Jean Marc Vital
Derek Thomas Cawley
Editors

Spinal Anatomy

Modern Concepts

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Jean Marc Vital
Spinal Unit
Centre Hospitalier
Universitaire de Bordeaux
Bordeaux
France

Derek Thomas Cawley
Spinal Unit
Centre Hospitalier
Universitaire de Bordeaux
Bordeaux
France

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Translated by Derek Thomas Cawley

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Foreword

It is difficult for the layman to understand anatomical research and discoveries, because anatomy is considered as a science of the dead, so long known without new phenomena. This book on the anatomy of the spine with its new concepts is a clear proof of this common mistake. Studying the dynamic anatomy of the living subject and using the most up-to-date technical means can open up new perspectives to elucidate the pathology of the spine and perfect its surgery!

The comparative anatomy of the spine through the vertebrate chain illustrates the Darwinian evolution of the spine to finally adapt to bipedal walking. Embryology, which is a repetition of phylogeny, shows this adaptation. Studies in erect standing have identified parameters, including "pelvic incidence," which quantifies the pelvic tilt relative to the lumbar curvature. Thus, from these parameters, it has been possible to identify four types of "vertebral equilibrium." It has appeared that a "reserve of the extension of the hips" must be considered in the operative state of sagittal imbalances.

The 3D study of vertebral movements, thanks to the "EOS system," made it possible to define an "articular chain of equilibrium" and a "cone of economy." To simplify this concept, the authors included the skull and pelvis in the spine as cephalic and pelvic vertebrae. This may seem logical and simplistic, but I doubt that anatomists agree. The new histological and chemical knowledge of the intervertebral disk enriches the chapter on this element. The posterior vertebral joints have general features specific to the cervical, dorsal, and lumbar vertebrae, which explain their dynamics and their role in the spinal balance; facet orientation variations are common. The study of ligaments and spinal muscles widens our conceptions on their structure and dynamics. In the muscles are isolated "sarcomeres" and fascicles whose angular orientation regulates their power. The tensegrity model helps in understanding the musculoskeletal system. It is necessary to emphasize the originality of the chapter on aponeuroses and fascia so little studied in classical works. The chapter on the vertebral canal makes it possible, in other interests, to discover the descriptions of the "lateral recess" and the "transverse canal." The spinal cord is the subject of an exhaustive review of our current knowledge. The spinal nerves and meninges happily complete this spinal anatomy!

It is obvious that this book deserves to be recommended to all those who are interested in the spine, including physiotherapists, rehabilitators, rheumatologists, and spinal surgeons. Congratulations to all the authors who participated in its realization!

Marseille, France René Louis

Preface

It is interesting to know that this book *Anatomy of the Spine: New Concepts* was born naturally, following our long experience concerning spinal surgical pathologies shared with Jacques Sénégas, founder of the school of spine surgery in Bordeaux, and to the interest we have in the anatomy of the vertebral column that we have long taught to medical students.

Thanks to this double cap, anatomist and surgeon of the spine, we have been able to develop an anatomy applied to physiology, degeneration, and surgical pathology.

We also collaborated with our friends in Montpellier, François Bonnel, who opened his collection of images of the School of Anatomy, and Alain Dimeglio, with his expertise on spinal growth.

All articles are from French anatomists and clinicians. These clinicians are spinal surgeons (orthopedic surgeons (pediatricians or adult surgeons) or neurosurgeons), rehabilitation specialists, physiotherapists, and biomechanists.

These French authors have all been able to develop rather original concepts concerning the growth of the vertebral column and its aging and functioning.

We thank them very much for their active participation.

All this has led to a book that we hope will allow readers to progress in terms of diagnostic and therapeutic knowledge of the spine.

Bordeaux, France

Jean Marc Vital
Derek Thomas Cawley

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Part I

Phylogenesis and Ontogenesis

Comparative Anatomy of the Axial Skeleton of Vertebrates

J. Sénégas

Introduction

Vertebrates (e.g. fish, amphibians, reptiles, birds and mammals, including primates) form a branch of the phylum chordata. They are distinguished from other animals by the existence of a bone or cartilaginous endoskeleton comprising two basic structures: the skull (hence the name Craniata) and the vertebral column which protect the central nervous system (encephalon and spinal cord). The oldest vertebrate fossils to date—*Mylokumingia fengjiaoa* and *Haikouichthys ercianunensis*—were discovered in China in 2003 in the Maotianshan Shales and date back to the early Cambrian period (535 million years ago).

It was above all, the physical constraints linked to the aquatic or terrestrial way of life that led to the selection of specific morphofunctional adaptations in these animals. They relate more specifically to the modes of respiration, locomotion, management of water loss and reproduction, and also behavioural constraints of survival (attack/defence, mating).

The Organization Plan for the Vertebrates

All vertebrates, without exception, present a bilateral symmetry which determines three axes of polarity (Fig. 1):

1. The anteroposterior axis (or craniocaudal axis) corresponds to the sequence: (1) of the head/neck complex which carries the sensory organs, the brain and the mouth; (2) the trunk complex that carries the appendicular system and (3) the tail.

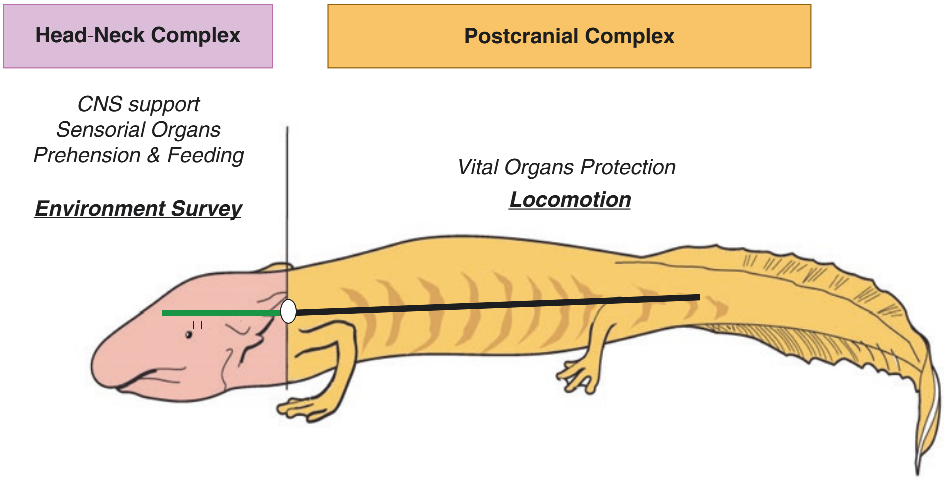

Fig. 1 The body of the vertebrates is characterized by the existence of an anteroposterior corporeal axis and a cephalocaudal bipolarization. Head and neck complex—support of the CNS and sensory organs for the analysis of environment and nutrition. Postcranial complex—protection of vital organs and locomotion

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J. Sénégas (✉)
Spinal Unit, University Hospital, Bordeaux, France

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The craniocaudal axis changes orientation during the transition from quadruped to biped with multiple angular variations between the horizontal and the vertical.

2. The dorsoventral axis with the vertebral column in dorsal position, the thorax and the abdomen in ventral position.
3. The left–right axis of symmetry in the coronal plane.

Adaptive Constraints of the Living Environment

Constraints of the Aquatic Environment

It is thought that the aquatic environment is the original environment. Oxygen is relatively rare (7.2 ml/l vs 209.5 ml/l in air) and diffuses more slowly. Oxygen is extracted by gills, extensions of the splanchnocranium. In the branchial system of fish, the partial pressure difference of oxygen between water and blood remains constant.

In the aquatic environment, postures and displacements constantly depend on Archimedes principles—the ratio of gravity/hydrostatic thrust which defines buoyancy. The force exerted on the water which determines the magnitude of the acceleration during the propulsion is a function of the displacement velocity and the viscosity of the liquid. In water, it is the axial structure (vertebral column periaxial musculature) that is the motor of locomotion, the fins (pterygium limbs) having in most fish only a directional or stabilizing role. The body, without a neck, moves as one, on itself around the three Cartesian axes, and advances in water by translation along the same axes. In attack/defence behaviours, the cephalic end of the fish is projected forward by the rest of the body [6]. Unlike amphibians, fish do not project the tongue to capture their prey, but some fish do so by suction such as anglerfish, heralding the behaviour of amphibians (sit and wait predators) (Fig. 2).

Constraints of the Terrestrial Air Environment

The terrestrialisation of tetrapods involves the extraction of oxygen from the air using lungs developed from the digestive tract. This active extraction requires the individualisation of a specific respiratory musculature whose action is reinforced by that of the appendicular musculature when the consumption of oxygen increases, especially in rapid displacements.

For the support of the body and terrestrial locomotion, the primordial adaptive stress is gravity (9.81 m/s^{-2}). It must be balanced by the resistance of the locomotor apparatus to ensure body retention. On land, it is the limbs which take on most propulsion forces. The axial system loses its flexibility, especially in large mammals, but it nevertheless contributes significantly to rapid propulsion through deformations in the sagittal plane which modify the orientation of the pelvis and thus the axis of thrust of the limbs. This intervention of the axial skeleton is essential in fast paces. The vertebral column also plays a pivotal role in postural flexibility through rotation.

Finally, to survive, an animal must be able to attack and defend itself. For this purpose, the axial skeleton of the tetrapod allows the rapid projection and retraction of the mouth, armed with teeth, towards the prey or the aggressor.

