Advanced maritime adaptation in the western Pacific coastal region extends back to 35,000–30,000 years before present

Masaki Fujita^{a,1}, Shinji Yamasaki^a, Chiaki Katagiri^a, Itsuro Oshiro^b, Katsuhiko Sano^c, Taiji Kurozumi^d, Hiroshi Sugawara^e, Dai Kunikita^f, Hiroyuki Matsuzaki^c, Akihiro Kano^g, Tomoyo Okumura^{g,h}, Tomomi Sone^g, Hikaru Fujita^g, Satoshi Kobayashiⁱ, Toru Naruse^j, Megumi Kondo^k, Shuji Matsuura^k, Gen Suwa^c, and Yousuke Kaifu^{l,1}

^aOkinawa Prefectural Museum & Art Museum, Okinawa 900-0006, Japan; ^bOkinawa Ishi no Kai, Okinawa 901-2206, Japan; ^cThe University Museum, The University of Tokyo, Tokyo 113-0033, Japan; ^dNatural History Museum and Institute, Chiba 260-8682, Japan; ^eBoard of Education, Urasoe City, Okinawa 901-2103, Japan; ^fGraduate School of Humanities and Sociology, The University of Tokyo, Tokyo 113-0033, Japan; ^gGraduate School of Social and Cultural Studies, Kyusyu University, Fukuoka 819-0395, Japan; ^hDepartment of Subsurface Geobiological Analysis and Research (D-SUGAR), Japan Agency for Marine-Earth Science & Technology, Kanagawa 237-0061, Japan; ⁱDepartment of Applied Biological Sciences, Faculty of Agriculture, Saga University, Saga 840-8502, Japan; ^jTropical Biosphere Research Center, University of the Ryukyus, Okinawa 907-1541, Japan; ^kLaboratory of Physical Anthropology, Ochanomizu University, Tokyo 112-8610, Japan; and ^lDepartment of Anthropology, National Museum of Nature and Science, Ibaraki 305-0005, Japan

Edited by James O'Connell, University of Utah, Salt Lake City, UT, and approved July 29, 2016 (received for review May 17, 2016)

Maritime adaptation was one of the essential factors that enabled modern humans to disperse all over the world. However, geographic distribution of early maritime technology during the Late Pleistocene remains unclear. At this time, the Indonesian Archipelago and eastern New Guinea stand as the sole, well-recognized area for secure Pleistocene evidence of repeated ocean crossings and advanced fishing technology. The incomplete archeological records also make it difficult to know whether modern humans could sustain their life on a resource-poor, small oceanic island for extended periods with Paleolithic technology. We here report evidence from a limestone cave site on Okinawa Island, Japan, of successive occupation that extends back to 35,000–30,000 y ago. Well-stratified strata at the Sakitari Cave site yielded a rich assemblage of seashell artifacts, including formally shaped tools, beads, and the world's oldest fishhooks. These are accompanied by seasonally exploited food residue. The persistent occupation on this relatively small, geographically isolated island, as well as the appearance of Paleolithic sites on nearby islands by 30,000 y ago, suggest wider distribution of successful maritime adaptations than previously recognized, spanning the lower to midlatitude areas in the western Pacific coastal region.

Homo sapiens | early modern humans | Late Pleistocene | Late Paleolithic | maritime adaptation

Modern humans first appeared on off-shore islands during the later half of the Late Pleistocene, as evinced from archaeological sites in Wallacea and Sahul dating back to at least 47,000 calendar years before present (cal BP; 0 cal BP = AD 1950) (1, 2). Such early maritime adaptation includes arguably purposeful water transportation (3, 4), exploitation of aquatic food resources including fast-moving marine fish (5), and use of bone and shell tools (6–9). However, the details of such early maritime culture, as well as its development and actual distribution beyond Wallacea and Sahul, remain unclear. Another unresolved question is whether people had enough skills to sustain life on small insular environments for extended periods. This last question is important in assessing the efficacy of Late Paleolithic technology in marine environments.

Okinawa Island is located in the middle of the Ryukyu Archipelago that stretches over the area of 1,200 km between the main islands of Japan and Taiwan (Fig. 1). Supposing sea-level lowering of 130 m during the Last Glacial Maximum (LGM; 26,000–19,000 cal BP) (10) and minimal uplifting, Okinawa was approximately triple the current area of 1,208 km², but was nevertheless comparatively small and isolated from both the Asian continent (~150 km) and the adjacent, smaller islands of

the archipelago (~20–130 km). This is in contrast with the general geography in Wallacea and eastern New Guinea, where large (>10,000 km²) and small islands are more tightly clustered.

