Megafaunal meiolaniid horned turtles survived until early human settlement in Vanuatu, Southwest Pacific

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Meiolaniid or horned turtles are members of the extinct Pleistocene megafauna of Australia and the southwest Pacific. The timing and causes of their extinction have remained elusive. Here we report the remains of meiolaniid turtles from cemetery and midden layers dating 3,100/3,000 calibrated years before present to approximately 2,900/2,800 calibrated years before present in the Teouma Lapita archaeological site on Efate in Vanuatu. The remains are mainly leg bones; shell fragments are scant and there are no cranial or caudal elements, attesting to off-site butchering of the turtles. The new taxon differs markedly from other named insular terrestrial horned turtles. It is the only member of the family demonstrated to have survived into the Holocene and the first known to have become extinct after encountering humans.

Meiolaniidae | taxonomy | extinction | Lapita people | middens

Meiolaniid turtles (Chelonia: Meiolaniidae) are an extinct group of large-bodied, fully terrestrial eucryptodire turtles that were confined to the Southern Hemisphere. These bizarre turtles are characterized by cranial horns or frills developed from the squamosals and a tail bearing a heavily ossified tail club (1–5). Meiolaniids were confined to the tertiary of South America and the Australia–southwest Pacific region (Fig. 1 and Table S1). Late Pleistocene Australian forms include the very large but poorly known *Ninjemys oweni* (5, 6) and an indeterminate *Meiolania* species (7). Their demise is included in the Pleistocene megafaunal extinctions that followed human arrival approximately 50,000 y ago (8); however, temporal overlap with humans has not been demonstrated (9). The most well known is *Meiolania platyceps* from Pleistocene calcretes on Lord Howe Island, 630 km east of Australia (1, 3, 5, 10). Elsewhere in the southwest Pacific, sparse and fragmentary meiolaniid remains, considered to be of Pleistocene age, have been found in New Caledonia (Pindai Caves, Walpole Island, Tiga Island), and on Vitilevu, Fiji (5, 11–13) (Fig. 1 and Table S1). Thus, although meiolaniids were widely distribution in the southwest Pacific, it is not known whether any survived into the Holocene, or if humans were implicated in their extinction. Here we report a previously undescribed locality and, geologically, the youngest occurrence for meiolaniids, providing evidence of temporal overlap with humans and unequivocal evidence that this interaction resulted in their extinction.

Results and Discussion

The meiolaniid bones reported here derive from the formerly-coastal Lapita cemetery and midden site at Teouma on the island of Efate, Vanuatu (14) (Fig. S1). People of the Lapita culture were the first humans to colonize the Vanuatu/New Caledonia/Fiji region of the southwest Pacific 3,100 to 3,000 y ago (15–17). The turtle remains reported here were excavated from 275 m^2 of the cultural deposits by two of the present authors (M.S. and S.B.) during 2004 to 2006 (*SI Text*). The site is well stratified, as shown in Fig. 2, with meiolaniid bones abundant and confined to the cemetery levels and basal layers of the later midden deposits (layer 2).

The site began as a cemetery, the oldest yet found in the Pacific Islands, approximately 3,100 or 3,000 calibrated years before present (cal BP) (14). After a subsequent period of only ephemeral visitation to the site, a village became established there approximately 2,900 cal BP. This sequence is underpinned by radiocarbon dating of shell, bone, and charcoal samples from associated human burials and midden materials (14,18) (*SI Text*).

The ages of the turtle bones are constrained by this archaeological sequence. Two accelerator MS radiocarbon dates on collagen from meiolaniid bones from the basal levels of layer 2, calibrated to 2,890 to 2,760 cal BP at 94.3% probability (*SI Text*), support this inference. The associated δ^{13}C values (−25.4, −23.1) are consistent with a terrestrial herbivorous diet for these turtles. The midden deposits in some areas exceed 1 m in thickness, but turtle bones were only ever found in situ in the lowest levels. The upper part of the midden cannot date to later than 2,500 cal BP on the basis of pottery typology, which is well dated at other Efate sites (19).

