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

V. Fischer\(^a, b, *\), A. Clément\(^c\), M. Guiomar\(^d\), P. Godet\(^a\)

\(^a\)Département de Paléontologie, Royal Belgian Institute of Natural Sciences, 29 Rue Vautier, 1000 Brussels, Belgium
\(^b\)Département de Géologie, Centre de Geosciences, Université de Liège, B-18, Allée du 6 Août, Liège, Belgium
\(^c\)5b Rue de Camargue, La Cigalière, 05000 Gap, France
\(^d\)Réserv naturelle géologique de Haute Provence, 10 montée Bernard Della Cassagrande, 04005 Digne-les-bains, France

ABSTRACT

A complete ichthyosaur rostrum, with 124 associated teeth, was recently discovered in Laux-Montaux locality, department of Drômes, southeastern France. The associated belemnites and ammonites indicate a late Valanginian age (\textit{Neocomites peregrinus Zone, Olostephanus 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 \textit{Aegirosaurus} outside the Tithonian (Upper Jurassic) lithographic limestones of Bavaria (southern Germany). Tooth morphology and wear pattern suggest that \textit{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.

1. Introduction

Ichthyosaurs were one of the most successful groups of Mesozoic marine reptiles, with a range that extends from the Olenekian (Early Triassic; \textit{Sander, 2000; Motani, 2005}) to the end of the Cenomanian (early Late Cretaceous; \textit{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. \textit{Bardet, 1994}). Several genera and species have been named from the Hauterivian of the Ul’yanovsk Region in Russia (\textit{Ochev and Efimov, 1985; Efimov, 1997}), but they have recently been considered as nomina dubia or subjective junior synonyms (\textit{McGowan and Motani, 2003}). The latest revision of Russian material by \textit{Storr 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 (\textit{Sander, 2000; Lingham-Solar, 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, 800 m East to the Laux-Montaux locality, Department of Drômes, southeastern France (Fig. 1). Other “Neocomian” marine reptiles from southeastern France include early Valanginian and Haueterian metriorhynchid crocodyliforms (respectively \textit{Endiosuchus macrospondylus} (\textit{Hua et al., 2000}) and \textit{Dakosaurus} sp. (\textit{Buffetaut, 1982})), late Valanginian teleosaurid crocodyliform (\textit{Steneosaurus} sp. (\textit{Cornée and Buffetaut, 1979})), and an Haueterian plesiosaurid (\textit{Plesiosaurus} indet. aff. \textit{Elasmosauridae} (\textit{Fournier et al., 1982})).

\begin{flushright}
* Corresponding author. Département de Paléontologie, Royal Belgian Institute of Natural Sciences, 29 Rue Vautier, 1000 Brussels, Belgium.
E-mail address: vfischer@ulg.ac.be (V. Fischer).
\end{flushright}

0195-6671/\$ – see front matter \textcopyright 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.cretres.2010.11.005

Please cite this article in press as: Fischer, V., et al., The first definite record of a Valanginian ichthyosaur and its implications on the..., Cretaceous Research (2010), doi:10.1016/j.cretres.2010.11.005
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 (≈ 10 cm) 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 southeast France has been intensively studied since 1993, using ammonites (Atrops and Reboulet, 1993; 1995; Reboulet, 1996; Reboulet et al., 2009) and belemnites (Clément, 1999; Janssen and Clément, 2002; Janssen, 2009). Ammonite zonation follows Reboulet et al., 2009. Belemnites guards 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 exstititorius (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 (Busnardoites campylotoxus Zone; Janssen and Clément, 2002).

- Duvalia binervia (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 D. binervia (Raspail, 1829), Pseudobelus brevis Paquier, 1900, Hibolithes gr. subusiformis 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, Neo- comites neocomiensis (d’Orbigny, 1841), Neolissoceras gracianum (d’Orbigny, 1841), Olcostephanus nicklesi Wiedmann and Dieri, 1968, Olcostephanus densicostatus (Weegener, 1909), and Phyllopachyceras sp. permits to refine the stratigraphic position of the specimen to the O. nicklesi Subzone, Neo- comites peregrinus Zone, upper Valanginian.

