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# SAUROPOD HABITS AND HABITATS

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## ABSTRACT

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Sauropod natural history has been a widely discussed and sometimes controversial topic. All amphibious theories of sauropod behavior from Cope and Marsh onward may have been inspired by Owen. Sauropod narial morphology might indicate either aquatic or terrestrial habits, and some sauropods may have had a complex narial structure, possibly a proboscis. Sauropods were vegetarians, but the specific diet of *Diplodocus* is unclear. Long necks could have been used for browsing in trees, or along streambanks, or under water. Sauropod axial and appendicular modifications point to primarily terrestrial behavior. Sauropods may have had a bird-like lung system. Sauropods sometimes dragged their tails on the ground and may have used them for defense. The deep thorax of sauropods is an adaptation to problems of terrestrial weight-bearing. Sauropod foot and limb structure is generally comparable to elephants, except in lack of joint ossification and development of large claws. Sauropods sometimes reared up on their hind limbs, and they definitely entered streams at least sometimes, but sedimentologic evidence does not support immersion in deep lakes as sauropods are frequently pictured. On the problem of terrestrial versus amphibious habits, most sauropod anatomy is equivocal, but where firm morphologic interpretations are possible, they usually point to terrestrial behavior.

## INTRODUCTION

No other fossil reptiles, perhaps no other fossil of any kind, has ever captured the imagination as thoroughly as have the sauropods. Considerable difference of opinion exists on the habits and habitat preferences of these curious beasts, ranging from "probably marine" (Owen, 1859b) to "specialized in terrestrial habits" (Riggs, 1904). Little information in the form of startling new specimens has been forthcoming for sauropods over the last forty years, and it is appropriate to make a critical retrospective analysis of the arguments bearing on sauropod natural history, particularly arguments developed on anatomical grounds. Aside from the specific question of sauropod behavior, this exercise has some application to the general problem of developing a complete picture of a fossil vertebrate which has no closely related descendents.

## ORIGINS OF THE AQUATIC-AMPHIBIOUS THEORY

The first pronouncement on a group of organisms, made by a respected authority, frequently has a lingering influence on later investigators. Sir Richard Owen was the first scientist to examine sauropod remains, the first to apply generic names, and the first to speculate on sauropod habits. Owen placed *Cardiodon* and later all Opisthocoelia (or Cetiosauria) in the Crocodilia and suggested they were aquatic or even marine (Owen, 1859a,b). In deference to Owen it must be pointed out that he had relatively poor material at his disposal, especially compared to specimens subsequently unearthed in North America. That Owen thought of sauropods as a subgroup of the Crocodilia undoubtedly predisposed him to think in terms of amphibious or aquatic behavior, but in support of his interpretation he specifically cited the tissue structure of sauropod long bones, a line of evidence later rejected by Hatcher (1903). It is difficult to assess the impact of Owen's theory on later authors, biassing them toward thinking of aquatic habits when dealing with sauropods. Few authors since Owen have insisted on marine or completely aquatic habits, but most have assumed some degree of amphibious behavior.

In North America both Cope and Marsh issued their first articles on sauropods the same year. Marsh (1877a,b,c) initially theorized a fully terrestrial habitat, characterizing *Atlantosaurus* (originally "*Titanosaurus*", preoccupied) as the largest animal to move on land and suggesting it fed on the vegetation of mountain forests. Cope (1877a, 1878b) likewise called his *Camarasaurus* the ". . . largest and most bulky animal capable of progression on land . . ." and stated: "That this species was capable of and accustomed to progression on land is certain from the characters of the bones of the limbs and their supports above described". Later, in a paper on the genus *Amphicoelias*, Cope (1878a) said: " . . . these beasts may have walked in deep water . . ." Vertebral structure was apparently the primary evidence for this new theory, and Cope was quick to get all sauropods in the swim: ". . . the species of *Camarasaurus* and *Amphicoelias* were dwellers in water of sometimes considerable depth . . ." (Cope, 1878c). Thus within the span of a single year Cope completely reversed himself on the question of sauropod habits. Was Cope influenced by Owen or had he developed an aquatic hypothesis independently?

Within the first year he published on sauropods, Cope (1877b) was aware of the similarity of *Camarasaurus* to European genera, particularly *Cetiosaurus*, yet when Marsh (1878) proposed the name Sauropoda, Cope uncharacteristically waited a full four years to point out the priority of Owen's Opisthocoelia (Cope, 1882). Marsh (1880b) had examined European sauropod literature as early as 1880, and included most European genera within his Sauropoda (Marsh, 1882). Following Cope's note on the Sauropoda—Opisthocoelia synonymy, Marsh stated that *Brontosaurus* was ". . . more or less amphibious". No specific justification is given, but Marsh was apparently influenced by geologic evidence: "The remains are usually found in localities where the animal had evidently become mired" (Marsh, 1883). Marsh makes no reference

to Owen's theory, but it is likely that he had at least read the aquatic hypothesis for Opisthocoelia at the time he altered his opinion.

In later papers Marsh continued to follow the "more or less amphibious" theory, while Cope insisted on more fully aquatic behavior. Both of their opinions may have been finally crystallized by the evidence of the narial position in *Diplodocus* (Cope, 1884; Marsh, 1884). It is interesting that both Marsh and Cope first thought of sauropods as terrestrial, then both switched to amphibious or aquatic theories. Neither of them cites Owen as the inspiration for their changes, but both had probably read Owen before altering their interpretations. There is reason to suspect that Owen is the ultimate source for all amphibious—aquatic theories of sauropod behavior.

## INTERPRETATION OF SAUROPOD ANATOMY

### *Narial openings*

Marsh (1884) compared the curiously positioned narial openings of *Diplodocus* to similarly placed nostrils of a phytosaur ("*Belodon*") and suggested that this similarity might indicate aquatic habits. Cope (1884) was very impressed by this feature and based his theory of aquatic habits primarily on the narial position of *Diplodocus.* Subsequent authors have also relied heavily on this feature to defend the amphibious—aquatic theory, and consequently the interpretation of sauropod narial morphology will be discussed at some length.

*Sauropod narial morphology*: There are three different narial patterns known for sauropods, each exemplified by a well-known genus.

(1) *Diplodocus* has a single narial aperture, of moderate size, positioned far dorsally above and between the orbits (Fig.1A and B).

(2) *Camarasaurus* has very large narial openings, with a median bar separating right from left. The nostrils occupy most of the rather short face anterior to the orbits, are directed laterally and somewhat anteriorly, and are visible in a dorsal view of the skull (Fig.1C and D). The nostrils are at about the same level as the orbits.

(3) *Brachiosaurus* has somewhat smaller nostrils than *Camarasaurus*, similarly divided by a bar, but which are distinctly higher than the level of the orbits.

*Narial morphology of aquatic and amphibious tetrapods:* Nostrils of many aquatic reptiles are positioned laterally on the snout just anterior to the orbits (Nothosauria, Sauropterygia, Placodontia, Ichthyosauria: Bakker, 1971a), but in other aquatic tetrapods the nostrils are on the extreme dorsal surface near the eyes (*Archelon*, Mosasauridae, Mysticeti, Sirenia, Desmostylia), and in others the nostril is "normally" positioned (most marine Chelonia, otters, Pinnipedia; Williston, 1914; Romer, 1956; Walker, 1968). Tetrapods of

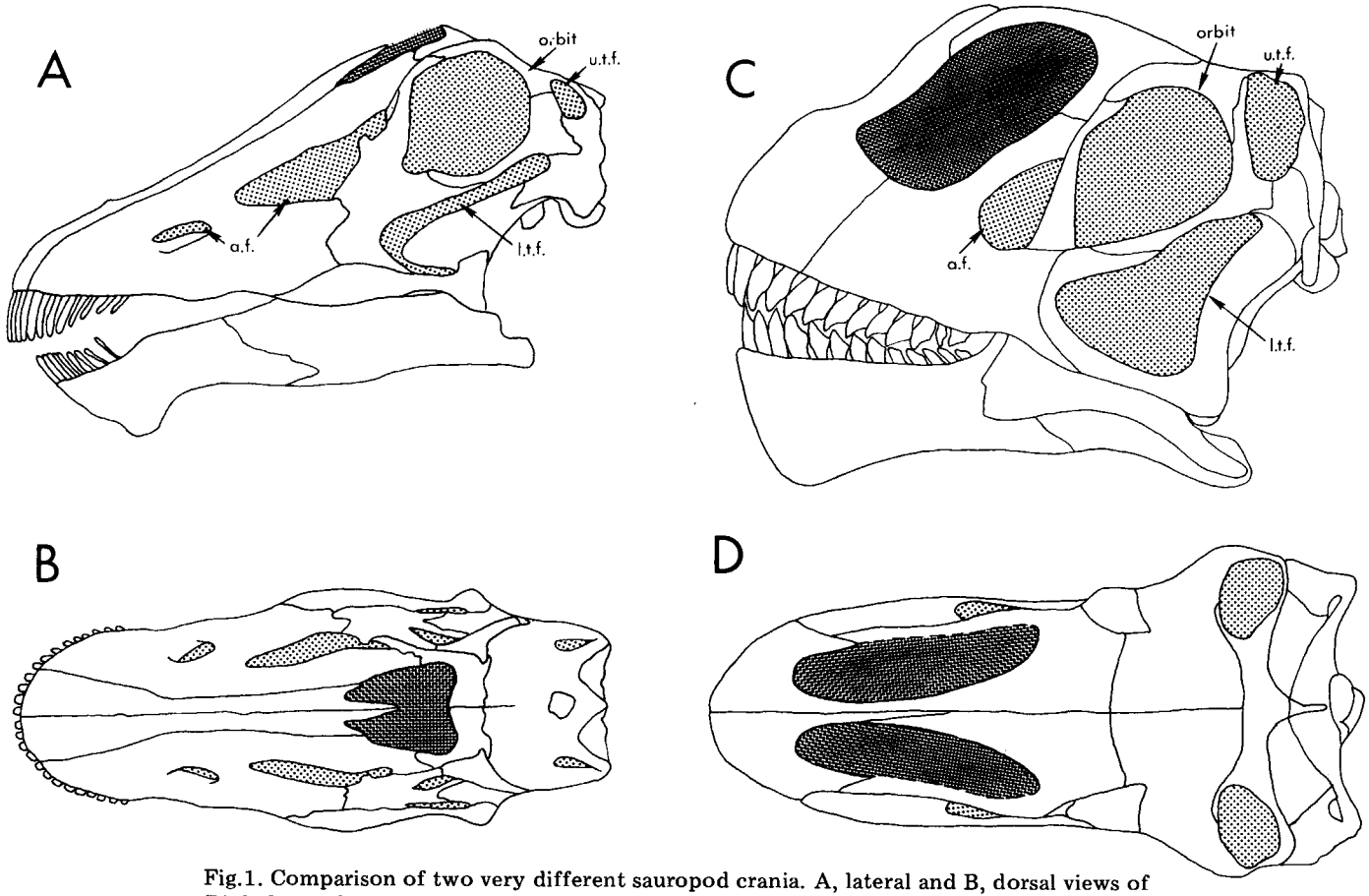


Fig.1. Comparison of two very different sauropod crania. A, lateral and B, dorsal views of *Diplodocus* showing the small, dorsally facing, retracted external nares and tiny pencil-like teeth. C, lateral and D, dorsal views of *Camarasaurus* showing the large external nares and robust, spatulate teeth. Nostrils shown in heavy stipple; other cranial openings in lighter stipple.
Abbreviations: *a.f.*, antorbital fenestra; *l.t.f.*, lateral temporal fenestrae; *u.t.f.*, upper temporal fenestrae. Skulls not drawn to same scale. (A and B after Ostrom and McIntosh, 1966; C and D after Gilmore, 1925.)

amphibious habits often have nostrils in the "normal" position (*Castor*, *Ondatra*, *Speothos*, *Hydrochoerus*, *Desmana*, *Amblyrhynchus*) but sometimes the nares are notably high on the skull (Phytosauria, Crocodilia, *Hippopotamus*). Thus there is no consistent narial pattern in amphibious or fully aquatic reptiles and mammals.

