**Anatomy.** — *Biologic-anatomical Investigations on the Bipedal Gait and Upright Posture in Mammals, with Special Reference to a Little Goat, born without Forelegs.* I. By E. J. SLIJPER (Utrecht). (From the Institute of Veterinary Anatomy of the State University, Utrecht, Holland; Director Prof. Dr. G. KREDIET).

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## I. *Introduction.*

In June 1939 our institute received a little he-goat, three months old, born without forelegs. On the left side it had only a scapula, just as GRAU (18) described of a new-born horse. This bone terminated in a little knob, which can be explained as the synostosis of the scapula with a vestigial humerus [see MURRAY (43) and GRAU (18) in opposition to JENNY (27)]. On the right side the animal possessed a very small and highly deformed little leg with a hoof, in the same way as has been described by GRAU (18) of a goat. Malformations of this kind are not uncommon at all; in our institute there are skeletons of new-born and young calves, goats and dogs without forelegs. They have for example been described by FULD (17; dog), REGNAULT (50; dog), GRAU (18; horse, goat), JENNY (27; sheep) and LESBRE (33) of man and all the domestic animals. Most of these animals were very well capable of living; REGNAULT (50) possessed a bipedal dog that was twelve years old. Unfortunately our little goat died at the age of one year owing to an accident. The first seven months of its life it passed its days on the grass-field, moving forward by jumps on its hindlegs in a semi-upright posture. The body made an angle of nearly 45° with the ground and the hoofs of the hindlegs were placed much farther forward under the body than in a normal goat, in order to bring the supporting surface under the centre of gravity. The manner of locomotion was quite similar to that of a jumping-hare or a kangaroo, both hindlegs leaving the ground at the same time. During the winter the animal lived in the stable.

Almost every author who has described animals born without forelegs, or animals whose forelegs had been amputated [see for example FULD (17; dog), COLTON (10; rat), KOWESCHNIKOWA und KOTIKOWA (32; cat), JACKSON (26; dog)] has restricted himself to an investigation of the vestigial foreleg or a few characteristics of the hindleg. In order to make a more intensive use of the material, the researches on my bipedal goat were connected with a biologic-anatomical investigation on the changes that have taken place in the locomotor-apparatus of mammals with a bipedal gait or an upright posture. So on the one side it was possible to give a better explanation of some characteristics of the bipedal goat, on the other side the changes in the structure of this animal served as a kind of proof of the explanation of the phenomena common to several or all bipedal and upright mammals.

On the whole these animals belong to three orders of mammals: the *Marsupialia, Rodentia* and *Primates*. If possible in each of this three orders I examined a skeleton of a representative of one of the following five types of locomotion (fig. 1): 1st. A walking or running animal [*Thylacinus cynocephalus* (Harris), *Lepus europaeus* Pall.]. 2d. An animal that walks on the branches of trees or that climbs with all four extremities [*Trichosurus vulpecula* (Kerr), *Phascolarctos cinereus* (Goldf.), *Sciurus vulgaris* L., *Cebus apella* L., *Trachypithecus pyrrhus* (Horsf.); for the kind of locomotion see MUYBRIDGE (44), BÖKER (5), SLIJPER (61)]. When climbing these animals now and then show an upright posture. 3d. A bipedal jumping animal [*Dendrolagus inustus* Müller u. Schlegel, *Bettongia lesueuri grayi* (Gould), *Macropus giganteus* (Zimm.), *Pedetes caffer* (Pall.), *Jaculus jaculus* (L.); for the kind of locomotion see BÖKER (5),

SLIJPER (61), MUYBRIDGE (44), ELFTMAN (14), HOWELL (25), HATT (21), LULL (36)]. These animals mainly jump by simultaneous propulsive strokes of both hindlegs. Their body makes an angle of nearly 45° with the horizontal plane, but is kept in balance on the hindlegs by the very long and heavy tail. At rest the tail serves as an adventitious support for the body-weight. 4th. A hanging-climbing animal. This type is only known of the Primates [I examined *Ateleus paniscus* (L.), *Hylobates lar leuciscus* Geoffr., *Pongo pygmaeus* (Hoppius); for the kind of locomotion see BÖKER (5), SLIJPER (61), PRIEMEL (49)]. These animals chiefly climb with their extremely elongated forelegs. When climbing their posture is nearly upright, they have no tail, but the body is kept in balance by the support of the forelegs. 5th. Man, the only real bipedal walker among the mammals. His posture is perfectly upright, there is no tail, but the body is kept in

