Refining the marine reptile turnover at the Early-Middle Jurassic transition (#53076)

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Refining the marine reptile turnover at the Early-Middle Jurassic transition

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Even though a handful of long-lived reptilian clades dominated Mesozoic marine ecosystems, several biotic turnovers drastically changed the taxonomic composition of these communities. A seemingly slow paced, within-System turnover took place across the Early-Middle Jurassic transition, seeing the demise of early neoichthyosaurians, rhomaleosaurid plesiosaurians and early plesiosauroids in favour of ophthalmosaurid ichthyosaurians and cryptoclidid and pliosaurid plesiosaurians, clades that will dominate the Late Jurassic and, for two of them, the entire Early Cretaceous as well. The fossil record of this turnover is however extremely poor, and this change of dominance appears to be spread across the entire middle Toarcian-Bathonian interval. We describe a series of ichthyosaurian and plesiosaurian specimens from successive geological formations in Luxembourg and Belgium that detail the evolution of marine reptile assemblages across the Early-Middle Jurassic, within a single sub-basin. These fossils reveal the continuing dominance of large rhomaleosaurid plesiosaurians, microcleidid plesiosaurians, and *Temnodontosaurus*-like ichthyosaurians up to the latest Toarcian, indicating that the structuration of the upper tier of marine ecosystems remained essentially constant up to the very end of the Early Jurassic. These fossils also suddenly record ophthalmosaurid ichthyosaurians and cryptoclidid plesiosaurians by the early Bajocian. As a result, the Early-Middle Jurassic marine reptile turnover appears restricted to the sole Aalenian stage, reducing the uncertainty of its duration, at least for ichthyosaurians and plesiosaurians, to 4 instead of 14 million years.

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Abstract

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Introduction

A series of diapsid clades dominated marine ecosystems during the entire Mesozoic (e.g. Motani, 2009; Benson, 2013; Pyenson, Kelley & Parham, 2014; Kelley & Pyenson, 2015). This long-term dominance was, however, pulsed by a series of extinctions and turnovers (Massare, 1987; Callaway & Massare, 1989; Bardet, 1994, 1995; Benson et al., 2010; Benson & Druckenmiller, 2014), the most-studied of which being those happening during the latest Triassic (Thorne, Ruta & Benton, 2011; Benson, Evans & Druckenmiller, 2012; Fischer et al., 2014c; Dick & Maxwell, 2015; Moon & Stubbs, 2020) and at the Jurassic-Cretaceous boundary (Tennant et al.; Fischer et al., 2012, 2013; Benson & Druckenmiller, 2014; Young et al., 2014a; Tennant, Mannion & Upchurch, 2016; Zverkov et al., 2018).

The dynamics of within-System marine reptile turnovers are less well known, despite evident modifications of assemblages outside System boundaries, such as during the early Late Cretaceous (Bakker, 1993; Bardet et al., 2008; Fischer et al., 2016, 2018). The composition of marine reptile communities clearly changed across the Early-Middle Jurassic transition (Maxwell, Fernández & Schoch, 2012; Vincent et al., 2013). Indeed, early neoichthyosaurian ichthyosaurians and microcleidid plesiosaurians seemingly met their demise and rhomaleosaurid plesiosaurians went near extinction (Maxwell, Fernández & Schoch, 2012; Fischer et al., 2013; Benson, Zverkov & Arkhangelsky, 2015), while ophthalmosaurid ichthyosaurians, thalattosuchian crocodylomorphs, cryptoclidid plesiosauroids, and pliosaurids radiated (Motani, 1999a; Ketchum & Benson, 2011a; Fischer et al., 2013; Benson & Druckenmiller, 2014; Moon, 2017; Foffa, Young & Brusatte, 2018). These newly diversified clades will then dominate the Late Jurassic and beyond.

However, the fossil record of marine reptiles across the middle Toarcian – Callovian interval is extremely poor (Benson et al., 2010; Maxwell, Fernández & Schoch, 2012) (Figure 1) and no region preserves fossiliferous successions spanning this transition. These biases blur both the tempo and the severity of this turnover. We tackle this issue by describing and analysing the composition of the late Toarcian-Bajocian marine reptile assemblages of Luxembourg and Belgium. We show that typical Early Jurassic forms such as rhomaleosaurid and microcleidid plesiosaurians and non-baracromian ichthyosaurians persisted in mid latitudes up to the latest Toarcian and that ophthalmosaurid ichthyosaurians and cryptoclidid plesiosaurians, the dominant Late Jurassic clades, suddenly appear during the early Bajocian, providing a refined timeline in a single sub-basin for what appears as an abrupt, Aalenian-restricted turnover.

Material & Methods

Upper Toarcian of Luxembourg: Thouarsense, Pseudoradiosa, and Aalensis zones

Towards the end of the Early Jurassic, the area of present-day Luxembourg was located in the northeast Paris Basin within the northwestern Peri-Tethys Ocean (e.g. Pieńkowski et al., 2008; Schintgen & Förster, 2013). In a shallow, near-coastal sea between the former landmasses of the Rhenish Massif in the north and the Vosges and Black Forest in the south, a thick siliclastic succession was deposited during the late Toarcian, with clayey to silty sediments in the lower parts and silty to sandy, iron-grain rich sediments in the upper part following a general coarsening upwards trend (Siehl & Thein, 1989). The material described herein includes a single, semi-articulated post-cranial ichthyosaur skeleton from the so-called "Couches à *Astarte voltzi*" (Dittrich, 1993), a clay-rich siltstone corresponding to level 11 of Delsate and Weis (2010), dated to the late Toarcian Thouarsense Ammonite Zone of the Grandcourt Formation.

All the other late Toarcian marine reptile remains from Luxembourg described herein were found in the overlying Minette ironstone Formation (Lucius, 1945). Deposition of the Minette successions took place under the influence of strong tidal currents (Teyssen, 1984) during the upper Toarcian Pseudoradiosa and Aalensis ammonite Zones (Di Cencio & Weis, 2020). The Aalenian Opalinum ammonite zone has not yet been detected in the area and probably forms a local hiatus (Maubeuge, 1972; Guérin-Franiatte & Weis, 2010).

Upper Toarcian of Belgium: Dispansum-Pseudoradiosa-Aalensis zones

The Mont-Saint-Martin Formation crops out in southern Belgium and includes iron-rich beds forming a slightly diachronous equivalent of the Minette ironstones in Luxembourg. These ironstones contain all the marine reptiles and were deposited in a shallow marine setting during the late Toarcian (Dispansum to Aaalensis ammonite zones; Boulvain et al., 2001). One fossil (IRSNB Vert-06455-0001) was found just outside the Belgian border, in the Meurthe-et-Moselle department, north-eastern France (Figure 2).

Middle-upper Aalenian of Luxembourg: Murchisonae and Concavum zones

The Toarcian part of the Minette ironstones in Luxembourg is locally overlain by a few meters of iron-rich marly sandstones and thin beds with calcareous nodules deposited during the Aalenian Murchisonae to Concavum ammonite zones (Guérin-Franiatte & Weis, 2010; Sadki, Weis & Braun, 2020). These deposits form the onset of a transgressive succession with increasingly finer sedimentation leading to the so-called "marnes micacées", a succession of poorly lithified silty claystones with thin layers of phosphatic nodules, dated to the lowermost Bajocian Discites ammonite zone (Guérin-Franiatte & Weis, 2010).

Lower Bajocian of Luxembourg: Humphriesianum Zone

The youngest marine strata in Luxembourg correspond to a succession of calcarenites, marl-limestone alternations and coral limestones deposited on the northeast margin of the Burgundy carbonate platform at the end of the lower Bajocian. The marine reptile remains described herein were all recovered from the so-called "Marnes sableuses d'Audun-le-Tiche", dated to the lower Bajocian Humphriesianum ammonite zone (Delsate et al., 2018; Popov, Delsate & Felten, 2019).

Fossilised diversity data

We extracted the number of fossil collections of Jurassic (Hettangian-Tithonian) marine reptiles (Ichthyosauria, Plesiosauria, Thalattosuchia, Pleurosauria, Angolachelonia) from the paleobiology database (https://paleobiodb.org) on the 26th March 2020. We binned these data per geological stage and generate a plot of the number of collections over time in R v3.6.2 (R Core Team, 2016), sing the geoscale v2.0 package (Bell, 2015).

Centra proportions

We gathered a series of measurements on centra, recording their position within the vertebral column (Table 1). We treated and plotted these data in R v3.6.2 (R Core Team, 2016) to visualize changes through time, if any.

Institutional abbreviations

IRSNB: Royal Belgium Institute of Natural Sciences, Brussels, Belgium. **MNHNL**: Muséum national d'histoire naturelle du Luxembourg, Luxembourg-ville, Luxembourg. **ULg-PA**: Collections de paléontologie animale de l'Université de Liège, Liège, Belgium.

Comparative Descriptions

Thouarsense zone fauna, upper Toarcian, Luxembourg

ICHTHYOSAURIA De Blainville, 1835
PARVIPELVIA Motani, 1999
THUNNOSAURIA Motani, 1999
BARACROMIA Fischer et al., 2013
Baracromia indet.
(Figure 3)

A single specimen (MNHNL TM212) is recorded from the Thouarsense zone: it is a partial articulated ichthyosaur comprising fifty-two centra, several ribs and gastralia, and two partial forefins, from the Dudelange locality. All the preserved pre-apical centra are markedly rounded and anteroposteriorly short, bearing close similarities with Jurassic thunnosaurians such as *Stenopterygius* and *Ophthalmosaurus* (Buchholtz, 2001; Massare et al., 2006). Posterior dorsal centra maintain clear bicipital rib articulations and all ribs have a 8-shaped cross-section, which also suggest that this specimen is a thunnosaurian (Sander, 2000; V.F. pers. obs. on NHMUK 2003, R5465, R498). The posterior apical centra are strongly compressed laterally, suggesting the presence of a lunate tailfin; although is the angle of the tailbent is unknown. The humerus is incompletely-preserved, lacking the capitulum. The dorsal trochanter is proximodistally short, as it does not extend to mid-shaft, while the deltopectoral crest is elongated and parallel to the long axis of the humerus. The small dorsal trochanter suggest that this taxon is not an ophthalmosaurid (Motani, 1999a). The humerus forms a prominent anterior process that possesses a conspicuous, anterodorsally facing facet. This facet exhibits a pitted bone texture which suggests the presence of a cartilaginous cap in vivo. While many Early Jurassic ichthyosaurians possess a mesiodistally-thick anterodistal expansion of the humerus (*Temnodontosaurus*, Leptonectidae, *Hauffiopteryx*, *Stenopterygius* (Johnson, 1979; McGowan & Milner, 1999; McGowan, 2003; McGowan & Motani, 2003; Maisch, 2008; Caine & Benton, 2011; Martin et al., 2012), this expansion here forms a flat facet but not for articulation with an anterior accessory epipodial element (the rounded and notched anterior surface of the radius confirms the absence of such an element). This combination of features rules out earliest neoichthyosaurians and ophthalmosaurids (e.g. Maisch & Matzke, 2000; McGowan & Motani, 2003) and has only been reported in the poorly known, ?late Toarcian-lower Bajocian taxon *Dearcmhara shawcrossi* (Brusatte et al., 2015), although the facet is smaller and deeper in *D. shawcrossi*. Epipodial and proximal elements closely resemble those of *Stenopterygius* spp. and *Chacaicosaurus cayi* (Johnson, 1979; Fernández, 1994; Maxwell, Fernández & Schoch, 2012), being polygonal and dorsoventrally thick, with no spatium interosseum. The radius and the radiale are notched as in many early neoichthyosaurians (e.g. Huene, 1922; McGowan, 1974; Maxwell, 2012; Lomax & Massare, 2016). The intermedium forms two distal facets unequal in size: a large, distally facing facet for articulation with distal carpal 3 and a smaller, posterodistally facing facet for articulation with distal carpal 4 (the ‘latipinnate’ condition, although the latipinnate-longipinnate dichotomy fails to capture what is essentially a trait with continuous spectrum; see Mazin (1982) and Motani (1999b) for discussions). The specimen MNHNL TM212 is regarded as a non-ophthalmosaurid baracromian, resembling *Stenopterygius* spp., *Chacaicosaurus cayi*, and *Dearcmhara shawcrossi*.

Pseudoradiosa zone fauna, upper Toarcian, Luxembourg

PLESIOSAURIA De Blainville, 1835
Rhomaleosauridae Nopcsa, 1928

Rhomaleosauridae indet.

(Figure 4)

Two large plesiosaurian propodials have been recovered from Pseudoradiosa zone: one (MNHNL DOU307) from the “Couche grise” of the Rodange locality, and one (MNHNL KA109) from the “Couche noire” of the Esch-sur-Alzette locality.

MNHNL DOU307 is a complete left propodial (proximal-distal length: 390mm; distal width: 210mm) with a weak posterior and dorsal curvature. The shaft is as wide as the capitulum, and there is no anterior expansion indicating that this propodial is an early plesiosaurian humerus (Storrs, 1997; Bardet, Godefroit & Sciau, 1999; O’Keefe, 2004; Smith & Vincent, 2010; Benson, Evans & Druckenmiller, 2012; Vincent & Storrs, 2019). The dorsal tuberosity is as anteroposteriorly wide as the capitulum and is weakly demarcated. A bulge with muscle scars is present on the ventral surface of the shaft, 30 mm distally to the capitulum. A very short prexial flange is present distally, forming a small, anterodistally facing triangular facet. The radial/tibial facet is flat and marks an angle of ca. 45° with the ulnar/fibular facet. This facet is convex and rugose, indicating the presence of an extensive cartilage layer. A larger postaxial flange is present, forming distally a semioval facet that is hardly discernible from the ulnar/fibular facet. There is no distal ridge, unlike in the cryptoclidid *Colymbosaurus* (Benson & Bowdler, 2014). The absence of a marked curvature (the anterior surface is straight in dorsal and ventral views) and the presence of a conspicuous postaxial flange suggest rhomaleosaurid affinities (Smith & Vincent, 2010; Smith & Benson, 2014; Smith, 2015) (with the exception of *Lindwurmia thiuda* Vincent & Storrs, 2019), which are reinforced by the large size of the propodial.

MNHNL KA109 is the distal end of a plesiosaurian propodial; the anterior-posterior asymmetry suggests it is also a humerus. It resembles MNHNL DOU307 in lacking a preaxial flange and the postaxial flange is smaller than in MNHNL DOU307. The distal surface is markedly rounded in dorsoventral view. A prominent, strongly pitted anteroposterior ridge textures of the distal surface, obliterating radial/tibial and ulnar/fibular facets. The postaxial flange forms a triangular and concave facet posterior to the distal ridge. A distal ridge is regarded as an autapomorphic feature of *Colymbosaurus* (Benson & Bowdler, 2014; Arkhangelsky et al., 2019) but the lack of an extensive postaxial flange precludes such a referral; the size of the humerus and its similarities with MNHNL DOU307 suggest rhomaleosaurid affinities.

Dispansum-Pseudoradiosa-Aalensis zones, upper Toarcian, Belgium

ICHTHYOSAURIA De Blainville, 1835

Ichthyosauria indet.

(Figure 5)

IRSNB Vert-06455-0001, IRSNB Vert-00000-00801, and IRSNB Vert-06659-0001 are ichthyosaurian centra, heavily eroded and damaged. Because their original shapes cannot be asserted, we refrained from calculating their shape ratios and assign them to Ichthyosauria indet.

IRSNB Vert-06462-0003 is a distal tooth that preserves the crown and the acellular cementum ring. The crown is recurved and robust (height: 14.83 mm, basal diameter: 8.14 mm, giving a crown shape ratio of 1.82), as is usually the case for distal ichthyosaurian teeth (Motani, 1997; McGowan & Motani, 2003). Apicobasal ridges texture the crown, unlike in leptonectids (Maisch, 1998; Maisch & Matzke, 2003; McGowan & Motani, 2003; Lomax, 2016) and the acellular cementum is itself ridged. This combination of features match that of *Ichthyosaurus*, *Protoichthyosaurus*, and *Temnodontosaurus* (McGowan, 1973; Godefroit, 1993a; Vincent et al., 2014; Brusatte et al., 2015; Lomax, Porro & Larkin, 2019). But it is also found in more primitive taxa such as *Contectopalatus* and *Cymbospondylus* (Maisch & Matzke, 2001; Klein et al., 2020). As a result, this specimen is referred to as Ichthyosauria indet.

IRSNB Vert-00000-00802 is a partial ichthyosaurian right quadrate, preserving the condyle, the stapedial facet and the posteroventral part of the anterior lamella. The condyle is massive, oval, but appears moderately short anteroposteriorly. The medial and lateral surfaces are pitted by numerous small foramina; the stapedial facet is semi-circular thickened ventral and posterior edges. This quadrate has the same size (maximal condylar width: 71 mm) and morphology as that of *Temnodontosaurus platyodon* (Godefroit, 1993a). In the absence of additional evidence, this quadrate is referred to Ichthyosauria indet. but indicates the presence of large ichthyosaurs by the latest Toarcian.

PARVIPELVIA Motani, 1999

Parvipelvia indet.

(Figure 5)

ULg-PA 35.961 is an ichthyosaurian anterior dorsal centrum with a damaged dorsal surface. Its height-length ratio is 78 mm/35 mm = 2.23. The centrum is rounded as in parvipelvians (Merriam, 1908; Maisch & Matzke, 2000) and the diapophyses and parapophyses strongly protrude from the body of the centrum, as in MNHNL TM 212.

IRSNB Vert-00000-00800 is a partial left ichthyosaurian surangular, probably associated with the angular IRSNB Vert-06462-0002. It consists of posterior third, where the angular in a mesiolaterally-flattened bone with a slightly convex lateral surface and a slightly concave medial surface for accommodation of the Meckelian canal. The dorsal surface of the surangular is saddle-shaped, forming a long and shallow concavity anterior to the coronoid process. The preserved morphology of IRSNB Vert-00000-00800 is not diagnostic, but we assign it to Parvipelvia indet. because of its probable association with the angular IRSNB Vert-06462-0002 (see below).

IRSNB Vert-06462-0002 is a partial left ichthyosaurian angular, bearing the typical double-grooved dorsal surface. The lateral wall of the angular is dorsoventrally short anteriorly, and only increases in size posterior to the level of the coronoid process. This narrow lateral exposure of the angular suggests that this specimen does not belong to Ophthalmosauridae, as this clade is notably characterized by large exposure of the angular in lateral view (Motani, 1999a).

IRSNB Vert-00000-00803 and IRSNB Vert-00000-00804 are large ichthyosaurian centra. IRSNB Vert-00000-00803 is 118 mm high and 48 mm long, giving a height-length ratio of 2.45; IRSNB Vert-00000-00804 is damaged on the edges and will not be measured but is of comparable size. The lateral surfaces of these centra are rounded in anteroposterior view, as in parvipelvians (Merriam, 1908; Maisch & Matzke, 2000), but their size departs from that of Early Jurassic thunnosaurians, even particularly large individuals (e.g. Maxwell, 2012; Lomax & Sachs, 2017). These centra rather match the size and shape of the dorsal-caudal centra of some large non-thunnosaurian neoichthyosaurians such as *Temnodontosaurus* spp. (Godefroit, 1993a; Martin et al., 2012) and *Excalibosaurus costini* (McGowan, 2003). IRSNB Vert-00000-00803 possesses a single apophysis (the parapophysis) placed laterally, suggesting it is middle preflexural caudal (Huene, 1922; McGowan & Motani, 2003). IRSNB Vert-00000-00804 possesses a diapophysis and a parapophysis placed ventrolaterally and is regarded as a posterior dorsal centrum. The size and shape of IRSNB Vert-00000-00803 and IRSNB Vert-00000-00804 match those of large early neoichthyosaurians and but are regarded as Parvipelvia indet. in the absence of unambiguous synapomorphies.

IRSNB Vert-00000-00808 is an ichthyosaurian anterior caudal centrum. Its height-length ratio is 65 mm / 22 mm = 2.94; this high shape ratio close to 3 might suggest thunnosaurian affinities (Buchholtz, 2001). The lateral surface of the centrum is rounded as in parvipelvians (Merriam, 1908; Maisch & Matzke, 2000) and slightly oval, as the ventral surface is flattened. The parapophyses are located lateroventrally.

IRSNB Vert-06462-0005 is an ichthyosaurian cervical centrum. Its height-length ratio is 63 mm / 24 mm = 2.62. The lateral surface of the centrum is rounded as in parvipelvians (Merriam, 1908; Maisch & Matzke, 2000). A faint ventral keel is present, giving the centrum a pentagonal shape. Such a shape is often seen in the cervical/anterior dorsals of parvipelvians (e.g. Huene, 1922; Fischer et al., 2014b; Lomax, Porro & Larkin, 2019) and is not of diagnostic value at a lower taxonomic level at the current state of our knowledge.

PLESIOSAURIA De Blainville, 1835

Plesiosauria indet.

IRSNB Vert-11312-00007 is a plesiosaurian dorsal centrum, as evidenced by the absence of transverse processes. Its height-length ratio is 67 mm / 44 mm = 1.52. The centrum is poorly preserved and we assign it to Plesiosauria indet.

Aalensis zone fauna, upper Toarcian, Luxembourg

The material from the Aalensis zone of the Minette ironstones is more abundant. We identified 12 ichthyosaurians and 8 plesiosaurians in the MNHL collections. Most of the material consist of isolated centra, complemented by three plesiosaurian propodials, one ichthyosaur coracoid, and one plesiosaurian tooth crown.

