

## A JUVENILE PLESIOSAUR FROM THE PLIENSBACHIAN (LOWER JURASSIC) OF ASTURIAS, SPAIN

NATHALIE BARDET,<sup>\*1</sup> MARTA FERNÁNDEZ,<sup>2</sup> JOSÉ CARLOS GARCÍA-RAMOS,<sup>3</sup>  
XABIER PEREDA SUBERBIOLA,<sup>4</sup> LAURA PIÑUELA,<sup>3</sup> JOSÉ IGNACIO RUIZ-OMEÑACA,<sup>3</sup> and PEGGY VINCENT<sup>1</sup>;

<sup>1</sup>UMR 5143 du CNRS, Département Histoire de la Terre, Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris, France, bardet@mnhn.fr, pvincent@mnhn.fr; <sup>2</sup>Departamento Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque, 1900 La Plata, Argentina, martafer@museo.fcym.unlp.edu.ar; <sup>3</sup>Museo del Jurásico de Asturias, 33328 Colunga, Spain, jcgramos@geol.uniovi.es, lpinuela@geol.uniovi.es, jigruiz@unizar.es; <sup>4</sup>Universidad del País Vasco/Euskal Herriko Unibersitatea, Facultad de Ciencia y Tecnología, Departamento de Estratigrafía y Paleontología, Apdo. 644, 48080 Bilbao, Spain, xabier.pereda@lg.ehu.es

Mesozoic marine reptiles are poorly known in Spain (see Quesada et al., 1998 for a bibliography). Up to now, the plesiosaur record of Spain consisted only of fragmentary remains coming from the Jurassic of Asturias (Schulz, 1858; Ruiz-Omeñaca et al., 2006) and the Cretaceous of the Basque Country and Castellón (Bardet et al., 1999a; Yagüe et al., 2003).

The Asturias record includes (1) an historical nineteenth century specimen (now lost)—one of the oldest fossil reptiles from Spain—briefly mentioned as “part of a skeleton and paddles of a plesiosaur, which largest vertebrae reach a diameter of 6 cm, found in Lower Jurassic rocks (most probably Rodiles Formation, Pliensbachian, J. C. G.-R. pers. obs.), between the localities of El Puntal and Tazones in Villaviciosa” (Schulz, 1858:108). Unfortunately, no figure was provided and we have no definitive certitude about the plesiosaurian affinities of this specimen. (2) isolated remains from the Lower Jurassic (Hettangian-Sinemurian; Gijón Formation) and Upper Jurassic (Kimmeridgian; Tereñes Formation) of the same area (Ruiz-Omeñaca et al., 2006).

Here we report on the discovery of an immature plesiosaur from the Pliensbachian of Asturias. It is the most complete plesiosaur specimen found in Spain, one of the very few juvenile plesiosaurs known worldwide, and an additional specimen from the very poor Pliensbachian fossil record.

**Institutional Abbreviations**—**MUJA**, Museo del Jurásico de Asturias (Colunga, Spain); **SMNS**, Staatliches Museum für Naturkunde Stuttgart (Germany).

### GEOLOGICAL BACKGROUND

The plesiosaur specimen was found in the Santa Mera cliffs, near Villaviciosa in Asturias, Northern Spain (Fig. 1A). As with most of the Mesozoic vertebrate remains and trackways from Asturias (García-Ramos and Gutiérrez-Claverol, 1995; García-Ramos et al., 2002, 2004), the plesiosaur specimen was unearthed at the foot of sea cliffs. The hard and dark matrix with pyrite in which the fossil is imbedded is part of the Santa Mera Member, Rodiles Formation (Valenzuela et al., 1986) of lower Pliensbachian age (*Jamesoni* Zone; Suárez Vega, 1974) (Fig. 1B). The Santa Mera Member of the Rodiles Formation consists of alternating limestones and dark marls, indicating an outer carbonate ramp

environment (García-Ramos et al., 2004). The region was part of an epeiric seaway that connected the northern interior Boreal sea to the southern Tethyan Ocean (Aurell et al., 2003; Robles et al., 2004). This specimen was probably exposed for a long time and could correspond to vertebrate remains (referred to as ichthyosaur) from the same locality and horizon previously mentioned by Suárez Vega (1974).

### SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860  
PLESIOSAURIA de Blainville, 1835  
PLESIOSAUROIDEA (Gray, 1825) Welles, 1943  
Gen. et sp. indet.  
(Fig. 2, Table 1)

### Referred Material

MUJA 0518, incomplete juvenile skeleton, preserved in five blocks (MUJA 0518a-e) and isolated elements (MUJA 0518f-m) (Fig. 2, Table 1) from Santa Mera near Villaviciosa, Asturias, Northern Spain; Santa Mera Member, Rodiles Formation, lower Pliensbachian age (*Jamesoni* Zone).

