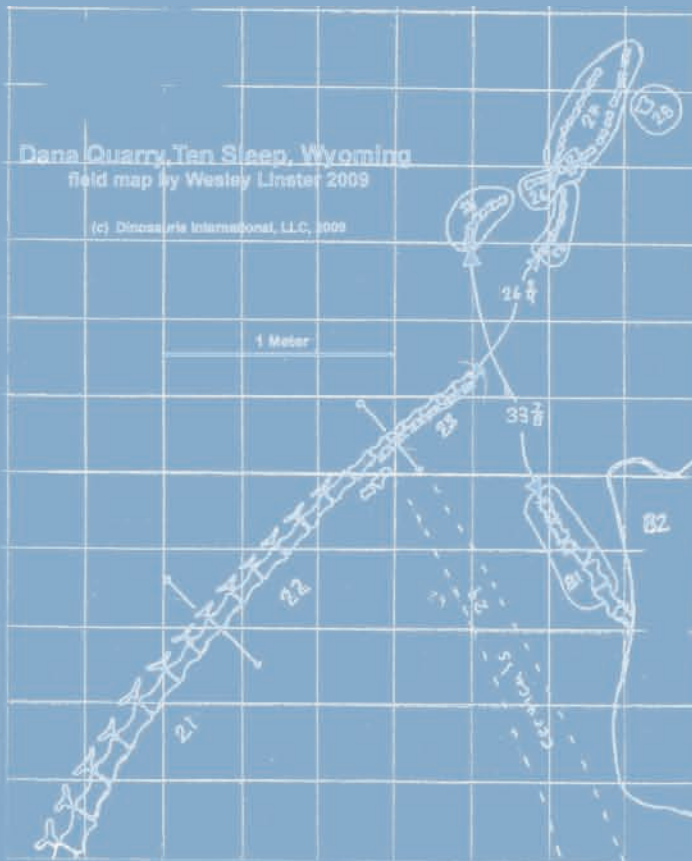# A NEW BASAL DIPLODOCID SPECIES, AMPHICOELIAS BRONTODIPLODOCUS FROM THE MORRISON FORMATION, BIG HORN BASIN, WYOMING, WITH TAXONOMIC REEVALUATION OF DIPLODOCUS, APATOSAURUS, BAROSAURUS AND OTHER GENERA
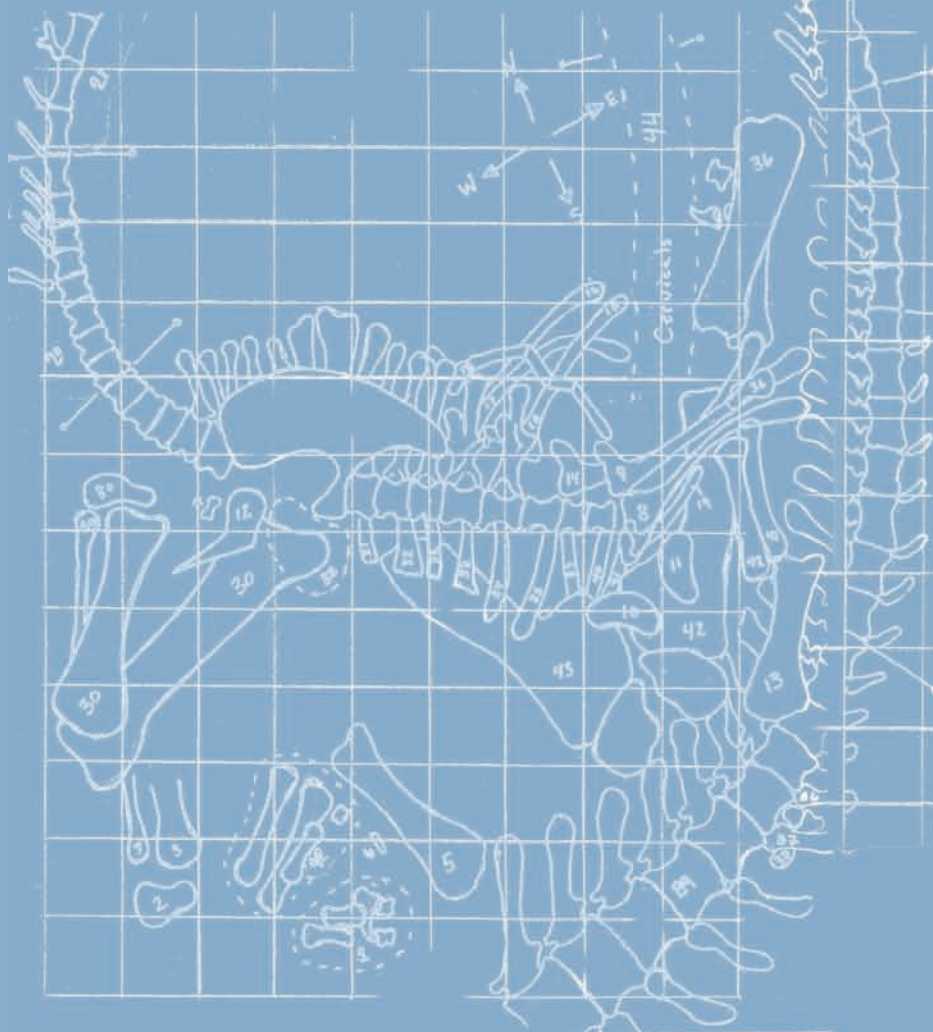
HENRY GALIANO and RAIMUND ALBERSDÖRFER

Dana Quarry, Ten Sleep, Wyoming
field map by Wesley Linster 2009

(c) Dinosauria International, LLC, 2009

1 Meter

Front Cover: Mounted skeleton of *Amphico-elias brontodiplodocus* **(DQ-EN) in Mexico - photo by Andres Estrada**

Inside Front & Back Covers: DQ-TY Bone Map by Wesley Linster

Back Cover: Skull with articulated cervical vertebrae exposed in matrix together with illustration depicting the reconstructed skull of *Amphicoelias brontodiplodocus*

A NEW BASAL DIPLODOCID SPECIES,

AMPHICOELIAS BRONTODIPLODOCUS

FROM THE MORRISON FORMATION, BIG HORN BASIN, WYOMING,

WITH TAXONOMIC REEVALUATION OF

DIPLODOCUS, APATOSAURUS, BAROSAURUS,

AND OTHER GENERA

HENRY GALIANO

AND

RAIMUND ALBERSDÖRFER

CONTENTS   **Page**

A NEW BASAL DIPLODOCID SPECIES, AMPHICOELIAS BRONTODIPLODOCUS FROM THE MORRISON FORMATION, BIG HORN BASIN, WYOMING, WITH TAXONOMIC REEVALUATION OF DIPLODOCUS, APATOSAURUS, BAROSAURUS, AND OTHER GENERA

HENRY GALIANO [1] AND RAIMUND ALBERSDÖRFER [2]

1. (henry@maxillaandmandible.com) Maxilla & Mandible, Ltd., 451 Columbus Avenue, New York, NY 10024, USA
2. (fossils@gmx .de) Bergstrasse 8, D-91220 Schnaittach, Germany

ABSTRACT - Five recently discovered, virtually complete, skeletons from the Dana Quarry, Ten Sleep, Wyoming, are recognized as belonging to a new basal diplodocid species, *Amphicoelias brontodiplodocus*. These fossils are part of a new fauna and flora occurring low in the Morrison Formation in the Big Horn Basin. Apparently no post mortem hydraulic transportation had taken place before burial. These skeletons were found close together within a small area, and therefore, represent a rarely preserved in situ death assemblage. These skeletons exhibit sexual dimorphism, with considerable ontogenetic and phenotypic variation. Of the two morphotypes that exist, one displays massive broad neck vertebrae with heavier limbs, while the other displays narrow cervicals, slender limb bones, and a proportionately longer tail. These morphs are regarded as male and female sexes, respectively. One immature specimen (DQ-TY) shows remarkable size disparity between the axial and appendicular skeletons, which clearly demonstrate that limbs reach adult lengths early in ontogeny. *Amphicoelias brontodiplodocus* is recognizable by the following diplodocid plesiomorphies: presence of basipterygoid recess, elongated overlapping cervical ribs, undivided neural spines on the 3rd – 9th cervical vertebrae, presence of both clavicles, and ossified calcanea.

The type specimen of *Amphicoelias altus* Cope, 1877, is regarded as a recognizable valid diplodocid taxon with priority status under the Code of Zoological Nomenclature. Compelling evidence provided by the new Dana Quarry specimens determines that the genera *Diplodocus* and *Barosaurus* are synonyms of *Amphicoelias.* Moreover, the recognized sexual dimorphism in the Dana Quarry sample demonstrates that *Apatosaurus* and *Supersaurus* are also synonyms of *Amphicoelias.* The taxonomic conclusions presented here strongly imply that the Morrison biota may not have had as diverse a sauropod fauna as previously believed.

A new life reconstruction is proposed for the genus *Amphicoelias.* Elongated skull, reduced dentition, grooved premaxillae, maxillae, and symphysis of lower jaws plus posterior placement of external nasal opening suggests the presence of a rostral bill designed for filter feeding. Sexual dimorphism is largely expressed in the hypertrophic development of cervical ribs in males. This uniquely male morphology facilitated defense and courtship display, combat, and subduing females during copulation. Graviportal limbs with digitigrade feet indicate that *Amphicoelias* was capable of long distance travel. A hyper-extended neck along with filter feeding capabilities supports the suggestion that a wading habit was their principal ecological niche.

INTRODUCTION

Nothing more symbolizes the image of a dinosaur than the long-necked sauropods. These largest creatures ever to walk on land thrived for 150 million years, are the quintessential icons of things big and prehistoric. Among sauropods, the family Diplodocidae is represented by some of the most gigantic dinosaurs known. Their popularity is huge, drawing visitors continuously to museums where they are exhibited. Two of the most famous dinosaur fossils known worldwide belong to this family – The American Museum of Natural History's (AMNH) "*Brontosaurus*" (*Apatosaurus*) in New York, and in Pittsburg, the Carnegie Museum's "Dippy", (*Diplodocus carnegii).* On exhibit, these colossal skeletons capture the imagination of the visitor in a way that is both humbling and thrilling.

Despite their popularity, sauropods are some of the most poorly understood dinosaurs. Much of their ontogeny,

functional morphology, and sexual dimorphism remain virtually unknown. So too are their taxonomic relationships, as seen, for example, in the history of *Brontosaurus*, which, alas, is noted for its rather embarrassing taxonomic paleontological blunders. Major examples include changing the name *Brontosaurus* to *Apatosaurus*, and replacing its skull that was mounted on the skeleton for more than 50 years. This skull was modeled after a *Camarasaurus*, a member of a different sauropod family. The correct cranium is completely different, in being smaller, more delicate, and proportionately longer in comparison. The name *Diplodocus* like *Brontosaurus* will never lose its popularity despite the rigors of taxonomic nomenclature.

Notwithstanding the popularity of these dinosaurs, this paper aims to change yet again, the way these creatures are viewed, with some rather radical conclusions with respect to their paleobiology and paleoecology. This report's principal objective is to document the most recently gathered

and updated paleontological information concerning the Dana Quarry diplodocids, and to make comparisons and to draw conclusions that reflect this new data.

The Dana Quarry site has produced some of the most important dinosaur discoveries made in North America. Since it is an active locality, its data must be revised often, and therefore, future reports are planned. Formal scientific publication is also intended for the Dana specimens once they are properly accessioned in institutional homes. Five outstanding specimens bearing the nicknames: Twinky (DQ-TY), Brontodiplodocus (DQ-BS), Sleeping Beauty (DQ-SB), Prince (DQ-PC) and Einstein (DQ-EN) are the newest discoveries, ranking as the best-preserved, most complete, diplodocid specimens known from this group of dinosaurs to date. Of the five specimens represented, four are adults and one is a half grown or adolescent individual all from the same species. Three other skeletons are also known from partially exposed elements, but they are still in the ground and will not be considered in this report. However, enough of their skeletons are exposed to allow some identification to be done, two are females and the third is male, all three examples represent adult individuals of *Amphicoelias brontodiplodocus*. Each additional stage of their skeletal preparation provides us with new information, enabling more accurate reconstructions of certain aspects of their paleobiology. Examination of these specimens has yielded substantial information on their species' phenotypic variation from a single bedding plane, an instance of time not previously documented. Thus these Dana Quarry specimens represent a "Rosetta Stone" for sauropod paleobiology.

Documented in this preliminary report, are the first crania found in direct association with their respective skeletons. Specimen DQ-BS is complete with uncrushed skull and lower jaws articulated to the cervical series. The skull in the largest specimen, DQ-PC, was found as complete but disarticulated, unquestionably associated with its cervical series in situ. The first discovered skull DQ-EN was found not as complete but is unquestionably associated with the skeleton. The teeth and braincase in the skulls in all these individuals differ only in proportional size, and otherwise are very similar.

The first completely known axial skeleton is preserved in the youngest individual (DQ-TY), this extraordinary specimen allows for the first time the location and identification of individual vertebrae to be made with accuracy, a critical aspect in determining the complicated ontogenetic development in vertebral transitions. It also displays elongated cervical ribs that overlap one another, the best specimen preserving this primitive diplodocid trait. This feature may occur early only in this diplodocid's ontogeny, since the cervical ribs in the adult specimen DQ-SB are not as long. Ontogenetic variation is also seen in the length of posterior cervical vertebrae. In DQ-TY these neck elements are proportionally shorter than in DQ-SB and DQ-BS demonstrating that the posterior cervical vertebrae continued to grow. This implies that the diagnostic differences cited in comparisons between *Diplodocus carnegii*

and *Barosaurus lentus* may be ontogenetic, not phylogenetic, in origin.

Mid caudal vertebrae in three specimens DQ-TY, DQ-SB and DQ-BS display variation not seen before in the degree of ventral sculpting in the vertebrae and diversity in chevron shapes and proportions. One specimen DQ-SB bears an interesting pathology, presumably caused by using its tail as a weapon.

All five skeletons preserve complete associated forelimbs allowing accurate limb bone ratios to be determined. The bones of the hind limb are equally complete and in three specimens the femoral shaft is rounded in cross-section. In DQ-EN and DQ-PC the femur is broadened, but otherwise, resembles in other details the holotype of *Amphicoelias altus*. Right and left ossified calcanea are preserved in the articulated feet of one specimen, DQ-SB. A well-preserved pair of clavicles were found in situ with the skeleton belonging to DQ-SB, and one isolated clavicle found near the scapula with DQ-TY.

These five Diplodocid skeletons are recognized as belonging to a new basal species, "*Amphicoelias brontodiplodocus*". They form part of a new fauna and flora originating low in the Morrison Formation, thus represent the oldest diplodocid species known in this formation. *Amphicoelias brontodiplodocus* is characterized as having considerable ontogenetic and individual variation. Moreover, sexual dimorphism in the Dana sample is recognized; of the two morphs that exist, one displays massive broad neck vertebrae with heavier limbs, in contrast with the other morph, which displays narrow cervicals, slender limb bones with a proportionately longer tail. These morphs are indentified as male and female respectively. It is believed that specimens referred to *Apatosaurus*, *Suuwaasea* and *Supersaurus* may also belong in *Amphicoelias*, representing males of this genus.

Institutional Abbreviations. AMNH, American Museum of Natural History, New York, New York; **BYU**, Brigham Young University, Provo, Utah; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **DMNH**, Denver Museum of Natural History, Denver, Colorado; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **NSMT**, National Museum of Tokyo.; **USNM**, United States National Museum, Washington D.C.; **SMA,** Sauriermuseum Aathal, Switzerland; **YPM**, Yale Peabody Museum, New Haven, Connecticut, and **UWGM**, University of Wyoming Geological Museum, Laramie.

DANA QUARRY STRATIGRAPHY & TAPHONOMY

The Dana Quarry site is located at the western edge of the Bighorn Mountains near the town of Ten Sleep in Washakie County, Wyoming. This site was discovered more than fifteen years ago by the present landowner, but its scope and importance were unknown until the summer of 2006, when the Dinosauria International, LLC team organized

Fig. 1. Excavation of DQ-BS in 2008 during the final stages of pedestaling the bones before plaster jackets were applied. At this spot numerous carnivore teeth were discovered belonging to species of *Allosaurus*, *Torvosaurus* and a small unidentified species.

proper excavation and documentation of it. These recent excavations have revealed a spectacular Morrison locality, preserving an enormous multi-species dinosaur death assemblage.

The Morrison Formation is a sedimentary rock unit with exposures most commonly seen in the Western States of New Mexico, Colorado, Utah and Wyoming. Throughout most of its range, the Morrison Fm. comprises mudstone, sandstone, siltstone and limestone and its layers are light grey, greenish gray, or red, Mook 1916, Dodson et al 1990, Foster 2003. In Wyoming, it ranges into the Bighorn basin where the Dana Quarry is located. Here the fossiliferous layers are comprised mostly of soft sandstones that are predominately yellow-ochre in color. These yellowish layers preserve both plant and animal remains possibly representing a unique depositional event. In these layers, gypsum inclusions are common together with lenses of grey mudstones. Moberly 1960 describes the Morrison Fm. in the Big Horn Basin as being an average of 200 feet thick containing calcareous sandstone beds that grade from silty or sandy limestone to pure limestone. The most common rock type is "calcareous, somewhat sandy mudstone or shale, colored shades of green, gray, olive, and yellow" (Moberly, 1960). Similar yellow rocks are also reported north of the Dana site at Howe Quarry but it is not certain how they correlate with each other. The Dana Quarry fossil layers sit just above the Morrison-Sundance Fm. contact whereas the Howe Quarry is mapped 120 feet above the Sundance Fm., Michelis 2004. However, these sites bear similar types of sediments and appear to represent temporal equivalents based on faunal similarities. We therefore believe that Dana

and Howe quarry sites represent approximately the same time periods despite the different stratigraphic levels.

In addition to the stratigraphic similarities, the mass accumulation of sauropods bones and close geographic proximity of Howe Quarry warrants comparisons with Dana Quarry. The diplodocid sample reported by Michelis 2004 from Howe Qu. is dimorphic in nature the two recognized taxa are *Apatosaurus* and *Barosaurus*. *Apatosaurus* is identified on the angle of neural spines in the anterior caudal vertebrae and from a small number of limb elements, curiously no cervical vertebrae have been reported belonging to this genus. Interestingly, cervical vertebrae identified as *Barosaurus* are well represented. Both sites are comparable in species richness, with Dana exceeding Howe in quality in terms of associated skeletons. According to Michelis 2004, 2,500 bones from twenty-five individuals have been excavated at Howe Quarry. By comparison, Dana has produced estimated 3,500 bones belonging to twelve individual skeletons, which are largely articulated and most possessing associated cranial material. The carnivores are also better represented in Dana with over 100 shed teeth belonging to *Allosaurus*, *Torvosaurus* and several unidentified small carnivores. *Allosaurus* makes up approximately 55% of the total sheds found so far. Howe Qu., on the other hand, reports 60 carnivore teeth. Moreover, Dana Quarry's mass mortality is largely of one species with young to adult individuals suggests that it represents a natural population sample, in contrast to Howe it is determined not representing a "herd". Dana has not produced skin impression or evidence of mummification as in Howe Quarry. Taphonomically, both sites are different, disarticulation of skeletons in the Dana specimens appear

Fig. 2. Above 2008 excavation of DQ-BS during the final stages of plaster jacketing ready for shipping. Morrison Formation exposures can be seen in the horizon north of the fossil site. The Dana fossil beds display a strong eastward tilt resulting from the uplift of the Big Horn Mountains. See close up of those exposures below.
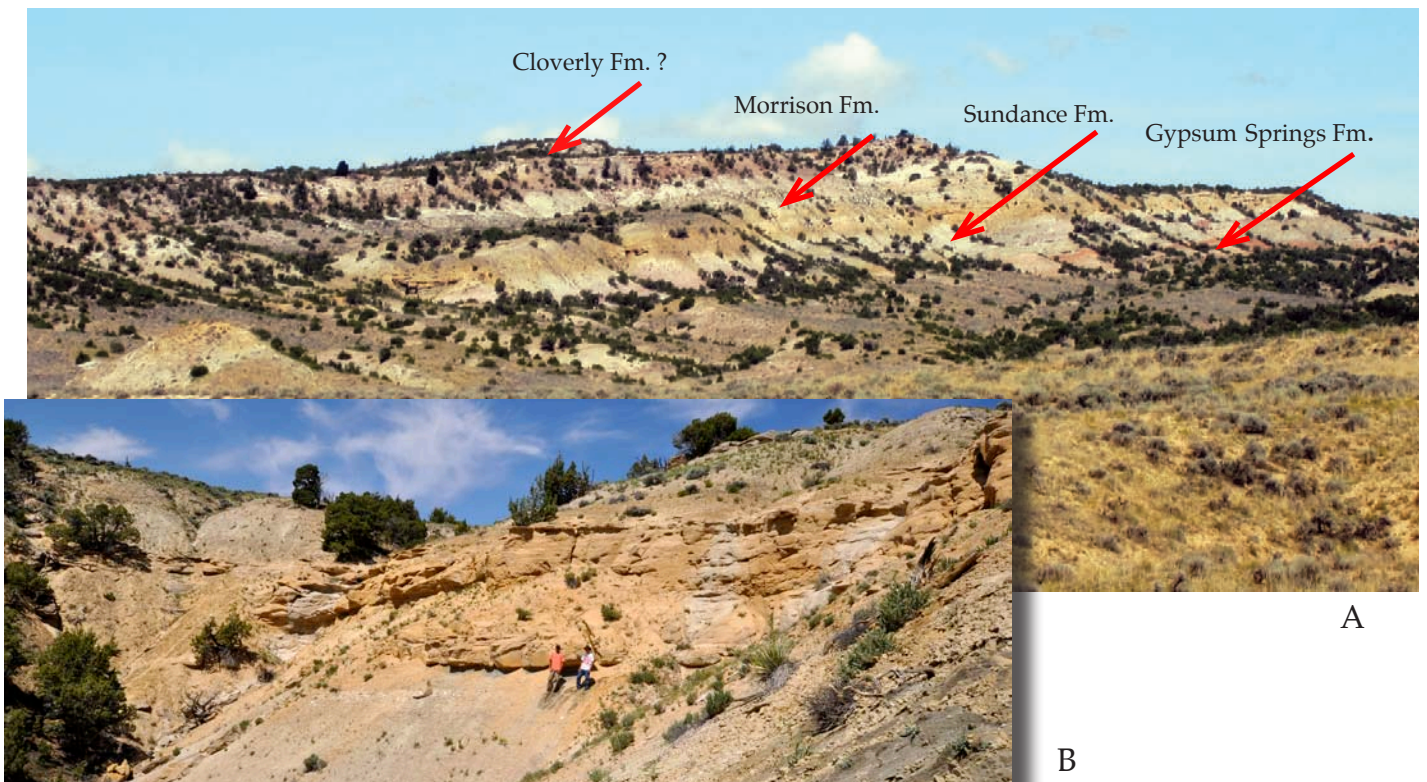

Fig. 3 A-B. Exposures with the various formations labelled. Contacts of the Gypsum Springs, Sundance , Morrison and possibly the Cloverly (Pryor Conglomerate?) on top. Wesley Linster and Steve Finch stand at the contact of the Sundance and Morrison Formations. The fossil layers are immediately above their heads. Note the distinctive yellowish color of that rock layer.

to be solely from scavenging while at Howe it is apparently from both scavenging and hydraulic disturbance.

