

## The Cuban Oxfordian herpetofauna in the Caribbean Seaway

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With 5 figures and 2 tables

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**Abstract:** The Oxfordian reptiles recorded in Cuba provide evidence of how the Caribbean Seaway acted as habitat and/or corridor for numerous pelagic predator groups, and even for those, such as pterosaurs, that flew over the area. The composition of the herpetofauna is provided as an Appendix, while remarks on the geologic setting, stratigraphic position, age, taphonomy, paleobiogeographic setting and biogeographic relationships of the Cuban Oxfordian reptiles are given. The fossils found in the lower to middle Oxfordian Jagua Vieja Member of the Jagua Formation (Western Cuba) include a wide range of marine invertebrates as well as fish, marine reptiles, dinosaurs and terrestrial plants. The abundance of plant remains (including tree trunks), some pterosaurs, a dinosaur, and even a primitive pleurodiran turtle, suggest a paleoenvironment not far from the coast. More “off shore” predators as plesiosaurs, pliosaurs, metriorhynchids and ichthyosaurs, probably crossed the seaway in seasonal migrations.

**Zusammenfassung:** Die Reptilfunde aus dem Oxfordium von Kuba geben Hinweise, wie der Hispanische Korridor als Lebensraum oder Wanderweg für zahlreiche pelagische Räuber diente, sogar für solche, die das Gebiet per Luft erreichten, wie Flugsaurier. Die oxfordische Herpetofauna wird zusammen mit Daten zu Fundorten, Fundschichten, Alter, Taphonomie und paläobiogeographischen Beziehungen als Anhang zusammengestellt. Die Fossilfunde aus dem unter- bis mitteloxfordischen Jagua Vieja-Member der Jagua-Formation (West-Kuba) beinhalten zahlreiche marine Invertebraten sowie Fische, Meeresreptilien, Dinosaurier und Landpflanzen. Die Häufigkeit von Landpflanzen, insbesondere Baumstämmen sowie die Nachweise einiger Flugsaurier, eines Dinosauriers und sogar einer primitiven pleurodiren

Schildkröte deuten auf ein küstennahes Habitat. Die pelagisch lebenden Räuber wie Plesiosaurier, Pliosaurier, Meereskrokodile und Ichthyosaurier passierten den Korridor vermutlich saisonal.

**Keywords:** Reptiles, Cuba, Oxfordian, Caribbean Seaway.

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## 1. Introduction

Late in the 19<sup>th</sup> century, the occurrence of Jurassic rocks dated using ammonites in Cuba was established by the Spanish mining engineer MANUEL FERNÁNDEZ DE CASTRO (1876), and later obtained wide recognition after the report by the famous Cuban naturalist CARLOS DE LA TORRE Y HUERTA (1912). Both discovered abundant Jurassic ammonites from a locality named Abra or Puerta del Ancón in the Viñales Valley of western Cuba (ALVAREZ CONDE 1957). During later explorations of the Sierra de los Órganos in the first half of the 20<sup>th</sup> century, DE LA TORRE Y HUERTA not only collected ammonites, but also numerous vertebrates, which were deposited in the Department of Geology and Paleontology of the University of Havana. In these early decades DE LA TORRE Y HUERTA and BARNUM BROWN collected Jurassic fossils for the American Museum of Natural History, and BROWN & O'CONNELL (1922) reported, for the first time, the occurrence of fossils marine reptiles in Cuba. Some of these specimens were described (e.g., DE LA TORRE Y MADRAZO & CUERVO 1939; DE LA TORRE Y MADRAZO & ROJAS 1949; DE LA TORRE Y CALLEJAS 1949), but many remained unidentified.

Field collecting of reptile bones continued during the entire century by different persons, generally guided by JUAN GALLARDO (an expert fossil hunter), and the specimens were housed in the Museo Felipe Poey of the University of Havana, in some private collections, and at the National Museum of Natural History (Washington, D.C.), the American Museum of Natural History (New York) and the Museum of Paleontology at Berkeley (California). None of this material was studied, with the exception of a pterosaur in the collection of the American Museum of Natural History (COLBERT 1969). A more recent report of a fossil Jurassic reptile (GUTIÉRREZ 1981) unfortunately can not be evaluated because of the lack of illustrations, and because the material is now lost. Furthermore, scarce and undescribed fossils of reptiles have been found in the Tithonian El Americano Member of the Guasasa Formation, and the Kimmeridgian-Tithonian Artemisa Formation (PSZCZÓLKOWSKI 1978; ITURRALDE-VINENT & NORELL 1996).

During the 1980's and 1990's, one of the authors (M.I.-V.) visited the Cuban fossil reptile collections in the museums of the United States (US National Museum of Natural History, American Museum of Natural History, and the Museum of Paleontology of the University of California in Berkeley) as well as all the paleontological collections in Cuba. Through collecting, exchange and donation, the collection of Jurassic reptiles of the Museo Nacional de Historia Natural de Cuba (MNHNCu) was created. Simultaneously, the fossilbearing localities reported both in the literature and on the museum specimen labels were revisited in order to establish their precise location. For this job JUAN GALLARDO and his senior son were instrumental, because they knew all the fossil-bearing sites. A catalogue of the Jurassic reptile-bearing localities with a preliminary discussion of the taxonomic position of the previously published taxa was published (ITURRALDE-VINENT & NORELL 1996).

A new step in the investigations of the fossil Jurassic reptiles started in 1999, with field expeditions supported by the National Geographic Society, and the beginning of a very successful collaboration between the Museo de La Plata (Argentina) and the Museo Nacional de Historia Natural (Cuba). As part of this cooperation, every important specimen was prepared in Argentina. Previous miss-identifications could be emended, and new taxa were described (FERNÁNDEZ & ITURRALDE-VINENT 2000; DE LA FUENTE & ITURRALDE-VINENT 2001; GASPARINI & ITURRALDE-VINENT 2001; GASPARINI et al. 2002; GASPARINI et al. 2004). At the same time, the geology and taphonomy of the fossil-bearing rocks were investigated, and Jurassic paleogeographic maps produced (ITURRALDE-VINENT 2003, 2004).

The fossil record of Oxfordian marine reptiles is poor worldwide (PERSSON 1963; BARDET 1995) and generally, discoveries are mainly reported from the Northern Hemisphere. These are for example the reptiles from the Oxford Clay (Callovian-Early Oxfordian) of England and equivalent deposits of France (MARTILL & HUDSON 1991; BARDET 1993, 1995; MCGOWAN & MOTANI 2003), those found in Russia and neighboring countries (STORRS et al. 2001), and the Sundance Formation and equivalents (Late Oxfordian) herpetofauna in Wyoming, Montana, and Alaska (BAKKER 1993b; MASSARE & SPERBER 1999; O'KEEFE & WAHL 2003a, b). In western Cuba, the middle-to-late Oxfordian marine herpetofauna is particularly important, not only for its taxonomic diversity, but also because the time span of the faunule, poorly represented in other latitudes (O'KEEFE 2001a; O'KEEFE & WAHL 2003a, 2003b). According to the record, the marine herpetofauna is dominated by plesiosauroids (18/34), but other groups including ichthyosaurians (5/34), metriorhynchids (3/34), pliosauroids (2/34), and turtles (1/32) are present. Likewise, pterosaurs (3/34) and dinosaurs (1/34) have been found.

