



# Mechanical analysis of the wide-hipped titanosaur *Savannasaurus elliottorum*

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## Abstract

Fossil material of the wide-hipped titanosaurian sauropod *Savannasaurus elliottorum* from the Winton Formation has been described precisely. The authors, Poropat et al. (2020), reconstruct the original owner of the bones and draw well-founded conclusions about the evolution of *Savannasaurus* by connecting its body shape with its environment. These conclusions are in the sense of Bock and von Wahlert (in *Evolution*, 19, 269–299, 1965), on the level of the ultimate “Biological Role”. In fact there are also arguments on the level of the more proximate “Mechanical Function” to strengthen this view. The investigation of the mechanical conditions leads to a confirmation of the conclusions drawn by the authors of the study, now on the proximate level of “Function”. Like each functional analysis it bridges the gap between the morphological trait and the use made of it during lifetime. The mechanical stresses (or internal forces) evoked by forces acting on it from outside (or the external forces) are the immediate causes which dictate its shape; in the case of fossils, the shapes of skeletal elements.

**Keywords** Biomechanics · Wide gauged tracks · Ground reaction forces · Area of support · Pelvis · Shoulder girdle

## Introduction

Poropat et al. (2020) describe exactly fossil material of the wide-hipped titanosaurian sauropod *Savannasaurus elliottorum* from the Winton Formation. The find comprises one neck vertebra, most of the vertebral column of the trunk, ribs, pelvis and nearly the complete forelimb. Most characteristic are the breadth, the barrel-shape of the trunk in contrast to the narrow, compressed trunks of other sauropods, and the width of the pelvis. Limbs are robust, and the gait obviously wide-gauged. The authors reconstruct the original owner of the bones and draw well-founded conclusions about the evolution of *Savannasaurus* by connecting its body shape with its environment. These conclusions are in the sense of Bock and von Wahlert (1965) on the level of the ultimate “Biological Role”. In fact there also are solid arguments on the level of the more proximate “Mechanical Function” to strengthen this view. This is what I am intending in this article.

## Methods

The essence of the methods used here is looking at the whole organism as a mechanical construction and investigate it from the viewpoint of an engineer. The approach implies two aspects: First, the *statics* of the respective animal or its parts must be looked at, second, the *kinetic* conditions during locomotion, or during acquisition and intake of food must be taken into consideration. Details of methods and procedures depend upon the investigated material and can be found in Preuschoft (in press) and earlier publications of the author.

## Results

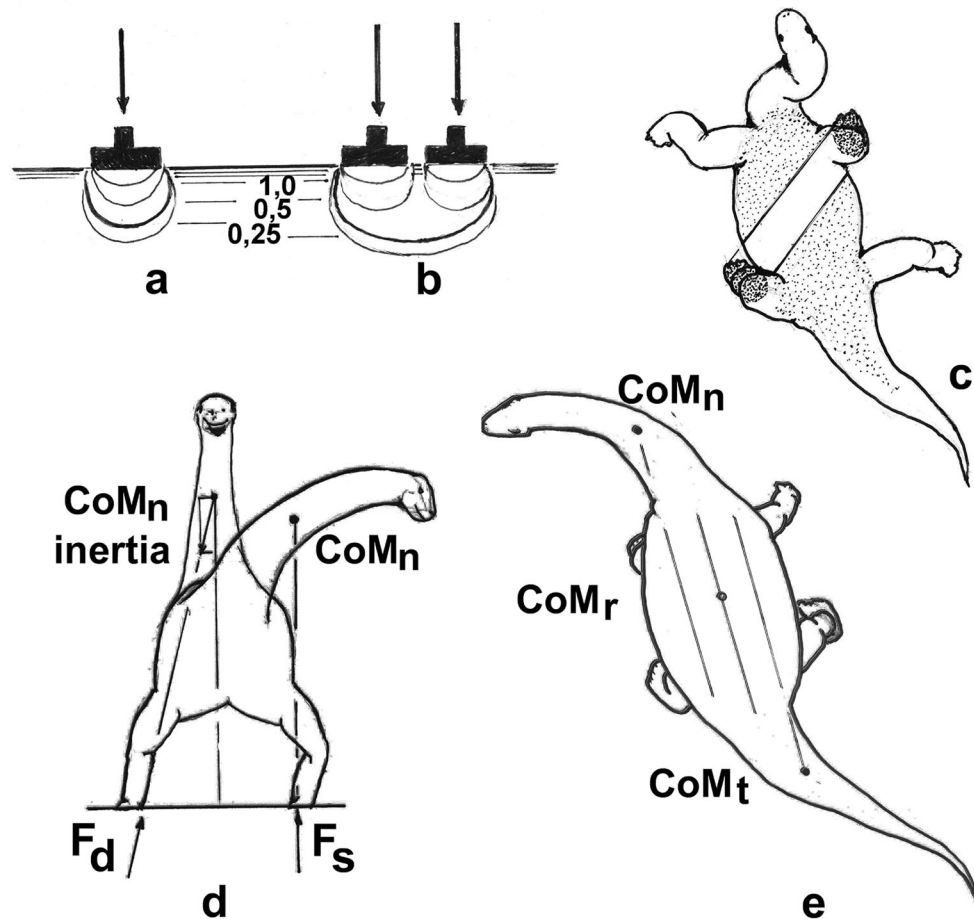
Wide gauged locomotion is claimed by Poropat et al. (2020), unfortunately without reference to original literature. The information seems to be taken from Coombs Jr and Molnar (1981). Underneath the autopodia, pressure in the ground distributes gradually, similar to onion-shells (Fig. 1a). If the individual footprints are close together, the “onion-shells” fuse and increase the local pressure by the ground reaction force (GRF) exerted by the second foot. This leads to deeper insertion of the respective autopodium (Fig. 1b). This effect is

