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A NEW SPECIMEN OF *NOTHOSAURUS* FROM THE LATEST ANISIAN (MIDDLE TRIASSIC) BESANO FORMATION (GRENZBITUMENZONE) OF ITALY

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Key words: *Nothosaurus* (Reptilia Sauropterygia), Besano Formation, Late Anisian, Middle Triassic, Monte San Giorgio, paleobiology, sympatric species, niche partitioning.

Abstract. A nearly complete but disarticulated skeleton of a small sized nothosaur is described. The specimen was collected in 2003 from an outcrop of the Besano Formation (Grenzbitumenzone of Swiss authors) of latest Anisian (Middle Triassic) age, in the Monte San Giorgio Area, northern Italy. The osteology of the postcranial skeleton supports the assignment to the genus *Nothosaurus*, and also excludes its belonging to *Nothosaurus giganteus/Paranothosaurus amsleri* already known from coeval localities of the Besano Formation in the Swiss part of the Monte San Giorgio area. Despite the lack of most of the skull, which contains diagnostic characters at the species level for *Nothosaurus*, the few preserved cranial elements suggest similarities with *N. juvenilis* which skull, and only known part, is also of comparable size. This specimen is particularly significant because it improves the knowledge of the osteology of *N. juvenilis* and because the second *Nothosaurus* species, smaller than *N. giganteus/P. amsleri*, suggests coexistence of sympatric species characterized by size and, probably, trophic differentiation within the genus *Nothosaurus* in the Monte San Giorgio area as occurred in the coeval Germanic Basin.

Riassunto. Viene descritto lo scheletro quasi completo, ma totalmente disarticolato e privo di quasi tutto il cranio, di un piccolo notosauriforme proveniente dalla Formazione di Besano (Grenzbitumenzone) risalente all'Anisico sommitale (Triassico Medio). I caratteri osteologici dello scheletro postcraniale consentono l'attribuzione al genere *Nothosaurus* ed escludono nel contempo la sua appartenenza alla specie *Nothosaurus giganteus/Paranothosaurus amsleri*, già nota da affioramenti svizzeri della Grenzbitumenzone. Purtroppo l'esemplare è quasi completamente privo del cranio, che contiene la maggior parte dei caratteri diagnostici a livello specifico per *Nothosaurus*, tuttavia le parti conservate permettono di ipotizzare la possibile appartenenza dell'esemplare a *N. juvenilis*. Il ritrovamento è particolarmente significativo perché se da una parte permetterebbe di aumentare considerevolmente le conoscenze sull'osteologia di *N. juvenilis*, in ogni caso testimonia la presenza di una seconda specie di *Nothosaurus* nella Formazione di Besano di dimensioni minori rispetto a *Nothosaurus giganteus/Paranothosaurus amsleri*. Questo suggerisce un scenario di compresenza di

specie simpatiche dello stesso genere nell'area del Monte San Giorgio, caratterizzate da dimensioni differenti, che quindi si cibavano di prede diverse con relativa suddivisione di nicchie trofiche, come è stato proposto per i notosauri coevi del Bacino Germanico.

Introduction

The rich vertebrate fauna of Besano-Monte San Giorgio (Lombardy, Italy and Canton Ticino, Switzerland) is among the most important in the world for the Middle Triassic even after the recent discoveries in China. The site represents an invaluable tool for comparisons among these faunas for a more complete delineation of the biogeography and evolution of Middle Triassic fishes and reptiles.

The first finds were reported by Curioni in 1847, and since then, vertebrates from the Besano-Monte San Giorgio have been studied extensively, with abundant material collected during palaeontological excavations and mining between the end of 19th and the first half of the 20th centuries. Fossils have been collected from different formations (Fig. 1), belonging to four horizons (Zangerl 1935) which age spans from the upper Anisian Besano Formation to the upper Ladinian Kalkschieferzone (Furrer 1995). The marine reptiles comprise ichthyosaurs, thalattosaurs, sauropterygians, while protosaurs were semi-aquatic (*Tanystropheus*) or terrestrial (*Macrocnemus*) and large rauischiids (*Ticinosuchus*) lived on land (Peyer 1937; Krebs 1963; Kuhn-Schnyder 1962). Eusauroptrygians, especially pachypleurosaurids are among the most abundant reptiles, with two genera and four species so far described (Carroll & Gas-kill 1985; Rieppel 1989; Sander 1989; Tschanz 1989).

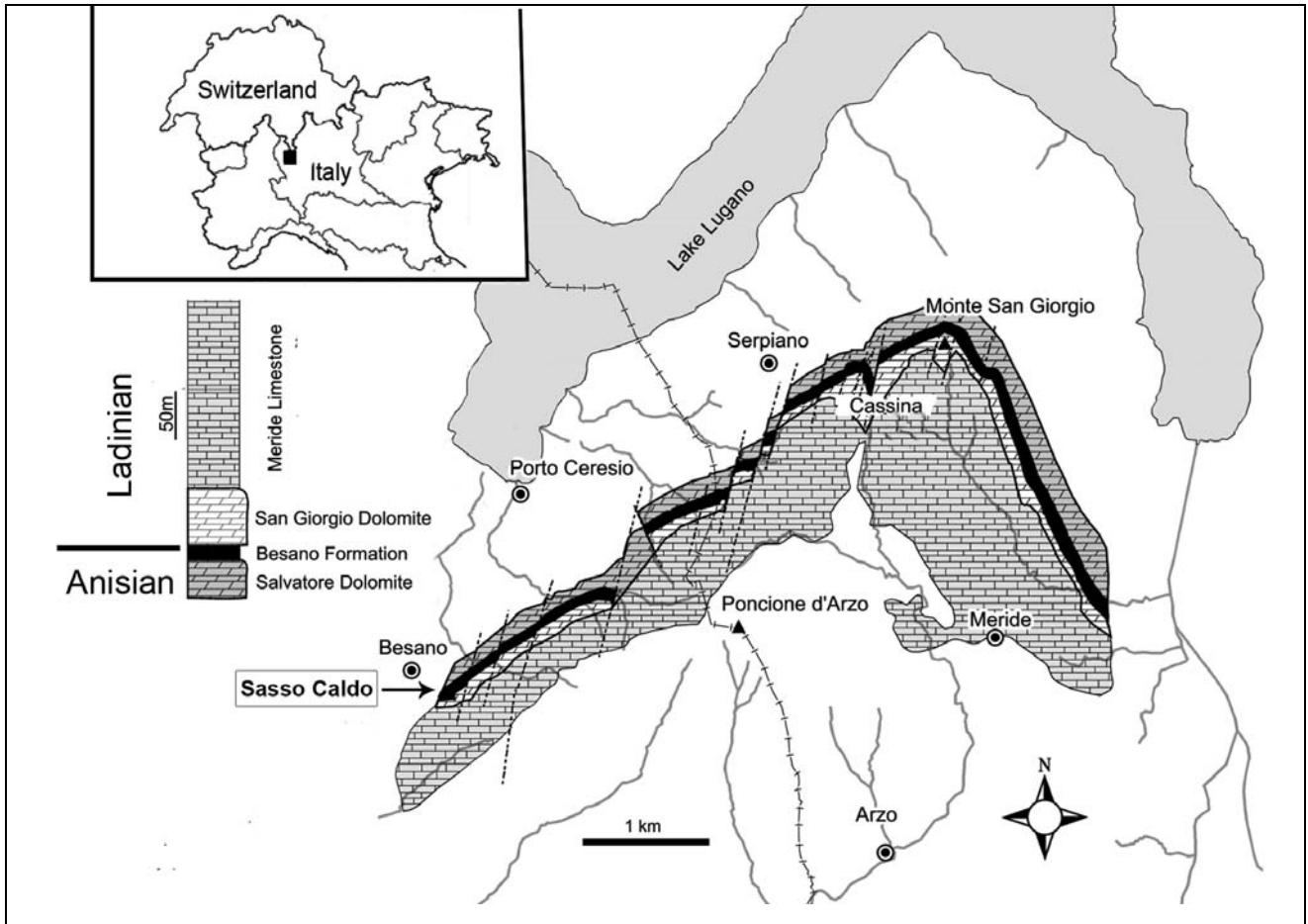


Fig. 1 - Map of the Besano-Monte San Giorgio areas showing the Anisian-Ladinian sequence along with the locality of Besano-Sasso Caldo (black arrow). Modified from Renesto & Stockar 2009.

In the Swiss localities of the Besano Formation both large (*Nothosaurus giganteus*= *Paranothosaurus amleri*) and small nothosauroids (*Lariosaurus buzzi*= *Silvestrosaurus*) were also found along with neusticosaur *Serpianosaurus* (Peyer 1939; Kuhn-Schnyder 1990; Tschanz 1989; Rieppel 1989; Sander 1989), while only *Serpianosaurus* has so far collected from the Italian localities of Besano.

