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SKELETAL REMAINS OF LARGE EUSAUROPTERYGIAN REPTILES (REPTILIA, SAUROPTERYGIA) FROM THE MIDDLE TRIASSIC OF THE AUPA VALLEY (NE ITALY)

RESTI SCHELETRICI DI GRANDI RETTILI EUSAUROPTERIGI (REPTILIA, SAUROPTERYGIA) DAL TRIASSICO MEDIO DELLA VAL AUPA (ITALIA NORD-ORIENTALE)

Abstract - Skeletal elements of large eusauropterygian reptiles are described from the uppermost Anisian Torbiditi d'Aupa Formation of the Aupa Valley, Friuli Venezia Giulia Autonomous Region. They include a tooth crown, an articulated dorsal segment of the vertebral column, eight isolated vertebral centra, five isolated neural arches, a caudal rib, a scapula, three coracoids, an ischium, a femur, and a mesopodial element. Size, morphological comparison and age suggest an affinity with '*Paranothosaurus amsleri*' from the Anisian-Ladinian boundary of Tessin (Switzerland and Italy). The scaling of some girdle and hind limb elements from the Aupa Valley according to the proportions of '*P. amsleri*' holotype gives total body length estimates of 385-320 mm for the Aupa Valley specimens. The late Anisian-early Carnian postcranial bones of large eusauropterygian reptiles with low neural spines from Germany and other European and middle Eastern localities have also been considered conspecific with the Tessin *taxon* or potentially such and variously referred as *Nothosaurus giganteus* (considering *P. amsleri* as a junior synonym of *N. giganteus*) or *Paranothosaurus giganteus* (considering *Paranothosaurus* as a valid genus). Whether these large and low-spined eusauropterygian reptiles all belong to a single and long-lived species or to more distinct species is still an unsolved question.
Key words: *Nothosaurus giganteus*, *Paranothosaurus amsleri*, Sauropterygia, Eusauropterygia, Osteology, Triassic, Anisian.

Riassunto breve - *Sono descritti gli elementi scheletrici di grandi rettili eusaurotterigi rinvenuti nelle Torbiditi d'Aupa (Anisico sommitale) della Val Aupa (Moggio Udinese, Udine). Includono una corona dentaria, un segmento dorsale articolato della colonna vertebrale, otto centri vertebrali isolati, cinque archi neurali isolati, una costola caudale, una scapola, tre coracoidi, un ischio, un femore e un elemento mesopodiale. Le dimensioni, il confronto morfologico e la datazione sugeriscono un'affinità con* 'Paranothosaurus amsleri' *del limite Anisico-Ladinico del Ticino (Svizzera e Italia). Facendo una proporzione tra la lunghezza di elementi dei cinti e dell'arto posteriore della Val d'Aupa e quella dei corrispondenti elementi dell'olotipo di* 'P. amsleri' *si ottiene una stima della lunghezza corporea totale di 385-320 mm per gli esemplari della Val d'Aupa. Il materiale postcraniale dei grandi rettili eusaurotterigi con spine neurali basse dell'Anisico superiore-Carnico inferiore rinvenuti in Germania e altre località europee e medio-orientali è stato considerato conspecifico con il* taxon *ticinese o potenzialmente tale e variamente riferito a* Nothosaurus giganteus *(considerando* P. amsleri *come un sinonimo più recente di* N. giganteus*) o a* Paranothosaurus *giganteus (considerando* Paranothosaurus *un genere valido). Se questi grandi rettili eusaurotterigi dalle spine neurali basse appartengano tutti ad una singola e longeva specie o a più specie distinte rimane una questione aperta.*
Parole chiave: Nothosaurus giganteus, Paranothosaurus armsleri, *Sauropterygia, Eusauropterygia, Triassico, Anisico.*

Introduction

The Middle Triassic Torbiditi d'Aupa Formation (Aupa Turbidites) of the eastern Carnic Alps (NE Italy) are being yielding abundant reptile skeletal remains since the beginning of this century. The specimens belong to tanystropheids, archosauriforms, sauropterygians and ichthyosaurs (Dalla Vecchia 2006b; 2008a; 2010; 2021). These remains were collected along the Aupa Torrent near Saps village (Moggio Udinese Municipality, Friuli Venezia Giulia Autonomous Region, NE Italy; Fig. 1). They come from 10 distinct outcrops (see Dalla Vecchia 2006b; 2010; Dalla Vecchia & Simonetto 2018). Although close to each other, these outcrops may represent different levels within the Torbiditi d'Aupa Formation, as suggested by the different lithologies containing the bones.

The Torbiditi d'Aupa Formation is 350 m thick in the Aupa Valley (Jadoul & Nicora 1979), but the vertebrate remains probably occur only in a few rela-

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tively thin horizons within the formation. According to Farabegoli *et* al. (1985) those horizons represent regressive events. The stratigraphic relationships of the ten fossil-bearing outcrops are difficult to establish because of the strong tectonic disturbance and the lacking of detailed studies.

The Torbiditi d'Aupa Formation was dated to the late Anisian-Anisian/Ladinian boundary by Jadoul & Nicora (1979) and to the latest Anisian (late Illyrian) by Farabegoli et al. (1985). Nicora et al. (2002, fig. 2) placed it in the upper Anisian. Dalla Vecchia (2006b) referred the Torbiditi d'Aupa Formation to the upper Anisian-lower Ladinian, most probably to the upper Anisian, based on the range of the ammonoid *Hungarites* gr. *zalaensis* (Böckh 1873) which was collected in the outcrop 6.

The Torbiditi d'Aupa Formation is approximately coeval with the Grenzbitumenzone/Besano Formation of Tessin (Switzerland and Italy), which yielded a reptile association that also include the long-necked tanystropheid *Tanystropheus*, archosauriforms (*Ticinosuchus ferox* Krebs 1965), a large eusauropterygian ('*Paranothosaurus amsleri*') and ichthyosaurs (Rieppel 2019).

The Torbiditi d'Aupa Formation have been considered to be a deep marine deposit (Jadoul & Nicora 1979; Farabegoli et al. 1985; Nicora & Rizzi 1998), as the word "turbidites" in the name of the formation suggests. However, according to Farabegoli et al. (1985) the bone-bearing horizons correspond to the progradation of fan deltas into the basin during the acme of the regressive cycles. Those fan deltas formed at the southern margin of the Anisian Paleocarnic Ridge, which was an emergent area located just north of the present day Aupa Valley (Farabegoli et al. 1985).

Fig. 1 - Provenance of the specimens. A) Location of the Aupa Valley in the Friuli Venezia Giulia Autonomous Region of NE Italy; B) Location of the fossil-bearing outcrops 1, 5-7 and 9 (sensu Dalla Vecchia & Simonetto 2018) mentioned in the text.
- *Provenienza degli esemplari. A) Posizione della Val Aupa nella Regione Autonoma Friuli Venezia Giulia dell'Italia nordorientale; B) posizione degli affioramenti fossiliferi 1, 5-7 e 9 (sensu Dalla Vecchia & Simonetto 2018) menzionati nel testo.*

Materials and methods

Objects of this paper are the skeletal elements from the Torbiditi d'Aupa Formation of the Aupa Valley belonging to large eusauropterygian reptiles. All the specimens (MFSN 31555, 31564, 31578, 31586, 34995, 37591, 37592/1, 37595-96, 37599, 37601, 37602-604, 37605, 44323, 46608-611, and 46669) are deposited at the MFSN, excluded MGC 479100, which is at the MGC. All the specimens have been found by Roberto Rigo, excluded MGC 479100 which was collected by Alfonso Tolazzi about 25 years ago. The latter specimen was found along the Broili Torrent, which flows into the Aupa Torrent between the Fus/Fous and Andri brooks, but on the left side of the valley (Fig. 1). Both the Torbiditi d'Aupa Formation and the unit once named "Terrigeno Ladinico" crop out along the Broili Brook (Jadoul & Nicora 1979). The "Terrigeno Ladinico" apparently corresponds to the upper Ladinian Acquatona Formation in Jadoul et al. (2002); the Torbiditi d'Aupa Formation and the higher Acquatona Formation are separated by the Buchenstein Formation. Because the sandstones of the Torbiditi d'Aupa Formation and those of the "Terrigeno Ladinico" are similar (Jadoul & Nicora 1979) and the specimen MGC 479100 is a block found in the torrent bed (G. Muscio, pers. comm.), it is impossible to establish its actual unit of provenance; it is assumed here that it is from the Torbiditi d'Aupa Formation, which yielded all the other specimens.

The sauropterygian systematics followed here is that of Rieppel (2000), being anyway aware of the fact that alternative phylogenetic relationships among eosauropterygians have been published in the following 23 years (for example, *Nothosaurus* results to be paraphyletic in the analysis by Liu et al. 2014).

The taxonomic history of the large eusauropterygians *Nothosaurus giganteus* Münster 1834 and *Paranothosaurus amsleri* Peyer 1939 and the debate on their validity and combination will be afforded in the Dis-

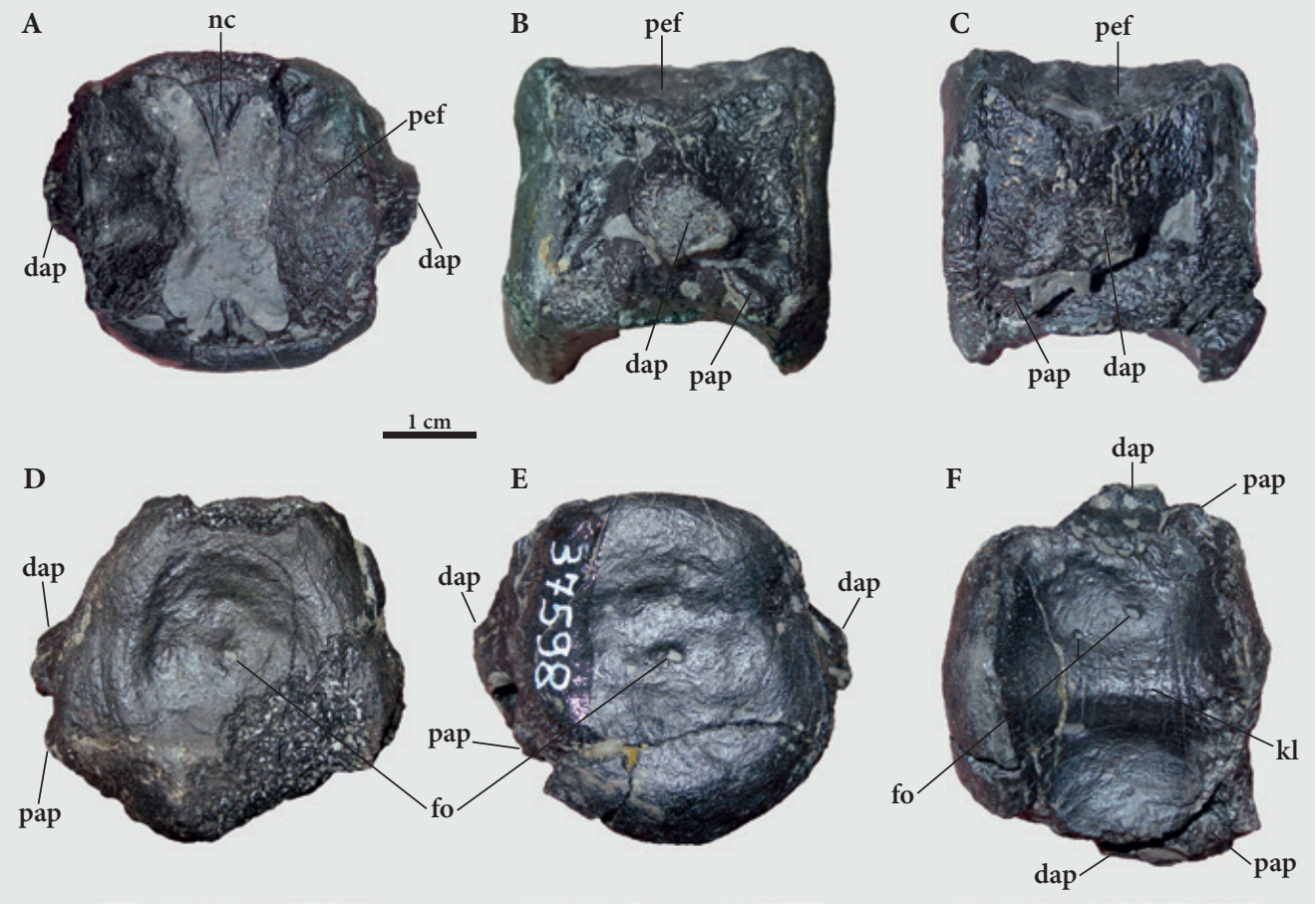


Fig. 2 - MFSN 37598, cervical vertebral centrum. A) Dorsal; B) right lateral; C); left lateral; D) anterior; E) posterior; and F) ventral views. Abbreviations: dap = diapophysis; fo = foramen; kl = keel; nc = neural canal; pap = parapophysis; pef = facet for pedicel of the neural arch.
- *MFSN 37598, centro vertebrale cervicale. A) Vista dorsale; B) laterale destra; C); laterale sinistra; D) anteriore; E) posteriore; F) ventrale. Abbreviazioni: dap = diapofisi; fo = forame; kl = carena; nc = canal neurale; pap = parapofisi; pef = facet for pedicel of the neural arc.*

cussion section. In the description and comparison of the specimens from the Aupa Valley, the names of these two taxa are used as in their original sense.

Gigantic apex predators have been defined by Liu et al. (2014) as those having body size ≥5 m long.

Institutional abbreviations: MFSN = Museo Friulano di Storia Naturale, Udine, Italy; MGC = Museo Geologico della Carnia, Ampezzo (Udine), Italy; PIMUZ = Paläontologisches Institut und Museum der Universität, Zürich, Switzerland; SMF = Naturmuseum Senckenberg, Frankfurt am Main, Germany; TWE = Museum TwentseWelle, Enschede, The Netherlands.

Description

The material consists of one tooth crown, an articulated dorsal segment of the vertebral column, several scattered skeletal elements from the vertebral column (eight centra, five neural arches and a caudal rib), four pectoral girdle elements (a scapula and three coracoids), one element of the pelvic girdle (an ischium), and two bones of the limbs (a femur and a mesopodial element).

Tooth

MFSN 31555 is a tooth crown from the outcrop 1. It was described, determined, and figured in Dalla Vecchia (2006b, fig. 5A), and figured in Dalla Vecchia (2008a, fig. 63C). It is conical and sigmoid, 18 mm long basoapically, with the surface ornamented by sharp and spaced basoapical ridges. There are no secondary and thinner basoapical ridges between the ridges, unlike the teeth referred to *Tanystropheus* (Dalla Vecchia 2006b, fig. 5; 2008a, fig. 63).

Axial skeleton

Cervical vertebra

MFSN 37598 (Fig. 2) is a vertebral centrum from the outcrop 6. It is 27 mm long; the anterior articular facet is 26.5 mm high and 27.5 mm wide. It is cylindrical with a flat dorsal surface bearing the neural canal and the

articular facets for the pedicels of the neural arch; the ventral surface is concave. The facets for the pedicels form with the neural canal a cruciform figure. The concave ventral surface is crossed longitudinally by a broad and blunt median keel. The ventral surface presents three small neurovascular foramina. The lateral surface bears the distinct diapophysis and parapophysis at the anteroventral corner; the small articular surfaces for the capitulum and tuberculum of the rib are rounded or elliptical, those of the left side are separated only by a shallow depression. The articular surfaces are flat, but with a shallow central depression bearing two small neurovascular foramina anteriorly and one posteriorly. The lateral surfaces are grooved and pitted suggesting osteological immaturity; therefore, this centrum probably belongs to an immature individual.