Ten specimens were identified as marine turtle, but are not hereafter discussed. The majority belong to a relatively large terrestrial turtle as shown by, for example, humeri and femora of similar length, proximal and distal ends expanded, and shafts markedly sigmoidal; pectoral girdle with angle between the dorsal scapular process and acromion markedly wider than the approximate 90° observed in marine turtles; coracoid short, fan-shaped caudally; phalanges short and robust; and unguals robust and slightly recurved (Figs. 2 and 3). The material includes 405 bones and numerous indeterminate bone/carapace fragments attributed to meiolaniids. Identifiable specimens are mainly limb bones from at least 30 individuals (Table 1), with cranial and caudal elements absent and shell pieces scant and fragmentary. Many of the bones are broken and often the epiphyses have been lost. They are identified as meiolaniid by the following apomorphies (4, 5): (*i*) humerus with ectepicondylar foramen beginning as a groove dorsally, but distally penetrating the condyle to open ventrally; (*ii*) ulna with a distinct ridge dorsoproximally, extending distally from articular facet, forming a flat radioulnar articulation medially; (*iii*) digits with two phalanges and a robust ungual; (*iv*) shell fragments that are relatively thin and bear pits and grooves without a regular pattern on their outer surface; and (*v*) presence of dermal armor on shell margin.

The Vanuatu meiolaniid differs from all named Pleistocene meiolaniids, so here we erect a new taxon for it.

Systematic Paleontology. Meiolaniidae Boulenger, 1887; ?*Meiolania* Owen, 1886 (20); and ?*Meiolania damelipi* sp. nov.

Holotype is AMF136641, right humerus, collected layer 2, Unit 3.3–3.4, Area 3B, Teouma Lapita site, Efate, Vanuatu, 2006 (Fig. 3). Etymology is for Willie Damelip, originally of Ambrym Island

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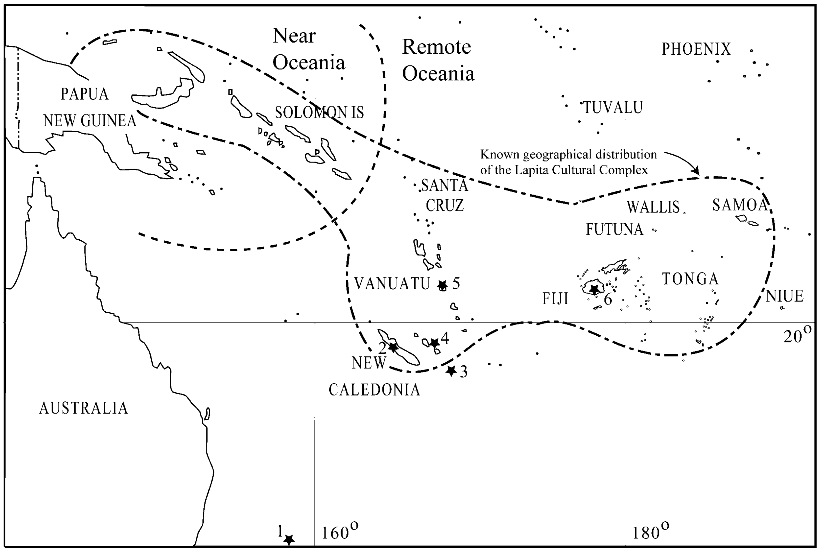

Fig. 1. Map of southwest Pacific showing locations where meiolaniid remains have been discovered: 1, Lord Howe Island (Australia); 2, Pindai Caves (New Caledonia); 3, Walpole Island (New Caledonia); 4, Tiga Island (New Caledonia); 5, Teouma, Efate Island (Vanuatu); and 6, Viti Levu Island (Fiji).

(*SI Text*). Diagnosis is a meiolaniid differing from other Pleistocene species with more gracile longbones; shoulder girdle with coracoid unfused, well developed dorsal and acromion processes diverge at approximately 105°; minor and major femoral trochanters ventrally enclose a deep intertrochanteric fossa; much smaller than *Ninjemys oweni*. Measurements of holotype are as follows: total length, 95 mm; maximum proximal width, 39 mm; minimum shaft width, 15 mm; and maximum distal width, 35 mm. Paratypes are all elements shown in Figs. 3 and 4; measurements are provided in Table 2.

Given the absence of the diagnostic material of the skull and the tail, and minimal peripheral material of the carapace or plastron, we only tentatively refer this new species to *Meiolania*. On biogeographic and temporal grounds, we consider it unlikely that the insular ?*M. damelipi* was conspecific with the Miocene taxa described from Australia (*SI Text* and Table S1). Whether it differed from other unnamed taxa from the New Caledonian region cannot be established from the material at hand. The pre-

Fig. 2. Southern section of Teouma excavation at the rear of the reef terrace (2009) showing the clearly stratified deposits. L1 indicates the black tephra-rich soil, L2 indicates the concentrated midden deposit, L3 indicates the yellow tephra, and L4 indicates the uplifted reef.