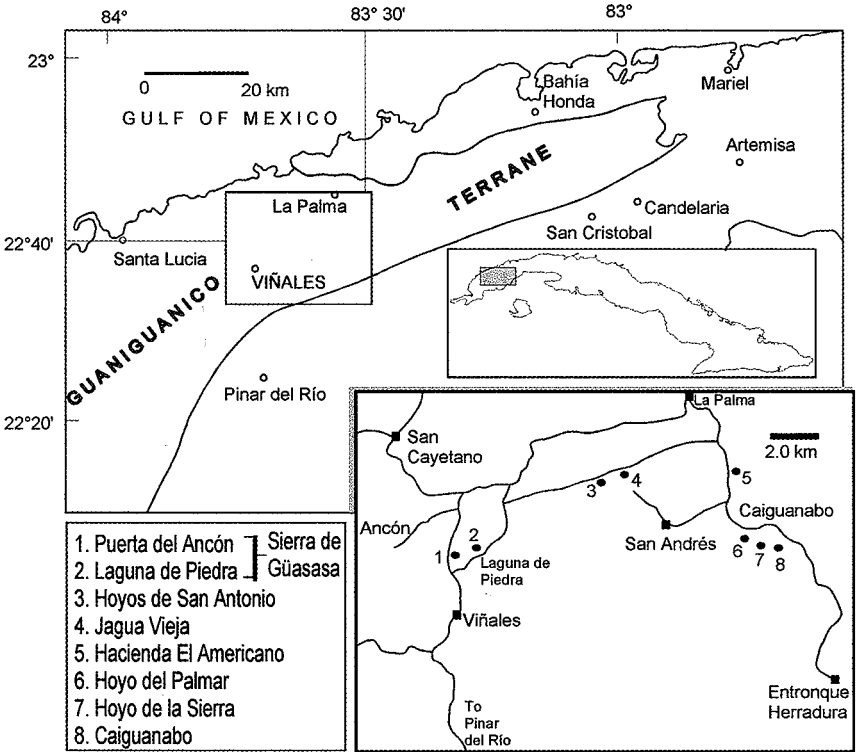


Fig. 1. Map of Jurassic fossil-bearing localities in western Cuba mentioned in this paper (Updated from ITURRALDE-VINENT & NORELL 1996).

In this paper we summarize our investigations of the Cuban Late Jurassic herpetofauna, and propose a paleoenvironmental scenario, analyzing the role of the Caribbean Seaway in the distribution of pelagic predators. In order to abridge the systematic information, an annotated list of the Oxfordian Cuban herpetofauna is included as Appendix. Cuban paleontological sites reported in this paper are located in Fig. 1 and Table 1.

## Acronyms:

USNM and NMHN. U.S. National Museum of Natural History, Washington, DC.

AMNH. American Museum of Natural History, New York.

MNHNCu. Museo Nacional de Historia Natural, Cuba.

IGP. Instituto de Geología y Paleontología, La Habana, Cuba.

## 2. Geological setting

The Jurassic fossil-bearing rocks in western Cuba outcrop in the Sierra de los Órganos and Sierra del Rosario of the Guaniguanico mountain range, as part of a ?Lower Jurassic to Middle Eocene sedimentary sequence (Fig. 1, Table 1). This sequence charts the evolution of Pangea (?Lower-Middle Jurassic to

**Table 1.** Additional details of the localities mentioned in this paper. Generally these paleontological sites represent around one square kilometer. The collecting terrains are slopes, creeks and farmlands near the karstified limestones hills (locally named Mogotes). Coordinates are referred to the Cuba: 1:50 000 scale topographic map.

Locality	Topographic sheet	Coord. X	Coord. Y
Cerca de Viñales (a)	Consolación del Sur and La Palma	—	—
Puerta de Ancón	Consolación del Sur	221 100	316 000
Laguna de Piedra	Consolación del Sur	222 900	316 300
Hoyos de San Antonio	La Palma	226 300	320 800
Jagua Vieja	La Palma	228 800	320 900
Hacienda El Americano (b)	La Palma	240 300	321 400
Hoyo del Palmar	La Palma	227 800	321 000
Caiguanabo	Herradura	244 200	316 900
Hoyo de la Sierra	Herradura	243 550	316 800

## Notes:

(a) This is an ambiguous locality reported in specimens collected early in the 20<sup>th</sup> century. It can be any place between Puerta del Ancón, Laguna de Piedra and Hoyos de San Antonio.

(b) The paleontologic sites in this table belong to the Jagua Vieja Member of the Jagua Formation, with the exception of the Hacienda El Americano, which belong to the Tithonian-Berriasian El Americano Member of the Guasasa Formation (PSZCZOLKOWSKI 1978; ITURRALDE-VINENT & NORELL 1996).

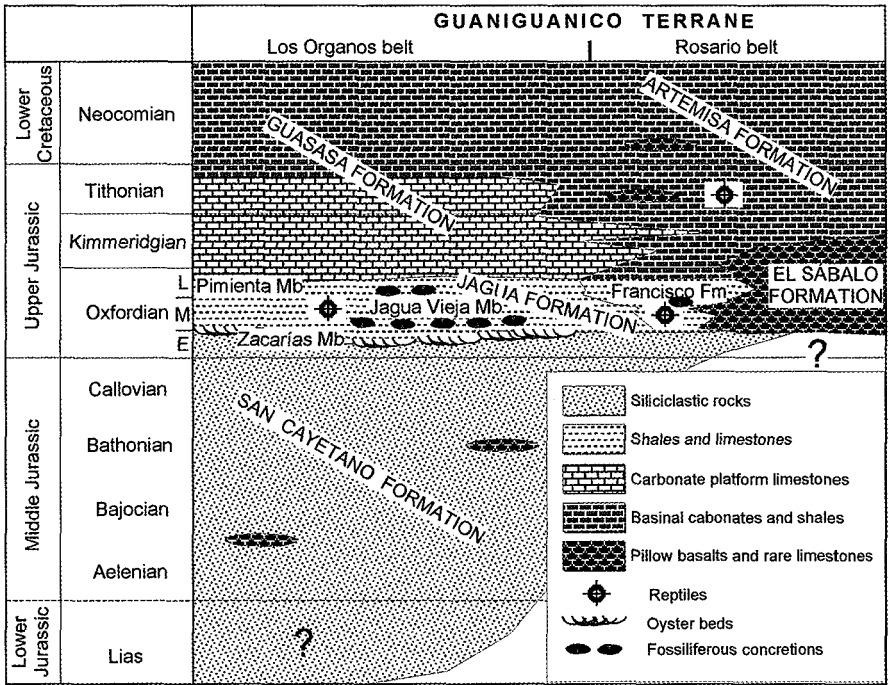
early Oxfordian siliciclastics with rare limestone and mafic igneous intercalations) into the Laurasian passive margin-early Caribbean sea (mid Oxfordian through Late Cretaceous shales, sandstones, basalts, limestones, and cherts), and the later development of the foreland basin (Paleocene through Middle Eocene limestones, shales, breccias and olistostromes with olistoplates). These rock suites are amalgamated within the Guaniguanico allochthonous terrane (ITURRALDE-VINENT 1994), which originated as part of the Maya (Yucatán) block borderland (ITURRALDE-VINENT 1994); probably close to the latitude of Belize and to the north (HUDSON et al. 1999). The whole unit is strongly deformed locally, with some degree of metamorphism, and piled up as a stack of allochthonous tectonic sheets verging north and northwest. The degree of deformation varies, but important for the preservation of the fossils is the fact that the siliciclastic members of the sections, as the fossil-bearing Jagua Formation, are usually much more folded and faulted than the limestone members (PIOTROWSKA 1978; PSZCZÓLKOWSKI 1978). This facilitated weathering and may have broken or dismembered some bones preserved in the shales.

