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Early Lapita skeletons from Vanuatu show Polynesian craniofacial shape: Implications for Remote Oceanic settlement and Lapita origins

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With a cultural and linguistic origin in Island Southeast Asia the Lapita expansion is thought to have led ultimately to the Polynesian settlement of the east Polynesian region after a time of mixing/integration in north Melanesia and a nearly 2,000-y pause in West Polynesia. One of the major achievements of recent Lapita research in Vanuatu has been the discovery of the oldest cemetery found so far in the Pacific at Teouma on the south coast of Efate Island, opening up new prospects for the biological definition of the early settlers of the archipelago and of Remote Oceania in general. Using craniometric evidence from the skeletons in conjunction with archaeological data, we discuss here four debated issues: the Lapita–Asian connection, the degree of admixture, the Lapita–Polynesian connection, and the question of secondary population movement into Remote Oceania.

Pacific Islands peopling | Polynesian origin | early Lapita | skull | morphometric analysis

The first human settlement of Vanuatu is indicated by the Lapita culture, whose earliest signature appears in the northwestern Melanesian islands toward the end of the interval 3,470–3,250 y B.P. or slightly later (1). The Lapita culture is defined by a set of artifacts including highly decorated pottery displaying a distinctive design system, long-distance exchanges of raw material and finished items, translocations of plants and animals, and the initial incursion of humans into the pristine island environments of Remote Oceania to the east of the main Solomon chain between 3,000 and 2,800 y B.P. (1, 2). In Vanuatu, as in the rest of Remote Oceania, Lapita quickly evolved, within 200–300 y, into distinctive local cultures in conjunction with increased population size and sedentism by the end of the Lapita period (3).

The question of the biological nature of the Lapita populations is routinely approached with data collected from protohistoric/historic or extant populations used as proxies. Analysis of skull morphology and morphometrics of protohistoric/historic populations from Oceania shows a geographical pattern of variation, separating northern and southern Melanesia from western and eastern Polynesia (4–6). More generally, the results indicate two contrasting divisions, an Australo-Melanesian pole comprising groups from the western part of Remote Oceania (Island Melanesia) and an Asian pole including groups from the (far) eastern part of Remote Oceania (Polynesia). This pattern suggests separate origins for the indigenous inhabitants of these two regions. Evidence from inherited genetic markers indicates that the populations living today in Vanuatu and generally in the region first settled by Lapita groups share a common origin in an area that encompasses Island South East Asia, the north coast of New Guinea, and the Bismarck Archipelago (7–13). These populations display haplogroups attributed both to the Pleistocene settlement of the northern Melanesian/Near Oceanic region and to the Lapita diaspora, with chronological estimates based on genetic data. Geographical variations in haplotype frequencies distinguish the western part of the initial Lapita

region from the eastern part, with a smaller diversity in the eastern populations in what is today Western Polynesia.

Studies on Lapita skeletal morphology (Table S1) have identified diversity in the physical makeup along with some level of local homogeneity, similarities with pre-Neolithic specimens from Island Southeast Asia and protohistoric/historic populations from southeastern Melanesia, and features not represented in any later Pacific Island groups (14–20). In a recent biodistance study of mandibles from Watom (New Britain), Pietrusewsky et al. (16) conclude that “expectation that skeletons associated with the Lapita Cultural Complex, Early or Late Lapita, biologically resemble the modern-day inhabitants of Remote Oceania is not supported” and challenge “the prevailing orthodox view that the origin of Polynesians is associated with Lapita culture.” However, whether the few analyzed individuals represent initial “Lapita people” is open to question. Because they postdate the initial appearance of the Lapita culture in the region (20), they may actually reflect subsequent gene flow and migratory events within the Melanesian region, saying more “about the contemporary indigenous inhabitants of eastern Melanesia than ... about the ancestors of the Polynesians,” as noted by Pietrusewsky et al. (18). Alternatively, the possibility that these late Lapita and (immediately) post-Lapita individuals derive directly from the initial “Lapita population” is not excluded, because heterogeneity among the early populations of the region and among the Lapita groups themselves might be expected (21–23).

