A NEW PTEROSAUR FROM THE JURASSIC OF CUBA

by ZULMA GASPARINI, MARTA FERNÁNDEZ *and* MARCELO DE LA FUENTE

ABSTRACT. *Cacibupteryx caribensis* gen. et sp. nov. is a new pterosaur of the family Rhamphorhynchidae found in western Cuba, in rocks of the Jagua Formation (Middle–Upper Oxfordian). The holotype, a skull and part of the left wing, is one of the few Jurassic pterosaurs that is well preserved in three dimensions. The new taxon shares characters with early and late Jurassic pterosaurs, and is one of the few late Jurassic taxa from western Laurasia and Gondwana. Furthermore, *Cacibupteryx* joins *Nesodactylus hesperius* Colbert from Cuba, and *Sordes pilosus* Sharov, from Kazakhstan as the most complete pterosaur recorded from the Middle–Upper Oxfordian. *Cacibupteryx caribensis* is one of the largest Jurassic pterosaurs known, and its skull possesses several distinct characters, including relatively broad roof elements (mainly frontal and parietal bones), a jugal with a prominent recess, occipital table trapezoidal in shape with the maximum width between the quadrate bones, and a small fenestra located in the posterior part of the pterygoid bones. In the Oxfordian, the Caribbean Corridor separated Laurasia and western Gondwana. The diversity of the marine herpetofauna found in the Jagua Vieja Member (Jagua Formation), and of teleostean fish, confirms that the corridor was an effective seaway over which flew at least *Nesodactylus* and *Cacibupteryx*.

KEY WORDS: Pterosauria, Rhamphorhynchidae, Cuba, Middle–Upper Oxfordian, Upper Jurassic.

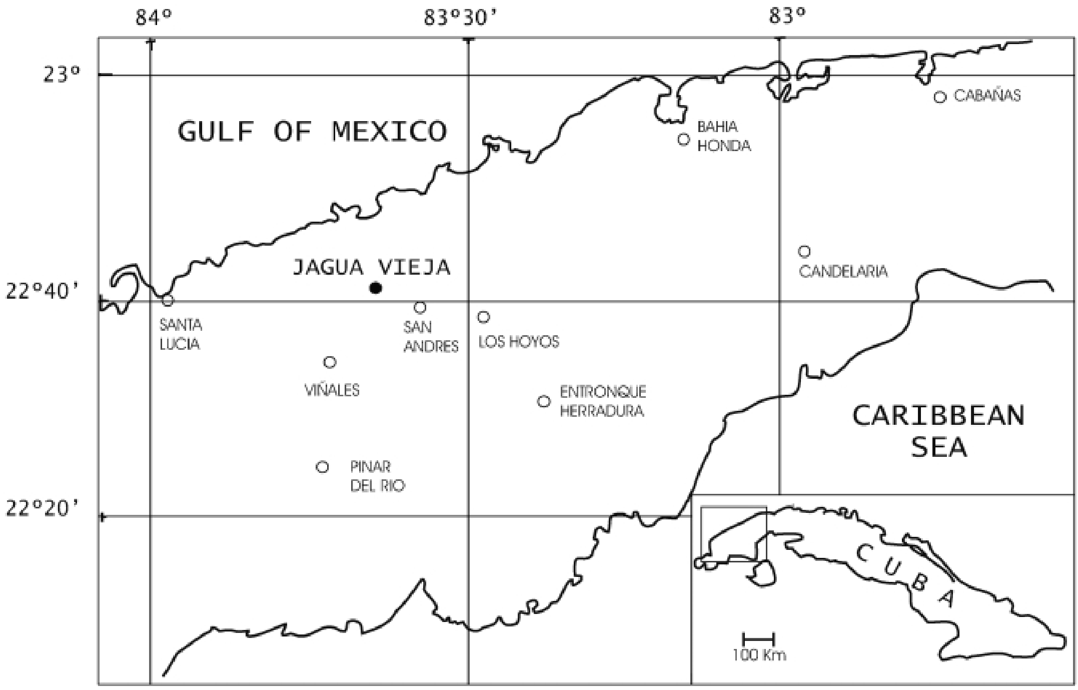
THE record of Jurassic pterosaurs in western Laurasia and Gondwana is relatively poor: specimens are rare and generally incomplete (Galton 1981; Padian 1984; Jensen and Padian 1989; Wellnhofer 1991; Gasparini *et al*. 1995; Clark *et al*. 1998; Harris and Carpenter 1998). Pterosaurs are almost unknown from the Upper Oxfordian, except for *Nesodactylus hesperius* Colbert, 1969, *Sordes pilosus* Sharov, 1971 and remains from France (Buffetaut *et al*. 1985; Buffetaut and Guibert 2001) and probably, Patagonia (Rauhut and Puerta 2001; Rauhut *et al*. 2001). Both situations highlight the importance of the Oxfordian pterosaurs found in western Cuba.

