

A NEW OXFORDIAN PLIOSAURID (PLESIOSAURIA, PLIOSAURIDAE) IN THE CARIBBEAN SEAWAY

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Abstract: A new pliosaurid, *Gallardosaurus iturraldei* gen nov. et sp. nov., was found in the Viñales area, western Cuba, in sediments of the Jagua Formation, middle–late Oxfordian. This new taxon is characterized by: wide participation of the premaxilla in the outer margin of the external naris; frontal not participating in the orbital margin; postorbital in contact with the jugal and squamosal; presence of anterior pterygoid vacuity; cultriform process of parasphenoid convex and exposed in palatal view; pterygoid flanges high; jaw articulation low relative to tooth row; trihedral teeth in cross-section and with smooth ridges at least in the labial face. A phylogenetic analysis suggests that *Gallardosaurus* forms a clade with *Peloneustes*, the most common pliosaurid genus occurring in the Oxford Clay. The Caribbean Seaway was, at least since the Oxfordian, a corridor that permitted the interchange for marine biota between Western Tethys and Eastern Pacific

realms. Among vertebrates, bony fish and long-necked plesiosaurs prevailed. However, marine pleurodiran turtles, metriorhynchid crocodylians, ophthalmosaurian ichthyosaurs, and pliosaurids (*G. iturraldei* gen. nov. et sp. nov.) have also been found, as well as at least two species of pterosaurs, and one camarasaurian dinosaur. Among these reptiles there were off-shore pelagic forms such as the ichthyosaurs and metriorhynchids, together with the pliosaurid *G. iturraldei* gen. nov. et sp. nov.; other taxa were presumably less pelagic, such as the pleurodiran turtles and the cryptoclidid plesiosauroids. *Gallardosaurus iturraldei* gen. nov. et sp. nov. would have played the role of an active predator taking advantage of nektonic fish recorded in the area.

Key words: Pliosaurid, Oxfordian, Cuba, Caribbean Seaway.

THE Oxfordian marine herpetofauna is known mainly from the Northern Hemisphere. These are, for example, the reptiles found in the Oxford Clay (Callovian–Early Oxfordian) of England, and equivalent deposits of France (Andrews 1913; Linder 1913; Martill and Hudson 1991; Bardet 1993, 1995; McGowan and Motani 2003); the middle Oxfordian of Russia and neighbouring countries (Storrs *et al.* 2000), and the late Oxfordian of the upper Sundance Formation and equivalents in Wyoming, Montana and Alaska (Bakker 1993; Massare and Sperber 1999; O’Keefe and Wahl 2003a, b). The herpetofauna from the middle–late Oxfordian of western Cuba joins these records (Gasparini and Iturralde-Vinent 2006).

Remains of Oxfordian reptiles were found in Cuba during the first half of the 20th century in several localities in the Sierra de los Organos and Sierra del Rosario of the Guaniguanico mountain range, located at the west of the island. These findings were published in Cuba and remained almost unknown elsewhere. During the 1990s, Manuel Iturralde-Vinent, from the Museo Nacional de Historia Natural de Cuba, started gathering information about those specimens, and made a detailed catalogue of

Jurassic reptile-bearing localities, with a preliminary discussion of the taxonomic position of the previously published taxa (Iturralde-Vinent and Norell 1996). Since the end of the 1990s there has been a close collaboration between Iturralde-Vinent and palaeontologists of the Museo de La Plata, in Argentina, that includes fieldwork, preparation of the specimens and corresponding systematic studies.

Ichthyosaurs, metriorhynchids, marine pleurodirans, plesiosauroids and pliosauroids, pterosaurs, and at least one camarasauromorph dinosaur are present in the Oxfordian Cuban herpetofauna (Gasparini and Iturralde-Vinent 2006). In this fauna, long-necked plesiosaur remains are the most abundant (Gasparini *et al.* 2002). By contrast, pliosaurid remains are very scarce and the only well-preserved specimen is the one here described (MNHN Cu P3005). This specimen was mentioned, without being prepared, by Iturralde-Vinent and Norell (1996), who pointed out that it generally resembled *Pliosaurus ferox* Sauvage, but that it needed adequate preparation. MNHN Cu P3005 was prepared at the Museo de La Plata and later was assigned to the pliosaurid *Peloneustes*

sp. (Gasparini and Iturralde-Vinent, 2006). However, a detailed analysis of the specimen justifies its assignment to a new taxon of Pliosauridae (*sensu* O'Keefe 2001, 2004).

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; CAMSM, Sedgwick Museum of Earth Sciences, Department of Earth Sciences, Cambridge University, UK; GPIT, Institut und Museum für Geologie und Paläontologie der Eberhard-Karls Universität, Tübingen, Germany; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Museum National D'Histoire Naturelle, Paris, France; MOZ, Museo Olsacher, Neuquén, Argentina; NHM, The Natural History Museum (formerly the British Museum, Natural History; BMNH R.), Palaeontology Department, London, UK; PETMG, Peterborough Museum and Art Gallery, Peterborough, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; YPM, Peabody Museum, Yale University, New Haven, USA.