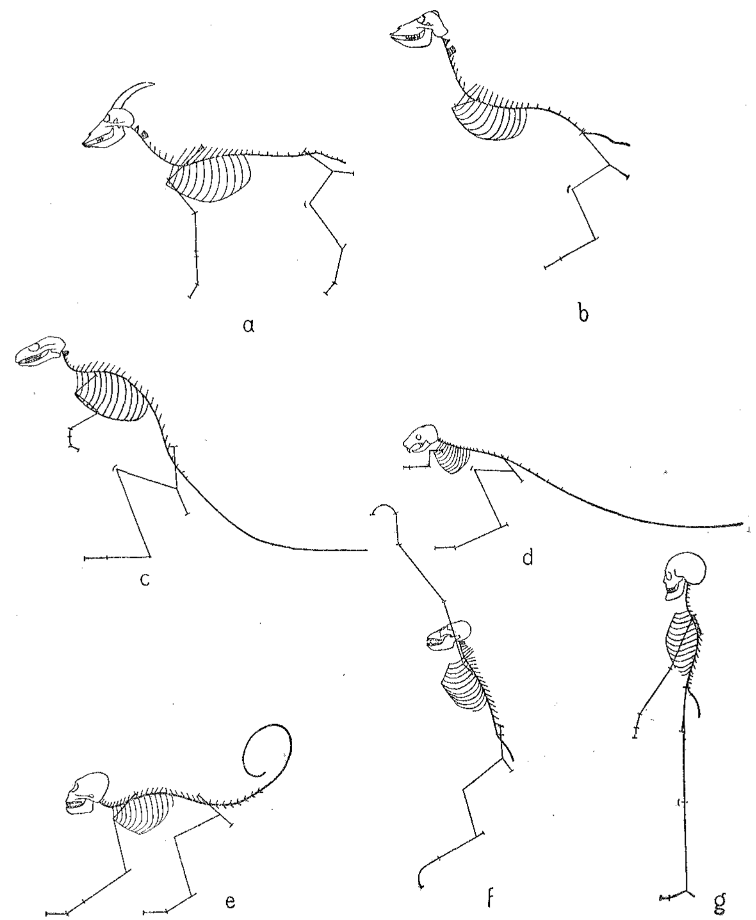

Fig. 1.

Schematic figures of the skeletons of the different types of mammals, described in this paper. *a.* Normal goat. *b.* Bipedal goat. *c.* Kangaroo (*Macropus giganteus* (Zimm.); bipedal jumping mammal). *d.* Jumping-mouse (*Jaculus orientalis* Erxl.; bipedal jumping mammal). *e.* Monkey (*Cebus apella* (L.); climbing mammal). *f.* Orang utan (*Pongo pygmaeus* (Hoppius); hanging-climbing mammal). *g.* Man (*Homo sapiens* L.; bipedal walking mammal).

balance on the hindlegs by the remarkable S-shaped vertebral column with a little aid of some muscles. The body-weight is supported entirely by the hindlegs; they move the body forward by alternating propulsive strokes. 6th. In connection with the upright posture of their body also some bats were included in the investigation.

Compared with the above-mentioned mammals the posture of the bipedal goat was a very unfavourable one. The body had to maintain a semi-upright posture without the aid of the counterweight of a tail or the support of forelegs. Moreover the total weight of the body was carried by the hindlegs alone, which were not stretched as in man but showed the same angles between the different parts as in most quadrupedal mammals. It was a priori to be expected, that these extremely unfavourable circumstances would cause some changes in the skeleton and the musculature. For the purpose of comparison I used a little female goat of nearly the same age. This control-animal was in a much better physical condition than the bipedal one. Its horns were already developed and it had five grinding teeth in stead of four. The chief measurements of the skulls were at a ratio of 84 to 100. All measurements of the control-animal therefore were converted into a ratio of 100 : 84. In table 1 is shown the difference of the dimensions of the skeleton between the two goats, calculated in % of the converted dimensions of the control-animal. Differences less than 6 % were always neglected.

In this paper special attention will be paid to the skeleton and musculature of the hindleg, the pelvis and the thorax. The changes that took place in the vertebral column and its musculature will be described in a special paper, devoted to the comparative anatomy of the body-axis of mammals.

At the end of this introduction I would like to express my most heartfelt thanks to Prof. Dr. Chr. P. Raven (Utrecht), Prof. Dr. H. Boschma (Leiden) and Dr. G. C. A. Junge (Leiden), for the kind and obliging way in which they placed the material of their collections at my disposal. Grateful acknowledgement is also made to Dr. L. D. Brongersma (Leiden) for the revision of the nomenclature and to Mr. W. Wijga (Utrecht) for the correction of the manuscript.

