

## **A New Pliosaurid from the Pliensbachian, Early Jurassic of Normandy, Northern France**

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# A new pliosaurid from the Pliensbachian, Early Jurassic of Normandy, Northern France

PEGGY VINCENT, NATHALIE BARDET, and EMANUELA MATTIOLI



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Complete plesiosaur skeletons are relatively abundant in the Lower Jurassic of England and Germany, but are exceptional in France. A new specimen from Normandy (northern France), including incomplete skull, palate and mandible with several associated vertebrae, is here described and its pliosauroid affinities are discussed. Comparison of this new specimen with other plesiosaurians indicates that it belongs to a new genus and species: *Cryonectes neustriacus*. This new plesiosaurian taxon represents one of the most complete pliosaurids reported from the Pliensbachian, a stage that has yielded very few diagnostic plesiosaurian remains. Our preliminary phylogenetic analysis places *Cryonectes* in a basal position among Pliosauridae, and suggests that the radiation of this clade occurred several millions of years earlier than previously thought. This new taxon contributes to our understanding of Early Jurassic plesiosaur diversity.

Key words: Reptilia, Plesiosauria, Pliosauroida, *Cryonectes*, Jurassic, Pliensbachian, France.

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## Introduction

Plesiosaurs are important members of Early Jurassic marine reptile faunas from England and Germany but are rare in France, being known from only a few specimens. Most of these are only partial skeletons, the only sub-complete specimen being *Occitanosaurus tournemirensis* (Sciau, Crochet, and Mattei, 1990) from the upper Toarcian of southern France (Bardet et al. 1999).

In the 1980s, the remains of a plesiosaur, including the incomplete skull and mandible with several associated vertebrae, were discovered by amateur palaeontologists in the Pliensbachian (Upper Lias) of Normandy, near Caen (Calvados Department, Northern France). The stratigraphic provenance of this specimen merits particular attention, because plesiosaurians of Pliensbachian age are rare compared to other stages of the Lower Jurassic. A partial postcranial skeleton of a plesiosaurid, *Westphaliasaurus simonsensii* Schwermann and Sander, 2011, has been found in the lower Pliensbachian of Germany, a plesiosaur from the Pliensbachian of Lincoln, England (Forrest 2006) is cur-

rently in preparation and an other one has been found in the Pliensbachian of Gloucestershire, England (Evans 2003, 2012). The other specimens from this stage are less complete and consist of postcranial remains, and most come from Europe: some remains of *Microcleidus* cf. *homalospondylus*, *Plesiosaurus* cf. *dolichodeirus*, and *Sthenarosaurus dawkinsi* from France mentioned by Persson (1963) but not figured; a juvenile specimen of a plesiosaur from Dorset, England (Storrs 1995); an adult plesiosaur from Lyme-Regis, England (Evans 2012); a juvenile plesiosaur from Asturias, Spain (Bardet et al. 2008); some remains of plesiosaurs of Denmark (Rees and Bonde 1999; Smith 2008); some vertebrae from an undetermined plesiosaurian from the Evergreen Formation (Pliensbachian–Toarcian?) of the Surat Basin, Queensland (Thulborn and Warren 1980); and some other briefly mentioned and undetermined plesiosaurian remains, which are perhaps Pliensbachian (Schulz 1858; Persson 1963; Thulborn and Warren 1980; Rees and Bonde 1999). In summary then, the only diagnostic plesiosaur taxon from this stage is *Westphaliasaurus simonsensii*.

The purposes of this paper are to describe the new specimen from Normandy and to compare it with other plesiosaurs, in order to improve our understanding of the evolution of the diversity of Liassic plesiosaurs.

**Institutional abbreviations.**—NHMUK, Natural History Museum, London, UK; BRSMG, Bristol Museum and Art Gallery, Bristol, UK; MAE, Musée de l'Agglomération d'Elbeuf, Elbeuf-sur-Seine, France; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

## Geographic and stratigraphic setting

The specimen MAE 2007.1.1(J) comes from the “Calcaire à Bélemnites” Formation (*Uptonia jamesoni* to *Pleuroceras spinatum* Ammonite Zone, Pliensbachian) outcropping in the Roche-Blain quarries, located in the commune of Fresney-le-Puceux near the city of Laize-la-Ville, approximately 10 km south of Caen (Fig. 1). The absence of associated diagnostic ammonite markers prevents direct age assignment of the specimen to the ammonite zone level.

The nannofossil assemblages from the rock matrix adhering to the specimen were examined in order to determine the age of the specimen. The assemblage is dominated (76.9% of specimens) by murolith-coccoliths (composed of a wall-like, sub-vertical rim; Fig. 2A–F), while placoliths (formed by two sub-horizontal shields; Fig. 2G–I) and the nannolith *Schizosphaerella* are rare. *Crepidolithus imponentus* (*C. cavus* in Bown 1987), *Bussonius prinsii*, and *Calyculus* sp. were recorded in the assemblage (Fig. 2A–C, I). In different sections from central and northern Italy these three taxa are recorded stratigraphically one after the other in sediments attributed to the *P. spinatum* Ammonite Zone, uppermost Pliensbachian (Mattioli and Erba 1999). The same record is reported by Veiga de Oliveira et al. (2005) in Portugal, and by Perilli et al. (2004) in northern Spain. Conversely, rare and sporadic occurrences of both *Calyculus* spp. and *Bussonius prinsii* have been reported as low as the lower Pliensbachian of NW Europe, but these taxa become consistently present in the uppermost Pliensbachian (Bown and Cooper 1998). These authors also report *Crepidolithus imponentus* from the *P. spinatum* Ammonite Zone. The first occurrence of *C. imponentus* is used to define the base of the NJ5b nannofossil subzone (Bown and Cooper 1998) that spans the uppermost Pliensbachian and the lowermost Toarcian. The lack of other, typical lowermost Toarcian species in the sample from the matrix of MAE 2007.1.1(J) leads us to correlate the sample with the uppermost Pliensbachian (Bown and Cooper 1998; Mattioli and Erba 1999; Perilli et al. 2004; Veiga de Oliveira et al. 2005; Mailliot et al. 2006). Very few small *Lotharingius* specimens, which are usually recorded stratigraphically below *C. imponentus* (Bown 1987; Bown and Cooper 1998; Mattioli and Erba

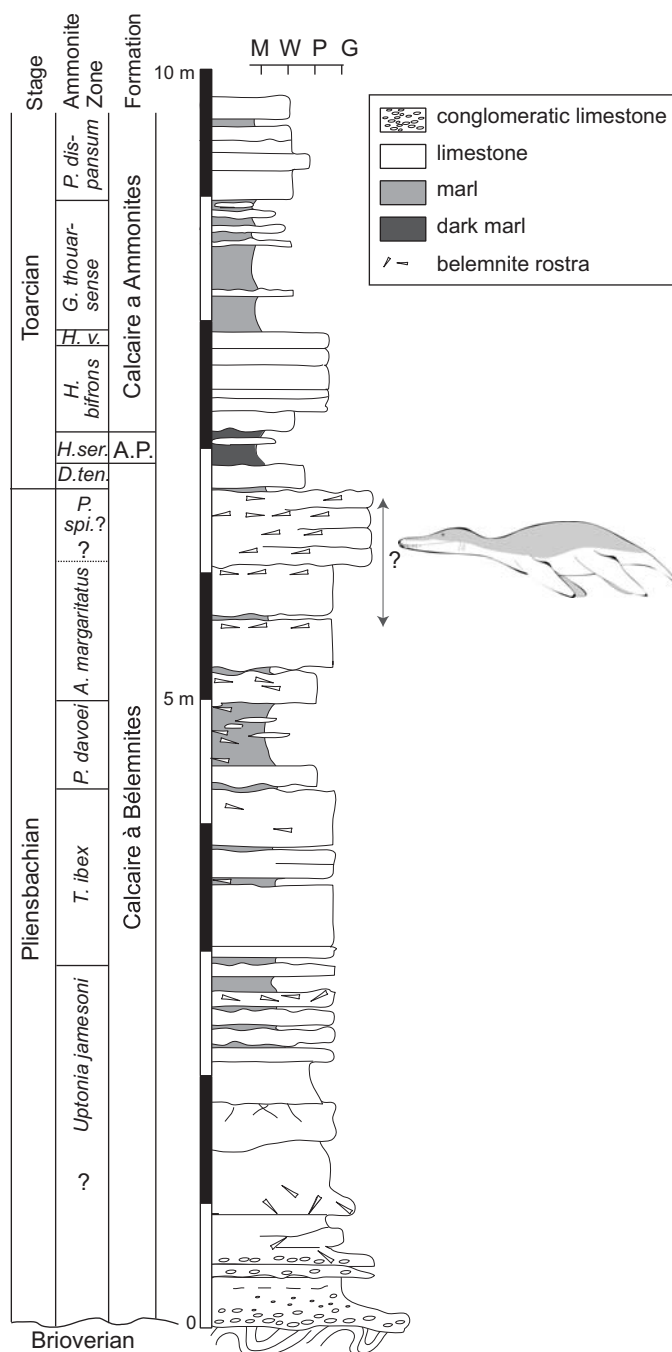


Fig. 1. Simplified stratigraphic section of the Lower Jurassic succession in the Roche-Blain quarry (modified from Dugué et al. 1998), with the possible stratigraphic position of the specimen *Cryonectes neustriacus* MAE 2007. 1.1(J), holotype, as indicated by arrows. Abbreviations: *P. spi.*, *Pleuroceras spinatum* Ammonite Zone; *D. ten.*, *Dactylioceras tenuicostatum* Ammonite Zone; *H. serp.*, *Harpoceras serpentinus* Ammonite Zone; *H. v.*, *Haugia variabilis* Ammonite Zone; A.P., “Argile à poissons” formation; M., mudstone; W., wackestone; P., packstone; G., grainstone.

1999), are present in the studied sample (i.e., *L. frodoi* in Fig. 2H). The dominance of muroliths in the studied sample is another argument to support a late Pliensbachian age. In fact, Mailliot et al. (2007) show that placoliths became dominant over muroliths in the basal Toarcian.