SYSTEMATIC PALAEOLOGY

SAUROPTERYGIA Owen, 1860
 PLESIOSAURIA Blainville De, 1835
 PLIOSAUROIDEA Welles, 1943
 PLIOSAURIDAE Seeley, 1874 (*sensu* O'Keefe, 2001)

Genus GALLARDOSAURUS gen. nov.

Derivation of name. Gallardo, in homage to Juan and Juanito Gallardo, Cuban farmers, who discovered most of the Oxfordian reptiles of Cuba; saurus, from the Greek lizard.

Type species. *Gallardosaurus iturraldei* gen. nov. et sp. nov.

Diagnosis. *Gallardosaurus* differs from other pliosaurids in the following combination of characters: participation of the premaxilla in the antero-medial margin of the naris. Nasal surpassing the anterior level of the orbits and participating widely in the posterior margin of the naris. Prefrontal expanded rostrally. Frontal excluded from the orbital margin. Parietal with expanded anterior margin. Lateral pillar of the postorbital merging with the jugal and squamosal. Presence of a slit-like anterior interpterygoid vacuity. Cultriform process of parasphenoid convex, exposed in palatal view and closing the anterior interpterygoid vacuity. The basisphenoid is 3/4, and the parasphenoid 1/4 inside the posterior interpterygoid vacuity. Pterygoid flanges high. Basioccipital tuber short. Coronoid area high and surangular short. The jaw articulation is low relative to the tooth row. Neural spine of the atlas and axis fused, forming a wide roof posteriorly, and upwardly oriented.

Gallardosaurus iturraldei sp. nov.

Text-figures 1–3

2006 *Peloneustes* sp. Gasparini and Iturralde-Vinent, pp. 350, 352, 357, 360, fig. 4C.

Derivation of name. In homage to Dr Manuel Iturralde-Vinent, distinguished Cuban geotectonist and palaeontologist, who dedicated a large part of his scientific work to recovering the Mesozoic fauna of his country, and interpreting it within the geotectonic evolution of the Caribbean.

Holotype. MNHNCu P3005. Incomplete skull and mandible, preserved in occlusion (Text-fig. 1; Text-fig. 2A; Text-fig. 3A–E). Atlas-axis and the third and fourth cervicals (Text-fig. 2B; Text-fig. 3F).

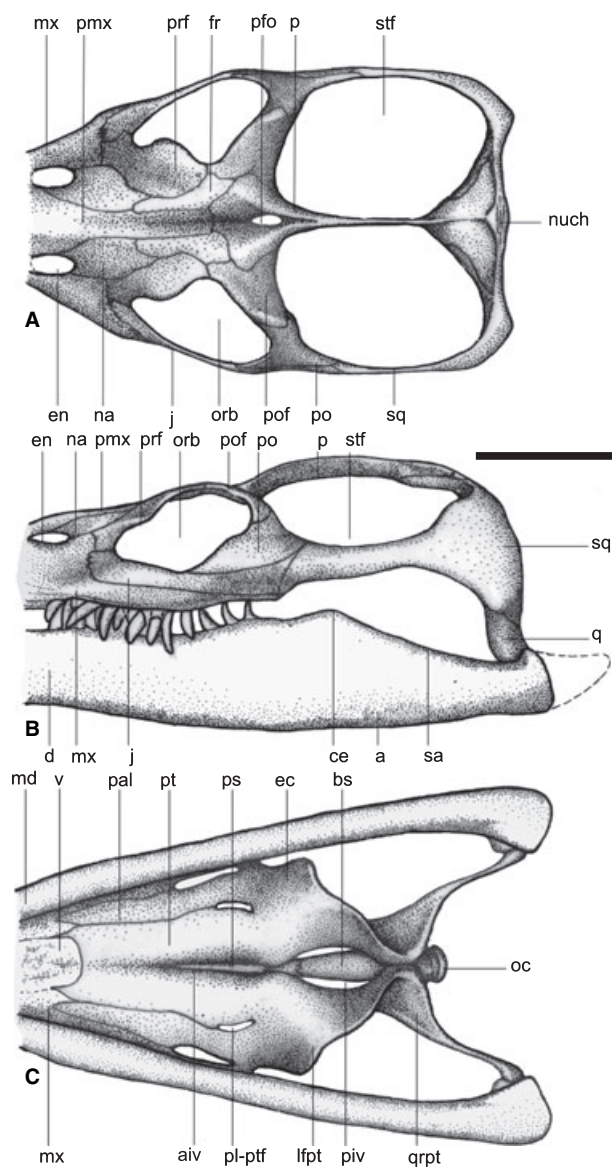
Type locality and horizon. MNHNCu P3005 was discovered by the farmer Juan Gallardo in 1946, in the Northern slope of the Sierra de Caiguanabo, 8 km east of Viñales, Pinar del Río Province, northwestern Cuba (Iturralde-Vinent and Norell 1996, fig. 4; Gasparini and Iturralde-Vinent 2006, fig. 1). This horizon corresponds to the Jagua Formation, Jagua Vieja Member, middle-late Oxfordian, Late Jurassic (Iturralde-Vinent and Norell 1996; Puszczkowsky 1999). The specimen MNHNCu P3005, as well as most of the Oxfordian reptiles from this formation, was found in a concretion '*in situ*' within the dark shales at the base of the slopes where the Jagua Member outcrops (Gasparini and Iturralde-Vinent 2006).

