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From sprawling to parasagittal locomotion in Therapsida: A preliminary study of historically collected museum specimens

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Abstract

Therapsids covered the entire spectrum of terrestrial locomotion from sprawling to parasagittal. Switching between sprawling and more erect locomotion may have been possible in earlier taxa. First, the axial skeleton shows little regionalization and allows lateral undulation, evolving then increasingly towards regionalization enabling dorsoventral swinging. During terrestrial locomotion, every step invokes a ground reaction force and functional loadings which the musculoskeletal system needs to accomodate. First insights into the functional loading regime of the fore- and hindlimb skeleton and the body stem of therapsids presented herein are based on the assessment and preliminary measurements of the historical collection of therapsids exhibited in the Paleontological Collection of Eberhard Karls Universität Tübingen, Germany. The specimens included are the archosaur *Hyperodapedon sanjuanensis*, the early synapsid *Dimetrodon limbatus* for comparison, and the therapsids *Keratocephalus moloch*, *Sauroctonus parringtoni*, *Tetragonias njalilus*, and *Belesodon magnificus*. The vertebral columns and ribs of the mounts were carefully assessed for original fossil material and, when preserved, ribs, sacral, and anterior caudal vertebrae were measured. The body of a tetrapod is exposed to forces as well as bending and torsional moments. To resist these functional stresses, certain musculoskeletal specializations evolved. These include: 1) compression resistant plate-like pectoral and pelvic girdle bones, 2) a vertebral column combined with tendinous and muscular structures to withstand compressive and tensile forces and moments, and 3) ribs and intercostal muscles to resist the transverse forces and torsional moments. The legs are compressive stress-resistant, carry the body weight, and support the body against gravity. Tail reduction leads to restructuring of the musculoskeletal system of the pelvic girdle.

Keywords

Bending, compressive stress, functional loading, ribs, synapsids, tensile stress, transverse forces, vertebrae

Introduction

Remarks on the chosen methodological framework

Therapsid locomotion and its evolution has been subject of various studies (e.g., Kemp 1978; King 1985; Walter 1986; Ray 2006 Kemp 1980 Ray 2006; see summary in Fröbisch 2006). Those studies often focussed on very specific taxa (e.g., Fröbisch 2006) or rather on isolated parts of the body, e.g., the vertebral column (Jones et al. 2021) or the hindlimbs (Fröbisch 2006). Very general re-occurring patterns of biomechanical adaptations found across Tetrapoda are rarely regarded.

We intend to establish a first overview on certain morphological and myological patterns of the body stem across Tetrapoda. The functional loading regimes of these locomotory systems will be discussed with the intent to improve our understanding of the sprawling to parasagittal locomotion in Tetrapoda in general and Therapsida in particular. Our approach is not a phylogenetic one because we first tried to establish a basic biomechanical understanding of certain locomotory systems. Nevertheless, in the future, studies on how these, often convergent, biomechanical patterns evolved in specific tetrapod and therapsid lineages will require a strict evolutionary framework to evaluate shifts in locomotory styles and posture in detail for specific taxa.

Evolutionary overview on quadrupedal locomotion

Fish

In contrast to terrestrial vertebrates (Fig. 1), the dominating external force acting on the external surface of an aquatic animal (Fig. 2A, B) is the water resistance. Fish fins, especially the fluke, act against the water resistance, and transmit the evoked force onto the body. If the paired pectoral fins are attached at the midline of the body (e.g., as in a tuna), they inhibit rolling along the longitudinal body axis (Fig. 2A, B) (Norman and Frazer 1963). Sarcopterygians have usually lobe-fins with smaller surface areas when compared to the ray-fins of ray-finned fish. Instead, lobe-finned fish have longer peduncles and, therefore, higher peripheral speeds, so that they can create the same water-resistance as the ray-finned fish. The attachment of the pectoral fins ventral to the body-midline (Fig. 2C, D) leads to rolling about the longitudinal axis, which must be counteracted by the dorsal fin, for example. However, the attachment of the pectoral fins ventral to the body midline is of advantage for lifting the body off the ground. If the anterior part of the body is lifted up by the pectoral fins, a transmission of forces near the belly is more effective than one closer to the body midline (Fig. 2C, D). This can be observed in ray-finned teleosts like mud-skippers. The pectoral fins of lobe-finned fish are divided into three segments which evolved into the

stylo-, zeugo-, and autopodium of Tetrapoda (Romer and Frick 1966).

Terrestrial Tetrapoda in general

Terrestrial tetrapods (Fig. 1) are continuously exposed to gravity, which acts primarily on those parts of the body with the largest mass, namely the body stem (from human anatomy, meaning the head, neck, trunk, and the tail, without the limbs). Gravity times mass results in a force, which is directed towards the ground, which means that the body weight has to be carried by the limbs (Fig. 2E–H). At the distal limb segments (hands and feet), ground resistance results in the ground reaction force directed away from the ground opposing the body weight. In order to sustain the body against gravity, tetrapods evolved various musculoskeletal structures to effectively transmit forces between ground and animal (Romer and Frick 1966). As tetrapod trace fossils show, toes can be pointing laterally, medially, or foreward. The zeugopodia do not need to be oriented vertically in an erect posture, but any deviation towards a more horizontal position and a more sprawling posture requires muscle activity of the elbow and knee joint flexors. This results in a force component in medial direction of the ground reaction force, which reduces the moments acting at the joints. An increase of muscle mass of the upper arm or thigh is limited, because the muscle belly diameters cannot exceed the length of the muscle bellies (Christian and Garland 1996). An abducted position of the upper arm and upper leg (Fig. 2E, F) leads to considerable torsional moments of the trunk and requires widely spread oblique muscles covering the rib cage to counter them. The elbows point slightly backwards and the knees forward (Fig. 2F). According to Preuschoft (2022), the forelimbs exert a braking, the hindlimbs show a re-accelerating function in each limb cycle, and the moderate backward and forward swinging of the knee and elbow joint reduces the moments in these joints (Loitsch 1991; Witte et al. 1991; Witte 1996). The glenoid and acetabulum are positioned ventral to the body midline. This way, the body can be lifted higher off the ground by muscle activity than if the glenoid or acetabulum were placed closer to the body midline (Fig. 2G, H).

Recent reptiles and salamanders keep their upper arms and thighs held laterally in an approximately horizontal position (=abducted or sprawling) (Fig. 2I) (e.g., Ashley-Ross 1995; Jenkins and Goslow 1983; Reilly and Elias 1998; Reilly and Delancy 1997). This sprawling posture of the limbs is generally considered to be the phylogenetically oldest, and indeed it can be derived convincingly from the limb position used in the earliest land-living animals. Lever arms of upright directed ground reaction force follow the cosine of the angle between the horizontal plane and the limb segment under consideration. Therefore, the maximum length of the lever arm equals the length of the respective limb segment. Because the angle of the knee or elbow in a sprawling extremity does not deviate much from 90° (Fig. 2E, F, I, L), and the ground reaction force acts at the distal end of the zeugopodium, the lever arms of the functional loads
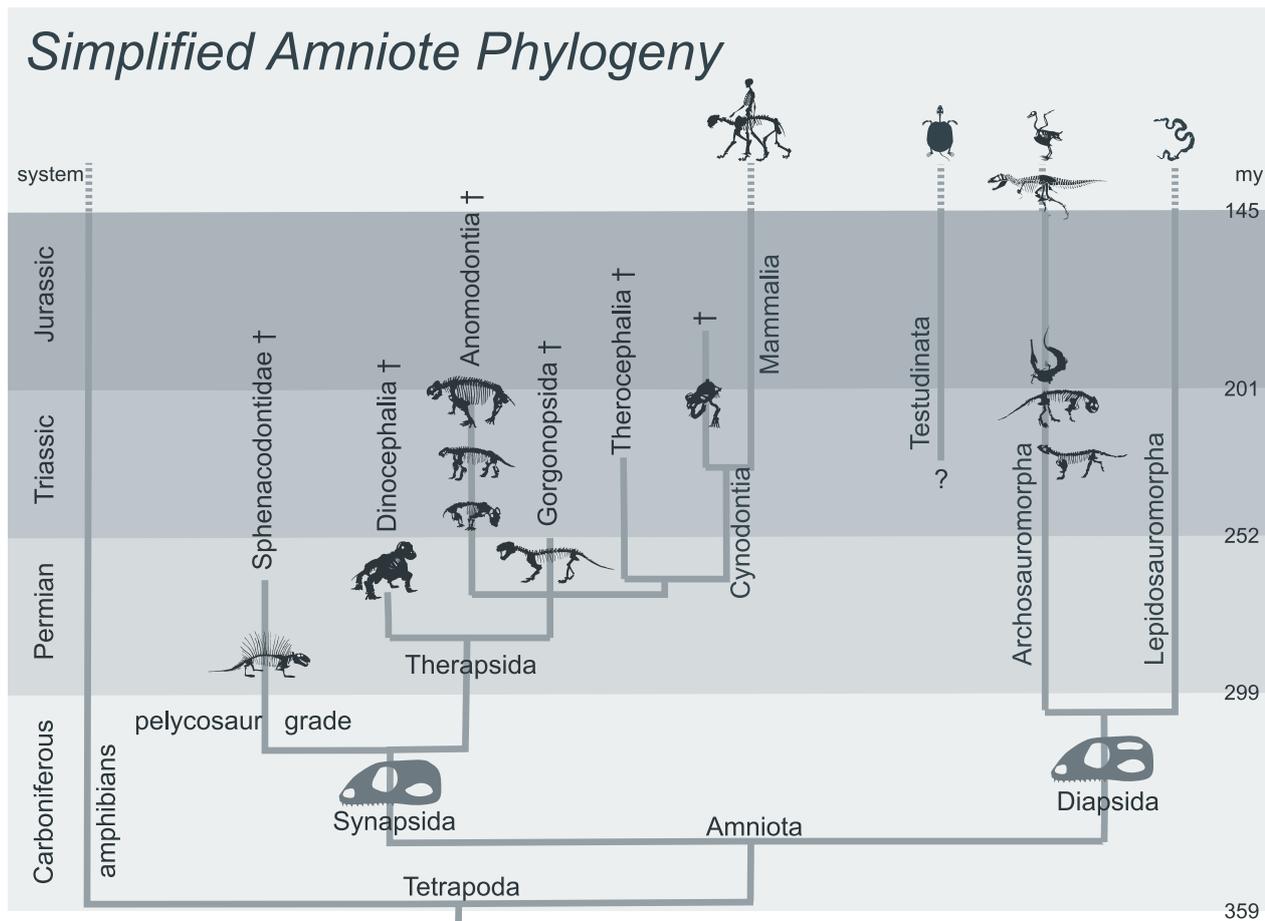
Simplified Amniote Phylogeny

Figure 1. Phylogenetic overview. Diapsida, represented by the archosaur *Hyperodapedon sanjuanensis* in our study, are the sister-group to Synapsida. Synapsids include the pelycosaur-grade *Dimetrodon limbatus* and Therapsida. From Therapsida, the dinocephalian *Keratocephalus moloch*, the anomodonts *Stahleckeria potens* and *Tetragonias njalilus*, the gorgonopsian *Sauroctonus parringtoni*, and the cynodont *Belesodon magnificus* were included in this study.

acting on the upper arm and thigh are as long as the stylopodium. It follows that high moments occur constantly in the joints that are the closest to the body. These moments are countered, irrespective of whether the tetrapod is walking or standing, by muscle activity.

In each stance phase of a lepidosaur or crocodilian (Fig. 2L, E–F), the horizontal position of the stylopodia and the approximately vertical position of the zeugopodia require that the trunk bends around the foot placed on the ground to avoid falling, because the center of mass is shifting. This lateral undulation of the body (Fig. 2L) is called a standing wave (Reilly and Delancey 1997; Reilly and Elias 1998). The lateral bending of the body is accompanied by laterally directed components of the ground reaction force with 17.7 % of the impulse created by the vertical component (Christian 1995; Fig. 2L, M, O). If the limbs are moving parasagittally, the laterally directed component of the ground reaction force becomes significantly smaller than those in reptiles (Fig. 2O) and may become zero.

Mammalia

The scapular blade of mammals swings (Jenkins 1974) and has therefore been functionally transformed into an additional limb segment (Fig. 2H; Schmidt 2001; Schmidt et al. 2002; Fischer and Lilje 2011). This results in a limb attachment to the body above the body midline (Fig. 2H). Yet, we would like to add that in kinematic studies, mostly in recent years of non-mammalian taxa, have shown that pectoral and even pelvic girdle movement is more common in Tetrapoda as have been acknowledged so far (Walker 1971; English 1977; Baier and Gatesy 2013; Mayerl et al. 2016; Schmidt et al. 2016). So far, this indicates that pectoral and pelvic swinging or oscillations during locomotion have been understudied in reptiles and inspire refinements of our understanding of tetrapod locomotion in general. The proximal point of rotation of the mammalian scapula is close to the vertebral border of the scapula. The musculature that is required for balancing the shoulder and the hip joint is integrated into the body contour (e.g., Nickel et al. 1968).

