

## A NEW PLEURODIRAN TURTLE FROM THE JAGUA FORMATION (OXFORDIAN) OF WESTERN CUBA

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**ABSTRACT**—The oldest Jurassic marine pleurodire is reported from the Jagua Formation in western Cuba. These remains are from levels of middle and late Oxfordian age. This turtle represents a new genus and species, *Caribemys oxfordiensis*. A phylogenetic hypothesis is proposed, whereby *Caribemys* is considered to be the sister group of *Notoemys* Cattoi and Freiberg, 1961, plus the Eupleurodira Gaffney and Meylan, 1988. The occurrence of *Caribemys oxfordiensis* n. gen. and sp. in the Jagua Formation along with plesiosauroids, pliosauroids, ophthalmosaurian ichthyosaurs, and metriorhynchid crocodiles, strongly suggests that during the Oxfordian a marine seaway was present in the Caribbean, connecting the western Tethys with the Pacific Ocean.

### INTRODUCTION

THE OCCURRENCE of Mesozoic marine reptiles in Cuba was poorly known until the publication of a general report about this faunule by Iturralde-Vinent and Norell (1996). But very few of these fossils, preserved in calcareous concretions, have been properly prepared, a requirement for any taxonomic study. As part of the effort to complete the study of these fossil reptiles, Zulma Gasparini (Museo de La Plata, Argentina) visited Cuba early in 1998, and together with M. Iturralde-Vinent (Museo Nacional de Historia Natural) investigated several outcrops and revised the fossil collections at both the Museo Nacional de Historia Natural in Havana and a small local museum in the Valle de Dos Hermanas, near Viñales. A small concretion was found in the latter museum, prepared partly mechanically, exposing the upper part of a turtle, the occurrence of which has never been reported before in the literature. This specimen was donated to the Museo Nacional de Historia Natural in Havana, and borrowed by the Museo de La Plata to be prepared and studied.

The only information accompanying the specimen was that Juan Gallardo collected it in the Jagua Formation, in Viñales. The fact that the fossil occurs in a carbonate concretion corroborates the provenance, as it is a typical style of preservation of Jagua's fossils.

The Cuban Oxfordian Jagua Formation contains a fairly rich fossil assemblage including plesiosauroids, pliosauroids, metriorhynchid crocodiles, ichthyosaurs, pterosaurs, fish, ammonites, belemnites and terrestrial plants (Iturralde-Vinent and Norell, 1996; Fernandez and Iturralde-Vinent, 2000). Some additional fossil reptiles are currently under investigation (Z. Gasparini and M. Iturralde-Vinent, personal commun., 1999).

In the Viñales area, the fossiliferous level where the saurians have been found is referred to the middle to late Oxfordian age, and is represented by the shales and limestones of the Jagua Vieja Member of the Jagua Formation (Iturralde-Vinent and Norell, 1996). The locality from which the specimen was collected is ambiguous, as “Viñales” refers both to a town and to a large valley where the middle to late Oxfordian Jagua Formation occurs (Fig. 1). Nevertheless, in western Cuba, Jagua is the only fossiliferous formation bearing reptiles in calcareous concretions, so the age of the fossils is certain.

The Jagua Vieja Member, up to 60 m thick, is composed of laminated black shales with thin intercalations of marly micritic to biomicritic limestones, containing fairly abundant lenticular calcareous concretions (Pszczolkowski, 1978).

The vertebrate fossils have been commonly found in the concretions of the Jagua Vieja Member, embedded within a horizontally laminated black limestone matrix. These concretions are len-

ticular in shape and of very different diameters, from a few centimeters up to nearly one meter. The analysis of a wackestone-packstone where the turtle was included yielded detrital vegetal remains and Oxfordian-kimmeridgian microfossils [*Favreina salvensis* (Parejas), *Favreina* sp., *Globochaete alpina* Lombard, ostracods with smooth hyaline shells]. These organisms suggest that the sedimentary environment was a shallow water protected platform (Sivia Blanco, personal commun., 2000).

To date, only two taxa of Jurassic pleurodires have been reported worldwide. The occurrence of an Oxfordian pleurodire in Cuba adds to the systematics and paleobiogeography of basal pleurodires and represents the third and the oldest record of a Jurassic marine pleurodire.

The followings abbreviations are used in the text and figures: MNHNCu-P—Museo nacional de Historia Natural, La Habana; MOZP—Museo Olsacher, Dirección Provincial de Minería, Zapala; NMB, Naturhistorische Basel Museum; SMSS, Sammlung des Museum der Stadt Solothurn.

### SYSTEMATIC PALEONTOLOGY

Order CHELONII Brongniart, 1800  
Infraorder PLEURODIRA Cope, 1864  
Genus CARIBEMYS new genus

*Type species.*—*Caribemys oxfordiensis* new species by monotypy.

*Diagnosis.*—Late Jurassic pleurodire having a carapace with continuous nuchal and neural bone series, seven or eight irregularly shaped neural bones, laterally placed cuneiform mesoplastra not in contact at the midline, carapace strongly depressed, iliac scar not reaching the peripheral bones. It differs from *Platychelys* in the absence of supramarginal scutes, absence of carapace protuberances, a rounded anterior plastral lobe, a large intergular scute and from *Notoemys* by the subquadrangular shape of the carapace, presence of a small plastral fenestra, and an elongated iliac scar.

*Etymology.*—“Caribe,” from Caribbean sea; “emys,” from the Greek “aquatic turtle.”

CARIBEMYS OXFORDIENSIS new species  
Figures 2–5

*Diagnosis.*—Same as for the genus, by monotypy.