Diagnosis. As for the genus.

Description

The skull and mandible are preserved in occlusion (Text-fig. 3B–E). Some sutures are incomplete, as in other skulls of Oxfordian reptiles of Cuba, which suggests diagenesis rather than the adult condition for all the specimens (Gasparini and Iturralde-Vinent 2006). MNHNCu P3005 is preserved in three dimensions, with only slight lateral plastic deformation.

In dorsal view (Text-figs 1A, 3A), the area of the supratemporal fenestrae is rectangular, with the medial axis shorter (16 cm) than the transverse (26 cm). The skull narrows from the posterior margin of the orbits, and more markedly anterior to the orbits, suggesting a narrow rostrum. The rostrum is preserved only up to the anterior margin of the external nares. Each naris is oval (antero-posterior diameter 3 cm; transverse, 1.5 cm), and limited medially by the premaxilla, caudally by the nasal and externally by the maxilla (Text-figs 1A–B, 3A, C). The premaxillae are fused. The area from the nares to the anterior margin of the orbits is convex, whereas caudally, up to the contact with the parietal, it is markedly concave. The premaxilla-parietal suture is straight. The nasal is widely exposed, extending caudally behind the anterior level of the orbit. The nasal contacts medially with the premaxilla, posteriorly with the frontal and prefrontal, and externally with the maxilla (Text-fig. 1A–B). In



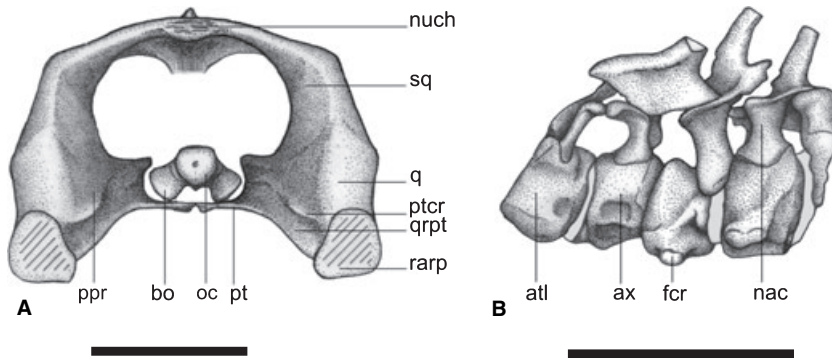
TEXT-FIG. 1. *Gallardosaurus iturraldei* gen. nov. et sp. nov. MNHNCu P3005, holotype. A, dorsal view. B, lateral view. C, palatal view. Key to abbreviations used in the Text-figure (Taylor and Cruickshank 1993; O'Keefe 2001): a, angular; aiv, anterior interterygoid vacuity; atl, atlas; ax, axis; bo, basioccipital; bs, basisphenoid; ce, coronoid eminence; d, dentary; ec, ectopterygoid; en, external naris; fcr, facets for cervical rib; fr, frontal; j, jugal; lfpt, lateral flange of pterygoid-ectopterygoid; md, mandible; mx, maxilla; nac, neural arch of cervical vertebra; na, nasal; nuch, scar of; nuchal ligament; oc, occipital condyle; orb, orbit; p, parietal; pal, palatine; pfo, parietal; foramen; pl-ptf, palatine-ptyergoid foramen; piv, posterior interptyergoid vacuities; pmx, premaxilla; po, postorbital; pof, postfrontal; ppr, paraoccipital process; prf, prefrontal; ps, parasphenoid; pt, pterygoid; pter, posterior transverse crest; q, quadrate; qrpt, quadrate ramus of pterygoid; rarp, retroarticular process; sa, surangular; sq, squamosal; stf, supratemporal fenestra; v, vomer. Scalebar represents 10 cm.

lateral view, the maxilla, with longitudinal striae below the naris, extends behind the posterior limit of the orbit. The prefrontals are broad, with a marked expansion covering the antero-dorsal area of the orbits. The prefrontal joins the postfrontal, excluding the frontal from the medial margin of the orbit (Text-figs 1A–B, 3A, C–D). The frontals are separated by premaxillae and parietals. Each frontal is narrow, with the medial margin almost straight, and the external margin sigmoid. The frontal contacts with the prefrontal, nasal, premaxilla, parietal and postfrontal (Text-figs 1A, 3A).

