A NEW SAUROPTERYGIAN REPTILE WITH PLESIOSAURIAN AFFINITY FROM THE LATE TRIASSIC OF ITALY

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Abstract. Bobosaurus forojuliensis, gen. et sp. nov., is a large sauropterygian from the Alpine Late Triassic (Early Carnian, northeastern Italy). The holotype is a moderately disarticulated skeleton consisting of the tip of the rostrum, part of the neck (including the atlas-axis complex), the trunk, most of the tail, parts of the limbs, and the pelvic girdle. The new taxon is characterized by a mosaic of "nothosaurian" and "plesiosaurian" features. It exhibits characters that were previously considered autapomorphies of different sauropterygian taxa. Dorsal neural spines are very high as in *Nothosaurus mirabilis*, and each dorsal rib has a distinct uncinate process, a diagnostic feature of the placodont *Paraplacodus*. The atlas-axis complex has the plesiosaurian pattern but is peculiar in several details. The neural spines of the anterior cervicals have an arched anterior margin. The spade-shaped pubis lacks an obturator foramen and an articulation with the ilium, and is associated with a stout, "hourglass-shaped" ilium that has a twisted shaft. Apomorphic characters include: cervical centra higher than wide and "pear-shaped" in anteroposterior view, a peculiar zygapophyseal articulation of pectoral to "caudal" vertebrae like that found in the dorsal vertebrae of *Simosaurus*, but with a reversed anteroposterior polarity, high neural spines on all vertebrae, neural spine of "sacral" to mid-caudal vertebrae with a bottle-shaped profile in lateral view, peculiar mid-posterior cervical ribs, lightened skeleton, and a comparatively large humerus. The new taxon was a specialized surface swimmer with a stiffened trunk and large forelimbs. It represents one of very few Late Triassic eusauropterygian taxa. It is probably a pistosaurid or, alternatively, could represent a different clade closer to Plesiosauria, occurring in the gap between the late Anisian pistosaurids and the earliest Rhaetian plesiosaurs.

Riassunto. Bobosaurus forojuliensis, gen. et sp. nov. è un grande rettile sauropterigio del Triassico superiore Alpino (Carnico inferiore, Italia nord-orientale). L'olotipo è uno scheletro moderatamente disarticolato e consiste nella punta del rostro, parte del collo (incluso il complesso atlante-asse), il tronco, la maggior parte della coda, parti degli arti e il cinto pelvico. Il nuovo taxon è caratterizzato da un mosaico di caratteri "notosauriani" e "plesiosauriani" e alcuni caratteri erano stati precedentemente ritenuti apomorfici di differenti taxa di sauropterigi. Le spine neurali dorsali sono molto alte come in *Notho-saurus mirabilis* e le coste dorsali presentano un distinto processo uncinato, carattere diagnostico del placodonte *Paraplacodus*. Il complesso atlante-asse ha l'aspetto generale di quello dei plesiosauri ma è peculiare nei dettagli. Le spine neurali delle vertebre cervicali anteriori hanno un margine anteriore arcuato. L'osso pubico, a forma di picca, è privo di un forame otturatorio e di una articolazione con l'ileo, il quale è tozzo, a forma di clessidra e con una diafisi torta. I caratteri apomorfici includono centri delle vertebre cervicali a "forma di pera" in vista antero-posteriore e più alti che larghi, una peculiare articolazione zigapofiseale dalle vertebre pettorali alle "caudali" simile a quella delle vertebre dorsali di *Simosaurus* ma con polarità antero-posteriore invertita, spine neurali alte in tutte le vertebre, spine neurali dalle vertebre "sacrali" fino a quelle medio-caudali a forma "di bottiglia" in vista laterale, coste cervicali peculiari, scheletro alleggerito e un omero proporzionalmente grande. Il nuovo taxon era un nuotatore di superficie specializzato, con un tronco irrigidito, grandi arti anteriori e uno scheletro alleggerito. Rappresenta uno dei pochi Eusauropterigi del Triassico superiore. È probabilmente un sauropterigio pistosauride o in alternativa potrebbe rappresentare un clade differente e più vicino a Plesiosauria, e si colloca temporalmente tra i pistosauridi dell'Anisico superiore e i primi plesiosauri retici.

Introduction

Plesiosaurians were among the most successful marine reptiles of Jurassic and Cretaceous times, disappearing at the end of the Cretaceous. Of all members of the extinct clade Sauropterygia, they were the best adapted to open sea life, and had limbs transformed into flippers. The earliest plesiosaurian remains come from the Rhaetian (203.6-199.6 mya; Gradstein & Ogg 2004) of France, Germany and England (Taylor & Cruickshank 1993; Storrs 1994). Pistosaurids are generally considered the most closely related to plesiosaurians among stem-group sauropterygians (Rieppel 2000; Rieppel et al. 2002). They are represented by two species, *Pistosaurus longaevus* Meyer, 1839 and *Augustasaurus hag-*

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dorni Sander, Rieppel & Bucher, 1997, both based on very few remains from the upper Anisian (237-240 mya) of Germany and Nevada, respectively (Sues 1987; Rieppel et al. 2002). No complete skeleton is known for either taxon. *Pistosaurus* is based on two skulls (Rieppel 2000); two partial skeletons and isolated bones (vertebrae, humeri, etc.) not associated with cranial elements have also attributed to this taxon (Sues 1987). *Augustasaurus* is based on a single incomplete specimen preserving the skull but lacking the posterior half of the skeleton (Sander et al. 1997; Rieppel et al. 2002). The affinity of pistosaurids with plesiosaurians is based mainly on cranial features.

The articulated skeleton of a large marine reptile has been recently discovered by Mr. Roberto Rigo in the lower Carnian (228-223 mya) of NE Italy and is here described as a new taxon. It preserves parts of the body that are unknown in *Pistosaurus* and *Augustasaurus*, and exhibits some plesiosaurian features in tandem with features previously considered diagnostic of other sauropterygian taxa. A gap of about 35 million years separates *Pistosaurus* and *Augustasaurus* from the first plesiosaurians: the new specimen occurs in this gap. Late Triassic eusauropterygian taxa are otherwise restricted to the small nothosaurian *Nothosaurus edingerae* Schultze, 1970 from the lowermost Carnian (upper Gipskeuper) of Germany (Hagdorn & Rieppel 1999), and the plesiosaurian *Thalassiodracon hawkinsi* (Owen, 1839) from the Rhaetian-Hettangian boundary (Storrs & Taylor 1996).

Abbreviations: MFSN = Museo Friulano di Storia Naturale, Udine, Italy; SMF = Natur-Museum Senckenberg, Frankfurt am Main, Germany.

Material and methods

The holotype, MFSN 27285, has been prepared for museum exhibition, with one side partly freed from rock and the rest still embedded in a large, thick limestone slab. Of course, this partial preparation limits the identification of some features, but available characters are enough to describe it as a new eusauropterygian taxon.

MFSN 27854, a partial neural arch, is also referred to the new taxon.

The neural spine is here considered as a part of the neural arch (Goodrich 1930; Romer 1956) in contrast to the reductivist approach that has sometimes appeared in literature (e.g., O'Keefe 2001) in which the neural arch is considered the part of the vertebra between the centrum and the neural spine. The neural arch height is measured from the top of the centrum to the apex of the neural spine as a line normal to the dorsal surface of the centrum. The neural spine height in the dorsal vertebrae is measured following Rieppel (2001) from the dorsal surface of the transverse process up to the dorsal margin of the spine. The neural spine height in cervical and caudal vertebrae is measured from the articular surface of the postzygapophysis up to the dorsal margin of the spine. The height of the neural arch exclusive of the spine is measured from the base of the neural canal to the dorsal surface of the transverse process. The centrum height is measured from the base of the neural canal to the bottom edge of the centrum, as suggested by Olivier Rieppel (pers. comm.).

The orientation of elements from the pelvic girdle is that of their original position in the uncrushed skeleton.

The work used as a reference for the systematics of the stem-group Sauropterygia is Rieppel (2000). The intention of this paper is not to perform a cladistic analysis of Sauropterygia including the new taxon. The published character matrices of stem-group sauropterygians (i.e., sauropterygians excluding Plesiosauria) are heavily biased toward cranial and shoulder girdle features that cannot be observed in the new taxon, while characters concerning the pelvic girdle and the axial skeleton (e.g, the atlas-axis) are scarcely represented. Furthermore, published cladistic analyses are focused on stem-group sauropterygians (placodonts, pachypleurosaurians, nothosauroideans and basal pistosaurians; e.g., Rieppel 2000), or on crown group sauropterygians (plesiosaurians, e.g. O'Keefe 2001) with a very limited overlapping, in order to resolve the phylogenetic relationships inside each separate group. The inclusion of the new taxon in a cladistic analysis will be performed after an adequate integration of the published character matrices, which is beyond the scope of the present paper.

Locality and age

MFSN 27285 was discovered by Mr. Roberto Rigo at the eastern end of the Tolmezzo Alps (southern Carnic Alps) at their border with the Julian Alps, 750 meters above sea level, along an unnamed left tributary of Pontuz Creek, near the village of Gran Colle, about two kilometres northwest of the town of Dogna, Udine Province, northern part of the Friuli Venezia Giulia
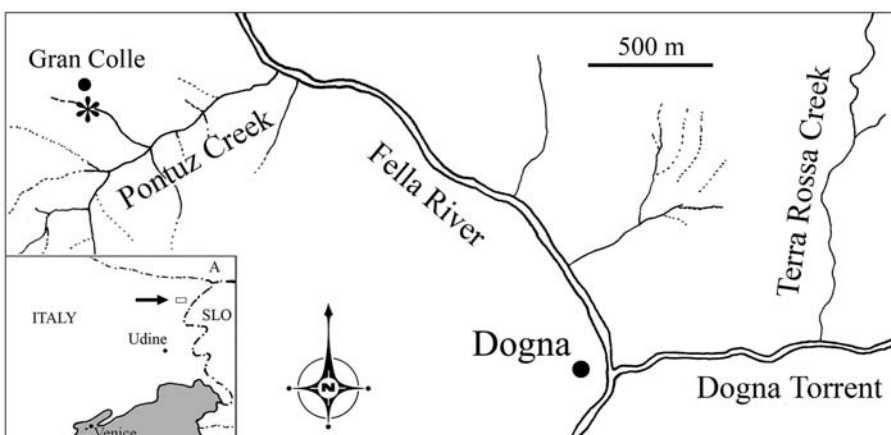

Fig. 1 - Location of the finding place (asterisk) close to the town of Dogna in northern Friuli, NE Italy.

Autonomous Region, NE Italy (Fig. 1). MFSN 27854 was also found along the left flank of Pontuz Creek.

MFSN 27285 comes from the lower part of an 8 m-thick section consisting of an irregular alternation of dark grey to blackish, bioturbated to nodular, often molluscs-rich limestone beds, and levels of blackish-dark greenish, clayey marls (Fig. 2). MFSN 27285 was preserved in a 20 cm-thick blackish limestone bed, grey or pale yellow when weathered. A Julian (lower Carnian; in the Alpine chronostratigraphy, the Carnian stage is subdivided into a lower part [Julian] and an upper part [Tuvalian]) palynomorph association is found in the section (Fig. 2) marked by the presence of *Concentricisporites bianulatus* (Neves, 1961), *Parcisporites* spp., *Duplicisporites verrucosus* (Leschik, 1956), *Enzonalasporites vigens* Leschik, 1956, *Duplicisporites granulatus* (Leschik, 1956) and *Araucariacites australis* Cookson, 1947 (Guido Roghi, pers. comm.). *Concentricisporites bianulatus* is restricted to the palynomorph Assemblage 1 of Preto et al. (2005) that is typical of

the lower Julian. The early Carnian bivalve *Myophoria kefersteini* Bronn, 1835 also occurs.