*Description.*—The carapace of *Caribemys* n. gen. is badly preserved, consisting of the anterior part, some fragments of lateral and posterior peripheral and pleural bones, and most of an internal mold (Figs. 2, 3). The carapace outline is subquadrangular with a straight anterior margin, slightly rounded anterolateral margin (second to fourth peripheral bones), and straight and converging

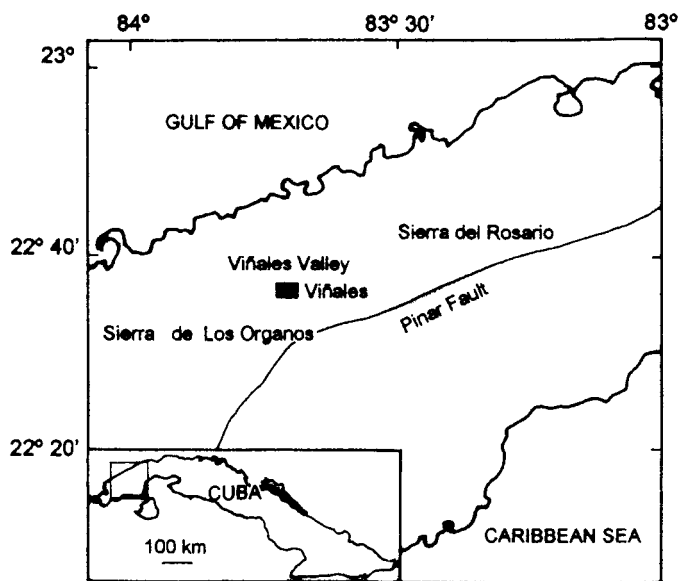


FIGURE 1—Location map of Viñales Valley in western Cuba.

posterolateral margins. The nuchal bone is poorly preserved. However, the position of the first pair of peripheral bones and the impression of the first neural bone suggest the presence of a short and wide nuchal. The shell is nearly as wide as long. The width/length carapace ratio is around 92 percent. A similar ratio is measured in *Notoemys*. Carapace protuberances below first costal scutes are absent.

Posterior to the nuchal bone fragments, the odd neural series continues with six irregular neural bones preserved as impressions on the surface of the internal cast (Figs. 2, 3). The first quadrangular one is the second neural bone. Unfortunately, the seventh and eighth neural bones, the seventh and eighth pair of pleural bones, and the first suprapygial bone are not preserved. The odd neural series ends in a fragment of the second suprapygial. The pygal bone is not preserved.

On both sides of this row there are bone remains and impressions of the eighth pleural bones (although the impressions of the last two pairs of pleural bones are not preserved) and most of the peripheral bones are represented. Seven peripherals (first, second, third, fourth, ninth, and fragments of the tenth and eleventh) on the left side, and the continuous peripheral series from first to eighth bones on the right side, are preserved. Normally 11 pairs of peripheral plates are present in casichelydian turtles. The preserved margin of the peripheral bones is smooth or slightly undulated as are the marginal scutes of *Notoemys*. This condition differs from *Platycheilus*, in which the peripheral margin is more serrated. The first, second, and third peripheral bones are trapezoidal. The posterior border of the first peripheral has a wide contact with the first pleural. Peripherals four to seven are partly preserved. Peripherals eight and nine have a high width/length ratio.

A quadrangular first vertebral scute can be reconstructed in *Caribemys*. This scute may have been considerably wider than long. The remaining vertebral scutes are not preserved.

As in other pleurodiran turtles, 12 pairs of marginal scutes appear to be present in *Caribemys*. However, only the first to ninth scutes are recognized on the right side and only the first to fourth scutes and isolated ninth and tenth scutes are distinguished on the left side. The first pair of marginal scutes was probably trapezoidal in shape and considerably wider than long. This condition does not preclude the presence of a short and wide cervical scute

in *Caribemys*, as with *Platycheilus* and *Notoemys*. However the presence of a nuchal scute cannot be determined. The remaining marginal scutes of the anterolateral margins of the carapace are subrectangular in shape and cover the distal third of the peripheral bones. The eighth left marginal scute is subrectangular and the ninth pair may have been subpentagonal. In the holotype of *Caribemys*, supramarginal scutes are absent, at least on the dorsal surface of the first through fourth peripheral bones, areas where these scutes are present in *Platycheilus*.

The isolated irregular and dentate dorsal surfaces of both ilia are distinguishable in the region of the eighth pleurals and the first suprapygial, to which this surface sutures in most pleurodirans (Figs. 2, 3).

Although the distal xiphiplastral extremity is not preserved in *Caribemys* the plastron was likely shorter than the carapace. The anterior plastral margin projects forward beyond the carapace, as with *Platycheilus* and *Notoemys*. The anterior lobe has slightly convergent lateral margins and appears to have been shorter than the posterior lobe, as in *Platycheilus*, *Notoemys*, and eupleurodiran turtles.

The plastron is attached to the carapace by a short bridge (Figs. 2, 3). This kind of attachment, as in *Platycheilus*, *Notoemys* and other pleurodire turtles, is sustained by the insertion of axillary and inguinal buttresses on the visceral surface of the carapace. In *Caribemys* the axillary buttress is attached to the lateral margin of the first pleural bone and the third peripheral bone, while the inguinal buttress extends onto the seventh peripheral and nearly contacts the eighth peripheral bone. The lateral parts of the plastron are curved upward and form an obtuse angle between the plastron and the buttresses as in all the Pleurodira, more so than in *Proganochelys* and *Kayentachelys*. The posterior plastral lobe is the longest component of the plastron, the length of the bridge being shorter.

The epiplastral bones in *Caribemys* are short and wide. The proportions and outline of these bones and the short contact between both bones in the plastral midline in *Caribemys* are similar to those of *Platycheilus* (see Bräm, 1965, pl. 1, fig. 2). In *Caribemys* the entoplastron outline (rounded anterolateral margin and tapering posterior margin) and the proportions (slightly longer than wide) are also very similar to those of *Platycheilus*. In both species the entoplastron does not extend anteriorly to separate the epiplastra, unlike the primitive condition seen in *Proterochersis* (ventrally) and other turtles such as *Proganochelys*, *Kayentachelys* (see Gaffney, 1990), or *Palaeochersis* (see Rougier et al., 1995).

*Caribemys* displays a simple intergular-gular scute pattern (Figs. 2, 3). A long and narrow intergular scute covers most of the entoplastron, and a pair of shorter but wider gular scutes extends over the anterolateral entoplastral extremity. Like *Notoemys*, but unlike *Platycheilus*, the intergular scute is three times the length of the interhumeral scute (see Table 1). The pattern of the remaining pectoral, abdominal, and femoral scutes is more similar to that seen in *Platycheilus* than to that of *Notoemys*.

In *Caribemys* the hyoplastra are the largest plastral bones. They include well developed axillary buttresses and the main part of the anterior plastral lobe. Their posteromedial margins form the anterolateral part of a small, subpentagonal central fenestra. *Caribemys* has (unlike *Platycheilus* and *Notoemys*) a single small hyo-hyoplastral fenestra. The humero-pectoral sulcus is posterior to the entoplastron. This sulcus is strongly curved anteriorly crossing the hyoplastra in their first third.

*Caribemys* has a pair of cuneiform mesoplastra, as do *Platycheilus* and *Notoemys*. They are sutured medially to the hyo-hyoplastra and to two peripherals laterally (Figs. 2, 3). These bones do not reach the margin of the small central fenestra.