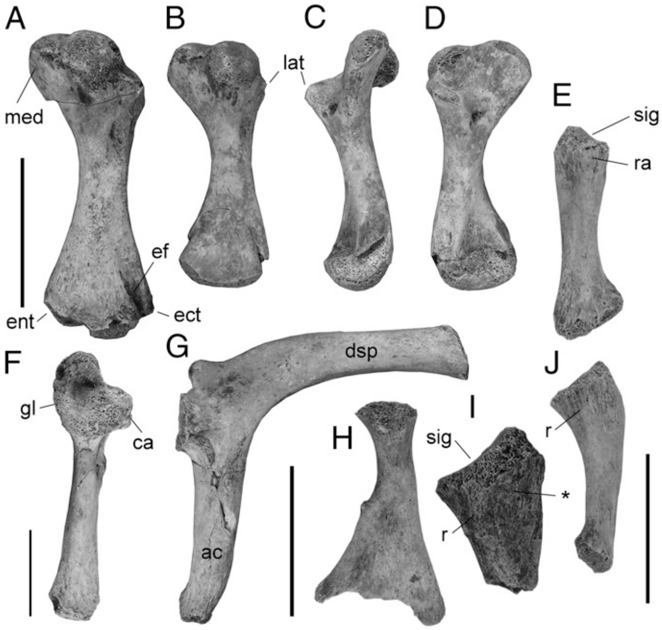

Fig. 3. Pectoral elements of ?*M. damelipi*. (*A*–*D*) Right humeri, Holotype AMF136641 (*A*) and AMF136640 (*B*–*D*), in (*A* and *B*) dorsal, (C) caudal, and (*D*) ventral aspects. (*E*, *I*, and *J*) Left ulnae, AMF136648 (*E* and *J*), and proximal half of AMF.136647 (*I*) in (*E*) medial and (*I* and *J*) dorsal aspect. (*F* and *G*) left scapula AMF136644 in (*F*) ventral and (*G*) lateral view. (*H*) Right coracoid AMF136652 in dorsal aspect. (ca, coracoid articulation; med, medial process; lat, lateral process; ac, acromion; dsp, dorsal scapular process; ect, ectepicondyle; ef, ectepicondylar foramen, which in unbroken specimens penetrates the ectepicondyle to emerge on the ventral facies; ent, entepicondyle; gl, glenoid; ra, radial-ulnar articulation; r, ridge forming boundary of dorsal-medial boundary low; sig, sigmoid notch.) *Area is flat, not a deep sulcus as in *M. platyceps*. See *SI Text* for associated data. (Scale bars, 50 mm.)

Table 1. Element frequency of meiolaniid remains from the 2004 to 2006 excavations at Teouma, Efate, Vanuatu

Element/body region	No. of specimens
Skull fragments	0
Vertebrae (presacral)	6
Pectoral (dorsal, acromion, glenoid)	64
Pectoral (coracoid)	37
Humeri	77*
Ulnae	6
Radii	12
Metacarpals	18
Pelvic elements	31
Femora	22
Tibia	12
Fibula	20
Metatarsals and astragalocalcaneum	5
Phalanges (manus and pedal)	95
Caudal vertebra	0
Total NISP	405

The minimum number of individuals was maximal for humeri (MNI of 30), but is an underestimate because 16 specimens remained unassigned to side. Miscellaneous fragments of bone or carapace are not listed here. See *SI Text* for details.

*Comprises 22 left, 3 proximal left, 3 distal left, 22 right, 8 proximal right, 3 distal right; 16 with side indeterminate.

served elements allow significant comparison with *M. platyceps* material in the Australian Museum, described by Gaffney (5).

