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A Jurassic Pterosaur from Cuba

By Edwin H. Colbert[1]

INTRODUCTION

Two or three years ago Richard Lund, then a graduate student at Columbia University and now at the Carnegie Museum in Pittsburgh, was etching a piece of Jurassic rock to expose any fossil fishes that it might have contained. The rock had been collected in Cuba a half century before by Barnum Brown, for many years Curator of Fossil Reptiles at the American Museum of Natural History, and came from a formation that was a known source for Jurassic fishes. In this case, however, the etching revealed not the remains of fish but a concentration of delicate reptilian bones which on examination proved to be those of a pterosaur. Consequently the material was submitted to the present writer for study.

Until the present time, the only published indication of Jurassic pterosaurs in the Western Hemisphere has been based on a single fragmentary bone, a right fourth metacarpal of a pterosaur, from the Morrison Formation at Como Bluff, Wyoming. The bone, originally described by Marsh under the name of *Pterodactylus montanus,* subsequently was placed by the same author in a new genus, *Dermodactylus.* It was slight evidence for the presence of an order of reptiles in the Western Hemisphere during Jurassic time.

Recently I was informed by José Bonaparte, of the Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina, that

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pterosaur bones, probably of Jurassic age, have been found in Argentina. These are as yet undescribed.

I wish to express my appreciation to Dr. Lund for his interest in, and his work devoted to, the preparation of the fossil described in the present paper. My thanks and appreciation are extended also to Dr. John Ostrom of Yale University, for making available to me the type of *Dermodactylus montanus* for study and comparisons, and to Dr. Craig Black of the Carnegie Museum, for lending a valuable skeleton of *Campylognathoides.*

The illustrations in this paper were prepared by Mr. Chester Tarka and Mr. Michael Insinna, and for their separate skills and assistance I wish to express my great appreciation. Valuable assistance in the preparation of the figures was given by Miss Marlyn Mangus.

Abbreviations of Institutions

A.M.N.H., the American Museum of Natural History
C.M., Carnegie Museum, Pittsburgh
Y.P.M., Peabody Museum of Natural History, Yale University

GEOLOGIC AND GEOGRAPHIC OCCURRENCE

During the years from 1911 to 1919, Barnum Brown made five trips to Cuba to study the geology and to collect fossils from that island. His first trip was made at the invitation of Carlos de la Torre, of the University of Havana, to investigate the occurrence of Pleistocene ground sloths in thermal springs at a locality northwest of Cienfuegos. While in Havana, Brown was given some Jurassic ammonites, collected near Viñales in western Cuba. De la Torre had, during the previous two years, published three papers announcing the occurrence of Jurassic strata in western Cuba, and describing some of the ammonites that had been collected from these beds.

Brown thus became interested in the Mesozoic geology and paleontology of western Cuba, and during four subsequent trips to the island he concentrated his efforts in this region. During the field season of 1918, Brown discovered beds of Oxfordian age near Viñales, and from these sediments he collected the matrix containing the pterosaur here described.

Cretaceous rocks extend through the length of Cuba, but apparently Jurassic sediments are limited to the western tip of the island, specifically to the Province of Pinar del Río. In this region the Jurassic rests upon pre-Oxfordian schists and shales, and in turn are covered by Cretaceous sediments. Oligocene, Miocene, and Pleistocene beds succeed the Cretaceous strata.

Four major divisions of the Jurassic have been recognized in the Province of Pinar del Río, namely, the Oxfordian, Lusitanian, Kimmeridgian, and Portlandian. The sequence, some 2000 feet in thickness, is made up of a series of limestones, generally black, blue-black, and gray in color, cut by calcite seams, and marked by intercalated shales, especially in the higher portions of the section. Conglomerates occur at the bases of the Portlandian and Kimmeridgian sections, and black, bituminous concretions are found throughout the extent of the Jurassic succession.

The age determinations and correlations of the Jurassic beds of Cuba, as based particularly on the ammonites found in them, were established in a series of papers by O'Connell, and one by Brown and O'Connell (1922). A few statements from this last-named publication give the reasons for the correlations that had been established for the Jurassic beds of Cuba.

"When the ammonite fauna of Cuba is compared with that of Europe, there is found to be a sufficiently close resemblance to indicate that both belong to the same geographical province—the Atlantic. A small number of cosmopolitan European species also occur in Cuba, while nearly all of the forms in the latter region show affinities with European species, thereby proclaiming themselves to be merely geographic variants" (Brown and O'Connell, 1922, pp. 656–657).

"So far, there has been found in the Cuban fauna only one of the European zonal fossils, namely, *Aspidoceras perarmatum* (Sowerby), [diagnostic for the Oxfordian] but, many of the species which are commonly associated with the zone fossils in Europe do occur in Cuba, so it has been possible to recognize the presence of the upper Oxfordian, the two lower zones of the Lusitanian, the lower Kimmeridgian, and the upper Portlandian" (Brown and O'Connell, 1922, p. 660).

Our interest centers on the lowest Jurassic as exposed in Cuba, because at the base of the Oxfordian sequence Brown found fishes and marine reptiles, along with the ammonites that characterize these sediments. The specimen described in this paper was found about 4½ miles, or about 7 kilometers, east of a mine known as Constancia, which in turn was about 5 miles, approximately 8 kilometers, north of Viñales. Brown and O'Connell described the Jurassic section in this region, in part as follows: "The best sections for the Oxfordian are seen near the Bodega La Guasasa, between Viñales and Vicente, in the mountain pass known as La Puerta del Ancón. The black limestones and shales are covered by a stalactitic drip which seals the bedding planes and preserves the rocks from erosion. It was here that de la Torre made his first collections, and the locality has since proved to be one of the richest for ammonites. The fossils occur in great numbers in the concretions which are found in the talus at the bottom of the cliffs. . . . Six miles northeast of Viñales is one of the massive limestone magotes with the pre-Oxfordian shales and schists forming the lower hills to the north. At the foot of this mountain and in many outcrops near the copper mine Constancia the black limestone accretions are abundant and they contain ammonites, pelecypods, gastropods, fishes, and marine reptiles" (Brown and O'Connell, 1922, pp. 647–648).

An Oxfordian age for the fossils collected in the vicinity of Viñales is well established. Although the fauna is of a characteristic marine facies, the presence in it of a pterosaur is not unique; the famous Solnhofen limestones of Bavaria, of Portlandian age, contain the remains of various flying vertebrates (pterosaurs, and the three known skeletons of *Archaeopteryx*).

Viñales is on the highway about 25 kilometers north of Pinar del Río.

