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MANUS CLAW FUNCTION IN SAUROPOD DINOSAURS

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ABSTRACT: The sauropod manus is characterised by phalangeal reduction on digits II-V and the presence of a claw on digit I. This claw is rarely seen in sauropod manus tracks. It has been suggested that the manus claw was used as a weapon, or played a role in feeding. These proposals, however, have not been tested against knowledge of the detailed structure and probable functional capabilities of the manus. Here, the anatomy of the best preserved sauropod mani is reviewed, with special emphasis on the structure of digit I. The shape, position, orientation and probable range of motion of the claw, suggest that it would not have made a very effective weapon. It may, however, have allowed the forelimb to grasp the trunk of a tree during "bipedal" high browsing. This would make the feeding position more stable and perhaps reduce the amount of muscular effort required. The Brachiosauridae probably did not need to employ this bipedal stance: instead the long forelimbs and vertical neck would have allowed browsing at high levels. This might explain the reduction of manus claw size in *Brachiosaurus*.

RESUMO: As mãos dos saurópodes são caracterizadas pela redução das falanges nos dedos II-V e pela presença de uma garra no dedo I. Esta garra raramente se observa nas impressões das mãos dos saurópodes. Tem sido sugerido que esta garra era usada como arma ou que tinha uma função na alimentação. Todavia, estas hipóteses não têm sido confrontadas com os conhecimentos da estrutura e funcionalidade das mãos. Neste artigo, a anatomia da mão melhor preservada é reavaliada, com particular cuidado no que respeita à estrutura do dedo I. A posição, forma, orientação e possível mobilidade da garra, sugere que não teria sido uma arma eficaz. Terá, sim, provavelmente ajudado o membro anterior a agarrar o tronco das árvores quando se erguiam apenas nos membros posteriores para alcançar a copa das árvores. Isto tornaria a posição bípede mais estável, durante o tempo em que se estavam a alimentar e talvez reduzisse o esforço muscular requerido. Os braquiosaurídeos, provavelmente, não necessitariam de adoptar esta posição bípede, pois os longos membros anteriores e o pescoço vertical permitir-lhes-iam alimentar-se nos ramos mais altos. Isto poderá explicar o menor tamanho das garras em *Brachiosaurus*.

INTRODUCTION

The tetrapod manus has been co-opted to serve a number of functions besides those associated with support and locomotion. In dinosaurs alone, we see the manus taking part in defence (*e.g. Iguanodon*, NORMAN, 1980) and grasping (*e.g. Prosauropoda*, GALTON, 1990). The relatively long forelimbs of sauropods and evidence from their trackways, leaves little doubt that these gigantic animals were habitual quadrupedal walkers (THULBORN, 1989). The robust nature of the sauropod manus, with the retention of a well developed fifth metacarpal, and the reduction of the number of phalanges on digits II-V, can also be related to the use of the forelimb during locomotion. The presence of a large claw on the pollex, therefore, is all the more puzzling. The probability that this claw would "snag" on ground debris (rocks, roots, etc.), suggests that this structure would hinder locomotion. This consideration, combined with the observation that manus claw imprints are rare in sauropod trackways (DUTUIT & OUAZZOU, 1980; JENNY & JOSSEN, 1982; ISHIGAKI, 1986; PITTMAN, 1989; FARLOW, PITTMAN & HAWTHORNE, 1989), has led to the proposal that the claw was held away from the substrate during locomotion (THULBORN, 1989). It should be noted, however, that sauropod manus tracks from the Morrison Formation (LOCKLEY, HOUCK & PRINCE, 1986), the Jurassic-Cretaceous of Niger (GINSBURG *et al.,* 1966), and the Middle Jurassic of Portugal (SANTOS *et al.,* 1994), do show claw marks. Thus, the possibility that the manus claw was occasionally used during locomotion (perhaps to gain purchase on particular substrates) cannot be ruled out at present. Indeed, THULBORN (1989) has suggested that both manus and pes claws were sometimes used in this way. Other authors have hypothesised that sauropods retained the large claw because it served some non-locomotor function, such as defence against predators (NORMAN, 1985), intraspecific combat (BAKKER, 1987), "pulling down vegetation" (THULBORN, 1989) or grasping tree trunks during high browsing (MCLOUGHLIN, 1979; TANIMOTO, 1991). Although plausible, these functions of the manus claw need to be examined with knowledge of the structure of the manus (especially digit I) in mind.

The large pollex claw is not unique to sauropods. Indeed, the use of different criteria for the estimation of relative size has led to disagreement over the taxonomic distribution of this "character". For example, CHARIG, ATTRIDGE & CROMPTON (1965) and GAUTHIER (1986) suggest that the Sauropodomorpha are characterised by the possession of a large claw on the pollex. UPCHURCH (1993) concluded that a "large" claw on digit I is present in at least some theropods as well as most sauropodomorphs, and did not include it in his cladistic analysis for this reason. SERENO (1989) listed the large claw as one of the synapomorphies uniting a monophyletic Prosauropoda. Whatever its true taxonomic distribution, we must ask why this large claw was retained in sauropods whilst the other manual digits underwent phalangeal reduction.