Dorsal vertebrae (Figs. 3-8)

MGC 479100 (Fig. 3) is a segment of the dorsal portion of the vertebral column made of eight articulated vertebrae with their corresponding ribs still in anatomical position. Here, the vertebrae are numbered progressively from the most proximal (1st) to the most distal (8th). The bones are preserved in a hard yellowish-grey sandstone. The bones have been worn away by erosion, exposing the neural arches in horizontal cross-section and the variably sectioned proximal portion of the ribs. The segment is exposed in dorsal view and the neural arches have been worn away almost to the pedicels. The articulated centra are plausibly preserved inside the rock. The distalmost vertebra exposes also the vertical cross- section of its centrum, which is ca. 25 mm high. The neural arches show all their main features variously sectioned. In dorsal/dorsolateral view, the sectioned neural arches have a rectangular outline, wider than long; the maximum width is ca. 70 mm (6th vertebra). The laterally projecting transverse processes are evident in the last four vertebrae (5th-8th). Because the section plane was not exactly perpendicular to the sagittal plane but variably inclined by a few degrees, the sections of both praezygapophyses and postzygapophyses are visible (Fig. 3). The interlocking zygosphene-zygantrum are evident in vertebrae 3rd to 8th (Fig. 3). Zygosphene and zygantrum are additional articular structures developed at the level of the zygapophyses, thus the section planes intercept them in this specimen. The zygantrum appears as a posterior (distal/caudal) broad notch with a median and thin vertical lamina ("septum" of Rieppel & Wild 1996, p. 23) that appears as a sharp point in cross-section. The zygosphene is a median, robust and long anterior (proximal/cranial) structure with a forked cross section. The zygosphene articulates to the zygantrum. The space between the two teeth of the fork accepts the median vertical lamina of the zygantrum.

The variously sectioned dorsal ribs were holocephalous and sickle-shaped, as it can be appreciated in the left ribs 4th to 6th. On the right side, the six anterior (proximal/cranial) ribs are slightly displaced posteriorly (distally/caudally) respect to their anatomical articulation.

The six isolated dorsal centra (MFSN 37591, 37592/1, 37599, 37601-602, and 46609) are amphiplatyan or platycoelous cylinders without a ventral keel and with unfused neural arches. The expanded facets for the pedicels of the neural arch are butterfly-shaped or cruciform, which is typical of the eosauropterygians (sensu Rieppel 2000). Five of them (MFSN 37591, 37592/1, 37599, and 37601-02) come from the outcrop 7.

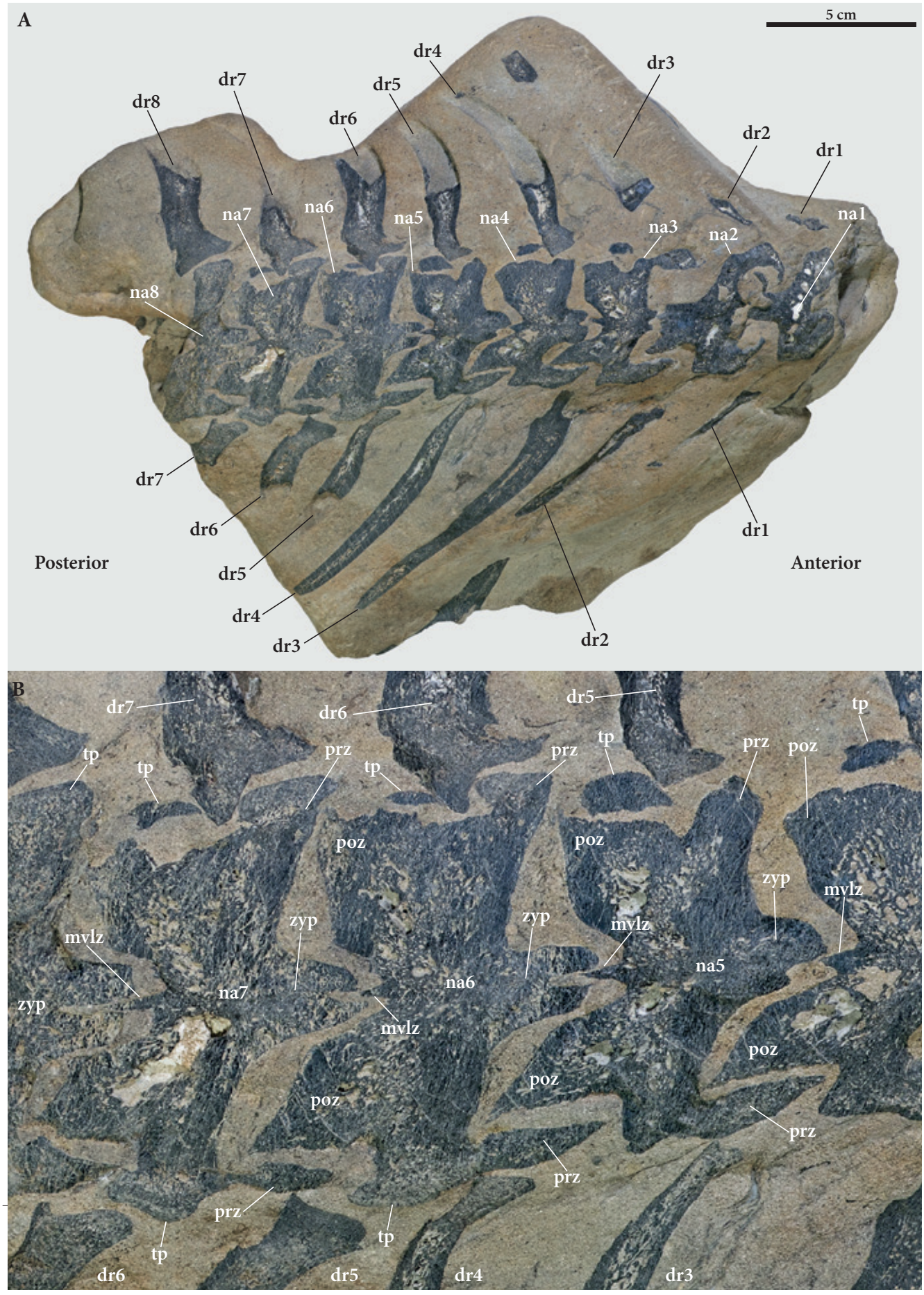
MFSN 37591 (Fig. 4A) is 36 mm long and still partly conglobated in the matrix. It dorsal side with the pedicel facets is damaged. The exposed articular facet is wider than high (39 mm wide and 34 mm high) and shallowly concave in the middle. The centrum shows no constriction. One small neurovascular foramen opens on each lateral side of the cylinder and two foramina occur ventrally.

MFSN 37592/1 (Fig. 4B) is 30 mm long, is still partly conglobated in the matrix and associated to a proximal caudal vertebra of *Tanystropheus*. Its articular facets are higher than wide (39-41 mm wide and 45-43 mm high) and shallowly concave in the middle. The facet for the pedicel of the neural arch slightly extends on the lateral side of the centrum. The exposed lateral side has two small neurovascular foramina close to each other and a further small foramen just dorsal to them.

MFSN 37601 (Fig. 4C) is 33 mm long. Its articular facets are wider than high (38.5-40 mm wide and 34.5-35 mm high) and shallowly concave in the middle, but with an evident central bulge. The facet for the pedicel of the neural arch slightly extends on the lateral side of the centrum. One lateral side has two small rounded neurovascular foramina, while the other has at least five foramina, four of them very small.

MFSN 37602 (Fig. 4D) is 41.5 mm long; its articular facets are higher than wide (45 mm wide and 47-51 mm high). One facet is nearly flat, whereas the other is shallowly concave. However, this centrum is distorted and slightly crushed because of the longitudinal (anteroposterior) compression and is constricted in the middle, thus appearing more spool-shaped than

Fig. 3 - MGC 479100, dorsal segment of the vertebral column in dorsal view. A) The whole segment; B) particular of the neural arches 5-7. Abbreviations: dr1-8 = dorsal rib 1-8; mvlz = mediovertical lamina («septum») of the zygantrum; na1-8 = neural arch 1-8; poz = postzygapophysis; prz = praezygapophysis; tp = transverse process; zyp = zygosphene.
- *MGC 479100, segmento dorsale della colonna vertebrale in vista dorsale. A) l'intero segmento; B) particolare degli archi neurali 5-7. Abbreviazioni: dr1-8 = costola dorsale 1-8; mvlz = lamina medioverticale dello zigantro; na1-8 = arco neurale 1-8; poz = postzigapofisi; prz = prezigapofisi; tp = processo trasverso; zyp = zigosfene.*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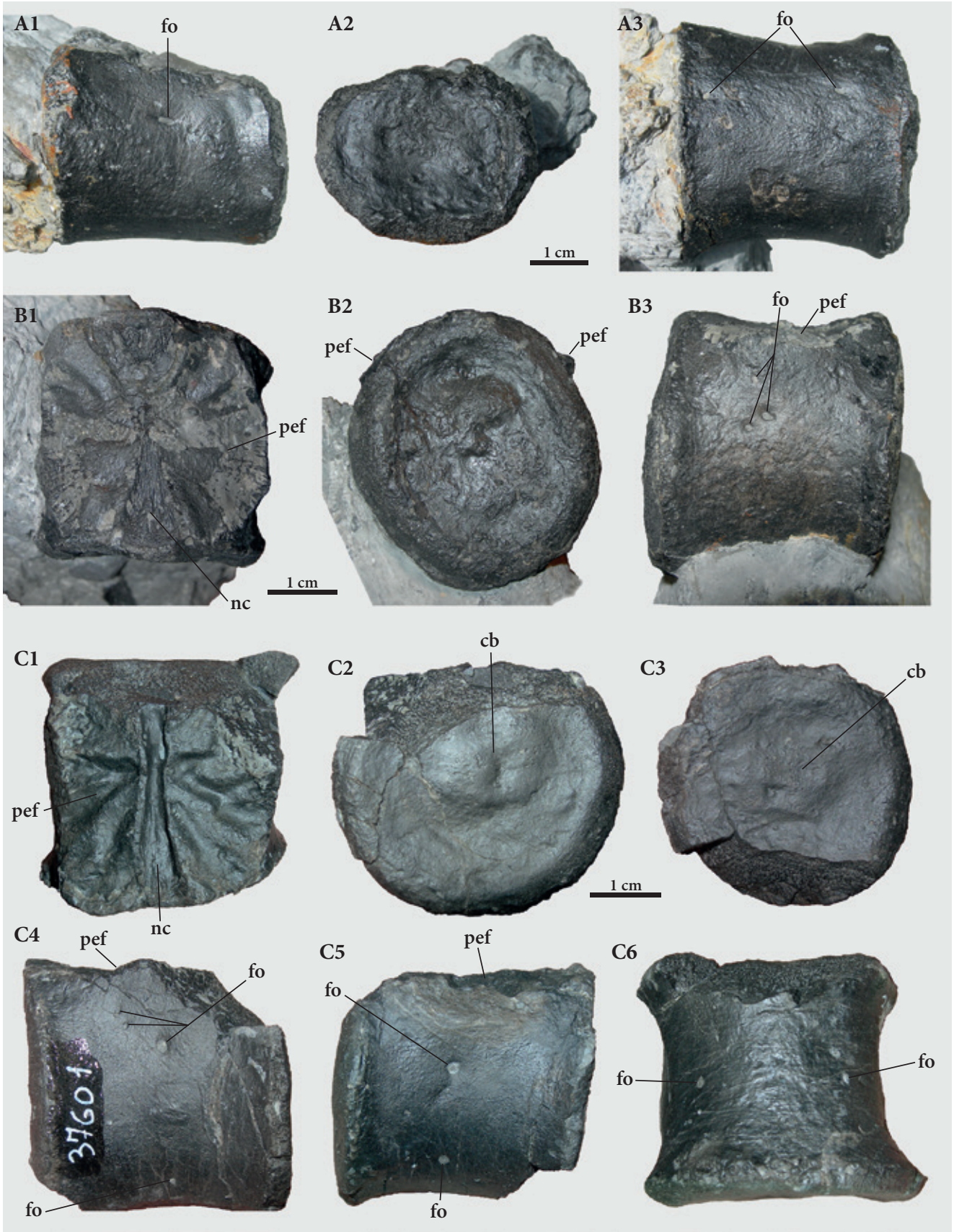

Fig. 4 - Vertebral dorsal centra. MFSN 37591 in ?right lateral (A1), ?anterior articular (A2), and ventral (A3) views; MFSN 37592/1 in dorsal (B1), articular (?posterior) (B2), and ?right lateral (B3) views; MFSN 37601 in dorsal (C1), anterior articular (C2), posterior articular (C3), ?right lateral (C4), left lateral (C5), and ventral (C6) views. Abbreviations: cb = central bulge; fo = neurovascular foramen; nc = neural canal; pef = facet for pedicel of the neural arch.

- *Centri vertebrali dorsali. MFSN 37591 in vista laterale ?destra (A1), ?anteriore (A2) e ventrale (A3); MFSN 37592/1 in vista dorsale (B1), articolare (?posteriore) (B2) e laterale ?destra (B3); MFSN 37601 in vista dorsale (C1), articolare (C2), posteriore (C3), laterale ?destra (C4), laterale sinistra (C5) e ventrale (C6). Abbreviazioni: cb = rigonfiamento centrale; fo = forame neurovascolare; nc = canale neurale; pef = faccetta per il pedicello dell'arco neurale.*

