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On Dinosaur Reconstruction: The Head

Georgios A. Florides, Paul Christodoulides

Faculty of Engineering and Technology, Cyprus University of Technology, Limassol, Cyprus
Email: paul.christodoulides@cut.ac.cy

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Abstract

This paper presents the current knowledge about the reconstruction of dinosaur heads. To reconstruct the dinosaur head, several features and functions of the head must be studied, namely osteology, musculature and soft tissue of the head, cranial kinesis, craniodental biomechanical characteristics, posterior part of the cranium, skin, and others. The main steps and points resulting from the study are the following. Firstly, the osteological remains of the head are studied for reconstruction according to the correct size and form in comparison with known remains belonging to the same family in case the remains were not complete. As the dinosaurs did not have facial muscles, their skin was pressed directly to the skull. The skin covering the large openings in front of the orbits of many dinosaurs probably bulged gently outward, and similarly, the jaw muscles bulged gently from the skull openings. Also, an investigation is performed to decide if sauropods were terrestrial or aquatic animals. Then, the individual characteristics of the head are examined in detail. These concern: 1) endocranial cast and nerves, 2) nostrils position, 3) the existence and kind of cheeks and lips, 4) Teeth types and function, 5) the palate shape and skin covering, 6) hyoid apparatus and tongues, 7) the details of the ear, 8) sclerotic rings and eyes, 9) skin and color. With the knowledge gathered about the various parts of the head in mind, decisions are made about the Amargasaurus (a sauropod) head in order to reconstruct a 3D, actual size head, as a worked example. Finally, the reconstruction procedure is described in detail.

Keywords

Amargasaurus Reconstruction, Dinosaur Head Details, Diplodocus Skull, Eye, Sclerotic Ring, Ear, Head Musculature, Teeth, Tongue, Oral Cavity, Nostrils, Cheeks and Lips, Skin

1. Introduction

This paper deals with the reconstruction of the head of dinosaurs. It is the third paper in a series and examines in detail the various parts of a dinosaur's head. Also, as an example, it explains step by step how to reconstruct the Amargasaurus head on a full scale. The first paper in the series covers the most important topics related to Paleontology and Dinosaurs and serves as a short guide that gives all the necessary knowledge in a comprehensible and compressed form [1]. The second paper in the series deals with the posture of dinosaurs and gives examples of how to visualize and reconstruct a dinosaur in an everyday life posture. In order to reconstruct the animal, the first and basic step to be taken is a decision about the posture of Dinosaurs, all discussed in [2].

The head of dinosaurs is probably the most important part in the reconstruction of the animal, since it contains the organs for vision, hearing, smelling and tasting, breathing, cropping, biting, cutting, chowing and swallowing food. Dinosaur heads come in many shapes, sizes and individual characteristics, depending on the species and the functions performed by the head. For example, meat-eating dinosaurs, such as Tyrannosaurids [3], had heads of about 1/10 to 1/8 of their total length, equipped with wide-opening powerful jaws with large and robust teeth with serrated edges that were made for penetrating and cutting flesh and meat. Other species, such as plant-eating ceratopsians [4], had a large head decorated with horns and frills. The head also had a beak like that of a tortoise or a bird and rows of teeth in the mouth. The length of the head and frill could be about 1/3 of the length of the animal, with the frill protecting the neck. Ornithopods, like duckbill hadrosaurs, had flattened broad and elongated snouts and toothless beaks. They also had sets of teeth in the mouth adapted for grinding vegetation. Parasaurolophus, a genus of duck-billed dinosaur, was characterized by a tubular crest extending over the top of the skull and beyond the occiput [5]. The crest was hollow and U-shaped, housing the nasal cavity. The size of the head in hadrosaurs was about 1/7 of their total lengths (for example, see restoration in [6]). Other ornithischian dinosaurs, such as Pachycephalosaurids, had cranial ornamentation and a uniquely enlarged dome [7]. In this group, the head was about 1/10 of their length (for example, see restoration in [8]). Sauropods, on the other hand, had small heads, long necks and tails, and pillar-like legs. They are notable for the enormous sizes that some species attained, reaching lengths of 40 m [9] or even more (implied by skeletal remains [10]). The size of the head was too small for the length and mass of the animal, roughly about that of a horse.

For the reconstruction of the dinosaur head several features and functions of the head must be studied, namely the osteology, musculoskeletal structures and soft tissue anatomy of the head, cranial kinesis, craniodental biomechanical characteristics, posterior part of the cranium, where the neck muscles connect and join the head with the neck, snout shape and other.

The reconstruction of the anatomy of the soft tissue of the dinosaurs' head is based on osteological marks, which indicate the attachment of muscles that consistently leave a fossa, crest, tuberosities, spurs, flanges, and other muscle-related bony structures. Other osteological correlates and concepts of bone surface homology (*i.e.*, the correspondence of general osteological regions that are continuous through evolution) and the development of precise hypotheses of structure and function help one to obtain the correct picture of the soft tissue anatomy. Thus, anatomical inferences can be drawn not only from fossil taxa, but also from closest-related clade, extant taxa (birds and crocodylians), and finally outgroup taxa (lepidosaurs and testudines) [11]. Another area of study for reconstructing the head anatomy is the variation of sizes and shapes of the dorsotemporal fossa and fenestra. The dorsotemporal fenestra is generally hypothesized to be analogous in size to the muscle forces acting upon the skull, as the jaw muscles fill the fossa in many vertebrates. However, this is not always the case, as in many animal groups, a wide variety of dorstotemporal fenestra in shapes and sizes, do not always appear to be directly corresponding to jaw muscle attachments only. The above hypothesis was examined through anatomical imaging and in vivo thermography techniques, comparing extant and extinct taxa, for the reconstruction of the soft tissues in the skull roofs of dinosaurs, pseudosuchians, and other reptiles [12]. The data did not support the hypothesis that the fossa was muscular, due to a complete lack of osteological correlates reflective of muscle attachment. The data inferred that the frontoparietal fossa contained a large vascular structure and adipose tissue. Also, the data suggested that the anatomy of non-avian dinosaurs could support significant vascular devices and/or vascular integumentary structures on their skull roofs [12].

Cranial kinesis in dinosaurs (streptostyly, pleurokinesis, and prokinesis) can be inferred from the analysis of the relevant musculoskeletal structures (like the synovial otic joints, synovial basal joints, protractor muscles, and permissive kinematic linkages) and comparison with extant diapsids [13]. The analysis can give an insight into feeding.

Analysis of craniodental biomechanical characteristics can provide information on the bite force and cranial robustness as well as the feeding abilities (*i.e.*, consumption of harder or softer food) of the dinosaur [14].

The posterior part of the cranium is also the area where the neck muscles connect and join the head with the neck. Detailed osteological studies of this area are provided in the literature, with the head musculature of the animal reproduced for a variety of animals in [14] [15] [16] [17].

To model the head more accurately, dimensional finite element analysis is used. The mechanical performance during biting and frontal butting can then be assessed. This technique is an effective tool that provides a good understanding of the cranial functional morphology. Such analyses can show the stress levels on the cranium, particularly on the braincase, during biting. The finite element analysis can also provide quantitative evidence suggesting the amount of forces that could be withstood at high velocity impacts and rapid frontal blows during agonistic encounters [18] [19]. Multibody dynamics models enable testing of hypotheses about an animal's feeding behavior, and show the influence of various anatomical parameters. In this context computed tomography (CT) scans can provide the model, while various properties (for bone, soft tissue, air spaces, etc.) can be attributed to studying the musculoskeletal dynamics [17].

To study the head of a dinosaur in detail, other methods utilize endocasts generated by computed tomography and three-dimensional (3D) rendering and visualization software. In this way, the nasal cavity can be constructed and its function studied, while the shape and size of the inner ear can reveal the hearing abilities and frequency ranges [20] [21] [22]. Additionally, the size of the various parts of the brain and the associated thickness of the nerves in comparison to extant animals and other dinosaur kinds can point to relevant functions. For instance, the size of the optic lobes can show the optic abilities of the animal, and the olfactory bulb size can indicate if the odor detection was of particular importance—for example in Tyrannosaurs [23] [24].

The goal of the current study is to show the reconstruction of a dinosaur's head. To achieve an accurate result, all features and functions of the head need to be studied through all methods available in the literature, as mentioned above.

2. Methods and Materials

In any animal reconstruction, the head that houses all the major senses of the animal and, also, important functions (such as breathing, and other) performed therein, must be studied in great detail. This is exactly the goal of the current study that deals with the head reconstruction of dinosaurs, presenting as a worked example the detailed reconstruction of the head of Amargasaurus.

This is done through presenting important information from paleontological studies found in the literature related to dinosaurs' head. A review of the available literature concerning the head features, with emphasis given on sauropods and Amargasaurus is performed. Every relevant topic concludes with the details concerning the steps taken for the reconstruction of the Amargasaurus head. In particular, to keep the paper handy and informative, the focus is on knowledge found in basic books of general Paleontology, and—for updates—in relevant journal articles. For offering further information to the reader, physical evidence from museums and open access scientific articles, freely available in the Web, are also included.

Many questions in Paleontology remain open, as information on many topics in the literature is questioned and there is no consensus. In such cases the main opinions are discussed in the paper. It is important to note that uncertainties about paleontological issues are resolved, with new information coming to light along with new findings and new tools and methods.

For the actual reconstruction of the dinosaur's head performed for the purposes of this study, the materials used are: wire rods, wire mesh, screed, various molds, paint, etc.

Thus, the rest of the paper is organized as follows. The skull bones of dinosaurs, and especially Amargasaurus, are addressed in Section 3, while the head musculature of dinosaurs is examined in Section 4. The details of the head of dinosaurs, including the nostrils, cheeks and lips, teeth, soft issue of palate, tongue and hyoid bone, ears, eyes, skin type and color, are presented in Section 5. Section 6 deals with the reconstruction procedure and details of processes. We conclude with Section 7.

3. The Skull

In any animal reconstruction, the head appearance is formed by the shape of its skull. The skull is the bone structure to which all the soft biological material of the head is attached. It is divided into 1) the cranium, which is the rigid upper portion that connects to the neck and includes the upper jaw, and 2) the mandible or lower jaw [1]. The cranium and mandible are composed of smaller bones. Also, in the skull there are some natural openings called the fenestra in anatomy (**Figure 1**).

3.1. Skull Remains of Amargasaurus

The procedure for the head reconstruction to be followed is similar for all animals. Firstly, all available information in the literature must be collected studied and compared in order to reach a sound decision on how to proceed. As an example, we present below the literature concerning the skull of Amargasaurus. The skull remains of Amargasaurus are described by Salgado and Bonaparte

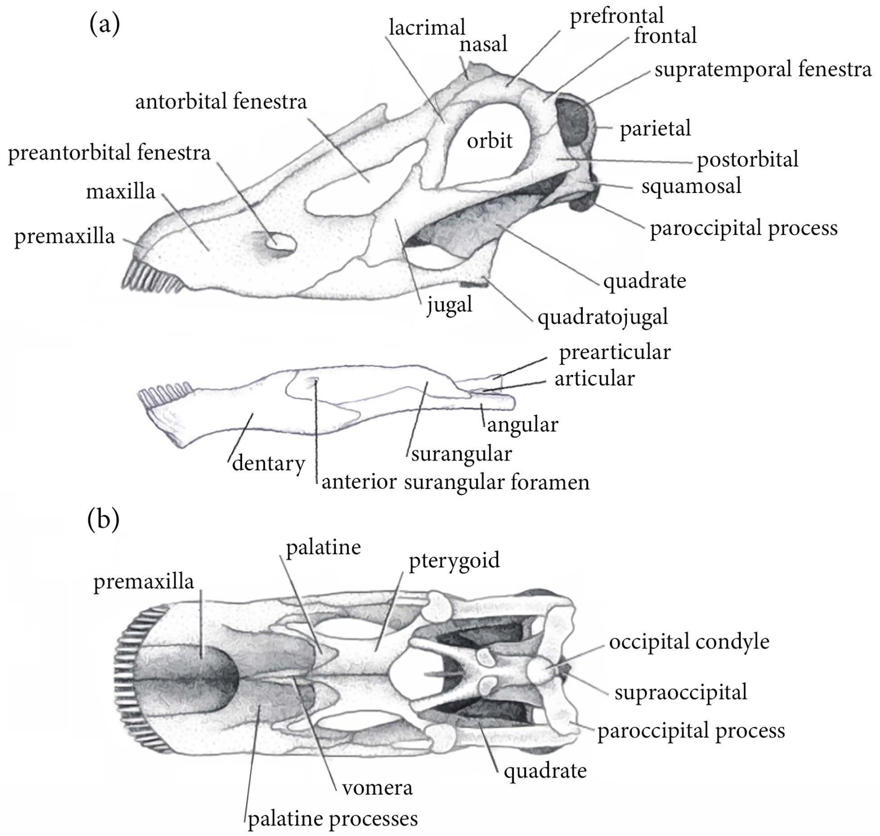


Figure 1. Diplodocus skull in lateral view (a) and cranium in ventral view (b) (see also [25] [26]).

[27], where Amargasaurus is identified as belonging to the family of dicraeosauridae, being comparable in size to Dicraeosaurus hansemanni. The preserved portion of the skull includes the temporal region and basicranium (**Figure 2**). The temporal region is complete, except for the ventral border of the infratemporal fenestra. The narial region is well preserved, with the prefrontals and frontals framing the opening. The nasals are missing. The braincase is intact up to the parasphenoid. The skull lacks the whole rostral and mandibular parts and no teeth were found.

Salgado and Calvo [28] attempted a preliminary analysis of the characteristics of the preserved skulls of Dicraeosaurus and Amargasaurus in order to recognize the derived cranial features that partly identify the group. They found some basic similarities with the skull of Diplodocus and proceeded to reconstruct the skull of Amargasaurus, with a length of 38 cm, as shown in **Figure 3(a)**.

The skull of Amargasaurus was also reconstructed by Novas [29], who identified the surviving cranium bones. This reconstruction does not differ from Salgado and Calvo [28].

Schwarz-Wings [30] mentions that dicraeosaurid sauropods skull remains are known only from Dicraeosaurus hansemanni (two braincases, several pieces of

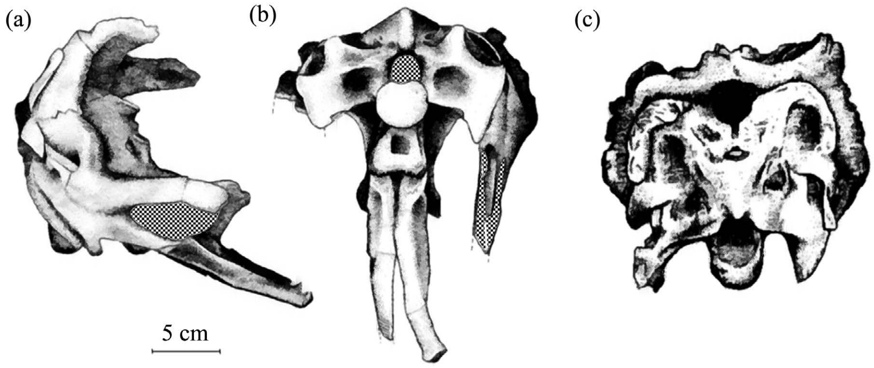


Figure 2. Amargasaurus cazaui. (a) Lateral view, (b) posterior, and (c) dorsal view of the preserved portion of the cranium (redrawn from [27]).

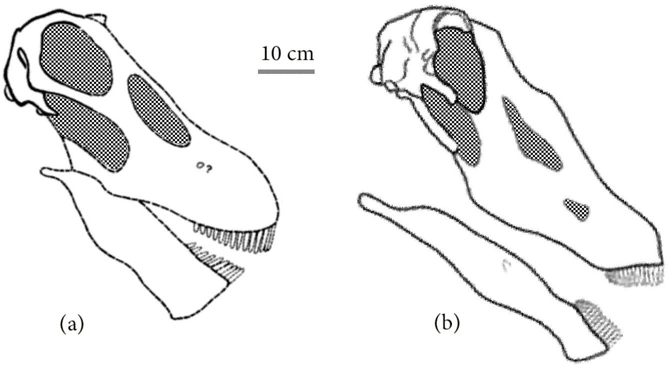


Figure 3. (a) Reconstruction of the skull of Amargasaurus by Salgado and Calvo [28] compared to (b) the reconstruction of Carabajal *et al.* [32], redrawn to the same scale for comparison.

the rostral part of the skull and additional isolated bones) and Amargasaurus cazaui (one braincase). A reconstruction of the skull of Dicraeosaurus hansemanni was given by Janensch [31], who then had only limited skull material of sauropods. The discoveries of many other sauropod skulls, *i.e.*, the Amargasaurus braincase, resulted in a more recent skull reconstruction of Dicraeosaurus. The new reconstruction changes the external appearance by little but suggests an inclination of the head position of about 65˚ downward from the horizontal instead of the 27˚ shown in Janensch's reconstruction. This Dicraeosaurus skull reconstruction may also have some implications for Amargasaurus.

Carabajal *et al.* [32] performed a CT scanning of the braincase of Amargasaurus cazaui to study the neurocranial material. They reconstructed the endocranium and the inner ear digitally in three-dimensions (3D). Based on a horizontal position of the lateral semicircular canal, they suggested that the head was held with the muzzle pointing downward at an angle of about 65˚ relative to the horizontal. This neck and head position was supported by the morphology of the atlas and axis and the reconstruction of the osteological neutral pose of the neck. The evidence presented for the skull and neck position of Amargasaurus fits with a mid-height food-gathering strategy. In alert position, the neck was directed upward in a very smooth s-shape and the head at around 270 cm from the floor with the lateral semicircular canal in a horizontal position. In osteological neutral position, the neck was directed downwards with the tooth row at around 80 cm from the floor and a rather straight neck. The skull reconstruction of this study is presented in **Figure 3(b)**.

Carabajal *et al.* [32] also observe that a major problem exists in the neural spines of the fourth and seventh cervicals, which are strongly inclined posteriorly and overlap the neural spines of the fifth and eighth cervicals respectively, which are themselves vertically oriented. As the authors suggest, the inclination of these spines is the result of postmortem deformation and restoration during specimen preparation. Therefore, in their restoration they present a vertical orientation of the deformed spines.

One can gain insights of the form and dimensions of the skull of Amargasaurus not only from the various studies presented above but also from reconstructions mounted in natural history museums. Two such reconstructions are displayed in [33] and [34], as presented in **Figure 4**. Obviously, there are differences, especially in the shape of the lower jaw.

Whitlock [35] examined the hypothesis that snout shape (square vs. round) and dental microwear are relevant to various browsing behaviors. The results show that the narrow snouts of Dicraeosaurus, Suuwassea and Tornieria, and the coarse scratches and gouges on the teeth of Dicraeosaurus, suggest mid-height selective browsing in these taxa. This could well apply for Amargasaurus, since it belongs to the same family (dicraeosauridae) as Dicraeosaurus. A comparison of the form of the snout of Dicraeosaurus skull to those reconstructed and displayed in exibitions [33] and [34] are shown in **Figure 5**.