The present paper describes the first *Nothosaurus* specimen collected in the Italian part of the Monte San Giorgio Area. The specimen is nearly complete but disarticulated. It is housed in the paleontological collection of the Museo Civico di Storia Naturale di Milano (Italy) with the catalogue number BES SC 1736. The specimen was collected in the Sasso Caldo Quarry (Fig. 1), an outcrop of the unit previously named Scisti Ittiolitici di Besano on the Italian side and “Grenzbitumenzone” (Frauenfelder 1916) on the Swiss side. The Besano Formation includes the Anisian-Ladinian boundary in its uppermost part (Brack et al. 2005). The described specimen was collected below the tuffitic layers and hence is of late Anisian age.

BES SC 1736 shows unequivocal characters that allow its assignment to the genus *Nothosaurus*, and

shows also some characters suggesting it could belong to the species *N. juvenilis* Edinger, 1921.

Systematic Paleontology

Sauropterygia Owen, 1860

Eosauropterygia Rieppel, 1994a

Eusauropterygia Tschanz, 1989

Nothosauridae Baur, 1889

Nothosaurinae Nopcsa, 1923

Nothosaurus Münster, 1834

Type species: *Nothosaurus mirabilis* Münster, 1834, Upper Muschelkalk, Middle Triassic of Germany.

Nothosaurus cf. **N. juvenilis** Edinger, 1921

Figs 2-8, Pl. 1-4

1921 *Nothosaurus juvenilis* Edinger fig.4.

1963 *Nothosaurus juvenilis* Edinger - Haas, p. 37 pl. 12

1970 *Nothosaurus juvenilis* Edinger - Schultze, p. 225 fig. 13

1994 *Nothosaurus juvenilis* Edinger - Rieppel, p. 735 fig. 1.

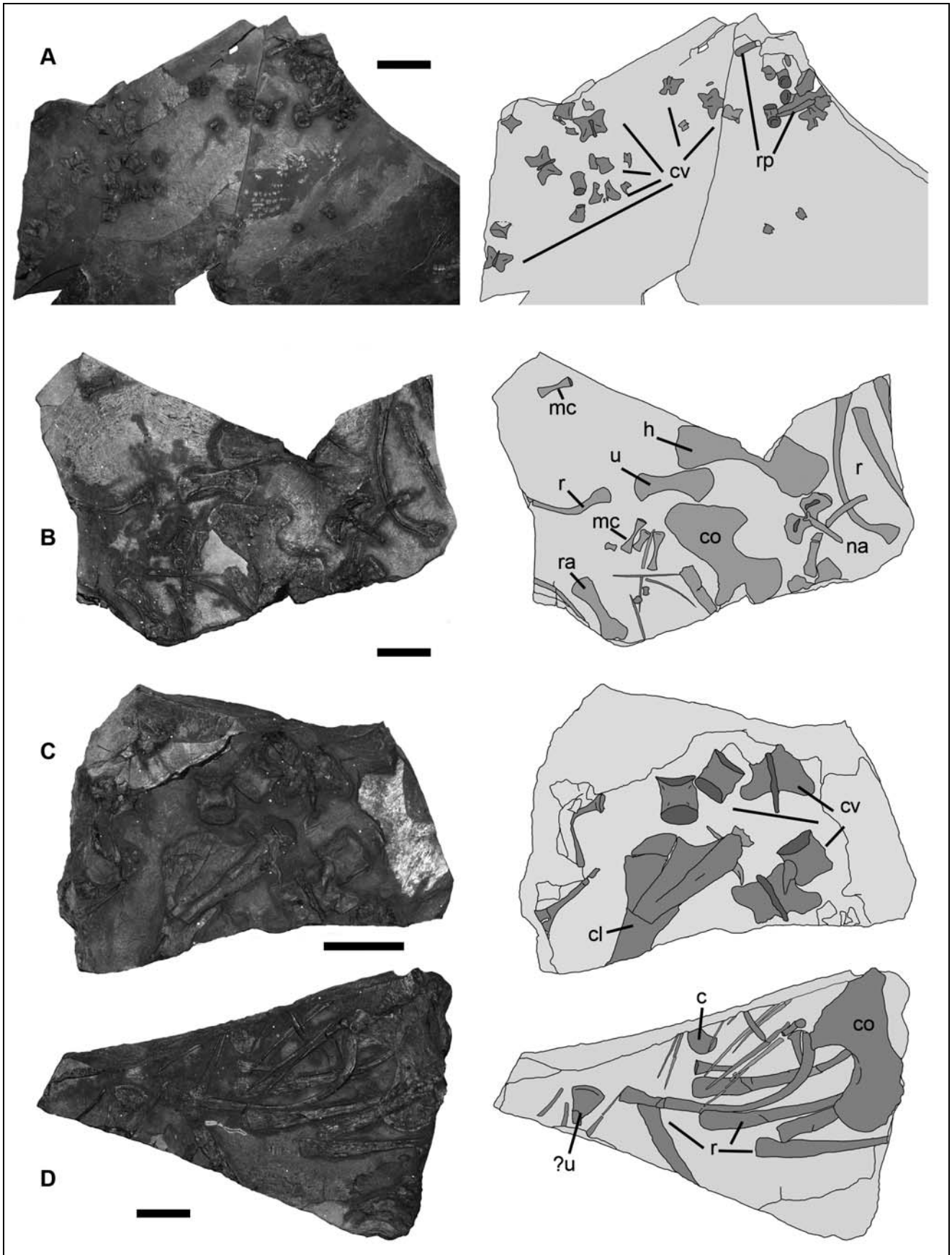


Fig. 2 - A-D, BES SC 1736, *Nothosaurus* cf. *N. juvenilis*. Photographs (left) and sketches (right) of the four small slabs showing the position of most relevant bones. Abbreviations are: c) carpal bone (unidentified), cl) clavicle, co) coracoid, cv) cervical vertebrae (both isolated centra and neural arches), h) humerus, mc) metacarpals, na) neural arches, r) ribs, ra) radius, rp) retroarticular process of the lower jaw, u) ulna. Scale bars equal 50 mm.

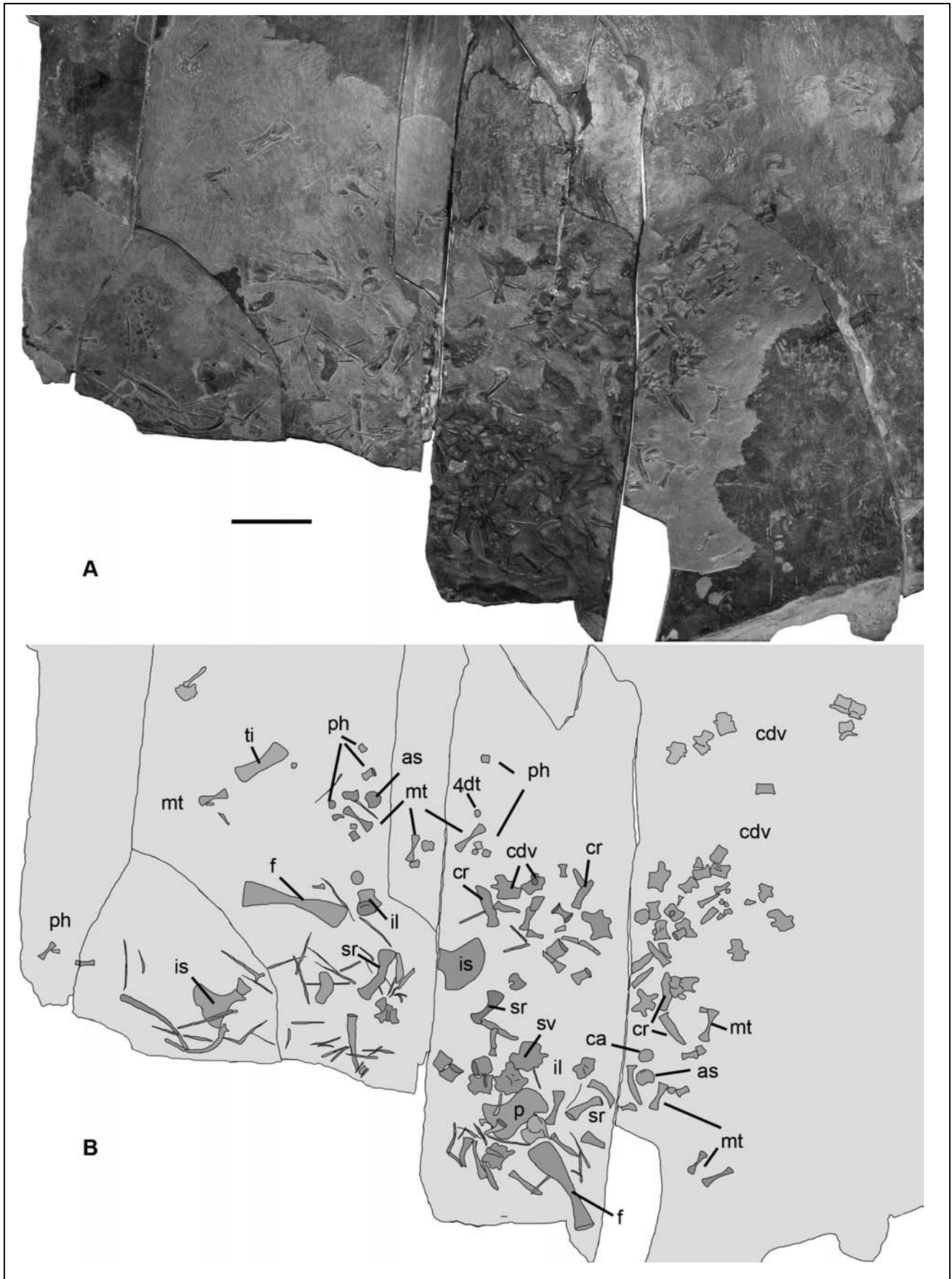


Fig. 3 - BES SC 1736, *Nothosaurus* cf. *N. juvenilis*. A) Photographs and B) sketch of the larger, composite slab showing the position of most relevant bones. Abbreviations are: as) astragalus, ca) calcaneum, cdv) caudal vertebrae, cr) caudal ribs, f) femur, il) ilium, is) ischium, mt) metatarsals, p) pubis, ph) phalanges, sr) sacral ribs, sv) sacral vertebrae, ti) tibia, 4dt) fourth distal tarsal. Scale bar equals 50 mm.