Past haplotype distribution reconstructed with ancient DNA (aDNA) data obtained from skeletal remains representing early human groups may theoretically be a means to investigate the

Significance

The question of the origin of Pacific Islanders has exercised scientists since the first explorers' voyages of the 16th century. Physical resemblance between Polynesians and Asian populations was detected, but in between were the islands of Melanesia, inhabited largely by people of different phenotype. However, the Lapita culture bridged this geographical divide 3,000 y ago. Morphological studies of early Lapita colonists from Teouma, Vanuatu align them with present-day Polynesian and Asian populations, whereas skeletal remains of later generations show a more Melanesian phenotype predominating. We suggest that migration streams from already-inhabited parts of Melanesia dating from the late-Lapita phase ultimately dominated the original Polynesian phenotype in eastern Melanesia, but not in Polynesia, which became relatively isolated soon after initial settlement.

Author contributions: F.V. and F.D. designed research; F.V. and F.D. performed research; F.V. and F.D. collated the data; F.V. and F.D. analyzed data; and F.V., F.D., M.J.T.S., and S.B. wrote the paper.

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issue. However, published data on prehistoric Pacific Islanders are sparse and mainly centered on Polynesia (24). Regarding the Lapita question directly, the current aDNA results include only one individual representing the first thousand years of settlement in Vanuatu [Efate, Taplins, midlate third millennium B.P. (25)] and four individuals representing the late Lapita (or immediately post-Lapita) human group from Watom (New Britain), all appearing in a separate mtDNA lineage to modern Polynesians (26). Although consistent with the morphological evidence (15, 16, 27), these pioneering results are still regarded as uncertain (24). The lack of preservation of aDNA is a major complication, as attested in early specimens from New Caledonia (WKO013B) and Mussau (Bismarck Archipelago) (18, 28) as well as in the Teouma human samples tested so far.

Here, we provide for the first time to our knowledge insights into the biological diversity and affinities of the human population in Vanuatu at the time of the settlement of Remote Oceania, using craniometric evidence recorded on a sample of the initial “Lapita population” dated to *ca.* 3,000–2,850 y B.P. (29) and comparisons with prehistoric and modern populations from the Asia-Pacific region. Large-scale excavations at the Teouma site have revealed a Lapita cemetery with 68 burial features where adults were preferentially treated by inhumation (30). However, inhumation was temporary; bones, including skulls and mandibles, were removed from burials postdecomposition and redeposited at the site but in a much smaller number than the incomplete inhumations recovered to date (31). The extant cranial elements consist of seven skulls in secondary deposits (B10 cache, B17, and B30) (Fig. 1), two partial skulls in a disturbed context (Quarry Area), single cranial fragments associated either with incomplete inhumation or secondary deposits (B10, B12, B29, and B45), six mandibles and a fragment of a seventh (B10, B17, B30, and B29), and 98 associated teeth. Although disconnected from the infra-cranial skeletons these cranial remains seem to have belonged to individuals of the same group, as shown by similarities in isotopic values measured in bone collagen (29) and in dental enamel (32). In the current study, we use five of the seven skulls (labeled TEO 10a, 10b, 10c, 17, and 30a) that, after reconstruction, are almost complete and suitable for metric study (Fig. 1).

Materials and Methods

To assess the biological affinities of these early Vanuatu settlers, we have generated two distinct comparison datasets (*SI Materials and Methods*). The first is a composite sample of 12 archaeological adult specimens that were chronologically selected to help in evaluating Lapita-associated population origins. It comprises Late Pleistocene and Holocene individuals from the Sahul region, pre-Neolithic individuals from Island Southeast Asia (ISEA), and immediately post-Lapita and more recent prehistoric individuals from Remote Oceania (Table S2). The second dataset consists of nine samples selected from the database of Howells (33), representing five geographically distinct human populations from East Asia (China), Western Micronesia (Guam), Island Melanesia (mainly Tolai from New Britain), Australia, and Eastern Polynesia (Table S3). This dataset originally included a total of 707 adult individuals out of which subsamples of 54 specimens (27 male and 27 female) were sampled in each of the five geographical groups ($n = 270$). Craniofacial shape affinities were assessed with series of multivariate analyses, including principal component analyses (PCA) on size-corrected measurements of the neurocranium and upper face and linear discriminant analyses (LDA), which have been used to predict the classification of the archaeological specimens, including the five Teouma individuals (*SI Materials and Methods* and Table S4).

