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Spencer G. Lucas
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CRETACEOUS-EOCENE CROCODILIANS FROM THE SAN JUAN BASIN, NEW MEXICO

SPENCER G. LUCAS
New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, New Mexico 87104-1375

Abstract—Crocodilian fossils from the Fruitland, Kirtland, Nacimiento and San Jose Formations in the San Juan Basin (Upper Cretaceous–lower Eocene) represent the genera *Akanthosuchus* (Nacimiento Formation), *Allognathosuchus* (Nacimiento and San Jose Formations), *Brachychampsa* (Fruitland and Kirtland Formations), *Diplocynodon* (Nacimiento Formation), *Goniopholis* (Fruitland and Kirtland Formations), *Leidyosuchus* (Fruitland, Kirtland, Nacimiento and San Jose Formations) and *Thoracosaurus*? (Fruitland Formation). The San Juan Basin taxa document some evolutionary turnover in crocodilians at the Cretaceous-Tertiary boundary and suggest that the feeding ecology of extant crocodilians was present among the Late Cretaceous–early Eocene crocodilians.

INTRODUCTION

Fossil crocodilians have been known from the Upper Cretaceous–lower Eocene strata of the San Juan Basin since Cope (1874) first reported them from the lower Eocene San Jose Formation. Since then, a diverse and diffuse literature has been published on San Juan Basin crocodilians, and several taxa have been proposed. However, most existing specimens have not been documented, and a need to revise the systematics of North American Late Cretaceous–Paleogene crocodilians has hampered precise identification and interpretation of the San Juan Basin crocodilians. Here, I review these crocodilians, document some new specimens, establish their stratigraphic ranges and discuss some of their evolutionary and ecological implications. AMNH = American Museum of Natural History, New York; MCZ = Museum of Comparative Zoology, Harvard University; NMMNH = New Mexico Museum of Natural History; PMU.R = Paleontologiska Museum, Uppsala Universität, Uppsala, Sweden; and UCMP = University of California Museum of Paleontology, Berkeley.

LATE CRETACEOUS CROCODILIANS

Overview

The first Late Cretaceous crocodilian reported from the San Juan Basin was the new species *Crocodilus stavelianus* named by Cope (1885). The holotype of this taxon, which I have not been able to locate (it should be in the AMNH collection), apparently is an isolated tooth morphologically similar to teeth of *Leidyosuchus* (cf. Cope, 1885). I consider *Crocodilus stavelianus* to be a nomen dubium.

Brown (in Sinclair and Granger, 1914) later mentioned crocodilian fossils in Upper Cretaceous strata of the San Juan Basin. Gilmore (1916, 1919; also see Reeside, 1924) discussed fragmentary crocodilian fossils, including blunt, broad isolated teeth from the Kirtland Formation he identified as *Brachychampsa*. Gilmore (1946) later identified isolated conical, bicarinate crocodilian teeth from the Naashoibito Member of the Kirtland Formation as *Crocodylus* sp. Although Lehman (1981) retained this identification, he (Lehman, 1985) later abandoned it without explanation. As Lambe (1908) and Armstrong-Ziegler (1980) argued, isolated, conical, bicarinate crocodilian teeth of Late Cretaceous age probably pertain to *Leidyosuchus*, not to the extant genus *Crocodylus*.

Hutchinson and Kues (1985, p. 48–50, fig. 14) assigned isolated teeth of crocodilians from the Fruitland Formation to *Brachychampsa*?, *Leidyosuchus* and indeterminate crocodilians. Armstrong-Ziegler (1978, 1980) identified isolated teeth from the Fruitland Formation as *Brachychampsa, Leidyosuchus* and ?*Thoracosaurus*. A large collection of isolated teeth, scutes, vertebrae and other postcrania from the Fruitland and Kirtland Formations listed by Kues et al. (1977) is now in the NMMNH and includes the same types of isolated teeth that have been identified as *Brachychampsa* and *Leidyosuchus*.

As Hutchinson and Kues (1985) well discussed, assigning isolated blunt, broad teeth to *Brachychampsa* is problematic since these teeth cannot be distinguished from isolated teeth of *Allognathosuchus*. Indeed, Lehman (1981) assigned such isolated teeth from the Naashoibito Member of the Kirtland Formation to ?*Allognathosuchus* but later abandoned the identification (Lehman, 1985). Here, I tentatively accept previous identifications of *Brachychampsa*, not *Allognathosuchus*, but note that this may artificially restrict the stratigraphic distribution of *Brachychampsa* in the San Juan Basin to the Late Cretaceous and *Allognathosuchus* to the Paleocene-Eocene. Isolated teeth and other fragmentary fossils thus suggest that ?*Thoracosaurus* is present in the Fruitland Formation and *Brachychampsa* plus *Leidyosuchus* are found throughout the Fruitland and Kirtland Formations.

