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## THE DIGITAL *PLATEOSAURUS* I: BODY MASS, MASS DISTRIBUTION AND POSTURE ASSESSED USING CAD AND CAE ON A DIGITALLY MOUNTED COMPLETE SKELETON

Heinrich Mallison

### ABSTRACT

*Plateosaurus* from the late Triassic of Central Europe is one of the best known dinosaurs. Despite the large number of finds, including complete and articulated skeletons, its posture and locomotion capabilities are still being debated. While recent assessments of the range of motion of the forelimb indicate that *Plateosaurus* was incapable of manus pronation, and thus an obligate biped, practically all other possible alternatives have been suggested in the literature. Here, I present evidence, derived from a detailed mounting of a 3D digital skeleton and a computer-aided engineering assessment of a digital 3D model of the living animal, that *Plateosaurus* was indeed an obligate biped. The position of the center of mass is assessed in several variations of the basic model to account for differing interpretations of soft tissue amounts. All models allow a stable bipedal pose with a subhorizontal back that is consistent with the requirements of both slow and rapid locomotion. Quadrupedal models, in contrast, suffer from locomotion restrictions due to highly uneven limb lengths and a limited motion range in the forelimb, and result in a smaller feeding envelope.

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**KEY WORDS:** Plateosaurus, locomotion, virtual skeleton

### INTRODUCTION

The prosauropod *Plateosaurus engelhardti* Meyer, 1837 from the Late Triassic of Central Europe is well known from many specimens from a number of locations, several of them in nearly perfect articulation. Among early dinosaurs, it is one of the best-known genera. The finds have caused heated debate about the locomotory adaptations of the animal. Huene (1907-08, 1926, 1928) argued for digitigrade bipedality and attributed a grasping function to the manus. He was convinced that *Pla-*

*teosaurus* was an obligate biped, much as the similar *Anchisaurus* that had been described as exclusively bipedal and digitigrade by Marsh (1893a, 1893b). A good indicator for this is the highly divergent length of fore- and hindlimbs. Huene had the mounts of GPIT1 and GPIT2 (Figure 1.1) set up in Tübingen in bipedal postures and adamantly stuck to this interpretation of the material, despite criticism from many sources.

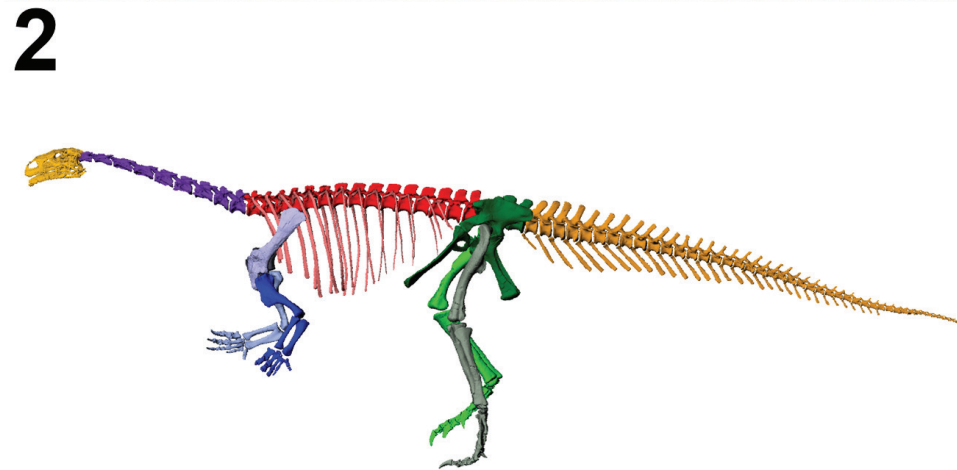
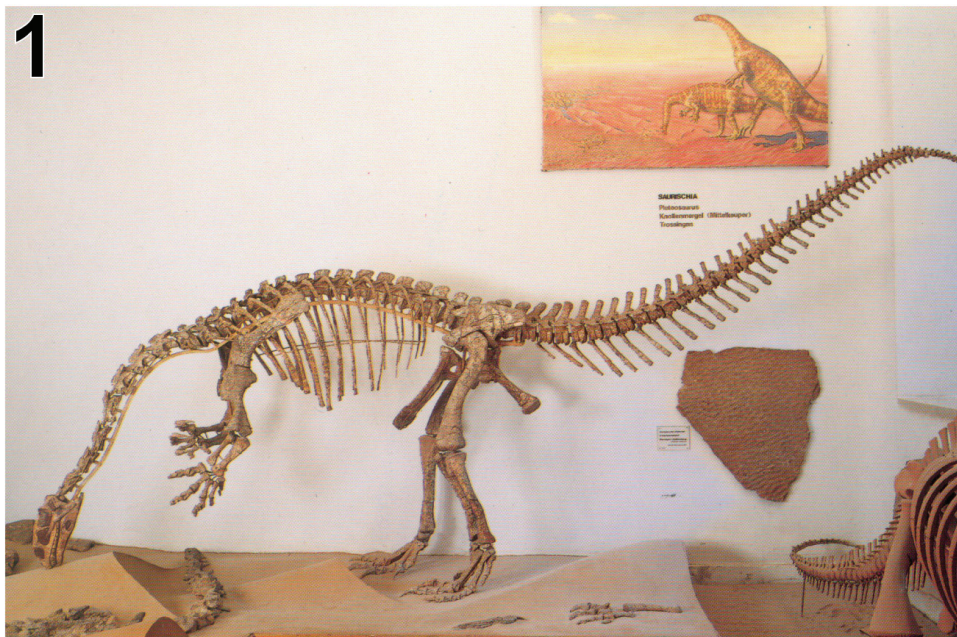
Other researchers have suggested practically any possible stance: obligate quadrupedality and plantigrady 'like lizards' was proposed by Jaekel

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**FIGURE 1.** GPIT1 *Plateosaurus engelhardti*. 1: Skeletal mount at IFGT. Photograph by the author. 2: Lateral view of digital mount (virtual skeleton) in bipedal pose. Skull from SMNS13200, various other elements from GPIT2. Length of left femur is 595 mm.

(1910), who later changed his mind and concluded a clumsy, kangaroo-like hopping as the only possible mode of locomotion (Jaekel 1911, 1913-14). Fraas (1912, 1913) referred to the (dorsoventrally compressed by sediment compaction) position of the skeletal finds in the field, arguing for a sprawling obligatorily quadrupedal gait. He had the skeleton SMNS 13200 mounted in this position in the Stuttgart museum.

Later, researchers began to agree with Huene on the issue of digitigrady, although plantigrady made a comeback in Sullivan et al. (2003). Weishampel and Westphal (1986) depicted *Plateo-*

*saurus* running digitigrade and bipedally, but they argued for facultative quadrupedality. Interestingly, the metacarpals were shown widely spread, in marked contrast to the interpretation by Huene (1926, but contra the reconstruction drawing in that publication), a position that does not seem to fit an active role of the manus in locomotion. Paul (1997) also argued for bipedality, but his outlined skeletal drawing seemed to imply permanent quadrupedality, not bipedality. Facultative bipedality was also proposed by Van Heerden (1997).

Among others, Galton (1971a, 1976, 1990, 2000) advocated facultative bipedality in prosauro-

poes. He based his opinion on the hindlimb to trunk ratio, which was also invoked by Bonaparte (1971). Wellnhofer (1994) also depicted *Plateosaurus* in a quadrupedal stance, based on characteristics of the tail of material from Ellingen now in the BSP, which he figured with a strong downward curve making a bipedal stance impossible.

In the first functional morphology approach on *Plateosaurus* locomotion, Christian et al. (1996) studied the vertebral column's resistance to bending in various vertebrates in order to determine their locomotory modes. Since *Plateosaurus* shows an intermediate pattern between obligate bipeds and obligate quadrupeds, exhibiting a medium peak of resistance to bending over the shoulders instead of either the small peak of bipeds or the large peak of quadrupeds, Christian et al. (1996) argued that the animal was probably facultatively bipedal at high speeds only. Christian and Preuschoft (1996) investigated the shape of the acetabulum and agreed with Huene 1926 on a near-vertical position of the femur in anterior view instead of a more sprawled configuration.

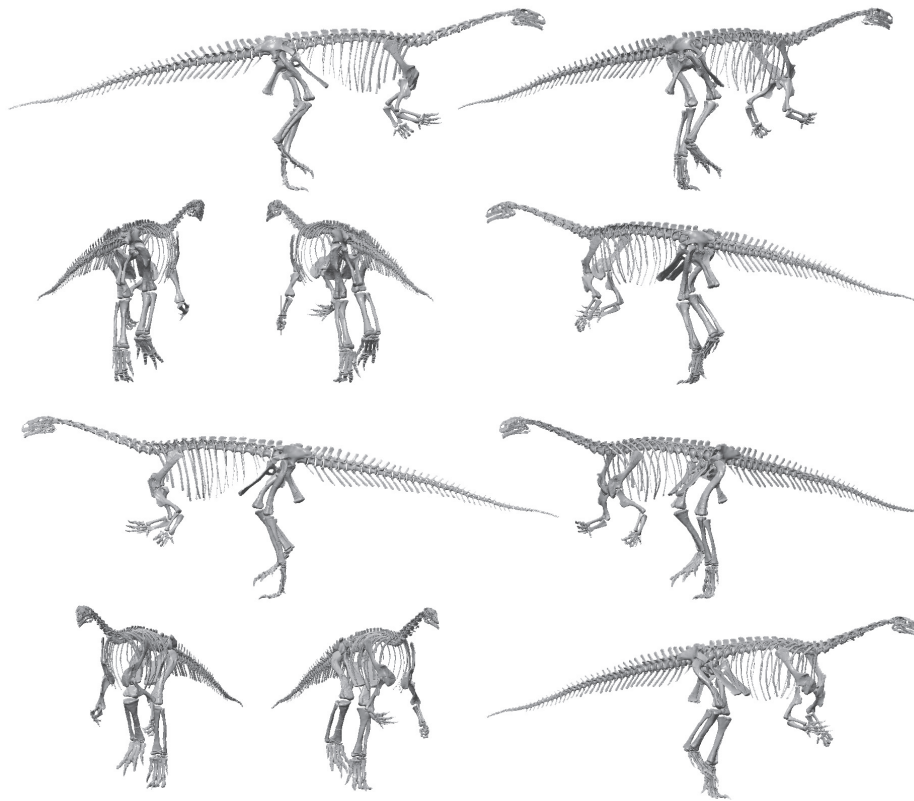
The latest extensive publication on the osteology of *Plateosaurus*, Moser (2003), claimed that *Plateosaurus* would only have been capable of tiny shuffling steps when walking bipedally. Moser also described the remounting of the skeletal mount previously exhibited in the BSP for the Naturhistorische Gesellschaft in Nuremberg. The animal was forced into what Moser called the track of a quadrupedal prosauropod (Moser did not specify which track exactly; probably he referred to the track depicted in Moser (2003: fig. 28, *Tetrasauropus unguiferus*, from Ellenberger [1972]), despite the fact that the track exhibits medially curving and rotated short toes and fingers, while almost all articulated finds of *Plateosaurus* and the morphology of the phalangeal articular surfaces indicate no longitudinal rotation of the toes or fingers. Also, the toes of *Plateosaurus* are long and slender. Moser (2003) suggested that this discrepancy may indicate an early sauropod instead of a prosauropod as the trackmaker. Galton (1971a, b) already suggested medial curving of the fingers in *Plateosaurus*, on the basis of GPIT1, and proposed a walking configuration of the manus that kept the laterally diverging first digit's claw off the ground. Baird (1980) concluded that the track of *Navahopus falci-pollex* from the Navaho Sandstone of Arizona was made by a quadrupedally walking plateosaurid dinosaur. The ichnofossil *Otozoum*, originally described by Hitchcock (1847) and redescribed by Rainforth (2003), is another candidate for a pro-

sauropod track: a bipedal track with two manus imprints on which the fingers point outward at a right angle to the direction of movement. The imprints fit the shape of the *Plateosaurus* manus and pes in a semi-plantigrade position. The pes of *Plateosaurus* has been claimed also to fit the pes print of, suggested as another possible quadrupedal prosauropod track by Lockley and Meyer (2000). Porchetti and Nicosia (2007) concluded that a *Plateosaurus*-like prosauropod is a possible creator of *Pseudotetrasauropus*, again requiring a more or less plantigrade position.

