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# *REBBACHISAURUS TESSONEI* SP. NOV. A NEW SAUROPODA FROM THE ALBIAN-CENOMANIAN OF ARGENTINA; NEW EVIDENCE ON THE ORIGIN OF THE DIPLODOCIDAE

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**ABSTRACT: A new species of Albian -Cenomanian sauropods, *Rebbachisaurus tessonei* sp. nov., is described. This new taxon is known from at least four specimens. One of them, the holotype is an almost complete and articulated specimen from the Rio Limay Formation of Northwestern Patagonia, and the most complete sauropod ever found in South America. Twelve autapomorphies support the creation of this new taxon. *Rebbachisaurus tessonei* sp. nov. shares eleven cranial and postcranial characters to support a close relationship to diplodocids; however, other ten postcranial characters, which characterize the family Diplodocidae, are not present in *R..tessonei* sp. nov. Therefore, the eleven synapomorphies allow the erection of a new lower taxon, Diplodocimorpha to include *R. tessonei* sp. nov. as the sister group of Diplodocidae.**

**RESUMO: Descreve-se una nova espécie de saurópode do AIbiano-Cenomaniano, *Rebbachisaurus tessonei* sp. nov., conhecida a partir de, pelo menos, quatro espécimes. Um destes exemplares, o holótipo, provém da Formação do Rio Limay, no noroeste da Patagónia, e é o mais completo saurópode encontrado na América do Sul. A definição deste movo táxone é apoiada por doze autopomorfias. *Rebbachisaurus tessonei* sp. nov. apresenta onze características cranianas e pós-cranianas que sustentan uma proximidade aos diplodocídeos; no entanto, outras dez características pós-cranianas (que caracterizam a família Diplodocidae) não estão presentes em *R. tessonei* sp. nov. Consequentemente, as onze sinapomorfias permitem a formalização de um novo táxone de categoria inferior, Diplodocimorpha (que inclui *R. tessonei* sp. nov.), grupo irmão dos Diplodocidae.**

## INTRODUCTION

In 1988, during a field trip, of the Museo de Ciencias Naturales de la Universidad del Comahue and the Museo de Ciencias Naturales "Bernardino Rivadavia" of Buenos Aires, an almost complete and articulated sauropod from the Albian-Cenomaian beds of the Ezequiel Ramos Mexía lake in Neuquén Province, Patagonia, Argentina was collected (Fig. 1). It was briefly reported on by CALVO & BONAPARTE (1988) and CALVO & SALGADO (1991), but no detailed informtation was given.

Some bones of the new sauropod from Neuquén resembled those of LAVOCAT (1954) from the Aptian-Albian of Morocco, Africa. In the first paper about the Morocco sauropod LAVOCAT (1951) listed an incomplete scapula, eight vertebrae, a sacrum, and seven ribs. ln his second paper LAVOCAT (1954) erected *Rebbachisaurus garasbae* LAVOCAT describing the scapula, a mid-dorsal verlebra, the sacrum and an anterior caudal, there Lavocat adds a humerus. The species is characterized by the very broad and racket-shaped blade of the scapula, a unique character among the Sauropoda (MCINTOSH, 1990a);and very tall neural spine relative to the height of the centra. The fragmentary nature of this material, however, has resulted in several hypotheses on the phylogenetic placement of *R. garasbae*.

Previous to Lavocat's description of *R. garasbae*, NOPCSA (1902) described and figured a dorsal vertebra from the Neuquén Province, Patagonia, Argentina.It strongly resembles that of *R. garasbae* and this new material, based on the morphology of the neural

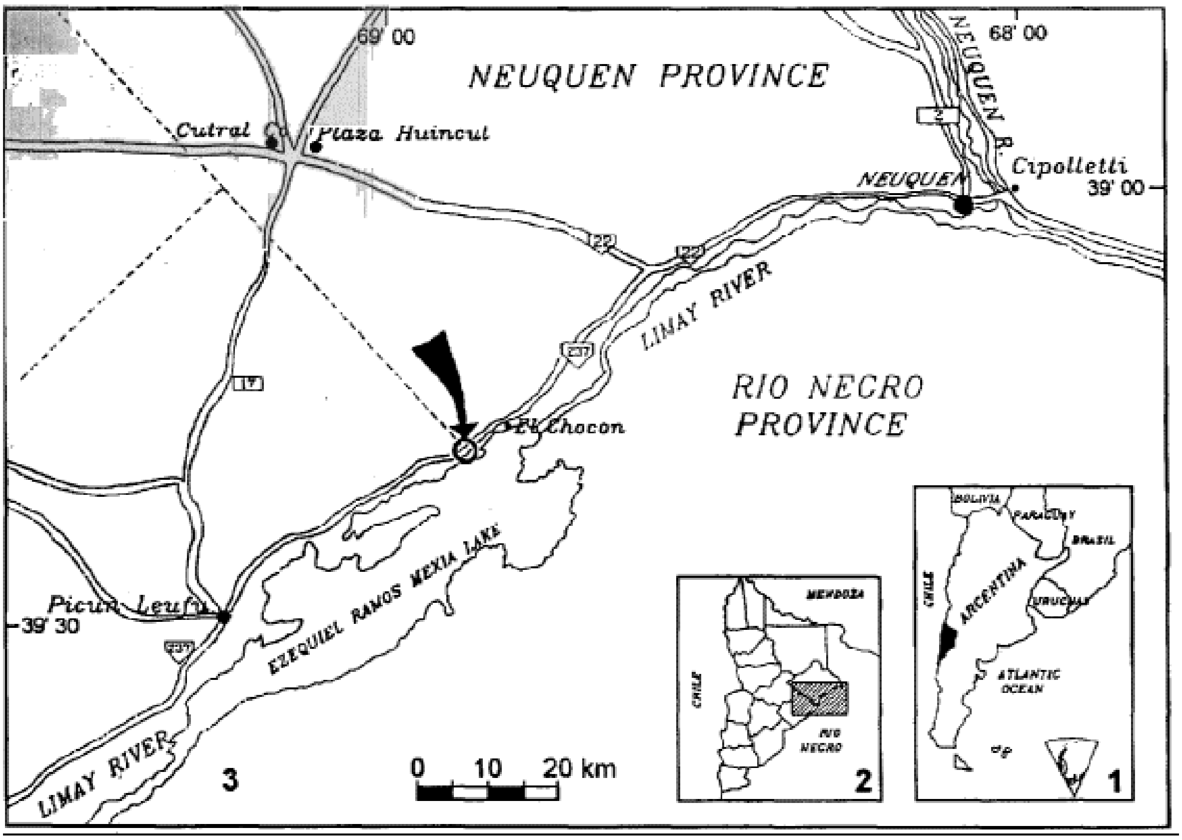


Fig. 1 - Map of Argentina (1) and Neuquén Province (2) detailing the area where *Rebbachisaurus tessonei* sp. nov. specimens were collected (3).

spine. He provisionally referred this vertebra to *Bothriospondylus* LYDEKKER. Later, HATCHER (1903) found that the morphology of Nopcsa's dorsal vertebra is not generically distinguishable from that of *Haplocanthosaurus priscus* HATCHER.

The deposits that yielded tile remains of *Rebbachisaurus tessonei* sp. nov. have also produced a diverse vertebrate fauna dominated by dinosaurs, including the sauropod *Andesaurus delgadoi* (CALVO & BONAPARTE, 1991), the theropod *Giganotosaurus carolinii* (CALVO, 1990; CORIA & SALGADO, 1995), frogs (BAEZ & CALVO, 1990),undescribed crocodiles, and a rich dinosaurian ichnofauna (CALVO, 1989, 1991). The paleoenvironment of the Candeleros Member was represented by a temperate climate with alternate rainy and dry seasons (CALVO & GAZZERA, 1989). The age of the Rio Limay Formation in this area of the basin has been interpreted as Albian-Cenomanian (CALVO, 1991).

We present a detailed description of the new sauropod and discuss the phylogenetic significance of this new material. We also discuss the validity of *R. garasbae* and the relationship between the Nopcsa's vertebra, *R. garasbae* and this new species in light of the present evidence.

## SYSTEMATIC PALEONTOLOGY

### DINOSAURIA OWEN

### SAUROPODA MARSH

### DIPLODOCIMORPHA new taxon

**Etymology** - Diplodoci, *Diplodocus*; morpha, with morphology of *Diplodocus.*

**Included taxa** - *Rebbachisaurus tessonei* sp. nov., Diplodocidae, and all descendants of their common ancestor.

**Diagnosis** - Sauropods with the following synapomorphies. (1) pencil like teeth, (2) anterior extension of the quadratojugal placed beyond the anterior border of the orbit, (3) basipterygoid processes directed forward, (4) quadrate inclined posterodorsally, (5) infrateniporal fenestra oval or slit-shaped, (6) narial opening placed above the orbit, (7) whip-lash tail, (8) tall neural arch in posterior dorsals being three times higher than that of the centra, (9) tall neural arch in caudals; at least 1.5 times higher than that of the centra, (10) wing-like transverse process in caudals, (11) humerus/femur ratio less than 0.70.

Genus *Rebbachisaurus* LAVOCAT, 1954

**Type species** - *Rebbacisaurus garasbae* LAVOCAT, 1954.

**Remarks** - LAVOCAT (1954) mentioned the differences of *Rebbacisaurus garasbae* with respect to other sauropods, but he did not do an adequate diagnosis for the genus.

**Diagnosis** - Paddle-like scapular blade, V-shape angle between the acromion and the scapular blade, absence of hyposphene-hypantrum in dorsals, tall neural arch and, although it is a primitive character, single neural spine, and parapophysis directed upward at approximately 45°

*Rebbachisaurus tessonei* sp. nov.

(Fig. 3-17)

**Assigned materials** - Unnominated dorsal vertebra; NOPCSA, 1902: 21, fig. 1-3.

**Holotype** - MUCPv-205, articulated, well-preserved skeleton, including basicranium, disarticulated cervical vertebrae, articulated vertebral column in posterior dorsals and all caudals. Complete pelvis and pectoral girdle, nearly complete hind and forelimbs lacking a manus. Gastric stones.

**Assigned materials** - MUCPv-206, a disarticulated skeleton composed of two posteriors and two anteriors cervical vertebrae, and one posterior dorsal vertebra, a sternal plate, four metacarpals, ribs and gastric stones. MUCPv-153 a partial articulated skeleton composed by two sacrals, the first six caudals, pubis and ischium. Unnumbered dorsal vertebra described by NOPCSA (1902).

**Locality and horizon** - Approximately 5 km Southwest of El Chocón locality, Neuquén Province, Patagonia, Argentina (Fig. 2). Top of the Candeleros Member (MUCPv-205 and 206) and base of the Huincul Member (MUCPv-153) of the Rio Limay Formation, Neuquén Group. Albian-Cenomanian, Middle Cretaceous.

Remains of the new sauropod were found in the continental deposits of the Candeleros Member of the Rio Liniay Formation, Neuquén Group (CAZAU & ULIANA, 1973). The Rio Limay Formation is composed of three Members, the lower one named Candeleros, the middle named Huincul and the upper one named Lisandro (Fig. 2). The Candeleros Member, in the southeastern sector of the Neuquén basin, is represented by thick sequences of siliclastic red beds. Silstones and fine sandstones are the most common component of this geological Member.

**Diagnosis** - *Rebbachisaurus tessonei* sp. nov. is diagnosed as a Diplodocimorph sauropod (see above). *Rebbachisaurus tessonei* sp. nov. has the following unique derived characters: basipterygoid processes very thin and short. Posterior process of the postorbital absent. Elongated anteroposteriorly articular condyle of the quadrate. Tuberas veiy reduced. Paraoccipital processes not distally expanded. Neural spine in posterior cervicals and dorsals with an accessory lamina connected the diapopostzygapophyseal laminae and the supraprezygapophyseal laminae. Anterior dorsals with both supraprezygapophyseal laminae contacting on the top of the spine. Transverse process in anterior caudals formed by a dorsal and ventral bar directed upward different to *R. garasbae* that has a true wing-like transverse process. Shaft of the pubis oval in cross section.