In contrast to the drier southern ranges of the Morrison Basin, the northern Dana site had most likely, a humid environment, being close to swamps and marshes near the Sundance Sea. While *Camarasaurus* is the most abundant dinosaur reported in the Morrison Formation, it is poorly represented in the Dana Quarry site. *Amphicoelias brontodiplodocus* is the most frequently occurring herbivore species preserved. These facts support the presence of different environmental conditions during that time in stark contrast to what is known in the upper beds in the southern parts of the Morrison Formation.

The Dana fossils are much older than most other Morrison localities - including those from the Salt Wash Member in Utah - possibly dating to latest Oxfordian Stage about 156 million years ago. The quarry is situated within the lower part of the Morrison Fm. The fossil producing layers are approximately twenty - thirty feet (6-9 meters) above the Sundance Formation (Fig. 3). The contact of these two formations is visible on the eastern slope of the site. Looking west from the quarry on the ranch property, one can see conglomerate sandstones that are possible remnants of what may be the basal Cloverly Fm. (Pryor Conglomerate), sitting on top of the Morrison Fm. Thus, at this locality, the Morrison Formation appears to be sandwiched between the Cloverly Fm. above and the Sundance Fm. below. Unless an unconformity exists between those two formations, the Dana Quarry can be considered Lower Morrison in age. The best example of the position of the fossil producing layer is about one mile north from Dana site here a section exposes clearly the contact layers of the Sundance and Morrison formations, (see Fig. 3)

Preliminary faunal comparisons support an older biostratigraphic position of the Dana Quarry. Supporting evidence for an older time period lies in the presence of two primitive dinosaur species of *Allosaurus* and *Hesperosaurus*. In the *Allosaurus* ("*jimmadsoni*"), skeleton, the skull is characterized by a horizontal lower boarder of the jugal, manus claws less hooked and the general slenderness of the skeleton, in comparison to the more derived, younger in age, *Allosaurus fragilis*. One primitive stegosaur discovered at the quarry, *Hesperosaurus mjosi*, is known only from Lower Morrison localities. These two dinosaur species are reported only from sites exposing the lowermost sedimentary layers of the Morrison Formation. Hence it is reasonable, based on Dana Quarry dinosaur paleobiological data, to assign to it a Lower Morrison age. In addition to *Amphicoelias brontodiplodocus*, the Dana Quarry "time capsule" has produced the following dinosaur fauna: *Camarasaurus sp., Brachiosaurus sp., Allosaurus jimmadsoni, Ornitholestes new species, cf. Coelurus, Torvosaurus sp., Ceratosaurus sp., Othnielosaurus consors, Camptosaurus sp., and Hesperosaurus mjosi.* Taking into account the synonymies presented in this report, the diversity of dinosaur species is as great in the lower biozones of the Morrison Formation as in the upper zones 2 and 3, Turner and Peterson 1999.

The Dana Quarry is rich in plant fossils too, containing the remains of many species of extinct plants including types of horsetails, ferns, cycads, and several families of conifers. An assortment of fossilized seeds and cones are quite common. This is a unique depositional site preserving both animal skeletons and plant remains that were not transported prior to burial. Lower vertebrates are rare, absent in fish, amphibians, lizards, and crocodilians; a sole exception, one turtle skeleton has been uncovered. This nearly complete shell with skeleton has been donated to the Houston Museum in Texas. Early mammals such as docodonts, symmetrodonts, and triconodonts have yet to be discovered. The paucity of aquatic species strongly implies that the Dana site was a seasonal, not a permanent, body of water, such as an ox-bow lake. Numerous small water-worn bone fragments are found scattered throughout the fossil layers demonstrating that constant moving water was present in the area. These bone fragments average less than twelve inches in length and are unidentifiable. Insect borings similar to ones seen, for example, at Bone Cabin Quarry West are common at this site. DQ-SB and DQ-TY show some acid etching to the bone surface. DQ-BS, DQ-PC and DQ-EN are scarred with tooth marks and insect borings, and the bones of these skeletons show the most amount of disturbance and disarticulation. The rib cages in all the skeletons are partially disarticulated, but not so much on the side facing down into the mud, suggesting that scavenging displaced these ribs apart, not a build-up of gas released from post-mortem decay.

The Dana Quarry is unique in offering great opportunities to study both dinosaur osteology and taxonomy from complete specimens. Its diverse associated fossilized fauna and flora are relevant in elucidating Morrison dinosaur paleoecology and biostratigraphy. Finally it has the potential of being one of the best North American terrestrial Jurassic paleobiological sites, since it surpasses most in completeness and quality of specimens.

SYSTEMATIC PALEONTOLOGY

Order SAURISCHIA
Suborder SAUROPODOMORPHA
Family DIPLODOCIDAE

Genus: *Amphicoelias* Cope

Type species: *Amphicoelias altus* Cope

Emended diagnosis: The genus *Amphicoelias* differs from other diplodocid genera in the following characteristics of primitive and derived features. Skull microcephalomorph, rostrum long; premaxillae caudally elongate, quadrate rostroventrally inclined; external nares opening dorsally above orbits; basipterygoid processes slender and elongate, occipital condyle ventrally positioned. Upper and lower teeth reduced in number and modified into sub-equal lengths of crown and root that are long and slender, spaced

Fig. 4. Left lateral profile close up of the *Amphicoelias brontodiplodocus* (DQ-BS) skull displaying exquisite preservation (see also back cover). The right quadrate, dentary, including several scattered teeth can be seen imbedded in the matrix. The lower jaws are preserved in articulation. Only the premaxillae are displaced and cannot be seen. Cranial openings are complete without distortion. The occipital condyle is ventrally positioned at near right angle to the long axis of skull. Note the textured surface displaying pits and grooves of the maxilla and dentary

apart and retained in front of jaws; jaws behind preantorbital fenestrae edentulous. Mandible long slender with expended symphysis. Fifteen cervical vertebrae, 2nd - 15th elongated with the 14th possessing the longest centrum, ten free dorsals, sacrum in adults normally comprised of one dorsal, two sacral and two caudal vertebrae. First dorsal (D 1) in the series has the longest centrum, 10th dorsal with body of neural spine off alignment with centrum, posterior dorsals, sacrum and anterior caudal vertebrae all with tall neural spines. Sacral vertebrae with ventral keels. Three sectioned caudal morphology, anterior caudals with pleurocoels (suppressed or absent in males) and expanded transverse processes; centrum of anterior caudals gradually decreasing posteriorly in size until, at a mid-point, they increase in size and robustness from (16th-20th) before decreasing again in size where they meet the supernumerary whiplash series. The approximately forty or so supernumerary caudals are sub-equal in length. The location of enlarged mid caudals or "disproportionately enlarged" transitional series is variable. Caudal fusion is also variable depending on the individual and age, and can occur in singles or in sets of two. Compact bone construction is dense in posterior caudals starting from "disproportionately enlarged" series. Anterior chevrons without anterior processes but remaining posterior ones diversely shaped depending on the location of the tail, starting in mid-tail from a simple elongated paddle then to forked and rod-like "double beam" shape types. Anterior processes become greater in size towards the end, and reach a near equal length with the main chevron body. Forked chevrons usually located in restricted areas within mid caudal series; ischia distal ends expanded; femur elongated, straight with reduced 4th trochanter with cross section sub circular to ovate. Sternal ribs ossified.

Females: In comparison to the male skeleton, the female is slender, her cervical vertebrae more elongated, narrow generally with low neural spines, ribs delicate; axial skeleton in mature individuals, with numerous pneumatic fosse more so than in young and males; mid caudal vertebrae elongated in comparison to males. Scapula with proximal end broadened, limb bones generally slender, femur with sub circular shaft in cross section. The shafts of sternal ribs are without excessive bone growth.

Males: The male skeleton is characterized by being more massive, displaying features associated with increased body weight. For example, femur shaft and distal humerus are broadened, pleurocoels and transverse processes on anterior caudal vertebrae reduced or absent. Shaft of femur and humerus laterally expanded, tibia relative to femur length shorter than in females. Adult males are neotenic in the retention of many of these features. Neck vertebrae powerfully constructed, cervical centrum broad, ribs hypertrophic, strongly built and extended ventrally, neural spines well developed, bifurcating in the anterior in C 4-6, caudal vertebrae shorter without ventral trough. Sternal ribs with excessive bone growth.

Ontogeny: Limb bones in juveniles disproportionately larger in comparison to the axial skeleton. This feature continues in half-grown individuals. Neural spines bifurcated v – shaped, dorsals and sacrum and anterior caudal vertebrae with short spines. Deep ventral trough in mid caudal vertebrae occurs in mature female individuals, but not in juveniles. Elongate pubic peduncle but reduced in adults. Ball or convex joint on whiptail caudals developed in mature individuals. Scapula longest skeletal element reduced in adults.

Synonyms*: Apatosaurus* Marsh*, Barosaurus* Marsh*, Diplodocus* Marsh*, Seismosaurus* Gillette*, Eobrontosaurus* Filla and Redman*, Supersaurus* Jensen*, Tornieria* Frass and *Suuwassea* Harris and Dodson

Included species: *Amphicoelias altus, A. brontodiplodocus* sp. nov., and possibly *A. emilieae*

Type Locality: Morrison Formation, Quarry 12, Garden Park, Colorado

Amphicoelias brontodiplodocus sp. nov.

Holotype: Although this study recognizes the Dana sample as representing a new species of *Amphicoelias*, we do not designate a type specimen until part of the collection is accessioned in an institution. The use of *A. brontodiplodocus* is temporary and for convenience in discussions presented herein, and not as an official nomenclatural declaration.

**Hypodigm**: Dana Quarry sample; DQ-BS, DQ-TY, DQ-SB, DQ-EN, and DQ-PC

Etymology: Marriage of two popular dinosaurs names *Brontosaurus* and *Diplodocus*

Locality: Dana Quarry, Ten Sleep, Washakie County, Wyoming. T. 48N, R. 89W, Sec.6, NW1/4 SW1/4. - GPS: N44o 03.078 W 107o 27.503

Horizon: Lower Morrison Formation

Diagnosis: Differs from *Amphicoelias altus* in the following combination of characters: Basipterygoid recess present; antiorbital fenestra proportionately small; proatlas present, neural spine bifurcate past the 9th cervical; cervical ribs elongate, overlapping, past centrum length; ossified calcaneum present; claws tapered. Axial skeleton in males generally less elongated with cervical ribs hypertrophic; unfused clavicles present, lack of pleurocoels on the anterior caudals, and lack of ventral sculpting on mid-caudal vertebrae until adult stage, and prezygapophysis on caudal vertebrae short. *Amphicoelias brontodiplodocus* is distinguishable from *Amphicoelias "Suuwassea" emilieae*, in lacking the following characters: no post parietal foramen, "optic" foramen not conjoined, neural spine bifurcation past 9th, and neural spines anteriorly position on cervical centra C 3-5.
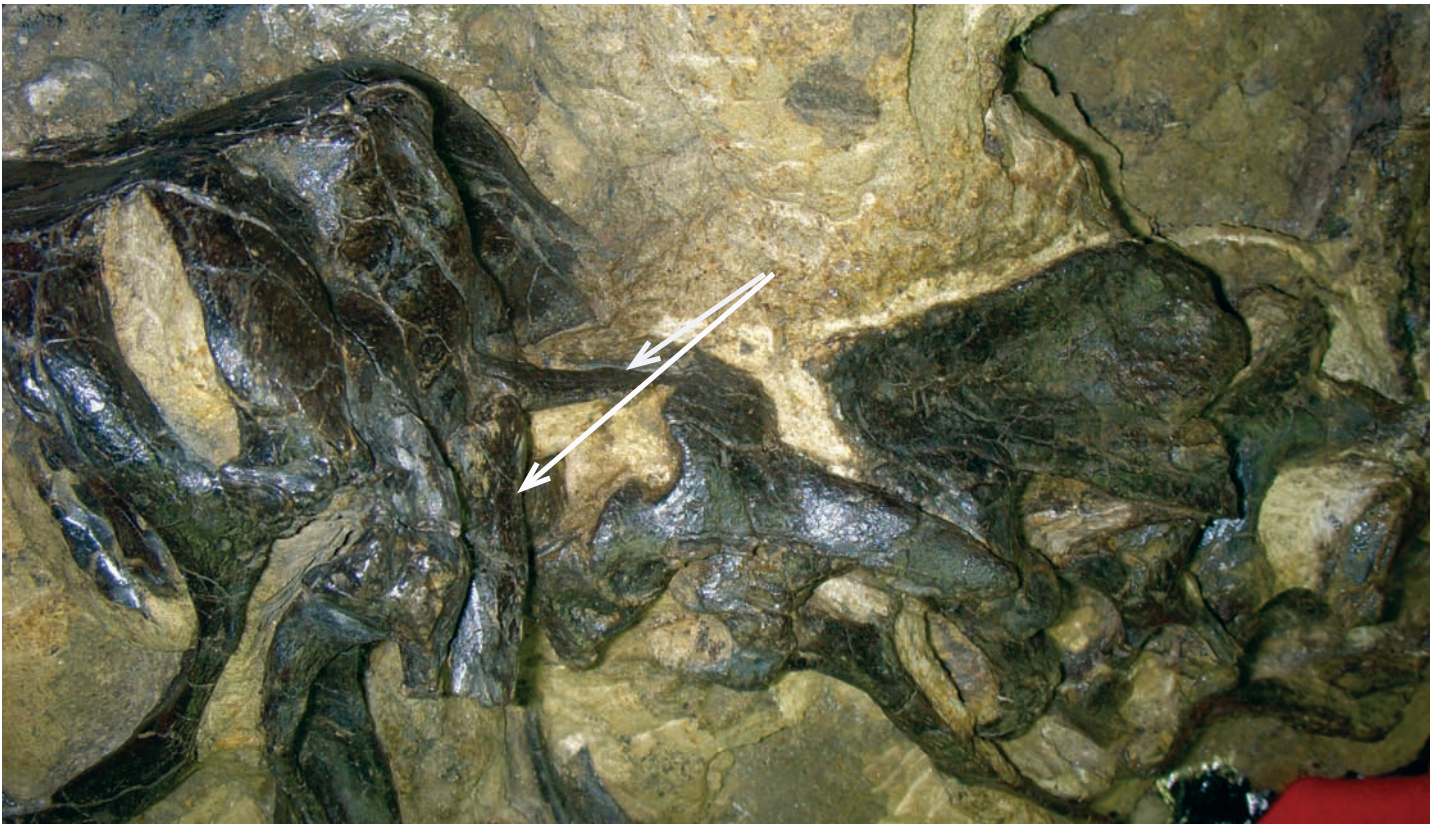
Fig. 5 A-C. Top photo shows proatlas bones in place, positioned above the occipital condyle in DQ-BS. Bottom photos B and C, shows the delicate sclerotic bones in place, and strongly flexed articulation of the anterior cervical vertebrae. Arrow in photo C indicates the elongated overlapping rib preserved on the axis. Photo C shows only 5 of the twelve vertebrae found completely articulated with the associated skull and lower jaws

Fig. 7 A-H. Right and left radii and ulnae A; right and left humerii in posterior and anterior views respectively B; Nicely preserved ilium, ischium, and pubis C.; left coracoid D; pes claw E; right and left fibulae F; left tibia posterior view G; and nearly complete left hindleg Barry James for scale. All elements belonging to the skeleton DQ-BS

Table 1. MEASUREMENTS FOR DQ-BS

SKULL:

Measurements taken from sufficiently exposed skull elements are as follows:

Length from laterally exposed edge of the left maxilla to sagital nuchal crest – 331 mm

Length of preantorbital foramen – 29.3 mm
Length antorbital fenestra - 80 mm
Greatest width of orbit - 119.8 mm
Dorsal ventral height of orbit - 82.3 m
Length of lateraltemporal fenestra – 123 mm
Length of left lower jaw – 269. 8 mm

AXIAL:

C 1 - 2.5cm centrum length 2.3 cm
C 2 - 16.5cm centrum length 9.2 cm
C 3 - 24.3cm centrum length 12.8 cm
C 4 - 28.9cm centrum length 13.9 cm
C 5 - 37.2cm centrum length 22 cm

C 6 - 38cm
C 7 - 39cm
C 8 - 41cm
C 9 - 45cm
C10 - 49cm
C11 - 55cm
C12 - 57cm
C13 - 59cm
C14 - 61cm
C15 - 53cm

Dorsal
D 6 - centrum 23 cm
D 7 - centrum 22.5cm
D 8 - centrum 21 cm
D 9 - centrum 20 cm
D10 - centrum 18.5cm
Pelvic
ischia rt & lt. 81cm
pubes rt. & lt. 89 cm

APPENDICULAR:

Humerus, rt. 91cm
Humerus, lt. 90cm
Ulna, rt. 76cm
Ulna, lt. 75cm
Radius, rt. 72cm
Radius, lt. 71cm
Scapula, lt. L, 115cm, W 51cm
Coracoid, lt. L, 46cm, W 35.5 cm
Femur, rt. 142 cm
Femur, lt. 141 cm
Tibia, rt. 102 cm
Tibia, lt. 101 cm
Fibula, rt.111 cm
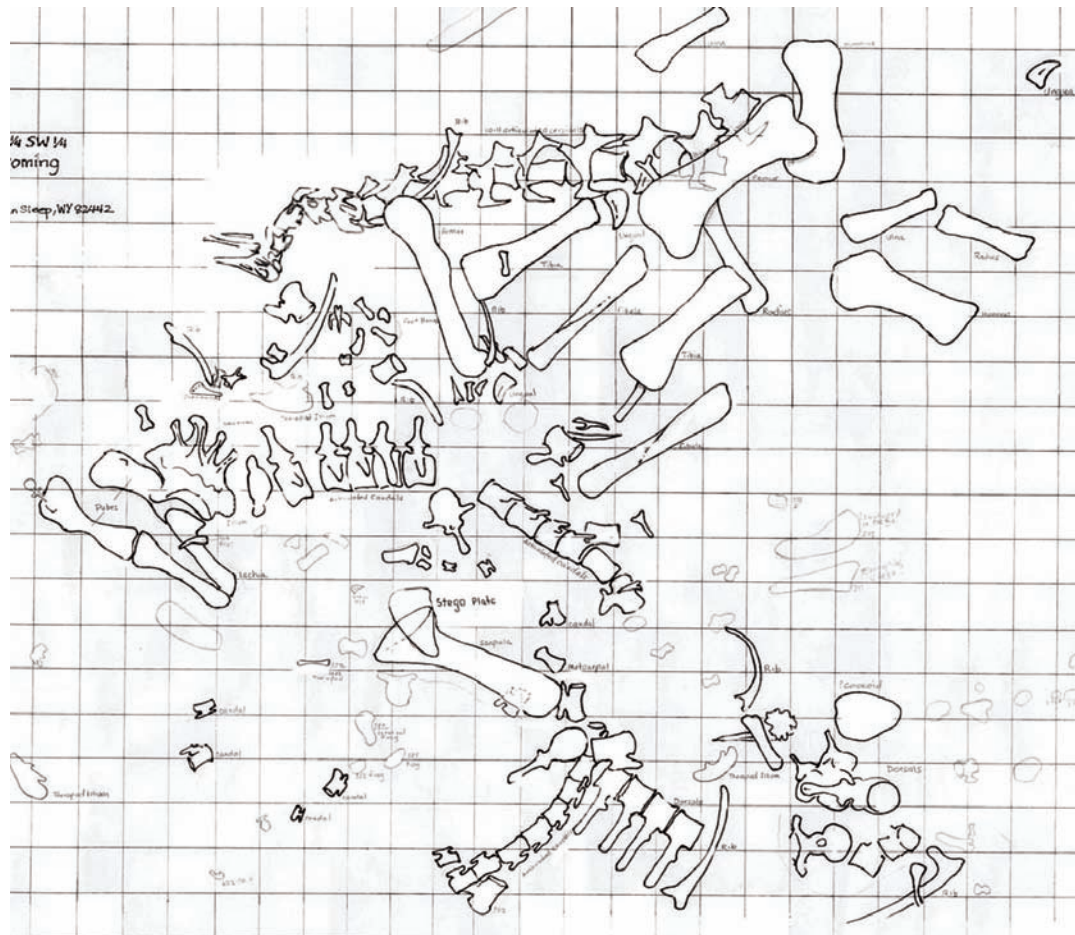Fibula, lt. 109 cm
Astragalus, rt., L 25 cm, W 15 cm

Fig. 8. The bone map above displays the position of the bones exposed in the quarry belonging to DQ-BS. Distribution of bones is attributed to scavenging as evident of the numerous tooth sheds and tooth scars on the bones. Map does not represent all the bones excavated. See also Fig. 1

Fig. 9. Wesley Linster poses with DQ-TY for scale. In the skeleton's death pose, the complete axial skeleton can be seen, which was found articulated without interruption. To the right of the line, is a partially exposed section of caudal vertebrae with femur lying visible to the right belonging to an specimen identified as an adult male individual.

DESCRIPTION AND COMMENTS FOR
AMPHICOELIAS BRONTODIPLODOCUS

In addition to first-hand examination, the skeleton descriptions belonging to Twinky (DQ-TY), Brontodiplodocus (DQ-BS), Sleeping Beauty (DQ-SB), Einstein (DQ-EN) and Prince (DQ-PC) were made from observations and notes taken in the field and laboratory over the years 2006-2010. The use of photography and drawings were also used to prepare descriptions when the actual specimen could not be examined while in plaster jackets. All five specimens are, at present, in various states of preparation and cannot individually be described in more detail at this time. The foregoing is therefore a preliminary description from a work-in-progress. Hence, future reports are planned including descriptions of new specimens. Many of the photographs presented here reflect these various states.

DQ-BS = "Brontodiplodocus", Table 1, Figs: 1, 5 - 8, 19, and 21

This specimen marks the first skeleton to be found with an intact skull preserved and articulated to a nearly complete series of cervical vertebrae. The skeleton is estimated to be 80-90% complete and, when mounted free standing, 24 meters (81-feet) in length. Preliminary observations suggest the individual was a young adult when it died. However, the exact age of this individual is under investigation at the Division of Paleontology, American Museum of Natural History. This study will rely on taking a thin section of sclerotic bone for dating; a first for sauropod paleobiology.

