Structure and Evolution of a Sauropod Tooth Battery

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D URING THE JURASSIC, SAUROPOD dinosaurs rose to predominance among vertebrate herbivores, in terms of both species diversity and biomass (e.g., Romer 1966; McIntosh 1990). Their perceived decline on northern landmasses during the Cretaceous has been linked to the evolution of tooth batteries in ornithischian herbivores (e.g., Lull and Wright 1942; Ostrom 1961; Bakker 1978; Lucas and Hunt 1989). On southern landmasses, in contrast, sauropod diversity increased during the Cretaceous (Weishampel 1990; Hunt et al. 1994), and a newly discovered southern sauropod, the rebbachisaurid *Nigersaurus taqueti*, is now known to have evolved a complex tooth battery (Sereno et al. 1999).

Rebbachisaurids are a poorly known sauropod clade, reported thus far only from Cretaceous rocks in South America (Calvo and Salgado 1995; Bonaparte 1996; Apestiguía et al. 2001; Lamanna et al. 2001), Africa (Lavocat 1954; Taquet 1976; Sereno et al. 1999), and Europe (Dalla Vecchia 1998; Pereda-Suberbiola et al. 2003). Many of these are fragmentary finds, leaving much of the skeletal anatomy of this group in question, especially the skull. In this

chapter, we describe the tooth-bearing bones and dental battery of *Nigersaurus taqueti* and provide an initial cranial reconstruction. We outline the feeding specializations common to diplodocoids and how these were modified within rebbachisaurids.

Institutional Abbreviation: MNN, Musée National du Niger, Niamey.

SYSTEMATIC PALEONTOLOGY

SAUROPODA MARSH 1878

EUSAUROPODA UPCHURCH 1995

NEOSAUROPODA BONAPARTE 1986

DIPLODOCOIDEA MARSH 1884

REBBACHISAURIDAE BONAPARTE 1997

NIGERSAURUS SERENO ET AL. 1999

TYPE SPECIES: *Nigersaurus taqueti* Sereno et al. 1999.

AGE: Early Cretaceous (Aptian–Albian).

DISCUSSION: *Nigersaurus taqueti* is the most common sauropod and one of the most common species recovered in the rich vertebrate fauna described from Gadoufaoua, Niger Republic
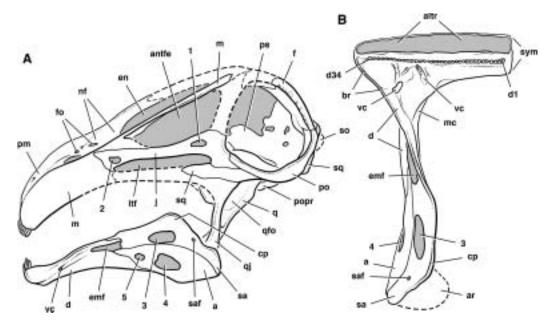
FIGURE 5.1. Preliminary reconstruction of the skull of *Nigersaurus taqueti* based on MNN GDF512. (A) Skull in left lateral view. (B) Left lower jaw in dorsal view with tooth batteries removed. **1–5**, accessory cranial fenestrae; **a**, angular; **altr**, alveolar trough; **antfe**, antorbital fenestra; **ar**, articular, **br**, buccal ridge; **cp**, coronoid process; **d**, dentary; **d1–d34**, replacement foramina for dentary tooth positions 1–34; **emf**, external mandibular fenestra; **en**, external naris; **f**, frontal, **fo**, foramen; **j**, jugal; **ltf**, laterotemporal fenestra; **m**, maxilla; **mc**, Meckel's canal; **nf**, narial fossa; **pm**, premaxilla; **po**, postorbital; **popr**, paraoccipital process; **ps**, parasphenoid; **q**, quadrate; **qfo**, quadrate fossa; **qj**, quadratojugal; **sa**, surangular; **saf**, surangular foramen, **so**, supraoccipital; **sq**, squamosal; **sym**, symphyseal surface; **vc**, vascular canal.

(Taquet 1976; Sereno et al. 1998, 1999, 2001, 2003; Larsson and Gado 2000). Nevertheless, because the skull and skeleton are delicately constructed and highly pneumatic, there are no complete skulls and only a few partially articulated skeletons. *Nigersaurus taqueti* was named and identified as a rebbachisaurid by Sereno et al. (1999). An earlier report from the same beds of a dicraeosaurid allied with titanosaurs (Taquet 1976:53) very likely pertains to the same species.

NIGERSAURUS TAQUETI SERENO ET AL. 1999
(FIGS. 5.1, 5.3–5.8)

HOLOTYPE: MNN GDF512, partial disarticulated skull and partially articulated neck preserved in close association on 1 m² of sandstone outcrop. Sereno et al. (1999:1346) also list a "scapula, forelimbs, and hind limbs" as part of the holotype. These and other bones, which we regard as referable to this species, were found at some distance from the skull and neck and

cannot be reliably associated with the holotypic specimen. The partial skeleton described by Taquet (1976) also was discovered in the vicinity of the holotype and may pertain to the same species.

LOCALITY AND HORIZON: Gadoufaoua (16° 27´N, 9°8´´E), eastern edge of the Ténéré Desert, Niger Republic; Elrhaz Formation.

REFERRED MATERIAL: MNN GDF513, worn crown. Additional skeletal and dental material is described elsewhere.

REVISED DIAGNOSIS: Rebbachisaurid sauropod characterized by five accessory fenestrae in the jugal, surangular, and angular; tooth number increased to 20 and to 34 in the maxilla and dentary, respectively; tooth replacement increased to as many as 10–12 in a single column; premaxilla and dentary lacking alveolar septa; maxilla with oval (vertically elongated) replacement foramina; extension of the dentary tooth row lateral to the sagittal plane of the

lower jaw; subcircular mandibular symphysis; crowns with prominent mesial (medial) and distal (lateral) ridges; scapula with prominent rugosity on the medial aspect of the proximal end of the blade.

DESCRIPTION

SKULL AND DENTITION

The skull and neck of the holotypic specimen of *Nigersaurus taqueti* were found in close association. Most of the dorsal skull roof is preserved (fig. 5.1A). The braincase is intact, with the proximal end of the stapes in place in the fenestra ovalis. The quadrate is the only palatal bone preserved. All of these bones, with the exception of the frontal and braincase, are composed of thin laminae or narrow struts and are extremely delicate. Five unique accessory fenestrae are present, two in the jugal and three in the surangular and angular (figs. 5.1–5.5). These accessory openings are bordered by bone that tapers gradually in width to a paper-thin edge that has a smooth margin. It is highly unlikely, therefore, that they represent lesions or some other kind of bone pathology, like the healed openings reported in aged individuals of other dinosaurian species (e.g., Brochu 2003).