The latest development in the controversy about the locomotory abilities of *Plateosaurus* is an assessment of the range of motion of the forelimb of *Plateosaurus* and the close relative *Massospondylus* by Bonnan and Senter (2007), which indicated that manus pronation was impossible. Therefore, Bonnan and Senter (2007) concluded that *Plateosaurus* was an obligate biped.

Recent research (Fechner 2006; Remes 2006, 2008) suggests that the paradigm of obligatorily bipedal ancestral dinosaurs may be wrong, and that the first dinosaurs were at most facultatively bipedal, holding their hind limbs in strongly flexed poses during quadrupedal locomotion. Such a posture allows subequal functional limb and thus stride lengths despite significantly different total limb lengths, and is similar to the posture of many small mammals. If this model of early dinosaurian locomotion is correct, then the obligate quadrupedal posture of sauropods is a primitive character, most small ornithischians with highly different limb lengths may have been facultatively quadrupedal as well, and bipedal posture would have evolved de novo and potentially separately in several dinosaurian lineages, such as theropods, some 'prosauropods', and some ornithopods.

The best approach to assess the locomotion capabilities of an extinct animal is to create an exact 3D digital mount of it, based on a well-preserved complete individual, and test all potentially possible postures for osteological and for kinematic probability. For the latter, it is necessary to create an accurate 3D model to determine the position of the center of mass (COM). Impossible postures can thus be eliminated. Here, I test the hypothesis that *Plateosaurus* was a facultative bipedal, using four-legged gaits for slow speed, while running bipedally. I used two possible basic postures of *Plateosaurus engelhardti* in various variations and assessed the position of the center of mass (COM) for a spread of mass distributions for each posture. If only the first posture, a quadrupedal stance,



**VIDEO 1.** Virtual skeleton of GPIT1 *Plateosaurus engelhardti* in bipedal posture (see website for full video).

results in a stable and probable posture, it is safe to assume that *Plateosaurus* was an obligate quadruped. The second posture, bipedal, would indicate an obligate biped if it is the sole feasible posture. If both postures are possible, at similar or different walking speeds, it is probable that *Plateosaurus* may indeed have been capable of both locomotory modes.

NOTE: Different researchers have articulated the bones of *Plateosaurus* differently, both in museum mounts and in reconstruction drawings. Those reconstructions that have a bearing on the investigations described here will be discussed below with the details of the articulation of the digital skeleton of *Plateosaurus*.

### MATERIAL AND METHODS

The basic postures were tested for feasibility by creating a digital mount (a virtual skeleton) of GPIT 1 (Figure 1.2, Video 1), a complete skeleton from Trossingen (GER), and posing it accordingly. Several versions were created that take different interpretations of shoulder girdle articulation, limb motion ranges, and foot position into account (see Mallison in press). Some of these variations are

osteologically feasible, others are impossible but were tested because they, or gaits based on them, were explicitly suggested in the literature. To determine whether a posture is stable, a CAD model of *Plateosaurus* was created on the basis of the virtual skeleton. For several variations of this model, accounting for different distributions of soft tissues on the skeleton, the position of the center of mass (COM) was determined in a CAE program.

### Institutional abbreviations

- AMNH American Museum of Natural History, New York, USA
- BSP Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany (formerly Bayerische Staatssammlung für Paläontologie und historische Geologie)
- GPIT see IFGT
- IFGT Institute for Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany (also IFG or UT in the literature)  
*Formerly Geologisch-Paläontologisches Institut Tübingen (abbreviated GPIT)*
- MB.R. see MFN

- MFN Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin  
*Formerly Museum für Naturkunde der Humboldt-Universität zu Berlin*  
*Also abbreviated MNHB. Collection numbers are MB.R.####.*
- MNHB see MFN
- MSF Sauriermuseum Frick, Frick, Switzerland

### Computer programs

Extraction of the bone surface shapes was performed in a time-limited trial version of AMIRA 3.11® by AMIRA Corp. CAD tasks (mounting the skeleton, CAD model creation) were conducted using McNeel Associates Inc. 'Rhinoceros® 3.0 NURBS modeling for Windows®' and 'Rhinoceros® 4.0 NURBS modeling for Windows®'. For polygon mesh editing I used a time-limited trial version of 'Geomagic Qualify 8.0®' from Geomagic Inc. CAE models were created and assessed in MSC.visualNastran 4D® by MSC Corp. and NX5® by Siemens PLM Software.

### 3D FILE EXTRACTION

The bones of GPIT1 were CT-scanned by B. Ludescher at the University Hospital of the Eberhard-Karls-University Tübingen on a Siemens™ Somatom Sensation© scanner. Slice thickness was 0.5 mm, with a 0.5 mm increment and a 0.25 mm overlap. The surface shapes of the bones were extracted from the resulting DICOM-format slice graphics using AMIRA® 3.11 and saved as polygon meshes in stereolithography format (\*.stl). This created artifacts (massive wrinkling of the surfaces), and a reduced set of every second slice was instead used. This removed overlap between neighboring slices and eliminated the artifacts. Internal surfaces and artifacts were removed, and the files were reduced in size to about 25% of original size using Geomagic Qualify 8.0®. Large (girdle and limb) bones were further reduced in size, to save computing time.

### Mounting the virtual skeleton

The bones were mounted in Rhinoceros® 3.0 and 4.0. The limbs were articulated separately from the vertebral column and girdle elements, and the partial assemblages later combined to create the two basic postures (bipedal and quadrupedal) and their variations.

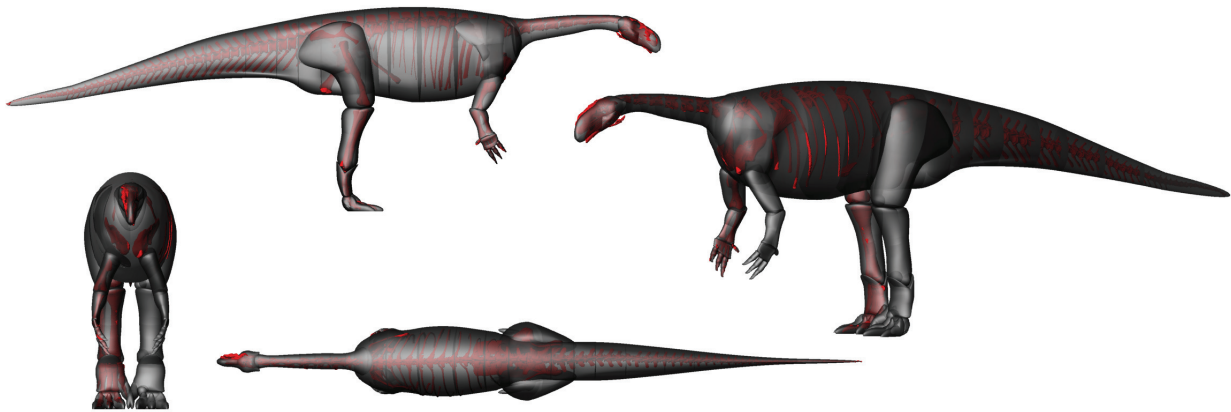
The vertebral column was placed into near-neutral articulation (ostgeologically neutral pose

[ONP], see Stevens and Parrish 1999) three separate times, with several weeks pause between the digital mountings, in order to avoid one mounting influencing decisions in the next mounting. In each case, the vertebrae were articulated with each other in pairs, so that only the last added vertebra and the one currently being placed were visible, to avoid errors in placement caused by apparent curvatures of the entire column. Two instances were created by proceeding along the vertebral column vertebra by vertebra, once from the front and once from the tail tip. The third mount was created in pieces, with the cervicals, dorsals, and caudals articulated separately and then combined in a final step. This redundancy in mounting was intended to remove bias caused by preconceived notions as far as possible. Neutral pose was determined by placing the anterior and posterior surfaces of the centra as parallel as possible while guaranteeing maximal overlap of the zygapophyses. Because nearly all dorsals in GPIT1 are distorted, with the transverse processes and zygapophyses rotated dorsally on the right and ventrally on the left side, and some show signs of slight antero-posterior compaction, neutral pose had to be approximated as a best guess in some of the articulations. However, comparison with other *Plateosaurus* material (SMNS 13200, GPIT2, SMNS F33) indicates that the induced errors are probably smaller than differences caused by intraspecific variation. All three digital mounts show highly similar curvatures and total lengths of the assembled spine, so only one was used in all further analyses. All differences were significantly smaller than even extremely conservative assessments of the range of motion in the intervertebral joints, and did not influence the overall trends in the spine. The limbs were also mounted repeatedly.

The bipedal and quadrupedal postures were created based solely on the osteology and poses suggested in the literature, even if the latter demanded impossible joint articulations. The expected position of the COM was not taken into account to avoid bias. The bipedal and quadrupedal poses resembled published reconstructions (Galton 1990, 2000; Paul 1987, 1997; Wellnhofer 1994; Weishampel and Westphal 1986), without regard for joint limits, center of mass, or other considerations.

### 3D model creation

Rhinoceros® 3.0 and 4.0 were used to create NURBS bodies for a 3D model for the living animal (Figure 2). Initially it consisted of ellipsoid bodies



**FIGURE 2.** Four views of the CAD model of *Plateosaurus engelhardti* and the virtual skeleton of GPIT 1 on which the model was based. Model is displayed in translucent mode to make segmentation and skeleton visible. Note that some bones stick out of the CAD model, mainly because the bones are deformed and were therefore ignored during model creation.

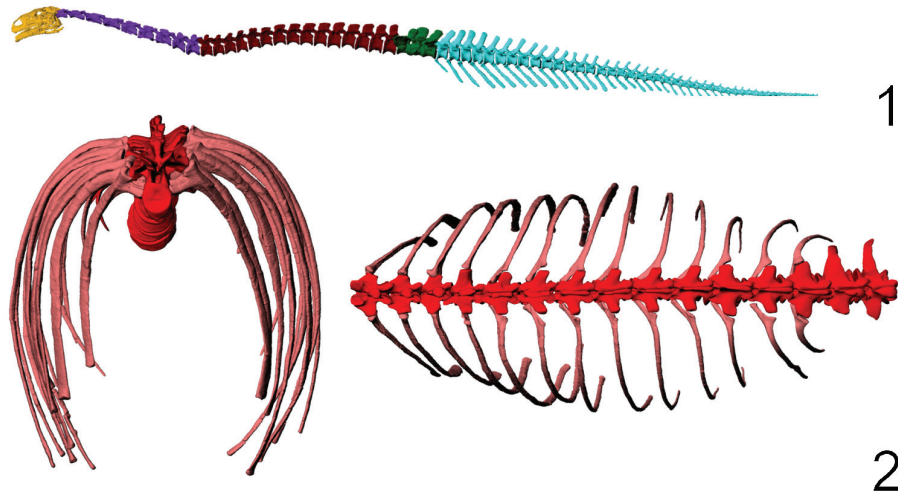
that were deformed to approximate the 3D shape defined by the extents of the skeleton. Then, the 3D bodies were further enlarged to incorporate room for soft tissues. This method differs from the ellipses-based method of Henderson (1999), allowing non-elliptical cross sections. The amount of soft tissue is conservative, except for the hips and upper hindlimbs. Here, relatively ample amounts of muscles were assumed, because dinosaurs produce most of the posteriorly directed force required for rapid locomotion not by limb extension, but by limb retraction (see Gatesy 1990), in contrast to mammals. Therefore, the iliofemoral, ischiofemoral, and especially caudofemoral musculature must have been relatively stronger than in mammals. The recent discovery of a hadrosaur mummy in North Dakota (US) confirms that at least hadrosaurs possessed much more musculature in the upper hindlimbs and tail than most previous reconstructions assumed (National Geographic Society 2007, Dec. 12). Since the musculoskeletal system of the all non-avian dinosaurs is relatively uniform, I feel that a robust soft tissue reconstruction of the hindlimb and basal tail of *Plateosaurus* is reasonable. Additional evidence comes from extant crocodylians. Persons (2009) found that all of the many extant taxa used for his study had a far larger amount of tail musculature than is usually assumed to be present in dinosaurs. Specifically, the muscle cross sections protrude far beyond the tips of the haemal arches and transverse processes (Persons 2009).

