First record of *Ichthyosaurus anningae* outside the United Kingdom: new evidence from the Lower Jurassic of northern Spain

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A new specimen of *Ichthyosaurus anningae* from Asturias (Northern Spain) is described in detail, representing the first unambiguous record of this species outside the type locality Dorset (UK). The associated ammonite assemblage firmly constrains the stratigraphic position of the specimen within the Rodiles Formation, Jamesoni Zone (Pliensbachian, Lower Jurassic). It aligns the Asturian faunal succession with coeval northwestern European basins. The new material preserves diagnostic cranial and postcranial features that refine the morphological characterization of *I. anningae*, including previously undocumented details of the skull anatomy. Based on the length of the humerus, the specimen described here represents the largest known individual of *I. anningae*. Incorporation of the specimen into an updated phylogenetic dataset supports the monophyly of *Ichthyosaurus* and reinforces the distinctiveness of *I. anningae* relative to other Pliensbachian taxa. The co-occurrence of *I. anningae* and *Leptonectes* sp. in the Rodiles Formation provides new evidence for niche partitioning among Early Jurassic ichthyosaurs in the Asturian Basin, paralleling patterns documented in localities in southwestern England. Taken together, these discoveries extend the paleobiogeographic range of Early Jurassic ichthyosaurs, provide new insights into the diversity and complexity of the faunas of the Iberian margin, and offer further evidence of the close affinities of marine communities in Northern Spain with those of the Jurassic subboreal sea of the United Kingdom.

Key words: Ichthyosauria, *Ichthyosaurus*, Pliensbachian, Jurassic, Asturias, Spain.

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Introduction

Ichthyosaurs were dominant components of marine ecosystems during most of the Mesozoic, particularly during the Jurassic. Their fossils are not only geographically widespread (they have been found in all continents including Antarctica, Campos et al. 2021) but are also abundant. Despite exquisite European Early–Middle Jurassic lagerstätten such as Lyme Regis, UK; Posidonia shales of Holzmaden Germany; the Callovian Oxford Clay, UK (e.g., McGowan 1974a, b; Hauff and Hauff 1981; Martill 1991; Stöhr and Werneburg 2022 ; Weedon and Chapman 2022) and worldwide rich Tithonian faunas like those from Svalbard, Russia and Patagonia (e.g., Campos et al. 2024; Zverkov and Efimov 2019; Delsett et al. 2019), there are still some gaps and/or poorly understood periods of ichthyosaurian evolutionary history. One of them

is the Pliensbachian, a time during which ichthyosaur records are comparatively scarce and patchy (Fischer et al. 2022). Based on the substantially different composition of pre- and post-Pliensbachian ichthyosaurian faunas Lomax et al. (2025) pointed out that this time interval was critical in their evolution and suggested that by the end of the early Pliensbachian a substantial turnover in the ichthyosaurian fauna of the Western Tethys had begun.

The iconic genus *Ichthyosaurus* de la Beche & Conybeare, 1821, has an evolutionary history that spans most of the Early Jurassic (Hettangian–Pliensbachian). The abundant and well-preserved Hettangian–Sinemurian records contrast with those of the last episode of their evolutionary history. The Pliensbachian record includes only a few specimens recovered from the southwestern coast of England and the two specimens that are sufficiently complete are referred to: *Ichthyosaurus anningae* Lomax & Massare, 2015, and *Ichthyosaurus conybeari* (Massare & Lomax, 2016). The paleogeographic distributions of *Ichthyosaurus* spp. in general, seem to have been restricted mainly to the Western Tethys, being frequently found in Early Jurassic deposits of England, but not so frequently in co-eval deposits of continental Europe (Zbyszewski and Moitinho de Almeida 1952; Godefroit 1996; Sousa and Mateus 2021). However, an isolated forefin of *Ichthyosaurus* sp. (CMNFV 9896) was described from the Lower Jurassic (likely Pliensbachian) of Alberta, Canada, unequivocally identified by its distinctive morphology (McGowan 1978; Massare et al. 2025).

The taxonomy of *Ichthyosaurus*, after an initial period when all Early Jurassic species were assigned to the genus, remained relatively stable for a long while. Thus, the *Handbook of Paleoherpetology* (McGowan and Motani 2003) included only three valid species: *Ichthyosaurus communis* de la Beche & Conybeare, 1821, *Ichthyosaurus breviceps* Owen, 1881, and *Ichthyosaurus conybeari* Lydekker, 1888. As is the case of other iconic names like *Ophthalmosaurus* Seeley, 1874, and *Platypterygius* Huene, 1922, *Ichthyosaurus*, and *I. communis* in particular, became in many cases a catch-all taxon of Early Jurassic broad-finned specimens with a digital bifurcation anterior to the primary axis and numerous closely-packed phalanges. This situation changed after the systematic review of British historic collections, which resulted in the revalidation of *Protoichthyosaurus* Appleby, 1979 (Lomax et al. 2017), which had been included in *Ichthyosaurus* by Maisch and Matzke (2000) and McGowan and Motani (2003). Additionally, three new *Ichthyosaurus* species were recognized: *Ichthyosaurus anningae* Lomax & Massare, 2015, *Ichthyosaurus larkini* Lomax & Massare, 2017, and *Ichthyosaurus somersetensis* Lomax & Massare, 2017. *Ichthyosaurus anningae* is known from its holotype (a skull and partial postcranium, including both humeri) and four other specimens from historic collections from Lyme Regis, Dorset, along the southwestern coast of England (Lomax and Massare 2015). This species is of particular interest as it helps to improve the still poorly known Pliensbachian records and thus contributes to understanding the last episode in the evolutionary history of the successful *Ichthyosaurus* lineage.

The specimen described herein (MUJA-3558) was initially discovered in 2009 as isolated ribs and a tooth at Vega Beach (Asturias, Spain). Continued surveys of the site in subsequent years resulted in the collection, with precise stratigraphic control, of the remainder of the same individual, including the skull and postcranial elements. In this study, we describe this material and refer the specimen to *Ichthyosaurus anningae.* This discovery is significant not only as the first record of the species outside of the United Kingdom but primarily for the anatomical data it provides. The specimen exhibits exceptional three-dimensional preservation of the cranial elements, bones that are typically crushed, absent, or obscured in previously described individuals. Furthermore, the humerus displays a morphology atypical for Early Jurassic parvipelvians, characterized by a compressed dorsal process that converges on the "plate-like" morphology seen in ophthalmosaurids. Furthermore, together with previous discoveries (Bardet et al. 2008; Fernandez et al. 2018), the new specimen expands the knowledge of the Pliensbachian marine tetrapod faunas, and together with the information provided by other Jurassic records from Portugal (Sousa and Mateus 2021; Pratas e Sousa et al. 2025), documents the composition of the Iberian marine faunas during the Early Jurassic. Our analysis reveals that the Pliensbachian faunas from Northern Spain are more compatible with those of Sinemurian–lower Pliensbachian of southwestern England than with post-Pliensbachian (Toarcian) ones.

Institutional abbreviations.—ANSP, Academy of Natural Sciences, Philadelphia, USA; BRSUG, University of Bristol, UK; CMNFV, Canadian Museum of Nature (Fossil Vertebrates), Ottawa, Ontario, Canada; DONMG, Doncaster Museum and Art Gallery, Doncaster, UK; MUJA, Museo del Jurásico de Asturias, Spain; NHMUK, Natural History Museum, London, UK; ROM, Royal Ontario Museum, Toronto, Canada.

Material and methods

As the skeleton was very fragile, MUJA-3558 was extracted with the matrix and then prepared manually at the MUJA. Although the skull and mandibles are not completely articulated, the elements preserved permit modeling the skull (Fig. 2). On this reconstruction, some relative dimensions (e.g., skull and mandible ratios) could be estimated.

To evaluate the phylogenetic position of MUJA-3558, we scored the specimen in the data matrix of Lomax et al. (2025), itself derived from Moon (2019). The resulting matrix consists of 287 characters and 116 terminal units (SOM 2 and 3, Supplementary Online Material available at http://app.pan.pl/SOM/app71-Fernandez_etal_SOM.pdf) and was analysed in TNT v. 1.5 (Goloboff and Catalano 2016) under equally weighted parsimony. A total of 112 characters (39%)

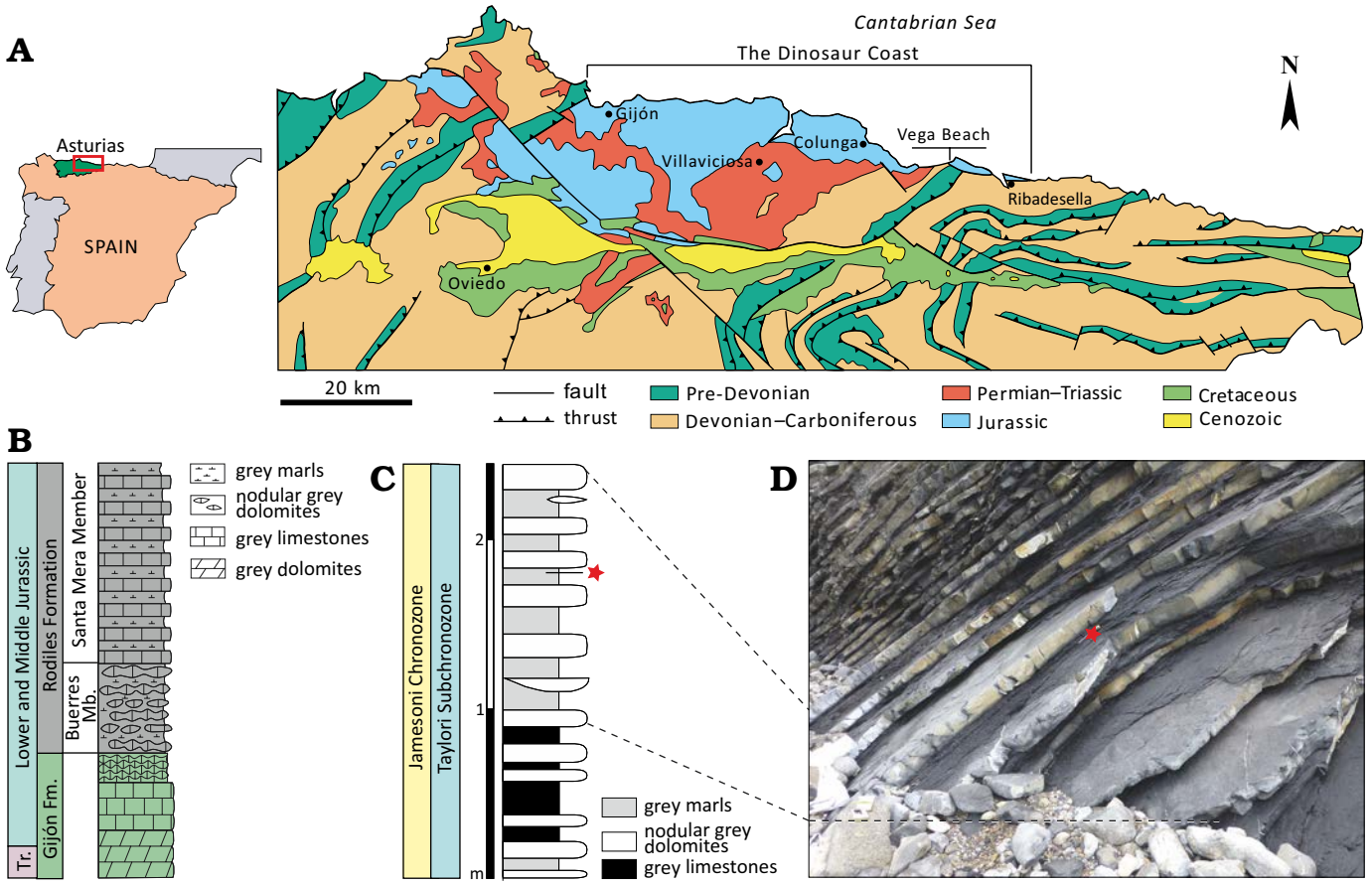

Fig. 1. **A**. Geological map of central-eastern area of Asturias (N Spain), showing the location of Vega Beach on the Ribadesella coastal cliffs where the specimen was found (modified from García-Ramos and Gutiérrez Claverol 1995). **B**. General stratigraphic log (not to scale) of the Tazones-Ribadesella sector (modified from García-Ramos et al. 2011). **C**. Detailed sedimentological log of the interval of the Rodiles Formation containing the ichthyosaur. **D**. Close-up of the alternation of limestone and marl beds. The red star indicates the position of the ichthyosaur bones.