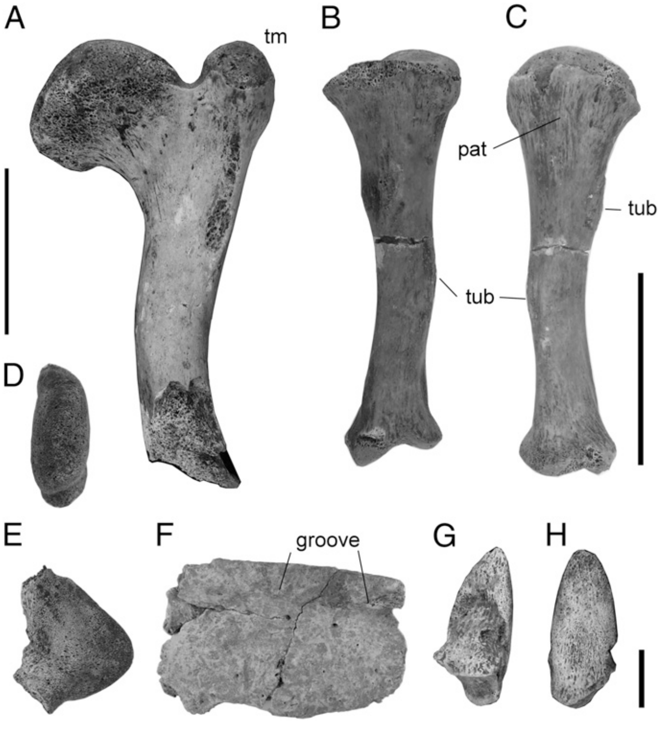

Fig. 4. Pelvic and carapace elements of ?*M. damelipi*. (*A*) Left femur AMF136642 in caudal view; (*B* and *C*) Right tibia AMF136651 in (*B*) ventral and (C) dorsal view. (*D* and *E*) Dermal armor of carapace in caudal (*D*) and ventral (*E*) views of AMF136646. (*F*) Marginal fragment of carapace with gutter AMF136649. (*G* and *H*) Ungual phal AMF136664 in (*G*) ventral and (*H*) dorsal aspects. (pat, patellar tendon attachment not raised in ridge; tm, trochanter major; tub, tuberosity.) See *SI Text* for associated data. (Scale bars, 50 mm in *A*–*F*, 10 mm in *G* and *H*.)

Humeri (Fig. 3 *A*–*D*) have less expanded ends than in *M. platyceps*. Estimated lengths range from 40 to 140 mm, with a maximum shaft diameter of 30 mm. As in *M. platyceps*, the proximal articular surface is hemispherical and offset dorsally from the shaft, the medial process is larger than the lateral one, and proximal width is greater than distal width. The ectepicondylar foramen begins as a distinct groove, wider than in *M. platyceps*, on the dorsal facies of the shaft, before penetrating the ectepicondyle to open ventrally. Humeri differ from *M. platyceps* and *M. mackayi* (11) with a less expanded lateral process and a more proximally projecting medial process.

Ulnae (Fig. 3 *E*, *I*, and *J*), as in *M. platyceps*, have proximally an extremely well developed olecranon process and sigmoid notch, and a well defined radioulnar articulation (5). Radii are more elongate and the rugosity for biceps superficialis on the shaft is smaller than in *M. platyceps*.

The shoulder girdle (Fig. 3 *F*–*H*) is triradiate: as in *M. platyceps*, the glenoid is not supported by a neck; the well developed dorsal and acromion processes diverge at approximately 105° compared with 120° in *M. platyceps* and other terrestrial turtles (5); the coracoid (Fig. 3*H*), unlike *M. platyceps*, is not fused to the glenoid and is more elongate. A wide scapular angle is usually correlated with a high body profile (5) suggesting that ?*M. damelipi* had a low body profile, somewhat more like marine turtles.

Femora (Fig. 4*A*) are stocky and range from 45 to 145 mm in shaft length; the head is large and hemispherical, being wider than long, and directed more dorsally to the shaft than in *M. platyceps*, such that it does not project proximally past the trochanter major. The minor and major trochanters are distinct from the femoral head, but unlike *M. platyceps*, have similar proximal extent and are linked ventrally by a bony web to enclose a deep intertrochanteric fossa.

Ankle, wrist, and digit elements are uncommon, but the few unguals are blunt, dorsoventrally thick, and ventrally flattened as in *M. platyceps* (Fig. 4 *G* and *H*).

Shell fragments of ?*M. damelipi* are similar to those of meiolaniids in having a thin dense outer bone layer and finely cancellous internal structure, but differ with a smoother external texture, and at least part of the carapace margin is concave dorsally. Dermal armor was present on the carapace (Fig. 4 *D* and *E*).

The size of ?*M. damelipi* can be compared with that of *M. platyceps* from the dimensions of the long bones. Femora and humeri were as long as 145 mm and 140 mm, respectively, similar to those in AMF57984 with a shell length of 1 m. However, larger turtles were present as one section of shoulder girdle preserves a glenoid cavity with a diameter of 40 mm compared with 30 mm in AMF57984.

These data show that the meiolaniid radiation in the southwestern Pacific region was more extensive than previously recognized (5). Dispersal to and between islands of this region would have been easily achieved by meiolaniids. Terrestrial turtles are highly buoyant (21) and some, e.g., *Dipsochelys giganteus*, are known to have survived in oceans without access to fresh water for many weeks (22). Although incapable of directed swimming, they are thus ideal candidates for ocean drifting, which dispersal mode explains the distribution of extant terrestrial turtles in the Indian Ocean (22, 23). There is nothing unique about Vanuatu to explain why meiolaniids survived there until the advent of humans, but could not have done so in other island groups, such as Fiji and New Caledonia. In the Lord Howe group, postglacial sea level rise greatly reduced land area, which in the absence of any evidence of pre-European occupation (24) could have facilitated the extinction of *M. platyceps*. For archipelagoes that retained islands of significant size in the Holocene, this cannot be the explanation. A poor or absent fossil record for most islands is the probable reason for a lack of other Holocene meiolaniids so discovery of further populations or taxa should be expected on other southwest Pacific islands where adequate habitat existed. Investigations of first contact human southwest Pacific sites will likely extend the record,