The snout is proportionately much shorter and the dental arcade is less prognathous than in diplodocids or dicraeosaurids (figs. 5.1, 5.2). As mentioned above, the external naris is not retracted above the orbit in *Nigersaurus*. A statement to the contrary—that the external naris is positioned as in diplodocids—was made on the basis of the maxilla before the premaxilla was exposed (Sereno et al. 1999:1344). Although the nasal and thus the posterior margin of the external naris are not known, the anterior portion of the border is far anterior to that in any known diplodocid. The external naris is large, laterally facing, separated in the midline from its opposite by a vertical premaxilla–nasal septum, and surrounded by a more pronounced narial fossa. As in other diplodocoids, the jaw articulation and laterotemporal fenestra are shifted anteriorly under the orbit (figs. 5.1, 5.2). The supratemporal fenestra is very reduced or absent altogether, in contrast to those in other diplodocoids (Holland 1924) or other sauropods.

The transversely expanded form of the alveolar ramus of the dentary is unique among dinosaurs (fig. 5.1B). No other dinosaur has a tooth row that extends lateral to the longitudinal plane of the lower jaw. The maximal width across the anterior end of the paired dentaries slightly exceeds the length of the entire lower jaw. Despite the gaping alveolar trough that housed hundreds of slender teeth packed together as a tooth battery, the dentary and other bones of the lower jaw in *Nigersaurus* are as lightly built as those in *Diplodocus* and much more slender than those in *Camarasaurus* (figs. 5.1, 5.2). The description below is limited to the tooth-bearing bones and the teeth.

PREMAXILLA

The premaxilla is a slender bone, the ventral third of which houses a battery of teeth aligned in four columns (fig. 5.3, table 5.1). The dorsal two-thirds of the premaxilla extends as a thin lamina appressed to its opposite in the midline. In lateral view, these two parts of the premaxilla meet at an angle of approximately 30°, greater than that in *Diplodocus* (figs. 5.1A, 5.2B). Four replacement foramina and a connecting groove for the dental lamina are visible on the posterior aspect of the bone. Unlike those in other diplodocoids, the alveolar margin and space within the premaxilla housing replacement teeth are not divided by bony septa into discrete alveoli. Rather, they are developed as an open trough, the arched anterior wall of which is thin and extends more than 1 cm farther ventrally than the posterior wall (figs. 5.3, 5.4).

Although the active, or functioning, teeth have fallen from the trough, a battery of replacement teeth is visible in computed tomography
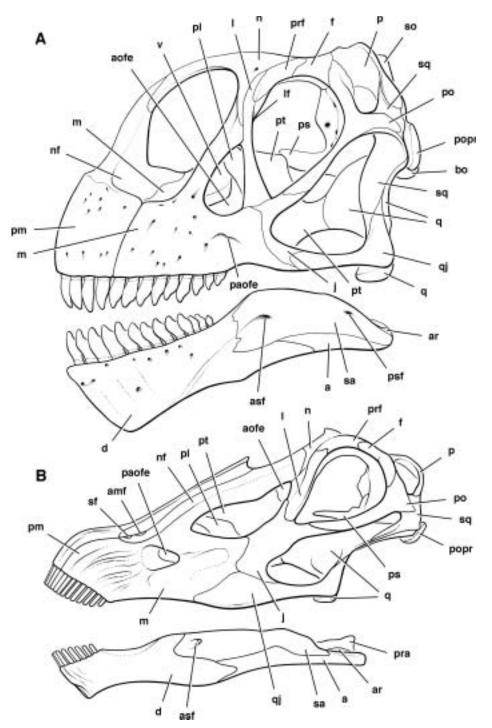
FIGURE 5.2. Skull reconstructions in lateral view of (A) the basal neosauropod *Camarasaurus lentus* and (B) the diplodocid *Diplodocus longus* (from Wilson and Sereno 1998). **a**, angular; **amf**, anterior maxillary foramen; **aofe**, antorbital fenestra; **ar**, articular; **asf**, anterior surangular foramen; **bo**, basioccipital; **d**, dentary; **f**, frontal; **j**, jugal; **l**, lacrimal; **lf**, lacrimal foramen; **m**, maxilla; **n**, nasal; **nf**, narial fossa; **p**, parietal; **paofe**, preantorbital fenestra; **pl**, palatine; **pm**, premaxilla; **po**, postorbital; **popr**, paraoccipital processes; **pra**, prearticular; **prf**, prefrontal; **ps**, parasphenoid; **psf**, posterior surangular foramen; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sf**, surangular foramen; **sq**, squamosal; **so**, supraoccipital; **v**, vomer.
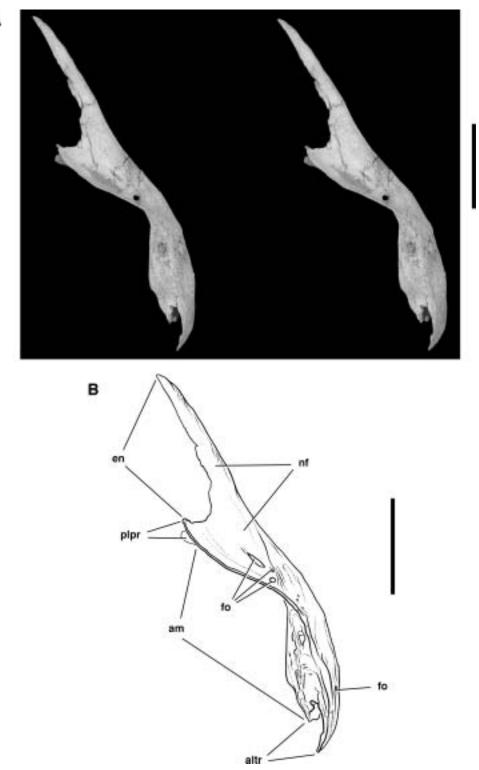
FIGURE 5.3. (A) Stereopair and (B) matching drawing of the right premaxilla of *Nigersaurus taqueti* (MNN GDF512) in lateral view. **am**, articular surface for the maxilla; **altr**, alveolar trough; **en**, external naris; **fo**, foramen; **nf**, narial fossa; **plpr**, palatal processes. Scale bars equal 5 cm.