The pectoral scutes of *Caribemys* cover most of the hyoplastra

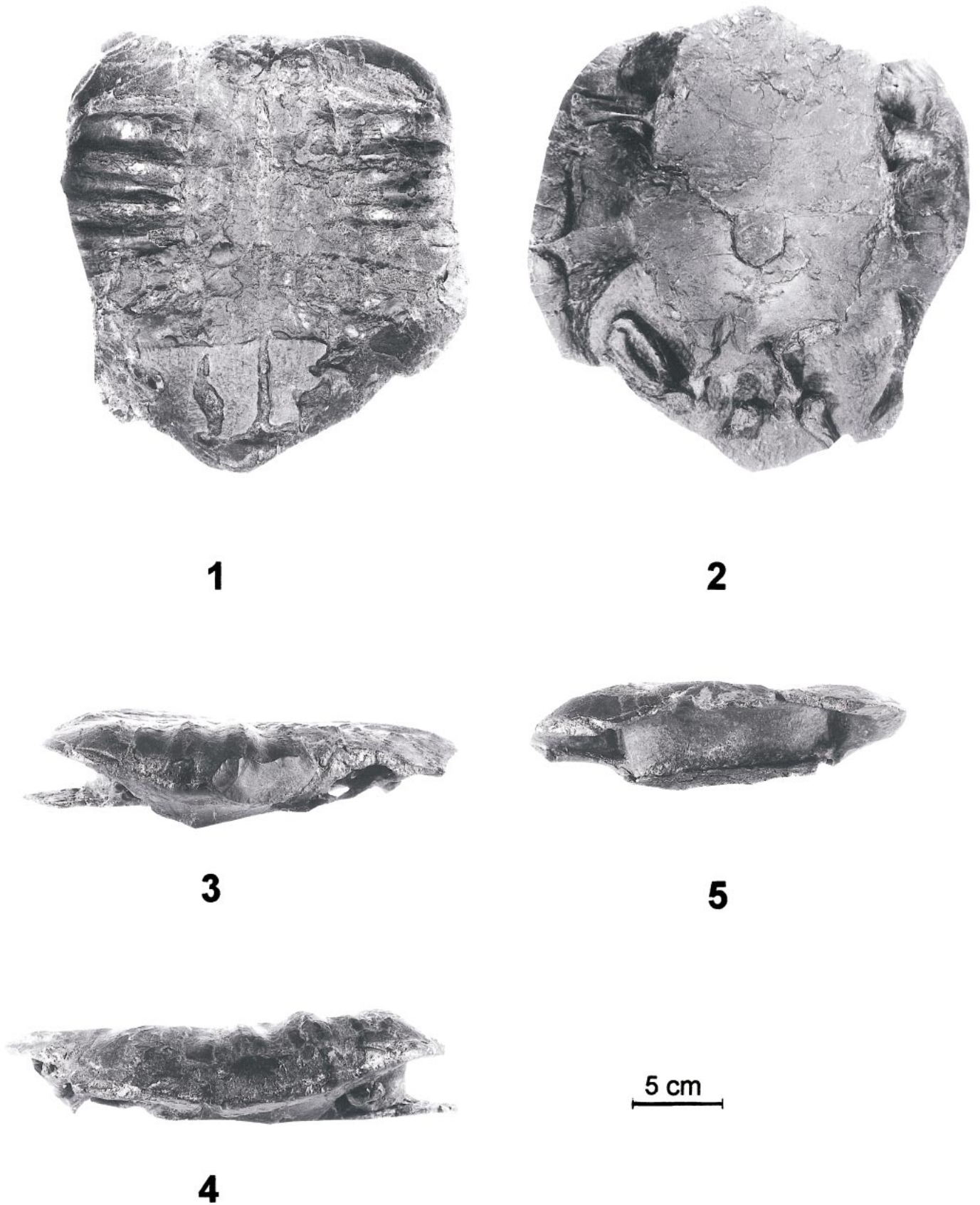


FIGURE 2—*Caribemys oxfordiensis* n. gen. and sp., MNHNCu-P 3209, shell. 1, Dorsal view; 2, ventral view; 3, left lateral view; 4, right lateral view; 5, anterior view.



