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New Extinct Mekosuchine Crocodile from Vanuatu, South Pacific

JIM I. MEAD, DAVID W. STEADMAN, STUART H. BEDFORD, CHRISTOPHER J. BELL, AND MATTHEW SPRIGGS

We describe a new species of crocodile (Reptilia: Crocodyloidea: Mekosuchinae) from a maxilla recovered at the Arapus archaeological site, on the island of Efate, Vanuatu, South Pacific. As with mekosuchine species in New Caledonia and Fiji, *Mekosuchus kalpokasi* sp. nov. was a small, possibly terrestrial carnivore that is now extinct. The differences between the Efate specimen and previously described species of *Mekosuchus* warrant recognition of a new species. Based on its association with Efate's earliest known human inhabitants, dating approximately 3000 cal yr B.P., the extinction of *M. kalpokasi* and other insular mekosuchines may have been anthropogenic. The lack of adequately dated pre-Quaternary and Quaternary vertebrate fossil records from Vanuatu, New Caledonia, and Fiji (as well as other smaller islands) precludes determining the timing and route of dispersal of mekosuchine crocodyloids.

LATE Quaternary extinctions (LQE) were perhaps the most profound biotic changes of the past two million years. Two major features of LQE are the loss of many large species of mammals on continents at the end of the recent glacial and the extinction of innumerable terrestrial species of reptiles, birds, and mammals on oceanic islands in the late Holocene. These losses were most catastrophic for large mammals in North America, South America, and Australia (Martin, 1984, 1990), and for birds in Oceania (= Remote Oceania; here the islands east of Australia and south and east of the Solomon Islands; Steadman, 1995; Martin and Steadman, 1999). Although changing climate and the first arrival of humans both have been blamed for the massive losses of large mammals on continents (see various chapters in MacPhee, 1999), few would question human involvement in the extinction of vertebrates on oceanic islands (Olson and James, 1982; Kirch, 1983; Steadman 1997). We report here a new species of extinct, mekosuchine crocodile from a prehistoric human context on the South Pacific island of Efate, Vanuatu. Aside from its zoogeographical implications, this discovery points once again to the first arrival of people as likely leading to the extinction of insular species.

Modern crocodylians (Reptilia, Archosauria, Eusuchia, Crocodylia) include the gavials (Gavialoidea), alligators and caimans (Alligatoridae), and crocodiles (Crocodylidae). Today, 13 species of crocodiles occur in tropical and subtropical regions. The only surviving crocodylian in Oceania is *Crocodylus porosus* (Indo-Pacific or Estuarine Crocodile), a large species (up to ~6 m total length and 1097 kg) that inhabits marine and freshwater habitats in Southeast Asia, Indonesia, northern Australia, New Guinea, the Solomon Islands, Vanuatu, and Palau (Allen, 1974; Alderton, 1991; Fig. 1). Its geographically closest relatives are *C. novaeguineae* (New Guinea Crocodile; predominantly freshwater habitats on New Guinea) and *C. johnstoni* (Johnston's Crocodile; predominantly freshwater habitats of northern Australia; Alderton, 1991).

The rich fossil crocodile fauna from the late Paleogene and Neogene of continental Australia featured many forms including mekosuchines (Salisbury and Willis, 1996; Willis, 1997, 2001). A Miocene crocodylian was reported by Molnar and Pole (1997) from New Zealand and is now thought to be a mekosuchine (R. E. Molnar March 2001, pers. comm.). From Pleistocene contexts, *Gavialis* (confined to tropical Asia today) was reported from Murua (Woodlark Island) in the Solomon Sea (Papua New Guinea) and *Crocodylus* sp. from northeastern New Guinea (Plane, 1967; Molnar, 1982). The late Quaternary crocodylian fauna in Oceania also included endemic species of terrestrial mekosuchine crocodiles (Crocodyloidea, Mekosuchinae; see below; Molnar et al., in press).

STUDY AREA AND METHODS

Vanuatu (formerly New Hebrides) is a group of 82 islands stretching 1300 km north–south, lying southeast of the Solomon Islands, just north and east of New Caledonia, and west of Fiji (Fig. 1). Efate (17°40′S, 168°20′E) is a geologically complex island (Quantin, 1972; Ash et al., 1978) of approximately 887 km^2 and 647 m elevation. It is the third largest island in Vanuatu, with a hot and rainy climate typical of the tropical southwest Pacific (Bregulla, 1992).

