

# An *in utero* foetus of the Middle Triassic ichthyosaur *Besanosaurus leptorhynchus* from Monte San Giorgio, Italy

Feiko Miedema<sup>1,2</sup>, Gabriele Bindellini<sup>3,4,5</sup>, Andrzej S. Wolniewicz<sup>6,7</sup>, Erin E. Maxwell<sup>2</sup>, Cristiano Dal Sasso<sup>3</sup>

<sup>1</sup> Universitetet i Oslo - Naturhistoriskmuseum, Kabelgaten 40, 0581 Oslo, Norway

<sup>2</sup> Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany

<sup>3</sup> Sezione di Paleontologia dei Vertebrati, Museo di Storia Naturale di Milano, Corso Venezia 55, 20121 Milan, Italy

<sup>4</sup> Dipartimento di Scienze della Terra, Sapienza Università di Roma, P.le Aldo Moro 5, 00085, Rome, Italy

<sup>5</sup> Dipartimento di Scienze della Terra, Università degli Studi di Milano, Via Luigi Mangiagalli 34, 20133 Milan, Italy

<sup>6</sup> Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland

<sup>7</sup> Department of Earth Sciences, University of Cambridge, Downing Street, CB2 3EQ, Cambridge, UK

<https://zoobank.org/411E1D4C-4E07-497E-835E-E55DF2978437>

Corresponding author: Feiko Miedema ([feiko.miedema@gmail.com](mailto:feiko.miedema@gmail.com))

Academic editor: Florian Witzmann ♦ Received 20 December 2025 ♦ Accepted 30 April 2026 ♦ Published 1 June 2026

## Abstract

*Besanosaurus leptorhynchus* is an early-diverging merriamosaurian ichthyosaur from the Middle Triassic Besano Formation of Alpine Europe. When the holotype specimen was first described, potential foetal material within the specimen was identified via X-ray imaging. Now, following further preparation, we describe this material in detail. The foetal remains consist of a single, slightly disarticulated individual located in the area corresponding to the right uterine cornu in the anterior trunk region. Much of the cranium, postcranial axial skeleton and part of the appendicular skeleton are preserved. The foetus is oriented in a manner suggesting tail-first birth, a trait common in more derived ichthyosaurs. Its developmental stage corresponds to the latest prenatal stage (stage 4) established for the parvipelvian ichthyosaur *Stenopterygius*. Several cranial elements demonstrate features influenced by ontogeny, such as the shape of the paracoronoid process of the surangular and the curvature of the jugal. A peculiar feature of the foetus is the presence of palatine teeth, previously reported among ichthyosauromorphs only in early-diverging ichthyosauriforms and the poorly known, small-bodied ichthyosaur *Wimanius*, which co-occurs with *Besanosaurus* at Monte San Giorgio. Our observations on the foetus confirm the original interpretation of this material as foetal rather than stomach contents, as has been more recently proposed. The new data allow us to discuss observations on the *in utero* carrying position of ichthyosaur fetuses more broadly.

## Key Words

*Besanosaurus*, foetus, Ichthyosauria, prenatal development, uterine morphology

## Introduction

Ichthyosaurs were a group of marine reptiles that lived throughout most of the Mesozoic (ca. 251–94 mya) (McGowan and Motani 2003; Motani 2005; Fischer et al. 2016). Over the course of their evolutionary history, the clade evolved several adaptations to the marine environment, including hydrofoil-like flippers, a dorsal fin, a

caudal fluke and insulating blubber (Lindgren et al. 2018; Renesto et al. 2020; Motani and Vermeij 2021; Gutarra et al. 2023). Due to these morphological traits, ichthyosaurs are often considered superficially convergent with cetaceans. However, they appear to differ from cetaceans in terms of feeding strategies (Motani et al. 2013; Delsett et al. 2023). A feature shared by both groups is a viviparous reproductive strategy, which may have evolved

either as an adaptation to marine life or as a trait acquired in terrestrial ancestors that proved advantageous during the early stages of marine invasion (the latter being the case in cetaceans) (Gingerich et al. 2009; Motani et al. 2014). Viviparity is evidenced by the discovery of numerous gravid ichthyosaur females from several taxa spanning ichthyosaur phylogeny (Miedema et al. 2023b). Furthermore, special attention has recently been given to the birthing strategies of early-diverging Triassic ichthyosauriforms (Motani et al. 2014; Klein et al. 2020; Miedema et al. 2023b).

*Besanosaurus leptorhynchus* is an early-diverging merriamosaurian ichthyosaur from the Middle Triassic of the southern Alpine region (Dal Sasso and Pinna 1996; Bindellini et al. 2021, 2024). All known specimens originate from the Besano Formation, which crops out on both sides of the Swiss-Italian border (Röhl et al. 2001; Bindellini et al. 2021). Currently, *B. leptorhynchus* is considered the only large-bodied shastasaurid (or shastasaur-grade) ichthyosaur from the Besano Formation (Bindellini et al. 2021). Shastasaurids (sometimes informally called “shastasaurids”) are early-diverging and often large-bodied merriamosaurian ichthyosaurs that were present throughout almost the entire Triassic (late Olenekian–latest Rhaetian) (Fischer et al. 2014; Lomax et al. 2024; Roberts et al. 2025). A recent, widely used definition of Shastasauridae is node based: the most recent common ancestor of *Besanosaurus leptorhynchus* and *Shastasaurus pacificus* and all of its descendants (Ji et al. 2015). However, there are conflicting hypotheses on whether “shastasaurids” actually form a clade e.g. (Ji et al. 2015), or if they represent a grade at the base of Euichthyosaria (Bindellini et al. 2021). Foetuses of “shastasaurids” in particular remain poorly known. Recently, foetal material was confirmed within specimens of *Shonisaurus popularis* from the Luning Formation (Carnian, Late Triassic) of Nevada, USA (Kelley et al. 2022). The discovery provided the first insight into the potential gregarious behaviour of female ichthyosaurs close to parturition, a phenomenon also potentially observed in an Early Cretaceous platypterygiine (Kelley et al. 2022; Pardo-Pérez et al. 2025). However, because the *Shonisaurus* foetal material has not yet been described in detail, developmental data for “shastasaurids” are still lacking. In the original description of the holotype of *Besanosaurus leptorhynchus*, the authors noted clusters of foetal (referred to as embryonic) elements on the basis of radiographs (Dal Sasso and Pinna 1996; Miedema et al. 2023b; Bindellini et al. 2024). However, since the original description of *B. leptorhynchus* was published, further preparation of the holotype specimen has fully exposed the foetal elements.

Here, we provide a detailed description of the foetal material preserved inside the body cavity of the holotype of *B. leptorhynchus* and qualitatively compare its morphology with that of the maternal specimen. Additionally, we compare the foetal remains with those of other known ichthyosaur prenatal developmental stages

and briefly discuss the inferred position of the ichthyosaurian uterine tract. The foetus provides further insight into ichthyosaur development, representing an evolutionary stage from which foetuses remain poorly known.

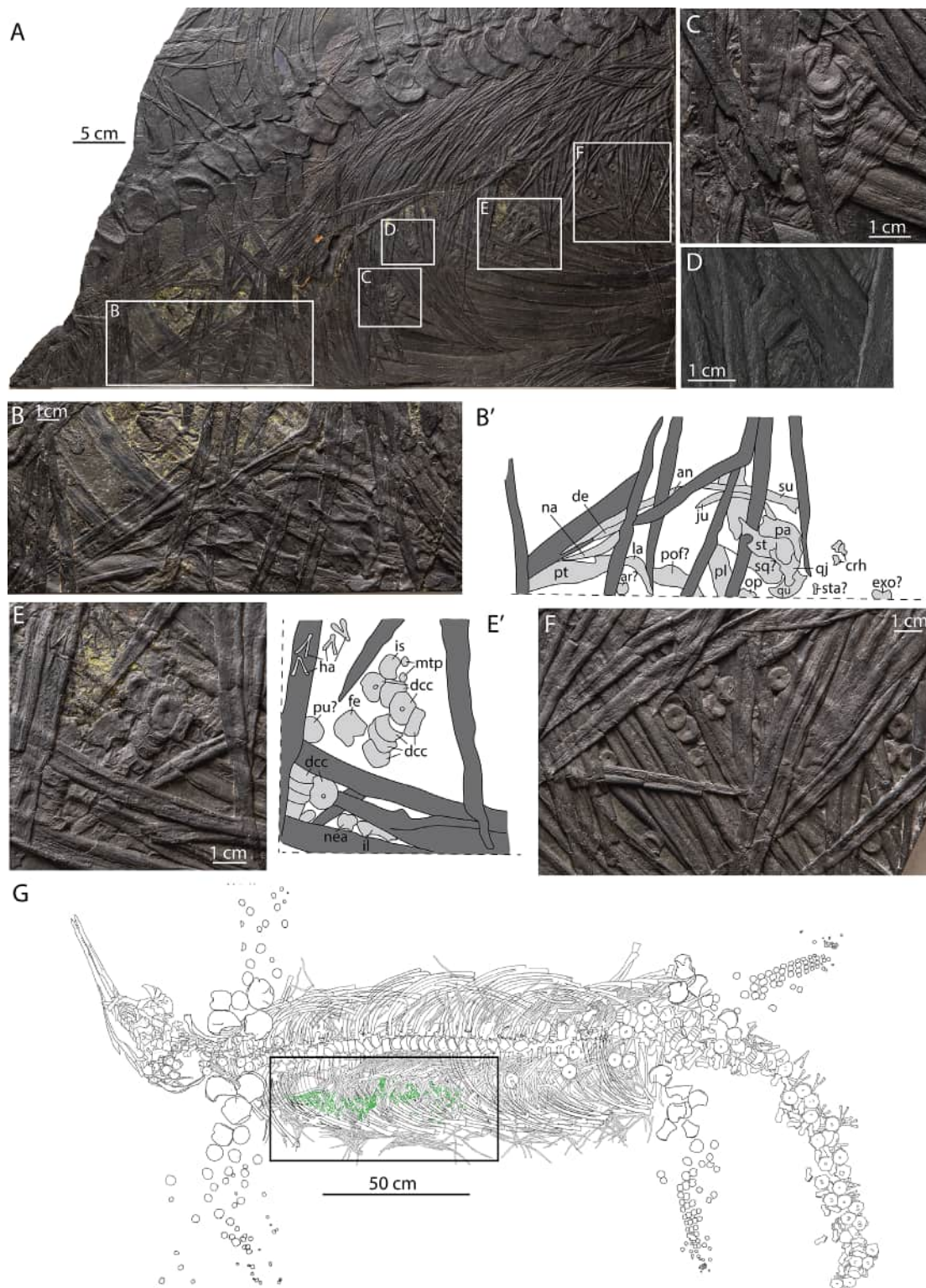
## Geological context

The Besano Formation (“Grenzbitumenzone”) crops out on Monte San Giorgio (Lombardy, Italy, and Canton Ticino, Switzerland; UNESCO WHL document 1090bis); its palaeobiodiversity is among the highest recorded for Middle Triassic marine reptile faunas (e.g., Benton et al. 2013; Furrer et al. 2024; Klug et al. 2024a). The Besano Formation is up to 16 m thick and consists of an alternation of black shales and laminated, organic-rich dolomitic layers, dated to the Anisian/Ladinian boundary (Brack et al. 2005; Wotzlav et al. 2018), deposited in a 30–130 m deep and approximately 20 km wide basin (Bernasconi 1991, 1994; Bernasconi and Riva 1993). The middle portion of the Besano Formation was deposited in a deep intraplateau basin, from which a large number of ichthyosaurian and other pelagic vertebrate remains have been recovered (Rieppel 2019). The holotype of *Besanosaurus leptorhynchus* (BES SC 999) was collected from the equivalent of layer 107 of the Besano Formation type section at the Sasso Caldo site (Dal Sasso and Pinna 1996; Bindellini et al. 2019, 2021, 2024; Bindellini and Dal Sasso 2022).

