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TAXONOMY AND SYSTEMATICS OF THE LATE CRETACEOUS PTEROSAUR *PTERANODON* (PTEROSAURIA, PTERODACTYLOIDEA)

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ABSTRACT A taxonomic revision of the Late Cretaceous pterosaur *Pteranodon* (Archosauria: Pterosauria) from the Niobrara and Pierre Formations of North America was undertaken as part of a comprehensive reexamination of the genus. There are only two valid species of *Pteranodon: P. sternbergi* from the upper Coniacian to lower Santonian, and *P. longiceps* from the upper Santonian to lower Campanian. *Pteranodon sternbergi* and *P. longiceps* differ primarily in the direction and shape of the large cranial crest found in males, and *Pteranodon sternbergi* seems to be ancestral to *P. longiceps*. All other named species are *nomina dubia* based on inadequate materials or junior synonyms based on specimens of different size, sex, or age than the type specimens of the valid species. A phylogenetic analysis of the Pterodactyloidea suggests that *Pteranodon* is the sister taxon of all other pteranodontids, that the Dsungaripteridae and Azhdarchidae are sister groups, and that the Dsungaripteridae + Azhdarchidae is the sister group of the Pteranodontidae.

Key Words: Pterosauria; *Pteranodon;* Systematics; Late Cretaceous; Niobrara Fm.

The large pterosaur *Pteranodon* from the late Cretaceous of Kansas was first described by O. C. Marsh in 1871. During the next 11 years Marsh named a total of seven species, and E. D. Cope named two more. In the 1890's, S. W. Williston published extensively on *Pteranodon*, but only reviewed the species. The osteology of *Pteranodon* was described by Eaton

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in 1910, and virtually all that was known of *Pteranodon*, and much of what was known about large pterosaurs in general, was found in or based on his description and reconstructions. *Pteranodon* became the archetypal large pterosaur in both the popular and scientific literature, and was the largest known pterosaur and flying vertebrate until the recent description of *Quetzalcoatlus* (Lawson, 1975a,b). In the years since Eaton's publication, new materials of *Pteranodon* and other large pterosaurs have been collected, and new questions about their osteology, functional morphology, and relationships have arisen. This necessitated a comprehensive reexamination of *Pteranodon*, of which this taxonomic revision is a part.

Pteranodon is better represented in the fossil record than any other pterosaur. There are more than 1100 specimens of *Pteranodon* from the Niobrara Formation of western Kansas in museum collections, including relatively complete skulls and articulated partial skeletons. Specimens of *Pteranodon* are excellently preserved because they were deposited in a low energy, deep-water environment. Consequently, they are not abraded, and fine features and fragile structures are preserved. The only disadvantage is that almost all of the elements have been crushed and distorted. Although the Solnhofen Limestone of Germany preserves complete skeletons, the Cambridge Greensand of England has produced more specimens, and the Santana Formation of Brazil has uncrushed bones in concretions, no other deposit has both large numbers of specimens and excellent preservation. This taxonomic revision is based on a reexamination of the large collections of *Pteranodon* including nearly every specimen in museum collections.

Most specimens of *Pteranodon* have been collected from the Smoky Hill Chalk Member of the Niobrara Formation of western Kansas. The Smoky Hill Chalk Member of the Niobrara Formation consists of approximately 200 m of impure chalks deposited on the eastern shelf of the Western Interior Seaway during a peak transgression from the late Coniacian to the early Campanian. It outcrops extensively in a band extending northeast to southwest across western Kansas. It is flat lying and contains many bentonite seams that make excellent stratigraphic markers (Hattin, 1982). General stratigraphic positions can be inferred from geographic locality (Stewart, 1988), but the formation has suffered local faulting, and precise determinations of stratigraphic position require examination of the specific outcrop. Within the outcrop area, most specimens of vertebrates have been collected from the upper parts of the Smoky Hill Chalk in Logan, Gove, and Graham counties, although Stewart (1988) noted that vertebrates occur throughout the Smoky Hill Chalk.

Most specimens collected from the Smoky Hill Chalk are not accompanied by accurate stratigraphic or locality data, even though this could have been recorded. For example, in the summer of 1874, B. F. Mudge and party began recording locality of each specimen as Section, Town, and Range, but stopped after about a month, perhaps because Marsh did not think the information was important. Even most specimens collected in this century do not have accurate locality information. This is unfortunate, because the lack of stratigraphic information made the taxonomic revision more difficult. Reasonably accurate stratigraphic data can be obtained for those specimens with accurate locality data, and I determined the approximate stratigraphic position of a number of important specimens from their locality data (Bennett, 1991).

In addition to the excellent record of *Pteranodon* from the Smoky Hill Chalk, the taxon also occurs in the overlying Sharon Springs Member of the Pierre Shale. The fauna of the Smoky Hill Chalk apparently continued without interruption into the Sharon Springs Member (Carpenter, pers. comm.) and *Pteranodon* occurs in the Sharon Springs Member of Kansas, Wyoming, and South Dakota. The single skull and all known postcranials from the Sharon Springs are indistinguishable from *Pteranodon longiceps* from the Smoky Hill Chalk.

Pteranodon has not been found north of Wyoming and South Dakota, and does not seem to have frequented higher latitudes. Despite the many specimens of pterosaurs from the Smoky Hill Chalk of Kansas, only two specimens of *Pteranodon* have been found in the Smoky Hill Chalk of South Dakota. No pterosaurs have been found in the Niobrara Formation of Canada, although the sample size is too small to be significant (E. S. Nicholls, pers. comm.). Similarly, although pterosaurs are known from the Sharon Springs Member of the Pierre Shale in Wyoming and South Dakota, they have not been found in the contemporaneous Pembina Member of Manitoba, despite collection of 856 fossil vertebrates (Nicholls and Russell, 1990). The collections from the Pembina Member are large enough that pterosaurs probably would have been found if they were present in the tetrapod fauna.

Pteranodon has not been definitely identified from other deposits. However, fragmentary pterosaur specimens that are not diagnostic of, yet are not inconsistent with, *Pteranodon* have been found in approximately contemporary deposits in the Gulf and Atlantic Coast regions. A small number of pterosaur specimens are known from the Selma Chalk Member of the Mooreville Formation of Alabama, and a short midcervical vertebra of a large pteranodontid (the only large short necked pterosaurs known in the Upper Cretaceous) and other pterosaur fragments are known from the Merchantville Formation (early Campanian) of Delaware (Baird and Galton, 1981). These materials are identified tentatively as *Pteranodon*.

A few indeterminate specimens of large pterosaurs from Europe and Japan have been referred to *Pteranodon* (Bogolubov, 1914; Nessov and Jarkov, 1989; Obata et al., 1972) but because of the great distances from the

Western Interior Seaway, there is no justification for referring these to the genus. *Pteranodon* appears to be endemic to the Western Interior Seaway and the Gulf and Atlantic Coasts of North America with a temporal range of late Coniacian through early Campanian.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York; BHI, Black Hills Institute of Geological Research, Hill City, South Dakota; BMNH, British Museum (Natural History), London; CM, Carnegie Museum of Natural History, Pittsburgh; CU, Museum, University of Colorado, Boulder; DMNH, Denver Museum of Natural History, Denver; FFM, Fick Fossil Museum, Oakley, Kansas; FHSM, Fort Hays State Museum (= SMM, Sternberg Memorial Museum), Fort Hays State University, Hays, Kansas; FMNH, Field Museum of Natural History, Chicago; KUVP, Natural History Museum, University of Kansas; LACM, Los Angeles County Museum of Natural History, Los Angeles; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNHN, Museum National d'Histoire Naturelle, Paleontologie, Paris; NMC, National Museum of Canada, Ottawa; ROM, Royal Ontario Museum, Toronto; SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City; SMNS, Staatliches Museum für Naturkunde, Stuttgart; TMM, Texas Memorial Museum, University of Texas at Austin; UALVP, Geology Museum, University of Alberta, Edmonton; UM, Museum of Paleontology, University of Michigan, Ann Arbor; UNSM, University of Nebraska State Museum, Lincoln; UOCM, Condon Museum of Natural History, University of Oregon, Eugene; "UNC," Uncatalogued specimens (see Bennett, 1991); USNM, U.S. National Museum of Natural History, Washington, D. C; UUPI, Palaeontological Institute, University of Uppsala, Uppsala; and YPM, Peabody Museum of Natural History, Yale University, New Haven.

LITERATURE REVIEW

The first specimens of *Pteranodon* were collected by O. C. Marsh in 1870 from the Niobrara Formation of western Kansas. The specimens, which consisted of the distal ends of two right wing metacarpals and a tooth of a *Xiphactinus* that Marsh believed came from the pterosaur, were described as *Pterodactylus oweni* (Marsh, 1871). In the summer of 1871, Marsh collected more material, including the remainder of one of the wing metacarpals described previously. Marsh (1872) described the additional remains and renamed the species *Pterodactylus occidentalis* because the former name was preoccupied by *Pterodactylus oweni* Seeley. In addition, he named a larger species, *Pterodactylus ingens*, based on wing elements of four individuals, and a smaller species, *Pterodactylus velox*, based on the distal end of a right wing metacarpal and the proximal end of the first wing phalanx. Marsh noted differences in the articular surfaces of the crushed limb bones of the three species and used the differences, as well as size, to separate the species. At the same time, E. D. Cope collected three or four specimens including distal ends of wing metacarpals, proximal ends of first wing phalanges, and fragments, which he believed represented large and small species. Cope wished to assign his species to *Ornithocheirus* Seeley, but misspelled the genus name as *Ornithochirus*. The descriptions of *Ornithochirus umbrosus*, the large species, and the smaller, *O. harpyia* (Cope, 1872), were published just 5 days after Marsh's second publication (Marsh, 1872). Cope stated that *Ornithochirus harpyia* was about the same size and probably the same species as Marsh's *Pterodactylus oweni*, but because that name was preoccupied, *Ornithochirus harpyia* should replace it. A reply by Marsh (Anon., 1872) to Cope's paper argued that *Ornithochirus umbrosus* and *O. harpyia* were junior synonyms of *Pterodactylus ingens* and *P. occidentalis*, respectively, because Marsh's (1872) publication had priority. Subsequently, Cope (1875) repeated his description of the type specimens of *Ornithochirus umbrosus* and *O. harpyia* with slight corrections, and provided illustrations of the specimens. Cope conceded that *O. harpyia* was a junior synonym of *Pterodactylus occidentalis*, but continued to view *O. umbrosus*, now called *Pterodactylus umbrosus*, as a separate species. Most later authors accepted the view that Cope's names are junior synonyms of Marsh's and, in fact, measurements of the type specimens do not support Cope's contention that *Ornithochirus umbrosus* was larger than *Pterodactylus ingens*. Widths of the crushed distal ends of wing metacarpals of *Pteranodon* from the Niobrara Formation are highly variable, depending in large part on the direction of crushing, and comparison of the more reliable diameters of the distal condyles of the syntypes of *Ornithochirus umbrosus* and *Pterodactylus ingens* shows them to be nearly the same size.

Starting in 1874, Marsh hired collectors, including B. F. Mudge and S. W. Williston, to work the exposures of the Niobrara Formation in western Kansas. During the next 6 years much more material was collected, including a well-preserved, nearly complete skull (YPM 1177) that showed that the pterosaurs from the Niobrara Formation differed from all other pterosaurs then known in their possession of edentulous jaws and a cranial crest. Marsh (1876a) erected a new genus and species, *Pteranodon longiceps*, based on the skull. The three previously named species from the Niobrara Formation were also placed in the genus *Pteranodon*, and a second smaller skull (YPM 1179) was referred to *Pteranodon occidentalis*. Marsh considered *P. longiceps* to be somewhat larger than *P. occidentalis*, but smaller than *P. ingens*. In the same publication he named another species, *Pteranodon gracilis*, based on wing bones and what he took to be a pelvis (actually a notarium with both scapulocoracoids). Subsequently, Marsh recognized his mistake, and without mentioning the misidentification of the notarium, he placed the species in the new genus *Nyctosaurus* (Marsh, 1876b) because the scapula and coracoid were not co-ossified as in *Pteranodon*. Marsh (1876a) also named *Pteranodon comptus* based on parts of three skeletons including "two distal ends of the characteristic metacarpal, ... and two sacral vertebrae" (actually the distal ends of tibiae of a small individual of *Pteranodon* and dorsal vertebrae of *Nyctosaurus*). The last species of *Pteranodon* named by Marsh was the very small, *Pteranodon nanus* (Marsh, 1881), based on jaw fragments, a partial notarium, humerus, and scapulocoracoid. The specimen is a small nyctosaur, but was placed in *Pteranodon* because the scapulocoracoid was fully co-ossified. Altogether, Marsh named six species of *Pteranodon* ranging in size from the very small *P. nanus* to the very large *P. ingens*. Although morphological characters were noted for each of the species, it is clear that size was the primary difference between them.

Williston (1892) reviewed the genus *Pteranodon* and listed seven species—viz., Marsh's six and *Pteranodon umbrosus;* he was not willing to accept the synonymy of *Pteranodon umbrosus* with *Pteranodon ingens*. He commented that *P. velox* was based on undiagnostic parts of the skeleton and that there was no evidence that *P. longiceps* was distinct from the other species. Williston did not suggest any taxonomic changes, but noted that Seeley (1871) mentioned an edentulous jaw fragment under the name *Ornithostoma*. Williston (1892) suggested that *Ornithostoma* might have priority over *Pteranodon*, and soon concluded that it did (Williston, 1893). All of Williston's subsequent publications through 1902 (Williston, 1895; 1896; 1897; 1902a,b) referred to *Pteranodon* as *Ornithostoma*. No specific name had been given to the edentulous jaw fragment of *Ornithostoma*, and so the "genus" *Ornithostoma* did not include any species until 1893 when Williston referred the species of *Pteranodon* to it. Plieninger (1901) discussed the question of priority of the name *Ornithostoma*, and concluded that because *Ornithostoma* had been neither described nor illustrated, it could not have priority. Subsequently, Williston (1903) gave up the name *Ornithostoma* and went back to *Pteranodon*.

Williston (1903) again reviewed the genus *Pteranodon*. *Pteranodon comptus* was referred to *Nyctosaurus gracilis* primarily on the basis of size because Williston did not realize that the "wing metacarpals" of the specimens were, in fact, tibiae, and *P. nanus* was also considered a synonym of *N. gracilis*. By this time, Williston had given up on *P. umbrosus*, and this left three species of *Pteranodon* based on postcranials (*P. ingens, P. occidentalis*, and *P. velox*) and one species (*P. longiceps*) based on a skull. Williston stated that *P. longiceps* "might be identical with either [*P.*] *occidentalis* or [*P.*] *velox*, possibly with both" (Williston, 1903:157), although the type specimen of *P. longiceps* could not be directly compared to the other type specimens. He concluded that there were three different-sized species and noted differences in the shape of the deltopectoral crests of the humeri. The deltopectoral crest of *P. ingens* was said to be "rounded and obtuse," whereas that of one or both of the smaller species was "more elongate and of a different shape." He also suggested that the large and small species differed in the curvature of the fourth wing phalanx.

Eaton (1910) presented the first detailed description of the osteology of *Pteranodon* and reviewed the taxonomy of the genus. He correctly identified the "wing metacarpals" of *P. comptus* as distal ends of tibiae from an individual about the size of the type of *P. occidentalis* and noted that the vertebrae might be referred to *Nyctosaurus*. Eaton stated that the appearance of the type specimen of *P. velox* was altered considerably by a concretion, and dismissed the specimen as not differing significantly from any other. Like Williston before him, he considered *P. nanus* to be a nyctosaur. This left the three species *P. occidentalis*, *P. longiceps*, and *P. ingens*. Eaton (1910) stated that most specimens of *Pteranodon* were too fragmentary to be of any systematic value. He characterized Marsh's original type specimens of *P. occidentalis* and *P. ingens* as "incomplete and fragmentary," and "a few poor fragments of wing bones," respectively, and ascribed all morphological differences in the postcranials described by Marsh to "extraneous causes" (Eaton, 1910:1). He discussed the variations of form of the humerus which resulted from crushing in different planes, and had even crushed clay models of humeri between two plates to examine the phenomenon. Eaton found no morphological differences in any of the postcranials of *Pteranodon* and concluded that size was the only important difference between the postcranials of *P. occidentalis* and *P. ingens*. Eaton decided arbitrarily to accept Marsh's referrals of the skulls YPM 1179 and 2594 to *P. occidentalis* and *P. ingens*, respectively, and then tried to separate those species and *P. longiceps* on the basis of differences in the skulls alone. He argued that to reject the referrals would be equally arbitrary and would lead to greater uncertainty. Eaton noted that the skull of *P. longiceps* (YPM 1177) presented "striking similarities" (Eaton, 1910:2) to the skull of *P. ingens* (YPM 2594), although only two-thirds the size, but he concluded that the three species could be differentiated on the basis of cranial morphology as well as size. Nevertheless, except for the type skull of *P. longiceps* (YPM 1177) and the postcranials and skulls referred by Marsh to *P. occidentalis* (YPM 1164, 1179) and *P. ingens* (YPM 1175, 2594), Eaton referred to all specimens as *Pteranodon* sp. [indet.].

Harksen (1966) described a new species, *Pteranodon sternbergi*, based on a large skull (FHSM VP 339) with an upright cranial crest and upward curving jaws, quite different from the skulls of *P. longiceps* (YPM 1177) and YPM 2594, which Eaton (1910) had referred to *P. ingens*. However, Harksen did not comment on the genus, and the taxonomy of *Pteranodon* was left untouched until Miller (1972) attempted a revision. Miller pointed out that it was impossible to distinguish between upright-crested and backward-crested species on the basis of postcranials. Therefore, he listed *P. occidentalis, P. ingens, P. velox, P. comptus, Ornithochirus umbrosus,* and *O. harpyia* as *nomina dubia* because they were based on fragmentary postcranials. This left only *P. longiceps* and *P. sternbergi*, which were based on skulls, and Miller named three new species based on isolated crania: (1) *P. marshi* (YPM 2594), the skull Eaton (1910) considered to be the type skull of *P. ingens;* (2) *P. eatoni* (YPM 1179), the skull Eaton considered to be the type of *P. occidentalis;* and (3) *P. walkeri* (FHSM VP 221) that Miller suggested had an upright crest somewhat like that of *P. sternbergi*. Miller placed the five species of *Pteranodon* in three subgenera: (1) *Longicepia*, later corrected to *Pteranodon* (Miller, 1973), that included *P. longiceps* and *P. marshi;* (2) *Sternbergia*, preoccupied and later replaced with *Geosternbergia* (Miller, 1978), that included *P. sternbergi* and *P. walkeri;* and (3) *Occidentalia* that included only *P. eatoni*. Miller also considered *Nyctosaurus* to be a subgenus of *Pteranodon*, and viewed the subgenera as steps in an evolutionary sequence in which the small, crestless *Nyctosaurus* gave rise to the small, crested *Occidentalia*, which in turn gave rise to the backward-crested *Longicepia* and the upright-crested *Sternbergia*.

Miller's revision contains a number of errors. He apparently was confused by Marsh's (1872) reference to five individuals in the description of *Pterodactylus occidentalis* and the statement by Eaton (1910) that YPM 1164 was the type of the species. As a result, Miller believed that YPM 1164 was the single type specimen of *P. occidentalis*, that consisted of the remains of five individuals collected at different places and times. A similar mistake was made in the case of *P. ingens*. Because of the apparently cursory nature of Miller's revision and his numerous mistakes, most subsequent workers have disregarded the revision.

Wellnhofer (1978) briefly reviewed the taxonomy of *Pteranodon*. In addition to the five species based on crania recognized by Miller, he recognized *P. ingens* and *P. occidentalis* based on postcranials. He did not list or comment on Miller's subgenera and argued against the inclusion of *Nyctosaurus* in the genus *Pteranodon*.

Schoch (1984) illustrated the type specimens of *Pteranodon* in the YPM collections and designated lectotypes for the species described by Marsh. He commented that there appeared to be three size classes, and then set about lumping the species, primarily on the basis of size. Schoch concluded that *P. longiceps* and *P. marshi* were junior synonyms of *P. ingens*, that *P. comptus* was a junior synonym of *P. velox*, and that *P. eatoni* was a junior synonym of *P. occidentalis*. In effect, Schoch disregarded Miller's revision and returned to the original scheme of Marsh (1872) with three species separated on the basis of size. Schoch did not comment on the upright-crested species, *P. sternbergi* and *P. walkeri*, or on Miller's point that it was not possible to distinguish between backward-crested and upright-crested species of *Pteranodon* solely on the basis of postcranials.