## II. *Hindleg.*

Neither the length of the whole leg, nor the proportional length of its separate bones, showed a marked difference from that of the control-animal (table 1, fig. 2). Only the first phalanx was a little bit elongated. This may cause no surprise, since in running mammals, to which the goat belongs, the proportional dimensions of the hindlegs and their different parts are nearly the same as in bipedal jumping mammals (table 2).

TABLE 1

DIFFERENCE OF THE DIMENSIONS OF THE SKELETON BETWEEN THE BIPEDAL AND A NORMAL GOAT

+6 (-6) means, that the dimension in the bipedal goat is 6% greater (lesser ) than that of the control-animal, calculated in % of the converted dimensions (100:84 ) of this control-animal.

HINDLEG

| | Length | Thickness of shaft | Dimensions of joint-surfaces | | | |
|---|---|---|---|---|---|---|
| | | | Proximal | | Distal | |
| Femur | + 5 | + 9 | +32 | +26 | +21 | +12 |
| Tibia | +11 | +20 | +26 | +21 | +20 | +31 |
| Tuber calcanei | +19 | +16 | | | | |
| Astragalus | +13 | +19 | +28 | +18 | +29 | 0 |
| Metatarsus | + 7 | + 6 | + 9 | +18 | +16 | +28 |
| 1st Phalanx | +26 | 0 | +18 | +21 | +18 | +18 |
| 2d Phalanx | + 6 | + 5 | +17 | + 8 | | |
| Patella | +11 | + 7 | +22 | +11 | | |
| Collum femoris | +20 | | | | | |

PELVIS

| Length of: | |
|---|---|
| Pelvis | +12 |
| Ilium | + 9 |
| Ischium | +23 |
| Pubis | - 5 |
| Symphysis | +27 |
| For.obturatum | + 1 |
| Distance betw. right and left: | |
| Tuber coxae | + 5 |
| Tuber ischii | +16 |
| Acetabulum | -38 |
| Breadth of: | |
| Ala ilii | + 3 |
| Sacrum at ilio-sacral joint | +13 |

| Thickness of: | | |
|---|---|---|
| Ilium | +41 | +22 |
| Acetabulum | +36 | +36 |
| Ischium | +21 | +54 |
| Pubis | +16 | +82 |
| Dimensions of joint-surface of acetabulum | +29 | +24 |

THORAX

The bipedal goat possessed 12 ribs,viz.: 7 true and 5 false ribs. The control-animal had 13 ribs,viz.: 7 true and 6 false. Both animals had 12 bicipital ribs.

Length of sternum with (without ) proc. xiphoideus: -4 (-9)
Breadth in the middle of sternebrae: 1st +103; 2d +38; 3d +29; 4th +32; 5th +38