Holotype: K.8698-1 Palaeontological and Geological Institute and Museum, University of Heidelberg, Germany.

Material: BES SC 1736 (Fig. 2-3) Museo Civico di Storia Naturale di Milano (Milan, Italy). Collected from the outcrop of Sasso Caldo (Fig. 1), near Besano (Lombardy, northern Italy), Formazione di Besano, latest Anisian (Middle Triassic).

Description

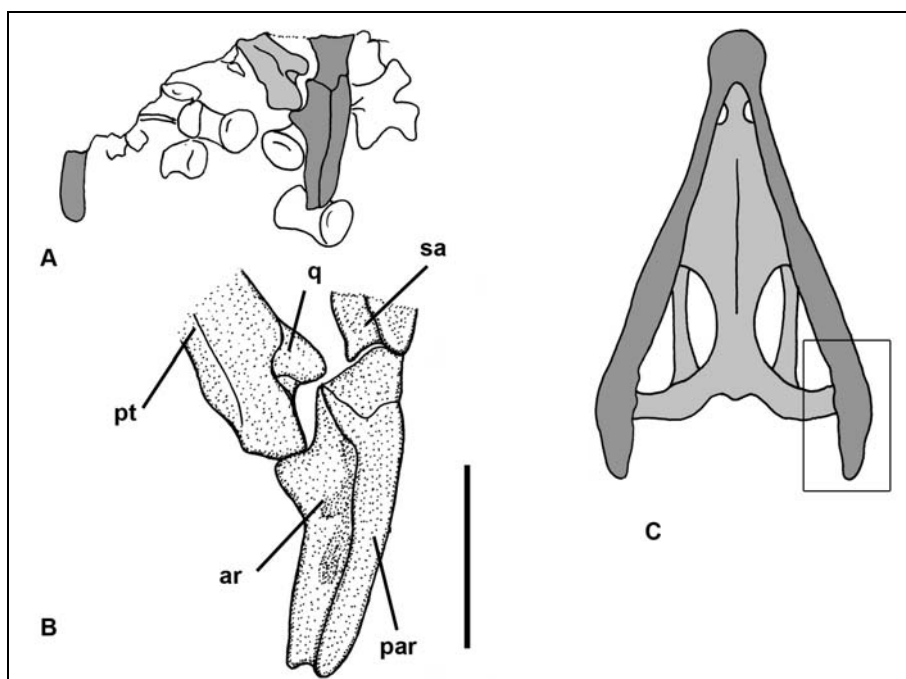
General remarks. BES SC 1736 is a nearly complete but almost completely disarticulated skeleton of a mid-sized eusauropterygian, lacking most of the skull, lower jaw and right fore limb. Bone measures are reported in Tab. 1. The specimen is preserved on several stone slabs (Figs 2-3), some of which do not match to each other because further slabs with missing elements were lost or destroyed during field work. By joining the matching portions of each slab, it has been possible to obtain six main slabs. In the first slab (Fig. 2A) are preserved a few cervical vertebrae, the left paroccipital process and the caudalmost portion of the lower jaws with both the right and left retroarticular processes and the left articular area for the quadrate. On the second, third and fourth slab (Figs. 2B-D) are preserved dorsal vertebrae and ribs, a few elements of the gastralia a partial clavicle, two coracoids, one humerus, left and right ulnae (on different slabs) one radius and elements of the carpus, metacarpus and few phalanges, presumably of the manus. The sixth slab (Fig. 3) is composed of smaller pieces that match together. This slabs preserves the last dorsal vertebrae and ribs; many gastralia; sacral, some caudal vertebrae and ribs, most elements of the pelvic girdle, two femora; one tibia and disarticulated elements of the tarsus, metatarsus and pes.

Skull. Only part of the occipital region is preserved (Fig. 4, Pl. 1A), the suspensorium process is strongly inclined caudolaterally, suggesting a distinct caudal displacement of the lower jaw articulation with respect to the (unpreserved) occipital condyle. The caudal portion of the left paroccipital process is very well preserved and shows how the pterygoid forms deep flanges running along the whole quadrate ramus of the pterygoid, which is typical for *Nothosaurus* (Rieppel 1984b; Rieppel & Wild 1996). The mandibular condyle of the quadrate is slightly compressed diagenetically, but is still articulated with the lower jaw.

Lower jaw. Part of the left articular area and both left and right retroarticular processes are well preserved (Fig. 4; Pl. 1A). The articular area for the quadrate is saddle shaped, with raised cranial and caudal margins. The retroarticular process is elongate and stout.

Vertebral column. Nearly all the centra are dissociated from their neural spines. The centra (Fig. 5 A, E, G, H; Pl. 1A) are slightly constricted assuming a faint hourglass shape, their ventral surfaces bear a small, slight keel, and their articular surfaces are platicoelous. In dorsal view, the disarticulated centra show cross-shaped facets for articulation of the pedicels of the neural arches as is typical for Eusauropterygia. The neural arches bear large, swollen pre- and post-zygapophyses with nearly horizontal articular surfaces (Fig. 5 B-D; Pl. 1 B-D). A deep zygantum is present between the post-zygapophyses, divided by a septum and the zygosphenes is bifurcated anteriorly (Fig. 5C-D; Pl. 1B). The transverse processes project laterally only slightly beyond

Fig. 4 - BES SC 1736, *Nothosaurus* cf. *N. juvenilis*. A) sketch of preserved elements of the skull (light grey) and of the lower jaw (dark grey), along with disarticulated cervical centra (outlined); B) detailed drawing of the right articular area; C) outline of a generalized nothosaurus skull (light grey) and lower jaw (dark grey), highlighting (rectangle) the portion of the skull detailed in (B). Scale bar equals 20 mm. Abbreviations are: ar) articular; par) prearticular; pt) pterygoid; q) quadrate; sa) surangular.