A third type of isolated tooth is found throughout the Fruitland and Kirtland Formations. This type of tooth (Fig. 1A–F) is nearly cylindrical and blunt-tipped, with weak carinae and longitudinal striations. Lehman (1981) assigned this tooth type to *Goniopholis*, and I concur with this identification because these teeth closely resemble the teeth in skulls of *Goniopholis* (e.g., Hulke, 1878, pl. 15, fig. 2a; Owen, 1878, pl. 1, figs. 3–8; Wiman, 1931, pl. 5, figs. 2–3). Isolated osteoscutes from the Fruitland and Kirtland Formations (e.g., Fig. 1G) also are assigned to *Goniopholis* because they closely resemble osteoscutes associated with *Goniopholis* skulls (e.g., Owen, 1878, pl. 4, fig. 1; Wiman, 1931, pl. 5, fig. 4). The density and shape of pitting of scutes of *Leidyosuchus* (Fig. 1J–L) and *Brachychampsa* (Fig. 1M–N) is much different (also see Lambe, 1908; Bryant, 1989, fig. 14A).

Goniopholis kirtlandicus Wiman

An incomplete skull of a Late Cretaceous crocodilian collected from the Kirtland Formation by Charles H. Sternberg and purchased by the University of Uppsala in Sweden was described by Wiman (1931) as a new species, *Goniopholis kirtlandicus*. *Goniopholis* is mostly a Late Jurassic–Early Cretaceous genus in Europe and North America, and its only Late Cretaceous occurrence is in the San Juan Basin. The holotype of *G. kirtlandicus* is an incomplete skull, PMU.R 230 (Fig. 2); an isolated tooth, PMU.R 231; and an isolated dorsal scute, PMU.R 231. The tooth and dorsal scute are presumably from the same individual as the incomplete skull (Mateer, 1981).

In a list attached to a letter to C. Wiman dated 14 November 1921, C. H. Sternberg stated that the holotype of *Goniopholis kirtlandicus* was collected at "Barell [sic] Springs 2½ miles South of [the Ojo Alamo] Trading Post, Kirtland Shales." On face value, this places the type locality in the upper shale member of the Kirtland Formation in approximately the extreme southern portion of sec. 20, T24N, R11W, San Juan County, New Mexico. However, Wolberg (1980, p. 40 and fig. 3) believed that Sternberg "overestimated the distance south of the trading post," so that the type specimen "probably came from near the middle of sec. 20, T24N, R11W." I agree with Wolberg's conclusion because there are few outcrops of the Kirtland Formation in the extreme southern portion of sec. 20. The holotype of *G. kirtlandicus* almost certainly came from the upper shale member, not from the overlying Naashoibito Member of the Kirtland Formation. Had it been derived from the Naashoibito Member, Sternberg would have identified the horizon as Ojo Alamo Sandstone, since what is now termed the Naa-