Colbert (1969) described the disjointed and incomplete skeleton of the first pterosaur found in Cuba, and referred it to a new taxon, *Nesodactylus hesperius*. This specimen (AMNH 2000) was found 10 km north-east of Viñales, Pinar del Río Province, in a horizon of the Jagua Formation that contains concretions in which invertebrates, fish and marine reptiles are frequently found (Iturralde-Vinent and Norell 1996). Colbert (1969) referred the new pterosaur to the Rhamphorhynchidae. Unwin (1995, 2003) and Unwin *et al.* (2000) confirmed the monophyly of this family and according to its definition *Nesodactylus* belongs to this clade.

Recently, the skull and some forelimb bones of a second pterosaur were found by local farmers in Jagua Vieja, also Pinar del Río Province (Text-fig. 1). It was recovered from levels assigned to the Middle–Upper Oxfordian of the Jagua Vieja Member of the Jagua Formation (Iturralde-Vinent and Norell 1996). At the beginning of 2002, during a palaeontological survey directed by Manuel Iturralde-Vinent (Museo Nacional de Historia Natural, Cuba) a third pterosaur (MNHNCu 3806P) was found at the same stratigraphic level as the new pterosaur described here, but at the Los Hoyos locality. Unfortunately, this specimen is indeterminate because of the erosion of the concretion in which it is preserved.

The purpose of this paper is to describe and name a new rhamphorhynchid pterosaur from Cuba. It demonstrates a greater level of pterosaur diversity in the Late Jurassic, and particularly in the Middle–Late Oxfordian, than previously supposed.

The holotype of the new pterosaur was prepared mechanically in the Departamento Paleontología Vertebrados of the Museo de La Plata, Argentina.



TEXT-FIG. 1. Map of the Viñales Valley area to show type locality for *Cacibupteryx caribensis*, IGO-V 208.

SYSTEMATIC PALEONTOLOGY

Order PTEROSAURIA Kaup, 1834
Family RHAMPHORHYNCHIDAE Seeley, 1870

Genus CACIBUPTERYX gen. nov.

Derivation of name. *Cacibu*, prefix, from the Taino language spoken by the aboriginals of Cuba (Tejera 1977) meaning lord of the sky; suffix *-pteryx* (Greek) wing.

Type and only known species. *Cacibupteryx caribensis* sp. nov.