## Materials and methods

We qualitatively studied the foetal material preserved in the body cavity of the holotype specimen of *Besanosaurus leptorhynchus* (BES SC 999, coded as 20.S288-2.2 in the Italian State Heritage Database). The holotype was collected in 1993 at the Sasso Caldo locality in northern Italy (Dal Sasso and Pinna 1996). The specimen was separated into 34 slabs collected by members and volunteers of the Museo di Storia Naturale di Milano and subsequently prepared. The foetal material associated with BES SC 999 is mostly preserved inside the maternal body cavity on slab no. 30, with some material also present on slab no. 31 (see Dal Sasso and Pinna 1996). All of the cranial material is preserved in association far anteriorly, close to the maternal pectoral girdle (Fig. 1A, B, G). The foetal pelvic girdle, posterior limb and haemal arches are associated and located more posteriorly (Fig. 1A, E, G). Preflexural/precaudal vertebrae are scattered between the maternal ribs and gastralia (Fig. 1A, C–G). To assist in our determination of foetal stage, we used the method outlined in Miedema and Maxwell 2026. We measured centrum width and height and notochordal canal width and height in articular view in seven vertebrae (three dorsal, three dorsal or anterior caudal and one possible posterior caudal). Measurements are provided in Suppl. material 1.

For comparison of the *in utero* position of ichthyosaur foetuses, we studied several pregnant ichthyosaur females



**Figure 1.** Overview and close-ups of selected areas of the foetal material preserved within the body cavity of the holotype of *Besanosaurus leptorhynchus* (BES SC 999), preserved on slab no. 30. Areas shown as close-ups correspond to areas marked in the overview photograph with the same letters, with their corresponding interpretative drawings denoted by an apostrophe. Dark gray denotes maternal ribs or gastralia, light gray indicates foetal bones: **A.** Overview of slab no. 30; **B.** Cranium remains; **C.** Cervical or anterior dorsal vertebrae; **D.** Dorsal vertebrae; **E.** Posterior dorsal or anterior caudal vertebrae, caudal ribs and podials; **F.** Sacral region; **G.** Position of the foetal remains within the entire trunk of BES SC 999. Abbreviations: an, angular; ar, articular; crh, cervical rib head; dcc, dorsal or caudal centrum; de, dentary; exo, exoccipital; fe, femur; ha, haemal arch; il, ilium; is, ischium; ju, jugal; la, lacrimal; mtp, (meta) tarsal or phalanx; na, nasal; nea, neural arch; op, opisthotic; pa, parietal; pl, palatine; pof, postfrontal; pt, pterygoid; pu, pubis; qj, quadratojugal; qu, quadrate; sq, squamosal; st, supratemporal; sta, stapes; su, surangular.

firsthand, including a large and representative sample of the Lower Jurassic parvipelvian species *Stenopterygius quadriscissus* housed in several museums (MHH, SMF, SMNS, GPIT, NHMUK) (Suppl. material 1). We also conducted a survey of the literature on all known pregnant female ichthyosaurs. We recorded litter size, foetal placement within the maternal body cavity, degree of disarticulation, foetal developmental stage and maternal taphonomic preservation (dorsal, lateral, ventral side up).

## Institutional abbreviations

**GPIT**, Palaeontological Collection of Tübingen University, Tübingen, Germany; **MHH**, Urweltmuseum Hauff, Holzmaden, Germany; **MSNM**, Museo di Storia Naturale di Milano, Milan, Italy (with BES SC as the acronym for Besano Sasso Caldo); **NHMUK**, Natural History Museum, London, United Kingdom; **PIMUZ**, University of Zürich, Paleontological Collections, Zürich, Switzerland; **SMF**, Senckenberg Museum Frankfurt, Frankfurt, Germany; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

## Description of the foetal remains preserved in BES SC 999

### Dermatocranium

#### Lacrimal

In the area containing the foetal nasal, articular and pterygoid, a left lacrimal is exposed in medial view (Fig. 1B). Its dorsal margin is covered by a maternal gastral element. The lacrimal is well ossified and its jugal facet is already clearly defined (Fig. 2A). The medial depression is divided centrally by a trough. Ossification lines indicate that the ossification centre is located within the medial depression (Fig. 2A).

#### Pterygoid

The right pterygoid is partially exposed in dorsal view and is the anteriormost preserved foetal cranial element (Fig. 1A, B). The anterior end of the palatal ramus and the posterolateral end of the quadrate ramus are partially covered by other elements (Fig. 2B). The pterygoid is well ossified. The palatal ramus bears an anteroposteriorly oriented furrow dorsomedially, which possibly marks the location of the fusion of two palatal prongs present in early development, as seen in *Stenopterygius* prenatal stage 3 (Miedema and Maxwell 2022). Medially, the pterygoid displays a thickened area, which may represent the parasphenoid facet. The quadrate ramus is quadrangular in outline, though it is unclear if the posterolaterally directed flange is fully developed (Fig. 2B).

#### Palatine

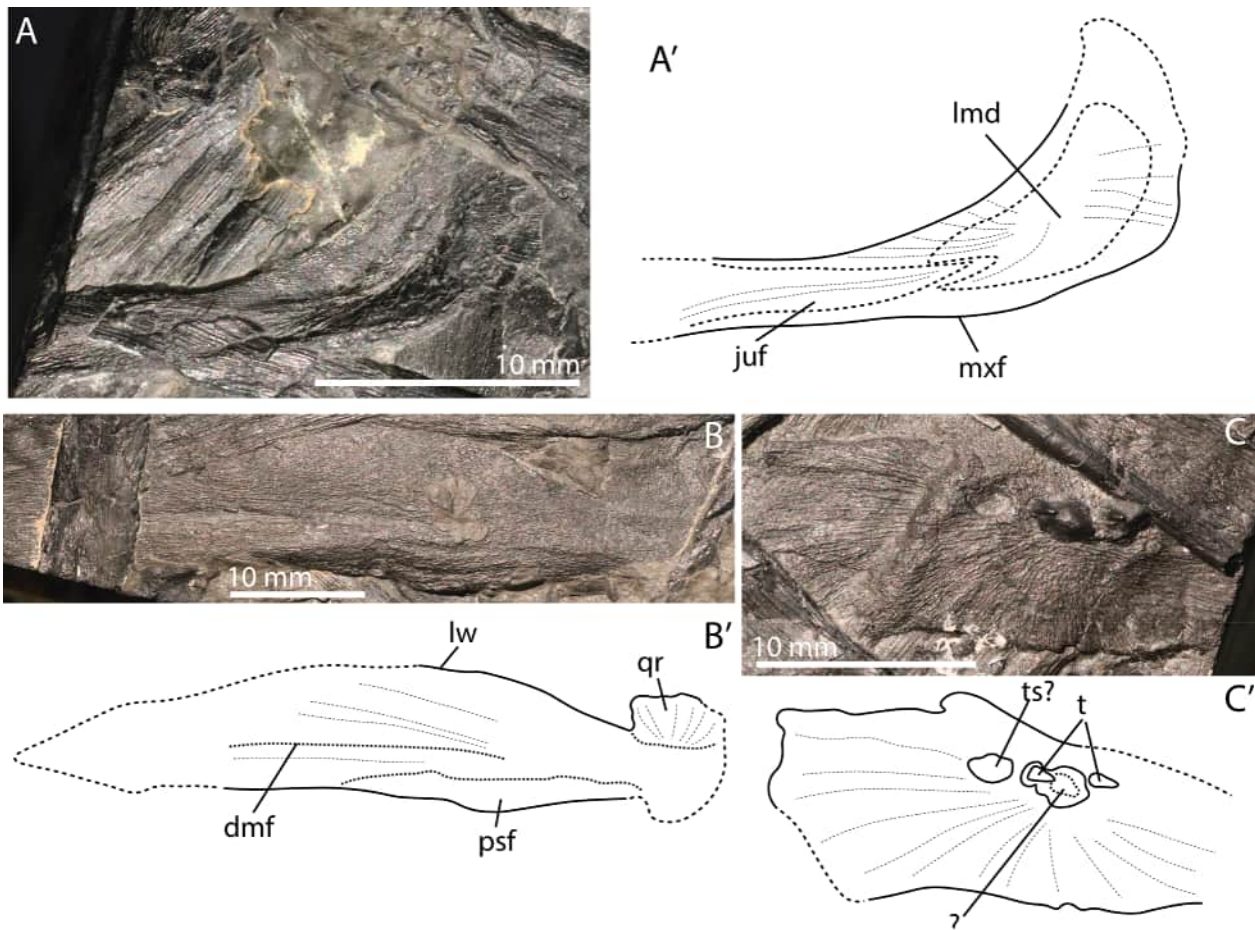
We identify a left palatine exposed in ventral view, located well posterior to the pterygoid and more closely associated with the elements of the cheek region (Fig. 1B). The element is well ossified (Fig. 2C). Striations indicate an ossification centre located just lateral to the tooth row. The element bears a tooth row with two teeth situated medially on the ventral surface (Fig. 2C). Between the two teeth there is a bulge and posterior to the teeth there is a gap. This gap does not seem to be diagenetic and may represent an empty alveolus. Alternatively, it may reflect incomplete ossification at this stage of development. The bulge is similar in size to the gap. We consider it unlikely that this element represents a rostral or mandibular dentigerous bone. If interpreted as being exposed in occlusal view, its mediolateral width would greatly exceed that expected for such elements, even when accounting for taphonomic flattening or distortion. Likewise, there is no indication of the presence of an alveolar groove or distinct sockets, apart from the gap between the two teeth. Moreover, the tooth row is not positioned along the midline of the element, which would be expected for the typical dentigerous elements in ichthyosaurs.

#### Nasal

A clearly visible right nasal bone is situated between the foetal angular and pterygoid anteriorly in the maternal body cavity (Fig. 1B). The nasal is preserved in direct medial view (Fig. 3A). The nasal is slightly sigmoidal in outline, thickened in the middle tapering markedly both anteriorly and posteriorly. Posterodorsally, there is an area demarcated by a ridge, likely representing the developing prefrontal facet. Ventrally, there is a small indentation which would also be visible laterally (Fig. 3A). This represents the dorsal border of the external naris, as seen postnatally (Bindellini et al. 2021). The nasal displays a distinct medial depression posterior to the external naris, likely corresponding to the internal nasal capsule (Miedema and Maxwell 2022) (Fig. 3A).

#### Jugal

A jugal is preserved between the foetal parietal and surangular (Fig. 1B). Its central portion is covered by both foetal and maternal elements, but the overlying elements are deformed, exposing the outline of the bone (Fig. 3B). The jugal is preserved in lateral view. It is J-shaped, with the dorsal ramus gradually transitioning into the horizontal ramus. The dorsal ramus projects posterodorsally and already displays a distinct postorbital/quadratojugal facet. The horizontal ramus exhibits a distinct facet for the maxilla, indicated by the heavily striated texture. The horizontal ramus does not appear to taper anteriorly, although the tip of the jugal may be hidden underneath other bones or slightly broken (Fig. 3B).



**Figure 2.** Dermatocranial elements of the foetus preserved inside the holotype of *Besanosaurus leptorhynchus* (BES SC 999). Interpretative drawings of specific elements are denoted by an apostrophe following their corresponding letter. **A.** Lacrimal (left, medial view); **B.** Pterygoid (right, dorsal view); **C.** Palatine (right, ventral view). Abbreviations: dmf, dorsomedial furrow; juf, jugal facet; lmd, lacrimal medial depression; lw, lateral wing; mxf, maxilla flange; psf, parasphenoid facet; qr, quadrate ramus; t, tooth; ts, tooth socket.

### Parietal

A foetal right parietal is exposed in ventral view and lies dorsal to the supratemporal (Fig. 1B). The parietal is generally well ossified. The occipital flange is present but is less well ossified than the rest of the parietal (Fig. 4A). A clear central depression is present and corresponds to the dorsal part of the optic lobe. The parietal foramen is posteriorly demarcated by a medially directed process and anteriorly by the medially curving edge of the medial side of the parietal, resulting in a concave lateral margin. The supratemporal ramus is relatively long and bears a surface defined by a ridge, which may represent either the supratemporal facet or a muscle attachment site (Fig. 4A). Striations indicate an ossification centre located directly posterolateral to the depression for the optic lobe.

