an opposite force $q$ with an arm $y$ act on the same vertebra, the most favourable direction ($S$) of the neural spine will be the direction that is intermediate between that perpendicular to $P(S')$ and that perpendicular to $q(S'')$. In fig. 86, however, it is shown that this

intermediate position is only the most favourable one, if the point of intersection of the lines $P$ and $q$ lies between the lines $S'$ and $S''$, which are the lines drawn from the point $V$ perpendicular to $P$ and $q$. Fig. 86 shows

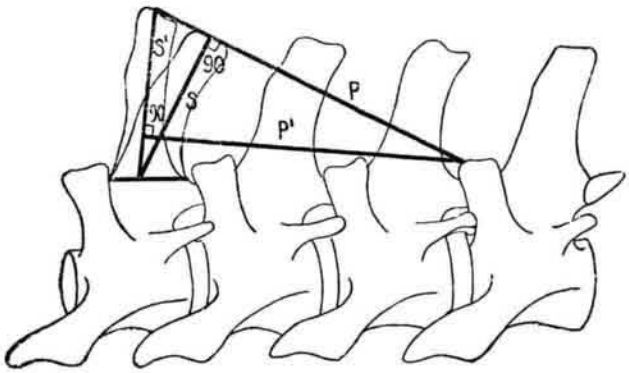


Fig. 84.

Schematic drawing of four lumbar vertebrae of a mammal with the m. multifidus inserted into one of the neural spines. The figure demonstrates that the direction ($S$) of the neural spine perpendicular to that of the highest fibre of the muscle ($P$) is the most favourable. For if the neural spine ($S'$) shows a direction perpendicular to the lowest fibre ($P'$), the spine must be longer.

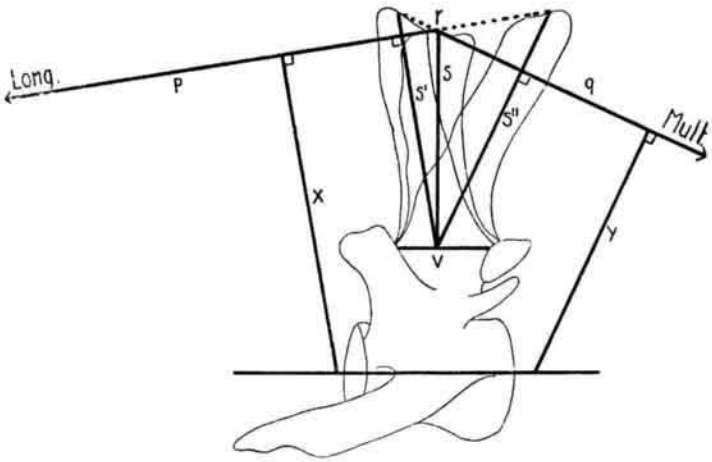


Fig. 85.

Schematic drawing of a lumbar vertebra of a mammal with two muscles with opposite action ($P$, m. longissimus dorsi; $q$, m. multifidus; lever-arms $x$ and $y$) inserted into the neural spine. The figure demonstrates that if the point of intersection ($r$) of $P$ and $q$ lies between $S'$ and $S''$, the direction of the neural spine represented by $S$ is the most favourable (shortest spine). See also fig. 97.

that, if this is not the case, the most favourable direction of the spine is the direction perpendicular to the line (representing the muscular force) that shows the highest point of intersection with the line $F$, erected in $V$ perpendicular to the longitudinal axis of the vertebral body. In this case

the neural spine is inclined to the side at which the muscle with the highest point of intersection is found.

Fig. 87 shows that the muscle with the highest point of intersection is the muscle whose origin lies closest to the vertebra of insertion ($q$ and $q'$), or the muscle that has the most remote centre of rotation ($P$ and $P'$; for example if a vertebra is almost immovably connected with its neighbours). The most important cause, however, for the shifting upward of the point

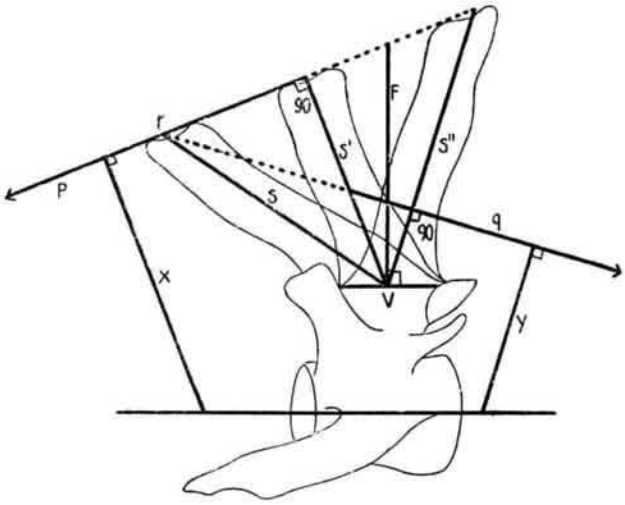


Fig. 86.

Schematic drawing of a lumbar vertebra of a mammal with two muscles with opposite action ($P$, m. longissimus dorsi; $q$, m. multifidus; lever-arms $x$ and $y$) inserted into the neural spine. The figure demonstrates that if the point of intersection of $P$ and $q$ ($r$) does not lie between $S'$ and $S''$, the most favourable direction of the neural spine ($S'$) is perpendicular to the muscle ($P$) that shows the highest point of intersection with the line $F$. $F$ is erected in $V$ perpendicular to the longitudinal axis of the vertebra.

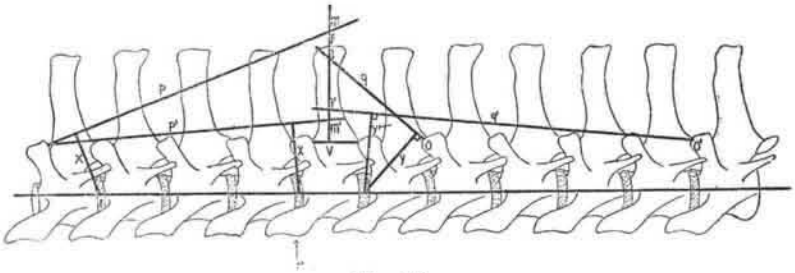

Fig. 87.

Schematic drawing of a series of lumbar vertebrae of a mammal with two muscles with opposite direction acting on the vertebra $V$ ($P$, $P'$, m. longissimus dorsi; $q$, $q'$, m. transverso-spinalis). The figure demonstrates: 1st, that if two muscles $q$ and $q'$ have the same lever-arm ($y$), the muscle ($q$) with the nearest point of insertion (o) shows the highest point of intersection with the line $F$. 2d, that if two muscles $P$ and $P'$ have the same lever-arm ($x$), the muscle ($P'$) with the nearest centre of rotation ($r'$) shows the lowest point of intersection ($m'$) with the line $F$. See also fig. 86.

of intersection will evidently be the increase in length of the arm. Generally we may suppose that, if the demands made on a certain muscle are increasing, the muscular force (the surface of the cross-section of the muscle), as well as the length of the arm will increase.

The length of the arm of a certain muscle, however, will not always depend on the demands made on the muscle and on the surface of its cross-section. It is also influenced by the length of the neural spine that is required by the other muscles, inserted into this spine. Suppose (fig. 88)

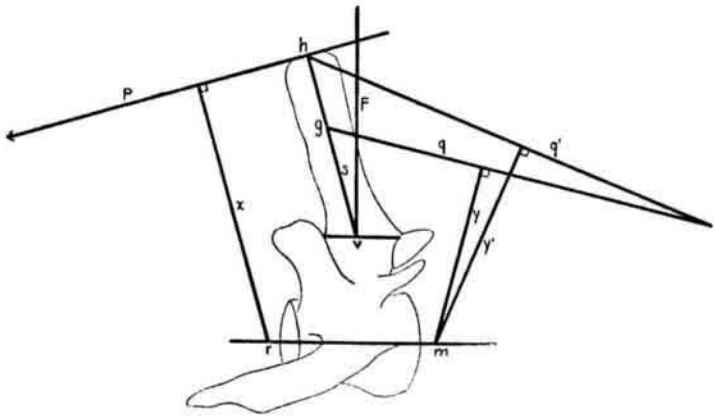


Fig. 88.

Schematic drawing of a lumbar vertebra of a mammal with two muscles with opposite action (*P*, m. longissimus dorsi, *q*, m. multifidus. The figure demonstrates that if *P* and *q* are attached to the neural spine, *P* shows the highest point of intersection with the line *F*. Consequently the most favourable direction of the neural spine will be perpendicular to *P*. In this case, however, *q* will not be attached at *g*, but at the summit of the spine *h*. Thus the lever-arm will be longer ($y'$) and the force can be proportionately diminished.

that a certain muscle $P$ with an arm $X$ and a certain muscle $q$ with an arm $y$ are inserted into a neural spine. Then $P$ has the highest point of intersection with $F$ and thus the neural spine will have a direction and a length represented by $s$. It will, however, be evident without more that in this case the area of insertion of the muscle $q$ will not end in the point $g$, but in $h$, that is the summit of the neural spine. Then the arm of the muscular force $q'$ is represented by $y'$ and the muscular force itself may proportionately be diminished.

Thus we may conclude that generally a neural spine will show the following directions:

1. Perpendicular to the direction of the muscle, if there is only one single muscle inserted into the spine.

2. An intermediate direction if there are two muscles that have an almost equal importance.

3. Perpendicular to the muscle that has the highest importance if the two or more muscles are not of an almost equal importance.

From the nature of the case, it is very difficult to obtain quite exact data about the importance of a muscle. For the present we must be satisfied to make a rough estimation, which is based on the thickness of the muscle and the position and extent of its area of insertion.

The second reason, why the direction of the neural spines is as perpendicular as possible to that of the muscles and ligaments, is based on the manner of insertion of the tendinous fibres and the structure of the bone.

PETERSEN (1930) and MOLLIER (1937) have shown that there are two different manners of attachment of a tendon to a bone, viz.: by direct transition of the tendon into the bone-substance and by transition into the fibres of the periosteum. After PETERSEN (1930) and SCHABADASCH (1935) the majority of the muscles is attached by the two different manners, although after their opinion there would be more fibres attached to the periosteum than directly to the bone.

In order to make a closer examination of the manner of attachment of the spinal muscles and ligaments to the neural spines, I made cross-sections of some of the anterior thoracic spines of a cow, with the attachments of the ligamenta interspinalia and the m. spinalis. With the naked eye the ligaments made the impression of being attached directly to the bone, the spinalis, on the contrary, made the impression of being attached to the periosteum. The sections were decalcified and stained with hemalun-eosine, hematoxilin- van Gieson and resorcin-fuchsin. The spongiosa was removed.

As is shown in fig. 89 (see also fig. 95), the ligamenta interspinalia are composed of a great number of elastic fibres (el.), connected by collagenous fibres. The majority of the elastic fibres makes a narrow angle with the caudal border of the neural spine, a number of cross-fibres, however, shows a direction perpendicular to that of the spine and attaches the above-described, nearly parallel fibres to the periosteum. A number of collagenous fibres has the same direction and evidently also the same task. The periosteum (per.) is a thick layer of collagenous fibres. At the lateral sides of the spine it is as thick as the compacta, but at the caudal side it is enormously thickened and forms a mighty cushion of collagenous fibres showing very different directions (per. cu.). An important part of these fibres forms the direct continuation of the above-described fibres of the ligamentum attached to the periosteum. Some of these fibres radiate into the lateral periosteum, so that we may say that the ligamentum is partly attached to the periosteum. The majority of its fibres, however, is directly continued into the bone of the caudal side of the spine.

The compacta borders on the periosteum with a very irregular border; several osteones have been found lying completely in the periosteum (ost. per.). The compacta of the caudal side of the neural spine shows the typical structure that has been described by PETERSEN (1930, p. 608) under the name of "Einstrahlungsknochen". The most important character of this kind of bone is the presence of very well developed bundles of collagenous fibres, which in different places intrude from the periosteum into the compacta (intr.). Here and there these fibres even reach the inner border of the compacta. They intrude themselves between the osteones of the outer and the lamellar bone of the inner layer of the compacta. Moreover they ramify several times and embrace the osteones. From the fact that these intruding bundles are not met with in every cross-section, we may conclude that they do not form a continuous layer, but that they are really separate bundles. In the sections stained with hemalun-eosine and resorcin-fuchsin the intruding bundles were markedly darker coloured than the other parts of the bone-tissue. This agrees

quite well with the statement of PETERSEN (1930; p. 609) that these fibres have a basophilous character.

In my sections of the neural spines I did not find a layer of fibrous cartilage between the inserting tendinous fibres and the bony tissue, as has been described by GEBHARDT

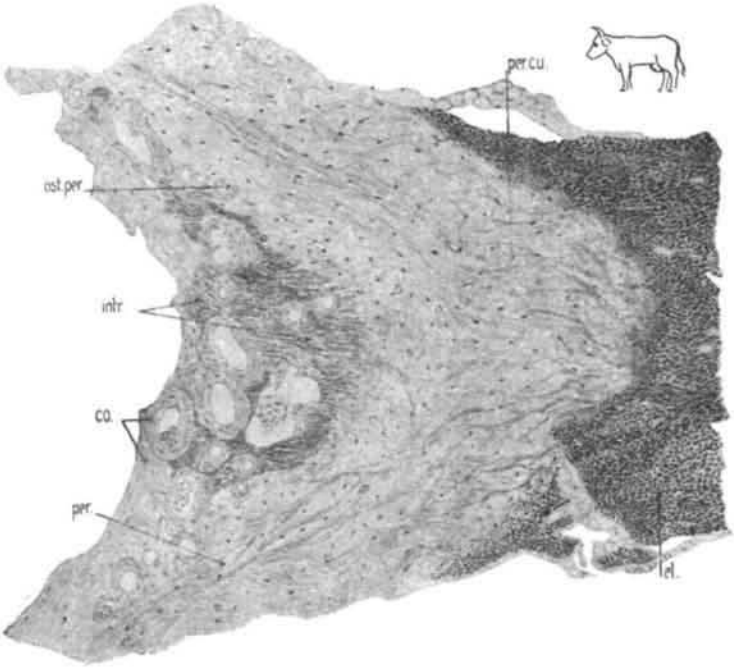


Fig. 89.
Horizontal section of the caudal part of an anterior thoracic neural spine of the cow, *Bos taurus* L. (dom.), with the attachment of the lig. interspinale. Spongiosa removed. Partly after hemalun-eosine, partly after resorcin-fuchsin sections. co = osteones and lamellar bone of compacta; per. = periosteum; ost. per. = osteones lying completely in the periosteum; per. cu. = cushion of collagenous fibres belonging to periosteum; el. = elastic fibres of lig. interspinale; intr. = collagenous fibres intruding into compacta and encircling the osteones. 2 ×.

(1901), WEIDENREICH (1923) and DOLGO-SABUROFF (1929). Since especially in the horse, however, some muscles and ligaments are inserted into little, but very distinct rough tuberosities of the spine (fig. 95), it is quite possible that here such a layer of fibrous and calcified cartilage may be found. The ligamentum nuchae is everywhere attached to the summits of the thoracic spines by means of a very thick layer of fibrous cartilage (fig. 90). The manner of attachment to the bone-substance, however, in these cases is principally the same as has been described above. The calcified tendinous fibres ("Faserknochen") intrude themselves and ramify everywhere between the osteones. Thus the tendon is very firmly anchored in the bone-substance. This has also been described by BENNINGHOFF (1925).

The attachment of a muscle to the periosteum I have studied at the m. spinalis cervicis and dorsi and the m. multifidus of the horse and cow. The m. spinalis cervicis of the horse and the m. spinalis dorsi of the cow were completely attached to the periosteum. The m. spinalis dorsi and the m. multifidus were only partly attached to the periosteum and partly directly to the bone. This was especially the case in the dorsal region. The

following description is based on the m. spinalis cervicis of the horse and the spinalis dorsi of the cow.

The periosteum of the neural spines is a comparatively thick layer of dense connective-

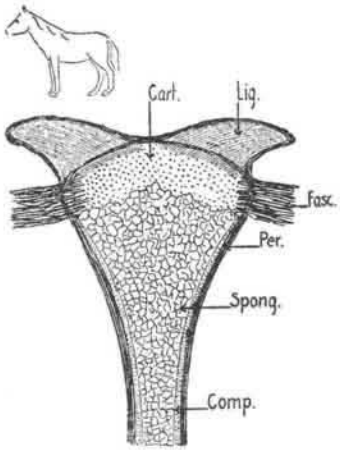


Fig. 90.
Schematic drawing of a transverse section of the summit of the 4th thoracic neural spine of a horse, *Equus caballus* L. (dom.). The figure demonstrates the attachment of the lig. nuchae (Lig.). Cart. = fibrous cartilage; Fasc. = fascia spino-transversaria and aponeurosis of latissimus dorsi; Per. = periosteum; Spong. = spongiosa; Comp. = compacta.

tissue. As is shown in fig. 91, the fibre-bundles run in various directions, but a great number of them encircle the neural spine in a direction that is almost quite or perfectly perpendicular to the longitudinal axis of the spine (o. per.). At its medial side the m. spinalis is provided with a flat and comparatively thin aponeurosis to which all its muscular fibres are attached. The muscle originates only by means of this aponeurosis. The angle of attachment of the aponeurosis with the periosteum is a very narrow one, so that the fibres of the aponeurotic layer run almost parallel to those of the periosteum (ap.). As is shown in fig. 91 and 92 the aponeurotic fibres are completely interwoven between the fibres of the outer layer of the periosteum (ap.). The majority of them is continued directly by the periostal fibres encircling the neural spine. Thus the manner of attachment of the tendinous fibres of the aponeurosis to the neural spine may be compared to a rope attached to a pile by means of a noose [fig. 93; see also PETERSEN (1930) and MOLLIER (1937)].

This noose, however, is everywhere firmly attached to the bone-substance by means of the inner layer of the periosteum (i. per.). This layer shows a denser and firmer structure than the outer one. It is almost exclusively composed of collagenous fibres, arranged concentrically round about the compacta. The direction of these fibres is perpendicular to the longitudinal axis of the spine. The border between the periosteum and the compacta is a very irregular one. There is an irregular layer of secondary periostal bone ["sekundärer Periostknochen"; PETERSEN (1930; p. 607)], composed of osteones that lie between the fibres of the periosteum. Some of these osteones are even partly dissolved and then the fibres of the periosteum cohere with the connective-tissue of the cavity of the osteone (diss.). Thus the periosteum and the compacta are attached to another by means of two very rough and irregular surfaces that work in with each other. There were no fibres perpendicular to the surface of the compacta (fibres of SHARPEY), as have been described above with regard to the attachment of the ligaments.

Principally, however, the manner of attachment of this periosteum to the compacta is the same as the manner of attachment of the ligaments and tendons that intrude directly into the bone-substance. For in both cases the fibres intrude between the osteones and encircle these tubes of bony substance in such a way, that we may also compare this manner of attach-

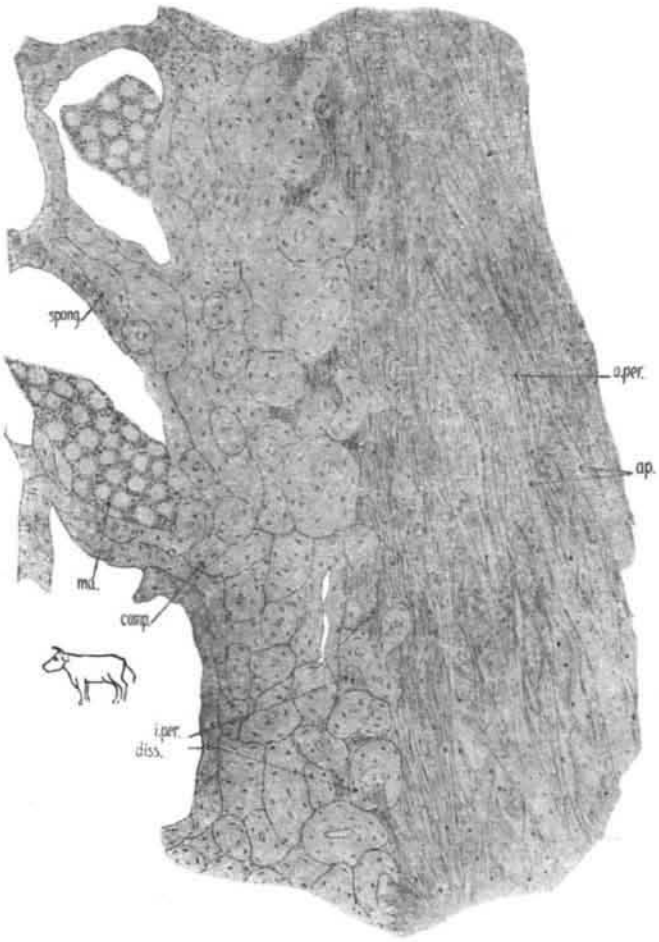


Fig. 91.

Horizontal section of the lateral part of an anterior thoracic neural spine of the cow, *Bos taurus* L. (dom.), with the attachment of the m. spinalis. Spongiosa removed. Partly after hemalun-eosine, partly after resorcin-fuchsin sections. o. per. = outer layer of periosteum; ap. = aponeurotic fibres of m. spinalis completely interwoven with outer layer of periosteum; i. per. = inner layer of periosteum intruding between osteones of compacta and encircling them; diss. = dissolved osteone; comp. = compacta; spong. = spongiosa; ma. = bone marrow.

ment to that of a rope, attached to a pile by means of a noose. Consequently as fig. 92 shows, every manner of attachment of a muscle or ligament to a neural spine, is based on this noose-principle. The nooses are either found round about the whole neural spine, or round about the osteones.

Now if a rope is attached to a pile by means of a noose, the direction of this rope must be perpendicular to that of the pile if a maximal effect will be obtained (fig. 93). For if the angle of attachment is not a straight one, we must take into account a longitudinal force that causes a slipping down

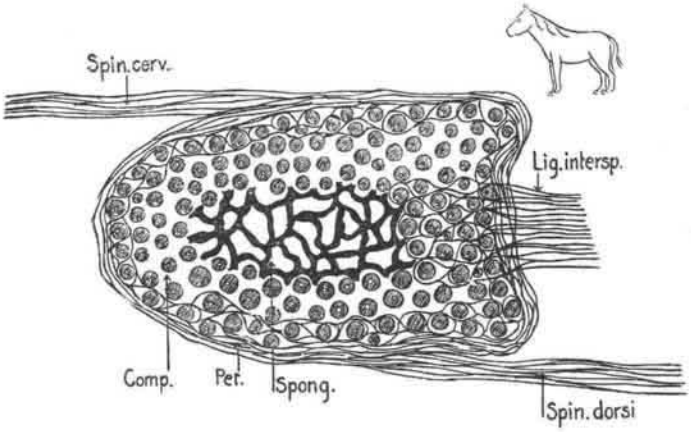


Fig. 92.
Very schematic drawing of a horizontal section of a neural spine (*3Th*) of the horse, *Equus caballus* L. (dom.), to demonstrate the manner of attachment of the ligaments and muscles to the bone. Per. = periosteum; Comp. = compacta; Spong. = spongiosa.

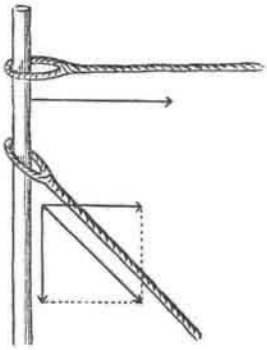

Fig. 93.
Schematic drawing to demonstrate that a rope attached to a pile by means of a noose is slipping down, if it is not attached perpendicular to the pile.

of the rope. And thus this noose-principle is the second reason why the direction of the muscles and ligaments perpendicular to that of the neural spines to which they are attached, is the most favourable.

That the direction of the osteones is the same as that of the whole neural spines, may already be evident from the fact that they are cut perfectly transversally in every cross-section (fig. 90, 91). This statement, however, is borne out by the results of BRUHNKE (1929), who made researches into the structure of the neural spines by means of the split-line-method ("Spaltlinienmethode") of BENNINGHOFF (1925) (fig. 94). These split-lines evidently show the direction of the osteones, as has been pointed out by BENNINGHOFF (1927) [and not the direction of the outer basic lamellae ("Generallamellen"), as BENNINGHOFF (1925) previously wrote].

As fig. 95 shows, the shape of the neural spines may be perfectly adapted to the attachment of the muscles and ligaments, especially to those muscles and ligaments that are attached directly to the bone. The more or less flat cranial and caudal sides of the spine and several little bony protuberances

make it possible that the muscles and ligaments are attached to the bone, perpendicular to the direction of the osteones.

The majority of the epaxial spinal muscles of the horse and cow is attached to the neural spines by means of the periosteum, as well as by

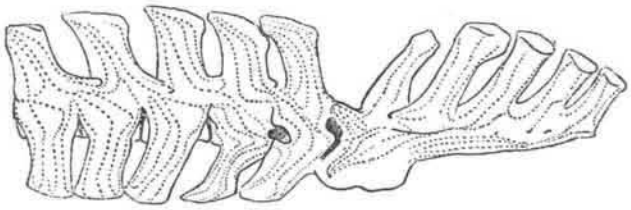

Fig. 94.
Lumbar and sacral vertebrae of the horse, *Equus caballus* P. (dom.), treated with split-line-method of BENNINGHOFF (1925), to demonstrate the direction of the osteones of the compacta. After BRUHNKE (1929).

a direct attachment to the bone. The number of fibres attached to the periosteum may vary considerably in the different regions of the vertebral column. A special manner of attachment is shown by the long tendons of the m. longissimus and spinalis dorsi, inserted into the summits of the lumbar neural spines. As is shown in fig. 19, they are attached partly to the

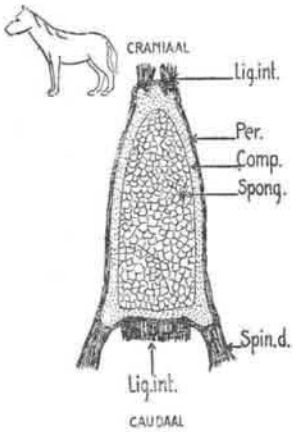


Fig. 95.
Very schematic horizontal section of the 3d thoracic neural spine of a horse, *Equus caballus* L. (dom.), to demonstrate the manner of attachment of the muscles and ligaments to the bone. See fig. 92.

periosteum, for the greater part, however, they are fused completely with the ligamenta interspinalia and consequently they are inserted by means of these ligaments into the bony substance of the cranial sides of the spines. The attachment of these tendons is further characterised by a very distinct fan-shaped radiating of these fibres, just as MOLLIER (1937) has described of the attachment of several other tendons to bones.