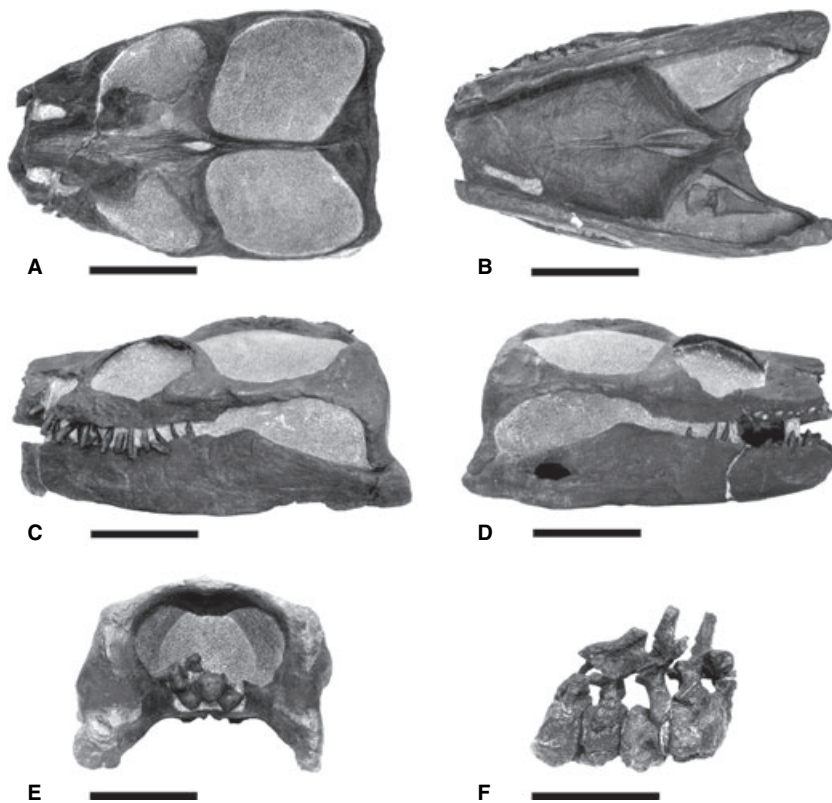
In *G. iturraldei* sp. nov. (MNHNCu P3005) the parietal is expanded anteriorly and surrounds the oval pineal foramen in a marked depression. The pineal foramen is 2/3rd of its length ahead the anterior margin of the supratemporal fenestrae. Behind the pineal foramen, the parietal forms a very thin crest, separating the large supratemporal fenestrae. The crest continues posteriorly over the triangular expansion of the parietal. On the anterior vertex of the triangle, the parietal crest reaches its highest point. The squamosals form a thin arch closing the skull roof behind the parietal. On the midline a rugose area with transverse furrows and striae form the scar of nuchal ligament (Text-figs 1A, 2A). These marks are conspicuous in other pliosauroids such as *Rhomaleosaurus zetlandicus* (Taylor, 1992) and *Maresaurus coccai* Gasparini, 1997. Laterally the postfrontal contacts the prefrontal, excluding the frontal from the upper margin of the orbit, and forming the posterior margin of the orbit (Text-figs 1A–B, 3A, C). In lateral view, the postfrontal-postorbital bar is sub-vertical, high and compressed. The postorbital widens laterally and contacts the squamosal and jugal (Text-figs 1B, 3C–D). The jugal, which is horizontally oriented, contacts the prefrontals, forming part of the ventral orbital border, and caudally it joins the postorbital and squamosal.

The supratemporal fenestrae are limited by the postorbitals, postfrontals, parietals and squamosals. The squamosal-quadrate arch is well marked, in approximately 90 degrees, as the anterior sector of the squamosal is straight and horizontal, whereas the posterior part of the squamosal and the quadrate are almost vertical. In many other pliosaurids from the Oxford Clay, such as *Peloneustes philarchus*, the arch formed by the squamosal and quadrate forms a more open angle, because the posterior ramus is slightly (BMNH R. 4058) or strongly (BMNH R. 3803 and BMNH R. 8574) posteriorly oriented, depending on the degree of plastic deformation during diagenesis.

The palate is exposed from the posterior part of the vomer up to the articulation of the quadrates with the mandible. The mandibular rami cover the lateral views of the palate (Text-figs 1C, 3B). The maxillae are at both sides of the vomer. The vomer contacts the pterygoids medially through a U-shaped suture, which is quite far from the anterior margin of the anterior interterygoid vacuity. The palatine and pterygoid form a convex plate, with a longitudinal depression, in which the palatine-ptyergoid suture is housed. Caudally the suture ends in a semilunar foramen. This foramen (Text-figs 1C, 3B) is found on both sides of the palate, suggesting that it is not a diagenetic artefact. In *P. philarchus* (SMNS 10113) there is a slight semilunar mark only on the left side. In *Pliosaurus brachyspondylus* (BRSMG Cc 332) there is a small subcircular foramen (Taylor and Cruickshank, 1993, fig. 7). This opening might correspond to the lateral



TEXT-FIG. 2. *Gallardosaurus iturraldei* gen. nov. et sp. nov. MNHNCu P3005, holotype. A, occipital view. B, atlas-axis and the next two cervical vertebrae. Key to abbreviations used in the figure: see explanation for Text-figure 1. Scale bar represents 10 cm.



TEXT-FIG. 3. *Gallardosaurus iturraldei* gen. nov. et sp. nov. MNHNCu P3005, holotype. A, dorsal view. B, ventral view. C, D, lateral views. E, occipital view. F, atlas-axis and the next two cervical vertebrae. Scale bar represents 10 cm.

palatine fenestra, characteristic of *Rhomaleosaurus victor* and *Rhomaleosaurus megacephalus* (O'Keefe, 2001, figs 7, 8). In the holotype of *G. iturraldei* sp. nov. the anterior interpterygoid vacuity is present. It is slit-like, well behind the vomer-ptyergoid contact, and closed by the cultriform process of the parasphenoid, which is markedly convex (Text-figs 1C, 3B).