The model's limbs were sectioned into functional units (manus, antebrachium, etc.), while the

neck, body, and tail were sectioned vertically into slices. Each part was thus turned into a separate entity, so that it could be given an individual density value. Theoretically, it would have been possible to subtract the bones from these volumes and give the remaining 3D bodies the average density of soft tissues. However, the gain in accuracy would have been minimal, especially given the uncertainty considering the amount of soft tissues, and the calculation demands for the computer programs would have increased massively.

#### CAE assessment of mass distribution

The center of mass (COM) was determined in a computer-aided engineering (CAE) software using NASTRAN. NASTRAN is a finite element analysis solver originally developed by NASA and today available in several versions able to handle kinetic/dynamic modeling of rigid body systems. Problems are time-discretized in NASTRAN, which solves them using the simple Euler integration, or the more complex and thus computer calculation time intensive Kutta-Merson integration. The latter allows a variable number of repeated integrations per (pre-defined) time step, and attempts to estimate the integration error. Thus, it delivers significantly more accurate results for highly unequal mass or speed combinations in the model (see Fox 1962 for details on the integration methods). For quasi-static analysis as presented here (i.e., standing models of *Plateosaurus* used to determine the position of the COM), Euler integration is sufficient. Tests using both methods on the same file failed to



**FIGURE 3.** GPIT1 *Plateosaurus engelhardti* 1: vertebral column with skull of SMNS13200 in neutral articulation, lateral view. Color code: cervicals in light blue, dorsals in red, sacrum in dark green, tail in dark blue. Total length of vertebral column is 5.17 m. 2: ribcage in anterior and 3: dorsal view. Total length 1.35 m. Note deformation of ribs and vertebrae that result in seemingly incorrect articulations.

show differences in the results. The exact position of the COM was calculated in the program.

## RESULTS

### Virtual skeletal mount of *Plateosaurus*

**Vertebral column.** *Plateosaurus* has 10 cervicals (plus a rudimentary proatlas), 15 dorsal and three sacral vertebrae. The tail is composed of 45 vertebrae in GPIT1. Figure 3.1 shows a lateral view of the cervical, dorsal, and caudal series of GPIT1 in osteologically neutral position.

The cervical column articulates in a nearly straight line, parallel to the long axis of the cervical centra. However, this line is not perpendicular to the anterior and posterior faces of the vertebrae, but ascends anteriorly. Therefore, ONP displaces the head dorsally, resulting in a skull position at or above shoulder height, depending on the angle of the anterior face of the first dorsal relative to the exterior.

The anterior dorsals arch dorsally (dorsals 1 through 4), while the middle part curves markedly ventrally (dorsals 5 through 10). Further posteriorly the dorsal column is nearly straight. In all, the downward curve results in a ventral rotation of the long axis of dorsal 5 by 22°, while the anterior upward curve angles the base of the neck up by 12° compared to dorsal 5, and 15° down compared to dorsal 15. Therefore, if the sacrum is placed with its long axis horizontal, the neck is attached at a

slight downward angle, and the 'stepping up' of the cervical is required to bring the head to above shoulder level in ONP. This position is similar to that of SMNS 13200 as figured in Huene (1926). The slightly different curvature of SMNS 13200 can be explained by the damaged dorsal 6 and the slight disarticulation between dorsals 4 and 5 (Huene 1926: plate II).

In the anterior tail, the neutral pose placing the centra faces parallel (ONP) cannot be created. Nearly all vertebra show slight keystoneing. As noted by Moser (2003), this keystoneing is intrinsic to the osteology, but its degree varies. In GPIT1 the variance is lower than in the material from Ellingen (Germany) described in detail by Moser (2003), which may be caused by a lower degree of taphonomic deformation. If the centra are placed at an angle to bring their anterior and posterior faces into a parallel position, the haemal arches can not be fitted to their articulation surfaces on the vertebrae. Neutral pose is supposed to provide the maximum contact of articular surfaces. Omitting the haemal arches, or moving them out of close articulation, would violate that principle. To accommodate the zygapophyses in articulation dorsally and the haemal arches in close articulation ventrally, the intervertebral disks were reconstructed as having slightly greater thickness ventrally than dorsally, i.e., slightly wedge-shaped. Adjustment for the haemal arches results in a straight tail, with varying intervertebral disc thickness and shape.

**Ribcage.** The articulations between ribs and dorsal vertebrae show that the anterior body was narrow from side to side (Figure 3.2). As in all dinosaurs, the ribs of *Plateosaurus* have two heads (Huene 1926), the dorsal capitulum that articulates with the diapophysis on the transverse process of the vertebra, and the ventral tuberculum, which contacts the parapophysis. The ribs move by rotating around the axis connecting the two articulations (Mallison in press). Whether the rib motion enlarges the ribcage volume, e.g., for breathing in as in humans, or whether the rib motion has no influence on the body volume depends on the orientation of the axis. In *Plateosaurus*, the first five dorsal ribs move antero-posteriorly, while all later body ribs swing outwards, increasing the volume of the body cavity (Mallison in press). For the analysis presented here, an intermediate position of the ribs was chosen. In- or exhalation does not significantly change the position of the COM, because there is practically no antero-posterior motion of large tissue volumes.

**Pectoral girdle and forelimb.** The pectoral girdle and the functionally associated axial elements are incompletely preserved in GPIT1. Only the co-ossified scapula and coracoid are preserved on each side, while the left clavicle and sternals are missing. The right clavicle is partially preserved and attached to the coracoid by sediment. It is a thin rod, as described by Huene (1926). The scapulacoracoids follow the usual prosauropod pattern in their general morphology, but show a number of peculiarities (Remes 2008), some of which have a profound impact on the interpretation of possible locomotion poses. Most importantly, the glenoid is a simple trough, restricted to the caudal margin of the scapulacoracoid. It does not extend to the lateral surface of scapula or coracoid, and only the anteromedial rotation of the entire scapulacoracoids leads to a caudoventrolateral orientation of the glenoid.

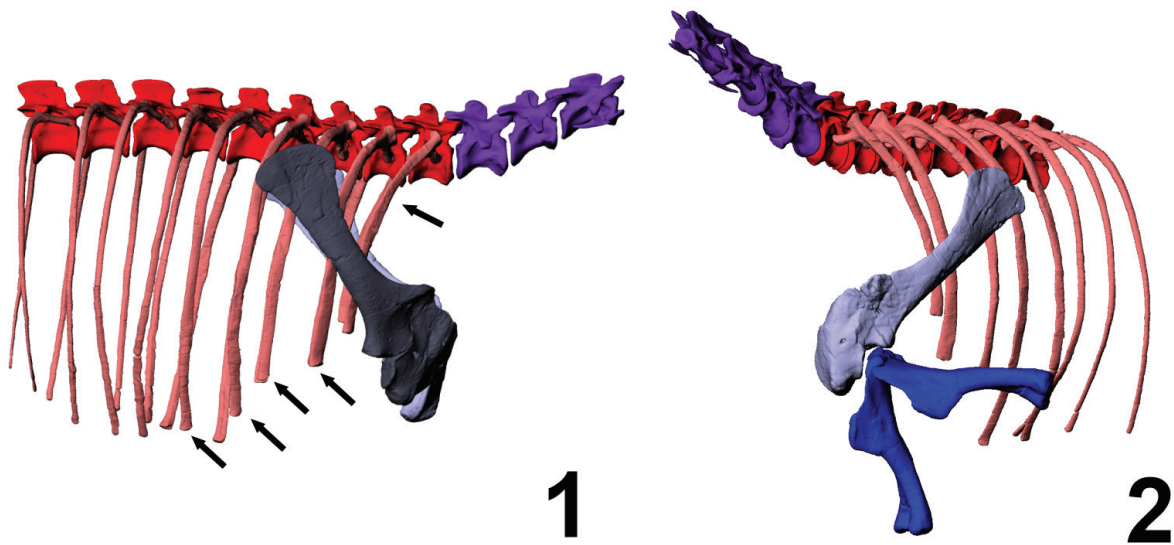
If the scapula is placed at an angle shallower than  $45^\circ$  in reference to the sacrum–1<sup>st</sup> dorsal line, either the pectoral girdle projects forward beyond the second to last cervical, a position contrary to all articulated finds, or the scapular blade overlaps beyond the fifth dorsal. Due to the lateral expansion of the ribcage during breathing, this would lead to lateral displacement of the dorsal end of the scapula, and thus require a hinge-joint motion between the coracoids. The forelimbs would therefore move laterally with each breath. Additionally, any force pressing dorsally on the glenoid, e.g., compressive forces in the forelimb during locomotion,

would tend to rotate the scapula anterodorsally. A placement of the scapula steeper than  $65^\circ$  is unreasonable, as it would lead to a nearly horizontal orientation of the coracoids, and direct the glenoid exclusively posteriorly.

Angles of the scapula between  $45^\circ$  and  $65^\circ$  appear reasonable, as they do not push the coracoids too far forward, but also place the tip of the scapular blade at the level of the fourth dorsal (Figure 4.1). Such a position, with tightly spaced coracoids, is biomechanically advantageous, as the girdle then can form a strong brace, both for projecting large forces through the arms, and as a support structure when the animal is lying on the ground. Remes (2008) also suggested this arrangement based on an analysis of the myology in basal sauropodomorphs. In *Massospondylus*, a close relative of *Plateosaurus*, Yates and Vasconcelos (2005) found articulated clavicles that were arranged in a furcula-like manner, touching at the midline. This further confirms the narrow arrangement of the shoulder girdle. For *Plateosaurus*, this condition of touching but not co-ossified coracoids and clavicles was already explicitly mentioned by Huene (1926) in several skeletons. The scapulae cannot be separated laterally and shifted dorsoposteriorly on the side of the ribcage as suggested by the mounts in the SMNS. It is important to note that dorsolaterally shifting the scapulacoracoids forces a quadrupedal *Plateosaurus* into a sprawled forelimb posture, with an extremely reduced functional forelimb length.

