

## Supersonic sauropods? Tail dynamics in the diplodocids

Nathan P. Myhrvold and Philip J. Currie

**Abstract.**—Computer models of the tail of *Apatosaurus louisae* show it could reach supersonic velocities, producing a noise analogous to the “crack” of a bullwhip. Similarity in tail structure suggests this was feasible for other diplodocids, and possibly for unrelated sauropods like *Mamenchisaurus* and the dicraeosaurids. Lengthening of caudal vertebrae centra between positions 18 and 25 is consistent with adaptation to the stresses generated by such tail motion, as is coossification of vertebrae via diffuse idiopathic skeletal hyperostosis (DISH), which occurs in the same region in about half the specimens. The noise produced may have been used for defense, communication, intraspecific rivalry, or courtship, in which case supersonic “cracking” may have been a sexually dimorphic feature. Comparisons with the club-bearing tails of the sauropods *Shunosaurus lii* and *Omeisaurus tianfuensis* show the diplodocid whiplash tail was not well adapted as a direct-impact weapon, bringing the tail-as-weapon hypothesis into doubt.

Nathan P. Myhrvold. Microsoft Research, One Microsoft Way, Redmond, Washington 98052-6399

Philip J. Currie. Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta T0J 0Y0 Canada

Accepted: 28 March 1997

### Introduction

The giant sauropod dinosaurs of the family Diplodocidae are known for their enormous and graceful tails that taper to thin tips. Lengthening of the tail also appears to have been characteristic of dicraeosaurid sauropods (Janensch 1929) and Late Jurassic Asian sauropods like *Mamenchisaurus* (Russell and Zheng 1993). These tails have fascinated observers for decades and have given rise to many suggestions as to their function or purpose.

The analogy to whips was inspired by the thin, tapering tails, particularly the “whiplash” section formed by the posterior 40 to 50 caudal vertebrae. The whip analogy gave rise to the notion that tails were used as defensive weapons (Osborn 1899; Hatcher 1901, 1903; Holland 1915; Coombs 1975; Bakker 1986) to flail potential enemies, whether predators or interspecific rivals.

Alexander (1989) speculated further that the analogy could be drawn more specifically with a bullwhip, which can produce a loud “crack” or sonic boom when the tip of the whip exceeds the speed of sound. We show that computer models of diplodocid tails could have reached supersonic velocities, and argue that this is physically plausible.

Mankind has used whips for tens of

thousands of years for a variety of purposes (Morgan 1972). Broadly speaking, there are two principal kinds of whips: flails are used to beat subjects (usually human), whereas noise-making whips (e.g., bullwhips, coach whips) are primarily used to create directed noises to maintain control over domestic animals.

The loud noise (“crack”) of a whip was attributed to many causes until detailed analysis (Bernstein et. al. 1958) showed that it was due to a surprising phenomenon—the tip of the whip actually exceeds the speed of sound to create a shock wave or sonic boom. The physics of whip cracking rely on two basic properties—flexibility and a decrease in the cross-sectional area (and therefore mass) from base to tip. The basic features of whip dynamics can be understood through conservation laws.

The process begins when the whip is swung in an arc and gains angular momentum given by  $mvr$ , where  $m$  is the mass,  $v$  is the tangential velocity, and  $r$  is the radius of the arc. A wave is sent down the whip, usually by abruptly reversing the direction of the base relative to the tip. As the wave moves toward the tip, the angular momentum of the wave must be conserved, as must the kinetic energy. The momentum of one section of tail must be trans-

TABLE 1. Specimens studied. AMNH = American Museum of Natural History, CM = Carnegie Museum, FM = Field Museum, NMMNH = New Mexico Museum of Natural History.

Species	Specimen	Data reference
<i>Apatosaurus louisae</i>	CM 3018 CM 3378	Gilmore 1936
<i>Apatosaurus excelsus</i>	FM 7163 CM 563	Gilmore 1936
<i>Barosaurus lentus</i>	AMNH 6341	J. McIntosh personal communication 1996
<i>Diplodocus</i> sp.	Howe Quarry, Wyoming	K. Siber personal communication 1996 (see Appendix)
<i>Diplodocus longus</i>	AMNH 223	Osborn 1899
<i>Seismosaurus hallorum</i>	NMMNH 3690	Gillette 1991
<i>Mamenchisaurus hochuanensis</i>		Young et al. 1972
<i>Camarasaurus</i> sp.	CM 11338	Gilmore 1925

ferred to the next. However, the mass of each successive portion of tail that the wave enters decreases because of the tapering cross-sectional area. In addition, the effective radius  $r$  also decreases because the wave is moving toward the end of the whip. With  $m$  and  $r$  dropping, the only way to keep the product  $mvr$  constant is for the wave to speed up, thereby reaching extreme velocity  $v$  at the tip.

The same mechanism, albeit at subsonic velocities, has been the subject of numerous biomechanical studies of athletic performance in humans, where it is responsible for obtaining peak velocity in karate chops, golf swings, and javelin throwing (Jorgensen 1970; Cavanaugh and Landa 1976; Terauds 1978; Joris et al. 1985; Kreighbaum and Barthels 1990). The process can be thought of as a form of mechanical leverage, similar to that of the lever and fulcrum or the pulley. Unlike those cases, this leverage is dynamic in nature, relying entirely on momentum transfer and conservation laws (Bernstein et al. 1958; Kreighbaum and Barthels 1990; Baht and Kearney 1996).

Whips intended primarily for noise-making are constructed of a wide variety of materials including paper, wood fiber, and leather. All share the basic principles of tapering cross sections and distal flexibility, but follow quite different designs. One common feature of many noise-making whips is a thin cord or string, known as the "popper" or "cracker," which forms the tip of the whip.

It is possible to make a whip crack without a popper at the end, but this requires more energy and the resulting shock wave is not as loud (Bernstein et al. 1958; Morgan 1972). The popper is typically frayed or unraveled at the

end, creating many fine threads, each of which can generate its own shock wave. Creating the shock wave stresses the popper and causes it to fray and wear, needing replacement after a few hundred to a thousand cracks.

### Diplodocid Tails

Data on the dimensions of caudal vertebrae and chevrons in several diplodocids and other sauropods were obtained (Table 1). The data show a high degree of regularity between the various diplodocids and *Mamenchisaurus* when the logarithms of caudal vertebrae height are plotted against tail position (Fig. 1). *Apatosaurus*, *Barosaurus*, and *Mamenchisaurus* fall on essentially the same line within the likely measurement accuracy.

The slope of a line fit through the data points for vertebral height shows that each successive caudal vertebra is about 6% smaller than its predecessor. The few data points for *Seismosaurus* fall on a geometric series roughly parallel to that of the other diplodocine sauropods, but one that is displaced upward. *Camarasaurus* falls below on a line with similar slope.

Similar geometric relationships exist for other measurements. However, instead of being fit to a single straight line on a semi-log chart, they have more structure and are best modeled with several line segments. Vertebral centrum-lengths (Fig. 2) can be fit to three geometric series in the diplodocids and *Mamenchisaurus*. The centrum lengths of *Camarasaurus* are quite different and show it has a very different sort of tail, without the thin "whiplash" possessed by the diplodocids (Gilmore 1925).