Larger qadrupedal mammals walk on adducted extremities and their limbs are moved in a parasagittal plane (Fig. 2G, H, N) (e.g., Bakker 1971). Limb segment length can be increased and therefore stride length can be increased as well. The metapodials have been elongated and, consequently, forearm and lower leg lengths are increased. The elbow points backward and the knee forward (Fig. 2P–Q). During the stance phase, the limbs of a large mammal function like an inverse pendulum:
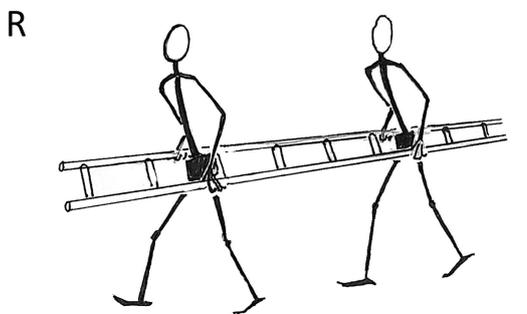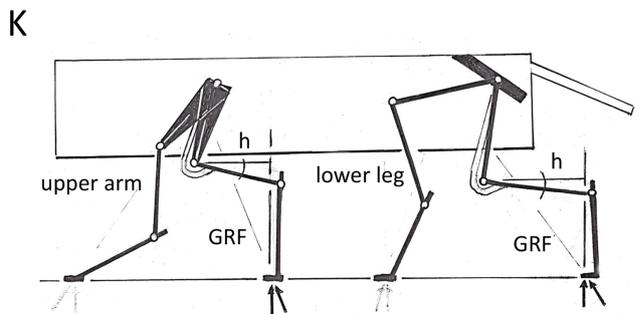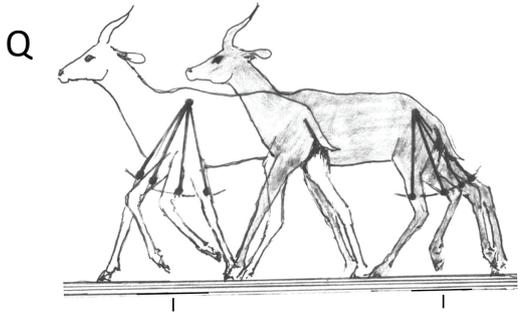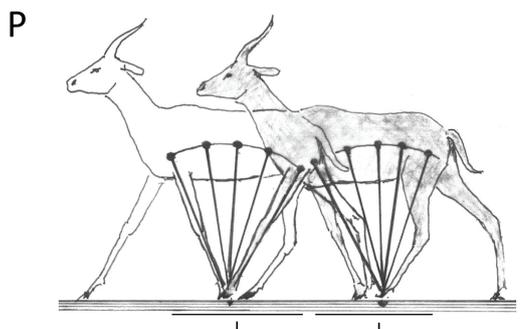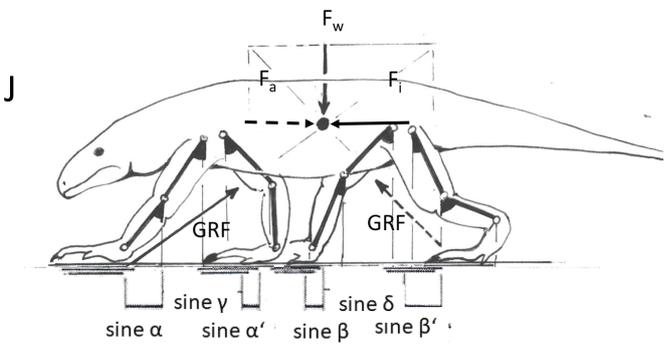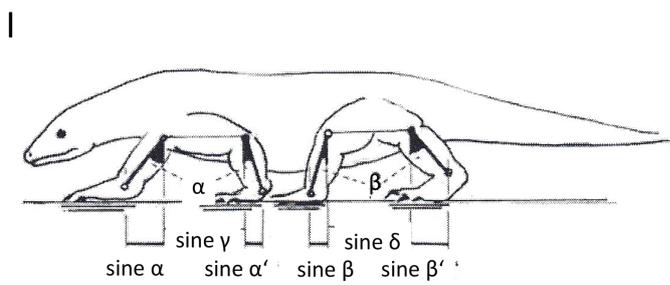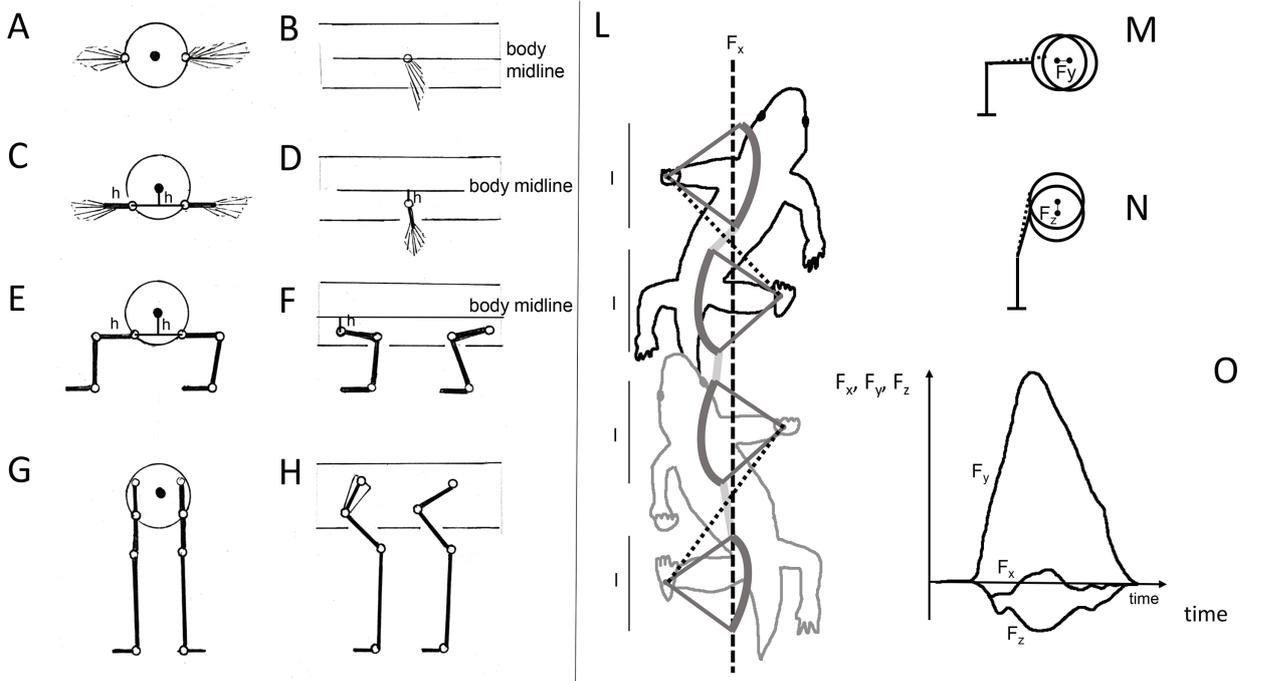
Parts of the body mass are lifted up on a circular pathway around the joint closest to the ground (lifted onto a higher level of potential energy) and then down again. The gain of kinetic energy compensates the internal friction within the system. During the swing phase, the limbs behave like suspended pendula. The length of the pendulum cord is the distance between the pivot and the limb's centre of mass. The time needed for swinging the limb forward determines the limb cycle frequency. By flexing the elbow/knee and carpal/tarsal joints, the length of the pendulum
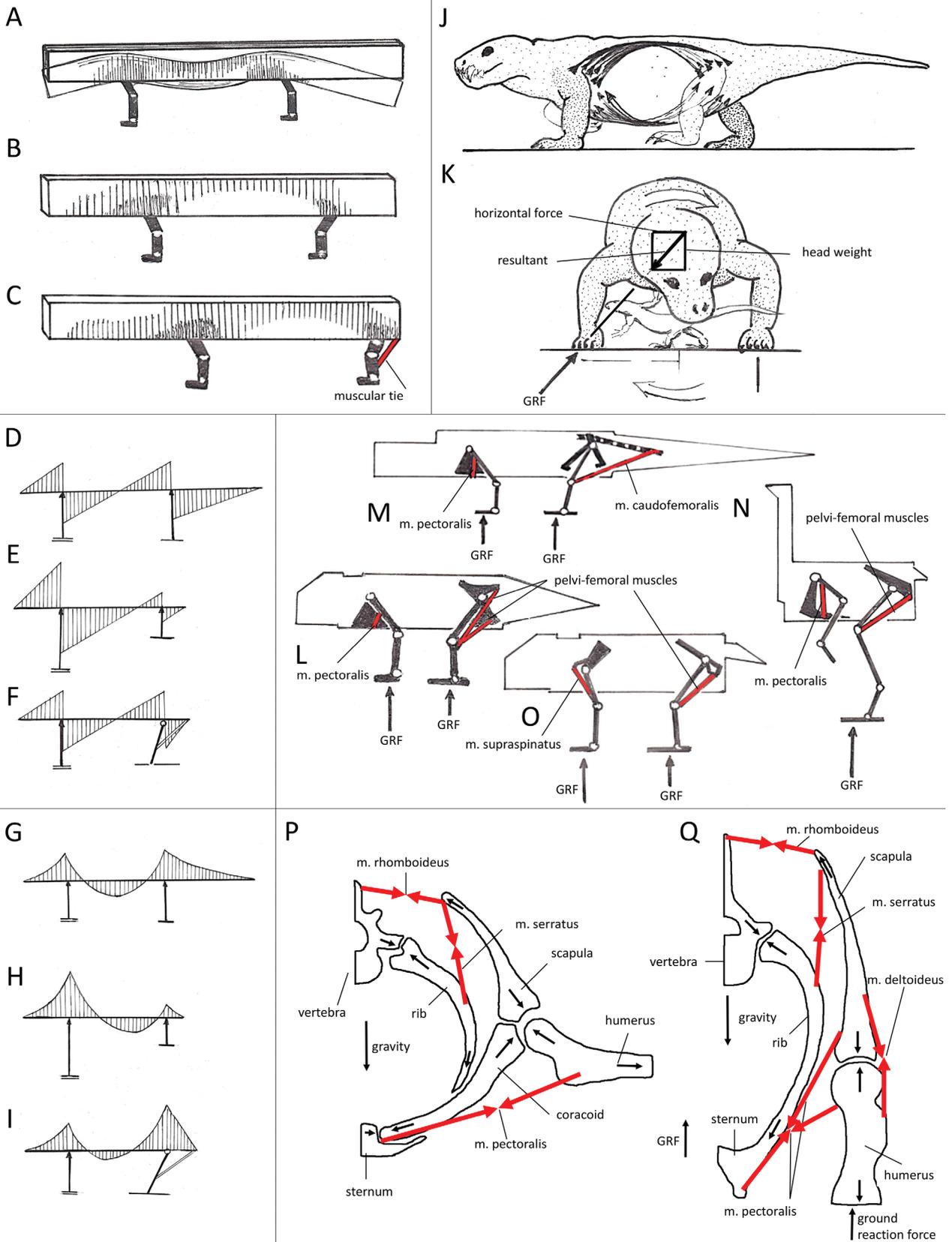
Figure 2. A–H Sprawling and parasagittal position of limbs. On the left side: anterior view; on the right side: lateral view. **A, B** Ray-fins, attached to the middle of the body have no lever arm in relation to the body midline and therefore generate no moment. **C, D** Lobe-fins attached to the ventral half of the body. Note the lever arm h multiplied with the force exerted by the lobe-fin, it leads to the moment h*F which rotates the animal about its long body axis. **E, F** For terrestrial sprawling locomotion, two additional joints (elbow/knee, wrist/ankle) are advantageous. If the shoulder and pelvic joints are near the ventral margin of the trunk, the latter is lifted higher off the ground than if the joints were more dorsally. The autopodia can be directed medially (as in frog-like anurans) or laterally (as often in crocodiles and lizards). The elbows are directed posteriorly and the knee anteriorly. For both, the lever arms (h) of the ground reaction forces are relatively long. This leads to great torques about the proximal joints, which must be counterbalanced by contractions of the m. pectoralis in the fore- and the m. caudofemoralis in the hindlimb (Gatesy, 1999). **G, H** In parasagittal digitigrade limbs two further additional limb segments have been added by a mobile scapula and elongated metacarpals and -tarsals. On the right side, the limb segments are above each other, so that no or only small moments occur in anterior view. On the left side, a common position is illustrated: a joint in the middle of the freely moving limb is approaching the midline, like in the famous valgus-position of the human knee, and the typical, though less observed carpal joints of cattle, other bovids, cervids. In the hindlimb, the hock joints are in many forms approached, while the fetlocks are directed laterally. In side view (**H**), the upper arm as well as the lower leg pass in each step from vertical (lever arm being zero) to horizontal (lever arm reaching cosine of joint angle, that is the length of the segment. Note in **E, F** the centre of mass is above the supporting limbs, while in **G, H** it is at the level and between the scapulae/iliac blades. **I, J** As long as segment lengths and angles between segments are not changed, stride length does not change with either a sprawling or parasagittal posture of the limbs, and the joint moments are not bigger in sprawling limbs. sin α, excursion angle of the forelimb; sin β, excursion angle of the hindlimb; sin γ, excursion angle of the forelimb; sin δ, excursion angle of the hindlimb. Progress made is proportional to the sine of the angles. **I** The excursion range of the fore and hindlimb depend on rotation of the humerus and femur. **J** Flexion and extension of elbow and knee joint permit greater excursion angles. F_a, inertial force against being accelerated; F_i, inertial force against being retarded/braking; F_w, weight force. **K** In many small mammals, the upper arms and lower legs are nearly held vertically during early phases of the limb cycle, while during later phases they are swung into a nearly horizontal position (Witte et al. 1999). The lever arms (h) of the vertical ground reaction forces (GRFs) are parallel to the horizontal and their length follows the cosine of the angle between the horizontal and the upper arm/leg or the lower arm/leg. The phases in which the lever arms have their shortest or greatest lengths, and in which the moments are the smallest and biggest are shown. These moments are opposed by muscle activity. **L–O** Wave-like trunk movements. **L** An early tetrapod seen from dorsally while walking. The stylopodia are swung laterally and forward during sprawling locomotion. During the stance phase, the stylopodia compel the trunk to give way laterally and the body moves approximately in a standing wave. l, length of the stance phase. **M** The schematic cross section at the level of the shoulder and hip joint show the lateral displacement of the trunk. **N** Extension of the limb joints lift the body up and down again in a wave-like curve because parasagittal locomotion can be described by inverse pendulum mechanics (Preuschoft 2022). **O** GRFs acting on a lizard foot. F_x, horizontal in the direction of walking; F_y, vertical; F_z, horizontal in transverse direction (changed and redrawn after Christian, 1995). **P, Q** Cursorial mammals exemplified by a medium-sized antelope. l, length of the stance phase. **P** Fore limb (left, white) and hindlimb (right, grey) in stance phase. The lower end of the inverted pendulum is the joint closest to the ground, the upper end is the hip joint, or the pivot about which the scapula rotates. **Q** A fore- (left, white) and a hindlimb (right, grey) in the swing phase. Pendulum length is defined by the distance between pivot and the respective leg's centre of mass. **R** Two people carrying a ladder. If both establish a firm, not mobile connection between their pelves and a ladder rung, they have to have an equal stride length and step frequency, i.e., walk in lock-step, to avoid disturbing each other. A free choice of stride length is only possible, if one of the two people loosens the connection between pelvis and rung. The plane in which the mass is moved forward is not essential, but the distance covered in the direction of locomotion.

cord can be modulated (Fig. 2P, Q). Extended joints make the limb pendulum long and increase the stride length.

Speed of walking is v = stride length (l) * frequency (F), whereby the frequency depends on the pendulum period (T): $F = T = 2 * \pi * $ square root from l/G (Preuschoft and Demes 1984; Witte et al. 1991; Witte 1995).

According to e.g., Witte et al. (2002) and Ren et al. (2008), the lever arms of the ground reaction force follow the cosine of the angles between the vertical and the mentioned segments and therefore are short in the first part and long in the second part of the limb cycle. Lever arm length can reach the length of the upper arm or the lower leg. Christian (1995) has pointed out that the position chosen by small mammals permits most rapid acceleration, because the pathway of the animal's center of mass follows the sine of the angle between vertical and segment axis. So, small mammals trade profiting from part of the possible energetic advantage of parasagittal locomotion for gaining the ability for rapid acceleration, by maintaining a flexed posture of the joints. Further, small mammals evolved to be digitigrade, so only the distal metatarsals/-carpals and phalanges are in contact with the ground. This way, an additional limb segment (in addition to the glenoid/acetabulum and elbow/knee joint) has evolved. The additional limb segment adds to an increased stride length (e.g., Witte et al. 2002; Ren et al. 2008; Fig. 2C). The proximal segments, scapula and femur, contribute the most to stride length. If elbows and knees are fully adducted and are moved in a parasagittal plane, flexion and extension of the elbow and knee joints allow larger stride lengths than in limbs held in a sprawling posture. This again refers to a more general biomechanical pattern. Although small mammals and birds do not move their extremities fully parasagittal (Bonnan et al. 2016; Jenkins 1971) their essential characteristics allow such an approximation.

A

B

C

muscular tie

J

K

horizontal force

resultant

head weight

GRF

D

E

F

M   m. pectoralis

m. caudofemoralis

N   pelvi-femoral muscles

GRF   GRF

L   m. pectoralis

pelvi-femoral muscles

GRF   GRF

O   m. supraspinatus

m. pectoralis

GRF   GRF

GRF

G

H

I

P

m. rhomboideus

m. serratus

scapula

vertebra   rib

humerus

gravity

coracoid

m. pectoralis

sternum

Q

m. rhomboideus

scapula

m. serratus

vertebra

m. deltoideus

gravity

rib

sternum

GRF

m. pectoralis

humerus

ground
reaction force

Evolution "towards" the origin of mammals

Synapsids show a variety of limb postures and associated changes of the locomotor system. Therapsids such as the dicynodont *Stahleckeria potens* (Fig. 1), span a continuum between sprawling and almost fully erect, adducted limb postures almost as partially attained by mammals (Jenkins 1971). Kemp (1978) inferred that some more advanced therapsids, i.e., members of Theriodontia, may have been able to use sprawling as well as more erect locomotory styles facultatively, convergent to modern