TABLE 2

PROPORTIONAL DIMENSIONS OF THE HINDLEG IN MAMMALS

| Species | Length of bone in % of total length of hindleg | | | | | |
|---|---|---|---|---|---|---|
| | Femur | Tibia | Tarsus | Metatarsus | Phalanges | Tuber calcanei |
| Thylacinus cynocephalus (Harris) | 36 | 38 | 6 | 11 | 19 | |
| Epimys norvegicus Erxl. | 31 | 37 | 4 | 13 | 15 | 6 |
| Lepus europaeus Pall. | 30 | 37 | 5 | 14 | 4 | 7 |
| Canis familiaris L. | 33 | 33 | 8 | 13 | 13 | 7 |
| Average of walking mammals | 32 | 36 | 6 | 12 | 13 | 7 |
| Equus caballus L. (dom.) | 27 | 27 | 7 | 23 | 16 | 8 |
| Giraffa camelopardalis (L.) | 19 | 21 | 4 | 40 | 16 | 5 |
| CAPRA HIRCUS L. CONTROL | 30 | 33 | 4 | 19 | 14 | 5 |
| CAPRA HIRCUS L. BIPEDAL | 30 | 34 | 4 | 19 | 13 | 6 |
| Average of running mammals | 25 | 27 | 5 | 27 | 15 | 6 |
| Phascolarctos cinereus (Goldf.) | 40 | 30 | 7 | 7 | 16 | |
| Ursus arctos L. | 36 | 29 | 4 | 10 | 11 | 5 |
| Hippopotamus amphibius L. | 42 | 26 | 10 | 10 | 14 | 13 |
| Rhinoceros sondaicus Desm. | 41 | 27 | 10 | 11 | 11 | 10 |
| Elephas maximus L. | 53 | 29 | 6 | 6 | 6 | 6 |
| Average of heavy mammals | 42 | 28 | 7 | 9 | 12 | 8 |
| Didelphis marsupialis L. | 35 | 37 | 8 | 8 | 12 | |
| Trichosurus vulpecula (Kerr.) | 34 | 34 | 7 | 7 | 18 | |
| Sciurus vulgaris L. | 30 | 38 | 7 | 7 | 18 | 4 |
| Anomalurus beecrofti Fraser | 35 | 35 | 5 | 9 | 16 | 3 |
| Trachypithecus pyrrhus (Horsf.) | 37 | 35 | 5 | 10 | 13 | 3 |
| Average of climbing mammals | 34 | 36 | 6 | 8 | 15 | 3 |
| Dendrolagus inustus Müll.u.Schleg. | 33 | 36 | 6 | 11 | 14 | 6 |
| Bettongia lesueuri grayi Gould. | 26 | 36 | 4 | 16 | 18 | 7 |
| Macropus giganteus Zimm. | 26 | 41 | 4 | 15 | 14 | |
| Pedetes caffer (Pall.) | 25 | 36 | 6 | 15 | 18 | 5 |
| Jaculus jaculus (L.) | 23 | 35 | 3 | 25 | 14 | 4 |
| Av. of bipedal jumping mammals | 27 | 37 | 5 | 16 | 16 | 5 |
| Ateleus paniscus (L.) | 35 | 33 | 7 | 11 | 14 | 5 |
| Hylobates lar leuciscus Geoffr. | 40 | 33 | 5 | 11 | 12 | 4 |
| Pongo pygmaeus (Hoppius ) | 33 | 30 | 8 | 13 | 16 | 6 |
| Av. of hanging-climbing mammals | 36 | 32 | 7 | 11 | 14 | 5 |
| Homo sapiens L. | 44 | 38 | 4 | 8 | 6 | 5 |

The factors, determining the proportional length of the femur ad tibia have been discussed by several authors. Regnault (50) and Fuld (17) found, that in dogs whose forelegs were amputated the femur proportionally was shortened and the tibia elongated. The differences between these dogs and the control-dogs, however, remained within the bounds of variability of the species, so that not too much value may be attached to their conclusions. On the contrary Colton (10) found, that in bipedal rats the femur was elongated and that it showed the same length-ratio as in man. His explanation, however, that this phenomenon might be caused by the fact that both man and rat are plantigrade, the dogs on the contrary digitigrade walkers, is not in accordance with the fact that the amputated dogs of Fuld just became plantigrade.

As is shown by the data collected in table 2, in bipedal jumping mammals on the whole the femur has been shortened, the tibia a little elongated and the metatarsus very much elongated [see also Howell (25), Schumann (59), Lyon (37) and Müller (41)]. In heavy quadrupedal mammals (especially in heavy Ungulates) as well as in hanging-climbing Primates and man, the femur is elongated and the tibia and metatarsus are shortened [see also Böker (5), Gregory (19) and others]. In both types of mammals the weight supported by the hindlegs is increased. In adaptation to this increase of weight in heavy quadrupedal mammals, in man and (to a lesser degree, however) in anthropoid apes, the femur has a more or less vertical position, while in bipedal jumping mammals its position is oblique or even nearly horizontal [*Macropus*; see Elftman (14)].

If the weight supported by the hindlegs is increased, then the femur is shortened if it has an oblique position, while it is elongated if its position is more or less vertical. This is easy to understand, because in a vertical position of the femur the distance between tuber ischii and knee-joint (length of the hamstring-muscles) is much shorter than in a horizontal position. The shortening of the fibers of the hamstring-muscles therefore must be compensated by the increase in length of the femur. On the other hand in mammals with a more or less horizontal femur this cannot be elongated, since in that case the transmission of power would be too unfavourable [see also Aichel (1)]. So the differences between the bipedal dogs and rats could perhaps be explained by the fact, that in dogs the femur is as long as the tibia, while in rats it is shorter. It is also possible, that the position of the femur in the dogs differed from that in the rats. Unfortunately the publications of FULD and COLTON do not give exact information on this point.