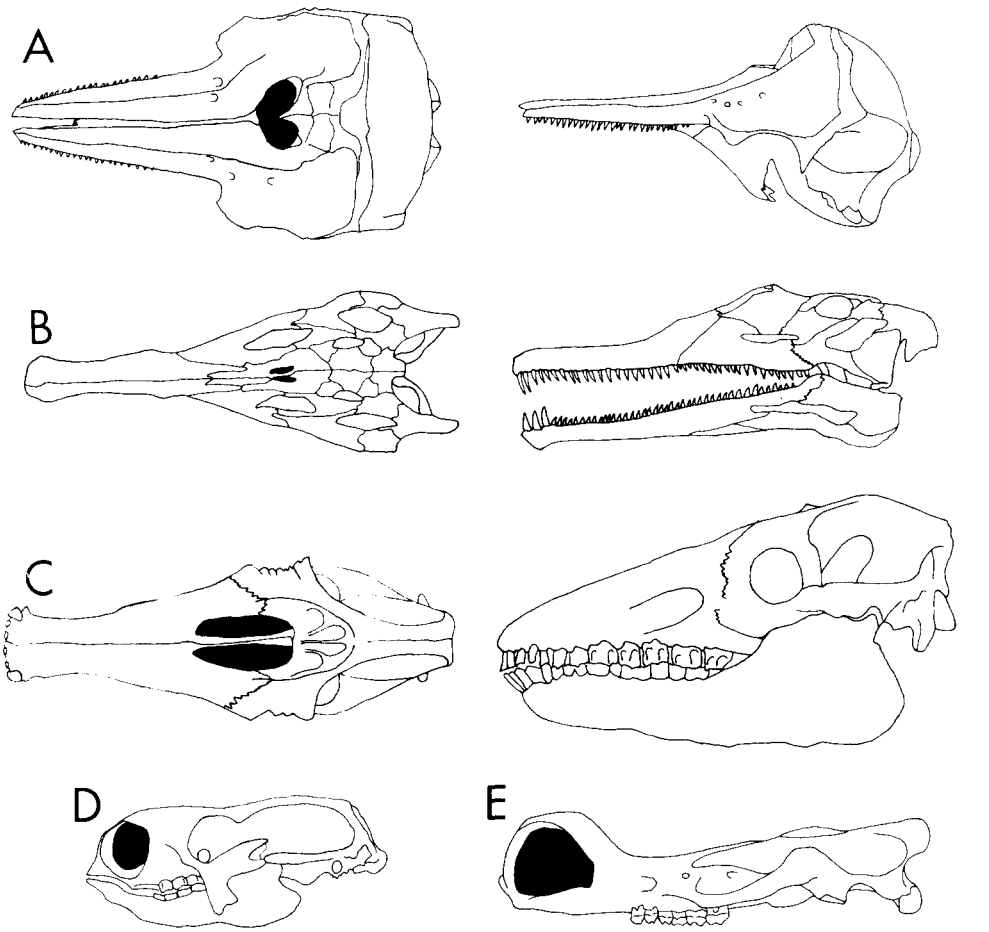


Fig.2. Dorsal and lateral views of three vertebrates with small dorsally positioned external nares similar to those of *Diplodocus*. A, *Lagenorhynchus*, an odontocete, fully aquatic habits; B, *Machaeroprosopus*, a phytosaur, amphibious habits; C, *Macrauchenia*, a litoptern, probably terrestrial. The general skull contour in *Macrauchenia* is most like *Diplodocus* of these genera, although differing in the development of muscle scars just posterior to the external nares, presumably indicating the presence of a proboscis. Below are shown two loop-snouted mammals reminiscent of *Camarasaurus* and *Brachiosaurus* but rarely compared to them. D, *Glossotherium*, an edentate; E, *Gobiatherium*, a dinocerate. The external nares are shown in black (very small in *Machaeroprosopus*). Skulls not drawn to same scale. (A after Kellogg, 1941; B after Colbert, 1947; C after Ameghino, 1889, and Zittel, 1923; D after Ameghino, 1889; E after Osborn and Granger, 1932.)

*Sauropod nares and habitat preference:* In view of the diversity of narial anatomy both within the Sauropoda and among amphibious—aquatic tetrapods, it is not possible to deduce sauropod habits from this feature. The narial arrangement of *Diplodocus*, so often cited in support of aquatic—amphibious habits, is paralleled in fully aquatic (Odontoceti), amphibious (Phytosauria), and fully terrestrial tetrapods (*Macrauchenia*, Fig.2; but some authors have called *Macrauchenia* amphibious because of its similarity to *Diplodocus*).

*Proboscis-bearing sauropods:* As observed by Bakker (1971a), the general cranial contour of sauropods, especially the size, shape, and position of the external nares, is similar in some respect to mammals which have, or are thought to have had, either a proboscis or at least a very large nose (Proboscidea, tapirs, Sirenia, Desmostylia, *Mirounga*, Pyrotheria, Astrapotheria; Fig.3). Among these animals the general cranial conformation is highly variable, but in most the narial opening is unusually large, faces somewhat dorsally, and is often retracted to near the orbits. Of these features increased size seems to be the most regular and reliable indicator of an exceptionally developed nose. Some mammals with unusually developed snouts show none of these cranial modifications (e.g. Macroscelididae).

There is a certain reluctance to accept a sauropod fitted with a proboscis because no living reptile has anything comparable to an elephantine or tapiroid nose. The closest approach is the elongate tubular nose of some turtles, an adaptation which allows the animal to remain almost fully submerged while breathing (e.g. *Chelus*, *Trionyx*). Narial projections of certain lacertilians do not contain the respiratory tract (see Fig.97 in Bellairs, 1970). Another objection is that reptiles have little superficial musculature anteriorly on the snout. Forward migration of branchiomeric muscle from the hyoid arch is the origin of almost all mammalian facial musculature, but in reptiles the bulk of this muscle still resides at the posterior extremity of the skull. Crocodiles have a sphincter mechanism associated with the nostril, an adaptation to their amphibious habits, but other amphibious and aquatic reptiles have non-muscular devices for occluding the respiratory tract (pp. 234—236 in Bellairs, 1970). In absence of any musculature, or at least with only a minimal amount, a sauropod proboscis might have been expanded for display as in *Mirounga* (Murphy, 1914). It is possible, therefore, to envision at least some sauropods with a proboscis, but there does not appear to be any reasonable way to prove such a structure existed (see theory of proboscis-bearing hadrosaurs by Wilfarth, 1938, 1939, 1940, 1948, 1949; rebuttal by Sternberg, 1939).

*Proboscises and habitat preference:* Assuming that sauropods had some kind of extensive narial structure, a proboscis in the widest sense of the word, what does this imply about habitat preferences? For mammals which have a proboscis or at least an expansive narial opening, the actual or inferred habits include fully aquatic (Sirenia, *Mirounga*, Desmostylia), amphibious (Pyrotheria, Astrapotheria, *Moeritherium*), and fully terrestrial (*Phiomia*, *Deinotherium*,

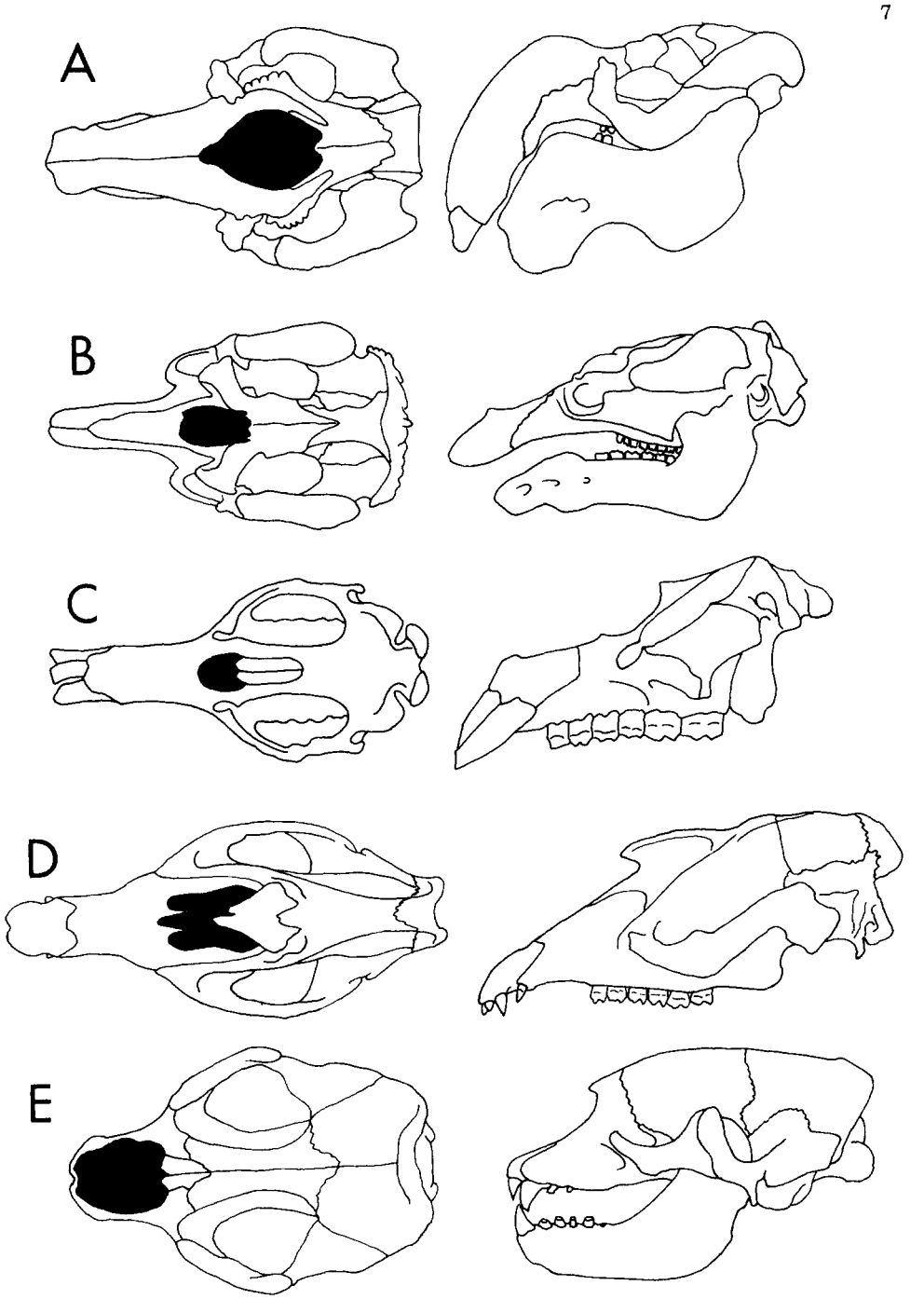


Fig.3. Dorsal and lateral views of several mammals which have fairly large, retracted external nostrils correlated with development of a proboscis or at least an extensive fleshy nose. A, *Dugong;* B, *Trichechus;* C, *Pyrotherium;* D, *Tapirus*; E, *Mirounga.* External nares are blackened in all dorsal views. Skulls not drawn to same scale. (A and B after Cuvier, 1825; C after Loomis, 1914; D and E after Hall and Kelson, 1959.)

