

# Comparative and Functional Anatomy of the Mammalian Lumbar Spine

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## ABSTRACT

As an essential organ of both weight bearing and locomotion, the spine is subject to the conflict of providing maximal stability while maintaining crucial mobility, in addition to maintaining the integrity of the neural structures. Comparative morphological adaptation of the lumbar spine of mammals, especially in respect to locomotion, has however received only limited scientific attention. Specialised features of the human lumbar spine, have therefore not been adequately highlighted through comparative anatomy. Mathematical averages were determined of 14 measurements taken on each lumbar vertebrae of ten mammalian species (human, chimpanzee, orang-utan, kangaroo, dolphin, seal, Przewalski's horse, cheetah, lama, ibex). The revealed traits are analysed with respect to the differing spinal loading patterns. All examined mammalian lumbar spines suggest an exact accommodation to specific biomechanical demands. The lumbar spine has reacted to flexion in a predominant plane with narrowing of the vertebral bodies in quadrupeds. Torsion of the lumbar spine is withstood by an increase in the transverse distance between the inferior articular processes in the upper lumbar spine in primates, but lower lumbar spine in humans, quadrupeds and the seal. Sagittal zygapophyseal joint areas resist torsion in the seal and humans. Ventral shear is resisted by frontal zygapophyseal joint areas in humans and primates, and dorsal shear by encompassing joints in the ibex. The human fifth lumbar vertebra is remarkable in possessing the largest endplate surface area and the widest distance between the inferior articular processes, as an indicator of the high degree of axial load and torsion in bipedalism. *Anat Rec* 264:157–168, 2001.

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**Key words:** lumbar spine; zygapophyseal joints; comparative anatomy; mammalian; human; locomotion; bipedalism; gait

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Due to the high incidence of spinal disorders, the human lumbar spine has maintained the stigma of being inadequately adapted to upright posture and locomotion. The converse point of view (Putz and Müller-Gerbl, 1996), however, suggests an exact accommodation of the spine of each mammalian species, including humans, to the specific biomechanical demands of the course of evolution, maintaining maximal stability while granting ideal mobility and securing the protection of neural structures. To date, the published literature on comparative lumbar vertebral anatomy has focused either on singular morphological aspects or selectively upon a mammalian subgroup


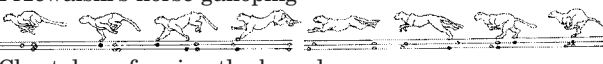


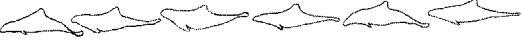
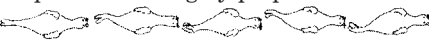
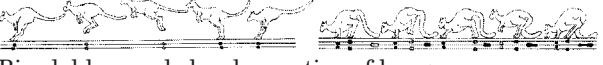
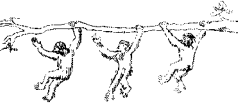


(Struthers, 1892; Odgers, 1933; Slijper, 1946; Rose, 1975; Pohlmeier, 1985; Shapiro, 1993; Wilke et al., 1997; Kumar et al., 2000). However, only in recognition of the spectrum

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TABLE 1. Presentation of mammalian species of the collective

| Species   | Number and gender     | Example of locomotion  |
|---|-----------------------|--|
| <i>Equus przewalski</i><br>(Przewalski's horse)   | 4 Female              | <br>Przewalski's horse galloping   |
| <i>Acinonyx jubatus</i><br>(Cheetah)              | 4 Female              | <br>Cheetah performing the bound   |
| <i>Lama vicugna</i><br>(Vicugna)                  | 3 Male                | <br>Lama pacing  |
| <i>Capra ibex ibex</i> (Ibex)                     | 2 Male                | <br>Ibex leaping in alpine terrain  |
| <i>Tursiops truncatus</i><br>(Bottlenose dolphin) | 2 Male<br>1 Not known | <br>Dolphin swimming by propulsion from vertical strokes of the fluke      |
| <i>Phoca vitulina</i><br>(Harbour seal)           | 2 Female<br>2 Male    | <br>Seal swimming by transverse strokes of the rear appendages             |
| <i>Macropus giganteus</i><br>(Kangaroo)           | 4 Male                | <br>Bipedal hop and slow locomotion of kangaroo                            |
| <i>Pongo pygmaeus</i><br>(Orang-utan)             | 3 Female              | <br>Brachiation of orang-utan (usually performed with support by the legs) |
| <i>Pan troglodytes</i><br>(Chimpanzee)            | 3 Male                | <br>Rare bipedal gait of chimpanzee                                      |
| <i>Homo sapiens</i><br>(Human)                    | 2 Female<br>2 Male    | <br>Human running  |

Only select modes of locomotion which are of relevance for the discussion are presented. Many of the common gaits are omitted for reason of space.

of morphological variability, may the functional individuality of a species be realistically assessed.

The purpose of this investigation is to establish a detailed correlation between the varied morphological features of a diverse collective of mammalian lumbar vertebrae and the differing compositions of spinal loading patterns in locomotion. Hereby, the human lumbar specialisation in respect to bipedalism may be more readily conceived.

## RESULTS

In order to facilitate the comparison of species with varying numbers of lumbar vertebrae, the sacrum (S) and last lumbar vertebra (LL) have been allocated the same level in the following tables with the preceding vertebrae listed above (L). The first two lumbar vertebrae of the cheetah and the lama and the first lumbar vertebra of the kangaroo and the ibex have been omitted. For the dolphin,

the obtained values of the thoracic vertebrae and lumbar vertebrae have been listed according to a separate axis on the right hand side of the tables.

### The Vertebral Bodies (Table 3)

**Vertebral body dimensions (Fig. 1a: e,f; Fig. 1b: k).** The terrestrial species all display a progressive sagittal narrowing of the vertebral bodies towards the sacrum, particularly pronounced in the quadrupedal species. The marine mammals, in contrast, reveal only a slight decrease in sagittal diameter. Remarkably, the posterior height of the vertebral bodies lies constantly between 2 and 3 cm for humans and the primates, but is generally between 3 and 5 cm for the rest of the collective. All species (disregarding the dolphin) reveal a loss in height of the last lumbar vertebra.

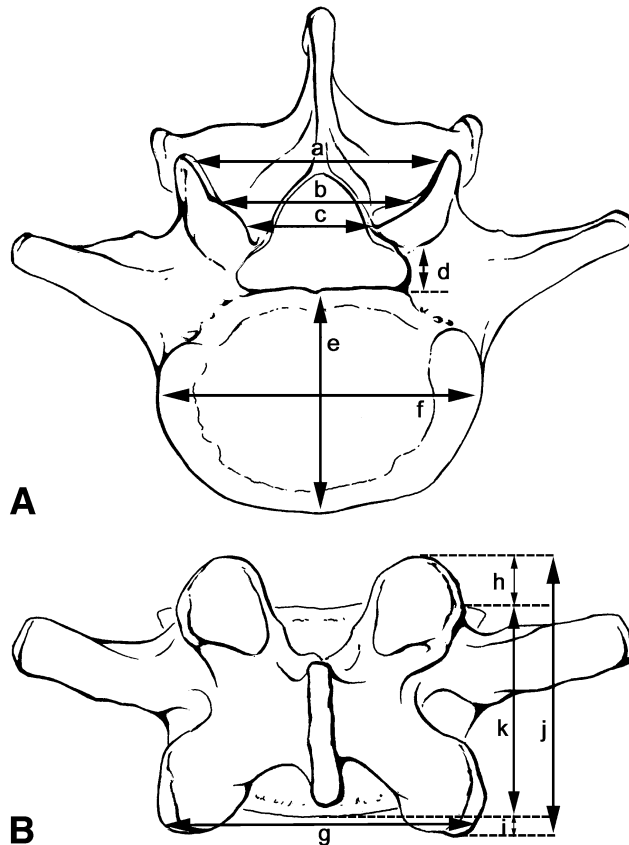


Fig. 1. **A:** Axial view of measurements taken on lumbar vertebrae and described in Table 2. **B:** Posterior view of measurements taken on lumbar vertebrae and described in Table 2.