The width of the shoulder girdle has been differently reconstructed with the ‘old’ museum mounts in the SMNS separating the coracoids by more than the length of a coracoid and placing the scapula blade almost parallel to the dorsal series. However, these mounts show a grossly exaggerated width of the ribcage. GPIT1 and GPIT2 were mounted with a narrower arrangement by Huene, as was AMNH 6810, another excellently preserved skeleton from Trossingen. As shown by Mallison (2007, in press), the ribcage is high-oval in the shoulder area, and only widens further posteriorly. Also, the anterior ribs sweep caudally slightly, allowing for a narrow girdle architecture, with steeply inclined scapula blades and medially almost contacting coracoids. Motion is restricted to antero-posterior sweeps (Mallison in press) only in the first five dorsal ribs, while further posteriorly there is a significant lateral expansion. Huene (1926) already mentioned that in SMNS 13200 these five ribs are significantly thicker and sturdier than those of more posterior dorsals (see Figure





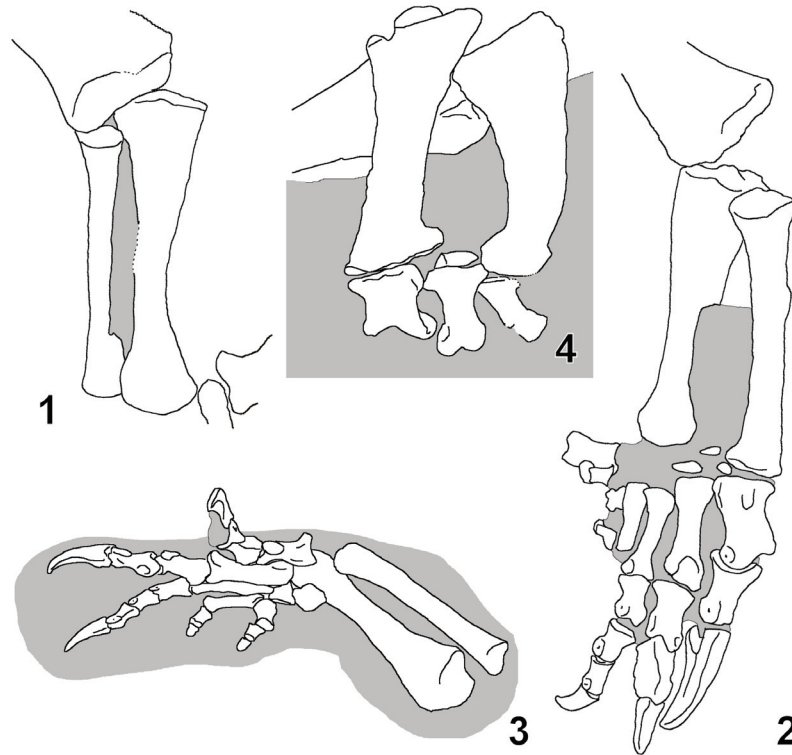
**FIGURE 4.** Pectoral girdle and forelimb of the virtual skeleton of GPIT1 *Plateosaurus engelhardti*. 1: lateral view of the pectoral girdle. Thick, flattened ribs indicated by arrows. 2: oblique view of the left scapula with two instances of the left humerus showing maximum rostrocaudal motion range in the glenoid.

4.1). They also have a flattened cross-section. This flattening is not caused by the ribs' attachment to the sternum, as the rough thickened distal ends indicating attachment are found on the first eight ribs. The most plausible explanation is that only the first five ribs had to absorb large forces transmitted through the pectoral girdle. Recently, Fujiwara et al. (2009) indeed found that more robust ribs are present where the *M. serratus* attaches to the ribcage in quadrupeds.

The proximal end of the humerus is broad and dorso-ventrally compressed. This indicates that a rotation of the humerus head in the glenoid, as is seen in animals with sprawling gaits (Goslow and Jenkins 1983; Landsmeer 1983, 1984; Meers 2003), was not possible. Due to the simple shape of the glenoid, protraction-extension is limited to an  $\sim 80^\circ$  angle, from  $55^\circ$  to  $135^\circ$  in relation to the long axis of the scapular blade (Figure 4.2). Therefore, if the scapula is placed at a  $35^\circ$  angle from the horizontal, the humerus can not be protracted beyond vertical. The possible amount of abduction can not be ascertained, but any angle greater than  $30^\circ$  leads to an unstable position, in which only limited forces can be placed on the joint. Large forces would lead to a medial shifting of the humeral head, as the glenoid does not contain it laterally in any way. These findings, more details on which can be found in Mallison (in press), confirm the results of Bonnan and Senter (2007). Due to the medial rotation of the glenoid axis, retraction of the

humerus displaces the elbow laterally. A purely parasagittal motion of the humerus seems not possible. The cranioventral torsion of the distal end of the humerus relative to the proximal end is usually  $45^\circ$  in prosauropods (Remes 2008), but only  $30^\circ$  in *Plateosaurus*.

Radius and ulna can only be articulated with the distal end of the humerus if they are placed into close proximity with each other (Mallison in press, fig. 5). The imperfect preservation of the distal humeral condyles allows separating radius and ulna by a few millimeters or up to about 2 cm. A tight arrangement seems more realistic, especially since the lateral side of the triangular distal end of the ulna forms an articular surface conforming to the shape of the proximal radius. Distally, both bones do not form contact surfaces, and are spaced slightly apart in all articulated finds (Figure 5). In GPIT2, the left radius and ulna each show a small deformation where they were pressed into each other during fossilization. This relatively tight placement allows only minimal motion between radius and ulna, making full pronation by rotation of the radius impossible. Several other factors also indicate that *Plateosaurus* was not capable of significantly pronating the hand this way: the proximal end of the radius is oval in circumference, with a ratio between the longest and shortest axes of 1.8:1 (Mallison in press, fig. 5). Rotating the radius head requires a circular circumference as seen in humans and cats. Only a sliding motion, which is

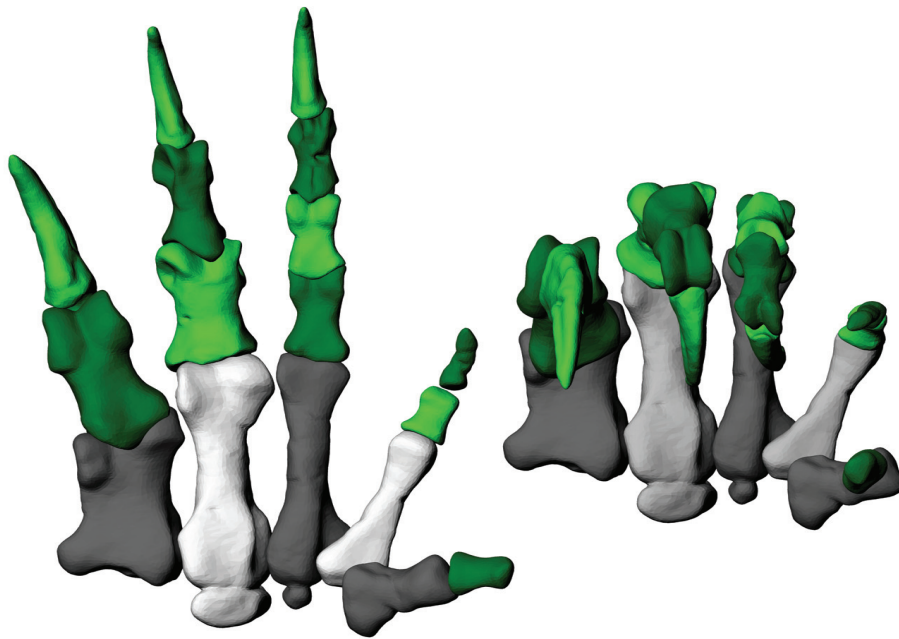


**FIGURE 5.** Articated forelimbs of *Plateosaurus* from Trossingen and Frick, drawn from photographs by the author 1. SMNS F33 left antebrachium and manus 2. SMNS F33 right antebrachium and manus. 3. MSF unknown number antebrachium and manus. 4. MSF 23 left antebrachium and manus.

not seen in any extant animal capable of pronation, remains possible. Bonnan and Senter (2007) investigated the ability to pronate the manus using an extant phylogenetic bracket approach and found none of the extant outgroup taxa capable of pronation. Additional evidence comes from the skeletons that were found in articulation in Trossingen (GER) and Frick (CH). The animals were trapped in mud (Sander 1992), their hindlimbs stuck while the forelimbs were still free. A quadruped should in such a situation attempt to push itself out of the mud with its forelimbs. However, not a single one of the skeletons shows a forelimb with a pronated manus close to the body midline. Rather, the arms are widely spread (SMNS F33), placed under the belly with the palm facing dorsally (MSF 23 right arm), or widely abducted with strongly flexed elbow, wrist, and fingers and medially directed palm in full supination (MSF 23 left arm). Huene (1928: plate X) figured a quarry map of GPIT1, the only find in which one arm potentially shows manus pronation (left forelimb). However, the overlap pattern of the girdle and limb bones (right scapula overlaps right humerus, left humerus

wedged between the coracoids, etc.) indicates that the skeleton was significantly displaced in a semi-macerated state, so that the position of the manus as found is not indicative of the potential motion range in vivo.

The carpus is not well preserved in GPIT1 and GPIT2, but MNHB Skelett XXV from Halberstadt has five carpals. The proximal row consists of two large elements that are shallow triangular in plantar view. The radiale has contact with the radius, metacarpal I, and the ulnare, as well as a small articulation with a distal carpal. The ulnare is situated between the ulna and the distal carpals. It is unclear whether it had any contact to the radius. The distal carpal row is formed by a flat, box-shaped bone closely corresponding to the form of and in close contact with the proximal end of metacarpal II, and two small rounded elements situated between the ulna and metacarpals III and IV. These do not block metacarpal V from contact with the ulna. The range of motion in the carpus is difficult to determine. Bonnan and Senter (2007) concluded that rotational or twisting motions are made impossible by the block-like structure of the carpus.



**FIGURE 6.** Left manus of the digital mount of GPIT2 *Plateosaurus engelhardti*, palmar view. 1: straight digits, 2: flexed digits. Length of metacarpal is 3 is 97 mm.

Extension and strong flexion, however, possibly to a similar degree as in humans, appear possible.

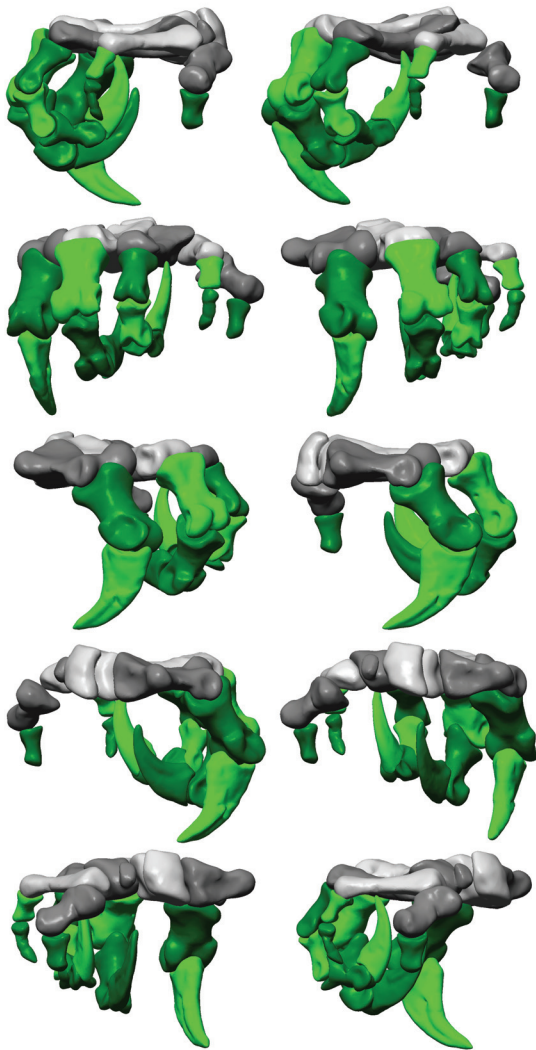
Metacarpals I through III articulate tightly with their proximal ends. Distally, they show minimal splaying. Metacarpal IV also has an articulation surface for metacarpal III, but angles laterally  $20^\circ$ . Metacarpal V has two distinct articulation surfaces, and contacts both metacarpal IV and the ulna. It angles laterally about  $50^\circ$  from metacarpal III.

The manus digits of *Plateosaurus* are highly unequal, with digit I developed as a strong grasping claw, and digit IV and V much reduced. Paul (1987, 1997, 2000) depicted *Plateosaurus* in a quadrupedal pose, with the first digit medially rotated by almost  $90^\circ$ , so that the claw is in a horizontal position at mid-stance. Digital manipulation of the scans of GPIT1 shows that this angle is close to  $27^\circ$  during hyperextension and decreases to only  $13^\circ$  at maximum flexion, because the significant size difference in the articular condyles of metacarpal I are partially countered by an asymmetrically shaped proximal articulation surface on the first phalanx of digit I. The significance of the size difference lies with the larger medial condyle being subjected to higher forces, not with a canting of the main axis of the digit. Additionally, as pointed out by Galton (1976), in *Anchisaurus*, which has a similarly shaped hand, during flexion the ungual phalanx rotates laterally, and thus nearly lines up with the second and third digits. The latter are

unremarkable, with strong claws. However, it is important to note that hyperextension is less pronounced than in the toes, even though there are distinct but shallow hyperextension pits. In contrast to the first three, digits IV and V do not show well-developed trochleae, resulting in greater freedom of motion but a reduced ability to withstand forces. The entire hand (Figure 6, Video 2) appears to be adapted to strong grasping, with some ability to oppose digits IV and V.

