The first definite record of a Valanginian ichthyosaur and its implications on the evolution of post-Liassic Ichthyosauria

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ABSTRACT

A complete ichthyosaur rostrum, with 124 associated teeth, was recently discovered in Laux-Montaux locality, department of Drôme, southeastern France. The associated belemnites and ammonites indicate a late Valanginian age (*Neocomites peregrinus* Zone, *Olcostephanus nicklesi* Subzone) for this fossil, which consequently represents the first diagnostic ichthyosaur ever reported from Valanginian strata. This specimen also represents the first occurrence of *Aegirosaurus* outside the Tithonian (Upper Jurassic) lithographic limestones of Bavaria (southern Germany). Tooth morphology and wear pattern suggest that *Aegirosaurus* belonged to the "Pierce II/ Generalist" feeding guild, which was hitherto not represented in post-Liassic ichthyosaurs. Most Late Jurassic ichthyosaurs actually crossed the Jurassic-Cretaceous boundary.

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Ichthyosauria; *Aegirosaurus*; Valanginian; Southeastern France; Vocontian Basin; Feeding guilds; Jurassic-Cretaceous extinction.

1. Introduction

Ichthyosaurs were one of the most successful groups of Mesozoic marine reptiles, with a range that extends from the Olenekian (Early Triassic; Sander, 2000; Motani, 2005) to the end of the Cenomanian (early Late Cretaceous; Bardet, 1992; 1994; 1995). However, this extensive stratigraphic record is interrupted by numerous gaps, one of the longest occurring during the Early Cretaceous, from the late Berriasian to the Barremian (about 13 my). Only indeterminate ichthyosaur remains have been discovered so far in sediments dating from this period (*e.g.* Bardet, 1994). Several genera and species have been named from the Hauterivian of the Ul'yanovsk Region in Russia (Ochev and Efimov, 1985; Efimov, 1997), but they have recently been considered as nomina dubia or subjective junior synonyms (McGowan and Motani, 2003). The latest revision of Russian material by Storrs et al. (2000) also mentioned two "Neocomian" Ichthyosauria indet. The poor record of Early Cretaceous ichthyosaurs strongly hampers our understanding of the evolution of post-Liassic ichthyosaurs, and gave support to the widely accepted idea that a major turnover in ichthyosaur history occurred between the Middle Jurassic and the Early Cretaceous (Sander, 2000; Lingham-Soliar, 2003).

In this paper, we describe the first diagnostic and well-dated ichthyosaur from that Lower Cretaceous gap. It was discovered by one of us (A.C.) in Upper Valanginian marls of the Northern Subalpine Chains, 800m East to the Laux-Montaux locality, department of Drôme, southeastern France (fig. 1). Other "Neocomian" marine reptiles from southeastern France include early Valanginian and Hauterivian metriorhynchid crocodyliforms (respectively *Enaliosuchus macrospondylus* (Hua et al., 2000) and *Dakosaurus* sp. (Buffetaut, 1982)), late Valanginian teleosaurid crocodyliform (*Steneosaurus* sp. (Cornée and Buffetaut, 1979)), and an Hauterivian plesiosauroid (Plesiosauria indet. aff. Elasmosauridae (Fournier et al., 1982)).

Institutional abbreviations. BSPHGM: Bayerische Staatssammlung für Paläontologie und historische Geologie Museum, Munich, Germany; GPIT: Geologisch-Paläontologisches Institut und Museum, Universität Tübingen, Germany; MOZ: Museo Professor J. Olsacher, Dirección Provincial de Mineriá, Zapala, Neuquén, Argentina; RGHP: Réserve naturelle géologique de Haute-Provence, Digne-les-Bains, France; SMC: Sedgwick Museum, Cambridge, England; SM: Schwegler Museum, Langenaltheim, Germany; UWGM: University of Wyoming Geological Museum, Laramie, U.S.A.
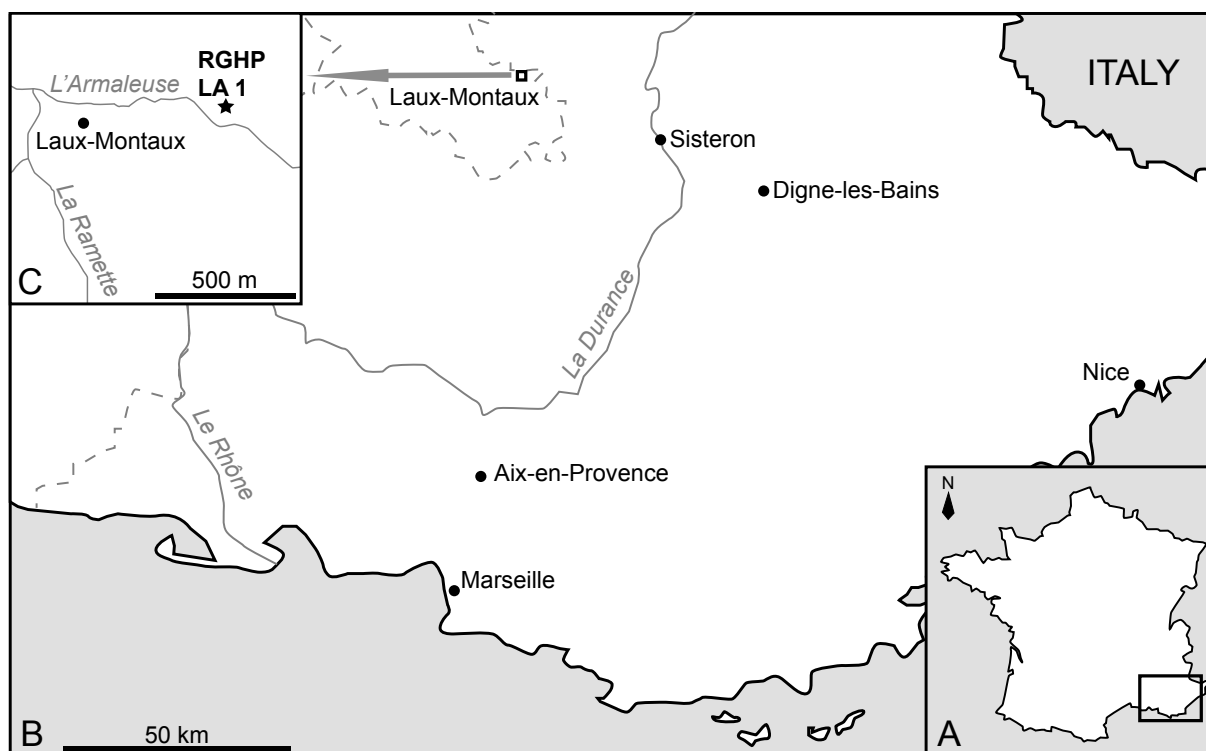
Fig. 1: A, France map; B, southeastern France map; C, local map of Laux-Montaux with the position of RGHP LA 1 marked by a star. The gray lines represent major rivers and the dashed line represents the boundary between the "Rhône-Alpes" and "Provence-Alpes-Côte d'Azur" regions. The empty square represents the area figured in the next map.