**TABLE 2. Measurements taken on the vertebrae of the collective**

1. Transverse distance between the posterior rims of the superior zygapophyseal joint surfaces (a in Fig. 1a)
2. Transverse distance between the midpoints of the superior zygapophyseal joint surfaces (b in Fig. 1a)
3. Transverse distance between the anterior rims of the superior zygapophyseal joint surfaces (c in Fig. 1a)
4. Surface area of the superior zygapophyseal articular facet (not depicted)
5. Length of the pedicle, measured from the posterior edge of the vertebral body to the base of the superior articular process (d in Fig. 1a)
6. Sagittal diameter of the vertebral body (e in Fig. 1a)
7. Transverse diameter of the vertebral body (f in Fig. 1a)
8. Surface area of the superior vertebral endplate (not depicted)
9. Angle of the superior vertebral endplate against the inferior endplate (not depicted)
10. Transverse distance between the inferior articular processes (g in Fig. 1b)
11. Prominence of the superior articular processes above the level of the superior vertebral endplate (h in Fig. 1b)
12. Prominence of the inferior articular processes below the level of the inferior vertebral endplate (i in Fig. 1b)
13. Total axial dimension of the articular processes (j in Fig. 1b)
14. Height of the vertebral body (k in Fig. 1b)

**Superior endplate surface area.** The largest superior vertebral endplate surface area is found consistently in the human lumbar spine, with the greatest value found at the fifth lumbar vertebra with almost 13 cm<sup>2</sup>. However, Przewalski's horse possesses a true joint between the transverse processes of the last lumbar vertebra and the sacral alae, which, when added to the endplate surface area amounts to the largest axial loading area of the collective with 21.54 cm<sup>2</sup>. A smaller surface area of the sacral endplate than the preceding lumbar vertebra is found in all species but the seal, which displays an increase in the sacrum.

**Superior endplate angle.** Consistently parallel endplates are found only in the dolphin. A slight anterior wedge shape of the vertebral bodies is found in all other species, except a unique dorsally tapering wedge shape of the human fifth lumbar vertebra. In general, a decrease of the angle is found towards the sacrum in all species with a ventral wedge shape. Przewalski's horse could not be measured due to the pronounced convex shape of the superior endplate.

#### The Articular Processes and Pedicles (Table 4)

**Articular process prominence (Fig. 1b: h, i).** The orang-utan, chimpanzee and kangaroo possess more prominent superior than inferior articular processes (length above or below the corresponding vertebral endplate), whereas for humans and the rest of the collective the opposite is true (excluding the thoracic spine of the dolphin). The cheetah consistently displays the least prominent superior articular processes of the collective and the kangaroo consistently the least prominent inferior articular processes.

**Total axial dimension of the articular processes (Fig. 1b: j).** A decrease towards the sacrum is found in all species. Przewalski's horse possesses the largest span in the upper lumbar spine with over 6 cm, but is surpassed by the kangaroo at the last two lumbar vertebrae. The primates, humans and the lama consistently remain below a 5-cm span and are surpassed by the rest of the collective.

**Transverse distance between the inferior articular processes (Fig. 1b: g).** An increase towards the sacrum is found in the seal, Przewalski's horse, cheetah, ibex, kangaroo and humans. Man possesses the largest value at the fifth lumbar vertebra with 5.1 cm. The primates (chimpanzee and orang-utan) reveal an opposite trait, with the maximum values found in the upper lumbar spine and tapering towards the lumbosacral junction. In the dolphin, the distance is widest in the first thoracic vertebra and tapers towards the lumbar spine.

**Pedicle length (Fig. 1a: d).** A tendency in decrease of length of the pedicles towards the sacrum is seen in all species, with the exception of the kangaroo. The latter reveals an increase in pedicle length of the sacrum compared to the last lumbar vertebra. The longest pedicles are found in the lower lumbar vertebrae of Przewalski's horse with 1.7 cm.

