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Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (Upper Hauterivian / Lower Barremian) Limestones of SW Istria (Croatia)

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Key words: Dinosauria, Sauropoda, Titanosauriformes, Diplodocimorpha, Upper Hauterivian-Lower Barremian, Cretaceous, Istria (Croatia).

Abstract

Remains belonging to sauropod dinosaurs have recently been discovered in Upper Hauterivian/Lower Barremian (Lower Cretaceous) limestones of SW Istria (Croatia). The material consists of a complete cervical vertebra, a nearly complete cervical centrum, fragments of possible cervical ribs, three partial dorsal and five more or less incomplete caudal vertebrae, parts of caudal neural spines, a chevron, the distal part of a femur, the proximal portion of a tibia and other fragments of bones. The bones were collected randomly from the sea bottom, therefore despite the fact that they come from the same outcrop, the same level and probably the same bed, they cannot be assigned with certainty to the same taxon. Their vastly different sizes indicate the presence of several individuals while different morphologies suggest the probable presence of more than one taxon. The complete cervical and the anterior to mid-caudal vertebrae present a more strict affinity with Brachiosauridae, a proximal cervical centrum resembles those of "*Chondrosteosaurus*", and a caudal neural spine is similar to those of the camarasaurids. The dorsal vertebrae have peculiar features (a very tall neural arch, well developed laminar complex, etc.) and characters suggesting their assignation to basal Titanosauriformes and, possibly, to Diplodocimorpha. A posterior dorsal vertebra testifies the presence of a new Diplodocimorph similar to *Rebbachisaurus* but more primitive.

1. INTRODUCTION

Dinosaur tracks of Cretaceous age are relatively common in the Istrian peninsula (NW Croatia), and have recently been reviewed by DALLA VECCHIA et al. (1993), DALLA VECCHIA & TARLAO (1995) and DALLA VECCHIA (1997a, b, c). They are preserved in Upper Barremian, Upper Albian and Upper Cenomanian limestones at several sites along the coast of the peninsula, and on the islands (Main Brijuni/Brioni island, Fenoliga islet, etc.).

The first discovery of dinosaur bones, on the Adriatic sea bottom at the Kolone locality near Bale/Valle village, south of Rovinj, was reported by BOSCAROLLI et al. (1993), and was followed by preliminary notes concerning the fossils and their stratigraphic and palaeoenvironmental context (DALLA VECCHIA, 1994a, b; DALLA VECCHIA et al., 1993; TUNIS et al., 1994; KOZARIĆ et al., 1996). Some specimens were identified as sauropod bones (DALLA VECCHIA, 1994b, 1997a, b, c; DALLA VECCHIA & TARLAO, 1995) but never described in detail. This paper presents a detailed description of the identifiable and attributable remains of the sample.

All of the material comes from the same outcrop, from the same stratigraphic level and, probably from the same bed (see below). However, most were collected randomly as scattered fragments on the beach and on the sea bottom, where the fossiliferous layer crops out. No systematic attempt had been made to collect the numerous bones still embedded in the rock. Since the fossiliferous bed, which seems to be particularly laden with bony remains (D. BOSCAROLLI, pers. comm.), lies below sea level, its excavation is difficult. However, this outcrop promises to be one of the most rich and interesting of present Europe.

2. DEPOSITIONAL ENVIRONMENT AND AGE

The age and depositional environment of this deposit are discussed in BOSCAROLLI et al. (1993), TUNIS et al. (1994) and DINI et al. (1998). The fossiliferous outcrop is characterized by the presence of beds of oncolitic rudstone with bone debris, and thinly laminated limestones with plant, shrimp and fish remains. Some bones (for example, the complete cervical vertebra WN-V1, the small dorsal MPCM-V1, the mid-caudal Nos IG-1 and other fragments) were preserved wholly in a yellow, thinly laminated limestone or with a side of the fossil in this laminated limestone and the other side in a grey, hard oncolitic rudstone. This seems to indicate that the preservation of complete bones is due to deposition in a relatively protected, low energy environment (laminated limestones) and to the probably rapid covering by the rudstone which testifies a high energy environment. However this should be confirmed by a detailed sedimentological and taphonomical study of the fossiliferous beds which is beyond the scope of this paper.

The stratigraphic sequence of the outcrop at Bale is composed of subtidal, intertidal and lacustrine limestones. The lower section is of Late Hauterivian/Early

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Barremian age due to the presence of the foraminifer *Campanellula capuensis* DE CASTRO; the upper section is probably Lower Barremian (BOSCAROLLI et al., 1993; TUNIS et al., 1994). Therefore the bones described here are the oldest record of dinosaurs currently known in Istria (DALLA VECCHIA & TARLAO, 1995) if possible sauropod tracks in the Berriasian of Fantazija Quarry (LOCKLEY et al., 1994) are excluded. The bones are approximately coeval with the theropod *pes* and sauropod *manus* prints found in a quarried limestone block from the Cansiglio Plateau (Northeastern Italy, Pordenone) described by DALLA VECCHIA & VENTURINI (1995). The sauropods of Bale are a rare case of dinosaur bone remains that are dated in correlation with the marine biochronology.

3. DESCRIPTION AND COMPARISON

The sample consists of more than 200 specimens, most of which are just bone fragments. The collected material was exposed to recent marine and shore weathering and was encrusted (and sometimes pierced) by living marine animals and algae. It was cleaned and prepared by the preparators of the Gruppo Speleologico Monfalconese A.D.F. at the Museo Paleontologico Cittadino of Monfalcone (Gorizia). Most of the bones are crushed, sometimes strongly, but otherwise the state of preservation of the bones still imbedded in the rocky matrix is very good. Only bones attributable to sauropods are described here; several specimens are too fragmented to identify the skeletal element to which they belonged, other fragments belong obviously to long and large bones which remain indeterminate.

The specimens will finally be stored or exhibited in a Museum dedicated to the local dinosaur remains in the village of Bale (Istria, Croatia). At present they are without the definitive number of this Museum therefore I will report here the numbers used during preparation (MPCM-V = Museo Paleontologico Cittadino di Monfalcone - Valle). The specimens that were not numbered during preparation and were at the Museum in Bale during the final version of this paper are identified with the abbreviation WN-V. Two bones are presently in the collection of the Institute of Geology, Zagreb (Nos IG-1 and Nos IG-2).

Because of the way the specimens were collected it is impossible to be immediately sure that they belong to the same taxon, or to a precise number of different taxa. In some occurrences, for example in some levels of the Morrison Formation (Upper Jurassic) of North America, six sauropod genera were found together (see CURTICE & WILHITE, 1996). Therefore each bone is compared with the corresponding bones of described sauropod taxa, in order to determine affinities particularly with the better known forms (*Brachiosaurus* RIGGS, *Haplocanthosaurus* HATCHER, *Camarasaurus* COPE, *Diplodocus* MARSH, and *Apatosaurus* MARSH) and the Neocomian-Barremian ones.

Acronyms: CD = caudal rib, CDL = centrodiapophysial lamina, CPR = centroprezygapophysial lamina, CO = condyle, COPR = condyloprezygapophysial lamina, DP = diapophysis, Has = articular surface for the hyposphene, HL = horizontal lamina (= diapo-prezygapophysial lamina, diapo-postzygapophysial lamina), HPN = hyposphene, HYP = hypantrum, IDL = infradiapophysial lamina, IHPNL = infrahyposphenal lamina, IPDL = infrapostdiapophysial lamina, IPDRL = infraprediapophysial lamina, IPPLa = infraparapophysial anterior lamina, IPPLb = infraparapophysial posterior lamina, IPRL = infraprezygapophysial lamina, IPZL = infrapostzygapophysial lamina, ISPZL = inner suprapostzygapophysial lamina, ITPZ = intrapostzygapophysial lamina, LIPPL = lateral infraparapophysial lamina; LIPZL = lateral infrapostzygapophysial lamina, NA = neural arch, NC = neural canal, NS = neural spine, OSPZL = outer suprapostzygapophysial lamina, PL = pleurocoel, PP = parapophysis, PR = prezygapophysis, PRL = prezygapophysial lamina, PRSPL = prespinal lamina, PSPL = postspinal lamina, PZ = postzygapophysis, SCL = "core" lamina of the neural spine, SDL = supradiapophysial lamina, SIPRL = subinfraprezygapophysial lamina, SPRZ = supraprezygapophysial lamina, SPZL = suprapostzygapophysial lamina.

AXIAL SKELETAL ELEMENTS

Cervical vertebrae

WN-V1 (Figs. 1 & 2; photographs in DALLA VECCHIA, 1994b, fig. 3, and DALLA VECCHIA, 1997c, fig. 2): two cervical vertebrae were preserved nearly in anatomical articulation. The posterior of the two is entire while only a posterior fragment (with the cotyle and the left postzygapophysis) of the other is preserved. The following description concerns the complete vertebra (Figs. 1 & 2). This is crushed laterally, the neural arch is bent to the left side and the left diapophysis with the corresponding horizontal lamina are crushed and bent to the centrum. The right side has been exposed to erosion on the sea bottom in recent times and was strongly weathered.

The centrum is opisthocoelous, very elongate and tubular. Its length is 350 mm, its height at the posterior end is 50 mm, the length/height ratio is therefore 7; maximum depth of the neural arch as preserved is 100 mm. The centrum has a cavernous, cancellate structure with thin external walls and relatively small, irregular internal cavities bordered by bone septa and ridges; the septa and walls are comparatively thicker than in the posterior cervical vertebra MPCM-V2 described below. The inner cavities are, at least in the anterior part of the centrum, antero-posteriorly elongated. A small pleurocoel, also antero-posteriorly elongated, is identifiable on the middle ventral part of the lateral side of the centrum (Fig. 2). "Pleurocoels" are also present anteriorly on the centrum, just above or at the base of the parapophysis. They actually are deep depressions and do not appear to communicate with the inner part of the

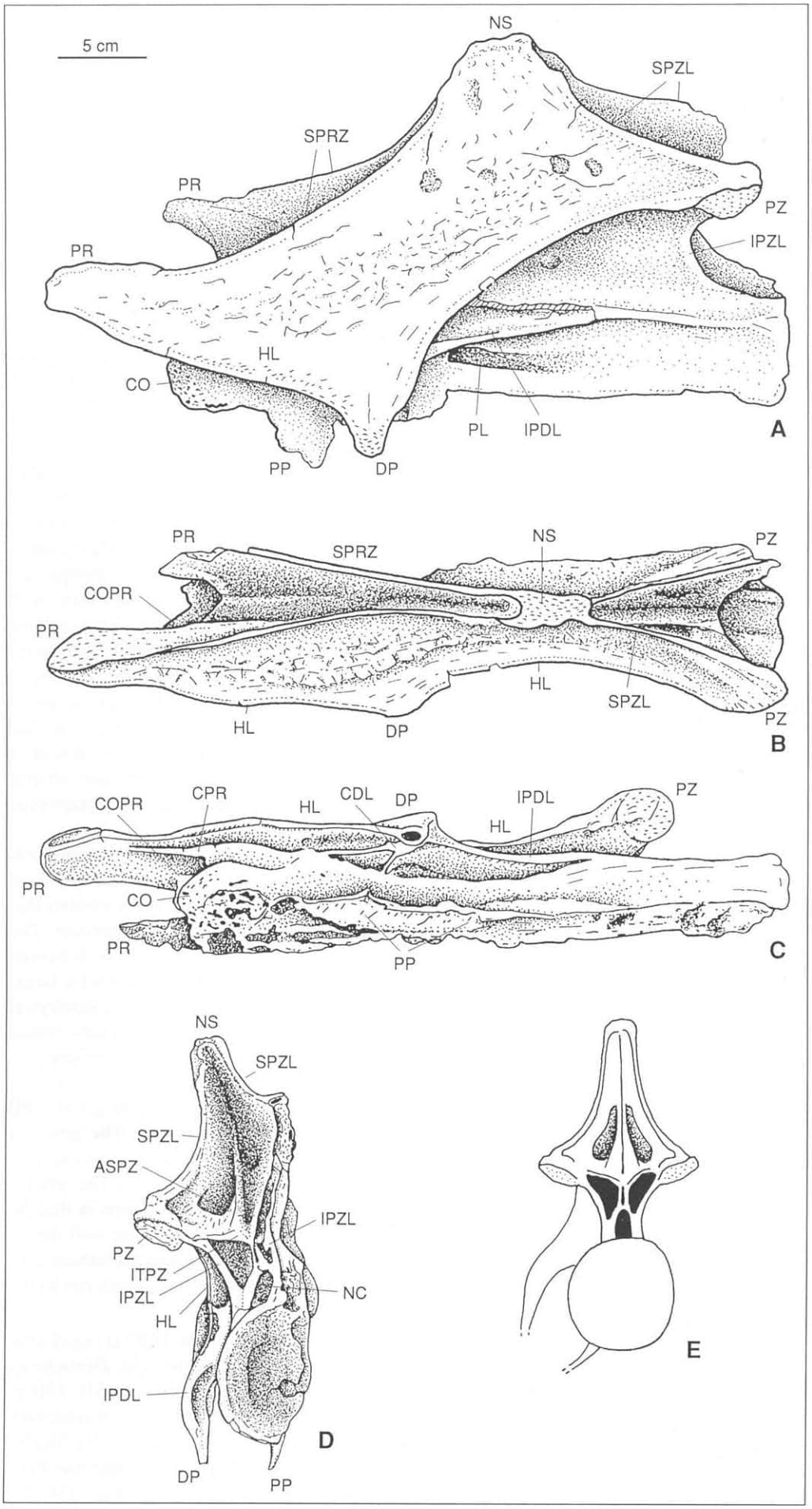


Fig. 1 Cervical vertebra WN-V1. Views: A) left lateral, B) dorsal, C) ventral, D) posterior. E) Reconstruction in posterior view. Acronyms: ASPZ = additional suprapostzygapophysial lamina.

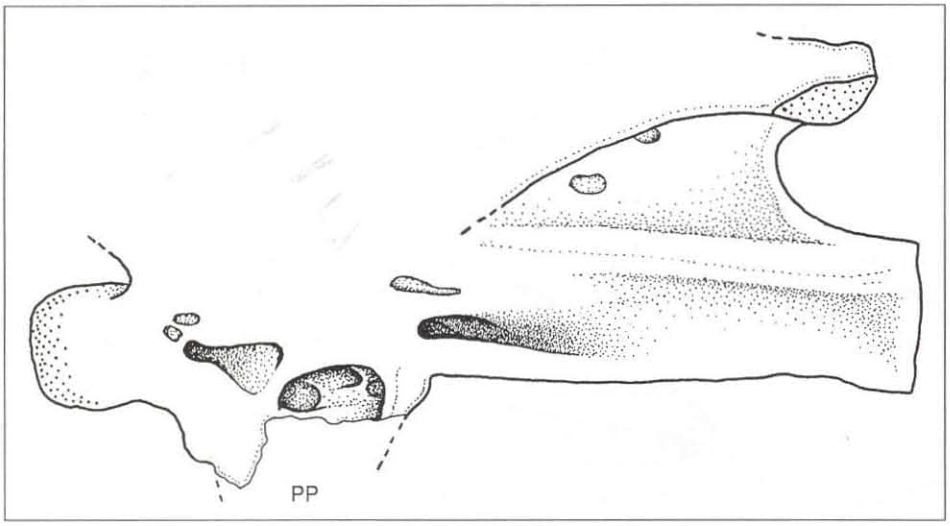


Fig. 2 Cervical vertebra WN-V1. Pattern of pleurocoels and small depressions.

centrum (they do not pierce the external wall) and are probably the *Aussenkaverne* reported in the cervicals of *Brachiosaurus brancai* JANENSCH by JANENSCH (1947, fig. 1). Small, rounded or oval (4-10 mm) shallow depressions are present in the anterior part of the centrum, and are most prevalent on the lateral side of the neural arch. Ventral excavations are not present. The "pleurocoels" and the depressions on the centrum are figured in Fig. 2.

The cotyle (the posterior articular cavity on the centrum) is deep and oval (main vertical diameter = 50 mm) but the shape is probably biased by compression, and the condyle is well developed, ball-like and small (maximum diameter = 35 mm).

The neural arch occupies nearly the entire dorsal surface of the centrum. The neural spine is low and not bifid. The parapophysis lacks the distal part and is oriented in the vertical plane; despite any compressional effects it is unlikely that this was originally oriented in the horizontal plane. The diapophysis is triangular in dorso-lateral view and tapers at the distal tip, which is broken and shows a circular outline of the section and a hollow inside. The tip of the diapophysis and the posterior margin of the anterior horizontal lamina are rough. From the diapophysis a well developed wing-like horizontal lamina is directed anteriorly to the prezygapophysis and posteriorly to the postzygapophysis. Where the posterior horizontal lamina begins a strong infrapostdiapophysial lamina is also obvious (Fig. 1C); this ends as a lamina at the dorsal-posterior third of the centrum and continues as a ridge with the relief tapering caudally, ending before reaching the caudal margin of the centrum. Where the infrapostdiapophysial lamina attaches to the diapophysis, the posterior side of the latter becomes wider and presents a shallow depression (this part has therefore a somewhat spoon-like aspect). There is a double, V-shaped inner centrodiapophysial lamina (Fig. 1C), with the point placed in correspondence to the narrowing of the tip of the diapophysis. The two branches of the lamina end at the dorsal-lateral part of the centrum; the anterior one is wider and very thin. There is a well developed centroprezygapophysial lamina, crushed against the anterior horizontal lamina, with a wide basal attachment on the dorsal-anterior part of the centrum, just caudal to the condyle. There is also a short condyloprezygapophysial lamina. The supraprezygapophysial and suprapostzygapophysial laminae are thin, well developed and separated (right from left) by very deep infra-supraprezygapophysial and infra-suprapostzygapophysial cavities (Fig. 1B). The supraprezygapophysial laminae are thinner than the suprapostzygapophysial laminae. The ventro-posterior part of the medial side of the suprapostzygapophysial lamina presents a deep cavity bordered medially by a very thin vertical lamina (ASPZ = additional suprapostzygapophysial lamina).