ICHTHYOSAURIA De Blainville, 1835

PARVIPELVIA Motani, 1999

Parvipelvia indet.

(Figure 6)

MNHNL DOU944 is an ichthyosaurian anterior dorsal centrum from an unknown locality. A central keel is not present but the centrum forms a ventral expansion, giving the centrum a slight pentagonal shape. The diapophysis is small and rounded, as in parvipelvians and unlike in more primitive forms (Merriam, 1908; Huene, 1922) and is strongly protruding and has a rounded distal surface. Shallow dorsoventral ridges connect to the base of the diapophysis, anterior and posteriorly. The parapophysis is flatter and less prominent and its anterior margin merges with the anterior edge of the centrum. Such a pentagonal shape is often seen in parvipelvians (e.g. Huene, 1922; Fischer et al., 2014b; Lomax, Porro & Larkin, 2019) and is not of diagnostic value at a lower taxonomic level at the current state of our knowledge.

MNHNL DOU998 is an anterior caudal centrum from an unknown locality. The centrum has a rounded outline, as in usually parvipelvian ichthyosaurians (Merriam, 1908; e.g. Maisch & Matzke, 2000; McGowan & Motani, 2003). Its height/length ratio is 90/31=2.9. This high ratio close to 3 might suggest thunnosaurian affinities (Buchholtz, 2001), but in the absence of additional data, this specimen is regarded as Parvipelvia indet.

MNHNL DOU369 is a series of disarticulated ichthyosaur centra. One originates from the mid-thoracic region and two others from the anterior caudal region, their respective height/length ratios are as follows: 68/32=2.1, 61/35=1.74, and 63/32=1.96. The mid-thoracic resembles MNHNL DOU944. The rather elongated anterior caudal suggest these centra do not belong to a thunnosaurian, but rather to an early parvipelvian (Buchholtz, 2001).

MNHNL DOU353 is a fragmentary left coracoid from an unknown locality. It preserves the lateral part and a fragment of the intercoracoid facet. The ventral surface is moderately saddle-shaped (intercoracoid facet is only 56mm thick while the mesiolateral length is 180mm). The glenoid facet is large (anteroposterior length=75mm) and oval, while the scapular facet forms a small triangle (anteroposterior length= 39mm) and forms a ca. 60° angle with the glenoid facet. The posterolateral emargination is wide and deep, the coracoid surface posterior to the glenoid faces posteriorly and not posterolaterally, similar to the condition seen in *Ichthyosaurus communis*, *Ichthyosaurus anningae*, *Protoichthyosaurus postaxialis*, and many but not all specimens of *Temnodontosaurus platyodon* (Home, 1819; Godefroit, 1993a; Lomax & Massare, 2015; Lomax, Porro & Larkin, 2019). The Triassic shastasaurid *Shatasaurus neoscapularis* also possesses a wide posterior notch, but the coracoid of that taxon is different, having a very wide anterior notch (McGowan, 1994). We regard this coracoid as belonging to a non-baracromian parvipelvian.

MNHNL DOU378 is a very large centrum from an unknown locality. It originates from the posterior dorsal – sacral – anterior caudal region (length: 65mm and diameter: 175mm, estimated height: 180-185mm, H/L ratio: 2.79-2.84). Its size departs from the Early Jurassic thunnosaurians (*Ichthyosaurus* and *Stenopterygius*, which have much smaller centra even particularly large individuals (e.g. Maxwell, 2012; Lomax & Sachs, 2017)). It rather matches the size and shape of the anteriormost caudal centra of some large non-thunnosaurian neoichthyosaurians such as *Temnodontosaurus* spp. (Godefroit, 1993a; Martin et al., 2012) and *Excalibosaurus costini* (McGowan, 2003) (the anterior caudals are much longer in *Eurhinosaurus longirostris* [V.F., pers. obs. on MNHN 1946-20]).

PLESIOSAURIA De Blainville, 1835

Plesiosauria indet.

(Figures 7, 8)

MNHNL DOU906 is a plesiosaurian tooth crown from the Esch-sur-Alzette locality. It is slender (length/basal diameter= 23/8= 2.875), labiolingually flattened and recurved indicating it does not belong to derived rhomaleosaurids and thalassophoneans (Owen, 1865; Smith & Vincent, 2010; Ketchum & Benson, 2011b; Smith & Benson, 2014). The crown bears fine striations along the entire surface.

MNHNL DOU724 is a plesiosaurian sacral vertebra probably originating from the Esch-sur-Alzette locality. The articular surface is strongly dorsoventral depressed and the centrum is as wide as long. As in MNHNL DOU722, MNHNL DOU723, and MNHNL DOU954, the subcentral foramina are widely spaced and are separated by a well-rounded/convex surface. Similar to the other centra, the dorsal edge of the articular surface is notched by the neural canal. The transverse process is elongated, stout, and points posterolaterally. The rib facet is 8-shaped (waisted), this time with a larger, ear-shaped dorsal part and a smaller, semioval ventral part. The neural canal is also 8-shaped, resembling a ‘plesiosauroid’ pectoral vertebra from the Aalenian-Bajocian of Australia (Kear, 2012). Despite having similar size to the vertebrae we referred to as Rhomaleosauridae indet., none of the feature we highlight above are recorded in *Rhomaleosaurus* (Smith, 2013; Smith & Benson, 2014) and their representation in other derived rhomaleosaurids is unclear. Accordingly, we regard this specimen as Plesiosauria indet.

Rhomaleosauridae Nopcsa, 1928

Rhomaleosauridae indet.

(Figures 7, 8)

MNHNL DOU722 and MNHNL DOU723 are two plesiosaurian pectoral vertebrae from the Esch-sur-Alzette locality. The articular surface of the centrum is oval, with a dorsal notch corresponding to the neural canal. The subcentral foramina are displaced laterally, being located on the ventrolateral surface. There is no ventral keel, but the ventral surface in between the subcentral foramina is clearly transversely convex. The rib facets are oval, connect to the neural arch, and their long axis is vertical; they extend ventrally below the level of the notochordal pit. The semi-circular prezygaphophyses face dorsomedially and are clearly separated from one another; their ventral margin is set below the centre of the neural canal, even though the neural canal is large. Anteriorly, the neural spine forms a basal triangular cavity containing a paired ridge. The height of this trough is about 1/3 of the total height of the neural spine. On the posterior surface, the basal region of the neural spines forms a deep tear-shaped concavity that extends for about one half of the total height of the neural spine, and appears similar to the condition of Microcleididae (Bardet, Godefroit & Sciau, 1999; Schwermann & Sander, 2011) and *Rhomaleosaurus* (Smith & Benson, 2014). However, the neural spines are much shorter than in microclidids (e.g. Owen, 1865; Bardet, Godefroit & Sciau, 1999). The neural spine possesses a posterior ridge while its anterior surface is concave, as in *Rhomaleosaurus thortoni* (Smith & Benson, 2014). The neural spine thickens dorsally and its dorsal half is posteriorly inclined, unlike in *Westphaliasaurus simonensii* (Schwermann & Sander, 2011). We assign these vertebrae to Rhomaleosauridae indet.

MNHNL DOU954 is a posterior pectoral/anterior dorsal vertebra from an unknown locality. It is essentially similar to MNHNL DOU722 and MNHNL DOU723. The main difference is the existence of ventral expansion of the centrum, even if a clear ventral keel remains absent. This ventral expansion gives the articular surface of the centrum a heart shape. The neural spine is concave anteriorly and bears a median ridges similar to the condition of *Rhomaleosaurus thorntoni* (Smith & Benson, 2014). We assign this vertebra to Rhomaleosauridae indet.

MNHNL DOU558 from the Belvaux locality and MNHNL DOU324A and MNHNL DOU324B (broken, juvenile) from the Esch-sur-Alzette locality are three plesiosaurian humeri. These strongly resemble MNHNL DOU307: the shaft is long and slightly curved posteriorly and dorsally, the dorsal tuberosity is wide, a boss with muscle scars is present ventrally to the capitulum, the preaxial lamella is very short and forms a small triangular distal facet, the postaxial lamella is longer and forms a semioval posterodistal facet, radial/tibial and ulnar/fibular facets form a 45-55° angle and no distal ridge is present. The only difference is the position of the dorsal tuberosity, which is offset ventrally, creating a flattened, dorsomedially-facing surface between the dorsal part of the capitulum and the ventral part of the dorsal tuberosity. The larger propodial (MNHNL DOU324A) measures 331mm in proximal distal length and 168mm is maximal distal width. The smaller 'adult' propodial (MNHNL DOU558) measures 309mm in proximodistal length and 150mm in distal width.

Microcleididae Benson et al. 2012
Microcleidus Watson, 1909
cf. *Microcleidus*
(Figure 7)

MNHNL DOU978 is a plesiosaurian cervical centrum from an unknown locality. The centrum is slightly wider than high and is markedly elongated (height=42mm, width=53mm, length=55mm) unlike in derived rhomaleosaurids and thalassophoneans, which have anteroposteriorly short centra (Owen, 1865; Smith & Vincent, 2010; Ketchum & Benson, 2011b; Smith & Benson, 2014). The ventral surface is flattened as in *Microcleidus* (Owen, 1865; Vincent et al., 2017) and bears two subcentral foramina. There is no ventral keel. The lateral surface bears a (very) faint anteroposterior ridge; a more conspicuous lateral ridge is present in *Microcleidus* spp. (Owen, 1865; Bardet, Godefroit & Sciau, 1999; Vincent et al., 2017). The neural arch is fused with the centrum. The orientation of bone fibers on the right side suggests that the suture is V-shaped, which is mainly seen in rhomaleosaurids (Benson, Evans & Druckenmiller, 2012) and in the early pliosaurid *Hauffiosaurus* (Benson et al., 2011). The neural canal is very small in diameter, resulting in zygapophyses that are located close to the centrum, as in *Microcleidus* (Owen, 1865; Bardet, Godefroit & Sciau, 1999) and unlike in *Plesiosaurus dolichodeirus* (Owen, 1865), *Westphaliasaurus simonensii* (Schwermann & Sander, 2011), *Hauffiosaurus* spp. (White, 1940; Benson et al., 2011) The prezygapophyses are clearly separated, medially-inclined and their ventral surface is located more ventrally than the centre of the neural canal. The rib facets is 8-shaped, being formed of two semi-ovals separated by an anterior and a posterior furrows, as in *Plesiosaurus dolichodeirus* (Owen, 1865; Storrs, 1997) and unlike in many microcleidids (Owen, 1865; Schwermann & Sander, 2011), *Hauffiosaurus* (White, 1940), and cryptoclidids (Andrews, 1910a; Brown, 1981; Knutsen, Druckenmiller & Hurum, 2012a,b). The rib facet in posterior cervical centra is separated by a groove *Microcleidus melusinae* (Vincent et al., 2017). This centrum thus bears strong similarities with *Microcleidus* and is regarded as cf. *Microcleidus*.

Upper Aalenian fauna

ICHTHYOSAURIA De Blainville, 1835

Ichthyosauria indet.

(Figure 9)

MNHNL HU242 (Concavum zone) is a small partial ichthyosaur rostrum from te Rumelange locality. It contains the anterior part of the left dentary (or right premaxilla), showing the labial and lingual walls. Two teeth are preserved in situ. The root and the acellular cementum ring have a circular cross-section and are perfectly smooth externally, unlike in *Ichthyosaurus*, *Protoichthyosaurus*, and *Temnodontosaurus* (McGowan, 1973; Godefroit, 1993a; Vincent et al., 2014; Brusatte et al., 2015; Lomax, Porro & Larkin, 2019) and there is no evidence for plicidentine (unlike other Jurassic ichthyosaurians for which this feature is known (Maxwell, Caldwell & Lamoureux, 2012)), but this latter feature cannot be used for a taxonomic purpose at the present state of our knowledge. The teeth are of a maximal diameter of 8mm and estimated 20mm apicobasal length; the size and shape of the tooth fits within the range of early baracromians (Godefroit, 1993b, 1994a; Fernández, 1994; Maisch, 2008; Maxwell, Fernández & Schoch, 2012) but in the lack of additional evidence, this material is here referred to Ichthyosauria indet.

PLESIOSAURIA De Blainville, 1835
Plesiosauria indet.
(Figure 9)

MNHNL HU384 (Murchisonae zone) is a small caudal centrum of a plesiosaurian of a juvenile individual, originating from the Tétange locality. Its height/width ratio is 32/36mm = 0.88. Two small triangular chevron facets are present ventrally, merging with the edge of the articular surface. The ventral surface is flat. A rounded rib facet is present on the lateral surface. The neural arc is disconnected from the centrum and absent; the facets appear diamond shaped. Sacral vertebrae usually have less diagnostic features than other vertebrae in plesiosaurians, as could be inferred from their respective number of phylogenetic characters (Benson & Druckenmiller, 2014); this, coupled to the immaturity of the specimen would make an assignment ambiguous and we refer this material to Plesiosauria indet.

PLESIOSAUROIDEA Gray, 1825
Plesiosauroidea indet.
(Figure 9)

MNHNL BU157 (Concavum or Murchisonae zone) is a moderately elongated plesiosaurian cervical vertebra from the Rumelange locality. The shape of the centrum suggestes it does not belong to derived rhomaleosaurids and thalassophoneans, which have anteroposteriorly short centra (Owen, 1865; Smith & Vincent, 2010; Ketchum & Benson, 2011b; Smith & Benson, 2014). The ventral surface is flattened and bears two subcentral foramina. No ventral keel is present. The edge of the centrum is rugose, as sometimes seen in various plesiosaurian clades (Owen, 1865; Seeley, 1874a; Fischer et al., 2020). An anteroposteriorly elongated bulge (rather than a ridge) is present on the dorsolateral surface. This bulge is separated from the rib facet by a median concave area. The rib facet is roughly oval but is very strongly waisted by an anterior and a posterior notch, giving the facet a marked 8 shape; this structure recalls – but is more marked than in – the late Toarcian centra MNHNL DOU978. The neural arch is fully fused to the centrum and no suture is discernible. A pair of supracentral foramina is present on the floor of foramen magnum. While MNHNL DOU978 could clearly be attributed to

Microcleidus, this vertebra – although superficially similar – is less elongated, possesses a lateral bulge rather than a ridge, and does not preserve the zygapophyses. As a result, a referral to Microclididae is too ambiguous. Nevertheless, the presence of an 8-shaped rib facet precludes a referral to cryptoclidids (Andrews, 1910a; Brown, 1981; Knutsen, Druckenmiller & Hurum, 2012a,b). Accordingly, this specimen is referred to as a non-cryptoclidid plesiosauroid.

Lower Bajocian fauna

ICHTHYOSAURIA De Blainville, 1835
Ichthyosauria indet.
(Figure 10)

MNHNL BM360 from the Rumelange locality contains one partial neural spine and two proximal parts of bicipital ribs. The neural spine bears a dorsoventrally-oriented median ridge on its anterior surface. The taxonomic values of these features is low and we assign this material to Ichthyosauria indet.

PARVIPELVIA Motani, 1999
Parvipelvia indet.
(Figure 10)

MNHNL BM758 is an ichthyosaurian caudal centrum from the Rumelange locality. Its shape is rounded, with a slightly flattened ventral surface, as in Parvipelvia (Merriam, 1908; Maisch & Matzke, 2000). Its height/length ratio is 100mm/38mm=2.63.

MNHNL BM725 from the Rumelange locality contains a cervical and a caudal ichthyosaurian centra. The cervical centrum has a height/length ratio of 83mm/38mm=2.18 while the same ratio for the caudal centrum is 56mm/26mm=2.15. The centra are rounded in shape and exhibit small and rounded apophyses, as in parvipelvians and unlike in more primitive forms (Merriam, 1908; Huene, 1922).

MNHNL BM461 is an ichthyosaurian cervical centrum from the Rumelange locality. Its height/length ratio is 72mm/30mm=2.4. The centrum is rounded in shape and exhibits small and rounded apophyses, as in parvipelvians and unlike in more primitive forms (Merriam, 1908; Huene, 1922).

MNHNL BM392 from the Rumelange locality contains five caudal centra and one sclerotic plate of a single ichthyosaurian specimen. The height/length ratios of the first four caudal centra are as follows: 72mm/30mm=2.4, 77mm/31mm=2.48, 72mm/29mm=2.48, 75mm/32mm=2.34. Their rounded shape indicates they belong to Parvipelvia (Merriam, 1908; Huene, 1922; Maisch & Matzke, 2000). The sclerotic plate bears radiating striations on its lateral surface and its internal and external edges are crenulated, as is usually the case in ichthyosaurians (Andrews, 1910a; McGowan, 1973; Fischer et al., 2014a). The external third of the plate is deflected, facing dorsally.

OPHTHALMOSAURIDAE Baur, 1897

Ophthalmosauridae indet.

(Figures 10, 11)

MNHNL BM780–BM781 is a nearly complete right ichthyosaurian surangular (MNHNL BM780), associated with seven teeth (bearing the collection number MNHNL BM781), originating from the Rumelange locality. The surangular is straight in all planes (only its posterior quarter is slightly deflected medially) and bears a thickened dorsal margin, giving it a tear-shaped cross-section. A lateral, anteroposteriorly elongated and posteriorly-deepening concavity is present on the lateral surface (‘surangular fossa’). This depressed area terminates anteriorly to the level of the coronoid process. The coronoid process is prominent and bears a rugose texture. A small, anteroposteriorly oriented ridge is present directly posteromedially to the coronoid process and is likely part of the muscle attachment. The dorsal margin of the surangular forms a concave plateau posteriorly to the coronoid process. A promiment M.a.m.e process is present directly posteromedially to the plateau; this process points dorsomedially. The angular facet extends anteriorly up to the level of the coronoid process and covers the ventral half of the surangular posteriorly. This indicates the presence of an extensive angular, which is an ophthalmosaurid synapomorphy (Motani, 1999a). The teeth are peculiar in forming externally-visible plicidentine, texturing the acellular cementum ring and the root by very deep apicobasal grooves, as in *Ichthyosaurus*, *Protoichthyosaurus*, and *Temnodontosaurus* (McGowan, 1973; Godefroit, 1993a; Vincent et al., 2014; Brusatte et al., 2015; Lomax, Porro & Larkin, 2019). The root cross-section is oval as in all parvipelvians bar most platypterygiines (Fischer et al., 2012; Fischer, 2016) and the base of the enamel is easy to discern, which is usually the case in ophthalmosaurids (Fischer et al., 2016). Accordingly, we refer this specimen as Ophthalmosauridae indet.

MNHNL BM779 is a fragmentary partially articulated ichthyosaurian, containing parts of the skull, axial skeleton, and scapular girdle, originating from the Rumelange locality. It belongs to Ophthalmosauridae, having a humerus with plate-like dorsal trochanter, a massive deltopectoral crest, a humeral facet for an anterior accessory element, a posterodistally deflected ulnar facet and a conspicuous acromial process on the scapula (Motani, 1999a; Fischer et al., 2012, 2013; Moon, 2017; Zverkov & Efimov, 2019). It resembles *Arthropterygius* in having an anteroposteriorly-short parietal symphysis, a deep ulnar facet on the humerus, a small humeral facet for an anterior accessory epipodial elements (Maxwell, 2010; Fernández & Maxwell, 2012; Zverkov & Prilepskaya, 2019). However, the presence of several autapomorphies on the cranial and appendicular elements indicates that this specimen constitutes a novel taxon, for which a dedicated manuscript is in preparation.

PLESIOSAURIA De Blainville, 1835
CRYPTOCLIDIDAE Williston, 1925
Cryptoclididae indet.
(Figure 10)

MNHNL BM782 is a left plesiosaurian propodial from the Rumelange locality. The propodial is straight in the proximodistal direction and slightly curves dorsally. The shaft is fairly elongated. The dorsal tuberosity is wide and weakly demarcated from the capitulum; they form together an evenly rounded proximal surface. A median dorsal boss surrounded by muscle scars is present close to the distal end of the dorsal tuberosity. This boss is median (along the axis of the shaft) and thus differs from the anteriorly placed boss seen in the humeri of rhomaleosaurids and microcleidids (Owen, 1865; Smith & Benson, 2014). The propodial markedly expands distally, forming a preaxial flange and a longer postaxial flange. The preaxial flange forms a dorsoventrally-narrow triangular facet distally. The postaxial flange forms a semioval posterior facet that forms a marked angle (ca. 45°) with the ulnar/fibular. Both the radial/tibial and the anteroposteriorly- and dorsoventrally-shorter ulnar/fibular facets are slightly convex. However, a distal ridge is absent, unlike in *Colymbosaurus* (Benson & Bowdler, 2014; Arkhangelsky et al., 2019). The shape of the propodial with its fairly slender shaft and large preaxial and postaxial flanges indicate cryptocleidid affinities (Andrews, 1910a; Mehl, 1912; Brown, 1981; O'Keefe & Wahl, 2003; Knutsen, Druckenmiller & Hurum, 2012c; Roberts et al., 2017, 2020); it resembles the humerus of humerus of *Murænosaurus leedsi* (Seeley, 1874b; Andrews, 1910a) and the femur of *Tricleidus seeleyi* (Owen, 1865).