#### The Zygapophyseal Joints (Tables 5 and 6)

**Zygapophyseal joint profile (Fig. 1a: a-c).** Six representative schematic shapes, displayed in Table 6,

**TABLE 3. Dimensions of the vertebral body\***

| Level     | Human <sup>a</sup><br>(n = 3-4) |      |     | Chimpanzee<br>(n = 3) |     |     | Orang-utan<br>(n = 3) |     |     | Kangaroo<br>(n = 4) |     |     | Przewalski's<br>horse <sup>b</sup><br>(n = 4) |     |      | Cheetah<br>(n = 4) |      |     | Lama <sup>c</sup><br>(n = 2-3) |     |      | Ibex (n = 2) |      |     | Seal (n = 4) |     |     | Dolphin <sup>d</sup><br>(n = 1-3) |   |            | Level      |
|-----------|---------------------------------|------|-----|-----------------------|-----|-----|-----------------------|-----|-----|---------------------|-----|-----|---|-----|------|--------------------|------|-----|--------------------------------|-----|------|--------------|------|-----|--------------|-----|-----|-----------------------------------|---|------------|------------|
|           | A                               | B    | C   | A                     | B   | C   | A                     | B   | C   | A                   | B   | C   | A   | B   | C    | A                  | B    | C   | A                              | B   | C    | A            | B    | C   | A            | B   | C   | A                                 | B | C          |            |
| <b>L</b>  | 3.2                             | 4.3  | 2.8 |                       |     |     | 2.3                   | 2.8 | 3.7 | 2.9                 | 3.7 | 4.3 | 2.0   | 2.6 | 4.2  | 1.6                | 2.6  | 3.6 | 2.0                            | 2.9 | 3.8  | 2.4          | 3.2  | 4.2 | 3.1          | 4.1 | 1.7 |                                   |   |            | <b>T1</b>  |
|           | 3.3                             | 4.5  | 2.8 | 2.7                   | 3.7 | 2.7 | 4.92                  | 12° |     | 10.01               |     |     | 4.88  | 8°  | 4.01 | 8°                 | 5.96 | 8°  | 5.96                           | 8°  | 6.79 | 8°           | 6.79 | 8°  | 10.50        | 0°  |     |                                   |   |            |            |
|           | 12.07                           | 2°   |     | 9.49                  | 17° |     | 2.3                   | 3.1 | 4.2 | 2.8                 | 3.7 | 4.4 | 2.0   | 2.6 | 4.5  | 1.6                | 2.6  | 3.5 | 2.0                            | 2.9 | 3.8  | 2.5          | 3.2  | 4.2 | 3.0          | 3.2 | 3.2 |                                   |   |            |            |
| <b>L</b>  | 3.3                             | 4.7  | 2.8 | 3.0                   | 3.8 | 2.7 | 2.4                   | 3.2 | 4.3 | 2.6                 | 3.8 | 4.5 | 2.0   | 2.8 | 4.6  | 1.6                | 2.6  | 3.4 | 2.0                            | 2.9 | 3.9  | 2.6          | 3.1  | 4.3 | 3.3          | 3.6 | 3.5 |                                   |   |            | <b>T5</b>  |
|           | 12.89                           | 0°   |     | 9.26                  | 13° |     | 5.89                  | 12° |     | 10.00               |     |     | 5.19  | 5°  | 4.12 | 10°                | 6.03 | 10° | 6.03                           | 10° | 7.01 | 8°           | 7.01 | 8°  | 8.70         | 0°  |     |                                   |   |            |            |
|           | 3.3                             | 4.9  | 2.6 | 3.1                   | 4.0 | 2.8 | 2.4                   | 3.4 | 4.2 | 2.6                 | 4.4 | 4.2 | 2.0   | 2.9 | 4.5  | 1.6                | 2.7  | 3.1 | 2.0                            | 2.9 | 3.9  | 2.7          | 3.2  | 4.2 | 3.8          | 4.2 | 3.0 |                                   |   |            |            |
| <b>L</b>  | 3.3                             | 4.9  | 2.6 | 3.1                   | 4.0 | 2.8 | 2.4                   | 3.4 | 4.2 | 2.6                 | 4.4 | 4.2 | 2.0   | 2.9 | 4.5  | 1.6                | 2.7  | 3.1 | 2.0                            | 2.9 | 3.9  | 2.7          | 3.2  | 4.2 | 3.8          | 4.2 | 3.0 |                                   |   |            | <b>L10</b> |
|           | 12.85                           | 0°   |     | 11.02                 | 13° |     | 7.07                  | 12° |     | 10.61               |     |     | 5.55  | 5°  | 4.32 | 10°                | 6.10 | 8°  | 6.10                           | 8°  | 7.43 | 3°           | 7.43 | 3°  | 10.95        | 0°  |     |                                   |   |            |            |
|           | 3.2                             | 5.1  | 2.3 | 3.3                   | 4.2 | 2.6 | 2.4                   | 3.6 | 4.0 | 2.1                 | 4.0 | 3.8 | 2.0   | 3.0 | 3.6  | 1.6                | 2.9  | 2.7 | 1.9                            | 3.2 | 3.5  | 2.8          | 3.2  | 3.8 | 4.3          | 4.6 | 2.9 |                                   |   |            |            |
| <b>LL</b> | 12.93                           | -17° |     | 11.83                 | 3°  |     | 7.93                  | 8°  |     | 8.32                |     |     | 5.67  | 5°  | 4.61 | 5°                 | 6.08 | 3°  | 6.08                           | 3°  | 7.92 | 0°           | 7.92 | 0°  | 11.67        | 0°  |     |                                   |   | <b>L20</b> |            |
|           | 2.9                             | 4.8  | —   | 2.9                   | 3.9 | —   | 1.9                   | 3.7 | —   | 1.9                 | 4.0 | —   | 1.7   | 3.1 | —    | 1.3                | 2.9  | —   | 1.6                            | 3.0 | —    | 2.9          | 2.9  | —   | 4.7          | 4.3 | 3.6 |                                   |   |            |            |
|           | 11.67                           | —    |     | 9.78                  | —   |     | 6.81                  | —   |     | 7.45                |     |     | 5.43  | —   | 4.54 | —                  | 5.34 | —   | 5.34                           | —   | 8.20 | —            | 8.20 | —   | 15.30        | 0°  |     |                                   |   |            |            |

\*A: Sagittal diameter of the vertebral body in cm; B: Transverse diameter of the vertebral body in cm; C: Height of the vertebral body, measured in the spinal canal in cm; D: Surface area of the superior vertebral endplate in cm<sup>2</sup>; E: Angle formed by the superior and inferior endplates of the vertebral body in degrees.

<sup>a</sup>In humans, height, sagittal diameter and endplate surface area were not measured in one individual due to partially preserved intervertebral disc structure. The negative angle indicates a dorsally-tapering wedge shape of the vertebral body.

<sup>b</sup>For Przewalski's horse, the joint surfaces of both lateral lumbosacral articulations (combining to an average of 14.09 cm<sup>2</sup>; Fig. 6d) were added to the endplate surface area (*cursor* value) and presented in addition to the conventional endplate surface area; the endplate angle could not be included due to the convex shape of the endplate.

<sup>c</sup>In the lama, reliable measurements could not be obtained in each motion segment due to the occasional preservation of ligaments.

<sup>d</sup>In the dolphin, the surface area of L10 and L20 were only measured in one individual.

may be deduced from the collective. The dolphin is unique in that it only possesses zygapophyseal joints up until the 7th thoracic vertebra, which are angled medially in contrast to the usual frontal joint orientation of the thoracic spine. In the seal, the joint surface is oriented mainly in the sagittal plane, while the terrestrial species possess a distinct frontal joint portion or orientation. Encompassing joints are found in the lumbar vertebrae and the sacrum of the lama and the ibex. Przewalski's horse reveals encompassing joints in the upper lumbar vertebrae, but not at the lumbosacral junction. The ibex is the only mammal of the collective that possesses an additional outward curvature at the dorsal rim of the articular surface (Fig. 9b). Encompassing joints are not found in the lumbar spines of the chimpanzee, orang-utan and kangaroo. The latter is unique in displaying almost perfectly plane joint surfaces. Humans and the primates reveal a curved joint, that of humans possessing a more pronounced sagittal and frontal joint area, while the joints of the primates are oriented more towards the frontal plane.

**Joint surface area.** Man is found to possess the largest joint surface area at the lumbosacral junction with over 2 cm<sup>2</sup>, but is surpassed by the chimpanzee at the prior levels. In the upper lumbar spine, Przewalski's horse has the largest joint surface area.

## DISCUSSION

To our knowledge, the presented study is currently the most comprehensive regarding the wide selection of ten mammalian species and the extent of morphological criteria compared in more than 200 lumbar vertebrae.

The choice of mammals was based upon selecting a collective with highly divergent strain patterns of the lumbar spine in locomotion, as distinguishable through the research published by Saunders et al. (1953), Hildebrand (1959), Gray (1968), Jenkins (1972), Dagg (1973), Gambaryan (1974), Kimura (1985), Eibel (1987), Fish (1988), Webb and De Buffrenil (1990) and Schmid and Piaget (1994). Detailed investigations were, however, not available for some of the rarer species such as the ibex and the lama.

Despite the overall extent of the study, certain limitations remain: The relatively small number of individuals examined from each of the species precludes reliable statistics and quantification as described by Panjabi et al. (1991a, 1991b and 1992). The averages determined, however, allow comparison of relative magnitudes and traits. Interpretation of the biomechanical function of the vertebrae is based solely upon the osseous structure. A more precise functional analysis would require the inclusion of the muscular and ligamentous attachments of the vertebrae. However, obtaining an adequate quantity of material suitable for dissection of each of the presented species is unlikely to be accomplished. For the same reason, a detailed examination of the spinous and transverse processes was not included as these are functionally closely linked to the structure of the muscles and ligaments of the spine. The zygapophyseal joints possess true three-dimensional surfaces. Correspondingly, an in depth analysis of the biomechanical function of these joints is only possible through three-dimensional analysis as described by Panjabi et al. (1993). However, for the purpose of functional comparative anatomy, regarding principle patterns of lo-

comotion, the most striking features are found in comparing the joint profile in the transverse plane.