The Jurassic stratigraphy of Guaniguanico has been described in detail by PSZCZÓLKOWSKI (1978, 1999), as has the Oxfordian strata (WIERZBOWSKI 1976). Herein we focus on the description of the lithology and taphonomy of the fossil-bearing Jagua Vieja Member of the Jagua Formation.

## 2.1. Jagua Vieja Member

A unique fossil-producing unit in western Cuba is represented by the middle to early Late Oxfordian Jagua Vieja Member of the Jagua Formation (Fig. 2). This unit is up to 60 meters thick black to grey coloured bituminous shales and calcareous shales, laminated or thin bedded, with intercalations of thin bedded limestone beds. Within the shale matrix occur fossil-bearing calcareous concretions at almost every level. In many localities, at the base of the Jagua Vieja Member occurs an oyster-rich horizon, just a few centimeters thick, which overlies the deltaic-marine shales and sandstones of the San Cayetano Formation. At other localities, below the Jagua Vieja Member are found the Pan de Azúcar and Zacarias members of the Jagua Formation, represented by well-bedded shales, some fine sandstones, as well as shelly and bioclastic limestones with oyster-rich coquinas (WIERZBOWSKI 1976; PSZCZÓLKOWSKI 1978). This oyster-rich level represents the facies transition between the marine-deltaic San Cayetano and the shallow marine Jagua Vieja Member, generally middle Oxfordian in age.

Concretions are lenticular and very variable in size, from a few centimeters up to nearly one meter across, and are composed of micritic limestone or dolostone with or without laminations. Most of them are fossiliferous.



**Fig. 2.** Jurassic-lowermost Cretaceous stratigraphy of Guaniguanico Terrane, modified from PSZCÓŁKOWSKI (1978, 1999) and WIERZBOWSKI (1976), including authors' field observations.

Concretions are found *in situ*, within the dark shales, as well as loose in the soil, at the base of the slopes where the Jagua Vieja Member outcrops, and in trails around the tobacco plantations where they have been piled up by the farmers. Fossils found in these concretions include vertebrates, invertebrates, and plant remains. The internal laminations of the concretions, when present, are planar and intersect the fossil elements, in opposition to sedimentary lamination that usually retains the shape of the fossil element. Outcrops are sparse, and the shales are usually weathered to form a reddish soil.

## 2.2. Depositional environment

The base of the Jagua Vieja Member was deposited in very shallow water depths, at perhaps no more than 10-12 meters, under aerobic conditions, as suggested by the oyster lumachelles with oncolites and algal crusts (WIERZBOWSKI 1976). According to WIERZBOWSKI (1976), those parts of the sequence dominated by bituminous shales, represent generally anoxic conditions, where benthic fauna was rather monotonous and impoverished, without benthic foraminiferans or macroburrowers, being represented mostly by pelecypods (primarily oysters), both overgrowing shells of dead ammonites (benthic island). However, those parts of the sections with abundant calcareous concretions, yielded microfossils characteristics of low energy, shallow water, near shore, generally protected areas (Table 2). The presence of benthic foraminifers, ostracods, pelecypods, gastropods and brachiopods in these levels, also suggests that the sea bottom was aerobic to slightly disaerobic. According to WIERZBOWSKI (1976) the marked predominance of perisphinctid ammonites in the Jagua Vieja Member seems to indicate sedimentation at shallow depths, but perhaps up to one or two hundred meters. The common occurrence of pycnodontiform fishes (*Gyrodus* sp. and others) also suggests shallow marine environment in the upper slope of the shelf (KRIWET 2001 a). Many pycnodont fishes were bottom dwellers that fed mainly on invertebrates (KRIWET 2001 b).

Indicators of the paleoenvironment are the marine reptiles which include both coastal and open marine dwellers. The presence of at least two pterosaur genera (*Nesodactylus* and *Cacibupteryx*), the coastal pleurodiran turtle *Caribemys*, and dinosaur remains also suggest that the coastline was close to the depositional centre. The analysis of the wackestones-packstone where the turtle *Caribemys* was included yielded detrital vegetal remains and Oxfordian-Kimmeridgian fossils such as *Favreina salevensis* (PAREJAS), *Favreina* sp., *Globochaete alpina* LOMBARDI, and ostracods with smooth hyaline shells. These organisms suggest that the sedimentary environment was a shallow water protected platform (DE LA FUENTE & ITURRALDE-VINENT 2001). The abundance of fish, suggests enough food for longnecked plesiosaurs, metriorhynchid crocodilians (*Geosaurus* sp.) and ichthyosaurs. A medium-sized pliosaur (*Peloneustes* sp.) played the top predator role.

Characteristic of the basin was the absence of coarse terrigenous input (no sandstone intercalations), suggesting that the surrounding lands were already invaded by the sea, and the surface topography was reduced to a low energy flat land.

Previous discussion suggests that the general Oxfordian scenario represented by the Jagua Vieja Member was one of a shallow marine continental margin (Laurasian) facing a deeper marine basin (Early ProtoCaribbean) and

**Table 2.** Oxfordian microfossils from the limestones of the calcareous concretions of the Jagua Vieja Member, suggesting aerobic to slightly anaerobic marine bottom waters. Identified by Silvia Blanco. Localities: 1 – Mogote Guacamaya, near Jagua Vieja (dolostone); 2 – Hoyo de la Sierra (wackestone-packstone); 3 – Mogote Jagua Vieja (wackestone); 4 – Sierra de Guasasa (wackestone-packstone). Localities see Fig. 1 and Table 1.

MICROFOSSILS	LOCALITIES			
	1	2	3	4
<i>Glomospira?</i> sp.			*	
<i>Colomisphaera</i> cf. <i>C. fibrata</i>			*	
<i>Favreina salevensis</i>				*
<i>Favreina</i> sp. indet.			*	*
<i>Globochaete alpina</i>	*			*
<i>Globochaete</i> sp.				
Small gastropods and pelecypods		*	*	
Ostracods with smooth hyaline shells			*	*
<i>Hedbergella</i> sp.		*		
Cadosinidae		*		
<i>Crustocadosina</i> aff. <i>C. semiradiata</i>		*		
<i>Committosphaera</i> sp.		*		
Calcisphaeres (or Radiolaria ?)		*		
Benthic foraminifera		*		

the coastal areas probably were mostly wetlands (ITURRALDE-VINENT 2003, 2004).

### 3. Taphonomic notes

The fossil assemblage of the Jagua Vieja Member is dominated by marine elements, but terrestrial plant remains are ubiquitous, and even very common as in Hoyo de la Sierra, where huge quantities of large elements occur. Some of the trunk fragments are isolated, without any portion of the concretions. This might suggest that they derived from the shales, as they show no signs of recent erosion. Under these conditions, the accumulation in the sediments of plant debris including large trunk and branch fragments (eventually bored by pelecypods) requires some mechanism to transport the fragments of terrestrial vegetation into the basin, as well as mud particles. Fine plant

debris may have been carried into the sea along tidal channels, but trunk and branch fragments probably were incorporated into the sediments during coastal erosion, characteristic of sea-level rise due to marine transgression.