Figure 3. A–C Body-stem simplified as a beam, resting on two pairs of supports at equal distances. Sketches based on finite element structure analysis-models. The trunk is assumed to have two times the weight of the head and neck and the tail. If the beam consists of soft material, gravity deforms it as shown in **A**. **A** Head and tail bend downwards and the trunk sags in the middle imposing tensile and compressive stresses onto the model. Compressive stress, vertically hatched; tensile stress, hatched horizontally. **B** The tail is reduced like in some therapsids. Only the compressive stresses are shown because the compression-resistant skeleton is the only preserved material we have. The highest values are indicated by darker hatching. The highest forces occur along an arch reaching from the anterior support along the back to the posterior support. That means the shoulder blade should be inclined posterodorsally and the ilium should be inclined anterodorsally. **C** Head and neck are elongated (which has the same effect as a heavier head in combination with a shorter neck) and the tail is completely reduced. The posterior support is connected to the trunk by a joint, which must be balanced by a muscular tie (double line). The pulling force causes very high stress in the beam behind the joint. **D–F** Transverse forces of the same beam. **D** Shows an equal amount of functional loading distributed onto the fore- and hindlimbs, and the long tail. **E** The combination of a short tail and a heavy head results in high loads on the fore limbs like in many therapsids. **F** A high load on the hindlimbs results from a forward inclination of the latter, like in the majority of mammals. The inclined limb is kept in balance by a muscular tie which connects the limb with the trunk. This leads to high transverse forces in the posterior cantilever. **G–I** Bending moments in the beam shown above in **A**, **B**, **C** The bending moments are the products of the transverse force at a certain length multiplied by distance to the nearest support. Therefore, their arrangement along the length of a body shows curvilinear outlines. Above the supports, positive values are high, between the supports, the sign changes, and reaches its lowest point where the transverse forces cross the zero line. **G** Long tail, stress peaks are about equally high, the highest negative values reached a maximum near the middle of the trunk. **H** Short tail and heavy skull result in a higher stress peak above the fore limb than in the hindlimb. **I** The hindlimb is inclined and balanced in the joint by a muscular tie. This results in very high transverse forces caudally to the joint, which create a very marked stress peak and reduce the negative values between the supports. **J, K** Torsional moments. **J** During locomotion between anterior and posterior extremities in the trunks of quadrupedal tetrapods. Torsional stresses concentrate near the external body wall and create a space free of functional loadings, i.e., the body cavity. **K** Torsion also occurs in the neck of therapsids, e.g., during feeding. The weight of the head combines with the horizontal force component to a resultant, in line with the sprawling legs, which reaches the ground within the area of support, otherwise the animal would fall over. **L–O** Different patterns of loading the extremity girdles. In **M** reptiles, **N** birds, **O** mammals, and **L** Therapsida. Skeletal elements black, active muscles red. Ground reaction force (GRFs) indicated by upward directed arrows, the length of which is roughly proportional to the size of the respective force. In **M** crocodilians and lepidosaurs, the retraction of the femur is performed by m. caudofemoralis. In **N** Aves, **O** Mammalia, and **L** Therapsida, femoral retraction is performed mostly by pelvi-femoral muscles originating from the pelvis caudally to the acetabular joint (ilium in Therapsida, ischium in Mammalia, synsacrum in Aves). Reptiles, synapsids, and birds have in common that the shoulder joint is balanced mainly by a very strong m. pectoralis. In mammals, the scapula is suspended by e.g., the m. supraspinatus. **P, Q** Suspension of the body stem from the pectoral girdle in cross section. **P** In reptiles, **Q** in cursorial mammals. **P** Please note that the most anterior ribs of reptiles primarily provide the insertion area for the m. serratus (which carries the body stem). **Q** In mammals the anterior ribs close the circle of forces via their rigid connection to the sternum. The m. pectoralis of mammals suspends the body and aids in keeping the glenoid joint in balance (changed after Hohn, 2011). Abbreviations: GRF, ground reaction force.

crocodilians that sprawl and shift to a semi-erect "high walk" (Reilly and Elias 1998). Further, within later dicynodonts, a more adducted hindlimb posture may have been achieved (King 1985; Walter 1986; Ray 2006) and their capability to change between a sprawling and a more erect gait could have been lost (Kemp 1980). Several examinations especially of hindlimb posture in therapsids were conducted in recent years (e.g., Ray 2006; see summary in Fröbisch 2006).

The humeral heads of the here studied therapsids seem to have been expanded in dorsoventral direction and strongly compressed anteroposteriorly. The proximal articulation surfaces are relatively rough and the joint congruency in the glenoid is relatively low, suggesting elaborate cartilaginous caps. There is little doubt that extensive humeral abduction and adduction were possible. The flattened shape of the humeral head inhibits long axis rotation, which is necessary for excursions of the anterior zeugopodium. In all synapsids, radius and ulna are well developed. The humerus is held in a sprawling position, the zeugopodium can be pronated so that the digits point forward (e.g., Romer and Frick 1966).

The femoral heads of the studied therapsids have a somewhat oval shape with a longer diameter in approximately anteroposterior direction than in dorsoventral direction. A moderate abduction of the thigh is possible, similar but to a lesser extend than the humerus. Femur abductors (e.g., m. iliofemoralis) are muscles, which insert into the proximal femur, while the femoral head is angled from the shaft. This means that the femoral head is proximal and medial to the trochanter major. The knee joint of synapsids is directed forward. Therefore, the zeugopodium of the hindlimb does not need to be pronated, the bony elements maintain their position during the entire walking cycle (e.g., Romer and Frick 1966).

Yet, studies on functional loading of skeletal elements are rare for Therapsida: Blob (2001) found that in terrestrial therapsids the change from a sprawling to a more adducted limb posture is accompanied by a change of the main functional loading regime in femora, from torsion to bending. Blob (2001) corroborated biomechanically Kemp's (1978) hypothesis that earlier therapsids were able to change locomotion, from sprawling to more erect postures.
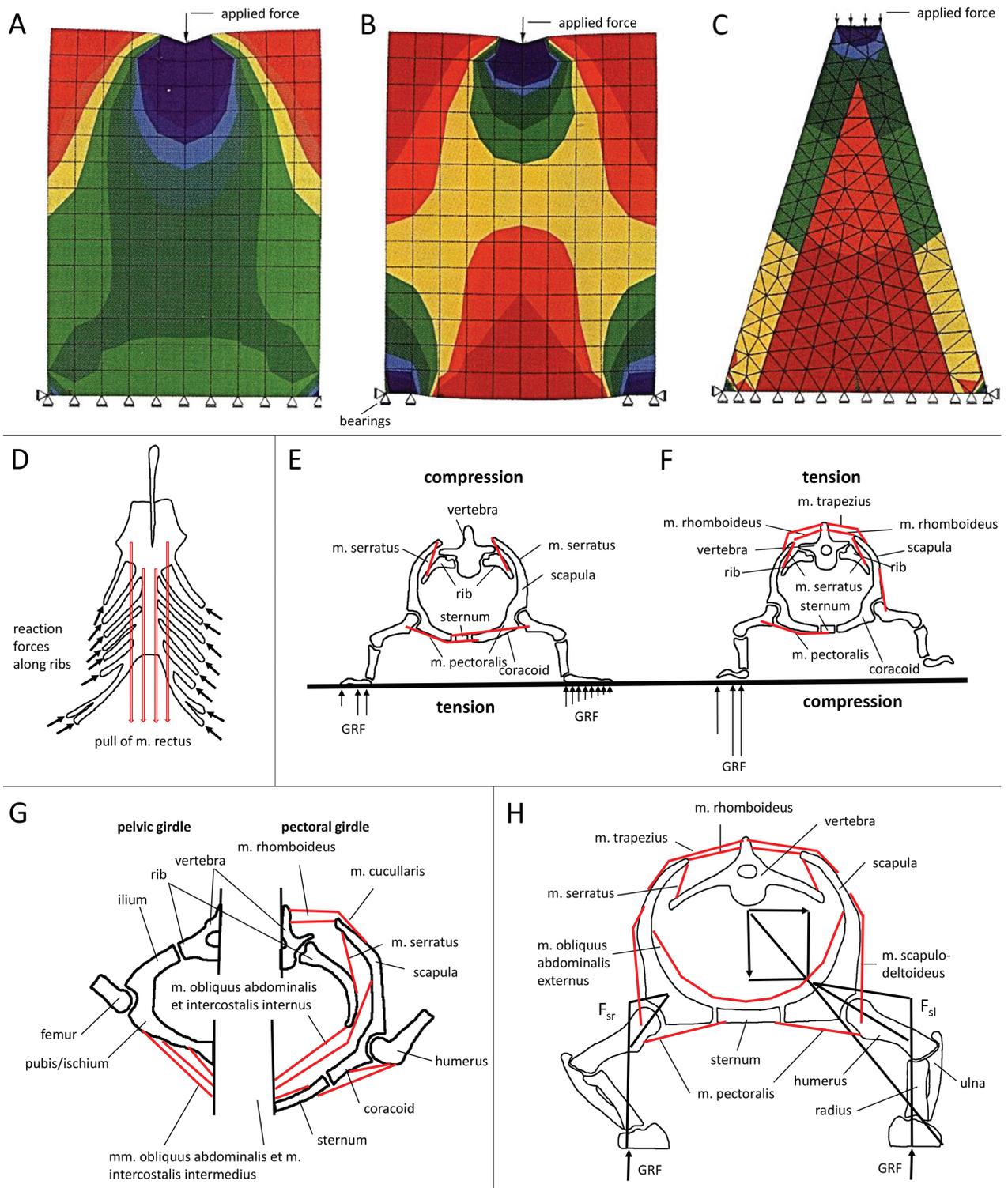
During therapsid evolution, their tails became lighter and shortened (Bakker 1971). The vertebral column of therapsids shows regions of intervertebral flexibility and stiffness corroborating that lateral undulation played an important role in locomotion (e.g., Cruickshank 1967; Hotton 1991; King 1981). Changes in vertebral morphology lead to increased stiffness of the vertebral column in lateral direction and increased flexibility in dorsoventral direction (Ray 2006), but also lead to increased long axis twisting especially in the more anterior vertebral column. This indicates very complex patterns of (in-)flexibility

of the vertebral column throughout therapsid evolution (Jones et al. 2021).

To our knowledge, studies focussing on the functional loading of the fore- and hindlimbs in combination with the axial skeleton, combining functional morphology with more technical observations, have not been conducted on therapsids. For our review, here we present first insights into the available data based on the historical collection of Friedrich von Huene (1875–1969) at the Paleonto-logical Collection, Eberhard Karls Universität Tübingen (GPIT), Germany. It is one of the largest collections with

Figure 4. A–D Sternum and rib angle in ventral view. Sternum, curvature of cartilaginous ribs, and rib angle in ventral view. **D** Morphology of the region in a crocodile as example. The black arrows indicate the direction of acting forces, not their sizes (changed and redrawn after Preuschoft 2022). **A** finite element structure analysis of a (weightless) plate, pushed by an external force (equivalent to the m. rectus abdominis) downward. Although the entire lower margin is available for transmission of this force, stresses tend to concentrate at both corners. **B** If the bearings along the lower margin are eliminated, this concentration becomes more pronounced, while the middle remains completely stress-free. **C** Following the yellow and green areas in (**C**), a new plate is created, and its most stressed parts are reinforced: Now the stressed parts deviate to both sides (forming the rib angle), and stresses become smaller downward (thinner ribs, longer cartilaginous parts). **E–G** Loading regime of the body stem in cross sections. **E** and **F** show the pectoral girdle, but in the pelvic girdle the same stress patterns occur. Loading depends upon the state of postural behavior: **E** If an animal is resting on both, fore- or hindlimbs, the lower part of the trunk is loaded by tensile stress and on its dorsal side by compressive stress (changed and redrawn after Hohn et al. 2013). **F** If one foot is lifted off the ground, the dorsal trunk is loaded by tensile stress and the ventral trunk as well as the remaining three legs by compressive stress (changed and redrawn after Hohn et al. 2013). **G** Left side pelvic girdle, right side pectoral girdle. The pelvic girdle as well as the pectoral girdle of reptiles and mammals are designed as ring-like structures (changed and redrawn after Preuschoft 2022). **H** Sketched frontal view of a tetrapod. Body cavity is suspended by muscles (red lines) from the most dorsal part of the shoulder girdle. Both limbs are sprawled but in a different way: on the left side with adducted, on the right side with a vertical zeugopodium. Accordingly, the ground reaction force (GRF) (upward directed black arrows) exerts different joint moments balanced by muscles. If the head moves to the left, the movement is opposed by the mass inertia, so the black arrow points to the right. In combination with the weight of the head (vertical black arrow) to a resultant, which reaches the ground within the field covered by the sprawled feet. A position is shown, in which the resultant just reaches the external margin of the left foot (changed and redrawn after Preuschoft 2022).

therapsid material in the world (Werneburg and Böhme 2018), but is still largely understudied regarding postcranial material. Thoroughly, the historical records on the recoveries of the specimens, the assembly of the skeletal mounts, as well as the vertebral columns including the ribs of the skeletal mountings themselves were studied and checked carefully for original fossil material (see Appendix 1; Fig. 1). Sacral and proximal tail vertebrae as well as ribs were measured where possible (Tables 1–11). Our starting point was the presumption that all skeletal elements of tetrapods must be strong enough to sustain the loads that gravity and locomotion impose on the skeleton (compressive forces, bending, and torsion). Changes in neck or tail length as well as increase in skull size are evaluated and show that minor local restructuring of the musculoskeletal system took place in order to adjust to the changing functional loading conditions. We do not follow a phylogenetic approach to interpret locomotory adaptations in our study, but focus on the basic physical conditions acting on any land vertebrate. In the future, the phylogenetic context will help interpreting specific adaptations and constrains through a taxon's specific evolutionary history.
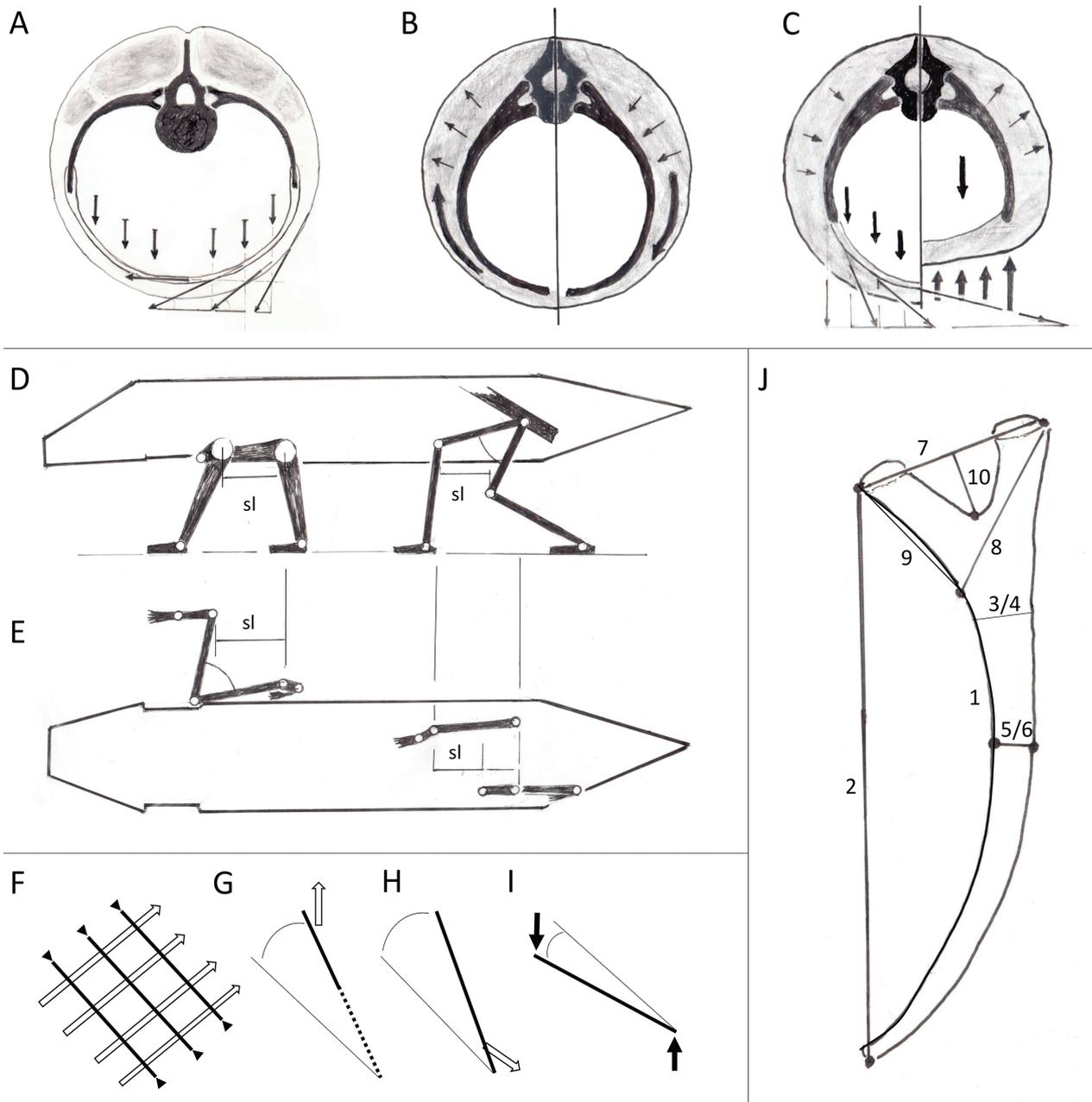
Results

Statics of the fore- and hindlimbs and the axial skeletons in vertebrates

Functional loading conditions in Tetrapoda in general

Fore- and hindlimb. In all tetrapods, the connection between the extremities and the trunk varies between the anterior and the posterior girdles (e.g., Brocklehurst et al. 2022). Preuschoft (2022) has proposed to explain why one girdle is mobile and the other rigid by an experiment: If two persons carry a ladder and press one ladder rung firmly against their hips, they have to adjust their stride length and frequency and walk in lock-step, otherwise they would interfere with each other. If one person loosens the ladder rung from the hip, both people can freely choose their stride lengths and frequencies. The model is based on parasagittal walking and a trunk with unvariable length, and therefore open to doubt. However, the disturbing interference comes from the shifting/pushing forward of the body stem (Fig. 2R). Exactly the same shifting/pushing forward does occur, if the limbs are held in a sprawling posture (Fig. 2L). In quadrupedal mammals, as well as in crocodiles, the decoupling of fore- and hind- limbs is given by a mobile shoulder girdle (e.g., Walker 1971; Jenkins 1974; English 1977; Baier and Gatesy 2013; Mayerl et al. 2016; Schmidt and Fischer 2000; Schmidt et al. 2002; Schmidt et al. 2016). If however, the trunk is very flexible (as for example in the Tambach reptiliomorphs), a curvature of the vertebral column can also change the distance between fore- and hindlimbs. The forces acting on the pectoral limb and girdle can be significantly higher than those acting on the pelvic limb and girdle in some behaviors, e.g., during deceleration of climbing. This is particularly relevant, if the centre of mass is closer to the shoulder than the hip (as in e.g., most mammals).

