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Feeding Mechanisms of the Sauropod Dinosaurs *Brachiosaurus, Camarasaurus, Diplodocus,* and *Dicraeosaurus*

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Skull morphologies and dental wear patterns have been examined in four sauropod genera to evaluate their probable feeding mechanisms. Wear facets on teeth are generally confined to their apices in *Brachiosaurus* and *Dicraeosaurus*, and they are sometimes also present on the mesial and distal carinae. Skull morphology and dental wear patterns in *Diplodocus* and *Dicraeosaurus* are consistent with a raking motion of the jaws during feeding. *Diplodocus* became mechanically adapted to feed in this way by evolving anteriorly directed teeth in the premaxilla and mesial parts of the maxilla, and by changing the direction of jaw adduction relative to the long axis of the skull. Similar features are present in the few known skulls of *Apatosaurus*, and they may also have been present in *Dicraeosaurus*. In *Brachiosaurus*, dental wear patterns also imply a raking motion of the jaws, although the more robust skull and teeth and the more vertically directed action of the jaw adductor muscles have led some to suggest the possibility of isognathous occlusion. *Camarasaurus* employed a powerful bite in its feeding, possibly with slight propaliny of the lower jaw, and its skull was modified to cope with increased stresses arising from mastication. Archaic sauropods appear largely to have employed isognathic occlusion in chopping off vegetation. The raking motion employed by diplodocids and dicraeosaurids was an advanced mode of cropping and stripping, linked evolutionarily to their highly apomorphic cranial morphology.

Keywords: Sauropod dinosaurs; *Brachiosaurus; Camarasaurus; Diplodocus; Dicraeosaurus;* Skull morphology; Jaws; Teeth; Feeding mechanisms

INTRODUCTION

The sauropod dinosaurs were very successful, evolving as a clade that includes numerous species. Their success raises challenging questions in regard to their paleoecology, notably on account of the enormous size attained by some taxa. More than ninety genera have been recognized (McIntosh, 1990a), but reasonably complete skulls are known from only a few species. These skulls are often peculiar in appearance. They seem small in relation to body size. In some advanced groups the teeth are long, slender, and pencil-like, and they are entirely mesial. No contemporary animal has a head like this, so it is difficult to infer sauropod feeding mechanisms.

Marsh (1896, 1898) recognized six and Huene (1927) five families of sauropods, but Janensch (1929a) recognized only two families, distinguished by their teeth. These later became known as the Brachiosauridae, with offset muzzles and strong, spoon or chisel shaped teeth, and the Titanosauridae, with slender muzzles and peg-like teeth. The former included cetiosaurs, brachiosaurs and camarasaurs, and the latter consisted of diplodocids, dicraeosaurs and titanosaurids. This grouping was accepted for

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decades until McIntosh (1990a, 1990b) realized that a dichotomy based mainly on tooth morphology did not properly represent sauropod phylogeny. His view has subsequently been affirmed by Yu (1990), Upchurch (1993, 1995), Wilson and Sereno (1994), Christiansen (1995) and most recently by Salgado and Calvo (1997) and Salgado *et al.* (1997).

For most of this century, sauropods have been regarded as aquatic or even near-shore marine animals. This view, together with the erroneous supposition that most sauropod teeth show little if any wear, has influenced hypotheses proposed to explain their feeding mechanisms. Janensch (1935/36) suggested that the strong jaws and teeth of *Brachiosaurus* were suited for ingestion of relatively tough plant material. He argued that the slender jaws and teeth of *Dicraeosaurus* would have made a good sieve for straining fishes or crustaceans, as they could not have been used to eat large water plants, lacking the means to cut them up into small, digestible pieces. Holland (1906) had inferred that *Diplodocus* used its comb-like dental arcade to rake seaweed off shore-line rocks, but Haas (1963) argued that these aquatic plants were too low in energy and insufficiently abundant to sustain such large animals. So, he supposed that *Diplodocus* used its teeth to strain freshwater invertebrates. Holland (1924) suggested that the wear on the teeth of *Diplodocus* was consistent with their use in harvesting and eating clams. Huene (1929) went so far as to imagine that the long tail of titanosaurids was used in a whip-like manner to strike at the fishes for which these sauropods hunted.

Subsequently, Bakker (1971) and Coombs (1975), following Riggs (1903, 1904), have shown that the postcranial morphology of sauropods is inconsistent with aquatic habits. Kermack (1951) had already pointed out the impossibility of sauropods living submerged at neck length, as some had supposed. The primarily terrestrial habits of sauropods have since been confirmed by other studies of their anatomy and taphonomy (Bakker, 1980, 1986; Dodson *et al.*, 1980; Russell *et al.*, 1980; Christiansen, 1997), as well as abundant trackway records (Lockley, 1987; Pittman and Gillette, 1989; Barnes and Lockley, 1994; Meyer and Hauser, 1994; Thulborn *et al.*, 1994; but see also Ishigaki, 1989, for the possibility that they occasionally swam). The only food abundant enough to support such massive, relatively slow moving animals, is vegetation. A vegetarian diet is consistent with the skull morphologies, tooth forms, and capacious abdominal regions of these animals, as well as the widespread occurrence of gastroliths (Christiansen, 1996).

Unlike mammals, with well differentiated incisors, canines, and molars, sauropods are largely isodont. Differences between premaxillary and maxillary teeth are apparent in several taxa, but these are modest even compared with the differentiation of teeth in many ornithischian dinosaurs. The jaw musculature of sauropodomorph dinosaurs was basically reptilian (Haas, 1963; Galton, 1985a, 1985b, 1985c, 1990), the posterior, external and internal adductors being most important. The main adductors were probably the external mandibular muscles, originating laterally on the jugale and postorbital and inserting on the laterodorsal surface of the surrangular, and the anterior pterygoideus, originating on the medial side of the maxilla and on the pterygoid, and inserting on the medial side of the surrangular-angular symphysis.

Sauropod cranial musculature was only moderately developed (Haas, 1963; Galton, 1986; Barrett and Upchurch, 1994), and there is little evidence of rotary action of the lower jaw. Living mammals have much more powerfully muscled jaws than reptiles of comparable size. Moreover, their lower jaws, which tend to be more rectangular than in reptiles, are capable of a more powerful bite at any given muscle size. Their teeth are closer to the midline of the resultant muscle force, which provides greater mechanical advantage (Young, 1981; Kemp, 1982; Greaves, 1988). Limited evidence bearing on the cranial myology of sauropods is available, so analyses of the feeding mechanisms of these animals have been based largely on wear patterns of their teeth.