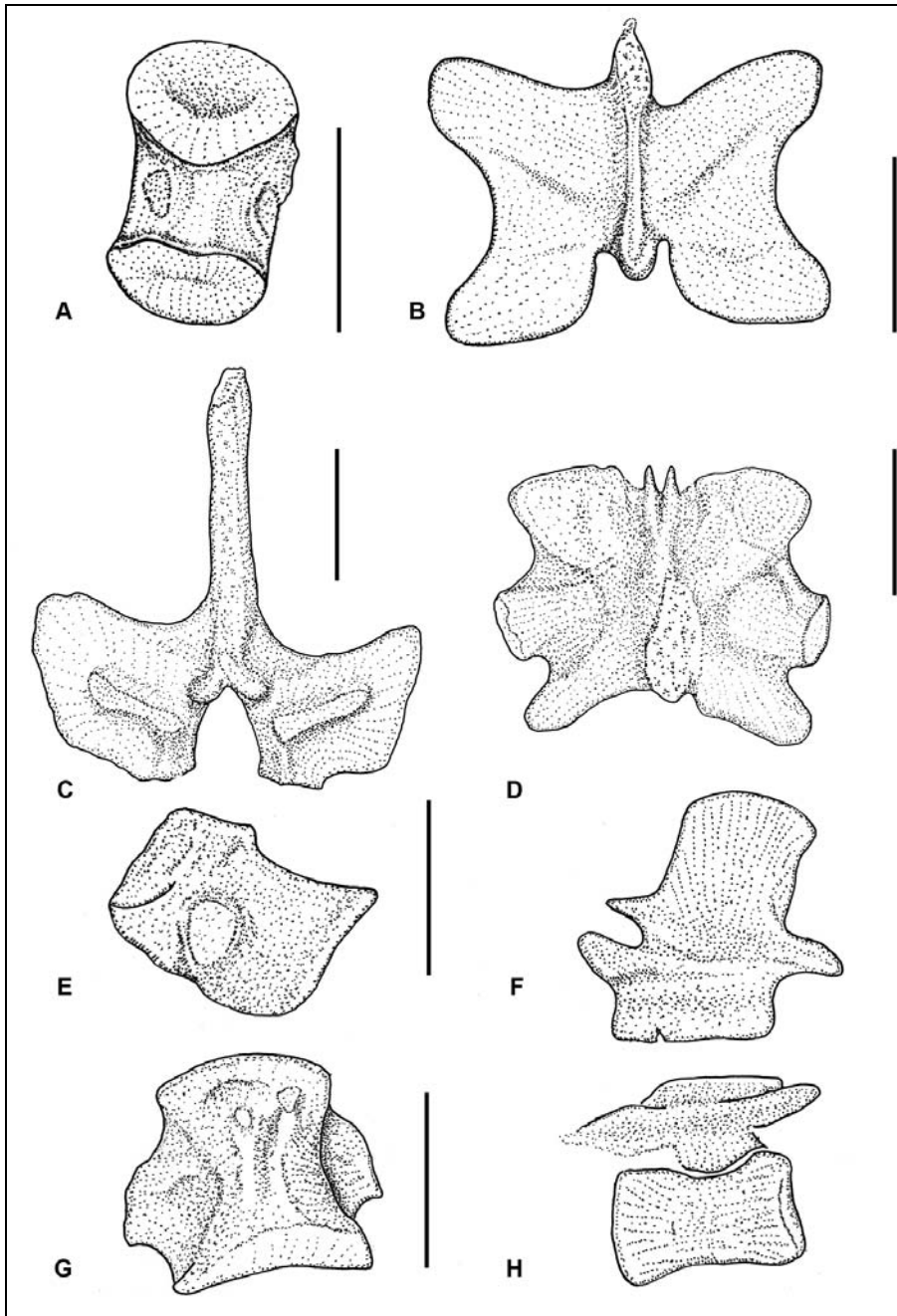


Fig. 5 - BES SC 1736, *Notbosaurus* cf. *N. juvenilis*. Drawings of various vertebral elements. A) Cervical centrum, ventral view; B) cervical neural arch, dorsal view; C) dorsal neural arch and spine, cranial view; D) dorsal neural arch, dorsal view; E) caudal centrum lateral view; F) caudal neural arch and spine lateral view; G) caudal centrum, ventral view; H) caudal vertebra lateral view. Scale bars equal 10 mm.

the zygapophyses, are strong with a wide base, reaching ventrally to the neurocentral suture (Fig. 5C; Pl. 1D). The transverse processes are separated from the postzygapophyses by a distinct notch. The neural spines of the dorsal vertebrae are subrectangular in shape, their axis slightly slanting caudally with no distal expansion as is typical for nothosaurs (Rieppel & Hagdorn 1997), approximately one and a half higher than long; the height of the neural spines does not vary much along the vertebral series, although their height decreasing gradually, starting from the mid-caudal region.

Ribs and gastralia. The cervical ribs (Pl. 2 B-C) are dicephalous, with broad pedicels, a short shaft and a

small free anterior process. The dorsal ribs (Pl. 2A) are holocephalous, with a flat or slightly convex articular area, evenly curved and expanded distally. The sacral ribs (Pl. 2 F-H) are stout and bear expanded heads at both ends. The caudal ribs (Pl. 2D) from the cranial region of the tail show a broad articular surface, a straight shaft tapering distally, ending in a broad, but not expanded, distal end. Several disarticulated gastralia are present, seemingly composed by three elements. The medial elements of the gastralia have an inverted "V" shape and bear a short but distinct cranial process (Pl. 2E).

Shoulder girdle. The craniolateral portion of the left clavicle and both coracoids are preserved. The pre-

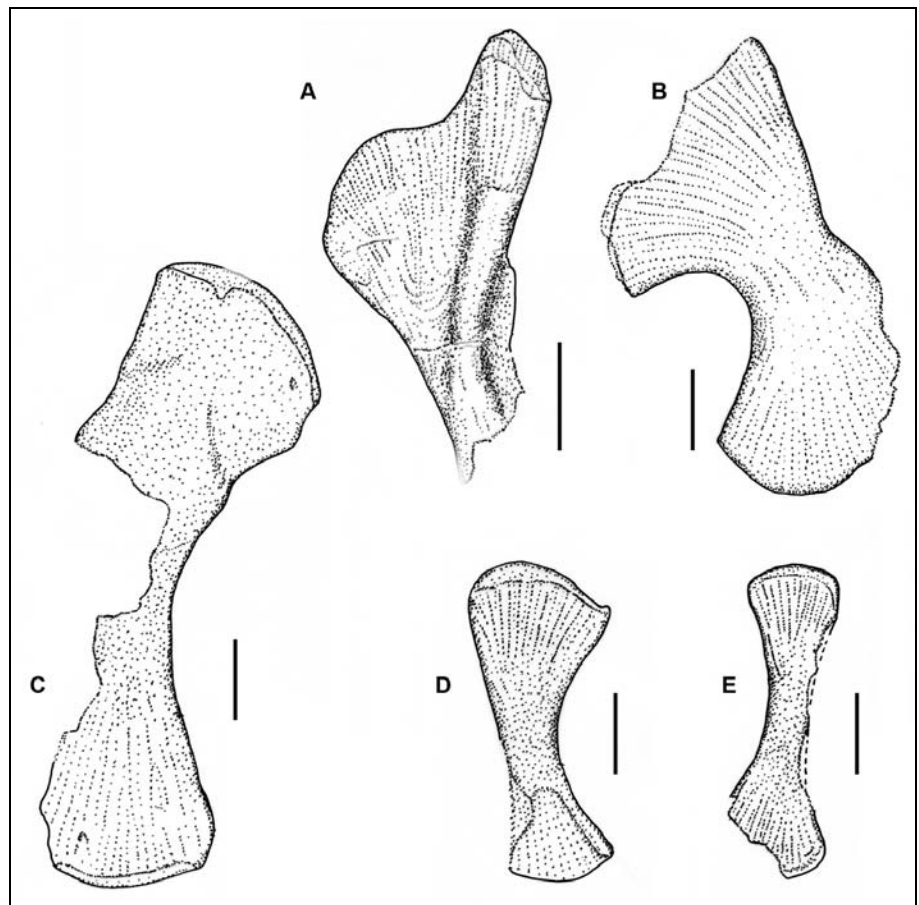
served fragment of the clavicle (Fig. 6A; Pl. 3A) shows an expanded horizontal blade which forms a pronounced craniolateral corner. The coracoids (Fig. 6B; Pl. 3B) are broad and flat, waisted bones with distinctly concave cranial and caudal margins and convex medial and lateral margins. Both coracoids are preserved at the borders of the slabs, so that their cranial and caudal margins are incompletely preserved, rendering impossible to check the shape and size of the preglenoid processes.

Pelvic girdle. The ilium is small, with a reduced iliac blade, which is separated from the acetabular area by a faint constriction (Fig. 7A-B; Pl. 3F-G). A small preacetabular process and a *spina praeacetabuli* are both present. The only preserved pubis is partially overlapped by a dorsal rib and part of its caudal margin is broken (Fig. 7D; Pl. 3F); it is a broad, plate-like bone, with concave cranial and caudal margins and convex lateral (dorsal) and medial (ventral) margins. The dorsal margin is expanded and thickened as it participates in the acetabulum; despite the presence of an overlapping rib, it can be noted that the medial margin shows a distinct embayment, similar to that figured by Peyer (1939, fig. 6) for *Nothosaurus giganteus/Paranotosaurus amsleri*. The obturator foramen is slit-like. The

ischium (Fig. 7C; Pl. 3B) is a subtriangular, fan-shaped bone, with distinctly concave cranial and caudal margins and convex lateral and medial margins. The ischium is greatly expanded toward its medial margins. The pronounced concavity of the caudal margin of the pubis, and of the cranial margin of the ischium form a wide fenestra thyroidea.

Fore limb. Only the right humerus is partially preserved: it lacks most of the preaxial portion of the shaft, while both proximal and distal heads are more complete (Fig. 6C; Pl. 3C). It is flattened and curved (with a convex preaxial and a concave postaxial border, Rieppel 1994a; Rieppel & Wild 1996), with slightly convex proximal and distal heads. The ectepicondyle is reduced. A well preserved ulna is present close to the humerus. The ulna is flat and broader than the radius and both the proximal and the distal heads are expanded (Fig. 6D; Pl. 3C), the proximal head being approximately 20% wider than the distal head (Tab. 1). The radius (Fig. 6E; Tab. 1) is narrower than the ulna, and its proximal and distal heads are slightly expanded. The morphology of these two bones is nearly identical to those of the radius and ulna of a *Nothosaurus* specimen from Winterswijk (Bickelmann & Sander 2008). Carpal bones are scattered along the slab surface or missing. A discoidal, flat bone with a subcircular margin inter-

Fig. 6 - BES SC 1736, *Nothosaurus* cf. *N. juvenilis*. Elements of the shoulder girdle and fore limb. A) lateral portion of clavicle, ventral view; B) coracoid, ventral view, C) humerus, ?ventral view, D) ulna, ?ventral view, E) radius ?ventral view. Scale bars equal 10 mm.