Human skeletal remains excavated from limestone fissure and cave sites, as well as other archaeological evidence, indicate that modern humans (*Homo sapiens*) appeared on the Ryukyu oceanic island chain no later than 35,000–30,000 cal BP (11). Okinawa was poor in lithic and animal food resources during the Late Pleistocene: There were no high-quality lithic raw materials, and large/medium-sized terrestrial animals were restricted to two species of dwarfed deer (*Cervus astylodon*, Muntjacinae gen. et sp. indet.) and wild boars (*Sus scrofa*) (12). This situation led some researchers to hypothesize that Okinawa and the other islands of the Ryukyus were too small for sustained occupation by Paleolithic people (13, 14). Indeed, clear evidence of human material culture in the Ryukyu Archipelago predating 10,000 cal BP has so far been scant, echoing the general “problem” with early modern human sites in southeastern Asia: the paucity of material evidence for innovative or modern behavior such as advanced lithic technology and personal ornaments (15–18).

Significance

Moving into oceanic islands after c. 50,000 years ago was a remarkable step forward in the history of worldwide expansion of modern humans. However, the developmental process of Pleistocene maritime technology remains unclear. So far, the only secure sources of information for such discussions were the Indonesian Archipelago and northern New Guinea as stepping-stones from the Asian continent to Australia. This article reports a successful maritime adaptation that extended from ~35,000 to 13,000 years ago on a small island environment in the southern Japanese Archipelago. The new evidence demonstrates a geographically wider distribution of early maritime technology that extended north to the midlatitude areas along the western Pacific coast.

Author contributions: M.F., S.Y., G.S., and Y.K. designed research; M.F., S.Y., C.K., I.O., K.S., T.K., H.S., D.K., H.M., A.K., T.O., T.S., H.F., S.K., T.N., M.K., S.M., and Y.K. performed research; M.F., D.K., A.K., and T.O. analyzed data; and M.F., S.Y., K.S., G.S., and Y.K. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence may be addressed. Email: fujiamsk@pref.okinawa.lg.jp or kaifu@kahaku.go.jp.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1607857113/-DCSupplemental.

Fig. 1. The location of Sakitari Cave and older dates of Pleistocene insular sites in the western Pacific regions. Symbols indicate the distribution of archaeological signs focused on in this article. Base map of the enlarged area around the Ryukyu Archipelago with approximate -130 m depth contour, created using the GeoMapApp software (www.geomapp.org/) and Global Multi-Resolution Topography synthesis (63).

AMS radiocarbon dates from 42 woody charcoal, seashell, snail, and crab samples are highly consistent with the stratigraphy, indicating little postdepositional disturbance (Fig. 3 and *SI Appendix*, Table S1 and *SI Appendix, Stratigraphy, Dates, and Periods of Human Occupation at Sakitari Cave*). These dates suggest near-continuous deposition from about 36,500–13,000 cal BP with no signs of erosion and minimal hiatus. Identified wood charcoal samples include genus *Camellia* and possibly *Symplocaceae*. The dates obtained for these samples may be older than the depositional dates by as much as their life durations of several hundreds to a thousand years. Other samples may have been variously affected by old carbon from the karst. Still, the remarkable stratigraphic consistency of the obtained dates suggest such effects are minimal, if any. The presence of two seashell species, *Callista chinensis* and *Haliotis diversicolor* (Osumi type) (*SI Appendix*, Table S2), the present-day distributions of which are restricted more than 400 km to the north, is consistent with the presumed cooler climate during and around the LGM.

Charcoal fragments and remains of freshwater crabs (Japanese mitten crab *Eriocheir japonica*) and freshwater snails (*Semisulcospira libertina*) are abundant in all layers. They are particularly dense in the dark-colored Layer II, which includes two charcoal belts (Layers II-1B and II-2 in Fig. 2). Artifacts from the terminal Pleistocene levels include possible seashell beads from Layer I

(c. 13,000–16,500 cal BP); fish hooks, shell-tools, and two types of shell beads from Layer II (c. 20,000–23,000 cal BP); and a shell-tool from the uppermost part of Layer III (c. 23,500–25,500 cal BP) (Fig. 4). Stone artifacts are rare and represented by only three tiny amorphous quartz flakes from Layer I (Fig. 4) (19, 20) and a possible grindstone from Layer II (Fig. 5B and *SI Appendix, Stone Artifacts*).

A few isolated human remains were found from Layers I and II (Fig. 4). Bones of a human infant are partially exposed on the eastern section of Pit 1 at the lower level of Layer III, dated to 29,000–31,000 cal BP (PLD-30878~30880 in [SI Appendix, Table S1](#)). At the current bottom of Pit 1, 10 cm below the infant skeleton, a charred deer bone and remains of freshwater crab (*E. japonica*), freshwater fish (Giant mottled eel *Anguilla marmorata*), and freshwater snail (*S. libertina*) were found with a charcoal fragment dated to c. 36,500 cal BP and land snails dated to c. 33,700 and 34,700 cal BP. The combined evidence of charcoal, human bone, and freshwater food residues (see *Seasonality of Cave Use*) indicate human activities at the cave extending to at least 30,000 cal BP, and probably to 35,000 cal BP.

The Seashell Artifacts

Fig. 2. Vertical section of Sakitari Cave and Trench I.

Fig. 3. Accelerator mass spectrometry ^{14}C dating obtained from Trench I and Pit 1 of Sakitari Cave.