could be scored for MUJA-3558. Multistate characters were treated as non-additive (unordered). Tree searches were carried out using a New Technology Search (50 iterations of the ratchet algorithm, drift algorithm default settings, minimum length found 100 times). The resulting most-parsimonious trees were subsequently subjected to a traditional search using TBR branch-swapping on trees stored in RAM. To identify wildcard taxa that could contribute to instability among the most parsimonious trees (MPTs), we employed IterPCR (Pol and Escapa 2009).

Geological setting

MUJA-3558 was found in the Asturian Basin, specifically at Vega Beach near the city of Ribadesella, at the eastern part of "The Dinosaur Coast" (Asturias, Northern Spain; Fig. 1A). On this beach, the Rodiles Formation crops out spectacularly, with very good exposures of both members of this formation (Fig. 1B). The lower one, Buerres Member, is late Sinemurian in age and consists of 30 m thick nodular limestones with some thin marl interbeds and represents the proximal part of a carbonate ramp. The overlying Santa Mera Member is characterized by a rhythmic alternation of tabular limestones and dark and light grey marl layers, including several intervals of black shales. It represents the middle and outer part of the carbonate ramp (Valenzuela et al. 1985, 1986; García-Ramos and Piñuela 2010). The member is up to 140m thick and spans the late Sinemurian to early Bajocian (Suárez Vega 1974). The skeleton was collected on top of a brachiopod-dominated shell bed belonging to the lower part of the Santa Mera Member (Fig. 1C, D). The age of this layer is early Pliensbachian, and it is included in the Jamesoni Chronozone (Taylori Subchronozone; Fig. 1C; Comas-Rengifo et al. 2023). The adjacent beds of the section contain abundant brachiopods, along with some ammonites, bivalves and belemnites. The most common associated trace fossils are *Chondrites*, *Phymatoderma*, and *Thalassinoides*.

Systematic palaeontology

Ichthyosauria de Blainville, 1835

Ichthyosauridae Bonaparte, 1841

Genus *Ichthyosaurus* de la Beche & Conybeare, 1821

Type species: *Ichthyosaurus communis* de la Beche & Conybeare, 1821, Lyme Regis, Hettangian–Sinemurian.

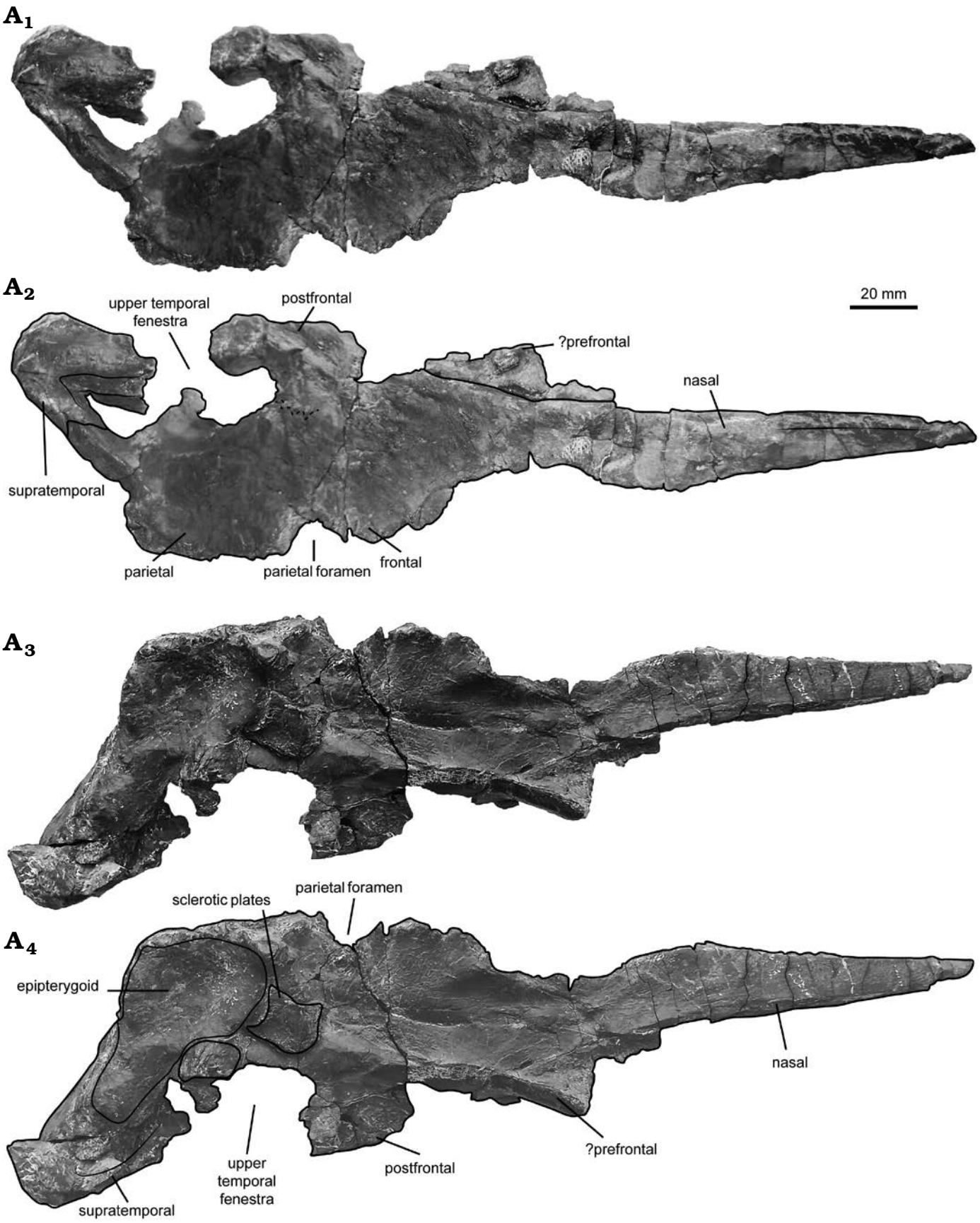

Fig. 2. Ichthyosaurid *Ichthyosaurus anningae* Lomax & Massare, 2015 (MUJA-3558) from Vega Beach, Asturias (Spain), lower Pliensbachian. Skull in dorsal (A_1, A_2) and ventral (A_3, A_4) views. Photographs (A_1, A_3), explanatory drawings (A_2, A_4).

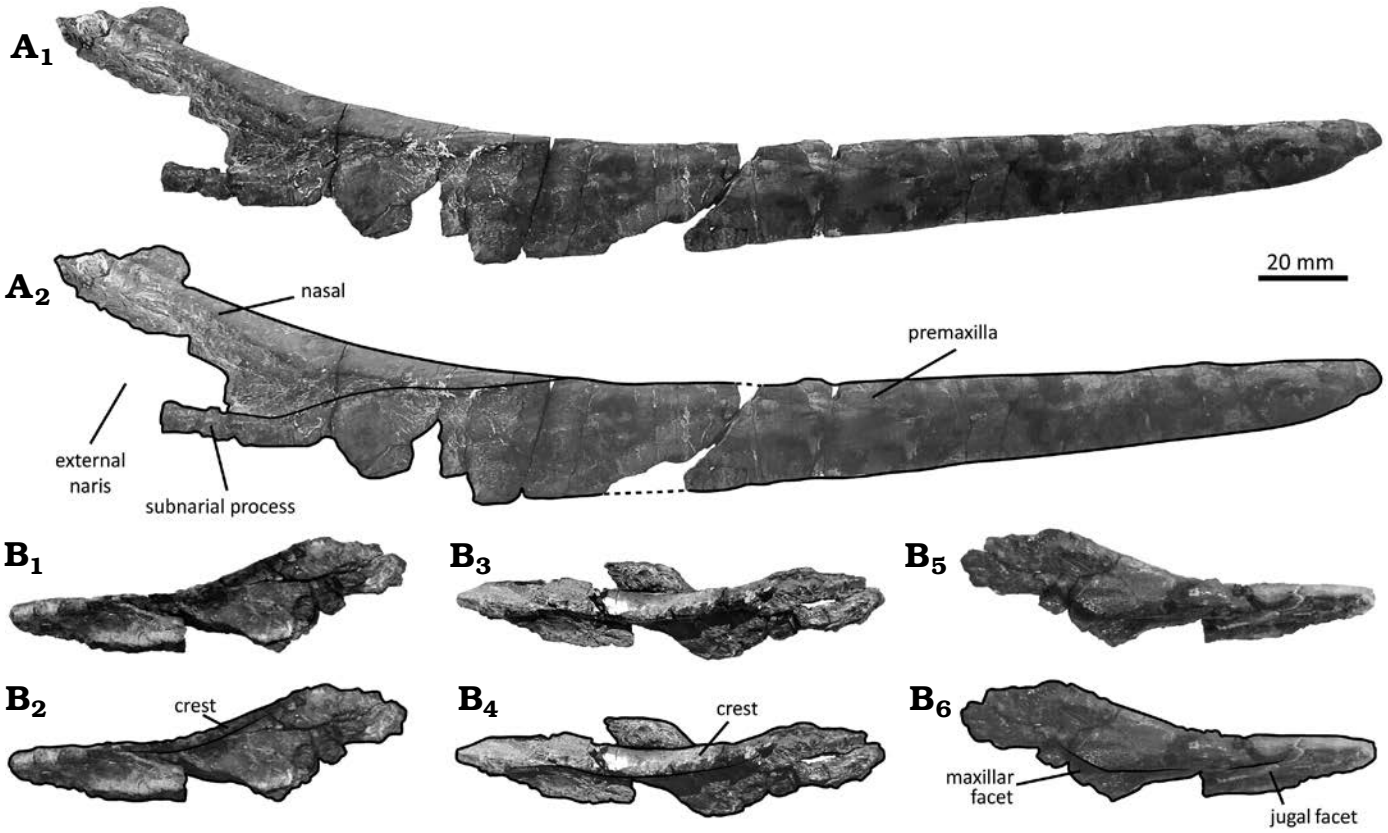

Fig. 3. Ichthyosaurid *Ichthyosaurus anningae* Lomax & Massare, 2015 (MUJA-3558) from Vega Beach, Asturias (Spain), lower Pliensbachian. **A**. Snout in lateral view. **B**. Lacrimal in lateral (B_1, B_2), dorsal (B_3, B_4), and ventral (B_5, B_6) views. Photographs (A_1, B_1, B_3, B_5), explanatory drawings (A_2, B_2, B_4, B_6).