### Squamosal

The right squamosal is located just anterior to the right quadratojugal and ventral to the right supratemporal, and is almost in articulation with those elements. It is trapezoidal in outline, being wider posteriorly. The centre of

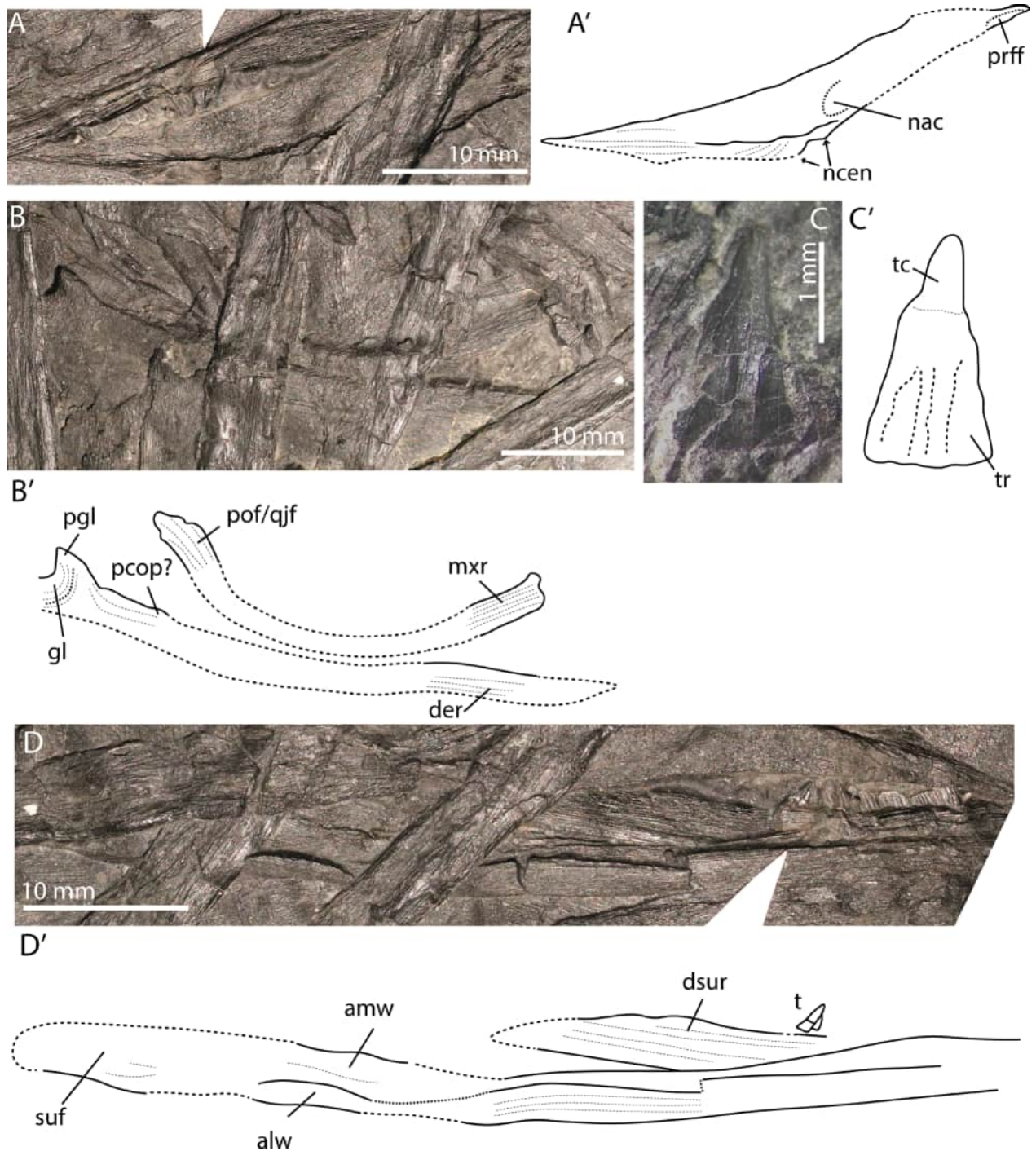
ossification is located anteriorly, with ossification lines radiating mainly posteriorly (Fig. 4B).

### Supratemporal

A right supratemporal can be observed between the foetal quadratojugal and parietal (Fig. 1A). The supratemporal is well ossified. Striations indicate an ossification centre located centrally on the lateral ramus (Fig. 4D). The supratemporal is strongly mediolaterally compressed. The medial (parietal) ramus bears a quadrate facet, which is partially preserved. It also bears a small depression posterodorsally, where the opisthotic would have contacted the supratemporal. The lateral ramus possesses a well-demarcated facet for the postorbital.

### Postfrontal

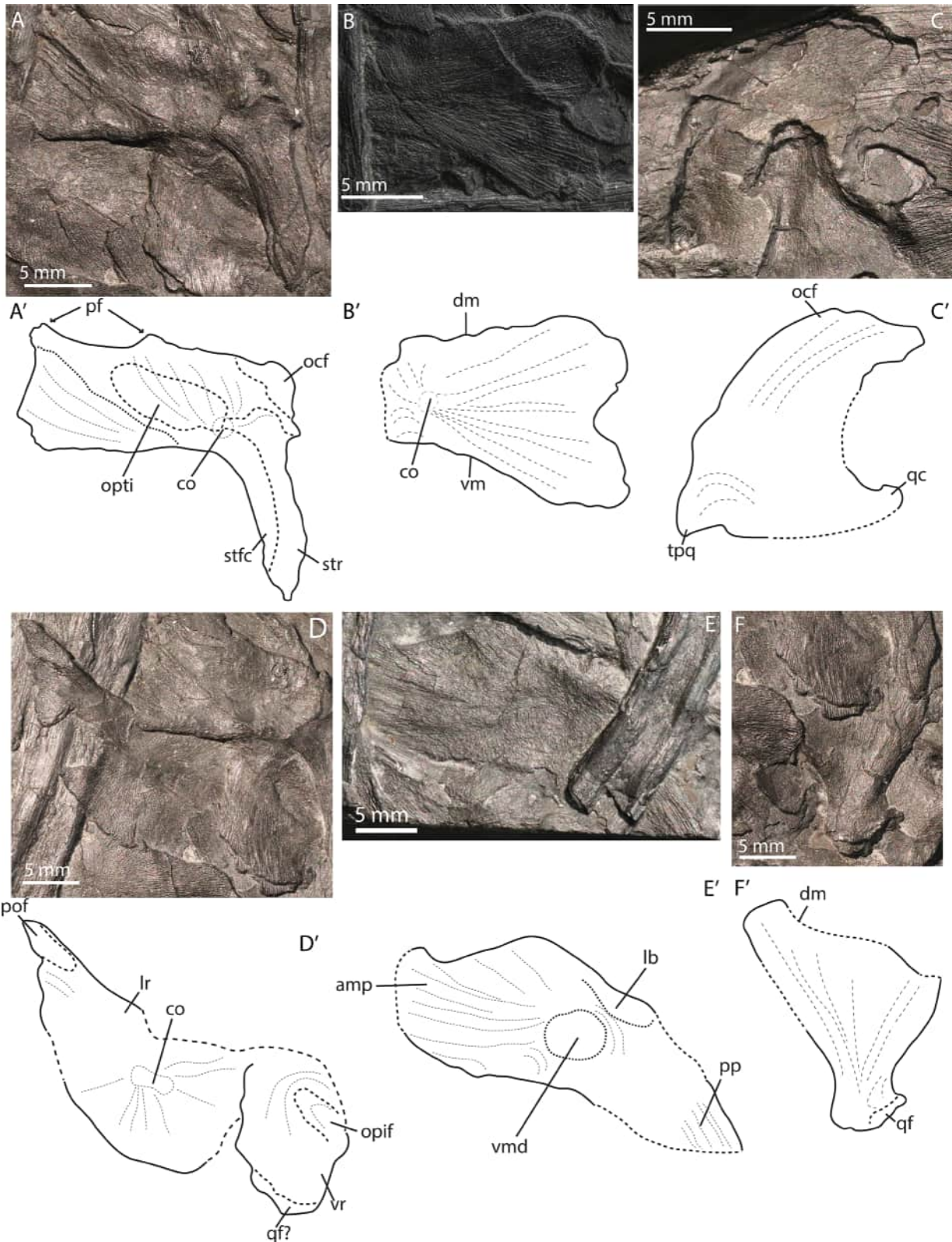
We tentatively identify a left postfrontal exposed in ventral view. It is situated between two maternal ribs, posterior to the foetal lacrimal (Fig. 1B). The tentative postfrontal is relatively broad and stout (Fig. 4E). It is slightly curved and consists of a broad anteromedial



**Figure 3.** Dermatocranial elements from the cranium and lower jaw of the foetus preserved inside the holotype of *Besanosaurus leptorhynchus* (BES SC 999). **A.** Nasal (left, medial view); **B.** Surangular (left, medial view) and jugal (right, lateral view); **C.** Tooth (labial? view); **D.** Angular (right, lateral view) and dentary (right, lateral view) (note white paper triangle visible on the surface of the specimen). Interpretative drawings are denoted by an apostrophe followed by their corresponding letter. Abbreviations: alw, angular lateral wall; amw, angular medial wall; der, dentary ramus; dsur, dentary surangular ramus; gl, glenoid; mxr, maxilla ramus; nac, nasal capsule; ncen, nasal contribution to the external naris; prff, prefrontal facet; pcop, paracoronoid process; pgl, preglenoid process; pof/qjf, postorbital/quadratojugal facet; suf, surangular facet; t, tooth; tc, tooth crown; tr, tooth root.

process and a more tapering posterior process (Fig. 4E). It exhibits a large ventromedial depression, which is also its ossification centre, as indicated by the outwardly radiating ossification lines. Lateral to this depression, a lateroventrally projecting boss is visible. We stress

that our identification of this element as a postfrontal is tentative. One aspect that could suggest a different identification (frontal?) is its relatively large size in comparison to other dermatocranial elements.



**Figure 4.** Dermatocranial elements from the cheek and skull roof regions and the quadrate of the foetus preserved inside the holotype of *Besanosaurus leptorhynchus* (BES SC 999). **A.** Parietal (right, ventral view); **B.** Squamosal (right, medial view); **C.** Quadrate (left, posteromedial view); **D.** Supratemporal (right, medial view); **E.** Postfrontal (left, ventral view); **F.** Quadratojugal (right, medial view). Interpretative drawings are denoted by an apostrophe followed by their corresponding letter. Abbreviations: amp, anteromedial process; co, ossification centre; dm, dorsal margin; lb, lateral boss; lr, lateral ramus; ocf, occipital flange; opif, opisthotic facet; opti, depression for optic lobe; pf, parietal foramen; pof, postorbital facet; pp, postfrontal posterior process; qc, quadrate condyle; qf, quadrate facet; stfc, supratemporal facet; str, supratemporal ramus; tpq, triangular process of quadrate; vm, ventral margin; vmd, ventromedial depression; vr, ventral ramus.

## Quadratojugal

A right quadratojugal is preserved in medial view between the quadrate, squamosal and supratemporal (all three elements are preserved almost in articulation) (Fig. 1B). The quadratojugal is well ossified and has well-defined medial and lateral surface outlines (Fig. 4F). The dorsal flange is partially covered by the medial process of the overlying supratemporal, whereas the dorsal portion of the quadratojugal covers the ventrolateral margin of the supratemporal medially (Figs 1B, 4F). The quadrate process, which bears the quadrate facet, is slightly offset posteriorly (Fig. 4F). The quadratojugal is widest dorsally and is anteroposteriorly constricted near the base, just dorsal to the quadrate process. Surface striations indicate an ossification centre near the base of the quadrate process (Fig. 4F).

## Lower jaw

Preserved foetal lower jaw elements include the surangular, angular and dentary. They lie in close association anterior to most other cranial elements on block 30 (Fig. 1A, B). All dermal lower jaw elements are well ossified (Fig. 3B, D). Surface striations indicate growth in a generally anteroposterior direction, but the ossification centres of the elements are indiscernible. The dentary preserves only the posterior surangular ramus and two disarticulated teeth (Fig. 3B–D). The angular displays well-formed lateral and medial walls, which enclose a very elongated surangular facet (Fig. 3D). The surangular is largely covered by other elements, but the glenoid area is exposed in medial view (Fig. 3B). The preglenoid process is already prominently developed, whereas the paracoronoid process is still small or absent at this stage. The glenoid area is characterized by a more roughened surface, indicating that it is less ossified than the rest of the element. Concentric striations in the glenoid region indicate a different ossification direction or centre compared to the rest of the element (Fig. 3B).