Phylogenetic Relationships.—The study of the phylogenetic relationships of pterodactyloids is in its infancy. Howse (1986) presented a cladistic analysis of the pterodactyloids based on characters of the cervical vertebrae. He noted that the primitive Jurassic pterodactyloids gave rise to two major groups, "long-necked" and "tall-spined" pterodactyloids. Bennett (1989) presented an analysis of the Cretaceous pterodactyloids based on characters of the pectoral girdle and forelimb in addition to Howse's characters. It was suggested that there are four major monophyletic groups of Cretaceous pterosaurs: the Pteranodontidae as diagnosed by Padian (1984) and Bennett (1989) on humeral characters; the Azhdarchidae as diagnosed by Nessov (1984) and Padian (1984, 1986) on cervical characters; the Dsungaripteridae as diagnosed by Bennett (1989) on characters of the forearm and carpus; and the Nyctosauridae as diagnosed by Bennett (1989) on characters of the pectoral girdle and forelimb.

Bennett (1989) suggested that the Azhdarchidae and Pteranodontidae are sister groups based on the form of the articulation between the scapula and notarium. The condition of the scapula and notarium in pterodactyloids seems to form a morphological series. In *Dsungaripterus*, the medial end of the scapula has an elongate oval articulation and is expanded and rugose for the attachment of ligaments, whereas in *Pteranodon* and *Quetzalcoatlus*, the articular surface of the scapula is subcircular and the scapula is not expanded for ligaments. Bennett (1989) suggested that the latter condition is a synapomorphy of the Pteranodontidae and Azhdarchidae. It was the only character cited to support the idea that the two clades are sister groups. Subsequently, characters have been noted that suggest that the Azhdarchidae and Dsungaripteridae are sister groups. Thus, the similarity in the form of the scapular articulation of *Pteranodon* and *Quetzalcoatlus* may be convergent. As a result of his cladistic analysis, Unwin (1992) identified the same major clades of Cretaceous pterosaurs as did Bennett (1989), but unfortunately, none of the characters used in Unwin's analysis was discussed.

MATERIALS AND METHODS

The recognition of fossil species usually presents problems, and the outcome of a taxonomic study of fossil materials is dependent upon the approach used by the taxonomist. In the past, authors usually adopted a typological approach and specimens that differed significantly in size or morphology were considered to represent separate species. This approach resulted in 11 named species of *Pteranodon* from the Niobrara Formation. Had this taxonomic revision of *Pteranodon* been done typologically, it would have been necessary to name at least three additional species based on slight variations in cranial crests and skull shape. A more realistic approach is to accept that within any population of a species there may be considerable morphological variation because of ontogenetic, sexual, and individual differences. When dealing with fossils, there also may be temporal and geographic differences (Ostrom and Wellnhofer, 1986). The problem then is to determine whether the morphological variation within a fossil assemblage reflects intraspecific or interspecific variation. An excellent example of this approach is the taxonomic revision of the ceratopsian dinosaur *Triceratops* by Ostrom and Wellnhofer (1986). They noted that the 16 nominal species of *Triceratops* differed primarily in the size and shape of the horns. They presented a study of the variation of horn morphology of extant artiodactyls, noted that the variation in horn morphology of *Triceratops* was no greater than the variation in horn morphology of extant artiodactyls, and concluded that there was only one species of *Triceratops* from the Lance Formation of the western United States.

I have attempted to employ a similar realistic approach to the taxonomic revision of *Pteranodon*, and have accepted that there may be considerable morphological variation within a species. There may also be temporal variations because of the more than four million years spanned by the fossil record of *Pteranodon* in the Western Interior Seaway. This taxonomic revision is part of a comprehensive reexamination of the over 1100 specimens of *Pteranodon* that made it possible to separate and identify much of the variation resulting from ontogenetic, sexual, and temporal differences (Bennett, 1991; 1992; 1993). Significant variation was noted in size, cranial morphology, size and shape of the cranial crest, and morphology of the pelvis.

A statistical analysis of measurements of *Pteranodon* from the Smoky Hill Chalk showed that there are two size classes (Bennett, 1991; 1992). The two size classes occur together throughout the Smoky Hill Chalk and differ in the relative size of the cranial crest and the morphology of the pelvis. Other than the difference in pelvic morphology, no morphological difference in the postcranial skeleton could be found between or within the size classes. The size classes are not year classes, or subadults and adults, because immature and mature individuals are present in each size class (Bennett, 1991; 1993). The size classes seem to be sexes, and the small class, which has a relatively large pelvic canal, is considered to be female, whereas the large class, which has large cranial crests (= display structures), is considered to be male.

The shape of the cranial crest varies in each size class. These variations are most noticeable in large individuals. In some large skulls, the cranial crest is directed backward and is a long, narrow blade, whereas in others, it is directed upward and is bulbous in profile (Figs. 1, 2). Stratigraphic positions of specimens from the Smoky Hill Chalk suggest that these two cranial morphs did not coexist (Fig. 3). Skulls with upright cranial crests are found in the lower part of the Smoky Hill Chalk from Marker Unit 4 up to Marker Unit 7, whereas skulls with narrow, backward-directed crests occur in the upper part of the Smoky Hill Chalk between Marker Units 13 and 20. Because the two morphs do not co-occur, they may be early and late forms of a single anagenetically evolving lineage; however, the differences in cranial morphology between the two morphs are sufficient to justify their recognition as separate species. In the following taxonomic revision, the upright-crested species from the lower part of the Smoky Hill Chalk is *Pteranodon sternbergi*, and the backward-crested species from the upper Smoky Hill Chalk is *Pteranodon longiceps*. All other species of *Pteranodon* are junior synonyms, *nomina dubia*, or referable to *Nyctosaurus* (Table 1).

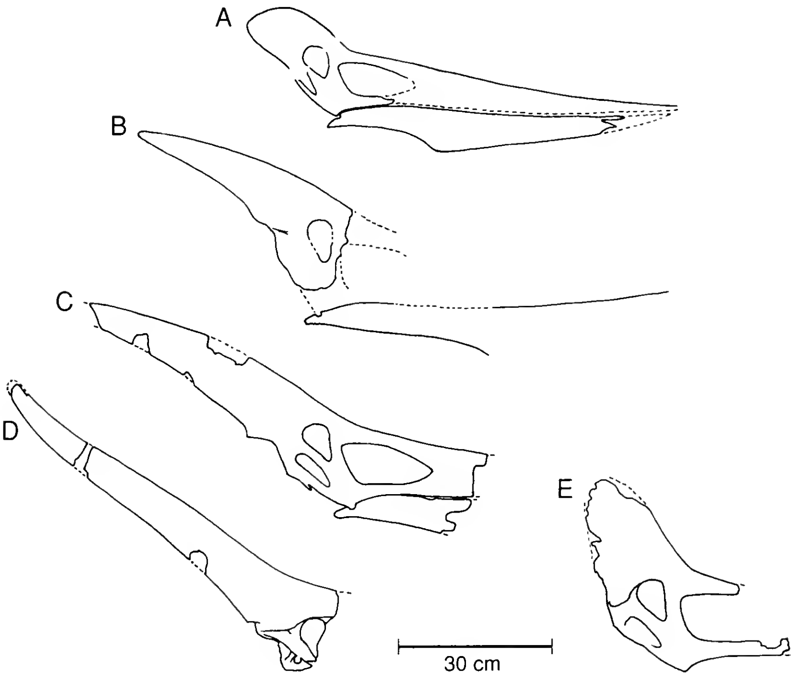

Fig. 1. Cranial crests of large specimens of *Pteranodon longiceps*. **A**. FHSM VP 221 (left lateral view reversed). **B**. DMNH 1732. **C**. YPM 2594. **D**. YPM 2473. **E**. KUVP 27821. The shallow mandibular ramus of DMNH 1732 may indicate that it is a subadult with the dentaries not fused to the rest of the mandible.

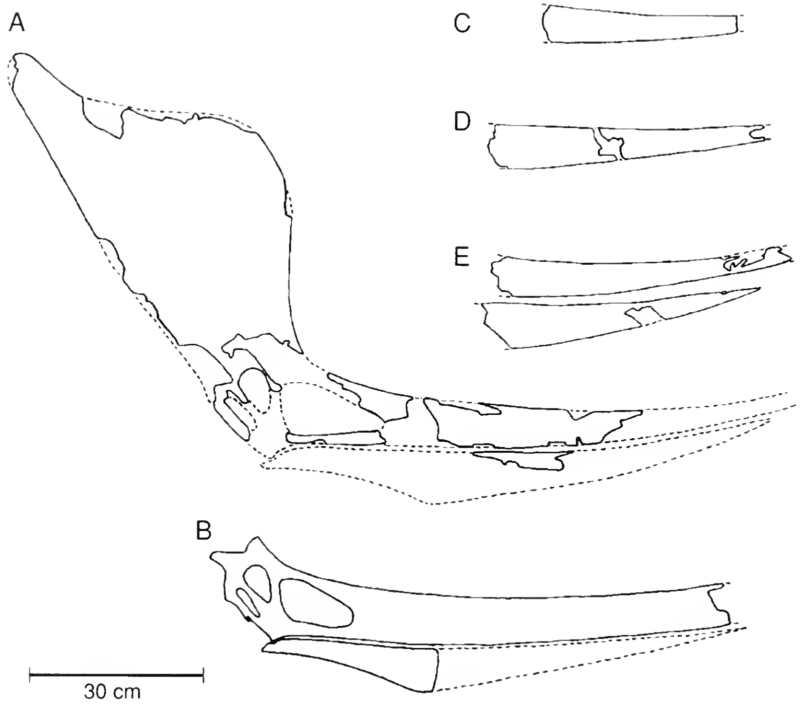

Fig. 2. Cranial crests of *Pteranodon sternbergi* and jaws of *Pteranodon*. **A**. FHSM VP 339 (left lateral view reversed). **B**. UALVP 24238. **C**. YPM 2489. **D**. AMNH 1974 (left lateral view reversed). **E**. KUVP 967. **A** and **B** are *P. sternbergi;* **C** and **E** are *P. longiceps;* and **D** is *Pteranodon* sp. indet.

There may be a minor difference in the angle of the occiput between the two species. In specimens of *Pteranodon sternbergi* (FHSM VP 339, UALVP 24238), the occiput lies at an angle of 38–41° to the palate, whereas in specimens of *P. longiceps*, the angle is 26.5–28° (Bennett, 1991; MS). This suggests that there was a trend toward lower angles. However, these differences in the angle of the occiput may be small enough that they could be attributed to individual, preservational, populational, or geographic variation. More specimens are needed to determine whether there was such a trend.

In view of the fact that the statistical analysis of *Pteranodon* showed that there are only two size classes, it is interesting to consider how the idea that there were three size classes became fixed. The notion of three size classes and three species of *Pteranodon* derives from Marsh's (1872) description of *P. ingens* (large), *P. occidentalis* (small), and *P. velox* (smallest). The type specimen of *P. velox* is small apparently because it is a subadult. The

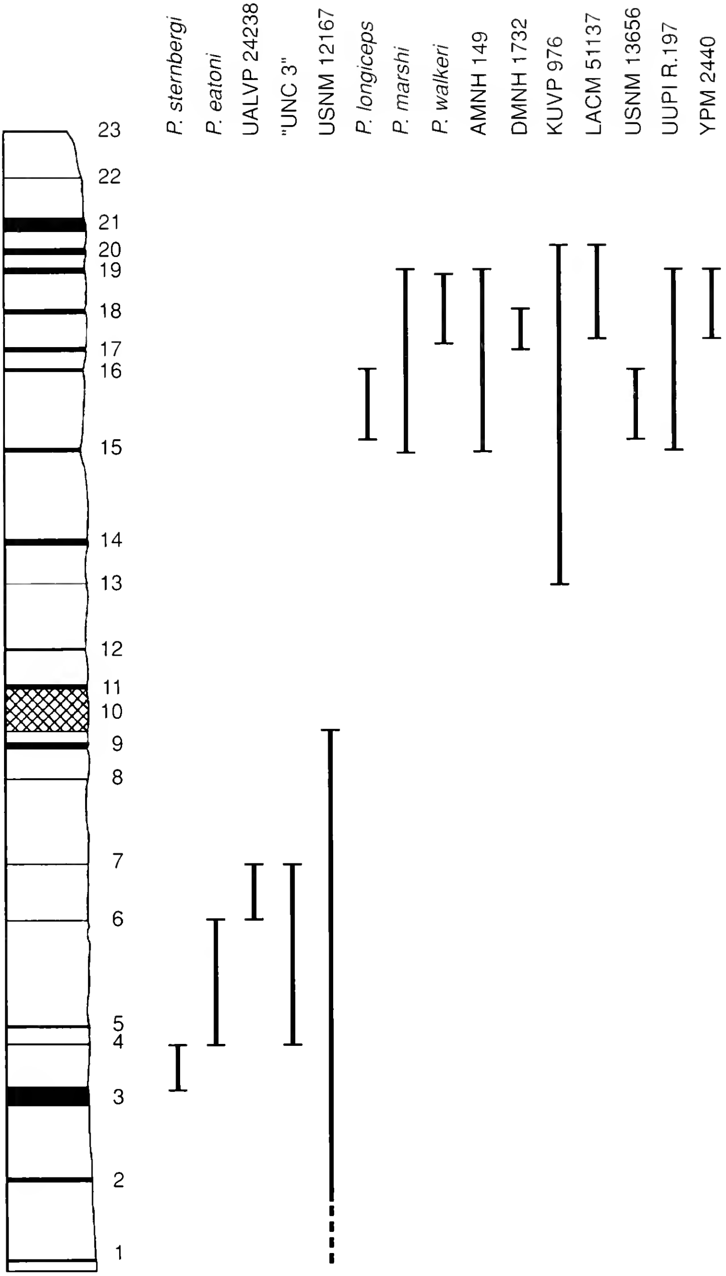

Fig. 3. Inferred stratigraphic positions or ranges of specimens of *Pteranodon* plotted against the composite stratigraphic column of Hattin (1982).

Table 1. Summary of named species of *Pteranodon* and *Nyctosaurus* from the Niobrara Formation of Kansas.

Species	Status here
Pterodactylus occidentalis Marsh, 1872 (= *Pterodactylus oweni* Marsh, 1871)	Nomen dubium
Pterodactylus ingens Marsh, 1872	Nomen dubium
Pterodactylus velox Marsh, 1872	Nomen dubium
Ornithochirus umbrosus Cope, 1872	Nomen dubium
Ornithochirus harpyia Cope, 1872	Nomen dubium
Pteranodon longiceps Marsh, 1876a	*Pteranodon longiceps*
Pteranodon gracilis Marsh, 1876a	*Nyctosaurus gracilis*
Pteranodon comptus Marsh, 1876a	Nomen dubium
Pteranodon nanus Marsh, 1881	*Nyctosaurus nanus*
Pteranodon sternbergi Harksen, 1966	*Pteranodon sternbergi*
Pteranodon marshi Miller, 1972	Junior synonym of *P. longiceps*
Pteranodon bonneri Miller, 1972	*Nyctosaurus bonneri*
Pteranodon walkeri Miller, 1972	Junior synonym of *P. longiceps*
Pteranodon eatoni Miller, 1972	Junior synonym of *P. sternbergi*

distal end of the wing metacarpal was not fully ossified and, thus is smaller than the fully ossified distal wing metacarpals of adults. No other specimens were referred to *P. velox*, yet the one specimen suggested that there was a third size class. The appearance of three size classes and three species was continued by the skull YPM 1179 when Eaton (1910) abandoned postcranials as useless in differentiating species of *Pteranodon*. Marsh had referred the skull to *P. occidentalis* when *P. longiceps* was described, and Eaton accepted the referral. YPM 1179 had been incorrectly reassembled and the dentary was not preserved with the mandible, so that the skull appeared to be smaller and more lightly built than that of *P. longiceps* (YPM 1177). However, YPM 1179 is not much smaller than YPM 1177. Miller's revision had three size classes and five species of *Pteranodon:* large and small backward crested "longicepias," large and small upright crested "sternbergias," and the even smaller *P. eatoni* based on the same incorrectly reassembled skull of YPM 1179. Miller (1972: 6) noted that the large and small forms might represent different sexes, but decided against that interpretation:

> It is possible that the larger crested species of the sternbergias and longiceps [sic] are males and the smaller crested species of those subgenera are females and thus the specific differencs [sic] cited herein are invalid. But it is equally possible that the smaller sized (and usually smaller crested forms) gave rise to the larger species and they form an evolutionary sequence. The problem is not solvable with our present lack of stratigraphic controls.

The incorrectly reassembled skull of YPM 1179 may have led Miller to reject the possibility of sexual dimorphism and adopt an evolutionary lineage interpretation of the size classes and morphs of *Pteranodon*.

Phylogenetic Analysis.—The cladistic analysis of the Pterodactyloidea is based on characters suggested by Nessov (1984), Padian (1984; 1986), Howse (1986), and Bennett (1989), plus additional characters (character transformations and data matrix in Appendix). Character information for the following taxa was based on published accounts and personal observations: *Anhanguera* (Campos and Kellner, 1985; Wellnhofer, 1985, 1991), *Azhdarcho* (Nessov, 1984), *Criorhynchus* (Hooley, 1914), *Brasileodactylus* (Kellner, 1984), *Ctenochasma* (Wellnhofer, 1970; de Buisonje, 1981), *Dsungaripterus weii* (Young, 1964, 1973), *Gallodactylus* (Fabre, 1976), *Germanodactylus* (Wellnhofer, 1970), *Gnathosaurus* (Wellnhofer, 1970), *Huanhepterus* (Dong, 1982), *Nyctosaurus* (Williston, 1902a,b, 1903), *Ornithocheirus* s.l. (Hooley, 1914; Seeley, 1870), *Ornithodesmus* (Hooley, 1913), *Pteranodon* (Bennett, 1991), *Pterodactylus* (Wellnhofer, 1970), *Quetzalcoatlus* (Lawson, 1975a,b; Langston, 1981), *Rhamphorhynchus* (Wellnhofer, 1975), *Santanadactylus araripensis* (Wellnhofer, 1985), and *Santanadactylus brasiliensis* (de Buisonje, 1980). I was unable to examine specimens of *Arambourgiania* (Arambourg, 1959), *Doratorhynchus* (Seeley, 1875), *Dsungaripterus parvus* (Bakhurina, 1982), and *Pterodaustro* (Bonaparte, 1970, 1971; Sanchez, 1973); thus character coding for those taxa is based solely on published accounts.

A phylogenetic analysis of the rhamphorhynchoid pterosaurs by Padian (pers. comm.) suggested that *Rhamphorhynchus* is the sister taxon of the Pterodactyloidea, and similarly, Unwin's (1992) analysis placed the Rhamphorhynchidae as the sister group of the Pterodactyloidea. Therefore, *Rhamphorhynchus* was used as an outgroup to polarize character transformations in the analysis. The data were analyzed using MacClade 3.01 (Maddison and Maddison, 1992). Numerous most parsimonious bifurcating trees were identified; however, collapsing branches to polytomies produced a single tree topology. The tree, based on 26 ingroup taxa and 37 characters, has 67 steps and a Consistency Index of 0.73. In all cases, taxa are placed on the tree as low as possible; that is, the character transformation is accelerated to more basal levels. Thus, *Brasileodactylus* may be an azhdarchid, but available information indicates only that it is an ornithocheiroid. Most character transformations have a single derived state, but Characters 9, 11, 13, 15, 17, 28, 29, 32, and 36 have more than one derived state and were not ordered for the analysis. In addition, the polarity of Characters 24–27 is unclear and they were not ordered. All other characters were ordered.

INCORRECTLY REFERRED MATERIALS

A number of specimens have been referred to *Pteranodon*, despite the fact that they either cannot pertain to the genus because of significant morphological differences, or should not be referred to *Pteranodon* because they are indeterminate.