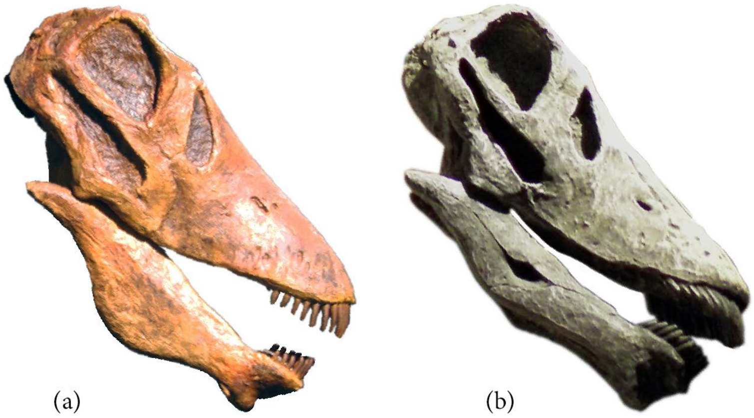

(a) (b)

Figure 4. Skull reconstructions of Amargasaurus displayed in (a) the Victoria Museum, Melbourne, Australia [34] and (b) the Victoria Memorial Museum of Ottawa in 2016 [34] (not to scale). Observe the difference in the shape of the lower jaw.

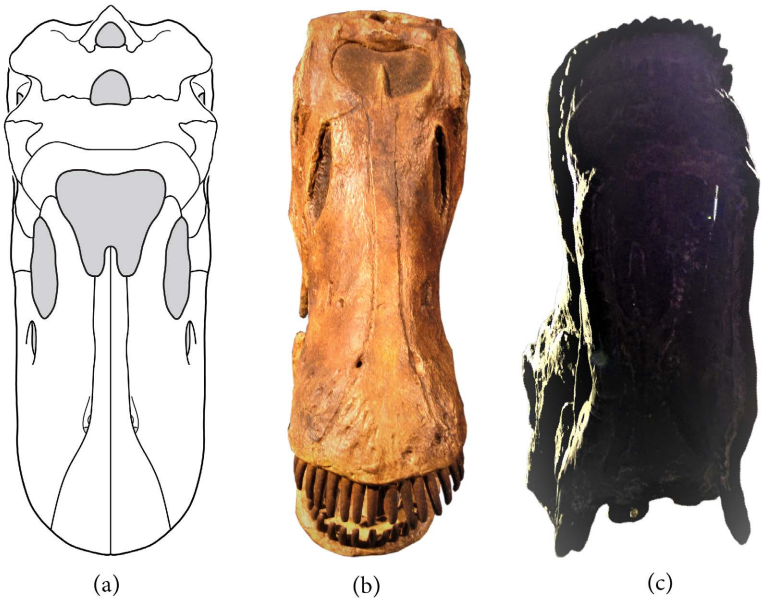
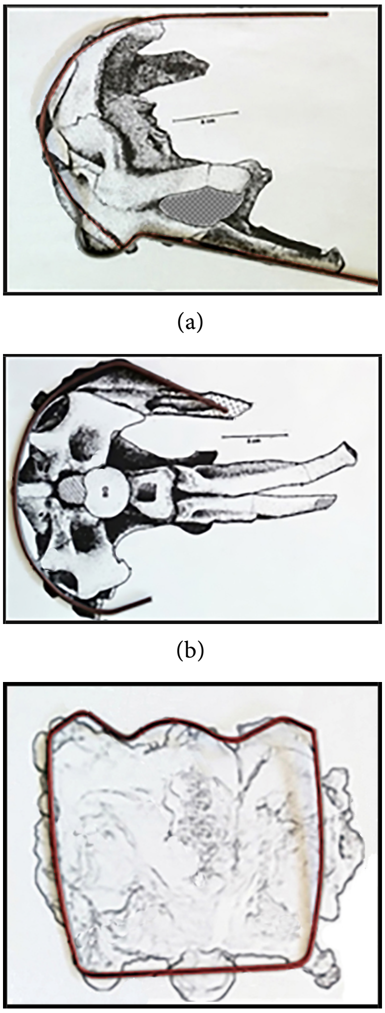

(a) (b) (c)

Figure 5. Comparison of snout shape between (a) The reconstruction of Dicraeosaurus skull by Whitlock [35], and the skull reconstructions as displayed in [33] in dorsal view and in [34] in ventral view.

3.2. Reconstruction of the Head

With the above in mind, a reasonably accurate construction can be accomplished. One can therefore start with known dimensions and shapes of **Figure 2** to construct the preserved portion of the skull, as shown in **Figure 6** and **Figure 7**, using 4 mm welded mild steel rods.

The same method of construction is followed for the remaining part of the head considering the dimensions of the reconstructions of **Figure 3(b)**. The rod wire head is then covered with a fine wire mesh needed to hold the plaster on which all the details of the flesh will be formed. The complete reconstruction of the head reinforcement is shown in **Figure 8**.



(a)

(b)

(c)

Figure 6. Working from the actual 1:1 drawings; 4 mm steel wire rods are bent over the appropriate drawing view to acquire the shape of the skull; (a) Lateral, (b) posterior, and (c) dorsal view.

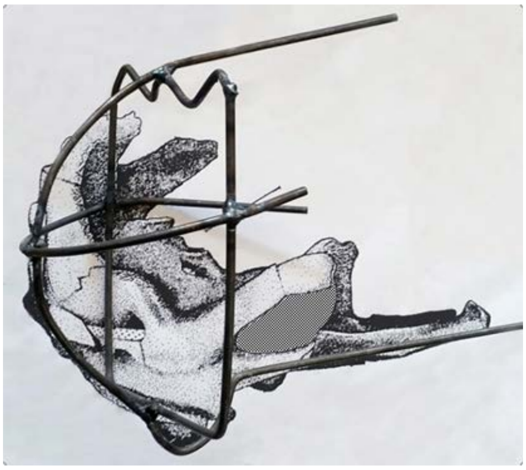
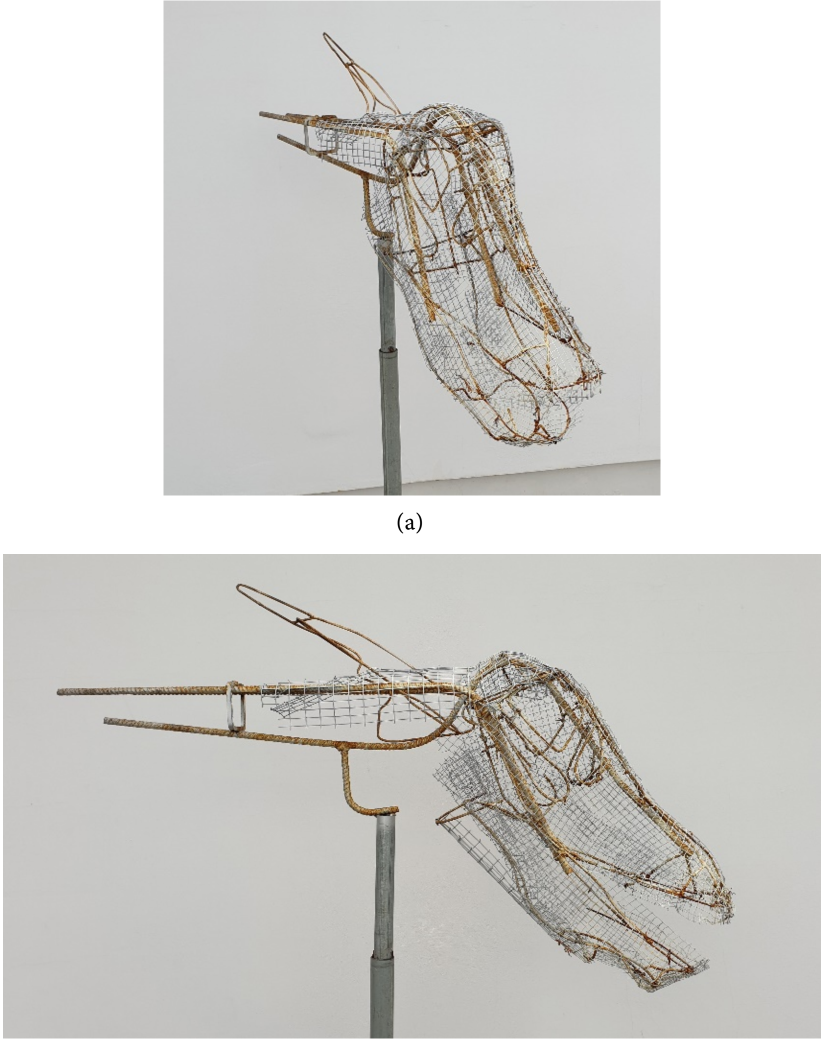


Figure 7. The shaped wires shown in **Figure 6** are welded together to acquire the three-dimensional shape of the preserved skull.



(a)

(b)

Figure 8. Welded rods forming the shape of the head covered with fine wire mesh to hold the plaster cover.

4. Head Musculature

Dinosaurs evolved a great diversity of cranial forms adapted to a variety of feeding (and other) behaviors. Transformations in head shape directly affect the reconstruction of muscles, and other important soft tissues of the head, rendering reconstructions not straightforward. Holliday [11] reconstructed, among others, the jaw muscles of a number of dinosaurs, after examining closely their living relatives, namely birds and crocodylians. The jaw muscles attach to the jaw on one side and on the cranium on the other side. Two of these reconstructions are shown in **Figure 9**, that of (a) Diplodocus (CM 3452) and (b) Majungasaurus (FMNH PR2100).

More cranial musculature reconstructions of ornithischian and herbivorous dinosaurs can be found in [15] and [36], and for theropod dinosaurs in [37] and [38].

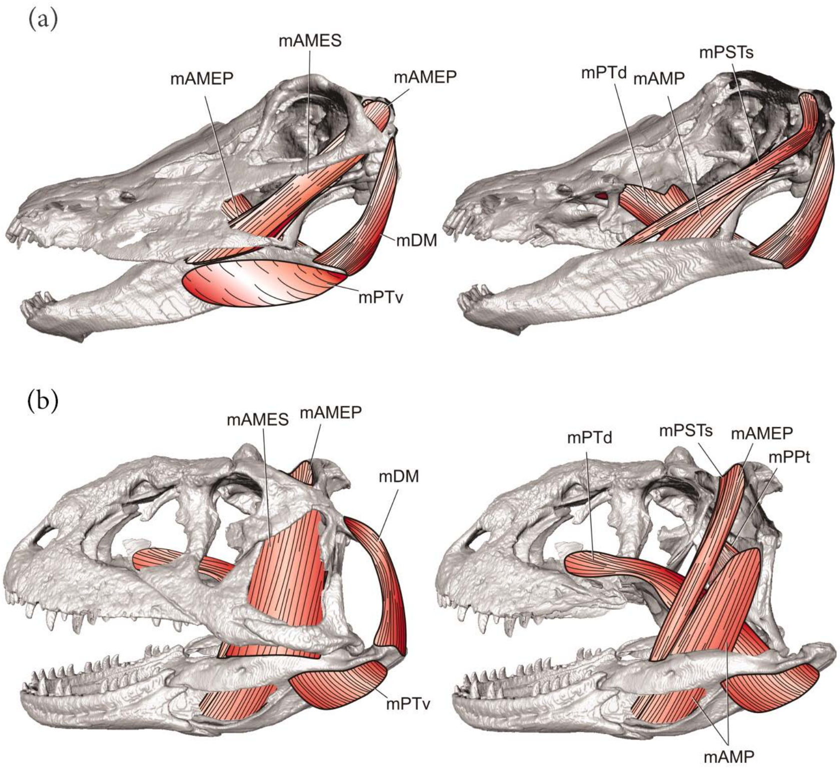


Figure 9. Jaw muscle anatomy in lateral view [11]. Left: superficial muscles; right: deeper muscles. (a) Diplodocus (CM 3452) and (b) Majungasaurus (FMNH PR2100). For abbreviations, see **Table 1**.

A good understanding on how the musculature reconstruction should appear in the mouth can be gained by observing the musculature of alligator mississippiensis in rostral and in caudal view [39] indicated in **Figure 10** and the 3D reconstruction of soft tissues of the bird Buteo buteo [40] indicated in **Figure 11**.

A rudimentary reconstruction of the jaw musculature of Amargasaurus cazaui was prepared by Salgado and Calvo [28], showing similar musculature with that of Diplodocus in **Figure 9**. These reconstructions mostly define the external shape of the head of Amargasaurus cazaui, since the rest of the head was covered with skin fitting directly on the skull bone. As Paul [41] ascertains, dinosaurs, like reptiles and birds, lacked facial muscles, so the skin was directly appressed to the skull. The skin covering the large openings in front of the orbits of many dinosaurs probably gently bulged outward. Jaw muscles likewise bulged gently out of the skull openings toward the eye sockets. Thus, dramatic reconstructions showing a depression of the skin covering the large openings in front of the orbits are not physical as such appearance shows underfed and crummy animals that are weak or sick in nature.

The insertion areas of the craniocervical musculature are present at the posterior part of the skull. This group of muscles connects the head to the neck and makes the head move relative to the neck. A study presenting the insertion areas of the craniocervical musculature of Diplodocus and Camarasaurus was performed by Button *et al.* [14], as shown in **Figure 12**.

Table 1. Anatomical abbreviations used in Figures 9-13.

Figures 9-11	Muscle (m.)	Figure 12	Muscle (m.)	Figure 13	Muscle (m.)
m.	muscle	m.c.	m. complexus	m. BC	m. biventer cervicis
mAMEM	m. adductor mandibulae externus medialis	m.i.c.	m. iliocastalis capitis	m. CPX	m. complexus
mAMEP	m. adductor mandibulae externus profundus	m.l.c.p.	m. longissimus capitis profundus	m. FC	m. flexor colli
mAMES	m. adductor mandibulae externus superficialis	m.l.c.s.	m. longissimus capitis superficialis	m. HY	m. hypoglossus
mAMP	m. adductor mandibulae posterior	m.r.c.v.	m. rectis capitis ventralis	m. IS	m. interspinales
mDM	m. depressor mandibulae	m.s.c.	m. splenius capitis	m. LCD	m. longus colli dorsalis
mIRA	m. intramandibularis	m.t.c.	m. transversospinalis capitus	m. LCV	m. longus colli ventralis
mPSTp	m. pseudotemporalis profunduis			m. PTv	m. pterygoideus ventralis
mPSTs	m. pseudotemporalis superificialis			m. RCd	m. rectus capitis dorsalis
mPTd	m. pterygoideus dorsalis			m. RCl	m. rectus capitis lateralis
mPTv	m. pterygoideus ventralis			m. RCv	m. rectus capitis ventralis
				m. SCm	m. splenius capitis medialis
				m. SCl	m. splenius capitis lateralis

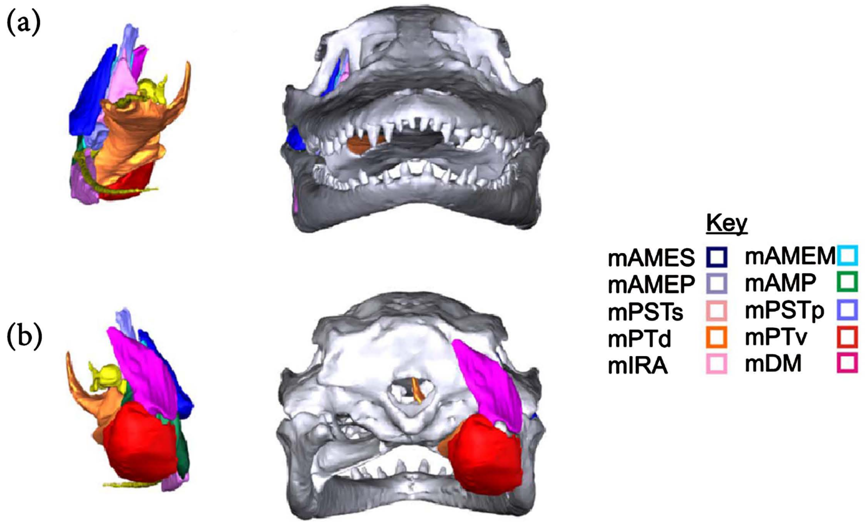


Figure 10. Musculature of alligator mississippiensis in (a) rostral and (b) caudal view (modified from [39]). For abbreviations see Table 1.

The way the craniocervical musculature should appear in a reconstruction, is again demonstrated in crocodilians and birds. As an example, the cervical musculature of the bird Buteo buteo [40] is shown in Figure 13 in (a) transverse and (b) sagittal section through the neck and skull.

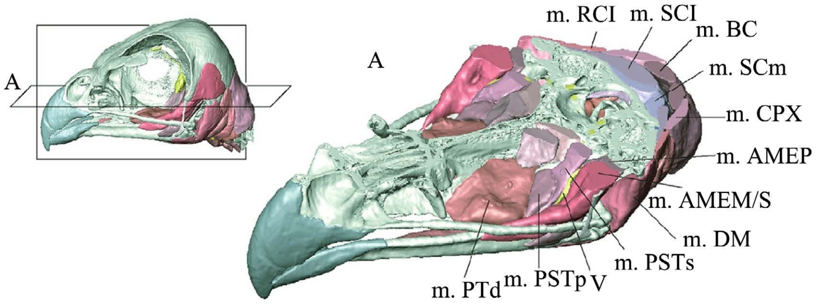


Figure 11. 3D reconstruction of soft tissues of the bird Buteo buteo in horizontal cross-section (modified from [39]). For abbreviations see **Table 1**.

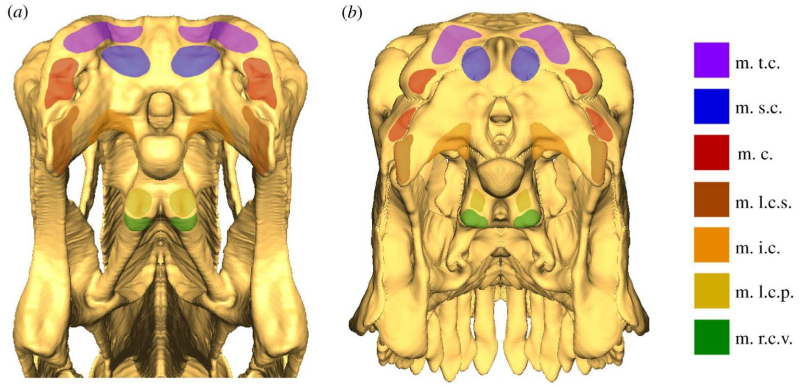


Figure 12. Posterior view of the skull models of (a) Diplodocus and (b) Camarasaurus, demonstrating the insertion areas of the craniocervical musculature for each (modified from [14]) (Skulls not to scale, for abbreviations see **Table 1**).