There are two thin, parallel and short vertical laminae just above the bony arch surrounding the neural cavity. The intrapostzygapophysial lamina reaches these laminae medially forming a Y-shaped structure. The short vertical lamina, infrapostzygapophysial lamina and intrapostzygapophysial lamina surround a large, deep cavity (Fig. 1E). Right infrapostzygapophysial lamina and intrapostzygapophysial lamina are crushed against one another and the corresponding cavity bordered by the two laminae is nearly closed.

The prezygapophysis is long and projects well beyond the anterior tip of the centrum. The articular surface is drop-shaped, facing medio-dorsally (orientation possibly partly modified by crushing). The postzygapophysis is similar to the prezygapophysis in that the articular surface faces ventro-laterally. The well developed, thin and wide (wing-like) horizontal lamina connects the prezygapophysis and postzygapophysis to the diapophysis.

Comparisons - elongated, "tube-like" cervical centra are present in *Brachiosaurus brancai*, *Diplodocus* and *Barosaurus lentus* MARSH (McINTOSH, 1990a, b). Cervical centra of the camarasaurids are relatively short and wide (OSBORN & MOOK, 1921; McINTOSH, 1990a, b). Diplodocids and *Camarasaurus* have bifid neural spines in the cervical vertebrae (McIN-

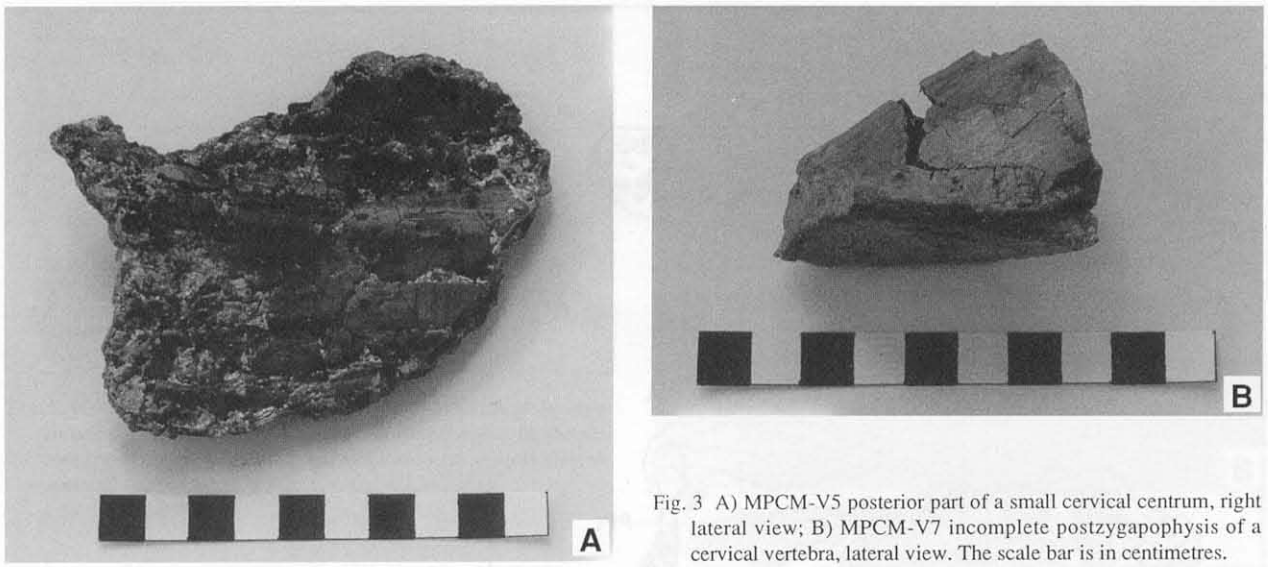


Fig. 3 A) MPCM-V5 posterior part of a small cervical centrum, right lateral view; B) MPCM-V7 incomplete postzygapophysis of a cervical vertebra, lateral view. The scale bar is in centimetres.

TOSH, 1990a, b; in *Diplodocus* and *Camarasaurus* they are bifid from cervical 3 onwards) whereas they are single in *Brachiosaurus*. The distribution of the "pleurocoels" in WN-V1 is similar, but not the same, as that of the anterior cervical vertebrae of *Brachiosaurus brancai* (JANENSCH, 1950, figs. 20, 23, 26, 29). In fact, the size of the posterior pleurocoel of the centrum is much smaller in the described specimen. Also the overall shape of the vertebra, the anterior elongation of the prezygapophysis, and diapophysis distally narrowing in a bottleneck manner, are similar to those of the anterior cervicals of *Brachiosaurus brancai* (JANENSCH, 1950, figs. 20, 23, 26, 29). The internal cavities are probably the same as the "longitudinal pneumatic tubes" observed in a presumed specimen of *Mamenchisaurus* YOUNG by RUSSELL & ZHENG (1993, p. 2089) and are present also in "*Chondrosteosaurus*" (e.g. HULKE, 1879, p. 756) and in another cervical centrum described below.

MPCM-V5 (Fig. 3A): this is the posterior part with the cotyle of a small centrum, with a basal-posterior fragment of the neural arch. The specimen is strongly crushed; it is 114 mm long and its height at the cotyle is 70 mm.

Comparisons - it is similar to the same region of the vertebra WN-V1 and represents another cervical vertebra belonging to a relatively small sauropod.

MPCM-V6: this specimen is probably the anterior portion (110 mm long) of a right infrapostdiapophysial lamina from a rather large vertebra: the corresponding part on the complete cervical WN-V1 is no longer than 20 mm.

MPCM-V7 (Fig. 3B): an incomplete posterior part of a postzygapophysis (48 mm long, 60 mm wide) clearly belonging to a vertebra much larger than the complete cervical vertebra WN-V1.

MPCM-V2 (Figs. 4 & 5): a nearly complete centrum, rather short, wide and low (length = 300 mm, height = 105 mm, and width = 175 mm at the posterior end) (Fig. 4). Its low profile is only partly due to dorsoventral crushing (the specimen, mainly in its anterior part, is crushed because of its extremely cavernous internal structure). A small part of the base of the neural arch is also preserved in the posterior part. The neural arch, the parapophyses, and the external bony wall in the cranial half have all been weathered away.

The posterior cotyle is rather deep and probably had an elliptical shape, wider than high, with a ratio W/h = 1.67. Its ventral side projects posteriorly more than the dorsal one.

There are three large pleurocoels on both lateral sides (Fig. 5A). The external margins of the anterior pleurocoel (APL) are weathered away, therefore what we see now is probably slightly different to the original external shape. It is the shallowest of the three openings and is separated from the posterior (PPL) and lower pleurocoel (LPL) by thin bony laminae.

The posterior pleurocoel is the largest and deepest opening (about 40 mm), elliptical, craniocaudally elongate, extending along most of the caudal half of the centrum. Though deep, the posterior pleurocoels do not occupy the whole inner part of the centrum, and are not separated from each other only by a medial lamina (as in the dorsals of *Camarasaurus* or *Brachiosaurus*). In fact the interior of the centrum of MPCM-V2 is wholly composed of small, honeycomb-like chambers. The dorsal and ventral rims of the pleurocoel are thick and lip-like. The anterior pleurocoel is elliptical and also anteroposteriorly elongated. This pleurocoel is deeper posteriorly and becomes more and more shallow ventro-anteriorly. It is separated from the posterior pleurocoel by a thin lamina. The lower pleurocoel opens latero-ventrally in the mid-anterior part of the centrum and is more developed ventrally (Fig. 4D). Its true outline has probably been affected by weathering on the lateral side where it possibly extended on the para-

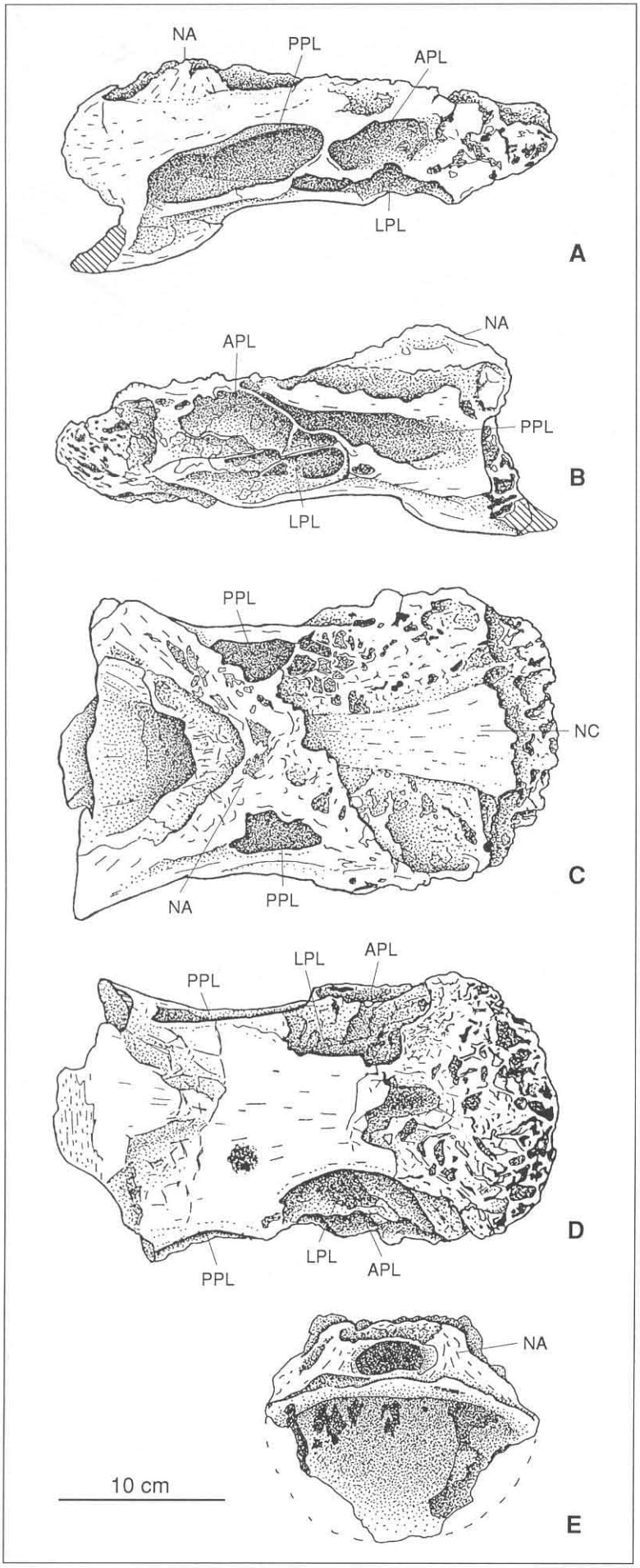
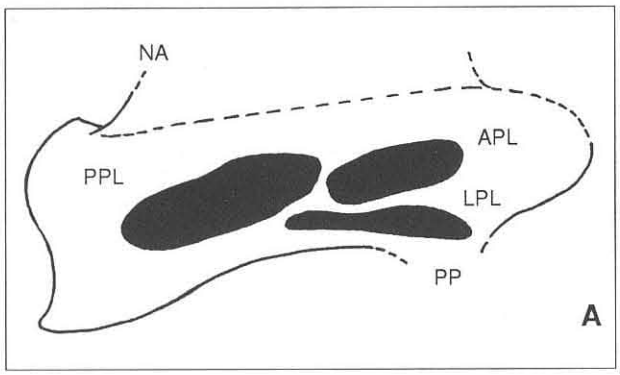


Fig. 4 MPCM-V2, posterior cervical centrum. Views: A) right lateral, B) left lateral, C) dorsal, D) ventral, E) posterior. Acronyms: APL = anterior pleurocoel, LPL = lower pleurocoel, PPL = posterior pleurocoel.



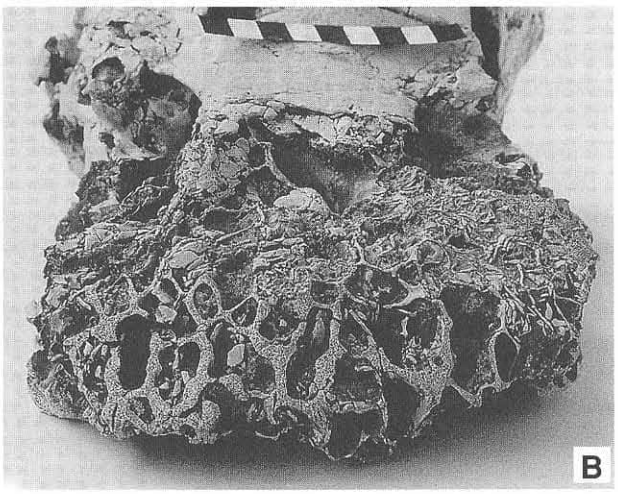


Fig. 5 MPCM-V2, posterior cervical centrum. A) Pattern of the pleurocoels, B) cancellate structure of the condylar region (in the picture the vertebra is upside down and shows the ventral-anterior surface). Acronyms as in Fig. 4.

pophyses. Its present shape is elliptical and antero-posteriorly elongate. The left one is partly subdivided into cells by thin bony septa.

The weathered dorsal surface of the centrum shows the cancellate structure of the inner vertebra. More or less irregularly shaped cells are separated by very thin septa; in some places (as in the left upper-mid part of the centrum) these cells are regularly divided by vertical septa into a "honeycomb" pattern. A regular "honeycomb" pattern, with antero-posteriorly elongated, tubular cells, is evident in the weathered anterior condylar part (Fig. 5B).

The trace of the neural canal on the dorsal side of the centrum shows that it is very expanded at both extremities: maximum posterior (at the exit from the neural arch) width is about 50 mm, maximum anterior width is 55 mm, minimum width is at midlength (about 25 mm); height in correspondence to the posterior exit from the neural arch is about 35 mm. The posterior opening of the neural canal is therefore elliptical, wider than high.

The ventral side of the centrum is very flat and without longitudinal depressions or ridges. In the anterior third the external, compact wall is weathered and the inner tubular, "honeycomb", cancellate structure is exposed (Fig. 5B). In the mid-anterior part there is a median, anteroposteriorly elongate, large (length = 45 mm) and deep (about 40 mm) hole. In the mid-anterior part of the centrum, the ventral external bony wall narrows because of the lower pleurocoel; here the medial margin of the opening is rimmed by the relatively thick wall.

Comparisons - the large pleurocoels are very different from the titanosaurid condition, and are characteristic of brachiosaurids, camarasaurids and diplodocids (mainly *Diplodocus*). Brachiosaurids and *Diplodocus*-like diplodocids seem to be excluded by the relative shortness and width of the centrum and its dorso-ventral flatness (McINTOSH, 1990b). The overall morphology of MPCM-V2 and the size and position of the pleurocoels strongly resemble cervical 10 of *Camarasaurus supremus* COPE (OSBORN & MOOK, 1921, figs. 7 & 32) and also the cervicals called *Chondrosteosaurus gigas* by OWEN (1876, see Pls. II-V). The latter are more or less coeval with MPCM-V2, being from the Barremian Wessex Formation (BLOWS, 1995) of England and have centra of the same proportions, overall outline, shape of articular surfaces, ventral aspect, very similar anterior pleurocoel and posterior pleurocoel and the particular, regular cancellate, "honeycomb" bone texture, mainly in the condylar region (see Pls. II, IV and V of OWEN, 1876 and the description by HULKE, 1879, p. 756-57). On the other hand, the cancellate texture is not present in *Camarasaurus* (P. UPCHURCH, pers. comm.). The size of MPCM-V2 is between that of the two specimens of *C. gigas* described by OWEN (1876, see Pl. V). They could differ in the presence and shape of the lower pleurocoel, but the shape and actual position of this opening in MPCM-V2 is effected by weathering which rubbed out completely the parapophyses, as reported above. Also variation of position of the posterior, lower and anterior pleurocoels may account for the differences. Therefore MPCM-V2 at the present state of knowledge should be referred to this taxon, whose validity, however, is doubtful (see below). *C. gigas* was based by OWEN (1876) on only a complete and a weathered cervical centrum. HULKE (1879) added at least another cervical centrum (n. 144, coll. H of HULKE, 1879) (actually he made a mistake in reporting the name and attributed it to *C. magnus*). *C. magnus* (= *Bothriospondylus magnus* OWEN, 1875 but type of *Ornithopsis hulkei* of SEELEY, 1870) is represented by two dorsal centra found in the same formation and locality of the cervicals called *C. gigas* (OWEN, 1876, p. 7). It appears plausible that *C. magnus* belongs to the same taxon of *C. gigas* as partly realized by Owen himself, who referred them, "provisionally", to distinct species on the base of the incorrect statement that they are both dorsal elements and that dorsals cannot be so different in the same species (p. 7). *C. magnus* was based on a vertebra (BMNH 28632) which OWEN (1875) had called *Bothriospondylus magnus* before recognizing its resemblance to the vertebrae of

C. gigas. Vertebrae of *C. magnus* (= *Ornithopsis hulkei*) have the same honeycomb-like texture in the condylar region as *C. gigas* (OWEN, 1875, Pl. IX). BMNH 28632 was indicated as one of the two types of *Ornithopsis hulkei* by SEELEY (1870) but OWEN (1876) rejected the name as "misleading" because of its Greek meaning which seems to suggest it is a bird bone. HULKE (1879) considered *Eucamerotus* HULKE and *Ornithopsis* to be synonyms because the type of the first (BMNH R2522, a partial neural arch), BMNH 28632 and a "mutilated centrum, retaining enough of the arch and superstructures" (p. 755) present an "extremely large-celled cancellous tissue" (p. 755). LYDEKKER (1888) accepted the synonymy of *Chondrosteosaurus* (both species) and *Ornithopsis* but suggested that *Pelorosaurus* MANTELL should be synonimized. In his recent review of *Ornithopsis* BLOWS (1995) does not include in *O. hulkei* the cervical vertebrae of *C. gigas* but considers it, as SEELEY (1870) did, as a lectotype of *O. hulkei* one of the two dorsal centra (the syntype of SEELEY, 1870, BMNH28632 - see LYDEKKER, 1888) called *C. magnus* by OWEN (1876). *C. gigas* was recently considered valid and tentatively assigned to the Camarasauridae by McINTOSH (1990b, p. 387) because of its close resemblance with cervical 10 of *Camarasaurus*. P. Upchurch, who is reviewing the British sauropod material, considers *C. gigas* a *nomen dubium* and probably a member of the Titanosauriformes (*Brachiosaurus* + Titanosauria) (P. UPCHURCH, pers. comm.).