The elongation of the first phalanx in the bipedal goat (table 1) may be connected with the fact that the feet had to be placed much more forward, in order to bring the supporting surface under the centre of gravity. As is shown in fig. 2 the more horizontal position of the metatarsus and the toes, required by the above-mentioned forward motion of the supporting surface, caused a change in the direction of the calcaneus and especially of the tuber calcanei. For in digitigrade and unguligrade mammals the direction of the tuber calcanei is always nearly parallel to that of the femur. This position guarantees the most favourable effect for the contraction of the m. gastrocnemius and flexor digitalis sublimis. In the normal goat there is an angle between the tuber calcanei and the metatarsus (fig. 2a). In the bipedal goat the position of the tuber calcanei with regard to that of the femur was nearly the same as in the control-animal. In connection with the altered position of the metatarsus, however, the tuber calcanei showed the same direction as this bone (fig. 2b). In consequence the angle between tuber calcanei and tibia was so much smaller than in the control-animal that the tarsal joint could not be completely stretched. The elongation of the tuber calcanei lengthened the lever of the tarsal joint.

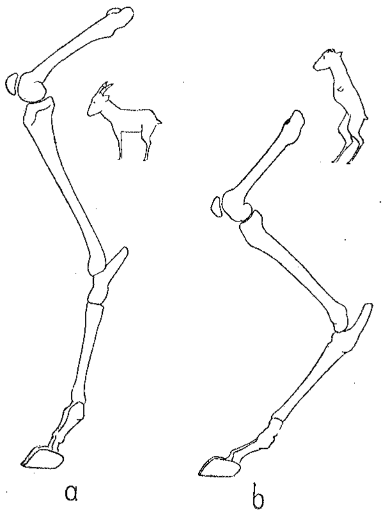

Fig. 2.
Left hindleg of the normal (*a*) and the bipedal (*b*) goat.

Neither an enlargement of the trochanter maior [RUDOLF (52)] or a limitation of the movements in the joints to one single plane, nor a reduction of the fibula [SCHAPIRO (55), SCHUMANN (59), LYON (37), HOWELL (25)] or of the number of toes could be expected in our goat, since these characters are already common to running and bipedal jumping mammals [SLIJPER (61)].

The very marked increase in thickness of all the bones of the hindleg and especially the increase of their proximal and distal ends and their joint-surfaces, without doubt have been caused by the increase of the weight supported by this leg. This is in perfect accordance with the considerations of WEIDENREICH (66) and the experiments of WERMEL (68) and STIEVE (62), but it does not quite agree with the data given by FULD (17) and COLTON (10). In the dogs of FULD the bones of the hindleg were not thickened, but only the quantity of bone had been augmented. The joint-surface of the distal epiphysis of the tibia of the dog of FULD was diminished, but in the rats of COLTON it had been increased. In the dogs the acetabular joint-surface too was diminished, while in the goat it has been increased, just as RUDOLF (52) has shown for the kangaroo. The elongation of the collum femoris is an adaptation to the narrowing of the pelvis at the acetabulum (see chapter III, sub 7).

The preservation of the muscles did not permit me to compare their weight with that of the control-animal. In general, however, it can be said that the greater part of the muscles in the bipedal goat were better developed than in the quadrupedal one, with the exception of the psoas-musculature, which showed a minor development. On the whole this observation agrees with the data given by FULD (17) for a bipedal dog, KOWESCHNIKOWA und KOTIKOWA (32) for a bipedal cat and by ALEZAIS (2), SCHAPIRO (55), ELFTMAN (14) and HOWELL (25) for bipedal jumping mammals. The psoas-musculature will be dealt with in chapter III.

## III. *Pelvis.*

1. **General remarks.** On the whole we may consider the structure of the pelvis as a compromise between the demands made by statical and mechanical forces, by the organs of the pelvic cavity, which have to take up a certain space and by the insertions of the muscles. An investigation into the differences in the structure of the pelvis thus must take into account these four demands and may not be restricted to one or two of them as ELFTMAN (14), BYKOV and KOTIKOWA (9) and many investigators of human anatomy have done [for a detailed discussion of the literature see ARIENS KAPPERS (3)].

As the pelvis is not a simple perpendicular pillar of the body-axis, the statical force (that is the gravitation) may be resolved into several different components [see for example MIJSBERG (45)]. The most important of these components are: 1st. A force going from the ilio-sacral joint through the ilium to the acetabular joint, where it is compensated by the counter-pressure of the supporting leg. Direction, length and thickness of the ilium, as well as the thickness of the acetabulum and the surface of the acetabular joint may be influenced by this force. 2d. A force that tries to rotate the right and left halves of the pelvis in an upward and outward direction. In future this force will be called the exorotation. In the first place, this exorotation is caused by the fact, that the point where the femoral head supports the acetabulum lies laterally to the ilio-sacral joint. In the second place it is caused by the rotation of the vertebral column round the transverse axis of the ilio-sacral joint. This rotation is caused by the weight of the body: the lumbar vertebral column tries to move downward, the sacrum tries to move upward. This bone transfers the upward force to the ischium by the broad ligaments and the lig. sacro-(caudo-) tuberosum. So it causes the exorotation of the ischium. The exorotation is compensated by the pubis and the symphysis pelvis. If the symphysis has been sawn through, the halves of the pelvis turn aside [FENEIS (15)]. The size of the exorotation-force depends on the position of the acetabulum, the divergence of the ischia and the size of the body-weight that rests upon the hindlegs.