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**Fig. 1** “External” forces acting against a *Savannasaurus*. **a, b** Compression propagated underneath one foot (**a**) or two feet (**b**) has nearly the same value (0.25), but if two feet are loaded close to each other, nearly twice the forces are acting and therefore roughly the twofold stress is acting against homogenous ground, which sooner will give way (Data from Nobiling, 1977). **c** *Savannasaurus*, seen from above, neck held upright and therefore shortened. Within the outline, the area of support (white band) is shown between the diagonal limbs. The soles of the autopodia which carry weight during their stance-phases are emphasised in dark grey, and the ventral surface of the trunk plus proximal tail, both resting on soft, muddy ground are illustrated in light grey. The size of this area reduces the local forces exerted against the

supporting underground. **d** *Savannasaurus* in anterior view, with CoM of the long neck flexed to the left of the animal. Ground reaction force  $F_s$  is directed vertical. In addition, on the right side of the animal the resultant of weight force and inertial force is shown, if the head and neck are moved to the right. It evokes the GRF named  $F_d$  and meets the ground only if the limb is sprawled. **e** The same animal seen from on top. The flexion of the neck to the left side causes a shift of the neck’s CoM<sub>n</sub> (marked by a dot), and makes a wide-gauged position of the forelimb useful. The same holds true for the tail (CoM<sub>t</sub>). The CoM<sub>r</sub> of the trunk (marked by a small black circle in the middle) is ignored, because it does not necessarily move with neck or tail

reliably diminished if the imprints of the manus or pes are kept widely apart – as is the case in wide-gauged locomotion.

On soft ground, which does not sustain the GRF, the feet may sink in deeply, until the ventral surface of the trunk gets into contact with it (Fig. 1c). Because the belly’s area is very large (roughly estimated about 10 times the area of one front plus one hindfoot), the animal will easily remain in its position, which is similar to “belly dragging” as described by Nyakatura et al. (2013). Sprawling limbs can be abducted, the autopodia lifted as high or higher than the dorsum of the animal, and this permits much more freedom for swinging forward to make the next step or for seeking a better, new support.

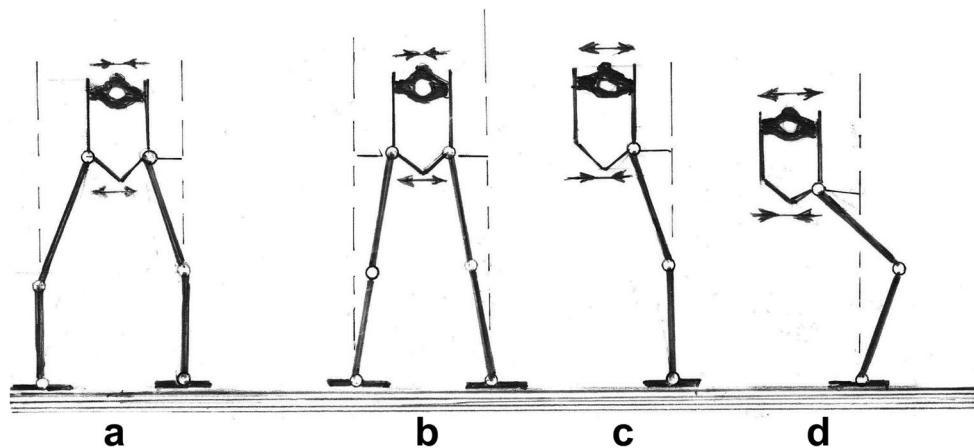
All this raises the question *why* the more energy-requiring position is assumed. A plausible reason is proposed in Preuschoft and Gudo (2006): Lateral excursions of the long neck shifts additional load to the forelimb on the concave side (Fig. 1d). This shift may lead, because of the length of the neck, to a position of the CoM lateral to the supporting limb, provoking torques, which unburden the contralateral autopodium, and make a more pronounced abduction of the foot advantageous. But, moving the long neck towards the left side (as in Fig. 1e) requires overcoming of the neck’s considerable mass moment of inertia, and therefore increases the horizontal component of load on the forelimb on the convex side during a short time

interval. The translation of neck mass can be counterbalanced to some degree by a lateral flexion of the tail in the opposite direction (Fig. 1e). In spite of this, the necessity to provide a very broad area of support remains the same, although it consumes additional muscle force. Because the trunk is not moved, it can be and has been left out from our consideration.

