

A new cryptoclidid Plesiosaur from the Oxfordian (Late Jurassic) of Cuba

Un nouveau plésiosaure cryptoclididé de l'Oxfordien (Jurassique supérieur) de Cuba

Un nuevo plesiosaurio criptoclidido del Oxfordiense (Jurásico superior) de Cuba

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Abstract

Cryptocleidus ? cuervoi caroli DE LA TORRE & ROJAS, 1949, a partial skull with associated mandible and atlas-axis from the Oxfordian of Cuba, has been completely prepared for the first time. It is here redescribed and assigned to a new cryptoclidid genus, *Vinialesaurus*, for which the species *caroli* is retained. *Vinialesaurus* is mainly diagnosed by palatal characters such as double internal nares, an anteriorly rounded vomer and a lack of anterior interpterygoid vacuities. It shares with other cryptoclidids large orbits and external nares, a small vertical jugal and a reduced tooth ornamentation. The occurrence of *Vinialesaurus caroli* in association with pliosauroids, ophthalmosaurian ichthyosaurs, metriorhynchid crocodylians and pleurodiran marine turtles, strongly suggests that a marine seaway was present in the Caribbean during the Oxfordian, connecting the western Tethys with the Oriental Pacific. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

Cryptocleidus ? cuervoi caroli DE LA TORRE & ROJAS, 1949, un crâne partiel avec la mandibule et l'atlas-axis associés provenant de l'Oxfordien de Cuba, a été entièrement préparé pour la première fois. Il est redécrit et attribué à un nouveau genre de cryptoclididé, *Vinialesaurus*, pour lequel l'espèce *caroli* est retenue. Des caractères du palais, tels qu'une double paire de narines internes, un vomer arrondi antérieurement et une absence de cavités interptérygoïdes antérieures caractérisent *Vinialesaurus*. Il partage avec les autres cryptoclididés de grandes orbites et narines externes, un petit jugal vertical et une ornementation dentaire réduite. L'association de *Vinialesaurus caroli* à des pliosauroïdes, ichthyosaures ophthalmosauriens, crocodiles méthriorhynchidés et tortues marines pleurodires, suggère fortement qu'un bras de mer était présent à l'Oxfordien au niveau des Caraïbes, mettant en contact la Téthys occidentale avec le Pacifique oriental. © 2002 Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Riassunto

La parte anterior del cráneo con la mandíbula y el atlas-axis asociados, referidos a *Cryptocleidus ? cuervoi caroli* DE LA TORRE & ROJAS, 1949, del Oxfordiano de Cuba, han sido completamente preparados por primera vez. En este trabajo, este ejemplar es redescrito

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y asignado a un nuevo género de criptocládido, *Vinialesaurus*, para el que se retuvo la especie *caroli*. *Vinialesaurus* es diagnosticado principalmente por caracteres del paladar tales como narinas internas dobles, vómer redondeado anteriormente y falta de vacuidades interpterigoideas anteriores. Comparte con otros criptocládidos las órbitas y narinas externas grandes, jugal vertical pequeño y dientes con ornamentación reducida. La presencia de *Vinialesaurus* asociado con pliosauroides, ictiosaurios ofthalmosaurianos, cocodrilos metriorrínquidos y tortugas marinas pleurodiras, indica la presencia de un pasaje marino en el Caribe durante el Oxfordiano, que conectaba el Tethys occidental con el Pacífico Oriental. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Keywords: Plesiosauria; Cryptoclididae; *Vinialesaurus*; Jurassic; Oxfordian; Cuba

Mots clés: Plesiosauria; Cryptoclididae; *Vinialesaurus*; Jurassique; Oxfordien; Cuba

Palabras claves: Plesiosauria; Cryptoclididae; *Vinialesaurus*; Jurásico; Oxfordiano; Cuba

1. Introduction

The fossil record of Oxfordian marine reptiles is very poor worldwide (Persson, 1963; Bardet, 1995). Most Middle Jurassic finds come from Europe, especially from the Oxford Clay (Callovian–Early Oxfordian) of England and equivalent deposits of France and the bulk of the material comes from the Callovian whereas Oxfordian specimens are very scarce (Andrews, 1910, 1913; Tarlo, 1960; Brown, 1981; Martill and Hudson, 1991; Bardet, 1993, 1995). In the Americas, material has been found principally in the Sundance Formation corresponding to the Western Interior Sea of North America (Knight, 1898, 1900; Gilmore, 1905, 1906; Marsh, 1895; Mehl, 1912; Bakker, 1993) and also in Chile (Gasparini, 1985) and Cuba (De la Torre and Rojas, 1949).

Since the beginning of the 20th century, numerous Oxfordian marine reptile remains have been unearthed in the Pinar del Rio Province, in western Cuba. However, they were poorly known prior to the comprehensive review by Iturralde-Vinent and Norell (1996).

The Cuban Oxfordian marine reptile assemblage is particularly important not only for its taxonomic diversity but also for its spatio-temporal occurrence. The fauna is dominated by the plesiosauroids but other groups such as pliosauroids, ichthyosaurians, crocodylians, turtles and pterosaurs are also present (Colbert, 1969; Iturralde-Vinent and Norell, 1996; Fernández and Iturralde-Vinent, 2000; De la Fuente and Iturralde-Vinent, 2001; Gasparini and Iturralde-Vinent, 2001).

The reptile-bearing outcrops are located in the Sierra de los Organos (Jagua Formation) and Sierra del Rosario (Francisco and Artemisa Formations) (Fig. 1), and range in age from the Oxfordian to the Tithonian (Iturralde-Vinent and Norell, 1996). The best preserved specimens come from concretions embedded in shallow marine nearshore shales and limestones of the Middle–Late Oxfordian Jagua Vieja Member of the Jagua Formation (Iturralde-Vinent and Norell, 1996).