### The Vertebral Bodies (Table 3)

**Marine mammals.** The dolphin and the seal, both displaying a balance in sagittal and lateral flexion during propulsion, possess nearly round vertebral endplates (Figs. 10b,c and 11b,c), with the dolphin, furthermore, possessing parallel endplates throughout.

**Terrestrial quadrupedal mammals.** A slight anterior wedge shape and a decrease in sagittal diameter towards the sacrum is recognisable in the quadrupedal species, in whom predominant sagittal flexion is found in locomotion (Figs. 6d, 7c, 8c and 9c).

**Terrestrial bipedal mammals and primates.** The vertebral bodies of humans provide a structural adaptation to a high degree of axial loading through a remarkably enlarged cranial endplate surface area. As the sagittal diameter does not greatly differ from the chimpanzee, it is the relatively increased transverse diameter of the superior endplate surface in humans which is responsible for the larger surface area. A dorsally-tapering wedge shape, found exclusively in the last lumbar vertebra of humans, enhances lordosis. Only results from studies by Preuschoft et al. (1988) on Japanese macaques trained for bipedalism reveal a similar trend, suggesting a functional adaptation to bipedal gait.

### The Pedicles (Table 4)

The similarity of lumbar pedicle length of approximately 1 cm in all species is remarkable, considering the difference in body size. Only Przewalski's horse displays a comparatively larger pedicle size in the caudal lumbar vertebrae. This finding suggests a common biomechanical denominator in lumbar spinal dynamics.

### The Articular Processes and Zygapophyseal Joints (Tables 4 and 5)

**Marine mammals.** Both species are subject to a lesser degree of ventral and dorsal shear than the terrestrial species. The lumbar spine of the dolphin is essentially subject to axial loading and is entirely devoid of vertebral joints (Fig. 11b and Table 6a). Significant torque may only be expected during steering with the pectoral fins (Webb and De Buffrenil, 1990) in the region of the upper thoracic spine, where resistance may be provided by the medially-angled zygapophyseal joints (Fig. 11b) and the wide transverse distance between the inferior articular processes (Fig. 11a). The higher level of torsion experienced by the lumbar spine of the seal finds a match in the essentially sagittal orientation of the zygapophyseal joints (Table 6d and Figs. 10a-c). Resistance to ventral shear is, however, reduced in comparison to terrestrial species (Gal, 1993).

**Terrestrial quadrupedal mammals.** As for the seal, an increase in the distance between the inferior articular processes towards the sacrum in the quadrupedal species is reflective of an increase in torsion in this region. In the lama, this feature was not anticipated in view of the expected lack of torsion in pacing. Review of the detailed process of pacing, however, reveals torsion

**TABLE 4. Dimensions of the articular processes and pedicles\***

| Level     | Human <sup>a</sup><br>(n = 3-4) |     |     | Chimpanzee<br>(n = 3) |     |     | Orang-utan<br>(n = 3) |     |     | Kangaroo<br>(n = 4) |     |     | Przewalski's<br>horse (n = 4) |     |     | Cheetah<br>(n = 4) |     |     | Lama <sup>b</sup><br>(n = 2-3) |     |     | Ibex (n = 2) |     |     | Seal (n = 4) |     |     | Dolphin<br>(n = 3) |     |     | Level     |
|-----------|---------------------------------|-----|-----|-----------------------|-----|-----|-----------------------|-----|-----|---------------------|-----|-----|-------------------------------|-----|-----|--------------------|-----|-----|--------------------------------|-----|-----|--------------|-----|-----|--------------|-----|-----|--------------------|-----|-----|-----------|
|           | A                               | B   | C   | A                     | B   | C   | A                     | B   | C   | A                   | B   | C   | A                             | B   | C   | A                  | B   | C   | A                              | B   | C   | A            | B   | C   | A            | B   | C   | A                  | B   | C   |           |
| <b>L</b>  | 0.5                             | 4.8 | 1.2 | 0.9                   | 4.3 | 0.7 | 0.8                   | 3.6 | 0.6 | 1.1                 | 5.2 | 0.5 | 1.1                           | 6.3 | 1.4 | 0.1                | 5.6 | 1.4 | 0.2                            | 4.6 | 0.7 | 0.6          | 5.4 | 1.1 | 0.4          | 5.7 | 1.1 | 0.7                | 2.7 | 0.1 | <b>T1</b> |
| <b>L</b>  | 0.6                             | 4.8 | 1.4 | 0.9                   | 4.3 | 0.7 | 0.8                   | 3.6 | 0.6 | 1.4                 | 5.6 | 0.4 | 0.9                           | 6.4 | 1.5 | 0.1                | 5.7 | 1.4 | 0.1                            | 4.5 | 0.8 | 0.5          | 5.7 | 1.1 | 0.4          | 5.7 | 0.9 | 0.9                | 3.5 | 0.2 | <b>T2</b> |
| <b>L</b>  | 0.5                             | 4.9 | 1.4 | 0.7                   | 4.4 | 0.7 | 0.8                   | 3.7 | 0.6 | 1.5                 | 5.8 | 0.4 | 0.8                           | 6.1 | 1.4 | 0.1                | 5.8 | 1.2 | 0.1                            | 4.3 | 0.5 | 0.5          | 5.6 | 1.2 | 0.5          | 5.9 | 1.2 | 1.1                | 4.0 | 0.4 | <b>T3</b> |
| <b>L</b>  | 0.7                             | 4.5 | 1.4 | 0.9                   | 4.6 | 0.8 | 0.8                   | 3.8 | 0.7 | 1.6                 | 5.9 | 0.3 | 0.6                           | 5.6 | 1.5 | 0.1                | 5.6 | 1.0 | 0.2                            | 4.1 | 0.5 | 0.5          | 5.6 | 1.2 | 0.5          | 5.7 | 0.9 | 1.0                | 4.4 | 0.4 | <b>T4</b> |
| <b>LL</b> | 0.8                             | 4.1 | 1.2 | 1.0                   | 4.4 | 0.8 | 0.9                   | 3.5 | 0.5 | 1.5                 | 5.7 | 0.4 | 1.0                           | 5.3 | 1.1 | 0.3                | 5.2 | 1.1 | 0.4                            | 3.7 | 0.5 | 0.6          | 5.4 | 1.2 | 0.7          | 5.3 | 1.0 | 0.8                | 4.3 | 0.3 | <b>T5</b> |
| <b>S</b>  | 0.5                             | —   | —   | 0.8                   | —   | —   | 0.8                   | —   | —   | 1.0                 | —   | —   | 0.5                           | —   | —   | 0.9                | —   | —   | 0.9                            | —   | —   | 0.8          | —   | —   | 0.6          | —   | —   | 0.8                | 4.3 | 0.2 | <b>T6</b> |
|           | —                               | 0.8 | —   | —                     | 0.7 | —   | —                     | 0.9 | —   | —                   | 1.4 | —   | —                             | 1.2 | —   | —                  | 0.5 | —   | —                              | 0.6 | —   | —            | 0.8 | —   | —            | 0.6 | —   | 3.1                | 2.1 | —   |           |

\*A: Prominence of the superior articular processes above the superior vertebral endplate in cm; B: Total axial dimension of the articular processes in cm; C: Prominence of the inferior articular processes below the inferior vertebral endplate in cm; D: Transverse distance between the inferior articular processes in cm; E: Length of pedicles in cm.