Fish

(Approximately 25,000 Species)

The axial skeleton of primitive fish such as cyclostomes (e.g. lamprey) is a flexible rod, the notochord which is formed of vacuolated chondrocytes, surrounded by a fibrous sheath. The stiffness of this hydrostatic skeleton depends on the osmotic pressure of the colloid in the vacuoles of the chondrocytes. Its mechanical properties can be compared to those of an elastic rod combining longitudinal compressive stiffness and lateral flexibility. With this configuration, the pro-

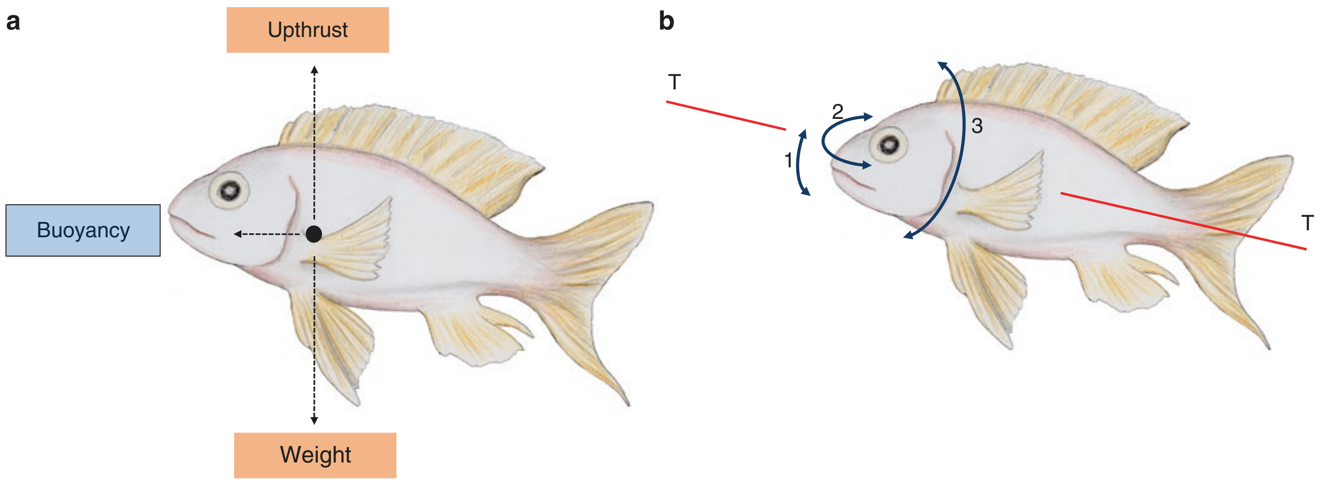

Fig. 2 (**a**) In the aquatic environment, the buoyancy depends on the hydrostatic weight/pressure ratio (Archimedes' thrust). (**b**) In fish the body uses six degrees of freedom. The linear displacements are carried out by axial translation. Buoyancy—Hydrostatic thrust—Gravity

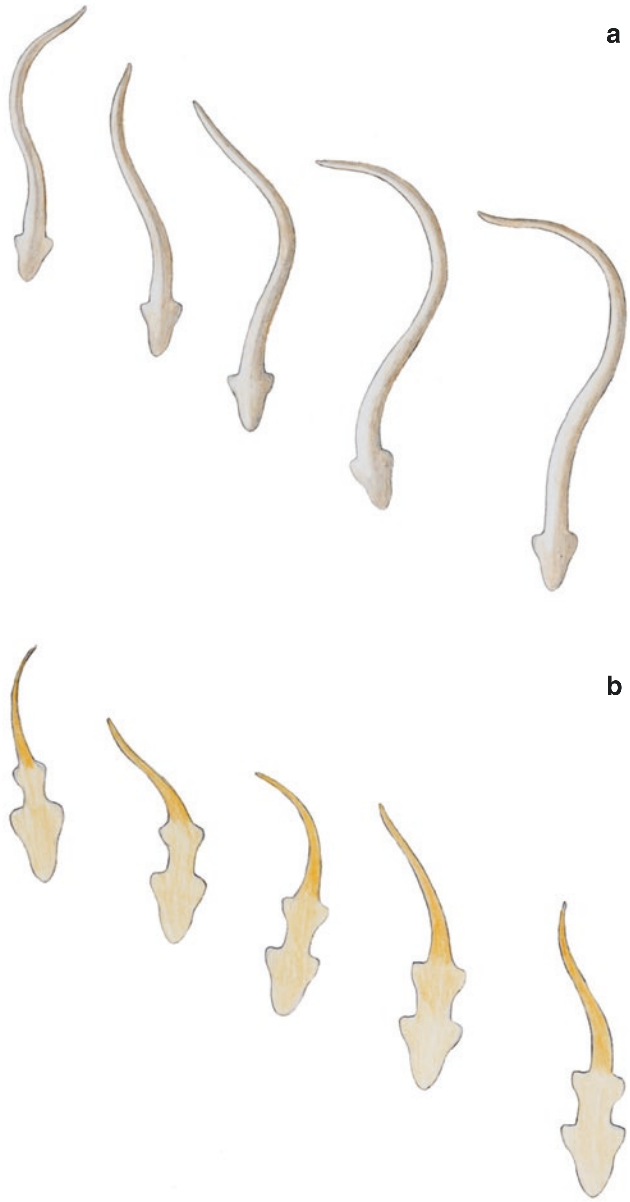

Fig. 3 The displacements of anguilliform fish (**a**) occur in an axial wave mode (the whole body is flexible and undulating). Most pelagic fish (**b**) move in an axial oscillatory mode (the propelling force originates mainly from the caudal fin). Certain fish with rigid bodies (e.g. balistidae, mormyridae and electric fish) move in a caudal oscillatory mode (the tail alone allows the propulsion)

pulsion of these species is the axial wave mode contraction of muscles composed of periaxial myotomes in sequence which generate a succession of undulating waves propagating from the head to the tail, while the animal moves forward [10].

Teleostean fish have a skeleton formed of identical cartilaginous or bony vertebrae, without zygapophyses. Although fish have no neck, there is a beginning of vertebral regionalisation, which distinguishes between a trunk segment and a more flexible caudal segment (Fig. 3).

In fish, the perivertebral musculature is organized into two groups, the dorsal epiaxial and ventral hypoaxial, separated by a horizontal septum. The myofibrils do not, however, attach directly into the vertebral parts. For pelagic fish (living neither close to the shore nor to the bottom), many myomeres regroup as large longitudinal fibre endings that resemble the organization of long muscles of tetrapods [15]. Propulsion of these species then takes place in the axial oscillatory mode, the lateral deformation of the body intensifying towards the caudal segment carrying a rigid fin.

The feeding of the fish is done either by suction/aspiration or by predators, by rapid acceleration of the mouth towards the prey. This gesture of rapid protraction of the head by impulse of the body involves the whole axial skeleton. This “push-forward-with-the-head” ability is evident with all tetrapods.

Tetrapodomorphic fish (actinistians such as coelacanth and rhipidistians like lungfish) have fleshy fins that participate in locomotion. Their pectorals have well-defined bony pieces prefiguring the anterior well-defined chiridian limbs. Tetrapod fish are characterized by the appearance of a cervical vertebra at the craniovertebral junction and chiridian limbs with three distinctly individual segments: stylopod, zeugopod and autopod. Thus, contrary to popular belief, the chiridian limbs first appeared in aquatic and non-terrestrial organisms. This is the principle of exaptation. At this stage, the functional coupling of the vertebral column of the appendicular skeleton for open-air locomotion is already in place.

In summary, fish are characterized by:

- A flexible cartilaginous or bony axial skeleton without vertebral differentiation but with truncal and caudal regionalization
- The presence of an epiaxial and hypoaxial musculature
- Only a lateral (in a horizontal plane) deformation of the column that ensures all locomotion with attack/defence behaviours.

Terrestrial Vertebrates

During life in the open air, the weight of the body is no longer balanced by hydrostatic thrust. It is the appendicular skeleton which counteracts gravity for the maintenance of the body and its displacements.

There are two spatial reference systems of terrestrial vertebrates:

At a minimum, two coordinate reference frames are needed to account for both the position and movements of the body in the environment and changes in the position of skeletal segments and organs within the body itself (Figs. 4 and 5).

1. The external (exocentric) reference frame is fixed, locked on the gravitational vertical force from which the coordinates of the centre of mass of the animal are defined.

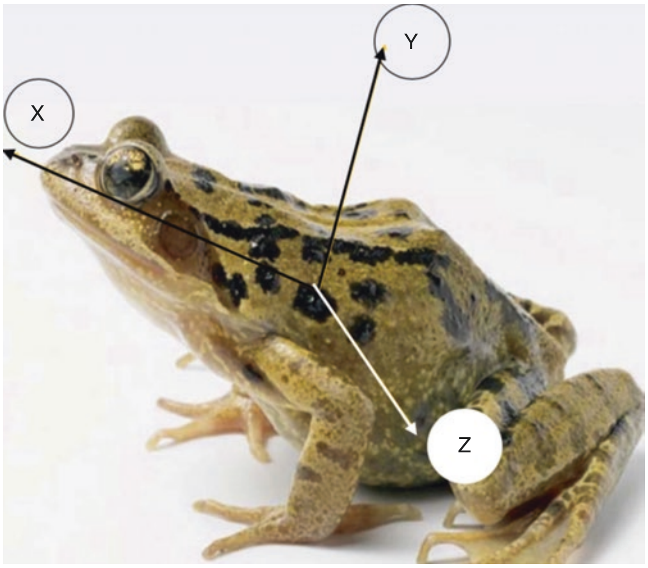

Fig. 4 Representation of the orthonormal reference formed by the three axes of polarity of the animal from the cephalocaudal axis of symmetry

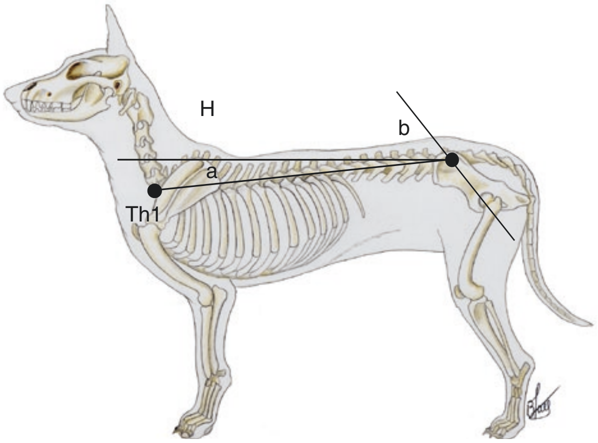

Fig. 5 In quadrupeds, the angular variations coupled between the thoracolumbar column and ilium can be measured by the spinopelvic angle. It is formed by the intersection of a line from T1 and the sacroiliac joint (the upper edge of the sacrum is very hard to visualize in animals) and the centre line between both the femoral heads (the bicoxo-femoral axis) and the sacroiliac joint. This is an adaptation of the spinopelvic angle described in humans

2. The general internal frame of reference (egocentric) corresponding to the three axes of polarity, which is an expression of the animal's body pattern (topological properties of the species).

To analyse the relative movements of the thoracolumbar spine and pelvic girdle, we propose to use the angle formed by the spinopelvic line from T1 to the centre of the sacroiliac joint (easier to locate in tetrapods than the sacral end plate), and the axis of the ilium represented by the line from the acetabulum to the same point of the sacroiliac joint.