SKULL MORPHOLOGY OF *BRACHIOSAURUS*

The skull of *Brachiosaurus brancai* is well known, based on a complete specimen HMN t1 from quarry S at Tendaguru Hill (Janensch 1929a, 1935/36). This skull is 70 cm long and 22.3 cm wide at the premaxillary/maxillary suture. Although a cast of this skull was mounted on skeleton HMN SII, the fragmentary skull HMN S116 belonging to this specimen appears to have been considerably larger (Christiansen, 1999). The skull of *Brachiosaurus* is quite heavily built, with a long muzzle (Figure 1A). The external nares are extremely large, separated by a long, thin internarial bar that is made up of the premaxilla rostrally and the nasal caudally. The orbital and lateral temporal fenestrae are very large and triangular in outline, reminiscent of those of *Camarasaurus.* As in that genus, the openings of the supratemporal fenestrae are mainly posterodorsal.

The quadrate is posteriorly inclined and quite heavily built, with a pronounced medial pterygoid process and a relatively planar articulation facet, also slightly posteriorly inclined, for the articular. Steptostylic movement of the quadrate appears unlikely due to the form of the pterygoid process and an apparently tight fit in the basicranium. The long muzzle is more clearly offset from the posterior part of the skull than in any other sauropod, consisting largely of long and very wide maxillae. Viewed dorsally, the skull is very wide and there is a distinct infranarial gutter, formed by the maxillae and premaxillae. The occipital condyle is directed posteroventrally and large rugosities are visible on the exoccipitale and supraoccipitale. These may have served for insertion of the ligamentum nuchae or the transversospinalis muscle.

The lower jaw is broadly U-shaped, not V-shaped as suggested by Calvo (1994), and it is quite massively constructed. The mandibular symphysis is anteriorly inclined, although not as much so as in *Diplodocus.* The surrangular slopes strongly posteriorly and the jaw articulation is situated well below the base of the tooth row in the dentary, creating a more even bite (Galton, 1986). Each ramus of the lower jaw broadens posteriorly, establishing a wide lower jaw joint. The articular is asymmetrically convex and rugose, indicating the former presence of a cartilaginous cover. The coronoid process consists largely of the surrangular and is moderately well developed. Although not as high as that of *Camarasaurus,* this is one of the larger coronoid processes among the sauropods, indicating the presence of well developed jaw adductors.

The jaws of *Brachiosaurus* are massive, up to 3.5 – 4 cm thick labiolingually in the mesial part of the jaw. Labially, a wall of bone, approximately 4 mm high, braces the premaxillary, maxillary and dentary teeth in the jaws (Christiansen, 1995). This structure, observed in other sauropods by Upchurch (1993), apparently strengthens the teeth proximally in response to bending stresses generated by caudal or lateral head motions during cropping. In *Brachiosaurus,* a similar wall of bone is also present lingually, in both the upper and lower jaws (Christiansen, 1995). Apparently, this bracing structure, which has only recently been recognized, occurs in all sauropods (Barrett and Upchurch, 1994).

The teeth extend far distally in the jaws. The premaxillary and maxillary tooth row of HMN t1 is 29.5 cm long and the dentary tooth row is 24 cm long. There are 4 premaxillary teeth, 11–13 maxillary teeth and 13–15 dentary teeth, all with long, robust roots. Premaxillary and maxillary teeth are longer than corresponding dentary teeth. Fully erupted *Brachiosaurus* teeth are stout and subconical or slightly ellipsoidal in cross-section along most of the proximal half (Figure 1B). Distally, they become broader and thinner, taking on a chisel-like appearance.