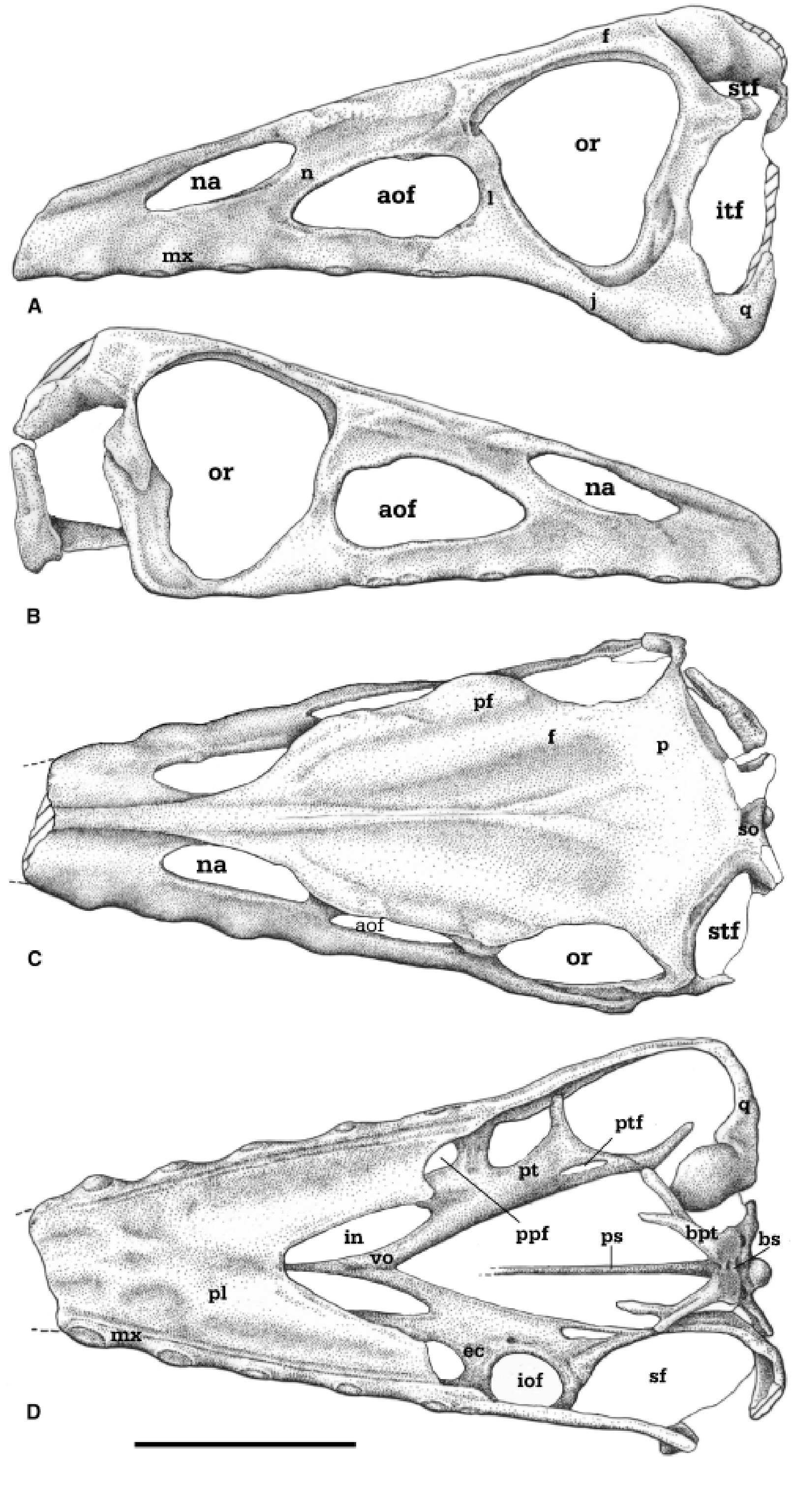
Diagnosis. As for the type and only known species.

Cacibupteryx caribensis gen. et sp. nov.

Text-figures 2–4

Derivation of name. Latin, *caribensis*, alluding to Caribbe.