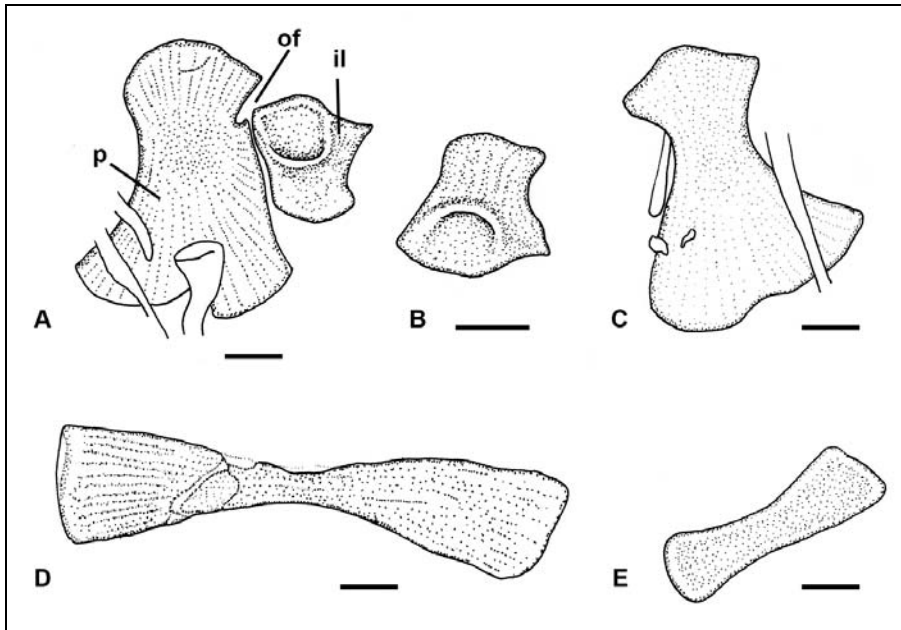


Fig. 7 - BES SC 1736, *Notosaurus* cf. *N. juvenilis*. Elements of the pelvic girdle and rear limb. A) Left pubis in ventral view and associated ilium (preserved tilted upside-down with respect to the pubis) in lateral view; B) right ilium in lateral view; C) left ischium in ventral view; D) femur, ?ventral view; E) tibia, ?ventral view. Abbreviations are: p) pubis, il) ilium, of) obturator foramen. Scale bars equal 10 mm.

rupted by a small embayment is preserved close to the right coracoid, and can be identified as an intermedium. A series of associated metacarpals are preserved with the left coracoid and most of other bones of the forelimb (Pl. 4B). The metacarpals are elongate, narrow bones, with slightly expanded heads. A further element is present, it is much shorter and less expanded at its distal end: it could be the first metacarpal. A few dissociated phalanges lie close to the metacarpals; they are short and broad, some, probably the more distal ones, are nearly discoidal in shape. Due to disarticulation and lack of elements, no phalangeal formula can be given.

Hind limb. The femur (Fig. 7D; Pl. 3D) is approximately the same length as the humerus, but with a straight and very narrow shaft. It has expanded proximal and distal heads, the latter showing a slightly convex outline. A thick ridge running close to the cranial margin of the proximal head could represent the internal trochanter. The femurs show a very shallow intertrochanteric fossa. A isolated tibia (Fig. 7E) is partially preserved at the margin of the larger slab, lacking the proximal head. It shows a hourglass outline with a straight shaft axis and slightly convex distal margin. The fibulae are missing. Among the preserved tarsal bones (Pl. 4C) is an astragalus with a rounded outline and an embayment of its proximal margin, which is also thickened by a small ridge. This concavity indicates that the perforating artery passed proximal to the tarsus as for other nothosaurs and *Simosaurus* (Rieppel 1994a). A subcircular bone, slightly smaller than the astragalus, is identified as the calcaneum (Pl. 4C). A third, very small discoidal bone close to the astragalus may represent a disarticulated fourth distal tarsal (Pl. 4C). The metatar-

sals are elongate with narrow shafts and expanded heads; one of the identified metatarsals is rather stubby and reaches half the length of the others and is identified as the first metatarsal. The pedal phalanges are short and broad, like those of the manus, the more distal ones being discoidal in shape. As in the manus, no phalangeal formula can be given for the pes.

Stomach contents. Several small bones and bony fragments are present as scattered elements between the ribs and vertebrae on the larger slab (Pl. 4D), in the area corresponding to the abdominal region and can thus be considered as stomach contents with some confidence. Fish scales and ribs are present along with tiny vertebrae, possible limb bones and some claw-like elements (very probably unguis phalanges), of some reptile. Poor preservation prevents any reliable identification of these elements.

Discussion

The osteological correlates, especially the morphology of the vertebrae and bones of the shoulder girdle, allow assignation of BES SC 1736 without doubt to the Eosauropterygia as diagnosed by Rieppel (1994a). Three eosauropterygian taxa are so far known from the Besano Formation: the pachypleurosaurid *Serpianosaurus mirigiolensis* (Rieppel, 1989), and the eosauropterygians *Lariosaurus* (*Silvestrosaurus*) *buzzi* (Tschanz, 1989) and *Paranotosaurus amsleri* (Peyer, 1939), considered by Rieppel & Wild (1996) as a junior synonym of *Notosaurus giganteus* Münster, 1834. The presence of platicoelous centra and of at least four sacral ribs support its assignment to the Eosauropterygia Tschanz,

Tab. 1 - Measurements (in mm) taken on the specimen.

Length of retroarticular process	20
Height of mid cervical rib	5.5
Length of disassociated cervical centra	15, 16, 17
Height of disassociated cervical neural arch	23
Maximum width of isolated cervical neural arch	24
Height of a disassociated dorsal neural arch and spine	34
Height of the neural spine of the same neural arch	15
Length of distal caudal centra	15, 14
Height of a distal caudal neural spine	12
Height of a distal caudal neural arch and spine	19
Length of the shaft of a dorsal rib	83
Length of the shaft of some disassociated sacral ribs	33, 31, 46
Length of dissociated caudal ribs	34.4, 32, 31, 25.5, 18, 14
Height of the coracoid	65
Pubis proximodistal (ventrodorsal) width	50
Ischium proximodistal (ventrodorsal) width	49.5, 48.5
Ilium height	21, 22
Humerus length	87
Humerus proximal width	24
Humerus distal width	28
Radius length	41.3
Radius proximal width	12
Ulna length	43.6
Ulna proximal width	20.5
Ulna distal width	16
Maximum diameter of dissociated intermedium	13.5
Length of preserved metacarpals	22, 20.5, 19.3, 13
Femur length	87, 86
Femur proximal width	20.7, 23
Femur minimum width	5, -
Femur distal width	20, 18
Tibia length	42
Tibia proximal width	13.5
Tibia distal width	14
Length of preserved metatarsals of ?left pes	26.6, 29, 25, 21.5, 12
Length of preserved metatarsals of ?right pes	27, 28, 24, 22, 13.5
Maximum diameters of the astragali	14, 15.3
Maximum diameters of the calcanei	11, 12.3

1989 as diagnosed by Rieppel (1994a). The morphology of the humerus of BES SC 1736 is like a scaled-up version of the humerus of *Lariosaurus* (*Silvestrosaurus*) *buzzi* (see Tschanz 1989: p. 167, fig. 7a-b) from the Grenzbitumenzone, rather than that of *Nothosaurus*. However, *Lariosaurus* (*Silvestrosaurus*) *buzzi*, apart for the much smaller absolute size, is different from BES SC 1736 for the presence of more developed and

sharper cranial processes of the cervical vertebrae, for the distally expanded ulna and the relatively wider and less inclined suspensorium (Fig. 8G; Tschanz 1989: p. 160-1, figs. 2-3; for other characters see Tschanz 1989: p. 164, fig. 5g, p. 167, fig. 7f). In particular, the presence of a distally expanded ulna is considered diagnostic for the genus *Lariosaurus* (Rieppel, 1998). Thus BES SC 1736 can not belong to *Lariosaurus* (*Silvestrosaurus*) *buzzi*.