In man these factors would be augmented by an outward directed component of the body-weight in the ilio-sacral joint. The existence of this component would depend on the fact, that at the ilio-sacral joint the caudal border of the ala sacralis is narrower than the cranial one. In consequence of this fact the sacrum would act as a kind of coping-stone in an arched roof [MEYER (39), BRAUS (6)]. Recently LÜHKEN (35), however, has shown, that this component does not cause an outward directed force at the symphysis pelvis but on the contrary an inward directed one. But his conclusion, that the symphysis in man has to resist pressure in stead of tension cannot be right, as FENEIS (15) has shown, that tension is prevalent in the symphysis of man. Moreover LÜHKEN has neglected the other exorotating forces. It is possible, however, that the symphysis of man has to resist less tension-force, than that of other mammals especially of other Primates. The fact, that man has a fibro-cartilagineous symphysis instead of a bony one, as well as the comparatively low symphyseal index (see table 3), might be an indication of this opinion. The theory of the coping-stone does not hold with regard to other mammals, because their sacrum does not rest upon the pelvis but is hung from the ala ilii [BRUHNKE (8)].

The mechanical forces, caused by the locomotion of the animal are the same as the above-described statical ones. Additional forces are the reciprocal shifting of the two halves of the pelvis in mammals that walk by alternating strokes of their hindlegs, as well as the rotation of the pelvis in a dorsal direction caused by the shock when the foot is planted on the ground. The first force is compensated by the symphysis, the second by the ligaments of the ilio-sacral joint, the tension of the m. rectus abdominis [STRASSER (63)] and the tension of the m. psoas minor. The capacity of the pelvis is influenced by the bulk of the different organs, the size of the faeces, but especially by the dimensions of the foetus at birth [ELFTMAN (14)]. This is illustrated by the different dimensions of male and female pelves [SCHMALTZ (56), BRAUS (6)] and by the fact that some sexual hormones are able to alter the structure of the pelvis [RUTH (54), HISAW (24), HAWRE, MEYER and MARTIN (23)]. Under the insertions of muscles that influence the structure of the pelvis, special attention must be paid to the m. glutaeus medius (length and width of ala ilii), the hamstring-muscles (length of ischium) and the adductor muscles (length of symphysis).

2. **Thickness of bones.** As already has been shown for the hindleg, it is not surprising at all that the increase of the weight supported by the pelvis has caused a considerable thickening of all bones, but especially of the acetabulum and pubis. The acetabular joint-surface too is enlarged to a very marked degree (fig. 3, table 1).

3. **Position of the pelvis.** Since the sacral vertebra principally transmits the power from the lumbar vertebral column to the pelvis and reciprocally, the angulus ilio-lumbalis has proved to be a safer indication of the different forces acting on the pelvis than the angulus ilio-sacralis, which has been determined by MIJSBERG (45), NAUCK (46) and others. The angulus ilio-lumbalis is the angle between the ilium and the axis of the lumbar vertebral column that is produced in a caudal direction. The angulus sacro-lumbalis is the angle between this caudally produced axis and the axis of the sacrum. In quadrupedal mammals a more or less vertical position of the ilium is the most favourable to support the body-weight, while a more or less horizontal position is the most favourable for the transmission of the locomotor-power from the hindleg to the vertebral column. In consequence the heavy quadrupedal mammals show a comparatively wide ilio-lumbar angle, while it is comparatively narrow in smaller or lighter mammals, especially in those species that have a more or less jumping locomotion (*Leporidae, Felidae*; see table 3).

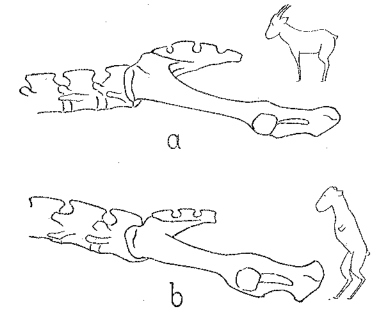

Fig. 3.
Lateral view on the pelvis of the normal (*a*) and the bipedal (*b*) goat.