## Splanchnocranium

### Quadrate

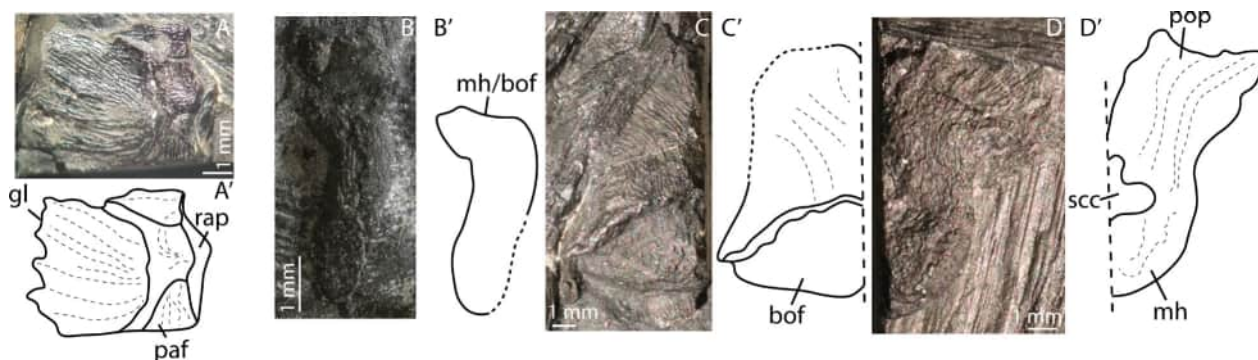
A left quadrate is preserved in posteromedial view, partially overlapped by the foetal quadratojugal (Fig. 1B). The quadrate displays a similar degree of ossification to the dermatocranial elements in the cheek (Fig. 4A–F). The occipital lamella curves posterolaterally (Fig. 4C). The anteroventral triangular process is already well developed and slightly offset from the rest of the pterygoid lamella. Surface striations indicate dorsoventral growth across most of the pterygoid lamella, except around the triangular process, where growth was more concentric (Fig. 4C). The quadrate condyle seems to be developed at this stage, although it is mostly hidden from view. No stapedial facet is visible due to the overlapping quadratojugal.

### Articular

An element located near the lacrimal and pterygoid (Fig. 1B) has a roughened surface texture, suggesting it is likely an endochondral element, which we tentatively identify as a right articular (Fig. 5A). The prearticular facet and a small retroarticular process appear well developed. In contrast, the anterior margin of the glenoid facet exhibits several indentations, indicating that this portion is still developing and less ossified than the posterior end (Fig. 5A).

### Stapes

We tentatively identify a stapes in close association with the quadrate and quadratojugal (Fig. 1B). It is relatively well ossified, although the rugose and striated surface texture indicates the presence of more cancellous bone, suggesting that the stapes is less ossified than the dermatocranial elements or the quadrate (Fig. 5B). The stapes is very slender, thickened only at its medial head, which is deflected ventrally and bears a basioccipital facet (Fig. 5B).



**Figure 5.** Chondrocranial and splanchnocranial elements of the foetus of *Besanosaurus leptorhynchus* (BES SC 999). **A.** Articular (right, medial view); **B.** Stapes (left?, medial? view); **C.** Exoccipital (left?, posterior? view); **D.** Opisthotic (left, anteromedial view). Interpretative drawings are denoted by an apostrophe followed by their corresponding letter. Abbreviations: bof, basioccipital facet; gl, glenoid; mh, medial head; paf, prearticular facet; pop, paroccipital process; rap, retroarticular process; scc, semicircular canal impression.

## Chondrocranium

### Exoccipital

We identify an element situated posterior to the other cranial elements as an exoccipital with a high level of confidence (Fig. 1B). The rough, ridged surface texture indicates an endochondral origin of the element (Fig. 5C). The exoccipital consists of a dorsoventrally projected column and a wide foot. The surface of the foot, which bears the basioccipital facet, is better ossified than the surface of the column. Unfortunately, the lateral and medial sides of the exoccipital are not preserved/exposed, which could explain the absence of a visible hypoglossal foramen.

### Opisthotic

A foetal opisthotic is observed anterior to the cluster of foetal elements representing the cheek and skull roof regions (Fig. 1B). The opisthotic exhibits the same roughened, ridged texture as the stapes and exoccipital. The paroccipital process is already evident and slightly deflected dorsolaterally. The medial head is not well-defined, but small impressions for the semicircular canals are already visible (Fig. 5D).

### Axial skeleton

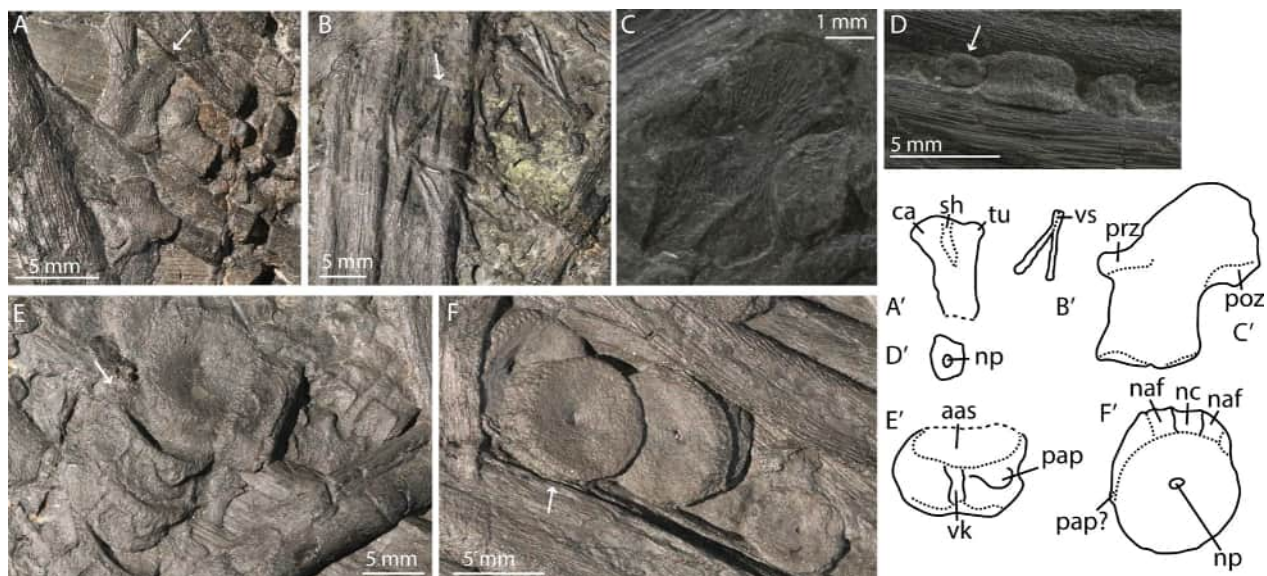
The foetal postcranial axial skeleton is represented by several associated and some articulated vertebral centra. Most of the preserved centra are preflexural, although posterior caudal vertebrae are also preserved in the

maternal body cavity (Figs 1B–E, 6D). All centra retain a small open notochordal pit, which is relatively larger in the posterior caudal centra (Fig. 6D–F). Rib facets (diapophyses), ventral keels and neural canals are already apparent in the preflexural centra (Fig. 6D–F). Neural arches are only rarely preserved and their surface texture indicates that they are less ossified than the centra. One anterior caudal neural arch exhibits developed pre- and postzygapophyses (Fig. 6C). Haemal arches are also already ossified, displaying two ossification centres that fuse ventrally, visible as a suture in some of the arches (Fig. 6B). Complete foetal ribs are absent, but several rib heads pertaining to cervical or anterior dorsal centra are evident just posterior to the area occupied by the foetal skull bones (Fig. 6A). The rib heads exhibit a distinct capitulum and tuberculum, connected by a sheath of bone (Fig. 6A). Thin but well ossified gastralia cluster along the ribs. Medial and lateral gastral elements can be distinguished. Their surfaces are striated, as are the cranial and caudal surfaces of both foetal and maternal ribs.

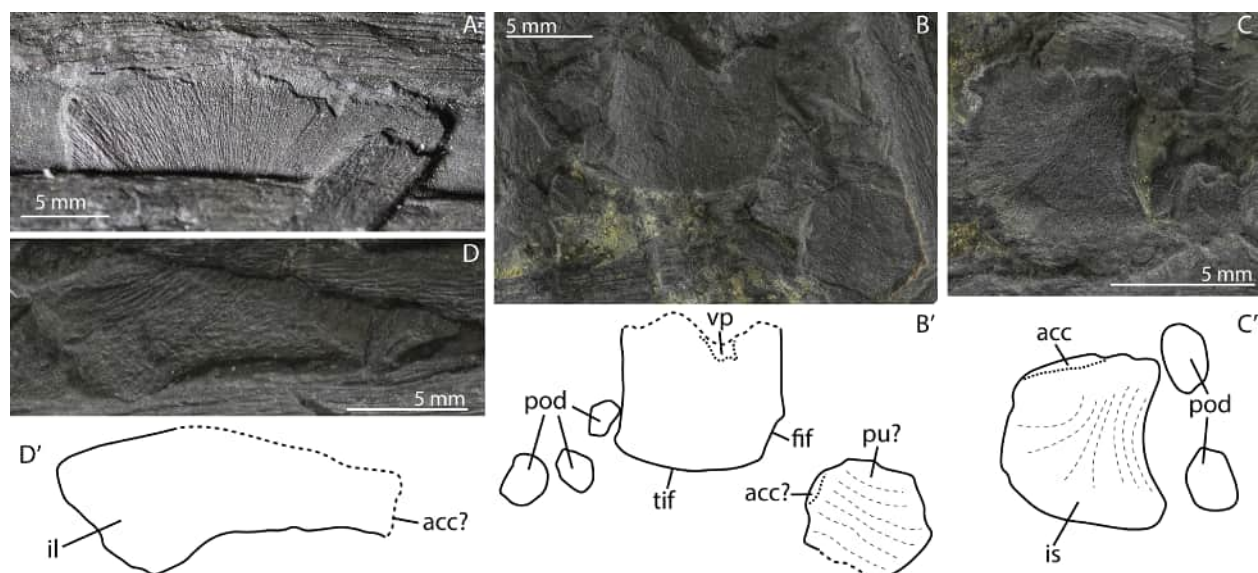
## Appendicular skeleton

### Pectoral girdle

A quadrangular to round element is preserved on block 31 and is mostly covered by a maternal rib. This element likely represents a coracoid or a scapula, given its shape and position in the maternal body cavity (ventral/posteroventral to the area occupied by the foetal cranial bones). The pectoral girdle element is well ossified, with striations indicating a centrally positioned perichondral ossification centre (Fig. 7A).



**Figure 6.** Axial postcranium of the foetus of *Besanosaurus leptorhynchus* (BES SC 999). **A.** Cervical rib heads; **B.** Haemal arches; **C.** Caudal neural arch; **D.** Posterior caudal centra; **E.** Dorsal vertebral centra; **F.** Posterior dorsal or anterior caudal centra. Interpretative drawings are denoted by an apostrophe following their corresponding letter. White arrows in A–F indicate elements figured in the interpretative drawing. Abbreviations: aas, anterior articular surface; ca, capitulum; naf, neural arch facet; nc, neural canal; np, notochord pit; pap, parapophysis; poz, postzygapophysis; prz, prezygapophysis; sh, sheet; tu, tuberculum; vk, ventral keel; vs, ventral suture.



**Figure 7.** Identifiable appendicular elements of the foetus of *Besanosaurus leptorhynchus* (BES SC 999). **A.** Pectoral element, coracoid? (dorsal/ventral view); **B.** Femur (left, dorsal view), pubis? and podials (dorsal/ventral view); **C.** Ischium (left?, ventral? view) and podials (dorsal/ventral view); **D.** Ilium (left?, lateral? view). Interpretative drawings are denoted by an apostrophe followed by their corresponding letter. Abbreviations: acc, acetabular contribution; fif, fibular facet; il, ilium; is, ischium; pod, podial element; pu, pubis; tif, tibial facet; vp, ventral process.