The unit where the specimens were collected is referred to the Rio del Lago Formation of the close Cave del Predil (formerly Raibl) area (Preto et al. 2005). The horizon with the specimen MFSN 27285 occurs about 10 meters above a 12 m-thick bank of oolitic limestone characteristic of the lower part of the formation. The same stratigraphic sequence seen at Pontuz Creek also crops out in the nearby valley of the Dogna Torrent and in the environs of Dogna village, only 2-3 km SE of Pontuz Creek (Fig. 1). Along Terra Rossa Creek, the over 200 m-thick Rio del Lago Formation overlies the "dolomia di Rio Terra Rossa" (about 30 m thick), in the middle of which a monospecific conodont fauna of *Pseudofurnishius murcianus murcianus* Van den Boogaart, 1966 indicates a latest Ladinian-early Carnian age (*aon* Subzone) (Jadoul & Nicora 2000; Preto et al. 2005). The basal part of the Rio del Lago Formation with the oolitic interval is missing in the Terra Rossa Creek because of a fault, but is seen in nearby Mas Creek (Preto et al. 2005). *Myophoria kefersteini* is present only in the lowest part of the Terra Rossa Creek section. Palynomorphs belong to Assemblage 1 (corresponding to the *Concentricisporites* cf. *C. bianulatus* Assemblage of Roghi 2004), characterized by *Concentricisporites* cf. *bianulatus* and *Kyrtomisporis ervii* Van der Eem, 1983. The ammonoids *Trachyceras* cf. *saulus* (Laube, 1869) and *Carnites floridus* (Wulfen, 1793), collected in the lower part of the unit, are typical of the middle Julian *aonoides* Subzone (Preto et al. 2005). All this supports an early Carnian age for the Rio del Lago Formation and the new sauropterygian.

The Rio del Lago Formation of Dogna area is rich in shallow water marine invertebrate (bivalves, gastropods, echinoderms, corals, etc.) and vertebrate macrofossils (Sirna et al. 1994; Rieppel & Dalla Vecchia 2001; Dalla Vecchia & Avanzini 2002). The mostly bioturbated limestone layers are interpreted as storm beds (Preto et al. 2005). The depositional environment of the lower-middle part of the unit is considered a subtidal carbonate-clastic ramp (Preto et al. 2005).
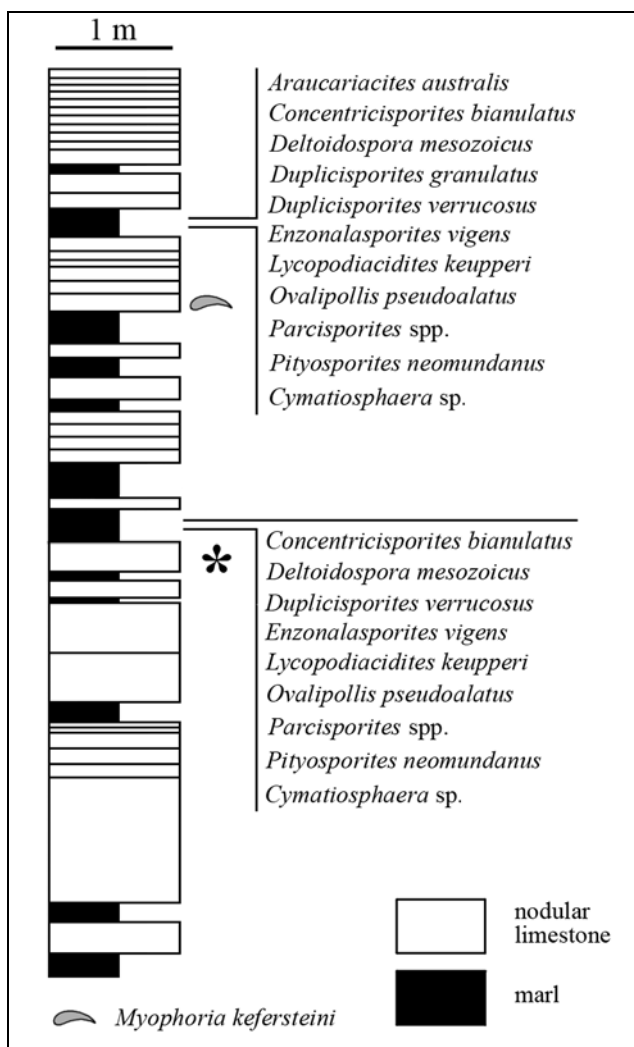

Fig. 2 - The section where MFSN 27285 was found (asterisk). The most significant palynomorphs from two sampled levels in the section are listed.

Systematic paleontology

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Sauropterygia Owen, 1860

Eusauropterygia Tschanz, 1989

Pistosauria Baur, 1887-1890

Bobosaurus gen. n.

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Derivation of name. After the nickname of the finder, Mr. Roberto "Bobo" Rigo (Udine, Italy); *sauros*, Greek for lizard.

Diagnosis. *Bobosaurus* is a sauropterygian that could reach a length in excess of 3 m diagnosed by the following unique combination

of characters: plesiosaurian massive atlas-axis complex made of eight sutured elements with double atlas and axis intercentra meeting ventrally; atlas centrum subequal in lateral extension to the atlantal arch and intercentrum, excluded both from the ventral margin of the complex and the lateral margin of the cotyle, with a fused, thorn-like axial rib; neural spines of anterior cervicals with wide, arched prespinal laminae, features found in some plesiosaurians but never in pistosaurids or other stem-group sauropterygians; posterior expansion in the mid-shaft of each dorsal rib forming a broad and blunt uncinate process (convergent in the placodont *Paraplacodus* Peyer, 1931); plesiosaurian, spade-shaped pubis with convex ventromedial margin lacking both an obturator foramen and an articulation to the ilium, associated with a stout, "hourglass-shaped" ilium with twisted shaft.

Bobosaurus has the following autapomorphies: cervical centra "pear-shaped" in anteroposterior view and higher than wide; presence of infraprezygapophysis and "infrapostzygapophysis" from the pectoral vertebrae 3-4 up to the first "caudal" vertebra and possibly as far posterior as "caudal" 11 like those found in the dorsals of *Simosaurus* but with a reversed anteroposterior polarity; tall neural spines on all cervical to caudal vertebrae including the axis; spines of the anterior cervicals at least 1.5 times the centrum height; spines of the dorsal vertebrae up to three times the centrum height; spines of mid-anterior caudal vertebrae 2.3-2.8 times the centrum height; neural spines of "sacral" vertebrae 4-9 to mid-caudal vertebrae with a bottle-shaped profile in lateral view; distal and backward-turned segments of the shafts of mid-posterior cervical ribs shorter or as short as the proximal segment and with a distally rounded, striated distal tips; lightened skeleton (hollow neural spines, coarsely spongy arches and cervical and possibly anterior dorsal ribs, spongy centra); large humerus (9 times the length of a mid-dorsal centrum).

Type and only species: *Bobosaurus forojuliensis* Dalla Vecchia n. sp.

Age: Early Carnian.

Bobosaurus forojuliensis n. sp.

(Figs 3-14)

Derivation of name. After Roman name *Forum Julii* of the Friulian part of the Region Friuli Venezia Giulia.

Holotype. MFSN 27285, a moderately disarticulated skeleton consisting in the tip of the snout, part of the neck (including the atlas-axis complex), the trunk, most of tail, parts of the limbs, and the pelvic girdle.

Referred material. MFSN 27854, dorsal neural arch.

Horizon. Lower part of the Rio del Lago Formation, lower Carnian (Julian).

Type locality. Unnamed tributary of Pontuz Creek, close to the small village of Gran Colle, about 2 km NW of the town of Dogna, Province of Udine, Friuli Venezia Giulia Autonomous Region, northeastern Italy. Geographic coordinates: N 46° 27' 25", E 13° 17' 28".

Repository. Museo Friulano di Storia Naturale, Udine, Italy.

Diagnosis. As for the genus.

Description

General features

The holotype is a partially preserved and moderately disarticulated skeleton exposing its right side (Figs. 3-4). Bones are in most cases uncrushed. Most of the skull and the lower jaw are missing. Only the tip of the skull with some teeth is exposed, in cross-section. The vertebral column is relatively well-articulated from the atlas-axis complex to the mid-caudal vertebrae, whereas the mid-distal caudal segment is more disarticulated. Most of the mid-posterior cervicals were lost because of weathering, but their cervical ribs are still preserved with little disarticulation. The length of the vertebral column (the sum of the central length from the atlas-axis to the smallest distal caudal vertebra, including an estimation of the cervical gap) is 2.450 mm. Considering also the intervertebral spaces, the missing distal caudals, and the skull, the length of the specimen was well in excess of 3 m. The rib cage is disarticulated and some of the dorsal ribs have shifted posteriorly and dorsally. Sacral ribs are found detached, but close to the sacral vertebrae. Sparse gastral elements are present on the slab. The caudal ribs are all disarticulated and scattered; the haemapophyses of the proximal caudals are detached from their natural articulation but still close to their respective vertebrae. Nothing is visible of the pectoral girdle, possibly because it has shifted below the vertebral column and is presently covered by the dorsal vertebrae and matrix. In fact, a convexity in the block and a partial disarticulation of the vertebral column occur in that region. The forelimbs are represented only by the right humerus. The hind limbs are represented only by a tibia, two tarsals and what is possibly a femur in cross section. Two metapodials and a phalanx are scattered along the vertebral column. The pelvic girdle is detached from the sacrum and had drifted slightly ventroposteriorly. An ilium and both ischia and pubis are exposed, slightly shifted from their original spatial relationships.

MFSN 27285 (Fig. 5) is an uncrushed, isolated neural arch lacking the mid-apical part of the neural spine. It belongs to an individual substantially smaller than the holotype (height is 50.8 mm, maximum width is 50.3 mm) and shows some differences in the outline of the cross-section of the neural spine, details of the prespinal and postspinal laminae, and the basal termination of the prespinal lamina. It is attributed to the new taxon because of the peculiar articular complex, well-developed prespinal and postspinal laminae, hollow spine, and geographic and stratigraphic provenance. It belongs to a dorsal vertebra, possibly a posterior one, because the neural spine does not slope posteriorly and the ventral end of the transverse process coincides with the sutural surfaces of the neural arch. Differences with neural arches of the holotype dorsals could be ontogenic or due to intraspecific variability.

Skull

Only the very tip of a rather narrow snout is preserved along the right flank of the atlas-axis complex, exposed as an inclined cross-section (i.e. not perpendicular to the main axis of the skull) 34 mm wide (Fig. 6). It comprises the anterior end of both premax-

Fig. 3   - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype.

illae which are sutured medially and bear two alveoli. A depression surrounding a large foramen occurs on each premaxilla. The left alveolus bears a tooth, whereas the right one is empty with the tooth preserved close by. An apparently separate bone, bearing an alveolate tooth, occurs ventromedial to the premaxillae; its position suggests it is the vomer. The ring-like section of an indeterminate bone (tip of the lower jaw?) occurs below the section of the premaxillae.

Dentition

Three partial tooth crowns and two sectioned teeth are preserved. Tooth crowns are straight or slightly curved, pointed and elongated cones with nu-

merous, strictly spaced and thin, apicobasal striations. The preserved portions are 13-27 mm long apicobasally. The cross-sections are circular. A cross-sectioned tooth base occurs in the probable vomer (Fig. 6). A median tooth in the tip of the snout is very rare in reptiles.