<sup>a</sup>In humans, pedicle length was measured in three individuals.

<sup>b</sup>In the lama, reliable measurements could not be obtained for each level in each individual due to the preservation of ligaments in singular motion segments.

**TABLE 5. Zygapophyseal joint profile and surface area of the superior articular processes\***

| Level     | Human<br>(n = 4) |     |     | Chimpanzee<br>(n = 3) |     |     | Orang-utan<br>(n = 3) |     |     | Kangaroo<br>(n = 4) |     |     | P. horse<br>(n = 4) |     |     | Cheetah<br>(n = 4) |     |     | Lama <sup>a</sup><br>(n = 2-3) |     |     | Ibex <sup>b</sup> (n = 2) |     |     | Seal <sup>c</sup><br>(n = 3-4) |     |     | Dolphin <sup>d</sup><br>(n = 2-3) |     |     | Level     |
|-----------|------------------|-----|-----|-----------------------|-----|-----|-----------------------|-----|-----|---------------------|-----|-----|---------------------|-----|-----|--------------------|-----|-----|--------------------------------|-----|-----|---------------------------|-----|-----|--------------------------------|-----|-----|-----------------------------------|-----|-----|-----------|
|           | A                | B   | C   | A                     | B   | C   | A                     | B   | C   | A                   | B   | C   | A                   | B   | C   | A                  | B   | C   | A                              | B   | C   | A                         | B   | C   | A                              | B   | C   | A                                 | B   | C   |           |
| <b>L</b>  | 1.7              | 2.6 | 2.8 | 1.5                   | 2.8 | 3.7 | 1.3                   | 2.1 | 2.4 | 1.0                 | 2.2 | 2.6 | 0.2                 | 1.8 | 1.7 | 0.8                | 1.9 | 2.1 | 0.7                            | 1.6 | 1.0 | 1.3                       | 2.0 | 1.3 | 2.5                            | 2.8 | 2.7 | 4.7                               | 5.6 | 5.6 | <b>T2</b> |
| <b>L</b>  | 1.7              | 2.7 | 2.8 | 1.5                   | 2.8 | 3.7 | 1.3                   | 2.1 | 2.4 | 1.1                 | 2.3 | 2.8 | 0.3                 | 1.9 | 1.9 | 1.0                | 2.2 | 2.3 | 0.9                            | 1.9 | 1.3 | 1.2                       | 2.2 | 1.4 | 2.3                            | 3.0 | 3.2 | 4.3                               | 5.2 | 6.0 | <b>T3</b> |
| <b>L</b>  | 1.8              | 3.0 | 3.2 | 1.7                   | 3.3 | 4.3 | 1.3                   | 2.1 | 2.6 | 1.4                 | 2.3 | 2.6 | 0.5                 | 2.1 | 2.2 | 1.1                | 2.2 | 2.4 | 1.3                            | 2.0 | 1.5 | 1.2                       | 2.4 | 1.4 | 2.5                            | 3.1 | 3.1 | 3.9                               | 4.7 | 5.4 | <b>T4</b> |
| <b>L</b>  | 1.8              | 3.2 | 3.5 | 1.6                   | 3.2 | 4.5 | 1.3                   | 2.1 | 2.9 | 1.7                 | 2.5 | 2.7 | 0.6                 | 2.3 | 2.4 | 1.3                | 2.1 | 2.5 | 1.8                            | 2.5 | 2.0 | 1.3                       | 2.6 | 1.7 | 2.5                            | 3.1 | 3.3 | 3.6                               | 4.3 | 5.0 | <b>T5</b> |
| <b>LL</b> | 2.0              | 3.7 | 4.0 | 1.6                   | 3.0 | 4.1 | 1.3                   | 2.0 | 2.7 | 1.9                 | 2.9 | 3.2 | 1.3                 | 2.8 | 2.9 | 1.7                | 2.4 | 2.8 | 2.3                            | 3.3 | 2.8 | 1.5                       | 2.8 | 1.8 | 2.6                            | 3.2 | 3.5 | 3.6                               | 3.9 | 4.2 | <b>T6</b> |
| <b>S</b>  | 2.5              | 4.7 | 5.2 | 1.7                   | 2.8 | 3.3 | 1.2                   | 1.7 | 2.1 | 1.9                 | 2.9 | 3.3 | 1.7                 | 2.9 | 3.2 | 2.3                | 3.1 | 3.8 | 3.0                            | 4.2 | 3.4 | 2.5                       | 3.3 | 2.2 | 3.0                            | 3.6 | 4.0 | 3.3                               | 3.3 | 3.3 | <b>T7</b> |
|           | 2.11             | —   | —   | 1.87                  | —   | —   | 0.81                  | —   | —   | 1.58                | —   | —   | 1.89                | —   | —   | 1.24               | —   | —   | 1.32                           | —   | —   | —                         | —   | —   | —                              | —   | —   | 0.8                               | 4.3 | 0.2 |           |

\*A: Transverse distance between the medial borders of the superior articular surfaces in cm; B: Transverse distance between the midpoints of the superior articular surfaces in cm; C: Transverse distance between the posterior borders of the superior articular surfaces in cm; D: Joint surface area of the superior articular processes in cm<sup>2</sup>.

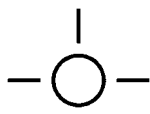
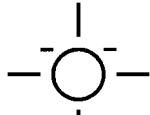
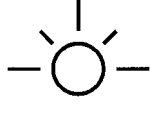
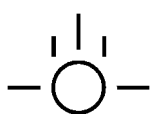
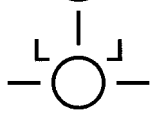
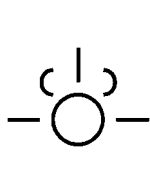
<sup>a</sup>In the lama, reliable measurements could not be obtained for each level in each individual due to the preservation of ligaments in singular motion segments.

<sup>b</sup>In the ibex, the additional outward curvature of the dorsal rim (Fig. 9b) and joint surface area were not included.

<sup>c</sup>In the seal, the joint surface areas of L4 and L5 of one individual could not be included because of damaged surfaces.

<sup>d</sup>In the dolphin the joint surface areas of T1, T3 and T5 of one individual could not be included because of damaged surfaces.