2. Geological setting

The specimen was discovered close to the top of a small hill formed by greyish to yellowish marls, interrupted periodically by small (≈10cm) limestone or marly limestone beds (fig. 2). Two large slumped units have been recognized near the top of the sequence. The whole sequence was deposited in the southern part of the Vocontian Basin, a highly subsident Mesozoic basin at the northwestern border of Tethys (Floquet et al., 2003; Danelian et al., 2006). The biostratigraphy of Valanginian sediments in southeastern France has been intensively studied since 1993, using ammonites (Atrops and Reboulet, 1993; 1995; Reboulet, 1996; Reboulet et al., 2009) and belemnites (Clément, 1999; Jansen and Clément, 2002; Jansen, 2009). Ammonite zonation follows Reboulet et al., 2009. Belemnites gards are much more abundant than ammonites in Valanginian strata from this area and are therefore a very useful biostratigraphic tool; ammonites were used to refine the biostratigraphy near the ichthyosaur remains. The following belemnites have been found along the path leading to the hill where the ichthyosaur was discovered: *Duvalia lata constricata* Uhlig, 1902, *Berriasibelus exstinctorius* (Raspail, 1829), *Conobelus conicus* (de Blainville, 1827) and *Castellanibelus orbignyanus* (Duval-Jouve, 1841). This association is typical for the lower Valanginian (*Busnardoites campylotoxus* Zone; Janssen and Clément, 2002). The occurrence of *Duvalia emericii* (Raspail, 1829), present along the upper section of the path to the hill, with the absence of the aforementioned species characterizes the base of the upper Valanginian (*Saynoceras verrucosum* Zone; Janssen and Clément, 2002). *Duvalia binervia*

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(Raspail, 1829) is particularly abundant on the hill, whereas the aforementioned species are absent. This indicates a late Valanginian age for that series (Janssen and Clément, 2002; Janssen, 2009). Near the top of the hill, where the ichthyosaur remains were discovered, the association of *Duvalia binervia* (Raspail, 1829), *Pseudobelus brevis* Paquier, 1900, *Hibolithes* gr. *subfusiformis* Raspail, 1829 and *Adiakritobelus* sp. is typical for the uppermost part of the Valanginian (Janssen, 2009). Ammonites have been collected just below the ichthyosaur remains, at the top and above the last slumped sequence (fig. 2). The presence of *Bochianites neocomiensis* (d'Orbigny, 1842), *Himantoceras acuticostatum* Thieuloy, 1964, *Neocomites neocomiensis* (d'Orbigny, 1841), *Neolissoceras grasianum*, (d'Orbigny, 1841), *Olcostephanus nicklesi* Wiedmann & Dieni, 1968, *Olcostephanus densicostatus* (Wegener, 1909), and *Phyllopachyceras* sp. permits to refine the stratigraphic position of the specimen to the *Olcostephanus nicklesi* Subzone, *Neocomites peregrinus* Zone, upper Valanginian.
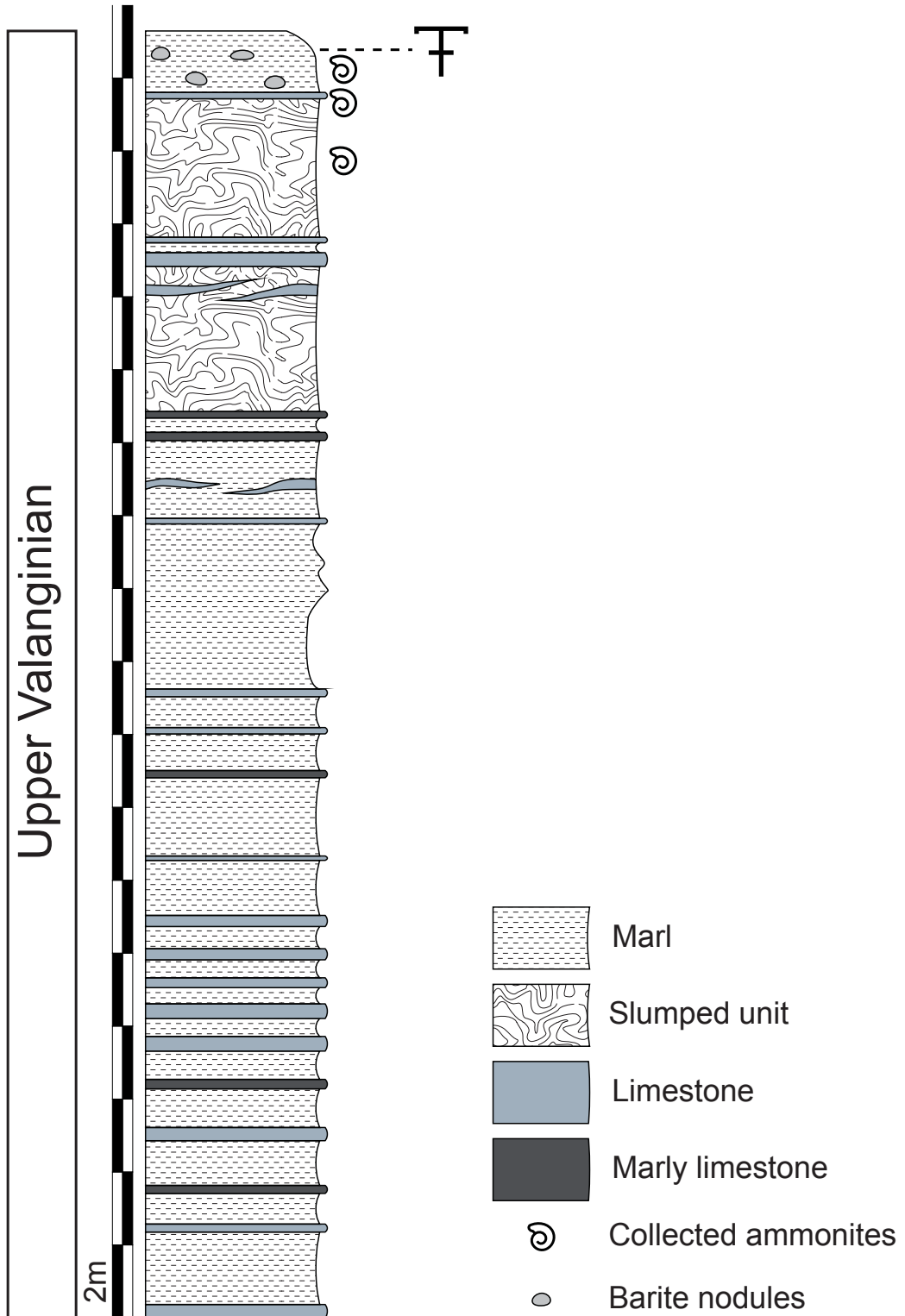
Fig. 2: Stratigraphic log of the hill where RGHP LA 1 has been found, northeast of Laux-Montaux.