Postcranial axial skeleton

Posterior to the atlas-axis complex and anterior to the first vertebra in which the articular facet for a rib spans both the centrum and the neural arch, there is room and partial evidence for at least 17 vertebrae. I consider as "cervicals" those vertebrae in which the articular facet/s for the rib is entirely on the centrum. Therefore the minimum number of cervical vertebrae

Fig. 4   - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. Abbreviations: aac = atlas-axis complex, ans = neural spine of the axis, as = astragalus, ca = calcaneum, ccv = centrum of a cervical vertebra, cCv = centrum of a caudal vertebra, cdv = centrum of a dorsal vertebra, cr = cervical rib, Cr = caudal rib, Cr* = the most proximal caudal rib, cv = cervical vertebra, Cv = "caudal vertebra", dr = dorsal rib, dv = dorsal vertebra, fe = femur, g = gastral rib, h = humerus, hm = hemapophysis (chevron), icv = isolated cervical vertebra, il = ilium, is = ischium, lcv = last cervical vertebra, mtp = metapodial, nCv = neural spine of a caudal vertebra, ndv = neural spine of a dorsal vertebra, ph = phalanx, pr = pectoral rib, pu = pubis, pv = pectoral vertebra, sk = anterior tip of the skull, sr = sacral rib, sv = "sacral" vertebra, ti = tibia,? = indeterminate bone. The articular surface for the rib in the transverse process is marked with a darker grey.

is 19, but it was possibly slightly higher. Six vertebrae follow in which the single articular facet for the rib is partly on the centrum and partly on the neural arch. I consider these pectoral vertebrae following Brown (1981) and Sues (1987), despite the arguments of Carpenter (1999). The articular facet for the rib is entirely on the neural arch, (i.e., the transverse process is formed largely or completely by the neural arch) in the successive 16 dorsal vertebrae. The articular facet migrates to the centrum again on the posterior vertebrae; it straddles the neural arch and centrum in the first nine vertebrae of this string (sacrals, according to Brown 1981),

Fig. 5 - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27854, neural arch of a dorsal vertebra. A) Posterior view, B) anterior view, C) left lateral view, D) dorsal view, E) ventral view. Abbreviations: ap = anterior process, ipoz = "infrapostzygapophysis", iprz = infraprezygapophysis, pl = prespinal lamina, pp = posterior process, poz = postzygapophysis, prz = prezygapophysis.
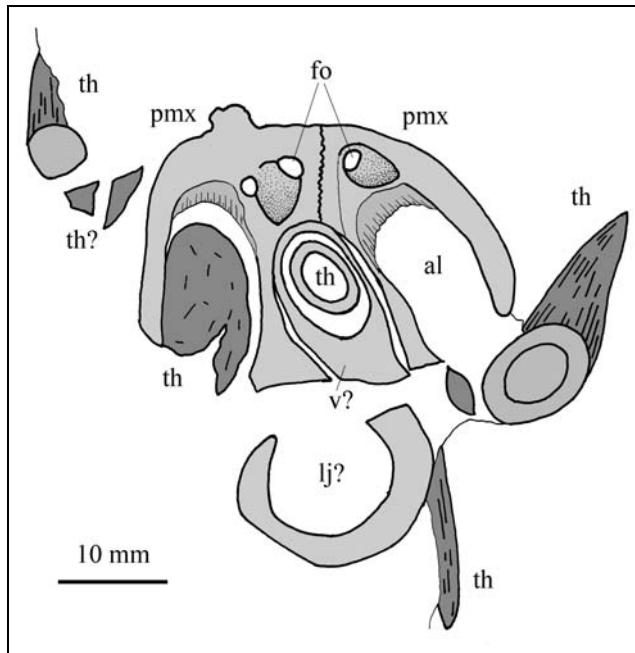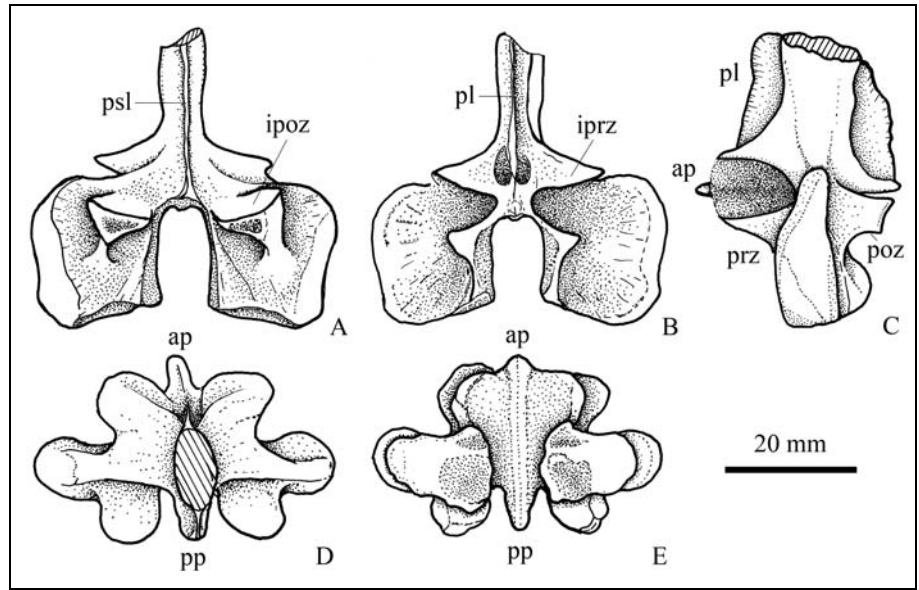

Fig. 6 - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. The tip of the snout in cross-section. Tooth crown remains are evidenced by dark grey colour. Abbreviations: al = alveolus, fo = foramen hosted in a depression of the premaxilla, lj = lower jaw, pmx = premaxilla, th = tooth, v = vomer.

and sits wholly on the centrum only in the successive 12 vertebrae which should therefore be considered caudals (Brown 1981). Following these are 22 other caudals and four small centra scattered in the slab. Of course, the presence of nine sacral vertebrae is unlikely: the four anteriormost are very probably posterior dorsals ("lumbars"). Because the sacral ribs are not articulated to their respective centra or to the pelvis, it is not possible to state unambiguously how many (or which) are true sacral vertebrae and where the transition to caudal verteb-

Fig. 7 - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. Atlas-axis complex. A) left lateral view; B) ventral view. Abbreviations: ac = atlas centrum, ana = atlas neural arch, ans = neural spine of the axis, axc = axis centrum, axic = axial intercentrum, atic = atlas intercentrum, pmx = premaxilla, poz = postzygapophysis, r. = right, tp = thorn-like process of the atlas centrum (axial rib), tu = tubercle of the axial intercentrum. The articular surfaces are in dark grey, the ventral surface of the complex in light gray, the lateral surfaces are in intermediate grey. The rock is in the lightest grey and the skull and dentition elements are white. The surfaces of broken parts are lined.

rae lies. For simplicity, I label as "sacral" the vertebrae with the articular facet for the rib partly on the neural arch and partly on the centrum, and, consequently, "caudals" are all those more posterior. The passage from pectoral to dorsal vertebrae, from dosals to "sacrals" and from "sacrals" to "caudals" is gradual. Neural arches are sutured to their centra.

Cervical vertebrae and ribs. The atlas-axis complex is a compact, massive bone formed by the aggregation of at least eight elements (Fig. 7). Its maximum length in ventral view is 65.8 mm, maximum anterior width is 52.3 mm; maximum posterior width and height of axial centrum are 41.7 mm and 38.8 mm, respectively. The exposed flat surface is the ventral one because the neural arch is on the other side (Fig. 7B), so the complex is upside-down. The complex exhibits the primitive condition of paired atlantal and axial intercentra, each formed by two elements (Goodrich 1930) for a total of four bones. The axial centrum is slightly separated from

both the atlantal centrum and the axial intercentrum, therefore it was not completely fused to either. The centrum of the atlas is sutured to the underlying axial intercentrum and the atlantal neural arch placed anteriorly. It is as wide as or slightly wider than the atlantal neural arch and intercentrum in lateral view. It bears a short, thorn-like process, probably a coossified axial rib. The square axial intercentra are sutured medially; they each bear a knob along the ventrolateral margin, possibly a remnant of an articular facet for the capitulum of an axial rib, also a primitive feature. The axial intercentra are square, sutured to each other medially and the atlantal centrum dorsally. They are slightly separated from the atlantal intercentra laterally, but they are sutured ventromedially. The dorsal margin of the cotyle for the occipital condyle (probably deeply concave, but still concealed by matrix) is placed more posteriorly than the ventral one (i.e., the margin of the cotyle in lateral view is slightly inclined anteroposteriorly like in many ple-
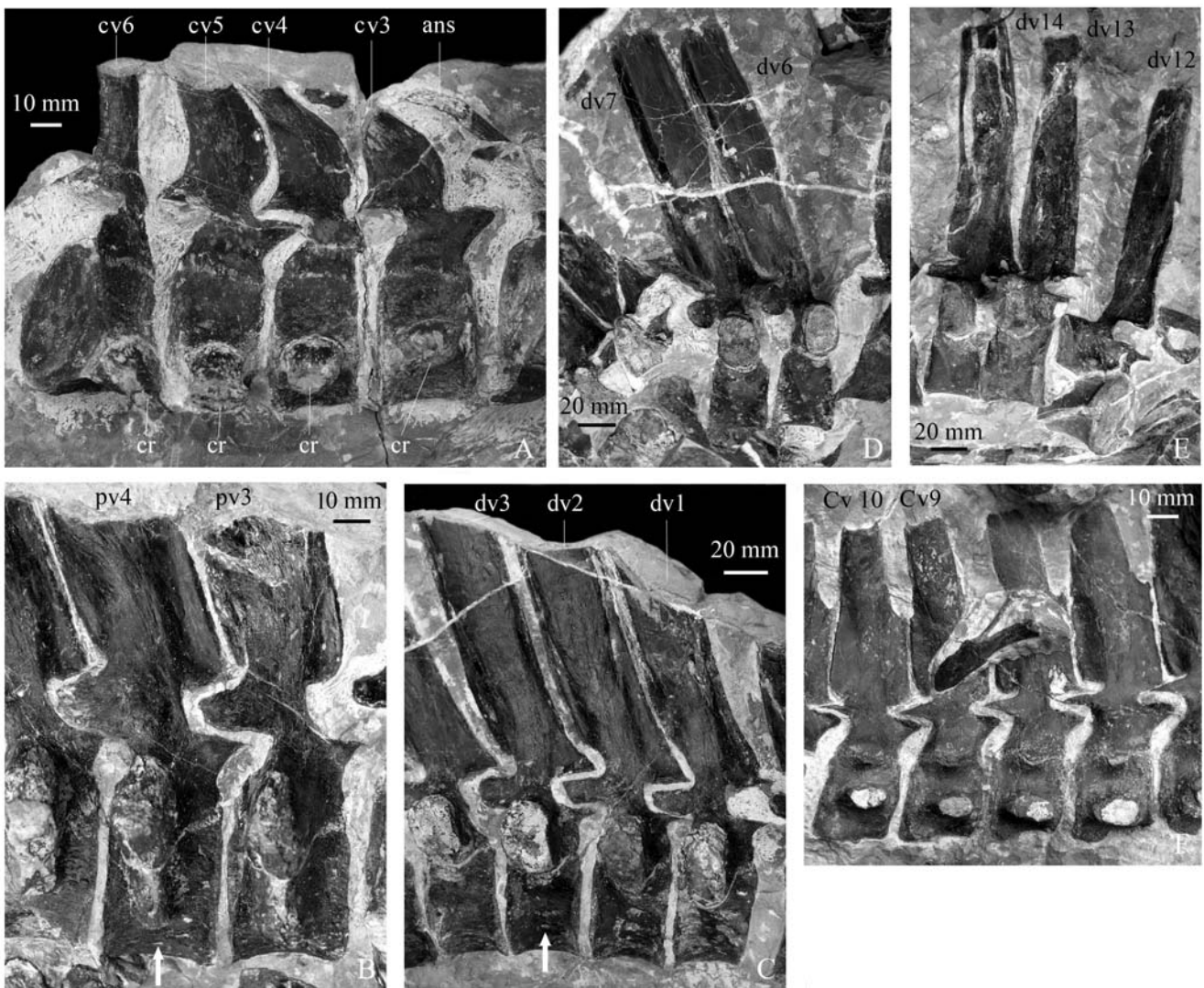

Fig. 8 - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. A) Cervical vertebrae 3-6, B) Pectoral vertebrae 3-4, C) dorsal vertebrae 1-3, D) dorsal vertebrae 6-7, E) dorsal vertebrae 12-14; F) Anterior caudal vertebrae ("caudals" 7-10). The white arrow indicates a subcentral foramen. Abbreviations as in figure 3.

siosaurians, e.g. Bakker 1993). The posterior articular face of the axis is only gently concave. The square neural arch of the atlas is sutured to its centrum. The neural arch of the axis is mostly covered by limestone. The postzygapophysis has an horizontal articular facet. The partially preserved neural spine, pointing out from below the centrum and partly concealed by the tip of the snout, is rather long, flat and narrow laterally, and slopes backward.