Ichthyosaurus anningae Lomax & Massare, 2015

Figs. 2–9; SOM 1: figs. 1, 2, 3A.

Material.—MUJA-3558, skull, mandible, vertebrae, ribs, partial left forefin including humerus, epipodium, carpals and phalanges, pectoral girdle (scapula and interclavicle) from Vega Beach (43°32'6.18'' N; 5°22'3.02'' W), Ribadesella, Asturias, Spain; Rodiles Formation, Jamesoni Zone, Pliensbachian, Lower Jurassic.

Description.—Two main parts of the skull have been preserved articulated: the left side of the skull roof and articulated nasal (Fig. 2) and the anterior part of the snout (including the complete prenarial segment) (Fig. 3A). The sutural patterns of the skull roof elements are difficult to discern in MUJA-3558. Consequently, the precise configuration of the parietal foramen and the exact contacts between the skull roof elements cannot be reliably established. The preservation of the larger elements of the mandible (dentary, splenial, angular, and part of the surangular), the ventral and posterior orbital margin (postorbital and jugal), and the partial snout and skull roof, permit the reconstruction of the skull profile (SOM 1: fig. 1). The reconstructed rostrum of MUJA-3558 exhibits a robust morphology and a straight dorsal margin. These characters align with the description of the *Ichthyosaurus anningae* holotype and its referred specimens (Lomax and Massare 2015). Most of the preserved skull roof corresponds to the left side. The supratemporal, parietal, frontal, prefrontal, and postfrontal (as well as most of the nasal) are articulated and the only missing part is the contact between the supratemporal and postfrontal. Due to compression, the supratemporal fenestra is distorted and, in dorsal view, the parietal, lateral ramus of the supratemporal and posterolateral part of the postfrontal seem to be wider than they should have been in life (Fig. 2A_1, A_2).

The best defined sutures are the supratemporal-parietal contact. The outline of the left prefrontal is not clear, and the right prefrontal is preserved and disarticulated. Based on its morphology, it is possible to infer that the contribution of the prefrontal to the skull roof was reduced (Fig. 4A). The skull bones with clear sutural edges, as well as the elements that could be completely extracted from the matrix, are described below.

Premaxilla: The right premaxilla is the best preserved and partially articulated with the right nasal (Fig. 3A). The lateral wall of the premaxilla tapers gently towards the tip. Posteriorly, the lateral surface bears a well-developed subnarial process forming the anterior and half of the ventral edge of the external naris. Due to the poor preservation of the dorsal margin of the external naris, it is not possible to precisely determine the presence or absence of the supranarial process. Unlike the premaxilla of the holotype (DONMG:1983.98), there is no conspicuous ornamentation on the anterior portion of the premaxilla. Two other fragments found disarticulated probably correspond to the left premaxilla.

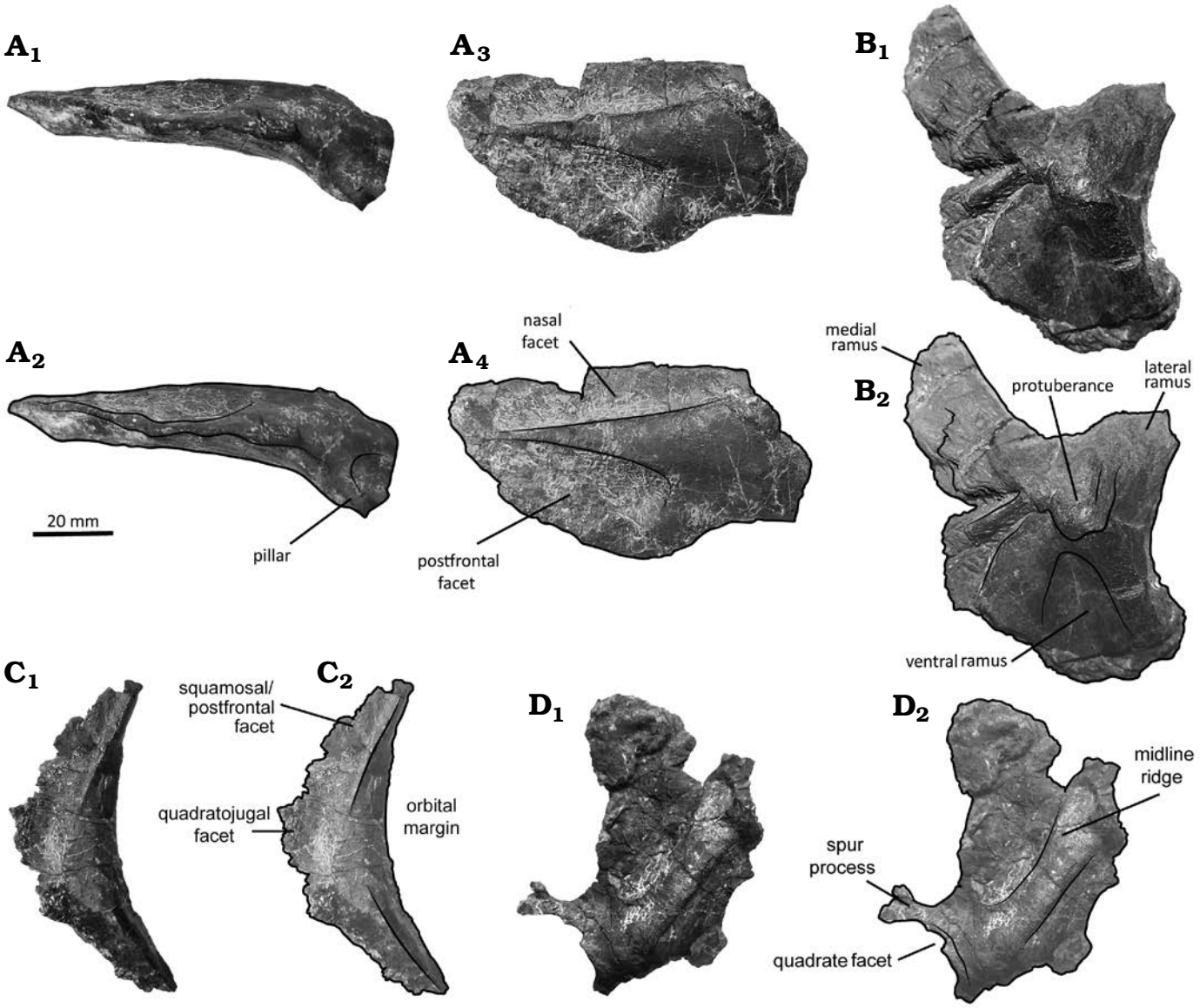

Fig. 4. Ichthyosaurid *Ichthyosaurus anningae* Lomax & Massare, 2015 (MUJA-3558) from Vega Beach, Asturias (Spain), lower Pliensbachian. **A**. Right prefrontal lateral (A_1, A_2) and dorsal (A_3, A_4) views. **B**. Right supratemporal in posterior view (B_1, B_2). **C**. Right postorbital in lateral view (C_1, C_2). **D**. Right quadratojugal in lateral view (D_1, D_2). Photographs (A_1, A_3, B_1, C_1, D_1), explanatory drawings (A_2, A_4, B_2, C_2, D_2).

Nasal: Both nasals are preserved but are exposed and articulated with other elements in very different ways. The left nasal is preserved in natural articulation with the ipsilateral postfrontal and frontal and the best preserved portion is the posterior dorsal surface; however, due to preservations, the sutural contacts among them cannot be traced (Fig. 2A_1, A_2). In contrast, the right nasal is preserved in natural articulation with the left premaxilla, and its well-exposed lateral surface bears a sharp crest. The dorsal surface of the left nasal is only well preserved in its anterior region. The contribution of the nasals to the dorsal surface of the snout is relatively short. Thus, in the dorsal view the nasal forms approximately 23% of the length of prenarial segment (from the tip of the snout up to the anterior margin of the naris).

Lacrimal: The right lacrimal was partially preserved and consists mostly of the ventroposterior process and the base of the dorsal process (Fig. 3B). As the anterior margin is poorly preserved, the sutural pattern between the lacrimal, maxilla, and prefrontal is unknown for the specimen. As in other species of the genus (e.g., *Ichthyosaurus communis*, *I. larkini*, *I. somersetensis*) and in the holotype of *I. anningae* (DONMG:1983.98) the ventroposterior process of the lacrimal makes up less than half of the anterior margin of the orbit (Lomax and Massare 2017). On the lateral surface, posteriorly, there is a crest that follows the orbital margin. A similar ridge has been also described in *Ichthyosaurus communis* and *Hauffiopteryx typicus* (Marek et al. 2015; McGowan 1973). On its ventral surface, there is a groove for the reception of the jugal.

Prefrontal: The right prefrontal was completely removed from the sedimentary matrix (Fig. 4A). It consists of a dorsal sheet of bone and a thicker anteroventrally directed pillar

forming the anterodorsal margin of the orbit. As the anterior portion of the bone is broken, the extent of the prefrontal contribution to the orbital rim cannot be determined. The dorsal sheet tapers posteriorly and its dorsal surface has two depressed and roughened areas that mark the overlapping contacts with the surrounding bones. They are separated by a smooth V-shaped and narrow surface indicating its narrow contribution to the skull roof.

Supratemporal: The supratemporal forms the posterolateral border of the supratemporal fenestra (Figs. 2, 4B). It branches into ventral, medial and lateral rami. In MUJA-3558, the left supratemporal is in its anatomical position and remains articulated with the skull roof via its sutural contact with the parietal, whereas the right one is completely disarticulated and compressed. Both lateral supratemporal rami are broken anteriorly and the left one is the more complete. The medial ramus of the left supratemporal is complete and has a robust anterior contact. In the posterior view, the ventral supratemporal ramus extends as a convex sheet of bone. On the most posterior portion of the supratemporal, there is a rounded and rugose protuberance probably ("knob") for the attachment of the M. depressor mandibulae, very similar to the one described by McGowan (1973) in *I. communis* (NHMUK R8177). Such a protuberance is frequent among ophthalmosaurids but it is generally more conspicuous, and it is particularly developed in some Late Jurassic forms like *Thalassodraco* (Jacobs & Martill, 2020).