CLASS REPTILIA

ORDER PTEROSAURIA

FAMILY RHAMPHORHYNCHIDAE

NESODACTYLUS,[1] NEW GENUS

DIAGNOSIS: A rhamphorhynchine pterosaur, comparable with *Rhamphorhynchus* in size. The bones are hollow throughout the skeleton. The tail is long, with the caudal vertebrae surrounded by long, ossified tendons. The quadrate is elongated, with an anterior flange broadening ventrally, and with an attenuated ventral process directed forward to meet the quadratojugal. The cervical vertebrae are large; the dorsal vertebrae, small. The scapula-coracoids are equal to each other in length, and slender. The sternum is very strongly keeled, but less expanded in outline than the same bone in *Rhamphorhynchus,* its posterior border being pointed rather than transversely straight. The forelimb is relatively large, the humerus being proportionally larger than that in *Rhamphorhynchus,* and having a greatly expanded deltopectoral crest. The fourth metacarpal is robust, and the proximal phalanx of this digit evidently is very long, and doubly keeled. The ilium is slender, its dorsal crest being produced anteriorly and posteriorly as long, rodlike processes. The prepubis is expanded and platelike, rather similar in shape to the prepubis of

[1] Nesos, νησος, island; and dactylos, δακτυλος, finger.

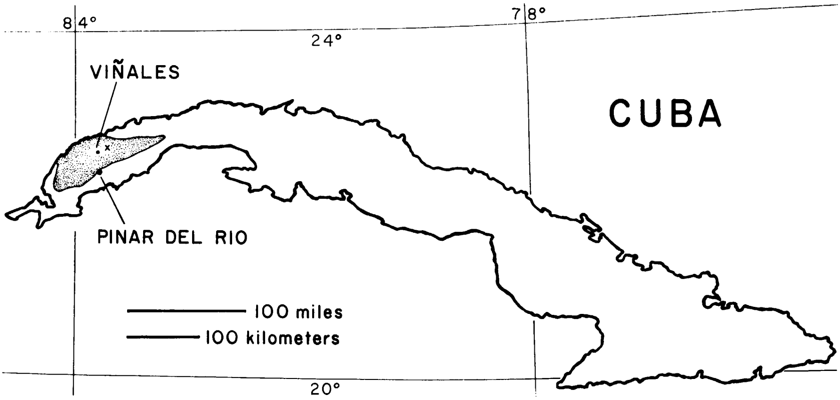

FIG. 1. Map of Cuba, showing Jurassic deposits of Pinar del Río in shaded area. The cross marks the approximate locality, east of Viñales, at which the type of *Nesodactylus hesperius,* new genus and species, was discovered. Scale: 1:10,000,000.

Dimorphodon. The hind limbs evidently were comparatively heavy and large.

TYPE: *Nesodactylus hesperius,* new species.

Nesodactylus hesperius,[1] new species

TYPE: A.M.N.H. No. 2000, a skeleton, consisting of the following parts: a skull fragment, presumably a right postorbital-squamosal bar; the quadrates, and possibly some other skull elements; scattered and isolated vertebrae, including at least five or six cervicals, several dorsals, one sacral, and an undetermined number of caudals; long, ossified, caudal tendons, indicating an elongated tail; left and right scapulae; left and right coracoids; a sternum; left and right humeri, radii, and ulnae; left and right carpi, metacarpals 1–4, and left and right proximal phalanges of the fourth digit; miscellaneous left and right phalanges from digits 1–3, including some unguals; left ilium; and ischium; left and right prepubes; head of left femur and distal end of right femur; one and perhaps more metatarsals; various ribs.

The bones listed above are preserved in seven small blocks of etched matrix, these blocks designated A to G for convenient reference. In addition there are a few loose bone fragments. Owing to the manner of preservation of these fossil bones, with some broken or partially obscured by bones overlying them, and with some incompletely etched, it is not pos-

[1] *Hesperius,* western.

sible to make definite statements as to the exact number of elements preserved, particularly so for the caudal vertebrae and the ribs. It is obvious, however, that, as there are no duplications of elements, all the bones within these matrix blocks represent a single individual.

Owing to the fragile nature of these bones, the etching that has thus exposed them cannot be carried beyond the point at which it now stands.

Horizon and Locality: Upper Jurassic, from the base of the Oxfordian as it is exposed in western Cuba. The locality is given as 4½ miles east of the Constancia Mine, which was about 5 miles north of Viñales. This position would be about 8 kilometers north and 7 kilometers east of Viñales, or about 10 kilometers northeast of the town. These distances can be regarded as only approximate. Viñales is about 24 or 25 kilometers on the highway due north of Pinar del Río, Province of Pinar del Río.

Diagnosis: See the diagnosis for the genus, above.

DESCRIPTION AND DISCUSSION

As is evident from the listing of the materials that comprise this new type, *Nesodactylus hesperius* is known from an agglomeration of bones that make up the considerable part of a skeleton. Unfortunately some of the most crucial parts are missing, the most serious being the absence of skull bones. Fortunately most of the elements of the postcranial skeleton are present; therefore good evidence is at hand on which to base a description of this pterosaur, and to make comparisons with related genera.

None of the bones have been removed from the black matrix in which they were originally enclosed; they are of such delicate construction that it has been thought wise to leave them in their original positions.

Nesodactylus hesperius is a rhamphorhynchine; various characters in the skeleton point to this relationship. Certain skeletal elements in particular are comparable to the same elements in *Rhamphorhynchus,* particularly the scapula-coracoid, the entire forelimb, the vertebral column, and the elongated tail in which the vertebrae are surrounded by elongated, ossified tendons. Other elements in the skeleton, notably the prepubes, show distinct differences from these elements of *Rhamphorhynchus,* but the differences are fewer than the resemblances. Consequently the relationship of this new pterosaur to *Rhamphorhynchus* appears to be close.

The Skull

A few skull bones are apparent among the materials comprising the type of *Nesodactylus hesperius*. There is a thin and delicate bar of bone,

