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COMMENTS ON THE SKELETAL ANATOMY OF THE TRIASSIC REPTILE *BOBOSAURUS FOROJULIENSIS* (SAUROPTERYGIA, PISTOSAUROIDEA)

COMMENTI SULL'ANATOMIA SCHELETRICA DEL RETTILE TRIASSICO *BOBOSAURUS FOROJULIENSIS* (SAUROPTERYGIA, PISTOSAUROIDEA)

Riassunto breve - *Bobosaurus forojuliensis* è un grande rettile eusaurotterigio proveniente dal Carnico marino (Fomazione di Rio del Lago, circa 235 milioni di anni) di Dogna (Regione Autonoma Friuli Venezia Giulia, Provincia di Udine, Italia nordorientale) rappresentato da due esemplari: l'olotipo (MFSN 27285) e un singolo, isolato arco neurale (MFSN 27854). È un pistosauroide che per alcuni è il plesiosauro più primitivo, per altri è il sister-group di Plesiosauria o comunque è al di fuori di tale clade. L'olotipo è costituito da uno scheletro parziale e moderatamente disarticolato che include la punta del muso con alcuni denti, parte del segmento cervicale della colonna vertebrale, i segmenti dorsale (inclusivo delle vertebre pettorali) e sacrale, la maggior parte del segmento caudale, alcuni elementi gastrali, l'omero destro, quasi tutto il cinto pelvico e alcuni elementi degli arti posteriori. Questi reperti sono stati descritti da Dalla Vecchia (2006). Con il presente articolo si completa la descrizione dell'olotipo, mostrando in particolare i vari elementi scheletrici in dettaglio e a colori. Inoltre, questi elementi scheletrici sono confrontati con le corrispondenti ossa degli altri Pistosauroidea, soprattutto *Yunguisaurus liae* e *Wangosaurus brevirostris* del Ladinico superiore cinese, che al tempo della prima pubblicazione di *Bobosaurus forojuliensis* non erano ancora noti. L'esemplare MFSN 27854 assomiglia, in parte, agli archi neurali del notosauroide *Simosaurus* che nel 2006 non era ancora noto nella Formazione di Rio del Lago della zona di Dogna e potrebbe appartenere, in alternativa, ad un taxon vicino a quest'ultimo.
Parole chiave: *Bobosaurus forojuliensis*, Sauropterygia, Eusauropterygia, Pistosauroidea, Osteologia, Triassico, Carnico, Friuli.

Abstract - *This paper integrates the osteological description of the holotype of the pistosauroid eusauropterygian* Bobosaurus forojuliensis *(lower Carnian, NE Italy), which was first described by Dalla Vecchia (2006), mainly showing in detail the various skeletal elements and by the use of colour photographs. Furthermore, comparisons with the corresponding bones of the other non-plesiosaurian pistosauroids are done, mainly with* Yunguisaurus liae *and* Wangosaurus brevirostris *from the upper Ladinian of China, which were still unknown at the time of the first publication of* Bobosaurus forojuliensis. *The referred specimen MFSN 27854 might belong to a taxon closer to the nothosauroid* Simosaurus *than to* Bobosaurus forojuliensis *and should be prudently excluded from the apodigm of the latter.*
Key words: Bobosaurus forojuliensis*, Sauropterygia, Eusauropterygia, Pistosauroidea, Osteology, Triassic, Carnian, Friuli.*

Introduction

Bobosaurus forojuliensis Dalla Vecchia, 2006 is a large eusauropterygian reptile from the lower Carnian of Dogna (Friuli Venezia Giulia Autonomous Region, Udine Province, NE Italy) represented by two specimens: the holotype (MFSN 27285) and a single isolated neural arch (MFSN 27854) (Dalla Vecchia 2006). The holotype is a moderately disarticulated and partially preserved skeleton including the tip of the rostrum with some teeth, part of the cervical segment of the vertebral column, the whole dorsal (including the pectorals vertebrae) and sacral segments, most of the caudal segment (including some haemapophyses), some gastralia, the right humerus, most of the pelvic girdle, some elements of the hind limbs, two metapodials and one phalanx (Dalla Vecchia 2006) (Figs 1-2).

Both specimens come from the lower part of the shallow marine Rio del Lago Formation, cropping out along the Pontuz Brook near the village of Gran Colle (NW of Dogna).

Bobosaurus forojuliensis is the oldest and most primitive plesiosaur, according to Fabbri et al. (2015),

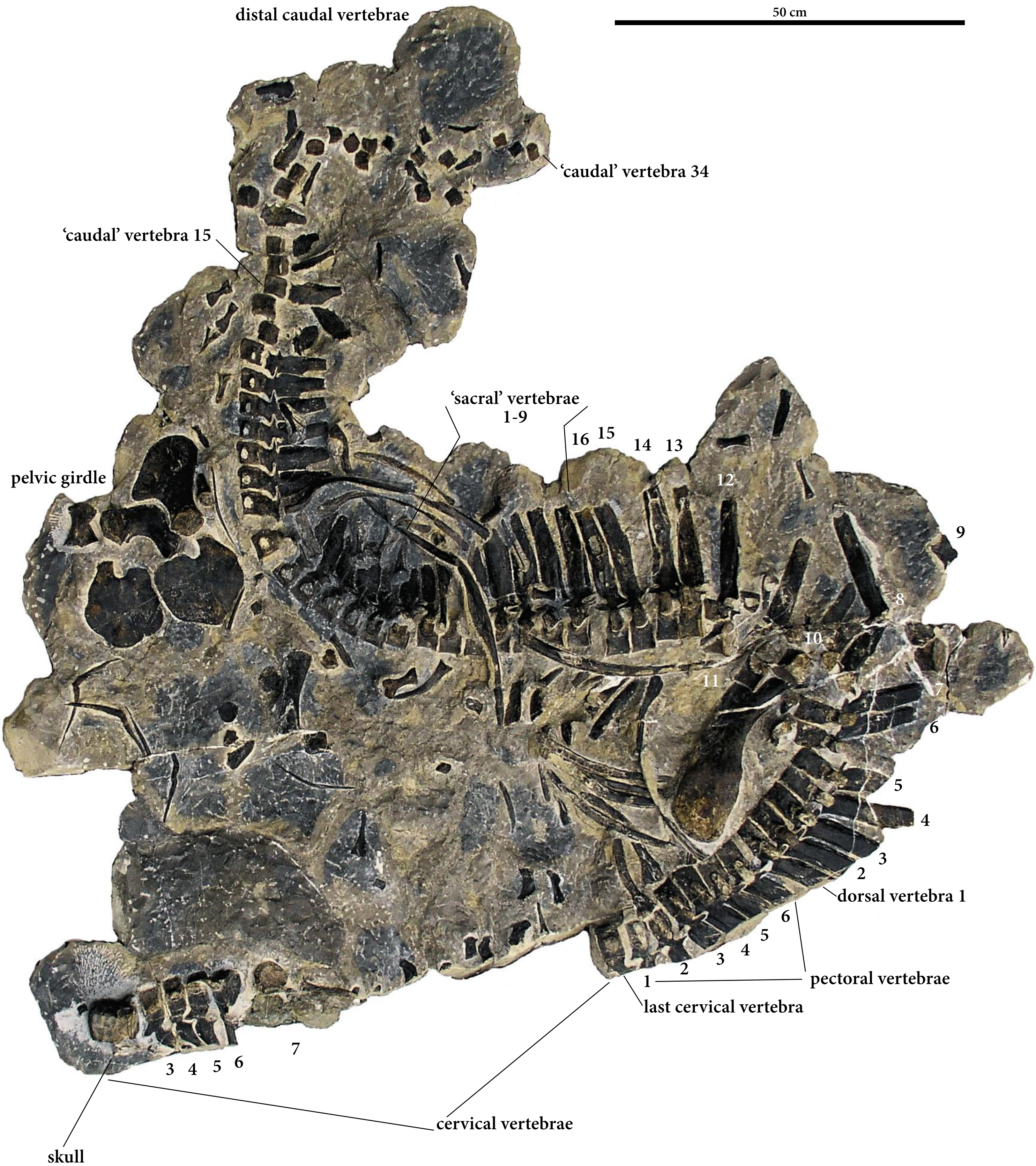

Fig. 1 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Numbers refer to the position of the vertebrae within each segment of the vertebral column. The isolate penultimate cervical vertebra (see DALLA VECCHIA 2006) is not reported. See DALLA VECCHIA (2006, fig. 4) for the identification of the other skeletal elements.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. I numeri si riferiscono alla posizione delle vertebre all'interno di ciascun segmento della colonna vertebrale. La penultima e isolata vertebra cervicale (si veda* DALLA VECCHIA 2006*) non è presente. Si veda* DALLA VECCHIA *(2006, fig. 4) per l'identificazione degli altri elementi scheletrici.*

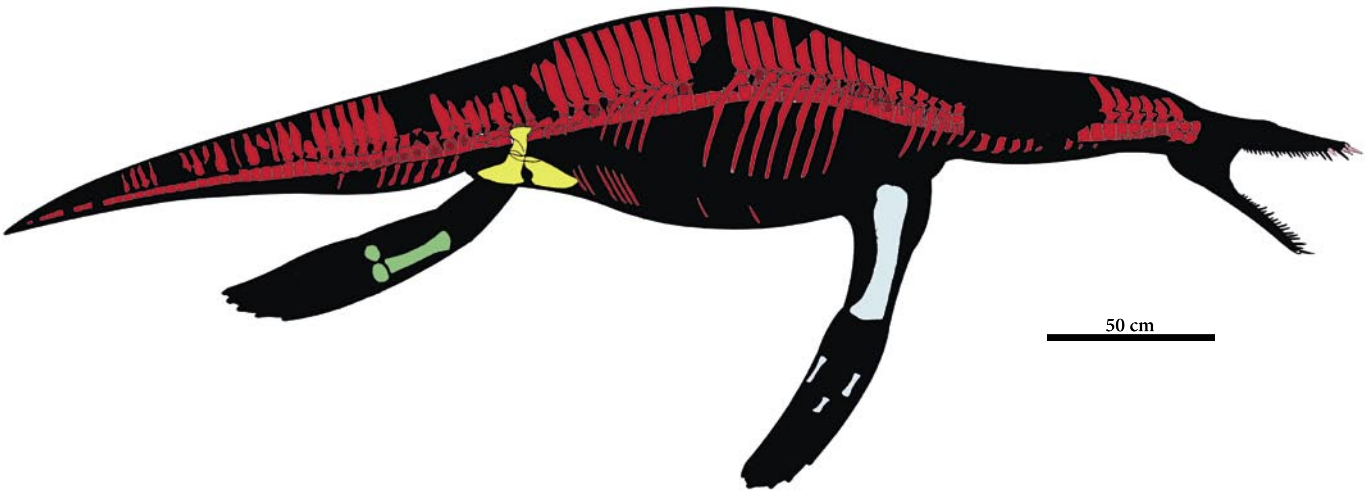

Fig. 2 - *Bobosaurus forojuliensis*, *silhouette* with the preserved skeletal elements. Pink: skull and teeth; red: axial skeleton and gastralia; pale blue: forelimb; yellow: pelvic girdle; and green: hind limb.
- Bobosaurus forojuliensis, silhouette *con riportate le ossa conservate. Rosa: cranio e denti; rosso: scheletro assiale e gastralia; azzurro: arto anteriore; giallo: cinto pelvico; verde: arto posteriore.*

Liu et al. (2015) and Ma et al. (2015), while it is the sister taxon of the Plesiosauria for Benson et al. (2012). As noted by Fabbri et al. (2015), *Bobosaurus forojuliensis* is or is not a 'plesiosaur' according to how the clade Plesiosauria is defined. Obviously, *Bobosaurus forojuliensis* is quite primitive with respect to the Rhaetian plesiosaurs, because it lived more than 30 million years before them. In any case, *Bobosaurus forojuliensis* has a significant importance for the sauropterygian evolution, also because it is one of the few records of non-placodont sauropterygians from the Upper Triassic.

This work is an addition and an update to the description by Dalla Vecchia (2006) and corrects a few mistakes present in it. Here, the osteology of the holotype skeleton is described and figured in detail, which was not possible in Dalla Vecchia (2006) because of publishing limits. Colour photographs are utilized, which could not be used in Dalla Vecchia (2006); large colour photographs can avoid misunderstandings and wrong interpretations that sometimes originate by observing black and white photographs and drawings. Comparisons with non-plesiosaurian pistosauroids that were unknown when Dalla Vecchia (2006) was written (e.g., *Yunguisaurus liae* Cheng, Sato, Wu & Li, 2006 and *Wangosaurus brevirostris* Ma, Jiang, Rieppel, Motani & Tintori, 2015, both from the upper Ladinian of China) are also undertaken. *Yunguisaurus liae* and *Wangosaurus brevirostris* are the first non-plesiosaurian pistosauroids represented by practically complete and articulated skeletons.

Institutional abbreviations: MFSN = Museo Friulano di Storia Naturale, Udine, Italy; NMNS = National Museum of Natural Science, Taichung, Taiwan, China; ZMNH = Zhejiang Museum of Natural History, Hangzhou, Zhejiang, China.

Systematic Palaeontology

Reptilia Linnaeus, 1758
Sauropterygia Owen, 1860
Pistosauroidea Baur, 1887-90

Bobosaurus forojuliensis
Dalla Vecchia, 2006

Holotype: MFSN 27285 (Fig. 1).

Referred specimen: the specimen MFSN 27854 (isolated dorsal neural arch) referred to *Bobosaurus forojuliensis* by Dalla Vecchia (2006) maight belong to a taxon closer to the nothosauroid *Simosaurus* (see below).

Type locality and horizon: Unnamed tributary of the Pontuz Brook, Udine Province, Northeastern Italy. Geographic coordinates: N 4682702500, E 1381702800. Lower part of the Rio del Lago Formation, lower Carnian (Julian) (Dalla Vecchia 2006).

Does MFSN 27854 belong to *Bobosaurus forojuliensis*?

Dalla Vecchia (2006) noted that the unusual "prezygapophyseal-infraprezygapophyseal/postzygapophyseal-infrapostzygapophyseal" articulations in the dorsal vertebrae of *Bobosaurus forojuliensis* occurred also in the nothosauroid *Simosaurus gaillardoti*, but apparently with a reversed craniocaudal polarity (the articular wedge is reported as cranial [anterior] and the articular cavity is cranial [posterior] in *Simosaurus*). Dalla Vecchia (2006) doubted about the correct identification of this orientation in *Simosaurus*, but recognized its correctness after the study (late

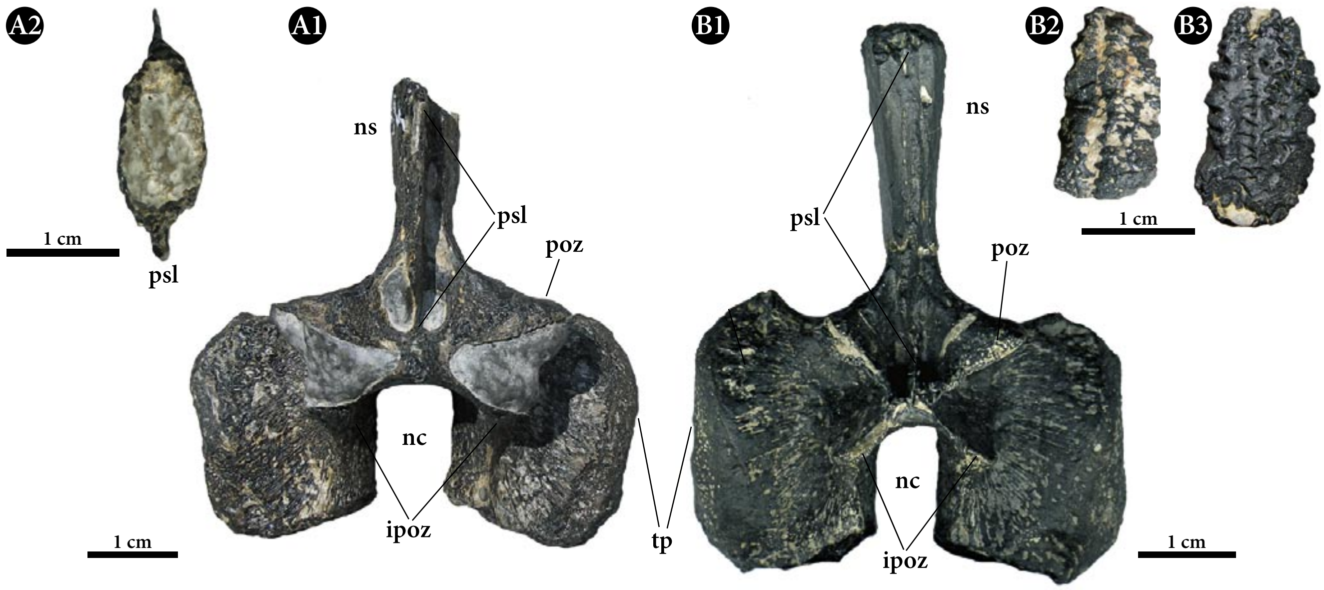

Fig. 3 - MFSN 27854, isolated neural arch (A) compared with a dorsal neural arch of *Simosaurus* aff. *gaillardoti* from the Rio dal Lago Formation of Dogna area (B). A1) Purported caudal view; A2) apical view in cross section; B1) MFSN 31870, caudal view; B2) MFSN 31870, apical view; B3) MFSN 34888, apical view. Structures of A are identified as it would belong to *Simosaurus* aff. *gaillardoti*. Abbreviations: ipoz = infrapostzygapophysis; nc = neural canal; ns = neural spine; psl = postspinal lamina; poz = postzygapophyis; tp = transverse process.

- *MFSN 27854, arco neurale isolato (A) confrontato con un arco neurale dorsale di* Simosaurus *aff.* gaillardoti *(MFSN31870) dalla Formazione Rio dal Lago dei dintorni di Dogna (B).* A1) supposta vista caudale; A2) vista apicale in sezione trasversale; B1) MFSN 31870, vista caudale; B2) MFSN 31870, vista apicale; B3) MFSN 34888, vista apicale. *Le strutture di A sono identificate come se appartenesse a* Simosaurus *aff.* gaillardoti. *Abbreviazioni: ipoz = infrapostzigapofisi; nc = canale neurale; ns = spina neurale; psl = lamina postspinale; poz = postzigapofisi; tp = processo trasverso.*

spring 2006) of an uncatalogued articulated skeleton of *Simosaurus* exhibited at the Geologisch-Paläontologisches Institut der Universität of Tübingen (Germany) (Dalla Vecchia 2008).

When *Bobosaurus forojuliensis* was first described (2006), the only other eusauropterygian known from the same area (surroundings of Dogna) and formation (Rio del Lago Formation) was the nothosauroid *Nothosaurus* (Rieppel & Dalla Vecchia 2001), thus the Middle Triassic *Simosaurus* (see Rieppel 1994) was not supposed to be present there. However, skeletal remains of *Simosaurus* aff. *gaillardoti* were discovered later in the Dogna area and were described by Dalla Vecchia (2008), showing that *Bobosaurus* and *Simosaurus* co-occurred in the Rio del Lago Formation.

The dorsal neural arch MFSN 27854 shares the following features with the dorsal neural arches of *Simosaurus* aff. *gaillardoti* from the Dogna area (cf. fig. 5 in Dalla Vecchia 2006 and fig. 3 in Dalla Vecchia 2008; here Fig. 3): 1) similar size (MFSN 27854 is much smaller than the neural arches of the holotype of *Bobosaurus forojuliensis*); 2) same wedge-cavity articular structure; 3) similar massive transverse processes; 4) similar proportions of the neural spine; and 5) the median spinal lamina is not confluent with the articular structures bordering dorsally the articular cavity (this occurs for sure only in one vertebra of the holotype of *Bobosaurus forojuliensis*; see below).

Being a single and isolate neural arch, the craniocaudal polarity of MFSN 27854 is unknown; it was deduce by Dalla Vecchia (2006) based on slope of the neural arch, which is supposed to be caudal (the spine is vertical in *Simosaurus*).

MFSN 27854 shares the following features with the dorsal neural arches of *Bobosaurus forojuliensis*: 1) the polarity of the wedge-cavity articular structure, if the slope of the neural arch is caudal; 2) broad prespinal and postspinal laminae (which, however, are extremely thin and could be broken in the neural arches of *Simosaurus*); and 3) the hollow neural spine (the inner part of the spine is made of finely spongy bone in *Simosaurus* aff. *gaillardoti*). The cross-section of the spine is elliptical in MFSN 27854 (see Dalla Vecchia 2006, fig. 5D and Fig. 3A2), while it is rectangular in the dorsal vertebrae of the holotype of *Bobosaurus forojuliensis* and rectangular and sometimes much flattened laterally in *Simosaurus* aff. *gaillardoti* (Fig. 3B2-3).

Thus, it cannot be excluded that MFSN 27854 belongs to a taxon closer to *Simosaurus* aff. *gaillardoti* than to *Bobosaurus forojuliensis* and it should be prudently be excluded from the apodigm of *Bobosaurus forojuliensis,* which results, consequently, formed by the sole holotype.

Description

The partial skeleton MFSN 27285 is exposed on its right side (Fig. 1). The vertebral column is relatively well-articulated and is S-like folded, with main disarticulation occurring in the middle of the dorsal segment (dorsal vertebrae 8-11), where the column is bent, and posterior to the 'caudal' vertebra 17 (Fig. 1). Most of the limb bones, the whole pectoral girdle and most of the gastralia are not preserved on the slab surface. While some pectoral girdle elements could be inside the slab (Dalla Vecchia 2006), limb bones and gastralia were probably lost during the drifting of the carcass.