TABLE 6. Basic zygapophyseal joint shapes

|   |   |
|---|---|
|  | a) Lumbar vertebra without zygapophyseal joints as found in the dolphin, indicating a lack of significant torsion and shear.  |
|  | b) Lumbar vertebra with mainly frontal zygapophyseal joint orientation, as found in the lower lumbar spine of the primates. Resistance is mainly afforded against ventral shear.  |
|  | c) Lumbar vertebra with inclined and plane joint surfaces, as found in the kangaroo. Resistance is provided to both shear and torsion. Rotation of the motion segment is limited to the range afforded by the joint space.  |
|  | d) Lumbar vertebra presenting mainly sagittal joint orientation, as found in the seal. Resistance is provided mainly against torsion.   |
|  | e) Lumbar vertebra presenting curved joints with frontal and sagittal areas, as found in humans and the tail of the kangaroo. Resistance is afforded against both torsion and shear. Rotation of the motion segment may be in excess of that allowed by the joint space through shifting of the centre of rotation. |
|  | f) Lumbar vertebra displaying curved, encompassing joints, as found in the ibex, lama and to a limited degree in Przewalski's horse. In addition to torsion and ventral shear, resistance is effectively provided against dorsal shear.   |

resulting from alternate positioning of the rear legs close to the midline through axial twisting of the lumbar spine, rather than singular ab- and adduction. The quadrupedal species which, in addition to ventral shear, experience dorsal shear within a motion-segment during locomotion may possess encompassing zygapophyseal joints (Table 6f). Przewalski's horse presents encompassing joints with a decrease in extent towards the lumbosacral junction (Figs. 6b,c). Here, dorsal shear acting upon the joints is limited by the fusion of the transverse processes of L5/L6 and the lateral lumbosacral joint formation (Figs. 6a,c,d). The lama and the ibex display encompassing zygapophyseal joints in all lumbar vertebrae and the sacrum (Figs. 8a–c and 9a–c). The male individuals of the ibex even have an additional outward curvature of the rim of the superior articular facet, likening the joint to a “key and lock” (Fig. 9b), in all but the lumbosacral joint. Adequate resistance is thus provided to the combination of high-grade torque and ventral and dorsal shear experienced in the alpine habitat. The cheetah, in contrast, does not display encompassing joints (Figs. 7a–c). This species, which actively contributes to acceleration through dynamic flexion and extension of the spine, may be assumed to counter dorsal shear through the tensed spinal musculature. Only the vertebrae of the thoracolumbar junction, where the flexed lumbar spine is forced against the relatively rigid thoracic spine, display moderately encompassing joints.

#### ***Terrestrial bipedal mammals and primates.***

Compared to the quadrupeds and the rest of the collective, the primates and humans possess a comparatively short

total axial span of the articular processes. This may be linked to the lesser extent of sagittal flexion during locomotion. Torsion, however, brings about a similar response in widening of the transverse distance between the inferior articular processes. The greatest distance is found at the human lumbosacral junction (Fig. 2a), providing resistance to the high degree of torque in the lower lumbar spine during bipedalism. Both primate species reveal the opposite trait, with the maximum values found in the upper lumbar vertebrae and tapering towards the sacrum (Figs. 3a and 4a); as previously described by Shapiro (1993) and correspondingly for the gorilla by Struthers (1892). The chimpanzee possesses the greatest distance of the collective in all vertebrae, except for the last lumbar vertebra, where it is surpassed only by Man. This finding may be explained through brachiation and quadrupedal climbing, whereby the stiffened lower body is rotated against the relatively fixed shoulder girdle, creating a gradient of torsion towards the thoracolumbar junction. Even in the rare event of bipedalism in the chimpanzee, rotation of the torso against the pelvis is very limited, thus not producing an equally high level of torsion and ventral shear at the lumbosacral junction as found in humans, in whom lumbar lordosis increases at heel strike—the moment of maximal pelvic rotation and highest vertical impulse (Thurston and Harris, 1983; Alexander, 1980). Accordingly, the increase in joint surface area measured in humans (corresponding to the calculated values of Panjabi et al. (1993)) reflects an increase in ventral shear towards the sacrum, where the largest joint surface area of the collective is found. A curved zygapophyseal joint shape is

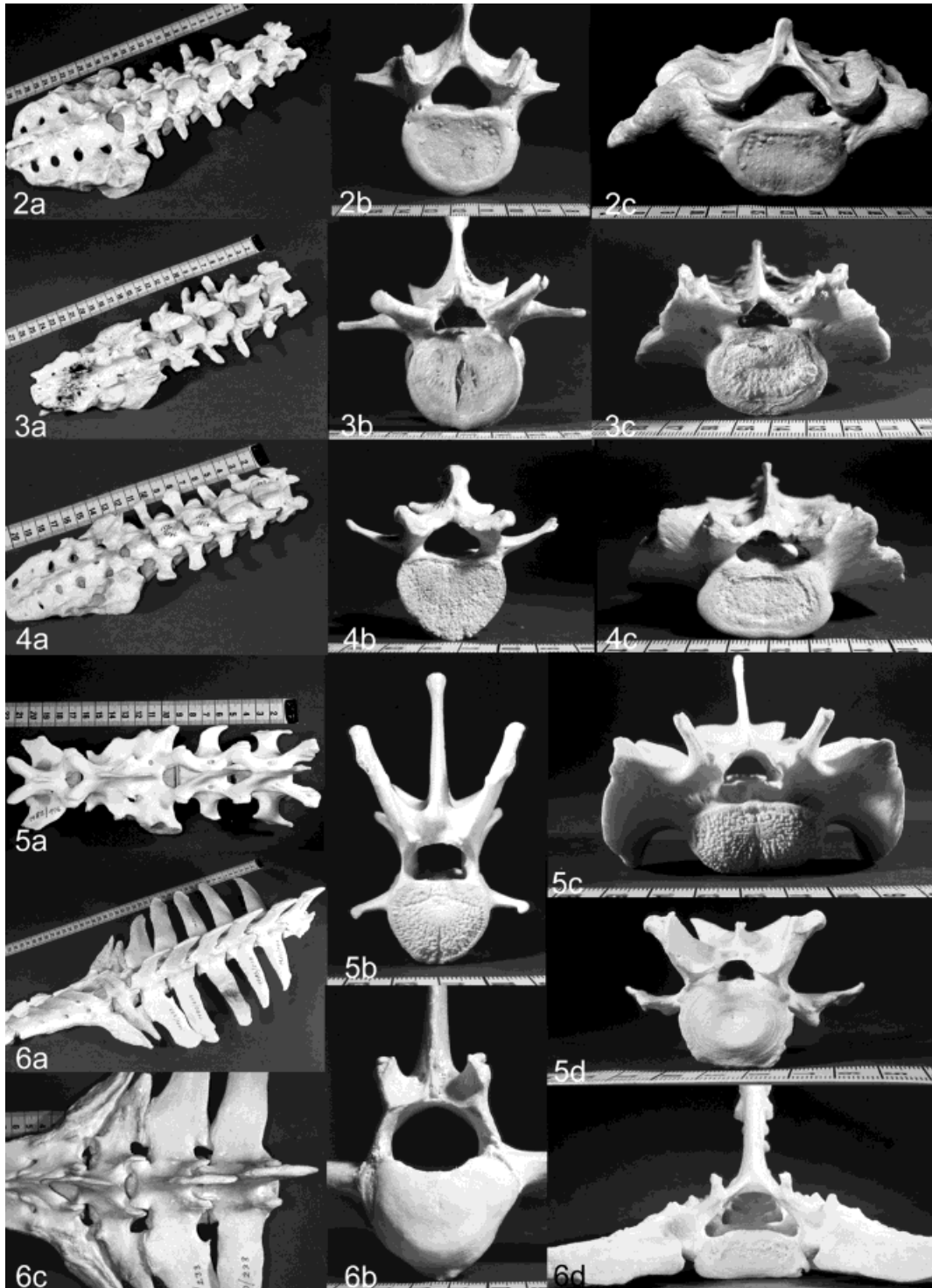


Fig. 2. Human lumbar spine (a), third lumbar vertebra (b) and sacrum (c). Fig. 3: Lumbar spine (a), third lumbar vertebra (b) and sacrum (c) of the chimpanzee. Fig. 4: Lumbar spine (a), third lumbar vertebra (b) and sacrum (c) of the orang-utan. Fig. 5: Lumbosacral junction with first tail vertebra (a), third lumbar vertebra (b), sacrum (c) and first tail vertebra (d) of the kangaroo. Fig. 6: Lumbar spine (a), third lumbar vertebra (b), lumbosacral junction (c) and sacrum (d) of Przewalski's horse.



