

A fragmentary leptonectid ichthyosaurian from the lower Pliensbachian of Luxembourg

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ABSTRACT

Despite abundant fossils, the quality of the fossil record of Early Jurassic marine reptiles strongly fluctuates with time and space. Pliensbachian strata have yielded very few marine reptile remains, especially outside of England, obscuring the evolution of marine reptiles during the middle part of the Early Jurassic. We report a new Pliensbachian locality from Luxembourg that contains abundant marine fauna and ichthyosaurian remains likely representing a single individual, composed of a partial snout, a possible surangular, two centra, and several ribs and gastralia. Ammonites and belemnites place this locality within the Valdani-Luridum Ammonite subzones of the Ibx Ammonite Zone, lower Pliensbachian. We assign the new ichthyosaur specimen to the clade Leptonectidae, using a combination of features from the snout and teeth. This specimen indicates that large neoichthyosaurians were present in multiple places of the European archipelago in all stages of the Early Jurassic and suggests that the ichthyosaurian faunas of western Europe remained essentially similar across the Sinemurian–Pliensbachian interval.

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INTRODUCTION

Mesozoic marine reptiles have an abundant fossil record, documenting the beginning of their radiation during the earliest Triassic (Motani et al., 2015, 2017) to centimetres below the Cretaceous-Palaeogene boundary horizon (Jouve et al., 2008; Gallagher et al., 2012). However, the quality of their fossil record strongly fluctuates with time and space (Benson et al., 2010; Benson and Butler, 2011; Butler et al., 2011), and possibly less so with phylogeny (Tutin and Butler, 2017). This fluctuation appears fractal, being also present within Early Jurassic ichthyosaurians: the early Toarcian shales have provided thousands of fossils in western Europe, with most specimens from Germany and England (Hauff, 1953; Godefroit, 1994; Benson et al., 2010), while the Pliensbachian and late Toarcian assemblages are extremely poorly sampled (Bardet et al., 2008; Fernández et al., 2018; Lomax and Massare, 2018a; Fischer et al., 2021). Pliensbachian ichthyosaurian faunas generally resemble those from the Sinemurian, with the presence of *Leptonectes* (McGowan and Milner, 1999; Fernández et al., 2018; Lomax and Massare, 2018a), *Ichthyosaurus* (Lomax, 2010; Lomax and Massare, 2015; Massare and Lomax, 2016), and *Temnodontosaurus* (Huene, 1931a; Hungerbühler and Sachs, 1996; Maisch and Hungerbühler, 1997), but also *Hauffiopteryx* (Maisch and Reisdorf, 2006; Maxwell and Cortés, 2020). However, the vast majority of Pliensbachian ichthyosaurians come from England and Germany; one (Maisch and Reisdorf, 2006) is from Switzerland and another (Fernández et al., 2018) is from Spain. In this context, documenting new Pliensbachian occurrences of ichthyosaurians is important to better understand how marine predator faunas changed throughout the entire Early Jurassic. In this paper, we describe the likely associated remains of a large ichthyosaur showing leptonectid affinities from a new lower Pliensbachian locality in central Luxembourg.

MATERIAL AND METHODS

Institutional Abbreviations

BRSMG: Bristol City Museum and Art Gallery, Bristol, UK. MHNH: Muséum d'Histoire Naturelle du Havre, Le Havre, France. MNHN: Muséum National d'Histoire Naturelle, Paris, France. MNHNL: Muséum National d'Histoire Naturelle du Luxembourg, Luxembourg-ville, Luxembourg. NHMUK: Natural History Museum, London, UK. OUM: Oxford University Museum, Oxford, UK.

The Cloche d'Or Locality

The remains described herein consist of a series of articulated and disarticulated remains of a large ichthyosaurian, MNHNL LM266 from the Cloche d'Or locality, in the Gasperich quarter in southern Luxembourg City, central Luxembourg (Figure 1). The outcrop at Cloche d'Or is situated along the banks of a recently re-natured Weierbaach creek. The first fragments were found during preliminary prospections in April 2021, and most of the remains were collected during controlled excavations and prospections lead by several of us (B.T., R.W., K.B., L.G., C.R., A.T., and Y.G.) in July 2021 (Figure 2), complemented by subsequent finds cropping out after the millennial floods of summer 2021.

Lithostratigraphy of Cloche d'Or

Along the Weierbaach creek, two lithostratigraphic formations, as defined by the Geological map of Luxembourg, are exposed. The lower one, the Li4 ("Marnes pauvres en fossiles") unit, consists of blue-greyish marls with occasional micritic nodules, and yields ammonites, bivalves (mostly *Gryphaea macculocchi*, as well as cardiniids and pectinids), brachiopods (notably *Spiriferina*, *Zeilleria*), crinoids (*Pentacrinites* sp.), and small passaloteuthid belemnites (*Nannobelus oppeli*). The Li4 succession corresponds to our units I and II (Figure 3). The lithological transition towards the overlying formation Lm1 is not clearly visible, and approximately corresponds to unit III or the basal part of



FIGURE 1. Map and location of the Cloche d'Or site, indicated by a star.