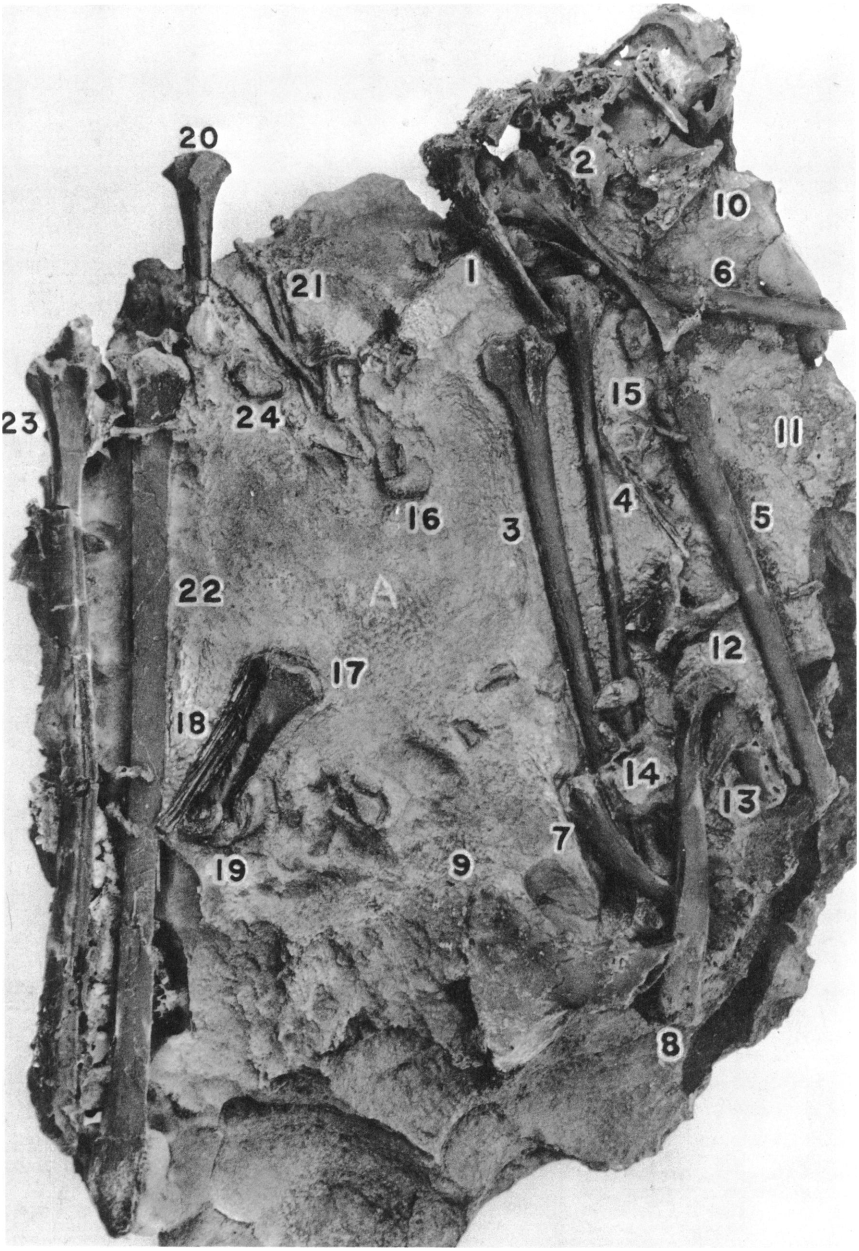

FIG. 2. *Nesodactylus hesperius,* new genus and species, A.M.N.H. No. 2000, from block A. 1. Right scapula. 2. Right coracoid. 3. Right radius. 4. Right ulna. 5. Left radius. 6. Left ulna. 7. Left scapula. 8. Right humerus. 9. Sternum. 10, 12, 13. Cervical vertebrae. 11, 14. Dorsal vertebrae. 15. Ribs. 16. Carpal. 17. Left metacarpal IV. 18. Left metacarpals I–III. 19. Carpal? 20. Right metacarpal IV. 21. Right metacarpals I–III. 22. Right digit IV, phalanx 1. 23. Left digit IV, phalanx 1. 24. Head of femur. ×1.

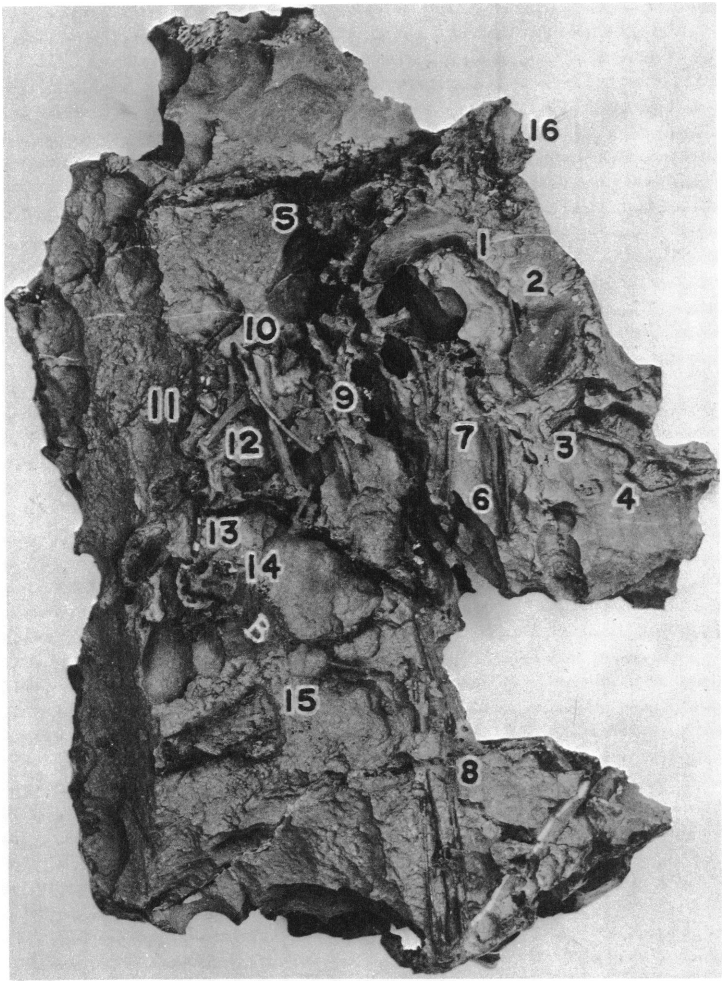

FIG. 3. *Nesodactylus hesperius,* new genus and species, A.M.N.H. No. 2000, from block B. 1, 2. Prepubes? 3. Sacral vertebra. 4. Right ilium. 5. Vertebra. 6. Ribs. 7, 8. Caudal vertebrae and ossified tendons. 9. Vertebra. 10. Metatarsal. 11. Vertebra. 12. Vertebra and rib. 13. Pubo-ischiatic plate. 14. Vertebra. 15. Distal end of femur. 16. Proximal end of femur. $\times 1$.

seemingly from the temporal region, tentatively identified as the right postorbitosquamosal bar. Two or three fragments appear to come from the cranial region. Finally, two bones have been identified as the quadrates.