MPCM-V4 (Fig. 6): this is a part of a larger bone and has a peculiar and somewhat puzzling shape and structure. Its identification is rather difficult but it appears to be part of a laminar system of the neural arch of a cervical or dorsal vertebra of a sauropod. In fact, even if it is strongly crushed and its original shape was deformed by compression, the specimen is a latticework of bone bridges and laminae, with pleurocoel-like openings. This frame, linked to the extreme lightening of the skeletal elements, is typical of sauropod cervical and dorsal vertebrae.

I chose an arbitrary orientation (see the caption of Fig. 6) of the specimen to describe it and I identify the main lamina-like structures which compose it with the acronyms S1, S2, etc. That which follows should be considered a tentative description.

S1 is the upper, longitudinal, lamina-like structure which is strongly crushed but not very deformed. Its outline in the anterior part, where it is possibly formed by two thinner laminae now strongly crushed one against the other, is rectangular in side view. At the anterior third, S1 becomes rib-like (*ar*), the profile becomes inclined, the upper part enlarges and its dorsal margin is sharply acute. The back side of S1 is nearly vertical; here the structure is divided into a rib-like arch (*bs*) which reaches S2 and a thin, central and inner lamina (*il*). S2 was originally nearly perpendicular to S1 but now is parallel to it because of crushing and deformation. S2 resembles a thick lamina, thicker posteriorly than anteriorly, and hollow inside. A large, oval pleurocoel opens in its present side surface, revealing the hollow inside. S3 is the left side structure corresponding to S2 but was mostly weathered away. If so, S1, S2 and S3 originally formed an upside down Y or T-shaped structure. S4 is a lamina crushed against S1, with a strong, rib-like upper margin (*um*) and the remaining part (*ts*) which is a thin sheet of bone crushed against *il*. The rib-like upper margin *um* begins in the dorsal margin of S1 where the latter becomes rib-like; therefore the two rib-like structures form (and formed before crushing) a V-shaped structure with the acute part pointing forward and downward. S4, now parallel to S1 was originally diverging from the latter posteriorly.

Comparisons - the shape of the structure S1 resembles one of a low neural spine of a cervical vertebra. However, the relation with the structure S4 cannot be recognized exactly in any described vertebra of *Haplocanthosaurus*, *Diplodocus*, *Apatosaurus* and *Camarasaurus* (pers. obs.). The shape of the specimen mostly resembles one of the bifid cervical neural spine of *Apatosaurus* (GILMORE, 1936). As reported above, in my opinion it is part of a complex laminar structure of a neural arch of a rather large and bizarre cervical or dorsal sauropod vertebra, but nothing more can be said until a more complete part of this structure is found.

Cervical ribs? (Fig. 7)

Seven rod-like bone fragments (among them is **MPCM-V8**, the others now on exhibit at Bale/Valle are without number), with oval or elliptical cross sections (about 10.5 x 14.5 mm in the longest fragment, the lower one in Fig. 7, 195 mm long). They have the same transverse sizes for all their lengths and are straight or slightly curved; they are not hollow and their surfaces present thin longitudinal striae. One surface is usually flatter (less convex) than the other.

Comparisons - They could be segments of the distal part of the shaft of long cervical ribs. They resemble the very characteristic, elongate rod-like shafts of the cervical ribs of *Camarasaurus*, *Brachiosaurus*, *Euhelopus* ROMER and *Mamenchisaurus*. On the other hand, McINTOSH (1990a) indicates short cervical ribs as a diagnostic feature of Diplodocidae. The identification as part of rib shafts is supported by the presence in the outcrop of similar bone fragments more than 500 mm long and perhaps as long as 1200 mm (D. BOSCAROLLI and F. BACCHIA, pers. comm.). If the identification is correct, their large size excludes them from belonging to a vertebra of the same size as the complete cervical vertebra WN-V1; they belong to a much larger vertebra of a large individual. Despite this, the fragments are very similar to the ossified tendons which strengthen the tail and the back of iguanodontids. However these skeletal elements are usually smaller and flatter. If the described specimens are ossified tendons there are two possibilities: 1) also iguanodontids are

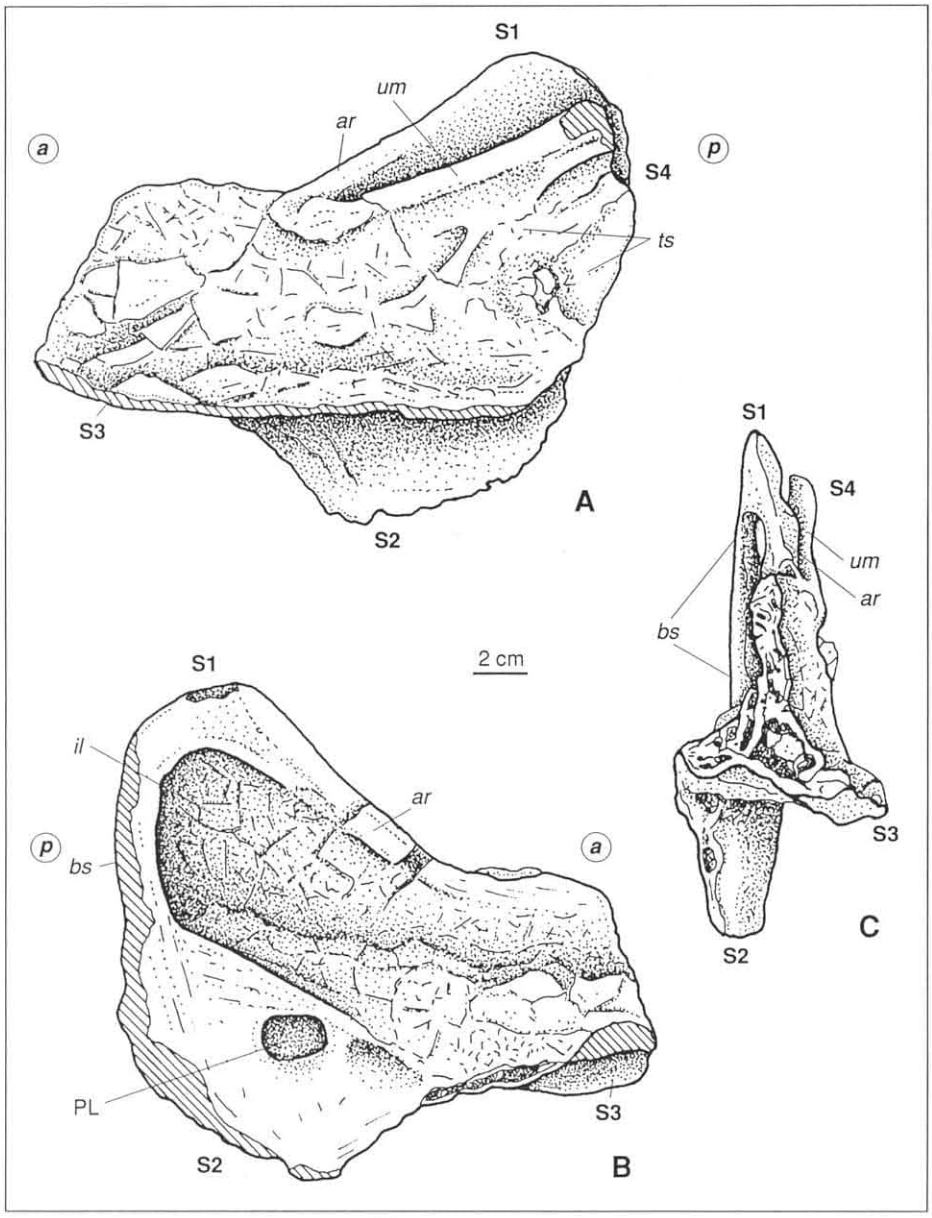


Fig. 6 MPCM-V4, possible fragment of the laminar complex of a large cervical or dorsal vertebra. A-B) "side" views, C) "front" view. Acronyms: a = "anterior", p = "posterior", S1 = lamina 1 , S2 = lamina 2, S3 = lamina 3, S4 = lamina 4. For the other abbreviations see text.

represented in the fossiliferous outcrop but we do not have other evidence of this, 2) there are sauropods with ossified tendons in the neck (calcified muscles are preserved in *Camarasaurus* - D. CHURE, pers. comm. in McINTOSH, 1990b) or in the tail.

Dorsal vertebrae

MPCM-V1 (Figs. 8 & 9): the specimen consists of a partly preserved, small centrum and corresponding neural arch without most of the spine. The neural arch is strongly crushed antero-posteriorly, due to the action of lithostatic pressure on the extremely hollow structure. The whole vertebra is in fact just a very complex latticework of thin bone laminae. After complete preparation it seems clear that in previous papers I wrongly identified the posterior part as the anterior (see DALLA VECCHIA, 1994b, fig. 4b). The anterior side of the vertebra was strongly weathered and to identify the original structures is not possible or at best very difficult.

The centrum has a kidney-like outline in posterior view, wider than high (about 80 x 55 mm) and the articular face is concave. It is a cylinder, therefore it has convex lateral sides.

On both lateral sides there is evidence of a very large pleurocoel, probably with an ovate outline (but see below) occupying most of the lateral side of the centrum (Figs. 8D & 9C). The pleurocoel is not a hole piercing the lateral wall of the centrum and in connection with its hollow inner part (Fig. 8B). It is just a deep depression rimmed ventrally (lip-like ventral margin), opening dorsally and partially (just in the ventral part) divided internally by a small, rib-like vertical septum (as in the dorsals of *Eucamerotus* sensu BLOWS, 1995 and many other sauropods). The inner structure of the centrum is extremely cavernous, cancellate, with thin

Fig. 7 Fragments of probable cervical ribs. Scale in centimetres.

vertical septa (mainly antero-posteriorly oriented but some smaller ones are transversally oriented) and reinforcing struts (Fig. 8B). The inner septa are as thin as less than 1 mm, whereas the external wall is thicker.

The neural canal is oval, large, about 29.5 mm wide and 21 mm high in posterior view, 25 and 16 mm respectively in anterior view.

The neural arch is comparatively very tall: the ratio H/h (H = distance between the base of the postzygapophysis and the top of the centrum, and h = centrum height) is 1.83; the preserved part of the neural arch is 2.8 times the height of the centrum. The neural arch is formed by very thin, long laminae which are difficult to identify because of the strong crushing; their original position is tentatively reconstructed in Figs. 9C and 10B.

The right postzygapophysis is nearly completely preserved. It is connected to the pedicels by a strong, straight, vertical lamina (infrapostzygapophysial lamina). There is no suture between the basal pedicels and the upper part of the arch. Between the two infrapostzygapophysial laminae the arch is depressed. Perhaps the two infrapostzygapophysial laminae were connected by a thin, horizontal intrapostzygapophysial lamina but crushing prevents further clarification. The cross-section of the postzygapophysis shows pneumatic cavities inside; the part with cavities is found dorsally with respect to a 5 mm thick layer of spongy bone which is just above the articular surface. The latter faces ventro-laterally and slightly anteriorly. There is no hypo-sphene: medially to the postzygapophyses the arch is deeply depressed and in the middle of the concavity there is the basal part of a rib-like (probably broken) postspinal lamina (Fig. 8A).

The articular surface of the prezygapophysis was probably borne by a large, triangular, dorso-laterally directed (in front view) structure, possibly formed by a thick, rib-like infraprezygapophysial lamina at the lateral margin and a thinner prezygapophysial lamina at the dorsal one (Figs. 8B & 9B). This apophysis is strongly crushed against the other laminae which comprise the neural arch. Nothing is preserved of the part of the prezygapophysis bearing the articular surface. Another triangular structure (indicated with the acronym AS in Figs. 8B and 9B) seems to start just above the neural canal, tapers dorsally and ends against the presumed prezygapophysial lamina. As in other vertebra this structure, which has been very damaged by weathering, is composed of a latticework of very thin laminae.

Above these structures there is the base of the neural spine. The rib-like trace of a possibly bifid (U-shaped in cross-section, Fig. 10) prespinal lamina can be recognized, with also the basal part of both supraprezygapophysial laminae. The latter taper toward the top and have a thickened margin in the upper half of the preserved part.

The pattern of lateral laminae is very complex (Figs. 8D, 9C & 10).

A wide and very thin lateral infrapostzygapophysial lamina starts from the lateral side of the base of the pedicel and reaches the posterior horizontal lamina just anterior to the postzygapophysis (Figs. 8D & 9C).

The thin infradiapophysial lamina seems to start from the same point as the lateral infrapostzygapophysial lamina (or a little above) and ends at the diapophysial "knob". Most of the diapophysis is completely weathered, and is recognizable only as a knob or strut, composed in its proximal part by the confluence of the laminae connected with it. The natural, unbroken outer margin of the infradiapophysial lamina is preserved in its basal part and shows that the infradiapophysial lamina was upwardly and laterally directed; this

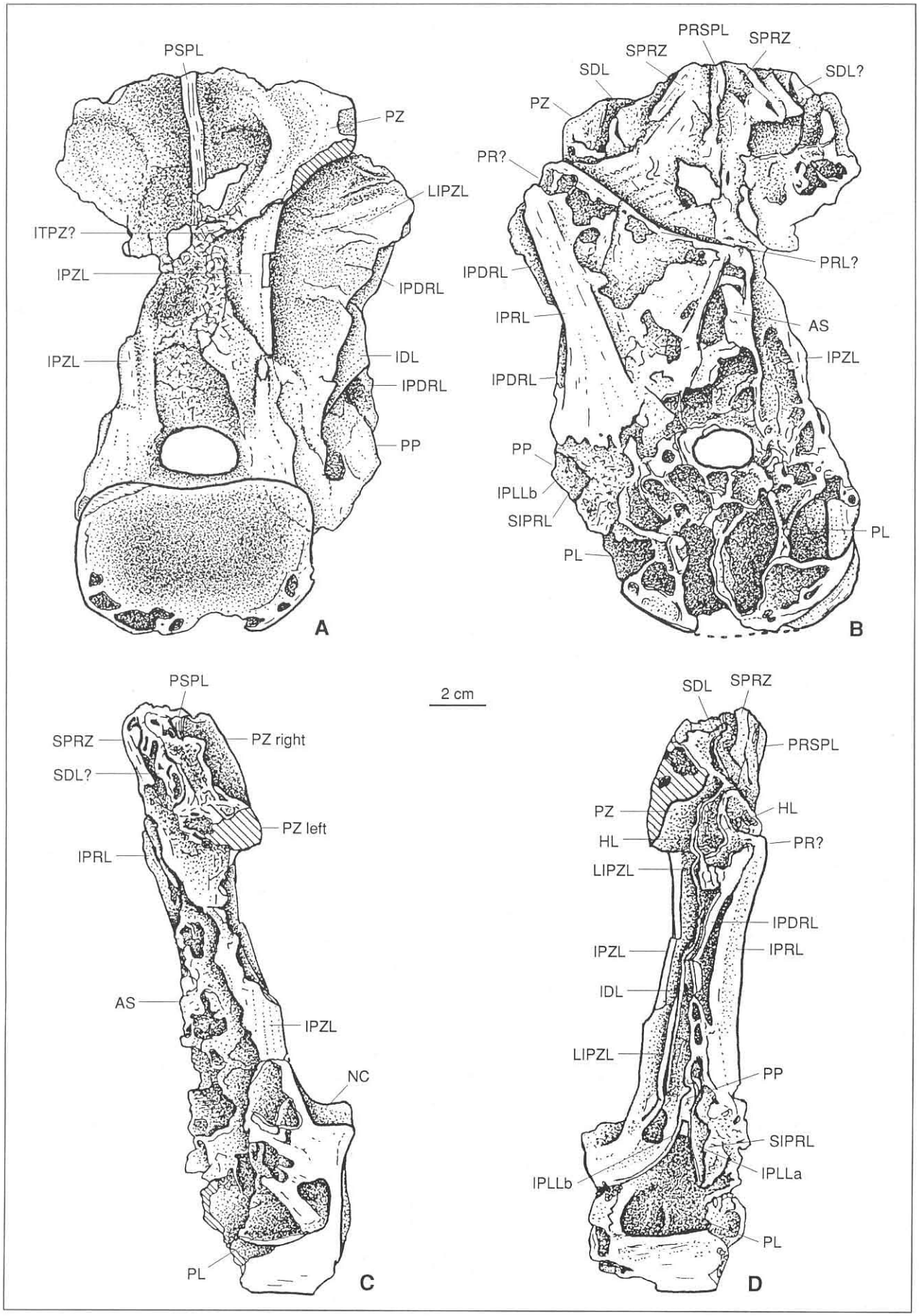


Fig. 8 MPCM-V1, anterior dorsal vertebra. Views: A) posterior, B) anterior, C) left lateral, D) right lateral. Acronyms: AS = anterior structure between prezygapophyses.