unit IV. The upper part of unit IV as well as the overlying units V-VII belong to the Lm1 (“Calcaire ocreux”) formation, which consists here of sandy, yellow marls yielding numerous ammonites, echinoderm remains, and a more diversified belemnite fauna than the underlying Li4 formation. Usually, this formation consists of three members, a lower calcareous member (“Raricostaten-Schichten”, roughly corresponding to the uppermost Sinemurian), a middle marly member (“Numismalis-Mergel”, corresponding to the lower Pliensbachian) and an upper calcareous member (“Davoei-Kalk”, also lower Pliensbachian) (Lucius, 1948; Maubeuge, 1950). The yellow marls at Cloche d’Or

are interpreted here as an equivalent of the middle marly member of the Calcaire ocreux formation. This means that the lower calcareous member is missing at Cloche d’Or. A similar hiatus at the base of the formation had previously been observed for some localities in Luxembourg (Lucius, 1948; Maubeuge, 1950; Maubeuge and Antun, 1967). A more complete succession of the Li4 and Lm1 formations has been recorded in other localities, for instance Capellen (Guérin-Franiatte, 2003), to the west of Luxembourg-City. The ichthyosaur remains described in the present paper were found in unit V, corresponding to the middle marly member of the Lm1 formation.



FIGURE 2. Photograph of the Cloche d'Or locality taken on 17 June 2021 during the main excavation activities. Most of the bone fragments (MNHNLM226) were found in the exposed layer between the two arrows.

Biostratigraphy of Cloche d'Or

The biostratigraphic interpretation of the exposed succession is based on ammonites (Figure 3). Two biozones are recognised: the Obtusum Zone of the upper Sinemurian and the Ibex Zone of the lower Pliensbachian. A characteristic association has been identified in unit VI: *Lytoceras fimbriatum* (Sowerby), *Acanthopleuroceras alisiense* (Reynès in Haug), and *Beaniceras luridum* (Simpson), an association corresponding to the upper part of the Ibex Zone (Valdani-Luridum subzones) (Christian Meister, personal communication). Belemnites retrieved from the succession corroborate and, in part, complement the ammonite-based zonation, although the biostratigraphic value of the belemnites is less precise compared to the ammonites (Riegraf, 1980; Combémorrel, 1997; Schlegelmilch, 1998). Belemnites of the genus *Nannobelus*, in particular *Nannobelus oppeli*, found in units I and II, indicate an upper Sinemurian age. Belemnites of the genus *Passaloteuthis*, known from the lower Pliensbachian onwards, were found in units IV to VII. Together with the ammonite association from unit VI, the belemnite evidence thus suggests that the ichthyosaur-bearing bed V is of lower Pliensbachian age. Multiple fragmentary specimens of the ammonite *Tragophylloceras* further corroborates the lower Pliensbachian age (Ibex Zone) of the ichthyosaurian specimen MNHNLM226.

Taphonomy

The ichthyosaurian remains described in the present paper were either collected directly in bed V or picked from the weathered surface below and in the creek downstream. In some cases, fragments collected from the stream bed could be associated with fragments directly retrieved from bed V (in particular the two fragments of a possible surangular), corroborating that all the remains, in fact, originate from the same bed. Unit V consists of conspicuously bright-coloured clayey marl, readily distinguishable from the over- and underlying strata. Furthermore, unit V has yielded an extraordinary microfauna, including numerous minute spines of the echinoid *Cuspidentechinus* Smith, 2016 and cyrtocrinid remains that are absent from the under- and overlying strata. Thanks to the distinctive colour and microfauna of the adhering matrix, even bone fragments that were found downslope or in the creek could be unambiguously assigned to unit V.

The marls of unit V show no signs of re-sedimentation, reworking, or condensation, neither in macroscopic terms (e.g., reworked ammonites or belemnites, intraclasts, encrusted pebbles) nor in the microfaunal spectrum. Furthermore, the bones show no evidence of encrusting organisms or adhering matrix other than the marls from unit V. We therefore exclude the possibility of reworking or condensation to explain the co-occurrence of the