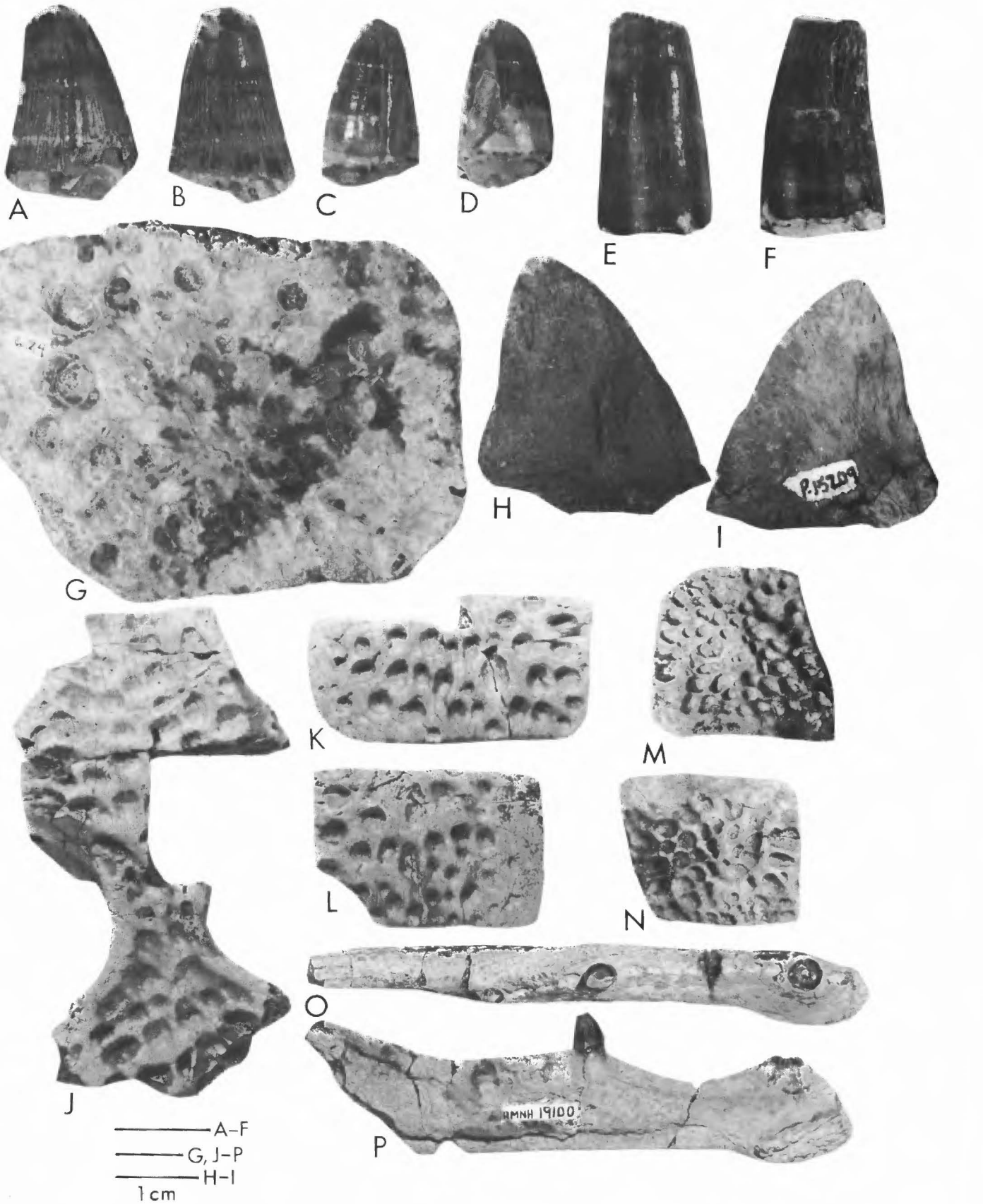


FIGURE 1. Some Late Cretaceous and Paleocene crocodilians from the San Juan Basin. A–B, *Goniopholis* sp., NMMNH P-20520, tooth. C–D, *Goniopholis* sp., NMMNH P-20522, tooth. E–F, *Goniopholis* sp., NMMNH P-20521, tooth. G, *Goniopholis* sp., NMMNH P-20523, osteoscute. H–I, *Akanthosuchus langstoni*, NMMNH P-15209, osteoscute. J–L, *Leidyosuchus* sp., NMMNH P-19320, frontal (J) and two osteoscutes (K–L). M–N, *Brachychampsa* sp., NMMNH P-20524, osteoscutes. O–P, *Allognathosuchus mooki*, NMMNH 19100, left dentary, occlusal (O) and medial (P) views. Fruitland Formation: G; Kirtland Formation: A–F, M–N; Nacimiento Formation: H–I (Puercan), J–L (Torrejonian), O–P (Puercan).