3. Systematic Palaeontology

Order: Ichthyosauria de Blainville, 1835

Thunnosauria Motani, 1999

Family: Ophthalmosauridae Baur, 1887

Genus: *Aegirosaurus* Bardet and Fernández, 2000

Type species. *Ichthyosaurus leptospondylus* Wagner, 1853a

Emended diagnosis. *Aegirosaurus* is characterized by the following potential autapomorphies within Ophthalmosauridae: small pointed teeth, densely packed (tooth density index 19) and strongly set in dental grooves; crown enamel smooth in juveniles and markedly ridged in adults; presence of a rugose, finely pitted surface on the apex of the teeth; puboischiatic complex without a foramen.

 Aegirosaurus is also characterized by the following combination of features: slender snout (snout depth ratio 0.047, the lowest of all ophthalmosaurids except *Platypterygius americanus*: 0.043 (McGowan, 1976)); reduced maxilla emerging well posteriorly to the nasal (character shared with *Maiaspondylus* (Maxwell and Caldwell, 2006a)); dorsal margin of external naris extends ventrally, giving it a kidney-shaped outline (shared with *Ophthalmosaurus* (Andrews, 1910)); humerus with three distal facets, the middle one, for intermedium, being the smallest (shared with *Brachypterygius extremus* and probably *Maiaspondylus* (McGowan, 1997; McGowan and Motani, 2003; Maxwell and Caldwell, 2006a)); six digits in the forefin, one of them being prexial (shared with some specimens of *Ophthalmosaurus* and *Brachypterygius* (McGowan and Motani, 2003)); polygonal and tightly packed phalanges (shared with *Caypullisaurus*, *Platypterygius* and *Maiaspondylus* (McGowan, 1972; Wade, 1990; Maxwell and Caldwell, 2006a; Fernández, 2007; pers. obs.); four digits in the hindfin (shared with *Undorosaurus* (Efimov, 1999; McGowan and Motani, 2003)).

Geographic distribution. Borscheim, Langenaltheim, Apfeltal, Bavaria, Germany (*locus typicus*); Laux-Montaux, department of Drôme, France.

Stratigraphic distribution. Basal Tithonian (stratum typicum) – late Valanginian.

Aegirosaurus sp.

(Figs. 3, 4)

Referred specimen. RGHP LA 1, the anterior part of a rostrum from upper Valanginian marls of Laux-Montaux, department of Drôme, France.

Description of the new referred specimen. RGHP LA 1 is the anterior part of a well-preserved snout, with 124 associated teeth or tooth fragments (fig. 3). The external bone texture is visible on the whole surface of the specimen. All the bones are articulated and have retained their 3-D morphology. Slight shear occurs between the left and right parts of the rostrum, and an intense deformation is seen on its proximal extremity, where the left dentary and the left splenial are bent laterally (fig. 3). The rostrum and mandible are nearly perfectly hemispherical in cross-section.

Premaxilla. The anterior 2 or 3 cm of both premaxillae are missing. Posteriorly, the premaxillae are preserved up to 6 cm posterior to the emergence of the nasals. They are long, straight, very slender, but robustly built: the bone is thick and there is no trace of internal vacuities. The premaxillae slightly thickens posteriorly, gradually increasing its diameter from 2.3 cm at the anterior part of the rostrum to 5 cm at the level of the contact with the nasals, 33 cm more posteriorly. At this point, the dorsal surface of the rostrum looks slightly concave. Fossa praemaxillaris runs along the whole length of the premaxilla, about 1 cm above the dental groove. It is narrow, shallow and continuous groove and becomes segmented on the anterior part of the premaxilla, ending anteriorly as a series of foramina. The dental groove is deep and continuous, but slightly constricted between the functional teeth. A dental groove of this kind is common for post-Triassic ichthyosaurs, such as *Platypterygius* (Mazin, 1983; Bardet, 1989; Motani, 1997). On the anterior part of the premaxilla, the dental groove is oriented vertically; posteriorly, it is slightly oriented laterally. The labial wall of the dental groove is thick along its whole height, whereas the base of the lingual wall is thin and quickly thickens ventrally. The labial and lingual walls have the same height, like in *Ophthalmosaurus* (Bardet et al., 1997). The maxilla is not preserved, even in the posterior-most sections of the rostrum, indicating this bone emerges far posteriorly to the level of emergence of the nasal.