These bones are elongated, as is typical for pterosaurs. In each, what

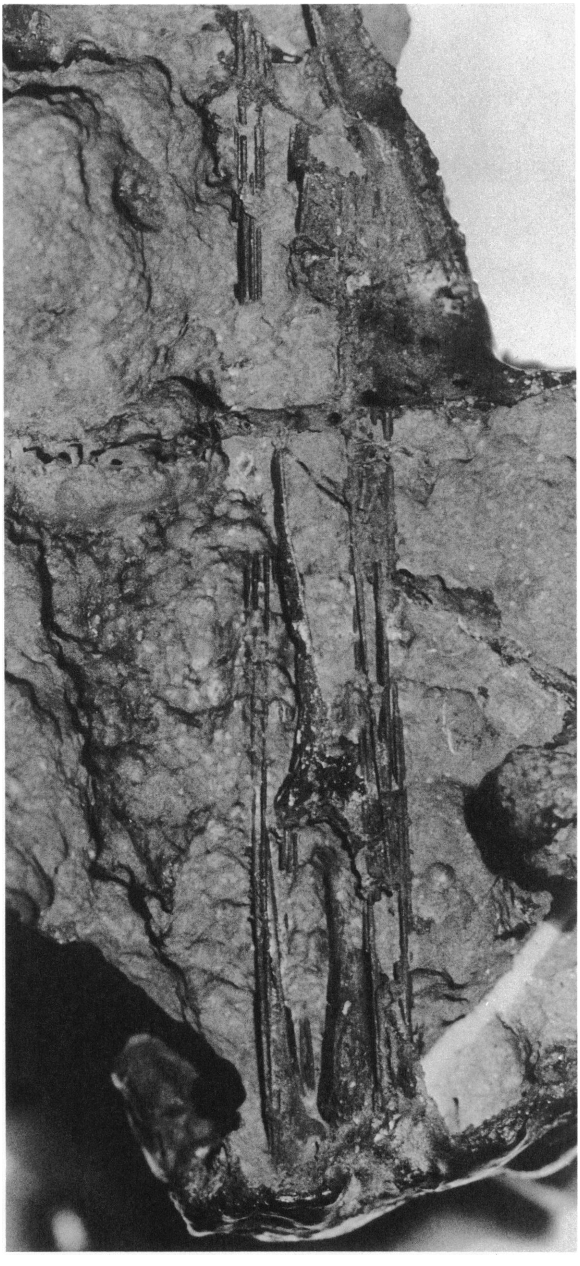

FIG. 4. *Nesodactylus hesperius,* new genus and species, A.M.N.H. No. 2000, ossified tendons around caudal vertebrae in block B. ×4.

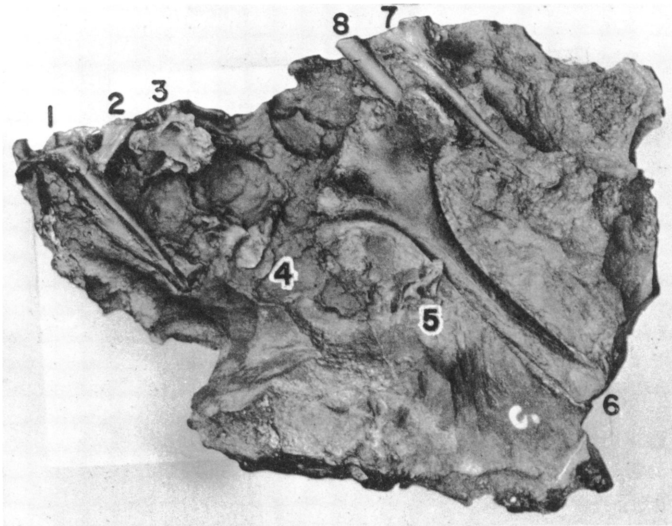

FIG. 5. *Nesodactylus hesperius,* new genus and species, A.M.N.H. No. 2000, from block C. 1. Right quadrate. 2–4. Possible cranial fragments. 5. Vertebra. 6. Left humerus. 7. Left coracoid. 8. Portion of an elongated bone, possibly a distal phalanx. ×1.

is here regarded as the upper end is bluntly tapered, to form a rounded articulation that must have fitted into a depression or socket in the squamosal. From this rodlike upper portion the bone, as seen in lateral view, widens ventrally in a thin, anteriorly directed flange, which becomes increasingly wider toward the ventral or articulating end of the bone. This flange, which is directed somewhat laterally as well as anteriorly, is exceedingly thin, and from its lowermost portion a very attenuated process extends forward to a considerable degree, presumably to articulate with the quadratojugal. Such a development is seen in various pterosaurs, notably *Campylognathoides* and *Scaphognathus.* Posteriorly the quadrate has the rodlike or barlike form so characteristic of the pterosaurs. It is a bar that widens, transversely from top to bottom, to terminate in the transverse articulating surface that impinged against the glenoid cavity of the articular of the mandible. Apparently the articulating surface of the quadrate was composed of an inner and an outer condyle, separated by a shallow sulcus. Along its outer edge, the ascending ramus of the quadrate shows a sharp ridge, separated from the flange mentioned above by a vertical, shallow concavity.

The quadrate of *Nesodactylus* thus differs from the same bone in *Rham-*

phorhynchus, being less rodlike in shape. The large flange on this bone and the ventral process possibly afforded increased areas of contact with the quadratojugal, thus bracing the quadrate against the stresses set up by the motion of the lower jaw.

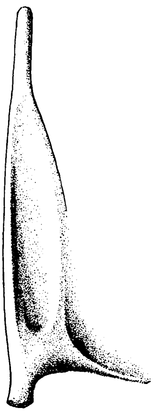

FIG. 6. *Nesodactylus hesperius,* new genus and species, A.M.N.H. No. 2000, right quadrate, lateral view. ×2.

THE AXIAL SKELETON

The disparity in size between the cervical and dorsal vertebrae is quite striking—in line with such disparity as seen in other pterosaurs. For example, the linear dimensions of a cervical vertebra in this new pterosaur may be more than double those of a dorsal vertebra, which means that the volume of the former exceeds that of the latter more or less by a factor of eight. This difference indicates that the skull of *Nesodactylus,* for which, unfortunately, we have little evidence, was relatively large. There is no way in which the number of presacral vertebrae can be determined; probably there were about 22 to 24 such vertebrae, of which perhaps eight may have been cervicals. In view of this difficulty it is possible only to compare a characteristic cervical with a characteristic dorsal vertebra, and to extend such comparisons to similar vertebrae in other genera.

The centrum of the procoelous cervical vertebra is elongated and relatively broad as well, its ventral surface being rather flat. On each side anteriorly, immediately behind the peripheral rim of the articulating surface, is a prominent facet for reception of the capitulum of the rib. The neural arch is very broad and rather heavy, and anteriorly it extends for a considerable distance in front of the articulation of the centrum. The anterior zygapophyses are rather widely separated and face forward and upward, for articulation with the similarly widely spaced postzygapophyses of the preceding vertebra. The neural spine is comparatively high and pointed.

The dorsal vertebra, in contrast, is small, with a narrow centrum, the articulating surfaces of which, instead of being broad and elliptical, are round. The neural arch is correspondingly narrow, and the zygapophyses are transversely close together. On each side of the centrum, in an anterior position, is the well-developed facet for the head of the rib. The neural spine is rather high. In their several described aspects the cervical and dorsal vertebrae of *Nesodactylus* are rather closely comparable with the vertebrae of *Rhamphorhynchus*.

