

# ICHTHYOSAURS FROM THE FRENCH RHAETIAN INDICATE A SEVERE TURNOVER ACROSS THE TRIASSIC–JURASSIC BOUNDARY

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**Abstract** Mesozoic marine reptiles went through a severe turnover near the end of the Triassic. Notably, an important extinction event affected ichthyosaurs, sweeping a large part of the group. This crisis is however obscured by an extremely poor fossil record and is regarded as protracted over the entire Norian–earliest Jurassic interval, for the lack of a more precise scenario. The iconic whale-sized shastasaurid ichthyosaurs are regarded as early victims of this turnover, disappearing by the middle Norian. Here we evaluate the pattern of this turnover among ichthyosaurs by analyzing the faunal record of two Rhaetian localities. One locality is Autun, eastern France; we re-discovered in this material the holotypes or partial ‘type’ series of *Rachitrema pellati*, *Actiosaurus gaudryi*, *Ichthyosaurus rheticus*, *Ichthyosaurus carinatus*, and *Plesiosaurus bibractensis*; a revised taxonomic scheme is proposed. The second assemblage comes from a new locality: Cuers, southeastern France. Both these assemblages provide several lines of evidence for the presence of shastasaurid-like ichthyosaurs in the Rhaetian of Europe. These occurrences suggest that both the demise of shastasaurids and the sudden radiation of neoichthyosaurians occurred within a short time window; this turnover appears more abrupt but also more complex than previously postulated and adds a new facet of the end-Triassic mass extinction.

**Keywords** Ichthyosauria; Shastasauridae; Rhaetian; Latest Triassic extinction; Turnover.

## **Introduction**

Ichthyosauria is a diverse clade of marine reptiles that spanned most of the Mesozoic (e.g. McGowan and Motani 2003). Until recently, most authors interpreted the fossil record as showing that three major extinction events affected this group: one during the Late or latest Triassic (LT), one at the Jurassic–Cretaceous boundary (JCB), and their total extinction at the Cenomanian-Turonian boundary (CTB) (e.g. Bardet 1992; Bakker 1993; Bardet 1994). Whereas the JCB extinction is now regarded as a minor event for ichthyosaurs (Fischer et al. 2012; Fischer et al. 2013), the LT and CTB extinctions are considered as severe (Thorne et al. 2011; Fischer et al. 2014). A very large portion of ichthyosaur diversity and disparity vanished in the course of LT extinction; only the open ocean-adapted parvipelvians survived (McGowan 1997; Thorne et al. 2011), and then rapidly radiated at the Triassic–Jurassic boundary and during the Jurassic (Fischer et al. 2013). However, the last unambiguous record of non-parvipelvic ichthyosaurs is middle Norian (e.g. McGowan 1997; Nicholls and Manabe 2004) and no diagnostic remains are known from the entire late Norian–Rhaetian interval, worldwide. The recent discovery of a possible non-parvipelvic ichthyosaur in the earliest Jurassic of

Wales (Martin et al. In Press) indicates that our understanding of the tempo and amplitude of these events remain largely unknown, as is their synchronicity with other biotic and abiotic events (Benson et al. 2012).

Only a handful of marine reptile occurrences have been reported in Rhaetian strata (see for example, the compilations of Bardet et al. 2014; Kelley et al. 2014). Besides the scarce material reported from southern France, Austria, and England (Corroy 1933; Zapfe 1976; Storrs 1994), Sauvage (1876, 1883, 1903) described abundant reptilian material and several new taxa from the ‘Pellat’ and ‘Dumortier’ collections, originating from latest Triassic strata in the Autun area, eastern France. This collection is therefore of crucial importance to understand the diversity dynamics near the end of the Triassic. However, this material was dispersed and considered as lost (Gand et al. 2012). S.G. and V.F. re-discovered most of this material in the collections of the Katholieke Universiteit Leuven (K.U. Leuven), Belgium (Table 1).

In order to evaluate the timing and modalities of the latest Triassic ichthyosaur turnover, (1) we reassess the ichthyosaur material of Sauvage, clarify its taxonomy and retrace its research history (see Electronic Supplementary Material [ESM]); (2) we describe new ichthyosaur remains and assess the stratigraphy of another Rhaetian locality, Cuers, in southern France. Then, (3) we review and discuss the ichthyosaur extinctions and radiations of the Norian–Hettangian interval in light of the new data and (4) replace it into a brief synoptic view of the end-Triassic turnover among marine reptiles, frequently considered as one of the ‘big five’ Phanerozoic mass extinctions (Wignall and Bond 2008).

**Table 1.** Amniotans from the Pellat Collection with their successive assignments and their current location.

<b>Sauvage 1883</b>	<b>Sauvage 1903</b>	<b>This work</b>	<b>Place curated and catalog number</b>
<b><i>Rachitrema pellati</i></b>		Nomen dubium, composite	
Neural arch (holotype)	<i>I. rheticus</i> neural arch	Ichthyosauria indet., Shastasaurid-like or cymbospondylid-like neural arch	PLV 1939
Ribs	—	Amniota indet., ribs or gastralia	PLV 1951, 1952
Scapula	<i>Toretocnemus (Leptocheirus)</i> scapula	Aff. Shastasauridae scapula	PLV 1942
Humerus	Indet.	Non-parvipelvian Ichthyosauria, ilium	PLV 1940

Left radius	<i>Toretocnemus</i> or <i>Shastasaurus</i> ilium	Plesiosauria indet., propodial	PLV 1938
Left pubis	Indet.	Amniota indet., possible ichthyosaur coracoid	PLV 1943
Mastoidien	—	Amniota indet., probable ichthyosaur surangular	PLV 1934
Skull element 1	—	Amniota indet., possible mandible fragment	PLV 1941
Skull element 2	—	Amniota indet., possible mandible fragment	PLV 1950 (connects to PLV 1959)
<b><i>Ichthyosaurus</i> <i>rheticus</i></b>		Nomen dubium, composite	
Centrum 1	—	—	Possibly in Autun seminary
Centrum 2	—	Aff. Shastasauridae thoracic centrum	PLV 1961
Centrum 3	—	—	?
Centrum 4	—	Aff. Shastasauridae thoracic centrum	PLV 1948
Centrum 5	—	—	?
Femur 1	—	Aff. Shastasauridae femur	PLV 1963
Femur 2	—	—	In MHNA
Scapula	—	Aff. Shastasauridae epipodial	PLV 1962
Ribs	—	Ichthyosauria indet. rib	PLV 1949?
Ribs	—	Amniota indet. (see PLV 1950 above)	PLV 1959
<b><i>Ichthyosaurus</i> <i>carinatus</i></b>		Nomen dubium, composite	
Centrum 1	—	Aff. Shastasauridae thoracic centrum	PLV 1949 partim
Centrum 2	—	Aff. Shastasauridae thoracic centrum	PLV 10bis
Centrum 3	—	—	In MHNA
Centrum 4	—	—	In MHNA
Mandible	—	Aff. Shastasauridae rostrum	? – PLV 1964 partim are compatible remains
Ribs	—	Ichthyosauria indet. rib	PLV 1957, but not entire series

<i>Plesiosaurus bibractensis</i>		Species inquirenda	
Cervical vertebra (holotype)	—	Pectoral or sacral plesiosaur vertebra	PLV 1936
Dorsal vertebra 1	—	—	Possibly in MHNA
Dorsal vertebra 2	—	caudal plesiosaur vertebra	PLV 1953 partim
Dorsal vertebra 3	—	dorsal plesiosaur vertebra	PLV 1949?
Dorsal vertebra 4	—	Pectoral or sacral plesiosaur vertebra	PLV 1953 partim
Caudal vertebra	—	dorsal plesiosaur vertebra	PLV 1948
Ribs	—	—	Possibly in MHNA
Femur	—	plesiosaur propodial	PLV 1954
<i>Plesiosaurus costatus</i>		Species inquirenda	
Cervical vertebra 1	—	cervical plesiosaur centrum	PLV 1935
Cervical vertebra 2	—	cervical plesiosaur centrum	PLV 1955
Cervical vertebra 3	—		Possibly in MHNA
<i>Actiosaurus gaudryi</i>		Species inquirenda	
Femur 1 (holotype)	—	Possible choristodere propodial	PLV 1937
Femur 2	—	—	?
Humerus	—	Possible choristodere propodial	PLV 1944 (broken original + cast)
Vertebra	—	—	?
<b>Additional material</b>			
—	—	Numerous plesiosaur and ichthyosaur centra	PLV 1945