Postorbital: The right postorbital is completely preserved (Fig. 4C). The lateral surface is divided into a smooth anterior crescentic portion that tapers dorsally and ventrally, and a posterior portion (also crescentic) characterized by a predominant roughened texture. The smooth and narrow anterior portion corresponds to the area of the postorbital exposed laterally. In MUJA-3558, the postorbital contribution to the cheek seems to be more reduced anteroposteriorly than in some *Ichthyosaurus* species such as *I. communis* (NHMUK PV R8I77, NHMUK PV R1162) (McGowan 1973: fig. 37, pl. 8; Lomax and Massare 2017: fig. 5), *I. larkini* (BRSUG 25300) and *I. somersetensis* (ANSP 15766) (Lomax and Massare 2017: figs. 1, 5). A thin posteroventrally directed crest separates the dorsal half of the laterally exposed region from a rough-textured posterior zone that delimits the area of overlap with the supratemporal/squamosal. In a similar manner, on the anteroventral part of the postorbital, a sharp crest separates the smooth and narrow anterior region from the posterior region, which has a groove where the jugal fits in and that is extended backward in an extensive rugose surface that marks the overlapping with the quadratojugal.

Quadratojugal: The right quadratojugal is almost completely preserved and was completely removed from the sedimentary matrix (Fig. 4D). On the lateral surface are two blunt vertical crests running parallel to one another and delimiting by a smooth raised surface between them. Anterior to this elevated surface is a roughened depressed area for the reception of the overlying postorbital (dorsally) and jugal (ventrally). As described by McGowan (1973) for

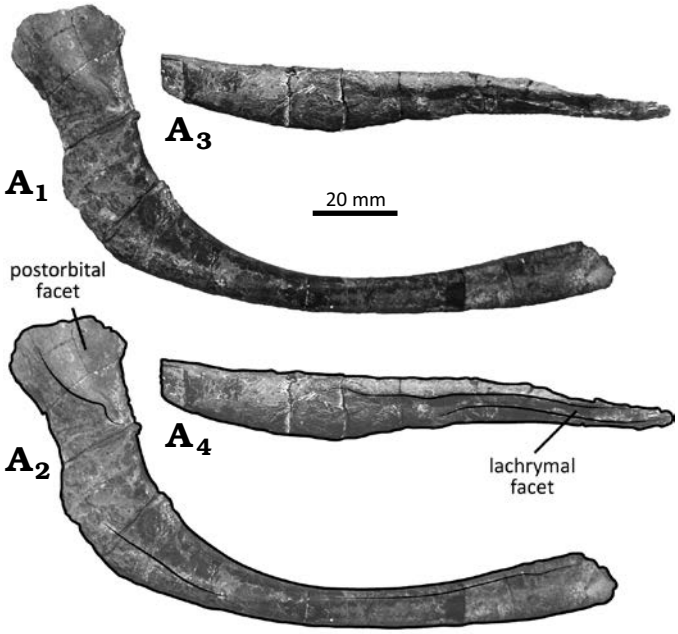

Fig. 5. Ichthyosaurid *Ichthyosaurus anningae* Lomax and Massare, 2015 (MUJA-3558) from Vega Beach, Asturias (Spain), lower Pliensbachian. Right jugal in lateral (A_1, A_2) and dorsal (A_3, A_4) views. Photographs (A_1, A_3) and explanatory drawings (A_2, A_4).

Ichthyosaurus communis, dorsally the quadratojugal widens out like a fan. In lateral view, at approximately one third of its length, the quadratojugal is constricted. On the posterior margin, ventral to the constriction, there is a process with a dorsal curved margin in the same location and similar to the "spur" process described by McGowan (1973). The medial surface is almost smooth except for a vertical crest. On the posteroventral margin is a concave facet for the articulation with the quadrate.

Jugal: Both jugals are disarticulated and, despite both being broken, the complete bone can be reconstructed (Fig. 5, SOM 1: fig. 2). The left jugal preserves the anterior process and most of the horizontal ramus that forms the ventral orbital rim whereas the right one is almost complete except for its most anterior tip. As in other species of *Ichthyosaurus*, the horizontal ramus tapers to a point anteriorly. The posterior part of the jugal, including the dorsal process, is more acute than in the holotype of *I. anningae*. Thus, the dorsal ramus is curved, forming an almost right angle with the horizontal ramus and the posterior bulge is more pronounced and it is in line with the horizontal ramus. On the lateral surface of the dorsal process, there is a facet for the articulation with the postorbital. Based on the reconstruction of the jugal-postorbital articulation it can be inferred that, as in the holotype of *I. anningae* the contribution of the jugal to the posterior border of the orbit less than one third of the height of the posterior margin of the orbit.

Epipterygoid: The shaft of the left epipterygoid is almost complete and it has been preserved attached to the ventral surface of the ipsilateral parietal and supratemporal exposed on its medial view (Fig. 2A_3, A_4; SOM 1: fig. 3). An isolated

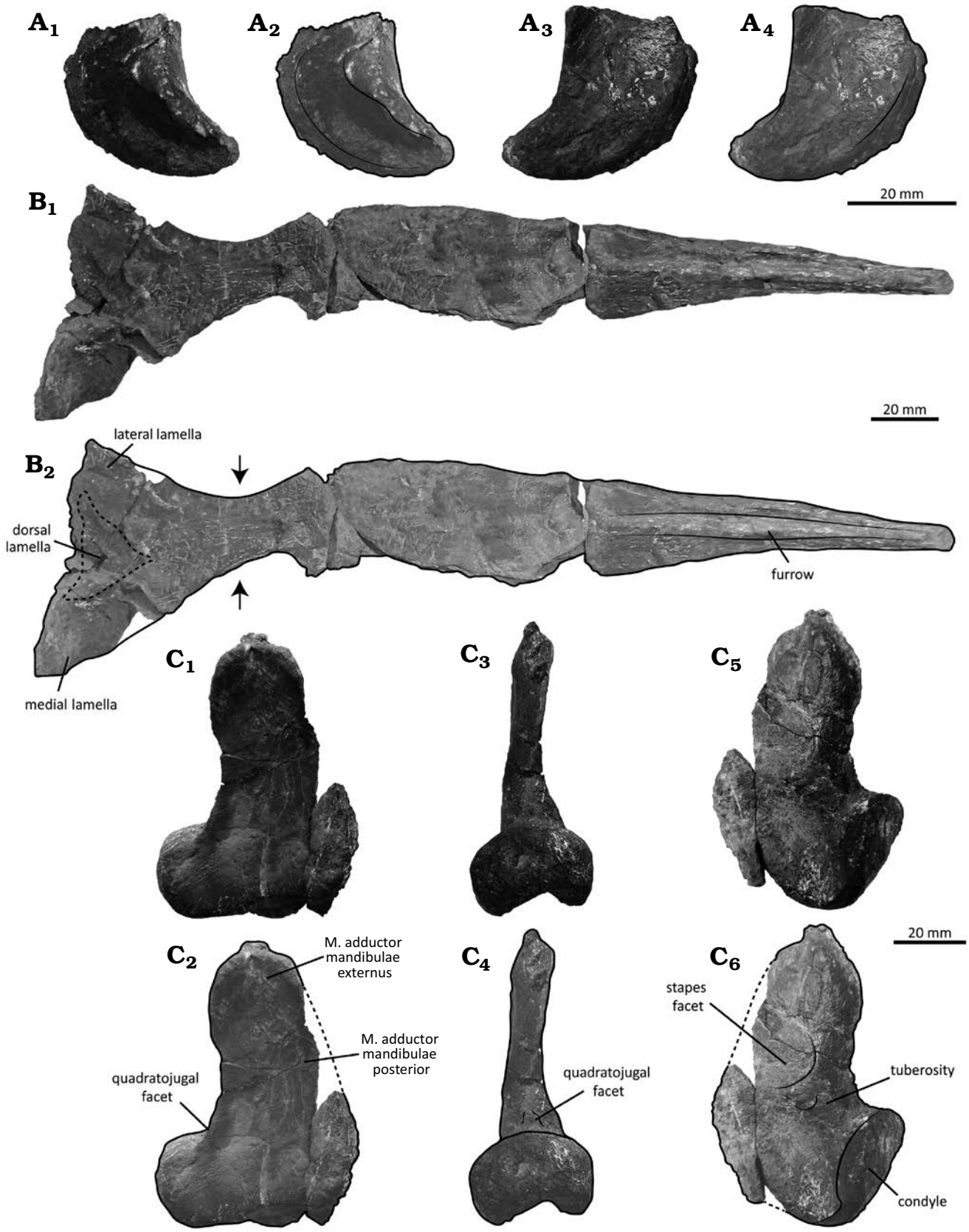

Fig. 6. Ichthyosaurid *Ichthyosaurus anningae* Lomax & Massare, 2015 (MUJA-3558) from Vega Beach, Asturias (Spain), lower Pliensbachian. **A**. Left epipterygoid (ventral portion, "foot") in lateral and slightly ventral (A_1) and medial (A_2) views. **B**. Left pterygoid in dorsal view (B_1, B_2). **C**. Right quadrate in anterior (C_1, C_2), lateral (C_3, C_4), and posteromedial (C_5, C_6) views. Black arrows indicate the pterygoid vacuites. Photographs (A_1, A_3, B_1, C_1, C_3, C_5), explanatory drawings (A_2, A_4, B_2, C_2, C_4, C_6).

element, laterally compressed with a grooved ventral surface (Fig. 6A; SOM 1: fig. 3), is here identified as the tip of the "foot" (sensu McGowan 1973: 22) of the same bone. As described by McGowan (1973), the dorsally expanded shaft of the epipterygoid of MUJA-3558 forms a flange and it bears a bulge approximately at mid-height. The only difference with *I. communis* is that the dorsal half of the bone (bearing the bony flange for the articulation with the parietal) of MUJA-3558 is more expanded in comparison with that figured by McGowan (1973: figs. 8, 37, pl. 2b); however, this could be due to compression during fossilization. The epipterygoid is a relatively large element and well ossified, indicating a stout connection between the skull roof and the palate.

Pterygoid: The left pterygoid is fairly complete but poorly preserved, and is exposed in dorsal view (Fig. 6B). While the quadrate ramus is clearly visible, the fragile palatal ramus, which forms the anterior portion of the element, remains embedded in the matrix to ensure its preservation. The quadrate and palatal rami are separated by emarginations of their medial and lateral margins; these, in turn, define the boundaries of the interpterygoid vacuity and the subtemporal fenestra, respectively. The palatal ramus takes the form of a thin sheet of bone that begins to taper from approximately its mid-length, eventually forming a pointed anterior extremity. On the dorsal surface, starting approximately at the point where the palatal ramus begins to taper, a shallow longitudinal groove appears and extends to the anterior extremity of the bone.