It may be presumed that there were four sacral vertebrae; of these one is well preserved and plainly visible. This vertebra has strong transverse processes, distally expanded for articulation with the ilium.

The matrix contains bundles of elongated ossified tendons, of the type that characteristically surround the caudal vertebrae of *Rhamphorhynchus*. The individual vertebrae contained within these ossified tendons are not readily visible. It is quite evident that the tail in *Nesodactylus* was long, and it may have consisted of 35 or 40 caudal vertebrae.

The etched blocks containing the bones of this pterosaur reveal numerous ribs, generally somewhat broken. They are hollow, as are the other bones of *Nesodactylus*, and slender.

The Appendicular Skeleton

Pectoral Girdle and Forelimb: The scapula and coracoid are both long and slender and virtually equal in length. These bones are closely comparable with the same bones in *Rhamphorhynchus*, but the scapula is somewhat more slender than that in the European form. The coracoid is distally expanded at the point of attachment with the well-developed sternum.

The sternum of *Nesodactylus* is a distinctive bone, in contrast to the other bones of the pectoral girdle, which are rhamphorhynchid in form. It is characterized by a very strong keel, seemingly heavier and more anteriorly projected than is the keel in *Rhamphorhynchus*. The plate of the sternum is not so expanded as the same portion in *Rhamphorhynchus*, but nevertheless is strongly constructed. It is not flat; rather its two sides extend obliquely upward from the midline. The anterior border of the sternal plate on each side is relatively straight, merging medially into the dorsal edge of the deep keel. At each of its two lateral extremities the sternal plate comes to a point, and from this point on each side the posterolateral border of the plate gently curves back on each side to the

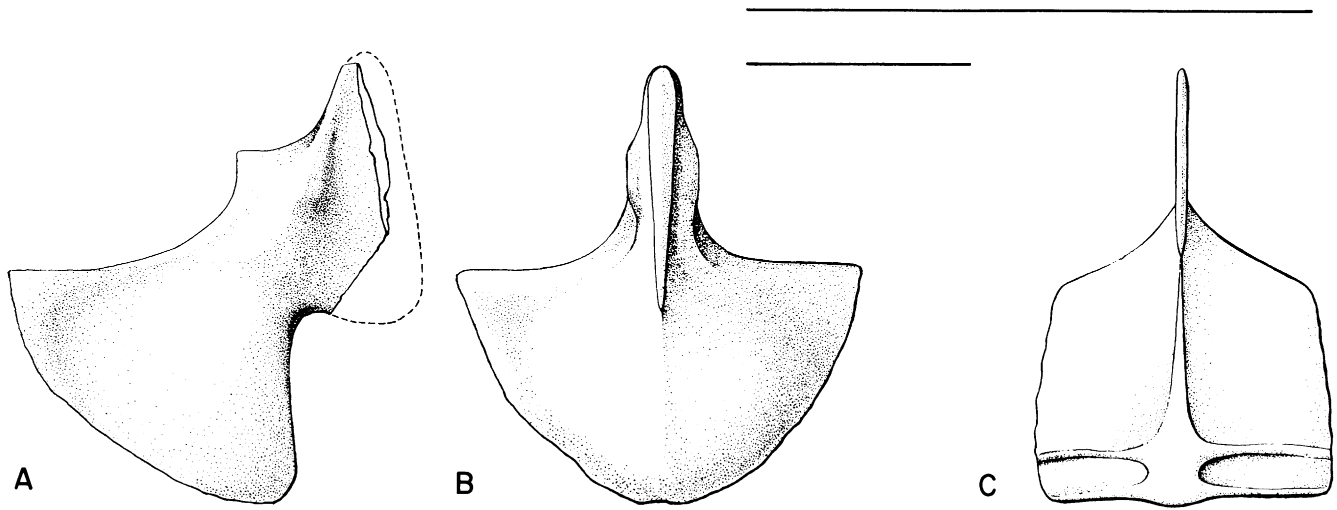

FIG. 7. A, B. *Nesodactylus hesperius*, new genus and species. A.M.N.H. No. 2000, sternum. A. Right lateral view. B. Ventral view. ×2. C. *Rhamphorhynchus gemmingi*, sternum, ventral view, after Stromer (1913), drawn at same unit length as A and B to facilitate comparisons. The black lines show the lengths at natural size, the one below being *Nesodactylus*, the one above *Rhamphorhynchus*.

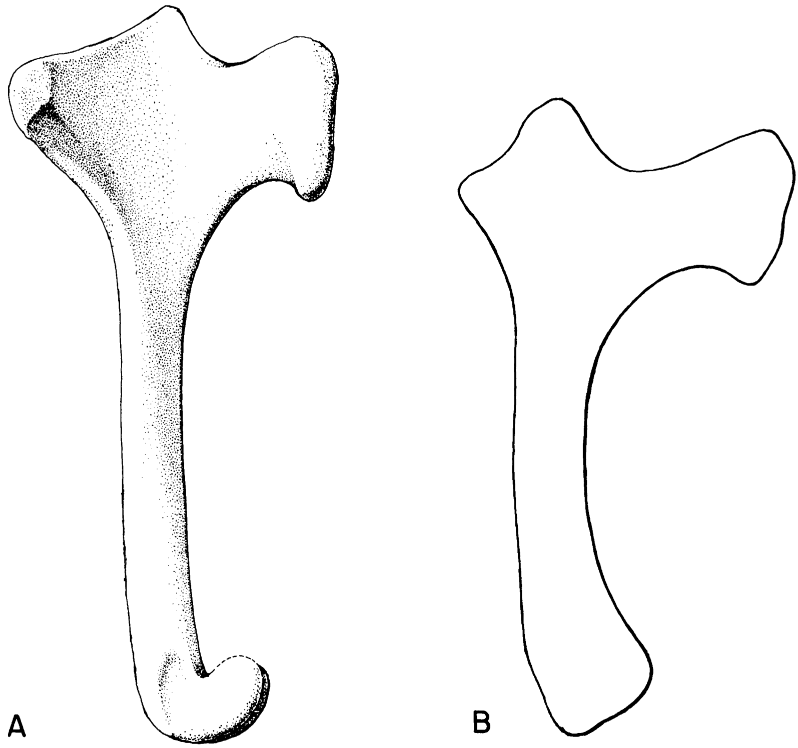

FIG. 8. A. *Nesodactylus hesperius,* new genus and species, A.M.N.H. No. 2000, left humerus, ventral view. B. *Rhamphorhynchus gemmingi,* outline of humerus, after Gross (1937). Both ×2.

midline. This condition may be contrasted with the sternal plate of *Rhamphorhynchus,* the back border of which is transversely straight, as are the sides. In other words, the sternal plate of *Rhamphorhynchus* in ventral view seems to be in the form of a broad quadrilateral plate; that of *Nesodactylus* is more like a broad triangle, the base of which faces posteriorly, the apex being directed anteriorly. This triangle is the platform from which the long, strong, sternal keel extends down. The sternal plate in *Nesodactylus,* although strongly developed, seems to be only about half as large, actually and proportionally, as the sternal plate in *Rhamphorhynchus* (see, Stromer, 1913). However, some illustrations of the sternum in this latter genus indicate a form and size similar to the sternum of *Nesodactylus* (for example, see Seeley, 1967, fig. 36).