TABLE 5.1

Measurements of the Tooth-Bearing Bones and Teeth of Nigersaurus taqueti

Premaxilla	
Maximum length	209
Maximum width of maxillary articular surface, midheight	18
Alveolar trough, anteroposterior width	10
Posterodorsal ramus, length	77
Maxilla	
Alveolar ramus	
Preserved width	94
Depth (to ventral rim of antorbital fenestra)	73
Replacement foramen, height	11
Replacement foramen, width	3
Dentary	
Alveolar ramus, width	115
Alveolar trough, anteroposterior width of medial end	12
Symphysis	
Dorsoventral height	21
Anteroposterior depth	23
Teeth	
Maxillary tooth	
Crown height	(25)
Basal crown width	4
Dentary tooth	
Crown height	(20)
Basal crown width	3

NOTE: Measurements are for the holotypic skull of *Nigersaurus taqueti* (MNN GDF512). Parentheses indicate estimated measurement. Measurements are in millimeters.
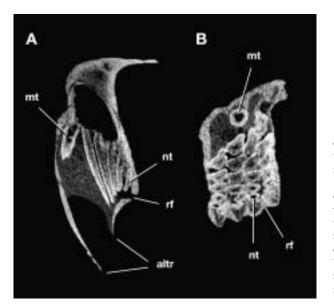

FIGURE 5.4. High-resolution computed tomographic sections through the right premaxilla of *Nigersaurus taqueti* (MNN GDF512) in (A) longitudinal and (B) cross-sectional views. The packing pattern of the tooth battery and the asymmetrical distribution of enamel on individual crowns are visible. **altr**, alveolar trough; **mt**, mature tooth; **nt**, new tooth; **rf**, replacement foramen.

(CT) scans in the upper half of the alveolar ramus (fig. 5.4B). The premaxillary teeth are self-supporting and in mutual contact along the lengths of their crowns, which presumably erupted and wore as a unit. The teeth originate just anterior to the replacement foramina. As the teeth increase in length, their roots extend into the upper half of the alveolar ramus before migrating ventrally toward the alveolar trough (fig. 5.4A).

MAXILLA

The ventral one-fifth of the maxilla houses a battery of teeth arranged in columns internal to each oval replacement foramen (Sereno et al. 1999:fig.2D; fig. 5.5, table 5.1). The dorsal four-fifths of the bone is developed proximally as a thin plate and distally as a narrow and delicate strut that divides the external naris and antorbital fenestra (fig. 5.1). As in the premaxilla, the alveolar margin is developed as an undivided trough, as seen in posterior view, with the labial (anterior) wall extending approximately 1 cm farther ventrally than the lingual (posterior) wall. Unlike the premaxilla and dentary, bony septa are present within the body of the alveolar ramus. These septa join the posterior and anterior walls, enclosing crypts for each replacement series that are approximately twice as deep labiolingually (anteroposteriorly) as mesiodistally (transversely).

Although all worn maxillary teeth have fallen from the alveolar trough, columns of replacement teeth are visible in the two most mesial (medial) tooth positions (Fig. 5.5). As in the premaxilla and dentary, the teeth originate just labially (anteriorly) to each replacement foramen, extend with growth dorsally and ventrally within the alveolar ramus, and then migrate in series toward the alveolar trough.

DENTARY

The dentary has a very unusual structure in *Nigersaurus taqueti* (figs. 5.1, 5.6, table 5.1). Other rebbachisaurids may eventually be shown to share some or all of these apomorphies. Several aspects of the dentary, however, currently have no parallel among reptiles.

In dorsal view, the T-shaped bone is divided into a mandibular ramus, oriented anteroposteriorly, and an alveolar ramus, oriented transversely (figs. 5.1B, 5.6). The posterior end of the mandibular ramus, as in other dinosaurs, is oriented in a parasagittal plane. It is divided into a slender dorsal process, which contacts the surangular, and a broader, tongue-shaped ventral process. The anterior end of the mandibular ramus, unlike that in any other sauropod, is dorsoventrally compressed and flares in transverse width before joining the alveolar ramus (fig. 5.1B). As a consequence, this portion of the mandibular ramus appears unusually slender in lateral view (fig. 5.1A). In dorsal view, this portion of the mandibular ramus is subtriangular with a concave dorsal surface. Laterally it is bounded by a sharp, upturned edge that joins the lateral extremity of the alveolar ramus. A large oval foramen opens in the center of this portion of the mandibular ramus. This foramen lies dorsal to a sizable vascular canal that passes anteriorly within the dentary toward the alveolar trough. Shallow grooves also exit the foramen and pass anteriorly toward the row of replacement foramina (Sereno et al. 1999:fig. 2C; fig. 5.6).

The breadth of the alveolar ramus exceeds the length of the mandibular ramus, a remarkable proportion that results in lower jaws that are as broad as they are long (figs. 5.1B, 5.6, table 5.1). The extraordinary width of the anterior end of the lower jaws is the result of the lateral extension of the alveolar ramus, approximately 30% of which is positioned lateral to the sagittal plane of the mandibular ramus. The medial portion of the alveolar ramus is subcylindrical. The mandibular symphysis, as a result, is subcircular (table 5.1). The symphysial surface is smooth and gently concave, suggesting that a small amount of flexion about the sagittal plane may have been possible.

The alveolar trough is nearly straight in dorsal view (fig. 5.1B). It narrows in width toward its lateral end. Other changes toward the lateral side of the trough include a decrease in the size of the replacement foramina and a
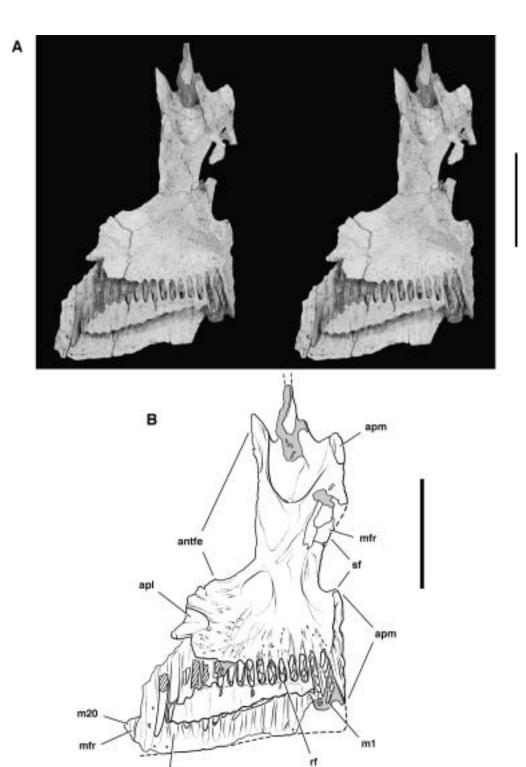
FIGURE 5.5. (A) Stereopair and (B) matching drawing of the left maxilla of *Nigersaurus taqueti* (MNN GDF512) in posterior view with two replacement tooth columns exposed by erosion. **al**, alveolus; **antfe**, antorbital fenestra; **apm**, articular surface for the premaxilla; **apl**, articular surface for the palatine; **m1– m20**, maxillary tooth positions 1–20; **mfr**, missing fragment; **rf**, replacement foramen; **sf**, subnarial foramen. Scale bars equal 5 cm.
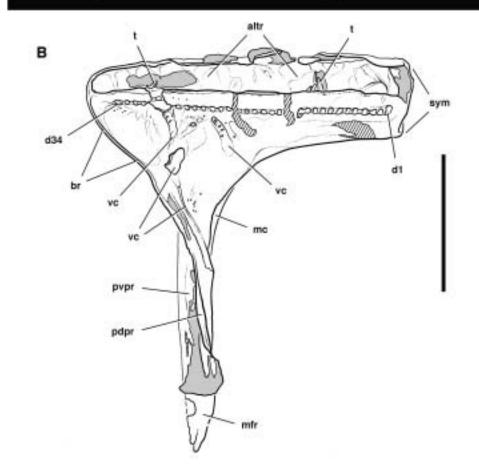
FIGURE 5.6. (A) Stereopair and (B) matching drawing of the left dentary of *Nigersaurus taqueti* (MNN GDF512) in dorsal view. **altr**, alveolar trough; **br**, buccal ridge; **d1–d34**, replacement foramina for dentary tooth positions 1–34; **mc**, Meckel's canal; **mfr**, missing fragment; **pdpr**, posterodorsal process; **pvpr**, posteroventral process; **sym**, symphysis; **t**, tooth; **vc**, vascular canal. Scale bars equal 5 cm.
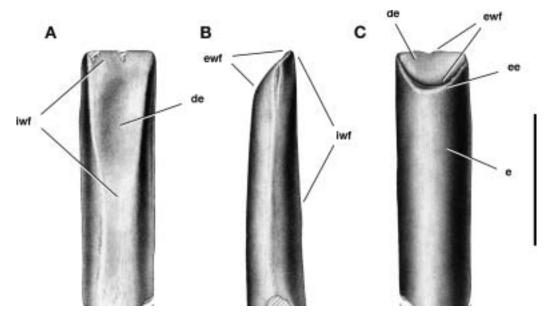
FIGURE 5.7. Isolated tooth of *Nigersaurus taqueti* (MNN GDF513) in (A) lingual (internal), (B) mesial or distal (medial or lateral), and (C) labial (external) views. **de**, dentine; **e**, enamel; **ee**, enamel edge; **ewf**, external wear facet; **iwf**, internal wear facet. Scale bar equals 1 cm.