(SI Appendix, Fig. S6). Smaller bivalves, *Septifer bilocularis*, were used as implements without prior modification (Fig. 5 D and I and SI Appendix, Fig. S7).

Beads are represented by three segmented tusk shells (*Dentalium* and *Pictodentalium*) and five perforated bivalve shells (*Sunetta kirai*) from Layer II (Fig. 5E), and by two perforated gastropod shells from Layer I (Fig. 4). Although traces of artificial modification are not evident for the *Dentalium* specimen, the *Pictodentalium* specimen shows clear concentric abrasions on both margins, probably caused by grinding (Fig. 5 J and K). The bivalve beads are perforated near their umbo by knapping internal side of the shell.

Well-preserved fishhook pieces, one finished and another unfinished, were excavated from Layer II and Layers I/II, respectively (Figs. 5 A and F and 6). These were single-piece hooks manufactured by splitting and grinding the flat bottom parts of *Trochus* shells. An allochthonous sandstone piece from the Layer II shows a smoothed surface that may have been used for the grinding process (Fig. 5B). Another broken shell fragment of the flat bottom part of *Trochus* from Layer II may have been a blank for fishhook production. The finished fishhook from Sakitari Cave was found in situ by M.F. from the uppermost Layer II-2, closely associated with two charcoals dated to 22,380–22,770 cal BP (PLD-23288 and PLD-23289 in SI Appendix, Table S1).

Seasonality of Cave Use

Freshwater crabs (*E. japonica*; minimum number of individuals = 709) and freshwater snails (*S. libertine*; minimum number of individuals = 431), possibly captured at a nearby river such as the

modern Yuhi River, dominate throughout the excavated terminal Pleistocene strata (SI Appendix, Fig. S8). Cases of nonhuman transport of aquatic organisms into caves have been reported (21). However, the known Late Pleistocene terrestrial fauna from Okinawa (dominated by small-bodied deer, boar, herons, egrets, and cranes) would not have selectively eaten large-bodied crabs. We therefore interpret these to represent human activities.

The dominance of the crab and freshwater snail remains applies to assemblages of all layers. About 3–12% of them are charred. X-ray diffraction analysis (SI Appendix, Fig. S9) indicates transformation of their mineralogical composition by heat above 500 °C. The human exploitation of freshwater crabs and snails at Sakitari Cave has a strong seasonal signal. The remains of *E. japonica* are distinctly biased toward larger individuals (SI Appendix, Fig. S10). Such large individuals of *Eriocheir* species are today captured in autumn when they migrate downstream for reproduction (22). This is also the season when they are the most delicious because their hepatopancreases are well developed. Our isotopic analyses of freshwater snails support their capture primarily in autumn (64%) and secondarily in summer (32%) (SI Appendix, Fig. S11, Table S5, and Faunal Analyses). The Sakitari faunal assemblage also includes a small number of Giant mottled eels [number of identified specimens (NISP) = 36], frogs (NISP = 328), marine fish (NISP = 9), small birds (NISP = 77), and small mammals (NISP = 509), some of which again show signs of burning and thus are considered to have been eaten by humans (SI Appendix, Fig. S8 and Table S4). Overall, aquatic nocturnal animals dominate the faunal assemblage, and terrestrial large/medium-sized mammals (deer and boars) are few (SI Appendix, Table S4).

	human remains	artifacts	notable food residues	
			middle/large mammals	abundant remains indicating seasonality
layer I				
13,291 ~ 16,625 cal yBP	deciduous canine carpal bone	quartz flakes shell beads	wild boar	freshwater crabs and snails
layer II				
19,635 ~ 23,425 cal yBP	lower molar tarsal bone	shell fishhook, possible grind stone shell scrapers shell beads	wild boar	freshwater crabs and snails
upper part of layer III				
23,450 ~ 25,480 cal yBP		shell scraper		freshwater crabs and snails
lower part of layer III				
26,104 ~ 36,701 cal yBP	infant atlas and rib(s)		extinct cervids	freshwater crabs and snails

Fig. 4. Notable remains obtained from Late Pleistocene layers of Sakitari Cave. The red square symbols in rightmost column indicate that seasonal hunting and gathering were suggested by size distribution of crabs and/or by isotopic analysis of freshwater snails, as described in SI Appendix, Faunal Analyses. (Scale bars, 1 cm.)

Fig. 5. Selected shell artifacts from the Pleistocene levels of Trench I. All the specimens are from Layer II unless indicated otherwise. Those portions with the arrows or squares are enlarged on the right. (A) Broken pieces of finished and unfinished fishhooks, (B) possible grind stone, (C) Veneridae shell scrapers shaped in a trapezoidal form, (D) shell scrapers of *Septifer bilocularis*, (E) two types of shell beads, (F) traces of grinding on the concave edge of a fishhook, (G) retouches on the concave edge of a bivalve shell tool, (H) use–wear (polish and striations) on the same edge as in G, (I) edge damages and striations on the ventral margin of a bivalve shell tool, and (J and K) ring-like striations on the inner side of the broken end of a tusk shell.