*Elephas, Loxodonta, Tapirus*, Macraucheniidae, *Palaeomastodon*; data for fossil Proboscidea from Osborn, 1936—1942). Allowing that many of these animals are extinct and their habits therefore conjectural (both *Deinotherium* and the Macraucheniidae have been called aquatic or amphibious), there is still sufficient range in habitat preference to make any correlation of behavior with proboscis development unrealistic.

Bakker (1971a) compared the expansive narial openings of *Camarasaurus*-like sauropods to living lepidosaurs which have "inverted sink trap" pathways in their respiratory passages. These lizards are highly terrestrial, and Bakker inferred similar habits for sauropods, but Bellairs (1970) suggests that some aquatic Lepidosauria may have similarly complex respiratory tracts.

*Narial structure, conclusion:* All of the data on sauropod narial morphology are inconclusive. *Diplodocus* can be called amphibious if compared to phytosaurs, terrestrial if compared to *Macrauchenia.* For other sauropods the habits inferred from narial morphology are entirely dependent on the choice of a modern analog (see comments below on the use of analogs).

*Teeth*

*Teeth and diet:* Sauropods have at least two different tooth morphologies. *Camarasaurus*-like sauropods have large spatulate teeth filling almost all of the jaws (Fig.1). Osborn (1905) in commenting on these "great cropping teeth" pointed out a correlated massiveness of premaxillaries, maxillaries, and mandibular rami (the skull under discussion was called *Morosaurus* by Osborn, 1905, but later referred to *Camarasaurus* by Osborn and Mook, 1921). Osborn was probably correct in speaking of cropping teeth, as the dental battery is unlike dinosaurian dentitions interpreted as grinding or shearing arrangements (e.g. Hadrosauridae and Ceratopsia; Ostrom, 1961, 1964b). It is likely that food, presumably plants, was swallowed with little or no mastication because little mechanical breakdown was necessary, or because a gizzard was present (evidence equivocal; Dorr, 1966), or because there was some unusual chemical or bacterial breakdown mechanism in the gut.

A second type of sauropod dentition, exemplified by *Diplodocus*, is composed of slender rod-like teeth confined to the extreme anterior regions of the jaws (Figs.1 and 4). Hay (1908) and Haas (1963) claimed that no wear facets whatever were present on *Diplodocus* teeth, but specimens at Dinosaur National Monument and Brigham Young University have well developed wear facets. A sophisticated replacement mechanism is indicated by numerous teeth hidden within the maxillaries (Marsh, 1880a, 1884; Edmund, 1960). That *Diplodocus* teeth are also cropping and not masticating teeth seems reasonable, but the apparent fragility of the teeth and supposed absence of wear has lead to the dubious supposition that only "soft" vegetation could be eaten. A modern horse or bovid artiodactyl, its skull stripped of molariform teeth, hardly presents a picture of a more "powerful" or extensive cropping dentition

than *Diplodocus*. It is possible, therefore, that *Diplodocus* and other pencil-toothed Sauropoda could nip off and ingest a wide variety of plants in the environment with mechanical breakdown provided by a gizzard or possibly all further breakdown accomplished chemically or bacterially.

Hay (1908) objected to sauropods consuming terrestrial vegetation on the grounds that plant material would become wedged in spaces between adjacent teeth. The spacing of *Diplodocus* teeth prompted a theory that the genus was a filter feeder, straining either fresh-water algae (Hay, 1908) or certain invertebrates (Haas, 1963) from stagnant pools. *Diplodocus* teeth are certainly spaced in such a way as to form an effective sieve, somewhat similar to the sieve mechanism of *Lobodon* although without the mammal's accessory cusps (Fig.4). A difficulty with the Hay and Haas theories aside from the presence of wear facets is the necessity of assuming an adequate supply of floating algae or invertebrates, both in terms of local concentration and abundance throughout the year.

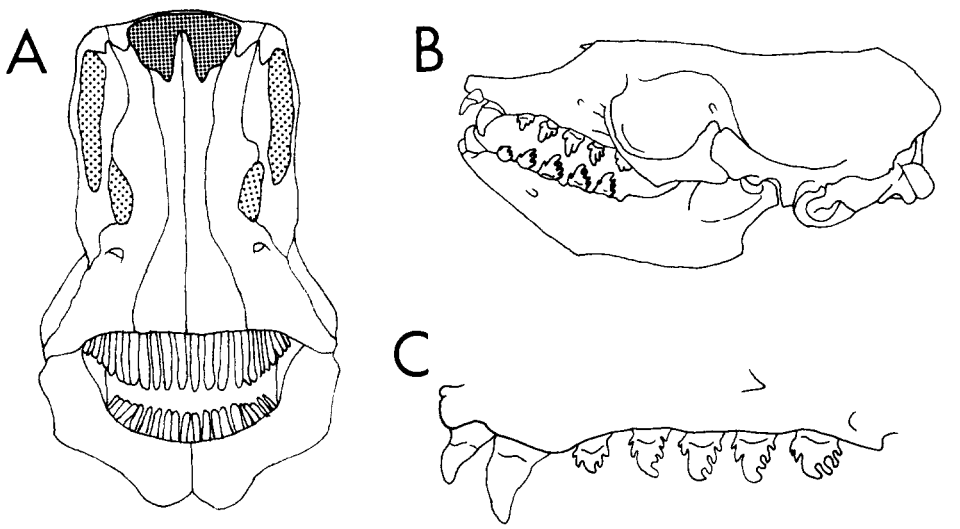


Fig.4. Comparison of *Diplodocus* and *Lobodon* to show the somewhat similar sieve-like mechanism set up by the teeth. A, *Diplodocus*, anterior view (see also Fig.1). B, *Lobodon*, lateral view: C, *Lobodon*, enlarged view of teeth. In *Diplodocus* the supposed sieve is created by uniform spacing of simple, rod-like teeth; in *Lobodon* the sieve is created by accessory cusps on widely spaced teeth. Skulls not drawn to same scale. (A after Ostrom and McIntosh, 1966; B after Hatt, 1958; C after King, 1964.)

*Teeth and habitat:* Riggs (1904) commented that the primary argument in support of semi-aquatic or marshy habitats for sauropods was based upon tooth morphology — upon the supposed necessity for sauropods to eat soft vegetation. Having thrown doubt on the latter conclusion, does it follow that sauropods are highly terrestrial? Not all aquatic vegetation is soft. The tooth replacement mechanism of *Trichechus* is an adaptation to cope with the

abrasive quality of some aquatic plants. Hippos are generally regarded as amphibious, yet terrestrial vegetation makes up the bulk if not the entirety of their diet, the animals wandering short distances from the water on nighttime forages (Walker, 1968). *Alces*, basically a terrestrial animal, spends an annual period as a wader feeding on aquatic vegetation (Walker, 1968). Because an animal can be as amphibious as a hippo yet feed on terrestrial plants, or be as terrestrial as *Alces* yet feed on aquatic plants, there does not appear to be any reasonable way to infer habitat preference from tooth morphology.

*Secondary palate*

A common but by no means universal feature of aquatic and many amphibious tetrapods is the development of a secondary palate. It is, of course, universal in mammals and is well developed in marine Chelonia and the Crocodilia. Partial secondary palates, occupying the snout but not forcing the choanae farther posterior than the orbits, are found in the Phytosauria, Mesosauria, and Ichthyosauria. Extensive bony palates with anteriorly positioned choanae occur in the Nothosauria, Sauropterygia, and Placodontia. Many turtles, *Champsosaurus*, and mosasaurs have essentially no secondary palate. Very little is known of sauropod palatal structure, but at least in *Diplodocus* the palate is more or less compatable with terrestrial archosaurs. Absence of a secondary palate is not proof of terrestrial habits, but the condition is more consistent with this interpretation than with highly aquatic behavior.

*Axial skeleton*

*The neck:* Almost as soon as the basic sauropod body configuration became known, the long neck of sauropods was compared to giraffes (Cope, 1877a, 1878c). Curiously, hardly any proponents of aquatic behavior for sauropods have compared sauropod necks with those of plesiosaurs. By implication from the giraffe analogy, sauropods were browsers on treetop vegetation. Another possibility is that sauropods, like hippos, were amphibious but fed primarily on terrestrial plants, the long neck providing access to near-shore vegetation without leaving the security of the water (Cope, 1878a). The neck might also allow sauropods to feed on aquatic plants while wading, somewhat in the manner of *Alces*, or might be used for sweeping—sieving movements as visualized by Hay (1908) and Haas (1963). Finally, the long neck might provide access to the surface for breathing while the animal was deeply submerged. This last image has been made popular by a number of restorations, all of which may be patterned after an original sketch by Cope (see Fig.21 in Osborn, 1931, and compare to the C. R. Knight painting made under Cope's direction, Fig.127 in Osborn and Mook, 1921). Foremost of several difficulties with this interpretation is the problem of ventilating the lungs against water pressure at the depths the restoration implies (Colbert, 1961). Although

an analogy with giraffes has merit, especially for long forelimbed genera such as *Brachiosaurus*, a long neck can equally well be interpreted as an adaptation for amphibious feeding.