## B. Explanation of the length [1]) and direction of the neural spines in mammals.

In the following pages we shall try to explain the differences in length and direction of the neural spines in mammals with the aid of the principles that have been dealt with above. So at the same time we are able to test the exactness of these principles. A survey of the most important characters of the neural spines is given in table 7.

### 1. *Mammals in general.*

#### a. *Neck.*

As follows from the data given in table 7, in a great many mammals the neural spines of the cervical vertebrae are very short or even wanting. There is, however, a very distinct correlation between the length of the cervical spines and the absolute size of the animals. Among the *Marsupialia* and *Rodentia* they show a moderate length only in the comparatively big *Macropodidae, Thylacinus* and *Hydrochoerus*. Among the other mammals they are comparatively well developed in the bigger Carnivores (*Ursidae, Canidae, Felidae*) and the Ungulates. The very long spines of the great apes will be dealt with on page 108. On page 30 it has been demonstrated that with increasing size of the animal its muscular force relatively diminishes. Thus it is evident without more that with relatively decreasing muscular force the length of the lever-arms of the muscles must increase.

The direction of the cervical neural spines is either upright, or they are inclined more or less in the cranial direction. This direction is very easy to explain, if we take into consideration that the only muscle of certain

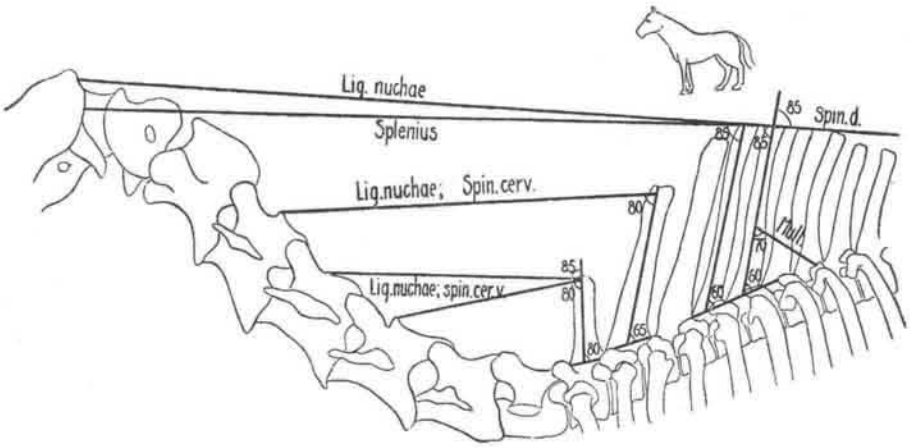


Fig. 96.
Schematic drawing of the cervical and anterior thoracic vertebrae of a horse, *Equus caballus* L. (dom.), to demonstrate the angle of attachment of the most important muscles and ligaments.

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[1]) By the length of the neural spine is meant its dorso-ventral diameter.

importance that is attached to the cervical spines, is the m. spinalis cervicis. This muscle originates at the 2d—7th cervical spine and is inserted into the neural spines of the cranial thoracic vertebrae (fig. 96, see also p. 19). The direction of the neural spines is quite or almost perpendicular to that of the muscle. The other cervical epaxial muscles are of very little importance. The direction of the mm. interspinales is always perpendicular to that of the spines, and the fascicles of the m. multifidus cervicis for the greater part originate at and insert into the zygapophyses; the remaining fibres are attached only to the bases of the neural spines. In the Ungulates the fibres of the ligamentum nuchae are also attached to the spines (see p. 29 and fig. 96). Since their direction is markedly obliquer than that of the spinalis cervicis, the cranial inclination of the neural spines in the Ungulates generally is greater than in the other mammals.

b. *Sacrum.*

In practically every mammal the neural spines of the sacral vertebrae stand upright or show a more or less caudal inclination. Into these spines are inserted the tendons of the m. longissimus dorsi and in some mammals also of the spinalis dorsi. These tendons would cause a cranial inclination of the spines. The upright position or caudal inclination, however, is evidently caused by the fact that several muscles of the hind leg originate at the sacral spines, viz.: the m. glutaeus maximus, glutaeus medius, biceps femoris and in some mammals also the m. semitendinosus. In a number of mammals these muscles are evidently of more importance than the m. longissimus dorsi.

c. *Trunk.*

From the data given in table 7, it is evident now that the great differences in inclination of the neural spines are met with in the trunk and especially in the postdiaphragmatic or postanticlinal region. Muscles that in all mammals exercise almost the same influence on the neural spines are: a. The mm. interspinales. Since in general two consecutive spines run almost parallel to another, these muscles are practically always attached nearly perpendicular to the direction of the spines. b. The m. trapezius thoracis, rhomboideus thoracis and latissimus dorsi. Since the direction of these muscles, however, is chiefly a lateral one, in the following considerations their influence on the neural spines may be neglected. c. This is also the case with the m. semispinalis capitis, which in some mammals is also attached to the anterior thoracic spines by means of the fascia spinotransversaria. For compared with that into the metapophyses this insertion, is of very little importance. d. Muscles exercising a comparatively great influence on the anterior thoracic spines are the m. splenius and spinalis cervicis (fig. 96, 98; see also p. 19, table 1 and p. 91). They are attached to the first 2—3, in some mammals even to the first 4 thoracic spines (fig. 101, 102). Their direction and their area of attachment is almost the same

in every mammal. This is also the case with the ligamentum nuchae in those mammals that are provided with this accessory supporting cord of the head and neck (see p. 30 and fig. 96, 98, 101, 102). As can be seen in fig. 96, the direction of the anterior thoracic spines with regard to these muscles and ligaments is the most favourable if they show a small or moderate caudal inclination. The first spines must show a smaller inclination than the other ones; in some mammals it would be even quite favourable if they stood upright.

All other epaxial muscles neither possess a constant area of attachment nor a constant direction or development in the different species of mammals. It is these muscles that cause the differences in the inclination of the neural spines. Several different cases successively will be dealt with.

*α. Reptiles.*

The simplest relations have been met with in the Reptiles. The only muscles that must be taken into account are the spino-articularis and the articulo-spinalis. As follows from fig. 36 and 97 the neural spines will have

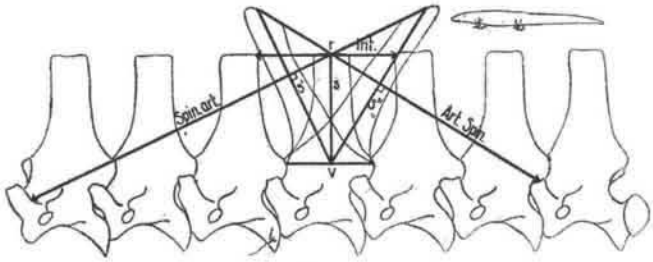



Fig. 97.
Schematic drawing of a number of thoracic vertebrae of a reptile with the most important muscles attached to the neural spines. The figure demonstrates that the most favourable direction of the neural spine is represented by the line S. Spin. art. = m. spino-articularis; Art. spin. = m. articulo-spinalis; Int. = m. inter-spinalis.

to show an intermediate position between that required by each of these two muscles. And indeed in almost every Reptile the neural spines of the trunk-vertebrae stand upright. This is also the case in the fossil Reptiles, the *Theromorpha* included. Only in some Dinosaurs and in the tail of some aquatic Reptiles (*Ichthyosauria, Plesiosauria, Mosasauria*) the spines show a small caudal inclination. The signification of this fact must still be the subject of accurate investigations. It is, however, highly probably that the articulo-spinalis in this region is better developed than the spino-articularis.

*β. Primitive relations in mammals.*

There are some mammals in which, apart from the splenius and the spinalis capitis, only the spino-metapophysial fascicles of the m. transverso-spinalis (m. semispinalis, multifidus, submultifidus) are attached to the neural spines. These relations were found in *Tachyglossus, Dasypus* and

*Choloepus*. In perfect accordance with the considerations given in the first part of this chapter, the neural spines of these animals are altogether inclined caudally (fig. 44, 48). In *Dasypus* the inclination of the anterior thoracic vertebrae is somewhat smaller than in the other regions of the vertebral column. Evidently this may be ascribed to the influence of the m. splenius, although here this muscle is of minor importance than the transverso-spinalis.

*γ. Specialised relations in mammals.*

In the majority of mammals, however, to the postdiaphragmatic neural spines are attached not only the above-described fascicles of the m. transverso-spinalis, but also the tendons of the m. spinalis, m. longissimus and even of the m. ilio-costalis. Thus a longer lever-arm for these muscles is obtained with increasing size of the animals and with increasing specialisation in the mobility of their body-axis (see p. 58). In some mammals the importance of the attachment of these muscles to the neural spines is still comparatively small with regard to that of the transverso-spinalis. In these cases we may expect that the neural spines will still be inclined altogether in the caudal direction. With increasing importance of these muscles, however, the point of intersection of the line representing the muscular force with the line perpendicular to the longitudinal axis of the vertebral body (see fig. 86, 87), shifts upward. Besides this point shifts upward in those mammals in which the mobility of the body-axis is localised more and more in the diaphragmatic region, since in these cases the distance between the neural spine and its centre of rotation is increasing (p. 83, fig. 87).

Thus we may expect that, with increasing importance of the muscles in question, the neural spines of the postdiaphragmatic region at first will show an intermediate position (upright) and that at last their direction will be perpendicular to that of the m. longissimus, so that they are inclined more or less in the cranial direction (fig. 98). In the thorax a comparatively

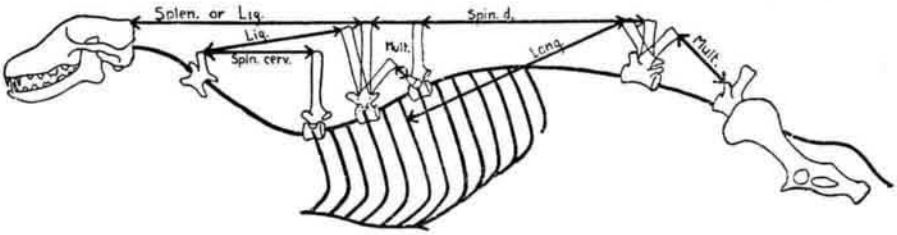



Fig. 98.
Schematic drawing of the vertebral column of a mammal to demonstrate the most favourable direction of the neural spines if only one muscle was attached to every spine.

great caudal inclination would be favourable with regard to the semispinalis and the shorter fascicles of the transverso-spinalis. The splenius and the spinalis, however, require a much smaller inclination or, especially with

regard to the cranial thoracic vertebrae, even an upright position (p. 92, fig. 96, 98). Fig. 99 shows that the greater difference in length there is between the anterior thoracic and the lumbar spines, the greater the caudal inclination of the anterior thoracic spines must be with regard to the demands of the m. spinalis dorsi.

On page 11 it has already been pointed out that a moderate caudal in-

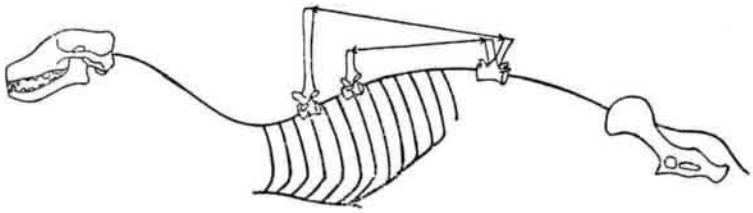


Fig. 99.
Schematic drawing of the vertebral column of a mammal to demonstrate that the greater the difference in height is between the prae- and postdiaphragmatic neural spines, the more the postdiaphragmatic spines are inclined caudally, as far as their direction depends on the action of the m. spinalis.

clination of the anterior thoracic spines, as well as a cranial inclination of the cervical spines, is quite favourable with regard to the cantilever-construction of the cranial part of the vertebral column. This, however, does not mean that this inclination is determined by the demands of the construction. On the contrary, in the following pages it will be demonstrated that even little differences in the direction of the neural spines may be ascribed to the different action of the muscles and ligaments.

In the following pages the above mentioned principles will be worked out in detail with regard to the different types of mammals.

2. *Terrestrial mammals.*

a. *Praediaphragmatic (prae-anticlinal) region.*

*α. Direction of neural spines.*

The data of table 7 and fig. 100 show that generally the neural spines of the first two thoracic vertebrae have only a small caudal inclination or even may stand upright. The inclination then rapidly increases up to a point that is found 1—3 vertebrae cranial of the anticlinal or the diaphragmatic (in mammals without anticliny) vertebra. Caudal of this point the inclination rapidly decreases. The anticlinal spine shows an upright position and even in the mammals without anticliny the inclination of the postdiaphragmatic neural spines is always less than that of the praediaphragmatic ones.

Fig. 101 and 102 show that the greater part of the surface of the first thoracic spines is occupied by the insertion of the m. spinalis cervicis, spinalis dorsi, splenius and the lig. nuchae. The influence of the semispinalis and the multifidus is quite subordinate to that of these muscles and the nuchal ligament. In the caudal direction, however, the importance of the semispinalis, multifidus and submultifidus is increasing and that of

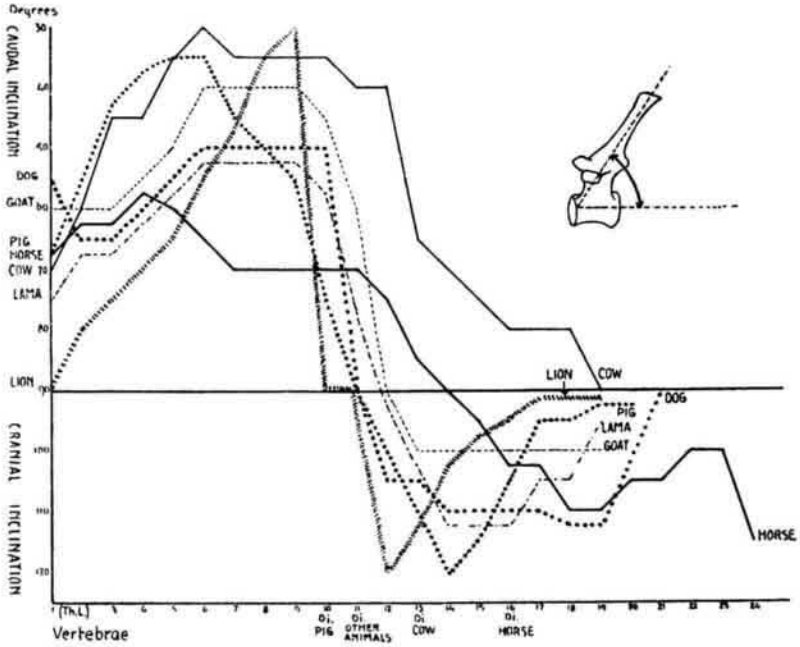



Fig. 100.

Curves of the inclination of the neural spines in several different mammals.

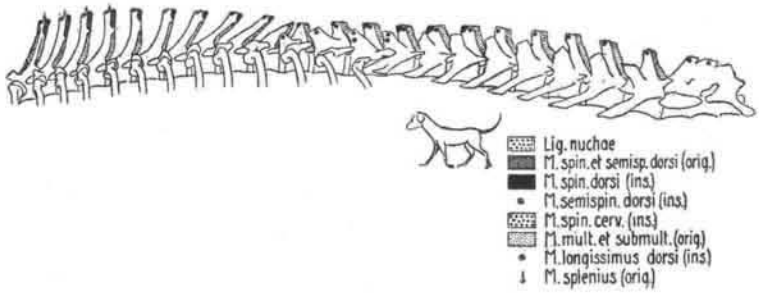



Fig. 101.

Schematic figure of the vertebral column of a dog, *Canis familiaris* L., with the area of attachment of the most important epaxial muscles.

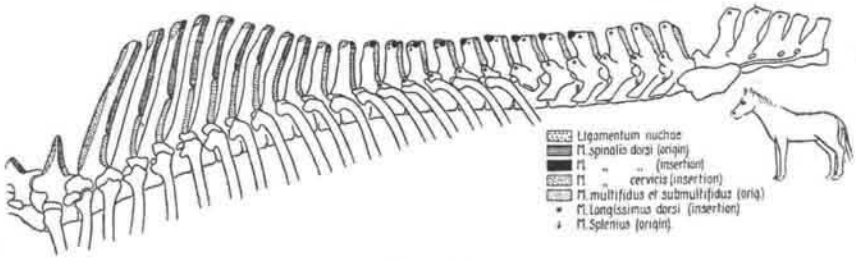



Fig. 102.

Schematic figure of the vertebral column of a horse, *Equus caballus* L. (dom.), with the area of attachment of the most important epaxial muscles.

the other muscles and the lig. nuchae decreasing. This may not only be concluded from the extent of the area of attachment (fig. 101, 102), but also from the strength of the muscular fascicles. Thus the first thoracic spines stand almost upright, while, with increasing importance of the spino-metapophysial fascicles of the transverso-spinalis, the inclination of the spines is increasing. Fig. 103 shows that the angle of attachment of the different muscles and ligaments in this region varies from 70—90° and consequently may be considered as a very favourable one.

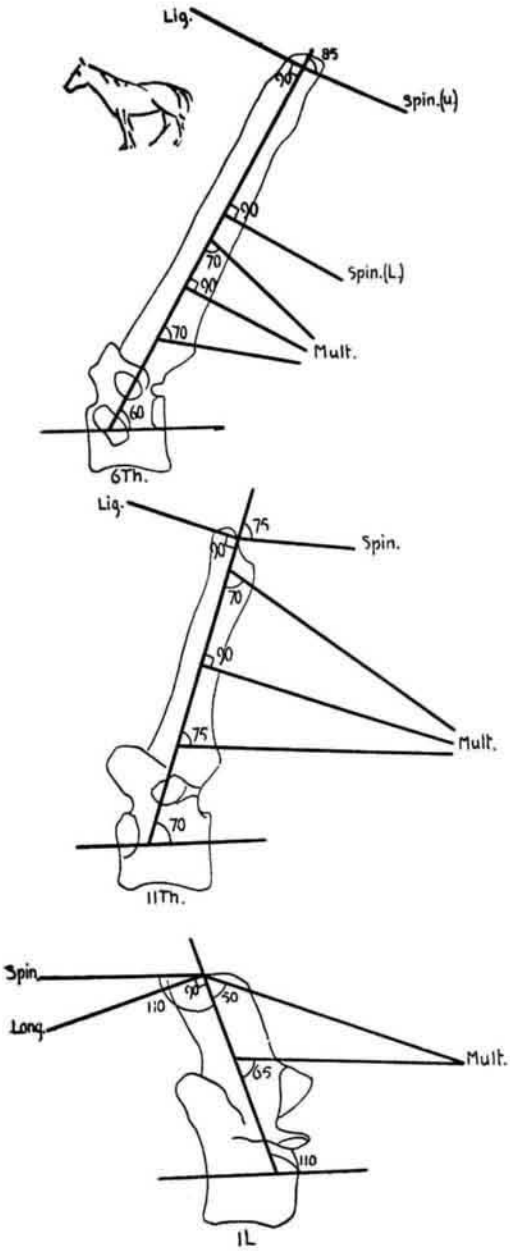



Fig. 103.
Schematic drawing of three vertebrae of a horse, *Equus caballus* L. (dom.), to demonstrate the angle of attachment of the most important muscles and ligaments.

It will be evident now that, within the scope of the above-described scheme, there may be a great number of little variations in the direction of the thoracic spines between the different terrestrial mammals. These variations may be ascribed to the differences in length and position of the neck, in length of the neural spines and in the importance of the different muscles and ligaments. So for example it is very obvious that in the cow and the goat there are so many thoracic vertebrae with a great caudal inclination (fig. 104).

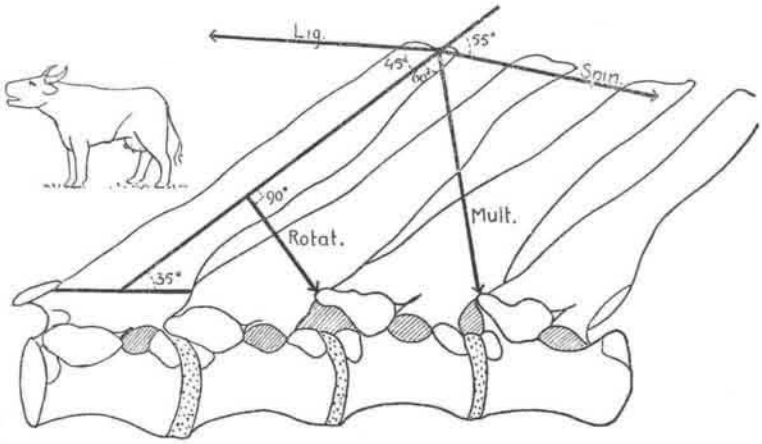



Fig. 104.
Schematic drawing of the 7th—10th thoracic vertebra of a cow, *Bos taurus* L. (dom.), to demonstrate the angle of attachment of the most important muscles and ligaments. The figure shows that especially the angle of attachment of the rotatores is very favourable.

It is highly probably that this phenomenon may be ascribed to the fact that in these animals the m. multifidus and the submultifidus of this region are especially strongly developed.

In some mammals the middle thoracic spines show a very characteristic nod. The basal part of the spine is inclined caudally, while the apical part stands upright. This nod is very well developed on the wolf, the dog and several species of bears (not, however, in *Ursus arctos* L.). It is much less developed in *Civettictis civetta* (Schreb.), *Herpestes fasciatus* Desm., *Cavia porcellus* (L.), *Lepus europaeus* Pall., *Centetes* and *Echinosorex albus* (Giebel). VIRCHOW (1913) was the first to show that this nod corresponds with the upper border of attachment of the mm rotatores. Thus the direction of the neural spine is as well adapted to the demands of the rotatores (a comparatively great caudal inclination), as to that of the other muscles (a small caudal inclination or an upright position).

## *β. Length of neural spines.*

The data given in table 7 show that the length of the neural spines, expressed in % of the length of the trunk, may be very variable (0—23 %). It was already to be expected in advance that a certain relation might be found between the length of the spines and the absolute size of the animals. For the fact that the body-weight increases in the third power and the muscular force only in the square, causes a certain disproportion between these two magnitudes that may be compensated by a lengthening of the lever-arm (the neural spine). A very distinct relation was found in horses of different size in which a certain thoracic spine varied from 18—20 and the 3d lumbar spine from 4,7—6,0 %. The relation is also very obvious in *Rodentia, Carnivora* and *Ungulata.*

Moreover the data of the Ungulates show that also the length of the neck and the

weight of the head may be of certain importance. Although after BACHOFEN-ECHT (1938) the weight of the antlers of deer is only 4% of the body-weight, the influence of this weight on the spines of the withers may be very important, since its lever-arm (the neck) is very long. In 8 different species of deer I compared the relative length of the fourth thoracic neural spine in the males, that bear antlers, and the females in which this headtire is wanting. The length of the spines varied in the males from 16,0—20,5% of the trunk-length, in the females from 14,0—16,0%. Further detailed researches on this subject, however, would be particularly interesting, since RÖRIG (1901) says that in deer the relative weight of the antlers is decreasing with increasing body-weight. In goats I found the same relation between the development of the horns and the length of the spines of the withers, as in deer. The relative length of the spines varied from 13% (young hornless animals) to 22% (old animals with big horns). SCOTT (1929) has shown that the same relation may be observed with regard to the phylogenetic development of the *Titanotheria*. With increasing body-size and length of the horns, the height of the withers increases too.

The above-described relation, however, has by no means been found in all groups of Ungulates. The extinct giant Rhinoceros *Baluchitherium* (Oligocene of Mongolia) has a comparatively short neck, a comparatively small head and no horns [GRANGER and GREGORY (1936)]. Nevertheless it has very high withers. The same may be said of the extinct giant piglike *Dinohyus* [Miocene of America; length 3,5 m; ROMER (1936)]. It is highly probably that the height of the withers in these animals is only caused by their absolute size (long lever-arm of the m. spinalis dorsi). No relation at all could be found on the *Bovinae*, of which I examined 14 different species. This phenomenon has already been demonstrated by BROWAR (1935, 1940). I can, however, not agree with the very remarkable way in which this author explains the height of the withers. The same absence of any relation was found by comparing the deer and the antelopes. The weight of the horns of antelopes is considerably less than that of the antlers of deer. Nevertheless the relative height of their withers was quite the same. Evidently there must be still other factors influencing the length of the neural spines, as for example the strength of the lig. nuchae. In the *Marsupialia, Insectivora* and not-anthropoid *Primates* also no distinct relation between the height of the withers and the absolute size of the animals, or the size of their heads and length of their necks could be found.

Fig. 105 shows that generally the 2d—4th thoracic vertebrae possess the longest neural spines. Their length then gradually decreases up to the diaphragmatic or anticlinal vertebra. After a comparatively small rising the course of the curve is further almost horizontal. This shape of the curve is easy to explain, since to the first thoracic vertebrae, the muscles and ligaments of the neck (splenius, spinalis cerv., lig. nuchae), as well as the m. spinalis dorsi are attached. To the postdiaphragmatic (or postanticlinal) spines are attached the tendons of the longissimus and spinalis. But the intermediate neural spines only serve as lever-arms for the multifidus and semispinalis. In a great many mammals these spines are not only the shortest, but also the narrowest (cranio-caudal diameter) and the thinnest (transversal diameter) (fig. 106).

### b. *Postdiaphragmatic (postanticlinal) region.*

On page 94 it has been pointed out that the better the spinal part of the m. longissimus and the m. spinalis dorsi are developed, and thus the more and the stronger tendons of these muscles are inserted into the neural spines of the postdiaphragmatic (postanticlinal) region, the more these spines will show the tendency to change their caudal inclination in an upright position, or a cranial direction.