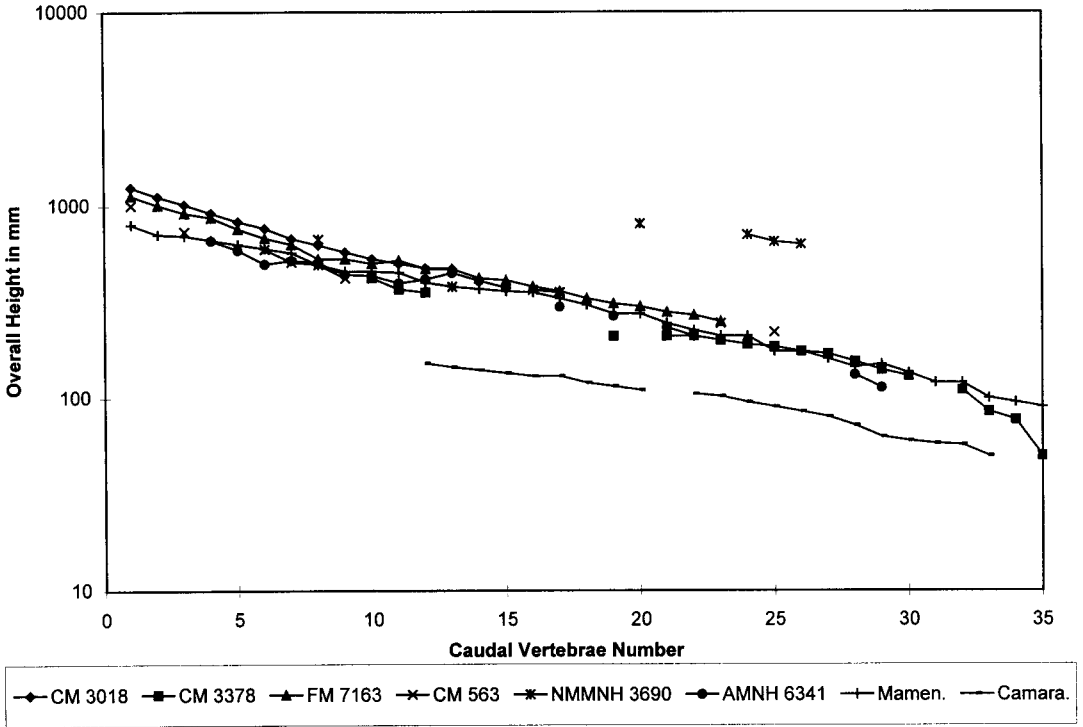


FIGURE 1. Overall height of sauropod caudal vertebrae plotted on a logarithmic scale against caudal position (vertebral segment number).

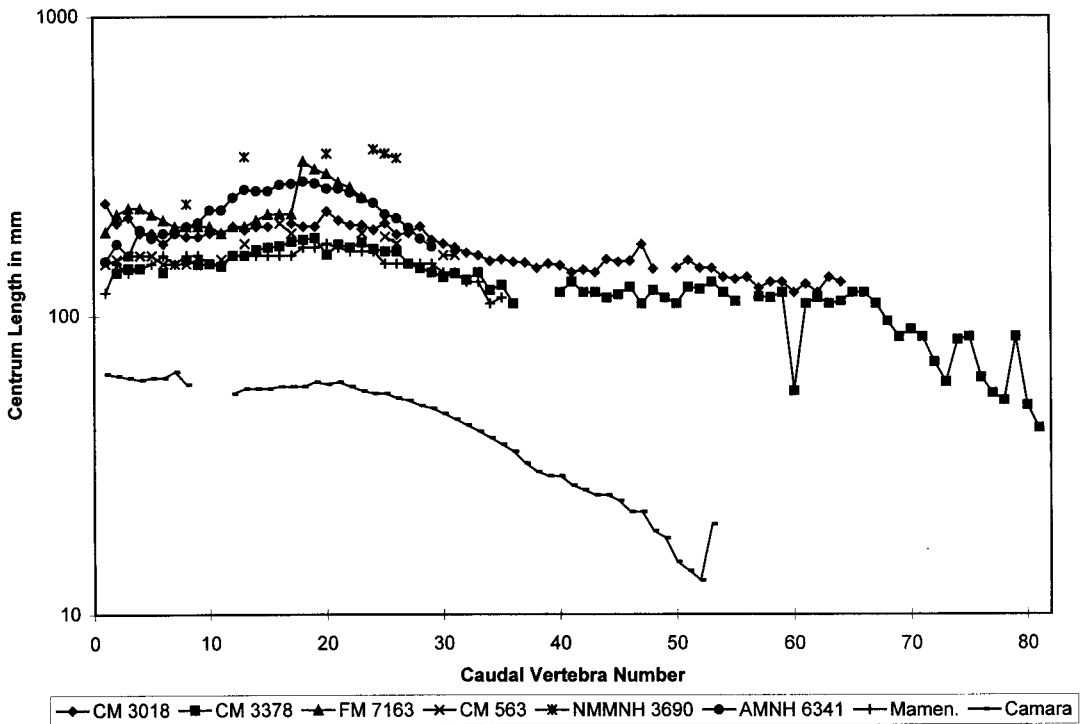


FIGURE 2. Central lengths of sauropod caudal vertebrae plotted on a logarithmic scale against caudal position (vertebral segment number).

TABLE 2. Physical parameters of reconstructed tail of *Apatosaurus* CM 3018, assuming a density of 1.0 g/cm<sup>3</sup>.

Mass	1449 kg
Length	12.48 meters
Center of mass	1.31 meters from proximal end (caudal 7)
Mass distal to caudal 35 (whiplash)	7.9 kg (0.54% of total tail mass)
Mass distal to caudal 22	55.5 kg (3.8% of total tail mass)
Torque on body when held horizontal	186,580 Newton-meters
Torque when horizontal to caudal 35	184,962 Newton-meters
Torque for tail truncated at caudal 22	158,676 Newton-meters
Torque for tail truncated at caudal 35	179,536 Newton-meters
Proximal/distal cross-sectional area	1309

Centrum length slowly increases in the series from the first caudal vertebra to a maximum between the 18<sup>th</sup> and 25<sup>th</sup> caudal vertebrae in all specimens studied here. The ratio of the maximum- to minimum-length caudals in this series is 2.11 in *Diplodocus* (AMNH 223) and 1.85 in *Barosaurus*, whereas *Apatosaurus* (CM 3018) has a more modest ratio of 1.28.

The lengthening of the caudal vertebrae in the region of vertebrae 18 through 25 corresponds to an area where coossification has fused one or more pairs of caudal vertebrae in approximately half of the known diplodocid specimens. This includes two of the *Apatosaurus* specimens (CM 3018 and 3378) studied here, three *Diplodocus* specimens (Hatcher 1901; Moodie 1916, 1923; Gilmore 1932, 1936), and many others (Rothschild and Berman 1991).

Early workers attributed this to trauma caused by contact with the ground, but this theory was discarded when it was realized that the dorsal elevation of the tail as it leaves the sacrum prevents the tail from touching the ground at that point. Another theory is that the tail was damaged when the sauropod reared up on its hind legs and used its tail as a support. However, the coossification of caudal vertebrae 22 and 23 in CM 3018 (Gilmore 1936: Fig. 8) shows that the fusion is confined to the centra and does not affect the neural spines. If the trauma occurred because the portion of the tail distal to caudal vertebra 23 was in contact with the ground while that proximal to caudal vertebra 22 was elevated by rearing up, this would compress the neural spines that overhang the centra and interlock closely. The lack of damage to the spines indicates that there was no vertical hyperextension of the joint. Instead, the injury is consis-

tent with overextension of the joint in a plane parallel to ground, as might be achieved while whipping the tail as proposed in this paper.

Recent CAT scan studies (Rothschild and Berman 1991) of a similar specimen have shown that the fusion resulted from ossification of the intervertebral ligaments through a physiological condition known as diffuse idiopathic skeletal hyperostosis (or DISH) rather than from injury.

Proximal to the region of maximum centrum length, the tail was stiffened by the thick muscles of the tail, and by the caudal ribs, which are present from caudal vertebrae 1 through 13 (in CM 3018). Distal to this area, the tail is thin and light; the reconstruction of CM 3018 as discussed below has 97.2% of its tail mass proximal to caudal vertebra 22, with only 3.8% distal (Table 2). The area where the caudal vertebrae achieve maximum centrum length therefore corresponds to the transition zone between the stiff muscular base and flexible whiplash section.

Simply holding the tail statically does not put a large stress load on this region, because the mass distal to it is such a small portion of the total mass. The maximum static torque occurs if the tail is held parallel to the ground. Even in this case the torque on the joint between caudal vertebrae 22 and 23 is only 15% of the torque on the joint proximal to the first caudal vertebra. Rapidly moving the tail distal to caudal vertebra 22 would put a dynamic load on this joint consistent with the lengthening found there.

Bullwhips and stock whips have very similar wear patterns in the area where the stiff handle section is joined to the more flexible body of the whip. This joint area is frequently

a point of failure that ends the useful life of a whip (Morgan 1972).

These observations suggest that the lengthening of the caudal vertebrae in the region of caudal vertebrae 18 through 25 is an evolutionary adaptation to the need for increased stiffness and reinforcement in this area. The increased lengthening observed in *Barosaurus* and *Diplodocus* is consistent with the observation that they are more lightly built than *Apatosaurus*. Adaptations reducing the robustness of the vertebrae might well be accompanied by compensating reinforcement at key stress points. The need for stiffness in the region is further supplemented in some individuals by vertebral fusion via DISH.

Distal to the point of maximum centrum length, the vertebrae steadily decrease in length via a slow geometric progression to vertebra 64, then drop off more rapidly distally from there (Fig. 2).