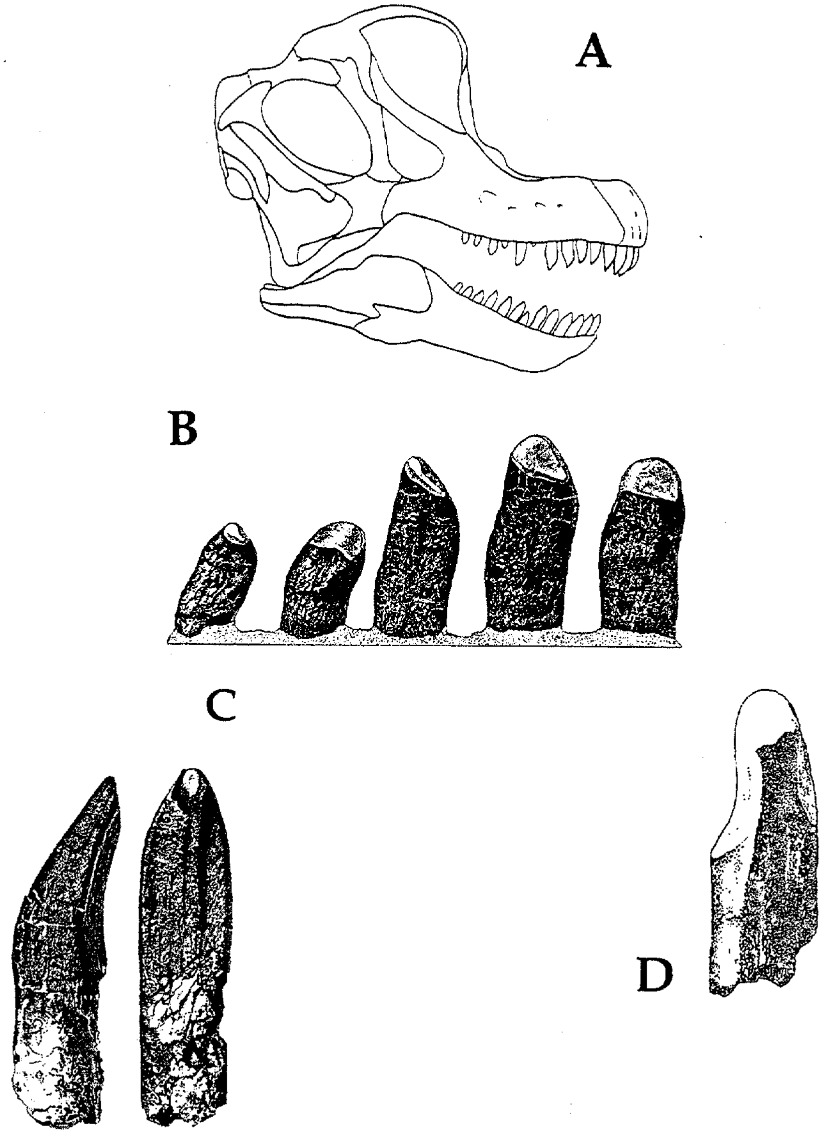

FIGURE 1 Skull and dental morphology of *Brachiosaurus*. **A**: New restoration of the skull of *Brachiosaurus brancai* based on specimen HMN t1, with a somewhat more massive mandible and coronoid process than in previous reconstructions. **B**: The last five maxillary teeth of specimen HMN WJ470 in lingual view. Length of entire jaw fragment, 110 mm. **C**: Medial maxillary tooth HMN S66–10 in mesial and lingual views, showing the characteristic, sharply inclined apical wear facet. Length of tooth, 76.5 mm. **D**: Severely worn dentary tooth HMN St, with large mesial and distal wear facets, merging with the apical wear facet. Length of tooth, 43 mm. **A** by the author, **B-D** affer Janensch (1935/36)

The upper parts of the teeth are planar lingually and convex labially, producing a "scooping" surface. Proximally, the dark enamel is finely grained but distally its surface becomes smoother. Denticles are present on the carinae of some (specimens HMN St) but not most of the known teeth. They are not nearly as pronounced nor as common here as they are in archaic sauropods such as *Vulcanodon* (McIntosh, 1990a), *Barapasaurus* (Jain *et al.*, 1975, 1979) and

Mamenchisaurus (Russell and Zheng, 1993). Toward their apices, the teeth become more pointed, terminating in blunt tips (Figure 1C). Distally, 20–40 % of overall tooth length is usually inclined lingually. In labial view the teeth are slightly convex, sometimes with a distinct ridge extending from the apex almost to the root.

Wear facets range from being indistinct in newly erupted teeth (HMN S116–3, S66–3, and S66–9) to severe in those subjected to long use (HMN WJ 4170 and Figure 1B). Wear facets on teeth of the upper jaw are always lingually situated, whereas dentary teeth display both lingual (usually larger) and labial wear facets. Wear on the distal part of each individual tooth is generally greater than in the mesial area (Figure 1B). Tooth wear is not generally correlated with size. Teeth in the upper jaw fragment HMN WJ 470 (Figure 1B), ranging from 28 to 43.5 mm in height, exhibit more wear than some teeth up to twice this size. Usually, the wear facets are confined to the apices of the teeth and are drop-shaped. In large teeth, the wear facets may be around 10–12 mm in diameter, corresponding to 12–15 % of overall tooth length. At the apex, the dark enamel is usually worn completely away, broadly exposing the pale brown dentine. Wear facet angles are steep, ranging from more than 60° to the long axis of the tooth to almost parallel to it. Comparing a large sample of premaxillary and maxillary teeth to dentary teeth, it is evident that the teeth of the upper jaw exhibit considerably greater wear than those of the dentary. On many wear facets, fine longitudinal scratches are evident, parallel to the long axis of the tooth. Pits and groves, commonly seen on wear facets of *Camarasaurus* teeth (see below), are generally absent.

Strange wear facets occasionally occur. One tooth from a lower jaw, not particularly worn, displays small lingual and labial facets that are confined to the apex. In addition, a distinct wear facet extends about 12 mm down the distal carina of the tooth. It is quite narrow and does not resemble the mesial and distal wear facets observed in *Camarasaurus*. Moreover, there does not appear to have been room for a tooth in the upper jaw to protrude far enough down along the carina to produce such a facet by dental occlusion. A similar pattern is observed in some more heavily worn, isolated teeth, found without associated skull remains (Figure 1D), although here heavy apical wear tends to merge with facets on the mesial and distal carinae. These wear patterns are reminiscent of facets seen on some *Camarasaurus* teeth, but there is no evidence of complementary wear facets on antagonist teeth of the upper jaw. Contrary to the suggestion of Barrett and Upchurch (1995), apical wear facets are typically developed on *Brachiosaurus* teeth and this latter type of wear is more uncommon.

INFERRED FEEDING MECHANISM OF *BRACHIOSAURUS*

Calvo (1994) and Barrett and Upchurch (1995) suggested that *Brachiosaurus* employed isognathic occlusion in its feeding, producing steeply inclined tooth wear facets as a result of biting tough vegetation. The observations reported here suggest rather that these animals used a raking motion to strip foliage, not unlike that inferred for *Diplodocus*. However, it is unlikely that their feeding mechanisms were identical, as the jaw of *Brachiosaurus* is rather different from those of diplodocids and dicraeosaurids.

Wear facets are usually symmetrical about the long axes of *Brachiosaurus* teeth, despite the fact that the upper and lower teeth appear not to have been symmetrically apposed in most cases. However, the possibility that this is due to distortion of the skull cannot be ruled out. Wear facets of the upper and lower jaws are at different angles to the tooth axis. Teeth of the upper jaw have wear facets extending down the lingual edges of the teeth when they are heavily worn, whereas dentary teeth have smaller wear facets that are usually confined to the apex, indicating that this pattern of wear was not produced by tooth to tooth abrasion. Smaller teeth from the posterior part of the jaw also display heavy wear facets (see Figure 1B), although they appear too small to have been brought into occlusion with the antagonist teeth. If the lingual facets on teeth in the upper jaw were produced by abrasion against teeth in the lower jaw, the labial sides of the dentary teeth must have been in contact with the lingual sides of teeth in the upper jaw. This does appear to have been the case in the only complete skull HMN t1, but well developed labial wear facets would have formed on the dentary teeth at angles comparable to those on teeth in the upper jaw, if they had been produced by mutual abrasion. No such wear facets were observed on any tooth attributable to the lower jaw of *Brachiosaurus,* in the course of this study. It is also hard to reconcile wear facets extending down the mesial and distal carinae on some teeth with tooth to tooth abrasion.