The data given in table 7 show that this relation holds good without more with regard to the *Monotremata, Marsupialia, Edentata, Rodentia*

and Ungulata. In *Tachyglossus*, for example, all neural spines are inclined caudally, but in *Ornithorhynchus* the spines into which the m. spinalis is inserted stand upright (1 L.—1 S.; fig. 43). In *Choloepus* and *Dasypus*,

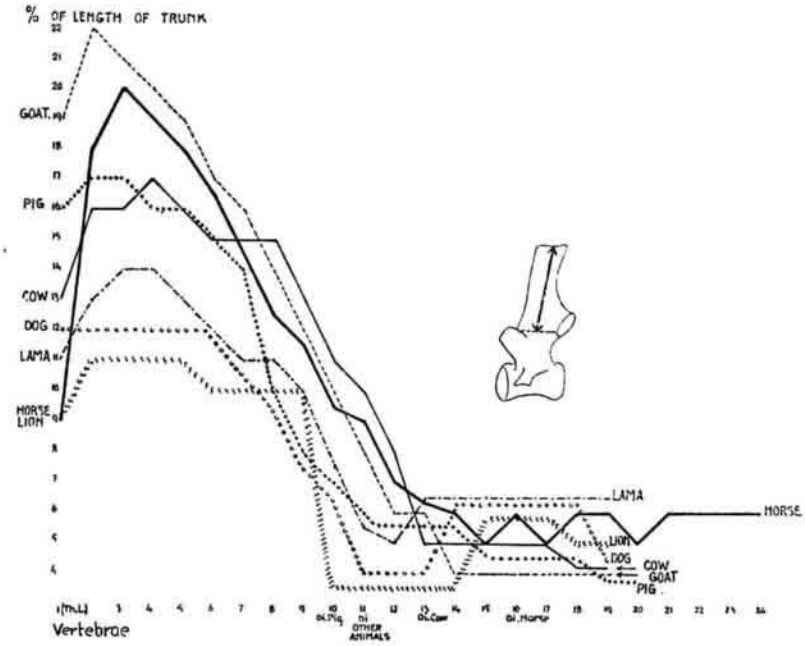



Fig. 105.
Curves of the length of the neural spines in several different mammals.

which possess only a multifidus or an undifferentiated transverso-spinalis, the neural spines are all inclined caudally (fig. 48). But in *Manis*, where comparatively weak tendons of the longissimus and spinalis are inserted into the summits of the spines, they show an almost upright position. This is also the case in the fossil relatives of these species [ABEL (1919), WEBER (1928), ROMER (1936)].

Among the *Marsupialia* the neural spines with the greatest caudal inclination have been found in *Phalanger*, in which the tendons of the longissimus and spinalis inserted into the neural spines, are only very weakly developed. The greatest cranial inclination is found in *Macropus* and *Dorcopsis*, in which these tendons are comparatively strongly developed.

The same relations are found in the *Rodentia*. A very marked but inexplicable exception is only found in *Psammomys*. Fossil Rodents show already the same differences in the slope of their neural spines as their recent relatives. The relations among the Ungulates will be dealt with later on (p. 103), as we shall first consider the neural spines and their musculature of the *Insectivora*, *Carnivora* and *Primates*.

Table 3 shows that in all *Carnivora* and *Primates* the tendons of the m. longissimus inserted into the summits of the neural spines, are very strongly developed. Besides there is always a m. spinalis, and in many

species this muscle also shows a comparatively strong development. In consequence one might expect that the representatives of these orders would show a very marked cranial inclination of their postdiaphragmatic neural spines. And indeed, the majority of the *Carnivora* and *Primates* show a very distinct anticliny. Among these orders even the most pronounced type of anticliny can be found, especially in the *Canidae* and *Felidae*, where the neural spines of the anticlinal vertebrae are very short or even absent (fig. 106). A very strong anticliny is already present in

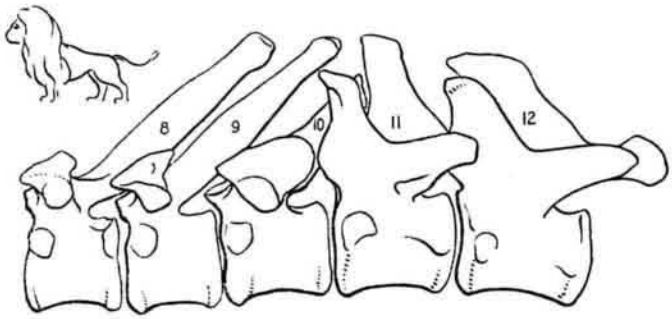



Fig. 106.

8th—12th thoracic vertebra of a lion, *Panthera leo* (L.), to show the very marked anticliny in this vertebral column. 10 Th. is the anticlinal and diaphragmatic vertebra.

many primitive fossil Carnivores [all *Creodonta*, primitive *Fissipedia*, primitive *Ursidae*, Oligocene *Felidae*; ROMER (1936)]. But in the Pleistocene North American *Smilodon* the cranial inclination of the lumbar spines is comparatively small. Next to these Carnivores and Primates with very distinct anticliny, however, there are several species in which the postdiaphragmatic neural spines stand upright or in which they even show a small caudal inclination. The development of the mm. longissimus and spinalis does not show the slightest relation with the phenomenon.

As table 7 shows, there is, however, a very marked relation between the inclination of the neural spines and the length (cranio-caudal diameter) of the postdiaphragmatic vertebral bodies. The shorter these vertebral bodies are, the more the neural spines show the tendency to an upright position or even to a caudal inclination. In fig. 10 it is demonstrated that, if the vertebral bodies are short, there is also but a short distance between the point of origin (neural spine) and the point of insertion (metapophysis) of the fascicles of the m. multifidus. On page 83 it has already been explained that this causes a high point of intersection of the line representing the muscular force and the line erected perpendicular to the longitudinal axis of the vertebral body. And the higher this point of intersection lies, the more pronounced the tendency of the neural spine will be to occupy a position perpendicular to the m. multifidus, instead of perpendicular to the m. longissimus or spinalis. So the shortness of the postdiaphragmatic

vertebral bodies causes the upright position or caudal inclination of their spines in some Carnivores and Primates.

From the nature of the case the length of the vertebral bodies is inti-

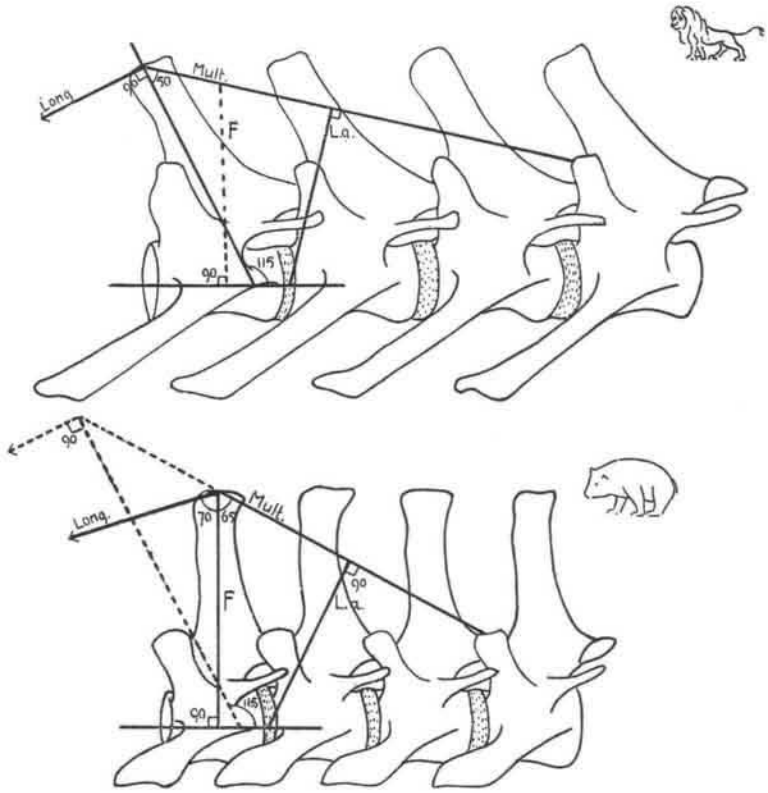



Fig. 107.

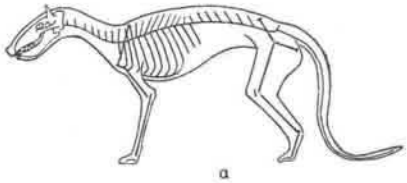
Schematic drawings of four lumbar vertebrae of a lion, *Panthera leo* (L.), and a bear, *Euarctos americanus* (Pall.). The figure demonstrates that if the vertebral bodies are comparatively short (bear), the point of intersection of the m. multifidus with the line *F* is so high, that the neural spine cannot be inclined in the cranial direction (perpendicular to the m. longissimus) as in the lion with its comparatively long vertebral bodies. The lever-arms (L. a.) have the same length.

mately connected with the general type of structure of the animal and its manner of locomotion. So it is, for example, a very striking fact that the North American Miocene precursor of the *Ursidae, Daphoenodon* [ROMER (1936), SCOTT (1929)], shows not only a very strong anticliny, but that the general structure of its skeleton is much more like that of the general type of light and slender Carnivores than like that of the comparatively heavy recent bears (fig. 108). The animals, for example, were not plantigrade but digitigrade.

The *Insectivora* in general show the same relations as the *Carnivora* and *Primates*. It is, however, not improbable that in this order the length of the

vertebral bodies, as well as the differences in strength of the tendons of the longissimus and spinalis cause the differences in the inclination of the neural spines. Detailed investigations on a greater materal of this order are wanted.

Table 7 shows that in the *Ungulata* there is also a certain relation



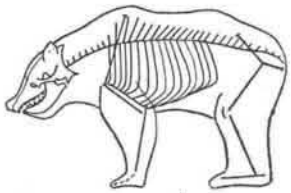




Fig. 108.
Schematic drawing of the body-outline and skeleton of: a. *Daphoenodon superbus* (Peterson), a North-American lower-Miocene forerunner of the bears; light animal with anticliny. b. Recent brown bear, *Ursus arctos* L.; heavy animal without anticliny.

between the length of the vertebral bodies and the inclination of the neural spines. The relation, however, is by no means so striking as in the abovementioned orders and the relation with the development of the muscles is much more characteristic.

On page 63 it has been shown that with decreasing mobility of their body-axis, the *Ungulata* show the tendency to a shifting backward of the spinal insertion of the m. longissimus. In some Ungulates this muscle is even inserted only into the sacral vertebrae and the ilium (fig. 62). This means, that with regard to the postdiaphragmatic neural spines, the importance of the m. longissimus decreases and consequently the importance of the m. transverso-spinalis (chiefly the m. multifidus) increases. Table 3 and 7 show very distinctly that parallel to this change in the reciprocal strength of these muscles, the neural spines of the postdiaphragmatic region change their cranial inclination into an upright position or even into a caudal inclination (fig. 62, 109). With regard to the generally very well developed m. spinalis, the upright position or — especially in Ungulates

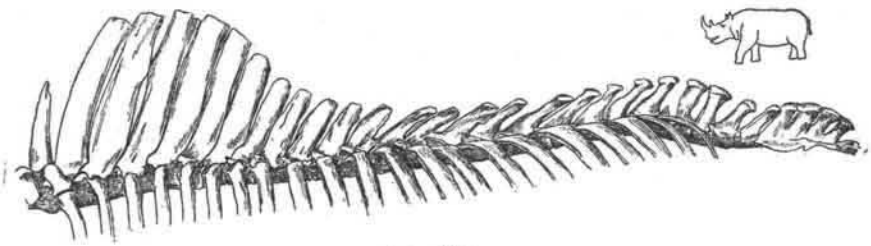


Fig. 109.
Vertebral column of the common African rhinoceros, *Diceros bicornis* (L.).

with high withers — even the caudal inclination of the lumbar spines is a very favourable one (fig. 99, 109).

Generally it may be said, that among the Ungulates the disappearance of the anticliny runs parallel with the reduction of the motion- and the better development of the tension-musculature of the back, a phenomenon that is intimately correlated with the type of locomotion and the general body-form. The upright or caudally inclined neural spines are chiefly found in the heavy Ungulates. This is very beautifully illustrated by the *Rhinocerotidae*. The light and slender North American, Eocene and Oligocene, "running" Rhinoceroses [*Hyrachyus, Hyracodon, Metamynodon*; OSBORN (1898)] show a distinct anticliny. The Oligocene *Caenopus tridactylus* Osborn was of moderate size and had upright standing lumbar spines. But in the heavy types, as for example *Baluchitherium* [Oligocene of Mongolia; GRANGER and GREGORY (1936)], *Teleoceras* [Pliocene of

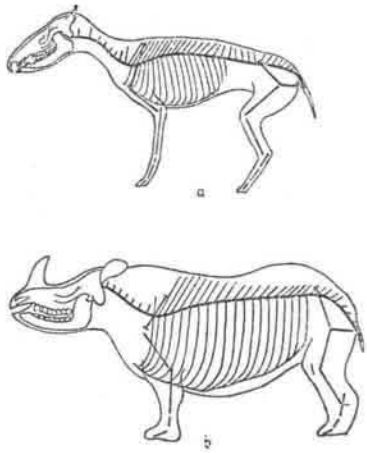


Fig. 110.
Schematic drawing of the body-outline and skeleton of: a. *Hyrachyus agrarius* Leidy, a running rhinoceros from the middle-Eocene of North-America; light animal with anticliny. b. Recent Javan rhinoceros, *Rhinoceros sondaicus* Desm., heavy animal with anticliny.

Kansas; ROMER (1936)], the other Pliocene *Rhinocerotidae* and the recent representatives of this family, as well as in the Oligocene Amynodontid *Metamynodon*, all postdiaphragmatic neural spines are more or less caudally inclined (fig. 110).

Other heavy forms with caudally inclined lumbar spines are, for example, the Oligocene African Embrithopode *Arsinoitherium*, the *Titanotheria*, (Eocene-Oligocene of North America), the Amblypod *Coryphodon* (Eocene of North America), the Miocene and Pliocene South American Notungulates *Toxodon* and *Homalodontherium* (*Protypotherium*, a light and slender Notungulate, however, shows a distinct anticliny) and all known fossil and recent representatives of the *Proboscidea* [OSBORN (1936)], with the exception, however, of *Elephas antiquus* Falc., whose neural spines all show a perfect upright position from the first thoracic up to the last lumbar vertebra [ANDREWS and COOPER (1928)].

Although they are certainly heavy animals, the *Hippopotamidae*, on the contrary, show a distinct anticliny, that is quite in accordance with the primitive arrangement of their epaxial musculature (table 3, 7, fig. 52). Among the *Tylopoda* the comparatively heavy Camels, that move forward in the characteristic amble or rack, show no anticliny. The Lama's and the Miocene *Oxydactylus*, on the contrary, have a distinct anticliny. In the

*Cervidae, Caprinae* and *Antilopinae* the postdiaphragmatic neural spines are inclined very little in the cranial direction or they stand upright. Although these animals belong to the light and slender type, their body-axis shows a very limited mobility and they move forward in a pace that may be considered as intermediate between the leaping-gallop and the horse-gallop (pag. 22). The spines of the heavier *Bovinae*, which move forward exclusively in a horse-gallop, are all inclined in the caudal direction. Among the primitive Ungulates, as for example the *Suidae, Tragulidae, Oreodontidae, Hypertragulidae* and primitive *Cervidae* (*Blastomeryx*) a very distinct anticliny can always be found.

The Horse-family (*Hippoidea*) is characterised by some remarkable facts that still need further investigation. As might be expected, the Eocene forerunner of this family (*Phenacodus primaevus* Cope) shows a comparatively distinct anticliny, and this character is also met with in the Eocene and Oligocene *Orohippus* and *Mesohippus* [LULL (1931), MATTHEW and CHUBB (1927)]. The recent horses (*Equus*) and the Pleistocene North American horse *Equus scotti* Gidley show almost the same type of anticliny, which is quite in accordance with the structure of their spinal musculature (table 3). In the Eocene *Eohippus*, the Miocene *Neohipparion* and the Pleistocene *Hippidium*, however, the lumbar neural spines stand almost upright [SCOTT (1929), ROMER (1936)].

## C. Anthropoid apes and man.

On page 65 it has been demonstrated that the body-axis of the hanging-climbing anthropoid apes and man shows some very characteristic adaptations to the special type of locomotion of these animals, as well as to their erect posture. On page 41 I have shown that, although the structure of the body-axis of quadrupedal terrestrial mammals is also quite adapted to the erect posture, the body-axis of bipedal mammals requires some special adaptations, since the muscles get tired if the animals move or stand on their hind-legs for a comparatively long time. The most striking adaptations

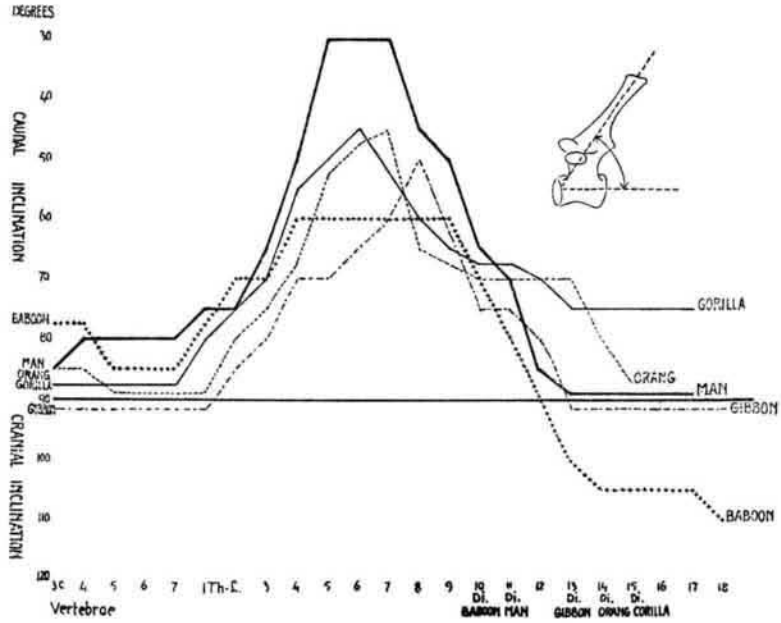



Fig. 111.
Curves of the inclination of the neural spines in several different Primates.

of the body-axis in man and the great apes are: 1. Shortening of the lumbar region. 2. Absence of the special mobility in the diaphragmatic region. 3. Comparatively small mobility of the whole body-axis. 4. Increase in strength of the erector spinae. 5. Shifting of the area of insertion of the longissimus dorsi in the cranial direction (far cranial from the diaphragmatic vertebra). 6. Reduction of the m. spinalis. 7. Increase in strength of the tension-elements of the spinal musculature in adaptation to the getting tired of the muscles.

The data given in table 7 show that especially in the thoracic region the length of the neural spines (10—12 %) is greater than in the quadrupedal monkeys (5—8 %). Without doubt this phenomenon is partly caused by the fact that with increase in length of their lever-arms the muscles do not get so quickly tired. For long neural spines have also been found in the bipedal jumping mammals *Macropus, Dorcopsis, Macroscelides* and *Jaculus* (table 7), as well as in the bipedal goat (p. 116).

Fig. 111 (see also table 7) shows that in quadrupedal monkeys the cranial thoracic neural spines have an inclination of 80—70°. In the caudal direction the slope of the neural spines increases (70—55°) up to a point that is situated 1—2 vertebrae cranial of the diaphragmatic vertebra. Caudal of this point the spines rise again. The hanging-climbing apes and

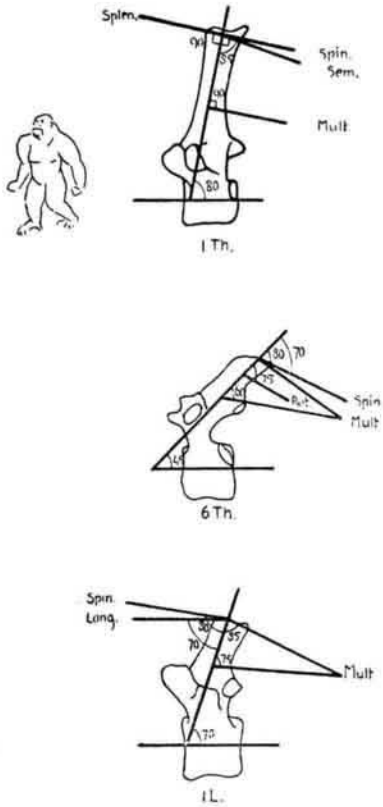



Fig. 112.
Schematic drawing of three vertebrae of a gorilla, *Gorilla gorilla* (Sav. et Wym.), to demonstrate the angle of attachment of the most important muscles.

man, however, are characterised by the fact that the middle thoracic spines show a much greater inclination (50—20°) than in the monkeys and that the summit of the curve lies 5—7 vertebrae cranial of the diaphragmatic vertebra (see also fig. 115). The greater inclination can be ascribed to the reduction of the m. spinalis dorsi and the increase in importance of the mm. semispinalis and multifidus.

Fig. 112—114 show that in the first thoracic vertebrae the muscles are

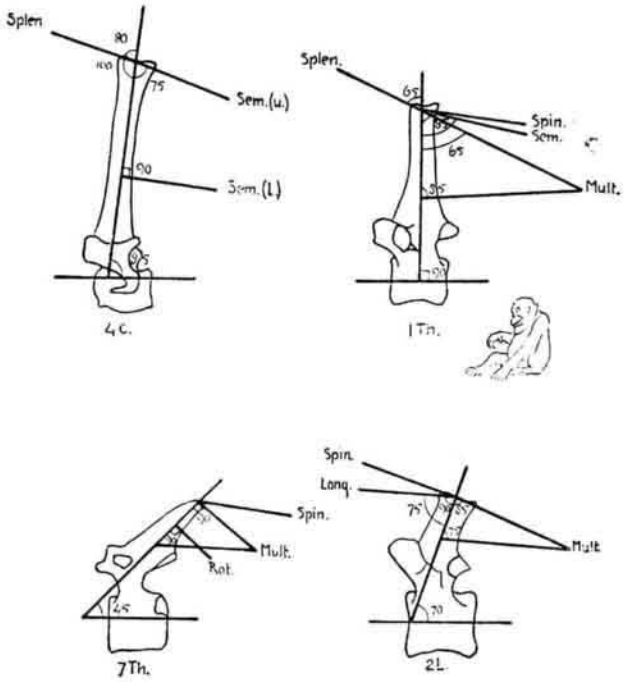



Fig. 113.
Schematic drawing of four vertebrae of the orang-utan, *Pongo pygmaeus* (Hoppius), to demonstrate the angle of attachment of the most important muscles.

attached almost perpendicular to the longitudinal axis of the neural spines. In the middle thoracic vertebrae, however, an angle of attachment of 90° has only been found with regard to the mm. rotatores. This may be an indication that, just as in the cow (p. 98, fig. 104), in this region these very short spinal muscles are of the greatest importance. The cranial shifting of the summit of the curve is evidently caused by the above-mentioned cranial shifting of the insertion of the m. longissimus. With regard to this characteristic the hanging-climbing monkeys *Ateles* and *Hylobates* show an intermediate position between the walking-climbing monkeys and the hanging-climbing apes.

Table 7 shows that the lumbar region of man and the great apes is characterised by the upright position (man) or the caudal inclination (apes) of the neural spines (fig. 115, 116). This position of the spines may be ascribed to the comparatively short vertebral bodies (see p. 101; the

shortening of the lumbar region is partly caused by a decrease in number of the lumbar vertebrae, partly by a shortening of the vertebral bodies), as well as to the reduction of the spinalis and the increase in strength of

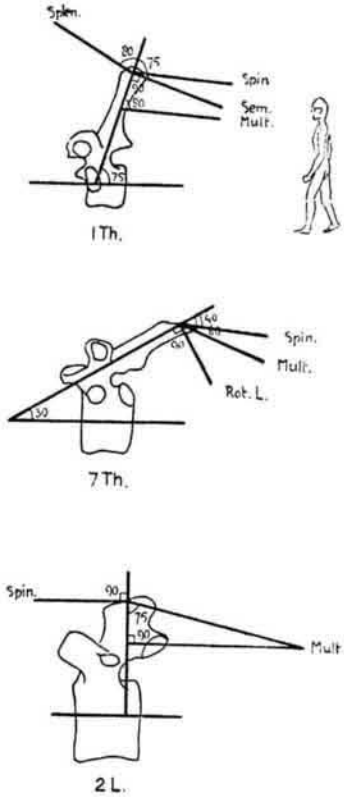



Fig. 114
Schematic drawing of three vertebrae of man, *Homo sapiens* L., to demonstrate the angle of attachment of the most important muscles.

the semispinalis and the multifidus. Fig. 112 and 115 show that in the gorilla the lumbar spines have a direction perpendicular to that of the transverso-spinalis. In the other apes and man the position of the spines is almost intermediate between a direction perpendicular to that of the transverso-spinalis and to that of the longissimus.

From the data given in table 7 it follows that the cervical neural spines of the anthropoid apes are extraordinarely long (10—19 %) while their length in man (4,8 %) is also greater than the average length in mammals (± 3 %; maximum of mammals 7 %). It is quite evident now that the length of the lever-arm of the force, necessary to hold up the head in a certain position, depends on several different factors. VALLOIS (1926) has already shown that one of these factors is the length of that part of the occiput that projects behind the occipital condyles. For this part of the occiput is the lever-arm by means of which the skull must be kept in balance upon the neck. A second factor is the absolute size of the head, which chiefly depends on the absolute size of the whole animal (see p. 30). The third factor is the development of the cervical muscles and ligaments. Man possesses a distinct ligamentum nuchae originating at the occipitale and the neural spines of the 2d—7th cervical vertebra and inserted into the anterior thoracic spines. In the anthropoid apes practically only ligamenta interspinalia are present. The cervical muscles show almost the same structure and development as in the quadrupedal monkeys.

It has already been demonstrated by VALLOIS (1926) that the most important cervical muscle is the m. splenius. The spinalis cervicis shows a comparatively weak and moreover a very various development. VON EGGELING (1922) showed the importance of the m. semispinalis cervicis.