The diameters of caudal vertebra centra decrease steadily through the first 35 segments with one slope (Fig. 3) after which there is a second, more gradual slope. Caudal vertebra 35 is typically the last one with a neural spine and chevron, suggesting it is the last vertebra with significant attachment to muscles and tendons.

The caudal vertebra dimensions of a complete tail were reconstructed on the basis of data from *Apatosaurus* CM 3018, supplemented as necessary. The dimensions of several damaged vertebrae were extrapolated from adjacent vertebrae. Vertebrae from 65 to 82 were reconstructed using the geometric series recovered from a line fit to the semi-log plot of the data from CM 3378 (Fig. 2), then applied to match up with the known vertebrae in CM 3018.

Chevrons are poorly preserved in most specimens. As an example, only three exist for CM 3018, although the caudal vertebrae show points of attachment for chevrons from vertebrae 1 through 35. Fortunately, a nearly complete set of chevrons is available for *Mamenchisaurus*, and these follow geometric scaling that yields a good fit to a straight line on a semi-log chart. Scaling for overall height, centrum length, and other metrics is similar in

*Mamenchisaurus* and *Apatosaurus*, so it is quite possible that chevron scaling is similar as well.

In lieu of better data, the geometric scaling law for *Mamenchisaurus* chevrons was fit to the existing chevrons of CM 3018 in order to estimate the size of the missing elements. It should be noted that it is not known whether *Mamenchisaurus* had a whiplash tail; however, this does not directly affect the chevron size. The structure of the chevrons is remarkably similar to that of *Diplodocus*, further justifying the substitution.

The softer tissue of the tail was reconstructed using a simple model that treats the cross section of the tail as two half ellipses joined at the midpoint of the centrum (Fig. 4). The transverse semi major axis of both ellipses is given by the maximum width of the vertebra (including the caudal rib or transverse process if present). The vertical semi major axis of the top ellipse runs from the midpoint of the centrum to the top of the neural spine, and that of the lower ellipse to the bottom of the chevron. In each case, the bone dimensions were increased by 10 mm to allow for skin thickness.

This model seems to be a reasonable point of departure for approximating the live tail. For the purposes of this study, it should be at least as good as making measurements from scale models constructed by artists (Colbert 1962; Alexander 1985). Note that the exact shape of the tail cross sections is not relevant for the studies in this paper—only the cross-sectional area matters.

If we assume a typical tissue density of 1000 kilograms per cubic meter (i.e., that of water), as is often used in biomechanical studies, the resulting tail has physical properties given in Table 2. The actual density of the tail may have been somewhat greater due to having a higher proportion of bone than typical tissue. Most of the mass is near the base, with the center of gravity of the tail (taken by itself) located just 1.3 meters from the base, which places it in the middle of caudal vertebra 7.

It is now widely believed that sauropods could keep their tails extended and off the ground (Coombs 1975). We can estimate the static torque placed on the body if the tail were held erect, parallel to the ground (Table

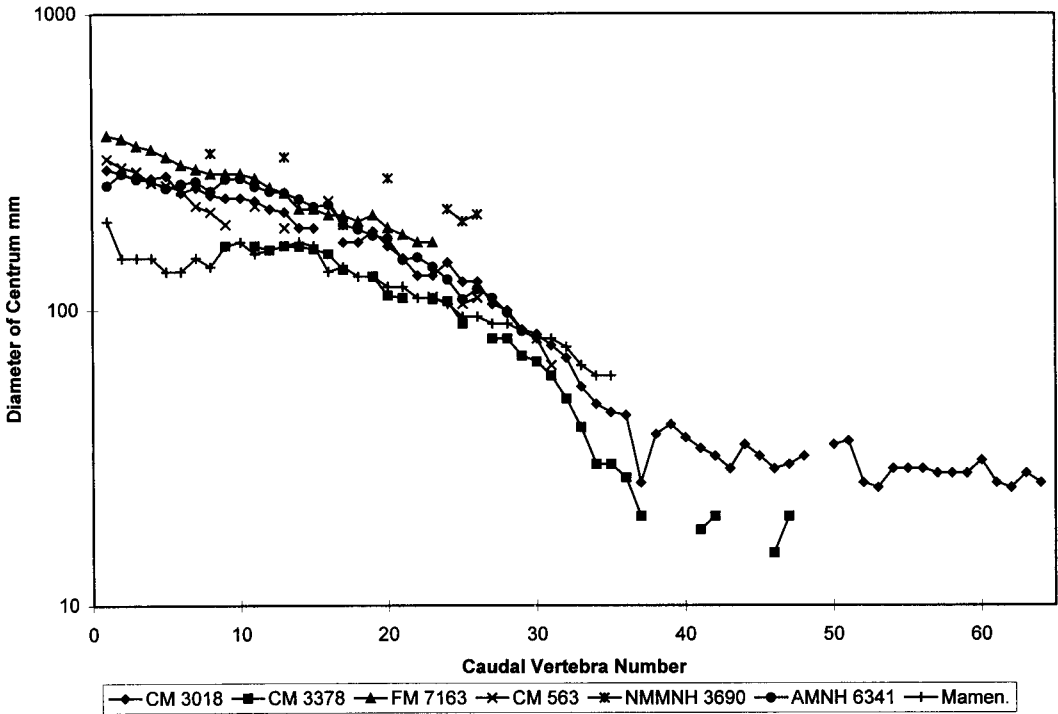


FIGURE 3. Diameters of sauropod caudal vertebra centra plotted on a logarithmic scale against caudal position (vertebral segment number).

2). Since neural spines and chevrons are absent distal to caudal vertebra 35, one can also calculate the torque resulting from holding the tail parallel only out to caudal vertebra 35 and letting droop the remainder distal to that point. Because the mass is heavily concentrat-

ed near the base, there is only a small difference in torque (Table 2).

The first step in comparing the model tail to a bullwhip was to examine how its cross-sectional area changes over its length. A braided kangaroo hide bullwhip 3.3 m long, weighing 700 grams was obtained from David Morgan, one of the few craftsmen in the United States still braiding whips by hand.

Cross sections of the whip were measured. In order to have a basis for comparing the mass distribution of the whip and tail, the ratio of cross-sectional area at each point to the cross-sectional area of the proximal end was plotted against the fraction of total length (Fig. 5). The cross-sectional area ratio is a measure of the mass decrease, and therefore velocity increase, and is thus analogous to the mechanical leverage of system.

The distal end of the CM 3018 tail ends with a cross-sectional area that is about 1300 times smaller than the proximal end (Table 2), a greater ratio of proximal to distal area than that for the bullwhip (with a 566:1 ratio). The

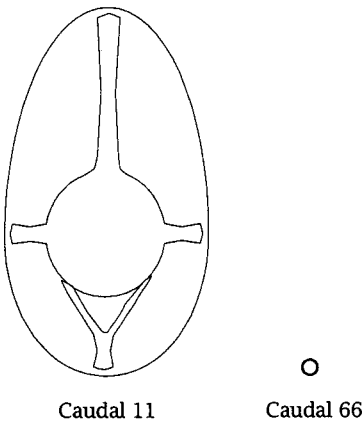


FIGURE 4. Sample cross sections of the reconstructed tail of *Apatosaurus* CM 3018, drawn to scale. Note that bone details in this figure are schematic only, rather than being exact outlines.