The skeletal elements exposed on the slab are shown in Fig. 2 in a *silhouette* of the animal body.

Skull

Only the distal extremity of the rostrum with some teeth is preserved of the skull and is exposed as an inclined cross-section. The remaining part was weathered away before the discovery of the specimen. The fused vomers reaches the tip of the snout as in *Pistosaurus longaevus* (see von Meyer 1847-55; de Saint Seine 1955, fig. 4D) and bear a single terminal tooth that is visible in cross-section.

The tip of the snout is evidently narrow; the peculiar structure of its cross-section is figured in Dalla Vecchia (2006, fig. 6) and can be observed here in Fig. 4A.

Because of the state of preservation of the skull and lower jaw, the arrangement of the teeth in the space is unclear and the presence or absence of 'fangs' cannot be established with certainty. Thus, the character states regarding the dentition that appear to be so important in the pistosauroid phylogeny by Sato et al. (2010) cannot be scored for *Bobosaurus*.

The elongate and conical tooth crowns can be seen in Fig. 4B; the apicobasal ridges are denser, thinner and less prominent than those in the enamel of typical *Nothosaurus* crowns.

Axial skeleton

Most of the vertebral column is preserved (82 vertebrae), showing only a moderate local disarticulation (Fig. 1). Dalla Vecchia (2006) divided it into cervical, pectoral, dorsal, 'sacral' and 'caudal' segments based fundamentally on the position of the articular facet for the ribs, which shows a clear sinusoidal pattern of migration along the vertebral column. First it is low on the centrum in the cervical vertebrae; then it migrates dorsally in the centrum moving gradually on the neural arch (pectoral vertebrae); then it remains totally on the neural arch (in the transverse process; dorsal vertebrae) to migrate gradually back on the centrum ('sacral' vertebrae) and finally to stay on the centrum

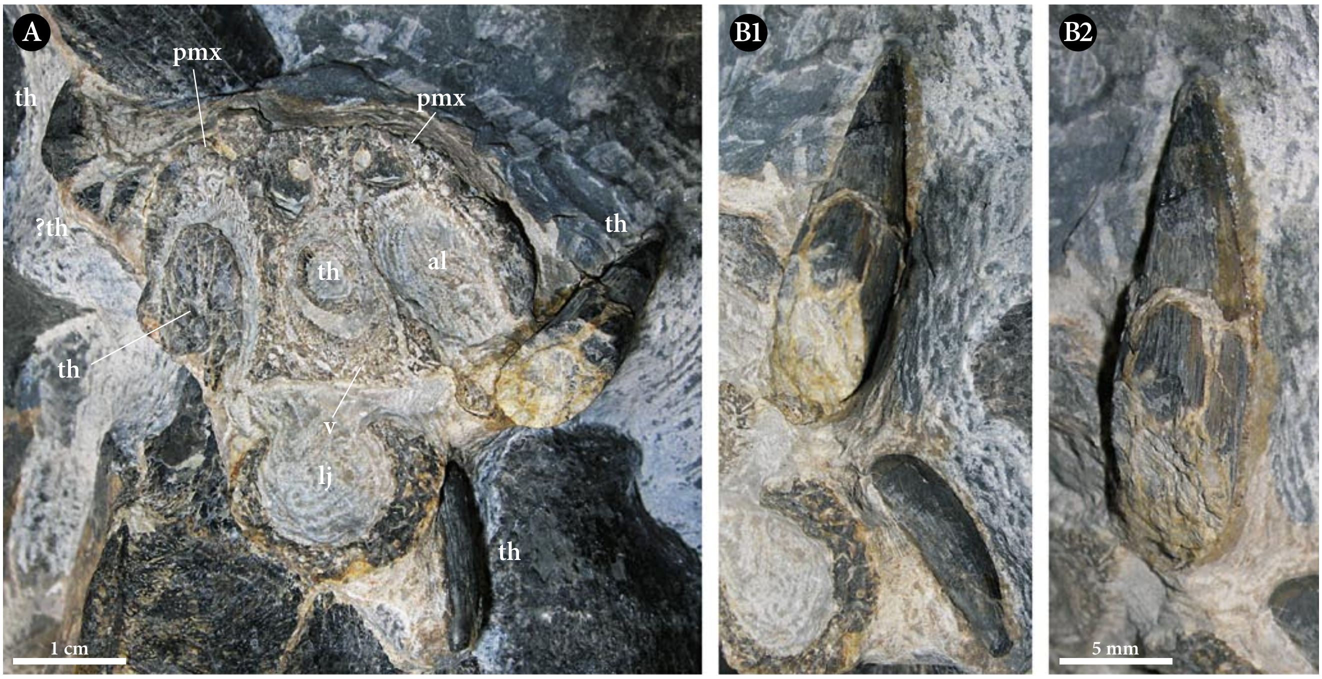

Fig. 4 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Skull and teeth. A) The cross section of the tip of the snout (cf. Dalla Vecchia 2006, fig. 6); B1-2) Tooth crowns. Abbreviations: al = alveolus; lj = lower jaw; pmx = premaxilla; th = tooth crown; v = vomer.

- Bobosaurus forojuliensis, *MFSN 27285, olotipo. Cranio e denti. A) la sezione trasversale della punta del muso (cf. Dalla Vecchia 2006, fig. 6); B1-2) corone dentarie. Abbreviazioni: al = alveolo; lj = mandibola; pmx = premascellare; th = corona dentaria; v = vomere.*

('caudal' vertebrae). The passage from pectoral to dorsal vertebrae, from dorsals to 'sacrals' and from 'sacrals' to 'caudals' is therefore gradual.

A peculiar articular structure between adjacent neural arches appears in the first pectoral vertebrae and is still present in 'caudal' vertebra 13, probably adding rigidity to the vertebral column, reducing drastically its vertical and possibly also its lateral mobility. It will be described in detail below.

Also the neural spines are peculiarly high in *Bobosaurus forojuliensis* (unlike *Pistosaurus longaevus* [see Geissler 1895; Sues 1987; Diedrich 2013]; *Augustasaurus hagdorni* [see Sanders et al. 1997; Rieppel et al. 2002]; *Yunguisaurus liae* [see Sato et al. 2010, 2014]; and *Wangosaurus brevirostris* [see Ma et al. 2015]) and have broad prespinal and postspinal laminae.

Neural arches are sutured to their centra and the neurocentral sutures are always open. As far as it can be seen, centra are non-notochordal and with parallel lateral edges (i.e., they are not much constricted) and there seems to be no zygosphene-zygantrum articulation between neural arches (because there is the peculiar articulation mentioned above).

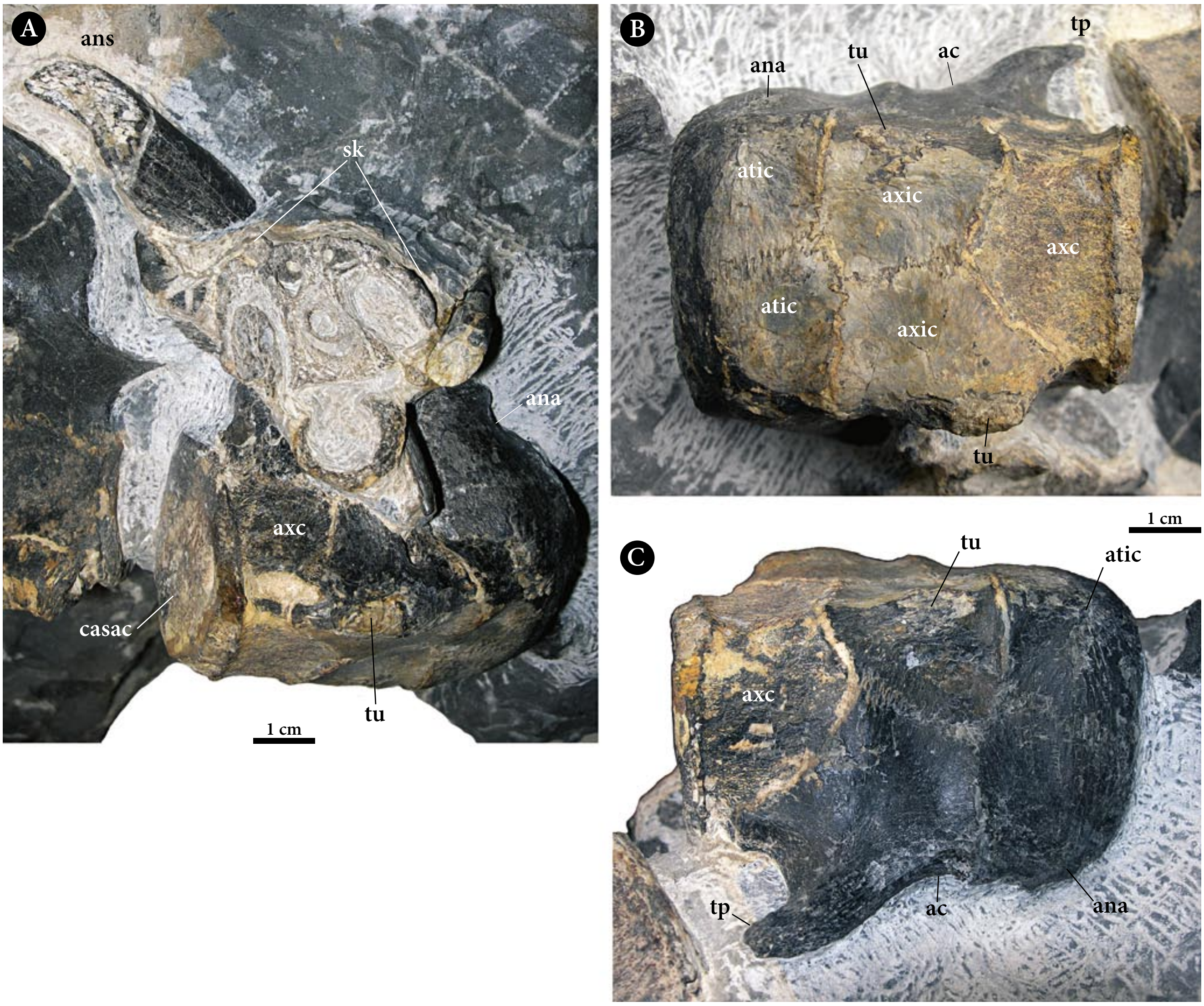

Fig. 5 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Atlas-axis complex. A) Right lateroventral view, the cross-sectioned tip of the snout covers most of the axis neural arch; B) ventral view; C) left lateral view (upside-down). Abbreviations: ac = atlas centrum; ana = atlas neural arch; ans = neural spine of the axis; atic = atlas intercentrum; axic = axial intercentrum; axc = axis centrum; casac = caudal articular surface of the axis centrum; sk = skull (cross-sectioned tip of the snout); tp = thorn-like process of the atlas centrum (fused atlas rib); tu = tubercle on the axial intercentrum.

- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Complesso atlante-asse. A) vista latero-ventrale destra, la sezione trasversale della punta del muso copre la maggior parte dell'arco neurale dell'asse (epistrofeo); B) vista ventrale; C) vista laterale sinistra (rovesciata). Abbreviazioni: ac = centro dell'atlante; ana = arco neurale dell'atlante; ans = spina neurale dell'asse; atic = intercentro dell'atlante; axic = intercentro dell'asse; axc = centro dell'asse; casac = superficie articolare caudale del centro dell'asse; sk = cranio (sezione trasversale della punta del muso); tp = processo del centro dell'atlante a forma di spina (costola dell'atlante fusa); tu = tubercolo dell'intercentro dell'asse.*

Cervical vertebrae (Figs 5-10)

Dalla Vecchia (2006) considered as cervical vertebrae the pre-dorsal vertebrae in which the articular facet/s for the rib is entirely on the centrum. This is not in agreement with other authors (e.g., Rieppel 2001) who consider as cervicals the vertebrae with distinct diapophyses and parapophyses for the bicipital cervical ribs.

The atlas-axis complex and the cervical vertebrae 3-6 are preserved in a row (Fig. 6), followed by the slightly disarticulated remains of cervicals 7-9. The following cervicals are missing because they had been weathered away. Anyway, their previous presence is testified by the corresponding cervical ribs that are still preserved on the slab (Fig. 11). The first following *in situ* vertebra has a single, large and sub-circular facet for the rib articulation that occurs entirely on the centrum (Fig. 10A). The successive vertebra is the first of a string of six vertebrae that have a single, dorsoventrally high and craniocaudally narrow articular facet for the rib that is partly on the neural arch. Those six vertebrae are here considered as pectoral vertebrae, following Brown (1981), Sues (1987), Storrs (1997) and Dalla Vecchia (2006).

A single, partially preserved vertebra with distinct diapophysis and parapophysis (Fig. 9) was found isolated near the rock layer preserving the skeleton; it appears to be the element just cranial to the vertebra with the large and sub-circular facet for the rib articulation. Dalla Vecchia (2006) considered it as the penultimate cervical vertebra and considered the vertebra with the large and sub-circular facet for the rib articulation as the last cervical vertebra.

Under these assumptions, *Bobosaurus forojuliensis* has at least 19 cervical vertebrae (based on the number of cervical ribs and the space between cervical vertebra

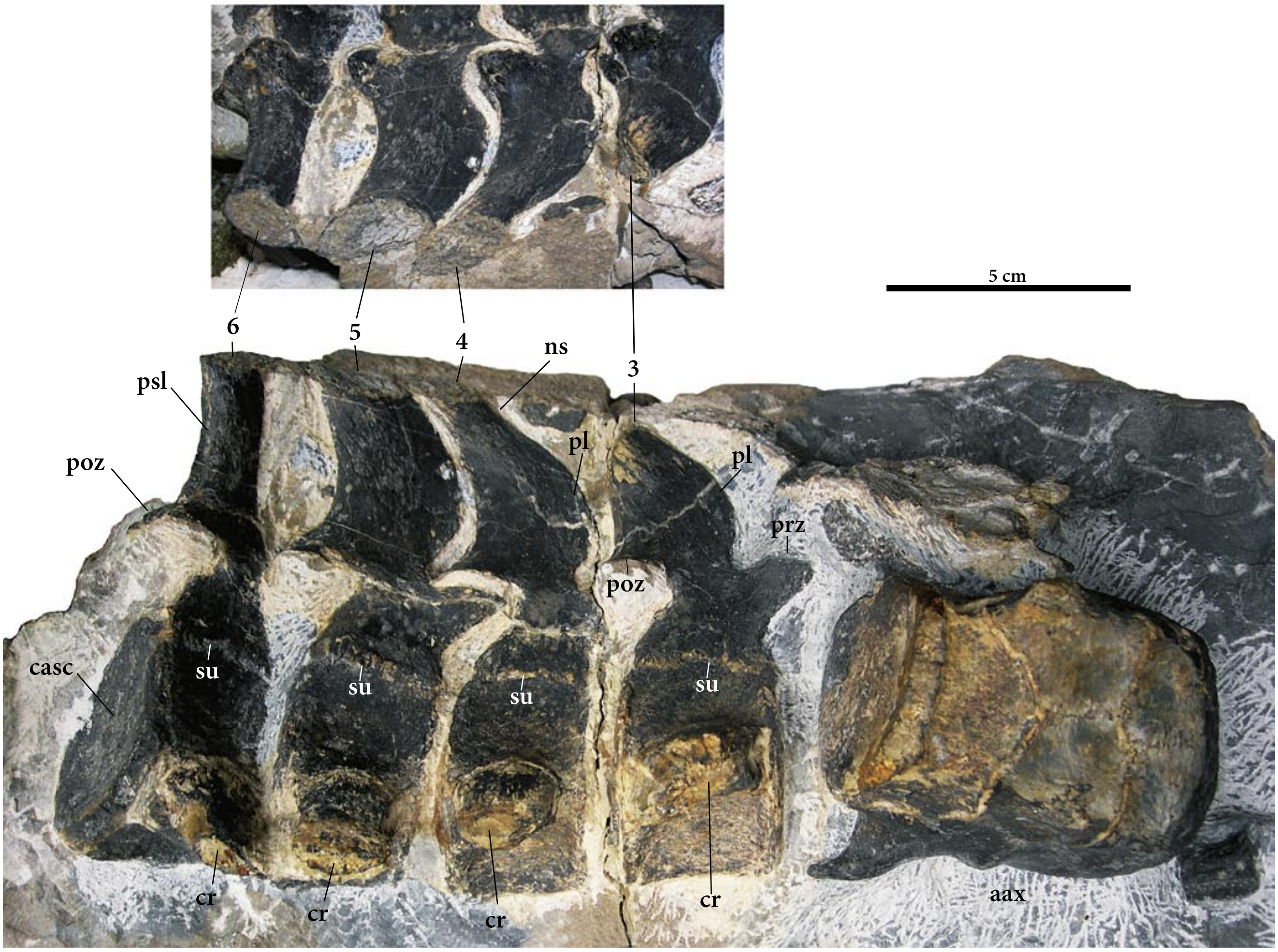

Fig. 6 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Cervical vertebrae 1-6. The smaller figure above shows the neural spines from a dorsolateral perspective (note their cross-sections). Abbreviations: 3-6 = cervical vertebrae 3-6; aax = atlas-axis complex; casc = caudal articular surface of the vertebral centrum; cr = cervical rib; ns = neural spine; pl = prespinal lamina; poz = postzygapophysis; prz = prezygapophysis; psl = postspinal lamina; su = neurocentral suture.

- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Vertebre cervicali 1-6. La figura piccola sopra mostra le spine neurali da una prospettiva dorso-laterale (si noti la loro sezione trasversale). Abbreviazioni: 3-6 = vertebre cervicali 3-6; aax = complesso atlante-asse; casc = superficie articolare caudale del centro vertebrale; cr = costola cervicale; ns = spina neurale; pl = lamina prespinale; poz = postzigapofisi; prz = prezigapofisi; psl = lamina postspinale; su = sutura neurocentrale.*

Fig. 7 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Cervical vertebra 7. A) Caudal view; B) right laterocaudal view. Abbreviations: afr = articular facets for the rib; cr = cervical rib; cvc 8-9 = cervical centra 8-9; ns = neural spine; psl = postspinal lamina; poz = postzygapophyis; prz = prezygapophyis.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Vertebra cervicale 7. A) vista caudale; B) vista latero-caudale destra. Abbreviazioni: afr = faccette articolari per la costola; cr = costola cervicale; cvc 8-9 = centro cervicale 8 e 9; ns = spina neurale; psl = lamina postspinale; poz = postzigapofisi; prz = prezigapofisi.*

9 and the last two cervicals; Dalla Vecchia 2006), but it could have more, if the segment of the vertebral column between cervical vertebra 9 and the penultimate cervical vertebra was disarticulated. However, it is improbable that *Bobosaurus forojuliensis* could have a high cervical count as *Yunguisaurus liae* (49-51, but including also the pectoral vertebrae; Sato et al. 2010, 2014), *Augustasaurus hagdorni* (36, but including also 4-5 pectoral vertebrae; Rieppel et al. 2002) and *Wangosaurus brevirostris* (at least 33, possibly including some pectoral vertebrae; Ma et al. 2015). Therefore, *Bobosaurus forojuliensis* was relatively short-necked like *Pistosaurus longaevus* (23-24 cervical vertebrae; Sues 1987; Diedrich 2013). Including the pectoral vertebrae (see below), *Bobosaurus forojuliensis* would have at least 25 pre-dorsal vertebrae. Whether this is a primitive feature or an apomorphy of *Bobosaurus forojuliensis,* it should be established considering on the whole the peculiar features of the vertebral column of this eusauropterygian and their functional meaning.

The atlas-axis complex is quite a massive element made of the sutured atlantal and axial double intercentra, axial and atlantal centra, and atlantal and axial neural arches (Fig. 5). The complex is rotated 90 degrees counterclockwise with respect to the cervical vertebra 3 and its cranial articular surface for the occipital condyle is obscured by the rock. Most of the right side of the axis neural arch is covered by the sectioned tip of the snout. The apically incomplete neural spine of the axis is slender and tall; it slopes caudally and has a C-like cross section (Fig. 5A).

Such a massive complex is not reported in *Pistosaurus longaevus* (see Sues 1987; Diedrich 2013), *Augustasaurus hagdorni* (see Sanders et al. 1997; Rieppel et al. 2002), *Yunguisaurus liae* (see Sato et al. 2015) and *Wangosaurus brevirostris* (see Ma et al. 2015), but it is common in plesiosaurs (e.g., Carpenter 1999).

Cervical vertebrae 3 to 5 (Fig. 6) show their lateral side, while cervical vertebra 6 is slightly rotated and shows also its caudal side. Their "pear-shaped" centrum was described in detail by Dalla Vecchia (2006). The articular surfaces of the centra cannot be fully seen, except for the caudal one of the cervical vertebra 6; they are shallowly concave. The diapophyseal and parapophyseal facets occur on a longitudinally elongate and slightly raised base, but they are obscured by the still sutured capitulum and tuberculum of the rib. No large subcentral foramina are visible. The intervertebral spaces corresponding to the intervertebral discs between the centra of cervical vertebrae 3 and 4 and 4 and 5 are 7.5 and 3 mm, respectively (thus, they are longer than those of later plesiosaurs; Wintrich & Sanders 2016). The neurocentral suture of the cervical vertebrae 3-6 is jagged but relatively straight, i.e. without significative ventral expansions. The articular surfaces of the zygapophyses are horizontal, allowing only lateral movements of the neck. The neural spines are arched backward. Their middle-apical portions are missing in cervicals 3-5 because they had weathered away (Fig. 6). A broad, "under sail"-like prespinal lamina with a convex cranial margin occurs cranially at the base of the spine; moving apically, the lamina tapers to a thin ridge (Fig. 6). The neural spine is rather craniocaudally narrow apical to the point of tapering of this lamina (as it can be appreciated in the cervical vertebra 4; Fig. 6). The postspinal lamina is visible in the cervical vertebra 6 and is just a thin basoapical ridge.