Wear patterns on the teeth of *Brachiosaurus* do not appear to indicate direct tooth to tooth contact, but a shearing action, suggested by Calvo (1994) and Barrett and Upchurch (1995), cannot be ruled out. The patterns of wear remain difficult to interpret. If *Brachiosaurus* employed a raking motion, stripping foliage with ventro-laterally directed movements of the head, labial wear facets would still be expected on the upper teeth, but these are not present. Horizontal, laterally oriented motion of the head is an alternative, but this is contradicted by the direction of fine scratches in the wear facets. The mode of cropping in *Brachiosaurus* must have been rather different from that of *Diplodocus* but the exact mechanism remains unclear.

SKULL MORPHOLOGY OF *CAMARASAURUS*

The skull of *Camarasaurus* is known completely from several very well preserved specimens, including a juvenile *C. lentus* (CM 11338, Gilmore, 1925) and larger, adult specimens from Dinosaur National Monument, in Utah. *Camarasaurus* has the largest and most powerfully developed skull, jaws and teeth of any known sauropod. The skull (Figure 2A) bears some resemblance to that of *Brachiosaurus.* The nares are quite large, the orbit and lateral temporal fenestra are very large, and the supratemporal fenestra is mainly dorsal in its exposure. Several features of the skull indicate that it was subjected to greater stress in food processing. The muzzle is very short and the more vertical orientation of the occiput, aligning the supratemporal fenestra more nearly above the coronoid process, indicates a more vertical action of the mandibular adductor muscles than in *Diplodocus, Dicraeosaurus* and *Brachiosaurus.* The internarial bar is massive, the maxilla is high, the premaxilla is robust, and the whole cranium is considerably more robust in build than that of *Diplodocus,* or even *Brachiosaurus.*

The robust quadrate is only slightly posteriorly inclined and it widens distally. The form of its articular facet bears some resemblance to that of *Brachiosaurus,* although it is usually more concave, with a fairly pronounced pterygoid flange. In the supratemporal fenestra, the parietals flare outward and upward, providing ample space for the posterior, external mandibular adductor muscles, which were presumably well developed. This is consistent with the fact that the surangular coronoid process is the largest seen in any sauropod skull, comparable in relative size to those of archaic cynodont therapsids such as *Thrinaxodon* and *Cynognathus.* As in *Brachiosaurus,* the jaw joint is situated below the level of the tooth row in the dentary, and the articular is convex, but slightly more triangular. The lower jaw is heavy and quite massive. One of *Camarasaurus supremus* measured 53.5 cm in length; it was 3.5 cm thick at the mandibular symphysis, narrowing to only 2.4 cm thick, 25 cm further back. The symphysis is anteriorly inclined, with a ventral projection that makes it the deepest part of the dentary. There is a well developed retroarticular process.

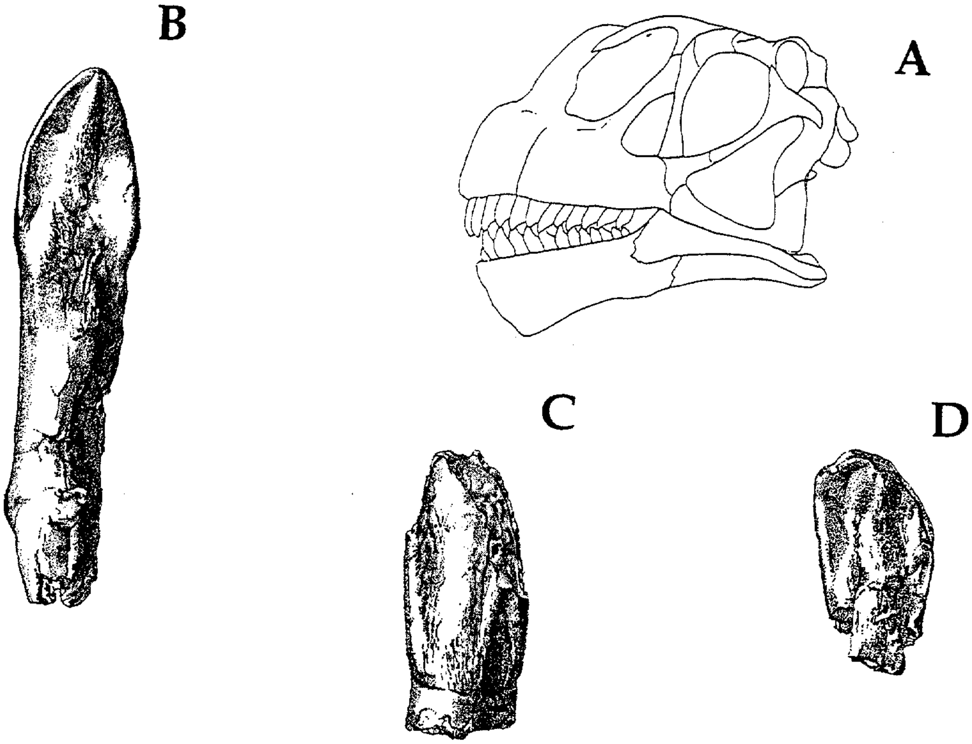

FIGURE 2 Skull and dental morphology of *Camarasaurus*. **A**: Reconstruction of the skull of *Camarasaurus lentus*. **B**: Presumed premaxillary tooth of *Camarasaurus supremus* in lingual view, showing little wear. Length of tooth and root, 139 mm. **C**: Presumed distal maxillary tooth of *C. supremus* in lingual view, showing heavy apical wear facets on the mesial and distal carinae. Length of tooth, 67 mm. **D**: Presumed mesial dentary tooth of *C. supremus* with less pronounced apical wear facets. Length of tooth 47 mm. **A** after Gilmore (1925), **B-D** after Osborn and Mook (1921)

There are 4 premaxillary, 8–10 maxillary, and 13 dentary teeth. The teeth are robust, ellipsoidal in cross-section around midlength, and narrow to a rounded point at the apex (Figure 2B). They have a distinctive, spoon-like shape in labial or lingual view. All teeth are anteriorly inclined, so the apex of each tooth overlaps the base of that in front of it, forming an interlocking, shearing tooth row (Carey and Madsen, 1972; Calvo, 1994; Barrett and Upchurch, 1995). Pronounced wear facets often occur on the mesial and distal carinae, on the triangular apices of the teeth (Figure 2C, D). Calvo (1994) suggested that these were formed by precise contact in shearing between the upper and lower teeth. He also suggested that some propaliny of the lower jaw provided a means of crushing vegetation, so *Camarasaurus* was capable of significant oral food processing. This is plausible, but it could not have amounted to real chewing like that of cynodont therapsids and mammals, given teeth that lacked broad, horizontal cuspate grinding surfaces.