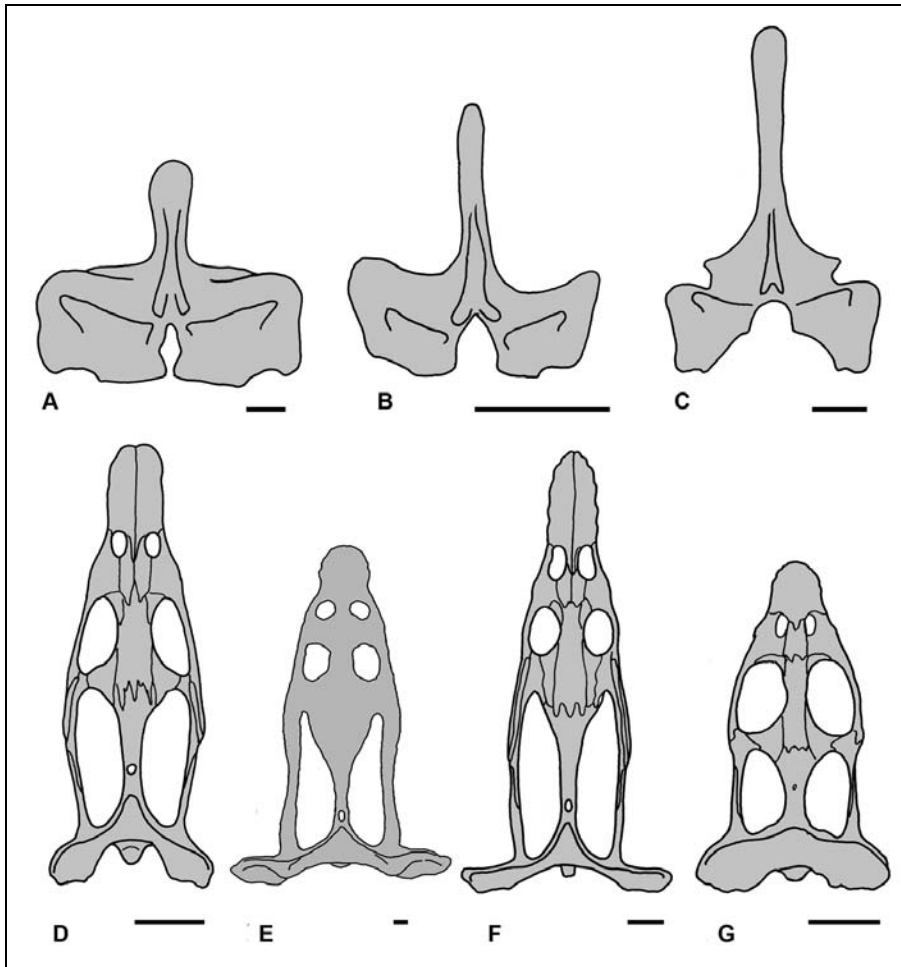


Fig. 8 - A-C: Comparisons among the dorsal neural arches and spines of A) *Nothosaurus giganteus/Paranothosaurus amsleri*; B) BES SC 1736; and C) *Nothosaurus mirabilis*. D-G: comparisons among the skulls of D) *Nothosaurus juvenilis*; E) *Nothosaurus giganteus/Paranothosaurus amsleri*; F) *Nothosaurus mirabilis* and G) *Silvestrosaurus buzzi*. A, C, modified from Rieppel & Wild (1996); D, F, modified from Rieppel (1994b); E, modified from Peyer (1939); G, modified from Tschanz (1989). Scale bars equal 20 mm.

Several characters support instead the attribution of BES SC 1736 to the genus *Nothosaurus*: transverse processes of the dorsal vertebrae extending along the entire height of the pedicels (Peyer 1939; Rieppel & Wild 1996); zygatronum divided by a vertical septum and zygosphenes bifurcated (Rieppel & Wild 1996); dorsal ribs not pachyostotic and distinctly expanded at their distal ends; presence of three sacral ribs with expanded distal ends (the fourth tapers distally); pubis notched at its ventral margin and with slit-like obturator foramen; ilium retaining a preacetabular process, femur with very shallow intertrochanteric fossa.

The assignment of BES SC 1736 to any known species of *Nothosaurus* is more difficult since most diagnostic characters at the species level concern the skull and very few relate to the postcranial skeleton. Apart from absolute size, the neural spines of BES SC 1736 are proportionally higher than in *Nothosaurus giganteus/Paranothosaurus amsleri* but lower than in *N. mirabilis* (Fig. 8A-C), being proportionally an intermediate between *N. giganteus* and *N. mirabilis*, suggesting that BES SC 1736 does not belong to these species. The lower jaw joint of BES SC 1736 is caudally displaced with respect to the occiput, a character which has been

considered diagnostic for *Nothosaurus juvenilis* Edinger, 1921 (Rieppel 1994b; Rieppel & Wild 1996). *N. juvenilis* is a small species of nothosaur from the Upper Muschelkalk of Germany (Rieppel 1994b) which is coeval with the Besano Formation. In the Germanic Basin *N. juvenilis* apparently shared the same environment with the large sized *N. giganteus* and the intermediate sized *N. mirabilis* (Rieppel & Wild 1996). Unfortunately the lack of most of the skull hinders further analysis, so attribution of BES SC 1736 to *N. juvenilis* should be considered tentative, and thus classified as *Nothosaurus* cf. *N. juvenilis*. *N. juvenilis* is so far known only by an isolated skull from the Middle Triassic of Germany (Rieppel 1994b), and its ontogenetic status remains controversial (Albers & Rieppel 2003): thus BES SC 1736, if correctly attributed to this species, may improve knowledge of the anatomy and development of this species.

The finding of BES SC 1736 is also of significance for palaeoecological reasons, because it testifies to the presence of sympatric species of *Nothosaurus* in the Besano Formation, which probably avoided competition by exploiting different niches. Rieppel (1994b) and Rieppel & Wild (1996), have already discussed the

coexistence of three *Nothosaurus* species of different absolute size (*N. juvenilis*, *N. mirabilis* and *N. giganteus*) in the Triassic Upper Muschelkalk of Germany; suggesting a scenario of niche partitioning. Closely related sympatric species, if using similar resources (as nothosauriforms were all aquatic predators), are potential competitors so, to coexist normally diverge on one of three niche axes (space, time or food: Pianka 1973, 1986). In the case of the nothosaurs of the Germanic Basin, according to Rieppel & Wild (1996) the most important niche dimension segregating the nothosaur species should have been food: the sympatric species, being of different size, avoided competition by presumably being characterized by different prey preferences. The discovery of BES SC 1736 testifies that a pattern of size differentiation and possibly trophic segregation may have also occurred for the nothosaurs of the Grenzbitumenzone, where a similar scenario has already been recognized for the predatory actinopterygian fish *Saurichthys* (Rieppel 1992). Identifiable stomach contents of *L. buzzii* (skull fragments of a juvenile cyamodontoid placodont, Tschanz 1989) suggest that *Lariosaurus* (*Silvestrosaurus*) *buzzii* fed on proportionally large, active prey rather than trapping smaller prey. In fact *L. buzzii* shares with nothosaurs a skull morphology and teeth suited for piercing and holding (Rieppel 2002) which support this suggestion. The size and typology of the stomach contents in BES SC 1736 are comparable with those of *L. buzzii*, despite the greater dimensions of this latter, testifying that at least a partial overlap in the range of prey dimensions occurred between *N. cf. juvenilis* and *L. buzzii* (the latter also being within the size range of potential prey for the former). Studies on living aquatic organisms (e.g. Scharf et al. 2000) have demonstrated that the range of prey sizes expands with increasing predator body size, resulting in an asymmetric relationships between prey size and predator size (as large predators continue to include small prey in their diets). It is feasible that coexistence in the same time and area of these two taxa with a partially overlapping range of prey sizes was made possible by habitat and/or microgeographical partitioning rather than simply food-size partitioning.

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PLATE 1

BES SC 1736, *Nothosaurus* cf. *N. juvenilis*. Skull and vertebral elements.

A) Retroarticular processes of the lower jaw, portion of the quadrate ramus of the pterygoid, of the quadrate in anatomical connection with the lower jaw; several disarticulated cervical vertebrae are visible between the two retroarticular processes; B) cervical neural arch, ventral view; C) dorsal neural arch, dorsal view; D) dorsal neural arch and spine, cranial view; E) caudal neural arch and spine, lateral view. Scale bars equal 1 cm.

PLATE 2

BES SC 1736, *Nothosaurus* cf. *N. juvenilis*; ribs.

A) Dorsal ribs; B-C) cervical ribs; D) caudal ribs; E) median element of a gastralium; F-H) sacral ribs. A, D-H, scale bars equal 10 mm, B, C scale bars equal 0.5 cm.

PLATE 3

BES SC 1736, *Nothosaurus* cf. *N. juvenilis*. Elements of girdles and limbs.

A) Clavicle; B) coracoid; C) humerus and ulna; D) femur; E) ilium; F) pubis and ilium turned upside-down with respect to the pubis; G) ischium. Scale bars equal 10 mm.

PLATE 4

BES SC 1736, *Nothosaurus* cf. *N. juvenilis*.

A) Radius; B) metacarpals (mc) and associated phalanges (ph); C) astragalus (as), calcaneum (ca) metatarsals (mt) and a dissociated caudal rib (cr); D) some of the unidentified stomach contents. Scale bars equal to 1 cm.