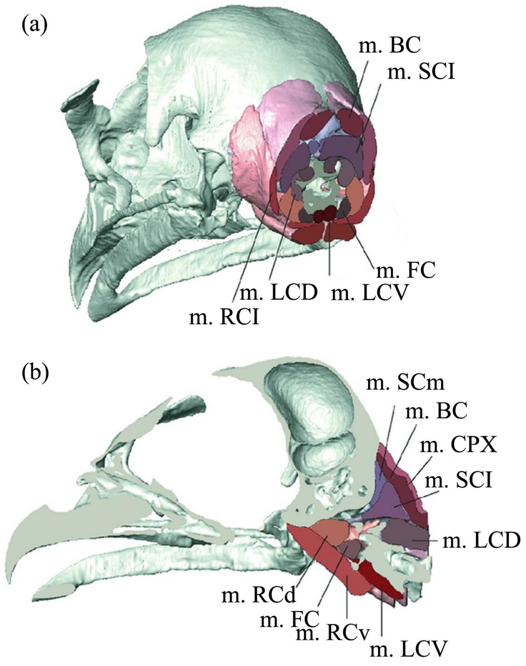


Figure 13. Cervical musculature of the bird Buteo buteo with (a) transverse and (b) sagittal section through the neck and skull (modified from [36]). For abbreviations, see **Table 1**.

5. Details of the Head

Scientists interpret different details of the animal head in a way to fit the functions of the head during life. The served functions depend on the physiology of the animal, its habits, and the environment in which the animal lived. Such is the case of sauropods, which for most of the 20th century were considered aquatic or even near-shore marine animals. This view influenced all hypotheses proposed to explain some head details and the habits of sauropods.

Coombs [42] acknowledges that sauropod natural history was sometimes controversial. From the beginning of their discovery – as above mentioned –, sauropods were considered amphibious. Their large bony nostrils and position could indicate either aquatic or terrestrial habits. Sauropods were vegetarians, but their long necks could have been used for browsing in trees, on long streambanks or underwater. The sauropod's anatomy is mostly unclear, but where firm morphologic interpretations are possible, they usually point to terrestrial behavior.

Of course, there are always uncertainties and questions, as for instance there are trackways consisting of "manus-only" prints that are interpreted as made by swimming sauropods [43]. Trackways also indicate that sauropods could and did wade and swim in streams, but also that sauropods sometimes dragged their tails on the ground [42].

The preserved trackways of sauropods indicate that these animals frequently walked across marine, intertidal zones and along the muddy margins of lakes. Sedimentological evidence also indicates that the muds and sands of these areas were often under water or exposed just when the animals left their impressions. The fossil remains of sauropods are known from coastal settings and are often found near, or mixed in with, fossils of marine organisms. The above indicates that sauropods could successfully walk in water and that they could associate with wet habitats (Henderson [44] and references therein).

Henderson [44] used computer modeling to investigate how the bodies of sauropods would have reacted when immersed in water. The investigation showed that the heavy sauropods were found to be exceptionally buoyant and unstable in water. Interpretations of "manus-only" trackways made by floating sauropods depend on the details of buoyancy of each species. Sauropods possessed highly pneumatized axial skeletons (see for instance [45]) and a system of thoracic and abdominal air sacs [46] reducing their density to about 80% that of water. The longer forelimbs of Brachiosaurus and Camarasaurus could have permitted them to propel themselves by poling along the bottom to produce manus-only trackways. By contrast, *Diplodocus* forelimbs would lift up well in advance of its hind limbs, allowing a maximum immersion depth for Diplodocus of just 2.4 m.

The diet of sauropods could perhaps shed more light in the discussion over whether sauropods were land or aquatic animals. A direct approach would be the study of plant remains in dinosaur coprolites. This approach is generally very difficult because specific fossilized coprolites cannot be traced in a particular plant-eating dinosaur. In the Mygatt-Moore Quarry, located in western Colorado, remains that include stegosaurs, ornithopods, ankylosaurs and sauropods (Apatosaurus and Camarasaurus) and Allosaurus were found. The Mygatt-Moore Quarry is interpreted as an attritional accumulation of abundant dinosaur remains at a permanent water hole. This interpretation is based on the abundance of carbonaceous plant material together with the presence of freshwater snails and fish [47]. In the Morrison Formation, of this quarry, fossils of possible coprolitic origin contain recognizable plant members that include gymnosperm seeds, fern sporangia, cycadophyte laminae and petioles, and conifer wood and cuticle. The nodules were almost certainly produced by herbivorous dinosaurs as these were the only large herbivores found in the Jurassic sediments [48]. Additionally, a locality of the Late Cretaceous in Central India has yielded a large number of coprolites attributed to titanosaurian dinosaurs (clade neosauropoda). The contained plant tissues come mostly from gymnosperms. Further analysis shows that plants of C3-type were the main diet of their producers and that gut fermentation may not have been an active mechanism in the digestion process of titanosaurs [49].

Fastovsky *et al.* [50] observe that tetrapods, which are most highly adapted for land locomotion, tend to have an erect stance that maximizes their movement efficiency on land. Tetrapods that are adapted for aquatic life, such as salamanders, extend their legs out of the body almost horizontally to aid them in swimming. Dinosaurs and mammals both have fully erect stances, which represent a full commitment to a terrestrial existence as well as to a more terrestrially-derived type of respiration. The remains of sauropods are found in a variety of environments from river floodplains to sandy deserts. Environments, such as those of the Upper Jurassic Morrison Formation in the American West, required sauropods to cope with long dry seasons during the year, forcing them to migrate in herds, when annual droughts were severe. In other places like Tendaguru in southeastern Tanzania, Glen Rose of Texas in the USA, and elsewhere, the sites were once close to the sea and the environment quite humid. Perhaps these were some of the conditions that sauropods found most pleasant. The bones of sauropods were also adapted for terrestrial life, locating the weight and strength of the skeleton where it was most needed, with denser bones in the lower parts and lighter ones in the upper parts of the skeleton.

As Bakker [51] explains, four-legged creatures first crawled out of the primordial swamps 400 million years ago. Dinosaurs appeared 200 million years after, in the land ecosystem, when the woodlands and waterways were already full of creatures. After a short geological period of 5 million years, the dinosaurs took control over all the land ecosystem, filling the roles of mega-predator and mega-herbivore. From there on, Bakker suggests that plant and dinosaur evolution worked both ways against each other. When plant-eating dinosaurs evolved more effective teeth or fermenting chambers, the plant species had to adjust or be destroyed and vice-versa. On average the record shows that plant-eating dinosaurs evolved faster than plants. Dinosaur species endured 2 to 3 million years before being replaced by a new species, but Mesozoic plants, lasted for 8 million years. Contrary to the above the Cretaceous, *Tyrannosaurus rex* was a variation of the basic form that evolved a 100 million years earlier in Late Triassic, with little difference as there was no need for change.

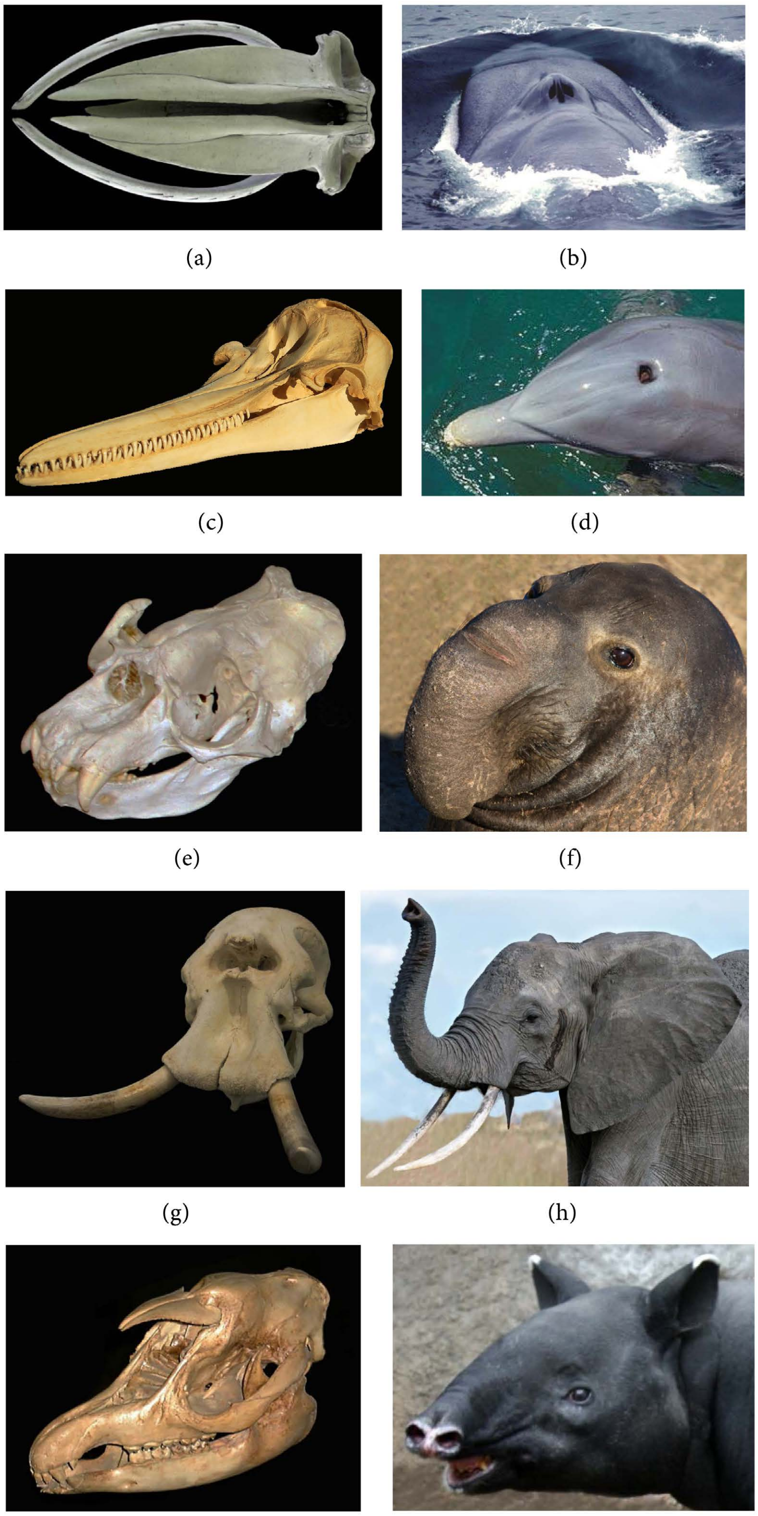
The herbivorous dinosaurs went three main periods of development: 1) *The Age of Anchisaurs*, with simple teeth, suitable for soft leaves and basic digestive system in Late Triassic and Earliest Jurassic; 2) *The Age of the High Feeders*, stegosaurs and brontosaurs, when the gigantic Diplodocus, Brachiosaurus and Brontosaurus evolved in Mid and Late Jurassic; 3) *The Age of the Low Feeders*, when all the terrestrial habitats were teeming with beaked dinosaurs that fed close to the ground in Cretaceous. Flowering plants first appeared in the Early Cretaceous just after the extinctions that occurred at the end of the age of the high feeders and when the low feeders appeared. Low shrubs and seedlings would now be driven to extinction as the nature of plant eating changed. In this context the plants reacted to the intense low cropping by fast spreading, fast growing, and fast reproduction that could be achieved by the early angiosperms. Conifers, cycadeoids and other non-angiosperms could not withstand the assaults of the new Cretaceous herbivores and, where this vegetation was thinned out, the very first flowering plants prevailed.

Seymour [52], on the other hand, brings into the discussion the cardiovascular physiology of dinosaurs and the blood pressure problem in tall, longnecked animals. He proposes that one attractive possibility that could solve the problem is that longnecked dinosaurs could have floated in the water with the lungs, neck, and nostrils at the surface, where lung inflation would not be a problem. The sauropod neck could be used to reach deep aquatic vegetation without any problems involving blood pressure. This lifestyle would be consistent with the limited upward flexion of sauropod necks, but with adequate downward flexion, down well below the level of the feet.

Having in mind the above, and as Christiansen [53] (see also references therein) mentions, the present belief is that sauropods were primarily terrestrial animals, confirmed by studies of their anatomy and taphonomy, abundant trackway records and the fact that vegetarian diet is consistent with the skull shapes, tooth forms, and the huge abdominal regions of their bodies, as well as the widespread occurrence of gastroliths [1] in the digging sites.

5.1. Nostrils

The above discussion about the details of the head affects the way that the bony nostril openings of Diplodocus, located in the forehead above the eyes, is explained. In his book, Bakker [51] explains that this position is a typical place for whale-like nostrils, the blowholes (**Figure 14(a)** and **Figure 14(b)**). Nostrils in this position give an obvious advantage to a swimming air breathing animal. It can inhale and exhale from the blowhole without the danger of water rushing



(a) (b)

(c) (d)

(e) (f)

(g) (h)

(i) (j)

Figure 14. Skulls showing bony nostrils and muscle attachments of living sea and land animals with blowholes and proboscides. (a) blue whale skull, (b) blowhole of a blue whale [54], (c) dolphin skull [55], (d) blowhole of a dolphin, (e) sea elephant skull, (f) sea elephant skull showing massive nostrils, (g) elephant skull, (h) african elephant proboscis, (i) tapir skull, (j) tapir short proboscis.

into its nostrils when keeping the head at or below water level. Therefore, if one assumes that diplodocus was spending time in water for feeding, it could simultaneously breathe and search around in the water for food.

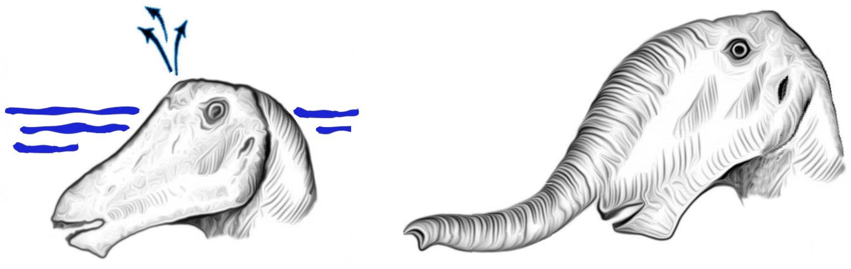
Conversely, if one believes that Diplodocus was entirely a land feeding animal then a comparison to extant mammals could suggest the presence of a proboscis. Diplodocus nostrils are positioned in the same place as the elephant's (**Figure 14(g)** and **Figure 14(h)**). A much smaller trunk in length is that of tapirs shown in **Figure 14(i)** and **Figure 14(j)**. A trunk is a highly specialized set of upper lip muscles that surround the fleshy nostrils and wrap around to form a mobile muscular tube with the fleshy nostril carried at the end of the tube. Proboscides, on the other hand, have muscle attachments on the skull bones around the nostrils, which Bakker could not find in the Diplodocus skull ([51], p. 143).

The appearance of the head of Diplodocus could thus be with or without a trunk, as indicated in **Figure 15**.

Knoll *et al.* [56] examined the possibility that Diplodocus had a trunk. They observed that in elephants, a large facial nerve emerges from the brain and that a branch of this nerve and a branch of the trigeminal nerve unite to form the proboscidial nerve. The proboscidial nerve controls the muscles of the complex motor system of the trunk. By examining the anatomy of the head and an endocranial cast, they found a relatively small facial nerve in Diplodocus (cranial nerve VII), which indicates that there is no evidence for the presence of an elephant-like proboscis.

Knoll *et al.* [56] also examined the case of Camarasaurus and Brachiosaurus, concluding that a proboscis, at least a large muscular one, was not present for Camarasaurus but was probably present for Brachiosaurus. Although not convincingly founded, this hypothesis remains acceptable for Brachiosaurus.

Furthermore, Bakker [51] suggests that alternative explanations for the locations of *Diplodocus* nostrils should also be explored, as they may have been adaptations for tooting and honking. The Diplodocus nasal chamber is roofed over by the snout bones (**Figure 16**). In this case the sound produced would be brassier than that of a Camarasaur or Brachiosaur that had huge bony nostrils probably covered with fleshy chambers.



(a) (b)

Figure 15. Suggestions as for the uncommon position of the bony nostrils of Diplodocus, for further study. (a) Nostrils for aquatic life, (b) an elephant like proboscis (after Bakker [51]).

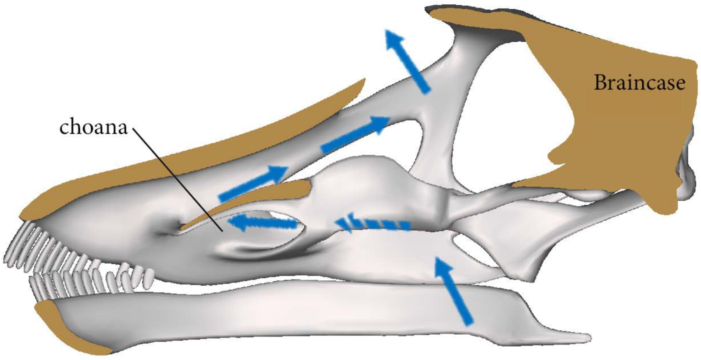


Figure 16. Sagittal section of diplodocus skull, showing the air passage through the right choana (internal nostril).

One such animal that uses its nose for producing sounds is the sea elephant with a proboscis increasing in size with age and body size independently (**Figure 14(e)** and **Figure 14(f)**. This animal spends most of its life in sea diving, returning to land to breed and molt. Sea elephant proboscis size is sexually attracting and is functionally related to the emission of agonistic vocalizations [57].

Concluding the discussion on nostrils, one could mention the work of Witmer [58] who has studied the location of the external opening in the skin of the bony nostrils. He has found that in all studied cases of extant dinosaur relatives, the fleshy nostril is located near the front end of the body (rostrally) within the bony nostril, in most cases being situated toward the lower surface of an animal (ventrally), as well. His findings have changed the traditional way of placing the fleshy nostril of dinosaurs at the back of the bony opening. The corrected position gives the advantage of placing the full length of the narial apparatus within the airstream, allowing it to function physiologically in a better manner. Moreover, a rostroventrally placed nostril is well disposed to collect odorants around the mouth (**Figure 17**).

Concerning sauropod dinosaurs, the conventional nostril position was high on the forehead so as to enable the animal to breathe when wading in water. This position was dictated by the habits of the animals believed to dwell primarily in the water. Since today it is believed that sauropods spent most of their time on land, Witmer [58]—based on the study of modern-day animals—found evidence that the nostrils of dinosaurs actually were parked in front. The new look of Diplodocus based on the above study is shown in **Figure 18**.

Amargasaurus Nostrils

In the case of Amargasaurus, there was no elephant-like proboscis. This is established by the study of Carabajal *et al.* [32] who examined the Amargasaurus cranial endocast and found that the cranial nerve VII, compared to other cranial nerves, is of small diameter with an unusually long canal through the bone.

The Amargasaurus bony nostril openings are located in the forehead, above the eyes as for Diplodocus. Therefore, the new position of the nostrils as for Diplodocus will be adopted.


(a) (b)

Figure 17. Head of Ceratosaur (a) restored in the traditional way, and (b) with the rostroventrally placed nostril opening, giving an obvious physiological advantage, as suggested by Witmer [58].