**STRATIGRAPHIC SEQUENCE OF THE NEUQUÉN GROUP**

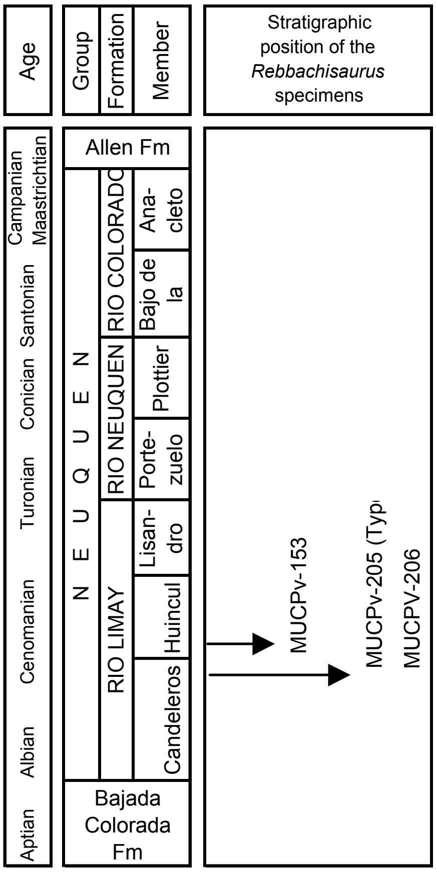


Fig. 2 – Scheme of the Neuquén Group sequence to show the stratigraphic position of the *Rebbachisaurus* specimens. MUCPv – Specimen collection number of *Rebbachisaurus tessonei* sp. nov. at the Museum of the University of Comahue-Patagonia, Argentina (data taken From CAZAU & ULIANA, 1972; ULIANA & DELLAPÉ, 1981; LEGARRETA & GULISANO, 1989; BONAPARTE 1991, and CALVO, 1991).

**Etymology -** This species is named in honor to Mr. Lieto Tessone, discoverer of the Holotype.

**DESCRIPTION**

**General remarks -** The three specimens of *Rebbachisaurus tessonei* sp. nov. from El Chocón area (MUCPv-153-205 and 206) are adults. Tue smallest is MUCPv-153 and the largest is MUCPv-206. For descriptions we have used the holotype (MUCPv-205) except where pointed out where we have used either MUCPv-153 or MUCPv-206.

**Skull -** The skull is represented by a basicranium including the following bones: frontal, parietal, lacrimal squamosal, postorbital, prefrontal, supraoccipital, exoccipital, and basioccipital, laterosphenoids, basisphenoids, basipterygoid processes, prootic, anthotic, opisthotic, nasals, quadratojugal, quadrate, jugal. The skull is tall and somewhat elongated. It is slightly deformed laterally by compression.

**Dorsal skull roof -** The nasals are poorly preserved, and the suture with the frontals is scarcely visible (Fig. 3). Part of the posterolateral rim of the nasal opening is present on the left side ; therefore the narial opening above the orbit as in Diplodocidae. The sutural contacts of the prefrontals include the nasal (not visible), lacrimal and frontal. The reduced prefrontals have a lenticular shape in dorsal view, despite the fact that they are displaced ventrally by postmortem deformation. The external margin involves part of the orbital rim although its contribution is reduced. In anterior view, the prefrontal overlaps the lacrimal.

The lacrimals are complete except for its anteroventral portion (Fig. 3-4). The dorsal end encloses the prefrontal and contacts the poorly preserved nasal. The lacrimal forms the anterior and anteroventral rim of the orbit. The distal end of the lacrimal has been slightly displaced backward by deformation. The jugal is poorly preserved, and part of the anteroventral rim of the orbit could have belonged to it. The anterior rim of the lacrimal forms the posterior margin of the antorbital fenestra.

The prefrontal contacts the nasal, lacrimal and frontal (Fig.7).The contact with the nasal is obscured by surface damage. The prefrontal has as a rhomboidal shape in antero dorsal view. The bone has been

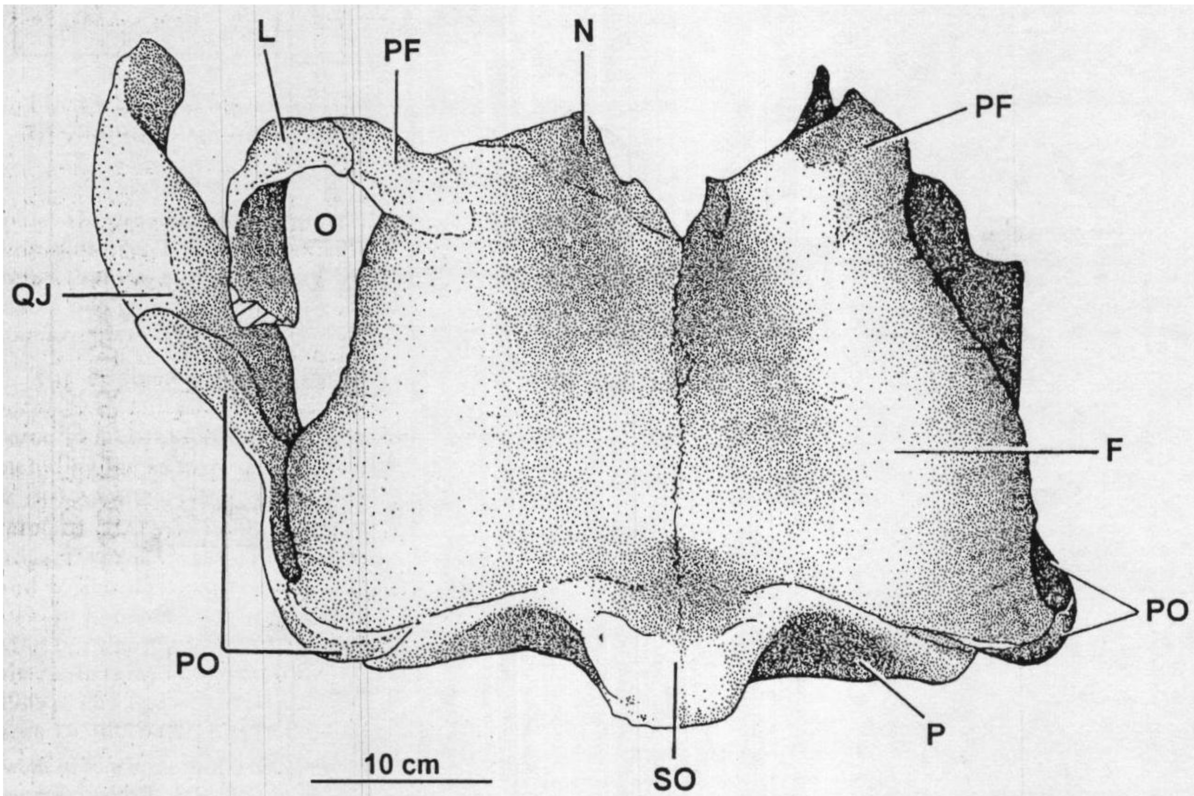


Fig. 3 - *Rebbachisaurus tessonei* sp. nov. Holotype. Skull roof in dorsal view. Abbreviatious: BO - basioccipital, BSD - basioccipital depression, BTP - basipterygoid process, CP - crista prootica, EO - exoccipital, F - frontal, FM - foramen magnum,J - jugal, L - lachrimal, LS - laterosphenoid, N - nasal, O - orbit, OS - orbitosphenoid, P - parietal, PF - prefrontal, PTF - postemporal fenestra, PO - postorbital, PP - paraoocipital prooess, PS - parasphenoid, QJ - quadratojugal, SO – supraoccipital, SQ -squamosal, STF -supratemporal fenestra, I to XII foramina for exit of nerves. Scale in centimeters.

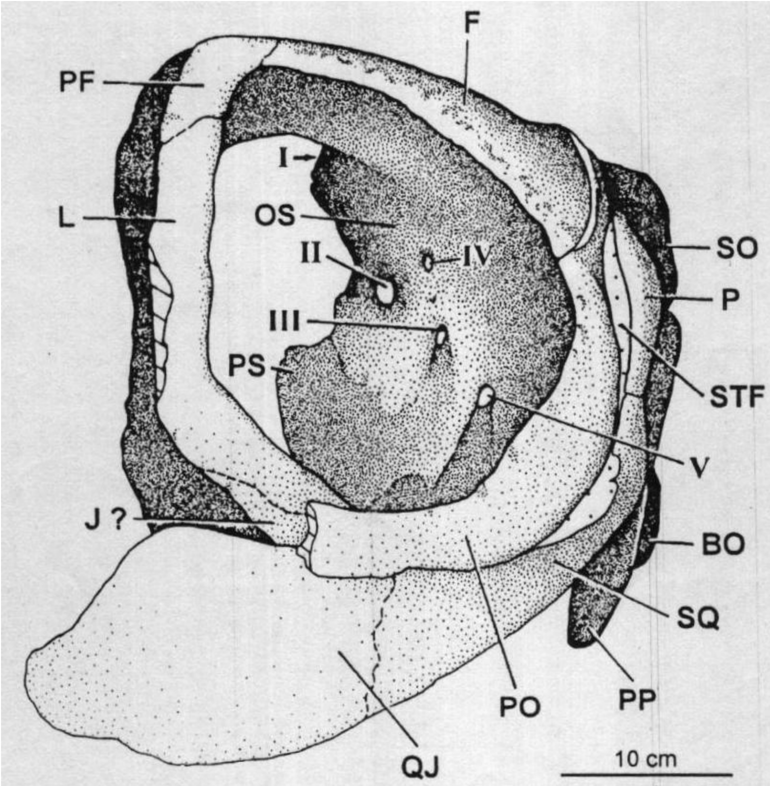


Fig.4 - *Rebbachisaurus tessonei* sp.nov. Holotype.Skull in lateral view.Abbreviations as in Figure 3.Scale in centimeters

little deformed. It participates on the anterodorsal rim of the orbit. The prefrontal overlaps the lacrimal and frontal.

The frontals are paired bones as in all sauropods except dicraeosaurids (Fig. 3). The frontal has a trapezoidal shape, with the posterior side wider than the anterior. and the lateral rim longer than the medial rim. The prefrontal and postorbital overlap the frontal. The frontal-parietal suture is well marked, and it faces concave posteriorly. As in *Amargasaurus* SALDAGO & BONAPARTE (SALGADO & CALVO, 1992) and *Dicraeosaurus* (JANENSCH, I935-36) the frontal does not participate in the supratemporal opening (Fig. 4). There is a marked depression at the contact of both frontals with both parietals.

The paired parietals join the frontal anteriorly, the postorbital and the supratemporal fenestra laterally, the squamosal, supraoccipital and paraoccipital process posteriorly (Fig. 3). The parietal is relatively wide and it presents a large depression near its contact with the supraoccipital. The posterolateral wing of the parietal twist into a vertical plane with its ventral edge resting in the dorsal margin of the squamosal (Fig. 4-5). There is no evidence of a median pineal foramen between the parietals. The supratemporal fenestra is very small, similar to that in Amargasaurus and Dicraeosaurus. It has a lenticular shape and it is bordered by the lateral rim of the parietal and squamosal and the medial border of the postorbital. The medial rim of the parietal contacts the paraoccipital process proximally and the squamosal distally. Between both bones the parietal participates shortly in the dorsal rim of the postemporal fenestra. The postemporal fenestra is elongated dorsoventrally. It is bordered by the paraoccipital process internally and the squamosal laterally (Fig. 5).

The postorbital is slender and curved. It does not have a posterior process present in all other sauropods, and it is considered an autapomorphic character of *Rebbachisaurus tessonei* sp. nov. (Fig. 4). The dorsal end contacts with the frontal. On the uppermost portion of the supratemporal fossa the parietal shares a narrow contact with the postorbital. On the ventral part of that fossa the postorbital has an extensive Contact with the squamosal. The elongated lenticular-shiaped supratemporal fenestra is bordered by among these three bones. The dorsal process of the postorbital is wedged between the parietal and frontal.