The right sides of cervical vertebrae 3 to 6 are exposed; vertebra 6 is visible also posteriorly, and the disarticulated and rotated vertebra 7 is exposed in right lateral and posterior views (Fig. 8A). The cervical vertebrae posterior to vertebra 9 are completely missing from the slab because of weathering. Only a single element of this missing string has been found scattered in the debris, completely freed from matrix (Fig. 9). Eight cervical ribs are regularly spaced and were probably in connection with, or close to, their relative, missing centra. The locations and number of ribs and the subdivision of the empty space by an average centrum length allow estimation of the minimum number of the cervical vertebrae reported above. Of course, in the case of disarticulation or bending of the missing portion, the actual number would be higher. However, the positions of the cervical ribs argues against a marked disarticulation of this neck segment. Preserved centra are higher than long, with lengths ranging from 28.5 to 33.5 mm; there is no clear trend toward elongation, although the two posterior centra are the longest. The centrum of cervical 6 has a maximum width of 39.5 mm, is 50 mm high and 29 mm long. The isolated centrum is 43 mm wide (excluding the apophyses for the ribs), 51.8 mm high and 33.5 mm long. Each cervical centrum has a slightly concave articular face that lacks a notochordal pit and is "pear-shaped" (Figs 9-10). Centra are coarsely spongy inside as shown by the section of cervical vertebrae 8-9, with a thin external layer of compacta. There is a low, blunt, mid-ventral longitudinal ridge. A longitudinally elongate apophysis separates the dorsolateral from the ventrolateral face of the centrum. Both faces are slightly constricted. The facets receiving the double-headed cervical rib occur on this low apophysis. They are elongate anteroposteriorly and set closely to each other, occupying most of the length of the centrum. The apophysis in the last cervical vertebra is longer and projects ventrolaterally from the mid-ventral lateral side of the centrum; it has a subcircular section and probably a single facet for the rib. A ridge connects its dorsal margin to the dorsal margin of the centrum. No subcentral foramina are present, at least in cervical vertebrae 3-6 and in the isolated one.

The height of the preserved part of the neural arch in cervical 6 reaches 101.8 mm (spine included), whereas the height of the spine alone is 82 mm. The ratio of
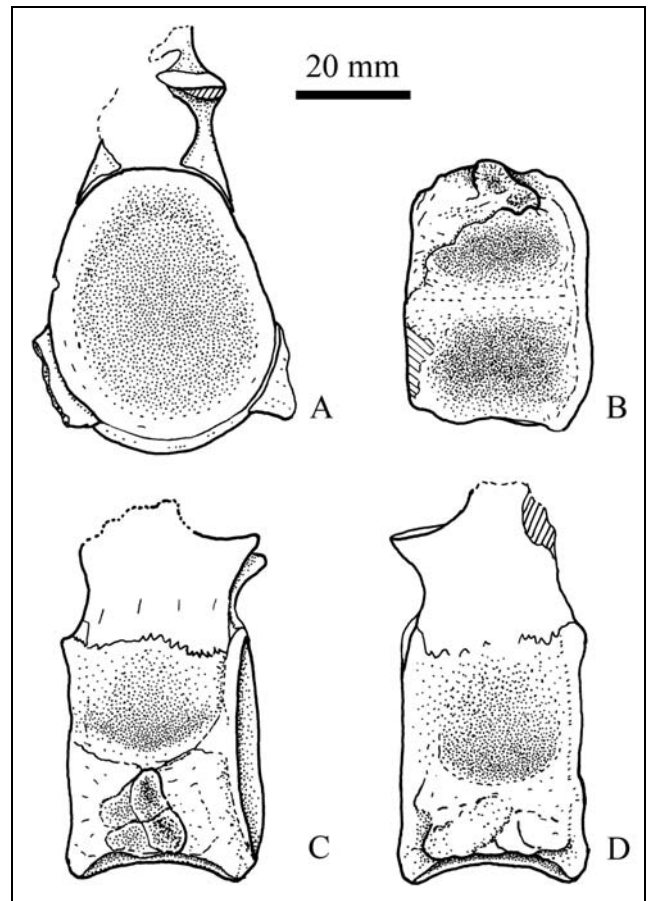

Fig. 9   - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. The isolated cervical centrum. A) Anterior view, B) ventral view, C) right lateral view, D) left lateral view.

neural arch/centrum height is 1.98. The neural spine is high (Fig. 10A) and the ratio of neural spine/centrum height is 1.64. The neural arches, excluding the spine, are shorter than the centrum. The neural arches bear simple postzygapophyses and prezygapophyses that project anteriorly and posteriorly beyond the centrum and have horizontal or slightly anteroposteriorly sloping (vertebra 7) articular facets. They are slightly narrower than their associated centra. The neural spines are hollow inside, with just a thin layer of compacta. They are inclined backward; the basal part is wide, with a strongly curved anterior margin, and tapers immediately above. The curved anterior part is made by a well-developed prespinal lamina that gives the basal part of the spine an "under sail" aspect, whereas the posterior lamina is much narrower and keel-like. The cross-section of the neural spine at mid-height is tear-drop-shaped (Fig. 10A).

The ribs of cervicals 3-6 are tightly appressed to the articular facets on their centra via curved and rough sutures. Although the vertebrae are slightly disarticulated from each other, the ribs are still firmly connected to their centra, whereas ribs posterior to this anterior
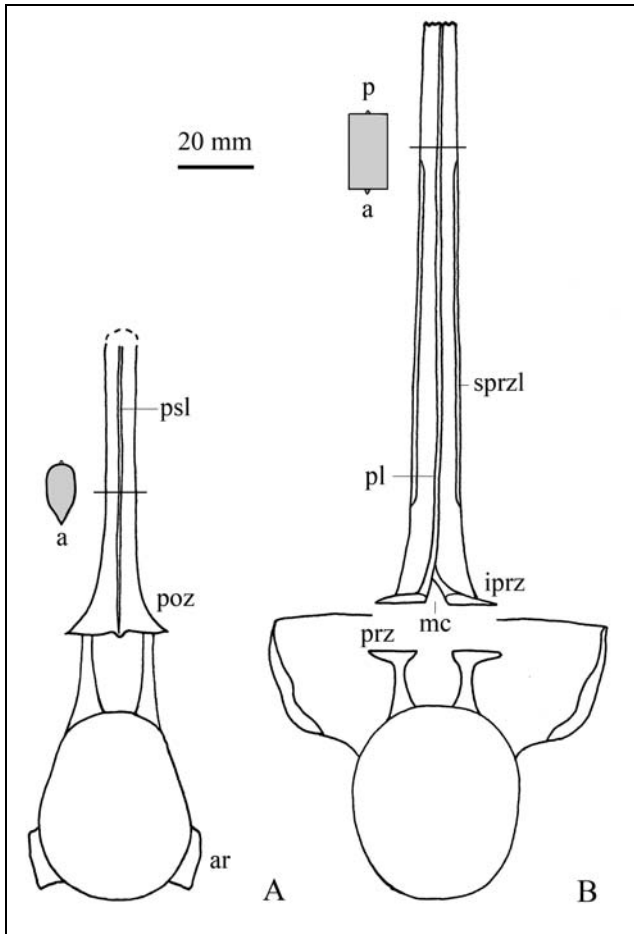
Fig. 10 - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. Reconstruction of vertebrae in anteroposterior view. A) cervical vertebra (based on cervical vertebrae 6-7), posterior view; B) dorsal vertebra (based on dorsal vertebra 13), anterior view. Cross-section of the neural spine is reported on the left side. Abbreviations: a = anterior, ar = sutural facets for the rib, iprz = infraprezygapophysis, mc = median cavity, p = posterior, pl = prespinal lamina, poz = postzygapophysis, prz = prezygapophysis, psl = postspinal lamina, sprzl = supraprezygapophyseal lamina.

their respective centra. The anterior ribs are dorsoventrally flattened and angled ventrolaterally. The rib of vertebra 6 preserves a large, hatched-shaped and blade-like anterior process. Capitula and tubercula are fan-shaped in dorsoventral view, Y-shaped in anteroposterior view, and separated by a slit-like spatium, possibly a narrow channel for a vertebral artery. Other 12 cervical ribs can be identified posteriorly. They are double-headed and "boot-shaped". The distal and backward-turned segments of the shaft (the "posterior processes" of Sander et al. 1997) increase in length and narrow posteriorly, but are never longer than the proximal segments (Fig. 11). The distal end of each rib is rounded and has a striated aspect due to presence of longitudinal ridges and grooves. The probably single anterior process is reduced and blade-like, with a rounded outline in more anterior members but becomes triangular posteriorly. The most posterior of the preserved ribs is 50 mm long, measured from the distal point of the shaft to the proximal margin; the smaller, complete posterior rib (Fig. 11A) is 38 mm long. The shafts of the ribs are coarsely celled (spongy) inside and practically hollow.

Pectoral vertebrae and ribs. The first vertebra after the last cervical has a dorsoventrally elongate (~37 mm) and anteroposteriorly narrow (maximum 11 mm) transverse process bearing an articular facet for the rib that is strikingly different from those of the preceding vertebrae. The neural arch participates in its uppermost part and increasingly forms a part of the process posteriorly. The area surrounding the suture between the portions of the process contributed by the centrum and neural arch forms a depression on the articular surface that distinguishes dorsal and ventral raised areas and gives the articular surface a "figure-8" shape in lateral view. A small foramen (2 to 4.5 mm long) is visible in the lower parts of the lateral sides of the centra in vertebrae 3, 4 and 6 (Fig. 8B). The centra of the six pectoral vertebrae range from 30-32 mm in length.

The articulation between the last cervical and the first pectoral vertebra is of the simple, plesiomorphic

segment of the vertebral column are mostly more or less detached. However, the proximal margins of the latter are saw-like (Fig. 11), suggesting they were sutured to
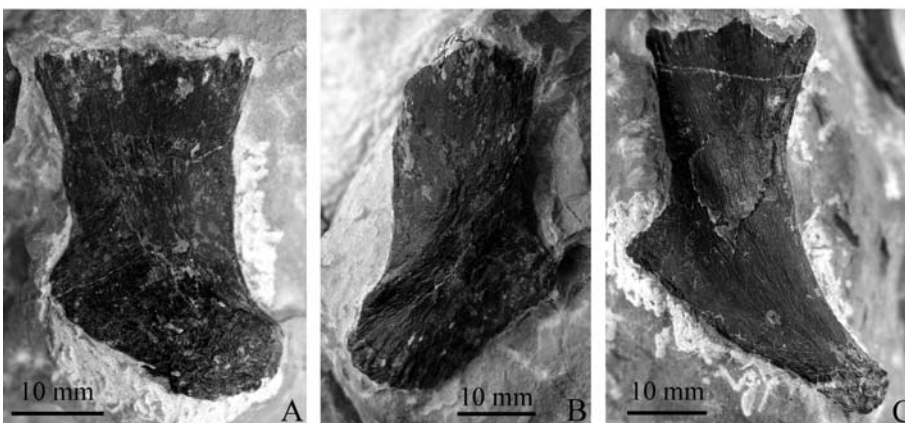

Fig. 11 - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. Cervical ribs. A) mid-posterior rib, B) mid-posterior rib with striated posterior tip of the shaft, C) more distal posterior rib. The posterior tip of the shaft is slightly damaged in specimens of figures A and B.

prezygapophysis-postzygapophysis type. The prespinal lamina has a rounded basal profile and is not confluent with the zygapophysis. The articulation between the first and second pectoral vertebra is also of this type. Between pectoral vertebrae 3 and 4, the vertebral articulation changes. Vertebra 3 has a well-developed posterior articular process projecting far beyond the posterior end of the centrum that has a rectangular outline in side view. This is the postzygapophysis-infrapostzygapophysis complex in the terminology of Rieppel (2000). Actually, the "infrapostzygapophysis" is not an apophysis, but a dorsal, articular facet on the postzygapophysis. A corresponding socket occurs anteriorly on the subsequent vertebra, bordered ventrally and dorsally by the prezygapophysis and infraprezygapophysis, respectively (Fig. 8B). Thus, the posteriorly-projecting and wedge-shaped process fits into a cavity on the posterior vertebra. This articular system is also found in the isolated neural arch MFSN 27854 (Fig. 5). It persists at least up to "caudal" vertebra 1 and possibly up to "caudal" vertebra 11 (see below), where only a side view is offered of the articular complex. There is a certain variability in the morphology of this structure along the vertebral column. Up to dorsal 14, the complex is more or less rectangular in side view, whereas it appears triangular in more posterior vertebrae. The shape of the complex and of the corresponding socket is wedge-like in MFSN 27285 and probably also in some dorsals, "sacrals" and possibly also "caudals" of the holotype, but it is probably "butterfly-like" in dorsal vertebrae 3-8 and square in dorsals 11 and 12.