The predominance of plesiosaur elements, specifically Plesiosauroidea, was confirmed both in the synopsis of marine reptiles from the Late Jurassic of Cuba (Iturralde-

Vinent and Norell, 1996) and in a recent review of the Cuban collections by two of the authors (Z. G. and M. I-V.). The specimens are in the collections of the Museo Nacional de Historia Natural de Cuba (MNHN Cu, formerly MNHNH). In the title of their paper, De la Torre and Rojas (1949) erroneously attributed the following plesiosaurs to ichthyosaurs: *Cryptocleidus*? (sic) *cuervoi* (two isolated cervical vertebrae, now lost); *Cryptocleidus*? (sic) *cuervoi quesadai* (a dorsal vertebra, MNHN Cu P 3007); and *Cryptocleidus*? (sic) *cuervoi caroli* (skull, MNHN Cu P 3008). All these specimens were found in different localities of the Viñales area which are not precisely described (De la Torre and Rojas, 1949). These fossils have received little attention in the scientific literature, having been discussed only by Welles (1962) and, more recently by Iturralde-Vinent and Norell (1996). Welles (1962) considered these species to be different from *Cryptocleidus* SEELEY and referred all three to *Muraenosaurus leedsii* SEELEY. Iturralde-Vinent and Norell (1996) considered the name *Cryptocleidus*? (sic) *cuervoi* as *nomen dubium* and the name *Cryptocleidus*? (sic) *cuervoi quesadai* as invalid. As far as the best preserved specimen is concerned, a partial skull with associated mandible (MNHNH P3008, now MNHN Cu P3008), it was partially prepared at the AMNH during 1991–1992 and referred to the genus *Cryptoclidus* (Iturralde-Vinent and Norell, 1996, p. 9, fig. 6). Since *Cryptocleidus*? (sic) *cuervoi* was considered a *nomen dubium*, Iturralde-Vinent and Norell (1996) named MNHN Cu P3008 *Cryptoclidus caroli* DE LA TORRE & ROJAS.

In 1997, the preparation of MNHN Cu P3008 was completed in the Museo de La Plata (Argentina). The skull and mandible were separated, exposing the atlas-axis. The fossil record of Oxfordian plesiosaurs, as previously noted, is very poor worldwide, so that MNHN Cu P3008 is important as it fills a gap in the record of Jurassic plesiosaurs and hence permits a more complete analysis of their phylogenetic relationships.

Repository abbreviations: AMNH, American Museum of Natural History, New-York; MNHN Cu, Museo Nacional de Historia Natural de Cuba, La Habana (formerly

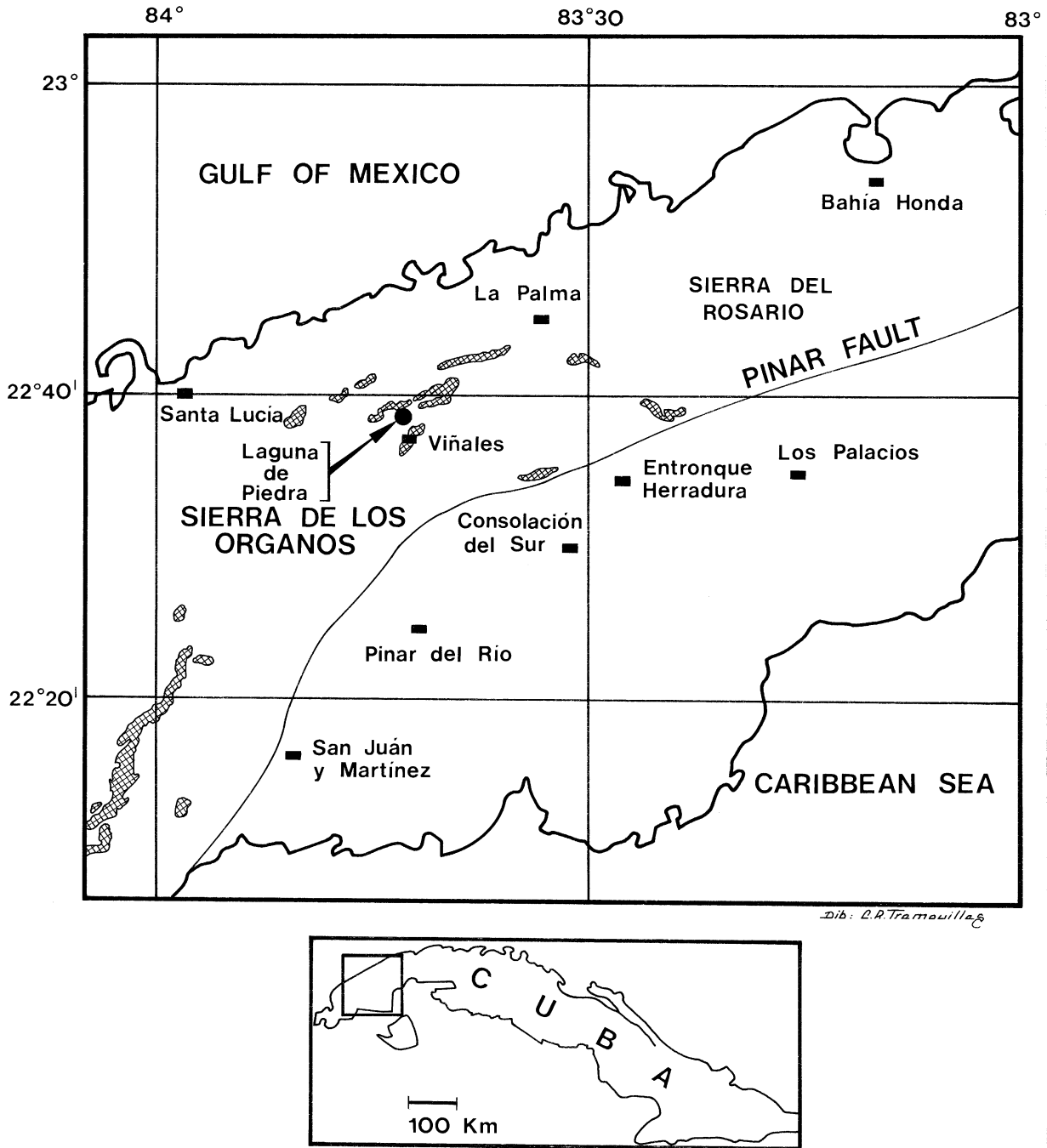


Fig. 1. Simplified geographical map of the Viñales area, western Cuba, showing the distribution of the fossil-bearing Jagua Formation and possible collecting sites.