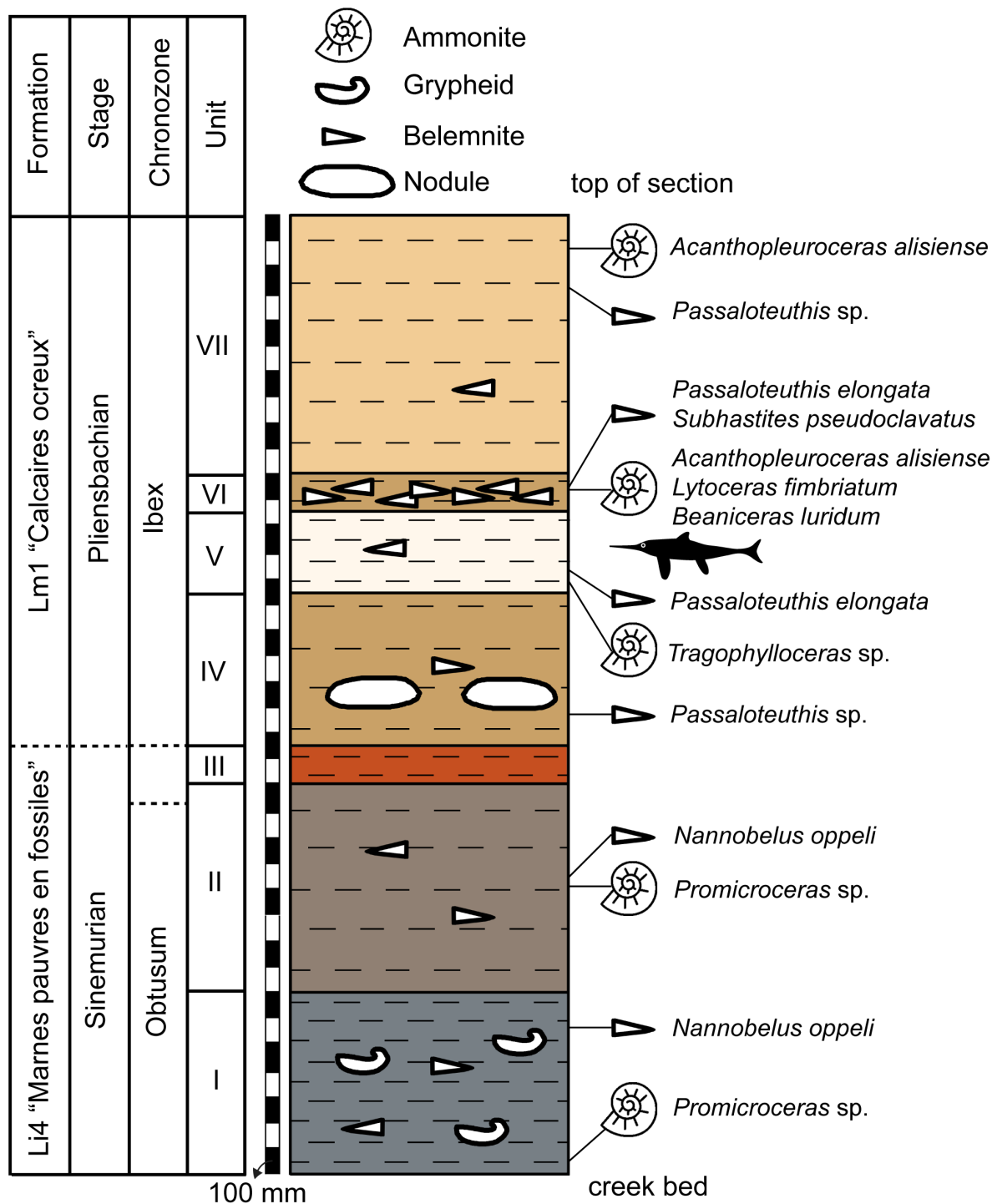


FIGURE 3. Stratigraphic log of the section at the Cloche d'Or locality.

bone fragments. While we cannot rule out that the bones belong to more than one individual, continuously controlled excavation allowed us to confirm the single origin of the bone fragments. All the remains can be traced down to a restricted area

within bed V, approximately 5 m wide, on both sides of the creek.

The bone tissue is well preserved in most cases. Interestingly, some fragments, in particular the vertebra and the possible surangular, show millimetric, radially oriented scratch marks (Figure 4).