Gilmore (1935) referred a proximal left humerus of a pteranodontid from the Eagle Ford Formation (late Cenomanian to late Turonian) of Texas (USNM 13804) to *Pteranodon*. The specimen differs from *Pteranodon* in the large size and proximal position of the pneumatic foramen on the dorsal side of the humerus near the posterior tuberosity, and the absence of a pneumatic foramen on the ventral surface near the deltopectoral crest. Therefore, it cannot pertain to *Pteranodon*. Additional materials from the Eagle Ford Formation include a proximal radius (TMM 40032–1) and a wing shaft fragment (TMM 42562–2), both of which are indeterminate. Because the humerus displays characters that are inconsistent with *Pteranodon*, it is possible that all the Eagle Ford materials represent a distinct pteranodontid, although the materials are not sufficient for the erection of a new genus.

Bogolubov (1914) described a single incomplete cervical vertebra from the Senonian of Russia as *Ornithostoma (Pteranodon) orientalis*. It is clear that he referred it to *Ornithostoma*, which at the time was considered by some to be a senior synonym of *Pteranodon*, because the vertebra was similar to those of *Pteranodon*. However, the specimen does not possess any characters that warrant its referral to *Pteranodon*, and recently Nessov and Jarkov (1989) erected the genus *Bogolubovia* for the specimen and referred it to the Azhdarchidae.

Obata et al. (1972) described a single incomplete bone of a large pterodactyloid from the Santonian to upper Campanian of Hokkaido and referred to it as *Pteranodon* sp. The element was not identified, but was said to resemble a fragment figured by Owen (1851: pl. 32, figs. 6, 6') that may be the proximal end of a first wing phalanx, and distal femora figured by Young (1964: fig. 10). Whatever the identity of the element, it is indeterminate and there is no justification for its reference to *Pteranodon*.

Gilmore (1928) described a large pterodactyloid pterosaur from the Hudspeth Formation (Albian) of Wheeler Co., Oregon, as *Pteranodon (?) oregonensis*. The type specimen (USNM 11925) includes a left humerus, with incomplete deltopectoral crest and damaged distal end, and two co-ossified dorsal vertebrae. The deltopectoral crest of the humerus is not warped like that of pteranodontids and the shaft does not taper evenly from the base of the deltopectoral crest to the distal end, which indicate that the species is not a pteranodontid (Padian, 1984; Bennett, 1989). Bennett (1989) suggested that the species was an azhdarchid "because no other taxa are known from the Upper Cretaceous that retain the primitive condition of the humerus" (Bennett, 1989: 675). This is wrong because the Albian is not Upper Cretaceous, and because there are other large pterodactyloids known from the Albian that exhibit the primitive condition of the deltopectoral crest. In fact, the humerus appears to resemble those of *Dsungaripterus* and an as yet unnamed pterosaur from the Santana Formation of Brazil (pers. observ.). Nessov (1991) placed the species in the new genus *Bennettazhia* and referred it to the Azhdarchidae, based primarily on Bennett's suggestion that the specimen was an azhdarchid.

The suggestion that *Ornithostoma* is congeneric with *Pteranodon* should be considered. The name *Ornithostoma* was given by Seeley (1871) to a bone fragment from the Cambridge Greensand that Owen (1859: pl. 4, figs. 4, 5) described as the proximal part of a wing metacarpal. Seeley reinterpreted the specimen as an edentulous jaw fragment. As noted above, Williston thought that *Ornithostoma* was the same as *Pteranodon* because both were toothless pterosaurs and suggested that *Ornithostoma* had priority over *Pteranodon;* however, Plieninger (1901) argued that *Ornithostoma* did not have priority. The edentulous jaw fragment of *Ornithostoma* differs from the jaw of *Pteranodon*. The jaws of *Pteranodon* have marginal ridges that extend 3–4 mm above the floor or roof of the mouth and that are composed of dense bone. The jaw of *Ornithostoma* lacks such ridges; instead, the jaw margins are rounded much like the jaws of the toothed *Ornithocheirus cuvieri*, although there are no teeth or alveoli. *Ornithostoma* presents a taxonomic problem because no specific name was given (Plieninger, 1901; and see Wellnhofer, 1978 for a brief discussion); however, because *Ornithostoma* is quite distinct from *Pteranodon*, it is not necessary to consider it further here.

NYCTOSAURUS

The taxonomy of *Nyctosaurus* has long been entangled with that of *Pteranodon*, probably because both are found in the Niobrara Formation and have elongate, tapering, edentulous jaws. Miller (1972) considered *Nyctosaurus* to be a subgenus of *Pteranodon*, but Bennett (1989) argued that it was distinct from *Pteranodon* and that it should be placed in a separate family. There are three named species of *Nyctosaurus* (Table 1): *N. gracilis*, *N. nanus*, and *N. bonneri*. *Nyctosaurus gracilis* is from the upper part of the Smoky Hill Chalk, whereas *N. nanus* is from quite low in the Smoky Hill Chalk. The two species differ considerably in size; although fully adult, *N. nanus* is much smaller than *N. gracilis*. The two species are also separated by a considerable temporal gap and so seem to be distinct. *Nyctosaurus bonneri* is from the upper part of the Smoky Hill Chalk, approximately contemporaneous with *N. gracilis*, and differs only in the proportions of the hind limb. Although a formal taxonomic revision of *Nyctosaurus* is beyond the scope of this paper, the difference between *N. gracilis* and *N. bonneri* does not seem to be significant, and I suspect that *N. bonneri* is a junior synonym of *N. gracilis*.

SYSTEMATIC PALEONTOLOGY

Class Reptilia

Subclass Archosauria

Order Pterosauria

Suborder Pterodactyloidea Plieninger, 1901

Infraorder Eupterodactyloidea, Infraordo Novum

Diagnosis.—Pterodactyloids with: helical jaw joint; atlas and axis fused; cervical vertebrae with exapophyses, tall neural spines, pneumatic foramina lateral to the neural canal; notarium of at least three fused dorsal vertebrae and fused ribs; scapula rotated with posterior/medial end approaching vertebral column; straight humeral shaft.

Definition.—That clade of pterodactyloids that shares the synapomorphy of the scapula rotated so that the posterior/medial end approaches the vertebral column.

Remarks.—The outward rotation of the scapula so that it serves as a brace for the wing is a remarkable innovation in pterodactyloid evolution. Unwin (1992) viewed this feature as having been evolved convergently in various lineages of large pterodactyloids. However, the rotation of the scapula is such an unusual feature that multiple evolution seems unlikely and the analysis supports that interpretation. Our current knowledge of pterodactyloid evolution suggests that a number of other innovations occurred at approximately the same point as the scapular rotation and so the members of this clade are remarkably different from the earlier pterodactyloids in morphology. The combination of these evolutionary innovations may have permitted a new radiation of pterodactyloids to evolve large size and replace more primitive pterodactyloids.

Superfamily Ornithocheiroidea, Seeley, 1870

Diagnosis.—Eupterodactyloids with: palate with median ridge and mandible with corresponding median groove; cranial crest on premaxillae, pneumatized with smooth surface and even dorsal margin; notarium with supraneural plate of fused neural spines; scapula articulating with supraneural plate of notarium.

Definition.—That clade of eupterodactyloids that shares the synapomorphy of the median palatal ridge and a corresponding median mandibular groove.

Remarks.—There has long been confusion regarding the identity of the Pteranodontidae and Ornithocheiridae. Seeley (1870) cited teeth prolonged anterior to the end of the premaxillae and a median ridge on the palate as important characters of *Ornithocheirus*. Marsh's (1876a) original diagnosis of the Pteranodontidae emphasized edentulous jaws and a cranial crest as the primary characters, although postcranial characters were mentioned as well. Wellnhofer (1978) diagnosed the Pteranodontidae (including *Nyctosaurus* and *"Ornithostoma"*) as having the following characters: (1) large pterosaurs; (2) skull very large with long, pointed, edentulous beak; (3) with or without parietal crest; (4) relatively small external skull openings; (5) mandible as deep as premaxillae are high; (6) pneumatic (cervical) vertebrae; (7) notarium of up to eight dorsals and sacrum with 6–10 sacrals; (8) wing extremely robust compared to hind limb; (9) some of proximal and distal rows of carpals fused; (10) Metacarpal IV substantially longer than antebrachium; (11) Metacarpals I–III reduced to splints without proximal ends and closely associated with Metacarpal IV; (12) manual Digits I–III with short clawed fingers; (13) femur slightly longer than humerus; (14) proximal tarsals fused to tibia; (15) fibula fused to tibia; and (16) Metatarsal V reduced. Many of these characters diagnose more general levels of pterosaurs and are symplesiomorphic for the Pteranodontidae. Padian (1984) rediagnosed the Pteranodontidae and included edentulous jaws and a cranial crest in his diagnosis, but stated that the warped deltopectoral crest was the "principal defining character" of the Pteranodontidae. Within the clade diagnosed by the warped deltopectoral crest, *Pteranodon* is the only genus known to possess edentulous jaws or a cranial crest formed primarily by the frontals. Rather than restrict the term Pteranodontidae to the genus *Pteranodon*, Padian (1984) and Bennett (1989) applied the name to the clade diagnosed by the warped deltopectoral crest.

Wellnhofer (1978) diagnosed the Ornithocheiridae as having the following characters: (1) long skull with very slender, laterally compressed snout; (2) snout blunt or tapering to end; (3) teeth short, strong, round to oval in cross section, with finely striated surface; (4) teeth of uniform size, separated by more than width of tooth, and extending far back in jaws; (5) palate with median keel and mandible with corresponding groove between two ridges; (6) lateral margins of dentigerous parts of jaws parallel; (7) cross section of mandible triangular; (8) confluent naris and antorbital fenestra larger than orbit; (9) end of scapula expanded and articulating with notarium; (10) proximal tarsals fused to tibia; and (11) fibula fused to tibia. This diagnosis is so general that *Doratorhynchus* could be considered to be an ornithocheirid, although its elongate cervicals indicate that it is an azhdarchid. Of the characters listed as diagnostic of the Ornithocheiridae (Wellnhofer, 1978), *Pteranodon* has Characters 1, 2, and 7–11; the only characters that *Pteranodon* lacks relate to teeth, the parallel section of the jaws, and the median ridge and groove of the jaws. The parallel section of the jaws is relatively short compared to the length of the dentigerous part of the jaws (e.g., *Anhanguera* [Wellnhofer, 1985; 1991; Campos and Kellner, 1985]), and in large part, the jaws taper evenly from the articulations to the anterior end as in *Pteranodon*. Similarly, of the characters listed by Wellnhofer (1978) as diagnostic of the Pteranodontidae, the genera considered to be ornithocheirids by Wellnhofer (1991) have Characters 1, 4–9, and 12–16, and those characters they lack relate to edentulous jaws, cranial crests, and the hyper-elongate metacarpus of *Pteranodon*.

The dental characters of the Ornithocheiridae (sensu Wellnhofer, 1978) are certainly symplesiomorphic (e.g., *Pterodactylus antiquus*), and the principal defining character of the Ornithocheiridae (sensu Seeley, 1870, and Wellnhofer, 1978) is the complementary median palatal ridge and mandibular sulcus. This character is found in *Santanadactylus*, *Anhanguera*, *Criorhynchus*, *Tropeognathus*, *Doratorhynchus*, *Brasileodactylus*, and *Ornithocheirus* s.s. The first four genera are pteranodontid or probably pteranodontid on the basis of the humeral morphology. *Doratorhynchus* is an azhdarchid on the basis of the hyper-elongate cervical vertebrae. *Brasileodactylus* was based on a single mandibular fragment, but it is notable that a second mandible of *Brasileodactylus* (SMNS 55414) is preserved with cervicals like those of some *Ornithocheirus* s.l. from the Cambridge Greensand (Owen, 1860, pl. 2, figs. 13–16) in the same concretion. Seeley (1875) noted the similarity between those *Ornithocheirus* cervicals and the cervical of *Doratorhynchus*, although the latter is longer. This may suggest that *Brasileodactylus* and the very similar *Ornithocheirus daviesi* and *O. sedgwicki* have affinities with the azhdarchids. Small humeri of primitive morphology from the Santana Formation and the Cambridge Greensand may pertain to *Brasileodactylus* and *Ornithocheirus daviesi*. Thus, the median palatal ridge and mandibular sulcus diagnose a large clade including pteranodontids, dsungaripterids, and azhdarchids. The term Ornithocheiridae should be applied to the clade diagnosed by the median palatal ridge and mandibular sulcus. Such a usage is consistent with the classifications of Williston (1903) and Plieninger (1901; 1907) who both viewed the Ornithocheiridae as including *Ornithocheirus* and *Pteranodon*. Because of the extent of the clade it is suggested that the term be elevated to superfamily rank as the Ornithocheiroidea.

Family Pteranodontidae Marsh, 1876a

Type genus.—*Pteranodon* Marsh, 1876a.

Included genera.—*Pteranodon* Marsh, 1876a; *Ornithodesmus* Seeley, 1887; *Santanadactylus* de Buisonje, 1980; *Anhanguera* Campos and Kellner, 1985.

Diagnosis.—Ornithocheiroids with: humerus with warped deltopectoral crest, thin proximal flange spanning between head and distal end of crest, terminal expansion at end of crest; posterior tuberosity directed posteriorly; shaft of humerus increasing in diameter from base of deltopectoral crest to distal end; distal end of humerus subtriangular.

Definition.—That clade of ornithocheiroids that shares the synapomorphy of a humerus with warped deltopectoral crest, having a thin proximal flange spanning between head and distal end of crest and terminal expansion at end of crest.

Remarks.—The Pteranodontidae were recently diagnosed (Bennett, 1989) on the basis of humeral characters, in particular the presence of a warped deltopectoral crest. One character cited by Bennett, proximal pneumatic foramen of humerus on dorsal surface distal to ulnar crest (= posterior tuberosity), apparently is not a synapomorphy. *Pteranodon* has a nutrient foramen there and the pneumatic foramen is on the ventral surface between the head and deltopectoral crest. Thus, the character cannot apply to the Pteranodontidae unless it can be shown to have been present in ancestral pteranodontids and reversed in *Pteranodon*. A second character requires clarification. Bennett (1989) suggested that the posterior tuberosity of pteranodontids differed from that of the primitive condition, and figured a proximal view of USNM 11925 to show the primitive condition. He suggested that in pteranodontids the posterior tuberosity is directed posteriorly, whereas in the primitive condition, it is directed ventrally. Recently, I became convinced that the posterior tuberosity of USNM 11925 had been larger but was damaged. There still appears to be a difference between the two forms of posterior tuberosity, but it is less marked than was suggested. In pteranodontids, the tuberosity is nearly twice as long anteroposteriorly than tall, whereas in the primitive condition, the measurements are subequal.

The Pteranodontidae include at least four genera—*Pteranodon*, *Ornithodesmus*, *Santanadactylus*, and *Anhanguera*—and probably include *Criorhynchus* (Owen, 1874), *Tropeognathus* (Wellnhofer, 1987), and some species referred to *Ornithocheirus* (Seeley, 1869, 1870).

Ornithodesmus was erected by Seeley (1887) for the species *O. cluniculus* and was based on a sacrum from the Wealden that Seeley considered to be that of a bird. Apparently, Seeley later decided *Ornithodesmus cluniculus* was a pterosaur and named a second species *O. latidens* (Seeley, 1901). Hooley (1913) described the materials of *O. latidens* and stated that the sacrum of *O. cluniculus* was a notarium. Examination of the type specimen of *O. cluniculus* convinced me that the specimen is not pterosaurian and, instead, bears a strong resemblance to the sacrum of ornithomimid dinosaurs (Howse and Milner, 1993). The species *O. latidens* is a pteranodontid pterosaur because the humerus has the diagnostic warped deltopectoral crest.

Santanadactylus was erected for *Santanadactylus brasiliensis* (de Buisonje, 1980), and was based on the proximal half of a pteranodontid humerus from the Santana Formation of Brazil. Additional species, *S. araripensis* and *S. pricei* (Wellnhofer, 1985), were also based on specimens including pteranodontid humeri. They are not necessarily congeneric with *S. brasiliensis*. "*Santanadactylus*" *spixi* is based on a specimen with a humerus of primitive morphology and is not a pteranodontid (Wellnhofer, 1985; 1990; 1991; Bennett, 1989).

The skull of *Araripesaurus santanae* (Wellnhofer, 1985), named in the same publication as *Santanadactylus araripensis*, is very similar to the skull of the latter species, and appears to be a subadult *S. araripensis* (Bennett, 1993). It was referred to *Araripesaurus* (Price, 1971) because the proximal and distal rows of carpals were not fused into syncarpals. Shortly thereafter, Campos and Kellner (1985) named *Anhanguera blittersdorfi* based on yet another skull. Wellnhofer (1991) transferred *Araripesaurus santanae* to *Anhanguera* because a second immature specimen (AMNH 22555) with unfused syncarpals included a skull with a small premaxillary crest like that of *Anhanguera blittersdorfi*. The skull of *Santanadactylus araripensis* does not include much of the premaxillary crest; however, the posterior end of the crest is present. In my opinion, both species of *Anhanguera* are junior synonyms of *Santanadactylus araripensis* (Bennett, 1988; Wellnhofer, 1989) and, therefore, are pteranodontids, although not necessarily congeneric with *Santanadactylus brasiliensis*. However, a taxonomic revision of the Santana Formation pterosaur fauna is beyond the scope of this work.

Postcranial remains from the Cambridge Greensand and English Chalk include humeri with warped deltopectoral crests that are pteranodontid. All postcranial remains from these deposits have been referred to the genus *Ornithocheirus* s.l., whereas the cranial remains have been placed in the genera *Ornithocheirus* s.s. and *Criorhynchus* (Wellnhofer, 1978). Some of the materials of *Ornithocheirus* s.s. from the Cambridge Greensand are similar to *Santanadactylus*, and probably are pteranodontid. *Criorhynchus* seems to be a pteranodontid because the only humeri from the Cambridge Greensand large enough to pertain to the *Criorhynchus* premaxillae fragments are pteranodontid. Likewise, *Tropeognathus* probably is pteranodontid because it is similar to *Criorhynchus* (Wellnhofer, 1987) and because the only humeri from the Santana Formation large enough to pertain to it are pteranodontid.

Wellnhofer (1991) suggested that *Pteranodon* did not have a warped deltopectoral crest because he could not see it in crushed specimens. Relatively uncrushed specimens do exist (e.g., YPM 1164, 2499; Fig. 4), and careful examination of typical crushed specimens also reveals the warped crest. In order to discuss the form of the warped deltopectoral crest,

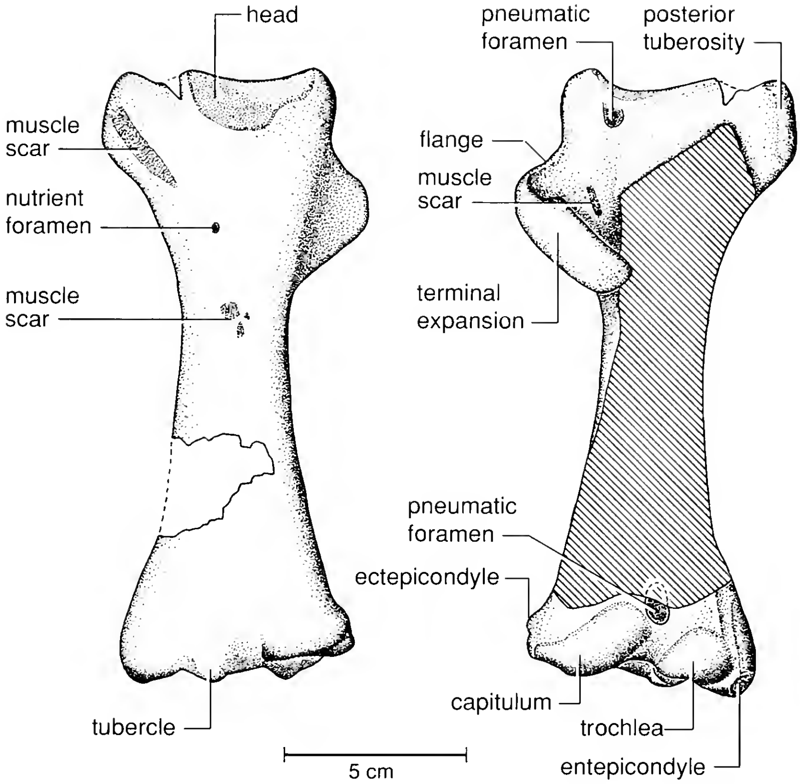

Fig. 4. Right humerus of YPM 1164. **A**. Dorsal view. **B**. Ventral view. Cross-hatched area is covered by matrix.