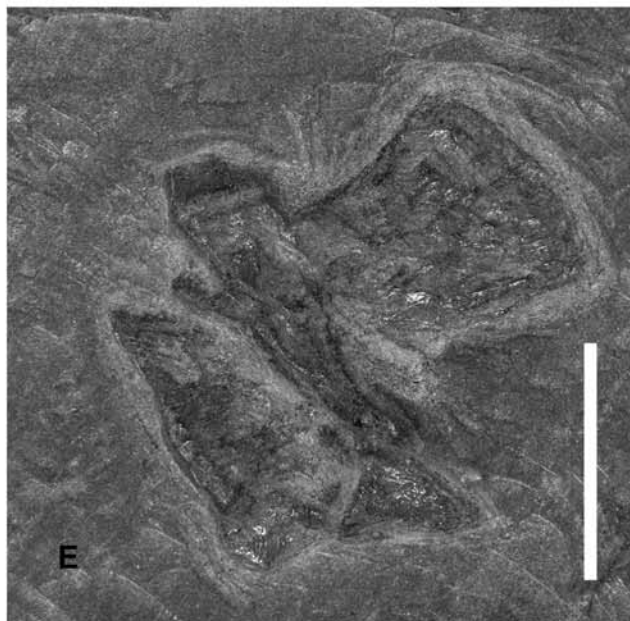
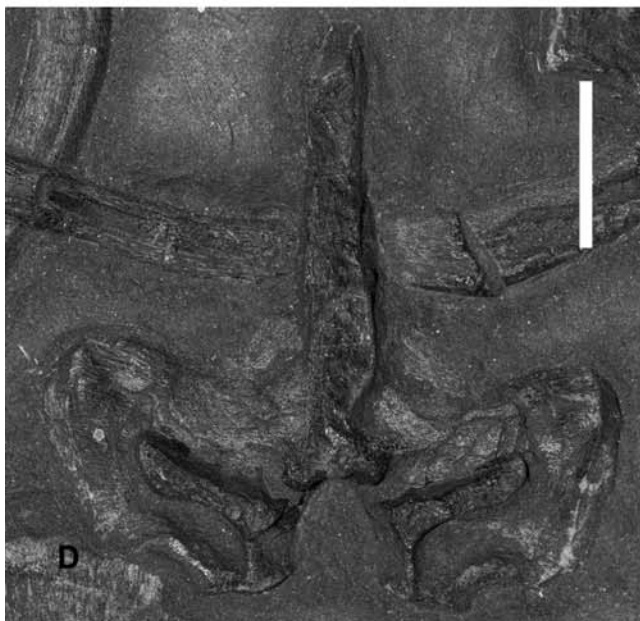
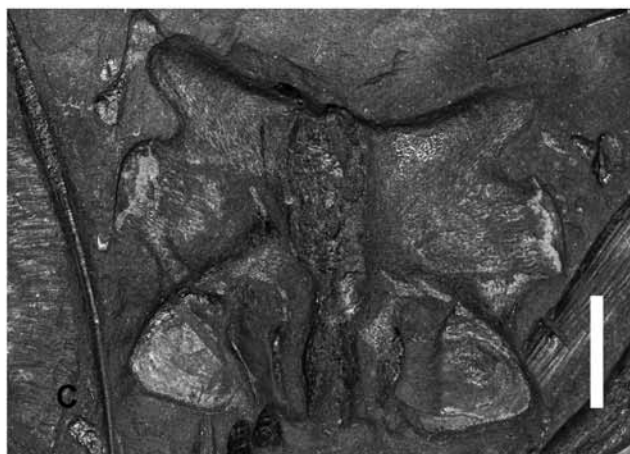
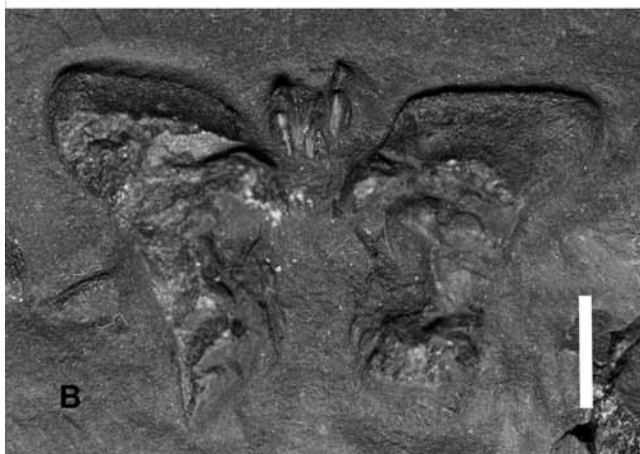
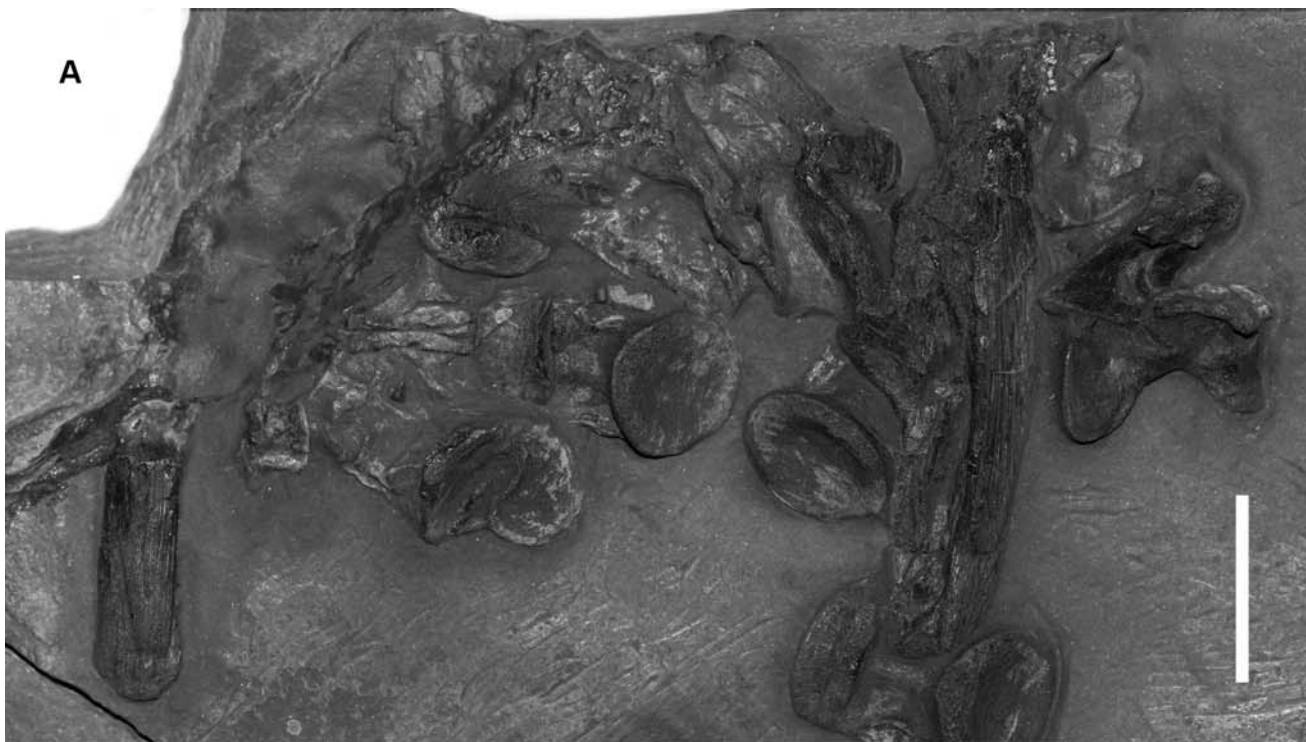