The posterior interpterygoid vacuities form a single oval vacuity, with the medial axis three times longer than the transverse. The basisphenoid is exposed medially, occupying 3/4 of the vacuity, and the parasphenoid completes the other anterior quarter. Both are fused and are markedly convex. On the anterior margin of the posterior interpterygoid vacuity, the pterygoids are very close but not completely fused, partially covering the cultriform process of the parasphenoid. Consequently, the parasphenoid is widely exposed at the palate, from the anterior section of the posterior interpterygoid vacuity up to the anterior

end of the anterior interteygid vacuity (Text-figs 1C, 3B). In palatal view, each pterygoid expands upwards and outwards, joining the ectopterygoid and forming a well-defined flange. Storrs (1997) and O'Keefe (2001) point out that the 'pterygoid flange' present in some pliosaurs is not a true pterygoid flange, because it is formed almost entirely by the ectopterygoid. In contrast, Drückenmiller (2002, fig. 10) states that the pterygoid flange is formed by the pterygoid and ectopterygoid. The quadrate ramus of the pterygoid is planar, with a sigmoid anterior external margin, and the posterior forming the arch, closing the palate. In palatal view, the occipital condyle is exposed and surrounded by a neck.

In *G. iturraldei* sp. nov. the occipital table is not deformed, maintaining the natural proportions (Text-figs 2A, 3E). This feature is important when evaluating characters. In most pliosauroids of the Oxford Clay housed in the collections of NHM,

GPIT and SMNS the occipital tables are strongly depressed, being rectangular in shape with the transverse axis quite long. BMNH R 4058, referred to *P. philarchus*, is one of the few specimens preserved without deformation, and the occipital table is higher, more quadrangular than in any of the other specimens referred to this taxon. The apex of the squamosal arch in the holotype (MNHNCu P3005) is elaborated into a posteriorly-directed bulb, as in most pliosaurs (O'Keefe 2001). In the medial sector, there is a rugosity with transverse furrows and striae that corresponds to the scar of the nuchal ligament (Text-fig. 2A). Ventral to this, on the supraoccipital, there is a deep depression, observed as well in *P. philarchus* (BMNH R. 4058). The posterior pillars of the occipital table are formed by the squamosal and quadrate, but no sutures marking the exact limits of these bones have been preserved. These pillars are vertical. Most of the exoccipitals-opisthotics are covered by sediment. The paraoccipital process is fused to the quadrate ramus of the pterygoid as in post-Liassic pliosauriomorphs (Taylor and Cruickshank 1993). A strong crest on the quadrate ramus of the pterygoid is parallel to the sutural margin with the paraoccipital process (Text-figs 2A, 3E). The pterygoids close the occipital table, very near to each other but not in contact (Text-fig. 2A). In the holotype, the occipital condyle is small, sub-spherical, with a neck and marked furrow. There is a central pit on the body of the condyle and projections of the basioccipital at both sides (basioccipital tubers) (Text-figs 2A, 3E). Because MNHNCu P3005 is not deformed, the occipital condyle is internally placed, and quite anterior to the posterior margin of the quadrates, being hidden in dorsal view. In MNHNCu 3005, the left quadrate has an inner condyle (mesial condyle) that is more developed and lower than the external (lateral condyle) as in all pliosaurs (Taylor and Cruickshank 1993).

The elements of the mandible are fused; hence, no sutures are evident (Text-figs 1B, 3C–D). Dorsal and externally, the area of the coronoid is high, and the surangular is short and descends abruptly toward the glenoid fossa. In MNHNCu P3005, the retroarticular processes are missing, and the jaw articulation is lower than the tooth row.

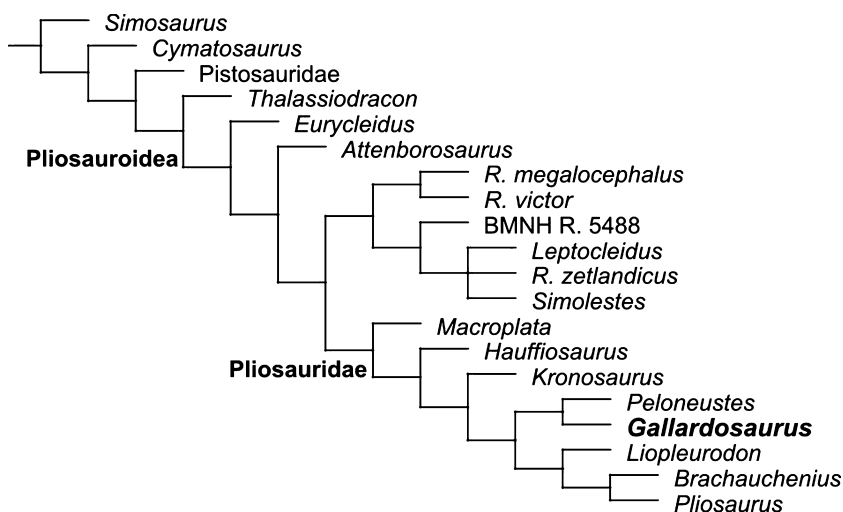
Most of the rostrum and the anterior mandible are missing; consequently it is impossible to know the number of alveoli. In occlusion, maxillary teeth cover partially or intercalate with lower teeth. The alveolar row of the maxilla reaches past the posterior margin of the orbit. The right mandible shows 14 alveoli with dental remains in different stages of preservation, but none of them complete, and they generally lack the enamel. Only one tooth bears enamel on its labial side, and it has smooth ridges. Another tooth, with the crown transversally cut off, shows that the section is trihedral (Tarlo 1960; Nøe *et al.* 2004). The left maxilla (Text-figs 1B, 3C) bears 13 teeth in different stages of preservation. The enamel is much damaged or lacking. The size of both teeth and alveoli increases anteriorly in the maxillary and dentary.