**Pelvic girdle and hindlimb.** The hindlimb of *Plateosaurus* (Figure 7) shows a number of adaptations to cursoriality compared to basal archosaur taxa. The femur is long, and its head is medially offset, indicating a parasagittal limb posture, as already concluded by Huene (1926, 1928). The distal femoral condyles in *Plateosaurus* face slightly caudally, which indicates that the knee could not be fully straightened. Combined with the longitudinal curvature of the femur shaft and its sub-circular cross-section this means that *Plateosaurus* had a permanently flexed limb posture, and that the femur was not held vertically during standing or at mid-stance.

In anterior view, the probable rotation axis of the knee joint is canted against the shaft of the femur by approximately  $70^\circ$  (Figure 7.1). The axis of the proximal end is hard to determine, but appears to be roughly parallel to that of the knee. If



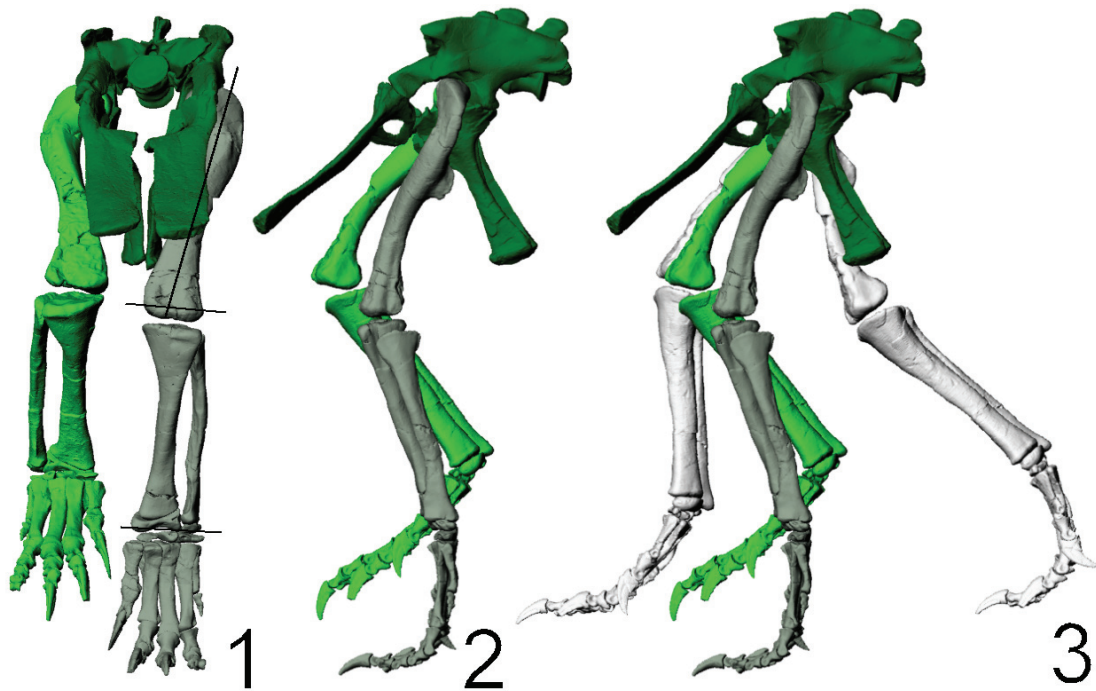
**VIDEO 2.** Virtual skeleton of GPIT1 *Plateosaurus engelhardti*: left manus in full flexion. For full video, see website.

the femur is placed in the acetabulum so that the axis of the knee joint is horizontal, the shaft is inclined medially and the approximate center of the knee is placed directly ventrally from the hip joint. In Figure 7.1, the femur is shown adducted slightly more, so that the first pedal digit is placed under the body midline. Such a position under or nearly under the COM is necessary for walking gaits in bipeds, and today seen in practically all quadrupeds.

Gatesy (1990) showed that non-avian dinosaurs use femur retraction as the major component in caudally directed foot displacement, thus generating most of the required force in the *M. caudofemoralis*. As this was certainly also the case in *Plateosaurus*, it is reasonable to assume that the femur covered a large arch during locomo-

tion. A limit on protraction is imposed by the pubes at low abduction angles. Retraction is not hindered by the ischia, so a maximum angle must be estimated based on the path of the *M. caudofemoralis longus* and its maximum contraction. This at best is educated guesswork, but it seems reasonable, given the position of the tail in relation to the pelvis, to assume that during locomotion retraction was limited to a position in which the femur shaft is parallel to the ischia, as at this point all ischiofemoral musculature has no retraction function left at all. If this is correct, then the angle that the femur can cover without significant abduction is  $65^\circ$ . Figure 7.2 depicts the hindlimbs and pelvic girdle in lateral view, with a suggested stride length of 1 m for a normal walk. This correlates roughly to a walking speed of 3.7 km/h, using an average of Alexander's (1976) and Thulborn's (1990) formulas. For this stride length, the femora need only cover a  $50^\circ$  angle. For angles larger than  $65^\circ$ , abduction is required so that the femur passes the pubis laterally, or retraction to beyond the level of the ischia. Compared to the neutral position chosen here (distal end of femur directly ventral from acetabulum in anterior view), the former requires  $20^\circ$  abduction. It appears therefore doubtful whether significantly larger protractions than to the level of the pubis were possible. Not only is all pubofemoral musculature ineffective for protraction when the femur is close to the pubis and has a purely adducting effect. Also, there is no greatly enlarged proacetabular process on the ilium of *Plateosaurus*. Therefore, the iliofemoral muscles that still have a protracting component are weak. Passive protraction, e.g. by transfer of rotational inertia from the shank to the thigh, is possible, but only effective at very high limb swing speeds (running gaits). One must assume that femur motion during normal locomotion was limited to the mentioned  $65^\circ$  at medium speeds, while slower speeds probably used less retraction. The center of mass was located in front of the acetabulum, and mid-stance position as reconstructed here was at slight protraction ( $20^\circ$  from vertical, Figure 7.2).

The tibia shaft is straight, and the tibia expands slightly proximally, but there is no distinct cnemial crest projecting anteriorly in lateral view. Knee extension therefore did not form a major part of locomotory limb motions, excluding the possibility of a hopping gait as suggested by Jaekel (1913-14), and probably also a bounding gallop as suggested by Paul (2000). In the tibia and fibula there is no canting between the long axis of the shaft and the apparent joint axes. Distally, the tibia articulates



**FIGURE 7.** Left hindlimb of the virtual mount of GPIT1 *Plateosaurus engelhardti*. 1: anterior, 2: lateral view. In 1, black lines mark probable joint axes. 3: as 2, with additional instances of the right hindlimb showing possible extreme range for a normal walking cycle. Length of left femur is 595 mm.

tightly with the massive astragalus. Four more carpals, a calcaneum and three distal tarsals, are preserved in GPIT1. On the left foot of MB.R.4404, three distal tarsals with very similar shapes to those of GPIT1 are preserved, so the likeliness of taphonomic deformation is low. The ankle is wide and flattened, with no bony structure forming a pronounced heel, and no indication of a large cartilaginous projection. Therefore, extension moments around the ankle were either low or created primarily through high muscular forces. In contrast, mammals use a large lever arm in their ankles, the tuber calcanei (Romer 1949). The ankle of GPIT1 forms a hinge joint, the axis of which is almost parallel to the knee (Figure 7.1). The range of motion is large, covering at least  $170^\circ$ . This would allow any limb pose from straight to completely folded, as in resting birds. Astragali of other individuals show a very similar morphology, if taphonomic deformation is taken into account. As a result of the arrangement of the joint axes, placing the femur canted inwards so that the knee axis is horizontal results in a vertical position of the lower limb, and places the third toe ventrally below acetabulum in anterior view (but not in lateral view, because the COM lies in front of the acetabulum).

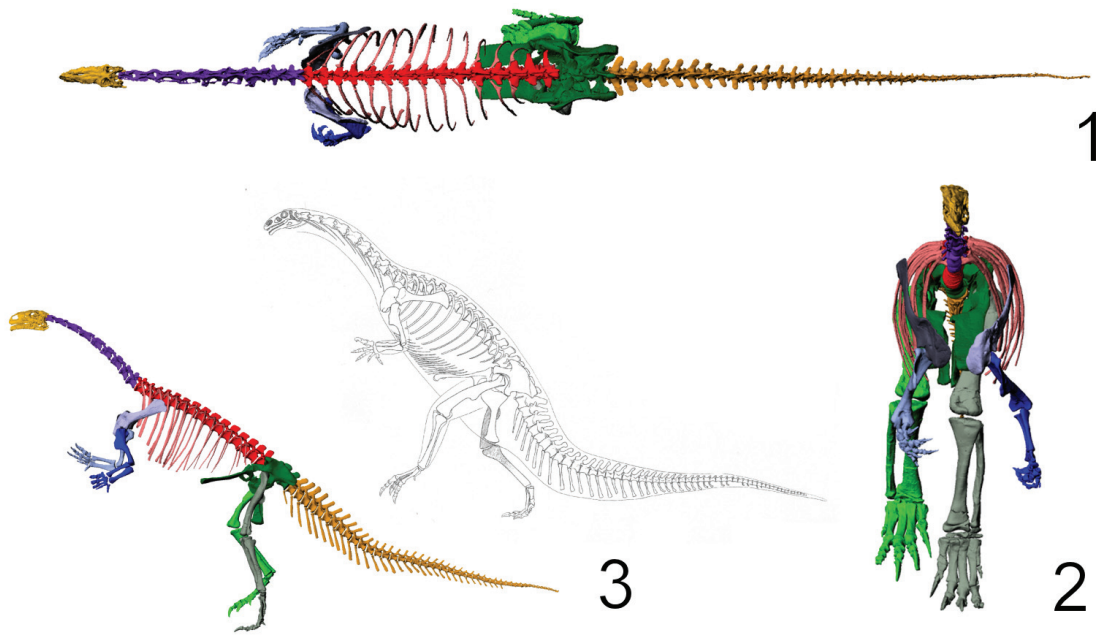
The metatarsals articulate tightly (Figure 8.1), with clearly demarcated, large articulation facets on their lateral sides. These, however, do not run down the shafts to a great extent, since the proximal articular ends are much wider than the shafts. Some previous reconstructions (e.g., the 'old' SMNS mounts) have therefore been created with splayed metatarsals. However, such a placement is not supported by the skeletons found in Trossingen, Halberstadt, and Frick, where all feet found in articulation show the metatarsals closely touching proximally and almost touching distally (Figure 8.2-4). There is no splaying in these finds, which would also be biomechanically unsound. Splayed metatarsals result in a larger, thus heavier foot, which decreases the swing frequency of the limb. Additionally, splaying causes lateral bending moments in the lateral and medial metatarsals. These could result in adaptation of the shape of the metatarsals and toes, e.g., unequal condyles on the interphalangeal joints and asymmetrical metatarsal shaft cross sections, as well as laterally curved metatarsal shafts, which are not present in *Plateosaurus*. A broader foot would offer more lateral stability, but in extant cursor feet are reduced in size, because the above mentioned factors outweigh the advan-



**FIGURE 8.** Pes of *Plateosaurus engelhardti* in dorsal view. 1: left pes of virtual mount of GPIT1. Length of metatarsal 3 is 234 mm. 2: left pes of SMNS F50 3: left metatarsus of SMNS F65 4: right pes MSF unnumbered. 2 – 4 not to scale.

tage of slightly greater stability. Only animals regularly walking on instable substrates such as snow and sand (e.g., arctic foxes and camels, respectively) show slightly larger support areas than their relatively moving on stable ground. Even in them the size increase in the foot is proportionally much smaller than splaying of the metatarsals would create in *Plateosaurus*.