An acceleration (in e.g., rapid flight, jumping etc.) imposes a higher functional loading onto the hindlimbs than onto the forelimbs. Therefore, a direct force transmission from the hindlimb onto the axial skeleton via a rather rigid sacral region is advantageous over a hypothetical rigid connection between the pectoral girdle and the axial skeleton. In slowing down or stopping, a tetrapod can afford minor delays in the transmission of force between the trunk and the anterior extremity. The reasons for this are a physical principle (illustrated in Fig. 2I), and hold true

for all animals including quadrupedal mammals. Further, the forces that result from slowing down and stopping are much greater than those occuring during the beginning to move. Longer braking distances, which are permitted by the extension of muscles, inhibit growth of negative accelerations to a certain degree (e.g., Preuschoft and Fritz 1977; Denoth et al. 1985; Preuschoft et al. 1991). Studies concerning these issues have been rarely based on postcranial morphology and metrics.

The morphology of the girdles and the associated myology differ between crocodilians, lepidosaurs, birds, and mammals (Fig. 3L–O), among others. The locomotory musculoskeletal system of mammals and birds has evolved from a state presumably similar to the one found in reptiles (Gatesy 1990). The ventral part of the pectoral girdle (interclavicle, clavicle, sternum, coracoid/procoracoid) form a massive bony plate in most tetrapods, except for mammals. These ventral bony elements usually serve

as origin surface for e.g., the m. pectoralis and act as a brace to stabilize the glenoid and keep the glenoid from being pulled medially. In birds, the same static situation is maintained during flight: The body weight is carried by the long laterally spread wings, which have a long lever arm, and are balanced by the huge m. pectoralis muscle. In contrast, mammals that have evolved to use parasagittal locomotion show a rearrangement of the locomotory musculoskeletal system. So, mammals do not need a strong humeral adductor like the m. pectoralis as sprawling tetrapods do, but instead the m. pectoralis aids the m. serratus in suspending and carrying the body. Lai et al. (2018) have described the shoulder girdle of *Massetognathus pascuali*, which actually shows the transition between the reptile-like and the mammalian (therian) condition (Fig. 3P). The scapula is inclined posteriorly in mammals (Fig. 2H). This is because the ground reaction force is lead through the articulation at its ventral end and

Figure 5. A–C Functional loading of ribs on cross sections. Skeletal elements drawn thicker than musculature. **A** The weight of the intestines pushes downward and is represented by six arrows. On the right side, the parts of weight combine with the pulling force of the muscles to resultants, which agree with the local direction of the muscles. The ventral tips of the ribs are pulled downward, and can be sustained because of the long, bifurcated collum and tuberculum. **B** Torsional moments compress the ribs on one side, while extending them on the other. In the first case, ribs tend to vault laterally, in the second, the curvature becomes flatter. **C** In contrast to the trunk carried freely above the ground (left side, also in **A**), a belly-dragging posture (right side) leads to compression of the ribs, not to tension. Ribs in side view. **D**, **E** Sketch of a synapsid, with sprawling forelimbs and parasagittally moving hindlimbs. **D** Lateral, **E** top view. Segment length is the same in both sketches, the excursion of the hip and shoulder joint are identical, as well as the step length sl. The excursion range of the zeugopodium is enabled by a rotation about the long axis of the stylopodium. **F** Direct transfer of body weight on the ground (bold arrows) leads to a more inclined position of the rib (after Preuschoft et al. 2007 a and b). This arrangement is suited to withstand the torsional stresses. It changes to its opposite at each step. **G** M. serratus pulls the anterior ribs cranially and hereby reduces their optimal angle of 45° as shown in **F**. **H** The muscles of the body wall pull the middle and posterior ribs downward and readjust their angle towards 90°. **I** Black arrows indicate compressed ribs, white arrows indicate tension of the intercostal muscles. **J** Rib measurements. We measured where possible due to preservation, the vertebrae and ribs (with calipers and a measureing tape) of *Sauroctonus parringtoni* (GPIT-PV-31579), *Stahleckeria potens* (GPIT-PV-30792), *Keratocephalus moloch* (GPIT-PV-31461), *Belesodon magnificus* (GPIT-PV-31575), *Hyperodapedon sanjuanensis* (GPIT-PV-31578), *Dimetrodon limbatus* (GPIT-PV-31373). We measured the vertebrae as follows: centrum hight (cranial side), width (cranial side), and length of the second last presacral vertebra to approximately half the tail length, if the respective vertebrae were preserved and if the state of preservation allowed it. Rib measurements included: measurements 1–10.

the scapula itself. The inclined scapula is connected to the humerus by strong muscles of which the largest one, m. supraspinam, takes its origin from the enlarged fossa supraspinam. The scapula is kept in equilibrium which is accomplished by the caudal part of the m. trapezius, which retracts, and by the m. rhomboideus and the cranial part of the m. trapezius (=m. cucullaris) which protracts. This equilibrium of the scapula has been investigated in detail by Preuschoft et al. (2003) (Fig. 3Q).

In the pelvic girdle of reptiles, associated with a posterodorsally expanding ilium (Fig. 3L, M), the sprawling posture of the hindlimb is maintained to a large extend by the m. caudofemoralis. M. caudofemoralis is a femoral retractor which originates from the transverse processes of the more cranial tail vertebrae in lepidosaurs and crocodilians (e.g., Russell and Bauer 2008; Snyder 1954; Romer 1923; Gatesy 1990; Gatesy 1997; Otero et al. 2010; Suzuki et al. 2011). Movements of the tail instead of the femur are excluded – without expenditure of energy – by the distribution of the insertion on the tail over several segments, and by the great mass moment of inertia of the tail (mass times square of lever arm, and lever arm being the distance between root of tail and its centre of mass). In contrast to reptiles, birds have the pygostyle (e.g., Romer 1923), and mammals and therapsids (Fig. 3N, O) have a slender and/or short tail (Bakker 1971; Kemp 1978; Romer and Frick 1966; Nickel et al. 1968). None of these skeletal structures possesses the mass moment of inertia to balance the body against movements of the hindlimbs, nor do they offer an adequate origin area for the m. caudofemoralis. Hence, the muscles that retract the femur originate from the post-coxal part of the pelvis. In birds these are the synsacrum and ischium and in mammals this is the complex formed by ischium and pubis (Romer and Frick 1966; Nickel et al. 1968). In several of the more advanced (Triassic) therapsids, the ilium as well as the ischium have posterior processes, which may well have served as origins of the femur retracting muscles (Fröbisch 2006). The exact differentiation of the

muscles is of minor importance in this context, because, from a biomechanical point of view, it is important that they muscularly connect the pelvis and the femur.

The pectoral and pelvic girdles are very similarly functionally loaded: On a transverse section, weight is approximately evenly distributed on all four limbs while standing (Fig. 4G). The ventral part of the girdles is stretched (tension), the dorsal part is compressed (Fig. 4E). During locomotion, at least one limb must be lifted off the ground. Then, the body weight is distributed onto the supporting limbs. This leads to compression of the ventral side of the girdle and stretching of the dorsal side of the pectoral girdle (Fig. 4F). The tensile forces are sustained by the muscles and ligaments and the compressive forces by the bony skeleton. On the dorsal side, these tensile forces are absorbed by the m. serratus (which also possesses a transverse component), the m. trapezius, and the m. rhomboideus. The same muscles also carry the weight of the limb in the swing phase. On the ventral body side lies a continuum of skeletal elements and the associated m. transverses thoracis.

In the skull, mass inertia and weight combine to form a resultant running in latero-ventral direction, which is in line with the sprawled position of the forelimbs (Fig. 4H). This can occur in combination with a vertical (as most frequent in reptiles) or with an adducted zeugopodium (like in frogs).

Axial skeleton. All tetrapods need to maintain their body off the ground against gravity. A theoretical model, a beam on two supportive structures, shows that the skull and neck and the tail bend downward, as well as the back sags between the two supportive structures (Fig. 3A). This means, compression resistant material is needed on the beam's lower margin above the anterior and the posterior supports and near the dorsal margin in the middle of the trunk, too, to avoid sagging. In contrast, tension-resistant structures are needed at the dorsal margins above the supports and along the ventral margin to maintain posture.
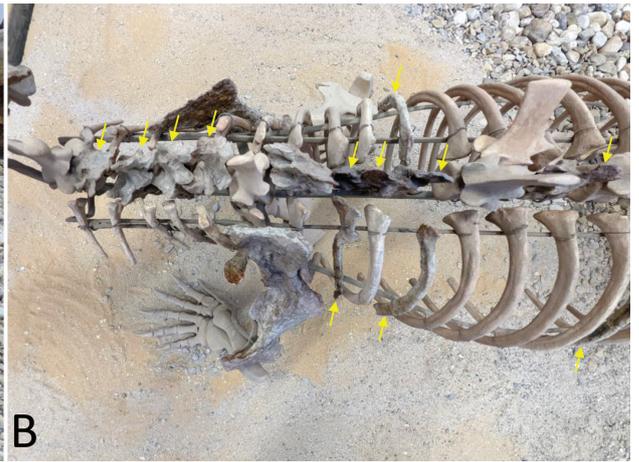
Figure 6. *Belesodon magnificus* (GPIT-PV-31575) and *Dimetrodon limbatus* (GPIT-PV-31373). **A** Overview over the mounted skeleton on display of *Belesodon magnificus*. **B** Cervical and anterior dorsal vertebral column. **C** Posterior dorsal, sacral, and caudal vertebral column. **D** The two first sacral vertebrae have been preserved, the third one was not preserved. Yellow arrows mark fossil vertebrae and ribs. The flattened ribs in the posterior part of the dorsal vertebral column were amended based on *Traversodon* and *Cynognathus* according to von Huene (1935–42). **E** Overview over the mounted skeleton of *Dimetrodon limbatus* on display. **F** Overview over the vertebrae and ribs of the cervical and cranial dorsal vertebral column. **G** Vertebrae and ribs of the caudal dorsal vertebral column. **H** Sacrum and caudal vertebral column. Yellow arrows mark fossil vertebrae and ribs; orange arrows mark exemplaric for one caudal vertebra the added parts made of plaster. Most vertebral centra, as well as the long dorsal spines of the dorsals are fossil material. Most ribs, and in the caudals also the dorsal spines are amended by plaster.

The vertebral column acts along the entire body length as a compression-resistant rod. The vertebral column is shifted slightly below the midline in the tail, and curves to the ventral side in the anterior thoracal region and at the neck's basis (Fig. 3A). As additonal stress-resistant elements, the pectoral and pelvic girdle and the gastralia expand along the ventral contour in many tetrapods. In contrast, the tension-resistant muscles are found in the nuchal region, along the ventral body wall between sternum and pelvis, and more on the dorsal than on the ventral side of the tail often enforced or replaced by tendinous structures. Shortening of the tail (Fig. 3B), or elongation of the neck (Fig. 3C), lead to several musculoskeletal changes, but do not fundamentally change the general tetrapod 'bauplan' (see below). If the beam would be cut into slices from head to tail, all sections in front of the anterior support structure would bend towards the ground. This is due to the often-missed transverse forces (Fig. 3D–F). The transverse forces increase either when the skull is relatively large or when the neck is relatively elongated. To illustrate the transverse forces, we call them positive at this stage. Behind the anterior support, the anterior section will remain high and the posterior will sink downward. The transverse forces turn negative and become smaller. Then, a point will be reached in which the anterior and the posterior parts of body mass are in balance. At this point, the transverse forces cross the midline of the body. Further caudally, towards the pelvis, transverse forces turn positive again. This means the more anterior section is bend ventrally to the ground and the more caudal section is bend relatively higher dorsally. Behind the posterior support structure, the transverse forces are negative and the tail is bend ventrally towards the ground. The longer and heavier the tail is, the greater the transverse forces, and the closer to the tip of the tail, the smaller the transverse forces are. The ribs and the intercostal muscles evolved to resist the transverse forces. In engineering strurctures, e.g., concrete beams, short tension-resistant wires are added at right angles to the long axis of the beam. Along the neck and the tail, the oblique structures, i.e., ribs and muscles, are means to sustain transverse forces. The long dorsal muscles, in contrast to those of the neck and tail, do not possess considerable non-axial components. An exeption poses the m. iliocostalis, which acts in reptiles as an oblique muscle at the lateral sides of the body wall, while it is seen in mammals as part of the longitudinal trunk extensors because of its innervation.

Multiplication of a transverse force at a given place by its lever arm results in the bending moment, which, if plotted along the trunk, unites to form a curvilinear function (Fig. 3G–I). If the trunk section between the two support structures has a higher weight than assumed in the drawings, the negative values increase. These curves representing the bending moment show how much the trunk tends to bend under the influence of gravity (see also Fig. 3A). If the supporting vertical force at the forelimbs is distributed over a broad region, as by e.g., the m. serratus of large mammals, functional loading peaks in a lowered and flattened curve.

During walking and trotting, body weight is supported in phases by only one limb of a pair, while the other swings foreward. In addition to the transverse forces and the bending moment, the trunk has to resist a torsional moment as well (Fig. 3J, K). To maintain stability, compression-resisting (ribs) and tension-resisting (oblique muscles) elements are necessary. The ribs follow a path intermediate between the path of the transverse forces and the compression induced by the torsional moment (from cranial-dorsal to caudal-ventral). Additionally, the ribs serve as origins of muscles, e.g., for the large m. serratus. Sprawled limbs induce a high torsional moment in the trunk region due to their long lever arms and high torsional moments. In the often narrow-shaped cursorial mammals, torsion plays a minor role in the trunk region because the lever arms are short and therefore the moments are minimized. Torsion resistance grows with the square of the diameters of the body. Therefore, the external layers of the body wall, that is ribs and trunk musculature, contribute most to its stability which leads to a generally relatively uniform arrangement of the trunk region in Tetrapoda. The body cavity is stress free. Nevertheless, there are minor differences in the arrangement of the trunk region in sprawling and parasagittaly moving tetrapods. In reptiles, nearly all trunk vertebrae carry ribs, and the m. iliocostalis covers the sides of the trunk as an oblique muscle. In mammals, ribs are confined to the anterior vertebrae and leave a longer (small mammals) or less long (large mammals) lumbar section free from ribs. The m. iliocostalis is confined to the dorsum, where it functions as a part of the "erector spinae-system" in extension or dorsiflexion. Additionally, ribs are also associated to ventilation, but the related forces are lower than those imposed by locomotion, therefore our discussion focusses on only the latter.
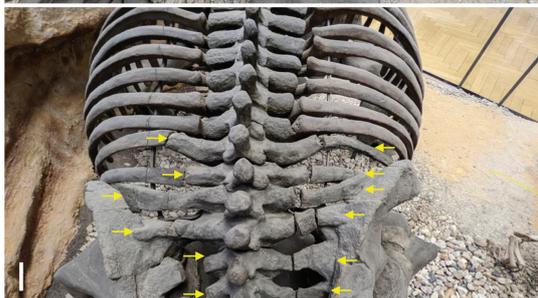
Figure 7. *Keratocephalus moloch* (GPIT-PV-31461) and *Sauroctonus parringtoni* (GPIT-PV-31579). **A** Overview over the mounted skeleton of *Keratocephalus moloch* on display. **C** Left side, cervical and cranial dorsal vertebral column. **E** Sacrum from lateroventral. Yellow arrows mark fossil vertebrae and ribs; curly bracket marks preserved dorsal vertebrae; orange arrows mark exemplaric for one rib and vertebra the added parts made of plaster. **G** Right side, cervical and cranial dorsal vertebral column. **I** Caudal dorsal vertebral column and sacrum. **B** Overview over the mounted skeleton of *Sauroctonus parringtoni* on display. **D** Caudal dorsal and caudal vertebral column. **F** Sacrum. Curly bracket marks the added vertebra of the tail. yellow and orange arrow mark exemplaric the original fossil material and the added plaster. Overall more caudal ribs consist of less fossil and more artificial material. **H** Cervical and cranial dorsal vertebral column. **K** Close-up of the sacral region and the cranial caudal vertebrae.