Nasal. The nasals are incomplete and broken off. The contact with the premaxilla begins approximately 36 cm posteriorly to the tip of the snout. The ventral surface of the nasal forms most of the internal dorsal surface of the rostrum, indicating a long overlapping area between the premaxilla and the nasal. Several narrow grooves ornament the ventral surface of the nasal, like in *Ichthyosaurus* (Sollas, 1916). Both nasals thicken medially near their suture.

Dentary. The anterior part of the dentaries is complete. As already mentioned, the posterior part (43 cm posteriorly to the tip) has been deformed and broken off. Fossa dentalis also ends anteriorly as a series of segments and foramina. An additional foramen is present on the left dentary, 3 mm ventrally to fossa dentalis and 12 mm posteriorly to the tip of the snout. The dental groove is also deep; its lingual wall thickens from its base to its top, whereas its labial wall remains thick along its whole height. Like in *Ophthalmosaurus*, the lingual wall is higher than the labial wall (Bardet et al., 1997). The posterior teeth are also oriented slightly more laterally than the anterior ones.

Splenial. The splenial is a long and slender bone with a quadrangular cross-section. Externally, the contact with the dentary begins 23 cm posteriorly to the tip of the snout. Therefore, the splenial emerges about 13 cm anteriorly to the nasal. In anterior or posterior view, the splenial contacts the dentary by a straight suture perpendicular to the curvature of the rostrum.

Teeth. One hundred and twenty-four complete or fragmentary teeth are preserved. Most are still well anchored and tightly packed in their dental groove. The height of the largest teeth ranges from 24 to 26 mm. Most are conical and straight, but the most posterior ones are slightly recurved. The crown is high and represents a bit less than half the height of the tooth (12 mm). The enamel bears numerous longitudinal striations. The apex is acute and pointed, which is unusual in post-Liassic ichthyosaurs. Teeth are round in cross-section below the apex, and become slightly oval above the root. The root is smooth, oval in cross-section, and slightly bulbous. The apices of many teeth, including all non-functional ones, are covered by a rugose