## Material and methods

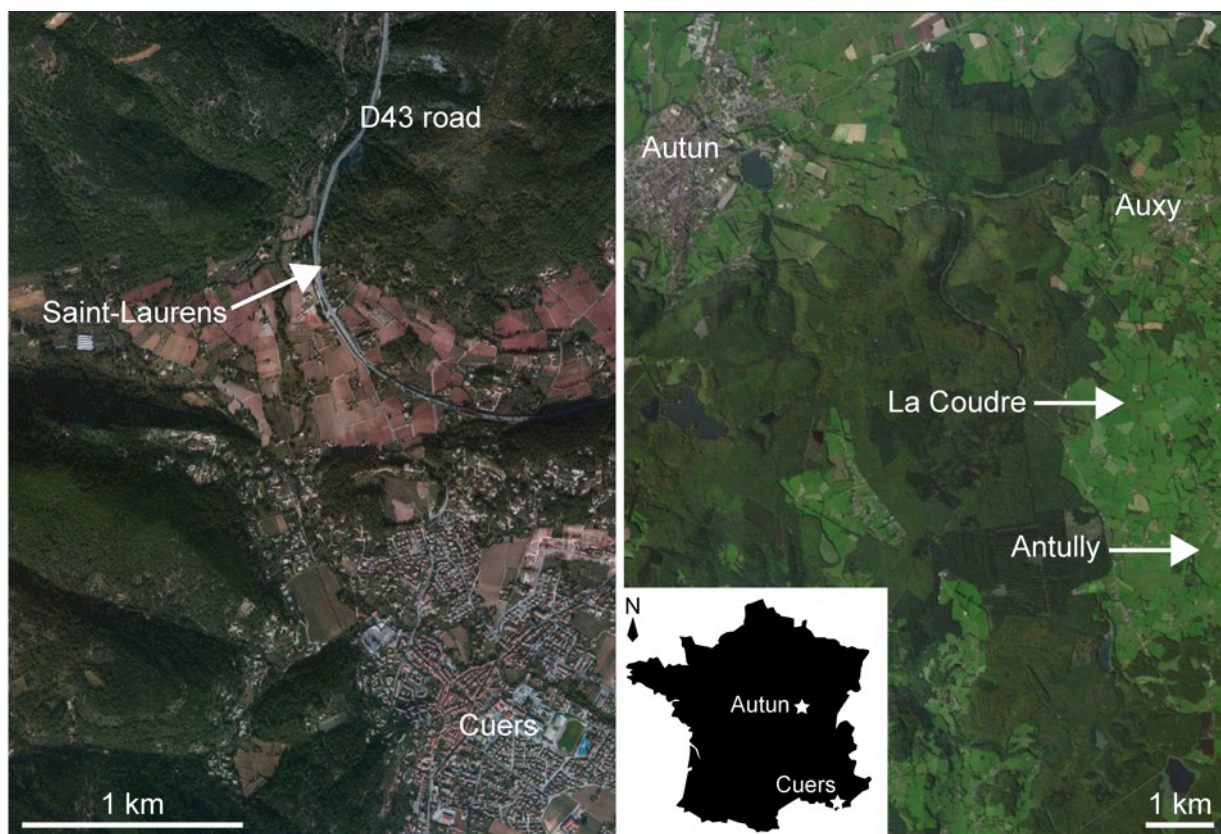
### Institutional Abbreviations

**MHNTV**, Muséum d'Histoire naturelle de Toulon et du Var, Toulon, France. **MHNA**, Muséum d'Histoire naturelle d'Auxerre, Auxerre, France ; **PLV**, Palaeontology collections, Katholieke Universiteit Leuven (K.U. Leuven), Belgium; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada. **UCMP**, University of California Museum of Paleontology,

Berkeley, U.S.A. **UM-CUE**, University of Montpellier<sup>2</sup>, Paleontological collections, Montpellier, France.

#### Geographic and geological setting

**Cuers** This site is located along the D43 road around ‘Saint-Laurens’, Var (83), France (Fig. 1). The section corresponds to a succession of Triassic bioclastic limestone beds containing numerous remains of chondrichthyans, teleosts, gastropods, crinoids, and bivalves, in association with ferruginous oolites and quartz. The bioclastic limestone is interbedded with numerous argillaceous beds (Fig. 2), as in other contemporaneous localities in the region (Caron 1967). The ichthyosaur remains studied here originate from a shale bed (Fig. S1 in ESM). Another shale bed a few meters above concentrates a diversified assemblage of teleosts (*Birgeria*, *Sargodon*, *Lepidotus*) and selachians (see below) (Agassiz 1833–43; Quenstedt 1856–1858; Corroy 1933; Charles 1948). Our sampling of the Saint-Laurens reveals an elasmobranch assemblage dominated by well-preserved hybodont remains, most of which being referable to *Lissodus minimus* (Agassiz, 1833–43). Other hybodonts (*Hybodus* sp., *Polyacrodus* sp., *Pseudodalatias barnstonensis* (Sykes, 1971), neoselachians (*Rhomphaiodon nicolensis* Duffin, 1993) and *Pseudocetorhinus pickfordi* Duffin, 1998 (order and family incertae sedis) complete this diverse assemblage (Cappetta 2012; Fig. S2 in ESM); a detailed account on the shark fauna from Cuers will be published in another venue. This assemblage closely resembles that of a nearby locality analyzed by Corroy (1933): *Hybodus minor* Agassiz, 1833–43, *H. cloacinus* Quenstedt, 1856–1858, *Lissodus minimus* and *Nemacanthus monilifer* (Agassiz, 1833–43) and that of Habay-la-vieille (Rhaetian of Belgium [Delsatte and Lepage 1991; Duffin and Delsatte 1993]), strongly suggesting a Rhaetian age for the Cuers locality.



**Fig. 1** Location of the two Rhaetian fossil sites analysed in this paper. Left: Saint-Laurens, near Cuers, Var, France. Right: La Coudre and Antully near Autun, Burgundy, France. Inset: France map with with Autun and Cuers.

**Autun** Most specimens originate from a bonebed in the “Grès à *Avicula contorta*” (Grès Blonds Formation) of the Autun area, Saône-et-Loire (71), Burgundy, France. The bivalve now known as *Rhaetavicula contorta* is indicative of the Rhaetian stage (e.g. Hautmann 2001). Two localities have yielded specimens analysed here: Antully and La Coudre; both are small villages in the vicinity of Autun (Fig. 1; Gand et al. 2012). Other specimens from the same area are preserved in a upper Rhaetian argillaceous limestone (Gand et al. 2012). All fossils from this area are thus unambiguously Rhaetian in age; however, more precise stratigraphic data for the bonebed is currently lacking.

#### Taxonomy assessment in bone-bed deposits

Sauvage (1883) recognized several taxa within the Autun material and referred several bones to them, creating ‘type’ series. In the following section, we re-describe these series but we assess the taxonomic affinities of each bone independently, as both the nature of their hosting formation (a sandstone bone-bed) and our re-assessment strongly suggest that these series are



composed of multiple individuals and taxa. Then, we summarize our taxonomic reassessments in the Systematic Paleontology section and in Table 1.

### **Comparative descriptions and affinities**

#### **Cuers ichthyosaur**

The ichthyosaur material from Cuers was discovered in close vicinity in a single bed and likely represents the remains of a single animal. This specimen was found during two distinct excavations by D.R. and X.V. and received two collection numbers, MHNTV PAL-1-10/2012 (premaxilla, centrum, partial ribs and indeterminate fragments) and MHNTV PAL-2/2010 (mandible, centrum, partial ribs and indeterminate fragments).

**Premaxilla (MHNTV PAL-1-10/2012)** A small rostrum fragment with a flat lateroventral facet (presumably for articulation with the maxilla), is interpreted as the premaxilla. A shallow fossa praemaxillaris is present. The dental groove is reduced and appears continuous, indicating an aulacodont or sub-theodont tooth implantation (Motani 1997). The labial wall is much higher and thicker than the lingual wall and possesses a flat maxillary facet.

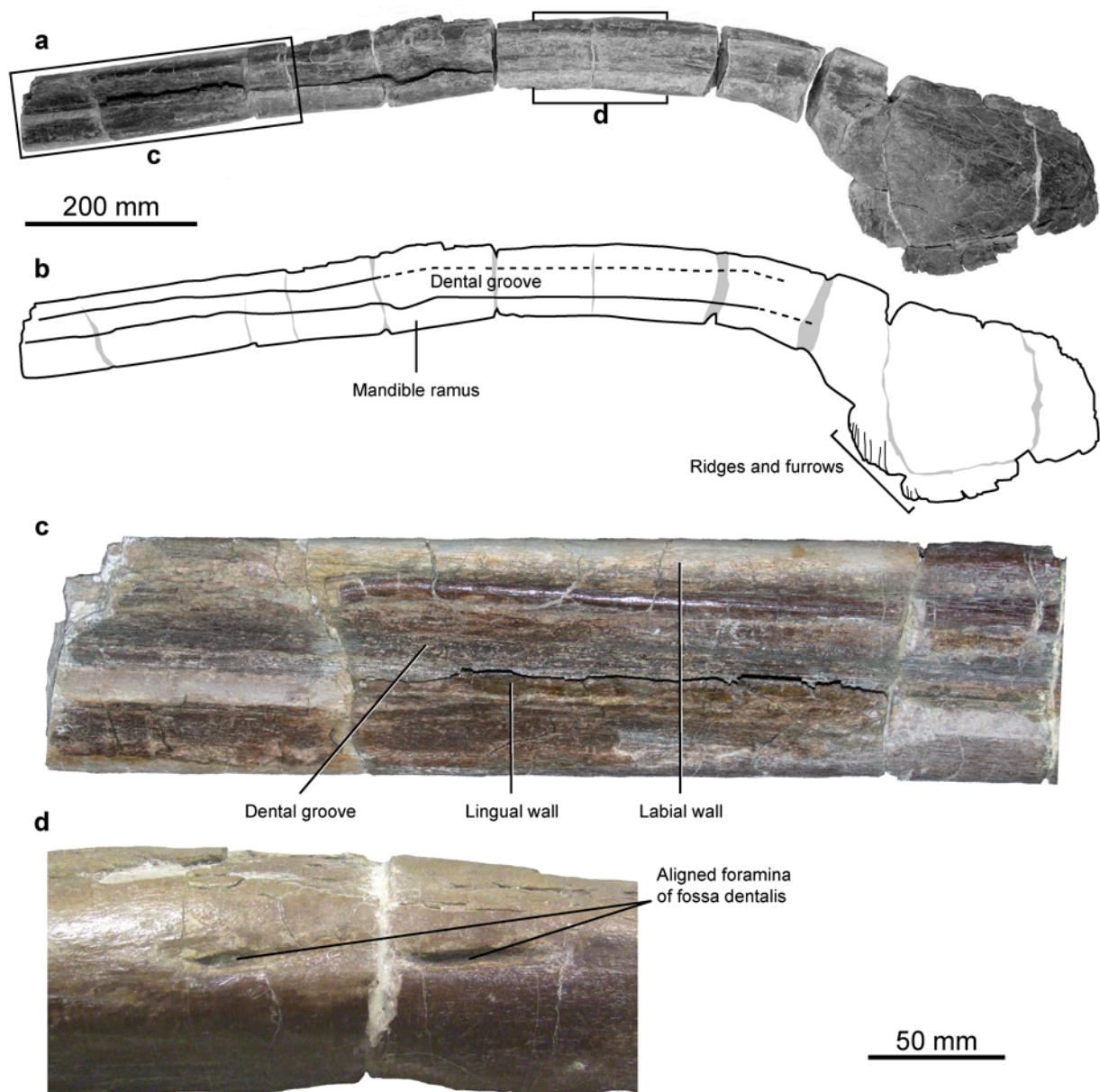
**Mandible (MHNTV PAL-2/2010)** This specimen is a mandible fragment measuring 1270 mm (Fig 2). The anterior part of the ramus is extremely slender (the long axis of its cross-section is only 79 mm long) and slightly arched, being markedly similar to that of *Shonisaurus sikanniensis* (see Figs 3, 4 in Nicholls and Manabe 2004) and the *Ichthyosaurus carinatus* mandible figured by Sauvage (1883: Pl. 8; see below). The fossa dentalis is discontinuous; it forms a straight succession of deep, anterolaterally-oriented foramina distant of 50 mm. They fuse to form a continuous groove over about 100 mm the middle part of the bone.