The angle of incidence formed by the axis of the ilium and that of the sacrum is not a reliable topological data in animals because, contrary to popular belief, the sacroiliac joint is mobile, varying within and between individual cases. In man also this mobility can vary from one subject to another.

The external and internal reference systems coincide only under certain conditions (as in the strict vertical position in human bipedalism). In all other cases, data switching is required to change the repository. In animals, this switching is performed automatically by the central nervous system, which reconstructs a global pattern of data from the two references, so that the animal knows the position, speed and acceleration of the elements, its environment, its body and its own components.

Amphibians (About 7000 Species)

In amphibians, the final regionalization of the vertebral column is in place. Although reduced to a single vertebra, the cervical segment articulates with two trochoid surfaces homologous to the occiput. This is the individualized subcranial junction.

In anurans (frogs), the trunk segment is limited to 4–8 elongated vertebrae connected to the pelvis by a longitudinal urostyle. Frogs have no ribs. The truncocaudal junction is the most mobile of the column. At rest, the column is flexed at this joint, while it extends during jumping.

In the urodeles (salamanders), the elongated truncal segment comprises 12–63 vertebrae with ribs connected to the sternum.

In amphibians, the posterior vertebral arch is complemented by three types of apophyses: diaphysis (transverse), zygapophysis (articular) and neurapophysis (spinous). The first segment of the upper limb (stylopod) is horizontal, characteristic of the transverse chiridium (buttressed limbs). In amphibians, the scapular girdle is independent of the vertebral column while the pelvic girdle is secured to the sacrum through the transverse sacral processes. The ilium houses the proximal end of the femur. The pubic and ischial parts play the role of levers for the proximal muscles of posterior limbs. The axial skeleton of amphibians shows no curvature in the sagittal plane (the functional sagittal curvature of the anurans corresponds to the truncopelvic junction). The axis of the ilium is vertical (sacropelvic angle = 90°). The lumbosacral angle is approximately 0°.

On land, the anurans move by alternate advances of the limbs, but choose the jump for fast displacements in the open air. There is then a great mobility of the short thoracic column, around the lumbosacral junction. In the urodeles, walking is affected by lateral oscillations of the column, which causes an inverse rotation of the pelvis. The main role of the limbs is to lift the body off the ground, while deformation of

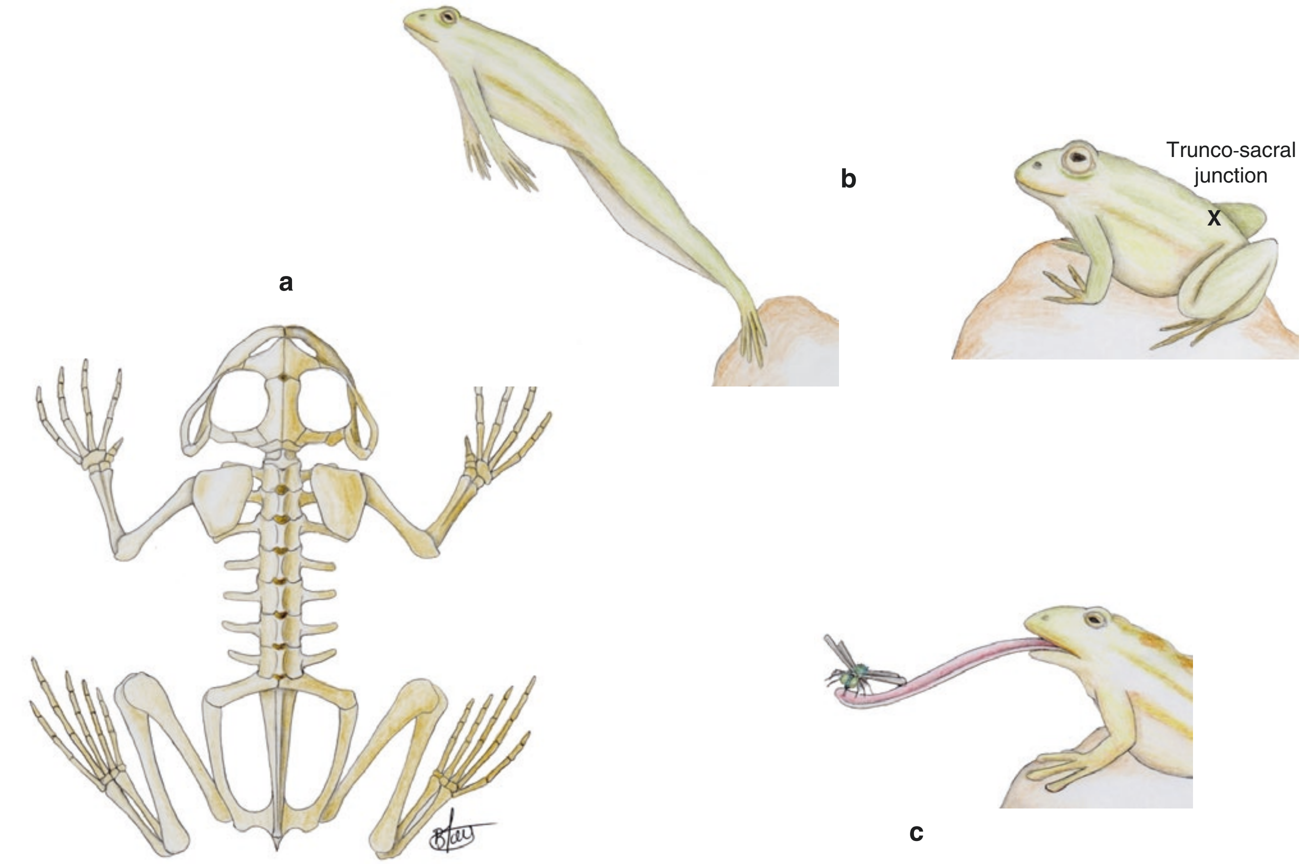

Fig. 6 (**a**) In Anurans (frogs) the craniovertebral junction is functional. The truncal segment is short and prolonged by the urostyle. (**b**) In the jump, the column is extended to the level of the truncosacral junction. (**c**) For amphibians and certain reptiles (geckos, iguanas, and chameleons), the projection of the tongue is more economical than that of the whole body for the capture of prey (sit-and-wait predators)

Fig. 7 Walking in Urodeles (salamanders) is done by side-to-side oscillations of the column causing an inverse rotation of the pelvis. The essential role of the limbs consists of lifting the body, while lateral deformations of the column pull the limbs forward

the vertebral column pulls the limbs forward. Different muscles ensure elevation and displacement [12] (Figs. 6 and 7).

The reduction of the cervical segment to a single vertebra does not make it possible to carry out a rapid protraction/retraction of the cephalic end of the animal for the capture of prey. The low mobility of the occipitocervical junction allows it only to bite and swallow. For reasons of saving energy that propulsion of the whole body would require, most of these species are "sit-and-wait predators" [6]. The solution of an extensible tongue projected rapidly and powerfully towards the prey was selected by evolution in many amphibians.

Respiration of amphibians is ensured by the contraction of the buccal floor, without any involvement of the appendicular musculature as seen in reptiles and mammals.

Reptiles (Approximately 8950 Species)

This class of terrestrial tetrapods remains heterogeneous and unclear in its definition. At the level of the axial skeleton, it is characterized by three major innovations:

1. a semi-independent craniocervical junction with significant mobility;
2. an epiaxial musculature differentiated into independent muscle groups;
3. and the strengthening of ties between the sacrum and the pelvis.

The Cervical Spine

The atlas articulates with a single occipital condyle. The testudines (turtles) have up to eight cervical vertebrae, the caudal aspect of which articulates with the first truncal vertebra which itself is fixed to the shell.

In reptiles, epiaxial cervical muscles become inserted on the occiput, differentiating into three groups (*vertebrocapitis superficialis* and *profundus*, and *intertransversalis capitis*). These extensor muscles of the craniocervical junction have an antigravity action which is essential for maintaining the head, which is sometimes very heavy (e.g. crocodiles).

The movements of protraction/retraction are particularly pronounced in turtles, whereas in crocodiles and most squamates (snakes), it is still the propulsion of the body that ensures the projection of the head forward. In geckos, iguanas and chameleons, the "sit-and-wait attitude" prevails, with the projection of the tongue towards the prey.

The thoracic column of the crocodiles comprises 10–11 vertebrae, 5 lumbar and 2 sacral, the transverse processes of which have a close connection with the ilium.

Like the cervical system, the muscular masses are segregated into organized bundles (*m. longissimus*, *m transverseo-spinalis* and *ilio costalis*), which generate the lateral movements of the column when they contract asymmetrically, but induce an extension of the column during a symmetrical contraction [15]. Crocodilian limbs have a first horizontal segment (buttressed limbs). It is the muscles of the pelvis that raise the body of the animal (sprawling posture).

The amplitude of mobility of the hip joint is low (less than 45°). The axis of the ilium is vertical, perpendicular to the vertebral axis at rest (pelvic version = 90°). The spinopelvic angle varies from 80 to 100° in crocodiles.

Slow locomotion in crocodiles is achieved by alternating oscillations of the column causing the front left leg and the rear right leg to move forward simultaneously with a caudal propulsion force. When the animal accelerates, as in catching prey, the entire column can participate in propelling the body forward. This new type of locomotion using a deformation of the column in the sagittal plane of flexion/extension induces backward (retroversion) and forward (anteversion) tilting of the pelvis leading to an increase in the amplitude of the stride, which increases the effect of the thrust of the posterior limbs. This new type of displacement is observed preferentially in young crocodilians, then disappears in adults as they become heavier [15] (Figs. 8 and 9).