Functional loading conditions in Therapsida

Fore- and hindlimb. In contrast to most diapsids, therapsids have a less long and heavy, in many cases a markedly reduced tail. However, at least anomodont heads were relatively large and heavy because of their large chewing apparatus and its associated muscles (e.g., Angielczyk 2004). This change of body proportions leads to high bending moments of the neck and lower bending moments in the tail region (Fig. 3H, I). Considerable compressive stresses in craniocaudal direction can be observed at the level of the two support structures. This requires a concentration of compression-resistant bony material in the respective areas, as indeed is present by the shoulder and pelvic girdles in early synapsids. The position of the limbs influences the structure of the trunk once the femoral retractors have shifted onto the postcoxal part of the pelvis. Then, high bending occurs above the posterior support and requires a massive development of the pubis-ischium-complex at the ventral side of the pelvic girdle (Fig. 3L–O). Already in the earliest known synapsids, the ventral part of the shoulder girdle, that is the coracoid, procoracoid, interclavicle, and clavicle, is well developed and either cartilaginous or bony (and a cartilaginous sternum that, although it often is not preserved, was likely present as well) (Buchholtz et al. 2021). The whole skeletal (or partially cartilagenous) plate is suited to sustain compressive stresses which result from bending which takes place above the anterior support. The large ventrally expanded girdles additionally provide origin surface area for the m. pectoralis (humeral adductor) and a bracing structure in phases of unilateral loading during walking. Corresponding to the pattern of compressive forces (Fig. 6), the scapular blade is inclined posterodorsally, like in nearly all quadrupeds. The arrangement of compressive stresses also explains the anterodorsal inclination of the ilium in contrast to e.g., reptiles that have a posterodorsally inclined ilium.

The skeleton of the pelvic girdle is expanded at its ventral side in anteroposterior direction as well as in lateromedial direction. This corresponds with the pattern of compressive forces in lateral (Fig. 3A–C) and anterior (Fig. 4G) view. The ilium expands behind the hip joint caudally which provides attachment surface for the hindlimb retractors while the tail is much reduced (see also Gebauer, 2007, Gebauer 2014). This expansion of the ilium in posterior direction does not alter the basic anterodorsal inclination of the ilium as shown in Fig. 3B.

Axial skeleton. Since the m. pectoralis profundus originates from the sternum in mammals, the connection between this element and the anterior often straight ribs is strong. In crocodiles and in lizards, the m. serratus acts on the short, very strong ribs which do not reach the sternum. In early synapsids, this muscle may have extended cranially onto the cervical vertebrae, e.g., in the sphenacodontid *Dimetrodon limbatus* five and in the gorgonopsian *Sauroctonus parringtoni* two cervical ribs are found. In line with this observation is that the innervation of the forelimb through the plexus brachialis comes from the lower neck segments and only one root comes from the first thoracic (e.g., Nickel et al. 1968).

The ribs of early therapsids differ from those of mammals and are similar to those of diapsid reptiles: proximally, they have two articular surfaces, the head and the tuberculum. This v-like shape provides stability and inhibits that the ribs are bend outward or inward. The force that induces outward or inward bending of the ribs is given in sprawling tetrapods when the stylopodia are abducted. In contrast, cranial or caudal bending of the ribs about an axis which connects both joints is easily taking place. Torsional moments are greater in reptiles than in mammals, because their ground reaction forces have longer lever arms. As a consequence, the trunk in extant reptiles is more rounded, or tube-like than in mammals that have a more laterally compressed trunk at the level of the pectoral and the pelvic girdles. Double-headed ribs are suited to sustain various loads (Fig. 5A–C, F–I):

1. The compressive components of torsion, which lead to bending of the rib outward (Fig. 5B, F): Compressive stress in walking alternates regularly with tensile stress, which leads to inward bending (Fig. 5C). In lateral view, the anterior ribs are approximately vertically arranged, more posterior ribs are inclined, and posterior ribs are less inclined again. Inclinations of 45° in lateral view are optimal for resisting torsional stress.

2. The force of the pulling and weight-carrying m. serratus (Fig. 4G): The resulting force acts against gravity, that is vertically upwards, and leads in the anterior ribs, that are aligned in the same direction, to functional loading by compressive stress.

3. Downward directed pull of the ventral body wall by gravity: The tension of the body wall leads to more vertically oriented ribs in the most posterior part of the dorsal vertebral column again.

Figure 8. *Stahleckeria potens* (GPIT-PV-30792). **A** Overview over the mounted skeleton on display. **B** Left side, cervical and cranial dorsal vertebral column. **C** Left side, caudal dorsal vertebral column. **D** Dorsal view of the sacral region. **E** Left side, caudal vertebrae. **F** Right side, cervical vertebral column. **G** Right side, cranial dorsals. **H** Right side, caudal dorsal. **I** Right side, ribs. Yellow arrows mark fossil vertebrae and ribs; curly bracket marks preserved dorsal vertebrae; orange arrows mark exemplaric for one rib and vertebra the added parts made of plaster.

4. Carrying the body weight in resting or sprawling belly-dragging (sensu Nyakatura et al., 2013): The body weight leads to compression of the most ventral bony body parts perpendicular to the body long axis (Fig. 5A, C)

It can be expected that the ribs are inclined to average angles mediating between the various functional loadings, which may vary dependending on the life-style. The independance from the most ventral part of the ribs, close to the sternum is secured by the not ossified and therefore mobile (see above) cartilaginous parts (Fig. 4A–D). Early therapsids have ribs on the cervical and the dorsal vertebral column. The small cervical ribs sustain high transverse forces at the pectoral region. The transverse forces extend far caudally and thus the ribs extend just as far caudally (Fig. 3E). On average, the more caudal ribs of the trunk are more slender than the more cranial ones. The tail in all therapsids is reduced, either quite short, or long but slender. For the respective taxa, we do not know how long the actual tails were. We presume, based on the preserved vertebrae of *Sauroctonus parringtoni* (gorgonopsian), *Stahleckeria potens* (anomodont), *Dimetrodon limbatus* (early synapsid), and *Hyperodapedon sanjuanensis* (archosaur) that their tails were still relatively long (see Appendix 1). In contrast, in *Belesodon magnificus* and *Keratocephalus moloch*, no tail vertebrae are preserved. For *Tetragonias njalilus*, we do not know, because Cruickshank (1967) merely stated that there are several caudal vertebrae, but he was unsure how many, and Fröbisch and Reisz (2011) gave a rough approximation of 12–15 caudal vertebrae for dicynodonts in general. So, it seems likely that a modern redescription of the postcranial material might shed light on this issue. This is because von Huene (1943) concentrated on the description of the skull and the skull fragments of the two specimens found (see Appendix 1) and Fröbisch (2006) concentrated on the hindlimb of *Tetragonias njalilus*. Complete caudal vertebral columns are only known for a few therapsids (Kemp 1986). Overall, Therapsida experienced a reduction of the tail length (Bakker 1971, but see also Fröbisch and Reisz 2011). The proximal tail vertebrae are not reinforced as in the taxa listed above (Tables 3, 5, 7, 9, 11), and the tail does not posses a markedly great mass moment of inertia.

Discussion

Observations on therapsids in comparison to fossil and living analogues

Fore- and hindlimbs

Therapsida evolved a relatively heavy head with a short neck and a short, or at least not heavy tail. These characteristics shifted the center of mass of the body forward, towards the forelimbs (Bakker 1971). As a consequence, the forelimbs are more massive and stronger than the hindlimbs. Although the neck was short and downward-directed bending moments were likely high. If a heavy head is moved, it offers a high moment of mass inertia. Further, depending on the feeding mode, external forces in e.g. lateral direction may have been acting on the skull as well. If so, body weight and external force combine to a laterally inclined resultant (Figs 3K, 4H). Only if this resultant meets the ground between the forefeet, the animal is able to keep itself balanced. In this case, the sprawling posture is advantageous as has been suggested by Kielan-Jaworowska and Gambaryan (1994) for multituberculate mammals. The lateral placement of the forelimb requires an extended origin of the adducting and very strong m. pectoralis as well as a compressive stress-resistant brace from the glenoid joint to the body midline via the sternum. Such a bracing structure, composed of varying bony and cartilaginous elements can be found in modern reptiles, amphibians, monotremes, and juvenile marsupials for example (Klima 1987; Preuschoft 2022). Careful reconstructions of the skeleton show that *Triceratops* had laterally abducted fore- and parasagittally adducted hindlimbs (Preuschoft and Gudo 2006). Our interpretation is in contrast to the erect posture of the species as reconstructed by Fujiwara (2009) and Fujiwara and Hutchinson (2012). Additionally, *Triceratops* had a large head with strong jaw muscles, a neck shield, and horns, which were used for defense and maybe also for intraspecific fights (Farke et al. 2004), imposing high external loadings on the skull. The ceratopsian hindlimbs experienced, like those of synapsids, lower functional loading than the forelimbs. This is due to their shorter and lighter tails and heavier heads (Kemp 1978, 2005;
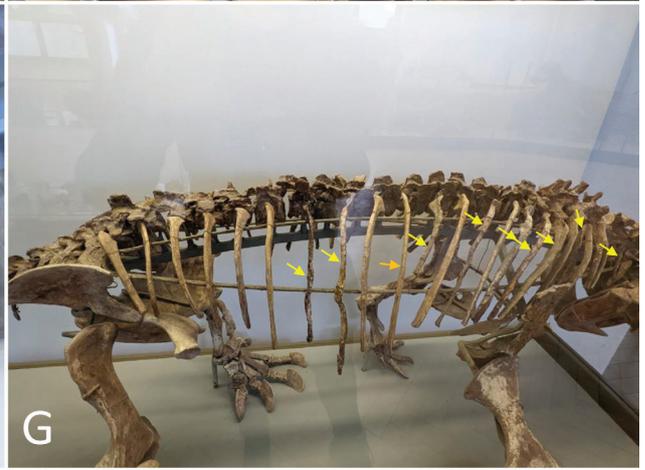
Figure 9. *Tetragonias njalilus* (GPIT-PV-31574) and *Hyperodapedon sanjuanensis* (GPIT-PV-31578). **A** Overview over the mounted skeleton. None of the mounted vertebrae and ribs are original fossil material, they are all made of plaster. **B**, **C**, **D** Drawers containing the mostly undescribed postcranial material of *Tetragonias njalilus*. **E** Overview over the mounted skeleton of *Hyperodapedon sanjuanensis*. **F** Left side, ribs. **G** Right side, ribs. **H** Sacrum and cranial caudal vertebrae. The vertebral column is mostly complete, the posterior part of the tail is artificial. **I** Sacral region. Orange arrows mark added material made of plaster. Yellow arrows mark fossil ribs.

Gebauer 2007; Gebauer 2014). The hindlimbs do not need to be held in a sprawling position because of the tail's low mass moment of inertia. Ceratopsians deviate in their morphology markedly from their closest relatives among ornithischians and are instead similar to the synapsids. Similar morphological adaptations seem to be present in recent monotremes, i.e., sprawling forelimbs and erect hindlimbs. This is not well supported by Jenkins (1970). Other adaptations, e.g., the aquatic adaptation of the platypus (*Ornithorhynchus*) and the specialized diet (ants) of echidnas (*Tachyglossus* + *Zaglossus*) riddle these other characters.

Most recent mammals walk with both limb pairs moved in a parasagittal plane. The swinging scapula provides an additional leg segment that adds to stride length. The necessity for strong leg adductors to maintain the sprawling posture becomes superfluous. Instead, recent mammals have a slender sternum which is craniocaudally oriented (Fig. 4A–D). The most anterior ribs attach to the sternum by a short cartilaginous portion which allows movements. While the coracoid, and in most cases also the clavicle, are absent in mammals, the m. pectoralis (profundus) takes its origin from the sternum and inserts above and below the glenoid joint without moving it. Because of this inclined direction, it helps carrying the heavy trunk (Fig. 2G, H, more information in Preuschoft 2022). The angle between humerus and scapula leads to considerable flexing moments. These are compensated by strong extensors: the m. supraspinam and m. deltoideus. The oldest known mammals from the Jurassic (e.g., *Haldanodon, Henkelotherium, Juramaia*) already had a comparable scapula-musculature configuration and their anterior ribs were strong enough to establish a compression-resistent connection between sternum and vertebral column. For parasagittal locomotion in mammals, a rotation along the long axis of the zeugopodium is unnecessary. This results in fusion of radius and ulna in highly evolved hoofed animals. The ulna contacts the elbow and forms part of the elbow joint, while the radius contributes to the carpal joint (e.g., Romer and Frick 1966; Nickel et al. 1968).

If the tail is reduced, it cannot provide a sufficiently stable insertion for the retractors of the femur. Instead postcoxal processes of the pelvis (synsacrum and ischium in birds, ischia and pubis in mammals) offer areas into which the retractors may insert (Fig. 3L–O). In birds, the muscles connect the distal femur or the knee area with the exceptionally strong synsacrum formed by fusion of ilium, ischium, and pubis. The synsacrum of birds is a strong box-beam. It sustains bending in side view, but also, together with the rigid transverse processes of the vertebrae, the bending in anterior view if only

one hindlimb contacts the ground during a limb cycle. In contrast to early mammals, neither in dinosaurs nor in crocodiles the pelvic girdle has a postcoxal process, which can serve as an origin for strong femur retracting muscles (e.g., Romer and Frick 1966; Nickel et al. 1968; Mickoleit 2005). In contrast, non-avian archosaurs have strong transverse processes of the proximal caudal vertebrae, from which the m. caudofemoralis originates. This muscle aids e.g., in undulatory swimming and compresses the proximal caudals, which as a consequence have large diameters (Preuschoft 1976). A shortened tail as in therapsids (Bakker 1971) is neither efficient for undulatory swimming, nor is its mass moment of inertia big enough to act as a counterforce against the contraction of a large m. caudofemoralis. All tetrapods with short tails will exhibit smaller diameters in their proximal caudal vertebrae. This expectation is confirmed by a comparison between *Hyperodapedon sanjuanensis*, *Dimetrodon limbatus*, *Sauroctonus parringtoni*, and *Stahleckeria potens* (Tables 3, 5, 9, 11; see Appendix 1). In most recent mammals, the tail has only a moderate mass, except for e.g., aquatic animals (whales and dolphins, otters, beavers) (Kuschel 1994; Preuschoft 2022), jumping animals (kangaroos, leaping prosimians, and Catarrhini), and climbing Platyrrhini with prehensile tails (e.g., Ankel 1962; Peters and Preuschoft 1974; Preuschoft 2022).

Skeleton of the body stem

An array of ribs, in especially the anterior part of the trunk is a characteristic of all Tetrapoda. In land-living vertebrates, ribs are part of the respiratory system (e.g., Perry 2010). Recent attempts for functional analyses of ribs were undertaken by e.g., Preuschoft et al. (2005) and Fujiwara et al. (2009). Following the principles of Pauwels (1965, 1980), the development of ribs is influenced by three mechanical factors: transverse forces, the muscular arrangement, and torsional moments. Ribs hamper flexing and extending the trunk dorsoventrally.

In the most cranial ribs the m. serratus pulls dorsally and in the more posterior ribs the muscular body wall (m. rectus abdominis, m. obliquus abdominis externus, m. obliquus abdominis internus, m. transversus abdominis) pulls ventrally. The m. serratus suspends the ribs and carries the body (Preuschoft 1976). It compresses the ribs and scapula. In contrast, the lateral posterior body wall imposes tensile forces onto the ribs. Carrying the weight of a large head results in large transverse forces. Like in many diapsid reptiles, all trunk segments bear ribs in early synapsids. This can partially be explained by negative transverse forces reaching far caudally (Fig. 3E). Similarly, the whole trunk region is subdued to high torsional

loading. Torsional loadings are imposed onto the neck region by different feeding styles (Fig. 3H) (e.g., by tearing off bites from prey or plants). The torsional moments have the same magnitude from head to thorax. The insertion of the m. serratus of reptiles at the distal ends of the most anterior dorsal ribs may have been extended in therapsids onto the cervical ribs. The compressive stress the m. serratus exerts may have induced the development and ossification of the cervical ribs (see e.g., in *Saurocto-nus parringtoni*, Fig. 7; and *Dimetrodon limbatus*, Fig. 6). This is confirmed by the innervation of the arm muscles via the brachial plexus, and the roots of this plexus mainly comes from the cervical segments. Only the first thoracic segment (Th_1) is involved in forming the brachial plexus (e.g., Romer and Frick 1966; Nickel et al. 1968).