Quadrate: Both quadrates have been partially preserved. The right one (Fig. 6C) is the most complete and preserves the articular condyle and most of the dorsal ramus whereas the left one is only represented by the articular condyle. It is formed by the stout articular condyle and a thin dorsal ramus. On the ventral surface, the condyle bears a well-defined triangular depression separating the rugose, convex articular facet and the facet for the surangular. In anterior view, the dorsal ramus is slightly concave dorsally and convex ventrally. Despite the dorsal ramus being partially broken, at the middle of its height, a sculptured area is visible, probably corresponding to the origin of the M. adductor mandibulae posterior; and dorsal to it is a shallow rugose depression probably for the M. adductor mandibulae externus (Moon and Kirton 2016). A pitted area along the ventral half of the medial margin of the quadrate marks the contact with the pterygoid. In lateral view, a triangular sculptured area, just above the articular condyle, indicates the area or articulation with the quadratojugal. In the posterior view, the dorsal portion of the lamella is gently convex. In this view, at one-half of the quadrate height is a shallow elliptical depression for the reception of the stapes. Just ventral to it is a tuberosity similar to one described for *Ophthalmosaurus icenicus* and interpreted by Kirton (1983) as the attachment point for the ligament that ties the quadrate and pterygoid. In all its views, the quadrate of MUJA-3558 is similar to that of *I. communis* (McGowan 1973: pls. 2c, 7e).

Opisthotic: The right opisthotic is completely preserved although distorted (Fig. 7A). Most of its anterior surface is roughened. As in *Ichthyosaurus communis*, the paroccipital process is short and stout, and it is not as slender as in most ophthalmosaurids (Fernández 1999; Fischer et al. 2012; Miedema et al. 2024). In anterior view, a deflection of the ventral edge continues into a slight depression on the ventral surface that forms the facet for articulation with the basioccipital. On the ventral surface, another elongated depression, larger than the former, indicates the facet for articulation with the stapes. On its posterior surface, there is a blunt ridge separating two rugose areas for muscle attachment, probably for the M. adductor mandibulae externus. The osteological correlates of the posterior components of the inner ear are shown on the medial surface and comprise two channels that join in a large concavity. The surfaces of these impressions are smooth. The channels probably housed the horizontal and posterior vertical semicircular canals, whereas the large concavity could have held the posterior ampulla and sacculus. Ventrally to these impressions is a deep and narrow groove probably for the hyomandibular branch of the facialis (VII) or the glossopharyngeal (IX). A small notch on the posterior border could correspond to the vagus foramen.

Supraoccipital: The supraoccipital was complete and was removed from the matrix (Fig. 7C). In anterior and posterior views, its outline is roughly quadrangular with a relatively straight dorsal margin. Running along the dorsal surface is a shallow roughened groove, suggesting cartilaginous contact with the ventral surface of the skull roof. As in other Early Jurassic *Ichthyosaurus*, and contrasting with the conditions of most derived forms (i.e., Ophthalmosauridae), the contribution of the supraoccipital to the foramen magnum is reduced. Thus, in MUJA-3558, *Ichthyosaurus communis*, *Stenopterygius* spp., and *Hauffiopteryx* (McGowan 1973; Marek et al. 2015; Miedema and Maxwell 2019), the contribution to the foramen magnum is less than one third of the total bone height. In anterior view, the dorsal half of the anterior surface is concave. Ventrally, the supraoccipital thickens to form the two short pillars. The impressions of the posterior portion of the otic capsule are clearly seen on the anterior surface of the pillars. A mirrored deflection of the ventral edges of the pillars forms the facet for the reception of the exoccipitals that extend to the ventral surface. In ventral view, the facets for the exoccipital are concave and triangular. The posterior surface of the supraoccipital is mainly convex and smooth except for its dorsal part, where this bone is overlapped by the parietals. Laterodorsal to the foramen magnum, the supraoccipital is pierced by a pair of foramina. Similar foramina have been identified in *Ichthyosaurus communis* (McGowan 1973) and ophthalmosaurids (e.g., *Ophthalmosaurus*, *Arthropterygius thalassonotus*, *Acamptonectes*) but are rare among *Stenopterygius* spp. (Miedema and Maxwell 2019).

Mandible: The right dentary is almost complete although poorly preserved. It is relatively slender and tapers to a point anteriorly (Fig. 7C). On its lateral wall, a longitudinal groove and some small foramina can be seen but,

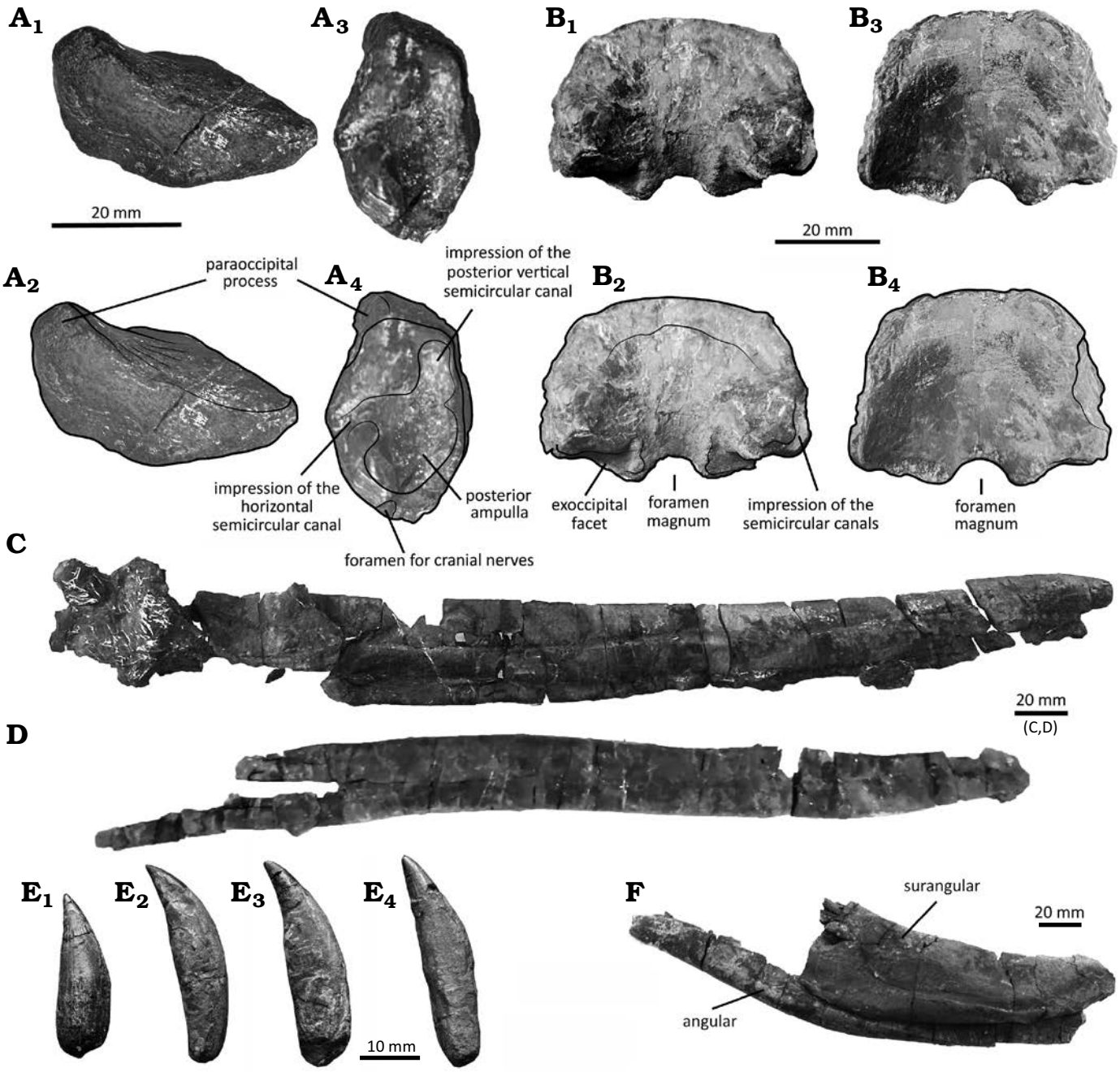

Fig. 7. Ichthyosaurid *Ichthyosaurus anningae* Lomax & Massare, 2015 (MUJA-3558) from Vega Beach, Asturias (Spain), lower Pliensabachian. **A**. Right opisthotic in posterior (A_1, A_2) and medial (A_3, A_4) views. **B**. Supraoccipital in anterior (B_1, B_2) and posterior (B_3, B_4) views. **C**. Right dentary in lateral view. **D**. Splenial in medial view. **E**. Teeth in lateral view (E_1–E_4). **F**. Right surangular and angular in lateral view. Photographs (A_1, A_3, B_1, B_3, C–F), explanatory drawings (A_2, A_4, B_2, B_4).

contrary to the mandible of the *I. anningae* holotype, there is no conspicuous ornamentation. The medial surface is still partially covered by the matrix so the extension of the symphysis cannot be traced accurately. Ventrally, a groove corresponding to the symphysial portion of the Meckelian canal can be distinguished. It widens posteriorly, being covered by the forked splenial to form the Meckelian fossa. The splenial (Fig. 7D) is a sheet of vertical bone, the largest element of the mandible, and it is deeply forked anteriorly. Posteriorly, the splenial tapers dorsoventrally fit with the angular. Both surangulars have been preserved, although incomplete. The right one lacks a third of the posterior part and was found partially articulated with the ipsilateral angular but both bones were completely separated during preparation (Fig. 7F). The left surangular is complete but detached from the remaining elements of the mandible. The surangulars are robust bones contrasting with the slenderness of the other elements of the mandible. The lateral wall is slightly convex and at its maximum height is almost double the height of the dentary.

Dentition: Several teeth were found associated with the material but none of them were found articulated. Most of the teeth that were complete, even those that retained enamel, display some degree of erosion. Although tooth morphology may change according to position in the jaws and/or ontogenetically (Cortés et al. 2021), all teeth associated with MUJA-3558 have a common pattern: they are conical, relatively short crowns with a pointed to rounded apex, and roots with coarse infoldings continuing as longitudinal striations towards the crown apex (Fig. 7E). In three teeth that are complete, the height of the crown is approximately or less than one third of the total height of the tooth (SOM 1: table 1)

Postcranium: vertebral column: The vertebral column was not preserved articulated except for some short sections formed by two or three vertebrae. Approximately 49 vertebral centra and ribs are scattered throughout the various blocks of the matrix (Fig. 8). Several vertebral centra were found in close association although not strictly articulated. Many vertebral centra were found in contact with each other. In lateral view the cervical and dorsal centra are roughly rectangular and have prominent anterior and posterior rims. The atlas and axis pleurocentra (Fig. 8A) are completely fused and the suture between them is only visible dorsally. The complex is comparatively larger than the isolated cervicals closest to it (e.g., atlas-axis complex: height 41 mm, width 42 mm; cervical centrum: height 32 mm, width 33.8 mm).

Pectoral girdle: An incomplete scapula, here identified as the left one, and the interclavicle are preserved in MUJA-3558 (Fig. 9). The scapula (Fig. 9B) consists of the complete shaft, strongly compressed, and most of the acromial process. Its general morphology resembles that of the *I. anningae* holotype (Lomax and Massare 2015: fig. 2) except for the acromial process, which in MUJA-3558 is more slender and anteriorly projected in MUJA-3558. However, this should be taken with caution because it may be diagenetic. The interclavicle (Fig. 9C) is complete, and its morphology is similar to the interclavicle of *I. communis* (NHMUK VP R288) described and figured by McGowan and Motani (2003: fig. 56).