The squamosal twist downwardly 90° in such a way that it is invisible in lateral view(Fig.4).The dorsal end is fused to the parietal. Below the level of the occipital condyle the squamosal twists 90°; so that, the articular surface for the quadrate head faces ventrally (Fog. 5). The distal portion of the squamosal extends widely foward and is fused to the quadratojugal, wich is wide and extends foward. Although

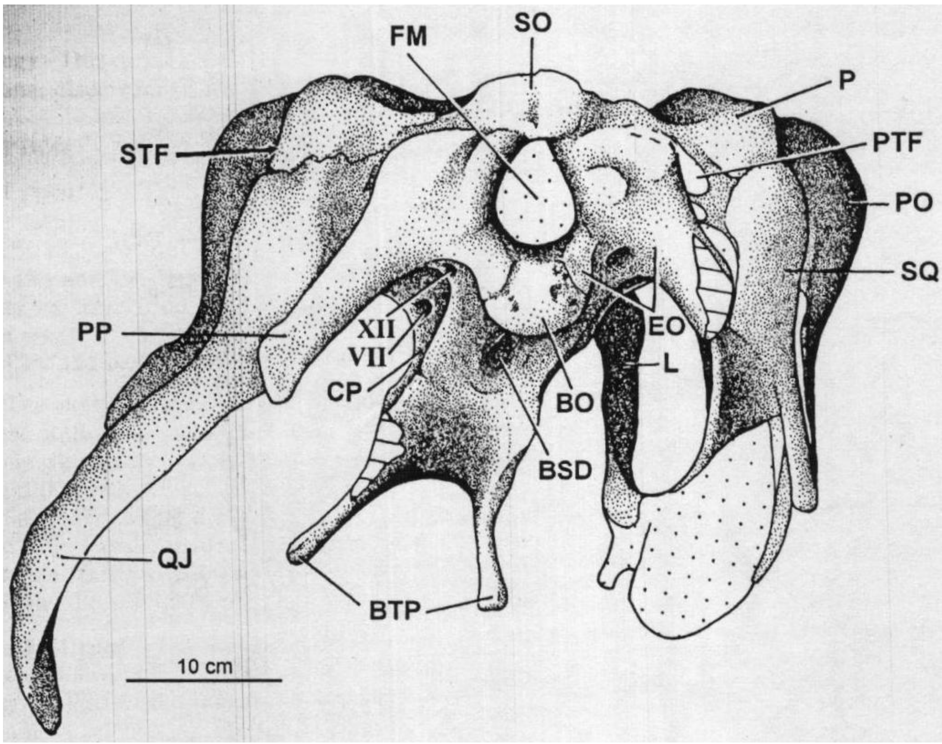


Fig. 5 - *Rebbachisaurus tessonei* sp. nov. Holotype. Skull in posteroventral view. Abbreviations as in Figure 3. Scale in centimeters.

the skull is somewhat deformed, the infratemporal opening is almost closed, with the squamosal and quadratojugal very close to the postorbital (Fig. 4). It is probably an autapomorphic character of *Rebbachisaurus tessonei* sp.nov. Anyway, the reduced slit-shaped infratemporal opening resembles that oval shape of *Diplodocus* MARSH, and it does not resemble the triangular shape seen in either *Camarasaurus* COPE or *Brachiosaurus* RIGGS.

The right quadrate is well preserved (Fig. 6). Its triangular shape in lateral view is formed by dorsal, ventral and anterior processes. The dorsal process has a relatively slender shaft formed by lateral and medial laminae, which form a "V' shape in cross section. In a posterior view a deep fossa is present as that of *Camarasaurus* and *Brachiosaurus.* The head is expanded at the end. Its articulation with the squamosal is large and triangular in shape. It is a rugose surface for a muscle attachment. The body of the quadrate angles anterodorsally in lateral view. The anterior pterygoid process of the quadrate is a flattened surface. The ventral process that articulates with the articular on the lower jaw is longer than the dorsal process. The articular condyle is four times longer than wide, and it is expanded antero-posteriorly. We consider this character an autapomorphy of *Rebbachisaurus tessonei* sp. nov. Although the quadrate was found disarticulated from the skull, putting the articular condyle horizontal to allow a normal movement of the lower jaw, the distal end of the quadrate inclines posterodorsally as in *Diplodocus.* The movement of the lower jaw was probably fore and aft like that of *Diplodocus* (CALVO, 1994a, 1994b).

**Braincase** - The small quadrangular supraoccipital resembles those in *Amargasaurus* and *Dicraeosau--rus,* and differ from the large ones present in *Diplodocus, Apatosaurus* MARSH, *Brachiosaurus* and *Camarasaurus* (Fig. 5). It contacts with the parietal dorsally and dorsolaterally and the paraoccipital process lateroventrally and ventrally.

The exposed contacts of the basioccipital include the exoccipital and basisphenoid. The basioccipital forms most of the occipital condyle. It is excluded from the border of the foramen magnum by having a medial process of the exoccipitals. The basal tuberas are poorly developed.

The basisphenoid contacts the basioccipital. In ventral view, a shallow central depression separates the basipterygoid processes, which are shorter than that in *Diplodocus,* and slender than that in *Camarasaurus,* and oval in cross section (Fig. 5). In lateral view, they project anteriorly as in diplodocids. The parasphenoid contacts posteriorly with the basisphenoid. Its cultriform process is transversely compresed (Fig. 7).

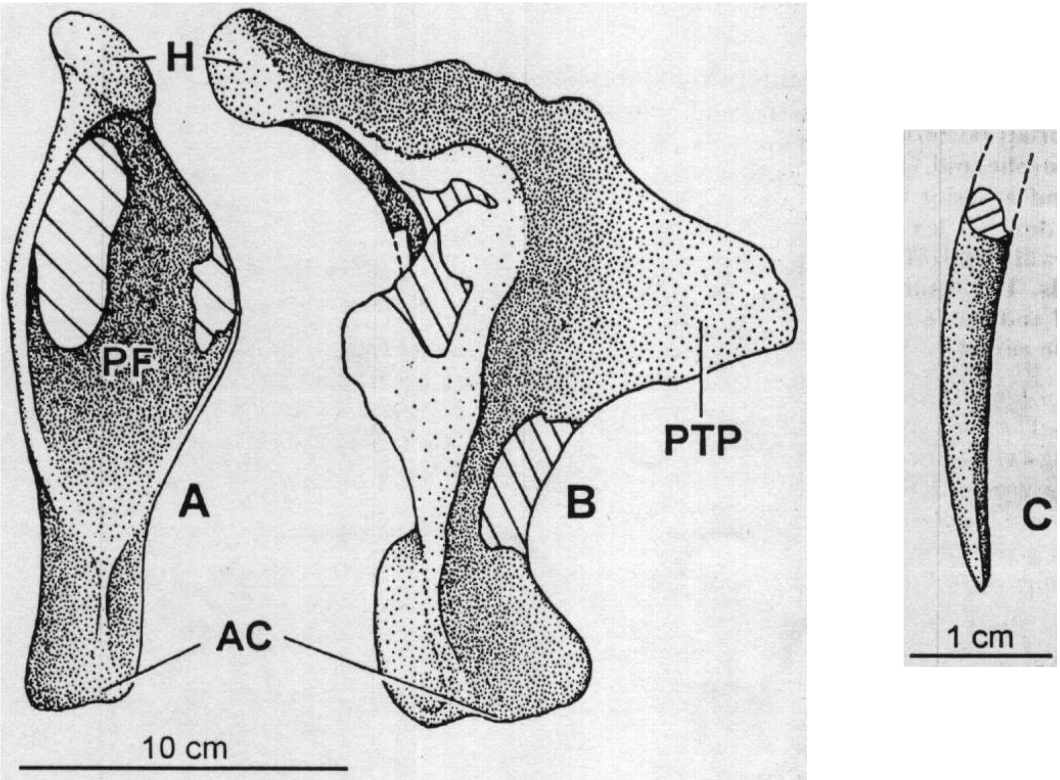


Fig. 6 - *Rebbachisaurus tessonei* sp. nov. Holotype. **A-B** - Rigth quadrate in posterior and lateral view. **C** - Tooth. Abreviations: AC -articular condyle, H - head, PF - posterior fossa, PTP - pterygoid process. Scale in centimeters.

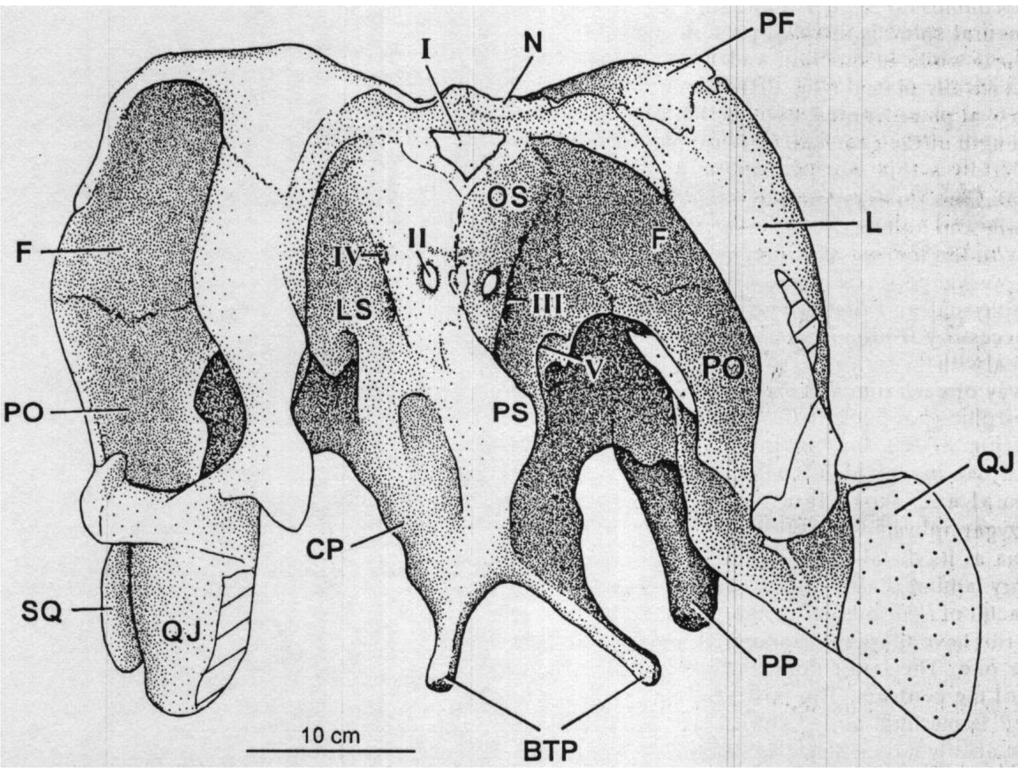


Fig. 7 - *Rebbachisaurus tessonei* sp. nov. Holotype. Skull in anterior view. Abbreviations as in Figure 3. Scale in centimeters.

The orbitosphenoids meet anteriorly (Fig. 7). They overlap posteriorly the frontal and anteriorly the laterosphenoid. The sutures are clearly seen in lateral and anterior views. The orbitosphenoids do not meet dorsally, leaving a large, subtriangular opening from which the olfactory tract emerged as in other sauropods. The sutural contact between the orbitosphenoid and the laterosphenoid is indicated by the exit of the spinal nerves II and IV (Fig. 4).

**Teeth** - OnIy a few isolated teeth was preserved (Fig.6C). The most complete is long, curved and slender having a circular cross section. Another tooth preserves the crown thaI is oval in cross section and it is slightly compressed. All teeth have unworn crowns ending in a very thin pencil-like tip. The crown tips of *Diplodocus* are broader than those of this specimen.

**Cervical vertebrae** - There are 8 cervical vertebrae preserved although probably 3 or 4 more vertebrae could have been present. Anterior cervicals are 1.5 times higlier than long (Fig. 8A); this ratio increases posteriorly reaching a value 2. The centra are strongly opisthocoelous. The narrow and single neural spine, placed in the middle of the centrum, is very tall, at least 1.5 higher than longer; this high ratio is shared with *Amargasaurus* and *Dicraeosaurus.* This is formed by four laminae, two suprapostzygapophysials, and two supraprezygapophysials, similar to those of *Haplocanthosaurus* HATCHER. In anterior cervicals the neural spine is inclined posteriorly as in *Amargasaurus* while in medium and posterior ones they are vertically placed (Fig. 8B). The centra bear two deep oval pleurocentral cavities that extend for half the length of the centrum. Cervical pleurocoelus are divided by a thin vertical septum or pleurocentral lamina. Tlie prezygapophysis are long and directed dorsally and anteriorly. The oval articular facets are flat with the longest axis directed anteroposteriorly. The prezygapophysis are reinforced by supraprezygapophyseal and diapoprezygapophyseal laminae. An accessory lamina connects the diapopostzygapophyseal with the supraprezygapophyseal lamina at the midway of each one and it is considered as an autapomorphic character of *Rebbachisaurus tessonei* sp. nov. (Fig. 8A-B). In posterior cervicals another accessory lamina is add; it is named a suprapostzygapophyseal accessory lamina and connects the postzygapophysis with the supraprezygapophyseal lamina at its distal end (Fig. 8B). This another accessory lamina is also considered an autapomorphic character of *Rebbachisaurus tessonei* sp. nov. The cervical ribs have short anterior branch and a longer posterior one. The latter does not reach the posterior face of the centrum. The postzygapophyses are preserved in medium and posterior cervicals, and they are relatively large. Articular facets are flat directed ventrally and internally. These articular facets are connected to the diapophyses by oblique postdiapophysial laminae and to the neural spine by suprapostzygapophyseal laminae. In the middle of the length of the infrapostzigapophyseal lamina is born another lamina that is connected to the neural spine. The short parapophyses are placed at the middle of the centrum and in ventral position. In lateral view, the diapophyses are reinforced by four laminae, two infradiapophysials and two supradiapophysials.