The search for the function (*i.e.* adaptive value) of the sauropod manus claw might be misplaced - the claw may have served no function. Instead, its presence in sauropods could have been maintained by some developmental constraint (perhaps a pleiotropic effect). It should be noted, however, that other dinosaurs were able to reduce or even lose the first digit. Sauropods themselves must have arisen from animals that possessed claws on digits II-IV. Most persuasive, is the fact that *Brachiosaurus* has greatly reduced the size of the pollex claw. It is, therefore, not unreasonable to hypothesize that the large manus claw was retained in the majority of sauropods because it served some "useful" function.

This paper examines the osteology of several well preserved sauropod mani and attempts to establish the functional capabilities of the pollex claw. In order for the manus claw to be used in feeding or fighting, sauropods must have been able to rear up into a bipedal stance. The evidence which suggests that sauropods could attain a bipedal stance is briefly reviewed here. Lastly, data on the structure and function of the manus is used to evaluate the various proposals for non-locomotor claw use.

THE STRUCTURE OF THE SAUROPOD MANUS

MATERIAL

Sauropod mani (as with their crania) are rarely well preserved. TABLE I lists the specimens upon which the following description is based. Some examples of the more complete sauropod mani are shown in Figure 1.

DESCRIPTION OF SAUROPOD MANI

Metacarpus: The sauropod metacarpus is very distinctive. The fifth metacarpal is very robust, especially compared to Mcs.III and IV. This situation is unlike that in other dinosaurs where the fifth metacarpal is often greatly reduced or lost. In most sauropod genera, Mcs.I and V are slightly shorter than Mcs.II-IV (Mc.III is usually the longest). However, in *Opisthocoelicaudia* and possibly *Alamosaurus,* Mc.I is the longest, although damage to the distal ends of Mcs.III and IV in USNM 15560 (see TABLE I) makes this difficult to confirm in the latter genus. The stoutness or robustness of sauropod metacarpals is variable. Brachiosaurids and camarasaurids appear to have relatively long and slender metacarpals compared to other sauropods (Fig. 1).

Sauropods typically have a digitigrade forelimb, with the metacarpals held in a vertically oriented "tubular" or semicircular arrangement (Fig. 2). As a result, the anterior portion of the manus is formed from Mcs.II-IV, with Mcs.I and V forming the posteromedial and posterolateral "corners" respectively. This arrangement, which has often been preserved in articulation (*e.g. Alamosaurus)* accords well with the "U"-shaped manus prints of sauropod trackways (FARLOW, PITTMAN & HAWTHORNE, 1989). Each metacarpal interlocks with its immediate neighbours in the proximal region of the metacarpus. Distally,

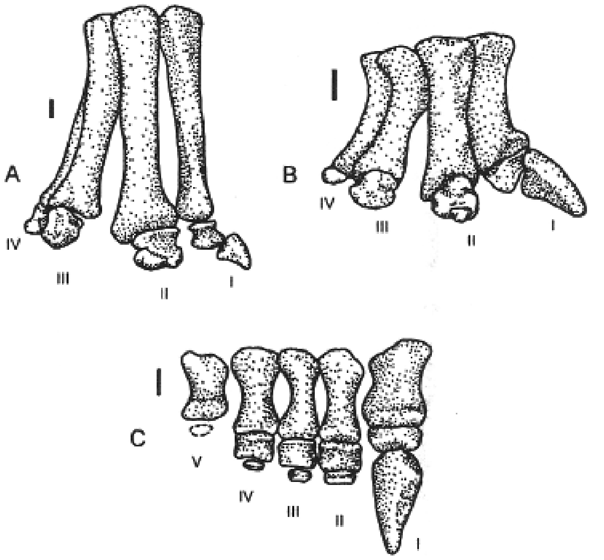

Fig. 1 - Sauropod mani: **A** - *Brachiosaurus brancai* (HMN SII, after JANENSCH, 1961), right manus in antero-internal view; **B** - *Janenschia robusta* (HMN Nr. 5, after JANENSCH, 1961), right manus in antero-internal view; **C** - *Shunosaurus lii* (IVPP T5402, after ZHANG, YANG & PENG, 1984), right manus in anterodorsal view. Scale bars: 50 mm.

TABLE I
Sauropod mani surveyed for this paper.

TAXON	SOURCE	INSTITUTION/ CATALOGUE Nº	PRESERVATION OF MANUS
Alamosaurus sanjuanensis	GILMORE (1946)	USNM 15560	Metacarpus only
Apatosaurus excelsus	HATCHER (1902)	CM563*	Complete (slight distortion of parts)
Apatosaurus louisae	GILMORE (1936)	CM3018	Complete
"Barosaurus lentus"	*Pers. obs.*	CM21744	Nearly complete (digit V, proximal end of Mc.III and distal end of ungual I-2 are missing)
"Bothriospondylus madagascariensis"	LAVOCAT (1955)	MHNP No. ? (on display)	Metacarpus only
Brachiosaurus brancai	JANENSCH (1961)	HMN SII	Complete
Camarasaurus grandis	*Pers. obs.*	FMNH P25126	Complete
Camarasaurus lentus	GILMORE (1925)	CM11338	Nearly complete (some parts obscured by matrix; some phalanges missing)
Janenschia robusta (= *"Tornieria robusta"*)	JANENSCH (1961)	HMN Nr. 5	Complete
Lapparentosaurus madagascariensis	OGIER (1975)	MHNP MAA 70, 95, 98-103, 142	Disarticulated metacarpals and phalanges (probably from more than one individual)
Opisthocoelicaudia skarzynskii	BORSUK-BIALYNICKA (1977)	ZPAL MgD-1/48*	Metacarpi only
Shunosaurus lii	ZHANG, YANG & PENG (1984)	IVPP T5402*	Complete
Vulcanodon karibaensis	RAATH (1972), COOPER (1984)	SAM QG24*	(?)Mcs.III-V, Ph.V-1