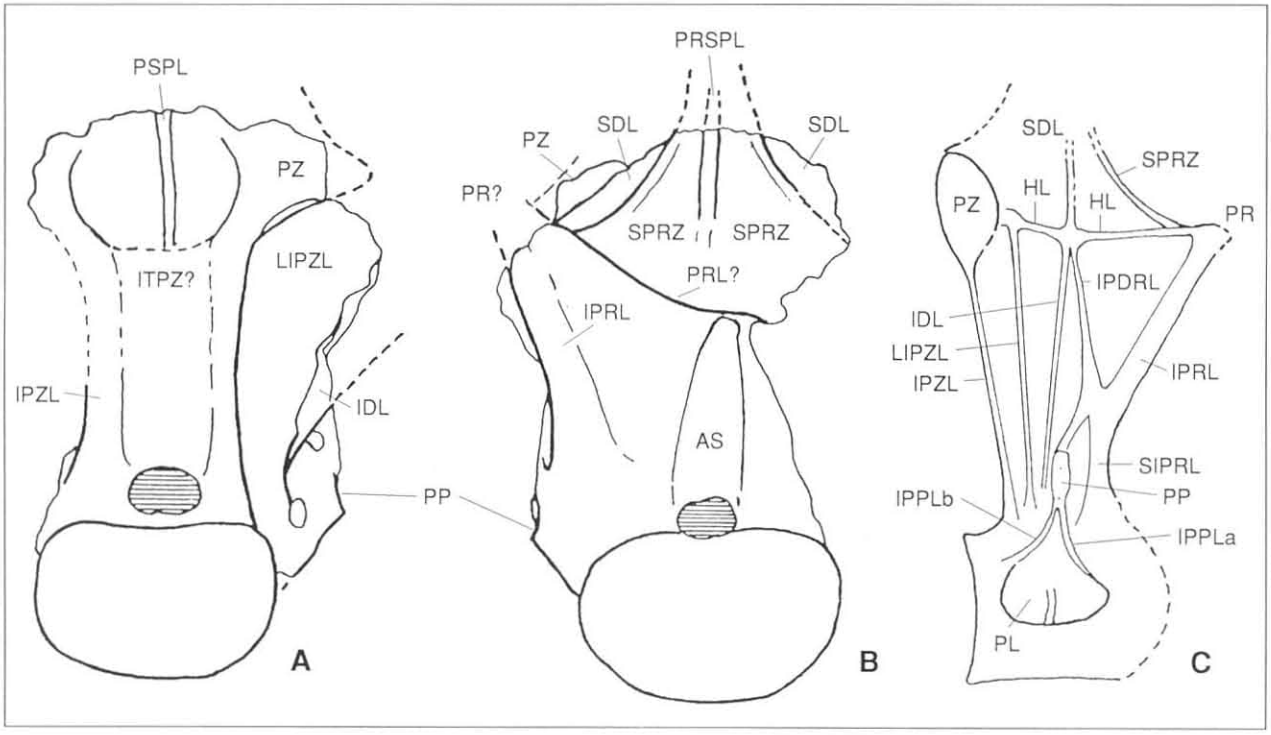


Fig. 9 MPCM-V1, anterior dorsal vertebra. Simplified drawing of the vertebra in A) posterior and B) anterior view; C) reconstruction of the laminar pattern in right lateral view.

lamina appears to have been a wide, wing-like structure projecting laterally (Fig. 9A).

Anterior to the described laminae there is evidence of a complex, laterally projecting structure placed at the base of the neural arch. In my opinion this structure could be the parapophysis or part of it. The position of the articular surface of the parapophysis is not clear. It is either the narrow facet shown in Figs. 8D and 9C as the parapophysis, or it was placed anteriorly and was weathered away. Two extremely thin laminae (infraparapophysial laminae, IPPLa,b, Figs. 8D & 9C) are present at the base of the structure; they join dorsally forming an upside down V and border the upper part of a vacuity connected with the pleurocoel. The resulting structure is a drop-shaped deep depression (Fig. 9C). The posterior lamina starts from the upper latero-posterior side of the centrum, the other probably from the upper latero-anterior. The two laminae meet at the presumed articular surface of the parapophysis. The latter continues dorsally as a short lamina which unites to another lamina (subinfraprezygapophysial lamina) coming probably from the upper latero-anterior part of the centrum. In posterior view two more or less circular deep cavities are visible respectively at the base and at the top of this laminar system. These cavities are probably true features of this part of the arch even if they were partly altered by crushing. In lateral view, just above the presumed parapophysis, two laminae bifurcate: a infraprediapophysial lamina (posteriorly) and the very thick, rib-like infraprezygapophysial lamina (anteriorly). At the bifurcation the infraprediapophysial lamina begins relatively thick and hollow inside, but rapidly tapers to become a thin, compact single sheet of bone. It was probably connected with the diapophysial "knob", but this part of the lamina is displaced because of strong crushing. There is a thin horizontal lamina between the prezygapophysis and the diapophysial "knob", and from this to the postzygapophysis. A thin supradiapophysial lamina can be identified but it is very crushed between the other laminae. The final part, extending to the diapophysial "knob", cannot be identified with certainty. The inner core of the spine is an antero-posteriorly directed, relatively thick lamina ("core" lamina of the neural spine, SCL), forming an I-shaped structure with the supraprezygapophysial lamina, suprapostzygapophysial lamina, postspinal lamina and prespinal lamina (and, of course, with the lateral insertion of the supradiapophysial lamina) (Fig. 10).

Comparisons - the probable low position of the parapophysis and the absence of the hyposphene (see below) suggest that this specimen is an anterior element, but not the first: it may be the 2nd to 4th since the parapophysis is not on the centrum. The small size of specimen MPCM-V1 would indicate that it belongs to a juvenile individual. Lack of fusion of the neural arches to the centra is considered an important diagnostic feature of immaturity (e.g CORIA, 1994; MARTIN, 1994; CURTICE & WILHITE, 1996) and has been observed in individuals of many genera: *Camarasaurus* (OSTROM & McINTOSH, 1966), *Haplocanthosaurus* (HATCHER, 1903), *Diplodocus* (CURTICE & WILHITE, 1996), *Patagosaurus* BONAPARTE (CORIA, 1994), *Phuwiangosaurus* MARTIN, BUFFETAUT & SUTEETHORN (MARTIN, 1994). The pedicels of the neural

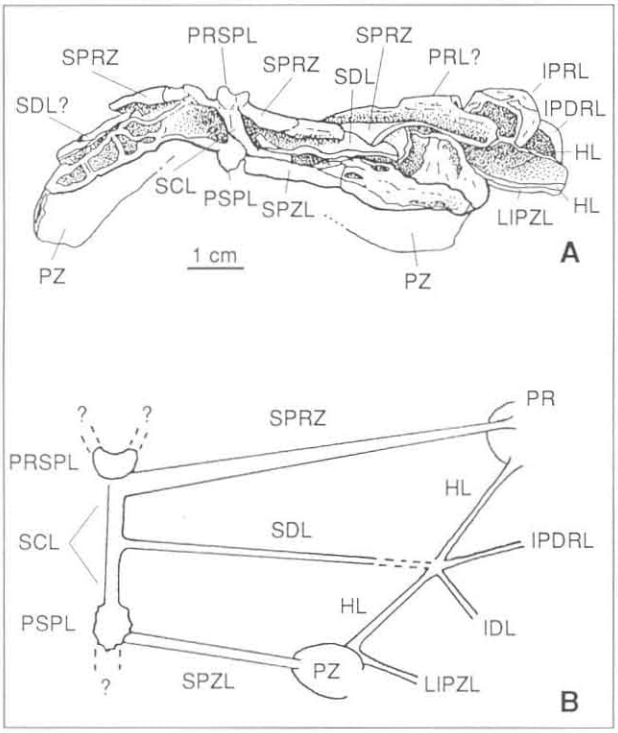


Fig. 10 MPCM-V1, anterior dorsal vertebra. A) dorsal view, B) reconstruction of the laminar pattern in dorsal view.

arch of MPCM-V1 are fused without evident suture to the centrum, therefore there is no evidence of immaturity except the small size.

Drop-shaped pleurocoels are present in the anterior dorsals of *Camarasaurus "supremus"* (OSBORN & MOOK, 1921, figs. 8 & 9) and *Camarasaurus grandis* MARSH (OSTROM & McINTOSH, 1966, pl. 23) and, less markedly, also in the mid-posterior dorsals of *Diplodocus carnegii* HATCHER (HATCHER, 1901, pl. VII), *Apatosaurus louisae* HOLLAND (GILMORE, 1936, pl. XXV), *A. excelsus* (MARSH) (GILMORE, 1936, pl. XXXII) and in some dorsals vertebrae of *Haplocanthosaurus priscus* HATCHER (HATCHER, 1903, pl. I). However the shape, size and position of pleurocoels in dorsal vertebrae are not always very reliable taxonomic features, since they change in the different elements even in the same individual, and in the same segment of the vertebral column (e.g GILMORE, 1936, pls. XXV & XXXII; HATCHER, 1901, pl. VII, 1903, pl. I; OSTROM & McINTOSH, 1966, pls. 23-25).

The specimen presents a peculiar, very high, neural arch. The anterior dorsal vertebrae of an immature *Camarasaurus grandis* figured in OSTROM & McINTOSH (1966, Pl. 23-24) and the dorsals of *Rebbachisaurus garasbae* LAVOCAT (RUSSELL, 1996, fig. 30) have also a rather tall neural arch, and *Haplocanthosaurus priscus* is the sauropod with the highest subzygapophysial part of the neural arch of the dorsal vertebrae. The ratio H/h (H = distance between the base of the postzygapophysis and the top of the centrum, and h = centrum height) in the dorsal ?6 of *Haplocanthosaurus priscus* (HATCHER, 1903, pl. 1), dorsal 5 of *Camarasaurus "supremus"* (OSBORN & MOOK, 1921, fig. 8) and an anterior dorsal of the immature *Camarasaurus grandis* is 1.60, 1.37, 1.22 respectively. In the Diplodocimorph (sensu CALVO & SALGADO, 1995) *Rebbachisaurus tessonei* CALVO & SALGADO (CALVO & SALGADO, 1995), in which the tall neural arch is a diagnostic feature, H/h is 0.55 in an anterior dorsal and 1.1 in the posterior ones, whereas in the dorsal of *R. garasbae* figured in RUSSELL (1996, fig. 30) it is at a maximum 1.3. The arch of MPCM-V1 is the highest in every case. Additionally in the figured anterior dorsals of *H. priscus* and *C. grandis* the shape of the centrum in posterior view is not kidney-like, the pleurocoel is smaller and the laminar pattern in the neural arch is different (HATCHER, 1903; OSTROM & McINTOSH, 1966). Unfortunately the most anterior dorsal vertebrae of sauropods are not as well known and described as the mid-posterior ones.

The absence of the hyposphene-hypantrum articulation in the dorsals is reported by SALGADO et al. (1997) for *Tornieria* and *Ornithopsis* (= *Eucamerotus* sensu BLOWS, 1995; but *Ornithopsis* has hyposphene-hypantrum, cf. HULKE, 1880, Pl. IV), in *Rebbachisaurus* LAVOCAT (CALVO & SALGADO, 1995; RUSSELL, 1996) and is common among titanosaurids (SALGADO et al., 1997). The absence of hyposphene-hypantrum articulation in the posterior dorsals is a synapomorphy of Titanosauridae sensu SALGADO et al. (1997). However the neural arch of the Titanosauridae is lower and the pleurocoel is much smaller and of a different shape (BONAPARTE & CORIA, 1993; BONAPARTE, 1996), therefore they are excluded. Following McINTOSH (1990b, p. 362) the hyposphene-hypantrum seems to be generally absent in the anteriormost dorsals of sauropods. It is absent on the dorsal 1 (which has a cervical-like aspect) in *Haplocanthosaurus priscus* but dorsals 2-5 are unknown and it is present in the other dorsal vertebrae (HATCHER, 1903). In *H. utterbacki* HATCHER the hyposphene-hypantrum is first seen on the dorsal 6 (HATCHER, 1903, p. 34), while in *Camarasaurus* only dorsals 1-2 are without the hyposphene (OSBORN & MOOK, 1921, p. 302). The dorsal vertebra 4 of *Brachiosaurus brancai* has a well developed hyposphene (JANENSCH, 1950, fig. 54), while in *Diplodocus carnegii* a hyposphene is present from dorsal 4 onwards but dorsals 1 and 2 are cervical-like. In *Apatosaurus excelsus* the hyposphene is present from dorsal 3 onwards (GILMORE, 1936) and the parapophysis of 1 and 2 remains on the centrum. There is some similarity with dorsal 2 of *Apatosaurus excelsus* and *A. louisae* but the position of the parapophysis and its laminae are different. Furthermore the shape of the neural spine was probably narrower (GILMORE, 1936).

Large, coarse cavitations in the internal structure of the centra is considered a brachiosaurid feature by BLOWS (1995), and a Titanosauriformes one by P. UPCHURCH (pers. comm. and in press). Following POWELL (1986) the great development of cavernous

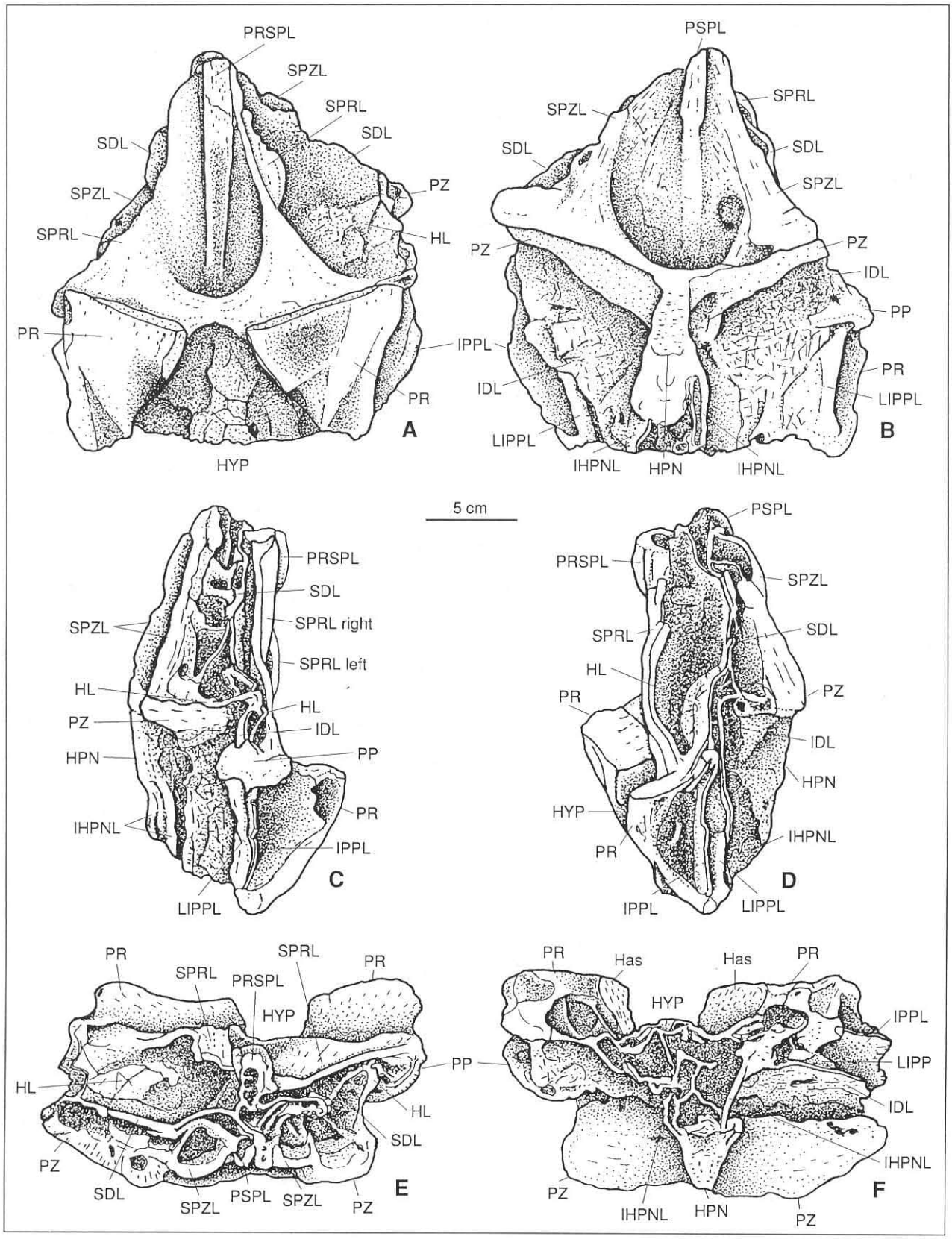


Fig. 11 MPCM-V3, part of a neural arch of a posterior dorsal vertebra. Views: A) anterior, B) posterior, C) right lateral, D) left lateral, E) dorsal, F) ventral. In these drawings broken surfaces are not showed by sloping lines. Acronyms: Has = articular surface for the hyposphene.

osseous tissue is a diagnostic character of Titanosauridae. ASTIBIA et al. (1990, p. 463) consider the "cellular bony structure of the vertebrae" an "autapomorphic titanosaurid feature". However SALGADO et al. (1997, p. 26) consider that the "phylogenetic relevance of the relative development of cavernous osseous tissue is unclear". In the dorsal vertebrae of *Brachiosaurus* and *Camarasaurus* the inner certrum is camerate (large cav-

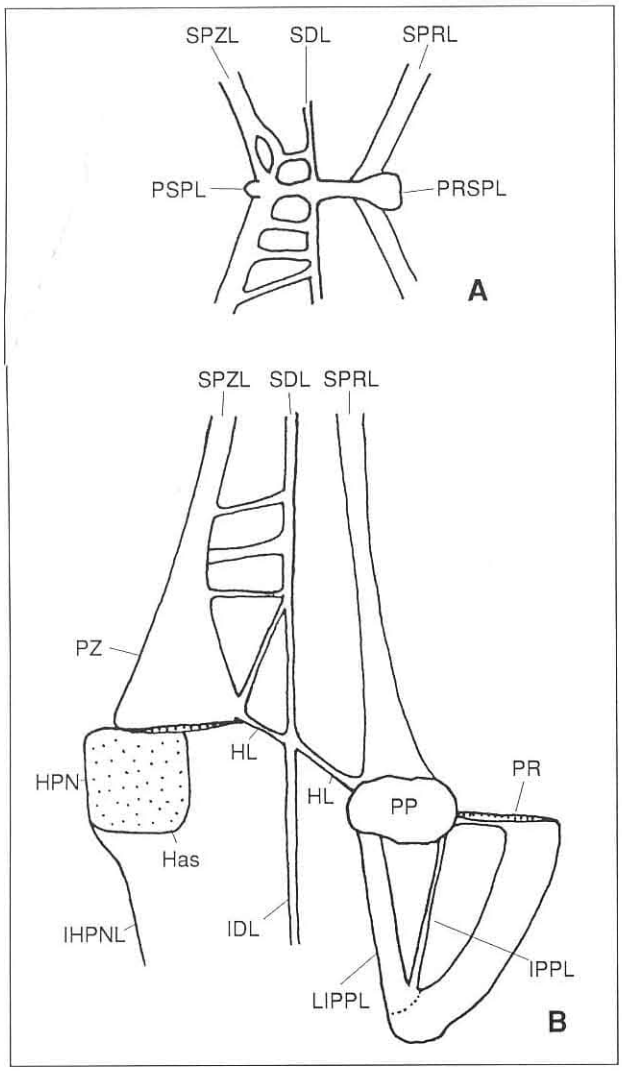


Fig. 12 MPCM-V3, part of a neural arch of a posterior dorsal vertebra. A) reconstruction of the laminar pattern in dorsal view, B) reconstruction of the preserved part of the basal neural arch in right lateral view. The Has of the prezygapophysis is projected in the corresponding position on the hyposphene.

ities) rather than cancellate. Since the individual represented by MPCM-V1 is very small, the extreme lightening of the vertebrae cannot solely be an adaptation to large size.