surface. This microtexture is not found on some functional teeth, including teeth with broken tip, indicating that it was probably worn out during food procurement (fig. 4). This peculiar feature has previously been reported only in some Liassic ichthyosaurs and crocodyliforms (Massare, 1987).
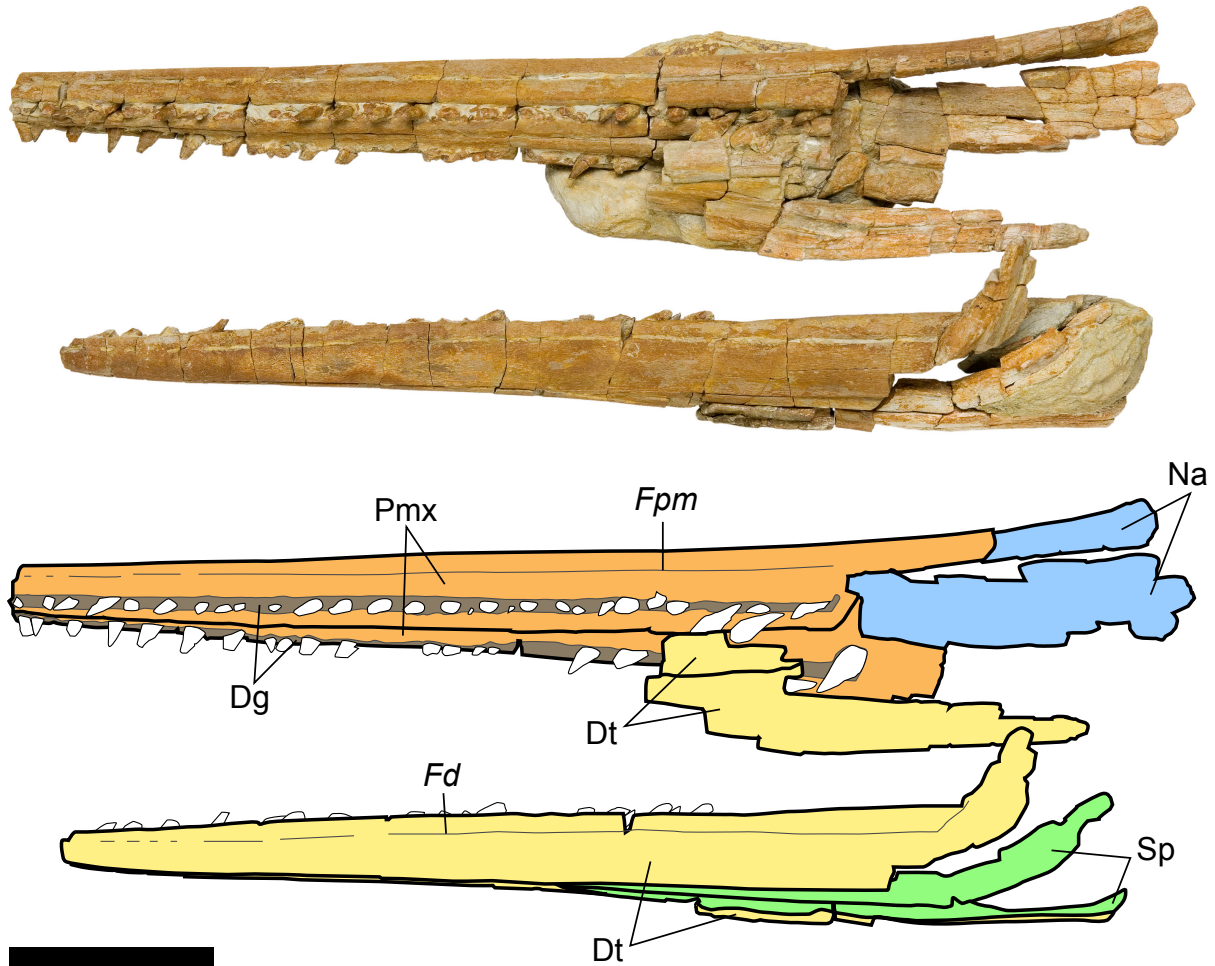
Fig. 3: *Aegirosaurus* sp. Photography and interpretation of RGHP LA 1 in left lateral view. Several teeth have been omitted in the interpretation for clarity. Dg: dental groove; Dt: dentary; Fd: fossa dentalis; Fpm: fossa praemaxillaris; Na: nasal; Pmx: premaxilla; Sp: splenial. Scale bar equals 100 mm.
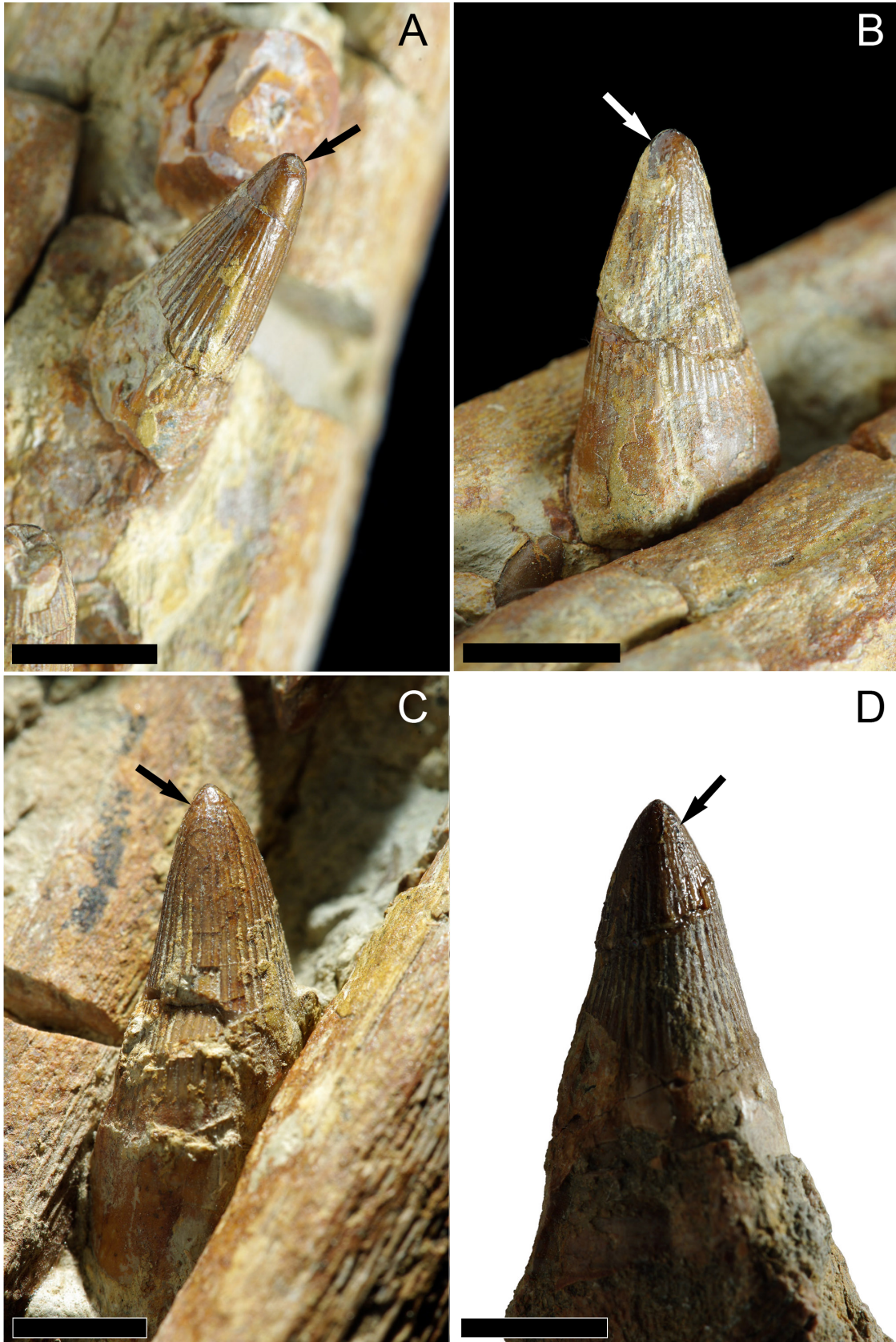
Fig. 4: *Aegirosaurus* sp. High-resolution photographs of selected teeth of RGHP LA 1. A, worn tooth with broken tip. The apex is nearly smooth. B, moderately worn tooth. The rugose surface on the apex is slightly smoothened. C, D, unworn functional teeth, showing the rugose surface of the apex. Scale bars equal 5 mm.

4. Discussion

4.1 Identification

Maturity. Criteria to establish the relative age of ichthyosaurs are mostly based on forefin morphology (Johnson, 1977). Some additional criteria have been proposed in the recent literature, including the relative size of sclerotic ring (Fernández et al., 2005) and the degree of fusion between the parasphenoid and the basisphenoid (Kear, 2005). However, all of these bones are missing in RGHP LA 1. The preserved part of the rostrum, including the anterior part of the nasals, measures 61 cm. This measurement represents a minimal value for the prenarial length, because the anterior end of the external nares, sets near the orbit in ichthyosaurs, is not preserved in this specimen. Table 1 compares the prenarial length and the total skull length in various post-Liassic ichthyosaurs. From these comparisons, the minimum skull length of RGHP LA 1 would range from 93 to 121 cm, suggesting that this specimen was probably a large adult individual. Adult post-Liassic ichthyosaurs for which cranial measurements are available have prenarial length ranging from 64 to 83 cm (table 1). RGHP LA 1 nearly falls in that range and is considered here as an osteologically mature ichthyosaur.

Table 1: Cranial measurements and ratios of some post-Liassic ichthyosaurs. The prenarial ratio is the prenarial length/mandible length. The ratio is then used to estimate minimal values of total skull length of RGPH LA 1. It has to be noted that the jaw length of *Brachypterygius* is slightly underestimated (Kirton, 1983) and that of *P. americanus* has been estimated by McGowan (1976), because the very tip of the snout is missing (Romer, 1968). The specimens used for *Aegirosaurus leptospondylus* are the two most complete specimens of the genus, but both are juveniles, as discussed in the text.