Conclusions

Evolution of parasagittal locomotion

Parasagittal locomotion evolved convergently in Aves, Meta-, and Eutheria. In therapsids, this posture was attained in the hindlimbs earlier than in the forelimbs (Fröbisch 2006). Some sprawling taxa are able to change to a semi-erect locomotion at higher speeds, e.g., the "high walk" of todays crocodiles (Reilly and Elias 1998) and big lizards (monitor lizards, iguanids) (Christian 1995; Preuschoft et al. 2007). The lack of endurance may be because the muscle fibres do not work at their optimal fibre length in this semi-erect stance (Christian 1995; Preuschoft et al. 2007). Extended joints save energy because they imply short lever arms. This option is used by the gigantic sauropods and by elephants as the largest among extant terrestrial mammals. Size, or a large body mass, may imply that a more erect way of walking would be more energetically efficient. Nevertheless, Clemente et al. (2011) showed that there is no correlation between body mass and the adduction angle between the femur and the sagittal plane.

Limb segments of the more extended parasagittal position can become longer without an increase of energy consumption. Many synapsids were of medium size [(e.g., *Dimetrodon limbatus* (Fig. 6)]*, Sauroctonus parringtoni* (Fig. 7)*, Tetragonias njalilus* (Fig. 9)*, Belesodon magnificus* (Fig. 6)), especially those considered to be ancestral to early mammals but some gained considerable body sizes (e.g., *Stahleckeria potens*, Fig. 8*, Keratocephalus moloch*, Fig. 7) and it seems that these also have not made use of extending the joints. Like early non-mammalian Therapsida, the earliest known mammals were small. Small animals can excert proportionally more muscle force (F) in relation to body mass (m; $F = m^{2/3}$) than large ones (Preuschoft 2022).

Possible evolutionary scenarios for the development of parasagittal locomotion are:

1. Small mammals hold their legs horizontally only during part of the locomotory cycle (roughly during one third) and save some energy this way (e.g., Witte et al. 2002; Ren et al. 2008).

2. The horizontal components of the ground reaction forces perpendicular to locomotion (F_y in Fig. 2O), which induce lateral undulation in sprawling tetrapods, are completely nullified when the limbs are moved in a parasagittal plane (Christian 1995; McElroy et al. 2014). By changing from horizontal (in reptiles and early tetrapods) to vertical movements using the inverted pendulum mechanics (stilt-like extremities of mammals), energy is saved and a possibility to utilize elastic rebounding is offered (Christian 1995; Witte et al. 1995, 2002) (Fig. 2P, Q).

3. For a digitigrade limb posture, an additional limb segment is formed by the tarsus and metapodium. This additional limb segment elongates the free limb and therefore step length (e.g., Witte et al. 2002; Ren et al. 2008).

4. During sprawling locomotion of synapsids, humeral long axis rotation may be limited, based on the oval humeral head surface observable in limbs (*Dimetrodon limbatus*, *Stahleckeria potens*, *Sauroctonus parringtoni*, *Tetragonias njalilus*, *Belesodon magnificus*). The digits are continuously pointing forward and the forearms are crossed during the entire limb cycle. This leads in many forms to a division of labor in which the ulna is loaded more in the proximal and the radius more in the distal part. In parasagittal locomotion, the manus is placed forward and extension and flexion of the elbow and knee joint increase the stride length (Romer and Frick 1966; Nickel et al. 1968).

5. A swinging scapula and an accordingly restructured thorax add to stride length by basically adding another additional limb segment to the leg (Fischer 1994a, b).

Therapsid heads have been rather large and presumably heavy. Lateral movements of the heavy head require a broad support from the forelimbs, especially when performed rapidly. Hindlimbs are not subject to this condition, especially, if the tail is never exposed to statical loading or lateral accelerations. A reason for a more parasagittal posture of the hindlimb in therapsids earlier in evolution than in the forelimbs may be that the reduced, lighter, and/or shortened tail did not constrain the hindlimb to a sprawling position earlier in locomotion than the forelimb was subjected to.

Table 1. *Belesodon magnificus* (GPIT-PV-31575) rib measurements. Abbreviations: n. m., not measurable.

	Measurement 1 (cm)	Measurement 2 (cm)	Measurement 3 (cm) (anteroposterior)	Measurement 4 (cm) (lateral-medial)	Measurement 5 (cm) (anteroposterior)	Measurement 6 (cm) (lateral-medial)	Measurement 7 (cm)	Measurement 8 (cm)	Measurement 9 (cm)	Measurement 10 (cm)
rib 9 (left)	n.m.	n.m.	0.6	1.0	0.3	1.1	2.6	1.7	1.5	n.m.
rib 11 (left and right)	n.m.	n.m.	0.6 and 0.6	1.0 and 1.1	0.4 and 0.5	1.0 and 1.0	Broken and 3.7	1.6 and 2.7	Broken and 2.1	n.m.
rib 16 (left)	n.m.	n.m.	0.7	1.1	0.7	1.0	2.3	1.6	1.8	n.m.
rib 19 (left)	n.m.	n.m.	0.5	0.8			2.3	1.4	1.8	n.m.

Table 2. *Dimetrodon limbatus* (GPIT-PV31373) rib measurements. Right side, left side is inaccessible.

	Measurement 1 (cm)	Measurement 2 (cm)	Measurement 3 (cm) (anteroposterior)	Measurement 4 (cm) (lateral-medial)	Measurement 5 (cm) (anteroposterior)	Measurement 6 (cm) (lateral-medial)	Measurement 7 (cm)	Measurement 8 (cm)	Measurement 9 (cm)	Measurement 10 (cm)
rib 1	n.m.	n.m.	0.6	1.1	0.5	0.6	1.9	1.7	1.0	0.3
rib 2	n.m.	n.m.	0.7	1.2	n.m.	n.m.	n.m.	2.1	n.m.	n.m.
rib 3	n.m.	n.m.	0.9	1.1	0.7	0.8	n.m.	n.m.	n.m.	n.m.
rib 8	n.m.	n.m.	1.2	1.8	0.8	0.7	n.m.	n.m.	n.m.	n.m.
rib 9	n.m.	n.m.	1.2	1.8	0.9	0.7	n.m.	n.m.	n.m.	n.m.
rib 12	n.m.	n.m.	n.m.	n.m.	0.8	0.9	3.5	2.5	2.8	2.3
rib 13	n.m.	n.m.	0.9	0.8	0.9	0.8	2.9	3.3	2.8	2.2
rib 16	n.m.	n.m.	0.8	1.3	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.

Table 3. *Dimetrodon limbatus* (GPIT-PV31373) vertebrae measurements (vertebrae measured until approximately half the tail length was reached).

	centrum width (cm)	centrum height (cm)	centrum length (cm)
second last presacral	3.6	3.0	3.8
last presacral	3.5	3.2	3.7
1. sacral	3.5	3.2	2.8
2. sacral	3.2	3.2	2.9
3. sacral	2.6	2.5	2.8
1. caudal	3.0	2.5	3.0
2. caudal	2.4	2.7	3.0
3. caudal	2.7	3.0	2.5
4. caudal	2.6	2.7	2.6
5. caudal	2.8	2.4	2.6
6. caudal	2.7	2.7	2.4
7. caudal	2.5	2.7	2.6
8. caudal	2.7	3.0	2.2
9. caudal	2.1	1.8	2.4
10. caudal	2.0	1.8	2.0
11. caudal	1.6	1.6	2.1
12. caudal	1.6	1.4	1.8
13. caudal	1.4	1.3	1.8
14. caudal	1.4	1.4	1.8

Table 4. *Hyperodapedon sanjuanensis* (GPIT-PV-31578) rib measurements. Ribs 22 and 23 on the left and rib 15 on the right side are not measurable because too incompletely preserved. Abbreviations: n.m., not measurable due to incomplete preservation or deformation.

	Measurement 1 (cm)	Measurement 2 (cm)	Measurement 3 (cm) (anteroposterior)	Measurement 4 (cm) (lateral–medial)	Measurement 5 (cm) (anteroposterior)	Measurement 6 (cm) (lateral–medial)	Measurement 7 (cm)	Measurement 8 (cm)	Measurement 9 (cm)	Measurement 10 (cm)
rib 1 (left)	n.m.	5.5	0.4	1.2	0.4	0.9	2.0	n.m.	n.m.	n.m.
rib 2 (right)	n.m.	5.5	0.5	0.6	0.4	0.5	2.0	1.5	1.6	0.9
rib 3 (right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	2.4	2.1	1.2	1.0
rib 4 (left)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	3.1	2.5	1.6	1.1
rib 7 (right)	15.0	15.5	0.5	1.3	0.5	1.0	3.2	2.5	3.4	0.4
rib 9 (right)	20.0	16.0	0.8	1.6	0.7	1.3	3.2	2.9	2.4	0.5
rib 10 (right)	20.6	17.0	0.7	1.1	0.8	1.1	2.9	2.4	1.7	n.m.
rib 11 (right)	20.9	16.0	1.0	1.5	1.0	1.0	n.m.	n.m.	n.m.	n.m.
rib 12 (left)	17.0	16.6	0.6	1.2	0.7	1.2	2.9	n.m.	n.m.	n.m.
rib 13 (right)	20.7	18.3	0.8	0.9	0.6	1.3	n.m.	n.m.	n.m.	n.m.
rib 14 (left)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.
rib 18 (right)	21.5	20.4	0.7	0.8	0.5	0.9	n.m.	n.m.	n.m.	n.m.
rib 19 (right)	17.7	15.8	0.5	0.8	0.5	1.1	n.m.	n.m.	n.m.	n.m.
rib 20 (left)	23.0	16.4	0.6	0.8	0.4	0.8	n.m.	n.m.	n.m.	n.m.

Table 5. *Hyperodapedon sanjuanensis* (GPIT-PV-31578) vertebrae measurements (vertebrae measured until approximately half the tail length was reached).

	centrum width (cm)	centrum height (cm)	centrum length (cm)
second last presacral	3.0	2.4	3.3
last presacral	2.5	2.8	2.5
1. sacral	2.8	2.3	3.5
2. sacral	2.9	2.5	3.4
1. caudal	2.0	2.4	2.6
2. caudal	2.3	2.3	2.4
3. caudal	2.0	2.2	2.3
4. caudal	1.8	2.4	2.1
5. caudal	2.0	2.2	2.0
6. caudal	1.5	2.0	1.8
7. caudal	1.2	1.8	1.8
8. caudal	1.0	1.6	2.0
9. caudal	1.1	2.0	1.7

Table 6. *Keratocephalus moloch* (GPIT-PV-31461) rib measurements. Abbreviations: n.m., not measureable.

	Measurement 1 (cm)	Measurement 2 (cm)	Measurement 3 (cm) (anteroposterior)	Measurement 4 (cm) (lateral–medial)	Measurement 5 (cm) (anteroposterior)	Measurement 6 (cm) (lateral–medial)	Measurement 7 (cm)	Measurement 8 (cm)	Measurement 9 (cm)	Measurement 10 (cm)
rib 12 (left and right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	13 and 16	7 and 7	12 and 13	n.m.
rib 13 (left and right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	15 and 15	6 and 7	12 and 13	n.m.
rib 14 (right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	15	7	12	n.m.
rib 15 (right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	13	5.5	12	n.m.

Table 7. *Keratocephalus moloch* (GPIT-PV-31461) vertebrae measurements (vertebrae measured until approximately half the tail length was reached).

	centrum width (cm)	centrum height (cm)	centrum length (cm)
second last presacral	9.0	7.2	4.5
last presacral	10.0	8.7	4.6
1. sacral	10.0	10.2	5.5
2. sacral	7.5	11.5	5.5
3. sacral	8.3	9.3	6.0
1. caudal	8.5	8.8	5.5

Table 8. *Sauroctonus parringtoni* (GPIT-PV-31579) rib measurements. All measured ribs are from the left side. Abbreviations: n.m., not measureable.

	Measurement 1 (mm)	Measurement 2 (mm)	Measurement 3 (mm) (anteroposterior)	Measurement 4 (mm) (lateral-medial)	Measurement 5 (mm) (anteroposterior)	Measurement 6 (mm) (lateral-medial)	Measurement 7 (mm)	Measurement 8 (mm)	Measurement 9 (mm)	Measurement 10 (mm)
rib 1	65 cm	65	6.82	9.75	5.8	7.61	21.27	14.8	11.4	3.1
rib 2	85	85	6.9	7.68	5.3	6.15	24.85	12.96	17.87	3.55
rib 3	115	110	7.07	8.67	7.2	7.38	23,2	15.28	11.54	3.34
rib 4	135	130	5.8	8.4	4.66	7.5	27.2	13.7	22.1	3.18
rib 5	150	135	7.32	11	7.3	8.45	32.12	13,5	18.3	3.55
rib 6	140	130	5.33	9	4.45	6.87	n.m.	n.m.	n.m.	n.m.
rib 7	155	135	6.3	9.6	7.36	7.76	n.m.	n.m.	n.m.	3
rib 8	180	135	6.84	7	5.75	7.09	21.7	14.3	17.34	2.8
rib 9	170	145	5.67	8.81	5,97	7.48	n.m.	n.m.	n.m.	n.m.
rib 10	190	165	4.22	10.4	5.42	5.5	n.m.	n.m.	n.m.	n.m.
rib 11	210	185	6.2	7.58	6.25	6.35	21.89	16.22	16.2	
rib 12	190	170	7.12	7.52	6.82	6.41	33.41	14.56	26	3.5
rib 13	180	145	5.87	8.54	6.01	7.61	34	17.5	25	1.2
rib 14	175	140	7.47	7.95	6.91	6.14	36.02	15.61	25.11	2.9
rib 15	170	135	9.42	7.64	7.63	4.55	32.53	14.34	25.11	4.3
rib 16	160	130	5.69	6.68	4.94	7.1	28.6	13.73	22.9	3.43
rib 17	130	110	8.33	9.12	6.43	8.48	n.m.	12.7	n.m.	4
rib 18	110	100	5.43	8.56	5.69	6.26	29.8	12.23	28.05	6
rib 19	100	80	5.73	7.2	4.42	4.75	20.4	13.43	19.7	1.85
rib 20	85	65	5.68	9.84	5.21	7.55	19.92	11	14.3	1
rib 21	90	70	5.86	8.25	5.62	9.11	18.2	10.2	17.4	1

Table 9. *Sauroctonus parringtoni* (GPIT-PV-31579) vertebrae measurements (if possible, vertebrae measured until approximately half the tail length was reached).

	centrum width(cm)	centrum height(cm)	centrum length (cm)
second last presacral	20.4	19	25
last presacral	18.7	18	15
1. sacral	36	20	18
2. sacral	23.7	18	19
3. sacral	21.4	16	17
1. caudal	25,4	22	22
2. caudal	23.3	12	19
3. caudal	24.2	14	22
4. caudal	22	12	14
5. caudal	16.2	14	14
6. caudal	19.20	12	10
7. caudal	18.2	14	16

Table 10. *Stahleckeria potens* (GPIT-PV-30792) rib measurements. Abbreviations: n.m., not measureable.

	Measurement 1 (cm)	Measurement 2 (cm)	Measurement 3 (cm) (anteroposterior)	Measurement 4 (cm) (lateral-medial)	Measurement 5 (cm) (anteroposterior)	Measurement 6 (cm) (lateral-medial)	Measurement 7 (cm)	Measurement 8 (cm)	Measurement 9 (cm)	Measurement 10 (cm)
rib 8 (left complete)	55	47.5	2.7	2.6	1.8	2.4	13.6	10.9	5.6	1.3
rib 9 (left)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.-	14.0	10.7	6.6	1.4
rib 12 (right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	10.6	7.6	7.0	n. m.
rib 14 (left)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	8.1	4.8	5.4	n. m.
rib 15 (left and right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	6.5 and 6.6	3.9 and 4.8	5.1 and 5.2	n. m. and 0.3
rib 16 (left and right complete)	110.5	76.5	3.8	4.5	3.7	4.4	7.5 and 7.2	4.7 and 4.3	4.4 and 4.6	n. m. and 0.2
rib 17 (right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	6.2	4.2	3.7	n. m.
rib 18 (right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	6.7	4.5	5.3	n. m.
rib 19 (right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	5.8	4.1	3.6	n. m.
rib 20 (left and right)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	6.1 and 6.2	4.0 and 4.2	3.7 and 4.6	n. m.
rib 23 (left)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	8.7	5.1	3.9	n. m.
rib 24 (left)	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	8.5	6.0	4.5	n. m.