Results

We visualized the size and shape of Toarcian and Bajocian ichthyosaur centra (Figure 12). These data reveal a decrease in overall size and a much smaller range of shapes from the late Toarcian to the Bajocian. However, a difference in sampling intensity between these two assemblages is evident. We randomly sampled our late Toarcian dataset to select 3 cervicals and 6 caudals 10000 times, yielding comparable datasets. We then compared the range of height-length ratios between these datasets. The Bajocian height-length ratios range is smaller than Toarcian height-length ratios range about 99.85% of the times and two times smaller about 98.56% of the times. The data at hand thus unambiguously suggest a reduction of the disparity of ichthyosaurian centrum shapes across the Early–Middle Jurassic transition, i.e. going from an early neoichthyosaurian-dominated to an ophthalmosaurid-dominated assemblage.

Discussion

The Early–Middle Jurassic transition in marine reptiles, a state of the art

The very well-sampled (Benson et al., 2010) Lower Jurassic marine ecosystems of western Europe housed a vast menagerie of neoichthyosaurians, thalattosuchians, and plesiosaurians (Owen, 1860; Huene, 1922, 1931; McGowan, 1974, 1979; Benton & Taylor, 1984; Maisch & Matzke, 2000; O'Keefe, 2004; Großmann, 2007; Maisch, 2008, 2010; Benson, Evans & Druckenmiller, 2012; Martin et al., 2012; Bardet et al., 2014; Lomax & Massare, 2016; Johnson, Young & Brusatte, 2020). Evidence from body size, craniodental shape, and swimming capabilities suggests that these taxa occupied several niches within shallow marine ecosystems (Hauff, 1953; Massare, 1987, 1997; Böttcher, 1989; Godefroit, 1994a; McGowan, 1996; Buchholtz, 2001; Buchy, 2010; Fischer, Guiomar & Godefroit, 2011; Martin et al., 2012; Dick, Schweigert & Maxwell, 2016; Maxwell & Cortés, 2020). Such a diversity of forms made the Early Jurassic marine ecosystems of western Europe an iconic representation of Mesozoic marine life (Taylor, 1997).

Even though a drastic reduction of apparent diversity is expected following the lagerstätten effect of the early Toarcian localities (Benson et al., 2010), the Middle Jurassic assemblages, when well sampled (i.e. not before the Callovian), are markedly distinct from their Toarcian counterparts. For ichthyosaurians, the dominant and diversified early neoichthyosaurians (leptonectids, *Suevoleviathan*, *Hauffiopteryx*, and *Temnodontosaurus*) are gone; the disappearance of non-thunnosaurian ichthyosaurians marks the end of large (>6m) ichthyosaurian top predators, at least up until the Aptian, when some derived platypterygiines will presumably fill similar roles (Fischer et al., 2014b, 2016; Bardet, Fischer & Machalski, 2016; Fischer, 2016). Ichthyosaurians will never re-evolve carinated teeth like those seen in *Temnodontosaurus platyodon* and *Temnodontosaurus trigonodon* (Conybeare, 1822; Godefroit, 1993a), nor the sawfish-like morphology of Leptonectidae (Swinton, 1930; Huene, 1951; McGowan, 1986, 2003; Lomax, 2016). From the Callovian onwards, ichthyosaur assemblages overwhelmingly consist of ophthalmosaurids (but see Fischer et al. (2013)), up to the final extinction of ichthyosaurians (Fischer et al., 2016). While diverse ophthalmosaurid assemblages are known by the Kimmeridgian (Fernández, 1997; Druckenmiller et al., 2012; Arkhangelsky

& Zverkov, 2014; Zverkov et al., 2015; Paparella et al., 2017; Moon & Kirton, 2018a; Delsett et al., 2019; Zverkov & Efimov, 2019; Campos, Fernández & Herrera, 2020; Zverkov & Jacobs, 2020), only the closely related *Ophthalmosaurus* and *Baptanodon* are known in the Callovian of Europe and North America, respectively (Seeley, 1874c; Marsh, 1895; Gilmore, 1902, 1906; Knight, 1903; Andrews, 1910b; Massare et al., 2006; Moon & Kirton, 2018b).

This leaves a fairly long interval (late Toarcian-Callovian) for which the ichthyosaur fossil record is very scarce and geographically dispersed: Sander & Bucher (1993) reported a large cf. *Stenopterygius* from the late Toarcian of southern France; Maisch & Matzke (2000: p72) mention the presence of *Temnodontosaurus* in the late Toarcian of southern Germany; Vincent et al. (2013) reported *Temnodontosaurus* sp., and *Stenopterygius*-like forms in the late Toarcian of southern France and a coracoid bearing many similarities with MNHN DOU353 from the early Aalenian of southern France; finally, Brusatte et al. (2015) described *Dearcmahara shawcrossi* from the late Toarcian-Bajocian of Scotland. The only diagnosable ichthyosaur remains unambiguously known from Aalenian deposits is the holotype of *Stenopterygius aalensis* from Germany (Maxwell, Fernández & Schoch, 2012) (see also Arnaud et al. (1976) and Maxwell et al. (2012) for additional indeterminate specimens). Fragmentary ophthalmosaurid specimens have been reported in the Aalenian-Bajocian boundary of Argentina (Fernández, 2003) and the early Bajocian of Argentina (Fernández, 1999; Gasparini et al., 2007) and Canada (Druckenmiller & Maxwell, 2014). It can be inferred from these data that a replacement of early neoichthyosaurians by ophthalmosaurids took place across the Early–Middle Jurassic transition, but the generalized absence of Aalenian-Bathonian ichthyosaur fossils worldwide and Early Jurassic fossils in South America make it difficult to identify a precise turnover.

While less abundant than ichthyosaurians in early Toarcian Lagerstätten (Hauff, 1953), plesiosaurians already had also evolved a vast array of morphotypes by the Toarcian (O'Keefe, 2001a,b; Benson, Evans & Druckenmiller, 2012; Smith & Araújo, 2017), presumably filling as many ecological niches: long-necked and small headed microclidids (Owen, 1865; Bardet, Godefroit & Sciau, 1999), gigantic, apex predatory rhomaelosaurids (Taylor, 1992; Cruickshank, 1994; Smith & Dyke, 2008; Smith & Vincent, 2010; Smith & Benson, 2014), and small-sized, moderately long-necked, and long-snout early pliosaurids (Benson et al., 2011; Ketchum & Benson, 2011a; Vincent, 2011; Fischer et al., 2017). Microcleidids supposedly go extinct after the Toarcian; their last definite record in the latest Toarcian of France (Sciau, Crochet & Mattei, 1990; Bardet, Godefroit & Sciau, 1999). However, an Aalenian specimen from France regarded as an indeterminate elasmosaurid by Vincent et al. (2007) possesses microcleidid features (8-shaped cervical rib facet, lateral ridge on cervical centra) and might possibly be regarded as a member of that clade. Nevertheless, the long-necked morphotype is then colonised by cryptoclydids by the Callovian-Oxfordian (Brown, 1981).

Only a couple of rhomaleosaurid lineages will survive up to the Middle/Late Jurassic, in high latitudes (Gasparini, 1997; Sato & Wu, 2008; Benson, Zverkov & Arkhangelsky, 2015). Thalassophonean pliosaurids concomitantly radiated and became the main marine apex predators from the Middle Jurassic to the early Late Cretaceous (Noe, 1999, 2001; Ketchum & Benson, 2011a; Benson et al., 2013; Benson & Druckenmiller, 2014; Fischer et al., 2017; Zverkov et al., 2018). A narrative where thalassophoneans filled (either competitively or passively) the niches previously occupied by *Temnodontosaurus* and derived rhomaleosaurids is sensible, but these animals have clearly distinct body plans and probably hunted differently (Massare, 1988; Buchholtz, 2001; O'Keefe, 2001b, 2002). In any case, there is evidence for the continuous presence of gigantic apex predatory plesiosaurians in Europe and elsewhere: *Simolestes keileni* from the upper Bajocian of eastern France (described by Godefroit (1994b), and currently under revision by S. Sachs), an indeterminate fragmentary jaw from the lower Bajocian of Switzerland (Sachs, Klug & Kear, 2019) and 'pliosauroid' tooth from the Aalenian-Bajocian of Australia (Long & Cruickshank, 1998; Kear, 2012). Whether these specimens are rhomaleosaurids or thalassophoneans obviously yields different outcomes as they might push the origin of apex predatory pliosaurids to the Bajocian, but these fossils suggest that the niche of very large apex predators was not vacated for a long period, if at all.

Recent evidence revealed a series of basal metriorhynchoid crocodyliforms in the late Toarcian–Aalenian interval (Wilberg, 2015; Ösi et al., 2018; Aiglstorfer, Havlik & Herrera, 2020) suggesting an intense diversification across the Early-Middle Jurassic transition (Aiglstorfer, Havlik & Herrera, 2020). The effect of this radiation is evident by the late Middle and Late Jurassic, where abundant thalattosuchian taxa are known, occupying several ecological niches (Gasparini, Pol & Spalletti, 2006; Young & de Andrade, 2009; Young et al., 2012, 2014b; Herrera, Gasparini & Fernández, 2013; Foffa et al., 2017, 2018). Teleosauroids do not appear much affected by this transition, but this might be due to the problematic taxonomy of the group (Johnson, Young & Brusatte, 2020).

An abrupt turnover

In light of the short review above, it appears clear that fossiliferous successions in a geographically-restricted areas are crucial to decipher both the tempo and the severity of the marine reptile turnover at the early–Middle Jurassic transition. The late Toarcian–Bajocian successions of Luxembourg and Belgium we analysed above yields novel biostratigraphic information that precise the turnover dynamics of ichthyosaurians and plesiosaurians during the Early–Middle Jurassic transition (the crocodyliform record, recently reviewed by Johnson et al. (2018), is scarce and does not provide relevant information regarding this turnover). In a global, broad-brush view of marine reptile macroevolution, the presence of rhomaleosaurids, microcleidids, and non-thunnosaurian ichthyosaurians in the late Toarcian of Luxembourg (Table 2) was expected, as these clades are already known to survive after the early Toarcian Lagerstätten (Bardet, Godefroit & Sciau, 1999; Vincent et al., 2013; Benson, Zverkov & Arkhangelsky, 2015). With the exception of possible remains from the Aalenian of France (Vincent, Bardet & Morel, 2007; see discussion above), MNHNL DOU978 and the holotype of *Microcleidus tournemirensis* (Sciau, Crochet & Mattei, 1990; Bardet, Godefroit & Sciau, 1999) are the youngest-known microcleidid to date and indicate that the clade extended at least up to the very end of the Early Jurassic. Recording microcleidids, large rhomaleosaurids, *Temnodontosaurus*-like forms, and more derived ichthyosaurians within the same basin that formed the early Toarcian Lagerstätten yields important palaeobiogeographic implications. These fossils indicate that the main marine reptile clades of the Early Jurassic remained abundant and dominant in mid-latitude, epicontinental seas up to the end of the Toarcian at least. Although much less prolific than the underlying strata, the upper Toarcian fossil record suggest that no major turnover took place within the Toarcian as the structuration of the upper tier of marine ecosystems remained intact. The taxonomic diversity crash that follows the early Toarcian appears to be mainly a Lagerstätten effect, confirming previous suspicions (Benson et al., 2010; Maxwell & Vincent, 2015).

In stark contrast with the sense of continuity displayed by the upper Toarcian occurrences, the Bajocian fossil record of Luxembourg suddenly records the dominant clades of the Late Jurassic: cryptoclidids, ophthalmosaurids, and probable pliosaurids, with no evidence – so far – for the presence of more ancient clades. The specimen MNHNL BM782 is oldest-known cryptoclidid and MNHNL BM770 and MNHNL BM780–BM781 are the oldest ophthalmosaurids known, after a single partial forefin from the Aalenian-Bajocian boundary of Argentina (Fernández, 2003) and fragmentary basicranium from an equivalent of the Sauzei Zone in Canada (Druckenmiller & Maxwell, 2014), which directly underlies the Humphresianum Zone. The new occurrences we report here indicate that ophthalmosaurids rapidly dispersed, being almost simultaneously recorded in Canada, Argentina, and Luxembourg by the Early Bajocian.

The Belgo-Luxembourgian marine reptile record provides a clearer picture of the marine reptile turnover occurring at the Early–Middle Jurassic transition, indicating that this replacement is restricted to the sole Aalenian stage instead of possibly spanning the entire middle Toarcian–Bathonian interval. This reduces the uncertainty on the timing and duration of this turnover to 4 instead of 14 million years and packs a series of extinctions and diversifications within a short period of abrupt climate cooling and changes in oceanic currents (Korte et al., 2015). This Aalenian shift from a Toarcian Warm Mode to Aalenian-Bajocian Cool Mode (Korte et al., 2015) also appears associated with a marked faunal disruption in belemnites, with random (i.e. non-morphologically-selective) extinctions leading to a distinct drop in belemnite biodiversity at least in the northwestern Peri-Tethys Ocean (Dera, Toumoulin & de Baets, 2016; Neige, Weis & Fara, 2020). This major disruption in the evolutionary history of Jurassic belemnites ended at the Aalenian-Bajocian boundary and resulted in a radiation of the suborder Belemnopseina that partially replaced the previously dominant Belemnitina in the Western Tethys (Weis, Mariotti & Riegraf, 2012; Weis, Sadki & Mariotti, 2017), furthermore entailing a distinct Boreal vs. Tethyan belemnite provincialism (Doyle, 1987; Mariotti, Santantonio & Weis, 2007; Weis & Mariotti, 2007; Mariotti et al., 2012; Dzyuba et al., 2019). At the present state of knowledge, we can only speculate about whether faunal changes in belemnites and marine reptiles were independently impacted by the same factors, or even causally connected, since belemnites are an essential component of the food spectrum in some marine reptiles (Massare, 1987; Böttcher, 1989; Dick, Schweigert & Maxwell, 2016), their faunal change could have triggered a disruption of the trophic chain up to the giant top predators.

Conclusions

A generalised turnover affected marine reptile communities across the Early–Middle Jurassic transition. However, the extremely poor fossil record of the middle Toarcian-Bathonian interval leaves a ca. 14 million years window of the uncertainty for this important event. Our thorough analysis of the marine reptile record of the late Toarcian to Bajocian successions in a confined palaeogeographic setting (the Belgo-Luxembourgian sub-basin) indicates that:

(i) the structuration of the upper tier of marine ecosystems remained unchanged up to the very end of the Early Jurassic, with the presence of large rhomaleosaurid plesiosaurians, microcroclidid plesiosaurians, as well as *Temnodontosaurus*-like and baracromian ichthyosaurians in the late Toarcian.

(ii) the dominant clades of the Late Jurassic, cryptoclidid plesiosaurians and ophthalmosaurid ichthyosaurians, arose and dispersed earlier than expected, being recorded in the early Bajocian of Luxembourg.

(iii) the within-System marine reptile turnover of the Early–Middle Jurassic transition is more abrupt than previously supposed, being restricted to the sole Aalenian stage, i.e. 4 million years.

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References

Aiglstorfer M, Havlik P, Herrera Y. 2020. The first metriorhynchoid crocodyliform from the Aalenian (Middle Jurassic) of Germany , with implications for the evolution of Metriorhynchoidea. *Zoological Journal of the Linnean Society* 188:522–551.

Andrews CW. 1910a. *A descriptive catalogue of the marine reptiles of the Oxford clay. Based on the Leeds Collection in the British Museum (Natural History), London. Part I.* London,: Order of the Trustees of the British Museum.

Andrews CW. 1910b. Note on the osteology of *Ophthalmosaurus icenicus* Seeley an ichthyosaurian Reptile from the Oxford Clay of Peterborough. *Geological Magazine* 4:202–208.

Arkhangelsky MS, Zverkov NG. 2014. On a new ichthyosaur of the genus *Undorosaurus*. *Proceedings of the Zoological Institute RAS* 318:187–196.

Arkhangelsky MS, Zverkov NG, Rogov MA, Stenshin IM, Baykina EM. 2019. Colymbosaurines from the Upper Jurassic of European Russia and their implication for palaeobiogeography of marine reptiles. *Palaeobiodiversity and Palaeoenvironments* 100:197–218. DOI: 10.1007/s12549-019-00397-0.

Arnaud M, Monleau C, Wenz S. 1976. Découverte de restes d'ichthyosaure dans l'Aalénien du Massif de la Loube (Var). *Bulletin du Musée d'Histoire Naturelle de Marseille* 36:3.

Bakker RT. 1993. Plesiosaur Extinction Cycles — Events that Mark the Beginning, Middle and End of the Cretaceous. In: Caldwell WGE, Kauffman EG eds. *Evolution of the Western Interior Basin: Geological Association of Canada, Special Paper*. Stittsville, Ontario, Canada, 641–664.

Bardet N. 1994. Extinction events among Mesozoic marine reptiles. *Historical Biology* 7:313–324.

Bardet N. 1995. Evolution et extinction des reptiles marins au cours du Mésozoïque. *Palaeovertebrata* 24:177–283.

Bardet N, Falconnet J, Fischer V, Houssaye A, Jouve S, Pereda Suberbiola X, Pérez-García A, Rage J-CJ-C, Vincent P. 2014. Mesozoic marine reptile palaeobiogeography in response to drifting plates. *Gondwana Research* 26:869–887. DOI: 10.1016/j.gr.2014.05.005.

Bardet N, Fischer V, Machalski M. 2016. Large predatory marine reptiles from the Albian–Cenomanian of Annopol, Poland. *Geological Magazine* 153:1–16. DOI:

10.1017/S0016756815000254.

Bardet N, Godefroit P, Sciau J. 1999. A new elasmosaurid Plesiosaur from the Lower Jurassic of Southern France. *Palaeontology* 42:927–952.

Bardet N, Houssaye A, Rage J-C, Suberbiola XP. 2008. The Cenomanian-Turonian (Late Cretaceous) radiation of marine squamates (Reptilia): the role of the Mediterranean Tethys. *Bulletin de la Société géologique de France* 179:605–622.

Bell MA. 2015. geoscale: Geological Time Scale Plotting.

Benson RBJ. 2013. Marine Reptiles. In: MacLeod N, Archibald JD, Levin P eds. *Grzimek's Animal Life Encyclopedia, Extinction*. Farmington Hills, Michigan: Gale Cengage Learning, 267–279.

Benson RBJ, Bowdler T. 2014. Anatomy of *Colymbosaurus megadeirus* (Reptilia, Plesiosauria) from the Kimmeridge Clay Formation of the U.K., and high diversity among Late Jurassic plesiosauroids. *Journal of Vertebrate Paleontology* 34:1053–1071. DOI: 10.1080/02724634.2014.850087.

Benson RBJ, Butler RJ, Lindgren J, Smith AS. 2010. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting the vertebrates. *Proceedings of the Royal Society B: Biological Sciences* 277:829–834.

Benson RBJ, Druckenmiller PS. 2014. Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. *Biological Reviews* 89:1–23. DOI: 10.1111/brv.12038.

Benson RBJ, Evans M, Druckenmiller PS. 2012. High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic boundary. *PLoS ONE* 7:e31838.

Benson RBJ, Evans M, Smith AS, Sassoon J, Moore-Faye S, Ketchum HF, Forrest R. 2013. A giant pliosaurid skull from the Late Jurassic of England. *PLoS ONE* 8:e65989. DOI: 10.1371/journal.pone.0065989.

Benson RBJ, Ketchum HF, Noè LF, Gómez-Pérez M. 2011. New information on *Hauffiosaurus* (Reptilia, Plesiosauria) based on a new species from the Alum Shale member (Lower Toarcian: Lower Jurassic) of Yorkshire, UK. *Palaeontology* 54:547–571.

Benson RBJ, Zverkov NG, Arkhangelsky MS. 2015. Youngest occurrences of rhomaleosaurid plesiosaurs indicate survival of an archaic marine reptile clade at high palaeolatitudes. *Acta Palaeontologica Polonica* 60:769–780.

Benton MJ, Taylor MA. 1984. Marine reptiles from the Upper Lias (Lower Toarcian, Lower Jurassic) of the Yorkshire coast. *Proceedings of the Yorkshire Geological Society* 44:399–429.

Böttcher VR. 1989. Über die Nahrung eines *Leptopterygius* (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonienschiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier. *Stuttgarder Beiträge zur Naturkunde Serie B (Geologie und paläontologie)* 155:1–19.

Boulvain F, Belanger I, Delsate D, Ghysel P, Godefroit P, Laloux M, Roche M. 2001. Triassic and Jurassic lithostratigraphic units (Belgian Lorraine). *Geologica Belgica* 4:113–119.

Brown D. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum (Natural History) Geology* 35:253–347.

Brusatte SL, Young MT, Challands TJ, Clark NDL, Fischer V, Fraser NC, Liston JJ, MacFadyen CCJ, Ross DA, Walsh SA, Wilkinson M. 2015. Ichthyosaurs from the Jurassic of Skye, Scotland. *Scottish Journal of Geology* 51:43–55. DOI: 10.1144/sjg2014-018.

Buchholtz EA. 2001. Swimming styles in Jurassic ichthyosaurs. *Journal of Vertebrate Paleontology* 21:61–73.

Buchy M-C. 2010. Morphologie dentaire et régime alimentaire des reptiles marins du Mésozoïque : revue critique et réévaluation. *Oryctos* 9:49–82.

Caine H, Benton MJ. 2011. Ichthyosauria from the upper Lias of Strawberry Bank, England. *Palaeontology* 54:1069–1093.

Callaway JM, Massare J. 1989. Geographic and stratigraphic distribution of the Triassic Ichthyosauria (Reptilia; Diapsida). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 187:37–58.