decrease in the distance between the replacement foramina and the edge of the alveolar trough. This gradual decrease in the width of the trough and the size and position of the replacement foramina suggests that the replacement rate and/or tooth size decreased toward the lateral end of the tooth row. Several loose teeth are preserved in the bottom of the alveolar trough and confirm the gradual decrease in tooth size laterally along the battery. There are 34 replacement foramina and, thus, 34 columns of teeth, which is 20 more than are typically present in the dentary of the diplodocid *Diplodocus* (Holland 1924; fig. 5.2B). As there are no septa at any depth within the alveolar trough, dentary teeth would have erupted and migrated toward the functioning wear surface as a self-supporting dental battery. No other sauropod has a dentary with an alveolar ramus of similar form lacking septa.

TEETH

The upper and lower teeth are virtually identical in form (Sereno et al. 1999: fig. 2C; fig. 5.7). These similarities are based on the pre-maxillary, maxillary, and dentary teeth in situ in MNN GDF513. Upper and lower teeth differ only in size; dentary teeth are smaller, perhaps by as much as 20%–30%. This is difficult to estimate more accurately because the available dentary teeth, a few of which remain within the alveolar trough, are of unknown maturity. A similar size differential, with upper teeth larger and longer than the lowers, has been observed in *Diplodocus* (Holland 1924:389) and the titanosaur *Nemegtosaurus* (Wilson 2005: 305).

The numbers of premaxillary, maxillary, and dentary tooth positions are 4, at least 24, and 34, respectively. Maxillary and dentary tooth counts are approximately double those in other diplodocoids such as *Diplodocus* (Holland, 1924; fig. 5.2B). Although the maxillary tooth row is incomplete laterally, there are probably only a few missing tooth positions, because the length of the combined premaxillary and maxillary tooth rows in MNN GDF513 is only slightly less than that for the dentary. The higher number of tooth positions in the dentary (34 versus approximately 30 for the premaxilla plus

maxilla) is consistent with the smaller size of the dentary teeth.

Crown shape and structure are uniform among upper and lower teeth. Unworn crowns are gently curved along their length and taper gradually to a narrow, rounded tip, which shows subtle wrinkles on its thickly enameled labial (external) surface. Teeth in place in the premaxilla and maxilla and near their natural position in the dentary confirm that the crowns are convex labially (anteriorly) in both the upper and the lower jaws.

At midlength, the crown has a trapezoidal cross section, with smooth enamel and a longitudinal groove on each side that accommodates the edges of adjacent crowns (Sereno et al. 1999:fig. 2D; fig. 5.7). Toward its tip, the crown has an oval cross section. The enamel is approximately eight times thicker on the labial (external), as opposed to the lingual (internal), side of the crown in both upper and lower teeth. Whereas other diplodocids and some titanosaurians have similar-shaped, narrow, cylindrical crowns, markedly asymmetrical enamel has not been reported previously among sauropods and is absent in other diplodocoids (*Dicraeosaurus* [Janensch 1935–1936:pl. 12, fig. 16], *Diplodocus* [Holland 1924:fig. 6].

TOOTH WEAR

Although wear facets are not present in teeth preserved in the holotypic jaw bones of *Nigersaurus taqueti*, worn teeth referable to this species have been recovered from many sites in the Gadoufaoua beds and show a distinctive pattern of wear. There is little reason to doubt the reference of these teeth to *Nigersaurus taqueti*, despite the presence of an unnamed titanosaurian in the same horizons; the crowns have narrow cylindrical proportions and highly asymmetrical enamel.

Unlike the teeth in nearly all other sauropods, those in *Nigersaurus taqueti* have a pair of wear facets located on opposite sides of the crown. The first—a labial (external) facet—is typical of dicraeosaurids and diplodocids; it cuts the crown at a high angle and appears to be

the product of nonocclusal abrasion (Holland 1924; Upchurch and Barrett 2000; fig. 5.7B, C). The elevated, rounded rim of thick enamel suggests that the wear facet was produced by ingested plant matter rather than the harder enameled edge of an opposing crown. The second—a lingual (internal) facet—resembles the internal facet on some narrow-crowned titanosaurians; it cuts the crown at a low angle and appears to be the product of occlusal abrasion (fig. 5.7B, C).

TOOTH BATTERY

STRUCTURE

Archosaur teeth, primitively, are anchored by alveoli that are separated from adjacent teeth by bony septa. They erupt *en echelon* along the jaw rather than in unison as a single unit. In most dinosaurian herbivores, wear facets develop from tooth-to-tooth occlusion at several points along the tooth row rather than developing as a continuous wear surface.

A *tooth battery*, by contrast, is here defined as a tooth composite composed of self-supporting teeth that erupt and wear in unison. The teeth are supported by adjacent teeth and erupt as a unit with wear surfaces that are continuous from one tooth to the next. In *Nigersaurus* part of the dentition fulfills these criteria—the premaxilla and dentary tooth rows. These bones do not have alveoli, intervening septa, or even well-developed grooves to guide erupting tooth columns. Rather, the teeth are packed into an open alveolar trough.