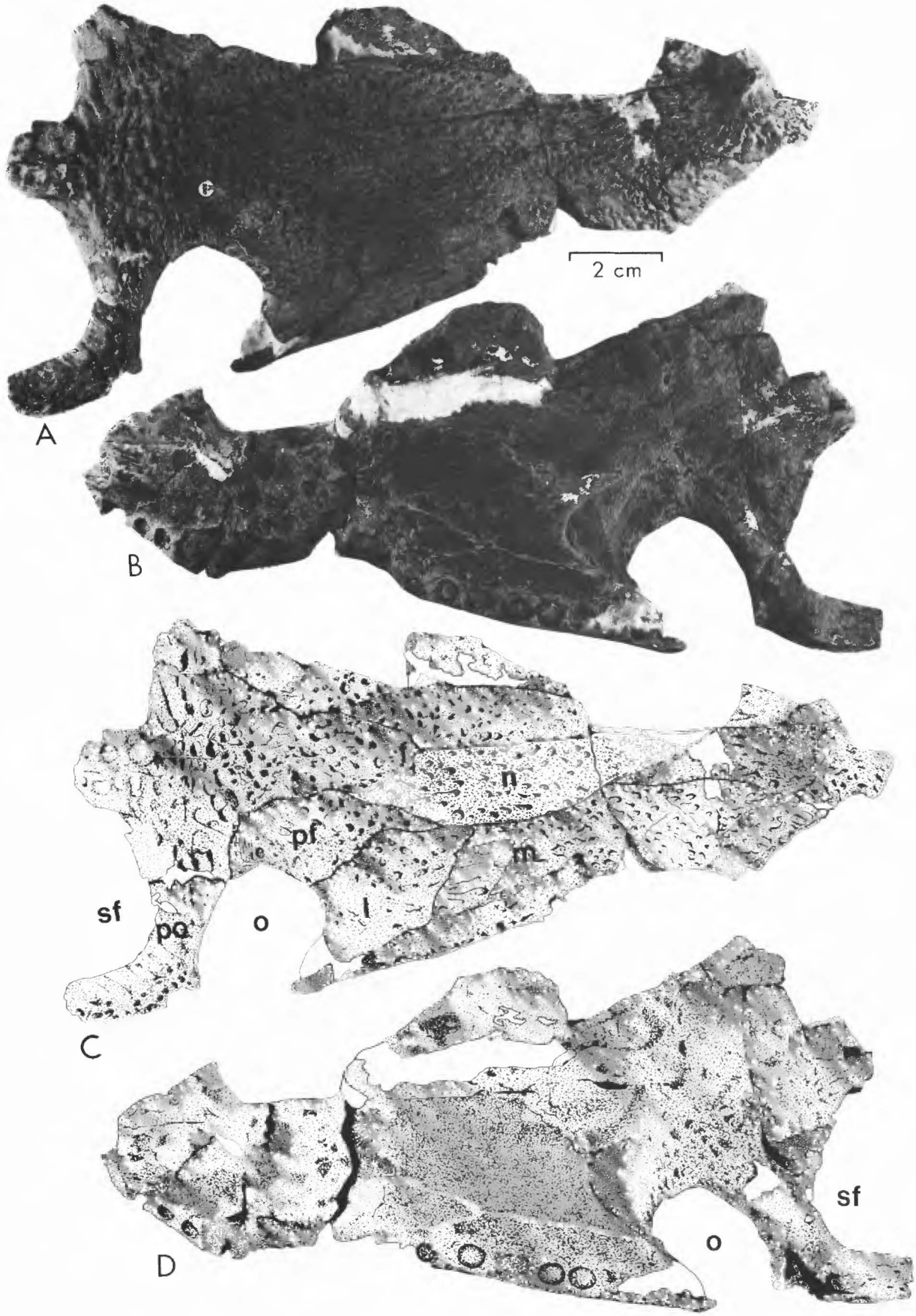


FIGURE 2. Holotype incomplete skull of *Goniopholis kirtlandicus*, PMU.R 230. A, C, dorsal views; B, D, ventral views. Abbreviations are: f—frontal; l—lacrimal; m—maxilla; n—nasal; o—orbit; pf—prefrontal; po—postorbital; sf—supratemporal fenestra.

shoibito Member was, in 1921, considered part of the Ojo Alamo Sandstone (Baltz et al., 1966).

Wiman (1931) provided an extensive and accurate description of the holotype of *G. kirtlandicus* (Fig. 2). He (p. 186) listed the following similarities shared by the Kirtland Formation crocodilian and *Goniopholis:* (1) general shape of the skull; (2) type of dermal sculpture; (3) configuration of the premaxillae; (4) lacrimals separate prefrontals from maxillae; (5) width between the orbits; (6) frontal participates very little in the orbit margin; (7) large size of supratemporal fenestrae; (8) frontal borders much of supratemporal fenestrae; (9) configuration of descending branch of postorbital; (10) number, shape and sculpture of teeth; and (11) development of a spine on the dorsal scute. These similarities are striking (see, for example, the skulls of *Goniopholis* described by Owen, 1878; Hulke, 1878 and Mook, 1925, 1942a) and justify inclusion of the Kirtland Formation specimens in *Goniopholis* as a distinctive species diagnosed by its exceptionally large, subrectangular supratemporal fenestrae, relatively short snout and possession of five small premaxillary teeth (Steel, 1973, p. 18). Mateer (1981, p. 59) listed a 1975 written communication from W. Langston to the effect that all North American specimens of *Goniopholis* pertain to *Eutretauranosuchus,* but this claim has never been substantiated.

PALEOCENE CROCODILIANS

Sullivan and Lucas (1986) listed the Paleocene crocodilians from the San Juan Basin. This listing of taxa is maintained here with documentation of some occurrences listed by Sullivan and Lucas (1986) and revisions that have been proposed since their list.