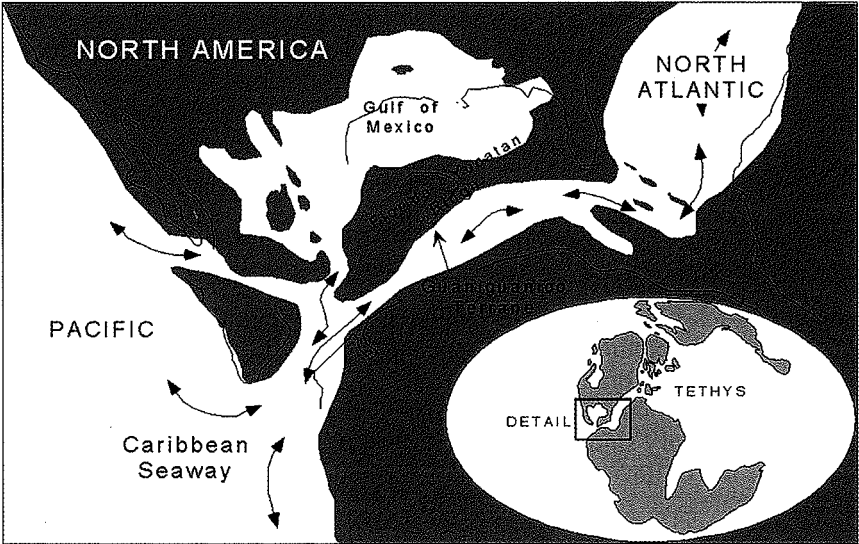
The vertebrate fossils are generally found in the concretions. They are very distinctive because the bones are black, while the color of the limestone matrix is usually grey. Skulls and postcranial bones are neither deformed nor crushed. Ammonite shells can be hollow or partially filled with calcareous sediment or sparry calcite, but they have lost the external nacre. Some reptiles are preserved with great details, as most fish (ARRATIA & SCHULTZE 1985) and the pterosaurs (COLBERT 1969; GASPARINI et al. 2004). Fish remains are often flattened, probably due to collapse of the skeleton, but three-dimensional specimens occur. They usually are not dismembered and retain the scales, suggesting that the bodies were not scavenged. Reptile bones present a shiny surface. They are generally recrystallized, and most skulls lack the sutures. All this suggests an early diagenetic origin for the fossiliferous concretions (PSZCZÓLKOWSKI 1978). The vertebrate fossils occur as complete or nearly complete carcasses, and as isolated fragmentary bones. Examples of articulated carcasses are mostly fish. The carcass of a small pterosaur is partially dismembered (COLBERT 1969). Only one carcass of a large marine reptile has been observed. But this one was not in a concretion but within a limestone bed of the El Americano Member (Guasasa Formation), now lost due to quarrying (G. FURRAZOLA, personal communication 1986). In many examples, fish carcasses occupy the equatorial plane of the concretions, partially protruding beyond the periphery. If the body is large and elongated, one or both ends of the fish can be missing. If the body is discoid, the entire periphery of the animal is usually missing. These examples suggest that the preservation was restricted to the concretions and parts of the animals may have been lost after fossilization. This last possibility is exemplified by the elongated elements of fossil plants which generally intersect the outer surface of the concretions, no matter the orientation of the element within the concretion. The same is true for some long reptile bones, single or several articulated vertebrae, or a reptile skull with some postcranial bones attached (GASPARINI & ITURRALDE-VINENT 2001; GASPARINI et al. 2002). Skulls can be fairly complete or fragmentary, due to the partial loss of the brain case or the tip of the rostrum. However, in many of the skulls the mandible is articulated although slightly twisted, e.g. *Vinialesaurus caroli*, *Peloneustes* sp., and *Geosaurus* sp. (Fig. 5 A-C, E). This suggests that the missing part of those bones may have been originally preserved in the embedding shales, but were later lost due to weathering or a secondary erosion of the concretion. Decomposition and partial alteration of the carcasses by microorganisms and bottom scavengers may have taken place, because some bones were exposed prior to burial. This is evidenced by

the ammonites attached to both long bones (DE LA TORRE Y CALLEJAS 1949) and fragmentary skulls (ITURRALDE-VINENT & NORELL 1996). However, no fossil bone has been recovered from the shales of the Jagua Vieja Member until now. The degree of weathering of the shales is very high, because the limestone mountains (Sierra de Los Órganos) receive as much as 2000 mm rainfall a year (Nuevo Atlas Nacional de Cuba 1988). The relative humidity is high because surface waters not only drain to the rivers, but also percolate and infiltrate the sediments in great quantities, due to the strong fracturing of the shales and karstification of the limestones. The high weathering level acts against the preservation of more complete carcasses. Probably large amounts of fossil material is currently dissolved within the shales. Some of the exposed concretions are eroded and further dissolved during transportation by surface drainage.

These observations suggest that the Cuban fossil material suffered a taphonomic history similar to that described by MARTILL (1987) for marine reptiles in the Callovian Oxford Clay Formation of central England. After death, the carcasses reached the sea floor intactly. The parts of the bodies in contact with the sediment, and those partially buried in the mud, suffered limited decay. Fish, for example, are fully preserved, even with skin impressions, probably due to rapid burial perhaps by sinking into a soupy substrate, very similar to the Brazil Santana concretions (MARTILL 1997). In large animals such as reptiles, burial rates were slow and probably did not cover the body so quickly. Parts of the flesh may have been exposed at the sea bottom to scavengers and accelerated decay. In these conditions the carcasses may collapse and the bones may be partially dispersed. Only some elements remain articulated and associated. In due time, loosely associated carcasses, as exemplified by the pterosaur *Nesodactylus hesperius* (Fig. 5B), may have been completely buried. There is no evidence of bones transport by bottom currents. After burial, diagenesis produced the calcareous concretions that enclosed parts of the carcasses, while other parts were probably preserved within the shales. Therefore, we hypothesize that some large marine reptiles in the Jagua Vieja Member may be more fully preserved, even as articulated carcasses, deep below the weathering horizon.

#### 4. General paleogeography during the Oxfordian

During the break up of Pangea in the Upper Jurassic the oceanic gap between North America and Gondwana widened (Fig. 3). This widening gap restricted the possibility of overland dispersal between the terrestrial biotas of these continental areas. Probably since the Bajocian, but surely since the Oxfordian, such faunal interchange ceased (ITURRALDE-VINENT & MACPHEE 1999).



**Fig. 3.** Simplified Oxfordian paleogeographic map of the Caribbean with a small insert of the world scenario. Shaded is land. Guanajuato-Terrane represents a section of the Caribbean margin of Yucatan (Maya Block) in this map. Arrows means marine interconnectivity among main oceans. Modified from ITURRALDE-VINENT (2004).

A marine basin with ocean crust was developing within the Gulf of Mexico region since the Callovian and within the Caribbean region since the Oxfordian. At this time the Gulf of Mexico was an independent marine extension of the Pacific Ocean until the latest Jurassic (Kimmeridgian-Tithonian), when finally communication with the Caribbean and the Atlantic was developed (SALVADOR 1991; MARTON & BUFFLER 1999). Before the Kimmeridgian, an emergent ridge was developed between present-day Florida and Yucatan, which separated the Gulf of Mexico from the Caribbean. This peninsular land ridge probably supported the terrestrial biota represented in the Jagua Formation. The Caribbean Seaway, a corridor only since the Oxfordian, was widely opened to allow exchange of pelagic-marine biota between Western Tethys and Eastern Pacific realms (Fig. 3; ITURRALDE-VINENT 2004).