The skull is preserved intact, displaying all the delicate cranial bones without distortion (Figs. 4 & 5). Even the fragile sclerotic bones are preserved complete in their orbital cavity. The lower jaws are preserved articulated. Only the premaxillae were displaced during excavation and cannot be seen in the accompanying photo. In addition to the orbtit and nasal openings, the preantorbital, antorbital, supratemporal, and lateral temporal fenestrae are all complete and without distortion. Resting above the occipital condyle are the small and rarely found proatlas bones, which are preserved in situ along with the atlas. The occipital condyle is ventrally positioned at near right angle to the long axis of the skull, as in all Morrison diplodocids.
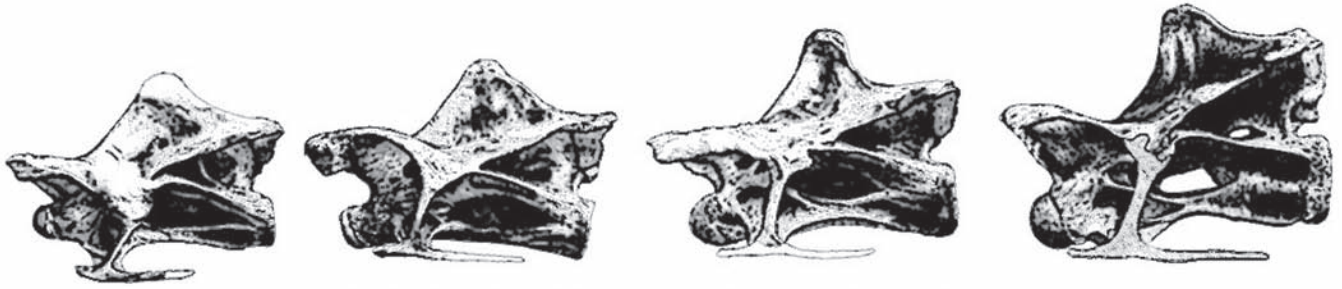
Every bony process, spine and rib along the cervical series is preserved on the thirteen vertebrae that were all found articulated to each other. The 14th cervical was in direct contact but not articulated, while the 15th was unearthed several feet away, near the pelvis. Thus, the bones of the head and neck in this individual are captured as they were in life. Interestingly, most of the neck vertebrae where preserved locked in a straight row except for the last six which are noticeably flexed in articulation. Moreover, the ends of the centra incline suggest that the neck was held normally in a somewhat flexed position.

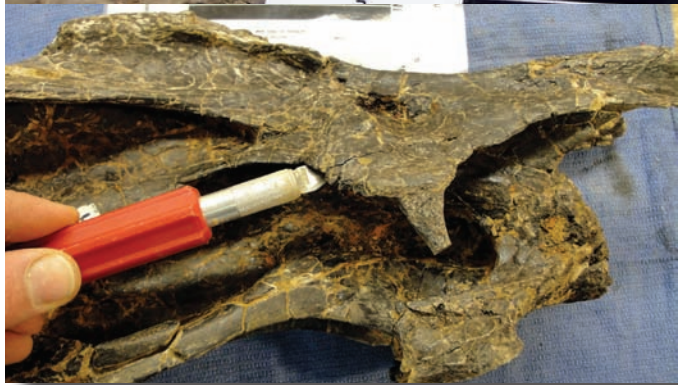The pelvic elements (Fig. 7) were also preserved
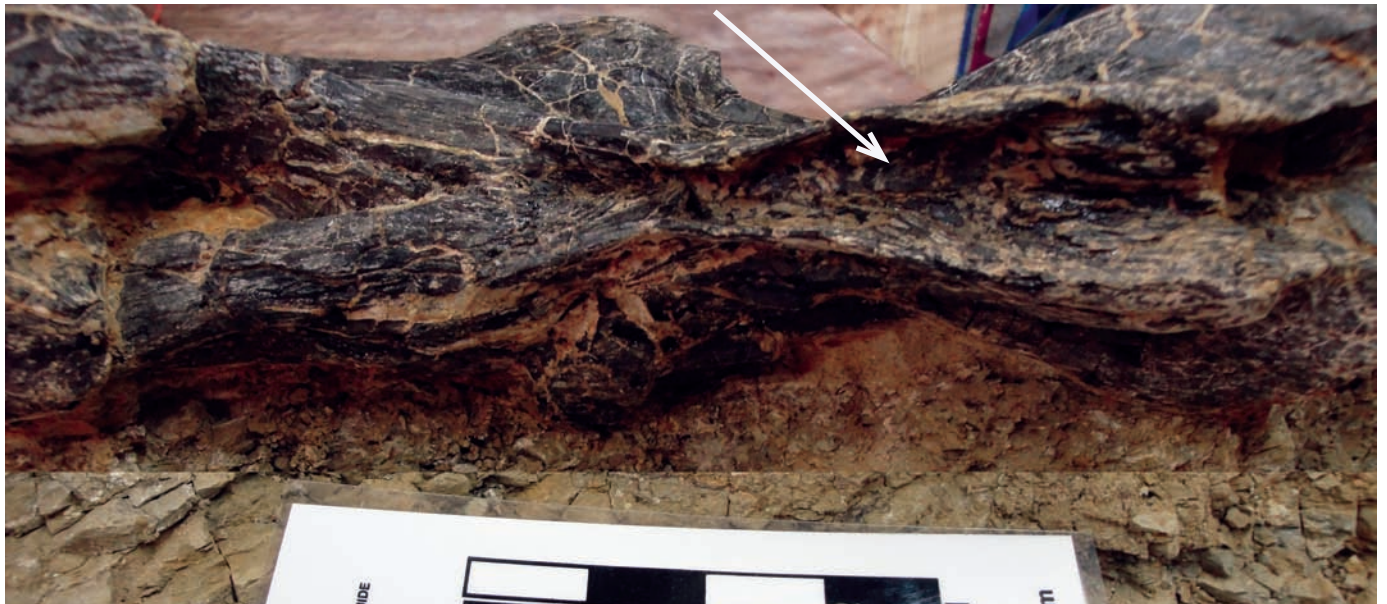
Fig. 10 A-D. Top, cervical vertebrae # 7-10 with ribs removed belonging to DQ-TY. Below (B) illustrations of C 7-10 from Hatcher 1901 reversed for comparison to show proportional similarity, not to scale with A. Dorsal view of C 9 showing first divided neural spine in the DQ-TY series, inserted below close up of C6 displaying fine detail. Divided neural spines commence at C 3 in the type of *D. carnegii*. Cervical ribs belonging to DQ-TY's vertebrae can be seen in jacket as found in Fig. 28a.

12

A

B

C

D

E

Fig. 11 A-E. A., right lateral view of dorsal, sacral, and anterior caudal vertebrae articulated with ilium, partially exposed in field jacket. B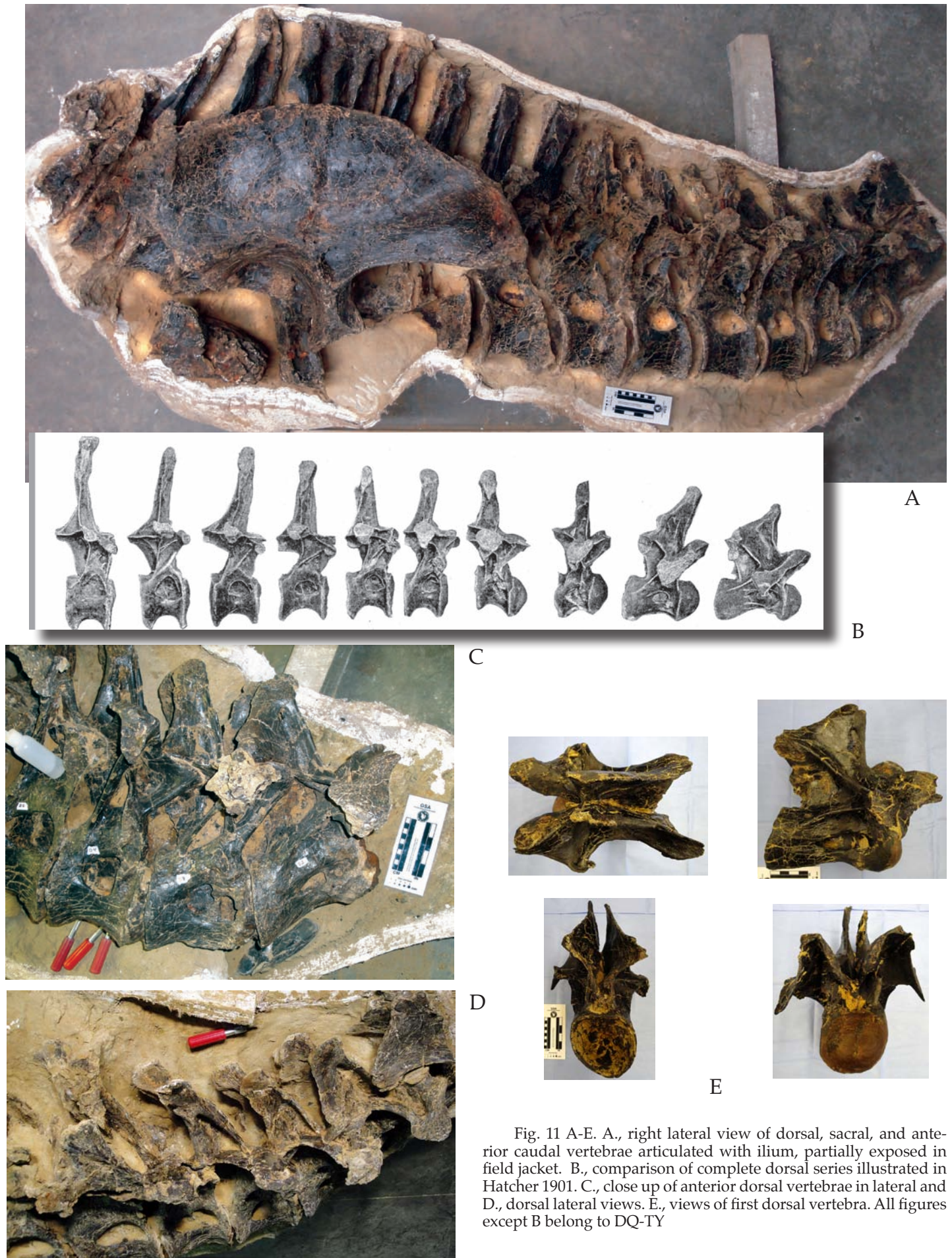., comparison of complete dorsal series illustrated in Hatcher 1901. C., close up of anterior dorsal vertebrae in lateral and D., dorsal lateral views. E., views of first dorsal vertebra. All figures except B belong to DQ-TY

A

B

C

D

E

Fig. 12 A-F. A., mid caudal vertebrae exposed in jacket showing chevrons articulated in place. Note the disproportionately large vertebrae with forked chevrons. B., Caudal vertebrae laid out on a table in order belonging to DQ-TY. C., close up of the same in photo but in more ventral view to show no ventral depression a typical feature of immature individuals. D., hook shaped neural spines are a distinct feature in both males and female in *Amphicoelias*. E., whiptail caudals are sub equal in length and were found spaced apart in the matrix, the elements pictured have not developed convex ends characteristic of fully adult individuals. F., "hooked " caudals displaying spacing between centra.
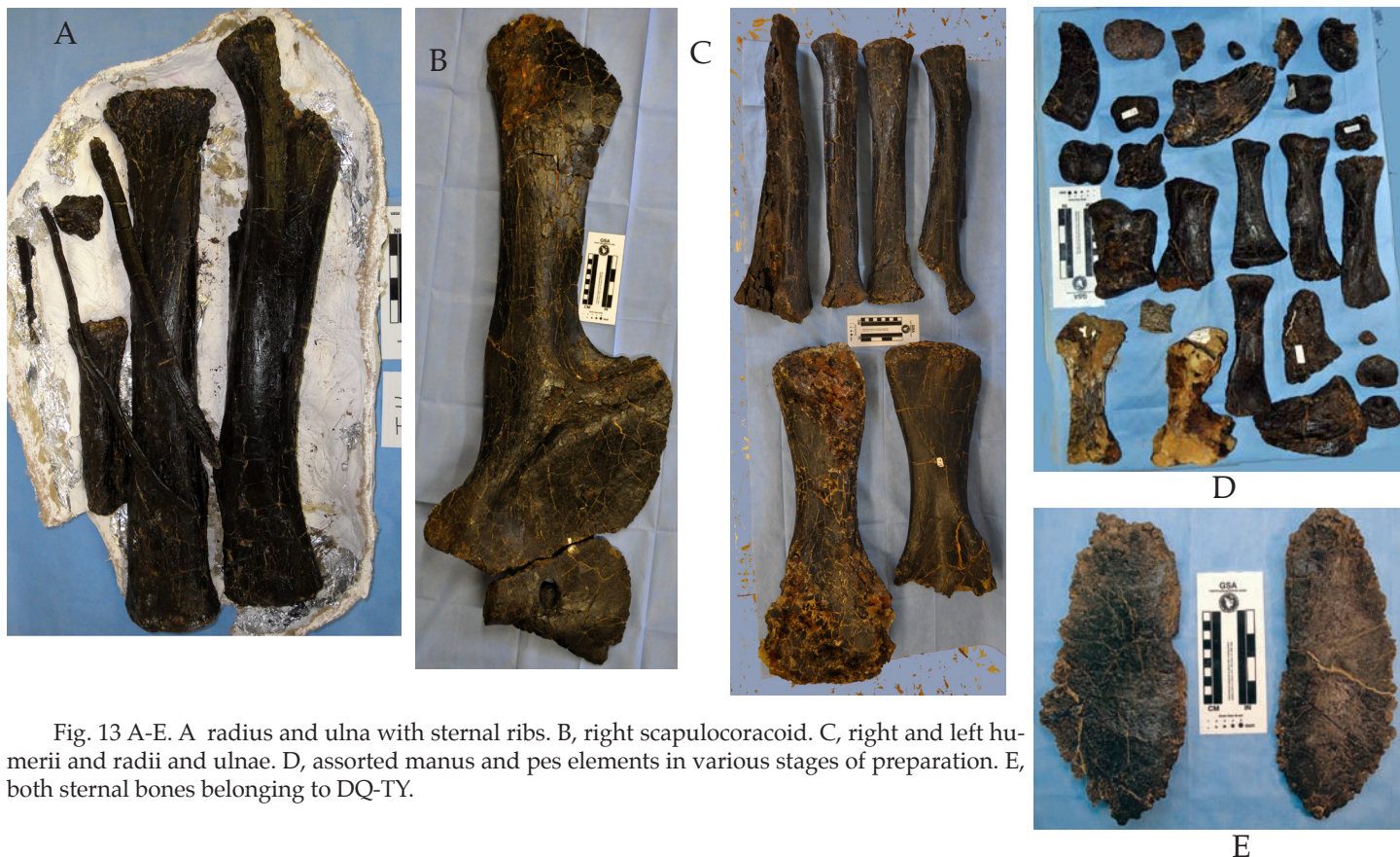

F

Fig. 13 A-E. A radius and ulna with sternal ribs. B, right scapulocoracoid. C, right and left humerii and radii and ulnae. D, assorted manus and pes elements in various stages of preparation. E, both sternal bones belonging to DQ-TY.

together in semi-articulation along with five fused sacral vertebrae. The sacral elements and the adjoining dorsals (D9 &10) suffer from considerable post-mortem distortion due to compression. The massive limbs are preserved complete and uncrushed without deformity, adding greatly to the skeleton's impressive appearance. Associated sets of foot bones, including claws, where also recovered. Only the right scapula and the whiplash section of the tail vertebrae are noticeably absent. Ongoing excavations may eventually expose them. Two pairs of mid caudal vertebrae are fused. Our quarry map (Fig. 8) illustrates the close distribution of the bones belonging to this associated skeleton.

DQ-TY = "Twinky", Figs: 9-13, 24, 28 A, and 32

The Dana Quarry has yielded magnificent dinosaur remains. One specimen, nicknamed "Twinky" (DQ-TY), is especially noteworthy due to its small size and exquisite preservation. Discovered in the spring of 2009, this new diplodocid is both the first complete specimen belonging to an adolescence individual, and the only one possessing a nearly complete axial skeleton. There are no comparable specimens housed in museum collections quite like DQ-TY. In complete paleontological context, as part of a population sample, this exceptional specimen offers unique opportunities to study ontogenetic development in sauropods.

Virtually all the bones are currently in the final stages of being carefully removed from their plaster jackets. Field observations taken from exposed bones indicate that the skeleton is approximately 70-80% complete and, if mounted free standing, may reach an estimated 12.19 -13.71 meters in length. Approximate measurements of the axial skeleton are: cervical series 3.65 m long, dorsal and sacrum 2.28 m and caudal vertebrae 7.01 m. The standing area the feet occupy may be less than 4.87 m long. Hence, DQ-TY measures about half the length of an adult specimen from the same quarry.

Several tiny teeth were uncovered besides a mass of thin bone about 20 cm long located beneath a section of caudal vertebrae, which provides some degree of probability that at least part of the skull may be preserved. These teeth are typically diplodocid in construction.

The complete axial skeleton (cervical, dorsal, sacral, and caudal vertebrae) was found articulated without interruption. This allows, with 100% certainty, identification of the exact number of elements in each vertebral group, thereby providing a template from which to compare other diplodocids. There are fifteen cervical, ten dorsal, five sacral and thirty-nine normal caudal vertebrae, unfortunately, information on the complete supernumery count is not available, as only twenty of these caudal elements were recovered.

In the skeleton's death pose, Fig 9, (see bone map inside front cover) the cervical vertebrae are flexed upward only from where they meet the dorsal vertebrae, and are positioned in straight alignment. In contrast, the preserved caudal vertebrae are arched over and positioned around the upper part of the body, suggesting that the tail, in life, can bend up and move much more freely than the elongated posterior neck vertebrae. All ten dorsal vertebrae were found intact articulated to the sacrum and positioned in a gradual

Fig. 14. Sue Wedekind and Henry Galiano carefully brush away lose sand from the well preserved skeleton belonging to DQ-SB, 2008.

downward direction from posterior to anterior, see Fig. 11. The eleventh dorsal is fused to the sacrum set of five. Only the centra of the 1st – 4th dorsal vertebrae are opisthocoelous. Neural spines bifurcate from D 1st – 5th while the remaining posterior dorsals terminate in a single knob. The centra of the five vertebrae making up the sacrum are fused, the three neural spines in the center also fused. These sacral elements (Fig. 24) are articulated without distortion to both ilia, which are complete. Unfortunately, both right and left pubes and ischia are damaged and cannot be described.

Together with the caudal vertebrae, a virtually continuous series of chevrons is preserved in exact placement showing a diversity of shapes along the tail not seen before. The most intriguing are the transitional chevrons located between the anterior single club-shaped ones and the characteristic straight double-beam types behind. In these transitional chevrons, the anterioposteriorly expanded distal processes are formed downward creating distinctive forks. This assortment of chevron shapes along the tail length is reminiscent of the condition seen in some mammalian groups that have powerful prehensile tails, as in anteaters (Edentata, Pilosa).

Another noteworthy feature is the occurrence of four over developed mid caudal vertebrae C 15th – 18th in DQ-TY. These caudals show what may be the early stages of ossified longitudinal ligaments, as seen in the fused tail vertebrae of USNM 10865 and type of *D. carnegii*. Interestingly, DQ-TY 's young individual age shows early stages of caudal vertebra fusion, a feature reported occurring only in fully-grown adults.

Towards the end of the DQ-TY tail, after the 32nd caudal, the neural spines in the whiplash section of vertebrae suddenly change into simple but robust freestanding processes with a distinctive backward hook. These spines are without zygopophysis. These hook-shaped neural spines may have helped to create a serrated edge along the tail, enhancing its flesh-cutting ability while in use.

These whiplash tail vertebrae were discovered lying buried in a continuous row and were preserved with a noticeable even spacing between each element indicating that a tough flexible tissue may have held them together in life. The spacing distance was greater in comparison to the other caudal vertebrae belonging to the same tail. Moreover, the ends of these vertebrae are not bi-convex suggesting that convexity develops in adults only. About twenty supernumerary vertebrae are present past the 32nd, but the exact number cannot be determined until complete preparation is completed. These caudal elements are subequal in length.