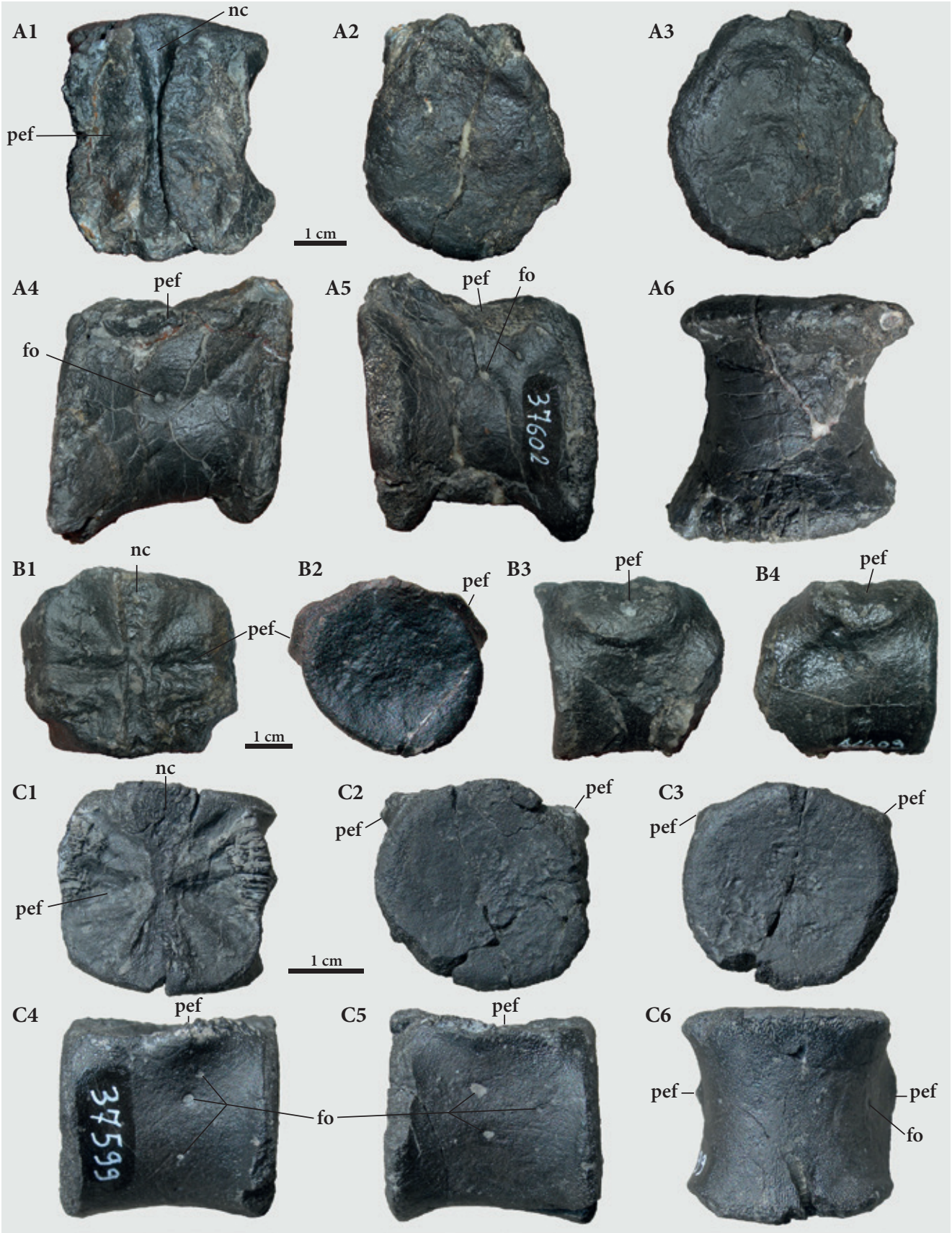

Fig. 5 - Vertebral dorsal centra. MFSN 37602 in dorsal (A1), anterior articular (A2), posterior articular (A3), right lateral (A4), left lateral (A5), and ventral (A6) views; MFSN 46609 in dorsal (B1), posterior articular (B2), right lateral (B3), left lateral (B4) views; MFSN 37599 in dorsal (C1), anterior articular (C2), posterior articular (C3), right lateral (C4), left lateral (C5), and ventral (C6) views. Abbreviations: fo = neurovascular foramen; nc = neural canal; pef = facet for pedicel of the neural arch.
- *Centri vertebrali dorsali. MFSN 37602 in vista dorsale (A1), anteriore (A2), posteriore (A3), laterale destra (A4), laterale sinistra (A5) e ventrale (A6); MFSN 46609 in vista dorsale (B1), posteriore (B2), laterale destra (B3), laterale sinistra (B4); MFSN 37599 in vista dorsale (C1), anteriore (C2), posteriore (C3), laterale destra (C4), laterale sinistra (C5) e ventrale (C6). Abbreviazioni: fo = forame neurovascolare; nc = canale neurale; pef = faccetta per il pedicello dell'arco neurale.*

cylindrical. One lateral side bears at least two-three small neurovascular foramina, while the other shows just one deeply sunk foramen.

MFSN 46609 (Fig. 4E) is from the outcrop 9. It is 36 mm long; its only completely preserved articular facet is shallowly concave and slightly wider than high (39 mm wide and 36.5 mm high). The facet for the pedicel of the neural arch extends on the lateral side of the centrum.

MFSN 37599 (Fig. 4F) is smaller than the others, being 26 mm long. Its articular facets are slightly wider than high (27.5-28 mm wide and 25-26.2 mm high) and shallowly concave. One lateral side has two small and rounded neurovascular foramina and a third very small foramen, while the other side has one small foramen and two further very small foramina. The surface is rough and pitted suggesting osteological immaturity; therefore, this centrum probably belongs to an immature individual.

The five isolated dorsal neural arches (MFSN 31578, 37603-604, and 37610-611) are dorsoventrally flattened and with broad and low pedicels.

MFSN 37603 (Fig. 6) is a neural arch from the outcrop 7 missing the left transverse process and most of the left praezygapophysis. The preserved portion is 59.5 mm wide, 49 mm long, and 44.5 mm high. The neural spine is damaged posteriorly and to a lesser extent anteriorly but complete for the remaining part, showing that it extends along the whole dorsal side of the arch and is low and probably rectangular in lateral view (ca. 32 mm long and 16 mm high). The neural spine is bent to the left probably due to taphonomic compression. The neural spine becomes thinner and lamina-like anteriorly where it connects to the zygosphene. The latter is broken and only the proximal portion is preserved. The deep zygantrum is crossed and divided into two parts by a broad mediovertical lamina, which is broken showing that its inner part is formed by thin and irregular laminae and vacuities. The basal floor of the zygantrum sends posteriorly a process whose most projecting part seems to correspond to the mediovertical lamina. Ventral to this process, two thin laminae (one per side) connetct the process with the pedicels, forming with the postzygapophyses a X-like structure. The ventral side of the process is slightly concave, bears a thin, median and longitudinal ridge, and forms the roof of the neural canal. The large and laterally projecting postzygapophyses have articular surfaces that slope at ca. 20° respect to the horizontal plane.

The transverse process is moderately projecting laterally and is higher than anteroposteriorly long; its ventral side is above the base of the pedicel, i.e. the transverse process did not extend on the centrum and does not take part in the formation of the neurocentral suture. This suggests that the neural arch is from a middle dorsal vertebra (see Dalla Vecchia 2006a; 2017). The articular facet for the rib is covered by the matrix.

The pedicels are complete and show the expanded articular facets that articulated on the corresponding butterfly-shaped or cruciform facets on the centrum.

The surface of the arch is finely pitted suggesting somewhat osteological immaturity despite to neural arch size.

MFSN 46611 (Fig. 7A) is a neural arch from the outcrop 5, still partly conglobated in the rock, missing most of the left postzygapophysis and with the neural spine broken at the base. As preserved, it is 71 mm wide, 43.5 mm long, and 41 mm high. The base of the neural spine extends along the whole dorsal side of the arch and connects anteriorly with the zygosphene without becoming thinner and lamina-like unlike MFSN 37603. The zygosphene is a robust process tapering distally but broken and missing the distal end. The zygantrum is filled by rock; its basal floor sends posteriorly a process extending beyond the level of the postzygapophyses. Ventral to this process two robust laminae (one per side) connetct the process with the base of the pedicels bordering the neural canal and forming with the postzygapophyses a X-like structure delimiting medially a large fossa below the postzygapophyses. The large and lateroposteriorly projecting postzygapophyses have articular surfaces that slope at ca. 12.5° respect to the horizontal plane. The praezygapophyses are slightly smaller than the postzygapophyses. The transverse processes are moderately projecting laterally and higher than anteroposteriorly long (the articular facet for the rib is 20 mm high and 10.5 mm long). The ventral side of the transverse processes is well above the base of the pedicel, i.e. the transverse process did not extend on the centrum and does not take part in the formation of the neurocentral suture. This suggests it is from a middle dorsal vertebra (see Dalla Vecchia 2006a; 2017). The posterior part of the ventral side of the transverse processes has a longitudinally elongated and slightly diagonal fossa. The pedicels are complete and show the articular facets, which are longer than wide and facing ventromedially, so that the neural canal is very narrow (ca. 4 mm).

MFSN 37604 (Fig. 7B) is an incomplete neural arch from the outcrop 6 that is still partly conglobated in the matrix, and lacks the right transverse process and praezygapophysis. The neural spine is broken at the base; the pedicels and part of the left transverse process had been worn away before burial. The preserved portion is 70 mm wide, 50 mm long, and 35mm high. The neural spine extends along the whole dorsal side of the arch. The zygosphene is broken. The deep zygantrum is still filled with rock. The basal floor of the zygantrum and the neural canal roof with a thin, median and longitudinal ridge can be seen in ventral view. The left one of the two thin laminae (one per side) connetcting the posterior process of the zygantrum with the pedicels, is exposed. The zygapophyses are large, the

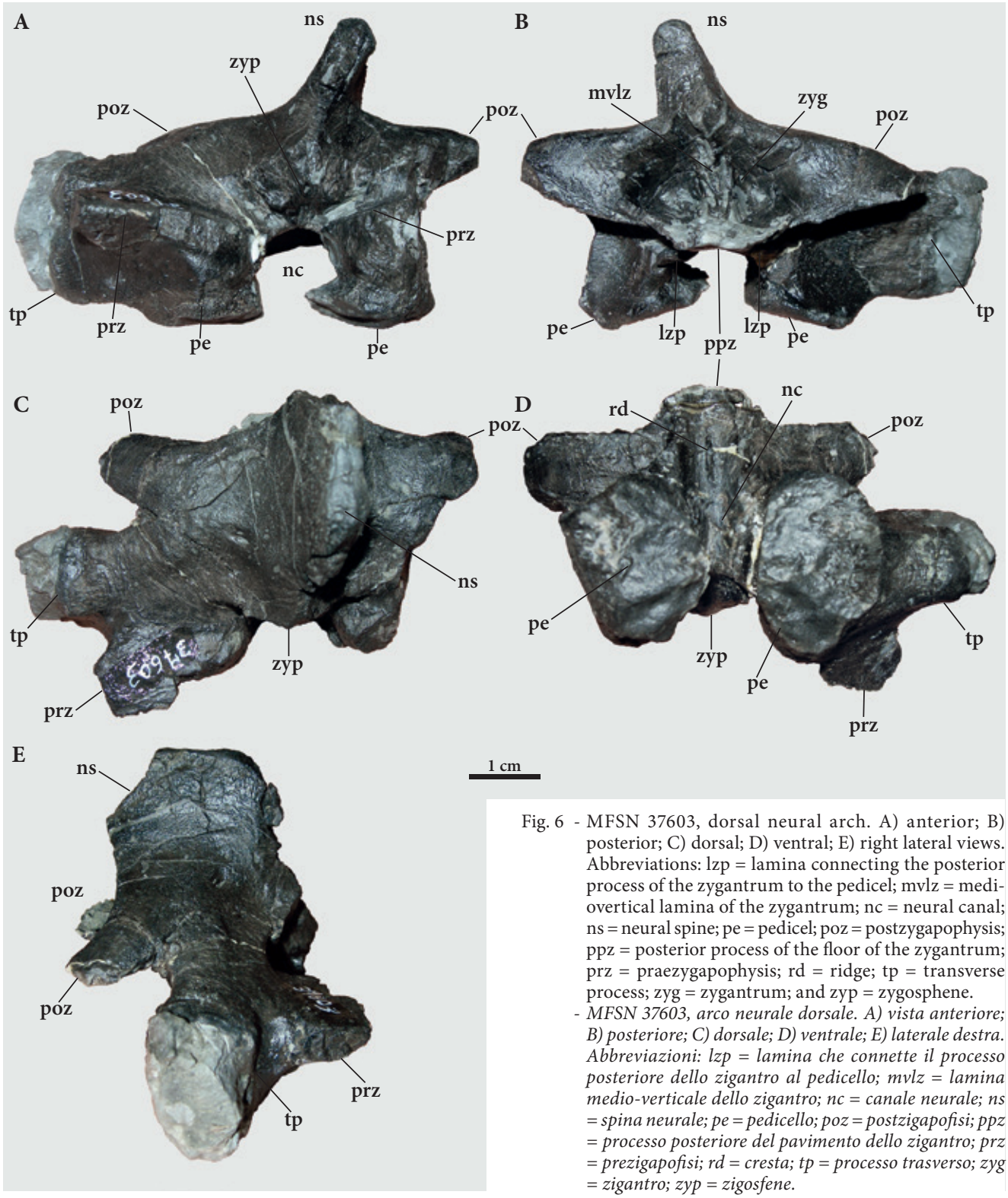

Fig. 6 - MFSN 37603, dorsal neural arch. A) anterior; B) posterior; C) dorsal; D) ventral; E) right lateral views. Abbreviations: lzp = lamina connecting the posterior process of the zygantrum to the pedicel; mvlz = medio-overtical lamina of the zygantrum; nc = neural canal; ns = neural spine; pe = pedicel; poz = postzygapophysis; ppz = posterior process of the floor of the zygantrum; prz = praezygapophysis; rd = ridge; tp = transverse process; zyg = zygantrum; and zyp = zygosphene.
- *MFSN 37603, arco neurale dorsale. A) vista anteriore; B) posteriore; C) dorsale; D) ventrale; E) laterale destra. Abbreviazioni: lzp = lamina che connette il processo posteriore dello zigantro al pedicello; mvlz = lamina medio-verticale dello zigantro; nc = canale neurale; ns = spina neurale; pe = pedicello; poz = postzigapofisi; ppz = processo posteriore del pavimento dello zigantro; prz = prezigapofisi; rd = cresta; tp = processo trasverso; zyg = zigantro; zyp = zigosfene.*

praezygapophysis more than the postzygapophysis. The praezygapophysis has a D-like outline in dorsal view and is directed anterolaterally. The articular surfaces of the praezygapophyses slope at ca. 22° and 11°. The transverse process is moderately projecting laterally in dorsal view.

MFSN 46610 (Fig. 7C) is a neural arch from the outcrop 9 that is still partly conglobated in the rock, thus it can be observed only in dorsal and left lateral views. In dorsal view it has a rectangular outline, 48 mm wide and 42 mm long. In lateral view it is low (the preserved part is 32 mm high) and massive. Its praezygapophyses are damaged as the left postzygapophysis (the right is still partly covered by the rock) and the neural spine is broken at the base. The left transverse processes appear to have been worn away before burial, whereas the