By the end of the Jurassic this Yucatan Laurasian continental margin (Guaniguanico terrane) resulted in deeper marine environments (PSZCZÓLKOWSKI 1978, 1999; SÁNCHEZ-BARRERA 1990; SCHAFFHAUSER et al. 2004), and sparse remains of marine reptiles have been reported in these deeper facies (Tithonian-Berriasian El Americano Member of the Guasasa Formation).

## 5. Paleobiogeographic implications

A shallow marine connection, perhaps intermittent, between the Western Tethys and Eastern Pacific through central Pangea ("Hispanic Corridor" of SMITH 1983), since the beginning of the Jurassic, has been proposed by numerous authors who recognized, in both geographic realms, the same genera and even species of marine invertebrates (DAMBORENEA & MANCENIDO 1979; HALLAM 1983; RICCARDI 1991; BALLENT & WHATLEY 2000; DAMBORENEA 2000; ABERHAN 2001). Accordingly, and at least since the Bajocian, these realms share several genera of marine reptiles. Hence, the possibility of the Caribbean Seaway acting as a connection, perhaps intermittent, cannot be discarded (GASPARINI 1978, 1992; GASPARINI & FERNÁNDEZ 1996, 2005). However, it was not until the Oxfordian, when marine reptiles are first recorded in the Caribbean realm. The opening of this oceanic seaway represents an important paleoceanographic event, as only since that time the Mesozoic deep circumequatorial oceanic circulation that linked the Tethys, Central Atlantic and Eastern Pacific oceans have commenced (ITURRALDE-VINENT 2003, 2004). Since SMITH (1983) several authors have used the name "Hispanic Corridor" for the Caribbean Seaway. Here we challenge the liberal use of this term, as "Corridor" implies full communication and faunal interchange, which is only true for the Caribbean Seaway since the Oxfordian (ITURRALDE-VINENT 2004). Previously, the Caribbean seaway was not well developed, and probably was represented by a system of intercontinental channels which probably were only temporarily connected during high sea level stands (ITURRALDE-VINENT 2004). In these conditions, before the Oxfordian, and probably since the Pliensbachian, the Caribbean was more a filter than a corridor for the marine faunas (DAMBORENEA 2000).

Based on the phylogenetic analysis of the teleosteans of the Oxfordian of northern Chile, Viñales (Cuba), and the Tithonian of Solnhofen (Germany), ARRATIA (1996) concluded that the fossil record supports a connection between European and Chilean fish fauna through the Caribbean seaway. Accordingly, MYCZYNSKI et al. (1998) recognized the same ammonite zones in the Middle-Late Oxfordian deposits of Chile, southern USA, Cuba and

Iberia. The record of marine reptiles in the Late Jurassic strata of Cuba, Mexico, western Americas, and Europe also demonstrates that they shared several genera.

The main North American exposures yielding upper Oxfordian marine reptiles are those of the Redwater Member of the Sundance Formation and equivalents, in Wyoming and Montana. They have been known since the beginning of the 20th Century, mainly through the ichthyosaur *Ophthalmosaurus* (= *Baptanodon*) (GILMORE 1906; MCGOWAN & MOTANI 2003). More recently BAKKER (1993 a, b) and O'KEEFE & WAHL (2003 a, b) have revealed a more diverse assemblage with plesiosauroids, pliosauroids and metriorhynchids. The middle-upper Oxfordian rocks of western Cuba, contain a related marine herpetofauna, but with higher taxonomic diversity. Likewise, most of the Oxfordian reptiles of North America and Cuba have close phylogenetic relationships with those of the Callovian-late Jurassic of Europe (FERNÁNDEZ & ITURRALDE-VINENT 2000; GASPARINI & ITURRALDE-VINENT 2001; GASPARINI et al. 2002; O'KEEFE & WAHL 2003 a, b). GASPARINI et al. (2002) indicated that the plesiosauroid *Vinialesaurus* from Cuba has strong affinities with *Kimmerosaurus* BROWN from the Kimmeridgian and with *Tricleidus* ANDREWS from the Callovian, both of England (ANDREWS 1910; BROWN 1981). In turn, O'KEEFE & WAHL (2003b) demonstrated similarities between the North American plesiosauroid *Tatenectes laramensis* KNIGHT, 1900 new comb., from the Sundance Formation and *Kimmerosaurus* and *Tricleidus*.

The ichthyosaur *Ophthalmosaurus* is recorded in the Sundance Formation (MCGOWAN & MOTANI 2003), and also from the Callovian-Tithonian of Europe (BARDET et al. 1997), and the Tithonian of northern Patagonia (FERNÁNDEZ, in press). In Cuba, the most complete ichthyosaur fragment was referred by FERNÁNDEZ & ITURRALDE-VINENT (2000) to an indeterminate ophthalmosaurian, recognizing traits such as the very large orbital cavity and sclerotic ring, as well as the reduced extracondylar area of the basioccipital, as seen in *Ophthalmosauridae*.

Several remains of metriorhynchid crocodylians were found in western Cuba, at least one of them assigned to *Geosaurus* sp. (GASPARINI & ITURRALDE-VINENT 2001). This is the oldest record of the genus. BAKKER (1993b) reported the presence of metriorhynchids in the Sundance Formation, but they have not been studied or illustrated so far. It is noteworthy that *Geosaurus* FRAAS, has been recorded in the Tithonian of eastern Mexico (STINNESBECK et al. 1993; FREY et al. 2002), the Tithonian of northern Patagonia (GASPARINI & DELLAPÉ 1976) and the Tithonian of Germany (BARDET 1995; VIGNAUD 1995), a distribution that encompasses at least the European Tethys, the Caribbean Seaway and the Eastern Pacific.

In the middle-upper Oxfordian of Cuba were also found a skull and mandible of *Peloneustes* sp. (ZG, in study). *Peloneustes* is a medium sized pliosaur frequent in the Callovian from the Oxford Clay (ANDREWS 1913; O'KEEFE 2001 a). BAKKER (1993 b) reported the presence of *Pliosaurus* sp. in the Sundance Formation, but no studies or illustrations of the material were published. A gigantic pliosaurid "The Monster of Aramberri" was found in Kimmeridgian rocks of northeastern Mexico (BUCHY et al. 2003). The presence of gigantic pliosaurs in the late Jurassic is not infrequent both in Europe and northern Patagonia (GASPARINI, in press).

*Caribemys oxfordiensis* is the oldest marine Pleurodiran turtle known. DE LA FUENTE & ITURRALDE-VINENT (2001) recognized its relationships to other pleurodirans from the Upper Jurassic, such as *Platychelys* from the Kimmeridgian and Tithonian of Europe and *Notoemys* CATTOI & FREIBERG, 1961, from the Tithonian of northwestern Patagonia (FERNÁNDEZ & DE LA FUENTE 1994).