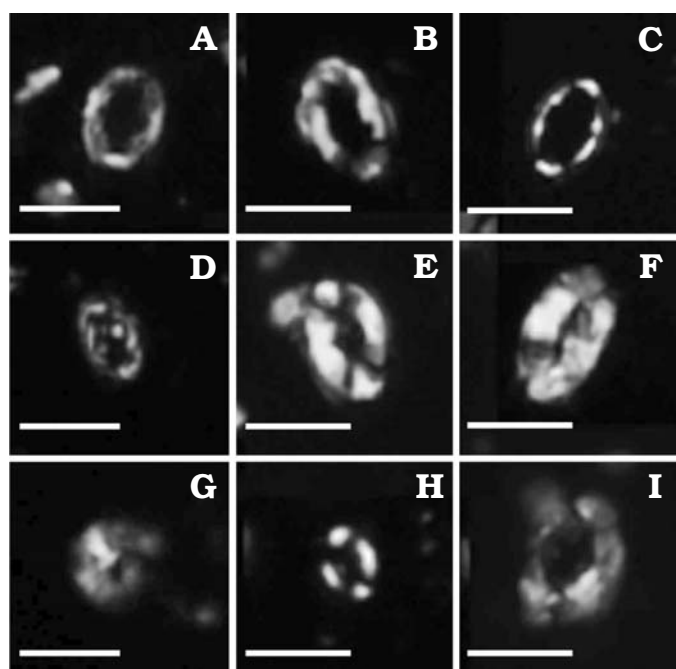


Fig. 2. Nannofossil assemblages present in the matrix of the specimen *Cryonectes neustriacus* sp. nov., MAE 2007.1.1(J) from Upper Pliensbachian, Calvados, France. **A, B.** Thick specimens of *Crepidolithus imponentus*. **C.** Thin specimen of *Crepidolithus imponentus*. **D.** *Parhabdololithus liasicus*. **E.** *Mitrolithus elegans*. **F.** *Crepidolithus crassus*. **G.** *Similiscutum cruciulus*. **H.** *Lotharingius frodoi*. **I.** *Calyculus* sp. ind. Scale bars 5  $\mu$ m.

## Systematic palaeontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Pliosauroida (Seeley, 1874) Welles, 1943

Pliosauridae Seeley, 1874

Genus *Cryonectes* nov.

*Type species:* *Cryonectes neustriacus* sp. nov., monotypic; see below.

*Etymology:* From Greek *kryos*, cold, and *nektris*, swimmer; in reference to the cool climatic conditions that prevailed during the latest Pliensbachian (e.g., Rosales et al. 2004; Suan et al. 2008, 2010).

*Cryonectes neustriacus* sp. nov.

*Etymology:* Derived from the Frank kingdom of Neustrie that covered northwest France, created after the death of Clovis in AD 511.

*Holotype:* MAE 2007.1.1(J), an incomplete skull and articulated mandible, and 10 associated vertebrae.

*Type locality:* Roche-Blain quarry, Fresney-le-Puceux, near Laize-la-Ville, south of Caen, Calvados Department, Northern France.

*Type horizon:* “Calcaire à Bélemnites” Formation, uppermost Pliensbachian (Lower Jurassic), Normandy (Dugué et al. 1998).

*Material.*—Holotype only.

*Diagnosis.*—Moderate-sized plesiosaurian (skull length: approximately 470 mm from the tip of the snout to the posterior end of the mandible) presenting the following unique combination of characters: contacts between premaxillae and

maxillae marked by a very slight constriction; snout well elongated; very thin anterior interpterygoid vacuity with pointed anterior and posterior margins; two ventrolaterally orientated low flanges on the posterior rami of the pterygoids; mandible with a long symphysis bearing seven tooth position and retaining a ventral mandibular ridge; cervical centra with relatively platycoelous articular surfaces; ventral sides of cervical centra almost flat, without ventral keel nor depression around the nutritive foramina.

### Description

*Preservation:* When discovered, the specimen was prepared first with acid, which unfortunately damaged some parts, especially the teeth, which are now broken and lack enamel. Mechanical preparation was subsequently performed. The premaxillae and maxillae are incompletely preserved (Fig. 3). The most important part of the palate is preserved separate from the skull (Fig. 4). It is damaged but some structures are recognizable. The complete mandible and the skull are in occlusion with teeth in situ (Figs. 5–7). One separated tooth is almost complete but lacks enamel as well (Fig. 7). Ten associated vertebrae are preserved in a non-natural sequence, nine being cervical, but the last one cannot be determined with confidence (Figs. 8–10).

*Ontogenetic stage:* Distinct neurocentral sutures are visible on all vertebrae preserving neural arches, except vertebra 9, which presents a closed suture. Accordingly, *Cryonectes* could be regarded as being at a relatively early stage in ontogenetic development (sensu Brown 1981). The closed neurocentral suture of vertebra 9 suggests that it was probably a subadult.

*Skull* (Figs. 3–6): The premaxillae are massive and the rostrum is long and narrow (Fig. 3). The skull roof is absent, thus preventing estimation of any snout elongation value. Nevertheless, the snout appears much longer than that of the Liassic plesiosauromorph taxa *Microcleidus* (NHMUK 36184; Brown et al. 2013), *Plesiosaurus* (Storrs 1997), *Occitanosaurus* (Bardet et al. 1999), *Hydrorion* and *Seeleyosaurus* (Großmann 2007), the basal plesiosaurian taxa *Thalassiodracon hawkinsii* (Storrs and Taylor 1996) and *Anningasaura lymense* Vincent and Benson, 2012, and Rhomaleosauridae (e.g., *Meyerasaurus victor*; Smith and Vincent 2010 and *Rhomaleosaurus zetlandicus*; Taylor 1992; Vincent and Smith 2009). The snout appears as elongated as those of *Attenborosaurus conybeari* (Sollas, 1881) and *Archaeonectrus rostratus* (NHMUK 38525; Owen 1865), but larger than that of *Hauffiosaurus zanoni* O’Keefe, 2001 and *Hauffiosaurus tomistomimus* Benson, Ketchum, Noè, and Gómez-Pérez, 2011b; and not as extended as that of *Hauffiosaurus longirostris* (MMUM LL 8004; O’Keefe 2001: fig. 9; Ketchum and Benson 2010: fig. A6; MCZ 1033: White 1940: fig. 4b). In dorsal view, the premaxillae unite in a well-developed medial suture along their whole preserved length. The long slender facial processes of the premaxillae, running back on the dorsal surfaces of the skull, are not preserved entire, but seem to constitute the anterior part of the low parasagittal ridge (Fig. 6A), as in



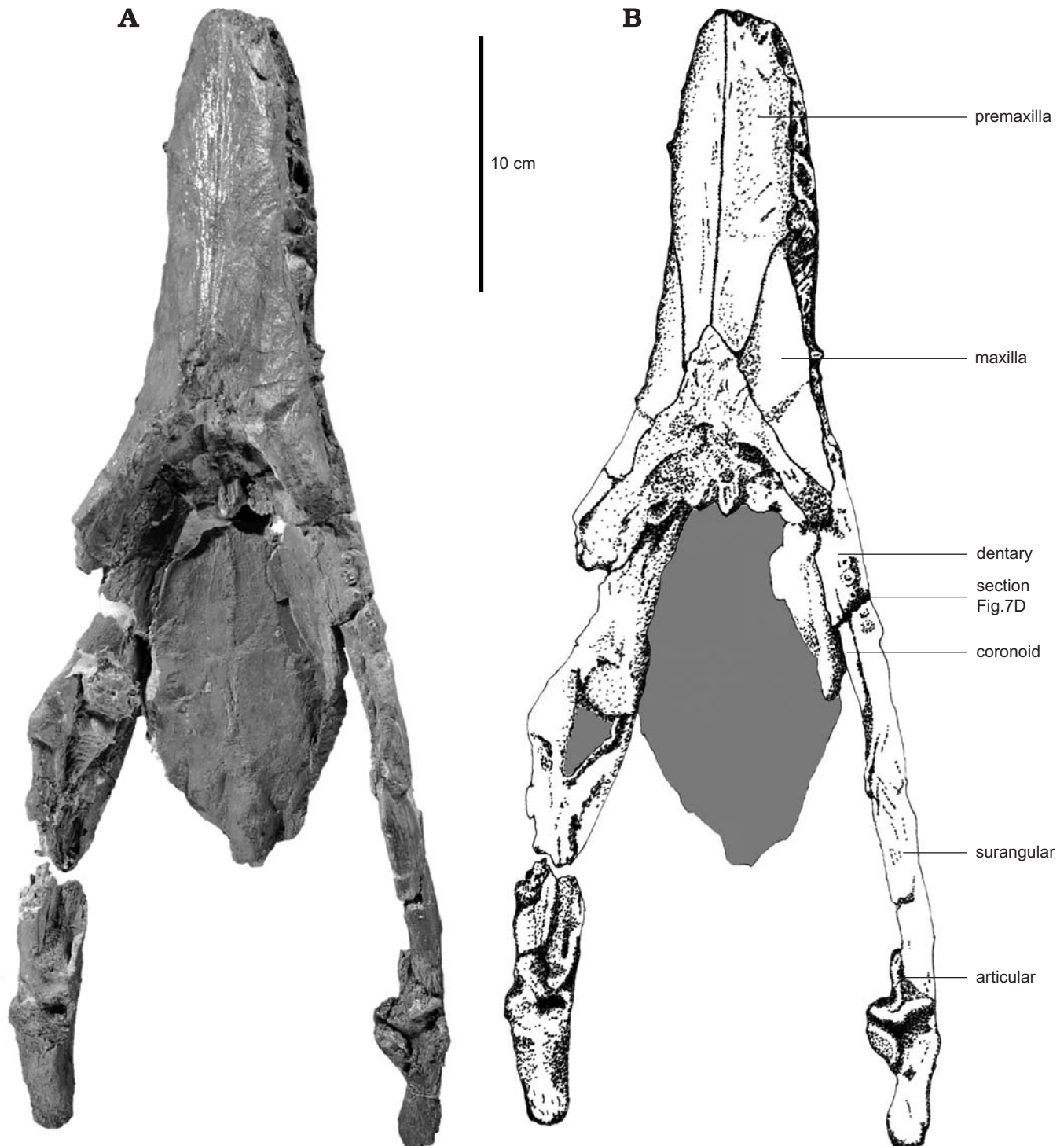


Fig. 3. Pliosaurid plesiosaur *Cryonectes neustriacus* gen. et sp. nov., MAE 2007.1.1(J), holotype; Late Pliensbachian, Early Jurassic, Calvados, France. Skull in dorsal view (A) and explanatory drawing (B).