The humerus in the new pterosaur from Cuba is similar to the same

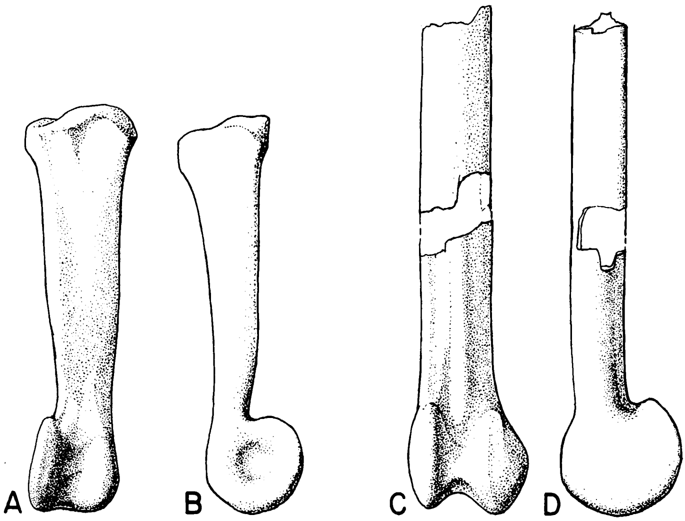

FIG. 9. A, B. *Nesodactylus hesperius,* new genus and species, A.M.N.H. No. 2000, left metacarpal IV. A. Ventral view. B. External lateral view. C, D. *Dermodactylus montanus,* type, Y.P.M. No. 2020, distal portion of right metacarpal IV. C. Ventral view. D. Internal lateral view. All ×2.

bone in *Rhamphorhynchus,* the chief difference being that in *Nesodactylus* this bone is proportionally slightly longer than that in the European genus. The most striking feature of the humerus is, of course, the enormous deltopectoral crest, this being in turn an indication of the powerful muscles for propulsive flight that obviously were present in this pterosaur. On the opposite side of the bone there is a prominent, rounded tubercle for the attachment of the subcoracoscapularis muscle. The shaft of the bone is slender, and distally there are prominent, rounded condyles.

The radius and ulna are greatly elongated, very slender bones, expanded at their extremities. These bones are in all respects similar to the same elements in *Rhamphorhynchus.*

The carpus is not fully preserved in *Nesodactylus,* but one rather large bone is here considered as being a part of the carpal complex and is tentatively identified as a fused radiale plus intermedium plus ulnare. On one side is a double facet that presumably accommodated the radius and the ulna; on the other, a broad facet that may have articulated with a large fourth distal carpal, which in turn would have articulated with the broad proximal facet of the fourth metacarpal. The relative size of this element and its articular surfaces seems to accord in a general way with the structure of the proximal fused carpal seen in *Rhamphorhynchus,* particularly *R. gemmingi.*

The manus in this new pterosaur is, as are other parts of the forelimb, strongly rhamphorhynchid. The first three digits are very slender, each terminating in a deep, compressed claw. The fourth digit, for the support of the wing membrane, is characteristically enlarged, but to a degree that perhaps surpasses the same digit in *Rhamphorhynchus.* The fourth metacarpal is very strong, with a broad proximal articular surface and a strong distal pulley, formed of the two expanded condyles.

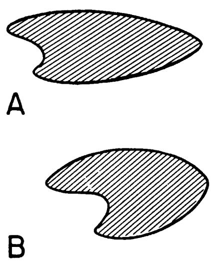

FIG. 10. Cross sections of the first phalanx of the fourth digit. A. *Nesodactylus hesperius,* new genus and species. B. *Rhamphorhynchus gemmingi,* after Gross (1937). Both ×4.

The proximal phalanx of this digit is large, seemingly proportionally larger than that in *Rhamphorhynchus.* Certainly the shaft of the bone seems to be heavier than the shaft of this same bone in *Rhamphorhynchus;* unfortunately the distal part of the bone is missing on both sides, so that the length of the phalanx can only be estimated. Anteriorly there is a sharp, knifelike edge; the posterior side of the bone is doubly keeled. The other phalanges from this digit are not present among the materials of *Nesodactylus hesperius* at hand.

The bones composing the wing in *Nesodactylus* are on the whole closely comparable with the same bones in *Rhamphorhynchus,* but perhaps relatively larger. Comparative measurements and proportions are given in tables 1 and 2.

PELVIC GIRDLE AND HIND LIMB: The ilium of *Nesodactylus* is composed of an elongated and low iliac crest, its anterior and posterior portions extending as long, rather thin rods, about equally extended in front of and behind the acetabulum. Apparently these projections of the ilium to front and rear are more elongated and less bladelike than is the case in *Rhamphorhynchus,* in which the ilium forms a rather deep and expanded plate. Thus the ilium of *Nesodactylus* shows a development in this respect that is comparable with what is seen in some species of *Pterodactylus.* The iliac portion of the acetabulum is large.

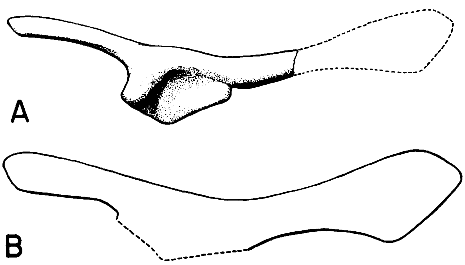

FIG. 11. A. *Nesodactylus hesperius,* new genus and species, A.M.N.H. No. 2000, right ilium, lateral view. B. *Rhamphorhynchus gemmingi,* outline of right ilium, lateral view, after Kuhn (1967). Both ×2.

Two paired bones preserved near the ilium are here interpreted as the prepubes. If this identification is correct, the prepubis in *Nesodactylus* was very large. The bones are here identified as prepubes because the

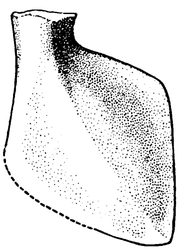

FIG. 12. *Nesodactylus hesperius,* new genus and species. A.M.N.H. No. 2000, element identified as a prepubis. ×2.

proximal articulation of each is restricted and occupies the termination of a rather narrow "neck," as would be expected in a prepubis. This surface gives no indication of having formed a part of the acetabulum. Moreover, the bone does not have the shape of a combined pubis-ischium, such as is typical of *Rhamphorhynchus,* for example, nor does it show a notch or an obturator foramen.