Results

The scatter plot of specimens on PC1 vs. PC2, which accounts for almost 48% of the total shape variation, shows rather large overlaps between the recent specimens of the five geographical groups (Fig. 2). However, the variation along PC1 distinguishes Australian and Melanesian specimens that mainly plot toward negative values from Chinese, Western Micronesian, and Polynesian specimens that mainly plot toward positive values. Contributions of variables indicate PC1 mainly opposes the variables NLH and OBH that are positively correlated with PC1, with the variables NLB and PAC that are negatively correlated with PC1

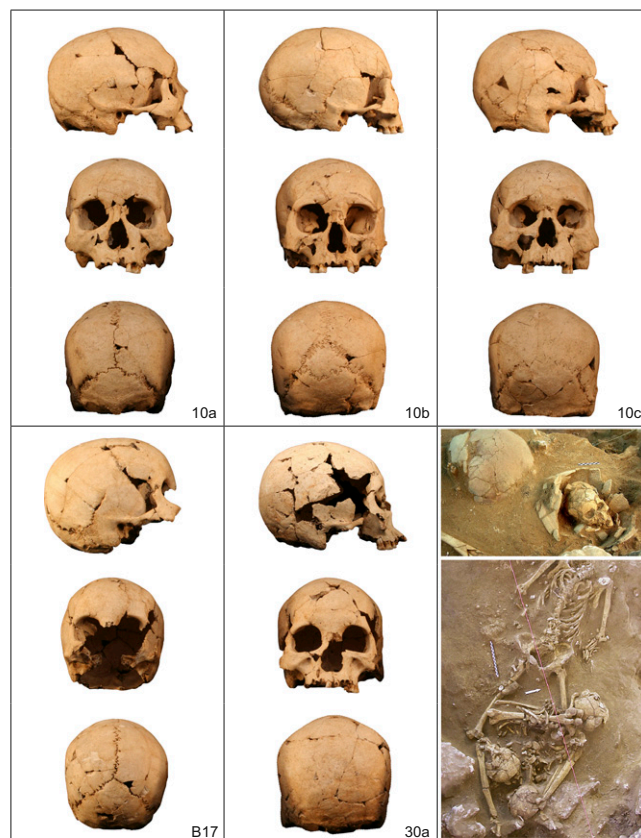


Fig. 1. Teouma Lapita skulls TEO 10a, 10b, 10c, 17, and 30a [images of the skull courtesy of Chris Smith (Anatomy Museum Curator, University of Otago)] and burial features B17 and B30 [bone collection B30 lies on the lower limbs of without-skull burial B44] [computer-assisted design courtesy of Michèle Ballinger (CNRS, UMR 7041)].

(Fig. 2). Australian and Melanesian individuals thus tend to display relatively long skulls (especially the parietal cord) and upper faces with relatively short and wide nasal apertures and low orbits. Chinese, Western Micronesian, and Polynesian individuals present the opposite morphological characteristics. The five Teouma specimens, as well as the Fijian Terminal Lapita or immediately Post-Lapita specimen Waya Y2-25-1, plot clearly among the variation range of these three recent “Asian-like” groups on PC1 vs. PC2. The post-Lapita Vanuatu individual from Mangaliliu presents rather different craniofacial shape affinities because it plots closer to recent Australo-Melanesian groups and archaeological Australian and pre-Neolithic Southeast Asian individuals. Two archaeological Australian specimens from the Coobool Creek series (CC28 and CC36) plot at the margin of the variation of recent Australians on PC1 vs. PC2; however, neither of these two individuals is described as artificially modified by head binding (34).