Table 11. *Stahleckeria potens* (GPIT-PV-30792) vertebrae measurements (vertebrae measured until approximately half the tail length was reached). Abbreviations: /, not measurable because fused; —, not measurable because not preserved; n.m., not measurable.

	centrum width(cm)	centrum height(cm)	centrum length (cm)
second last presacral	—	—	-
last presacral	9.2	8.9	5.4
1. sacral	9.4	11.6	42.4
2. sacral	n.m.	n.m.	n.m.
3. sacral	n.m.	n.m.	n.m.
4. sacral	n.m.	n.m.	n.m.
5. sacral	n.m.	n.m.	n.m.
6. sacral	n.m.	n.m.	n.m.
7. sacral	n.m.	n.m.	n.m.
8. sacral	6.2	5.6	n.m.
1. caudal	n.m.	n.m.	n.m.
2. caudal	7.5	8.6	4.0
3. caudal	8.4	8.0	4.1
4. caudal	7.8	6.5	4.5
5. caudal	7.0	6.4	4.8
6. caudal	7.1	8.2	4.2
7. caudal	7.3	4	3.4

Table 12. Segments of body stem. The remains of the vertebral columns of *Stahleckeria potens*, *Belesodon magnificus*, *Keratocephalus moloch*, and *Tetragonias njalilus* are too fragmentary to determine the number of vertebrae, their regionalization, and which are rib-bearing or carrying wide transverse processes.

Taxon	no. of cervical vertebrae	no. of dorsal vertebrae	no. of sacral vertebrae	no. of caudal vertebrae	cervical vertebrae with ribs	dorsal vertebrae without ribs	tail vertebrae with transverse processes	citation
Sauroctonus parringtoni (GPIT-PV-31579)	7	21	3	33–34	2	0	7	Gebauer 2007; 2014
Hyperodapedon sanjuanensis (GPIT-PV-31578)	6	19	2	35–40	6	0	Impossible to determine	von Huene (1939–42)
Dimetrodon limbatus (GPIT-PV-31373)	unknown	27 presacrals (Case 1910)	3 (Romer 1927)	> 20 in e.g. the specimen described by Romer (1927) (observed in the GPIT specimen)	all	0	Impossible to determine	

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References

Angielczyk KD (2004) Phylogenetic evidence for and implications of a dual origin of propaliny in anomodont therapsids (Synapsida). Paleobiology 30: 268–296. https://doi.org/10.1666/0094-8373(2004)030<0268:PEFAIO>2.0.CO;2

Ankel F (1962) Vergleichende Untersuchungen über die Skelettmorphologie des Greifschwanzes südamerikanischer Affen (Platyrrhina). Zeitschrift für Morphologie und Ökologie der Tiere 52: 131–170.

Ashley-Ross MA (1995) Patterns of hind limb motor output during walking in the salamander *Dicamptodon tenebrosus* with comparisons to other tetrapods. Journal of Comparative Physiology A 177: 273–285. https://doi.org/10.1007/BF00192417

Baier DB, Gatesy SM (2013) Three-dimensional skeletal kinematics of the shoulder girdle and forelimb in walking *Alligator*. Journal of Anatomy 223(5): 462–473. https://doi.org/10.1111/joa.12102

Bakker RT (1971) Dinosaur physiology and the origins of mammals. Evolution 25(4): 636–658. https://doi.org/10.2307/2406945

Blob RW (2001) Evolution of the hindlimb in nonmammalian therapsids: biomechanical test of paleontological hypothesis. Paleobiology 27(1): 14–38. https://doi.org/10.1666/0094-8373(2001)0272.0.CO;2

Bonnan MF, Schulman J, Varadharajan R, Gilbert C, Wilkes M, Horner A, and Brainerd EL (2016) Forelimb kinematics of rats using XROMM, with implications for small eutherians and their fossil relatives. PLoS ONE 11:e0149377. https://doi.org/10.1371/journal.pone.0149377

Brocklehurst RL, Fahn-Lai P, Regnault S, Pierce SE (2022) Musculoskeletal modelling of sprawling and parasagittal forelimbs provides insight into synapsid postural transition. iScience 25(1): 1–21. https://doi.org/10.1016/j.isci.2021.103578

Buchholtz EA, Yozygur ZM, Feldman A, Weaver AA, Gaudin TJ (2021) The therian sternum at the lateral somitic frontier: Evolution of a composite structure. Journal of Zoology 315(1): 19–28. https://doi.org/10.1111/jzo.12809

Case EC (1910) Description of a skeleton of *Dimetrodon incisivus* Cope. Bulletin of the American Museum of Natural History 28: 189–196.

Christian F (1995) Zur Biomechanik der Lokomotion vierfüßiger Reptilien (besonders der Squamata). Courier Forschungsinstitut Senckenberg, Band 180, Naturforschende Gesellschaft. Frankfurt, 58 pp.

Christian A, Garland J (1996) Scaling of limb proportions in monitor lizards (Squamata, Varanidae). Journal of Herpetology 30: 219–230. https://doi.org/10.2307/1565513

Clemente CJ, Withers PC, Thompson G, Lloyd DG (2011) Evolution of limb bone loading and body size in varanid lizards. Journal of Experimental Biology 2011: 3013–3020.

Cruickshank ARI (1967) A new dicynodont genus from the Manda Formation of Tanzania (Tanganyika). Journal of Zoology, 153: 163–208. https://doi.org/10.1111/J.1469-7998.1967.TB04059.X

Denoth J, Gruber K, Ruder H, Keppler M (1985) Forces and torques during sports activities with high accelerations. In: Perren SM, Schneider E (Eds) Biomechanics: Current Interdisciplinary Research, International Series on Biomechanics. Martinus Nijhoff, Amsterdam, 663–668.

English AWM (1977) Structural correlates of forelimb function in fur seals and sea lions. Journal of Morphology 151: 325–352. https://doi.org/10.1002/jmor.1051510303

Farke AA, Wolff EDS, Tanke DH (2009) Evidence of combat in *Triceratops*. PLoS ONE 4(1): e4252. https://doi.org/10.1371/journal.pone.0004252

Fujiwara S (2009) A reevaluation of the manus structure in *Triceratops* (Ceratopsia: Ceratopsidae). Journal of Vertebrate Paleontology 29: 1136–1147.

Fujiwara S, Hutchinson JR (2012) Elbow joint aductor moment arm as an indicator of forelimb posture in extinct quadrupedal tetrapods. Proceedings of the Royal Society of London, Series B 279: 2561–2570.

Fischer M (1994a) Die Lokomotion von *Procavia capensis* (Mammalia, Hyracoidea). Habilitationsschrift Fakultät Biologie, Universität Tübingen.

Fischer M (1994b) Crouched posture and high fulcrum, a principle in the locomotion of small mammals: The example of the rock hyrax (*Procavia capensis*) (Mammalia, Hyracoidea). Journal of Human Evolution 26: 501–524. https://doi.org/10.1006/JHEV.1994.1030

Fischer M, Lilje KE (2011) Hunde in Bewegung. Franckh Kosmos Verlags G.m.b.H. , Stuttgart.

Fröbisch J (2006) Locomotion in derived dicynodonts (Synapsida, Anomodontia): a functional analysis of the pelvic girdle and hind limb of *Tetragonias njalilus*. Canadian Journal of Earth Science 43: 1297–1308. https://doi.org/10.1139/e06-031

Fröbisch J, Reisz RR (2011) The postcranial anatomy of *Suminia getmanovi* (Synapsida: Anomodontia), the earliest known arboreal tetrapod. Zoological Journal of the Linnean Society 162: 661–698. https://doi.org/10.1111/j.1096-3642.2010.00685.x

Fujiwara S-I, Kuwazuru O, Inuzuka N, Yoshikawa N (2009) Relationship between scapula position and structural strength of rib cage in quadrupedal animals. Journal of Morphology, 270: 1084–1094. https://doi.org/10.1002/jmor.10744

Gatesy SM (1990) Caudofemoral musculature and the evolution of theropod locomotion. Paleobiology 16(2): 170–186. https://doi.org/10.1017/S0094837300009866

Gatesy SM (1997) An electromyographic analysis of hindlimb function in *Alligator* during terrestrial locomotion. Journal of Morphology 234(2): 197–212. https://doi.org/10.1002/(SICI)1097-4687(199-711)234:2<197::AID-JMOR6>3.0.CO;2-9

Gebauer E (2007) Phylogeny and Evolution of the Gorgonopsia with a special reference to the skull and skeleton of GPIT/Re/7113 ("*Ailurognathus?*" *parringtoni*). PhD Thesis. Geowissenschaftliche Fakultät, University of Tübingen, Tübingen.

Gebauer E (2014) Re-assessment of the taxonomic position of the specimen GPIT/RE/7113 (*Sauroctonus parringtoni* comb. nov., Gorgonopsia). In: Kammerer C, Angielczyk KD, Fröbisch J (Eds) Early Evolutionary History of the Synapsida. Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-6841-3_12

Gregory WK (1926) The skeleton of *Moschops capensis* Broom, a dinocephalian reptile from the Permian of South Africa. Bulletin of the American Museum of Natural History 56: 179–251. http://hdl.handle.net/2246/1323

Hohn B (2011) Walking with the shoulder of giants: Biomechanical conditions in the tetrapod shoulder girdle as basis for sauropod shoulder reconstruction. In: Klein N, Remes K, Gee CT, and Sander M (eds.) Biology of the Sauropod dinosaurs. Indiana University Press.

Hohn-Schulte B, Preuschoft H, Witzel U, Distler-Hoffmann C (2013) Biomechanics and functional preconditions for terrestrial lifestyle in basal tetrapods, with spevial consideration of *Tiktaalik roseae*. Historical Biology 25: 167–181.

Hotton N (1991) The nature and diversity of synapsids: prologue to the origin of mammals. In: Schultze H-P, Trueb L (Eds) Origins of the Higher Groups of Tetrapods. Cornell University Press, Ithaca, N.Y. 598–634.

Huene F von (1931) Beitrag zur Kenntnis der Fauna der Südafrikanischen Karooformation. Geologische und Paläontologische Abhandlungen 18: 159–227.

Huene F von (1942) Die Anomodontier des Ruhuhu-Gebietes in der Tübinger Sammlung. Palaeontographica Abteilung A 94: 154–184.

Huene F von (1935–42) Die fossilen Reptilien des Südamerikanischen Gondwanalandes – Ergebnisse der Sauriergrabungen in Südbrasilien 1928/29. C.H. Beck'sche Verlagsbuchhandlung, Munich, 375pp.

Jenkins FA Jr. (1971) Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. Journal of Zoology 165: 303–315. https://doi.org/10.1111/j.1469-7998.1971.tb02189.x

Jenkins FA Jr (1974) The movement of the shoulder in claviculate and aclaviculate mammals. Journal of Morphology 144: 71–84. https://doi.org/10.1002/jmor.1051440105

Jenkins FA Jr, Goslow GE Jr (1983) The functional anatomy of the shoulder of the savannah monitor lizard (*Varanus exemanthicus*). Journal of Morphology 175: 195–216. https://doi.org/10.1002/jmor.1051750207

Jones KE, Dickson BV, Angielczyk KD, Pierce SE (2021) Adaptive landscapes challenge the "lateral-to-sagittal" paradigm for mammalian vertebral evolution. Current Biology 31(9): 1883–1892. https://doi.org/10.1016/j.cub.2021.02.009

Kemp TS (1978) Stance and gait in the hindlimb of a therocephalian mammal-like reptile. Journal of Zoology 186: 143–161. https://doi.org/10.1111/j.1469-7998.1978.tb03362.x

Kemp TS (1980) Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. Journal of Zoology 191: 193–239. https://doi.org/10.1111/j.1469-7998.1980.tb01456.x

Kemp TS (1982) Mammal-Like Reptiles and the Origin of Mammals. Academic Press, London UK.

Kielan-Jawaroska Z, Gambaryan PP (1994) Postcranial anatomy and habits of asian multituberculate mammals. Fossils and Strata Monograph Series 36: 1–92.

King GM (1981) The functional anatomy of a Permian dicynodont. Philosophical Transactions of the Royal Society of London, Series B, 291: 243–322. https://doi.org/10.1098/rstb.1981.0001

King GM (1985) The postcranial skeleton of *Kingoria nowacki* (von Huene) (Therapsida: Dicynodontia). Zoological Journal of the Linnean Society 84: 263–298. https://doi.org/10.1111/j.1096-3642.1985.tb01801.x

Klima M (1987) Early development of the shoulder girdle and sternum in marsupials (Mammalia, Metatheria). Advances in Anatomy, Embryology and Cell Biology, Vol. 109, Springer, Berlin.

Kuschel T (1994) Vergleichende Funktionell-morphologische Untersuchungen der Vorderextremitäten von Ohren- und Hundsrobben (Otariidae und Phocidae). Diplom-Arbeit Fakultät für Biologie, RUB, Bochum, Germany.

Lai PH, Biewener AA, and Pierce SE (2018) Three-dimensional mobility and muscle attachments in the pectoral limb of the Triassic cynodont *Massetognathus pascuali* (Romer, 1967). Journal of Anatomy 232: 383–406.

Loitsch C (1993) Kinematische Untersuchungen über den Galopp von Pferden (*Equus caballus*). Doctoral Thesis, Fakultät für Biologie, RUB, Bochum, Germany.

Mayerl CJ, Brainerd EL, Blob RW (2016) Pelvic girdle mobility of cryptodire and pleurodire turtles during walking and swimming. Journal of Experimental Biology 219(17): 2650–2658. https://doi.org/10.1242/jeb.141622

McElroy EJ, Wilson R, Biknevicius AR, Reilly SM (2014) A comparative study of single-leg ground reaction forces in running lizards. Journal of Experimental Biology 217: 735–742. https://doi.org10/1242/jeb.095620

Mickoleit G (2005) Phylogenetische Systematik der Wirbeltiere. Verlag Dr. Pfeil, München, Germany.

Nickel R, Schummer A, Seiferle E (1968) Anatomie der Haustiere Bd. I: Bewegungsapparat. Verlag Parey, Berlin.

Norman JR, Frazer FC (1963) Riesenfische, Wale und Delphine. Verlag Parey, Berlin.

Nyakatura J, Andrada E, Curth S, Fischer MS (2013) Bridging "Romer's gap": Limb mechanics of an extant belly-dragging lizard inform debate on tetrapod locomotion during the Early Carboniferous. Evolutionary Biology 41: 175–190. https://doi.org/10.10007/sll692-013-9266-z

Otero A, Gallina PA, Herrera Y (2010) Pelvic musculature and function of *Caiman latirostris*. Herpetological Journal 20: 173–184. https://www.ingentaconnect.com/contentone/bhs/thj/2010/00000020/00000003/art00008#expand/collapse

Pauwels F (1965) Gesammelte Abhandlungen zur funktionellen Anatomie des Bewegungsapparates. Springer, Berlin.

Pauwels F (1980) Biomechanics of the locomotor apparatus. Completely revised and enlarged, including seven new chapters. Springer, Berlin.

Perry S (2010) Atmungsorgane. In: Westheide & Rieger, Spezielle Zoologie, Wirbel- oder Schädeltiere. Spectrum, Heidelberg, 127–141.

Peters A, Preuschoft H (1984) External biomechanics of leaping in *Tarsius* and its morphological and kinematic consequences. In: Niemitz C (Ed.) Biology of Tarsiers. Fischer-Verlag, Stuttgart, New York 227–255.

Preuschoft H (1976) Funktionelle Anpassung evoluierender Systeme. Aufsätze und Reden der Senckenbergischen Naturforschenden Gesellschaft. Waldemar Kramer-Verlag, Frankfurt, 98–117.

Preuschoft H (2022) Understanding Body Shapes in Animals. Springer, Berlin.