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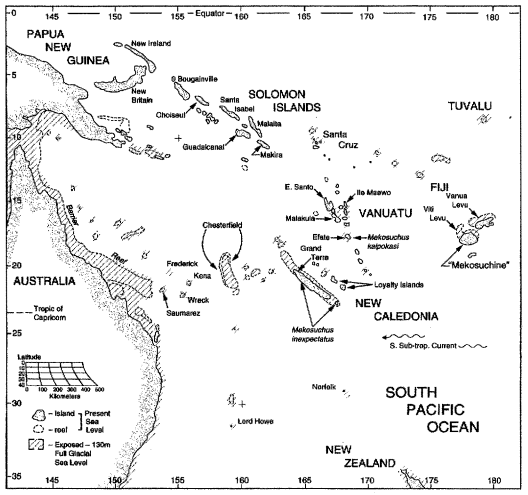

Fig. 1. Map of the South Pacific region showing the locality of mekosuchine fossils including *Mekosuchus kalpokasi* on Efate, Vanuatu. Reefs are indicated by dotted lines. The approximate expansions of islands and reefs during glacial intervals are illustrated by hachuring (except for those of Solomon Islands and greater New Guinea). The estimates of island size at maximum low sea level stands are taken from bathymetric navigational charts and from Spriggs (1997).

Excavations at the Arapus archaeological site were conducted by SHB and MS in 1999. The Arapus site is located immediately southwest of the famed Mangaasi site on the opposite side of Pwanmwou Creek in northwest Efate. A grid of one by one meter testpits (labeled ST 1, etc.) was excavated at Arapus during the six-week field season (for details of the site, see Bedford and Spriggs, 2000).

The evidence for initial human habitation of the Arapus-Mangaasi area is at the Arapus site along a former beach ridge located some 10–12 m above mean sea level (Bedford and Spriggs, 2000). The lowest cultural levels in the Arapus excavations were concentrated deposits of large shellfish, especially *Trochus maculatus*. Associated with the shellfish were bones of several individuals of fish, bird, flying fox, sea turtle, and the crocodile described here. A distinctive style of pottery, named Arapus, was present but relatively sparse. The basal deposits in ST 20 and 27, where the mekosuchine remains were recovered, are similar stratigraphically and in their cultural materials to those in ST 14 and 17. These lower deposits consist of a dark, sandy, human-occupation layer lying directly above culturally sterile, coral beach deposits. Two radiocarbon determinations (^{13}C-adjusted and calibrated using Calib REV 4.1.2 (see Stuiver et al., 1998a,b) including Delta R as 0 for marine shell) on a large *Trochus maculatus* shell from the lowest cultural levels in ST 14 and 17 (one shell per sample) provide ages of 2868–2706 calibrated years before present (cal yr B.P.; ANU-11160; Australian National University radiocarbon laboratory number) and 3200–2853 cal yr B.P. (ANU-11159); therefore, we assume that the mekosuchine remains described here are stratigraphically and chronologically associated and date to approximately 3000 cal yr B.P.

Mekosuchine crocodiles.—Mekosuchinae contains seven extinct Australian and South Pacific genera (*Australosuchus, Baru, Kambara, Mekosuchus, Pallimnarchus, Quinkana, Trilophosuchus*; Salisbury and Willis, 1996). A new taxon will soon be added to this list (Worthy et al., 1999; Molnar et al., in press). The diversity of mekosuchine crocodiles in Australia was greatest during the Neogene, although details about the timing of originations and extinctions are lacking for most taxa (Salisbury and Willis, 1996:fig. 15).

Among the seven genera, only *Mekosuchus* has been found on the islands in Oceania. Molnar et al. (in press) are describing a new taxon of mekosuchine from Viti Levu, Fiji. The Fijian specimens are thought to date to the late Pleistocene and are not associated with cultural material. *Mekosuchus inexpectatus* was described from archaeological contexts containing Lapita pottery on New Caledonia and its offshore islands (Balouet and Buffetaut, 1987; Balouet, 1991; Fig. 1). At least the New Caledonian species is thought to have been a terrestrial form based on the presence of anterolaterally opening nares along with attributes of the vertebrae and limb bones (Balouet, 1991). The other species of *Mekosuchus* are *Mekosuchus whitehunterensis* (Oligocene) and *Mekosuchus sanderi* (Miocene), both from northeastern continental Australia (Willis, 1997, 2001).

There is debate as to where the mekosuchines fit within the overall phylogeny of Crocodylia (Fig. 2). Location number 1 in Figure 2 has the mekosuchines as a sister taxon of Crocodylidae, a position preferred by Salisbury and Willis (1996) and Molnar et al. (in press). Location number 2 in Figure 2 is equally plausible, given available data, and is a position preferred by Brochu (1997; pers. comm. December, 2001). This position is not as thoroughly presented in the literature as that of Location number 1. Location number 3 is an inferred position outside of Alligatoroidea and Crocodyloidea, but its actual assignment is vague (inferred from Balouet, 1991:fig. 4).