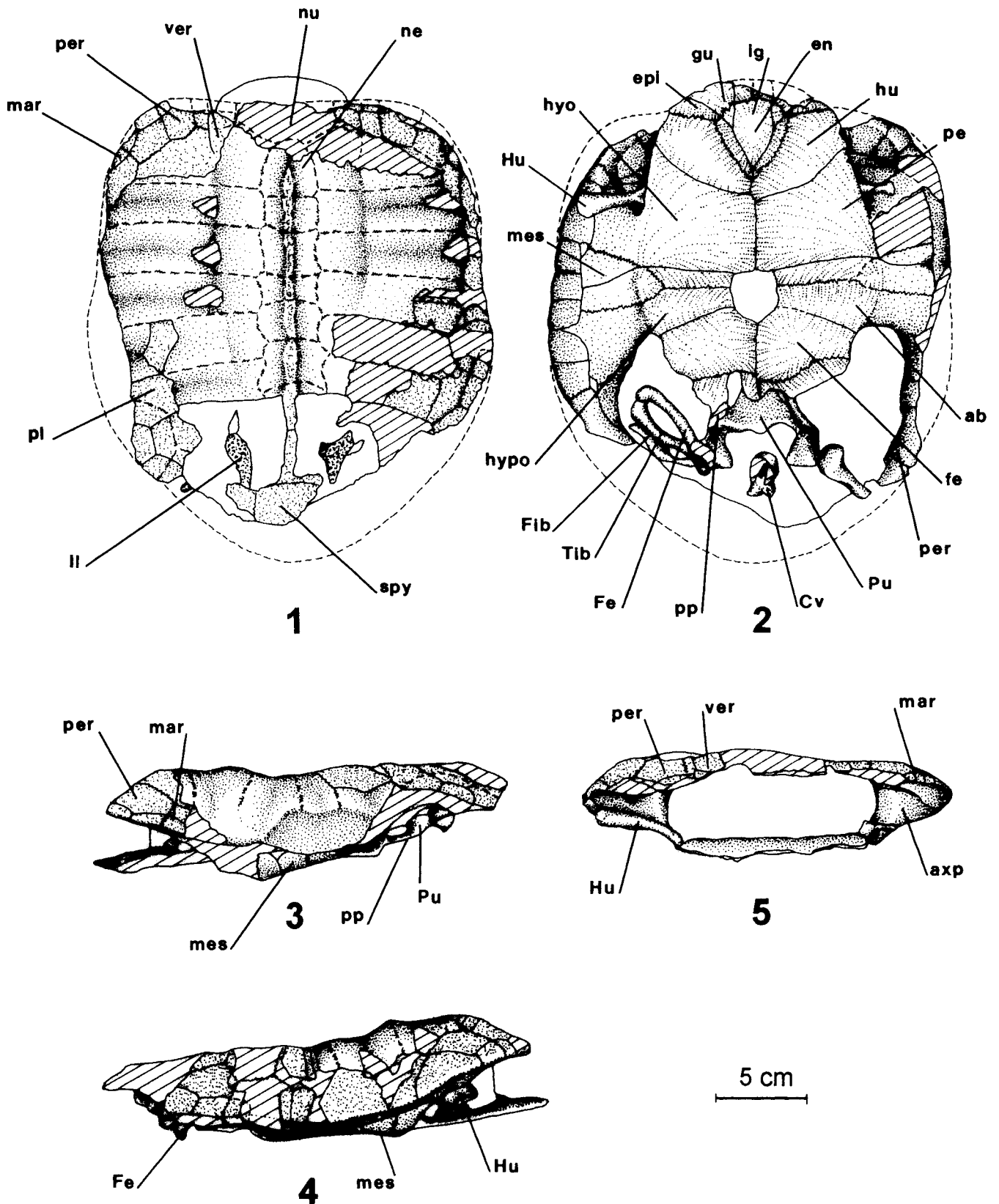


FIGURE 3—*Caribemys oxfordiensis* n. gen. and sp., MNHNCu-P 3209, shell. 1, Dorsal view; 2, ventral view; 3, left lateral view; 4, right lateral view; 5, anterior view. Abbreviations: ab = abdominal scute, ax p = axillar process, cv = caudal vertebrae, en = entoplastron, epi = epiplastron, fe = femoral scute, Fe = femur, Fib = fibula, gu = gular scute, hyo = hyoplastron, hu = humeral scute, Hu = humerus, ig = intergular scute; Il = ilium, mar = marginal scute, mes = mesoplastron, ne = neural bone, nu = nuchal bone, pe = pectoral scute, per = peripheral bone, pp = pectinal process, Pu = pubis, spy = suprapygial bone, Tib = tibia, ver = vertebral scute.

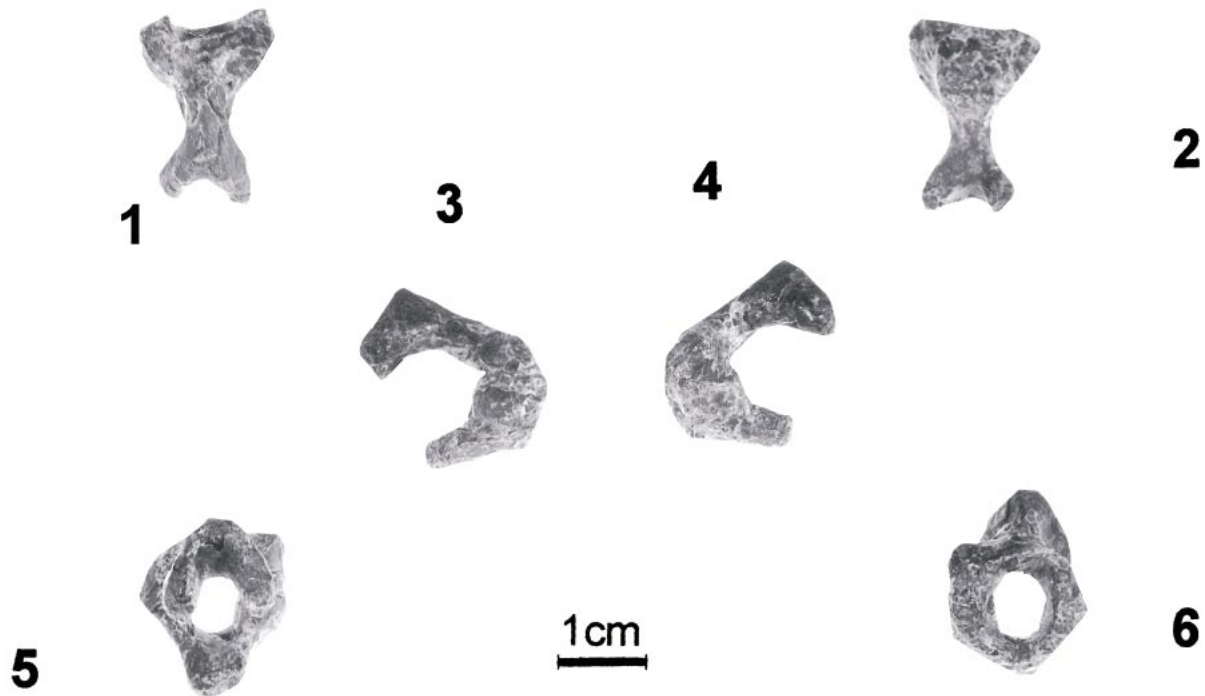


FIGURE 4—*Caribemys oxfordiensis* n. gen. and sp., MNHNCu-P 3209,? eight cervical vertebra. 1, Dorsal view; 2, ventral view; 3, lateral right view; 4, lateral left view; 5, posterior view; 6, anterior view.

and extend onto the anterior portion of the mesoplastron, as with *Platycheilus* and *Notoemys*. The pectoro-abdominal sulcus runs transversally across the posterior edge of the hyoplastron and the mesoplastron where it has a slightly posterolateral bend.

The hypoplastron of *Caribemys*, as usual, forms the inguinal notch and the inguinal buttress. These bones also form the posterolateral margin of the central plastral fenestra and are the main component of the posterior lobe.

The abdominal scute is as narrow as the humeral scute and covers the posterior part of the hyoplastron, most of the mesoplastron and the anterior part of the hypoplastron. The abdomino-femoral sulcus runs obliquely from the central plastral fenestra across the hypoplastron to the inguinal notch.

In *Caribemys* only the proximal fragment of both xiphiplastra are preserved, but unlike *Platycheilus* and *Notoemys*, they are not separated along the midline anteriorly. Unfortunately, most of both xiphiplastra are not preserved, preventing complete knowledge of the ventral contacts of the pelvic girdle. On the right side, a narrow lateral pubic process attached to the right xiphiplastral plate can be seen.