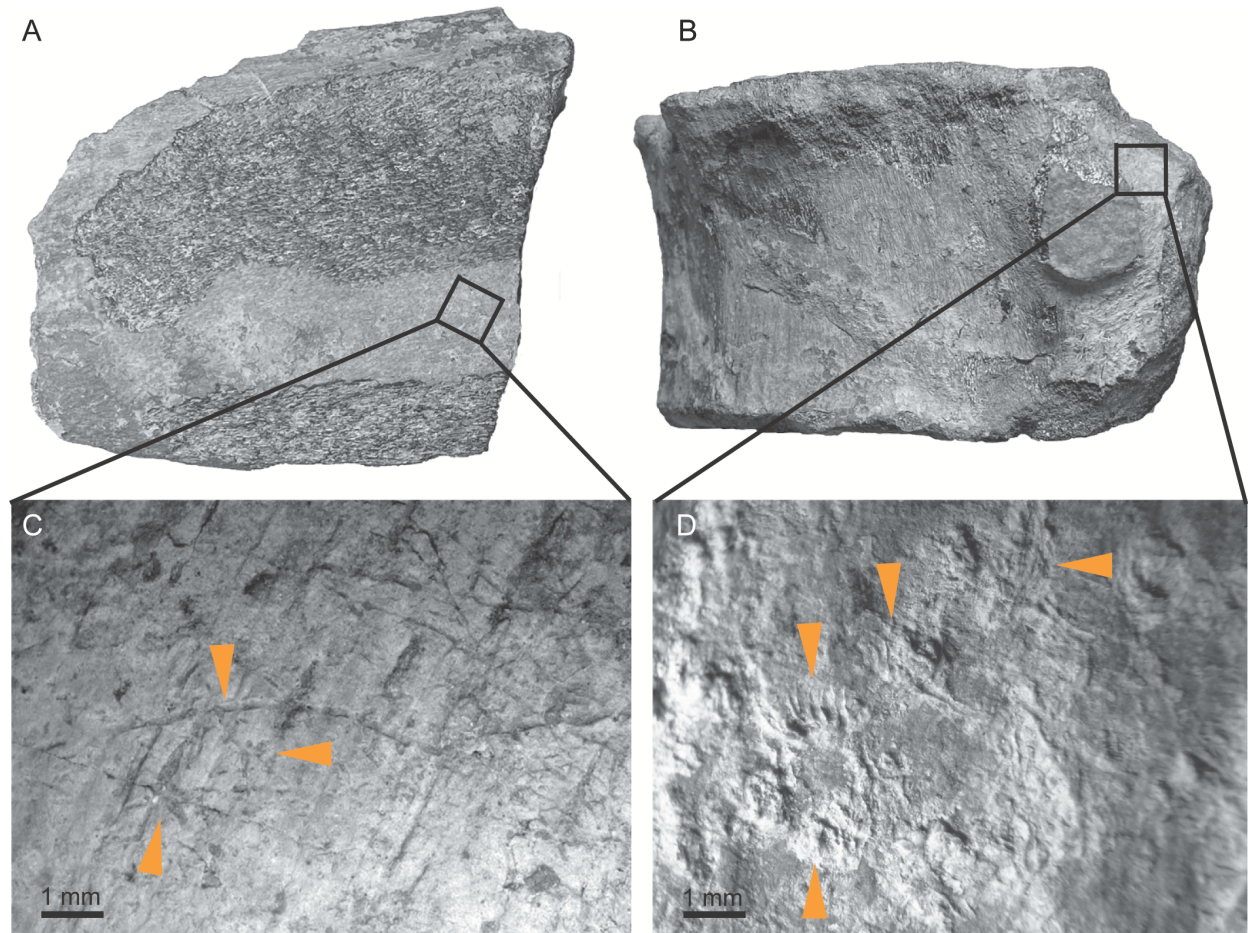


FIGURE 4. Post-mortem scratch marks. Details of the bone surface of the possible surangular (A) and a vertebral fragment (B) of MNHNL LM226. These scratch marks with their characteristic radial shape are assignable to the ichnogenus *Gnathichnus* sp. and attributed to the grazing activities of regular echinoids. The orange arrows indicate some of best-preserved marks.

The size, depth, orientation, and arrangement of the scratch marks are typical features of *Gnathichnus*, an ichnogenus attributed to the grazing activity of regular echinoids (Bromley, 1975). *Gnathichnus* is usually found on invertebrate shells or skeletal parts (e.g., Breton et al., 1992; Carrasco, 2003) but also on vertebrate bones (Meyer, 2011; Reolid et al., 2015), including on ichthyosaur remains (Danise et al., 2014). The sediment surrounding the bone fragments yields abundant spines, test plates, and masticatory apparatus components of a small regular echinoid with teeth of trapezoidal cross-section, reminiscent of the common and widespread Early Jurassic echinoid genus *Cunidentechinus*, which therefore qualifies as a possible producer of the grazing traces on the bones.

SYSTEMATIC PALAEOLOGY

Order ICHTHYOSAURIA De Blainville, 1835
 Clade PARVIPELVIA Motani, 1999
 Clade NEOICHTHYOSAURIA Sander, 2000
 Family LEPTONECTIDAE Maisch, 1998
 Leptonectidae indet.

Referred material. MNHNL LM266, from the lower Pliensbachian (Valdani to Luridum Ammonite sub-zones of the Ibex Ammonite Zone) of the Cloche d'Or locality, central Luxembourg.

Snout

Two contiguous fragments of a rostrum are preserved over 51 mm, containing articulated premaxillae, dentaries, splenials, and teeth (Figure 5). The premaxilla and the dentary are slender, being as dorsoventrally high as the apicobasal height of the corresponding tooth crowns. The premaxillary and dentary fossae are present, in the form of a

