

A plesiosaur specimen from the Lias of Lyme Regis: the second ever discovered plesiosaur by Mary Anning

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ABSTRACT

A historical specimen of plesiosaur, discovered by Mary Anning and kept in the Muséum national d'Histoire naturelle, Paris, under the number MNHN A. C. 8592 is here described. Discovered in 1824 by the first palaeontologist woman, Mary Anning, the specimen was sold by her to Constant Prévost who took it to Paris. This specimen is the second ever discovered plesiosaur and is here described for the first time even though it was figured by Cuvier (1825). The specimen is preserved in articulation and retained almost the entire post cranium but lacks the skull and most part of the neck. It preserves 56 vertebrae, most of the pectoral and pelvic girdles and most of the limbs. It was referred to *Plesiosaurus dolichodeirus* by Storrs (1997). Comparison with other specimens of *Plesiosaurus dolichodeirus* indicates that MNHN A. C. 8592 is an adult of advanced age. It reveals some unique features that may be attributed to ontogenetical and/or intraspecific variations. A better understanding of these variations among several individuals of the same species may help to clarify the problematic taxonomy and phylogeny of plesiosaurs.

KEY WORDS

Plesiosauria,
Plesiosauroidea,
Plesiosaurus,
Lower Jurassic,
England,
intraspecific variation.

RÉSUMÉ

Un spécimen de plésiosaure du Lias de Lyme Regis: le deuxième plésiosaure découvert par Mary Anning.

Un spécimen historique de plésiosaure, découvert par Mary Anning, conservé au Muséum national d'Histoire naturelle, Paris, et enregistré sous le numéro MNHN A. C. 8592 est décrit. Découvert en 1824 par la première femme paléontologue, Mary Anning, le spécimen a été vendu par elle à Constant Prévot qui le rapporta à Paris. Ce spécimen est le second plésiosaure découvert, il est décrit ici pour la première fois, bien qu'il fût figuré par Cuvier en 1825. Le spécimen est conservé en connexion anatomique et préserve la presque totalité du squelette postcrânien, à l'exception du crâne et d'une grande partie du cou. Il comprend 56 vertèbres, une partie de la ceinture pectorale et de la ceinture pelvienne et une partie des membres. Il a été rapporté à l'espèce *Plesiosaurus dolichodeirus* par Storrs (1997). Sa comparaison avec les autres spécimens rapportés à cette espèce indique que MNHN A. C. 8592 est un adulte « âgé ». Il révèle quelques caractères uniques qui peuvent être attribués à une variation ontogénétique et/ou intraspécifique. Une meilleure compréhension de ces variations parmi plusieurs individus de la même espèce pourrait aider à clarifier les problèmes de taxonomie et de phylogénie chez les plésiosaures.

MOTS CLÉS

Plesiosauria,
Plesiosauroidea,
Plesiosaurus,
Jurassique inférieur,
Angleterre,
variation intraspécifique.

INTRODUCTION

The plesiosaurs form a group of predatory marine reptiles whose stratigraphical range is uppermost Triassic to uppermost Cretaceous (Brown 1981). They are important members of marine reptile fauna from the Lias of Europe. The first genus of plesiosaur erected is *Plesiosaurus* De la Beche & Conybeare, 1821. Plesiosaur specimens described during 19th century were most often attributed to this genus, even if they commonly displayed some very different morphological characters. For example, some species originally attributed to this genus are no further classified as plesiosauroid but as pliosauroid specimens. This is the case for *Archaeoneotrus rostratus* (Owen, 1865) Novozhilov, 1964, *Thalassiodracon hawkinsi* (Owen, 1838) Storrs & Taylor, 1996, *Rhomaleosaurus megacephalus* (Stutchbury, 1846) Cruickshank, 1994, *Rhomaleosaurus zetlandicus* (Phillips, 1854) (Taylor 1992), or *Macropata longirostris* (Tate & Blake, 1876) (O'Keefe 2001). Therefore, the genus *Plesiosaurus* should be considered as a waste-basket taxon (Storrs 1997: 146) and some studies have been recently undertaken to clarify the taxonomic position of the species

referred to this genus. Brown (1981) and Tarlo (1960) clarified the taxonomy of late Jurassic Plesiosauroidea and Pliosauroida. More recently, Storrs (1997) has excluded nearly all species previously referred to this taxon and proposed that only three valid species should be attributed to *Plesiosaurus*: *P. dolichodeirus* Conybeare, 1824, *P. guilelmiimperatoris* (Dames, 1895) and *P. brachypterygius* (Huene, 1923). More recently, Großmann (2007) revised the taxonomic position of the German Liassic plesiosaurs *P. guilelmiimperatoris* and *P. brachypterygius* and erected two new genera, *Seeleyosaurus* White, 1940 for *P. guilelmiimperatoris* and *Hydrorion* Großmann, 2007 for *P. brachypterygius*. As a result, the only persisting valid species of *Plesiosaurus* is *P. dolichodeirus*.

The first description of the genus *Plesiosaurus* was based on isolated remains from the Lower Jurassic of Lyme Regis, Dorset (De la Beche & Conybeare 1821). Three years later, Conybeare (1824) provided the first exhaustive plesiosaur description based on the first sub-complete skeleton of plesiosaur discovered in the Lower Jurassic of Lyme Regis by Mary Anning and defined it as *Plesiosaurus dolichodeirus*, the type species of *Plesiosaurus*. Since this discovery, many

specimens of *P. dolichodeirus* were discovered in the Lower Jurassic of England and Storrs (1997) reported 25 specimens belonging to this species.

Here we present a description of the second plesiosaur specimen discovered by Mary Anning and now exposed in the permanent exhibition of the Muséum national d'Histoire naturelle, Paris, under the number MNHN A. C. 8592.

ABBREVIATIONS

BGS British Geological Survey, Nottingham;
 MNHN Muséum national d'Histoire naturelle, Paris;
 BMNH Natural History Museum, London;
 OXFUM Oxford University Museum of Natural History, Oxford.

HISTORY OF THE SPECIMEN

From 1800 to 1824, Georges Cuvier obtained a great deal of informations, such as documents, drawings, casts and original fossils related to marine reptiles (ichthyosaurs and plesiosaurs) from the Lower Jurassic (Liassic) of Great Britain (Taquet 2003). He knew everything about the discoveries made by Mary Anning in Lyme Regis (Dorset).