Carte géographique simplifiée de la région de Viñales à l’Ouest de Cuba, montrant les affleurements de la formation fossilifère de Jagua et les sites possibles de récolte.

MNHNH, Museo Nacional de Historia Natural de La Habana); NHM, Natural History Museum, London.

2. Geographical and geological settings

The locality from which MNHNCu P3008 was collected was identified as ‘near Viñales, between Laguna de Piedra and La Palma’, where Late Jurassic rocks are exposed (De

la Torre and Rojas, 1949). Ammonites adhering to the bones of MNHNCu P3008 were identified by R. Myczyński (in Iturralde-Vinent and Norell, 1996) and date the fossil skull as Middle to Late Oxfordian in age. This age interval is well represented in the Sierra de los Organos of western Cuba, especially in the area near Viñales, by the isochronous Jagua Formation (Pszczolkowski, 1978; Iturralde-Vinent and Norell, 1996). However, the Oxfordian Jagua Formation outcrops in several long and narrow strips between Laguna

de Piedra and La Palma, and it is not known from which precise locality MNHNCu P3008 was collected (Fig. 1).

The Jagua Formation has been subdivided into the Zacarías, Jagua Vieja, and Pimienta Members (Pszczolkowski, 1978). The Zacarías Member (Middle Oxfordian) consists of up to 40 m of clayey shales with thin intercalations of mudstone and bivalve coquinas (Pszczolkowski, 1978). The saurian-bearing Jagua Vieja Member (Middle to Late Oxfordian) is up to 60 m thick, and is composed of laminated black shales with thin intercalations of marly micritic to biomicritic limestones, containing fairly abundant lenticular calcareous concretions. The Pimienta Member (Middle to Late Oxfordian) is represented by 60 m of thick, well stratified, black to dark gray limestones and shales, containing the first planktonic foraminiferans identified in the local Jurassic section (Pszczolkowski, 1978).

The Cuban Jurassic vertebrate fossils are commonly found in concretions that are imbedded within horizontally laminated black shales and limestones of the Jagua Vieja Member of the Jagua Formation. These concretions are lenticular in shape and of very variable size, from a few centimeters up to nearly one meter across. Fossil found in these concretions include vertebrates (fishes and reptiles), abundant ammonites, belemnites, and other invertebrates, as well as plant remains. These concretions are found in situ, as well as at the base of the slopes where the Jagua Vieja Member outcrops and around the farm plantations where they have been removed from the soil and piled up along the trails. They are neither deformed nor compressed. Ammonites can be hollow and partially filled with calcareous sediment or sparry calcite. Fossil bones are generally characterized by a highly polished surface and, as in MNHNCu P3008, most of them are recrystallized so that they have lost most sutures. Fish remains are often flattened, probably due to desiccation, but three-dimensional specimens are not uncommon (Pszczolkowski, 1978; Iturralde-Vinent and Norell, 1996). This suggests an early diagenetic origin for the fossiliferous concretions (Pszczolkowski, 1978).

The Jurassic rocks of western Cuba have been identified as part of the 'Guaniguanico Terrane', because it is an allochthonous suite of rocks that reached its present-day position sometime in the mid-Tertiary (Bralower and Iturralde-Vinent, 1997). During the Jurassic, this terrane was located in the southeastern part of the present-day Yucatán peninsula, facing the Caribbean (Hudson et al., 1999). In this scenario, the shallow marine section of the Jagua Formation represents a major marine transgression within the evolving southern continental margin of Laurasia (Iturralde-Vinent, 1994). In the Guaniguanico Terrane, occurs a thick unit of pillow basalts (El Sábalo Formation), partially isochronous with the Jagua Formation, suggesting that the oceanic crust was under development in the Caribbean during the Oxfordian (Iturralde-Vinent, 1994). These facts strongly suggest that the Caribbean seaway—a marine channel with oceanic crust—was well developed

between Laurasia and Gondwana during the Oxfordian (Pindell, 1994; Iturralde-Vinent and MacPhee, 1999), enhancing the dispersal of the marine biota between the western Tethys and the eastern Pacific.

3. Systematic palaeontology

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA De Blainville, 1835

PLESIOSAUROIDEA (Gray, 1825) Welles, 1943

CRYPTOCLIDIDAE Williston, 1925

Vinialesaurus nov. gen.

Derivation of name: from *Viñales*, town in western Cuba in which area the fossil was found, and *Sauros* (Greek), lizard.

Type species: *Cryptocleidus* ? (sic) *cuervo caroli* DE LA TORRE & ROJAS, 1949.

Diagnosis: as for type and only species of the genus, *Vinialesaurus caroli* (DE LA TORRE & ROJAS, 1949).

Vinialesaurus caroli (DE LA TORRE & ROJAS, 1949),
new combination

Cryptocleidus ? (sic) *cuervo caroli* DE LA TORRE & ROJAS, 1949, p. 199, pl. 6, figs. 1–2.

Muraenosaurus leedsii SEELEY, 1874 - Welles, 1962, p. 9.

Cryptoclidus caroli (DE LA TORRE & ROJAS, 1949) - Iturralde-Vinent & Norell, 1996, p. 10, fig. 6.

Type specimen: MNHNCu P3008, anterior part of skull and mandible with associated atlas-axis.