The LDA is able to correctly discriminate the five geographical groups of the 270 recent specimens. The scatter plot on LD1 vs. LD2 mainly distinguishes two major geographical groups along LD1 (Fig. 3). Australian and Melanesian individuals plot toward negative values of LD1, whereas Chinese, Micronesian, and Polynesian individuals plot toward the positive. Discriminations inside each of these two major geographical groups are mainly expressed along LD2, but at lower magnitudes. Australians are separated with some overlap from Melanesians that tend to have positive values for LD2. The same trend is observed for Polynesians that have generally higher values for LD2 than Chinese and Micronesians. These two last groups are largely overlapping on LD1 vs. LD2 and their 95% ellipses are only slightly discriminated.

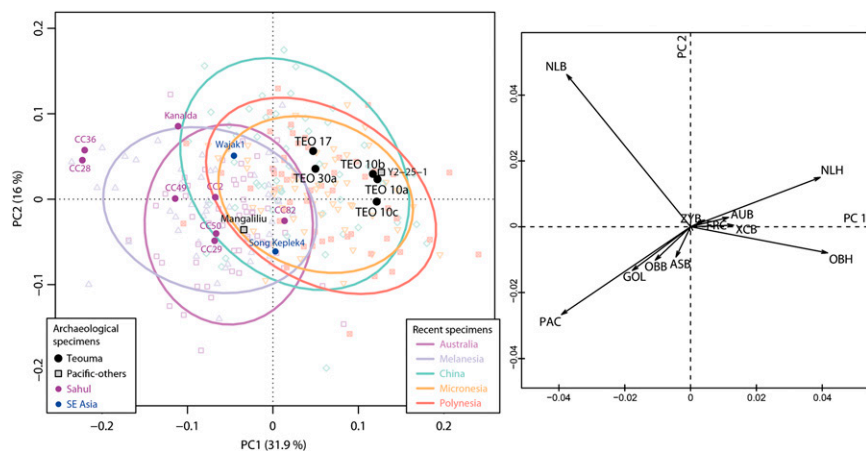


Fig. 2. PCA on the log-shape ratios of 11 craniofacial variables for 270 recent and 17 archaeological specimens: scatter plot of specimens on PC1 vs. PC2, with 95% ellipses for the five geographical groups of recent specimens and plot of the 11 craniofacial variables (log shape ratio) scores for PC1 vs. PC2.

The predicted values on LD1 and LD2 of the 17 archaeological specimens with no a priori geographical assignments fall well inside the overall variation of the 270 recent specimens.

The cross-validation procedure indicates that 72.6% of the 270 recent specimens are correctly assigned to their original group (Table 1). This percentage is significantly higher than the 20% probability of a correct assignment by chance only for five geographical groups. The results indicate 77.8% of correct assignments for Australians, 75.9% for Melanesians, 75.9% for Chinese, 70.4% for Polynesians, and 63% for the Western Micronesian group that provides the highest number of incorrectly assigned specimens. If one takes into account the two larger geographical groups that are distinguished in the PCA and the LDA scatter plots (i.e., Australian and Melanesian on the one hand and Chinese, Micronesian and Polynesian on the other hand), percentages of correctly assigned specimens significantly increase to, respectively, 88.9% and 95.7%. This implies that despite a significant percentage of incorrect assignments the discriminant functions computed with the 11 craniofacial shape variables for 270 recent specimens divided into five geographical groups provide a good discrimination between all of the groups, and, at a higher geographical level, a very good discrimination between an Australian and Melanesian pole and a Chinese, Micronesian, and Polynesian pole.

The results of the predicted classifications of the 17 archaeological specimens computed with the discriminant functions are presented in Figs. 4 and 5. Seven of the eight Australian archaeological individuals present high assignment probabilities to Australian and/or Melanesian groups (Fig. 4A). The eighth Australian archaeological specimen, Coobool Creek 82, presents a completely different profile of its predicted assignment. The probabilities indicate more than 84% for an assignment to the Polynesian group and negligible probabilities for assignments to the Australian and Melanesian groups. This particular specimen has been systematically identified as artificially modified in previous work (34, 35), which could explain its particular craniofacial shape.