TEXT-FIG. 2. *Cacibupteryx caribensis* gen. et sp. nov., IGO-V 208, holotype. A, skull in left lateral view. B, right lateral view. C, dorsal view. D, ventral view. Abbreviations: aof, antorbital fenestra; bpt, basipterygoid; bs, basisphenoid; ec, ectopterygoid; f, frontal; in, internal naris; iof, infraorbital fenestra; itf, infratemporal fenestra; j, jugal; l, lachrymal; mx, maxilla; n, nasal; na, naris; or, orbit; p, parietal; pf, prefrontal; pl, palatine; ppf, postpalatal fenestra; pt, pterygoid; ptf, posterior pterygoid fenestra; ps, parasphenoid; q, quadrate; sf, subtemporal fenestra; so, supraoccipital; stf, supratemporal fenestra; vo, vomer. Scale bar represents 5 cm.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Holotype. IGO-V 208, Museo Mario Sánchez Roig, Instituto de Geología y Paleontología, La Habana, Cuba. Incomplete but three dimensional, uncrushed skull, without mandibles, distal end of the left ulna, fragments of the left radius, left phalanx 1 of the wing-finger, and phalanx 4 of the wing-finger(?). The bones of the forelimb lay against the palate IGO-V 208 buried in sediment; thus all are considered to belong to a single individual.

Locality and horizon. Mogote Jagua Vieja, north-east of Viñales, Viñales Valley, Pinar del Río Province, Cuba (Text-fig. 1); Jagua Vieja Member of the Jagua Formation (Middle–Upper Oxfordian) (Iturralde-Vinent and Norell 1996).

Diagnosis. Rhamphorhynchid pterosaur with broadly expanded skull roof elements (mainly frontal and parietal bones). Subcircular orbits with their ventral half more compressed. Orbital ventral margin level with the dental border. The section of the jugal that forms the postero-ventral border of the orbit bears a well-developed pocket-like recess. A small fenestra is located in the posterior part of the pterygoid.

DESCRIPTION

Skull

The skull is partially complete, three-dimensionally preserved, with a slight displacement to the right. Sutures are not visible. This may be either because in other specimens of adult pterosaurs these bones are fused together, or because of fossilisation effects. The anterior part of the skull in front of the nares is missing. The orbit is the largest opening of the skull (Table 1). The skull roof is even, rising smoothly backwards; it is remarkably wide between the orbits, with a low central crest bordered on either side by smooth depressions. The lateral walls of the rostrum up to the posterior border of the external nares flare downwards and outwards but behind the nares, they are vertical. Consequently, in dorsal view the antorbital fenestra is hardly visible. The occipital is trapezoid-shaped with the quadrates directed outwards. The palate is extensively fenestrated.

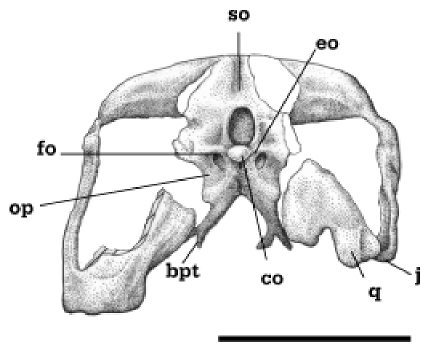
The premaxillae of the holotype (IGP-V 208) form a bar separating the nares, and extend backward as a smooth ridge between the frontals. Behind the nares the roof of the rostrum and skull expand so that the antorbital fenestrae and orbits are hardly visible in dorsal view. The large frontal expansion obscures the lachrymals in this view. In front of the orbits there are smooth lateral expansions probably formed by the prefrontals. The frontal-parietal suture cannot be determined. The parietal region is the most elevated and convex part of the skull roof. The posterior border of the supratemporal fenestrae has not been preserved, but based on the preserved part of the squamosal, the supratemporal fenestrae were probably subcircular in shape with the longest axis transverse to the sagittal axis of the skull, and predominantly dorsal since they are little exposed in lateral view.

The maxilla is slightly festooned in lateral view; each arch belongs to one alveolus. The nares are longer than high (Table 1) and placed dorsolaterally. A wide and even bar, formed by the nasals and maxillae, separates the nares from the antorbital fenestrae. The nasal, located in the posterodorsal corner of the nares, is exposed in both dorsal and lateral views.