**Dorsal vertebrae** - There are 12 dorsal vertebrae preserved, four of them not complete. They are very tal. Pleurocentral cavities are present in an dorsals. The anterior ones have very small pleurocoels (Fig. 8D). The neural arch is very high bearing long transverse processes and a single neural spine (Fig. 8C-D). Anterior dorsals are strongly opisthocoelous with the centrum compressed latero and dorsoventrally. The neural arch is taller than that of the posterior cervicals, like those of *Haplocanthosaurus.* The neural canal is large and oval with the longest axis directed dorsoventrally. The neural arch, below the beginning of the neural spine is very high, at least twice as tall as the centrum.This height increases posteriorly. The diapophyses are placed at a lower level than the zygapophyses. Anterior dorsals lack hyposphene-hypantrum. The prezygapophyses are short with oval-shaped articular facets inclined axially. They are placed almost over the diapophysis. They are separated by a short diapoprezygapophyseal lamina oriented horizontally. The prezygapophyses are connected lo the neural spine through a supraprezygapophyseal lamina and to the centrum through a infraprezygapophyseal lamina; therefore, a long and deep channel is formed between laminae. Moreover, a preespinal !amina is present in between two supraprezygapophysial laminae.

The postzygapophyses are placed al a higher level than the prezygapophyses. The articular facets are large and oval in shape with the longest axis directed downward and toward the axial plane. The postzygapophyses are reinforced ventrally by a infrapostzygapophyseal and a diapopostzygapophyseal lamina (Fig. 8D). Dorsally they are reinforced by a suprapostzygapophyseal lamina and the suprapostzygapophyseal accessory lamina already seen in posterior cervicals. The suprapostzygapophyseal and infrapostzygapophyseal laminae form a long and deep channel. The four principal laminae that form the spine are connected dorsally forming an arc.

Toward the middle dorsals, the postzygapophysis are in contact with the neural spine and are closer to each other. In midposterior dorsals they are fused, as are the suprapostzygapophyseal laminae forming the postespinal lamina (Fig. 9); This pattern of postespinal construction is present also in *Apatosaurus exceisus* MARSH. The same occurs with both infrapostzigapophiseal laminae but they finally disappear in most medial dorsal.

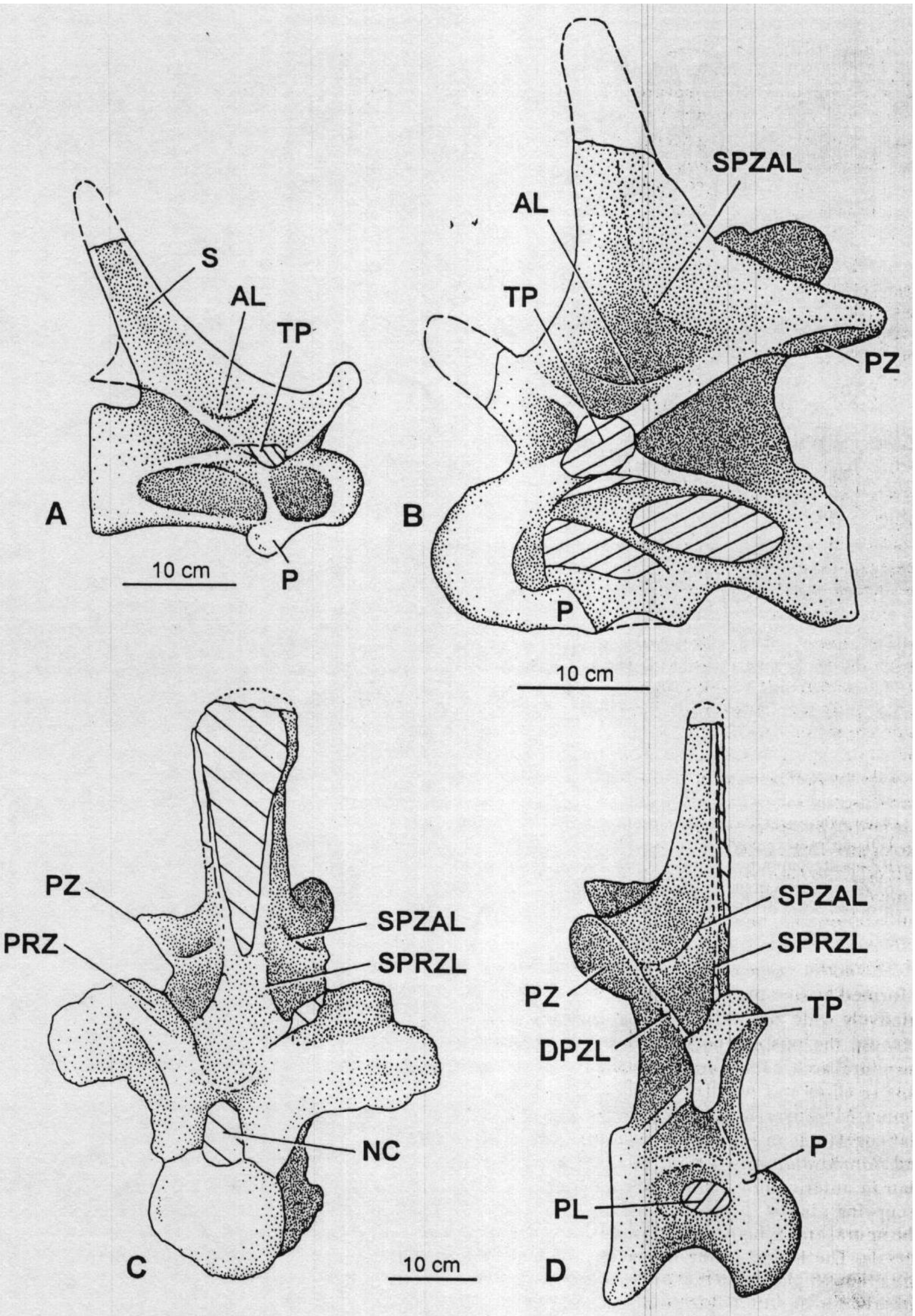


Fig. 8 - *Rebbachisaurus tessonei* sp. nov. Holotype. Cervical and anterior dorsal vertebra. **A** - Anterior cervical in lateral view. **B** - Posterior cervical in lateral view. **C, D** - Anterior dorsal vertebra in anterior and lateral views. Abbreviations: AL - accessory lamina, DPZL - diapopostzygapophyseal lamina, NC - Neural canal, P – parapophysis, PL - pleurocoel, PRZ - prezygapophysis, PZ - postzygapophysis SPRZL - supraprezygapophyseal lamina, SPZAL - suprapostzygapophyseal accesory lamina, TP - transverse process. Scale in centimeters.

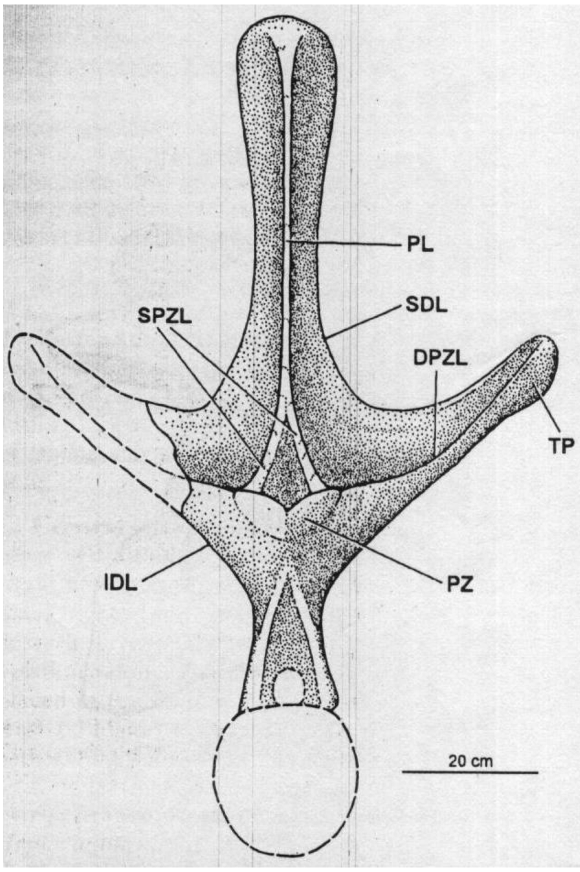


Fig. 9 - *Rebbachisaurus tessonei* sp. nov. MUCPv-206. Mid-posterior dorsal vertebra in posterior view. Abbreviations: DPZL- diapopostzygapophyseal larnina, IDL- infradiapophyseal lamina, PL- postespinal larnina, PZ- postzygapophysis, SDL- supradiapophyseal larnina, SPZL - suprapostzygapophyseal lamina, TP - transverse process. Scale in centimeters.

The neural spine of the posterior dorsal vertebrae is formed by one prespinal, one postespinal and two relatively wide supradiapophyseal laminae (Fig. 9). Because the postzygapophyses are almost fused to the neural arch, each diapopostzygapophyseal lamina runs to close and parallel to the supradiapophyseal lamina. Moreover, in posterior dorsals, the centra are platicoelus as in *Haplocanthosaurus*, Diplodocidae and *Barapasaurus* JAIN *et al.* The centra are longer than in anterior dorsals. Pleurocoels are very large occupying almost the entire Iength of the centrum. The neural arch is higher than in anterior and medium dorsals. The height of the neural arch is more than three times higher than that of the centra in posterior dorsaís similar to Diplodocidae and *Andesaurus* CALVO & BONAPARTE.

**Sacral vertebrae -** Two small sacral fragments were found in the holotype; but one complete sacral centra was found in MUCPv-153 showing both end amphyplatian.

**Caudal vertebrae -** Forty articulated caudal vertebrae are preserved in the holotype. The vertebral centra are platicoelous (Fig. 10B); the most anterior centra are short and high. Posteriorly, the centrum decrease in height but increase in length. The lateral side is slightly concave. The ventral side in anterior and middle caudals is flat, with a wide longitudinal groove that disappears in posterior caudals. The most anterior caudals present robust, short and relatively wide transverse processes directed upward and forward (Fig. 10A); although no true wing-like processes are present, the dorsal component of the transverse process is well developed as in diplodocids. In MUCPv-153 the most anterior caudals were articulated; the first three showed a perforated transverse process, that is formed by a dorsal (diapophysis) and a ventral (parapophysis) bar as in *Apatosaurus* (Fig. l0C). This condition differs from that of *R. garasbae* in which the transverse processes are typical wing-like as in Diplodocidae.Therefore, we think that the ancestral condition for *Rebbachisaurus* is the presence of wing-like transverse process. The condition in *R. tessonei* sp. nov. is an autapomorphy. The neural arch in anterior caudals is twice higher than the height of the centra, as in *Dicraeosaurus*, and it is born on the anterior border of the centrum. The neural spine in these caudals is formed by a prespinal, postespinal and two lateral laminae (Fig. 10A-B). Each lanima becomes thicker and slightly wider ending in a bulky bone. The neural arches in medium and posterior caudals are placed on the middle of the centrum and decrease in height (Fig. 11). In anterior view, the centra has a semilunar shape with the concavity ventrally placed. The neural spines are triangular in shape becoming laterally compressed lacking the lateral laminae present in the anterior ones. The spine extends backward over the posterior border of the centrum (Fig. 11A-B). The dorsal border of the spine is straight in middle caudals (Fig. 11A). The prezygapophysis are long extending anteriorly over the anterior border of the centrum. The postzygapophysis are long and well developed. The middle and posterior caudals have a very short spine with the dorsal border inclined foreward (Fig. 10B). The posterior caudal vertebrae are long and very thin pencil-like (Fig. 1IC-D). The tail is whip-lash like those in *Diplodocus* and *Barosaurus* MARSH.

**Chevron -** The tail is complete and only the anterior caudals bear chevrons. Anterior chevrons are unforked and the proximal ramus are unfused as in *Haplocanthosaurus*, brachiosaurids and camarasaurids.