The upper half of the neural spine is missing in all pectoral vertebrae. The basal portion slopes posteriorly and is flattened laterally with a rectangular cross section (the section is six times anteroposteriorly longer than wide in pectoral vertebra 2). The prespinal lamina is well-developed anteroposteriorly, as is the postspinal lamina, which has a convex, rounded outline.

At least two ribs are related to the pectoral series and were originally articulated to the pectoral vertebra 1 or 2 and 2 or 3. The single articular heads are greatly expanded dorsoventrally and fan-like.

Dorsal vertebrae and ribs. There are 16 dorsal vertebrae (Figs. 8C-E). Each centrum is spool-shaped, with slightly constricted lateral sides. Centra range from 28-34 mm in length, and show no clear trend of either elongation or shortening. The articular faces are oval and shallowly concave, higher than wide. The centra of all dorsals display a distinct, shallow, arcuate groove crossing the right lateral side diagonally from the posterior dorsal corner to the mid-ventral margin. This feature, the purpose of which is unknown, has also been observed in centra of *Nothosaurus* Münster, 1834 (R. Wild, pers. comm.). Two-three, very small, closely spaced subcentral foramina that are 1.5-2.5 mm long

are present in dorsal vertebrae 1 and 3, and 13 to 16. A "cruciform" platform for the articulation of the neural arch is visible on centra 10 and 11.

The transverse process migrates dorsally and then ventrally again along the series. Its ventroproximal part maintains a tongue-like lateral projection of the centrum in dorsal vertebra 1; this projection reduces progressively its extent in dorsals 2 to 5. The transverse process is formed entirely by the neural arch in vertebrae 6-16. Each arises perpendicular to the neural arch and is more elongate laterally than those of the pectoral vertebrae. The rectangular articular surface for the rib narrows dorsoventrally compared to the pectoral vertebrae. The neural spines of dorsal vertebrae 1-7 and 12 and 13 angle backward 18-25°, whereas those of the posterior dorsals are less inclined. The ratios of neural arch/centrum height and neural spine/centrum height are 3.8/3.1 and 3.7/3.2, respectively, in dorsal vertebrae 7 and 12. The heights of the neural arches without the spines are 31 and 23 mm, respectively, in the same elements, significantly less than the 45 mm centrum height. The oval cross-section of the neural spine in MFSN 27285 (Fig. 5D) shows that it is hollow inside with a layer of compacta less than 0.5 mm thick. The mid to apical cross-section of the neural spine in the dorsal vertebrae of the holotype reveals that they too are hollow. This is also the case for the cervical and the pectoral vertebrae. The cross-section is rectangular and laterally narrow (the anteroposterior length is twice the width in the upper part of the spine; Fig. 10B). The apex of the spine generally has a concave, jagged margin, and apicobasal grooves and ridges at the top of the lateral face, giving it a striated aspect. The well-developed prespinal and postspinal laminae are extremely thin, probably around 1 mm in the holotype and less in MFSN 27854. They both expand basally in a foot-like articular structure, just above the neural channel (Fig. 5C-E) in MFSN 27854; two small, arranged symmetrically to the right and to the left, subcircular cavities occurring in the neural arch at the base of the prespinal lamina are the places for the attachment of tendons connecting the neural spines. The prespinal lamina starts at the apex of the spine in the mid-dorsal vertebrae of the holotype and widens basally where, at least in posterior dorsals, it is confluent with the right infraprezygapophysis. The basal segment of the prespinal lamina and a short lamina starting from the left infraprezygapophysis and confluent with prespinal lamina roof a small, median, longitudinal cavity with an upside-down V-shaped morphology (see Fig. 10B), which could be another articular structure. Thin and low, keel-like suprainfrazygapophyseal laminae occur in the spine in the holotype (Fig. 10B).

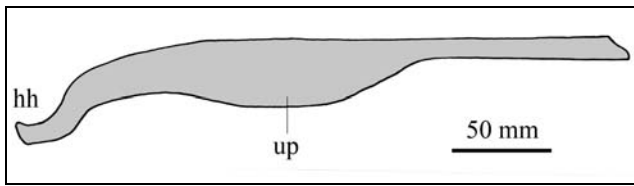Twenty-one to 23 dorsal ribs are identifiable in the slab. Their overall shapes resemble a sickle, and

Fig. 12   - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. Posterior dorsal rib, lateroposterior view. Abbreviations: hh = holocephalous head, up = uncinate process.

the rib shafts curve gently and do not expand distally. No longitudinal grooves are observed. The mid-shaft bears a posterior, wing-like expansion that forms a broad and blunt uncinate process (Fig. 12). The shafts of many anterior dorsal ribs are evidently collapsed, suggesting they were hollow or coarsely spongy inside, whereas some smaller, posterior elements are undoubtedly solid (i.e., finely spongy) distally.

"Sacral" vertebrae and ribs. The distinctive feature of the "sacral" vertebrae is the partial migration on the centrum of the articular surface for the rib. The transverse processes gradually reduce their lateral extension posterior to the dorsal vertebrae. In "sacral" vertebra 1, the process is reduced to two-thirds the length of that of the dorsal vertebra 7. The centrum of "sacral" vertebra 1 forms only a small portion of the articular facet for the rib, whereas it forms nearly one-third of the facet in "sacral" 2. The facet is borne on a very short process whose distal end is crater-like in "sacrals" 6-9, and possibly in "sacral" 5, which is nearly completely covered by a rib. The dorsal part of the process is formed by a ventral expansion of the neural arch. Whereas the dorsoventally elongated facets in "sacrals" 1 to 4 are slightly convex, in "sacrals" 6-9 they are concave, have each a median, dorsoventral groove, and occupy most of the lateral surfaces of the centra. The facet is larger in "sacral" 9 (the longest dimension is 30 mm) and possibly in "sacral" 8. Here, the facets resemble those of the four sacral vertebrae of the plesiosaur *Cryptoclidus* figured by Brown (1981). "Sacrals" 7-9 are probably the true sacral vertebrae; "sacral" 6 may also participate, if there are four sacral vertebrae. The shape of the neural spine changes with "sacral" 4 in which the prespinal lamina ends abruptly with a step at mid-spine, giving the spine a somewhat "bottle-shaped" profile. This feature is much more visible in mid-anterior caudals (Fig. 8E). The centrum lengths in "sacral" vertebrae range from 30.5-33 mm. The centrum of "sacral" 1 has three very small foramina below the transverse process; "sacral" 6 has a single, very small foramen. "Sacral" 5 has a large, 3 mm long, oval foramen and a possible second foramen that is narrow (1 mm) and elongate (7 mm).

The ribs situated before the sacrum, which are decidedly shorter and straighter than the preceding dor-

sal ribs (e.g., Brown 1981), are sometimes reported in literature as "lumbar" ribs. One short, curved, disarticulated element, that occurs in the "lumbar" region is labeled in Figure 4 as the most proximal caudal rib, but it cannot be excluded as a "lumbar" rib.

Three robust bones that are expanded at both extremities are identified as sacral ribs; four more are also tentatively identified as such. Two of the distally expanded ribs and one that is unexpanded lie parallel and close to each other. They are probably the right sacral ribs 1-3, slightly displaced from their articulations with the corresponding vertebrae. The unexpanded rib is the anteriormost of the group and could, alternatively, be the last "lumbar" rib. A similar, isolated rib is tentatively identified as a "sacral" in Figure 4, but it could be a "lumbar" or even an anterior caudal rib. The middle rib of the triad is 53 mm long and has a "bifid" (Y-shaped) distal expansion. The posteriormost element is also 53 mm long but is not "bifid" distally. Another, much more clearly exposed sacral rib is "bifid" distally and 57 mm long. The two rami of the expanded distal part are short, separated by a wide and deep central groove and bear slightly convex and rough distal articular surfaces. The surfaces are elongate anteroposteriorly and extend for 25 mm. One, probably the ventral, is wider dorsoventrally than the other. They would articulated with the ilium. The articular facet on the opposite expanded part of the rib has an axis of elongation rotated 90° with respect to that of the distal facets and fits with the articular facet on the centra of sacral vertebrae 8 and 9. Because this proximal articular surface is inclined, the rib was directed ventrolaterally when articulated.

Caudal vertebrae, ribs and haemapophyses. A total of 38 "caudals" are preserved. The upper part of the low process that bears the crater-like articular facet for the rib in the first "caudal" vertebra is formed by a tongue-like, ventral expansion of the neural arch that does not contribute the articular facet. The shape of the latter is similar to that of the last "sacral" vertebra. The distal surface of the rib-bearing process is less elongate dorsoventrally in "caudal" 2 and becomes triangular in "caudals" 3-5, where it also bears a ridge connecting its dorsal margin to the base of the neural arch. The surface has a large, elliptical, and anteroposteriorly elongate depression. Beginning with "caudal" 6, the elliptical depression is coincident with the whole distal surface of the rib-bearing process. Its size diminishes gradually posterior to this element. From "caudal" 13 to at least 18, the process and facet are replaced by a small knob. The posterior centra have two parallel, closely spaced longitudinal ridges on the lateral surface.

The lengths of the centra with the articular facet for the rib range from 28.5-32 mm; posteriorly, the lengths decrease gradually so that the shortest centrum

is 15 mm long. The centra are always higher than wide, and have ventrally flattened, oval articular faces in posterior view. Projecting posterior facets for the haemapophysis are present only in "caudal" vertebrae 7-10. Singular subcentral foramina 2 to 4 mm long can be seen in vertebrae 2-4.

On each, the neural spine is slightly inclined backward, square and laterally flattened in its basal half due to the wide prespinal and postspinal laminae. The prespinal lamina terminates dorsally around mid-spine at a step, whereas the postspinal lamina tapers more gradually, ending at roughly the same elevation. The upper (apical) portion of the spine is narrower; its cross-section changes posteriorly from subrectangular and laterally flattened to subcircular. All this imbues the neural spine with a "bottle-like" profile in lateral view (Fig. 8E). The neural spines of the posterior caudals are not hollow.

There are six probable caudal ribs, all detached from their articulations with their respective centra. Five have straight and dorsoventrally flat shafts with "squared" distal ends; the longest has a curved shaft. Their lengths are 92, 65, 65, 54, 25 and 22 mm according to their original positions along the vertebral series. As mentioned above, the longest element could eventually prove to be a "lumbar" rib. If it is a caudal rib, it would be the most proximal caudal rib preserved.

Six haemapophysis, ranging from 40-47 mm in length, occur in the proximal part of the tail; one is far removed on the slab. They are Y-shaped and have haemal spines that are fan-shaped in lateral view.

Gastralia. Eight gastralia are preserved scattered across the slab. Three V-shaped, medioventral elements are preserved close to each other (one is broken into two parts by a fault). They have small anterior projections, and their lateral shanks enclose an angle of 130-135°. Straight, slender, and spindle-shaped elements with pointed extremities represent intermediate or lateral gastral rib segments.

In summary, the holotype of *Bobosaurus* has at least 19 cervical vertebrae, six pectorals, 16 dorsals, 9 "sacrals" and at least 38 "caudals", for a total of 82 elements. The minimum count for the presacral vertebrae is 45 or 46, considering 4 or 5 "sacrals" as "lumbars".

Girdles

The pelvic girdle (Fig. 13) is relatively small in comparison with the overall size of the specimen. Pubic and ischiadic bones are exposed in the same view that, because the exposed surface is flat, must be dorsomedial.