Locality and horizon: somewhere between Laguna de Piedra and La Palma, in the Sierra de Los Organos, Pinar del Río Province, western Cuba (Fig. 1); Jagua Vieja Member, Jagua Formation, Middle-Late Oxfordian, Late Jurassic (Iturralde-Vinent and Norell, 1996).

Diagnosis: skull with lateral supraorbital process on frontal; large external nares and orbits; small vertical jugal; vomer anteriorly rounded; anterior interpterygoid vacuities lacking; large double internal nares divided by a maxillary-vomer bar; reduced tooth ornamentation.

4. Description

4.1. Preservation

The skull is preserved from the tip of the rostrum to the anterior rims of the temporal fenestrae. The anterior parts of both mandibular rami are preserved, the right one back to the coronoid process of the surangular. They are slightly compressed but not distorted. Most sutures are not visible. This feature may be ontogenetic (if the specimen was an old adult sensu Brown, 1981) or due to recrystallization within the fossil-bearing concretion (see previous discussion).

4.2. Skull (Figs. 2A–C and 3A, B)

In front of the external nares, the snout is low, short and convex; more posteriorly, the skull gently rises up to the pineal foramen. Between the nares, the premaxillae is markedly convex from side to side and meet the frontal without visible suture in a rugose area exhibiting two deep grooves (Figs. 2A and 3A). In ventral view, the premaxillae bears five pairs of alveoli, some of the left side bearing teeth. The first is the smallest whereas the third and the fourth are the largest (anteroposterior diameters of the alveoli in cm: 0.7–1.1–1.4–1.3–1.1). Posteromedially to the main alveoli, are located five replacement ones, some showing teeth in eruption.

The premaxillary–maxillary suture is marked by a slight constriction visible in dorsal and ventral views. The teeth around this suture are smaller than the other. Dorsally, this suture is difficult to distinguish but seems to be straight and to run from the lateral border of the snout, behind the fifth premaxillary alveolus to the anterolateral corner of the external naris margin.

Posterior to the premaxillary–maxillary constriction, the maxilla is slightly sinuous from the first to the fifth maxillary alveolus and then becomes straight up to the posteriormost and smallest alveolus. The maxilla's anterior orbital margin exhibits a small protuberance (Figs 2C, 3C). A similar structure has been observed in *Cryptoclidus eurymerus* SEELEY (Brown, 1993, fig. 1b). Below the orbit, the maxilla is slender as in cryptoclidids and in contrast to 'plesiosaurids' and elasmosaurids (excepting *Muraneosaurus*) where it forms a wide bar. The maxilla bears 10–11 alveoli but it is incomplete. The first alveolus is small and marks the beginning of the slight curvature previously mentioned. This undulation bears five alveoli of which the three median are the largest (diameters in cm: 0.6–0.9–1.1–1.2–0.6). Posteriorly, there are five or six small alveoli equisized, but difficult to observe because of poor preservation in this area. As in the premaxillae, replacement alveoli are also present on the maxilla, posteromedially to the main ones.

The frontal is roughly quadrangular so that the interorbital bar is wide. It is deeply grooved along its dorsal midline so that it seems composed of two bones not completely united, a condition often observed in plesiosaurs. Laterally, at about the middle of the orbit, the frontal shows a small supraorbital process (Figs. 2A and 3A). Because of the absence of a clear suture in this area, there is no evidence for the presence or absence of prefrontal and postorbital.

The nares are of different sizes, which could be due to preservation and/or preparation. The better preserved left naris is circular and relatively large compared to the size of the snout and orbit, as is typical for cryptoclidids (Brown, 1993).

The orbits are relatively large compared to the length of the snout as in cryptoclidids (orbit length = 2/3–1 snout

length) and in contrast with 'plesiosaurids' and elasmosaurids (orbit length = 1/2 snout length). It is dorsolaterally oriented, and pear-shaped (posterior transverse diameter about 5 cm, anterior transverse diameter about 2.5 cm).

The jugal appears a delicate L-shaped bone, vertically oriented and expanded anteriorly where it contacts the maxilla (Fig. 2C).

Only the anterior portion of the parietal is preserved, enclosing the pineal foramen and delineating the anterior border of the temporal fenestrae. Its sutural contact with the frontal is not identifiable.

In ventral view, the suture between premaxillae and vomer is almost rounded in outline and not V-shaped as is typical for other plesiosaurs (Figs. 2B and 3B). The vomer forms a strong bar between the internal nares, convex from side to side and projecting ventrally below the level of the maxilla. The vomer expands posterior to the internal nares and its suture with palatine and pterygoid is also rounded. The premaxillary–maxillary suture ends in the anterolateral corner of the anterior pair of internal nares, whereas the vomero–palatine suture ends in the posterolateral corner of the posterior pair of internal nares. The maxilla enters the lateral margin of the internal nares.

The pterygoid–palatine region is slightly convex. It has not been possible to identify the sutures of these two bones with the maxilla or with the ectopterygoid. The pterygoids enclose large posterior interpterygoid vacuities, but anterior interpterygoid vacuities are absent.