**Scapula -** Both scapula are preserved (Fig. 12A). They are long and very wide, rectangular in shapes with acute corners. Both distal and proximal ends are

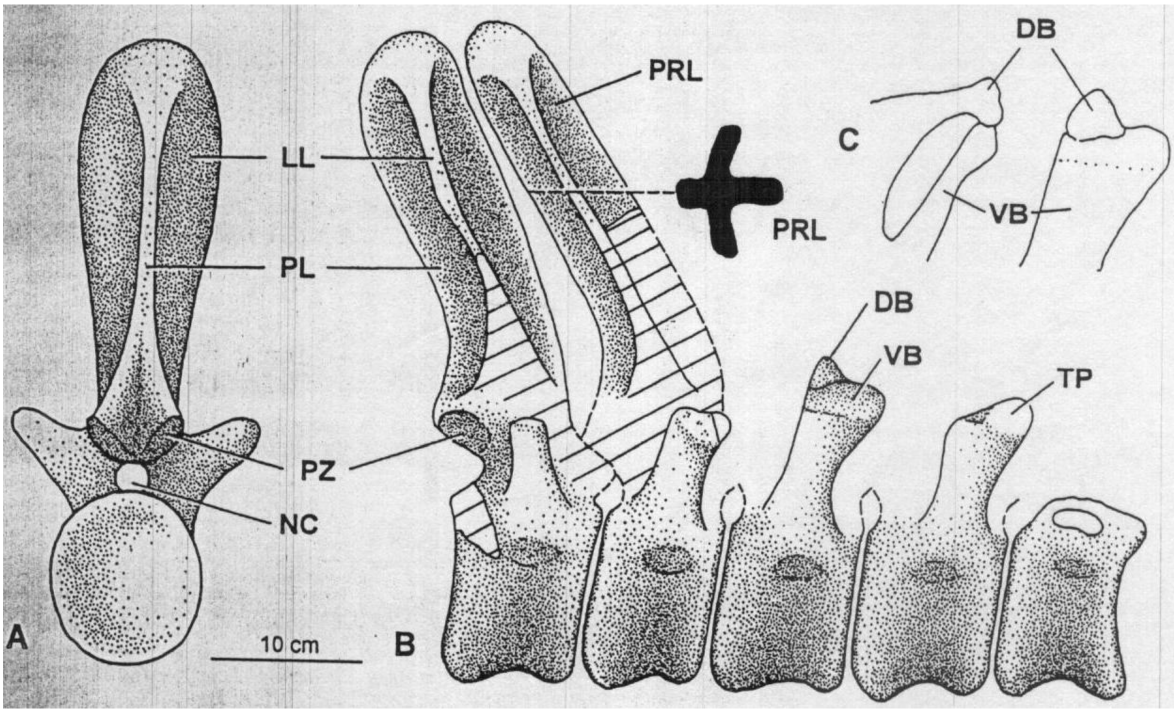


Fig. 10 - *Rebbachisaurus tessonei* sp. nov. MUCPv-153. Anterior caudal vertebra. **A** - Fifth caudal vertebra in posterior view. **B** - Caudals 1-5 in lateral view. **C** - Transverse process of caudal 3 in posterior and lateral views. Abbreviations: DB - dorsal bar, LL – lateral lamina, NC - neural canal, PL - postespinal lamina, PRL - preespinal lamina, TP – transverse process, VB - ventral bar. Scale in centimeters.

expanded. The former is paddle-like as in *Rebbachisaurus garasbae* and as broad as in *Haplocantosaurus priscus* in which the maximum wide is three times wider than the minimun ones. The proximal end is thick in its contact with the coracoids. In dorsal view, the scapula is slightly curved. In lateral view, a ridge born froin its anteromedial border goes to the posteroinferior border. The acromion is thick, acute and directed upward.

**Coracoid** - Both coracoids are preserved (Fig. 12A). Coracoids have trapezoidal shapes with a robust glenoid articular surface for the humerus. The glenoid cavity is thick, and it forms 1/3 of the socket. The articulation with the scapula is a broad and relatively long surface. The coracoid foramen is closed and oval in shape.

**Sternal plate** - The sternal plate is very bad preserved in the holotype, but it is complete in MUCPv-206. The sternal plate is a semilunar, laminar and thin bone. The lateral border is concave while the medial one is convex. This shape is also present in Titannosauridae, but we consider this character an autapomorphy of *Rebbachisaurus tessonei* sp. nov.

**Humerus** – The left humerus and the proximal end of the rigth one are preserved (Fig. 12B). The humerus is robust, relatively short (90 cm in length). The humerus/femur ratio is 0.62. It is less than 0.70 as in Diplodocids. The deltoid crest is placed near the proxinial end. It is high with rounded corners, and is inclined with respect to the humeral axis. The internal tuberosity is well marked. The proximal corner is straight and slightly convex. The diaphysis is robust and subcircular in section. The anterior depression of the proximal end is wide and subtriangular in shape. The distal end is smaller than the proximal one. The entepicondyle and ectepicondyle are not well marked.

**Ulna** - Only the left ulna is preserved (Fig. 12C). The ulna of 66 cm of length is straight and thin. The robust proximal end is triradiate. The diaphysis is subcircular in cross section. The medial face is the widest; the proximal half is concave forming sharp angles with the other faces. The antero-lateral face is almost flat. The distal articulation is thin, and a little expanded posteriorly. The distal corner is convex with a small depression in the anterolateral face. The Ulna/tibia ratio is 0,78.

**Radius** - The left radius is preserved (Fig. 12 D). The radius is elongated and it has 69 cm of length; the diaphysis is straight and oval in cross section. The expanded distal end is asymmetrical. The ulnar face is slightly convex. It is marked by a ridge. It begins on the posterior proximal end and lasts in the middle of the diaphysis; from there, a bulge occurs in the middle of the distaI end of the sane ulnar face. The proximal articulation is slightly concave and quadrangular in shape. The antiulnal face is flat.

**Metacarpals** - The holotype does not preserve metacarpals but they are preserved in MUCPv- 206. Despite that MUCPv-206 is a bigger animal than the holotype, according to the cervical and dorsal vertebra sizes, the metacarpal III? of MUCPv-206 is only a 30% of the radius length of the holotype. This comparative evidence shows that metacarpal II-III - radius length ratio in the holotype should have been smaller than 0.45 as in other diplodocids and primitive sauropods. Four metacarpals are preserved in the *Rebbachisaurus* MUCPv-206. They were found disarticulated, so that the position of them is uncertain. Metacarpais II-IV and V are well preserved but slightly crushed. Metacarpal III is incomplete.

Metacarpal II? is long (20 cm) and much the widest bone of the series, the proximal end is compressed, the articular surface is rugose and oval in shape. It has a notch on the medial side to articulate with metacarpal III. The anterior surface is relatively flat and smooth. The distal end is expanded into a subacuminate process on its infero-mesial margin. The distal articular surface is rugose, concave latero-mesially. The posterior surface is convex with a smooth ridge coming from its upper-rnesial border to the lower-lateral border. Metacarpal III? (20.5 cm) is the longest of the series. It is slender than Mc II. the proximal portion is incomplete as well as a small portion of the middle of the shaft.The anterior surface is convex proximally and flattened distally. The distal articular surface is wider than the proximal one, and it has a subcuadrangular shape. The shaft is oval in cross section. The posterior surface, not well preserved, has a ridge in the middle of the medial side. Metacarpal IV? (19 cm) is shorter than Mc II and III, and more slender than Mc III. It is greatly constricted internally making the shaft cross section of subtriangular shape. The proximal articulation is very broad and subcircular. The anterior view is flat proximally and convex distally. The posterior view is convex proximally and strongly convex distally. The distal articulation has a subcircular shape. The medial border has a ridge in its proximal half. Metacarpal V? (17 cm) is the shorter of the series. It is wider than Mc III and more

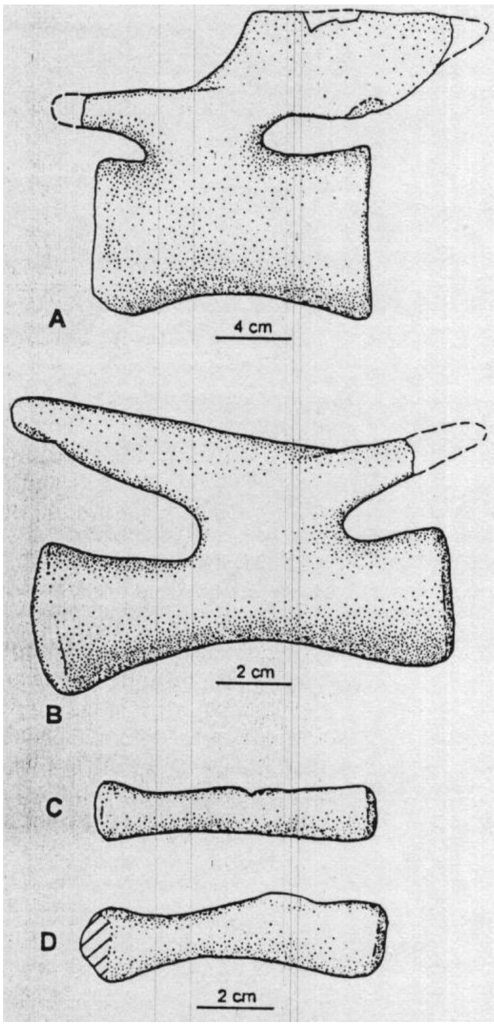


Fig. 11 - *Rebbachisaurus tessonei* sp. nov. Holotype. Caudal vertebrae. **A** - Middle caudal. **B** - Mid-posterior caudal. **C, D** - Posterior caudals. Scale in centimeters.

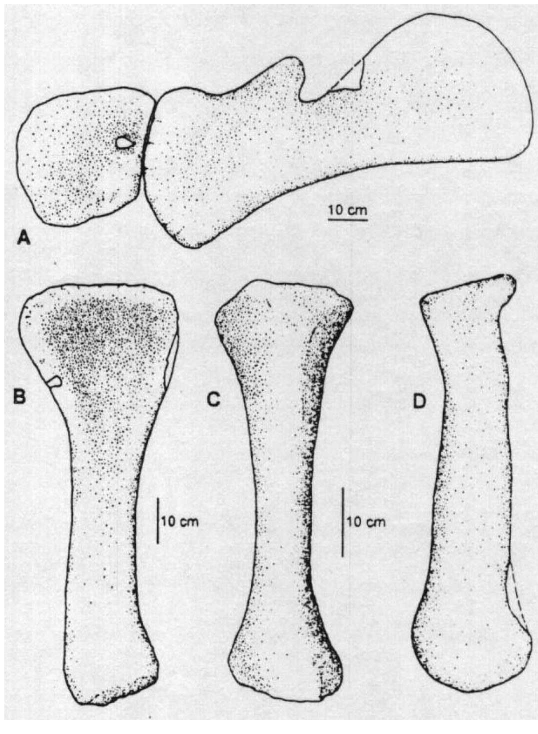


Fig. 12 - *Rebbachisaurus tessonei* sp. nov. Holotype. Pectoral girdle and fore limb. **A** - left scapulo-coracoid in lateral view. **B** - Left humerus in anterior view. **C** - Left ulna in lateral view. **D** - left radius in anterior view Scale in centimeters.

robust than Mc II and III. The anterior surface is convex with a twisted and smooth ridge coming from its upper-lateral side to the lower-medial side. The proximal end has a subcuadrangular shape and the articulation has an oval shape. The posterior side is smooth and flat. The widest portion is on the proximal end.

**Ilium** - The left ilium is not well preserved; it is short and low (Fig. 13). The ventral border, behind of the acetabulum, is slightly convex forming a reduced preacetabular lamina. The postacetabular process is also small. The pubic peduncle is wider mediolaterally than anteroposteriorly. The ischial peduncle is poorly exposed. The articular surface of the acetabulum belongs mostly to the ilium, The anterior corner of the ilium is directed upward and forward.

**Pubis** - Both pubes are preserved (Fig. 13). The pubis is long (98 cm) and straight. The shaft is massive and rounded in section a character not developed in any other sauropod. The ischial and pubic peduncle form an angle of more than 100°. The pubic foramen is apparently open and oval in shape. The acetabular surface of the pubis is small. Both the ischial and the iliac articulation are reduced. The ambiens process is not present as that of *Diplodocus* and *Apatosaurus.*

**Ischium** - Only the rigth ischium of the holotype is preserved (Fig. 13-14). The ischium has smaller areas for articulation with the ilium and pubis; between them there is a deep and well-marked concavity forming part of the acetabulum. The ischium is long (94 cm) with the ischionic shaft long and thin occupying approximately the 80% of its length. It takes the shape of a twisted shaft. The distal end is thin and narrow; it has almost the same size as the shaft.