Puercan crocodilians

Puercan crocodilians from the San Juan Basin are *Akanthosuchus langstoni, Allognathosuchus mooki* and *Leidyosuchus* sp. When O'Neill et al. (1981) originally described *Akanthosuchus langstoni,* it was known only from Torrejonian horizons of the Nacimiento Formation. Since then, keeled osteoscutes characteristic of *A. langstoni* have been discovered at two Puercan localities: (1) NMMNH locality 626, SW¼ SW¼ SW¼ SE¼ sec. 4, T24N, R11W, *Taeniolabis* zone in De-na-zin Wash, three osteoscutes catalogued as NMMNH P-8611; (2) NMMNH locality 1120, SE¼ NW¼ SE¼ sec. 28, T23N, R9W, *Ectoconus* zone in Kimbeto Arroyo, a scute catalogued as NMMNH P-15209 (Fig. 1H–I).

Simpson (1930) described *Allognathosuchus mooki* from a skull, lower jaw and partial postcranial skeleton, and it is the most abundant Puercan crocodilian in the San Juan Basin. Puercan specimens range from adult sized (Figs. 1P, 3A–C, E–F) to extremely small juveniles (Fig. 3G–N). Storrs et al. (1983), Lucas (1984) and Lucas and Sullivan (1986) documented fragmentary specimens of *Leidyosuchus* sp. from Puercan horizons of the Nacimiento Formation.

Torrejonian crocodilians

Torrejonian crocodilians from the San Juan Basin are *Akanthosuchus langstoni, Allognathosuchus mooki, Diplocynodon multidentatus* and *Leidyosuchus acutidentatus*. The most common Torrejonian crocodilian in the San Juan Basin is *Allognathosuchus*. The only named species from the San Juan Basin is *A. mooki* Simpson, 1930, based on a skull, lower jaw and partial skeleton from the Puercan *Taeniolabis* zone of the Nacimiento Formation in De-na-zin Wash. This excellent specimen has never been fully described or adequately illustrated, which explains why the cranial anatomy of *Allognathosuchus* has not been widely known. However, it is now clear that *Wannaganosuchus* Erickson, 1982 is a junior subjective synonym of *Allognathosuchus,* as is *Navajosuchus* Mook, 1942b (Sullivan et al., 1988). Furthermore, *Albertochampsa* Erickson, 1972 also cannot be distinguished from *Allognathosuchus* except for the degree to which the lacrimals are excluded from contact with the nasals by the prefrontals, a variable feature among skulls of *Allognathosuchus*. This synonymy is particularly significant because *"Albertochampsa"* is based on a Late Cretaceous skull; *Allognathosuchus* thus crosses the Cretaceous-Tertiary boundary.

Further information on the cranial anatomy of *Allognathosuchus* is provided by MCZ 8381 (Fig. 4; Table 1), collected in the Torrejonian interval of the Nacimiento Formation in Alamita Wash (sec. 19, T22N, R6W) by C. B. Wood and C. Schaff in 1980. This juvenile skull displays characteristic features of *Allognathosuchus* that include: (1) short and blunt snout; (2) heterodont dentition (Fig. 5) in which the anterior teeth are long, conical and blade-like, whereas the posterior teeth are short, blunt and globose; (3) third and fourth maxillary teeth (numbers 8–9 in Fig. 4) are the largest teeth; (4) U-shaped suture between frontal and nasals; (5) supratemporal fenestrae approximately half the size of the orbits; (6) narrow, flat interorbital plate; and (7) undulating tooth row. Other Torrejonian specimens of *A. mooki* from the San Juan Basin include adult-sized individuals (Fig. 3D) and very small juveniles (Fig. 3O–P). Bartels (1988) suggested that there are eight species of *Allognathosuchus*. Only one of these species is represented in the San Juan Basin Paleocene. Like the Puercan specimens of *Allognathosuchus,* the San Juan Basin Torrejonian specimens all appear to pertain to *A. mooki.*

Lucas and Sullivan (1986) documented a Torrejonian skull and lower jaw of *Leidyosuchus acutidentatus* from Kimbeto Arroyo. Other Torrejonian specimens of *Leidyosuchus* (e.g., Fig. 1J–L) are much less complete. *Diplocynodon multidentatus* is known from a single jaw (Mook, 1930; Berg, 1966), and its assignment to *Diplocynodon* is tentative (Lucas and Sullivan, 1986).