*Vertebral structure:* A unique feature of sauropod postcranial anatomy is the curious structure of vertebrae anterior to approximately the fifth caudal. Centra are deeply excavated, sometimes almost completely hollow, and neural spines, transverse processes, and zygapophyses are reinforced by thin laminae and struts presumably aligned with stress patterns thus strengthening the vertebrae with minimal addition of weight (these generalities apply to many, but not all Sauropoda). Also, the posterior dorsals have an extra set of articular surfaces lying ventral to the normal zygapophyses. These accessory articulations, called hyposphen and hypantrum (former coined by Cope, 1878c), are thought to greatly restrict the range of movements possible between adjacent vertebrae (Osborn and Mook, 1919, 1921) and are absent from all cervicals and most caudals. Bakker (1971a) interpreted these accessory articulations as a weight-bearing adaptation, but somewhat similar structures in mammals are not associated with problems of large body size (Pholidota, Edentata, *Scutisorex;* despite the complexity of *Scutisorex* vertebrae, there is apparently little or no restriction of movement: Walker, 1968). Cope (1878a) compared the hollow vertebrae of *Amphicoelias* and other sauropods to vertebrae of deep-sea fishes and concluded that *Amphicoelias* was amphibious and fed ". . . on precipitous shores". Although there is some similarity to certain teleost fishes, both the buttressing system and accessory articulations of sauropod vertebrae are more believable as terrestrial adaptations. Riggs (1904) ". . . failed to discover in the skeletal structure of aquatic or semi-aquatic animals, either reptilian or mammalian, any of that fluting and hollowing of the vertebrae which have been interpreted as evidence of aquatic habits in the Opisthocoelia" (see similar observation by Bakker, 1971a). Although sauropod vertebral structure is inconsistent with a theory of fully aquatic behavior, sauropods could still be amphibious. Amphibious tetrapods may have vertebrae little different from more fully terrestrial genera because the vertebrae must sometimes support the animal's weight on land (e.g. *Hippopotamus*, Crocodilia, Phytosauria).

*Lung diverticula:* The theory of lung diverticula invading the cavities of sauropod vertebral centra originated with Seeley (1870) who erroneously identified some sauropod vertebrae as a gigantic, ground-dwelling pterodactyl. Owen (1875) maintained the lung-diverticula hypothesis even after recognizing the dinosaurian nature of Seeley's *Ornithopsis* material. Cope (1878c, 1884) suggested that lung diverticula in vertebral cavities of sauropods acted as "pneumatic floats" while the animal was submerged, and Marsh (1877a) interpreted cavities in the sacral mass as a pneumatic, weight-reducing adaptation. Janensch (1947) was a particular champion of the lung-diverticula theory and deduced a lung structure comparable to birds (see also Bakker, 1971b).

Assuming that adipose or loose connective tissue rather than lung sacs or gas bladders filled the cavities would still support the hypothesis that the cavities were a weight-reducing adaptation. If the air-sac theory is accepted, it can be interpreted as either a terrestrial or aquatic adaptation. Storage space for extra air is of benefit to a submerged tetrapod, and objections raised to the air-storage interpretation of hadrosaur crests would largely not apply to a lung-diverticulum system (Ostrom, 1961; see review in Heaton, 1972). A difficulty with associating lung diverticula and aquatic habits is the presumably high buoyancy which would result (see further discussion of sauropod buoyancy deduced from footprint evidence below).

*Vertebrae and limbs:* The lightness of sauropod vertebrae relative to their size contrasts sharply with sauropod limb bones which lack a medullary cavity and are relatively massive. Sauropods do not have a pachyostosis comparable to the Sirenia or Odobenidae, bony tissue of the long bones being primarily cancellous somewhat as in the Cetacea, Otariidae, and Phocidae (Williston, 1914). Matthew (1910, 1915) and Williston (1925) suggested that a "water line" could be drawn from hip joint to shoulder blade on a sauropod with all the bones above this line being lightly constructed, below this line being relatively massive. By this theory the limb bones ". . . served the same purpose as the lead in a diver's shoes . . ." to keep the animal erect while wading (Matthew, 1915). Although this analogy has some appeal, the combination of light but strong vertebrae and massive limbs can equally well be interpreted as terrestrial adaptations.

*Axial skeleton: the tail*

*General caudal morphology:* There are at least two slightly different patterns of caudal morphology among sauropods. In *Diplodocus* and *Apatosaurus* the tail is extremely long, with over eighty vertebrae (Osborn, 1899a; Hatcher, 1901; Holland, 1906, 1915; Gilmore, 1936). The last thirty or so vertebrae of these genera form a whip-lash, as it has frequently been called. In contrast, substantially shorter tails of just over fifty vertebrae are found in *Camarasaurus* and *Brachiosaurus* (Osborn and Mook, 1921; Gilmore, 1925). In all sauropods the proximal caudals have tall neural spines, short transverse processes, and are fitted with rather long chevrons (Fig.5). Toward the middle of the tail the transverse processes become obsolete and the chevrons short, but the neural spines remain moderately tall. By the distal third of the tail the chevrons are absent and the neural spines have become short.

*Tail dragging:* The slope of a sauropod tail when the animal was walking has been the subject of some disagreement. *Diplodocus* was originally reconstructed with the tail sloping fairly steeply downward from the hips, with ground contact first made by approximately the twentieth vertebra. Evidence for this reconstruction included a change in chevron morphology at about caudal

twenty and a tendency for caudals near this region to coalesce (Osborn, 1899a; Hatcher, 1901; Holland, 1906, 1910; Moodie, 1916, 1923). However, during the assembly of a *Diplodocus* for the United States National Museum, Gilmore (1932) fitted the caudals as closely as possible, producing a slightly upward inclination of the tail immediately posterior to the hips and delaying ground contact until caudal 28 or 29. The upward slant at the base of the tail is also found in *Camarasaurus* and *Apatosaurus* (Lull, 1930; Gilmore, 1932). The overall appearance of the tail in this attitude compares favorably to *Varanus komodoensis* (Gilmore, 1932). Bakker (1968) doubted that sauropods dragged

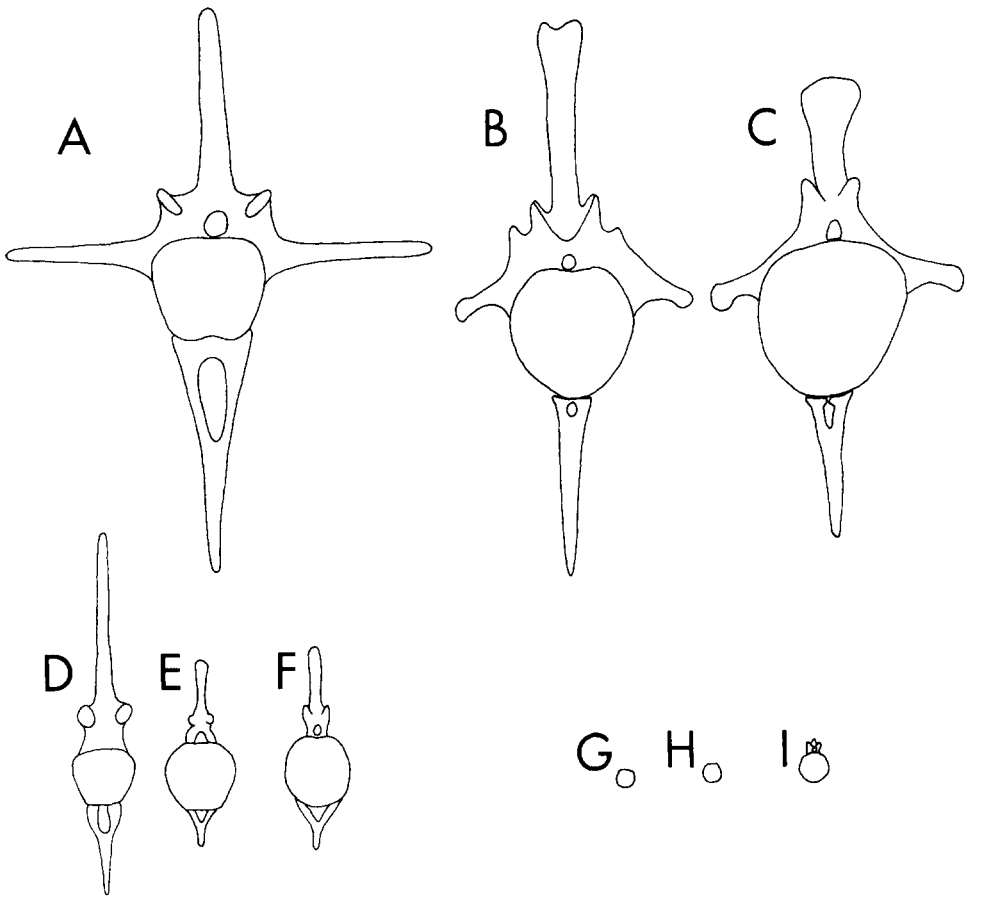


Fig.5. Comparison of caudal vertebrae from two sauropods with those of a crocodile. A, D, and G are *Crocodilus;* B, E, and H are *Apatosaurus;* C, F, and I are *Camarasaurus.* A, B, and C are fourth caudals; D, E, and F are eighteenth caudals; G and I are the 36th caudals, while H is the 32nd caudal. The two sauropods are drawn to the same scale but the *Crocodilus* vertebrae are enlarged so that the diameter of the fourth caudal centrum is about the same as in the two sauropods. (A, D, and G after Mook, 1921; B, E, and H after Gilmore, 1936; C, F, and I after Osborn and Mook, 1921.)

their tails at all, and certainly no more effort should be required to keep the tail off the ground than to support the head and neck. That sauropods at least sometimes dragged their tails is witnessed by probable sauropod trackways with what appears to be the imprint of a heavy tail (Bird, 1944). Absence of tail drags in the famous Glen Rose trackways is discussed below.

*Tail as a weapon:* The long whip-like caudal extension in *Diplodocus* has been compared to tails of living monitors, and sauropods have been pictured swinging their tails lizard-fashion as a defensive measure (Osborn, 1899a; Hatcher, 1901, 1903; Holland, 1915). Injury attending defensive strikes could account for the occasional fusion of sauropod caudals, but fusion has also been explained as resulting from dragging on the ground (Moodie, 1916, 1923), senility (Gilmore, 1932), and other sauropods stepping on the tail (Holland, 1906, commenting on *Cetiosaurus leedsi*). If fusion is a result of combat injury, it is curious that damage is habitually in the vicinity of the twentieth caudal rather than among the smaller, presumably more fragile, distal caudals. As Gilmore (1936) noted: "There must have been great liability of loss from the tip of such a slender appendage . . ."

*Tail used for swimming:* Osborn (1899a, 1905) went farther than any author in visualizing the tail as a "propeller" used for swimming. He even suggested that *Diplodocus* had a caudal fin, although his evidence and his interpretation of its appearance are nowhere stated. Osborn seems to have quietly dropped this idea in later publications, and other authors who have invoked the tail for swimming have been less extreme (e.g. Hatcher, 1903). Proximally a sauropod tail is deep and narrow, with long chevrons and tall neural spines but with short transverse processes (Fig.5). The apparently flattened shape of this region has probably influenced many into believing it suitable for aquatic propulsion. For example, Riggs (1904) compares the elevated neural arches of *Haplocanthosaurus* to those of *Stegosaurus* with the comment: ". . . it may be due to acquired aquatic habits, as such a tendency is found in certain cetaceans". The small size of transverse processes in sauropods indicates substantially lesser development of caudal muscles than in crocodilians (Fig.5; Gregory, 1919). Long transverse processes are to be expected in animals using lateral caudal undulations for swimming, as the lengths of the moment arms of caudal muscles are determined in part by the lengths of the processes. It must be admitted, as Hay (1908) pointed out, that colubrid snakes have tails no more modified for swimming than that of *Diplodocus* and yet snakes make fair progress in the water.