* Denotes those specimens not examined by the author (*i.e.* data were derived solely from the literature).

the metacarpals diverge slightly. Some trackways show sauropod manus prints with Mcs.II-IV bound together into a digital pad somewhat separate from Mcs.I and V (*e.g. Brontopodus*, FARLOW, PITTMAN & HAWTHORNE, 1989). Other trackways suggest a more truly semicircular arrangement, with Mcs.I and V more tightly bound to the central metacarpals (*e.g. Breviparopus*, DUTUIT & OUAZZOU, 1980, but see FARLOW, PITTMAN & HAWTHORNE, 1989 for comments). Unfortunately, it is not yet possible to assign these different tracks to particular sauropod taxa on this basis.

"U"-shaped sauropod manus prints have been discovered in deposits of Lower Jurassic age (JENNY & JOSSEN, 1982; ISHIGAKI, 1986), suggesting that some of the earliest sauropods possessed fairly typical sauropod mani, with full digitigrady. The body fossils are less informative. Only Mcs.III-V are known from *Vulcanodon* (the earliest and most plesiomorphic sauropod, from the Lower Jurassic of Zimbabwe). The *Vulcanodon* manus appears to be sauropod-like insofar as the fifth metacarpal is long and robust, but it cannot be confirmed that these metacarpals were held in a vertical tubular arrangement. The manus of *Shunosaurus*, from the Middle Jurassic of China (Fig. 1C) has been illustrated by ZHANG, YANG &

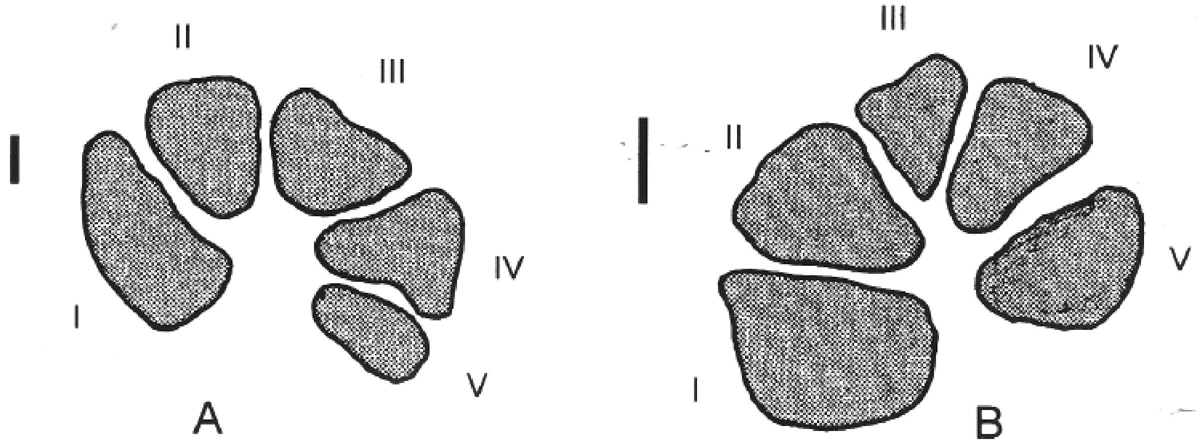

Fig. 2 - Proximal view of two sauropod mani, showing the tubular or semicircular arrangement of the metacarpals. **A** - right manus of *Brachiosaurus brancai* (HMN SII, after JANENSCH, 1961). **B** - right manus of *Janenschia* (HMN Nr. 5, after JANENSCH, 1961). Scale bars: 50 mm.

PENG (1984) as if the metacarpals simply lay side-by-side. Unfortunately, these authors do not mention whether this arrangement was chosen for clarity of illustration, or because it represents the natural articulation. Therefore, although it seems highly likely that early sauropods had a digitigrade stance, with a tubular metacarpus, the presence of these derived states can only be confirmed in the Brachiosauridae, Camarasauridae, Titanosauridae, *Opisthocoelicaudia,* and the Diplodocidae (all *sensu* UPCHURCH, 1993, 1994b).

Phalanges: In most dinosaurs there are three and four phalanges on manual digits II and III respectively. Terminal phalanges are easily lost as a result of post-mortem decay and disturbance. The phalangeal formulae of tetrapods, therefore, should be treated with some caution. Probable sauropod phalangeal counts are: *Shunosaurus,* 2-2-2-2-? (ZHANG, YANG & PENG, 1984); *Janenschia,* 2-2-1-1-1; *Apatosaurus, Brachiosaurus* and *Camarasaurus,* 2-1-1-1-1. Phalangeal reduction is consistent with the known sauropod trackway data and probably reflects the use of the forelimb as part of the animal's locomotor system.

Except for the first phalanx on digit I (see below), proximal phalanges are typically rectangular or trapezoidal in dorsal view. The proximal articular surfaces are flat and somewhat expanded dorsopalmarly. The distal ends are compressed dorsopalmarly and widened transversely. The distal articular surfaces are divided into two rounded "condyles" by a deep midline groove. The second row of phalanges, as seen in *Shunosaurus* and possibly *Janenschia*, appear to be greatly reduced. They are little more than rounded, 'button-like', lumps of bone.