The two archaeological specimens Song Keplek 4 and Wajak 1 (Eastern Java, Indonesia) present different profiles for their respective predicted assignments (Fig. 4B). Song Keplek 4 presents very clear craniofacial shape affinities with the recent Melanesian group, with probabilities of more than 83% for an assignment to this group. The probabilities for Wajak 1 are largely distributed among the Melanesian, Chinese, Micronesian, and Polynesian groups, with higher probabilities for the Polynesian group (53.5%). This points to shared affinities for the craniofacial shape variables of Wajak 1 with the Australian and Melanesian pole as well as with the Chinese, Micronesian, and Polynesian pole.

The two non-Teouma archaeological comparison specimens from the Pacific present two opposite profiles for their predicted assignments (Fig. 4C). The Terminal Lapita or immediately post-Lapita individual Y2-25 from Waya (Yasawa, Fiji) presents dominant affinities with recent Micronesians and Chinese (respectively

68.6% and 29.9%), whereas the post-Lapita specimen from Mangaliliu (Efate, Vanuatu) shows almost exclusive craniofacial shape affinities with recent Australian and Melanesian specimens, with probabilities of predicted assignments to these two groups of, respectively, 71.5% and 27.5%.

The five Lapita specimens from the Teouma cemetery show craniofacial shape affinities with the Chinese, Western Micronesian, and Polynesian geographical pole, with only minor or null percentages of predicted assignments to recent Australian and Melanesian groups (Fig. 5). However, the detailed results of individual predicted assignments distinguish two groups. Teouma B10A, B10B, and B30A present largely dominant percentages of predicted assignments to the recent Polynesian group (respectively 70.3%, 94.0%, and 88.8%), whereas Teouma B10C and B17 present dominant affinities with the recent Chinese sample (respectively 78.2% and 72%). These contrasted craniofacial shape affinities at a finer scale among the Teouma specimens are also found in the scatter plot on LD1 vs. LD2 (Fig. 3). The five Teouma individuals, as well as the Terminal Lapita or immediately post-Lapita specimen from Waya (Y2-25-1), are clearly aligned with the recent specimens on the Asian pole toward

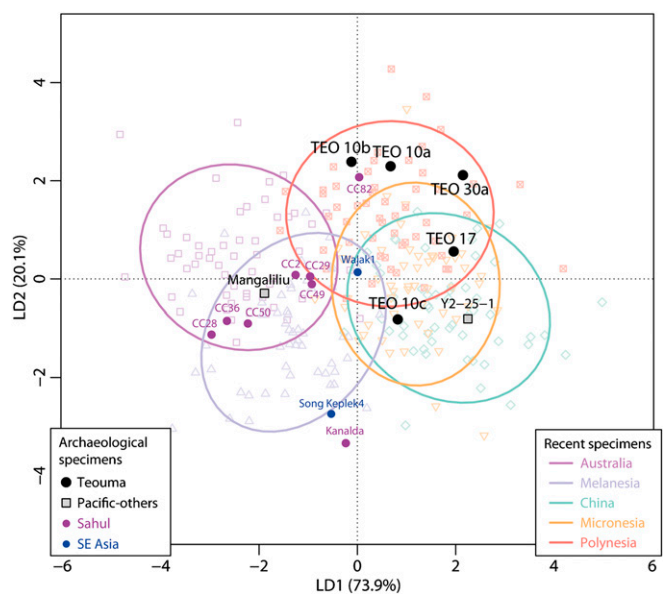


Fig. 3. LD1 vs. LD2: scatter plot of the 270 recent specimens (with 95% ellipses for the five geographical groups) used to compute the discriminant functions and 17 archaeological specimens (predicted values).

Table 1. Discriminant analysis: Assignations of specimens to geographical groups after cross-validation

Geographical groups	Australia	Melanesia	China	Micronesia	Polynesia	Total (original)	Percent correct, %	Pooled geographical groups (original)	Percent correct (pooled geographical groups), %
Australia	42	9	0	1	2	54	77.8	108	88.9
Melanesia	4	41	2	4	3	54	75.9		
China	0	1	41	6	6	54	75.9	162	95.7
Micronesia	0	3	11	34	6	54	63.0		
Polynesia	2	1	5	8	38	54	70.4		
Total	48	55	59	53	55	270	72.6	270	92.3

positive values on LD1, but they tend to be distinguished into two subgroups along LD2.