*H. longirostris* (MCZ 1033; White 1940), *Archaeonectrus* (NHMUK 38525; Owen 1865), and *Macroplata tenuiceps* (Ketchum and Smith 2010). The premaxillae bear five pairs of teeth, whose relative sizes are not easily observable because of bad preservation. Weak ridges ornament the external surface of the premaxilla. The sockets for the large premaxillary teeth run posteriorly, medially and dorsally, deep into the bone. The

contacts between premaxillae and maxillae are marked by a very slight constriction of the muzzle as in *Marmornectes candrewi* Ketchum and Benson, 2011a, *Peloneustes philarchus* (SMNS 10113; Ketchum and Benson 2011b), *Pliosaurus brachyspondylus* (BRSMG Cc332; Taylor and Cruickshank 1993), and *H. zanoni* O'Keefe, 2001 (see also Vincent 2011), but not as marked as in Rhomaleosauridae (e.g., *Meyera-*

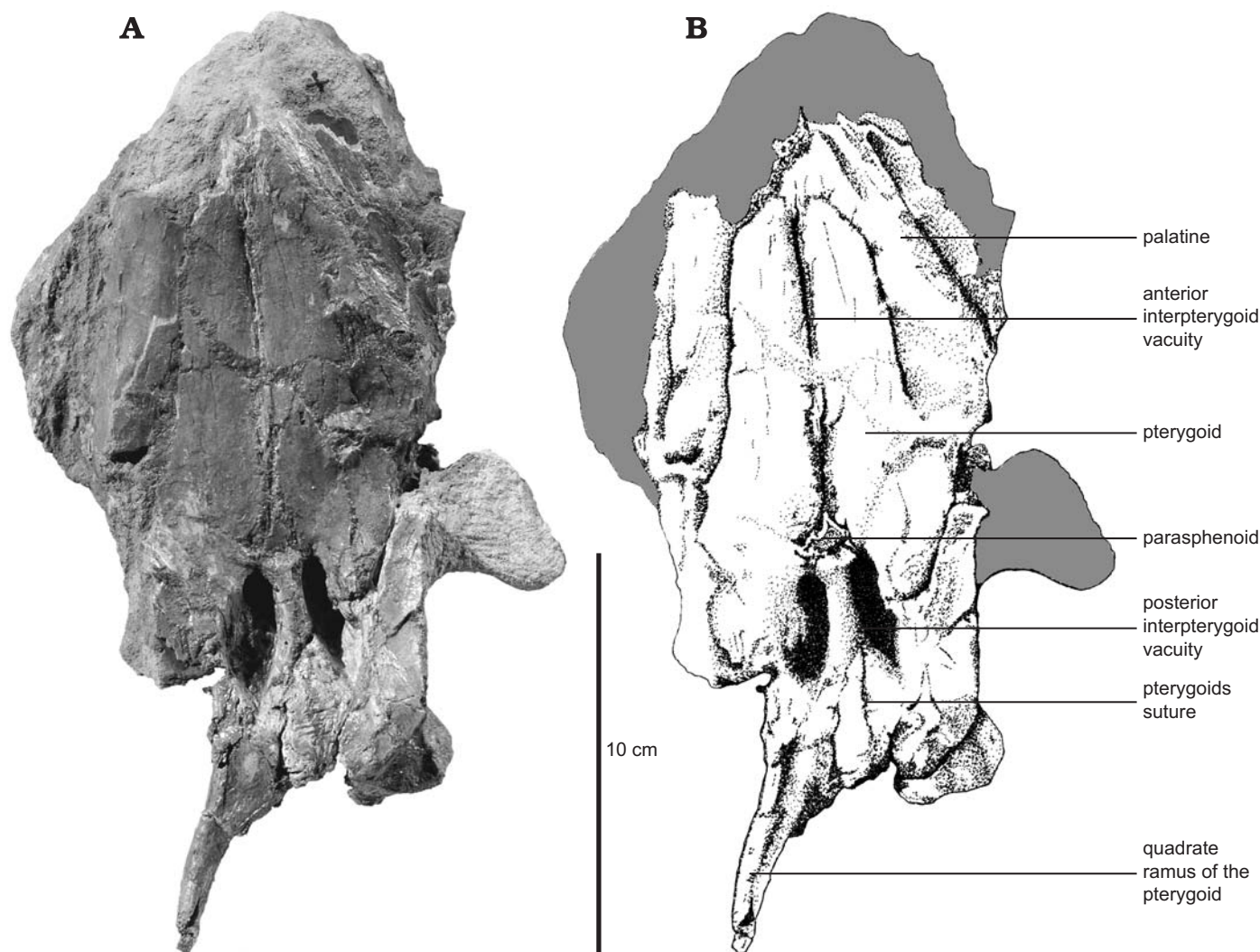


Fig. 4. Pliosaurid plesiosaur *Cryonectes neustriacus* gen. et sp. nov., MAE 2007.1.1(J), holotype; Late Pliensbachian, Early Jurassic, Calvados, France. Palate in ventral view (A) and explanatory drawing (B).

*saurus victor*, Smith and Vincent 2010; *Rhomaleosaurus zetlandicus*, Taylor 1992). The premaxillae-maxillae sutures are straight on the right side and slightly interdigitating on the left. They run posteromedially from the margin of the tooth row. The maxillae are long and slender and not entirely preserved. The right maxilla bears at least nine alveoli.

The palatines are partially preserved, the left one being the most complete of the two (Fig. 4). It is an elongate bone running from the anteriormost part of the snout towards the posterior part of the ectopterygoid, which is not preserved. Their medial margins contact the pterygoids. They are not preserved anteriorly but probably join the vomers. The specimen does not present lateral palatal fenestration bordered by palatine and pterygoid as in *Plesiosaurus* (Storrs 1997), *Leptocleidus capensis* (Cruickshank 1997), *Peloneustes* (Ketchum and Benson 2011b), and *Liopleurodon* (Andrews 1910).

The pterygoid is a large bone forming the main part of the palatal surface (Fig. 4). It includes the anterior, lateral, poste-

rior and quadrate ramus. The anterior ramus is very long, broad and flat, with a thickened front portion. Laterally it contacts the palatine in a nearly straight suture. In the median line, the anterior ramus parts to form a very narrow anterior interpterygoid vacuity as in *Plesiosaurus brachyspondylus* (Taylor and Cruickshank 1993), small individuals of *Peloneustes* (Ketchum and Benson 2011b), and *Hauffiosaurus tomistomimus* (Benson et al. 2011b), but much more extended. The two pterygoids meet for a short distance anteriorly and posteriorly to the anterior interpterygoid vacuity (Figs. 4, 6B, C). Behind, they are separated by the anterior part of the parasphenoid. Posteriorly, the medial edges of the pterygoids curve away from the parasphenoid to enclose the posterior interpterygoid vacuities. They meet again posterior to the posterior interpterygoid vacuities (Fig. 6B, D). Behind the posterior interpterygoid vacuities, the posterior portion of each pterygoid bears a slight and short flange ventrolaterally orientated (Figs. 4, 6D). Only the quadrate ramus of the right pterygoid is preserved; it is poorly preserved. It is a long, lat-

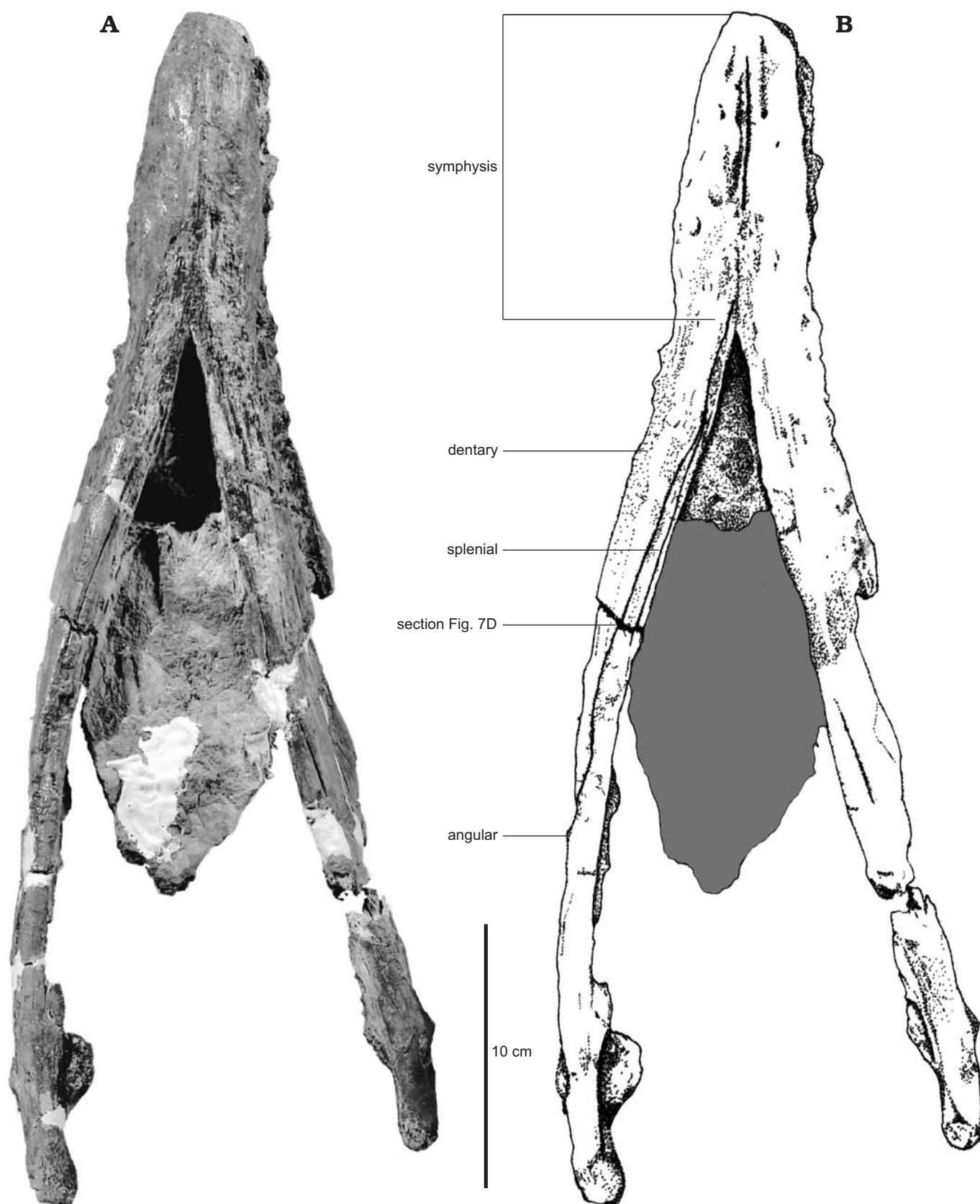


Fig. 5. Pliosaurid plesiosaur *Cryonectes neustriacus* gen. et sp. nov., MAE 2007.1.1(J), holotype; Late Pliensbachian, Early Jurassic, Calvados, France. Skull in ventral view (A) and explanatory drawing (B).