Importantly, the overall pattern of faunal food residue appears consistent throughout the documented terminal Pleistocene sequence, from lower Layer III to Layer I.

Discussion and Conclusions

Little has so far been known about the Paleolithic lifeways in the Ryukyu Archipelago, but the rich archeological evidence found from Sakitari Cave improves this situation substantially. Here, a chronologically successive record shows near-continuous occupation on the island since c. 35,000 cal BP. Although the density of the archeological remains varies, there are no noticeable changes in their compositions within the excavated sequence. Therefore, contrary to the previous predictions (13, 14), the Paleolithic people of Okinawa probably had sustained their life on this small, resource-poor island for about 25,000 y or more until Neolithic components first appeared at c. 10,000 cal BP. Alternatively, if the occupational record actually was truncated by short hiatuses, this would imply recurrent colonization by maritime people of similar subsistence strategies. Either possibility would have been accompanied by considerable technological sophistication and behavioral complexity, as discussed below.

First, instead of stones, the Paleolithic people here used seashells, often modifying them into standardized tool-forms to process organic materials. In eastern Asia, until now, knapped opercula of *Turbo* sp. and unmodified limpet shell tools dated to c. 35,000–30,000 cal BP (7, 8), from Gebe, a Wallacean island, have been the single documented case of shell tools predating 20,000 cal BP. The shell tools from Sakitari Cave, the second such example, are remarkable because they are more diverse, are standardized, and include morphologically unique examples. The use of seashells as raw materials may not be unique to *H. sapiens* because there is evidence that Neanderthals produced scrapers on shells as an alternative to stones at some Mediterranean coastal sites (23). However, the trapezoidal shell-scrapers from Sakitari Cave can be considered a unique invention that is not dependent on lithic industry templates.

Marine shell beads are reported from the Late Pleistocene modern human sites in Sri Lanka, Australia, and northern China (24–26), but have so far been unknown in southeastern Asia. The evidence reported here fills this void. Together with a recent report of perforated animal teeth and incised stones from northern Vietnam (27) and perforated *Nautilus* shell from Timor

(9), the Sakitari evidence substantiates the presence of ornament manufacturing and symbolism (28, 29) extending from Southeast Asia to the western Pacific coastal region.

The Sakitari seashell artifacts include the world's oldest fishhook, found in situ from a layer dated to 23,000 cal BP. These single-piece fishhooks, made of *Trochus* shells, are comparable or older in age than the similar fishhooks reported from Timor (~23,000–16,000 cal BP) (5) and New Ireland (c. 18,000–20,000 ¹⁴C BP) (30). The new Sakitari Cave evidence demonstrates that fishhook technology was widely distributed from Wallacea northward to the western Pacific margin by LGM times.

Another signal of complexity regards evidence for a sophisticated seasonal pattern of subsistence: Late Pleistocene seasonal

Fig. 6. Pieces of finished (*Upper*) and unfinished (*Lower*) fishhooks from Sakitari Cave.

hunting and gathering has been demonstrated in Tasmania (31) and suggested from Vietnam (27). The faunal remains from Sakitari Cave provide the first secure evidence of such behavior in the eastern Asian Paleolithic record. At Sakitari Cave, people knew the seasonal behaviors of aquatic animals (and perhaps also taste) and repeatedly visited the cave to target them at the best time of year.

In the context of modern human origins and dispersals, traces of early sophisticated behaviors have been widely acknowledged from the Late Pleistocene of Africa and through western to northern Eurasia (28, 32, 33), whereas paucity of such evidence from southeastern Asia has been a conundrum. However, recent studies highlight still sporadic but gradually accumulating signatures of modern behavior in this region. These examples include capturing arboreal animals (34) or fast-moving marine fish (5); use of bone and shell technology (5–9, 35); and use and possible processing of plants (36, 37), pigment (27, 36), and ornaments (27); as well as cultural adaptation to rainforest environment (38). The importance of aquatic foraging strategies in human evolution has been repeatedly mentioned (e.g., refs. 39–41). The findings from Sakitari Cave add to these and corroborate the idea that modern human behaviors in the southeastern to eastern Asia regions are difficult to detect archaeologically because of emphasis in technology based on nonlithic, perishable materials (6, 42).

Finally, our discoveries provide insights into the potential and extent of Paleolithic maritime culture. At this time, the oldest evidence for human presence in the central Ryukyu Archipelago comes from the Yamashita-cho Cave I site in Okinawa Island, dated to c. 36,000 cal BP from a single charcoal sample taken from well-stratified contexts but analyzed more than 40 y ago (43). The new dates from Sakitari Cave provide additional support for such an early timing of human occupation. This must have occurred via successive ocean crossings, probably from the south (44–47), the route of which were, in some places, more than 140–200 km distant without visible targets, and/or confronted by strong ocean currents (11). Further additions to the Ryukyu Archipelago case are the evidence of repeated narrow water crossing from the Korean Peninsula to Kyushu Island of Japan (48, 49), obsidian transport from an island south of central Honshu Japan (50), and the suggested modern human presence in northern Luzon by 30,000 cal BP (51). Overall, the evidence reported here, combined with the above emerging evidence, indicates that successful maritime adaptation was not restricted to Wallacea and northern Sahul, but was more widely distributed along the 8,000-km-long southwestern Pacific coastal region by ~35,000 cal BP.