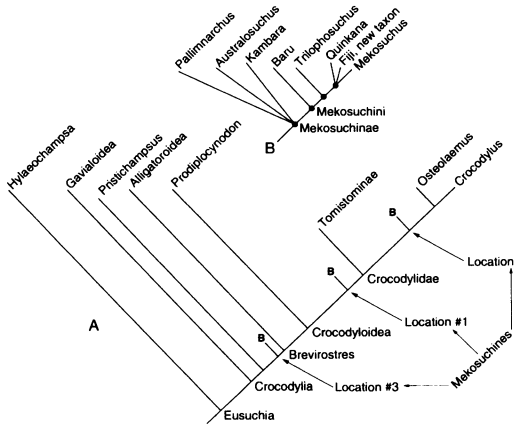

Fig. 2. Relationships among living and some extinct crocodyloids based on data from parsimony analyses by a number of authors (A), especially Brochu (1997). The cladogram is not a new analysis of data, rather a generalized diagram to illustrate the various placements of the mekosuchines (B) within the overall Crocodylia. Location number 1 places the mekosuchines outside of Crocodylidae (adapted from Salisbury and Willis 1996:fig. 14; Molnar et al., in press: fig. 13). Location number 2 places the mekosuchines within Crocodylidae (based in part on Brochu, 1997, and pers. comm., December, 2001). Location number 3 places the mekosuchines outside of Alligatoroidea and Crocodyloidea, but its actual placement is vague (inferred from Balouet, 1991:fig. 4).

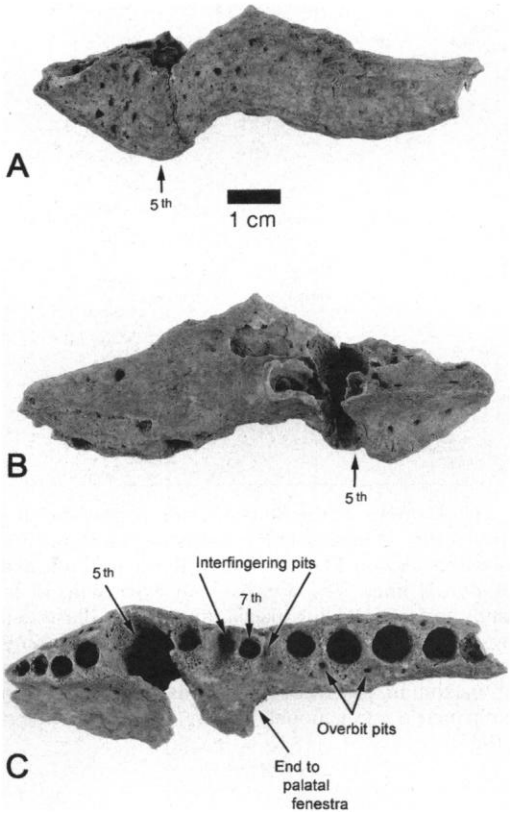

Fig. 3. *Mekosuchus kalpokasi* holotype, left edentulous maxilla fragment (UF 162724) from Arapus archaeological site, Efate Island, Vanuatu. (A) Lateral (labial) aspect; anterior end to the left. (B) Medial (lingual) aspect; anterior end to the right. (C) Ventral (palatal) aspect; anterior end to the left. The orientation of the maxilla in C is such that it would appear that the palatal fenestra ends at the posterior side of m7, but in reality it ends equal to the anterior edge of this tooth. Scale equals 1 cm.

Systematic Paleontology

Crocodylomorpha Walker, 1970

Neosuchia Benton and Clark, 1988

Eusuchia Huxley, 1875

Crocodylia Gmelin, 1788

Crocodyloidea Cuvier, 1807

Mekosuchinae Willis, Molnar, and Scanlon, 1993

Mekosuchus Balouet and Buffetaut, 1987

Three elements from Arapus (all fragmentary) are identified as crocodylian. A fragmented tibia and fibula are from an adult crocodilian and likely belong to a mekosuchine, although they are not diagnosable at present. The description and character analysis below are based on the maxilla. Specimens are curated at the Florida Museum of Natural History, University of Florida (UF).

Mekosuchus kalpokasi sp. nov.
Figure 3

Holotype.—Edentulous fragment of left maxilla (UF 162724; Fig. 3).

Referred specimens.—Proximal fragments of right tibia (UF 162726) and left fibula (UF162725).