Table 8 shows that generally the quadrupedal monkeys of small size have very short

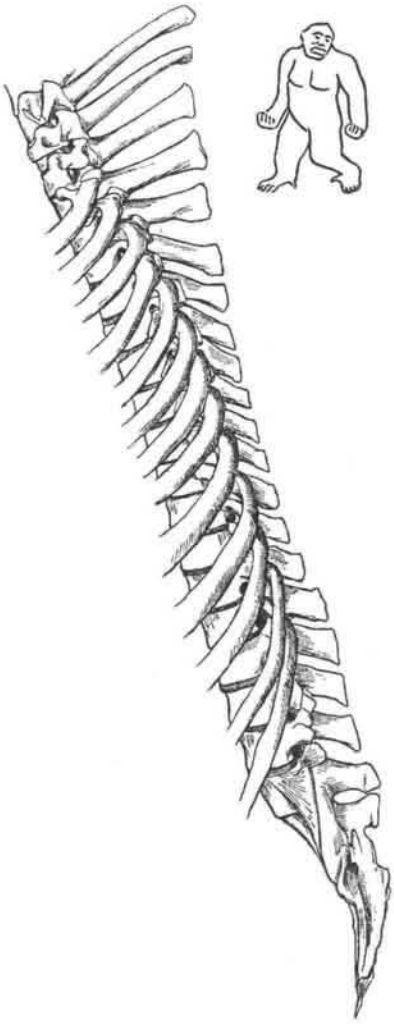


Fig. 115.
Vertebral column of the gorilla, *Gorilla gorilla* (Sav. et Wym.).

cervical spines with the exception of *Loris tardigradus* (L.) in which the postcondylar part of the occiput is very short. The quadrupedal monkeys of moderate size have already longer neural spines. Among these monkeys the longest spines are found in those species that possess the shortest postcondylar part of the occiput. In the big apes that have a comparatively short postcondylar lever-arm, the spines are extraordinarely long; in man whose skull shows a much more favourable lever-arm, the cervical spines are of moderate length. The Neanderthal-man, who had a shorter postcondylar part of the occiput, the cervical spines were longer than in recent man [VALLOIS (1926)]. Thus it has been demonstrated that the demands made on the cervical muscles and ligaments are increasing in the series: quadrupedal monkeys — recent man — Neanderthal-man — anthropoid apes, and that the length of the cervical spines is adapted to these increased demands. This

order of succession is somewhat different from that given by VALLOIS (1926), who did not take account of the absolute size of the animals.

The inclination of the cervical neural spines (see fig. 113) may be of great importance for the reconstruction of the position of the head and neck in fossil man [WEINERT (1941, p. 108)]. For the inclination of the spines depends on their own length as well as on the length and position of the postcondylar part of the occiput. This question, however, must still be the subject of more detailed investigations.

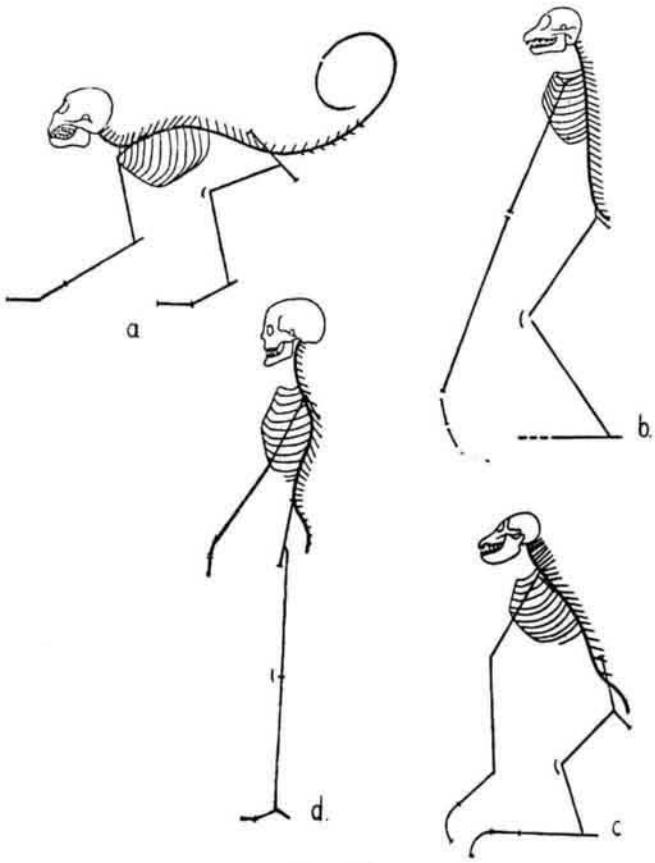



Fig. 116.
Schematic figures of the skeletons of the different types of Primates. a. Capuchin monkey, *Cebus capucinus* (L.), walking-climbing monkey. b. White-handed gibbon, *Hylobates lar leuciscus* Geoffr., hanging-climbing monkey. c. Orang-utan, *Pongo pygmaeus* (Hoppius), hanging-climbing ape. d. Man, *Homo sapiens* L., bipedal walking mammal. The length of the neural spines is exaggerated.

## D. The aquatic mammals.

In chapter V it has been pointed out that the mobility of the body-axis and the structure of the spinal musculature of the otter [*Lutra lutra* (L.)] do not differ very much from the terrestrial mammals. In consequence the length and direction of the neural spines are also the same as in the land-mammals.

The *Pinnipedia* still possess a distinct diaphragmatic vertebra in the

caudal part of the thoracic region. The mobility of their body-axis, however, is greater than in their terrestrial relatives. A very striking characteristic is the shortness of their neural spines (table 7), a phenomenon that without doubt is intimately connected with the poor development of the m. spinalis and the tendons of the m. longissimus inserted into the neural spines. This reduction of the neural spines and their muscles depends on the fact that an important part of the swimming-movements are exercised in the lateral in stead of in the sagittal direction (see p. 70). This increase of the lateral movements also caused an increase in strength of the m. ilio-costalis as well as the lateral projection of the ala ilii and the metapophyses. In the seal (*Phoca*) the lateral movements are still of more importance than in the sea-lion (*Zalophus*). Consequently in *Phoca* the neural spines are shorter and the metapophyses are projecting more laterally than in *Zalophus* (fig. 117). The distance between left and right

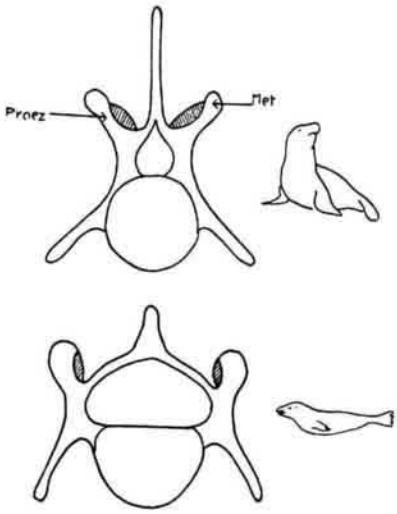



Fig. 117.
Schematic drawing of the 3d lumbar vertebra of a sea-lion, *Zalophus californianus* (Lesson), and a common seal, *Phoca vitulina* L., to show the differences in the length of the neural spines and the position of the praezygapophyses and metapophyses. Cranial view.

metapophysis is in *Phoca* 7 % of the trunk-length, in terrestrial Carnivores 4,5—5,5 % and in *Zalophus* 4,5 %.

With regard to the inclination of the neural spines, the sea-lion (first two lumbar spines upright, 3—5 L caudally inclined) also takes an intermediate position between the land-mammals and the seals (all neural spines caudally inclined). The caudal inclination of the spines must evidently be ascribed to the poor development of the m. spinalis and the tendons of the m. longissimus attached to the neural spines, as well as to the comparatively short bodies of the lumbar vertebrae (table 7 and 101).

In the permanent aquatic mammals (*Cetacea, Sirenia*) the length of the thoracic neural spines does not differ very much from that in the terrestrial mammals. The lumbar spines, however, are distinctly longer (in *Phocaena* for example 7,2 % of the trunk-length). This characteristic may be directly connected with the increased mobility of this region.

In a previous paper [SLIJPER (1936, p. 415) see also p. 77 of this paper] I have already pointed out that with regard to the inclination of the neural spines, several different groups may be distinguished, although I must recant my explanation of this phenomenon.

In the *Sirenia, Archaeoceti, Mystacoceti* and *Ziphiidae* the neural arches are short, the neural spines very long; the metapophyses are attached to the arches on a low level and very well developed (fig. 119, 120). The zygapophyses show the tendency to disappear, the diaphragmatic vertebra is shifted in the cranial direction or all articular surfaces may even be of the tangential type; the neural spines do not limit the mobility of the body-axis in the sagittal plane. It is highly probably that the animals swim by means of undulating

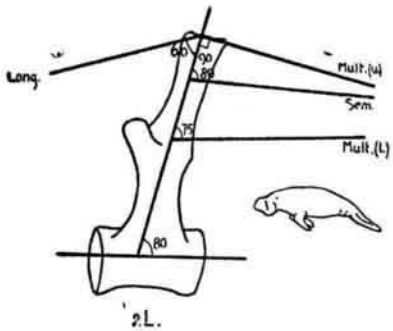



Fig. 118.
Schematic drawing of the 2d lumbar vertebra of the dugong, *Dugong australis* (Owen), to demonstrate the angle of attachment of the most important muscles.

movements of their whole body, although it is quite evident that these movements will increase in the caudal direction. The neural spines are all inclined caudally. This may be ascribed to the following facts: 1st. There is no m. spinalis that originates at the prae- and is inserted into the postdiaphragmatic vertebrae. 2d. With the exception of the *Mystacoceti*, the tendons of the m. longissimus inserted into the neural spines show the same or even a weaker development than those inserted into the metapophyses. 3d. The m. transverso-spinalis is very strongly developed, especially in the lumbar region. Thus as fig. 118 shows, this muscle is attached perpendicular to the neural spines. 4th. The lumbar vertebral bodies are comparatively short (3,3—5,0 % of the trunk-length; see also p. 101).

In the *Odontoceti* (with the exception of the *Ziphiidae*) the following phenomena may be observed (fig. 119, 120): 1st. The metapophyses of the lumbar region shift dorsally; the neural spines are caudally inclined: *Physeteridae, Eurhinodelphidae, Inia, Stenodelphis, Pseudorca*. 2d. Dorsally shifted metapophyses. The neural arches of a part of the lumbar vertebrae are inclined cranially. Neural spines caudally inclined: *Acrodelphidae, Delphinapteridae, Kogia, Lipotes, Kentriodon, Grampus orca, Orcella, Globicephalus*. 3d. Very marked dorsal shifting of the metapophyses. In a certain part of the lumbar region the neural spines as well as the arches are inclined cranially, so that there is a kind of anticliny. The greatest caudal inclination is 75°, the greatest cranial inclination 145°: *Platanista, Delphinidae* with the exception of the above-mentioned species. *Phocaenidae*.

Almost parallel with these changes in the position of the neural spines, arches and metapophyses, an increase in number of the zygapophyses, a shifting backward of the diaphragmatic vertebra and the appearance of other factors limiting the sagittal movements may be observed (table 7). And indeed, the mobility of the cranial part of the trunk in these animals seems to be less than in the other permanent aquatic mammals. The movements especially take place in the posterior lumbar and the caudal region (p. 72).

In consequence of the appearance of a more localised mobility, the importance of the m. longissimus is increasing, that of the m. transverso-

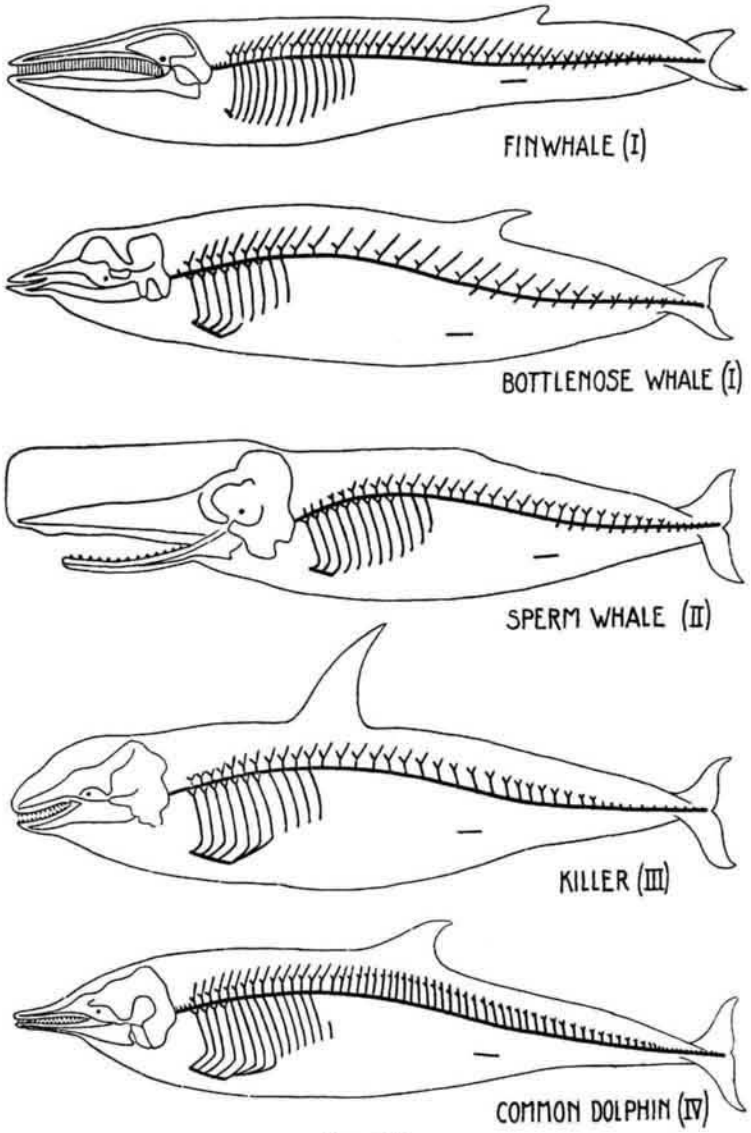



Fig. 119.

Schematic figure of the body-outline and skeleton of five Cetacea, to show the four different types that may be distinguished with regard to the position of the metapophyses and the direction of the neural arches and spines. I. All neural spines caudally inclined, position of all metapophyses low; Fin-whale, *Balaenoptera physalus* (L.) (*Mystacoceti*), Bottlenose whale, *Hyperoodon ampullatus* (Forst.) (*Ziphiidae*). II. All neural spines caudally inclined, metapophyses shifting upward in the lumbar and anterior caudal region; Sperm-whale, *Physeter macrocephalus* L., (*Physeteridae*). III. Neural spines inclined caudally, neural arches of posterior lumbar region cranially inclined, metapophyses shifting upward; Killer, *Grampus orca* (L.) (*Orca-Globicephalus*-group of *Delphinidae*). IV. Neural arches and neural spines of posterior lumbar and anterior caudal region inclined cranially, metapophyses shifting upward; Common dolphin, *Delphinus delphis* L. (*Delphinidae*).

spinalis, on the contrary, decreasing. The shifting upward of the metapophyses gives a greater lever-arm to the metapophysial tendons of the longissimus, but makes the area of origin of the transverso-spinalis smaller.

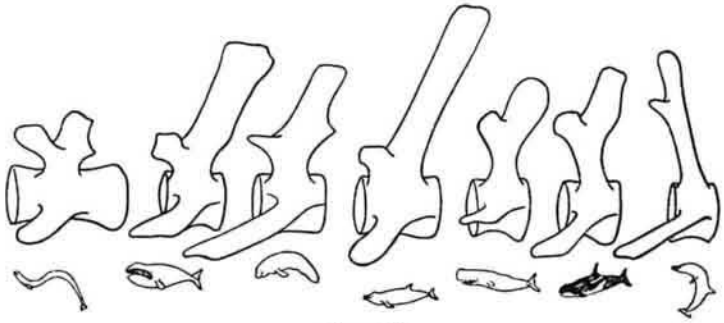
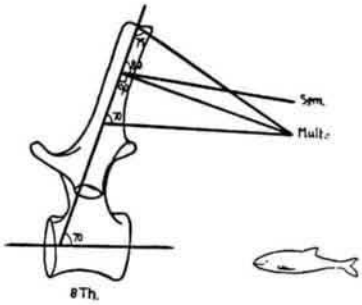


Fig. 120.
Schematic figures of one of the last lumbar vertebrae of six Cetacea and one Sirenian belonging to the four different types of the vertebral column, reproduced in fig. 119. From left to right: Eocene Archaeocete, *Basilosaurus cetoides* (Owen) (*Archaeoceti;* type I); Greenland right whale, *Balaena mysticetus* L. (*Mystacoceti;* type I); *Dugong australis* (Owen) (*Sirenia;* type I); Sowerby's whale, *Mesoplodon bidens* Sowerby (*Ziphiidae;* type I); Sperm whale, *Physeter macrocephalus* L. (*Physeteridae;* type II); Killer, *Grampus orca* L. (*Orca-Globicephalus*-group of *Delphinidae;* type III); Common dolphin, *Delphinus delphis* L. (*Delphinidae;* type IV).

And indeed, in the lumbar region of these animals the transverso-spinalis does not show such a big development as in the other *Cetacea*. Thus in a certain area of the lumbar region the importance of the longissimus is greater than that of the transverso-spinalis and consequently the neural spines are inclined cranially. Fig. 121 shows that although these spines are



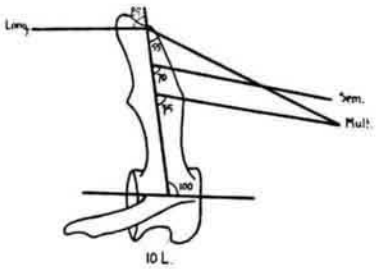




Fig. 121.
Schematic drawing of two vertebrae of a common porpoise, *Phocaena phocaena* (L.) to demonstrate the angle of attachment of the most important muscles.

inclined cranially, the angle of attachment of the semispinalis-fascicles is not so unfavourable as might be expected, since the metapophyses of the caudal vertebrae lay on a comparatively high level.

E. The bipedal goat.

Although it would be very attractive to prove the exactness of the considerations given in this chapter in an experimental way, the technical difficulties of these experiments make them almost impossible. MORITA (1912, 1913) has made some attempts in this direction by cutting or extirpating the ligaments and muscles of the anterior thoracic vertebrae of the rabbit. In my opinion, however, his conclusions are not exact. The fact that the inclination of the apical part of the anterior thoracic spines diminished when the ligaments were cut, may be better explained by supposing that then the importance of the splenius and spinalis increased. It is not impossible that, when MORITA extirpated both the muscles and ligaments, the little fascicles of the multifidus and submultifidus were left intact and that they caused the greater caudal inclination of the spines.

Fortunately, however, the changes that had taken place in the vertebral column of the bipedal goat [see p. 5 and SLIJPER (1942)], gave the opportunity to draw some conclusions based on a kind of natural experiment. The vertebral column of this bipedal goat (fig. 122) was more bent in the

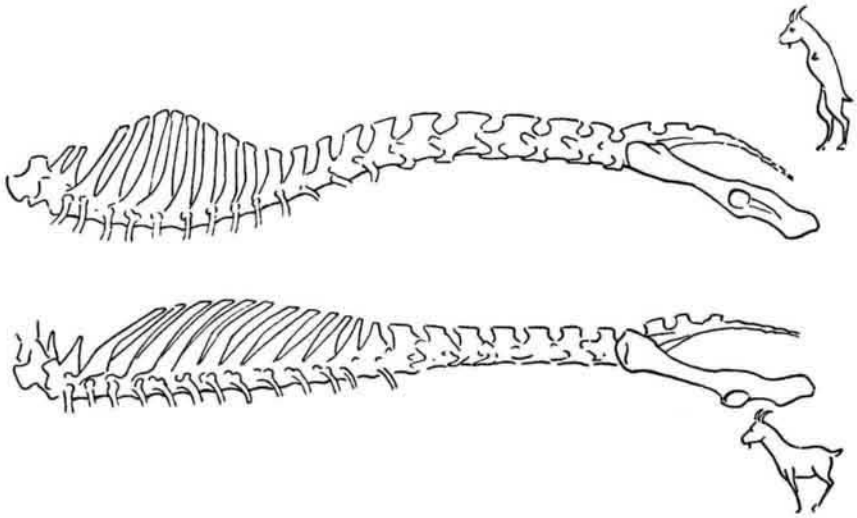


Fig. 122.
Vertebral column of a normal and of the bipedal goat.

dorsal direction (ventral concave) than in the control-animal, evidently in order to bring the centre of gravity above the supporting surface. With regard to the epaxial muscles I had the impression that the longissimus was a little better developed, that the spinalis showed the same, but the transverso-spinalis a minor development than in the control-animal. The

other spinal muscles showed no differences. Moreover I established the remarkable fact that the abdominal muscles showed a minor development than in the control-animal, but that the tunica flava was much stronger developed. With the differences in shape of the vertebral bodies I have already dealt with on page 41.

Fig. 123 shows that all neural spines of the bipedal goat were longer

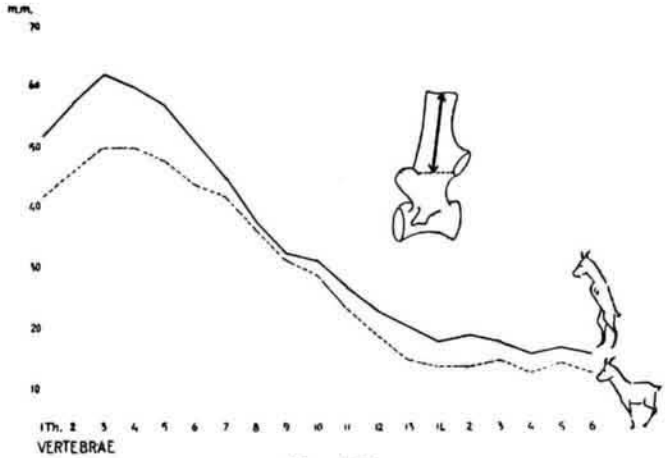



Fig. 123.
Curves of the length of the neural spines in a normal and in the bipedal goat. The measurements of the control-animal were converted into a ratio of 100 : 84, since the normal goat was greater than the bipedal one. See SLIJPER (1942).

than those of the control-animal. In the 1st—6th thoracic vertebra, however, the difference was very great, a moderate difference was found in the 10th thoracic—6th lumbar vertebra and only a very small difference in the 7th—10th thoracic vertebra (see also fig. 122). Since the most important area of origin of the m. spinalis is found at the 1st—6th thoracic and its most important area of insertion at the 1st—6th lumbar vertebra, this increase in length has evidently taken place to give the m. spinalis a greater lever-arm. The curves of the breadth of the neural spines (cranio-caudal diameter; fig. 124) show the same shape and the same differences as the

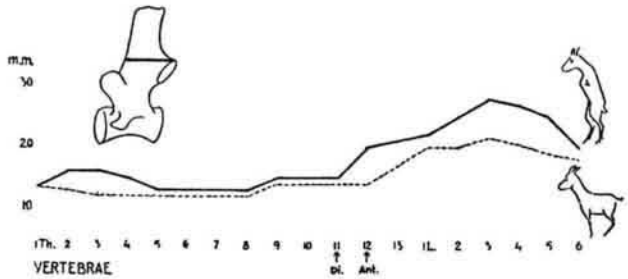



Fig. 124.
Curves of the breadth of the neural spines in a normal and in the bipedal goat. See fig. 123.

curves of the length. This is not a very astonishing fact, since the longer the lever-arms, the greater their moments of resistance and consequently the greater the breadth of the spines (the $h$ of the $bh^2$; see p. 32) must be.

Fig. 122 and 125 show that in the bipedal goat the neural spines of the anterior 10 thoracic vertebrae show a much less inclination than those of the quadrupedal one; they stand almost upright. In stead of showing a

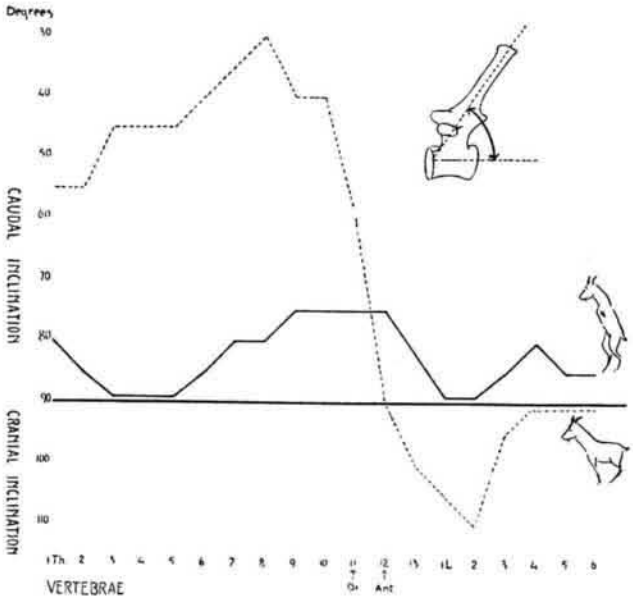



Fig. 125. Curves of the inclination of the neural spines in a normal and in the bipedal goat. *Di* = diaphragmatic, *Ant.* = anticlinal vertebral.

moderate cranial inclination, the neural spines of the 12th thoracic—6th lumbar vertebra stand also almost upright, or they show even a weak caudal inclination. Thus the changes in the position of the neural spines have taken place in the same regions as the changes in their length and evidently these changes must also be connected with the m. spinalis. Since all lever-arms of this muscle are lengthened, the importance of the muscle is greatly increased, not only with regard to the m. longissimus, but also with regard to the multifidus and submultifidus. Consequently the neural spines show the tendency to place their longitudinal axes perpendicular to the direction of the m. spinalis.

The fact that the fatigue of the muscles in this bipedal animal sooner sets in (see also p. 41 and 105), has thus been anticipated by an increase in length of the lever-arms of the m. spinalis. Then the increased importance of the m. spinalis caused the upright position of the neural spines.