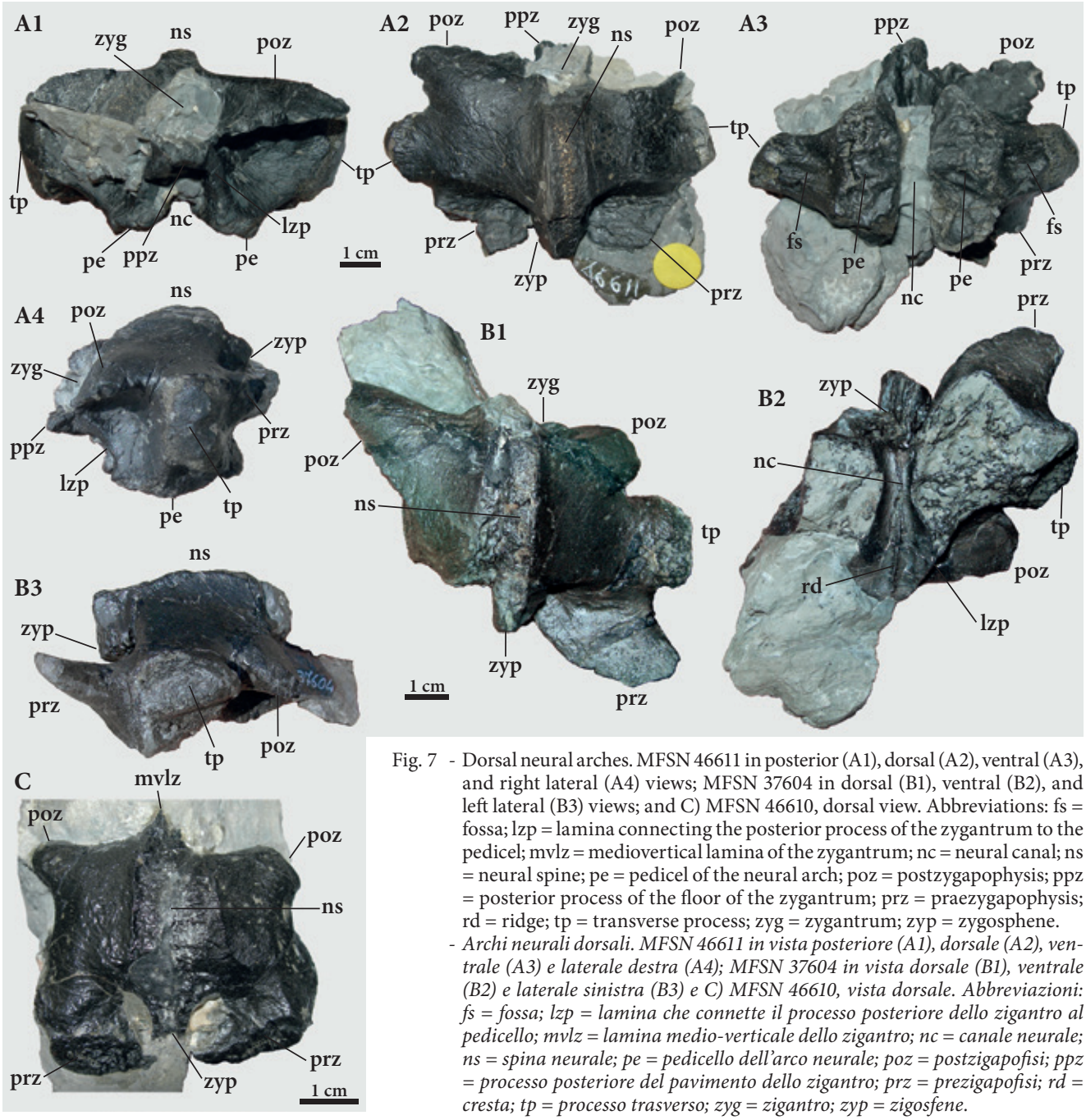

Fig. 7 - Dorsal neural arches. MFSN 46611 in posterior (A1), dorsal (A2), ventral (A3), and right lateral (A4) views; MFSN 37604 in dorsal (B1), ventral (B2), and left lateral (B3) views; and C) MFSN 46610, dorsal view. Abbreviations: fs = fossa; lzp = lamina connecting the posterior process of the zygantrum to the pedicel; mvlz = mediovertical lamina of the zygantrum; nc = neural canal; ns = neural spine; pe = pedicel of the neural arch; poz = postzygapophysis; ppz = posterior process of the floor of the zygantrum; prz = praezygapophysis; rd = ridge; tp = transverse process; zyg = zygantrum; zyp = zygosphene.

- *Archi neurali dorsali. MFSN 46611 in vista posteriore (A1), dorsale (A2), ventrale (A3) e laterale destra (A4); MFSN 37604 in vista dorsale (B1), ventrale (B2) e laterale sinistra (B3) e C) MFSN 46610, vista dorsale. Abbreviazioni: fs = fossa; lzp = lamina che connette il processo posteriore dello zigantro al pedicello; mvlz = lamina medio-verticale dello zigantro; nc = canale neurale; ns = spina neurale; pe = pedicello dell'arco neurale; poz = postzigapofisi; ppz = processo posteriore del pavimento dello zigantro; prz = prezigapofisi; rd = cresta; tp = processo trasverso; zyg = zigantro; zyp = zigosfene.*

right one is nearly entirely concealed by the rock. The zygapophyses are nearly at the same level. The praezygapophyses are large in dorsal view and slope at about 16-18° respect to the horizontal plane in anterior view. The mediovertical lamina of the zygantrum appears as short point in dorsal view, while the zygosphene is a robust, rectangular and bifid anterior process between the praezygapophyses.

These neural arches resemble that from the lower Muschelkalk of Oberdorla (Thuringia, Germany) figured in Peyer (1939, fig. 22).

MFSN 31578 (Fig. 8) is a neural arch from the outcrop 6 that was described and figured in Dalla Vecchia (2006b) and figured in Dalla Vecchia (2008a). It differs from the other neural arches described above. It is a massive element 49.5 mm high from the base of the preserved part of the pedicels (they lack the articular portion) to the apex of the neural spine, 56 mm wide and at 51 mm long considering also the long posterior process of the floor of the zygantrum. The rectangular neural spine is low (ca. 20 mm). The postzygapophyses are robust but not much enlarged. In the place of the prezygapophyses, there are two thin ridges that border dorsally the shallowly concave anterior surface of the pedicels; the praezygapophyseal articular facets, if present, are extremely riduced. The right transverse process is damaged; only a small dorsoposterior portion seems to be present of the left one. Anyway, the transverse

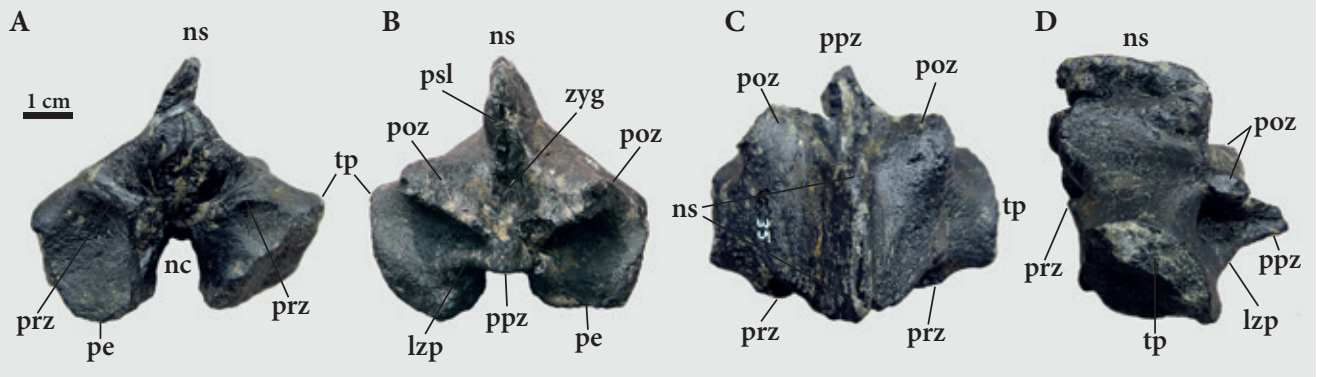

Fig. 8 - MFSN 31578, ?dorsal neural arch. A) Anterior; B) posterior; C) dorsal; and D) left lateral views. Abbreviations: lzp = lamina connecting the posterior process of the zygantrum to the pedicel; nc = neural canal; ns = neural spine; pe = pedicel; poz = postzygapophysis; ppz = posterior process of the floor of the zygantrum; prz = 'praezygapophysis'; psl = prespinal lamina; tp = transverse process; zyg = zygantrum.
- *MFSN 31578, arco neurale ?dorsale. A) Vista anteriore, B) posteriore, C) dorsale e D) laterale sinistra. Abbreviazioni: lzp = lamina che connette il processo posteriore dello zigantro al pedicello; nc = canale neurale; ns = spina neurale; pe = pedicello; poz = postzigapofisi; ppz = processo posteriore del pavimento dello zigantro; prz = 'prezigapofisi'; psl = lamina prespinale; tp = processo trasverso; zyg = zigantro.*

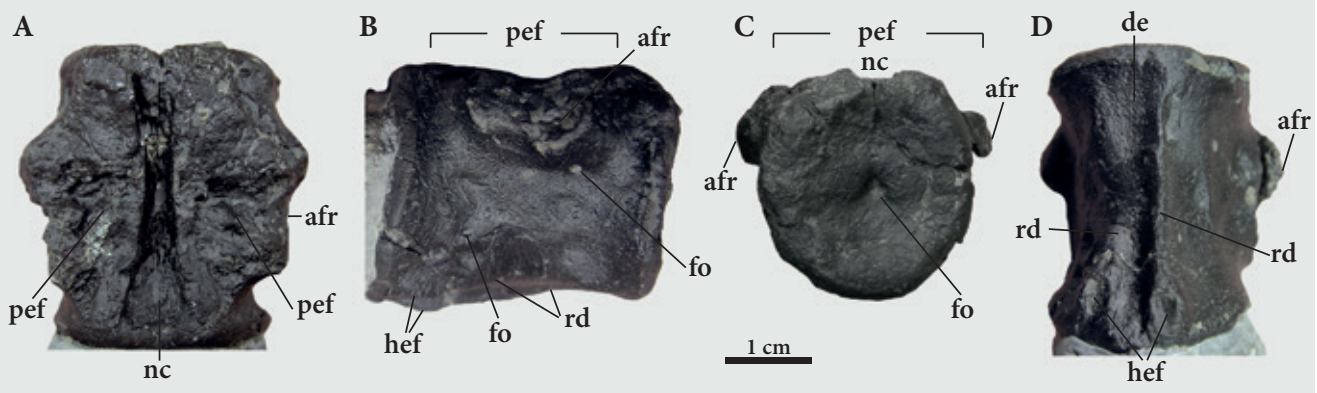

Fig. 9 - MFSN 31564, caudal vertebral centrum. A) Dorsal; B) right lateral; C) anterior; and D) ventral views. Abbreviations: afr = articular facet for the rib; de = median depression; fo = neurovascular foramen; hef = haemapophyseal facet; nc = neural canal; pef = facet for pedicel of the neural arch; rd = ridge.
- *MFSN 31564, centro vertebrale caudale. A) Vista dorsale, B) laterale destra, C) anteriore e D) ventrale. Abbreviazioni: afr = faccetta articolare per la costola; de =depressione mediana; fo = forame neurovascolare; hf = faccetta articolare per l'emapofisi; nc = canale neurale; pef = faccetta per il pedicello dell'arco neurale; rd = cresta.*

process was clearly massive and scarcely projecting laterally, forming a single block with the pedicel. The part of the arch between the 'praezygapophyses' is damaged and nothing remains of the zygosphene. The zygantrum is relatively narrow and crossed vertically in its dorsal part by a thick postspinal lamina (corresponding to the mediovertical lamina of the zygantrum mentioned in the other arches). From the floor of the zygantrum projects posteriorly a long and tapering process connected by laminae to the postzygapophyses and to the pedicel; the laminae form an X-like figure bordering a fossa below each postzygapophysis like in MFSN 37603 and MFSN 46611.

The extremely reduced 'praezygapophyses' suggest it is a misshapen neural arch; the shape of the transverse processes may indicate that it is from a transitional element to the sacral or pectoral segment of the vertebral column (Dalla Vecchia 2017).

Caudal vertebra

MFSN 31564 (Fig. 9) is a proximal caudal centrum from the outcrop 6 that had been described and figured in Dalla Vecchia (2006b). It is 32 mm long, 25 mm wide, 26 mm high anteriorly and 29 mm high posteriorly. The posterior articular surface is still covered by rock. The expanded facets for the pedicels form with the narrow neural canal a butterfly-like figure. The facets extend on the lateral sides of the centrum and bear the lower part of the articular facet for the rib, which apparently was developed mainly on the neural arch. Small neurovascular foramina open on the lateral sides (the left lateral side counts at least five of those foramina, the largest just below the facet for the pedicels). The surface is finely pitted and grooved, suggesting osteological immaturity. The anterior articular surface is slightly higher than wide and concave; it presents a foramen exactly at the centre, thus the centrum may be

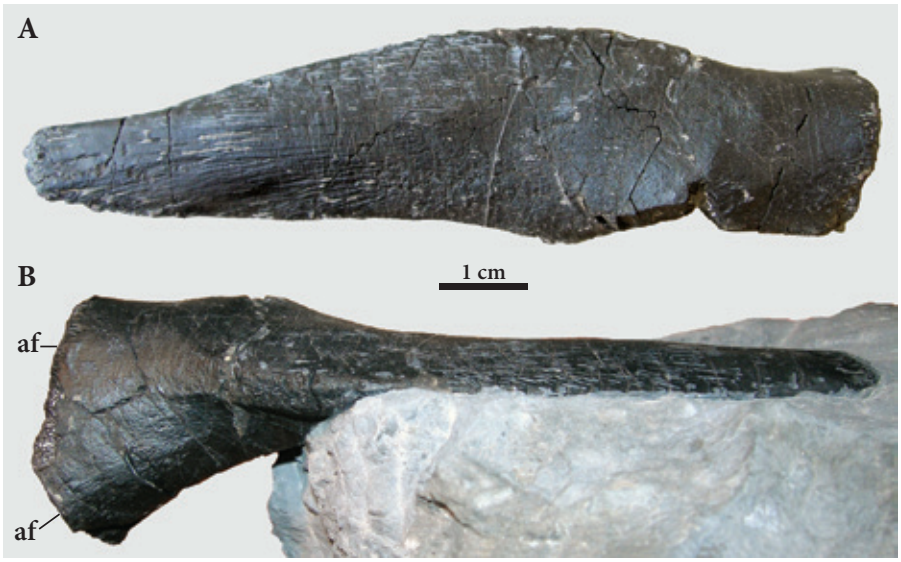

Fig. 10 - MFSN 37596, left proximal caudal rib. A) Dorsal view; B) anterior view. Abbreviations: af = articular facet.
- *MFSN 37596, costola caudale prossimale sinistra. A) Vista dorsale; B) vista anteriore. Abbreviazioni: af = facetta articolare.*

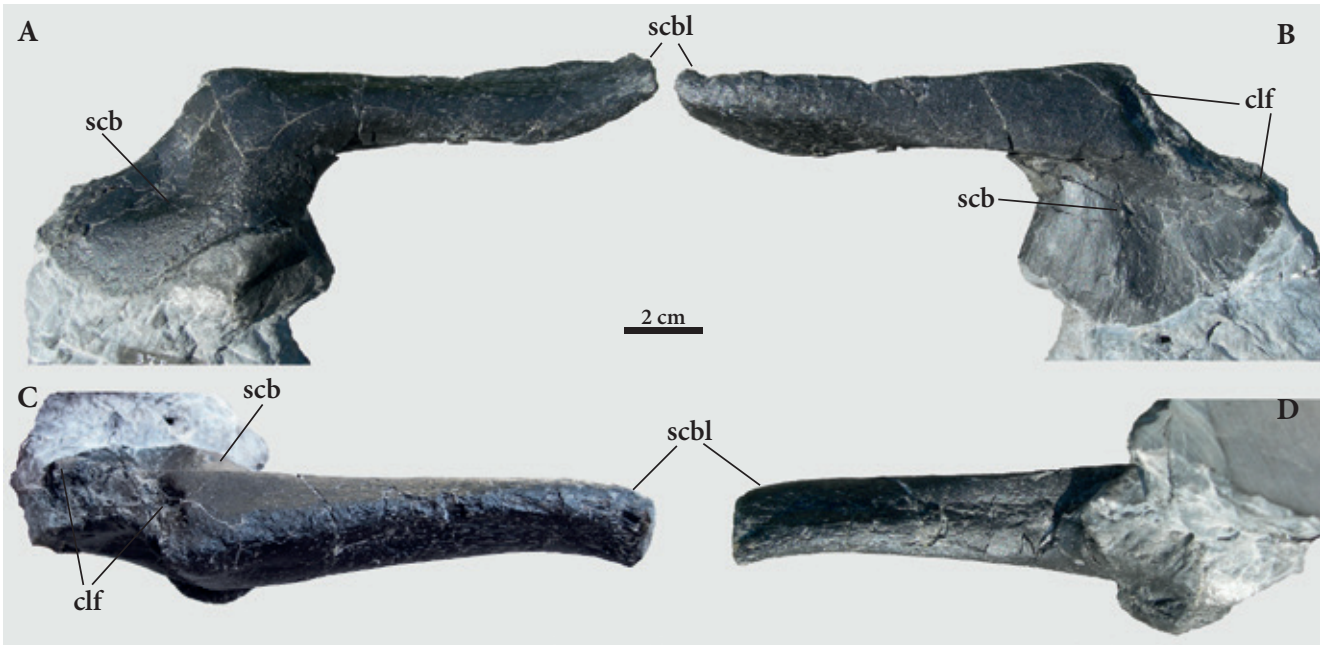

Fig. 11 - MFSN 37595, left scapula. A) Lateral; B) medial; C) dorsal; and D) ventral view. Abbreviations: clf = clavicular facet; scb = scapular body; scbl = scapular 'blade'.
- *MFSN 37595, scapola sinistra. A) Vista laterale; B) mediale; C) dorsale; D) ventrale. Abbreviations: clf = facetta per l'articolazione clavicolare; scb = corpo scapolare; scbl = 'lama' scapolare.*

notochordal. The ventral side presents two longitudinal and parallel ridges. The left ridge is thin and extends along most of the ventral margin of the centrum; the right ridge is blunter, wider and nearly disappears at mid-centrum. They border a narrow and longitudinal median depression and each ridge ends posteriorly with a small, concave and ventroposteriorly directed facet for the articulation of the haemapophysis. The latter facets are the main features suggesting that this centrum is from a caudal vertebra.