DETAILED STRUCTURE OF DIGIT I

The tubular arrangement of sauropod metacarpals can create confusion with regard to descriptions of position and orientation. For example, the palmar surfaces of the metacarpals face laterally, posteriorly and medially, deepening on which metacarpal is selected. I therefore utilise two sets of terms for the description of orientation and position. The first set includes "medial", "lateral", "dorsal", "palmar", "proximal" and "distal". These refer to structures and surfaces on the metacarpal itself, as if it were laid with its palmar surface on the ground, with the long-axis parallel to the midline of the animal, and the distal end projecting anteriorly. The second set of terms includes: "external", "internal", "anterior" and "posterior". These refer to orientation with regard to the whole animal. For example, external means that a structure faces away from the midline of the animal, whereas internal means that it faces towards the midline. Thus, the dorsal surface of Mc.I faces internally, and its palmar surface faces externally; the dorsal and palmar surfaces of Mc.III face anteriorly and posteriorly respectively, and so on. Such a nomenclature may seem over-elaborate, but many of the earlier descriptions (HATCHER, 1902; GILMORE, 1936) lack clarity as a result of imprecise terminology.

Mc.I lies at the postero-internal corner of the manus. Its proximal end is approximately semicircular in outline, with the convex margin forming the dorsal, medial and palmar edges. The proximal portion of the lateral surface is flat or concave and faces anteriorly. This concave area receives part of the medial margin of the proximal end of Mc.II. The shaft of the metacarpal is constricted with respect to the proximal and distal ends. The palmar surface is broad near its distal end, but more proximally it becomes an acute ridge. As a result, a transverse section through the shaft is subcircular or subquadrangular near the distal end, but becomes subtriangular near the proximal end. As in other metacarpals, the distal end of Mc.I is wider lateromedially than dorsopalmarly. The distal articular surface bears a dorsopalmarly oriented groove on its midline. This extends well onto the dorsal and palmar surfaces. In *Apatosaurus, Camarasaurus* and *Lapparentosaurus,* the groove slants somewhat medially as its runs towards the palmar edge. In many sauropods, including *Apatosaurus, Camarasaurus, Janenschia, Opisthocoelicaudia* and *Lapparentosaurus,* the lateral portion of the distal end is expanded relative to the medial part (Fig. 3). As a result, the lateral distal condyle projects more distally than the medial condyle. These unusual features of the distal end are not present on any of the other metacarpals, and they also appear to be absent on the first metacarpals of *Brachiosaurus* and *Shunosaurus.*

In *Apatosaurus, Janenschia* and *Camarasaurus,* the proximal phalanx of digit I is wedge-shaped in dorsal view. The proximal and distal margins are long, the lateral margin is shorter, and the medial surface is shorter still (Fig. 4). This is in contrast to *Brachiosaurus,* where the phalanx is rectangular in outline. In *Apatosaurus,* the proximopalmar margin is drawn out into a thin flange. GILMORE (1936), however, noted that this flange was less well developed in *Apatosaurus louisae* (CM3018) compared to *A. excelsus* (CM563), and suggested that it had been exaggerated by crushing in the latter. Nevertheless, there was probably a small portion of the proximal articular surface which "underlay" the distal end of Mc.I. The proximal surface is concave and bears a low broad keel running dorsopalmarly. This keel fits into the groove on the distal surface of Mc.I. The distal end of the phalanx is convex dorsopalmarly and concave lateromedially (*i.e.*, mildly ginglymoid). The lateral distal condyle is relatively large, and possesses an articular surface which extends onto the dorsal and palmar faces.

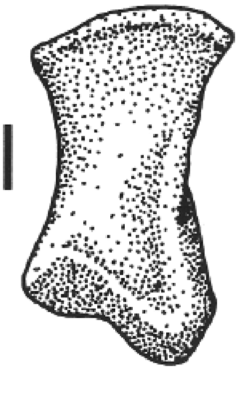

Fig. 3 - Metacarpal I (dorsal view) of *Apatosaurus louisae* (CM3018, after GILMORE, 1936), from the left manus. Scale bar: 50 mm.

The ungual (Ph.I-2) is typically large, laterally compressed and mildly recurved in side view (Fig. 5). The long-axis of the proximal articular surface runs dorsopalmarly. This surface is usually mildly concave and articulates with the large lateral distal condyle on the proximal phalanx. The medial surface of the ungual is typically convex dorsopalmarly, whereas the lateral surface is nearly flat. Distally, the claw tapers to a blunt tip. This is usually rather thin transversely and rounded in outline in side view (Fig. 5). The palmar surface is wide at the proximal end, tapering distally, and does not form a sharp cutting edge. Certain sauropods may not have possessed claws like that described above. In *Brachiosaurus,* the ungual is greatly reduced in size. Part of the claw belonging to "*Barosaurus lentus*" (CM21744) suggests that this animal possessed a much longer, less transversely compressed ungual. The proximal end of this claw, as in one tentatively assigned to *Vulcanodon* by COOPER (1984), is more circular or quadrangular in outline.

TANIMOTO (1991) claimed that no claw was present in *Opisthocoelicaudia.* In fact, no manual phalanges of any kind are known in this form, and the right manus also lacks Mcs.IV-V (BORSUK-BIALYNICKA, 1977). The fact that only one partial skeleton (and a few isolated elements) of this genus has been discovered so far, suggests that the absence of the manus claw is most parsimoniously interpreted as the result of taphonomic loss.