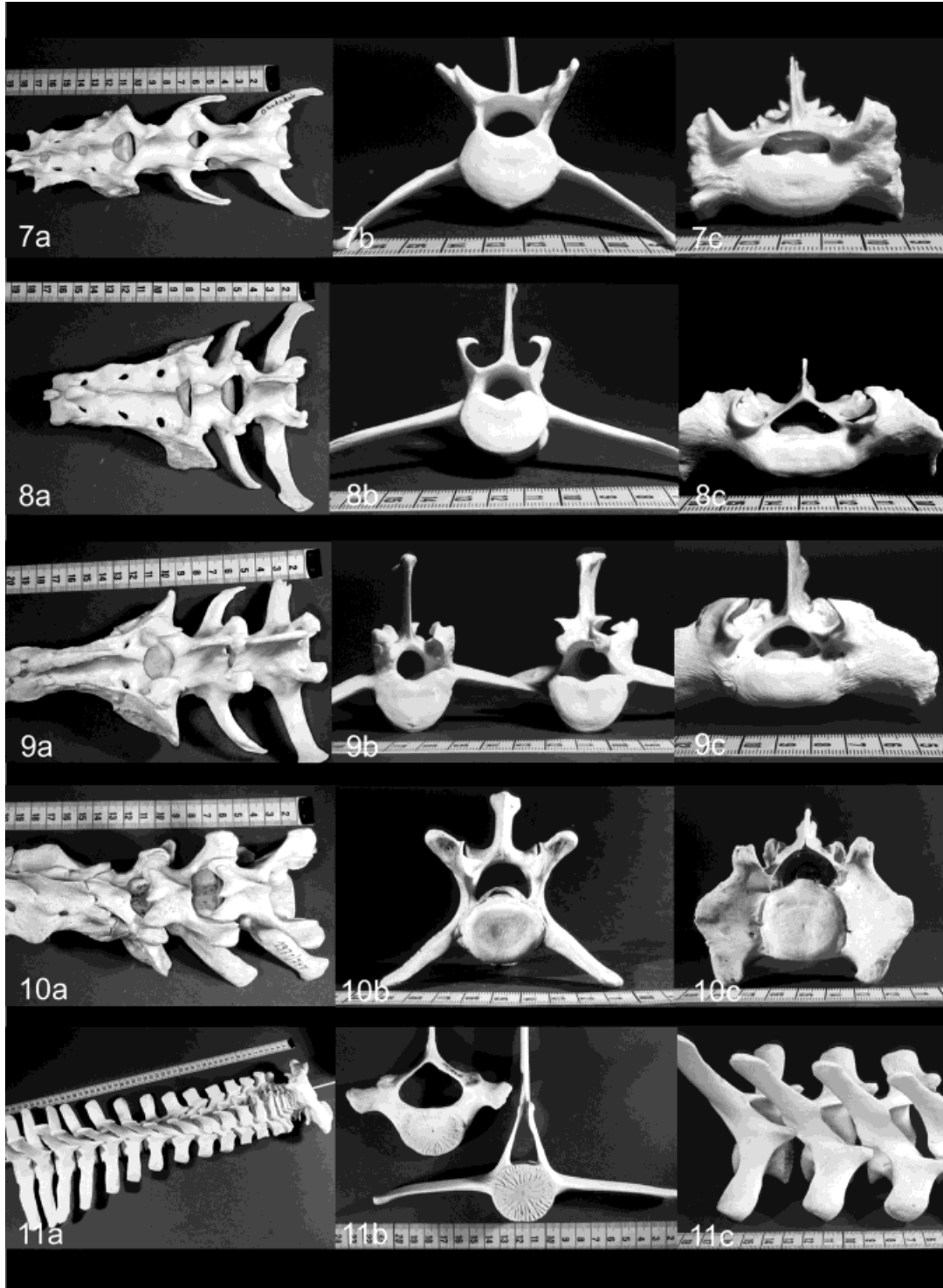


Fig. 7. Lumbosacral junction (a), third lumbar vertebra (b) and sacrum (c) of the cheetah. Fig. 8: Lumbosacral junction (a), third lumbar vertebra (b) and sacrum (c) of the lama. Fig. 9: Lumbosacral junction (a), third lumbar vertebra (b) and sacrum (c) of the ibex Fig. 10: Lumbosacral junction (a), third lumbar vertebra (b) and sacrum (c) of the seal. Fig. 11: Cervical, thoracic and upper lumbar spine (a), fifth thoracic (left) and third lumbar (right) vertebra (b) and lower thoracic spine (c) of the dolphin.

present in humans and to a lesser extent in the primates, which present a more frontal orientation (Figs. 2b,c; 3b,c; 4b,c and Table 6b,e). A curved joint is necessary for rotation within a motion segment beyond the range allowed by the joint space alone, as it enables the superior vertebra to rotate about the engaged joint until movement is limited by the contralateral joint capsule and the annulus fibrosus (Putz, 1985; Shirazi-Adl et al., 1986; Hafer et al., 1992; Nägerl et al., 1992; Boszczyk et al. 2001). Rotation within the lumbar spine is particularly apparent in humans, as the shoulder girdle is rotated against the pelvis in walking or running. In contrast, the plain lumbar joint surfaces of the kangaroo (Figs. 5b,c; Table 6c) limit rotation to the range granted by the joint space. Remarkably however, the first tail vertebra of the kangaroo (Fig. 5a) reveals a pronounced curvature (Fig. 5d). This may be explained through the slow gait, during which the base of the tail is subject to a large degree of rotation, as the direction of travel is changed in support phases by the tail (Table 1).

## CONCLUSION

Regarding the spine, two principles of evolution appear to compete—increasing structural support while maintaining segmental mobility. This requires the judicious arrangement of a minimum of material to achieve sufficient stability. All mammals examined suggest an exact accommodation of the lumbar spine to the specific biomechanical demands sustained during the course of evolution. The mammalian lumbar spine appears to react to flexion in a predominant plane with narrowing of the vertebral bodies in that plane (e.g., sagittal narrowing of lower lumbar vertebrae in quadrupeds), while increased axial load induces an increase in superior endplate surface area (e.g., lower lumbar spine of humans). Torsion of the lumbar spine is withstood by an increase in the transverse distance between the inferior articular processes (e.g., upper lumbar spine in primates, lower lumbar spine in humans and quadrupeds) and a sagittal zygapophyseal joint orientation (e.g., the seal). Ventral shear is resisted by frontal zygapophyseal joint portions (e.g., humans), while extreme dynamic dorsal shear is countered by encompassing joints (e.g., the ibex).