EARLY EOCENE CROCODILIANS

Lucas (1988) reviewed the early Eocene crocodilians from the San Juan Basin, assigning them to *Allognathosuchus* sp. (includes *Alligator chamensis* Cope, 1874; *Crocodilus wheeleri* Cope, 1875; and *Diplocynodon sphenops* Cope, 1875, all of which are nomina vana) and *Leidyosuchus* sp. (includes *Crocodilus grypus* Cope, 1875). Crocodilian fossils are common in the lower Eocene Regina and Tapicitos Members of the San Jose Formation but are almost exclusively isolated teeth and vertebral centra that defy precise identification.

DISCUSSION

The Late Cretaceous–early Eocene crocodilians from the San Juan Basin (Fig. 6) closely resemble contemporaneous crocodilians from elsewhere in the Western Interior, especially Montana and Wyoming (e.g., Bartels, 1983; Bryant, 1989). No significant extinction of crocodilians took place at the end of the Cretaceous according to Sullivan

TABLE 1. Measurements (in mm) of MCZ 8381, juvenile skull of *Allognathosuchus mooki*.

1. Greatest width of quadratojugals	66.0
2. Width, level of last (12th?) maxillary tooth	56.3
3. Width, level of last (4th) premaxillary tooth	43.2
4. Width at premaxillary-maxillary suture	30.2
5. Length, posterior border of cranial table to posterior edge of external nasal opening	94.6
6. Anterior width of cranial table	93.9
7. Posterior width of cranial table	49.1
8. Length, posterior border of cranial table to posterior rim rim of orbit	29.1
9. Length, enternal narial opening	9.2
10. Width, orbit	20.0
11. Length, orbit	30.4
12. Minimum width, interorbital space	7.6
13. Length, supratemporal fenestra	18.8
14. Width, supratemporal fenestra	12.6
15. Minimum width between supratemporal fenestrae	8.9



FIGURE 3. Some Paleocene specimens of *Allognathosuchus mooki* from the San Juan Basin. A–B, NMMNH P-19361, dorsal view of posterior end of skull (A) and occlusal view of maxillary fragment (B). C, NMMNH P-8812, occlusal view of maxillary fragment. D, NMMNH P-8991, occlusal view of maxillary fragment. E–F, UCMP 100029, lateral (E) and medial (F) views of lower jaw fragment. G–N, NMMNH P-8929, parts of juvenile skeleton: quadrate (G–H), partial metatarsal (I), vertebral centrum (J–L), osteoscutes (M–N). O–P, NMMNH P-20525, juvenile lower jaw, lateral (O) and occlusal (P) views. Puercan: A–C, E–N; Torrejonian: D, O–P.