### Description

**Preservation**—The specimen is preserved in five blocks (MUJA 0518a-e). Some elements were recovered free of matrix (MUJA 0518f-m), probably due to sea wave erosive action. Eight vertebral centra including three cervicals, two pectorals and three dorsals, seven neural arches, sixteen ribs and eight gastralia, one humerus, one incomplete femur, one pubis, one ilium and three additional indeterminate bones (possibly the other ilium and two epipodial bones) have been recovered. Based on their size and proportions, it can be reasonably assumed that all these bones come from the same individual.

**Ontogenetic Stage of Development**—The small size of the specimen (vertebral centra about 3 cm long), its poor degree of ossification with neural arches and ribs not fused to centra, almost flat vertebral articular surfaces, and propodials with poorly defined extremities, tuberosity/trochanter and rugosities, suggest that it was a juvenile (*sensu* Brown, 1981). Curiously, the Asturias specimen lacks other typical juvenile characters such as deep V-shaped neuro-central lateral suture, low dorsal neural spines and semi-lunate pubis (Brown, 1981; Storrs, 1995, 1997). The size of the specimen indicates it was a young (estimated body length about 1.8 m) but not a neonate individual.

\*Corresponding author.

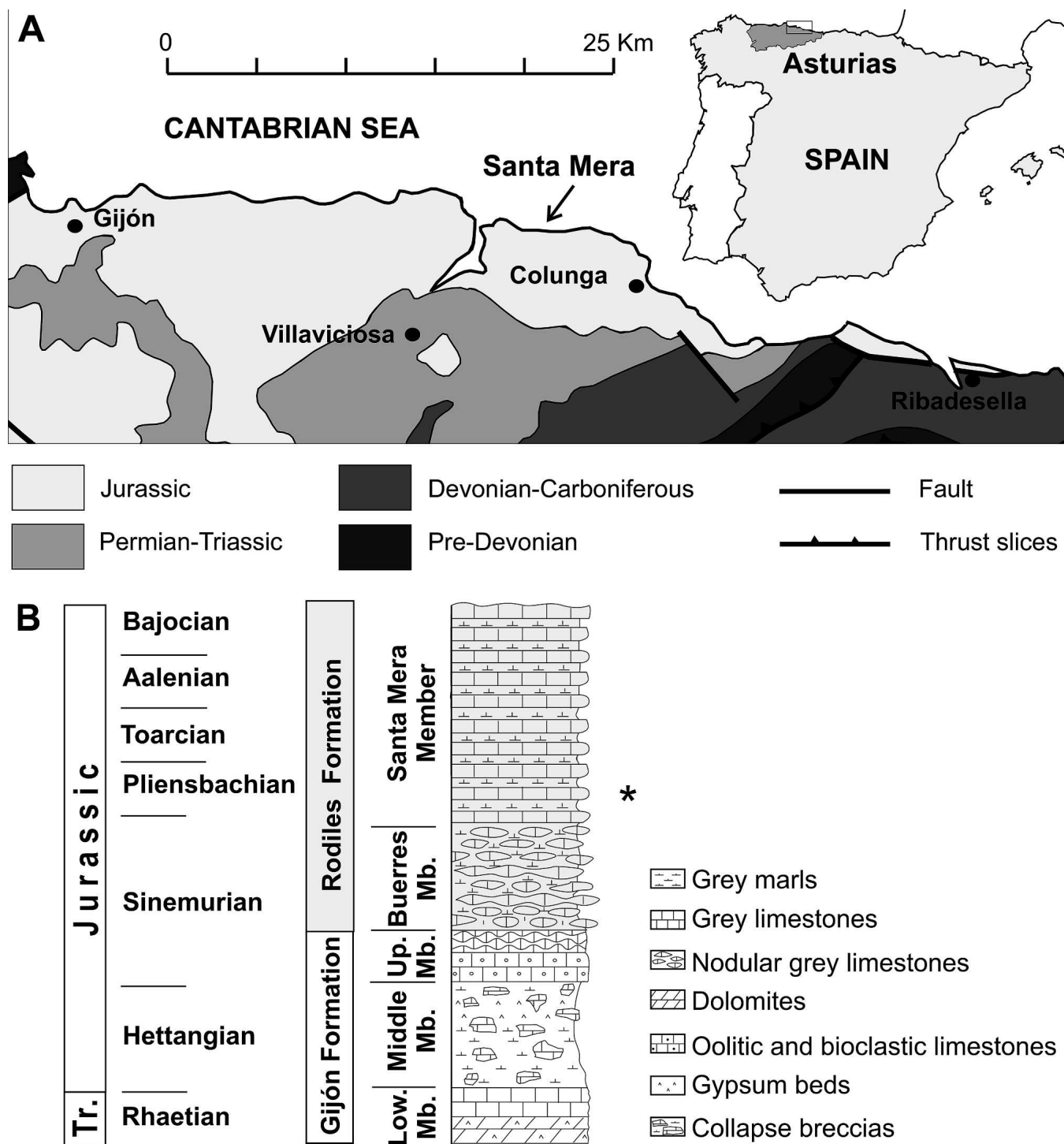


FIGURE 1. **A**, Geographical (Santa Mera) and **B**, stratigraphical (asterisk) locations of the specimen in northern Spain.