Caudal ribs

MFSN 37596 (Fig. 10) is a proximal, probably left, caudal rib from the outcrop 6 still partly conglobated in the rock. It is 97 mm long. The shaft is flattened dorsoventrally and spear point shaped (expanded in the middle and tapering distally), but slightly asymmetrical in dorsal view (Fig. 10A) and with a blunt end. The dorsal surface of the shaft shows fine longitudinal striae. The articular head is much expanded dorsoventrally in an asymmetrical way (it is 29 mm high and is plausibly more expanded ventrally) and bears two articular facets for the corresponding articular facets on the vertebra. The dorsal facet is larger than the ventral and the facets are separated by a ridge. In dorsal view, the specimen resembles the caudal ribs of *Paranothosaurus amsleri* (see Peyer 1939, pl. 66), mainly those in median position (caudal vertebrae 5-7). The asymmetry of the

caudal ribs of the holotype of *Paranothosaurus amsleri* suggests that MFSN 37596 is a left element.

Appendicular skeleton

Pectoral and pelvic girdles

Scapula. MFSN 37595 (Fig. 11) is a scapula from the outcrop 6. It is 162 mm long craniocaudally, about 60 mm high and has a maximum lateromedial width of 45 mm. As "the clavicular facet expands onto the medial surface" in the scapula of *Simosaurus* (Rieppel 1994, p. 23) and "clavicles applied to medial surface of scapula" in all sauropterygians (Rieppel 1994, p. 5), the position of the facet in this scapula (Fig. 11C) indicates that it is a left one. The scapular body (the "glenoidal portion" of Rieppel 2000, p. 13) is massive, ventrally expanded and fan-shaped in lateral and medial views. The scapular body is 74 mm long craniocaudally and is lateromedially crushed, so that it locally collapsed. The articular facet for the coracoid and the scapular contribution to the glenoid are concealed by the rock or damaged; the specimen should be further prepared to allow for their identification. The elongated and anteriorly placed clavicular facet (cf. Rieppel 1994, figs. 25A, 26A, and 54C-D) is narrow and probably distorted by the lateromedial crushing. There is no clear evidence of the presence of a notch corresponding to the coracoid foramen along the ventromedial margin of the scapular body. The scapular 'blade' ("dorsal wing" of Rieppel 1994, p. 23) is rod-like, very long (120 mm), robust and posteriorly directed. The distal half of the 'blade' is compressed dorsolaterally-ventromedially and its extremity is curved dorsolaterally and has a 'cut' (i.e., not pointed nor tapering) distal end (Fig. 11C-D). The flat distal surface of the 'blade', which is still covered by rock in MFSN 37595, has been interpreted as an articular facet in the similar left scapula of a large eusauropterygian from the Lower Muschelkalk of Winterswijk (The Netherlands) described by Voeten et al. (2014).

The scapula MFSN 37595 is quite unlike that from the lower Carnian site of Lavaz Brook (Dogna municipality, Friuli Venezia Giulia Autonomous Region) figured in Dalla Vecchia (2008b, fig. 7C) and tentatively referred to *Simosaurus*, which has a more gracile and probably shorter 'blade'. It is also unlike that of *Nothosaurus* cf. *mirabilis* Münster 1834 figured in Peyer (1939, fig. 20; see also Rieppel 2000, fig. 7), which has a shorter and distally tapering 'blade', as well as those of *Nothosaurus* cf. *giganteus* from the upper Muschelkalk of Israel figured in Rieppel (2000, fig. 8) and *Nothosaurus giganteus* from the lower Keuper (Ladinian) of Hoheneck, southern Germany (Rieppel et al. 1999, fig. 18), which have both a comparatively shorter, lanceolate and more dorsally directed 'blade'. It differs also from the scapula of *Nothosaurus* figured in Rieppel (1994, fig. 54C-D), which has a comparatively shorter, distally expanded and striated 'blade' and a large coracoid foramen notch.

The resemblance is closer with the *Nothosaurus* scapula figured in Rieppel (1994, fig. 54A-B), which has a robust, straight and distally 'cut' blade, and with the scapula of *Simosaurus gaillardoti* Meyer 1842 (see Rieppel 1994, fig. 26A), which, however, has a comparatively shorter 'blade' and a marked coracoid foramen notch. As anticipated above, MFSN 37595 is rather similar, at least in dorsal view, to the scapula of a large indeterminated eusauropterygian from the lower Muschelkalk of Winterswijk (The Netherlands), which also lacks a ventromedial notch (Voeten et al. 2014, fig. 2A). There is some resemblance also with the scapula of *'Paranothosaurus giganteus'* from the upper Muschelkalk (Illyrian) of Bad Sulza (Thuringia, Germany) figured in Dietrich (2013, fig. 9/3), because of the shape and length of the scapular 'blade'. Dietrich (2013, p. 142) considered the "elongated processus" as typical of the scapula of *'Paranothosaurus giganteus'*. Even more striking appears to be the resemblance with the scapula of *'Paranothosaurus giganteus'* from the upper Muschelkalk of the Bayereuth region (Bavaria, Germany) figured in Dietrich (2012, fig. 10/3). Unfortunately, these bones have not been described in detail.

Coracoid. The sample includes three coracoids: MFSN 37605 from the outcrop 6, MFSN 44323 from site 5, and MFSN 46608 from the outcrop 9.

MFSN 37605 is nearly complete and 217 mm long (Fig. 12A). It s preserved in a dark grey gravelly siltstone. MFSN 44323 is nearly complete and 250 mm long (Fig. 12B); it is also preserved in a dark grey gravelly siltstone with plant remains. MFSN 46608 preserves the proximal portion as bone and the shaft and part of the distal portion as impression of the bone (Fig. 12C). The preserved part is 220 mm long. It is preserved in grey sandstone with plant remains.

These coracoids are elongated and ventrodorsally flattened. Their medial margin is concave, whereas the lateral margin is concave in the proximal half and convex in the distal half. MFSN 44323 exposes both dorsal and ventral views; the main difference is that the surface of the distal expansion is shallowly concave in one (the dorsal), whereas it is slightly convex in the other.

The expanded proximal portion is flattened dorsoventrally (dorsomedially-ventrolaterally) and bears two processes for the long articulation to the scapula (cf. Fig. 13C); these processes are separated by an open and U-like coracoid foramen, which is narrower in MFSN 44323 than in MFSN 46608 (Fig. 12B-C). The lateral process, which participates to the glenoid, is much more robust and thicker than the anterior process; it has a rectangular outline in dorsal (dorsomedial) and ventral (ventrolateral) view. The proximal end of this process bears two distinct articular facets (Fig. 14); one is for the scapula, whereas the other participates to the

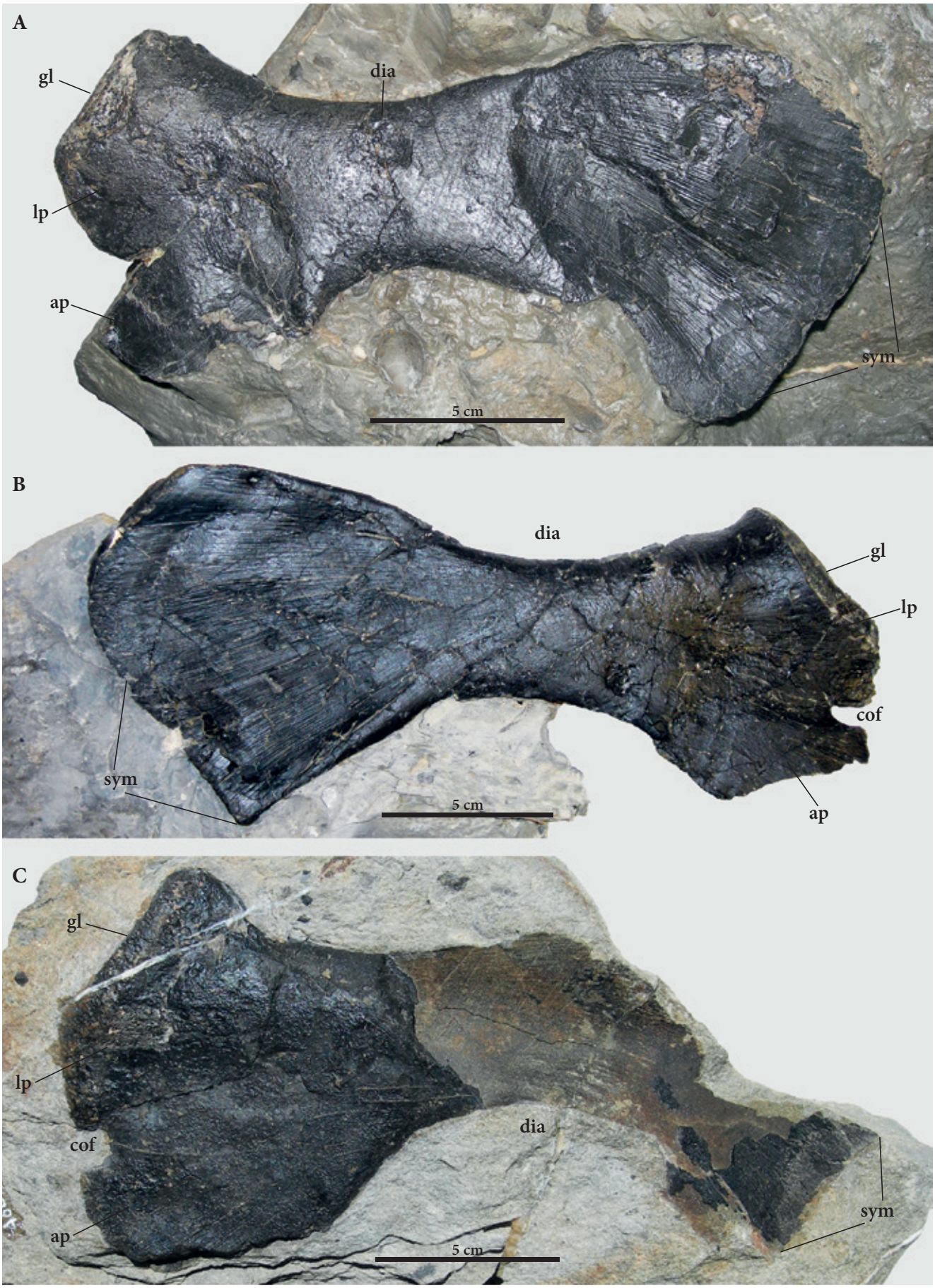

Fig. 12 - Coracoids. A) MFSN 37605; B) MFSN 44323 (right element in ventral view); and C) MFSN 46608. Abbreviations: ap = anterior process; cof = coracoid foramen; dia = diaphysis; gl = glenoid; lp = lateral process; sym = symphyseal margin.
- *Coracoidi. A) MFSN 37605, B) MFSN 44323 (elemento destro in vista ventrale) e C) MFSN 46608. Abbreviazioni: cof = forame coracoideo; dia = diafisi; gl = glenoide; sym = margine sinfisiale.*

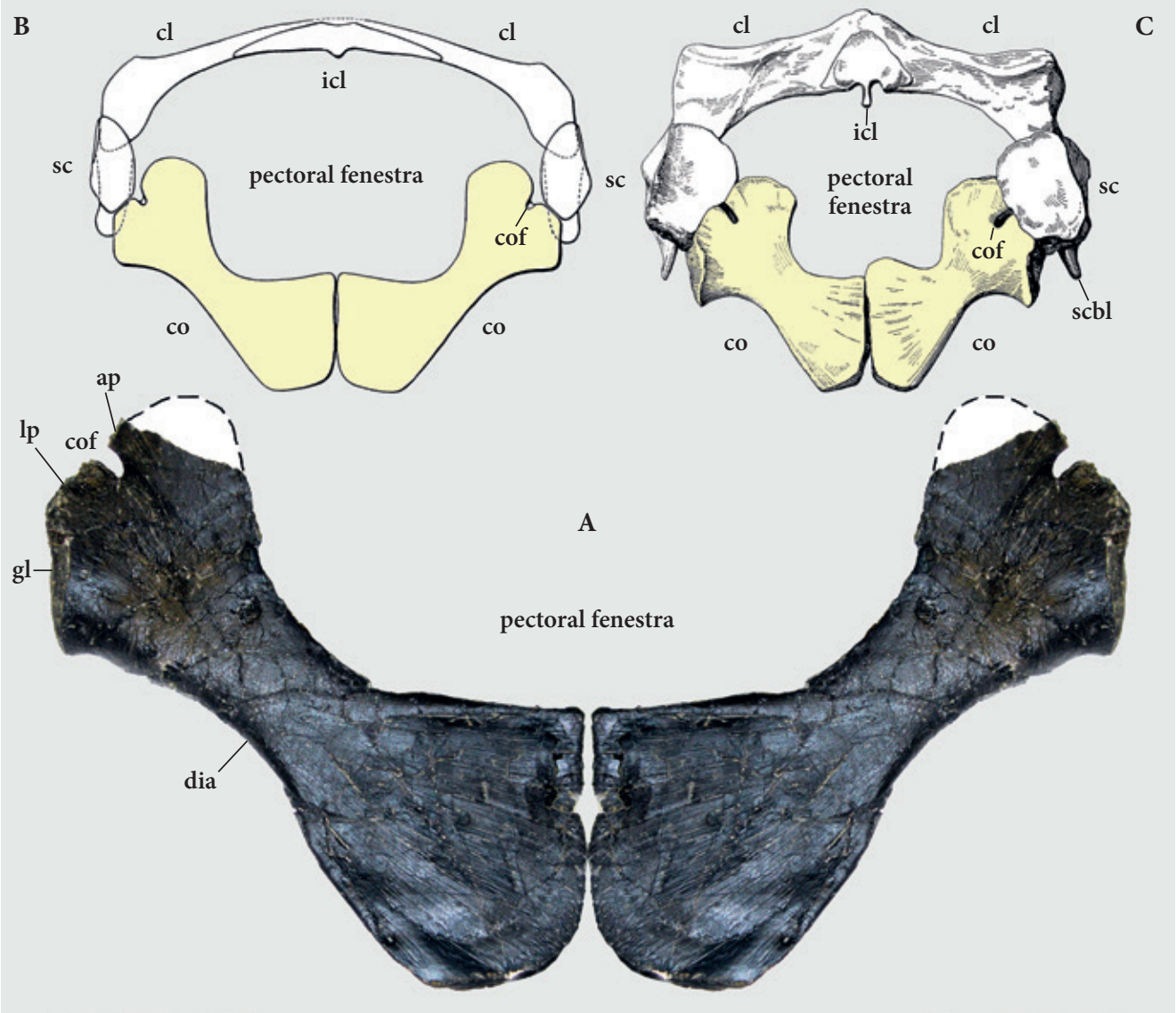

Fig. 13 - Pectoral girdles reconstructions in ventral (ventrolateral) view. A) MFSN 44323 and its mirror image to reconstruct the articulation between the two coracoids in ventral (ventrolateral) view; B) reconstruction of the pectoral girdle of '*Paranothosaurus amsleri*' (after Peyer 1939, fig. 4); and C) the pectoral girdle of *Nothosaurus* cf. *mirabilis* (after Peyer 1939, fig. 20). Abbreviations: ap = anterior process; cl = clavicle; co = coracoid; cof = coracoid foramen; dia = diaphysis; gl = glenoid; icl = interclavicle; lp = lateral process; sc = scapula; scbl = scapular 'blade'.