Cervical vertebra 7 (Fig. 7) is disarticulated and rotated, exposing the right lateral and the caudal sides (Fig. 7). The right cervical rib is not articulated and the craniocaudally elongate diapophyseal and parapophyseal facets, which are parallel and close to each other, are visible on their raised base (Figs 7 and 8). The postzygapophyses bear horizontal articular facets that are slightly craniocaudally sloping. Only

Fig. 8 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Double articular facets for the rib in the cervical centrum 7 (right laterocaudal view). Abbreviations: dap = diapophysis; pap = parapophysis.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Faccette articolari doppie per la costola nel centro cervicale 7 (in vista latero-caudale destra). Abbreviazioni: dap = diapofisi; pap = parapofisi.*

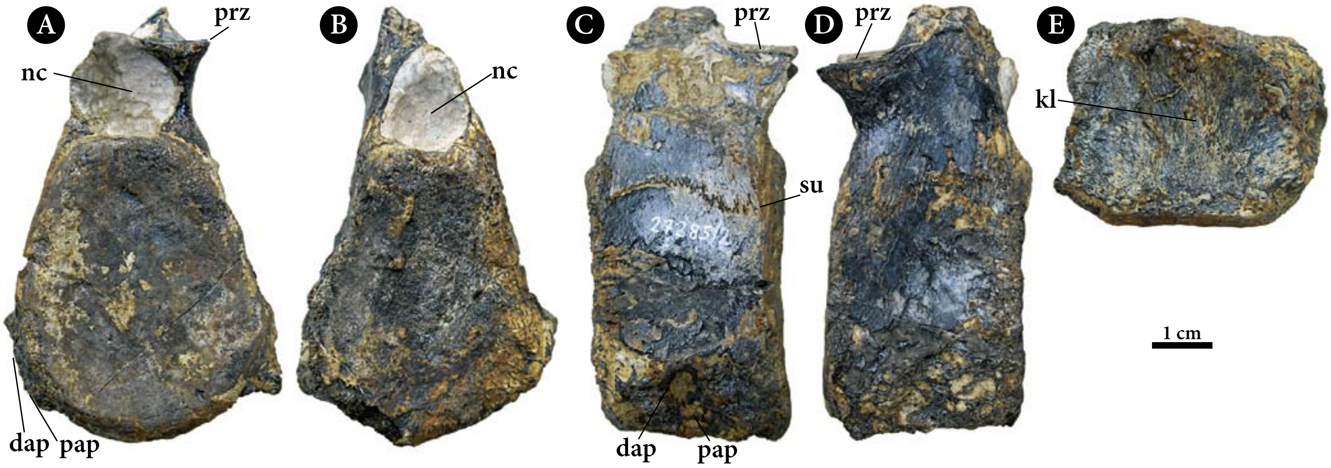

Fig. 9 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Penultimate cervical vertebra. A) Cranial view; B) caudal view; C) right lateral view; D) left lateral view; and E) ventral view. Abbreviations: dap = diapophysis; kl = keel; nc = neural canal; pap = parapophysis; prz = prezygapophysis; su = neurocentral suture.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Penultima vertebra cervicale. A) vista craniale; B) vista caudale; C) vista laterale destra; D) vista laterale sinistra; E) vista ventrale. Abbreviazioni: dap = diapofisi; kl = carena; nc = canale neurale; pap = parapofisi; prz = prezigapofisi; su = sutura neurocentrale.*

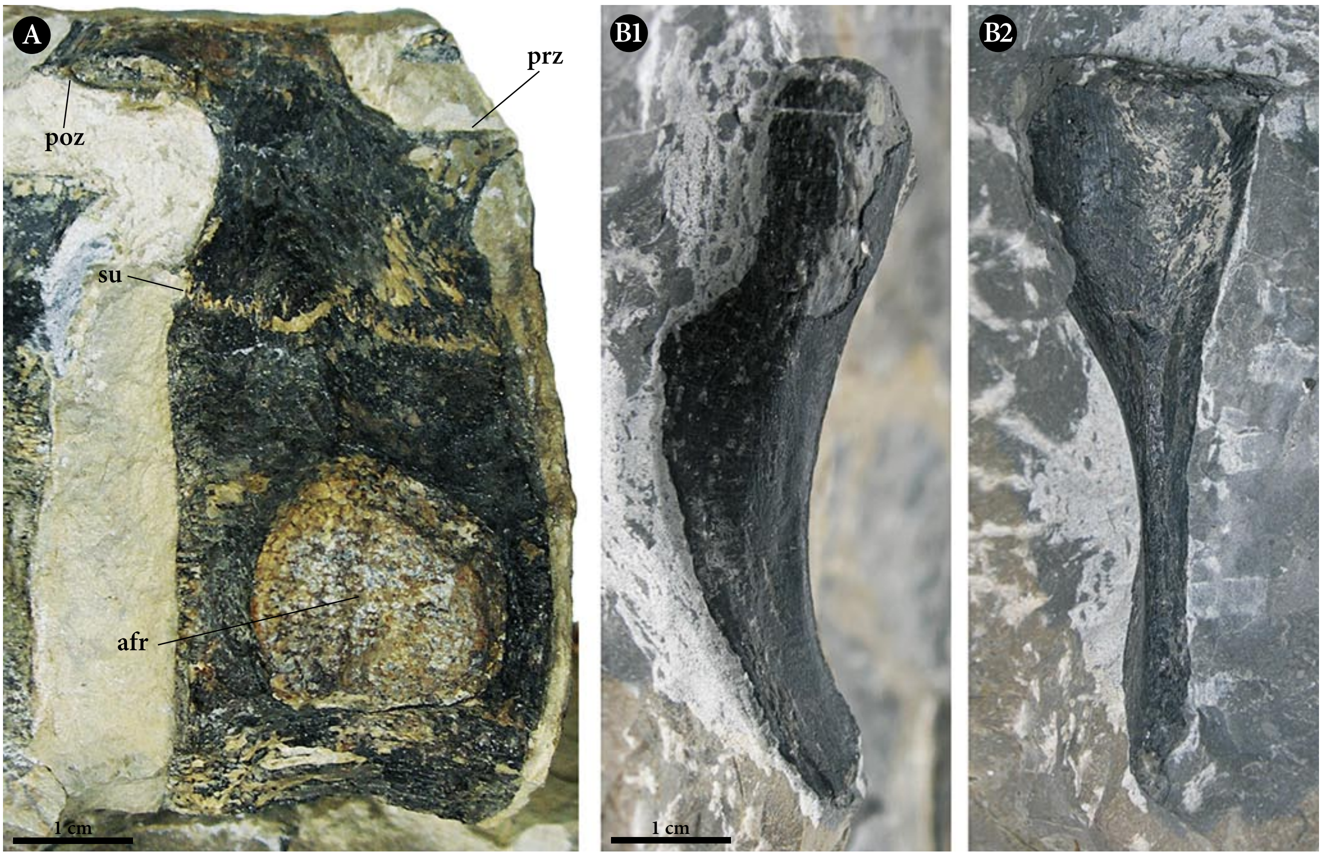

Fig. 10 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Last cervical vertebra and rib. A) Last cervical vertebra (transitional between the cervicals and the pectorals) in right lateral view. B) a probable last cervical rib in dorsoventral (B1) and cranial (B2) views. Abbreviations: afr = articular facet for the rib; poz = postzygapophysis; prz = prezygapophysis; su = neurocentral suture.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Ultima vertebra e costola cervicale. A) ultima vertebra cervicale (di transizione fra cervicali e pettorali) in vista laterale destra. B) una probabile ultima costola cervicale in vista dorso-ventrale (B1) e craniale (B2). Abbreviazioni: afr = facetta articolare per la costola; poz = postzigapofisi; prz = prezigapofisi; su = sutura neurocentrale.*

the caudal view of the nearly complete neural spine is exposed; it is tall, inclined backward and craniocaudally narrow apically. The postspinal lamina is just a thin ridge.

As said above, only a single element of the missing string of cervical vertebrae has been found scattered in the debris at the base of the rock wall containing the skeleton-bearing stratum. It is totally freed from the

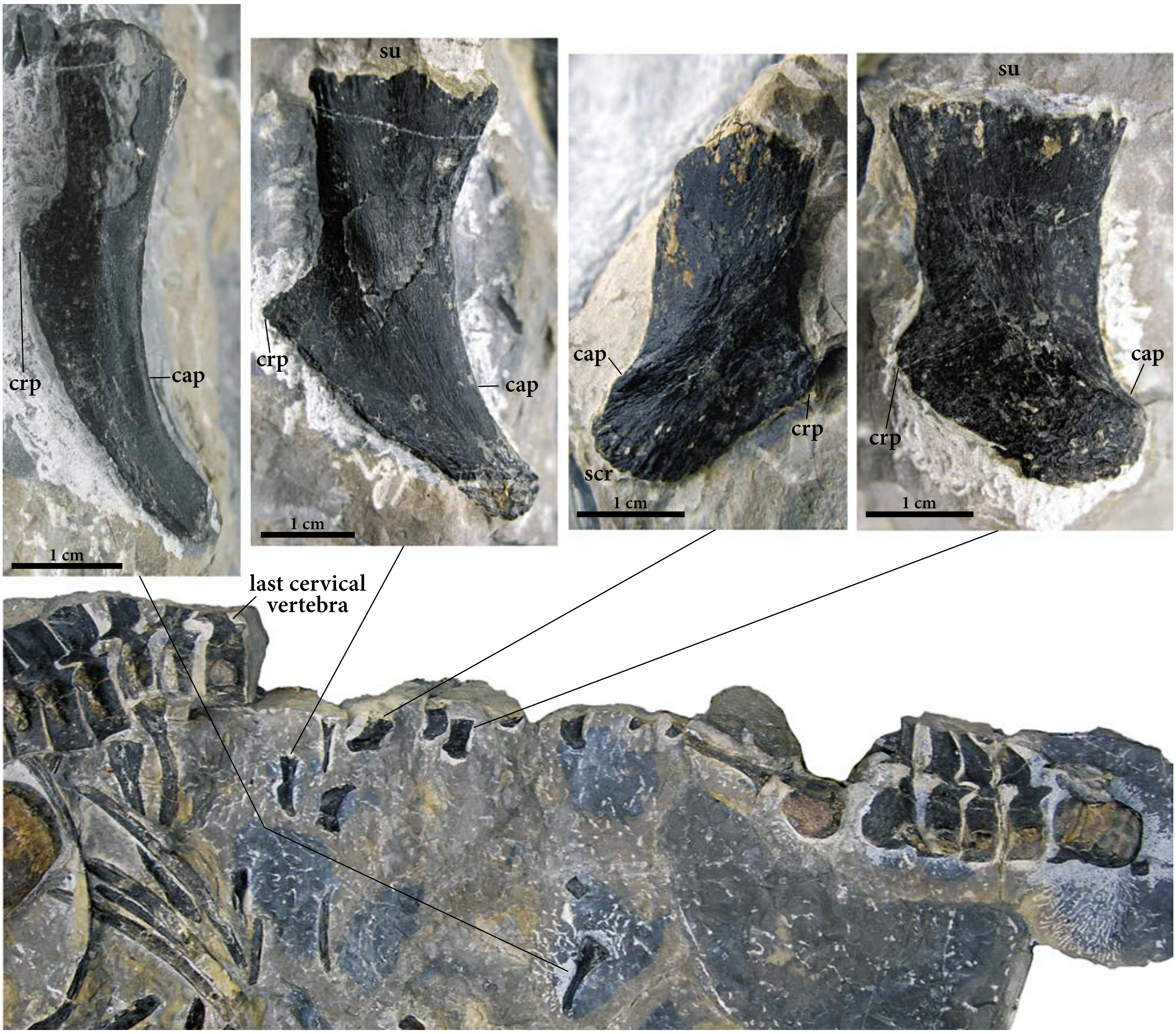

Fig. 11 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Cervical ribs. Below: panoramic view of the cervical segment of the vertebral column. Above: the better preserved cervical ribs in dorsoventral view; the proximal-distal direction is from right to left. The last to the left is the probable last cervical rib. Note the change in morphology of the elements from the middle to the distal positions. Abbreviations: cap = caudal process; crp = cranial process; scr = "saw-cut" rugosities; su = sutural margin.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Costole cervicali. Sotto: panoramica del segmento cervicale della colonna vertebrale. Sopra: le costole cervicali meglio conservate, in vista dorso-ventrale; la direzione prossimo-distale va da destra a sinistra. L'ultima a sinistra è probabilmente l'ultima costola cervicale. Si noti il cambio di morfologia dagli elementi mediani a quelli distali. Abbreviazioni: cap = processo caudale; crp = processo craniale; scr = rugosità "saw-cut"; su = margine suturale.*

conglobating rock and lacks most of the neural arch (Fig. 9). Its prezygapophyses have horizontal articular facets. There is a longitudinal, low and blunt keel on the ventral surface (Fig. 9E), showing (with also cervicals 3-7) that the cervical vertebrae of *Bobosaurus forojuliensis* are keeled ventrally.

Diapophyses and parapophyses in all these cervical vertebrae are parallel and close to each other; there is not shifting backwards of the parapophyses on centrum along the cervical segment of the vertebral column.

As said above, the last cervical vertebra is characterized by a single and large articular surface for the rib that is entirely on the centrum, only slightly raised on it and has a circular outline (although it is damaged ventrally and probably was deeper than it appears; Fig. 10A). According to Rieppel (2001) it should not be considered a cervical vertebra because it has a single articular surface for the rib. However, the articular surfaces of the following pectoral vertebrae are totally different, being craniocaudally narrow and placed on a dorsoventrally elongate transverse process that is partly formed by the neural arch. I keep considering it as the last cervical, although this vertebra is clearly transitional between the cervical and the pectoral

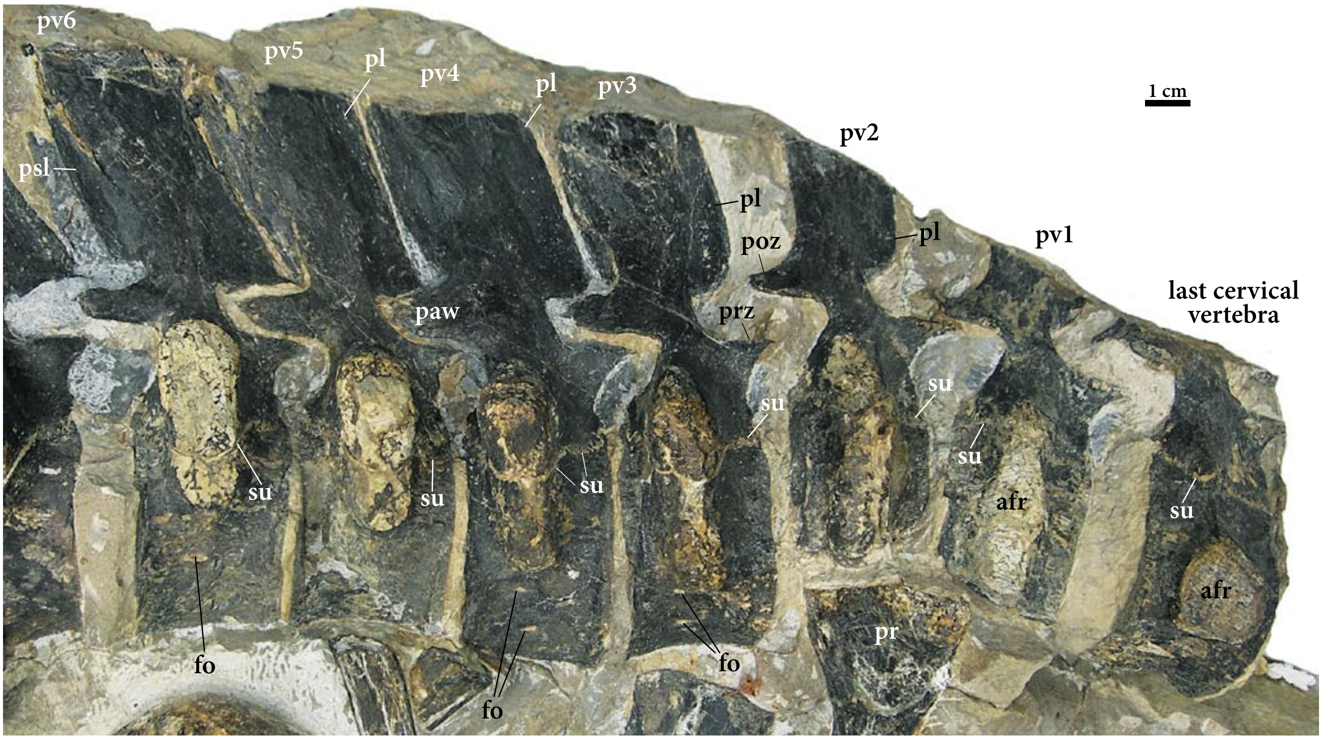

Fig. 12 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Pectoral vertebrae. Abbreviations: afr = articular facet for the rib; fo = foramen; paw = posterior (caudal) articular wedge; pl = prespinal lamina; poz = postzygapophysis; pr = pectoral rib; prz = prezygapophysis; psl = postspinal lamina; pv1-6 = pectoral vertebrae 1-6; su = neurocentral suture.
- Bobosaurus forojuliensis, *MFSN 27285, olotipo. Vertebre pettorali. Abbreviazioni: afr = faccetta articolare per la costola; fo = forame; paw = cuneo articolare posteriore (caudale); pl = lamina prespinale; poz = postzigapofisi; pr = costola pettorale; prz = prezigapofisi; psl = lamina postspinale; pv1-6 = vertebre pettorali 1-6; su = sutura neurocentrale.*

vertebrae. This vertebra is separated by the successive pectoral vertebra 1 by a relatively wide intervertebral space (12.5 mm long).

The horizontal articular facets of the zygapophyses and the tall and backward sloping neural spines of the cervical vertebrae suggest that the dorsal mobility of the neck was limited; the articular facets of the zygapophyses favoured instead the lateral movement.

Cervical ribs

The right ribs of cervical vertebrae 3-6 are still articulated with their centra; only the tubercula and capitula are preserved, while the shaft and processes were weathered away. The remains of at least other 13 cervical ribs can be identified on the slab. Most of them were disconnected from the sutural articulation with their centra (which is testified by the jagged margins of the tubercula and capitula; Fig. 11), but remained in the neck region. All ribs here referred to as cervicals have a distinct free cranial process, which has a triangular outline becoming more and more pointed moving caudally, and a long caudal process (the "posterior processes" of Sander et al. 1997). The shape of the ribs changes along the vertebral segment: the rib becomes longer and slender, due mainly to the elongation of the caudal process (Fig. 11). The distal end of the caudal process has "saw-cut" rugosities (sensu Sander et al. 1997), at least in some mid-cervical ribs (Fig. 11).

A bone labeled ?lr in Dalla Vecchia (2006, fig. 4, but the abbreviation is missing in the legend of the caption) is probably the last cervical rib by comparison with those of *Pistosaurus longaevus* (see Dietrich 2013, fig. 2C) and *Nothosaurus jagisteus* (see Rieppel 2001, fig. 6D). It was not described by Dalla Vecchia (2006) and it was not considered in his count of the cervical ribs. Unlike preceding cervical ribs, it has a single articular head, which is dorsoventrally elongate with finished margins (Fig. 10B1-2), thus its articulation on the centrum was not sutural. Its articular head corresponds with the articular facet for the rib on the last cervical vertebra (Fig. 10A). Like the other cervical ribs, it has a triangular cranial process and a posterior process; however, the latter is much longer and slender than in the other cervical ribs (Fig.11).

Pectoral vertebrae (Figs 12-13)

The last pre-sacral vertebra with the facet for the rib articulation occurring entirely on the centrum is followed by six vertebrae where the single articular facet for the rib is partly on the centrum and partly on the neural arch (Fig. 12). Their articular facet is quite different from those of the preceding cervical vertebrae. These vertebrae are transitional between the

Fig. 13 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Migration of the neurocentral suture at the pectoral-dorsal transition. The arrows indicate the sutures. Abbreviations: dv1-3 = dorsal vertebrae 1-3; fo = foramen; paw = posterior (caudal) articular wedge (postzygapophysis with two articular facets); pl = prespinal lamina; pv4-6 = pectoral vertebrae 4-6; tp = transverse process; uprz = upper prezygapophysis.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Migrazione della sutura neurocentrale alla transizione tra vertebre pettorali e dorsali. Le frecce indicano le suture. Abbreviazioni: dv1-3 = vertebre dorsali 1-3; fo = forame; paw = cuneo articolare posteriore (postzigapofisi con due faccette articolari); pl = lamina prespinale; pv4-6 = vertebre pettorali 4-6; tp = processo trasverso; uprz = prezigapofisi superiore.*

cervical vertebrae and the dorsal vertebrae where the single articular facet for the rib is totally on the neural arch. As said above, they were considered as pectoral vertebrae by Dalla Vecchia (2006). The count of the pectoral vertebrae of *Augustasaurus hagdorni* seems to be 4-5, but it is uncertain (Rieppel et al. 2002). *Yunguisaurus liae* has an unreported number of pectoral vertebrae that Sato et al. (2010) include in the cervical count. Ma et al. (2015) do not mention the presence of pectoral vertebrae in *Wangosaurus brevirostris*.