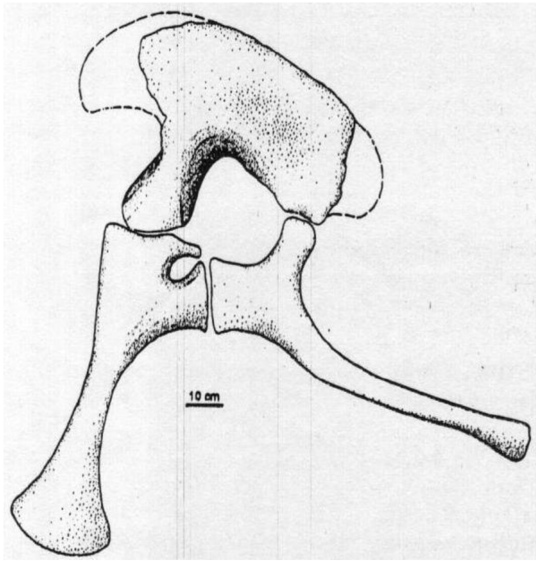


Fig. 13 - *Rebbachisaurus tessonei* sp. nov. Holotype. Reconstruction of the pelvic girdle in lateral view. Scale in centimeters.

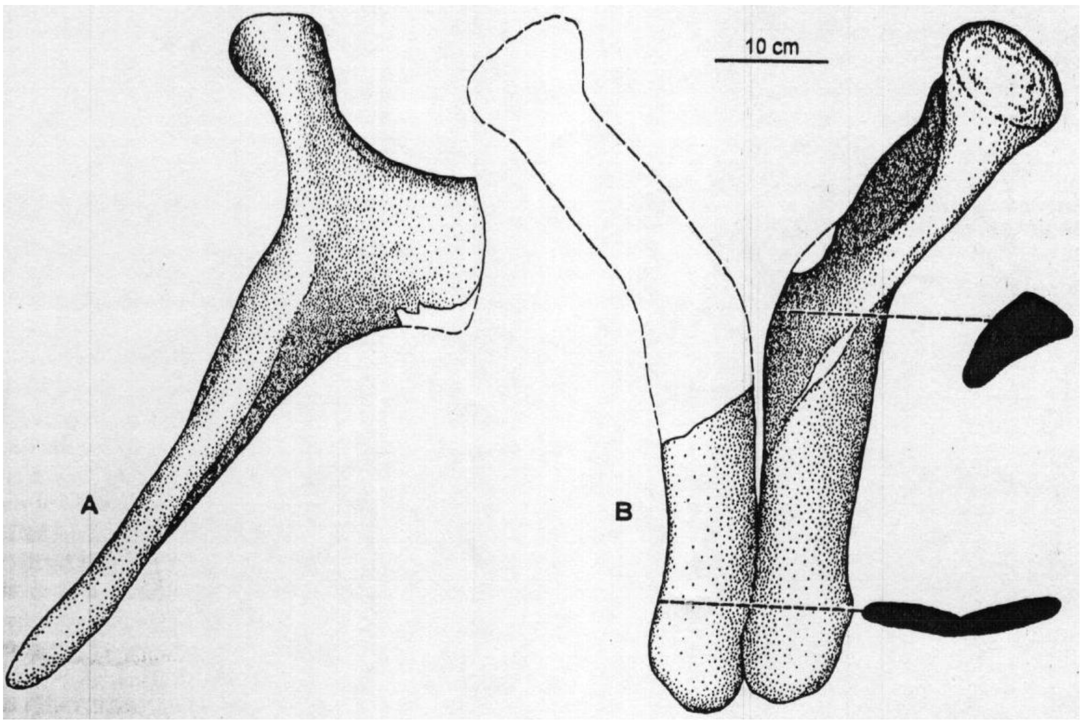


Fig. 14 - *Rebbachisaurus tessonei* sp. nov. MUCPv-153. Ischia. **A** - in lateral view. **B** - dorsal views. Scale in centimeters.

Both ischia contact side by side horizontally (articulated in MUCPV-153) as in *Brachiosaurus* and *Haplocanthosaurus priscus* (Fig. 14). The pubic peduncle is small but it is bigger than the iliac peduncle. The proximal region has an apparently reduced ventral keel (obturator process).

**Femur** - The complete Ieft femur and the distal part of the right one are preserved (Fig. 15A). The femur is robust, straight and long (144 cm). In a posterior view the greater trochanter, placed on the upper third portion, is restricted lo a small longitudinal bulge. Thus, the lateral projection of it is thin showing sharp corners. In lateral view, the medial condyle is better developed than the lateral one on the distal end. The lateral bulge is not prominent. Distal condyles are separated by a deep intercondylar groove. Thr fourth trochanter is not well preserved, but appears to be poorly developed, above midlength of the femur.

**Tibia** - Both tibiae are preserved (Fig. 15B). The tibia of *Rebbachisaurus tessonei* sp. nov. (85 cm in length) is considerably shorter than the femur. It has suffered postmortem deformation. The distal end is more broadly expanded transversely than the proximal one. The proximal end is much more developed anteroposteriorly than the distal end. The articular surface of the tibia is almost flat. The tibia/femur ratio is 0.55.

**Fibula** - Both fibulae are preserved (Fig. 15C). The fibula is much more slender than the tibia and slightly exeeeds it in length (88 cm). In lateral view it has a sigmoid shaped. The external face is convex along its length and above its midlength is a vertically ovale roughened tubercle for insertion of M. iliofibularis. The internal face is flat except at the proximal end where it is convex. The proximal end is slightly expanded antero-posteriorly. The whole bone is flattened transversely.

**Astragalus** - The left astragalus is partially preserved; only the distal end of the tongue is missing. In proximal view it is triangular; a eoncavity developed on the posteromedial surface fits into the blunt knob of the tibia. The convexity developed on the anteromedial surface receives the concave arca of the distal end of the tibia. Laterally, the astragalus is concave to receive the expanded projection from the mesiodistal end of the fibula. The distal surface of the astragalus is broadly convex.

**Metatarsals** - Metatarsals are deformed by compression and they were not found articulated. Metatarsals II, IV and V were found in both feet, and Metatarsal I of the right foot (Fig 16). Metatarsal I is the shortest and stoutest bone of the series. It is constricted medially. The proximal end is expanded anteriorly and transversely. The distal end is expanded anteriorly and compressed transversely. The

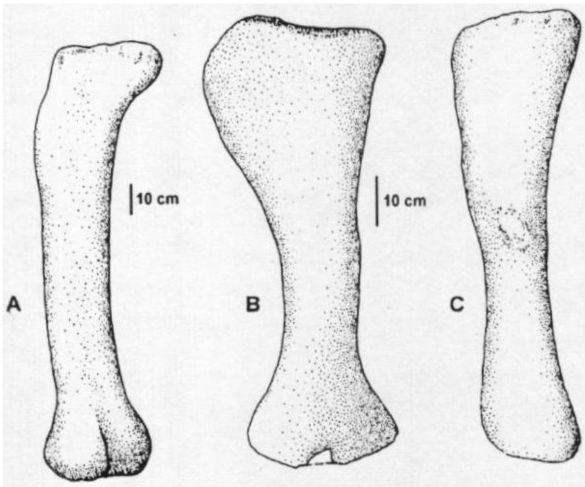


Fig. 15 - *Rebbachisaurus tessonei* sp. nov. Holotype. Hind limb. **A** - Left femur in posterior view. **B** - Rigth tibia in medial view. **C** - Left fibula in lateral view. Scale in centimeters.

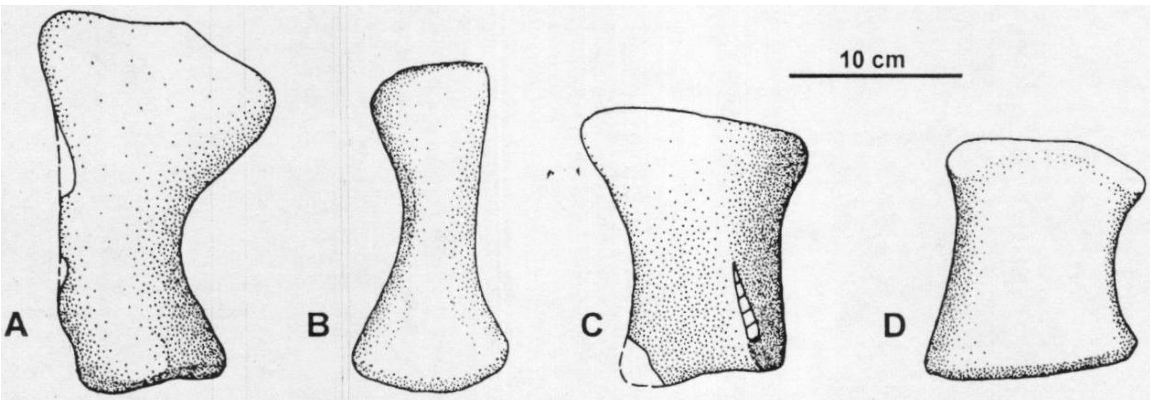


Fig. 16 - *Rebbachisaurus tessonei* sp. nov. Holotype. Rigth metatarsals. **A** - V. **B** - IV. **C** - II. **D** – I in anterior views. Scale in centimeters.

proximal surface is nearly flat. The medial proximal end is concave anteroposteriorly for articulation of the Metatarsal II. Metatarsal II is stout and slightly longer than metatarsal I. The proximal end is wider than the distal one. A prominent ridge is developed on the anterior surface from the distal end and extends diagonally up the middle of the proximal end. The distal articular end presents a convex articular surface anteroposteriorly but is concave transversely. Metatarsal III is missing. Metatarsal IV is longer and much more slender than Metatarsal II. There is a prominent carina running dorsoventrally on the posterior side. The proximal articular surface is flat. Metatarsal V is the longest preserved; it is greatly expanded proximally and little enlarged distally. The distal end, in ventral view, has a quadrangular shape. On the lateral distal end there is a prominent notch. Both falanges I are preserved; they are short. The proximal end is broader anteroposteriorly than transversely, and it has an elongated oval curved shape. In anterior view, falange I has a semilunar shape; both the proximal and distal condyles have projections from their posterolateral corners, and a deeply concave rim unites both corners. The medial rim is strongly convex.

**Gastroliths -** Gastric stones are rarely associated to sauropod bones (CALVO 1994a; 1994c). However, in the *Rebbachisaurus tessonei* sp. nov. holotype (MUCPv-205), we have found six gastric stones together in an abdominal position; two of them were adhered to the ribs. Five stones weighed from 350 to 375 g, but the other one weighed 850 g. The stones are igneous rocks, some granties and some quarzitic. They have rounded and rugose surfaces. The stones are not highly colored. MUCPv-206 also preserved six stones in between its ribs and dorsal vertebra they weighed from 190 to 420 g.

## DISCUSSION AND COMPARISONS

The discovery of the nearly complete sauropod *Rebbachisaurus tessonei* sp. nov. has forced a reconsideration of the phylogenetic relationships of the genus *Rebbachisaurus garasbae.* Both *R. tessonei* sp.nov. and *R. garasbae* are contemporary. *R. garasbae* is represented by very few bones, which, though incomplete allows some comparison witlh the complete *R. tessonei* sp. nov. The synapomorphic characters of both genera are: 1) Broadly expanded scapular blade with rounded distal rim paddle-like. The scapular blade in *Rebbachisaurus* is very broad and racket-like with the distal rim rounded. The major expansion of the blade is at a half of its length. In prosauropods and other diplodocids there are a small expansion exactly on the distal end, but not in the complete blade. The widest expansion is seen in *HapIocanthosaurus* (HATCHER, 1903;MCINTOSH & WILLIAMS, 1988) but this is fan-like. In *Camarasaurus,* and *Brachiosaurus* only the third distal end of the scapular blade is expanded, but lesser than that of *Rebbachisaurus.* Therefore, we consider this a sinapomorphy character for *Rebbachisaurus.* 2) V-shape angle between the acromion and the scapular blade. 3) Absence of hyposphene-hypantrum in posterior dorsals. The hyposphene-hypantrum is plesiomorphycally present In all sauropods except in the most derived genera of Titanosauridae. We consider this character a sinapomorphy for *Rebbachisaurus.* 4) Tall neural arch and, although it is a primitive character. 5) Single neural spine. 6) Parapophysis directed upward at approximately 45°. Up to now only one autapomorphic character in *R. tessonei* sp. nov., no true wing-Iike transverse process in anterior caudals, differences it from *R. garasbae.*

MCINTOSH (1990a) also recognized that a dorsal vertebra described and illustrated by NOPCSA (1902) resembles that of *R. garasbae.* Nopcsa's vertebra was collected in the Alarcon Barda, 80 km southwest of Neuquén City, Patagonia Argentina. Coincidentally the type and other specimens described and illustrated here as *Rebbachisaurus tessonei* sp. nov. came from the same area. Therefore, McIntosh's assignment is certainly correct in including the Nopcsa's vertebra as *Rebbachisaurus,* now *Rebbachisaurus tessonei* sp. nov. Finally one more species of *Rebbachisaurus* was described and illustrated by LAPPARENT (1960) as *Rebbachisaurus tamesnensis.* However, such as MCINTOSH (1990a) recognized, that species does not belong to *Rebbachisaurus,* at least by having the following characters: presence of spoon shaped teeth, slightly distal expansion of the ischium and presence of Hyposphene-hypantrum in dorsal vertebrae. *R. tamesnensis* is excluded in the present analysis from belonging to the Diplodocimorpha. We believe "*R. tamesnensis"* is a camarasaurid such as Lapparent proposed.