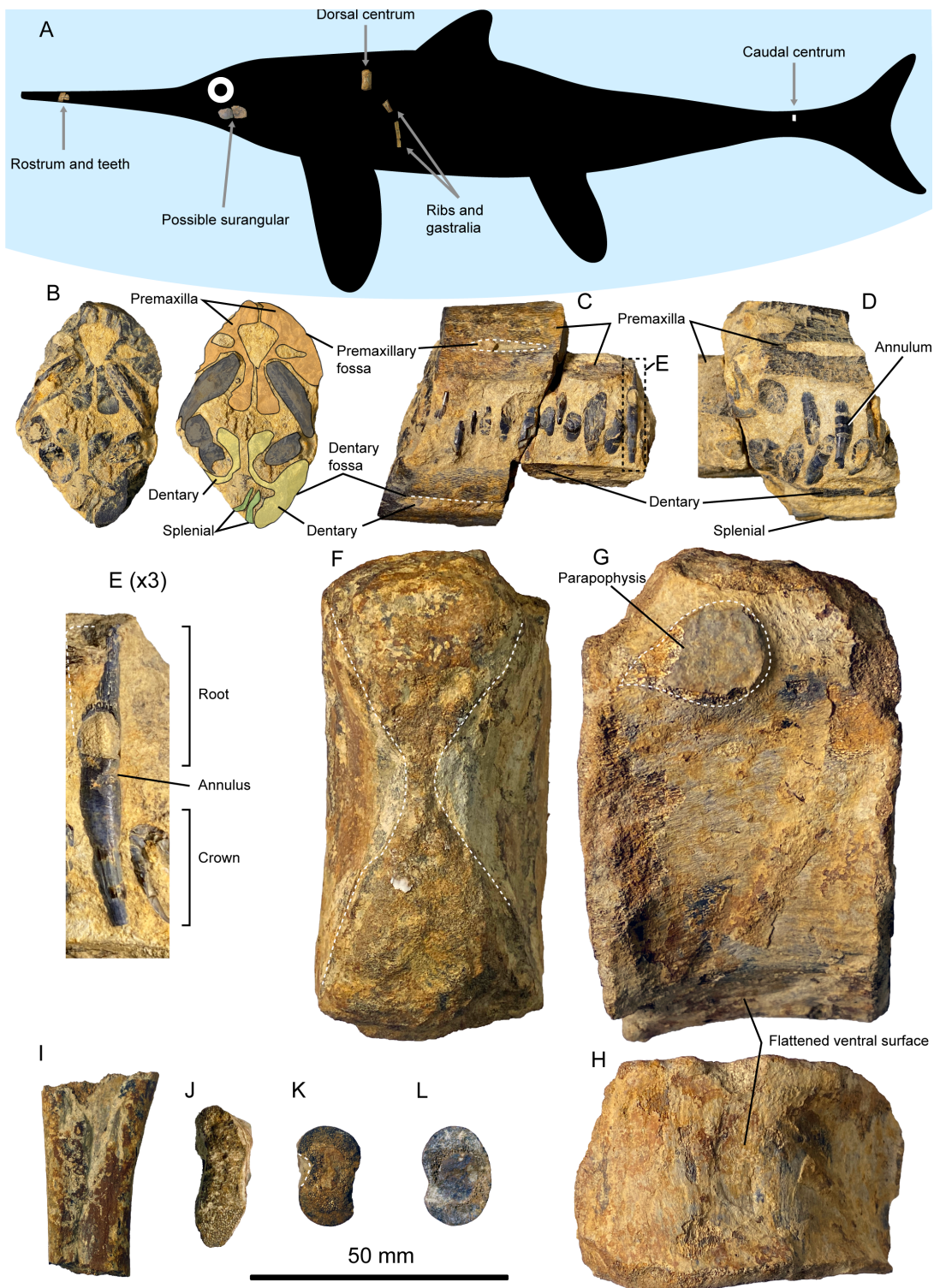


FIGURE 5. Location and anatomy of selected remains of the leptonectid ichthyosaurian MNHNL LM226. (A) silhouette with the location of selected remains; the total size of the animal is difficult to assess. (B) photograph and interpretation of the rostrum in ?anterior view. (C, D) rostrum in lateral views. (E) Detail of a tooth, magnified three times with respect to the other elements, showing the elongated crown and the near absence of striations on the root and acellular cementum ring. (F–H) fragmentary dorsal centrum in (F) medial, (G) lateroventral, (H) ventral views. (I) large rib fragment in internal view. (J) proximal cross-section of a rib, showing the 8-shaped cross-section. (K) cross-section of a rib, showing the 8-shaped cross-section. (L) distal cross-section of a rib showing the loss of one of the anterior/posterior grooves.

series of elongated foramina that are 13 mm long and 3 mm high for the premaxillary fossa and slightly longer for the dentary fossa. The anterior part of the splenial is preserved in articulation with the dentary and has a slit-like ventral exposure. The splenial thus possesses a long ventral exposure, which is similar to that of *Leptonectes moorei* (V.F. pers. obs. holotype specimen NHMUK PV R 14370) and differs from the condition seen in the rather short-snouted *Hauffiopteryx* spp., where the nasal rapidly protrude from the dorsal margin of the rostrum, extending anteriorly as far (or further) than the splenial (Marek et al., 2015; Maxwell and Cortés, 2020). In MNHNL LM266, the nasal is not even present internally, indicating its dorsal exposure is de facto set more posteriorly than that of the splenial.

The tooth crowns are slightly recurved and markedly elongated: the apicobasal height / basal diameter ratio is 11 mm / 4 mm = 2.75 (Figures 5, 6), very similar to some species of *Stenopterygius* (Maxwell, Fernández, et al., 2012), *Hauffiopteryx* (Maxwell and Cortés, 2020), and in leptonectids such as most species of *Leptonectes* (Fraas, 1892; Huene, 1922; McGowan, 1989, 1993) (with the exception of *Leptonectes moorei* [McGowan and Milner, 1999]), *Eurhinosaurus longirostris* (Reisdorf et al., 2011), and *Wahlisaurus massarae* (Lomax, 2016) (Figure 6). This condition is clearly distinct from the stouter teeth seen in *Temnodontosaurus* spp. (Fraas, 1891; McGowan, 1974; Godefroit, 1993), *Suevoleviathan* spp. (Maxwell, 2018), *Protoichthyosaurus* (Lomax and Massare, 2018b; Lomax et al., 2019), and some species of *Ichthyosaurus* (Fraas, 1891; Maisch, 1997; Maisch et al., 2008). Another similarity with *Stenopterygius*, *Hauffiopteryx*, and leptonectids is the reduction of longitudinal striations along the crown (Maisch, 1998; Maxwell, 2012; Lomax, 2016; Fernández et al., 2018) (Figures 5, 6). Yet, sparse striations are present in MNHNL LM266 but do not reach the apical quarter of the crown (as in *Leptonectes* spp.; Figure 6), and many crowns exhibit a single basal ring, as in *Wahlisaurus massarae* (Lomax, 2016), *Leptonectes* spp. (Figure 6), and *Eurhinosaurus longirostris* (in which more than one basal ring is usually present (e.g., Godefroit, 1994; Fischer et al., 2011)). The acellular cementum ring is not ridged, unlike in *Temnodontosaurus* (Godefroit, 1993; Maxwell, Caldwell, et al., 2012), *Ichthyosaurus* (McGowan, 1973; Vincent et al., 2014), and *Protoichthyosaurus* (Lomax et al., 2019). The root bears fine striations, but only in the basal half, as in some leptonectids (Fraas, 1892; Godefroit, 1994).