Locality.—Arapus archaeological site, Efate Island, Vanuatu.

Age.—Late Holocene, associated with radiocarbon dates between 3200 and 2706 cal yr B.P.

Etymology.—Named for the Honorable Donald Kalpokas of Lelepa Island, the traditional landowners of the Arapus site. Prime Minister of Va-

TABLE 1. MESO-DISTAL (M-D) AND MEDIO-LATERAL (M-L) MEASUREMENTS (MM; * = MINIMUM) OF MAXILLAR ALVEOLI OF *Mekosuchus kalpokasi* HOLOTYPE (UF 162724). Alveoli are numbered from anterior to posterior.

Tooth no.	M-D	M-L
1	3.56	3.03
2	3.89	3.56
3	4.41	4.23
4	5.22	4.76
5	10.43*	10.05*
6	4.29	4.62
7	4.31	3.96
8	5.62	5.04
9	7.00	5.27*
10	7.91	6.56
11	6.78	5.72
12	5.23*	5.35

nuatu at the time of the discovery of the mekosuchine remains, Kalpokas has always been strongly supportive of archaeological research at the site.

Diagnosis.—Short maxillary tooth row (maxillary teeth m1-m12; 88.7 mm); palatal fenestra reaching anteriorly to the position of m7; tooth pits for dentary teeth interfingering between m6 and m7, and m7 and m8, with an overbite posterior to m8; internal medial wall steeply inclined to palate forming a high palatal arch (= high alveolar process of Salisbury and Willis, 1996; Molnar, 1991); lateral side of maxilla vertically inclined for at least 20 mm before rounding to dorsal surface of face (indicating a tall face); maxillary alveoli circular to slightly ovate (implying no ziphodonty; i.e., highly medio-laterally compressed teeth with serrated, keel-edge carinae, see Salisbury and Willis, 1996); deep curvature (= extreme festooning) to lateral profile of tooth row.

Description.—The holotype is a fragmentary left maxilla (UF 162724) with edentulous alveoli for teeth m1 through m12 (Fig. 3C). The alveoli vary from circular to slightly ovate (Table 1), with no indication that the teeth were ziphodont (as in the extreme medio-lateral compression in *Quinkana*; see below; Salisbury and Willis, 1996; Willis, 1997). The great disparity in tooth size (Table 1) features m5 as the largest (typical of derived crocodyloids; see Brochu, 1999), m1-m4 and m6-m8 the smallest, and m9-m12 from slightly to much larger than m1-m4. Anteriorly, the maxilla is broken at the rostal notch ("canine notch" for the fourth dentary tooth) but does not preserve any pattern of the notch (Fig. 3). Tooth pits for dentary teeth indicate an interfingering bite, with pits located prominently between m6-m7, slightly medially between m7 and m8 and an overbite occlusal pattern medial to teeth m8-m9 and m9-m10 (following character description of Brochu 1999; Fig. 3C). The preserved portion of the palatine fenestra begins at m7 (Fig. 3C). The attachment area of the ectopterygoid borders the tooth row beginning at m10 and, with the flange of the maxilla, forms a shelf 4 mm wide. The entire tooth row from m1 to m12 is 88.7 mm long. The lateral wall of the palate is steeply inclined, with the exterior surface of the maxilla oriented vertically for at least 20 mm (Fig. 3B–C). These characters indicate that the face of *Mekosuchus kalpokasi* was short (= brachycephalic) and vaulted, not long and thin (flat) as in most living crocodiles.

Discussion.—A detailed analysis of characters on the maxilla permits confident placement of the Efate specimen with the extinct crocodylian clade Mekosuchini (Salisbury and Willis, 1996, 1997). The posterior portion of the maxilla preserves an articular facet for the ectopterygoid. This facet is situated immediately medial to the posterior tooth alveoli, indicating that the ectopterygoid was in close association with the posterior maxillary teeth. This is a primitive condition for eusuchian reptiles. The derived condition, in which a posteromedially expanded maxilla separates the ectoptergoid from the posterior tooth row, occurs in alligatoroid crocodylians (Salisbury and Willis, 1996, 1997; Brochu, 1997; both character states illustrated by Norell et al., 1994). The separation of the tooth row and the ectopterygoid is present in all but one (*Purussaurus neivensis*) of the alligatoroids in which the character can be evaluated (Brochu, 1999). The maxilla from Efate lacks this synapomorphy of the Alligatoroidea.