Immediately after the spectacular discovery of the first skeleton of *Plesiosaurus* by Mary Anning and its announcement made by William Conybeare on February 20, 1824, Cuvier received numerous letters from Great Britain with details of this event.

"This new fossil animal was found at Lyme in Dorsetshire, in the Blue Lias on the coast, in January 1824, or earlier [...] has been purchased by the Duke of Buckingham for £100 – and is now before the Geological Society in London – who are of opinion at present that it is an entire animal – at least it is thought to be so by Mr Conybeare who considers it as *Plesiosaurus* – Mr Cuvier must see it and decide its genus [...]" (letter of Mr Cumberland of 4 March 1824 in Taquet 2003). Cuvier received also a splendid drawing of the skeleton made by Mary Morland (the future Mrs Buckland) and sent 3 April 1824.

In order to acquire new specimens for the Paris museum (after the fossils of the Bullock Museum bought to Colonel Birch in May 1820), Cuvier decided to send the French geologist Constant Prévost (1787-1856) to Great Britain for an official geological

trip, appointed by the administration of the Muséum national d'Histoire naturelle. Very quickly, Prévost left Paris and, in May 1824, received the following note by the British geologist Charles Lyell:

"I am to receive here on Friday Monsieur Constant Prévost, an eminent French Geologist who received me last year in France with great hospitality. In a fortnight I am to commence a tour with him from Purbeck along the coast of Dorset and Devon to Cornwall to return by Wales, Bristol, Oxon..." (letter of 8 May 1824 from C. Lyell to Dawson Turner in Wilson 1972: 126). On May 29th, the two geologists left Oxford for Bristol, where they met Reverend W. D. Conybeare. The three men, together, visited Cornwall, travelled back along the coast, and stopped in Lyme Regis, just to see "[...] a magnificent specimen of an Ichthyosaurus which had recently been discovered in the cliffs there by the celebrated Mary Anning of which Prévost made a sketch" (Wilson 1972: 129).

Prévost explained later that he had the opportunity to buy a specimen of plesiosaur just when he was in Lyme Regis:

"[...] the nicest specimen of the same species of Plesiosaur, after the one we were speaking on [the specimen bought by the Duke of Buckingham], is the specimen which possesses now the Muséum d'Histoire naturelle de Paris; we have nearly seen the discovery which was made of it on the beach of Lyme-Regis by seamen of the small harbor; these, after taking all possible care of it for the extraction, under the surveillance of miss Mary Anning, were just selling it to her, when we visited this place. We have been lucky enough to benefit from a so favorable opportunity to be of some utility to the scientists of our country, and we have offered to the Muséum of comparative anatomy, a unique piece which would have lacked always to its nice collection, without the chance allowing us to precede the British amateurs and scientists. Except for the neck and for the head which are missing, the rest of the body is nearly completely preserved; and this part even has the advantage on the fossil of the Duke of Buckingham, that the dorsal vertebrae have not been displaced [...] All the Reptiles we were speaking on are altogether, either in the solid beds, either in the clay layers of the Lias, and sometime the portions of the same skeleton are even embedded inside beds of different kind; the bone

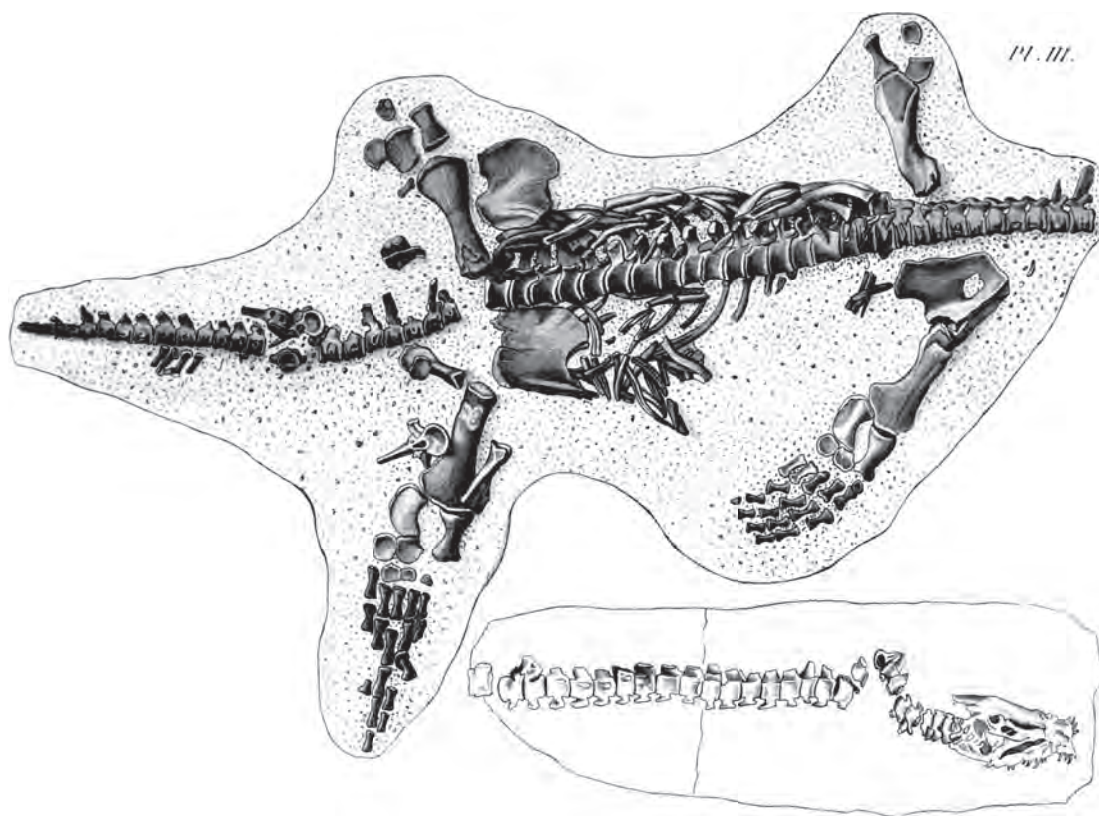


FIG. 1. — Skeleton of *Plesiosaurus dolichodeirus* Conybeare, 1824 (MNHN A. C. 8592) in ventrolateral view, Lias, Lyme Regis, England. Drawing realized by Cuvier (1825), from the third edition of his “Discours sur les révolutions de la surface du globe”. Head and neck are from another specimen (see text).

which seems to have been part of a same individual are generally linked, so that the discovery of a single vertebrae or of a single phalange allow to search in the same place the others parts of the animal, because these researches have been (as we learned from miss Mary Anning herself) successful” (Prévost 1825 *in* Taquet 2003).