The holotype (MNHNCu P3005) preserves the atlas-axis and the next two cervicals (Text-figs 2B, 3F). All these elements, originally articulated and in natural position with respect to the condyle, were separated during preparation. The centra of the atlas-axis are not fused, suggesting that the holotype of *G. iturraldei* was not an old animal. The atlas, although larger than the

axis, has the typical proportions of the vertebral centra of pliosaurs: length (2.7 cm) less than height (4.2 cm), and wider (5 cm) than high (4.2 cm). In anterior view, the atlas has a neat central odontoid process and is markedly concave. It is ventrally surrounded by the subvertebral intercentrum and laterally by the arch of the atlas. The neural spine of the atlas fuses with that of the axis, forming a wide roof posteriorly, and is dorsally oriented. Both the atlas and axis have a smooth ventral crest. On the left side of the atlas body there is a protuberance similar to that of *P. philarchus* (Andrews, 1913, text-figs 16A, 3). A rib facet occurs on the axis. The third and fourth cervicals are joined by an intervertebral disc of cartilage. The articular surfaces are slightly concave and in the ventral side of the centrum, there is a central crest or keel with a pore at both sides. Short ribs are fused to the articular facets for ribs. A figure-eight shape of this area suggests that the facet had two articular surfaces. The neural arches of the cervicals are high and the neural spines are high and circular in section. A smooth ventral keel occurs on the cervical centra.

PHYLOGENETIC POSITION OF *GALLARDOSAURUS ITURRALDEI*

The work of O'Keefe (2001, 2002, 2004) yielded improvement in the understanding of the phylogenetic relationships of Plesiosauria. His hypotheses were analysed mainly in the context of plesiosauroids (Kear 2003; Grossmann 2007). In order to analyse the phylogenetic affinities of *G. iturraldei*, I chose the analysis of O'Keefe, (2001) because it is the most comprehensive. The cladistic analysis was conducted using a dataset of 107 skull and 23 postcranial characters. This dataset was modified from that used by O'Keefe (2001, appendices 1, 2). Twenty taxa were used in this analysis, and the basal Sauropterygia *Simosaurus* Meyer, *Cymatosaurus* Fritsch, and *Pistosauridae* Zittel, were considered as the outgroup. The ingroup included: *Thalassiodracon* Storrs and Taylor, *Eurycleidus* Andrews, *Attenborosaurus* Bakker, *Rhomaleosauridae* (*sensu* O'Keefe, 2001, fig. 20), *Macroplata* Swinton, *Hauffiosaurus* O'Keefe, *Kronosaurus* Longman, *Peloneustes* Lydeker, *Liopleurodon* Sauvage, *Brachauchenius* Williston, *Pliosaurus* Owen, and *Gallardosaurus* nov. gen. Only characters 1–130 from 166 (O'Keefe 2001, appendices 1, 2) were considered, because no materials of *G. iturraldei* are available for the rest of the characters. For *Peloneustes* and *Pliosaurus*, some of the state characters coding were modified in respect to those of O'Keefe (2001) (Text-fig. 4; Appendix 1). The dataset was analysed with equally weighted parsimony using TNT (Tree Analysis Using New Technology, vers. 1.1; Goloboff *et al.* 2003). A heuristic tree-search strategy was conducted, consisting of 1000 replicates of random addition sequences using TBR branch swapping (holding 10 trees



TEXT-FIG. 4. Phylogenetic position of *Gallardosaurus iturraldei*.

per replicate). The collapsing rule utilized was the minimum length rule. This analysis resulted in one most parsimonious tree of 203 steps (CI, 0.576; RI, 0.645). The inclusion of *G. iturraldei* does not modify the monophyly of the Pliosauridae (O'Keefe 2001, 2004). *Gallardosaurus* shares the following synapomorphies with pliosaurids: strong narrowing of the rostrum ahead the orbits; occipital condyle short, vomers extending posteriorly and meeting pterygoids in a wide suture, pterygoids meeting anterior to posterior interpterygoid vacuity, and posterior articulation for succeeding neural spine in cervical neural spines absent. *Gallardosaurus* is the sister taxon of *Peloneustes* and the two share the following synapomorphies: occipital condyle hemispherical with groove (43), and jaw articulation lower than tooth row (98). Likewise, the autapomorphies of *Gallardosaurus* are: triedral teeth in cross-section (planar face) (104) atlas and axis intercentra exclude atlas centrum ventrally (110) (see O'Keefe 2001, appendix 1).