Species (specimen)	Total mandibular length (cm)	Prenarial length (cm)	Prenarial ratio	Estimation RGHP LA 1 (cm)	Reference
Chacaicosaurus cayi (MOZ 5803)	98	64	0.65	93.4	Fernández, 1994
Ophthalmosaurus icenicus (GPIT specimen)	98	64	0.65	93.4	Maisch and Matzke, 2000
Caypullisaurus bonapartei (MOZ 6139)	141	71	0.5	121.1	Fernández, 2007
*Aegirosaurus leptospondylus** (SM)	56.5	38	0.67	90.7	Bardet and Fernández, 2000
*Aegirosaurus leptospondylus** (BSPHGM)	31.4	16	0.51	119.7	Bardet and Fernández, 2000
Brachypterygius extremus (SMC J68516)	123	71	0.58	105.7	McGowan, 1976
Platypterygius americanus (UWGM 2421?)	130	74	0.57	107.2	McGowan, 1976

Identification. Because the stratigraphic position of RGHP LA 1 is intermediate between the well-known Late Jurassic and late Early Cretaceous forms, we decided to compare it to all post-Liassic taxa. Despite its incompleteness, RGHP LA 1 displays four diagnostic characters: the order of emergence of cranial bones from the tip to the back of the snout (splenial>>nasal>>maxilla), the slenderness of the snout, the tooth morphology, and the tooth density. Many Late Jurassic to Early Cretaceous taxa are characterized by a well-developed maxilla that extends anteriorly up to the level of emergence of the nasals, or even further anteriorly, like *Platypterygius americanus*, *P. bannovkensis*, *P. longmani*, and *Caypullisaurus* (Romer, 1968; McGowan, 1972; 1976; Arkhangel'skii, 1998; Sirotti and Papazzoni, 2002; Kear, 2005; Fernández, 2007). The slenderness of the rostrum does not match the robust jaws of *Brachypterygius* (McGowan, 1976), *Mollesaurus* (Fernández, 1999), and *P. hercynicus* (Kuhn, 1946; Kolb and Sander, 2009). The retention of small, yet robust, and pointed teeth at adult stage also differs from most post-Liassic taxa, which exhibit either toothlessness or a

reduced number of very small and delicate teeth (*Mollesaurus*, *Ophthalmosaurus*, *Caypullisaurus*, *Chacaicosaurus*; McGowan, 1976; Fernández, 1994; 1999; 2007; Buchy, 2010), or are characterized by medium-sized, recurved, robust teeth with an acute but rounded apex (*Undorosaurus*, *Brachypterygius*, *Platypterygius*; McGowan, 1972, 1976; Massare, 1987; Bardet, 1989; 1990; McGowan and Motani, 2003; pers. obs.). *Maiaspondylus lindoei* from the Albian of Canada differs from RGHP LA 1 in having smooth crowns and ridged, bulbous roots (Maxwell and Caldwell, 2006a). Only *Aegirosaurus leptospondylus* shares all these characters with RGHP LA 1 (Wagner, 1853b; Meyer, 1863; Fraas, 1891; Bardet and Fernández, 2000).

The tooth density index (TDI) is one of the ratios used by McGowan (1976) to differentiate post-Triassic ichthyosaurs. Although some of these ratios are probably influenced by ontogeny (Godefroit, 1994), the TDI seems particularly useful in identifying some post-Liassic ichthyosaurs. The TDI measures the number of premaxillary and dentary teeth over 10% of the jaw length, at the middle of the rostrum. Nineteen teeth have been counted over a distance of 9 cm in the posterior part of the dental grooves of RGHP LA 1 (near the level of emergence of nasals), giving a TDI of 19. This clearly differs from other taxa such as *P. americanus* (TDI 7) and *Brachypterygius* (TDI 12), but matches the TDI 18 measured on photographs of the neotype of *Aegirosaurus leptospondylus* published in Bardet and Fernandez (2000). According to McGowan's paper (1976), these are the highest TDI measured in ichthyosaurs, with the exception of some Liassic *Stenopterygius* specimens having a TDI of 21. Despite possible slight variations due to the state of preservation of the jaw, the TDI values calculated here are considered sufficiently segregated to be used as an additional clue to

refer RGHP LA 1 to *Aegirosaurus*. Given the scarcity of the material, we refrained to assign this specimen to the specific level, even if *Aegirosaurus* is currently a monotypic genus.

RGHP LA 1 is the only adult *Aegirosaurus* specimen currently in existence. Indeed, the two specimens described in detail by Bardet and Fernández (2000) are much smaller and are regarded as juveniles (the same can be said about the other specimens they briefly describe in the appendix of their paper). The only difference between these specimens and RGHP LA 1 is the enamel ornamentation of the crown: the smaller specimen (BSPHGM 1954 I 608: skull length 30 cm) has smooth crowns, the neotype ("SM", skull length 56 cm) has minute ridges, and RGHP LA 1 (≥90 cm-long skull) has well developed ridges in the crown enamel. A specimen referred to *Ichthyosaurus leptospondylus* by Meyer (1863, prenarial length over 25 cm) also exhibits ridged enamel. This could either reflect intrageneric variation or a possible ontogenetic series.