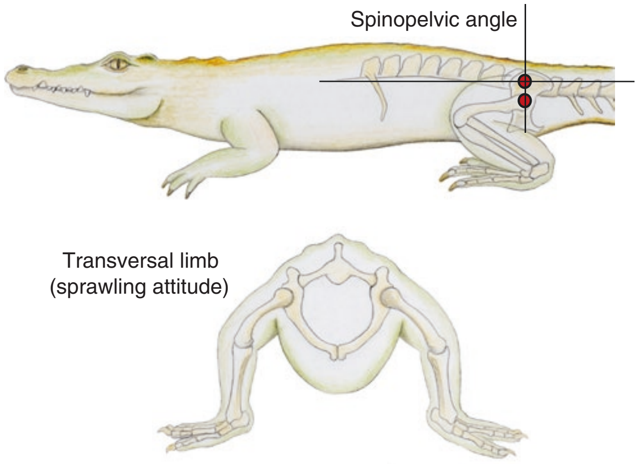

Fig. 8 In crocodiles, the axis of the ilium is perpendicular to the column. The posterior spinopelvic angle and the pelvic version approximate 90°

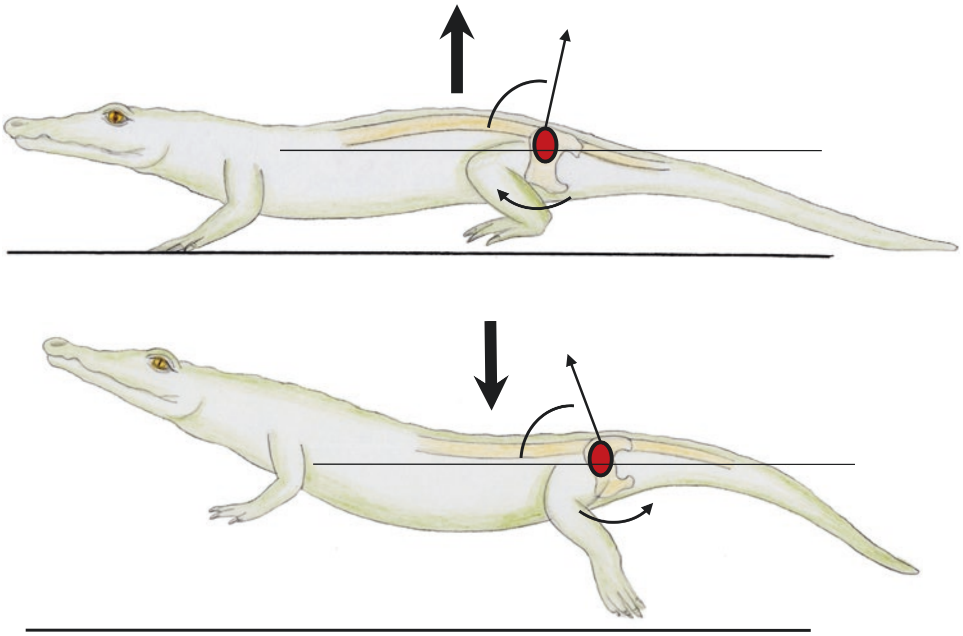

Fig. 9 Young crocodiles can mobilize their column in the sagittal plane which changes the orientation of the pelvis and thus improves the thrust of the posterior limbs. The weight of the adult makes this impossible

It is interesting to note that it is in reptiles that the coupling respiration/locomotion appears. However, the two functions cannot be carried out concomitantly. In locomotion, the appendicular musculature contracts asymmetrically, in the respiration symmetrically. This strict alternation is possible only because of the low energy expenditure of these ectothermal species.

In summary, amphibians and reptiles are characterized by:

- defining the final regionalization of the column, an SP angle varying from 80 to 120°
- locomotion by lateral oscillations or by sagittal deformation of the column for rapid displacements
- protraction/retraction of the isolated head or with the whole body creating the "push-forward-with-the-head" characteristic or the capture of prey by the tongue—"sit-and-wait predators".

Birds (Approximately 10,000 Species)

Birds have the most flexible neck of vertebrates with a rigid thorax to allow for flight. This is the most extreme example of the substitution of limbs for the axial skeleton for all movements. They are bipeds.

Birds emerge from the lineage of the middle Jurassic theropod dinosaurs that survived the Triassic-Cretaceous extinction, 65 million years ago. This line is characterized by a long moving neck that stabilizes the posture of the head during running and flight, and by its rapid projection (protraction/retraction) for the capture of prey (Fig. 10).

The vertebrae of the thoracic, lumbar and the sacral spine are fused to form the synsacrum. The truncated column only intervenes in flight and walking as a fulcrum of the muscles of the pelvis. In contrast, the S-shaped cervical segment includes many vertebrae (up to 25 in swans). The axis of the cervical spine is vertical, perpendicular to the trunk.

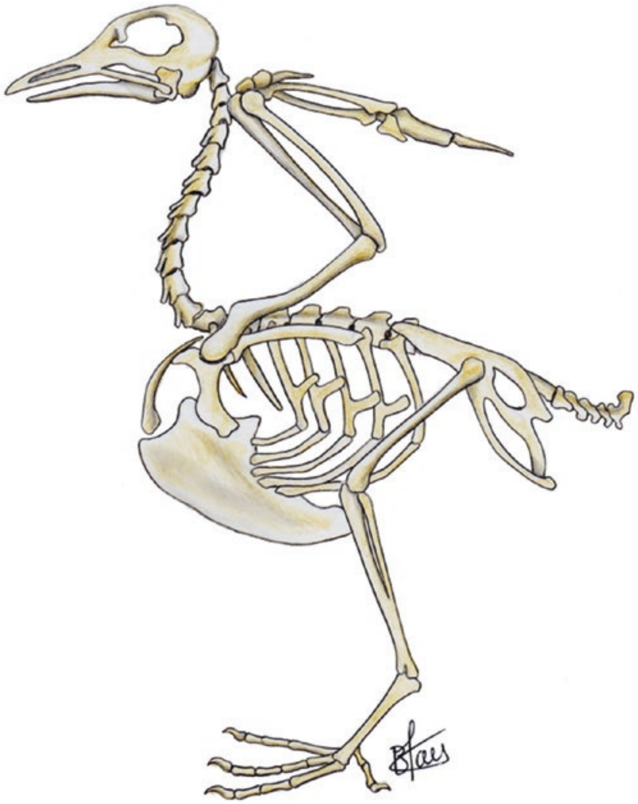

Fig. 10 In birds, the long and flexible neck allows it to project or retract the head quickly. The posterior vertebrae of the trunk are fused to form the synsacrum. The trunk is sufficiently rigid to allow flight

Mammals (About 5500 Species)

Adaptation to open-air lifestyles is fully expressed in mammals, the most widely spread and most morphologically diverse vertebrate group. This great ecological independence is the result of many evolutionary innovations [12]:

- Firstly, they benefit from permanent homeothermia from the embryonic stage (unlike birds).
- They also exhibit an exceptional neopallium development of the brain which allows them to perform complex behaviours "culminating in man, with language, conceptualization and symbolic thought" [12].
- Finally, their musculoskeletal system is optimized for an important metabolic energy conservation thanks to the nature and organization of the elastic connective structures of the musculature of the column and the limbs [9]; thus referred to as a spring mechanism. Indeed, the potential (slow-paced) and kinetic (fast-paced) energy released during stride is temporarily stored in the stretched muscles in the form of "elastic energy" which will be restored immediately to the same muscle group for the next phase of the locomotor cycle without metabolic cost. One of the most characteristic examples of this phenomenon is the high jump. Whatever the technique, the jumper starts by stretching the propulsion muscular chain by lowering its centre of gravity, which has the effect of passively storing

the elastic energy and thus considerably reinforcing the vertical thrust force.

At high speeds, some mammals, and man more than quadrupeds, can thus save more than half the metabolic energy that their movements would otherwise require without this mechanism.

The protein macromolecule, Titin, which is incorporated into the sarcomeres, plays a major role in this mechanism by giving its deformation to the frequency of the locomotive cycle, which reduces the dissipation of energy in the form of heat [13].

This phenomenon applies as much to the musculature of the limbs as to that of the spine. It is therefore preferable to compare the column with a bowstring or retaining bridge (by Arcy Thompson 1917).

The Cervical Spine

Functionally, the cervical column is coupled to the head and ensures its spatial orientation. The survival of terrestrial animals depends on information from one's external frame of reference. The information is captured by the visual, vestibular and somatosensory organs and then directed to the brain, whose interpretation of the data allows navigation through a complex environment without falling or failing. The vestibular system contributes to postural balance and locomotion by vestibulocollic reflexes and vestibuloocular reflexes. With the acquisition of bipedalism, the role of vision becomes predominant thanks to the high definition of macular perception and the acquisition of stereoscopic vision. This multisensory information supplies the middle and anterior brain as well as the hippocampus. The simultaneous cerebral integration of the data from the two repositories makes it possible to reconstitute and constantly update an internal map of the environment for navigation.

This central navigation function devolved mainly to the head/neck complex implies in sthenic tasks (exploration, alert, racing, combat) the possibility of horizontalizing the cephalic end which corresponds to the plane of terrestrial activity. This results in a de facto empowerment of the spatial frame of reference of the head relative to that of the rest of the body. Thus, irrespective of the inclination of the body or the type of locomotion, quadruped or biped, the plane of the base of the skull, parallel to the lateral (or horizontal) semicircular canals, presents only a slight angulation with respect to the skull [5, 8]. The neck is thus the instrument for adjusting the position of the head.

This neurological constraint is not without consequence in terms of energy. Indeed, the head/neck assembly presents itself as an inverted pendulum which poses problems of equilibrium, especially in quadrupeds. The weight of the head represents approximately 10% of body weight in large herbivores, 8% in humans and chimpanzees [16], and 6% in lemur prosimians [5]. This difference of 2–4% may seem small in absolute value, but becomes significant in relative value, given the total mass of large quadrupeds (about 500 kg for the horse). Proportionally, bending moments are 10–11 times greater than in humans and chimpanzees. Bipedalism also results in a considerable reduction in the bending moment of the head.

In aquatic mammals (whales, dolphins) secondarily adapted to life in water 50 million years ago, the cervical vertebrae became fused, with only a mobile cranial junction. Similarly, the fusion of the vertebrae of the lower cervical segment is observed in the armadillo and in some rodents such as the kangaroo rat and the jerboa, which has the effect of reducing the inertia of the weight of the head when jumping. The same applies to burrowing species such as the mole rat [11], where fusion of the vertebrae of the lower cervical spine increases its resistance to axial stresses (Fig. 11).

The centre of gravity of the head in quadrupeds is located very forward of the craniovertebral junction due to the development of the splanchnocranium, the horizontality of the base of the skull (platybasia) and the very posterior position of the occipital condyles, so that the occipitoatloid line is almost vertical. In primates and even more markedly in humans, basicranial flexion is observed in the sphenoid, with the clivus then forming an angle with the anterior part of the base of the skull. This process, probably related to the development of the cerebral hemispheres and the reduction of facial mass, coincides with the forward migration of the occipital condyles, which has the effect of considerably reducing the bending moment of the centre of mass of the head. In humans, the occipitoatloid articulation is horizontal and the head gravity line passes right in front of the dens (Fig. 12).