Forefin: A partial left forefin (the humerus and a partial articulated zeugopodium, proximal carpals and two distal carpals) and other isolated elements scattered next to the other fin bones are preserved in MUJA-3558.

The humerus (Fig. 9A, D) is almost complete except for the distal portion of the dorsal process and a small posterodistal portion of the surface for the articulation with the ulna. Despite being partially eroded, the extension of the dorsal process on the dorsal surface of the humerus can be traced. The humerus of MUJA-3558 is short and robust, with a slightly constricted shaft, a morphology consistent with other species of *Ichthyosaurus* but distinct from other Pliensbachian taxa such as *Xiphodracon goldencapensis*, *Hauffiopteryx typus*, and *Leptonectes* spp. (Maxwell and Cortés 2020; Lomax et al. 2025). Specifically, the proximal and distal widths in MUJA-3558 are subequal (ratio 0.94), whereas the humeri of *X. goldencapensis*, *H. typus*, and *Leptonectes* spp. are relatively elongated and characterized by a distal expansion that is significantly broader than the proximal end (e.g., proximal/distal width < 0.90). In dorsal view, the most conspicuous feature is the dorsal process. In MUJA-3558, the base of the process outlines a narrow and compressed structure projecting from the shaft. The dorsal process resembles, despite being less developed, the "plate-like" process of ophthalmosaurids. It rises from the proximal end but slightly more posteriorly than in *I. communis* (ROM 30148; Motani 1999: fig. 2I). Distally, the dorsal process descends antero-distally and extends for more than the half of the proximodistal length of the humerus. The relative extension of the dorsal process of MUJA-3558 is the same as in the holotype of *Ichthyosaurus anningae* (DONMG:1983.98) and differs from the short process described in *I. communis* (ROM 30148; Motani 1999: fig. 2I). The relative length of the dorsal process also resembles the condition present in some ophthalmosaurids such as *Ophthalmosaurus icenicus* (Moon and Kirton 2016: text-fig. 33a; pl. 30: 5, 6), *Sveltonectes* (Fischer et al. 2011: fig. 4H) and *Myobradypterygius* (Campos et al. 2024: fig. 2).

The pattern and morphology of the zeugopodium and proximal carpal row (Fig. 9A) are consistent with those of the holotype (Lomax and Massare 2015: fig. 2). The radius and ulna are subequal in size, and the hexagonal intermedium separates the radiale from the ulnare and supports two digits distally. From the distal carpal row, two carpals identified as 3 and 4 are the only articulated element preserved.

Stratigraphic and geographic range.—At least upper Sinemurian–Pliensbachian and its geographic range comprises Lyme Regis and Charmouth, Dorset (southern England), Vega Beach, Ribadesella (northern Spain)

Phylogenetic analysis

The phylogenetic analysis under equal weights resulted in 74 most-parsimonious trees (MPTs), each with a length of 1684 steps. The strict consensus tree shows relatively well-resolved relationships among Triassic forms; however, this is not the case for Parvipelvia, in which only some of the major clades (Temnodontosauridae, Ichthyosauridae, and Hauffiopterygia) are recovered, while others, such as Stenopterygiidae and Ophthalmosauridae, are completely collapsed internally. Despite this, MUJA-3558 is recovered deeply nested within Ichthyosauridae, as the sister taxon of *Ichthyosaurus anningae*. The IterPCR procedure identified more than 35 unstable taxa, most of which correspond to representatives of Ophthalmosauridae. This instability appears to result from conflicting character information and missing data. The subsequent removal of these unstable taxa substantially improved the resolution of the consensus tree (Fig. 10). The reduced consensus topology recovers *Ichthyosaurus* spp. as a monophyletic group, representing the most basal member of Jurassic Parvipelvia. This position for the clade is consistent with the most recent phyloge-

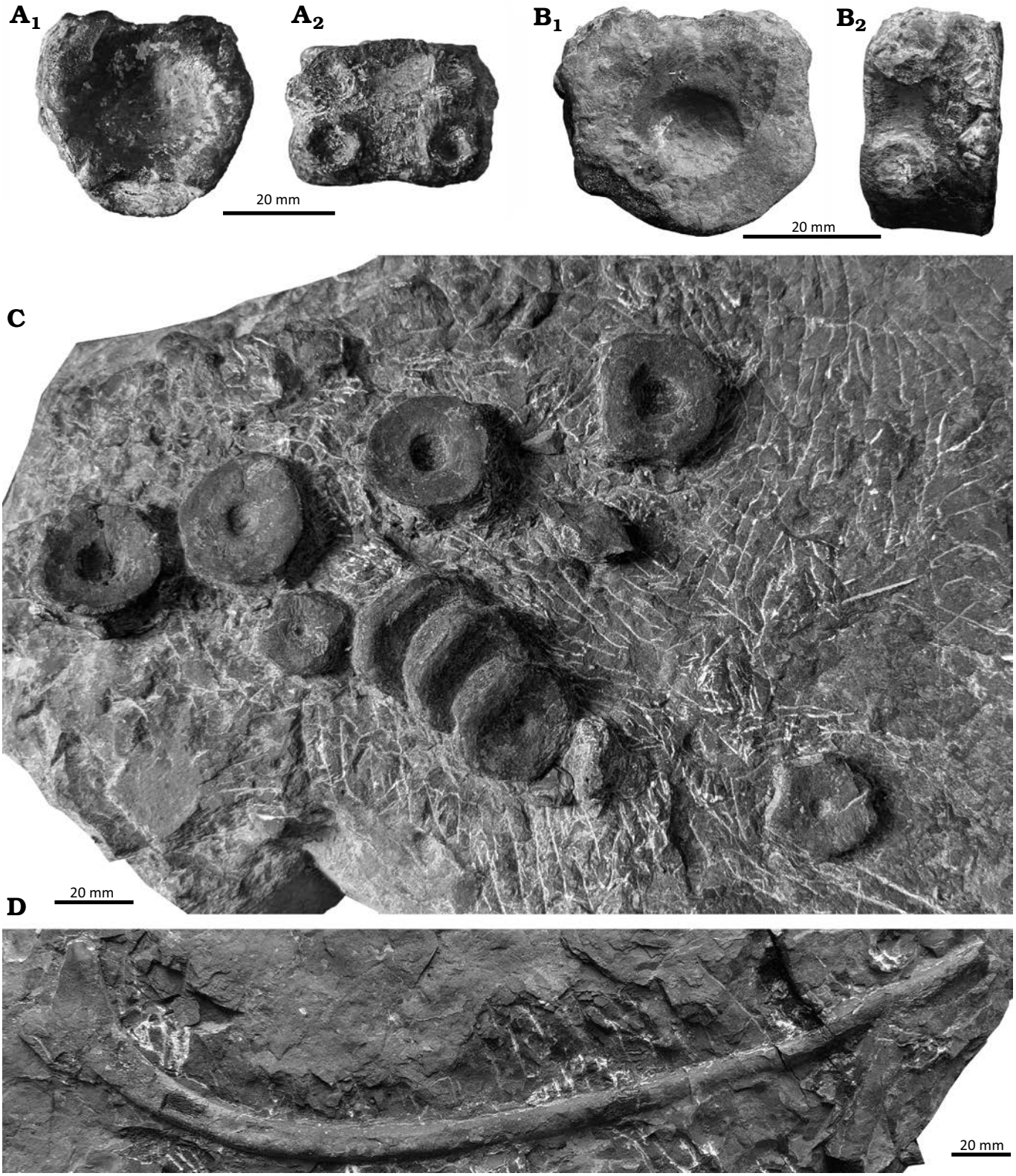

Fig. 8. Ichthyosaurid *Ichthyosaurus anningae* Lomax & Massare, 2015 (MUJA-3558) from Vega Beach, Asturias (Spain), lower Pliensabachian. **A**. Atlas-axis complex centrum in anterior (A_1) and dorsal (A_2) views. **B**. Dorsal vertebra centrum in anterior (B_1) and dorsal (B_2) views. **C**. Caudal centra in anterior or posterior view. **D**. Dorsal rib in anterior view.

netic hypothesis (e.g., Maxwell and Cortés 2020; Laboury et al. 2022; Lomax et al. 2025). The *Ichthyosaurus* clade is supported by the following synapomorphies: (i) a tail shorter than the precaudal length of the body; (ii) an ulna larger than the intermedium; (iii) subequal distal facets of the intermedium; (iv) an ischium with a rod-like shape and