- *Ricostruzione dei cinti scapolari in vista ventrale (ventrolaterale). A) MFSN 44323 e la sua immagine speculare per ricostruire l'articolazione tra i due coracoidi in vista ventrale (ventrolaterale); B) ricostruzione del cinto scapolare di* 'Paranothosaurus amsleri' *(da Peyer 1939, fig. 4) e C) cinto scapolare di* Nothosaurus *cf.* mirabilis *(da Peyer 1939, fig. 20). Abbreviazioni: ap = processo anteriore; cl = clavicola; co = coracoide; cof = forame coracoideo; dia = diafisi; gl = glenoide; icl = interclavicola; lp = processo laterale; sc = scapola; scbl = 'lama' scapolare.*

glenoid (the latter is the largest facet in MFSN 44323). The position and orientation of the two facets suggest that MFSN 44323 is a right coracoid showing the entire ventral view and part of the dorsal one.

The anterior process is thin and blade like. For this reason it is damaged in all specimens and its exact outline cannot be established, although it was probably rounded as that of *'Paranothosaurus' amsleri* (see Peyer 1939, fig. 4; Fig. 13A-B). In MFSN 37605, its medial margin had clearly been damaged before the final burial; Fig. 12B).

The distal (posterior) portion of the coracoid is much expanded, fan-like and massive. The posteromedial symphyseal margin with the other coracoid (Fig. 13) forms the medial half of the distal surface of the fan; this margin is long and straight, making a 90° angle with the anterior margin of the fan. The posteromedial half of the distal margin of the fan is rounded. In distal view, the medial half of the distal portion of the fan (the symphyseal one) is very thick (with a broad symphyseal surface) and tapers posteriorly (MFSN 46608; Fig. 15). The shape of the distal end (Fig. 13) suggests that the coracoids were posteriorly united by cartilage. The distal expanded portion of the coracoid is slightly concave ventrally (ventrolaterally) and convex dorsal-

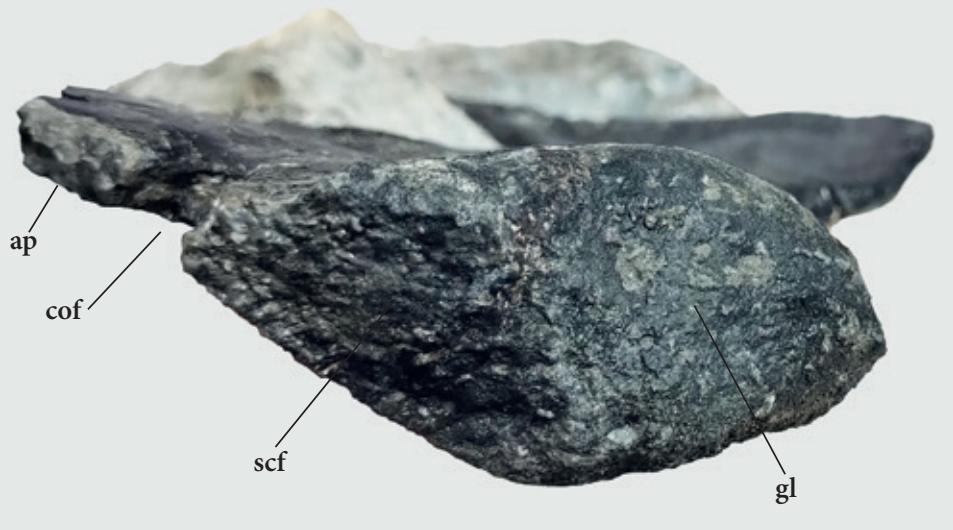

Fig. 14 - MFSN 44323, right coracoid, proximal lateral process in proximal view. Abbreviations: ap = anterior process; cof = coracoid foramen; gl = glenoid; scf = scapular facet.
- *MFSN 44323, coracoide destro, processo prossimale laterale in vista prossimale. Abbreviazioni: ap = processo anteriore; cof = forame coracoideo; gl = glenoide; scf = faccetta scapolare.*

Fig. 15 - MFSN 37605, coracoid in distal and perspective view showing the thick distal and symphyseal portion.
- *MFSN 37605, coracoide in vista distale e prospettica che mostra la spessa porzione distale e sinfisiale.*

ly (dorsomedially). Between the proximal and distal expanded portions, there is the short, lateromedially waisted and dorsoventrally flattened shaft.

In MFSN 44323, both ventral and dorsal surfaces of the coracoid are ornamented by thin and closely spaced longitudinal striae, which are less marked in the shaft and more evident in the distal fan-like portion. This is unlike the condition in the coracoids of a specimen referred to *Nothosaurus* sp. (TWE 480000475) from the upper Anisian of Winterswijk (The Netherlands) that have a smooth ventral surface and a striated dorsal surface (Klein et al. 2015).

Because of their size, overall shape and slenderness, the coracoids from the Aupa Valley are very similar to those of '*Paranothosaurus amsleri*' as reconstructed by Peyer (1939, fig. 4; Fig. 13B). Also, the large coracoids from the uppermost Anisian/lower Ladinian of Germany figured by Dietrich (2012, fig. 10/1; 2013, fig. 9/4) and referred by this author to '*Paranothosaurus giganteus*' are slender as MFSN 44323. According to Rieppel (2000), an incomplete enclosure of the coracoid foramen between the coracoid and scapula is a potentially diagnostic feature of *N. giganteus*.

The pectoral fenestra bordered by the coracoids and the other elements of the pectoral girdle (Fig. 13) appears to be comparatively broader in the Aupa Valley taxon than in the pectoral girdle of *Nothosaurus* cf. *mirabilis* figured in Peyer (1939, fig. 20; see also Rieppel 2000, fig. 7; Fig. 13C) and in that of '*Paranothosaurus*' *amsleri* (see Peyer 1939, fig. 4; Fig. 13B), because the medial margin of the coracoid is straighter in MFSN 44323. While the posterior part of the pectoral fenestra is rectangular in the reconstruction of the pectoral girdle of '*Paranothosaurus*' *amsleri* (Fig. 13B), it was semicircular in the Aupa Valley specimen MFSN 44323 (Fig. 13A).

Ischium. MFSN 34995/1 (Fig. 16) is a nearly complete left ischium from the outcrop 6 that has already been figured in Dalla Vecchia (2008a). The ischia of the eusauropterygian reptiles are expanded and fan-like ventral plates that meet their opposites in the midline (Fig. 17A-B). MFSN 34995/1 is 155 mm long and has a maximum width of 130 mm. The bone has a slightly expanded proximal head for the articulation with ilium and pubis and the participation to the glenoid (Fig. 17C). The iliac facet is small and triangular; the pubic facet is not clearly separated from the glenoid facet, but the latter extended more ventrally and abutted on the thickened part of the diaphysis. The diaphysis is short, thick in the middle and with a sharp posterolateral margin. Its ventral (ventrolateral) side (that exposed in Fig. 16) is convex, whereas the dorsal (dorsomedial) is flat. The fan-like and dorsoventrally (ventrolaterally-dorsomedially) flattened distal portion (the "foot" of Storrs 1991, p. 30) is much expanded and slightly asymmetrical (the medial portion is more lateromedially elongated than the lateral portion; Fig. 17A). A fragment of the posterolateral part is missing; there the maximum thickness of

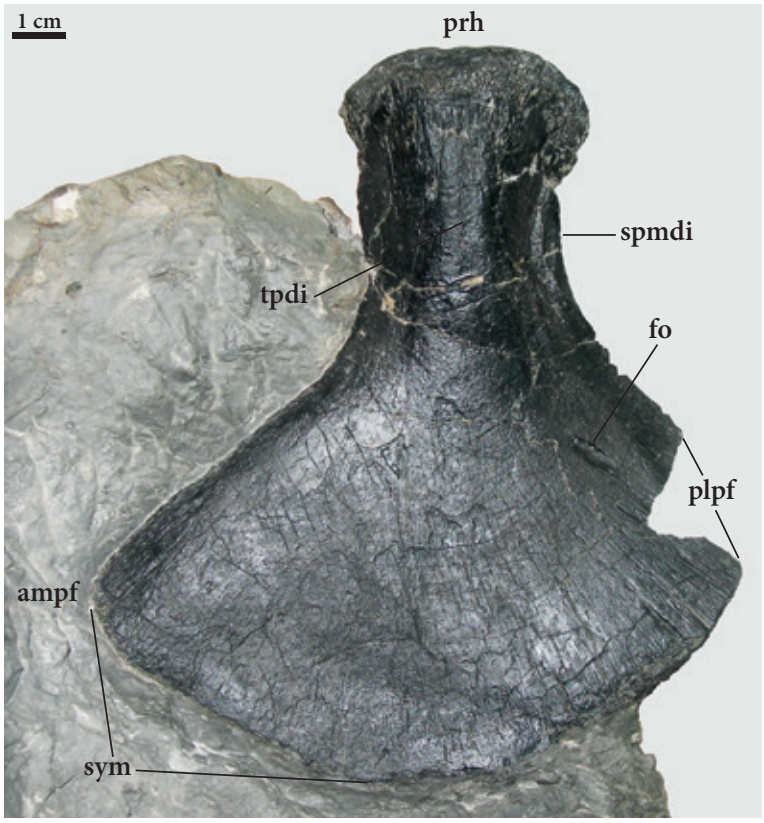

Fig. 16 - MFSN 34995, left ischium, ventral (ventrolateral) view. Abbreviations: ampf = anteromedial portion of the 'fan'; fo = neurovascular foramen; plpf = posterolateral portion of the 'fan'; prh = proximal articular head; spmdi = sharp posterolateral margin of the diaphysis; sym = symphyseal margin; tpdi = thickened part of the diaphysis.
- *MFSN 34995, ischio sinistro in vista ventrale (ventrolaterale). Abbreviazioni: ampf = porzione anteromediale del 'ventaglio'; fo = forame neurovascolare; plpf = porzione posterolaterale del 'ventaglio'; prh =testa articolare prossimale; spmdi = margine posterolaterale affilato della diafisi; sym = margine sinfisiale; tpdi = parte inspessita della diafisi.*

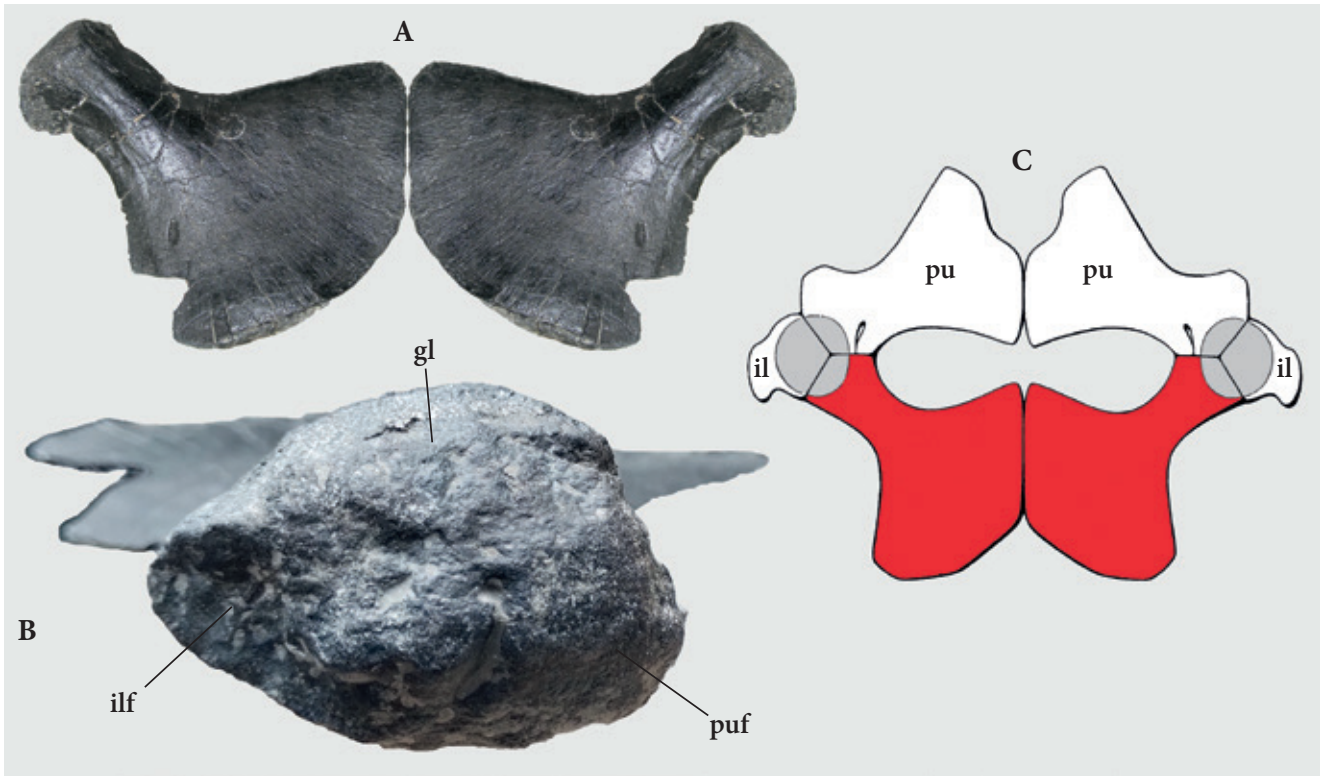

Fig. 17 - Reconstruction of the ischial articulation and of the pelvic girdle. A) MFSN 34995 and its mirror image to reconstruct the articulation between the two ischia in ventral view; B) MFSN 34995, articular head in proximal view; and C) reconstruction of the pelvic girdle of '*Paranothosaurus amsleri*' in ventral view (after Peyer 1939, fig. 6). In C, the glenoid is emphasized in grey colour and the ischia are in red. Abbreviations: gl = glenoid; il = ilium; ilf = iliac facet; pu = pubis; puf = pubic facet.
- *Ricostruzione dell'articolazione ischiatica e del cinto pelvico. A) MFSN 34995 e la sua immagine speculare per ricostruire in vista ventrale l'articolazione tra i due ischi; B) MFSN 34995, testa articolare in vista prossimale e C) ricostruzione del cinto pelvico di* 'Paranothosaurus armsleri' *in vista ventrale (da Peyer 1939, fig. 6). In C, il glenoide è evidenziato in grigio e gli ischi in rosso. Abbreviazioni: gl = glenoide; il = ilio; ilf = faccetta iliaca; pu = pube; puf = faccetta pubica.*