4.2 A new feeding guild for post-Liassic ichthyosaurs

Massare (1987) used various tooth characteristics, such as the relative size, the apex morphology, and the presence of cutting edges, to establish general feeding "guilds" among Mesozoic marine reptiles. According to this paper, most post-Liassic ichthyosaurs belong to the "Smash" guild. Members of that feeding guild include *Platypterygius*, *Brachypterygius*, *Ophthalmosaurus* (at least juveniles) and probably *Undorosaurus*, and are characterized by robust, conical, slightly recurved teeth, with an acute but rounded apex. The small pointed teeth of *Aegirosaurus* do not correspond to that morphotype, neither to any other feeding

guild described amongst Mesozoic marine reptiles. Indeed the teeth of *Aegirosaurus* appear much smaller than in any of the species studied by Massare (1987). The "relative tooth size" index was defined as the ratio "height of the largest crown / skull width" (distance between quadrates). Shell-crushing taxa have the lowest "relative tooth size" index (0.1) in Massare's paper. Even with such a low ratio, the skull width of RGHP LA 1 would measure only about 12 cm, which is unrealistically narrow for an ichthyosaur with a skull length close to 1 m. Consequently, the relative tooth size index was probably much lower than 0.1 in *Aegirosaurus*. Massare (1987) also defined the "tooth shape" index as the ratio "height / basal diameter" of the largest crown. The "tooth shape" index is about 1.7 in RGHP LA 1, similar to marine reptiles belonging to the "Pierce II" and "Crunch" guilds. The "Pierce II" guild includes marine vertebrates eating medium-sized fishes and tetrapods (such as the extant Orca *Orcinus orca*), and the "Crunch" guild includes some Jurassic ichthyosaurs and some marine crocodyliforms, characterized by blunt teeth that were best suited to crack shelled cephalopods or armoured fishes (Massare, 1987; 1997).

The presence of a rugose surface on the apex of unworn teeth in RGHP LA 1 was also reported in representatives of the "Crunch" guild. On the other hand, the general morphology of the crown, with a fairly pointed apex only slightly rounded by wear, more closely resembles representatives of the "Generalist" guild. Thus, the teeth of *Aegirosaurus* display characteristics that can be observed in three distinct predatory guilds ("Pierce II", "Crunch", and "Generalist"), but they are much smaller than in reported representative of these guilds. These teeth were probably too small to efficiently pierce and tear flesh from medium-sized to large preys (the "Pierce II"

guild) and far too pointed to crush shelled invertebrates (the "Crunch" guild). However, they seem well designed for impaling a wide range of small fleshy preys, such as fishes and soft cephalopods, resembling that of extant delphinine odontocetes, such as *Tursiops* or some species of *Lagenorhynchus*, which also have a generalist diet of cephalopods and fishes (Ridgway and Harrison, 1999; Lingham-Soliar, 2003). The long and slender snout also suggests a diet of small and rather soft preys. Furthermore, in a subsequent work, Massare (1997) merged the "Pierce II" and "Generalist" guilds into one ("Pierce II / General"), characterized by the following tooth morphology: "Pointed, somewhat slender, curved teeth of moderate length. Two carinae or fine longitudinal ridges are often present. Worn teeth have a rounded apex or the tip may be broken". Most of these characteristics can also be observed in RHGP LA 1. Although its teeth are much smaller than in other representatives of this guild, *Aegirosaurus* is therefore tentatively reported to this "Pierce II / General" guild. This guild was previously restricted to some pliosauroids, plesiosauroids, and thalattosuchians (Massare, 1997; Pierce et al., 2009). *Aegirosaurus* thus marks the colonization of this guild by Late Jurassic to Early Cretaceous ichthyosaurs, but in their "own way", probably feeding on much smaller preys than other representatives of that guild.
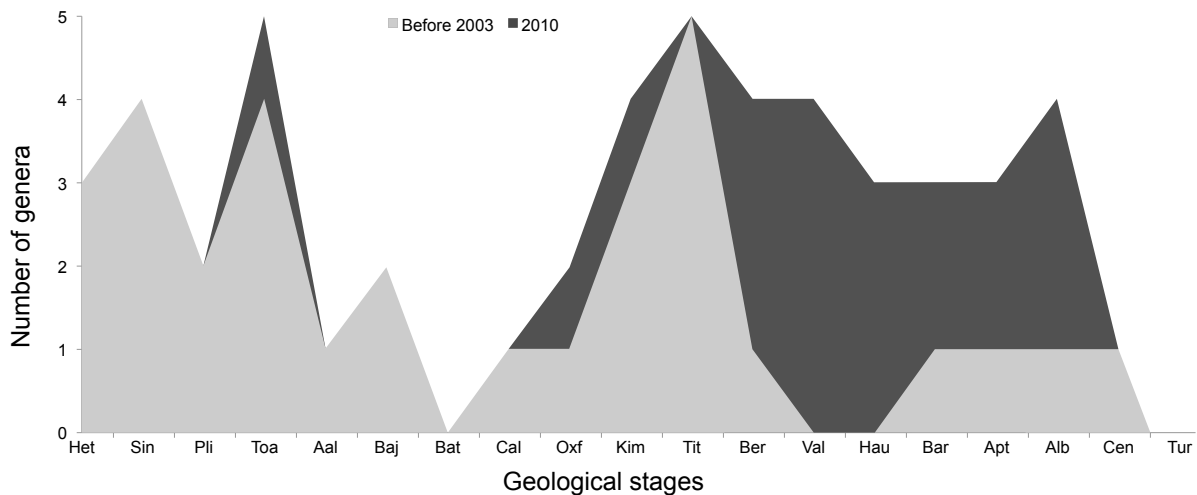
4.3 The biodiversity evolution of post-Liassic Ichthyosauria

Before 2003, no Late Jurassic ichthyosaur genus was known in Lower Cretaceous deposits, and the diversity of Cretaceous ichthyosaurs was very low (one genus: *Platypterygius*). According to these observations, Lingham-Soliar (2003) suggested that the strong decline of

ichthyosaurs during the Early Cretaceous was due to competition from newly evolved teleost fishes that occupied similar ecological niches. Indeed, the evolutionary radiation of teleost fishes started in the Middle Jurassic; because of more "aggressive" reproduction habits, they would have progressively driven ichthyosaurs to extinction by outcompeting them in their ecological niche of fast swimmers.