Several cranial and postcranial charaeters of *Rebbachisaurus tessonei* sp. nov. are not present in other sauropods and are regarded here as autapomorphies (see TABLE I an Appendix for character-state distributions). 1) Basipterygoid processes very thin and short. In *Rebbachisaurus tessonei* sp. nov. the shortness together with the extreme slenderness of the basipterygoid processes is not seen in other Sauropods. In prosauropods, *Camarasaurus* and Titanosauridae, they are short but robust; in *Diplodocus, Apatosaurus, Amargasaurus,* and *Dicraeosaurus* they are long and relatively slender, although they are more robust than in *R. tessonei* sp. nov. 2) Infratemporal fenestra almost closed. The quadratojugal, squamosal, postorbital and jugal form a big triangular infratemporal opening in Prosauropoda, *Camarasaurus, Brachiosaurus* and Titanosauridae (CALVO, 1994a, 1994b). It is oval and anteroposteriorly elongated in *Diplodocus* and *Apatosaurus* and more reduced in *Amargasaurus* and *Dicraeosaurus.* In *R. tessonei* sp. nov. the infratemporal fenestra is

TABLE I
Character and taxon matrix.

| TAXON | CHARACTER | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 5 | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 49 |
| PROSAUROPODA | 00000 | 00000 | 00000 | 00000 | ?0?00 | ???00 | 00?00 | 00000 | 00000 | 0000 |
| *Barapasaurus tagorei* | ?00?? | ????? | ????0 | 00000 | 00?00 | 00000 | ?0??? | ????0 | 00000 | ?0?0 |
| *Omeisaurus* | 00000 | 00000 | 00001 | 00000 | 01001 | 00000 | 00000 | 01000 | 00010 | 100? |
| *Camarasaurus* | 00100 | 00000 | 00001 | 01010 | 01001 | 00000 | 00010 | 00100 | 10010 | 1001 |
| *Brachiosaurus* | 01100 | 00000 | 0?011 | 0000? | ?1?01 | 11000 | 00011 | 00101 | 10110 | 1101 |
| *Andesaurus delgadoi* | ????? | ????? | ????? | ????? | ???11 | 11011 | 00?11 | ?0??? | 10011 | 1101 |
| TITANOSAURIDAE | 011?0 | 0000? | 01011 | 00?00 | 01101 | 21012 | 00011 | 00011 | 10011 | 1101 |
| *Haplocantosaurus delfsi* | ????? | ????? | ????1 | 00001 | 01100 | 2?000 | 00010 | ?0100 | 00000 | 10?? |
| *Haplocantosaurus priscus* | ????? | ????? | ????1 | 00001 | 01100 | 21000 | 00010 | ?02?0 | 00110 | 10?? |
| *Rebbachisaurus tessonei* | 02101 | 11111 | 110?1 | 10101 | 11110 | 21000 | 02210 | 10210 | 00110 | 1010 |
| *Apatosaurus lousiae* | 12111 | 11010 | 10021 | 01011 | 01010 | 21001 | 01?00 | 1?0?0 | 01000 | 0010 |
| *Diplodocus* | 12111 | 11010 | 10021 | 01010 | 01010 | 21001 | 11100 | 11000 | 01000 | 0010 |
| *Barosaurus lentus* | ????? | ????? | ????1 | ?1?10 | 01010 | 21001 | 11100 | 1100? | ?10?? | ?0?? |
| *Dicraeosaurus* | ?21?? | 1???1 | ?1120 | 11011 | 10010 | 21101 | 01200 | 110?0 | 01000 | 0010 |
| *Amargasaurus cazaui* | ????? | 1?111 | ?11?0 | 11111 | 10?10 | 21101 | 0??00 | ??1?0 | 0???? | ?01? |

vestigial slit shaped. 3) Posterior process ol Postorbital absent. In *R. tessonei* sp. nov. the postorbital, in lateral view, has the posterior and anterior border perfectly curved; therefore, no trace of a postorbital process is present. This condition has not been reported elsewhere among dinosaurs. 4) The articular condyle of the quadrate is elongated anteroposteriorly, the length is 4 times the width; in *R. tessonei* sp. nov., it is elongated anteroposteriorly. In sauropod outgroups, *Camarasaurus, Brachiosaurus,* Titanosauridae and in other diplodocids the articular condyle, in ventral view, is of triangular shape. This shape contrasts strongly with that of *R. tessonei* sp. nov. in which it is rectangular. A similar articular condyle is apparently present in *Quaesitosaurus* (KURZANOV & BANIKOV, 1983), regarded as an advanced titanosaurid with a brachiosaurid-like skull (CALVO, 1994a, 1994b). In the context of all the evidence, we think that this character was developed independently both in *Quaesitosaurus* and *R. tessonei* sp. nov. 5) Basal tuberas very reduced. In *R. tessonei* sp. nov. the basal tuberas seem to have been very reduced. In other sauropoda and other dinosaura basal tuberas are bulbous and well developed. 6) Paraoccipital process not distally expanded. The distal portion of the paraoccipital process in *R. tessonei* sp. nov. is narrow and straight. This configuration of the distal part of the paraoccipital process is unknown among diplodocids and sauropod outgroups. However, narrow distal end of the paraoccipital process is present in derived Titanosauridae such as *Antarctosaurus* (HUENE, 1929) and *Saltasaurus* BONAPARTE & POWELL (POWELL, 1986). The difference between the paraoccipital process in those Titanosauridae and *R. tessonei* sp. nov. is that in the former they are curved inward the skull plane axis. 7) Neural spine in cervicals bears an accessory lamina connecting the diapopostzygapophyseal with the supraprezygapophyseal lamina al midway of each one. Prosauropods have simple neural spine without the neural spine complexity present in sauropods. In *Barapasaurus* (JAIN *et al.,* 1979), some "cetiosaurids" such as *Patagosaurus* (BONAPARTE, 1979) *Cetiosaurus medius* (MARTIN, 1987: fig. 1) we can only see the diapopostzygapophyseal and the suprapreziygapophyseal laminae; in lateral view, a slight concavity is developed between these laminae. In other sauropods a deep concavity is enclosed by the diapopostzygapophyseal, the supraprezygapophyseal and the suprapostzygapophyseal laminae. In *R. tessonei* sp. nov. that deep concavity is divided by an accessory lamina that connects the supraprezygapophyseal and the diapopostzygapophyseal laminae. 8) Neural spine in posterior cervicals and anterior dorsals present a suprapostzygapophyseal accessory lamina that connects the postzygapophysis with the supraprezygapophyseal lamina at its distal end. In other Sauropoda the area enclosed, by the diapopostzygapophyseal, the suprapostzygapophyseal and the supraprezygapophyseal, does not present any accessory lamina as that. 9) Anterior dorsals with both supraprezygapophyseal laminae contacting on the top of the spine.

In sauropods with unforked neural spines, the supraprezygapophyseal lamina in anterior dorsals is placed anterolaterally rising upward. These laminae either disappear or form a massive bone on the top of the spine. In *R. tessonei* sp. nov. both laminae reach each other on the top of the spine following its curvature. Therefore, both supraprezygapophyseal laminae contact each other forming an arc. This character is not seen in other sauropod. 10) Transverse processes in anterior caudals formed by a dorsal (diapophysis) and a ventral (parapophysis) bar directed upward. 11) Sternal plate of semilunar shape. This condition is also present in derived Titanosauridae. Th condition in *R. tessonei* sp. nov. is interpreted as an autapomorphic character of this genus. 12) Shaft of the pubis oval in cross section. The pubis is an elongated bone in which the distal end is separated from the proximal one by a long and slender shaft. Tiis morphology is unknown atiiong otuer sauropods in which the shaft of the pubis is somewhat platelike.

**PHYLOGENETIC RELATIONSHIPS OF *REBBACHISAURUS TESSONEI* SP. NOV.**

The phylogenetic relationships of *Rebbachisaurus tessonei* sp. nov. were investigated by a phylogenetic analysis using the branch-and-bound option of PAUP 3.0.The taxa analyzed were 13 sauropod species, the monophyletic Titanosauridae and the monophyletic Prosauropoda. Characters were polarized using Prosauropoda, *Barapasaurus* and *Omeisaurus* YOUNG as outgroups. *Camarasaurus, Brachiosaurus, Andesaurus,* Titanosauridae, *Haplocanthosaurus priscus, H. delfsi* MCINTOSH & WILLIAMS and *Rebbachisaurus tessonei* sp. nov. were used as terminal taxa.

For the analysis, 49 cranial and postcranial characters were employed, none of which were autapomorphic for any terminal taxa. The analysis yielded one parsimonious tree with 85 steps and a consistence index of 0.655. The tree summarizing these results is provided in Fig. 18. The present evidence suggests that the genera within the family Diplodocidae:*Apatosaurus, Diplodocus, Amargasaurus, Dicraeosaurus* and *Barosaurus* form a monophyletic clade as has already been demonstrated by BERMAN & MCINTOSH (1978), MCINTOSH (1990a) and YU (1993). We have excluded from this family to *Nemegtosaurus* NOWINSKY and *Quaesitosaurus* for belonging to Titanosauridae (CALVO, 1994a, 1994b; SALGADO, CORIA & CALVO, *in press*; SALGADO & CALVO, *in press).*

Several synapomorphies unite *Rebbachisaurus tessonei* sp. nov. with Diplodocidae: (1) Pencil like teeth, (2) Anterior extetision of tíle quadratojugal placed beyond the anterior border of the orbit, (3) Anteriorly directed basipterygoid processes, (4) Quadrate inclined posterodorsally, (5) Infratemporal fenestra oval or slit shaped, (6) Narial opening placed above

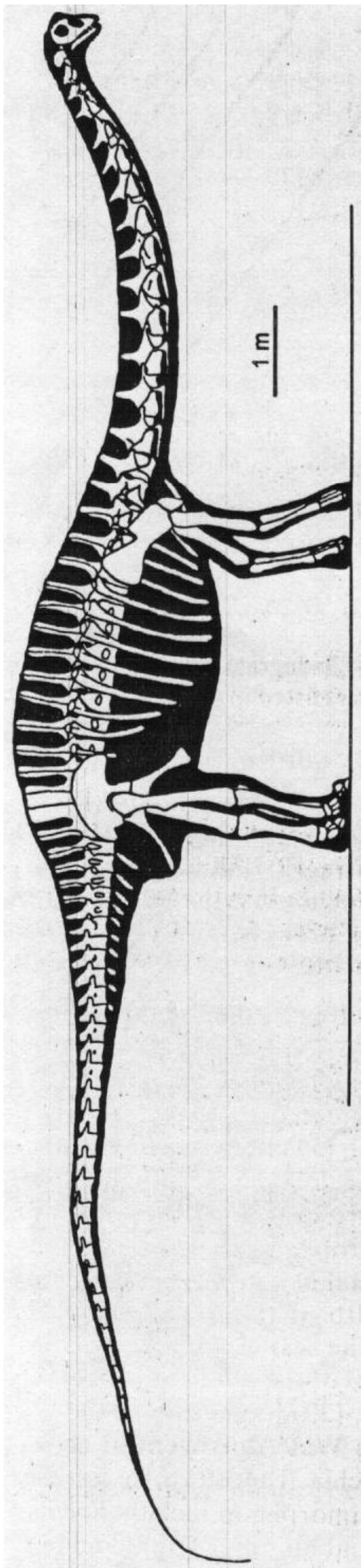


Fig. 17 - *Rebbachisaurus tesonei* sp. nov. Holotype. Reconstruction of the skeleton. Scale 1 m.