Both humeri are preserved with the holotype of *Caribemys*, but only the right one is preserved in good condition (although the distal end is damaged). The right and left humeri are exposed in ventral view (Figs. 2, 3).

The plastral lobe hides the proximal ends of both humeri. Only on the right humerus are the lateral and medial process partially visible. As in other pleurodires they are roughly equal in size. Between them, there is a C-shaped intertubercular fossa, a concavity equal in size and shape to that of other pleurodires.

The humerus narrows distally to a subcylindric axis in cross section. As in other pleurodiran turtles, the shaft of the humerus in *Caribemys* has a slightly sigmoidal curve. Distally the shaft of the humerus of *Caribemys* flattens and expands in a broad distal end. Unlike the humeri of *Notoemys* and *Chelus*, the shaft of the

humerus in *Caribemys* is less flattened dorsoventrally. The distal end of the right humerus is damaged and cannot be described.

The pelvic girdle is seen in ventral view and partially in lateral view (Figs. 2, 3). The ilium, pubis, and ischium are united to compose the acetabulum, seen on the left side where the head of the femur is slightly displaced. The ilium, as usual, is dorsally directed and has an irregular dorsal dentate surface that could be sutured to the carapace. Pubes are the best preserved and most conspicuous elements of the pubo-ischiadic plate. Unlike *Platycheilus*, an extensive pubic plate with an ossified epipubis is present in *Caribemys*. The narrow lateral or pectinal pubic processes are firmly attached to the anterolateral margins of the xiphiplastra. As in *Platycheilus*, the ventral parts of the pubes are not vertically directed. Although the ischiadic plates are not well preserved in *Caribemys*, a large thyroid fenestra can be distinguished. It appears to have been partly separated as in *Platycheilus* and unlike the Eupleurodiran turtles, in which both fenestrae are completely connected.

The right and left femora are preserved in *Caribemys* (Figs. 2, 3), but the right femur is more completely preserved and it is articulated with the pelvic acetabulum. The femur in *Caribemys* is slightly longer than the humerus with both ends slightly expanded. The right femoral head is hidden, though laterally exposed. The head is partly damaged in the left femur. The articular head surface is set off from the dorsal surface of the femur at an angle of approximately 110 degrees with the longitudinal axis of the femur.

The proximal end of the femur of *Caribemys* is slightly expanded by two processes, partially damaged. They limit a relatively shallow intertochanteric fossa. The femoral shaft in *Caribemys* is subcylindric in cross section and arched dorsoventrally as in other turtles. Although the distal end on the right femur in *Caribemys* is partially exposed the condyles that bear the tibial articulation are visible.

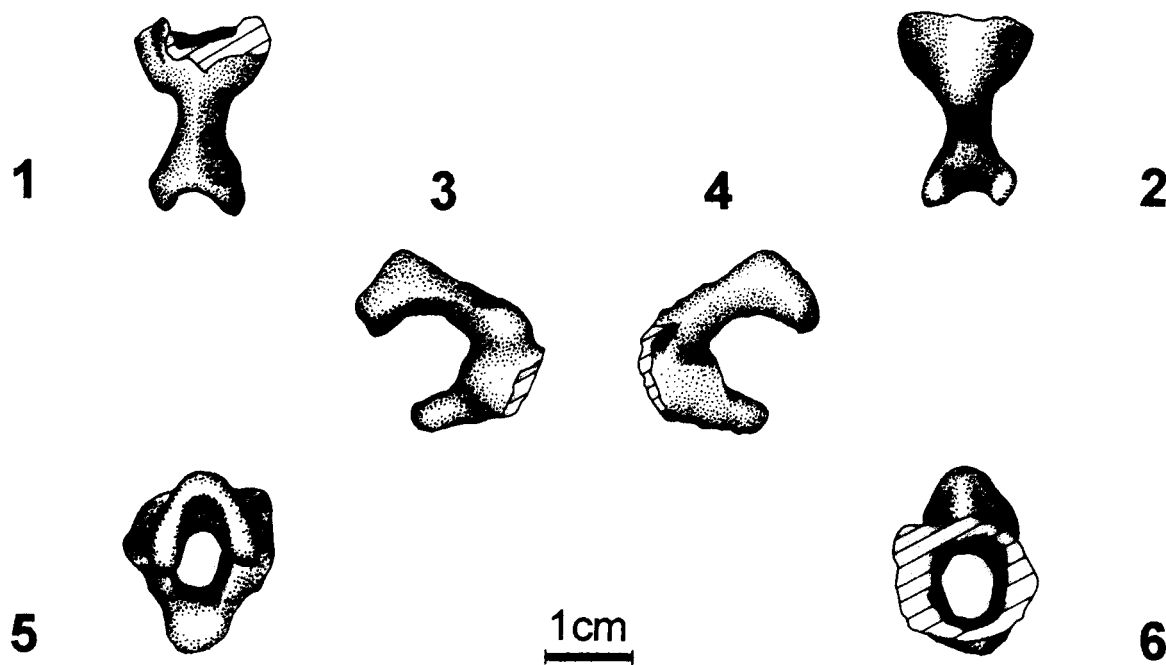


FIGURE 5—*Caribemys oxfordiensis* n. gen. and sp., MNHNCu-P 3209,? eight cervical vertebra. 1, Dorsal view; 2, ventral view; 3, lateral right view; 4, lateral left view; 5, posterior view; 6, anterior view.

Only the right tibia is preserved in the holotype of *Caribemys* (Figs. 2, 3). This bone is slightly displaced from its natural position, lying beside and under the femur. The tibia in *Caribemys* is a massive bone expanded at both ends, and the shaft is unnaturally bent. Although the proximal end is partially hidden under the femur it can be seen that the end expands twice the width of the shaft at its narrower point. Unfortunately, the proximal third and the articular surface are damaged and are not available for an accurate description. The distal articular surface is partially exposed and only a medial dome is recognized.

Only the right fibula is preserved in *Caribemys* (Figs. 2, 3). The shaft is partially damaged and strongly bent. As the fibula is turned and displaced from its original position, the distal end is lying beside the tibia while the proximal end of the fibula is superposed on the tibia. As in other turtles, the fibula is a slender element, more gracile than the tibia. The proximal articular surface is rounded. The distal extremity of the fibula of *Caribemys* is expanded and the distal fibular shaft seems to be slightly concave on the dorsal side and convex on the ventral side.

A single nearly complete cervical vertebra is preserved (Figs.