(a) (b)

Figure 18. The position of the nostrils on Diplodocus (a) in the traditional view with the nostril located more to the rear of the head, and (b) new look as suggested by Witmer [58].

5.2. Cheeks and Lips

The appearance of lips of extinct animals is still debated. Many extinct animals had lizard-like lips, with thin muscular bands running along the inner edges of their lips that could just flare the lips to expose the teeth. The attachment site of this type of lips is a lightly beveled edge on the fossil gum-line along the outer edge of the upper and lower jaw. A series of holes (foramina canal openings) in the jawbones where the lips would lie in life, allowed blood vessels to nutriate the lips and nerve fibers to carry sensory signals to the brain. As Bakker [51] mentions, Massospondylus, an older relative of Diplodocus, had lizard lips. Allosaurus, Ceratosaurus and the tyrannosaurs retained this lizard-lip form in later periods (**Figure 19**).

However, as Bakker [51] observes, Diplodocus lips were not lizard-like because the gum lines along its jawbones were not beveled, and the holes for blood vessels and nerves did not make an evenly spaced row as in lizards (**Figure 20**). Diplodocus lips were different from those of crocodiles as well. Crocodile facial skin is thin and tightly fixed to the skull bones, so there are no movable lips along the gum line. The skull bone beneath the thin scaly lip tissue is pitted and

Figure 19. Tyrannosaurus skull with a series of holes in the upper and lower jawbone to allow the blood vessels to pass for nutrition and nerve fibers to carry sensory signals to the brain [59].

Figure 20. Diplodocus jawbones. The gum lines along Diplodocus jawbones were not beveled, and the holes for blood vessels and nerves did not make an evenly spaced row as in lizards [60].

grooved so that the horny skin can attach very firmly to the bone surface, but contrary to crocodile bone Diplodocus jawbones are quite smooth.

Concerning cheeks, Upchurch and Barrett [61] mention that sauropods did not have a muscular cheek and this is indicated by the absence of ridges on the mandible and upper jaw (buccal emargination). This would allow a wider gape and more amount of food to be collected in each mouthful. On the other hand, some food would be lost through the sides every time foliage was chopped.

In addition to the above, Morhardt [62] examined the hypothesis that foramina density is correlated to some degree to extra-oral structures. Foramina canal openings can be observed as holes in the external bone surfaces and exist in varying amounts among the major taxonomic groups. Data analysis showed that the number of extra-oral foramina is statistically correlated with the presence or absence of extra-oral tissues. The data suggested that a mean count of over 100 foramina for a single bone is indicative of the absence of a significant extra-oral tissue covering (e.g., crocodilians). Those organisms that fall into a range above 50 appear to either have no extra-oral soft tissue (bare), or hard, cornified soft tissue (beak). Compared to the rest of the sample, Ornithischian and Saurischian dinosaurs included in the study (Diplodocus as well) fall into the range of organisms that have extra-oral coverings (well below 50). The coverings would have been soft, pliable extra-oral tissues similar to "lips" or "cheeks". In this case, Bakker's [51] reconstruction in **Figure 15(a)** is correct.

Wiersma & Sander [63], in their article on Camarasaurus dental morphology, describe inter alia, the presence of gingival connective tissue in specimen SMA 0002 exhibited in the Sauriermuseum Aathal, Switzerland (**Figure 21**). This specimen was found at Howe-Stephens Quarry, Bighorn Basin, WY, USA. A slab of sediment with soft tissue impressions extending to the middle part of the teeth crowns suggests the existence of a gingival soft tissue structure that partially covers the teeth. It is also believed that the cover of gingival connective tissue is indicated by the wrinkled enamel on the crown of the teeth. In addition, the authors mention that the labial side of the gingiva may well have been covered by a keratinous beak or large scales that, together with the gingiva, held the teeth in the jaw.

Feeding mechanisms and buccal anatomy for Ornithischian Dinosaurs with a review of previous literature on the subject is given in Nabavizadeh [36]. Individual studies for specific animals are also available, such as for example the parrot-like structure and function of the psittacosaur skull referring to the buccal musculature [65].

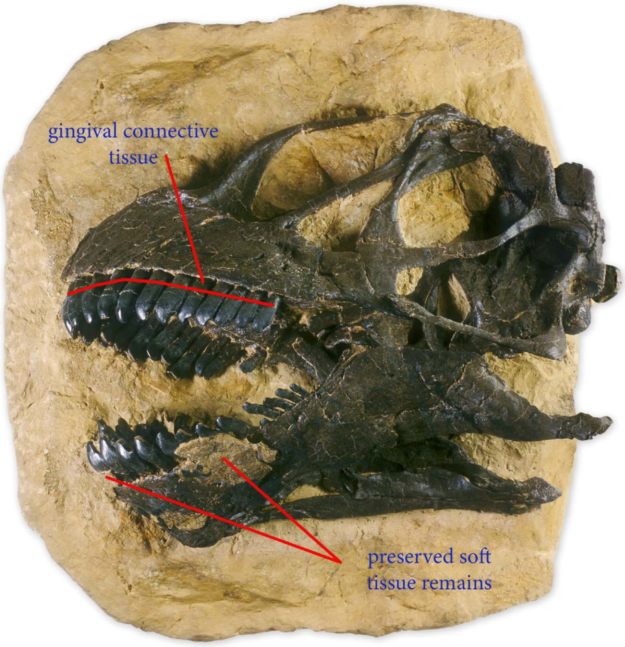


Figure 21. Camarasaurus specimen SMA 0002 exhibited in the Sauriermuseum Aathal, Switzerland. Wrinkled enamel on the crown of the teeth possibly indicates the presence of gingival connective tissue. Soft tissue remains are also present [64] (Credit: Sauriermuseum Aathal, Switzerland, Courtesy: National Science Foundation).

Amargasaurus Cheeks and Lips

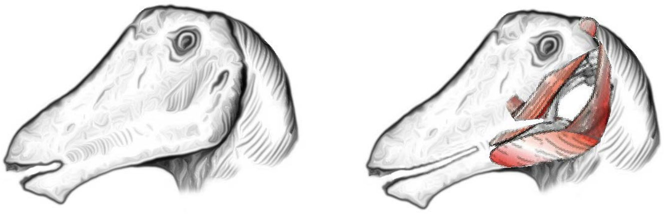
Similar to Diplodocus, the jaw of Amargasaurus can be separated into three regions, the front one that bears the teeth, the area at the back where the muscles are attached to, and an intermediate whose functional relationship to the rest of the jaw is relatively unknown. In the absence of muscular cheeks, the opening could extend closer to the muscle attachments and therefore Bakker's [51] Diplodocus restoration can be adapted to show this modification (**Figure 22**), as suggested by Upchurch and Barrett [61]. An opening extending just behind the last teeth will be adopted in the restoration.

5.3. Teeth

Teeth are typical of the function they perform in animal feeding. For this reason, they are specific in terms of their shape and size (**Figure 23**). As the interest of the current study is for the reconstruction of Amargasaurus, a review of the teeth and feeding habits of its nearest known relatives, Dicraeosaurus and Diplodocus, is presented below.

Barrett and Upchurch [69] reconstructed the jaw musculature of Diplodocus as well as the jaw movement, in order to understand its feeding mechanics. The reconstruction suggests that the lower jaw could be moved fore and aft (propaliny). This motion might allow a wider gape and might aid in foliage stripping during high browsing. The tooth wear indicates high browsing (grabbing a small branch in the mouth and moving the head downward to strip it) and low browsing (moving the head upward to strip the branch). These features imply a shift from powerful cropping of vegetation exercised by Brachiosaurus and Camarosaurus to a more precise and prolonged stripping and raking action for diplodocids and dicraeosaurids.

Another investigation of the feeding behavior of Diplodocus was performed by Young *et al.* [70]. They used biomechanical modeling with finite element analysis, to examine the performance of the Diplodocus skull in three feeding behaviors. Specifically, they modeled muscle-driven static biting, branch stripping and bark stripping. They concluded that the skull was not constructed for bark stripping due to the high evolving stresses, but that the stresses were well endured for static biting and branch stripping, indicating the feeding behavior for diplodocids.



(a) (b)

Figure 22. Restoration of Diplodocus. (a) Bakker's [51], (b) adapted to show openings extending very close to the muscle attachments, as suggested by Upchurch and Barrett [61].

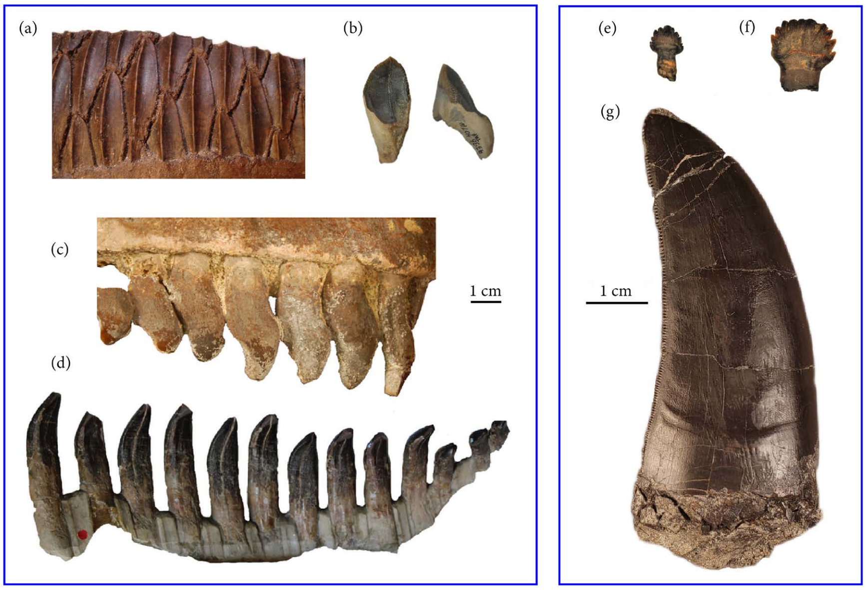


Figure 23. Various shapes and sizes of Dinosaur teeth: (a) Hadrosaurid teeth, right dentary tooth battery of the lambeosaurine Lambeosaurus lambei in lingual view [66]; (b) ceratopsid teeth, isolated right maxillary tooth in lingual (left) and mesial (right) views [66]; (c) toothrow of Camarasaurus [67]; (d) toothrow of Giraffatitan [67]; (e) ankylosaurid tooth in lingual view [66]; (f) nodosaurid tooth in lingual view [66]; 2 ceratopsid teeth [66]; (g) shed lateral tooth of *Allosaurus* with distal denticles at the left side [68].

Whitlock [35] examined the relation between the snout shape (square or round), the dental microware and the browsing behavior (*i.e.*, selective to non-selective browsing at ground height, mid-height or in the upper canopy) of diplodocoidea. Although for Amargasaurus there were no sufficient data, the study indicated that dicraeosauridae lived in forested ecosystems and were selective browsers (**Figure 24**). The closest functional analogs of sauropods in feeding are birds, whose toothless beaks likewise cannot grind the food and reduce it to small particles easy to digest. Of course, the great difference in size stops the analogy at this point.

Christiansen [53] studied the feeding mechanisms of Dicraeosaurus together with those of the sauropod dinosaurs, namely Brachiosaurus, Camarasaurus and Diplodocus. Sauropods were largely isodonts unlike mammals that have well differentiated teeth. The teeth of Dicraeosaurus were elongated and slender. In cross section, the teeth were cylindrical proximally (at the root), but distally they were broader and flatter. There were 4 premaxillary teeth – as in Diplodocus –, but in this case, there were 12 maxillary and more than 16 dentary teeth. Some large teeth were hardly worn but there were others that were heavily worn, with the wear facets of the latter, forming an angle of approximately 40˚ with their long axes, as in Diplodocus. There are great skull similarities and dental wear patterns in Diplodocus and Dicraeosaurus that point to similar habits in feeding. During feeding there was a raking motion of the jaws and the substantial wear suggests extensive contact with material sliding between the teeth. As with all

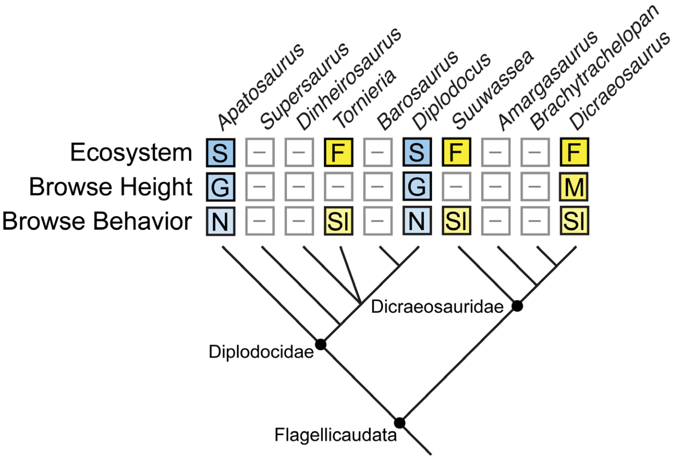


Figure 24. Phylogeny of Flagellicaudata sauropods, with ecosystem, inferred browse height, and inferred browse behavior. Data suggest that ground-height, non-selective browsing evolved in open, savanna-like environments, whereas selective, mid-height browsing was most common in diplodocoids living in closed environments dominated by mid- and upper-canopy browse. Blue tones indicate data suggestive of ground-height, non-selective browsing; yellow tones indicate data suggestive of mid-height, selective browsing. Inferences for which insufficient data exists are represented by a dash (–) within frames. Abbreviations: S, savanna type ecosystem; F, forested ecosystem; G, ground-height browser; M, mid-height browser; N, nonselective browser; Sl, selective browser (modified from [35]).

sauropods, there was hardly any oral processing of the food. The sauropod heads were designed to crop vegetation. Even Camarasaurus, whose skull was modified to cope with increased stresses in powerful bites, was not involved in true chewing, but was confined to shearing or crushing. A restored Dicraeosaurus hansemanni maxillary tooth has a total length of 63 mm, approximately 50 mm of which appears to have protruded from the jaw [53]. **Figure 25** shows (a) Dicraeosaurus hansemanni restored teeth on display at the Museum für Naturkunde, Berlin [71] and (b) Diplodocus longus teeth from Utah, USA [72].

To satisfy the feeding needs of sauropods, the teeth were used to crop massive amounts of vegetation and, hence, they were often severely worn. A quick replacement mechanism was evolved to equip sauropods with less worn teeth over their lifetimes and allow their skulls to be light. Emic [73] estimated that Diplodocus had a small volume of narrow-crowned teeth that were replaced very quickly. Tooth formation time in Diplodocus was 185 days, with the average tooth replacement rate being about one tooth every 35 days. For Nigersaurus the average tooth replacement rate was 14 - 30 days. **Figure 26** shows analogous details for neosauropoda taxa.

A method used for calculating tooth formation times and tooth replacement rate in extinct organisms is the extrapolation of the space between incremental lines in dental tissues representing daily growth (von Ebner Line Increment Width). Such a study giving details for many species (both herbivore and carnivore) is presented in [74]. An example of tooth replacement of a carnivore dinosaur is shown in **Figure 27** [75].


(a) (b)

Figure 25. Sauropod teeth. (a) Dicraeosaurus hansemanni restored teeth, on display at the Museum für Naturkunde, Berlin [71]; (b) Diplodocus longus—sauropod dinosaur teeth (DNM 974, Dinosaur National Monument, Utah, USA), Credit: James St. John [72].

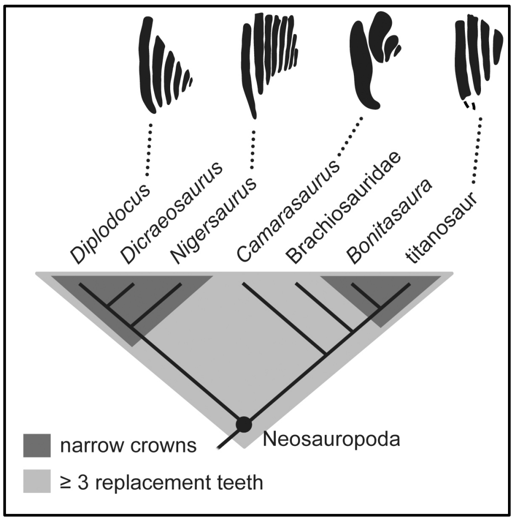


Figure 26. Cladogram of Neosauropoda showing tooth replacement rates. Light gray indicates taxa that have at least three replacement teeth at each tooth position. Dark gray shows taxa that have narrow tooth crowns. Silhouettes along the top of the cladogram show the number and size of replacement teeth in one tooth position (modified from [73]).

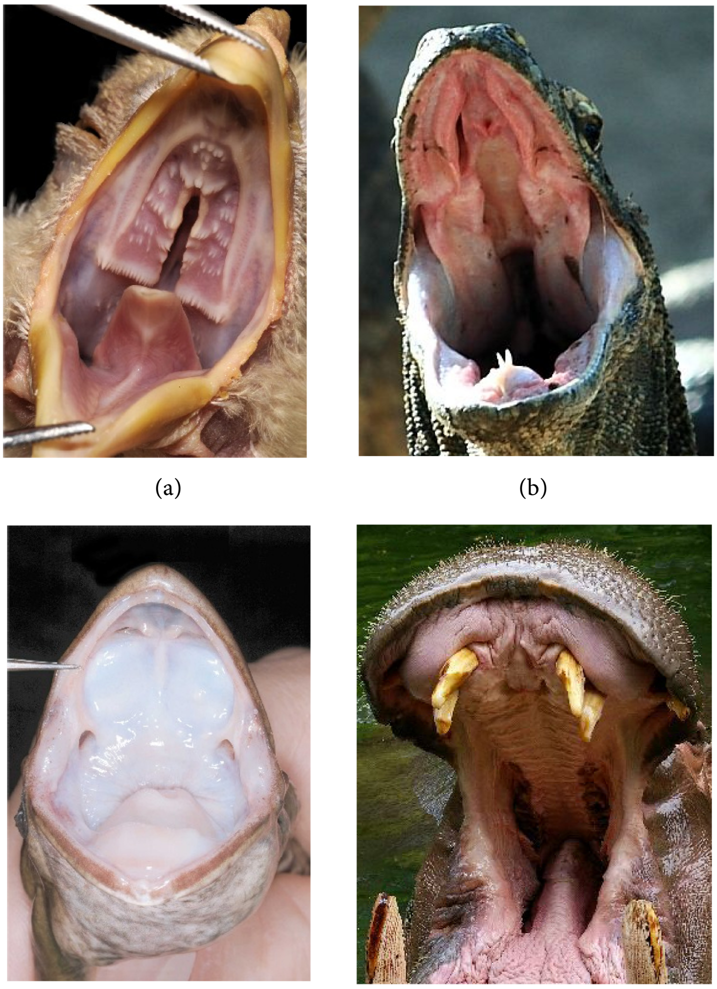
Figure 27. Tyrannosaur lower jaw showing emerging new teeth that would replace existing ones [75].