From pectoral vertebra 1 to 6 the neurocentral suture gradually 'migrates' ventrally on the transverse process and the latter decreases in dorsoventral height and slightly increases in craniocaudal length and in lateral extent (Figs 12 and 13).

The intervertebral spaces among the pectoral vertebrae are much shorter that the space between the last cervical and the first pectoral vertebra: they are 3.5 mm (pectorals 1-2), 4.2 mm (pectorals 2-3), 2 mm (pectorals 3-4), 3 mm (pectorals 4-5), and 2.2 (pectorals 5-6) mm long.

Small neurovascular foramina are randomly distributed in the pectoral vertebrae (Figs 12 and 13).

The peculiar articulation between the neural arches in post-cervical vertebrae of *Bobosaurus forojuliensis* was reported in detail by Dalla Vecchia (2006). The vertebrae from pectoral 3 to at least 'caudal' 13 do not have a 'simple' zygapophyseal pachyostosis: it is instead an unusual kind of zygapophyseal articulation that is not observed in any other sauropterygians (Fig. 14). Unfortunately, this articular complex can be seen only in lateral view, except than in the dorsal vertebra 12 (Fig. 21A) where the prezygapophyseal complex is exposed in cranial view. A further preparation done after the publication of Dalla Vecchia (2006) shows some more detail of this peculiar articulation in a few other vertebrae, but the fact is that the specimen would require much more preparation to describe the neural arches articulation in detail.

As a general rule, the postzygapophysis has a dorsal articular facet in addition to the usual ventral articular facet (Fig. 15B). Dalla Vecchia (2006) used the term "infrapostzygapophysis" for this surface following

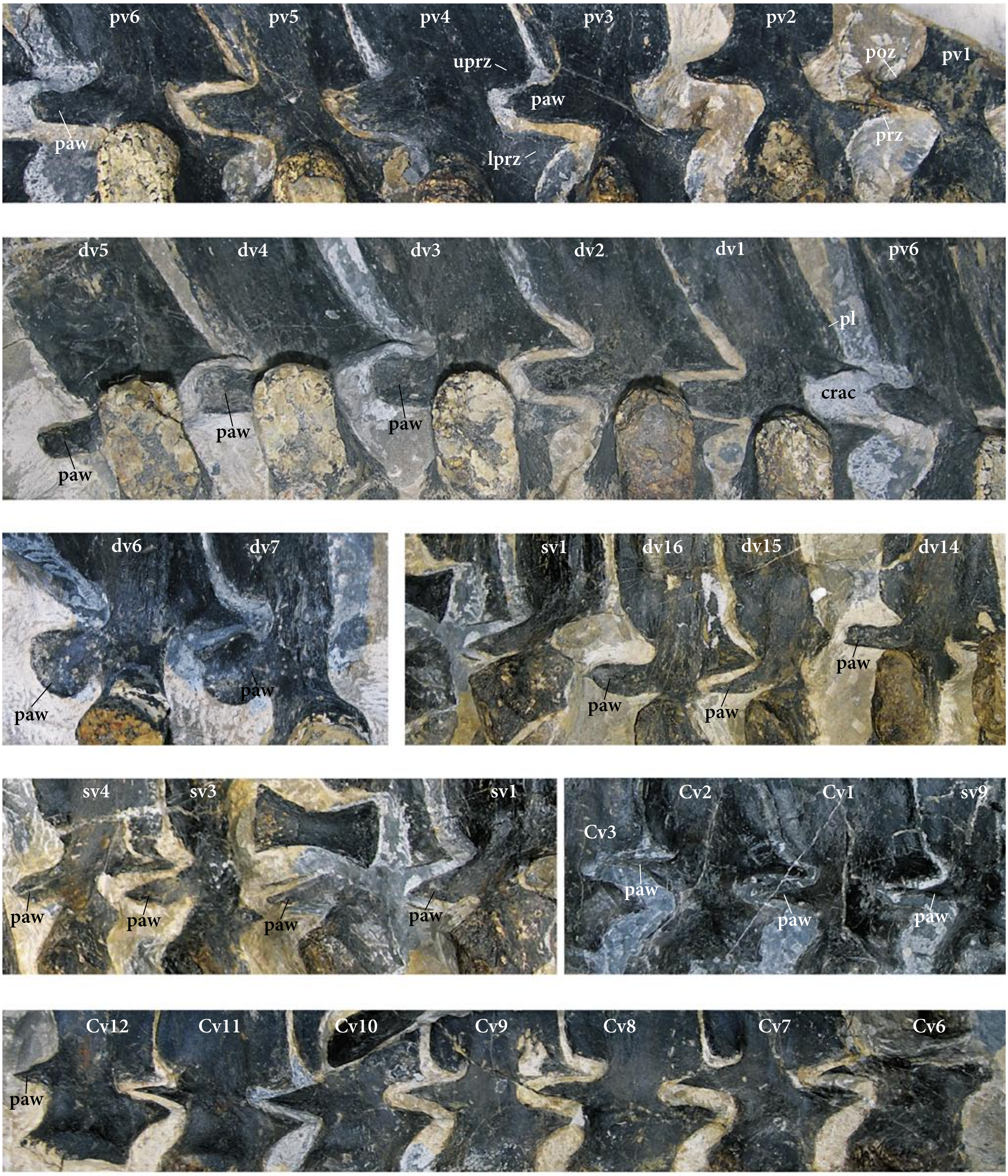

Fig. 14 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Neural arch articulation among post-cervical vertebrae. Cranio-caudal direction from the upper right to the lower left corners of the figure. Abbreviations: crac = cranial (anterior) articular cavity; Cv = 'caudal' vertebrae; dv = dorsal vertebrae; lprz = lower prezygapophysis; paw = posterior (caudal) articular wedge; pl = prespinal lamina; poz = postzygapophysis; prz = prezygapophysis; pv = pectoral vertebrae; sv = 'sacral' vertebrae; uprz = upper prezygapophysis. Not drawn to scale. As for scale, see the other figures of the post-cervical segments of the vertebral column.

- Bobosaurus forojuliensis, *MFSN 27285, olotipo Articolazione degli archi neurali nelle vertebre post-cervicali. La direzione cranio-caudale va dall'angolo in alto a destra a quello in basso a sinistra. Abbreviazioni: crac = cavità articolare craniale (anteriore); Cv = vertebre 'caudali'; dv = vertebre dorsali; lprz = prezigapofisi inferiore; paw = cuneo articolare posteriore (caudale); pl = lamina prespinale; poz = postzigapofisi; prz = prezigapofisi; pv = vertebre pettorali; sv = vertebre 'sacrali'; uprz = prezigapofisi superiore. Non in scala. Per quanto riguarda la scala si vedano le altre figure dei segmenti post-cervicali della colonna vertebrale.*

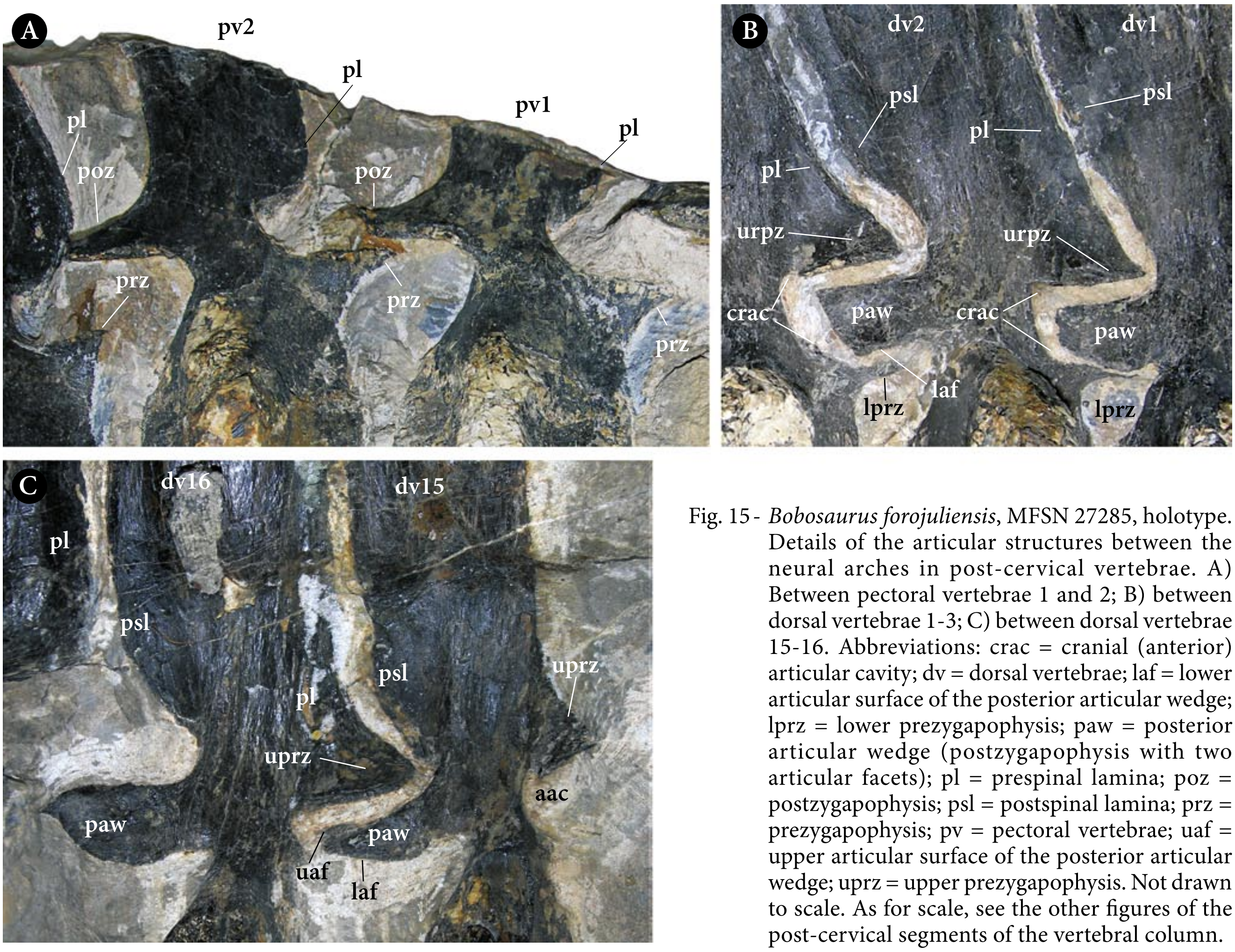

Fig. 15 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Details of the articular structures between the neural arches in post-cervical vertebrae. A) Between pectoral vertebrae 1 and 2; B) between dorsal vertebrae 1-3; C) between dorsal vertebrae 15-16. Abbreviations: crac = cranial (anterior) articular cavity; dv = dorsal vertebrae; laf = lower articular surface of the posterior articular wedge; lprz = lower prezygapophysis; paw = posterior articular wedge (postzygapophysis with two articular facets); pl = prespinal lamina; poz = postzygapophysis; psl = postspinal lamina; prz = prezygapophysis; pv = pectoral vertebrae; uaf = upper articular surface of the posterior articular wedge; uprz = upper prezygapophysis. Not drawn to scale. As for scale, see the other figures of the post-cervical segments of the vertebral column.

- Bobosaurus forojuliensis, *MFSN 27285, olotipo. Dettagli delle strutture articolari tra gli archi neurali nelle vertebre post-cervicali. A) tra le vertebre pettorali 1 e 2; B) tra le vertebre dorsali 1-3; C) tra le vertebre dorsali 15-16. Abbreviazioni: crac = cavità articolare craniale (anteriore); dv = vertebre dorsali; laf = superficie articolare inferiore del cuneo articolare posteriore; lprz = prezigapofisi inferiore; paw = cuneo articolare posteriore (postzigapofisi con due faccette articolari); pl = lamina prespinale; poz = postzigapofisi; psl = lamina postspinale; prz = prezigapofisi; pv = vertebre pettorali; uaf = superficie articolare superiore del cuneo articolare posteriore; uprz = prezigapofisi superiore. Non in scala. Per quanto riguarda la scala si vedano le altre figure dei segmenti post-cervicali della colonna vertebrale.*

Rieppel (2000), but it is just a dorsal articular facet of the postzygapophysis. This additional dorsal facet articulates with a facet present ventrally on an expansion of the base of the broad prespinal lamina of the following vertebra (Fig. 15B; of course, the prespinal lamina bifurcates basally to form the two - right and left - articular expansions; Fig. 21A); for clarity, this additional cranial (anterior) structure (the infraprezygapophysis of Dalla Vecchia 2006) is reported here as 'upper prezygapophysis', while the 'normal' prezygapophysis is reported as 'lower prezygapophysis'. Therefore, the postzygapophysis is a caudally (posteriorly) oriented wedge that fits into the cranial (anterior) articular cavity of the following vertebra, which is bordered by the lower prezygapophysis ventrally and by the upper prezygapophysis dorsally (Fig. 15B). As far as it can be observed at the present state of preparation, the shape of the articular wedge (i.e., the postzygapophysis) changes along the vertebral column (Fig. 14).

The articulation between the last cervical vertebra and the first pectoral vertebra seems to be of the normal prezygapophysial-postzygapophysial type (Fig. 15A); the prespinal lamina has a rounded basal termination without any expanded articular structure. The upper prezygapophysis is surely developed in the pectoral vertebra 4 and the caudal articular wedges (only the right one is exposed) occur in the preceding pectoral vertebra 3 and has a sub-rectangular to trapezoidal outline in lateral view (Figs 12 and 14). This morphology is retained up to the dorsal vertebra 2 (Fig. 14). The orientation of the articular facets cannot be seen, but it was plausibly horizontal. Starting from dorsal vertebra 3, the lateral outline of the articular wedge becomes more rounded to heart-like and remains such at least up to dorsal vertebra 7 (Fig. 14), but possibly up to dorsal vertebra 11. This change in morphology could be related with the change in inclination of the articular surfaces on the wedge (facing dorsomedially and ventromedially). In the dorsal vertebra 12 (Fig. 21A), the prezygapophyseal complex in cranial view shows horizontal articular surfaces that allowed only lateral movements. The posterior articular wedge of the following dorsal vertebra 13 has a sharp triangular outline in lateral view; the upper prezygapophysis of the dorsal vertebra 14 articulates on a caudomedial facet on the dorsal side of the wedge. The posterior articular wedge of the dorsal vertebra 14 has, again, a sub-rectangular outline in lateral view (Fig. 14). The posterior articular wedge of the dorsal vertebra 15 is like that of dorsal vertebra 13 and its articulation with the following dorsal vertebra 16 is of the same type (Figs 14 and 15C). The posterior articular wedge of the dorsal vertebra16 has a peculiar, sub-rectangular outline with a caudal point in lateral view (Fig. 15C). The following vertebrae have an articulation like that of dorsal vertebra 13 up to 'caudal' vertebra 13: the articular wedge has a sharp triangular outline in lateral view and the upper prezygapophysis of the following vertebra just overlaps it caudomedially (Fig. 14). The articular surfaces are not fully exposed, but they appear to be more complex than the simple horizontal type and possibly limited the vertebral movement in every direction. Probably, the changes in the morphology of the articular joints along the vertebral column correspond with a diverse mobility of the vertebrae in the different segments. The study of the morphofunctional implications of these changes are beyond the scope of this paper.

Fig. 16 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Pectoral ribs 2 and 3.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Costole pettorali 2 e 3.*

Pectoral ribs

At least two ribs are related to the pectoral series and were probably articulated to the pectoral vertebrae 2 and 3, being associated with them (Fig. 16). Their single articular heads are greatly expanded dorsoventrally (unlike the articular heads of the dorsal vertebrae; see below) and distinctly fan-like; they correspond with the dorsoventrally elongated transverse processes of the proximal pectoral vertebrae. The proximal part of the shaft of the rib is curved; the distal segment is still inside the rock.

Dorsal vertebrae (Figs 17-21)

The vertebrae with the articular facet for the rib entirely on the neural arch, (i.e., the corresponding transverse process is formed largely or completely by the neural arch) were considered dorsal vertebrae by Dalla Vecchia (2006). Under this assumption, *Bobosaurus forojuliensis* has 16 dorsal vertebrae (but see below). The count is 21 in *Augustasaurus hagdorni* (see Sander et al. 1997; probably this count is inclusive of the pectoral vertebrae); *Pistosaurus longaevus* has at least 20 dorsal vertebrae (Sues 1987). *Yunguisaurus liae* and *Wangosaurus brevirostris* have 23 (Sato et al. 2010) and 16 (Ma et al. 2015) dorsal vertebrae, respectively. However, those counts cannot be compared with that reported here for *Bobosaurus forojuliensis*, because of the different definition of 'sacral' vertebrae given for those taxa (see below).

The intervertebral space between the last pectoral vertebra and the first dorsal vertebra is again broader (13 mm long) than the intervertebral spaces between the adjacent pectoral vertebrae and those between the dorsal vertebrae 1-5 (3 mm between dorsal vertebrae 1-2; 4 mm between dorsal vertebrae 2-3; 2.5 mm between dorsal vertebrae 3-4; and 1.7 mm between dorsal vertebrae 4-5).

The arched groove crossing diagonally the right lateral side of the centrum of all dorsals from the caudal dorsal corner to the mid-ventral margin, mentioned by Dalla Vecchia (2006), is shown in Fig. 18C, but can be seen also in Figs 13, 17 and 19-20.

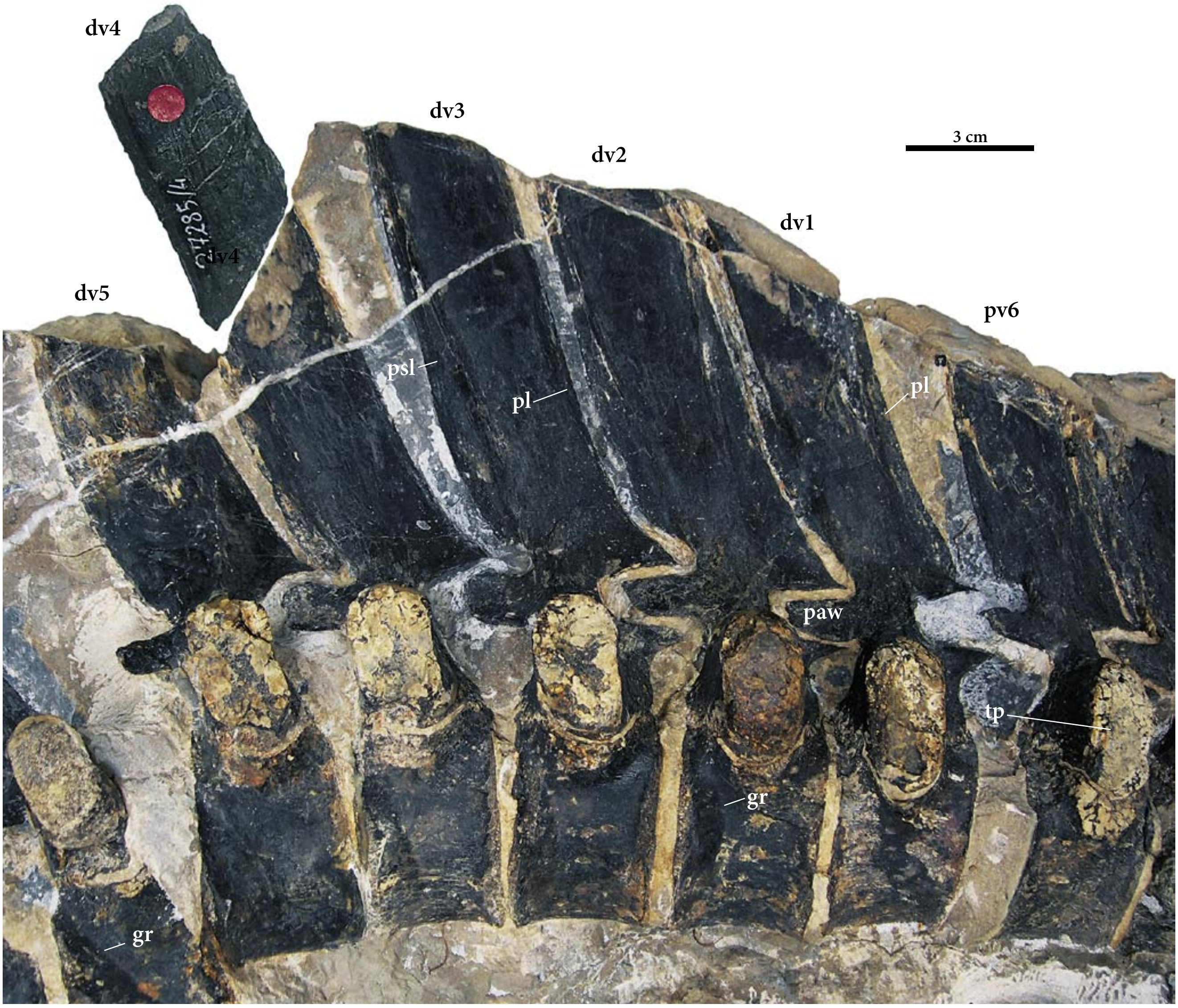

Fig. 17 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Proximal dorsal vertebrae. Abbreviations: dv1-5 = dorsal vertebrae 1-5; gr = groove; paw = posterior articular wedge; pl = prespinal lamina; psl = postspinal lamina; pv4-6 = pectoral vertebra 6; tp = transverse process.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Vertebre dorsali prossimali. Abbreviazioni: dv1-5 = vertebre dorsali 1-5; gr = solco; paw = cuneo articolare posteriore; pl = lamina prespinale; psl = lamina postspinale; pv6 = vertebra pettorale 6; tp = processo trasverso.*

Centra are shallowly amphicoelous. The sutural facets receiving the pedicels of the neural arch on the dorsal surface of centrum are expanded into a cruciform or 'butterfly-shaped' platform that can be seen in centra 10 and 11 (Fig. 19A).