Structure

The cervical spine of terrestrial mammals has 7 vertebrae, except the Folivora (sloth) which has 6–9 and Sirenia (manatee) which has 6 [11].

The upper cervical spine consists of the atlas and axis; morphology varies little from one species to another, except the dens (C-shaped in herbivores and vertical in carnivores and primates). The length of the spinous processes and the width of the transverse processes are much more prominent in quadrupeds and large primates than humans. Similarly, the superior articular surfaces of the atlas corresponding to the

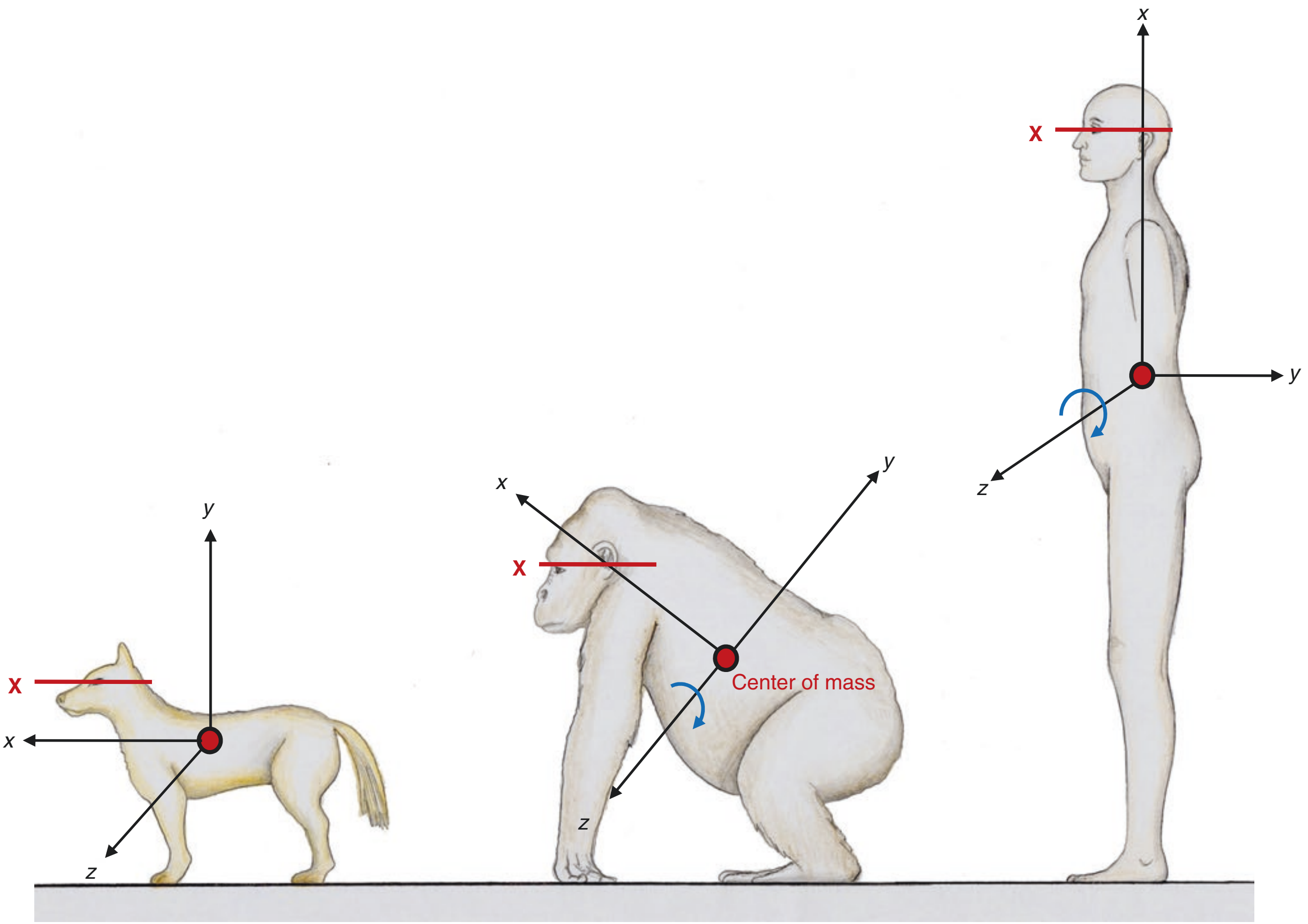

Fig. 11 In the internal frame of reference, the coordinate axes of the head are kept approximately fixed relative to the external reference frame by changes in the orientation of the cervical column, irrespective of the position of the trunk, horizontal (quadrupeds) or vertical (bipeds). This autonomy of the cephalic coordinates facilitates the switching of data between the two reference frames and allows the brain to permanently recreate a new global pattern of navigation

occipital condyles occupy in quadrupeds about 75% of the atlas ring but only 40% in humans [7].

The lower cervical spine includes the lower 5 cervical vertebrae whose configuration minimally varies. The total volume of the vertebral bodies is relatively greater among bipeds.

Movements

Mobility of the occipitocervical junction is important in the sagittal plane in quadrupeds (flexion/extension range of motion of 90–105°), whereas it is much lower in primates, including humans (13° in monkeys and 25° in man) [8]. Rotations take place in the atlantoaxial joint (Tables 1 and 2).

The mechanical coupling of both OC1 and C1C2 joints generate a toggle effect which allows more lateral tilting movements of the head (induced rotation).

It is worth noting that in quadrupeds, mobility between the vertebrae of the lower cervical spine is very small (unlike humans). It is also interesting to note that the cervicothoracic articulation encompasses more than the C7T1 anatomical junction. It encompasses C6 to T2 in small quadrupeds [8], and as far as T3 in humans. The range of motion of the cervicothoracic junction ranges from 6 to 80° in all mammals [8].

In the neck, as well as the very important intrinsic ligament mechanism, there is an extrinsic ligament (septum nuchae) specifically developed for large herbivores. This system plays a vital role in the passive stabilization of the craniocervical kinetic chain (which is not provided by the

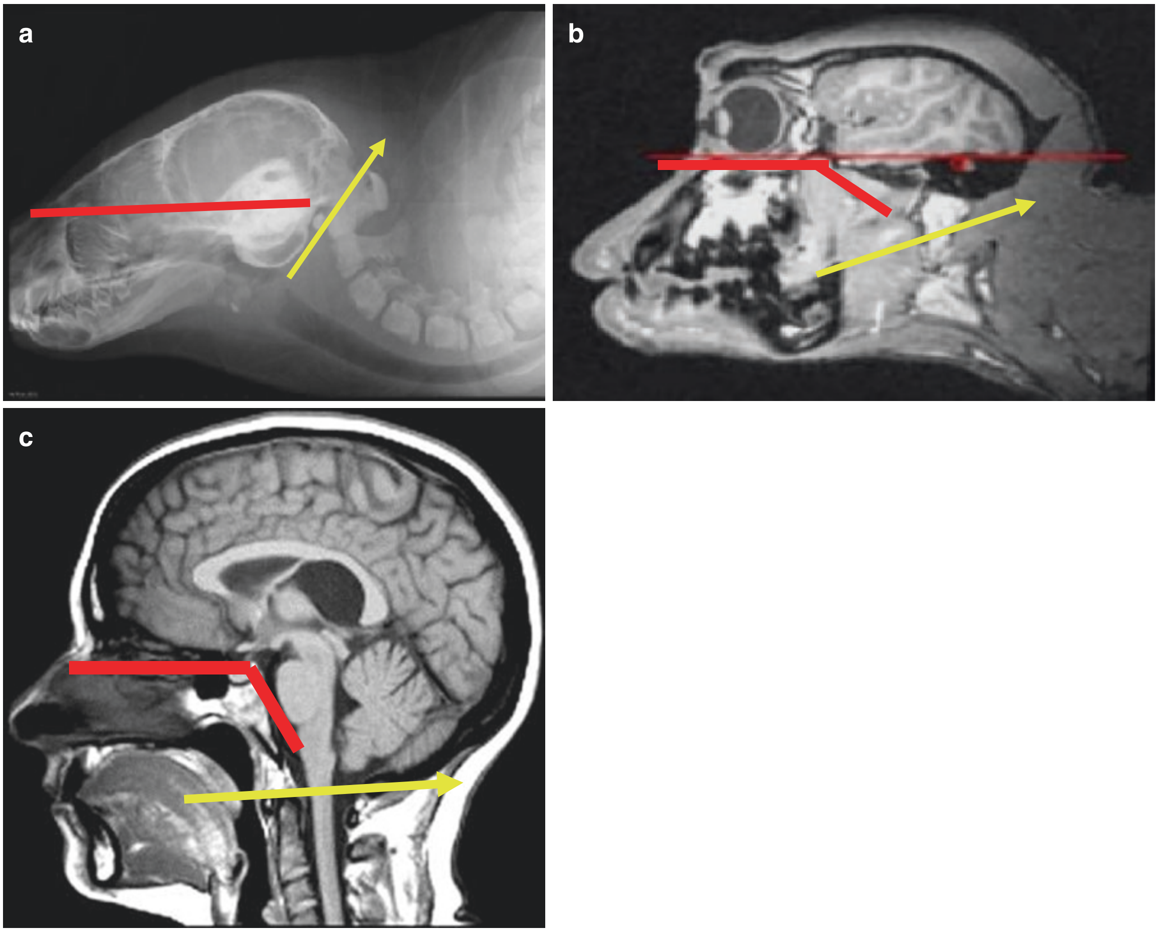

Fig. 12 In quadrupeds (**a**) the skull base is horizontal (platybasia), the occipital condyles are located at the back of the skull and the foramen magnum is tilted back and top. In monkeys (**b**) there is a basicranial bending at the sphenoid bone, the occipital condyles are located further forward. The foramen magnum tends to horizontalize. In humans (**c**) basicranial flexion is more important between the anterior floor of the skull base and clivus, the occipital condyles are almost under the skull and the foramen magnum is horizontal

Table 1 Amplitude of mobility in the sagittal plane of the atlantooccipital articulation (OC1) in various mammals [7]

Rabbit	104.6° (±15.7)
Guinea pig	106.6° (±5.9)
Cat	88.6° (±11.2)
Rhesus	13° (±14.8)
Man	25°

Table 2 Range of mobility in the sagittal plane at the cervicothoracic junction (C6T3) [8]

Rabbit	96°
Cat	82°
Rhesus	68°
Man	33°

bone passive locking cam effect, as applied to most musculoskeletal joints). This elastic passive locking allows optimum use of the inertia of the head and neck in running.