*Ossified tendons:* A minor point bearing on the question of sauropod caudal functions is the absence of ossified tendons. The function of ossified tendons has frequently been misinterpreted. Such structures do not add rigidity to the vertebral column because they could easily bend through any arc which could be assumed by the vertebrae. The tendency of a tendon to a stretch dampens

out the effect of muscles attached to it. Ossification greatly reduces stretching where tendons are long and must transmit considerable tension. Presumably this accounts for ossified tendons in hadrosaurs where epaxial muscles were used either for swimming or for holding the tail off the ground (Lull and Wright, 1942; Ostrom, 1964b) and in some ankylosaurs where a heavy tail club was swung for defense (Coombs, unpublished). Ossified tendons might therefore be expected in sauropod tails if they were regularly used for swimming or defense, or if the tail was habitually carried free of the ground. Absence of ossified tendons weakens but certainly doesn't disprove all these theories.

*Axial versus appendicular locomotion:* There is no reason to assume that an amphibious or aquatic reptile will of necessity use axial rather than appendicular locomotion (Williston, 1914). Aquatic reptiles may use axial locomotion (Phytosauria, Crocodilia, *Champsosaurus*, Ichthyosauria, Hydrophiidae, *Amblyrhynchus*), or appendicular locomotion (Nothosauria, Sauropterygia, Placodontia, Chelonia), or possibly a combination of both (Mesosauria, Mosasauridae). Among aquatic mammals the more amphibious forms commonly used appendicular locomotion (*Hippopotamus*, otters, *Speothos*, *Castor*, *Cuniculus*, *Ondatra*, *Hydrochoerus*, *Desmana*, *Ornithorhynchus*), whereas more fully aquatic forms may use appendicular (Pinnipedia, Desmostylia), axial (Cetacea), or a combination of both (Sirenia). Therefore, the fact that sauropod tails show no modifications for use in aquatic locomotion has only limited significance to the question of amphibious versus terrestrial habits. There is reason to believe that when in water sauropods moved by paddling with their limbs (see discussion of footprints below).

*Thorax*

*Body shape:* As with other anatomical features, sauropods show some diversity in the shape of the body cross-section. *Diplodocus* has "a short thick, slab sided body" (Matthew, 1905, 1915; see also Holland, 1906), but *Camarasaurus* is broader through the thorax (Osborn and Mook, 1919, 1921; Gilmore, 1925). Many amphibious and especially aquatic tetrapods tend to have roughly circular or at least very broad cross-sections (Sauropterygia, Chelonia, Cetacea, Ichthyosauria, Mosasauridae, *Hippopotamus*, *Potomagale*, *Speothos;* see comment of Bakker, 1971a). There are a few amphibious or aquatic tetrapods which are little different in body shape than more terrestrial genera (most Phytosauria, Crocodilia, Pinnipedia). The one living tetrapod which is a wading browser has a moderately narrow body with long limbs (*Alces*).

*Why large terrestrial tetrapods are narrow bodied:* (refer to Fig.6 for all discussion in this paragraph). The shape of the body, particularly the attitude of the ribs with respect to their vertebrae, is responsive to weight-bearing problems in any very large tetrapod which is not fully aquatic. A tetrapod's

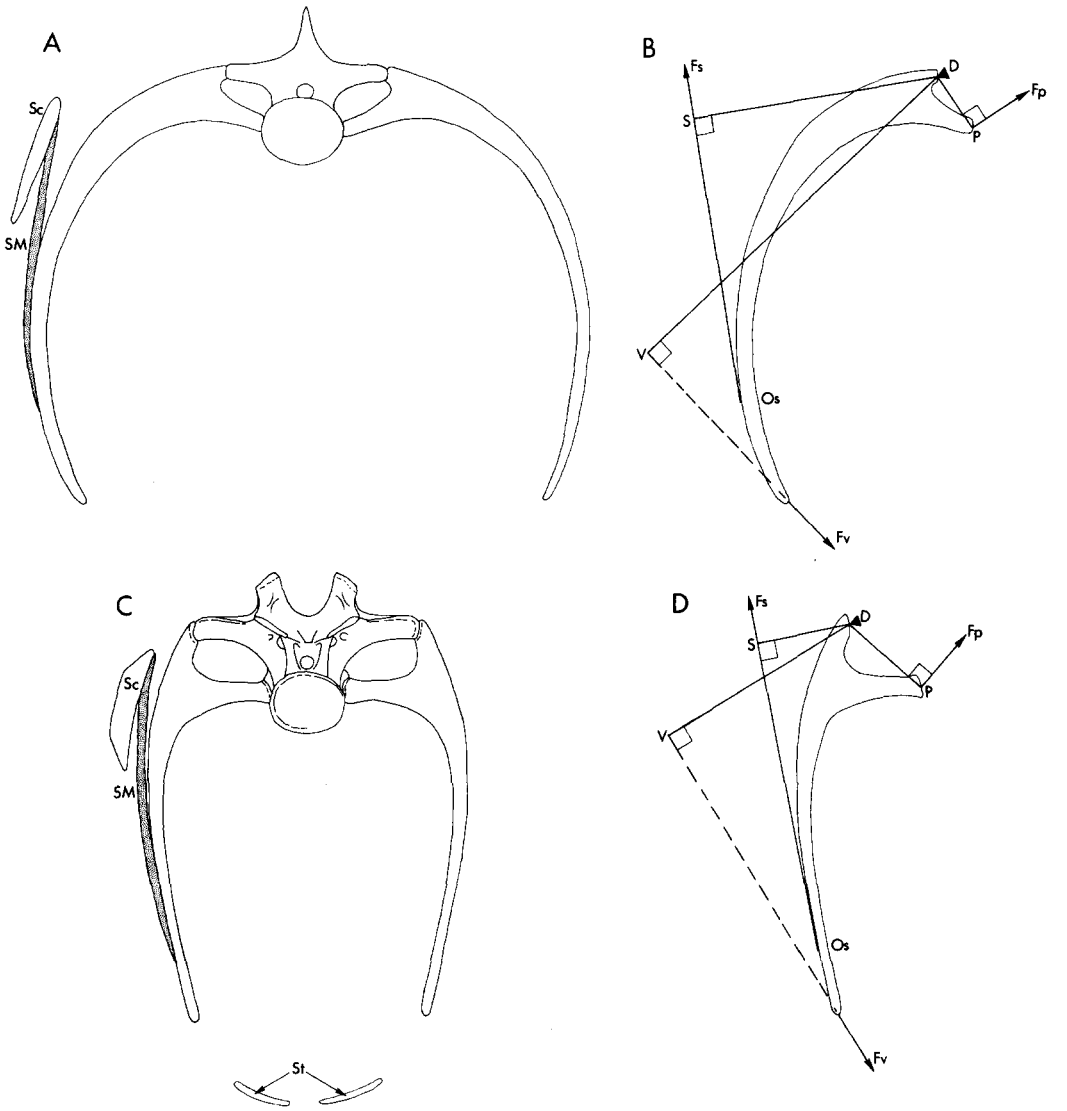


Fig.6. Comparison of a hypothetical round-bodied tetrapod with an actual sauropod, showing cross-sections through the anterior thoracic area. A, hypothetical round-bodied tetrapod; B, simplified analysis of forces acting on one rib. C, actual sauropod (*Camarasaurus*) cross-section through approximately the fourth dorsal vertebra; D, simplified analysis of forces. See text for further discussion.
Abbreviations: *D*, diapophysis, arbitrarily designated the pivot point; *Fs*, force transmitted by the serratus muscles to the ribs; *Fv*, ventral forces applied to the distal tip of the ribs by body muscles, sternal elements, and cartilages; *Fp*, force generated at the parapophysis by ligaments, a passive force; *Os*, origin of the serratus muscles on the rib; *P*, parapophysis; *Sc*, scapula (in section); *SM* serratus muscles (shown in stipple); *St*, sternal plates (in section). Moment arms for the various forces are as follows: *DP* for force *Fp*; *DS* for force *Fs*; and *DV* for force *Fv*. (C after Osborn and Mook, 1921.)

weight is transmitted from the forelimbs to the ribcage primarily by the serratus muscles (*SM*) and also, when present, by ventral pectoral elements (e.g. coracoids). Forces transmitted by the serratus muscles (*Fs*) operate tangential to the rib surface at the point of the muscle's origin (*Os*). These forces (*Fs*) tend to pivot the ribcage around the diapophyseal articulation (*D*) and to bow or bend the ribs outward depending on their compliancy. (Choice of the diapophyseal articulation as the pivot point is purely arbitrary. The pivot point can equally well be visualized at the parapophysis or at some point between the rib heads.) These tendencies to rotate and bend are resisted in several ways: (1) ribs become "T" shaped in section reducing their compliancy (reduces bending); (2) there is a force (*Fp*) at the parapophyseal articulation (resists rotation); (3) there is a force (*Fv*) generated by the resistance of ventral thoracic elements — cartilages, ventral ribs, sternal elements, and body wall musculature (counters both bending and rotation). The magnitude of *Fs* is determined by the animal's weight and activity. When the animal is standing squarely on all four limbs, *Fs* is somewhat less than one-fourth the total body weight. In a moving animal the size of *Fs* increases rapidly, and in a running tetrapod the instantaneous value of *Fs* may be several times greater than the body weight. The sum of the moments of resisting forces must slightly exceed the maximum moment experienced at *Os*. Expressed symbolically:

$$DV\ (Fv) + DP\ (Fp) > DS\ (Fs)$$

Within certain weight limits, and what the critical weight might be is uncertain, *Fv* and *Fp* can be increased sufficiently to allow almost any shape in the thorax. *Fp*, which is primarily a consequence of ligaments binding rib head to vertebra, is probably a very large force in all tetrapods. Thus some rather large terrestrial tetrapods may have rotund body cross-sections (e.g. rhinos). However, in the largest terrestrial tetrapods, as well as in moderately large cursorial forms, a further modification enters. The length of the moment arm of *Fs* (*DS* in Fig.6) is reduced while the moment arm of *Fp* (*DP* in Fig.6) is lengthened. This is accomplished by having tall straight ribs and by increasing the length of the transverse processes. The tall straight ribs also have less tendency to bend because *Fs* is nearly parallel to the long axis of the ribs (i.e., the component of *Fs* acting normal to the rib surface at *Os* is very small). The difference made by these alterations is shown in comparing a hypothetical round-bodied tetrapod to an actual sauropod as shown in Fig.6. In the round-bodied tetrapod, the moment arm *DS* is longer than the resistance arm *DP*, but in a sauropod the resistance arm *DP* is longer than *DS*.