In addition to the exceptional axial skeleton, the limbs are also preserved in near-correct anatomical position. For example, the right hind limb (femur, tibia, fibula, and pes) is preserved in articulation folded immediately under the pelvis, in a kind of squat position. The other limbs, including the complete scapulocoracoid and sternum sets, are similarly preserved in situ very close to the front portion of the torso, suggesting rapid burial after death. Several
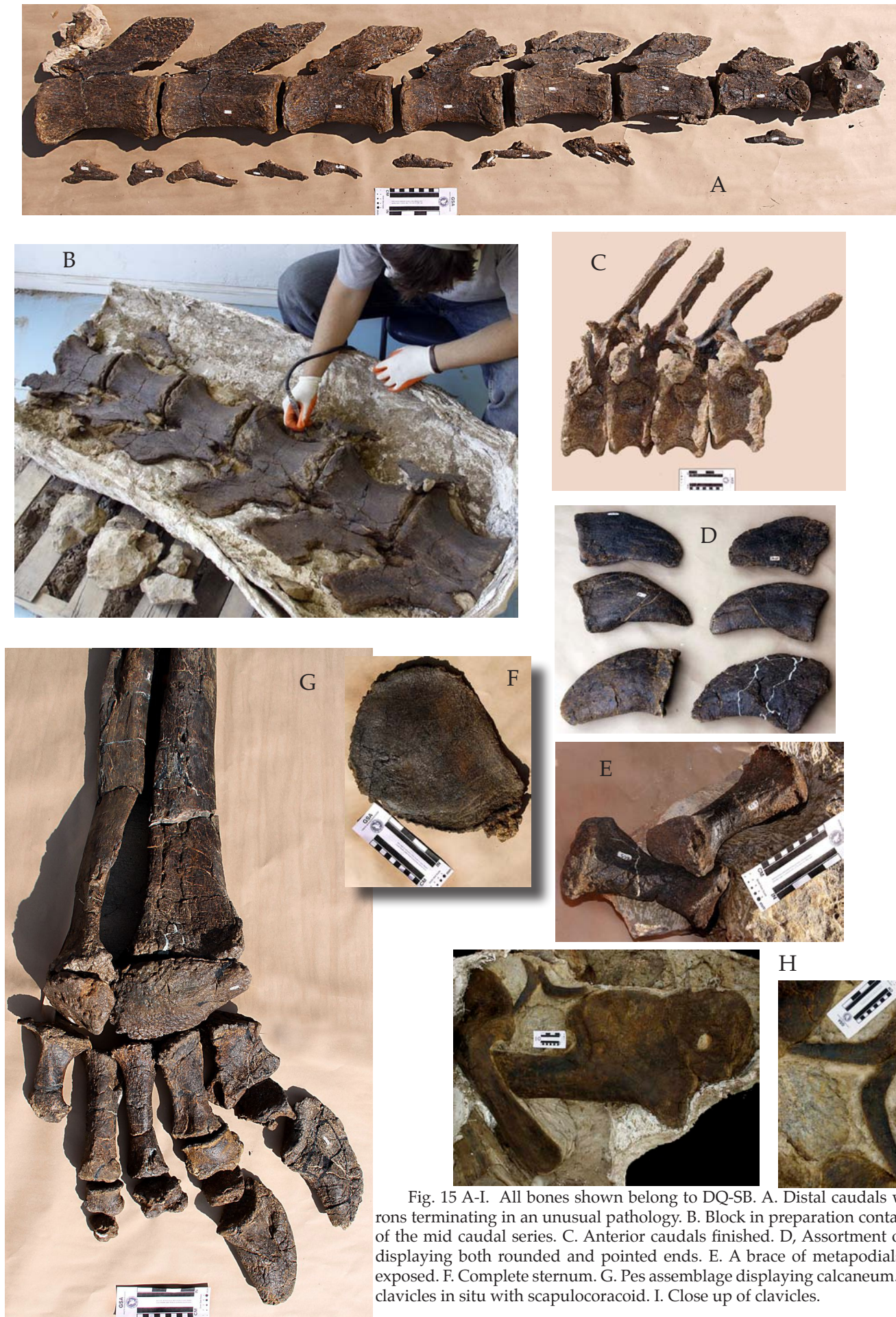
Fig. 15 A-I. All bones shown belong to DQ-SB. A. Distal caudals with chevrons terminating in an unusual pathology. B. Block in preparation containing part of the mid caudal series. C. Anterior caudals finished. D, Assortment of unguals displaying both rounded and pointed ends. E. A brace of metapodials partially exposed. F. Complete sternum. G. Pes assemblage displaying calcaneum. H. Paired clavicles in situ with scapulocoracoid. I. Close up of clavicles.

Fig. 16. Partially exposed block in preparation containing part of the skeleton belonging to DQ-SB. Visible are: ilium, femur , ribs, and both scapulacoracoid elements. In this block the paired clavicles were found.

sternal ribs have been recovered in fine condition, but some show distortion from being pushed against the other limb bones (Fig. 13 A). Much of the limb and foot bones belonging to DQ-TY have been cleaned and removed from their plaster jackets and are now waiting to be mounted. From field observation, we have been able to see the pelvic elements preserved semi-articulated, remarkably preserving, virtually complete sacrum and ilium without displacement. The pubes and ischia were badly damaged by the backhoe blade that initially led to its discovery. Also damaged are the left femur, tibia and fibula. One complete isolated clavicle has been recovered so far, and compares favorably with the complete set found in situ next to the scapula with the DQ-SB skeleton.

Another unique aspect of this specimen lies in the disproportionately large limbs in comparison to the axial skeleton. This immature individual exhibits striking size disproportion between axial and appendicular skeletons, which clearly demonstrate that limbs reach adult lengths early in ontogeny. The reconstructed skeleton may recall the ungainly appearance seen in a pony.

DQ-SB = "Sleeping Beauty", Figs: 14-16, and 28C

This specimen is the most beautiful in-situ dinosaur skeleton discovered in the Dana Quarry, hence the name "Ten Sleep Beauty" or "Sleeping Beauty." The bone is preserved dense and hard with fine surface detail. The exquisite preservation allowed us to expose a significant area of the skeleton while in the ground. The skeleton is preserved, articulated, for the most part, but with the cervical vertebrae noticeably dislocated behind

the tail section. The cervicals are all articulated together with the posterior ones locked together in a straight row, while the anterior ones are flexed similarly as preserved in "DQ-TY and DQ-BS. The axis is preserved but the skull has not yet been located. Since the Dana Quarry skeletons were not washed in before they were buried, it is hopefully that cranial material will be found in the large blocks removed from the quarry. Otherwise, all the remaining dorsal, sacral and caudal vertebrae are preserved in articulation. The dorsal and sacral bones are positioned in a fairly straight row, but the anterior caudal vertebrae flex upward above the level of the sacral spines, and then bend inward abruptly, as if the carcass had shifted against the tail at some point before its burial. It is possible that the body of water that preserved all the individual dinosaurs may have had a high bank rim around it that added to the trapping strength of the mud hole.

Except for the left ilium, all the pelvic elements are together in place with the sacrum. No "floating" bony ossicles have been found in the sacral region indicating that this individual may have not been as old. Floating sacral ossicles occur in the type of *D. carnegii* and in the USNM *D. longus* specimen. Many ribs are attached to the dorsal vertebrae on the right side but the left ones are not. The left ribs are displaced possibly due to expansion of post-mortem gasses from the belly and not from scavenging, as no tooth sheds or any other evidence exists supporting this activity. Located in the abdominal area are gastralia and or sternal ribs, which indicate that the carcass was buried rapidly after death before scavengers could tear away the soft organs within the abdominal area.
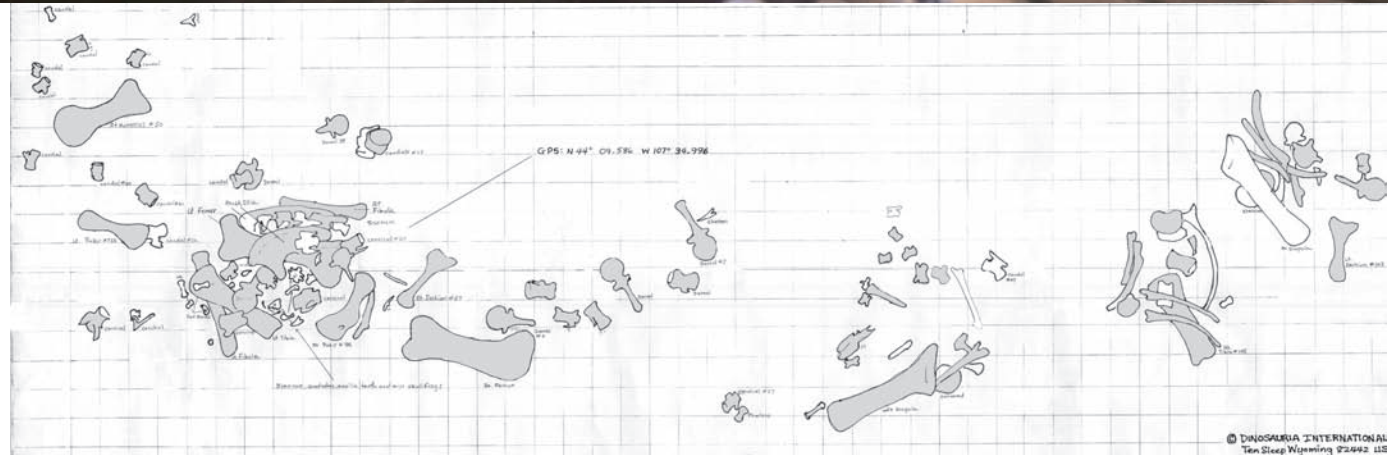
Fig. 17 A-D. Mounted skeleton belonging to "Einstein" on display in Monterrey Mexico 20009 and in Abu Dhabi International Airport 2008. Photo and accompanying bone map of DQ-EN's skeleton. The distribution of bones were probably due to scavenging as suggested by the numerous carnivore teeth found mixed with the skeleton and tooth marks present on the bones. DQ-EN displayed the most disarticulation of bones in comparison to the other specimens from the quarry.

Fig. 18 A-C. Partially exposed skull and lower jaws belonging to DQ-PC. Caudal view of the braincase can be seen in the upper left corner, and prezygapophysis and centrum can be seen in the middle (see arrow). B. Close up of teeth found with skull. C., distal caudal vertebrae from the associated skeleton.

The last preserved caudal shows a pathology indicating that DQ-SB had lost the terminal part of its tail due to an injury. Whether it was bitten or broken off during battle is not known, hence DQ-SB lacks the whiptail section of vertebrae, other than the occurrence of fusion, this may be the first recorded pathology of this type in the tail vertebrae of a sauropod.

The appendicular skeleton is another exceptional aspect of DQ-SB, because it preserves the bones of the front limbs and feet better than any other known diplodocid specimen. These forelimb elements were preserved semi-articulated. Even the well-known Carnegie Museum skeleton has reproduction forelimbs modeled after the Houston Museum specimen (type of *D. hayi*). The presence of forelimb bones, in diplodocids, is vital in establishing a humerus-to-femur ratio.

Preserved in associated with the shoulder girdle is a fine pair of clavicle bones, Fig. 15. Discovered in situ, these rarely found bones are first documented here as proof of their presence and position. Their presence is important in establishing the distribution of this poorly known element in sauropods. Superficially boomerang in shape, these clavicle elements thicken at the lateral and taper at their median extensions.

Articulated manus and pes elements emphasize the systematic importance of the skeleton of DQ-SB, Preserved in situ, for both hind feet, are calcified calcanea, Fig. 15. Absence of this tarsal has been often cited as a synapomorphy of Diplodocidae, see discussion in Bonnan, 2000.

All five *A. brontodiplodocus* skeletons, were excavated within a relatively small area no longer than one hundred meters, and the skeletons were not separate from each other in distances exceeding seven meters. There's one interesting footnote with regards to their excavations - no stomach stones or gastroliths have been found in or near the rib cage area belonging to any one of the *Amphicoelias brontodiplodocus* skeletons.

DQ-EN = "Einstein", Front cover and Fig 17 A-D

"Einstein" received its nickname after it was realized that the braincase was preserved along with the rest of the skeleton. "Einstein" is also the first skeleton representing a typical *Apatosaurus* morphology found directly associated with its skull. In addition to the braincase, several other cranial elements comprising "Einstein's" skull include both

20

quadrates, a left maxilla displaying unerupted dentition in the alveoli, isolated teeth and several indeterminate fragments. Of possible systematic importance, the Dana Quarry braincase displays a clear basipterygoid recess, a feature associated solely with specimens indentified as *Apatosaurus*, Balanoff, et al, 2010. The basipterygoid recess in "Einstein's" cranium is a clear depression, circular in outline at the base where the pterygoid processes converge. Comparison with the holotype braincase of *Diplodocus hayi* HMNS 175 and *Apatosaurus* braincase BYU 17096 (digimorph.org/specimens/Diplodocus sp/and digimorph. org/ specimens/Apatosurus_sp/) shows close similarity with DQ-EN.

The association of the skull with the skeleton is unquestionable; its discovery was made in the lab, in the largest plaster jacket, within the main mass of the skeleton tangled between the bones of the hindquarters (see quarry map Fig. 17 D). Its postcranial skeleton is approximately 70-80% complete, with a nearly complete pelvis and hind leg elements, most of the cervical and dorsal vertebrae including a good portion of anterior caudals, a humerus, many foot bones. In addition to numerous thoracic ribs, several sternal ribs showing massive rugosities are preserved. In over all size, DQ - EN is approximately 10 -15% smaller in comparison to the mounted specimen at the AMNH, but exceedingly more complete.

DQ-EN is especially intriguing, because we can interpret many of the differences between it and the other Dana specimens as part of observable sexual dimorphism in *Amphicoelias brontodiplodocus* Except for the overall skeletal robustness and development of massive laterally expanded cervical ribs, there exist few features not associated with ontogenetic or individual variation separating DQ-EN from the other Dana Quarry individuals. In other words, there is little reason to suspect that DQ-EN is a different species than the rest of the sample preserved. Reasons to suspect the presence of another species is greatly diminished by the DQ-PC skeleton, which has a complete skull and the postcranial skeleton better articulated. The most critical dimorphic feature in DQ-EN lies with the hypertrophic development of the cervical ribs, which expand the neck skeleton outwardly in a unique fashion. We speculate that this immensely broad neck, in life, was used for the purpose of bearing down on the female's neck, using its stronger construction together with the greater body weight for the purpose of subduing its mate during copulation. Reinforcing this idea are the low neural spines and narrow overall width of the cervical ribs in specimens we consider female (DQ-BS and DQ-SB), which appear to be designed specifically to under-fit with those of male neck vertebrae like the ones we see in DQ-EN and DQ-PC. The limbs in DQ-EN are typical apatosaur in morphology in their massive proportions to bear added weight, the humerus is distinctly broad at both ends, while the femur is also broaden transversely.

"Einstein" is the first Dana Quarry dinosaur that has been reconstructed and mounted in a freestanding life-like pose. In the summer of 2008, "Einstein" made his public debut at the Abu-Dhabi International Airport where his spectacular skeleton went on exhibit, Fig. 17 B. The unveiling caused a media event and, for several months, "DQ-EN was a major attraction, which amazed and thrilled thousands of visitors at the airport; many had never seen an actual dinosaur before in their lives. Today, "Einstein" has a good home in Mexico, where it will be the centerpiece in a forthcoming museum planned to celebrate the first National Museum of Natural History in that country.

DQ-PE = "Prince", Fig. 18, and 28B

During the preparation of this manuscript in 2010, another remarkable skeleton was discovered immediately next to Sleeping Beauty (DQ-SB), hence "Prince Charming". The skeleton representing DQ-PC is complete with an exceptionally well-preserved skull and the lower jaws. This skull was found at the end of the anterior cervical series. The exact number of cervicals will remain unknown until the large blocks can be prepared. This skull is massive and much larger than that of "Einstein" - it is possibly 20-30% greater in overall proportion, thereby providing another large male from which to make comparisons. The skull is buried with its snout pointing downward and a series of anterior cervicals articulated can be seen immediately behind the braincase. Numerous displaced teeth (Fig. 18 b) can be seen concentrated on one side of the skull, due to their proximity, these may belong to the lower jaws. The posterior cervical vertebrae, tentatively identifies as C 13th -15th with dorsals 1st & 2nd attached, are huge massive elements rivaling the largest known specimens from the Morrison. In these cervicals, the ribs display primitive features, massive and long prominent anterior processes. The posterior cervicals are well preserved and mostly articulated so we have for the first time the opportunity to study this osteological aspect in male example. Numerous long bones are preserved without distortion and are dimensionally comparable with the type of *Apatosaurus louisae*. For example, the length of humerus in *A. louisae* is 114.80 cm and in DQ-PE it is 106.68 cm.

DISCUSSION

Our initial attempts to identify the new Dana specimens were made difficult largely and ironically due to their extraordinary completeness. Each of the Dana Quarry specimens, are more than 80% complete and trying to locate equivalent skeletons for comparison, a futile task. However, it should be noted that the skeleton of *Apatosaurus louisae* Gilmore, 1936 is by far the most complete, and comparable diplodocid example published. Although there are few disappointing features in this specimen, the most notable being the damaged posterior cervicals, which prevent relative size comparisons to be made in the sequence of those vertebrae. Past informal reports by us have conveniently referred the present material to *Diplodocus* and to *Apatosaurus*, but to avoid adding further confusion, we thought it best to dispense with the traditional approach of trying to fit and to indentify the Dana material to the current taxonomic state of affairs. The traditional approach

would have provided us with two new species to add to the Morrison list of sauropods. Instead we employed a novel approach by attempting to fit previously reported Morrison fossils within the context of the *A. brontodiplodocus* sample. The results are astoundingly radical by comparison with previous studies. Comparisons show that most characters used to distinguish various Diplodocid taxa were found within the Dana sample, allowing an excellent opportunity for taxonomic reevaluation.

Hidden by taxonomy, sexual dimorphism, ontogeny and variation, has gone unrecognized. Over seventeen Diplodocid species have been proposed from the Morrison since the bitter feuding days between Edward Drinker Cope and Othniel Charles Marsh. Unfortunately, many of the type specimens are based on fragmentary material, and many of the exhibited skeletons representing these species are unassociated composites. At present, roughly twelve species dispersed within six genera are recognized as valid. Considering the remarkably close morphology uniting these taxa, the number seems unrealistically high. Amazingly, most of these genera occur together in many quarry sites and no study aimed at distinguishing sexual dimorphism or ontogeny has been attempted. Given that the Morrison Formation's paleontology is over 120 years old, such a study is well over due. A census of significant specimens is listed below to demonstrate the paucity of diplodocid skeletons more than 50% complete.

Amphicoelias Cope 1877

The genoholotype material of *Amphicoelias altus*, AMNH 5764, consists of two dorsal vertebrae, incomplete pubis and femur, see Fig. 19. These bones were collected at the highest levels in the Morrison Formation in Quarry 12 at the Garden Park area in Colorado. The tall neural spine together with other features are diagnosistic and identifies without question the dorsal vertebrae as belonging to Diplodocidae, Osborn & Mook 1921, McIntosh 2005, Carpenter 2006. The type femur is also a diagnosistic element displaying typical diplodocid features - elongation, reduced trochanter and a rounded mid shaft cross section. This femur morphology is a shared derived character present in many specimens including the types of *D. hayi*, *D. carnegii*, and in the skeleton at the USNM *D. longus*. The dorsal identified as D 6 and pubes belonging to the type are unfortunately fragmented and do not help establish additional characters of taxonomic value beyond diplodocid level.

Resolving the correct position of the type vertebra is crucial in extending comparisons with other specimens. In *Amphicoelias brontodiplodocus*, there are 15 cervical and 10 free dorsal vertebrae and one fused dorsal to the sacral membership. The first of the five fused vertebrae making up the sacrum is a dorsal and the last two are caudals. The more complete of the two dorsal vertebrae belonging to the holotype AMNH 5764 can be identified with 100% certainty as not belonging to the last free dorsal as previously judged by Osborn & Mook, 1921, McIntosh 2005 and others, (see Fig. 22). Gilmore, 1932 (p.11) accurately points out in his description

of the 10th dorsal in the USNM mounted *Diplodocus longus* skeleton: "The spine is strongly inclined forward of the vertical axis of the vertebra as a whole. In other words, when the vertebra is placed in an articulated position the lower half is inclined backward, which brings the forwardly inclined spine into a nearly vertical position. Special mention is made of this feature for the reason that in previous restorations the tenth vertebral spine has been either restored or replaced in the vertical axis, and when articulated a faulty spacing of the spine top in relation to others of the series has resulted. This forward angulation in the present specimen results in a uniform spacing of the spines, as would be expected". The tenth dorsal in all Morrison diplodocid specimens is an important diagnostic element marking a vertebral transition that can be immediately recognized and distinguished from other sauropods. Thus, the type dorsal of *A. altus* is in all basic construction more similar to any one of the preceding vertebrae without spinal bifurcation, but its position in the series will remain uncertain until more information becomes available. For now is it reasonable to conclude that this dorsal fits the morphology seen in the Dana sample and other more complete Morrison specimens in agreeing morphologically with D7, D8, or D9, with a best guess at number D9. There exists a disparity between the illustrations provide by Cope and Osborn, see Fig. 19A. The type of *Amphicoelias* is clearly more similar to the same elements in the mounted skeleton at the Carnegie Museum (type *D. carnegii*) than to *Apatosaurus louisae*, in that the neural spine in these two dorsals have well developed posterior centroparapophyseal lamina and the proportions of centrum to spine are the same. Therefore, except for absolute size differences, the posterior dorsals in all Morrison diplodocids are in accord with the type dorsal of *A. altus*. Except for their larger size, the specimens referred to *A. altus* differ little from *Amphicoelias brontodiplodocus* The femur in *A. altus* is noticeably more elongated as compared to *Amphicoelias brontodiplodocus*, but otherwise similar in its sub circular cross section and construction, see Fig. 19.

Diplodocus longus Marsh 1878

According to McIntosh and Carpenter, 1998, the holotype of *Diplodocus longus*, Marsh 1878, YPM 1920 consists of two mid caudal vertebrae, and a chevron, see Fig. 20 & 21. This specimen was recovered in Quarry 1 located near Canon City, Colorado. McIntosh and Carpenter, 1998, determined that the two type caudal vertebrae were probably 20th & 21st by comparison with the AMNH 223, USNM 10865, and DMNH 1494. Our comparisons with the Dana sample agree with the caudal position of the type vertebrae provided there is given room for individual variation. For example, in comparison with DQ-TY the holotype of *D. longus* fits the general proportions, and horizontal lower boarder of the centrum seen in the caudals 24th -25th, but without a ventral depression. The lack of ventral depression is a result of the immature growth stage in the axial skeleton and also involves the sexual dimorphism as observed in the Dana sample discussed below.

The best-preserved caudal vertebra of the two comprising the holotype does not display the degree

22

Table 2. Census of diplodocid skeletons

Diplodocus

Houston Museum of Science and Natural History, Texas, HMNS 175,(type of *Diplodocus hayi*), partial skeleton with braincase

Carnegie Museum, Pittsburgh, type of *D. carnegii*, a composite of three skeletons with cast reconstructions from *D. hayi,* HMNS 175 = CM 84 type: Right femur, pelvis without left ilium, right scapula and coracoid, both sterna, eighteen ribs, fourteen cervical, eleven dorsal, four sacral, and twelve caudal vertebrae. CM 94, nine cervical, eight dorsal, and twenty caudal vertebrae; left femur, right tibia, fibula, and pes; complete pelvis, both scapulae and coracoid, and one sternum.

Denver Museum of Natural History, Colorado skeleton, DMNH 1494 is about 30% complete. Ten dorsals, sacrum with right ilium, thirteen caudal vertebrae, assorted chevrons, ribs, and right femur. Neck cast of *D. carnegii.*

US National Museum, Washington, DC, USNM 18865, composite of two individuals and casts from the Carnegie specimen= Ten dorsal, five sacral, and thirty two caudal vertebrae; nine ribs, complete pelvis; right scapula, coracoid, both humerii, ulnae, and one radius, left hind leg and foot, and eighteen chevrons.

Senckenberg, Germany, fragmentary specimen with mostly casts from the Carnegie specimen

Apatosaurus

American Museum of Natural History, New York, *Apatosaurus excelsus* less than 30-40% Composition of the *Brontosaurus* Skeleton. AMNH 460, Consists of the 5th, 6th, and 8th to 13th cervical vertebrae, 1st to 9th dorsal and 3rd to 19th caudal vertebrae, all the ribs, both coracoids, parts of sacrum and ilia, both ischia and pubes, left femur and astragalus, and part of left fibula.