The nature of the association of the dentary teeth with those of the maxilla is a systematically informative character in crocodylians. In extant forms, the dentary teeth are situated lingual to those of the maxilla when the mouth is closed (a condition referred to as "overbite" as seen in extant *Alligator*) or are situated between those of the maxilla ("interfingering" as in extant *Crocodylus*). More recent analyses (Brochu, 1997, 1999) indicate that the variation in this character, especially its expression in fossil forms, is greater than previously recognized. Many fossil taxa show intermediate conditions where some teeth interfinger, whereas others

show an overbite. These morphologies represent three discrete character states (Brochu, 1997, 1999), but the Efate crocodylian represents an additional state not previously recognized. Tooth pits (for reception of dentary teeth) on the maxilla can reveal the position of the dentary teeth relative to the maxillary teeth in species where the dentary is not available (Brochu, 1997, 1999). In the Efate specimen, no clear tooth pits are present adjacent to m1-m4, but subtle depressions suggest an overbite in that region (Fig. 3C). A dentary tooth was clearly interfingered between m6 and m7 and an interfingering condition was also present between m7 and m8, although the latter tooth pit is placed somewhat more medially than the former (Fig. 3C). An overbite pattern is clearly present between m8 and m9 and between m9 and m10. The phylogenetic significance of this pattern is uncertain. However, a similar condition is found in *Baru*, *Mekosuchus*, and *Trilophosuchus*.

In many crocodilians (gavialoids being the exception), the fourth and fifth maxillary alveoli are enlarged relative to others. In the Efate specimen, the fifth maxillary alveolus is enlarged (Fig. 3C), a condition seen in *Pristichampsus* but considered by Salisbury and Willis (1996, 1997) to be independently derived and synapomorphic for the clade at their "Node G," including {*Brachyuranochampsa* {*Harpacochampsa* + Crocodylidae}} + {"*Crocodilus*" *affinis* {*Asiatosuchus germanicus* + Mekosuchinae}} (for a similar but alternative scenario, see Brochu, 1997). This character supports placement of the Efate fossil within this clade. "Tooth disparity" is a qualitative (sometimes quantitative, when expressed as a ratio; Salisbury and Willis, 1996) evaluation of the variation in size and/or morphology of the dentition. Great disparity is diagnostic for the clade {Meckosuchinae + *Asiatosuchu*, but such disparity is also found within Alligatoridae, "*Crocodilus*" *affinis*, and *Harpacochampsa* (Salisbury and Willis, 1996, 1997). We interpret the condition in the Efate specimen (Table 1) as a synapomorphy uniting the fossil with {Mekosuchinae + *Asiatosuchus*}.

Two additional characters in the Efate maxilla support its phylogenetic position within the Mekosuchini. The antero-lateral margin of the palatal fenestra extends to a point just anterior to the seventh maxillary alveolus (see note in figure caption). This anterior extension unambiguously places the fossil in Mekosuchini (Salisbury and Willis, 1996, 1997:character 14). The deep snout (= vaulted or tall palate and face versus the thin, flattened appearance of most crocodylians) diagnoses the fossil further as a member of the {*Mekosuchus* + *Quinkana*} clade (this feature also evolved independently in *Pristichampsus*; Salisbury and Willis, 1996, 1997). Many mekosuchine crocodiles are considered altirostral in having a short but tall snout and face (however, this is not found on *Pallimnarchus*, *Australosuchus*, or *Kambara*). These altirostral crocodiles may have occupied a terrestrial or semiarboreal habitat than aquatic.

Among mekosuchines, *Baru* and *Quinkana* have ziphodont dentition. The m1 through m5 are ziphodont in *Quinkana*. The alveoli of the Efate specimen clearly did not support ziphodont teeth, so we rule out an affinity with *Quinkana*. *Mekosuchus* is at present inadequately diagnosed. In *Mekosuchus*, the postorbital bar is level with the margin of the jugal, but in most other crocodylians, it is inset from the lateral margin of the jugal (Salisbury and Willis, 1996, 1997). The condition in *Mekosuchus* is also present in *Osteolaemus tetraspis* and *Pristichampsus* and is considered in all three taxa to be an independent reversal of a synapomorphy of Crocodylia according to Salisbury and Willis (1996, 1997). This reversal was proposed as one of two potential synapomorphies for *Mekosuchus* by Salisbury and Willis (1996, 1997). The second possible synapomorphy is that the pterygoids form more than one-third of the ventral surface of the narial canal between the palatal fenestrae, a condition found in *Mekosuchus* and *Trilophosuchus rackhami* (the sister taxon to {*Mekosuchus* + *Quinkana*}), but not in *Quinkana*; it is therefore not clear at what level this character applies. It may be a synapomorphy of {*Trilophosuchus rackhami* +{*Mekosuchus* + *Quinkana*}}, with a subsequent reversal in *Quinkana*, or it may be independently derived in both *Mekosuchus* and *Trilophosuchus rackhami*. Neither of the potential synapomorphies for *Mekosuchus* proposed by Salisbury and Willis (1996, 1997) are preserved in the Efate specimen, and we know of no maxillary characters that will unambiguously permit referral to that taxon. Because the Efate specimen lacks the diagnostic synapomorphy for *Quinkana* (ziphodonty), it must represent either *Mekosuchus* or a new taxon within the {*Mekosuchus* + *Quinkana*} clade. We feel that it is more conservative and reasonable to refer our specimen to *Mekosuchus* than to diagnose a new genus on the basis of a fragmentary maxilla.