The antorbital fenestra is longer than high and its anterior border has a more acute angle than its posterior border, which is slightly concave. There is a slight projection into the fenestra on the posterior third of the dorsal margin.

The orbits are almost vertical; thus they are little exposed in dorsal view. The orbits are subcircular with a constriction caused by a slight posterior expansion of the lachrymal, and on the opposite margin, by a greater anterior expansion of the jugal. The lower border of the orbit is much more concave than the upper border. The jugal just below the orbit is rather slender and, hence, the lower orbital margin lies below the level of the antorbital fenestra. The section of the jugal that forms the postero-ventral border of the orbits bears a well-developed, pocket-like recess. The borders of the jugal, quadratojugal and quadrate are uncertain. Fragments of each quadrate close the infratemporal fenestrae posteriorly. The quadrates are subvertical in position with the posterior border of the quadrate inclined slightly backward forming an angle of approximately 107 degrees with the ventral margin of the skull.

The skull is trapezoid-shaped in occipital view, narrower dorsally than ventrally with an almost flat roof. The maximum width of the skull is reached between the ventral part of the quadrates. The supraoccipital is triangular and recessed in the central region. It is exposed in dorsal and occipital views. A fragment of the left parietal marks the posterior border of the supratemporal fenestra. The occipital condyle is small, while the foramen magnum is suboval and twice as high as the condyle. On a vertical, but recessed, plane the exoccipital is fused externally with the opisthotics, and internally they form the lateral margins of the foramen magnum. From the base of the condyle, the exoccipitals change their orientation, slanting down and forward. The foramen ovale, next to the contact with the basioccipital, is bordered internally by the exoccipital and externally by the opisthotic. The opisthotic is columnar with concave lateral margins. Beneath the condyle, the basioccipital extends as a relatively narrow furrow between the



TEXT-FIG. 3. *Cacibupteryx caribensis* gen. et sp. nov., IGO-V 208, holotype. Skull in occipital view. Abbreviations: bpt, basipterygoid; co, condyle; eo, exoccipital; fo, foramen ovale; j, jugal; op, opisthotic; q, quadrate; so, supraoccipital. Scale bar represents 5 cm.

exoccipitals. Two projections of the basipterygoids contact the basioccipital and exoccipitals. The left quadrate, though incomplete, borders the infratemporal fenestra.

In palatal view the maxillae are narrow and undulate laterally where they expand around the alveoli. There are six preserved alveoli on both sides. Although incomplete it is likely that there were fewer than 11 pairs of teeth in the rostrum. The anteroposterior diameter of each alveolus is longer than the transverse, and the intra-alveolar spaces widen toward the posterior part of the maxilla, except for the last two alveoli, which are close to each other. The last alveolus is level with the ectopterygoid. The rostrum of the holotype is incomplete; thus, the true length of the skull cannot be estimated.

The palatines occupy most of the anterior part of the palate, surrounding the internal nares, and forming the anterior border of the postpalatinal fenestrae.

The ectopterygoids, located between the maxillae and pterygoid, are flat and form the posterior margin of the post-palatinal fenestra, and the anterior margin of the infraorbital fenestra. The vomer is a narrow bar tapering anteriorly that, together with the anterior end of the pterygoids, divides the internal nares, which are very large.

The pterygoid bifurcates anteriorly; the anterior ramus contacts the vomer while the external ramus fuses with the palatine, forming the internal margin of the post-palatinal fenestra. It contacts the ectopterygoid, almost encloses the infraorbital fenestra, and has a lateral bar that contacts the jugal, separating the infraorbital and subtemporal fenestrae. The posteromedial part of the pterygoid bears a small, elongate fenestra.