Discussion

A Lapita–Asian Connection. Our analyses, involving five *ca.* 3,000- to 2,850-y-old skulls associated with the Lapita culture uncovered from the Teouma site (Efate, Vanuatu) and 270 recent skulls from the five geographic regions of Australia, Melanesia, Western Micronesia, Polynesia, and China clearly point to a Lapita–Asian biological connection. The results show little or no affinities between the Teouma cranial series and the modern Australian and Melanesian cranial series but strong similarities to Chinese, Western Micronesian, and especially Polynesian cranial series; in other words, the Teouma individuals fit into the Asian pole and not into the Australo-Melanesian pole (5, 6). Our results also confirm the East Asian affinity previously identified in the Terminal Lapita or immediately post-Lapita individual Y2-25 from Waya (Yasawa) in the Fiji group (19) and the resemblances with modern Melanesians already observed for the post-Lapita specimen recovered at Mangaliliu (Efate, Vanuatu) (36).

Our results also highlight a lack of morphological resemblance between the individuals uncovered at Teouma and the late Pleistocene–early Holocene individuals from Australia and Island Southeast Asia, which in turn display similarities with modern-day inhabitants of Australia and northern Melanesia. The only notable exceptions to this pattern are Coobool Creek 82, whose proximity with recent Polynesians could be a side effect of artificial cranial modification by head binding (34, 35), and the Pleistocene Javanese specimen Wajak 1 recently related to 37,400–28,500 y B.P. (37). This individual has been described in previous studies as a very large specimen with some resemblances to early anatomically modern humans (38). However, several studies also pointed out its “Asian characteristics,” especially in its facial features (37, 39, 40). According to our analysis, those attributes are shared with the Lapita individuals. Interestingly, Early Holocene (11,000-8,000 y B.P.) and Mid-Late Holocene (4,000/3,000–2,200 y B.P.) individuals from Niah West Mouth Cave (41) have been shown to share similar cranial and facial morphology (42). These observations suggest that the identified Lapita–Asian biological connection, regardless of the