The **pelvic girdle** (depicted in fig. 20, and the sacrum in fig. 30 of the original paper by Poropat et al. 2020), shows an extended contact between the pubic bones of both sides. The symphyseal contact area is under tension (Fig. 2a, b) during standing, for example at rest. If a part of the body weight is carried by only one hindlimb (a stage inevitable for any sort of terrestrial locomotion!), the symphyseal region is compressed (Fig. 2c, d). Compression requires a considerable amount of pressure-resisting (bone) material – which in *Savannasaurus* indeed exists. In addition, this expanded pubis offers, in addition to the probably existing *M. caudofemoralis*, large areas for the insertion of the necessarily strong adductor muscles. A sprawling position and in particular a wide gauge of the hindlimbs makes the torques in the pelvic girdle greater than a narrow gauge would do. According to a paper of Christian et al. (1996), there exist Prosauropods and Sauropods, which have developed the opposite “adaptation”: keeping biacetabular width very narrow, so that the hip joints can be balanced reliably by the strong adductor muscles, without activity of the weak abductors (Fig. 2c, d). Evidently, the width of the pelvis in *Savannasaurus* leads to greater torques than a narrow pelvis would be exposed to. Therefore, the extension of the sacrum (as depicted in fig. 13, Poropat et al., 2020), just confirms what

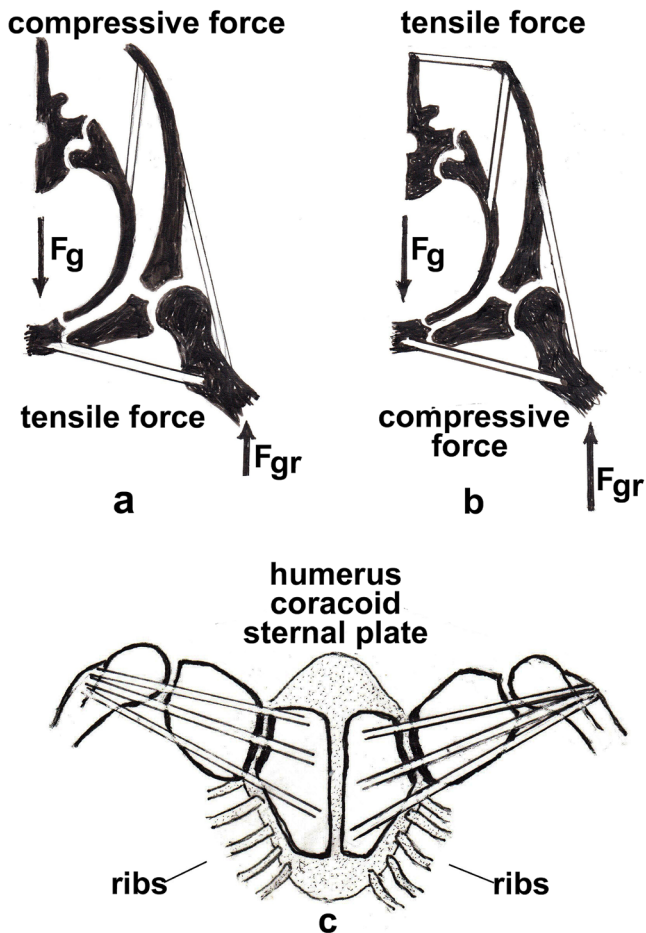
has been said above: massive bone construction offers strength against mechanical stress. The pubis of *Savannasaurus* is of uncommon, extreme strength and so can sustain high compressive and tensile forces. The sacrum, which closes the “ring” structure of the pelvis, consists in *Savannasaurus* of unusual four segments, whereas in other sauropods exist only two or three of them.