Bennett (1989) illustrated an uncrushed pteranodontid humerus (USNM 13804) rather than a *Pteranodon* humerus because it showed the morphology of the crest better than crushed humeri of *Pteranodon* from the Niobrara Formation.

Genus *Pteranodon* Marsh, 1876a

Type species.—*Pteranodon longiceps* Marsh, 1876a.

Included species.—*Pteranodon longiceps* Marsh, 1876a; *Pteranodon sternbergi* Harksen, 1966.

Distribution.—Smoky Hill Chalk Member of the Niobrara Formation (Coniacian to lower Campanian) of western Kansas and South Dakota; Sharon Springs Member of the Pierre Shale (lower Campanian) of western Kansas, South Dakota, and Wyoming. Indeterminate pteranodontid materials that may be *Pteranodon* have been collected from the Mooreville Chalk

Member of the Selma Formation (lower Campanian) of Alabama, and the Merchantville Formation (lower Campanian) of Delaware.

Diagnosis.—Pteranodontids with: cranial crest formed by frontals and directed upward or backward from skull; premaxillary crest with relatively straight dorsal margin, not rounded in profile; edentulous jaws with raised marginal ridges; beaks long and slender with premaxillae and dentaries tapering to points; premaxillae extending beyond end of mandible; mandibular symphysis approximately two thirds of length of mandible; ceratobranchials of hyoid apparatus greatly reduced or unossified; nasal process reduced; neural spines of dorsal and sacral vertebrae narrow anteroposteriorly; notarial and synsacral supraneural plates formed of ossified interspinous ligaments; postacetabular process of ilium contacting neural spines of posterior synsacral vertebrae and fused with them in mature adults; proximal caudal vertebrae with duplex centra; distal caudal vertebrae reduced and co-ossified to form caudal rod; proximal pneumatic foramen of humerus on ventral surface near proximal end of deltopectoral crest; nutrient foramen on dorsal surface of humerus; distal pneumatic foramen of humerus on ventral surface just proximal to and between condyles; metacarpus length equal to or greater than 1.5 times length of antebrachium; proximal ends of Metacarpals I–III not reaching distal syncarpal; distal syncarpal lacking facets for Metacarpal I–III; distal end of wing metacarpal without an elevation between condyles.

Some of these characters may not be synapomorphies of *Pteranodon*, but none of them is known to be shared with other pteranodontid taxa. New information on related taxa may show some characters to be symplesiomorphies.

Pteranodon does not display the widely spaced, trenchant teeth, and palatal ridge and mandibular groove of *Ornithocheirus* s.s., *Brasileodactylus*, *Santanadactylus araripensis*, *Anhanguera*, *Criorhynchus*, and *Tropeognathus*. *Pteranodon* lacks the rounded or bulbous premaxillary and mandibular crests of *Anhanguera*, *Criorhynchus*, and *Tropeognathus*. *Pteranodon* lacks the interlocking triangular teeth and rounded distal end of the beaks, deeply keeled cristospine and asymmetrical sternocoracoid articulations of *Ornithodesmus latidens*. *Pteranodon* lacks the large pneumatic foramen on the dorsal surface of the humerus near the posterior tuberosity found in other pteranodontid humeri, having instead a small nutrient foramen in its place and a large pneumatic foramen on the ventral surface near the deltopectoral crest.

Hypodigm.—Specimens from the Niobrara Formation include: **AMNH** 138A, 139–141, 144, 145, 147–153, 153A, 154, 155, 167, 168, 219, 1571–1573, 1644, 1800, 1974, 2004, 2085, 2094, 2095, 2122, 2123, 2169–2177, 2180, 4906–4908, 5098, 5099, 5819, 6158, 7515, 7519, 7608, 8595, 23701. **BHI**, eight uncatalogued specimens. **BMNH R** 2929–2939, 2945, 2959, 3299, 4006–4008, 4010, 4011, 4078, 4534–4539, 4541–4546, 4549, and one uncatalogued specimen. **CM** 1539, 1540, 11400, 11400-A, 11402–11413, 11415, 11416, 11418–11421, and nine uncatalogued specimens. **DMNH** 1732. **FFM**, one uncatalogued specimen. **FHSM** 184, 221, 339, 696, 2059, 2062–2067, 2070, 2072, 2119, 2120, 2140–2147, 2183, 2232, 2288, 4515, 4522, 4526, 5316, 8224. **FMNH P** 27476, **FMNH PR** 139, 494, 1144, 1602, **FMNH UR** 895, **FMNH UC** 609, 1336–1338, 1341, and one uncatalogued specimen. **KUVP** 917–926, 928–931, 933, 935, 937–945, 947–949, 951–955, 957–959, 961, 963–981, 983, 987–991, 993–995, 997, 998, 5071, 9786, 16487, 27827–27829, 28709, 28710, 40012, 40302–40304, 40332, 40335, 49164, 49398–49400, 49417, 49502, 56648–56650, 57291, 60617, 65724, 65725, 65737, 65742, 65748, 66111, 66115, 66137, 66141, 69446–69449, 84836, 84844, 84851, 85027, 85371–85393, 85395–85441, 85444, 85446–85450, 85452–85462, 85464–85470, 85472, 85590. **LACM** 50924–50927, 51129, 51131–51134, 51136–51138, 51760, 51762, and two uncatalogued specimens. **MCZ** 279, 3815, and five uncatalogued specimens. **MNHN**, two uncatalogued specimens. **NMC** 8167. **ROM** 26104–26107. **UALVP** 24238, 24239. **UM** 3222, 3611, 9074, 9075, 9083, 12396–12404, 12407. **UM V** 56571. **UNSM** 50128–50130, 50036, 50037. **UOCM F** 746, 747, 31157–31160, 31162, 31203, 31224, 31228, 31231–31233. **USNM** 6075, 9050, 11642, 12167, 13656, 13804, 13868, 16837, 20621, 20711, 407634–407644. **UUPI R**.197. **YPM** 1160–1162, 1164–1166, 1169–1172, 1175–1177, 1179–1181, 1183–1186, 1188, 1189, 1191–1199, 1455, 2264–2267, 2269–2289, 2300–2302, 2304–2311, 2320, 2331–2333, 2335–2340, 2342–2348, 2350, 2352–2364, 2366, 2371–2381, 2390, 2391, 2396, 2397, 2399–2410, 2412–2481, 2483–2512, 2514, 2520–2526, 2528–2568, 2570–2599, 2599 1/2, 2600–2602, 2604–2620, 2623–2630, 2635–2701, 2703–2716, 2720–2728, 2728 1/2, 2728 3/4, 2729–2761, 2767–2769, 2771–2790, 2799, 2810–2813, 2830–2834, 5775, 42794–42797, 42800–42827, 42829, 42835–42837. "**UNC** 2–8": seven uncatalogued specimens in private collections (see Bennett, 1991). Specimens from the Pierre Shale include: **AMNH** 5819, 5840, 5841. **BHI**, one uncatalogued specimen. **CU** 45062, 47280. **FMNH PR** 464, 468–470, 676, 1332. **KUVP** 27821, 33564, 36116, 50011, 50013, 50015–50019, 50089, 85445. **LACM** 126163, 127314. **SDSM** 497, 5817, 5818, 51141, 54358, 56128. **USNM** 18266.

Remarks.—*Pteranodon* accounts for almost all of the pterosaur specimens from the Niobrara Formation, whereas specimens of *Nyctosaurus* (the only other pterosaur known from the Niobrara Formation) constitute less than 3% of the materials. In addition, *Pteranodon* is the only pterosaur known from the Pierre Shale. *Pteranodon* has not been identified from any other formations. However, fragmentary specimens that are not diagnostic of, yet are not inconsistent with, *Pteranodon*, have been found in the Selma

Chalk Member of the Mooreville Formation of Alabama (FMNH P 27476, PR 139, 1144, and undescribed materials in the Red Mountain Museum; not in the Cleveland Museum of Natural History as stated in Lawson, 1975a), and the Merchantville Formation of Delaware (YPM-PU 21820 and 22359; Baird and Galton, 1981). These specimens are approximately contemporary with, and not too far removed geographically from, the known occurrences of *Pteranodon;* thus, it is possible that these specimens are *Pteranodon.* Pteranodontid materials from the Mowry Shale (Albian) of Montana and the Eagle Ford Formation (late Cenomanian to late Turonian) of Texas (Gilmore, 1935), which differ from *Pteranodon* in the position of the proximal pneumatic foramen and in the shape of the distal end of the humerus, cannot be referred to *Pteranodon.*

The relationships of *Pteranodon* to other pterodactyloid pterosaurs are not fully understood and more work is needed to resolve the relationships within the Pteranodontidae. *Pteranodon* has the diagnostic humeral characters of the Pteranodontidae (Bennett, 1989). Among pteranodontids, *Pteranodon* is derived relative to *Santanadactylus* and *Ornithodesmus* in possessing edentulous jaws, the proximal ends of Metacarpals I–III not articulating with the distal syncarpal, and an extremely long metacarpus. *Pteranodon* seems to be primitive in regard to the apparent retention of a pneumatic foramen on the ventral side of the humerus near the deltopectoral crest. (See cladistic analysis below.)

Miller (1972; 1973; 1978) erected three subgenera of *Pteranodon, Pteranodon (= Longicepia), Geosternbergia (= Sternbergia),* and *Occidentalia,* and also considered *Nyctosaurus* to be a subgenus of *Pteranodon.* Bennett (1989) showed that *Nyctosaurus* is quite distinct from *Pteranodon* and placed it in a separate Nyctosauridae as had earlier authors. The present study suggests that all species included in the subgenera *Pteranodon, Geosternbergia,* and *Occidentalia* are based on skulls of *Pteranodon longiceps* and *P. sternbergi.* Consequently, there is no reason to retain the subgenera.

Pteranodon longiceps Marsh, 1876a

1876a *Pteranodon longiceps:* Marsh, p. 508.
1910 *Pteranodon longiceps* Marsh: Eaton, p. 2.
1972 *Pteranodon (Longicepia) longiceps* Marsh: Miller, p. 9.
1972 *Pteranodon (Longicepia) marshi:* Miller, pp. 9–10.
1972 *Pteranodon (Sternbergia) walkeri:* Miller, pp. 15–16.
1973 *Pteranodon (Pteranodon) longiceps* Marsh: Miller, p. 100.
1973 *Pteranodon (Pteranodon) marshi:* Miller, p. 100.
1978 *Pteranodon (Geosternbergia) walkeri:* Miller, p. 194.
1978 *Pteranodon longiceps* Marsh: Wellnhofer, pp. 61–62.
1984 *Pteranodon longiceps* Marsh: Schoch, pp. 12–14.

Holotype.—YPM 1177. Skull and atlas-axis complex in slab; additional remains not preserved in the slab include skull fragments, cervical rib, partial radius, proximal end of Wing Phalanx 2, and other fragments.

Horizon and Locality.—Smoky Hill Chalk Member of the Niobrara Formation. Collected by S. W. Williston on May 2, 1876 near the Smoky Hill River, "Wallace" Co., Kansas. Williston's (1876) field notebook reads: "Loc. 3 mi. NE of Monument Rocks in fine yellow chalk. Wash gentle for 20 feet + then quite precipitous." Three miles northeast of Monument Rocks is in Gove Co., not Wallace or Logan. Based on examination of the exposures northeast of Monument Rocks, Bennett (1991) reported that the skull probably was collected from between 2 m above Marker Unit 15 and Marker Unit 16.

Paratypes.—None.

Distribution.—Upper part of the Smoky Hill Chalk Member of the Niobrara Formation (between Marker Units 13 and 20, upper Santonian to lower Campanian) of western Kansas, and the Sharon Springs Member of the Pierre Shale (lower Campanian) of Kansas, Wyoming, and South Dakota.

Diagnosis.—*Pteranodon* with: posteriorly directed, bladelike cranial crest. *Pteranodon longiceps* differs from *P. sternbergi* in that the crest is directed posteriorly, and in males, is arcuate and tapers evenly from the base to the end. In addition, the occiput may be more reclined than in *P. sternbergi*.

Referred Materials.—AMNH 149; DMNH 1732; FHSM VP 221, 2183; KUVP 965, 976, 2122, 27821; LACM 51137; USNM 13656; UUPI R.197; YPM 1179, 2431, 2440, 2473, 2594. Postcranials from the Smoky Hill Chalk referred on the basis of stratigraphic position include: AMNH 1571–1573; CM 1539, "UNC A"; FHSM VP 184; FMNH PR 494; KUVP 977; LACM 50926; UNSM 50130; YPM 1160, 1161, 1169–1172, 2335, 2425, 2470. Postcranials from the Sharon Springs Member of the Pierre Shale referred on the basis of stratigraphic position include: AMNH 5819, 5840, 5842; BHI "UNC C"; CU 45062, 47280; FMNH PR 464, 468–470, 676, 1332; KUVP 33564, 36116, 50011, 50013–50019, 50089, 85445; LACM 126163, 127314; SM 497, 5817, 5818, 51141, 54358, 56128; USNM 18266.

Remarks.—The well-preserved type skull of *Pteranodon longiceps*, which was collected 5 yr after the first description of postcranial materials from the Niobrara Formation, showed that the Niobrara pterosaurs had edentulous jaws and could not be placed in *Pterodactylus*. Marsh (1876a) consequently erected a new species, genus, family, and order of pterosaurs based on the skull. The original description of Marsh (1876a:507–508) is as follows.

> This genus is readily distinguished from any Pterodactyles hitherto described by the cranial characters, which are well shown in a nearly perfect skull, and portions of others, in the Yale Museum. The cranium preserved is very large, and the facial portion greatly elongated. There is a high sagittal crest, which projects backward some distance beyond the occipital condyle. The latter is directed backward, and somewhat downward. The quadrate is long, and inclined well forward. The orbits are large, as are also the antorbital and nasal apertures. The maxillary bones are closely coossified with the premaxillary, and the whole forms a long, slender beak, which, in the specimens examined, tapers gradually to the pointed apex. There are no teeth, or sockets for teeth, in any part of the upper jaws, and the premaxillary shows some indications of having been encased in a horny covering. The lower jaws, also, are long and pointed in front, and entirely edentulous. The rami are closely united by a symphysis which extends from the apex to beyond the posterior extremity of the dentary bone …
>
> The nearly complete skull mentioned above may be regarded as the type of the genus *Pteranodon*….
>
> The species represented by this specimen is well marked, and may be called *Pteranodon longiceps*. It is somewhat larger than *P. occidentalis* Marsh, which apparently has more slender jaws [presumably referring to YPM 1179]. The Yale collection contains portions of a skull indicating a much larger species [YPM 2594], which is probably *P. ingens* Marsh.

Marsh's description provided 10 characters to diagnose *Pteranodon longiceps*. Seven of the characters diagnose more general levels of pterosaurs: large skull; elongate facial portion of skull; backward-directed occiput; long, inclined quadrate; large orbits; large confluent naris and antorbital fenestra; and mandibular rami united by a long symphysis. Two characters are diagnostic of the genus *Pteranodon:* edentulous jaws; and premaxillae tapering to a point. Lastly, high sagittal crest projecting backward, is diagnostic of the species *P. longiceps*. The type specimen displays the raised marginal ridges of the jaws and the greatly reduced nasal process, which are additional characters diagnostic of *Pteranodon;* the backward-directed crest distinguishes *P. longiceps* from *P. sternbergi*. Therefore, the description and type specimen provide enough information to define the species adequately and *P. longiceps* is a valid species. *Pteranodon longiceps* is the sister taxon of *P. sternbergi* and is distinguished from it by the posteriorly directed cranial crest that is a long, narrow blade in males, and possibly a slightly smaller angle between the occiput and the palate. The stratigraphic ranges of the two species suggest that *P. longiceps* descended from *P. sternbergi*.

Pteranodon marshi and *P. walkeri*, erected by Miller (1972) for isolated crania, are junior synonyms of *P. longiceps*. *Pteranodon marshi* was based on the skull (YPM 2594) that Eaton (1910) considered to be a type of *P. ingens*. The skull displays the posteriorly directed cranial crest that shows it to be *P. longiceps*, and its large size and large crest identify it as a male.

Miller (1972) placed *P. marshi* in the subgenus *Longicepia* (later corrected to *Pteranodon* [Miller, 1973]) with *P. longiceps; Longicepia* was diagnosed by Miller (1972:9) as follows:

> Members of this subgenus are relatively large forms characterized by elongate crests extending posteriorly from the occipital-parietal region of the skull. The humerus to radius-ulna ratio is 1:1.25, and the humerus to metacarpal IV ratio is 1:2.4.

Miller's (1972:10) diagnosis of the species *Pteranodon marshi* is as follows:

> A large skull characterized by a long crest projecting posteriorly. The crest has a relatively wider base and rises more abruptly than the crest of *P. longiceps*. Furthermore the crest apparently is arc-like in form and is not recurved as is that of *P. longiceps*.

Miller's subgenus *Longicepia* corresponds to *Pteranodon longiceps* in the present revision, and Miller's concepts of the species *P. longiceps* and *P. marshi* are female and male, respectively. The differences in form between the crests of *P. marshi* (YPM 2594) and *P. longiceps* (by which Miller meant YPM 2473) can be ascribed to individual and possibly temporal variation. The cranial crest of YPM 2473 is quite similar to that of YPM 2594 in overall shape, although the crest of the former appears to have been slightly more upright (Fig. 1). The character, crest arclike and not recurved like that *P. longiceps* [= YPM 2473], cannot be demonstrated because the posterior end of the crest of YPM 2594 is not preserved. The type skull of *P. marshi* agrees well with *P. longiceps* except for absolute size and the size relative of the cranial crest, both of which are sexually dimorphic.

Pteranodon walkeri (Miller, 1972) is based on the partially disarticulated skull and axis of a subadult (FHSM VP 221) in a plaque mount. The type specimen was collected, prepared, and reconstructed in the plaque mount by G. F. Sternberg. Miller (1972) noted that the specimen had been incorrectly reconstructed, suggested it belonged to an upright crested form like *P. sternbergi*, and "photographically reassembled" the parts of the skull. The original diagnosis (Miller, 1972:15) of *Pteranodon walkeri* is as follows:

> A large *Pteranodon* with a upright crest, but not bulbous or as large as that of *P. sternbergi*. The mandible is like that of the longicepias in form.

Of the three characters mentioned by Miller—large size, upright but not bulbous crest, and mandible like that of longicepias—none is useful for defining a species. The large size indicates that the specimen is a male. The skull has unfused quadrates, jugals, and atlas-axis complex, and is clearly a subadult. This may explain why the cranial crest is not particularly long (The margins of the crest are not preserved and it might have been longer.) There is no evidence that the crest was upright. The braincase-crest fragment has been rotated anteriorly relative to the jugal; and if this displacement is considered, the crest would be directed posterodorsally as in DMNH 1732 and YPM 2594. It is not clear what Miller meant by the character "mandible like longicepias in form." Possibly he thought that the jaws were straight and not curved upward as are the jaws of the type of *Pteranodon sternbergi;* this may have resulted from his misinterpretation of the elements preserved in the plaque mount. Miller apparently interpreted the midline of the premaxillae, preserved in dorsal view, as the edge of the upper jaw preserved in lateral view. Because the midline of the premaxillae is preserved in dorsal view, it is straight, not curved like the reconstructed jaws of *P. sternbergi.* Examination of FHSM VP 221 indicates that both Sternberg's and Miller's reconstructions are incorrect; moreover, examination reveals that the skull does not differ significantly from *P. longiceps.*

Pteranodon longiceps seems to persist into the Sharon Springs Member of the Pierre Shale. The only *Pteranodon* skull from the Sharon Springs (KUVP 27821) is indistinguishable from *P. longiceps* from the Smoky Hill Chalk. The skull is that of a large male; the crest tapers from the base and is not bulbous in profile.

Pteranodon sternbergi Harksen, 1966

1966 *Pteranodon sternbergi:* Harksen, p. 75.
1972 *Pteranodon (Sternbergia) sternbergi:* Miller, p. 14.
1972 *Pteranodon (Occidentalia) eatoni:* Miller, pp. 16–18.
1978 *Pteranodon (Geosternbergia) sternbergi:* Miller, p. 194.
1978 *Pteranodon sternbergi:* Wellnhofer, p. 63.

Holotype.—**FHSM VP 339** (Originally SMM 5426). Incomplete skull with large, upright cranial crest in a plaque mount; additional fragments not in the plaque mount include the left quadrate, articular region of left mandible, occipital condyle and basioccipital fragment, and other fragments.