MPCM-V3 (Figs. 11 & 12; figured in DALLA VECCHIA, 1994b, fig. 4A, and DALLA VECCHIA & TARLAO, 1995, fig. 2). This specimen represents the zygapophysial segment of the neural arch and the basal part of the neural spine of a dorsal element. The position of the parapophysis and diapophysis suggests a mid-posterior position. It is 220 mm high and 200 mm wide, and therefore belongs to a large individual. Some parts have been weathered so that the present margins seem to be the original margins of the bone but actually are not. Erosion destroyed the projecting part of the hyposphene, the complete transverse processes, most of the processes for the capitulum and most of the neural spine. The bone was strongly crushed antero-posteriorly and this affected mainly the laminae visible in lateral view (i.e. horizontal lamina, infradiapophysial lamina, supradiapophysial lamina, etc.) which are therefore deformed and artificially approached.

The specimen is composed of a latticework of thin laminae, above all the axial part of the arch. Also the thickest and strongest parts (i.e. zygapophyses) are cavernous. For example, a large deep cavity divided by a thick septum (Fig. 11F) opens medially at the base of the prezygapophysis, just below the articular surface for the hyposphene.

The prezygapophyses are large, with wide articular surfaces facing dorso-medially. There is a wide, more or less quadrangular articular facet for the hyposphene bordering the upper part of the hypantrum, and articulating with the hyposphene. At the ventral end of this facet the prezygapophysis narrows forming a step-like structure, (i.e. the articular surface for the hyposphene is on a low, ventro-medial projection of the prezygapophysis) and the prezygapophysis assumes a hammer-like shape. A thin lamina starts from the base of the articular surface for the hyposphene to reach the axis of the arch in the middle of the hypantrum. The hypantrum is very wide, deep and with an isosceles trapezium outline.

The postzygapophyses are united to the hyposphene forming a very strong, Y-shaped articular structure (Fig. 11B). The postzygapophysis articular surface is very wide and elongated. The hyposphene is triangular and dorsoventrally elongate, but unfortunately the posterior portion is strongly weathered. The hyposphene originally was probably much more developed posteriorly. In fact there is no clear indication of the presence of the accessory articulation, which should fit in the corresponding step-like structure of the prezygapophysis, nor a complete articular facet corresponding to the articular facet in the prezygapophyses (Has, Figs. 11 & 12). The infrahyposphenal laminae start from the ventral end of the hyposphene and are ventrally and slightly laterally directed. The ventral cross-section of the specimen shows that the axial core of the neural arch is formed of a latticework of thin laminae (Fig. 11F). It is possible that there was something like an infrahyposphenal cavity entering the hyposphene from inside the neural arch.

The parapophysis stalk is preserved but weathered at the outer end, on the right side just behind the prezygapophysis. On this side there is also a knob which is probably the proximal part of the "core" of the transverse process (=diapophysis) since all laminae are confluent to it (Fig. 11C). On the left side, the position of the parapophysis and diapophysis is shown only by convergence of the laminae, since the processes have been completely removed by weathering (Fig. 11D). The position of the transverse process seems to be near the postzygapophysis in the left side, while it is midway between the postzygapophysis and parapophysis in the right one.

Two laminae start from the base of the prezygapophysis. The thin anterior lamina reaches the parapophysis anteriorly or in the middle, and is therefore an infraparapophysial lamina. It borders posteriorly a very deep lateral depression excavated into the prezygapophysis. The posterior lamina is very thick, rib-like, reaches the parapophysis posteriorly (Fig. 11C), and is here identified as a lateral infraparapophysial lamina. The presence of a very thin infradiapophysial lamina is clear on the left side (Fig. 11D) while the right one is very strongly crushed.

The thin horizontal lamina was somewhat shortened, deformed and bent to a S-shaped structure by antero-posterior compression (Figs. 11C-D).

The supraprezygapophysial lamina is a thick lamina. It has a wide base (about 70 mm) in front view and tapers quickly toward the top of the preserved part, where it is at least 20 mm wide, and therefore does not end against the prespinal lamina. Interpretation of the actual morphology of this lamina is difficult since the right one seems different from the left one, perhaps because of weathering and crushing. It was probably antero-laterally directed (Fig. 12A), with a thick, lip-like anterior margin which rims the deep, axial depression formed by the two supraprezygapophysial laminae, at the bottom of which the prespinal lamina starts. No bony struts or laminae seem to connect the supraprezygapophysial lamina to the supradiapophysial lamina. The prespinal lamina is weathered and appears more as a rib than a lamina. It probably did not project beyond the level of the supraprezygapophysial lamina. It starts at the base or very near the base of the neural spine, becomes wider and stronger toward the top and perhaps was bifid (but this aspect could be due to weathering), at least at the base.

The suprapostzygapophysial laminae, which are more affected by weathering, mimic the supraprezygapophysial laminae but are thicker above all at the base where they are confluent with the postzygapophysis. The left one bifurcates just above the postzygapophysis and becomes single again soon after (Fig. 11D-E). A complex latticework of transverse laminae, thin in the basal part of the neural spine, thicker and strut-like above, connects the suprapostzygapophysial lamina to the supradiapophysial lamina. The postspinal lamina is similar and preserved like the prespinal lamina but its width is constant. The supradiapophysial lamina is thinner than the suprapostzygapophysial and supraprezygapophysial laminae. There is a relatively short "core" lamina of the neural spine that means the spine was narrow in lateral view and roughly of rectangular appearance in cross-section (Fig. 12A), at least at the apex of the preserved part. It seems narrow also in antero-posterior view but it is impossible to know if it widened again above the preserved part or not.

Comparisons - the presence of a medial prespinal lamina in posterior dorsals is considered a synapomorphy of the Titanosauriformes [*Brachiosaurus brancai* + (*Chubutisaurus insignis* DEL CORRO + Titanosauria)] sensu SALGADO et al. (1997) and its development down to the base of the neural arch is considered a character of derived titanosaurids. However, Titanosauridae sensu SALGADO et al. (1997) lack a hypantrum-hyposphene complex in the posterior trunk vertebrae. A prespinal lamina in posterior dorsals is also present convergently in the Diplodocidae (op. cit.). *Eucamerotus foxi* BLOWS, considered a brachiosaurid by BLOWS (1995), does not present a prespinal lamina in the posterior dorsals (see HULKE, 1880, pl. IV, fig. 5).

The development and morphology of the preserved supraprezygapophisial-prespinal laminae and suprapostzygapophysial-postspinal laminae is similar to those of the Diplodocidae (see posterior dorsals of *Diplodocus*, HATCHER, 1901; *Apatosaurus*, GILMORE, 1936, pls. XXV & XXXII; *Amphicoelias* COPE, OSBORN & MOOK, 1921, figs. 119 & 120) and *Haplocanthosaurus priscus* (HATCHER, 1903, pl. I). A narrow neural spine of the dorsal vertebrae is also a feature of the Diplodocidae.

The infrahyposphenal lamina and corresponding cavity are structures which seem to be present only in the Diplodocidae (CURTICE et al., 1996) but apparently the posterior dorsals of *Eucamerotus foxi* also have them (see HULKE, 1880, pl. IV, fig. 7).

The step-like structure on the medial side of the prezygapophysis seems to be present also in the holotype of *Eucamerotus foxi* (BLOWS, 1995, fig. 1C). The whole prezygapophysis-hypantrum complex appears to be somewhat similar, on the basis of BLOWS (1995, fig. 1C) to that of the holotype of *Eucamerotus foxi*. However, the hypantrum-hyposphene articulation is also similar to that of some basal titanosaurs, and in particular that of the anterior dorsal of *Argentinosaurus huinculensis* BONAPARTE & CORIA, where the step-like structure has been called "accessory articulation of the hypantrum" (cf. BONAPARTE & CORIA, 1993, figs. 4 & 6), and is considered a diagnostic feature of the genus (BONAPARTE & CORIA, 1993, p. 272). As suggested by the authors themselves (p. 276, 280) the development of these structures is related to the large size of the individuals, and is therefore very probably a homoplastic character.

The presence, absence or shape of lesser laminae on the neural arch of sauropod dorsals probably lacks great taxonomic value because of the variability existing in the same individual (cf. *Diplodocus* in HATCHER, 1901, and *Apatosaurus* in GILMORE, 1936).

WN-V6 (Fig. 13D-E), is a nearly complete dorsal vertebra still under preparation, showing mainly its right and posterior side. The specimen will be stored at the Museum of the Municipality of Bale and is at present without number. It is less crushed than the other presacral vertebrae found in the outcrop. The right pedicel of the neural arch is detached from the centrum and this could mean that it was not completely fused to it (but crushing should be considered the main cause of this detachment) and that the specimen does not belong

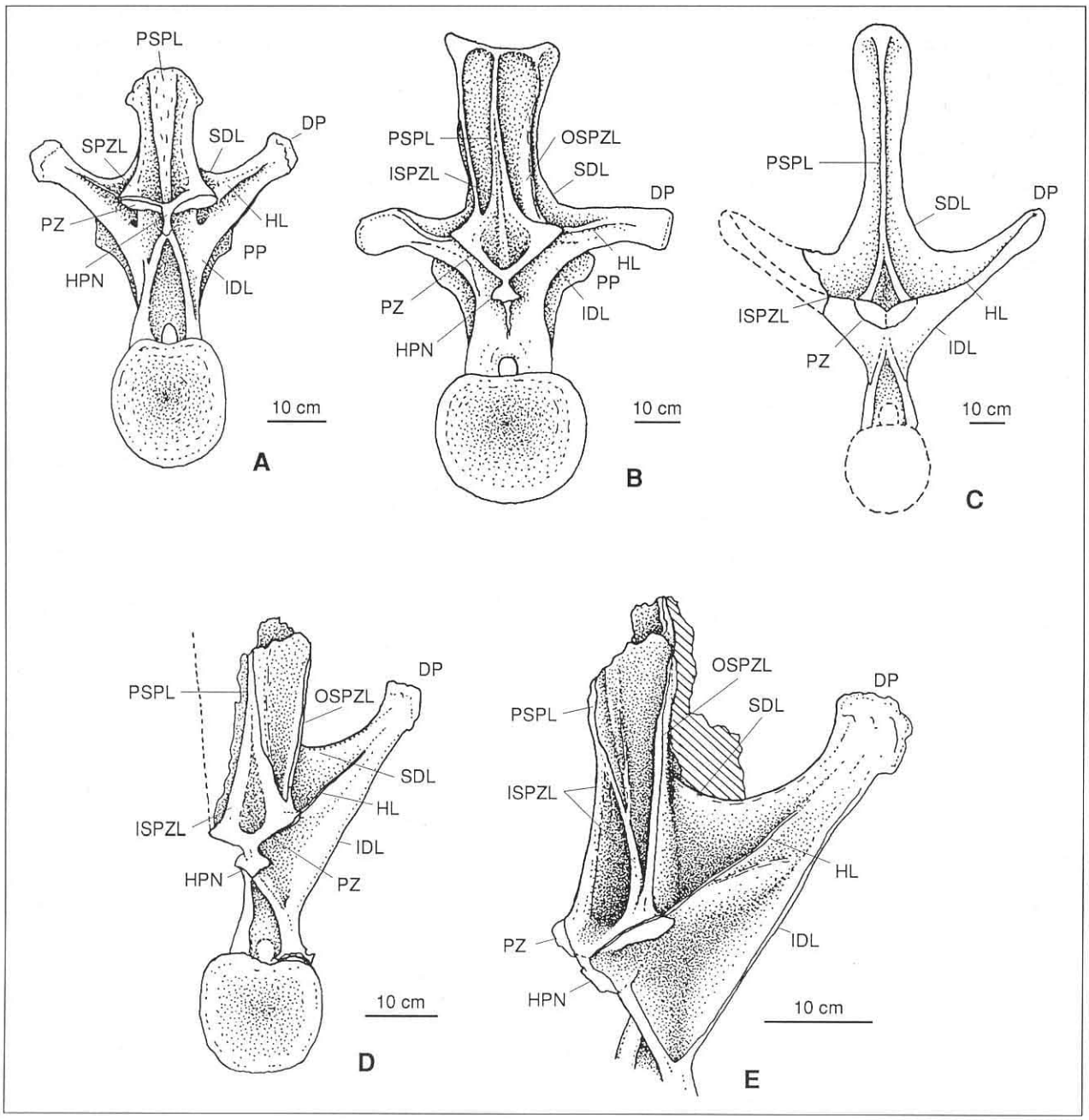


Fig. 13 Mid-posterior dorsal vertebrae in posterior view. A) Dorsal 13 of *Haplocanthosaurus priscus* (redrawn from HATCHER, 1903), B) dorsal 5 of *Apatosaurus louisae* (redrawn from GILMORE, 1936), C) mid-posterior dorsal of *Rebbachisaurus tessonei* (redrawn from CALVO & SALGADO, 1995), D) WN-V6, nearly complete posterior dorsal vertebra, E) postero-lateral view of the neural arch of WN-V6.

to a fully mature individual. The overall morphology and the relative position of the diapophysis and parapophysis indicate that it is a posterior dorsal vertebra. It is larger than MPCM-V1 and smaller than MPCM-V3 and has a characteristic tall neural arch, with long diapophysis extending sharply upward (the angle is about 45°). There is a hyposphene-hypantrum complex and the neural spine is undivided (but only the lower part is preserved). The neural arch is a latticework of thin and wide laminae. Each suprapostzygapophysial lamina is double. The relatively narrow inner suprapostzygapophysial laminae taper rapidly, coming together to form a postspinal lamina. The outer suprapostzygapophysial laminae are wide and antero-posteriorly directed. They run parallel to the main axis of the spine, tapering upward, and abutting nearly perpendicularly the supradiapophyseal lamina (Fig. 13E). A similar suprapostzygapophysial laminar pattern is sometimes present in the diplodocid *Apatosaurus* (see GILMORE, 1936, Pl. XXV; here Fig. 13B). The diapo-postzygapophyseal lamina (= horizontal lamina) ends in the middle of the transverse process without reaching the diapophysial articular surface. The centrum is relatively small and elongate (its maximum dorso-ventral height is about 150 mm, and length is more than 200 mm), the articular facets are circular and a large pleurocoel is

present antero-dorsally on the lateral side. The inner structure of the centrum is not cancellate (i.e. it is finely spongy).

Comparisons - the overall morphology is reminescent of the mid-posterior dorsal vertebrae of *Haplocanthosaurus* (Fig. 13A) and *Rebbachisaurus* LAVOCAT (reference is made mainly to *R. tessonei* CALVO & SALGADO, Albian-Cenomanian of Argentina (Fig. 13C), because the only prepared dorsal vertebra of *R. garasbae* LAVOCAT, Aptian - ?Cenomanian of Morocco, was never figured and was only poorly described by LAVOCAT, 1954). Reference to Dicraeosauridae is excluded by the presence of the pleurocoel (the absence of pleurocoels in the dorsal vertebrae is considered an important apomorphy of dicraeosaurids, see McINTOSH, 1990b). *Haplocanthosaurus*, which shares with the vertebra under examination the high inclination of the diapophysis and the presence of the hyposphene-hypantrum, has, on the other hand, a postspinal lamina with a very different morphology, single suprapostzygapophysial laminae, a taller subzygapophysial portion of the neural arch, and is known presently only in the Upper Jurassic of North America (McINTOSH, 1990b). *Rebbachisaurus* does not present an outer suprapostzygapophysial lamina (see CALVO & SALGADO, 1995, fig. 9; here Fig. 13C) and, most important, does not present a hyposphene-hypantrum complex in dorsal vertebrae (CALVO & SALGADO, 1995). The neural spine of *R. tessonei* is more slender in antero-posterior view than that of the specimen here described. However, the spine of *R. garasbae* is wider than that of the South American species. The preserved part of the neural spine of WN-V6 is most reminescent of the neural spines of some dorsal vertebrae of *Apatosaurus louisae* (Fig. 13B).