**Axial Skeleton**—All centra are slightly wider than long and high ( $W > L > H$ ) (Fig. 2, Table 1). They bear slightly concave articular surfaces with rugose margins, small central pit, large foramina subcentralia and slightly concave neuro-central lateral suture. The cervical centra bear two rib processes, slightly dumbbell-shaped articulation surfaces and slightly concave ventral surface without a keel (Fig. 2A, C, E). The pectoral centra bear large single-headed rib facets (Fig. 2A, C). The dorsal centra exhibit round articular surfaces and convex lateral surfaces (Fig. 2A, D).

The neural arches are strongly built and bear large pre- and postzygapophyses which are narrower than the centrum (Fig. 2A, C, F). The neural spines are astonishingly high for a juvenile specimen, blade-like, with a slightly convex or straight apex. They probably correspond to neural arches from the dorsal series.

They are sixteen ribs and eight gastralia (Fig. 2), including small hatched-shaped double-headed cervical ribs, long and robust recurved single-headed dorsals ribs, a short and robust sacral rib, and typically sigmoidal gastralia. The dorsal ribs and

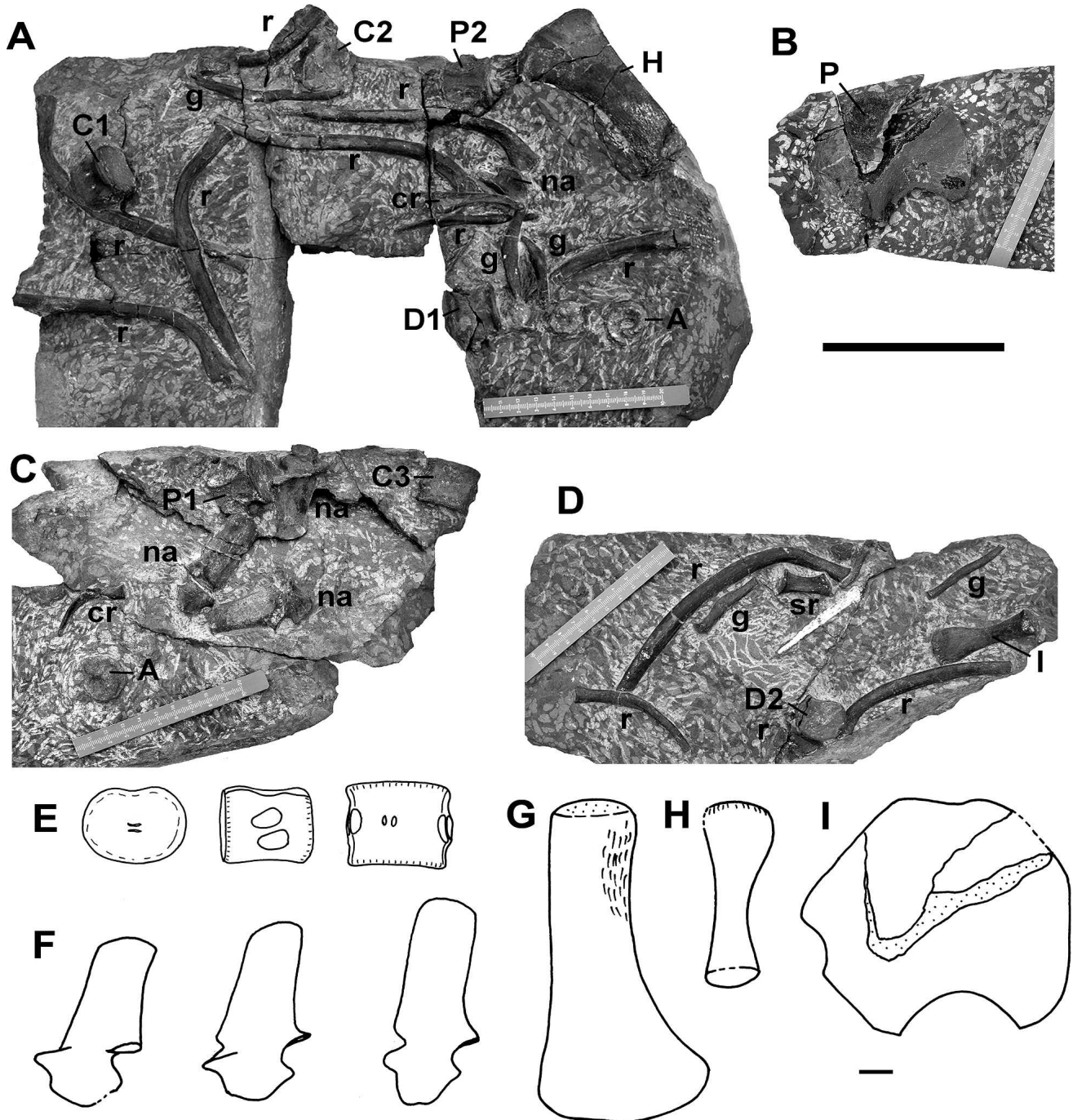


FIGURE 2. MUJA 0518, Santa Mera near Villaviciosa, Asturias, Northern Spain; Rodiles Formation, Santa Mera Member, Lower Jurassic, Pliensbachian age (*Jamesoni* Zone). **A**, MUJA 0518a (left) and 0518c (right); **B**, MUJA 0518e; **C**, MUJA 0518d; **D**, MUJA 0518b; **E**, detail drawings of C: cervical C3 in articular, lateral and ventral views; **F**, detail drawings of C: neural arches in lateral views; **G**, detail drawing of A: right humerus in ventral view; **H**, detail drawing of D: right ilium in ventral view; **I**, detail drawing of B: pubis. Scale = 10 cm for A–D and 1 cm for E–I. **Abbreviations:** A, ammonite; C1–3, cervical vertebrae; cr, cervical rib; D1–2, dorsal vertebrae; g, gastralia; H, humerus; I, ilium; na, neural arch; P, pubis; P1–2, pectoral vertebrae; r, rib; sr, sacral rib.

gastralia are probably pachyostotic, being swollen in their median part, which is in agreement with the ontogenetical growth pattern proposed for plesiosaurs by Wiffen et al. (1995).