Amargasaurus Teeth

Salgado and Bonaparte [27] mention that no teeth were found at the digging site of Amargasaurus. Consequently, we refer again to the teeth of Dicraeosaurus. The teeth of Dicraeosaurus [53] were confined to the mesial edges of the jaws and placed 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. Therefore, the teeth of Amargasaurus can be similar in shape and size to those of Dicraeosaurus and Diplodocus and, hence, they can be placed in a similar way in the mouth.

5.4. The Palate Soft Tissue

The roof of the oral cavity is covered with the palate soft tissue. The palate soft tissue will appear in a reconstruction of an open mouth and, thus, needs to be studied. The palate varies in shape for different animals, but generally in the front of the mouth it is covered with ridged skin. Some forms of palates are shown in **Figure 28**.



(a) (b)

(c) (d)

Figure 28. Variations in the roof of the oral cavity: (a) Chicken [76], (b) Komodo dragon [77], (c) frog [76], (d) hippopotamus [78].

The Palate Soft Tissue of Amargasaurus

There are no detailed studies about the soft tissue covering the roof of the oral cavity in dinosaurs. However, there are studies dealing with the air passages in the cavities of the cranium, such as ankylosaurs [79], Pachycephalosaurids (**Figure 29**) [80], Lambeosaurine Hadrosaurids [81] and others, which marginally touch the subject. In the case of the Amargasaurus restoration it was chosen a view at which the teeth will cover completely the oral cavity. Therefore, a serrated skin similar to that of the hippopotamus will be adopted without any details.

5.5. The Tongue and Hyoid Bone

A wide variety of tongue shapes, sizes and features exist in the animal kingdom (**Figure 30**). The tongue is a muscular organ and is part of the lingual apparatus, which also includes cartilaginous and bony skeletal elements, muscles, salivary glands, epithelial structures, etc., and is a component of the feeding apparatus. Other elements also connect the lingual apparatus to other components of the feeding apparatus, such as the skull, jaw apparatus, and larynx.

The lingual apparatus cooperates with the jaw apparatus and the larynx in generating coordinated movements during various behaviors, such as feeding and drinking [83]. The fusion of the hyoid, a U-shaped bone, and remnants of the branchial arches form a Y-shaped bone (hyobranchium) that serves to support the tongue and its muscles and is also connected to the larynx. In general, the hyobranchium comprises a midline body (corpus hyoidei) and paired, laterally extending horns (cornua) [84].

The swan hyobranchium is shown in **Figure 31**.

The reptilian hyobranchial apparatus is partly cartilaginous and is incompletely preserved in fossils. Among non-avian dinosaurs, the elements most commonly fossilized are the usually rod-shaped first ceratobranchials and lack distinguishing anatomical landmarks. Therefore, in fossil Dinosauria the hyobranchium remains poorly understood [86].

In birds the tongue is thin, often covered with a horny layer, and is generally limited to fore–aft movement. In crocodilians the tongue is broad, fatty, and

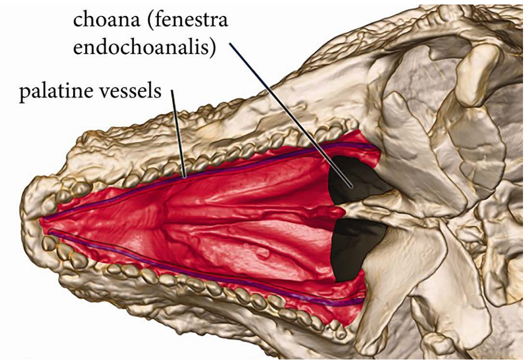


Figure 29. Stegoceras validum cranium in ventral view with restored soft palate and vasculature [80].

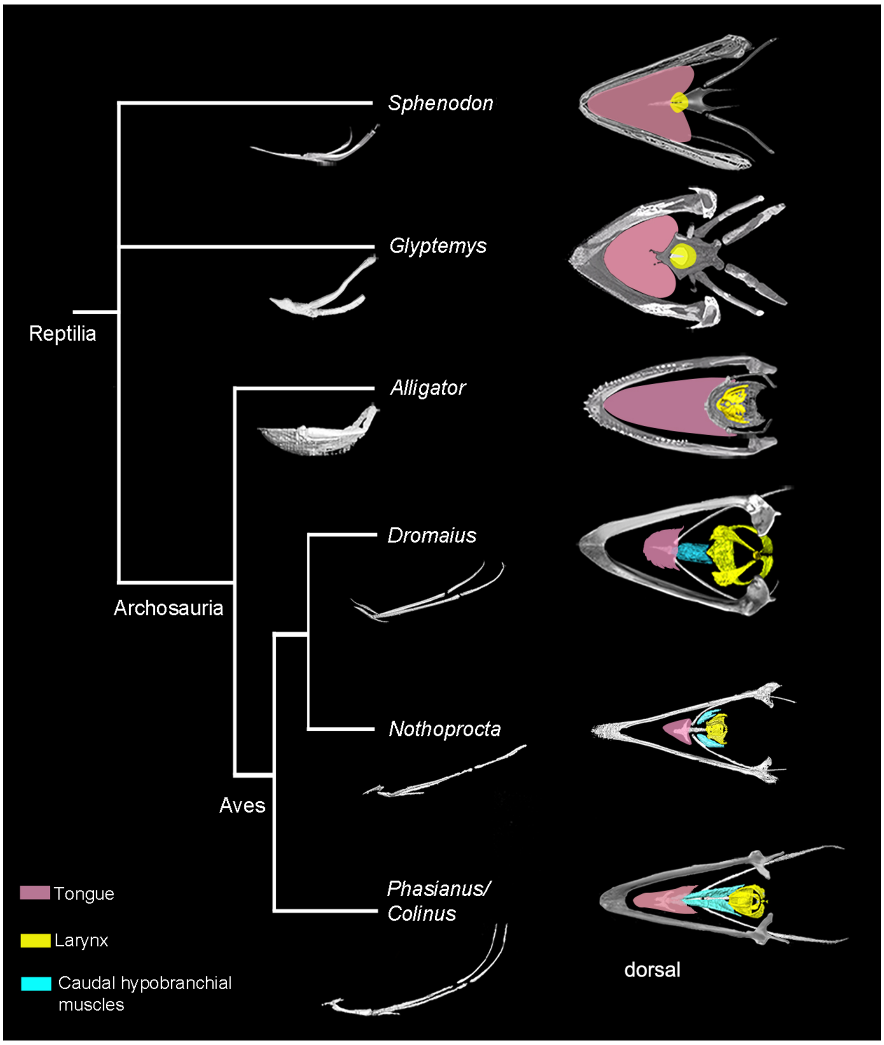


Figure 30. Variation of hyoid bone and tongue form in extant archosaurs and outgroups (modified from [82]).

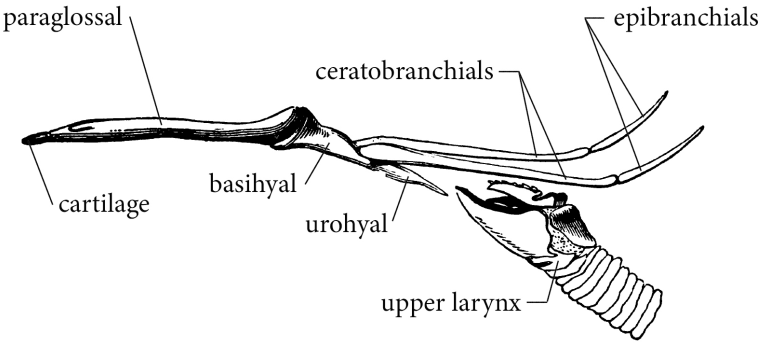


Figure 31. The hyobranchium of swan (modified from Owen [85]).

only weakly mobile. Therefore, the mobility of the tongues of birds and crocodilians, which belong to the archosaur group together with dinosaurs, cannot match the mobility seen in mammalian and lepidosaurian tongues, which have a complicated intrinsic musculature that archosaurs lack [87].

According to Paul [41], dinosaurs lacked flickering tongues since they were not lizards or snakes. Also, because dinosaurs had well-developed hyoids that supported the tongues, their tongues were similarly well-developed. In predatory theropods the tongue was probably simple and inflexible. The tongues of herbivorous dinosaurs may have been more flexible and complex in order to help in the manipulation of fodder and, in the case of ornithischians, in the chewing of fodder.

As a robust hyoid apparatus was found specifically in sauropods, it has been assumed that the latter possessed a powerful tongue. The tongue would be used to guide and manipulate food, reducing some of the losses from the sides of the mouth [61].

The Tongue and Hyoid Bone of Amargasaurus

As a robust hyoid apparatus was present in Amargasaurus (as in sauropods), a powerful tongue can be adopted for Amargasaurus as well. An example of a strong hyoid apparatus is the one found with the skull remains of Tapuiasaurus macedoi. Tapuiasaurus is a new sauropod dinosaur from the Early Cretaceous of Brazil, a titanosaurian with low and elongated diplodocid-like skull morphology (**Figure 32** [88]).

5.6. Ears

The ears of archosaurs (the group that includes the crocodilians, extinct dinosaurs, and birds) function basically in a common way, although specific anatomical details vary [89]. The archosaurs, lack the outer ear that mammals have, therefore there is no earflap (called the pinna). The external auditory entrance was developed independently in mammals and birds. In reptiles, the eardrum

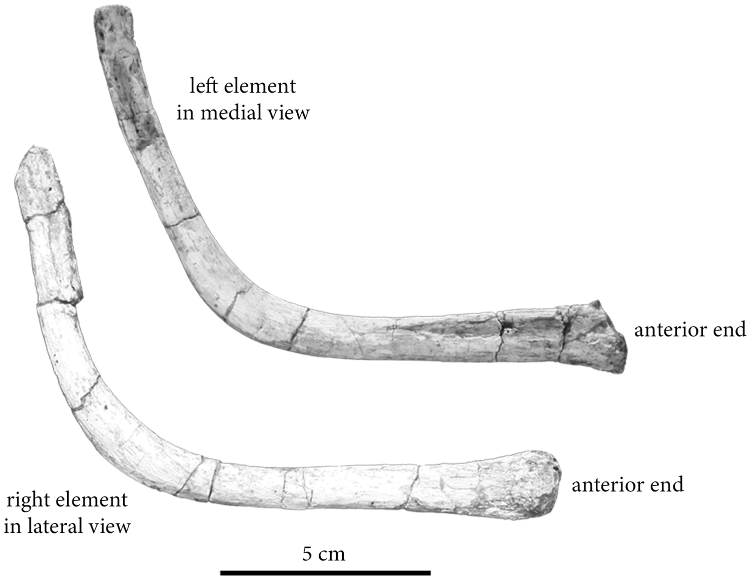


Figure 32. Hyoid apparatus of Tapuiasaurus macedoi, a titanosaurian with low and elongated diplodocid-like skull morphology (modified from [88]).

generally lies directly on the exterior surface, at the bottom of a shallow depression or, it may be covered by a flap of skin like in crocodilians. In birds, it is a relatively short tract without any particular osseous covering. It is partially limited by the occipital bones and the quadrate, but its lining remains membranous [90]. In dinosaurs, the outer ear was a deep, small depression, between the quadrate and jaw-closing muscles at the back of the head, and the eardrum was set in the depression [41]. Specifically, the tympanum of Shunosaurus and Camarasaurus was situated caudomedially to the shaft of the quadrate, while for Edmontosaurus regalis, Corythosaurus Casuarius, Brachylophosaurus canadensis, and Maiasaura peeblesorum, the tympanum was presumably located at the head of the quadrate [91].

The various anatomical structures of an avian ear (**Figure 33**) are used here for describing the basic anatomy. The main bone of the middle ear is the stapes (also called columella for avis), which transmits vibrations from the eardrum, called the tympanum, to the inner ear. This differs from the mammalian middle ear that has three articulated small bones, namely the malleus attached to the eardrum, the incus in the middle and the stapes attached to a smaller membrane covering the oval window. Many extinct species had massive stapes suited for conducting terrestrial vibrations to the inner ear, like the case of an animal listening with its head touching the ground ([92], p. 80). An example of preserved stapes (columella) can be seen in **Figure 34**. The inner ear, although varying greatly in vertebrates, is basically a membraneous apparatus (the membraneous labyrinth), which is filled with a fluid (the endolymph) and is embedded in bone, called the bony labyrinth (otic capsule), at the back of the skull. The membraneous labyrinth is separated from the surrounding bone by a thin layer of liquid (the perilymph), which serves to transmit vibrations from the stapes ([92], p. 80). The upper portion of the membraneous labyrinth (the vestibular organ) has three semicircular canals at right angles to each other. The dissimilar fluid

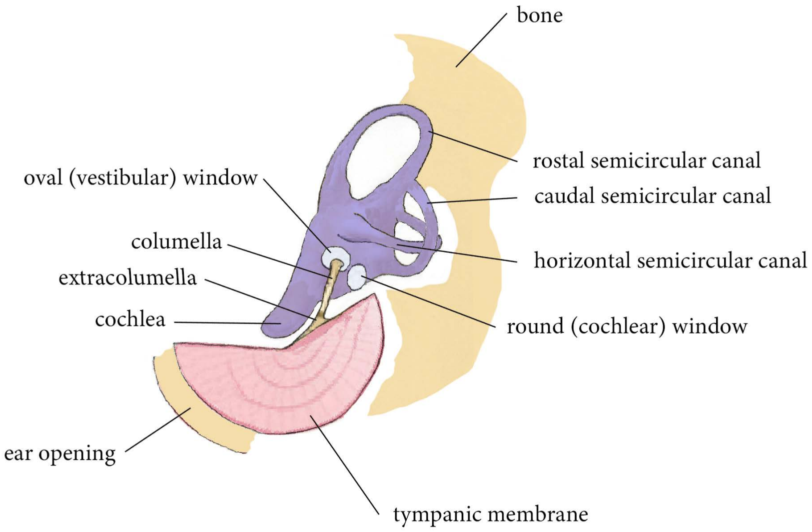


Figure 33. Schematic view of an avian ear with its basic parts.

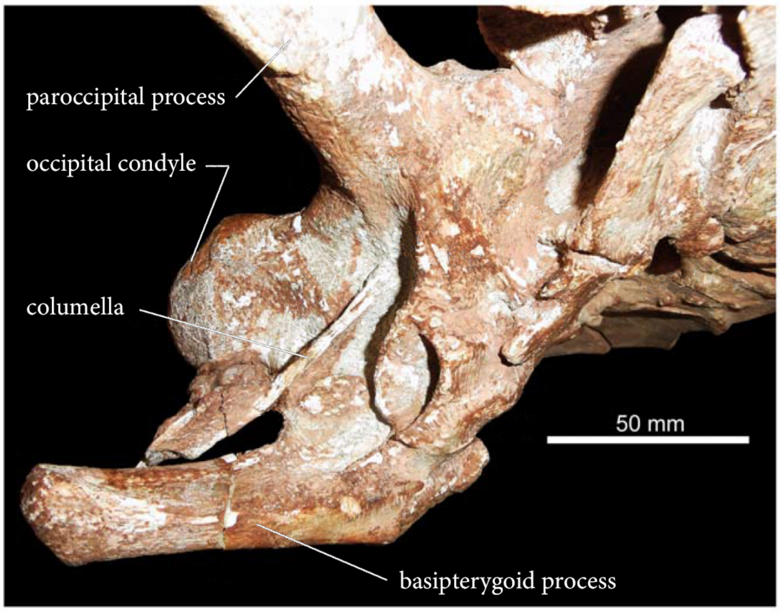


Figure 34. Preserved columella of the sauropod dinosaur Spinophorosaurus nigerensis from the Jurassic of Aderbissinat, Niger [93].

movement inside the canals excites sensory cells within, which transmit information to the brain about the head position and balance.

The lowermost portion of the bony labyrinth, the cochlear organ, is related with hearing and contains the membraneous labyrinth (**Figure 35**). The membraneous labyrinth contains the sensory cells. The cochlear organ contains in part the basilar papilla as a sensory epithelium for hearing. The bony cochlea has two openings: the oval (vestibular) window where the columella is connected, and the round (cochlear) window that is sealed from the middle ear by a membrane. The cochlea is divided by a cartilagenous frame, which spans the basilar membrane that supports the cochlear duct. This duct is composed of different epithelial specializations and encloses a space, the scala media, which is filled with endolymph. On each side of the cochlear duct there are spaces filled with perilymph. The narrow space on the oval window side is called the scala vestibuli, and the wider one on the round window side is called the scala tympani. The scala vestibule communicates with the scala tympani both at the base and the apex. The basilar papilla of birds consists of hair cells and of supporting cells. The basilar membrane is agitated by the motion of fluid around it, and this is detected by the hair cells activating the sense of hearing [94]. It is worth mentioning that the description above is far from complete. There are other organs like the utriculus, the sacculus and more, for which no mention has been made here. More information can be found, for example, in [89] and [95].

In reptiles and birds, the cochlear duct is uncoiled and short, unlike in mammals where it is coiled and lengthy. With the coiled arrangement, mammals can hear high-frequency sounds. Humans can hear up to 20 kHz, dogs 60 kHz, and bats 100 kHz. In comparison, the auditory range of many reptiles and birds is

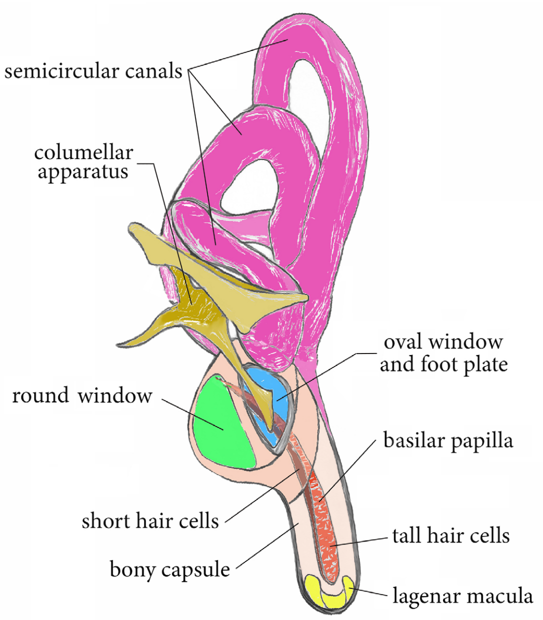


Figure 35. Schematic presentation of the chicken's otic capsule and columellar apparatus. The bony capsule of the cochlear duct is drawn in section and transparent to show the basilar papilla and lagenar macula inside. The semi-circular canals of the vestibule are shown above (after Tanaka and Smith [96]).

between 1 and 5 kHz, with the exceptions of the owl, with a range from 250 Hz to 12 kHz, and geckos that can hear as high as 10 kHz. There are also exceptions for the lower frequency range, with cassowaries that can detect 25 Hz and use this ability to communicate over long distances, and pigeons that can hear as low as 2 Hz and detect approaching storms [41].