A narrow, continuous dental groove is present; as in *Ichthyosaurus carinatus* (see below) but unlike other ichthyosaurs, the dental groove lies on the medial surface of the rostrum. As in the premaxilla, the labial wall is thick, whereas its lingual wall appears markedly reduced. Preservation and preparation damage have further reduced it to 5 mm thin lamella. As preserved, the dental groove is only 10 mm deep, which appears extremely small compared to the size of the mandible. Shastasaurids are the only ichthyosaurs known to have substantially reduced their dental grooves; they are completely absent in *Guanlingsaurus liangae* and *Shonisaurus sikanniensis* (Nicholls and Manabe 2004; Sander et al. 2011). The floor of the dental groove of the Cuers ichthyosaur is smooth, continuous and there is no evidence of alveoli. This indicates an aulacodont mode of tooth implantation (Motani 1997).

No bone sutures are visible in MHNTV PAL-2/2010, suggesting that many bones of the mandible are fused or that the fossil recrystallized during diagenesis. The shape of the posterior

part of the mandible is also unusual: the jaw ramus narrows laterally and expands dorsoventrally, forming a biconcave spatula. Deep striations ornate the anterodorsal edge of this region. Whereas the posterior part of the bone is unlike that of any ichthyosaur we are aware of, this bone is unmistakably ichthyosaurian in having an aulacodont tooth implantation and a lateral fossa dentalis. Because the anterior and the posterior ends of the mandible are missing, the total length of the mandible cannot be adequately estimated, but could have reached 2 m or more, since the ramus is still 80 mm high at the anterior-most section and the entire symphysis is missing.

**Axial skeleton** Two centra and rib fragments are preserved (Fig. S3 in ESM). The centrum of MHNTV PAL-2/2010 is 119 mm wide and its height/length ratio is high, reaching 4.76. The centrum of MHNTV PAL-1-10/2012 is similar, being 115 mm wide and has a height/length ratio of 5.47. Given the three-dimension preservation mode of the other remains, it is unlikely that this ratio results from excessive compaction, although it certainly influenced the value. The lateral surface of both centra is weathered so that no apophysis can be recognized accurately. The floor of the neural canal is preserved and is hourglass-shaped in dorsal view, as in the Autun material (see below) and *Shonisaurus popularis* (see Camp 1980) and unlike the straight, rectangular shape found in neoichthyosaurians (e.g. Godefroit 1993; McGowan and Motani 2003; Kolb and Sander 2009). The floor of the neural canal is pierced by numerous small foramina, as in the material from Autun). The ribs are markedly compressed anteroposteriorly. Median grooves are present on both their anterior and posterior surfaces, giving the ribs an 8-shaped cross-section. The depth of these grooves decreases distally.



**Fig. 2** Mandibular remains from the Cuers ichthyosaur (MHNTV PAL-2/2010). **a**, photograph of the ?right mandible in lingual view; **b**, interpretative drawing; shaded zones in the interpretation represent cracks and missing bone. The posterior part of the mandible has been flattened along the bedding plane. **c**, close-up of the dental groove. **d**, close-up of fossa dentalis.

**Affinities** Besides its large to gigantic size, the Cuers ichthyosaur displays two important characters: an aulacodont dentition and flattened centra. Increase of body size (skull length  $\geq$  40 cm in adults) is regarded as a synapomorphy for Longipinnati without Torectonemidae (Maisch and Matzke 2000:character 33). Amongst remaining Longipinnati, aulacodonty characterizes Neoichthyosauria, but can also be observed in the shastasaurid *Shastasaurus pacificus* (see Motani 1997; Table S1). Neoichthyosaurians do not have extremely flattened

centra (e.g. Buchholtz 2001); such centrum morphology has not been described in *Shastasaurus* itself either, but definitely in other shastasaurids: the cervical centra of *Himalayasaurus* and the thoracic centra of some *Shonisaurus* species are characterized by a height/length ratio  $\geq 3$  (Motani 1999; Maisch and Matzke 2000; Dalla Vecchia and Avanzini 2002; McGowan and Motani 2003; Nicholls and Manabe 2004). Finally, the extremely long and slender mandibles with nearly absent dental groove do not correspond to any parvipelvian taxa known so far; large neoichthyosaurians are present in the Hettangian–Sinemurian of western Europe, but either have robust mandible and dentition (*Temnodontosaurus*; e.g. Godefroit 1993) or a slender and diminutive mandible (Leptonectidae; e.g. McGowan 2003). The Cuers remains closely match the mandible morphology of shastasaurids, especially that of *Shonisaurus sikanniensis*, in forming a long, arched rod, that implies a reduced symphysis (Nicholls and Manabe 2004), unlike in leptonectid parvipelvians (e.g. McGowan 2003). The detailed morphology of shastasaurid mandible is however incompletely understood except in *Shonisaurus popularis* (see Camp 1980); as far as we know, the peculiar morphology of the posterior part of the Cuers mandible has not been documented in any ichthyosaurs.

The available data indicate that the Cuers ichthyosaur should be related to shastasaurid-like ichthyosaurs (as the monophyly of Shastasauridae is still debated: e.g. Maisch 2010; Ji et al. 2013). This specimen possesses a unique combination of characters: *Shonisaurus*- or *Himalayasaurus*-like centra and skull size but *Shastasaurus*-like aulacodont tooth implantation. The diversity of Late Triassic shastasaurids in terms of tooth implantation and tooth shape is surprisingly high, with the presence of edentulous, small-toothed aulacodont, subthecodont, and thecodont forms (Table S1 for details and references). In this context of high intragroup diversity and questioned monophyly of Shastasauridae, we assign this specimen to aff. Shastasauridae.