The internal nares are located medially on the palate, separated by the wide vomer. They are characteristically very large and divided by a superficial maxillary–vomer transversal bar, so that they appear as double internal nares, although they communicate below the bar (Figs. 2B and 3B). This is considered here as an autapomorphy of this genus. It should be noted that these large and divided into two parts internal nares are not the result of an artifact of preservation or preparation because they are symmetrical and bear natural margins. The anterior openings are elliptical, posterolaterally oriented and larger than the posterior ones which are circular. Some plesiosaurs show specializations around the internal nares, comparable to but not identical with that of *Vinialesaurus*. In *Rhomaleosaurus megalcephalus* (STUTCHBURY), there is a pair of grooves on each side of the palate. The medial one runs to the internal naris and the lateral one to a large, posteriorly located foramen (Cruickshank, 1994). In *Rhomaleosaurus thornstoni* ANDREWS, there are two closed foramina located in front of the internal naris, both lying in the same groove (Cruickshank, 1996). Finally, *Pliosaurus brachypondylus* (OWEN) also exhibits two foramina located in the same groove but behind the internal nares (Taylor and Cruickshank, 1993). In all of these species, both the choanae and the additional foramina remain very small. In MNHNCu P3008, there is no groove around the internal nares which are very large and divided into two by a maxillary–vomer bar although remaining in connection

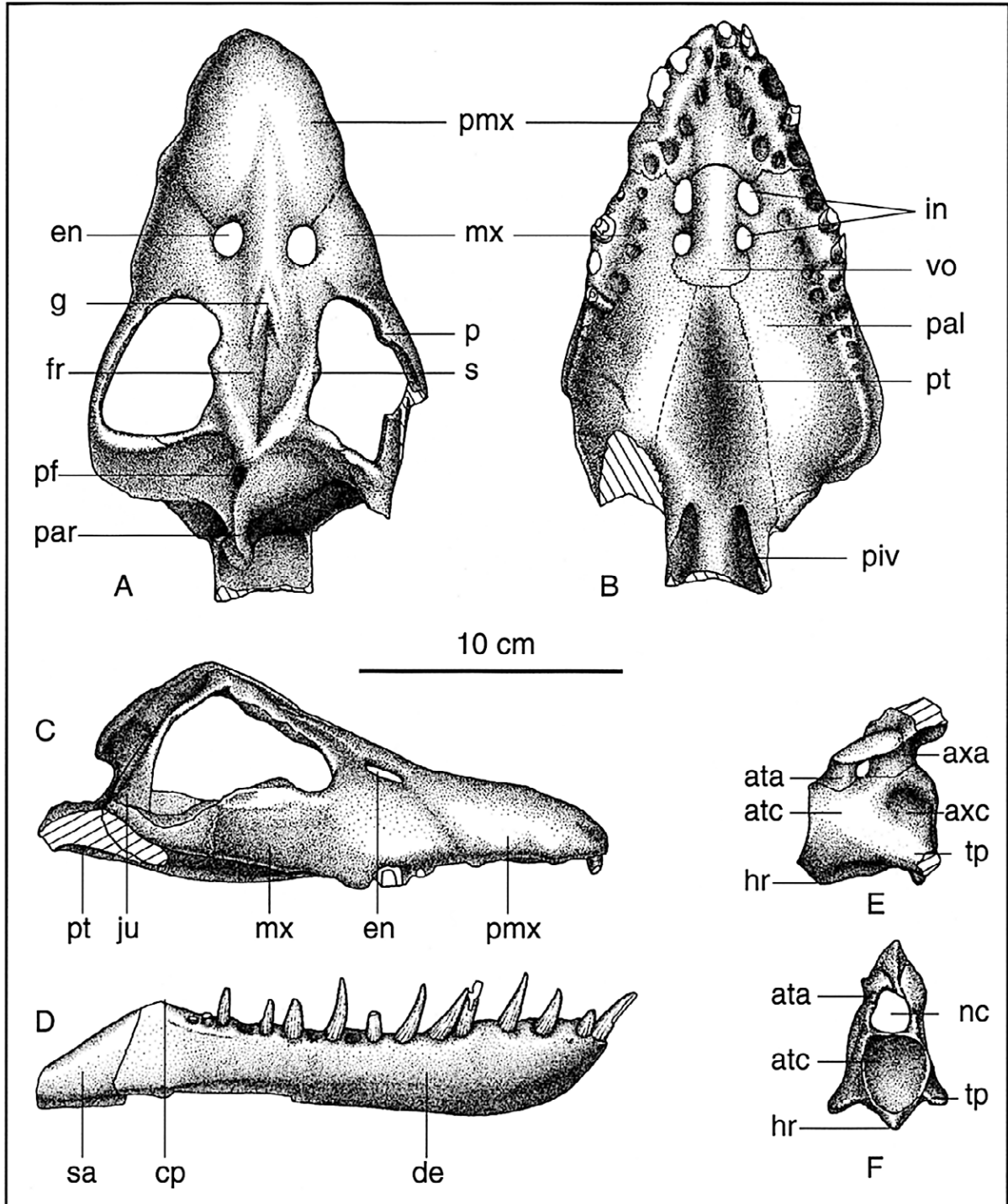


Fig. 2. *Vinalesaurus caroli* (DE LA TORRE & ROJAS, 1949) new combination, MNHNCu P 3008, near Viñales, western Cuba, Jagua Vieja Member, Jagua Formation, Middle to Late Oxfordian, Late Jurassic. **A, B, C**: skull in dorsal, ventral and right lateral views; **D**: mandible in right lateral view; **E, F**: atlas-axis in left lateral and anterior views. Graphic scale: 10 cm. Abbreviations used: ata, atlas arch; atc, atlas centrum; axa, axis arch; axc, axis centrum; cp, coronoid process; de, dentary; en, external nares; fr, frontal; g, frontal groove; hr, hypapophyseal ridge; in, internal nares; ju, jugal; mx, maxilla; nc, neural canal; p, maxillary protuberance; pal, palatine; par, parietal; pf, pineal foramen; piv, posterior interpterygoid vacuity; pmx, premaxilla; pt, pterygoid; s, supraorbital process; sa, surangular; tp, transverse process; vo, vomer.