Nowadays with new tools in hand, like the computed tomography-based digital visualization techniques, very detailed reconstructions of the endocranial (inside the skull) soft-tissues can be accomplished. In this way it is easy to study and compare the hearing abilities of dinosaurs. For example, such studies exist for archosauria [23], for Saurischia [93] and for theropoda [97] (see **Figure 36**).

In general, dinosaurs did not have fleshy outer ears and their inner ears were not complex, suggesting that their hearing abilities were similar to those of reptiles and birds. The inner ear is connected to the cranial nerve VIII that brings sound and information about one's position and movement in space into the brain [98].

Ears of Amargasaurus

Carabajal *et al.* [32] CT scanned the skull of Amargasaurus cazaui, allowing for the generation of three-dimensional models for both the cranial endocast (the cast of the brain cavity) and the inner ear. The inner ear was 30 mm tall and 22 mm wide. The lagena that housed the cochlear tube was rather short, indicating that the sense of hearing would have been poorer in Amargasaurus than in other sauropods for which inner ears have been studied. The fenestra ovalis, visible in the CT scans, is oriented posterolaterally.

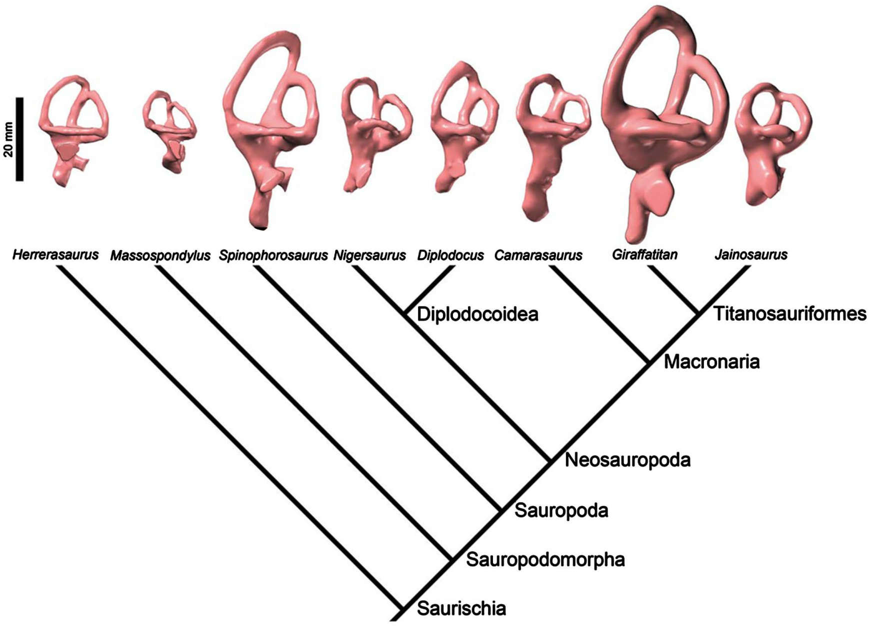


Figure 36. Cladogram of some saurischian taxa showing the endosseous labyrinths of the left inner ears of the species, derived from CT images [91].

Since the interest is in finding the correct position of the ears of Amargasaurus on the head externally, the position and direction of the columella on the skull must be observed. Salgado and Calvo [28] indicate that the columella was arranged on the anteroventral edge of the paroccipital process. Amargasaurus cazaui in this sense differs from Plateosaurus, Dromaeosaurus and Corythosaurus by having its columella lateroventrally oriented. The authors believe that the different orientation of the columella was also accompanied by a different position of the tympanic membrane, although the exit of this structure does not seem to be certain in several dinosaurs. They propose that the columella changed its orientation to follow the inclination of the paroccipital processes (**Figure 37**).

5.7. Eyes

The size of the eye and its position in the orbit is important for a realistic representation. Fortunately, many reptiles and birds as well as fishes have a series of bony plates embedded in the white part of the eye ([92], p. 76). These plates articulate together to form a ring called the sclerotic ring, whose size gives a good estimation of the size of the eye. The diameter of the inner ring tends to closely match the area of the visible eye when the eyelids are open [41]. **Figure 38** shows the position and size of the sclerotic ring in a bird's eye, while **Figure 39** shows the position and size in some dinosaurs. Sclerotic rings were found in many extinct groups, including dinosaurs, pterosaurs and ichthyosaurs.

Usually, if vision is a predominant sense, eyes are large. Large eyes contain more light-receptor cells than smaller eyes and are therefore more sensitive to light. Most dinosaurs had large eyes in absolute sense, although on a large head they may seem relatively small. Birds have circular or slit pupils, with the latter

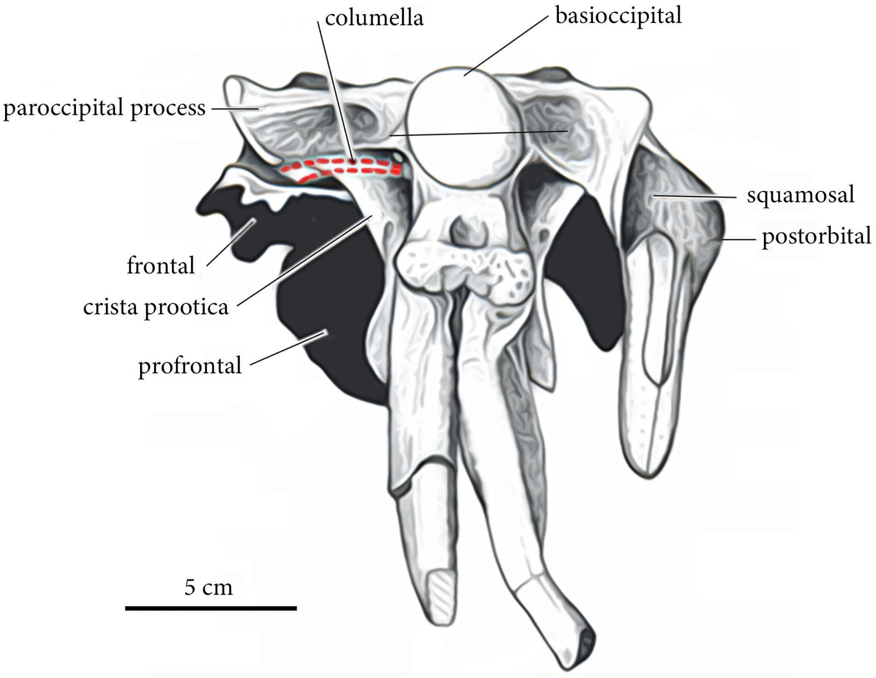


Figure 37. Posteroventral view of the brain case of Amargasaurus cazaui, showing the position of the columella (modified from Salgado and Calvo [28]).

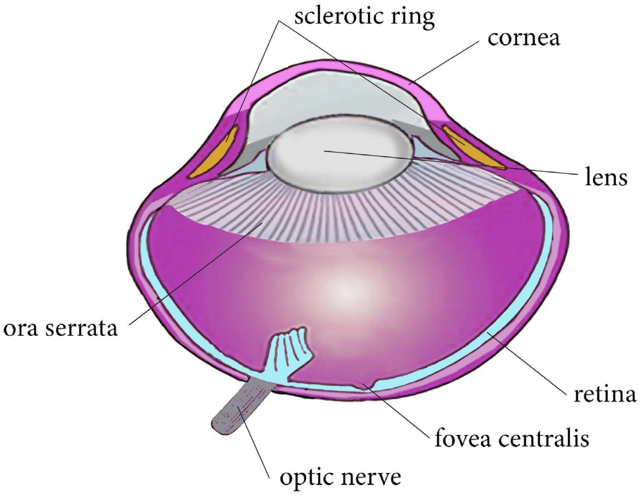


Figure 38. Simplified sketch of bird's eye showing basic parts and position of sclerotic ring. More details can be found in [99].

most commonly present in nocturnal animals. There is no way at present to specify the type of dinosaur eyes, although either of them may have been present in different species. In addition, the eyes of birds and reptiles are protected by both lids and nictitating membranes and the same could be assumed for dinosaurs too. Concerning the position of the eye in the orbit, in some large dinosaurs the eyes were in its upper part [41].

Sclerotic ring types vary as do their sizes and number of plates per species. **Table 2** shows sclerotic ring details for various dinosaur species [102].

(a)

(b)

(c)

Figure 39. Position of sclerotic rings in some dinosaurs. (a) Oviraptorosaur (Dinosauria, Theropoda) [100], (b) Opisthocoelicaudia (a camarasaurid sauropod) [101], (c) Tarbosaurus bataar (Theropoda, Tyrannosauridae) [101].

Because dinosaur eyes were bird- or reptile-like and not mammal-like, they lacked white surrounding the iris. Dinosaur eyes may have been solid black or brightly colored, just like those of many reptiles and birds ([41], p. 33).

Table 2. Sclerotic ring details for various dinosaur species [102].

Species	Outer diameter [mm]	Inner diameter [mm]	Width of the sclerotic ring [mm]	Number of plates
Nemegtosaurus mongoliensis	76	44	16	10
"Struthiomimus samueli"	≈60	≈33	≈13	20
Plc.teosaurus frasianus	-	-	-	16
Brachiosaurus brancai	≈83	≈43	19 - 20	≈10
Diplodocus hayi	-	25 - 30	-	-
Saurolophus osborni	88	52	≈18	10
Anatosaums annectus	-	-	-	13
Lambeosaurus lambei	60	-	-	14
Corythosaurus casuarius	70	-	-	14

Eyes of Amargasaurus

The exact position of the eyes on the head of Amargasaurus should be similar to what is demonstrated in Diplodocus skull CM 11,161, a replica of which is shown in **Figure 40**. The well-preserved sclerotic ring in the orbit shows this position. The eye is quite large, but the diameter of the inner ring which shows the visible eye is small. Measurements of the specific sclerotic ring show an inner diameter of about 3.5 cm and a head length of 57 cm, approximately similar to the length of Amargasaurus head. Therefore, a similar size eye should be fitted.

5.8. Skin Type and Color

Skin impressions in the sediments show that the sauropods together with many other kinds of dinosaurs, such as hadrosaurs, iguanodontids and theropods, were covered with small polygonal scales (**Figure 41**). Czerkas [104] gives the history of skin discovery and its description in the Howe Quarry, located below the Big Horn Mountains near Shell, Wyoming, USA. Describing the impressions found, he mentions that the scales vary in size from less than 1 cm to more than 3 cm. Unlike most other examples from other dinosaurs, almost all skin impressions from the Howe Quarry preserved the actual epidermis as a thin carbonaceous layer of about 1 to 2 mm thickness. The external surface has tiny bumps (1 to 2 mm wide) covering each scale. Larger tubercles (2 to 3 mm wide) are usually below the carbonaceous layer. These are interpreted as the tiny papilliform texture being made by the contact layer of the epidermis and the underlying dermis. Some sections of skin are identified with their natural positions on the lower sides and belly region where the scales are moderate in size, usually 2 to 3 cm wide. In typical dinosaurian fashion, they are in rosette patterns and non-overlapping. No additional ornamentation, such as diamond shaped clusters like that on some hadrosaurs is discernible.

Czerkas [106] (as in [104]) also describes dermal spines found in the same quarry. The spines most probably were arranged over the tail, on the dorsal

Figure 40. Cast of a diplodocid skull (possibly a species of Diplodocus [CM 11161]) showing the position of the sclerotic ring in the orbit [103].

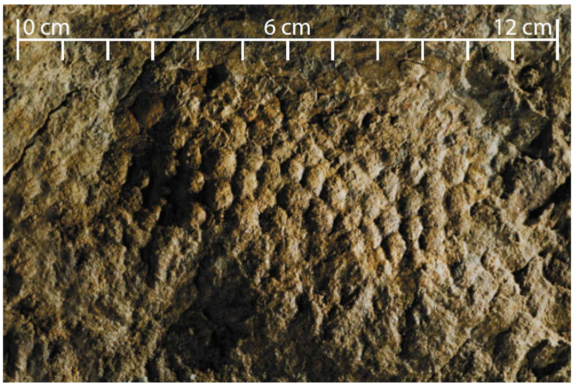


Figure 41. Skin impression found along the rib cage of Victoria's right side on which it came to rest. "Victoria" is a stegosaur excavated at the Howe-Stephens Quarry, from the Morrison Formation in northcentral Wyoming, USA. The "honeycomb" pattern of the skin shows polygons of approximately 1cm diameter [105].

median line and in a single row. It is unclear if the spines continued and how they were arranged along the sauropod's body and neck. The spines are smallest over the distal part of the tail and increase in size anteriorly. The largest spine size (although not complete) would be about 18 cm in height. Also, a variety in shape of the dermal spines was found in the quarry. Some spines are quite narrow, and others are broader and more conical. Also, some of them are sharply pointed and straight, and others are recurved possibly having blunter tips.

Many other researchers have also published data on skin impressions found in different places of the world. Mateus and Milan [107] describe a dinosaur track-assemblage from the Upper Jurassic Lourinha Formation in central-west Portugal (Lusitanian Basin), consisting of medium to large-sized sauropod tracks with preserved impressions of skin, together with stegosaur and theropod tracks. Sauropod tracks were identified as pes tracks that vary in size from 58 to 105 cm in length, with impressions of short, pointy, outward facing digits. Some specimens show short blunt claws and a division into digital pads. Several patches of skin impressions are found on the underside and sides of some casts in two patterns: In the palmar surface of the feet, the skin pattern is rough and scaly with the scales arranged in a hexagonal pattern and ranging from 2 to 3 cm in diameter. On the sides, the skin scales overlap and the pattern becomes pointy with the pointy end facing upward.

Romano and Whyte [108] mention that sauropod skin textures are rare and only about fifteen of them have been described, out of which two are of actual skin and the rest are sediment impressions. The scale shapes are mostly hexagonal or pentagonal, although they range from tetragonal to octagonal, with their size (longest diameter) varying from 4 to 40 mm. The authors also present skin on Sauropod manus cast from the Saltwick Bay, UK, with the same general skin pattern. They comment that when scale size is fairly uniform over a limited area, scale arrangement is comparatively regular. In some cases, though, where scale size is more irregular, occasionally prominent "rosettes" are present, but without any obvious regular distribution or pattern. Although Czerkas [106] (see above) had noted that the scales tended to be moderate in size (2 - 3 cm), non-overlapping and in "rosette pattern", Romano and White [108] only noticed rosettes rarely, with no apparent relationship to position on the body or age of the material. Additionally, the authors present excellent examples of restoration of sauropod manus from a sideritic cast, and sauropod pes from a sandstone cast, from the Cornelian Bay, UK.

Bell [109] examined the possibility to utilize skin impressions in the characterization of palaeospecies. He examined skin impressions (**Figure 42**) from various parts of the body of two species of the hadrosaurine Saurolophus, one from Mongolia and one from Canada, and found that they can be differentiated solely by scale shape and pattern. Therefore, he suggests that taxonomic descriptions should include possible skin impression descriptions, including their position and orientation on the body.

In some titanosaurs that belonged to the same group of dinosaurs called neosauropods, the skin additionally contained osteoderms. Also, Saltasaurus, a

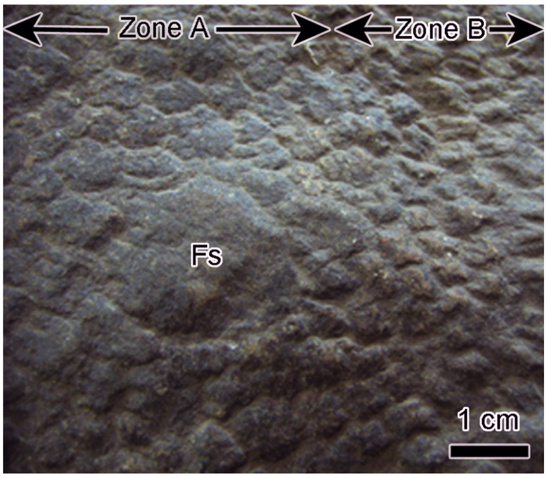


Figure 42. Hadrosaurid Skin Impressions shown to allow differentiation of the species, solely by scale shape and pattern. The figure shows detail of transition between polygonal basement-scales in zone A and shell basement-scales of zone B. Fs, feature-scale [96].

genus of titanosaurid sauropod from northwestern Argentina was covered with a fully armored skin [110].

Eggs and embryos of titanosaurid sauropods were found in Auca Mahuevo, Argentina, and the embryonic skin structure was examined by Chiappe and Dingus [110]. The skin presents a diverse array of scale patterns. In one case, a triple row of larger scales crosses an area of smaller scales. In other cases, scales are found arranged in rosette patterns, in which a circle of eight smaller scales surrounds a large central scale. In other specimens several triangular scales converge toward a central point, like the petals of a flower. Unfortunately, it is not possible to identify where these scale arrangements were located on the body, because the patches of fossilized skin did not overlap identifiable bones in the skeleton. The scales of the skin of embryos do not overlap one another; the skin is similar to the fossilized skin of adult dinosaurs. In this respect, the skin of dinosaurs and embryos is more similar to the beadlike or pearl-shaped skin of Gila monsters than that of typical lizards.

Concerning skin colors, although it is now possible to restore the actual colors of dinosaur feathers ([111] [112]), there is still no method to restore the colors of scales. As Paul ([41], p. 33) mentions, it was proposed that different scale patterns on a particular species of dinosaur may correspond to differences in coloration, but this may not be true since some reptiles are uniformly colored regardless of variations in the scales. Paul [41] proposes that dinosaur scales were better suited to carry bold and colorful patterns, like those of reptiles, birds, tigers and giraffes, instead of the dull gray, non-scaly skin of big mammals, as the color vision of dinosaurs may have encouraged the evolution of colors for display and camouflage. As an example, he mentions that dinosaurs adapted to living in forested areas may have used greens for covering. Another observation from nature is that big reptiles and birds tend to be earth tinged despite their color vision, leading to the conclusion that small dinosaurs were more likely to have bright color patterns as do many small lizards and birds.

Vivid colors within a species could also be used, especially in the breeding season, together with crests, frills, skin folds and taller neural spines, or to declare the presence of a fearsome predator.

Skin Type and Color of Amargasaurus

Amargasaurus skin should be similar to other sauropods, but as belonging to a separate species it should have some differentiations in scale shape and pattern. Skin impressions of sauropods, like Diplodocus and Barosaurus, found in Utah, USA, in Late Jurassic beds (150 million years ago), show the beadlike shape (**Figure 43**), a patent that will be followed in the reconstruction of the skin that follows.