The direction of the vertebral column in upright going and bipedal mammals makes it possible to combine a nearly vertical ilium with a very narrow ilio-lumbar angle [see table 3, especially the Primates; see also NAUCK (46), PRIEMEL (49)]. In the normal goat there is an ilio-lumbar angle of 23°. In the bipedal one this angle had been reduced to 0° (fig. 3). The angle between the ilium and the horizontal plane amounted from 25° to about 65 à 75°.

4. **Position of the sacrum.** In literature one can find several different explanations for the position of the sacrum and especially for its position in man, which is characterized by the possession of the remarkable promunturium. Several authors try to explain the nearly right angle between the lumbar and sacral vertebrae in man by the tension of the dorsal back-musculature or its demands for insertion [LE DAMANY (12)]. Other investigators on the contrary believe, that it is the demand of space in the pelvic cavity that determines the position of the sacrum. Recently BLUME (4) has shown, that the development of the promunturium is in no way connected with statical or mechanical forces. From the data given in table 3 it is evident now, that the width of the angulus lumbo-sacralis (see sub 3) completely depends on the other factors determining the capacity of the pelvic cavity. So it can be seen that a wide lumbo-sacral angle occurs in those mammals that have a long sacrum and a narrow ilio-lumbar angle [compare for example *Ursus arctos* L. (6 sacral vertebrae) with *Panthera leo* (L.) (2 sacral vertebrae, same ilio-lumbar angle) or *Bos taurus* L. (ilio-lumbar angle of 30°) with *Rhinoceros sondaicus* Desm. (70°)]. The possession of a promunturium is not limited to man, but it occurs in several different quadrupedal mammals (*Sus, Dicotyles, Haplomys, Ursus*). Among the bipedal mammals a widening of the lumbo-sacral angle only occurs in the *Macropodidae*. For in the other species there was no marked change of the ilio-lumbar angle or the number of sacral vertebrae. The increase of the number of these vertebrae in Primates certainly has been the chief factor that caused the widening of the lumbo-sacral angle.

The above-mentioned opinion is fully borne out by the fact, that in the bipedal goat the ilio-lumbar angle decreased by 23° while the lumbo-sacral angle increased by 16° (see also table 1 and fig. 3).

TABLE 3. POSITION AND PROPORTIONAL DIMENSIONS OF THE PELVIS IN MAMMALS.