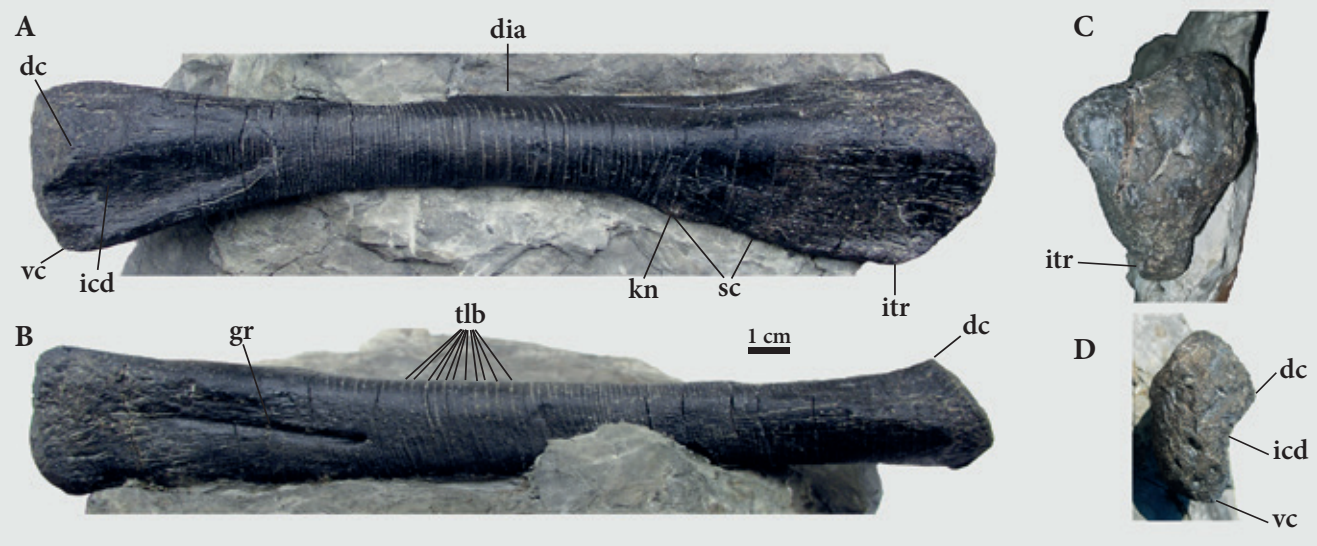

Fig. 18 - MFSN 31586, left femur. A) Posterior; B) dorsal; C) proximal; and D) distal views. Abbreviations: dc = dorsal condyle; dia = diaphysis; gr = groove; icd = intercondylar depression; itr = internal trochanter; kb = knob; sc = muscle scar; tlb = thin light bands; vc = ventral condyle.
- *MFSN 31586, femore sinistro. A) Vista posteriore; B) dorsale; C) prossimale; D) distale. Abbreviazioni: dc = condilo dorsale; dia = diafisi; gr = solco; icd = depressione intercondilare; itr = trocantere interno; kb = nodo; sc = cicatrice muscolare; tlb = sottili bande chiare; vc = condilo ventrale.*

the bone is 6 mm. The ventral (ventrolateral) surface is flat and crossed by thin and closely spaced longitudinal striae (Fig. 16). A large neurovascular foramen opens at the end of a groove on the proximal part of the posterolateral portion of the fan. The dorsal (dorsomedial) surface is concealed by the rock.

The distal margin of the fan is arched with a straight symphyseal (medial) edge where the element articulated with the other ischium (Fig. 17A). The thickness of the symphyseal edge cannot be appreciated because the articular surface is concealed by the rock.

This ischium has been referred to a nothosauroid by Dalla Vecchia (2008a) because of its morphology and large size compared to that of the other ischia from the tetrapod sample of the Aupa Valley, which is composed mainly of *Tanystropheus* bones (Dalla Vecchia 2006b; 2008a). However, the ischia of the eusauropterygians (Peyer 1939, fig. 6, pls. 66 and 72; Storrs 1991, figs. 15A and 16; Rieppel 1994, fig. 28d; Klein et al. 2022, fig. 17A, B, E, G) and large tanystropheids (Wild 1973, figs 71 and 92) have a similar overall shape. MFSN 34995/1 resembles the ischium of *'Paranothosaurus amsleri'* (Fig. 17B), but the lateroposterior portion of the fan is less expanded in the Friulian specimen.

Limb bones

MFSN 31586 (Fig. 18) is a femur from the outcrop 6 and is still partly conglobated in the rock. According to Rieppel (1994, fig. 33A), it is a left femur and the fully exposed sides are the posterior and the dorsal ones. This element has been described and figured in Dalla Vecchia (2006b) and figured in Dalla Vecchia (2008a). It is 247 mm long, straight, slender and expanded at both extremities. The proximal third of the bone is just more expanded dorsoventrally (45 mm) than the distal one (43 mm), but it is more robust. This proximal part has a triangular cross section due to the thick and long internal trochanter. The internal trochanter ends distally with a small knob; its distalmost tract (30 mm) presents a muscle scar. The dorsal side of the proximal expanded part is flat and contains a 67 mm long longitudinal groove, deep and narrow, ending distally with a neurovascular foramen. The distal expanded portion is flattened and slightly twisted with respect to the proximal one. There are two distal condyles that are separated by a broad intercondylar depression extending on the posterior surface of the distal expanded portion; two small neurovascular foramina open in the depression. The articular facets of the condyles are confluent. The dorsal condyle is larger than the ventral one. The diaphysis is straight and constricted (the nearly circular cross section at mid-diaphysis has a diameter of 22 mm). The diaphysis appears to be transversally crossed by very thin (submillimetric) light bands which could be related to the bone growth or to diagenesis.

The limited sigmoidality of the femur and a pronounced internal trochanter were considered as deviations from the typical *Nothosaurus* morphology by Voeten et al. (2014).

MFSN 46669 (Fig. 19) is a disk-like bone from the outcrop 5. It has a somewhat crescentic outline given by a slightly concave (constricted) proximal («dorsal» according to the orientation chosen by Klein et al. 2022, p. 45) side opposite to the convexity of the rest. It is evidently a large mesopodial element with the wider surfaces that are the dorsal (lateral) and ventral

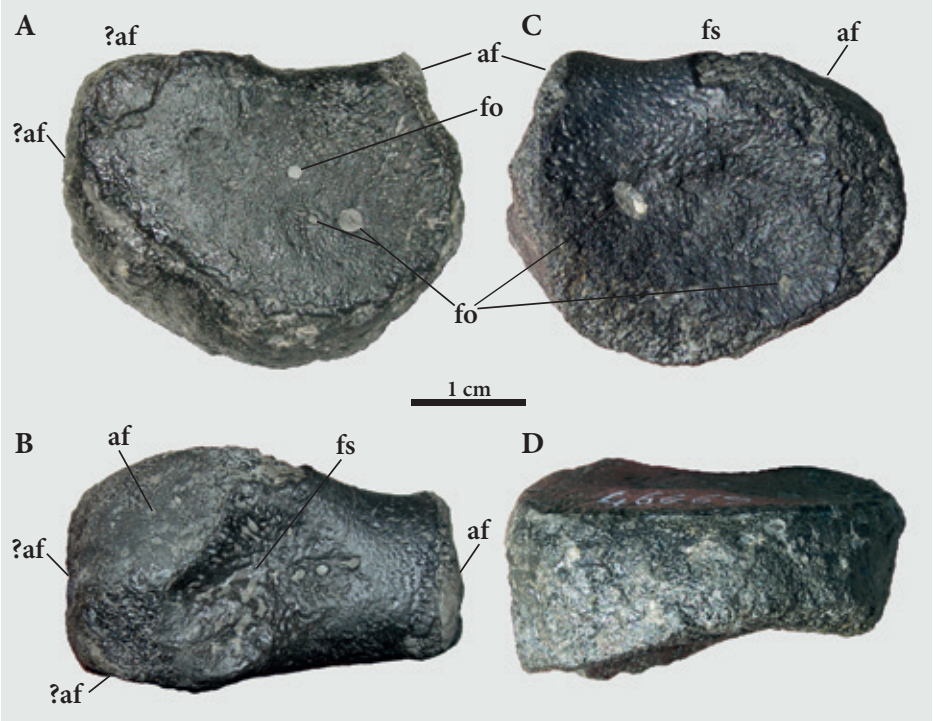

Fig. 19 - MFSN 46669, large mesopodial element. A) dorsal or ventral; B) ventral or dorsal; C) proximal; and D) distal views. Abbreviations: af = articular facet; fo = neurovascular foramen; fs = fossa.
- *MFSN 46669, grande elemento mesopodiale. A) Vista dorsale o ventrale; B) ventrale o dorsale; C) prossimale; D) distale. Abbreviazioni: af = facetta articolare; fo = forame neurovascolare; fs = fossa.*

(medial) ones (cf. Saint Seine 1955, fig. 25; Romer 1956, fig. 189D; Rieppel 1994, fig. 64). It is 29 mm long proximodistally, 36 mm wide, 21 mm thick proximally and 10.5 mm thick distally. The surface shown in Fig. 19A (dorsal or ventral) is flat and finely pitted but with three larger neurovascular foramina, one of which is much larger than the other two. The opposite side (Fig. 19B) is slightly concave and finely pitted and also shows three larger neurovascular foramina, one of which is much larger than the other two. The proximal side (Fig. 19C) presents a 'cut' extremity (right in Fig. 19C) and an expanded opposite estremity. The latter presents a broad and flat articular surface and a possible smaller articular facet, which, however could be due to bone erosion. A third articular facet could be contiguous to these two in the lateral/medial side of the bone (Fig. 19C). An articular facet occurs also on the opposite medial/lateral side (the 'cut' one; Fig. 19A-C). There is a distinct fossa (depression) in the middle of the proximal side; here the bone texture is coarsely pitted and grooved (Fig. 19C). The curved distal surface has a spongy aspect, probably because the bone was slightly damaged.

This mesopodial element might be an astragalus because of its size and the presence of a distinct proximal concavity for the perforating artery as reported for *Simosaurus* by Rieppel (1994, p. 30, figs. 31B and 34) and *Nothosaurus* (Saint Seine 1955, fig. 25; Rieppel 1994, fig. 64) and the presence of articular facets for the tibia and fibula (Saint Seine 1955, fig. 25). In *Nothosaurus* both the intermedium and the astragalus are large mesopodials with a somewhat crescentic outline in dorsoventral view, but the astragalus is anteroprossimally longer (Saint Seine 1955, fig. 25). However, the intermedium of '*Paranothosaurus amsleri*' appears to be nearly as large as the astragalus and is even more crescentic according to Peyer (1939, pls. 66 and 71-72). Furthermore, the intermedium can also have articular facets for the radius and ulna (Romer 1956, fig. 186B). The astragalus of *Nothosaurus mirabilis* has just a slightly more concave proximal margin with respect to the intermedium; they are identified as such because the tarsals are associated with the femur (Klein et al. 2022).

Discussion

Middle Triassic large eusauropterygian taxa

The systematics of the Eusauropterygia is traditionally based on features of the skull and lower jaws. This is particularly true for the genus *Nothosaurus* (Rieppel & Wild 1996; Rieppel 2000). Unfortunately, the sample from the Aupa Valley does not include skull and lower jaw material.

The scattered nature of the specimens, their provenance from distinct outcrops of the same formation and the difference in size do not allow to refer them unambiguously to a same taxon, although this cannot be excluded. Furthermore, the just partial preparation of most of them sometimes hampers the identification of structures allowing to a satisfactory comparison, especially among neural arches.

Because of the geological age (probably uppermost Anisian), large size and palaeogeographical provenance of the eusauropterygian skeletal elements described above, comparison is made firstly with the large notho-

saurid from the Grenzbitumenzone/Besano Formation of the Tessin (Switzerland and Italy) that was named *Paranothosaurus amsleri* by Peyer (1939). The taxonomy of this taxon is debated.

Peyer (1939) referred a complete and articulated skeleton (PIMUZ T 4829) from the Cava Tre Fontane site of the Monte San Giorgio locality deposited then at the Zoological Museum of the University of Zürich, Switzerland (now at the Paläontologisches Institut und Museum of the same university) to the new genus *Paranothosaurus,* with the species *P. amsleri*. The diagnoses of the genus and species by Peyer (see below) are a general description of the specimen without actual diagnostic features (except, possibly, the low neural spine of the vertebrae), which do not allow a true distinction from *Nothosaurs*.

Generic diagnosis of *Paranothosaurus* by Peyer (1939, p. 79): Skull with the features of *Nothosaurus*, i. e. with a pair of wide parietal openings, which are separated by a median part of the skull that is wide in front and narrow behind. Large parietal foramen. The medium-sized orbits are located in front of the middle of the skull. Bony exterior nostrils located slightly posterior to mid-range orbit-tip of snout; the choanae just very little behind the nostrils, almost vertically below. Large pterygoids up to the posterior edge of the skull united by suture. Dentition limited to the edges of the jaws; the teeth of the premaxilla, the corresponding teeth in the lower jaw and two teeth of the maxilla considerably enlarged; between the large maxillary teeth and the teeth of the premaxilla there are a number of smaller teeth. Posterior cervical and the entire thoracolumbar region of the vertebral column with very low spinous processes. Trunk ribs except for the foremost, which are transitional in shape, one-headed. Pectoral and pelvic girdles *Nothosaurus*-like, as are the limbs. Formula of the phalanges of the feet 2 3 4 5 4; terminal phalanges approximately semicircular. Each element of the gastral apparatus consists of five pieces, namely an obtuse-angled symmetrical middle piece, and one inner and one outer side piece each.

Specific diagnosis of *Paranothosaurus amsleri* by Peyer (1939, p. 80): [species] Reaching a total length of up to ca. 4 m, skull length up to ca. 50 cm, length of the lower jaw up to ca. 60 cm. 19 cervical, 26 thoracolumbar, 5 sacral vertebrae. Approximately 60 caudal vertebrae (33 preserved). The space enclosed by the ventral elements of the pectoral girdle is very large. Interclavicle with large transversal width and small cranio-caudal length. The margin of the ulna bordering the spatium interosseum medially presents an arched notch, the fibula is curved with an arched notch in the middle of its convex margin (on the side of the fifth finger). In the 5th to about 12th caudal vertebrae, the posterior end of the vertebral body bears strong basal processes for the haemapophyses.