6. Reconstruction Procedure and Details of Processes

6.1. Placing the First Layer of the Plaster

With the above determination of the final details we proceed with the placing of

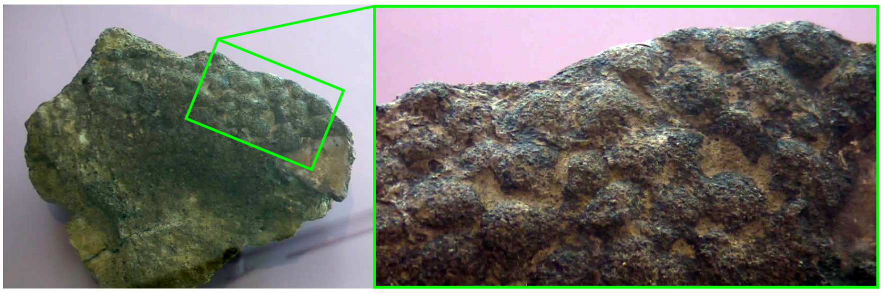


Figure 43. Skin impressions of sauropods like Diplodocus and Barosaurus, found in Utah, USA, in Late Jurassic beds (150 million years ago) [113], with enlargement of a segment. Scale (diameter) about 2 cm.

the first layer of the plaster on top of the wire mesh on the head construction. In order to make sure that the eye and ear openings will be positioned symmetrically on the predetermined places, tubes of the appropriate size are inserted first, through the head structure, as indicated in **Figure 44**. When layering the plaster, it is made sure that the wire mesh is covered on both sides with a minimum amount of plaster placed on the outer side in order not to change the dimensions of the construction. Steel bars holding the weight of the structure are covered all over with ample material in order to reinforce the structure and avoid future oxidation of the bars.

6.2. Reconstruction of the Teeth

The general form and dimensions of the teeth are shown in **Figure 25**. To reconstruct the whole denture, each one of the teeth can either be individually constructed, which is very tedious, or a number of teeth can be constructed, with molding techniques used to replicate them. It was chosen to construct about ten individual teeth and then use the replicating technique.

In the market there are a number of air hardening modeling clay materials that do not change significantly in dimension during the hardening process and can be formed easily. Such material can be used for constructing the prototype teeth. In the beginning, a tube of internal diameter about 10 mm can be used to extrude a cylinder of the right length and then form the edge by hand, as shown in **Figure 45**. Water on the clay surface helps to easily shape and smooth it.

Another way of forming the teeth is to use cylindrical rods of wood of the proper diameter, bought from a DIY store. After wetting the rod in a bucket for some hours, the rod is placed in a vise and bent gradually in steps until the required curvature along the length is achieved. A permanent deformation remains on the wood when left in the vise to dry. Then the rod can be cut to the correct length, filed accordingly to acquire the required end shape and finally polished with a very fine sand cloth (see **Figure 46**).

When a sufficient number of teeth are constructed, room-temperature-vulcanizing (RTV) silicone rubber can be used to produce a mold for creating the replica teeth. This type of mold allows a good flexibility for easy extraction of the poured material.

(a) (b)

Figure 44. Plastic tubes of the appropriate size are inserted first through the head structure, for symmetrically positioning the eye and ear openings at the predetermined places. The first plaster layer is then placed on the wire mesh: (a) front view, (b) side view.

Figure 45. Extruding clay from the tube and forming the correct shape of teeth by hand.

(a) (b)

Figure 46. Wood teeth. (a) Bending the wood rod in a vise, and (b) finished shapes of teeth.

To produce the mold the following steps should be followed. 1) The prototype teeth must be glued on the middle of one of the sides of a plastic container, as shown in **Figure 47**. 2) The volume of the silicone rubber needed to fill the

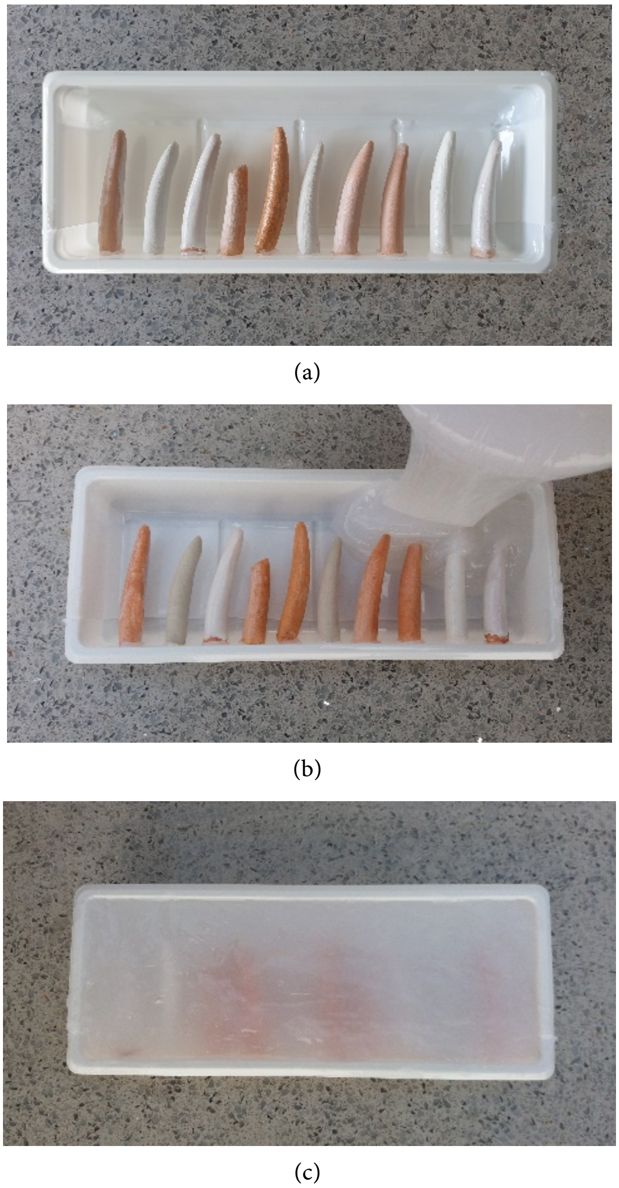


Figure 47. Preparation of the mold. (a) The prototype teeth are glued on the middle of one of the sides of the container, (b) pouring of the silicone rubber, (c) formed mold.

container must be estimated. This can be done by filling the container with water and emptying the water in a cup, marking the height of water. 3) The cup and the container with its content must be dried. 4) The surfaces that will be wetted by the silicone rubber in the container must be sprayed with a thin layer of anti-stick material (mold release agent). 5) The constituents of the silicone rubber must be mixed in the cup, using slow motion in order not to trap air in the mixture. 6) The mixture must be steadily poured into the container so that it runs by itself very slowly, until it covers completely all teeth and reaches to the top. Slow pour is necessary to allow time for air to escape from around the teeth. 7) Once poured, the mold must be lightly tapped to help move any bubbles, which were trapped, to the surface. 8) The liquid material must be left to harden for the time suggested by the manufacturer. 9) The plastic container and then the prototype teeth from inside the mold must be removed.

There are also other, less expensive, methods of producing molds. One such method is to dissolve silicone with acetone and produce the mold [114], or use a mold produced with mixing silicone to corn starch or soapy water [115], or even use hot glue [116]. For these methods, one should try not to trap air in the mold, work in a ventilated place and, if possible, in an environment with warm temperature for quick drying of the mixture of silicone.

In the market, there is a variety of materials that can be used to construct the teeth replica, varying from acrylic resins to cement-based mixtures and liquid porcelains. Materials that are dimensionally stable, weatherproof and UV resistant should be chosen. When the material is in hand, one should spray the mold with release agent and follow the manufacturer directions to mix the components. Then the liquid should be poured in the tooth mold. To facilitate the work, a syringe can be used (**Figure 48**) for allowing the liquid to reach to the depth of the mold cavity and for allowing pouring from the depth up, thus minimizing the possibility of trapping air. **Figure 49** shows the silicone mold, the teeth prototypes and casted teeth with various materials.

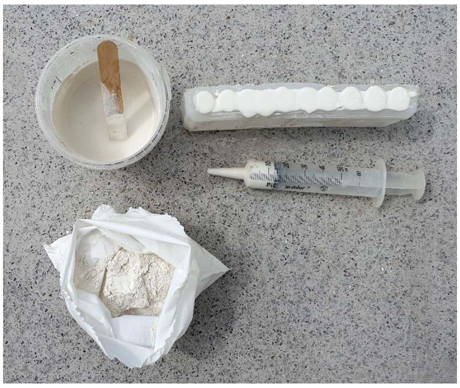


Figure 48. Mixing the components and pouring with the help of a syringe.

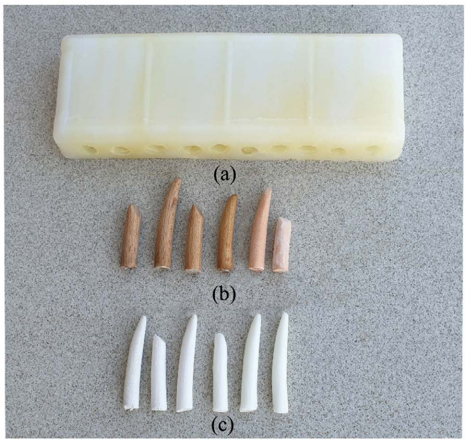
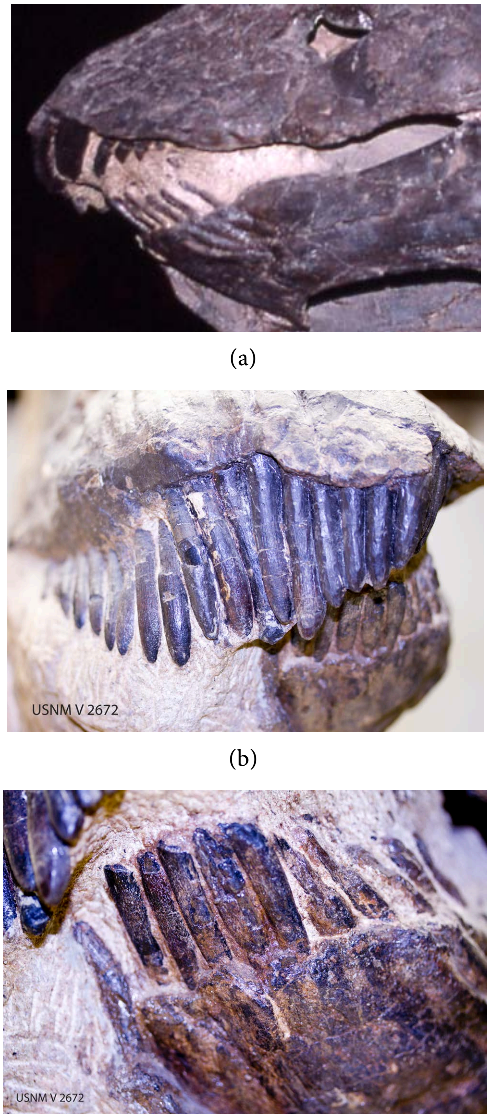


Figure 49. Silicone mold (a), teeth prototypes (b) and casted teeth (c) with various materials.

6.3. Denture Reconstruction

For reconstructing the denture, 4 premaxillary teeth, 12 maxillary and 16 dentary teeth are used as in Diplodocus. As **Figure 25(b)** shows, the teeth in sauropods were not replaced all at once, but individual teeth were replaced at random. Therefore, some of the teeth were heavily worn, while others were new. Also, the teeth wore out in various directions depending on which teeth of the upper jaw came in contact with particular teeth of the lower jaw during chewing. Another observation is that the lower jaw, when drawn slightly aft, allows its teeth to slide under the upper jaw teeth and let the mouth close, as shown in **Figure 50**. At the front position, the teeth close together, allowing the animal to bide.



(a)

(b)

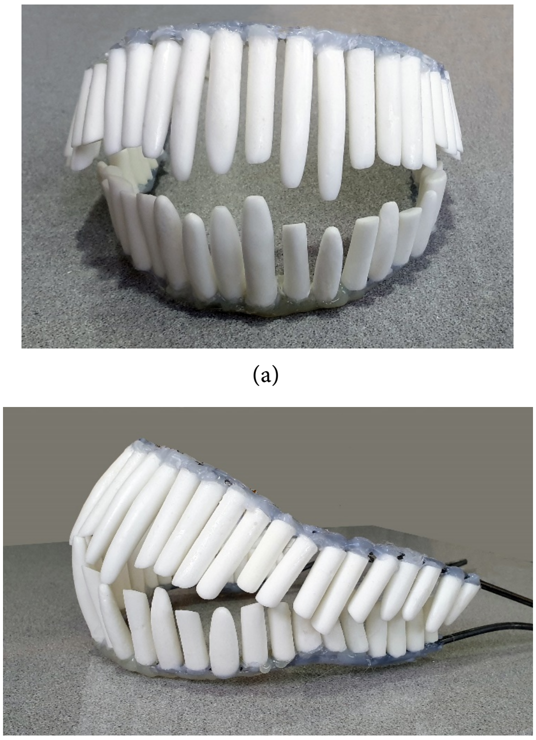
(c)

Figure 50. Diplodocus longus, specimen USNM V 2672. (a) Diplodocus skull showing relative position of upper and lower jaws, (b) close-up of dentary of upper jaw, (c) close-up of dentary of lower jaw. (Michael Brett-Surman, Smithsonian Institution—Department of Paleobiology [60]).

Based on the above observations, the construction continues with steel wire rods bended to the shape and dimensions of the upper and lower alveolar bones (the thickened ridge of jaw bones that contains the tooth sockets or dental alveoli) and the replica teeth glued, as shown in **Figure 51**.

6.4. Reconstruction of the Skin

Stamps with the exact shape of the finished skin need to be produced if large areas of finished surface are to be covered with skin impressions. A way to produce the stamps is by using the traditional method of sculpting a sample piece and then producing a cylindrical stamp from that in the following way: At the beginning a sketch of the skin for a square area should be drawn, making sure that the top edge is a continuation of the bottom edge and the left one is a continuation of the right one. In this way, when the stamp is rolled on the surface, it will produce uninterrupted skin that will match with the next rolling line. Using air hardening modeling clay, a flat surface of about 1 cm thickness should be produced, the sketch of the skin on the clay should then be transferred, and sculpting the skin texture manually should follow, as in **Figure 52**. When the material dries up, the next step is to spray the surface with a thin layer of anti-stick material (mold release agent) and cover it with a silicone layer of about 0.5 cm thickness. When hardened, the silicone layer can then be rolled and clued around an appropriate diameter tube to form the cylindrical stamp, as shown in **Figure 53**.

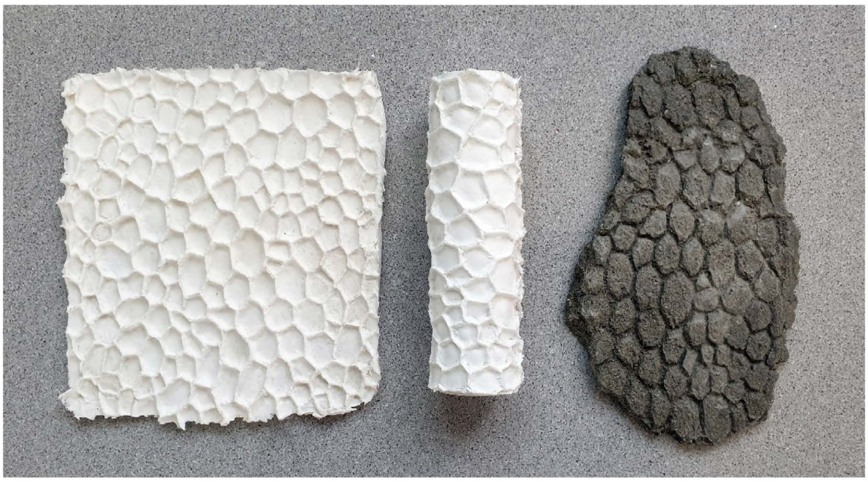


(a)

(b)

Figure 51. Reconstructed dentaries. (a) front view, (b) side view.

Figure 52. Sculping the skin on the modeling clay.



(a) (b) (c)

Figure 53. The silicone layer (a) rolled and clued around an appropriate diameter tube (b) to form a cylindrical stamp, producing the corresponding skin texture onto the plaster surface (c).

Another method is to use computer software, namely (for example) Adobe Photoshop [117], to draw the skin sketch shown in **Figure 54**, adjusting the shapes at the corresponding edges to match as explained above. In order to produce the virtual 3D stamp, another software, namely the free online "Image to Lithophane" [118], can be used and the skin sketch adjusted in color and details, to suit the needs of the software; for example, in order to produce the concave shape of every scale, darker color should be drawn in the middle that will fade to the borders by using the gradient tool in Photoshop.

The outcome of "Image to Lithophane" software is a .STL file that can be viewed and edited (if needed) on other free software, like Autodesk Meshmixer [119], and then printed on any 3D printer, as shown in **Figure 55**.

When producing the finished skin surface in our reconstruction, it was found easy to press the rolling stamp on the fresh mortar by placing a clear thin food membrane in between. In this way the rolling stamp was maintained clean and the finish on the fresh mortar was improved.

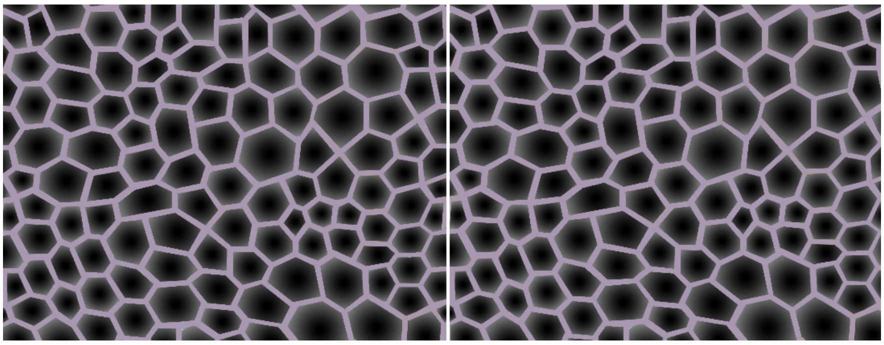
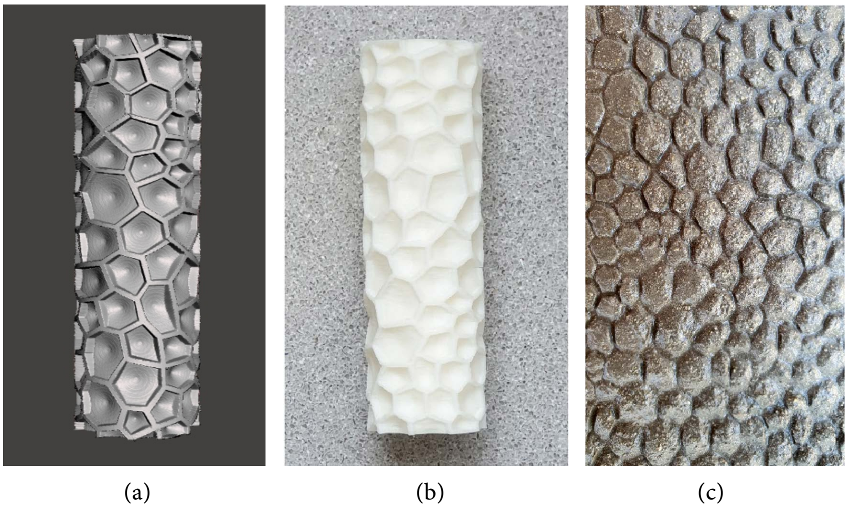


Figure 54. Skin sketches drawn in Photoshop, with matching shapes of the corresponding edges.