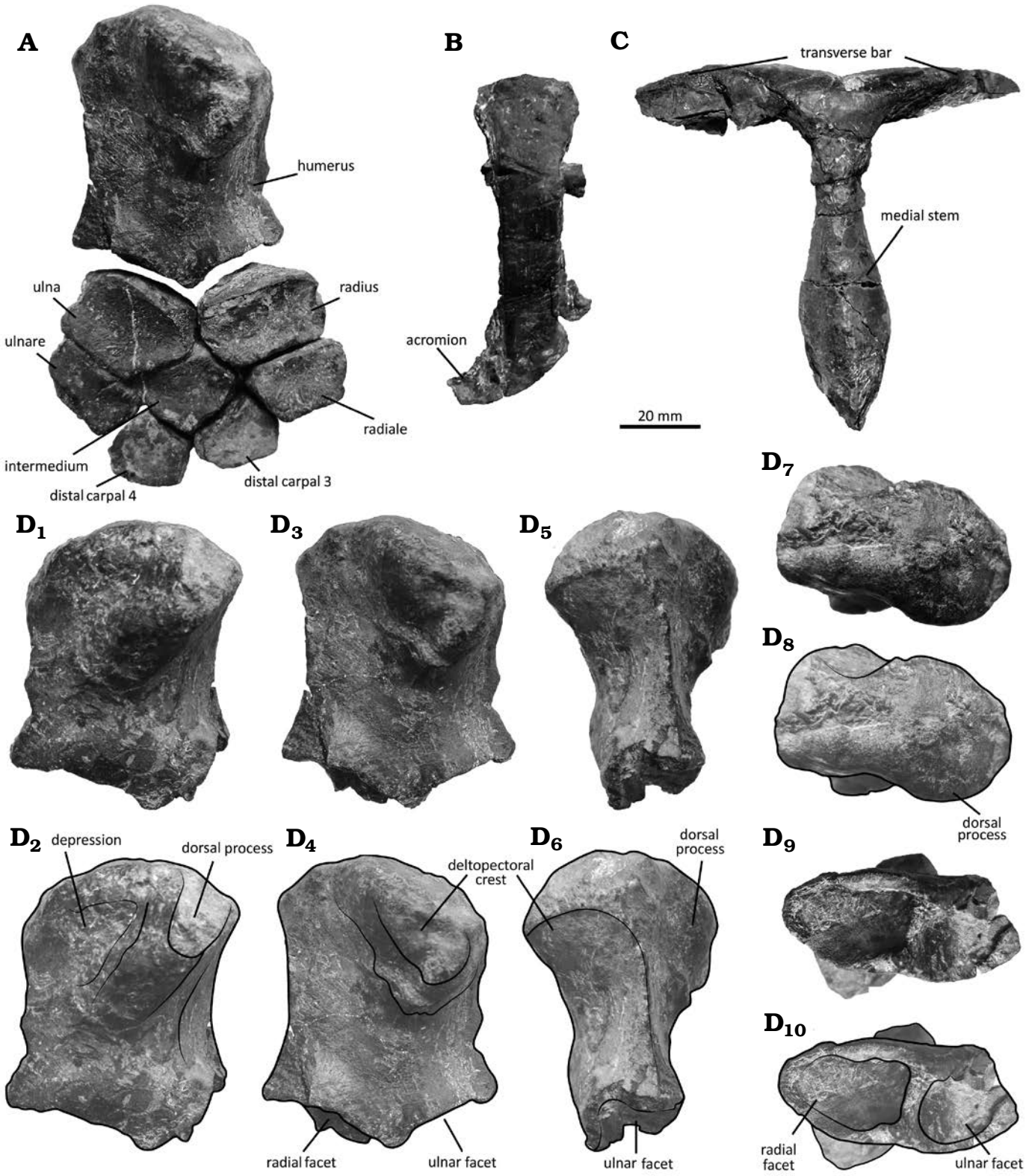

Fig. 9. Ichthyosaurid *Ichthyosaurus anningae* Lomax & Massare, 2015 (MUJA-3558) from Vega Beach, Asturias (Spain), lower Pliensabachian. **A**. Partial forefin in ventral view. **B**. Left scapula in lateral view. **C**. Interclavicle in ventral view. **D**. Left humerus in dorsal (D_1, D_2), ventral (D_3, D_4), posterior (D_5, D_6), proximal (D_7, D_8), and distal (D_9, D_{10}) views. Photographs (A–C, D_1, D_3, D_5, D_7, D_9), explanatory drawings (D_2, D_4, D_6, D_8, D_{10}).

an acetabular contribution greater than that of the pubis; (v) a femur with subequal proximal and distal ends; (vi) a straight or convex anterior margin of the tibia; (vii) polygonal metatarsals. Temnodontosaurids, leptonectinids, hauffiopterygians, and stenopterygids are retrieved as successive outgroups to Ophthalmosauridae.

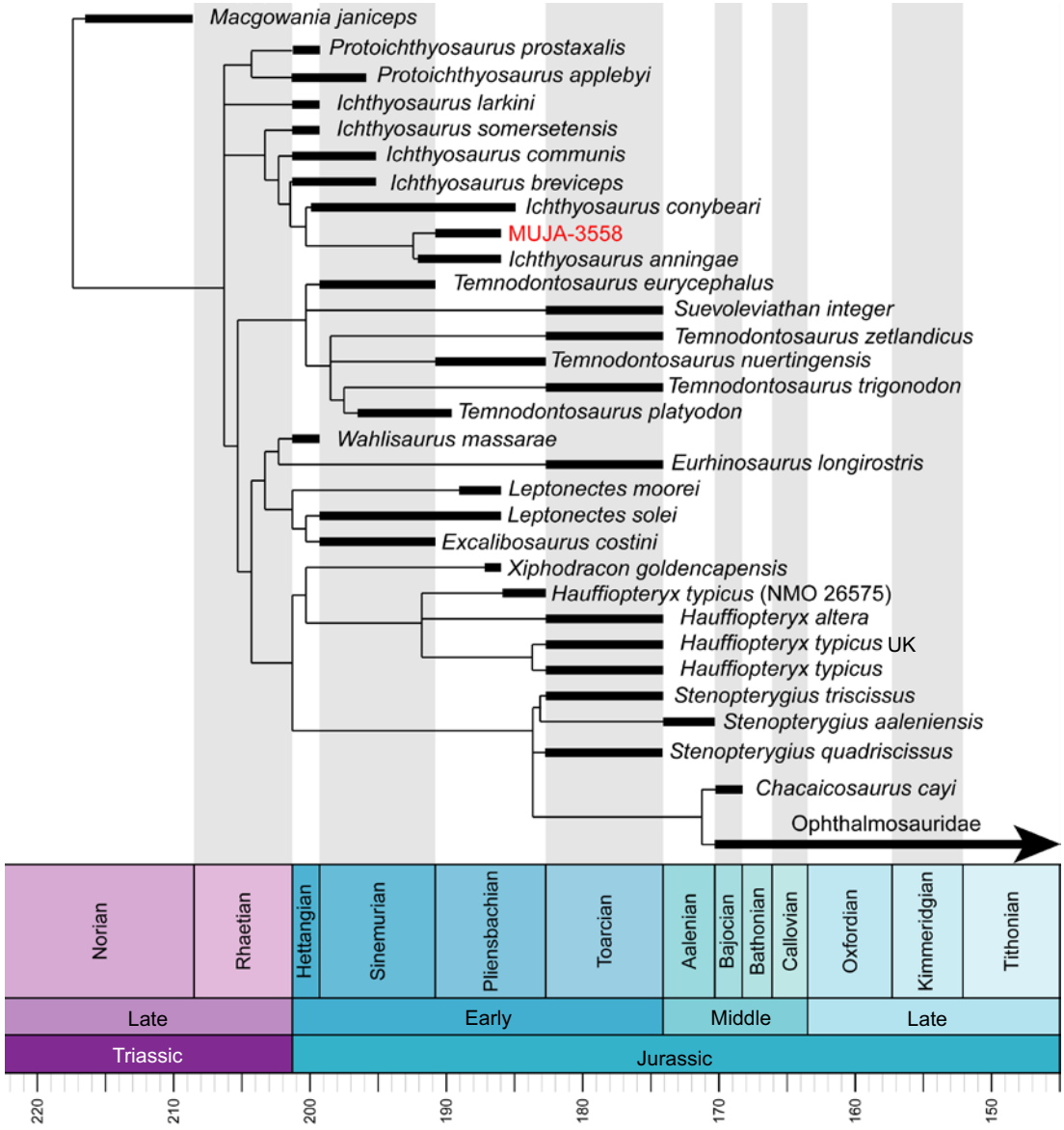

Fig. 10. Time-calibrated strict consensus of arising equal weights resulted in 74 most-parsimonious trees of 1684 steps.

Discussion

Identification of the Northern Spain ichthyosaur and phylogenetic affinities.—MUJA-3558 is clearly distinguished from other Pliensbachian ichthyosaurs like *Leptonectes* sp, *Hauffiopteryx* sp., *Xiphodracon goldencapensis* by its shorter rostrum and robust dental morphology, lacking the extreme rostral elongation and the distal explanation of the humerus typical of these forms. The comparison with *Fernatator prenticei* from the Pliensbachian of British Columbia (Canada) is more complicated since there are few comparable elements between holotype, and the only known specimen of this species, and MUJA-3558. However, the curved dorsal ramus of the jugal forming an almost right angle with the suborbital process contrasts with *F. prenticei* jugal characterized by the lack of dorsal bend, and a short, wide and relatively straight posterior process. On the other hand, MUJA-3558 can be assigned to a species of *Ichthyosaurus*, and distinguished from its closely related *Protoichthyosaurus*, based on a combination of skull and forefin features. Thus, the rostrum of MUJA-3558 is relatively robust, as in *Ichthyosaurus communis*, contrasting with the long slender one of *Protoichthyosaurus* spp. and *I. larkini*; however, the slenderness of the rostrum is not easily quantified (Lomax and Massare 2018). The morphology of the preorbital region, specifically the sutural relationships and the relative contributions of the circum-narial and circum-orbital elements, is considered taxonomically significant within Parvipelvia (e.g., Fischer et al. 2016; Zverkov and Jakobs 2020). In the particular case of Lower Jurassic ichthyosaurs, and more specifically within *Ichthyosaurus*, these cranial characters are diagnostic for differentiating *I. communis*, *I. larkini*, and *I. somersetensis*, and serve as key fea-

tures for distinguishing the genus from *Protoichthyosaurus* (Lomax and Massare 2017, 2018; Lomax et al. 2020). The premaxilla, prefrontal, jugal, and lacrimal are all preserved in MUJA-3558 but their disarticulation precludes a reliable reconstruction of the narial and orbital margins however, in lateral view, the left prefrontal of MUJA-3558 depicts the same pattern described for *Ichthyosaurus communis* and *I. anningae*. That is, the ventral process of the prefrontal is short and robust with a reduced contribution to the anterior orbital rim contrasting with the dorsoventrally long anteriorly process extending along part of the anterior orbit margin of *Protoichthyosaurus* spp. and *Ichthyosaurus larkini* and *I. somersetensis*. Beyond the combination of these skull features, the most conspicuous and unequivocal evidence to distinguish MUJA-3558 from *Protoichthyosarus* species, and referred to as *Ichthyosaurus*, is provided by the arrangement of the carpal rows. While in *Protoichthyosaurus* species distal carpal 3 contacts the ulnare, in MUJA-3558 as in *Ichthyosaurus* spp. the intermedium bears two subequal articular facets for distal carpal 3 and 4 precluding distal carpal 3-ulnare contact. Within the *Ichthyosaurus*, MUJA-3558 differs from all other species and it can be assigned to *Ichthyosaurus anningae* based on the following autapomorphies: (i) a short, robust humerus with a prominent deltopectoral crest extending over more than half of the shaft length; (ii) an anterior margin of the humeral shaft markedly shorter than the posterior margin in ventral view; (iii) a distinct dorsoventral constriction of the humeral head. Although the circular depression anterior to the dorsal process of the humerus, previously described as an autapomorphy of *I. anningae* (Lomax and Massare 2015), is not evident in MUJA-3558, a constriction and subtle depression are present in the same region. This discrepancy is plausibly attributable to individual or ontogenetic variation. Crucially, the absence of a distinct circular depression does not compromise the taxonomic referral, as MUJA-3558 aligns with the diagnosis of *I. anningae* in all other significant aspects of its cranial and postcranial anatomy.

Based on humeral length, the MUJA-3558 represents the largest known individual of *I. anningae*, with humeral dimensions comparable to those of the largest *Ichthyosaurus somersetensis* specimens (Lomax and Massare 2015: table 2; SOM 1: table 1). Furthermore, the morphology of all directly comparable preserved elements between the holotype of *I. anningae* and MUJA-3558 is entirely consistent. The only notable difference is the absence of surface ornamentation on the snout. Of all the specimens referred to this species to date, MUJA-3558 is the largest. The basal neoichthyosaur position and monophyly of *Ichthyosaurus*, indicate that early neoichthyosaur diversification involved the early establishment of geographically widespread, morphologically conservative lineages that persisted alongside more derived specialists during the Pliensbachian such as the hauffiopterygian *Xiphodracon* (Lomax et al. 2025).