Campos L, Fernández MS, Herrera Y. 2020. A new ichthyosaur from the Late Jurassic of north-west Patagonia (Argentina) and its significance for the evolution of the narial complex of the ophthalmosaurids. *Zoological Journal of the Linnean Society* 188:180–201. DOI: 10.1093/zoolinnean/zlz095.

Di Cencio A, Weis R. 2020. Revision of upper Toarcian ammonites (Lytoceratidae, Graphoceratidae and Hammatoceratidae) from the Minette ironstones, southern Luxembourg. In: Di Cencio A, Sadki D, Weis R eds. *Paléontologie au Luxembourg (2) Les ammonites de la Minette*. Ferrantia, in press.

Conybeare WD. 1822. Additional notes on the fossil genera *Ichthyosaurus* and *Plesiosaurus*. *Transactions of the Geological Society of London* 2:103–123.

Cruickshank a. RI. 1994. Cranial Anatomy of the Lower Jurassic Pliosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Reptilia: Plesiosauria). *Philosophical Transactions of the Royal Society B: Biological Sciences* 343:247–260. DOI: 10.1098/rstb.1994.0024.

Delsate D, Suberbiola XP, Felten R, Felten G. 2018. First thyreophoran dinosaur from the Middle Jurassic (Bajocian) of Luxembourg. *Geologica Belgica* 21:19–26.

Delsate D, Weis R. 2010. La Couche à Crassum (Toarcien moyen) au Luxembourg: stratigraphie et faunes de la coupe de Dudelange-Zoufftgen. *Ferrantia* 62:35–60.

Delsett LL, Roberts AJ, Druckenmiller PS, Hurum JH. 2019. Osteology and phylogeny of Late Jurassic ichthyosaurs from the Slottsmøya Member Lagerstätte (Spitsbergen, Svalbard). *Acta Palaeontologica Polonica*:717–743. DOI: 10.4202/app.00571.2018.

Dera G, Toumoulin A, de Baets K. 2016. Diversity and morphological evolution of Jurassic belemnites from South Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology* 457:80–97. DOI: 10.1016/j.palaeo.2016.05.029.

Dick DG, Maxwell EE. 2015. The evolution and extinction of the ichthyosaurs from the perspective of quantitative ecospace modelling. *Biology letters* 11:20150339-. DOI: 10.1098/rsbl.2015.0339.

Dick DG, Schweigert G, Maxwell EE. 2016. Trophic niche ontogeny and palaeoecology of early Toarcian *Stenopterygius* (Reptilia: Ichthyosauria). *Palaeontology*:n/a-n/a. DOI: 10.1111/pala.12232.

Dittrich D. 1993. *Erläuterungen zur geologischen Karte von Luxemburg, 1.25000: Blatt 11 Grevenmacher und Blatt 13 Remic*.

Doyle P. 1987. Lower Jurassic-Lower Cretaceous belemnite biogeography and the development of the Mesozoic Boreal Realm. *Palaeogeography, Palaeoclimatology, Palaeoecology* 61:237–254. DOI: https://doi.org/10.1016/0031-0182(87)90052-6.

Druckenmiller PS, Hurum J, Knutsen EM, Nakrem HA. 2012. Two new ophthalmosaurids (Reptilia: Ichthyosauria) from the Agardhfjellet Formation (Upper Jurassic: Volgian/Tithonian), Svalbard, Norway. *Norwegian Journal of Geology* 92:311–339.

Druckenmiller PS, Maxwell EE. 2014. A Middle Jurassic (Bajocian) ophthalmosaurid (Reptilia, Ichthyosauria) from the Tuxedni Formation, Alaska and the early diversification of the clade. *Geological Magazine* 151:41–48. DOI: doi:10.1017/S0016756813000125.

Dzyuba OS, Schraer CD, Hults CP, Blodgett RB, Schraer DJ. 2019. Early Bajocian belemnites of Southcentral Alaska: new data and new perspectives on mid-Middle Jurassic Megateuthididae and Belemnopseidae biogeography. *Journal of Systematic Palaeontology* 17:911–935. DOI: 10.1080/14772019.2018.1486335.

Fernández M. 1994. A new long-snouted ichthyosaur from the early Bajocian of Neuquén basin (Argentina). *Ameghiniana* 31:291–297.

Fernández M. 1997. A new ichthyosaur from the Tithonian (Late Jurassic) of the Neuquén Basin (Argentina). *Journal of Paleontology* 71:479–484.

Fernández M. 1999. A new ichthyosaur from the Los Molles Formation (Early Bajocian), Neuquén basin, Argentina. *Journal of Paleontology* 73:677–681.

Fernández M. 2003. Ophthalmosauria (Ichthyosauria) forefin from the Aalenian-Bajocian boundary of Mendozo Province, Argentina. *Journal of Vertebrate Paleontology* 23:691–694.

Fernández MS, Maxwell EE. 2012. The genus *Arthropterygius* Maxwell (Ichthyosauria: Ophthalmosauridae) in the Late Jurassic of the Neuquén Basin, Argentina. *Geobios* 45:535–540.

Fischer V. 2016. Taxonomy of *Platypterygius campylodon* and the diversity of the last ichthyosaurs. *PeerJ* 4:1–21. DOI: 10.7717/peerj.2604.

Fischer V, Appleby RM, Naish D, Liston J, Riding JB, Brindley S, Godefroit P. 2013. A basal thunnosaurian from Iraq reveals disparate phylogenetic origins for Cretaceous ichthyosaurs. *Biology Letters* 9:1–6. DOI: 10.1098/rsbl.2013.0021.

Fischer V, Arkhangelsky MS, Uspensky GN, Stenshin IM, Godefroit P. 2014a. A new Lower Cretaceous ichthyosaur from Russia reveals skull shape conservatism within Ophthalmosaurinae. *Geological Magazine* 151:60–70. DOI: 10.1017/S0016756812000994.

Fischer V, Bardet N, Benson RBJ, Arkhangelsky MS, Friedman M. 2016. Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. *Nature communications* 7:1–11. DOI: 10.1038/ncomms10825.

Fischer V, Bardet N, Guiomar M, Godefroit P. 2014b. High Diversity in Cretaceous Ichthyosaurs from Europe Prior to Their Extinction. *PLoS ONE* 9:e84709. DOI: 10.1371/journal.pone.0084709.

Fischer V, Benson RBJ, Druckenmiller PS, Ketchum HF, Bardet N. 2018. The evolutionary history of polycotylid plesiosaurians. *Royal Society Open Science* 5. DOI: 10.1098/rsos.172177.

Fischer V, Benson RBJ, Zverkov NG, Soul LC, Arkhangelsky MS, Lambert O, Stenshin

IM, Uspensky GN, Druckenmiller PS. 2017. Plasticity and convergence in the evolution of short-necked plesiosaurs. *Current Biology* 27:1667–1676. DOI: 10.1016/j.cub.2017.04.052.

Fischer V, Cappetta H, Vincent P, Garcia G, Goolaerts S, Martin JE, Roggero D, Valentin X. 2014c. Ichthyosaurs from the French Rhaetian indicate a severe turnover across the Triassic–Jurassic boundary. *Naturwissenschaften* 101:1027–1040. DOI: 10.1007/s00114-014-1242-7.

Fischer V, Guiomar M, Godefroit P. 2011. New data on the palaeobiogeography of Early Jurassic marine reptiles: the Toarcian ichthyosaur fauna of the Vocontian Basin (SE France). *Neues Jahrbuch für Geologie und Paläontologie* 261:111–127. DOI: 10.1127/0077-7749/2011/0155.

Fischer V, Maisch MW, Naish D, Kosma R, Liston J, Joger U, Krüger FJ, Pardo Pérez J, Tainsh J, Appleby RM. 2012. New ophthalmosaurid ichthyosaurs from the European Lower Cretaceous demonstrate extensive ichthyosaur survival across the Jurassic-Cretaceous boundary. *PLoS ONE* 7:e29234. DOI: 10.1371/journal.pone.0029234.

Fischer V, Zverkov NG, Arkhangelsky MS, Stenshin IM, Blagoveschensky IV, Uspensky GN. 2020. A new elasmosaurid plesiosaurian from the Early Cretaceous of Russia marks an early attempt at neck elongation. *Zoological Journal of the Linnean Society*:in press. DOI: 10.1093/zoolinnean/zlaa103.

Foffa D, Young MT, Brusatte SL. 2018. Filling the Corallian gap : New information on Late Jurassic marine reptile faunas from England. *Acta Palaeontologica Polonica* 63:287–313.

Foffa D, Young MT, Brusatte SL, Graham MR, Steel L. 2017. A new metriorhynchid crocodylomorph from the Oxford Clay Formation (Middle Jurassic) of England, with implications for the origin and diversification of Geosaurini. *Journal of Systematic Palaeontology* 2019:1–21. DOI: 10.1080/14772019.2017.1367730.

Foffa D, Young MT, Stubbs TL, Dexter KG, Brusatte SL. 2018. The long-term ecology and evolution of marine reptiles in a Jurassic seaway. *Nature Ecology and Evolution* 2:1548–1555. DOI: 10.1038/s41559-018-0656-6.

Gasparini Z. 1997. A new pliosaur from the Bajocian of the Neuquen Basin, Argentina. *Palaeontology* 40:135–147.

Gasparini Z, Fernández MS, de la Fuente MS, Salgado L. 2007. Reptiles marinos Jurásicos y Cretácicos de la Patagonia Argentina: su aporte al conocimiento de la herpetofauna mesozoica. *Ameghiniana* APA Public:125–136.

Gasparini Z, Pol D, Spalletti LA. 2006. An unusual marine crocodyliform from the Jurassic-Cretaceous boundary of Patagonia. *Science* 311:70–73.

Gilmore CW. 1902. Discovery of teeth in *Baptanodon*, an ichthyosaurian from the Jurassic of Wyoming. *Science* 16:913–914.

Gilmore CW. 1906. Notes on osteology of *Baptanodon*. *Memoirs of the Carnegie Museum* II:325–337.

Godefroit P. 1993a. Les grands ichthyosaures sinémuriens d'Arlon. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Sciences de la Terre* 63:25–71.

Godefroit P. 1993b. The skull of *Stenopterygius longifrons* (Owen, 1881). *Revue de Paléobiologie de Genève volume spécial* 7:67–84.

Godefroit P. 1994a. Les reptiles marins du Toarcien (Jurassique inférieur) belgoluxembourgeois. *Mémoires pour servir à l'Explication des Cartes Géologiques et Minières de la Belgique* 39:98.

Godefroit P. 1994b. *Simolestes keileni* sp. nov., un Pliosaure (Plesiosauria, Reptilia) du Bajocien supérieur de Lorraine (France). *Bulletin des Académie et Société Lorraines des sciences* 33:77–95.

Großmann F. 2007. The taxonomic and phylogenetic position of the Plesiosauroidea from the Lower Jurassic Posidonia shale of south-west Germany. *Palaeontology* 50:545–564.

Guérin-Franiatte S, Weis R. 2010. Le passage Aalénien-Bajocien près de Rumelange: la série biostratigraphique dans le Bassin d'Esch-sur-Alzette (Grand-Duché de Luxembourg). In: Weis R, Guérin-Franiatte S eds. *Le Jurassique inférieur et moyen au Luxembourg*. Luxembourg ville, Luxembourg: Ferrantia, 73–96.

Hauff B. 1953. *Das Holzmadenbuch*. Öhringen.

Herrera Y, Gasparini Z, Fernández MS. 2013. A new Patagonian species of Cricosaurus (Crocodyliformes, Thalattosuchia): First evidence of Cricosaurus in Middle-Upper Tithonian lithographic limestone from Gondwana. *Palaeontology* 56:663–678. DOI: 10.1111/pala.12010.

Home E. 1819. Reasons for giving the name Proteo-Saurus to the fossil skeleton which has been described. *Philosophical transactions of the Royal Society of London* 109:212–216.

Huene F von. 1922. *Die Ichthyosaurier des Lias und ihre Zusammenhänge*. Berlin: Verlag von Gebrüder Borntraeger.

Huene F von. 1931. Neue Studien über Ichthyosaurier aus Holzmaden. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 42:345–382.

Huene F von. 1951. Ein neuer Fund von *Eurhinosaurus longirostris*. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 93:277–283.

Johnson R. 1979. The osteology of the pectoral complex of *Stenopterygius* Jaekel (Reptilia: Ichthyosauria). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 159:41–86.

Johnson MM, Young MT, Brusatte SL. 2020. Emptying the wastebasket: a historical and taxonomic revision of the Jurassic crocodylomorph Steneosaurus. *Zoological Journal of the Linnean Society* 189:428–448. DOI: 10.1093/zoolinnean/zlaa027.

Johnson MM, Young MT, Brusatte SL, Thuy B, Weis R. 2018. A catalogue of teleosauroids (Crocodylomorpha: Thalattosuchia) from the Toarcian and Bajocian (Jurassic) of southern Luxembourg. *Historical Biology* 2963:1–16. DOI: 10.1080/08912963.2018.1427090.

Kear BP. 2012. A revision of Australia's Jurassic plesiosaurs. *Palaeontology* 55:1125–1138. DOI: 10.1111/j.1475-4983.2012.01183.x.

Kelley NP, Pyenson ND. 2015. Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* 348:aaa3716. DOI: 10.1126/science.aaa3716.

Ketchum HF, Benson RBJ. 2011a. A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early–Middle Jurassic pliosaurids. *Special Papers in Palaeontology* 86:109–129.

Ketchum HF, Benson RBJ. 2011b. The cranial anatomy and taxonomy of *Peloneustes* *philarchus* (Sauropterygia, Pliosauridae) from the Peterborough Member (Callovian, Middle Jurassic) of the United Kingdom. *Palaeontology* 54:639–665. DOI: 10.1111/j.1475-4983.2011.01050.x.

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. DOI: 10.1080/14772019.2020.1748132.

Knight WC. 1903. Notes on genus *Baptanodon*. *American Journal of Science, Fourth Series* 16:78–81.

Knutsen EM, Druckenmiller PS, Hurum JH. 2012a. A new plesiosauroid (Reptilia: Sauropterygia) from the Agardhfjellet Formation (Middle Volgian) of central Spitsbergen, Norway. *Norwegian Journal of Geology* 92:213–234.

Knutsen EM, Druckenmiller PS, Hurum JH. 2012b. Two new species of long-necked plesiosaurians (Reptilia: Sauropterygia) from the Upper Jurassic (Middle Volgian) Agardhfjellet Formation of central Spitsbergen. *Norwegian Journal of Geology* 92:187–212.

Knutsen EM, Druckenmiller PS, Hurum JH. 2012c. Redescription and taxonomic clarification of “Tricleidus” svalbardensis based on new material from the Agardhfjellet Formation (Middle Volgian). *Norwegian Journal of Geology* 92:175–186.

Korte C, Hesselbo SP, Ullmann C V., Dietl G, Ruhl M, Schweigert G, Thibault N. 2015. Jurassic climate mode governed by ocean gateway. *Nature Communications* 6:10015. DOI: 10.1038/ncomms10015.

Lomax DR. 2016. A new leptonectid ichthyosaur from the Lower Jurassic (Hettangian) of Nottinghamshire, England, UK, and the taxonomic usefulness of the ichthyosaurian coracoid. *Journal of Systematic Palaeontology*:1–15. DOI: 10.1080/14772019.2016.1183149.

Lomax DR, Massare JA. 2015. A new species of *Ichthyosaurus* from the Lower Jurassic of West Dorset, England, U.K. *Journal of Vertebrate Paleontology*:903260. DOI: 10.1080/02724634.2014.903260.

Lomax DR, Massare JA. 2016. Two new species of Ichthyosaurus from the lowermost Jurassic (Hettangian) of Somerset, England. *Papers in Palaeontology*. DOI: 10.1002/SPP2.1065.

Lomax DR, Porro LB, Larkin NR. 2019. Descriptive anatomy of the largest known specimen of Protoichthyosaurus prostaxalis (Reptilia: Ichthyosauria) including computed tomography and digital reconstruction of a three-dimensional skull. *PeerJ* 7:e6112. DOI: 10.7717/peerj.6112.

Lomax DR, Sachs S. 2017. On the largest Ichthyosaurus : A new specimen of Ichthyosaurus somersetensis containing an embryo. *Acta Palaeontologica Polonica* 62:575–584.

Long JA, Cruickshank ARI. 1998. Further Records of Plesiosaurian Reptiles of Jurassic and Cretaceous Age From Western Australia. *Records of the Western Australian Museum* 19:47.

Lucius M. 1945. Die Luxemburger Minetteformation und die jüngeren Eisenerzbildungen unseres Landes. Beiträge zur Geologie von Luxemburg. *Service Carte géologique du Luxembourg* 4:1–347.

Maisch MW. 1998. A new ichthyosaur genus from the Posidonia Shale (Lower Toarcian, Jurassic) of Holzmaden, SW-Germany with comments on the phylogeny of post-Triassic ichthyosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 209:47–78.

Maisch MW. 2008. Revision der Gattung *Stenopterygius* Jaekel, 1904 emend. von Huene, 1922 (Reptilia: Ichthyosauria) aus dem unteren Jura Westeuropas. *Palaeodiversity* 1:227–271.

Maisch MW. 2010. Phylogeny, systematics, and origin of the Ichthyosauria - the state of the art. *Palaeodiversity* 3:151–214.

Maisch MW, Matzke AT. 2000. The Ichthyosauria. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 298:1–159.

Maisch MW, Matzke AT. 2001. The cranial osteology of the Middle Triassic ichthyosaur Contectopalatus from Germany. *Palaeontology* 44:1127–1156.

Maisch MW, Matzke AT. 2003. The cranial osteology of the ichthyosaur *Leptonectes* cf. *tenuirostris* from the Lower Jurassic of England. *Journal of Vertebrate Paleontology* 23:116–127. DOI: 10.1671/0272-4634(2003)23[116:TCOOTI]2.0.CO;2.

Mariotti N, Santantonio M, Weis R. 2007. Aalenian-Early Bajocian Belemnite Assemblage From Peri-Mediterranean Tethyan Sediments (Calabria , Southern Italy). *Geologica Romana* 40:1–19.

Mariotti N, Weis R, Di Cencio A, Clément A, De Baets K. 2012. New records of early Middle Jurassic belemnites in the French Subalpine Basin and their paleobiogeographic significance. *Geobios* 45:99–108. DOI: https://doi.org/10.1016/j.geobios.2011.11.012.

Marsh OC. 1895. The Reptilia of the *Baptanodon* Beds. *American Journal of Science* 50:405–406.

Martin JE, Fischer V, Vincent P, Suan G. 2012. A longirostrine *Temnodontosaurus* (Ichthyosauria) with comments on Early Jurassic ichthyosaur niche partitioning and disparity. *Palaeontology* 55:995–1005. DOI: 10.1111/j.1475-4983.2012.01159.x.

Massare JA. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7:121–137.

Massare JA. 1988. Swimming capabilities of Mesozoic marine reptiles: implications for the methods of predation. *Palaeobiology* 14:187–205.

Massare JA. 1997. Faunas, behavior, and evolution. In: Callaway JM, Nicholls EL eds. *Ancient Marine Reptiles*. San Diego: Academic Press, 401–421.

Massare JA, Buchholtz EA, Kenney J, Chomat A-M. 2006. Vertebral morphology of *Ophthalmosaurus natans* (Reptilia: Ichthyosauria) from the Jurassic Sundance Formation of Wyoming. *Paludicola* 5:242–254.

Maubeuge PL. 1972. *Etudes stratigraphiques sur la formation ferrifère de Lorraine et ses morts-terrains*. Metz: Self-edited.

Maxwell EE. 2010. Generic reassignment of an ichthyosaur from the Queen Elizabeth Islands, Northwest Territories, Canada. *Journal of Vertebrate Paleontology* 30:403–415.

Maxwell EE. 2012. New metrics to differentiate species of *Stenopterygius* (Reptilia: Ichthyosauria) from the Lower Jurassic of southwestern Germany. *Journal of Paleontology* 86:105–115. DOI: 10.1666/11-038.1.

Maxwell EE, Caldwell MW, Lamoureux DO. 2012. Tooth histology, attachment, and replacement in the Ichthyopterygia reviewed in an evolutionary context. *Paläontologische Zeitschrift* 86:1–14.

Maxwell EE, Cortés D. 2020. A revision of the Early Jurassic ichthyosaur *Hauffiopteryx* (Reptilia: Ichthyosauria), and description of a new species from Southwestern Germany. *Palaeontologia Electronica* 23:1–43. DOI: 10.26879/937.

Maxwell EE, Fernández MS, Schoch RR. 2012. First diagnostic marine reptile remains from the Aalenian (Middle Jurassic): a new ichthyosaur from southwestern Germany. *PLoS ONE* 7:e41692. DOI: 10.1371/journal.pone.0041692.

Maxwell EE, Vincent P. 2015. Effects of the early Toarcian Oceanic Anoxic Event on ichthyosaur body size and faunal composition in the Southwest German Basin. *Paleobiology*:1–10. DOI: 10.1017/pab.2015.34.

Mazin J-M. 1982. Affinités et phylogénie des Ichthyopterygia. *Geobios, mémoire spécial* 6:85–98.

McGowan C. 1973. The cranial morphology of the Lower Liassic latipinnate ichthyosaurs of England. *Bulletin of the British Museum (Natural History) Geology* 24:1–109.

McGowan C. 1974. A revision of the longipinnate ichthyosaurs of the Lower Jurassic of England, with description of the new species (Reptilia, Ichthyosauria). *Life Science Contributions, Royal Ontario Museum* 97:1–37.