However, new data on the evolution of the biodiversity of post-Liassic ichthyosaurs do not support this hypothesis. McGowan and Motani (2003) examined isolated basioccipitals from the Albian Upper Greensands (England) and proposed that both *Ophthalmosaurus* and *Brachypterygius*, originally described from the Callovian to Tithonian of Europe, Argentina and North America and from the Kimmeridgian to Tithonian of Eurasia, respectively, were still present by Albian times. Moreover, *Caypullisaurus* was described both from the Tithonian (Fernández, 1997) and Berriasian (Fernández and Aguirre-Urreta, 2005; Fernández 2007) of the Neuquén Basin (Argentina). The discovery of RHGP LA 1 also considerably extends the stratigraphic and geographic range of *Aegirosaurus* from the Tithonian of Germany (Bardet and Fernández, 2000) to the late Valanginian of southeastern France. In the current state of our knowledge, only the very rare *Nannopterygius*, from the Kimmeridgian Kimmeridge Clay of Dorset (England;

McGowan and Motani, 2003), the taxonomically doubtful *Undorosaurus*, from the middle Volgian (Tithonian) of Ul'yanovsk Province and Moscow region (Russia; McGowan and Motani, 2003), and *Arthropterygius* from the Oxfordian-Kimmeridgian boundary of Melville Island, Canada (Maxwell, 2010) appear be restricted to the Late Jurassic. Consequently, what seemed to be a major turnover in ichthyosaur history after the end of Jurassic, as previously pointed out by Sander (2000), Bardet (1994) and Lingham-Soliar (2003), turns out to be an artefact of preservation biases/Lagerstätte effects, as a great part of Late Jurassic ichthyosaurs are also found in Early Cretaceous strata, despite a much lower number of specimens. Indeed, whereas an intermediate extinction event occurs at the Jurassic-Cretaceous boundary (Hallam and Wignall, 1997; Arens and West, 2008), some authors have already hypothesised that a significant part of that extinction could be explained by a decrease in the quality of the fossil record (Bardet, 1995; Benton, 1995; Hallam and Wignall, 1997). Still, Benson et al. (2009), studying Mesozoic marine tetrapod diversity as a whole, regarded the J-K boundary extinction event as unbiased. The extremely poor record of ichthyosaurs from the earliest Cretaceous and the new data presented here contradict this study, at least for ichthyosaurs.

Fig. 5: Evolution of the generic diversity of post-Triassic ichthyosaurs through time. For each stage, the number of genera integrates the whole stage duration and is placed at the middle of the stage. Ghost-lineages have been included. The light gray curve represents the data known just before 2003 and the dark gray curve represents the current state of knowledge. Het: Hettangian, *Ichthyosaurus, Leptonectes, Temnodontosaurus*; Sin: Sinemurian, *Ichthyosaurus, Leptonectes, Temnodontosaurus, Excalibosaurus*; Pli: Pliensbachian, *Leptonectes, Temnodontosaurus*; Toa: Toarcian, *Temnodontosaurus, Suevoleviathan, Eurhinosaurus, Stenopterygius, Hauffiopteryx*; Aal: Aalenian, *Stenopterygius*; Baj: Bajocian, *Mollesaurus, Chacaicosaurus*; Bat: Bathonian, —; Cal: Callovian, *Ophthalmosaurus*; Oxf: Oxfordian, *Ophthalmosaurus; Arthropterygius*; Kim: Kimmeridgian, *Ophthalmosaurus, Brachypterygius; Arthropterygius; Nannopterygius* Tithonian, *Ophthalmosaurus, Brachypterygius, Aegirosaurus, Caypullisaurus, Undorosaurus*; Ber: Berriasian, *Ophthalmosaurus, Brachypterygius, Aegirosaurus, Caypullisaurus*; Val: Valanginian, *Ophthalmosaurus, Brachypterygius, Aegirosaurus, Caypullisaurus*; Hau: Hauterivian, *Ophthalmosaurus, Brachypterygius, Platypterygius*; Bar: Barremian, *Ophthalmosaurus, Brachypterygius, Platypterygius*; Apt: Aptian, *Ophthalmosaurus, Brachypterygius, Platypterygius*; Alb: Albian, *Ophthalmosaurus, Brachypterygius, Platypterygius, Maiaspondylus*; Cen: Cenomanian, *Platypterygius*; Tur: Turonian, —. Fernández, 1994; 1997; 1999; 2007; Bardet et al., 1997; Maisch and Matzke, 2000; McGowan and Motani, 2003; Fernández and Aguirre-Urreta, 2005; Maxwell and Caldwell, 2006a; 2006b; Maisch, 2008; Ensom et al., 2009; Maxwell, 2010.

Consequently, ichthyosaurs cannot be considered as a group on the decline since the Middle Jurassic anymore; they were apparently not strongly affected by the Jurassic-Cretaceous Boundary Extinction Event either, which apparently had a more severe impact on terrestrial faunas (Benton, 1995; Orcutt et al., 2007; Benson et al., 2009) and on marine microorganisms (Lethiers, 2001; Bambach, 2006). In fact, the biodiversity of ichthyosaurs remains somewhat constant from the Lower Jurassic up to the late Early Cretaceous (fig. 5) with the presence of four to five genera each time ichthyosaur-rich sediments are present

(Early and Late Jurassic and late Early Cretaceous shales, Late Jurassic lithographic limestones). Lingham-Soliar's (2003) hypothesis of a "slow" and inescapable ichthyosaur extinction by increasing ecological stress since the Middle Jurassic is unsatisfactory, even though the radiation of teleost fishes is a parameter that must be considered when considering the demise of ichthyosaurs, among others (*e.g.* a break in the food-chain at the level of belemnites (Bardet, 1992) or the middle Cretaceous anoxic events). New data suggest a more sudden extinction event for ichthyosaurs during the middle Cretaceous (Maxwell and

Caldwell, 2006a; 2006b; Fischer et al., 2009). But the tempo and mode of this extinction at the beginning of the Late Cretaceous still needs to be investigated in detail.

5. Conclusions

The discovery of a fragmentary specimen of *Aegirosaurus* sp. in upper Valanginian deposits of southeastern France confirms that a great part of Late Jurassic ichthyosaur genera crossed the J-K boundary. Ichthyosaurs were thus not severely affected by the extinction event occurring at that boundary, or by biological competition with teleost fishes since the Middle Jurassic as it was previously supposed. During the whole Early Cretaceous, ichthyosaurs were still well diversified both from taxonomical (6 genera identified so far) and ecological (at least 2 feeding guilds represented) points of view.

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