The palatal part of both quadrates is incomplete. The parasphenoid extends forward to a point level with the last alveolus, but is twisted to the right by post-mortem deformation. The basipterygoids lie ventral to the basioccipital, and bifurcate anteriorly.

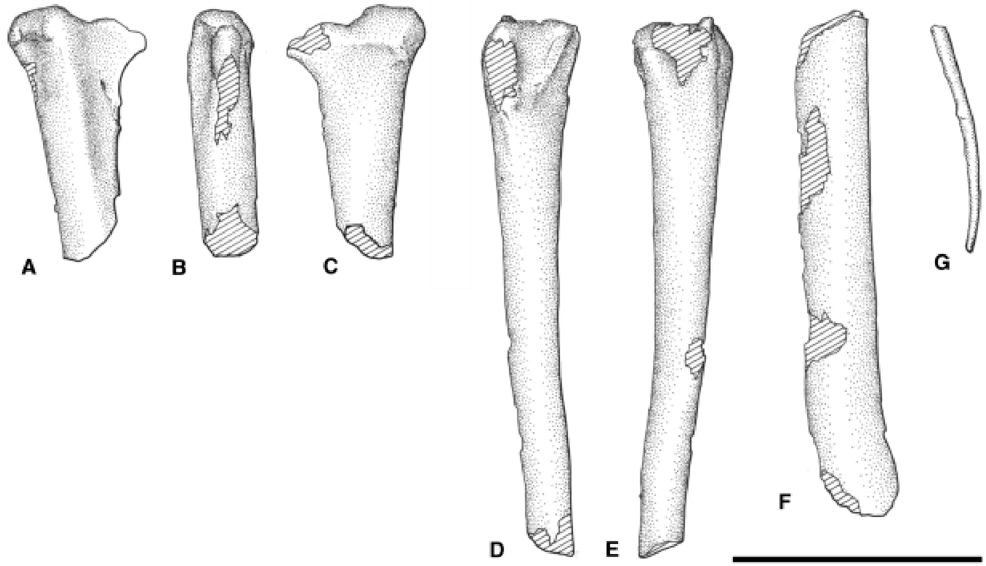
Forelimb

The radius and ulna are both from the left wing and are partially preserved. The ulna, as usual in pterosaurs, is the strongest bone. Only the distal articular surface and about one-third of the shaft of a left ulna are preserved. The shaft is oval in cross section. The anterior surface of this part of the bone is characterised dorsally by a strong, blunt crest. The distal articular area is dorsoventrally elongate and irregular in shape. Remains of a large condyle forming the dorsal half of this extremity is recognised. Unfortunately the diagnostic convex tubercle and the concave fovea carpalis are not identified.

The distal end and approximately two-thirds of the shaft of a left radius are preserved. The shaft is oval in cross section. This bone is narrow, as usual, and has a tall, narrow articulation with two large condyles oriented at an acute angle to each other.

A short section of the distal part of the left wing phalanx 1 is preserved. Its shaft seems to be heavily built and dorsoventrally flattened, and is subtriangular in cross section. No groove could be identified on its rear margin. A small elongated and slightly twisted bone is partially preserved. This element is tentatively identified as a distal fragment of the left wing-finger phalanx 4.

Remarks. The holotype (skull and left wing) is uncrushed and three-dimensional. This kind of preservation is unusual in Jurassic pterosaurs as most of them are preserved in two dimensions, compressed in limestones (Wellnhofer 1991). Usually the occipital and palatal views are hidden in pterosaurs preserved in two dimensions, restricting comparisons with IGO-V 208. Sutures of the skull are not visible either because in other specimens of adult pterosaurs these bones are fused together, or because of fossilisation



TEXT-FIG. 4. *Cacibupteryx caribensis* gen. et sp. nov., IGO-V 208, holotype. A, distal fragment of the left ulna in anterior view. B, distal fragment of the left ulna in posterior view. C, distal fragment of the left ulna in ventral view. D–E, distal fragment of left radius in anterior and posterior view. F, fragment of the wing, phalanx 1. G, distal fragment of left wing, phalanx 4 . Scale bar represents 5 cm.

effects. It is noteworthy that sutures of other marine reptiles from the same stratigraphic level (Gasparini and Iturralde-Vinent 2001; Gasparini *et al*. 2002) have not been preserved either; consequently, diagenetic processes may also act to efface sutures.