This differs from the condition of *Leptonectes moorei* (Figure 6), *Leptonectes solei* (Figure 6), *Stenopterygius* (Godefroit, 1994), and *Hauffiopteryx* (Maxwell and Cortés, 2020), where the root ridges reach the base of the acellular cementum ring. The root is slightly expanded mesiodistally and slightly compressed labiolingually, another usual feature that is often present in leptonectids (Fraas, 1891; Reisdorf et al., 2011; Lomax, 2016).

The small size of these rostral fragments can be interpreted in two ways: (i) it belongs to a small individual, distinct from the other remains from the site or (ii) it represents the anterior extremity of a long snouted ichthyosaurian, where the tip of the rostrum can be extremely small compared to the size of the animal (McGowan, 1993, 2003). The presence of a discontinuous premaxillary fossa and, to a lesser extent, the absence of both a nasal and a maxilla (even internally) suggests that this fragment was located from the anterior quarter of the rostrum. The exposure of the splenial is less indicative of a position within the rostrum, because at least one leptonectid (*Leptonectes moorei*) possesses a very long ventral splenial exposure (V.F. pers. obs. holotype specimen NHMUK PV R 14370). In the absence of other evidence and given the taphonomy, stratigraphy, and the controlled excavations, we regard all the ichthyosaur fragments described here as likely belonging to a single individual. Even so, we detail the taxonomic information present in all fragments in isolation (Table 1), and the conclusions of the paper do not rely on this association.

Possible Surangular

Two contiguous fragments are interpreted here as the posterior part of a large right surangular (Figures 4, Supplementary Information Figure 1). The lateral surface is convex and forms a shallow anteroposterior ridge at mid-height. The medial surface is concave and forms a wide prominent ridge located within the ventral half of the medial surface. The ventral surface is rounded while the bone tapers dorsally to a thin, saddle-shaped ridge, as might be seen close to the coronoid process in neoichthyosaurians (Sollas, 1916; McGowan, 1973). The perfectly straight and parallel bone fibres on the concave side (Figures 4, Supplementary Information Figure 1) are features of ichthyosaurian surangulars (V.F. pers. obs. on material from MNHNL, MHNH). We do not derive taxonomic information from these fragments, because we consider their identification too tentative.