All toes of GPIT1 are almost straight, in contrast to Skelett XXV (MB.R.4404) from Halberstadt, in which the fourth toe curves laterally. Similarly, in GPIT1 toes 1 through 3 are canted slightly medially compared to the long axis of the metatarsus, though beveled distal condyles of the metatarsals. The fourth metatarsal, however, is canted laterally. In contrast, in Skelett XXV, toes 1 through 3 are



**FIGURE 9.** Virtual skeleton of GPIT1 in bipedal posture in 1: subhorizontal back, lateral view, 2: subhorizontal back, anterior view. 3: back angled 30° in comparison to reconstruction drawing redrawn from Huene 1928. Left femur length is 595 mm.

canted strongly medially, and the base of the fourth toe is perpendicular to the long axis of the metatarsus. It is unclear whether this difference is caused by intraspecific variation, or indicates that the two individuals belong to separate species.

The hindlimb digits of GPIT1 allow somewhat larger hyperextension angles than in the forelimb, indicative of a highly digitigrade to unguligrade stance just before toe lift-off. This adds to the greater effective limb length in the hindlimb compared to the lower hyperextension angles in the forelimb. Further indicators for digitigrady are the dorsoventrally flattened cross-sections of the metatarsal shafts and the lack of proximal-distal arching in the metatarsus, both indicating low craniocaudal bending moments.

#### Poses of the entire skeleton

In the following, both bipedal and quadrupedal poses are described, and their biomechanical implications are addressed.

**Bipedal poses.** For a bipedal, theropod-like posture, the hindlimb of *Plateosaurus* can be placed in accordance with the evidence on bone loading derived from longbone curvature and cross sections. The femur is inclined forward at a protraction angle around 20°. The knee is flexed, and the tibia and fibula inclined slightly posteriorly. The ankle is also slightly flexed, placing the metatarsus in a ver-

tical or, more probably, sub-vertical position at mid-stance (Figures 1.2, 9.1, 9.2, Video 1).

Any bipedal posture is only feasible if the COM is supported by the hindfeet. If the COM rests close to the hips, the exact orientation of the vertebral column does not matter. If it is placed further forward, so that the hindlimb does not support it when the back is in a subhorizontal position, the simplest way to change the anteroposterior position of the COM is to tilt the vertebral column. The steeper it is placed, the further back the COM moves. Huene 1928 suggested a fairly steep position for rapid locomotion (Figure 9.3), similar to the then prevailing view of *Iguanodon* (Dollo 1893) and other bipedal dinosaurs. Later, a paradigm shift led to almost universal agreement that most dinosaurs had subhorizontal backs when walking bipedally (e.g., Norman 1980; Bakker 1986; Paul 1987). The main reason for the latter posture is the far greater femur retraction range that it allows compared to a more upright posture. *Plateosaurus* can be placed bipedally in either position (Figures 1.2, 9.1-3), but the more upright posture limits locomotion speed significantly. An upwards angle of at least 45° is required for the long axis of the sacrum to create a significant backwards shift of the COM. However, already at 30° (Figure 9.3), the femur must be retracted to the level of the ischia, so that only very small steps are possible. Also, if the

COM lies so far posteriorly that this pose (30° upwards rotation) is balanced, rotating the body around the hips requires very little energy, due to the small moment arm. Therefore, it seems more reasonable to assume that a bipedal *Plateosaurus* might feed with a steeply inclined vertebral column (Figure 9.3), but use a subhorizontal posture (Figure 1.2) for locomotion.

In a bipedal pose with a subhorizontal back, the neutral pose of the vertebral column leads to a head position above the highest point of the back. The animal can thus cover a 360° arc by a small neck motion alone, i.e., there is no blind area. In order to bring the snout to the ground, e.g. for drinking, a slight increase in hindlimb flexion and moderate ventriflexion of the anterior two thirds of the thoracic vertebral column and maximum ventriflexion of the neck is sufficient (Mallison in press, contra Huene 1928), but even a slight seesaw motion that rotates the anterior body down (as suggested to be necessary by Huene [1928]) does not inhibit rapid flight. In contrast, to bring the hands to the ground for grasping requires significant flexion of the hindlimbs, with greatly increases joint torques required to sustain the pose. Essentially, the animal must kneel or squat down when manipulating objects at ground level for a prolonged time, or use a front limb for support. Dual-handed grasping is then impossible. Rainforth's (2003) re-description of the ichnofossil *Otozoum* pointed out that one track shows a bipedal animal, potentially a prosauropod, using both hands, palms facing medially, to support itself, probably while squatting down.

**Quadrupedal poses.** In a quadrupedal pose the forelimbs must be able to take strides of a significant length. If a stride length of only 0.4 m is to be possible, the height of the glenoid above the ground when placing the manus on the ground can not be more than 0.6 m. Due to this extremely short forelimb length, the vertebral column slope downwards so that the 1<sup>st</sup>dorsal – 2<sup>nd</sup>sacral line slopes by 19° for a digitigrade (Figure 10.1), and 9° for a semi-plantigrade model (Figure 10.2). In a fully plantigrade (FVP) model, whether with a strongly protracted or nearly vertical femur position, the head is at or slightly above the same height as the sacrum (Figure 10.3-4). These postures bring the manus on the ground without introducing strong ventriflexion in the dorsal series, and retain room for femur excursions during locomotion. The effective forelimb/hindlimb length ratios (i.e., height of glenoid divided by height of acetabulum in mid-stance pose) are 0.45 for the digitigrade, 0.54 for

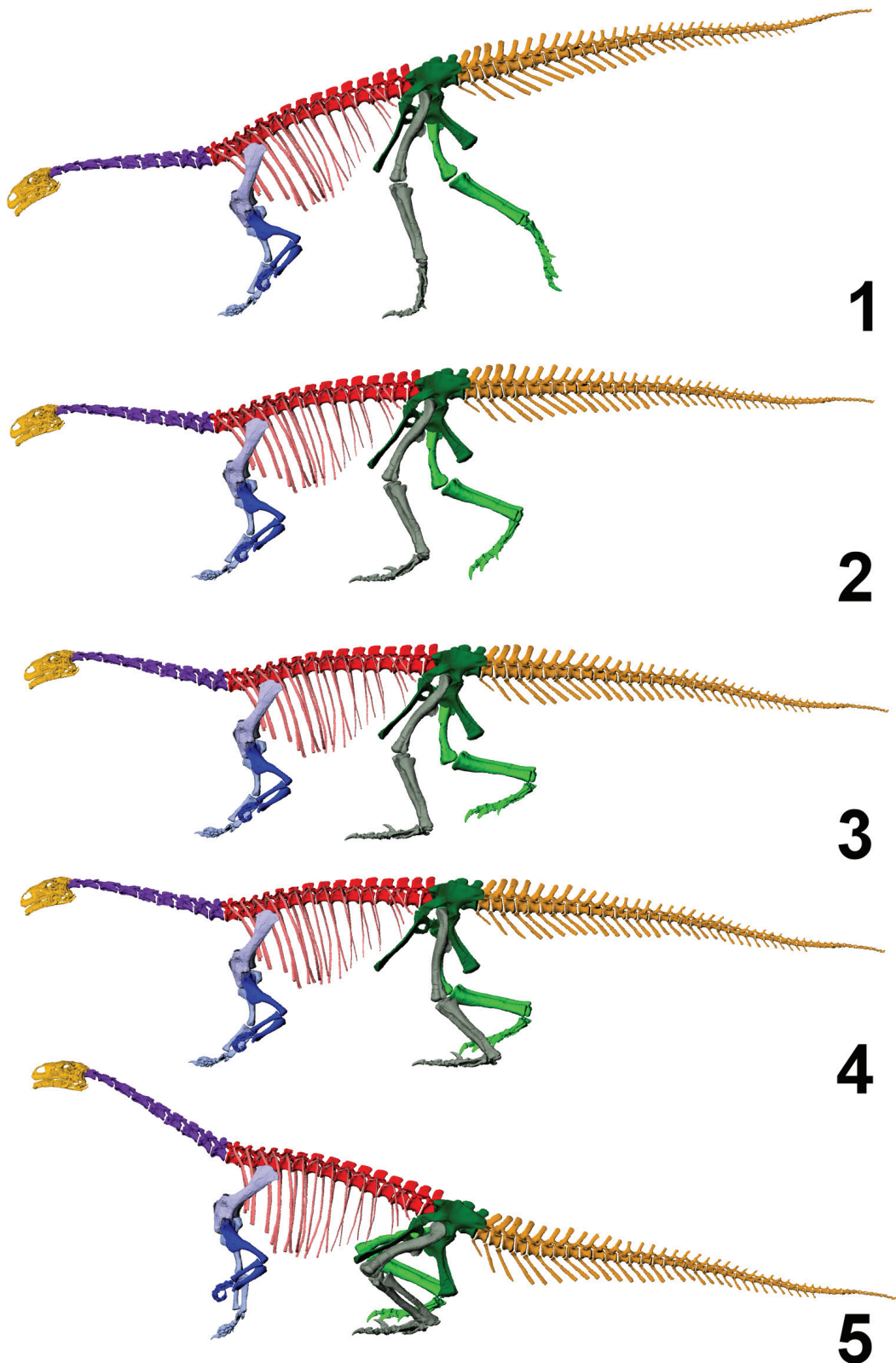
the semi-plantigrade, and 0.59 for the plantigrade model. In all these positions the motion of the hindlimb is significantly limited compared to a bipedal posture. In the digitigrade model, the femur can be protracted roughly 20° less than in a bipedal pose, reducing stride length. In the semi- and plantigrade models, limb protraction requires extreme flexion of the ankle while the free limb passes the supporting limb, due to the great length of the pes compared to the tibia. In such a pose femur retraction cannot be the main component of protraction unless the animal uses a sprawling posture, in direct contradiction to the osteological evidence (see Gatesy 1990).

Subequal fore and hind limb lengths cannot be created, even with a pronated manus and parasagittal forelimbs, as it requires femur protraction to beyond the pubes at midstance, and to subhorizontal for limb protraction (Figure 10.5, Video 3). Note that in this position the height of the glenoid was artificially increased to 0.7 m by using a standing instead of a walking pose in the forelimb. This position does not allow proper walking at all, as it limits stride length to 0.2 m.

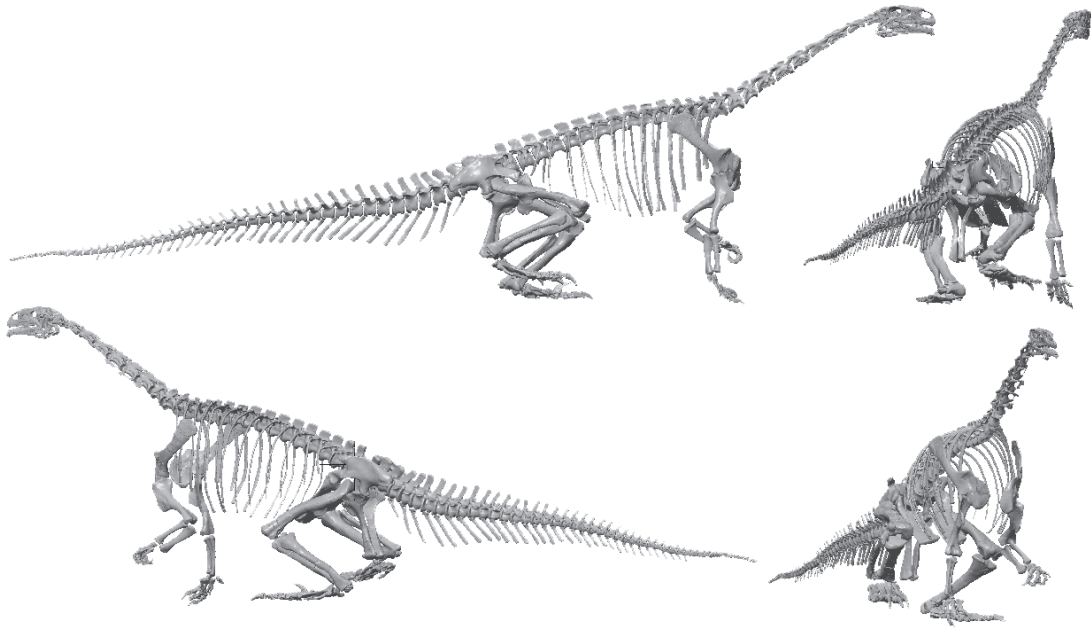
However, all these poses were created with a pronated manus. If the forelimb is placed in correct articulation with regards to the wrist and elbow, strong humerus abduction is required to turn to palm ventrally. This would essentially create a sprawling pose. However, it is not possible to rotate the humerus around its long axis to create a subvertical antebrachium, so that the animal would touch the ground with its ribcage. If the hindlimbs are placed in a sprawling position (following Fraas 1912; contra Huene 1926, 1928; Gatesy 1990; Christian and Preuschoft 1996; Christian et al. 1996), the femora must be disarticulated from the pelvis, and the tibia and fibula must be disarticulated from the distal femoral condyles. Alternatively to a sprawling pose, *Plateosaurus* might have walked on non-pronated hands, but Bonnan and Senter (2007) show clearly that the required adaptations are missing.