The Craniovertebral Musculature

There is a large musculature variation in mammals related to the complexity of stabilization and precise mobilization of head/neck system. One can distinguish schematically:

(1) the short muscles of the craniocervical junction (*m. recti* and *obliqui capitis anterior* and *posterior*)
(2) short intervertebral muscles, including intermetameric (*m. intertransversalis* and *m. interspinalis*) and long spinal muscles (*m. longus capitis* and *cervicis, m. longissimus and m. semispinalis*) which mainly act as stabilizers cervical flexible
(3) finally, cephalothoracoscapular muscles (*m. splenius capitis, m. levator scapulae, m. scalenius, m. trapezius* and *m. sternocleidomastoid*) that are specifically dedicated to the active mobilization of the neck and secondarily, respiration during effort. Cats have a muscle (*m.*

occipitoscapularis) that is absent in humans. The cervical muscle volume is comparatively much higher in quadrupeds than in primates, including humans.

Postures

At rest, the cervical spine of small mammals (rabbits, guinea pigs, cats) resembles an "S" shape whose average orientation is vertical. In this configuration, the craniocervical junction is maximally flexed and the cervicothoracic junction is stabilized at full extension [8]. This attitude, according to these authors, is totally passive, only assured by the tensioning of the pervertebral tissues (resting posture). In this position, the plane of the lateral semicircular canals is inclined to the horizontal at approximately 5–10° upwards. The same authors describe, next to the posture of rest, the alert or active posture, in which the head is raised by extending the occipito-cervical hinge. The cervicothoracic junction is then flexed in this posture and the plane of the lateral semicircular canals moves upward [8].

However, extending the generalization of this functional dichotomy to all terrestrial mammals of the complex head/neck seems too simplistic. It is enough to be persuaded to observe the diversity of the postures of the head and the neck of large ungulates (e.g. cattle, deer and sheep) (Fig. 13).

The mechanical model of the head/neck is that of an inverted pendulum whose rod represents the cervical spine and the sphere, the head. Schematically, the rod moves around the cervicothoracic joint, while the sphere is mobilizing around the occipitocervical junction. However, it is not exactly centred on the end of the cervical rod. In quadrupeds, it is forward due to the very posterior position of the occipital condyles, which induces a significant bending moment at 0C1. In primates and even humans, that moment is greatly reduced by adopting the biped posture.

In quadrupeds, verticalisation of the neck reduces the bending moment of the head. This attitude of retraction is analogous to the term used in humans. It involves an extension of the cervicothoracic junction. This posture cannot be completely passive, as in this position, the perivertebral tissues are not stretched sufficiently. Contraction is combined with two different positions of the head. When in this position the OC1 joint remains flexed, the posterior tendinoligamentous structures are likely to develop an effective passive muscle moment so that the energy cost is low (standing alert position). When the OC1 joint is actively maintained in extension, the tension moment of the passive structures decreases. The maintenance of this position necessitates contraction of the occipitocervicothoracic muscles as seen in trotting or parrying (sthenic retraction).

When the neck is flexed around the cervicothoracic joint, the bending moment increases horizontally and then decreases. This protraction movement stops when the elastic tension of ligament and muscle (whose deformation is non-linear) reaches the value required to cancel the bending moment of the head/neck. When the protraction is combined with a bending of the OC1 joint, posture is mainly passive, energy-saving (like grazing, watering or extreme tiredness states). By contrast, when protraction is combined with an active extension of the OC1 and/or a straightening of the neck above the horizontal, it is then a sthenic posture (as in the gallop). This position optimizes the moment of inertia of the head and neck in fast running (Fig. 14).

We find these same two basic stereotypes (retraction-protraction) in primates including humans. Protraction corresponds to a passive rest position when the OC1 joint is flexed (as in reading or sleeping in a sitting position), or to an active position when the OC1C2 joint is extended under the effect of the posterior musculature. This is in fact a "push-forward-with-the-head" attitude which one observes in particular through efforts of pushing (as in the collision sports). According to Ordway et al. [14], it is in this posture that the

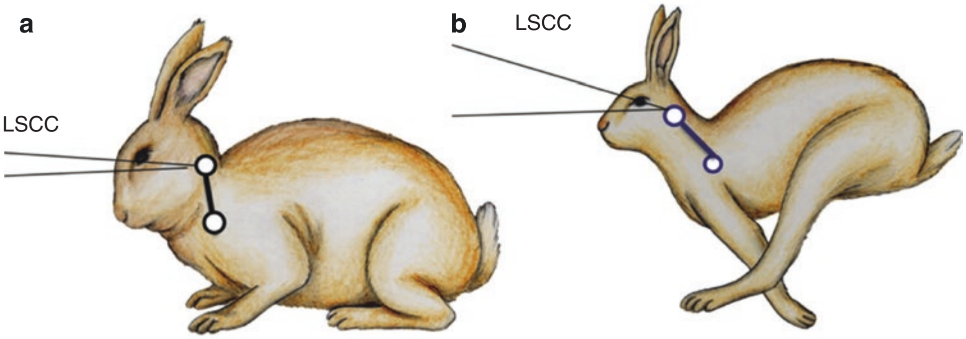

Fig. 13 In small mammals: In the rest position (**a**) the cervical spine is vertical, the craniovertebral junction is maintained in full flexion and the cervicothoracic junction in extension [4]. The plan of the lateral semicircular canals (LSCC) is slightly inclined to the horizontal (5–10°). In the alert position (**b**) the positions of the two joints are reversed. The plan of the lateral semicircular canals is shifted upwards

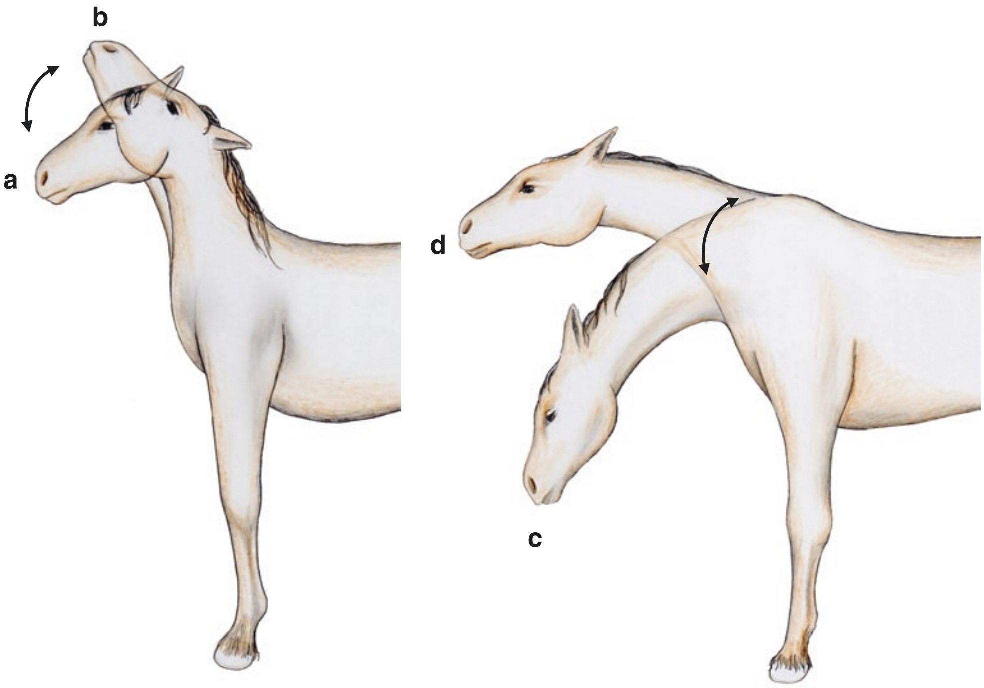

Fig. 14 Reverse coupling of the craniovertebral and cervicothoracic joints: (**a**) when the craniovertebral junction is flexed (static posture without large energy expenditure), the other (**b**) is extended (sthenic posture). Displacements at the craniovertebral junction, flexion (**c**) or extension (**d**)

craniocervical junction reaches its maximum amplitude in extension.

Retraction behaves in the same way through flexion of the OC1 joint (OC1 position where it reaches its maximum amplitude in flexion) and active extension (e.g. to charge with the head or to wear a headlight). Each of these attitudes implies a new choice of orientation of the field of view depending on the position of the eyes of the animal, the side of the head in quadrupeds and front of the head in humans and primates [5] (Fig. 15).

In running, the cervical spine plays, in quadrupeds, a significant role in breathing (respiratory locomotion coupling). Inspiration occurs when the neck is in ventral flexion, expiration when dorsi-flexing.

Thoracic Spine and Lumbosacral

The trunk of quadrupeds is almost horizontal and approximately cylindrical shaped. Its centre of mass is positioned approximately centrally. Its forward displacement, as in ungulates, promotes running, whereas the most posterior position is observed in small mammals [2].

Limbs articulate with the trunk by the shoulder and pelvic girdles. The shoulder girdle is independent of the axial skeleton and maintains a single connection to the trunk through the clavicle (collarbone). The upper limbs are involved in locomotion more as carriers and for steering than that as propellants. In many small mammals, the upper limbs acquire the faculties of grasping and manipulating objects within the field of view, which will become their primary role in bipeds. One notes by contrast, at the pelvis, increased strengthening ties between the ilium and sacrum without the loss of sacroiliac joints whose mobility in locomotion persists in many animals and also in man. In humans, it is 3–17° in adults, and up to 30° in gymnasts. In certain athletes one can even observe an opposite displacement of each iliac bone in the sagittal plane.

The proximal segments of the limbs are, in mammals, situated in a parasagittal plane, which has the effect of symmetrically supporting the body and raising the centre of gravity. This configuration reduces ground frictional force, improves manoeuvrability and allows the use of the elastic potential energy (spring effect). At the point of rapid reaction, manoeuvrability and acceleration capabilities outweigh stability however, especially in humans.