Morphological information provided by MUJA-3558.—MUJA-3558 provides relevant morphological information for future comparisons as it preserves some bones in three dimensions and others that were either not preserved in other known specimens of the species and/or were not fully exposed and available for examination, such as the supraoccipital, opisthotic and quadratojugal. Another interesting feature is that the specimen confirms the presence of a well-developed epipterygoid, comparable to that known for *Ichthyosaurus communis* (McGowan 1973). The morphofunctional significance and the evolution of the epipterygoid among ichthyosaurs has not been deeply explored. This is partly because in the more derived forms of neoichthyosaurs, except for some *Stenopterygius* and *Argovisaurus* (Miedema and Maxwell 2022; Miedema et al. 2024) , the bone is reduced and/or probably remained cartilaginous. MUJA-3558 shows that the epipterygoid was not only present but also, as in *I. communis*, well-developed and formed a constituent part of the skull. The morphology of the "foot" (McGowan 1973) of the epipterygoid (Fig. 6A; SOM 1: fig. 3) indicates that this bone was not sutured to the palate (more specifically to the pterygoid) suggesting a certain degree of flexibility and/or moving, especially during feeding. Such an epipterygoid could have provided strength to the skull but without losing flexibility.

The other interesting feature displayed by MUJA-3558 is the morphology of the humerus. The fins of ichthyosaurs depict a unique modification pattern among secondarily marine tetrapods and have been used (particularly the forefin) as a source of taxonomic, phylogenetic and evolutionary information (Campos et al. 2024). Since the rise of the Neoichthyosauria, one of the most significant changes that occurred in the forefins is linked to the humerus, specifically to the development of a dorsal, plate-like process. This feature, defined by Motani (1999), has been recovered in all subsequent phylogenetic analyses as an unambiguous synapomorphy of ophthalmosauria, the diverse clade that dominated the seas worldwide since the Middle Jurassic. The unusual development of this process, and its plate-like shape, resembles the process present in *Ichthyosaurus anningae*. This apomorphy, in accordance with most phylogenetic analyses, including the one presented here, is better explained in terms of a parallelism.

Pliensbachian faunas from Asturias, trophic differentiation and niche partitioning.—The presence of *Ichthyosaurus anningae* adds to previous records of *Leptonectes* sp. in the Pliensabachian of Northern Spain (Fernández et al. 2018). The two taxa exhibit markedly different cranial and dental morphologies, which imply distinct trophic strategies. *Ichthyosaurus anningae*, as other *Ichthyosaurus* species, had robust, moderately conical teeth with rounded apices typical of a generalist feeder. *Leptonectes* sp., in contrast, possessed slender, finely striated, and more delicate teeth, often associated with specialized piscivore and, combined with its extremely elongate rostrum, indicates rapid lateral snapping and the capture of small, agile prey items (Massare 1987; Foffa et al. 2018). The co-occurrence of both ichthyosaurs with contrasting feeding strategies suggests that the

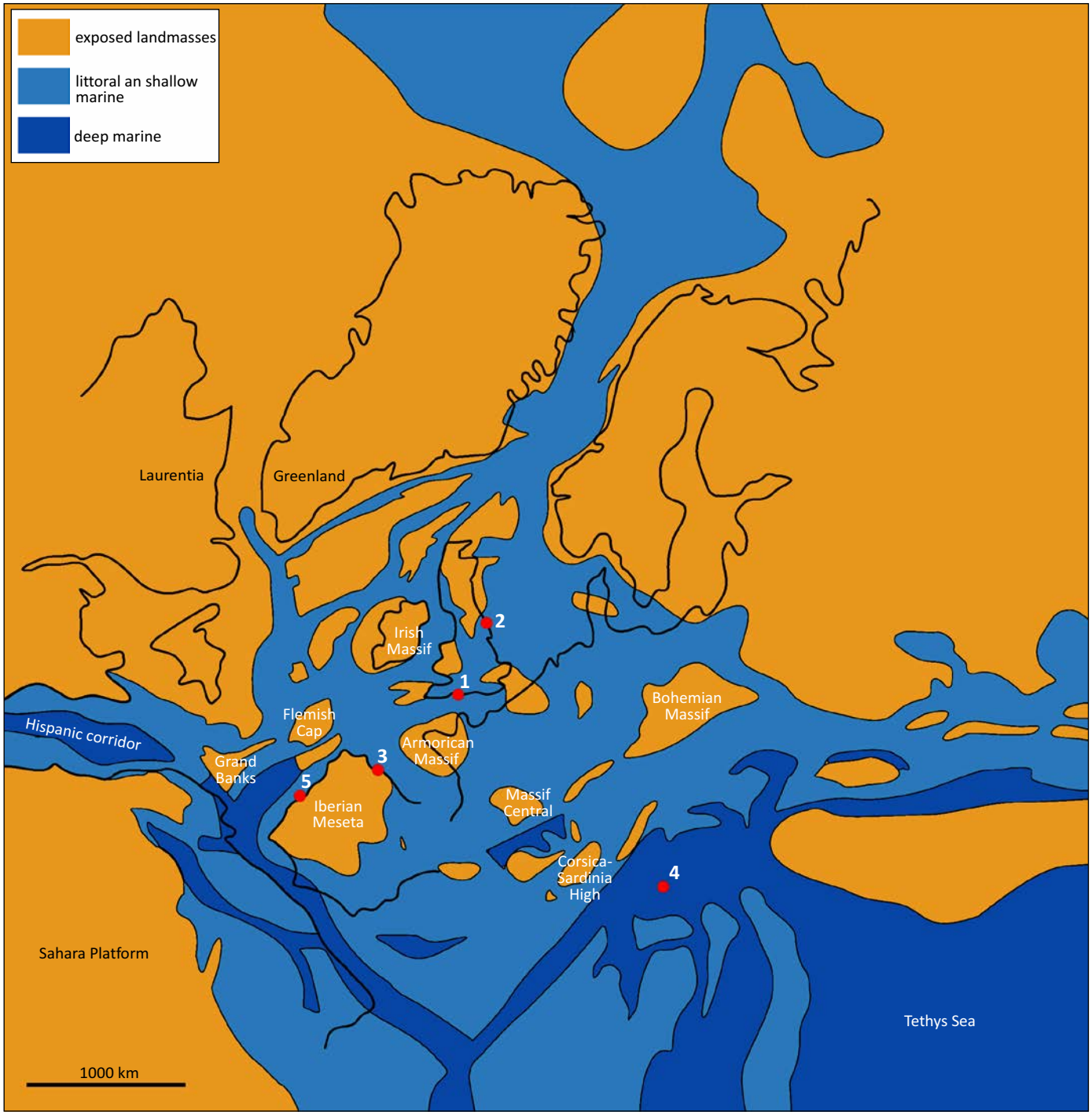

Fig. 11. *Ichthyosaurus* occurrences in the Early Jurassic. Palaeogreographic map for the Sinemurian–Toarcian interval modified and redrawn from Ziegler (1988: pl. 11). 1, Dorset (UK); 2, Cleveland Basin (UK); 3, Asturian Basin (Spain); 4, Southern Alps of Northern Italy; 5, Lusitanian Basin (Portugal).

Asturian Basin supported a diverse prey community and niche partitioning. *Leptonectes* may have exploited fast-moving schooling fishes (in open water), whereas *I. anningae* occupied a broader niche, consuming a mixture of fish and softer-bodied organisms. This trophic separation mirrors patterns observed in the rich Early Jurassic marine assemblages from the UK and where multiple ichthyosaur taxa coexisted (Lomax and Massare 2012, 2015) by partitioning ecological space (Dick and Maxwell 2015).

Paleobiogeographic significance.—The ammonite assemblages in the lower Pliensbachian of Spain are like those established in UK, France, and Germany (Northwest European Province), although some intervals such as Taylori Subchronozone include several species typical of the Mediterranean Province (Comas-Rengifo et al. 2023). During this time the Asturian Basin, was situated in the northern sector of the Iberian Seaway, between the Tethys Ocean and the southwestern region of the European epicontinental sea (Fig. 11),

and exhibited a subboreal affinity (Thierry 2000). The evidence provided by the ichthyosaurs from Northern Spain are also consistent with the information based on invertebrates. Although the Asturian Basin was geographically positioned between the Tethyan and Northern European marine realms, its faunal character is notably distinct from a "true" Tethyan assemblage. The latter, representing the Mediterranean Province, is defined by a high abundance of phylloceratid and lytoceratid ammonites and specialized carbonate-platform benthos (Comas-Rengifo et al. 2023). In contrast, the Asturian Basin exhibits a consistent Subboreal affinity, characterized by cooler-water taxa typical of the Northwest European Province. The presence of *Ichthyosaurus annigae* in Northern Spain further reinforces this link, suggesting that ecological filters, likely temperature-driven, maintained a biological boundary that aligned the basin with northern faunas despite the physical connectivity of the Iberian Seaway. Although the Early Jurassic ichthyosaur record in the Iberian Peninsula is sparse, recent discoveries in both Northern Spain (Fernández et al. 2018) and Portugal (Sousa and Matteus 2021; Pratas e Sousa et al. 2025) significantly improve our understanding of paleobiogeographic relationships along the western margin of the Tethys Sea. The occurrence of *I. anningae* on the Northern Iberian margin extends the known palaeogeographic range of this species and reinforces the subboreal affinity of the lower Pliensbachian ichthyosaur assemblage in Asturias, complementing earlier reports of *Leptonectes* sp. (Fernández et al. 2018). These taxonomic links are concordant with high-resolution ammonite correlations that place the studied horizon within the Jamesoni Zone, and thus within the temporal window in which the extensive epeiric sea along the NW European margin facilitated faunal exchange (Comas-Rengifo et al. 2023).

A recent contribution of Lomax et al. (2025) documents a complex ichthyosaur faunal turnover through the Pliensbachian, marked by the stratigraphic appearance of morphologically novel, narrow-snouted forms (Hauffiopterygiidae) in higher Pliensbachian levels. Placed in that broader framework, the *Ichthyosaurus anningae* from the Jamesoni Zone described here represents part of the pre-turnover Subboreal assemblage.

Additional discoveries in both Portugal and Spain will undoubtedly help to develop a better understanding of the dynamics of ichthyosaur faunas during the Early Jurassic.

Conclusions

The discovery of MUJA-3558 provides new anatomical and palaeobiogeographic data on Early Jurassic ichthyosaurs from the western Tethyan margin. The specimen is referred to *Ichthyosaurus anningae* based on a diagnostic combination of cranial and humeral characters, including a strongly developed deltopectoral crest and a dorsoventrally constricted humeral head, and represents the first record of the species from the Iberian Peninsula as well as the largest individual known. Three-dimensional preservation allows the first description of the supraoccipital, opisthotic, and quadratojugal in this taxon, while a well-developed, non-sutured epipterygoid indicates cranial mobility in basal neoichthyosaurs. The plate-like dorsal humeral process resembles the ophthalmosaurian condition and is interpreted as morphological parallelism. Co-occurrence with the longirostrine *Leptonectes* sp. in the Asturian Basin supports ecological differentiation within a structured Pliensbachian marine ecosystem comparable to those of north-western Europe. The presence of *I. anningae* in northern Spain supports subboreal affinities and faunal continuity between the NW European epicontinental sea and the Iberian Seaway during the Jamesoni Chronozone, prior to the Pliensbachian faunal turnover.

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