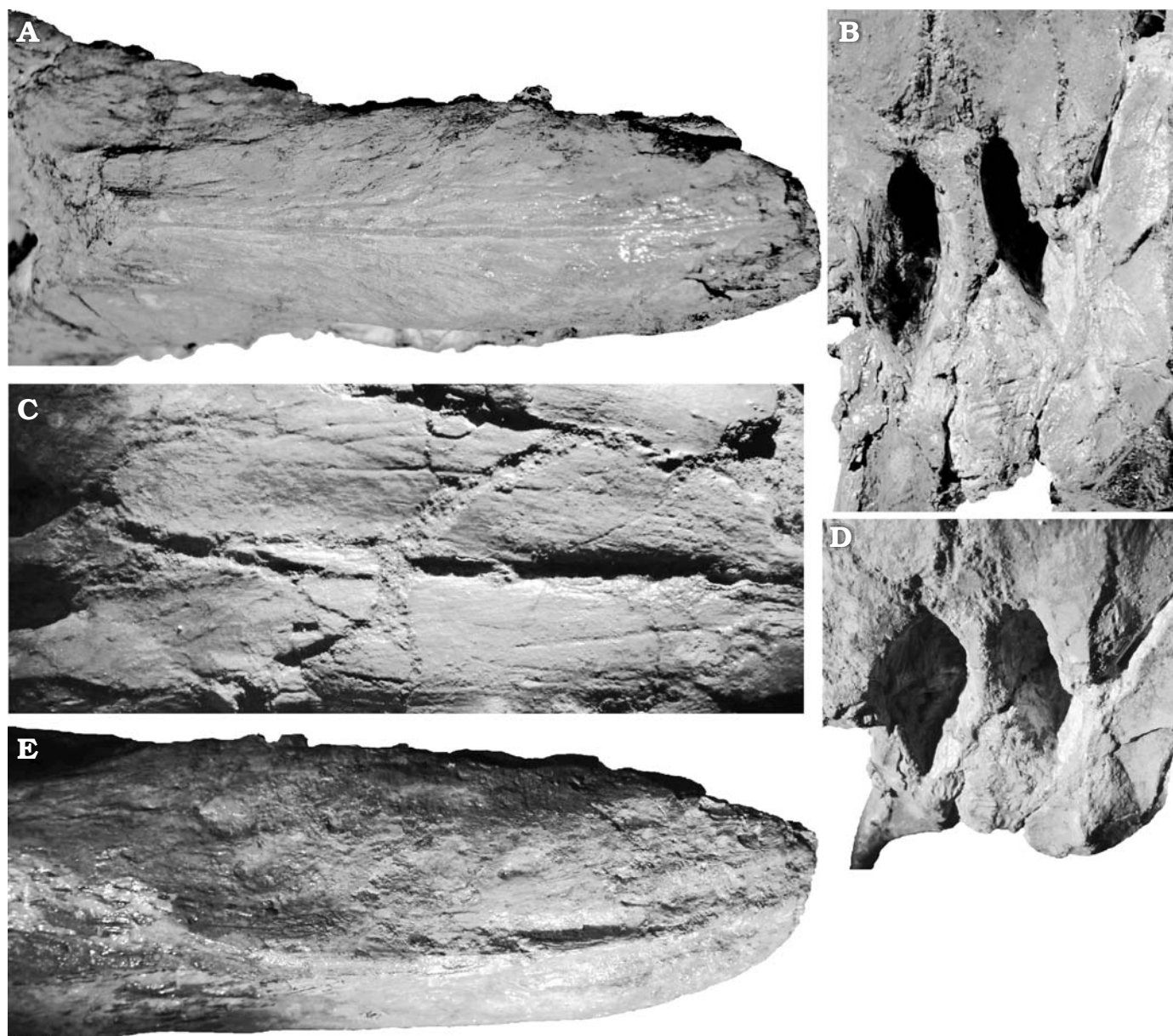


Fig. 6. Pliosaurid plesiosaur *Cryonectes neustriacus* gen. et sp. nov., MAE 2007.1.1(J), holotype; Late Pliensbachian, Early Jurassic, Calvados, France. **A.** Rostrum in dorsal view. **B.** Close-up photograph of the parasphenoid and posterior interpterygoid vacuities. Close-up photograph of the anterior interpterygoid vacuity (**C**) and the posterior part of the palate in oblique anterior view (**D**). **E.** Rostrum in ventral view.

erally compressed process running posterolaterally from the basicranium to the non-preserved quadrate.

The anterior interpterygoid vacuity, very long and slender, is present on the middle of the palate (Figs. 4, 6C), distinguishing *Cryonectes* from *Hauffiosaurus zanoni* (O'Keefe 2001; Vincent 2011), which does not possess an anterior interpterygoid vacuity. The anterior interpterygoid vacuity of *Cryonectes* has very pointed anterior and posterior margins. The posterior interpterygoid vacuities are bordered laterally by the pterygoids and are separated on the midline by the parasphenoid. These are deep, anteroposteriorly extended, mediolaterally orientated and kidney-shaped (Figs. 4, 6B).

The parasphenoid is a thin flat bone anteriorly, forming a short triangular cultriform process that extends onto the sur-

face of the palate and tapers to a sharp anterior point (Figs. 4, 6B). The parasphenoid extends well anterior to the anterior border of the posterior interpterygoid vacuities, but less than the parasphenoid of *Peloneustes* (Ketchum 2007) or *P. brachyspondylus* (Taylor and Cruickshank 1993), and divides the pterygoids along their midline. It contacts the pterygoids with strong interdigitating sutures. The parasphenoid divides the posterior interpterygoid vacuities into two openings and is ventrally keeled between them. The palate is here slightly concave from side to side. The posterior portion of the parasphenoid cannot be differentiated from the basisphenoid because of damages.

**Mandible** (Figs. 5–7): The mandible is well preserved and complete. It is narrow and tapers anteriorly (Fig. 5).



From the anterior extremity to the posterior end of the retroarticular process, it is 470 mm long. The mandible is slightly bowed when viewed in ventral view, but less than that of Rhomaleosauridae (the condition in *Archaeonectrus* is unknown). A natural break provides a section (Fig. 7D) revealing the internal arrangement of the mandibular elements.

The dentary rami are joined anteriorly in an elongated symphysis (Fig. 6E), about 110 mm long, approximately one quarter of the length of the mandible; the ratio is approximately the same for *Archaeonectrus* (NHMUK 38525; Owen 1865). The snout tip is narrow and slightly transversally expanded, as in *Marmornectes candrewi* Ketchum and Benson, 2011a, being intermediate between the unexpanded snout tip of longirostrine polycotyliids (e.g., *Dolichorhynchops herschelensis*, Sato 2005; *Thililua longicollis*, Bardet et al. 2003), *Hauffiosaurus* (Vincent 2011; Benson et al. 2011b), and *H. longirostris* (White 1940; Benson et al. 2011b), and the spatulated snout tip of longirostrine pliosauroids (e.g., *Peloneustes*, Ketchum 2007; *Liopleurodon*, Noè 2001) and Rhomaleosauridae (e.g., *Meyerasaurus victor*, Smith and Vincent 2010). The condition in *Archaeonectrus* is unknown as the mandible is preserved laterally compressed. In the symphyseal region, the two rami form a median crest where they join (Fig. 6E), here poorly preserved, as in *H. longirostris* (White 1940) and distinguishing *Cryonectes* from *Hauffiosaurus* and *Marmornectes* which do not possess ventral mandibular ridge (Vincent 2011; Benson et al. 2011b; Ketchum and Benson 2011a). The condition is unknown in *Archaeonectrus*, as the mandible is preserved laterally compressed. Posteriorly, the two dentary rami are separated by the splenials entering into the symphyseal region for a short distance on the ventral side. Posteriorly, the rami diverge by about 40° and increasingly become laterally compressed and more vertical. Posteriorly, the dentary contacts the surangular and overlaps internally the suture between the surangular and the coronoid. The lateral surface of the dentary is flat without a trough occupying the lateral surface, as is the case in *H. tomistomimus* (Benson et al. 2011b).

The splenial is a long, transversely compressed bone (Fig. 7). It takes part in the symphysis for a short distance where it forms the internal and ventral border of the mandibular ramus. Throughout its length, it is very closely applied to the medial face of the coronoid extremity. The splenial is not preserved over the Meckelian canal because it is thin and liable to breakage, as is the case in many other plesiosaurs (O'Keefe 2001).

The coronoid is a very thin and long bone extending from the coronoid eminence, to the anterior part of the mandible posterior to the symphysis so that it does not participate into the symphyseal region. It is not exposed in lateral view (Fig. 7B). Its ventral surface contacts the splenial and is overlapped by it ventrally. Posteriorly, it deepens over the Meckelian canal, forming its roof (Fig. 7C). It unites with the surangular in an almost vertical suture. Its dorsal edge is close to and nearly parallel with the alveolar border of the dentary bone.

The angular is prolonged forwards as a narrowing process ending a few centimetres from the symphysis. In this region, it joins the dentary on the lateral side of the mandible and the

coronoid on its medial side (Fig. 7B). It forms the ventral surface of the coronoid eminence. In lateral view, the angular forms a well-marked suture with the surangular.

The surangular forms the dorsal part of the mandible between the coronoid eminence and the glenoid. Its dorsal surface is transversally expanded as in *Marmornectes* (Ketchum and Benson 2011a), broader than that of *Thalassiodracon* (Storrs and Taylor 1996; Benson et al. 2011a), but narrower than that of *Peloneustes* (Ketchum and Benson 2011b). It does not bear any depression anterior to the glenoid dorsally nor a foramen on its medial surface. The suture between articular and surangular is clearly visible in this specimen (Fig. 7B), whereas it is generally closed, and thus not visible, in almost all plesiosaurs (e.g., Brown 1981; Ketchum and Benson 2011a; Sato 2003, 2005). The suture runs from a point situated at the level of the coronoid eminence on the ventral surface of the mandible, to a point situated dorsally, anterior to the anterior margin of the glenoid.

The articular is a robust bone, exposed mainly dorsally and forming the dorsomedial flange of the jaw ramus between the surangular, the glenoid fossa and the retroarticular process. The glenoid fossa is laterally expanded and has two concavities to fit the double condyles of the quadrate. The medial area is deeply concave from side to side and the small lateral area is only slightly concave. The anterior border of the glenoid cavity forms a prominent lip. The retroarticular process is long, narrow, almost vertical and medially recurved.

**Dentition** (Fig. 7): About 34 teeth are represented. Each premaxilla bears 5 tooth sockets, distinguishing *Cryonectes* from *Peloneustes* (6 teeth in each premaxilla), *H. zanoni* (7), *H. longirostris* (10), and *Marmornectes candrewi* (6). The left maxilla bears 9 sockets and the right 6, but the maxillae are not entirely preserved. Fifteen sockets are exposed on the left dentary and 19 on the right. Since some sections of the dentaries are obscured or slightly damaged, it is most likely that there were originally a few more than 19 teeth on both sides, a number close to that observed for *Archaeonectrus* (NHMUK 38525; Owen 1865), which presents approximately twenty teeth on each dentary. It is likely that there were at least 66 functional teeth in the specimen. The mandibular symphysis occupies at least seven tooth positions, and is in this regard similar to that of *Archaeonectrus* (NHMUK 38525; Owen 1865) and *Macroplata tenuiceps* (NHMUK R5488; Ketchum and Smith 2010), which both present seven or eight dentary tooth pairs adjacent to the mandibular symphysis (Ketchum and Smith 2010). This number is higher than in *Attenborosaurus conybeari* (Sollas, 1881) and NHMUK 39514 (Vincent 2012), which both present a mandibular symphysis occupying less than seven tooth positions, and distinctly lower than in *Peloneustes* (Ketchum 2007), *Marmornectes candrewi* Ketchum and Benson, 2011a, and *H. longirostris* (White 1940), which all have a mandibular symphysis occupying at least 12 tooth positions. The mandibular teeth of *Cryonectes* are close to each other, distinguishing it from *Archaeonectrus* (NHMUK 38525; Owen 1865) in which the teeth are well separated; Owen