Because sauropods show exactly those modifications of body shape which would be expected in a highly terrestrial megatetrapod, it is reasonable to conclude they had regular if not exclusively terrestrial habits. Riggs (1904) pictured *Brachiosaurus* as more terrestrial than other sauropods because of its notably deep thorax, but it is doubtful that more terrestrial and more amphibious genera could be distinguished by body shape alone. Problems of packing

an extensive gut into the body cavity may influence overall body conformation in some sauropods.

*Limbs and feet*

*Limb posture:* Some uncertainty is present in reassembling the limbs of an extinct animal into what can be considered a "normal" or "typical" posture for the species. Sauropods are particularly troublesome because the articular ends of their long bones are not as well ossified or meticulously modeled as in most large tetrapods. The rough, incompletely ossified ends of sauropod elements have been compared to similar bones of aquatic tetrapods and have sometimes been cited as indicating amphibious or aquatic habits (Osborn, 1898; Hatcher, 1901; Hay, 1910; Lull, 1915). The arguments follow one of two lines: (1) The extensive cartilaginous pads indicated by the roughened articular surfaces could not support a sauropod's weight without suffering damage; and (2) habitually terrestrial megavertebrates never have such extensive cartilaginous pads. The first argument is probably not valid. The greater compliancy of cartilage compared to bone could allow a greater contact area at the joint through a wide variety of limb angles, thus distributing forces over a greater surface area at the joint. There is some credence to the second argument if analogies with other terrestrial megavertebrates have any validity. Large, presumably terrestrial dinosaurs all have more fully ossified joint surfaces than sauropods (carnosaurs, iguanodontids, stegosaurs, ankylosaurs, ceratopsians, ?hadrosaurs). Well-ossified joint surfaces are also the rule in large terrestrial mammals (Proboscidea, Rhinocerotidae, Dinocerata, Brontotheriidae). Only in the most highly aquatic mammals and reptiles are the long bone joints poorly ossified (Cetacea, Sirenia, Ichthyosauria, Sauropterygia, Mosasauridae, marine Chelonia, Thalattosuchia), but the limbs of these forms are otherwise so unlike sauropod limbs, and the lack of joint modeling so much more extreme, that the comparison does not seem altogether reasonable. Why sauropods should be the single exception to a consistent pattern of well-ossified joint surfaces in terrestrial megatetrapods is unclear.

The attitude of sauropod limbs, particularly those of *Diplodocus*, was once the subject of a lively debate. The famous life-size drawing of *Camarasaurus* made by Ryder in 1877 under Cope's direction, the first attempt at a complete sauropod skeletal reconstruction, portrays the genus with approximately straight, elephantine limbs (see plate 82 in Osborn and Mook, 1921). Similarly Marsh (1883) from the very beginning restored *Brontosaurus* (later made *Apatosaurus*) with a more or less mammal-like limb posture. Many later authors, including Osborn, Mook, Hatcher, Holland, Riggs, Matthew, Gilmore, Gregory, and Janensch, several of whom were engaged in preparing full skeletal mounts, also tended to align proximal and distal limb elements producing elephantine, pillar-like legs. Objections were raised by Hay (1908, 1910, 1911) and Tornier (especially 1909a, but see also 1909b,c, 1910a,b,c) both of whom insisted on a crocodile-like or "reptilian" sprawling attitude for *Diplodocus*

limbs (there is no indication that Hay or Tornier were thinking of the high walk of crocodiles; see Cott, 1961). Both Hay and Tornier, despite their detailed arguments, appear to have been biassed by an initial assumption that all reptiles must be posed alike, i.e. in the manner of lizards. Hay assumed that the entire proximal end of a sauropod femur constituted an articular surface, rather than accepting the existence of a trochanter towards the lateral edge of the proximal end (problem of poor ossification). A scathing rebuttal by Holland (1910) and milder more analytic replies by Matthew (1910) and Abel (1910) did not succeed in convincing either Hay or Tornier that their ideas were erroneous, but hardly any authors since have reconstructed sauropods with a sprawling limb posture. A remarkable specimen of *Camarasaurus*, almost complete and in natural articulation, demonstrated the correctness of the majority opinion that sauropods had essentially an elephant-like posture (Gilmore, 1925), and the final, virtually indisputable evidence came from sauropod trackways (Bird, 1939, 1941, 1944). There is little room for dispute on the basically pillar-like attitude ascribed to sauropod limbs.

Riggs (1904) pointed out that the straight limbs of sauropods were similar to "uplands" vertebrates and that by analogy with proboscideans and Dinocerata this indicated basically terrestrial habits. In fact, there are some marine reptiles that have little or no flexion at the elbow or knee (Ichthyosauria, Sauropterygia, Mosasauridae; Osburn, 1906; Williston, 1914), but the limbs of these forms are otherwise so unlike sauropod limbs that the comparison is not appropriate (see below). Despite their similar post-like limbs, sauropods and proboscideans have different musculature (Romer, 1923) demanding slightly different limb movements for sauropods (Gregory, 1919). The very short moment arms of some major limb muscles in sauropods (no olecranon process or calcaneal tuber) together with the relatively immobile pectoral girdles (immobility correlated with presence of large ventral elements; see Hildebrand, 1974, pp. 493—495) point to very sluggish ambulation for sauropods even compared to elephants.

*Bipedalism:* In an early paper on *Camarasaurus*, Cope (1878a) makes the following statement: "It must be born in mind that the caudal vertebrae retain the solid character seen in those genera which stood habitually on their hind limbs." Aside from anticipating a later theory of bipedal origins for sauropods, there is an intimation of at least occasional bipedality for sauropods. Elsewhere during the same year Cope explicitly stated that sauropod forelimbs did not leave the ground (Cope, 1878b), and Marsh regularly stated that bipedal locomotion was hardly possible for sauropods (e.g. Marsh, 1883, 1896). Osborn (1898) resurrected the idea of a bipedal stance for submerged sauropods and suggested an analogy with the terrestrial pose of hadrosaurs. Osborn may have been inspired by Knight's restoration made under Cope's direction (see Fig.127 in Osborn and Mook, 1921). Later, when discussing the construction and functions of sauropod tails, Osborn speculated that the tail could act as a counterbalance to all of the body anterior to the pelvic girdle for raising up to

a bipedal stance, or that sauropods could sit up on their hind limbs and tail in a "tripodal" position both on land and in the water (Osborn, 1899a). Riggs (1904) suggested that long neural spines on sacral and posterior dorsal vertebrae, bifurcated neural spines on anterior dorsal and cervical vertebrae, and a short stocky body all indicated that some sauropods ". . . were adapted to rearing up on the hind legs . . .". Bifurcated anterior neural spines, as in *Diplodocus* and *Apatosaurus*, presumably accommodated the tendons and musculature required for lifting the front of the body. The theory of sauropod bipedality culminated with "Scientific American" commissioning Charles R. Knight to execute a painting showing two *Diplodocus*, one completely submerged save for the neck and head, the other rearing up on its hind legs on the nearby shore either to nibble the top of a cycad or in response to the approach of the submerged animal. This fascinating painting thus encompasses and attempts to reconcile almost the entire gamut of opinions on sauropod habits ("Scientific American", 1907, vol. 96, page 483). Sauropods might have been as bipedal as elephants, which can be trained to stand and even walk bipedally, and which sometimes rear up on the hind limbs in the wild to reach high leaves and branches. Some very unlikely quadrupeds are capable of briefly assuming a bipedal stance, e.g. stallions and bighorn sheep when engaged in hierarchy or mating battles (the latter actually run bipedally when tilting with an opponent). Occasional bipedality is therefore not as outlandish for sauropods as it might seem, but such activity was probably so rare as to be trivial to an overall picture of sauropod natural history.

*Feet:* "The short, stout metapodials and blunted phalanges characteristic of the Opisthocoelia would be as ill adapted for propulsion in water or upon marsh lands as are those of the elephant" (Riggs, 1904). Sauropod feet are not so easily compared to those of modern elephants. Some sauropod metacarpals stood nearly vertically in a semicircular array like a ring of doric columns below a capital dome (Fig.7; Hatcher, 1902; Osborn, 1899b, 1904), and in this respect a sauropod manus is closer to hippo and rhino feet than to the more platigrade elephant manus. The abbreviated phalangeal segment of a sauropod manus is similar to elephants (Bakker, 1971a). Sauropod metatarsals are less uniform in length than the metacarpals and the whole pes has a peculiar asymmetrical entaxonic structure not comparable to ungulate or subungulate mammals (Fig.7; Hatcher, 1901). Still more unusual in sauropod feet is the presence of large claws, at least one in the manus and three in the pes (Fig.7; Osborn, 1899b). These claws differ strikingly from the hooves of most large terrestrial herbivores, including elephants, and are unlike the wide, hoof-like unguals of large, supposedly terrestrial herbivorous reptiles (Ceratopsia, Ankylosauria, Stegosauria, ?Hadrosauridae). Such claws do not look suitable for hard dry ground or cursorial habits, but there are some large herbivorous mammals which had similar claws (ground sloths, chalicotheres, homalodotheres), and many medium-sized mammalian carnivores as well as very large predatory reptiles (carnosaurs) combine large claws with highly terrestrial,