McGowan C. 1979. A revision of the Lower Jurassic ichthyosaurs of Germany with descriptions of two new species. *Palaeontographica. Abteilung A. Paläozoologie, Stratigraphie* 166:93–135.

McGowan C. 1986. A putative ancestor for the swordfish-like ichthyosaur *Eurhinosaurus*. *Nature* 322:454–456.

McGowan C. 1994. A new species of *Shastasaurus* (Reptilia: Ichthyosauria) from the Triassic of British Columbia; the most complete exemplar of the genus. *Journal of Vertebrate Paleontology* 14:168–179.

McGowan C. 1996. Giant ichthyosaurs of the Early Jurassic. *Canadian Journal of Earth Sciences* 33:1011–1021.

McGowan C. 2003. A new specimen of *Excalibosaurus* from the English Lower Jurassic. *Journal of Vertebrate Paleontology* 23:950–956.

McGowan C, Milner AC. 1999. A new Pliensbachian ichthyosaur from Dorset, England. *Palaeontology* 42:761–768.

McGowan C, Motani R. 2003. *Part 8. Ichthyopterygia*. München: Verlag Dr. Friedrich Pfeil.

Mehl MG. 1912. *Muraenosaurus*? *Reedii*, Sp. Nov and *Tricleidus*? *Laramiensis* Knight, American Jurassic plesiosaurs. *The Journal of Geology* 20:344–352.

Merriam JC. 1908. Triassic Ichthyosauria with special reference to the American forms. *Memoirs of the University of California* 1:1–154.

Moon BC. 2017. A new phylogeny of ichthyosaurs (Reptilia: Diapsida). *Journal of Systematic Palaeontology* 17:129–155. DOI: 10.1080/14772019.2017.1394922.

Moon BC, Kirton AM. 2018a. Ichthyosaurs of the British Middle and Upper Jurassic Part 2 *Brachypterygius*, *Nannopterygius*, *Macropterygius* and Taxa invalida. *Monographs of the Palaeontographical Society* 172:85–197. DOI: 10.1080/02693445.2018.1468139.

Moon BC, Kirton AM. 2018b. Ichthyosaurs of the British Middle and Upper Jurassic Part

1, *Ophthalmosaurus*. *Monographs of the Palaeontographical Society* 170:1–84. DOI: 10.1080/02693445.2016.11963958.

Moon BC, Stubbs TL. 2020. Early high rates and disparity in the evolution of ichthyosaurs. *Communications Biology* 3:1–8. DOI: 10.1038/s42003-020-0779-6.

Motani R. 1997. Temporal and Spatial Distribution of Tooth Implantation in Ichthyosaurs. In: Callaway JM, Nicholls EL eds. *Ancient Marine Reptiles*. San Diego, California: Academic Press, 81–103.

Motani R. 1999a. Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology* 19:473–496.

Motani R. 1999b. On the evolution and homologies of ichthyosaurian forefins. *Journal of Vertebrate Paleontology* 19:28–41.

Motani R. 2009. The Evolution of Marine Reptiles. *Evo Edu Outreach* 2:224–235.

Neige P, Weis R, Fara E. 2020. Ups and downs of belemnite diversity in the Early Jurassic of Western Tethys. *Palaeontology*:In Press.

Noe LF. 1999. The Callovian pliosaurs of the Oxford Clay–evidence and implications for the consumption of marine invertebrates. In: *Secondary Adaptation to Life in Water/La réadaptation au milieu aquatique*. 13–17.

Noe LF. 2001. A taxonomic and functional study of the Callovian (Middle Jurassic) Pliosauroidea (Reptilia, Sauropterygia). University of Derby.

O'Keefe FR. 2001a. Ecomorphology of plesiosaur flipper geometry. *Journal of Evolutionary Biology* 14:987–991.

O'Keefe FR. 2001b. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia:Sauropterygia). *Acta Zoological Fennica* 213:1–63.

O'Keefe FR. 2002. The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). *Palaeobiology* 28:101–112.

O'Keefe RF. 2004. Preliminary description and phylogenetic position of a new Plesiosaur (Reptilia : Sauropterygia) from the Toarcian of Holzmaden, Germany. *Journal of Paleontology* 78:973–988. DOI: 10.1666/0022-3360(2004)078<0973:pdappo>2.0.co;2.

O'Keefe FR, Wahl WJ. 2003. Preliminary report on the osteology and relationships of a new aberrant cryptocleidoid plesiosaur from the Sundance Formation, Wyoming. *Paludicola* 4:48–68.

Ösi A, Young MT, Galácz A, Rabi M. 2018. A new large-bodied thalattosuchian crocodyliform from the Lower Jurassic (Toarcian) of Hungary, with further evidence of the mosaic acquisition of marine adaptations in Metriorhynchoidea. *PeerJ* 6:e4668. DOI: 10.7717/peerj.4668.

Owen R. 1860. On the orders of fossil and recent Reptilia and their distribution in time. *Report of the British Association for the Advancement of Science* 29:153–166.

Owen R. 1865. A monograph of the Fossil Reptilia of the Liassic Formations, part third: *Plesiosaurus*, *Dimorphodon*, and *Ichthyosaurus*. *Monograph of the Palæontographical society*:12–130.

Paparella I, Maxwell EE, Cipriani A, Roncacè S, Caldwell MW. 2017. The first ophthalmosaurid ichthyosaur from the Upper Jurassic of the Umbrian-Marchean Apennines (Marche, Central Italy). *Geological Magazine* 154:837–858. DOI: 10.1017/S0016756816000455.

Pieńkowski G, Schudack ME, Bosák P, Enay R, Feldman-Olszewska A, Golonka J, Gutowski J, Herngreen GFW, Jordan P, Krobicki M, Lathuiliere B, Leinfelder RR, Michalík J, Mönnig E, Noe-Nygaard N, Pálfy J, Pint A, Rasser MW, Reisdorf AG, Schmid DU, Schweigert G, Surlyk F, Wetzel A, Wong TE. 2008. Jurassic. *The Geology of Central Europe Volume 2: Mesozoic and Cenozoic* 2:0. DOI: 10.1144/CEV2P.2.

Popov E V, Delsate D, Felten R. 2019. A New Callorhinchid Genus (Holocephali, Chimaeroidei) from the Early Bajocian of Ottange-Rumelange, on the Luxembourg-French Border. *Paleontological Research* 23:220–230. DOI: 10.2517/2018PR021.

Pyenson ND, Kelley NP, Parham JF. 2014. Marine tetrapod macroevolution: Physical and biological drivers on 250 million years of invasions and evolution in ocean ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology* 400:1–8. DOI: 10.1016/j.palaeo.2014.02.018.

R Core Team. 2016. R: A language and environment for statistical computing.

Roberts AJ, Druckenmiller PS, Cordonnier B, Delsett LL, Hurum JH. 2020. A new plesiosaurian from the Jurassic-Cretaceous transitional interval of the Slottsmøya Member (Volgian), with insights into the cranial anatomy of cryptoclidids using computed tomography. *PeerJ* 2020. DOI: 10.7717/peerj.8652.

Roberts AJ, Druckenmiller PS, Delsett LL, Hurum JH. 2017. Osteology and relationships of *Colymbosaurus* Seeley, 1874, based on new material of *C. svalbardensis* from the Slottsmøya Member, Agardhfjellet Formation of central Spitsbergen. *Journal of Vertebrate Paleontology* 4634:e1278381. DOI: 10.1080/02724634.2017.1278381.

Sachs S, Klug C, Kear BP. 2019. Rare evidence of a giant pliosaurid-like plesiosaur from the Middle Jurassic (lower Bajocian) of Switzerland. *Swiss Journal of Palaeontology* 138:337–342. DOI: 10.1007/s13358-019-00200-9.

Sadki D, Weis R, Braun P. 2020. Graphoceratidés (Ammonitina) de l'Aalénien moyen (Jurassique) de Rumelange-Hutberg (Grand-Duché de Luxembourg). In: Di Cencio A, Sadki D, Weis R eds. *Paléontologie au Luxembourg (2). Les ammonites de la Minette*. Ferrantia, in press.

Sander PM. 2000. Ichthyosauria: their diversity, distribution, and phylogeny. *Paläontologische Zeitschrift* 74:1–35.

Sander PM, Bucher H. 1993. An ichthyosaur from the uppermost Toarcian of southern France. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* 1993:631–640.

Sato T, Wu XC. 2008. A new Jurassic pliosaur from Melville Island, Canadian Arctic Archipelago. *Canadian Journal of Earth Sciences* 45:303–320. DOI: 10.1139/E08-003.

Schintgen T, Förster A. 2013. Geology and basin structure of the Trier-Luxembourg Basin – implications for the existence of a buried Rotliegend graben. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* 164:615–637. DOI: 10.1127/1860-1804/2013/0025.

Schwermann L, Sander PM. 2011. Osteologie und Phylogenie von Westphaliasaurus simonsensii: Ein neuer Plesiosauride (Sauropterygia) aus dem Unteren Jura (Pliensbachium) von Sommersell (Kreis Höxter), Nordrhein-Westfalen, Deutschland. *Geologie und Paläontologie in Westfalen* 79:5–56.

Sciau J, Crochet J-YY, Mattei J. 1990. Le premier squelette de plésiosaure de France sur le Causse du Larzac (Toarcien, Jurassique inférieur). *Geobios* 23:111–116. DOI:

10.1016/0016-6995(90)80021-7.

Seeley HG. 1874a. Note on some of the generic modifications of the plesiosaurian pectoral arch. *Quarterly Journal of the Geological Society* 30:436–449. DOI: 10.1144/GSL.JGS.1874.030.01-04.48.

Seeley HG. 1874b. On *Murænosaurus Leedsii*, a Plesiosaurian from the Oxford Clay. Part I. *Quarterly Journal of the Geological Society of London* 30:197–208. DOI: 10.1144/GSL.JGS.1874.030.01-04.35.

Seeley HG. 1874c. On the pectoral arch and fore limb of *Ophthalmosaurus*, a new ichthyosaurian genus from the Oxford Clay. *Quarterly Journal of the Geological Society of London* 30:696–707.

Siehl A, Thein J. 1989. Minette-type ironstones. In: *Phanerozoic ironstones*. Geological Society of London, Special Publications, 175–193.

Smith AS. 2013. Morphology of the caudal vertebrae in *Rhomaleosaurus zetlandicus* and a review of the evidence for a tail fin in Plesiosauria. *Paludicola* 9:144–158.

Smith AS. 2015. Reassessment of "*Plesiosaurus*" *megacephalus* (Sauropterygia: Plesiosauria) from the Triassic-Jurassic boundary, UK. *Palaeontologia Electronica* 1820:1–19.

Smith AS, Araújo R. 2017. *Thaumatodracon wiedenrothi*, a morphometrically and stratigraphically intermediate new rhomaleosaurid plesiosaurian from the Lower Jurassic (Sinemurian) of Lyme Regis. *Palaeontographica Abteilung A* 308:89–125. DOI: 10.1127/pala/308/2017/89.

Smith AS, Benson RBJ. 2014. Osteology of Rhomaleosaurus thorntoni (Sauropterygia: Rhomaleosauridae) from the Lower Jurassic (Toarcian) of Northamptonshire, England. *Monographs of the Palaeontographical Society* 168:1–40. DOI: 10.1080/02693445.2014.11963953.

Smith AS, Dyke GJ. 2008. The skull of the giant predatory pliosaur *Rhomaleosaurus cramptoni*: implications for plesiosaur phylogenetics. *Naturwissenschaften* 95:975–980. DOI: 10.1007/s00114-008-0402-z.

Smith AS, Vincent P. 2010. A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. *Palaeontology* 53:1049–1063. DOI: 10.1111/j.1475-4983.2010.00975.x.

Storrs GW. 1997. Morphological and taxonomic clarfification of the genus *Plesiosaurus*. In: *Ancient marine reptiles*. 145–190.

Swinton WE. 1930. On a new species of *Eurhinosaurus* in the British Museum. *Geological Magazine* 67:275–277.

Taylor M. 1992. Functional anatomy of the head of the large aquatic predator *Rhomaleaosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. *Philosophical Transactions of the Royal Society B: Biological Sciences* 335:247–280. DOI: 10.1098/rstb.1992.0022.

Taylor MA. 1997. Before the Dinosaur: The historical significance of the fossil marine reptiles. In: Callaway JM, Nicholls EL eds. *Ancient Marine Reptiles*. San Diego California: Academic Press, xix–xlvi.

Tennant JP, Mannion PD, Upchurch P. 2016. Sea level regulated tetrapod diversity dynamics through the Jurassic/Cretaceous interval. *Nature Communications* 7:12737. DOI: 10.1038/ncomms12737.

Tennant JP, Mannion PD, Upchurch P, Sutton MD, Price GD. Biotic and environmental dynamics through the Late Jurassic – Early Cretaceous transition : evidence for protracted faunal and ecological turnover. *Biological Reviews*. DOI: 10.1111/brv.12255.

Teyssen TAL. 1984. Sedimentology of the Minette oolithic ironstones of Luxembourg and Lorraine: a Jurassic subtidal sandwave complex. *Sedimentology* 31:195–2011.

Thorne PM, Ruta M, Benton MJ. 2011. Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. *Proceedings of the National Academy of Sciences of the United States of America* 108:8339–8344. DOI: 10.1073/pnas.1018959108.

Vincent P. 2011. A re-examination of *Hauffiosaurus zanoni*, a pliosauroid from the Toarcian (Early Jurassic) of Germany. *Journal of Vertebrate Paleontology* 31:340–351. DOI: 10.1080/02724634.2011.550352.

Vincent P, Bardet N, Morel N. 2007. An elasmosaurid plesiosaur from the Aalenian (Middle Jurassic) of Western France. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 243:363–370.

Vincent P, Martin JE, Fischer V, Suan G, Khalloufi B, Sucheras-Marx B, Lena A, Janneau K, Rousselle B, Rulleau L, Suchéras-Marx B, Léna A, Janneau K, Rousselle B, Rulleau L. 2013. A marine vertebrate fauna from the Toarcian-Aalenian succession of southern Beaujolais, Rhône, France. *Geological Magazine* 150:822–834. DOI: doi:10.1017/S0016756812000982.

Vincent P, Storrs GW. 2019. *Lindwurmia*, a new genus of Plesiosauria (Reptilia: Sauropterygia) from the earliest Jurassic of Halberstadt, northwest Germany. *Science of Nature* 106. DOI: 10.1007/s00114-018-1600-y.

Vincent P, Taquet P, Fischer V, Bardet N, Falconnet J, Godefroit P. 2014. Mary Anning's legacy to French vertebrate palaeontology. *Geological Magazine* 151:7–20. DOI: 10.1017/S0016756813000861.

Vincent P, Weis R, Kronz G, Delsate D. 2017. *Microcleidus melusinae*, a new plesiosaurian (Reptilia, Plesiosauria) from the Toarcian of Luxembourg. *Geological Magazine*:In Press. DOI: 10.1017/S0016756817000814.

Weis R, Mariotti N. 2007. A belemnite fauna from the Aalenian-Bajocian boundary beds of the Grand Duchy of Luxembourg (NE Paris Basin). *Bollettino della Societa Paleontologica Italiana* 46:149–174.

Weis R, Mariotti N, Riegraf W. 2012. The belemnite family Holcobelidae (Coleoidea) in the European Jurassic: systematics, biostratigraphy, palaeobiogeography and evolutionary trends. *Palaeodiversity* 5:13–49.

Weis R, Sadki D, Mariotti N. 2017. Aalenian-Bajocian belemnites from the Middle and High Atlas, Morocco: taxonomy, biostratigraphy and palaeobiogeographical affinities. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 284:215–240. DOI: 10.1127/njgpa/2017/0659.

White TE. 1940. Holotype of *Plesiosaurus longirostris* Blake and classification of the plesiosaurs. *Journal of Paleontology* 14:451–467.

Wilberg EW. 2015. A new metriorhynchoid (Crocodylomorpha, Thalattosuchia) from the Middle Jurassic of Oregon and the evolutionary timing of marine adaptations in thalattosuchian crocodylomorphs. *Journal of Vertebrate Paleontology* 902846. DOI: 10.1080/02724634.2014.902846.

Young MT, de Andrade MB. 2009. What is *Geosaurus*? Redescription of *Geosaurus giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. *Zoological Journal of the Linnean Society* 157:551–585.

Young MT, Brandalise de Andrade M, Cornée J-J, Steel L, Foffa D. 2014a. Re-description of a putative Early Cretaceous “teleosaurid” from France, with implications for the survival of metriorhynchids and teleosaurids across the Jurassic-Cretaceous Boundary. *Annales de Paléontologie* 100:165–174. DOI: 10.1016/j.annpal.2014.01.002.

Young MT, Brusatte SL, de Andrade MB, Desojo JB, Beatty BL, Steel L, Fernández MS, Sakamoto M, Ruiz-Omeñaca JI, Schoch RR. 2012. The cranial osteology and feeding ecology of the metriorhynchid crocodylomorph genera *Dakosaurus* and *Plesiosuchus* from the Late Jurassic of Europe. *PLoS ONE* 7:e44985. DOI: 10.1371/journal.pone.0044985.

Young MT, Steel L, Brusatte SL, Foffa D, Lepage Y. 2014b. Tooth serration morphologies in the genus *Machimosaurus* (Crocodylomorpha, Thalattosuchia) from the Late Jurassic of Europe. *Royal Society Open Science* 1:1–14. DOI: 10.1098/rsos.140269.

Zverkov NG, Arkhangelsky MS, Pardo-Pérez J, Beznosov PA. 2015. On the Upper Jurassic ichthyosaur remains from the Russian North. *Proceedings of the Zoological Institute RAS* 319:81–97.

Zverkov NG, Efimov VM. 2019. Revision of *Undorosaurus*, a mysterious Late Jurassic ichthyosaur of the Boreal Realm. *Journal of Systematic Palaeontology*:in press. DOI: 10.1080/14772019.2018.1515793.

Zverkov NG, Fischer V, Madzia D, Benson RBJ. 2018. Increased Pliosaurid Dental Disparity Across the Jurassic – Cretaceous Transition. *Palaeontology* 61:825–846. DOI: 10.1111/pala.12367.

Zverkov NG, Jacobs ML. 2020. Revision of Nannopterygius (Ichthyosauria: Ophthalmosauridae): reappraisal of the ‘inaccessible’ holotype resolves a taxonomic tangle and reveals an obscure ophthalmosaurid lineage with a wide distribution. *Zoological Journal of the Linnean Society*:1–48. DOI: 10.1093/zoolinnean/zlaa028.

Zverkov NG, Prilepskaya NE. 2019. A prevalence of *Arthropterygius* (Ichthyosauria: Ophthalmosauridae) in the Late Jurassic—earliest Cretaceous of the Boreal Realm. *PeerJ* 7:e6799. DOI: 10.7717/peerj.6799.

Figure Captions

Figure 1. Number of collections of marine reptiles (Ichthyosauria, Plesiosauria, Thalattosuchia, Pleurosauria, Angolachelonia) per stage. Data extracted from the paleobiology database on the 26th March 2020 (see Acknowledgements for the main contributors of these data). Silhouettes originate from phylopic: *Dakosaurus* by Dmitry Bogdanov & T Michael Keesey; *Meyerasaurus*, *Eurhinosaurus*, *Temnodontosaurus*, *Plesiopterys*, and *Ophthalmosaurus* by Gareth Monger; *Rhomaleosaurus* and *Stenopterygius* by Scott Hartmann; *Peloneustes* by Nobu Tamura & T Michael Keesey; *Albertonectes* by Frank Denota.

Figure 2. Map of the fossiliferous localities investigated. Produced using data from Esri, HERE, Garmin, and OpenStreetMap.

Figure 3. Thoursense Zone fauna, late Toarcian, Luxembourg. Selected anatomy of specimen MNHNL TM212. (A–B) left coracoid in ventral (A) and anteroventral (B) views. (C, E, F) left humerus in anterodorsal (C), distal (E), and proximal (F) views. (D) left forefin in ventral view.

Figure 4. Pseudoradiosa Zone fauna, late Toarcian, Luxembourg. (A–E) rhomaleosaurid left humerus MNHNL DOU307 in ventral (A), anterior (B), dorsal (C), proximal (D), and distal (E) views. (F–H) rhomaleosaurid humerus MNHNL KA109 in dorsal/ventral (F), proximal (H), and distal (H) views.

Figure 5. Ichthyosaurians of the late Toarcian of Belgium and Luxembourg. (A–B) large, *Temnodontosaurus*-like caudal centrum IRSNB Vert-00000-00803 in anterior (A) and lateral (B) views. (C–D) probable thunnosaurian caudal centrum IRSNB Vert-00000-00808 in anterior (C) and dorsal (D) views. (E–F) ichthyosaurian distal tooth IRSNB Vert-06462-0003 in labial (E) and mesial (F) views. (G–H) probable non-ophthalmosaurid left angular IRSNB Vert-06462-0002 in lateral (G) and medial (H) views. (I–K) ichthyosaurian right quadrate IRSNB Vert-00000-00802 in lateral (I), medial (J), and posterior (K) views.

Figure 6. Ichthyosaurians of the Aalensis Zone, late Toarcian, Luxembourg. (A–C) left coracoid of a non-baracromian parvipelvian MNHNL DOU353 in ventral (A), lateral (B), and posterior (C) views. (D–E) large parvipelvian caudal centrum MNHNL DOU378 in dorsal (D), anterior (E), and cross-sectional (F) views. (G) small parvipelvian caudal centrum MNHNL DOU998 in anteroventral view. (H–I) parvipelvian dorsal centrum

MNHNL DOU944 in anterior (H), and lateral (I) views. (J) parvipelvian dorsal centrum MNHNL DOU352 in anterior view.