RELATIONSHIPS

The Rhamphorhynchidae are represented in the fossil record from the Lower Jurassic (Toarcian) to the Upper Jurassic (Tithonian) (Unwin *et al*. 2000). The last episode of this long history is well documented by Tithonian rhamphorhynchids from Solnhofen, whereas Oxfordian and Kimmeridgian forms are poorly known (Wellnhofer 1975*a–c*, 1991; Bakhurina and Unwin 1995; Bennett 1995). In this context, the holotype of *Cacibupteryx caribensis* represents the best preserved Middle–Late Oxfordian pterosaur skull found so far.

Cacibupteryx caribensis is referred to the Rhamphorhynchidae (*sensu* Unwin in press) based on the reduction in size of the nares and antorbital opening compared to the orbit, the estimated tooth count of 11 pairs or less, and downward curvature of the posterior ventral profile of the skull. Unfortunately, in *Cacibupteryx* several of the synapomorphies diagnostic of the subfamilies Rhamphorhynchinae and Scaphognathinae have not been preserved (i.e. anterior tip of the snout, mandibles and complete wing-finger). These facts hampered further resolution of *Cacibupteryx* within the family. It exhibits characters of both subfamilies as defined by Unwin (2003). Thus, it shares with the Rhamphorhynchinae an antorbital fenestra that is twice as long as it is deep, but lacks synapomorphies supporting this taxon such as the location of the antorbital fenestra below the nares and a wing-finger with a grooved rear margin.

In *Cacibupteryx* the nares and antorbital fenestrae are somewhat reduced when compared with those of most Liassic rhamphorhynchids such as *Parapsicephalus* Arthaber, but they are not so reduced as in the Tithonian *Rhamphorhynchus* H. von Meyer.

Cacibupteryx shares with the Liassic *Dorygnathus* Wagner a relatively small degree of inclination of the infratemporal fenestra and quadrate, an infratemporal fenestra that is not visible in dorsal view, and the absence of an abrupt elevation of the skull roof in the parietal area. In addition, it also shares with both *Dorygnathus* and *Rhamphorhynchus* the slight exposure of the antorbital fenestra in dorsal view and the

TABLE 1. Measurements of skull of *Cacibupteryx caribensis* gen. et sp. nov., IGO-V 208.

Skull	Measurement (mm)	Skull	Measurement (mm)
Preserved skull length	154	Estimated maximum dorsal width of occiput	70
Height of skull in front of the orbits	39	Estimated maximum ventral width of occiput	78
Height of skull behind the orbits	67	Length of internal naris	32
Length of external naris	34	Width of internal naris	7
Height of external naris	12	Length of interpterygoid fenestra	67
Length of antorbital fenestra	39	Maximum width of interpterygoid fenestra	31
Maximum height of antorbital fenestra	18	Length of intrapterygoid fenestra	11
Height of orbit	45	Width of intrapterygoid fenestra	2
Maximum length of orbit	39		