3. Systematic palaeontology

Order: Ichthyosauria de Blainville, 1835

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 intermediate, 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 and 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 thicken 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 a 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).

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).
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 RGHP 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."

<table>
<thead>
<tr>
<th>Species (specimen)</th>
<th>Total mandibular length (cm)</th>
<th>Prenarial length (cm)</th>
<th>Prenarial ratio</th>
<th>Estimation RGHP LA 1 (cm)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chacaiosaurus cayi (MOZ 5803)</td>
<td>98</td>
<td>64</td>
<td>0.65</td>
<td>93.4</td>
<td>Fernández, 1994</td>
</tr>
<tr>
<td>Ophthalmostomas icenicus (CPT specimen)</td>
<td>98</td>
<td>64</td>
<td>0.65</td>
<td>93.4</td>
<td>Maisch and Matzke, 2000</td>
</tr>
<tr>
<td>Caypullisaurus bonapartei (MOZ 6139)</td>
<td>141</td>
<td>71</td>
<td>0.5</td>
<td>121.1</td>
<td>Fernández, 2007</td>
</tr>
<tr>
<td>Aegirosaurus leptospondylus (SM)</td>
<td>56.5</td>
<td>38</td>
<td>0.67</td>
<td>90.7</td>
<td>Bardet and Fernández, 2000</td>
</tr>
<tr>
<td>Aegirosaurus leptospondylus (BSPHGM)</td>
<td>31.4</td>
<td>16</td>
<td>0.51</td>
<td>119.7</td>
<td>Bardet and Fernández, 2000</td>
</tr>
<tr>
<td>Brachypterygius extremus (SMC J68516)</td>
<td>123</td>
<td>71</td>
<td>0.58</td>
<td>105.7</td>
<td>McGowan, 1976</td>
</tr>
<tr>
<td>Platypterygius americanus (UWGM 24217)</td>
<td>130</td>
<td>74</td>
<td>0.57</td>
<td>107.2</td>
<td>McGowan, 1976</td>
</tr>
</tbody>
</table>

Please cite this article in press as: Fischer, V., et al., The first definite record of a Valanginian ichthyosaur and its implications on the..., Cretaceous Research (2010), doi:10.1016/j.cretres.2010.11.005
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 RHGP 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 tetrappeds (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 RHGP 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 fleshly preys, such as fishes and soft cephalopods, resembling that of extant delphinine odontocetes, such as Tursiops or some species of Lagophyrynchus, 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 carinæ 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 Ichthyosaurus

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 Aguira-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 Nanopterygius, from the Kimmeridgian Kimmeridge Clay of Dorset (Engladn; McGowan and Motani, 2003), the taxonomically doubtful Undorosaurus, from the middle Volgan (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 to 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 (Fig. 5), 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. 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., 2005) and on marine faunas (Floquet, 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,b; 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.

Acknowledgements

The authors wish to thank Dr. Nathalie Bardet (CNRS, MNHN, Paris) and Pr. Edouard Poty (Ulg, Liège) for revising earlier versions of this manuscript. Pr. François Atrops (Claude Bernard Lyon 1 University, Lyon) receive our most sincere acknowledgements for determining the collected ammonites, and providing a precise biostratigraphic canvas. Dr. Erin Maxwell (University of Alberta) and Dr. Darren Naish (University of Portsmouth) are sincerely thanked for their insightful and very constructive comments, which greatly improved this manuscript. V.F. was supported by a FNRS grant (Aspirant du F.R.S. — FNRS).

References


Please cite this article in press as: Fischer, V., et al., The first definite record of a Valanginian ichthyosaur and its implications on the... Cretaceous Research (2010), doi:10.1016/j.cretres.2010.11.005