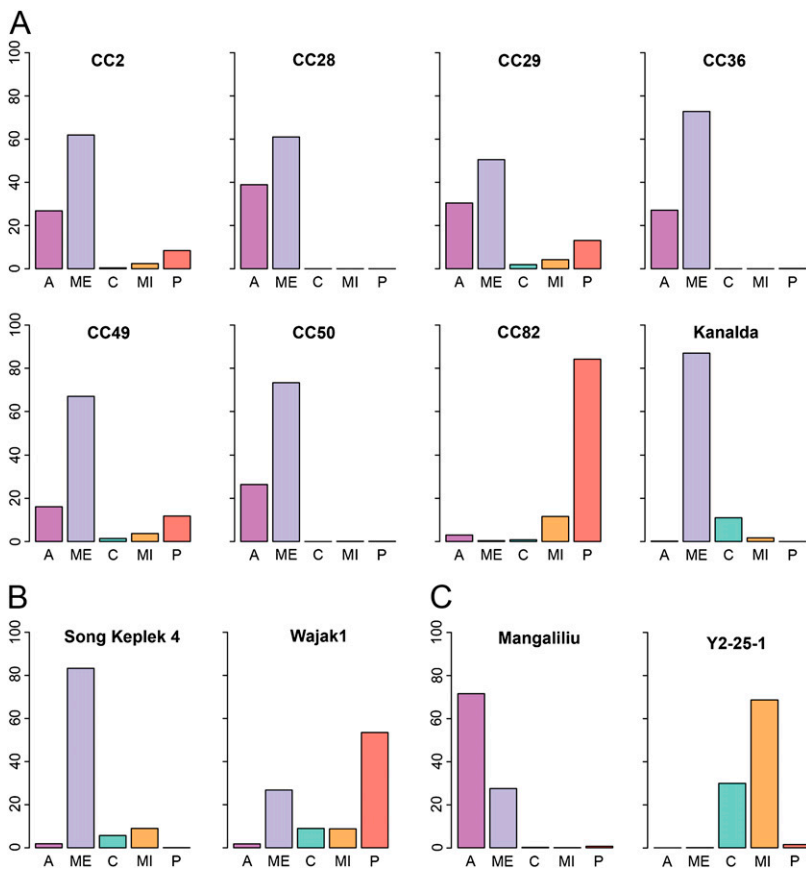


Fig. 4. Bar plot of the predicted probabilities of posterior assignments to the five geographical groups: (A) Australian archaeological specimens; (B) Javanese archaeological specimens; (C) Pacific archaeological specimens. A, Australia; ME, Melanesia; C, Chinese; MI, Micronesia; P, Polynesia.

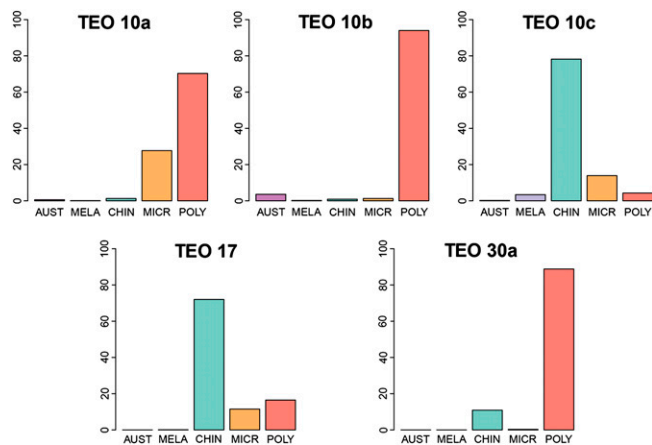


Fig. 5. Teouma archaeological specimens: bar plot of the predicted probabilities of posterior assignments to the five geographical groups (AUST, Australia; MELA, Melanesia; CHIN, Chinese; MICR, Micronesia; POLY, Polynesia).

time period it was transferred to Remote Oceania, could have an antiquity predating “neolithization” in ISEA and roots in the late Pleistocene/early Holocene populations already established in the greater Southeast Asian region. Even if phenotypic and genetic markers are not necessarily connected, it is worth noting that the observed pattern finds parallels in genetic evidence pointing to the presence of Asian features as early as the Early-Mid Holocene in Island Southeast Asia and Near Oceania and indicating multiple phases of dispersals within this region (11, 43, 44). The population movement associated with the Lapita culture could therefore have been of much shorter distance than usually thought (45).

The Question of Admixture. Our results otherwise echo earlier morphometric conclusions formulated by Howells (46), affirming no important gene exchange between Melanesians and pre-Polynesians. Indeed, the observed lack of similarity between the five individuals recovered at Teouma and the modern-day inhabitants of Australia and northern Melanesia suggests little or no admixture between individuals, either male or female, associated with the Lapita culture who colonized Central Vanuatu *ca.* 3,000 y ago and the population already established/resident in Near Oceania. This interpretation, differing from that of genetic studies that indicate a mixed (varying with sex) Asian/Near Oceanian ancestry of Remote Oceanians (8–10, 12, 47), could be related to the time of admixture, with estimates calculated via genomewide data analyses being imprecise: around 3,000 y ago [ABC simulation analysis (10)] and even 2,700 y ago (wavelet transform analysis, 95% confidence interval: 2,300–3,900 y (48)). Conflicting with what is implied in the Triple I model for Lapita (21, 49), incorporation of Near Oceanian biological features and the spread of Lapita culture could therefore have been time-dissociated processes. Nevertheless, absence of evidence of Near Oceanian admixture in our sample does not rule out previous expectations of heterogeneity among the early populations of the region and among Lapita-associated groups themselves (21–23). In fact, heterogeneity does exist in the Teouma group, a sample representing a single community. Our results point to morphological diversity within the Asian range of variation (Figs. 2, 3, and 5), suggesting a composite group with multifocal origins. Results of isotopic studies, showing diversity in geographical origins of the individuals buried at Teouma (32), support this view as well as long-distance exchanges of obsidian (50) and pots (51) during the earliest phases of site use.