Later, Rieppel & Wild (1996, pp. 3 and 14-15) considered *Paranothosaurus amsleri* as a junior synonym of *Nothosaurus giganteus*. Rieppel et al. (1999) retained *Paranothosaurus* as a subjective junior synonym of *Nothosaurus*; they stated that *Nothosaurus* (*Paranothosaurus*) *amsleri* Peyer, 1939 is most probably conspecific with *Nothosaurus giganteus*, but that unequivocal assessment of synonymy of these two species requires further study of the material. According to these authors, *N.* (*Paranothosaurus*) *amsleri* has an autapomorphic vertebral structure that corresponds to the structure of the large vertebrae from the Germanic Triassic, referred to *N. giganteus*. Rieppel (2000, pp. 74 and 79) again considered *Paranothosaurus amsleri* as a junior synonym of *Nothosaurus giganteus*. *Nothosaurus giganteus* was erected by Münster (1834) based on skull fragments (holotype) and the posterior part of a left lower jaw ramus (paratype) from the Upper Muschelkalk (*atavus* through *postspinosus* biozones, uppermost Illyrian) of Oschengerg near Lainek east of Bayreuth, Bavaria, Germany. Therefore, the diagnostic features of this species are necessarily all in the cranial and mandibular elements. Rieppel (2000, p. 75) formulated an emended diagnosis of the species based on the large size, shape of the rostrum, number of fangs per premaxilla and shape of the fifth tooth, shape of the mandibular symphysis, shape of the postorbital, and development of the ectopterygoid flanges. Rieppel (2000) reported the species from the Upper Muschelkalk (Illyrian-Fassanian) of Germany (Bayreuth, Stuttgart-Zuffenhausen, and Crailsheim) and the upper Lower Keuperdolomit (Ladinian, early Longobardian) of Hoheneck near Ludwisburg (Germany). Rieppel & Wild (1996, pp. 14-15) and Rieppel (2000, p. 79) added to the list of the referred specimens also PIMUZ T 4829 holotype of *Paranothosaurus amsleri* from the Anisian-Ladinian boundary of Tessin, because of size, skull proportions and stratigraphic occurrence. This complete specimen could allow referring to *Nothosaurus giganteus* by comparison also the isolated large-sized postcranial elements. This was done by Rieppel & Wild (1996), but not by Rieppel (2000).

As noticed by Peyer (1939), PIMUZ T 4829 has much lower neural spines respect to those of the genotypical species *Nothosaurus mirabilis*. According to Rieppel & Wild (1996) and Rieppel (2000) the low neural arch on the dorsal vertebrae represents the plesiomorphic condition within *Nothosaurus* by comparison with the outgroups (e.g., *Simosaurus*), as well as with nothosaurs from the lowermost Muschelkalk. Neither Rieppel & Wild (1996) nor Rieppel (2000) included "low neural spine in the dorsal vertebrae" as a diagnostic feature of *Nothosaurus giganteus*.

Nevertheless, Rieppel & Wild (1996) referred to this species a lot of postcranial bones of large-sized eusauropterygians collected in the same horizons where the

skull and mandibular elements of *Nothosaurus giganteus* have been found, but also from other horizons. They include the following elements from the Upper Muschelkalk of Germany: a cervical and two sacral vertebrae**,** two articulated vertebrae, another three isolated vertebrae, a coracoid and a scapula with parts of the clavicle from Bayreuth (N Bavaria); a humerus from Bindlach near Bayreuth; several vertebrae and a humerus from different horizons (biozones) of Hegnabrunn near Kulmbach (N Bavaria); vertebrae, girdle and appendicular elements from several different horizons and localities near Crailsheim, NE Baden-Württemberg (a coracoid and an ischium from Crailsheim; a vertebra from Neidenfels; a vertebra, a coracoid, two humeri, and a femur from Heldenmuhle; several vertebrae, a humerus, and a femur from Tiefenbach; several vertebrae and a coracoid from Schmalfelden); a pubis from Sattelweiler (NE Baden-Württemberg); a coracoid from Hofingen near Leonberg and Stuttgart- Zuffenhausen (central Baden-Württemberg); a vertebra from Bedheim-Ehrlichsgraben (NW Baden-Württemberg), Rublingen (NE Baden-Württemberg), Berlichingen (N Baden-Württemberg), Bettenfeld near Rothenburg (NW Bavaria), Eschenau (N Bavaria), Rugendorf (N Bavaria), Forstlahm-Herlas (N Bavaria), Grossenbehringer near Gotha (Thuringia), and Kleinromstedt near Weimar (Thuringia); a vertebra, a pectoral girdle, an ischium, and an ilium from Bad Sulza (Thuringia).

A vertebra and a neural arch are reported from the Muschelkalk of "Montdessus, Neurthé" and Luneville (Meurthe- et- Moselle), NE France, respectively.

An ilium is reported from the lower Keuper (Ladinian, Longobardian) of Zwingelhausen (central Baden-Württemberg). Finally, 11 articulated dorsal vertebrae with fragmentary ribs and gastralia have been found in the Middle Triassic of Belogradcik, NW Bulgaria.

Curiously, Rieppel & Wild (1996) do not include in the referred specimens the dorsal vertebra from the "Ladinian" of "Southern Alps" that they mention in the text (p. 15) and figure in fig. 9 referring it to *Nothosaurus giganteus*. That vertebra and other eusauropterygian material from the latest Ladinian-early Carnian site of Fusea (Tolmezzo municipality, Friuli Venezia Giulia Autonomous Region, NE Italy) were later described by Rieppel & Dalla Vecchia (2001). A sacral vertebra (actually a cervical; Dalla Vecchia 2008a, fig. 90A); two dorsal vertebrae (Fig. 20); an anterior dorsal neural arch; an isolated centrum; a partial skull; a lower jaw fragment; a lower jaw fragment with tooth; and the distal end of a left clavicle were referred to *Nothosaurus* cf. *N. giganteus*, mainly based on specimens' size and the low spines in the neural arches, because other bones from the same layer and outcrop were referred just to *Nothosaurus* sp.

Rieppel et al. (1999, p. 15) referred a neural arch with low neural spine; the posterior end of a left mandibular ramus; a large vertebral centrum; large girdle elements (including a scapula); and large proximal limb bones from the Muschelkalk (Illyrian-Fassanian) of Makhtesh Ramon in the Negev desert, Israel, to *Nothosaurus* cf. *N. giganteus* "or a very closely related species".

Later, several vertebrae from the upper Ladinian of Fuencaliente de Medinaceli (Soria Province, Castilla y León, Spain) have been referred to *Nothosaurus* cf. *giganteus* by de Miguel Chaves et al. (2016). Recently, a skull fragment of *N. giganteus* has been described from the Lower Keuper (Longobardian) of Kupferzell (Baden-Württemberg) (Hinz et al. 2020).

Diedrich (2012) also accepted that the large 'nothosaur' material from the upper Muschelkalk of Germany and PIMUZ T 4829 (*Paranothosaurus amsleri* holotype) belong to the same species. However, according to this author (p. 30) there are "very strong cranial and postcranial anatomic differences" between PIMUZ T 4829 and *Nothosaurus* as represented by the type species *N. mirabilis*, thus the genus *Paranothosaurus* should be considered valid. As the specimens referred to *Nothosaurus giganteus* and *Paranothosaurus amsleri* are considered to belong to the same species, the correct combination is *Paranothosaurus giganteus* because of priority. Short neural spines and short cervical to dorsal vertebra centra with extended zygapophyses are the main features distinguishing *Paranothosaurus giganteus* from *Nothosaurus* species (Diedrich 2012, p. 30).

Later, Liu et al. (2014) described a new taxon - *Nothosaurus zhangi* Liu, Hu, Rieppel, Jiang, Benton, Kelley, Aitchison, Zhou, Wen, Huang, Xie & Lv - from the upper Anisian (Pelsonian) of China, whose size approached or slightly exceeded that of *Nothosaurus giganteus*, but it has relatively higher neural spine respect to the western large-sized species (Liu et al. 2014, fig. 2a-b and e).

Size and comparisons

According to Liu et al. (2014), *Nothosaurus giganteus* reached 500-700 mm in total body length; this estimate is clearly based on the isolated largest skulls from the Germanic Muschelkalk. In fact, the total length of PIMUZ T 4829 (*Paranothosaurus amsleri* holotype) is sensibly lower (385 mm) according to Peyer (1939). The coracoids, femora and ischia of PIMUZ T 4829 are 250-260 mm, 260 mm and 185-187 mm long, respectively. The same skeletal elements from the Aupa Valley sample are 250-217 mm, 247 mm, and 155 mm long, respectively. Therefore, the Friulian individuals appear to be slightly smaller than that from the Tessin. Using the measurements reported in Peyer (1939), it is possible to estimate the total body length of the large eusauropterygians from the Aupa Valley on the basis of Peyer's body length estimate under the assumption that the Friulian individuals had the same body proportions of PIMUZ T 4829.

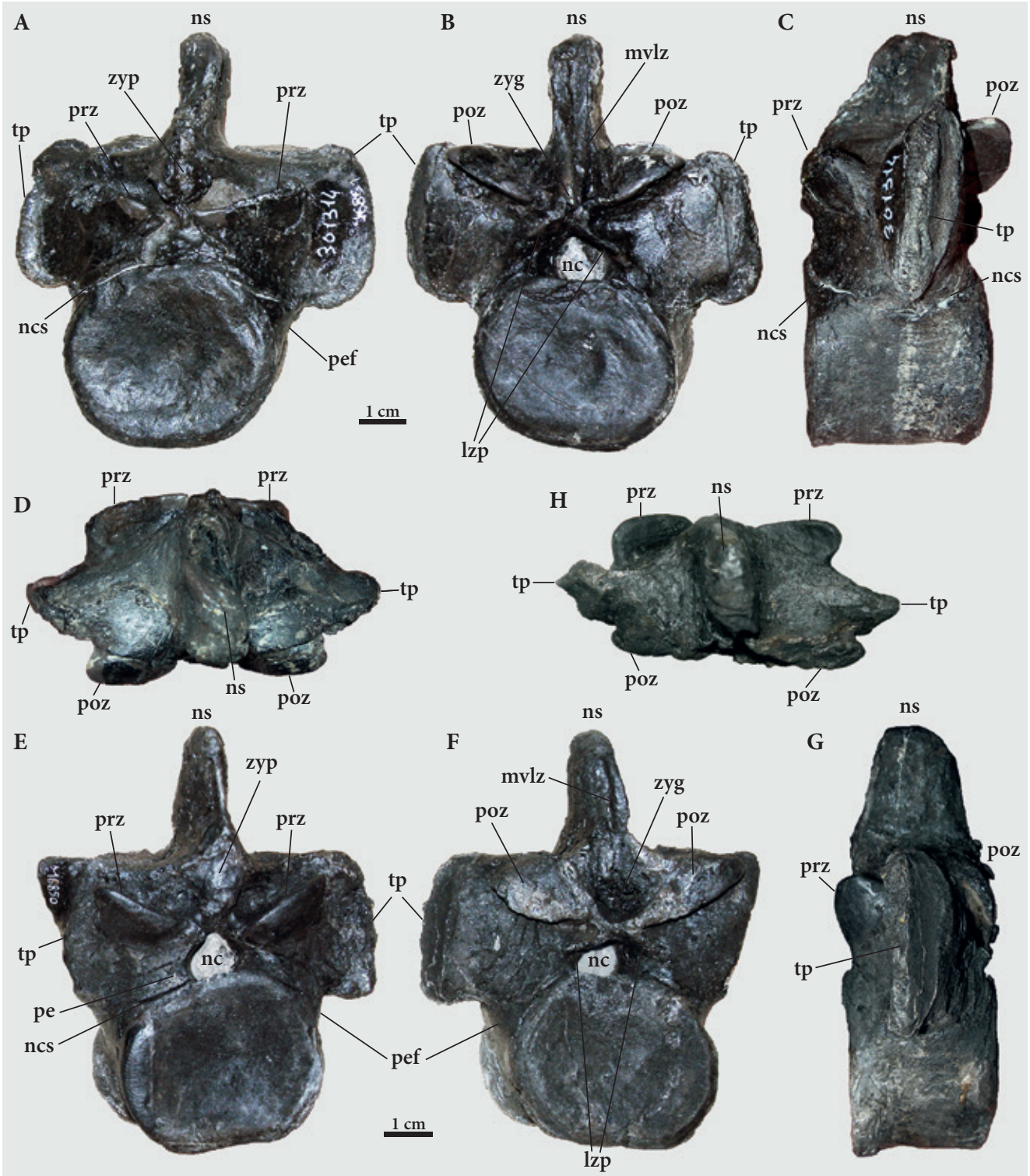

Fig. 20 - Dorsal vertebrae of *Nothosaurus* cf. *N. giganteus* from the Fusea locality. A-D) MFSN 16851 in anterior (A); posterior (B); left lateral (C); and dorsal (D) views; E-G) MFSN 16850 in anterior (E); posterior (F); left lateral (G); and dorsal (H) views. Abbreviations: lzp = lamina connecting the posterior process of the zygantrum to the pedicel; mvlz = medio-vertical lamina of the zygantrum; nc = neural canal; ncs = neurocentral suture; ns = neural spine; pe = pedicel of the neural arch; pef = facet/base on the centrum for pedicel of the neural arch; poz = postzygapophysis; prz = praezygapophysis; tp = transverse process; zyg = zygantrum; zyp = zygosphene.

- *MFSN vertebre dorsali di* Nothosaurus *cf.* N. giganteus *dalla località di Fusea. A-D) MFSN 16851 in vista anteriore (A), posteriore (B), laterale sinistra (C) e dorsale (D); E-G) MFSN 16850 in vista anteriore (E), posteriore (F), laterale sinistra (G) e dorsale (H). Abbreviazioni: lzp = lamina che connette il processo posteriore dello zigantro al pedicello; mvlz = lamina medio-verticale dello zigantro; nc = canale neurale; ncs = sutura tra centro e arco neurale; ns = spina neurale; pe = pedicello dell'arco neurale; pef = faccetta/base sul centro per il pedicello dell'arco neurale; poz = postzigapofisi; prz = prezigapofisi; tp = processo trasverso; zyg = zigantro; zyp = zigosfene.*

The coracoids, the femur and the ischium gave a total body length estimate of 385-320 mm, 365 mm, and ca. 320 mm, respectively. Although large, the late Anisian eusauropterygians of Friuli were not giant in size.

The 228 mm long partial skull (MFSN 19288) from the site of Fusea (which occurs only 16 km SW to the Aupa Valley) described in Rieppel & Dalla Vecchia (2001, fig. 22) and referred to *Nothosaurus* cf. *giganteus* corresponds to a total skull length of ca. 460 mm using as reference the skull of *Nothosaurus giganteus* SMF R-475 figured in Rieppel (2000, fig. 10B). Comparing this estimated skull length to that of PIMUZ T 4829 (485 mm) and using the estimated total length of PIMUZ T 4829, the resulting total length of the Fusea nothosaur would be 365 mm, comparable to the geologically older individuals of the Aupa Valley. Unfortunately, the site did not yield scapulae, coracoids and ischia for comparison. The dorsal vertebrae (e.g., MFSN 16850-51, which were found close to each other; Dalla Vecchia 1994, fig. 6; Rieppel & Dalla Vecchia 2001, fig. 24A-B; Fig. 20) are similar to those from the Aupa Valley in having a low neural spine, but differ in the absence of the posterior process of the floor of the zygantrum and in the apical tapering of the neural spines. Furthermore, the age difference between the two localities spans approximately the whole Ladinian, which means ca. 5 million years. The transverse processes are unusually flattened anteroposteriorly, but this may be a taphonomic bias. The large eusauropterygians from the Fusea and Aupa valley localities may belong to a long-lived *Nothosaurus*/*Paranothosaurus giganteus* ranging the late Anisian-early Carnian interval as hypothesized by Rieppel (2000). As an alternative, several distinct large eusauropterygian taxa with low-spined neural arches existed during this interval, which may be distinguished only through an accurate anatomical study and the comparison of the postcranial material and the discovery/description of specimens preserving associate skull and postcranial material.

At the present state of the knowledge, most of the eusauropterygian from the Aupa Valley can be referred to *Nothosaurus*/*Paranothosaurus giganteus* as represented by the late Anisian/earliest Ladinian material from Switzerland and Germany.

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