From the biography of Constant Prévost published by Jules Gosselet (1896), we know that the Paris specimen of *Plesiosaurus* was bought for 3 pounds by Mary Anning from the sailors, and then sold for 10 pounds to Constant Prévost. The fossil arrived in Paris just after Cuvier had sent to the printer the manuscript of his chapter V “De l’Ichthyosaurus et du Plésiosaurus” of his last volume of the second edition of the “Ossements fossiles”. So Cuvier was unable to

include in this volume, which was published in June 1824, the description or a drawing of this splendid plesiosaur specimen.

A year later, in 1825, Cuvier published a third edition of his “Discours sur les révolutions de la surface du globe” (Cuvier 1825). This was an opportunity for him to introduce among the plates the engraving (Fig. 1) of the specimen bought from Mary Anning, to which he added the engraving of the head and the neck of the first specimen of *Plesiosaurus* (bought by the Duke of Buckingham). This latter was originally published by Conybeare (1824).

Since 1825, the Paris *Plesiosaurus* has not been described. The specimen is on display since 1898 in the gallery of Palaeontology of the Muséum national d’Histoire naturelle, Paris.

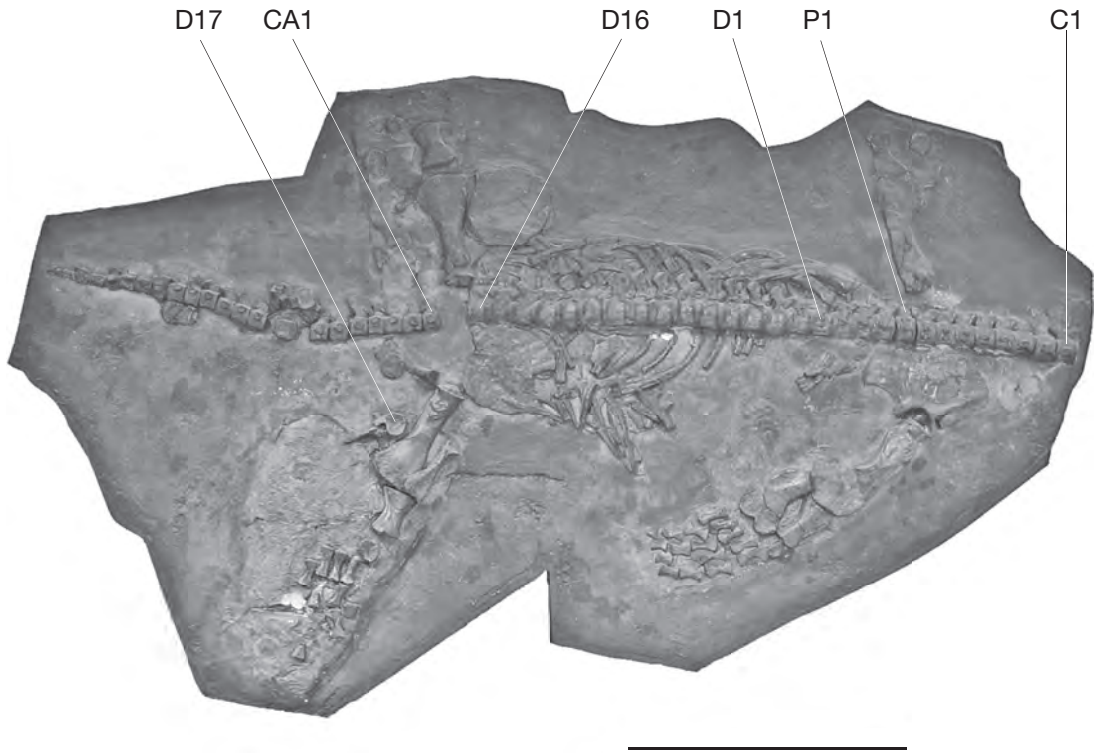


FIG. 2. — Skeleton of *Plesiosaurus dolichodeirus* Conybeare, 1824 (MNHN A. C. 8592) in ventrolateral view, Lias, Lyme Regis, England. Abbreviations: **C1**, cervical vertebra number 1; **CA1**, caudal vertebra number 1; **D1**, dorsal vertebra number 1; **D16**, dorsal vertebra number 16; **D17**, dorsal vertebra number 17; **P1**, pectoral vertebra number 1. Scale bar: 50 cm.

SYSTEMATIC PALEONTOLOGY

Clade SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Family PLESIOSAURIDAE Gray, 1825

Genus *Plesiosaurus* De la Beche & Conybeare, 1821

Plesiosaurus dolichodeirus Conybeare, 1824

MATERIAL EXAMINED. — Skeleton MNHN A. C. 8592.

GEOGRAPHICAL OCCURENCE. — Lyme Regis, Charmouth coastal region, Dorset, England.

STRATIGRAPHICAL OCCURRENCE. — No information is available for the stratigraphical occurrence of the specimen MNHN A. C. 8592, but it is possibly the same as for other *Plesiosaurus dolichodeirus* specimens, that is uppermost Sinemurian (Lower Lias) *Echioceras raricostatum* zone, Black Ven Marl Formation (Storrs 1997).

DESCRIPTION

Preservation and size (Fig. 2; Table 1)

The specimen is preserved in one block of original matrix and exposes its ventrolateral aspect. It is articulated and comprises the almost complete postcranial skeleton. In its general aspect, the position of the specimen indicates that the skeleton was little displaced after the death of the animal. The vertebral column includes 56 vertebrae from the tail to the base of the neck. Most of the anterior part of the neck is lost. Of the pectoral girdle, only the dorsal aspects of the scapulae and the distal parts of the coracoids are visible (the main part is not preserved or is buried into the matrix). The pelvic one is partially preserved and includes the two ilia and pubes. The right forelimb and hindlimb are almost completely preserved, approximately in life position; the left ones are only partially preserved.

TABLE 1. — Axial skeleton measurements (in cm) of *Plesiosaurus dolichodeirus* Conybeare, 1824 (MNHN A. C. 8592). The vertebral sequence is not the natural one and the numbers indicate the position of the vertebrae within the preserved vertebral column. Abbreviations: **C**, cervical vertebrae; **CA**, caudal vertebrae; **D**, dorsal vertebrae; **P**, pectoral vertebrae; **?**, missing data; **l**, length; **h**, height; **w**, width.