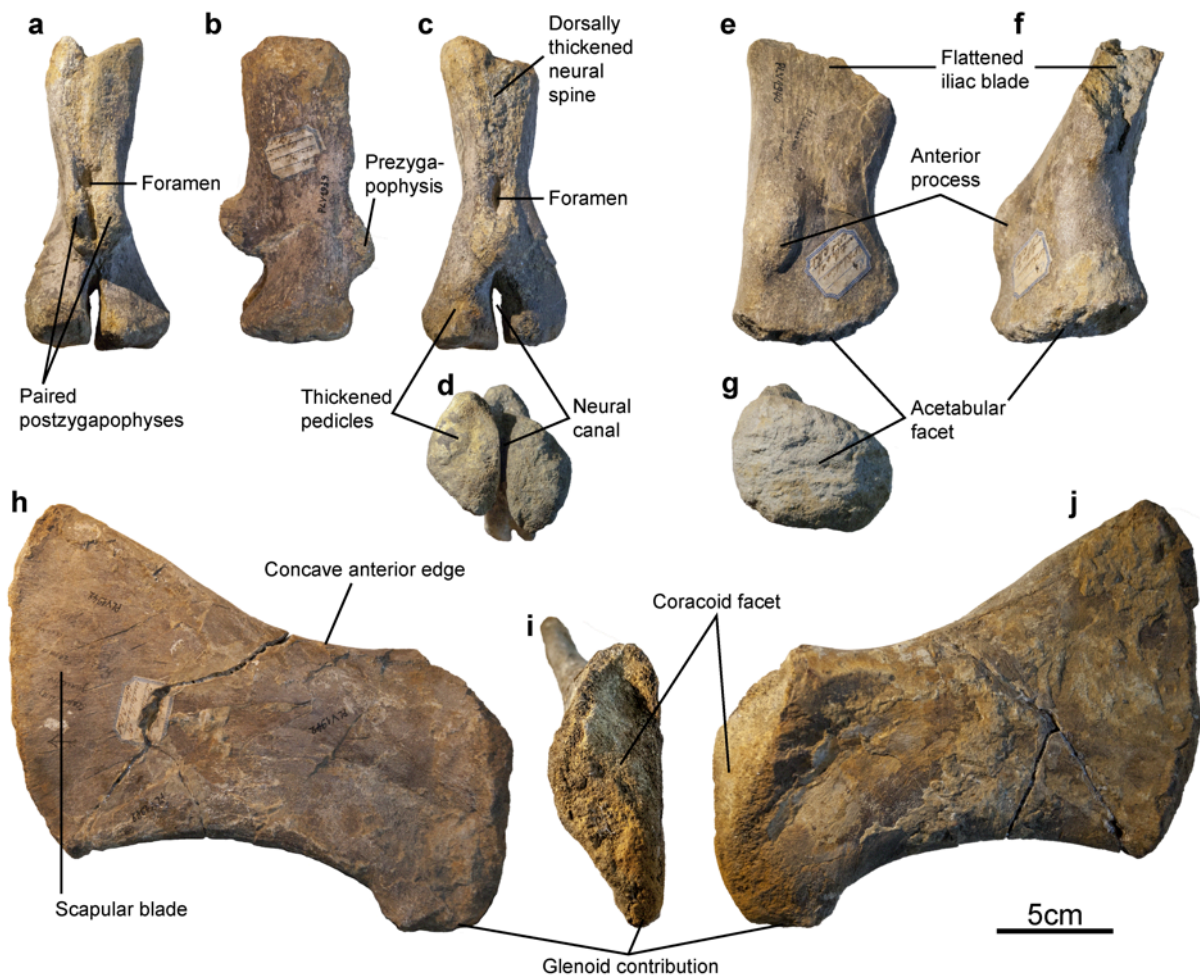
#### *Rachitrema pellati* type series

**Neural arch (PLV 1939)** The holotype of *R. pellati* is a large complete neural arch that is 242 mm high (Fig 3). This taxon was previously assigned by Sauvage (1883) to Dinosauria; Huene (1902) and Sauvage (1903) then recognized its ichthyosaurian affinities. The pedicle has a semi-oval cross-section and is greatly thickened, strongly reducing the width of the neural canal to a narrow cleft. Unlike in neoichthyosaurians, the postzygapophyses are paired (Maisch and Matzke 2000). The neural spine thickens dorsally, a feature encountered in *Cymbospondylus* (see Maisch and Matzke 2000) and several shastasaurid taxa for which the neural spine is known ('*Shastasaurus altispinus*' [= *S. pacificus* according to McGowan and

Motani 2003], *Callawayia neoscapularis* and *Shonisaurus sikanniensis*; Merriam 1908; Nicholls and Manabe 2001, 2004). More primitive and more derived ichthyosaurs, including *Mixosaurus* and the early neoichthyosaurian *Temnodontosaurus platyodon*, lack this feature (Merriam 1908; Godefroit 1993; Maisch and Matzke 2000); the neural spine of the early parvipelvians *Hudsonelpidia* and *Macgowania* is however unknown. The neural spine of *R. peltati* is straight and not offset posteriorly, as in *Callawayia neoscapularis*, *Hudsonelpidia brevirostris*, and *Californosaurus perrini* (Merriam 1908; McGowan 1995; Nicholls and Manabe 2001) and unlike in *Shastasaurus pacificus* (see Merriam 1908). Unusually, the neural spine is pierced by a large oval foramen situated above the zygapophyses.

**Scapula (PLV 1942)** The scapular blade is wide, unlike in *Callawayia neoscapularis* and parvipelvians, which possess a slender scapular blade (McGowan 1994, 1996b; Maisch and Matzke 2000) (Fig. 3). The scapula markedly differs from that of *Cymbospondylus* in seemingly lacking a prominent, isolated acromial process (Merriam 1908; Sander 1989), although the medial part of the scapula is not complete. The scapula closely resemble to that of *Shonisaurus popularis* in its general shape (see McGowan and Motani 1999; Maisch and Matzke 2000) and in lacking an anterior flange. Among non-parvipelvic ichthyosaurs, only *Shonisaurus* lacks this anterior flange (e.g. Maisch and Matzke 2000). PLV 1942 also lacks a medial notch, unlike in *Shastasaurus* (see Merriam 1902, 1908; Ji et al. 2013).

**Ilium (PLV 1940)** This specimen was previously regarded by Sauvage (1883) as a dinosaur humerus; he latter regarded it as a indeterminate ichthyosaur bone (Sauvage 1903); we regard it as an ichthyosaur ilium. The acetabular surface is round in cross-section and slightly dome-shaped (Fig 3). The ilium then becomes transversely flattened, and appears similar to the condition seen in *Cymbospondylus* (see Merriam 1908). The shape of the ilium indicates non-neoichthyosaurian affinities: the ilium possesses an anterior process, as many Middle–Late Triassic taxa such as *Cymbospondylus petrinus*, *Californosaurus*, and *Hudsonelpidia* (Merriam 1908; McGowan 1995; McGowan and Motani 2003). The neoichthyosaurian *Suevoleviathan* is the only post-Triassic ichthyosaur exhibiting this feature (Maisch 1998). Furthermore, the flattened shape of the iliac blade and the large size of the ilium (the preserved part, lacking a great part of the iliac blade is 126 mm high) indicate it does not belong to parvipelvic ichthyosaurs, which are characterized by a reduction of the pelvic girdle size and a styloidal iliac blade (Motani 1999).



**Fig. 3** Unambiguous ichthyosaur remains from the *Rachitrema pellati* type series. **a-d**, PLV 1939, a shastasaurid-like or cymbospondylid-like neural arch in **a**, posterior; **b**, lateral; **c**, anterior; **d**, ventral views. Note the thick pedicles and the central foramen. **e-g**, PLV 1940, a non-parvipelvic ichthyosaur ilium in **e**, anterior; **f**, lateral; **g**, ventral views. Note the anterior process and the robust acetabular portion. **h-j**, PLV 1942, a *Shonisaurus*-like right scapula in **h**, anterior, **i**, medial; **j**, posterior views. Note the elongated shape and distal fan.

**Affinities** We agree with Huene (1902), Sauvage (1903) and Bardet & Cuny (1993) on the ichthyosaurian affinities of *Rachitrema pellati*. However, each fossil should be evaluated individually and some bones of the type series are not ichthyosaurian. The holotype specimen, a neural arch, was referred to as *I. rheticus* by Sauvage (1903). It is not compatible with neoichthyosaurians and bears numerous similarities with shastasaurid and cymbospondylid ichthyosaurs. It is unique in possessing a foramen dorsally to the zygapophyses. Another element of the type series of *R. pellati*, the scapula (PLV 1942), closely resembles that of shastasaurids, particularly *Shonisaurus popularis*. The ilium (PLV 1940) cannot be determined more precisely than Ichthyosauria indet., but its morphology is distinct from that of

parvipelvian ichthyosaurs. The ribs (PLV 1951, PLV 1952) are of moderate to very large size (404 + 415 mm long for PLV 1951 and 305 mm long for PLV 1952), may indicate ichthyosaur affinities, but this attribution should be taken with caution; accordingly, we regard these remains as Amniota indet. here. Finally, some bones of the type series of *R. pellati* belong to other groups, notably a plesiosaur propodial (PLV 1938) and other elements (PLV 1934, PLV 1941, PLV 1943, PLV 1950\_59) of unclear affinities (Table 1; Fig. S4 in ESM).

#### *Ichthyosaurus rheticus* series

*Ichthyosaurus rheticus* and *Ichthyosaurus carinatus* were named and diagnosed by Sauvage (1876) on the basis of centra from the Pellat Collection, but this paper did not describe any specific remains, so that no holotype material can be selected. Sauvage (1883) latter described a series of remains that he assigned to *I. rheticus* and another that he assigned to *I. carinatus*; we assess these series below. Most specimens of these series are housed at the K.U. Leuven, but some others are located at the MHNA (Gand et al. 2012).