Very small neurovascular foramina occurs in the dorsal centra 1, 3 and 13-16 (Figs 13 and 23).

The ventral-dorsal-ventral migration of the neuro-central suture on the transverse process in the pectoral to 'sacral' vertebrae can be seen in Figs 12, 13, 17, 18A, 19, 23 and 24. Correspondingly, the articular facet for the rib migrates from the neural arch (dorsal vertebrae) to the centrum ('sacral' vertebrae).

Transverse processes of dorsal vertebrae are moderately elongated and projecting (Figs 19-21); at least some of them are similar to those of *Pistosaurus longaevus* (Fig. 21B; cf. Diedrich 2013, fig. 16A). The articular surface for the rib on the transverse processes is not evenly rounded, but always dorsoventrally higher than craniocaudally long, although not as in the pectoral vertebrae. The distal end of the transverse processes is not much thickened (Figs 20 and 21), but some processes slightly flares dorsoventrally distally (Fig. 21B).

The shape, caudal inclination and laminae of the peculiar neural spines of the dorsal vertebrae of *Bobosaurus forojuliensis* can be can be seen in Figs 17, 18A, 19, 20 and 23.

The complete neural spine of dorsal vertebra 4 (the first complete of the dorsal vertebrae) is 127 mm tall (apico-basal length). The upper half of this spine is detached from the lower half, is stored separately and

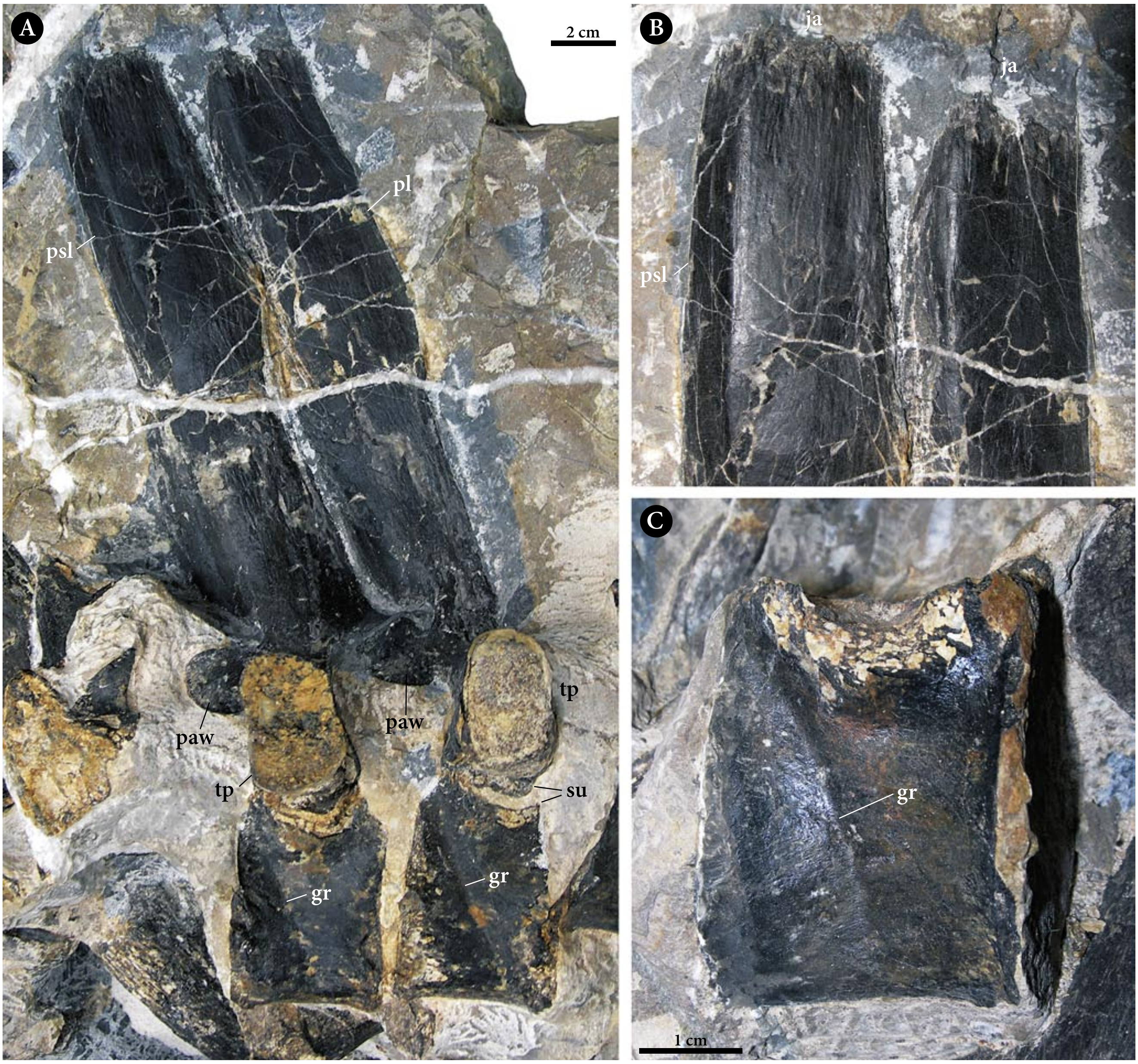

Fig. 18 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. The dorsal vertebrae 6 and 7 and their structures. A) The two vertebrae in right lateral view; B) particular of the upper part of the neural spines; and C) particular of the diagonal groove on the lateral side of the centrum (dorsal vertebra 11). Abbreviations: gr = groove; ja = jagged apex of the neural spines; paw = posterior articular wedge; pl = prespinal lamina; psl = postspinal lamina; tp = transverse process; su = neurocentral suture.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Le vertebre dorsali 6 e 7 e le loro strutture. A) le due vertebre in vista laterale; B) particolare della parte superiore delle spine neurali; C) particolare del solco diagonale sulla faccia laterale del centro (vertebra dorsale 11). Abbreviazioni: gr = solco; ja = apice sfrangiato delle spine neurali; paw = cuneo articolare posteriore; pl = lamina prespinale; psl = lamina postspinale; tp = processo trasverso; su = sutura neurocentrale.*

Fig. 19 - [Following page] *Bobosaurus forojuliensis*, MFSN 27285, holotype. The dorsal vertebrae 6-16 and the 'sacral' vertebrae 1-6. A) The segment with dorsals 6-13; B) the segment with dorsal 12-'sacral' 6. The centrum of the dorsal vertebra 10 was removed to expose the entepicondyle of the humerus; the centrum of dorsal vertebra 9 is preserved at the slab margin and falls outside the upper part of figure A. Abbreviations: cdv11= centrum of the dorsal vertebra 11; dr = dorsal rib; dv5-16 = dorsal vertebrae 5-16; g = gastrale; h = humerus; lprz = lower prezygapophysis; nsdv8-11 = neural spine of the dorsal vertebrae 8-11; paw = posterior articular wedge; ph = phalanx; pl = prespinal lamina; prz = prezygapophysis; psl = postspinal lamina; sv = 'sacral' vertebra; tp = transverse process; uprz = upper prezygapophysis.
- [a destra] Bobosaurus forojuliensis*, MFSN 27285, olotipo. Le vertebre dorsali 6-16 e le vertebre 'sacrali' 1-6. A) il segmento con le dorsali 6-13; B) il segmento con la dorsale 12-'sacrale' 6. Il centro della vertebra dorsale 10 è stato rimosso per visualizzare l'epicondilo dell'omero; il centro della vertebra dorsale 9 è conservato nel margine della lastra e ricade fuori della parte superiore della figura A. Abbreviazioni: cdv11= centro della vertebra dorsale 11; dr = costola dorsale; dv5-16 = vertebre dorsali 5-16; g = gastrale; h = omero; lprz = prezigapofisi inferiore; nsdv8-11 = spine neurale delle vertebre dorsali 8-11; paw = cuneo articolare posteriore; ph = falange; pl = lamina prespinale; prz = prezigapofisi; psl = lamina postspinale; sv = vertebra 'sacrale'; tp = processo trasverso;* uprz = prezigapofisi superiore.


A
1 cm
dv12
dv13
dv14
nsdv8
nsdv11
nsdv10
dv8
dr
pl
nsdv9
dv7
dv6
dv5
cdv11
h
B
1 cm
dr
g
sv3
sv2
sv1
dv16
dv15
dv14
dv13
dv12
dr
sv5
sv6
pl
psl
ph
paw
tp
dr
tp
sv4
uprz
lprz
dr

Fig. 20 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. The last five dorsal vertebrae and the first 'sacrals' in perspective view. Abbreviations: ipzl = lateral prespinal lamina (infraprezygapophysial lamina of Dalla Vecchia 2006); lprz = lower prezygapophysis; nc = neural canal; pl = prespinal lamina; tp = transverse process; uprz = upper prezygapophysis. For scale see Fig. 19.
- Bobosaurus forojuliensis, *MFSN 27285, olotipo. Le ultime vertebre dorsali e le prime 'sacrali' in vista prospettica. Abbreviazioni: ipzl = lamina prespinale laterale (lamina infraprezigapofisiale di* Dalla Vecchia *2006); lprz = prezigapofisi inferiore; nc = canale neurale; pl = lamina prespinale; tp = processo trasverso; uprz = prezigapofisi superiore. Per la scala si veda la Fig. 19.*

is not present in the figures of this paper (excluding Fig. 17 where it was added).

The apex of the neural spine, at least in mid-dorsal vertebrae, is jagged (Fig. 18B) or concave (Fig. 23) in lateral view.

There is a certain degree of variability in the lamination pattern of the neural arches of the dorsal vertebrae that cannot be fully appreciated because the arches are mostly still surrounded by rock and mostly show the right lateral side only. Dalla Vecchia (2006) based his description of the prespinal and 'suprainfrazygapophyseal' laminae (Dalla Vecchia 2006, fig. 10B) mainly on the dorsal vertebra 12, which is exposed in cranial view (see Figs 20 and 21A). Actually, the scarcely developed 'suprainfrazygapophyseal' laminae do not originate or reach the 'suprainfrazygapophysis (here upper prezygapophysis), thus a more appropriate definition would be 'lateral prespinal laminae'.

As anticipated above, the prespinal lamina (which has a median position with respect to the 'lateral prespinal laminae) seems to divide basally to reach each of the two upper prezygapophyses with a short but distinct ramus (Fig. 21A; see also Dalla Vecchia 2006, fig. 10B). However, the prespinal lamina of dorsal vertebra 1 seems to be median and distinct with respect to the upper prezygapophysis (Fig. 13).

Dorsal ribs

The rib cage is disarticulated and some of the dorsal ribs have shifted caudally and dorsally. The slab surface contains remains of 21-23 dorsal ribs. Some of them can be seen in Fig. 22.

The shafts of the dorsal ribs do not flare distally like in *Simosaurus* (Dalla Vecchia 2008) and do not show pachyostosis. Unlike the 'uncinate' processes described by Klein & Sichelschmidt (2014), the 'uncinate' processes in the dorsal ribs of *Bobosaurus forojuliensis*

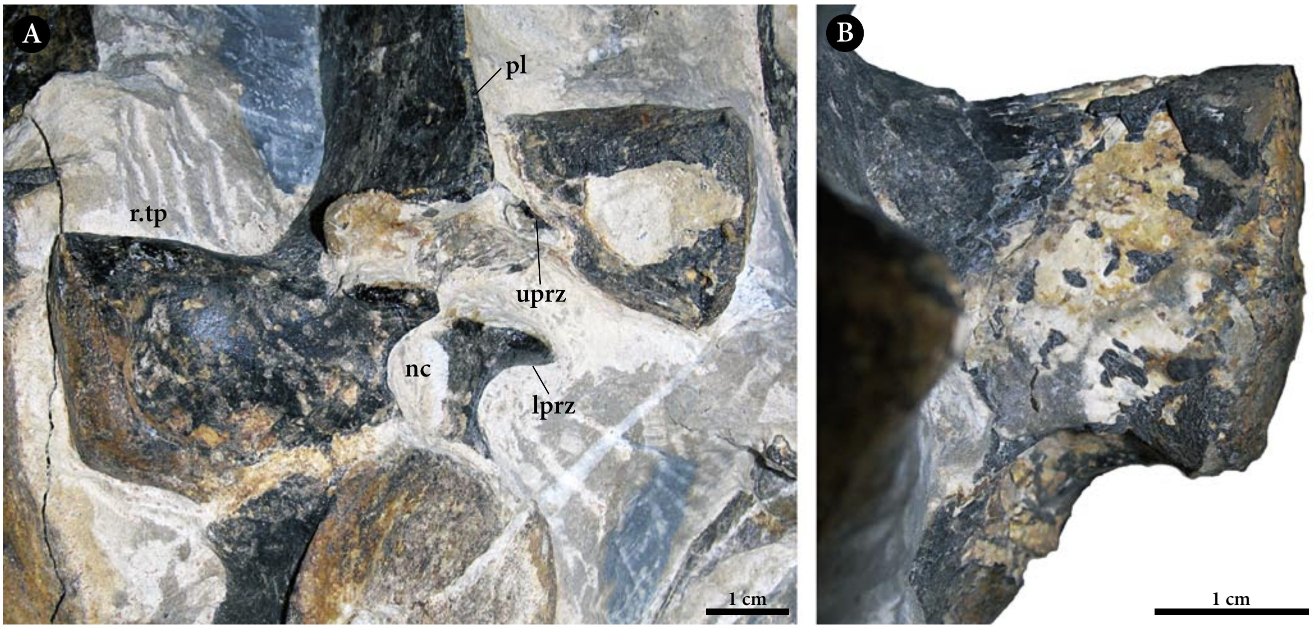

Fig. 21 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Transverse processes of the dorsal vertebrae. A) Dorsal vertebra 12; B) right transverse process of dorsal vertebra 7 in caudal view. Abbreviations: lprz = lower prezygapophysis; nc = neural canal; pl = prespinal lamina; r = right; tp = transverse process; uprz = upper prezygapophysis.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Processi trasversi delle vertebre dorsali. A) vertebra dorsale 12; B) processo trasverso destro della vertebra dorsale 7 in vista caudale. Abbreviazioni: lprz = prezigapofisi inferiore; nc = canale neurale; pl = lamina prespinale; r = destro; tp = processo trasverso; uprz = prezigapofisi superiore.*

Fig. 22 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Dorsal ribs. Abbreviations: ah = single articular head of the dorsal rib; Cr = caudal rib; Cv = 'caudal' vertebra; sh = shaft of the dorsal rib; sr = sacral ribs; sv = 'sacral' vertebra; up = 'uncinate' process of the dorsal rib.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Costole dorsali. Abbreviazioni: ah = testa articolare singola della costola dorsale; Cr = costola caudale; Cv = vertebra 'caudale'; sh = diafisi della costola dorsale; sr = costola sacrale; sv = vertebra 'sacrale'; up = processo 'uncinato' della costola dorsale.*

Fig. 23 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. The dorsal-'sacral' transition. The arrows point to the neurocentral suture that migrates downward on the centrum. Abbreviations: dv13-16 = dorsal vertebrae 13-16; fo = foramen; paw = posterior articular wedge; pl = prespinal lamina; psl = postspinal lamina; sv1-2 = 'sacral' vertebra 1-2; tp = transverse process.
- Bobosaurus forojuliensis, *MFSN 27285, olotipo. La transizione dorso-'sacrale'. Le frecce indicano la sutura neurocentrale che migra verso il basso sul centro vertebrale. Abbreviazioni: dv13-16 = vertebre dorsali 13-16; fo = forame; paw = cuneo articolare posteriore; pl = lamina prespinale; psl = lamina postspinale; sv1-2 = vertebre 'sacrali' 1-2; tp = processo trasverso.*

are developed at about mid-shaft and are long and relatively craniocaudally narrow flanges along the caudal sides of the ribs (Fig. 22). *Pistosaurus longaevus* (see Gleissner 1895; Diedrich 2013), *Augustasaurus hagdorni* (see Sander et al. 1997), *Yunguisaurus liae* (see Sato et al. 2010, 2014) and *Wangosaurus brevirostris* (see Ma et al. 2015) do not have 'uncinate' processes in their dorsal ribs.

'Sacral' vertebrae (Figs 23-24)

Dalla Vecchia (2006) referred to as 'sacrals' the post-pectoral vertebrae with the articular facet for the rib partly on the centrum partly on the neural arch (i.e., the articular facet for the rib is cut by the neurocentral suture), following Brown (1981). Under this assumption, *Bobosaurus forojuliensis* has nine 'sacral' vertebrae. This segment is not well-exposed and 'sacral' vertebrae 5 and 6 are still mostly concealed by rock. The transition from dorsal to 'sacral' vertebrae so defined is gradual (Fig. 23); only a very small portion of the articular facet is on the centrum in the first 'sacral' vertebra. Of course, *Bobosaurus forojuliensis* does not

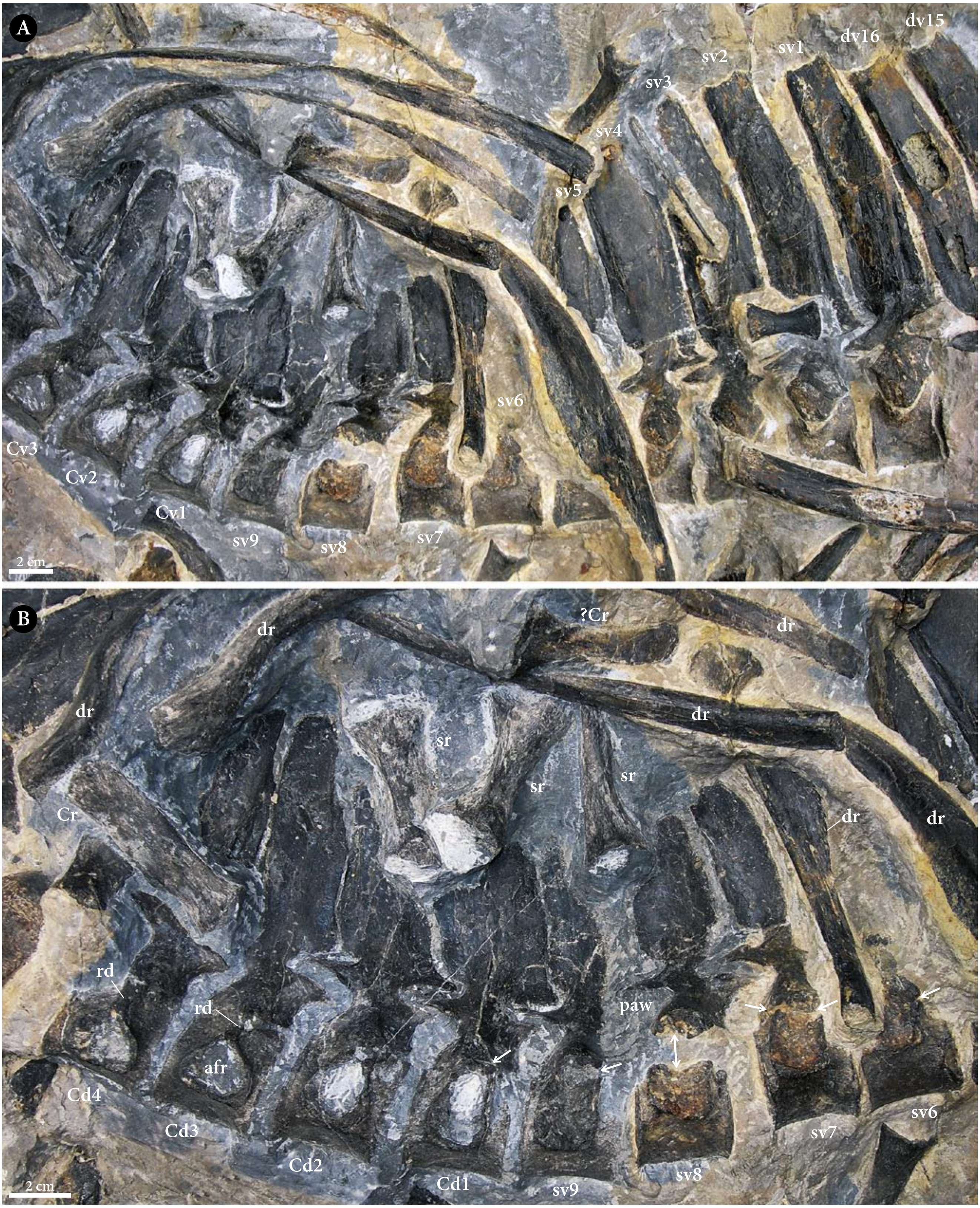

Fig. 24 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. The 'sacral' segment of the vertebral column. A) The whole segment and the adjacent dorsal and 'caudal' vertebrae; B) detail of the 'sacro-caudal' transition. Arrows point to the neurocentral suture. Abbreviations: afr = articular facet for the rib; Cr = caudal rib; Cv1-4 = 'caudal' vertebrae 1-4; dr = dorsal rib; dv13-16 = dorsal vertebrae 13-16; paw = posterior articular wedge; rd =ridge; sr = sacral rib; sv1-9 = 'sacral' vertebra 1-9.

- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Il segmento 'sacrale' della colonna vertebrale. A) l'intero segmento e le vertebre dorsali e 'caudali' adiacenti; B) dettaglio della transizione 'sacro-caudale'. Le frecce indicano la sutura neurocentrale. Abbreviazioni: afr = facetta articolare per la costola; Cr = costola caudale; Cv1-4 = vertebre 'caudali' 1-4; dr = costola dorsale; dv13-16 = vertebrae dorsali 13-16; paw = cuneo articolare posteriore; rd =cresta; sr = costola sacrale; sv1-9 = vertebre 'sacrali' 1-9.*

have nine true sacral vertebrae, but the actual number of true sacral vertebrae cannot be known, because their corresponding sacral ribs are not still articulated to them. In fact, the only way to know which are the true sacral vertebrae is by their association with the sacral ribs, which are usually expanded at their extremities and articulate with the ilia. Only one isolated sacral vertebra with a fused rib having expanded extremities is referred to *Pistosaurus longaevus* (see Diedrich 2013); the sacrum is unknown in *Augustasaurus hagdorni* (see Sander et al. 1997; Rieppel et al. 2002). The four sacral vertebrae of *Wangosaurus brevirostris* are identified based on their articulated ribs, which are robust and distally expanded (Ma et al. 2015). Sato et al. (2010) do not explain on which bases the three sacral vertebrae are identified in *Yunguisaurus liae*; Sato et al. (2014, p. 6) based their identification on the presence of ribs with "wide" distal ends and on the observation that "the combined width of the three ends on the left side is only slightly narrower than the sacral end of the ilium".

Three parallel ribs in a row (Fig. 24B) are plausibly sacral ribs because of their expanded distal extremities, but they occur in correspondence of the last two 'sacral' vertebrae and the first 'caudal' vertebra. If they are in their original anatomical position, then *Bobosaurus forojuliensis* would have at least three sacral and 23 dorsal vertebrae (like *Yunguisaurus liae*). Dalla Vecchia (2006) tentatively identified other four bones as sacral ribs. If this is correct, *Bobosaurus forojuliensis* would have four sacral vertebrae (but see below). In the case that the three sacral ribs are shifted backward from their original position (this was the interpretation by Dalla Vecchia 2006), it is possible that only the middle three or four of the nine 'sacral' vertebrae (thus, 'sacrals' 4-6, or 4-7/3-6) are true sacrals. However, according to Dalla Vecchia (2006), the true sacral vertebrae are probably the 'sacrals' 7-9 (with the possible addition of 'sacral' vertebra 6, if *Bobosaurus forojuliensis* has four sacral vertebrae), based on the morphology of the articular facets for the ribs compared to those in the sacral vertebrae of the plesiosaur *Cryptoclidus* figured by Brown (1981) (in 'sacrals' 6-9 of MFSN 27285, the articular facets occupy most of the lateral surfaces of the centra, are concave and have each a median dorsoventral groove; Fig. 24B). In that case, *Bobosaurus forojuliensis* would have 21-22 dorsal vertebrae.

The centra of the 'sacral' vertebrae have neurovascular foramina like the last dorsal vertebrae (Fig. 23).

The shape of the tall neural spines of the 'sacral' vertebrae can be seen in Figs 23 and 24.

Sacral ribs

As discussed above, sacral ribs are usually identified based on their expanded extremities. *Bobosaurus forojuliensis* seems to have at least three sacral ribs per side, which were sutured and not fused to their respective vertebrae. The row of three sacral ribs detached, but close to the vertebrae mentioned above is shown in Fig. 25A. As anticipated above, Dalla Vecchia (2006) tentatively identified other four bones as sacral ribs. One of them can be observed in Fig. 25A and is shown in detail also in Fig. 28E. Dalla Vecchia (2006) referred with doubt that rib as a sacral rib, mostly because of its position and distinct morphology from the caudal ribs, although it is unexpanded at one extremity; its referral will be discussed below in the description of the caudal ribs. Other two purported sacral ribs are fragmentary. The only well-preserved and exposed is that in Fig. 25B.

In Fig. 25A, the three sacral ribs in a row are indicated with the letters *a-c*, with *a* the most cranial and *c* the most caudal of the three. Ribs *b* and *c* have both extremities expanded; the extremity toward the vertebra of rib *a* is expanded, while the other extremity was considered as "unexpanded" by Dalla Vecchia (2006), but it is actually still covered by rock, therefore it could be expanded too. As rib *a* is very similar to the other two associated ribs, it is plausibly a sacral rib too, not the last "lumbar" as alternatively proposed by Dalla Vecchia (2006). These three ribs are probably from the right side because of their position on the right side of the vertebral column. One of the expanded extremities of the better exposed isolated sacral rib (Fig. 25B) is forked (bifid) with a central groove separating two rough articular facets; this bifid extremity occurs also in the sacral rib *b* of the string and it is the iliac extremity. The articular facet of the opposite expanded extremity (which can be observed in the rib of Fig. 25B) fits into the articular facet for the rib in the 'sacral' vertebra 9.

The still articulated sacral ribs of *Yunguisaurus liae* (NMNS 004529/F003862) appear to be scarcely expanded at the extremities in dorsal view, but these are mostly damaged (Sato et al. 2010, fig. 8); those of specimen ZMNH M8738 (figured by Sato et al. 2014, fig. 8C-D) appear to be more slender than those of *Bobosaurus forojuliensis*. Ma et al. (2015) do not describe the sacral ribs of *Wangosaurus brevirostris* in detail. In the sacral vertebra referred to *Pistosaurus longaevus* by Diedrich (2013, fig. 13K), the rib is fused with the centrum and its extremities are dorsoventrally expanded. The expansion of the extremities is dorsoventral also in *Simosaurus gaillardoti* and the rough and thicker extremity is the iliac one (see Rieppel 1994, fig. 20A-C and F).

'Caudal' vertebrae (Figs 24 and 26-27)

As the actual sacral vertebrae cannot be unambiguosly identified, also the beginning of the caudal segment remains dubious. Consequently, Dalla

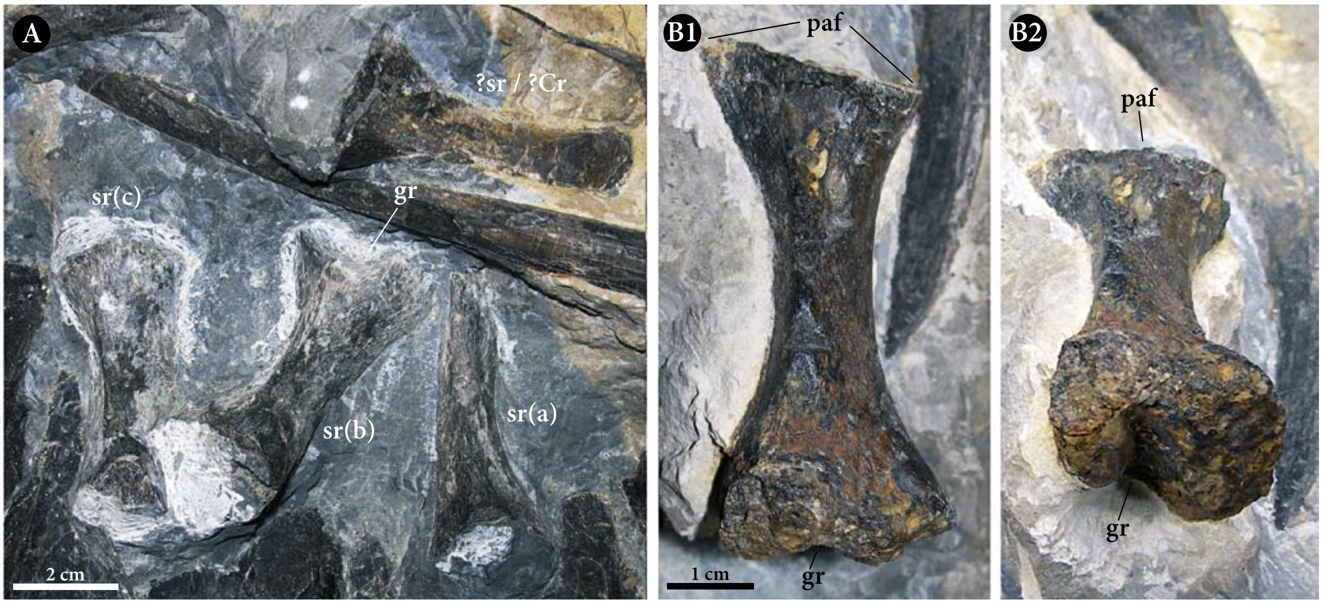

Fig. 25 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Sacral ribs. A) Three associate sacral ribs, probably right elements; B) isolate sacral rib, in cranial or caudal view (B1) and in latero-cranial or latero-caudal view (B2). The proximal extremity in B1 is the original one (i.e., it is not cut or damaged). Abbreviations: gr = groove; paf = proximal articular facet; sr(a-c) = sacral ribs (a-c), alphabetical order corresponds to the cranio-caudal position.

- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Costole sacrali. A) tre costole sacrali associate, probabilmente destre; B) costola sacrale isolata in vista craniale o caudale (B1) e in vista latero-craniale o latero-caudale (B2). L'estremità prossimale in B1 è quella originale, vale a dire che non è tagliata o danneggiata. Abbreviazioni: gr = solco; paf = faccetta articolare prossimale; sr(a-c) = costole sacrali (a-c), l'ordine alfabetico corrisponde alla posizione cranio-caudale delle costole.*

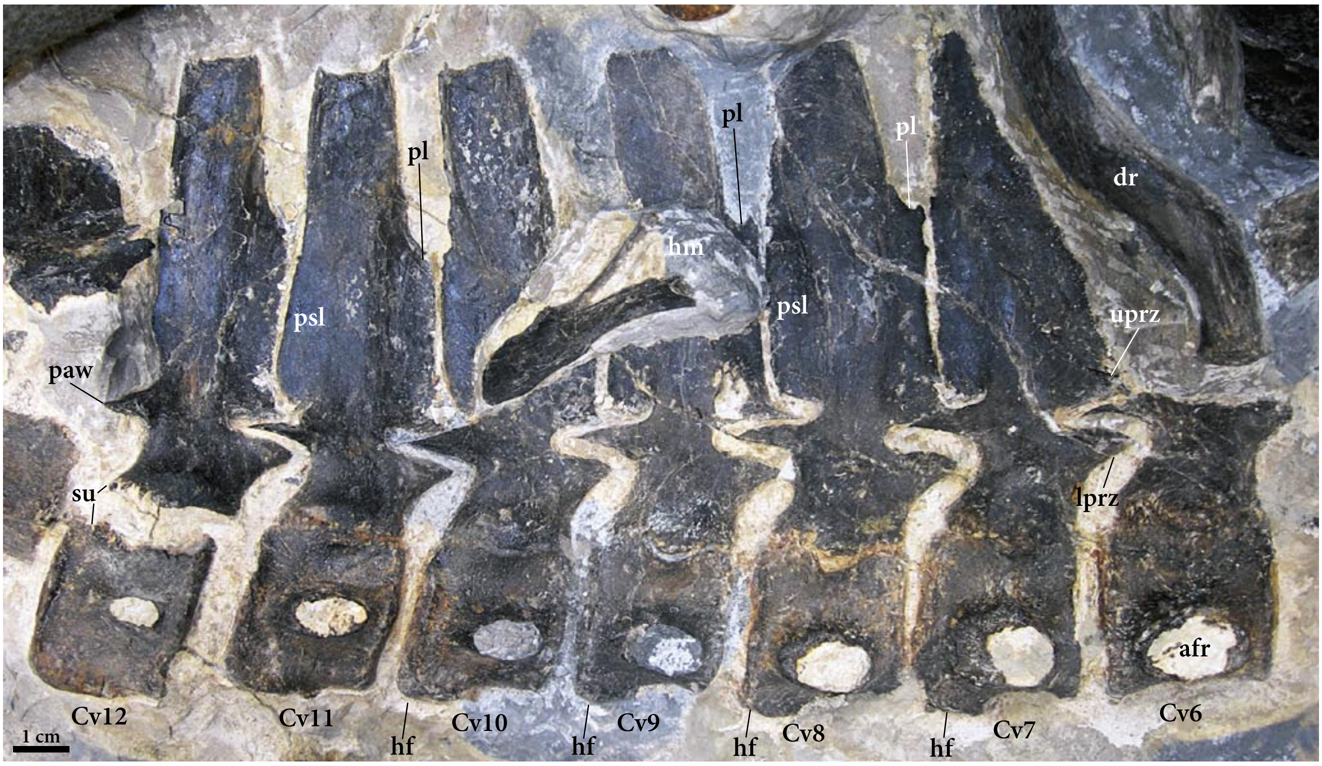

Fig. 26 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Proximal caudal vertebrae. Abbreviations: afr = articular facet for the rib; Cv 6-12 = caudal vertebrae 6-12; dr = dorsal rib; hf = haemapophysial facet; hm= haemapophysis; lprz = lower prezygapophysis; paw = posterior articular wedge; pl = prespinal lamina; psl = postspinal lamina; su = neurocentral suture; uprz = upper prezygapophysis.

- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Vertebre caudali prossimali. Abbreviazioni: afr = faccetta articolare per la costola; Cv 6-12 = vertebre 'caudali' 6-12; dr = costola dorsale; hf = facetta articolare per l'emapofisi; hm= emapofisi; lprz = prezigapofisi inferiore; paw = cuneo articolare posteriore; pl = lamina prespinale; psl = lamina postspinale; su = sutura neurocentrale; uprz = prezigapofisi superiore.*

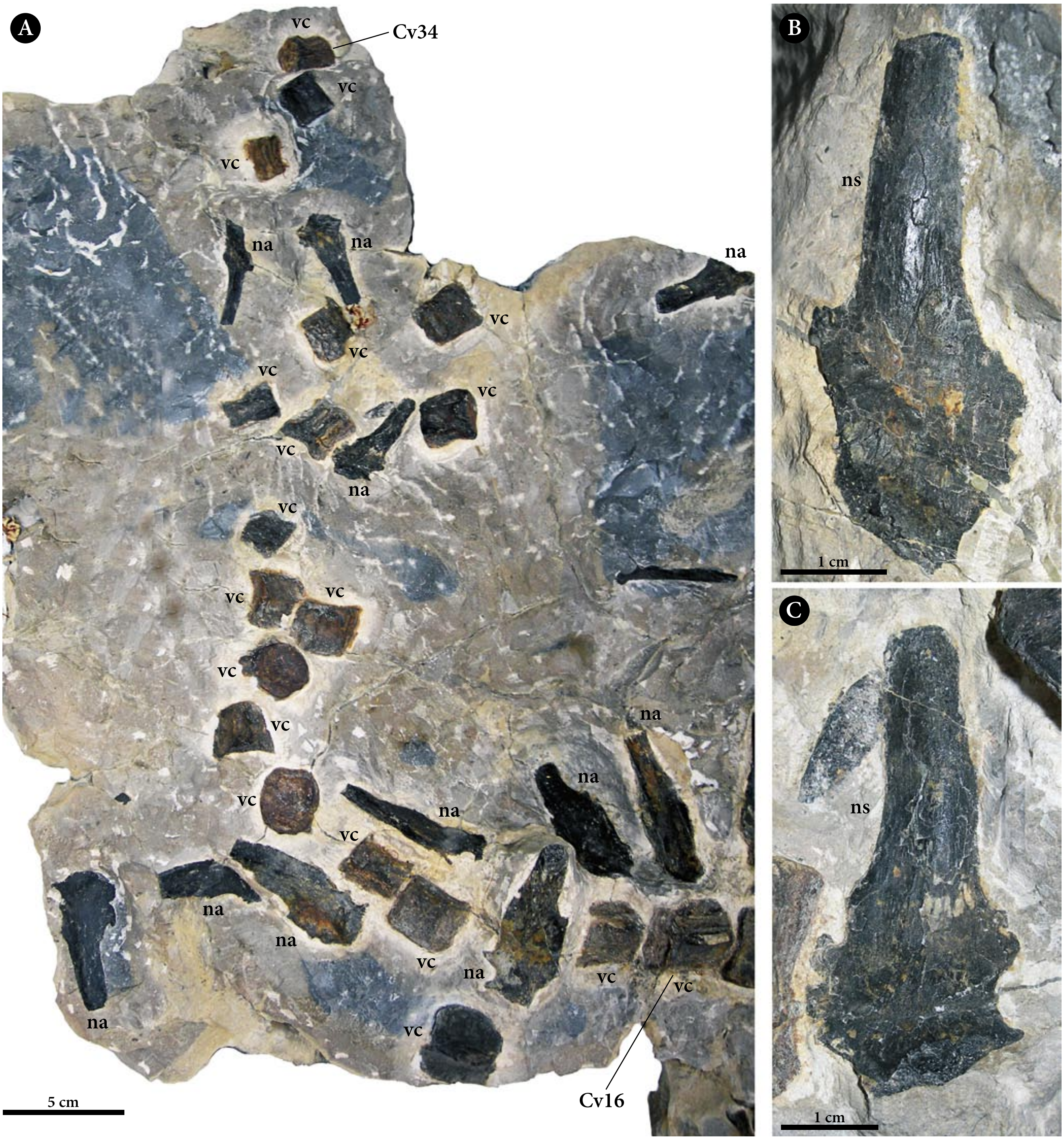

Fig. 27 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Middle-distal caudal vertebrae. A) Panoramic view of the distal preserved portion of the tail; B-C) detail of two isolated neural arches. Abbreviations: Cv = caudal vertebrae; na = neural arch; ns = neural spine; vc = vertebral centrum.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Vertebre caudali medio-distali. A) panoramica della porzione distale della parte conservata della coda; B-C) dettaglio di due archi neurali isolati. Abbreviazioni:* Cv = vertebre caudali; *na = arco neurale; ns = spina neurale; vc = centro vertebrale.*

Vecchia (2006) considered as 'caudal' vertebrae those with the articular facet for the rib that sits wholly on the centrum, following (Brown 1981). As I said above, the first 'caudal' vertebra might be the last true sacral vertebra.

The preserved 'caudal' vertebrae are 38, including four small distal elements scattered on the slab (Dalla Vecchia 2006). The articulated segments 1-4 (Fig. 24) and 6-12 (Fig. 26) are separated by a gap containing the isolated 'caudal' vertebra 5 (Fig. 1); the segment following 'caudal' 12 is more disarticulated (Fig. 27A).

The details of the 'caudal' vertebrae described by Dalla Vecchia (2006) can be observed in Figs 24, 26 and 27. Fig. 27B-C shows the neural arches of the mid-distal caudal vertebrae in detail. The neural spines slightly taper apically, as it is the case of the apical half of the spines of all 'caudal' vertebrae (Figs 24 and 26). The articular structures in neural arches of mid-distal caudal vertebrae are not clearly identifiable.

Projecting posterior facets for the haemapophyses are visible only in 'caudal' vertebrae 7-10 in lateral view (Fig. 26). Haemapophyseal facets are probably present also in the successive centra, but they cannot be seen because they are concealed by rock.

Caudal ribs

Five to seven caudal ribs, all disarticulated and scattered, were identified by Dalla Vecchia (2006). The uncertainty in the number is caused by the possible confusion between proximal caudal and 'lumbar' ribs when they are not connected with their relative vertebrae.

Dalla Vecchia (2006) referred a slender and curved element (Fig. 28A) as a possible first caudal rib by comparison with the "anterior" caudal rib of *Simosaurus gaillardoti* figured by Rieppel (1994, fig. 20D), underlining, however, that it could alternatively be a 'lumbar' rib (the element is marked with an asterisk in Dalla Vecchia 2006, fig. 4). This latter identification is supported by the comparison with *Wangosaurus brevirostris* (see Ma et al. 2015, fig. 1), but the comparison with *Yunguisaurus liae* supports the first identification (Sato et al. 2014; the first caudal rib is recurved in fig. 8C).