Vinalesaurus caroli (DE LA TORRE & ROJAS, 1949) nouvelle combinaison, MNHNCu P 3008, près de Viñales, Ouest de Cuba, Membre Jagua Vieja, Formation Jagua, Oxfordien moyen-supérieur, Jurassique supérieur. **A, B, C**: crâne en vues dorsale, ventrale et latérale droite; **D**: mandibule en vue latérale droite; **E, F**: atlas-axis en vues latérale gauche et antérieure. Echelle graphique: 10 cm. Abréviations utilisées: ata, arc de l'atlas; atc, centrum de l'atlas; axa, arc de l'axis; axc, centrum de l'axis; cp, processus coronoïde; de, dentaire; en, narines externes; fr, frontal; g, sillon du frontal; hr, ride hypapophysaire; in, narines internes; ju, jugal; mx, maxillaire; nc, canal neural; p, protubérance du maxillaire; pal, palatin; par, pariétal; pf, foramen pineal; piv, cavité interptérygoïde postérieure; pmx, prémaxillaire; pt, ptérygoïde; sa, surangulaire; tp, processus transverse; vo, vomer

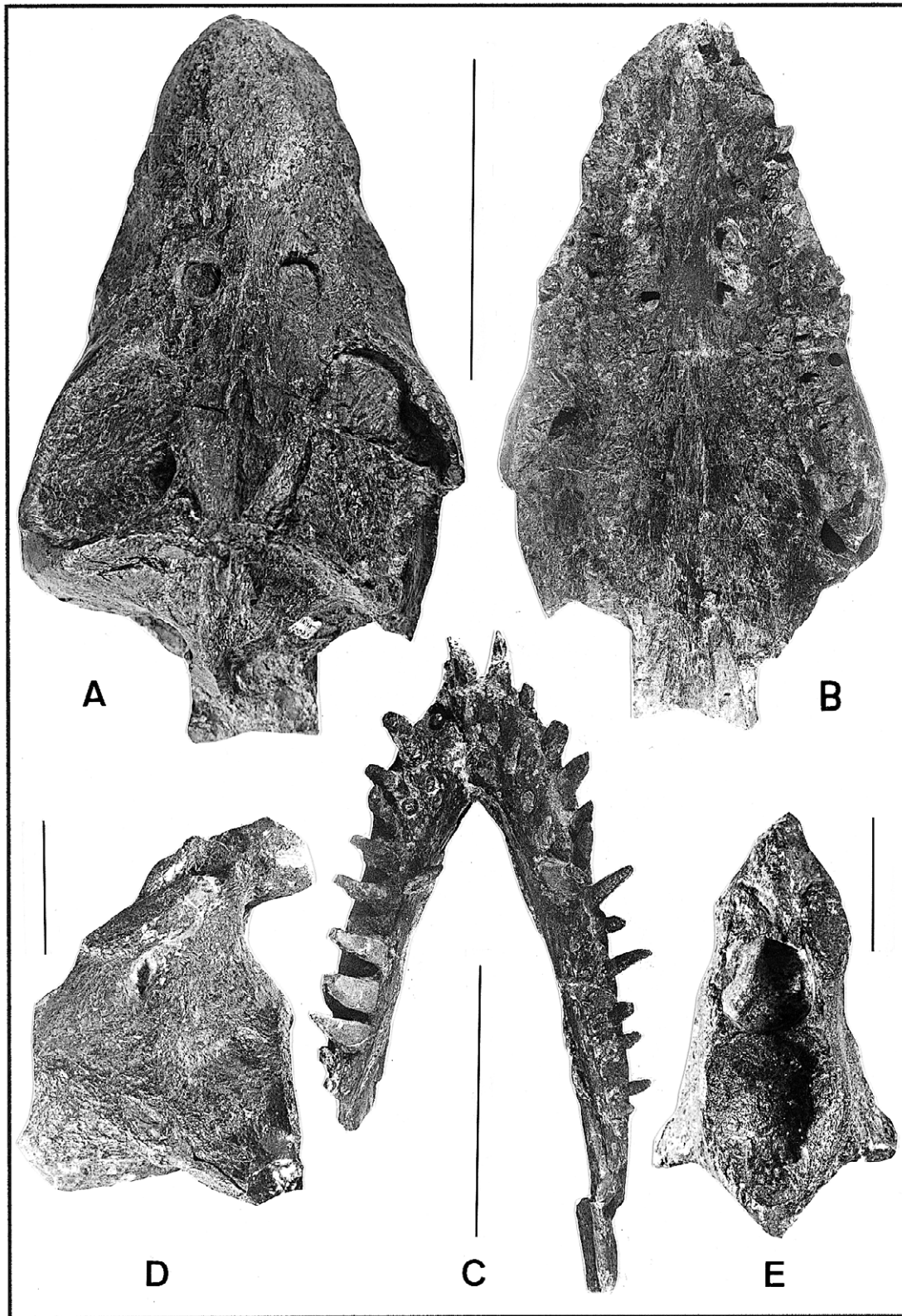


Fig. 3. *Vinalesaurus caroli* (DE LA TORRE & ROJAS, 1949) new combination, MNHNCu P 3008, near Viñales, western Cuba, Jagua Vieja Member, Jagua Formation, Middle to Late Oxfordian, Late Jurassic. Photographs of skull, mandible and atlas-axis. **A, B**: skull in dorsal and ventral views; **C**: mandible in dorsal view; **D, E**: atlas-axis in left lateral and anterior views. Graphic scale: 10 cm for A, B, C and 2 cm for D and E.

Vinalesaurus caroli (DE LA TORRE & ROJAS, 1949) nouvelle combinaison, MNHNCu P 3008, près de Viñales, Ouest de Cuba, Membre Jagua Vieja, Formation Jagua, Oxfordien moyen-supérieur, Jurassique supérieur. **A, B**: crâne en vues dorsale et ventrale; **C**: mandibule en vue dorsale; **D, E**: atlas-axis en vue latérale gauche et antérieure. Échelle graphique: 10 cm pour A, B et C, 2 cm pour D et E.

below this bar. The communication between the anterior and posterior part of the nares excludes the possibility of being large nutritive foramina.

4.3. Mandible (Figs. 2D and 3C)

The mandible is narrow. The symphysis reaches the anterior border of the fourth alveolus dorsally and the anterior border of the fifth alveolus ventrally.