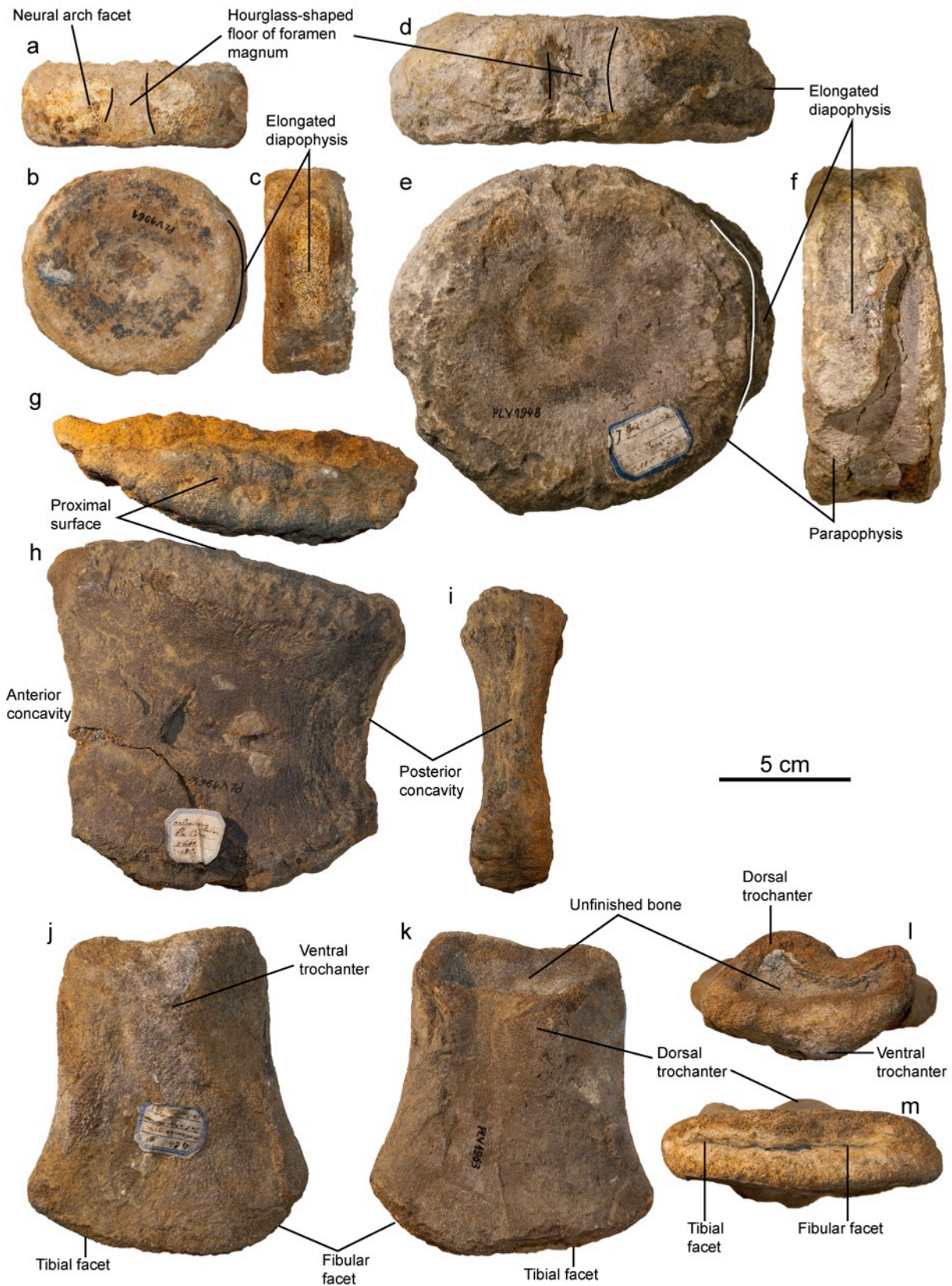
**Centra (PLV 1948 partim, PLV 1961)** Sauvage (1883) provided a number of measurements and descriptions of the centra he regarded as belonging to *I. rheticus*. Only two of them match these measurements and are labeled as such (PLV 1948 partim, PLV 1961). Other centra from Antully and La Coudre are present in the Pellat Collection at the K.U. Leuven (PLV 1932, PLV 1948 partim, PLV 1949 partim). All these centra have a prominent, extremely dorsoventrally elongated diapophysis, as in the thoracic centra of shastasaurids (Sander 1997; Lucas 2002) (Fig. 4). In PLV 1948 partim, the diapophysis merges with the anterior margin of the centrum ventrally. When present (in PLV 1948 partim), the parapophysis is a small but prominent bulge that merges with the anterior margin of the centrum. As in the centra of the Cuers ichthyosaur, the floor of the foramen magnum of these centra is hourglass-shaped in dorsal view and is pierced by numerous foramina in PLV 1932 and PLV 1949 partim.

**Epipodial (PLV 1962)** We interpret the specimen PLV 1962, regarded as a femur by Sauvage (1883), as an ichthyosaur epipodial of exceptionally large size, resembling that reported in Martin et al. (In Press). Both the proximal and distal surfaces are thicker than the shaft and are covered by pitted, unfinished bone. These surfaces are not parallel; the distal surface is offset by an angle of approximately 20° (Fig. 4). The proximal surface is the longest and the thickest; this facet is straight and eye-shaped in proximal view. The distal surface is poorly preserved but its edge appears rounded in dorsal view. The shaft is proximodistally short and markedly flattened dorsoventrally, unlike in basal ichthyosaurs, where the shaft is more columnar, as in mixosaurids and *Cymbospondylus* (e.g. Merriam 1908; McGowan and Motani 2003). Both the

anterior and posterior surfaces of the shaft are gently concave, indicating the presence of a large and oval spatium interosseum unlike in *Toretocnemus* and parvipelvians (e.g. Merriam 1908; McGowan 1995; Maisch 1998; McGowan and Motani 2003). There is no peripheral flange. This element resembles the radius of *Pessopteryx*, *Besanosaurus* and *Shonisaurus popularis* (Dal Sasso and Pinna 1996; McGowan and Motani 1999; Maisch 2002) but more closely resembles the tibia of *Californosaurus* (Merriam 1908) and shastasaurids, notably those of *Guanlingsaurus liangae* and *Guizhouichthyosaurus tangae* (Shang and Li 2009; Sander et al. 2011; Ji et al. 2013). Given the much older occurrence of *Pessopteryx* (Lower Triassic of Svalbard: Maisch 2010), PLV 1962 is here considered as an epipodial probably belonging to a shastasaurid or a closely related form (both *Besanosaurus* and *Californosaurus* are usually recovered as closely related or within shastasaurids: Maisch and Matzke 2000; Fröbisch et al. 2013; Ji et al. 2013).

**Femur (PLV 1963)** Although flattened dorsoventrally, the femur closely resembles that of shastasaurids, especially to those of *Guanlingsaurus liangae* and *Shastasaurus osmonti* Merriam 1908 (= *Shastasaurus pacificus* according to McGowan 1994) (Merriam 1908; Sander et al. 2011; Ji et al. 2013). It is short, unlike in *Cymbospondylus* (see Merriam 1908). The capitulum region is deeply concave, suggesting an immature age (Johnson 1977) (Fig. 4). A wide and low longitudinal trochanter is present on both the dorsal and ventral surfaces. According to Maxwell et al. (2012) the trochanter lying close to the anterior edge of the femur is the dorsal process. Thus, PLV 1963 is regarded as a right femur. It differs from that of *Cymbospondylus*, *Toretocnemus zitteli* and *Californosaurus perrini* in having a protruding anterodistal process (Merriam 1908). As in *Shastasaurus pacificus*, *Shonisaurus popularis*, *Phantomosaurus*, *Besanosaurus*, *Mikadocephalus* and *Californosaurus* but unlike in *Toretocnemus zitteli*, and basal neoichthyosaurians, the fibular facet is small and oriented posterolaterally (Merriam 1908; Camp 1980; Maisch and Matzke 2000; McGowan and Motani 2003).





**Fig. 4** Shastasaurid-like remains from the *Ichthyosaurus rheticus* series. **a-c**, PLV 1961, a centrum in **a**, dorsal; **b**, anterior; **c**, right lateral views. Note the elongated diapophysis. **d-f**, PLV 1948, a centrum in **d**, dorsal; **e**, anterior; **f**, right lateral views. Note the elongated diapophysis. **g-i**, PLV 1962, an epipodial in **g**, proximal, **h**, dorsal; **i**,

posterior views. Note the anterior and posterior concavities. **j-m**, PLV 1963, a right femur in **j**, ventral, **k**, dorsal; **l**, proximal; **m**, distal views.

**Affinities** As for *Rachitrema pellati*, the type series cannot be considered as belonging to a unique individual. Based on the drawing of Sauvage (1883, 1903), Bardet & Cuny (1993) and Gand et al. (2012) regarded this species as a nomen dubium, and proposed shastasaurid affinities for this material. Our first-hand examination of the material indicates all remains attributed to *I. rheticus* are compatible with shastasaurids or closely related Triassic taxa, even when considered individually.

#### *Ichthyosaurus carinatus* series

**Mandible (PLV 1964)** Sauvage (1883: Pl. 8) assigned a gigantic mandibular fragment to *I. carinatus*. This fragment, as well as centra and a femur are not in K.U. Leuven but the latter two are housed in the MHNA (Gand et al. 2012). Other mandibular remains (PLV 1964 partim) of similar size and morphology are part of the re-discovered material and may constitute the missing parts of the original fragment; we describe these remains below. PLV 1964 consists of a dentary fragment and a partial splenial. The dentary (Fig. S5 in ESM) is similar to that of the Cuers ichthyosaur and the specimen figured by Sauvage (1883: Pl. 8) in having a continuous dental groove that lies on the medial face of the dentary; the medial wall of the dental groove is reduced to a thin lamella, as in the Cuers ichthyosaur and the specimen figured by Sauvage. The dental groove in PLV 1954 appears however much deeper than that of the Cuers ichthyosaur. A shallow but continuous fossa dentalis is present. As in the Cuers material, there is no evidence for the presence of a symphysis, hinting at an unusual mandible morphology for an ichthyosaur; more complete remains are however needed to unambiguously assess the mandible shape of the shastasaurid-like ichthyosaurs of the French Rhaetian. Yet, an extremely shortened mandibular symphysis has been described the shastasaurid *Guanlingsaurus liangae* (see Sander et al. 2011). The partial splenial is 335mm-long and is J-shaped, with a thickened ventral portion.

**Centra (PLV 1949 partim, PLV 10bis)** Two centra from Pellat Collection in K.U. Leuven match the measurements and descriptions of Sauvage (1883); PLV 1949 partim and PLV 10bis. The morphology of the centra, including the peculiar floor of foramen magnum is similar to that of the Cuers ichthyosaur and the remains attributed to *I. rheticus*.

**Rib (PLV 1957)** A partial rib from the Pellat Collection in the K.U. Leuven possesses two grooves giving the rib a number 8-shaped cross-section, as in the Cuers material.

**Affinities** Bardet & Cuny (1993) regarded *Ichthyosaurus carinatus* as nomen dubium with possible shastasaurid affinities, but each remain should be analyzed individually. Our analysis indicates these remains closely resemble the material from Cuers and Autun are therefore regarded as belonging to shastasaurid-like ichthyosaurs.