Preuschoft H, Fritz M (1977) Mechanischen Beanspruchungen im Bewegungsapparat von Springpferden. In: Nachtigall W (Ed.) Physiology of Movement – Biomechanics; Bewegungsphysiologie-Biomechanik. Fortschritte der Zoologie 24: 75–98, Fischer-Verlag, Stuttgart.

Preuschoft H, Demes B (1984) Biomechanics of brachiation. In: Preuschoft H, Chivers DJ, Brockelmann W, Creel N (Eds.), The Lesser Apes. Edinburgh Univ. Press., Edinburgh, 96–118.

Preuschoft H, Gudo M (2006) Die Schultergürtel von Wirbeltieren. Biomechanische Überlegungen zu den Bauprinzipien des Wirbeltierkörpers und zur Fortbewegung der Tetrapoden. Zentralblatt für Geologie und Paläontologie, Teil II, 339–361, Schweizerbart, Stuttgart.

Preuschoft H, Reif W, Loitsch C, Tepe E (1991) The function of labyrinthodont teeth: Big teeth in shallow jaws. In: Schmitt-Kittler N, Vogel K (Eds.), Constructional Morphology and Evolution. 151–171, Springer-Verlag, Berlin/Heidelberg.

Preuschoft H, Schmidt M, Hayama S, Okada M (2003) The influence of three-dimensional movements of the forelimbs on the shape of the thorax and ist importance on erect body posture. In: Franzen JL (Ed.), Walking Upright. Courier Forschungs-Institut Senckenberg 243: 9–24.

Preuschoft H, Distler C, Witzel U, Sick H (2005) Ribs and rib cages in terrestrial vertebrates. Their mechanical function and stressing, analysed with the aid of FESA. Journal of Vertebrate Paleontology 25(3)A: 101.

Preuschoft H, Witzel U, Hohn B, Schulte D, Distler C (2007) Biomechanics of locomotion and body structure in varanids with spezial emphasis on the forelimbs. In: Horn HG, Boehme, Krebs WU (Eds.), Advances in Monitor Research III, Mertensiella: 59–78, Chimaera-Buchhandelsgesellschaft, Frankfurt a. M.

Ray S (2006) Functional and evolutionary aspects of the postcranial anatomy of dicynodonts (Synapsida, Therapsida). Palaeontology 49(6): 1263–1286. https://doi.org/10.1111/j.1475-4983.2006.00597.x

Reilly SM, Delancey MJ (1997) Sprawling locomotion in the lizard *Sceloporus clarkia*: the effects of speed on gait, hindlimb kinematics, and axial bending during walking. Journal of Zoology 243: 417–433. https://doi.org/10.1111/J.1469-7998.1997.TB02791.X

Reilly SM, Elias JA (1998) Locomotion in *Alligator mississippiensis*: kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. Journal of Experimental Biology 201: 2559–2574. https://doi.org/10.1242/jeb.201.18.2559

Ren L, Butler M, Miller C, Paxton H, Schwerda D, Fischer MS, Hutchinson JR (2008) The movements of limb segments and joints during locomotion in African and Asian elephants. The Journal of Experimental Biology 211: 2735–2751. https://doi.org/10.1242/jeb.018820

Romer AS (1923) Crocodilian pelvic muscles and their avian and reptilian homologues. Bulletin of the American Museum of Natural History 48: 533–552. https://hdl.handle.net/2246/1307

Romer AS (1927) Notes of the Permo-Carboniferous reptile *Dimetrodon*. Journal of Geology 35(8): 673–689. https://doi.org/10.1086/623462

Romer AS, Frick H (1966) Vergleichende Anatomie der Wirbeltiere. Parey, Berlin.

Russell AP, Bauer AM (2008) The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. In: Gans C, Parsons TS (Eds) Biology of the Reptilia, volume 21. Academic Press, New York, 465 pp.

Schmidt M (2001) Zur Evolution der Fortbewegung der Primaten. Doctoral thesis, Biologisch-Pharmazeutische Fakultät der Universität Jena.

Schmidt M, Fischer M (2002) Cineradiographic study of forelimb movements during quadrupedal walking in the brown lemur (*Eulemur fulvus*, Primates, Lemuridae). American Journal of Physical Anthropology 111: 245–262. https://doi.org/10.1002/(SICI)1096-8644(200002)111:2<245::AID-AJPA9>3.0.CO;2-3

Schmidt M, Voges D, Fischer M (2002) Shoulder movement during quadrupedal locomotion in arboreal primates. Zeitschrift für Morphologie und Anthropologie 83: 235–242. https://doi.org/10.1127/zma/83/2002/235

Schmidt M, Mehlhorn M, Fischer MS (2016) Shoulder girdle rotation, forelimb movement and the influence of carapace shape on locomotion in *Testudo hermanni* (Testudinidae). Journal of Experimental Biology 219(17): 2693–2703. https://doi.org/10.1242/jeb.137059

Snyder RC (1954) The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. The American Journal of Anatomy 95(1): 1–45. https://doi.org/10.1002/aja.1000950102

Suzuki D, Chiba K, Tanaka Y, Hayashi S (2011) Myology of crocodiles III: pelvic girdle and hindlimb. Fossils (The Palaeontological Society of Japan) 90: 37–60.

Walker WF (1971) A structural and functional analysis of walking in the turtle, *Chrysemys picta marginata*. Journal of Morphology 134(2): 195–214. https://doi.org/10.1002/jmor.1051340205

Walter LR (1986) The limb posture of kannemeyeriid dicynodonts: functional and ecological considerations. In: Padian K (Ed) The Beginning of the Age of Dinosaurs. Cambridge University Press, Cambridge, UK, 89–97.

Werneburg I, Böhme M (2018).The paleontological collection Tübingen. In: Beck L.A., Joger U. (ed.) Paleontological Collections of Germany, Austria, and Switzerland. Springer, Berlin, S. 505–512.

Witte H, Preuschoft H, Recknagel S (1991) Human body proportions on the basis of biomechanical principles. Zeitschrift für Morphologie und Anthropologie 78: 407–423. https://doi.org/10.1127/zma/78/1991/407

Witte H, Lesch C, Preuschoft H, Loitsch C (1995) Die Gangarten der Pferde. Sind Schwingungsmechanismen entscheidend? Federschwingungen bestimmen den Trab und den Galopp. Pferdeheilkunde 11(4): 265–272.

Witte H (1996) Beiträge zur Funktionellen Anatomie und Biomechanik elastischer Elemente im Bewegungsapparat. Habilitationsschrift Medizinische Fakultät der RUB, Bochum.

Witte H, Preuschoft H, Fischer M (2002) The importance of the evolutionary heritage of locomotion on flat ground in small mammals for the development of arboreality. In: Okada M, Preuschoft H (Eds.) Arboreal Locomotor Adaptation in Primates and its Relevance to Human Evolution. Zeitschrift für Morphologie und Anthropologie 83(2/3): 221–233. https://doi.org/10.1127/zma/83/2002/221

Appendix 1

The material we examined includes the skeletons of the archosaur *Hyperodapedon sanjuanensis* (GPIT-PV-31578) (Figs 1, 9), the early synapsid pelycosaur-grade *Dimetrodon limbatus* (GPIT-PV-31373) (Figs 1, 6), and the therapsids *Sauroctonus parringtoni* (GPIT-PV-31579) (Figs 1, 7), *Stahleckeria potens* (GPIT-PV-30792) (Figs 1, 8)*, Keratocephalus moloch* (GPIT-PV-31461) (Figs 1, 7), *Belesodon magnificus* (GPIT-PV-31575) (Figs 1, 6), and *Tetragonias njalilus* (GPIT-PV-31574) (Figs 1, 9), all displayed at the Paleontological Collection, Eberhard Karls Universität Tübingen (GPIT), Tübingen, Germany. Most of these specimens were collected in digging campaigns by Friedrich von Huene (1875–1969) in various parts of the world over time. So, *Sauroctonus parringtoni* and *Tetragonias njalilus* are from the Upper Permian of the Ruhuhu region in Tanzania. *Stahleckeria potens*, *Belesodon magnificus*, and *Hyperodapedon sanjuanensis* are from the Middle Triassic of Rio Grande do Sul, Brazil. *Keratocephalus moloch* is from the Middle Permian of the Karoo, RSA. *Dimetrodon limbatus* is from the Lower Permian of Texas, USA, and was bought by Sternberg.

1. *Hyperodapedon sanjuanensis* (Rhynchosauria, Archosauromorpha, GPIT-PV-31578) (Fig. 9) has been found in Sao José, close to Santa Maria, Brazil, and is from the Santa-Maria-Formation, Middle to Upper Triassic. Von Huene (1935–1942) suggested that the vertebral column consists of six cervical, 25 presacral, and two sacral vertebrae. The vertebrae are amphicoelous. During the excavation, three specimens of *Hyperodapedon sanjuanensis* were recovered. Based on all three, von Huene (1935–42) estimated that *Hyperodapedon* has a total of about 35–40 caudal vertebrae. This is based on two relatively complete specimens (specimens "19,2" and "23") that had three and eight caudals preserved (Table 5). The third specimen (from excavation 46) had 32 articulated caudal vertebrae of which presumably the first two and some of the last vertebrae are missing. The identification of the cervicals is not unequivocal. The first eight vertebrae have a different shape than the following, but the sixth vertebra is the first one with ribs and the seventh vertebra articulates with a double-headed rib. This way, von Huene (1935–1942) defined that the first six are cervicals and that the seventh vertebra is the first dorsal or a transitional vertebra. *Hyperodapedon* had tail ribs and haemapophyses. The mounted skeleton is a composit skeleton based on specimen "19,2" and amended by the other specimens. Specimen "19,2" had ribs 7–10, 12, 16, and 20 preserved. In the mounted composit skeleton, the vertebrae 1–24, two sacrals, and nine caudal vertebrae are mounted. Further, on the right side, ribs 2, 3, 7, 9, 10, 11, 13, 15, 18, 19, and two fused sacral ribs, ribs 1, 4, 9–15, 18–20, 22, and 23 are mounted, as well as the two sacral ribs are fused to the sacral vertebrae on the left side of the skeleton (Table 4).

2. The mounted skeleton of *Dimetrodon limbatus* (GPIT-PV-31373) (Fig. 6) is a composit skeleton and was bought by Sternberg in 1911. The fossil remains are recorded to be from the Wichita-Formation, Lower Permian, from the Craddocks Ranch in Texas, USA. Which parts of the skeleton belong to different individuals has not been documented. There are different states of preservation noticeable though. As e.g., the first ribs on the right body side appear to be smoother and partially white crystallized and preserved in contrast to the generally more reddish state of preservation. The vertebral column appears to be relatively complete (Table 3) including the long dorsal spines

of the dorsal vertebral column. Many transverse processes of the posterior dorsals and the proximal caudals have been amended by colored plaster. Further, many dorsal spines of the caudal vertebrae have been amended by plaster, too. 43 caudal vertebrae were counted. The vertebrae are amphicoelous. On the right side, ribs 1–3, 8, 9, 12, 13, 16, and three sacral ribs have been partially preserved (Table 2). The left side of the body is inaccessible due to the mounting's placement in the diorama.

3. *Sauroctonus parringtoni* (Gorgonopsia) (GPIT-PV-31579) (Fig. 7) is from the Usili-Formation, Songea Group, Upper Permian from the Usili-Mountain, Ruhuhu-region, Tanzania. The vertebral column is relatively well preserved including seven cervicals, three sacrals, and the first seven caudal vertebrae (Table 9). The ribs are often broken and especially the distal ends have been amended by plaster as was noted by Gebauer (2007). The more caudal ribs, cervicals, and anterior dorsals, are all double-headed and more complete than the more posterior ones which have been largely amended by plaster, so the rib length measurements have to be looked at based on this condition (Gebauer 2007; Table 8). In the mounting, the third and second sacral vertebra have been transposed we concluded after comparison to Gebauer (2007).

4. *Stahleckeria potens* (GPIT-PV-30792) (Fig. 8) (von Huene 1935–1942) is a kannemeyeriiform from Chiniquá close to Saõ Pedro do Sul, Rio Grande do Sul, Brazil, Santa Maria Formation (Middle Triassic). The vertebrae and ribs were sorted and assigned to their position in the skeleton solely by size by von Huene and are from an undocumented number of specimens by von Huene, so the mounted skeleton is a composit skeleton (von Huene 1935–1942). At least partially preserved are the vertebrae 1, 2, 4, 6, 8–11, 13–17, 19–22, 24–32, 34–45, 47. The second last presacral and the first caudal vertebra are not preserved and made from plaster, and therefore, could not be measured. In *Stahleckeria potens*, the sacrum consists of eight fused vertebrae. The vertebrae are amphicoelous (von Huene 1935–1942). We measured the width and height of the anterior side of the centrum of the first sacral vertebra and the posterior side of the eighth sacral vertebra and measured the length of the whole fused sacral complex as it was not possible to measure each single centrum (Table 11).

No cervical ribs have been preserved. Only two ribs, ribs 8 (left side) and 16 (right side), are complete (von Huene 1935–1942). Many ribs are partially preserved (right side: 12, 14, 16–22; left side: 8, 9, 11–17, 20, 21, 23, 24), but only those where the proximal head was fully preserved were measured (measurements 12–15). All rib fragments have been amended by plaster and it is not possible to identify how correctly they have been assigned to their position in the vertebral column. We collected data on rib 8, 9, 14, 15, 16, 20, 23, 24 from the left side and rib 12, 16–20 from the right side (Table 10).

5. *Belesodon magnificus* (GPIT-PV-31575) (Fig. 6) was found in Chiniquá (São Lucas), Rio Grande do Sul, Brazil, Santa-Maria-Formation (Middle to Upper Triassic). The vertebrae are amphicoelous. Eleven presacral vertebrae are preserved (3, 5–11, 14) but not the second last and last one before the sacrum. Three diagenetically dorsoventrally flattened sacral vertebrae are preserved. The fourth sacral vertebra is missing. No caudal vertebrae are preserved. Due to the state of preservation, only the first sacral vertebra can be measured (centrum height: 1.7 cm; centrum width: 2.4 cm; centrum length: 2.5 cm). Ribs 9, 11, 16, and 20 from the left side and 11 from the right side are preserved (Table 1). All others are modelled and based loosely on *Traversodon* and *Cynognathus* (Huene 1935–1942, p.112).

6. *Tetragonias njalilus* (GPIT-PV-31574) (Fig. 9) (Anomodontia, Dicynodontia) von Huene 1943a (synonym *Dicynodon njalilus*), Njalila, Ruhuhu-Gebiet, Tansania; Middle Triassic, Manda-Formation (235 Ma). The species (*Dicynodon njalilus*) has been based on the skull of a juvenile specimen. Parts of the postcranium of the juvenile specimen, as well as part of the skull and the postcranium of an ontogenetically older specimen of presumably the same species has been been mentioned but not been described by von Huene (1942). Before we could measure the preserved vertebrae and ribs, the postcrania would need a redescription because otherwise it it impossible to know their position within the skeleton. von Huene did not document how the skeletal mounting was conceptualized (von Huene, 1942). The skull and limb bones of the mounted skeleton are labelled as 292 (the number of the fossil digging campaign) but none of the vertebrae or ribs are original. Because the skull looks fairly complete, we presume that the juvenile specimen on which the species is based on, has been mounted as well as the fore- and hindlimb of either one of the individuals.

7. *Keratocephalus moloch* (tapinocephalid dinocephalian; Synapsida: Therapsida) (GPIT-PV-31461) (Fig. 7) was found in the *Tapinocephalus*-Zone of the Lower Beaufort Beds, Early Capitanian, Middle Permian in Abrahamskraal, Karoo, RSA. Part of the presacral vertebrae of *Keratocephalus moloch* are preserved including the last two presacrals, the three sacral vertebrae, and the first tail vertebra (i.e., vertebrae: 1, 2, 8–17, 27–33) (Table 7). In the mounted skeleton, cervicals and the first dorsal/presacrals are added, as well as the tail and the missing ribs. The

vertebrae are amphicoelous. Presumptions by von Huene were based on *Moschops capensis* by Gregory (1926) according to von Huene himself (von Huene, 1931, p.20.). The specimen was found upside down, so with the back on the ground, so the more dorsal parts have been preserved rather than the ventral parts (von Huene, 1931). On the left side, part of the proximal rib 12, 13, 15, 26, and 28 and from the right side rib 11–14, 16, 26, and 27 are preserved. Only the three respective left ribs and rib 12, 13, and 14 are complete enough (Table 6) to measure the most proximal measurement sections (Tables 7–9).