Most of the caudal ribs from proximal positions have long, straight and dorsoventrally flat shafts with

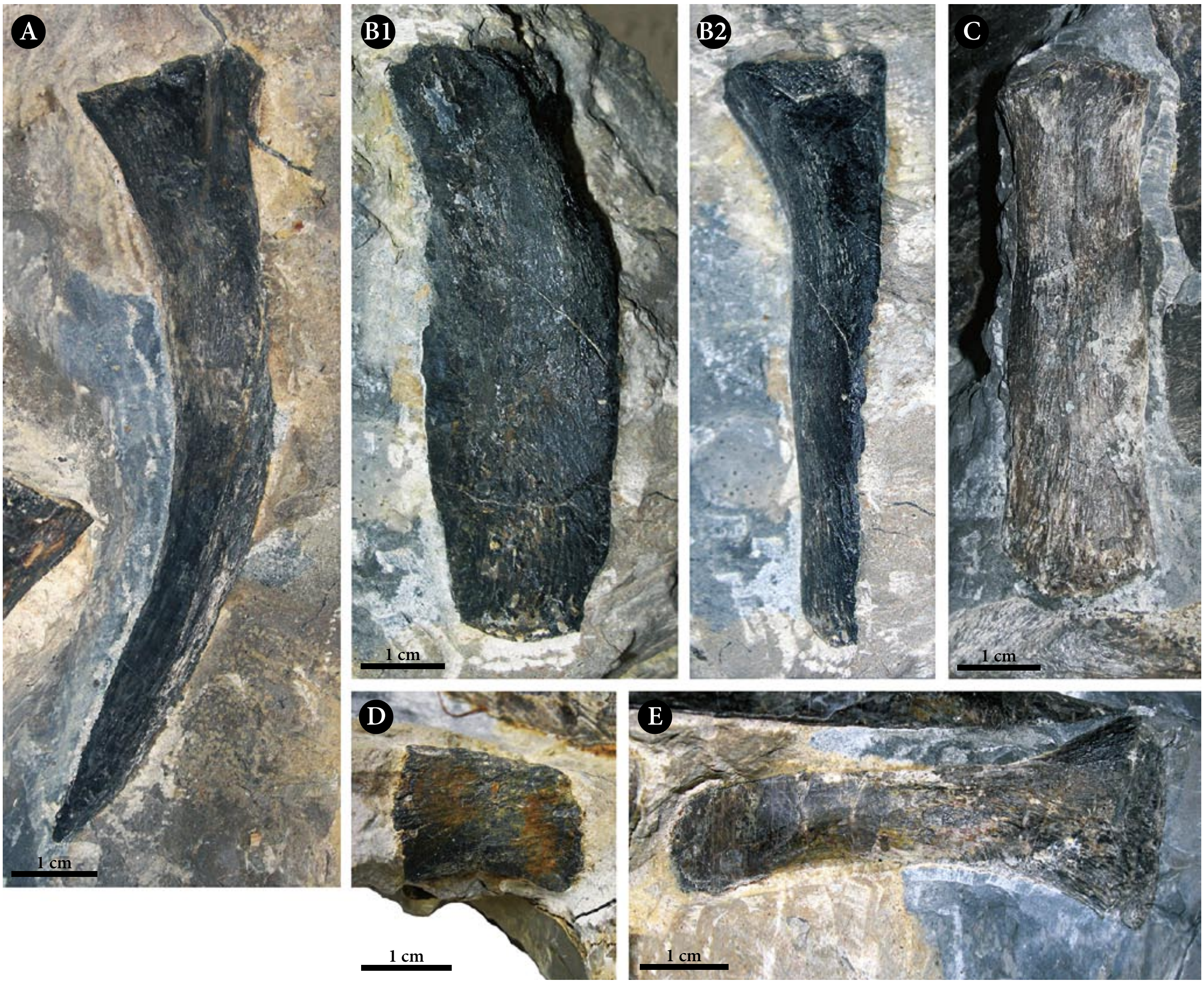

Fig. 28 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Caudal ribs. A) Proximal caudal rib or alternatively 'lumbar' rib; B) proximal caudal rib in dorsoventral (B1) and cranial (B2) views; C) proximal caudal rib in dorsoventral view; D) distal caudal rib in dorsoventral view; E) possible proximal caudal or sacral rib in dorsoventral view.

- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Costole caudali. A) costola caudale prossimale o in alternativa costola 'lombare'; B) costola caudale prossimale in vista dorso-ventrale (B1) e craniale (B2); C) costola caudale prossimale in vista dorso-ventrale; D) costola caudale distale in vista dorso-ventrale; E) possibile costola caudale prossimale o sacrale in vista dorso-ventrale.*

"squared" distal ends (Fig. 28B-C). Those from more distal positions have also dorsoventrally flattened shafts, but are very short (Fig. 28E). The rib in figure 28D appears to differ a little from the proximal caudal ribs, because its shaft is more slender and appears to be slightly expanded 'distally'. However, the apparent 'distal' end of the bone is not its actual extremity, which is probably concealed by rock. As it is preserved close to the string of three sacral ribs, Dalla Vecchia (2006) identified it as a sacral with doubt, underlining that, alternatively, it could be a 'lumbar' or a drifted caudal rib. The descriptions of *Yunguisaurus liae* and *Wangosaurus brevirostris* are not sufficiently detailed to help in solving the doubt.

Unlike *Bobosaurus forojuliensis*, the proximal caudal ribs of *Yunguisaurus liae* are fused to their centra (Sato et al. 2014).

Haemapophyses

Haemapophyses are disarticulated and scattered. At least seven of them can be identified in the slab, mostly in correspondence of the proximal tail segment (Fig. 1). Each haemapophysis is made of two distinct pedicels that unite at the distal end where the haemal spine begins, closing the haemal canal ventrally (Fig. 29). The haemal spines of the largest hemapophyses are fan-shaped in lateral view, with a broad distal portion (Fig. 29).

Yunguisaurus liae appears to have rod-shaped haemapophyses that are not united medially like those of plesiosaurs (Sato et al. 2010; 2014). Their spines taper distally in lateral view (Sato et al. 2014, fig. 6A-B). Haemapophyses are undescribed in *Wangosaurus brevirostris* (see Ma et al. 2015).

Gastralia

The slab contains the remains of at least eight gastralia. The gastral plastron disarticulated during the decay of the carcass and the elements are scattered on the slab surface. Three medio-ventral elements are characteristically angulated and with sharp extremities; they have a single and small cranial

Fig. 29 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Three proximal haemapophyses (chevrons).
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Tre emapofisi prossimali.*

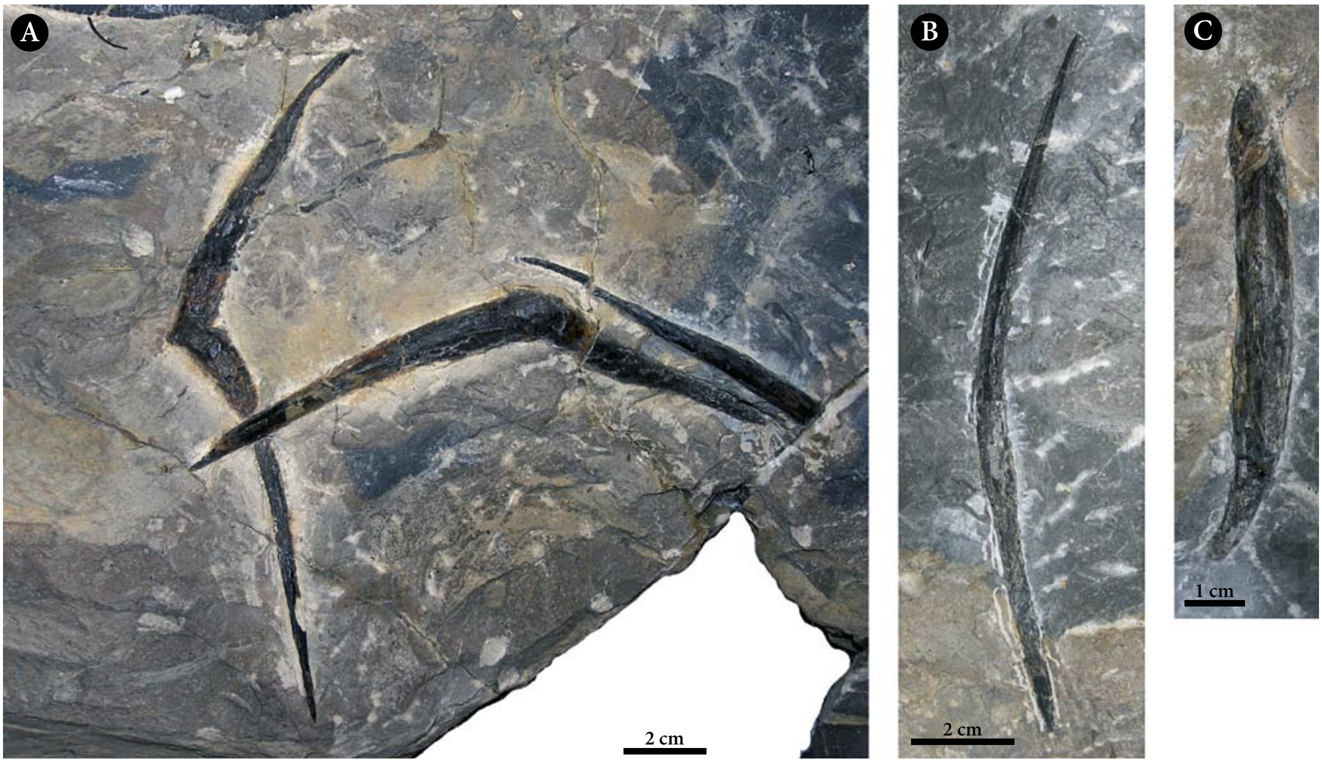

Fig. 30 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Gastralia. A) Medioventral gastral 'rib' segments; B) intermediate gastral 'rib' segment; C) possible lateral gastral 'rib' segment.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Gastrali. A) segmenti medio-ventrali di 'costole' gastrali; B) segmento intermedio di una 'costola' gastrale; C) possibile segmento laterale di una 'costola' gastrale.*

process (Fig. 30A). Slightly curved, slender, and spindle-shaped elements are intermediate or lateral gastral segments (Fig. 30B), while a shorter and more robust element (Fig. 30C) with a curved extremity could be a lateral segment (Rieppel 2001). Gastralia are unreported in *Wangosaurus brevirostris* (see Ma et al. 2015). Sato et al. (2010) do not describe the gastralia of *Yunguisaurus liae*, but according to Sato et al. (2014, p. 6), the specimen ZMNH M8738 has 48 disarticulated gastralia and the "medial" ones are "boomerang-shaped".

Appendicular skeleton

Forelimbs

The right humerus is the only exposed forelimb element and shows its dorsal side (Fig. 31A). It is much larger than the humerus of *Wangosaurus brevirostris* (see Ma et al. 2015, figs 1 and 3A-B), but it is impossible to establish exactly how much larger, because Ma et al. (2015) do not report any measurement; it is three times longer than the right humerus of the holotype of *Yunguisaurus liae* and 2.24 times that of the second specimen (ZMNH M8738; Sato et al. 2014); it is 1.52 times the length of the humerus of the holotype of *Augustasaurus hagdorni* and over 1.5 times that of *Pistosaurus longaevus* figured in Sues (1987). It is club-like with a postaxially curved and expanded distal end. The distal two-thirds of the postaxial margin are concave, while the whole preaxial margin is practically straight.

At the time of the first study of MFSN 27285, the distal portion of the humerus was partly covered distally by rock and the centra of the dorsal vertebrae 10 and 11, but it was further prepared after the publication of Dalla Vecchia (2006) exposing the entepicondyle (Fabbri et al. 2014). The proximal extremity of the humerus is concave and has a rough surface (Fig. 31B) that is suggestive of the presence of an extensive cartilage cap in the living animal (Diedrich 2013). The proximal extremity is concave also in *Pistosaurus longaevus* (see Sues 1987; Diedrich 2013) and *Yunguisaurus liae* (see Sato et al. 2010), while the state in *Augustasaurus hagdorni* and *Wangosaurus brevirostris* is unknown (Sander et al. 1997; Ma et al. 2015). Sato et al. (2010) considered this feature as caused by the lack of the epiphysis and probably suggestive of individual immaturity, while it is a structural feature to give more rigidity to the limb according to Diedrich (2013). The humerus of *Bobosaurus forojuliensis* has no trace of the deltopectoral crest like the humeri of *Pistosaurus longaevus* and *Augustasaurus hagdorni* (see Sander et al. 1997); the state appears to be unknown in *Wangosaurus brevirostris* (see Ma et al. 2015) and *Yunguisaurus liae* (Sato et al. 2010, 2014; the humerus of *Yunguisaurus liae* is not described is sufficient

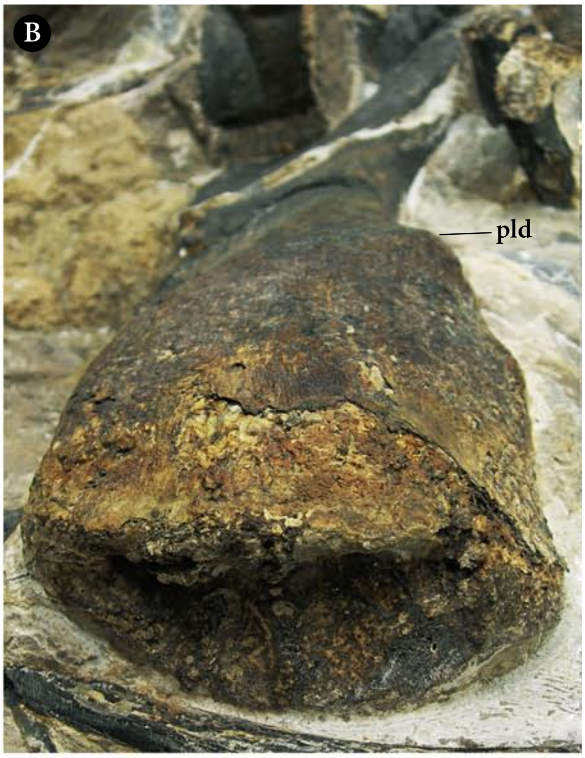

Fig. 31 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Humerus. A) Right humerus in dorsal view (the centrum of dorsal vertebra 10 was removed); B) particular of the concave proximal end. Abbreviations: cdv11 = centrum of the dorsal vertebra 11; cpf = concave proximal face; ent = entepicondyle; pld = protuberance for the *latissimus dorsi*.

- Bobosaurus forojuliensis, *MFSN 27285, olotipo. Omero. A) omero destro in vista dorsale (con il centro della vertebra dorsale 10 rimosso); B) particolare dell'estremità prossimale concava. Abbreviazioni: cdv11 = centro della vertebra dorsale 11; cpf = faccia prossimale concava; ent = entepicondilo; pld = protuberanza per il* latissimus dorsi.

detail). Dalla Vecchia (2006) identified a distinct protuberance occurring dorsally near the postaxial margin (Fig. 31A) as the possible point of insertion of the *latissimus dorsi* muscle, based on Rieppel (2001) and figures in Sues (1987). However, the purported insertion of the *latissimus dorsi* muscle is broader and without relief in *Corosaurus alcovensis* (see Storrs 1991), while it has a broader surface and is placed more centrally on the dorsal surface in other sauropterygians (Klein 2010). In any case, the structure occurring in *Bobosaurus forojuliensis* is a knob-like protuberance, not a crest.

The cleaning of the distal termination of the humerus (mainly removing the centrum of the dorsal vertebra 10, which is not present in the figures of this paper, excluded Fig. 1) exposed the entepicondyle and allowed detecting the absence of the entepicondylar foramen (Fabbri et al. 2014) like in *Pistosaurus longaevus* and *Augustasaurus hagdorni* (see Sander et al. 1997) and *Yunguisaurus liae* (see Sato et al. 2010), but unlike *Wangosaurus brevirostris* (see Ma et al. 2015). The entepicondyle is moderately developed. Unfortunately, it was not possible to further expose the distal end of the humerus (which is still covered by the centrum of the dorsal vertebra 11) in order to observe the presence or the absence of the ectepicondylar foramen and the morphology of the distal articular facets for the ulna and radius.

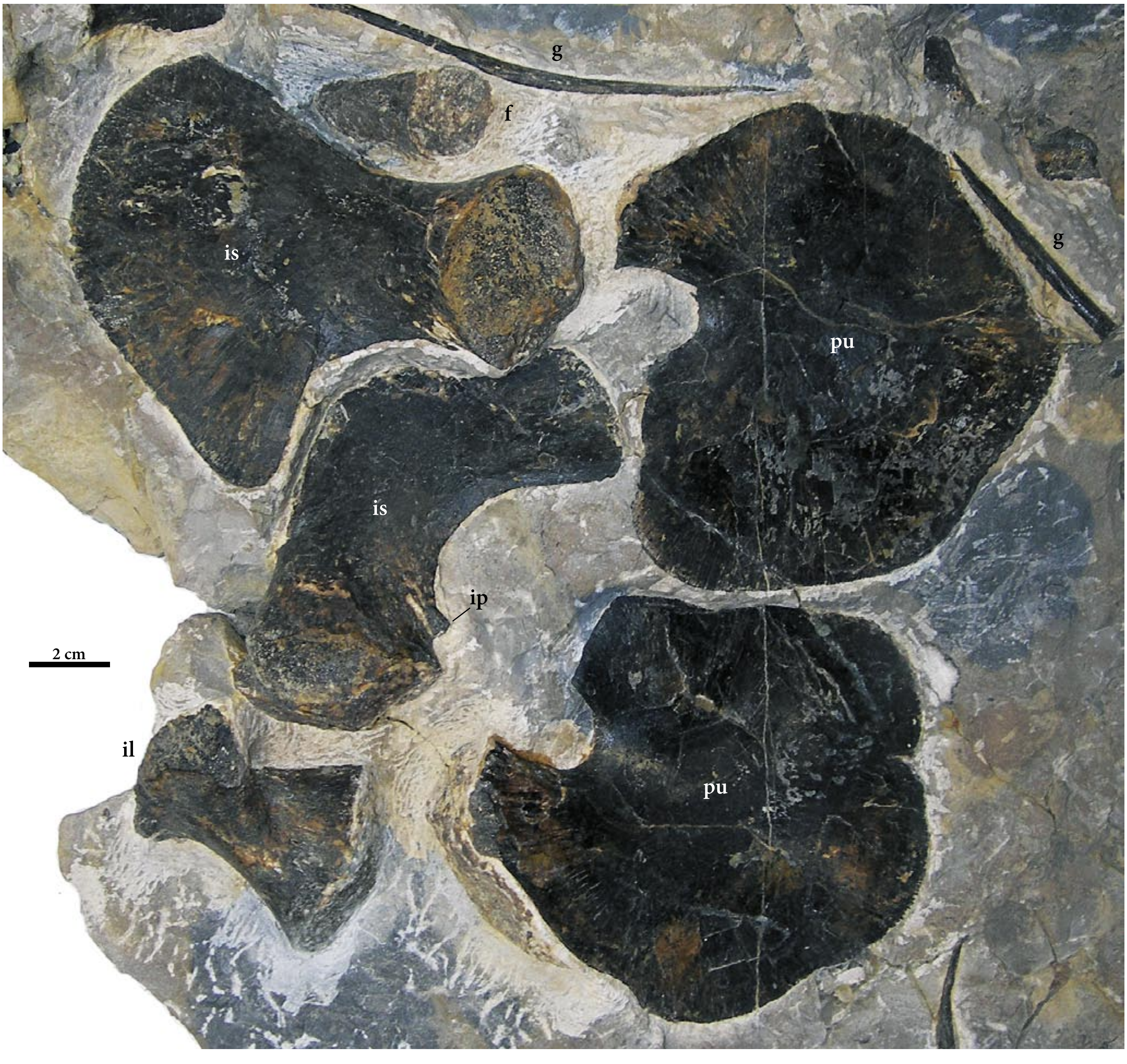

Fig. 32 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Pelvic girdle in dorsomedial view. Abbreviations: f = femur; g = gastrale; il = ilium; ip = small cranioproximal process of the ischium; is = ischium; pu = pubis.
- Bobosaurus forojuliensis*, MFSN 27285, olotipo. Cinto pelvico in vista dorso-mediale. Abbreviazioni: f = femore; g = gastrale; il = ilio; ip = piccolo processo cranio-prossimale dell'ischio; is = ischio, pu = pube.*

Pelvic girdle

Contra Diedrich (2013), the pelvic girdle is well-exposed and nearly complete in the holotype of *Bobosaurus forojuliensis* (only the left ilium is not visible; Fig. 32). The ischia and pubes are still paired and suffered only a limited disarticulation, while the right ilium is close to them. The ischia and pubes form expanded ventral plates that meet their opposites in the midline.

According to Dalla Vecchia (2006), ischia and pubes show their dorsomedial side, based on comparison with the ischium of *Simosaurus gaillardoti*. In fact, the ventrolateral side of the latter is convex, while the dorsomedial surface is flat (Rieppel 1994, fig. 28D); this seems to be the case of the similarly shaped ischium of *Tanystropheus* too (Wild 1973). The ischia of the holotype of *Bobosaurus forojuliensis* show the flat dorsomedial surface.

The only preserved ilium (Fig. 33) shows four sides: a lateral or medial one (Fig. 33A), a caudal or cranial one (Fig. 33C), part of the ventral and part of the dorsal sides. As the exposed lateral or medial side has no trace of the articular facets for the sacral ribs (Fig. 33A-B), it is presumably the lateral side, not the medial one as reported by Dalla Vecchia (2006) based on the asymmetrical development of the craniocaudally elongated iliac blade. If the pelvis is in dorsal view, the position of the element suggests it is a right ilium in lateral and cranial views. Although cranially damaged, the preacetabular process is therefore more developed than the postacetabular process, unlike *Nothosaurus* and *Simosaurus* (Rieppel 2000) and *Corosaurus alcovensis* (see Storrs 1991). The postacetabular process is longitudinally divided into two parts in lateral view; Fig. 33A-B).

The craniocaudally elongated iliac blade is relatively well-developed and the postacetabular process is not projecting beyond level of posterior margin of acetabular portion of ilium, but this is not comparable with the state in other sauropterygians because of the peculiar morphology of the ilium of MFSN 27285. The shaft is twisted and the laterocaudally-mediocranially expanded distal end bears a ventrolateral acetabular facet and a ventromedial articular surface for the ischium (Fig. 33). Therefore, the ilium of *Bobosaurus forojuliensis* seems to contact the ischium only.