This supposed prepubis not only is characterized by a well-developed "neck" with an articulation at its end, but also below this neck expands into a large, diamond-shaped, or lozenge-shaped area, transversely convex on one side and concave on the other. In shape the bone is perhaps most like the prepubis of *Dimorphodon.*

Somewhat more distant from the ilium is a flat bone that may be a portion of the pubio-ischiatic plate. On one side of it there is a deep, rounded notch, possibly the remnant of an enlarged obturator foramen. At best this identification is tentative, as is the identification of the supposed prepubes.

If this analysis of the pelvis is correct, then *Nesodactylus* shows a girdle quite different from that of *Rhamphorhynchus*. Perhaps this might be called a more "primitive" girdle than the typical rhamphorhynchid pelvis.

The two fragments of femur preserved indicate that the hind limb in *Nesodactylus* was relatively large, considerably larger in proportion than the *Rhamphorhynchus* hind limb.

One definitely identifiable metatarsal is preserved in the matrix, near the pelvic elements. This bone, too, is relatively large. It seems obvious that *Nesodactylus* had strong hind limbs as well as large wings.

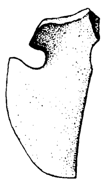

FIG. 13. *Nesodactylus hesperius,* new genus and species. A.M.N.H. No. 2000, element tentatively identified as a portion of a puboischiatic plate. ×2.

COMPARISONS AND RELATIONSHIPS

Perhaps the relationship of *Nesodactylus hesperius* to *Dermodactylus montanus,* the one other described pterosaur from the Jurassic of the Western Hemisphere, should be clarified. *Dermodactylus montanus* was first described by Marsh as *Pterodactylus montanus,* the type, described in 1878, being a single right fourth metacarpal, lacking its proximal end. The bone was collected from the Morrison Formation at Como Bluff, Wyoming, having been found in the famous "Quarry 9" by Samuel Wendell Williston, then a collector for Marsh.

As Marsh indicated in his description of this type, the shaft of the bone is thin-walled and hollow, its transverse section being oval in its proximal portion, but trihedral distally, with a strong longitudinal ridge on its under surface. The outer distal condyle is obliquely placed, separated from the inner condyle by a very narrow groove, and the inner condyle has an almost circular vertical outline. The condyles of the fourth metacarpal are similar to the condyles of the same bone in *Nesodactylus,* and of *Rhamphorhynchus* for that matter, but this bone in *Dermodactylus* is quite different from the same element in the other genera by virtue of its length. Because the proximal part of the bone is missing, we can only speculate as to its total length; certainly it was relatively long, perhaps in this respect not unlike the same bone in the Asiatic genus *Dsungaripterus,* recently described by Young (1964). This difference in itself is enough to show quite clearly that *Nesodactylus* and *Dermodactylus* are distinct genera.

The type description of *Dermodactylus montanus* mentioned only the partial metacarpal on which the species was founded. In the subsequent publication in which Marsh (1881) established the genus *Dermodactylus,*

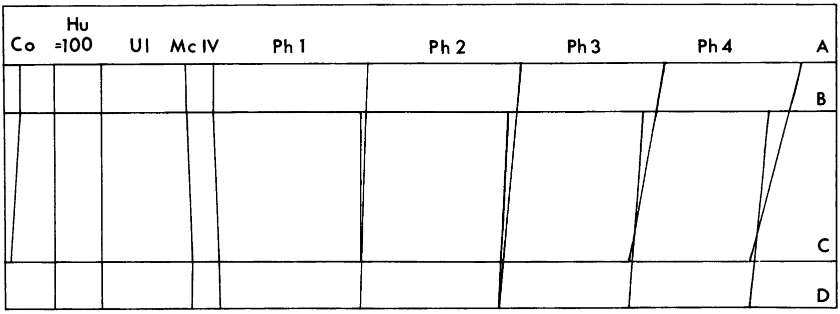

FIG. 14. A comparison of lengths of the coracoid (Co), humerus (Hu), ulna (Ul), fourth metacarpal (McIV), and phalanges (Ph1, Ph2, Ph3, Ph4) based on a unit of length for the humerus. A. *Nesodactylus hesperius,* new genus and species, with the phalangeal lengths restored on the basis of a comparison with *Rhamphorhynchus münsteri* Goldfuss. B. *Nesodactylus hesperius,* new genus and species, with the phalangeal lengths restored on the basis of a comparison with *Rhamphorhynchus gemmingi* Meyer. C. *Rhamphorhynchus muensteri* Goldfuss. D. *Rhamphorhynchus gemmingi* Meyer.

the existence of other materials was indicated, including "portions of wing bones," scapula, coracoid, vertebrae, and teeth. But in discussing these fossils Marsh remarked, "The size of these specimens indicates a spread of wings of about five or six feet" (Marsh, 1881, p. 342). Such a statement seems quite out of line with the dimensions of the type metacarpal of *Dermodactylus,* a bone that indicates an animal more or less comparable in size with *Rhamphorhynchus.* Therefore it seems possible that Marsh had before him some mixed materials, and that by error he attributed the remains of some other reptile or reptiles to *Dermodactylus montanus.*

It was perhaps on the basis of this statement by Marsh that Mook in 1916 attributed to *Dermodactylus montanus* "various remains of wings, teeth, and vertebrae" (Mook, 1916, p. 149).

The resemblances and differences between *Nesodactylus* and *Dermodactylus* are clear; the resemblances and differences between *Nesodactylus* and *Rhamphorhynchus* are equally clear. The new pterosaur from Cuba is

TABLE 1

COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF JURASSIC PTEROSAURS

	Nesodactylus hesperius A.M.N.H. No. 2000	*Rhamphorhynchus muensteri* A.M.N.H. No. 1943	*Rhamphorhynchus gemmingi* (from Gross, 1937)	*Campylognathoides zitteli* C.M. No. 11424
Cervical vertebra				
Length of centrum	10.0	10.0	10.9	8.2
Breadth at prezygapophyses	10.2	—	—	6.7
Height	12.3	11.0	—	—
Dorsal vertebra				
Length of centrum	6.0	7.4	—	—
Breadth of neural arch	2.8	—	—	—
Height	7.0	—	—	—
Sacral vertebra				
Length of centrum	4.5	4.8[a]	—	—
Breadth of transverse process	15.7	13.0[a]	18.0	—
Scapula, length	30.3	31.1	31.5	33.1
Coracoid, length	32.2	33.4	—	31.0
Sternum, length	29+	54.5	—	49.4
Sternal plate				
Length	23.0	32.0	—	34.0
Breadth	34.0	42.0	—	53.7
Depth of keel	15e[b]	14.4	—	10.0