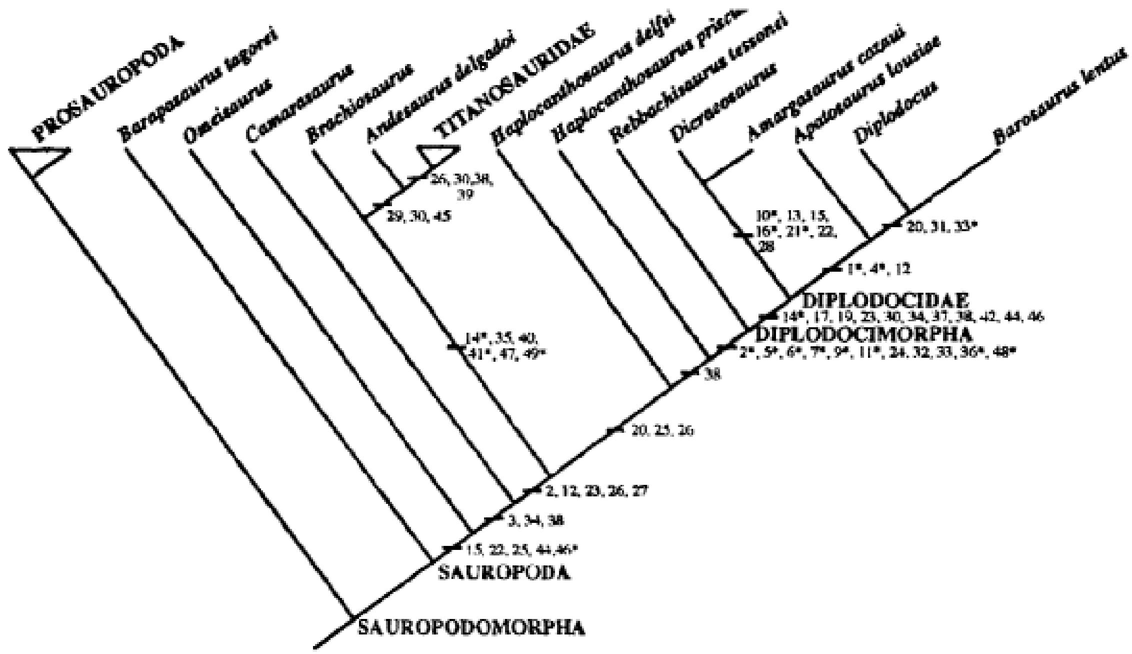


Fig. 18 - Cladogram showing relationships of *Rebbachisaurus tessonei* sp. nov. among Sauropoda. Numbers refer to derived characters usted in the Appendix (asterisked characters have ambiguous optimization).

the orbit, (7) Whip-lash tail, (8) Tall neural arch in posterior dorsals being three times higher than that of the centra, (9) Tall neural arch in caudals; at least 1.5 times higher than that of the centra, (10) Wing-like transverse process, and (11) humerus/femur ratio less than 0.70.

By contrast, other synapomorphies that characterizes the Diplodocidae are not present in *Rebbachisaurus tessonei* sp. nov.: (12) Cervical neural spine bifurcated, (13) Anterior dorsal neural spine bifurcated, (14) Presence of Hyposphene-hypantrum in anterior dorsals, (15) Slightly procoelous anterior caudal vertebras, (16) Presence of rnidcaudal chevrons with fore and aft directed processes, (17) Closed hemal canal in anterior caudals, (18) The ratio maximum width of the distal scapular blade/minumun width of the scapular blade is 2, (19) Presence of the prominent of the ambiens process in anterior part of the pubis, (20) Expansion of the distal end of the ischia, (21) Wide dorsoventral contact of both distal ends of ischia. Therefore, we have erected a new taxa Diplodocimorpha to include *Rebbachisaurus tessonei* sp. nov. and all other Diplodocidae presenting characters 1 to 11. Diplodocidae is considered the sister group of *Rebbachisaurus tessonei* sp. nov. presenting characters 12-21.

The present analysis has shown that *Haplocanthosaurus* is a paraphyletic taxon. *"H." delfsi* shares with *"H." priscus* + Diplodocimorpha the following characters: 1) The high of the neural arch in anterior dorsals is at least three times longer than the length of the centra; 2) Dorsal centra in posterior dorsals are amphyplatian or amphycoelus; and 3) Mid-preespinal lamina in posterior dorsals occupy all the length of the spine. *"H."priscus,* in turn, is considered the sister gro up of the Diplodocimorpha by having a distal scapular blade widely expanded (maximum width/minimum width > 3). Unfortunately, no part of the skull in *"H." priscus* and "H." *delfsi* is known; therefore, several cranial characters here considered diagnostic for Diplodocimorpha could be synapomorphies of a more inclusive group.

**PALEOGEOGRAPHIC CONSIDERATIONS**

The presence of R. *garasbae* in the Aptian-Albian of Morocco and *R. tessonei* sp. nov. in the Albian-Cenomanian? of Argentina increase our knowledge about the Africa - South Anicrica faunal community during mid-Cretaceous times (PATTERSON, 1975). It also allows to establish a land bridge connection in between both continents up to Albian times.

The Africa - South Anierica connection during Aptian-Albian times is based by the presence of the following vertebrates: The Mesosuchian crocodiles *Araripesuchus* from the Aptian of Northeastern Brazil and Niger (BUFFETAUT & TAQUET, 1979); the giant crocodilian *Sarcosuchus* from the Aptian of Brazil and Niger(BUFFETAUT & TAQUET, 1977); the turtles *Araripemyidae* from the Aptian of Niger and Brazil (DE BROIN, 1980) and the Coelacanths *Mawsonia* from the Aptian-Albian of Brazil and Africa (WENZ, 1980).

**CONCLUSIONS**

*Rebbachisaurus tessonei* sp. nov. a sauropod from the Albian-Cenomanian of Patagonia is the most complete species of *Rebbachisaurus* ever found. Twelve autapomorphies support the erection of this new taxa. *Rebbachisaurus tessonei* sp. nov. is the latest diplodocimorph so far known. *Rebbachisaurus tessonei* sp. nov. exhibits many synapomorphies that justify its position as the sister group of Diplodocidae, and it also confirms the interpretation of this specimen as part of a large clade of Diplodocimorpha. Eleven synapomorphies unite *R. tessonei* sp. nov. to diplodocids: pencil like teeth; anterior extension of the quadratojugal placed beyond the anterior border of the orbit; quadrate inclined posterodorsally; narial opening placed above the orbit; anteriorly directed basipterygoid processes; infratemporal fenestra oval or slit shaped; tall neural arch in posterior dorsals being three times higher than that of the centra; tall neural arch in caudals (at least 1.5 times higher that that of the centra); whip-lash tail wing-like transverse process in anterior caudals; humerus/femur ratio less than 0.70. These characters allow us to recognize the presence of a large clade that we call Diplodocimorpha.

*Rebbachisaurus tessonei* sp. nov. does not present typical characters that support the monophyly of the family Diplodocidae such as bifurcated cervical and anterior dorsal neural spine, hyposphene-hypantrum in anterior dorsals, prominent ambiens process on anterior part of the pubis, slightly procoelous anterior caudal vertebra, closed hemal canal in anterior caudals, midcaudal chevrons with fore and aft directed processes, wide dorsoventral contact of both distal ends of ischia, and expansion of the distal end of the ischia. These characters are regarded as synaponiorphies of the Diplodocidae. The genus *Rebbachisaurus* includes two species, *R. garasbae* from Morocco and *R. tessonei* sp. nov. from Argentina; *R. tasmesnensis* from Algeria is considered a camarasaurid sauropod. The presence of the genus *Rebbachisaurus* in rocks of Argentina and Morocco documents that an intercontinental land bridge between South America and Africa was present at least up to the Albian age.

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**APPENDIX**

List of 49 character and character status of Sauropoda used for cladistic analysis (TABLE I). Character codes: 0, primitive; 1,2, derived; ?, missing or uncertain. Some sources for the character analysis are: BERMAN & MCINTOSH,1978; GAUTHIER, 1986; MCINTOSH, 1990b; YU, 1993; SALGADO *et al.* (*in press*).

1) Fossa posterior in quadrate: present (0), absent (1).

2) Tooth shape: spoon shaped (0), cone and pencil chisel-like (1), pencil-like (2).

3) Serration in teeth: present (0), absent (1).

4) Angle lacrimal-parietal: posteriorly inclined (0), vertical (1).

5) Quadrate position: vertical (0), inclined posterodorsally (1).

6) Direction of the basipterygoid process: ventrally (0), anteriorly (1)

7) Narial opening position: in front of the orbit (0), above the orbit (1).

8) Posterior rim of infratemporal fenestra: back of the posterior rim of the orbit (0), well in front of the posterior rim of the orbit (1).

9) Infratemporal fenestra shape: subtriangular (0), oval / slit-shaped (1).

10) Supratemporal fenestra: big (0), small (1).

11) Anterior rim of the quadratojugal: placed before the anterior border of the orbit (0), beyond the anterior border of the orbit (1).

12) Supraoccipital width: supraoccipital width 50% of skull width (0), supraoccipital width 30% of skull width (1).

13) Frontals: unfused (0), fused (1).

14) Ascending process of the maxilla: placed in the middle of it (0), placed posteriorly of it (1), placed anteriorly of it (2).

15) Cervical centra: without pleurocoels (0), with pleurocoels (1).

16) Height of the anterior cervical neural arch: height of the neural arch > length of the centra (0), height of the neural arch > length of the centra (1).

17) Shape of the neural spine in cervicals: undivided (0), bifid (1).

18) Neural spine in anterior cervicals: directed upward (0), directed backward (1).

19) Neural spine in anterior dorsals: fused (0), unfused (1).

20) Neural arch on anterior dorsals: height of the neural arch / length of the centra < 3 (0), height of the neural arch / length of the centra > 3 (1).

21) Tall neural spine on anterior dorsals: height of neural spine is less than 65% of height of the neural arch (0), height of neural spine is more than 65% of height of the neural arch (1).

22) Pleurocoels in dorsal centra: absent (0), present (1).

23) Hyposphene-hypantrum on anterior dorsals: present (0), absent (1).

24) Tall neural arch on posterior dorsals: neural arch height / centra height < 3 (0), neural arch height / centra height > 3 (1).

25) Dorsal centra in posterior dorsals: amphiplatian-platicoelous (0), strongly opistocoelous (1).

26) Midpreespinal lamina on posterior dorsals: absent (0), present on the superior part of the spine (1), present over all the spine (2).

27) Postespinal lamina on posterior dorsals: absent (0), present (1).

28) Tall neural spine on posterior dorsals: neural spine height is less than 75% of neural arch height (0), neural spine height is more than 75% of neural arch height (1).

29) Pleurocoels shape: no eye shaped (0), eye shaped (1).

30) Centrum on anterior caudals: amphicoelous (0), sligthtly procoelous (1), strongly procoelous (2).

31) Pleurocoelus on anterior caudals: absent (0), present (1).

32) Wing-like process: absent (0), present well developed (1), formed by a dorsal and ventral bar (2).

33) Neural arch on anterior caudals / height of 1.5 (0), 1.5 - 2 (1), > 2 (2).

34) Hemal canal on anterior caudals: closed (0), open (1).

35) Neural arch on middle-posterior caudals:, placed in the middle of the centra (0), anteriorly placed (1).

36) Whip-lash tall: absent (0), present (1).

37) Forked midcaudal chevrons: absent (0), present (1).

38) Width of the distal scapular blade: maximum width / minimum width < 2 (0), maximum width / mini- mum width 2 to 3 (1), maximum width / minimum width > 3 (2).

39) Shape of sternal plate: oval (0). semilunar (1).

40) Lobe of the ilium: acute (0), expanded upward

41) Length of the articular surface of the pubis for ischia: 30% or less length of pubis shaft (0), more than 30% length of pubis shaft (1).

42) Prominent ambiens process on pubis: absent (0), prominent (1).

43) Ventral rim of the distal end of ischium: V-shaped (0), horizontal (1).

44) Distal end of ischium: expanded (0), narrow (1).

45) Pubis / ischium lenglit ratio: pubis shorter than ischium (0), pubis considerably longer than ischium (1).

46) Dorsoventral contact of the distal end of ischium: higher than the dorsal exposition (0), shorter than dorsal exposition (1).

47) Bulge in femur: absent (0), present (1).

48) Humeral proportion: less than 70% of femoral length (0), more than 70% of femoral length (1).

49) Metacarpal proportion: less than 45% of the radius length (0), more than 45% of the radius length (1).

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*Reviewer's comment:*

[This is] one of the most important papers I have read in recent years, [...].

John S. McIntosh

Este artículo [...] tiene un gran interés para el conocimiento de la historia evolutiva de los Saurópodos.

José Luis Sanz