The Rhamphorhynchidae (UNWIN 2003) are represented in the fossil record from the Toarcian to the Tithonian, but the Oxfordian and Kimmeridgian forms are poorly known (WELLNHOFFER 1991). In Cuba there are two taxa *Nesodactylus hesperius* and *Cacibupteryx caribensis*, and a third one which has a crest on the sagittal plane of the rostrum (CODORNIÚ & GASPARINI in study). The holotype of *Cacibupteryx caribensis* is the best preserved middlelate Oxfordian pterosaur skull reported so far (GASPARINI et al. 2004) but at the moment the phylogenetic relationships are not resolved. The probable record of a camarasauromorph in western Cuba, probably derived from the Florida-Yucatan Ridge (Fig. 3), would be consistent with their distribution in the Kimmeridgian-Tithonian of North America (MCINTOSH 1990).

## 6. Conclusions

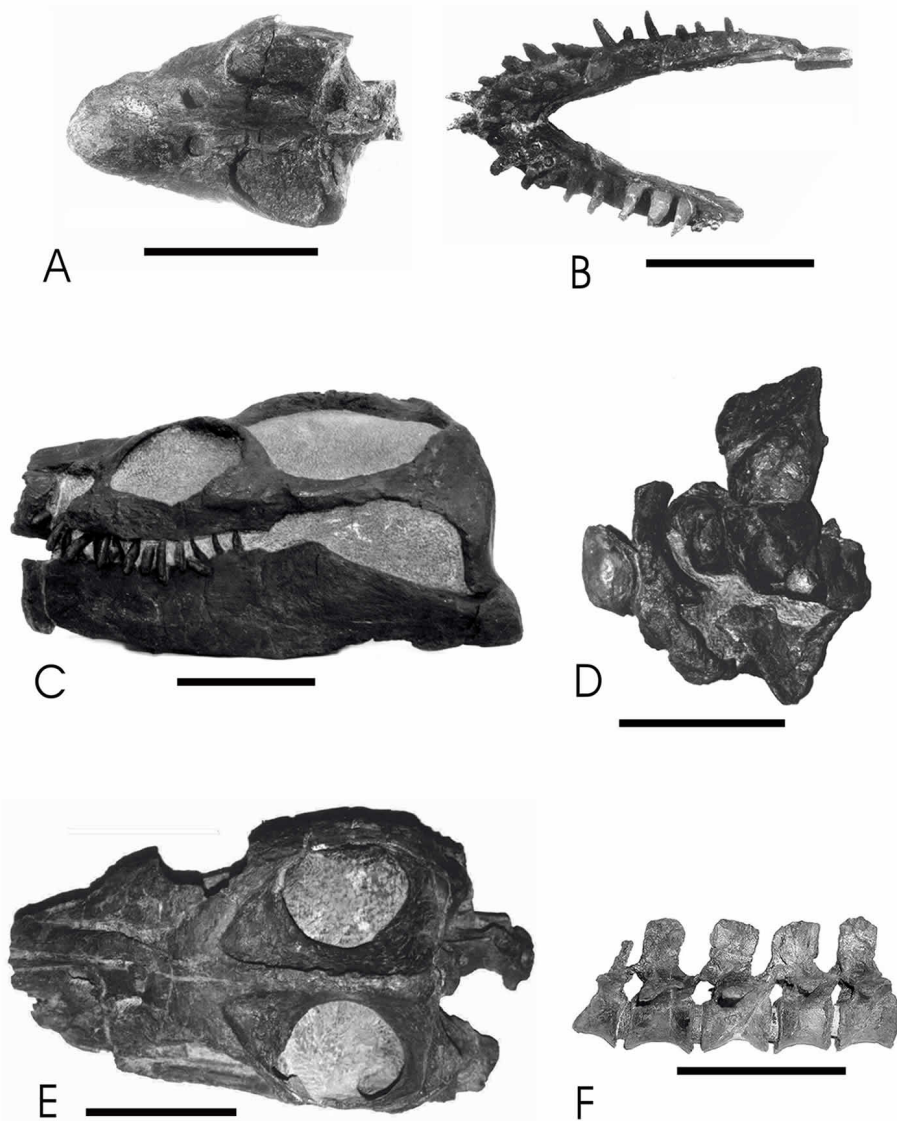
Given the present state of knowledge of the Cuban Oxfordian reptiles, it may be concluded that: (1) Fossil remains of Jurassic reptiles from western Cuba occur (Guaniguanico Terrane), mainly in the middle-upper Oxfordian Jagua Vieja Member of the Jagua Formation, cropping out in the Sierra de los Órganos (Pinar del Río province). (2) These fossil-bearing strata were deposited in shallow marine conditions on the continental margin of Laurasia (with coastal wetland) facing the deeper Caribbean oceanic seaway. (3) The vertebrate fossils reported from the Jagua Vieja Member have been historically recovered from calcareous concretions embedded in black shales, where small animals such as fish, turtles and pterosaurs are almost complete, but the skeletons of the largest reptiles are always incomplete.

These remains include well-preserved isolated bones, articulated skulls and mandibles, and segments of vertebral columns. (4) The taphonomic analysis suggests that there was no active predation on carcasses on the sea floor prior to fossilization. (5) Most of the fossil reptiles of the Jagua Vieja Member are marine and include thalattosuchians (*Geosaurus* sp.), pliosauro-morphs (*Peloneustes* sp.), plesiosauro-morphs (*Vinialesaurus caroli*), ichthyosaurians (Ophthalmosauridae), chelonians (*Caribemys oxfordiensis*) and pterosaurs (*Nesodactylus hesperius*, *Cacibupteryx caribensis*). At least one remain of a dinosaur suggests the presence of terrestrial animals whose carcasses were carried to the sea. (6) Most of the marine reptiles from the middle-upper Oxfordian of Cuba have close phylogenetic relationships with those of the Callovian-late Jurassic of the European Tethys and late Jurassic forms of the Eastern Pacific (Oxfordian Sundance Formation of north-western North America and Tithonian Vaca Muerta Formation of north-western Patagonia). (7) The Jurassic Caribbean Seaway was a corridor for the dispersion of pelagic reptiles between the European Tethys and the Eastern Pacific since the Oxfordian, as well as a barrier to dispersion of continental forms between Laurasia and Gondwana.

## 7. Appendix – Systematic paleontology

The first papers describing the Cuban Jurassic herpetofauna were published during the first half of the 20th Century by graduate students under the guidance of RICARDO DE LA TORRE Y MADRAZO (senior professor of Paleontology at the University of Havana). Several new taxa were introduced, generally described as ichthyosaurs (DE LA TORRE Y MADRAZO & CUERVO 1939; DE LA TORRE Y MADRAZO & ROJAS 1949), but actually representing plesiosaurs, crocodiles and fish (ITURRALDE-VINENT & NORELL 1996; GASPARINI & ITURRALDE-VINENT 2001). A long bone of a dinosaur was also described as a humerus or femur of a “diplodocus” or “brontosaur” (DE LA TORRE Y CALLEJAS 1949). In these early works, the specimens were poorly prepared, inadequately described and improperly allocated taxonomically. Since the study of COLBERT (1969) on the pterosaur *Nesodactylus*, the Cuban Jurassic reptiles catalog (ITURRALDE-VINENT & NORELL 1996), and the preparation and study of old specimens plus others discovered more recently, knowledge of the Cuban Oxfordian herpetofauna has increased greatly. A synthesis is presented here.