Materials and Methods

General Information About Sakitari Cave. Sakitari Cave is a limestone cave located at the southern end of the Okinawa Island, 26° 08' 15" N and 127° 44' 57" E (Figs. 1 and 2). It is located about 1 km upstream from the Minatogawa Fissure site from where four relatively complete skeletons of modern humans were excavated during the 1970s, associated with charcoals dated to c. 20,000 cal BP. At Sakitari Cave, fragments of Neolithic Jomon potteries, lithic artifacts, and vertebrate remains had been collected by previous workers, but the presence of Late Pleistocene cultural strata was first demonstrated by our systematic excavation initiated in 2009. Much of the central area of the cave floor and parts of the cave entrances had been paved for tourism before our excavation, but we found undisturbed prehistoric sediments in recessed areas near the entrances (*SI Appendix, Figs. S1 and S2*). The present report focuses on Trench I and Pit 1 near the west entrance. At present, terminal Pleistocene strata are minimally exposed at Trenches II and III.

Excavation Methods. We first dug a 1 × 2 m pit, Pit 1, to the depth of 2.5 m below the ground surface immediately inside the west entrance. Then we dug a 2.5 × 3 m trench, Trench I, which partially overlaps Pit 1, to the depth of 1.5 m (Fig. 2 and *SI Appendix, Figs. S1 and S2*). Excavation was carried out following stratigraphic layers, not by vertical levels. Soft brushes and bamboo skewers were used to dig the relatively incompact Late Pleistocene strata (Layers I–III described later) to recover the majority of the artifacts and osseous

remains in situ. All the excavated sediments were brought to the laboratory for water screening with 0.5–3 mm mesh. All Pleistocene layers of Trench I and Pit 1 were dug by three researchers (M.F., S.Y., and C.K.) spending 505 d on site.

Dating Methods. Woody charcoal, crab shell, snail shell, and marine shell samples collected in situ from the stratigraphic layers were radiocarbon dated, using accelerator mass spectrometry at the Micro Analysis Laboratory, Tandem Accelerator, the University of Tokyo, and Paleo Laboratory Co., Japan (*SI Appendix, Table S1*). Direct ^{14}C dating of human and other vertebrate remains were unsuccessful because of poor collagen preservation. ^{14}C dates were calibrated using the calibration program OxCal v4.2.3 (c14.arch.ox.ac.uk) based on the IntCal13 calibration curve for the charcoal, land snail, and freshwater snail and crab samples, and based on the Marine13 data set for the marine shell samples. We used the Marine13 calibration curve for brackish-water shells (*Geloina erosa*), assuming they lived in 100% marine water environments, although no data are available for the percentage contribution of freshwater to their habitats.

Observation and Experiment on the Shell Artifacts. All seashell fragments were sorted into Bivalvia, Scaphopoda, and Gastropoda (*SI Appendix, Table S2*). To evaluate authenticity and function of the shell artifacts, macroscopic and microscopic use–wear traces were examined using a metallographic microscope Olympus BXFM and a digital microscope Keyence VHX-600, at magnifications ranging from 25× to 500× (*SI Appendix, Figs. S4–S7*).

Although the experimental use–wear analysis of stone artifacts has a half-century history (52–58), few systematic studies on use–wear patterns of shell tools have been undertaken (but see refs. 59–61). Hence, a preliminary experimental program was undertaken to better understand use–wear formation on the Sakitari Cave shell tools. First, we broke and knapped modern shells of Veneridae (*Meretrix petechialis*) to obtain fragments similar to the Sakitari Cave Veneridae tools. The broken edges thus produced were then used to process antlers, bones, hides, bamboos, and woods (*SI Appendix, Fig. S4*). The use–wear created on these experimental specimens were compared with those observed on the archaeological shell specimens.

Faunal Analyses. Animal remains were sorted into the following taxonomic categories; extinct cervids, wild boar, unidentifiable medium-sized mammals, small mammals (rodents and insectivores), birds, reptiles (lizards and snakes), frogs, freshwater fish (eel), marine fish, unidentifiable fish, unidentifiable small vertebrates, freshwater crabs (Japanese mitten crab, *E. japonica*), freshwater snails (*S. libertina*), and land snails (six species were identified). We counted the minimum number of individuals for the crabs, freshwater snails, and land snails, and the NISP for the other animal taxa (*SI Appendix, Fig. S8 and Table S4*). Some of these animal remains exhibit dark colors. To examine whether this indicates burning, we carried out an X-ray diffraction analysis of freshwater snail samples. A black-colored and a white-colored snail shell excavated from Layer II were powdered and analyzed by a Rigaku X-ray Diffractometer RINT 2100 V (Kyushu University), using $\text{CuK}\alpha$ radiation (40.0 kV, 30.0 mA), in a step of 0.02°, with a scan speed of 2°/min (*SI Appendix, Fig. S9*).