**Appendicular Skeleton**—The ventral side of the right humerus is exposed on block MUJA 0518c (Fig. 2A, G; Table 1). It is approximately 11.1 cm long. Discrete rugosities are present on the anterior surface and on the dorsal third of the ventral surface, as usually so in plesiosaurs (Brown, 1981). The proximal

extremity is rounded in cross-section and regularly convex from side to side. The tuberosity is poorly differentiated from the rugose head. The distal extremity is compressed dorsoventrally, convex, and does not bear distinct surfaces for radius and ulna, a juvenile trait. The shaft of the bone is almost straight anteriorly and convex posteriorly, a primitive character found in Liassic plesiosaurs (Storrs, 1997; Bardet et al., 1999b; O'Keefe, 2001).

TABLE 1. Measurements (in mm) of MUJA 0518 main bones.

Vertebrae	Length	Width	Height
Cervical 1	27	31	25
Cervical 2	?	34	25
Cervical 3	26	31	24
Pectoral 1	25	30	>25
Pectoral 2	25	30	23
Dorsal 1	27	31	26
Dorsal 2	?	28	29

Appendicular bones	Length	Proximal width	Median width	Distal width
Humerus	111	28	30	57
Ilium	58	16	10	22
Pubis	85	85	30	57

Vertebra numbers do not refer to anatomical position but only to their location on matrix blocks.

The proximal half of a left femur (MUJA 0518m) has been found free of matrix. The proximal head is rounded, and the trochanter is poorly differentiated from the head. The femur is oval in cross-section at mid-part. Both anterior and posterior edges are straight. Discrete rugosities are present on the ventral surface.

A presumed right ilium is exposed in ventral view on block MUJA 0518b (Fig. 2D, H). It is narrow and half the size of the humerus, being 5.8 cm long. The proximal end is broad and flattened and the distal end is rounded in cross-section, both being convex. The shaft is narrow and not twisted. The anterior and posterior edges are concave.

It is unknown if the damaged pubis (block MUJA 0518 e) is the left or right element (Fig. 2B, I). The medial edge is straight and the lateral one is slightly convex with a small notch located just anterior to the femoral articulation surface. The anterior surface is regularly convex with also a small notch located near the antero-medial corner. The posterior surface has poorly defined articulation surfaces for the femur and ischium. The surface corresponding to the obturator foramen is concave.

### Systematical Attribution

The occurrence of foramina subcentralia on the vertebral centra, high dorsal neural spines, massive propodials with expanded distal end and dorsal trochanter/tuberosity as well as large, plate-like pubis lacking iliac articulation, are plesiosaurian synapomorphies (Brown, 1981; O'Keefe, 2001).