All the specimens reported here were recovered from the Jagua Vieja Member of the Jagua Formation (see Geological Setting; Figs. 1-2). However, they can not be understood as a natural association or assemblage, because they are usually found isolated, even within the same locality. It is important to underline that most of the specimens are incomplete, due to



**Fig. 4.** Oxfordian reptiles of Cuba. **A-B** – (MNHNCu P3008) *Vinialesaurus caroli* (DE LA TORRE Y MADRAZO & ROJAS, 1949); **C** – (MNHNCu P3005) *Peloneustes* sp.; **D** – (MNHNCu P3068) *Ophthalmosauria* indet skull, right view; **E** – (MNHNCu P3009) *Geosaurus* sp.; **F** – (NMNH 419640) dorsal thalattosuchian vertebrae. Scale 10 cm.

both taphonomy and collection biases. The concretions had to be broken for inspection, because not always is there external evidence of the fossil content. In addition, many concretions have been found broken with their fragments separated due to plugging for agriculture. Finally, some specimens have been damaged due to inappropriate preparation.

Plesiosauria DE BLAINVILLE, 1835

Plesiosauroidea (GRAY) WELLES, 1943

Cryptoclididae WILLISTON, 1925

*Vinialesaurus* GASPARINI, BARDET, ITURRALDE-VINENT, 2002

*Vinialesaurus caroli* (DE LA TORRE Y MADRAZO & ROJAS, 1949)

Synonyms: *Cryptocleidus?* (sic) *cuervoi caroli* DE LA TORRE Y MADRAZO & ROJAS (1949).

Material: MNHNCu P3008 (holotype) (Fig. 5A, B; ITURRALDE-VINENT & NORELL 1996, fig. 6). Anterior part of skull and mandible with associate atlas-axis (GASPARINI et al. 2002, figs. 2-3)

Locality: Near Viñales, between Laguna de Piedra and La Palma (Fig. 1).

Comments: DE LA TORRE Y MADRAZO & ROJAS (1949) reported the occurrence of long-necked plesiosauria from the Sierra de los Órganos and described the taxon *Cryptocleidus?* (sic) *cuervoi caroli* (ITURRALDE-VINENT & NORELL 1996, fig. 6). Recently the holotype (Fig. 4A, B) was prepared and described as Cryptoclididae *Vinialesaurus caroli* nov. comb., belonging to the sister-group of *Cryptoclidus-Kimmerosaurus* (GASPARINI, BARDET & ITURRALDE-VINENT 2002, figs. 2-3).

Plesiosauroidea indet.

Comments: Many other postcranial elements (vertebrae, fragmentary long bones, ribs, and pectoral girdle), as well as a fragmentary unidentified mandibles and skulls, have been found in different localities at the same stratigraphic level.

Pliosauroida WELLES, 1943 (sensu O'KEEFE 2001 a)

Pliosauridae SEELEY, 1874

*Peloneustes* sp.

Material: MNHNCu P3005 (Fig. 4C). Partial skull and mandible.

Locality: Northern slope Sierra de Caignanabo (Fig. 1, Table 1).

Comments: A comparison with pliosauroids stored at the Natural History Museum (London), especially one of the few specimens preserved in 3D (R 4058), and at the Geologisch-Paläontologische Institut der Universität, Tübingen, suggested that the Cuban pliosaurid corresponds to a new species of *Peloneustes* LYDEKKER (Z.G. under study).

Pliosauroida indet.

Material: MNHNCu P0828.

Locality: Hoyos de San Antonio.

Comments: A mandibular fragment with widely spaced circular alveoli. Very damaged material that cannot be prepared and therefore not identified.

Ichthyosauria DE BLAINVILLE, 1835

Ophthalmosauria APPLEBY, 1956 (sensu MOTANI 1999)

Ophthalmosauridae BAUR, 1887

Ophthalmosaurid gen. et sp. indet.

Material: MNHNCu P3068 (Fig. 4D). Several bones of one skull partially disarticulated (both pterygoids, the basisphenoid, the basioccipital and part of the sclerotic ring) (FERNÁNDEZ & ITURRALDE-VINENT 2000, figs. 2-3).

Locality: Probably on the southern slope of Sierra de Guasasa (Fig. 1, Table 1)

Comments: As remarked FERNÁNDEZ & ITURRALDE-VINENT (2000), the most striking feature in this specimen is the large orbit inferred on the large size of the sclerotic ring (estimated diameter: 15cm). This character, together with the extracondylar area of the basioccipital reduced, in posterior view, are present in Ophthalmosauridae (MCGOWAN & MOTANI 2003).

Ichthyosauria indet.

Material: MNHNCu P3864, mandibular fragment; MNHNCu P3807, fragment of rostrum very damaged with eroded teeth; MNHNCu P3808, very damaged fragment of rostrum.

Locality: MNHNCu P3864, MNHNCu P3807: Jagua Vieja (Fig. 1, Table 1); MNHNCu P3808: Hoyos de San Antonio.

Ichthyosauria indet.

Synonyms: *Ichthyosaurus torrei* DE LA TORRE Y MADRAZO & CUERVO, 1939.

Material: MNHNCu P3001, skull fragment with mandibular rami attached.

Locality: Laguna de Piedra (Fig. 1, Table 1).

Comments: This specimen was described as holotype of *Ichthyosaurus torrei* by DE LA TORRE Y MADRAZO & CUERVO (1939) but this description was poor. The specimen was prepared in the Museo de La Plata, and then referred to a Metriorhynchidae (GASPARINI & ITURRALDE-VINENT 2001). However, a new analysis of the material suggested that the latter determination was incorrect, and that MNHNCu P3001 belongs to an Ichthyosauria (Z.G. & M.F. in study).

Crocodyliformes BENTON & CLARK, 1988  
Metriorhynchidae FITZINGER, 1843  
*Geosaurus* CUVIER, 1824

*Geosaurus* sp.

Material: MNHNCu P3009 (Fig. 4E), skull and mandible attached with damaged atlas-axis (ITURRALDE-VINENT & NORELL 1996, fig. 7; GASPARINI & ITURRALDE-VINENT 2001, fig. 2).

Locality: Southern slope of the Sierra de Guasasa (Fig. 1, Table 1).

Comments: The skull is slightly flattened and displaced to the right; consequently, the mandible can be seen in dorsal view (Fig. 4E). Characters such as oval shaped supratemporal fenestrae and angle formed by the sagittal and postorbital rami of the frontal more acute than in *Metriorhynchus* (VIGNAUD 1995), suggest the assignment of MNHNCu P3009 to *Geosaurus* sp.. This is the oldest record of the genus, as it has been recorded hitherto only in the late Kimmeridgian and Tithonian of Germany, Switzerland, Mexico, Chile and Argentina (GASPARINI & ITURRALDE-VINENT 2001; FREY et al. 2002).

Metriorhynchidae indet.