INFERRED FEEDING MECHANISM OF *CAMARASAURUS*

Skull morphology and tooth wear indicate that the jaws of *Camarasaurus* were involved in more biting action than those of other sauropods. Cropping by members of this genus appears to

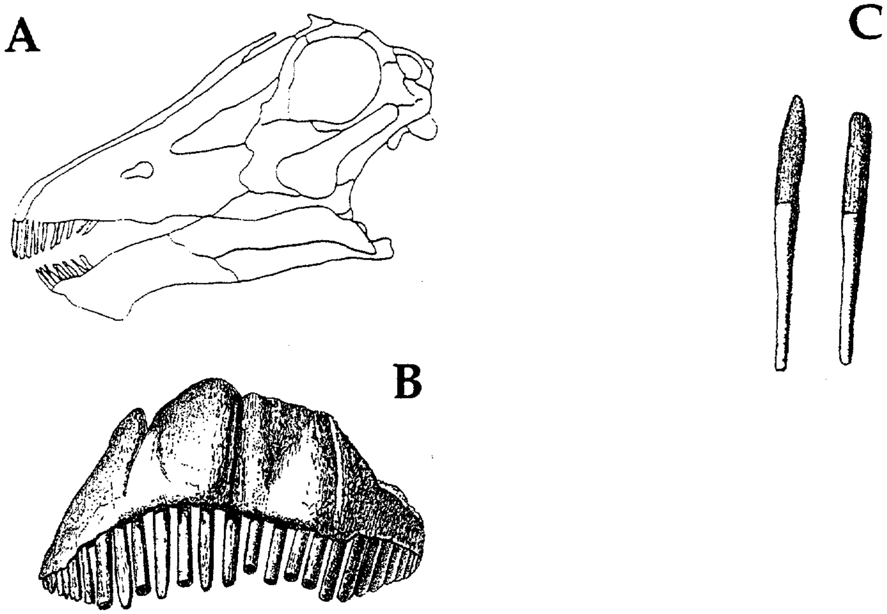

FIGURE 3 Skull and dental morphology of *Diplodocus*. **A**: Reconstruction of the skull of *Diplodocus longus*, specimen CM 11161. **B**: Anterior view of the premaxillae and maxillae of CM 11161, showing both rather planar and inclined wear facets on the teeth. **C**: Mesial maxillary teeth of *D. longus* showing little wear. **A, B** after Holland (1924), **C** after Marsh (1884)

have involved biting off foliage, with little if any of the raking or combing employed by *Brachiosaurus* and *Diplodocus*. The skull of *Camarasaurus* acquired derived characters designed to cope with the compressive stresses generated by mastication. Wear facets on teeth situated far distally in the jaw clearly indicate that *Camarasaurus*, unlike grazing mammals, employed the entire tooth row in cropping, as did *Brachiosaurus*. Microwear on the teeth of *Camarasaurus* is dominated by rough scratches and pits, indicating that these animals fed on tougher and more resilient food than *Diplodocus* and *Brachiosaurus*, in which finer tooth wear is observed (Fiorillo, 1998). This documents one dimension of niche differentiation among these sauropod genera, which are sympatric, at least in North America.

SKULL MORPHOLOGY OF *DIPLODOCUS*

Diplodocus is the only diplodocid for which complete skulls and mandibles are known. The partial skull of *Apatosaurus*, lacking a lower jaw, is very similar to those of *Diplodocus*, albeit somewhat larger and broader (Holland, 1915, 1924; Berman and McIntosh, 1978; Chatterjee and Zheng, 1997). Another skull and neck of *Apatosaurus* have recently been discovered in Wyoming (Connely, 1997; Connely and Hawley, 1998) but this has yet to be described. The skull of *Diplodocus* is highly modified from the plesiomorphic condition of archaic sauropods (Figure 3A).

The quadrate is markedly posteriorly inclined, displacing the jaw articulation rostrally compared with other sauropods. The jaw joint, unlike those of *Camarasaurus* and *Brachiosaurus*, is situated slightly above the level of the tooth row in the dentary. The orbits are large, as are the elongated lateral temporal fenestra, whereas the supratemporal fenestra are much smaller and more laterally exposed than in *Camarasaurus* or *Brachiosaurus*. The nares are situated dorsally and there is no internarial bar. The occipital condyle faces ventrally, in contrast to its posteroventral orientation in most other sauropods, especially archaic forms. Salgado and Calvo (1997) see most of these characters as a complex related to a posteroventral re-orientation of the long axis of the skull in the horizontal plane. The muzzle is elongated, although not sharply demarcated as in *Camarasaurus* and *Brachiosaurus*. Overall, the skull is considerably more delicate than those of these sauropods, and the muscle scars are indistinct.

The lower jaw is long and thin in construction; mesially it is wide. Viewed from above, it is almost rectangular, with subparallel rami. A beautifully preserved skull of *Diplodocus longus* (Figure 3A) is 52.2 cm long from the tip of its premaxillae to the occipital condyle (cf. Holland, 1924; Berman and McIntosh, 1978). The lower jaw of this specimen is 44.9 cm long, with slender rami that decrease substantially in labiolingual thickness, distally. The articular does not form a distinct glenoid, but rather a shallow, somewhat elongated, fossa. The coronoid process of the surrangular is modest, indicating that the mandibular adductor muscles were not well developed.

The mandibular symphysis is markedly inclined (Figure 3A) with a process that projects posteroventrally. The mesial part of the lower jaw turns a little ventrally, relative to the long axis of the rami. The mandibular symphysis is completely fused, unlike those of *Brachiosaurus* and *Camarasaurus*. Curiously, there is a fairly well developed retroarticular process, consisting dorsally of the surrangular and the articular and ventrally of the angular. This appears to have provided relatively more leverage for the mandibular depressor muscle than existed in *Brachiosaurus*.