When *Gallardosaurus* is compared with *Peloneustes* there are differences that justify its assignment to a new taxon. In *Gallardosaurus* the premaxilla participates in the margin of the naris, a primitive condition that is lost in *Peloneustes* (O'Keefe, 2001); the nasals are more expanded than in *Peloneustes* (O'Keefe, 2001, and personal observations in specimens BMNH R. 8572, R. 4058), extending behind the anterior level of the orbits (Text-fig. 1A). The pineal foramen is 2/3 in front of the anterior margin of the supratemporal fenestrae, while in *Peloneustes* it is backwards, as the anterior margin of the pineal foramen coincides with the anterior margin of the supratemporal fenestrae. In *Gallardosaurus* the anterior interpterygoid vacuity is present; in *Peloneustes* it is absent. In *Gallardosaurus*, the basisphenoid and parasphenoid, inside the posterior interpterygoid vacuity, are fused, forming a markedly convex bar. In *Peloneustes* the basisphenoid is rectangular and the parasphenoid is triangular, and more

exposed in the vacuity (O'Keefe 2001, figs 11, 22). In *Gallardosaurus* the anterior section of the squamosal is horizontal and low, while in *Peloneustes* (BMNH R 4058; R 8574) it is higher. The neural spine of the atlas and especially the axis are fused, forming a wide roof posteriorly and upwardly oriented, a character that is absent in *Peloneustes*.

THE NEW PLIOSAURID IN THE CARIBBEAN SEAWAY

The Caribbean Seaway, opened as a corridor only since the Oxfordian, allowed the exchange of pelagic marine biota between the Western Tethys and the Eastern Pacific realms (Iturralde-Vinent 2004). Ophthalmosaurian ichthyosaurs (Fernández and Iturralde-Vinent 2000), metriorhynchid crocodylians (*Geosaurus* sp.) (Gasparini and Iturralde-Vinent 2001), marine pleurodiran turtles (*Caribemys oxfordiensis* De La Fuente and Iturralde-Vinent, 2001), cryptoclidid plesiosauroids (*Vinialesaurus caroli* De La Torre *et al.*, 1949) (Gasparini *et al.* 2002), and the new pliosaurid *Gallardosaurus iturraldei* were found in the Jagua Vieja Member of the Jagua Formation in western Cuba. Together with these marine reptiles, pterosaurs (*Nesodactylus hesprius* Colbert, 1969 and *Cacibupteryx caribensis* Gasparini *et al.*, 2004) and a probable camarasaurian dinosaur (Gasparini and Iturralde-Vinent 2006) have been found.

The base of the Jagua Vieja Member was deposited in very shallow water depths, at perhaps no more than 10–12 metres, under aerobic conditions as indicate the oyster lumachelles with oncolites and algal crusts (Wierzbowski 1976). Parts of the section with abundant calcareous concretions yielded microfossils characteristics of low energy, shallow water, near shore and protected areas (Gasparini and Iturralde-Vinent 2006). The proximity of the coast

(Florida-Yucatan ridge) (Iturralde-Vinent 2004) is also suggested by the record of dinosaur remains, pterosaurs, plant debris and large trunk and branch fragments (Gasparini and Iturralde-Vinent 2006).

Coincidentally, the pleurodiran *C. oxfordiensis* has no morphological characters in the carapace or limbs suggesting adaptations for life in the offshore sea (De La Fuente and Iturralde-Vinent 2001). Another fact to take into account is the predominance of long-necked plesiosaurs. It is generally accepted that these plesiosauroids inhabited shallow environments near the coast, feeding on very soft or very small bony prey (Massare 1997), and/or probably bottom invertebrates (Mchenry *et al.* 2005; Buchy 2007). The proximity to the coast was not a limiting factor for other reptiles that might have preferred more open seas. Such is the case of the metriorhynchids, ophthalmosaurians and the new pliosaurid. The diversity of the marine herpetofauna and the predominance of fish, suggest that the Caribbean Seaway was not merely passage for *G. iturraldei*. In this context, *G. iturraldei* could have crossed the Caribbean seaway in seasonal migrations, while acting as an active predator taking advantage mainly of the large amount of nectonic fish (Arratia and Schultze 1985).

CONCLUSIONS

A new pliosaurid, *G. iturraldei* gen. nov. et sp. nov., is described from the Jagua Formation, middle–late Oxfordian, Viñales area, western Cuba. This new taxon is characterized by: wide participation of the premaxilla in the external naris; frontal not participating in the orbital margin; postorbital in contact with the jugal and squamosal; presence of anterior pterygoid vacuity; cultriform process of parasphenoid convex and exposed in palatal view; pterygoid flanges high; jaw articulation lower than the tooth row and trihedral teeth in cross-section with smooth ridges at least in the labial face.