4, 5). Unfortunately, this vertebra lacks the anterior central articulation and the prezygapophyses, but the posterior convex central articulation and the postzygapophyses are well preserved. The close similarity between the cervical vertebra of *Caribemys* and the eighth cervical vertebra of *Platycheilus* from the Basel Museum suggests that an eight cervical vertebra is represented. A posteriorly protruded articular condyle with a convex and rounded articular centrum, as is seen in *Platycheilus*, pleurodiran turtles, and cryptodiran such as *Chelydra*, is present on the eighth cervical of *Caribemys*. The neural spine of the cervical vertebra of *Caribemys* is very low and continuous with the processes bearing the postzygapophyses. These structures are very close to each other and faced ventrally. The posterior part of the ventral surface of the centrum is smooth and slightly convex without a keel. The major differences between the eighth cervical vertebrae of the holotype of *Caribemys* and the Basel specimen of *Platycheilus* are the narrowness of the processes that support the postzygapophyses and the shape of the condyle. An unfortunate mistake caused by incomplete preparation of the firmly articulated cervical vertebrae of *Notoemys* led Fernández and de la Fuente (1994) to

TABLE 1—Comparison of the shell in *Caribemys* and the other Late Jurassic pleurodires.

Characters	<i>Platycheilus</i>	<i>Caribemys</i>	<i>Notoemys</i>
Carapace shape	Suboval	Subquadrangular	Cordiform
Carapace protuberances below costals and vertebrals	Present	Absent	Absent
Shell flatness	Moderate	Extreme	Extreme
Supramarginals	Present	Absent	Absent
Number of plastral fontanelles	2	1	1
Form and shape of the plastral fontanelles	Small and irregular outline	Small pentagonal	Large and slightly narrow and elongated in antero-posterior way
Intergular scute	Small intergular scute covers the anterior half of the entoplastral bone	A long and narrow intergular scute covers most of the entoplastral bone	Probably a long intergular scute that covers most of the entoplastron bone
Intergular scute/interhumeral seam ratio	Intergular scute is equal in length to the interhumeral seam	Intergular scute is three times the length of interhumeral seam	Probably an intergular scute three times the length of the interhumeral seam
Anterior plastral lobe shape	Trapezoidal	Rounded	Subquadrangular

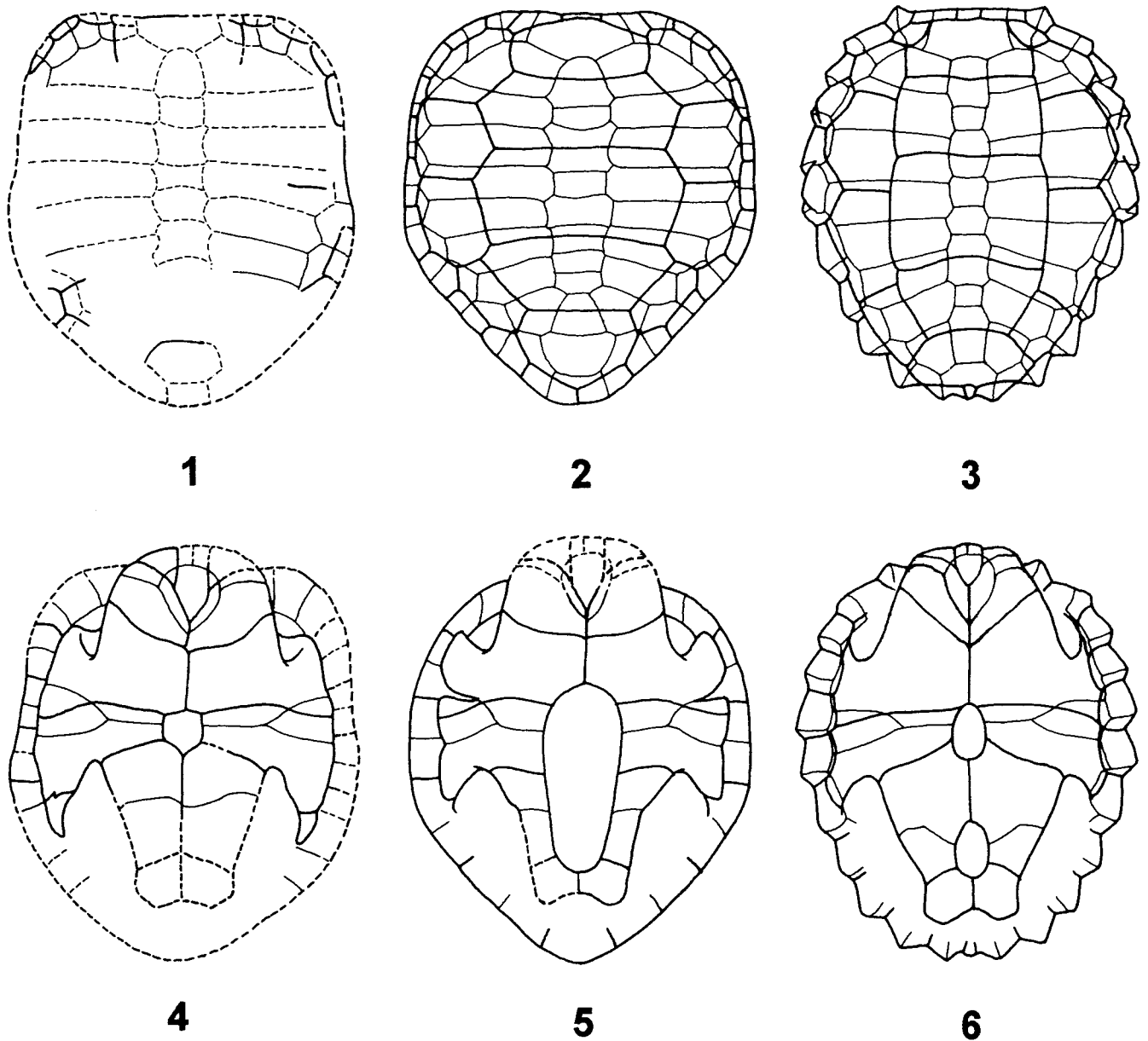


FIGURE 6—Comparisons of shell of Late Jurassic pleurodires. 1–3, dorsal view; 4–6, ventral view. 1, 4, *Caribemys oxfordiensis* n. gen. and sp. (MNHNCu-P 3209); 2, 5, *Notoemys laticentralis* (MOZP 2487); 3, 6, *Platycheilus oberndorferi* (SMSS 56).

describe the opisthochoelus second, third and fourth cervical vertebrae as amphicoelous. The opisthochoelus cervical vertebrae of *Notoemys* together with the condition seen in the posterior cervical vertebrae of *Platycheilus* and *Caribemys* suggested the presence of the full formed articular centra preserved in the three taxa of Late Jurassic pleurodires: )1( 2( 3( 4(in *Notoemys* (MOZP 2487); )7( 8) in *Platycheilus* (uncatalogued NMB specimen), ?(8) in *Caribemys* (MNHNH-P 3209).