There are 4 teeth in the premaxilla, usually 9–10 and sometimes 11 in the maxilla, and 10 in the dentary. The teeth are never denticulate. They are straight, slender and peg-like, usually of subequal diameter proximally and distally (Figure 3B, C). Distally, the teeth become slightly flattened, but there is no lingual curvature, as in *Brachiosaurus*. Teeth are confined to the front of the jaws, so in lateral view there does not appear to be a very large cropping surface. However, as noted above, the skull and lower jaw are almost rectangular, so the muzzle is very wide compared to skull length. The teeth of both the upper and lower jaws slope distinctly forward, resulting in a protrusion beyond the premaxilla of about 20 mm. The bases of the teeth are supported by labial and lingual rims of bone, like those described above for *Brachiosaurus*. The labial rim is always the more massive of the two.

Haas (1963) and Dodson (1990), among others, have suggested that diplodocid teeth generally show little wear. To the contrary, fully erupted teeth in three *Diplodocus* skulls I have observed are more or less severely worn (Figure 3B), as also noted by Upchurch (1993), Barrett and Upchurch (1994, 1995), Calvo (1994), Salgado and Calvo (1997), and even long ago by Holland (1924).

Wear facets on the teeth of *Diplodocus* are not nearly as steeply inclined, relative to the long axis of the tooth, as those of *Brachiosaurus*. Calvo (1994) and Salgado and Calvo (1997) reported wear facets with an inclination of less than 40°. I have observed facets at angles approaching 50° on some teeth, but most have a lower inclination. Calvo (1994) suggested that wear facets on corresponding upper and lower teeth match, indicating direct tooth to tooth abrasion. Barrett and Upchurch (1994) disagree, arguing that facets on teeth of the upper and lower jaws are labially situated, indicating that they were produced by extensive tooth to food contact. Skull CM 11161 (Figure 3A) has several severely worn teeth with facets cut almost perpendicular to their long axes. Other teeth in the upper and lower jaws have both labial and lingual wear facets, the labial ones usually being considerably more pronounced.

Overall, wear facets do not appear to support precise tooth to tooth contact in *Diplodocus*. They are heterogeneous in form, and facets on corresponding upper and lower teeth are often quite different from one another, cut at angles that match rather poorly. The predominant pattern of microwear on these abraded surfaces consists of fine scratches (Fiorillo 1998). This suggests that sauropods with peg-like teeth usually fed on soft vegetation, such as low growing ferns or young shoots high in the trees.

INFERRED FEEDING MECHANISM OF *DIPLODOCUS*

The direction of force developed by contraction of the external mandibular adductor muscles seems not to have been perpendicular to the long axis of the skull in *Diplodocus*, unlike that of most tetrapods. It was somewhat posteriorly inclined, due to the ventral twisting of the occipital region noted above, whereas the anterior pterygoideus muscles acted with a marked anterior inclination, as shown by Barrett and Upchurch (1994). This dual jaw adductor action, together with the shallow, elongate articular facet, would have permitted propaliny of the lower jaw, but not cranial kineticism (Calvo 1994). Barrett and Upchurch (1994) suggested that this would have allowed the jaw to gape more widely during abduction. In opening the lower jaw, the mandibular depressor muscles would tend to pull it posteriorly, and this effect was reversed in adduction. The wider gape would have allowed a larger bite size, more even stripping, and hence a faster rate of ingestion (Barrett and Upchurch, 1994). Propaliny of the lower jaw has also been inferred in *Apatosaurus* (Connely and Hawley, 1998).

Barrett and Upchurch (1994) have argued that labial wear facets on the upper and lower teeth of *Diplodocus* were formed independently by tooth to food abrasion. Facets on the premaxillary and maxillary teeth were formed during high browsing, as branchlets were pulled off inside the oral cavity by ventro-lateral motion of the head. Dentary teeth acquired labial wear in low browsing, as the animal pulled its head upward and to one side. Thus, the comb-like dental arcade was employed in a raking motion, to strip foliage off larger branches, and not in a biting or shearing action, which would involve more precise tooth to tooth contact.

This interpretation is plausible, given wear facets in the upper and lower jaws that do not match and the pronounced labial wear on all teeth. Stripping would have set up substantial stresses in the thin peg-like teeth, tending to distort them about their long axes. Under these circumstances, anteriorly protruding teeth are appropriate, as their long axes are more closely aligned with the forces generated by tearing and stripping, reducing bending moments. However, the common occurrence of horizontal wear facets on upper and lower teeth suggests either stripping in low browsing where the long axis of the head would have been almost vertical, or some degree of tooth to tooth contact, but surely less than suggested by Calvo (1994). Under no circumstances could *Diplodocus* have processed plant matter orally.

SKULL MORPHOLOGY OF *DICRAEOSAURUS*

Dicraeosaurus is one of the fascinating sauropods that emerged from the German Tendaguru expedition of 1909–1913. A mount was prepared, based on the fine partial skeleton HMN m of *D. hansemanni*. Unfortunately, the skull is only partially known. Two basicrania and isolated bones, including some from the muzzle region, have been found. The orbital part of the skull remains largely unknown. A skull was reconstructed from the available parts (Figure 4A), with unknown parts modeled on those of *Diplodocus* (Janensch, 1935/36).

It is not known for certain if the internarial bar was absent, as in the reconstruction, but the length of the ascending premaxillary process indicates that the nares faced dorsally. As in *Diplodocus* the supratemporal fenestra is small