### **Systematic palaeontology**

Amniota Heckel 1866

Ichthyosauria Blainville 1835

Merriamosauria Motani 1999

Shastasauridae Merriam 1902

Aff. Shastasauridae

Referred specimens. MHNTV PAL-2/2010 and MHNTV PAL-1\_10/2012 (incomplete skeleton comprising partial rostrum, centra, and rib fragments from the Rhaetian of Cuers); PLV 10bis (centrum); PLV 1942 (scapula); PLV 1948 (centrum); PLV 1949 partim (centrum); PLV 1961 (centrum); PLV 1962 (epipodial); PLV 1963 (femur); PLV 1964 partim (rostrum). All PLV material are from the Rhaetian of Autun area.

Ichthyosauria indet.

Referred specimens. PLV 1939 (neural arch, holotype of *R. pellati*); PLV 1940 (ilium); PLV 1949 partim (rib); PLV 1957 (rib). All remains are from the Rhaetian of Autun area.

Plesiosauria Blainville 1835

Plesiosauria indet.

Referred specimens. PLV 1938 (propodial from the Rhaetian of the Autun area).

Amniota indet.

Referred specimens. PLV 1934 (possible surangular); PLV 1941 (possible mandible fragment); PLV 1943 (possible coracoid); PLV 1950 (possible mandible fragment); PLV 1951 (rib or gastralium); PLV 1952 (rib or gastralium); PLV 1959 (possible mandible fragment). All remains are from the Rhaetian of Autun area.

### **Species inquirenda**

*Plesiosaurus bibractensis*: PLV 1936 (vertebra); PLV 1948 (vertebra); PLV 1949 partim (vertebra); PLV 1953 (two vertebra); PLV 1954 (propodial). All remains are from the Rhaetian of Autun area.

*Plesiosaurus costatus*: PLV 1935 (vertebra); PLV 1955 (vertebra).

*Actiosaurus gaudryi* (PLV 1937, PLV 1944), two propodials resembling those of choristoderes (e.g. Storrs and Gower 1993).

## **Discussion**

Several lines of evidence presented in the comparative descriptions above indicate that the Cuers and Autun localities contain an ichthyosaur assemblage dominated by large shastasaurid-like forms. Discrepancies in sizes (e.g. the small femur PLV 1963, the moderately-sized scapula PLV 1942 and the very large ilium PLV 1940 and the centra PLV 1949 partim and PLV 10bis) indicate the presence of multiple individuals in Autun, and possibly distinct taxa. Although rare in Europe (Callaway and Massare 1989), the presence of shastasaurid-like ichthyosaurs in northwestern Tethys is not surprising from a biogeographic point of view, as this group was one of the first ichthyosaur clades to attain a very broad biogeographic range, colonizing both Tethys and Panthalassa (Callaway and Massare 1989; Sander 1997; Motani et al. 1999; Ji et al. 2010; Bardet et al. 2014). However, shastasaurids and shastasaurid-like ichthyosaurs (depending on taxonomic opinions) were hitherto restricted to the Anisian–middle Norian interval (Callaway and Massare 1989; McGowan and Motani 2003; Nicholls and Manabe 2004; Ji et al. 2010). The specimens from Cuers and Autun therefore represent the youngest record of that group and morphotype and imply a substantial range extension to the latest stage of the Triassic. Interestingly, Storrs (1994) reported the presence of very large centra, matching those of *Shonisaurus sikanniensis*, in Rhaetian strata of England. Further sampling may thus reveal additional occurrences of shastasaurid-like forms in latest Triassic strata. Rather than representing a genuine biological signal, the supposed Norian demise of shastasaurids was thus at least partially biased by a decrease of the quality of the fossil record. Although the record of Rhaetian ichthyosaurs is still too poorly sampled, our new data unambiguously indicate this group reached the end of the Triassic, dominating the French Rhaetian marine ecosystems. Combined with the recent discovery of a possible shastasaurid-like ichthyosaur in the lowermost Jurassic of Wales (Martin et al. In Press), our new data suggest that the extinction of the peculiar, gigantic shastasaurid-like ichthyosaurs forms a new

facet of the Triassic-Jurassic mass extinction, which was probably not an instantaneous catastrophic event like often postulated for the K-Pg extinction.

An equally unexpected feature of Cuers and Autun assemblages is the absence of remains compatible with neoichthyosaurians, giving these assemblages a typically ‘Triassic’ aspect. Small remains appear generally rare in Autun, possibly because of a depositional bias; this may alter the fossil record towards large taxa. Yet, we do not expect the lack of neoichthyosaurians to be due to this bias, as early neoichthyosaurians are generally large forms (e.g. *Leptonectes*, *Temnodontosaurus* and some specimens of *Ichthyosaurus*: McGowan 1989; Godefroit 1993; McGowan 1996a; Maisch et al. 2008; Martin et al. 2012). By contrast, the earliest Jurassic of Western Europe contains an extremely rich record of neoichthyosaurians from distinct lineages (e.g. McGowan 1974b, a; Maisch 1999). Neoichthyosauria thus probably arose elsewhere (its sister taxa are from the Norian of British Columbia: McGowan 1995, 1996b; Motani 1999) and massively colonized Western Europe during or after the end-Triassic events. From a global point of view, the current data indicates that both the disappearance of a significant part of the Late Triassic ichthyosaur diversity and disparity (carried by shastasaurid-like forms; Thorne et al. 2011) and the rapid radiation of Neoichthyosauria (Fischer et al. 2013) are restricted to the Rhaetian stage, which is about 7.2 Ma in duration (Gradstein et al. 2012) and form a rather short-lived turnover that profoundly affected the evolutionary history of ichthyosaurs.

Other marine reptile clades, placodonts and thalattosaurs (Müller 2007; Kelley et al. 2014), went totally extinct during the Rhaetian; numerous invertebrate groups were also affected (e.g. Hallam and Wignall 1997; Wignall and Bond 2008; Smith et al. 2014). But other groups such as plesiosaurs and neoichthyosaurians radiated immediately after (Benson et al. 2012; Fischer et al. 2013), implying a Rhaetian or older divergence of lineages. Under this revised scheme, the Rhaetian and the Triassic–Jurassic boundary therefore concentrate a massive faunal turnover for marine reptiles. Severe environmental changes have also been reported in the same interval, notably a meteorite impact (Olsen et al. 2002; Smit et al. 2014) and flood volcanism (Schoene et al. 2010; Whiteside et al. 2010). However, precise stratigraphic correlation in between all these biotic events and between the biotic and abiotic events is still wanting (see reviews of Hesselbo et al. 2002; Deenen et al. 2010; Van de Schootbrugge et al. 2013). On the other hand, close analyses reveal that many groups, especially among invertebrates and microvertebrates, have a rather diffuse, non-catastrophic Late Triassic turnover characterized by elevated extinction rates during the entire Norian–Rhaetian interval (Cuny 1995; Tanner et al. 2004; Bambach 2006; Mander et al. 2008). While

our data modifies our understanding of the Late Triassic history of ichthyosaurs, it also leave an open question: is the entire extinction of shastasaurid-like forms a severe event restricted to the Triassic-Jurassic boundary or did it happen as a series of minor extinctions from the Norian to the earliest Jurassic? What appears currently clear is that this extinction and its context are more complex than previously postulated and that the final demise of shastasaurid-like ichthyosaurs may likely be a supplementary facet of the end-Triassic mass extinction.

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## ELECTRONIC SUPPLEMENTARY MATERIAL

### Research history of the material from Autun

The Pellat collection refers to Edmont Pellat (°July 19th 1832 – †July 10th 1907), a celebrated French amateur paleontologist who gathered his enormous collection of fossils during numerous travels throughout France and Algeria during his career. Having frequent contacts with scientists, a large number of his specimens were chosen as type specimens for vertebrate and invertebrate taxa. Pellat amassed a collection of Rhaetian vertebrates gathered by quarrymen from the Autun area (Gand et al. 2012). Sauvage (1876, 1883) established five taxa based on this material: *Ichthyosaurus rheticus*, *Ichthyosaurus carinatus*, *Rachitrema pellati*, *Actiosaurus gaudryi*, and *Plesiosaurus bibractensis*. These taxa were variously considered as ichthyosaurs, plesiosaurs, theropods, and therapsids (Huene 1902; Sauvage 1903; McGowan and Motani 2003).