Characters present mainly in the Diplodocimorpha (sensu CALVO & SALGADO, 1995) indicate that the specimen belongs to this clade: 1) the neural arch is three times the dorso-ventral centrum height (the height of the only partially preserved neural arch is 2.85 times the dorso-ventral centrum height), 2) the suprapostzygapophysial laminar pattern is relatively complex, with inner suprapostzygapophysial laminae which are confluent to form a postspinal lamina, and outer suprapostzygapophysial laminae parallel to the axis of the spine and tapering upward, 3) the tall neural spine is relatively narrow in antero-posterior and lateral view.

The Early Cretaceous diplodocimorphs are represented mainly by a group of Gondwanian taxa (*Rebbachisaurus garasbae*, *R. tessonei*, and the Neocomian *Amargasaurus cazaui* SALGADO & BONAPARTE from Argentina) with extremely tall neural spines and upwardly directed diapophyses in the dorsal vertebrae. This suggests a Gondwanian affinity of the Istrian sauropod fauna.

WN-V6 represents a new diplodocimorph taxon because of the combined presence of an hyposphene-hypantrum complex, a well developed outer suprapostzygapophysial lamina running parallel to the axis of the spine and a high (about 45°) inclination of the long diapophyses. It is very probably related to *Rebbachisaurus* but is less derived because of the presence of the hyposphene-hypantrum in dorsal vertebrae. The name *Histriasaurus boscarollii* is proposed for this new taxon, in honour of the discoverer of the site, mr. Dario Boscarolli, and referring to the region where the specimen was found (*Histria* = Latin name of Istria).

Caudal vertebrae

WN-V3 (Fig. 14). The specimen was figured in BOSCAROLLI et al. (1993, figs. 25-27). The centrum is 100 mm long, 120 and 115 mm high respectively at the anterior and posterior articular side. The shape of the articular facets is roughly elliptical, with the longer axis (150 mm in the anterior facet) horizontal. The posterior is nearly flat, the anterior is a little weathered and was originally flat or shallowly concave. The ventro-posterior part of the centrum projects downward and slightly backward; this projection is related to the chevron articulation, but there is no clear mark of the articular facet, only a thin, transversally flat area. There are no pleurocoels and not even longitudinal ridges or grooves on the ventral side. The ventral side is slightly depressed but the cross-section of the centrum is not "heart-shaped". The proximal part of the coalesced caudal rib is placed high on the dorsal-lateral side of the centrum and is laterally and backwardly directed. The rib is spine-like and slightly dorso-ventrally flattened. The neural arch is only partly preserved. It is tall and placed anteriorly on the centrum, so the distal third of the latter is not covered by the arch. The circular neural canal is very large. The pedicels are slightly medially inclined. The postzygapophysis is far above the base of the neural canal and is posteriorly elongate. The articular facet is a shallow depression, anterodorsally-posteroventrally elongated, facing laterally and only slightly ventrally, placed on the ventral part of the postzygapophysis. The prezygapophyses are not preserved but the position of the articular facet in the postzygapophyses suggests it was anteriorly and upwardly directed. The neural spine is not preserved but its base was rather far above the base of the neural canal. Shortness of the centrum and the presence of a strong rib identify this as an anterior caudal element.

MPCM-V14 (Fig. 15), is a centrum lacking the posterior half and with the basal part of the neural arch. The centrum is more broad than high (about 115 x 70 mm), with a kidney-shaped, concave anterior articular surface. The left rib (only the anterior, basal part is preserved) placed on the dorsal-lateral side of the centrum, is strong and probably latero-posteriorly directed. There is a shallow depression in the centrum just below the rib. The neural canal is subcircular to oval and very large, of greater height than width (26 x 20 mm) in posterior view, the opposite in front view. The neural arch is fused without suture to the centrum. The pedicels are strong and inclined medially. The prezygapophyses

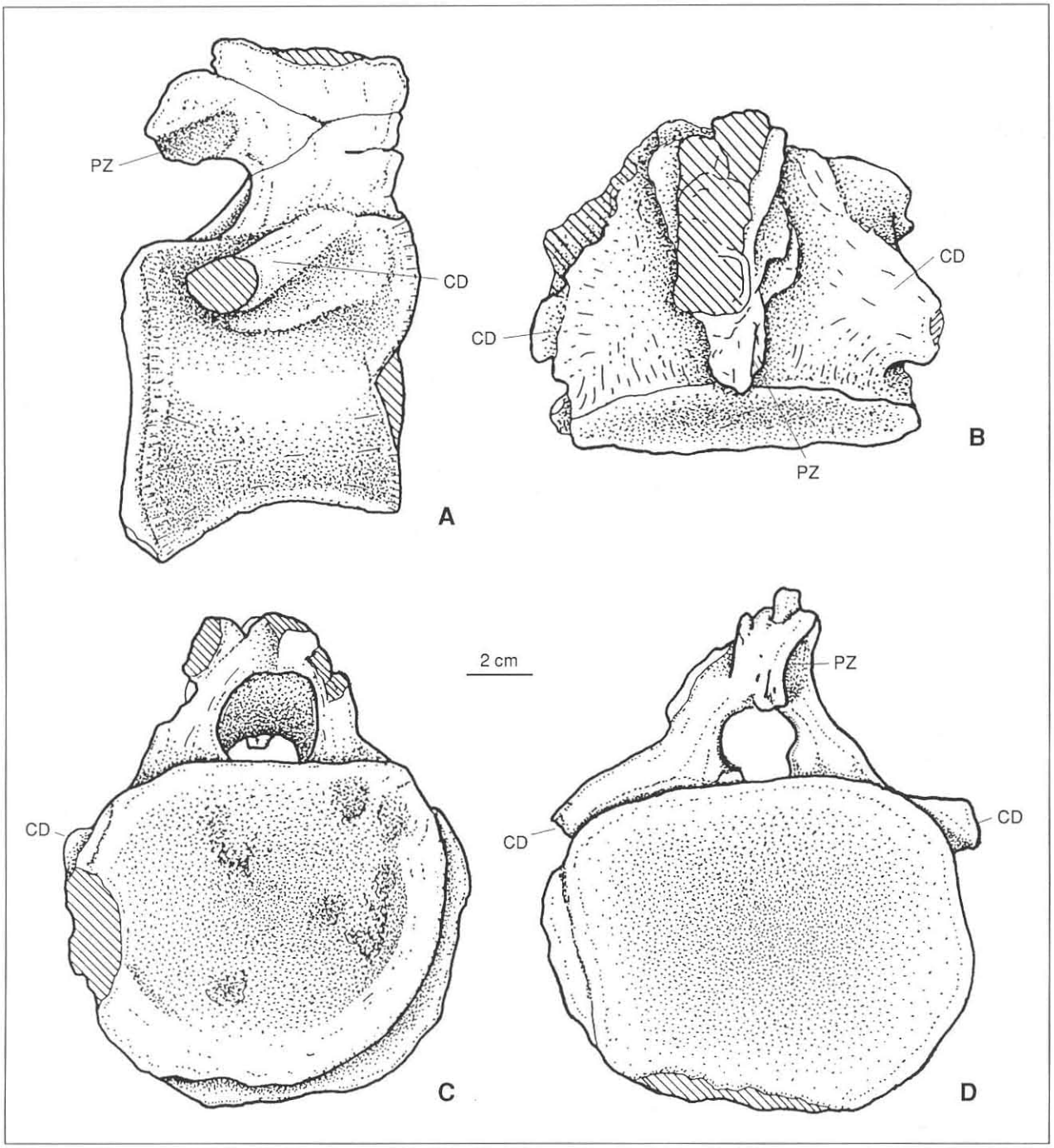


Fig. 14 WN-V3, anterior caudal vertebra. Views: A) right lateral, B) dorsal, C) anterior, D) posterior.

lack the distal part with the articular surfaces. They start at the base of the neural arch and rise from the anteriormost part of the centrum, are forwardly inclined at about 45° in side view, and are flattened laterally with the outer side which faces laterally, upward and backward. Only the basal anterior part of the neural spine is preserved. It is not far above the base of the neural arch. The basal parts of the prespinal and supraprezygapophysial laminae are preserved. The neural spine appears to be caudally inclined, at least in the basal part and its base was antero-posteriorly narrow.

The evident shortness of the centrum and the presence of a strong rib placed down on it identify it as an anterior caudal element.

MPCM-V15 (Fig. 16) comprises most of a relatively short centrum with a fragment of the right basal part of the neural arch. The right side of the centrum and, partly, the posterior articular surface are sufficiently preserved for description. The centrum is elliptical, of greater width than height (about 127 x 105 mm) in posterior view, short (75-80 mm), and with a practically flat posterior articular surface. Its shape was spool-like,

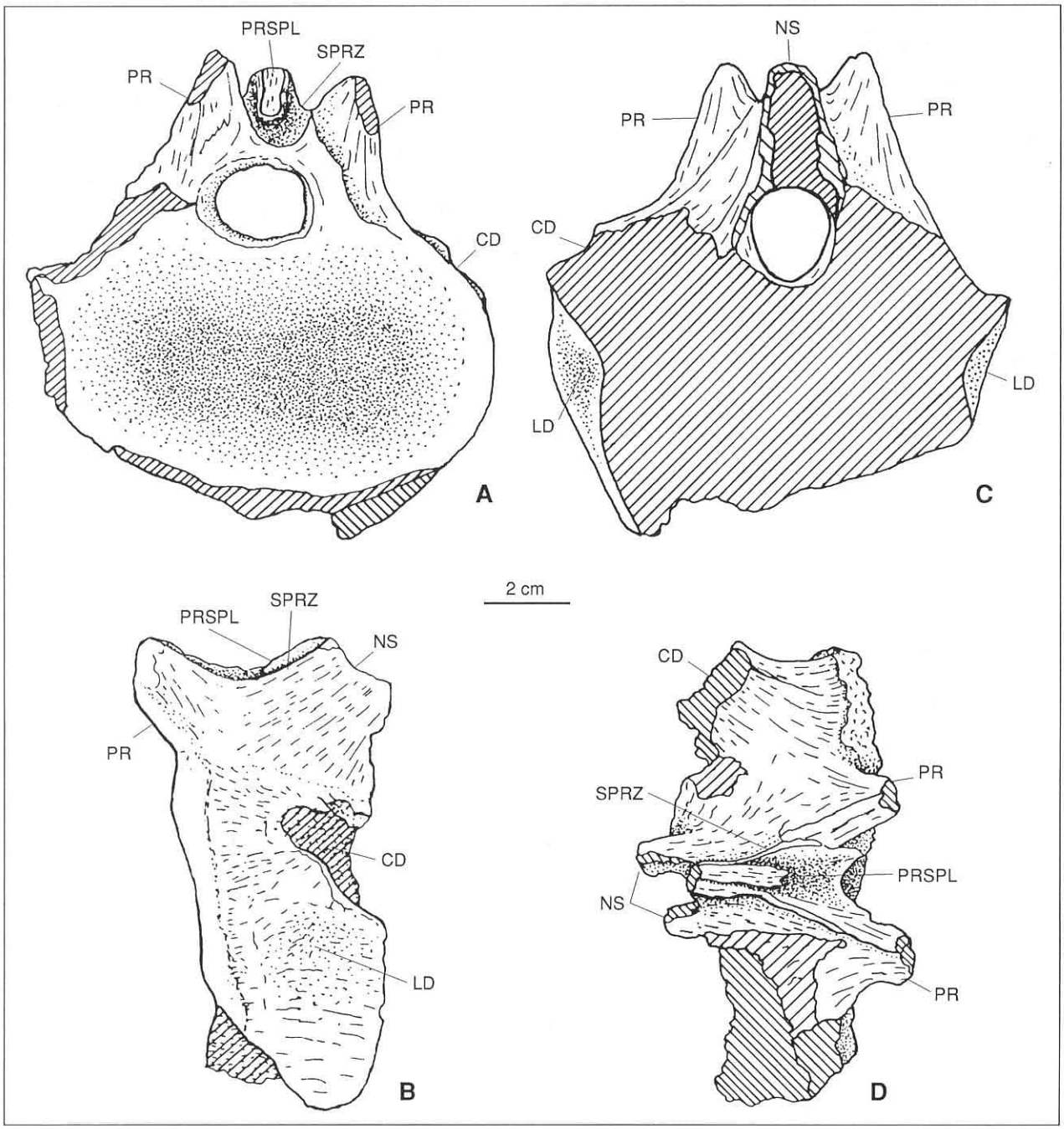


Fig. 15 MPCM-V14, fragmentary anterior caudal vertebra. Views: A) anterior, B) left lateral, C) posterior, D) dorsal. Acronyms: LD = lateral depression.

with a marked oval to semicircular depression in the dorsal lateral half just below the rib. The right rib (only the basal segment is preserved) is placed in the uppermost, dorso-lateral side of the centrum at the attachment of the neural arch. It is strong, slightly flattened dorso-ventrally and directed latero-posteriorly.

The shortness of the centrum and the presence of a strong rib identify it as an anterior caudal element.

Nos IG-1 (Fig. 17, photograph in DALLA VECCHIA, 1997c, fig. 4). The centrum is nearly complete (the left side was weathered) and there is part of the neural arch without most of the neural spine. The centrum is typically spool-shaped and relatively elongate (length l = 120 mm; height h at the extremities = 90 mm; l/h ratio = 1.33), and amphicoelous with the anterior facet shallow and the posterior one slightly deeper. These facets are elliptical and slightly greater in width than height. There are moderately developed, separate facets for the chevron on a relatively shallow ventro-posterior projection of the centrum. Pleurocoels, ventral ridges and grooves are absent. There is no true caudal rib or transverse process, only an antero-posteriorly elongate knob (LK in Fig. 17) at the base of the neural arch. The latter is placed on the anterior half of the centrum and its base is 48 mm long. The zygapophyses are

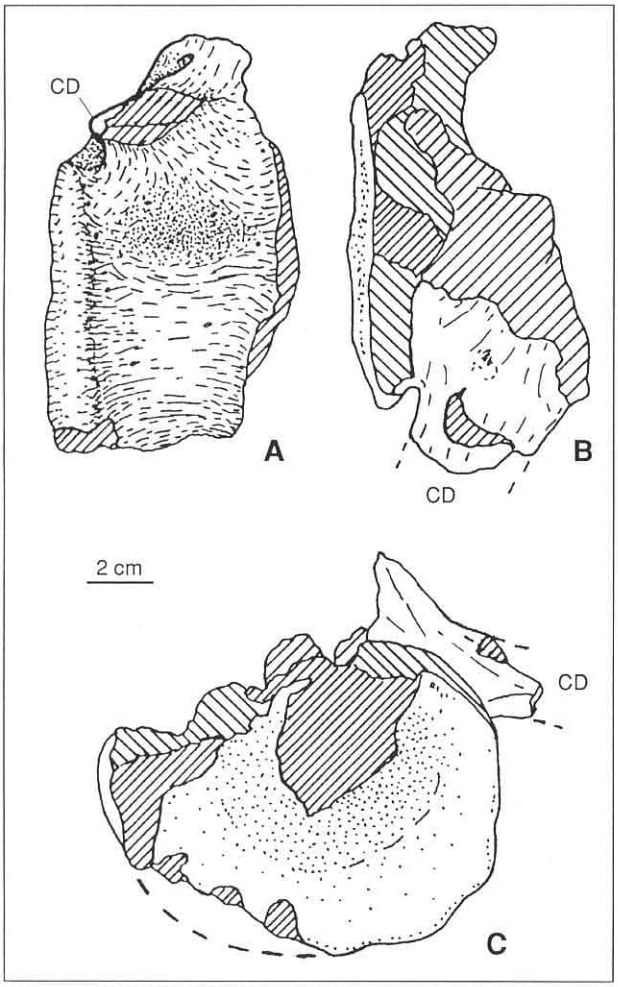


Fig. 16 MPCM-V15, fragmentary anterior caudal vertebra. Views: A) right lateral, B) dorsal, C) posterior.

badly and incompletely preserved. The postzygapophysis is far above the base of the neural canal, the articular region faces laterally and slightly ventrally. The prezygapophysis is lower on the arch and probably antero-dorsally elongate. Only the basal part of the spine is preserved.

A relatively elongate centrum, lacking a caudal rib but possessing a knob at the base of the arch, together with a well developed neural arch, indicate that this is a mid-caudal vertebra (approximately posterior to the 15 - 16 caudal because of the absence of a rib, see McINTOSH, 1990b).

WN-V4 (Fig. 18). This vertebra consists of a nearly complete centrum. It is amphicoelous with shallow articular facets, spool-shaped and more elongated than the centrum of Nos IG-1 (length = 116 mm, height at the extremities = 70.5 mm, l/h ratio = 1.55). The articular facets of the centrum are more or less elliptical, slightly greater in width than in height. Pleurocoels, ventral ridges and grooves are absent. The facets for the chevron do not project. The only difference that may be found with the vertebra Nos IG-1, if we exclude elongation, is a shorter (40 mm) basal part of the neural arch. Only the basal part of both pedicels are preserved; the neural canal is narrow (11 mm minimum width). The neural arch is placed decidedly on the anterior half of the centrum. The resemblance with Nos IG-1 and its greater elongation and shorter base of neural arch (perhaps related to a smaller and lower arch) suggest it is mid-caudal but more distal than the vertebra Nos IG-1.