Unfortunately the authors, who made researches upon the skeleton of bipedal dogs and cats [see SLIJPER (1942)], give no data about the body-axis. KRÜGER (1927 a) made researches upon a dog with an immovable knee-point. The body-weight of this animal was chiefly carried by the fore-legs. From his fig. 4 it might be concluded that in this dog corresponding changes in length and inclination of the neural spines had taken place as in the bipedal goat.

# VII

# SUMMARY AND CONCLUSIONS

## A. General considerations.

The body-axis (vertebral column and spinal musculature) of mammals may neither be compared to an arched roof, nor to a bridge. In the first place it forms part of the construction of the whole trunk-skeleton. This construction may be considered as an elastic bow (pelvis and body-axis of the trunk) bent in the dorsal direction (ventral concave) by a string (sternum, abdominal muscles, linea alba, extrinsic muscles of the legs). The head and neck may be compared to a loaded beam supported at one end only. On the other hand the whole body-axis may be compared to such a beam if the animal stands or sits on its hind quarters only, a posture that is attained by every mammal now and then. Thus the principal static function of the body-axis is to resist bending in the dorsal direction. The elastic resistance is caused by the strength of the intervertebral discs and ligaments, but chiefly by the tonus of the epaxial musculature.

In the second place the body-axis is an organ of locomotion. It has to transmit the locomotive power from the hind quarters to the forehand (this means chiefly: to resist bending in the dorsal direction) and it has to bend and extend the back in the sagittal plane, especially when the animal moves in a leaping-gallop.

With these considerations as starting-point, an attempt was made to explain the structure and development of the vertebral bodies, the epaxial musculature and the neural spines. For that purpose the skeletons of 90 and the musculature of 80 different species of mammals were studied. The results were affirmed by the aberrant characters of the body-axis of a one year old goat, born without forelegs.

## B. Vertebral bodies.

Since the principal static function of the body-axis is to resist bending in the sagittal plane, the moment of resistance against bending ($bh^2$) of all vertebrae (intervertebral discs) was determined and plotted out in a curve. The stress of an architectural construction must be adapted to that situation at which the demands made on it are maximal. With regard to the vertebral column of quadrupedal mammals this is the erect or semi-erect posture. Thus it could be expected that the diagram of moments would have the shape of a straight line, rising uniformly in the caudal direction. That in reality the curve has a quite different shape, and that there are also marked differences between the different mammals, must be ascribed to the fact that the stress of the body-axis does not depend on

the vertebral bodies only, but also more or less on the other elements of this axis. The better these additional supporting elements in a certain region are developed, the smaller the moments of resistance of the vertebral bodies may be.

In the neck the additional support is given by the dorsal musculature and the lig. nuchae. Since the strength of these supports is inversely proportionate to the absolute size of the animal body, the diagram of the bigger quadrupedal mammals shows a characteristic summit in the lower cervical region. The aberrant shape of the curve in the thorax must be ascribed to the development of the anterior thoracic neural spines and to the true ribs. The horizontal course of the line or its decline in the lumbar region of some species is caused by the lig. ilio-lumbale, accessory articulations between the transverse processes, the increased diameter between the zygapophyses or the embracing zygapophyses. In the whole vertebral column the bodies are always more broad than high, while the additional strengthening is much greater in the sagittal than in the transverse direction.

In the *bipedal mammals* the shape of the diagram agrees quite well with that of a beam supported at one end only. For in these mammals the additional supports are of very small importance since the muscles become tired if the animals retain the erect posture for a comparatively long time. In the *aquatic mammals* only the locomotive power and the resistance of the water must be taken into account. The shape of the curve is the same as that of a beam supported at its middle. In the *Pinnipedia* the shape is intermediate between that of the terrestrial and the permanent aquatic mammals.

## C. The epaxial musculature and the mobility of the vertebral column.

The epaxial musculature of mammals has chiefly to prevent or to exercise movements in the sagittal direction. In primitive terrestrial mammals the mobility of the body-axis is almost the same in every region of the trunk. The more the animals, however, move forward in the leaping-gallop, the more the mobility of the body-axis is limited to the diaphragmatic region (the region where the direction of the zygapophyses is changing).

Hence with increasing specialisation of their type of locomotion, the following adaptations of the musculature may be observed: 1st. A distinct tendency to the development of long fascicles, instead of the short metameric ones, in all three systems of epaxial muscles (ilio-costalis, longissimus, transverso-spinalis). The fibres chiefly originate at the prae- and are inserted into the postdiaphragmatic vertebrae. 2d. A distinct tendency to a shifting upward of the insertion of all three systems from the transverse processes and metapophyses into the summits of the neural spines, in order to get a longer lever-arm in the sagittal direction. This tendency is especially

demonstrated by the reduction of the ilio-costalis and its fusion with the caudal part of the longissimus (erector spinae) as well as by the development of the m. spinalis and the aponeurosis of the m. longissimus.

Moreover, the attention may be directed to the development of the m. ilio-lumbalis and the gluteal tongue.

With increasing specialisation, in the *Ungulata* the leaping-gallop is replaced by the horse-gallop or the amble. Both paces are characterized by the fact that the mobility of the back is practically limited to the lumbo-sacral joint. Special adaptations of the musculature are its transformation from a motion- into a tension-musculature and the shifting of the insertion of the longissimus dorsi from the lumbar into the sacral spines.

The mobility of the body-axis of the *anthropoid apes* and *man* is only very small. Hence an increase in development of the tension-musculature (semispinalis, multifidus) at the cost of the motion-musculature (chiefly of the spinalis) can be observed. The special loss of mobility in the diaphragmatic region is attended with an extension of the area of insertion of the longissimus and semispinalis from the post- into the praediaphragmatic region.

In the permanent *aquatic mammals* (*Cetacea, Sirenia*) the centre of mobility of the body-axis lies at the base of the tail. The special fascicles of the semispinalis and longissimus between the prae- and postdiaphragmatic vertebrae have disappeared. There is no spinalis dorsi, but a special type of spinalis. All three systems of the trunk-musculature are fused with the corresponding elements of the neck and tail. The ilio-costalis is very well developed and completely separated from the longissimus (lateral movements). In the specialised *Cetacea* the lever-arm of the metapophysial tendons of the longissimus and transverso-spinalis is enlarged by a shifting upward of the metapophyses in the posterior lumbar and anterior caudal region.

## D. The neural spines.

*General considerations:*

1. Although in certain mammals and in certain regions of the body-axis the height and inclination of the spines go very well with the bow and-string-construction of the trunk, these characters of the spines are in no way directly determined by the demands of this construction, nor by any other static demands made on the vertebral column.

2. The neural spines must be considered as levers, transmitting the muscular force to the vertebral bodies. Height and direction of the spines are determined by this force.

3. The most important factor determining the differences in height of the spines between the different mammals, is the absolute size of the animals. For with increasing body-size the strength of the muscles relatively decreases and thus the length of their lever-arms must increase.

The length of the neck and the weight of the head may have a certain

influence. Both factors also may be held responsible for the development of the ligamentum nuchae (*Canidae, Ungulata*). The height of the cervical spines in the *Primates* is determined by the absolute body-size and by the length of that part of the occiput that projects behind the condyles.

The differences in height of the spines between the different regions of the vertebral column are determined by the importance of the muscles attached to them. The height increases with increasing importance of the muscles.

4. The most favourable direction of the spines is the direction perpendicular to that of the muscular and ligamentous forces acting on them. This fact is based on two different reasons:

a. If the neural spines show this direction a maximal effect is attained with a minimal length of the spines. Thus: economizing of material. The direction of the spines is intermediate if two or more muscles of almost equal importance are attached to them. In other cases the direction is perpendicular or nearly perpendicular to the muscle with the highest importance.

b. The manner of attachment of the muscles to the periosteum of the neural spines (encircling fibres) as well as the manner in which the periosteum and the directly intruding tendons are attached to the compacta (fibres intruding between the osteones and encircling them) may be compared to a rope attached to a pile by means of a noose. Since the direction of the osteones is the same as that of the whole neural spines, the perpendicular attachment prevents the slipping down of the rope.

*Explanation of characters of neural spines:*

With the aid of the above-mentioned principles the differences in the direction of the neural spines in the different regions of the body-axis as well as in the different species of mammals could be explained. The fact that it was possible to give a satisfactory explanation affirmed the exactness of the principles.

From the terrestrial mammals in general it can be said that the upright position or cranial inclination of the cervical spines is chiefly determined by the m. spinalis cerv. and the lig. nuchae. In the praediaphragmatic region all spines are inclined more or less caudally. This direction gives the most favourable angle of attachment (70—90°) to the different muscles. Mutual differences in the slope of the spines can be explained by mutual differences in the development of the muscles.

Two factors may chiefly be held responsible for the differences in the postdiaphragmatic region. In the *Monotremata, Marsupialia, Edentata* and *Rodentia* with increasing importance of the spinalis and the spinal tendons (aponeurosis) of the longissimus, the caudally inclined spines show the tendency to attain an upright position or a cranial inclination (appearance of anticliny). In the *Carnivora* and *Primates* the direction is chiefly determined by the length of the vertebral bodies. For the angle of attach-

ment of the multifidus depends on this length. In the *Insectivora* and *Ungulata* both factors influence the direction of the spines. The caudal shifting of the insertion of the longissimus in Ungulates is responsible for the loss of anticliny in the specialised representatives of this order.

The very great caudal inclination of the middle thoracic spines in the *anthropoid apes* and *man* is caused by the reduction of the m. spinalis and the increased importance of the multifidus and submultifidus. The upright position or caudal inclination of the lumbar spines depends on the same factors as well as on the comparatively short vertebral bodies. In the primitive *aquatic mammals* the uniform caudal inclination of the spines is chiefly caused by the reduction of the spinalis and the increased importance of the other elements of the transverso-spinalis. The shifting upward of the metapophyses in the posterior lumbar region of the specialised *Cetacea* caused a decrease in importance of the transverso-spinalis and an increase of the longissimus in this region. This phenomenon may be held responsible for the cranial inclination of the neural spines in this region.

The exactness of the above-given considerations was affirmed by the aberrant characters of the vertebral column of the *bipedal goat*. The fact that the fatigue of the muscles in this animal sooner appears has been anticipated by an increase in length of the lever-arms of the m. spinalis. The increased importance of this system caused the upright position of the neural spines throughout the whole vertebral column.

## E. Final conclusions.

1. Shape and size of the *vertebral bodies* of mammals depend on the static function of the body-axis to resist bending in the dorsal direction (ventral concave). Their dimensions are highly influenced, however, by the development of the other elements of the body-axis.

2. Structure and development of the *epaxial musculature* are influenced by static factors (for example by the absolute size of the animal body), but they depend chiefly on the type of locomotion of the animals and the corresponding type of mobility of the vertebral column.

3. Structure, development and inclination of the *neural spines* chiefly depend on the structure and development of the epaxial musculature and thus in the last instance also chiefly on the type of locomotion.

# VIII

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TABLE 1.

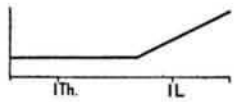
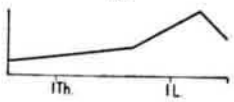
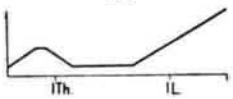
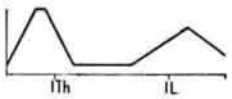
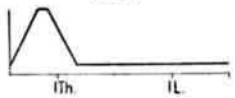
*Origin and insertion of the mm splenius, semispinalis capitis, serratus ventralis and pectoralis profundus in mammals.*

| Species [1]) | M. splenius | | M. semispinalis capitis. Origin from metapophyses of thoracic and from articular processes of cervical vertebrae [3]) | M. serratus ventralis. Origin from cervical vertebrae and ribs [3]) | M. pectoralis profundus. Caudal border of origin [3]) |
|---|---|---|---|---|---|
| | Development [2]) | Insertion [3]) | | | |
| *Monotremata.* | | | | | |
| Tachyglossus aculeatus (Shaw) | | | 2 C.— 1 Th. | | |
| Ornithorhynchus anatinus (Shaw) | + | O. | | | |
| *Marsupialia.* | | O. | | | |
| Phalanger orientalis (Pallas) | ++ | O. | 3 C.— 6 Th. | 3 C.— 8 R. | |
| Metachirops opossum (L.) | ++ | O. | 3 C.— 5 Th. | 3 C.— 7 R. | 8 Cart., Xiph. |
| Metachirus nudicaudatus (E. Geoffr.) | + | O. | 3 C.— 6 Th. | 3 C.— 6 R. | |
| Macropus (Wallabia) ruficollis (Desm.) | ++ | O., 1—2 C. | 2 C.— 5 Th. | 3 C.— 6 R. | Xiph. |
| Macropus giganteus (Zimm.) | ++ | O., 1—2 C. | 2 C.— 6 Th. | 4 C.— 6 R. | 5 Cart. |
| Dorcopsis veterum (Less.) | ++ | O. | 2 C.— 5 Th. | 3 C.— 7 R. | Xiph. |
| Echimypera kalabu (Fischer) | + | O. | 2 C.— 7 Th. | 3 C.— 8 R. | Xiph. |
| *Edentata.* | | | | | |
| Choloepus didactylus (L.) | ± | O. | 3 C.— 2 Th. | 4 C.— 8 R. | 9 Cart. |
| Dasypus novemcinctus L. | ± | O. | 2 C.— 8 Th. | 3 C.— 6 R. | |
| Manis spec. | ++ | O. | [5]) | 3 C.— 8 R. | |
| *Insectivora.* | | | | | |
| Erinaceus europaeus L. | + | O. | 2 C.— 6 Th. | 2 C.— 9 R. | |
| Echinosorex spec. | ++ | O., 1—3 C. | 2 C.— 7 Th. | 3 C.— 9 R. | Xiph. |
| Tupaia spec. | ++ | O., 1—3 C. | 3 C.— 6 Th. | 3 C.— 9 R. | 8 Cart., Xiph. |
| Ptilocercus lowii Gray | ++ | O. | 3 C.— 3 Th. | 3 C.— 8 R. | Xiph. |
| Macroscelides spec. | + | O. | 3 C.— 6 Th. | 3 C.—10 R. | Xiph. |
| Talpa europaea L. | + | O. | 3 C.— 3 Th. | 3 C.— 7 R. | 6 Cart. |
| *Rodentia.* | | | | | |
| Cricetus cricetus (L.) | ++ | O. | 3 C.— 5 Th. | 3 C.— 6 R. | 6 Cart. |
| Arvicola terrestris (L.) | + | O. | 3 C.— 8 Th. | 2 C.— 8 R. | 8 Cart. |
| Cavia porcellus (L.) | | | 3 C.— 5 Th. | | |
| Psammomys algiricus Thomas | ++ | O. | 3 C.— 7 Th. | 3 C.— 8 R. | |
| Jaculus hirtipes (Lichtenstein) | +++ [4]) | O. | 3 C.— 6 Th. | 3 C.— 7 R. | |
| Cuniculus paca (L.) | + | O. | 2 C.— 8 Th. | 3 C.— 7 R. | 7 Cart. |
| Sciurus vulgaris L. | | | 7 C.— 6 Th. | | |
| *Carnivora fissipedia.* | | | | | |
| Putorius putorius (L.) | + | O. | 3 C.— 5 Th. | | |
| Lutra lutra (L.) | ++ | O. | 3 C.— 6 Th. | 3 C.— 7 R. | 9 Cart. |
| Mydaus javanensis (Lesch.) | ++ | O. | 3 C.— 8 Th. | 3 C.— 7 R. | 7 Cart. |
| Canis familiaris L. | ++ | O. | 3 C.— 4 Th. | 3 C.— 7 R. | Xiph. |
| Panthera leo (L.) | ++ | O. | 3 C.— 6 Th. | 3 C.— 8 R. | |
| Euarctos americanus (Pall.) | + | O. | 3 C.— 7 Th. | 1 C.— 8 R. | 7 Cart. |
| Helarctos malayanus (Raffles) | + | O. | 3 C.— 4 Th. | 4 C.— 9 R. | 9 Cart. |
| *Carnivora pinnipedia.* | | | | | |
| Zalophus californianus (Lesson) | ++ | O. | 4— 7 C. | 3 C.—10 R. | |
| Phoca vitulina L. | ++ | O. | 3 C.— 1 Th. | 3 C.— 9 R. | |
| *Tubulidentata.* | | | | | |
| Orycteropus afer (Pall.) | + | O. | 3 C.— 4 Th. | 1 C.— 8 R. | |
| *Ungulata.* | | | | | |
| Tragulus javanicus (Osb.) | + | O., 1—3 C. | 3 C.— 3 Th. | 2 C.— 9 R. [6]) | 9 Cart., Xiph. |
| Equus caballus L. (dom.) | ++ | O., 1—5 C. | 3 C.— 7 Th. | 3 C.— 8 R. | 9 Cart., Xiph. |
| Lama glama (L.) | — | — | 2 C.— 4 Th. | 4 C.— 8 R. | |
| Hippopotamus amphibius L. | ++ | O. | 3 C.—10 Th. | | |
| Sus scrofa L. (dom.) | + | O., 1 C. | | 2 C.— 7 R. | 8 Cart., Xiph. |
| Capra hircus L. (dom.) | + | O., 1—5 C. | 3 C.— 8 Th. | 3 C.— 9 R. | Xiph. |
| Gazella spec. | + | O., 1—6 C. | 3 C.— 5 Th. | 4 C.— 8 R. | |
| Mazama americana (Erxl.) | + | O., 1—5 C. | 2 C.— 7 Th. | 3 C.— 9 R. | Xiph. |
| Capreolus capreolus (L.) | + | O., 1—5 C. | 2 C.— 7 Th. | 3 C.— 9 R. | Xiph. |
| Odocoileus virginianus gymnotis (Wiegm.) | + | O., 1—5 C. | 3 C.— 6 Th. | 3 C.— 9 R. | Xiph. |
| Camelus bactrianus L. | — | — | 3 C.— 5 Th. | 4 C.— 9 R. | Xiph. |
| Tapirus terrestris (L.) | + | O., 1 C. | 3 C.— 8 Th. | 3 C.— 7 R. [7]) | 10 Cart. |
| Bos taurus L. (dom.) | + | O., 1—2 C. | 3 C.— 8 Th. | 3 C.— 9 R. | Xiph. |
| Diceros bicornis (L.) | +++ | O., 1—4 C. | | | |
| Rhinoceros sondaicus Desm. | | | 3 C.— 7 Th. | 2 C.— 7 R. | 7 Cart. |
| Elephas maximus L. | ++ | O. | 3 C.—14 Th. | 3 C.—11 R. | |
| *Sirenia.* | | | | | |
| Dugong australis (Owen) | + | O. | 2 C.— 9 Th. | 3 C.— 7 R. | |
| *Cetacea.* | | | | | |
| Balaenoptera acutorostrata Lacép. | | | 1 Th.— 3 L. | | |
| Delphinapterus leucas (Pallas) | + | O. | [5]) | 3 C.— 4 R. | |
| Phocaena phocaena (L.) | + | O. | 2 C.— 6 Th. | | |
| *Primates.* | | | | | |
| Nycticebus spec. | + | O. | 1— 4 Th. | 3 C.—11 R. | 9 Cart. |
| Tarsius tarsius (Erxleb.) | + | O. | | 3 C.— 7 R. | Lin. |
| Saimiri sciureus (L.) | + | O. | 3 C.— 6 Th. | 3 C.— 9 R. | 8 Cart. |
| Erythrocebus patas (Schreb.) | + | O., 1—2 C. | 3 C.— 5 Th. | | |
| Lemur spec. | | | 3 C.— 6 Th. | | |
| Callithrix spec. | | | 3 C.— 6 Th. | | |
| Cercopithecidae | | | 2 C.— 5 Th. | | |
| Cercopithecus spec. | + | O., 1 C. | 2 C.— 7 Th. | 3 C.— 9 R. | 9 Cart. |
| Papio cynocephalus (L.) | + | O. | 3 C.— 7 Th. | 3 C.—10 R. | 10 Cart. |
| Macaca mulatta (Zimmerm.) | + | O., 1 C. | 3 C.— 7 Th. | | |
| Ateles paniscus (L.) | | | 3 C.— 4 Th. | 3 C.— 8 R. | 5 Cart. |
| Hylobates lar leuciscus Geoffr. | + | O., 1—2 C. | 2 C.— 4 Th. | | |
| Pan paniscus Schwarz | + | O., 1—3 C. | 3 C.— 5 Th. | | |
| Gorilla gorilla (Sav. et Wym.) | + | O., 1 C. | 3 C.— 7 Th. | 3 C.— 9 R. | |
| Pongo pygmaeus (Hoppius) | | | 2 C.— 3 Th. | | |
| Homo sapiens (L.) | + | O., 1—3 C. | 3 C.— 4 Th. | 1—4 C.; 1—9 R. | 6 Cart. |

1) For the age of the animals and the authors of the publications from which some of the data are taken, see table 3.
2) — = absent. ± = present; weakly developed. + = present; normal development. ++ = present; strongly developed. +++ = extremely strong development.
3) O. = occipitale. C. = cervical vertebrae. Th. = thoracic vertebrae. L. = lumbar vertebrae. R. = rib. Cart. = costal cartilage. Xiph. = xiphoid cartilage of sternum. Lin. = linea alba half-way the abdomen.
4) Caudal border of origin lies in the middle of the thoracic region.
5) No separate semispinalis capitis, it is the cranial part of the undifferentiated m. transverso-spinalis.
6) The origin from the ribs lies more ventral than in other mammals.
7) The origin from the ribs lies more ventral than in other mammals. There is a separate dorsal part, originating from the 1st—5th rib.

TABLE 2.

*Survey of the characteristics of the curves representing the bending-moment ($bh^2$) of the vertebral bodies in quadrupedal terrestrial mammals.*

| Type of curve | Species | Summit of curve in the neck | Beginning of rising of curve in thorax | Beginning of decline of curve in lumbar region | Author |
|---|---|---|---|---|---|
| Ia   | Loris tardigradus (L.) | — | 10 Th. | — | Original |
| | Macaca irus fascicularis (Raffles) | — | 8 Th. | — | " |
| | Manis javanica Desm. | — | 12 Th. | — | " |
| | Sciurus vulgaris L. | — | 8 Th. | — | " |
| | Didelphis spec. | — | 8 Th. | — | " |
| | Hydrochoerus hydrochaerus (L.) [1]) | — | 12 Th. | — | VIRCHOW (1910a) |
| | Castor fiber L. [1]) | — | 12 Th. | — | NAUCK (1932) |
| Ib   | Pongo pygmaeus (Hoppius) | — | 8 Th. | 3 L. | Original |
| | Gorilla gorilla (Sav. et Wym.) | — | 8 Th. | 3 L. | NAUCK (1932) |
| | Euarctos americanus (Pall.) | — | 10 Th. | — | VIRCHOW (1910) |
| | Felis catus L. | — | 9 Th. | 5 L. | AUER (1914) |
| | Choloepus hoffmanni Pet. | — | 10 Th. | 2 L. | Original |
| II   | Panthera leo (L.) | 6 C. | 9 Th. | 4 L. | Original |
| | Vulpes vulpes (L.) | 5—7 C. | 7 Th. | — | " |
| | Canis familiaris L. | 6—7 C. | 9 Th. | — | " |
| | Sus scrofa L. (dom.) | 4 C. | 10 Th. | — | " |
| IIIa   | Choeropsis liberiensis (Mort.) | 5—6 C. | 13 Th. | — | Original |
| | Elephas maximus L. | 4 C. | 15 Th. | — | " |
| IIIb   | Lama glama (L.) | 7 C. | 12 Th. | 3—6 L. | Original |
| | Hippopotamus amphibius L. | 1 Th. | 12 Th. | 3 L. | " |
| | Bos taurus L. (dom.) | 6—7 C. | 12 Th. | 3 L. | " |
| | Equus caballus L. (dom.) | 6—7 C. | 9—12 Th. | 1 L. | Orig. See also WENGER (1915) |
| | Equus (Asinus) asinus L. | 5 C. | 10 Th. | 3 L. | NAUCK (1932) |
| | Taurotragus oryx (Pall.) | 6 C. | (11 Th.) [2]) | (3 L.) [2]) | Original |
| IIIc   | Diceros bicornis (L.) | 6 C. | — | — | VIRCHOW (1910b) |
| | Capra hircus L. (dom.) | 7 C. | — | — | Original |
| | Ovis aries L. (dom.) | 7 C. | — | — | " |
| | Dama dama (L.) | 7 C. | — | — | " |
| | Capricornis sumatraensis (Bechst.) | 7 C. | — | — | " |

[1]) *Hydrochoerus* and *Castor* show already the beginning of a cervical summit.
[2]) Only a very slight rising and decline in the posterior thoracic and lumbar region.