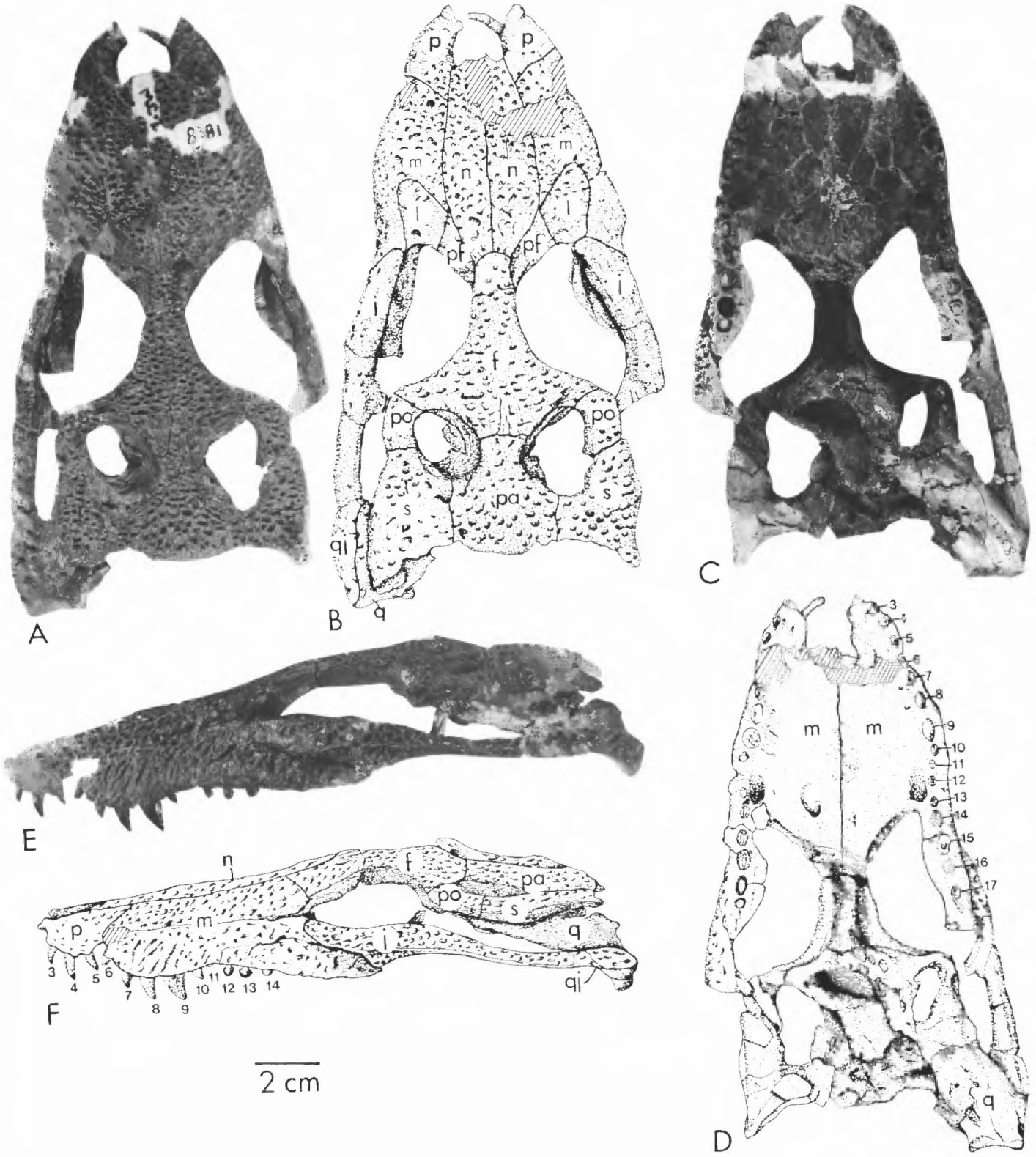


FIGURE 4. Juvenile skull of *Allognathosuchus mooki*, MCZ 8381 from the Nacimiento Formation. A, B, dorsal views. C, D, ventral views. E–F, lateral views. Abbreviations are: f—frontal, j—jugal, l—lacrimal, m—maxilla, n—nasal, p—premaxilla, pa—parietal, pf—prefrontal, po—postorbital, q—quadrate, qj—quadratojugal, s—squamosal.

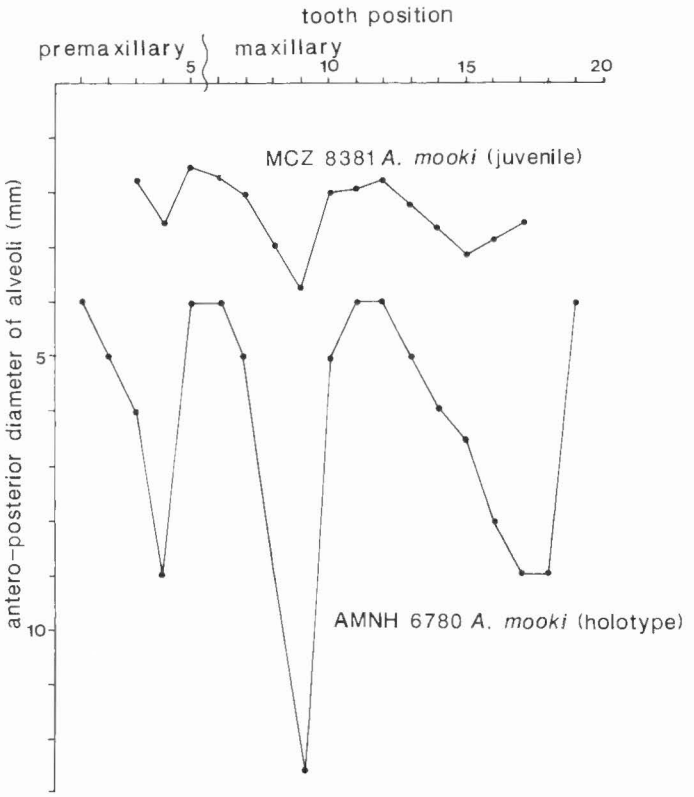


FIGURE 5. Plot of measurements of alveoli of two specimens of *Allognathosuchus mooki* from the Paleocene of the San Juan Basin.