*Etymology*.—"oxfordiensis," from Oxfordian age.

*Type*.—Holotype, MNHNP 3209. A partially preserved shell, a probable eighth cervical vertebra and remains of the appendicular skeleton of a single individual.

*Occurrence*.—Shales and limestones of the Jagua Vieja Member of the Jagua Formation of middle to late Oxfordian age (Iturralde-Vinent and Norell, 1996) from "Viñales" area, western Cuba (Fig. 1).

*Discussion*.—A sutural attachment between the pelvis and the shell has been considered the main postcranial synapomorphy to distinguish pleurodiran turtles from Triassic *Proterochersis* (see Gaffney and Meylan, 1988; and references therein). However, Rougier et al. (1995), in describing preliminarily the Late Triassic turtle *Palaeochersis talampayensis*, suggested that the "pelvis fusion" was produced prior to the appearance of the Pleurodira, excluding *Proterochersis* as a basal pleurodire and regarding *Proterochersis* as sister taxa of Casichelydian turtles. Others disagree with this statement (Gaffney, personal commun., 1997; Lapparent de Broin, personal commun., 1997) and consider *Proterochersis* to be a basal pleurodire, suggesting that Rougier et al. (1995) misinterpreted the pelvis-shell linkage condition present in *Palaeochersis*. In this work we assume the traditional position until the condition of the *Palaeochersis* pelvis attachment can be adequate explained.



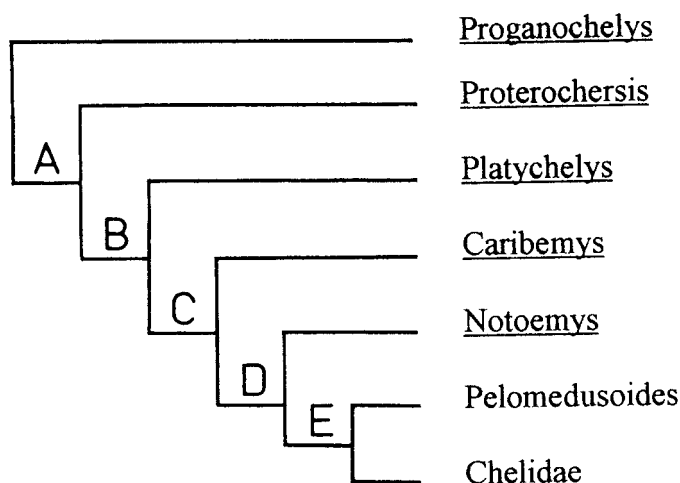


FIGURE 7—Cladogram showing phylogenetic relationships of *Caribemys*.

Character and character states are listed in appendix. Node A: 8(1), 10(1), 28(1). Node B: 7(1), 15(2), 21(1), 23(1), 24(1), 25(2), 27(1), 29(1), 30(1). Node C: 11(2), 17(1). Node D: 3(1), 4(1), 12(2), 13(1), 26(1). Node E: 1(1), 2(1), 5(1), 6(1), 9(2), 14(1), 16(1), 18(3), 19(2), 20(1), 22(1).

In the holotype of *Caribemys oxfordiensis* n. gen. and sp., remains of the sutural attachment between the pelvis and shell could be recognized 1) in the contact by suture on the right pubis; and 2) in the dentate attachment on the dorsal surface of the ilium.

Two taxa of Upper Jurassic pleurodire have been discovered previously. *Platycheilus orbendorferi* Wagner, 1853, in Laurasia, in the Kimmeridgian of Solothurn (Switzerland), Guimarota (Portugal) and the Tithonian of Kelheim (Germany) (Wagner, 1953; Bram, 1965; Broin, 1988); and *Notoemys laticentralis* Cattoi and Freiberg, 1961, recorded in Gondwana, in the Tithonian of Neuquén Basin (Argentina) (see Cattoi and Freiberg, 1961; Wood and Freiberg, 1977; de la Fuente and Fernández, 1989; Fernández and de la Fuente, 1993, 1994; Gasparini and Fernández, 1997). The main shell differences among *Caribemys* and these other two Jurassic pleurodires (Table 1) justify a generic distinction for the Cuban Oxfordian turtle (see Fig. 6).

A detailed discussion of the phylogeny of the Pleurodira is beyond the scope of this study; however, a preliminary cladistic analysis based in Gaffney (1988), Gaffney and Meylan (1988) Gaffney et al. (1991), Fernández and de la Fuente (1994); Meylan (1996); and Lapparent and Murelaga (1999), was carried out in order to determine the position of *Caribemys oxfordiensis*. The new genus and species described above is only known from a single shell and an incomplete cervical vertebra. The absence of a skull in the holotype of *Caribemys* (as well as in *Platycheilus* and *Proterochersis*), and consequently the cranial data, does not weaken the hypothesis proposed herein, which is based mainly on postcranial characters. To provide a preliminary assessment of its relationships, a data matrix containing 30 osteological characters across seven taxa was constructed (see appendix). The data matrix was analyzed using Hennig86 version 1.5 applying the "i.e." option. To calculate consistency (C.I.) and retention (R.I.) indices, autapomorphies were excluded. The characters were treated as non-additive (=unordered) to preclude an a priori polarity assumption. The trees were rooted by using *Proganochelys* as outgroup. The analysis of the data matrix yielded one most parsimonious tree with a tree length of 39, a C.I. of 0.97 and a R.I. of 0.96. The new taxon is placed as the sister taxa of the *Notoemys* + *Eupleurodira* (see below).

This analysis (see Fig. 7) suggests that the Pleurodira (Node

A) form a natural group defined by: pelvis narrower than posterior lobe; pelvis sutured to the shell and posterior plastral lobe bifid. Within the Pleurodira, *Caribemys* appears as the sister group of *Notoemys* and the *Eupleurodira*. This clade (Node C) is supported by the following characters: ilium scar does not extend below the peripheral bones, and supramarginal scutes absent. The unnamed node formed by *Notoemys* and the *Eupleurodira* is characterized by the following synapomorphies: quadrate with medial process extending medially to braincase below cranioquadrate space; hyomandibular branch of facial nerve lies in its own canal; ilium suture shape oval; sacral ribs reduced; entoplastral process reduced to entoplastral posterior length. It is worthy to remark that cranial characters, although known in *Notoemys* and *Eupleurodira*, are unknown in *Caribemys*, *Platycheilus*, and *Proterochersis*.