TABLE 3

*Some characteristics of the epaxial spinal musculature in mammals.*

In the different orders the species are arranged after the inclination of their post-anticlinal neural spines.
C. = cervical (vertebrae, spines, region), Th. = thoracic, L = lumbar, S = sacral, Ca. = caudal, Sk. = skull.

| Species | Sex, age, length in cm [1] | Vertebral column: Maximal inclination of post-anticlinal vertebrae in degrees [2] | Vertebral column: Anticlinal vertebra (Th.) [3] | Vertebral column: Diaphragmatic vertebra (Th.) [4] | Number of vertebrae: Th. | Number of vertebrae: L. | Number of vertebrae: S. | Musc. ilio-costalis: Fusion with m. longissimus [5] | Musc. longissimus dorsi: Insertion into: Metapophyses (proc. mamm.) [6] | Musc. longissimus dorsi: Insertion into: Neural spines [6] | Musc. longissimus dorsi: Strongest developed inserting tendons [7] | Musc. transverso — spinalis: General structure [8]: Praediaphragmatic region | Musc. transverso — spinalis: General structure [8]: Postdiaphragmatic region | Musc. transverso — spinalis: Development in relation to m. longissimus [9] | Musc. transverso — spinalis: Musc. semispinalis [10]: Origin | Musc. transverso — spinalis: Musc. semispinalis [10]: Insertion | Musc. transverso — spinalis: Musc. semispinalis [10]: Manner of insertion [11] | Musc. transverso — spinalis: Musc. semispinalis [10]: Development in relation to other parts of m. transv. [12] | Musc. transverso — spinalis: Musc. spinalis [10]: Origin | Musc. transverso — spinalis: Musc. spinalis [10]: Insertion | Musc. transverso — spinalis: Musc. spinalis [10]: Manner of insertion [13] | Musc. transverso — spinalis: Musc. spinalis [10]: Development in relation to other parts of m. transv. [12] | Author (when not original) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Monotremata.* | | | | | | | | | | | | | | | | | | | | | | | |
| Tachyglossus aculeatus (Shaw) | | (70) | — | — | 16 | 5 | 4 | + [14] | — [15] | — [15] | — | Tr. | Tr. | ++ | — | — | — | — | — | — | — | — | VALLOIS (1922) |
| Ornithorhynchus anatinus (Shaw) | A. 25 | 100 | 16 | — | 17 | 2 | 3 | — | — [15] | — [15] | — | Tr. + Sp. | Tr. | ++ | — | — | — | — | 13—14 Th. | 15 Th.—1 S. | S. | ++ | VIRCHOW (1929) |
| *Marsupialia.* | | | | | | | | | | | | | | | | | | | | | | | |
| Phalanger orientalis (Pallas) | N. 22 | (75) | — | 9 | 13 | 6 | 2 | ± | 12 Th.—5 L. | 2 L.—2 S. | M. | Sm. + Sp. | Tr. | | 1—13 Th. | 8 Th.—4 L. | S.—F. | ++ | 1—13 Th. | 2—4 L. | F. L. | —— | |
| Metachirops opossum (L.) | ♂ A. 24 | (85) | — | 9 | 13 | 6 | 2 | + | 11 Th.—3 L. | 3 L.—2 S. | M.—P. | Sm. + Sp. | Tr. | | 1—12 Th. | 11 Th.—3 L. | F. | ++ | 1—13 Th. | 3—4 L. | F. L. | —— | |
| Metachirus nudicaudatus (E. Geoffr.) | ♀ A. 10 | (85) | — | 9 | 13 | 6 | 2 | ± | 11 Th.—5 L. | 1—5 L. | M. | Tr. + Sm. | Tr. + Sm. | + | 1—10 Th. | 11 Th.—1 L. | S. | + | — | — | — | — | |
| Macropus (Wallabia) ruficollis (Desm.) | ♂ Y. 30 | 110 | 10 | 11 | 13 | 6 | 2 | + | 12 Th.—2 L. | 12 Th.—2 S. | M.—P. | Sm. + Sp. | Tr. [16] | + | 1—11 Th. | 12 Th.—2 L. | F. | + | 1—11 Th. | 12 Th.—2 L. | F. L. | + | |
| Macropus giganteus Zimm. | ♀ Y. 60 | 110 | 11 | 10 | 13 | 6 | 2 | + | 12 Th.—1 L. | 12 Th.—2 S. | P. | Sm. + Sp. | Tr. | + | 1—6 Th. | 10 Th.—2 L. | S.—F. | ± | 1—11 Th. | 12 Th.—3 L. | F. L. | + | |
| Dorcopsis veterum (Less.) | ♀ Y. 25 | 115 | 12 | 11 | 13 | 6 | 2 | + | 1—3 L. | 1 L.—2 S. | P. | Sm. + Sp. | Tr. [17] | + | Sk.—10 Th. | 9—13 Th. | S. | + | Sk.—10 Th. | 11 Th.—1 L. | F. L. | — | |
| Echimypera kalabu (Fischer) | ♂ Y. 23 | 115 | 12 | | 13 | 7 | 3 | (±) | 12 Th.—2 L. | 2 L.—3 S. (F.) | M.—P. | Sm. + Sp. | Tr. | | 1—12 Th. | 5 Th.—2 L. | S.—F. | ++ | 1—12 Th. | 2—4 L. | F. F. | —— | |
| *Edentata.* | | | | | | | | | | | | | | | | | | | | | | | |
| Choloepus didactylus (L.) | ♀ Y. 25 | — | — | 21 | 24 | 3 | 8 | — | 1 Th.—3 L. | — | M. | M. | M. | | — | — | — | — | — | — | — | — | |
| Dasypus novemcinctus L. | ♂ A. 37 | (55) | — | 8 | 11 | 5 | 9 | — | 8 Th.—5 L. | — | M. | Tr. | Tr. | + | — | — | — | — | — | — | — | — | |
| Manis spec. | ♀ A. 24 | (80) | — | 10 | 14 | 5 | 5 | — | 1 Th.—5 S. (F.) | 1 Th.—5 S. (F.) | M. | Tr. + Sp. | Tr. | ++ | 1 Th.—5 S. | 1 Th.—5 S. | S. | ++ | ? | 15 Th.—5 L. | F. F. | —— | |
| *Insectivora.* | | | | | | | | | | | | | | | | | | | | | | | |
| Erinaceus europaeus L. | ♂ A. 29 | (90) | — | 13 | 14 | 6 | 4 | (±) | 3—8 Th. | 12 Th.—4 S. | P. | Tr. | Tr. | + | — | — | — | — | — | — | — | — | |
| Echinosorex spec. | ♀ A. 19 | 100 | 12—13 | | 15 | 5 | 4 | (±) | 15 Th.—3 S. | 3 L.—3 S. | | Sm. + M. | Tr. | | 1—13 Th. | 15 Th.—2 L. | F. L. | — | — | — | — | — | |
| Talpa europaea L. | ♂ A. 13 | 100 | 9 | 12 | 13 | 7 | 6 | ++ | 12 Th.—3 L. | 1 L.—3 S. (F.) | M. | Tr. + Sm. + Sp. | Tr. | | 1—11 Th. | 12 Th.—1 L. | F. L. | — | 1—11 Th. | 1—2 L. | F.L.—F.F. | — | |
| Tupaia spec. | ♀ A. 19 | 110 | 10 | 10 | 12 | 7 | 3 | ± | 12 Th.—4 L. | 1—4 L. (F.) | M. | Sm. + Sp. | Tr. | + | 1—11 Th. | 12 Th.—4 L. | F. L. | + | 1—11 Th. | 1—4 L. | F.L.—F.F. | —— | |
| Macroscelides spec. | ♀ A. 7 | 120 | 10 | 12 | 13 | 8 | 2 | ± | 13 Th.—8 L. | 5 L.—2 S. (F.) | M. | Tr. + Sm. | Tr. | | 1—9 Th. | 10 Th.—2 L. | S. | ± | — | — | — | — | |
| Ptilocercus lowii Gray | | 120 | 11 | 10 | 14 | 6 | 3 | — | 11—14 Th. | 12 Th.—3 S. [18] | | Sm. + M. | Sm. + M. | — | 4—6 Th. | 11—14 Th. | F. L. | — | — | — | — | — | LE GROS CLARK (1924) |
| *Chiroptera.* | | | | | | | | | | | | | | | | | | | | | | | |
| Chiroptera | | — | — | | 11—13 | 5 | 5 | ++ | O [26] | 3 L.—5 S. [27] | P.? | Tr. | Tr. | + [28] | — | — | — | — | — | — | — | — | VALLOIS (1922) |
| *Rodentia.* | | | | | | | | | | | | | | | | | | | | | | | |
| Cricetus cricetus (L.) | ♂ A. 12 | (80) | — | 11 | 13 | 6 | 2 | ++ | 12 Th.—5 L. | 2 L.—2 S. | M.—P. | Sm. + M. + Sp. | M. | | 1—11 Th. | 12 Th.—2 L. | S. | ++ | 1—11 Th. | 1—2 L. | F. L. | —— | |
| Arvicola terrestris (L.) | ♂ A. 16 | (90) | — | 11 | 13 | 7 | 3 | ++ | 1 L.—3 S. | 1 L.—3 S. | M.—P. | Sm. + M. + Sp. | M. | | 1—10 Th. | 12 Th.—1 L. | S. | ++ | 1—11 Th. | 1—3 L. | F. L. | —— | |
| Cavia porcellus (L.) | ♀ A. 31 | 130 | 11 | 12 | 13 | 6 | 4 | ++ | 13 Th.—5 L. | 1 L.—4 S. | M.—P. | Sm. + M. + Sp. | M. | | 3 C.—12 Th. | 1—13 Th. | S. | + | 3 C.—12 Th. | 13 Th.—3 L. | S.—F. | + | |
| Thomomys bottae (Eyd. et Gerv.) | | 130 | 10—11 | | 12 | 7 | 5 | ++ | | | | Tr. | Tr. | | + | + | | | — | — | — | — | HILL (1937) |
| Psammomys algiricus Thomas | ♀ A. 16 | 130 | 10 | 10 | 12 | 6 | 3 | ++ | 1—6 L. | 5 L.—2 S. | M. | Tr. + Sm. | Tr. | ++ | 1—10 Th. | 11 Th.—4 L. | S. | + | — | — | — | — | |
| Jaculus hirtipes (Lichtenst.) | ♂ A. 10 | 130 | 12 | 11 | 12 | 7 | 3 | ++ | 12 Th.—4 L. | 1 L.—3 S. | P. | Tr. + Sm. + Sp. | Tr. | ++ | 1—10 Th. | 11 Th.—4 L. | S. | + | 1—11 Th. | 1—5 L. | F. L. | + | |
| Jaculus orientalis Erxleb. | A. 14 | 130 | 12 | 11 | 12 | 7 | 4 | + | 1 Th.—4 S. | + | | Tr. + Sp. | Tr. | | | | | | 12 Th. | 4 S. | | —— | HOWELL (1932) |
| Allactaga siberica (Forst.) | A. 13 | 130 | 12 | 11 | 12 | 7 | 4 | + | 1 Th.—4 S. | + | | Tr. + Sp. | Tr. | | | | | | 7 Th. | 4 S. | | —— | HOWELL (1932) |
| Dipodomys spectabilis Merr. | A. 14 | 130 | 11 | 11 | 12 | 7 | 5 | + | 1 Th.—4 S. | + | | Tr. | Tr. | | | | | | — | — | — | — | HOWELL (1932) |
| Cuniculus paca (L.) | ♀ Y. 25 | 135 | 12 | 13 | 14 | 6 | 3 | + | 1—5 L. | 1 L.—3 S. | P. | Sm. + M. + Sp. | Tr. | | 3 C.—12 Th. | 11 Th.—1 L. | S. | + | 3 C.—12 Th. | 1—4 L. | S. | + | |
| Sciurus vulgaris L. | ♂ A. 19 | 135 | 10 | 10 | 12 | 7 | 3 | ++ | — | 12 Th.—3 S. | P. | M. + Sp. | M. | | — | — | — | — | 1—11 Th. | 12 Th.—4 L. | S. | + | |
| *Carnivora fissipedia.* | | | | | | | | | | | | | | | | | | | | | | | |
| Helarctos malayanus (Raffles) | ♀ Y. 24 | (75) | — | 11 | 15 | 4 | 5 | + | 11 Th.—3 S. | 1—10 Th. 1 L.—3 S. | P. | (Sm. + Sp.) + M. | M. | + | 1—12 Th. | 11 Th.—1 L. | F. L. | + | 1—12 Th. | 13 Th.—2 L. | S.—F | + | |
| Mydaus javanensis (Lesch.) | ♀ A. 40 | (85) | — | 14 | 15 | 5 | 3 | ++ | 2 Th.—2 L. | 14 Th.—3 S. | P. | Tr. + Sp. | Tr. | + | — | — | — | — | 2—9 Th. | 14 Th.—1 L. | F. L. | — | |
| Euarctos americanus (Pall.) | ♂ N. 23 | 90 | 14 | 11 | 15 | 5 | 5 | + | 12—15 Th. | 1 L.—4 S. | P. | (Sm. + Sp.) + M. | M. | + | 1—14 Th. | 12 Th.—1 L. | S.—F. | + | 1—14 Th. | 15 Th.—2 L. | S.—F. | ± | |
| Canis familiaris L. | ♂ A. | 110 | 11 | 10 | 13 | 7 | 3 | + | 11 Th.—1 L. | 12 Th.—2 S. | P. | Sm. + Sp. + M. | M. | + | 6 C.—9 Th. | 13 Th.—1 L. | F. L. | —— | 6 C.—9 Th. | 13 Th.—3 L. | F. L. | + | |
| Panthera leo (L.) | ♀ A. 150 | 110 | 11 | 11 | 13 | 7 | 3 | ++ | 12 Th.—7 L. | 13 Th.—2 S. | P. | Sp. + M. | M. | + | — | — | — | — | 3—12 Th. | 13 Th.—7 L. | F. L. | ++ | |
| Lutra lutra (L.) | ♂ Y. 20 | 120 | 12 | 12 | 14 | 6 | 2 | — | 1 L.—2 S. | 1 L.—2 S. [19] | P. | Sm. + Sp. + M. | M. | ± | 1—12 Th. | 13—14 Th. | S. | — | 1—12 Th. | 13—14 Th. | S. | ± | |
| Putorius putorius (L.) | ♂ A. 40 | 135 | 11 | 10 | 14 | 6 | 2 | ++ | 1—2 L. | 12 Th.—2 S. | P. | Sp. + M. | M. | + | — | — | — | — | 1—9 Th. | 11 Th.—3 L. | S.—F. | + | |
| *Carnivora pinnipedia.* | | | | | | | | | | | | | | | | | | | | | | | |
| Phoca vitulina L. | ♂ F. 51 | (65) | — | 11 | 15 | 5 | 3 | (±) | 4 Th.—3 S. | 15 Th.—3 S. (F.) | M. | M. + Sm. + Sp. | Tr. | + [20] | 1—12 Th. | 9—14 Th. | S. | ++ | 1—12 Th. | 13 Th.—1 L. | F. L. | —— | |
| Zalophus californianus (Lesson) | ♂ F. 39 | 90 | 1 L. | 12 | 15 | 5 | 3 | ± | 7 Th.—3 S. | 1 L.—3 S. | M. | M. + Sm. + Sp. | Tr. | + [21] | 7 C.—8 Th. | 7 Th.—3 L. | S.—F. | — | 7 C.—8 Th. | 1—3 L. | F. L. | — | |
| *Tubulidentata.* | | | | | | | | | | | | | | | | | | | | | | | |
| Orycteropus afer (Pall.) | ♂ F. 23 | 100 | 9 | 10 | 13 | 8 | 7 | — [22] | 11 Th.—7 S. | 1 L.—7 S. | M. | Sm. + M. + Sp. | Tr. | + | 1—10 Th. | 12 Th.—5 L. | S. | ++ | 1—10 Th. | 1—4 L. | F. F. | —— | |
| *Ungulata.* | | | | | | | | | | | | | | | | | | | | | | | |
| Loxodonta africana (Blumenb.) | F. | (35) | — | 17—1 L. | 20 | 3 | 3 | ++ (s.) | O. [26] | 1—3 S. | | Sm. | | | | | | | | | | | EALES (1928) |
| Elephas maximus L. [15] [42] | ♂ F. 69 | (35) | — | 17—1 L. | 21 | 3 | 3 | ++ (s.) | 3 Th.—3 S. | 1—3 S. [42] | M. | (Tr. + Sp.) | Tr. | ++ | 1 Th.—1 S. | 3 Th.—1 S. | | | 2—9 Th. | 1—3 S. | F. L. | —— | |
| Diceros bicornis (L.) | ♂ A. 290 | (65) | — | — | 20 | 3 | 5 | ++ (s.) | — | 19 Th.—5 S. [24] | P. | Sm. + M. + Sp. | M. | + [25] | 1—11 Th. | 8—13 Th. | S. | — | 1—11 Th. | 14—20 Th. | S. | ++ | |
| Rhinoceros sondaicus Desm. | ♀ F. 37 | (65) | — | — | 20 | 3 | 5 | ++ (s.) | — | 20 Th.—3 S. [23] | P. | Tr. + Sp. | Tr. | + | — | — | — | — | Cran. Th. | 10—19 Th. | S. | ++ | |
| Camelus bactrianus L. | ♂ A. | (65) | — | 11 | 12 | 7 | 4 | ++ (l.) | — | 4 L.—5 S. | P. | Sm. + M. + Sp. | M. | + | 6 C.—7 Th. | 11 Th.—7 L. | S.—F. | ± | 6 C.—7 Th. | 10 Th.—4 S. | S.—F. | ++ | |
| Bos taurus L. (dom.) | ♀ A. | (70) | — | 13 | 13 | 6 | 5 | + | — | 1—5 S. | P. | Sm. + M. + Sp. | M. + Sm. | + | 6 C.—4 Th. | 7 Th.—2 L. | S. | —— | 6 C.—11 Th. | 12 Th.—3 S. | S.—F. | ++ | |
| Tapirus terrestris (L.) | F. 28 | (70) | — | — | 18 | 5 | 4 | + | 1—10 Th. | 1 L.—4 S. | P. | Tr. + Sp. | Tr. | + | — | — | — | — | 3 C.—11 Th. | 12 Th.—4 L. | S. | ++ | |
| Odocoileus virginianus gymnotis (Wiegm.) | ♂ N. 41 | 90 | 12—13 | 11 | 13 | 6 | 5 | ++ (l.) | — | 3 L.—3 S. | P. | Sm. + M. + Sp. | M. | + | 2—13 Th. | 9—13 Th. | S. | — | 2—13 Th. | 13 Th.—3 S. | S.—F. | ++ | |
| Mazama americana (Erxl.) | A. | 90 | 11—13 | 12 | 13 | 6 | 5 | ++ (l.) | — | 2 L.—4 S. | P. | Sm. + M. + Sp. | M. | + | 1—10 Th. | 12 Th.—1 L. | S. | —— | 1—10 Th. | 11 Th.—6 L. | S. | ++ | REISER (1903) |
| Capreolus capreolus (L.) | A. | 90 | 11—13 | 12 | 13 | 6 | 5 | ++ (l.) | — | 2 L.—4 S. | P. | Sm. + M. + Sp. | M. | + | 1—10 Th. | 12 Th.—1 L. | S. | —— | 1—10 Th. | 11 Th.—6 L. | S. | ++ | REISER (1903) |
| Gazella spec. | ♀ Y. 90 | 90 | 11—13 | 11 | 13 | 7 | 5 | + | — | 5 L.—4 S. | P. | Sm. + M. + Sp. | M. | + | 1—11 Th. | 13 Th.—7 L. | S. | — | 1—11 Th. | 13 Th.—7 L. | S. | ++ | |
| Capra hircus L. (dom.) | ♀ Y. 100 | 100 | 12 | 11 | 13 | 6 | 4 | ++ (l.) | 1—4 S. | 3 L.—4 S. | P. | Sm. + M. + Sp. | M. | + | 1—11 Th. | 12 Th.—2 L. | S. | — | 1—11 Th. | 12 Th.—6 L. | S. | ++ | |
| Hippopotamus amphibius L. | ♂ F. 54 | 110 | 1 L. | 10 | 15 | 4 | 3 | ++ (s.) | 1—3 L. | 14 Th.—3 S. | P. | Sm. + M. + Sp. | Tr. | + | 1—12 Th. | 11—15 Th. | S. | ± | 1—12 Th. | 13 Th.—1 L. | F. L. | + | |
| Lama glama (L.) | ♂ A. | 110 | 12 | 11 | 12 | 7 | 4 | ++ (l.) | 6 L.—4 S. | 4 L.—4 S. | P. | Sm. + M. + Sp. | Tr. | + | 1—6 Th. | 11 Th.—5 L. | F. L. | + | 1—6 Th. | 10 Th.—4 L. | S. | + | |
| Equus caballus L. (dom.) | ♂ A. | 110 | 14 | 16 | 18 | 6 | 5 | ++ (l.) | 14 Th.—6 L. | 14 Th.—3 S. | P. | M. + Sp. | Tr. | + | — | — | — | — | 6 C.—10 Th. | 11 Th.—3 L. | F. L. | ++ | |
| Sus scrofa L. (dom.) | ♀ A. | 115 | 11 | 10 | 14 | 7 | 4 | ++ (l.) | —? | 1 L.—1 S. | P. | M. + Sp. | Tr. | + | — | — | — | — | 5 C.—8 Th. | 9 Th.—4 L. | S.—F. | + | |
| Tragulus javanicus (Osb.) | ♀ F. 25 | 140 | 11 | 11 | 13 | 6 | 5 | ++ (l.) | 11 Th.—3 L. | 12 Th.—5 S. | P. | Sm. + M. + Sp. | Tr. | + | 1—11 Th. | 11 Th.—3 L. | F. L. | + | 1—11 Th. | 12 Th.—5 L. | F. L. | ++ | |
| *Sirenia.* | | | | | | | | | | | | | | | | | | | | | | | |
| Dugong australis (Owen) | ♀ F. 110 | | — | 12—3 L. | 19 | 3 | 1—30(20) [31] | ++ (l.) | Ext. caud. lat. included [30] 16 Th.—31 C. | 13 Th.—31 C. | M.—P. | M. | M. (Tr.) | ± | Extensor caudae medialis included see table 7. — | — | — | — | (Sk.—5 Th.) | (7—12 Th.) | | ++ | |
| Trichechus inunguis (Natt.) | ♂ A. 184 | | — | 10—17 | 18 | 2 | 1—24 (14) | — | 6 Th.—24 C. | 6 Th.—24 C. | M.—P. | Tr. | Tr. | + | — | — | — | — | — | — | — | — | |
| *Cetacea.* | | | | | | | | | | | | | | | | | | | | | | | |
| Balaenoptera musculus (L.) | ♂ F. 110 | | — | — | 14 | 16 | 25(18) [32] | — | Ext. caud. lat. included [29] 1 Th.—15 L. | 1 L.—16(25) C. | P. | M. | Tr. | Extensor caudae medialis included see table 7. Th.—L.+ | — | — | — | — | (Sk.) | (1 Th.—3 L.) | S. | ++ | |
| Balaenoptera acutorostrata Lacép. | ♂ F. 122 | | — | — | 11 | 13 | 18 (12) | — | 1 Th.—13 L. | 3 L.—11(18) C. | P. | M. | Tr. + M. | Th.—L.+ | — | — | — | — | (Sk.) | (1 Th.—3 L.) | S. | ++ | |
| Balaenoptera borealis Lesson | ♀ F. 25 | | — | — | 13 | 16 | 19 (12) | — | 1 Th.—16 L. | 1 L.—11(19) C. | P. | Tr. | Tr. | + | — | — | — | — | — | — | — | — | SCHULTE (1916) |
| Hyperoodon ampullatus (Forst.) | ♂ Y. 265 | | — | — | 9 | 10 | 19 (14) | — | Fused with transv. sp. | | P. | Fused with longissimus | | | | | | | | | | | |
| Delphinapterus leucas (Pall.) | ♂ F. 41 | | — | — | 11 | 11 | 20 (11) | — | 2 L.—10 C. | 2 L.—10(20) C. | M.—P. | Tr. + Sm. | Tr. + Sm. | ++ | Sk.—10 L. | 1 Th.—11 L. | S. | +++ | (Sk.) | (Th.) | | ± | |
| Pseudorca crassidens (Owen) | ♂ A. 352 | | — | 4 | 10 | 11 | 21 (14) | — | 1 L.—15 C. | 1 L.—15(21) C. | M.—P. | Tr. | Tr. | ++ | — | — | — | — | (Sk.) | (caud. Th.) | | + | |
| Grampidelphis griseus (Cuv.) | ♀ Y. 180 | | 12 L. | 3—6 | 13 | 18 | 31 (11) | — | 1 L.—18 C. | 1 L.—18(31) C. | M.—P. | Tr. | Tr. | ++ | — | — | — | — | | | | | |
| Tursiops truncatus (Mont.) | ♂ Y. 100 | | 7 L. | 5 | 13 | 16 | 26 (9) | — | 1 L.—18 C. | 1 L.—18(26) C. | M.—P. | Tr. | Tr. | ++ | — | — | — | — | | | | | |
| Delphinus delphis L. | ♂ A. 160 | | 7 L. | 5 | 14 | 21 | 33 (11) | — | 1 L.—19 C. | 1 L.—19(33) C. | M.—P. | Tr. | Tr. | ++ | — | — | — | — | | | | | |
| Phocaena phocaena (L.) | ♂ Y. 66 | | 8 L. | — | 13 | 16 | 30 (18) | — | 1 Th.—19 (30) C. | 1 L.—14 C. | M. | Tr. + M. | Tr. | ++ | — | — | — | — | — | — | — | — | |
| Phocaena phocaena relicta Abel. | ♀ F. 14 | | 8 L. | — | 13 | 16 | 29 (19) | — | 3 Th.—18 (29) C. | 1 L.—15 C. | M.—P. | Tr. | Tr. | ++ | — | — | — | — | — | — | — | — | |
| *Primates.* | | | | | | | | | | | | | | | | | | | | | | | |
| Gorilla gorilla (Sav. et Wym.) | ♂ A. 90 | (65) | — | 2 L. | 13 | 4 | 6 | + | — | 11 Th.—4 L. [39] | P. | (Sm. + Sp.) + M. | Sm. + M. | ++ | 3 C.—4 L. | 6 Th.—4 S. | S. | ++ | 3 C.—6 Th. | 7—11 Th. | S.—F. | -- | |
| | | | | | | | | + | 12 Th.—4 L. [37] | 8 Th.—1 S. | | (Sm. + Sp.) + M. | M. | ++ | 2 C.—5 Th. | 1—12 Th. | | | 2 C.—8 Th. | 4 Th.—1 L. | F. L. | | PLATTNER (1922) |
| | | | | | | | | + | 10 Th.—3 L. | 10 Th.—1 S. | | (Sm. + Sp.) + M. | M. | ++ | | | | | | | | | STEWART (1936) |
| | | | | | | | | + | 7 Th.—3 L. | 8 Th.—1 S. | | Sm. + M. | M. | ++ | 2 C.—5 Th. | 1—10 Th. | | | — | — | — | — | VALLOIS (1928) |
| Pan paniscus Schwarz | | (75) | — | 1 L. | 13 | 4 | 6 | + | 12 Th.—4 L. [36] | 9 Th.—1 S. | | (Sm. + Sp.) + M. | M. | ++ | 2 C.—1 Th. | 1—9 Th. | S. | + | 6 C.—6 Th. | 6—11 Th. | F. L. | + | PLATTNER (1922) |
| | | | | | | | | + | 6 Th.—2 L. | 7 Th.—4 S. | | (Sm. + Sp.) + M. | M. | ++ | 2 C.—7 Th. | 1—10 Th. | | | 2—9 Th. | 10—13 Th. | F. L. | | VALLOIS (1922; 1928) |
| | | | | | | | | + | ? [36] | 10 Th.—4 S. | | (Sm. + Sp.) + M. | M. | ++ | 2 C.—3 Th. | 1—9 Th. | S. | | 7 C.—9 Th. | 10 Th.—2 L. | | | VIRCHOW (1909) |
| | | | | | | | | | 13 Th.—1 L. | 8 Th.—1 S. | | (Sm. + Sp.) + M. | M. | ++ | | | | | | | | | STEWART (1936) |
| Pongo pygmaeus (Hoppius) | | (80) | — | 1 L. | 12 | 4 | 5 | + | 7 Th.—3 L. | 3 Th.—1 S. | | Tr. + Sm. | Tr.? | | 5 C.—5 Th. | ? | | | — | — | — | — | VALLOIS (1928) |
| | | | | | | | | + | | | | | | | | | | | | | | | |
| Nycticebus spec. | ♀ A. | (80) | — | 15 | 15 | 7 | 3 | + | 15 Th.—7 L. | 4 Th.—3 S. | P. | Tr. + Sp. | Tr. | ++ | — | — | — | — | 1—5 Th. | 6—11 Th. | S. | —— | |
| Homo sapiens L. | | 90 | 12 | 11 | 12 | 5 | 5 | + | 10 Th.—2 L. [38] | 1 L.—4 S. | P. | Sm. + M. + Sp. | M. | ± | 6 C.—4 Th. | 6—11 Th. | S. | ± | 2—9 Th. | 11 Th.—2 L. | F. L. | — | EISLER (1912) VALLOIS (1922) WINCKLER (1938, 1939) |
| Hylobates lar leuciscus Geoffr. | | 90 | 10—13 | 13 | 13 | 5 | 4 | + | 12 Th.—3 L. [35] | 6 Th.—1 S. | P. | (Sm.+Sp.)+M. [40] | M. | | 1—2 C. | 1—4 Th. [41] | S. | —— | 4—7 Th. | 6 Th.—2 L. | F. L. | ++ | PLATTNER (1922) |
| Macaca mulatta (Zimmerm.) | A. | 90 | 12 | 10 | 13 | 6 | 4 | + [33] | 11 Th.—6 L. | 12 Th.—6 L. | M.—P.? | (Sm. + Sp.) + M. | M. | ± | 6 C.—11 Th. | 11 Th.—6 L. | F. L. | + | 6 C.—11 Th. | 12 Th.—6 L. | F. L. | + | NISHI (1938) |
| Papio cynocephalus (L.) | ♀ Y. 27 | 95 | 11 | 11 | 12 | 6 | 2 | + | 11—12 Th. | 12 Th.—2 S. | P. | (Sm. + Sp.) + M. | M. | ± | 1—10 Th. | 10—12 Th. | F. L. | — | 1—10 Th. | 12 Th.—2 L. | F. L. | ± | |
| Ateles paniscus (L.) | ♂ Y. 24 | 100 | 14 | 12 | 14 | 4 | 3 | + | — | 11 Th.—3 S. | P. | Sm. + Sp. + M. | Tr. | ++ | 1—14 Th. | 5 Th.—4 L. | S. | ++ | 5—9 Th. | 13 Th. | F. L. | —— | |
| Cercopithecus spec. | ♀ A. 54 | 110 | 10 | 11 | 12 | 7 | 2 | + | 10 Th.—4 L. | 12 Th.—2 S. | P. | Sm. + M. + Sp. | Tr. | | 1—6 Th. | 7—10 Th. | S. | — | 1—10 Th. | 12 Th.—1 L. | F. L. | — | |
| Cercopithecidae | | 110 | 10—11 | 11 | | | | + | 10—12 Th. | 11 Th.—3 S. | P. | Sm. + M. + Sp. | Tr. | | 2 C.—6 Th. | 6 Th.—2 L. | | | 1—9 Th. | 11 Th.—2 L. | | | VALLOIS (1928) |
| Erythrocebus patas (Schreb.) | | 140 | 10 | 11 | 12 | 7 | 3 | + | 1—4 L. [34] | 12 Th.—3 S. | P. | Sm. + M. + Sp. | Tr. | + | 2 C.—4 Th. | 4 C.—9 Th. | S. | | 7 C.—9 Th. | 12 Th.—4 L. | F. L. | ± | VIRCHOW (1916) |
| Lemur spec. | | 140 | 12 | 10 | 11 | 8 | 3 | + | 12 Th.—5 L. | 11 Th.—5 L. | P. | Sm. + M. + Sp. | Tr. | | 2—9 Th. | 10—12 Th. | | | 2—9 Th. | 6 Th.—2 L. | | | VALLOIS (1922) |
| Callithrix spec. | | 140 | 12 | 10 | 11 | 8 | 3 | + | 12 Th.—5 L. | 11 Th.—5 L. | P. | Sm. + M. + Sp. | Tr. | | 2—9 Th. | 10—12 Th. | | | 2—9 Th. | 6 Th.—2 L. | | | VALLOIS (1922) |
| Saimiri sciureus (L.) | ♂ A. 23 | 145 | 11 | 11 | 13 | 7 | 3 | + | 12 Th.—3 S. | 13 Th.—3 S. | P. | Sm. + M. + Sp. | Tr. | ++ | 1—11 Th. | 10—13 Th. | S.—F. | — | 1—11 Th. | 13 Th.—1 L. | F. L. | --- | |
| Tarsius tarsius (Erxleb.) | ♂ A. 13 | 145 | 10 | 10 | 13 | 8 | 3 | + | — | 12 Th.—3 S. | P. | Sm. + M. + Sp. | Tr. | ++ | 1—11 Th. | 10—13 Th. | S. | + | 1—11 Th. | 12 Th.—1 L. | F. L. | --- | |