Horizon and Locality.—Smoky Hill Chalk Member of the Niobrara Formation. Collected by G. F. Sternberg in the Fall of 1952 from "1 mile West of Bogue, about 200 steps North of the [South Fork of the Solomon] River and South of Hwy. [24], Graham Co., Kansas." Based on examination of the exposures west of Bogue, Bennett (1991) suggested that the skull probably was collected from approximately Marker Unit 4 or a short distance below it.

Paratypes.—None.

Distribution.—Lower part of the Smoky Hill Chalk Member of the Niobrara Formation (Marker Units 4–7, upper Coniacian to lower Santonian) of western Kansas.

Diagnosis.—*Pteranodon* with: upward-directed crest, that is bulbous in profile and broader above base than at base in males; premaxillae extending a moderate distance up the front of crest; seems to have a median process formed by palatines or vomers extending posteriorly into confluent choanae.

Pteranodon sternbergi differs from *P. longiceps* in the upright cranial crest that is bulbous in lateral view, and in the premaxillae extending further up the anterior margin of the crest. In addition, it is possible that *P. sternbergi* has a somewhat greater angle between the occiput and the palate than *P. longiceps*, and possibly is distinguished further by the presence of the median process of the palatines or vomers.

Referred Materials.—UALVP 24238; "UNC 3"; "UNC 8"; USNM 12167. Postcranials referred on the basis of stratigraphic position: ROM 26104; UNSM 50036; YPM 1181, 2493.

Remarks.—The type specimen is a large skull with an immense, upward-directed crest; the specimen was collected and reconstructed in a plaque mount by G. F. Sternberg (Fig. 5). Harksen (1966) recognized that the specimen was distinct from *Pteranodon longiceps*, and named it *Pteranodon sternbergi*. The typographical error *Pteranodon sternberg* [sic] appeared in the systematic section, but it is clear from the text that the correct name is *Pteranodon sternbergi*. The original description (Harksen, 1966:75) is as follows:

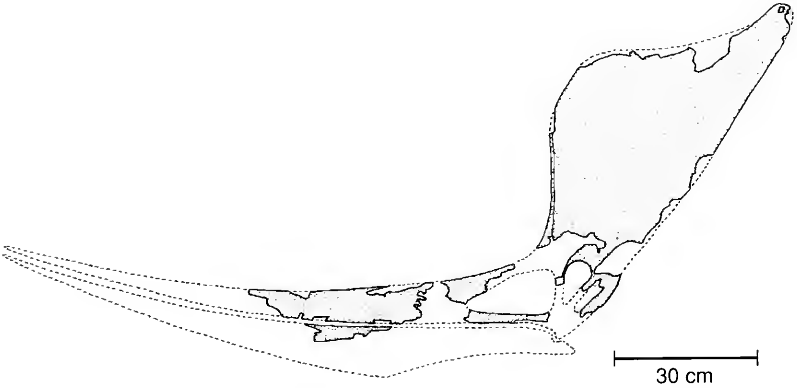

Fig. 5. Skull of FHSM VP 339, holotype of *Pteranodon sternbergi* (Harksen, 1966), as reconstructed in plaque mount by G. F. Sternberg. Bone is stippled; the dashed line shows Sternberg's reconstruction. My reconstruction of the jaws is shown in Figure 2.

> The distinguishing characteristics of this species are the bulbous outline of the supraoccipital crest and the high angle formed between the long axis of the supraoccipital crest and the long axis of the mandible.

The characters mentioned by Harksen are valid and separate *Pteranodon sternbergi* from *P. longiceps*. The crest is upright and bulbous in profile and is at a high angle to the palate. Therefore, *P. sternbergi* is a valid species. However, there is some uncertainty regarding the reconstruction of the specimen. According to Miller "Sternberg … stated (personal communication, 1957) that the complete outline of jaws, as restored, was visible in the chalk when the specimen was collected" (Miller, 1972:14). However, that is directly contradicted by a description of the specimen written by Sternberg (G. F. Sternberg, unpublished letter in FHSM files) when the specimen was sold to the Fort Hays State University Museum:

> The nearly complete crest and skull forward to beyond the center of the beak. In many cases the bone had been badly eaten by roots and is covered by plaster to hold it in place. All bone is present in the actual position in which it was found.
>
> The condyle has been removed from the specimen and is preserved separately, also the union of the lower jaw with the quadrate from one side. This may be the right one. It was washed out when found. The restoration as I have restored the extreme back of the lower jaw with quadrate may not be heavy enough. It seems on examining the bone from this region which is stored with the fragments of the skull that I have not made the restoration heavy enough.
>
> The curve of the beaks has been governed by the sections of both lower and upper jaws shown in the mount. They are in the exact position they were in when found.
>
> The bone around the orbit was badly eaten and had to be covered with a thin layer of plaster but the general shape is quite correct. This crest which is quite remarkable for its size does not extend back as is shown in other specimens. It turns up and takes an entirely different angle with relation to the skull than do any other long crested skulls I have ever seen. It is the largest crest I have ever seen. It is the largest crest I have ever seen [sic] and though there are several small patches of restoration on it, the outline is correct in every detail unless at the back just above the orbit. Here I was unable to be absolutely sure because the roots had destroyed the contact.
>
> The distal ends of both beaks were not present when the specimen was found, but the small sections of both jaws which are in the exact place as found, gives a very accurate shape and I am enclined [sic] to believe that the upward curve toward the front end is not overdone. The general shape of the skull which is exactly as found seems to take on an entirely different shape than most other known specimens and is not flattened out backwards, but is much more forward and up.

As stated in the letter, there is somewhat more bone preserved around the orbit, confluent naris and antorbital fenestra, and lower temporal fenestra than can be seen from a distance. If one examines the specimen closely, the bone is visible, though covered in most places by plaster. The remains suggest that the skull was not broken up and that the crest and jaw fragments are in their proper position; however, little is preserved of the jaws. UALVP 24238 suggests and "UNC 8" shows that the premaxillae extended beyond the end of the mandible; probably this was also the case in FHSM VP 339. Thus, the mandible was probably not as long as reconstructed. The upward curvature of the premaxillae reconstructed by Sternberg seems to have been taken from the dorsal margin of the preserved fragments. The curvature of those fragments may reflect the development of a premaxillary crest like that of UALVP 24238 rather than the curvature of the jaws. In UALVP 24238, the mandible is not as deep as in *Pteranodon longiceps* and this may be an additional character of *P. sternbergi*. However, more specimens are needed before this can be determined.

Pteranodon eatoni (Miller, 1972), based on an incomplete skull in a plaque mount (YPM 1179) that Eaton (1910) considered to be a type of *P. occidentalis*, is considered a junior synonym of *P. sternbergi*. The specimen includes the braincase region and right quadrate; a fragment including parts of the left jugal, maxilla, and premaxilla; the left ramus of the mandible; and a fragment of the distal end of the dentary or premaxilla. The specimen was reconstructed in a plaque mount, which is incorrect in that the jugal-maxilla-premaxilla fragment is mounted upside down so that it gives the appearance that the dorsal margin of the premaxilla curved downward and the confluent naris and antorbital fenestra was large (Fig. 6). Miller (1972) considered this to be the only species in the subgenus *Occidentalia*. His subgeneric diagnosis (Miller, 1972:16) is as follows:

> Pteranodonts characterized by relatively short supraoccipital crests. The narial fenestra is relatively large. The only known specimen consists of an incomplete skull that is relatively small.

Because *Pteranodon eatoni* was the only species in the subgenus *Occidentalia*, Miller did not provide a diagnosis of the species. The character "short supraoccipital crest" cannot be demonstrated. The type skull was cleaned recently and there is no evidence of a finished edge on the crest. Therefore, the crest must have been larger than it is at present, although how large and exactly what shape is unclear. The character "large narial fenestra" is based on the incorrect reconstruction of the specimen, with the jugal-maxilla-premaxilla fragment inverted. If one corrects for the inver-

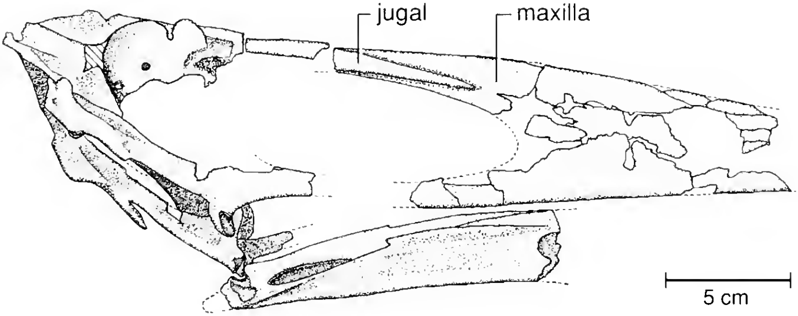

Fig. 6. Skull of YPM 1179, holotype of *Pteranodon eatoni* (Miller, 1972), in right lateral view as mounted in plaque. Note that the left jugal-maxilla-premaxilla fragment is inverted and that the dentary is not preserved with the mandibular ramus.

sion, the skull resembles those of small specimens of *P. longiceps*, and the specimen appears to be a female. However, it is slightly smaller than the type of *P. longiceps*, appears to have a more erect occiput, and slender mandibular rami like those of FHSM VP 339 and UALVP 24238. Thus, *P. eatoni* cannot be shown to differ from *P. sternbergi*, and is considered to be a junior synonym of *P. sternbergi*.

TAXA OF UNCERTAIN TAXONOMIC POSITION

The following six nominal species of *Pteranodon* are based on postcranial materials. The characters given in the original descriptions are inadequate to diagnose a species and the type specimens are inadequate for identification to the species level. Therefore, all six are considered *nomina dubia*. The type specimen of *Pteranodon velox* is inadequate for identification to the generic level. It cannot be determined to which genus it might belong, although it probably is *Pteranodon*. The other five nominal species seem to have come from the upper half of the Smoky Hill Chalk Member of the Niobrara Formation and, thus probably are based on specimens of *Pteranodon longiceps*.

Pteranodon occidentalis **(Marsh, 1872) nomen dubium**

1871 *Pterodactylus oweni:* Marsh, p. 472.
1872 *Pterodactylus occidentalis:* Marsh, p. 241.
1876a *Pteranodon occidentalis* (Marsh): Marsh, p. 508.

1972 *Pteranodon occidentalis* (Marsh): Miller, p. 7.
1978 *Pteranodon occidentalis* (Marsh): Wellnhofer, pp. 62–63.
1984 *Pteranodon occidentalis* (Marsh): Schoch, pp. 3–6.

Lectotype.—YPM 1160. Right Metacarpal IV, broken proximal end of Wing Phalanx 1, distal end of Wing Phalanx 2, and fragments.

Horizon and Locality.—Smoky Hill Chalk Member of the Niobrara Formation. Collected by O. C. Marsh on November 30, 1870, and in July or August, 1871, from the north side of the Smoky Hill River, 5 mi W of Russell Springs, Logan Co., Kansas. Examination of outcrops west of Russell Springs indicates that the specimen probably was collected between Marker Units 18 and 20 (Bennett, 1991).

Other Syntype.—YPM 1161. Distal end of the right Metacarpal IV. Collected by O. C. Marsh, November, 1870, from the Smoky Hill Chalk Member, Niobrara Formation, east side of the North Fork of the Smoky Hill River, 1 mi from mouth, Logan Co., Kansas. Examination of outcrops west of Russell Springs indicates that the specimen was probably collected between Marker Units 18 and 20 (Bennett, 1991).

Remarks.—Marsh (1871) described the species *Pterodactylus oweni* on the basis of distal ends of two wing metacarpals collected in 1870. The original description (Marsh, 1871:472) is as follows:

> The remains belonged to two or more individuals. They are fragmentary, but some of them are quite characteristic. The distal ends of two long bones [YPM 1160 and 1161], similar in form to the tibia of a bird, are evidently portions of the peculiar metacarpal of the wing-finger. One of these [YPM 1160], which retains the lower part of the shaft, resembles in its proportions the corresponding bone in *Pterodactylus Suevicus*. The condyles are well developed, and have a sweep of two thirds of a circle. They appear to have been originally somewhat oblique. In size and general form, they are not unlike those of the specimen figured by Owen in his Memoir on Cretaceous Reptiles, 1851 (Sup. I, Pl. IV, fig. 9–11), but there was apparently no longitudinal elevation between them. The shaft, where broken, is subtrihedral, with the posterior face concave. The bones are light, with thin compact walls. The long bones are pneumatic. The teeth are smooth, and compressed. The length of the metacarpal with the part of the shaft preserved is six and one-half inches; the fore and aft extent of the condyles fourteen lines; the transverse extent about thirteen lines. This would indicate an expanse of wings of not less than twenty feet! The species, which is the first found in this country, may be named *Pterodactylus Oweni*, in honor of Professor Richard Owen of London. The remains now representing it were discovered by the writer, in November last, in the upper Cretaceous formation of Western Kansas.

Marsh wrote "two or more individuals" because he had two distal ends of right wing metacarpals and at least one tooth. YPM records indicate that

Marsh and his field party collected only two specimens of *Pteranodon* in 1870 (YPM 1160 and 1161) each of which consisted of distal right wing metacarpal. The distal end of the wing metacarpal of YPM 1160 is preserved with some shaft still attached and is 65 mm long, whereas YPM 1161 preserves almost no shaft and is only 38 mm long. YPM 1160 is certainly the specimen Marsh described.

In 1871, Marsh collected more material, including the remainder of the wing metacarpal of YPM 1160, two other specimens, and more teeth. Marsh (1872) described the new material, adding to the description of the species, which he renamed *Pterodactylus occidentalis* because it was preoccupied. The name *Pterodactylus oweni* Marsh was preoccupied by, and a primary junior homonym of, *P. oweni* Seeley (1864). According to the International Code of Zoological Nomenclature (Art. 59), primary junior homonyms must be permanently rejected. Thus, even though *Pterodactylus occidentalis* (Marsh) was transferred to *Pteranodon*, the species name *oweni* cannot be restored. The description of the additional materials (Marsh, 1872:241–242) is as follows:

> An excavation at the point where the first specimens [YPM 1160 and 1161] were found yielded portions of the same skeleton.... The additional remains of this species, discovered by our party during the past summer, consist of portions of five individuals, which differed somewhat in size, but all tend to confirm the conclusions based on the fragments first examined. From the locality which furnished one of the original specimens, we recovered the proximal end of the right wing-finger metacarpal, which evidently belonged with the distal extremity described [YPM 1160], and proves the entire bone to have been at least fifteen inches in length, or much more elongated than any hitherto known. With this specimen were found portions of the second and third phalanges of the same wing-finger, all indicating the great size and power of the wings. Another specimen [YPM 1165], found by the writer at a higher level, in the yellow chalk, pertained to a larger individual, and is of much interest. It consists of the distal extremity of the left wing metacarpal, articulated to the adjoining proximal end of the first phalanx. Both bones are in excellent preservation, and show this characteristic joint most perfectly.
>
> The most important remains of this species yet discovered, however, consist of nearly all the bones of a right wing [YPM 1164], from the humerus to the last phalanx inclusive, which were found by the writer in place in the gray Cretaceous shale, during our investigations near the Smoky River. Although more or less fractured, the bones are in general well preserved, and show clearly the peculiar structure of the Pterosaurian wing, as well as the especial characters that mark the present species.

The specimens to which Marsh referred apparently are YPM 1160, 1161, 1164, and 1165; of these, only YPM 1160 and 1161 were collected before the original description and can be considered syntypes. Marsh described

Table 2. Measurements (mm) of teeth described by Marsh (1872) as pertaining to *Pteranodon*, and teeth of *Xiphactinus audax* in the YPM collections.

Specimen	Length	Greatest diameter at base	Least diameter at base
P. occidentalis (Marsh, 1872)	25.0	9.0	5.5
YPM "UNC A"	24.9	8.5	4.6
P. ingens (Marsh, 1872)	18.6	7.25	5.0
YPM 1171	18.1	7.3	5.0
P. ingens (Marsh, 1872)	48.0	14.0	11.3
YPM 1173	48.3	14.3	11.2
YPM 1163 "A"	15.5	5.8	4.1
YPM 1163 "B"	20.2	—	—
YPM 1174	35.6	5.8	7.4

YPM 1164 in detail, and then went on to describe (Marsh, 1872:244) the teeth found with the specimens:

> The teeth found with remains of this species, and supposed to belong with them, are very similar to the teeth of Pterodactyls from the Cretaceous of England. They are smooth, compressed, elliptical in transverse outline, pointed at the apex, and somewhat curved.

There are six teeth in the YPM collections that apparently were considered to be pterosaur teeth by Marsh. I located the teeth in the fossil fish collection, without any note to indicate that they were the "pterosaur" teeth, but five of them (YPM 1163 "A," 1163 "B," 1171, 1173, and 1174) are numbered in sequence with specimens of *Pteranodon* collected in 1870 and 1871, and two of those teeth match the dimensions given for *Pterodactylus ingens* (Table 2). The sixth tooth is uncatalogued, but was collected in December 1870, and matches the dimensions given by Marsh (1872) for the tooth of *Pterodactylus occidentalis*. It seems likely that this is the tooth to which Marsh (1871, 1872) referred. All six teeth can be referred to the ichthyodectiform fish *Xiphactinus audax*. The variations in size and shape noted by Marsh are apparently normal variation of tooth size in *Xiphactinus*, but there are also variations in degree of crushing of the teeth.

Schoch (1984) designated the distal end of the wing metacarpal of YPM 1160 as the lectotype of *Pteranodon occidentalis*, and the other fragments of YPM 1160 and YPM 1161 as paralectotypes. Schoch designated only the distal end of the wing metacarpal as the lectotype because he thought that there was some confusion as to when the materials had been collected. He noted that the distal end of the wing metacarpal was only 65 mm long, not the 6.5" (165 mm) that Marsh (1871) reported, and suggested that there might have been more of the specimen present when Marsh described it. Unfortunately, Schoch did not reassemble the fragments; when I did so, they all fit perfectly with adjoining pieces except for the joint at 65 mm from the distal end. It is possible that a small portion may be missing, but the length of the reassembled wing metacarpal (410 mm) matches that given by Marsh (1872: 412 mm). It is clear that YPM 1160 was collected in two different years, but with the nature of the outcrops of the Niobrara Formation in Logan County, it would not be difficult to return to the exact locality two years in a row. Because the materials collected the second year perfectly match the distal wing metacarpal in size, morphology, and quality of preservation, all of YPM 1160 should be the lectotype. YPM 1161 is the only other syntype, because YPM 1164 and YPM 1165 were collected after the original description and cannot be considered part of the type series.

None of the characters used by Marsh to diagnose *Pterodactylus occidentalis* is valid. *Pteranodon* does differ from *Ornithocheirus* s.l. (Owen, 1859) in the lack of the longitudinal elevation between the condyles of the distal wing metacarpal, but this character is of no value at the specific level. Likewise, the size of the wing metacarpal indicates the specimen is a female, but this fact is of no value in separating species. The provenance and morphology of the material indicate that it is *Pteranodon*, and its stratigraphic position suggests that it is a specimen of *Pteranodon longiceps*, but it is indeterminate at the species level. Consequently, *P. occidentalis* must be considered a *nomen dubium*.

Pteranodon ingens (Marsh, 1872) nomen dubium

1872 *Pterodactylus ingens:* Marsh, p. 248.
1876a *Pteranodon ingens* (Marsh): Marsh, p. 508.
1972 *Pteranodon ingens* (Marsh): Miller, pp. 7–8.
1978 *Pteranodon ingens* (Marsh): Wellnhofer, p. 62.
1984 *Pteranodon ingens* (Marsh): Schoch, pp. 6–9.

Lectotype.—YPM 1170. Distal ends of the radius and ulna, proximal and distal ends of Metacarpal IV, shaft and distal end of Wing Phalanx 1, and shaft fragments.

Horizon and Locality.—Smoky Hill Chalk Member of the Niobrara Formation. Collected by O. C. Marsh in July, 1871, from the north side of the Smoky Hill River, 18 mi E of Fort Wallace, Kansas. That is approximately 5 mi W of Russell Springs, and examination of outcrops west of Russell Springs indicates that the specimen was probably collected from between Marker Units 18 and 20 (Bennett, 1991).