Because the Asturian plesiosaur exhibits centra slightly wider than long and high, cervical centra bearing two rib articular surfaces and no ventral keel, and blade-like dorsal neural spines, it can be referred to the Plesiosauroidea (Brown, 1981; Bardet et al., 1999b; O'Keefe, 2001).

The Asturian specimen has been compared to a number of Liassic plesiosauroids from the Hettangian-Sinemurian of England (*Plesiosaurus dolichodeirus* Conybeare, 1824, see Storrs, 1997; *Eretmosaurus rugosus* (Owen, 1840), see Brown, 1981, N.B. pers. obs.), the Pliensbachian of England (?*Plesiosaurus* sp., see Storrs, 1995) and the Toarcian of France (*Occitanosaurus tournemirensis* (Sciau, Crochet, and Mattei, 1990), see Bardet et al., 1999b), Germany (*Seeleyosaurus guilelmiimperatoris* (Dames, 1895), see Fraas, 1910 and Grossman, 2006; *Hydrorion brachypterygius* (Huene, 1923), see Grossman, 2006) and England (*Microcleidus homalospondylus* (Owen, 1865), P.V. pers. obs.).

Some of these taxa (*Plesiosaurus*, *Seeleyosaurus*, *Hydrorion*) include juvenile referred specimens. This new discovery is thus of notable interest as it adds to our knowledge of the plesiosaur

earliest ontogenetical growth stages and permits interesting comparisons between immature plesiosaur specimens, which remain very scarce worldwide (see Cruickshank, 1994; Storrs, 1995; Wahl, 2006 for a review).

First of all, MUJA 0518 differs from the only plesiosaur—and moreover juvenile specimen—identified in the Pliensbachian stage up to now. This specimen, referred to as ?*Plesiosaurus* sp. by Storrs (1995), bears short cervicals ( $H > L$ ) with monocephalous ribs and a ventral keel. Though Storrs (1995) mentioned that the vertebrae of this specimen are identical to that of *Plesiosaurus dolichodeirus*, this systematic attribution could be questioned as at least the suite of characters exhibited by the cervical vertebrae is typically pliosauroid (see O'Keefe, 2001).

As a whole, MUJA 0518 exhibits cervical vertebrae with bi-cephalous ribs, a Plesiosauria plesiomorphy present in *Plesiosaurus*, *Microcleidus*, *Hydrorion*, *Seeleyosaurus* (including its junior synonym *Plesiopterys*, see Grossman, 2006) and *Occitanosaurus*. Monocephalous ribs are only known in *Eretmosaurus*.

The cervical centra of MUJA 0518 are moderately elongated ( $W > L > H$ ), as in *Plesiosaurus*, *Seeleyosaurus*, *Hydrorion* and *Eretmosaurus*. In *Microcleidus* and *Occitanosaurus* the centra are more elongated ( $L > W > H$ ).

All centra of MUJA 0518 bear curiously slightly concave neuro-central lateral suture. This suture is typically deeply V-shaped in *Plesiosaurus* and *Seeleyosaurus* (*Plesiopterys*) juvenile specimens (Storrs, 1995, 1997; O'Keefe, 2004).

The neural spines of MUJA 0518, considered as probably dorsal ones, are high for a juvenile. But they are lower than those of adult specimens of *Plesiosaurus*, *Seeleyosaurus*, *Hydrorion*, *Microcleidus*, *Occitanosaurus* and of *Seeleyosaurus* juvenile specimen (*Plesiopterys*). On the contrary, they are higher than those of *Hydrorion* juvenile specimen SMNS 51141 (P.V., pers. obs., see Grossman, 2006). This could imply that MUJA 0518 was probably older than *Hydrorion* juvenile SMNS 51141 (size about 1.5 m) but younger than *Seeleyosaurus* one (*Plesiopterys*) (size about 2.2 m).

The humerus bears a shaft about twice the distal extremity width, poorly defined extremities and tuberosities/rugosities, and an almost straight anterior surface. In all other Liassic plesiosauroids, the humerus is proportionally longer and slender (shaft more than twice the distal width) with expanded extremities. The anterior face is very convex in *Plesiosaurus* giving the bone a bowed shaft but it is almost straight in all other Liassic plesiosauroids. Only the juvenile specimen of *Hydrorion* (SMNS 51141) shows a stouter and shorter shaft. It should be noted that these characters are probably related to ontogeny, not to systematic differences.

The ilion is plesiomorphically not twisted (Storrs, 1995), as in *Plesiosaurus* and the juvenile specimen of *Seeleyosaurus* (*Plesiopterys*, SMNS 16812; see O'Keefe, 2004). In other Liassic plesiosauroids the ilion is twisted. In MUJA 0518, as well as in *Seeleyosaurus* juvenile specimen (*Plesiopterys*), the ilion is more slender—especially the flat sacral end—than in other Liassic plesiosauroids, but this could be related to ontogeny.