No.	l	h	w	No.	l	h	w
C1	3.7	3.7	?	D17	?	3	3.2
C2	3.8	~3.3	?	CA1	2.7	2.7	?
C3	3.5	~3.5	?	CA2	2.9	?	?
C4	3.8	~3.5	?	CA3	2.6	?	?
C5	3.5	~3.5	?	CA4	2.7	?	?
C6	3.5	~3.5	?	CA5	2.7	?	?
C7	3.4	?	?	CA6	2.7	?	?
C8	3.2	?	?	CA7	2.7	?	?
P1	3.4	?	?	CA8	?	2.9	3.4
P2	3.3	?	?	CA9	?	2.8	3.5
P3	3.3	?	?	CA10	2.8	2.8	3.2
P4	3.5	?	?	CA11	2.7	?	?
D1	3.7	?	?	CA12	2.7	?	?
D2	3.8	?	?	CA13	2.5	?	?
D3	3.9	?	?	CA14	2.6	?	?
D4	3.8	?	?	CA15	2.6	?	?
D5	3.8	?	?	CA16	2.6	?	?
D6	3.6	?	?	CA17	2.5	?	?
D7	3.5	?	?	CA18	2.5	?	?
D8	3.5	?	?	CA19	2.4	?	?
D9	3.8	?	?	CA20	2.4	?	?
D10	3.9	?	?	CA21	2	?	?
D11	3.8	?	?	CA22	~1.6	?	?
D12	3.8	?	?	CA23	~1.4	?	?
D13	3.5	?	?	CA24	1.2	?	?
D14	3.8	?	?	CA25	~1.1	?	?
D15	3.5	?	?	CA26	~1.1	?	?
D16	~3.3	?	?	CA27	1.3	?	?

Vertebral column (Figs 2; 3; Table 1)

Fifty-six vertebrae are preserved, including 8 basal cervicals, 4 pectorals, 17 dorsals and 27 caudals. No sacrals are preserved. Most of the vertebrae are preserved in lateral aspect. The articular facet of the centra is generally not visible with exception of the posterior articular facet of the anteriormost preserved cervical vertebra (C1), which is partially observable, and the anterior articular facet of one dorsal vertebra (D17) and two caudal vertebrae (CA8 and CA9).

Cervical vertebrae (Figs 2; 3A, B; Table 1)

With the exception of the two anterior-most preserved vertebrae, which are seen from the left, all cervicals present the right lateral side (Fig. 3A). It

is difficult to envisage a taphonomical mechanism that may explain such an unusual position. It is therefore most likely that the two anterior-most cervicals were inaccurately repositioned during preparation of the specimen. The articular surface of the cervical centra can be partially observed thanks to the anterior-most cervical C1. It is a rounded oval in outline, gently concave and is surrounded by a sharply-defined, rounded border. A small pit is situated in the center of the articular facet, and likely marks the original position of the notochord.

The centrum of the anterior-most preserved cervical vertebrae is approximately as long as it is high (see Table 1). Though their precise height cannot be measured with the same degree of confidence, the observation of the lateral aspect of the other cervicals suggest that the centrum of these latter are also as long as or slightly longer than they are high (see Table 1).

The lateral face of the centra beneath the bases of the neural arch are almost flat. Only one half of the ventral surfaces of the cervical centra are observable. The ventral surfaces are concave in longitudinal direction and probably transversally too. No sign of a presence of a ventral longitudinal keel is observable. The prezygapophyses are oval in longitudinal direction and orientated almost vertically. Both the pre- and postzygapophyses project beyond the level of the articular surfaces of the centrum, the prezygapophyses more than the postzygapophyses. Only the anterior-most cervical (C1) preserves the entire neural arch, which is higher than long (height/length ratio \approx 2.5) and gently inclined posteriorly. The neural spine is sub-rectangular in outline with a rounded dorsal extremity. The remaining cervical vertebrae preserve only fragmentary neural arches. The cervical ribs are double-headed, however, this is not evident for the anterior-most cervical vertebrae (C1, C2 and C3), where the articular facets for the ribs are very closely spaced. The following cervical vertebrae present a distinct longitudinal groove between the rib facets, showing distinct tuberculum and capitulum. Towards the base of the neck, the rib facets are progressively located higher on the centra, and thus the width of the grooves between the double-headed rib facets increase. None of the cervical ribs is preserved.