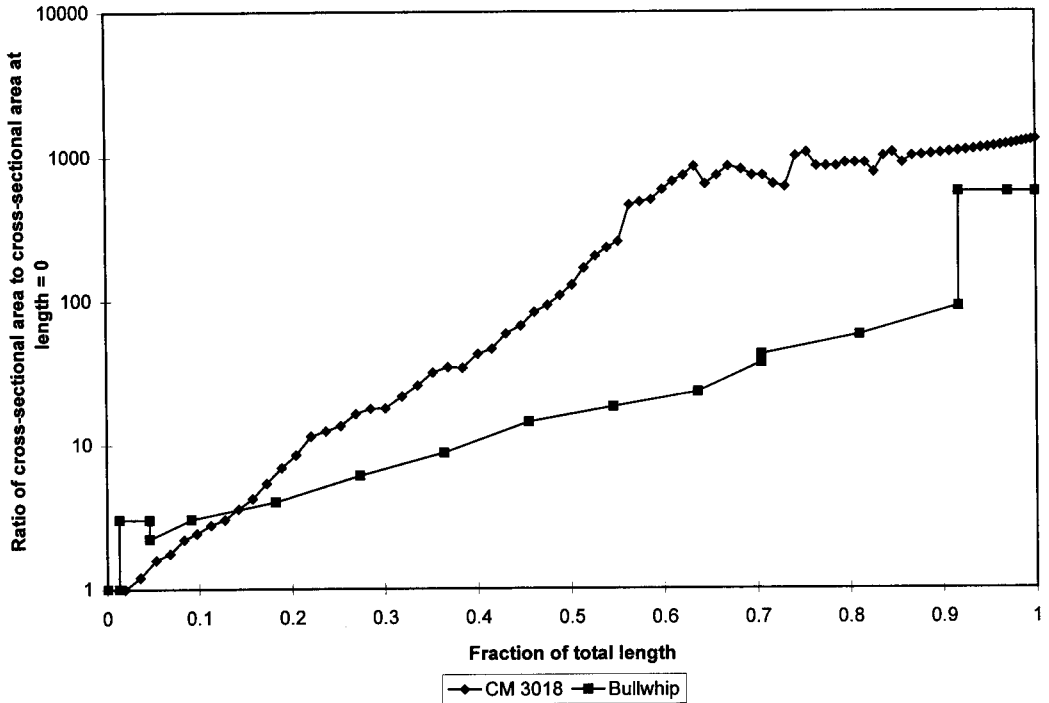


FIGURE 5. Comparison of cross-sectional area ratios plotted on a logarithmic scale against fraction of total length, for the reconstructed tail of *Apatosaurus* CM 3018 and for a bullwhip.

TABLE 3. *Apatosaurus* tail model parameters. The models are composed of 14 sections, each of which represents a series of caudal vertebrae. The table shows the length and mass for each section. In some simulations an additional three popper sections were used. Simulations were run at the mass values shown, and at one half and twice these values. Constraints on the maximum intervertebral joint angles were chosen from one of the joint angle columns.

Caudal vertebrae	Section length (m)	Section mass (kg)	Joint angles 1 (degrees)	Joint angles 2 (degrees)	Joint angles 3 (degrees)	Joint angles 4 (degrees)
1-8	1.590	1075.305	11.25	5.63	2.0	2.0
9-16	1.560	259.968	11.25	5.63	2.0	2.0
17-23	1.445	71.711	12.86	6.43	2.5	3.0
24-30	1.333	27.795	12.86	6.43	5.0	5.0
31-36	0.953	6.681	15.00	7.50	7.0	7.0
37-42	0.877	1.827	15.00	7.50	10.0	10.0
43-47	0.774	0.994	18.00	9.00	15.0	15.0
48-52	0.732	1.086	18.00	9.00	20.0	15.0
53-57	0.672	0.777	18.00	9.00	20.0	15.0
58-62	0.628	0.715	18.00	9.00	20.0	15.0
63-67	0.646	0.655	18.00	9.00	20.0	15.0
68-72	0.538	0.533	18.00	9.00	20.0	15.0
73-77	0.413	0.380	18.00	9.00	20.0	15.0
78-82	0.317	0.271	18.00	9.00	20.0	15.0
Popper	0.330	0.022				
Popper	0.330	0.015				
Popper	0.330	0.009				

bullwhip has the added advantage that the final 10% of its length is a thin popper, whereas the final portion of the tail as charted (Fig. 5) has a bone core. Adding a popper-like tail extension to CM 3018 would increase its ratio even further. The mass distribution gives the tail of CM 3018 the potential of behaving like a whip. In order to investigate this further, computer models were developed of both the CM 3018 tail and the bullwhip.

A commercial physical simulation software package, *Working Model* (Knowledge Revolution 1995, 1996) was used to create a model whip and tail. *Working Model* includes a full representation of Newtonian mechanics, using the variable step size Kutta-Merson or 5<sup>th</sup>-order Runge-Kutta algorithm (Gear 1971) for accurate integration of the equations of motion. It also allows approximate air resistance and frictional forces to be modeled.

Performance considerations prevented modeling every vertebra individually. Instead, the tail was modeled as sections of four to eight vertebrae connected by joints (Table 3). A similar approach to modeling whip mo-

tions via discrete links is used in other biomechanical studies (Kreighbaum and Barthels 1990; Baht and Kearney 1996).

The rod-like caudal vertebrae of the whip-lash portion of the tail are, as an early observer noted, "remarkable because of the fact that they articulate both in front and behind by convex, or almost conical surfaces, showing that the posterior extremity of the tail possessed the very largest degree of flexibility" (Hatcher 1901).

Further evidence of flexibility comes from a well-preserved *Diplodocus* specimen from the Howe Quarry, Wyoming, in which the whip-lash portion of the tail is fully articulated and encased by skin impressions, making it likely that the vertebrae were fossilized in position. In the whiplash portion of the tail, this specimen shows gaps between distal caudal vertebrae of between 10 and 12 mm (K. Siber personal communication 1996). The gaps suggest the presence of soft tissue caps, probably cartilaginous, on the ends of the vertebrae, which would again maximize flexibility.

This flexibility must be numerically estimated, as constraints on the maximum intervertebral joint angles. One approach is to estimate the angles of the "almost conical" joint surfaces (for example, those illustrated in Gilmore 1936: Plate XXVII); however, this would not allow for any missing soft tissue. Another is to look at fossil specimens with articulated columns of caudal vertebrae. Another *Diplodocus* from Howe Quarry has just such an articulated column of caudal vertebrae arranged in a nearly circular loop. Using the site map (K. Siber personal communication 1996), we can estimate the angles between the caudal vertebrae in situ. The most highly curved portion of this loop executes a 180-degree bend over six caudal vertebra joints, for an average angle per joint of 30 degrees. Contraction of the tendons or other processes after death might have caused this tail to assume a position not possible during life. However, the articulated tail is quite straight both proximal and distal to the bend, suggesting that this specimen did not undergo any overall distortion or contraction.

In order to allow for the uncertainty in this parameter, we simulated four different sets of

angular constraints, with maximum intervertebral joint angle varying from 9 to 20 degrees (Table 3). For comparison, Gertsch (1994) used a 20-degree maximum joint angle in a diplodocid tail model.

The likely mode of using a tail as whip would have been to move it in a plane parallel to the ground, as suggested by several factors. The tail has far greater potential for horizontal flexibility in the first 35 caudal vertebrae, which are braced for rigidity in the vertical direction by neural spines, chevrons, and (presumably) tendons, all of which helped support the tail. There would not have been much room to move the tail vertically, because it is much longer than the height of the sacrum. For these reasons, all simulation was done in two dimensions, simulating a tail moving side to side in a plane parallel to the ground.

Human whip artists have developed an enormous repertoire of different motions that can be used to generate supersonic cracks (Allen 1989). The common characteristics are that the crack is achieved by moving the whip within a single plane, while abruptly changing the direction of the base. Because we do not know what methods *Apatosaurus* might have used in cracking its tail, trial and error was used to adjust initial conditions to create a suitable crack. Insight was gained by manual practice with a bullwhip.

Broad ranges of initial conditions led to supersonic cracking in both the simulated whip and tail. A typical set of initial conditions was to apply a torque to the base of the tail at 50,000 Newton-meters (N-m) for 0.2 seconds, then to apply a counter torque of 60,000 N-m in the opposite direction. Other simulations produced a crack with as little as 20,000 N-m of torque. Another approach to initial conditions was to move the base of the tail in a quasi-periodic motion with period of one to two seconds, and with sufficient amplitude to achieve the maximum intervertebral joint angles in caudal vertebrae 1 through 8.