See for the notes next page.

1) F. = fetus. N. = neonatus. Y. = young. A. = adult.
The length is given from tip of snout to base of tail.

2) In mammals without anticliny the maximal inclination of the spines of the *lumbar* vertebrae is filled in in brackets (see table 7).

3) — = no anticliny. Caudal of the thoracic vertebrae with maximal caudal inclination the inclination of the spines gradually diminishes (see table 7).

4) — = no diaphragmatic vertebra; throughout the whole vertebral column the zygapophyses are of the tangential type (see page 7).

5) — = m. iliocostalis lumborum perfectly free.
± = m. iliocostalis lumborum (origin: last ribs and transverse processes of lumbar vertebrae) connected with pars ilio-lumbalis of m. longissimus dorsi.
(±) = m. iliocostalis lumborum connected with pars ilio-lumbalis of m. longissimus dorsi, but only to a small extent.
+ = m. iliocostalis lumborum fused with pars ilio-lumbalis of m. longissimus dorsi and inserted into the spinous processes of the lumbar vertebrae by means of the aponeurosis of the m. longissimus dorsi, or by means of the fascia spino-transversaria. A certain limit, however, is discernible between the fibres of the longissimus and those of the ilio-costalis.
++ = m. iliocostalis lumborum completely fused with m. longissimus dorsi. No limit discernible. M. iliocostalis dorsi terminating in the region of the last ribs.
++(l.) = m. iliocostalis lumborum completely fused with m. longissimus dorsi. M. iliocostalis dorsi terminating in the lumbar region.
++(s.) = m. iliocostalis lumborum completely fused with m. longissimus dorsi. M. iliocostalis dorsi terminating at the ilium.

6) **+** = insertion present.
**–** = insertion absent.
O. = no insertion described.
(F.) = by means of the fascia spino-transversaria.
S. = only inserted into sacral spines or insertion into sacral spines much stronger developed than into the lumbar ones.

7) M. = the tendons, inserted into the metapophyses (proc. mammillares) are much stronger developed than those, inserted into the neural spines.
M.—P. = the tendons inserted into the metapophyses and into the neural spines show an equal development.
P. = the tendons inserted into the neural spines are much stronger developed than those inserted into the metapophyses.

8) Tr. = undifferentiated transverso-spinalis, composed of semispinalis and all kinds of shorter fibres between the neural spines and the metapophyses.
Sm. = origin of semispinalis and shorter fibres.
Sp. = origin of spinalis. Example: Sm. + Sp. = separate semispinalis and spinalis. (Sp. + Sm.) = spinalis and semispinalis fused.
M. = only multifidus and shorter fibres.

9) ++ = very strongly developed, almost as strong as the m. longissimus.
+ = strongly developed.
± = moderate development.
— = weakly developed.
Th. = thoracic region.
L. = lumbar region.

10) Tr. = semispinalis-fibres form a part of the undifferentiated transverso-spinalis.
**–** = separate semispinalis (or spinalis) absent.
**+** = " " " " present.

11) S. = tendons inserted separately.
F. = inserting tendons fused with those of m. longissimus dorsi.
S.—F. = cranial tendons inserted separately, caudal tendons fused with those of m. longissimus.

12) ++ = very strongly developed.
+ = strongly developed.
± = moderate development.
— = weakly developed.
—— = very weakly developed.

13) S. = tendons inserted separately into neural spines.
F.L. = tendons fused with those of the m. longissimus dorsi; sometimes this gives the impression as if the m. spinalis is inserted into the superficial aponeurosis of the m. longissimus.
F.F. = tendons fused with the fascia spino-transversaria.
S.—F. = cranial tendons inserted separately, caudal tendons fused with those of m. longissimus.

14) The lumbar vertebrae of *Tachyglossus* do not possess transverse processes. The m. ilio-costalis is inserted with a very strong aponeurosis into the neural spines of 14 Th.—3 L.

15) No real m. longissimus dorsi. There is only present the so-called m. ilio-lumbalis (pars ilio-lumbalis m. long. dorsi), originating at the vertebral bodies of the lumbar vertebrae (there are no transverse processes) and inserted into the ilium.

16) In the lumbar region of *Macropus ruficollis* Desm. a separate accessory semispinalis has been found. Origin: neural spines of 1—3 L. Insertion: 25 % into metapophyses of 4—6 L., 75 % into metapophyses of 1—2 S.

17) In the lumbar region of *Dorcopsis mülleri* Schleg. only an accessory semispinalis has been found. Origin: neural spines of 1—5 L. Insertion: metapophyses of 1—2 S.

18) Additional insertion into transverse processes of 1 L.—3 S.

19) The m. longissimus dorsi is not inserted into the ilium. The pars ilio-lumbalis m. long. dorsi is fused with the m. levator caudae lateralis, just as in the *Cetacea* and *Sirenia*. The fibres inserted into the neural spines of the sacral vertebrae are comparatively weakly developed. There are also some fibres inserted into the neural spines of the anterior caudal vertebrae.

20) As strongly developed as the m. longissimus.

21) Strongly developed, but not as strong as m. longissimus.

22) Iliocostalis thoracis narrow; iliocostalis lumborum broad.

23) M. longissimus dorsi comparatively weakly developed and very tendinous. Pars ilio-lumbalis entirely wanting; no fibres originating at lumbar transverse processes or inserted into the ilium.

24) M. longissimus dorsi strongly developed but fairly tendinous. No insertion into ilium, but there are fibres that originate at the lumbar transverse processes.

25) M. multifidus in the prae-diaphragmatic region moderately developed. In the post-diaphragmatic region, however, the muscle is very strongly developed, nearly as strongly as the m. longissimus.

26) No insertion into metapophyses described.

27) Weakly developed.

28) In the prae-diaphragmatic region weakly, in the post-diaphragmatic region strongly developed.

29) The m. longissimus dorsi of the *Cetacea* is completely fused with the m. extensor caudae lateralis. Three systems of inserting tendons can be distinguished:

1. Superficial tendons, inserted into the summits of the neural spines. They are homologous with the superficial tendons of the terrestrial mammals and the *Sirenia*.
2. Deep tendons, inserted into the metapophyses, homologous with the corresponding tendons of the terrestrial mammals and the *Sirenia* (m. extensor caudae lateralis, pars medialis; SLIJPER, 1936).
3. Long tendons, inserted into the dorsal surface of the posterior caudal vertebrae. These vertebrae possess neither a neural spine nor a metapophysis. Almost all of them are included into the tail-fin. This system of tendons (m. extensor caudae lateralis, pars lateralis; SLIJPER, 1936) may be considered as a continuation of both the superficial and the metapophysial tendons.

Survey of insertion:

| Species. | Superficial tendons. | Metapophysial tendons. | Long tendons. |
|---|---|---|---|
| Balaenoptera musculus (L.) | 1 L.—16 Ca. | 1 Th.—15 L. | 17—25 Ca. |
| Balaenoptera acutorostrata Lacép. | 3 L.—11 Ca. | 1 Th.—13 L. | 12—18 Ca. |
| Balaenoptera borealis Lesson. | 1 L.—11 Ca. | 1 Th.—16 L. | 12—19 Ca. |
| Delphinapterus leucas Pallas | 2 L.—10 Ca. | 2 L. —10 Ca. | 11—20 Ca. |
| Pseudorca crassidens (Owen). | 1 L.—15 Ca. | 1 L. —15 Ca. | 15—21 Ca. |
| Phocaena phocaena L. | 1 L.—14 Ca. | 1 Th.—19 Ca. | 20—30 Ca. |
| Phocaena phocaena relicta Abel. | 1 L.—15 Ca. | 1 Th.—18 Ca. | 19—29 Ca. |

This table shows that the first long tendon is nearly always inserted into the vertebra immediately caudal of the vertebra with the last superficial tendon. There may be a gap between the region of insertion of the metapophysial and the long tendons. In the *Phocaenidae*, however, the relations are quite the reverse.

30) In the *Sirenia* the m. longissimus dorsi is completely fused with the m. extensor caudae lateralis. In opposition to the *Cetacea*, however, there is no system of long tendons, exclusively inserted into the vertebrae of the tail-fin.

31) With regard to the *Sirenia*, in this column is filled in the number of sacral vertebrae, the total number of caudal vertebrae and (in brackets) the number of caudal vertebrae included in the tail-fin.

32) With regard to the *Cetacea*, in this column is filled in the total number of caudal vertebrae and (in brackets) the number of caudal vertebrae included in the tail-fin.

33) Only a few fibres inserted into the neural spines.

34) Also inserted into the transverse processes of 1— 9 Th.

35) " " " " " " " 4— 7 Th.

36) " " " " " " " 1— 9 Th.

37) " " " " " " " 4—12 Th.

38) " " " " " " " 6—10 Th.

39) Pars ilio-lumbalis weakly developed.

40) Spinalis, semispinalis and multifidus almost entirely fused.

41) According to VALLOIS (1922) the m. semispinalis is inserted into 1 Th.—1 L.

42) I dissected also the spinal musculature of an adult female (45 years). In opposition to the fetus, the m. longissimus dorsi of this animal appeared to be strongly developed, but it was very tendinous and completely fused with the m. transverso-spinalis. The tendons, inserted into the neural spines, were not so very weakly developed as in the fetus, although they were not stronger than those inserted into the metapophyses.

TABLE 4.

*Survey of the mobility of the vertebral column in the trunk of mammals.*

| SPECIES | MOBILITY IN THE SAGITTAL PLANE (DORSO-VENTRAL) [1] | | | | | | | | MOBILITY IN THE HORIZONTAL PLANE (LATERAL) [1] | | | APOPHYSES | AUTHOR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Praediaphragmatic region | | Diaphragmatic region | | Postdiaphragmatic region | | Lumbo-sacral joint | | Prae-diaphragm. region | Post-diaphragm. region | Lumbosacral joint | | |
| | Dorsal concave | Ventral concave | Dorsal concave | Ventral concave | Dorsal concave | Ventral concave | Dorsal concave | Ventral concave | | | | | |
| Didelphis spec. | ++ | ++ | ++ | ++ | ++ | ++ | ++ | ++ | | | | | COUES (1872) |
| Macropus giganteus Zimm. [5] | +++ | ++ | +++ | +++ | — | —— | ± | ± | +++ | —— | ———— | | Original |
| Choloepus spec. | ++ | ++ | ++ | ++ | ++ | ++ | ++ | ++ | | | | Accessory metap. | LUCAE (1882) |
| Hydrochoerus hydrochaerus (L.) | + | ++ | + | ++ | ——— | ——— | | | | | | Some short anap. | VIRCHOW (1910a) |
| Oryctolagus cuniculus (L.) | ———— | + | + | + | ——— | ——— | +++ | +++ | +++ | —— | ———— | No anap. | VIRCHOW (1915) |
| Lutra lutra (L.) | +++ | +++ | +++ | +++ | — | ± | | | +++ | + | | No anap. | LUCAE (1876) |
| Felis spec. | + | ++ | ++ | ++ | ——— | + | | | ++ | —— | | 1—2 L. with anap. | LUCAE (1876) |
| Canis familiaris L. [2] | ++ | — | ++ | + | —— | ± | ++ | ++ | ++ | + | ———— | No anap. | Original |
| Phoca vitulina L. | +++ | +++ | +++ | +++ | ++ | + | | | +++ | + | | No anap. | LUCAE (1876) |
| Equus caballus L. (dom.) [3] | ——— | —— | ——— | ± | ——— | ——— | ——— | ++ | + | ——— | ———— | No. anap. 28 Th.—4 L. embracing zygap. 5 L.—1 S. proc. transv. with access. joints | Original |
| Lemur spec. | + | ++ | ++ | ++ | ———— | ++ | | | + | ——— | ———— | | LUCAE (1882) |
| Saimiri sciureus (L.) | + | ++ | ++ | ++ | ——— | ++ | + | + | — | ——— | ———— | All L. with anap. | Original |
| Ateles paniscus (L.) | ——— | ++ | — | ++ | ——— | —— | + | + | — | —— | ———— | | " |
| Cercopithecus spec. | —— | + | + | ++ | —— | ± | ———— | + | + | ——— | ———— | Anap. prevent dorsal mobility in postdiaphr. region. | " |
| Cebus capucinus (L.) | + | +++ | + | +++ | ——— | —— | + | + | +++ | —— | ———— | All L. with anap. | LUCAE (1876) |
| Macaca spec. | ++ | + | ++ | +++ | —— | + | | | | | | | BLUNTSCHLI (1912) |
| Papio cynocephalus (L.) | + | ++ | ++ | ++ | ——— | —— | + | + | — | —— | ———— | 1—3 L. with anap. | Original |
| Pan paniscus Schwarz | —— | + | —— | ± | ± | ——— | | | ++ | —— | ———— | No anap. | BLUNTSCHLI (1912) |
| Homo sapiens L. [4] | —— | + | —— | ± | ± | ——— | ± | ++ | ++ | —— | ———— | | FICK (1911); BLUNTSCHLI (1912) |

[1] +++ = highly mobile — = very moderate mobility
++ = very mobile —— = small mobility
+ = fairly well mobile ——— = almost not mobile
± = moderate mobility ———— = immobile
cran. = only in the cranial region

[2] REUTER (1933) believes that in the lumbar region there is no sagittal mobility at all. This, however, has been proved to be not exact.

[3] The data of WENGER (1915) correspond quite well with my own experiments. Some data of KRÜGER (1939a) therefore cannot be exact.

[4] The data of VIRCHOW (1911) and those of ANDERSSON and EKSTRÖM (1940) do not correspond quite well with those of FICK (1911) and BLUNTSCHLI (1912).

[5] The statement of VIRCHOW (1925) that the whole vertebral column of the kangaroo is very mobile, is not quite exact.

TABLE 5.

*Survey of factors influencing the mobility of the vertebral column in the aquatic mammals.*

| Species | Last vertebra with articulating zygapophyses [1] | Diaphragmatic vertebra [2] | Factors limiting the mobility of the vertebral column | |
|---|---|---|---|---|
| | | | Neural spines [3] (Dorsal direction) | Embracing metapophyses (Lateral direction) [4] |
| *Lutrinae.* | | | | |
| Lutra lutra (L.) | 1 S. | 12 Th. | — | An. 14 Th.—1 L. |
| *Pinnipedia.* | | | | |
| Phoca vitulina L. | 1 S. | 11 Th. | — | — |
| Zalophus californianus (Lesson) | 1 S. | 12 Th. | — | — |
| *Sirenia.* | | | | |
| Halitherium schinzi Kaup (Oligocene) | 1 S. | one of last Th. | — | — |
| Miosiren kocki Dollo (Miocene) | 1 S. | one of last Th. | — | — |
| Dugong australis (Owen) | 1 S. | 12 Th.—3 L. | — | — |
| Trichechus inunguis (Natt.) | 1 S. | 10—17 Th. | — | — |
| *Archacoceti.* | | | | |
| Protocetus atavus Fraas (Middle Eocene) | 1 S. | 7—11 Th. | — | — |
| Eocetus schweinfurthi (Fraas) (Middle Eocene) | 1 S. | one of last Th. | — | — |
| Dorudon stromeri (Kellogg) (Upper Eocene) | 8—11 Th. | tang. | — | — |
| Dorudon zitteli (Stromer) (Upper Eocene) | cranial L. | tang. | — | — |
| Zygorhiza kochii (Stromer) (Upper Eocene) [5] | cranial L. | tang. | — | — |
| Prozeuglodon isis (Andrews) (Upper Eocene) | 6 Th. | tang. | — | — |
| Basilosaurus cetoides (Owen) (Upper Eocene) [5] | 8 Th. | tang. | — | — |
| *Mystacoceti.* | | | | |
| Balaena glacialis Bonnat. | 2 (4) Th. | tang. | — | — |
| Megaptera nodosa Bonnat. | 5 Th. | tang. | — | 9 Th.—7 L. |
| Balaenoptera physalus L. | (4) Th. | tang. | — | 5 Th.—11 Ca. |
| Balaenoptera brydei Olsen | (4) Th. | tang. | — | 5 Th.—10 L. |
| Balaenoptera borealis Lesson. | (5) Th. | int. | — | 5 Th.—5 L. |
| Balaenoptera acutorostrata Lacép. | 4 Th. | 3 Th. | — | 4 Th.—12 L. |
| *Physeteridae.* | | | | |
| Physeter macrocephalus L. | | | — | 8 Th.—8 L. |
| Kogia breviceps Blainv. | — | — | — | 9 Th.—8 L. |
| *Ziphiidae.* | | | | |
| Hyperoodon ampullatus (Forster) | 4 (3) Th. | int. | — | — |
| Mesoplodon bidens (Sowerby) | 4 (7) Th. | 3 Th. | — | — |
| *Eurhinodelphidae.* | | | | |
| Eurhinodelphis cocheteuxi du Bus (Miocene) [6] | 9 Th. | | — | — |
| *Platanistidae.* | | | | |
| Platanista gangetica Lebeck | 3 (5) L. | 4 Th. | + | 1—11 L. |
| Inia geoffroyensis Blainv. | | | + | 1—5 L. |
| Stenodelphis blainvillei Gerv. | 8 Th. | | — | — |
| *Delphinapteridae.* | | | | |
| Delphinapterus leucas (Pallas) | 5 Th. | int. | — | — |
| Monodon monoceros L. | 8 (9) Th. | tang. | — | 10 Th.—3 Ca. |
| *Delphinidae.* | | | | |
| Kentriodon pernix Kellogg (Miocene) [7] | 10 Th. | tang.—int. | — | — |
| Grampus orca (L.) | 5 (7) Th. | int. | — | 7 Th.—4 L. |
| Orcella brevirostris Owen | 6 Th. | | | |
| Pseudorca crassidens (Owen) | 5 (7) Th. | 4 Th. | — | — |
| Globicephalus melas (Traill) | 5 (7) Th. | int. | — | — |
| Grampidelphis griseus (Cuv.) | 8 (9) Th. | 3—6 Th. | + | — |
| Tursiops truncatus (Mont.) | 6 (9) Th. | 5 Th. | + | 10 Th.—4 L. |
| Lagenorhynchus acutus (Gray) | 8 (10) Th. | 6 Th. | + | 11 Th.—5 L. |
| Lagenorhynchus albirostris Gray | 8 (10) Th. | 6 Th. | + | 11 Th.—5 L. |
| Delphinus delphis L. | 7 (8) Th. | 5 Th. | + | 10 Th.—5 L. |
| *Phocaenidae.* | | | | |
| Phocaena phocaena L. | 8 (9) Th. | tang. | + | 10 Th.—4 L. |

[1]) C. = cervical, Th. = thoracic, L. = lumbar, S. = sacral, Ca. = caudal vertebrae.
The first 2 or 3 vertebrae caudal of the last vertebra with articulating zygapophyses often are connected to another by a syndesmosis between the inner sides of the metapophyses and the foregoing neural spines. The last of these vertebrae is indicated in brackets. Some *Mystacoceti* possess no synarthroses but only these syndesmoses.
— = No articulations at all.

[2]) See page 7 and fig. 2.
tang. = all zygapophyses are of the tangential type.
int. = the zygapophysial facets show an intermediate position between the radial and the tangential type.

[3]) + = The neural spines, especially of the lumbar vertebrae, are placed so closely together that they touch another when the vertebral column is only slightly bent in the dorsal direction (dorsal concave).
— = No special limiting factors.

[4]) Vertebrae whose metapophyses embrace the foregoing neural spines in such a manner that the mobility of the vertebral column, especially in the lateral direction, is limited to a comparatively high degree.
An. = Anapophyses present from.....
— = No special limiting factors.

[5]) After KELLOGG (1936).

[6]) After ABEL (1931).

[7]) After KELLOGG (1927).

TABLE 6.