Other Syntypes.—YPM 1169. Bones of right wing: the proximal end of Wing Phalanx 1, proximal and distal ends of Wing Phalanx 2, proximal end of Wing Phalanx 3, shaft fragments from the wing phalanges, and the distal end of Metacarpal III; and two *Squalocorax* teeth. Collected by O. C. Marsh on July 27, 1871, from the Smoky Hill Chalk Member, Niobrara Formation, south side of the Smoky Hill River, 20 mi E of Fort Wallace, Kansas. That is approximately 3 mi W of Russell Springs. **YPM 1171**. Distal end of Metacarpal IV, proximal end of the coracoid, and one tooth of *Xiphactinus*. Collected by O. C. Marsh on July 26, 1871, from the Smoky Hill Chalk Member, Niobrara Formation, south side of the Smoky Hill River, 20 mi E of Fort Wallace, Kansas. That is approximately 3 mi W of Russell Springs. **YPM 1172**. Distal end of right Metacarpal IV and two fragments probably from the distal ends of the radius and ulna. Collected by O. Harger on July 31, 1871, from the Smoky Hill Chalk Member, Niobrara Formation, north side of the Smoky Hill River, 26 mi E of Fort Wallace, Kansas. That is approximately 3 mi E of Russell Springs. Examination of outcrops around Russell Springs indicates that these three specimens were probably collected from between Marker Units 17 and 20 (Bennett, 1991).

Marsh (1872) based the species on four specimens and three fish teeth collected the summer of 1871. The original description (Marsh, 1872:246–247) is as follows:

> The existence of a second and much larger species of Pterodactyl, in the same strata with the remains just described [*Pterodactylus occidentalis*], is clearly indicated by a number of specimens, pertaining to four individuals, which were discovered last summer during the explorations of the Yale party along the Smoky River and its tributaries. One series of these specimens [YPM 1170] consists of the greater portion of an ulna, part of a radius, the distal end of a wing-metacarpal, and portions of the corresponding phalanges, evidently belonging to the right wing of the same animal. The other specimens secured are equally characteristic, and serve to supplement this series.
>
> A comparison of these various remains, especially the bones of the forearm, with the corresponding parts of the preceding species [*P. occidentalis*], shows several important differences, aside from that of size. In the former species, the ulna, or larger anti-brachial bone, has, on its proximal end, two large articular faces for union with the condyles of the humerus, and between them a low elevation, which extends only to a line joining the proximal margins of these surfaces. In the large species, this elevation is represented by a very prominent, flattened protuberance, which projects far beyond the rest of the proximal extremity. The smaller articular face in this specimen, moreover, is much less inclined from the axis of the shaft. The distal ends of the same bones show equally marked differences. In *Pt. occidentalis*, the articular face on the outer side extends transversely only to the margin of the

> central tubercle. In the species under consideration, this face does not terminate until it reaches a point opposite the middle of the corresponding projection, which is much more compressed than in the smaller specimen. The radii, also, of the two species exhibit essential differences, especially in their proximal extremities.
>
> The metacarpal bone of the wing-finger is very similar at its distal end to that of the species above described. It shows, however, unmistakable indications of a median ridge on its anconal side; and since this is also the case with all the other specimens preserved, there can be little doubt that this feature was a specific character. The remaining portions of the phalanges, so far as the present material allows of comparison, show no essential differences in the two species.
>
> With one series of the above specimens [YPM 1169], a small bone was found, which is probably the distal end of a metatarsal. In its general features it agrees most nearly with the bone figured by Seeley [1870, pl. 6, figs. 8, 9] as a metacarpal or metatarsal. The fact that this specimen is nearly solid bone would be an argument for considering it the latter, as all the wing-bones examined during the present investigation are clearly pneumatic.
>
> The dental characters of this species are at present only known from a single crown of a tooth [YPM 1171], found with one series of the specimens, and from two larger and very perfect teeth found by themselves [YPM 1173 and 1174?], which agree so closely with the former that they deserve notice in this connection. These specimens are less curved and less compressed than the teeth referred to *Pt. occidentalis*, but in other respects they are nearly identical.

Marsh mentioned four characters in his description of *Pteranodon ingens;* of these, the characters of the ends of the ulna and radius, and the median ridge on the anconal side of the wing metacarpal, are artifacts of crushing and preservation. They cannot be demonstrated in better-preserved material. The dental characters do not apply to *P. ingens*, because the teeth are those of *Xiphactinus*. The last character, large size, indicates that the specimens are males, but is of no value in differentiating between the species of *Pteranodon* from the Niobrara Formation. The provenance and morphology of the specimens indicate that they are *Pteranodon*, and their stratigraphic position suggests that they are specimens of *Pteranodon longiceps*, but the lectotype of *P. ingens* is indeterminate, as are the three syntypes. Consequently, the name *P. ingens* is a *nomen dubium.*

***Pteranodon velox* (Marsh, 1872) nomen dubium**

1872 *Pterodactylus velox:* Marsh, p. 247.
1876a *Pteranodon velox* (Marsh): Marsh, p. 508.
1972 *Pteranodon velox* (Marsh): Miller, p. 8.
1978 *Pteranodon velox* (Marsh): Wellnhofer, p. 65.
1984 *Pteranodon velox* (Marsh): Schoch, pp. 9–12.

Holotype.—YPM 1176. Distal end of Metacarpal IV and proximal end of Wing Phalanx 1 lacking the extensor tendon process. The wing metacarpal had ferruginous concretions on the anterior and posterior surfaces that altered its appearance considerably.

Horizon and Locality.—Smoky Hill Chalk Member of the Niobrara Formation. Collected by O. C. Marsh on July 27, 1871, from the south side of the Smoky Hill River, 26 mi E of Fort Wallace, Kansas. That is approximately 3 mi E of Russell Springs. Examination of outcrops east of Russell Springs indicates that the specimen was probably collected between Marker Units 17 and 20 (Bennett, 1991).

Paratypes.—None.

Remarks.—Marsh (1872) based this species on a single, isolated specimen, and no other specimens have been referred to the taxon. The original description (Marsh, 1872:247–248) is as follows:

> This species, which was apparently about two thirds the size of *Pterodactylus occidentalis*, is at present represented, so far as known, by the distal end of a right metacarpal of the wing-finger, and by the proximal extremity of the adjoining first phalanx. These bones, however, are among the most characteristic parts of the Pterosaurian skeleton, and in the present instance the specimens appear to show several points of distinction from the species already described [*P. ingens* and *P. occidentalis*].
>
> In the metacarpal bone, the articular distal extremity is smaller in proportion to the size of the shaft which supports it, than in either of the species above described. In other respects it appears to present no essential difference except that of size. The first phalanx, however, shows in its proximal end several differences which are clearly of specific importance. The outer articular surface in the present specimen is proportionally much narrower, and has its posterior margin more extended proximally. There is, moreover, no indication, on the inner side of the bone, of the large obtuse tubercle which is a prominent feature in all the corresponding specimens of the other two species. The epiphysis which bears the olecranoid process has disappeared from the present specimen, leaving an elongated oval depression, with a well defined margin. Both of the above bones are somewhat distorted by pressure.

Of the characters mentioned by Marsh—distal end of the wing metacarpal smaller in proportion to the shaft, and the unfused extensor tendon process of the first wing phalanx—are characters that indicate that the specimen is a subadult. The distal end of the wing metacarpal appears smaller because the condyles were not fully ossified. The apparent absence of the tubercle is a result of the concretion altering the appearance of the wing metacarpal. Eaton (1910) noted that the form of the specimen was altered considerably by the ferruginous concretion, and commented that there were no significant differences from other specimens of *Pteranodon* that could not be explained by crushing.

The provenance and morphology of the specimen suggest that it is *Pteranodon*, and the specimen probably is a subadult female *Pteranodon*, but it could possibly be a subadult male *Nyctosaurus*. In either case, the specimen is indeterminate and *P. velox* must be considered a *nomen dubium*.

Pteranodon umbrosus (Cope, 1872) nomen dubium

1872 *Ornithochirus umbrosus:* Cope, pp. 420–421.
1875 *Pterodactylus umbrosus* (Cope): Cope, pp. 65–66.
1892 *Pteranodon umbrosus* (Cope): Cope, 1892, p. 2.
1972 *Ornithochirus umbrosus* Cope: Miller, p. 8.
1978 *Pteranodon umbrosus* (Cope): Wellnhofer, p. 65.

Syntypes.—AMNH 1571. Distal end of the left Metacarpal IV and proximal of the right Wing Phalanx 1 from separate individuals. Cope (1872; 1875) referred to a phalanx of one of manual Digits I–III and a preaxial carpal, but they cannot be located.

Horizon and Locality.—Smoky Hill Chalk Member of the Niobrara Formation. Collected by E. D. Cope in 1871 from [Twin] Butte Creek, Logan Co., Kansas. Examination of outcrops along Twin Butte Creek suggests that the specimen was probably collected from between Marker Units 8 and 20 (Bennett, 1991).

Paratypes.—None.

Remarks.—Cope (1872) described *Pteranodon umbrosus* on the basis of wing fragments of what he apparently thought represented a single individual. The original description is as follows (Cope, 1875:421–422; figures mentioned in square brackets refer to Cope, 1875: pl. 7, reproduced here as Fig. 7):

> Represented by the distal portion (ten inches) of the wing finger metacarpal [Fig. 7:1]; the proximal portion (eight inches) of the first phalange of the same digit [Fig. 7:2], with two phalanges of claw-bearing digits [Figs. 7:3 and 7:4]. The distal condyles of the first named bone are separated by the usual deep groove above and below, and wind spirally to their terminations on the inferior face. The narrow base which supports the inner condyle is bounded posteriorly by an acute edge; directly outside of the base of this ridge is a deep groove or foramen, which is bounded next the external condyle by another ridge which rises to the base of the inner condyle on the trochlear side. The transverse diameter of the condyles is M. 0.043 or seventeen lines.
>
> The proximal end of the first phalange is perfect, but flattened by pressure. It presents the two usual cotyloid cavities well separated by an elevated ridge. Anteriorly it presents an elevated crest for muscular insertion. This terminates abruptly, and is followed distally by a deep notch. Distal to this is

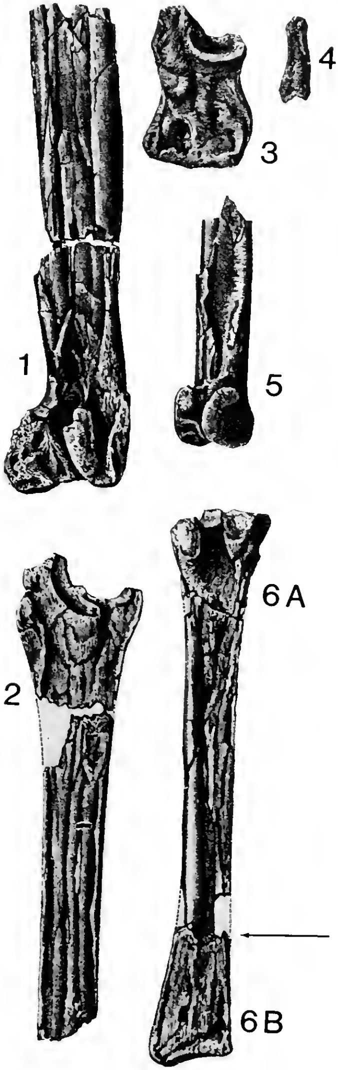

Fig. 7. Illustrations of type specimens of *Ornithochirus umbrosus* and *O. harpyia* from Plate 7 of Cope (1875). **1**, **2**. AMNH 1571, distal left Metacarpal IV and proximal right Wing Phalanx 1 of two individuals: part of type specimen of *Ornithochirus umbrosus*. **3**, **4**. Preaxial carpal and manual phalanx: part of type specimen of *Ornithochirus umbrosus*, missing. **5**, **6A**, **B**. AMNH 1572, distal right Metacarpal IV, proximal left Wing Phalanx 1, and proximal left Wing Phalanx 2 (?) of at least two individuals: type specimen of *Ornithochirus harpyia*. Note that **2** and **5** seem to be from the same individual.

> another prominence of the bone; also probably, an insertion. Antero-posterior diameter (flattened) 24 lines.
>
> The claw phalange [= preaxial carpal] is short and wide; both its articulations are simple and concave. Both outlines are keeled, one very strongly at one end, and at the other presenting beyond the articular surface, a wide prolonged process for muscular insertion. Length of phalange without process, thirteen lines; process four lines; diameter widest extremity eleven lines. This indicates a very stout digit. The other digit is penultimate, and is remarkable for its small size, perhaps indicating an external rudimental digit. It is only supposed to belong to the anterior limb, from its having been found with the preceding bones. It is more slender than the other and differs in having the convex distal articulation, divided by a trochlear groove, and the concave proximal one in like manner divided by a trochlear carina. Length nine lines; proximal depth three lines.
>
> This species is the largest Pterodactyle as yet known from our continent, the end of the wing metacarpal exceeding in diameter that of the species described by Professor Marsh from the same region [*Pterodactylus occidentalis*] by four lines.
>
> From near Butte Creek, from the yellow chalk.

The original description of *Ornithochirus umbrosus* makes it clear that Cope was placing the species in Seeley's genus *Ornithocheirus*, because Seeley had commented on the large size of the phalanges of the clawed digits and Cope believed the preaxial carpal was a large phalanx of a clawed digit. The description was repeated with minor corrections (the "claw phalange" was reidentified as a preaxial carpal) and the specimens were illustrated (Cope, 1875).

Apparently some time after Cope described the species, the type specimen of *Ornithochirus umbrosus* (AMNH 1751) was mixed with the type of *O. harpyia* (AMNH 1752) and AMNH 1753. I have separated the three specimens as much as possible based on the original description and the illustrations in Cope (1875: pl. 7, figs. 1–4). The distal end of Metacarpal IV (Fig. 7:1) and the proximal Wing Phalanx 1 (Fig. 7:2) can be readily identified from the description and the illustration. The preaxial carpal (Fig. 7:3) and the small phalanx from one of the Digits I–III (Fig. 7:4) cannot be located. They were not present among the three mixed specimens, and they also do not appear to be mixed in with other specimens in the AMNH collections.

Although Cope implied that the type specimen of *Ornithochirus umbrosus* was a single individual, that is not possible. The distal end of Metacarpal IV clearly does not belong with proximal Wing Phalanx 1. The metacarpal is a left and the phalanx is a right; the phalanx is from a smaller individual than the metacarpal, and the phalanx is covered by cirriped borings, whereas the metacarpal does not show any borings. Instead, the first wing phalanx seems to belong with the distal wing metacarpal of the type of *Ornithochirus harpyia*. The metacarpal of *O. harpyia* is also a right, shows cirriped borings and an identical quality of preservation, and is the same size as the proximal first wing phalanx of *O. umbrosus*. It seems likely that the wing metacarpal and first wing phalanx of one individual were separated and mixed with other specimens before Cope described them.

The main criterion for separating this species from others was its large size. Cope stated that the width of the wing metacarpal exceeded that of *Pterodactylus occidentalis* by four lines (8.5 mm). After Marsh synonymized *Ornithochirus umbrosus* with *P. ingens*, Cope claimed that *O. umbrosus* was larger than *P. ingens*, although measurements of the type specimens do not support Cope's contention. The width of the crushed distal ends of wing metacarpals of *Pteranodon* from the Niobrara Formation is variable, depending in large part on the direction of crushing, and comparison of the more reliable diameters of the distal condyles of *O. umbrosus* and *P. ingens* shows them to be nearly the same size (Table 3).

Despite problems in determining which specimens actually constitute the type specimen, the point is moot, because AMNH 1571–73 do not exhibit any species-specific characters. Likewise, the descriptions and illustration of the missing elements do not allow separation of the species. The provenance and morphology of the specimens indicate that they are *Pteranodon*, and their stratigraphic position suggests that they are specimens of *Pteranodon longiceps*, but they are indeterminate at the species level and *P. umbrosus* must be considered a *nomen dubium*.

Pteranodon harpyia (Cope), 1872 nomen dubium

1872 *Ornithochirus harpyia:* Cope, pp. 421–422.
1875 *Pterodactylus occidentalis* Marsh: Cope, pp. 66–67.
1972 *Ornithochirus harpyia* Cope: Miller, p. 9.
1978 *Ornithochirus harpyia* Cope: Wellnhofer, p. 65.

Syntypes.—AMNH 1572. Shaft and distal end of right Metacarpal IV, proximal end of left Wing Phalanx 1 and shaft, and proximal end of Wing Phalanx 2, from at least two individuals.

Horizon and Locality.—Smoky Hill Chalk Member of the Niobrara Formation. Collected by E. D. Cope in 1871 from [Twin] Butte Creek, Logan Co., Kansas. Examination of outcrops along Twin Butte Creek suggests that the materials were probably collected from between Marker Units 13 and 20 (Bennett, 1991).

Remarks.—Cope (1872) based this species on wing metacarpals and phalanges of three individuals, which differed from *Ornithochirus umbrosus* in size and in certain characters of the distal wing metacarpal and proximal Wing Phalanx 1. Cope's (1872:421–422) description is as fol-

Table 3. Measurements (mm) of the distal wing metacarpals of Marsh and Cope type specimens.

Species	Specimen	Mc IV–d	Mc IV–v	Determination
Pterodactylus occidentalis	YPM 1160	26.1	29.5	♀ *Pteranodon* sp. indet.
	YPM 1161	—	24.8	♀ *Pteranodon* sp. indet.
	YPM 1170	—	34.6	♂ *Pteranodon* sp. indet.
Pterodactylus ingens	YPM 1171	33.6	36.1	♂ *Pteranodon* sp. indet.
	YPM 1172	—	38.6	♂ *Pteranodon* sp. indet.
Ornithochirus umbrosus	AMNH 1571	36.7[a]	35.4	♂ *Pteranodon* sp. indet.
Ornithochirus harpyia	AMNH 1572	24.8	25.0	♀ *Pteranodon* sp. indet.
Pterodactylus velox	YPM 1176	21.7	20.2	Subadult; ♀ *Pteranodon* or ♂ *Nyctosaurus*

[a] Estimated.

lows; figures in brackets refer to Plate 7 of Cope (1875), which is reproduced here as Figure 7:

> Established on wing metacarpals and phalanges of three individuals. The articular extremities indicate a species from one-half to two-thirds the size of the last named [*Ornithochirus umbrosus*]. Those of the metacarpal [Fig. 7:5] are very prominent above as well as below, and there is no distinct ridge in the trochlear groove between them. The inner condyle does not stand on a base with an acute posterior ridge, but overhangs a rather obtusely edged support. There is no second ridge on the outer (trochlear) side of it. The same condyle terminates abruptly posteriorly on the superior face of the shaft. Width of condyle in No. 1, eleven lines; in No. 2, thirteen lines; vertical diameter inner condyle, eleven lines (No. 1); transverse diameter shaft above, right [sic, read "eight"] lines.
>
> The proximal articular surface of the proximal wing phalanges [Fig. 7:6A] are deeply concave, the inner protected by an elevated margin behind,

> that of the outer much lower. They are separated chiefly by a deep emargination, but on their short adjacent portions by a low ridge. The process for ligamentary insertion is well developed. The distal extremity [Fig. 7:6B] is slightly widened, and its articular surface is wedge-shaped with a very convex base. Its surface is slightly concave in both directions and without median ridge. The margin of the shaft terminates in a short tuberosity bearing articular surface. Transverse diameter, sixteen lines. Length of shaft preserved, but incomplete, 9 inches 1 line.
>
> This species is about the size of the pterodactyle found by Professor Marsh in the same region [*Pterodactylus occidentalis*], and probably belongs to the same genus, and possibly the same species. This cannot, however, be definitely ascertained, as his species is imperfectly described; all the characters adduced except the measurements being generic. The name given by Professor Marsh has also been previously used both in this genus and in *Pterodactylus* and must therefore be given up.
>
> Remains of the two *Ornithochiri* [= *O. umbrosus* and *O. harpyia*] above described are not rare in the yellow chalk of the Niobrara group, and those obtained were mostly from different parts of the course of the bluffs of Butte Creek.

The distal end of the wing metacarpal (Fig. 7:5) illustrated by Cope (1875) can be readily identified. I have been able to piece together more shaft than Cope illustrated. The entire shaft of the metacarpal is covered by small cirriped borings. As noted in the discussion of *Ornithochirus umbrosus* above, the proximal Wing Phalanx 1 and shaft described as part of the type of *Ornithochirus umbrosus* probably belong with the distal wing metacarpal included in the type of *Ornithochirus harpyia*. The first wing phalanx (Fig. 7:6) illustrated by Cope actually is a composite of two bones—the proximal end of a Wing Phalanx 1 and some shaft (Fig. 7:6A) and the proximal end of a left Wing Phalanx 2 (Fig. 7:6B). The first wing phalanx is of approximately the same size as the wing metacarpal, but it lacks cirriped borings, shows a different quality of preservation, and is clearly from a different individual.