Figure 7. Plesiosaurian centra of the Aalensis Zone, late Toarcian, Luxembourg. (A–B) rhomaleosaurid pectoral vertebra MNHNL DOU954 in anterior (A) and ventral (B) views. (C–G) cf. *Microcleidus* cervical vertebra in anterior (C), ventral (D), dorsal (E), lateral (F), and oblique (G) views. (H–J) rhomaleosaurid pectoral vertebra MNHNL DOU723 in anterior (H), lateral (I), and posterior (J) views. (K–N) plesiosaurian sacral vertebra MNHNL DOU724 in dorsal (K), anterior (L), posterolateral (M), and ventral (N) views. (O–Q) rhomaleosaurid pectoral vertebra MNHNL DOU722 in anterior (H), lateral (I), and posterior (J) views.

Figure 8. Plesiosaurians of the Aalensis Zone, late Toarcian, Luxembourg. (A) plesiosaurian tooth crown MNHNL DOU906 in ?mesial view. (B) rhomaleosaurid right humerus MNHNL DOU558 in dorsal view. (C–F) rhomaleosaurid right humerus MNHNL DOU324a in proximal (C), dorsal (D), posterior (E), and distal (F) views. (G) juvenile rhomaleosaurid propodial MNHNL DOU324b.

Figure 9. Late Aalenian fauna, Luxembourg. (A–D) non-cryptoclidid plesiosauroid cervical centrum MNHNL BU157 in anterior (A), dorsal (B), ventral (C), and oblique (D) views. (E–G) plesiosaur juvenile caudal centrum in lateral (E), anterior (F), and anteroventral (G) views. (H–I) fragmentary ichthyosaurian rostrum.

Figure 10. Humphresianum Zone fauna, early Bajocian, Luxembourg. (A–F) cryptoclidid propodial MNHNL BM782 in anterior (A), proximal (B), dorsal (C), ventral (D), posterior (E), and distal (F) views. (G–H) parvipelvian MNHNL BM392 centra (G) and sclerotic element in lateral view (H). (I–O) ophthalmosaurid surangular and teeth MNHNL BM780_781: anterior tooth in labial (I) and basal (J) views; mid-rostrum tooth in labial (K) and basal (L) views; posterior tooth in labial view (M); right angular in lateral (N) and medial (O) views.

Figure 11. The new Humphresianum Zone ophthalmosaurid, early Bajocian, Luxembourg. Selected anatomy of specimen MNHNL BM779. (A–C) right exoccipital in anterolateral (A), posteromedial (B), and posterior (C) views. (D–E) suraoccipital in posterior (D) and ventral (E) views. (F–H) left scapula in anterior (F), medial (G), and lateral (H) views. (I–K) right quadrate in lateral (I), anterior (J), and condylar (K) views. (L) right parietal in dorsal view. (M–N) right humerus in posterior (M) and dorsal (N) views. (O–P) right ulna in posterior (O) and dorsal (P) views.

Figure 12. Ichthyosaurian centra proportions. (A) Height over length; the grey lines indicate a ratio of 2 and 3. (B) Height-length ratio, emphasizing the reduction of shape disparity from the late Toarcian to the Bajocian. The silhouette originate from phylopic: *Stenopterygius* by Scott Hartmann.

Figure 1

Number of collections of marine reptiles (Ichthyosauria, Plesiosauria, Thalattosuchia, Pleurosauria, Angolachelonia) per stage.

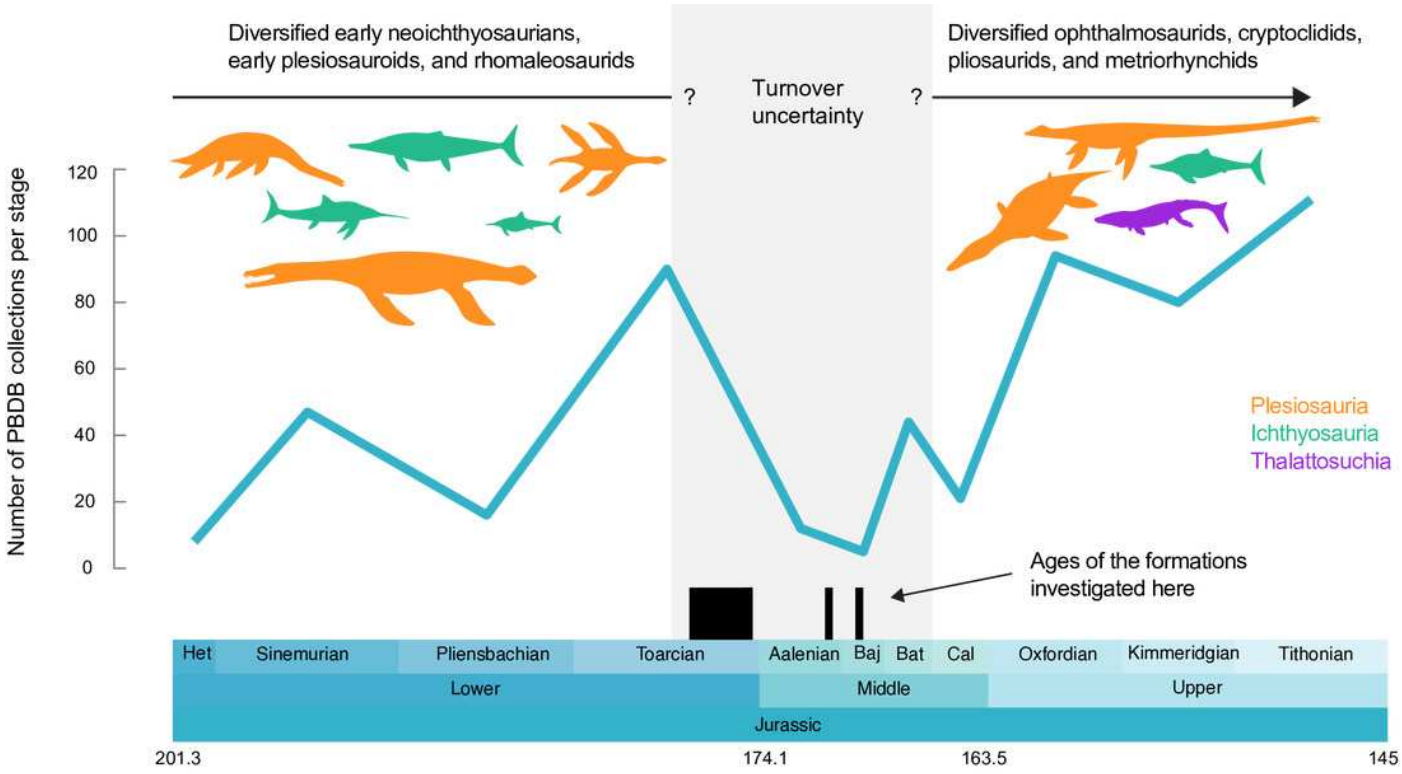
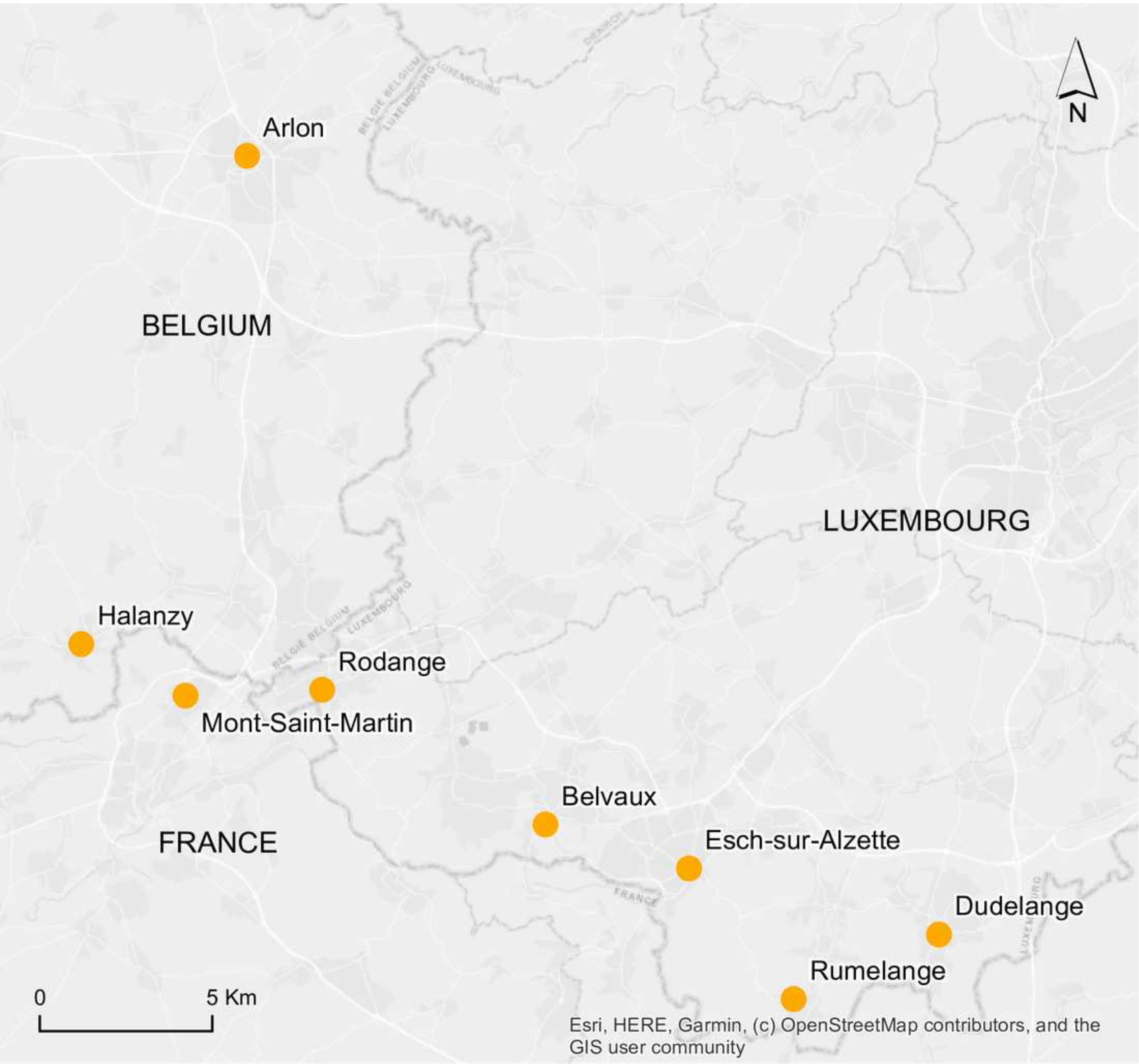


Figure 2

Map of the fossiliferous localities investigated



Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Figure 3

Thoursense Zone fauna, late Toarcian, Luxembourg.

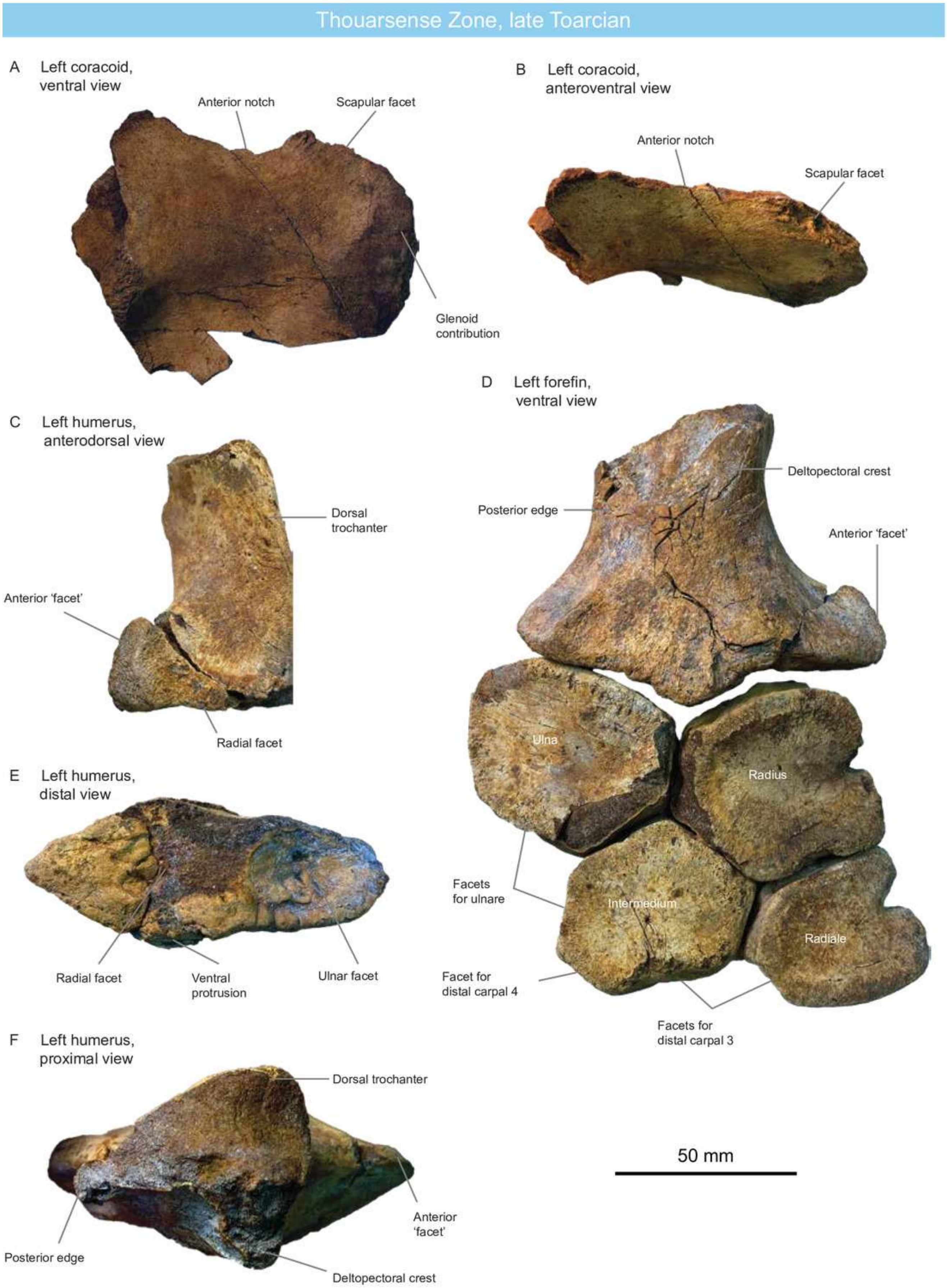

Thouarsense Zone, late Toarcian
A Left coracoid, ventral view
Anterior notch
Scapular facet
Glenoid contribution
B Left coracoid, anteroventral view
Anterior notch
Scapular facet
C Left humerus, anterodorsal view
Dorsal trochanter
Anterior 'facet'
Radial facet
D Left forefin, ventral view
Deltopectoral crest
Posterior edge
Anterior 'facet'
Ulna
Radius
Intermedium
Radiale
Facets for ulnare
Facet for distal carpal 4
Facets for distal carpal 3
E Left humerus, distal view
Radial facet
Ventral protrusion
Ulnar facet
F Left humerus, proximal view
Dorsal trochanter
Anterior 'facet'
Posterior edge
Deltopectoral crest
50 mm

Figure 4

Pseudoradiosa Zone fauna, late Toarcian, Luxembourg.

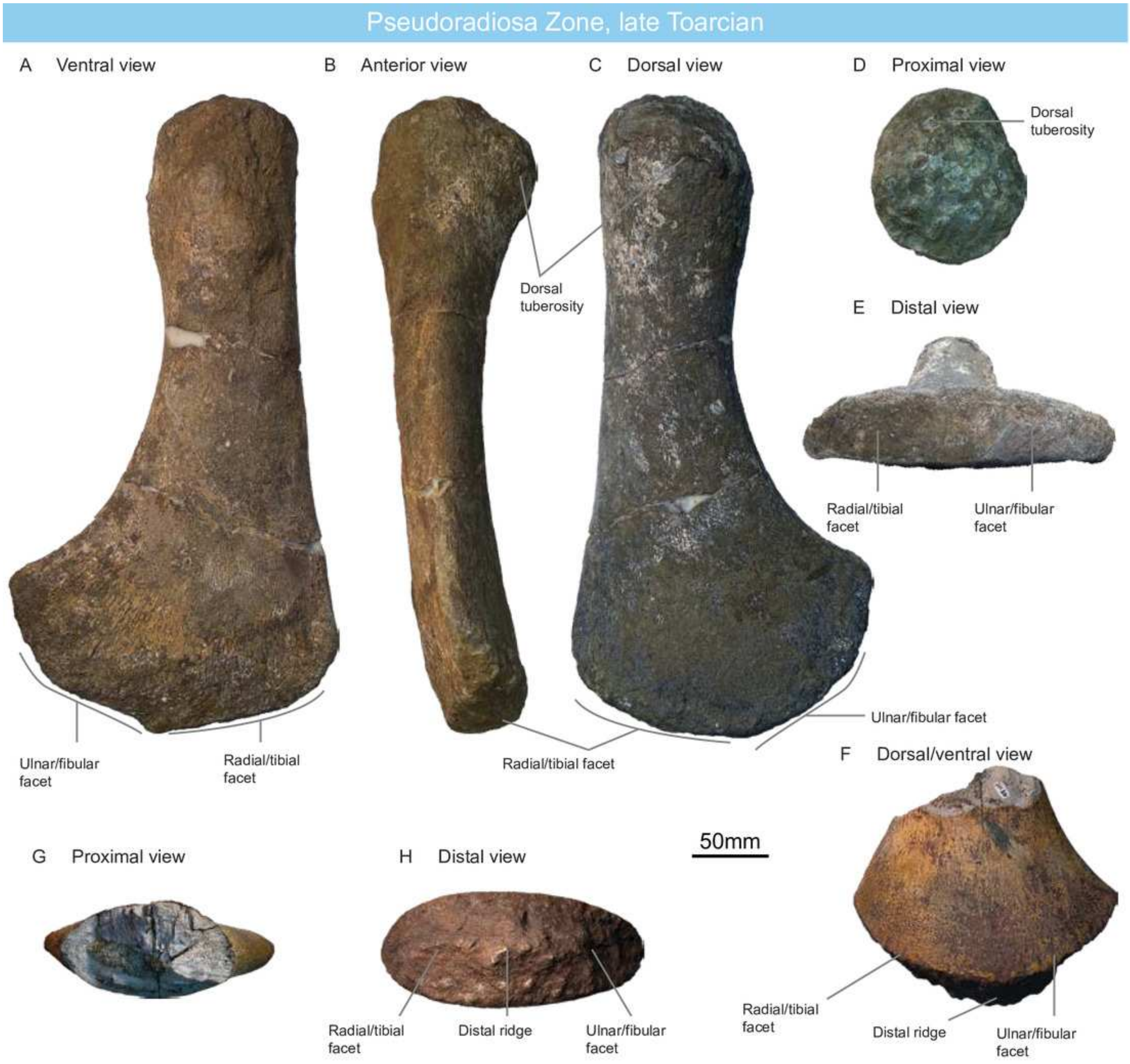


Figure 5

Ichthyosaurians of the Aalensis Zone, late Toarcian of Luxembourg and Belgium.