(a) (b) (c)

Figure 55. Production steps of the "skin". (a) STL file resulting from photoshop drawing, (b) 3D printed in a rolling stamp, (c) skin texture printed onto the plaster surface (right).

6.5. Reconstruction of the Soft Tissue of the Roof or the Oral Cavity

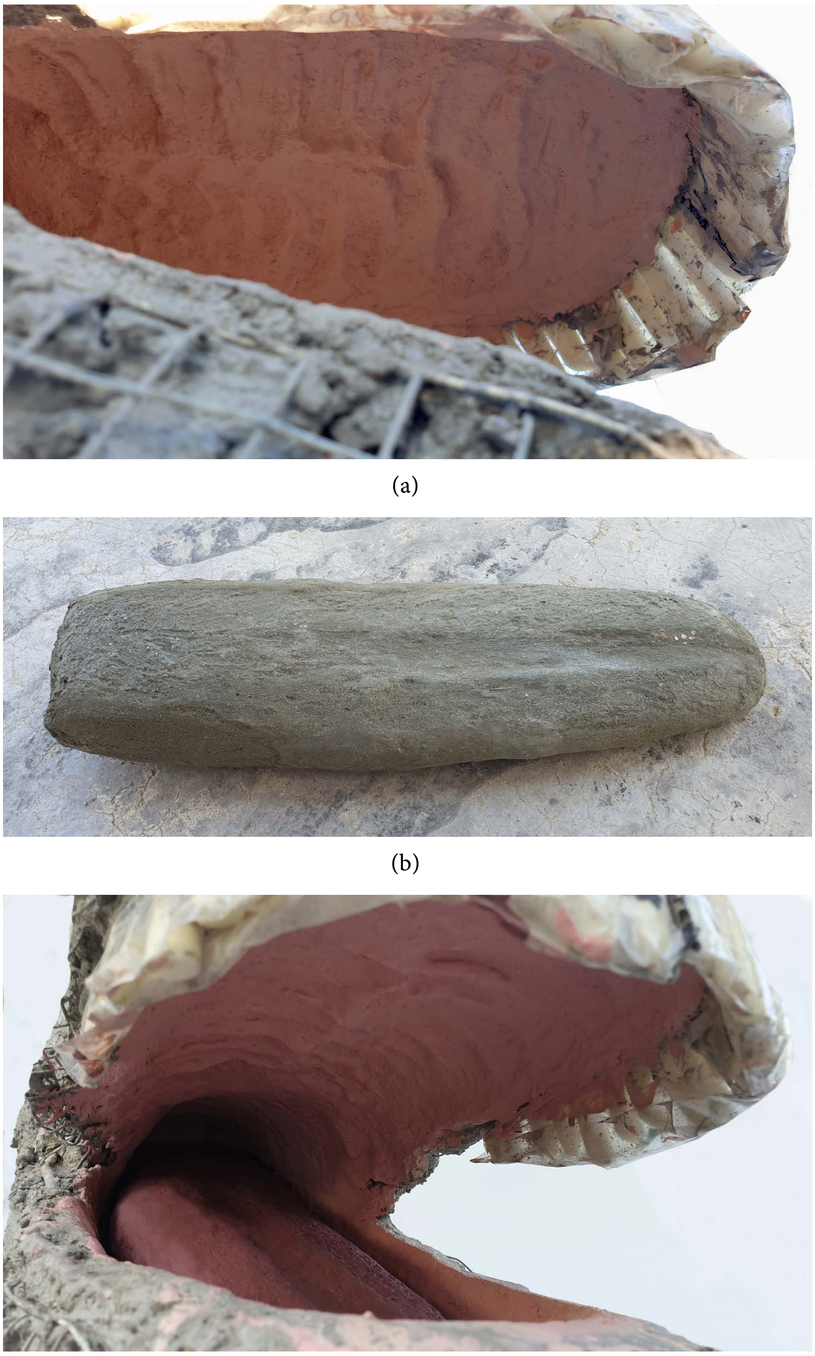
The next step is to place the top denture in position and construct the oral cavity. A serrated surface was produced on the roof of the cavity without much detail, as this area is not visible in the finished reconstruction. The tongue was also produced to fit its position in the mouth, while the cavity was painted as no access in this area is possible in a later stage (**Figure 56**).

6.6. General External Appearance

To proceed with the reconstruction, one must have a general model that will be followed. A selected example for our case is the head of the Iguana and the turkey (**Figure 57**). Specific points to observe on this model are the nostrils, eyelids, ear opening and scales around the mouth (for Iguana). These features will be generally adopted in the reconstruction.

6.6.1. Reconstruction of the Nostrils and Roof of the Head

The reconstruction proceeded with the marking of the nostrils on the head. The



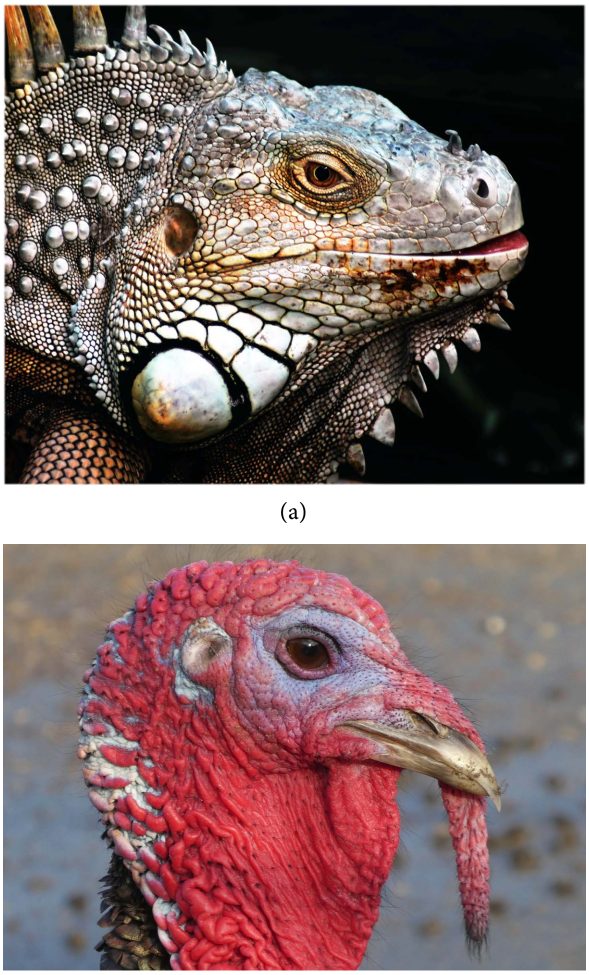
(a)

(b)

(c)

Figure 56. Oral cavity. (a) Top denture in position with the serrated surface produced on the top of the oral cavity, (b) tongue, (c) finished oral cavity.

reconstruction of **Figure 18**, showing two separated nostrils running along the whole length of the nose, is not generally encountered in nature, we believe. **Figure 14** indicates this feature only on tapirs, but in this case the nostrils separate at a small distance only at their ends. Therefore, at the end of the nose the two nostrils deviate slightly from the midline, allowing the animal to smell not only directly from the front of the snout but from the sides as well (**Figure 58**).


(a)

(b)

Figure 57. Models for the reconstruction of Amargasaurus head. (a) Iguana head [120], (b) turkey head [121].

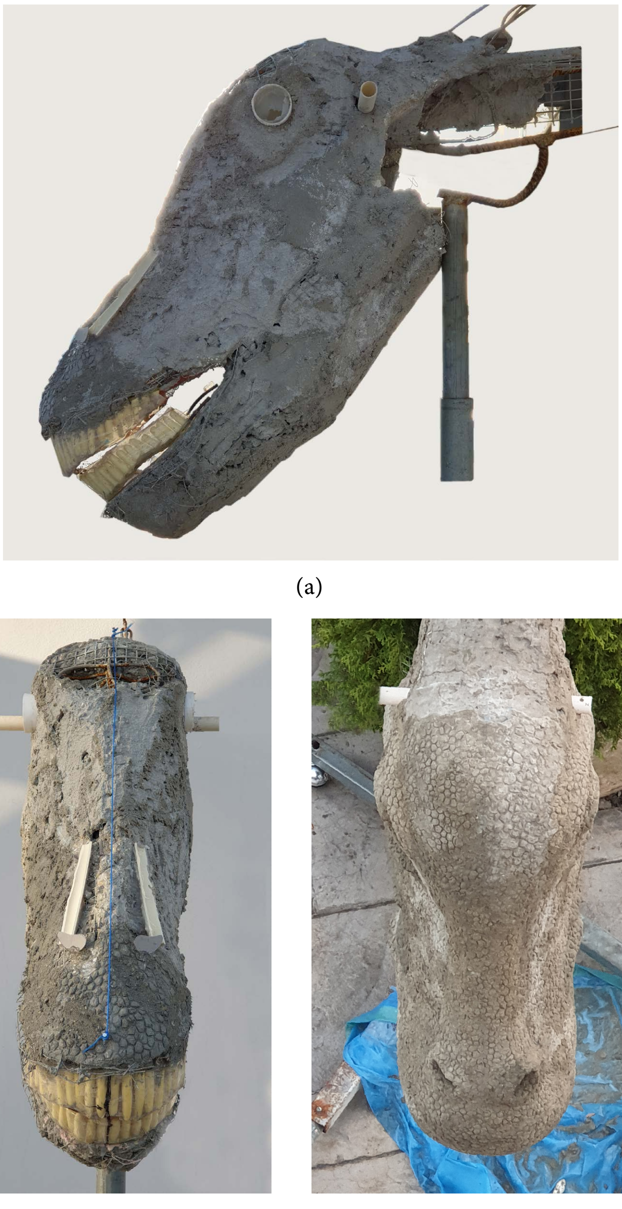
6.6.2. Reconstruction of the Eyes and Ear Opening

Realistic glass eyes that fit any animal (or human) can be found in the market. These eyes come in various sizes, shapes and designs, and are replicas of the eyes of mammals, birds, fishes and reptiles and amphibians. Such eye replicas can be found, for example, in [112] [113]. Eye replicas can also be customized in design and color to fit any requirement. In our case the eyes chosen are shown in Figure 59.

The ear opening is presented as a shallow depression, according to the model of Figure 57, as shown in Figure 59.

6.6.3. Reconstruction of the Lower Side of the Head and Jaw Musculature

Finally, the lower side of the head is constructed. Also, the position of the jaw muscles is slightly enhanced by bulging slightly the appropriate areas. Final touches then follow to complete the reconstruction stage (Figure 60). For example, the lips are modeled in a way to decrease the mouth opening and reach behind the last tooth.


(a)

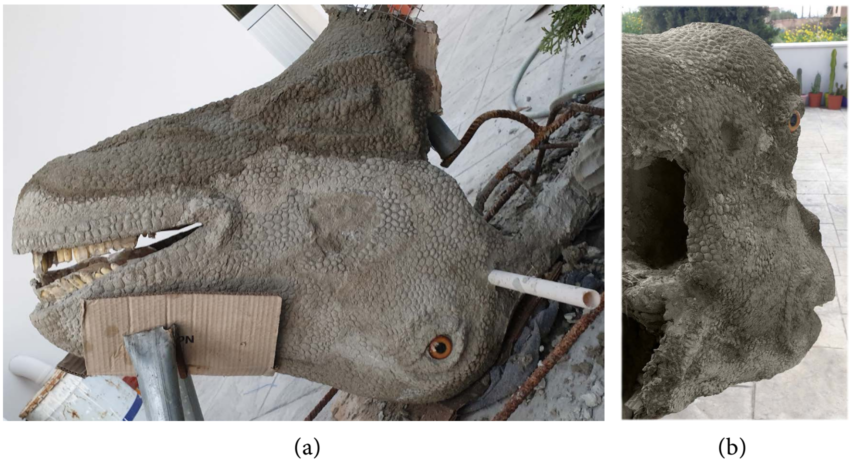
(b) (c)

Figure 58. Nose construction. (a) Side view indicating the nostril position, (b) front view and (c) top view of the finished nostrils.

Figure 59. Amargasaurus fitted eyes (diameter = 32 mm) and ear opening.

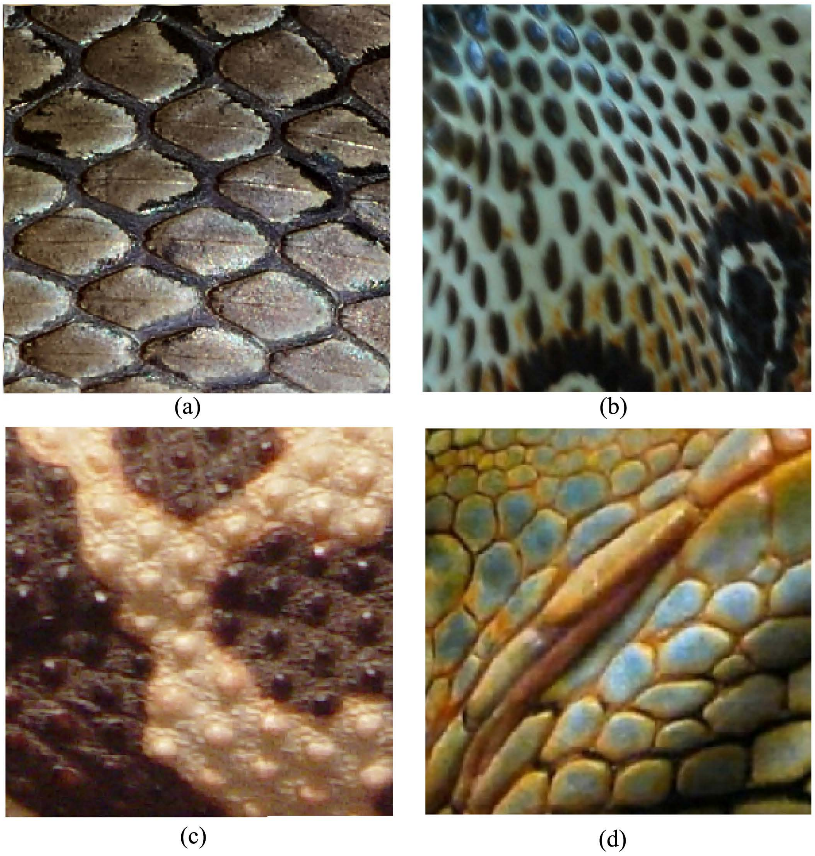
6.6.4. Painting the Head

The next and final step is to paint the head. Vivid colors are selected as encountered in reptiles. The scale color can be lighter, darker or the same as the color of the space in between the scales, as shown in **Figure 61**. The colors chosen for the head of Amargasaurus are shown in **Figure 62**.



(a) (b)

Figure 60. Construction stages: (a) construction of the lower side of the head, (b) bulging the area of the jaw muscles and finalizing the lips.



(a) (b)

(c) (d)

Figure 61. Scale color compared to the color in between the scales. (a) Snake, (b) back of Cobra, (c) Gila monster, (d) Iguana.

Figure 62. Completed reconstruction of the head of Amargasaurus.

7. Conclusions

In any animal reconstruction, the head is one of the most important parts since there, all the major senses of the animal are housed and important functions are performed. This paper has presented the current knowledge concerning the reconstruction of the heads of dinosaurs. Dinosaur heads come in many shapes, sizes and individual characteristics, depending on the species and the use that served. For the reconstruction of the dinosaur head, several features and functions of the head should be studied, namely the osteology, musculature and soft tissue of the head, cranial kinesis, craniodental biomechanical characteristics, posterior part of the cranium, skin, and others. As a worked example, the Amargasaurus (a sauropod) head in full scale has been chosen to be reconstructed in this paper. The main steps and resulting points of the study are as follows.

As a first step, the osteological remains of the head were studied for reconstruction according to their correct size and form by comparison to known remains belonging to the same family in the case they were not complete.

As dinosaurs lacked facial muscles, their skin was directly appressed to the skull. The skin covering the large openings in front of the orbits of many dinosaurs probably gently bulged outward, and likewise, jaw muscles bulged gently out of the skull openings.

Although sauropods were vegetarians, they had long necks that could have been used for browsing in trees, long streambanks or under water. The sauropods anatomy is mostly unclear, but firm morphologic interpretations usually point to terrestrial behavior. A full commitment to a terrestrial existence for dinosaurs is indicated by their fully erect stances (like mammals). The diet of sauropods through the study of plant remains in dinosaur coprolites could perhaps shed more light on whether sauropods were land or aquatic animals. The bones of sauropods were also adapted for terrestrial life, with the weight and strength of the skeleton located where it was mostly needed, *i.e.*, denser bones at the lower parts and lighter ones at the upper parts of the skeleton. Thus, the dominating view is that sauropods are land animals and are reconstructed as such.

Concerning the individual characteristics of the head:

1) The proboscidean nerve controls the muscles of the complex motor system of the trunk. By examining the anatomy of the head and the endocranial cast this can be addressed in detail for any individual animal

2) Observation of the nostrils of extant animals can suggest the correct position of the nostrils of dinosaurs.

3) The existence and kind of cheeks and lips is a subject of discussion but indications as foramina canal openings (type and density) in the jawbones, and the skull bone morphology at the area of probable cheeks give indications as to their form.

4) Teeth types vary according to their function and use. Nature provided dinosaurs with a teeth replacement rate. This remarkable method provided dinosaurs with new teeth throughout their life to serve their needs. Incremental lines in dental tissues are an indication of tooth replacement rate.

5) The palate varies in shape for different animals, but generally, at the front of the mouth, it is covered with ridged skin. Some forms of palates are shown in the article.

6) Dinosaurs had robust hyoid apparatus that supported well-developed tongues. The tongues of predatory theropods were probably simple and in-flexible. The tongues of herbivorous dinosaurs may have been more flexible and complex in order to help in the manipulation of fodder.

7) In dinosaurs, the outer ear was a deep, small depression, between the quadrate and jaw-closing muscles at the back of the head, and the eardrum was set in the depression. Many extinct species had massive stapes suited for conducting terrestrial vibrations to the inner ear, like the case of an animal listening with its head touching the ground.

8) Sclerotic rings (a series of bony plates embedded in the white part of the eye) were found in many extinct groups, including dinosaurs, pterosaurs and ichthyosaurs. The sclerotic ring inner diameter gives a good estimation of the size of the visible eye when the eyelids are open. Concerning the position of the eye in the orbit, in some large dinosaurs, the eye was in the upper part of the orbit.

9) Skin impressions in the sediments show that the sauropods together with many other kinds of dinosaurs, such as hadrosaurs, iguanodontids and theropods, were covered with small polygonal scales. A comparison to extant animals shows that the skin of dinosaurs is more similar to the beadlike or pearl-shaped skin of Gila monsters than that of typical lizards.

Having in mind the gleaned knowledge on the various parts of the head, decisions concerning the head of Amargasaurus have been taken in order to reconstruct a 3D, actual size head. The reconstruction procedure and details of the processes have been described in this paper.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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