Although Cope mentioned that the species was based on three specimens, his description does not refer to any specimens other than the wing metacarpal and first and second wing phalanges, which he figured. All the characters to which he referred can all be ascribed to differences in the planes of crushing of the different specimens. Despite problems in identifying which specimens belong to the types of *Ornithochirus umbrosus* and *O. harpyia* (see above), none of the postcranials is of any value. The morphology and provenance of the specimens indicate that they pertain to the genus *Pteranodon*, and their stratigraphic position suggests that they are specimens of *Pteranodon longiceps*, but they are indeterminate at the species level. Therefore, *Pteranodon harpyia* must be considered a *nomen dubium*.

Pteranodon comptus Marsh, 1876a nomen dubium

1876a *Pteranodon comptus:* Marsh, p. 509.
1972 *Pteranodon comptus* Marsh: Miller, p. 8.
1978 *Pteranodon comptus* Marsh: Wellnhofer, p. 65.
1984 *Pteranodon comptus* Marsh: Schoch, pp. 14–17.

Lectotype.—YPM 2335. Distal ends of both tibiae, right tarsals, and a metatarsal fragment, all poorly preserved.

Horizon and Locality.—Smoky Hill Chalk Member of the Niobrara Formation. Collected by B. F. Mudge on May 17, 1875 from T8S, R23W, Graham Co., Kansas. Examination of outcrops in that township suggests that the specimen was probably collected from between Marker Units 15 and 19 (Bennett, 1991).

Other Syntypes.—YPM 2287. Limb-shaft fragments and two dorsal centra referable to *Nyctosaurus*, fragments of fish, and the mandible and marginal scutes of a small toxochelyid(?) turtle. This "specimen" probably was collected along Twin Butte Creek and is in yellow chalk, which suggests that it came from between Marker Units 13 and 20 (Bennett, 1991). **YPM 2397**. Distal end of a femur collected April 29, 1876, from "Wallace Co." Little can be said about the stratigraphic position of this specimen.

Remarks.—Marsh (1876a:509) described *Pteranodon comptus* on the basis of three specimens, including what he interpreted as the distal ends of small wing metacarpals, a distal ulna, and two vertebral centra. The original description is as follows:

> The smallest Pterodactyle known from American strata is indicated by portions of three skeletons in the Yale Museum. Among these remains are two distal ends of the characteristic metacarpal of the wing finger [YPM 2335], other portions of the wing bones, and two sacral vertebrae [YPM 2287]. The large metacarpal is very slender, and elongated, and its outer distal condyle has its superior margin elevated above the shaft, and terminated proximally in a point. The ulna [YPM 2397?] is comparatively large, and the proximal carpal has an oval air cavity on its radial side. The sacral vertebrae have their centra short, and medially constricted.

As usual, no specimen numbers were given in the original description, but Eaton (1910) noted that YPM 2335 and 2287 were labeled "*P. comptus*, type in part" and that YPM 2397 was associated with the other two specimens. In addition, Eaton described the specimens briefly. He noted that YPM 2335 consisted of the distal ends of both tibiae and a right tarsus, although today this specimen also includes a fragment of a metatarsal. YPM 2287 consisted of two posterior dorsal centra lacking neural arches, and this agrees with the specimen as it is today. Lastly, YPM 2397 was said to include parts of two individuals—a distal femur, distal tibia, and fragmentary metatarsals. However, today there is no trace of the distal tibia or metatarsals.

Eaton correctly identified the "wing metacarpals" of YPM 2335 as distal tibiae of an individual about the size of *Pteranodon occidentalis*, and suggested that the "distal ulna" was the distal femur of YPM 2397. The measurements of tibiae and tarsus of YPM 2335 compare well with those published by Marsh (Table 4). Schoch designated YPM 2335 as the lectotype of *P. comptus*, but did not consider the other two specimens, YPM 2287 and 2397, to be paralectotypes. However, there is little doubt that YPM 2287 and 2397 are the other syntypes of *P. comptus*. YPM 2287 is referred to *Nyctosaurus* because of the very small size and crescentic shape of the dorsal centra, which differ from the oval centra of *Pteranodon*. The limb-shaft fragments of YPM 2287 probably pertain to the same individual as the dorsal vertebral centra because of the small size and the quality of preservation.

The provenance and morphology of YPM 2335 and 2397 indicate that they are *Pteranodon*, and stratigraphic position suggests that they are

Table 4. Comparison of Marsh's (1876a) measurements (in mm) *Pteranodon comptus* "wing metacarpals and carpals" with distal tibiae and tarsals of YPM 2335.

		YPM 2335	
Measurement	Marsh (1876a)	Right	Left
"Transverse diameter of proximal carpal"	17.0	—	—
Greatest length of distal tarsals as preserved	—	17.1	—
"Antero-posterior diameter of outer distal condyle of wing metacarpal"	12.8	—	—
Anteroposterior diameter of lateral condyle of tibia	—	12.3	12.8
"Longitudinal extent of condyle"	11.6	—	—
Longitudinal extent of lateral condyle of tibia	—	11.0	11.7
"Transverse diameter of shaft above condyle"	11.5	—	—
Transverse diameter of shaft of tibia above condyle	—	11.6	—

specimens of *Pteranodon longiceps*, but they are indeterminate at the species level. Therefore, *P. comptus* must be considered a *nomen dubium*.

PHYLOGENETIC ANALYSIS

A phylogenetic analysis of the rhamphorhynchoid pterosaurs by Padian (pers. comm.) suggested that *Rhamphorhynchus* is the sister taxon of the Pterodactyloidea, and similarly, Unwin's (1992) analysis placed the Rhamphorhynchidae as the sister group of the Pterodactyloidea. Therefore, *Rhamphorhynchus* was used as an outgroup to polarize character transformations in the analysis. Numbered nodes refer to the cladogram in Figure 8, and numbered characters refer to character transformations in the Appendix.

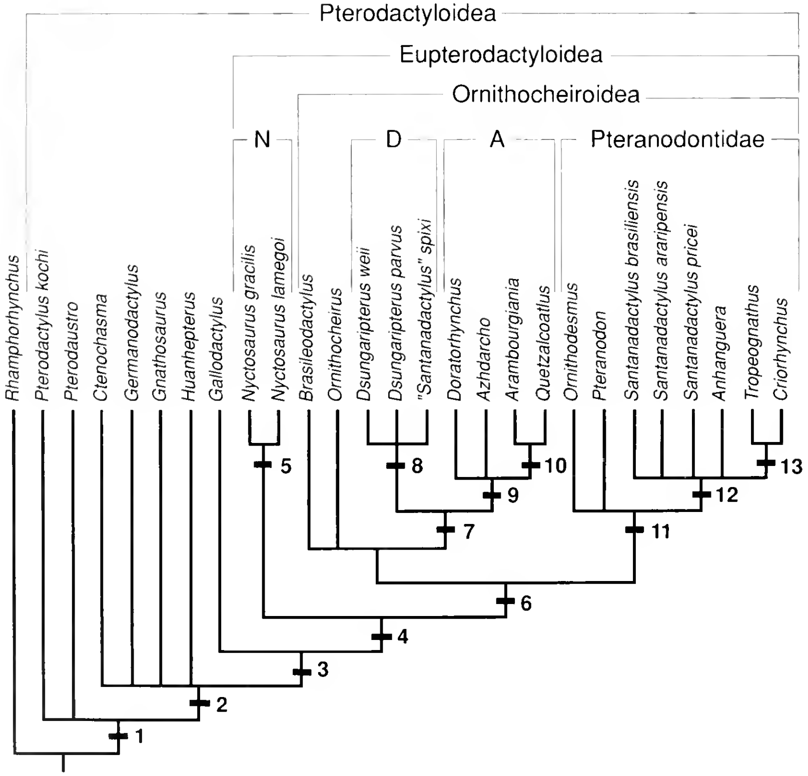

Fig. 8. Cladogram of the Pterodactyloidea based on 37 characters (see Appendix). Numbers by nodes correspond to those discussed in the text. Abbreviations: A, Azhdarchidae; D, Dsungaripteridae; N, Nyctosauridae.

It should be emphasized that the cladogram presented here is not a phylogenetic tree, but merely represents the present state of knowledge of the relationships of the various taxa. Unfortunately, the analysis still is plagued by a lack of morphological information about Jurassic pterodactyloids, and more work is needed to elucidate their relationships. Too little is known about *Noripterus*, *Cearadactylus*, *Tapejara*, and *Tupuxuara* to place these taxa on the cladogram with any confidence. *Noripterus* was considered a dsungaripterid by Young (1973), but I have been unable to confirm that. *Cearadactylus* and *Tupuxuara* are known only from partial skulls, and although they probably belong in the Ornithocheiroidea, little more can be said. *Tapejara* is known from skulls and cervical vertebrae. The cervicals have pneumatic foramina lateral to the neural canal, and so *Tapejara* is an eupterodactyloid and probably an ornithocheiroid, but again little more can be said. The analysis suggests that a number of characters found in Cretaceous pterodactyloids are convergent. Edentulous jaws are found in *Nyctosaurus*, *Quetzalcoatlus*, *Pteranodon*, *Tapejara*, and *Tupuxuara*, yet they belong to at least three different families. Similarly, hyper-elongation of the wing metacarpal, and the apparently concomitant reduction of Metacarpals I–III so that they do not reach the carpus, is found in *Nyctosaurus*, *Quetzalcoatlus*, and *Pteranodon*.

Pterodactyloidea (Node 1).—Synapomorphies of the Pterodactyloidea include: confluent naris and antorbital fenestra, reclined occiput, seven cervical vertebrae, cervical ribs absent, tail shorter than trunk, length of metacarpus greater than one-half length of antebrachium, and pedal Digit V with only one short phalanx. These characters contrast with the condition in *Rhamphorhynchus* and other non-pterodactyloid pterosaurs—viz., separate naris and antorbital fenestra, relatively vertical occiput, eight cervical vertebrae, cervical ribs carried by Cervical Vertebrae 3–8, long tail, metacarpus much shorter than antebrachium, and pedal Digit V with two long phalanges. These pterodactyloid characters are not listed in the data matrix.

Node 2.—This clade shares the following synapomorphy:

1.1 Sagittal premaxillary crests. Of the taxa within this clade for which the skull is known only *Gallodactylus*, *Nyctosaurus*, and *Ornithodesmus* appear to lack premaxillary crests, but *Gallodactylus* has a parietal crest. *Pterodactylus* and *Pterodaustro* are excluded from this clade because they appear to lack premaxillary crests, but see the discussion under Node 3.

Node 3.—This clade shares the synapomorphy of:

2.1 First two dorsal vertebrae cervicalized. Cervicalization refers to the fact that these vertebrae, the sixth and seventh postaxial vertebrae, are longer and broader than the subsequent dorsals, and generally more like the cervicals in morphology. The first two dorsal vertebrae are cervicalized in the Nyctosauridae, Azhdarchidae, Pteranodontidae, and Dsungaripteridae (Bennett, 1989, 1991), and in these forms they also have exapophyseal articulations like the cervicals. Bennett (1991) suggested that the two vertebrae may have been cervicalized as a result of the fusion of dorsal vertebrae into a notarium. However, in *Gallodactylus suevicus*, the two anterior dorsal vertebrae are cervicalized with the centra broad, low, and longer than the subsequent dorsals, although there is no evidence of a notarium.

The branching pattern produced by Characters 1 and 2 (sagittal premaxillary crest and cervicalized dorsal vertebrae) may be misleading. The case of *Ctenochasma* suggests that we approach the absence of a premaxillary crest with caution; one species, *C. porocristata*, has a premaxillary crest, whereas two others, *C. roemeri* and *C. gracile*, appear to lack crests. Bennett (1992) noted sexual dimorphism in crest size in *Pteranodon* and other large pterodactyloids and suggested that the presence and absence of crests in *Ctenochasma* may reflect sexual dimorphism. In addition, recent work (Bennett, MS) has suggested that the crestless species of *Pterodactylus* may be juveniles of other species that had cranial crests.

Similarly, the separation of *Gallodactylus* from other non-eupterodactyloids may result from our incomplete understanding of the evolution of the pterodactyloids. In *Rhamphorhynchus* and other non-pterodactyloids, there are eight cervical vertebrae and cervical ribs are present on C2 or C3 through C8 (Wellnhofer, 1975). In eupterodactyloids (see below), the ribs of the first two dorsals are short and do not reach the sternum, whereas those of the first notarial vertebra do. It is not clear what the condition is in primitive pterodactyloids. The character of seven cervical vertebrae in pterodactyloids may actually be that C1–C7 lack ribs; thus, it is possible that there were the plesiomorphic eight cervicals or perhaps nine, if the sixth and seventh postaxial vertebrae are actually cervicals rather than cervicalized dorsals. More work is needed to clarify this. In short, our knowledge of the relationships of the Jurassic pterodactyloids might be better represented by an unresolved polytomy. More work is needed to resolve the relationships of the basal pterodactyloids.

Eupterodactyloidea, infraorder novum (Node 4).—The clade [Nyctosauridae + Dsungaripteridae + Pteranodontidae + Azhdarchidae] shares the following synapomorphies:

4.1 Scapula rotated outward so that the posterior/medial end approaches vertebral column. The scapula is certainly rotated outward in the Nyctosauridae + Dsungaripteridae + Azhdarchidae + Pteranodontidae (Bennett, 1989).

5.1 Helical jaw joint (?reversed in *Ornithodesmus*). Among this clade the helical jaw joint is present in all taxa for which the jaw articulation is known except *Ornithodesmus* (Hooley, 1913). I have not been able to examine the articulation in *Ornithodesmus* to confirm its absence.

6.1 Atlas fused to axis. Howse (1986) used fusion of the atlas and axis as a synapomorphy of the "tall-spined pterodactyloids" (= [Pteranodontidae + Nyctosauridae]), but the character is also present in *Azhdarcho* (Nessov, 1984) and *Dsungaripterus* (pers. observ.). In addition, this character may also have been present in some Jurassic pterodactyloids.

7.1 Cervical vertebrae with exapophyses. Exapophyses, accessory articulations ventrolateral to the central articulation, are present in all members of this clade for which the cervicals are known. Howse (1986) stated that *Pteranodon* had the autapomorphy of preexapophyses on the cervical vertebrae. However, the condition in *Pteranodon* is identical to that of other pteranodontids, nyctosaurids, dsungaripterids, and azhdarchids (Bennett, 1989; 1991).

8.1 Cervical vertebrae with pneumatic foramina lateral to neural canal. Pneumatic foramina lateral to the neural canal are found in pteranodontids, nyctosaurids, and azhdarchids. Among pteranodontids, *Anhanguera santanae* does not have pneumatic foramina lateral to the neural canal; instead, the foramina on the sides of the centra are particularly large (Wellnhofer, 1991). *Dsungaripterus* lacks pneumatic foramina lateral to the neural canal, but the skeleton of *Dsungaripterus* has thick-walled bones and little postcranial pneumaticity.

9.0 Cervical vertebrae with tall neural spines. Tall neural spines on cervical vertebrae are found in pteranodontids, nyctosaurids, and dsungaripterids, but not in azhdarchids. The most parsimonious arrangement is for tall neural spines to evolve at Node 4 and be lost in the azhdarchids. This is not unreasonable, because in taxa with elongate vertebrae, tall neural spines would not be needed to provide area for muscle insertions and for leverage to flex the neck. But it is also possible that the tall neural spines could be developed convergently in response to a need for additional area for muscle origins and insertions and for additional increase leverage, as different short-necked pterosaurs increased in size.

10.1 Notarium of three or more fused dorsal vertebrae and fused dorsal ribs. A notarium formed of fused dorsal vertebrae and anterior dorsal ribs is found in nyctosaurids, dsungaripterids, azhdarchids, and pteranodontids. The notarium of *Nyctosaurus* is not well known, but consists of at least three vertebrae and three pairs of dorsal ribs. In *Dsungaripterus*, the notarium consists of four vertebrae and four pairs of ribs, and in *Pteranodon*, the notarium consists of six dorsal vertebrae and four pairs of dorsal ribs. *Azhdarcho* has a notarium, but it is not well known (Nessov, 1984).

11.1 Scapula shorter than coracoid. In *Nyctosaurus* and pteranodontids the scapula is slightly shorter than the coracoid when measured from the center of the glenoid to the medial ends. Dsungaripterids and azhdarchids differ from this condition and seem to share a synapomorphy of coracoid shorter than the scapula and with a deep supracoracoid flange (see below).

12.1 Humeral shaft straight. Straight humeral shafts are known in *Nyctosaurus*, *Dsungaripterus*, *Quetzalcoatlus*, and pteranodontids. The shaft of the humerus is curved in *Pterodactylus*, *Gallodactylus*, and *Rhamphorhynchus*. The straightening may be related to the increased diameter of the shaft of the humerus in larger pterosaurs.

This clade, the Eupterodactyloidea, is named because the rotation of the scapula and the development of a notarium seem to be critical innovations that permitted this new radiation of pterodactyloids to evolve large size and replace more primitive pterodactyloids. Young (1964) proposed a third suborder of the Pterosauria, the Dsungaripteroidea, in addition to the Rhamphorhynchoidea and Pterodactyloidea, and diagnosed it by the primary character of a notarium. Such a clade may exist, but it is not clear what exactly Young meant by "notarium." I have defined a notarium as consisting of at least three fused dorsal vertebrae and fused dorsal ribs. It seems that Young considered a notarium to include an articulation on a supraneural plate for the scapula, in which case the Nyctosauridae would be excluded and his Dsungaripteroidea would correspond to the Ornithocheiroidea discussed below.

Nyctosauridae (Node 5).—The Nyctosauridae (Williston, 1903; = subfamily Nyctosaurinae) share the following synapomorphy:

13.1 Humerus with hatchet-shaped deltopectoral crest. The humerus of *Nyctosaurus* is distinctive. The deltopectoral crest does not have an elongate base and the long axis of the base of the crest is parallel to the long axis of the humerus. In these respects, it is similar to the humerus of azhdarchids and displays the primitive condition. In anterior view, the deltopectoral crest is gently curved with the concave side down. The crest widens and ends with a rounded margin producing the characteristic hatchet shape and there is a small flattened terminal expansion at the proximal end of the crest (See Williston, 1903 for the best figure to date). Muscle attachment scars form a characteristic pattern, quite unlike that of the pteranodontid humerus; unfortunately, the pattern of muscle scars in dsungaripterids and azhdarchids is not known. The pneumatic foramen is on the ventral surface of the humerus between the head and deltopectoral crest. This may be the primitive position of the pneumatic foramen because it is also located there in *Bennettazhia*. The Nyctosauridae include *Nyctosaurus gracilis* from the late Coniacian to early Campanian of North America, and a large indeterminate nyctosaurid, *Nyctosaurus lamegoi* (Price, 1953), based on a single incomplete humerus from the Maestrichtian of Brazil.

Autapomorphies of *Nyctosaurus gracilis* include the following characters:

14.1 Edentulous jaws.

15.1 Hyper-elongate Metacarpal IV (length ≥ 1.5 × antebrachium), and Metacarpals I–III reduced and not reaching carpus (convergent with *Quetzalcoatlus* and *Pteranodon*).

16.1 Only three phalanges in wing finger (Brown, 1986).

17.1 Neural spines of midnotarial vertebrae T-shaped in anterior view. Although *Nyctosaurus* has a notarium and the scapula is rotated so its posterior end approaches the vertebral column, the scapula does not articulate with the vertebral column. Instead, the T-shaped neural spines and the posterior/medial end of the scapula are expanded for ligaments that fixed the end of the scapula (Bennett, 1989).

18.1 Dorsal centra crescentic in cross section.

Nyctosaurus lamegoi may share many of these characters with *N. gracilis*, in which case they would be synapomorphies of the Nyctosauridae, but only its humerus is known. The humerus of *N. lamegoi* differs from that of *N. gracilis* only in its greater size.