Carnegie Museum of Natural History, Pittsburgh, type of *A. louisae,* nearly complete skeleton, 85-90% complete= possible skull, ninety four vertebrae, thirty eight cervical and dorsal ribs, complete pelvis; right femur, tibia, fibula, and astragulus; left partial pes; left scapula, coracoid, humerus, ulna, radius, and most of manus; right scapula, coracoid and humerus

Carnegie Museum of Natural History, Pittsburgh, found with type of *D. carnegii,* (CM 84 & 94 near Sheep Creek, WY), CM 563, nine cervical, nine, dorsal, five sacral, and eighteen caudal vertebrae, left ilium, both pubes and ischia, many ribs, three chevrons, left scapula and coracoid, both humerii, radii, and ulnae, complete right manus, right femur, both tibiae, fibulae, and astragulas.

Field Museum of Natural History, Chicago, *A. ajax* about 40-50%
Ten dorsal five sacral, and twenty third caudal vertebrae, eighteen right and left ribs, right ilium, both pubes and ischia, fragmentary right ilium, left femur, and thirteen chevrons.

Los Angeles County Museum, California, (CM field no. 40) specimen unearthed below the type of A. louisae. Eleven cervical, ten dorsal, five sacral, and forty caudal vertebrae, complete pelvis, left femur, tibia and fibula, and most ribs.

Peabody Museum of Natural History, New Haven, type of *Brontosaurus excelsus*, 50-60% According to illustrations Ostrom and McIntosh 1975: Eleven incomplete cervical, nine dorsal, five sacral, and eighteen caudal vertebrae, complete pelvis, left scapula and coracoid, eight complete ribs, eight chevrons, right and left humerii, radii, ulnae, femora, tibiae, fibulae, astragalii, and metapodials, and phalange.

National Museum of Tokyo, NSMT – PV 20375, Nine cervical, ten dorsal, sacrum, and twenty nine caudal vertebrae. Thirteen chevrons, fifteen ribs, right scapulocoracoid, right forelimb and hindlimb elements, and partial manus and pes. Left hindlimb possible *Camarasaurus*.

University of Wyoming Geological Museum, Laramie, UWGM 15556, 50 -60% partial skeleton - no published data available.

Barosaurus

AMNH 6341 six cervicals, 9 dorsal, 29 caudal vertebrae; 1 chevron; complete pelvis, left scapula, right partial scapula, left humerus, right hindlimb and partial pes.

YPM 429 17 presacral, 15 caudal, and partial sacral vertebrae; fragmentary scapula, ilium, pubis, ischium, femur, tibia and fibula; complete sternum.

Sauriarmuseum, Aathal, Switzerland, SMA 009 ("Toni") unidentified skeleton more than 80% complete

Others

There exists no skeletons of, *Supersaurus, Suuwassea, Eobrontosaurus* or *Tornieria* more than 50% complete belonging to a single individual on exhibit or housed in institutional collections.
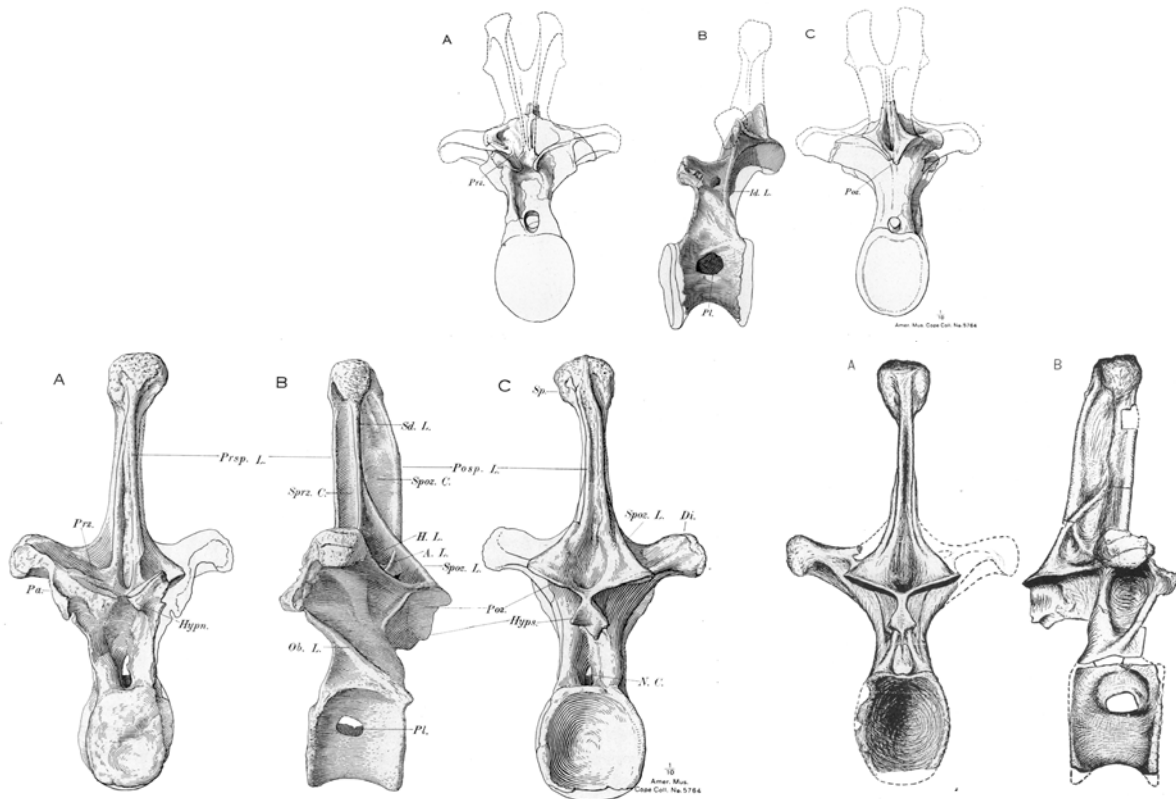
Fig. 19A. Holotype vertebrae belonging to *Amphicoelias altus*, illustrations after Osborn and Mook 1921 and Cope 1877. Top row, dorsal vertebra (D6) after Osborn and Mook, 1921. Bottom row, dorsal vertebra possibly D9, note the misleading disparity between both sets of drawings, left drawings from Osborn and Mook 1921. Lateral view reserved in the Osborn and Mook.

Fig. 19B. Femora of *A. altus*, type (after Osborn and Mook 1921) and *A. brontodiplodocus* DQ-BS. Drawings of mid shaft cross sections of left femur (CM 94) mounted with type of *D. carnegii* (Hatcher 1901). An elongate straight femur with sub circular - ovate shaft is characteristic feature of *Amphicoelias*. Depending on shaft location some variation exists in shape of cross section.

24

of sculptured ventral surface. Its illustration in Marsh's monograph is grossly misleading, the ventral surface of the caudal is not sculpted the way it is reconstructed. This specimen has suffered damages and if the repairs could be made accurately the ventral surface would not be so deep. The caudal's ventral trough is exaggerated by lateral compression, and the plaster repair and reconstruction work is visually misleading in creating a deeper than normal recess. In fact the ventral surface is no different in depth from specimens referred to *Diplodocus, Barosaurus* or the adult individuals preserved in the Dana Quarry, and therefore indistinguishable. The small prezygapophyses and short centrum bring to mind *Apatosaurus, Barosaurus* and individuals from the Dana sample. By comparison with the caudal series, housed in USNM, AMNH, and CM, the prezygapophyses are noticeably long and well developed.

McIntosh and Carpenter, 1998 recognized the differences in caudals between *D. carnegii* and the type of *D. longus*. It was stated that the type of *D. longus* was morphologically distinct from the Carnegie specimen (type of *D. carnegii*). " The caudals, YPM 1920, appear to be more primitive in being shorter and with pleurocoels not extended as far back in the tail." The opportunity to compare *Amphicoelias* and *Barosaurus* was not made in that report after it was clear that the assignment of the Carnegie specimen to the genus *Diplodocus* was in question and may be in error.

These comparisons reveal numerous differences that suggest that the type material is not diagnostic below generic level, and assignment to a species is impossible, therefore, it is claimed that the type, YPM 1920 is *nomen dubium*. For that reason, the genus *Diplodocus* is considered a synonym of *Amphicoelias.* The name *Amphicoelias* Cope 1877 is regarded as a valid and recognizable genus with priority status over *Diplodocus* Marsh 1878 under the Code of Zoological Nomenclature. The *Amphicoelias altus* type represents a diagnosistically superior material in comparison with the type specimen of *D. longus.* The genus *Diplodocus longus* cannot be distinguished reliably because of incompleteness and limited morphology.

Fig. 20. Fig. 20. Holotype of *Diplodocus longus*, illustrations from Marsh. Note the differences in the degree of ventral sculpting in comparison to photographs of the original fossil shown in Fig. 21A

Diplodocus carnegii Hatcher 1901

So much of our current knowledge of diplodocid osteology stems from comparisons bridged by the use of one incomplete skeleton to another incomplete skeleton, resulting in the creation of "concept species", the mounted skeleton of *Diplodocus carnegii* is a perfect example. The best-known sauropod skeleton, *Diplodocus carnegii* Hatcher 1902, is on display at the Carnegie Museum. The type specimen is partial skeleton that was unearthed in Quarry C near Camp Carnegie, Sheep Creek, Albany County, Wyoming. The type of *Diplodocus carnegii* is represented by a less than a 40% complete skeleton. According to Hatcher 1901, the type (CM 84) includes forty-one associated vertebrae, right femur, rt. scapula and coracoid, both sternal plates, eighteen ribs, and pelvis lacking the left ilium. Thus, it lacks a skull, most of the tail, front limbs, and bones of the feet. The anterior cervical and sacral vertebrae are damaged in this specimen. This specimen was discovered in 1899 near another but smaller individual CM 94 (CM 307 is also included in the mounted skeleton) Both of these partial skeletons were also excavated nearby the remains of an *Apatosaurus* skeleton less than three meters apart. Historically, this specimen despite its incomplete and composite state defines the genus *Diplodocus*. The similarity of dorsal vertebra and femur between *Diplodocus carnegii* and the type of *Amphicoelias altus* is all too great. The overall structure of the dorsal vertebra differs only in having a less prominent spinopostzygapophyseal lamina, a variable feature. The femora are also similarly constructed in being long slender and having a sub circular cross section shafts. Based on these observations, *D. carnegii* should be recognized as a synonym of *Amphicoelias altus*.

Barosaurus lentus Marsh 1890

The concept of *Barosaurus* is essentially based on two incomplete skeletons YPM 429 and AMNH 6341. The YPM specimen was described by Lull, 1919 from Piedmont, South Dakota and the better of the two specimens now housed at the ANMH originated from Dinosaur National Monument Quarry in Utah. Both these specimens exhibit immense cervical vertebrae. The Yale specimen was collected from isolated and scattered bones with no clues that it represented one or more individuals. While the AMNH specimen preserves articulated vertebrae in two series, cervical and dorsal, it was buried directly underlying another skeleton in the same quarry. This other skeleton is now mounted on display at USNM (*Diplodocus longus*). Apart from the extraordinarily massive cervical series discovered at the quarry, both skeletons are very close in morphology including length of limbs, the AMNH specimen measuring slightly larger. It's not clear why after preparation these two skeletons were not considered members of the same species, a logical question suggested by their direct association in the quarry. Nor is it clear why the cervical series together with the floating limb and foot bones were assigned to AMNH

6341 and not to the USNM skeleton. Therefore, it is possible, although unlikely, that parts of these two specimens have been mixed up.

McIntosh, 2005 characterizes *Barosaurus* as having a mixture of primitive and derived features in comparison to *Diplodocus*. The features given by McIntosh 2005 are: cervicals and anterior dorsals are up to 50% more elongated, divided neural spines commencing in the middle of the neck, cervicalization of vertebrae in the shoulder region = reducing dorsals to nine; tail with short centra and short undivided spines, pleurocoels, and transverse processes not extending as far back, with ventral sculpting less extreme; forelimbs relatively longer, scapula with less expanded proximal end.

Divided neural spines commence in the middle of the neck, recalls the condition that exists in *Amphicoelias brontodiplodocus.* In *Amphicoelias brontodiplodocus* neural spine bifurcation starts at the 9th cervical, which is remarkably similar to *Barosaurus* provided that the nine cervical vertebrae are correctly identified in the AMNH specimen. In other diplodocids, bifurcation is seen in the anterior cervicals, usually before the 6th. Another similarity shared by all Morrison diplodocids is unique size sequence of the posterior cervicals, in which the 14th bears the longest centrum while the 13th and 15th are subequal in length. The sympleisomorphy between the Dana sample and *Barosaurus* establishes a close relationship from other specimens and helps to reinforce the identifications put forth in this report regarding the number of cervical vertebrae in *Barosaurus*. The only difference between *A. brontodiplodocus* and *Barosaurus* is the condition of the cervical ribs. In *A. brontodiplodocus* they are noticeably longer and overlap each other in comparison to the rather short ribs in *Barosaurus*.

McIntosh, 2005 reasoned that the vertebra described by Lull, 1919 belonging to the type specimen as the 10th dorsal was the dorsal-sacral (11th). The 10th dorsal vertebra is incomplete and damaged lacking much of the neural spine. This is a difficult calculation to make based on comparisons bridged by the use of one incomplete skeleton to composite with another incomplete skeleton, and assumes without direct evidence that there exists sixteen cervicals and nine dorsals in *Barosaurus*. As described above under *Amphicoelias* the 10th dorsal is a recognizable diagnostic element impossible to identify without a complete specimen with to judge the position of the neural spine against the centrum. The Dana sample provides us with an accurate template for *Amphicoelias*, in having a total of twenty five presacral, fifteen cervical, ten free dorsal vertebrae excluding the one fused dorsal to the sacrum.

The characters cited by McIntosh, 2005 that pertain to the tail are all affected by the ontogenetic stage and gender of the individual. As described below the axial skeleton is developed after the development of appendicular elements as clearly indicated in the immature DQ-TY and "Toni" skeletons. Males develop massive necks and heavier skeletons. In addition, tail with short centra, short undivided

spines, pleurocoels, transverse processes not extending back, and less ventral sculpting, are all consistent with characters associated with sexual dimorphism. Notwithstanding the condition of the entire cervical ribs series, which is unknown in *Barosaurus*, we identify both AMNH and YPM *Barosaurus lentus* skeletons as probably those of male individuals based on the exaggerated proportions of the posterior cervicals and massive limbs structure. It should be noted that there is only one *Apatosaurus* skeleton (CM 3018 type *A. louisae*) that supposedly has the complete cervical series including the posterior and anterior dorsal series preserved. However, in this specimen C 13th -15th are badly crushed and plaster reconstructions mounted on the skeleton. Therefore it is unknown what the true morphology of the posterior neck vertebrae is in the apatosaur morphotype. Hopefully, after preparation, the Dana specimen DQ-PC will shed more light on this important feature.

Apatosaurus Marsh 1877

Uncertainty exists surrounding the taxonomic status of *Apatosaurus ajax* Marsh 1877. Marsh in his original announcement cited a skeleton in the YPM collection belonging to new genus and species *Apatosaurus ajax*. In this announcement a brief description exaggerated the completeness of the skeleton and only noted four vertebral specimens (syntypes) of which one was a sacrum. In 1879 Marsh described and compared more of the fossils he attributed to *A. ajax* and for the first time stated that the sacrum was the holotype. Hence, the holotype was designated two years after establishment of that taxon. Again in 1896 (p. 166) Marsh in reference to *Apatosaurus ajax* (YPM 1860) states: "The sacrum represented in fig. 2, Pl. XVll, may be regarded the as the type specimen. It has the same general features as the sacrum of *Atlantosaurus*, shown on the plate, but it has only three coossified vertebrae instead of four." Marsh was very clear in this description and in the accompanied illustration that the name bearer for *Apatosaurus* is a sacrum (lectotype). The direct implication here is that the sacrum is not part of the skeleton mentioned originally.

Riggs 1903 acknowledges the sacrum as the type but only makes comparisons with the referred elements designated by Marsh as belonging to *Apatosaurus ajax,* in the same paper he placed *Brontosaurus* into synonymy. The type specimen of *Apatosaurus ajax* has not received broad level of acceptance, Riggs 1903 concluded "the species *A. ajax* cannot be recognized as in the adult"… and Gilmore 1936, evaded comparisons with *A. ajax* in his description of *A. louisae* probably for its incomparable standing. Berman and McIntosh 1978, based on color preservation, old field numbers and because of "appropriate size", deduced that a partial cranium, quadrates and other elements assumed to be from the type locality Quarry 10 near Morrison Colorado, must belong to *Apatosaurus* YPM 1860 presumably in reference to the collection of bones catalogued under the same number as the type sacrum YPM 1860. Here again is another indication of additional material not belonging with the type and species diagnosis shifting to referred material. Unfortunately, the size of the quadrate described by Berman

Fig. 21A. Two of the three elements comprising the holotype of *Diplodocus longus*, Marsh 1878, YPM 1920. Lateral and ventral views of the mid caudal vertebra exhibits extensive incorrectly done repair work exaggerating the degree of sculpting on the ventral surface. Note the short prezygapophysis in comparison to AMNH 223, (see Fig. 29), which is a distinguishing feature separating *Amphicoelias altus* from *Amphicoelias brontodiplodocus.* In the chevron, the slight downward position of the processes indicates that it belongs to the close to the forked series and its location would have been more anterior than the probable position of the caudal vertebra.

Fig. 21B. Two complete caudal vertebrae, from the same mid section belonging to the DQ-BS tail, displaying different depth and configuration on the ventral side. Right lateral and left ventral views. Important feature to note is the deep sculptural configuration in #403 which is exaggerated due to compression during fossilization. 447A on the other hand, is shallow in comparison. If these caudal elements were found separately unassociated, 403 would be identified as *Diplodocus longus* and 447A as *Barosaurus*. Note, the characteristic "double beam " chevron kept in articulated with caudal (447a). Dana Quarry field numbers are used to identify the bones in DQ-BS.

and McIntosh and assumed to belong to the holotype sacrum is from a large individual exceeding the expected dimensions, so it is not possible that the quadrates and the braincase that fits so well together belong to the same individual as the sacrum. The 21cm-long quadrate from Quarry 10, places this cranial material outside the size range of the holotype sacrum. By comparison with the type of *A. lousiae*, the sacrum against the quadrate would represent an individual approximately half the size. The size of the quadrate in the "probable skull" belonging to *A. lousiae* is 18.5 cm. According to Ostrom and McIntosh 1966, Quarry 10 has produced the remains of three sauropod skeletons – *Atlantosaurus immanis*, *Apatosaurus laticollis* and *A. ajax*. So, it doesn't seem possible that the holotype of *A. ajax* can ever be sorted reliably. Furthermore, it is not clear if the collection from Quarry 10 belongs to one taxon or a mixture. Illustrations for many of these specimens and other Marsh types were subsequently published in Ostrom and McIntosh 1966.

Apatosaur cervical vertebrae and limbs are often mistaken for bones of *Camarasaurus*, and vice versa, which may be the case in the type of *A. ajax*. There exists a point of similarity with *Camarasaurus* and type of *A. ajax*, which has not been addressed. The illustrations in Marsh 1896 *D. longus* (pl xxv111), *Morosaurus lentus* (pl XXX111) *Atlantosaurus montanus* (pl XV11) and Ostrom & McIntosh 1966 of *A. amplus* YPM 1981 type, *Brontosaurus excelsus* YPM 1980, and *Morosaurus grandis* YPM 1900, reveal an interesting disparity in the relative proportional lengths of S2 & S3 against S4 in the sacrum. In *Morosaurus* S2-4 are near equal in overall size and ventral lengths whereas in the other specimens, S4 is proportionately larger in comparison to the adjoining S2-S3. The holotype of *A. ajax* YPM 1860 is more similar to *Camarasaurus* ("*Morosaurus*") in this aspect. Furthermore, Marsh 1877 stated that both type specimens of *A. ajax*, and *Camarasaurus (Morosaurus) grandis* originated from the same locality. Thus, reexamination is urgent, the type needs to be compared and described properly to resolve these issues. The taxonomic status of *A. ajax* is therefore at present Sauropodomorph incertae sedis. However, if the holotype can be shown to be part of a more complete individual with

Fig. 11 F. View of sacral spines and ribs belonging to DQ-TY

definable specific diplodocid characters then the genus name *Apatosaurus* may have priority over *Amphicoelias*, but as a fragmentary sacrum the type can only be judged nomen dubium.