Congeneric species.—There are currently three published species of *Mekosuchus*: *M. inexpectatus* from the Holocene of New Caledonia, and *M. whitehunterensis* (Oligocene) and *M. sanderi* (Miocene) of Queensland, Australia (Balouet and Buffetaut, 1987; Willis, 1997, 2001). The Efate specimen differs from *M. inexpectatus* in

having some dentary teeth interfingering with teeth in the maxillary row (a complete overbite was present in *M. inexpectatus*). In *M. whitehunterensis*, most maxillary tooth alveoli are too close together to permit interfingering (i.e., an overbite was likely present), although two "occlusion pits" (= tooth pits) were present, one between m6 and m7, and one posterior to m7 (Willis, 1997). This is similar to the condition in the Efate specimen where tooth pits for reception of dentary teeth are present medial to the maxillary teeth in the anterior tooth row and posterior to the alveolus for m8. Unlike the Efate specimen, dentary tooth pits are found lingual to m6–7 and interfingering between m7–8 on *M. sanderi* (Willis, 2001).

Post-m5 teeth of *M. sanderi* were laterally compressed (Willis, 2001; contra the condition in the Efate specimen). *Mekosuchus inexpectatus* had molariform posterior teeth (a bulbous or durophagus configuration) for crushing. *Mekosuchus whitehunterensis* had no such crushing teeth but instead had 16 teeth with "unserrated anterior and posterior carinae, becoming laterally compressed posteriorly so that posterior teeth [were] blade-like" (Willis, 1997:425–426). The alveoli of *M. kalpokasi* are circular to slightly ovate, but the teeth themselves were not recovered.

The palatal fenestrae are placed more anteriorly relative to the maxillary alveoli in mekosuchines than in most other crocodylians. The palatal fenestra in the Efate specimen and in *Mekosuchus whitehunterensis* extends to the anterior edge of the m7 alveolus (see note in caption, Fig. 3); in *M. inexpectatus* and *M. sanderi* this fenestra extends anteriorly to just in front of the alveolus for m6, possibly a derived character state.

Long-snouted crocodilians, such as *Gavialis gangeticus* and *Crocodylus johnstoni*, have maxillae and dentaries with linear orientations in lateral aspect (= "no festooning" of Molnar, 1981). A broad, curvature of the tooth row is observed in *C. acutus* (some undulation of Brochu, 1999: fig. 49; = slight festooning). Short-faced crocodiles have deep curvature (= strong or extreme festooning or undulation). The profile in *Mekosuchus whitehunterensis* is undulating but not extreme (Willis, 1997:fig. 4). The condition in *M. inexpectatus* is unknown, but its short snout probably had at least some undulation. In contrast, *M. kalpokasi* had extreme undulation of the tooth row, with distinct bimodal curvature in its short toothrow (Fig. 3A). The degree of curvature also is much greater in *M. kalpokasi* than in the Fijian mekosuchine specimen (pers. comm. R. E. Molnar June 2000; Molnar et al., in press).

The degree of curvature and undulation can vary ontogenetically and as anomalies (often caused by adverse dietary or captivity conditions) within a population as shown by the study of *C. novaeguineae* (Hall, 1985; Hall and Portier, 1994). Although crania and mandibles of crocodilians can develop a brachycephalic growth pattern, it does not change the dorso-ventral shape of the face from one of a flattened arrangement (typically of living crocodiles; see Iordansky, 1973) to one of a more vaulted (taller) design as seen on *M. kalpokasi* and some other mekosuchines (e.g., the Fijian species; Molnar et al., in press). Growth stage I of Hall and Portier (1994) is a first year phase in which teeth are typically in a common alveolar groove (Iordansky, 1973) or where the more anterior teeth are in weakly divided alveoli. Crocodylians in growth stage I also have a somewhat brachycephalic growth pattern (this changes quickly in stage II; Hall and Portier, 1994). The maxilla of *M. kalpokasi* clearly shows an adult-stage growth to its alveoli (Fig. 3C), and therefore appears to be from a small adult, brachycephalic (yet vaulted faced) individual, one not due to an early ontogenetic stage of growth.