A potentially negative effect of the only quadrupedal poses in which the hindlimbs can be moved in a realistic gait cycle (hindlimbs digitigrade, Figure 10.1) is the forwardly inclined vertebral column combined with the low shoulder height. At neutral articulation of the neck, the view the animal can see is quite limited. A blind angle extends posteriorly, and lateral excursions of the neck to 'check six' result in a large blind area on the contralateral side. Extreme dorsiflexion of the neck is required to bring the head to a sufficient height so





**FIGURE 10.** Virtual skeleton of GPIT1 in quadrupedal poses in lateral view. 1: Digitigrade, 2: semi-plantigrade, 3: plantigrade hindlimb. 4: as 3, but with vertically positioned femur at midstance. 5: equal limb length posture. Length of left femur is 595 mm.



**VIDEO 3.** Virtual skeleton of GPIT1 *Plateosaurus engelhardti* in quadrupedal posture with equal effective fore and hind limb lengths. For full video, see website.

that a 360° view is possible. While possibly feasible when feeding, during rapid locomotion such a neck position carries a high risk, because all articulations are at their bony stops. Therefore, even slight impulses, e.g., from stumbling, can lead to serious injury. Extant animals appear to carry their necks close to neutral articulation during rapid locomotion (Christian and Dzemplski 2007), potentially because of this risk. For *Plateosaurus*, running in a quadrupedal posture carrying the neck near neutral articulation leads to a head height below hip height, close enough to the ground that a misstep in the forelimbs leads to an impact on the ground.

A further potential disadvantage is the maximum possible head height, and thus size of the feeding envelope. The base of the neck is at two thirds the height of a bipedal pose (0.99 m compared to 1.49 m). Additionally, in a bipedal pose the animal can tilt the body up to increase shoulder and thus feeding height (Figure 9.3). While *Plateosaurus* could theoretically be envisaged as an obligate quadruped that uses quadrupedal gaits for slow locomotion, then gets up into a bipedal pose to feed, and then back down again into a quadrupedal stance for locomotion, this makes sense only if there are bipedal stances suitable for feeding but not for locomotion. These could only be postures with a steeply inclined vertebral column, akin to a

rearing elephant. However, as shown above, there are no bipedal poses that do not allow locomotion.

### Body mass

The CAD model of *Plateosaurus* based on GPIT1 has a total volume of 740 l. There are no indications of air sacs invading bone to form post-cervical pneumatic cavities in *Plateosaurus* or other prosauropods (Wedel 2007), but the dorsal vertebrae show shallow troughs on the centra. In combination with the ability to breathe through rib motion, this indicates that prosauropods probably possessed pulmonary air sacs. An extant phylogenetic bracket (EPB) approach (Witmer 1995) confirms this: both theropods and sauropods had (and have) bird-like lungs (Perry and Reuter 1999; Wedel 2005, 2007; O'Connor and Claessens 2005), as indicated by the extensive pneumaticity of their skeletons. Birds have densities as low as 0.73 kg/l (Hazlehurst and Rayner 1992), and sauropod density is therefore probably best assumed to be about 0.8 kg/l or even lower (Wedel 2005). Crocodiles have lungs that, albeit simpler in structure than those of birds, are interpreted as a preadaptation for the formation of true air sacs and a unidirectional lung (Perry 1998; Farmer and Sanders 2010). Therefore, it is most parsimonious to assume the existence of small pulmonary air sacs in *Plateosaurus*, even though they did not invade

bones and thus left no clear marks on the preserved parts of the animals. Rib motion probably was the main mode of lung ventilation in *Plateosaurus*, because the architecture of the costovertebral articulations (dual headed hinge joints) is the same as is generally the case in saurischians (basal Saurischia: Langer 2004; *Tyrannosaurus*: Hirasawa 2009), and the air exchange volume can be estimated at a value typical for birds (Mallison in press). The air sacs may have been large, but in the absence of solid evidence (skeletal pneumaticity) for a large size they must be assumed to have been so small that the overall density can be modeled on that of extant terrestrial vertebrates. As a consequence, the average density should cautiously be assumed at a value between 0.9 kg/l and 1.0 kg/l.

Additionally, density is not uniform across the entire animal, and various body parts were accordingly given values that reflect the relative abundance of bone, flesh, intestines, and air volumes in them. Skull, tail, limbs, and the pelvic region are assumed to be heavier than water ( $d = 1.05$  kg/l to  $1.1$  kg/l), while the neck and anterior trunk region are significantly lighter ( $d = 0.7$  kg/l). This basic model has an average density of  $0.94$  kg/l and a total weight of  $693$  kg. Variations of the density of model parts to account for different soft tissue amounts, details of which are given in Table 1, result in average densities between  $0.89$  kg/l and  $1.13$  kg/l. The basic model has a very posteriorly placed COM, so most variations were designed to move the COM forward. This was achieved by reducing the mass of the tail and posterior trunk, and/or increasing the mass of neck and anterior trunk. However, one variant was produced in which the limbs were given higher density, too, although this partly cancels the effect that a heavier neck and anterior body have on shifting the center of mass. Total mass varies between  $600$  kg and  $838$  kg. Scaled to the size of the largest and smallest known individuals (total length  $10$  m and  $4.8$  m, Sander and Klein 2005) of *Plateosaurus*, the basic model gives a weight range from  $476$  kg to roughly  $4300$  kg for an average density of  $0.89$  kg/l.

#### Position of the center of mass (COM)

In the basic model, the COM rests  $0.23$  m in front of and  $0.16$  m below the acetabulum in a bipedal standing pose. The mass variations result at most in an anterior shift by  $0.06$  m to  $0.29$  m (Table 1). The dorsoventral shift is negligible.

**Bipedal poses.** In the bipedal poses created on the basis of a best fit of the skeletal elements, in all

but one the COM rests comfortably above the support area (Figure 11.1). This is true in both the digitigrade and the semi-plantigrade pose, and requires only modest femur protraction (maximum value  $20^\circ$  from vertical, in combination with a fully digitigrade stance and a metatarsus inclination of  $65^\circ$  from horizontal). For the most front-heavy mass variation at full digitigrady the COM plots just in front of the longest digit. Femur protraction to  $25^\circ$  ( $+5^\circ$  compared to the basic model) brings the support area under the COM in this model.

**Quadrupedal poses.** In all models with an inclined femur the COM plots in the support area of the hind foot or at its anterior edge, unless the lower hindlimb is placed at an unrealistic strong posterior inclination (as in Figure 10.4). If the hind limb is posed as deemed anatomically correct here, with a protracted femur, limited knee and ankle flexion and fully digitigrade, the ratio of effective limb lengths is  $0.45$ , and the hindlimb carries between  $90\%$  and all of the weight. Unrealistically flexing the knee so that the tibia is strongly inclined leads to a maximum of  $35\%$  of the weight supported on the forelimbs, albeit with a low effective limb length ratio of  $0.52$ . Increased limb flexion, which results in less massively unequal limb lengths, moves the support area forward, due to increases in femur protraction and ankle flexion. In fact, even absurdly light-tailed versions of the model with a significantly inflated pectoral region and neck have a COM plotting solidly within the area of the hindfoot in mid-stance at effective limb length ratios between  $0.7$  and  $1$ . Subequal fore and hind limb lengths in a sprawling position place up to  $40\%$  of the weight on the forelimbs but are osteologically impossible.

Models with a vertical femur position place more weight on the forelimbs, by shifting the support point of the hind limbs posteriorly. However, they either require a strongly inclined position of the lower hindlimb, which creates large bending moments because of the long moment arm of the COM and high torques in the knee and ankle joints, or cause an extreme difference in limb length. In extant animals with parasagittal limbs, the hindfoot is almost always placed under the hip joint, or close to such a position. The *Plateosaurus* models with a vertical femur and strong limb flexion, however, result in a foot position far behind the acetabulum. Such a posture causes extreme flexing moments in the knee and ankle, and can thus be dismissed as unrealistic, especially considering the short moment arms of the extensor muscles of the ankle and knee. The alternative pose, with a steeply placed lower hindlimb (low limb flexion),

**TABLE 1.** Mass variations of CAD model of *Plateosaurus engelhardti*. For each model version, the densities and masses for all model parts are given, along with the resulting average density of the model and the shift in position of the COM in craniocaudal (d pos COM y) and dorsoventral (d pos COM z) direction relative to model 1 (basic model). Positive numbers indicate caudal/dorsal shift, negative numbers indicate cranial/ventral shift.

PART NAME	Model No.	1	1	2	2	3	3	4	4	5	5
	VOLUME	basic model DENSITY kg/l	basic model MASS kg	DENSITY kg/l	MASS kg	DENSITY kg/l	MASS kg	DENSITY kg/l	MASS kg	DENSITY kg/l	MASS kg
head	5.88	1.10	6.46	1.10	6.46	1.10	6.46	1.10	6.46	1.10	6.46
neck 1	1.50	0.70	1.05	0.70	1.05	0.80	1.20	0.80	1.20	0.80	1.20
neck 2	1.17	0.70	0.82	0.70	0.82	0.80	0.94	0.80	0.94	0.80	0.94
neck 3	1.48	0.70	1.03	0.70	1.03	0.80	1.18	0.80	1.18	0.80	1.18
neck 4	1.88	0.70	1.32	0.70	1.32	0.80	1.50	0.80	1.50	0.80	1.50
neck 5	2.17	0.70	1.52	0.70	1.52	0.80	1.73	0.80	1.73	0.80	1.73
neck 6	2.32	0.70	1.63	0.70	1.63	0.80	1.86	0.80	1.86	0.80	1.86
neck 7	6.20	0.70	4.34	0.70	4.34	0.80	4.96	0.80	4.96	0.80	4.96
trunk 1	41.03	0.70	28.72	0.70	28.72	0.80	32.82	0.80	32.82	1.20	49.23
trunk 2	75.47	0.70	52.83	0.70	52.83	0.80	60.37	0.80	60.37	1.20	90.56
trunk 3	103.91	0.70	72.74	0.70	72.74	0.80	83.13	0.80	83.13	1.20	124.69
trunk 4	84.77	0.90	76.29	0.90	76.29	1.00	84.77	1.00	84.77	1.00	84.77
trunk 5	52.90	1.00	52.90	1.00	52.90	1.00	52.90	1.00	52.90	1.00	52.90
trunk 6	68.91	1.00	68.91	1.05	72.35	1.25	86.14	1.25	86.14	1.25	86.14
tail 1	31.92	1.00	31.92	1.10	35.11	1.25	39.90	1.00	31.92	1.00	31.92
tail 2	23.65	1.00	23.65	1.10	26.01	1.25	29.56	1.00	23.65	1.00	23.65
tail 3	25.77	1.00	25.77	1.10	28.35	1.25	32.21	1.00	25.77	1.00	25.77
tail 4	23.46	1.00	23.46	1.10	25.80	1.25	29.32	1.00	23.46	1.00	23.46
tail 5	11.47	1.00	11.47	1.10	12.61	1.25	14.33	1.00	11.47	1.00	11.47
tail 6	8.72	1.00	8.72	1.10	9.59	1.25	10.90	1.00	8.72	1.00	8.72
tail 7	3.84	1.00	3.84	1.10	4.22	1.25	4.80	1.00	3.84	1.00	3.84
tail 8	2.07	1.00	2.07	1.10	2.28	1.25	2.59	1.00	2.07	1.00	2.07
thigh	51.26	1.00	51.26	1.10	56.39	1.25	64.08	1.25	64.08	1.25	64.08
shank	12.74	1.00	12.74	1.10	14.02	1.25	15.93	1.25	15.93	1.25	15.93
foot	4.72	1.00	4.72	1.10	5.20	1.25	5.90	1.25	5.90	1.25	5.90
toes	3.29	1.00	3.29	1.10	3.62	1.25	4.11	1.25	4.11	1.25	4.11
arm complete	7.38	1.00	7.38	1.10	8.12	1.25	9.23	1.25	9.23	1.25	9.23
total axial	580.46	0.86	501.44	0.89	517.97	1.01	583.58	0.95	550.85	1.10	639.01
total hindlimb	72.02	1.00	72.01	1.10	79.22	1.25	90.02	1.25	90.02	1.25	90.02

Table 1 (continued).