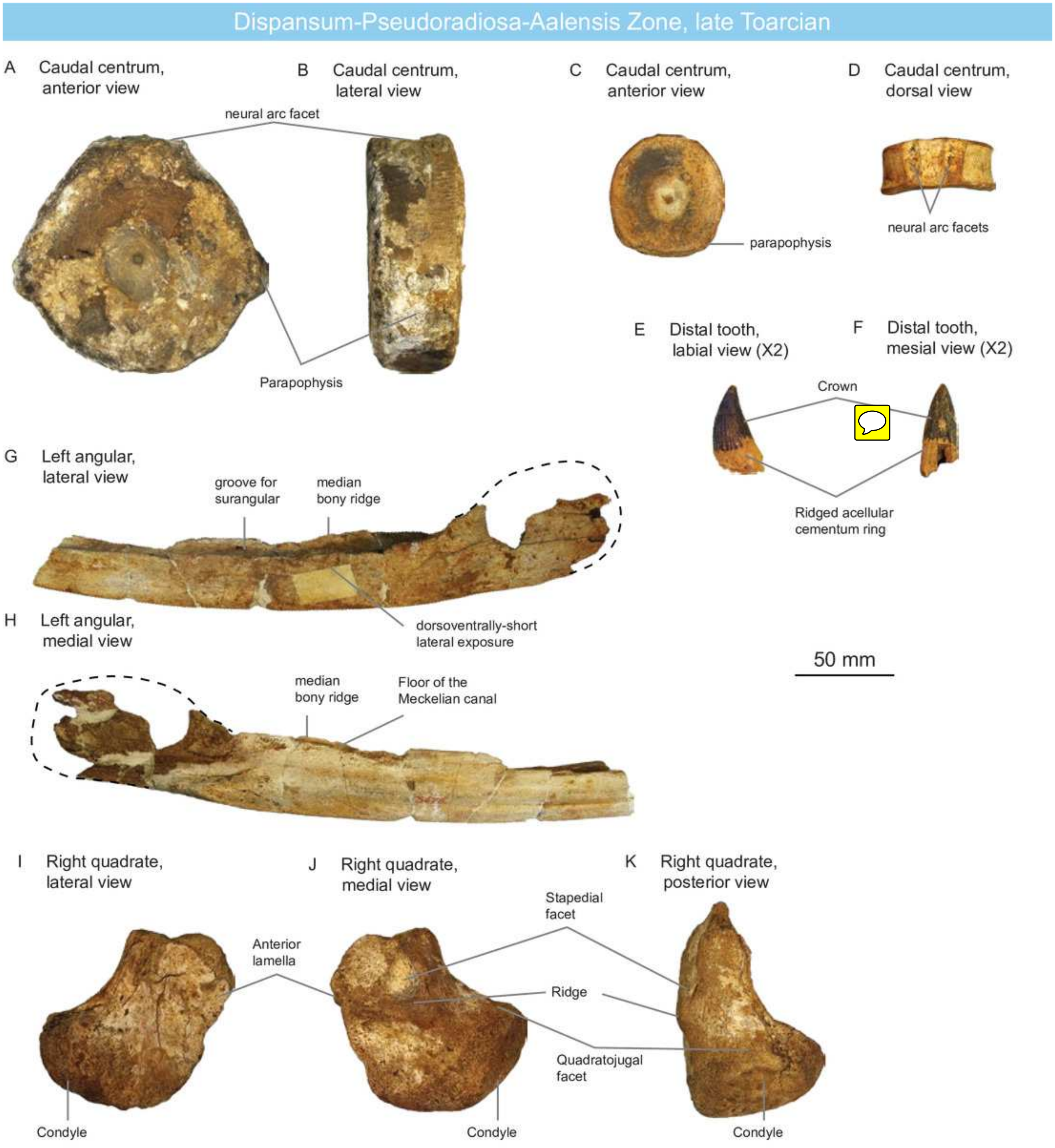

Dispansum-Pseudoradiosa-Aalensis Zone, late Toarcian
A Caudal centrum, anterior view
B Caudal centrum, lateral view
C Caudal centrum, anterior view
D Caudal centrum, dorsal view
neural arc facet
parapophysis
neural arc facets
Parapophysis
E Distal tooth, labial view (X2)
F Distal tooth, mesial view (X2)
Crown
Ridged acellular cementum ring
G Left angular, lateral view
groove for surangular
median bony ridge
dorsoventrally-short lateral exposure
H Left angular, medial view
median bony ridge
Floor of the Meckelian canal
50 mm
I Right quadrate, lateral view
J Right quadrate, medial view
K Right quadrate, posterior view
Stapedial facet
Anterior lamella
Ridge
Quadratojugal facet
Condyle
Condyle
Condyle

Figure 6

Ichthyosaurians of the Aalensis Zone, late Toarcian, Luxembourg.

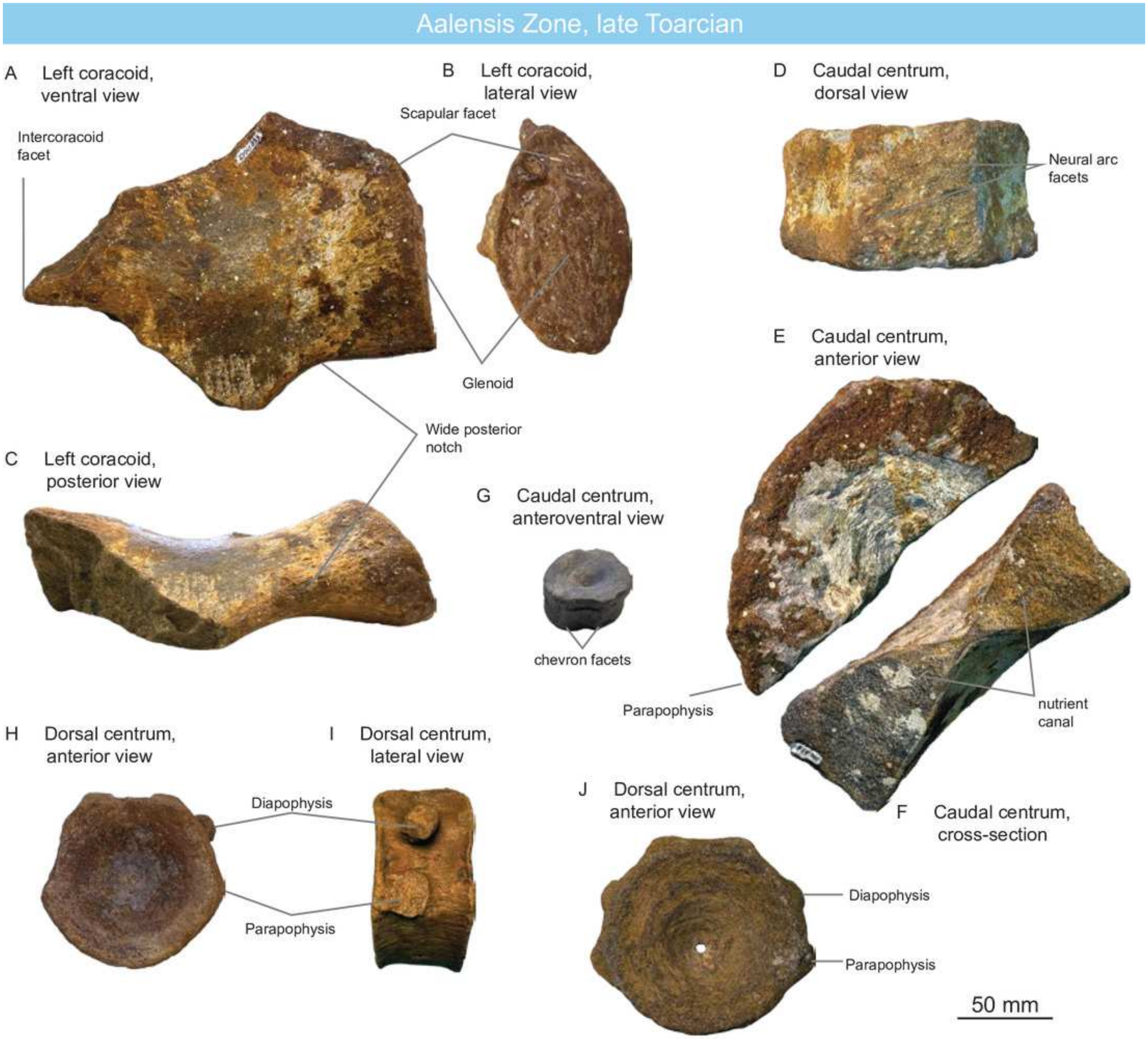


Figure 7

Plesiosaurian centra of the Aalensis Zone, late Toarcian, Luxembourg.

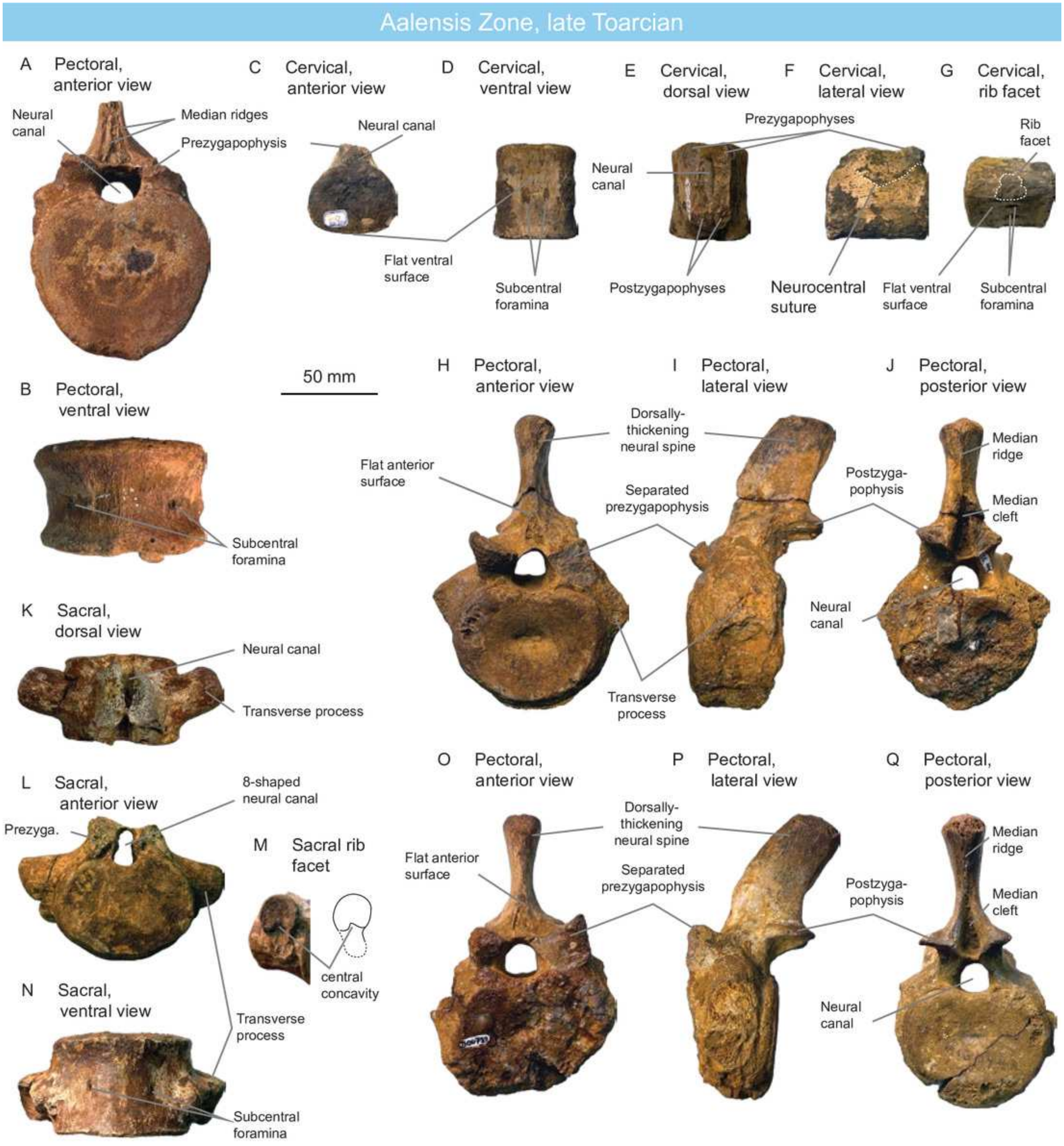

Aalensis Zone, late Toarcian
A Pectoral, anterior view
Neural canal
Median ridges
Prezygapophysis
C Cervical, anterior view
Neural canal
Flat ventral surface
D Cervical, ventral view
Subcentral foramina
E Cervical, dorsal view
Neural canal
Postzygapophyses
F Cervical, lateral view
Prezygapophyses
Neurocentral suture
G Cervical, rib facet
Rib facet
Flat ventral surface
Subcentral foramina
B Pectoral, ventral view
Subcentral foramina
50 mm
H Pectoral, anterior view
I Pectoral, lateral view
J Pectoral, posterior view
Dorsally-thickening neural spine
Flat anterior surface
Separated prezygapophysis
Postzyga-pophysis
Median ridge
Median cleft
Neural canal
Transverse process
K Sacral, dorsal view
Neural canal
Transverse process
L Sacral, anterior view
Prezyga.
8-shaped neural canal
M Sacral rib facet
central concavity
N Sacral, ventral view
Transverse process
Subcentral foramina
O Pectoral, anterior view
P Pectoral, lateral view
Q Pectoral, posterior view
Dorsally-thickening neural spine
Flat anterior surface
Separated prezygapophysis
Postzyga-pophysis
Median ridge
Median cleft
Neural canal

Figure 8

Plesiosaurians of the Aalensis Zone, late Toarcian, Luxembourg.

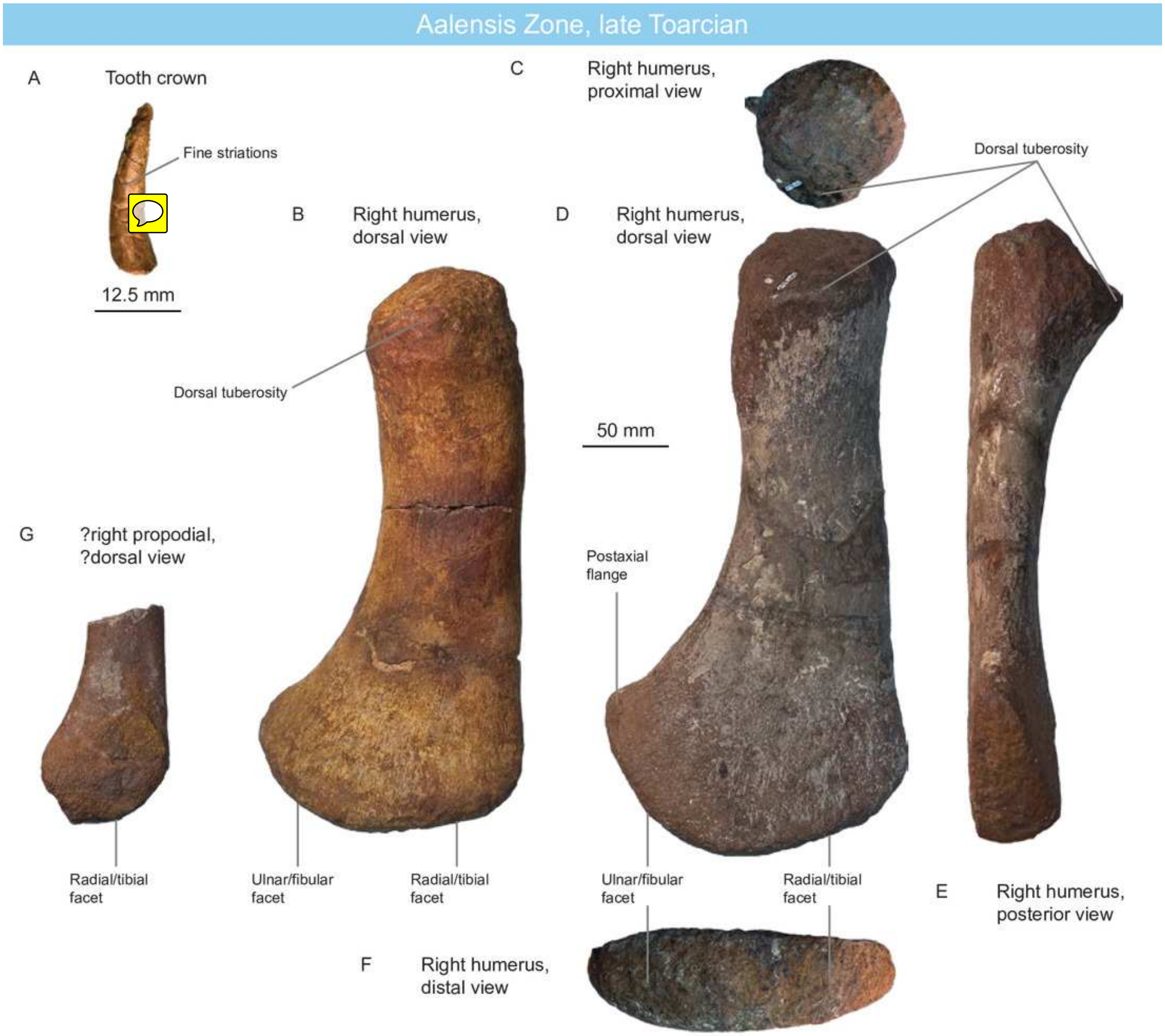


Figure 9

Late Aalenian fauna, Luxembourg.

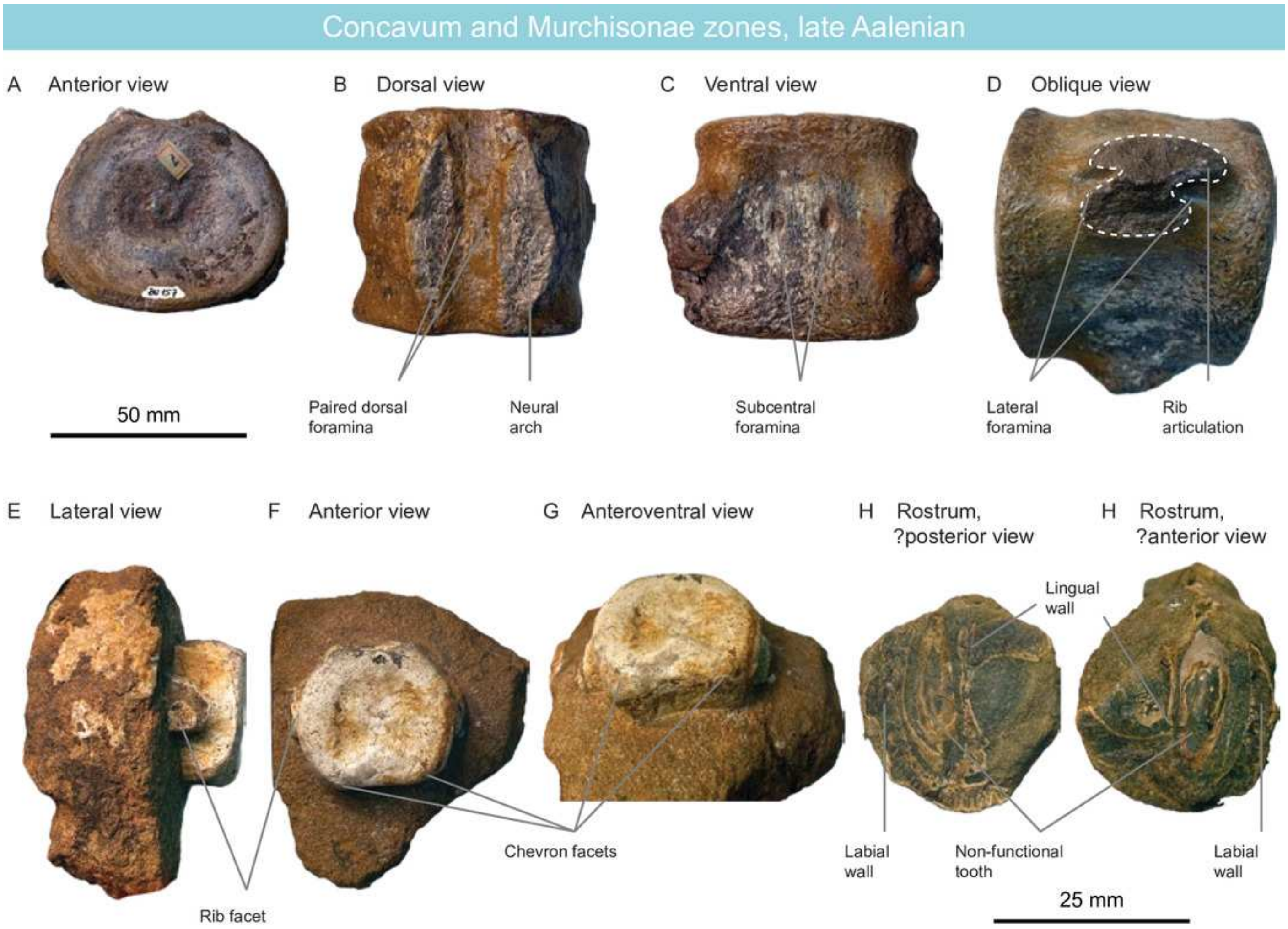


Figure 10

Humphresianum Zone fauna, early Bajocian, Luxembourg.