The pubis is not semi-lunate as in juveniles but typically notched anteriorly and laterally, as in *Seeleyosaurus* (including *Plesiopterys*) and *Occitanosaurus*. It is semilunate, even in adult specimens, in *Plesiosaurus*, *Hydrorion*, *Microcleidus* and *Eretmosaurus*.

In summary, the Asturias specimen shares with *Seeleyosaurus* cervical centra moderately elongated, a not twisted ilion and a notched pubis. However, due to the incomplete nature of the specimen, a precise identification is not possible and the specimen is here referred to an indeterminate Plesiosauroidea.

TABLE 2. Plesiosaurian specimens mentioned or described from the Pliensbachian stage worldwide.

	Ammonite zone	Plesiosaur taxa	Material	Locality	Formation	Reference
Pliensbachian	<i>P. spinatum</i>					
	<i>A. margaritatus</i>	<i>M. cf. homalospondylus</i> <i>P. cf. dolishodeirus</i> <i>S. dawkinsi</i> <i>? Plesiosaurus</i> sp.	Vertebrae Vertebrae Girdle elements Incomplete postcranial skeleton (juvenile)	Lorraine, France	?	Persson, 1963
	<i>P. davoei</i>		Subcomplete skeleton (adult)	Dorset, UK	Green Ammonite Beds	Storrs, 1995
	<i>T. ibex</i>	New taxon?		Gloucestershire, UK	Charmouth MudStone Fm.	Evans, 2003
	<i>U. jamesoni</i>	Plesiosaur	Teeth, vertebrae, limb bones	Denmark	Haste Fm.	Rees and Bonde, 1999
		Plesiosauroid	Incomplete postcranial skeleton (juvenile)	Asturias, Spain	Rodiles Fm.	This work
Unknown zone		<i>Archaeonectrus</i> n.sp.	Incomplete cranium, vertebrae	Normandie, France	Calcaire à Belemnites Fm. ( <i>Margaritatus</i> or <i>Jamesoni</i> zone)	Vincent, 2004
Possible other stage		Plesiosaur?	Vertebrae	Asturias, Spain	Rodiles Fm. ?	Schulz, 1858
		<i>Plesiosaurus</i> sp.	Incomplete skull	Portugal	Charmouthian or Toarcian	Sauvage, 1897–1898
		Plesiosauroid	Vertebrae	Queensland, Australia	Evergreen Fm. Pliensbachian or Toarcian	Thulborn and Warren, 1980

Standard Ammonite Zone from Harland et al. (1989).

## DISCUSSION

### Filling the “Pliensbachian gap”

Plesiosaurian abundance and diversity are particularly high during the Jurassic, especially in the Lower Early Jurassic of England (Hettangian–Sinemurian) and Germany (Toarcian), as well as in the Middle–Upper Mid–Late Jurassic of England and France (Brown, 1981). On the contrary, plesiosaur remains are very scarce in the Pliensbachian (Lower Jurassic) and Aalenian (Middle Jurassic) rocks.

Numerous marine reptile genera are known in the under- and overlying stages of the “Pliensbachian gap” (i.e., Evans, 2003; O’Keefe, 2004; Maisch & Reisdorf, 2006): six plesiosaurs and four ichthyosaurs in the Sinemurian, as well as eight plesiosaurs, four ichthyosaurs and three thalattosuchian crocodiles in the Toarcian (Bardet, 1995; Mc Gowan & Motani, 2003; O’Keefe, 2001, 2004). Conversely, from the Pliensbachian, only two ichthyosaur genera are known (Mc Gowan & Motani, 2003) and, concerning plesiosaurs, only the genus *Plesiosaurus* has been identified (Storrs, 1995).

Indeed, up to recently, only fragmentary and indeterminate plesiosaur remains were described or briefly mentioned from the Pliensbachian worldwide, the age of some of them being moreover uncertain (Schulz, 1858; Sauvage, 1897–1898; Persson, 1963; Thulborn & Warren, 1980; Rees & Bonde, 1999) (Table 2).

Recent more complete discoveries made in England (Storrs, 1995; Evans, 2003), France (Vincent, 2004) and the here described specimen from Spain, permit to significantly improve our knowledge of Pliensbachian plesiosaurs (Table 2). Moreover, the Asturian specimen represents one of the oldest Pliensbachian occurrences (basal Pliensbachian, *Jamesoni* Zone). These records suggest that the paucity of Pliensbachian plesiosaurs may be more due to incomplete sampling than to their actual absence.