#### Pelvic girdle

The foetal pelvic girdle is represented by an ilium, an ischium and possibly a pubis. All these elements lie relatively close to each other, posterior to the other foetal elements in the maternal body cavity (Fig. 1E). The ischium is well ossified, displaying a quadrangular shape and a concave posterolateral margin, giving the element a semilunate outline. The overall degree of ossification is high, except for the anterior (pubic) margin and the acetabular contribution (Fig. 7C). We tentatively identify a pubis located close to the femur (Fig. 7B). The overall degree of ossification of this element is similar to that of the ischium. The putative pubis is round in outline and a large portion of it is obscured by maternal ribs. The round outline precludes the identification of this element as a tibia or fibula, which are more elongated and narrow, and its size excludes identification as a metatarsal or phalanx (Bindellini et al. 2024). There is a possibility that this element is the astragalus, but its relative size suggests that an identification as a pubis is more likely. The area occupied by the obturator foramen is hidden from view if the identification of the element as a pubis is correct. The ilium is partially covered by a maternal rib anteriorly. It is laterally curved and its overall degree of ossification is high (Fig. 7D).

#### Femur and distal hindlimb

A femur is preserved close to the pelvic elements (Fig. 1E). It is quadrangular in outline and well ossified, although its dorsal portion is broken off (Fig. 7B). The tibial and fibular facets are already weakly developed and a small possible ventral process is visible proximally on the dorsal surface at the broken margin. A few irregularly

shaped meso- and autopodial elements are present in the vicinity of the ischium and the femur (Fig. 7B, C). These elements are slightly less ossified than the femur and pelvic elements, as indicated by their rougher surface texture. They have likewise not yet acquired their postnatal morphology, as postnatal tarsals and phalanges are either almost completely round or more elongated anteroposteriorly and display a distinct central constriction (Bindellini et al. 2024). None of the preserved distal hindlimb elements can be confidently identified in terms of their position within the hindlimb.

## Discussion

### Ontogenetic changes in *Besanosaurus*

Overall, the foetus closely resembles the adult morphology, although distinct differences are present. The paracoronoid process on the surangular is underdeveloped compared to postnatal stages (Bindellini et al. 2021). In *Stenopterygius quadricissus*, this process is present in stage 4 foetuses and is distinctly separate from the preglenoid process, as in sexually mature specimens. However, the paracoronoid area undergoes significant postnatal ontogenetic changes in *Stenopterygius*, as the paracoronoid and preglenoid processes are nearly confluent in postnatal stage 2 before reverting to separation (Miedema and Maxwell 2022). In *Besanosaurus*, the foetal jugal has a more pronounced curvature, whereas in postnatal stages it is more angular posteriorly and the curvature is more acute (Bindellini et al. 2021). This ontogenetic variation is comparable to that observed in *Stenopterygius* (Miedema and Maxwell 2022). In addition, the medial edge of the foetal pterygoid

in *Besanosaurus* is less concave than in postnatal stages. The dorsal part of the paroccipital process of the opisthotic is not as wide as in postnatal specimens and the basioccipital facet is probably not yet ossified. Alternatively, the facet may not be preserved, as the opisthotic lies at the edge of the block. (Bindellini et al. 2021). A substantial difference in paroccipital process development between perinatal and postnatal specimens has also been reported for the Late Cretaceous parvipelvian *Platypterygius australis* (Kear and Zammit 2013). Determining whether the shape of the semicircular canal indentations on the opisthotic varies substantially throughout development is challenging. However, the angle between the horizontal and vertical canal indentations appears similar in pre- and postnatal individuals of *Besanosaurus*, with the indentations being relatively wider prenatally (Bindellini et al. 2021). In contrast, *Stenopterygius* exhibits a substantial ontogenetic change in this angle (Miedema and Maxwell 2019). The triangular process on the quadrate seems relatively larger in the foetus of *Besanosaurus* than in some postnatal specimens (Bindellini et al. 2021). The curvature of the pterygoid lamella of the quadrate remains relatively constant throughout ontogeny, a pattern also observed in *Stenopterygius* and *Platypterygius australis* (Kear and Zammit 2013; Miedema and Maxwell 2019). However, this differs from *Mixosaurus cornalianus*, where the lamella differs in orientation between pre- and postnatal specimens: in which the pterygoid lamella curves more strongly posteriorly in the foetus, whereas in adults the lamella is straight and directed more dorsally (Miedema et al. 2023a).

### Relative prenatal stage of the *Besanosaurus* foetus

Staging fossil foetuses is difficult, as the material is often incomplete and represents only a snapshot of prenatal development. Recently, relative developmental stages were proposed for the ichthyosaur *Stenopterygius quadriscissus* on the basis of cranial ossification patterns (Miedema and Maxwell 2022). The cranium of the *Besanosaurus* foetus exhibits advanced stages of ossification in both dermal and endochondral elements. All dermatocranial elements are well ossified and display a similar degree of development. The dermatocranium is generally better ossified than the endochondral elements, except for the quadrate, which shows a degree of ossification similar to that of the dermatocranium (Fig. 1, Fig. 4C). Delayed endochondral ossification relative to the dermatocranium is a well-documented pattern in *Stenopterygius quadriscissus* and *Mixosaurus cornalianus* and is common among Diapsida (Rieppel 1993; Khannoon and Evans 2015; Danielson and Sheil 2017; Miedema and Maxwell 2022; Miedema et al. 2023a). It is noteworthy that the parietal and pterygoid do not lag behind other dermatocranial elements in ossification in *Besanosaurus*, which is the case in all stages of

development in *Stenopterygius* and in late-stage development of *Mixosaurus* (Miedema and Maxwell 2022; Miedema et al. 2023a). The parietal is well ossified, with a distinct offset supratemporal ramus, a well-defined optic lobe depression and an occipital flange. The pterygoid exhibits a dorsomedial furrow along its palatal ramus, suggesting that the palatal ramus may have been split at an earlier stage of development, similar to stage 3 *Stenopterygius* (Miedema and Maxwell 2022). The overall well-ossified cranium, along with the lack of ossification delay in the parietal and pterygoid relative to other dermatocranial elements, suggests that the developmental stage of the *Besanosaurus* foetus is comparable to stage 4 *Stenopterygius* (Miedema and Maxwell 2022).

We applied the recently published method outlined in Miedema and Maxwell (2026) to assess if a notochordal canal size proxy (Notochordal Canal Index; NCI) in *Besanosaurus* is consistent with the developmental pattern in other ichthyosaurs. We were able to measure seven vertebral centra preserved in (almost) full articular view, three of which likely represent dorsal centra, at least three represent anterior caudals and one possible posterior caudal. The mean measured NCI is 0.09 and significantly different from that of stage 4 *Stenopterygius* (perinatal) (Miedema and Maxwell 2026) (Suppl. material 1). This indicates that the NCI is significantly lower in the perinatal stage of *Besanosaurus* than in the perinatal stage in *Stenopterygius*. This was also the case in the foetus of the large-bodied *Platypterygius australis*, which also had a significantly lower NCI compared to other perinatal ichthyosaur foetuses including *Stenopterygius* (Miedema and Maxwell 2026). We therefore conclude that substantial differences in terminal foetal body size (and thereby total adult body size) influence the usefulness of the NCI, with larger-bodied taxa having lower NCI values (at least perinatally) (Miedema and Maxwell 2026). Taking all this into account, we propose that the foetus of *Besanosaurus* was in the latest stages of prenatal osteological development, immediately prior to birth.

### Notes on taxonomic identification and a discussion of the predation versus reproduction hypotheses

The discovery of an individual assigned to the megapredatory ichthyosaur *Guizhouichthyosaurus*, with thalattosaurian remains preserved in the abdominal region, led to the suggestion that *Besanosaurus leptorhynchus* might have also exhibited a megapredatory feeding ecology (Jiang et al. 2020). Additionally, it was proposed that the small vertebrae originally discovered within the maternal body cavity of the holotype, previously interpreted as embryonic/foetal, could represent mixosaurid centra (Jiang et al. 2020). However, we consider the material preserved in the maternal body cavity to be unambiguously foetal based on the following evidence: 1) the remains are associated and arranged in an anteroposterior

sequence; 2) the bones are in pristine condition and show no signs of digestive alteration (Serafini et al. 2025); 3) clear ossification differences between elements, particularly in the cranium, are consistent with the ossification pattern observed in other ichthyosaur fetuses (Miedema and Maxwell 2019, 2022; Miedema et al. 2023a); and 4) the vertebral centra contain a small notochordal pit (contra Jiang et al. 2020), further supporting their foetal identity (Miedema and Maxwell 2026).

Although the foetal material differs from the maternal skeleton in some respects due to ontogeny (see above), it is clearly attributable to *Besanosaurus leptorhynchus* based on several character states unique to *Besanosaurus* among Besano Formation ichthyosaurs (and notably different from *Mixosaurus*), including a triangular process of the quadrate, a large preglenoid process of the surangular, and a quadrangular proximal end of the femur. Moreover, the foetus clearly exhibits bicipital rib heads in which the heads are connected by a bony sheath and low, wide neural spines, which are far more similar to those present in mature individuals of *Besanosaurus* than to mixosaurids (Økland et al. 2018; Bindellini et al. 2024; Fang et al. 2024). Lastly, other discussions of ecological roles in ichthyosaurs, and in *Besanosaurus* specifically, deem a megapredatory feeding ecology in this ichthyosaur unlikely. This is based on the slender rostrum and small, narrow tooth morphology, as well as stomach contents preserved in a referred specimen of *Besanosaurus* (coleoid hooklets) (Bindellini et al. 2021, 2024). Macropredatory ichthyosaurs *sensu* Bennion et al. (2023a, 2023b) usually have robust rostra and wide, robust teeth, which are sometimes serrated, crenulated or bear deep enamel ridges, all of which is absent in *Besanosaurus* (Fröbisch et al. 2013; Bindellini et al. 2021; Bennion et al. 2023a).

## Presence of palatal teeth

Although palatal teeth are widely distributed among many early-diverging diapsids and extant lepidosaurs, they are largely absent in ichthyosaurs (Matsumoto and Evans 2017). However, teeth are present on the pterygoid in an early-diverging ichthyopterygian identified as cf. *Utatusaurus hataii* from the Lower Triassic of Japan (Motani 1999; Yoshizawa and Tsuihiji 2026). Teeth are also recognized on the palatine of *Wimanius odontopalatus*, a poorly known ichthyosaur from the Middle Triassic of Monte San Giorgio, which is one of the defining features of the taxon (Maisch and Matzke 1998). Moreover, the early diverging ichthyosauriform *Chaohusaurus brevifemoralis* from the Lower Triassic of South China has a single tooth row on the posterior part of the palatine (Yin et al. 2021).

Given these comparisons, we consider the presence of palatal dentition in the foetus of *Besanosaurus* very likely. In the foetus, the putative palatal teeth are also arranged in a single row, as in *Wimanius* and *Chaohusaurus* (Maisch

and Matzke 1998; Yin et al. 2021). Unfortunately, no distinct palatine has been identified in any of the other postnatal specimens of *Besanosaurus leptorhynchus*, making ontogenetic comparisons impossible (Bindellini et al. 2021). It therefore remains uncertain whether these palatal teeth persisted throughout ontogeny. The presence of palatal teeth in early-diverging ichthyosauriforms and in the *Besanosaurus* foetus may indicate that this feature is a developmental remnant lost in postnatal stages. In a recently studied ontogenetic sequence of *Mixosaurus cornalianus* (Miedema et al., 2023b), fetuses of the taxon do not exhibit teeth on the vomer. The only preserved perinatal pterygoid is exposed in dorsal view and no clear perinatal palatine has been identified, which limits the identification of perinatal palatal dentition. The absence of well-preserved perinatal palatal elements means that the presence of palatal teeth in early mixosaurid development cannot yet be completely ruled out. The complete loss of palatal dentition likely occurred around the origin of Parvipelvia, as fetuses of *Stenopterygius* clearly lack this feature (Miedema and Maxwell 2022).