Two analyses were made to examine the seasonality of the hunting and collecting activity at Sakitari Cave. First, we investigated size variation of *E. japonica*, using its carapace width as a parameter. Because almost all of the crab remains from Sakitari Cave were pincers, their carapace widths were estimated from the lengths of the movable pincers, using allometric equation derived from 14 modern individuals (seven males and seven females) captured in the Ryukyu Archipelago. Here, the male and female individuals were pooled because it was impossible to identify sex for the archaeological crab remains. The resultant equation, $y = 1.36x + 2.71$ (x , movable pincer length; y , carapace width; $r^2 = 0.985$), was applied to 709 movable pincers from Sakitari Cave.

Second, oxygen isotopic analysis was carried out on 35 freshwater snail specimens (20 from Layer II and 15 from Layer I) to investigate the water temperature and the seasons at their death. For each specimen, about 25 samples were taken, using a dental drill along the spiral growth axis of the whorl, from the outer lip toward the apex, at 2-mm intervals. The analysis was performed by a mass spectrometer (Finnigan MAT Delta Plus) accompanied by a Gas Bench. This system measures isotopic ratio of CO_2 generated by acid reaction (purified H_3PO_4 at 50 °C for 3 h) in a glass vial filled with He gas. Obtained oxygen isotopic values are expressed in parts per thousand relative to Vienna Pee Dee Belemnite ($\delta^{18}\text{O}$ vs. Vienna Pee Dee Belemnite). Repeated measurements of the laboratory standard typically show reproducibility of ~0.2‰ (2 σ). More details about the analytical methods are available in ref. 62.

ACKNOWLEDGMENTS. We thank Nanto Co. Ltd. for the permission of excavation at Sakitari Cave. Part of this study was conducted under the

Grant-in-aid for Scientific Research (Nos. 23905004 and 25905002) from the Japan Society for the Promotion of Science.