Table 2. Measurements (mm) of the Holotype (AMF.136641) and the paratypes of ?*M. damelipi* n. sp

Element	Cat no.	Total length maximum	Maximum proximal width	Minimum shaft width	Maximum distal width
Humerus	AMF.136641	95	39	15	35
Humerus	AMF.136640	80	32	12	24
Femur	AMF.136642	122	63	23	—
Coracoid	AMF.136652	58	26	10	29
Coracoid	AMF.136653	65	26	29	41
Radius	AMF.136654	65	21	14	—
Ulna	AMF.136647	80	33	14	29
Ulna	AMF.136648	61	26	12	21
Tibia	AMF.136651	98	30	13	22
Astragalocalcaneum	AMF.136655	55			
Dermal armor	AMF.136646		39, across base of triangular process		
Dermal armor	AMF.136650		29, across base of triangular process		
Pectoral element	AMF.136644	146, length dorsal process; 83, length acromion process; 47, maximum diameter glenoid			

The maximum diameter of the femoral ball (AMF.136642) is 36 mm.

and reexamination of bones previously interpreted as marine turtle might reveal that some are in fact those of terrestrial turtles.

The discovery of meiolaniid remains at Teouma provides conclusive evidence that they survived into the late Holocene and that humans encountered them. Relatively large numbers of meiolaniid bones occur, particularly in the basal levels of the Teouma midden, dating to approximately 2,900 or 2,800 cal BP, where they overlay burials dated 3,100 to 3,000 cal BP (14). Some burials were associated with meiolaniid carapace fragments (*SI Text*). In younger layers, they are absent. Remarkably for a Pacific coastal site, bones of marine turtles are rare in the lower layers. Early colonizers of the western Pacific normally hunted sea turtles and impacted many populations (25). At Teouma, large comparatively heavy bodied and fleshy terrestrial turtles were available and were the preferred prey until their disappearance by approximately 300 y after the initial encounter. Skeletal representation (Table 1) is markedly biased toward legs and associated fleshy parts. We infer that most turtles were killed and butchered elsewhere with mainly the fleshy upper limbs being taken back to the village. It seems probable that the first colonists, who created the cemetery at Teouma, and whose habitation sites have not yet been found, had eliminated proximate populations of turtles.

Hunting undoubtedly contributed to the extinction of ?*M. damelipi*, but may not have been the only cause. In the Mascarenes (Indian Ocean), where Europeans were the first humans to encounter the terrestrial turtles on Mauritius and Rodrigues, and initial densities were high, intensive exploitation for food rendered all populations extinct in a little more than one century (22). This rapid extirpation of turtles was partly attributed to the introduction of pigs, which prey on young and eggs. Similarly, pigs introduced by Lapita people may have affected the survivorship of Vanuatu meiolaniids. Whatever the exact synergy of factors, meiolaniids were extinct on Efate in Vanuatu within 300 y of the arrival of Lapita people.

The discovery of ?*M.damelipi* and that it became extinct soon after human arrival fits a recurring pattern across the Pacific. In Vanuatu, similar timed extinctions include a crocodilian and several birds (26, 27). Such losses are widespread and numerous and include crocodilians and large birds in New Caledonia (5, 27), these and large iguanids in Fiji (13), with losses of birds on every island for which a record exists (ref. 27 and references therein). Whether the turtle species known from fossil sites in New Caledonia (12) and Fiji (13) also survived until human arrival has yet to be established. The overall situation is such that in terms of total species, the loss of diversity in the late Holocene for the Pacific exceeds all other areas on Earth.

Materials and Methods

The Teouma Lapita site, located on the south coast of Efate Island, Central Vanuatu, was found in January 2004, following removal of approximately 1,000 m^2 of the overlying black ash-rich soil during quarrying. In 2004 to 2006, an area of 275 m^2 was excavated using trowels only, and all material was sieved dry or, as in most cases, wet-sieved to retrieve the most complete sample possible (18). Turtle bones were sorted from midden materials by one of the present authors (S.H.). Identification to taxon, element, and side was by two other authors (A.W. and T.H.W.). Radiocarbon analyses were carried out by the Radiocarbon Dating Laboratory at the University of Waikato, Hamilton, New Zealand, with accelerator MS determinations made on the graphitized carbon at the Rafter Laboratory in Lower Hutt, New Zealand (*SI Text* describes details). The turtle bones described herein are deposited in the Australian Museum, Sydney, and in the Vanuatu National Museum, Port Vila.