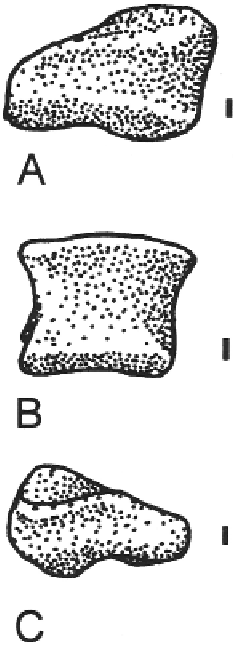

Fig. 4 - Phalanx I-1 from three sauropods, in dorsal view. **A** - *Apatosaurus louisae* (CM3018, after GILMORE, 1936), from left manus. **B** - *Brachiosaurus brancai* (HMN SII, after JANENSCH, 1961), from right manus. **C** - *Janenschia robusta* (HMN Nr. 5, after JANENSCH, 1961), from right manus. Scale bars: 10 mm.

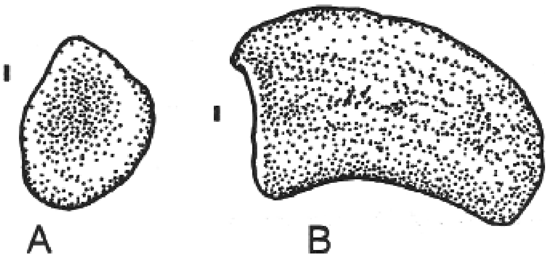

Fig. 5 - Ungual (Ph.I-2) from the left manus of *Apatosaurus louisae* (CM3018, after GILMORE, 1936). **A** - medial view. **B** - proximal view. Scale bars: 10 mm.

RANFE AND ORIENTATION OF MOVEMENT OF THE SAUROPOD MANUS CLAW

The above description suggests that the first manual digit of many sauropods possessed a number of features not found on digits II-V. These include: enlargement of the laterodistal condyle of Mc.I; intercondylar groove on distal end of Mc.I extends onto dorsal and palmar surfaces; palmomedial slant of condyles across distal end of Mc.I; wedge-shaped Ph.I-1, with an enlarged laterodistal condyle; and a vertical keel on the midline of the proximal end of Ph.I-1. When the first manual digit is articulated, these features allow the claw to be flexed and extended through a wide arc. Given that Mc.I occupies the postero-internal corner of the manus, with its dorsal surface facing towards the midline of the animal, the arc of rotation of the claw would lie in an approximately transverse, rather than parasagittal, plane. The claw could, therefore, be hyperextended holding it away from the substrate, as suggested by THULBORN (1989). In this position, the claw would lie internal to, and perhaps a little behind, the rest of the first digit, with the tip of the claw projecting upwards and inwards. If the digit was flexed, starting in the hyperextended position, the claw would swing internally and forwards through the first half of the arc, and then, depending on the resistance of the substrate, it could continue to swing externally and a little backwards. At maximum flexure the claw lies below the level of the rest of the manus.

BIPEDAL STANCE IN SAUROPODS

Many authors have envisaged sauropods utilising a bipedal ("tripodal") stance (OSBORN, 1899; RIGGS, 1904; COOMBS, 1975; NORMAN, 1985; BAKKER, 1986, 1987; JENSEN, 1988), thus freeing the forelimb (and manus claw) for other purposes. There is, however, little agreement with regard to the osteological characters which would permit bipedality, and as a consequence there is also little consensus concerning the sauropod taxa that were capable of this behaviour (see TABLE II). The evidence for sauropod bipedality is briefly reviewed here.

The data in TABLE II gives the impression that virtually all types of sauropod either have been, or at least could be, argued to possess adaptations for bipedality. In general terms, these osteological characters can be arranged into several categories, including specialisations which: shift the centre of gravity to a point nearer the acetabulum; allow the tail to act as an effective "third leg"; aid in weight support and general stability of the trunk region during bipedality; increase the mechanical advantages of the various muscles involved in raising the pre-acetabular portion of the body. For example, shortening of the forelimbs and trunk, lightening of the presacral vertebral column, and retention of a heavy tail, would place the centre of gravity near to the fulcrum used during bipedality (*i.e.* the acetabulum). ALEXANDER (1989) showed that the centre of gravity in *Apatosaurus* was nearer to the sacrum than that in *Brachiosaurus*. The diagonal bracing ligaments, discussed by JENSEN (1988), attach at the tops of the presacral neural spines, and pass posteroventrally to the base of the spine or transverse process of the succeeding vertebra. This network of ligaments, coupled with the well-developed hyposphene-hypantrum articulations, would effectively immobilise the middle and posterior portion of the dorsal series.

The "mosaic" distribution of bipedal characters might have resulted from separate groups of sauropod independently producing their own particular methods for attaining and maintaining a bipedal posture. It might also be related to sauropod groups exploiting bipedality to different extents (see "Conclusion"). It is also probable, however, that some of these characters are partly, or perhaps wholly, unrelated to bipedality. For example, rotation of the ilium may have helped weight support during bipedality, but it could also be correlated with increased forelimb length (JENSEN, 1988). This would explain why *Brachiosaurus*, the sauropod least likely to have employed bipedality, has an anteroventrally rotated ilium. Similarly, BAKKER's (1986) suggestion that forked chevrons are an adaptation allowing the tail to rest on the ground, is also questionable. Other sauropods which may have used bipedality, such as *Cathetosaurus* and titanosaurids, possess conventional blade-like chevrons. There may be a better correlation between the presence of forked chevrons and the use of the tail as a weapon (UPCHURCH, *submitted*).