- O'Connell JF, Allen J (2015) The process, biotic impact, and global implications of the human colonization of Sahul about 47,000 years ago. *J Archaeol Sci* 56:73–84.
- Higham TFG, et al. (2009) Radiocarbon dating of charcoal from tropical sequences: Results from the Niah Great Cave, Sarawak, and their broader implications. *J Quaternary Sci* 24(2):189–197.
- O'Connell JF, Allen J, Hawkes K (2010) Pleistocene Sahul and the origins of seafaring. *The Global Origins and Development of Seafaring*, eds Anderson A, Barrett JH, Boyle KV (McDonald Institute for Archaeological Research, Cambridge, UK), pp 57–68.
- O'Connor S (2010) Pleistocene migration and colonization in the Indo-Pacific region. *The Global Origins and Development of Seafaring*, eds Anderson A, Barrett JH, Boyle KV (McDonald Institute for Archaeological Research, Cambridge, UK), pp 41–55.
- O'Connor S, Ono R, Clarkson C (2011) Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. *Science* 334(6059):1117–1121.
- O'Connor S, Robertson G, Aplin KP (2014) Are osseous artefacts a window to perishable material culture? Implications of an unusually complex bone tool from the Late Pleistocene of East Timor. *J Hum Evol* 67:108–119.
- Szabó K, Brumm A, Bellwood P (2007) Shell artefact production at 32,000–28,000 BP in Island Southeast Asia: Thinking across media? *Curr Anthropol* 48(5):701–723.
- Szabó K, Brent K (2015) Limpet shells as unmodified tools in Pleistocene Southeast Asia: An experimental approach to assessing fracture and modification. *J Archaeol Sci* 54:64–76.
- Langley MC, O'Connor S, Piotto E (2016) 42,000-year-old worked and pigment-stained *Nautilus* shell from Jerimalai (Timor-Leste): Evidence for an early coastal adaptation in ISEA. *J Hum Evol* 97:1–16.
- Clark PU, et al. (2009) The Last Glacial Maximum. *Science* 325(5941):710–714.
- Kaifu Y, Fujita M, Yoneda M, Yamasaki S (2015) Pleistocene seafaring and colonization of the Ryukyu Islands, Southwestern Japan. *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*, eds Kaifu Y, Izuhu M, Goebel T, Sato H, Ono A (Texas A&M Univ Press, College Station, TX).
- Kawamura A, Chang CH, Kawamura Y (2015) Middle Pleistocene to Holocene mammal faunas of the Ryukyu Islands and Taiwan: An updated review incorporating results of recent research. *Quat Int* 397:117–135.
- Takamiya H (1996) Initial colonization, and subsistence adaptation processes in the late prehistory of the Island of Okinawa. *Indo-Pacific Prehistory Assoc Bull* 15:143–150.
- Bellwood P (2015) Migration and the origins of *Homo sapiens*. *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*, eds Kaifu Y, Izuhu M, Goebel T, Sato H, Ono A (Texas A&M Univ Press, College Station, TX).
- Bellwood P (1997) *Prehistory of the Indo-Malaysian Archipelago* (Univ of Hawai'i Press, Honolulu).
- Haidle MN, Pawlik AF (2010) Pleistocene modernity: An exclusively Afro-European issue? An introduction to Session A1. *IPPA Bull* 30:3–8.
- Barker G, et al. (2013) The Niah Caves, the 'human revolution', and foraging/farming transition in Island Southeast Asia. *Reforest Foraging and Farming in Island Southeast Asia*, ed Barker G (McDonald Institute for Archaeological Research, Cambridge, UK), pp 341–366.
- Simanjuntak T, Sémah F, Sémah A-M (2015) Tracking evidence for modern human behavior in Paleolithic Indonesia. *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*, eds Kaifu Y, Izuhu M, Goebel T, Sato H, Ono A (Texas A&M Univ Press, College Station, TX).
- Yamasaki S, et al. (2012) Excavations (2009–2011) at Sakitari-do cave site, Nanjo city, Okinawa prefecture—A new late Pleistocene paleoanthropological site. *Anthropol Sci* 120:121–134.
- Yamasaki S, Fujita M, Katagiri C, Kurozumi T, Kaifu Y (2014) Human use of marine shells from Late Pleistocene layers of Sakitari-do cave site, Nanjo city, Okinawa prefecture. *Anthropol Sci* 122(1):9–27.
- Erlandson JM, Moss ML (2001) Shellfish feeders, carrion eaters, and the archaeology of aquatic adaptations. *Am Antiq* 66(3):413–432.
- Kobayashi S (2011) Growth patterns of the Japanese mitten crab *Eriocheir japonica* (de Haan) in its river phase in Fukuoka Prefecture, Japan. *J Crustac Biol* 31(4):653–659.
- Douka K, Spinapolice EE (2012) Neanderthal shell tool production: Evidence from Middle Palaeolithic Italy and Greece. *J World Prehist* 25(2):45–79.
- Perera N, et al. (2011) People of the ancient rainforest: Late Pleistocene foragers at the Batadomba-lena rockshelter, Sri Lanka. *J Hum Evol* 61(3):254–269.
- Habgood PJ, Franklin NR (2008) The revolution that didn't arrive: A review of Pleistocene Sahul. *J Hum Evol* 55(2):187–222.
- Pei WC (1939) The Upper Cave Industry of Choukoutien. *Palaeontologia Sinica New Ser. D* 9:1–58.
- Nguyen V (2015) First archeological evidence of symbolic activities from the Pleistocene of Vietnam. *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*, eds Kaifu Y, Izuhu M, Goebel T, Sato H, Ono A (Texas A&M University Press, College Station, TX).
- McBrearty S, Brooks AS (2000) The revolution that wasn't: A new interpretation of the origin of modern human behavior. *J Hum Evol* 39(5):453–563.
- Kuhn SL, Stiner MC (2007) Body ornamentation as information technology: Toward an understanding of the significance of early beads. *Rethinking the Human Revolution*, eds Mellars P, Boyle K, Bar-Yosef O, Stringer C (McDonald Institute for Archaeological Research, Cambridge, UK), pp 45–54.
- Smith A, Allen J (1999) Pleistocene shell technologies: Evidence from Island Melanesia. *Australian Coastal Archaeology*, eds Hall J, McNiven (Australian National University, Canberra, Australia), pp 291–297.