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Supporting Information

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Background and Location

The Teouma Lapita site, located on the south coast of Efate Island, Central Vanuatu (Fig. S1), was found in January 2004, following a series of opportune events (1). Tectonic uplift, volcanic ashfall, and alluvial deposits have repositioned this once immediately coastal colonization-period site, situated on an uplifted karstic reef terrace, to a current location approximately 800 m from the sea. Subsequent volcanic activity, postdating its use, has buried the site beneath as much as 80 cm of black tephra-rich sediment. Earthmoving activity in 2003 removed 1,000 m^2 of the overlying black ash-rich layer and in the process exposed the Lapita site. Initial excavations in 2004 quickly revealed that the first use of the site was as a cemetery and it was therefore both important at a local Vanuatu level but also provided the first real opportunity in more than 50 y of research to describe a group of Lapita people themselves and at the same time glean insights into their ritual and mortuary practices. Five field seasons have been undertaken at the site (2004–2006 and 2008–2009). Those of 2004 to 2006 (total excavated area of 275 m^2) have been outlined (1) in some detail. In 2008 and 2009, a further 76 m^2 were excavated. This expanded on previously excavated areas primarily further west and south. These excavations provided refinement of the boundaries of the cemetery, site stratigraphy, and chronology, and brought the total number of burials to 59, representing a maximum of 80 individuals. The excavation of the cemetery deposits was undertaken using trowels only, and all material was sieved dry or, as in most cases, wet-sieved to retrieve the most complete sample possible. The later midden deposits were excavated using both trowel and spade in some cases as a result of the hard-packed nature of the deposits, and all were dry sieved, with sample squares being sieved in water. From 2006 a laser theodolite total station has been used during excavations to facilitate detailed recording of the excavated areas, including burial features and artifacts, and to complete a topographic map of the wider site.

It has been established that just before human arrival at Teouma, a thick and still largely unweathered orange/yellow tephra, which has been identified in other areas of Efate (2–4), was deposited across the uplifted terrace (Fig. S2). This created a level surface across the once jagged uplifted reef. Burials were subsequently placed in shallow graves dug into the tephra in gaps in the uplifted reef and in the upper beach zone. The cemetery is concentrated along a northeast to southwest trending zone, 10 to 15 m wide and adjacent and parallel to the former beach. Evidence of initial habitation, possibly contemporary with the use of the cemetery, was identified in the form of concentrated midden dumping, adjacent and east of the cemetery, in area 6B and the east/west aligned trench extension of area 2. Further excavation in this area is required to confirm the nature of this deposit.

After the cessation of burial activity and a loss of the cemetery's significance, as much as 100 cm of midden was deposited across the site (Fig. S2). The deposit is associated with habitation activities dating to the Latest Lapita, Arapus, and Early Erueti phases of Central Vanuatu at approximately 2900–2500 BP (1, 4). It is in the lowest layers of this deposit, directly overlying the burials, that we find more concentrated faunal remains, including those of the meiolaniid turtles. These are found in association with concentrated deposits of shellfish comprising very large examples of a broad range of species.

The later midden deposits provide insights into changing settlement pattern and site use over time. They overlie the earlier Lapita deposits but also cover a significantly larger area of the site. The southern extent of the Erueti deposits parallels that of the Lapita deposits on the edge of the old reef but extends at least a further 20 m north, east, and west of the Lapita cemetery. This pattern of deposition, representing realigned and expanding settlement relates to adaptation to ongoing tectonic activity, which created a progressively prograding shoreline. The preferred location for habitation remained adjacent and parallel to the contemporary beach, requiring episodic realignment of the settlement. The continued uplift and alluvial infilling of the bay ultimately led to the abandonment of the settlement as access to the sea became increasingly problematic.

When it had been abandoned the site was further built up by a weathered tephra-rich black layer perhaps associated with volcanic activity on Nguna Island to the north at approximately 2300 BP, and which has again been identified across much of west coast Efate. Finally a later deposit of tephra-rich soil completes the stratigraphy of the site, and this may relate to further activity on Nguna or indeed to the massive 1452 AD Kuwae eruption to the north (5). The site shows no signs of use or occupation after 2500 BP until the development of the coconut plantation on the site approximately 100 y ago. There is no sign at Teouma of any Late Erueti or Mangaasi-style pottery (c. 2500–1200 BP) that is common in many other archaeological sites on Efate and the Shepherds (4).

Taxonomy of Meiolaniidae

There is considerable confusion in the literature as to who the author of Meiolaniidae is, e.g., Megirian (6). We found that the name is attributable to Boulenger, not Lydekker, who provided a junior synonym, as follows.