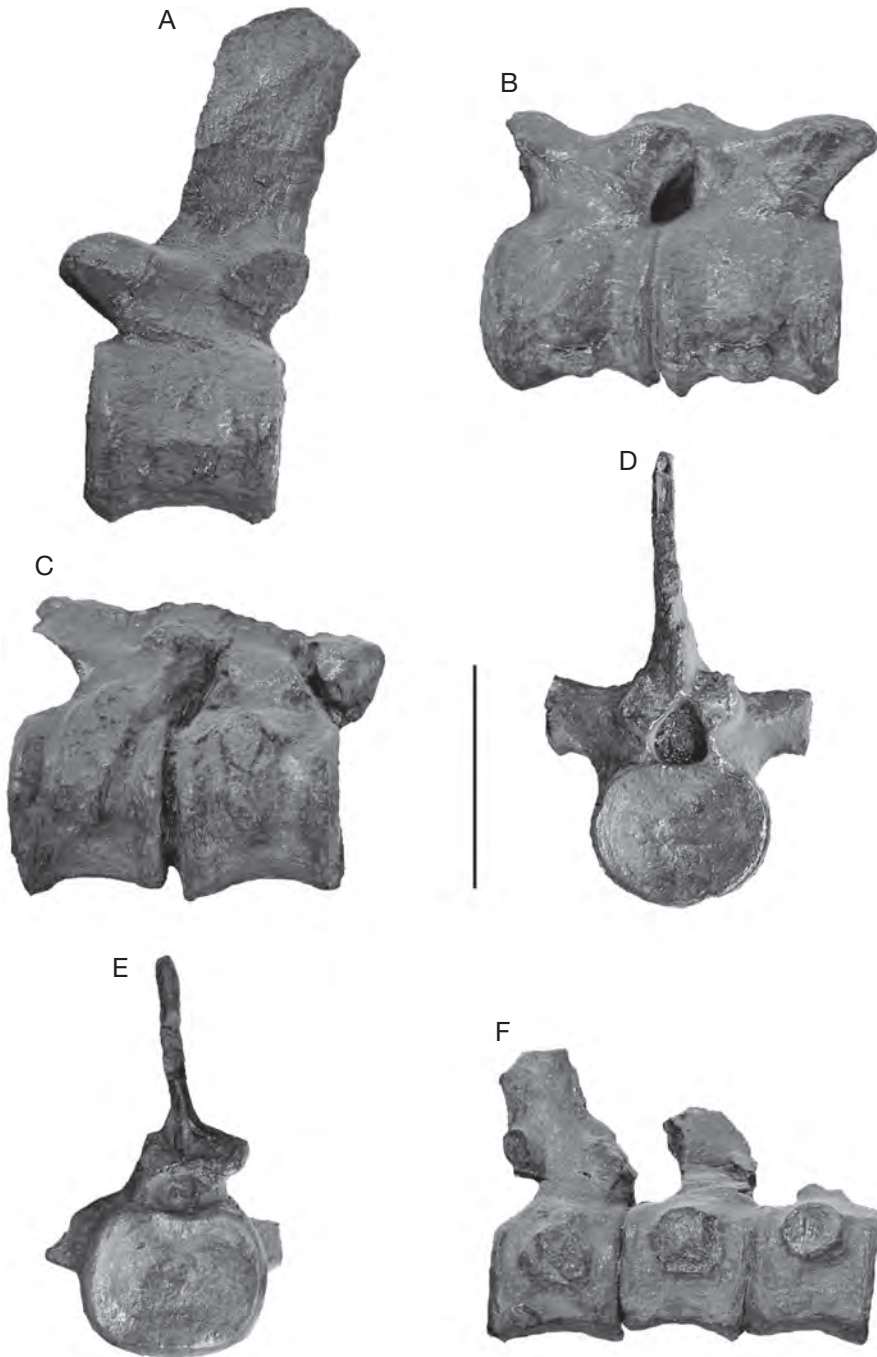


FIG. 3. — *Plesiosaurus dolichodeirus* Conybeare, 1824 (MNHN A. C. 8592), Lias, Lyme Regis, England: **A**, cervical vertebra C1 in left lateral view; **B**, cervical vertebrae C4 and C5 in right lateral view; **C**, pectoral vertebrae P1 and P2 in right lateral view; **D**, dorsal vertebra D17 in anterior view; **E**, caudal vertebra CA9 in anterior view; **F**, caudal vertebrae CA3, CA4 and CA5 in right lateral view. Scale bar: 5 cm.

TABLE 2. — Skeleton measurements (in cm) of *Plesiosaurus dolichodeirus* Conybeare, 1824 MNHN A. C. 8592 (except axial skeleton – see Table 1).

Bones	Length
Left ilium	10.9
Rigth ilium	10.7
Left humerus	21.5
Rigth humerus	21.4
Left ulna	8
Left radius	8
Rigth radius	7.9
Left femur	18.4
Rigth femur	18.6
Left tibia	7

Pectoral vertebrae (Figs 2; 3C; Table 1)

Four pectoral vertebrae are present, which represents the common number in plesiosaurs (Brown 1981). They are morphologically intermediate between cervicals and dorsals. The centra are sub-circular in cross section. The large oval rib facets are carried by both the centra and the neural arch.

Dorsal vertebrae (Figs 2; 3D; Table 1)

Seventeen dorsal vertebrae are preserved, which represent the standard count for plesiosaurs (Brown 1981). However, Storrs (1997) indicated 21 dorsal vertebrae for *P. dolichodeirus*. In MNHN A. C. 8592, the absence of the sacra indicate that the posterior part of the trunk is incomplete (Fig. 2); it is therefore impossible to unambiguously estimate the original dorsal count in the specimen. Most of the dorsal vertebrae are preserved in right lateral view with the exception of the D17, which is exposed in anterior view. The dorsal centra are more rounded than those of the cervical vertebrae. The articular facets for the ribs are located on the neural arches, well rounded in outline and slightly concave. The ventral surface of the centra is smooth and evenly convex transversally. The nutritive foramina are well spaced and located on the lateral surfaces of the centra. Most of the neural arches of the dorsal vertebrae are obscured by overlying dorsal ribs or not preserved. The only observable neural arch is that of D17, which is slightly broken and shows its ante-

rior margin. It consists of a narrow neural spine, which appears about 10% shorter than the neural spine of the anterior-most cervical vertebra (C1). Several dorsal ribs are preserved. They are single-headed, thick, and curved, with a flat and enlarged articular head. The dorsal ribs, being enlarged in their medial part, are probably pachyostotic *s.s.*, a conclusion also reached by Storrs (1997) for the genus *Plesiosaurus*.

Caudal vertebrae (Figs 2; 3E, F; Table 1)

Twenty seven caudal vertebrae are preserved. Storrs (1997) count 28 caudal vertebrae for the species *Plesiosaurus dolichodeirus*, suggesting that this portion of the vertebral column is probably sub-complete in MNHN A. C. 8592. The caudal centra are quadrate-shaped in anterior view and have almost platycoelous articular surfaces. All neural arches and spines of the caudals are only partially preserved, except for the caudal CA5. Most of the caudal vertebrae are preserved in lateral view with the exception of CA8 and CA9 (see Table 1 for measurements). The caudal centra are wider than long and high. They possess well-developed rib facets, which are more or less pentangular in outline and are located on the centra. Towards the back of the neck, the rib facets are located more ventrally on the centra. The size of the centra decreases rapidly towards the posterior part of tail. Towards the posterior part of the tail, the preserved parts of the neural spines are increasingly inclined posteriorly. Haemal arch facets are located on both anteroventral and posteroventral edges of the centra, the posterior ones being generally larger than the anterior ones. Zygapophyses were probably present, but are not preserved on the specimen.

Girdles (Figs 2; 4; Table 1)

The pectoral girdle of MNHN A. C. 8592 is only partially visible, possibly because some of its elements were not preserved or buried in the matrix. The left scapula and coracoid are almost complete and are observable in ventral view (Fig. 4A). The right portion of the preserved pectoral girdle and articulated humerus of the specimen MNHN A. C. 8592 was figured by Hulke (1883), based on its cast (BGS GSM 118412).

Scapula (Figs 2; 4A)

The scapula is partially preserved, the dorsal ramus is almost totally missing or hidden by matrix. A small plate of unidentified bone near the glenoid fossa may represent a fragment of the dorsal ramus of the scapula. A strong ridge separates the ventral surface of the scapula from its dorsal ramus. The posterior ramus bears a posterolaterally-orientated facet that forms the anterior part of the glenoid fossa. The scapula contribution to the glenoid is less extensive than the coracoid one. Given the general outline of the left scapula, there was probably no middle contact between the two scapulae, as proposed by Storrs (1997) for its reconstruction of the pectoral girdle of *P. dolichodeirus*.