PLATE 1

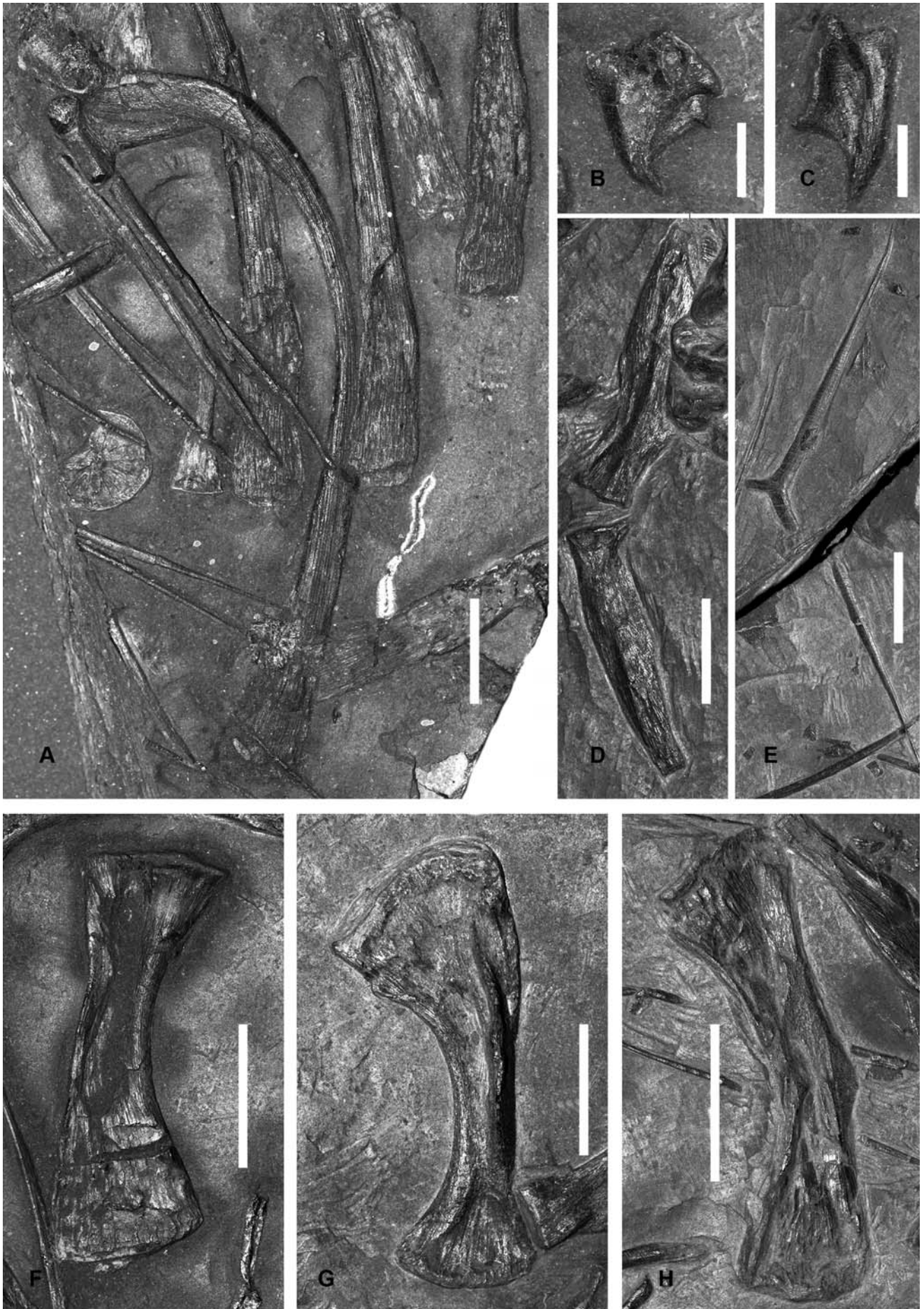


PLATE 2

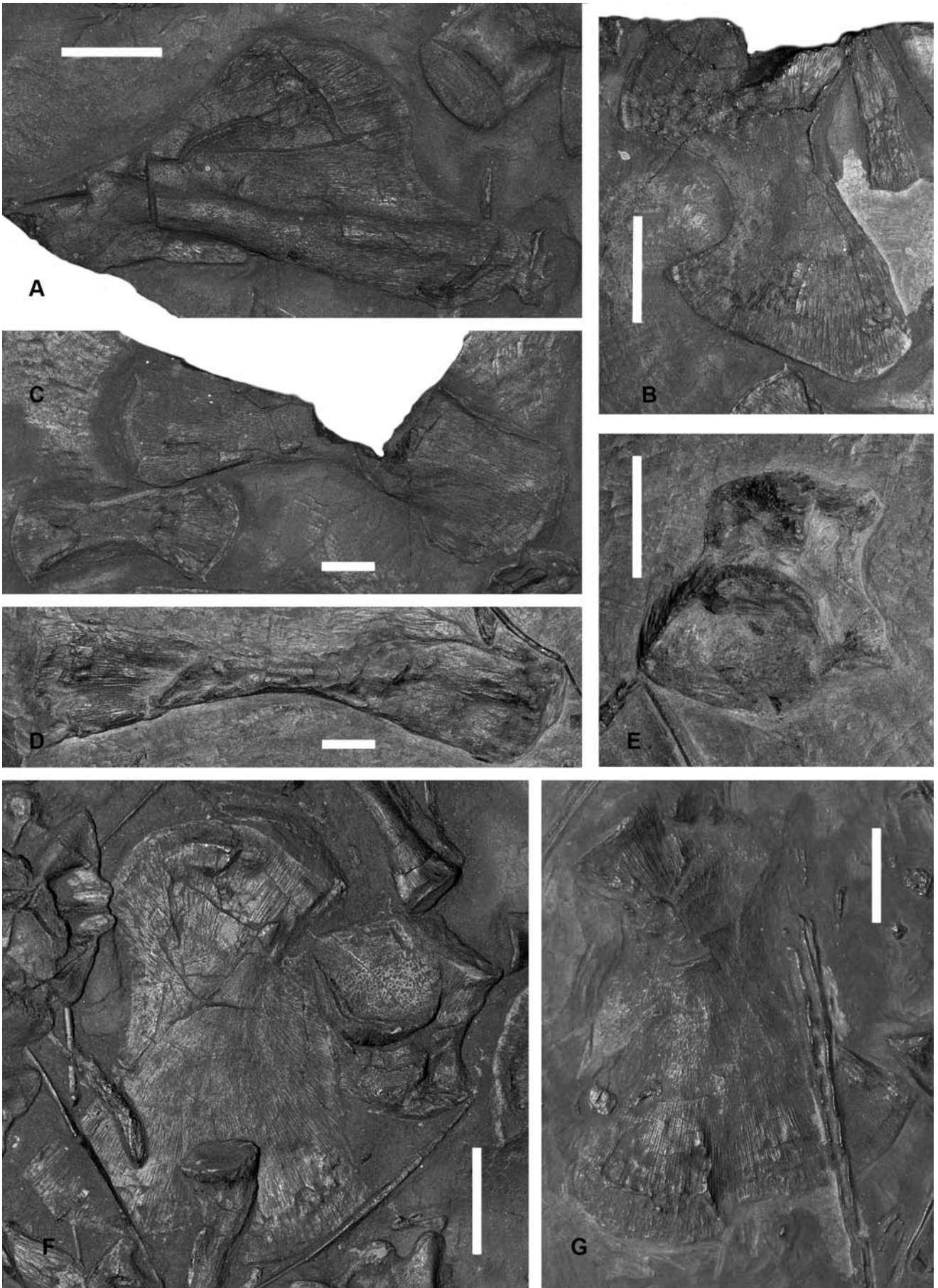


PLATE 3

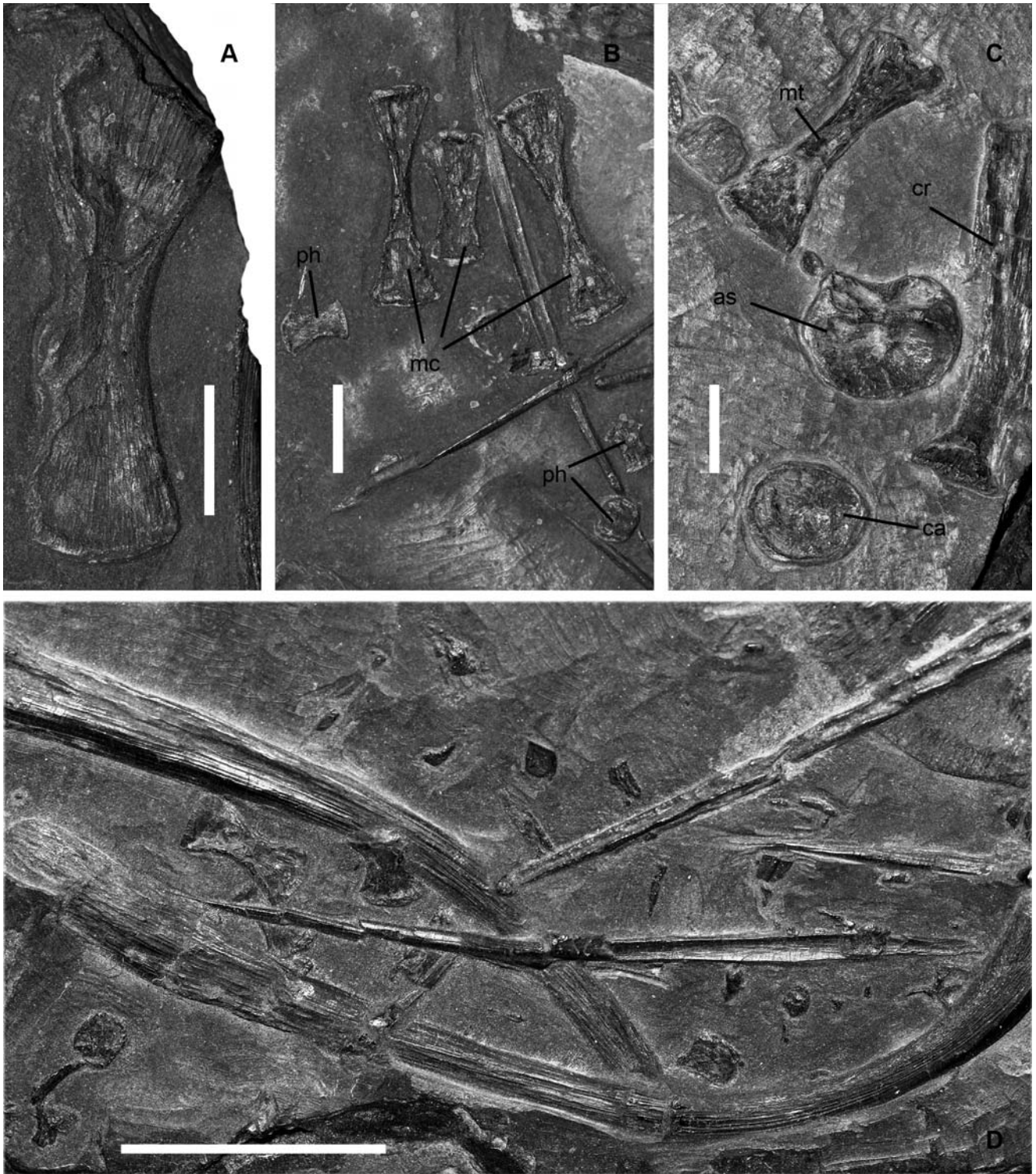


PLATE 4

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