These initial conditions accelerated the center of mass of the tail to a maximum velocity of between 1.5 and 2.5 meters per second. The motion culminated in a wave that momentarily moved the tip at over 350 m/s, the speed of sound at sea level in typical atmospheric



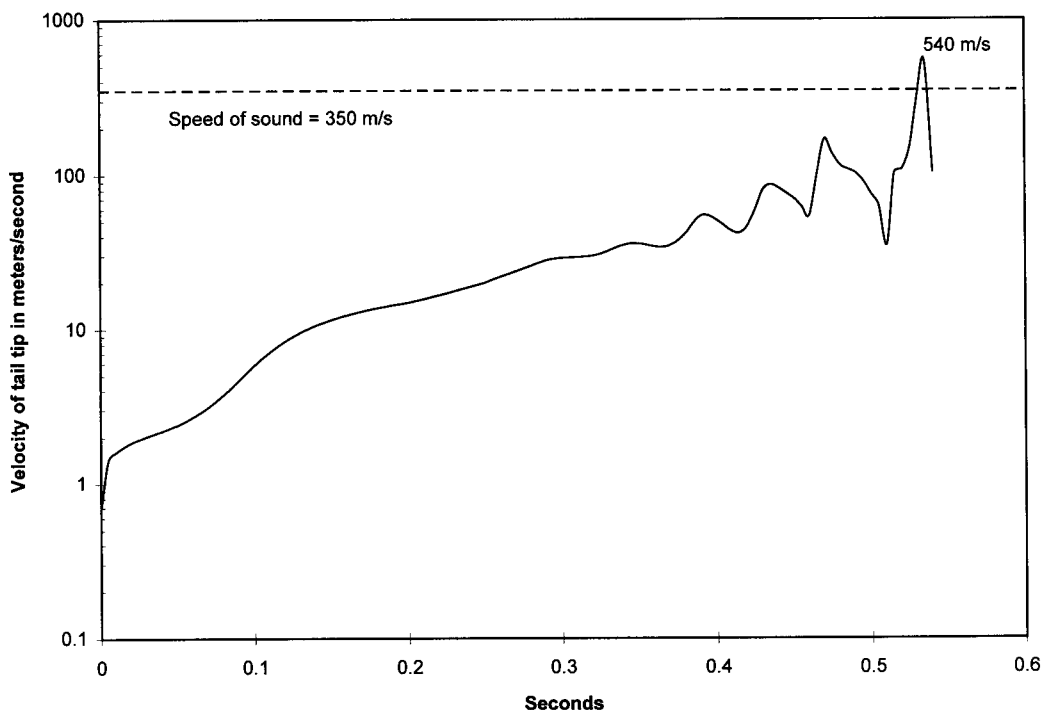


FIGURE 6. Distal tail tip velocity versus time from one simulation for the reconstructed tail of *Apatosaurus* CM 3018.

conditions. The tail tip velocity produced by a typical simulation is plotted in Figure 6.

The motions required by these simulations seem physically reasonable. The torque applied is less than a third that exerted to keep the tail parallel to the ground. The total energy expended is equivalent to moving the tail at the velocity achieved by the center of mass, which varied between 0.5 and 2 m/s. This can be compared to the velocity and energy requirements for walking.

Walking speed can be estimated from foot spacing in trackways and from knowledge of the basic limb geometry. Estimates for diplodocid sauropods result in average walking velocities of 0.8 to 1.2 m/s (Alexander 1976, 1989; Thulborn 1982, 1990; Lockley et al. 1986). The velocity of the proximal part of the tail seems quite reasonable since it is only twice the average walking speed.

Trackways of fast-moving sauropods have not been reported, but the maximum speed of walking or running attainable by diplodocids can also be estimated, albeit with considerable uncertainty. One approach is to invoke an empirical relationship between body size or mass

and maximum speed (Bakker 1975; Garland 1983); another is to make an estimate of maximum stride and use the same analysis as for trackways (Thulborn 1982). The result is a maximum velocity of between 3.3 and 11.9 m/s (depending on the method) for *Apatosaurus* and between 3.3 and 14.4 m/s for *Diplodocus* (Bakker 1975; Garland 1983; Thulborn 1982, 1990).

The mass of *A. louisae* has been estimated at 33,500–37,500 kg (Colbert 1962; Anderson et al. 1985; Alexander 1985, 1989), although some favor a lower value of 18,000 kg (P. Christiansen personal communication 1997). The tail as modeled here is 1449 kg, or only 4.2% of the total mass. Moving this tail at an average velocity of 2 m/s gives it only 17% of the kinetic energy of an entire 33,500-kg *Apatosaurus* moving at 1 m/s. The energy required for cracking thus seems to be much less than that required for walking. When compared with the hypothesized maximum speeds, the tail energy is tiny—between 1.5% and 0.12% depending on which estimate is used.

A major inadequacy in the simulation is that

it treats the tail as a passive element. The proximal end of the tail remains pinned in one location, rotating due to torque applied to it. This helps demonstrate the basic dynamics of momentum transfer in the tail, which leads to supersonic motion. However, it is a very simplified model of the full mechanics of tail motion that would have been possible in life.

*Apatosaurus* is likely to have swung its tail by moving its hindquarters rather than keeping them still as modeled here. Such hindquarter motion might have occurred by shifting weight between its rear legs, or perhaps by stamping its rear feet. Alexander (1985, 1989) estimated that 70% of the weight of *Apatosaurus* was carried on the rear legs, amounting to 23,450 kg for an individual of total mass 33,500 kg. The tail as modeled here is only 6% of this. Thus even a very slow motion of the hindquarters of 0.5 to 1 m/s (i.e., the average walking speed estimated from trackways) would have transferred an enormous amount of momentum to the tail.

The same supersonic velocities could therefore have been achieved with lower torque, and thus less effort, because of the assistance of the pelvic and leg muscles. It is even possible that *Apatosaurus* could have produced supersonic cracks incidentally while walking, in time with its footfalls.

Another area where the simulation is unrealistic is that in life, *Apatosaurus* is likely to have had the ability to apply torque at more places than just the extreme proximal end, and would also have been able to control its tail, rather than treating it as an entirely passive object. Caudal ribs extend from caudal vertebrae numbers 1 through 13, so significant transverse torque could be exerted at least throughout this series. Smaller tendon attachment points are found throughout the caudal vertebrae and these could allow *Apatosaurus* to distribute some muscular forces along a larger portion of the tail than modeled here. In addition, *Apatosaurus* likely could have sensed joint position (at least in the base of the tail and possibly throughout) and thus could have coordinated timing of the motion.

Either of these capabilities would have allowed much finer control of the waves moving down the tail, potentially enabling tail crack-

ing for an even wider range of initial conditions, including some with even lower torque and less abrupt changes in torque. It is known that very simple control logic can yield highly efficient control of whip motion with reduced torque and energy requirements (Baht and Kearney 1996). Thus, any control capability would have enhanced the ability of *Apatosaurus* to crack its tail.

As will be discussed below, it is possible that the tail extended beyond the last caudal vertebra as a kind of "popper." This extension would presumably have been made of some combination of skin, tendon, and keratin. As one would expect, simulations that include a popper also generate supersonic motion and in general require smaller torque to do so.

Various combinations of alternative parameter sets (Table 3) and initial conditions were attempted to determine the robustness of supersonic motion. This included varying the mass (or density) by a factor of four, varying the intervertebral joint angle constraints by more than a factor of two, and using widely different initial conditions. In all cases, it was easy to find simulations that produced supersonic motion.

We conclude that a broad range of physical conditions allow for the possibility of supersonic motion for tails similar to that of *Apatosaurus*. The geometric scaling of vertebral dimensions found in the various diplodocids strongly suggests that any of them, or non-diplodocid sauropods with "whiplash" tails, would share this capability. The large dynamic leverage created by the ratio of proximal to distal cross-sectional area and the flexibility of the tail practically guarantee that supersonic motion is possible.

A previous biomechanical study (Gertsch 1994) used a methodology quite different from this paper to calculate tail dynamics of a model diplodocid tail. Instead of employing a full simulation of Newtonian physics for a passive tail controlled at the base, Gertsch used a computer model that applied constant transverse angular acceleration at every intervertebral joint. This presumably was meant to model muscle forces bending the tail at the joints, simplified for the calculation. The points of large muscle attachment (such as

caudal ribs), and thus the largest transverse muscular forces, are confined to the base of the tail in real specimens. Some transverse angular acceleration of the joints might have been possible in the whiplash section of the tail, but it seems unlikely that the value would have been constant for all intervertebral joints.

The initial conditions used were also different. Gertsch assumed that the tail began tightly coiled at the maximum joint angle, then uncoiled rapidly with constant interjoint angular acceleration in the manner of a tightly wound clock spring unwinding. Supersonic motion was not reported in this scenario (Gertsch 1994).

Despite these differences, the results are not inconsistent with those reported in this paper. The initial conditions used by Gertsch would not be expected to give rise to supersonic motion. Gertsch recognized this and speculated that supersonic motion might be possible, although he considers it unlikely. Further, Gertsch stipulated that this would occur under initial conditions in which the motion of the base of the tail changes direction during the simulation, as those in this paper do.

### Discussion

At first, the results might seem rather surprising, given that tails are flesh and blood and do not seem capable of supersonic motion. Is supersonic motion physically reasonable for a flesh and blood dinosaur?

Although we intuitively think of supersonic motion in terms of the exotic materials and engineering required for aircraft, ordinary leather bullwhips show that no special materials or stresses are involved. If whips made from the skins of cows and kangaroos are able to withstand supersonic motion, why not dinosaur skin and tendons?