The right ilium is hourglass-shaped; the thick iliac blade is expanded anteroposteriorly and has a rough dorsal surface. This suggests the presence of a cartilaginous covering that would have increased the articular surface for the sacral ribs. In fact, the ilium alone seems
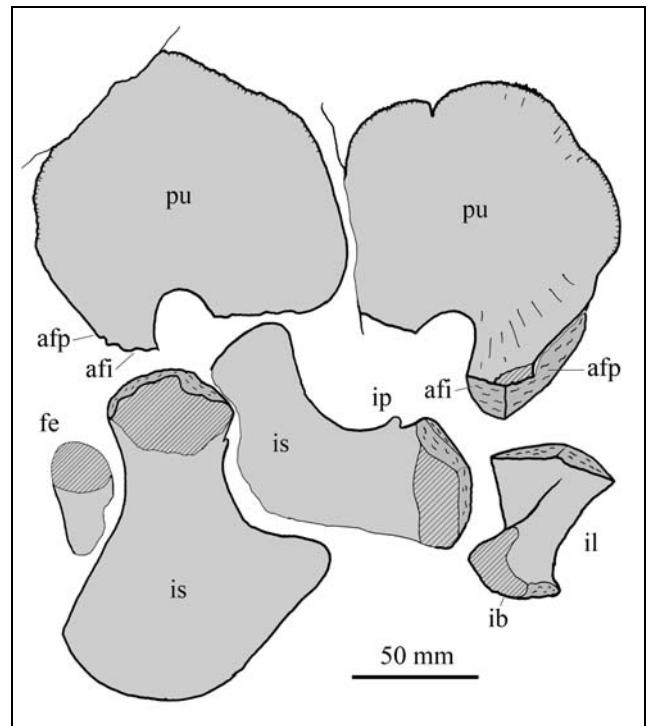

Fig. 13 - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. Elements of the pelvic girdle. Abbreviations: afi = articular face for the ischium, afp = acetabular facet of the pubis, fe = femur, ib = iliac blade, il = ilium, ip = small process of the ischium (obturator process?), is = ischium, pu = pubis. Damaged surfaces are lined and articular surfaces are in darker grey.

too small to host all the sacral ribs. No articular faces for the ribs are visible. One of the two processes of the iliac blade, although damaged, is more developed than the other. The most developed is the posterior one in *Nothosaurus* and *Simosaurus* (Rieppel 2000); if also true for *Bobosaurus*, the ilium exposes its posteromedial surface. The height of the ilium is 58.5 mm and the maximum length of the blade is 53 mm, whereas the maximum dimension of the ventral end is 56 mm. The shaft is twisted in such a way that the iliac blade is directed anteroposteriorly whereas the ventral part, with the articular surfaces, is expanded anteromedially-posterolaterally. The ventral surface, only partially freed from matrix, is convex and appears divided into two large, probably ischiadic and acetabular facets.

The ischium is a fan-shaped bone with a slightly expanded laterodorsal head that is damaged in both elements. The head carries the facet for the pubis and participates in the acetabulum; the facet for the ilium cannot be recognized because of damage. Distal to the short shaft is an expanded, ventromedial portion like in most sauropterygians. Along the anterior margin of the shaft, close to the head, there is a very small, thin (obturator?) process. The maximum breadth of the ischium is 125.5 mm and the anteroposterior length is 121-122 mm.
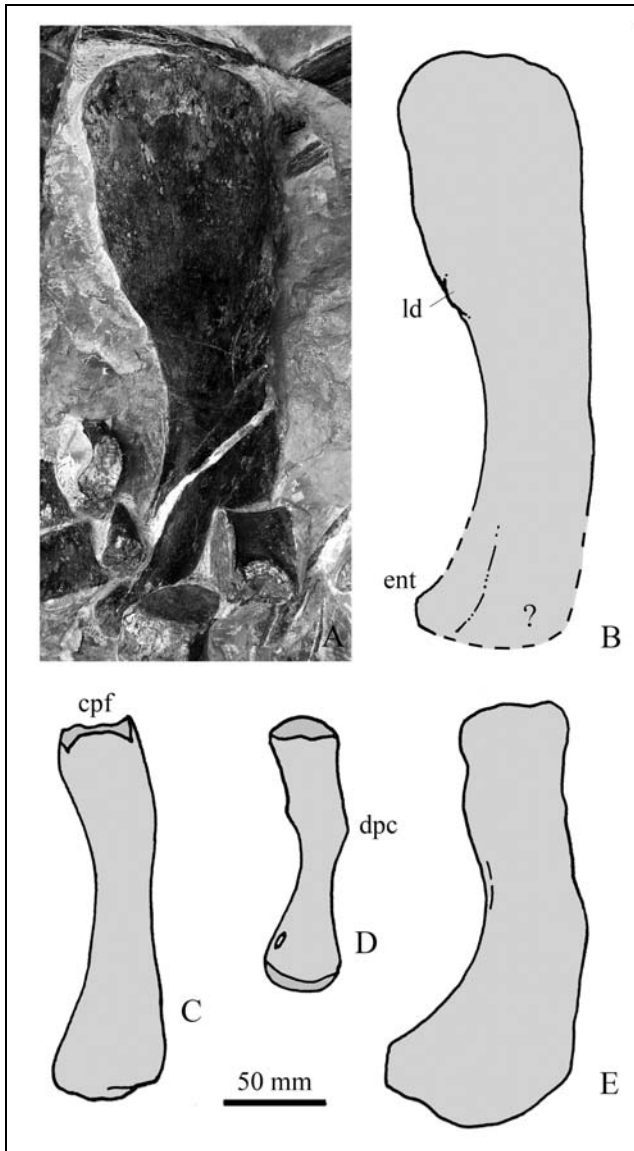
Fig. 14 - *Bobosaurus forojuliensis* n. gen. et sp., MFSN 27285, holotype. Humerus. A) Right humerus of *Bobosaurus*, dorsal view, B) drawing of the humerus of figure A, C) humerus referred to *Pistosaurus* (from Sues 1987), D) humerus of *Nothosaurus* (from Rieppel 2000, reversed), E) humerus of *Plesiosaurus* (from Storrs 1997). Abbreviations: cpf = concave proximal face, dpc = deltopectoral crest, ent = entepicondyle, ld = knob for the muscle latissimus dorsi,? = portion covered by the vertebral centra.

process bears a posterior articular surface for the ischium and a doubly wide, posterolaterally facing acetabular facet. The pubis makes up the anterior part of the acetabulum. An articular facet for the ilium is lacking.

Limbs

The proximally swollen right humerus, exposed in dorsal view, is a rather robust bone (Fig. 14 A-B) whose maximum preaxial-postaxial width is 83 mm; it becomes flatter distally. It is partly covered distally by matrix and the centra of dorsal vertebrae 10-11. The exposed part, from the proximal end to the entepicondyle, is 280 mm long and is probably close to the total length. It is more robust than the humeri of *Pistosaurus* and *Augustasaurus* and comparatively larger (Fig. 14): both Anisian taxa have a total lengths estimated at around 2.5 to 3 m and have humeri that are 169 and 184 mm long, respectively (Sander et al. 1997). This proportional difference is also shown by the ratio of humerus/mid-dorsal vertebral centrum length, which is ~9 in *Bobosaurus*, ~ 4.7 in *Pistosaurus* (SMF R 4041), and 4.6 in *Augustasaurus*. This indicates that the forelimb of the new taxon was proportionally larger. The mid-distal shaft postaxial margin is decidedly curved, whereas the preaxial margin is straight, at least up to the covered distal end of the bone. There is no trace of a deltopectoral crest, whereas a knob, possibly for the insertion of the M. latissimus dorsi, occurs close to the postaxial margin. The proximal face of the bone is rough and concave in the middle.

Only two metapodials are preserved. They are gracile bones that are slightly expanded at their extremities, 55 and 46 mm long, and 9 and 11 mm wide at midshaft, respectively. A stouter and more robust bone with expanded extremities is most probably a proximal phalanx. It measures 32.5 mm long and 10 mm wide at midshaft.

The hind limbs are disarticulated and only a tibia and what is probably a femur are preserved. The femur is exposed close the ischia as a circular cross-section of a diaphysis (Fig. 13). The distal part of the tibia is displaced by a fault. It is a straight, relatively slender bone that has moderately expanded extremities and is 145 mm long and 23 mm wide at midshaft (minimum width). The proximal articular face is flat, whereas the distal face is convex. The tibia is about half the length of humerus, a proportion shared with the nothosaurid *Lariosaurus valceresii* Tintori & Renesto, 1990 that has hind limbs nearly the same length as the forelimbs. The hind limbs of *Bobosaurus* could have been comparatively long, as are the forelimbs.

Two tarsals lie near the tibia. Both are disc-like with circular outlines and without indentations. One is larger than the other, with longest diameters 35 mm and 28 mm, respectively. According to Romer (1956, p. 401), the tarsi of "nothosaurs" have "two relatively large

The pubis is a plate-like bone that is subcircular or spade-shaped in dorsomedial view and measures 140 mm in its greatest dimension. The anterior, dorsolateral, and ventromedial margins of the bone are finely fringed, suggesting that an outer part of the element was made of cartilage. The posterior border is emarginated by a deep, semicircular notch, that constitutes the anterior part of a reduced puboischiadic (thyroid) fenestra. There is no obturator foramen. The posterolateral (ischioacetabular) process is narrow in dorsomedial view, but is very thick in the dorsomedial-ventrolateral direction. The

proximal plates, of which one representing the astragalus was much larger than the calcaneum; distal ossifications are smaller and variable." *Nothosaurus* has three tarsals (Peyer 1939; Rieppel & Wild 1996), as does *Simosaurus* (Rieppel 1994), and the calcaneum and astragalus are markedly larger than the distal tarsal. The astragalus is decidedly larger than the calcaneum in *Simosaurus*, and is slightly larger than the calcaneum in *Nothosaurus giganteus* Münster, 1834 (= *Paranothosaurus amsleri* Peyer, 1939). Because of their size, the larger element is identified as the astragalus and the smaller as the calcaneum.

Comparison and discussion

Characters diagnostic of the Sauropterygia are: absence of cervical intercentra (excluding the atlas-axis complex); cervical ribs with free anterior processes; and humerus curved with the crest for insertion of the M. latissimus dorsi muscle reduced. One character is diagnostic of the Eosauropterygia: the facet on the centrum for the neural arch pedicels is "butterfly-shaped" or "cruciform". In addition to large body size and tall neural spines, diagnostic features that distinguish *Bobosaurus* from Pachypleurosauria include: dorsal iliac blade not reduced to simple dorsal process; vertebral centra relatively constricted in ventral view; and sacral ribs with distal expansions.

Characters autapomorphic relative to all sauropterygians. Cervical centra that are "pear-shaped" in anteroposterior view and higher than wide have not been reported in any sauropterygian. Prezygapophyseal-infraprezygapophyseal/postzygapophyseal-infrapostzygapophyseal articulations in the dorsal vertebrae are an autapomorphy of *Simosaurus gaillardoti* H. v. Meyer, 1842 (Rieppel 2000). The vertebrae of *Bobosaurus* exhibit the same complex zygapophyseal articular structures as *Simosaurus*, but have a reversed anteroposterior polarity. In fact, according to Rieppel (1994), the condyle is anterior and the cotyle is posterior in *Simosaurus*. No other sauropterygian has such a high cervical and caudal neural spines, and the "bottle-like" outline of the "sacral" and caudal neural spines is also unique (Owen 1865; Tarlo 1960; Brown 1981; Storrs 1991, 1997; Rieppel & Wild 1996; Rieppel 1994, 1997, 1998, 2000, 2001; Rieppel et al. 1999; 2002). The hollow neural spines, coarsely spongy ribs and lightened vertebrae are autapomorphic (ibidem). The shape of the mid-posterior cervical ribs differs from those of *Simosaurus* and *Nothosaurus* (Rieppel 1994), *Corosaurus* (Storrs 1991), *Pistosaurus* (Geissler 1895), *Augustasaurus* (Rieppel et al. 2002) as in many plesiosaurians (Owen 1865; Brown 1981). The humerus is comparatively much larger than that of pistosaurids and other

stem-group sauropterygians (Peyer 1939; Storrs 1991; Sanders et al. 1997; Rieppel 1994, 2000).