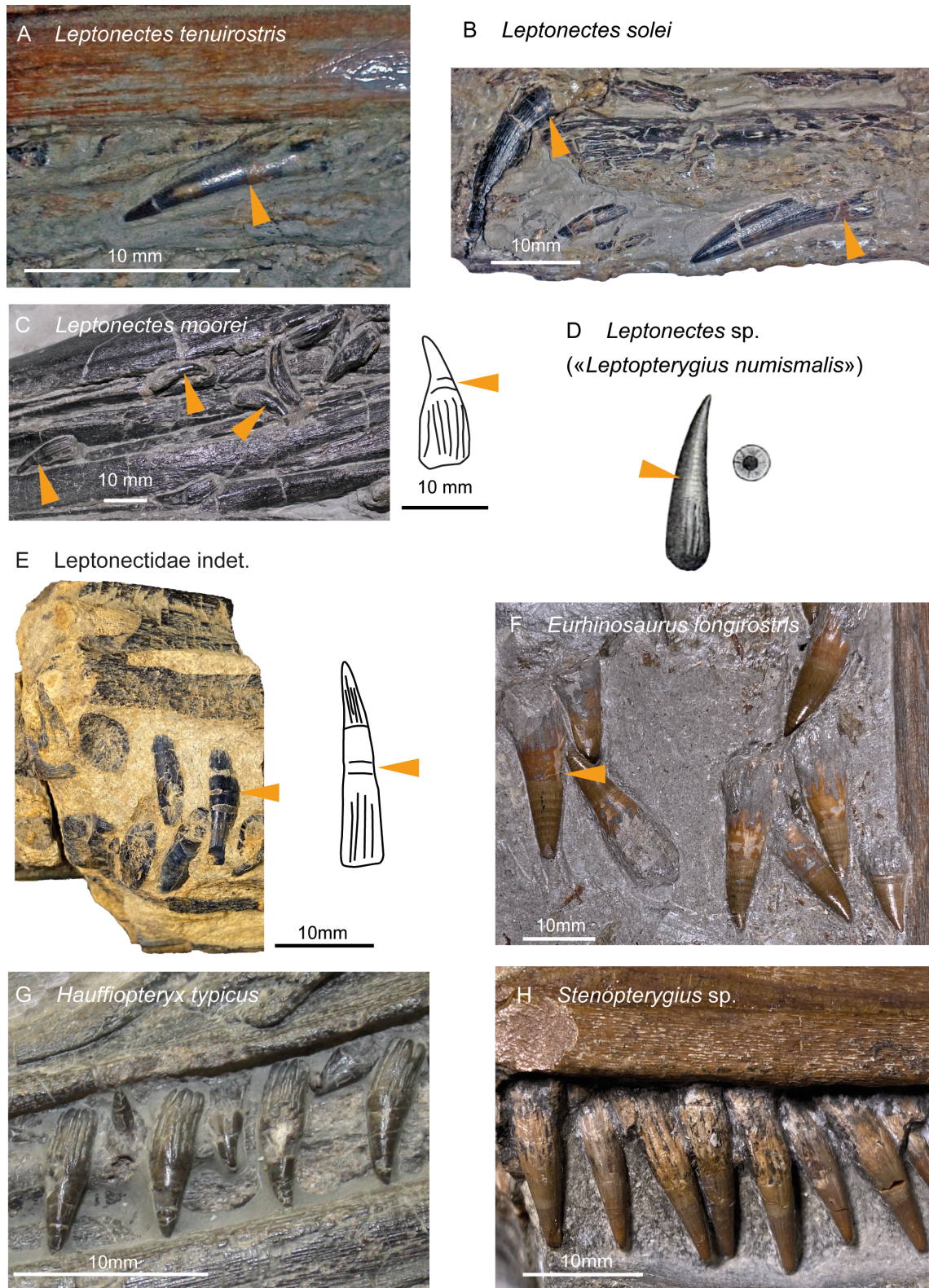


FIGURE 6. Diagnostic dental features of Early Jurassic ichthyosaurs with small and elongated tooth crowns. The distribution of concave ring at the level of the acellular cementum ring, which we term here “annulus” (indicated by orange arrows) appears restricted to leptonectids but are not fully expressed in all the teeth of an individual. (A) OUM J10305. (B) BRSMG Ce9856. (C) NHMUK R PV14370. (D) drawing extracted from Fraas (1892). (E) MNHNL LM226. (F) MNHNL TU112. (G) SMNS 81965. (H) MNHNL TV178.

Centra

Two centra fragments are present. One (Figures 4, 5) is a large dorsal centrum with an antero-posterior length of 52 mm and a diameter certainly above 100 mm (as the preserved portion is 100 mm wide), and probably between 120 and 130 mm. One apophysis is visible; the fact that the dorsal part of the centrum is missing suggests that this apophysis is the parapophysis. This apophysis is >20 mm long anteroposteriorly and 15 mm high dorsoventrally. It is teardrop-shaped, with anterior ridge connecting to the anterior margin of the centrum, as is typically of parvipelvians and clearly distinct from the dorsoventrally elongated diapophyses and often minuscule parapophyses seen in shastasaurids (Merriam, 1902; Sander, 1997; Fischer et al., 2014). Ventrally, the centrum forms a slightly concave surface. We interpret this as a parapophysis, present on the lateral surface of the centrum at mid-height. Accordingly, this centrum is regarded as an anterior dorsal centrum. The large size and the aspect ratio match with the morphology of *Temnodontosaurus* spp. (McGowan, 1974; Godefroit, 1993; Martin et al., 2012; Swaby and Lomax, 2021) and *Leptonectes solei* (McGowan, 1993). However, most other leptonectids have smaller centra, with diameters ranging from 25 to 65 mm (Huene, 1951; McGowan and Milner, 1999; McGowan, 2003; Lomax, 2016).

A second fragmentary bone solely consists of the margin of the articular surface of a small centrum. The lateral or ventral surface is concave and lacks chevron facets or apophyses. It is interpreted as a posterior caudal centrum, given the small size.

Ribs and Gastralia

Several tens of rib fragments are preserved (Figures 5, Supplementary Information Figure 1). Most have wide anterior and posterior grooves, giving the rib an “8” shape in cross-section, as is usually the case in neoichthyosaurians. However, the dorsal ribs of *Leptonectes tenuirostris*, *Temnodontosaurus azerguensis*, and some species of *Ichthyosaurus* seem to lack the grooves, giving

their ribs a rounded cross-section (Martin et al., 2012; Lomax and Massare, 2016). In one fragment, one of the grooves can be observed vanishing medially; the largest fragments have a single groove, and the opposite side is gently convex (Figure 5). A series of other, small fragments are straight and exhibit a rugose texture; we interpret these as fragmentary gastralia.