The presence of palatine teeth in the foetus of BES SC 999 raises the possibility that *Wimanius odontopalatus*, an ichthyosaur that co-occurs with *Besanosaurus leptorhynchus* at Monte San Giorgio, is a junior synonym of the latter. *Wimanius* is known only from a single specimen, a partial cranium exposed in ventral view (Maisch and Matzke 1998). The holotype of *Wimanius* is consistent in size (mandible length of just over 20 cm) between the estimated size of the *Besanosaurus* foetus (mandible length of 10–12 cm) and the smallest currently recognized postnatal *Besanosaurus* specimen (PIMUZ T 4376, mandible length of 41 cm) (Maisch and Matzke 1998; Bindellini et al. 2021). This raises the possibility that the *Wimanius* holotype represents an early postnatal referred specimen of *Besanosaurus*. The validity of *Wimanius* has been questioned in previous studies (Motani 1999; Sander 2000; McGowan and Motani 2003; Klug et al. 2024b), with these authors noting morphological similarities between *Wimanius* and *Besanosaurus*. A detailed revision of the holotype of *Wimanius* is warranted based on our new observations but is beyond the scope of the present study.

## Litter size, uterine position and parturition orientation

The foetal material of BES SC 999 is disarticulated, but its relative *in vivo* positioning of the separate body regions remains largely intact. All cranial material is positioned far anteriorly, directly posterior to the maternal pectoral girdle (Fig. 1). Although the foetal vertebrae are somewhat scattered and may appear evenly distributed, we observe a clear anterior-posterior gradient, with caudal vertebrae being the only type of vertebrae clustered more posteriorly in the maternal body cavity. The pelvic girdle and femur are closely associated and positioned further posteriorly than the foetal cranium.

In the original description of BES SC 999, the authors noted three or four clusters of vertebrae lying in sequence, leading to some confusion as to whether multiple foetuses or a single foetus were present (Dal Sasso and Pinna 1996). The absence of obvious contralateral cranial or appendicular elements, together with the clear anteroposterior gradient in element distribution, leads to the most parsimonious conclusion that all the material represents a single foetus. The foetus is located in the right uterine cornu, as the maternal specimen is preserved with the trunk exposed in ventral view (Fig. 1). The anterior orientation of the foetal cranium suggests a future caudal (tail-first) presentation at birth. Caudal presentation appears to be the preferred, though not exclusive, method of parturition in Merriamosauria (Böttcher 1990; Miedema et al. 2023b), but future discoveries of shastasaurid/shastasaur-grade ichthyosaurs might reveal different preferred birth orientations within the group (Kelley et al. 2022; Miedema et al. 2023b).

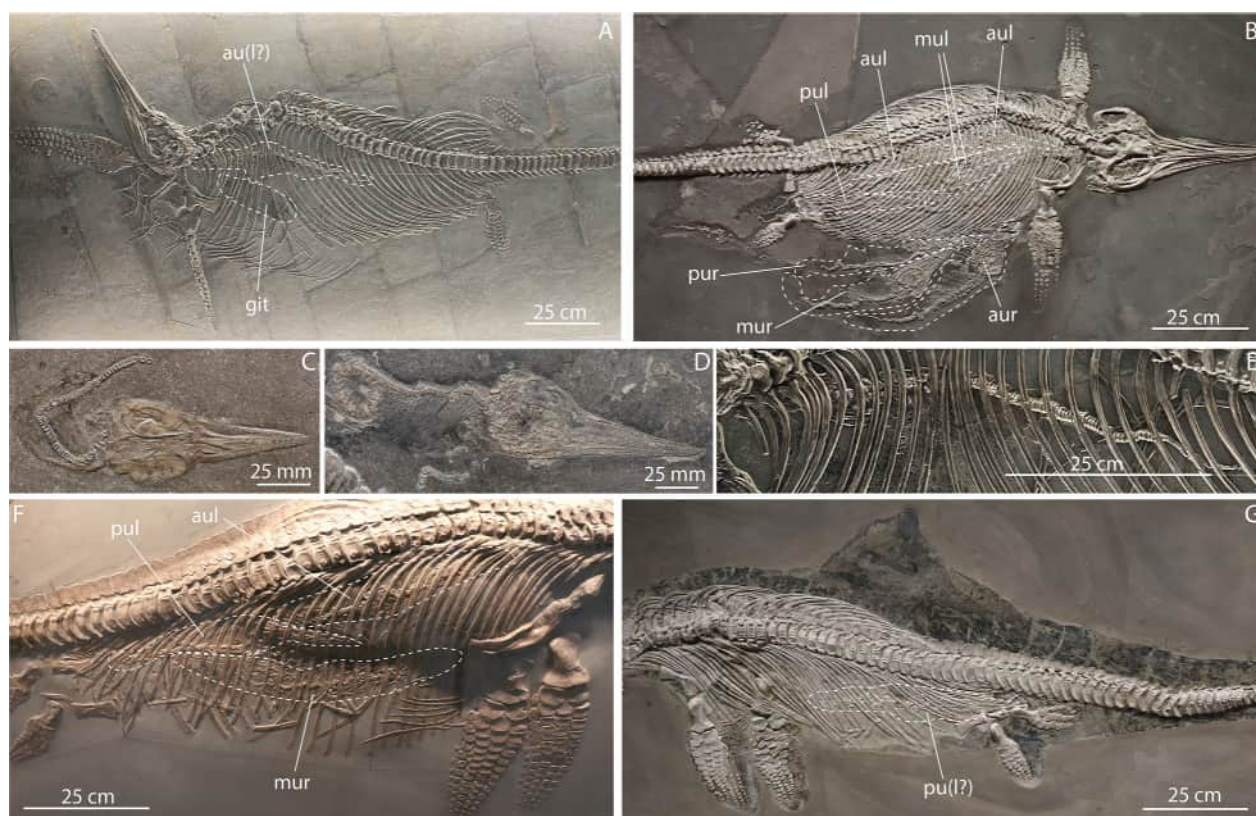
The litter size for the *Besanosaurus* holotype is one foetus. This is not uncommon within Ichthyosauria and is the most common litter size in the best-studied genus *Stenopterygius* (Böttcher 1990; Miedema et al. 2023b). Litter size varies greatly among Ichthyosauria, but the three genera with multiple known pregnant females (*Stenopterygius*, *Ichthyosaurus*, *Mixosaurus*) suggest that between two and four foetuses is the norm within Ichthyosauria and six or more foetuses occur only exceptionally (Miedema et al. 2023b; Miedema and Maxwell 2026). Litter size is relatively difficult to study in ichthyosaurs, as many factors need to be considered. In fossilized pregnant females with perinatal (stage 4) foetuses, there is a high chance of seeing fewer foetuses than were originally present due to late births or deceased, unaborting foetuses. Moreover, the sample size needs to be considered for robust statistical testing. The sample of *Stenopterygius* attests to this, as litter size ranges from 1 to 10–11 in this taxon (Böttcher 1990).

The far anterior placement of the cranium of BES SC 999 at ca. 20% maternal coelomic length (measured between the anterior and posterior margins of the pectoral and pelvic girdles, respectively) suggests that the foetus was still *in utero* and had not yet begun migrating posteriorly in preparation for parturition. However, the far anterior position of the BES SC 999 foetus could be at least partially taphonomic. The maternal specimen is preserved with the ventral side facing away from the sediment, allowing greater time for movement before burial. In *Stenopterygius*, more anterior placement of the foetus is sometimes seen in maternal specimens that arrived head-first on the sea-floor, such as SMF-R-4131 (Fig. 8A) (Reisdorf 2007a, 2007b; Reisdorf et al. 2012). In contrast, in maternal specimens interpreted as having landed laterally, ventrally or dorsally, foetuses tend to be more evenly distributed along the trunk (Fig. 8B, F–G) (Suppl. material 1). In general, the original foetal position is likely best preserved in maternal specimens that came to rest laterally on the seafloor (Suppl.

material 1). In dorsal presentations (landings), disarticulation of foetal material is most common (e.g. SMNS 50007, SMNS 54062; Suppl. material 1). In some cases, the original foetal position cannot be determined due to late expulsion of the foetus, preserving it outside the maternal body cavity (e.g. Fig. 8A, B, F, G). In maternal specimens with lateral presentation (lateral landing) and a single foetus, three main modes of foetal preservation occur: foetus preserved in the anterodorsal part of the maternal body cavity, foetus preserved dorsally in the mid-trunk region, and foetus preserved in the birth canal. In maternal specimens with higher foetal counts, foetuses tend to be stacked both dorsoventrally and anteroposteriorly, often lying with the cranium close to the trunk or tail of the neighbouring foetus (Fig. 8B, F). Regardless of taphonomic maternal landing position, anterior foetal placement is consistently observed in euichthyosaurs. In the only gravid specimen of *Cymbospondylus* (head-first arrival?), three foetuses are preserved, lying in an anteroposterior sequence, with the most anterior foetus lying close to the maternal pectoral girdle and all foetuses lying in positions consistent with head-first birth (Klein et al. 2020). In *Mixosaurus*, the pattern is more ambiguous. In PIMUZ T 4830 (lateral view), foetuses are situated posteriorly in the maternal trunk close to the birth canal. In PIMUZ T 1902 (preserved in lateral view), the single preserved foetus is somewhat disarticulated and almost completely spans the maternal trunk, with the cranium lying close to the maternal pectoral girdle, similar to the condition in the *Besanosaurus* holotype (Miedema et al. 2023b). In *Stenopterygius*, foetuses are observed in the anterior, mid- and posterior trunk regions (e.g. Fig. 8A, B, F, G). Posterior (pelvic) foetal positioning is rarer and in *Stenopterygius* is typically observed in near-birth foetuses, such as GPIT-PV-30054, SMNS 6293 and SMNS 16811 (Fig. 8G), with SMNS 50963 being the exception, in which two early-stage foetuses are located just posterior to the birth canal. We interpret SMNS 50963 as involuntary early abortion associated with maternal death.

The reproductive tract lies dorsal to the gastrointestinal tract in ichthyosaurs (Böttcher 1990), a condition similar to that in other viviparous reptiles (Blackburn 1998) (Fig. 8A). Ichthyosaur foetuses are coiled in early prenatal development, as in modern squamates (prenatal stage 1) (Fig. 8C) (Blackburn 1998; Stewart 2015; Miedema et al. 2023b), but acquire a straightened posture from stage 2 onward (Fig. 8D, E). This suggests that, throughout gestation, foetuses occupy various positions within the trunk, particularly in females carrying multiple foetuses in a single litter.

Foetuses are generally arranged in a partial anterior-posterior sequence within both uterine cornua (Fig. 8B, F, G). In individuals with multiple foetuses, however, substantial dorsoventral overlap between foetuses seems to occur within the same cornu (Fig. 8B, F). We hypothesize that in early prenatal development, coiled foetuses are arranged in sequence akin to that of modern viviparous reptiles. After transitioning to an elongated body alignment (i.e. after stage 2), foetuses likely lost relative



**Figure 8.** Position and orientation of stage 4 foetuses of *Stenopterygius* in the reproductive tract and coiled or straightened morphology of foetuses at various developmental stages. **A.** Pregnant *S. quadricissus* SMF-R-4131 in lateral view, with a foetus in the left(?) uterine cornu dorsal to gastrointestinal material and located in the maternal anterior trunk region. **B.** Pregnant *S. quadricissus* SMNS 52036, with foetuses lying in both uterine cornua in an anteroposterior sequence, with substantial dorsoventral overlap and showing a distinct straightened axial skeleton (note the high number of foetuses is atypical in *Stenopterygius*). **C.** Postmortem aborted stage 1 foetus of *S. quadricissus* SMNS 10460, still in a coiled position. **D.** Postmortem aborted stage 2 foetus of *S. quadricissus* SMNS 50963, showing a straightened axial skeleton. **E.** *S. quadricissus* stage 4 foetus *in utero* SMF-R-4131, showing a distinct straightened axial skeleton. **F.** Pregnant *S. quadricissus* MHH 1981/33, with foetuses lying in both uterine cornua in anteroposterior sequence with substantial dorsoventral overlap in the maternal mid-trunk region, showing both cranial and caudal presentation. **G.** Pregnant *S. quadricissus* SMNS 16811, with foetus lying in the maternal posterior trunk region, likely close to birth. Abbreviations: a, anterior; git, gastrointestinal tract; l, left; m, mid-trunk; p, posterior; r, right; u, uterine cornu. Note: scale bars in **A** and **E** should not be used for further analyses, as photos and measurements were taken through a glass cover.

positional freedom *in utero*, causing them to stack largely dorsoventrally, overlapping and underlapping their siblings while continuing to develop along the antero-posterior axis during later stages of gestation. This pattern suggests that the uterus was not tightly constricted around each individual foetus, as seen in modern viviparous squamates and mosasauroids (Blackburn 1998; Caldwell and Lee 2001), but was instead more tube-like and flexible, providing ample space for foetal growth during later developmental stages. The distribution of foetuses in females carrying more than three individuals also suggests that both uterine cornua were present and well developed (Fig. 8B, F), precluding the possibility of marked uterine size asymmetry or complete loss, as observed in modern squamates and birds (Blackburn 1998; Yoshimura and Barua 2017).