**Acknowledgments**—Support provided by Protocolo de colaboración CN-04-226 between the Consejería de Cultura, Comunicación y Turismo del Principado de Asturias and Universidad de Oviedo, and Consejo Nacional de Investigaciones Científicas y Tecnológicas (grant PIP5156). Contribution to the “Convenio específico de colaboración / Convention de Collaboration” between the UPV/EHU (Bilbao), the CNRS (France) and the MNHN (Paris, France). Thanks to A. García-Ramos for the photographs.

## LITERATURE CITED

- Aurell, M., S. Robles, B. Bádenas, I. Rosales, S. Quesada, G. Meléndez, and J. C. García-Ramos. 2003. Transgressive-regressive cycles and Jurassic palaeogeography of northeast Iberia. *Sedimentary Geology* 162:239–271.
- Bardet, N. 1995. Evolution et extinction des reptiles marins au cours du Mésozoïque. *Palaeovertebrata* 24(3-4):177–283.
- Bardet, N., J. C. Corral, and X. Pereda Suberbiola. 1999a. Marine reptiles from the uppermost Cretaceous of the Laño quarry (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Alava* 14 (Num. Esp. 1):373–380.
- Bardet, N., P. Godefroit, and J. Sciau. 1999b. A new elasmosaurid genus from the Upper Lias of Southwestern France. *Palaeontology* 42: 927–952.
- 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 d’Histoire naturelle de Paris* 3:233–296.
- Brown, D. S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauroidea. *Bulletin British Museum Natural History (Geology)* 35: 253–347.
- Conybeare, W. D. 1824. On the discovery of an almost perfect skeleton of *Plesiosaurus*. *Transactions of the Geological Society of London, Second series* 1:381–389.
- Cruickshank, A. R. I. 1994. A juvenile plesiosaur (Plesiosauroidea: Reptilia) from the Lower Lias (Hettangian: Lower Jurassic) of Lyme Regis, England: a plesiosauroid-plesiosauroid intermediate? *Zoological Journal of the Linnean Society* 112:151–178.
- Dames, W. 1895. Die Plesiosaurier der süddeutschen Liasformation. *Physikalische und Mathematische Abhandlungen der königlichen Akademie der Wissenschaften zu Berlin* 1895:1–83.
- Evans, M. 2003. An intriguing new plesiosaur from the Pliensbachian of England. 51st Symposium of Vertebrate Palaeontology and Comparative Anatomy, Oxford, Abstracts: p. 17.
- Fraas, E. 1910. Plesiosaurier aus dem oberen Lias von Holzmaden. *Palaeontographica* 57:105–140.
- García-Ramos, J. C., and M. Gutiérrez-Claverol. 1995. La Geología de la Franja Costera Oriental y de la Depresión Prelitoral de Oviedo–Cangas de Onís; pp. 247–258 in C. Aramburu and F. Bastida (eds.), *Geología de Asturias*. Gijón, Spain: Trea.
- García-Ramos, J. C., J. Lires, and L. Piñuela. 2002. Dinosaurios. Rutas por el Jurásico de Asturias. *La Voz de Asturias*, Lugones, Spain, 204 pp.
- García-Ramos, J. C., L. Piñuela, and J. Lires. 2004. Guía del Jurásico de Asturias. Rutas por los yacimientos de huellas de dinosaurios. Ed. Zinco Comunicación, Gijón, Spain, 118 pp.