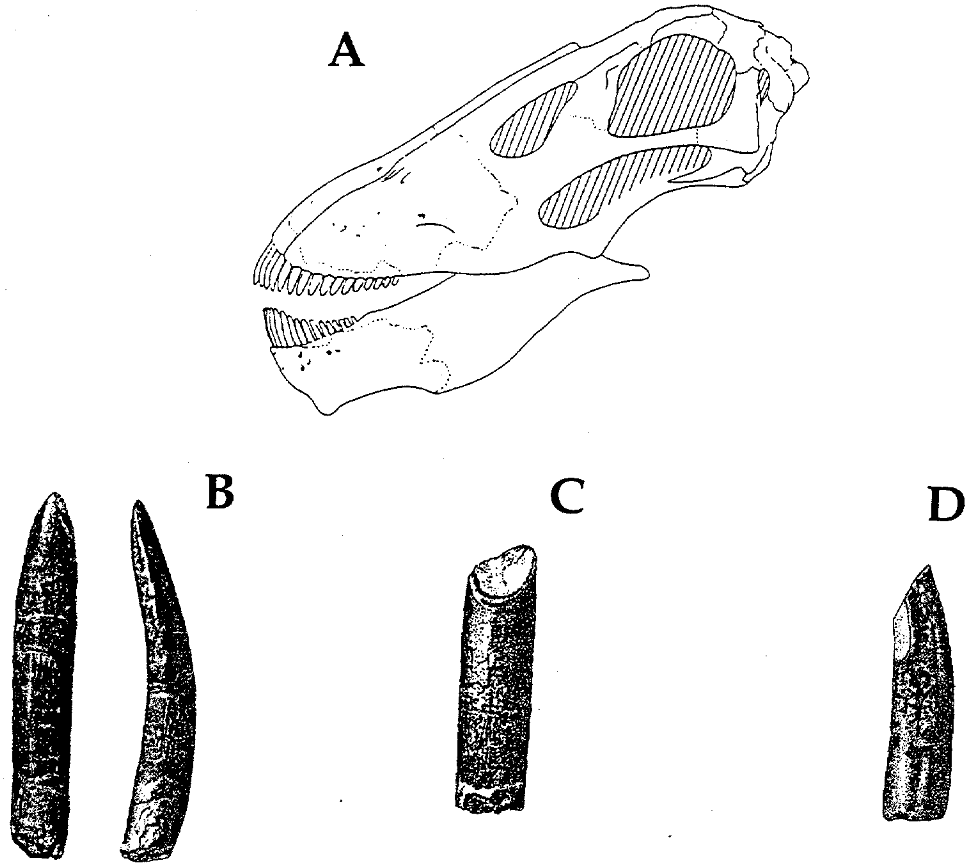

FIGURE 4 Skull and dental morphology of *Dicraeosaurus*. **A**: Outline of the restored skull of *Dicraeosaurus hansemanni*. **B**: Maxillary tooth HMN EH in labial and distal views, with only a small, indistinct apical wear facet. Length of tooth and root fragment, 63 mm, of which approximately 50 mm appears to have protruded from the jaw. **C**: Tooth HMN St in labial view, with a heavy, inclined terminal wear facet. Length of tooth, 37 mm. **D**: Tooth HMN St in mesial view showing a mesial wear facet that has merged with the terminal wear facet. Length of tooth, 34 mm. All after Janensch (1935/36). According to Janensch, **C** and **D** were most probably from *Dicraeosaurus*, although he did not consider it certain. Having examined all the material, this author is convinced that these are teeth of *Dicraeosaurus*

and faces laterally. The skull is restored with a more strongly inclined occipital region than *Diplodocus*. Not known directly, this is nonetheless plausible, given the very long basipterygoid processes, which are relatively much longer than those of *Diplodocus*.

The lower jaw is known only from the dentaries. The mesial part is rectangular, but more U-shaped than in *Diplodocus*, with subparallel rami. The jaw has been restored with a moderate coronoid process and a fairly large retroarticular process, based on that of *Diplodocus*, in the absence of any real knowledge of these structures. As in *Diplodocus*, there is an anterior, ventrally projecting dentary process and the mandibular symphysis is anteriorly inclined. The restored skull is 59 cm long but the lower jaw spans only 43.5 cm, due in part to the great inclination of the occiput, which displaces the jaw joint rostrally. The jaw is relatively shorter than that of any other known sauropod. As in *Diplodocus*, teeth are confined to the mesial edges of the jaws. The teeth are restored with their long axes set almost vertically in the dentary, but markedly inclined in relation to the long axis of the skull, as in *Diplodocus.* This is plausible, given the probable inclination of the skull, and hence of the premaxillary and maxillary bones, but this is not known for certain.

Replacement teeth have been found in *Dicraeosaurus* jaw material (Janensch, 1935/36), but teeth subjected to wear have been found only in isolation (Figure 4B, C, D). The teeth are elongate, slender, and lingually curved. Proximally, they are cylindrical in cross section, but distally they are broader and flatter. As in *Diplodocus* there are 4 premaxillary teeth, but here there are 12 maxillary and no less than 16 dentary teeth. Some large teeth are barely worn, whereas others are extremely worn. Heavily worn teeth have terminal wear facets at a fairly low angle to their long axes, approximately 40°, as in *Diplodocus.* Janensch (1935/36) suggested that lingual facets occurred on teeth of the upper jaw and labial facets on those of the lower jaw, indicating dental occlusion. In fact, isolated teeth were identified as coming from the upper or lower jaw by the form of the terminal wear facet, so this rested on circular reasoning. It is just as likely that wear facets on corresponding upper and lower jaw teeth did not match, as in *Diplodocus,* given the similarities in jaw and dental morphology between these two genera.

INFERRED FEEDING MECHANISM OF *DICRAEOSAURUS*

The skull of *Dicraeosaurus* is not well enough known to constrain its jaw mechanisms with any degree of certainty. The angles at which upper and lower jaw teeth would have met are not known, so the possibility that some of the wear facets were caused by tooth to tooth abrasion cannot be evaluated. If the basicranium was less inclined than in the existing reconstruction of the skull, the teeth in the upper jaw would probably not have protruded much beyond the edges of the premaxillae. However, the forms of the teeth and known skull parts resemble those of diplodocids. Several heavily worn teeth in the collections of the Museum für Naturkunde in Berlin display wear facets extending far down their mesial and distal carinae, as seen in *Brachiosaurus.* These teeth are so heavily worn that is uncertain whether they belonged to *Dicraeosaurus* or not, but the difference between them and undisputed *Dicraeosaurus* teeth seems minimal. Such substantial wear suggests extensive contact with material sliding between the teeth, which implies a mode of cropping not unlike that inferred for *Diplodocus.*

DISCUSSION

The inferred relative sizes of the jaw adductor muscles, the robustness of the skull and teeth, and the angles between the tooth axes and the long axis of the skull are mutually well correlated in these sauropods. *Diplodocus* and *Dicraeosaurus* appear to have had relatively weak jaw musculatures. Given thin, peg-like teeth and relatively limited tooth to tooth contact in feeding, the bite would not have been very strong. The inclination of the teeth also precludes strong jaw adduction, which would have set up considerable bending stresses in the teeth themselves. These animals probably did not close the mouth completely during feeding, as this would bend the branches between the upper and lower tooth rows, interfering with efficient stripping of foliage.