Phylogenetic analysis suggests that *Gallardosaurus* does not modify the monophyly of the Pliosauridae (O’Keefe 2001, 2004) and the new taxon forms a clade with *Peloneustes*, a pliosaurid genus from the Oxford Clay. The Caribbean Seaway was, at least since the Oxfordian, a corridor that permitted the interchange for marine biota between the Western Tethys and Eastern Pacific realms. Among vertebrates, bony fish and long-necked plesiosaurs prevailed. However, marine pleurodiran turtles, metriorhynchid crocodylians, ophthalmosaurian ichthyosaurs, and pliosaurids (*G. iturraldei* sp. nov.) were also found, as well as at least two species of pterosauroids, and one camarasaurian dinosaur. *Gallardosaurus iturraldei* would have played the role of an active predator taking advantage of nectonic fish recorded in the area.

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APPENDIX 1

Data matrix for the cladistic analysis following O’Keefe (2001, appendix 1, 2, see Supporting Online material: <http://www.science.marshall.edu/okeefe/links.html>).

Simosaurus, *Cymatosaurus*, *Pistosauridae*, *Thalassiodracon*, *Eurycleidus*, *Attenborosaurus* and the *Rhomaleosauridae* comprise the outgroup. The ingroup included: *Thalassiodracon* Storrs and Taylor, *Eurycleidus* Andrews, *Attenborosaurus* Bakker, *Rhomaleosauridae* (*sensu* O’Keefe, 2001, fig. 20), *Macroplata* Swinton, *Hauffiosaurus* O’Keefe, *Kronosaurus* Longman, *Peloneustes* Lydeker, *Liopteroodon* Sauvage, *Brachauchenius* Williston, *Pliosaurus* Owen, and *Gallardosaurus* nov. gen. Inapplicable characters are coded as ‘x’; unknown characters are coded as ‘?’.

In the Appendix 1 the new taxon *Gallardosaurus* gen. nov., and *Peloneustes* and *Pliosaurus* are included because few of the state characters coding were modified from O’Keefe 2001, appendix 2). Modifications are in bold. In *Peloneustes* the state coding of character 43 (0) has been modified because some specimens of *Peloneustes philarchus* (BMNH R 4058) have the occipital condyle hemispherical with groove; character 46 is (1) because specimens like BMNH R 4058 have the paraoccipital process robust; character 98 (1) the jaw articulation in relation to tooth row is lower (BMNH R 4058; 8574). In *Pliosaurus* the state coding of the character 9 (1) has been modified because there is a constriction at premaxilla/maxilla suture (BRSMG Cc 332 see Taylor and Cruickshank 1993); character 60 (1) modified because in BRSMG Cc 332 there is an anterior slit-like interpterygoid vacuity (see Taylor and Cruickshank 1993); character 78 (1) because hay especimenes con lateral fenestration bordered by palatines and pterigoids (BRSMG Cc 332; BMNH R 2860); character 98 (1) jaw articulation lower than tooth row (BMNH R 3891).

Character-taxa matrix

Peloneustes

1	2	3	4	5	6	7	8	9	0
1	2	1	1	1	1	1	2	1	0
1	1	0	X	X	0	0	0	1	1

1	2	3	4	5	6	7	8	9	0
0	0	0	0	2	0	1	0	1	0
0	1	0	0	1	0	1	0	0	0
0	0	0	1	0	1	0	0	1	1
0	0	1	1	1	1	0	2	0	0
1	1	1	0	1	0	0	0	2	0
2	2	X	0	0	2	1	1	0	0
1	1	1	1	0	0	0	0	1	1
0	1	0	1	0	0	0	1	1	1
0	0	1	0	0	1	1	0	0	0
2	2	0	1	0	0	0	1	0	2
0	0	1	0	0	1	1	1	2	0

Pliosaurus

1	2	3	4	5	6	7	8	9	0
1	2	?	?	?	1	?	2	1	0
1	1	0	X	X	0	0	0	?	1
0	0	0	0	2	?	1	1	1	0
0	1	0	1	1	1	0	?	?	0
0	0	1	1	?	1	?	?	1	?
?	0	0	1	1	?	?	2	0	1
1	1	0	0	?	?	0	?	3	?
?	?	X	?	?	0	?	1	1	?
1	?	1	1	?	0	0	0	2	1
0	1	0	1	1	0	0	1	1	1
0	0	1	1	1	1	1	?	?	?
?	2	?	0	0	0	0	1	1	2
?	0	?	0	0	1	1	1	?	0

Gallardosaurus

1	2	3	4	5	6	7	8	9	0
1	?	?	?	?	?	?	2	?	0
1	0	?	X	X	0	0	0	1	1
0	0	0	0	2	0	1	0	1	0
0	1	0	1	1	0	?	0	0	0
0	0	0	1	0	1	0	0	1	1
?	?	?	1	1	?	0	?	?	1
1	1	?	0	1	0	0	0	2	0
2	2	X	0	?	0	?	1	?	0
?	1	1	1	0	?	?	?	?	?
0	?	0	?	?	?	?	1	?	?
?	?	1	1	?	?	?	0	?	2
?	2	?	1	0	0	0	1	?	2
?	0	?	0	0	?	?	1	?	0