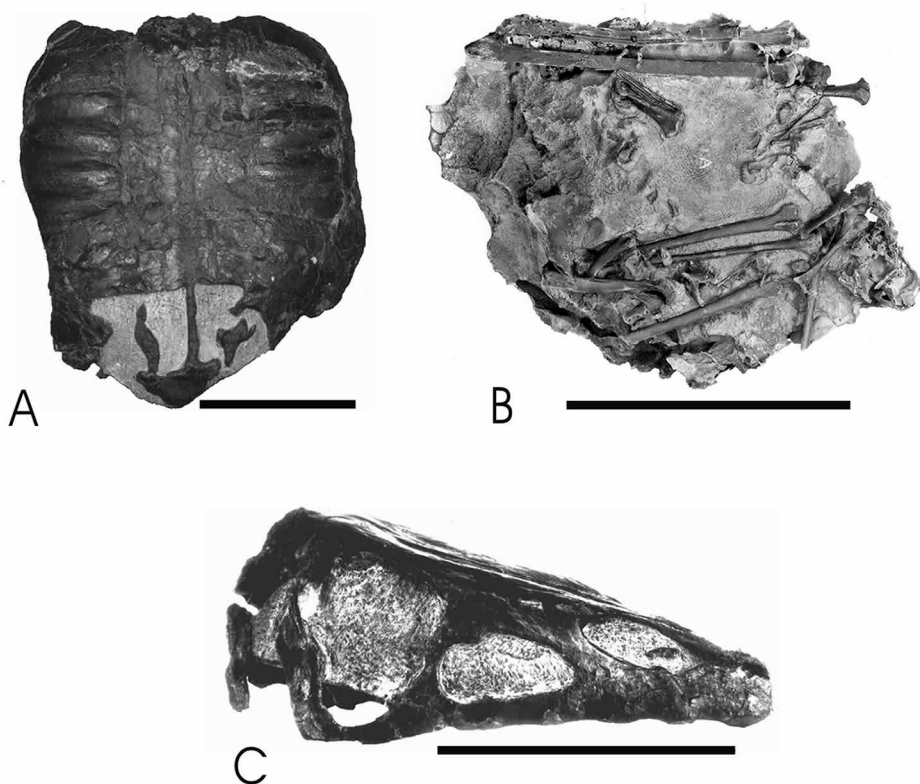
Synonym: *Geosaurus* sp. (GASPARINI & ITURRALDE-VINENT 2001), *Cryptocleidoid* (O'KEEFE 2003b).

Material: Access Number 419640 (previously NMNH 18699). Incomplete skull and mandible Locality: Puerta de Ancón (Fig. 1, Table 1).

Comments: Recently, O'KEEFE (2003b, fig. 6) described this specimen and referred it to an aberrant cryptocleidoid. Previously, GASPARINI & ITURRALDE-VINENT (2001) referred the same specimen, with the number NMNH 18699, to *Geosaurus* sp. The features observed in the palate and the dorsal side of the skull are those of a metriorhynchid crocodile.

*Thalattosuchia* indet.

Material: USNM 451942. Access Number 186997. Five articulated dorsal vertebrae (Fig. 4F).



**Fig. 5.** Oxfordian reptiles of Cuba. **A** – (MNHNCu P3125) carapax of *Caribemys oxfordiensis* DE LA FUENTE & ITURRALDE-VINENT, 2001; **B** – (AMNH 2000) *Nesodactylus hesperius* COLBERT, 1969; **C** – (IGP-V208) *Cacibuptyryx caribensis* GASPARINI, FERNÁNDEZ & DE LA FUENTE, 2004. Scale 10 cm.

Locality: Hoyo de la Sierra (Fig. 1, Table 1).

Comments: The dorsal vertebrae are articulated. The centrum in lateral view is sandglass shaped with the anterior and posterior ends with conspicuous striae. This kind of vertebra is seen both in teleosaurids and metriorhynchids (VIGNAUD 1995), hence it is impossible to assign them to one of these families.

Chelonii BRONGNIART, 1800  
Pleurodira COPE, 1864

*Caribemys oxfordiensis* DE LA FUENTE & ITURRALDE-VINENT, 2001

**Material:** MNHNCu P3125 (holotype) (Fig. 5A). DE LA FUENTE & ITURRALDE-VINENT (2001, fig. 2) incorrectly cited this specimen as MNHNCu 3209. The holotype is an incomplete shell, a probable cervical eight vertebra, and remains of the appendicular skeleton of a single specimen (DE LA FUENTE & ITURRALDE-VINENT 2001, figs. 2-6).

**Locality:** Near Viñales (Fig. 1, Table 1).

**Comments:** The only Cuban specimen of marine turtle, *Caribemys oxfordiensis*, is at the same time the oldest pleurodiran yet known. Previously, there were described two taxa of Upper Jurassic pleurodires, *Platychelys obendorferi* WAGNER from the Kimmeridgian of Solothurn, Switzerland and Portugal and the Tithonian of Germany, and *Notoemys laticentralis* CATTOI & FREIBERG, 1961 from the Tithonian of northern Patagonia (DE LA FUENTE & ITURRALDE-VINENT 2001). The phylogenetic analysis suggests that *Caribemys* belongs in Pleurodira, and appears to be the sister group of *Notoemys* + Eupleurodira (DE LA FUENTE & ITURRALDE-VINENT 2001, fig. 7).

Pterosauria KAUP, 1834  
Rhamphorhynchidae SEELEY, 1870 (sensu UNWIN 2003)

*Cacibupteryx caribensis* GASPARINI, FERNÁNDEZ & DE LA FUENTE, 2004

**Material:** IGP-V 208. (Fig. 5C). Incomplete three dimensional skull; distal end of the left ulna, fragments of the left radius, and left phalanx 1 of the wing-finger (GASPARINI et al. 2004, text-figs. 2-4).

**Locality:** Jagua Vieja (Fig. 1, Table 1).

**Comments:** It is a rhamphorhynchid with broadly expanded skull roof elements, mainly frontal and parietal. The orbits are subcircular with the ventral half more compressed. The orbital ventral margin is level with the dental borders; the section of the jugal that forms the postero-ventral border of the orbit bears a well-developed pocket-like recess; a jugal with a prominent recess (GASPARINI et al. 2004, text-fig. 2B, C), and the occipital table trapezoidal in shape with the maximum width between the quadrate bones (GASPARINI et al. 2004, text-fig. 3). The Rhamphorhynchidae (UNWIN 2003) are represented in the fossil record from the Toarcian to the Tithonian, but the Oxfordian and Kimmeridgian forms are poorly known (WELLNHOFER 1991; CARPENTER et al. 2003). Consequently, the holotype of *Cacibupteryx caribensis* is the best preserved middle-late Oxfordian pterosaur skull found so far (GASPARINI et al. 2004).

## Rhamphorhynchinae NOPCSA, 1928

*Nesodactylus hesperius* COLBERT, 1969

Material: AMNH 2000, holotype (COLBERT 1969; Fig. 5B).

Locality: Hoyo del Palmar (Fig. 1, Table 1).

Comments: COLBERT (1969) described the first pterosaur found in Cuba, and identified it as a new Rhamphorhynchidae. According to WELLNHOFER (1991), *Nesodactylus* is a Rhamphorhynchidae indet., but UNWIN (2003), assigned it to the Rhamphorhynchidae Rhamphorhynchinae. The only elements preserved that allow a comparison between the holotypes of *Nesodactylus* and *Cacibupteryx* are the quadrate, and the distal ends of the left radius and ulna, and they are different (GASPARINI et al. 2004), justifying the validity of these genera.

Dinosauria OWEN, 1842

Sauropodomorpha v. HUENE, 1932

## Camarasauromorph ?

Locality: Jagua Vieja (Fig. 1, Table 1).

Comments: The specimen referred here to Dinosauria was originally described by DE LA TORRE Y CALLEJAS (1949) as a long bone, about 45 cm long, without the epiphyses. The specimen is lost, but it was illustrated by a fairly good photograph. According to L. SALGADO (pers. comm. 2002), this element can be tentatively referred to as a tarso-metatarsus of a camarasauromorph dinosaur.

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