Although all functioning (worn) teeth have fallen away from the jaws of the holotypic specimen, the tooth battery is intact within the body of the premaxilla (fig. 5.3), as visualized in cross and longitudinal sections with high-resolution CT (fig. 5.4). Embryonic teeth migrate into the alveolar trough via replacement foramina. As they grow in length and diameter, they migrate deeper into the body of the premaxilla before passing ventrally out of the alveolar trough (fig. 5.4A). There appear to be as many as 10 teeth at a single tooth position, from embryonic tooth to

wearing crown. The four tooth columns in the premaxilla are arranged *en echelon* so that the widest portion of a given crown contacts the more tapered portion of adjacent crowns, with the prominent edge of enamel lodged in a groove on the side of adjacent crowns (fig. 5.4B).

Less is known about the structure of the tooth battery of the dentary, although it was probably very similar. The crowns have the same shape, structure, and orientation. The position of the replacement foramina near the margin of the alveolar trough indicates that embryonic teeth began their trajectory closer to the open end of the trough and grew deep into the alveolar trough before emerging at the functional end of the tooth battery. The most distal (lateral) tooth columns in the dental battery of the dentary must have angled anterolaterally as shown by the extension of the trough lateral to the lateral most replacement foramen (fig. 5.1B).

The body of the maxilla has septa separating columns of teeth (fig. 5.5). Closer to the ventral end of the maxilla, the septa give way to an open trough with a groove for each tooth column on anterior and posterior walls. As in the premaxilla, there appear to have been at least 10 teeth to a column medially and fewer laterally; an incomplete sequence of 8 teeth is visible in the first column (fig. 5.5). The maxillary teeth, presumably, emerged from the alveolar trough as a self-supported tooth battery.

FUNCTION

Exactly how the tooth batteries of *Nigersaurus* functioned to produce the wear facets evident on isolated teeth remains unsolved, despite knowledge of the general structure of the tooth batteries. What we can outline at this point are several observations that provide some insight into the mystery.

We know that teeth in lower and upper tooth rows do not match one-to-one given their differing sizes and numbers. We also know that both upper and lower tooth batteries were constructed in a similar manner, with the convex, thickly enameled crown surface facing labially (anteriorly). Many mammals, such as rodents, have analogous anteriorly positioned, self-sharpening lower and upper incisors with lingual (internal) wear facets (Taylor and Butcher 1951). As in *Nigersaurus*, both lower and upper incisors are externally convex, with thickened enamel on their labial (external) sides and wear facets facing lingually (internally). This is the closest analogy to the structure and orientation of the individual teeth in *Nigersaurus*. Mammalian incisors like these, however, are much more robust and are sharpened in a manner very different from that in any dinosaur. The chisel-shaped edge is maintained by breakage (preferential chipping of the softer dentine) and by tooth-to-tooth abrasion. Unlike *Nigersaurus*, the facets on lower and upper incisors are not symmetrical (the uppers typically have higher-angle, stepped facets), and the shearing breakage that keeps the leading edge sharp rarely produces facets that are uniformly planar.

We strongly suspect that the low-angle, lingual (internal) wear facet was produced by tooth-to-tooth abrasion, because the facet is extremely flat and cuts smoothly across the external margin of enamel. The high-angle labial (external) wear facet, in contrast, appears to have been produced by tooth-to-plant abrasion, because the facet is concave, with a rounded, polished rim of enamel along its trailing labial (external) edge (fig. 5.7).

Because all of the isolated teeth from Niger, England (Naish and Martill 2001), and Brazil (Kellner 1996) show a similar pattern of wear—with the low-angle facet first to appear—it is likely that both lower and upper teeth are represented and wear in a similar manner. Yet it is not clear how this is functionally possible. Hadrosaurid and ceratopsian tooth batteries have opposing, mirrored patterns of tooth wear: the enamel is thickest on opposing sides of the crown (medially in maxillary teeth, laterally in dentary teeth); the crowns curve in opposite directions (laterally in maxillary teeth, medially in dentary teeth); and the wear facets occur in opposing orientations (medially or ventromedially in maxillary teeth, laterally or dorsolaterally

in dentary teeth). Although an isolated ornithischian tooth from a tooth battery may be difficult to assign to either the upper or the lower tooth row (when upper and lower crowns have a similar shape and ornamentation), these teeth have mirrored positions when they are found in place. One possible explanation for the uniform pattern of wear in *Nigersaurus* is that the lingual (internal), low-angle facet is produced by the lower crowns passing lingually (internally) to the upper crowns (the usual tetrapod condition) but that the lower crowns are worn away and eventually obliterated in the process. If this were true, the entire sample of isolated teeth of *Nigersaurus* and related taxa found now on several continents would include only premaxillary and maxillary teeth from the upper tooth batteries. If not, and if we are correct that the low-angle facet is produced by tooth-to-tooth occlusion, there must have existed an occlusal mechanism unlike any described to date among tetrapods—a mechanism capable of producing low-angle, lingual (internal) wear facets on both lower and upper crowns.

Another conundrum involves the cutting edge of the crown. In ornithischians with tooth batteries and in mammalian herbivores, thickened enamel is always positioned along the cutting edge. This is not the case in *Nigersaurus*. Not only are the lower and upper teeth oriented with their curvature and thickened enamel on the same (external) side, but the leading wedge-shaped edge of the crown is formed entirely of dentine. It is difficult to understand how this edge, which is perfectly straight, is maintained in the course of wear without the protection of enamel (fig. 5.7). Even if one envisages adjacent crowns, it is hard to understand how the soft leading edge of dentine would not be concave from wear rather than straight.

A final observation suggests that the tooth battery of *Nigersaurus* is quite different from that in ornithischians. To produce an elongate, low-angle wear facet on the lingual (internal) side of the crown (fig. 5.7A), most of this side of the crown must have been exposed. The succeeding replacement crown, in other words,

must have been positioned at a good distance from the cutting edge of the functional crown. Only one crown in each tooth column could have been functional. In ornithischian dentitions, higher-angle wear facets allow more than a single crown in the same tooth column to participate in the active, cutting surface of the dental battery.

In the future, we plan to digitally define and prototype the intact portion of the tooth battery within the premaxilla in the hope that it will shed further light on how the battery functioned during mastication.