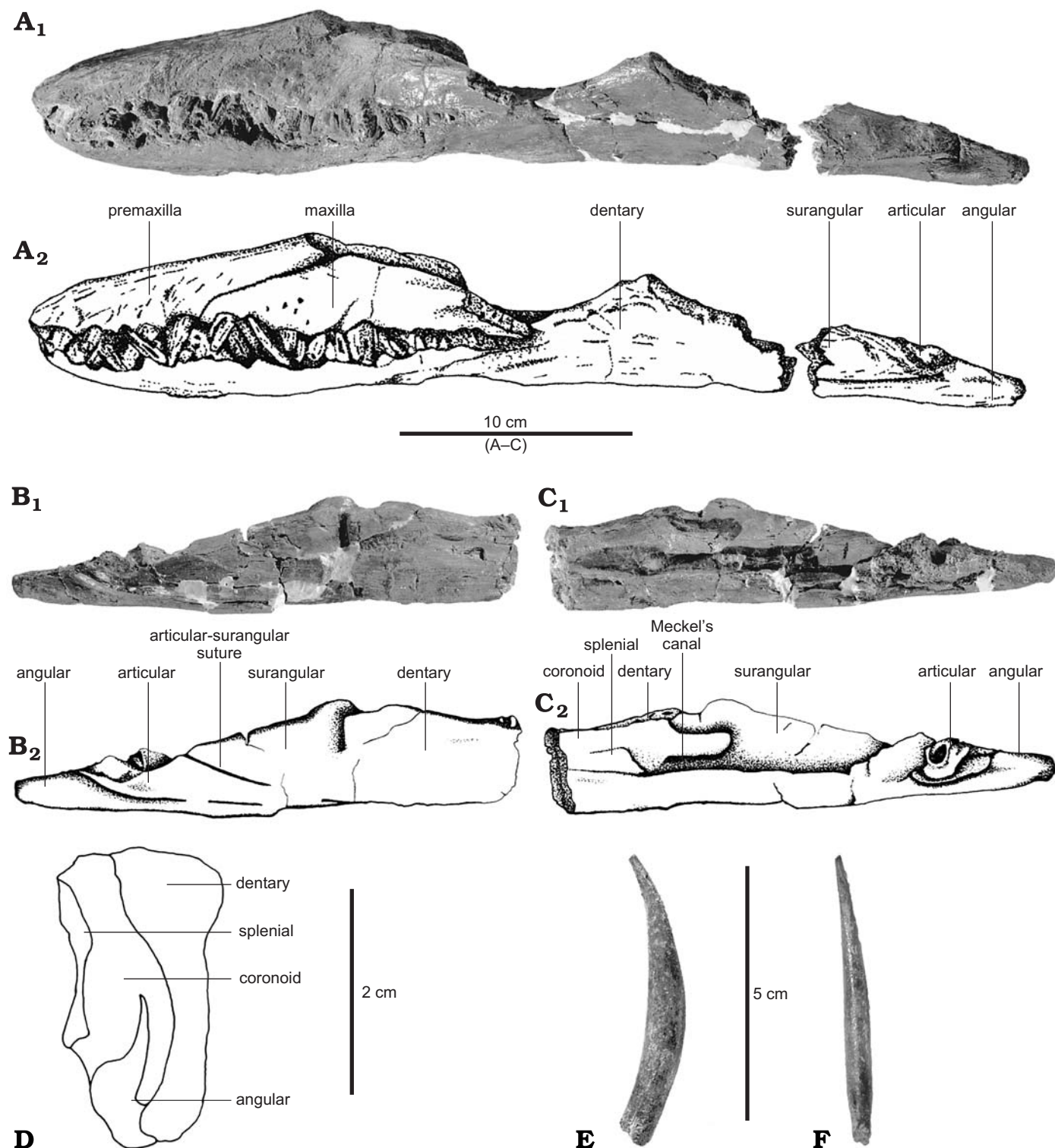


Fig. 7. Pliosaurid pliosaur *Cryonectes neustriacus* gen. et sp. nov., MAE 2007.1.1(J), holotype; Late Pliensbachian, Early Jurassic, Calvados, France. A. Skull in left lateral view. Posterior part of the right mandibular ramus in lateral (B) and lingual (C) views. Photographs (A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub>) and explanatory drawings (A<sub>2</sub>, B<sub>2</sub>, C<sub>2</sub>). D. Section of the right mandibular ramus (see Fig. 2 and 4 for actual line of section). E, F. Teeth.

(1865) noted that “the teeth are divided by intervals of rather more than their own basal breadth”.

The teeth vary in size and orientation along the jaw. The anteriormost teeth are tilted whereas the posterior ones are

more vertical. The first pair of teeth is very small in comparison to adjacent teeth. The teeth are broadly similar in size and shape across the premaxilla-maxilla suture. They all show the typical pliosaurian form with curved, conical crowns and

thin roots. Each tooth is subcircular in cross section without carinae, distinguishing *Cryonectes* from *Pliosaurus brachydeirus* (Owen, 1842) and *P. brachyspondylus* (BRSMG Cc332; Taylor and Cruickshank 1993) which exhibit trihedral teeth in cross-section with carinae. The crowns of the best-preserved teeth are needle-like, slightly curved, slender and sharp, and their tips are compressed (Fig. 7E, F) contrary to those of *Attenborosaurus conybeari* (Bakker 1993), *Archaeonectrus* (NHMUK 38525), *H. zanoni* (Vincent 2011), *Peloneustes* (Ketchum 2007), and *Liopleurodon* (Noè 2001) which have more robust and large teeth without compression. Most of the tooth row in *Cryonectes* is slightly higher than the glenoid fossa.

**Axial skeleton** (Figs. 8–10, Table 1): The centra of the cervical vertebrae are relatively short, with their width slightly exceeding their length and their height ( $W > L > H$ ) (Table 1). Broad and short cervical centra are also seen in *Archaeonectrus* (Owen 1865). The cervical proportion of *Cryonectes* ( $H < L$ ; Table 1) differs from *Attenborosaurus* (Sollas 1881), *P. brachyspondylus* (BRSMG Cc332; Taylor and Cruickshank 1993) and *H. tomistomimus* (Benson et al. 2011b), whose cervical vertebrae are higher than long. Brown (1981) proposed short cervical centra as a character of Pliosauroida and Andrews (1913) and Ketchum (2007) stated that the cervical centra of pliosaurids are approximately half as long as they are high or wide. Accordingly, the cervical centra of *Cryonectes* show pliosauroid, but not pliosaurid, proportions.

In Table 1 and in Figs. 8, 9, and 10, the vertebral numbers refer to their position in the vertebral column as preserved, not the natural position. The articular surfaces are elliptical and moderately amphicoelous, and the margins form an abrupt angle with the centrum side. Each articular surface possesses a marked, central, horizontally elongated pit. The ventral sides are almost flat and lack a keel, distinguishing *Cryonectes* from *H. zanoni* (Vincent 2011), *Archaeonectrus* (NHMUK R.1337; Owen 1865), *P. brachydeirus* (Tarlo 1960), and Rhomaleosauridae (e.g., *M. victor* Smith and Vincent, 2010), which possess a ventral keel on cervical vertebrae. This character is probably not ontogenetic because juvenile specimens of *Thalassiodracon* (e.g., NHMUK 2018; PV personal observations)

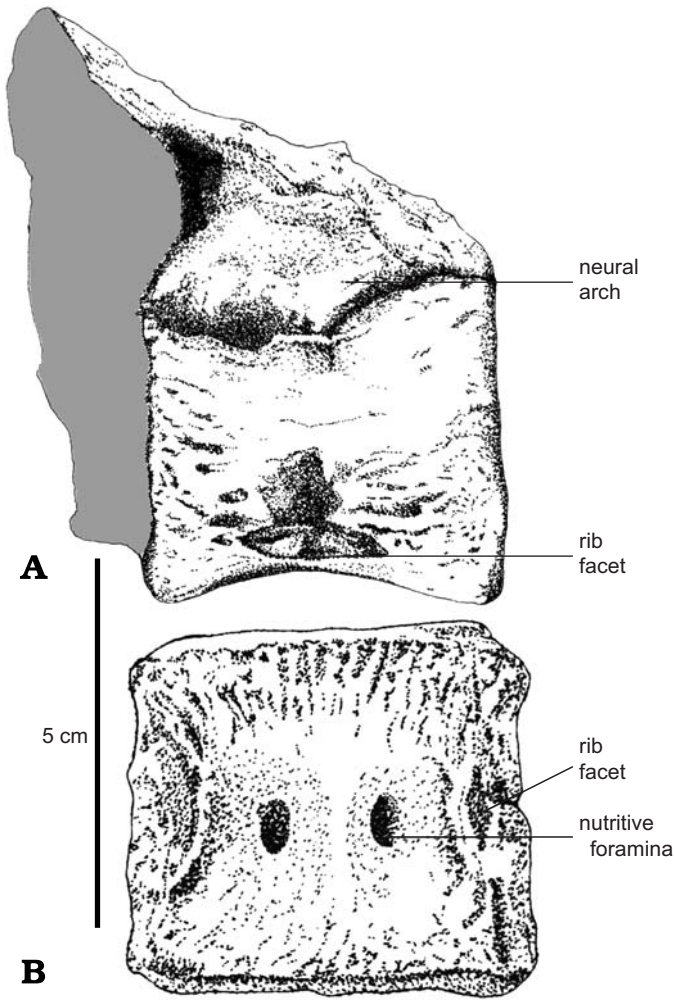


Fig. 8. Pliosaurid plesiosaur *Cryonectes neustriacus* sp. nov., MAE 2007. 1.1(J), holotype; Late Pliensbachian, Early Jurassic, Calvados, France. **A.** Cervical vertebra 1 in right lateral view. **B.** Cervical vertebrae 3 in ventral view. Note that the number of each of the vertebrae refers to its position in the vertebral column as preserved, not its natural position.

already possess this feature. The ventral paired nutritive foramina are well developed and form ovate depressions. They are close to each other. The lateral surfaces of the centrum beneath the bases of the neural arch are moderately concave lengthwise. The margins of the lateral surfaces show marked rugosities. There are two distinct articular facets for the ribs. The first facet is oval whereas the second is sub-circular. The rib facets are located ventrally and slightly nearer to the posterior than the anterior edge of the centrum. Only partial neural arches are preserved for vertebrae 1, 2, 3, and 9 and a partial isolated one is also preserved. The neural spine appears to have been narrow. The zygapophyses are poorly preserved and few characters are observable. The posterior zygapophyses are small, with elongate and only slightly concave articular surfaces. No groove runs on the posterior surface of the neural spine dorsally to the postzygapophyses.

The undetermined vertebra is not well preserved. Its centrum is shorter than high and the articular facets appear more rounded ventrally than other accompanying vertebrae.

Table 1. Axial skeleton measurements (in mm) of *Cryonectes neustriacus* gen. et sp. nov., MAE 2007. 1.1(J). The number of each vertebra refers to its position in the vertebral column as preserved, not its natural position. ~ approximately; ? missing data.

	No.	Height	Length	Width
Cervical	1	45	48	50
Cervical	2	41	48	54
Cervical	3	~41	45	56
Cervical	4	45	52	56
Cervical	5	~45	~51	~58
Cervical	6	49	50	60
Cervical	7	~48	52	~60
Cervical	8	51	~49	61
Cervical	9	54	~66	?