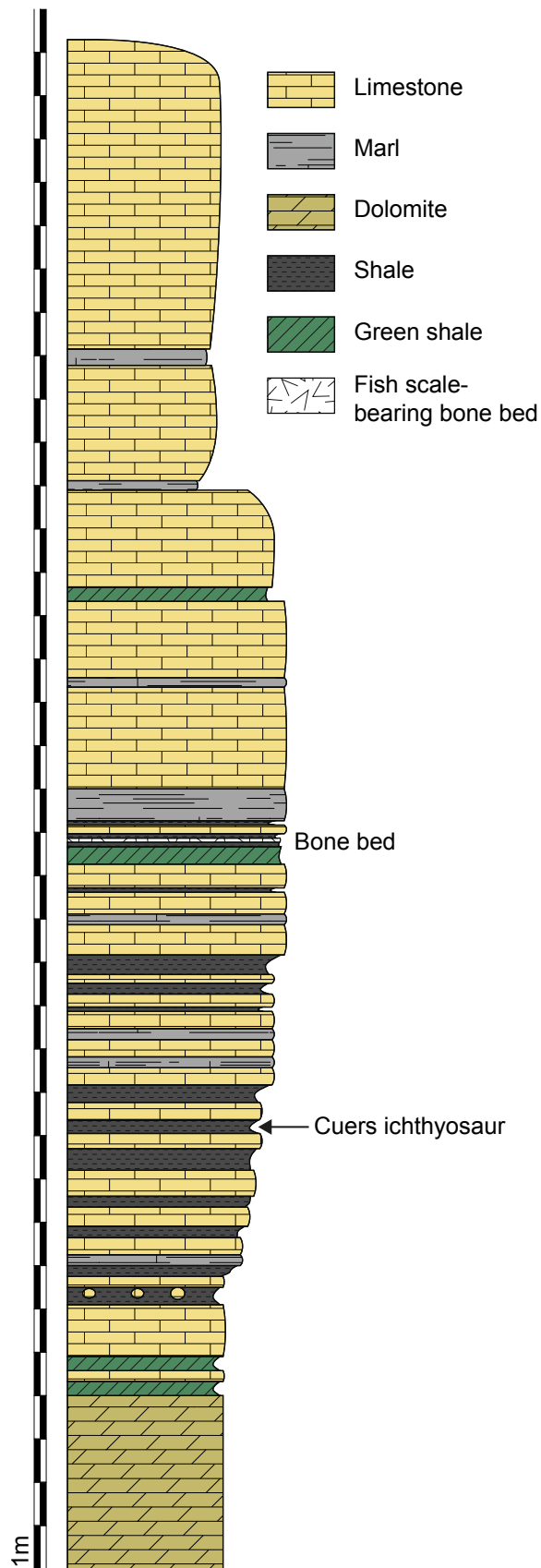
By intermittences of the ‘comptoir géologique les fils d’ E. Deyrolles’ (Paris), the Pellat collection was, after his death, sold to Henri de Dorlodot (°August 15<sup>th</sup>, 1855 – †January 4<sup>th</sup>, 1929), professor in geology and paleontology at the K.U. Leuven, for a sum of 41,417 francs. At first, the name of the buyer was kept secret, as requested by the family. The sale and more importantly the possibility that the collection left France created a lot of fuzz (Burnotte 1985). But according to several documents, the K.U. Leuven was preferred by E. Pellat himself and his family (see Burnotte 1985 for a detailed account).

Some years before, in 1904, a part of the collection of the French geologist Eugène Dumortier (1801-1876) arrived at the K.U. Leuven. The precise details about the sale were not recovered, but the university archives note the intermediary of Adolphe Piret, head of the ‘comptoir belge de minéralogie et de paléontologie’ at Tournai (Belgium) (Burnotte 1985). A substantial part of the Dumortier collection, containing vertebrates and invertebrates fossils, was donated to the Université de Lyon, France. Sauvage’s types from the Pellat and Dumortier went to the fossil vertebrate collections of K.U. Leuven. For more than a century, these specimens remained in the K.U. Leuven collections, surviving both the bombing of Leuven in the 1st and 2nd world wars, and two consecutive relocations (late 60ies and 2005). In the mean time, these specimens and their associated taxa disappeared from the literature. It was by accident that S.G. and V.F. relocated the specimens in 2012.

**Table S1** Tooth implantation modes of shastasaurid-like ichthyosaurs. Edentulous refers to a complete absence of alveoli, dental groove, and bony fixation. The taxonomy of *Shastasaurus*

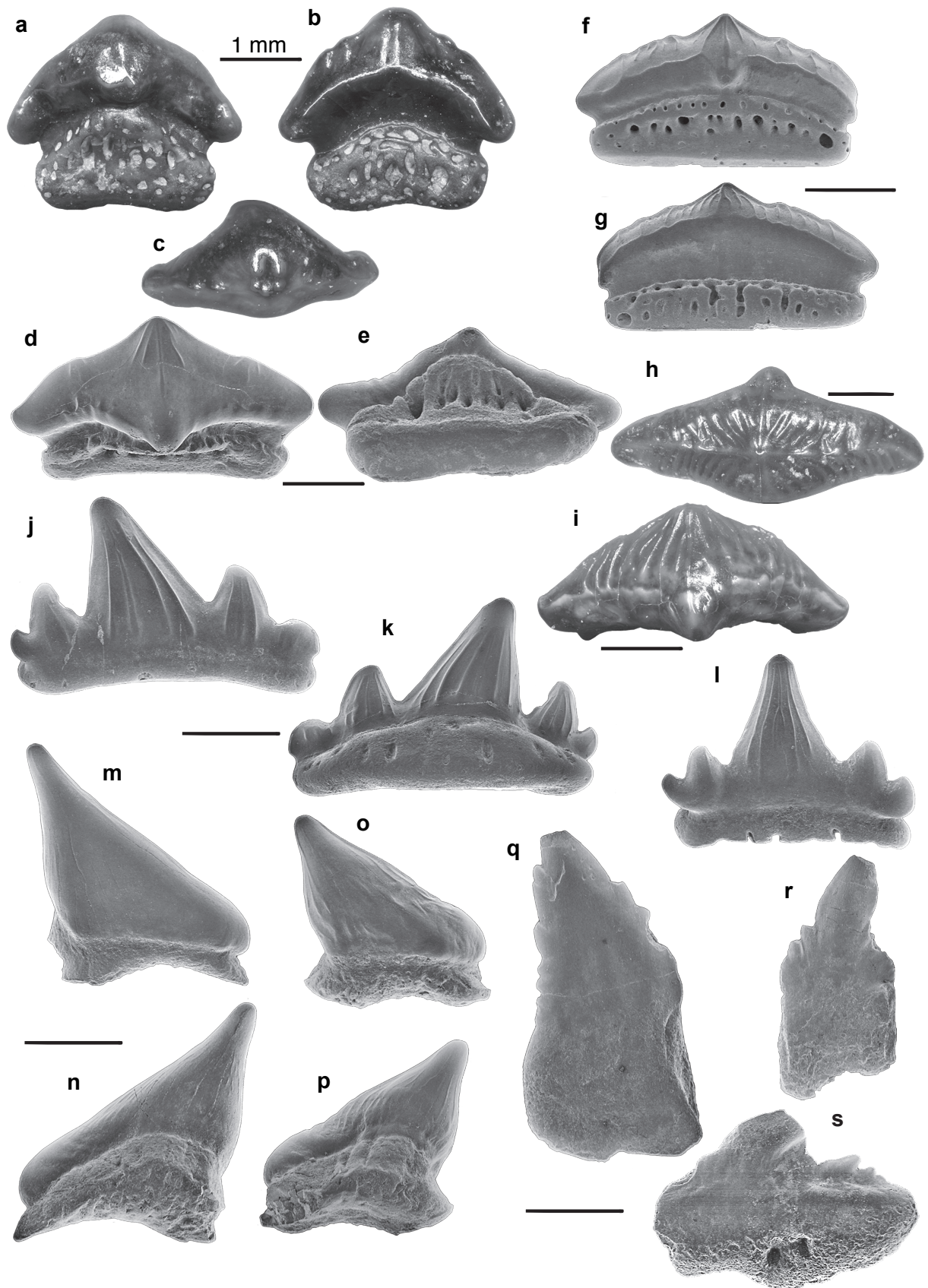
follows McGowan 1994. The asterisk (\*) indicates that specimen was firstly described as *Shastasaurus altispinus* by Callaway & Massare (1989b), but referred to *Shonisaurus* sp. by Motani (1999).

Taxon or specimen	Tooth implantation	Reference
ROM 44296	subthecodont?	McGowan 1997
<i>Besanosaurus leptorhynchus</i>	thecodont	Dal Sasso and Pinna 1996
<i>Shastasaurus pacificus</i>	aulacodont	Motani 1997; Maisch and Matzke 1998
<i>Guanlingsaurus liangae</i>	edentulous	Sander et al. 2011
<i>Shastasaurus sikanniensis</i>	edentulous	Nicholls and Manabe 2004; Sander et al. 2011
<i>Shonisaurus popularis</i>	thecodont	Camp 1980; McGowan 1997; Motani 1997; McGowan and Motani 1999
<i>Shonisaurus popularis</i>	thecodont in juveniles, edentulous in adults	Nicholls and Manabe 2004
<i>Shonisaurus</i> sp. (UCMP 27141)*	thecodont	Callaway and Massare 1989a
<i>Himalayasaurus tibetensis</i>	? (ridges)	Motani 1997; Motani et al. 1999
" <i>Callawayia</i> " <i>neoscapularis</i>	aulacodont	McGowan 1994; Motani 1997
" <i>Callawayia</i> " <i>neoscapularis</i>	subthecodont	Nicholls and Manabe 2001
<i>Guizhouichthyosaurus tangae</i>	thecodont	Maisch et al. 2006