| Species | Dimensions in % of the distance between occipital crest and cranial border of sacrum | | | | | | | | | Situation of pelvic inlet with regard to the sacral vertebrae 1) | Number of sacral vert. | Angle between ( in degrees ) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Length of bone | | | | | Breadth at | | | Height of pelvis | | | Ilium and lumbar vertebrae 2) | Sacrum and lumbar vertebrae | Ilium and pubis |
| | Ilium | | | Ischium | Symphysis | Pelvic inlet | Acetabulum | Tuber ischii | | | | | | |
| | Presacral | Postsacral | Total | | | | | | | | | | | |
| Thylacinus cynocephalus (Harris) | 6 | 6 | 12 | 10 | 12 | 7 | 6 | 7 | 6 | c.2S. | 2 | 28 | 0 | 117 |
| Lepus europaeus Pall. | 8 | 8 | 16 | 12 | 8 | 6 | 6 | 9 | 7 | c.2S. | 2 | 8 | 20 | 105 |
| Panthera leo (L.) | 7 | 8 | 15 | 11 | 12 | 8 | 6 | 8 | 6 | c.2S. | 2 | 15 | 15 | 130 |
| Canis familiaris L. | 7 | 7 | 14 | 9 | 7 | 7 | 6 | 11 | 9 | c.3S. | 3 | 18 | 35 | 135 |
| Ursus arctos L. | | | | | | | | | | 5S. | 6 | 12 | 56 | 140 |
| Sus scrofa L. ( dom.) | 6 | 9 | 17 | 11 | 9 | 9 | 8 | 8 | 7 | c.3S. | 3 | 15 | 50 | 105 |
| Average of walking mammals | 7 | 8 | 15 | 11 | 10 | 7 | 6 | 9 | 7 | | | 15 | 29 | 122 |
| CAPRA HIRCUS L. CONTROL | 4 | 14 | 18 | 11 | 8 | 9 | 9 | 9 | 9 | c.4S. | 4 | 23 | 36 | 140 |
| CAPRA HIRCUS L. BIPEDAL | 4 | 13 | 17 | 14 | 10 | 10 | 4 | 9 | 7 | c.4S. | 4 | 0 | 52 | 130 |
| Lama glama (L.) | 3 | 8 | 11 | 7 | 7 | 7 | 6 | 5 | 8 | 2S. | 4 | 53 | 10 | 135 |
| Equus caballus L. (dom.) | 2 | 11 | 13 | 10 | 10 | 8 | 9 | 7 | 10 | 3S. | 5 | 33 | 20 | 90 |
| Bos taurus L. (dom.) | 3 | 11 | 14 | 12 | 12 | 10 | 9 | 10 | 11 | 3S. | 5 | 30 | 36 | 100 |
| Giraffa camelopardalis (L.) | 2 | 9 | 11 | 6 | 8 | 8 | 8 | 7 | 13 | 2S. | 4 | 70 | 0 | 85 |
| Average of running mammals | 3 | 11 | 14 | 9 | 9 | 8 | 8 | 7 | 10 | | | 42 | 18 | 110 |
| Hippopotamus amphibius L. | 4 | 14 | 18 | 16 | 12 | 10 | 9 | 8 | 11 | 2S. | 3 | 75 | 0 | 90 |
| Rhinoceros sondaicus Desm. | | | | | | | | | | 2S. | 4 | 70 | 0 | 90 |
| Elephas maximus L. | | | | | | | | | | 2S. | 3 | 75 | 0 | 90 |
| Average of heavy mammals | 4 | 14 | 18 | 16 | 12 | 10 | 9 | 8 | 11 | | | 73 | 0 | 90 |
| Trichosurus vulpecula (Kerr) | 10 | 12 | 22 | 12 | 12 | 9 | 10 | 15 | 10 | c.2S. | 2 | 22 | 0 | 135 |
| Phascolarctos cinereus (Goldf.) | 13 | 7 | 20 | 8 | 7 | 8 | 7 | 7 | 7 | c.3S. | 3 | 30 | 0 | 112 |
| Sciurus vulgaris L. | 10 | 13 | 23 | 14 | 12 | 7 | 7 | 10 | 10 | c.2S. | 2 | 0 | 20 | 150 |
| Trachypithecus pyrrhus (Horsf.) | 12 | 10 | 22 | 9 | 12 | 9 | 9 | 8 | 11 | c.2S. | 2 | 10 | 20 | 100 |
| Average of climbing mammals | 11 | 11 | 22 | 11 | 11 | 8 | 8 | 10 | 10 | | | 15 | 10 | 124 |
| Dendrolagus inustus Müll.u.Schl | 14 | 9 | 23 | 15 | 9 | 13 | 13 | 18 | 12 | c.2S. | 2 | 36 | 0 | 130 |
| Bettongia lesueuri grayi Gould | 14 | 10 | 24 | 21 | 14 | 13 | 13 | 20 | 7 | c.2S. | 2 | 22 | 0 | 130 |
| Macropus giganteus (Zimm.) | 14 | 8 | 22 | 16 | 16 | 11 | 10 | 15 | 9 | c.2S. | 2 | 22 | 18 | 130 |
| Pedetes caffer (Pall.) | 17 | 13 | 30 | 19 | 8 | 15 | 15 | 23 | 16 | c.3S. | 3 | 0 | 20 | 115 |
| Jaculus jaculus (L.) | 15 | 11 | 26 | 20 | 17 | 15 | 11 | 20 | 20 | c.3S. | 3 | 0 | 20 | 150 |
| Av.of bipedal jumping mammals | 15 | 10 | 25 | 18 | 13 | 13 | 12 | 19 | 13 | | | 16 | 12 | 131 |
| Ateleus paniscus (L.) | 11 | 24 | 35 | 14 | 13 | 12 | 12 | 16 | 24 | c.3S. | 3 | 5 | 23 | 112 |
| Hylobates lar leuciscus Geoffr. | 11 | 22 | 33 | 9 | 12 | 13 | 20 | 15 | 26 | c.4S. | 4 | 22 | 16 | 90 |
| Pongo pygmaeus (Hoppius ) | 15 | 23 | 38 | 19 | 15 | 15 | 16 | 19 | 23 | 3S. | 3 | 5 | 35 | 120 |
| Av. hanging-climbing mammals | 12 | 23 | 35 | 14 | 13 | 13 | 16 | 17 | 24 | | | 11 | 25 | 107 |
| Homo sapiens L. | 9 | 12 | 21 | 16 | 8 | 20 | 21 | 19 | 15 | 1S. | 5 | 5 | 85 | 80 |

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[1] c. 2 S. = caudal of the 2d sacral vertebra.

[2] See sub 3.

*(To be continued.)*