PART NAME	Model No.	1	1	2	2	3	3	4	4	5	5
	VOLUME	DENSITY kg/l	MASS kg	DENSITY kg/l	MASS kg	DENSITY kg/l	MASS kg	DENSITY kg/l	MASS kg	DENSITY kg/l	MASS kg
total forelimb	7.38	1.00	7.38	1.10	8.12	1.25	9.23	1.25	9.23	1.25	9.23
total complete	739.26	0.89	660.24	0.94	692.64	1.06	782.07	1.01	749.34	1.13	837.50
av. density			0.8931		0.9369		1.0578		1.01		1.1328
d pos COM y (m)			0		0.023		0.026		-0.06		-0.062
d pos COM z (m)			0		-0.003		-0.005		-0.004		0.003

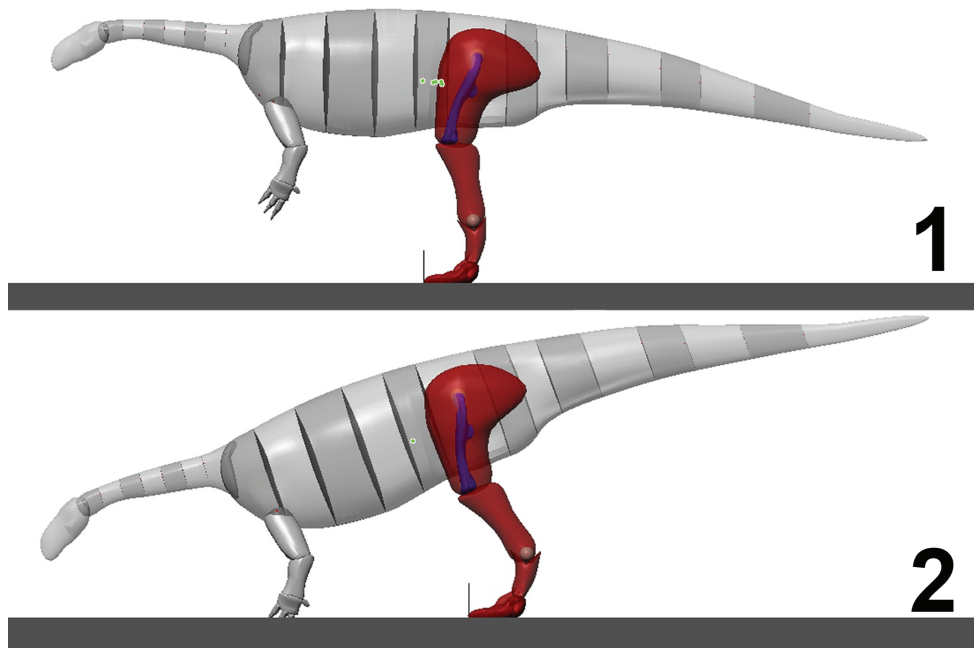
causes similarly low limb length ratios as those models with an inclined femur and a slightly flexed hind limb. At most, using the unreasonable mass distribution of the most front-heavy model ( $d = 1.13$  kg/l), the forelimbs carry about 41% of the body weight (Figure 11.2), with a limb length ratio of 0.45. Note, however, that for this hindlimb posture the acetabulum is not above, but far in front of the point of support, and the hind limb thus permanently subjected to large bending moments.

In all quadrupedal poses that do not shift the pectoral girdle to an absurdly low position on the ribcage, the COM lies significantly higher than the glenoid (e.g., at 1.5 times the height in the model shown in Figure 11.2). This means that the stability of the anterior body part when supported by only one forelimb is reduced compared to the pattern seen in nearly all extant quadrupeds, in which the limb articulation with the trunk rests higher than or roughly at the level of the COM.

**Stability of slow gaits.** The extremely posterior position of the COM has consequences for the stability of even slow gaits. Slow locomotion means that the body, due to its low moment of inertia, has ample time to react to small lateral imbalances. Unless one is balanced well, much energy is expended correcting the balance instead of moving forward. When walking slowly and bipedally, the body must sway laterally or the feet must be placed

in front of each other, on the track midline, so that the COM passes exactly over the support area. These two solutions, or any combination of them, require strong limb adduction to bring the foot under the COM. A more longitudinal support area, such as a plantigrade instead of a digitigrade foot, or quadrupedal instead of bipedal gaits, reduce the risk of toppling as well as the need to adduct the hindlimbs fully. A wider track is possible, creating a wide support triangle (Henderson 2006). To be effective, the quadrupedal posture should thus increase both the width and the length of the support area compared to a bipedal pose. The latter, a minor factor, is obviously the case in practically any quadruped, but the former relies on allowing a wider track in the forelimbs and hindlimbs for creating a wide support triangle when any one limb is lifted.

In *Plateosaurus* this is not the case in any osteologically possible quadrupedal pose, even assuming manus pronation, as is best shown by a test of the balance in a three-point support pose. If a hindfoot is lifted off the ground in a CAE model, using the most front-heavy mass variant, in a standing pose with only  $10^\circ$  femoral abduction in both limbs, the animal tends to topple caudolaterally, because the COM lies behind the support triangle formed by the forefeet and the remaining hindfoot. The supporting hindlimb must be



**FIGURE 11.** CAD 3D model of GPIT1 in lateral view. 1: bipedal pose. 2: quadrupedal pose with most anterior COM position. Green dots indicate position of the COM for all (1) and most front-heavy (2) model variations.

adducted to nearly the same angle as in a biped to avoid this. Therefore, a quadrupedal pose does not offer a significant advantage with regard to stability, because an accidental imbalance in the supporting hindlimb is as dangerous as in a bipedal stance. A detailed discussion of walking cycles in *Plateosaurus* is beyond the scope of this paper.

**Potential trackways.** The virtual skeleton cannot be placed in a quadrupedal pose that allows normal locomotion. Therefore, none of the quadrupedal trackways assigned to prosauropods, such as *Tetrasauropus unguiferus* (Ellenberger 1972) or *Navahopus falcipollex* (Baird 1980) were created by a plateosaurid. In contrast, the skeleton can be placed to conform to the ichnofossil *Otozoum moodii* (Hitchcock 1847, Rainforth 2003), contra Farlow (1992). Porchetti and Nicosia (2007) fitted the scaled-down pes of *Plateosaurus* into the track of *Tetrasauropus* in a plantigrade stance. As shown, this posture is highly unlikely for *Plateosaurus*.

## DISCUSSION

The total body volume and mass obtained for *Plateosaurus engelhardti* falls within the range of previous estimates. Seebacher (2001) calculated 1073 kg for AMNH 6810, an animal roughly the same size as GPIT1. Gunga et al. (2007) con-

structed two CAD models based on a high resolution laser scan of the mount of GPIT1. One of the models has significant volumetric errors (Mallison in press) and results in a weigh estimate of 912 kg. The other model follows the contours of the mount closely and results in a 630 kg estimate. Sander and Klein (2005) estimate the largest individuals of *Plateosaurus* to have reached 4000 kg at an overall length of 10 m, which is nearly identical to the results presented here. Henderson (2006) derived a total mass of only 279 kg for *Plateosaurus* by 3D mathematical slicing. However, it seems that the scale of the drawing cited by Henderson (2006: p. 919) as source data (Paul 1987) has been unintentionally altered. The animal is roughly two thirds as long as GPIT1, much smaller than the smallest known individual of *Plateosaurus* (4.8 m total length, Sander and Klein 2005). Scaling the model used here down to equal size as Henderson's 2006 model results in a mass of 418 kg (d = 0.6 kg/l neck, 0.9 kg/l remaining body parts as in Henderson 2006). The main reason for the discrepancy in total mass appears to be the more slender belly of the model used by Henderson 2006, which is unusual for a herbivore. Also, the drawing the model is based on has a relatively slender tail and hindlimbs.

Posing the virtual skeleton of GPIT1 digitally resulted in a bipedal pose in which the COM is well supported by the support area formed by either one adducted foot, or both feet with the limbs held vertically in anterior view (Figures 1.2, 9.1-2). Bipedal locomotion appears easily possible at any speed, because the feet can be adducted at mid-stride sufficiently to support the COM. Due to the wide pubes, very rapid locomotion with long strides requires significant abduction of the femora. Therefore, at a run *Plateosaurus* had to sway from side to side, or rotate the pelvis around the vertical axis. However, the claim by Moser (2003) that *Plateosaurus* could only take tiny steps in a bipedal pose is not supported by the virtual mount. A stride length of 1.34 m is easily possible for GPIT1, without requiring any abduction of the femora (Mallison in press). Rather, the stride length limitation is true for the extremely upright pose suggested by Huene (1926, see Figure 9.3). While rapid running gaits probably require massive abduction of the femora, rapid walking can easily be achieved bipedally with a subhorizontal back, as the femur can easily cover a 65° angle without significant abduction (Mallison in press). Additionally, a bipedal, digitigrade pose appears to create bending moments in the limb bones that conform to the observed shapes; however, a detailed biomechanical analysis is required. It also frees the manus for other uses than locomotion, e.g., inter- and intraspecific combat or manipulation of food.

None of the tested quadrupedal poses offers any locomotory advantage over a bipedal pose, because neither mobility nor stability is increased. To the contrary, locomotion is limited to extremely slow speeds, and energetically ineffective due to high flexion angles in the hind limb joints in most tested postures. The problem of limited femur protraction at low abduction angles due to a collision with the pubes is aggravated compared to a bipedal pose. Additionally, a quadrupedal pose either does not place a significant part of the weight on the forelimbs, or exposes them to high compressive loads while inhibiting the step cycle in the hindlimbs through extreme flexion. Furthermore, the potential feeding envelope in a quadrupedal stance is smaller, and circumferential vision is limited to an extreme neck posture, while a bipedal stance offers easy 360° sight.

It seems counterintuitive that *Plateosaurus* should have used a posture and gaits that offer no advantage, while suffering from several potentially severe restrictions. For very slow locomotion over an unusual substrate, a slippery, muddy river bank,

at least one ornithischian adopted a very clumsy quadrupedal gait (Wilson et al. 2009), and for such circumstances or for climbing steep inclines *Plateosaurus* may have similarly used a crawl on all fours. However, the pedal morphology of *Plateosaurus* is more similar to the theropod discussed by Wilson et al. (2009) that did not use a wide-gauge, crawling quadrupedal gait on the same substrate, so that even this possibility seems unlikely. For normal locomotion, it appears unreasonable for *Plateosaurus* to have adopted a quadrupedal posture, even if one assumes that manus pronation was somehow possible without strong humeral abduction.

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