Ornithocheiroidea (Node 6).—The clade [*Ornithocheirus* s.s. + *Brasileodactylus* + Dsungaripteridae + Azhdarchidae + Pteranodontidae] shares the following synapomorphies:

19.1 Palate with median ridge and mandible with corresponding median groove. The palatal ridge and mandibular groove was one of the characters used by Seeley (1870) to diagnose the Ornithocheiridae (= subfamily Ornithocheirae). It is found in *Ornithocheirus* s.s., *Brasileodactylus*, *Doratorhynchus*, *Santanadactylus araripensis*, *Anhanguera*, *Criorhynchus*, and *Tropeognathus*. In *Azhdarcho*, the extreme anterior end of the fused premaxillae has a weak median ridge and the dorsal surface of the fused dentaries is gently concave. It is not clear if this is homologous with the ridge and groove of other forms. The fact that it is not found in the edentulous forms such as *Pteranodon* is apparently a loss. *Ornithocheirus* s.s. and *Brasileodactylus* are in this clade, but no other characters are known that would further resolve their relationships. As noted elsewhere, a mandible of *Brasileodactylus* (SMNS 55414) is preserved with cervicals like those of some *Ornithocheirus* s.l. from the Cambridge Greensand (Owen, 1860: pl. 2, figs. 13–16) in the same concretion. Seeley (1875) noted the similarity between those *Ornithocheirus* cervicals and the cervical of *Doratorhynchus*, although the latter is longer. This may suggest that *Brasileodactylus* and the similar *Ornithocheirus daviesi* and *O. sedgwicki* have affinities with the azhdarchids.

17.2 Notarium with supraneural plate of fused neural spines. The notarium with supraneural plate and scapular articulation are found in all members of this group in which the notarium or scapula is known. The Nyctosauridae differ from this group in that the neural spines of the notarium are not coalesced into a supraneural plate, and, although the scapula is rotated so that it forms a steep angle to the vertebral column, the medial end of the scapula does not articulate with the notarium.

20.1 Scapula articulates with supraneural plate of notarium.

Node 7.—The clade [Dsungaripteridae + Azhdarchidae] shares the following characters:

11.2 Coracoid shorter than scapula with deep supracoracoid flange. Dsungaripterids and azhdarchids share a distinctive scapulocoracoid morphology with the coracoid shorter than the scapula, with a deep supracoracoid flange, and with the coracoid appearing to form a 90° angle below the glenoid. This character may be linked to the overlapping sternocoracoid joints. Altogether, the pectoral girdle of these two families seems to be more powerfully built and more mobile than that of pteranodontids.

13.2 Deltopectoral crest long and curving ventrally (Bennett, 1989).

21.0 Sternocoracoid joints overlap (?convergent with *Ornithodesmus*).

22.1 Midshaft of humerus subcylindrical (Bennett, 1989).

23.0 Preaxial carpal process short giving distal syncarpal rectangular shape.

24.1 Distal articular surfaces of distal syncarpal of unequal size.

Bennett (1989) cited five characters of the forearm and carpus as diagnostic of the Dsungaripteridae, and termed them the "dsungaripterid carpus." It has become clear that some of these characters occur in the Azhdarchidae. Therefore, they are coded separately, rather than as a single character. D. M. Unwin (pers. comm.) suggested that the "dsungaripterid carpus" was merely the primitive condition of carpus in pterodactyloids and *Rhamphorhynchus*. This may be the case, but I have not been able to confirm it, and the conditions do differ from those of pteranodontids and nyctosaurids.

Dsungaripteridae (Node 8).—The Dsungaripteridae (Young, 1964; Bennett, 1989) share the following synapomorphies:

25.1 Short, squat preaxial carpal.

26.1 Distal end of radius subtriangular with large process on anterior side. The character "distal end of radius subtriangular" is not listed in the data matrix. However, the condition differs significantly from that of *Santanadactylus* in which distal end is subrectangular. The condition in *Nyctosaurus* and *Pteranodon* is unclear because of crushing.

27.0 Ventrally offset tuberculum of distal ulna.

Included taxa are *Dsungaripterus weii* (Young, 1964), *D. parvus* (Bakhurina, 1982), and "*Santanadactylus*" *spixi* (Wellnhofer, 1985; Bennett, 1989).

Azhdarchidae (Node 9).—The Azhdarchidae, as diagnosed by Nessov (1984; = subfamily Azhdarchinae) and Padian (1984; 1986), share the synapomorphies:

9.2 Cervical vertebrae with low, vestigial, or absent neural spines (?convergent with *Huanhepterus*).

28.2 Extreme elongation of midcervical vertebrae (length ≥ 5 × width), with round cross section in middle of centrum (?convergent with *Huanhepterus*).

An additional character, cervical vertebrae with unossified neural canals, was cited by Padian (1984; 1986) as a synapomorphy, has not been demonstrated in all the genera assigned to the group, and may diagnose a smaller clade within the Azhdarchidae. In the shorter anterior or posterior cervicals of *Azhdarcho*, the neural canal is ossified. The canal might still be unossified in the long midcervicals of *Azhdarcho*, or the unossified condition in *Quetzalcoatlus* may be ontogenetic or an autapomorphy. Nessov (1984) included the character of median pneumatic foramen above the neural canal in his diagnosis, but this has not been reported in *Arambourgiania* and *Quetzalcoatlus*, and it is present in *Pteranodon*. The Azhdarchidae include *Azhdarcho*, *Quetzalcoatlus*, *Arambourgiania*, and *Doratorhynchus*.

Node 10.—*Quetzalcoatlus* and *Azhdarcho* share the following synapomorphy:

14.1 Edentulous jaws. *Doratorhynchus* has toothed jaws, and the condition of the jaws in *Arambourgiania* unknown.

29.3 Shafts of wing phalanges 2 and 3 with inverted T-shaped cross section. These phalanx shafts have rather thick walls compared to those of phalanges with suboval cross sections. This might be an adaptation to prevent damage to the phalanges from striking objects.

Pteranodontidae (Node 11).—As discussed earlier, the Pteranodontidae include at least four genera, *Pteranodon*, *Ornithodesmus*, *Santanadactylus*, and *Anhanguera*. *Criorhynchus* from the Cambridge Greensand is probably also pteranodontid, because the only postcranials large enough to pertain to it are pteranodontid. *Tropeognathus* from the Santana Formation of Brazil is very similar to *Criorhynchus*, and probably is also pteranodontid. The Pteranodontidae share the synapomorphies:

13.3 Humerus with warped deltopectoral crest, thin proximal flange spanning between head and distal end of crest, and terminal expansion at end of crest.

22.1 Shaft of humerus increasing in diameter from base of deltopectoral crest to distal end.

26.1 Subtriangular distal end of humerus.

Within the Pteranodontidae there is an unresolved trichotomy consisting of *Ornithodesmus*, *Pteranodon*, and a clade consisting of all other pteranodontids (Node 12).

Autapomorphies of *Ornithodesmus* include:

21.0 Overlapping sternocoracoid joints (?convergent with dsungaripterids and azhdarchids).

34.1 Deep cristospine.

35.1 Ulna with ridge supporting radius (Hooley, 1913).

Autapomorphies of *Pteranodon* include:

14.1 Edentulous jaws (convergent with *Nyctosaurus*, *Quetzalcoatlus*, *Tapejara* [Kellner, 1989], and *Tupuxuara* [Kellner and Campos, 1988]).

15.2 Hyper-elongate Metacarpal IV (length ≥ 1.5 × antebrachium), and Metacarpals I–III reduced and not reaching carpus (convergent with *Nyctosaurus* and *Quetzalcoatlus*).

17.3 Supraneural plate of ossified ligaments.

30.1 Frontal crest.

31.1 Duplex caudal vertebrae. The centra of the proximal caudals are low and broad and appear as if they consisted of two normal spool-shaped centra fused together at the midline.

32.2 Distal pneumatic foramen of humerus on ventral surface.

Additional autapomorphies and probable autapomorphies not listed in the data matrix are discussed in the Systematic Paleontology section above.

All non-*Pteranodon* pteranodontids share the synapomorphy:

33.1 Radius less than half the diameter of ulna. This character is seen in *Santanadactylus* and *Ornithodesmus*. The radius is greater than one half the ulna diameter in *Pteranodon*, "*Santanadactylus*" *spixi*, and *Nyctosaurus*.

Bennett (1989) suggested that a pneumatic foramen on the dorsal surface of the humerus near the posterior tuberosity (= ulnar crest) was a synapomorphy of the group. However, in *Pteranodon* the pneumatic foramen is on the ventral surface. Based on the position of the pneumatic foramen in *Nyctosaurus* and *Bennettazhia*, this is the primitive condition for the foramen. Therefore, this character seems to diagnose a clade within the Pteranodontidae, and cannot be considered a synapomorphy of the Pteranodontidae unless it can be shown to have been reversed in *Pteranodon*. The position of the pneumatic foramen at the proximal end of the humerus is not known in *Ornithodesmus*. If it is on the dorsal surface of the humerus, then *Ornithodesmus* would be within the polytomy at Node 12, and *Pteranodon* would be the sister taxon of all other pteranodontids. However, if the position of the foramen in *Pteranodon* is the result of a reversal, then the overlapping sternocoracoid joints of *Ornithodesmus* might share a common origin with those of dsungaripterids and azhdarchids at Node 6. The character then would have been reversed, to symmetrical sternocoracoid joints, in other pteranodontids. This latter arrangement would be more consistent with the stratigraphic position of the various taxa, and would be as parsimonious as the alternate convergent evolution of overlapping sternocoracoid facets in *Ornithodesmus* and at Node 7.

Wellnhofer (1991) stated that the humeri of the indeterminate pteranodontid USNM 13804 and *Santanadactylus* have a ridge and depressed area on the head, and noted that it was not present in *Anhanguera*. This ridge is also visible in a few relatively uncrushed specimens of *Pteranodon* (e.g., YPM 1191, Fig. 9). The ridge appears to represent the limit of a thick articular cartilage that covers the ventral half of the head. It is not visible in immature specimens. Specimens considered by Wellnhofer

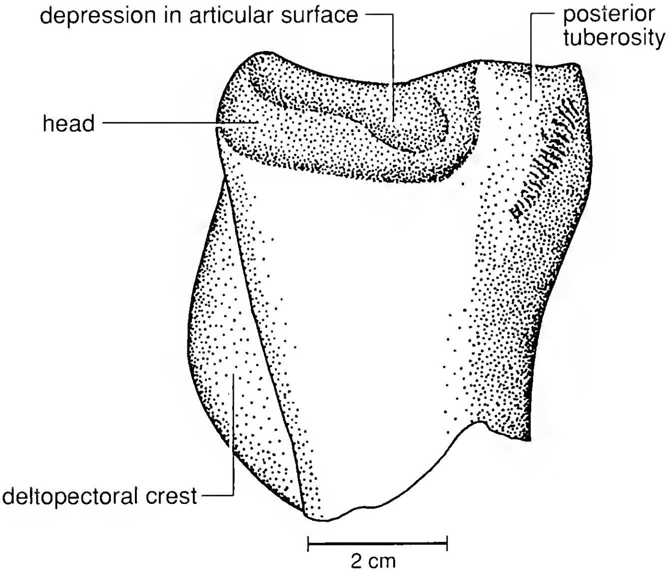

Fig. 9. Proximal left humerus of YPM 1191 in dorsal view showing the depressed area on the articular surfac

(1991) to be *Anhanguera santanae* (e.g., AMNH 22555) lack the ridge because they are subadults as shown by the unfused notaria, scapulocoracoids, and pelvic girdles. All characters listed by Wellnhofer to separate *Santanadactylus araripensis* and *Anhanguera santanae* are ontogenetic differences between adults and subadults (Bennett, 1993).

Node 12.—This clade, which includes *Santanadactylus brasiliensis, S. araripensis, S. pricei, Anhanguera, Criorhynchus,* and *Tropeognathus,* shares the following synapomorphy:

36.2 Pneumatic foramen on dorsal surface of humerus.

Within this clade, *Santanadactylus pricei* and some postcranials from the Cambridge Greensand referred to *Ornithocheirus* s.l. have an elevation between the condyles of the wing metacarpal. Note that *Anhanguera* and *Santanadactylus araripensis* seem to be synonyms.

Node 13.—*Tropeognathus* and *Criorhynchus* share the synapomorphy:

37.1 Large rounded terminal premaxillary and mandibular crests. However, as noted by Bennett (1992), specimens assigned to these genera may be males of sexually dimorphic species, and the females of their species are referred to other genera. If this were the case, the large terminal crests might still be a synapomorphy of the sexually dimorphic species.

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APPENDIX

CHARACTERS AND DATA MATRIX

Character transformations used in the cladistic analysis.

1. Premaxillary crest.
    0: Absent.
    1: Present.
2. Eight and ninth postcranial vertebrae.
    0: Morphological dorsals.
    1: Cervicalized.
3. Parietal crest.
    0: Absent.
    1: Present.
4. Scapula.
    0: Lies subparallel to vertebral column.
    1: Rotated outward.
5. Helical jaw joint.
    0: Absent.
    1: Present.
6. Atlas and axis vertebrae.
    0: Unfused.
    1: Fused.
7. Exapophyseal articulations.
    0: Absent.
    1: Present.
8. Midcervical vertebrae
    0: Without pneumatic foramina lateral to the neural canal.
    1: With pneumatic foramina lateral to the neural canal.
9. Neural spines of cervical vertebrae.
    0: Tall.
    1: Low.
    2: Reduced/obsolescent neural spines.
10. Notarium of fused dorsal vertebrae.
    0: Absent.
    1: Present.
11. Scapulocoracoid.
    0: Scapula and coracoid lengths subequal.
    1: Scapula shorter than coracoid.
    2: Coracoid shorter than scapula, and with deep supracoracoideus flange.

12. Humerus shaft.
    0: Bowed.
    1: Straight.
13. Deltopectoral crest.
    0: Short and proximally placed
    1: Long, straight, and distally expanded into a hatchet shape.
    2: Long and curving ventrally.
    3: Warped.
14. Jaws.
    0: Toothed.
    1: Edentulous.
15. Metacarpus.
    0: Metacarpals I–III the same length as Metacarpal IV and articulating with the carpus.
    1: Metacarpal I articulating with the carpus, but Metacarpals II and III are reduced and do not.
    2: Hyper-elongate Metacarpal IV (length ≥ 1.5 × antebrachium, and Metacarpals I–III reduced and not reaching the carpus.
16. Wing finger.
    0: With four phalanges.
    1: With three phalanges.
17. Supraneural plate of notarium.
    0: Absent.
    1: Absent, but neural spines of midnotarial vertebrae T-shaped.
    2: Formed of fused neural spines.
    3: Formed of ossified interspinous ligaments.
18. Dorsal centra.
    0: Suboval in cross section.
    1: Crescentic in cross section.
19. Palate and mandible.
    0: Without ridge and sulcus.
    1: With ridge on palate and sulcus on mandible.
20. Scapula.
    0: Does not articulate with notarium.
    1: Articulates with notarium.
21. Sternocoracoid articulations.
    0: One in front of the other.
    1: Side by side.
22. Midshaft of humerus.
    0: Straight.
    1: Tapers.

23. Preaxial carpal process of distal syncarpal.
    - 0: Short, giving the syncarpal a rectangular appearance.
    - 1: Long, giving the syncarpal a teardrop shape.
24. Articular facets of distal syncarpal.
    - 0: Unequal, ventral facet larger.
    - 1: Subequal in size.
25. Preaxial carpal.
    - 0: Long.
    - 1: Short and squat.
26. Distal end of humerus.
    - 0: Oval to D-shaped.
    - 1: Subtriangular.
27. Tuberculum of ulna.
    - 0: Offset ventrally.
    - 1: Not offset ventrally.
28. Midcervical vertebrae.
    - 0: Short and of relatively uniform length.
    - 1: Elongated.
    - 2: Extremely elongated (length $\geq 5 \times$ width).
29. Cross section of wing phalanges.
    - 0: Concave posteriorly.
    - 1: Round to subtriangular.
    - 2: Suboval with longitudinal ridges on anterior and posterior surfaces.
    - 3: Round to subtriangular, but Wing Phalanges 2 and 3 with inverted T-shaped cross section.
30. Frontal crest.
    - 0: Absent.
    - 1: Present.
31. Caudal vertebrae.
    - 0: With simple centra.
    - 1: With duplex centra.
32. Distal pneumatic foramen of humerus.
    - 0: Absent.
    - 1: On distal end.
    - 2: On ventral surface just proximal to and between the condyles.
33. Radius.
    - 0: Greater than half diameter of ulna.
    - 1: Less than half diameter of ulna.
34. Cristospine.
    - 0: Shallow.
    - 1: Deep.

35. Ulna.
    - 0: Without longitudinal ridge.
    - 1: With longitudinal ridge.
36. Proximal pneumatic foramen of humerus.
    - 0: Absent.
    - 1: On ventral surface.
    - 2: On dorsal surface.
37. Rounded terminal premaxillary and mandibular crests.
    - 0: Absent.
    - 1: Present.

Data matrix of character states for cladistic analysis. Characters 9, 11, 13, 15, 17, 24–29, 32, and 36 were unordered.

	0 0 0 0 0 0 0 0 0 1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3
Character	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7
Rhamphorhynchus	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 – – – – 0 0 0	0 0 0 0 0 0 0
Pterodactylus kochi	0 0 0 0 – 0 0 – 1 0	0 0 0 0 0 0 0 – – 0	– 0 0 – – – – 1 1 0	0 0 0 0 0 0 0
Pterodaustro	0 – 0 0 – – 0 – 1 –	– – 0 0 – – – – – –	– 0 – – – – – 1 0 –	– – – – – 0 0
Ctenochasma	1 – 0 – – – – – – –	– – – 0 – – – – – –	– – – – – – – – – –	– – – – – 0 0
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Gallodactylus	0 1 1 0 – 0 0 – 1 –	0 0 0 0 0 0 – – – 0	– 0 0 – – – – 1 1 0	– – – – – 0 0
Nyctosaurus gracilis	0 1 0 1 1 1 1 1 1 1	1 1 1 1 2 1 1 1 0 0	1 1 1 1 – 0 0 0 1 0	0 – – 0 0 1 0
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Dsungaripterus weii	1 1 1 1 1 1 1 – 0 1	2 1 2 0 – 0 2 0 0 1	0 – 0 0 1 1 0 0 2 0	0 – – 0 0 – 0
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"*Santanadactylus*" *spixi*	– – – – – – – – – –	– – – – 2 – – – – –	– 0 0 0 1 1 – 1 – –	– – 0 – – – –
Doratorhynchus	– – – – – – – 1 2 –	– – – 0 – – – – 1 –	– – – – – – – 2 – –	– – – – – – –
Azhdarcho	– 1 – – 1 1 1 1 2 1	– 1 2 1 – – – 0 – –	– – – 0 – – 0 2 3 –	– – – – – 1 –
Arambourgiania	– – – – – – 1 1 2 –	– – – – – – – – – –	– – – – – – – 2 – –	– – – – – – –
Quetzalcoatlus	1 1 – 1 1 – 1 1 2 –	2 1 2 1 2 0 2 – 0 1	0 0 0 0 1 – 0 2 3 –	– – – – 0 1 0
Pteranodon	1 1 0 1 1 1 1 1 0 1	1 1 3 1 2 0 3 0 0 1	1 1 1 1 0 0 1 0 1 1	1 2 0 0 0 1 0
Ornithodesmus latidens	0 1 – 1 0 – 1 – 0 1	1 1 3 0 – – 2 0 0 1	0 0 – – – – 1 – – –	– 1 1 1 1 – 0
Santanadactylus brasiliensis	– – – 1 – – – – – –	– – 3 – – – – – – –	– 1 1 – – – – – – –	– – – – – 2 –
Santanadactylus araripensis	1 – 0 – 1 – – – 0 –	– 1 3 0 1 – – – 1 –	– 1 1 1 0 – 1 – – 0	– 1 1 – 0 2 –
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Anhanguera	1 1 0 1 1 1 1 0 0 –	1 1 3 0 1 0 2 – 1 1	– 1 1 1 0 0 1 0 1 0	0 – – – 0 2 –
Tropeognathus	1 – 1 – 1 – – – – –	– – – 0 – – – – 1 –	– – – – – – – – – 0	– – – – – – 1
Brasileodactylus	– – – – – – – – – –	– – – 0 – – – – 1 –	– – – – – – – – – –	– – – – – – 0
Ornithocheirus s.s.	– – – – – – – – – –	– – – 0 – – – – 1 –	– – – – – – – – – –	– – – – – – 0
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