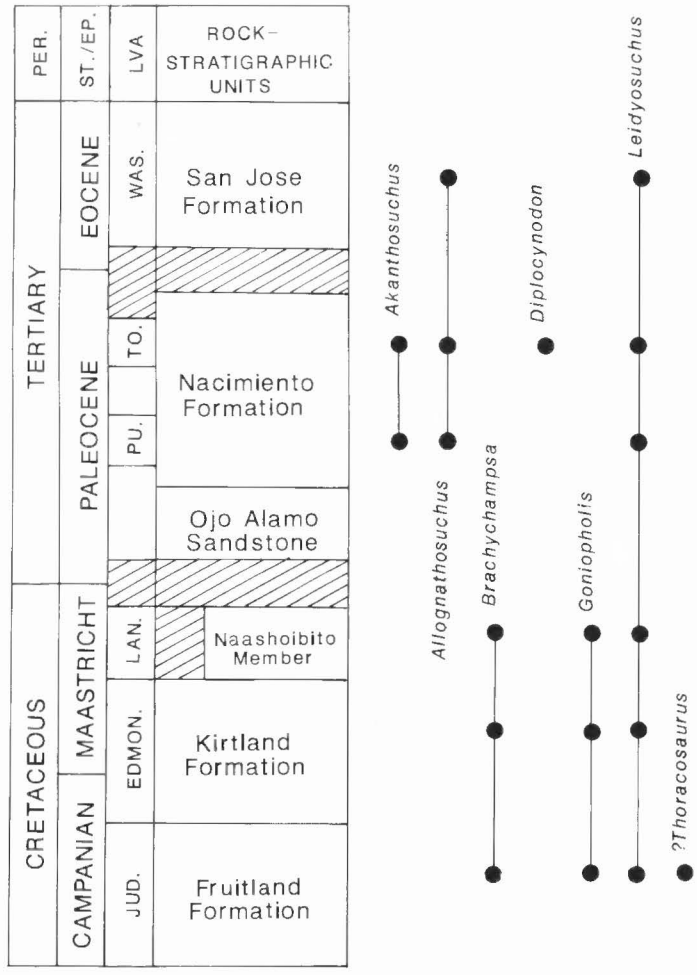


FIGURE 6. Stratigraphic distribution of Late Cretaceous–early Eocene crocodilians in the San Juan Basin. Land-vertebrate ages are: EDMON. = Edmontonian, JUD. = Judithian, LAN. = Lancian, PU. = Puercan, TO. = Torrejonian, WAS. = Wasatchian.

(1987), but the San Juan Basin crocodilians document clear evolutionary turnover at the Cretaceous-Tertiary boundary (Fig. 6). The persistence of *Allognathosuchus* and *Leidyosuchus* throughout the Paleocene–early Eocene is striking.

An interesting aspect of the ecology of extant crocodilians is that "in each of the major areas of distribution there is a single large, dangerously predaceous species, and a number of freshwater dwellers that either feed on a general selection of smaller prey or which are piscivorous" (Dowling and Duellman, 1971, p. 118.2). Large, living predaceous species (for example, *Crocodilus niloticus*) have massive, moderately elongate snouts and either isodont or heterodont dentitions. In contrast, living generalized feeders (for example, *Caiman*) have broad flattened snouts and heterodont dentitions that include blunt, broad crushing teeth in the posterior portion of the tooth row (Aoki, 1989). Extant fish-eating crocodilians, such as *Gavialis*, have very elongate snouts and isodont dentitions.

The San Juan Basin crocodilians indicate that the same type of crocodilian feeding ecology seen today was present during the Late Cretaceous–early Eocene. Thus, during the late Campanian, when the Fruitland Formation was deposited near the shores of an epeiric seaway, fish-eating (*?Thoracosaurus*), predaceous (*Leidyosuchus*) and generalized feeding (*Brachychampsa, Goniopholis*) crocodilians were present. The freshwater floodplains represented by the Kirtland Formation were the sites of continued co-existence of predaceous (*Leidyosuchus*) and generalized (*Brachychampsa, Goniopholis*) feeders. Paleocene–early Eocene freshwater floodplains, in which *Allognathosuchus* "replaced" *Brachychampsa*, also supported these two types of feeding strategies among the crocodilians. Note that earlier suggestions of specialized feeding by either *Brachychampsa, Allognathosuchus* or *Leidyosuchus* (Case, 1925; Abel, 1928; Carpenter and Lindsey, 1980; Erickson, 1984) do not stand up to functional analysis and comparison with the dietary habits of similar extant crocodilians (Aoki, 1989), although occasional turtle- or clam-eating by one or more of these crocodilians cannot be discounted. Therefore, the San Juan Basin crocodilians apparently demonstrate the persistence of crocodilian feeding ecology since at least the Late Cretaceous.

ACKNOWLEDGMENTS

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