The right dentary is complete and bears 17 alveoli with teeth, some of them damaged during preparation when separating the skull from the mandible. The first five teeth are about equal in size (diameter from 1 to 1.3 cm). The sixth to the 17th alveoli gradually decrease in size to 0.5 cm.

The splenial is a very thin, vertical plate of bone, which reaches the symphysis but does not enter it. Posteriorly, it rises up from the level of the 10th alveolus to form the internal face of the coronoid process together with the surangular. The coronoid process is incomplete but appears to be low. Remains of the angular are preserved on the right mandibular ramus, below the coronoid process.

The teeth are conical, acute, slightly recurved and procumbent. The enamel crown ornamentation is reduced and consists of very dense fine striations. Because the teeth have been damaged, more details are not available.

4.4. Vertebrae (Figs. 2E, F and 3D, E)

During preparation, the atlas-axis complex was found articulated with the skull. The anterior articular surface of the atlas is subtriangular with a ventral crest (hypapophysal ridge) that is more distinct and compressed than that of *Muraenosaurus* (Andrews, 1910, text-fig. 49) (Figs. 2E, F and 3D, E). Posteriorly, this crest becomes a lower promontory. The atlas neural arch is large and high, being 2/3 that of the atlas centrum and surrounds a circular neural canal. It is fused to the axis neural arch with a foramen between them (Figs. 2E and 3D). Transverse processes are short.

4.5. Measurements

Rostrum length from tip to anterior orbital border: 11 cm.
 Rostrum width at anterior margin of external nares: 8.8 cm.
 Rostrum width at anterior margin of orbit: 10 cm.
 Anteroposterior diameter of right orbit: 6 cm.
 Anteroposterior diameter of left orbit: 5.4 cm.
 Transverse diameter of left orbit: 5.0 cm.

Anteroposterior and transverse diameters of left naris: 1.2 cm (circular).

Anteroposterior and transverse diameters of right naris: 1.6 cm and 1.2 cm (oval).

5. Discussion

A cladistic analysis, including six species and nine cranial characters, has been performed to understand the phylogenetic affinities of *Vinialesaurus* among Plesiosauroidea (Appendix 1). Comparisons have been made with a selection of Middle–Late Jurassic plesiosaurs, namely the *cryptoclidids* *Cryptoclidus eurymerus* (PHILLIPS), *Tricleidus seeleyi* ANDREWS and *Kimmerosaurus langhami* BROWN, and the elasmosaurid *Muraenosaurus leedsii* SEELEY (see Brown, 1981). The cryptoclidid *Colymbosaurus trochanterius* (OWEN) has not been included in the analysis because it is known only from postcranial material and may be synonymous with *Kimmerosaurus* (BROWN et al., 1986). The basal *Plesiosaurus dolichodeirus* CONYBEARE (see Storrs, 1997) has been chosen as outgroup. All taxa have been personally inspected, on the basis of the specimens from the collections of the Natural History Museum of London (see Table 1). Characters have been mainly selected from the Bardet et al. (1999) database. The data matrix (Appendix 2) was analysed using Hennig86 version 1.5 (Farris, 1988) implementing the implicit enumeration option. The characters were treated as non-additive (= unordered) to preclude an a priori knowledge of character evolution. The analysis of the data matrix generated one tree of 11 steps, a C.I. of 0.90 and a R.I. of 0.85 (Fig. 4).

Muraenosaurus is the sister taxon of the cryptoclidids, based on the long and narrow rostrum (character 1), which reverses in *Tricleidus*, probably because of its juvenile status. The monophyly of cryptoclidids is supported by large external nares (character 2), absence of prefrontal (character 3)—a missing data in *Vinialesaurus*—and strongly emarginated cheek (character 4). Within this clade, *Vinialesaurus* forms a natural group with *Cryptoclidus* and *Kimmerosaurus*, supported by the reduced teeth ornamentation (character 9₁). *Vinialesaurus* is the sister-group of *Cryptoclidus* and *Kimmerosaurus* which share more than five premaxillary teeth (character 8). The absence of teeth ornamentation and of anterior pterygoid vacuities are autapomorphies of *Kimmerosaurus* and *Vinialesaurus*, respectively. Two other autapomorphies of *Vinialesaurus* (not

Table 1

List of specimens from the collections of the NHM (London) inspected for comparisons.

Liste des spécimens de la collection du National History Museum de Londres examinés pour comparaison.

<i>Plesiosaurus dolichodeirus</i> CONYBEARE, 1824 - BMNH 22656, 41101, Sinemurian of Dorset
<i>Cryptoclidus eurymerus</i> (PHILLIPS, 1871) - BMNH R2860, Callovian of Cambridgeshire
<i>Tricleidus seeleyi</i> ANDREWS, 1909 - BMNH R3539, Callovian of Cambridgeshire
<i>Kimmerosaurus langhami</i> BROWN, 1981 - BMNH R8431, Kimmeridgian of Dorset
<i>Muraenosaurus leedsii</i> SEELEY, 1874 - BMNH R2421, R2422, R2678, R2861, Callovian of Cambridgeshire

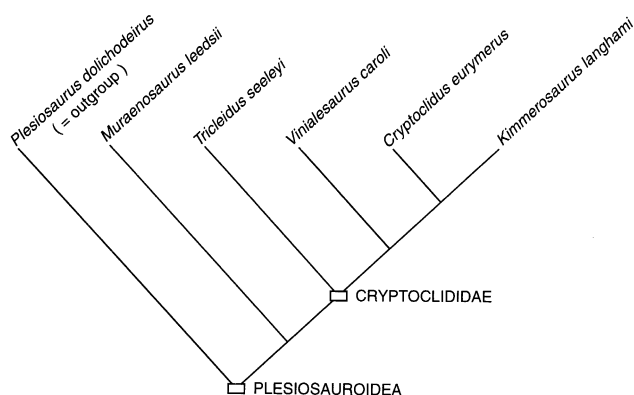


Fig. 4. Cladogram showing the phylogenetical affinities of *Vinalesaurus caroli* among a selection of Plesiosauroidea.