Bobosaurus forojuliensis displays two features that were previously reported as autapomorphies of other sauropterygian taxa. High dorsal neural spines were considered a synapomorphy of a clade composed of *Nothosaurus mirabilis* Münster, 1834, *N. haasi* Rieppel, Mazin & Tchernov, 1997 and *N. tchernovi* Haas, 1980 (Rieppel 2000). The highest are found in *N. mirabilis* where "high neural spines on dorsal vertebrae" was considered a diagnostic feature of the species (Rieppel 2000). The dorsal neural spines of *Bobosaurus* are decidedly higher than those of *N. mirabilis* figured in Rieppel (2000, p. 12) where the ratio of neural spine/centrum height is only 1.75. "Dorsal ribs with distinct uncinate process" was thought to diagnose the placodont *Paraplacodus* (Rieppel 2000).

The concomitant presence of paired atlantal and axial intercentra, an atlantal centrum subequal in lateral extension to the atlantal neural arch and intercentrum, the exclusion of the atlantal centrum from both the anterior and ventral margins of the complex in lateral view, and the fusion of the axial rib high on the atlantal centrum, is a unique combination of characters in the new taxon. The axial and atlantal intercentra of MFSN 27285 meet ventrally and exclude the atlantal centrum from the ventral face of the complex as in *Trinacromerum* Cragin, 1888, and all other polycotylids (Romer 1956). The centrum is also excluded from the lateral margin of the cotyle in those plesiosaurs and in *Bobosaurus*. This is the derived condition in plesiosaurians according to O'Keefe (2001). However, the structure in the complex of MFSN 27285 differs from that of *Trinacromerum* in the larger size of atlantal centrum and the absence of a hypapophyseal ridge. A large atlantal centrum is a feature of the Cryptoclididae, but the bone has an anterior position (participating in the lateral margin of the cotyle) in those plesiosaurians (Bakker 1993). Unlike *Bobosaurus*, the axial and atlantal intercentra in plesiosaurians are both single elements (however, Goodrich [1930, p. 58] reported the presence of paired "hypocentra" in the cervical region of plesiosaurians), and a hypapophyseal ridge often arises ventrally in the complex. According to O'Keefe (2001), the broad articulation of the axial rib with the atlantal centrum and/or other elements is the primitive condition among plesiosaurians and is found in members of different clades (*Thalassiodracon* Storrs & Taylor, 1996, *Cryptoclidus* Phillips, 1871, *Muraenosaurus* Seeley, 1874, *Mortuneria* Chatterjee & Small, 1989, and *Peloneustes* Lyddeker, 1889). However, the only rib in the atlas-axis complex of *Plesiosaurus dolichodeirus* Conybeare, 1824 is short, thorn-like, and posteriorly projecting like that of *Bobosaurus*, but it is fused to the ventral margin of the axial

centrum (Storrs 1997) as in many other plesiosaurians (Bakker 1993).

The concomitant presence of a plesiosaurian pubis (plate-like, spade-shaped, without an obturator foramen and an iliac contact) with a stout, hourglass-shaped ilium with a twisted shaft is also unique to *Bobosaurus*.

Characters autapomorphic relative to Nothosauroidea. Unlike members of the Nothosauroidea (*Simosaurus* and Nothosauria), *Bobosaurus* has a pubis with a convex ventromedial margin and an astragalus that lacks a concave proximal margin. The nothosauroidean pubis is characteristically waisted and has a concave ventromedial margin. Teeth of the new taxon are decidedly unlike the distolateral teeth of *Simosaurus* which are characterized by broad and blunt crowns distinctly set off from the tooth bases, and are more slender than its mesial (anterior) teeth (Rieppel 1994). They also differ from those with widely-spaced and sharp ridging of *Nothosaurus* (Vickers-Rich et al. 1999; Dalla Vecchia & Avanzini 2002). The Nothosauridae (*Nothosaurus* + *Lariosaurus* Curioni, 1847) have vertebral centra with parallel lateral edges (i.e., they are laterally unconstricted cylinders) and sacral ribs lacking distinct expansions at their distal ends (Rieppel 2000).

Synapomorphies of stem-group sauropterygians. The cervical vertebral count of *Bobosaurus* (probably 19) is more similar to that of *Pistosaurus* (22 according to Geissler 1895, 24 according to Sues 1987) and *Nothosaurus* (19 to at least 24; Rieppel 2001) than to the diagnostic >28 of "plesiosauroid" plesiosaurians and the ~30 of primitive "pliosauroid" plesiosaurians per Brown (1981). Cervical ribs and neural arches are fused to the centra, but a suture is still visible. Usually they are completely fused, with sutures obliterated, in adult plesiosaurians, although the presence of sutures is an immature trait (Brown 1981). The centra are never wider than high, whereas plesiosaurians always show the reverse (Brown 1981). The zygapophyseal facets of the cervical vertebrae never slope mediolaterally in *Bobosaurus* whereas they do in plesiosaurians (e.g., Owen 1865; Brown 1981; Taylor & Cruicksank 1993; Storrs & Taylor 1996). Accessory articulations on the vertebrae are common in stem-group sauropterygians, but their absence is a diagnostic character of the Plesiosauria (Storrs 1991; O'Keefe 2001; Smith 2003). The transverse processes of plesiosaurians are generally more slender and longer than those of the new taxon, and have subcircular articular facets (Brown 1981). The tibia is relatively slender in *Bobosaurus*, like in stem-group sauropterygians, whereas it is characteristically a stouter bone in members of the Plesiosauria (e.g., Brown 1981; Storrs 1997). Gastralia in *Bobosaurus* are not so robust as to form a ventral plastron, whereas they are pachyostotic in plesiosaurians. The ilium is stout and low in the new

taxon, more like those common to stem-group sauropterygians (e.g., Storrs 1991; Rieppel 2000) than the slender and high shafts typical of the Plesiosauria. The tail is longer than the short appendage of plesiosaurians that have an average of 25 vertebrae (Bardet et al. 1999).

Synapomorphies of the Plesiosauria. Plesiosaurian teeth are often slender and straight or slightly curved cones with closely-striated surfaces, like those of *Bobosaurus* (Brown 1981; Massare 1987; Taylor & Cruicksank 1993; Storrs 1997). The atlas, axis, and their respective neural arches and intercentra are firmly interconnected and interlocked to form a robust single element in adult plesiosaurs, although sutures can be visible among individual components (e.g. Jaekel 1907; Romer 1956; Bakker 1993, Storrs 1997; Carpenter 1997; Gasparini et al. 2003). The plesiosaurian condition that occurs in *Bobosaurus* is unusual among reptiles (Bakker 1993). The neural spine of the axis slopes posteriorly and ends far beyond the posterior end of the centrum in *Libonectes morgani* (Welles, 1949) (Carpenter 1997), *Plesiosaurus dolichodeirus* (Storrs 1997) and *Thalassiodracon* (Storrs 1997), as well as in *Bobosaurus*.

Having cervical zygapophyses narrower than the widths of their centra is a diagnostic feature of the Plesiosauria according to Storrs (1991) and O'Keefe (2001). Parapophyseal and diapophyseal facets in the cervical vertebrae of *Plesiosaurus* are distinctly paired on the centrum and anteroposteriorly elongate (Storrs 1997). The posterior cervical vertebrae have rounded and pedicelate rib facets (Storrs 1997). Dorsal neural arches (excluding the spine) are apomorphically shorter than centrum height in plesiosaurians according to O'Keefe (2001) and Smith (2003). High neural spines are listed as a diagnostic feature of the Plesiosauria by Storrs (1991). The neural spines have a recurved anterior profile in the cervical vertebrae of the Early Liassic pliosauroid *Attenborosaurus conybearei* (Sollas, 1881) (Owen 1865), the anterior cervicals of the Sinemurian *Plesiosaurus dolichodeirus* (Owen 1865) and the upper Toarcian elasmosaurid *Occitanosaurus tournemirensis* (Sciau, Crochet & Mattei, 1990) (Bardet et al. 1999). This feature is not found in any stem-group sauropterygian. The cervical ribs are sutured or fused without suture to their respective centra in plesiosaurians, whereas in pistosaurids they are not (Rieppel et al. 2002). Cervical ribs are fused to the centra only in the small *Corosaurus* among stem-group sauropterygians (Storrs 1991). Having pubes developed into large, ventral plates is a diagnostic plesiosaurian feature according to Brown (1981). "Anterior border of pubis expanded" and "....iliopubic contact lost" are apomorphic characters of Plesiosauria (Storrs 1991). The pubes of plesiosaurians are rounded, sometimes spade-shaped, and have a narrow contact with the ischia mainly in juvenile specimens (Storrs 1997; Bardet et al. 1999; Carpenter

1999). *Corosaurus alcovensis* Case, 1936 has a rounded pubis, but retains an obturator foramen and a dorsal articular facet for the ilium. The absence of an obturator foramen is an apomorphy of Plesiosauria (Storrs 1991). O'Keefe (2001) reports this feature in the pistosauroid *Cymatosaurus* and the nothosaurian *Lariosaurus*. However, *Cymatosaurus* is known only from skull material and gastralia (Rieppel 2000) and the pubis of *Lariosaurus* has an obturator foramen (Rieppel 2000). The lack of articulation between ilium and pubis is an apomorphic character of the Plesiosauria per Storrs (1991), O'Keefe (2001) and Smith (2003). All these plesiosaurian features occur also in *Bobosaurus*.

The overall shape of the humerus in *Bobosaurus* is intermediate between those of nothosaurids and *Plesiosaurus*, which is primitive among plesiosaurians (Storrs 1997). *Bobosaurus* shares with *Plesiosaurus* the absence of a deltopectoral crest (a pistosaurid feature as well; Rieppel et al. 2002), a concave postaxial margin, a robust shaft, and an entepicondyle projecting posteriorly.

Typically, not all the features characteristic of the later members of a successful group appear at the same time during its early history. It is possible that many of the plesiomorphic characters of *Bobosaurus* are those that only later attained the "plesiosaurian condition."

Synapomorphies of the Pistosauridae. Unfortunately some characters shared by *Bobosaurus* and plesiosaurians cannot be checked in *Pistosaurus* and *Augustasaurus*. The few pistosaurid remains overlap little with available *Bobosaurus* material. As a result, comparison is easier with plesiosaurs than with pistosaurids, making it difficult to decide whether or not the new taxon is a pistosaurid. Most of the known diagnostic features of *Pistosaurus* and *Augustasaurus* are in the skull and are therefore unknown in *Bobosaurus*. The pelvic girdle, sacrum, and caudal vertebrae are not preserved in the only *Augustasaurus* specimen, and the atlas-axis complex has never been described (Sander et al. 1997; Rieppel et al. 2002). Only a partial reconstruction of the ischium and ilium is available for the pelvic girdle of the supposed *Pistosaurus* postcrania (Sues 1987). *Bobosaurus* could share with pistosaurids some skeletal features that cannot be checked in the scarce described material.

However, some pistosaurid features occur in *Bobosaurus*. The rostrum of pistosaurids is characteristically elongate, tapering, pointed, and has anterior premaxillary and dentary fangs (Rieppel et al. 2000), like that suggested by the cross-section of the tip of the snout of the new taxon. The vertebrae referred to *Pistosaurus* are laterally constricted, with oval, taller than wide, slightly amphicoelous articular faces; the dorsals have wide prespinal and postspinal laminae, and the neural spines are relatively tall (Sues 1987; pers. obs.).

The presence of subcentral foramina, considered apomorphic of the Plesiosauria by Brown (1981) and Storrs (1991), is a diagnostic feature of the Pistosauria (Pistosauridae + Plesiosauria) per Rieppel et al. (2002). Those foramina are unevenly present in *Bobosaurus*: they are absent in the cervicals, present in some pectorals, dorsals, "sacrals", and anterior "caudals" but sometimes number 2-3. Subcentral foramina are occasionally found also in centra referred to *Nothosaurus* (Rieppel 2000, fig. 4B; pers. obs.), suggesting that they are more widespread among the Eusauropterygia. As in *Bobosaurus*, the subcentral foramina can sometime be absent in polycotylid plesiosaurians (Sato & Storrs 2000) suggesting that the feature could be unevenly distributed among pistosaurians.