Structures

The mammalian thoracic region comprises 12–15 vertebrae. The thoracic vertebrae of large herbivores have very long spinous processes. At the transition between the thoracic and lumbar vertebrae is at the anticlinal vertebra (diaphragmatic vertebra, to which all other vertebrae are inclined) where the spinous process is short. On both sides, chest spinous processes are inclined caudally, the lumbar cephalad.

There are usually from four to seven lumbar vertebrae (the latter figure is typical of the cat and rabbit). The body of

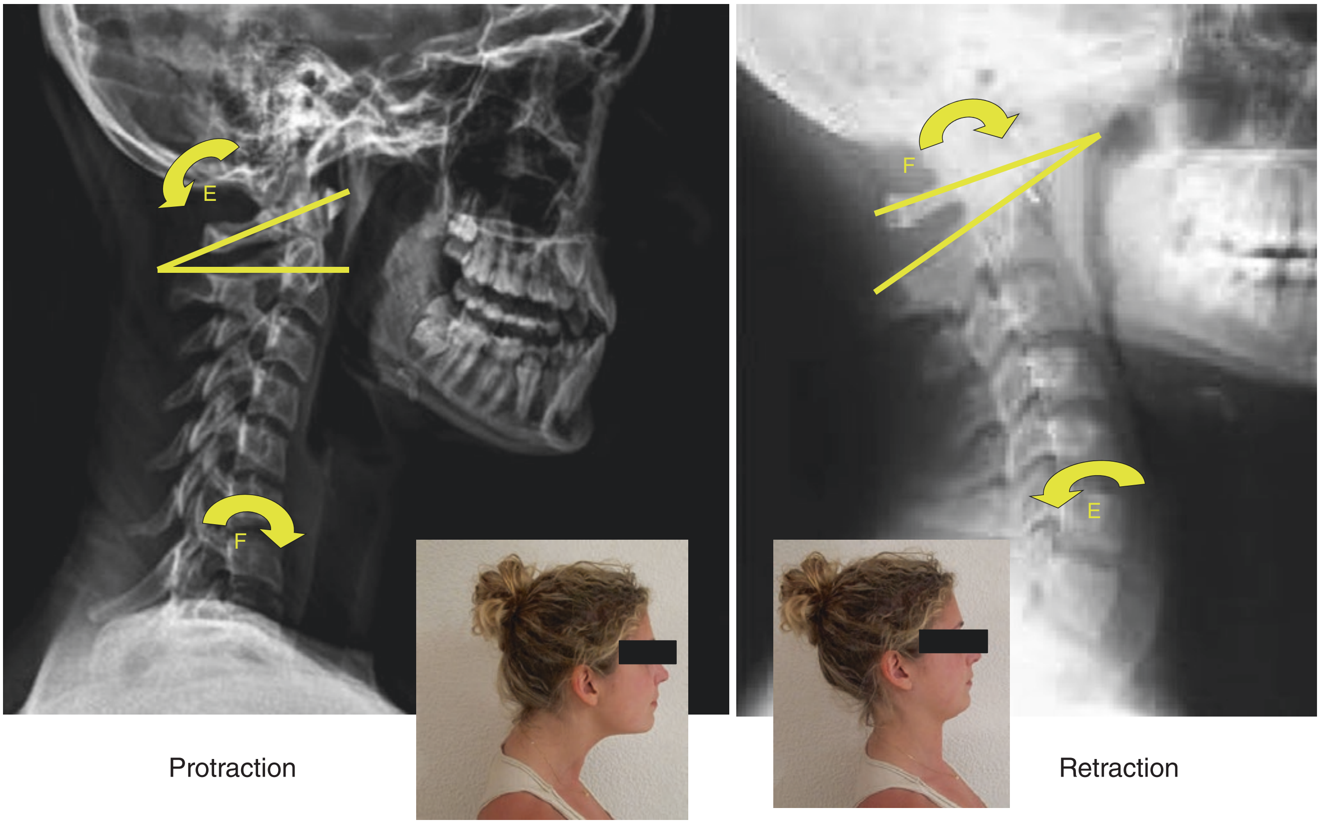

Fig. 15 Primates, including humans, use like quadrupeds, the reverse coupling of the two extreme neck positions for protraction and retraction of the neck and head

the lumbar vertebrae is proportionally larger in men and increases down to L5.

The sacrum is composed of a varying number of fused vertebrae (three in cats, four in rabbits and usually five in humans). This number can reach six to eight in perissodactyla (odd-toed ungulates—e.g. horse, zebra and rhino) and up to thirteen in edentulous (e.g. anteater and sloth). The first sacral vertebrae articulates with the ilium through its transverse processes.

The coccygeal vertebrae also vary in number, depending on the tail length (up to fifty, but usually three to five); Merged, they form the coccyx in humans [11].

Musculature

Both the body of quadrupeds and that of the bipeds present a “bowstring construction” represented by tight dorsal musculature bow and the chord of the ventral muscles, especially the *recti*. As in the neck, in terrestrial mammals there is a regression of epiaxial muscles concomitant with the trans-girdle musculature (*mm. trapezius, rhomboid, latissimus dorsi* and *glutei*) [12]. The local system of intervertebral short muscles (*m. interspinalis, m. intertranversalis*) is distinguished from a global system (*m. erector spinae*, *m. quadratus lumborum* and *m. rectus* and *obliqui abdominalis* and *m. psoas)* [3].

Postures

The quadruped truncal column is generally horizontal or kyphotic. The diaphragmatic vertebrae represents in quadrupeds, the flexion/extension hinge of the trunk.

- In all quadrupeds the lumbosacral angle (LSA) is minimal while it becomes important especially in primates and hominids. Abitbol [1] has in particular studied variations of this angle: in dogs, it varies from 4 to 14° (average 9.3°); rhesus monkeys, 20 to 35° (mean 26.7°); chimpanzee 22 to 44° (average 32°) and in humans 71 to 83° (average 77°). This angle is related to the acquisition of erect posture and the ontogeny of biped locomotion.
- The pelvic tilt that expresses the orientation of the ilium relative to the horizontal for quadrupeds and to the vertical for bipeds varies in quadrupeds from 30 to 60°. In chimpanzees, which are alternately quadru-

ped and biped, it varies from 25 to 60° (average 42°). In humans, the angle of pelvic tilt varies from 7 to 25°.

- The spinopelvic angle (SP) (Fig. 5) varies from 60 to 75° in quadrupeds, from 30 to 60° in chimpanzees and from 15 to 45° in humans.

The thoracolumbar spine helps to maintain posture and locomotion in quadrupeds as well as bipeds. In extension there is a relative shortening of the column that has the effect of pulling the sacroiliac junction forward in quadrupeds and upward among bipeds.

Contrary to what one might think, it is not the posterior limbs that guide the pelvis, but the vertebral column. This rocker promotes forward momentum when pushing off from the rear. Conversely, the bending of the thoracolumbar spine causes the pelvis to retrovert, increasing the amplitude of pushing off from the front (Fig. 16).

Primates generally move in quadrupedalism, especially in fast running, but adopt bipedal posture in either static or in slow movements or jumps (lemurs).

The physical problem of verticalisation of the body is that of balance on a considerably reduced support surface, in addition to maintenance of balance through effective musculature. In primates, the centre of mass is located at the base of the thorax which is relatively high compared to the hips. Moreover, the absence of lordosis does not allow easy adjustment of the line of gravity on the support polygon if the femurs are not bent over the pelvis. This posture is difficult to maintain in large part because of weak *glutei maximi* muscles in these animals, and instead use the *g. medius* and *g. minimus* for hip extension.

It is likely that bipedalism evolved as an adaptive process in the three-dimensional arboreal environment (Rose 1991; Preuschoft 1991). In this situation, the body weight is often supported only by the posterior limbs so that the anterior limbs are liberated for their gripping function (Fig. 17).

In humans, during walking and running, the deformation of the lumbar spine allows pelvic tilt. Pelvic retroversion increases hip flexion amplitude and extends the stride. Anteversion favours the rear step thrust by increasing the extension of the hip beyond the vertical (Fig. 18).

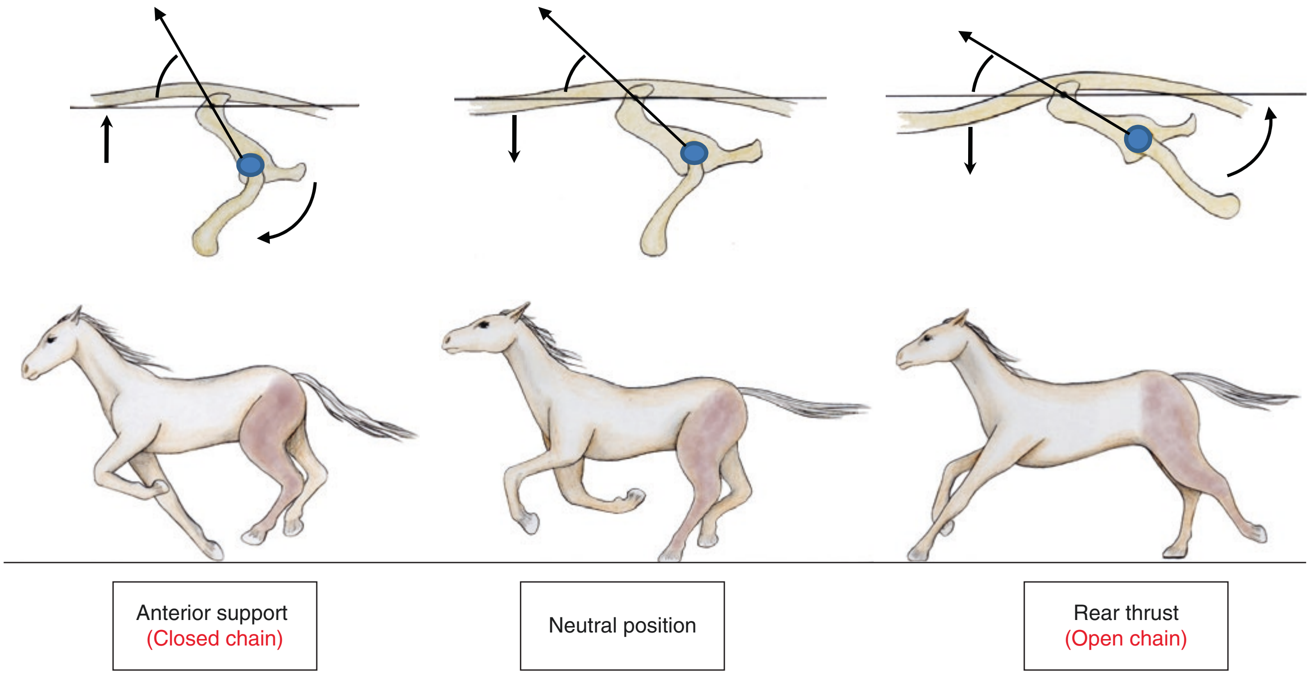

Fig. 16 In mammalian runners, the bending of the thoracolumbar spine induces pelvic retroversion which increases the amplitude of the previous step. The extension brings the pelvis in anteversion which has the effect of increasing the extension of the femur and the thrust of the posterior pitch