Coracoid (Figs 2; 4A)

The coracoid is a large and broad plate of bone. Its medial margin is nearly straight. The posterior margin of the coracoid is irregular, suggesting that its posterior part is probably not complete and may thus have been originally more expanded posteriorly. Its lateral margin is concave. Anteriorly, it contacts the posterior ramus of the scapula. Its glenoid contribution is anterolaterally orientated. The medial suture between the coracoid and the anterior ramus of the scapula is marked medially by a notch and run posterolaterally to the pectoral fenestra. The glenoid fossa is shared by the scapula and coracoid and is oval in outline and concave.

Pectoral fenestration (Figs 2; 4A)

The pectoral fenestra is elliptical, and diagonally orientated, with well-rounded margins. It is laterally formed by the scapula and posteromedially by the coracoid.

Ilium (Figs 2; 4B, C)

Both ilia are preserved in ventral view, the distal portion of the right one being partially hidden by an indeterminate metatarsus. The ilium is expanded at both extremities, whereby the sacral extremity is more expanded than the acetabular. It is twisted and has a constricted shaft. The dorsal margin of the ilium, corresponding to the surface for the sacral ribs, is relatively broad. The

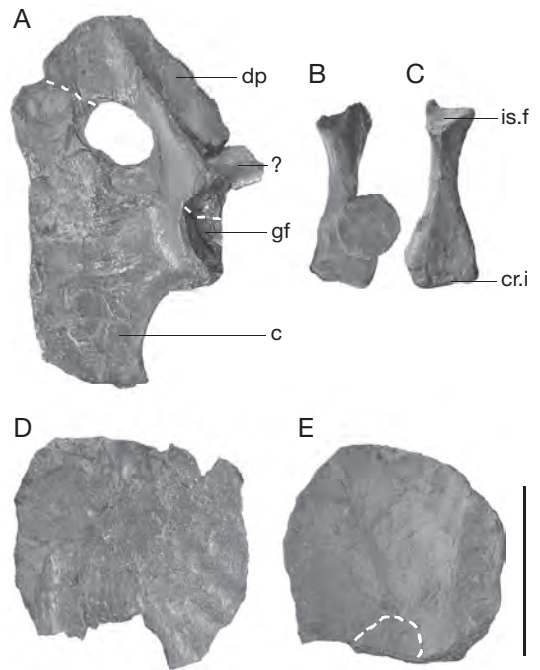


FIG. 4. — *Plesiosaurus dolichodeirus* Conybeare, 1824 (MNHN A. C. 8592), Lias, Lyme Regis, England: **A**, left scapula and coracoid in ventral view, the dotted line represents the hypothetical limit between the scapula and the coracoid; **B**, left ilium in ventral view; **C**, right ilium in ventral view; **D**, left pubis in ventral view; **E**, right pubis in ventral view, the dotted line represents the hypothetical limit of the pelvic foramen. Abbreviations: **c**, coracoid; **cr.i**, crista illii; **dp**, dorsal process of the scapula; **gf**, glenoid surface; **is.f**, facet for ischium. Scale bar: 10 cm.

anterior facet is reduced whereas the posterior one is well expanded and slightly concave. The acetabular end articulating with the pelvic plate is rod-like.

Pubis (Figs 2; 4D, E)

Both pubic bones are partially preserved in ventral view. They are large and nearly pentagonal. Only the left one (Fig. 4D) presents a deep semicircular notch on its posterior border, forming the anterior margin of the pelvic aperture. Nevertheless, Cuvier (1825) figured a notch at this level in his original drawing (Fig. 1), indicating that a piece of bone has been subsequently added on the mediolateral border of the right pubis. The anteromedial margins of the pubis is slightly concave and its anterior edge is convex.

*Forelimbs (Figs 2; 5; Table 2),
humerus (Figs 2; 5A, B)*

Both humeri are well preserved. The left one is observable in ventral view and the right one in dorsal view. The humerus is markedly asymmetrical with its anterior margin being nearly straight, and its posterior margin being concave due to the distinctive enlargement of its posterodistal part. The proximal portion of the humerus is almost flat and bears rugosities on its ventral surface, which correspond to scars of the adductor muscles. The humeral head is surrounded by a lipped edge with tuberosities. A channel of finished periosteal bone between these tuberosities and the articular face of the glenohumeral condyle divides the proximal articular area into two. The deltopectoral crest, marking the insertion of the *M. coracobrachialis*, is more strongly developed than the dorsally situated tricipital crest, which marks the insertion of the *M. subcoracoscapularis*, *M. subscapularis* and *M. subcoracoideus*. A very pronounced projection is present near the proximal end and runs axially down the posterior border of the humeral shaft. Sato *et al.* (2003) interpreted this projection as the attachment site for *M. latissimus dorsi* and/or other muscles that pull the humerus backward and upward for *Bishanopliosaurus youngi* author, date.

On the dorsal and ventral surfaces of the distal end of the humerus, there are extensive areas of shallow ornamentation. The distal end of the humerus possesses two well-developed epipodial facets, an anterior one for the radius and a posterior one for the ulna. The radial facet is nearly straight and the facet for the ulna is slightly concave.

Radius and ulna (Figs 2; 5A, B)

The left radius and ulna are preserved in ventral view, whereas the right radius and the right ulna are preserved in dorsal view. The left and right radii as well as the left ulna are complete; the right ulna preserves only its proximal half.

Both the radius and ulna are longer (proximally to distally) than broad (preaxially to postaxially). The proximal margin of the radius is nearly straight, while the distal margin is convex in outline and

bears a large articular facet for the radial and a smaller one for the intermedium. The preaxial and postaxial margins of the radius are both concave, in a way that the radius has an hourglass outline.

The ulna is lunate, with a posteriorly convex margin. It has a small and slightly convex proximal articular facet for the humerus and two distinct distal articular facets for the intermedium and ulnare. Both the postaxial margin of the radius and the preaxial margin of the ulna are concave. Together they enclose a narrow spatium interosseum.