The actual portion of the tail that would have exceeded the speed of sound is quite limited. Only the very distal section (perhaps as small as the final centimeter) would have done so. The rest of the tail would not have been subjected to these velocities for several reasons.

The maximum velocity experienced by each portion of the tail declines exponentially with distance from the tip (i.e. proximally) (Fig. 7).

This is in keeping with the prior observations that the decrease in cross-sectional area (which is also exponential) is a primary factor in accelerating the tail. The momentum transfer mechanism allows slow motion of the massive proximal region to be concentrated in the far lighter distal region.

As soon as part of the tail started to exceed the speed of sound, the shock wave would have been generated, dissipating energy from the tail into the surrounding air, and thereby producing the noise. This would have caused a dramatic energy loss, preventing any more of the tail from being accelerated past the sound barrier. High-speed photography of bullwhips shows that only the very tip—from one centimeter down to a few millimeters—exceeds the speed of sound and generates shock waves (Bernstein et. al. 1958).

Thus, only the very extreme tip of the tail would have borne the brunt of the stress. Little of the actual flesh or blood supply would have been required at the extreme distal end, because it was little more than skin stretched over the last vertebrae. Consequently, delicate features such as blood vessels would not have been subjected to these terminal stresses.

A further way to protect the tail proper from these stresses would have been to extend the tail past the last caudal vertebra with skin, tendon, or keratin. Such a feature would have absorbed all the stresses of creating the shock wave, just as their counterparts—the popper—does on bullwhips. The tail popper would have frayed through wear, but could have been renewed through constant growth from the tip of the tail outward.

Christiansen (1996) examined several anatomical characters, including morphology of the central articulating faces and the angulation of the zygapophysical facets of the caudal vertebrae of several of diplodocids, and compared them with those of other sauropods, primarily *Camarasaurus* and *Brachiosaurus*. He found they are quite similar, at least within the proximal series of caudal vertebrae at the base of the tail. The non-diplodocids had no equivalent of the rod-like “whiplash” vertebrae at the distal end of the tail.

Christiansen (1996) concluded that this similarity is inconsistent with the proposition that

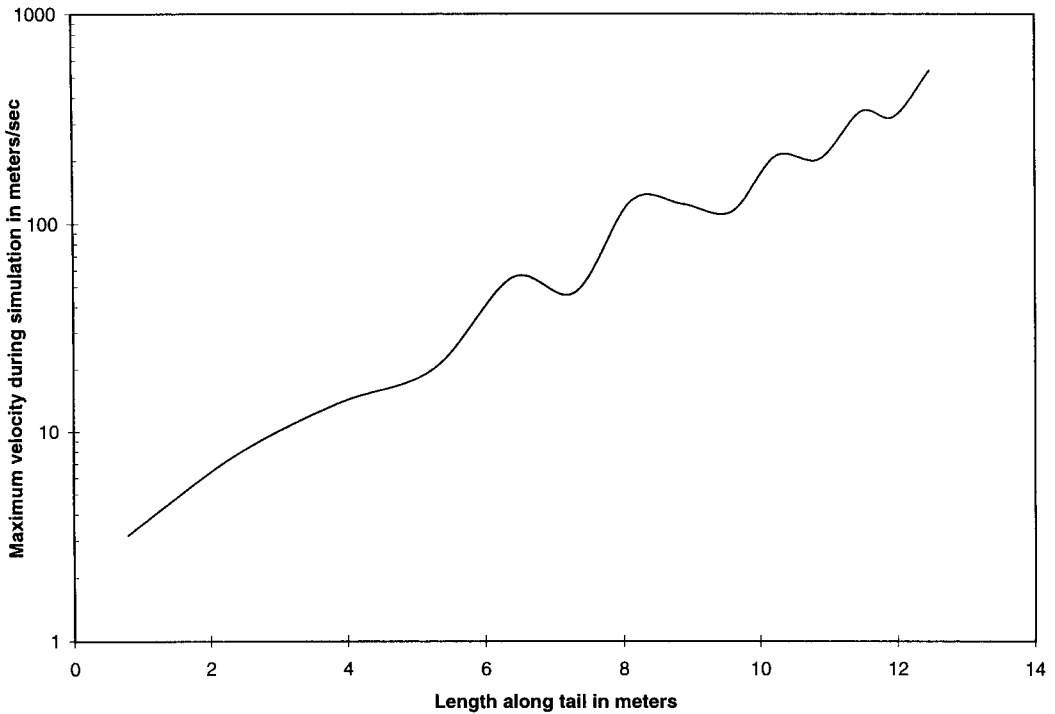


FIGURE 7. Maximum velocity achieved during an entire simulation, plotted versus the length along the tail where it occurred for the reconstructed tail of *Apatosaurus* CM 3018.

diplodocids used their tails as weapons. Findings here tend to support his overall conclusion that the tails were not weapons (as treated below). However, Christiansen's arguments could be interpreted to rule out supersonic motion of the tail, and thus should be examined.

That various sauropods had roughly similar tails in the proximal region is not surprising. The whiplash portion, which so differentiates the tails of the diplodocids, is, structurally speaking, a very small addition. If the tail of *Apatosaurus*, as modeled here, were truncated and the portion distal to caudal vertebra 22 removed, the remaining proximal portion would have 96.2% of the original mass, and would require 85% of the original torque to be held parallel to the ground (Table 2). The whiplash region itself is smaller yet—the portion distal to caudal vertebra 35 is just 7.9 kg, or only 0.54% of the total tail. The basic structural properties of the tail proximal to caudal vertebra 22 should therefore be dominated by the requirements of its mass.

As shown in Figure 1, the overall height of

the caudal vertebrae of *Camarasaurus* obeys a scaling relationship with caudal vertebra number very similar to that for the diplodocids. Overall height is the largest contributor to cross-sectional area and mass because the neural spines are so high in the distal caudal vertebrae (e.g., Figure 4). Therefore, we would expect *Camarasaurus* to have a similarly massive tail at the base. It is not surprising that the mechanisms for supporting a massive tail (including the central articulating faces and the zygapophyses) could be shared by various sauropods.

Likewise, we would expect that the musculature should be basically similar (Christiansen 1996) among various sauropods, since the addition of the whiplash tail only adds a tiny fraction of the mass of the *Apatosaurus* tail—just 7.9 kg. (Table 2). Momentum transfer allows quite ordinary motion of the proximal portion of the tail to be accelerated to extreme velocity when transferred distally to the whiplash.

It is entirely likely that *Camarasaurus* and *Brachiosaurus* could move the proximal por-

tion of their tails at velocities similar to those we assume for *Apatosaurus*, since it is just twice the average sauropod walking speed. This is quite reasonable for a limb or tail. However, the distal portions of the *Brachiosaurus* or *Camarasaurus* tails would not achieve supersonic motion, because they do not possess the diplodocid whiplash. An analogy is that a man holding a whip can achieve supersonic velocities at the distal end of the whip. The same arm without the whip will have similar proximal velocity, but its distal end will not be supersonic.

Christiansen (1996) assumes that to be a weapon, the diplodocid tails would be differentiated from the tails of *Camarasaurus* and *Brachiosaurus* in two ways: more flexible in the proximal caudal vertebrae (as evidenced in the central articulating faces and zygapophyses) and more muscular. As discussed above, neither condition should be expected for tail cracking. A stiff proximal portion is desirable, and no special musculature is required.

The existence of the whiplash is the most important distinction between diplodocid and non-diplodocid tails, but as Figure 2 shows, the length of the centra and their scaling behavior with caudal vertebra number clearly distinguishes the diplodocid specimens from *Camarasaurus*. Not only is the curve of a very different form, but the *Camarasaurus* shows no tendency to achieve a maximum length in the region between caudal vertebrae 17 and 24. The increased stiffness in the mid-caudal series is consistent with the requirements of supersonic tail cracking.

### The Tail as Weapon

The theory that the tail was used as a weapon has been popular with many investigators (Osborn 1899; Hatcher 1901, 1903; Holland 1915; Coombs 1975; Bakker 1986; Dodson 1990), yet it has substantial problems (Christiansen 1996).

Presumably, a sauropod would have wielded its tail as a weapon against two possible classes of adversaries—predators and intraspecific rivals. Given their enormous size, it is not clear that adult diplodocids needed any weapon against predators. In any event, either

sort of adversary is likely to have been large and would not have been easily deterred.

In the reconstruction of CM 3018, however, the final two-meter section of the tail has a mass of only 1.8 kg and an overall diameter of 32 mm. In order to impart enough force or energy to harm a large adversary, a weapon this light would have to travel at an extreme velocity. The simulation results suggest that such velocities could have been attained, but contact with the target would have damaged the tail itself.