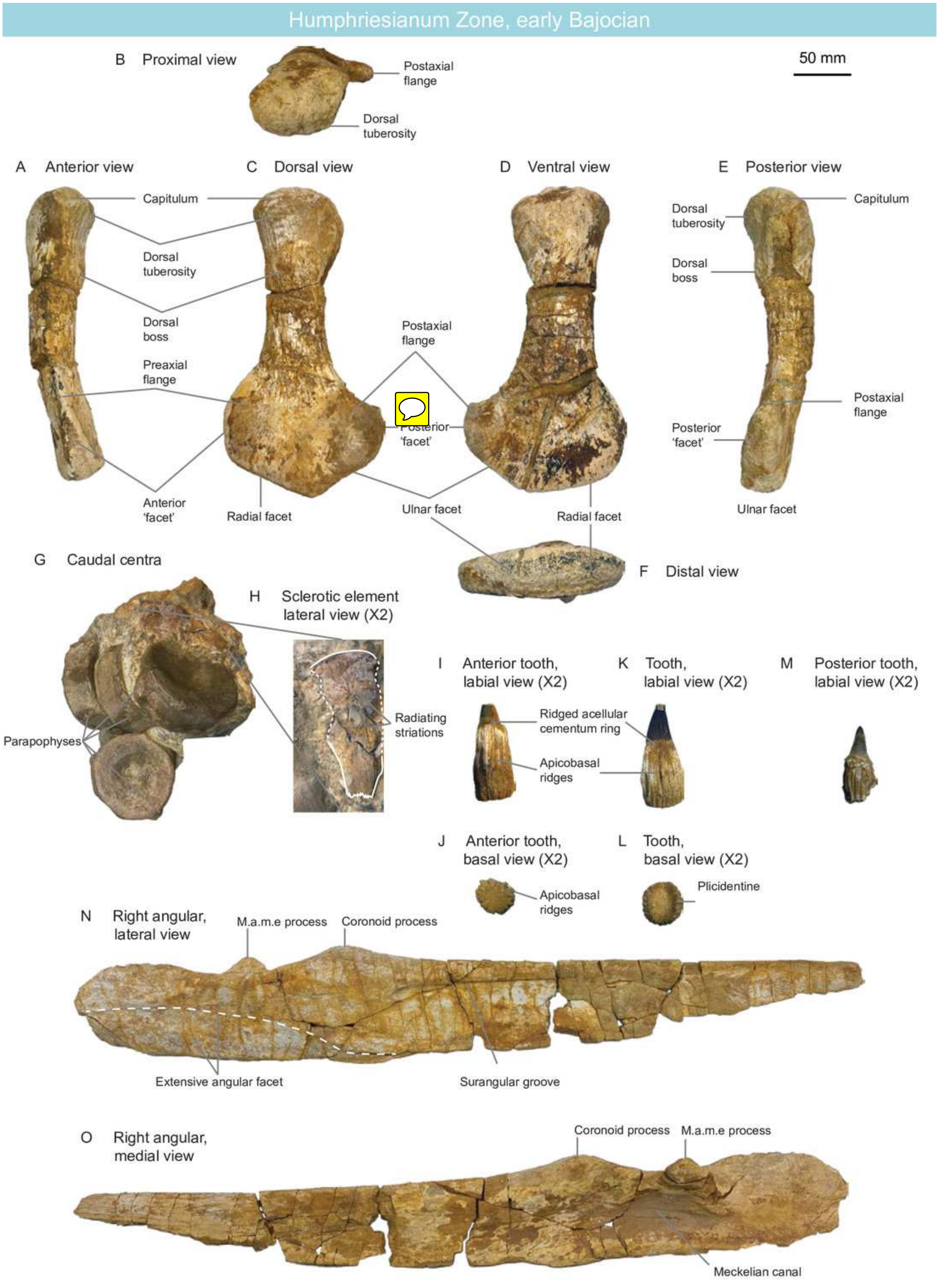

Humphriesianum Zone, early Bajocian
B Proximal view
Postaxial flange
Dorsal tuberosity
50 mm
A Anterior view
C Dorsal view
D Ventral view
E Posterior view
Capitulum
Dorsal tuberosity
Dorsal boss
Preaxial flange
Postaxial flange
Posterior 'facet'
Anterior 'facet'
Radial facet
Ulnar facet
Radial facet
Capitulum
Dorsal tuberosity
Dorsal boss
Postaxial flange
Posterior 'facet'
Ulnar facet
G Caudal centra
F Distal view
H Sclerotic element lateral view (X2)
Radiating striations
Parapophyses
I Anterior tooth, labial view (X2)
K Tooth, labial view (X2)
M Posterior tooth, labial view (X2)
Ridged acellular cementum ring
Apicobasal ridges
J Anterior tooth, basal view (X2)
L Tooth, basal view (X2)
Apicobasal ridges
Plicidentine
N Right angular, lateral view
M.a.m.e process
Coronoid process
Extensive angular facet
Surangular groove
O Right angular, medial view
Coronoid process
M.a.m.e process
Meckelian canal

Figure 11

The new Humphresianum Zone ophthalmosaurid, early Bajocian, Luxembourg.

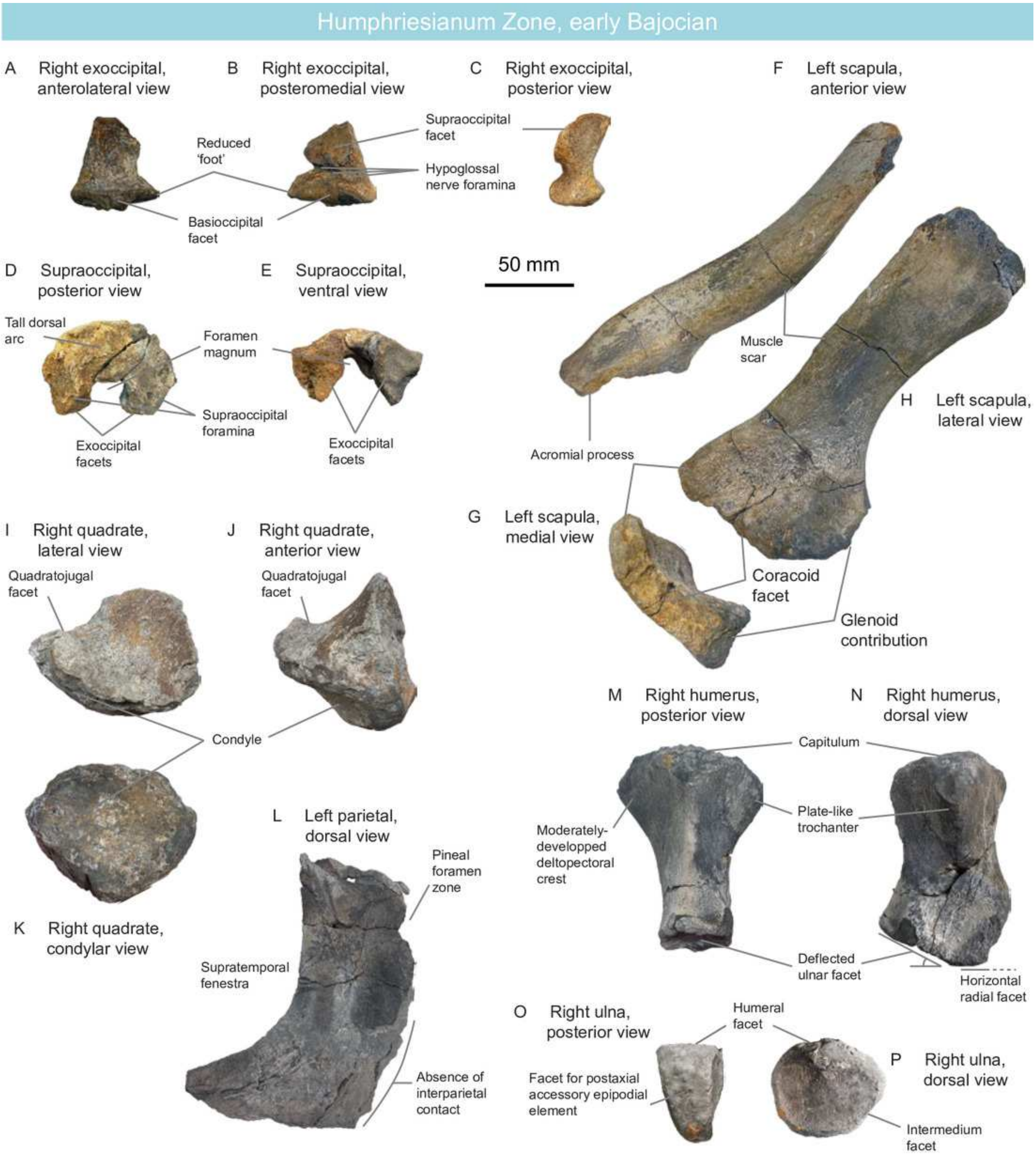

Humphriesianum Zone, early Bajocian
A Right exoccipital, anterolateral view
B Right exoccipital, posteromedial view
C Right exoccipital, posterior view
F Left scapula, anterior view
Supraoccipital facet
Reduced 'foot'
Hypoglossal nerve foramina
Basioccipital facet
D Supraoccipital, posterior view
E Supraoccipital, ventral view
50 mm
Tall dorsal arc
Foramen magnum
Supraoccipital foramina
Exoccipital facets
Exoccipital facets
Muscle scar
H Left scapula, lateral view
Acromial process
I Right quadrate, lateral view
J Right quadrate, anterior view
G Left scapula, medial view
Quadratojugal facet
Quadratojugal facet
Coracoid facet
Glenoid contribution
Condyle
M Right humerus, posterior view
N Right humerus, dorsal view
Capitulum
Plate-like trochanter
Moderately-developped deltopectoral crest
L Left parietal, dorsal view
Pineal foramen zone
K Right quadrate, condylar view
Supratemporal fenestra
Deflected ulnar facet
Horizontal radial facet
O Right ulna, posterior view
Humeral facet
P Right ulna, dorsal view
Facet for postaxial accessory epipodial element
Absence of interparietal contact
Intermedium facet

Figure 12

Ichthyosaurian centra proportions.

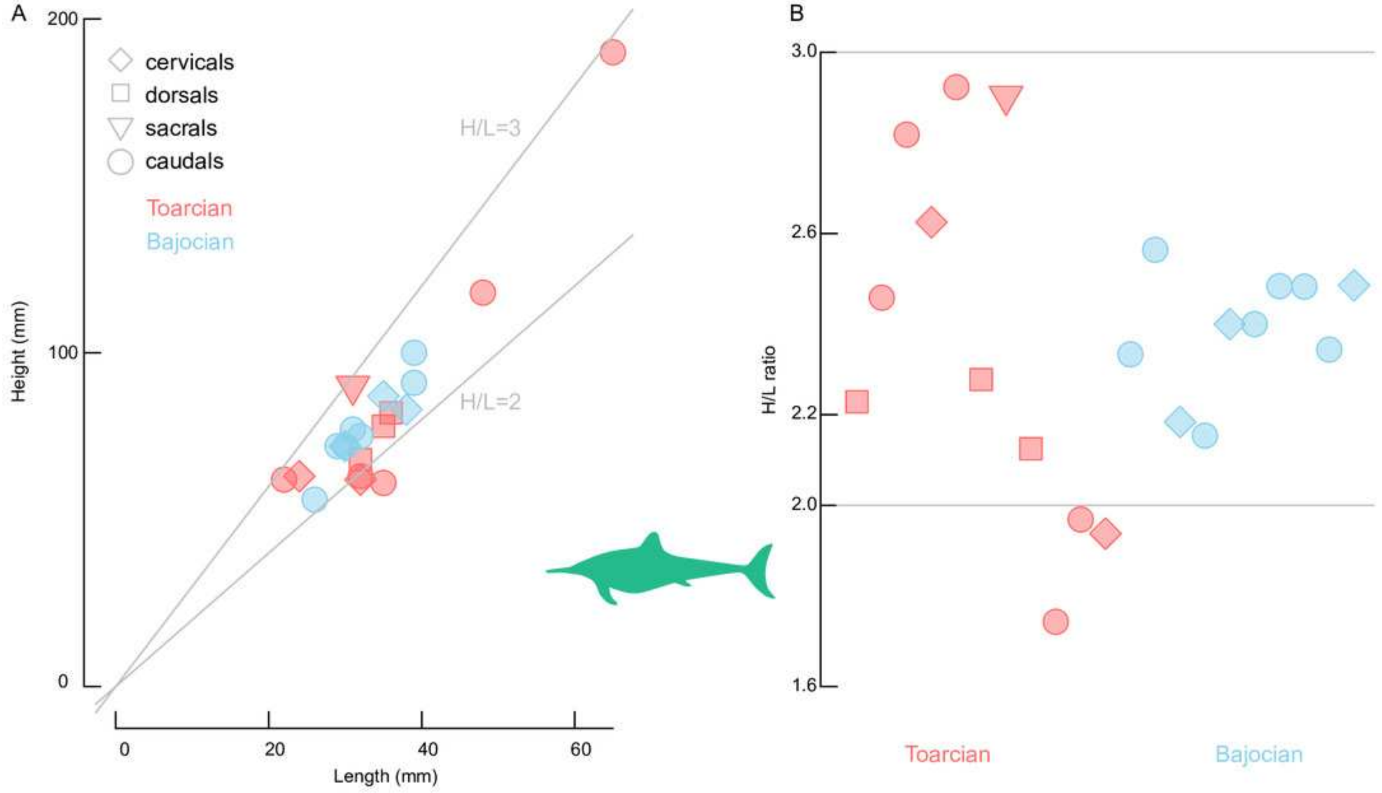


Table 1(on next page)

Centra dimensions (in millimeters).

Table 1. Centra measurements in millimeters.

Specimen	Clade	Age	Axial_zone	Height	Length	Width
ULgPA35961	Ichthyosauria	Toarcian	dorsal	78	35	86
IRSNB_Vert-00000-00803	Ichthyosauria	Toarcian	caudal	118	48	118
IRSNB_Vert-00000-00808	Ichthyosauria	Toarcian	caudal	62	22	60
IRSNB_Vert-06462-0005	Ichthyosauria	Toarcian	cervical	63	24	64
IRSNB_Vert-11312-00007	Plesiosauria	Toarcian	dorsal	67	44	81
MNHNL_DOU378	Ichthyosauria	Toarcian	caudal	190	65	NA
MNHNL_DOU978	Plesiosauria	Toarcian	cervical	41	55	53
MNHNL_DOU944	Ichthyosauria	Toarcian	dorsal	82	36	NA
MNHNL_DOU998	Ichthyosauria	Toarcian	sacral	90	31	NA
MNHNL_DOU722	Plesiosauria	Toarcian	dorsal	50	37	60
MNHNL_DOU723	Plesiosauria	Toarcian	dorsal	55	30	63
MNHNL_DOU954	Plesiosauria	Toarcian	pectoral	63	42	73
MNHNL_DOU724	Plesiosauria	Toarcian	sacral	39	40	57
MNHNL_DOU369a	Ichthyosauria	Toarcian	dorsal	68	32	NA
MNHNL_DOU369b	Ichthyosauria	Toarcian	caudal	61	35	NA
MNHNL_DOU369c	Ichthyosauria	Toarcian	caudal	63	32	NA
MNHNL_HU384	Plesiosauria	Aalenian	caudal	32	NA	NA
MNHNL_BU157	Plesiosauria	Aalenian	cervical	67	62	71
TMNHNL_MP212	Ichthyosauria	Toarcian	cervical	62	32	56
MNHNL_BM779	Ichthyosauria	Bajocian	caudal	91	39	NA
MNHNL_BM758	Ichthyosauria	Bajocian	caudal	100	39	NA
MNHNL_BM725a	Ichthyosauria	Bajocian	cervical	83	38	NA
MNHNL_BM725b	Ichthyosauria	Bajocian	caudal	56	26	NA
MNHNL_BM461	Ichthyosauria	Bajocian	cervical	72	30	NA
MNHNL_BM392a	Ichthyosauria	Bajocian	caudal	72	30	NA
MNHNL_BM392b	Ichthyosauria	Bajocian	caudal	77	31	NA
MNHNL_BM392c	Ichthyosauria	Bajocian	caudal	72	29	NA
MNHNL_BM392d	Ichthyosauria	Bajocian	caudal	75	32	NA
MNHNL_BM779	Ichthyosauria	Bajocian	cervical	87	35	90

Table 2(on next page)

List of the material and taxonomic identifications.

Table 2. List of the material and taxonomic identifications.

Specimen	Locality	Stage	Zone	Element	Clade	Identification	Note
ULgPA35961	Arlon region	Toarcian	Dispansum to Aalensis	Dorsal centrum	Ichthyosauria	Parvipelvia indet.	
IRSNB Vert-06455-0001	Mont-Saint-Martin (France)	Toarcian	Dispansum to Aalensis	Centrum	Ichthyosauria	Ichthyosauria indet.	
IRSNB Vert-00000-00801	Halanzy (Belgium)	Toarcian	Dispansum to Aalensis	Centrum	Ichthyosauria	Ichthyosauria indet.	
IRSNB Vert-06659-0001	NA (Luxembourg)	Toarcian	Dispansum to Aalensis	Centrum	Ichthyosauria	Ichthyosauria indet.	
IRSNB Vert-06462-0003	Halanzy (Belgium)	Toarcian	Dispansum to Aalensis	Tooth	Ichthyosauria	Ichthyosauria indet.	
IRSNB Vert-00000-00802	NA	Toarcian	Dispansum to Aalensis	Right quadrate	Ichthyosauria	Ichthyosauria indet.	
IRSNB Vert-00000-00800	Halanzy (Belgium)	Toarcian	Dispansum to Aalensis	Left surangular	Ichthyosauria	Parvipelvia indet.	Probable non-ophthalmosaurid
IRSNB Vert-06462-0002	Halanzy (Belgium)	Toarcian	Dispansum to Aalensis	Left angular	Ichthyosauria	Parvipelvia indet.	Probable non-ophthalmosaurid
IRSNB Vert-00000-00803	NA (Luxembourg)	Toarcian	Dispansum to Aalensis	Caudal centrum	Ichthyosauria	Parvipelvia indet.	*Temnodontosaurus*-like
IRSNB Vert-00000-00804	NA (Luxembourg)	Toarcian	Dispansum to Aalensis	Dorsal centrum	Ichthyosauria	Parvipelvia indet.	*Temnodontosaurus*-like
IRSNB Vert-00000-00808	NA	Toarcian	Dispansum to Aalensis	Caudal centrum	Ichthyosauria	Parvipelvia indet.	Possible thunnosaurian
IRSNB Vert-06462-0005	Halanzy (Belgium	Toarcian	Dispansum to Aalensis	Cervical centrum	Ichthyosauria	Parvipelvia indet.	

IRSNB Vert-11312-00007	Halanzy (Belgium	Toarcian	Dispansum to Aalensis	Dorsal centrum	Plesiosauria	Plesiosauria indet.	
MNHNL TM212	Dudelange	Toarcian	Thouarsense	Partial skeleton	Ichthyosauria	Baracromia indet.	Non-ophthalmosaurid
MNHNL DOU944	NA (Luxembourg)	Toarcian	Aalensis	Dorsal centrum	Ichthyosauria	Parvipelvia indet.	
MNHNL DOU998	NA (Luxembourg)	Toarcian	Aalensis	Caudal centrum	Ichthyosauria	Parvipelvia indet.	
MNHNL DOU369	NA (Luxembourg)	Toarcian	Aalensis	Centra	Ichthyosauria	Parvipelvia indet.	Probable non-thunnosaurian
MNHNL DOU353	NA (Luxembourg)	Toarcian	Aalensis	Coracoid	Ichthyosauria	Parvipelvia indet.	Non-baracromian
MNHNL DOU378	NA (Luxembourg)	Toarcian	Aalensis	Posterior dorsal to anterior caudal centrum	Ichthyosauria	Parvipelvia indet.	Probable non-thunnosaurian
MNHNL HU242	Rumelange	Aalenian	Concavum	Partial rostrum	Ichthyosauria	Ichthyosauria indet.	
MNHNL BM360	Rumelange	Bajocian	Humphriesianum	Partial neural spine and ribs	Ichthyosauria	Ichthyosauria indet.	
MNHNL BM758	Rumelange	Bajocian	Humphriesianum	Caudal centrum	Ichthyosauria	Parvipelvia indet.	
MNHNL BM725	Rumelange	Bajocian	Humphriesianum	Cervical and caudal centra	Ichthyosauria	Parvipelvia indet.	
MNHNL BM461	Rumelange	Bajocian	Humphriesianum	Cervical centrum	Ichthyosauria	Parvipelvia indet.	
MNHNL BM392	Rumelange	Bajocian	Humphriesianum	Five caudal centrum and one sclerotic plate	Ichthyosauria	Parvipelvia indet.	
MNHNL BM780_781	Rumelange	Bajocian	Humphriesianum	Surangular, teeth	Ichthyosauria	Ophthalmosauridae indet.	
MNHNL BM779	Rumelange	Bajocian	Humphriesianum	Partial skeleton	Ichthyosauria	Ophthalmosauridae indet.	
MNHNL DOU307	Rodange	Toarcian	Pseudoradiosa	Humerus	Plesiosauria	Rhomaleosauridae indet.	

MNHNL KA109	Esch-sur-Alzette	Toarcian	Pseudoradiosa	Humerus	Plesiosauria	Rhomaleosauridae indet.	
MNHNL DOU906	Esch-sur-Alzette	Toarcian	Aalensis	Tooth crown	Plesiosauria	Plesiosauria indet.	
MNHNL DOU724	Probably Esch-sur-Alzette	Toarcian	Aalensis	Sacral vertebra	Plesiosauria	Plesiosauria indet.	
MNHNL DOU722	Esch-sur-Alzette	Toarcian	Aalensis	Pectoral vertebra	Plesiosauria	Rhomaleosauridae indet.	
MNHNL DOU723	Esch-sur-Alzette	Toarcian	Aalensis	Pectoral vertebra	Plesiosauria	Rhomaleosauridae indet.	
MNHNL DOU954	NA (Luxembourg)	Toarcian	Aalensis	Posterior pectoral/anterior dorsal	Plesiosauria	Rhomaleosauridae indet.	
MNHNL DOU558	Belvaux	Toarcian	Aalensis	Humerus	Plesiosauria	Rhomaleosauridae indet.	
MNHNL DOU324A	Esch-sur-Alzette	Toarcian	Aalensis	Humerus	Plesiosauria	Rhomaleosauridae indet.	
MNHNL DOU324B	Esch-sur-Alzette	Toarcian	Aalensis	Humerus	Plesiosauria	Rhomaleosauridae indet.	Juvenile
MNHNL DOU978	NA (Luxembourg)	Toarcian	Aalensis	Cervical centrum	Plesiosauria	cf. Microcleidus	
MNHNL HU384	Esch-sur-Alzette	Aalenian	Murchisonae	Caudal centrum	Plesiosauria	Plesiosauria indet.	Juvenile
MNHNL BU157	Rumelange	Aalenian	Concavum or Murchisonae	Cervical vertebra	Plesiosauria	Plesiosauroidae indet.	Non-cryptoclidid
MNHNL BM782	Rumelange	Bajocian	Humphriesianum	Propodial	Plesiosauria	Cryptoclididae indet.	