We acknowledge taphonomic concerns regarding the exact position of the *in utero* foetuses in ichthyosaurs,

but based on all specimens observed, a more anterodorsal (maternal pectoral area) carrying position in either left or right uterine cornu, followed by perinatal posterior migration, seems to be the most parsimonious condition inferred in ichthyosaurs. The anterior placement of the foetus during gestation supports the “trim control” hypothesis as explanation for the preference of tail-first birth in Euichthyosauria (Miedema et al. 2023b). The trim control hypothesis proposes that foetuses of ichthyosaurs should be carried with the heaviest portion (the head) as close as possible to the maternal centre of buoyancy (the lungs) to reduce maternal energy expenditure during pregnancy (Miedema et al. 2023b). However, this observation does not exclude the “mechanical” hypothesis, which proposes that the anterior placement of the cranium is energetically advantageous during peristaltic contractions during birth (Miedema et al. 2023b). Both factors could have contributed.

## Conclusion

The holotype of *Besanosaurus leptorhynchus* contains a single well-preserved foetus. Preserved foetal remains include parts of the cranium of all developmental origins, as well as postcranial axial and posterior paraxial elements. Based on the degree of cranial ossification, the developmental stage of the foetus is comparable to stage 4 in *Stenopterygius*. We interpret the foetus as possessing teeth on the palatine, potentially representing a developmental atavism that was completely lost in parvipelvians. The presence of these palatal teeth may have future taxonomic implications, especially regarding the validity of the genus *Wimanius*. Several ontogenetically variable features are evident between the foetal and adult morphologies, including the shape of the paracoronoid process on the surangular and the curvature of the jugal; these features are also variable in ontogenetic series of other ichthyosaurs. The *Besanosaurus* foetus is carried in the right uterine cornu in a far anterior placement (ca. 20% along the maternal body cavity) and seems to be oriented for tail-first birth, as is common in members of Merriamosauria. Observations on the more derived Early Jurassic genus *Stenopterygius* show that foetuses lie in anterior-posterior sequence but are also partially dorsoventrally stacked during late gestation in both uterine cornua. This contrasts with most modern viviparous reptiles and mosasauroids, which exhibit strict uterine compartmentalization of individual foetuses.

## Author contributions

Conceptualization: FM, GB, CDS. Methodology: FM, GB, ASW, EEM, CDS. Investigation: FM, GB, ASW, CDS. Visualization: FM, GB, CDS. Supervision: CDS, EEM. Writing—original draft: FM. Writing—review & editing: FM, GB, ASW, EEM, CDS.

## Acknowledgements

We thank the Italian Ministry of Culture and the “Soprintendenza Archeologia, belle arti e paesaggio per le province di Como, Lecco, Sondrio e Varese” for permission to study the BES SC material. We would like to express our immense gratitude to the volunteers of the former “Gruppo paleontologico di Besano”, who unearthed the specimen and to D. Affer, F. Fogliazza, and L. Magnoni (MSNM) for skilful preparation of BES SC 999. Although not as successful as we hoped for in relation to the foetal material, we thank L. Forzenigo, C. Bonelli, and G. Terribile (Fondazione IRCCS “Cà Granda” Ospedale Maggiore Policlinico di Milano) for assistance with the CT analysis of BES SC 999. FM thanks Omar Rafael Regalado Fernandez for his assistance during a collection visit at the Senckenberg Museum Frankfurt. ASW received funding from the Polish National Agency for Academic Exchange (grants BPN/BEK/2022/1/00194; BPN/BKK/2025/1/00005). We also thank Jelle Heijne

(Universität Bonn, LVR- Amt für Bodendenkmalpflege im Rheinland, NRW Germany) and Neil Kelley (Vanderbilt University, Nashville, USA) for constructive feedback on an earlier version of this manuscript.

## References

- Bennion RF, Maxwell EE, Lambert O, Fischer V (2023a) Craniodental ecomorphology of the large Jurassic ichthyosaurian *Temnodontosaurus*. *Journal of Anatomy* 244: 22–41. <https://doi.org/10.1111/joa.13939>
- Bennion RF, MacLaren JA, Coombs EJ, Marx FG, Lambert O, Fischer V (2023b) Convergence and constraint in the cranial evolution of mosasaurid reptiles and early cetaceans. *Paleobiology* 49: 215–231. <https://doi.org/10.1017/pab.2022.27>
- Benton MJ, Zhang Q, Hu S, Chen Z-Q, Wen W, Liu J, Huang J, Zhou C, Xie T, Tong J, Choo B (2013) Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth-Science Reviews* 125: 199–243. <https://doi.org/10.1016/j.earscirev.2013.05.014>
- Bernasconi S, Riva A (1993) Organic geochemistry and depositional environment of a hydrocarbon source rock: the Middle Triassic Grenzbitumenzone Formation, southern Alps, Italy/Switzerland. In: Spencer AM (Ed.) *Generation, Accumulation and Production of Europe's Hydrocarbons III*. Springer Berlin Heidelberg, Berlin, Heidelberg, 179–190. [https://doi.org/10.1007/978-3-642-77859-9\\_15](https://doi.org/10.1007/978-3-642-77859-9_15)
- Bernasconi SM (1991) Geochemical and microbial controls on dolomite formation and organic matter production/preservation in anoxic environments: a case study from the Middle Triassic Grenzbitumenzone, Southern Alps (Ticino, Switzerland). Dr. Phil. Thesis. Swiss Federal Institute of Technology Zürich. [https://doi.org/10.1007/978-3-642-77859-9\\_15](https://doi.org/10.1007/978-3-642-77859-9_15)
- Bernasconi SM (1994) Geochemical and microbial controls on dolomite formation in anoxic environments: A case study from the Middle Triassic (Ticino, Switzerland). *Contributions to Sedimentology* 19: 1–109.
- Bindellini G, Dal Sasso C (2022) First skeletal remains of *Helveticosaurus* from the Middle Triassic Italian outcrops of the southern alps, with remarks on an isolated tooth. *Rivista Italiana di Paleontologia e Stratigrafia* 128(3): 625–641. <https://doi.org/10.54103/2039-4942/17397>
- Bindellini G, Balini M, Teruzzi G, Dal Sasso C (2019) Ammonoid and *Daonella* zonation of the Sasso Caldo quarry (Besano Formation, Middle Triassic). In: Strati 2019, 3<sup>rd</sup> International Congress on Stratigraphy—ST2.4 Ammonoids in stratigraphy. <https://doi.org/10.3301/absgi.2019.04>
- Bindellini G, Wolniewicz AS, Miedema F, Scheyer TM, Dal Sasso C (2021) Cranial anatomy of *Besanosaurus leptorhynchus* Dal Sasso & Pinna, 1996 (Reptilia: Ichthyosauria) from the Middle Triassic Besano Formation of Monte San Giorgio, Italy/Switzerland: taxonomic and palaeobiological implications. *PeerJ* 9: e11179. <https://doi.org/10.7717/peerj.11179>
- Bindellini G, Wolniewicz AS, Miedema F, Dal Sasso C, Scheyer TM (2024) Postcranial anatomy of *Besanosaurus leptorhynchus* (Reptilia: Ichthyosauria) from the Middle Triassic Besano Formation of Monte San Giorgio (Italy/Switzerland), with implications for reconstructing the swimming styles of Triassic ichthyosaurs. *Swiss Journal of Palaeontology* 143: 32. <https://doi.org/10.1186/s13358-024-00330-9>
- Blackburn DG (1998) Structure, function, and evolution of the oviducts of squamate reptiles, with special reference to viviparity and placenta-