Notwithstanding the taxonomic status of *Apatosaurus ajax*, the genus concept essentially rests on two specimens, the holotype skeleton of *Apatosaurus louisae* Holland, 1915, and the mounted skeleton of *Brontosaurus excelsus* (Como Bluff, YPM 1980 and YPM 4633). *A. louisae* is by far the most widely acclaimed example, and *B. excelsus* skeleton mounted and exhibited in the Peabody Museum. Despite the familiarity of these *Apatosaurus* specimens various aspects of it skeleton remain poorly known particularly the cervical vertebrae. However, Riggs 1902 and Upchurch et al 2004 have described reasonably complete specimens, but in these specimens the cervical series are as incomplete and fragmentary as in the Peabody *B. excelsus* and American Museum skeletons. In fact the cervical vertebrae which forms part of the type of A. *louisae* was not found directly articulated to the dorsals and may have been from a different individual. Moreover, the posterior vertebrae are badly crushed and modeled plaster reconstructions are mounted on the skeleton and illustrated in Gilmore's description. The reconstructed cervicals are C13-15 together with the centra proportions and lack of certain diplodocid details (for example transverse central buttress Berman and Rothschild 2005) gives more the impression of a camarasaurid than diplodocid morphology. It should be pointed out that these cervicals were reconstructed during a time when ideas of Morrison sauropods relationship were vague and not widely accepted, so reconstruction may be incorrect. It is not possible to judge the length of the 14th against the 15th and the relation to the first dorsal. Verification of anterior rib process is also wanting. As a result generic and species level diagnoses remain vague particularly in the cervical region. Another feature indicating that the cervicals may be incorrectly reconstructed and misleading is the noticeably short length of the 14th in *A. louisae*. Comparisons show in specimens preserving the required articulation, that the 14th cervical vertebra is the longest in the series and is an *Amphicoelias* synapomorphy. If the cervicals are correctly reconstructed in *A. louisae* then it is suspicious as belonging to one individual or represents an aberrant form displaying an abnormal post-cervical skeleton. An aberrant individual is also suggested by the odd fact that no other skeleton preserving similar associated cervicals has been reported belonging to *A. louisae.*
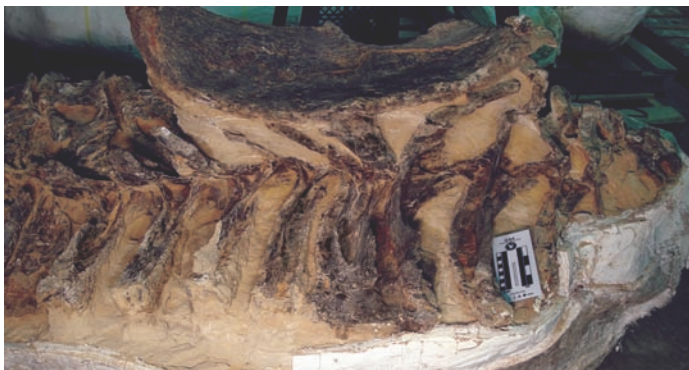
And yet, one observation should be clear, that the post cervical skeleton of *Apatosaurus* represents one of the two morphs that occur frequently in the same sites together with *Diplodocus* morphs. The apatosaur morph displays massive skeleton with heavier limbs, less pneumatic axial skeleton and shorter tail in contrast with the other morph or diplodocoid which displays delicate skeleton, slender limb bones, highly pneumatic axial skeleton with a proportionately longer tail. These morphs are identified as male and female respectively and this sexual dimorphism is an important autapomorphy in *Amphicoelias*. These morphs all share
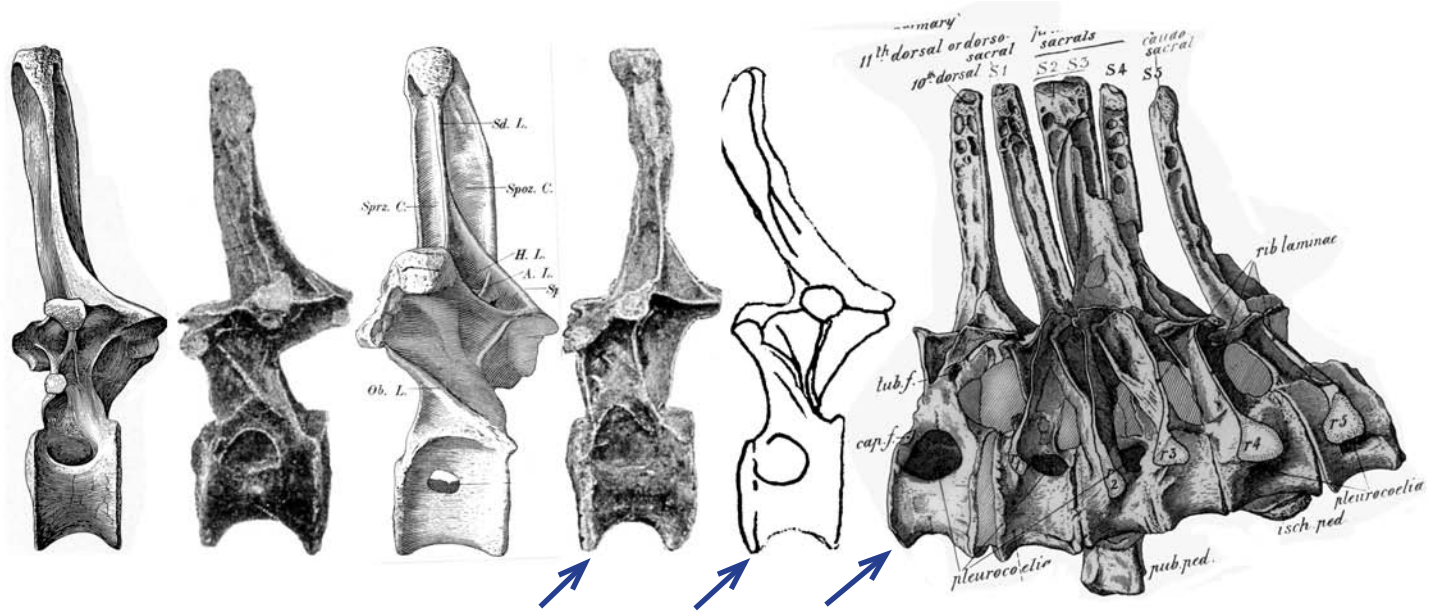
Fig. 22. Left lateral views of diplodocid dorsal vertebrae. From left to right: *Apatosaurus lousiae* D9, CM 3018, Type (after Gilmore 1932); *Diplodocus carnegii* D8 (reversed) Type (Hatcher); *Amphicoelias altus* D 9? Type AMNH 5764 (reversed Osborn 1924); *D. carngeii,* D10 Type; *D. longus*, USNM 10865, D 10 (Gilmore 1932); *Diplodocus longus* AMNH 516 (Osborn 1904). Note the variability and off align position of neural spine in the tenth dorsals (arrows). AMNH 516 illustrates clearly spinal modification of the tenth dorsal to fit against the sacral series. Figures not to scale
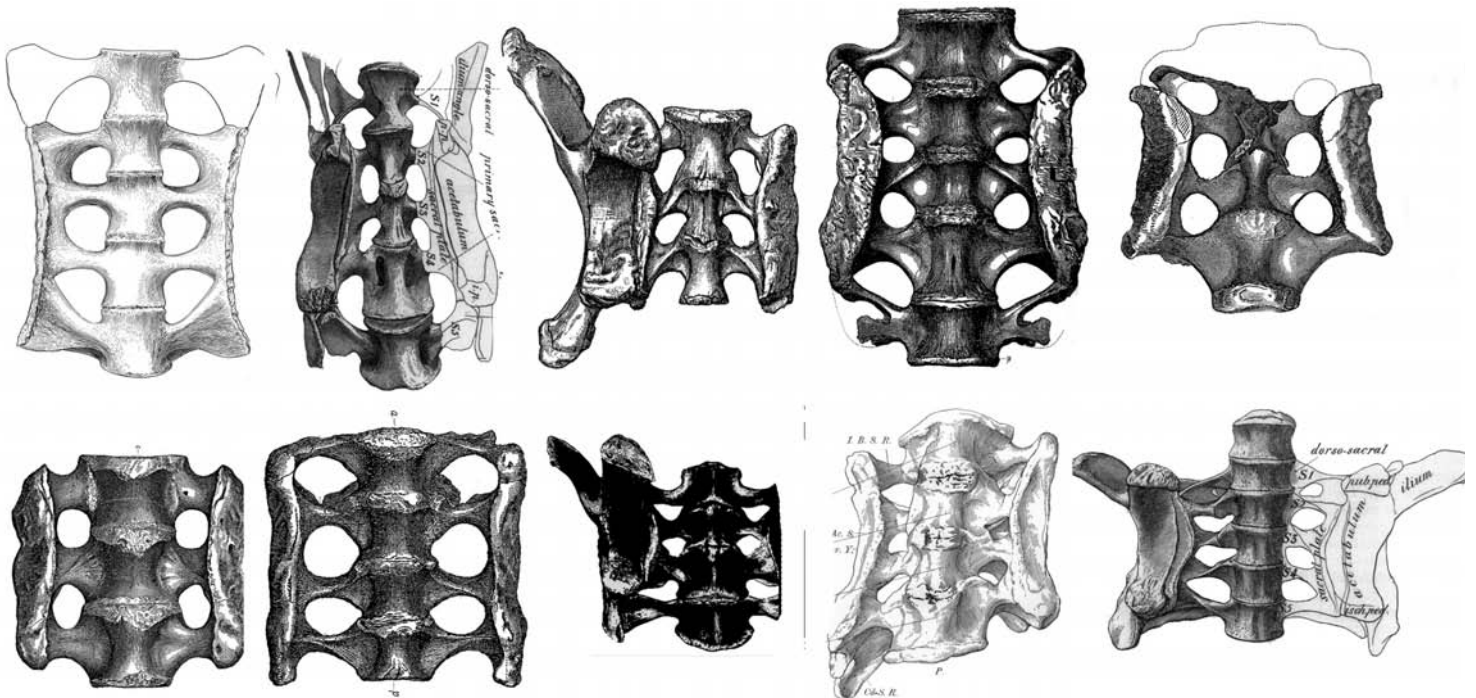

Fig. 23. Morrison sauropod sacra in ventral views.

Top row from left to right: *Apatosaurus lousiae* Type CM 3018; *Diplodocus longus* AMNH 516 (Osborn 1904); "*D. longus* "Type"; *Brontosaurus excelsus* YPM 1980 Type; and "*Atlantosaurus montanus*",Type, YPM 516.

Bottom from left to right - *Apatosaurus ajax* Type; "*Morosaurus" grandis*, Type of *Morosaurus impar*, YPM 1900; *Diplodocus carnegii* Type; YPM 1900; *Camasaurus supremus*, AMNH 5761; and *Camarasaurus* species, AMNH 690.

Note the distribution of ventral constriction and keeling of centra, except for *A. louisae*, the diplodocids show this distinctive feature in contrast to the more rounded centra in camarasaurids. Sacral vertebrae in DQ-TY and DQ-BS are keeled. Figures not to scale

the same uniquely derived characters, which can best be interpreted as representing a single species displaying sexual dimorphism. In addition to the well known post cranial similarities, the cranial characters described by Berman and McIntosh 1978 furthermore supports the closeness of *Apatosaurus* and *Diplodocus* morphology.

The type skeleton *Apatosaurus louisae* Holland, 1915 was discovered in Dinosaur National Monument, Utah in the same quarry that produced the *Barosaurus lentus* (AMNH) and *D. longus* (USNM) specimens discussed above. Positioned akin to these specimens, the skeleton of *Apatosaurus louisae* was found together with other skeletons in overlapping positions. One of these other skeletons was identified as *Diplodocus*, and the other a juvenile *Apatosaurus*. The point being made is that there is corroborative evidence of the same assortment of diplodocids morphotypes occurring directly together as they do in the Dana Quarry.

Suuwassea emilieae Harris and Dodson, 2004

This important specimen is from the lower part of the Morrison Formation in Montana, which immediately warrants comparison with *A. brontodiplodocus*. *Amphicoelias brontodiplodocus* is distinguishable from *Suuwassea emilieae*, in lacking the following characters: no post parietal foramen, "optic" foramen not conjoined, neural spine bifurcation past 9th, and neural spines anteriorly position on cervical centra 3-5. Otherwise, all the other elements referred to *Suuwassea emilieae* compare favorably with *Amphicoelias brontodiplodocus*. The ball or convex joint on whiptail caudal vertebra is not developed in *S. emailieae* suggesting that the specimen is an immature individual, and probably a male as judged by the hour-glass shaped humerus, and tall neural spines on the cervical vertebrae. Therefore, the genus *Suuwassea* is referable to *Amphicoelias* but the species *A. emilieae* may be kept in validity until further comparisons can be made.

Eobrontosaurus yahnahpin Filla and Redman 1994

This specimen originates from the Bertha Quarry in the eastern part of the Como Bluff area in Wyoming. Comparisons with the type of *Eobrontosaurus yahnahpin* from a cast of the hind leg in the exhibit collection at the Black Hill Institute in Hill City, SD suggests that it is a small or young male individual of *Amphicoelias*. The ossified sternal ribs are also very similar in this specimen with ones preserved in DQ-EN - both display a clear excessive bone growth not seen in female examples.

Tornieria africana Frass 1908

The Tendaguru species, *Tornieria africana*, is based on poorly documented, isolated bones of uncertain association, (Remes, 2006). Many of the described features point to both *Apatosaurus and Diplodocus* morphotypes, suggesting that it may represent a composite diplodocid taxon. These characters include; robust distal ischium, distal scapula without expansion, femur flattened, tibia & fibula short, humerus broad. In *Tornieria africana*, the illustrated caudal

vertebrae are excavated ventrally, recalling *Diplodocus* and *Barosaurus*, which we have seen is a variable character in the Dana sample of *Amphicoelias brontodiplodocus* The *Tornieria africana* bones appear to represent a composite of male and female morphotypes that need to be better characterized with more complete material. The genus *Tornieria* is here included in *Amphicoelias*.

Amphicoelias brontodiplodocus new species

The Dana specimens are sufficiently distinct morphologically to warrant the establishment of a new species, *A. brontodiplodocus*. Thus, we recognize two or possibly three *Amphicoelias* species, a more primitive form *A. brontodiplodocus* in the lower part of Morrison and a more derived species *A. altus* in the upper part. A possible third species *A. emailieae* may prove to be valid. Whether these two species overlap in time is not known. However, it is likely that future discoveries of more complete specimens particularly from classic upper Morrison localities will close the morphological gap between *A. brontodiplodocus* and *A. altus* in which case only one Morrison species can be recognized. Although this study recognizes a new taxon, we do not designate a type specimen until part of the collection is accessioned in an institution. The species name is used for the sake of communication and discussion in this report and it is understood that the unofficial and temporary name *A. brontodiplodocus* may be changed.
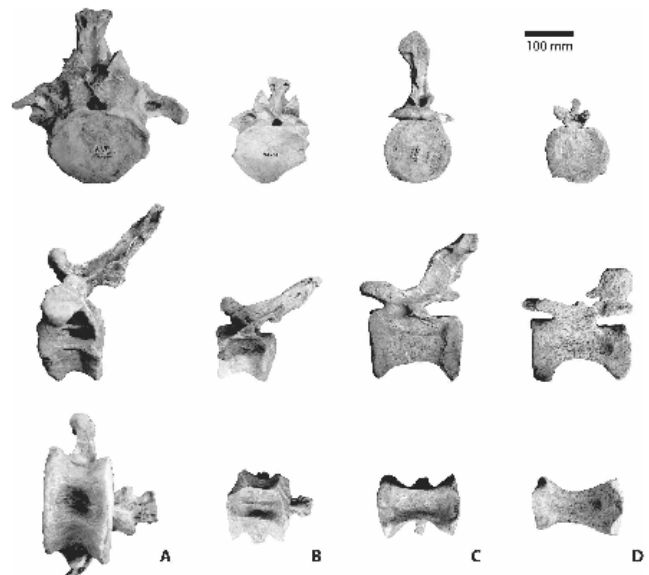

Fig. 25. Caudal vertebrae belonging to *Tornieria africana* not from one individual after Remes 2006

RECONSTRUCTION OF LIFE HABITS AND PALEOECOLOGY OF *AMPHICOELIAS*

Since their initial discovery scientist have speculated about the life habits of sauropods in opposing scenarios. Originally depicting them as feeble brained, solitary, aquatic reptiles and then in later years, to herding animals

with complex behavior, living in open dry savannah environments Dodson 1990, . Current speculation, based on Dana discoveries, portrays diplodocids somewhere in the middle of these two scenarios, as highly evolved creatures well suited for extensive overland travel but preferring to live and to feed in watery shore environments, a niche filled primarily by today's wading birds. The key adaption for this niche is the ability to travel from one body of water to another, in the case of birds, flying is their method of travel while diplodocids are perfectly adapted for long distance walking. The ability to migrate and to explore new resources confers a substantial ecological advantage to a species so that it is not restricted to a habitat in the same way aquatic animals are to water. This form of opportunistic feeding may have varied their food intake regionally and seasonally. Long before wading birds, the shore or wetland habitats may have been dominated by sauropod and hadrosaur species throughout most of the Jurassic and Cretaceous Periods. Fossil evidence for the existence of wading birds is not known until the Eocene, (Green River Formation/ Messel) where a large diversity of species occupied this niche until today.

The Head

One of the most extraordinarily derived features in *Amphicoelias brontodiplodocus* is the microcephalomorphic condition of its skull. The skull in DQ-BS measures approximately fourteen inches against its estimated body length of eighty feet, which amazingly calculates to approximately 1.4 % of body length. Among quadruped animals, *Amphicoelias brontodiplodocus* may have evolved, proportionately, the smallest known skull, paralleling in proportion birds and toothless mammalian edentates. The braincase is also incredibly small which apparently, in life, housed a brain no larger than a man's thumb (measured from the base at the wrist). During preparation, matrix sand carefully removed and saved from Einstein's braincase measured 80 cubic centimeters or approximately less than a half of a cup in volume. DQ-EN is a massive individual specimen from the Dana Quarry, almost the size of the American Museum of Natural History "*Brontosaurus*" skeleton. Like microchip technology, this reduce sized brain must be respected as an organ optimized to maintain a substantial body morphology as this, that also needs to be acknowledged as a derived sauropod character. *Apatosaurus* brain morphology is the subject of a recently published research by Balanoff, et al, 2010. The cranial skeleton in *Amphicoelias brontodiplodocus* is lightweight in construction featuring, thin bones, proportionately large openings, and nearly toothless upper and lower jaws, all to minimize the cantilever weight stress the neck had to support.

The skull drawing (Fig. 26) of *Amphicoelias brontodiplodocus* (DQ-BS) accurately depicts how the animal holds its head naturally taking into account the ventral position of the occipital condyle. This is critical in that it shows two important features about these amazing creatures not previously described. With head held in this position, its eyes would see without obstruction, and were clearly stereoscopic, positioned similarly like those in birds for

example. This is best appreciated when the skull is examined in front view. All the other known Diplodocid skulls may be incorrectly reconstructed or preserved distorted, as they do not seem to show this feature to the same degree. The other feature is orientation, which is determined by the identifying the top of the head in connection with orbital position. The skull in *Amphicoelias brontodiplodocus* is flexed, by the downward position of the occipital condyle, which does not face directly back as in most other dinosaurs. In a relaxed pose the head is held with the snout pointing down while the frontal (top of skull) is kept horizontal to the ground. Therefore, to point its head to look straight ahead the neck needs to curve in below the skull, which tends to agree with the idea that the entire neck was not kept rigid and low to the ground. Head and neck posture in sauropods is the subject of debate (Taylor et al 2009, Stevens & Parrish 2005). The downward angle of the occipital condyle allows the skull to be held in an inverted position when the neck is lowered while feeding, see Fig. 27.

The Feeding System

Amphicoelias brontodiplodocus and other diplodocids, display a unique dental morphology somewhat reminiscent of the specialization seen in certain insectivorous mammals (e. g. *Proteles*, *Manis*), which share a significant reduction in the number of cheek teeth with weak slender jaws, where chewing has been effectively abandoned as an adaption for feeding on small and relatively soft foods such as insects. The feeding preferences might have been for similar types of foods in *A. brontodiplodocus.* The tooth crowns in *Amphicoelias brontodiplodocus* have been greatly simplified, narrowed and like its roots also elongated. In other words the individual teeth are long and skinny, and situated in the jaws evenly and slightly protruding so to appear like the teeth in a comb. Descriptions by Holland 1924 points out similar features in the dentition belonging to the skulls CM 11161 and 11162.

The entire dentition may have functioned similarly as in the comb-like incisors of certain mammal species. Like the incisors in other animals, the teeth are retained only in the front edges of the upper and lower jaws. These dental features are derived in comparison to more primitive sauropods *Camarasaurus* and *Brachiosaurus*, and point to a unique feeding adaptation. Analyses based on cranial structure, dental micro wear and feeding mechanisms, Barrett & Upchurch 1994, 1995, Calvo 1994, Christiansen 2000, Upchurch & Barrett 2000, and Sereno & Wilson 2005 concluded that the diplodocid dentition does not interlock and the jaws are used primarily in a back and forth movement, however, these studies have speculated that branch stripping may have been employed. Stripping would require that swallowing of virtually complete vegetation without being processed into a lump through mastication, and pushed by muscle contractions in a twenty- thirty foot long neck, which seems highly improbable. Effective processing orally of plant material requires the food to be chewed into a lump for throat muscles to be able to swallow. It is clear that Morrison diplodocids were incapable of chewing plant material with their front teeth therefore it is believed that the reduced
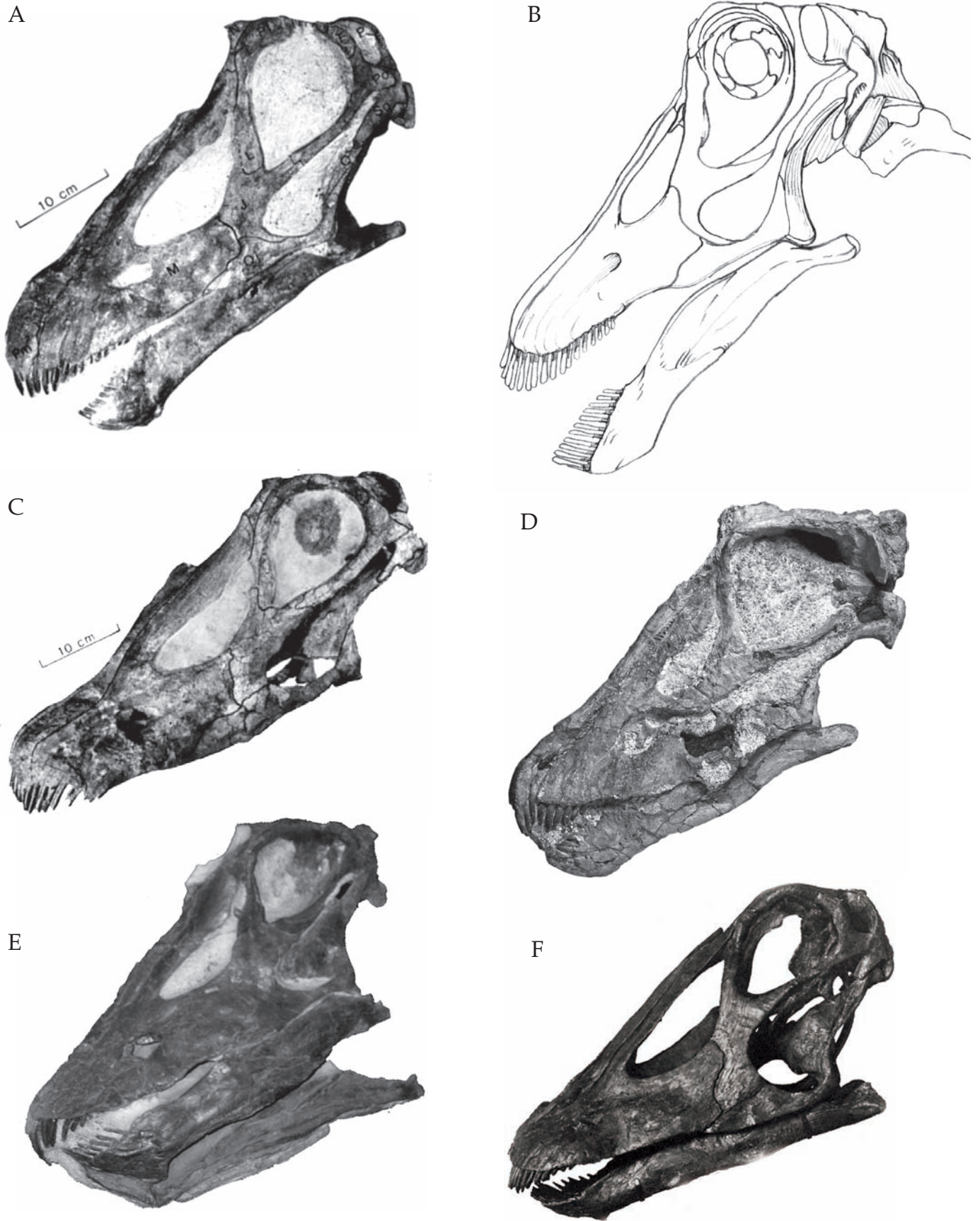
Fig. 26. Comparison of Diplodocid skulls including reconstruction drawing of the new Dana Quarry specimen. Skulls have been reoriented, to reflect a more anatomically natural pose based on the position of the occipital condyle: A., CM 3452 Berman and McIntosh 1978. B., DQ-BS Dana Quarry. C., CM 11161 Berman and McIntosh 1978. D., CM 11255 reversed after Whitlock 2010. E., USNM 2672 Holland 1906. F., AMNH 969. Figures not to scale

dentition was part of a feeding system, which incorporated a type of rostral bill.