DISCUSSION

The presence of long and slender teeth, with faint longitudinal striations, a ring/annulus at the base of the crown, and with a slightly rectangular root, combined with a slender rostrum suggest leptonectid affinities for the rostral fragments of MNHNL LM266 (Figure 6). Within leptonectids, the absence of an overbite and the slender teeth rule out *Eurhinosaurus longirostris*, *Excalibosaurus costini*, and *Leptonectes moorei* (Huene, 1931b; McGowan, 1986, 2003; McGowan and Milner, 1999). The large size of the associated centra – if they, as we think is the case, belong to the same individual – suggests an animal of large size, comparable to *Leptonectes solei*, and multiple species within *Temnodontosaurus*, notably *Temnodontosaurus platyodon* and *Temnodontosaurus trigonodon* (Godefroit, 1993; McGowan, 1993, 1996). *Leptonectes* is known to be present in the European Archipelago from the Hettangian to the Pliensbachian, including in nearby Belgium (Godefroit, 1992; McGowan and Milner, 1999; Lomax and Massare, 2018a) (if one regards the Pre-Planorbis beds as earliest Hettangian in age, as suggested by Hillebrandt and Kystyn (2009)) and is thus a solid candidate for the remains from the Cloche d’Or locality. However, we assign these remains to Leptonectidae indet., pending discovery of cranial and appendicular material that could clarify the taxonomic relationships of this specimen. It should be stressed here that the presence of leptonectids in the Luxembourg-Trier basin (see also Godefroit, 1992) during the early Pliensbachian does not require the skeletal elements we describe here to

TABLE 1. Diagnostic value of the elements of MNHNL LM266 if taken individually.

Anatomical element	Individual diagnostic value
Snout fragment (premaxillae, dentaries, splenials, teeth)	Leptonectidae
Possible surangular	Vertebrata
Centra (one dorsal and one posterior caudal)	Neoichthyosauria
Ribs (and possible gastralia)	Neoichthyosauria

origin from a single individual; only the presence of a large leptonectid does (Table 1).

Even if leptonectid neoichthyosaurians have been abundantly described (e.g., Fraas, 1891; Huene, 1922; McGowan, 1989, 1993; Godefroit, 1994; McGowan and Milner, 1999; Maisch and Matzke, 2003; Lomax, 2016), the details of the dental morphology of leptonectids are rarely documented, notably the concentric rings found towards the base of the tooth crown (but see Godefroit, 1994; Reisdorf et al., 2011; Lomax, 2016). These slightly concave rings, which we term here “annuli”, clearly differ from the similarly positioned “enamel bands” of pliosaurids, which have a positive relief (Zverkov et al., 2018). Because it is not well distributed among neoichthyosaurians, this feature can be useful to segregate leptonectids from other taxa with smoothed and elongated tooth crowns, such as *Hauffiopteryx* and *Stenopterygius* (Figure 6). Indeed, even if *Hauffiopteryx* spp., *Stenopterygius* spp., and leptonectids all share a reduction of longitudinal ridges on tooth crown (Reisdorf et al., 2011; Maxwell, Fernández, et al., 2012; Fernández et al., 2018; Maxwell and Cortés, 2020), the presence of a such annuli has not been reported yet in *Hauffiopteryx* and *Stenopterygius*. A slightly labiolingually compressed root whose apicobasal ridges do not reach the acellular cementum ring, combined with the occurrence of one of more annuli close to the base of the crown can, therefore, at the current state of our knowledge, identify a tooth belonging to a leptonectid (Figure 6). Several of these rings have been reported on the crown of *Eurhinosaurus* (Godefroit, 1994; Fischer et al., 2011; Reisdorf et al., 2011) and might represent a diagnostic feature of this taxon.

The continued absence of baracromian ichthyosaurians in Pliensbachian strata suggests a sense of continuity in the ichthyosaurian assemblages during the Hettangian–Pliensbachian interval, which essentially (but not exclusively) contains leptonectids, *Ichthyosaurus*, and *Temnodontosaurus* (McGowan and Motani, 2003). A novelty of the

Pliensbachian is to record the slightly more derived taxon *Hauffiopteryx* (Maxwell and Cortés, 2020). Thanks to the Cloche d’Or locality, all stages of the Early Jurassic are now known to contain large early neoichthyosaurians (with centra diameter > 10 cm) in many places of the European Archipelago (Godefroit, 1993; McGowan, 1996; Martin et al., 2012; Maxwell and Vincent, 2015; Fischer et al., 2021). By contrast, baracromians dominate ichthyosaurian assemblages in the European Archipelago by the early Toarcian with the ubiquitous presence of multiple species of *Stenopterygius* (Huene, 1931b; Hauff, 1953; Godefroit, 1994; Maisch, 2010; Maxwell, 2012; Dick et al., 2016) and are the only ichthyosaurians found after the Bajocian, with the exception of *Malawania anachronus* (Fernández, 1994; Fischer et al., 2013, 2021). The Pliensbachian gap in the fossil record of ichthyosaurians might contain this change of dominance; in any case, these remains further highlight the importance of the Luxembourg–Trier basin deposits in understanding the diversity dynamics of Jurassic marine reptiles.

CONCLUSIONS

Marine reptile remains are rare in Pliensbachian strata, worldwide. We describe remains of large ichthyosaurians from a new lower Pliensbachian locality in central Luxembourg (Ibex Ammonite zone). At least some of these remains belong to Leptonectidae, confirming the continuous presence of early neoichthyosaurians during the entire Hettangian–Pliensbachian interval in Western Europe.

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SUPPLEMENTARY INFORMATION

A fragmentary leptonectid ichthyosaurian from the lower Pliensbachian of Luxembourg.

SUPPLEMENTARY INFORMATION FIGURE 1. Additional remains of MNHNL LM226. (A, B) possible partial surangular (posterior quarter) in (A) lateral and (B) anterior views. (C) rib fragments with a single, shallow groove.