TABLE 1—(*Continued*)

	Nesodactylus hesperius A.M.N.H. No. 2000	*Rhamphorhynchus muensteri* A.M.N.H. No. 1943	*Rhamphorhynchus gemmingi* (from Gross, 1937)	*Campylognathoides zitteli* C.M. No. 11424
Humerus				
Length	46.5	37.2	40.0	49.5
Breadth across deltopectoral process	21.5	20.6	22.0	23.0
Radius, length	79.0	66.2	70.0	59.8
Ulna, length	80.0	67.1	72.5	60.0
Carpus, length	6.0	5.4	2.5	7.1
Metacarpal IV, length	26.7	20.6	21.0	22.5
Digit IV				
Phalanx 1, length	137e	109.3	116.0	88.0
Phalanx 2, length	[135][c]	107.8	114.0	95.1
Phalanx 3, length	[122]	97.7	106.5	84.2
Phalanx 4, length	[115]	92.3	98.0	96.6
Metacarpal I, length		19.5	17.5	—
Digit I, phalanges 1–2, length	—	11.0	11.8	12e
Metacarpal II, length	—	19.5	18.0	—
Digit II, phalanges 1–3, length	—	18.8	15.9	22.2
Metacarpal III, length	—	—	—	—
Digit III, phalanges 1–4, length	—	18.7	18.4	24.9

TABLE 1—(*Continued*)

	Nesodactylus hesperius A.M.N.H. No. 2000	*Rhamphorhynchus muensteri* A.M.N.H. No. 1943	*Rhamphorhynchus gemmingi* (from Gross, 1937)	*Campylognathoides zitteli* C.M. No. 11424
Ilium	—			
Length	20+	13.2	35.0	—
Diameter of acetabulum	4.7	—	5.7	5.5e
Prepubis				
Length	17.2	—	—	16.8
Breadth	12.0	—	—	19.3
Femur				
Length	—	34.5	34.6	37.4
Breadth, distal	9.3	4.3	—	—
Tibia, length	—	49.4	49.0	47.4
Metarsal III, length	19.8	26.3	26.0	21.9
Digit III, phalanges 1–4, length	—	17.0	17.2	—

[a] Second sacral.
[b] e, estimated length.
[c] Measurements in brackets are lengths as restored.

TABLE 2
RATIOS (HUMERUS = 100) OF FORELIMB BONES IN JURASSIC PTEROSAURS

	Nesodactylus hesperius A.M.N.H. No. 2000	*Rhamphorhynchus muensteri* A.M.N.H. No. 1943	*Rhamphorhynchus gemmingi* (from Gross, 1937)	*Campylognathus zitteli* C.M. No. 11424
Coracoid	69	90	—	63
Humerus	100	100	100	100
Ulna	172	180	181	121
Metacarpal IV	57	55	52	45
Digit IV				
Phalanx 1	305/318[a]	294	290	178
Phalanx 2	300/312[a]	290	285	192
Phalanx 3	270/292[a]	262	266	170
Phalanx 4	257/278[a]	248	245	142

[a] Extrapolations, based on *R. muensteri* and *R. gemmingi.*

obviously closely related to the European genus. Resemblances are close in the form of the large cervical and much smaller dorsal vertebrae, the obviously long tail in both, the form of the scapula-coracoid and the humerus, which indeed show striking similarities, and in the structure of the carpus, the wing metacarpal, and the phalanges. Differences are apparent in the form of the quadrate and the proportions of the wing finger and, so far as we can see it, of the hind limb. *Nesodactylus* seems to have had slightly larger, heavier wings than did *Rhamphorhynchus,* and considerably larger, stouter legs. Furthermore, the structure of the pelvis is quite different in the two genera, *Nesodactylus* being characterized by a relatively "primitive" pterosaurian pelvis, with large, platelike prepubes.

Thus the balance of resemblances and differences indicates that *Nesodactylus* is a rhamphorhynchid, closely related to *Rhamphorhynchus,* but nonetheless generically distinct. This taxonomic distinction is to be expected, not only because of the distant geographic separation of *Nesodactylus* from the European form, but also, and more particularly, because of its slightly earlier geologic age. Recall that *Nesodactylus* is of Oxfordian age; *Rhamphorhynchus* is of Kimmeridgian age. The differences in morphology and age are not great. Perhaps it is valid to consider *Nesodactylus* and *Rhamphorhynchus* as two contiguous evolutionary branches from a common stem.

SUMMARY AND CONCLUSIONS

Nesodactylus hesperius, a rhamphorhynchid pterosaur from the Oxfordian of western Cuba, adds a new detail to our knowledge of Jurassic flying reptiles. This new pterosaur, obviously closely related to *Rhamphorhynchus,* seems to indicate that, although the rhamphorhynchids of late Jurassic age were a closely knit group, they nevertheless developed some evolutionary divergence. As is becoming apparent among many groups under continued detailed study of the fossil record, this evolutionary divergence was marked by a "mosaic" pattern of development. *Nesodactylus* in most respects was a specialized rhamphorhynchid, as progressive as *Rhamphorhynchus* itself, and certainly well advanced beyond the condition seen in some of the earlier Jurassic members of the family, such as *Campylognathoides.* Thus the adaptations for flying, as indicated by large wings with hypertrophy of the fourth digit and a sternum with an unusually large keel, are particularly noteworthy in *Nesodactylus,* surpassing in this genus the similar adaptations in *Rhamphorhynchus.* In contrast, the pelvis seems to show some primitive features, particularly in the form of the ilium and the prepubis. In addition the hind legs seem to have been relatively large in *Nesodactylus,* which may indicate the retention of a primitive character, if descent from a strongly bipedal thecodont is considered as the line of origin for the flying reptiles.

It is particularly useful to have this record of a rhamphorhynchid in Cuba, thereby extending the range for these flying reptiles. Of course, there is every reason to think that the pterosaurs were world wide in distribution during middle and late Mesozoic time, but because of their supposed habits and the fragility of their bones the fossil record is very spotty. *Rhamphorhynchus* is, of course, a characteristic European genus of late Jurassic age, and this same form has been identified in the Tendaguru deposits of eastern Africa. (*Rhamphorhynchus* has been described recently by Rao and Shah, 1963, from the lowermost Jurassic Kota beds of central India. The materials are fragmentary, and whether this fossil can be regarded as *Rhamphorhynchus* in a strict sense is questionable. More recently [Anonymous, 1966] there has been a report in the popular press of the discovery of *Rhamphorhynchus* in Soviet Asia.) Now that the discovery of *Nesodactylus* confirms the tenuous evidence hitherto embodied in the single metacarpal of *Dermodactylus* for the presence of late Jurassic pterosaurs in the Western Hemisphere, it is possible to consider with confidence the cosmopolitan distribution of flying reptiles during late Jurassic time.

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