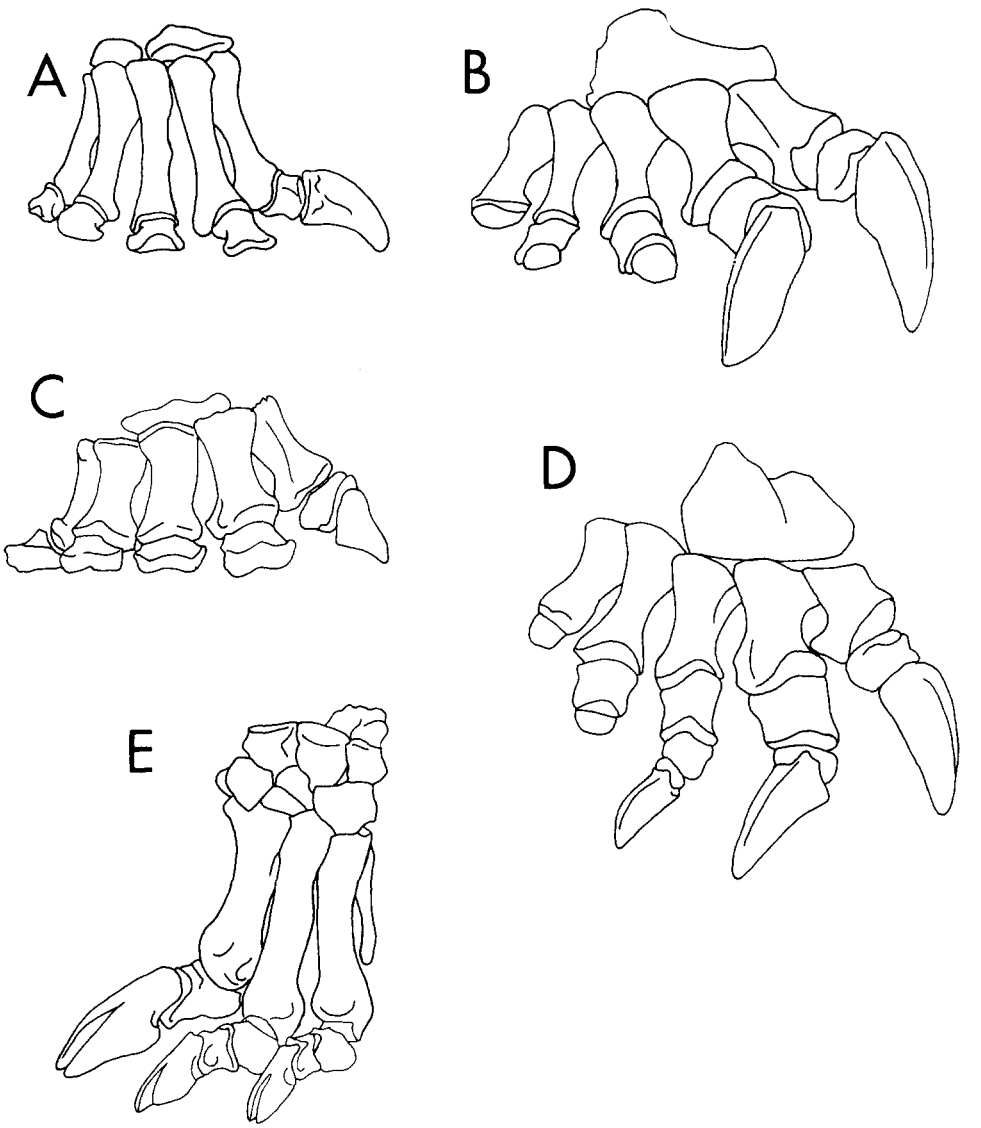


Fig.7. Manus and pes of two sauropods and the manus of a clawed herbivorous mammal. A, manus and B, pes of *Diplodocus*. C, manus and D, pes of *Apatosaurus*. E, manus of *Moropus*, a chalicothere. Not drawn to the same scale. (A after Osborn, 1904; B and D after Hatcher, 1901: C after Gilmore, 1936; E after Holland and Peterson, 1914.)

cursorial behavior. What use sauropods made of their claws is unclear — gaining purchase on a muddy streambed is certainly plausible — but on the whole Riggs' (1904) final conclusion is probably correct: ". . . if the foot structure of these animals indicates anything, it indicates specialization for terrestrial locomotion".

*Limbs and feet, summary:* Perhaps the most revealing analysis of sauropod limb and foot structure comes by measuring sauropods against the fourteen trends found by Osburn (1906) to be common in the feet of aquatic and amphibious reptiles and mammals. In the listing below, an exclamation mark indicates a trend totally unlike, even diametrically opposed to the condition in sauropods.

| Aquatic limb and foot trends | Are sauropods comparable? |
|---|---|
| 1. Abbreviation of the limbs as a whole. | 1. No! |
| 2. Curvature or backward extension of the limb. | 2. No! |
| 3. Distal dilation of the limb. | 3. No! |
| 4. Parallelism or convergence of the fore and hind limbs. | 4. Yes, but qualitatively different from aquatic tetrapods. |
| 5. Tendency towards loss of hind limbs. | 5. No! |
| 6. Tendency toward similarity in shape and function of all the bones of the limbs. | 6. No. |
| 7. Elongation of the digits. | 7. Metacarpals long, but otherwise no. |
| 8. Hyperphalangy. | 8. No! |
| 9. Hyperdactyly. | 9. No. |
| 10. Formation of smaller skeletal parts. | 10. For non-ungual phalanges, yes, but not for pre-, meso-, and metapodial elements, nor for unguals. |
| 11. Concentration of all skeletal parts except the digits. | 11. No! |
| 12. Cartilaginous progression in joints. | 12. Yes, although not as extreme as in most aquatic tetrapods. |
| 13. Loss of mobile articulations in joints. | 13. No. |
| 14. Loss of tuberosities for muscle attachment. | 14. Some, but similar to other large quadrupedal dinosaurs (e.g. *Stegosaurus*). |

In terms of Osburn's criteria for evaluating aquatic adaptations in the limbs and feet, sauropods fare very badly. The opinions of Hatcher (1903), Riggs (1904), Gregory (1919), and Bakker (1971a) that sauropods had essentially terrestrial limbs and feet are certainly correct.

*Use of modern analogs*

Virtually every author who has dealt with sauropods has used modern analogs in deducing habits, the most popular being elephants because of similar large size, limb posture, and thorax conformation, and also giraffes because of their long neck (e.g. Cope, 1877a, 1878b; Riggs, 1904; Matthew, 1905, 1915; Bakker, 1971a; and the present paper). Aside from the fact that no modern animal is comparable in all respects to sauropods (Matthew, 1905, 1915), there is an inherent, almost inescapable temptation to overextend such analogies. For example, if sauropods are like elephants in being large, having pillar-like legs and a deep narrow thorax, what then may be said of sauropod habits? Elephant habitat preferences are difficult to categorize because they are so

variable, for *Elephas* encompassing thick jungles and open grassy plains, for *Loxodonta* including dry savannas, desert scrub, river valleys, thorn brush, and dense forests (Bere, 1966; Walker, 1968; Sikes, 1971). Both savannas and dense jungles form major refugia, but the most critical parameter controlling elephant distribution is the presence of large permanent bodies of water (Bere, 1966; Sikes, 1971). The east African *Loxodonta* may only recently have entered savanna terrain, a consequence of human deforestation over the past 150 years (Sikes, 1971). Habitat preferences ascribed to fossil Proboscidea are highly diversified (Osborn, 1936—1942). If an analogy is drawn and sauropods are said to be "like elephants", it is pertinent to ask not only which elephants and why, but also in what part of their range and during what part of the year. It is a subtle trap, the ease with which an entire reptilian suborder can have its habits and habitat preferences deduced by comparison not with all proboscideans, not with the family Elephantidae, not with a particular genus or even a single species, but by comparison with certain populations of a single subspecies.

Deciding that a particular modern animal is most like sauropods is no guarantee of solving the problem of sauropod behavior.

## NON-ANATOMICAL EVIDENCE

### *Taxonomic diversity*

Osborn (1898) observed: "It is *a priori* improbable that so many different genera of gigantic Saurians of similar size co-existed". Bakker (1971a) modified Osborn's theory, arguing that paludal—lacustrine environments could not support the diversity of sauropods found in a single assemblage. Assuming that sauropods fossilized together also lived sympatrically (i.e. thanatocoenose = biocoenose) and that errors in present sauropod nomenclature are minor, it is certainly true that the number of sauropod taxa found in single quarries in the Morrison Formation exceeds the number of megamammals (= size and weight range of modern elephant, rhino, and hippo) found living sympatrically. Modern paludal—lacustrine environments support few megatetrapods, the bulk of the tetrapods being amphibious—aquatic birds, an element not present in Jurassic time. Bakker (1971a) is probably correct in objecting to crowding all sauropods together in an aquatic situation, but concluding that no sauropods fed on aquatic plants is probably unwarranted. The diversity in sauropod dentitions probably reflects a diversity in dietary and consequently habitat preferences.

### *Footprints*

As noted above, Riggs (1904) believed that sauropod feet were ill adapted to swampy or muddy terrain, yet evidence in the form of footprints indicates that sauropods, like elephants, could and did cross muddy and swampy ground.

Elephants may occasionally get stuck in mud holes, but there is no evidence that this is common or that elephants avoid swampy ground because of the danger. On the contrary, elephants are notoriously fond of wallowing and wading (Bere, 1966; Sikes, 1971). The famous sauropod trackways near Glen Rose, Texas, were made in mud sufficiently soft to allow huge sauropod feet to sink to depths of twelve to eighteen inches (Bird, 1939, 1941, 1944). Absence of tail drags at Glen Rose has long been explained by assuming the presence of sufficient water to float the tails free of the bottom. Support for this explanation comes from possible sauropod trackways which do have a tail imprint (Bird, 1944). One set of sauropod prints is composed almost exclusively of forefoot impressions, there being only a single hind foot imprint (Fig.8). The animal apparently floated his hindquarters while "walking" along the bottom with his forelimbs, then kicked the bottom with his left hindfoot as he turned to his right (Bird, 1944). This trackway, if correctly interpreted, indicates that sauropods were too buoyant to stand fully submerged with all four feet planted firmly on the bottom as they are portrayed in many popular restorations. The trackway also throws some doubt on the Matthew—Williston theory of the limbs acting as ballast, and indirect support is given to the lung-diverticulum theory (see above).

*Gregarious behavior:* Bird (1944), Bakker (1968, 1971a), and Ostrom (1972) have all supported the idea that sauropods traveled in herds, the evidence

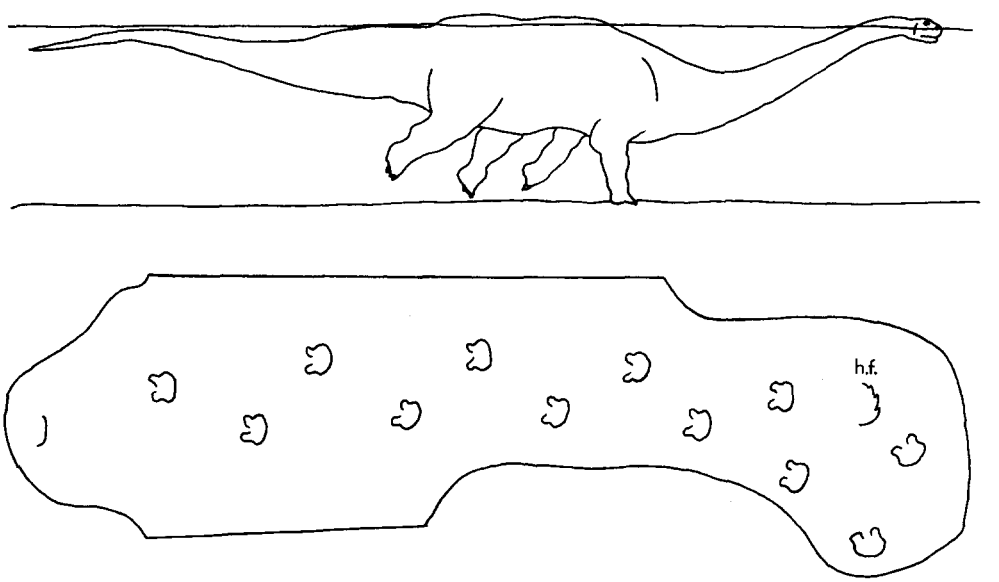


Fig.8. A trackway consisting of sauropod forefoot prints with only a single hindfoot impression. The lower sketch is a map of the trackway with the single left hindfoot imprint indicated at *h.f.* The upper sketch shows the manner in which a partially floating sauropod could make such a trackway. (After Bird, 1944.)

coming from a particular assemblage of trackways at Glen Rose. The use of the word "herd" is troublesome because it is usually reserved for ungulate mammals and its application implies mammal-like behavior, interaction, and coordinated activity. Sauropod aggregates might equally well be called "pods", or "flocks", or "troops", or "packs", or any one of many collectives each implying more than simple aggregation. There is, of course, some doubt on the "herding" interpretation for the Glen Rose assemblage. Basking crocodiles (or turtles, or *Amblyrhynchus*) suddenly startled will dash to the water leaving, conditions permitting, several subparallel trackways over a small area. The Glen Rose aggregate might be no more than a fortuitous assemblage at a feeding ground prompted to flight by approaching danger (tracks of a large theropod are present), or the several individuals may have crossed the area over a period of many hours. There appears to be no other instance of multiple sauropod trackways on a single bedding plane, all headed in the same direction. There are trackways of single individuals, as for example the famous sauropod followed by a carnosaur (Bird, 1944), and many sauropod ichnites are single footprints (Marsh, 1899; Hatcher, 1903). Sufficient sauropod trackways may not exist for statistical treatment such as Ostrom (1972) applied to Triassic footprints.