Biogeography.—Understanding the time and distribution of mekosuchines in Oceania is in its infancy largely because of the rare finds and the inadequate chronological controls related to the specimens. At least three species of insular mekosuchine crocodylians inhabited the South Pacific in the late Quaternary: *Mekosuchus inexpectatus* (New Caledonia), *M. kalpokasi* (Vanuatu), and the new genus from Fiji. The oldest insular fossils of a mekosuchine belong to the new taxon from Fiji (Molnar et al., in press); although these remains are stated as presumed late Pleistocene in age, this has yet to be demonstrated or confirmed. *Mekosuchus inexpectatus* is known from Holocene deposits on New Caledonia, dating as old as 3000 to 3900 yr B.P. and possibly as young as 1670 to 1810 yr B.P., although these are not direct analyses of the *Mekosuchus* skeleton (Balouet and Buffetaut, 1987; Balouet, 1991). As presented here, *M. kalpokasi* is thought to date about 3000 cal yr B.P.

Among the three island groups on which mekosuchians are known, New Caledonia is closest to Australia. The New Caledonian biota can be accounted for by dispersal as well as vicariance (Morat, 1993). New Caledonia (16,650 km^2) became isolated from Australia by about 65 Ma, and from New Zealand by the mid-Miocene (Kroenke, 1996). It now lies at the southern lim-

it of tropical climates. New Caledonia has considerable intraisland habitat differentiation and one of Oceania's richest and most highly endemic biotas (Bauer and Sadlier, 1993; Morat, 1993). According to Bauer (1999) the oldest component of its lizard fauna is the diplodactylid geckos (*Bavayia, Eurydactylodes, Rhacodactylus*), which have their closest affinities with carphodactyline geckos of Australia and New Zealand, and may be Gondwanan in origin. At the species level, New Caledonia shares less than 12% of its modern lizard fauna with Vanuatu, Fiji, Tonga, and Samoa, whereas the nearby Loyalty Islands share > 30% of its species with these same islands (Fig. 1; Bauer, 1999).

The species-level similarities among lizard faunas of different island groups probably reflect dispersal, whereas the lizard dissimilarities among island groups have been attributed to the geological origins of the Inner Melanesian Arc (IMA) and the Outer Melanesian Arc (OMA; see also Polhemus, 1996; Bauer, 1999). The IMA is Gondwanan in origin and consists wholly or in part of rifted continental fragments from Australia (Dickinson and Shutler, 2000). The IMA includes New Caledonia, eastern New Guinea, and the Norfolk ridge (and Island) south to New Zealand (Fig. 1). The OMA is believed to have developed only since the mid-Tertiary, and includes the Bismarck Archipelago, Solomon Islands, Vanuatu, Fiji, and Tonga, regions that probably never had direct continental connections (Dickinson and Shutler, 2000; Dickinson, 2001). Within the OMA faunal similarity is high but species richness and taxonomic diversity decrease from west to east (see various chapters in Keast and Miller, 1996).

Is the tropical, South Pacific Ocean an avenue or a barrier relative to crocodylian distributions? Osmoregulation (maintenance of salt and water balance) poses a problem for vertebrates that live within or extensively use marine habitats, such as the Pacific Ocean. Most crocodiles solve this problem with salt glands in the tongue that can excrete concentrated salt (hyperosmotic sodium chloride) solutions with a minimum of water loss (the alligatoroids do not have this ability; Taplin, 1989; Taplin and Grigg, 1989). Because of this, the saline habitat of oceans is not a barrier to many species of *Crocodylus*, although, it is not known what the ability of osmoregulation was for any of the mekosuchines.

As rifting separated New Caledonia and New Zealand (IMA) from Australia in the latest Cretaceous (Kroenke, 1996), mekosuchines could not have occupied the initial rafting continental-crust islands because the earliest evidence of a mekosuchine is *Kambara* from the early Eocene (Willis et al., 1993; Salisbury and Willis, 1996). Given the knowledge of the fossil record of mekosuchines, vicariance likely has not played a part in the distribution of these crocodyloids in Oceania.