- Gray, J. E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. *Annals of Philosophy* 26:193–217.
- Grossmann, F. 2006. Taxonomy, phylogeny and palaeoecology of the plesiosauroids (Sauropterygia, Reptilia) from the Posidonia Shale (Toarcian, Lower Jurassic) of Holzmaden, south west Germany. Ph.D. dissertation, Eberhard-Karls-Universität Tübingen, Tübingen, 135 pp. Available at: <http://tobias-lib.ub.uni-tuebingen.de/volltexte/2006/2639/> Accessed December 21, 2007.
- Harland, W. B., R. L. Armstrong, A. V. Cox, L. E. Craig, A. G. Smith, and D. G. Smith. 1989. *A Geologic Time Scale*. Cambridge, UK: Cambridge University Press; 263 pp.
- Huene, F. von 1923. Eine neuer Plesiosaurier aus dem oberen Lias Württembergs. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 1923: 3–23.
- Maisch, M. W. and A. G. Reisdorf. 2006. Evidence for the longest stratigraphic range of post-Triassic Ichthyosaur: a *Leptonectes tenuirostris* from the Pliensbachian (Lower Jurassic) of Switzerland. *Geobios* 39:491–505.
- Mc Gowan C. and R. Motani. 2003. Ichthyopterygia. *Handbook of Paleoherpology*. Verlag Dr. Friedrich Pfeil, München, Germany, 175 pp.
- O'Keefe, F. R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). *Acta Zoologica Fennica* 213: 1–63.
- O'Keefe, F. R. 2004. Preliminary description and phylogenetic position of a new plesiosaur (Reptilia: Sauropterygia) from the Toarcian of Holzmaden, Germany. *Journal of Paleontology* 78(5):973–988.
- Owen, 1840. Report on British fossil reptiles, Part 1. Reports of the British Association for the Advancement of Science 9:43–126.
- Owen, R. 1860. On the orders of fossil and recent Reptilia, and their distribution in time. Reports of the British Association for the Advancement of Sciences for 1859 29:153–166.
- Owen, R. 1865. A Monograph on the Fossil Reptilia of the Liassic Formations. Part III. Sauropterygia. *Palaeontographical Society Monographs* 17:1–40.
- 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 årsskrift, Andra avdelningen: Medicin samt matematiska och naturvetenskapliga ämnen. Ny Följd* 59: 1–59.
- Quesada, J. M., M. de la Fuente, F. Ortega, and J. L. Sanz. 1998. Bibliografía del registro español de vertebrados mesozoicos. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geología)* 94:101–137.
- Rees, J. and N. Bonde. 1999. Plesiosaur remains from the Early Jurassic Hasle Formation, Bornholm, Denmark. Secondary Adaptation to Life in Water, Copenhagen, Abstracts: 70.
- Robles, S., S. Quesada, I. Rosales, M. Aurell, and J. C. García-Ramos. 2004. El Jurásico marino de la Cordillera Cantábrica. pp. 279–285 in J. A. Vera (ed.), *Geología de España*. Madrid, Spain: Sociedad Geológica de España-Instituto Geológico y Minero de España.
- Ruiz-Omeñaca, J. I., J. C. García-Ramos, L. Piñuela, N. Bardet, D. D. Bermúdez-Rochas, J. I. Canudo, and X. Pereda Suberbiola. 2006. Restos directos de vertebrados del Jurásico de Asturias. pp. 171–173 in E. Fernández-Martínez (ed.), *XXII Jornadas de la Sociedad Española de Paleontología y simposios de los proyectos PICG 493, 503, 499, y 467*. Libro de resúmenes. León, Spain: Universidad de León.
- Sauvage, H.-E. 1897–1898. Vertébrés fossiles du Portugal. Contribution à l'étude des poissons et des reptiles du Jurassique et du Crétacé. Direction des travaux Géologiques du Portugal, Lisbonne, 46 pp.
- Schulz, G. 1858. Descripción Geológica de Asturias. Gonzalez, Madrid: Imprenta y Librería de Don José Gonzalez, Madrid, Spain, 138 pp.
- Sciau, J., J. Y. Crochet, and J. Mattei. 1990. Le premier squelette de plésiosaure de France sur le Causse du Larzac (Toarcien, Jurassique inférieur). *Géobios* 23:111–116.
- 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*. pp. 145–190 in Callaway, J. M., and E. L. Nicholls (eds.), *Ancient Marine Reptiles*. San Diego: Academic Press.
- Suárez Vega, L. C. 1974. Estratigrafía del Jurásico de Asturias. *Cuadernos de Geología Ibérica* 3:1–368.
- Thulborn, T. and Warren, A. 1980. Early Jurassic plesiosaurs from Australia. *Nature* 285:224–225.
- Valenzuela, M., J. C. García-Ramos, and C. Suárez de Centi. 1986. The Jurassic sedimentation in Asturias (N Spain). *Trabajos de Geología* 16:121–132.
- Vincent, P. 2004. Etude d'un spécimen de plésiosaure (Sauropsida, Sauropterygia) provenant du Jurassique de Normandie: anatomie, systématique, phylogénie et paléobiogéographie. DEA de Paléontologie, Muséum National d'Histoire Naturelle de Paris, 45 pp. (unpublished).
- Wahl, W. R. 2006. A juvenile plesiosaur (Reptilia: Sauropterygia) assemblage from the Sundance Formation (Jurassic), Natrona County, Wyoming. *Paludicola* 5:255–261.
- Welles, S. P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. *Memoirs of the University of California* 13:125–254.
- Wiffen, J., V. de Buffrénil, A. de Ricqlés, and J. M. Mazin. 1995. Ontogenetic evolution of bone structure in Late Cretaceous Plesiosauria from New Zealand. *Geobios* 28(5):625–640.
- Yagüe, P., F. Ortega, L. Noè, J. M. Gasulla, and M. D. García. 2003. Reptiles marinos (Plesiosauria) del Aptiense inferior de Morella (Castellón); pp. 399–404 in Pérez-Lorente, F. (coord.), *Dinosaurios y Otros Reptiles Mesozoicos en España*. Logroño, Spain: Instituto de Estudios Riojanos (IER, Ciencias de la Tierra, 26).

Submitted May 12, 2007; accepted July 25, 2007.