Gasparini (Chong and Gasparini, 1972, 1976; Gasparini, 1978; Gasparini and Chong, 1977) already suggested a close affinity between the Jurassic marine herpetofauna of the Neuquén Basin (Central-Western Argentina) and those of the Western Tethys. Based on the paleoposition of the continents, Gasparini (1977) proposed that the most important seaways for marine reptiles linking both faunas was the early Caribbean seaway (=Hispanic Corridor of Bartok et al., 1985). The affinities of the invertebrate fauna from west-central South America and the West Tethys (Damborenea and Manceñido, 1979; Manceñido and Dags, 1992; Riccardi, 1991) help to support this hypothesis as do later papers on the marine reptile faunas (i.e., Gasparini, 1980, 1985, 1992; Gasparini and Fernández, 1996, 1997). However, direct evidence of marine reptiles using the Caribbean seaway during Late Jurassic is scarce. Consequently, the descriptions of ichthyosaur, plesiosaur, crocodile, and turtle remains (see Fernández and Iturralde Vinent, 2000; Gasparini, personal commun., 1999; herein) from the Oxfordian of the Guaniguanico terrane in western Cuba is of particular interest as they fill a paleobiogeographic gap. The Guaniguanico terrane originated at the Caribbean borderland of the Maya block (Yucatan peninsula) during the Jurassic period, and was transported to the present day position during the early Tertiary (Iturralde-Vinent, 1994).

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## APPENDIX I

Character, character states, and character matrix used to determine the phylogenetic position of *Caribemys*. Characters 2–4, 10 and 17 were selected from Gaffney et al. (1991), character 8, 9, 11, 13, 15, 18, 20, 23, 26, 28–29 were selected from Lapparent and Murelaga (1999); characters states in 7, 27 were modified from Gaffney et al. (1991) and characters states in 1, 14, 16, 21, 22 were modified from Lapparent and Murelaga (1999).

1. Skull emargination  
absent (0); present (1)
2. Processus throchlearis pterygoidei  
absent (0); present (1)
3. Quadrate with ventral process extending medially to contact braincase below cranioquadrate space  
absent (0); present (1)
4. Hyomandibular branch of facial nerve  
lies within canalis cavernosum (cranioquadrate passage) (0); lies in its own canal (1)
5. Shortening of the posterior descending opisthotic process  
absent (0); present (1)
6. Posterior descending opisthotic process closing the recessus scalae tympani  
absent (0); present (1)
7. Cervical vertebrae  
lack formed central articulations (0); well formed central articulations (1)
8. Pelvis width  
pelvis wider than posterior lobe (0); pelvis narrow than posterior lobe (1)
9. Thyroid fenestra  
two small and separated openings (0); two larger openings united (1); united as one large openings (2)
10. Pelvis-Shell attachment  
ligamentous link (0); sutured to shell (1)
11. Ilium scar  
absent (0); extends below the peripheral bones (1); does not extend below the peripheral bones (2)
12. Ilium suture shape  
absent (0); narrow and pointed posteriorly (1); ovaloid (2)

- 13. Sacral rib  
well developed (0); reduced (1)
- 14. Nuchal bone  
width  $\gg$  length (0); width  $>$  or  $=$  length (1)
- 15. Pygal notch  
large (0); reduced (1); absent (2)
- 16. Cervical scute  
width  $>$  length (0); width  $<$  length or absent (1)
- 17. Supramarginals  
present (0); absent (1)
- 18. First thoracic ribs  
unreduced and separated from rib 2 (0); unreduced and laterally linked to rib 2 (1); laterally partly reduced in size and laterally linked to rib 2 (2); much reduced in size to a thin medial part and medially linked to rib 2 (3)
- 19. Costo-vertebral tunnel  
wide and still wider anteriorly and posteriorly (0); wide and slight posterior reduction in width (1); all along reduced in width (2)
- 20. Neural series  
irregular series (0); regular series or absence of neurals (1)
- 21. Axillary process contact with pleural 1  
absent (0); present (1)
- 22. Inguinal process contact with pleural 5  
no contract (0); contract (1)
- 23. Epiplastral reduction  
long posterior part (0); reduced posterior part (1)
- 24. Epiplastral process present (0); absent (1)
- 25. Entoplastral participation in anterior border  
ventral and dorsal participation (0), ventral participation (1); no participation (2)
- 26. Posterior entoplastral process  
unreduced (0); reduced to posterior limit of entoplastron (1)
- 27. Mesoplastra  
midline contact (0); without midline contact (1)
- 28. Posterior lobe rounded (0); bifid (1)
- 29. Intergular number  
two (0); one (1)
- 30. Inframarginal scutes  
present (0); absent (1)

Taxa	Characters														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Proganochelys</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Proterochersis</i>	?	?	?	?	?	?	?	1	0	1	1	1	0	?	1
<i>Platycheilus</i>	?	?	?	?	?	?	1	1	1	1	1	1	0	0	2
<i>Caribemys</i>	?	?	?	?	?	?	1	1	?	1	2	1	?	0	?
<i>Notoemys</i>	?	?	1	1	0	0	1	1	?	1	2	2	1	0	2
<i>Pelomedusoides</i>	1	1	1	1	1	1	1	1	2	1	2	2	1	1	2
Chelidae	1	1	1	1	1	1	1	1	2	1	2	2	1	1	2

Taxa	Characters														
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Proganochelys</i>	0	0	0	0	?	0	0	0	0	0	0	0	0	0	?
<i>Proterochersis</i>	0	0	0	0	?	0	0	0	0	1	0	0	1	0	0
<i>Platycheilus</i>	0	0	1	1	0	1	1	1	1	2	0	1	1	1	1
<i>Caribemys</i>	?	1	?	?	0	1	0	1	1	2	?	1	?	1	1
<i>Notoemys</i>	0	1	2	1	0	1	0	1	1	?	1	1	1	1	1
<i>Pelomedusoides</i>	1	1	3	2	1	1	1	1	1	2	1	1	1	1	1
Chelidae	1	1	3	2	1	1	1	1	1	2	1	1	1	1	1