DISCUSSION

COMPARISONS

SKULL

In general proportions, the skull of *Nigersaurus taqueti* bears little resemblance to that of diplodocids (figs. 5.1, 5.2B). It has a more abbreviate, less prognathous snout; the depth of the cranium is approximately 90% of its length (as measured from the snout to the quadrate condyle). This cranial proportion is even more abbreviate than that of *Camarasaurus* (fig. 5.2A) and *Jobaria* (Sereno et al. 1999), which have a cranial depth between 50% and 60% of its length. The external naris in *Nigersaurus* is large and parasagittal in position as in *Camarasaurus* and *Jobaria*. In diplodocids, in contrast, the external naris is smaller, dorsally facing, and retracted to a position anterodorsal to the orbit (the condition in dicraeosaurids is as yet unknown). The laterotemporal fenestra in *Nigersaurus* is proportionately elongate and extends anteriorly as far as the antorbital fenestra and external nares, farther than in any sauropod described to date. There is no development of a preantorbital fenestra as occurs in other neosauropods (fig. 5.2B). The dermal bones of the skull roof in *Nigersaurus* are remarkably slender and delicate compared to those of other sauropods including diplodocids. The posterodorsal ramus of the maxilla, which separates the external naris and antorbital fossa, is reduced to an extremely delicate, strap-shaped

lamina 1 mm thick and a few millimeters wide (fig. 5.1).

The lower jaw is easy to distinguish from that in diplodocids (figs. 5.1, 5.2B). The coronoid process on the surangular is prominent and deep in lateral view, more closely resembling that in the titanosaurian *Rapetosaurus* (Curry Rogers and Forster 2004) than the low profile jaws of diplodocids (fig. 5.2B). In *Nigersaurus* the teeth are restricted to the transverse portion of the anterior end of the skull, and at least the lower tooth row extends lateral to the parasagittal plane of the lower jaw. In both of these attributes, *Nigersaurus* is unique among dinosaurs. Diplodocids show an incipient condition in these regards; all but the lateral extremities of the tooth rows are positioned along the anterior, transverse margin of the skull, and the dentary tooth row flares just beyond the parasagittal plane of the posterior portion of the lower jaw.

A dentary from Upper Cretaceous rocks in South America referred to *Antarctosaurus wichmannianus* (Huene 1929:69, pl. 29, fig. 5) is similar to that in *Nigersaurus taqueti* in the extreme breadth of the transverse portion of the ramus and the concomitant increase in tooth count. There are at least 24 teeth in the dentary, with the majority (approximately 18) located in the broad, transverse portion of the ramus. The dentary of this South American form, however, is not as derived as that in *Nigersaurus*. The teeth are set in sockets rather than an undivided alveolar trough, the tooth row is L-shaped rather than straight and restricted to the transverse portion of the ramus, and the symphysial surface is narrow rather than circular. Despite these similarities, the phylogenetic affinity of *Antarctosaurus* is not yet resolved. There is a possibility that this taxon, which was found together with titanosaur cranial and postcranial remains, may have acquired these features convergently with *Nigersaurus*.

TEETH AND TOOTH WEAR

Teeth that closely match those of *Nigersaurus taqueti* in form, structure, and wear have been described recently from slightly older Barremian-age beds on the Isle of Wight (Naish

and Martill 2001:pl. 36) and from the Upper Cretaceous Bauru Group in Brazil (Kellner 1996:fig. 7). The crowns are narrow and subcylindrical and, at midlength, have a trapezoidal cross section. The size, form, and angle of the pair of wear facets are exactly like those described above for *Nigersaurus taqueti*. As noted by Kellner (1996:619), the low-angle lingual (internal) facet is the first to appear and is always more elongate than the labial (external) facet, as preserved in progressively worn crowns. The enamel may have an asymmetrical distribution on the crown, but this needs firsthand verification. Kellner provisionally regarded these teeth as titanosaurian, because of the predominance of titanosaurian postcranial bones from the same beds. It is very probable, however, that these Brazilian teeth belong to a rebbachisaurid diplodocoid that lived on South America in the Late Cretaceous. (e.g., *Limaysaurus;* Salgado et al. 2004).

In other diplodocoids, the teeth are larger relative to the jaw bones and anchored in individual alveoli (fig. 2B; *Dicraeosaurus* [Janensch 1935–1936:figs. 107, 111]; fig. 2B). The crowns have a circular cross section, symmetrical enamel, and a single low-angle, labial (external) wear facet (Holland 1924). Despite some variation, isolated teeth of *Dicraeosaurus* show the same external facet (Janensch 1935–1936:pl. 12, figs. 23, 25). This facet is characterized by a rounded lip of enamel along its trailing (external) edge (fig. 5.7; ewf) and scratches that course across the dentine from the internal to the external sides (Fiorillo 1991; Calvo 1994b; Upchurch and Barrett 2000). How this wear facet formed has remained a mystery ever since Holland (1924) summarized early speculation, which included scraping cycad trunks (Holland), procuring fish hiding in stream beds (Tornier), and munching on freshwater bivalves (Sternfeld). Because Holland (1924:fig. 4) depicted "*Diplodocus* seizing a mussel," that hypothesis gained the upper hand, although Holland maintained no personal preference. More recent proposals include stripping leaves from branches (Dodson 1990; Barrett and Upchurch 1994) and raking
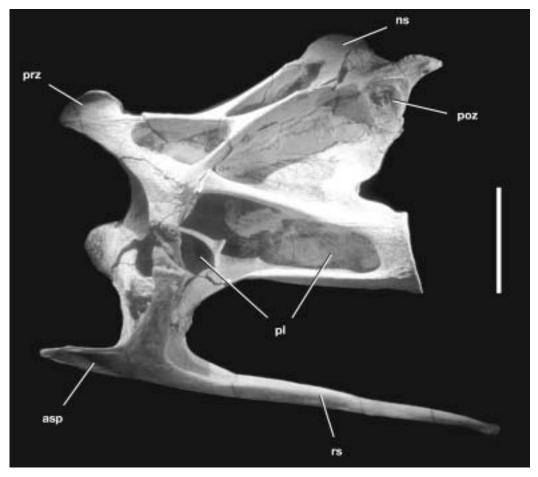
FIGURE 5.8. Fifth cervical vertebra and co-ossified rib of *Nigersaurus taqueti* (MNN GDF512) in lateral view. **asp**, anterior spine; **ns**, neural spine; **pl**, pleurocoel; **poz**, postzygapophysis; **prz**, prezygapophysis; **rs**, rib shaft. Scale bar equals 5 cm.

bark (Bakker 1986). *Nigersaurus* adds a new wrinkle. Here we see the same kind of external facet in teeth set into a tooth battery. These batteries, in turn, are housed in a skull with a very different shape and even more delicate construction than in diplodocids (fig. 5.2).

Some titanosaurians have narrow-crowned teeth that bear a general resemblance to those of *Nigersaurus taqueti*, but these teeth have more robust proportions (e.g., Kellner and Mader 1997:fig.2; *Rapetosaurus* [Curry Rogers and Forster 2004:fig. 32]). The internal (lingual) facet—the only one present—cuts the crown at a low angle. An external (labial) facet has never been described outside Diplodocoidea. *Nemegtosaurus*, which has internal V-shaped and apical wear facets (Nowinski 1971; Wilson

2005), has continued to confuse discussions of tooth form and masticatory style among diplodocoids (e.g., Upchurch and Barrett 2000). *Nemegtosaurus* and the conspecific, or closely allied, *Quaesitosaurus* from the Late Cretaceous of Asia are better understood as titanosaurians rather than diplodocoids (Calvo 1994a; Wilson and Sereno 1998; Wilson 2002, 2005).