JENSEN (1988) voiced some doubts about the bipedal ability of most sauropods, apart from *Cathetosaurus* which possesses numerous adaptations for sustained bipedality. Some of Jensen's concerns may be unfounded, since he uses estimates of sauropod weights which are probably too high. For example,

TABLE II
Summary of recent studies which have examined sauropod bipedality.

1 CHARACTER	2 FUNCTION	3 AUTHOR/TAXA	4 OTHER TAXA
Bifurcation of neural spines from cervical 3 to the sacrum	Complete involvement of pre-acetabular region in bipedality	JENSEN (1988); *Cathetosaurus*	Less extreme development in *Camarasaurus*, *Euhelopus*, *Mamenchisaurus*, *Opisthocoelicaudia*, Diplodocidae, Dicraeosauridae
Pre-epipophyseal ridges on cervicals	Attachment of "diagonal bracing ligaments"	JENSEN (1988); *Cathetosaurus*	-
Short back region	Places centre of gravity nearer to the acetabulum; increases stability	BAKKER (1986); Diplodocidae, Stegosauria	Sauropodomorpha
Flexible back region	Allows centre of gravity to be shifted posteriorly	BAKKER (1987); *Camarasaurus*, Stegosauria	-
"Metapophyseal spurs" on dorsal neural spines	Attachment of "diagonal bracing ligaments"	JENSEN (1988); *Cathetosaurus*	*Brachiosaurus*, *Camarasaurus*, *Haplocanthosaurus*
Anteriorly directed spurs on transverse processes	Attachment of "diagonal bracing ligaments"	JENSEN (1988); *Cathetosaurus*	-
Tall dorsal neural arches	Increased height of transverse processes and proximal ends of thoracic ribs; better leverage for iliocostalis and longissimus muscles	BAKKER (1987); *Camarasaurus*, Stegosauria	Most Sauropoda
Tall sacral neural spines	Improved leverage of muscles	BAKKER (1986, 1987); Diplodocidae, Stegosauria	*Dicraeosaurus*, *Amargasaurus*
Procoely/opisthocoely of anterior caudal centra	Increased flexibility of tail - better "prop" during tripodal stance	TANIMOTO (1991); *Opisthocoelicaudia*, Titanosauridae	*Bellusaurus*, *Mamenchisaurus*, mildly expressed in Dicraeosauridae and Diplodocidae
Long chevrons	Increases weight of tail (better counterbalance for pre-acetabular body weight)	BAKKER (1987); Stegosauria. JENSEN (1988); *Cathetosaurus*	-
"Forked" chevrons	Support underside of tail whilst resting on ground	BAKKER (1986); Diplodocidae	Dicraeosauridae, *Datousaurus*, *Mamenchisaurus*, *Omeisaurus*, *Shunosaurus*
Shortened forelimbs	Shifts centre of gravity nearer to acetabulum	BAKKER (1986); Diplodocidae	Dicraeosauridae
20 degree rotation of ilium	Allows weight to pass through strongest part of ilium during bipedal stance	JENSEN (1988); *Brachiosaurus*, *Cathetosaurus*	-
Outward turning of the anterior iliac process	Support of viscera during bipedal stance	BORSUK-BIALYNICKA (1977); *Opisthocoelicaudia*, Titanosauridae	The rotation of the ilium has a similar function in *Cathetosaurus* (JENSEN, 1988)

Column 1, "Character": the osteological character linked with bipedality. Column 2, "Function": the role played by the osteological character in sauropod bipedality. Column 3, "Author/Taxa": the author(s) who proposed the character and the taxa supposed to possess it. Column 4, "Other Taxa": other taxa possessing the character (according to UPCHURCH, *pers. obs.*).

Brachiosaurus and *Apatosaurus* are thought to have weighed 80 and 30-40 t respectively. These estimates are based on the work of COLBERT (1962) who used scale models as a means of finding the volumes of dinosaurs. These volumes can be multiplied by the probable density of the dinosaur (usually that of water, 1,000 kg.m^{-3}) in order to find its mass. This technique has two disadvantages. Firstly, the volume of the model depends greatly on the amount of muscle mass reconstructed (compare Colbert's and Alexander's estimates in ALEXANDER, 1989). Secondly, the assumption that sauropods had a density close to that of water is almost certainly unrealistic. Sauropod vertebrae are famous for their weight saving structures. For example, the presacral vertebrae are reduced to a complex array of struts and laminae, and the centra are greatly lightened by the presence of extensive pleurocoels. In *Brachiosaurus* even the thoracic ribs are hollow. These features are particularly important for bipedality, since they are located in the presacral region. Much lower, and perhaps more realistic, estimates of sauropod weights have been obtained using a method based on the correlation between body mass and limb bone circumferences in extant mammals (ANDERSON, HALL-MARTIN & RUSSELL, 1985). For example, these authors estimate the weights of *Apatosaurus, Diplodocus* and *Brachiosaurus* to be 37.5, 5.8 and 31.6 t respectively, compared to (no estimate for *Apatosaurus*), 18.5 and 46.6 t respectively by ALEXANDER (1989). Even Jensen admits that some limited bipedality was possible in most sauropods. He writes (JENSEN, 1988: 128): "Some sauropods may have been able to rise up momentarily to a semibipedal, or tripodal posture, but none, prior to the discovery of *C. lewisi*, display any convincing structural, or morphological, evidence of a capability for a sustained, bipedal posture" ["*C. lewisi*" is *Cathetosaurus*].