- Pike-Tay A, Cosgrove R, Garvey J (2008) Systematic seasonal land use by late Pleistocene Tasmanian Aborigines. *J Archaeol Sci* 35(9):2532–2544.
- Mellars P, Boyle K, Bar-Yosef O, Stringer C, eds (2007) *Rethinking the Human Revolution* (McDonald Institute for Archaeological Research, Cambridge, UK).
- Klein RG (2009) *The Human Career* (Univ of Chicago Press, Chicago), 3rd ed, p 989.
- Piper PJ, Rabbett RJ (2014) Late Pleistocene subsistence strategies in Island Southeast Asia and their implications for understanding the development of modern human behaviour. *Southern Asia, Australia and the Search for Human Origins*, eds Dennell R, Porr M (Cambridge Univ Press, Cambridge, UK), pp 118–134.
- Rabbett R (2005) The early exploitation of Southeast Asian mangroves: Bone technology from caves and open sites. *Asian Perspect* 44(1):154–179.
- Reynolds T, et al. (2013) The first modern humans at Niah, c. 50,000–35,000 years ago. *Reforest Foraging and Farming in Island Southeast Asia*, ed Barker G (McDonald Institute for Archaeological Research, Cambridge, UK), pp 135–172.
- Barton H, et al. (2013) Late Pleistocene foragers, c. 35,000–11,500 years ago. *Reforest Foraging and Farming in Island Southeast Asia*, ed Barker G (McDonald Institute for Archaeological Research, Cambridge, UK), pp 173–215.
- Roberts P, et al. (2015) Direct evidence for human reliance on rainforest resources in late Pleistocene Sri Lanka. *Science* 347(6227):1246–1249.
- Erlandson JM (2001) The archaeology of aquatic adaptations: Paradigms for a new millennium. *J Archaeol Res* 9:287–350.
- Erlandson JM (2010) Food for thought: The role of coastlines and aquatic resources in human evolution. *Human Brain Evolution*, eds Cunnane SC, Stewart KM (John Wiley & Sons, Inc., Hoboken, NJ), pp 125–136.
- Erlandson JM, Fitzpatrick SM (2006) Oceans, islands, and coasts: current perspectives on the role of the sea in human prehistory. *J Island Coast Archaeol* 1(1):5–32.
- Langley MC, Clarkson C, Ulm S (2011) From small holes to grand narratives: The impact of taphonomy and sample size on the modernity debate in Australia and New Guinea. *J Hum Evol* 61(2):197–208.
- Kaifu Y, Fujita M (2012) Fossil record of early modern humans in East Asia. *Quat Int* 248:2–11.
- Suzuki H (1982) The Minatogawa Man. *Bull Univ Museum* 19:7–49.
- Baba H, Narasaki S, Ohyama S (1998) Minatogawa hominid fossils and the evolution of Late Pleistocene humans in East Asia. *Anthropol Sci* 106:27–45.
- Kaifu Y, Fujita M, Kono RT, Baba H (2011) Late Pleistocene modern human mandibles from the Minatogawa Fissure site, Okinawa, Japan: Morphological affinities and implications for modern human dispersals in East Asia. *Anthropol Sci* 119:137–157.
- Suwa G, Fukase H, Kono RT, Kubo D, Fujita M (2011) Mandibular tooth root size in modern Japanese, prehistoric Jomon, and Late Pleistocene Minatogawa human fossils. *Anthropol Sci* 119(2):159–171.
- Norton CJ, Jin JH (2009) The evolution of modern human behavior in East Asia: Current perspectives. *News Rev (Melb)* 18(6):247–260.
- Morisaki K (2015) Appearance of Hakuhen-Sentoki (HS Points) and second modern human migration into Kyushu, Japan. *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*, eds Kaifu Y, Izuhu M, Goebel T, Sato H, Ono A (Texas A&M Univ Press, College Station, TX).
- Ikeya N (2015) Maritime transport of obsidian in Japan during the Upper Paleolithic. *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*, eds Kaifu Y, Izuhu M, Goebel T, Sato H, Ono A (Texas A&M Univ Press, College Station, TX).
- Mijares ASB (2008) The Late Pleistocene to early Holocene foragers of northern Luzon. *Bull IPPA* 28:99–107.
- Semenov SA (1964) Prehistoric technology: An experimental study of the oldest tools and artefacts from traces of manufacture and wear (Cory, Adams & Mackay, London, United Kingdom).
- Tringham R, Cooper G, Odell G, Voytek B, Whitman A (1974) Experimentation in the formation of edge damage: A new approach to lithic analysis. *J Field Archaeol* 1(1/2):171–196.
- Keeley LH (1980) *Experimental Determination of Stone Tool Uses: A Microwear Analysis* (Univ. of Chicago Press, Chicago).
- Vaughan PC (1985) *Use-Wear Analysis of Flaked Stone Tools* (Univ of Arizona Press, Tucson).
- Van Gijn AL (1990) The wear and tear of flint: Principles of functional analysis applied to Dutch Neolithic assemblages. *Annales Préhistoriques et Archéologiques* 22:1–181.
- Rots V (2010) *Prehension and Hafting Traces on Flint Tools: A Methodology* (Luvén Univ Press, Leuven, Belgium).
- Sano K (2012) *Functional variability in the Late Upper Palaeolithic of North-Western Europe* (Rudolf Habelt, Bonn).
- Luik H, Choyke AM, Batey C, Lougas L (2005) From hooves to horns, from mollusc to mammoth: Manufacture and use of bone artefacts from prehistoric times to the present. *Proceedings of the 4th Meeting of the ICAZ Worked Bone Research Group at Tallinn* (Tallinn Book Printers Ltd., Tallinn, Estonia), pp 319–324.
- Lammers-Keijsers YMJ (2007) *Tracing Traces From Present to Past: A Functional Analysis of Pre-Columbian Shell and Stone Artefacts From Anse à la Gourde and Morel, Guadeloupe, FWI*. (Leiden Univ Press, Leiden, The Netherlands).
- Cuenca Solana D, Gutiérrez Zugasti I, Conte IC (2011) The use of mollusc shells as tools by coastal human groups: The contribution of ethnographical studies to research on Mesolithic and early Neolithic technologies in Northern Spain. *J Anthropol Res* 67:77–102.
- Hori M, Hoshino K, Okumura K, Kano A (2008) Seasonal patterns of carbon chemistry and isotopes in tufa depositing groundwaters of southwestern Japan. *Geochim Cosmochim Acta* 72(2):480–492.
- Ryan WBF, et al. (2009) Global multi-resolution topography synthesis. *Geochim Geophys Geosyst* 10(3):Q03014.