Cladogramme montrant les affinités phylogénétiques de *Vinalesaurus caroli* au sein d'une sélection de Plesiosauroidea.

included in this analysis) are large and divided into two internal nares and anteriorly rounded vomer.

The family Cryptoclididae is classically considered to range from the Callovian to the Maastrichtian and to include the Middle–Late Jurassic genera *Cryptoclidus*, *Tricleidus*, *Kimmerosaurus* and *Colymbosaurus*, as well as *Aristonectes* CABRERA and *Morturneria* CHATTERJEE & CREISLEY, from the Late Cretaceous (Brown, 1981; Chatterjee and Small, 1989). Recently, Bardet et al. (1991) have suggested that *Aristonectes* and *Morturneria* may be elasmosaurids rather than cryptoclidids and, as a result, the known Cryptoclididae were restricted to the Callovian–Tithonian interval, a view confirmed by work in preparation (Gasparini et al., in press). Cryptoclidids are mainly known in Europe where numerous complete skeletons have been unearthed (Brown, 1981). Outside Europe, incomplete postcranial remains of cryptoclidids have been found in the Lower Callovian of northwestern Patagonia (Gasparini and Spalletti, 1993) and in the Oxfordian of western North America (Mehl, 1912). The discovery of a new cryptoclidid in Cuba, namely *Vinalesaurus caroli*, indicates a greater diversity of this family during the Late Jurassic than was previously assumed, and fills a gap in the Oxfordian fossil record. Moreover, the marine reptiles from the Jagua Formation of Cuba are evidence that, as early as the Oxfordian, the Caribbean seaway (Iturralde-Vinent and McPhee, 1999) showed a notable pelagic faunal diversity.

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Appendix 1.

1. Rostrum (short and high = 0, long and low = 1). In *Plesiosaurus dolichodeirus* the rostrum is short and high in lateral view. In more derived plesiosauroids with the exception of *Tricleidus*, the rostrum is longer and lower. The fact that *Tricleidus* retains the plesiomorphic condition could be linked to the possible immaturity of the holotype and only known specimen of this taxon.

2. External naris size (small = 0, large = 1). In *P. dolichodeirus* and in elasmosaurids the external nares are small compared to the size of the snout. In cryptoclidids the nares are large.

3. Prefrontal (present = 0, absent = 1). The prefrontal is present in all member of the Plesiosauroidea and the external nares are bordered by the premaxillae, maxillae, prefrontals and frontals. In cryptoclidids there is no indication of the occurrence of a prefrontal so that the nares are surrounded only by premaxillae, maxillae and frontals (Brown, 1981).

4. Cheek emargination (weakly emarginated = 0, strongly emarginated = 1). In *P. dolichodeirus*, the cheek is weakly emarginated, the jugal is a large horizontally-oriented quadrilateral element and the ventral surface of the jugal-squamosal is almost flat, a plesiomorphic character retained by elasmosaurids. Cryptoclidids on the other hand exhibit a deep ventral emargination of the cheek, resulting from the enlargement of the orbit and the remodeling of the jugal into a small, narrow and vertically oriented bone (Brown, 1993; Brown and Cruickshank, 1994).

5. Maxilla–internal nare contact (yes = 0, no = 1). In *P. dolichodeirus* and in most plesiosauroids, the maxillae participate in the lateral margin of the internal nares. In *Cryptoclidus* (Brown & Cruickshank, 1994) and *Occitanosaurus* (Bardet et al., 1999), the maxillae are excluded from the margin of the internal nares by an anterior extension of the lateral part of the palatines.

6. Anterior pterygoid vacuities (present = 0, absent = 1). In most plesiosauroids anterior pterygoid vacuities are present. In elasmosaurids and in *Vinalesaurus*, the palate is closed anteriorly. This could be linked to cranial kinesis in relation with food habits. In *Muraenosaurus*, anterior pterygoid vacuities have been mentioned by Andrews (1910, fig. 47) but the poor preservation of this area does not allow confirmation of this observation.

7. Occipital condyle (formed by basioccipital only = 0, formed by basioccipital and exoccipitals = 1). Primitively, the occipital condyle is formed by the basioccipital only

(Rieppel, 1994), a plesiomorphic condition found in plesiosauroids, elasmosaurids and in *Tricleidus*. Only advanced cryptoclidids exhibit a participation of exoccipitals in the formation of the occipital condyle.

8. Number of premaxillary teeth (five = 0, more than five = 1). The plesiomorphic number of premaxillary teeth in Plesiosauria is five (Brown, 1981), a condition retained in Jurassic elasmosaurids. In Cryptoclididae, there is a tendency to increase this number as *Cryptoclidus* possesses six teeth and *Kimmerosaurus* eight. *Tricleidus* and *Vinialesaurus* remain plesiomorphic on this character.

9. Teeth ornament (present = 0, reduced = 1, absent = 2). In *P. dolichodeirus* and most plesiosauroids including *Tricleidus*, the teeth are slender and ornamented by fine and numerous longitudinal enamel ridges. In cryptoclidids, there is a trend to reduce the ornament of the teeth, ranging from the presence of few ridges (*Cryptoclidus* and *Vinialesaurus*) to a complete lack of ornament (*Kimmerosaurus*) (Brown, 1981).

Appendix 2.

	12345	6789
<i>Plesiosaurus dolichodeirus</i>	00000	0000
<i>Cryptoclidus eurymerus</i>	11111	0111
<i>Tricleidus seeleyi</i>	0111?	0000
<i>Kimmerosaurus langhami</i>	1111?	?112
<i>Muraenosaurus leedsii</i>	10000	?000
<i>Vinialesaurus caroli</i>	11??0	?01

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