Carpals, metacarpals and phalanges (Figs 2; 5A, B)

The proximal rows of left carpals preserve (from the postaxial to the preaxial margin of the limb) the intermedium and the ulnare. On the right forelimb, only the intermedium (recognized by comparison with the shape and size of the proximal rows of left carpals) is preserved. The other elements of the right forelimb are missing.

The distal row of left carpals is only represented by one bone element, which probably corresponds to the distal carpal I according to its position with respect to other elements.

The metacarpals are phalangiform. The distal-most end of the paddle are missing. The digits one to four preserve three phalanges. The phalanges are hourglass-shaped.

Hindlimbs (Figs 2; 5; Table 2),

femur (Figs 2; 5C, D)

Both femora are preserved in ventral aspect. The femur is shorter and more slender than the humerus (see Table 1). The difference between propodial proportions is generally considered as an important taxonomic character (Welles 1943; Brown 1981), when considered in adult forms. The proportion of propodial of MNHN A. C. 8592 is in accordance with the assumption correlating long-neck taxa with relatively longer humeri. In ventral view, the femur expands nearly symmetrically from its head to its distal part, its preaxial border being slightly more expanded than the postaxial one in the distal region. The head of the femur is moderately convex and rugose, which indicates the presence of a thick cap of cartilage in life. The trochanter

is located along the ventral margin of the femoral shaft and projects distodorsally to the capitulum. The trochanter, which marks the insertion of the *M. puboischiofemoralis externus*, is separated from the head by a strip of finished periosteal bone, which divides the usually single cartilaginous area into two. In outline, the distal articular surface is convex, with shallow epipodial facets for the tibia and fibula.

Tibia and fibula (Figs 2; 5C, D)

Both tibiae are preserved in ventral view. In general shape and proportions, the tibia mirrors the radius. The tibia is longer than broad and presents a preaxially to postaxially constricted shaft in the medial region. It possesses a straight proximal margin and a slightly convex distal one.

Only the right fibula is preserved. The left one is depicted on the engraving of the specimen by Cuvier (1825) but is now lost (see Fig. 1). The preaxial edge of the fibula is deeply concave. Distally, the fibula bears two straight and distinct facets for the astragalus and calcaneum.

Tarsals, metatarsals and phalanges (Figs 2; 5C)

Two rounded elements are preserved on the right hindlimb. One of them contacts the fibula into a straight facet and could therefore correspond to the calcaneum. The other one is hardly identifiable; considering its size, it could correspond to a metatarsal. One tarsal element of the left hindlimb is preserved. Given its position and general shape, it is difficult to identify it with confidence. Nevertheless, two tarsal elements were drawn by Cuvier (1825) on the left hindlimb on the original engraving of the specimen (see Fig. 1). Neither of these is positioned as the element currently present in the specimen, indicating that the latter has been displaced and that the other one has been lost. The remaining element, given its shape and original position on the figure of Cuvier (1825), probably corresponds to the calcaneum (Fig. 1). Accordingly, the lost element could correspond to the astragalus. Another tarsal element is preserved and partially overlaps the left ilium (Fig. 4B). It is unfortunately impossible to assign it to one of the hindlimbs.

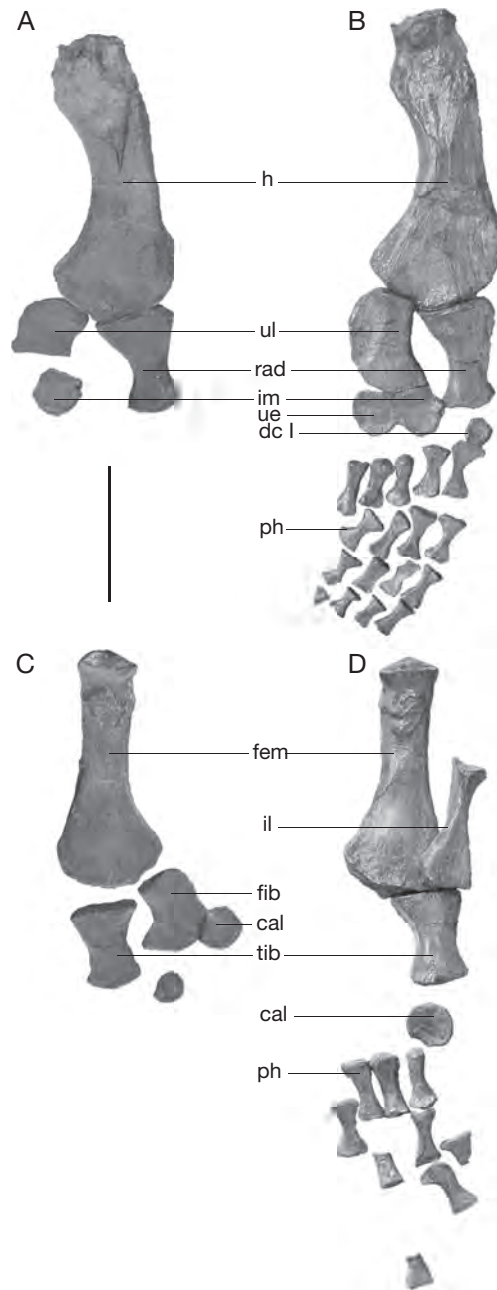


FIG. 5. — *Plesiosaurus dolichodeirus* Gonybeare, 1824 (MNHN A. C. 8592), Lias, Lyme Regis, England: **A**, right forelimb in dorsal view; **B**, left forelimb in ventral view; **C**, right hindlimb in ventral view; **D**, left hindlimb in ventral view. Abbreviations: **cal**, calcaneum; **dc I**, distal carpal I; **fem**, femur; **fib**, fibula; **h**, humerus; **il**, ilium; **im**, intermedium; **ph**, phalanx; **rad**, radius; **tib**, tibia; **ue**, unlnare; **ul**, ulna. Scale bar: 10 cm.

TABLE 3. — *Plesiosaurus dolichodeirus* Conybeare, 1824, measurements (in cm) of the holotype BMNH 22656, OXFUM J.10304 (taken from Storrs 1997) and MNHN A. C. 8592.

Length	BMNH 22656	OXFUM J.10304	MNHN A. C. 8592
Humerus	19	21	21.5
Femur	18	20	18.5
Radius	8	8	8
Ulna	8	10	8
Ilium	11	?	10.8
Tibia	7	7	7
Posterior cervical	4	?	3.2
Caudal series	68	88	> 63

All metatarsals are missing. Judging from engraving of the specimen of Cuvier (1825), three left metatarsals were originally preserved.