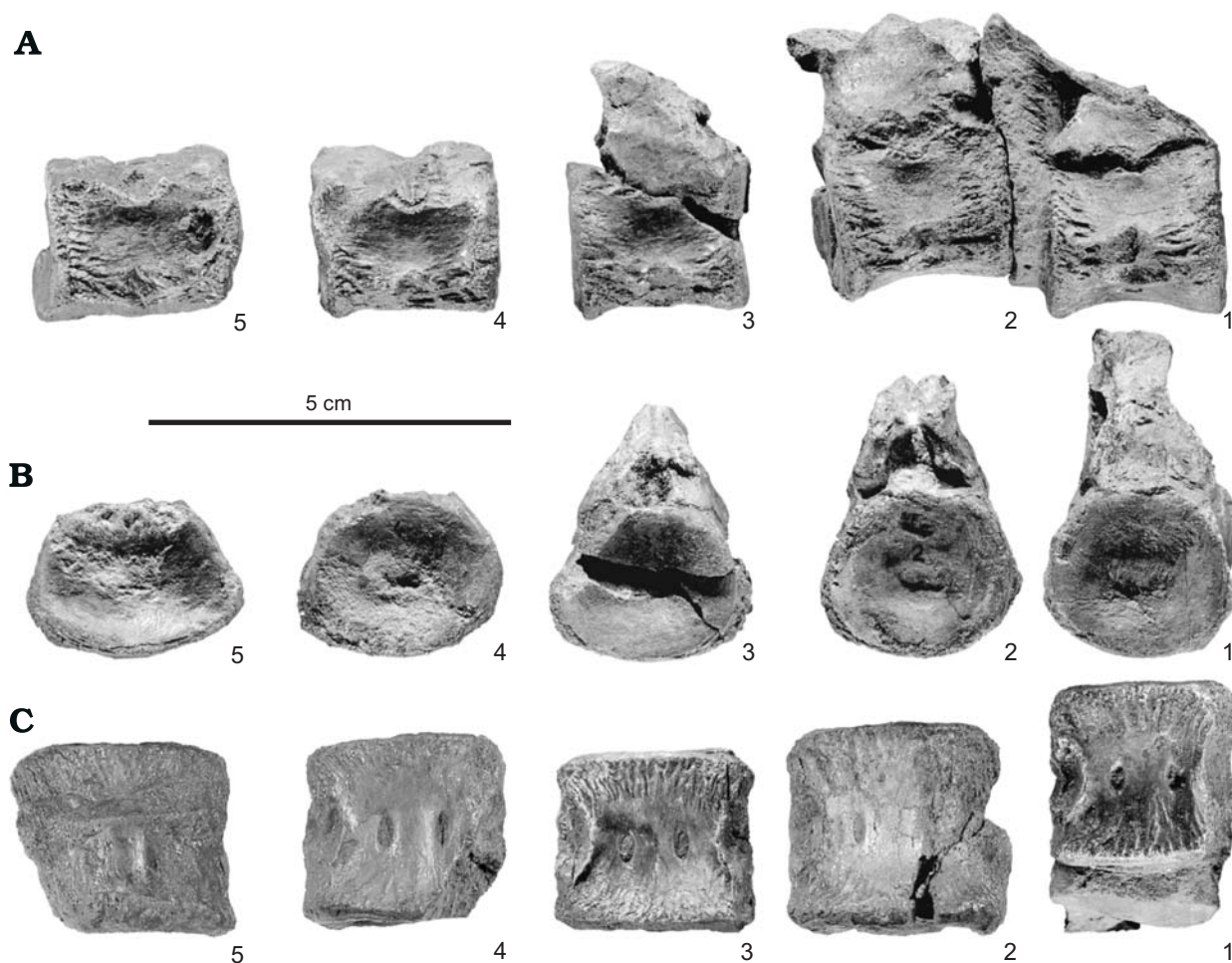


Fig. 9. Pliosaurid pliosaur *Cryonectes neustriacus* gen. et sp. nov., MAE2007.1.1(J), holotype; Late Pliensbachian, Early Jurassic, Calvados, France. A. Cervical vertebrae 1 to 5 in right lateral view. B. Vertebrae 1 to 5 in anterior view. C. Vertebrae 1 to 5 in ventral view.

The two nutritive foramina are laterally placed. The ribs articulations are not preserved.

**Remarks.**—In general morphology *Cryonectes* does not resemble any known plesiosaurian taxon. Long-snouted plesiosaurs are present among pliosauroids and Leptocleidia (Ketchum and Benson 2010). No leptocleidian has been described from the Lower Jurassic, and the absence of a trough-like ventral surface of the posterior ramus of the pterygoid lateral to the posterior interpterygoid vacuity excludes *Cryonectes* from Leptocleidia (diagnosis of Ketchum and Benson 2010). *Cryonectes* differs from all other Early Jurassic pliosauroids in its cranial and postcranial skeleton. *Attenborosaurus conybeari* differs from *Cryonectes neustriacus* in that the mandibular symphysis extends for fewer than seven teeth, the teeth are robust and large and the cervical vertebrae are higher than long (Sollas 1881). *Cryonectes* differs from *Hauffiosaurus*, which possesses 7–10 premaxillary teeth, no anterior interpterygoid vacuity, no ventral mandibular ridge and a ventral keel on cervical vertebrae (O’Keefe 2001; Vincent 2011; Benson et al. 2011b). *Hauffiosaurus longirostris* Benson, Ketchum, Noè, and Gómez-Pérez, 2011b (MCZ 1033; *Macroplata* in White 1940) presents a very long snout,

much more extended than in *Cryonectes neustriacus*, including 10 teeth in each premaxilla and at least 13 tooth positions along its mandibular symphysis (White 1940). *Cryonectes* and *Archaeonectrus* (NHMUK 38525; Owen 1865) share a long, narrow snout and a long mandibular symphysis bearing seven teeth, the ratio between the length of the mandibular symphysis and the length of the mandible is approximately the same. However, the premaxillae of *Archaeonectrus* (NHMUK 38525) are more laterally expanded than those of the specimen studied here; the teeth are not so curved and not so large in *Cryonectes* than in *Archaeonectrus* (NHMUK 38525); *Archaeonectrus* possesses cervical vertebrae with width always exceeding their length and their height and with two deep depressions around the ventral nutritive paired foramina, separated by a sharp keel (NHMUK R.1337; personal observations). *Cryonectes* also differs markedly from Rhomaleosauridae, which exhibit a marked constriction at the premaxillary-maxillary suture, a short and spatulate mandibular symphysis, a bowed mandible, a broad anterior interpterygoid vacuity with round extremities, robust teeth, a ventral keel on the ventral side of its cervical vertebrae and both large nutritive foramina sunk in deep depressions on cervical

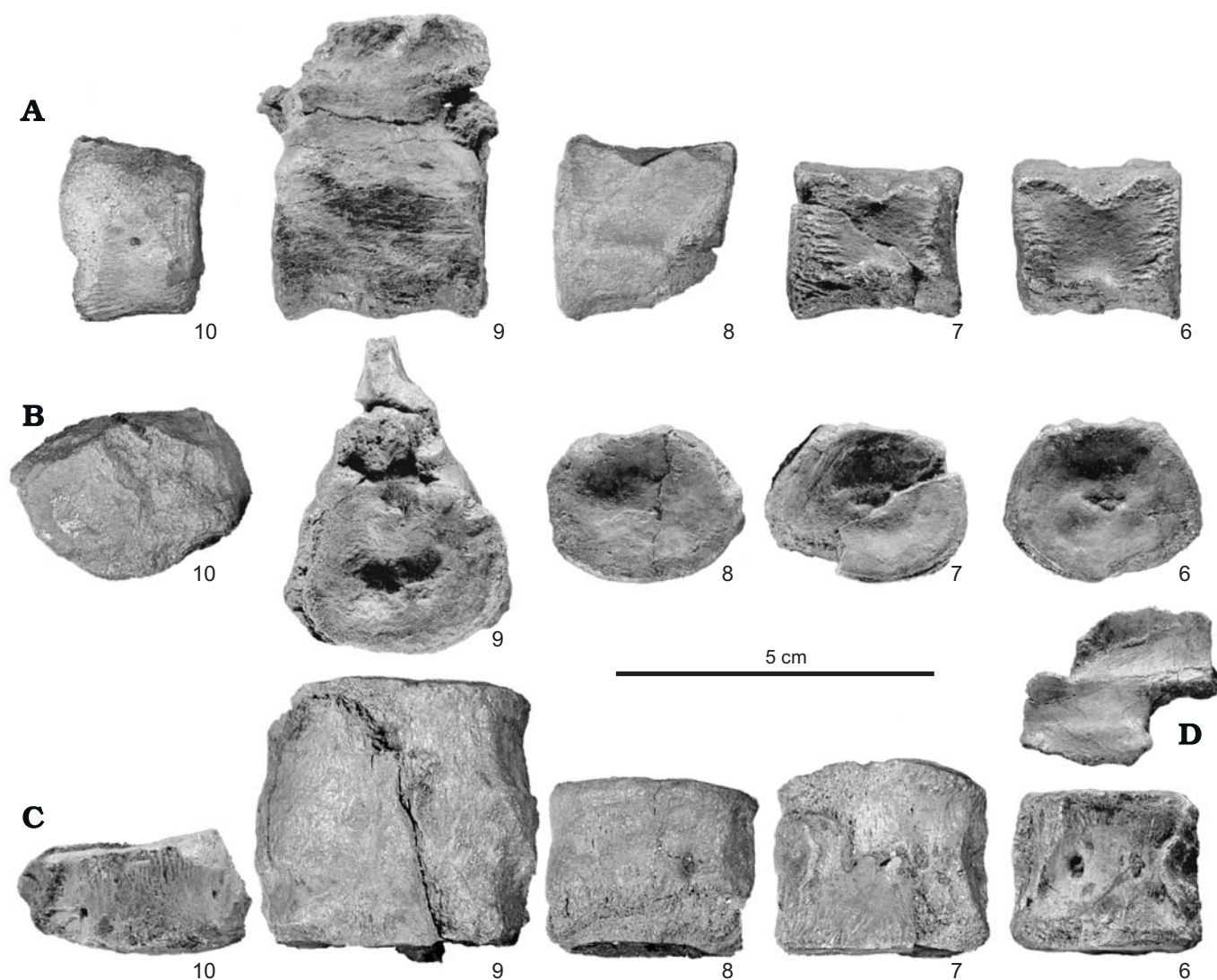


Fig. 10. Pliosaurid plesiosaur *Cryonectes neustriacus* gen. et sp. nov., MAE2007.1.1(J), holotype; Late Pliensbachian, Early Jurassic, Calvados, France. **A.** Vertebrae 6 to 10 in right lateral view. **B.** Vertebrae 6 to 10 in anterior view. **C.** Vertebrae 6 to 10 in ventral view. **D.** An isolated neural arch in left lateral view.

vertebrae (Watson 1909; Taylor 1992; Cruickshank 1994, 1996; O'Keefe 2001; Ketchum and Benson 2010: character 86.0; Ketchum and Smith 2010; Smith and Dyke 2008: characters 60.1 and 64.1; Smith and Vincent 2010).