Comparisons - all five caudals present a centrum greater in width than in height, a feature also shared with the cervical MPCM-V2 and the dorsal MPCM-V1. This is not the most common state for sauropods even if it is present, for example, in *Brachiosaurus brancai* (JANENSCH, 1950), in the anterior dorsals of *Diplodocus carnegii* (HATCHER, 1901), sometimes in the dorsals of *Andesaurus* BONAPARTE & CALVO (BONAPARTE & CORIA, 1993), in the dorsals of *Eucamerotus foxi* (BLOW, 1995).

A ball-and-cup articulation is not present, and the centra are amphicoelous or amphiplatyan. Therefore Titanosauridae sensu SALGADO et al. (1997) are excluded, at least for the anterior elements sufficiently complete, since mid-caudals can be amphiplatyan or even gently amphicoelous in primitive forms of the Titanosauria. This is the case of *Malawisaurus* JACOBS, WINKLER, DOWNS & GOMANI (amphicoelous; JACOBS et al., 1993), an undetermined genus from Argentina (SALGADO & CALVO, 1993), "andesaurid" titanosaurs (BONAPARTE & CORIA, 1993) and the Late Maastrichtian *Magyarosaurus* HUENE (pers. obs.).

In the two mid-caudals, and in the most complete anterior caudal, the neural arch is displaced toward the anterior half of the centrum, a feature which was considered apomorphic for Titanosaurids (e.g McINTOSH, 1990a), but is considered a synapomorphy of the wider clade Titanosauriformes by SALGADO et al. (1997). There are no pleurocels, no ventral sulcus (excavation) in the two mid-caudals and in the most complete anterior caudal; the ribs of the three anterior elements are not wing-like, and the centra are always short or moderately elongated. This excludes the Diplodocidae as diagnosed by McINTOSH (1990a, b).

The shape of the centrum of WN-V3 and Nos IG-1, and the postero-laterally directed ribs of WN-V3, MPCM-V14 and MPCM-V15, are more reminiscent of the anterior to mid-tail vertebrae of *Brachiosaurus brancai* (JANENSCH, 1950). The anterior caudals of *Camarasaurus* are similar to the described anterior vertebrae but do not possess a posteriorly directed rib (OSTROM & McINTOSH, 1966; McINTOSH, 1990a, b). Also the position of the neural arch on the centrum, its overall morphology, the shape and position of the postzygapophysis, the orientation of the prezygapophysis and the shape of the caudal rib correspond to the anterior and mid-caudals of *Brachiosaurus brancai* (JANENSCH, 1950; McINTOSH, 1990b).

The comparison with the caudals of this species (JANENSCH, 1950, Pls. II-III) and the l/h ratio (0.87) show that the vertebra WN-V3 might be the 6 - 8 cau-

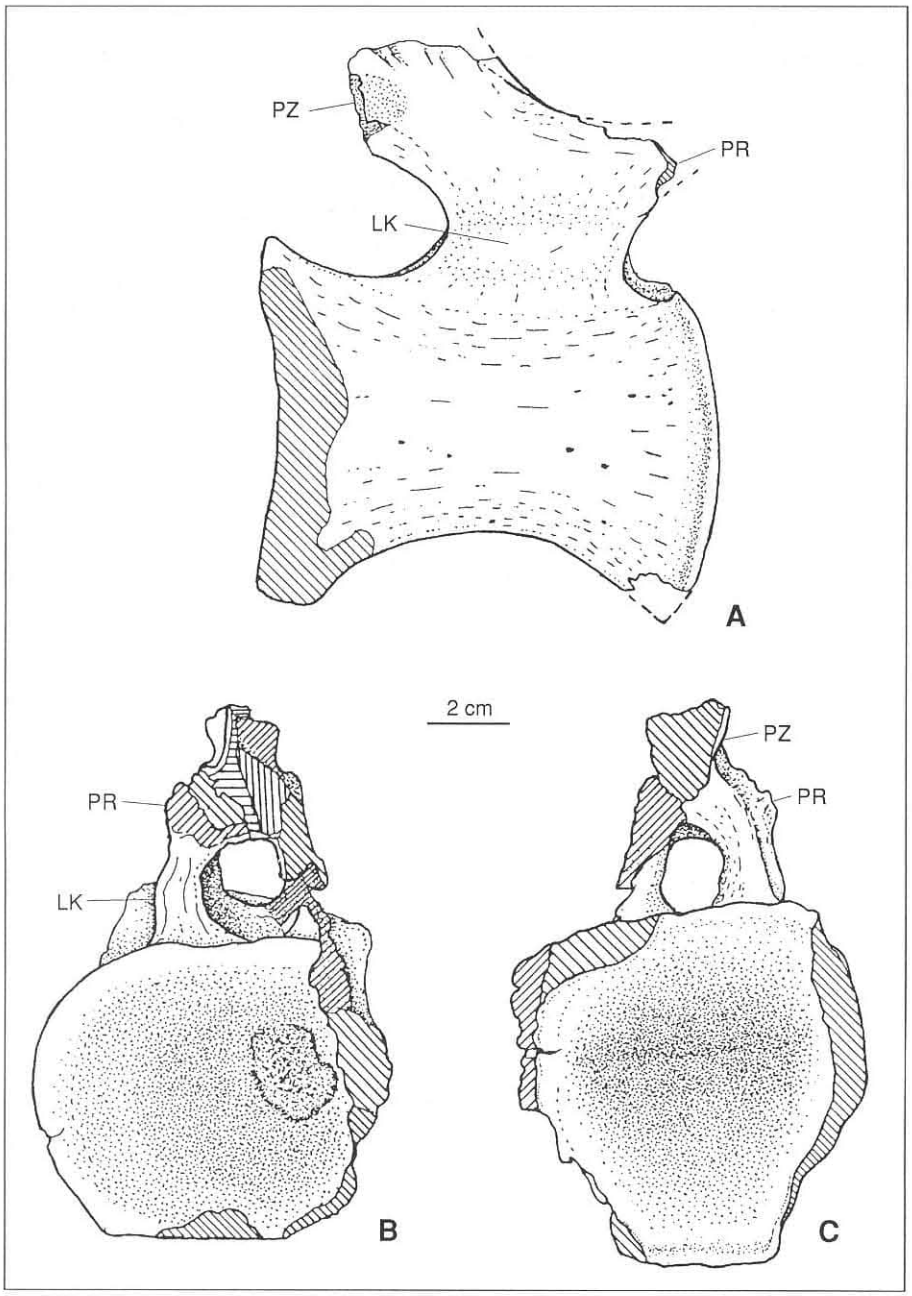


Fig. 17 Nos IG-1, mid-caudal vertebra. Views: A) right lateral, B) anterior, C) posterior. Acronyms: LK = lateral knob at the base of the neural arch.

dal. The mid-caudals Nos IG-1 and WN-V2 are comparable, considering mainly the elongation of the centra, respectively, to the 18 - 20 and 22 - 25 caudal (JANENSCH, 1950, *ibid.*).

MPCM-V14 differs from the anterior caudal WN-V3 because the base of the spine is lower on the arch.

Isolated caudal neural spines

MPCM-V13 (Fig. 19), is the basal segment (95 mm tall) of a neural spine probably from a small anterior caudal vertebra. It is rectangular in cross section, 30 mm wide in side view and narrow in front (12 mm) and back (15 mm) view. The anterior and posterior sides are wrinkled (rough). There seem to be very short (about 30 mm), small supraprezygapophysial laminae, which end just above a short prespinal lamina. There were probably corresponding small postzygapophysial laminae which however, are badly preserved. On the outer (lateral) sides there is a stronger lamina (lateral spinal lamina, LSL), antero-laterally directed, which tapers and ends at the upper broken margin of the spine.

Comparisons - it is very different from a brachiosaurid spine. A vaguely similar laminar pattern is present in the proximal caudals of *Apatosaurus* (cf. OSTROM & McINTOSH, 1966, pl. 35; pers. obs.).

MPCM-V9 (Fig. 20). This specimen is the upper portion (90 mm) of a neural spine. It is club-shaped, "triangular" in antero-posterior view, rectangular in the ventral cross-section of the broken lower part, with flat, smooth outer (lateral) sides and flat and wrinkled (rough) anterior and posterior sides. The tip is rounded,

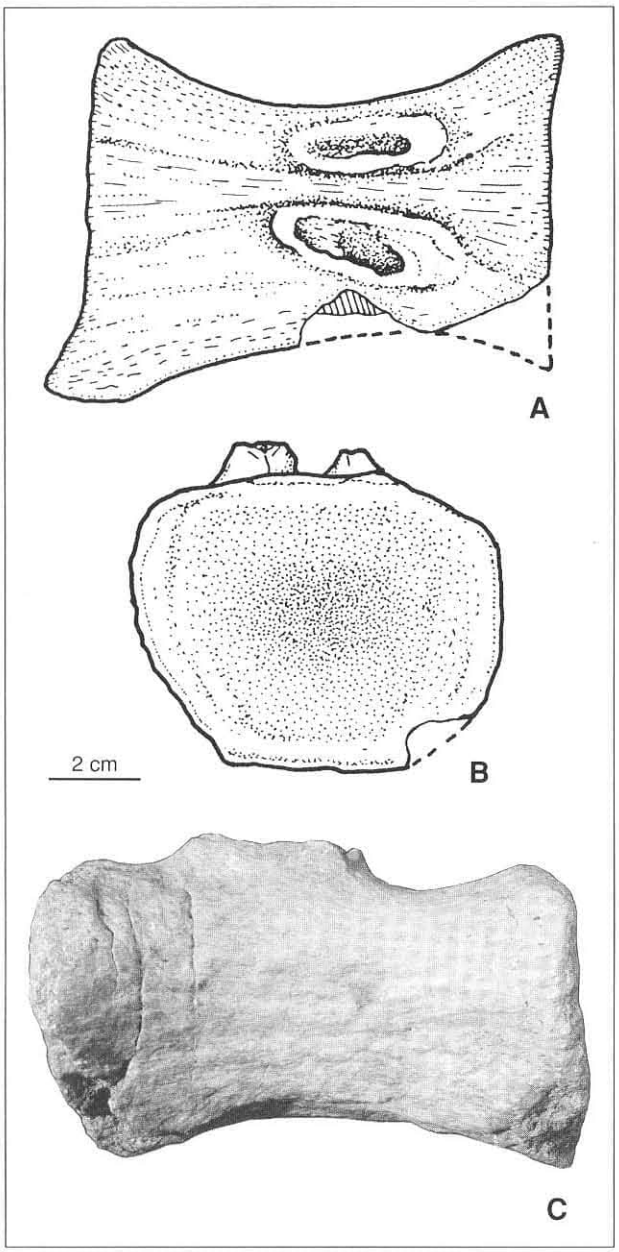


Fig. 18 WN-V4, mid-caudal vertebra. Views: A) dorsal, B) posterior, C) left lateral.

and is formed by the fusion, represented by a suture, of a semicylindrical element. The spine was inclined at about 15° with respect to the vertical.

Comparisons - it is very similar to the neural spines of the anterior (2?) and mid-caudals (12-13?) of "*Morosaurus grandis*" (= *Camarasaurus grandis*) figured in OSTROM & McINTOSH (1966, pls. 37-38). Also the anterior caudal vertebra of *Aragosaurus ischiaticus* SANZ, BUSCALIONI, CASANOVAS & SANTAFE from the Hauterivian of Spain has a similar neural spine (SANZ et al., 1987). The tip of the spine is generally rectangular in diplodocids.

Haemapophyses

WN-V5 (Fig. 21). The specimen (175 mm long) is the only nearly complete element among the discovered chevron remains. It is Y-shaped, the proximal, articular part is not preserved, the distal shaft is straight and spatulate.

Comparisons - haemapophyses are of poor taxonomic value. Only Diplodocidae (*Diplodocus*) and some sauropods from China (Shunosaurinae) have haemapophyses with a characteristic shape on the middle segment of the tail but this is not the case in our specimen which is similar to the mid-tail chevrons of both *Camarasaurus* (OSBORN & MOOK, 1921) and *Brachiosaurus* (JANENSCH, 1950). No remains indicating the presence of the typical diplodocid mid-caudal chevrons have been collected up to now in the outcrop.

APPENDICULAR SKELETON ELEMENTS

Femur

Nos IG-2 (Fig. 22), is the distal, condylar part (not the "proximal quarter" as reported by KOZARIĆ et al., 1996, p. 745) of a quite large right femur, 375 mm long and about 300 mm wide in antero-posterior view. The fragmentary bone is partly very crushed and weathered. Its main recognizable feature is the presence of an undeformed condyle with a lumpy surface which indicates a well developed cartilaginous covering. This condyle is asymmetrical in side view (Fig. 22B), with an articular surface more developed posteriorly (cf. OSTROM & McINTOSH, 1966, pls. 71-73), and is slightly splayed outward in front view. The preserved condyle appears to occupy less than half the width of the femur in antero-posterior view and is identifiable as the tibial one (cf. OSTROM & McINTOSH, 1966, pls. 71-73). Lateral to the condyle (Fig. 22A) the bone is very crushed in correspondence with the *sulcus intercondiloideus* and the fibular condyle, which is nearly completely eroded.

Comparisons - the bone obviously belonged to a large animal, and is here attributed to a sauropod, because of its size and comparison with the femora illustrated by GILMORE (1936), HATCHER (1901), OSBORN & MOOK (1921) and in OSTROM & McINTOSH (1966, pls. 71-73). It is very similar to the femora of *Camarasaurus grandis* figured in OSTROM & McINTOSH (1966, pls. 72-73) and *Camarasaurus* in OSBORN & MOOK (1921, figs. 107-109), but the preserved part has no taxonomic value.

Tibia

MPCM-V16 (Fig. 23): this is the proximal part of a left tibia. The specimen is 220 mm long, and is damaged in the anterior part, therefore the cnemial crest is partly missing. The latter structure was proportionally rather small (cf. SALGADO et al., 1997, fig. 11). The proximal articular part is spongy in aspect, and there is a moderate caudal projection in this region. In the lateral side there is a marked groove for the accomodation of the proximal part of the fibula; there is also a small and shallow depression on the medial side. The proxi-

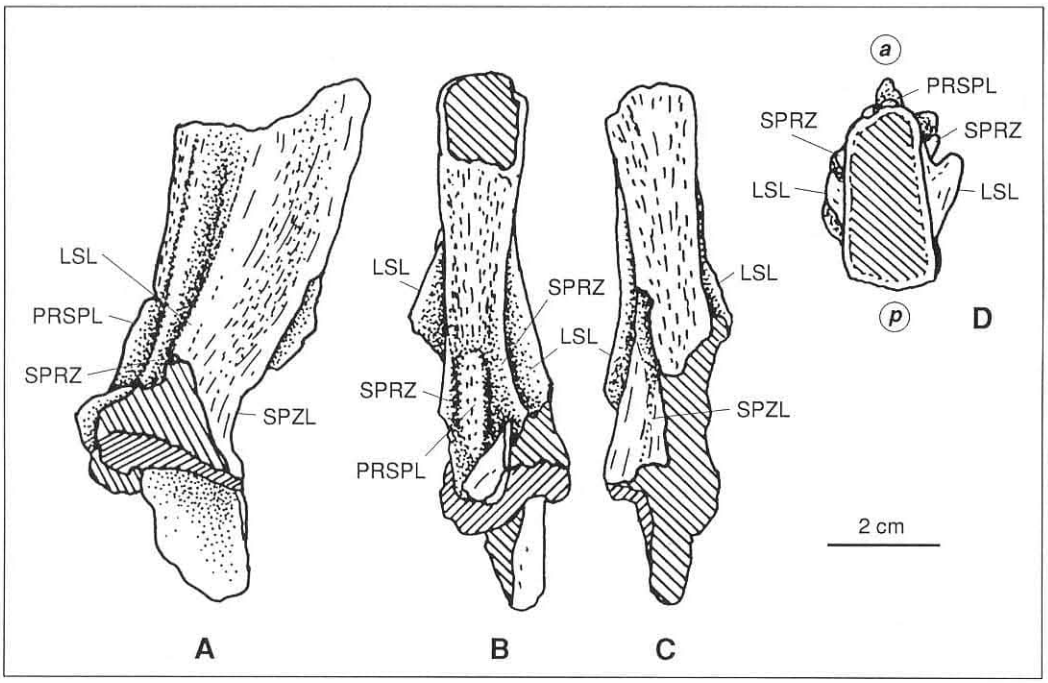


Fig. 19 MPCM-V13, fragmentary neural spine. Views: A) left lateral, B) anterior, C) posterior, D) dorsal. Acronyms: LSL = lateral spinal lamina, a = anterior, p = posterior.

mal tibia is flattened medioanteriorly-posterolaterally and expanded proximally, and narrows sensibly below the cnemial crest (the anterolateral-medioposterior width at the base of the cnemial crest is only 75 mm). This suggests that the tibia under examination had a shaft more slender than those of most sauropods (cf. McINTOSH, 1990, figs. 16-17, and SALGADO et al., 1997, fig. 11).

Comparisons - Diplodocids (*Diplodocus carnegii* and *Barosaurus lentus* in McINTOSH, 1990, figs. 16-17) have the most slender tibiae among sauropods, probably because of the relative elongation of the hind limbs. The specimen is very similar to the proximal end of tibia of the Late Jurassic "*Gigantosaurus megalonyx*" (see GLUT, 1997, p. 439).