Meiolaniidae Boulenger, 1887. Miolaniidae Boulenger, 1887 [October]: *Proc Zool Soc Lond* 1887(III): 554; type genus *Meiolania* Owen, 1887.

Miolaniidae Lydekker, 1889: Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History), part III, containing the order Chelonia: 159; type genus *Meiolania* Owen, 1887.

Both names *Meiolania* and *Meiolania platyceps* are attributable to Owen, 1886 (17) in an abstract in *Proceedings of the Royal Society of London* [1886(40):315–316]. This publication has precedence over Owen, 1887 (18), not 1886 as commonly cited, because Owen's article was in part 2 of the *Philosophical Transactions of the Royal Society of London* for 1886, which was not published until 1887. In Table S1, we provide a list of all described taxa of meiolaniids, and significant records from Australia and the Southwest Pacific, arranged by geological age and with the relevant references (7–21).

Etymology of ?*M. damelipi*

The species is named for the late Willy Damelip of Ambrym Island, Vanuatu (died 2007). He was an archaeologist at the Vanuatu Cultural Centre and worked with S.B. and M.S. for more than a decade during archaeological research in Vanuatu, organizing the logistics of many surveys and excavations including that at Teouma.

Accelerator MS Radiocarbon Dates for Meiolaniids from Teouma, Vanuatu

Two bone samples were prepared and analyzed by the Radiocarbon Dating Laboratory at the University of Waikato in Hamilton, New Zealand. Samples were cleaned and ground, decalcified in 2% HCl, rinsed and dried, then gelatinized at pH 3 with HCl at 90° degrees for 4 h, then ultrafiltered and freeze-dried before graphitization. Accelerator MS determinations were made on the graphitized carbon at the Rafter Laboratory in Lower Hutt, New Zealand (Tables S2 and S3).

The dates presented in Table S2 were calibrated using the Northern Hemisphere calibration curve INTCAL04 (22), which is appropriate for Vanuatu, given its position relative to the "thermal equator" of the Intertropical Convergence Zone at the South Pacific Convergence Zone [e.g., McCormac et al. (23); Petchey et al. (24), p. 2238; Fig. 1]. McCormac et al. (23) pointed out that, where the Intertropical Convergence Zone seasonally shifts south of the geographic equator, plants use CO_2 from the Northern Hemisphere for part of the year and from the Southern Hemisphere for the remainder.

The isotope determinations presented in Table S3 provide quality control regarding the radiocarbon ages obtained. Modern collagen has approximately 43% carbon and 16% nitrogen, and should have a C:N ratio of approximately 3.2. Most well preserved archaeological bone averages 35wt% carbon with between 11 and 16 wt% nitrogen and a C:N ratio of 3.1 to 3.5. The Teouma results therefore fall within acceptable parameters (e.g., refs. 25, 26).

Meiolaniid Samples Associated with Burials

Burial 19 was excavated in 2005 and was found in squares C1 and D1. The excavation of burial 19 revealed that, after the grave was infilled with earth, a turtle shell or parts thereof were placed over it, and then coral boulders were used to seal it.

The turtle shell fragments from square D1, samples 4,170 and 4,171, were many and small, and had no patterning or pitting, so were classified as indeterminate turtle. However, samples 4,243, 4,244, 4,245, and 4,246, from square C1, included some with evidence of ornamental pitting on the external surface characteristic of meiolaniid. Sample 4,244 (Fig. 3*F*) contains a marginal shell fragment with characteristic surface texture of meiolaniids, but which differs from known taxa by the marginal being recurved or concave dorsally forming a gutter. Therefore a meiolaniid turtle shell was interred with burial 19.

In addition to burial 19, six meiolaniid long bones (Table S4) were associated with burials: samples AW161 an AW365, burial 10; AW193, burial 12; AW359, burial 20; AW391, burial 32; and AW111, burial 31.