As noted earlier, the single diagnostic Pliensbachian plesiosaurian taxon is the plesiosaurid *Westphaliasaurus simonsensii* Schwermann and Sander, 2011 from the lower Pliensbachian (*Tragophylloceras ibex* Ammonite Zone), and so slightly older than *Cryonectes*. Since *W. simonsensii* is known from postcranial remains, the two specimens preserve only a few overlapping portions. The cervical vertebrae of *Westphaliasaurus* and *Cryonectes* present both ventral sides almost flat lacking a keel, gently amphicoelous articular facets, with a marked, central pit (the pit of *Cryonectes* being more elongated), and two distinct articular facets for the ribs. Nevertheless, the articular margins of the cervical vertebrae of *Cryonectes* form an abrupt angle with the centrum side, whereas they are more rounded in *Westphaliasaurus*.

*Cryonectes* presents characters that are consistent with the diagnosis of Pliosauridae proposed by Druckenmiller and Russell (2008), namely ventral pterygoid flanges lateral and posterior to the posterior interpterygoid vacuities and a flat ventral surface of the cervical centra. In addition, *Cryonectes* has a coronoid with a long lingual process and cervical centra with flat ventral surfaces, characters that are consistent with the diagnosis of Pliosauridae proposed by Ketchum and Benson (2010).

*Stratigraphic and geographic range.*—Type locality and horizon only.

## Phylogenetic analysis

In order to develop a hypothesis of phylogenetic relationships of *Cryonectes neustriacus* among Plesiosauria, a preliminary cladistic analysis was performed using a data matrix



(Supplementary Online Material at [http://app.pan.pl/SOM/app58-Vincent\\_et\\_al\\_SOM.pdf](http://app.pan.pl/SOM/app58-Vincent_et_al_SOM.pdf): SOM 1) including 15 species scored for 66 characters (SOM 2). Two taxa were specified as outgroup, *Serpianosaurus mirigiolensis* Rieppel, 1989 and *Simosaurus gaillardoti* Meyer, 1842, and these were defined prior to the analysis and constrained to be paraphyletic relative to the ingroup. All characters were coded as unordered. Because missing data may influence cladistic analysis in rather unpredictable ways (Platnick et al. 1991), the phylogenetic reconstruction has been based on a selection of plesiosaurian taxa for which the skeletal morphology is sufficiently known. The characters have been scored using the literature and personal observations. Ontogenetic characters (sensu Brown 1981) have been excluded from the analysis.

A branch-and-bound search for the most parsimonious trees was performed using PAUPv.4.0b10 (Swofford 2002). The parsimony analysis of the data matrix yielded two trees (Fig. 11) of length 133 steps, consistency index excluding uninformative characters (CI) = 0.52, and retention index (RI) = 0.63.

This phylogenetic analysis places the Early Jurassic taxa *Thalassiodracon* and *Hauffiosaurus tomistomimus* as successive basalmost members of the ingroup that consists of three unresolved subclades. The first subclade includes the polycotilid *Dolichorhynchops osborni*, and the leptocleidid *Nichollssaura borealis*, the second consists of two pairs of sister-taxa, *Archaeonectrus rostratus* and *Hauffiosaurus longirostris*, and *Meyerasaurus victor* and *Rhomaleosaurus cramptoni*, and in the third subclade, corresponding to the Pliosauridae, *Cryonectes neustriacus* is recovered in basal position, sister taxon of a clade including *Pliosaurus brachyspondylus*, *Peloneustes philarchus*, *Liopleurodon ferox*, and *Simolestes vorax*.

The present preliminary analysis groups *Archaeonectrus*, *Meyerasaurus*, and *Rhomaleosaurus* into a clade, and in this regard is consistent with the analysis of Smith and Dyke (2008). Our results however differ from those of Ketchum and Benson (2010), who recovered *Archaeonectrus* in a basal position among Plesiosauroidea, and that of O'Keefe (2001), who found a monophyletic clade including, among others, *Meyerasaurus*, *Rhomaleosaurus*, and *Simolestes*. In the present study, the clade including *Archaeonectrus*, *Meyerasaurus*, *Hauffiosaurus*, and *Rhomaleosaurus* is only supported by three unambiguous synapomorphies (7.1: presence of a dorsomedian foramen between premaxillae; 58.1: presence of diastema between premaxillae and maxillae; 64.1: presence of ventral keel on cervical vertebrae). It should be noted that *Archaeonectrus rostratus* has not been re-described since its description by Owen (1865), so that a large part of its skull anatomy remains unclear.

Our analysis places *Cryonectes neustriacus* in a basal position within the clade Pliosauridae (Fig. 11). Pliosauridae is here defined by seven ambiguous synapomorphies and three unambiguous ones (41.1: presence of a ventrally projecting flange of the pterygoid—a synapomorphy of Pliosauroida sensu Druckenmiller and Russell (2008); 62.1: presence of

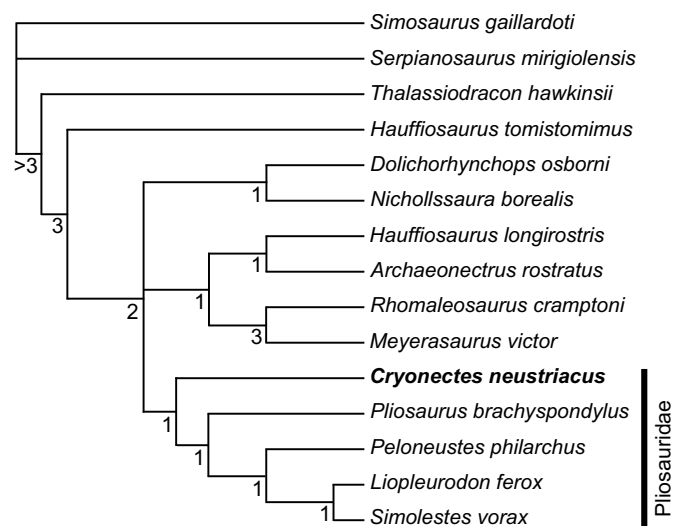


Fig. 11. Cladogram showing the phylogenetic relationships of *Cryonectes neustriacus* gen. et sp. nov. Tree length: 133. CI = 0.52, RI = 0.63. For character list and taxa/ character matrix see SOM 1 and SOM 2. Bremer indices are indicated for each node.

gently convex or platycoelous articular facets for the cervical centra; 33.0: contact between the pterygoids posterior to the anterior interpterygoid vacuity (this character is only known for *Cryonectes* and *Pliosaurus*). Pliosauridae classically includes the taxa *Liopleurodon*, *Simolestes*, *Peloneustes*, and *Pliosaurus* (Druckenmiller and Russell 2008; Smith and Dyke 2008; Ketchum and Benson 2010). Importantly, these taxa are Callovian in age (Noé 2001). If our attribution of *Cryonectes* to the Pliosauridae is correct, our results then imply that the radiation of this clade must have occurred before the late Pliensbachian, more than 15 millions of years earlier than previously thought.

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## References

- Andrews, C.W. 1910. *A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay. Part 1*. 205 pp. British Museum (Natural History), London.