*Footprints, summary:* Trackways indicate that sauropods could and did wade and swim in streams, and that sauropods sometimes dragged their tails on the ground. One set of tracks suggests that sauropods sometimes may have occurred in groups. What sauropod footprints do not demonstrate is habitual preference for stream or swampy, muddy habitats, nor do they show whether aggregates were accidental or purposeful.

*Sedimentology*

Interpretation of geologic evidence bearing on the problem of sauropod habitat preferences is very difficult. It is most tempting to assume that where sauropods are most abundant as fossils, there also they lived by choice, yet there is always the possibility that abundance of fossils says more about the suitability of the depositional environment for preservation than about habitat preferences of the animals present. Even if sauropods only came to rivers or lakes to drink, their bones would sometimes turn up in stream channel or lake deposits. It would be quite beyond the scope of this paper to evaluate every geologic formation which has yielded sauropods, so the discussion will be limited to three well-known and generally well-studied situations.

*Morrison Formation:* The Morrison Formation may have produced more than half of all the known specimens of sauropods. Additionally, the Morrison has been thoroughly studied by both paleontologists and geologists (e.g. Mook, 1915, 1916, 1918; Stokes, 1944, 1953; Untermann and Untermann, 1954, 1964; Moberly, 1960; Mirsky, 1962). A few simple arguments suggest that the environmental setting in which the Morrison formed was also the preferred

habitat of the Sauropoda there entombed. Foremost is the enormous area over which the Morrison was laid down. The numerous sauropods could not possibly have wandered accidentally into the Morrison environment from elsewhere. Post-mortem transport for any considerable distance is also very unlikely, as witnessed by the large size of sauropod bones compared to the fineness of Morrison sediments, the presence of many partially articulated skeletons often with long stretches of vertebrae intact, and finally the good preservation of fragile struts and buttresses on the vertebrae. Therefore, describing the Morrison environment also describes the favored habitat of many sauropods. The Morrison Formation is generally thought to have been laid down over a surface of very little relief only slightly elevated above sea level. The bulk of the sediment is fine variegated mudstone and shale, but some coarse cross-bedded sandstones are present and coal seams are found toward the top of the Morrison, especially in the Brushy Basin Member (Mirsky, 1962). Depositional settings include floodplain-overbank, fluviatile, and presumably paludal as evidenced by coal. Lacustrine deposition seems to be very rare if present at all, and much of the fluvial sediment was deposited under very shallow water (Stokes, 1953). The Morrison climate has been called somewhat arid (Stokes, 1944) and ". . . no more than semi-arid and probably much more humid" (Mirsky, 1962). Faunal elements requiring at least an annual wet season are present (Hecht and Estes, 1960). The environment has often been compared to a lowland river floodplain, but without large, deep, permanent lakes and extensive, thick, long-standing swamps. Whether sauropods frequented streams more than the dry ground between is impossible to determine, though it seems inevitable they spent some time in both. Sauropod bones are scattered throughout the formation, but are somewhat more common toward the top. A famous quarry is located in a very coarse sandstone near the top of the Morrison (Osborn and Mook, 1921), and the Dinosaur National Monument quarry is also in relatively coarse matrix, but does the abundance of sauropods in these quarries point to a preference for the high energy streams indicated by coarse sediments, or was the rapidly moving water a "death-trap" for sauropods unwary enough to enter it? Most probably the high rate of sediment deposition was conducive to preservation.

*Wealden Beds:* Another well-studied formation in which sauropods are the most abundant terrestrial tetrapod is the Wealden (Allen, 1949a,b, 1954, 1959). The situation is very different from the Morrison in that most sauropod remains are dissociated, isolated elements, partially articulated skeletons being very rare, indicating considerable post-mortem transport of sauropod bones (not all Wealden reptiles show signs of transport, e.g. the Bernissart *Iguanodon*). The Wealden environment has been variously interpreted (Allen, op. cit.) but the general picture is one of a large freshwater lake with offshore reed beds. Streams bringing in sediments from the London Platform and depositing these in cyclic deltaic sequences were sometimes pooled to form backwater swamps. At times, the sea breached barriers surrounding the lake converting

it to a brackish inland sea. Here is a wet environment — lacustrine, lagoonal, paludal and estuarine — with sauropods on the fringes, probably somewhat inland on the London Platform, but not commonly or regularly venturing out into the larger bodies of water.

*Tendaguru:* Another formation worthy of note, though not as thoroughly studied as the previous examples, is the dinosaur-bearing deposit at Tendaguru. This formation is similar to the Morrison in terms of the preponderance of sauropod bones compared to all other tetrapods. Tendaguru sediments include shales and mudstones apparently similar in lithology to much of the Morrison (Schuchert, 1918). In some places coarser sediments show cross-bedding and ripple marks. Three brackish to freshwater deposits interbed with three zones of marine molluscs. Sauropod bones, which are not found in the marine deposits, are generally more dissociated and scattered than in the Morrison, thus indicating transport. The environment was fluviatile and floodplain, with some lagoonal and marsh deposits. There is some evidence in the form of articulated upstanding feet that at least sometimes sauropods died in situ, suggesting that at least sometimes they wandered into soft, muddy, or swampy areas, but this is not common.

No other formations have quite the relative and absolute abundance of sauropods as have the Morrison, Wealden, and Tendaguru. Upper Cretaceous formations, particularly the Oldman, Edmonton, Lance, and Hell Creek, have produced large numbers of dinosaurs, primarily species regarded as terrestrial, yet sauropods are conspicuous by their absence (Russell, 1964; Russell, 1967). Sauropods definitely survived as late as the Campanian in very restricted numbers and diversity. Absence of sauropods in the most productive Upper Cretaceous sediments may reflect a real decline of the group, but possibly it is a consequence of environmental limitations not immediately obvious in the sedimentology.

## SUMMARY

(1) The aquatic—amphibious theory of sauropod habits originated with Owen, possibly as the result of a taxonomic error.

(2) Owen may have inspired or biassed Cope, Marsh, and all later authors toward an amphibious interpretation of sauropod behavior.

(3) There is no simple or obvious way to interpret sauropod narial structure.

(4) The narial position of *Diplodocus* suggests amphibious habits if compared to phytosaurs, terrestrial habits if compared to *Macrauchenia.*

(5) *Camarasaurus* and similar genera had a complex narial structure, possibly a proboscis, which could indicate either amphibious or terrestrial habits.

(6) Absence of a secondary palate speaks against highly aquatic habits.

(7) Teeth of *Camarasaurus* and similar genera could nip off almost any available vegetation.

(8) *Diplodocus* teeth are difficult to associate with a specific food, but can be interpreted either as cropping teeth or as a sieve mechanism.

(9) The long neck of sauropods might be an adaptation for either terrestrial or aquatic feeding.

(10) Sauropods may have had a bird-like system of air sacs in the vertebrae and ribs.

(11) Buttresses, accessory articulations, and central cavities of sauropod vertebrae are best explained as terrestrial weight-bearing adaptations.

(12) Sauropod tails are not specially modified for aquatic propulsion, but they could have served that function.

(13) Sauropods may have swung their tails as a defensive measure.

(14) Sauropods at least sometimes dragged their tails on the ground.

(15) Sauropod axial skeletons show no clearly amphibious or aquatic adaptations.

(16) Sauropod body shape indicates regular if not constant exposure to stresses of terrestrial locomotion.

(17) Poorly modeled articular surfaces on sauropod limb bones are unlike all other terrestrial megavertebrates.

(18) Sauropods had a straight-limbed posture similar to modern elephants.

(19) Sauropod limbs and feet show few if any modifications consistent with amphibious or aquatic habits.

(20) Sauropods may have occasionally assumed a bipedal or "tripodal" stance.

(21) Sauropods show a higher taxonomic diversity in single assemblages than do comparably large mammals.

(22) Sauropods sometimes occurred in groups.

(23) Sauropods sometimes waded, paddled, and swam in streams.

(24) Sauropod remains are common in moist lowland, floodplain, and fluviatile deposits.

(25) Large lakes and swamps are either uncommon where sauropods abound, or when sauropod bones are present in lacustrine or paludal deposits, they show signs of transport.

## CONCLUDING REMARKS

Assessment of all the data and arguments presented above is no simple matter. Many features of sauropod anatomy can be interpreted in several ways, and it is not always possible to defend one hypothesis over another which is diametrically opposed. The aquatic—amphibious theory rests primarily on two features: (1) dorsally positioned nostrils (esp. of *Diplodocus*); and (2) cartilaginous articulations in the limbs. This is remarkably slim evidence in view of the popularity of the amphibious theory. Many features of the appendicular and axial skeleton speak strongly for primarily terrestrial behavior. Geologic evidence indicates occasional ventures into streams, but does not support constant submersion in deep lakes as sauropods are often

portrayed. However, an amphibious reptile may show few if any of the anatomical modifications found in other amphibious or aquatic tetrapods. Tetrapods of amphibious habits may be distressingly similar to closely related terrestrial species (e.g. *Thalarctos maritimus* and *Ursus horribilis*). Calling the entire suborder Sauropoda a homogeneous group is probably misleading (e.g. Hatcher, 1903), as the diversity of sauropod morphology probably reflects diversity in habits and habitat preferences. Great caution must be exercised in any attempt to correlate anatomy with natural history, to deduce habitat preference from osteology, to estimate relative time spent wading versus walking by an extinct animal. Sauropods are basically alien animals with an alien morphology insofar as there is no living species anatomically similar in all parts of its anatomy. What can be said of the habits of an animal with the nose of a *Macrauchenia*, the neck of a giraffe, the limbs of an elephant, the feet of a chalicothere, the lungs of a bird, and the tail of a lizard? With so many plausible but conflicting interpretations, it is unlikely there will be general agreement on sauropod habits as long as more than one paleontologist has an opinion on the matter.

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