The distal caudal vertebrae are very thin and delicate and do not appear to have been built for high-speed impacts. The biconvex joints project from the shaft of the vertebral centra enough so that they would be involved in any lateral impact, risking injury that would render them inoperative, or at least be evident in the fossil record.

The whiplash caudal vertebrae are only from 4 to 12 cm long, much smaller than the size scale of important body parts of any likely adversary. A single impact with a 1- to 3-meter target might damage 8 to 25 or more consecutive vertebrae. Repeated use through a lifetime should leave an ample record, yet fossil evidence of coossification or other trauma in the distal whiplash caudal vertebrae has not been reported.

A dramatic example of adaptation for the stress of impact is shown in the tails of *Shunosaurus lili*, and *Omeisaurus tiefuensis*. These Chinese sauropods have the final caudal vertebrae fused into tail clubs reminiscent of those of ankylosaurs (Dong et al. 1989). The club is formed from the fusion of the final three to five caudal vertebrae, which are also modified to have greatly enlarged centra (compared with the nearby distal caudal series). The distal non-club vertebrae and their joints are protected from contacting the target of impact by the enlarged central diameter of the club. These thick bony structures are quite different from the tail tips of *Apatosaurus*, or other diplodocids for which the entire caudal series is known.

Connective tissue or a covering of horny or keratinous armor might have served the same function as a tail club in protecting the distal caudal vertebrae and their joints. However,

there is no reported fossil evidence of such a cover. In contrast, *Diplodocus* specimens with intact skin impressions associated with the distal caudals have been found and they appear to be inconsistent with an armored cover (Czerkas 1992).

Extending the tail beyond the last caudal vertebrae with a flexible flail from one to three meters long is another way to allow impact without involving the caudal vertebrae, their joints, or other delicate tissue. Such a flail might be composed of tough tendon, skin, and/or keratin. A 10-mm to 20-mm diameter flail moving at several hundred kilometers an hour could be tough enough to withstand impact, yet deal a formidable cutting blow to a target of soft tissues. The effect of impact could be further enhanced if the flail contained sharp horny "beads," modified scales, or other armored projections (likely made of keratin), analogous to human-designed impact flails such as "cat-o'-nine-tails" (Morgan 1972).

Like the popper of a bullwhip, a weapon-oriented flail would still be capable of being cracked at supersonic velocity to create a noise. For use in an impact, subsonic (but still extremely high) velocity would be better because a supersonic shock wave would dissipate energy to the air rather than the target. There is no known fossil evidence of such a feature, so this must be regarded as entirely speculative. Obviously, another and perhaps simpler option is to discard the tail-as-weapon theory.

Several species of monitor lizards, including the water monitor, *Varanus salvator*, use tail slapping during intraspecific interaction and for defense, and this behavior partially inspired the tail-as-weapon hypothesis for diplodocids (Holland 1915). Varanids usually strike their opponents with their tails on the side of the body (Auffenberg 1981, 1988). Captive specimens of *V. salvator* at the Woodland Park Zoo in Seattle frequently lash out at their keeper, upon occasion striking him on the arms, legs, and forehead (D. Paine personal communication 1996). These blows, although startling, do not break human skin or cause any lasting injury.

Monitor tail lashing is not supersonic, be-

cause the tail is not thin enough. The ratio of extreme proximal to distal cross-sectional areas as measured from a prepared skeleton of *V. salvator* at the Woodland Park Zoo is approximately 80:1. This can be compared with 1300:1 for CM 3018 (Table 1). The 80:1 figure is not too far from the 90:1 ratio found for the bullwhip without popper, but in addition, the tail is much less flexible. The caudal vertebrae of *V. salvator* are not similar to those of the diplodocids, in that they do not possess the rod-like whiplash vertebrae or biconvex joints. All caudals of *V. salvator* have neural spines, chevrons, and transverse processes that tend to restrict the joint motion. Due to these projections from the centrum, these vertebrae are arguably even more delicate than those of the diplodocids, yet they survive being used as a defensive weapon. This is due to the much lower velocities and lower mass of the tail.

#### The Tail as Noisemaker

Suppose instead that the noise created by the supersonic crack of the tail were itself the primary objective. This is supported by the shape and mass distribution of the tail, which seem optimized for supersonic cracking.

Although the tail could crack without a flexible tail extension or popper, there would be advantages to having one. A popper even a centimeter or two in length, made of skin and tendon, would improve shock wave generation and protect other tissues from the stress of cracking. Human-designed whips generally have a popper that is somewhat longer—roughly 10% of the overall length. The tail popper is likely to be frayed distally by shock wave generation and could be renewed by growing proximally.

If fossil evidence of a distal tail extension or popper were found, it would strongly confirm tail cracking. Also, the nature of such an extension might resolve whether it was used primarily as a weapon or noisemaker. The Howe Quarry in Wyoming has produced skin impressions and dermal spines from diplodocid sauropods (Czerkas 1992), up to what appears to be the distal end, without evidence of a tail extension or popper (K. Siber personal communication 1996). However, the extension might have been lost. This would not be sur-

prising given that we conjecture it to be an expendable feature, often lost during use. If DISH tail fusion is indeed sexually dimorphic, tail extensions might also be, leaving the possibility that this specimen is the wrong sex.

A supersonic crack might have been useful to a sauropod in many ways. Predators might be deterred by the level of the sharp sound generated. The precise amount of energy released depends on details of the popper and on the specific motion used. However, it should scale linearly with the mass of the tail, and thus be a factor of 2000 times greater than a conventional bullwhip. A shock wave of this intensity could be a deterrent, especially to a predator with sensitive hearing.

The primary use for bullwhips is to herd mammalian herbivores used in agriculture and transportation. Likewise, interactions within a sauropod group may have been one of the primary uses of tail cracking. Trackway (Bird 1944; Lockley et al. 1986) and bonebed (Coria 1994) evidence suggests that sauropods traveled together in orderly groups. Tail cracking would have been an excellent way to enforce discipline within a group, and to communicate between the various members of it. The sound from the crack of a sauropod tail would have carried for kilometers.

Social animals that congregate in groups often have some sort of dominance contest, display, or intraspecific combat designed to establish hierarchy, either generally or as part of mate selection. Although we do not know much about sauropod social life, dominance may have been established by some form of intraspecific contest or combat. Tail cracking as a display would have been an excellent way to establish dominance or resolve disputes without actually needing to resort to physical contact that could cause injury.

Rothschild and Berman (1991) noted that DISH-based vertebral fusion is found in approximately half of all specimens and suggested that it was a sexually dimorphic physiological adaptation to the stress of intraspecific combat using tails. One sex (presumably the males) would have engaged in this behavior and would have possessed the physiological adaptation of fused vertebral centra from repeated use. Supersonic tail cracking pro-

vides a better explanation as the mechanism for intraspecific combat.

Tail cracking could have been used as a non-lethal form of male-versus-male dominance contests or displays. Alternatively, or in addition, tail cracking might have had other sexually related uses. It could have been used by males as an auditory means to call or attract females over distances, or have been an element in courtship displays or rituals (individually or in the context of a lek). Another use might have been controlling access to females or herding them in a harem.

Since no diplodocids have been reported where the existence of the whiplash caudal series itself was a sexually dimorphic feature, the tails were presumably useful for both sexes—and so, potentially, was tail cracking. Females might have used cracking for female-to-female dominance or displays, which are known in many social animals.

If tail cracking had a sexually related function, then it might have developed after a period in which diplodocid ancestors evolved through sexual selection on tail length alone. Later, tail cracking behavior could have developed, and sexual selection could have further optimized the tails for it. This would explain how to get a tail long enough to crack in the first place. However, it also suggests an alternative explanation for the tails—perhaps sexual selection on length was sufficient by itself.

In any event, the intriguing possibility of DISH-based vertebral fusion as a sexually dimorphic feature could be verified by correlation with other, as yet unidentified, signatures of sex determination in the diplodocids.

### Conclusion

The arguments and simulations presented in this paper are at best only circumstantial evidence. It is very difficult to prove any behavioral characteristic like tail cracking from the fossil record. We have demonstrated that the fundamental potential for supersonic motion is plausible from the biomechanical structure of diplodocid tails. Tentative confirmation can be found in several aspects of the osteology—increased length of caudal vertebrae in the proximal series and DISH-based verte-

bral fusion in the same region. Computer modeling gives us a new tool for determining the dynamic characteristics of species known only from the fossil record. Each of these lines of evidence is strongly suggestive of supersonic motion; however, they fall short of being conclusive that such behavior actually occurred. We hope that future fossil evidence can be found to clarify the issue.