- Andrews, C.W. 1913. *A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay, Based on the Leeds Collection in the British Museum (Natural History)*, London, Part II. 305 pp. British Museum, London.
- Bakker, R.T. 1993. Plesiosaur extinction cycles—Events that mark the beginning, middle and end of the Cretaceous. In: W.G.E. Caldwell and E.G. Kaufman (eds.), *Evolution of the Western Interior Basin. Geological Association of Canada, Special paper 39*: 641–664.
- Bardet, N., Godefroit, P., and Sciau, J. 1999. A new elasmosaurid plesiosaur from the Lower Jurassic of southern France. *Palaeontology* 42: 927–952.
- Bardet, N., Pereda Suberbiola, X., and Jalil, N.-E. 2003. A new polycotyloid plesiosaur from the Late Cretaceous (Turonian) of Morocco. *Comptes Rendus Palevol* 2: 307–315.
- Bardet, N., Fernández, M., Garcia-Ramos, J.C., Pinuela, L., Pereda Suberbiola, X., and Vincent, P. 2008. A juvenile plesiosaur from the Pliensbachian (Lower Jurassic) of Asturias, Spain. *Journal of Vertebrate Paleontology* 28: 258–263.
- Benson, R.B.J., Bates, K.T., Johnson, M.R., and Withers, P.J. 2011b. Cranial anatomy of *Thalassiodraco hawkinsii* (Reptilia, Plesiosauria) from the Early Jurassic of Somerset, United Kingdom. *Journal of Vertebrate Paleontology* 31: 562–574.
- Benson, R.B.J., Ketchum, H.F., Noë, L.F., and Gómez-Pérez, M. 2011a. New information on *Hauffiosaurus* (Reptilia, Plesiosauria) based on a new species from the Alum Shale Member (Lower Toarcian: Lower Jurassic) of Yorkshire, UK. *Palaeontology* 54: 547–571.
- Blainville, H.D. de 1835. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'Erpétologie et d'Amphibiologie. *Nouvelles Annales du Muséum (national) d'Histoire naturelle, Paris, Serie 3* 4: 233–296.
- Bown, P.R. 1987. Taxonomy, evolution and biostratigraphy of late Triassic–early Jurassic calcareous nannofossils. *Special Papers in Paleontology* 38: 1–118.
- Bown, P.R. and Cooper, M.K.E. 1998. Jurassic. In: P.R. Bown (ed.), *Calcareous Nannofossil Biostratigraphy*, 34–85. British Micropalaeontological Society Publication Series, Kluwer Academic Publishers, London.
- Brown, D.S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum (Natural History), Geology* 35: 253–347.
- Brown, D.S., Vincent, P., and Bardet, N. 2013. Osteological redescription of the skull of *Microcleidus homalospondylus* (Sauropterygia, Plesiosauria), from the Lower Jurassic of England. *Journal of Paleontology* 87: 537–549.
- Cruikshank, A.R.I. 1994. Cranial anatomy of the Lower Jurassic pliosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Reptilia: Plesiosauria). *Philosophical Transactions of the Royal Society of London, Series B* 343: 247–260.
- Cruikshank, A.R.I. 1996. The cranial anatomy of *Rhomaleosaurus thorntoni* Andrews (Reptilia, Plesiosauria). *Bulletin of the British Museum (Natural History), Geology* 52: 109–114.
- Cruikshank, A.R.I. 1997. A Lower Cretaceous pliosauroid from South Africa. *Annals of the South African Museum* 105: 207–226.
- Dugué, O., Fily, G., and Rioult, M. 1998. Le Jurassique des côtes du Calvados. *Bulletin trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre* 85: 1–132.
- Druckenmiller, P.S. and Russell A.P. 2008. A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. *Zootaxa* 1863: 1–120.
- Evans, M. 2003. An intriguing new plesiosaur from the Pliensbachian of England. In: T. Kemp, P. Barrett, M. Nowak-Kemp, J. Hay, and B. Thomas (eds.), *51<sup>st</sup> Symposium of Vertebrate Palaeontology and Comparative Anatomy, Oxford, 17–19.09.2003, Abstracts Volume*, 17. Oxford University Museum of Natural History, Oxford.
- Evans, M. 2012. *A New Genus of Plesiosaur (Reptilia: Sauropterygia) from the Pliensbachian (Early Jurassic) of England, and Phylogeny of the Plesiosauria*. 397 pp. Unpublished Ph.D. dissertation, University of Leicester, Leicester.
- Forrest, R. 2006. A plesiosaur from the Pliensbachian of Lincoln. In: E. Buffetaut (ed.), *54<sup>th</sup> Symposium of Vertebrate Palaeontology and Comparative Anatomy, Paris, 12–16.09.2006, Abstracts Volume*, 12. SGF, ENS, Paris.
- Großmann, F. 2007. The taxonomic and phylogenetic position of the Plesiosauroidea from the Lower Jurassic Posidonia Shale of south-west Germany. *Palaeontology* 50: 545–564.
- Ketchum, H.F. 2007. *The Anatomy, Taxonomy and Systematics of Three British Middle Jurassic Pliosauroids (Sauropterygia: Plesiosauria), and the Phylogeny of Plesiosauria*. 273 pp. Unpublished Ph.D. dissertation, University of Cambridge, Cambridge.
- Ketchum, H.F. and Benson, R.B.J. 2010. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. *Biological Reviews* 85: 361–392.
- Ketchum, H.F. and Benson, R.B.J. 2011a. A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early Jurassic pliosauroids. *Special Papers in Palaeontology* 86: 109–129.
- Ketchum, H.F., and Benson, R.B.J. 2011b. The cranial anatomy and taxonomy of *Peloneustes philarchus* (Sauropterygia, Pliosauridae) from the Peterborough Member (Callovian, Middle Jurassic) of the UK. *Palaeontology* 54: 639–665.
- Ketchum, H. and Smith, A.S. 2010. The anatomy and taxonomy of *Macropotamo teneiceps* (Sauropterygia, Plesiosauria) from the Hettangian (Lower Jurassic) of Warwickshire, United Kingdom. *Journal of Vertebrate Paleontology* 30: 1069–1081.
- Mailliot, S., Mattioli, E., Guex, J., and Pittet, B. 2006. The Early Toarcian anoxic crisis, a synchronous event in the Western Tethys? An approach by quantitative biochronology (unitary associations), applied on calcareous nannofossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 240: 562–586.
- Mailliot, S., Elmi, S., Mattioli, E., and Pittet, B. 2007. Calcareous nannofossil assemblages across the Pliensbachian/Toarcian boundary at the Peniche section (Ponta do Trovão, Lusitanian Basin). *Ciências da Terra (UNL)* 15: 1–14.
- Mattioli, E. and Erba, E. 1999. Biostratigraphic synthesis of calcareous nannofossil events in the Tethyan Jurassic. *Rivista Italiana di Paleontologia e Stratigrafia* 105: 343–376.
- Meyer, H. von 1842. *Simosaurus*, die Stumpfschnauze, ein Saurier aus dem Muschelkalke von Lunéville. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde* 1842: 184–197.
- Noë, L.F. 2001. *A Taxonomic and Functional Study of the Callovian (Middle Jurassic) Pliosauroids (Reptilia, Sauropterygia)*. 354 + 182 pp. Unpublished Ph.D. dissertation, University of Derby, Derby.
- O'Keefe, R.F. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). *Acta Zoologica Fennica* 213: 1–63.
- Owen, R. 1842. Report on British fossil reptiles, Part II. *Report of the British Association for the Advancement of Science for 1841* 11: 60–204.
- Owen, R. 1860. On the orders of fossil and recent Reptilia, and their distribution in time. *Report of the British Association for the Advancement of Science for 1859* 29: 153–166.
- Owen, R. 1865. A monograph on the fossil Reptilia of the Liassic formations. Part III. *Monograph of the Palaeontographical Society* 17: 1–40.
- Perilli, N., Comas-Rengifo, M.J., and Goy, A. 2004. Calibration of the Pliensbachian–Toarcian calcareous nannofossil zone boundaries based on ammonites (Basque-Cantabrian area, Spain). *Rivista Italiana di Paleontologia e Stratigrafia* 110: 97–107.
- Persson, P.O. 1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. *Lunds Universitets Arsskrift, Serie 2* 59: 1–59.
- Platnick, N.I., Griswold, C.E., and Coddington, J.A. 1991. On missing entries in cladistic analysis. *Cladistics* 7: 337–343.
- Rees, J. and Bonde, N. 1999. Plesiosaur remains from the Early Jurassic Hasle Formation, Bornholm, Denmark. In: E. Hoch and A.K. Brantsen (eds.), *Secondary Adaptation to Life in Water, Copenhagen, 13–17.09.1999, Abstracts Volume*, 70. Geologisk Museum, Copenhagen.
- Rieppel, O. 1989. A new pachypleurosaur (Reptilia: Sauropterygia) from

- the Middle Triassic of Monte San Giogio, Switzerland. *Philosophical Transactions of the Royal Society of London, Series B* 323: 1–73.
- Rosales, I., Quesada, S., and Robles, S. 2004. Paleotemperature variations of Early Jurassic seawater recorded in geochemical trends of belemnites from the Basque-Cantabrian basin, northern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203: 253–275.
- Sato, T. 2003. *Terminonatator ponteixensis*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Saskatchewan. *Journal of Vertebrate Paleontology* 23: 1–89.
- Sato, T. 2005. A new polycotylid plesiosaur (Reptilia: Sauropterygia) from the Upper Cretaceous Bearpaw Formation of Saskatchewan, Canada. *Journal of Paleontology* 79: 969–980.
- Schulz, G. 1858. *Descripción geológica de Asturias. First Edition*. 138 pp. Imprenta y Librería de Don José Gonzalez, Madrid.
- Schweremann, L. and Sander, M. 2011. Osteologie und Phylogenie von *Westphaliasaurus simonsensii*: Ein neuer Plesiosauride (Sauropterygia) aus dem Unteren Jura (Pliensbachium) von Sommersell (Kreis Höxter), Nordrhein-Westfalen, Deutschland. *Geologie und Paläontologie in Westfalen* 79 (1): 1–56.
- Sciau, J., Crochet, J.-Y., and Mattei, J. 1990. Le premier squelette de plésiosaure de France sur le Causse du Larzac (Toarcien, Jurassique inférieur). *Geobios* 23: 111–116.
- Seeley, H. 1874. Note on some generic modifications of the plesiosaurian pectoral arch. *Quarterly Journal of the Geological Society of London* 30: 436–449.
- Smith, A.S. 2008. Plesiosaurs from the Pliensbachian (Lower Jurassic) of Bornholm, Denmark. *Journal of Vertebrate Paleontology* 28: 1213–1217.
- Smith, A.S. and Dyke, G.J. 2008. The skull of the giant predatory pliosaur *Rhomaleosaurus cramptoni*: implications for plesiosaur phylogenetics. *Naturwissenschaften* 95: 975–980.
- Smith, A.S. and Vincent, P. 2010. A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. *Palaeontology* 53: 1049–1063.
- Sollas, W.J. 1881. On a new species of *Plesiosaurus* (*P. conybeari*) from the Lower Lias of Charmouth; with observation on *P. macrocephalus*, Stutchbury, and *P. brachycephalus*, Owen. *Quarterly Journal of the Geological Society of London* 37: 440–480.
- Storrs, G.W. 1995. A juvenile specimen of ?*Plesiosaurus* sp. from the Lias (Lower Jurassic, Pliensbachian) near Charmouth, Dorset, England. *Proceedings of the Dorset Natural History and Archaeology Society* 116: 71–75.
- Storrs, G.W. 1997. Morphological and taxonomic clarification of the genus *Plesiosaurus*. In: J.M. Callaway and E.L. Nicholls (eds.), *Ancient Marine Reptiles*, 145–190. Academic Press, London.
- Storrs, G.W. and Taylor, M.A. 1996. Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian/Hettangian) of Street, Somerset, England. *Journal of Vertebrate Paleontology* 16: 403–420.
- Suan, G., Mattioli, E., Pittet, B., Mailliot, S., and Lécuyer, C. 2008. Evidence for major environmental perturbation prior to and during the Toarcian (Early Jurassic) oceanic anoxic event from the Lusitanian Basin, Portugal. *Paleoceanography* 23 (PA1202): 1–14.
- Suan, G., Mattioli, E., Pittet, B., Lécuyer, C., Suchéras-Marx, B., Duarte, L.V., Philippe, M., Reggiani, M.L., and Martineau, F. 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. *Earth and Planetary Science Letters* 290: 448–458.
- Swofford, D.L. 2002. *PAUP\*: Phylogenetic Analysis Using Parsimony (\* and other methods) for Macintosh. Version 4.0b10*. Sinauer Associates, Sunderland.
- Tarlo, L.B.H. 1960. A review of the Late Jurassic Pliosaurus. *Bulletin of the British Museum (Natural History), Geology Series* 4: 147–189.
- Taylor, M.A. 1992. Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria; Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. *Philosophical Transactions of the Royal Society of London, Series B* 335: 247–280.
- Taylor, M.A. and Cruickshank, A.R.I. 1993. Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. *Philosophical Transactions of the Royal Society of London, Series B* 341: 399–418.
- Thulborn, T. and Warren, A. 1980. Early Jurassic plesiosaurs from Australia. *Nature* 285: 224–225.
- Veiga de Oliveira, L.C., Duarte, L.V., Perilli, N., Rodrigues, R., and Lemos, V.B. 2005. Estratigrafia química (COT,  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ ) e nanofósseis calcários na passagem Pliensbaquiano–Toarciano no perfil de Peniche (Portugal): resultados preliminares. *Pesquisas em Geociências* 32: 3–16.
- Vincent, P. 2011. A re-examination of *Hauffiosaurus zanoni*, a pliosauroid from the Toarcian (Early Jurassic) of Germany. *Journal of Vertebrate Paleontology* 31: 340–351.
- Vincent, P. 2012. Re-description of a basal plesiosaur (Reptilia, Sauropterygia) from the Lower Jurassic of England. *Journal of Paleontology* 86: 1187–1196.
- Vincent, P. and Benson, R.B.J. 2012. *Anningasaura*, a basal plesiosaurian (Reptilia, Plesiosauria) from the Lower Jurassic of Lyme Regis, United Kingdom. *Journal of Vertebrate Paleontology* 32: 1049–1063.
- Vincent, P. and Smith, A.S. 2009. A redescription of *Plesiosaurus propinquus* Tate & Blake, 1876 (Reptilia, Plesiosauria), from the Lower Jurassic (Toarcian) of Yorkshire, England. *Proceedings of the Yorkshire Geological Society* 57: 151–160.
- Watson, D.M.S. 1909. A preliminary note on two new genera of Upper Liassic plesiosaurs. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 54: 1–28.
- Welles, S.P. 1943. Elasmosaurid plesiosaurs with a description of new material from California. *Memoirs of the University of California* 13: 125–254.
- White, T.E. 1940. Holotype of *Plesiosaurus longirostris* Blake, and classification of the plesiosaurs. *Journal of Paleontology* 14: 451–467.