Physiological constraints may have prevented sauropods from exploiting bipedality. The main difficulties arise from the vertical distance between heart and head, and blood pressure changes during raising or lowering of the head. Recent work, however, has suggested that sauropods may have possessed a number of adaptations (some of which are also found in the giraffe), which would have lessened these problems (CHOY & ALTMAN, 1992). For example, additional "pumps" and valves along the cerebral arteries, combined with thickening of the artery walls and fascia of the neck, may have enabled blood to be pumped 8-12 m vertically. The collapse and re-inflation of the jugular vein, alteration in heart rate and thick, tight skin on the legs, may have prevented dangerous changes in blood pressure resulting from alterations in neck elevation. For further discussion see DODSON (1990), HICKS & BADEER (1992), TAYLOR (1992) and DENNIS (1992).

In summary, several osteological characters suggest that sauropods were capable of attaining a *stationary* bipedal stance, and maintaining it for at least short periods. The wide distribution of characters associated with bipedality, lower estimates of sauropod weights, and the probable need for bipedality during mating (DODSON, 1990), make it difficult to argue that sauropods were forced to remain quadrupedal at all times. This is not to say, however, that bipedality did not have its costs, and may have been used only rarely by some sauropods, such as *Brachiosaurus*.

THE FUNCTION OF THE SAUROPOD MANUS CLAW

FIGHTING

Large body size, herding, the presence of tail clubs (*Shunosaurus* and *Omeisaurus*, DONG, PENG & HUANG, 1989) or whiplashes (Diplodocidae), and body armour (Titanosauridae, JACOBS *et al.*, 1993; *Diplodocus*, CZERKAS, 1992), leaves little doubt that many sauropods needed to be able to defend themselves. NORMAN (1985: 97) depicts the large manus claw used as a weapon to fend off predators. BAKKER (1987) suggests that it could also have played a role in intraspecific combat. Rearing up into a bipedal position would have made an impressive threat display, making the sauropod appear even taller and larger. A blow from the flailing sauropod forelimb could also have carried considerable force. However, the large manus claw does not seem well suited to this role.

The claw itself does not resemble either the stabbing thumb-spike of *Iguanodon*, or the cutting/slicing claws on the hindfeet of dromaeosaurid theropods. Of course, only the bony core of the claw is available for inspection, and the original keratinous sheath may have transformed the claw into a more effective weapon. However, the blunt rounded tip and moderate curvature of the claw suggest that it was not used for stabbing. The broadly rounded palmar margin of the claw also implies that it would not have been effective as a slashing/cutting weapon.

The position of the claw at the postero-internal corner of the manus also casts doubt on its status as a weapon. The manus would have to be rotated (about the long-axis of the limb) through approximately 90° in order to bring the claw into a more useful position. Unfortunately, little is known about the structure of the sauropod wrist. Some twisting of the forelimb could have occurred at the elbow, although this joint appears to have mainly been concerned with parasagittal flexure and extension of the lower forelimb. The shoulder joint also seems to have been restricted to fore and aft motion of the forelimb. Trackway evidence suggests that some rotation of the manus and pes was possible, with many tracks showing a 10-15° outward rotation (FARLOW, PITTMAN &

HAWTHORNE, 1989). Although this amount of rotation may not represent the maximum possible value, it would not be enough to bring the claw into a useful position for fighting. Without rotation of the manus, the parasagittal movement of the forelimb during bipedality could only swing the flat surface of the claw towards an attacker.

Alteration in the position of the body was probably difficult, if not impossible, for a sauropod standing bipedally. The great weight of these animals, and the "columnar" nature of the forelimbs (with poor leverage for most of the muscles), suggests that they probably lacked the speed and dexterity needed to wield the claw effectively, especially against smaller and more agile theropods. In short, the sauropod forelimb may have been used as a weapon in extreme circumstances, but the claw probably did not play an important role in this behaviour.

FEEDING

THULBORN (1989) suggested that the sauropod manus claw was used in "... pulling down vegetation". It is, however, difficult to see how the manus could be used in this way. The forelimbs of sauropods were shorter, and almost certainly less flexible, than their necks. In most cases, the head would feed in positions where the manus could not reach. Pulling down vegetation using the forelimbs may make sense when the manus can reach a point higher than the head, but this was never the case in sauropods.

MCLOUGHLIN (1979) and TANIMOTO (1991) suggest that the large manus claw was used to grasp the trunk of a tree during high browsing. Extra height would be obtained by adopting the bipedal (or tripodal) stance, and greater stability could be achieved by placing the forelimbs against the trunk of the tree. The manus claws could then be used to grip the tree trunk, locking the mani in place. These authors did not relate their ideas to details of manus anatomy and function. Nevertheless, the shape, position, orientation and range of motion of the sauropod manus claw, could be well suited to "trunk-gripping".

During high browsing, the mani would be placed on the surface of the tree trunk, either side of the midline. The cylindrical shape of the trunk would result in a tendency for the mani to slip outwards (away from the midline). If digit I was flexed in this position, the large manus claw would rotate forwards and inwards, towards the surface of the trunk. The claw could then increase the ability of the manus to grip the trunk's surface. The postero-internal position of digit I means that the claw would be well situated for resisting the outward "slide" of the manus.