Finally, we must confess that it is pleasing to think that the first residents of Earth to exceed the sound barrier were not humans, but rather the diplodocid sauropods. Following their demise, a hiatus in supersonic motion of over a hundred million years ensued until this capability was rediscovered by our species.

### Acknowledgments

The authors would like to thank R. McNeil Alexander, P. Christiansen, B. Curtice, D. Gillette, and S. Vogel for helpful comments.

### Literature Cited

- Allen, M. 1989. The art of the bullwhip. Mark Allen Productions, Las Vegas. [Videotape.]
- Alexander, R. McN. 1976. Estimates of speeds of dinosaurs. *Nature* 261:129–30.
- . 1985. Mechanics of posture and gait of some large dinosaurs. *Zoological Journal of the Linnaean Society* 83:1–25.
- . 1989. Dynamics of dinosaurs and other extinct giants. Columbia University Press, New York.
- Anderson, J. F., A. Hall-Martin, and D. A. Russell. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology, London A.* 207:53–61.
- Auffenberg, W. 1981. The behavioral ecology of the Komodo monitor. University of Florida Press, Gainesville.
- . 1988. Gray's monitor lizard. University of Florida Press, Gainesville.
- Baht, D. N., and J. K. Kearney. 1996. On animating whip-type motions. *Journal of Visualization and Computer Animation* 7: 229–249.
- Bakker, R. T. 1975. Experimental and fossil evidence for the evolution of tetrapod bioenergetics. Pp. 365–399 in D. M. Gates and R. B. Schmerl, eds. *Perspectives of biophysical ecology*. Springer, Berlin.
- . 1986. The dinosaur heresies. Morrow, New York.
- Bernstein, B., D. A. Hall, and H. M. Trent. 1958. On the dynamics of a bull whip. *Journal of the Acoustical Society of America* 30:1112–1115.
- Bird, R. T. 1944. Did *Brontosaurus* ever walk on land? *Natural History* 53:60–67.
- Cavanagh, P. R., and J. Landa. 1976. A biomechanical analysis of the karate chop. *The Research Quarterly* 47:610–618.
- Christiansen, P. 1996. The “whiplash” tail of diplodocid sauropods: was it really a weapon? In M. Morales, ed. *The continental Jurassic*. Bulletin of the Museum of Northern Arizona 60:51–58.
- Colbert, E. H. 1962. The weights of dinosaurs. *American Museum Novitates* 2076:1–16.
- Coombs, W. P. 1975. Sauropod habits and habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology* 17:1–33.
- Coria, R. A. 1994. On a monospecific assemblage of sauropod dinosaurs from Patagonia: implications for gregarious behavior. *Gaia* 10:209–213.
- Czerkas, S. A. 1992. Discovery of dermal spines reveals a new look for sauropod dinosaurs. *Geology* 20:1068–1070.
- Dodson, P. 1990. Sauropod paleobiology. Pp. 402–407 in D. B. Weishampel, P. Dodson, and H. Osmolska, eds. *The Dinosauria*. University of California Press, Berkeley and Los Angeles.
- Dong, Z. M., G. Z. Peng, and D. X. Huang. 1989. The discovery of the bony tail clubs of sauropods. *Vertebrata Palasiatica* 27: 219–224.
- Garland, T. 1983. The relationship between maximal running speed and body mass in terrestrial mammals. *Journal of Zoology* 199:157–70.
- Gear, C. W. 1971. Numerical initial value problems in ordinary differential equations. Prentice-Hall, Englewood Cliffs, N.J.
- Gertsch, L. 1994. Dinosaur tail dynamics. In G. E. Nelson, ed. *The dinosaurs of Wyoming*. Wyoming Geological Association 44th Annual Field Conference Guidebook:25–38.
- Gillette, D. D. 1991. *Seismosaurus halli*, gen. et sp. nov., a new sauropod dinosaur from the Morrison Formation (Upper Jurassic/Lower Cretaceous) of New Mexico, USA. *Journal of Vertebrate Paleontology* 11:417–433.
- Gilmore, C. W. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument. *Memoirs of the Carnegie Museum* 10:347–384.
- . 1932. On a newly mounted skeleton of *Diplodocus* in the United States National Museum. *United States National Museum Proceedings* 81 (Art. 18):1–21.
- . 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum* 11:175–300.
- Hatcher, J. B. 1901. *Diplodocus* (Marsh): its osteology, taxonomy and probable habits, with a restoration of the skeleton. *Memoirs of the Carnegie Museum* 1:1–63.
- . 1903. Additional remarks on *Diplodocus*. *Memoirs of the Carnegie Museum* 2:72–75.
- Holland, W. J. 1915. Heads and tails; a few notes relating to the structure of the sauropod dinosaurs. *Annals of the Carnegie Museum* 9:273–278.
- Janensch, W. 1929. Die Wirbelsäule der Gattung *Dicraeosaurus*. *Palaeontographica Supplement* 7:27–93.
- Jorgensen, T., Jr. 1970. On the dynamics of the swing of a golf club. *Americal Journal of Physics* 38:644–651.
- Joris, H. J. J., A. J. Edwards van Muyen, G. J. van Ingen Schenau, and H. C. G. Kemper. 1985. Force, velocity and energy flow during the overarm throw in female handball throwers. *Journal of Biomechanics* 18:409–414.
- Knowledge Revolution. 1995. Working Model (software package and associated documentation). Knowledge Revolution, San Mateo, Calif.
- . 1996. World Wide Web site, <http://www.krev.com>
- Kreighbaum, E., and K. M. Barthels. 1990. Biomechanics, a qualitative approach for studying human movement. Macmillan, New York.
- Lockley, M. G., K. J. Houck, and N. K. Prince. 1986. North America's largest dinosaur trackway site: implications for Morrison paleoecology. *Geological Society of America Bulletin* 97: 1163–1176.
- Moodie, R. L. 1916. Two caudal vertebrae of a sauropodous dinosaur exhibiting a pathological lesion. *American Journal of Science* 41:530–531.
- . 1923. Paleopathology. University of Chicago Press, Chicago.



- Morgan, D. 1972. Whips and whipmaking. Cornell Maritime Press, Centerville, Md.
- Osborn, H. F. 1899. A skeleton of *Diplodocus*. Memoirs of the American Museum of Natural History 1:191-214.
- Rothschild, B. M., and D. S. Berman. 1991. Fusion of caudal vertebrae in Late Jurassic sauropods. *Journal of Vertebrate Paleontology* 11:29-36.
- Russell, D. A., and Z. Zheng. 1993. A large mamenchisaurid from the Junggar Basin, Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* 30:2082-2095.
- Terauds, J. 1978. Computerized biomechanical analysis of selected javelin throwers at the 1976 Montreal Olympics. *Track and Field Quarterly Review* 78:29-31.
- Thulborn, R. A. 1982. Speeds and gaits of dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 38:227-56.
- . 1990. *Dinosaur tracks*. Chapman and Hall, New York.
- Young, C. C., M. N. Bien, and T. H. Mi. 1972. *Mamenchisaurus* from Ho Chuan. *Academia Sinica, Institute of Vertebrate Paleontology and Paleoanthropology Monographs A* 8:1-30. [In Chinese.]

## Appendix

Length of centrum data for *Diplodocus* sp. excavated at Howe Quarry, Wyoming. Assignment of the first vertebra in the series to caudal position number 33 is hypothetical as the vertebrae proximal to it are unavailable in this specimen at this time. However, this assumption matches the scaling of *Diplodocus* specimen AMNH 223 (Osborn 1899) and yields the same total number of caudal vertebrae as *Apatosaurus* (AMNH 3378). Remaining vertebrae in this series were found articulated in place. Missing lengths (\*) are either incomplete, missing in the specimen, or were not prepared at time of measurement. Data provided by K. Siber (personal communication 1996).

Caudal no.	Length	Caudal no.	Length	Caudal no.	Length
33	145	50	85	67	50
34	150	51	80	68	51
35	153	52	65	69	46
36	155	53	73	70	44
37	150	54	72	71	*
38	*	55	65	72	*
39	145	56	67	73	*
40	140	57	66	74	40
41	130	58	62	75	41
42	125	59	*	76	39
43	115	60	*	77	42
44	110	61	*	78	*
45	105	62	57	79	*
46	96	63	55	80	45
47	95	64	56	81	43
48	90	65	54	82	38
49	87	66	50		