The **shoulder girdle** (shown in figs. 15 and 16 of the original paper by Poropat et al. 2020), includes the coracoid and the sternal plates. Again the sprawling position of the extremities leads to very high torques, simply because of the long lever arms of the ground reaction force (which is applied to the manus) at the shoulder joint. Hohn-Schulte has investigated in her thesis (Hohn-Schulte, 2010, see also Hohn, 2011) the shoulder region of the sauropod *Diplodocus* with the aid of the Finite Element Systems-method. Her results can be transferred largely to *Savannasaurus*: In the latter form (Fig. 3), the coracoid is not fused to the scapula (as realised in *Diplodocus* and *Brachiosaurus*), and extremely massive. Its medial margin is slightly rounded, so giving the impression that it was sliding along a contact with the sternal plate, like in lizards. The excavation on the sternal plate is visible and emphasised in the description. According to Hohn’s reconstruction the sternal plates are the bony cores of the partly cartilaginous origins for the pectoral muscle (Fig. 3c), which keeps the sprawling humerus in balance at the glenoid joint. The shapes of these structures fit perfectly to the assumption that *Savannasaurus* possessed a thorax much wider than in other sauropods.



**Fig. 2** According to Christian et al. (1996), strong adductor muscles of the hip are common among all reptiles, while abductors are notoriously weak. Therefore, equilibrium against the moment of GRFs can best be maintained in the hip joint, if the pes is placed lateral to the hip. In all drawings, **a–d**, the lever arm of the vertical component of GRF at the hip joint GRF is the same. The position of the knee is unimportant (**b, c, d**). This configuration is secured in *Plateosaurus* and in several Sauropods by a very narrow pelvis with short distance between the acetabulae (=interacetabular distance; Christian et al., 1996). This keeps the hip reliably medial to the GRF. The pelvis in

reptiles and mammals is exposed to contradicting stresses: If weight is supported by two limbs, as in standing, the symphysis is under tension (**a, b** horizontal arrows), and the sacrum compressed from one side to the other (**a, b**). If weight is supported by one limb alone, like in walking or trotting, the pubic region is under compressive stress, and the sacrum tensed (**c, d**). In the wide-hipped *Savannasaurus*, the width of the pelvis induces a markedly sprawling gait. This leads to particularly long lever arms and high forces in the pelvis which require high strength. (Inspired by Christian et al., 1996)



**Fig. 3** Schematic cross section through the shoulder region of a Titanosaur is sketched for two-limb support (a) and one-limb support (b). In the former, the sternal region is under tension. In the latter, the sternal area is compressed from both sides. The ways of loading are the same as those in the pelvis, shown in Fig. 2. The pectoral muscle must be active in one-limb support as well as in two-limb support. This in particular, if load arms (i.e. horizontal distance between manus and shoulder joint) are long. Contraction of the (strong) pectoral muscle evokes compressive stresses in the coracoid (which is traversed, Fig. 3 c) as well as in the sternal plates (from where the muscle takes its origin). In addition to the activity of the *M. pectoralis*, the *M. serratus*, which carries trunk weight, exerts in two-limb standing a dorso-medial torque at the scapula, because of which the (weak) abducting muscles must be activated. The dorso-medially directed torque becomes greater if only one limb supports trunk weight, since *M. rhomboideus* and *M. trapezius* are acting to sustain the tensile forces by which the free limb is suspended. Both muscles rotate the scapula medially. Their rotating moments are much smaller than that of body weight in the gleno-humeral joint, but anyway must be compensated by abducting muscles. (Inspired by Fig. 11.9 in Hohn, 2011). c Schematic view from ventral side on the major elements of the shoulder girdle. The size and exact outline of the cartilaginous sternal plate (stippled) are difficult to predict. It probably contained joints, like in modern lizards and crocodiles. In its centre, bony plates (white, heavy outlines) reinforce the cartilage. The humeri are abducted (as in sprawling positions) and three fibres of the *M. pectoralis* are illustrated as double lines. The system sustains compressive as well as tensile forces such as shown in Fig. 4. (Inspired by fig. 11.10 B in Hohn, 2011)

## General conclusion

The investigation of the mechanical conditions leads to a confirmation of the conclusions drawn by the authors of the study (Poropat et al., 2020) on the proximate level of “function” in the sense of Bock and von Wahlert (1965). Like each functional analysis it bridges the gap between the morphological traits (in the case of fossils shapes of skeletal elements) and their being mechanically loaded, and therefore the causes which dictate their shapes.

In addition, the foregoing analysis opens access to a more general observation: Several mammal-like reptiles (*Scymnognathus*, *Stahleckeria*, *Lystrosaurus* from the collection of the University of Tübingen) possess a reduced tail, and the rather heavy head typical of mammals. According to carefully made reconstructions, their hindlimbs are based on a pelvis with rearward extended ilium and pronounced post-coxal ischium, and seem to have been moved mainly in parasagittal planes. Their frontlimbs, however, are based on a shoulder girdle with strong and heavy ventral coracoids and clavicle. This indicates, like in sauropods, sprawled positions of the frontlimbs. The reasons behind this situation seem to be very similar to those described here. They are being investigated in an ongoing study of Preuschhof, Krahl and Wernburg (in prep.).

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## Declarations

**Conflict of interest** The author declares that he has no conflict of interest.

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