The use of the forelimbs during high browsing might have several advantages. Firstly, a small component of the animal's weight would still be carried through the forelimbs. Secondly, the forelimbs could help give the sauropod greater lateral stability. Finally, although rearing up into the bipedal stance would require substantial muscular effort, the use of the forelimbs to brace the body (resisting the tendency of the body to fall forwards), could have facilitated the maintenance of this position.

The feeding scenario outlined above is only feasible if Mesozoic trees were large enough to resist the forces imposed by the "leaning" sauropod. A typical large sauropod, such as the 23 m long *Apatosaurus louisae* (CM3018) has a manus approximately 500-600 mm in transverse width. The distance between the forelimbs (measured perpendicular to the midline of the animal) is about 2 m. This distance could have been reduced by angling the forelimbs so that the mani lay closer to the midline. The diameter of the thoracic region places limits on the extent to which this is possible (though see "2 -" below). Even if the forelimbs could be directed a little towards the midline, a tree trunk would need to have a diameter of at least 2.5-3 m if this sauropod was to be able to rest both mani on its surface. Although such trunk diameters are not inconceivable (especially for some of the larger conifers), it must be admitted that the majority of Mesozoic trees would probably have been somewhat smaller than this. This "problem" with the "trunk-gripping" hypothesis might be circumvented in several ways:

1 - Trunk-gripping and bipedality were easier for, and therefore employed most often by, the smaller sauropod genera (and perhaps the subadults of larger forms).

2 - Some sauropods may have been able to bring their mani closer to the midline. FARLOW, PITTMAN & HAWTHORNE (1989, and references therein), LOCKLEY, FARLOW & MEYER (1994) and LOCKLEY *et al.* (1994) discuss some sauropod trackways where the manus and pes prints impinge on the midline.

3 - Larger sauropods may have used only one manus against the trunk (but this would have been less stable).

Whether a tree was capable of supporting the weight imposed on it by a sauropod is a complex issue. The forces applied to the tree would depend on the weight of the sauropod, the component of this weight transmitted by the forelimbs, and the point on the tree where the mani were placed. The ability of the trunk to resist this force would depend on trunk diameter, the mechanical properties of the wood and the strength of the root system. It seems likely that most of the sauropod's weight would have been carried by the hindlimbs and tail. Large trees may have been able to easily withstand the forces applied to them by sauropods. It is even possible that sauropods would occasionally demolish trees by pushing against them in this way, allowing access to the entire foliage mass.

CONCLUSION

None of the proposed functions of the sauropod manus claw can be entirely ruled out. Some trackway evidence does suggest that the claw was not always carried above the substrate. Outward rotation of the manus would have brought the claw into a more useful position with regard to defence. However, the postero-internal position, and the transverse arc of rotation, make the manus claw particularly well suited to the "trunk-gripping" function suggested by MCLOUGHLIN (1979) and TANIMOTO (1991).

Information on the nature of Jurassic and Cretaceous floras is somewhat patchy. Recent studies of the flora of the Morrison Formation provide some data on at least one habitat favoured by sauropods. Western North America, during the Upper Jurassic, was dominated by lowland basins, with numerous shallow lakes and swamps (MILLER, 1987). The vegetation was "savanna-like", dominated by ferns. Conifers, and other tall trees (cycads and gingkos) were probably distributed in "clumps" over this area (COE *et al.,* 1987; MILLER, 1987). The canopy formed by these trees was probably around 20 m above ground level (TIFFNEY, 1989). In these conditions, bipedal feeding would have had two major advantages. Firstly, it would generally increase the amount of foliage that could be reached by a sauropod. Even so, any foliage above about 15 m would have been safe from the attention of sauropods (unless the entire tree was demolished). Secondly, the "clumped" distribution of the tall trees may have encouraged sauropods to increase the vertical range over which they could feed. Whilst a sauropod moved from one feeding site to the next, it would have to stop feeding, and at the same time it would be using energy at an increased rate. It would be to the sauropod's advantage, therefore, to minimise the amount of time travelling from place to place, and maximise the amount of food gathered at each feeding site. The manus claw, by prolonging the amount of time a sauropod could feed whilst in a bipedal posture, may have allowed more extensive feeding on each tree. Very large brachiosaurids, such as *Brachiosaurus* and *Ultrasaurus,* probably did not use bipedal postures during feeding, and this may explain why the manus claw is reduced in size. Some sauropods, such as *Cathetosaurus,* titanosaurids and *Opisthocoelicaudia,* were probably specialised for prolonged periods in a bipedal stance. Other groups, such as the diplodocids, dicraeosaurids, camarasaurids and the Chinese "euhelopodids", may have preferred to remain quadrupedal whenever possible, but could have used bipedal feeding (with trunk-gripping) when food was scarce, or perhaps when, as subadults, they faced competition at lower feeding heights from ornithopods and stegosaurs.

ABBREVIATIONS

CM - Carnegie Museum of Natural History, Pittsburgh, USA.
FMNH - Field Museum of Natural History, Chicago, USA.
HMN - Humboldt Museum of Natural History, Berlin, Germany.
IVPP - Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, People's Republic of China.
MHNP - National Museum of Natural History, Paris, France.
SAM - South African Museum, Cape Town, South Africa.
USNM - United States National Museum, Smithsonian Institute, Washington DC, USA.
ZPAL - Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

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