Dorsoventrally narrow transverse processes in the dorsal vertebrae is a feature shared by the new taxon, pistosaurids, and plesiosaurians; they are wider in nothosaurians. The humerus of *Bobosaurus* has a concave proximal face like those humeri referred to *Pistosaurus* from the Muschelkalk Basin (see Sues 1987) and an incomplete humerus from the upper Anisian of NE Italy attributed to cf. *Pistosaurus longaevus* (Dalla Vecchia & Avanzini 2002; actually very unlike the humeri of *Pistosaurus* in its general morphology).

The new taxon does not share with pistosaurids the diagnostic character "parapophysis shifted backward on centrum along cervical vertebral column" (Rieppel et al. 2002).

Conclusions

Bobosaurus is a large sauropterygian with plesiosaurian affinities, but also many peculiar features. The trunk was stiffened, as shown by the tall neural spines, narrow neural arches and their articulation, and the uncinate process in the dorsal ribs, all of which are features useful in preventing torsion of the vertebral column (Carroll 1988). The skeleton was lightened, the opposite of the pachyostotic condition observed in many sauropterygians. The forelimbs were particularly well-developed, as indicated by the large and robust humerus. *Bobosaurus* dwelled in the shallow sea covering the northwestern coasts of Tethys during the early Carnian. All this suggests it was a surface swimmer that mainly used its forelimbs, and possibly hind limbs, in swimming.

Bobosaurus is a further representative of the sauropterygian fauna that lived in the subtidal environment of the Dogna area, represented to date by cyamodontoid placodonts (*Protenodontosaurus italicus* Pinna, 1990) and *Nothosaurus* sp. (Rieppel & Dalla Vecchia 2001).

The phylogenetic position of *Bobosaurus* is presently difficult to resolve because the holotype lacks most of the skull. It is probably a specialized pistosaurian sauropterygian, possibly close to *Pistosaurus* and *Augustasaurus*. Alternatively, it could belong to a Late Triassic clade closer to Liassic plesiosaurians than are pistosaurids, whose existence was hypothesized by Bakker (1993). In a cladistic analysis the Anisian pistosaurids could be perceived as the sister-group of the plesiosaurians simply because the actual sister-group lived during the long (20 million years) Late Triassic gap in the eusauropterygian fossil record. The crown-group sauropterygians that dominated the Jurassic and Cretaceous seas probably evolved their characteristic features during that interval. *Bobosaurus* lived at the beginnings of the gap and a minimum of 9 million years after the only two pistosaurids known to date. This second possibility could be supported or disproved only by increasing the Late Triassic eusauropterygian record.

REFERENCES

Bakker R.T. (1993) - Plesiosaur extinction cycles - events that mark the beginning, middle and end of the Cretaceous. In: Caldwell W.G.E. & Kauffman E. G. (eds) - Evolution of the Western Interior Basin, Geological Association of Canada, special paper, 39: 641-664, Toronto.

Bardet N., Godefroit P. & Sciau J. (1999) - A new elasmosaurid plesiosaur from the Lower Jurassic of southern France. *Palaeontology*, 42 (5): 927-952, London.

Brown D. S. (1981) - The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bull. British Mus. (Nat. Hist.)*, Geology Series, 35: 253-247, London.

Carpenter K. (1997) - Comparative cranial anatomy of two North American Cretaceous plesiosaurs. In: Callaway J.M. & Nicholls E. L. (eds) - Ancient Marine Reptiles, pp. 191-216, Academic Press, London and New York.

Carpenter K. (1999) - Revision of North American elasmosaurs from the Cretaceous of the Western Interior. *Paludicola*, 2 (2): 148-173, Rochester.

Carroll R.L. (1988) - Vertebrate Paleontology and Evolution. V. of 698 pp. Freeman W.H., New York.

Dalla Vecchia F.M. & Avanzini M. (2002) - New findings of isolated remains of Triassic reptiles from northeastern Italy. *Boll. Soc. Paleont. It.*, 41(2/3): 215-235, Modena.

Gasparini Z., Bardet N., Martin J.E. & Fernandez M. (2003) - The elasmosaurid plesiosaur *Aristonectes* Cabrera from the latest Cretaceous of South America and Antarctica. *J. Vert. Paleont.*, 23 (1): 104-115, Lawrence.

Geissler G. (1895) - Über neue Saurier-Funde aus dem Muschelkalk von Bayereuth. *Zeitschr. deut. geol. Ges.*, 47: 331-355, Berlin.

Goodrich E. S. (1930) - Studies on the structure and development of vertebrates. V. of 837 pp. University of Chicago Press edition 1986, Chicago.

Gradstein F. M. & Ogg J.G. (2004) - Geologic Time Scale 2004 - why, how, and where the next! *Lethaia*, 37: 175-181, Oslo.

Hagdorn H. & Rieppel O.C. (1999) - Stratigraphy of marine reptiles in the Triassic of Central Europe. *Zbl. Geol. Paläont.* Teil I (7-8; 1998): 651-678, Stuttgart.

Jadoul F. & Nicora A. (2000) - La discontinuità stratigrafica del Ladinico sommitale del Rio di Terra Rossa (Dogna, Alpi Giulie). *Riassunti delle comunicazioni orali e dei posters - 80° Riunione Estiva S.G.I.*, 287-288, Trieste.

Jaekel O. (1907) - *Placochelys placodonta* aus der Obertrias des Bakony. In: Resultaten der wissenschaftlichen Erforschung des Balatonsee, 1. Band. 1. Teil. Palaeontologischer Anhang. Pp. 91 pp., Victor Hornyanszky, K. und K. Hofbuchdruckerei, Budapest.

Massare J. A. (1987) - Tooth morphology and prey preference of Mesozoic marine reptiles. *J. Vert. Paleont.*, 7 (2): 121-137, Lawrence.

O'Keefe F. R. (2001) - A cladistic analysis and taxonomic revision of Plesiosauria (Reptilia: Sauropterygia). *Acta Zool. Fennica*, 213: 1-63, Helsinki.

Owen R. (1865) - A monograph on the fossil Reptilia of the Liassic Formations. Part 1. Order Sauropterygia. *Palaeontogr. Soc. Monogr.*, 17: 1-40, London.

Peyer B. (1939) - Die Triasfauna der Tessiner Kalkalpen. XIV. *Paranothosaurus amsleri* nov. gen. nov. spec. *Abh. schweiz. paläont. Gesellschaft.*, 62: 1-87, Zurich.

Preto N., Roghi G. & Gianolla P. (2005) - Carnian stratigraphy of the Dogna area (Julian Alps, northern Italy): tessera of a complex palaeogeography. *Boll. Soc. Geol. It.*, 124: 269-279, Roma.

Rieppel O. C. (1994) - Osteology of *Simosaurus gallairdoti* and the relationships of stem-group Sauropterygia. *Fieldiana*, Geology n. ser., 28: 1-85, Chicago.

Rieppel O. C. (1997) - Sauropterygia from the Muschelkalk of Djebel Rehach, Southern Tunisia. *N. Jahrb. Geol. Paläont. Mitt.*, 1997-9: 517-530, Stuttgart.

Rieppel O. C. (1998) - The status of the Sauropterygian Reptile genera *Ceresiosaurus*, *Lariosaurus*, and *Silvestrosaurus* from the Middle Triassic of Europe. *Fieldiana*, Geology n. ser., 38: 1-46, Chicago.

Rieppel O. C. (2000) - Sauropterygia I. In: Wellnhofer P. (ed.) - *Handbuch der Paläoherpetologie*, Part 12A. V. of 134 pp., Verlag Friedrich Pfeil, München.

Rieppel O. C. (2001) - A new species of *Nothosaurus* (Reptilia: Sauropterygia) from the Upper Muschelkalk (Lower Ladinian) of southwestern Germany. *Palaeontographica* Abt. A, 263: 137-161, Stuttgart.

Rieppel O. C. & Dalla Vecchia F. M. (2001) - Marine Reptiles from the Triassic of the Tre Venezie area, northeastern Italy. *Fieldiana*, Geology n. ser., 44: 1-25, Chicago.

Rieppel O. C., Mazin J.-M. & Tchernov E. (1999) - Sauropterygia from the Middle Triassic of Makhtesh Ramon, Negev, Israel. *Fieldiana*, Geology n. ser., 40: 1-85, Chicago.

Rieppel O. C., Sander P. M. & Storrs G. W. (2002) - The skull of the pistosaur *Augustasaurus* from the Middle Triassic of nortwestern Nevada. *J. Vert. Paleont.*, 22(3): 577-592, Lawrence.

Rieppel O. C. & Wild R. (1996) - A revision of the genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic, with comments on the status of *Conchiosaurus clavatus*. *Fieldiana*, Geology n. ser., 34: 1-82, Chicago.

Roghi G. (2004) - Palynological investigations in the Carnian of Cave del Predil area (Julian Alps, NE Italy). *Rev. Palaeobot. Palynol.*, 132: 1-35, Amsterdam.

Romer A. S. (1956) - Osteology of the Reptiles. Third impression (1976). V. of 772 pp., The University of Chicago Press, Chicago & London.

Sander P. M., Rieppel O. C. & Bucher H. (1997) - A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of the plesiosaurs. *J. Vert. Paleont.*, 17(3): 526-533, Lawrence.

Sato T. & Storrs G. W. (2000) - An early polycotylid plesiosaur (Reptilia: Sauropterygia) from the Cretaceous of Hokkaido, Japan. *J. Paleont.*, 74(5): 907-914, Lawrence.

Sirna G., Dalla Vecchia F.M., Muscio G. & Piccoli G. (1994) - Catalogue of Paleozoic and Mesozoic Vertebrates and Vertebrate localities of the Tre Venezie area (North Eastern Italy). *Mem. Sci. Geol.*, 46: 255-281, Padova.

Smith A. S. (2003) - Cladistic analysis of the Plesiosauria (Reptilia: Sauropterygia). Master thesis in Palaeobiology, University of Bristol, pp. 91 (Unpublished).

Storrs G. W. (1991) - Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. *Bull. Peabody Mus. Nat. Hist.*, 44:1-151, New Heaven.

Storrs G. W. (1994) - Fossil vertebrate faunas of the British Rhaetian (latest Triassic). *Zool. J. Linn. Soc.*, 112: 217-259, London.

Storrs G.W. (1997) - Morphological and taxonomic clarification of the genus *Plesiosaurus*. In: Callaway J.M. & Nicholls E. L. (eds) - Ancient Marine Reptiles, pp. 145-190, Academic Press, London and New York.

Storrs G.W. & Taylor M. A. (1996) - Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian/Hettangian) of Street, Somerset, England. *J. Vert. Paleont.*, 16(3): 403-420, Lawrence.

Sues H.-D. (1987) - Postcranial skeleton of *Pistosaurus* and interrelationships of the Sauropterygia (Diapsida). *Zool. Journ. Linn. Soc.*, 90: 109-131, London.

Tarlo L.B.H. (1960) - A review of the Upper Jurassic pliosaurs. *Bull. Br. Mus. Nat. Hist.*, A4: 147-189, London.

Taylor M. A. & Cruickshank A.R.I. (1993) - A plesiosaur from the Linksfield Erratic (Rhaetian, Upper Triassic) near Elgin, Morayshire. *Scottish J. Geol.*, 29: 191-196, Edimburgh.

Tintori A. & Renesto S. (1990) - A new *Lariosaurus* from the Kalkschieferzone (Uppermost Ladinian) of Valceresio (Varese, N. Italy). *Boll. Soc. Paleont. Ital.*, 29(3): 309-319, Modena.

Vickers-Rich P., Rich T.H., Rieppel O. C., Thulborn R.A. & McClure H.A. (1999) - A Middle Triassic Vertebrate fauna from the Jilh Formation, Saudi Arabia. *N. Jahrb. Geol. Paläont. Abt.*, 213 (2): 201-232, Stuttgart.