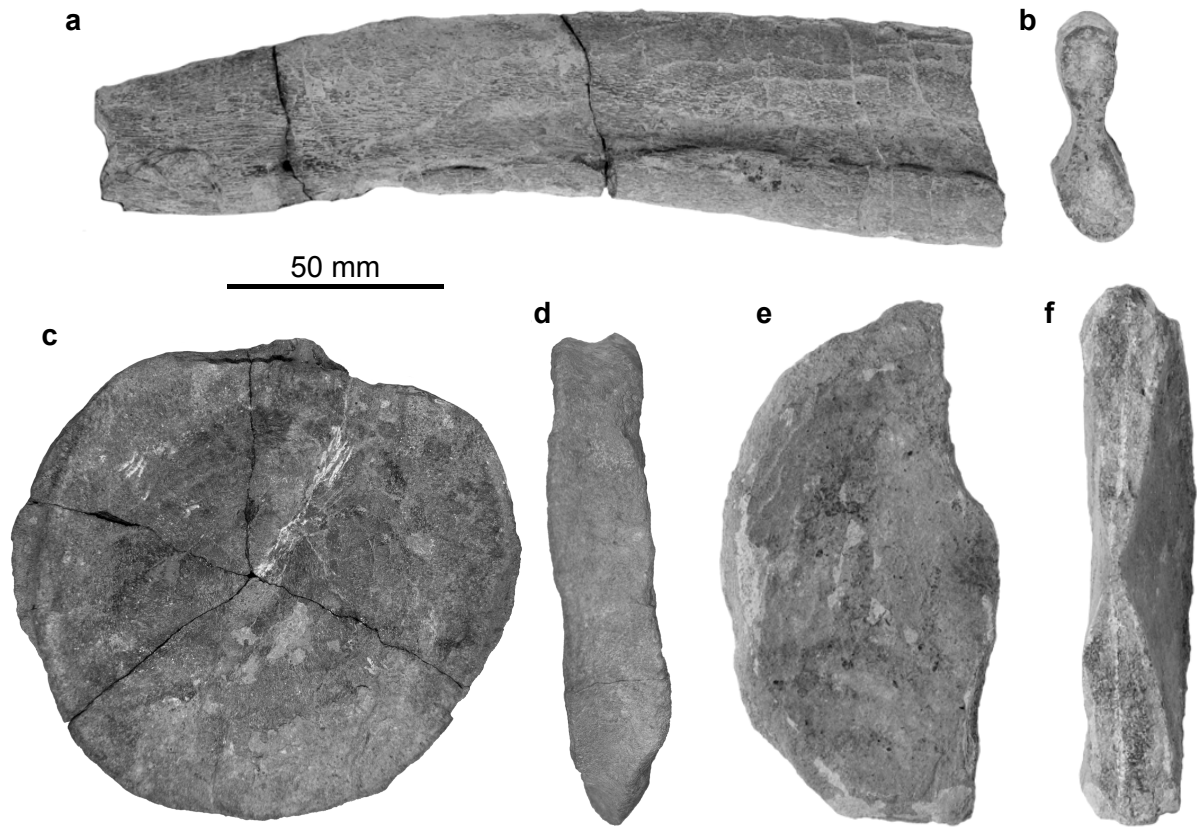
**Fig. S1** Stratigraphic log of the discovery site of the Cuers ichthyosaur, in Saint-Laurens, Var, France, surveyed by X.V.





**Fig. S2** Stratigraphically relevant elasmobranchs from the Saint-Laurens site. **a-i**, *Lissodus minimus*; **a-c**, anterior tooth, UM-CUE 3; **a**, labial view; **b**, lingual view; **c**, occlusal view; **d-**

**e**, anterolateral tooth, UM-CUE 4; **d**, labial view; **e**, basal view; **f-g**, anterolateral tooth, UM-CUE 5; **f**, labial view; **g**, lingual view; **h**, lateral tooth, UM-CUE 6, occlusal view; **i**, lateral tooth, UM-CUE 7, labial view; **j-l**, *Rhomphaiodon nicolensis*; **j-k**, upper antero-lateral tooth, UM-CUE 8; **j**, labial view; **k**, lingual view; **l**, lower lateral tooth, UM-CUE 9, labial view; **m-p**, *Pseudocetorhinus pickfordi*; **m-n**, antero-lateral tooth, UM-CUE 10; **m**, labial view; **n**, lingual view; **o-p**, more lateral tooth, UM-CUE 11; **o**, labial view; **p**, lingual view; **q-s**, *Pseudodalatias barnstonensis*; **q**, lower anterior tooth, UM-CUE 12, labial view; **r**, lower lateral tooth, UM-CUE 13, lingual view; **s**, very lateral tooth, UM-CUE 14, lingual view. Scale bars = 1 mm.

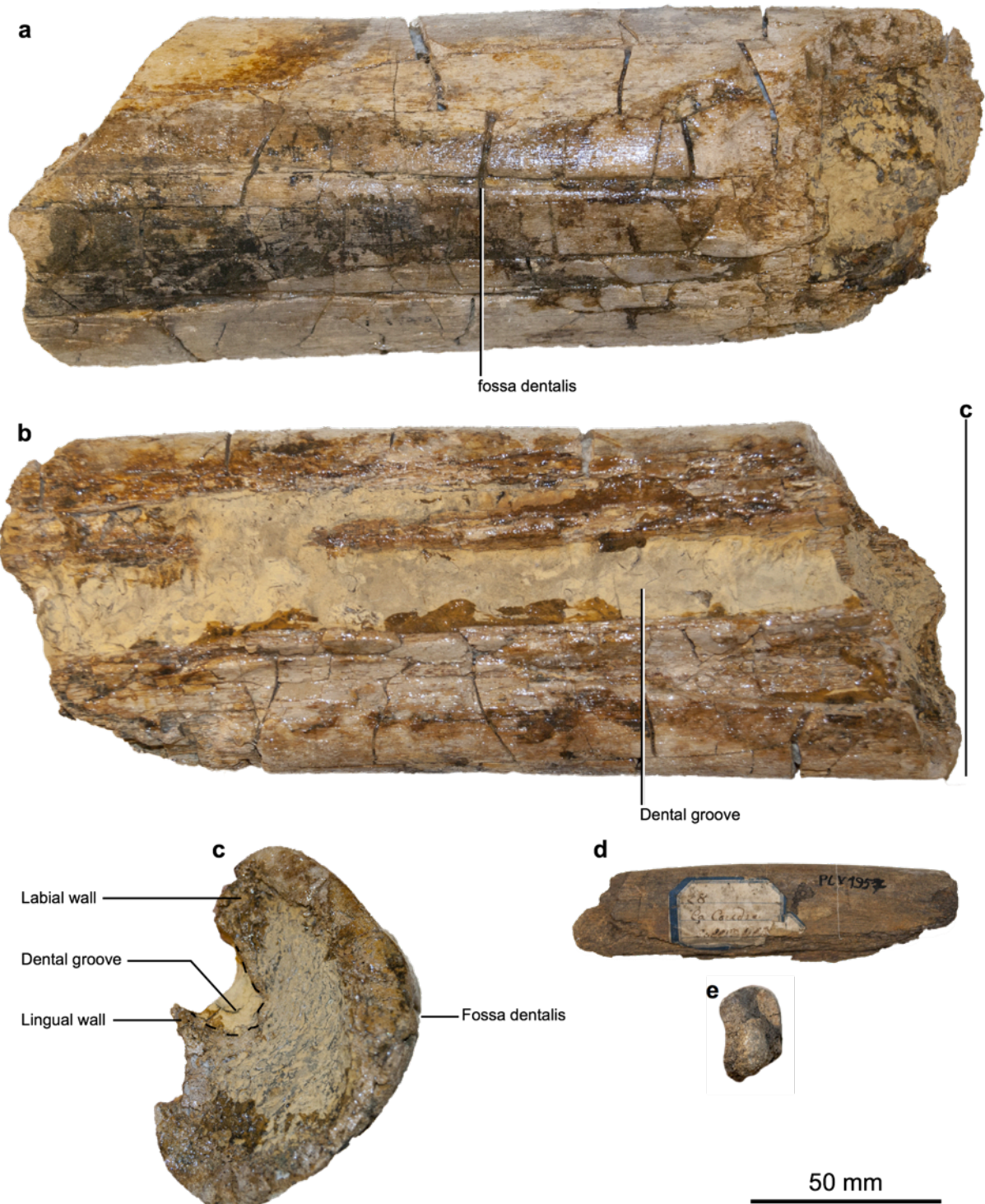


**Fig. S3** Axial skeleton remains from the Cuers ichthyosaur. **a**, distal end of a rib (MHNTV PAL-2/2010). **b**, cross-section of the proximal part of **a**; note the conspicuous ‘8’-shaped cross-section. **c**, centrum (MHNTV PAL-1\_10/2012) in anterior view. **d**, centrum (MHNTV PAL-1\_10/2012) in lateral view. **e**, centrum (MHNTV PAL-2/2010) in anterior view. **f**, centrum (MHNTV PAL-2/2010) in medial view.



**Fig. S4** Other remains from the *Rachitrema pellati* type series. **a**, PLV 1950 possible posterior of a mandible in medial view, that connects to PLV 1959 (**b**), a indeterminate bone regarded by Sauvage as belonging to *Ichthyosaurus rheticus*. **c-d**, PLV 1943, a possible ichthyosaur coracoid severely weathered in **c**, medial; **d**, anterior views. **e-f**, PLV 1941, a fragmentary bone similar to but larger than PLV 1950 (**a**), in **e**, medial; **f**, anterior; **g**, lateral views. **h-i**, PLV 1938, a partial sauropterygian propodial in **h**, capitular; **i**, anterior views. **j-k**, PLV 1934, probable posterior part of an ichthyosaur surangular in **j**, medial; **k**, lateral views. **l-l'**, PLV 1951, a probable ichthyosaur rib or gastralia of very large size. **m**, PLV 1952, a probable ichthyosaur rib or gastralia.





**Fig. S5** Remains compatible with the series of *Ichthyosaurus carinatus*. **a-c** mandible fragment in **a**, lateral; **b**, medial; **c**, posterior views. Note the lateral fossa dentalis and medial dental groove. A similar condition is found in the original material of Sauvage (1883) and in the Cuers ichthyosaur. **d**, **e**, rib fragment labeled as *Ichthyosaurus carinatus*, in **d**, lateral view; **e**, cross-section.

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