The ilium of *Pistosaurus longaevus* is quite different: the iliac blade has nearly parallel cranial and caudal margins, has a sharply truncated dorsal end and contacts distally also the pubis (Sues 1987, fig. 5). The holotype of *Yunguisaurus liae* also has a different paddle-like ilium, with a narrow and short shaft, a moderately expanded distal (acetabular) end and a much expanded iliac blade, which however is relatively short craniocaudally and its postacetabular part is slightly more developed than the preacetabular (Sato et al. 2010, fig. 8). However, the ilium of the referred specimen ZMNH M8738, with its craniocaudally elongated iliac blade and expanded articular end (Sato et al. 2014, fig. 8-C-D), is more similar to that of *Bobosaurus forojuliensis*, but differs in its longer shaft and apparent absence of twisting. Unfortunately, the ilium is unknown is *Augustasaurus hagdorni* (see Sander et al. 1997) and it is not yet described in *Wangosaurus brevirostris* (see

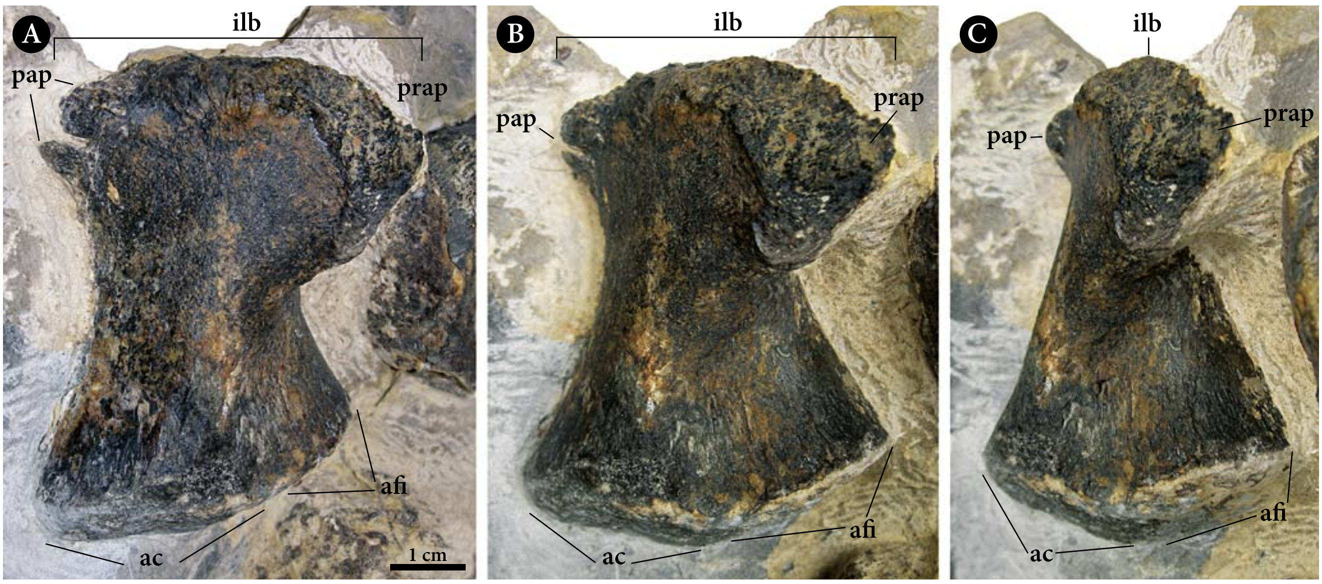

Fig. 33 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Right ilium. A) Lateral view; B) laterocranial view; C) cranial view. Abbreviations: ac = iliac contribution to the acetabulum; afi = articular facet for the ischium; ilb = iliac blade; pap = postacetabular process of the iliac blade; prap = preacetabular process of the iliac blade.

- Bobosaurus forojuliensis, *MFSN 27285, olotipo. Ilio destro. A) vista laterale; B) vista latero-craniale; C) vista craniale. Abbreviazioni: ac = contributo dell'ileo all'acetabolo; afi = faccetta articolare per l'ischio; ilb = lama iliaca; pap = processo postacetabolare della lama iliaca; prap = processo preacetabolare della lama iliaca.*

Ma et al. 2015). The ilium of *Bobosaurus forojuliensis* has a primitive overall morphology resembling the ilia of *Nothosaurus* and *Simosaurus* (Rieppel 2000) and *Corosaurus alcovensis* (see Storrs 1991), which, however, do not present the twisting of the shaft and articulate with the pubis (Sues 1987).

The pubes are exposed in dorsomedial view (Fig. 32); the thickened articular portion of the right one was freed from the conglobating rock to show the articular facet for the ischium and the acetabular contribution of the pubis. Each element is a broad, semi- to sub-circular and very thin plate that thickens very much in correspondence of the articular facet for the ischium and the pubic contribution to the acetabulum (Fig. 34). The caudal margin has a semicircular notch which forms the cranial part of the puboischiadic fenestra. There is no open and slit-like obturator notch like that occurring in the pubes of *Nothosaurus* (see Rieppel 1994) and *Paranothosaurus amsleri* (see Peyer 1939), nor the obturator foramen of *Simosaurus gaillardoti* (see Rieppel 1994).

The rounded pubes are very similar to those of *Yunguisaurus liae* (see Sato et al. 2014) and possibly also to those of *Pistosaurus longaevus* (see Diedrich 2013), which resemble those of the plesiosaur *Plesiosaurus* (Storrs 1997) and the plesiosaurs in general (e.g., Andrews 1910; Carpenter 1999; Ketchum & Smith 2010). The semicircular pubis of *Corosaurus alcovensis* is similar to those of *Bobosaurus* and *Yunguisaurus* (Storrs 1991), but it has a slit-like obturator notch and an articular facet for the ilium. The general morphology of the pubes of the more primitive eusauropterygians *Simosaurus* and *Nothosaurus* is completely unlike the overall morphology of the pubis of *Bobosaurus forojuliensis*: their pubes are craniocaudally waisted (i.e., cranially concave) and notched medially (Rieppel 1994).

The right ischium shifted below the left ischium (Fig. 32). The left ischium rotated nearly 90 clockwise from its anatomical position and covers the caudal process of the right ischium. Along the cranial margin of the shaft and close to the articulated head, there is a small process surrounding a slit-like opening that Dalla Vecchia (2006) identified as a possible obturator process. Process and opening appear to be rather similar to those present in the pubes of *Nothosaurus* (e.g., Rieppel 1994, fig. 29; 2001, fig. 6J), where the opening is considered to be the obturator foramen (Rieppel 1994). However, such a structure is absent in the ischium of *Simosaurus gaillardoti* (see Rieppel 1994), *Nothosaurus* cf. *N. juvenilis* (see Renesto 2010), *Cymatosaurus* sp. (Sander et al. 2014), *Pistosaurus longaevus* (see Diedrich 2013), and *Yunguisaurus liae* (see Sato et al. 2014). The articular head of both ischia is damaged in correspondence of the articular facet for the ilium.

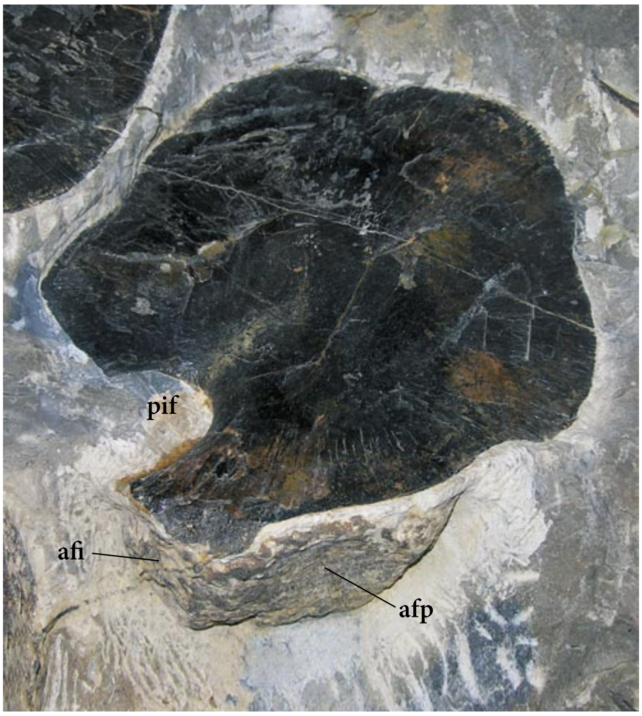

Fig. 34 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. The right pubis in mediodorsal and perspective view, with the articular region in foreground. Abbreviations: afi = articular face for the ischium, afp = acetabular facet of the pubis; pif = cranial part of the puboischiatic fenestra. For scale see Fig. 32.
- Bobosaurus forojuliensis, *MFSN 27285, olotipo. Il pube destro in vista medio-dorsale e prospettica, con la regione articolare in primo piano. Abbreviazioni: afi = faccetta articolare per l'ischio; afp = contributo del pube all'acetabolo; pif = parte craniale della finestra puboischiatica. Per le dimensioni si veda la Fig. 32.*

Hind limbs and metapodials/phalanges

The circular cross-section of the diaphysis of a long bone occurs close to the left ischium (Fig. 32). Because of its position, size and cross-section outline, Dalla Vecchia (2006) referred this bone to as a femur. If this identification is correct as it seems, the femur is much more slender than the humerus and has a cylindrical shaft.

The only preserved zeugopodial element is a tibia (Fig. 35A), which is much longer than wide and only moderately expanded distally like the tibiae of *Yunguisaurus liae* (see Sato et al. 2014) and *Wangosaurus brevirostris* (see Ma et al. 2015), but it is more slender than that of *Yunguisaurus liae* and similar to that of *Wangosaurus brevirostris*.

Only two bones can be referred to as carpals or tarsals (Fig. 35B-C). They are disc-like and comparatively large and are preserved close to the tibia (Fig. 1). Dalla Vecchia (2006) identified them as proximal tarsals because of their location and size: the largest as the astragalus and the smaller as the calcaneum (cf. Sato et al. 2010, fig. 10). There is no proximal concavity in the astragalus.

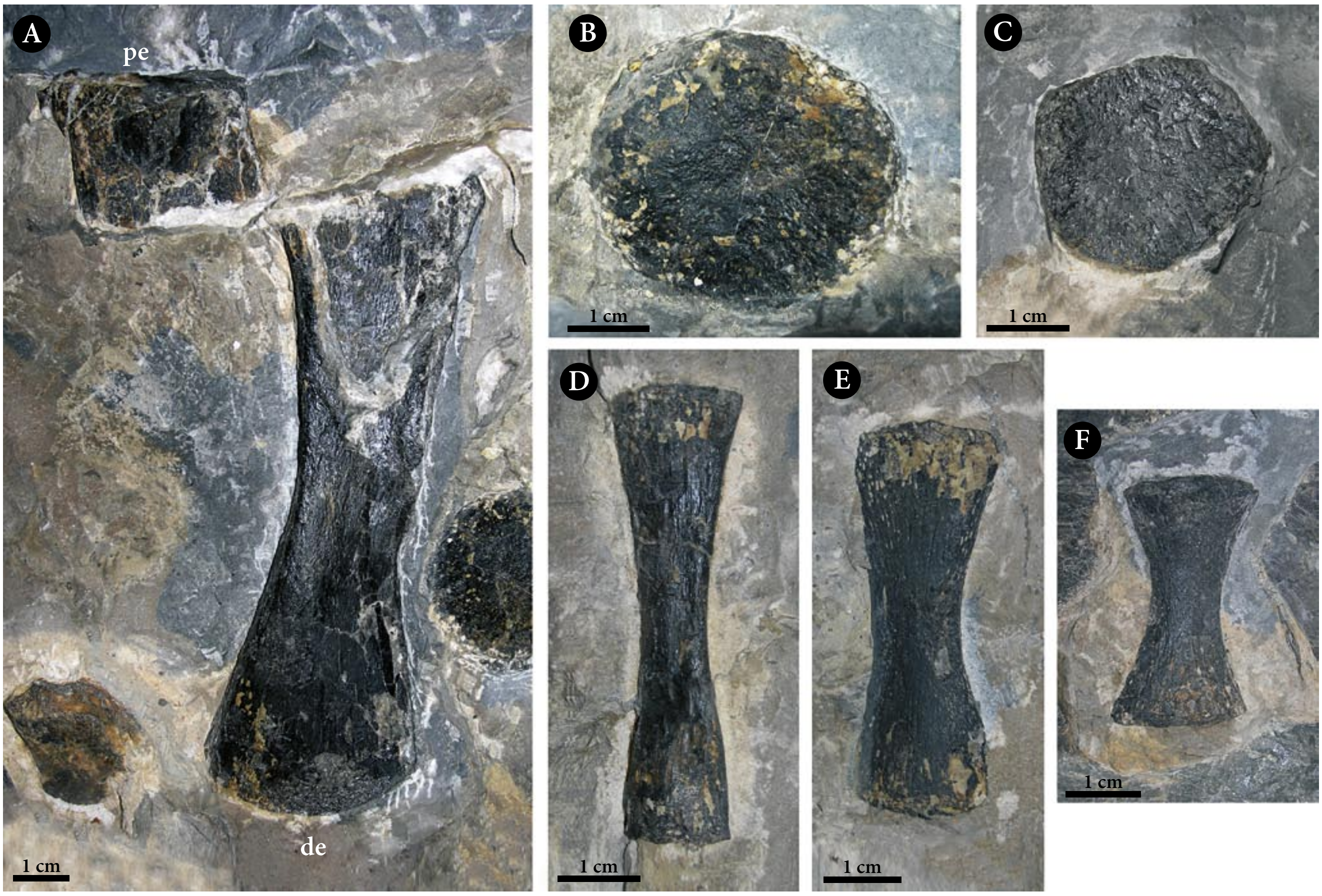

Fig. 35 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Other limb bones. A) Tibia; B) astragalus; C) calcaneum; D-E) metapodials; F) possible phalanx. Abbreviations: de = distal extremity; pe = proximal extremity.
- Bobosaurus forojuliensis, *MFSN 27285, holotype. Altri elementi degli arti. A) tibia; B) astragalo; C) calcagno; D-E) metapodiali; F) possibile falange. Abbreviazioni: de = estremità distale; pe = estremità prossimale.*

Only two slender and relatively short bones can be identified as metapodials on the slab (Fig. 35D-E). A third shorter and stouter element is probably a proximal phalanx (Fig. 35F). Although all of the three bones were considered forelimb elements in the reconstruction of Fig. 2, it cannot be established for sure whether the metapodials are metacarpals or metatarsals and the phalanx is from manus or pes. Comparison with the articulated limbs of *Yunguisaurus liae* (see Sato et al. 2010, fig. 10) suggests they are all from the forelimbs, because those from the hind limbs are more massive. However, the distinction in *Wangosaurus brevirostris* is not so evident as in *Yunguisaurus liae* (Ma et al. 2015, fig. 3). Furthermore, the size of the humerus compared to the tibia and the cross-section of the femur suggest that the forelimbs were more robust than the hind limbs in *Bobosaurus forojuliensis,* unlike *Yunguisaurus liae* and *Wangosaurus brevirostris*.

Lightened skeleton

A peculiarity of *Bobosaurus forojuliensis* taht was underlined in Dalla Vecchia (2006) is its lightened postcranial skeleton, which is the opposite of the pachyostotic skeleton of some other sauropterygians (Rieppel 2000; Taylor 2000). Broken or cross-sectioned bones show that they are coarsely spongy internally, with a framework of minute and spaced trabeculae (osteoporosis of Sheldon 1997) and a very thin external layer of compacta (which often is less than 0.5 mm thick). This can be observed in the cross-sectioned neural spine of the axis (Fig. 36A), in several cross-sectioned pedicels of the cervical ribs (Fig. 36B), in the eroded or broken transverse processes of the pectoral vertebrae (Fig. 36C), in some broken neural arches of the dorsal vertebrae (Fig. 36E), and in cross-sectioned centra of the cervical vertebrae 8-9 (Fig. 36F). The hollow inside of some neural spines seems to be totally filled in with calcite (Fig. 36D). Long skeletal elements are locally collapsed showing that the inner part was hollow or very coarsely spongy (e.g., the tibia [Fig. 36G]). This is the case of the shafts of many dorsal ribs and at least one pectoral rib, while some smaller ribs from distal positions are finely spongy distally and were probably heavier than the others.

The most probable function of a lightened skeleton was to increase natural buoyancy (Sheldon 1997) and

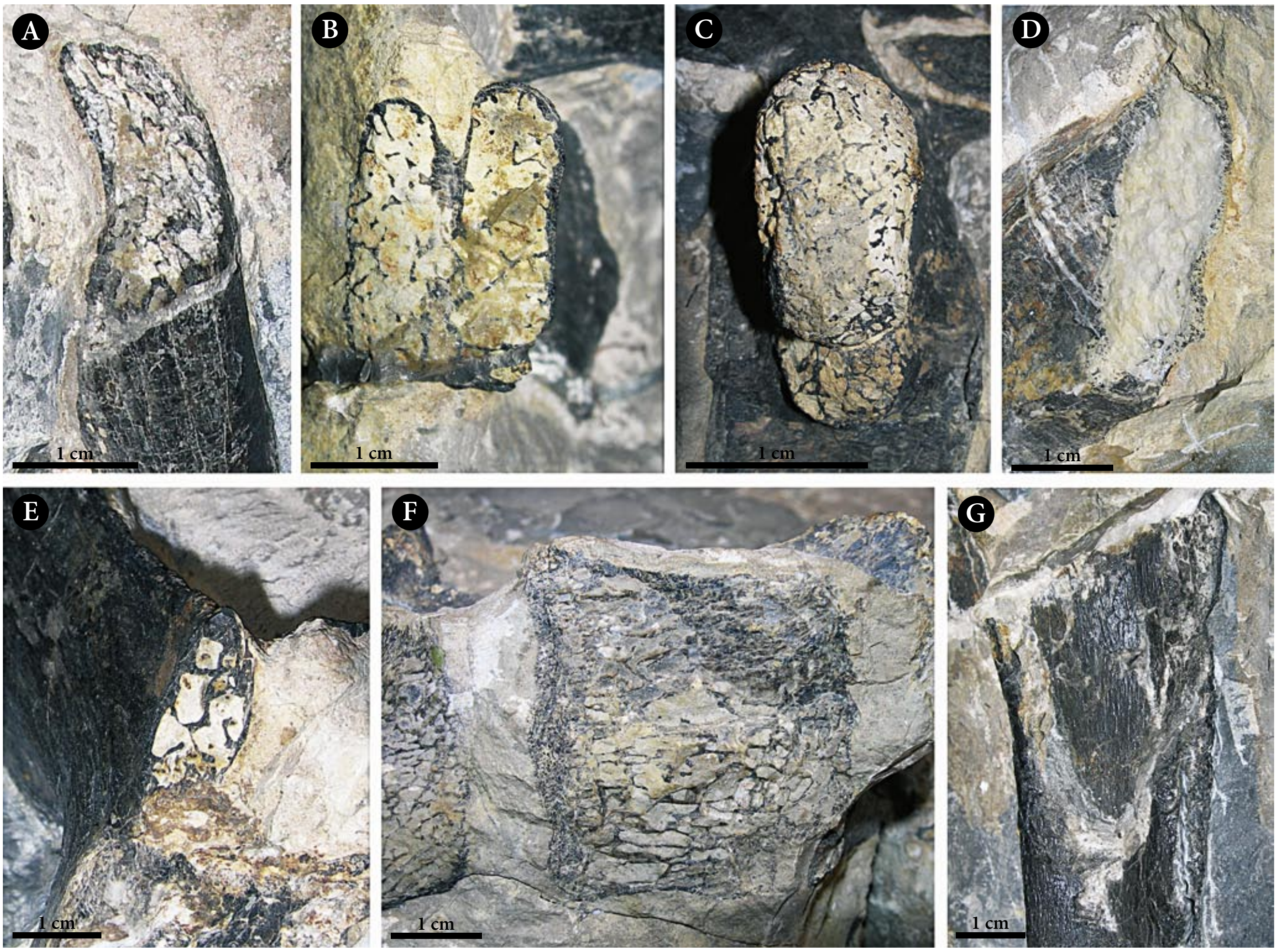

Fig. 36 - *Bobosaurus forojuliensis*, MFSN 27285, holotype. Evidences of the coarsely cancellous inside of the *Bobosaurus* bones. A) Sectioned neural spine of the axis; B) sectioned tuberculum and capitulum of a cervical rib; C) worn right transverse process of pectoral vertebra 6; D) sectioned neural spine of dorsal vertebra 5; E) sectioned upper prezygapophysis of dorsal vertebra 8; F) longitudinal section of the centrum of cervical vertebra 9 (sectioned centrum 8 to the left); G) collapsed portion of the tibial shaft. Voids are filled by white calcite.
- Bobosaurus forojuliensis, *MFSN 27285, olotipo. Evidenze del riempimento grossolanamente spugnoso delle ossa di* Bobosaurus. *A) sezione della spina neurale dell'asse; B) sezione del tuberculum e del capitulum di una costola cervicale; C) processo trasverso destro della vertebra pettorale 6, dalla superficie erosa; D) sezione della spina neurale della vertebra dorsale 5; E) sezione della prezigapofisi superiore della vertebra dorsale 8; F) sezione longitudinale del centro della vertebra cervicale 9 (a sinistra il centro sezionato della vertebra cervicale 8); G) porzione collassata della tibia. I vuoti sono stati riempiti da calcite bianca.*

could be related to fast swimming and active predation on mobile food (Taylor 2000). Dalla Vecchia (2006) hypothesized that *Bobosaurus forojuliensis* were a surface swimmer that dwelled in the shallow sea existing along the north-western coasts of Tethys during the early Carnian. However, according to Sheldon (1997, p. 349), the reduced bone density is consistent with the reduced effect of gravity and occurs in amniotes frequenting the deeper portion of the water column. The depositionary environment where the carcass of MFSN 27285 deposited was a shallow carbonate-clastic ramp (Preto et al. 2005), with maximum water depths of a few dozen of metres. However, the carcass could be transported by storms from the close deep water Julian Basin, which occurred a few kilometres to the east during the early Carnian, as it is probably the case also of the few ammonoids found in the Rio del Lago Formation (Preto et al. 2005). This would explain the rarity of *Bobosaurus forojuliensis* remains in the Rio del Lago Formation.

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