In *Brachiosaurus,* the teeth and jaw adductor muscles were stronger, implying that this species employed some degree of dental occlusion in addition to a raking motion in its feeding. In *Camarasaurus,* the teeth, jaws, and jaw adductors appear to have been much more powerfully developed. These animals were capable of powerful biting and crushing, involving regular, direct dental occlusion as indicated by the development of wear facets on their teeth.

The only known lower jaw of *Mamenchisaurus* resembles that of *Brachiosaurus,* and the same is true of its teeth (Russell and Zheng, 1993). The teeth are only slightly worn, so there is little evidence on which to infer its feeding mechanism. A mode of cropping not unlike that of *Brachiosaurus* is plausible. *Euhelopus zdanskyi* has a skull and teeth resembling those of *Brachiosaurus* and *Camarasaurus.* Wear facets on its teeth are quite similar to those of *Camarasaurus* (Wiman, 1929), supporting Calvo's (1994) suggestion that their modes of cropping were similar.

Titanosaurid sauropods apparently did not employ a mode of cropping like that of diplodocids, despite superficial resemblances in their cranial and dental morphologies. The morphologies of basal titanosaurids, such as *Malawisaurus* (Jacobs *et al.,* 1993), and recent phylogenetic analyses (Salgado *et al.,* 1997) suggest that narial retraction and the development of non-denticulate, peg-like teeth confined to the mesial part of the jaws reflect convergence of titanosurids with diplodicids and dicraeosaurids. The wear facets on titanosaurid teeth suggest that these animals employed isognathic dental occlusion in cropping (Calvo, 1994; Salgado and Calvo, 1997).

Nemegtosaurus is traditionally considered to be the sister taxon of either diplodocids or dicraeosaurids (McIntosh, 1990a; Christiansen, 1995; Upchurch, 1995), but it emerged from a recent analysis as a titanosaurid (Salgado *et al.,* 1997). The wear facets on its peg-like teeth (Nowinski, 1971) suggest a mode of cropping similar to that inferred for other titanosaurids. Salgado and Calvo (1997) argued that the appearance of a diplodocid-like, elongate skull, with a strongly inclined occipital region, was due to distortion, and that the skull was really much taller, more like that of a brachiosaurid. However, the presence of very long basipterygoid processes (Nowinski, 1971) casts some doubt on this interpretation.

Interestingly, archaic sauropod genera, largely represented only by fragmentary skull material, appear to have employed isognathic dental occlusion in feeding, possibly in combination with slight propaliny of the lower jaw. In the Lower Jurassic genus *Barapasaurus,* which is probably the sister taxon of all other sauropods except for the most primitive taxon, *Vulcanodon* (Upchurch, 1993, 1994, 1995; Christiansen, 1995), the teeth are heavy and spoon-shaped, with coarse denticles on the mesial and distal carinae (Jain *et al.,* 1975). The forms of the wear facets have yet to be described for this genus.

In the Middle Jurassic, cetiosaur-like dinosaurs *Amygdalodon* and *Patagosaurus* from South America, the teeth are large and spoon-shaped, with wear patterns reminiscent of those of *Camarasaurus* (Cabrera, 1947; Bonaparte, 1979, 1986, 1996). These suggest extensive tooth to tooth contact along the apical part of the carinae. The teeth of *Omeisaurus,* from the Middle Jurassic of China, resemble those of *Brachiosaurus* or *Camarasaurus,* although they are more slender than those of the latter, and have well developed denticles on the mesial and distal carinae (He *et al.,* 1984).

Sauropods evolved from prosauropods, or more likely, the two are sister groups. Prosauropods had more or less spoon-shaped teeth, with coarse denticles on both their mesial and distal carinae, and relatively little wear, implying isognathic occlusion (Galton, 1986, 1990). Archaic sauropods apparently retained this mode of cropping, with teeth not too different from those of prosauropods, whereas diplodocids and dicraeosaurids evolved highly apomorphic skull and tooth forms, adapted to a new mode of cropping. The isognathic occlusion that seems to have been employed by titanosaurids thus seems to represent a reversal in function, based on a different cranial and dental morphology.

Curiously, the yunnanosaurids developed cylindrical teeth like those of diplodocids and titanosaurids, although they were not confined to the mesial part of the maxillae, and they display well developed wear facets (Galton 1986, 1990). Basal sauropods did not share this dental morphology, so the slender teeth of yunnanosaurids evolved convergently with those of advanced sauropods. The feeding mechanism of *Yunnanosaurus* is not well understood, and the suggestion that its mode of cropping was sauropod-like (Galton 1986, 1990) is not very informative, given the heterogeneity of feeding mechanisms within the Sauropoda. The possibility that yunnanosaurids employed a raking motion in cropping cannot be ruled out. The suggestion that peg-like, adenticulate teeth have erroneously been assigned to the Yunnanosauridae is incorrect (Christiansen, 1999).

It is clear that sauropods did little if any oral processing of their food. Their heads were designed to crop vegetation. Even in *Camarasaurus,* oral trituration must have been confined to shearing or crushing that did not involve true chewing. Since sauropod teeth are often severely worn, they were evidently used to crop enormous amounts of fodder during their presumably fairly short spans of use, compared with mammalian teeth. As reptiles shed their teeth throughout life, the individual tooth is usually not operational for nearly as long as mammalian teeth.

The rates of ingestion and feeding energetics of sauropod dinosaurs cannot simply be compared with those of mammals on the basis of head size, as oral mastication of food, requiring a substantial chewing apparatus, plays such a large part in the feeding of the latter (Owen-Smith, 1988; Christiansen, 1999). In sauropods, the mechanical breakdown of food required to maintain the cellular metabolism of such large animals was most probably carried out in muscular ventricula, assisted by gastroliths as in certain birds (Janensch, 1929b; Galton, 1986; Gillette, 1994; Christiansen, 1996). So, sauropod heads are morphologically homologous with the heads of other advanced tetrapods, but they were not functionally analogous to the heads of either mammals or ornithischian dinosaurs. The closest functional analogs of sauropods in feeding are birds, whose edentulous beaks likewise make oral trituration impossible. However, the significance of ecological and physiological comparisons between sauropods and birds, even including the ratites, is limited by the great differences in size between them.

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