The functional individuality of mammalian species should therefore be appreciated, when considering nonhuman spines as biomechanical models for humans. In this light, a highly advanced level of differentiation of lumbar spinal morphology is recognised for humans. It may be more reasonable to attribute the high incidence of low back afflictions to our evolving modern lifestyle rather than to imperfect morphological adaptation.

## EXPERIMENTAL PROCEDURES

### Selection of Mammalian Lumbar Spines

The lumbar spines of ten mammalian species (human, chimpanzee, orang-utan, kangaroo, dolphin, seal, Przewalski's horse, cheetah, lama, ibex) were chosen for investigation. Only clearly taxonomised, undamaged adult mammalian spines without extensive degenerative changes from a zoological collection and human spines from an anatomical collection were selected.<sup>1</sup> All specimens were dried and free of soft tissue, except for occasionally preserved spinal ligaments and intervertebral discs. Lumbar vertebrae, as defined by the lack of costovertebral articulations, and the first sacral vertebra of

each species were studied. In the dolphin, the thoracic spine was added, as zygapophyseal joints are exclusively present in this region and the analysis of their morphology is paramount in understanding the regression of the zygapophyseal joints in the lumbar spine. Selection was limited to one gender in four species with substantial size discrepancy between genders: the kangaroo, the chimpanzee, the orang-utan and the ibex. For most species four suitable lumbar spines were found; however, in certain species only a lesser number could be obtained due to the rarity of the species (Table 1).

### Selection of Mammalian Species

The ten mammalian species were selected according to their highly contrasting motion and loading patterns of the lumbar spine (Table 1).

**Strain and motion of the lumbar spine in locomotion.** Movement of the lumbar spine is limited to flexion in the sagittal and frontal planes and rotation of vertebrae against each other along the longitudinal axis of the spine. For functional comparison, the forces acting upon the lumbar spine have to be broken down into basic components: axial compression, torsion and shear in the transverse plane. The spinal column at rest, which may be compared to a strung bow (Slijper, 1946; Kummer, 1959; Putz, 1981), will ideally only be subjected to axial loading without shear or torsion. This axial force is absorbed by the intervertebral discs and bodies without integration of the zygapophyseal joints. In locomotion, however, axial torsion (Gray, 1968) and anterior or posterior shear within the motion segment is induced according to the mode used. The zygapophyseal joints are instrumental in the management of these forces, providing stability, while maintaining and guiding flexibility. The sagittal portions have been shown to resist torsion (Putz, 1977; Müller-Gerbl, 1992; Nägerl et al., 1992), while the frontal and encompassing areas withstand ventral and dorsal shear, respectively. Dorsal shear is induced in phases of support solely by the front legs, especially at moderate speeds which do not provide for enough velocity to propel the body mass without significant vertical oscillation. In this situation, the caudal vertebra of a motion-segment is subject to a ventrally directed force, resisted by the cranial vertebra through encompassing joints or through muscular resistance. All quadrupeds incorporating flight phases in their gait, or travelling over uneven terrain, are necessarily subject to dorsal shear of the lumbar spine.

**Marine mammals.** The dolphin (*Tursiops truncatus*) and the seal (*Phoca vitulina*) were selected in view of the reduced gravitational influence of body mass upon the mode of locomotion (Badoux, 1968) and the far lesser degree of ventral and dorsal shear than in terrestrial mammals. The dolphin is subject only to minor shear and torsion of the lumbar spine (Gray, 1968; Klima, 1992), presenting mainly axial loading during the propulsion through sagittal strokes of the tail fluke (Table 1). The seal, in contrast, displays a lateral stroke of the rear appendages in propulsion (Fish, 1988; Table 1) and subjects its lumbar spine to a high degree of torsion during steering with interaction of both pairs of appendages.

**Terrestrial quadrupedal mammals.** Przewalski's horse (*Equus przewalski*), the cheetah (*Acinonyx jubatus*),

the lama (*Lama vicugna*) and the ibex (*Capra i. ibex*), were selected in view of their contrasting gaits. Przewalski's horse performs the gallop with a stiff lower back, limiting sagittal flexion selectively to the lumbosacral junction and highly restricting axial rotation (Townsend and Leach, 1984; Table 1). The cheetah, when bounding, characteristically incorporates the whole lumbar spine through powerful flexion and extension (Table 1), with rapid changes in direction and lead inducing a high degree of torsion in the lumbar spine. In the ibex, the degree of dorsal and ventral shear may be assumed to be the greatest of the collective due to its extreme leaping in the alpine habitat, which it performs in addition to the usual quadruped gaits (Gambaryan, 1974; Table 1). The lama was included as a representative of the camelids, which are known as frequent pacers.

**Terrestrial bipedal mammals and primates.** The kangaroo (*Macropus giganteus*) was selected for its bipedal hop (Table 1), which is not dependent upon axial pelvic rotation. The slow gait of the kangaroo is characterised by quadrupedal support phases, alternating with phases of support by the front appendages and the tail, while the rear legs are suspended (Eibel, 1987; Table 1). In disparity to the lumbar spine, extensive rotation is required of the base of the tail in the frequent changes of direction. Two species of primates were included due to the anthropological interest in comparison with humans. The orang-utan (*Pongo pygmaeus*) is assumed to be best adapted to arboreal life amongst the great apes (Schmitt and Larson, 1995). The female of the latter was examined as, in contrast to the larger male, it very rarely descends to the ground and almost exclusively performs either quadrupedal climbing or supported brachiation, which place only moderate demand upon the short trunk regarding flexibility. Bipedalism is not normally observed in nature. The chimpanzee (*Pan troglodytes*), moving with far more vigour than the orang-utan and often travelling on the ground, was seen as taking up an intermediate position between the orang-utan and humans. According to a report by Hunt (1991), bipedalism is only infrequently displayed by this primate in the wild, next to quadrupedal climbing, running and brachiation. When present, bipedalism is performed with kyphotic trunk posture, pronounced flexion of the hips and a lack of countering rotation of the pelvis and shoulder girdle (Jenkins, 1972; Prost, 1980). Stride length is far shorter than in humans (Kimura, 1985) and running with flight phases has not been observed (Schmid and Piaget, 1994). Finally, human-kind (*Homo sapiens*) was included in the collective. In human bipedalism, the lordotic lumbar spine is the focus of axial load and torsion through the countering rotation of shoulder girdle and pelvis, with an increase during faster walking and running (Schmid and Piaget, 1994).

### Measurements

Fourteen measurements, described in Table 2 and illustrated in Figure 1, were taken on each vertebra using precision callipers. Measurements of the surface area of the superior vertebral endplates and superior zygapophyseal joint surfaces were obtained by outlining modelling clay casts on millimetre paper. The sagittal angle between the superior and inferior endplates (latter defined as parallel to the horizontal plane), was measured by aligning the tangent of the superior endplate on millimetre paper,

where the angle to the horizontal plane was determined with a standard protractor.

Mathematical averages of the measurements were determined for each species and provided the basis for comparison between the species.

A profile of the zygapophyseal joints in the transverse plane was established by measuring the distance between the superior articular facets of a vertebra at the anterior joint rim, the facet midpoints and the posterior joint rim. A smaller difference between the values indicates a more sagittal joint alignment. An encompassing joint is reflected in a smaller posterior than midpoint value, while a small anterior value with a larger midpoint value indicates a frontally-oriented joint region.

### ACKNOWLEDGMENTS

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