EVOLUTION OF A SAUROPOD TOOTH BATTERY

Nigersaurus taqueti must be placed within the context of diplodocoid phylogeny to better understand how its novel tooth battery evolved (fig. 5.9). Diplodocoids include diplodocids, dicraeosaurids, and rebbachisaurids. Diplodocids are best known from the Late Jurassic of North America and include *Diplodocus*, *Apatosaurus*,
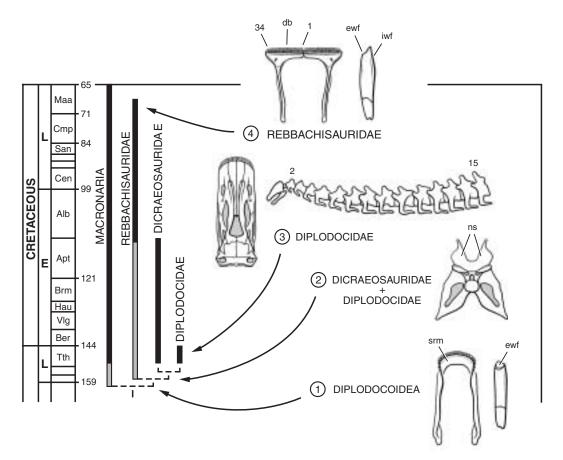
FIGURE 5.9. Phylogram showing the relationships and recorded durations of the three principal diplodocoid clades (Rebbachisauridae, Dicraeosauridae, Diplodocidae) and some of their feeding specializations. Node 1 (Diplodocoidea): slender cylindrical crowns, low-angle external (labial) wear facet, teeth restricted anteriorly in subrectangular muzzle. Node 2 (Dicraeosauidae + Diplodocidae): bifid cervical neural spines. Node 3 (Diplodocidae): nares retracted, 15 cervical vertebrae. Node 4 (Rebbachisauridae): low-angle, internal wear facet, increase in tooth number, asymmetrical enamel, dental batteries in some taxa. **1–34**, dentary teeth 1 through 34; **2–15**, cervical vertebrae 2–15; **db**, dental battery; **en**, external naris; **ewf**, external wear facet; **iwf**, internal wear facet; **ns**, neural spine; **srm**, subrectangular muzzle.

Barosaurus, and others (Hatcher 1901; Holland 1924; Berman and McIntosh 1978; Ostrom and McIntosh 1999). Dicraeosaurids include *Dicraeosaurus* (Janensch 1935–1936) from the Late Jurassic of Africa and the long-spined *Amargasaurus* from the Early Cretaceous of South America. Rebbachisaurids include *Limaysaurus* (Calvo and Salgado 1995; Salgado et al. 2004) from the Early Cretaceous of South America and *Nigersaurus* (Sereno et al. 1999) and *Rebbachisaurus* (Lavocat 1954) from the mid- and Late Cretaceous of Africa. Rebbachisaurid teeth and other fragmentary remains indicate that the group was also present in Europe and persisted

to the end of the Cretaceous at least in South America. As a sister taxon to dicraeosaurids and diplodocids, rebbachisaurids must have diverged from other diplodocoids before the end of the Late Jurassic, although no trace of the group has yet been found from this period (fig. 5.9).

Although the teeth of *Nigersaurus* are particularly slender, all diplodocoids are characterized by proportionately narrow, subcylindrical crowns that are only weakly expanded and flattened (fig. 5.9, node 1). The rate of tooth replacement, in addition, appears to have been accelerated across the group, although this is most apparent in *Nigersaurus*. In this regard, we

assume that the number of teeth in a single column is related to the replacement rate. *Diplodocus*, for example, has as many as six teeth in a single column in the maxilla (Marsh 1884:pl. 4, fig. 3). Worn diplodocoid teeth have a characteristic external, low-angle, wear facet on both upper and lower teeth (fig. 5.7 ewf) that must have formed from tooth-to-plant abrasion (*contra* Calvo 1994b; Barrett and Upchurch 1994; Upchurch and Barrett 2000). Most diplodocoid teeth are positioned in a transverse row along the squared anterior margin of the snout (fig. 5.9, node 1).

Nigersaurus has further developed a number of these features (fig. 5.9, node 2). Tooth size decreases relative to the size of the jaw bones, and tooth number increases to 30 or more in lower and upper tooth rows. In *Nigersaurus* the teeth are restricted to the anterior margin of the snout and extend lateral to the sagittal plane of the lower jaw, features unknown elsewhere among dinosaurs. More teeth are present in a single column, and the rate of replacement, presumably, has increased as well. Most of the teeth in the jaws are pressed so close to one another that there are no intervening septa and, for the first time among sauropods, batteries of self-supporting teeth erupt as a single unit. Although still a functional conundrum, an additional low-angle wear facet appears on the lingual (internal) side of the active crowns in both lower and upper tooth batteries.

Dicraeosaurids and diplodocids evolved other features that likely impacted food procurement but are not present in *Nigersaurus* or other rebbachisaurids. These include a reduction in the number of teeth, a projecting "chin" on the dentary, a relative lengthening of the snout, retraction of the external nares, and an increase in the length and number of cervical vertebrae (fig. 5.9, nodes 3, 4). In dicraeosaurids and diplodocids, in addition, the resting curvature of the neck arches anteroventrally (Janensch 1929; Stevens and Parrish 1999). This is not the case in *Nigersaurus*, as exemplified by the fifth cervical vertebra (fig. 5.8).

COMPARISON TO ORNITHISCHIAN TOOTH BATTERIES

Tooth batteries evolved twice among ornithischian dinosaurs from a hypothetical common ancestor with a simple dentition characterized by a suite of ornithischian features related to herbivory—a predentary, cheek embayments on the dentary and maxilla, asymmetrical enamel in dentary and maxillary crowns, and wear facets from tooth-to-tooth occlusion on the buccal (lateral) and lingual (medial) sides of dentary and maxillary teeth, respectively. Evolution of tooth-supported batteries occurred first among ornithopods, with initial changes toward a dentition occurring before the close of the Jurassic, and later among ceratopsian dinosaurs, where all structural changes occurred during the Late Cretaceous (Sereno 1997, 2000).

The fully developed tooth batteries in hadrosaurids and ceratopsids are structurally very similar, evolved in comparable stages, and involved an increase in body size of approximately an order of magnitude (Sereno 1997: fig. 7; 2000: fig. 25.9). Independent but similar structural changes include a relative decrease in tooth size and increase in tooth columns and replacement rate, the loss of alveolar septa, restriction of the enamel to opposing sides of the crown in maxillary versus dentary teeth, an increase in the prominence of a ridge on the enameled side of the crown, adjustment of the crown shape for efficient packing, an increase in the volume of supporting bone in the maxilla and dentary, a reduction of postdentary elements in the lower jaw, and the development of a coronoid process with an expanded process for muscular attachment.