- tion. *The Journal of Experimental Zoology* 282: 560–617. [https://doi.org/10.1002/\(SICI\)1097-010X\(199811/12\)282:4/5%3C560::AID-JEZ10%3E3.0.CO;2-J](https://doi.org/10.1002/(SICI)1097-010X(199811/12)282:4/5%3C560::AID-JEZ10%3E3.0.CO;2-J)
- Böttcher R (1990) Neue Erkenntnisse über die Fortpflanzungsbiologie der Ichthyosaurier (Reptilia). *Stuttgarter Beiträge zur Naturkunde Ser. B* 164: 1–51.
- Brack P, Rieber H, Nicora A, Mundil R (2005) The Global boundary Stratotype Section and Point (GSSP) of the Ladinian Stage (Middle Triassic) at Bagolino (Southern Alps, Northern Italy) and its implications for the Triassic time scale. *Episodes* 28: 233–244. <https://doi.org/10.18814/epiugs/2005/v28i4/001>
- Caldwell MW, Lee MSY (2001) Live birth in Cretaceous marine lizards (mosasauroids). *Proceedings of the Royal Society B: Biological Sciences* 268: 2397–2401. <https://doi.org/10.1098/rspb.2001.1796>
- Dal Sasso C, Pinna G (1996) *Besanosaurus leptorhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the Middle Triassic of Besano (Lombardy, N. Italy). *Paleontologia Lombarda, Nuova Serie* 4: 1–22. <http://www.getcited.org/pub/100399614>
- Danielson SC, Sheil CA (2017) Patterns of chondrification and ossification in the skull of *Graptemys pseudogeographica*, the false map turtle (Emydidae). *Journal of Morphology* 278: 1739–1753. <https://doi.org/10.1002/jmor.20747>
- Delsett LL, Pyenson N, Miedema F, Hammer Ø (2023) Is the hyoid a constraint on innovation? A study in convergence driving feeding in fish-shaped marine tetrapods. *Paleobiology* 49: 684–699. <https://doi.org/10.1017/pab.2023.12>
- Fang Y, Wolniewicz AS, Liu J (2024) A new species of mixosaurid ichthyosaur from the Middle Triassic of Luxi County, Yunnan Province, South China. *Acta Palaeontologica Polonica* 69: 263–280. <https://doi.org/10.4202/app.01133.2024>
- Fischer V, Bardet N, Benson RBJ, Arkhangel'sky MS, Friedman M (2016) Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. *Nature Communications* 7: 1–11. <https://doi.org/10.1038/ncomms10825>
- Fischer V, Cappetta H, Vincent P, Garcia G, Goolaerts S, Martin JE, Roggero D, Valentin X (2014) Ichthyosaurs from the French Rhaetian indicate a severe turnover across the Triassic–Jurassic boundary. *Naturwissenschaften* 101: 1027–1040. <https://doi.org/10.1007/s00114-014-1242-7>
- Fröbisch NB, Fröbisch J, Sander PM, Schmitz L, Rieppel O (2013) Macro-predatory ichthyosaur from the Middle Triassic and the origin of modern trophic networks. *Proceedings of the National Academy of Sciences* 110: 1393–1397. <https://doi.org/10.1073/pnas.1216750110>
- Furrer H, Lagerstaetten K, Giorgio MS (2024) The history of palaeontological research and excavations at Monte San Giorgio. *Swiss Journal of Palaeontology* 143: 1–25. <https://doi.org/10.1186/s13358-024-00314-9>
- Gingerich PD, Ul-Haq M, Von Koenigswald W, Sanders WJ, Smith BH, Zalmout IS (2009) New protocetid whale from the middle Eocene of Pakistan: Birth on land, precocial development, and sexual dimorphism. *PLoS ONE* 4: e4366. <https://doi.org/10.1371/journal.pone.0004366>
- Gutarra S, Stubbs TL, Moon BC, Heighton BH, Benton MJ (2023) The locomotor ecomorphology of Mesozoic marine reptiles. *Palaeontology* 66: e12645. <https://doi.org/10.1111/pala.12645>
- Ji C, Jiang D, Motani R, Rieppel O, Hao W, Sun Z (2015) Phylogeny of the Ichthyopterygia incorporating recent discoveries from South China. *Journal of Vertebrate Paleontology* 0–18. <https://doi.org/10.1080/02724634.2015.1025956>
- Jiang D, Motani R, Tintori A, Rieppel O, Ji C, Zhou M, Wang X, Lu H, Li Z (2020) Evidence supporting predation of 4-m marine reptile by Triassic megapredator. *iScience* 25: 101347. <https://doi.org/10.1016/j.isci.2020.101347>
- Kear BP, Zammit M (2013) In utero foetal remains of the Cretaceous ichthyosaurian *Platypterygius*: Ontogenetic implications for character state efficacy. *Geological Magazine* 151: 71–86. <https://doi.org/10.1017/S0016756813000113>
- Kelley NP, Irmis RB, Depolo PE, Noble PJ, Montague-judd D, Little H, Blundell J, Rasmussen C, Percival LME, Mather TA, Pyenson ND (2022) Grouping behavior in a Triassic marine apex predator. *Current Biology* 32: 5398–5405. <https://doi.org/10.1016/j.cub.2022.11.005>
- Khannoon ER, Evans SE (2015) The development of the skull of the Egyptian cobra *Naja h. haje* (Squamata: Serpentes: Elapidae). *PLoS ONE* 10: 1–25. <https://doi.org/10.1371/journal.pone.0122185>
- Klein N, Schmitz L, Wintrich T, Sander PM (2020) A new cymbospondylid ichthyosaur (Ichthyosauria) from the Middle Triassic (Anisian) of the Augusta Mountains, Nevada, USA. *Journal of Systematic Palaeontology* 18: 1167–1191. <https://doi.org/10.1080/14772019.2020.1748132>
- Klug C, Scheyer TM, Klein N, Liu J, Albiseti D, Furrer H, Stockar R (2024a) Special Issue: 100 years of scientific excavations at UNESCO World Heritage Site Monte San Giorgio and global research on Triassic marine Lagerstätten. *Swiss Journal of Palaeontology* 143: 37. <https://doi.org/10.1186/s13358-024-00328-3>
- Klug C, Sivgin T, Miedema F, Scheffold B, Reisdorf AG, Stössel I, Maxwell EE, Scheyer TM (2024b) Swiss ichthyosaurs: a review. *Swiss Journal of Palaeontology* 143: 31. <https://doi.org/10.1186/s13358-024-00327-4>
- Lindgren J, Sjövall P, Thiel V, Zheng W, Ito S, Wakamatsu K, Hauff R, Kear BP, Engdahl A, Alwmark C, Eriksson ME, Jarenmark M, Sachs S, Ahlberg PE, Marone F, Kuriyama T, Gustafsson O, Malmberg P, Thomen A, Rodríguez-Meizoso I, Uvdal P, Ojika M, Schweitzer MH (2018) Soft-tissue evidence for homeothermy and crypsis in a Jurassic ichthyosaur. *Nature* 564: 359–365. <https://doi.org/10.1038/s41586-018-0775-x>
- Lomax DR, Salle PD, Perillo M, Reynolds J, Reynolds R, Waldron JF (2024) The last giants: New evidence for giant Late Triassic (Rhaetian) ichthyosaurs from the UK. *PLoS ONE* 19: ee0300289. <https://doi.org/10.1371/journal.pone.0300289>
- Maisch MW, Matzke AT (1998) Observations on Triassic ichthyosaurs. Part II: A new ichthyosaur with palatal teeth from Monte San Giorgio. *Neues Jahrbuch für Geologie und Paläontologie - Monatshefte* 1: 26–41. <https://doi.org/10.1127/njgpm/1998/1998/26>
- Matsumoto R, Evans SE (2017) The palatal dentition of tetrapods and its functional significance. *Journal of Anatomy* 230: 47–65. <https://doi.org/10.1111/joa.12534>
- McGowan C, Motani R (2003) *Copeia Handbook of Paleoherpology* part 8 Ichthyopterygia. Sues H-D (Ed.) Verlag Dr. Friedrich Pfeil, München, 175 pp. <https://doi.org/10.2307/1442949>
- Miedema F, Maxwell EE (2019) Ontogeny of the braincase in *Stenopterygius* (Reptilia, Ichthyosauria) from the Lower Jurassic of Germany. *Journal of Vertebrate Paleontology* 39: e1675164. <https://doi.org/10.1080/02724634.2019.1675164>
- Miedema F, Maxwell EE (2022) Ontogenetic variation in the skull of *Stenopterygius quadriscissus* with an emphasis on prenatal development. *Scientific Reports* 12: 1707. <https://doi.org/10.1038/s41598-022-05540-0>
- Miedema F, Maxwell EE (2026) Use of the notochordal canal as a reliable proxy for prenatal stage, a case study in Ichthyosauria. *Royal Society Open Science* 13: 251986. <https://doi.org/10.1098/rsos.251986>

- Miedema F, Bindellini G, Dal Sasso C, Scheyer TM, Maxwell EE (2023a) Ontogenetic variation in the cranium of *Mixosaurus cornalianus*, with implications for the evolution of ichthyosaurian cranial development. *Swiss Journal of Palaeontology* 142: 27. <https://doi.org/10.1186/s13358-023-00289-z>
- Miedema F, Klein N, Blackburn DG, Sander PM, Maxwell EE, Griebeler EM, Scheyer TM (2023b) Heads or tails first? Evolution of fetal orientation in ichthyosaurs, with a scrutiny of the prevailing hypothesis. *BMC Ecology and Evolution* 23: 12. <https://doi.org/10.1186/s12862-023-02110-4>
- Motani R (1999) Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology* 19: 473–496. <https://doi.org/10.1080/02724634.1999.10011160>
- Motani R (2005) Evolution of Fish-Shaped Reptiles (Reptilia: Ichthyopterygia) in Their Physical Environments and Constraints. *Annual Review of Earth and Planetary Sciences* 33: 395–420. <https://doi.org/10.1146/annurev.earth.33.092203.122707>
- Motani R, Vermeij GJ (2021) Ecophysiological steps of marine adaptation in extant and extinct non-avian tetrapods. *Biological Reviews* 96: 1769–1798. <https://doi.org/10.1111/brv.12724>
- Motani R, Jiang DY, Tintori A, Rieppel O, Chen GB (2014) Terrestrial origin of viviparity in Mesozoic marine reptiles indicated by Early Triassic embryonic fossils. *PLoS ONE* 9: e88640. <https://doi.org/10.1371/journal.pone.0088640>
- Motani R, Ji C, Tomita T, Kelley N, Maxwell E, Jiang DY, Sander PM (2013) Absence of suction feeding ichthyosaurs and its implications for Triassic mesopelagic paleoecology. *PLoS ONE* 8: e66075. <https://doi.org/10.1371/journal.pone.0066075>
- Økland IH, Delsett LL, Roberts AJ, Hurum JørnH (2018) A *Phalarodon fraasi* (Ichthyosauria: Mixosauridae) from the Middle Triassic of Svalbard. *Norwegian Journal of Geology* 98: 267–288. <https://doi.org/10.17850/njg98-2-06>
- Pardo-Pérez JM, Malkowski M, Zambrano P, Lomax DR, Gascó Martín C, Kaluza J, Ortiz H, Pérez Marín A, Villa-Martínez R, Yurac M, Cáceres M, Zegers A, Delgado J, Scapini F, Astete C, Maxwell EE (2025) The first gravid ichthyosaur from the Hauterivian (Early Cretaceous): a complete *Myobradypterygius hauthali* von Huene, 1927 excavated from the border of the Tyndall Glacier, Torres del Paine National Park, southernmost Chile. *Journal of Vertebrate Paleontology* 45: e2445705. <https://doi.org/10.1080/02724634.2024.2445705>
- Reisdorf AG (2007a) Der Ichthyosaurier vom Hauensteiner Nebelmeer. *Mitteilungen der Naturforschenden Gesellschaft Solothurn* 40: 9–15. <https://doi.org/10.5169/seals-543333>
- Reisdorf AG (2007b) No Joke Movement: Mehr über den Hauensteiner Ichthyosaurier und rezente marine Lungenatmer. *Mitteilungen der Naturforschenden Gesellschaft Solothurn* 40: 25–49. <https://doi.org/10.5169/seals-543366>
- Reisdorf AG, Bux R, Wyler D, Benecke M, Klug C, Maisch MW, Fornaro P, Wetzel A (2012) Float, explode or sink: Postmortem fate of lung-breathing marine vertebrates. *Palaeobiodiversity and Palaeoenvironments* 92: 67–81. <https://doi.org/10.1007/s12549-011-0067-z>
- Renesto S, Dal Sasso C, Fogliazza F, Ragni C (2020) New findings reveal that the Middle Triassic ichthyosaur *Mixosaurus cornalianus* is the oldest amniote with a dorsal fin. *Acta Palaeontologica Polonica* 65: 511–522. <https://doi.org/10.4202/app.00731.2020>
- Rieppel O (1993) Studies on skeleton formation in reptiles: Patterns of ossification in the skeleton of *Chelydra serpentina* (Reptilia, Testudines). *Journal of Zoology* 231: 487–509. <https://doi.org/10.1111/j.1469-7998.1993.tb01933.x>
- Rieppel OC (2019) Mesozoic sea dragons: Triassic marine life from the ancient tropical lagoon of Monte San Giorgio. Indiana university press, Bloomington, Indiana, 312 pp. <https://doi.org/10.2307/j.ctvd58t86>
- Roberts AJ, Rucinski M, Kear BP, Hammer Ø, Engelschön VS, Scharling TH, Larsen RB, Hurum JH (2025) Earliest oceanic tetrapod ecosystem reveals rapid complexification of Triassic marine communities. *Science* 390: 722–727. <https://doi.org/10.1126/science.adx7390>
- Röhl HJ, Schmid-Röhl A, Furrer H, Frimmel A, Oschmann W, Schwark L (2001) Microfacies, geochemistry and palaeoecology of the Middle Triassic Grenzbitumenzone from Monte San Giorgio (Canton Ticino, Switzerland). *Geologia Insubrica* 6: 1–13.
- Sander PM (2000) Ichthyosauria: their diversity, distribution, and phylogeny. *Paläontologische Zeitschrift* 74: 1–35. <https://doi.org/10.1007/BF02987949>
- Serafini G, Miedema F, Schweigert G, Maxwell EE (2025) *Temnodontosaurus* bromalites from the Lower Jurassic of Germany: hunting, digestive taphonomy and prey preferences in a macropredatory ichthyosaur. *Papers in Palaeontology* 11: e70018. <https://doi.org/10.1002/spp2.70018>
- Stewart JR (2015) Placental specializations in lecithotrophic viviparous squamate reptiles. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 324: 549–561. <https://doi.org/10.1002/jez.b.22632>
- Wotzlaw J-F, Brack P, Storck J-C (2018) High-resolution stratigraphy and zircon U–Pb geochronology of the Middle Triassic Buchenstein Formation (Dolomites, northern Italy): precession-forcing of hemipelagic carbonate sedimentation and calibration of the Anisian–Ladinian boundary interval. *Journal of the Geological Society* 175: 71–85. <https://doi.org/10.1144/jgs2017-052>
- Yin Y, Ji C, Zhou M (2021) The anatomy of the palate in Early Triassic *Chaohusaurus brevifemoralis* (Reptilia: Ichthyosauriformes) based on digital reconstruction. *PeerJ* 9: e11727. <https://doi.org/10.7717/peerj.11727>
- Yoshimura Y, Barua A (2017) Female Reproductive System and Immunology. In: Sasanami T (Ed.) *Avian Reproduction*. Advances in Experimental Medicine and Biology. Springer Singapore, Singapore, 33–57. [https://doi.org/10.1007/978-981-10-3975-1\\_3](https://doi.org/10.1007/978-981-10-3975-1_3)
- Yoshizawa K, Tsuihiji T (2026) Skeletal morphology of an early ichthyopterygian, cf. *Utatusaurus hataii*, from Japan with an emphasis in CT scan data of the skull. *Journal of Vertebrate Paleontology* 45: e2621687. <https://doi.org/10.1080/02724634.2026.2621687>

## Supplementary material 1

### Supplemental file

Authors: Feiko Miedema, Gabriele Bindellini, Andrzej S. Wolniewicz, Erin E. Maxwell, Cristiano Dal Sasso

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/fr.29.183128.suppl1>