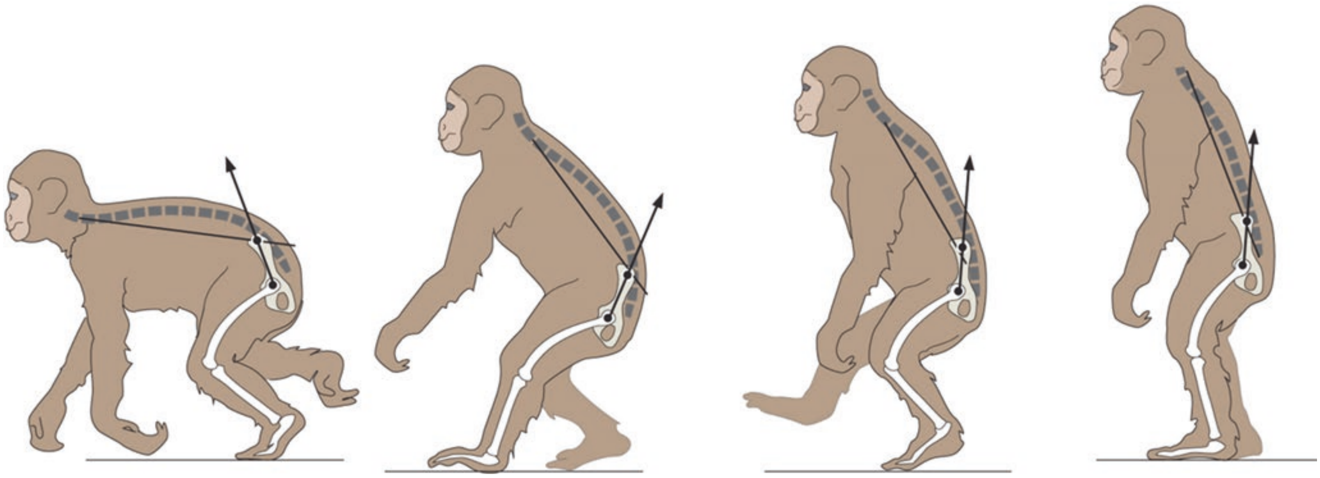

Fig. 17 Chimpanzees adopt quadrupedalism for quick trips (semibrachiateurs). They can maintain a stable bipedal posture but the lack of lumbar lordosis forces flexion of the femur on the pelvis to bring the projection of the centre of mass into the area of elevation. This position requires a significant effort from the glutei muscles

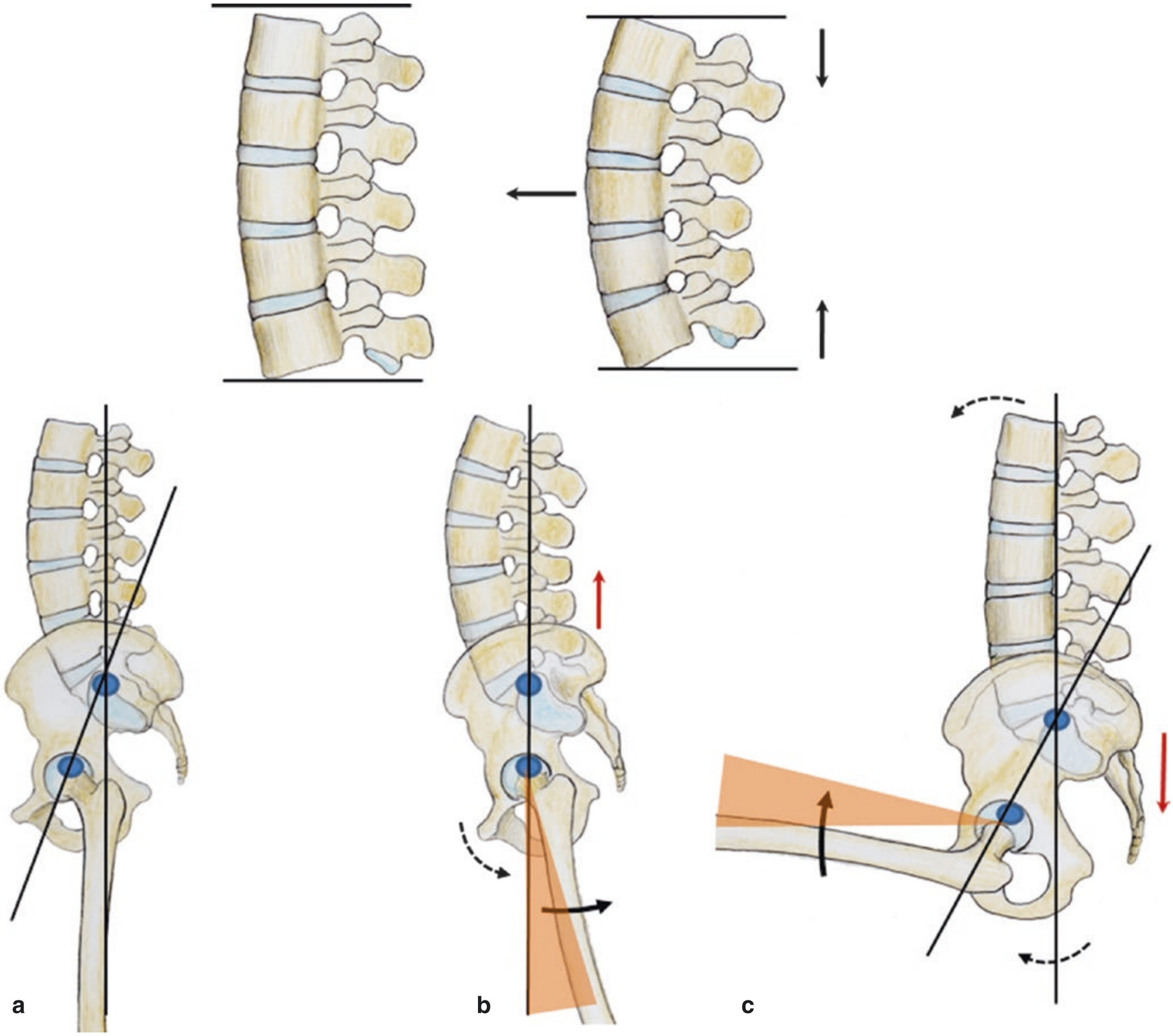

Fig. 18 The extension of the lumbar spine (**a**) pulls the pelvis in anteversion, which has the effect of granting a supplementary extension to the femur relative to the vertical (**b**) (without gain in amplitude of the hip joint). Conversely, lumbar flexion (**c**) causes pelvic retroversion and, consequently, an equivalent gain in femur flexion

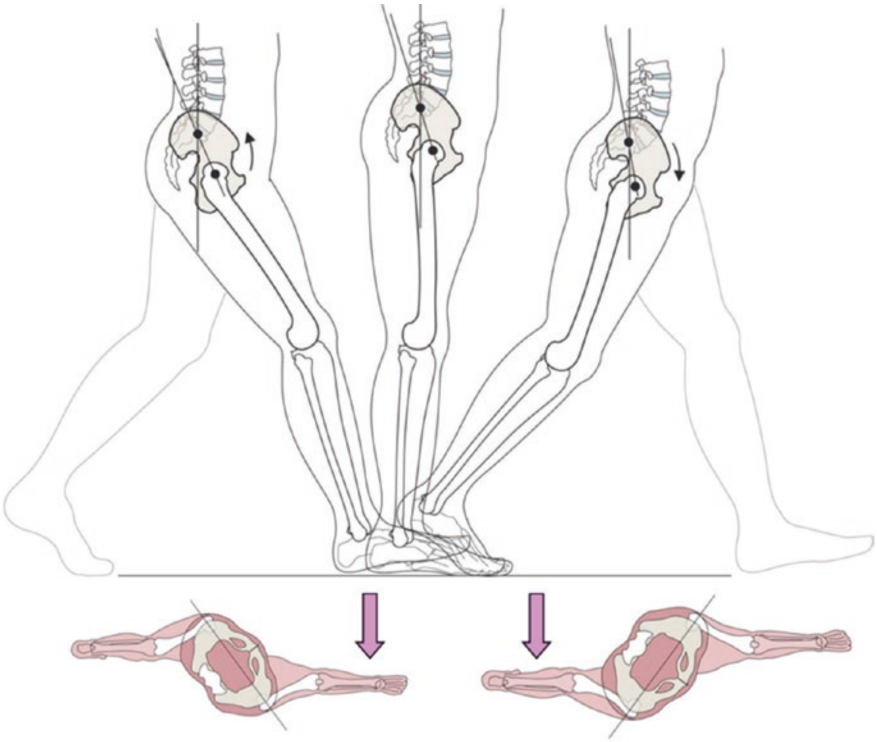

Fig. 19 In humans when walking and running, the shoulders and pelvis rotate in opposite direction with a tipping point approximately at the thoracolumbar junction

In mammals, the vertebral column plays an essential role both in posture and in movement by the axial rotational movements which are usually coupled to displacements in the coronal and sagittal planes. When walking and running the shoulders and pelvis move in opposite directions. The thoracolumbar spine is thus "twisted" from either side of the thoracolumbar junction. Rotations are expressed as the background kinematics of the spinal kinematics. This contributes to a better understanding of their role in the genesis of spinal degenerative process (Fig. 19).

In summary, the mammals are characterized by:

- A very mobile cervical spine capable of powerful and rapid protraction and retraction movements
- A thoracolumbar spine that permits the awareness and stability of postures. It is also involved in locomotion by a "spring effect" in flexion/extension which changes the orientation of the pelvis
- In bipeds exclusively, the lumbar column intervenes in locomotion. Moreover, it plays an essential role in the axial rotation of the body.

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