*Survey of the development of the m. transverso-spinalis in the aquatic mammals.*

c = cervical (vertebrae, spines, region), Th. = thoracic, L. = lumbar, S. = sacral, Sk. = skull.

| Species. | General structure of m. transverso-spinalis thorac. et lumb. [1]) | | Development of m. transverso-spinalis [2]) | | M. spinalis [3]) | | Development of m. spinalis [2]) | Development of m. multifid |
|---|---|---|---|---|---|---|---|---|
| | Thorax | Lumbar region | Thorax | Lumbar region | Origin | Insertion | | |
| Lutra lutra (L.) | Sm. + Sp. + M. | M. | ± | ± | 1—12 Th. | 13—14 Th. | — | + |
| Zalophus californianus (Lesson) | Tr. + (Sm. + Sp.) | Tr. | + | + | 7 C.—8 Th. | 1—3 L. | — | ++ |
| Phoca vitulina L. | Sm. + Sp. + M. | Tr. + (Sp. + Sm.) | ++ | ++ | 1—12 Th. | 13 Th.—1 L. | —— | ++ |
| Dugong australis (Owen) | M. | M. | ± | ± | Sk.—5 Th. | 7—12 Th. | ++ | ++ |
| Trichechus inunguis (Natt.) | Tr. | Tr. | + | + | ▬ | ▬ | ▬ | + |
| Balaenoptera musculus L. | M. | Tr. | — | ++ | Sk. | 1 Th.—3 L. | ++ | ± |
| Balaenoptera borealis Lesson [4]) | Tr. | | | | | | | ± |
| Balaenoptera acutorostrata Lacép. | M. | Tr. (M.) | — | + | Sk. | 1 Th.—3 L. | ++ | — |
| Delphinapterus leucas (Pallas) | Tr. | Tr. | + | + | Sk. | Th. [5]) | ± | ++ |
| Pseudorca crassidens (Owen) | Tr. | Tr. | + | + | Sk. | caud. Th. | + | ++ |
| Phocaena phocaena relicta Abel | Tr. | Tr. | + | + | ▬ | ▬ | ▬ | ++ |
| Phocaena procaena (L.) | Tr. (M.) | Tr. | + | + | ▬ [6]) | ▬ [6]) | ▬ [6]) | ++ |

[1]) Tr. = undifferentiated transverso-spinalis composed of semispinalis and all kinds of shorter fibres between the neural spines and the metapophyses.
Tr. (M.) = undifferentiated transverso-spinalis but chiefly multifidus.
Sm. = semispinalis and shorter fibres.
Sp. = spinalis.
M. = only multifidus and shorter fibres.
Sm. + Sp. + M. = separate semispinalis, spinalis and multifidus.
(Sm. + Sp.) = spinalis and semispinalis fused.

[2]) ++ = very strongly developed.
+ = strongly developed.
± = moderate development.
— = weakly developed
—— = very weakly developed.

[3]) ▬ = spinalis absent.

[4]) After SCHULTE (1916).

[5]) Intimately fused with the other parts of the transverso-spinalis.

[6]) Between 1 Cerv. and 11 Th. the m. interspinales here and there pass one or two neural spines over.

TABLE 7.

*Some characteristics of the vertebral column in mammals.*

In the different orders the species are arranged after the inclination of their neural spines in the postanticlinal region.

C. = cervical (vertebrae, spines, region), Th. = thoracic, L. = lumbar.

| Species | Number of vertebrae | | Diaphragmatic vertebra (Th.)[1] | Length of trunk (Th. + L.) in cm | Length in % of length of trunk (Th. + L.) | | | Length of body of 3d L. in % of length of trunk (Th. + L.) | Length of longest neural spines in % of length of trunk (Th. + L.) | | | Thoracic vertebrae with longest neural spines | Inclination of neural spines in degrees. Caudal incl. = less than 90°; cranial incl. = more than 90° | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | | | C.[2] | Prae-anticlinal vert. | | Anticlinal vertebra (90°) (Th.)[3] | Postanticlinal vertebrae | | |
| | Th. | L. | | | C. | Th. | L. | | C. | Th. | L. | | | Inclination in degrees | Th. with maximal inclination | | Maximal inclination in degrees[4] | Vertebrae with maximal inclination (L.)[4] | Inclination of spines caudal of these vert.[5] |
| *Monotremata.* | | | | | | | | | | | | | | | | | | | |
| Ornithorhynchus anatinus (Shaw) | 16 | 3 | — | 12 | 40 | 91 | 9 | 5.8 | 0 | 6.6 | 5.8 | 4—10 | — | 70 | 1—16 | 1 L. | 100 | 2—3 | — |
| Tachyglossus aculeatus (Shaw) | 16 | 5 | — | 15 | 35 | 77 | 23 | 4.8 | 0 | 6.6 | 6.0 | 2—4 | — | 60 | 6—16 | — | (70) | 3 | 90 |
| *Marsupialia.* | | | | | | | | | | | | | | | | | | | |
| Echimypera kalabu (Fischer) | 13 | 7 | 11 | 11 | 14 | 50 | 50 | 6.7 | | | | | | | | 12 | 115 | 1—3 | 100—90 |
| Dorcopsis veterum (Less.) | 13 | 6 | 11 | 33 | 23 | 54 | 46 | 6.6 | 2.7 | 10.1 | 7.2 | 3—4 | cr. | 90—60 | 4—8 | 11 | 116 | 1—4 | 100—90 |
| Macropus spec. | 13 | 6 | 11 | 43 | 21 | 54 | 46 | 7.8 | 0—3.6 | 9.8 | 5.0 | 2 | cr. | 80—60 | 7—8 | 11 | 110 | 1—2 | 105—90 |
| Thylacinus cynocephalus (Harris) | 13 | 6 | 9 | 44 | 32 | 59 | 41 | 6.8 | 2—5.5 | 9.1 | 4.0 | 1—3 | u. | 90—50 | 7—9 | 10 | 100 | 1—5 | 90 |
| Didelphis marsupialis L. | 12 | 7 | 9 | 18 | 27 | 60 | 40 | 7.7 | 7.7 | 8.8 | 4.4 | 3 | u. | 70 | 1—7 | 12 | 85 | 3—5 | 90 |
| Phascolarctos cinereus (Goldf.) | 11 | 8 | 9 | 31 | | | | 6.8 | 3.2 | 6.4 | 4.0 | 1—2 | ca. | 70—40 | 5—6 | — | (85) | 1—8 | — |
| Phalanger orientalis (Pallas) | 13 | 6 | 9 | 27 | | | | 6.8 | 2.2 | 5.5 | 4.4 | 1—4 | u. | 90—50 | 7—9 | — | (75) | 1—6 | — |
| Trichosurus vulpecula (Kerr.) | 13 | 6 | 10 | 25 | 16 | 58 | 42 | 8.0 | 0 | 8.0 | 6.4 | 1 | — | 75—55 | 5—7 | — | (60) | 1 | 70—90 |
| *Edentata.* | | | | | | | | | | | | | | | | | | | |
| Euphractus sexcinctus (L.) | 11 | 3 | 8 | 15 | 25 | 75 | 25 | 7.3 | 0 | 16.0 | 6.6 | 1 | — | 60—40 | | — | (55) | 1—3 | — |
| Priodontes giganteus (Geoffr.) | 13 | 2 | 13 | 30 | 30 | 90 | 10 | 6.7 | 0 | 19.0 | 8.0 | 1—2 | — | 40 | | — | (70) | 1—2 | — |
| Myrmecophaga jubata L. | 15 | 2 | 14 | | 54 | 86 | 14 | | | | | | | | | | | | |
| Choloepus didactylus (L.) | 23 | 3 | 21 | 32 | 12 | 86 | 14 | 4.3 | 3.4 | 4.3 | 0 | 1—6 | u. | 70—55 | | [6] | [6] | [6] | — |
| Smutsia gigantea (Ill.) | 14 | 5 | 10 | 37 | 21 | 60 | 40 | 5 7 | 2.0 | 3.7 | 5.4 | | cr. | 90—60 | | — | (80) | 4—5 | — |
| *Insectivora.* | | | | | | | | | | | | | | | | | | | |
| Tupaia glis ferruginea Raffles | 12 | 7 | 10 | 9 | | | | 10.6 | 0 | 7.0 | 6.0 | 2—4 | — | 70—50 | 7—9 | 10 | 130 | 1—7 | — |
| Elephantulus rozeti (Duv.) | 13 | 7 | 12 | 4 | 20 | 44 | 56 | 8.0 | 0 | 10.0 | 10.0 | 1—4 | — | 70—35 | 7—9 | 12 | 125 | 1—3 | 120—105 |
| Ptilocercus lowii Gray | 13 | 5 | 10 | 5 | | | | 9.0 | 0 | 5.0 | 4.0 | 2—4 | — | 70 | 1—8 | 9 | 120 | 1—5 | — |
| Talpa europaea L. | 13 | 7 | 12 | 6 | 23 | 57 | 43 | 6.8 | 0 | 3.0 | 2.6 | 12—13 | — | — | — | 11 | 110 | 1—7 | — |
| Echinosorex albus (Giebel) | 15 | 5 | | 12 | | | | 6.6 | 0 | 13.2 | 5.0 | 2 | — | 60—45 | 5—11 | 12 | 100 | 1—5 | — |
| Centetes spec. | 18 | 5 | 14 | 13 | 25 | 69 | 31 | 6.5 | 3.1 | 10.0 | 3.5 | 4 | r | 80—40 | 9—11 | 16—18 | 90 | 1—5 | — |
| Erinaceus europaeus L. | 15 | 6 | 13 | 12 | 25 | 60 | 40 | 5.8 | 0 | 7.0 | 5.0 | 3 | — | 45 | 1—7 | 15—18 | 80 | 4—6 | — |
| Chrysochloris asiatica (L.) | 18 | 4 | 18 | 5 | 26 | 70 | 30 | 6.4 | 0 | 6.0 | 5.0 | | — | 40 | 1—13 | — | (70) | 1—4 | — |
| *Rodentia.* | | | | | | | | | | | | | | | | | | | |
| Dasyprocta aguti (L.) | 13 | 6 | 12 | 24 | 26 | 56 | 44 | 7.5 | 0 | 10.8 | 8.3 | 3—6 | — | 80—60 | 7—9 | 11 | 145 | 1—4 | 125 |
| Lepus europaeus Pall. | 12 | 7 | 10 | 20 | | | | 8.3 | 0 | 11.4 | 5.5 | 4 | cr. | 60—35 | 5—7 | 10 | 140 | 1—4 | 130 |
| Cuniculus paca (L.) | 13 | 6 | 13 | 22 | 21 | 58 | 42 | 5.4 | 0 | 7.7 | 4.5 | 2—4 | — | 90—40 | 8—11 | 12 | 135 | 1—6 | — |
| Sciurus vulgaris L. | 12 | 7 | 10 | 10 | 23 | 44 | 56 | 8.0 | 0 | 6.0 | 4.5 | 4—8 | — | 80—60 | 3—10 | 11 | 130 | 1—3 | 120—115 |
| Jaculus jaculus (L.) | 11 | 7 | 11 | 5 | 10 | 40 | 60 | 10.0 | 0 | 0 | 6.0 | 1—11 | — | [6] | [6] | [6] | 130 | 1—5 | 115 |
| Cavia porcellus (L.) | 13 | 6 | 12 | 14 | 25 | 53 | 47 | 7.8 | 0 | 8.5 | 5.0 | 2—5 | — | 75 | 1—8 | 10—11 | 130 | 2—6 | — |
| Psammomys algiricus Thomas | 12 | 7 | 10 | 6 | | | | 8.0 | 0 | 7.0 | 7.0 | 2—4 | — | 80—65 | 4—9 | 10 | 130 | 1—4 | 110 |
| Castor canadensis Kuhl. | 14 | 5 | 11 | 30 | 15 | 66 | 34 | 6.0 | 0 | 10.0 | 5.3 | | — | 40 | 3—8 | 11 | 90 | 1—5 | — |
| Arvicola terrestris (L.) | 12 | 6 | 11 | 7.5 | 20 | 42 | 58 | 8.0 | 0 | 5.3 | 4.0 | 4—7 | — | 90—55 | 6—8 | 9 | 90 | 1—6 | — |
| Cricetus cricetus (L.) | 13 | 6 | 11 | 9.5 | 20 | 50 | 50 | 8.4 | 0 | 6.3 | 3.7 | 2 | — | 80—55 | 6—8 | 9 | 80 | 5—6 | — |
| Bathyergus suillus (Schreb.) | 14 | 6 | 11 | 13 | 21 | 53 | 47 | 7.0 | 0 | 6.1 | 6.1 | 1—4 | — | 90—60 | 6—9 | 13 | 80 | 5—6 | — |
| *Carnivora fissipedia.* | | | | | | | | | | | | | | | | | | | |
| Martes (Martes) foina (Schreb.) | | | 10 | 23.5 | 37 | 65 | 35 | 7.1 | | 5.8 | 3.5 | 2—3 | cr. | 80—40 | 7—9 | 10 | 135 | 1—2 | |
| Civettictis civetta (Schreb.) | | | 11 | 32 | 48 | 58 | 42 | 6.6 | | 10.0 | 5.3 | 1—2 | cr. | 80—60 | 7—10 | 11 | 135 | 1—4 | |
| Mungos mungo (Gmel.) | | | 11 | 17 | 30 | 63 | 37 | 6.5 | | 9.8 | 5.3 | 2 | cr. | 85—70 | 7—9 | 10 | 130 | 1—4 | |
| Felis catus L. | 13 | 7 | 10 | 24.5 | 24 | 54 | 46 | 7.5 | 2.0 | 8.8 | 3.2 | | cr. | 90—45 | 4—9 | 10 | 130 | 1—3 | 110—90 |
| Meles meles (L.) | | | 12 | 33 | 36 | 70 | 30 | 6.0 | | 9.0 | 4.2 | 1—2 | u. | 75—60 | 8—12 | 13 | 125 | 1—3 | |
| Lutra lutra (L.) | | | 12 | 31 | 36 | 68 | 32 | 6.1 | | 6.1 | 3.2 | 4 | u. | 85—55 | 8—11 | 12 | 120 | 1—4 | |
| Nasua rufa Tied. | 14 | 6 | 11 | 25 | 26 | 48 | 52 | 6.8 | 2.8 | 7.3 | 5.4 | 1 | u. | 65—50 | 5—9 | 11 | 115 | 1—3 | 100—90 |
| Canis lupus L. | 13 | 7 | 11 | 53 | 46 | 60 | 40 | 6.7 | 3.4 | 12.4 | 6.2 | | cr. | 60—35 | 7—10 | 11—12 | 115 | 1—6 | 100 |
| Canis familiaris L. | 13 | 7 | 10 | 50 | 38 | 60 | 40 | 6.0 | 2.4 | 12.0 | 6.0 | 1—6 | cr. | 65—50 | 6—10 | 11 | 110 | 1—6 | 90 |
| Panthera leo (L.) | 13 | 7 | 11 | 88 | 32 | 54 | 46 | 6.3 | 4.5 | 11.3 | 5.6 | 2—5 | cr. | 90—30 | 9 | 10 | 110 | 1 | 100—90 |
| Arctictis binturong (Raffles) | 14 | 6 | 11 | 40 | 27 | 62 | 38 | 5.7 | 3.0 | 7.3 | 3.5 | | cr. | 65—60 | 3—11 | 12 | 110 | 1—4 | 90 |
| Latax lutris (L.) | 14 | 6 | 12 | 50 | 18 | 60 | 40 | 5.2 | 2.0 | 6.4 | 6.0 | | cr. | 80—50 | 7—11 | 12—14 | 105 | 2—5 | 80 |
| Thalarctos maritimus (Phipps) | 14 | 6 | 11 | 90 | 41 | 66 | 34 | 4.9 | | | | | | | | | 90 | 1—6 | — |
| Mellivora capensis (Schreb.) | 15 | 4 | | 33 | | | | 5.1 | 2.8 | 8.7 | 3.9 | 2—4 | cr. | 90—70 | 6—11 | 12—15 | 90 | 1—4 | — |
| Mydaus javanensis (Lesch.) | 16 | 5 | 14 | 18 | 22 | 70 | 30 | 5.0 | 3.8 | 10.0 | 5.0 | | cr. | 85—65 | 6—14 | 15—16 | 85 | 1—5 | — |
| Conepatus mapurito (Gmelin) | 16 | 5 | 14 | 18 | 23 | 71 | 29 | 5.0 | 3.8 | 9.4 | 5.0 | | cr. | 85—65 | 6—14 | 15—16 | 85 | 1—5 | — |
| Ursus arctos L. | 14 | 6 | 11 | 55 | 40 | 67 | 33 | 5.5 | | 11.0 | 5.4 | 2—4 | cr. | 70—30 | 6—12 | — | (75) | 1 | 80—85 |
| *Carnivora pinnipedia.* | | | | | | | | | | | | | | | | | | | |
| Zalophus californianus (Lesson) | 15 | 5 | 12 | 100 | 38 | 72 | 28 | 4.2 | 3.5 | 6.5 | 3.0 | | cr. | 65 | 1—12 | 13—15 | 85 | 3—5 | — |
| Phoca vitulina L. | 15 | 5 | 11 | 45 | 35 | 69 | 31 | 5.3 | 1.0 | 3.7 | 3.3 | | u. | 60 | 1—15 | — | 65 | 1—5 | — |
| *Tubulidentata.* | | | | | | | | | | | | | | | | | | | |
| Orycteropus afer (Pall.) | 13 | 8 | 10 | 40 | 24 | 54 | 46 | 6.0 | 3.0 | 13.0 | 11.0 | 5—7 | u. | 90—40 | 4—7 | 12—13 | 100 | 3—6 | 95 |
| *Ungulata.* | | | | | | | | | | | | | | | | | | | |
| Tragulus javanicus (Osb.) | 13 | 6 | 11 | 18 | 29 | 60 | 40 | 6.9 | 3.3 | 11.6 | 6.1 | 5 | cr. | 80—55 | 9—10 | 11 | 140 | 1—5 | 120 |
| Sus scrofa L. (dom.) | 14 | 7 | 10 | 70 | 25 | 60 | 40 | 5.7 | 3.3 | 17.1 | 5.0 | 2—3 | cr. | 90—35 | 5—6 | 11 | 120 | 1 | 105—90 |
| Equus caballus L. (dom.) | 18 | 6 | 16 | 110 | 52 | 78 | 22 | 4.5 | 0 | 20.0 | 5.9 | 4 | — | 65—55 | 4 | 14 | 110 | 1 | 105—100 |
| Hippopotamus amphibius L. | 15 | 4 | 10 | 125 | 35 | 75 | 25 | 5.5 | 5.5 | 16.0 | 5.5 | 3—5 | u. | 80—40 | 6—9 | 1 L. | 110 | 2—3 | 100 |
| Lama glama (L.) | 12 | 7 | 11 | 82 | 81 | 58 | 42 | 5.2 | 0 | 14.0 | 5.4 | 3—4 | — | 75—50 | 6—9 | 12 | 110 | 2—4 | 100—90 |
| Capra hircus L. (dom.) | 13 | 6 | 11 | 51 | 40 | 60 | 40 | 6.6 | 6.4 | 21.6 | 5.5 | 2 | cr. | 60—40 | 6—9 | 12 | 100 | 1—6 | — |
| Cervus spec. | 13 | 7 | 12 | 54 | 50 | 64 | 36 | 5.3 | 0 | 13.7 | 5.0 | 4—5 | cr. | 80—45 | 5—9 | 11—13 | 90 | 1—7 | — |
| Odocoileus virgin. gymnotis (Wiegm.) | 13 | 6 | 11 | 55 | 48 | 62 | 38 | 6.2 | 4.0 | 14.9 | 6.2 | 2—5 | cr. | 65—40 | 4—9 | 12—13 | 90 | 1—6 | — |
| Giraffa camelopardalis (L.) | 14 | 5 | 14 | 110 | 129 | 72 | 28 | 4.0 | 0 | 21.8 | 6.0 | 5 | u. | 90—60 | 10—13 | — | (70) | 1—2 | 80—90 |
| Tapirus indicus Desm. | 19 | 4 | — | 85 | 32 | 76 | 24 | 4.1 | 3.5 | 15.2 | 4.1 | 3 | u. | 45 | 1—8 | 14—19 | (70) | 2—4 | — |
| Bos taurus L. (dom.) | 13 | 6 | 13 | 110 | 40 | 64 | 36 | 5.4 | 3.2 | 16.3 | 5.0 | 4 | cr. | 70—30 | 6 | — | (70) | 1 | 75—90 |
| Camelus bactrianus L. | 12 | 7 | 11 | 145 | 66 | 60 | 40 | 4.6 | 0 | 16.6 | 6.0 | 2—5 | — | 60—40 | 4—8 | — | (65) | 1—3 | 70—90 |
| Rhinoceros sondaicus Desm. | 19 | 3 | — | 150 | 28 | 85 | 15 | 4.0 | 5.0 | 20.1 | 4.0 | 2—3 | u. | 60—45 | 6—8 | — | (65) | 1—3 | — |
| Elephas maximus L. | 19 | 3 | 17—1 L. | 150 | 22 | 80 | 20 | 4.6 | 3.5 | 23.3 | 9.0 | 2—4 | cr. | 80—20 | 10—13 | — | (65) | 1—3 | — |
| *Primates.* | | | | | | | | | | | | | | | | | | | |
| Tarsius tarsius (Erxl.) | 13 | 6 | 10 | 5.2 | 25 | 51 | 49 | 9.6 | 0 | 5.7 | 5.7 | | — | 80—55 | 7—9 | 10 | 145 | | |
| Saimiri sciureus (L.) | 13 | 7 | 11 | 14 | 18 | 50 | 50 | 8.6 | 0 | 7.1 | 5.6 | | — | 90—55 | 7—8 | 11 | 145 | | |
| Cebus apella (L.) | 14 | 5 | 11 | 17.5 | 20 | 65 | 35 | 8.4 | 2.9 | 5.8 | 6.0 | | u. | 80—65 | 8—10 | 11 | 140 | | |
| Lemur macaco albifrons E. Geoffr. | 12 | 7 | 10 | 16 | 21 | 47 | 53 | 8.2 | 0 | 5.1 | 7.8 | | — | 90—60 | 9—11 | 12 | 140 | | |
| Erythrocebus patas (Schreb.) | 12 | 6 | 11 | 23 | 32 | 44 | 56 | 8.2 | 3 0 | 6.5 | 6.1 | | u. | 80—70 | 7—9 | 10 | 110 | | |
| Ateles paniscus (L.) | 14 | 4 | 12 | 20 | 30 | 65 | 35 | 6.7 | 3.5 | 6.5 | 6.0 | | u. | 75—40 | 5—6 | 14 | 100 | | |
| Papio cynocephalus (L.) | 12 | 6 | 10 | 21 | 25 | 50 | 50 | 7.6 | 2.0 | 7.8 | 5.0 | | ca. | 70—55 | 6—8 | 11 | 95 | | |
| Hylobates lar leuciscus Geoffr. | 13 | 5 | 13 | 30 | 23 | 65 | 35 | 7.3 | 4.0 | 5.0 | 3.0 | | u. | 90—55 | 6—8 | 10—13 | 90 | 1—5 | — |
| Homo sapiens L. | 12 | 5 | 11 | 45 | 26 | 60 | 40 | 7.3 | 4.8 | 10.0 | 8.2 | 5 | u. | 70—20 | 5—6 | 12 | 90 | 1—5 | — |
| Nemestrinus nemestrinus (L.) | 13 | 6 | 10 | 22 | 22 | 56 | 44 | 6.8 | 4.1 | 6.3 | 4.6 | | u. | 70 | 1—8 | 12 | 90 | 1—6 | — |
| Loris tardigradus (L.) | 16 | 7 | 15 | 14.5 | 15 | 55 | 45 | 5.5 | 5.0 | 4.2 | 2.8 | | ca. | 80—75 | 8—15 | 16-2 L. | 80 | 3—7 | — |
| Pongo pygmaeus (Hoppius) | 12 | 4 | 1 L. | 34 | 20 | 70 | 30 | 7.3 | 13.0 | 10.0 | 4.4 | 1 | u. | 60—25 | 5—6 | — | (80) | 1—4 | — |
| Pan paniscus Schwarz | 13 | 3 | 1 L. | 30 | 23 | 77 | 23 | 7.3 | 10.5 | 11.0 | 8.6 | 1 | ca. | 80—55 | 7—9 | — | (75) | 1—3 | — |
| Gorilla gorilla (Sav. et Wym.) | 13 | 3 | 2 L. | 45 | 26 | 67 | 33 | 6.9 | 19.0 | 12.0 | 7.1 | 1 | u. | 80—45 | 6—9 | — | (65) | 1—3 | — |

[1]) — = no diaphragmatic vertebra; throughout the whole vertebral column the zygapophyses are of the tangential type (see page 7 and fig. 2).

[2]) cr. = larger or smaller cranial inclination.
u. = upright (90°).
ca. = small caudal inclination.
— = practically no neural spine.

[3]) — = no anticliny. Caudal of the vertebra with maximal caudal inclination the inclination of the spines gradually diminishes (the number of degrees increases).

[4]) In mammals without anticliny, the maximal inclination of the spines of the *lumbar* vertebrae is filled in in brackets.

[5]) — = The last lumbar vertebra belongs to the vertebrae with maximal inclination.

[6]) Practically no neural spines.

TABLE 8.

*Survey of the relation between the length of the cervical neural spines and the size and structure of the skull in Primates.*

| Species | Length of trunk (Th. L.) in cm | Length of cervical neural spines in % of length of trunk | Total length of skull in mm | Length of praecondylar part of skull, divided by length of postcondylar part, multiplied by 10 |
|---|---|---|---|---|
| *Small monkeys.* | | | | |
| Tarsius tarsius (Erxl.) | 5,2 | 1,0 | 39 | 25 |
| Saimiri sciureus (L.) | 14 | 1,0 | 66 | 15 |
| Lemur macaco albifrons E. Geoffr. | 16 | 1,0 | 86 | 33 |
| Cebus apella (L.) | 17,5 | 2,9 | 95 | 21 |
| Loris tardigradus (L.) | 14,5 | 5,0 | 68 | 47 |
| *Monkeys of moderate size.* | | | | |
| Papio cynocephalus (L.) | 21 | 2,0 | 131 | 22 |
| Erythrocebus patas (Schreb.) | 23 | 2,0—4,0 | 109 | 20 |
| Ateles paniscus (L.) | 20 | 3,5—5,0 | 117 | 24 |
| Nemestrinus nemestrinus (L.) | 22 | 4,1 | 113 | 24 |
| Hylobates lar leuciscus Geoffr. | 30 | 4,0—5,6 | 141 | 29 |
| *Big apes and man.* | | | | |
| Homo sapiens L. | 45 | 4,8 | 165 | 10 |
| Pongo pygmaeus (Hoppius) | 34 | 13,0 | 255 | 29 |