Mekosuchines could have dispersed short distances across marine habitats to the rifting continental islands during the Oligocene and Miocene (Kroenke, 1996), although the fossil record is lacking such evidence. We propose that insular mekosuchines were Neogene (possibly only Quaternary) colonizers from Australia, but precisely when this may have happened (or how many times it may have happened) is not understood. Interisland dispersal may even account for mekosuchines on New Caledonia, the closest and largest island mass to Australia. Traveling at 20° S from Australia (approximately 150° E) eastward to New Caledonia (165° E), one passes through the Great Barrier Reef, small isolated reefs (e.g., Frederick, Kena), and the large reef complex of Chesterfield (Fig. 1). All of these reef-island masses have insignificant land area above present sea level. With a lowering of sea level by as much as approximately 130 m during the last glacial maximum at 22,000 to 18,000 yr B.P. (and presumably similar values during at least several of the many previous glacial maxima throughout the Pleistocene; Chappell and Shackleton, 1986; Nunn, 1998; Yokoyama et al., 2000), these reefs and small islands became significant land masses with elevations as high as approximately 120+ m. Bathymetry indicates that the Chesterfield reef complex became an exceedingly large island that we calculate to be approximately 80 by 320 km (> 20,000 km^2, here named Greater Chesterfield Island for its glacial maximum appearance; Fig. 1). We assume that basic reef development has been stable through the Quaternary.

Efate was not appreciably larger at the glacial maximum sea level, although other islands in Vanuatu did coalesce into larger islands, such as Epi joining the Shepherd Islands, or Maewo with Pentecost. The largest island in Vanuatu at glacial maximum would have been the coalesced Santo, Malo, and Malakula. Vanuatu became a tighter set of larger islands with an appreciable increase in landmass. Islands and reef clusters today in the Santa Cruz Group also became larger and less isolated at glacial maximum. Figure 1 does not show details of the land expansion of New Guinea, New Ireland, and New Britain, which remained, however, as separate islands (Spriggs, 1997). In the Solomon Islands, Buka and Bougainville coalesced with

Choiseul, Isabel, and nearby smaller islands north of New Georgia Sound (Spriggs, 1997). Other islands in the southern Solomons (Guadalcanal, Malaita, and Makira) expanded in area individually. With deglaciation, sea level began to rise approximately 18,000 years ago, with levels approaching those of today being reached by approximately 9000 yr B.P. (Yokoyama et al., 2000).

The importance of glacially lowered sea levels is probably profound for biotic dispersal between Australia and/or New Guinea and tropical Pacific islands. In particular, the Greater Chesterfield Island between New Caledonia and Australia would have facilitated island-hopping dispersal. This stepping-stone arrangement is within today's tropical climate zone. Even in a late Pleistocene climate with air temperatures averaging 3–4 C cooler (Hope and Tulip, 1994; Kershaw, 1994) and cooler sea temperatures as well (Beck et al., 1997; Ganopolski et al., 1998), the Greater Chesterfield Island region would have provided potential dispersal routes into the South Pacific for tropical and subtropical species, including mekosuchine crocodiles. If dispersal rather than vicariance accounts for the former presence of mekosuchines in the tropical Pacific, the ancestral mekosuchine must have had some marine swimming/drifting capabilities such as *Crocodylus porosus* has today. During interglacial sea level highs, insular mekosuchines may have been able to persist only on the largest islands of New Caledonia, Vanuatu, and Fiji. We predict that mekosuchine crocodile fossils eventually will be found elsewhere in the southwest Pacific, such as Santa Cruz, Loyalty Islands, other islands in Vanuatu and Fiji, and possibly even the larger islands in Tonga and Samoa. Short- and long-distance dispersal of mekosuchines out into Oceania would require an ability to osmoregulate.

Extinction.—Considerable extinction of vertebrates followed the arrival of Lapita peoples in New Caledonia, Vanuatu, and Fiji (Balouet and Olson, 1989; D. W. Steadman, unpubl. data). For Vanuatu, the losses of birds documented thus far by DWS are less than in the other two island groups but include shearwaters (*Puffinus pacificus*, P. cf. *gavia*), a booby (*Papasula abbotti*), a hawk (*Accipiter* sp.), a megapode (*Megapodius* undescribed sp.), rails (*Gallirallus* undescribed sp., *Porzana* undescribed sp.), and a parrot (*Eclectus* undescribed sp.).

The extinction of insular mekosuchine crocodiles postdate the arrival of people and is consistent with an anthropogenic cause as suggested for the prehistoric losses of lizards (Pregill and Dye, 1989; Pregill, 1993, 1998), bats (Koopman and Steadman, 1995), and birds (Steadman, 1995) in Oceania—direct human predation, predation by introduced mammals (rats, dogs, pigs), and habitat alteration (see Holdaway, 1999). For these small crocodiles, predation might have been especially important. The recovery of *M. kalpokasi* in clear association with cultural debris at the Arapus site almost certainly constitutes it being food consumed by the earliest human visitors to the site.

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