The Lapita/Polynesian Connection. Contrasting with previous morphometric studies of Lapita cranial elements (14–16, 18, 19), evidence presented in this study definitively supports the consensual view that the origin of the Polynesians is associated with the Lapita culture (28, 52–54). Our results, illustrating strong similarities between *ca.* 3,000-

y-old cranial remains from Teouma in Vanuatu and the Polynesian cranial series in this study, demonstrate a common ancestry for at least some of the people associated with the early Lapita cultural complex in Vanuatu and the Polynesian peoples, and a Lapita foundational contribution to the Polynesian gene pool. This common ancestry seems to be shared with early people established in Fiji. The late Lapita individual from Naitabale (Moturiki) is reported to display Polynesian features (20), and the Terminal Lapita or immediately post-Lapita Y2-25 individual from Waya (Yasawa) presents East Asian affinities (19). These data give little support to the ideas of distinctiveness between Fijian and Tongan founding populations and of an emergence of a distinctive Polynesian phenotype in West Polynesia (55). The Polynesian physical makeup seems to predate the development of Ancestral Polynesian society and its spread to East Polynesia (56).

Secondary Population Movement into Remote Oceania. In this context, the recurring observations of similarities between the skeletons associated with the late Lapita and immediately post-Lapita periods in Near and Remote Oceania and protohistoric/historic skeletons from island Melanesia reported by previous studies need explanation. Affinities with modern inhabitants of Melanesia are recognized for the skeletons associated with the late Lapita period from Watom Island (New Britain) (15, 16). Similarities with East Melanesian populations, including New Caledonia, are diagnosed in the WKO013B (18) and in WKO013C (17) skeletons, both excavated from the site of Lapita in Koné (New Caledonia) and dated to the immediately post-Lapita period. Melanesian morphological features are identified (27) in skeletons uncovered at the Taplins site in Mele (Efate, Vanuatu) also dated to the immediately post-Lapita period (25). We suggest that impact from a northern Melanesian gene flow, in at least some regions of Remote Oceania such as Vanuatu and New Caledonia, could account for this pattern of morphological variation over time (57, 58). Twenty years ago, Green (59) proposed that this movement started by 2,500 y B.P. We propose here that it occurred earlier, shortly after the initial colonization and before the end of the Lapita period. This suggestion, biologically plausible considering the short duration of the Lapita period in Remote Oceania (200–300 y, 12–15 human generations), is consistent with the results of genetic studies. There is a larger Near Oceanian contribution to the gene pool in populations living today in the western part of Remote Oceania (10, 12) with the possibility of an admixture time at about 2,700 y ago (48).

This interpretation is also supported by cultural evidence. Earlier there were suggestions of a post-Lapita secondary migration from Near Oceania into western parts of Remote Oceania, supposedly associated with the spread of incised and applied relief pottery of the Mangaasi style (54). However, the end of the Lapita period is marked by a major decrease in mobility indicated by cessation of obsidian long-distance exchange (22, 50), by the divergence and ultimate end of production of Lapita pottery itself, and by radical changes in dietary and funerary practices as observed at the Teouma site (31).

This alternative prospect, considering a modification/alteration of the initial morphology of the population associated with the Lapita culture as occurring during the Lapita period rather than immediately afterward, reconciles the contradictory archaeological and bioarchaeological views on the origins of Polynesians better than other explanations such as selection, adaptation, secular change, bottleneck, and founder effect (60, 61), or the addition of a significant later Asiatic migration via Micronesia (16, 62). The late Lapita individuals that have been the subject of study before the discovery of the Teouma site are simply not representative of the biology of the initial Lapita dispersal through Remote Oceania into Polynesia. In Island Melanesia this original migratory push was overlain by further migration from Near Oceania that did not significantly affect Tonga, Samoa and adjacent regions of Western Polynesia.

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