The circumstances surrounding the evolution of tooth batteries in rebbachisaurid sauropods bear a few similarities to and many striking differences from those in ornithischians. Similarities include the reduction of tooth size, increase in number of tooth columns, increase in replacement rate (or at least the number of teeth per column), loss of alveolar septa between tooth columns, thickened

enamel on one side of the crown and near-loss of enamel on the other, and adjustment of crown shape for efficient packing. These similarities, thus, are confined to the size, shape, number, and rate of replacement of the teeth and the asymmetrical distribution of enamel.

Fundamental differences begin with timing. Available rebbachisaurid fossils suggest that a tooth battery among sauropods had evolved sometime during the Early Cretaceous; the teeth from the Isle of Wight (Naish and Martill 2001) look very similar to those of *Nigersaurus* and are Barremian (ca. 125 Ma; middle Early Cretaceous) in age. This postdates the establishment of tooth-supported dentitions in ornithopods (Late Jurassic) but predates the appearance of ceratopsian tooth batteries (Late Cretaceous). Another basic difference involves body size. There was no increase in body size among sauropods concomitant with the development of tooth batteries. Although *Rebbachisaurus* ranks among the largest of sauropods, *Nigersaurus* ranks among the smallest, with a body length of approximately 15 m.

The orientations of the tooth batteries are diametrically opposed. The tooth batteries have an anteroposterior, rather than a transverse, orientation in ornithischians and rebbachisaurids, respectively. The ornithischian tooth battery is located posteriorly within the jaws and used for food processing; cropping is a function of an expanded, toothless bill. The sauropod dental battery, in contrast, is located anteriorly and may have been used primarily in cropping.

The presence or absence of gastroliths as an accessory means to break down plant matter may be correlated with the aforementioned fundamental functional differences. The absence of gastroliths among ornithischians with advanced dentitions (euornithopods, neoceratopsians) including dental batteries suggests that more efficient oral processing of plant matter has replaced gut-processing by gastroliths (Sereno 1997:473). In sauropods, in contrast, the group in which dental batteries evolved (diplodocoids) has the greatest proven incidence of gastroliths, suggesting that their derived dental features did not function primarily in the breakdown of plant matter.

Gastroliths are present in rebbachisaurids (Calvo 1994b), dicraeosaurids (Janensch 1929), and diplodocids (Cannon 1906; Brown 1941; Gillette 1990). The absence of gastroliths among nondiplodocoid sauropods is based on many articulated skeletons of *Shunosaurus*, *Camarasaurus*, *Jobaria*, and *Opisthocoelicaudia*. *Cedarosaurus*, a macronarian sauropod of uncertain affinity, is thus far the only nondiplodocoid sauropod with gastroliths (Sanders et al. 2001).

The pattern of wear in the rebbachisaurid tooth battery is completely different from that in ornithischians, which uses thickened enamel and tooth-to-tooth occlusion to form a self-sharpening cutting margin. In rebbachisaurids, only one of a pair of wear facets is formed by tooth-to-tooth occlusion, the sharp leading edge of worn crowns is formed in dentine rather than enamel, the thickened enamel is located on the same (labial) side of lower and upper crowns, and lower and upper crowns apparently have identical wear patterns.

The locus of the most rapid replacement and wear is different in ornithischian and rebbachisaurid tooth batteries. In ornithischians, the crown size, the number of teeth in a column, and the distance of the replacement foramen from the alveolar margin are all greatest in the middle of the tooth battery. In *Nigersaurus*, in contrast, the crown size, the number of teeth in a column, and, to a lesser degree, the distance of the replacement foramen from the alveolar margin are all greatest toward the midline.

Finally, the tooth-bearing bones are constructed differently in ornithischians and sauropods with dental batteries. In ornithischians with tooth batteries, the dentary, in particular, is robustly constructed, with a thick and prominent coronoid process for attachment of substantial adductor musculature. Postdentary elements are greatly reduced in size. This pattern of change in the lower jaw closely mirrors changes that occurred earlier in the evolution of the mammalian masticatory apparatus (Allin 1975). In *Nigersaurus*, in contrast, the tooth-bearing elements are constructed of thin laminae, the dentary does not gain in relative

length in the lower jaw, the coronoid process is developed as a thin plate of bone, and the supratemporal fenestra (the usual origin of adductor musculature) is closed by approximation of surrounding bones.

CONCLUSIONS

Early in their evolution, sauropods adopted tooth-to-tooth occlusion and, in consequence, evolved lower and upper tooth rows of equivalent length, characteristic patterns of wear facets, a more substantial coronoid process, and a robust mandibular symphysis (McIntosh 1990; Calvo 1994a; Wilson and Sereno 1998; Upchurch and Barrett 2000). Among sauropods, it is now apparent that diplodocoids evolved complex dentitions during the Cretaceous, as exemplified by the dental batteries of a recently named African rebbachisaurid, *Nigersaurus taqueti* (Taquet 1976; Sereno et al. 1999).

The dental battery on each side of the upper and lower jaws is composed of more than 30 columns of teeth that are packed into a tight self-supporting unit in the premaxilla and dentary. Individual teeth have slender rod-shaped crowns characterized by highly asymmetrical enamel. Dentary teeth are somewhat smaller than but otherwise similar to premaxillary and maxillary teeth. The crowns in both lower and upper jaws have thickened enamel on their convex labial (external) side. Wear produces two stereotypical facets, the first appearing as a low-angle, lingual (internal) facet produced by tooth-to-tooth occlusion and the second as a high-angle, labial (external) facet produced by tooth-to-plant abrasion. Both facets are well developed on crowns with significant wear, resulting in a straight, sharp apical wedge of dentine where the facets intersect. How either of these facets was produced remains a significant, and largely unanswered, question.

Unlike the parasagittal dental batteries of ornithischians, the dental battery in *Nigersaurus* is oriented transversely and may have been used for cropping rather than prolonged oral processing. Although the rebbachisaurid dental battery is preserved only in *Nigersaurus*, isolated teeth from Lower Cretaceous horizons on the Isle of Wight and rocks of Late Cretaceous age in Brazil suggest that related forms with potentially a similar degree of dental complexity were present on other continents. It is highly unlikely, however, that rebbachisaurids with dental batteries ever achieved the taxonomic diversity of ornithischians with dental batteries (hadrosaurids, ceratopsids) in Late Cretaceous faunas of North America and Asia.

Dental batteries evolved three times independently within Dinosauria—in euornithopod and neoceratopsian ornithischians and in rebbachisaurid sauropods. Fundamental functional differences coupled with their diachronous appearance suggest that dinosaurian dental batteries did not evolve in response to a single environmental cue, such as the rise of angiosperms during the mid-Cretaceous (Sereno 1997: Sereno 1999; Barrett and Willis 2001).

ACKNOWLEDGMENTS

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