Fig. 27. Illustration depicts the head of *Amphicoelias brontodiplodocus* in an inverted feeding position as indicated by the right angle of the occipital condyle against the long axis of skull.

Rostral Bill

The presence of a rostral bill is indicated by the distinct grooves, channels, pits and foramina on the surface bone of the upper and lower jaws. This rostral bill may have been formed by durable keratinous/ramphotheca or from reinforced or thick epidermal tissue, which may have been formed with a degree of leather like flexibility. This rostral bill probably covered the snout in areas of the premaxilla, maxilla and dentary. Additionally, it is possible that a cutting edge or notch also existed on the long post dental diastema, which, as indicated on the skull, may have been created by the angle of the lower boarder along the maxilla and quadrajugal contact, and from below the posterior ridge of the dentary. This rostral bill may have resembled and functioned both like a duck's bill and a turtle's beak.

As in a duck or flamingo's bill equipped with fine ridges, the teeth in *Amphicoelias brontodiplodocus* may have had a double function, one being the incorporation of these thin teeth into a rostral bill to form ridges necessary for filter feeding, possibly by dabbling. Dabbling for soft aquatic vegetation, algae, insect larvae and crustaceans may have been an energy efficient way of consuming highly nutritious foods in large quantities. The inter-dental spaces creating a comb-like structure may have functioned as a straining apparatus in the imbedded teeth. A secondary function may have been to use the protruding peg-like teeth as a functional beak for probing in soft mud, nipping and manipulation. The section of the jaws behind the teeth may have had a keratin cutting edge for slicing Gand reducing larger food matter into manageable pieces, in the same way turtles use the side of their jaws equipped with double rows of sharp ridges for shearing and chopping.

With the ability to wade, *Amphicoelias brontodiplodocus* may have had access to a larger menu of food in comparison to other contemporary herbivores. During seasonal migrations from one body of water to another when it could not filter feed or dabble for microscopic aquatic plants and animals, *Amphicoelias brontodiplodocus* may have taken advantage of its long neck and specialized bill to browse on both low and high vegetation with a selective picking and browsing capability not available to other herbivores. Fungi, fruit, tree sap, and insects may have been some of the selected sought after foods.

Nasal Repositioning

The presence of a rostral bill in *Amphicoelias brontodiplodocus* is also evident in the harmonious character complex seen in the skull skeleton. Principally these characters include the posterior-dorsal position of the opening for the external nares above the orbits, modification and caudal elongation of the premaxillae, and size reduction of nasal bones. Many vertebrate species with reduce or absent dentition, evolve beaks or bills as an alternative efficient lightweight food processing mechanism. As a developmental consequence of this feeding mechanism, the nasal opening must be relocated behind the area of the continually growing horny keratin in order to the protect the air passages from obstruction. Virtually all bird species have their nostril openings located at the posterior end of their bill or beak but in front of the nasal-frontal hinge. Several duckbilled hadrosaurs also show backward, close to the orbit, repositioning of the nasal openings. The highly speculative and sometimes controversial nasal position in diplodocids (Coombs 1975, Witmer 2001, and others) can be explained as a response to a neomorphic structure such as a keratin bill, and not as an adaption seen in animals that are truly aquatic (Bakker, 1971, 1986). The position of the nasal opening is compelling evidence in favor of a rostral bill structure, which seems to have been overlooked in discussions attempting to explain this unique dinosaur trait. The external shape of this bill structure may have extended the snout considerably. The caudally placed nasal opening may have also aided in the ability to simultaneously breath while filter feeding during long periods of wading in *Amphicoelias brontodiplodocus*. The posterior position of the obits and nasal openings in the skull is well suited to allow the elongated snout to be submerged in water or mud for extended periods. Moreover, the right angle position of the occipital condyle against the long axis of the skull is another unique diplodocid synapomorphy that would allow the skull to be held in an inverted position while feeding. The inverted position of the head would make the intake of water easier while at the same time permitting the rejection of water through the nasal openings to be blown away from the face, see Fig. 27. Therefore, nasal repositioning, and flexed angle of the skull is consistent with the presence of a rostral organ for the purpose of filter feeding.

Neck

As a primary function, the long sauropod neck was designed for the obvious purpose to have a better reach. With respect to feeding, such a reach had to take advantage of the resources available from one feeding zone into another, thus making sense for its extreme length. In the case of *A. brontodiplodocus*, reaching into tall treetops or from a body of water onto a shoreline seems to present the best logical explanation for natural selection to favor a long neck. To feed or to graze on plants at your feet, neck length need only be as long as the legs. So the notion that diplodocids like *A. brontodiplodocus*, kept their heads normally low can be rejected if only for these reasons. The secondary function for an elongated neck is for wading in a safe distance from land predators. With the help of an elongated neck, *Amphicoelias brontodiplodocus* may have been able to reach from a deeper part of a lake or river to the shoreline where soft vegetation, algae and arthropods were abundant. In deeper water the pneumatic axial skeleton may have had an advantage in keeping the body buoyant, while drifting or floating from one feeding area to another with little effort.

From three Dana specimens that were found with articulated cervical vertebrae (DQ-BS, DQ-TY and DQ-SB), we can see that the morphology of the anterior vertebrae is designed for flexibility, enabling the head to look about independently. For example, the ends of the centra are inclined, indicating that the neck was held naturally in a flexed position. The posterior cervical vertebrae, (C10-14) may have been held rigidly together but the anterior ones (C2-9) were flexible so the head could move in various directions and in addition to looking about, to help reach considerable distances up from the ground. Although, the head and neck may have been held low while feeding, it had to be nearly straight up, much higher than the level of the hips, when walking. To avoid cantilever stress during walking, the head and neck probably had to be elevated and positioned back to a point where much of that weight could be balanced over its forelimbs.

How the cervical vertebrae articulated below and not behind the braincase is another important observation from the Dana specimens. The head and neck in this position, helps support the idea that the neck must have been flexible at least in the forward section - in our specimens, flexibility was probably above the 9th cervical. Recent studies (Stevens and Parrish, 2005) argue that the entire neck in Diplodocids was kept stiff and held low to the ground. Our Dana specimens demonstrate the opposite condition in showing flexibility at the anterior set of neck bones. Part of the evidence is based on three *Amphicoelias brontodiplodocus* cervical series that were preserved with the anterior section articulated loosely and the back section rigidly articulated. It makes sense for a head equipped with stereoscopic vision to have the added ability to look around especially behind itself to detect danger and to be able to use the whiplash tail effectively. Moreover, the cotyle joint in the centra are slanted allowing a great range of movement indicating that the neck
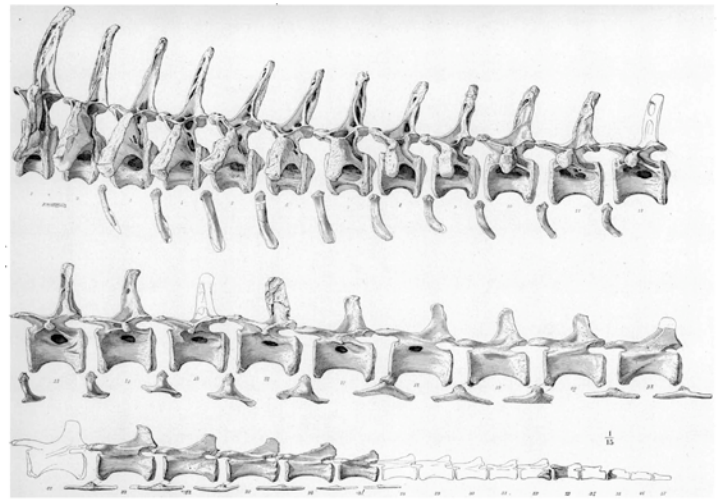

Fig. 29. Illustration of AMNH 223 after Osborn 1900 here referred to *Amphicoelias altus* exhibits elongated prezygapophysis not seen in *A. brontodiplodocus*

had the ability to flex. With cervical flexibility, *Amphicoelias brontodiplodocus* could look about freely at the end of its long rigid neck, in the same manner as in living ostrich for example. In contrast, in living giraffes, the atlas and axis act as the only pivot point of movement for the head's ability to look about from the end of its long and rigid neck.

Neural Spines

In both DQ-TY and DQ-BS the neural spine processes of the cervical vertebrae from C 2-8 are undivided, which provides additional evidence supporting flexible movement in the neck. Starting with the ninth cervical, there is slight notch, and from 11th -15th bifurcation is progressively deep. This condition seems to be unique in the Dana specimens, and thus marks the most primitive state known in Diplodocidae. In comparison, bifurcation begins in the following cervical position by number in these taxa: C5 *Suuwassea emilieae*; C6 *Apatosaurus lousiae*; C2 *Apatosaurus excelsus*; C6 *Apatosaurus ajax*; C3 *Diplodocus carnegii*; and C2 *Dicraeosaurus*. It should be point out that in the (AMNH) partial skeleton of *Barosaurus* described by McIntosh, 2005 may share the same condition of mid cervical neural spine bifurcation as in the Dana sample, which commence at C 9.

Cervical Ribs

The most surprising feature seen in the cervical vertebrae are the elongated overlapping ribs. DQ-TY is the best-known diplodocid example displaying in completeness this primitive morphology, Fig. 28 A. This condition is also visible in DQ-SB and DQ-BS, but not as well and complete as in DQ-TY. Equally fascinating are the cervical ribs in DQ-PC, which are noticeably shorter proportionately in length but exceedingly more robust, Fig. 28 B. In DQ-PC, the parapophyses are massive, well developed laterally extending the width of the vertebra considerably beyond the other Dana individuals. The DQ-PC skeleton represents

a large individual with a humerus length of 104.1 cm, and was preserved immediately next to the DQ-SB skeleton. To reiterate the conclusions reached herein, the condition in the cervical ribs are osteological traits displaying sexual dimorphism.

Whiplash

Like the neck, the tail in *A. brontodiplodocus* was designed for extended reach as can be seen not only by the elongation of vertebral centra but also from the unique development of supernumerary caudal elements. This specialization is a well-established autapomorphy occurring in Morrison diplodocids, which essentially doubles the tail length. These supernumerary elements also double the number of caudal elements forming the tail. DQ-TY and DQ-SB have the greatest number of caudal vertebrae complete with chevrons preserved in articulation amongst the Dana sample. These specimens exhibit a diverse morphology obviously designed for a use much more sophisticated than simple counterbalance. Myhrvold and Currie, 1997, explored the capabilities of diplodocid tails of being used as supersonic noisemakers. However, we compare these whiplash vertebrae to martial arts weapons (Bakker 1994), specifically, flexible long-range flail weapons - Chinese Three Section Staff, the Plum Flower Chain, and Okinawa Nunchaka. The tail similarities to these weapons include loosely connected equal length sturdy segmented rods that deliver fast and crushing powerful blows from built up speed and momentum. Speed and momentum is generated in part by the loosely connected and elongated streamline length of the caudals creating a whip like extension. Direct impact application is possible due to the well-developed thick and dense compact bone in the posterior section of tail vertebrae. In *Amphicoelias brontodiplodocus*, the compact surface bone of these caudal is noticeably thicker in proportion to the same in other skeletal elements. A dual purpose their articulation can be used to strike over or around an object in the same manner martial arts weapons do by allowing a greater chance of hitting a target.

Towards the end of the DQ-TY tail, after the 32nd caudal or so, the neural spines suddenly change into simple but robust freestanding processes with a distinctive backward hook. These spines are without zygopophysis, and seem to have developed density to add both weight and strength to control better the free action in the tail. The major feature here is the densely weighted bone, (synapomorphy) which would not be ideal as a bullwhip-like structure but to strengthen the striking power of the tail. The hooked shaped neural spines may have helped to create a serrated edged along the tail, enhancing the flesh cutting ability of the tail during its use. Discoveries at Howe Quarry, (Czerkas, 1992, Ayer, 2000 Michelis, 2004), that preserved skin impressions from a tail section belonging to a diplodocid shows clearly that dermal spines were present, which may have been supported internally by these dense bone neural spines. In life, the whiplash vertebrae are spaced apart indicating that a tough flexible tissue may, have held these elongated elements, together. The presence of tissue between these elements is demonstrated by the evidence observed in the in situ discovery belonging to DQ-TY, see Fig. 12 F. Past the 40th vertebra or so, the supernumerary caudal elements become sub-equal in length developing biconvex ends in mature adults. In the immature specimen (DQ-TY) the ends of these caudal elements are nearly flat while in adults they are convex suggesting an ontogenetic feature.

Fused or coossified vertebrae are a characteristic *Amphicoelias* trait but it is not found in all specimens where the tail is complete enough to be sure of its presence. This caudal vertebrae fusion shows various degrees of ossification in individual specimens. It is always restricted to the centra where the surface bone is scarred with extra growth that form horizontal rod like ridges identifiable as ossified longitudinal ligaments, possibly to create addition tail reinforcement. Interestingly, the same type of condition is present in the prehensile tails of living anteaters of South America. These fused vertebrae may have helped in the same way that a handle of a long range weapon employed from a man's arm responds, by helping to transmit power and speed through the unique combination of rigidity and looseness of the tail. A dual function may include the strengthening of an area from which to rest body weight during tripod standing as explained below. Examination of a series of kangaroos tail skeletons would be an interesting study to see if there is a connection in caudal reinforcement as in *Amphicoelias.* In DQ-TY these caudals show what may be early stages of ossified longitudinal ligaments seen in advanced stages in the tail vertebrae of USNM 10865 and type of *D. carnegii.* DQ-TY's young individual age in opposition to early stages of fused caudal vertebra, a feature seemingly for fully-grown adult, provides some evidence against conclusions reached in Rothschild & Berman, 1991 study. Their study concluded that the fusion was the result of a condition similar in humans of advance years named "diffuse idiopathic skeletal hypostosis" or DISH. They hypothesized that the fused caudal may have helped tail lifting in females during copulating, thereby explaining the distribution of this feature as gender based.

Thus, the extraordinary functional morphology in the tail region of these dinosaurs supports the presence of a capability more sophisticated than the side swiping tail defensive behavior of a monitor lizard or crocodile. In life, *Amphicoelias brontodiplodocus* had a tail designed to slash flesh and strike with bone crushing power, with the added capability to hit a target with deadly accuracy.

In DQ-SB the last preserved caudal shows a pathology indicating that it had lost the terminal whiptail section of vertebrae due to an injury. Whether it was bitten or broken off during battle is not clear, but it does record the first pathology of this type found in a tail of a sauropod. Remarkably, this caudal vertebra shows bone growth around the centrum, similarly as in the "club tailed" sauropods from Asia *Omeisaurus* and *Mamenchisaurus*. It is possible that the club tail, in these genera, is a traumatized caudal and not a true club as in ankylosaurs. This specimen shows no fusion of mid caudal vertebrae as seen in DQ-TY and DQ-

A

B

C

Fig. 28 A-C. A - B., Comparison of mid cervical ribs in *Amphicoelias brontodiplodocus* belonging DQ-TY and DQ-PC from Dana Quarry. Note the proportionately more robust rib and the massive, well developed laterally extending parapophyses in DQ-PC (posterior end of rib is not shown) in comparison to the elongated overlapping ribs in DQ-TY. C., cervicals belonging to DQ-SB, an adult specimen displaying a shorten length in comparison to DQ-TY.

BD. The loss of whiplash in life perhaps is a common feature in diplodocids and is connected in some way to the absence of mid caudal fusion. The specimens listed in Rothschild and Berman, 1991, which are lacking mid caudal fusion are not complete with whiptail sections. For example, AMNH 223 is not a complete tail section see Fig. 29. Fusion occurs in different locations in the mid caudal section of the tail in various individuals.

Rearing

Diplodocids inherited strongly constructed hips, hind legs and tail from their bipedal ancestors, so rearing may have been possible at least in young individuals. The hind legs and tail would act as anchors for the body in a tripod stance. Attempting to stand a body as elongated as *Amphicoelias* would demand a coordinated effort in the animal's ability to quickly bring the head, neck and forelimbs as close over the center of gravity without losing balance. Before the body is thrown up in elevation by the upward spring of the forelimbs, the hind feet would need to have been rotate inward to begin the process of balancing the huge towering body. To help in balancing, the astragalus has developed on the ventral articulation a flatten surface to allow flexibility and looseness in the joints, thereby, permitting the pes to rotate inward against the tibia and fibula to obtain stability during the ascent of the forward part of the body. The condition in the ankle of *Amphicoelias* is an interesting sauropod / theropod character that needs to be explored more thoroughly. Also supporting the idea that rearing was possible is the presence of forked chevrons in concert with the disproportionately enlarged or transitional series of the mid caudal vertebrae where the tail would have touched the ground during erect tripod standing. While the body is being lifted up and tail presumable held in a somewhat horizontal position, the section of caudal vertebrae that would touch the ground first would be the mid section series (C 14-28) where the bones are densely reinforced and bear forked chevrons. The Dana specimens are the only diplodocids to have chevrons preserved in place, and this sample exhibits variability in the location of fused caudal vertebrae and forked chevrons. The variability in the location of coossification of caudal vertebrae would depend on the frequency of rearing and growth of the individual. The forked chevrons are the key feature here in that they probably protected the neural spines from compression and therefore damage. Thereby, rejecting the reasons given against the idea that rearing was not possible, Myhrvold and Currie 1997.

With the ability to rotate the pes, and presence of three well-developed claws, digging in the ground for the purpose of nesting may have also been possible in Amphicoelias. In the same way living turtles and tortoises dig into the earth to build nests for the laying of their eggs.

Fig. 30. Comparison of hindlimbs in adults belonging *Diplodocus* and *Apatosaurus*, from Osborn 1899. Except for size and robustness these elements are virtually the same.

Sexual Dimorphism

Sexual dimorphism in dinosaurs is poorly understood largely due to insufficiently large population samples from a single time plane, permitting a study via morphometrics. Many previously established dinosaur species are probably based on gender-related characters. We interpret the dimorphism in *Amphicoelias brontodiplodocus*, as representing male and female individuals. The hypertrophic condition of the cervical ribs in the Dana sample provides compelling evidence in the present working hypothesis. Only the Dana sample (DQ-EN & DQ-PC) and *Apatosaurus,* poses this enigmatic cervical rib autapomorphy, which expands the width and depth of the neck skeleton substantially. We speculate that in life, this immensely broad, and strongly constructed, neck was used in a courtship behavior involving the neck while bearing down on the back of the female's neck for the purpose of subduing and holding the body steady during copulation, Fig. 31. In the same manner bull elephants use their oversized heads and heavy tusks to bear weight on the back of the female before copulation. The height, bifurcation of neural spines and ventral width of centrum between males and females is another sexual dimorphic feature seen in the cervical vertebrae. The neural spines' narrower width on the cervical vertebrae in DQ-SB, DQ-BS, and DQ-TY are quite slender in comparison to DQ-PC. In other words, the width of the cervical across the ribs in Prince allows it to fit over the slender female necks. Moreover, a broaden neck may have also played a role in courtship display and in male rivalry. The courtship displays may have had a cobra-like effect in their swaying heads and necks, but of course, looking much bigger. Intraspecfic combat, territorial defense, and dominance could have been achieved among males by pushing or slamming with their necks, in the same way male giraffes compete using their necks and heads against each other. The small size or absence of pleurcoel fossae in the anteríor caudals may be a response to the necessary weight increase in males. Most of

the features recognized as gender specific can be seen in very young individuals; it is probable that most male features were neotenic in origin. For example, the hypertrophic cervical ribs, short axial skeleton, absent pluerocoels, and short neural spines can be seen in SMA 0009. These observations support in part Senter's 2007 discussion of neck elongation in sauropods, which may have been driven by sexual selection, and not by feeding competition.

Fig. 31. Adult male and female *Amphicoelias brontodiplodocus* in speculative mating positions displaying the use of broad neck in males for subduing their mates before copulation.

Morrison diplodocids may have occupied a proboscidean-like niche with a gregarious population of males and females analogous to African elephant herds. Males (*Apatosaurus*) with larger and more massive bodies would have powerful broad necks for courtship display and subduing females. African elephants vary greatly, but males are generally much more massive than same age adult females. In addition to over all greater size and stature, male elephants may be twice the weight as in females. Principle courtship display in male elephants is their larger tusks. *Amphicoelias* females may have formed herds to help rear calves, which were led by a dominating, harem keeping male. Males may have lived a solitary existence away from the herd appearing only during courtship. This may explain why, in the best fossil sites, *Amphicoelias / Diplodocus* is found in multiples while *Apatosaurus*, only as occasional isolated occurrences.

The morphological distances between *Camarasaurus* and *Brachiosaurus* are similar in many ways to what exists in the Dana sample, thus, the need to reconsidered these taxa as gender based.

Ontogeny

Great morphological variation exists in one documented Saurischian population, the mass mortality collection of *Coelophysis*, from Ghost Ranch New Mexico, Colbert 1989. Colbert reports on the proportions of limb to cervical lengths, in *Coelophysis,* which can vary greatly, as much as 20% or more, demonstrates that axial vs. appendicular development is not equally synchronized. As exemplified in two immature specimens, DQ-TY and SMA 0009, the same ontogenetic condition appears to exist in both *Amphicoelias* and *Coelophysis*. The recognition of ontogenetic features is of great taxonomic importance not only for diplodocids but other sauropods. In addition to sexual dimorphism and individual variation, ontogeny helps to indentify character polarity in a clear biological manner.

The baby sauropod skeleton "Toni", described by Schwarz, et al, 2007 (SMA 0009, Howe Stephens Quarry, Shell, Wyoming, belongs in the genus *Amphicoelias* and probably represents *A. brontodiplodocus*. As Toni's clavicle is the same boomerang-like shape as in DQ-SB and DQ-TY. In comparison to the fragment described as a possible clavicle belonging to *Suuwassea*, by Harris, 2007, the Dana Quarry clavicles are not similar in being more bent and without rugosities on the end of the process. The same difference is true for the clavicle figured by Hatcher 1901 for *D. carnegii.* It is not certain without the benefit of better material if these feature represent species difference between *A. brontodiplodocus* and *A. altus*.