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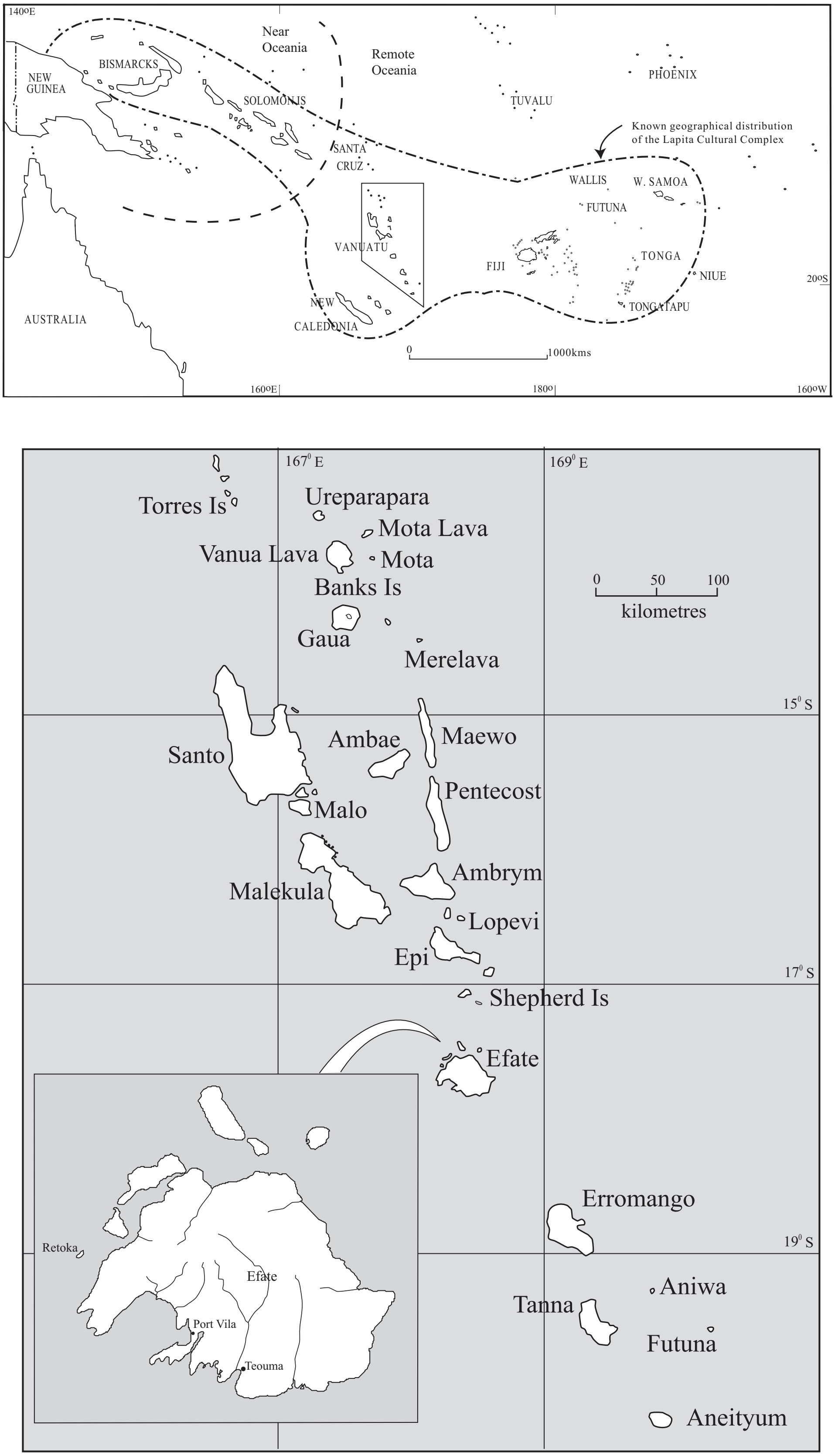

Fig. S1. Location of the Teouma site on Efate, in the Vanuatu archipelago, from Bedford et al. (1).

Fig. S2. An exemplary section through the Teouma deposits as revealed in the southern section of the Teouma excavation in 2009. The basal rock of uplifted reef is overlain by a layer of yellow ash. Above this lie the midden deposits from which the turtle bones described here were obtained.

Table S1. Taxonomy, geologic age and geographical distribution of taxa referred to the family Meiolaniidae Boulenger, 1887

Table. S1

Table S2. Accelerator MS determined radiocarbon results from meiolaniid bone from Teouma, Vanuatu

Table. S2

Table S3. Isotope determinations from meiolaniid bone gelatin from Teouma, Vanuatu

C:N is the carbon to nitrogen ratio. Carbon and nitrogen isotopes were determined with a precision of ± 0.2% at the Radiocarbon Dating Laboratory, University of Waikato, Hamilton, New Zealand. The sulfur isotope data were determined by ISO Analytical (Isolytix), Dunedin, New Zealand, by the EA-IRMS method.

Table. S3

Table S4. List of specimens showing identified long bones of meiolaniid turtles: Indeterminate shell fragments and bone shards are not listed

In column 1, AMF (Australian Museum Paleontology Department catalog number) or AW number (not prefixed, our working catalog number); ID Number is the Archaeological identifier that sometimes had multiple specimens within. NISP is number of individual specimens.

Table. S4