Only one phalanx is preserved in the right hindlimb and nine phalanges for the left. They are hour-glass-shaped. Nevertheless, eight have been lost since Cuvier realised the drawing of the specimen.

COMPARISON

Specimen MNHN A. C. 8592 has been attributed to *P. dolichodeirus* by Storrs (1997). The reconstruction of the pectoral girdle of *Plesiosaurus dolichodeirus* is partially based on MNHN A. C. 8592 (Hulke 1883; Storrs 1997). According to the diagnosis proposed by Storrs (1997) for genus and species of *P. dolichodeirus*, MNHN A. C. 8592 and this species share: paired rib facets on the cervical vertebrae; a coracoid of moderate breadth; a humerus with prominent shaft curvature and marked posterodistal (postaxial) expansion but weak anterodistal (preaxial) corner; robust, pillar-like anterior epipodials offset to extend distally beyond posterior epipodials; broad crescentic posterior epipodials; a convex anterior margin of the pubis; an ilium with a little twist to shaft; and the forelimbs slightly longer than hindlimbs. *Plesiosaurus dolichodeirus* is known by 25 partial to sub-complete specimens. The recent revision and comprehensive description of the species by Storrs (1997) allow some detailed comparison between MNHN A. C. 8592 and other specimens of *Plesiosaurus dolichodeirus*.

The species *Plesiosaurus dolichodeirus* usually shows a centrum slightly longer than high (Storrs

1997), as observed in MNHN A. C. 8592. Storrs (1997) reported 41 cervical vertebrae in BMNH 22656 (holotype), 42 cervical vertebrae in OXFUM J.10304 and 38 or 39 cervical vertebrae in BNMH 1313. He also noted the presence of 4 or 5 pectorals, about 21 dorsals, 3 sacrals and 28 caudals for BNMH 22656. A broadly similar number of pectoral, dorsal and caudal vertebrae is present in MNHN A. C. 8592. Because MNHN A. C. 8592 preserves 8 cervicals, 4 pectorals, 17 dorsals and 27 caudals, it can be estimated that 38 to 42 vertebrae are lacking in MNHN A. C. 8592 by comparison with others specimen of *Plesiosaurus dolichodeirus*, between 30 and 34 of them being cervical vertebrae. Additionally, Storrs (1997) describes the sacral end of the ilium as flattened in *Plesiosaurus dolichodeirus*, a condition also observed in MNHN A. C. 8592.

There are some notable differences between the specimen MNHN A. C. 8592 and the other specimens referred to *Plesiosaurus dolichodeirus*. The proximal portion of the humerus of MNHN A. C. 8592 bears a prominent projection, which is absent in other specimens of *Plesiosaurus dolichodeirus* (Storrs 1997: 173). The humeral projection observed in MNHN A. C. 8592 is unique among Plesiosauroidea, but has been reported in several Pliosauroida. A similar humeral projection is observed in the same position in *Bishanopliosaurus youngi* Dong, 1980 (Sato *et al.* 2003), *Liopleurodon ferox* Sauvage, 1873 (Andrews 1913) and *Eurycleidus arcatus* (Owen, 1840) (Andrews 1922), and at the midway of the posterior edge of the shaft in *Simolestes vorax* Andrews, 1909 (Andrews 1913).

Size ratios of bone elements between BMNH 22656 and MNHN A. C. 8592 are also observable: in BMNH 22656 the humerus and femur are slightly shorter but the caudal series is longer than in MNHN A. C. 8592, suggesting that MNHN A. C. 8592 could have been shorter than BMNH 22656 but more massive.

DISCUSSION

Several anatomical characters provide evidence about the ontogenetic stage of development of MNHN

A. C. 8592. The presence of neural arches fused to the vertebral centra, cervical centra bearing concave articular faces and round ossified margins, as well as well-achieved closed limb bones with well-defined edges, indicate that this specimen was probably an “adult” (*sensu* Brown 1981). The humerus presents a nearly straight anterior margin and a concave posterior margin, which is also typical in humerus of “adult” plesiosaurs (see Brown 1981: 276–280). Moreover, the division of the usually single proximal articular area of both the humerus and femur in two indicates an “old adult” stage for this specimen (Brown 1981).

It is thus arguable that the humeral projection observed in MNHN A. C. 8592 but absent in other specimens referred to *Plesiosaurus dolichodeirus* was only present in adults of advanced age (*sensu* Brown 1981). Nevertheless, other specimens referred to *Plesiosaurus dolichodeirus* and previously considered as “old” adults (e.g., OXFUM J.10304; Storrs 1997) lack any humeral projection. These observations suggest that the humeral projection was probably not related to an advanced ontogenetic stage of development. Similarly, an advanced ontogenetic stage of development appears unlikely to be at the origin of the more massive proportions of MNHN A. C. 8592 compared to other large specimens of *Plesiosaurus dolichodeirus*. A simple explanation could be that these morphological differences might reflect intraspecific variations among this species not connected with ontogenetical development. However, most plesiosaur species are known by only one specimen or at most relatively few, generally incomplete specimens. Consequently, morphological differences between individuals of the same species are almost unknown, thus preventing any further interpretations of these morphological differences in terms of intraspecific variations. Interestingly, several researchers have pointed out sexual dimorphism, particularly in the differentiation of the humerus shape (differences in muscular attachments development) within pachypleurosaurs (Rieppel 1989; Sander 1989; Rieppel & Lin 1995) or champsosaurs (Katsura 2004). Additionally, Welles (1962: 38) also proposed that plesiosaur males were larger and heavier than the females. Considering these statements, the observed differences between

MNHN A. C. 8592 and other specimens referred to *Plesiosaurus dolichodeirus* could be a result of sexual dimorphism.

SUMMARY AND CONCLUSIONS

In addition to its historic importance, the specimen MNHN A. C. 8592 presents a unique character on its humerus, not described in other specimens of this species, and body proportions that differ from that of several other specimens of *P. dolichodeirus* of the same ontogenetical age. It is here suggested that these morphological differences could reflect intraspecific variations or sexual dimorphism. Nevertheless, it should be noted that intraspecific variations within species of plesiosaurs are not well understood, as most plesiosaurian species are represented by only one specimen. Even so, a better understanding of these variations among several individuals of the same species may help to clarify the problematic taxonomy and phylogeny of plesiosaurs. As *P. dolichodeirus* is one of the best-documented plesiosaur species, a detailed reexamination and comparison of all the specimens referred to this species should contribute to improve our knowledge concerning this topic.

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