4. DISCUSSION AND CONCLUSIONS

Sauropod systematics are chaotic and in a state of flux, as the very different classifications of JANENSCH (1929), McINTOSH (1990a, b), BONAPARTE (1986), UPCHURCH (1994, 1997) and SALGADO et al. (1997) demonstrate. In most classifications the sauropod families are based mainly on just one more or less well known genus and the other members are tentatively included, "weighting" the characters shared with

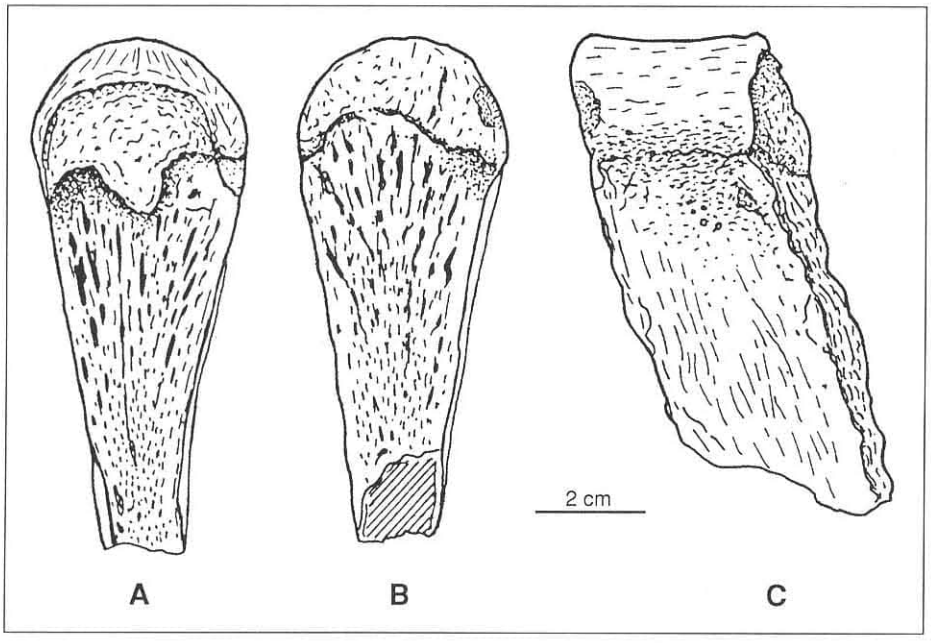


Fig. 20 MPCM-V9, fragmentary neural spine. Views: A) anterior, B) posterior, C) right lateral.

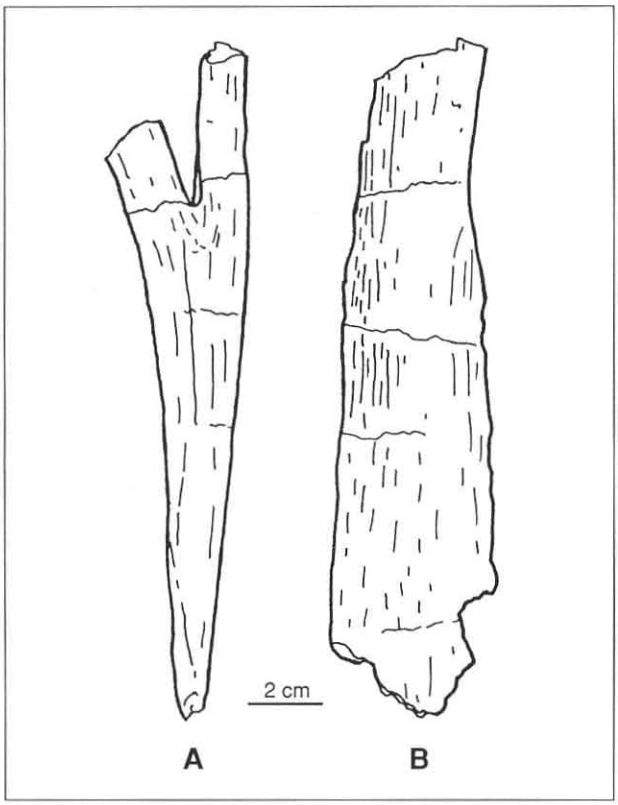


Fig. 21 WN-V5, haemapophysis. Views: A) anterior, B) left lateral.

those well known forms. In this way *Haplocanthosaurus*, which is one of the best known sauropods, but lacks the skull and has "mixed" characters, is included in the Cetiosauridae by McINTOSH (1990b), in the Dicraeosauridae by BONAPARTE (1986), in the Camarasauridae by UPCHURCH (1994) and finally considered, in a cladistic analysis, the sister-taxon of the Neosauropoda (Brachiosauria + Diplodocoidea) by UPCHURCH (1997).

Early Cretaceous sauropods appear to be widespread and diversified but they are not well known since most species and genera are based on scarce or undiagnostic remains. This was underlined by McINTOSH (1992) who stated that most sauropod genera "might be termed *nomina dubia*", "as they can be distinguished from the 12 well known genera but not from each other because they are based on fragmentary postcranial skeletons or teeth" (HUNT et al., 1994, p. 263).

Therefore comparisons with the Istrian remains are in many cases practically impossible. This is clearly evident from the taxonomic list of Hauterivian - Barremian sauropods after McINTOSH (1990b; this list of course follows McIntosh's Linnean classification), completed here following JACOBS et al. (1993), HUNT et al. (1994), BLOWS (1995), and BONAPARTE (1996). Most taxa are based on incomplete, fragmentary remains.

Cetiosauridae (mentioned by HUNT et al., 1994, but not in McINTOSH, 1990b). Probably none of these taxa are actually "cetiosaurids".

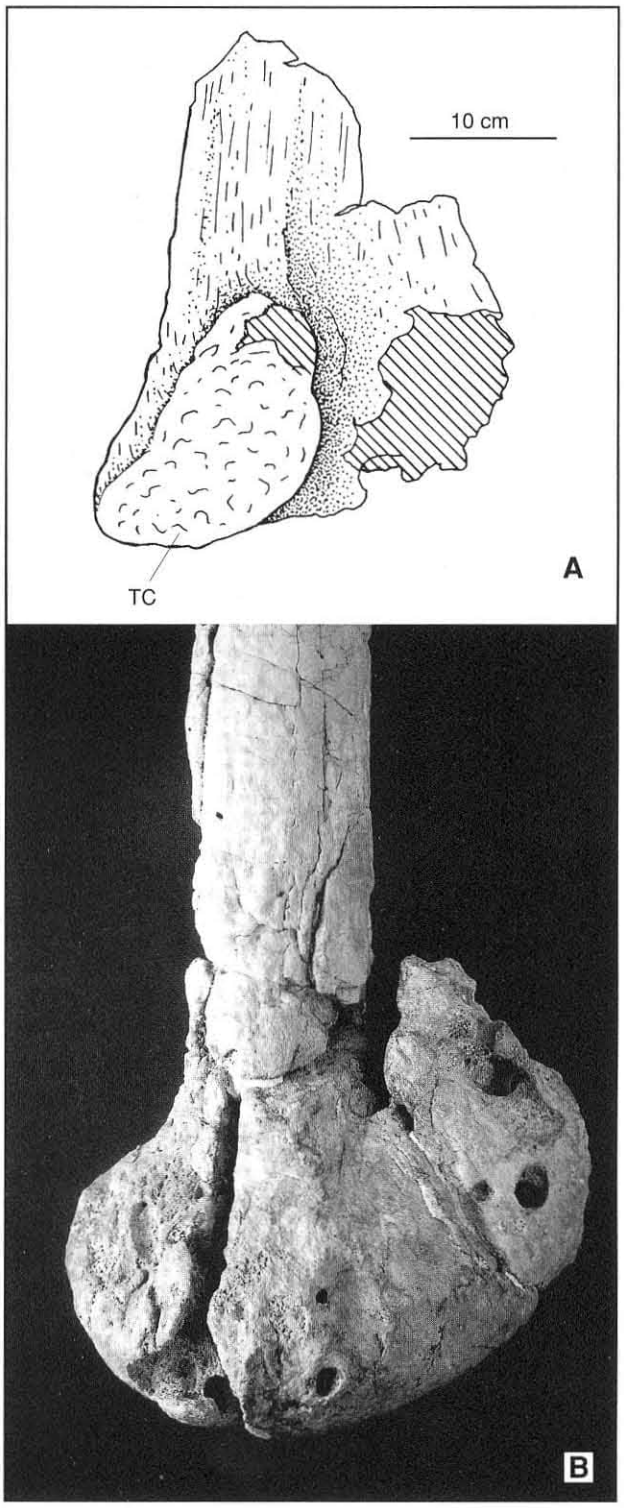


Fig. 22 Nos IG-2, distal end of a right femur in A) posterior view, B) medial view (tibial condyle). Acronyms: TC = tibial condyle.

Cetiosaurus conybeari MELVILLE (wrongly cited as C. *oxoniensis* by HUNT et al., 1994) (England, Valanginian - Barremian, vertebrae).

Cetiosaurus brevis OWEN (England, Valanginian - Barremian) in LYDEKKER (1888) are reported vertebrae, chevrons, metatarsals, phalanges and frag-

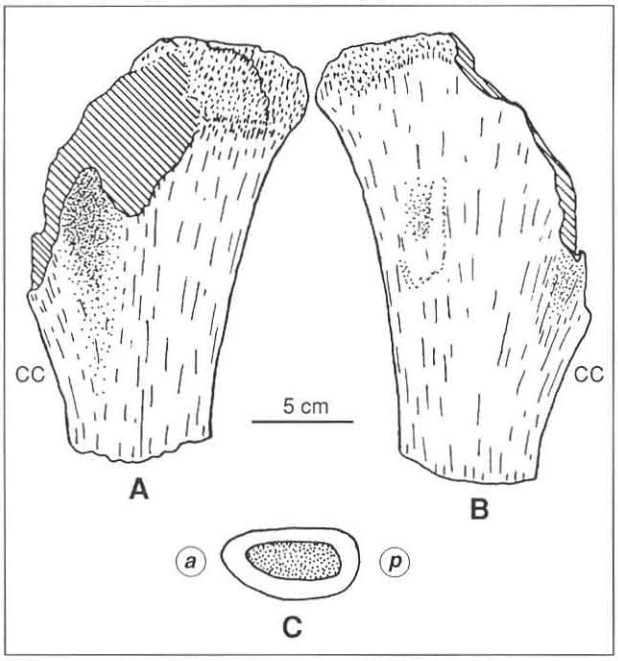


Fig. 23 MPCM-V16, proximal part of a left tibia. A) posterolateral view, B) anteromedial view, C) distal cross-section. Acronyms: CC = cnemial crest, a = anterior, p = posterior.

ments of long bones from the Wealden and attributed to this taxon; no other author mentions them.

Cetiosaurus sp. (Spain, Valanginian - Barremian).

Brachiosauridae

Ornithopsis hulkei (England, Barremian, dorsal vertebra, following BLOWS, 1995).

Eucamerotus foxi (England, Barremian, dorsal vertebrae, following BLOWS, 1995).

Pelorosaurus conybearei MANTELL (England, Valanginian, following BLOWS, 1995, only a humerus is considered to belong to this species).

Pleurocoelus nanus MARSH (USA, Hauterivian - Barremian, isolated remains of more than 6 individuals, including skull elements).

P. altus MARSH (USA, Hauterivian - Barremian, tibia and fibula).

P. valdensis LYDEKKER (England, Valanginian - Barremian, teeth, dorsal and caudal centra).

Cf. *Pleurocoelus* sp. (Spain, Barremian).

Camarasauridae

Aragosaurus ischiaticus (Spain, Early Barremian, caudal vertebrae, scapula, fore limb, ischium, pubis).

Chondrosteosaurus gigas (England, Barremian, cervical vertebrae; *nomen dubium* following P. UPCHURCH'S pers. comm.).

Titanosauridae

Unnamed titanosaurid (="*Titanosaurus*" *valdensis*) (England, Valanginian - Barremian, several caudal vertebrae).

Malawisaurus dixeyi JACOBS, WINKLER, DOWNS & GOMANI (Malawi, Early Cretaceous, premaxilla, dentary teeth, cervical, dorsal and caudal vertebrae, sternal plates, ischium). This taxon could be more recent than the others reported in this list (JACOBS et al., 1993).

Macrurosaurus semnus SEELEY (England, Valanginian, isolated caudal vertebrae).

Diplodocidae

Amargasaurus cazaui SALGADO & BONAPARTE (Argentina, Neocomian, a nearly complete skeleton).

Incertae sedis

Mongolosaurus haplodon GILMORE (Mongolia, Berriasian - Albian, teeth, basioccipital, 3 cervical vertebrae).

Unnamed sauropod (England, Hauterivian - Barremian, fore limb, epidermal impressions).

Following the list of HUNT et al. (1994) from this stratigraphic interval there are indeterminate or undescribed "brachiosaurids" also in Spain and the USA, diplodocids in England and Argentina and indeterminate sauropods in China, South Korea, Mongolia, Japan, Niger, France and England.

It can be observed that the record comes mainly from the Wealden of England and there is little information about Gondwanian sauropods and none (just undescribed bones from Niger) about northern African which are better known in the Albian - Cenomanian interval.

Of the abundant but scattered English remains a plethora of new taxa were created during the 19th century, and this led to inextricable confusion. Following BLOWS (1995) and P. UPCHURCH (pers. comm.) the Wealden sauropod fauna is dominated by brachiosaurids whereas camarasaurids are absent. Titanosauria and diplodocids are scarcely represented, as seen above. Unfortunately a satisfying recent revision of the English material has not been published yet and comparison with Wealden sauropods is still at best very difficult. The presence of "*Chondrosteosaurus gigas*" both in Istria and Southern England could have palaeogeographic significance but the diplodocimorph similar to *Rebbachisaurus* is more important under this point of view. This aspect should be investigated further.

The study of the described material suggests the following points:

1) On the basis of size, at least two "forms" are present: a large form (fragments of cervical vertebrae, ?cervical ribs, bony laminae MPCM-V4, part of the neural arch of a dorsal vertebra MPCM-V3, distal part of the femur Nos IG-2) and a small one (cervical vertebra WN-V1, fragmentary cervical vertebra MPCM-V5, posterior cervical centrum MPCM-V2, anterior dorsal vertebra MPCM-V1, all the caudals and the fragmentary neural spines, the proximal tibia MPCM-V16). There is too great a difference in size among some remains, and no evidence of immaturity of small specimens (in all small vertebrae the neural arch is fused to the corresponding centrum), to support the idea that all the specimens belong to the same species. Even if we consider the Istrian sauropods as insular inhabitants with the typical intraspecific size variability of Pleistocene insular mammals (KOTSAKIS, 1985) the size difference is still too great.

2) A new Diplodocimorph similar to *Rebbachisaurus* but more primitive because it still retains a hyposphene-hypanthrum, is represented by a posterior dorsal vertebra.

3) The posterior cervical vertebra MPC-V2 is very similar to those of the coeval "*Chondrosteosaurus gigas*" of England, and in the shape and pleurocoels but not the bone texture, to *Camarasaurus* of North American Late Jurassic. It is very different from the cervical WN-V1 and probably belongs to a different taxon. The latter cervical is most reminescent of the anterior cervicals of *Brachiosaurus brancai*.

4) Since long cervical ribs are not known in diplodocids (considering *Mamenchisaurus* does not belong to them, UPCHURCH, 1997) the fragments of rib shaft here reported, if correctly identified, belong most probably to a brachiosaurid or a camarasaurid (the state in Titanosauria sensu SALGADO et al., 1997 is not known).

5) All preserved cervical and dorsal vertebral parts (excepted WN-V6) are extremely lightened having A) centra with a "honeycomb"-like, cancellate structure, a feature considered by most specialists typical of the Brachiosauridae (sensu McINTOSH, 1990b) or the most inclusive Titanosauriformes (sensu SALGADO et al., 1997), and B) neural arches made by a complex network of thin laminae.

6) The posterior cervical MPCM-V2, the anterior dorsal MPCM-V1 and all the caudals present elliptical, kidney-shaped or, at least, wider than high articular facets of the centra.

7) The articular facets of the anterior dorsal MPCM-V1 and the posterior cervical MPCM-V2 have a great difference in size which suggests that they belongs to individuals of rather different size. Whether this is due to ontogeny, sexual dimorphism or because they belong to different taxa, is indeterminated from the few remains collected.

8) The anterior dorsal MPCM-V1 is peculiar in being very small, with the relatively tallest neural arch ever described in a sauropod, cancellate texture of the centrum and with a very developed laminar complex with peculiar structures. However, it cannot be stated with certainty that it does not belong to the same taxon as MPCM-V2, and therefore possibly to "*Chondrosteosaurus gigas*". This suggests to avoid the creation of a new taxon, pending the excavation of further material.

9) The developed prespinal lamina of MPCM-V3 suggests that it belongs to the Titanosauriformes sensu SALGADO et al. (1997) and most specifically to the advanced Titanosauria, or to the Diplodocidae. Other features exclude the Titanosauria.

10) The anterior and mid-caudals resemble mostly the Titanosauriformes sensu SALGADO et al. (1997) and *Brachiosaurus brancai* in particular, but they are not diplodocid or titanosaurid.

11) Surprisingly, the fragmentary caudal neural spine MPCM-V9 is very similar to those of *Camarasaurus* and *Aragosaurus*. Since the other fragmentary caudal neural spine MPCM-V13, which has a relatively well developed system of laminae, represents a different part of the spine, these two specimens could belong to the same taxon. Both broken spines are very different from the typically low spines of *Brachiosaurus brancai*.

HUNT et al. (1994) suggested that "isolated, but distinct, postcrania may be considered valid type specimens and disassociated specimens from the same bed should be grouped as much as possible. These usually questionable taxonomic procedures are only tolerated in sauropods because these immense animals are so often represented by such fragmentary or jumbled specimens." (p. 266). The adoption here of this procedure is prevented by the presence of individuals with very different sizes and bones with features suggesting that they belong to different families (sensu McINTOSH, 1990b) (for example, all the caudals seem to be referable to brachiosaurids while the isolated caudal neural spines are not brachiosaurid spines, cervicals seem to belong to different families, etc.).

However, most of the bones seem to come from non-Titanosauria Titanosauriformes (sensu SALGADO et al., 1997) sauropods.

Therefore both Titanosauriformes, Diplodocimorpha and, possibly, Camarasauridae are present in the site.

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