The striking disproportionately large limbs in comparison to the axial skeleton in SMA 0009, is consistent with the condition that exists in DQ-TY. Both show rapid lengthening of the appendicular elements in contrast to slow development exhibited in the axial skeleton. A reconstructed skeleton of either SMA 0009 or DQ-TY would recall the ungainly appearance seen in puppies or in a pony. For example, the Houston *Diplodocus hayi* is 27.43 meters in length with a humerus that 91 cm long, in contrast DQ-TY is 12.80 meters in length with a humerus measuring almost 81.28 cm, but much more slender in comparison.

The most interesting and observable aspect of Toni's skeleton is its short neck and tail. Both of these features suggest that in very early in its life history, the individual was not fully capable to survive on its own. The neck's reach and tail's whiplash may have not been effectual at that stage of development, thereby, implying that a social behavior in *Amphicoelias* may have existed if parental care was involved. The early development of long legs suggests that this was essential for survival and supports the idea that SMA 0009 may have been part of a herd in that the appendicular elements were highly developed and very well suited for traveling, a critical aspect in keeping up with its members for protection. Intermediate in size between SMA 0009 and DQ-TY is the type of *Elosaurus parvus* (CMNH 566) Peterson and Gilmore 1902 from Sheep Creek, Wyoming, which demonstrates that gender related features, can be seen early in ontogeny. In this specimen the scapula is near

equal to the femur in length just as in the SMA 0009 skeleton, but the humerus has already taken the typical hour-glass shape seen in adult male specimens. The scapula in SMA 0009's skeleton is the largest bone while in adults it is the femur. Schwarz, et al, 2007 made no comparisons between the two disproportionately longer than femur scapulae in the specimens comprising SMA 0009 and type of *Elosaurus parvus*, a key factor in determining the age and gender of these two specimens.
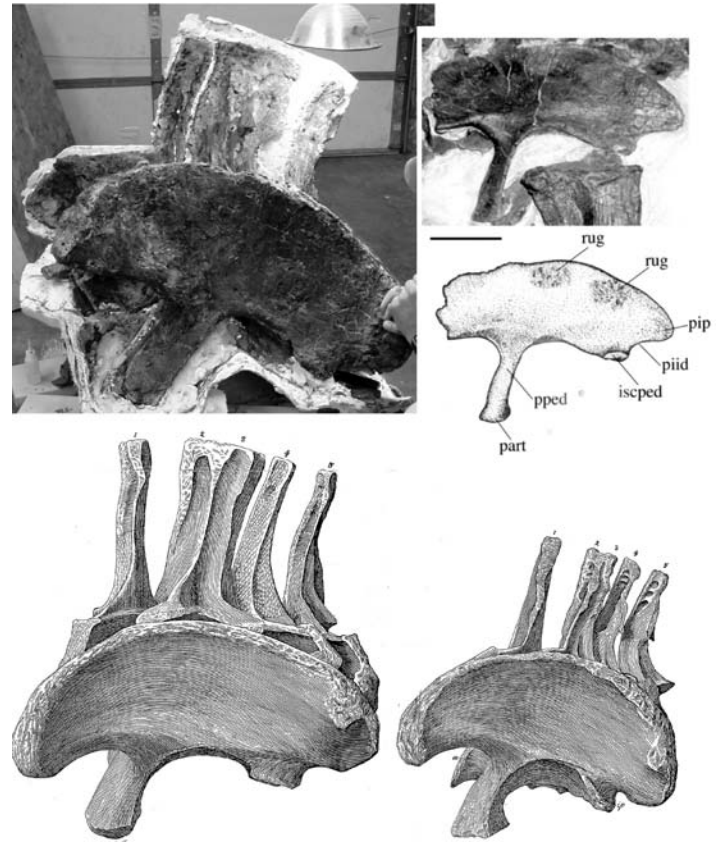

Fig. 32. Comparison of illia belonging to DQ-TY and SMA 0009 illustrating the elongated pubic peduncle in juveniles of *Amphicoelias*. Bottom row adult *Apatosaurus* and *Diplodocus* illia for comparison.See also Fig. 7C, DQ-SB. Illustrations from Schwarz 2007 and Hatcher 1903

Whitlock, et al, 2010 identified the skull CM 11255 as belonging to a juvenile individual with a snout that is more rounded, and teeth distributed much further back along the jaws, in comparison to adult skulls referred to *Diplodocus*. CM11255 was discovered in Dinosaur National Monument near two partial skeletons AMNH 6341 (*Barosaurus)* and USNM 10865 (*Diplodocus).* CM 11255 may not belong to a juvenile individual based on comparison with the Dana sample. The skull in DQ-BS is approximately twelve and half inches long (length from laterally exposed edge of the left maxilla to sagital nuchal crest – 331 mm) and the femur is 4.65 feet (142 cm). The skull length in CM 11255 is 13.77 inches, which by comparison with *A. brontodiplodocus* (DQ-BS) the femur should measure little more. AMNH 6341 (*Barosaurus*) femur length is 4.72 feet (1440 mm) and USNM

10865 femur 5.16 feet, so it is possible that CM 11255 may actually belong to one of these adult skeletons.
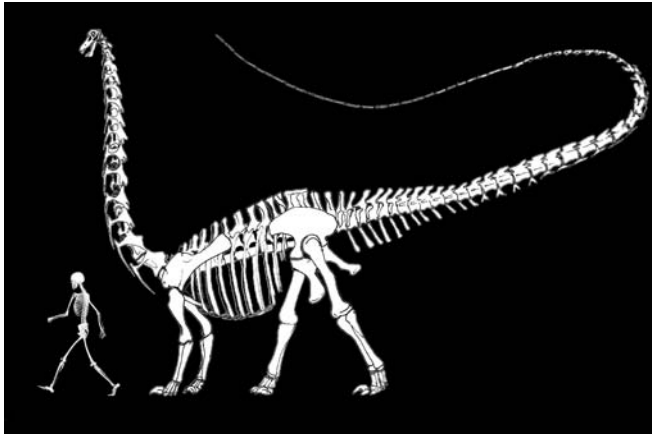

Fig. 33. Skeletal reconstruction of *Amphicoelias brontodiplodocus* based primarily on the present specimens DQ-TY and DQ-BS, which are determined to be young adult females. This silhouette drawing is a revision in progress aimed at deriving an accurate osteological reconstruction incorporating new information based on complete material. The short forelimbs against tall hindquarters suggests a more crouching pose bringing the dorsal and caudal vertebrae into an upward angle thereby allowing greater freedom in the range of motion for the use of the tail as a weapon. Our new skeletal reconstruction is in some respects reminiscent of a scorpions' attack pose, and contrasts with previous attempts which incorrectly portraits the axial skeleton in a stiff horizontal position.

Body Weight

Their elephantine bodies supported extremely long necks and tails making them look gigantic in proportions and dimensions of length, but their weight has been overestimated. Previous reported calculated weight estimates, suggests that sauropods like *Diplodocus* and *Apatosaurus* may have reached 11 and 33 tons respectively, Colbert, 1962, Alexander, 1985. Although, we disagree with these weight estimates despite their size, sauropods may have not been as heavy as speculated. However, what's interesting and relevant to sexual dimorphism seen in this study, *Apatosaurus* was determined to be three times the weight of *Diplodocus*. It would seem odd that an animal with a massive skeleton as in apatomorphs would not develop weight reducing features as seen in other diplodocidmorphs, unless it there is a distinct advantage in being heavier. In terrestrial animals bigger and heavier are generally linked with defense or sexual dimorphism.

Diplodocid skeletons were architecturally designed to incorporate weight reducing air cavities throughout much of their axial skeleton in the same way birds lighten their bones. The pneumatic skeleton is the evolutionary advantage, which saurischians had in developing gigantism as a survival strategy. In sauropods there exists a correlation between increase size and degree of pneumatization Wedel, 2003, 2005. The method of calculating weight by using water displacement is misleading when taking into account the pneumatic condition of these skeletons – imagine the erroneous calculated heavy weight of an inflated balloon. Another technique relies on the measurement of long bones such as humerii and femora in deriving estimated weights. This alternative method of determining the weights of dinosaurs from living mammalian quadrupeds, assumes the body mass to be similar, which is of course it is not. Until a reliable method is developed to calculate the estimated body weight of a pneumatically designed skeleton as in living birds, dinosaurs, especially sauropods, will remain a challenge.

Gastroliths

Given that the skeletons in the Dana Quarry represent in situ mortalities, it is interesting to note that no stomach stones or gastroliths have been found in or near the rib cage area belonging to any one of the five *Amphicoelias brontodiplodocus* skeletons. These specimens were excavated within a relatively small area no longer than 100 meters and were not separate from each other by distances exceeding seven meters. This evidence is in direct contridiction to the reported gastroliths found with *Seismosaurus* in New Mexico, Gillette 1991. We interpret this absence of gastroliths as evidence that *Amphicoelias brontodiplodocus* did not feed on hard vegetation, and furthermore speculate that gastroliths found in Morrison sites of younger age may instead belong to the tree top browsers *Camarasaurus or Brachiosaurus* where the occurrence of these taxa is exceedingly more abundant.

REFERENCES CITED

Ayer J. 2000. The Howe Ranch dinosaurs. Aathal, Switzerland: Sauriermuseum Aathal.

Alexander, R. McNeill. 1985. Mechanics of posture and gait of some large dinosaurs: Zoological Journal of the Linnean Society 83: 1-25

Balanofff, A. M., Bever, G. S., and Ikejiri, T. The Braincase of Apatosaurus (Dinosauria: Sauropoda) Based on Computed Tomography of a New Specimen with Comments on Variation and Evolution in Sauropod Neuroanatomy. AMNH Novitates Number 3677, 29 pp., 10 figures, 1 table March 4, 2010

Bakker, R. T. 1971. Ecology of the brontosaurs. *Nature* 229, 172-174.

Bakker, R. T. 1986. *The Dinosaur Heresies. New Theories Unlocking the Mystery of Dinosaurs and their Extinction*. William Morrow, New York.

Barrett, P. M. & Upchurch, P. 1994. Feeding mechanisms of *Diplodocus*. *Gaia* 10, 195-203.

Barrett, P. M. & Upchurch, P. 1995. Sauropod feeding mechanisms: their bearing on palaeoecology. In Sun, A. & Wang, Y. (eds) *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press (Beijing), pp. 107-110.

Berman, D. S. and J. S. Mclntosh. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). Bulletin of the Carnegie Museum of Natural History 8:1–35.

Calvo, J.O. 1994. Jaw mechanics in sauropod dinosaurs. *Gaia*, 10:183-193.

Carpenter, Kenneth. 2006. Biggest of the big: A critical re-evalustion of the mega-sauropod Amphicoelias fragillimus Cope, 1878. pp. 131-137 in J. Foster and S. G. Lucas (eds.), Paleontology and Geology of the Upper Jurassic Morrison Formation. New Mexico Museum of Natural History and Science Bulletin, 36.

Christiansen, P. 2000. Feeding mechanisms of the sauropod dinosaurs *Brachiosaurus*, *Camarasaurus*, *Diplodocus*, and *Dicraeosaurus*. *Historical Biology* 14, 137-152.

Coombs, W. P. 1975. Sauropod habits and habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology* 17, 1-33.

Cope, E. D. 1877. On Amphicoelias, a Genus of Saurians from the Dakota Epoch of Colorado. Pal. Bull. No. 27, pp. 1-5

Colbert, E.H. 1962. The weights of dinosaurs, Novitates 2076: 1-16

Colbert, E. H. 1989. The Triassic Dinosaur Coelophysis. Museum of Northern Arizona Bulletin.

Czerkas, S. A. 1992. Discovery of dermal spines reveals a new look for sauropod dinosaurs. Geology 20: 1068-1070.

Dodson, P. 1990. Sauropod paleoecology. pp. 402–407 in D. B. Weishampel, P. Dodson and H. Osmolska (eds.), The Dinosauria (First Edition). University of California Press, Berkeley.

Foster, J. R. 2003. Paleoecological Analysis of the Vertebrate Fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region U.S.A. New Mexico Museum of Natural History and Science, Bulletin 23

Fraas, E. 1908. Ostafrikanische Dinosaurier. Palaeontographica 55: lton, P.M. 1977.

Filla, J., Redman, P.D., 1994. *Apatosaurus yahnahpin* a preliminary description of a new species of diplodocid dinosaur from the Late Jurassic Morrison Formation of southern Wyoming the first sauropod dinosaur found with a complete set of 'belly ribs'. In: Nelson, G.E. (Ed.), The dinosaurs of Wyoming. Wyoming Geological Association, Casper, pp. 159–178.

Gillette, D. D. 1991 Journal of Vertebrate Paleontology 11(4): 417-433, the Society of Vertebrate Paleontology *Seismosaurus halli*, gen. et. sp. nov., A New sauropod Dinosaur from the Morrison Formation (Upper Jurassic/ Lower Cretaceous) of …

Gilmore, C.W. 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum of Natural History*, 11:175-274.

Harris, J. D. and P. Dodson. 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. Acta Palaeontologica Polonica 49:2197–210.

Harris, J. D. 2007. The appendicular skeleton of *Suuwassea emilieae* (Sauropoda: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana (USA). Gobios 40 501-522

Hatcher, J.B. 1901. *Diplodocus* Marsh: its osteology, taxonomy, and probable habits, with a restoration of the skeleton. *Memoirs of the Carnegie Museum of Natural History*, 1:1-63.=

Holland, W.J. 1906. The osteology of *Diplodocus* Marsh: with special reference to the restoration of the skeleton of *Diplodocus*. *Memoirs of the Carnegie Museum of Natural History*, 2:225-276.

Holland, W.J. 1924. The skull of *Diplodocus*. *Memoirs of the Carnegie Museum of Natural History*, 9:279-403.

Holland, W. J. 1924. The skull of *Diplodocus*. Memoirs of the Carnegie Museum 9:379–403.

International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature (Fourth Edition). International Trust for Zoological

Nomenclature, London, 232 pp.

Lull, R. S. 1919. The sauropod dinosaur *Barosaurus* Marsh. Memoirs of the Connecticut Academy of Arts and Sciences 6:1–42.

Marsh, O. C. 1877. Notice of new dinosaurian reptiles from the Jurassic formation. Am. Jour. Sci. 3rd Series Vol. 14

Marsh, O. C. 1884. Principal characters of American Jurassic dinosaurs. Part VII. On the Diplodocidae, a new family of the Sauropoda. American Journal of Science (Series 3) 27:161–167.

Marsh, O. C. 1890. Description of new dinosaurian reptiles. American Journal of Science (Series 3) 39:81–86.

Marsh, O. C. 1895. On the affinities and classification of dinosaurian reptiles. American Journal of Science (Series 3) 50:483–498.

Marsh, O.C., 1896. The dinosaurs of North America. The Annual Report of the U. S. Geological Survey 1895–1895, 135–244.

McIntosh, J.S. and Berman, D.S. 1975. Description of the palate and lower jaw of the sauropod dinosaur *Diplodocus* (Reptilia: Saurischia) with remarks on the nature of the skull of *Apatosaurus*. Journal of Paleontology, 49:187-199.

McIntosh, J. S. 1990a. Species determination in sauropod dinosaurs with tentative suggestions for their classification. pp. 53–69 in K. Carpenter and P. J. Currie (eds.), Dinosaur systematics. Approaches and Perspectives. Cambridge University Press, Cambridge.

McIntosh, J. S. 1990b. Sauropoda. pp. 345–401 in D. B. Weishampel, P. Dodson and H. Osmolska (eds.), The Dinosauria (First Edition). University of California Press, Berkeley.

McIntosh, J. S, and Carpenter, K. 1998. The Holotype of *Diplodocus longus* with Comments on other specimens of the genus. Modern Geology, Vol. 23, pp. 85-110

McIntosh, J. S. 2005. The genus *Barosaurus* Marsh (Sauropoda, Diplodocidae). pp. 38–77 in V. Tidwell and K. Carpenter (eds.), Thunder-Lizards: The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington.

Michelis, I. 2004 Vergleichende Taphonomie des Howe Quarry's (Morrison Formation, Oberer Jura), Bighorn County, Wyoming, USA. Ph.D. thesis, University of Bonn, Bonn.

Moberly, Ralph. 1960. Morrison, Cloverly, and Sykes Mountain formations, northern Bighorn Basin, Wyoming and Montana. *In* Geological Society of America Bulletin, v. 71, no. 8, pp. 1137-1176.

Mook, C.C. 1916. Study of the Morrison Formation Ann New York Acad. Sci. 27: 39-191

Myhrvold, N. P. & Currie, P. J. 1997. Supersonic sauropods? Tail dynamics in the diplodocids. Paleobiology 23, 393-409.

Osborn, H.F. 1899. A skeleton of *Diplodocus*. *Memoirs of the American Museum of Natural History*, 1:191-214.

Osborn, H. F., 1904. Manus, Sacrum, and Caudals of Sauropoda. Bull. Amer. Mus. Nat. Hist., XX, pp. 181-190

Osborn, H.F. and Mook, C.C. 1921. *Camarasaurus, Amphicoelias*, and other sauropods of Cope. *Memoirs of the American Museum of Natural History*, 3:247-387.

Ostrom, J.H. and McIntosh, J.S., 1966; Marsh's Dinosaurs. *Yale Univ. Press*, New Haven, 388

Paul, G. S. 1988. The brachiosaur giants of the Morrison and Tendaguru with a description of a new subgenus, *Giraffatitan*, and a comparison of the world's largest dinosaurs. Hunteria 2:31–14.

Peterson OA, Gilmore CW. 1902. Elosaurus parvus, a new genus and species of Sauropoda. Annals Carnegie Mus. 1:490–499.

Riggs, E.S. 1903. Structure and relationships of opisthocoelian dinosaurs. Part 1: *Apatosaurus* Marsh. *Field Columbian Museum, Geological Series*, 2:165-196.

Remes, K. 2006. Revision of the Tendaguru sauropod dinosaur Tornieria africana (Fraas) and its relevance for sauropod paleobiogeography. Journal of Vertebrate Paleontology 26: 651–669.

Rothschild, B.M., and Berman, D. S., 1991, Fusion of Caudal Vertebrae in Late Jurassic Sauropods. Journal of Vertebrate Paleontology 11 (1): 29-36

Schwarz, D., Ikeijiri, T., Breithaupt, B., Martin, P., and Klein, S & N. A nearly complete skeleton of an early juvenile diplodocid (Dinosauria: Sauropoda) from the Lower Morrison Formation (Late Jurassic) of north central Wyoming and its implications for early ontogeny and pneumaticity in sauropods. Historical Biology, 2007; 19(3): 225–253

Sereno, P. C. & Wilson, J. A. 2005. Structure and evolution of a sauropod tooth battery. In Wilson, J. A. & Curry-Rogers, K. (eds) *The Sauropods: Evolution and Paleobiology*. University of California Press, Berkeley, pp. 157-177.

Senter, P. 2007. Necks for sex: sexual selection as an explanation for sauropod dinosaur neck elongation. *Journal of Zoology* 271, 45-53.

Stevens, K. A . and Parrish, J. M. 2005. Digital reconstructions of sauropod dinosaurs and implications for feeding. In The Sauropods: Evolution and Paleobiology, 178-200. University of California Press, Berkeley, California.

Taylor, M. P., Mathew J. W. and Darren N.. 2009. Head and neck posture in sauropod dinosaurs inferred from extant animals. Acta Palaeontologica Polonica 54(2): 213-230.

Turner and Peterson. 1999. Vertebrate Paleontology in Utah, Miscellaneous Publication 99-1, Utah Geological Survey. 77-106

Upchurch, P. and P. M. Barrett. 2000. The evolution of sauropod feeding mechanisms. pp. 79–122 in H.-D. Sues (ed.), Evolution of Herbivory in Terrestrial Vertebrates. Cambridge University Press, Cambridge.

Upchurch, P., P. M. Barrett, and P. Dodson. 2004a Sauropoda. pp. 259–322 in D. B. Weishampel, P. Dodson and H. Osmolska (eds.), The Dinosauria (Second Edition). University of California Press, Berkeley.

Upchurch, P., Y. Tomida, and P. M. Barrett. 2004b. A new specimen of *Apatosaurus ajax* (Sauropoda: Diplodocidae) from the Morrison Formation (Upper Jurassic) of Wyoming, USA. National Science Museum Monographs 26:1–107.

Wilson, J. A. and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Memoirs of the Society of Vertebrate Paleontology 5:1–68.

Wedel, M.J. 2003. The evolution of vertebral pneumaticity in sauropod dinosaurs. *Journal of Vertebrate Paleontology*, 23:344-357.

Wedel, Mathew J. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates. pp. 201-228 in: Jeffrey A. Wilson and Kristina Curry-Rogers (eds.), *The Sauropods: Evolution and Paleobiology*. University of California Press, Berkeley

Witmer, L. M. 2001. Nostril position in dinosaurs and other vertebrates and its significance for nasal function. *Science* 293, 850-853.

Whitlock, J., Wilson, J., & Lamanna, M. 2010. Description of a Nearly Complete Juvenile Skull of Diplodocus (Sauropoda: Diplodocoidea) from the Late Jurassic of North America Journal of Vertebrate Paleontology, 30 (2), 442-457
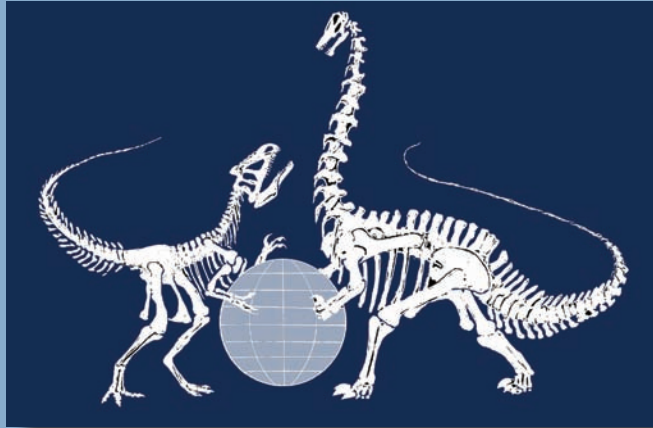
Galiano, H., and R. Albersdörfer, 2010. A new basal diplodocid species, *Amphicoelias brontodiplodocus* from the Morrison Formation, Big Horn Basin, Wyoming, with a taxonomic reevaluation of *Diplodocus, Apatosaurus, Barosaurus* and other genera. Dinosauria International (Ten Sleep, WY) Report No. 1 Sept., 2010, p 1 - 42, figures 1 - 33

Amphicoelias brontodiplodocus new species