slender jugal bar below the orbit. Likewise, it shares with *Parapsicephalus* and *Scaphognathus* Wagner from the Lower Jurassic of the United Kingdom and the Tithonian of Solnhofen, and with *Sordes* from the Oxfordian of Kazakhstan, the ventral position of the mandibular articulation with respect to the maxillary alveoli. The trapezoidal occiput of *Parapsicephalus* (Wellnhofer 1991, p. 32) is remarkably similar to that of *Cacibupteryx*. In this regard, it should be noted, however, that the occiput is exposed and/or has been illustrated in only a few taxa. Nevertheless it is remarkably different from that of *Rhamphorhynchus* (Wellnhofer 1975*a*, fig. 4a), which shows an occipital table with rounded margins and the quadrate medially oriented. In addition, *Cacibupteryx* is different from early rhamphorhynchids such as *Dorygnathus*, *Parapsicephalus* and from the 'rhamphorhynchoid' *Rhamphinion* Padian, because in these taxa the jugal bar that surrounds the orbit ventrally is wide (Padian 1984), whereas in *Cacibupteryx* it is almost as narrow as in *Rhamphorhynchus*. *Cacibupteryx* shares with *Rhamphorhynchus* the subequal size of the nares and the antorbital fenestrae, which are smaller than the orbits (Bennett 1995); the position of the ventral margin of the orbit below the level of the maxillary alveoli, a character that is linked to the narrowing of the jugal; and the extensive fenestration of the palate. However, *Rhamphorhynchus* can be differentiated from *Cacibupteryx* by the strong ventral inclination of the quadrate and infratemporal fenestra, the laterodorsal exposure of the supratemporal fenestra, the domed shape of the occiput caused by the medial direction of the quadrates, and the absence of the small fenestra in the posterior part of the pterygoid.

The only elements preserved that may be compared between the holotype of *Nesodactylus* and *Cacibupteryx* are the quadrate, and the distal ends of the left radius and ulna. There is no correspondence in either size or shape between these elements. The quadrates of *Nesodactylus* and *Cacibupteryx* have particularly distinctive features. Thus, the posterior border of the quadrate and the ventral process meet at almost a right angle in *Nesodactylus*. When the quadrates of both taxa are overlapped at the same scale, they do not match. In *Cacibupteryx* the angle formed by the posterior border and the ventral edge is more obtuse (approximately 107 degrees). In *Nesodactylus* the ventral border of the quadrate has an embayment which is absent in *Cacibupteryx.* The distal ends of the ulna of *Cacibupteryx* and *Nesodactylus* are also quite distinctive: in *Cacibupteryx* there is a strong, blunt crest on the anterior surface whereas in *Nesodactylus* (according to Colbert 1969, fig. 2) this crest is sharper and shorter; in *Cacibupteryx* the ventral area of the distal end is more expanded than in *Nesodactylus*.

OXFORDIAN REPTILES IN THE CARIBBEAN CORRIDOR

A large number of bony fish (Arratia and Schultze 1985) and marine reptiles (Iturralde-Vinent and Norell 1996) have been found in Middle–Upper Oxfordian levels of the Jagua Formation of western Cuba. These sediments were deposited in an oceanic seaway located between North and South America, named the Caribbean Corridor. The opening of the Caribbean Corridor represents an important palaeoceanographic event, since it resulted in a deep circum-equatorial oceanic circulation that linked the biotas of West

Tethys, Central America and the Eastern Pacific (Iturralde-Vinent and McPhee 1999; Iturralde-Vinent 2000). The study of the herpetofauna found in the Jagua Formation has revealed that several marine reptiles, most of them indicators of near-shore environments, lived in, or used this corridor as, a seaway. This is the case of the numerically dominant plesiosauroids, among them *Vinialesaurus caroli*, referable to the Cryptoclididae (Gasparini *et al*. 2002), and a pleurodiran turtle, *Caribemys oxfordiensis* (de la Fuente and Iturralde-Vinent 2001). Other pelagic predators used this seaway, including ophthalmosaurian ichthyosaurs (Fernández and Iturrale-Vinent 2000), metriorhynchid crocodiles (Gasparini and Iturralde-Vinent 2001) and a middle-sized pliosaur. The amount and diversity of bony fish justifies the diversity of marine predators and pterosaurs in this seaway. Likewise, the presence of at least two different taxa of pterosaurs reinforces the hypothesis that the Jagua Vieja Member corresponds to near-shore environments (Iturralde-Vinent 2000).

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