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Chapter

# The Migration, Culture, and Lifestyle of the Paleolithic Ryukyu Islanders

Masaki Fujita, Shinji Yamasaki and Ryohei Sawaura

### Abstract

Roughly 35,000 years ago, hunting-fishing-gathering people occupied the Ryukyu Islands of Japan, a chain of small-sized islands in the western Pacific. There are Paleolithic sites scattered over most of the relatively large islands, thereby suggesting an extensive human dispersal over the sea at least 30,000 years ago. Recent morphological and genetic studies of the human fossils found in this area revealed that Paleolithic occupants might have an affinity with the modern and prehistoric populations of Southeast Asia. Recent excavation of Paleolithic sediments at Sakitari Cave, Okinawa Island, provided a variety of shell artifacts, including beads, scrapers, and fishhooks, and evidence of seasonal consumption of aquatic animals, especially freshwater crabs. The Paleolithic Ryukyu Islanders' culture and lifestyle, which made use of unique resources, demonstrate behavioral adaptations to living on relatively small islands.

**Keywords:** Paleolithic, Ryukyu Islands, maritime adaptation, human remains, material culture, shell artifacts, aquatic animals, seasonality

### 1. Introduction

Intensive immigration to the island is a tremendous environmental adaptation achieved by *Homo sapiens* [1]. Recently, pre-sapiens hominin has been reported to enter the islands [2–4]. But *H. sapiens* has been much more aggressive in immigrating to the islands, especially relatively small and remote islands [5], and utilization of marine resources even at the late Pleistocene [6–10]. Intensive colonization to the island demands complex planning and technological innovation such as seagoing craft, navigation on the ocean, adaptation to unfamiliar fauna, flora, and landscapes [1, 5].

The Ryukyu Islands are one of the oldest oceanic islands to which Pleistocene people immigrated, comparable with the islands of Southeast Asia [1, 11]. Early modern humans inhabited this area no later than 30,000 years ago and probably earlier than 36,500 years ago [1, 11, 12]. The Paleolithic sites cover most of the relatively large islands of this area (**Figure 1**, **Table 1**). The human remains found in this area consist of male and female adults, and children [13–16]. These facts suggest the intentional voyages of early modern humans with their families to the islands.

In Australia, researchers found evidence of the oldest voyage in the world from the islands of Southeast Asia; that voyage occurred earlier than 50,000 years ago [17, 18]. The maritime technology for open sea fishing seems to have been developed prior to the journey, as reported in the case of Timor [19]. Although the use of aquatic resources by early modern human developed before Out-of-Africa,



#### Figure 1.

Paleolithic sites of the Ryukyu archipelago. The white circle represents the sites with stone tools, and the black circle represents the sites with human remains. The dark gray area represents the current land, and the light gray area represents the contour at 120 m depth.

Region	Site	Island	Area of the island	Age of the oldest layer	Artifacts	Human remains
Northern Ryukyus	Tachikiri	Tanega- shima	444 km <sup>2</sup>	35k	Cobble tools, grinding stones, polished adze blades, flakes	
_	Yokomine C	Tanega- shima	444 km <sup>2</sup>	35k	Cobble tools, grinding stones, flakes, anvil stones	
Central Ryukyus	Tsuchihama- Yaya	Amami-O- shima	712 km <sup>2</sup>	>30k?	Shale flakes	
	Kishikawa	Amami-O- shima	712 km <sup>2</sup>	30k?	Chert flakes	
	Amangusuku	Tokuno- shima	248 km <sup>2</sup>	>30k?	Chert flakes	7 [] [
_	Garazo	Tokuno- shima	248 km <sup>2</sup>	>30k?	Granite and sandstone cobbles	
_	Yamashita- cho Cave 1	Okinawa	1,207 km <sup>2</sup>	36k	Sandstone cobbles	Partial infant
_	Sakitari Cave	Okinawa	1,207 km <sup>2</sup>	35k	Shell artifacts and sandstone (whetstone) (23k~20k) Quartz flakes (16k~14k)	Partial adults and infants (14k~16k, 23k, 30k)
_	Minatogawa	Okinawa	1,207 km <sup>2</sup>	20k~23k		Four adults
	Shimojibaru	Kume-jima	56 km <sup>2</sup>	18k		Infant

Region	Site	Island	Area of the island	Age of the oldest layer	Artifacts	Human remains
Southern Ryukyus	Pinza-abu	Miyako	158 km <sup>2</sup>	29k~32k		Partial adult(s)
	Shiraho- Saonetabaru Cave	Ishigaki	223 km <sup>2</sup>	27k		Four adults and more (18k~27k)
<b>Table 1.</b> Paleolithic sites	of the Ryukyu Isla	ands.				

much earlier than 100,000 years ago [20–22], the populations who came to Islands Southeast Asia (ISEA), in the course of the worldwide dispersal of early modern humans, may have developed much more extensive uses of marine resources [19, 23–26].

Developed maritime technology and flexible resource usage would have enabled Paleolithic people to advance into the island environment beyond the tropical zone. The Ryukyu Islands consist of relatively small islands that are distributed on the margins of the tropical to temperate zone, and which are isolated from each other and mainland Japan. Natural resources such as stone materials and terrestrial animals differ among the islands. Between 30,000 and 36,500 years ago, Paleolithic people immigrated to these variable islands, which spread over 1200 km. Their entry into these diverse environments for a relatively short period provides evidence of the malleable behavior of the early modern humans who adapted to these islands. The purpose of this paper is to review the Paleolithic archeological sites of the Ryukyu Archipelago and to clarify how people adapted to sub-tropical remote islands with limited resources, especially in contrast with the ISEA, thus providing the basis for the global distribution of Paleolithic people.

#### 2. Geographic setting and paleofauna of the Ryukyu Islands

The chain of Ryukyu Islands stretches roughly 1200 km between Kyusyu Island of Japan and Taiwan in the west Pacific. More than 150 relatively small islands (<1207 km<sup>2</sup>) are dispersed from the northeast to the southwest at roughly 27° north in latitude (**Figure 1**). A dry and sandy climate generally exists at this latitude around the world, but the Ryukyus are covered with subtropical forests nourished by the hot and humid atmosphere created by the Kuroshio ocean current.

Previously, the Ryukyu Islands were at the eastern end of the Eurasian continent. The tectonic plate movements of the Eurasian and Philippine plates formed the deep ocean basin named the "Okinawa trough" to the west of the Ryukyus and divided the islands from the continent. This geological event probably occurred no later than the early Pleistocene [27]. Today the islands are divided into three parts by the sea, which is over 1000 meters deep: the northern, central, and southern Ryukyus. Some of the northern Ryukyu Islands were connected to the Kyushu Island of Japan during the Last Glacial Maximum (LGM) around 20,000 years ago. The fauna and prehistoric culture of these islands were closely related to those of Kyusyu. By contrast, the central and the southern Ryukyus were isolated throughout the Pleistocene.

The islands now are located at the margin of two biogeographic areas: the Oriental and Sino-Japanese regions [28]. The fauna and flora of the Ryukyus



#### Figure 2.

Overviewed stratigraphy of the Minatogawa site. The uppermost part of the fissure deposit contained Holocene Jomon. The lower level (layers III and IV) contained late Pleistocene animal and human fossils. Although only medium-sized animals are drawn in the figure, many small animal fossils were found in the lower deposit.

gradually shifted from Sino-Japanese species to Oriental species from the north to the south. The basis of the terrestrial fauna was formed before the isolation from the Eurasian Continent in the early Pleistocene [29–31].

Nearly two million years of isolation have fostered many of the islands' endemic animals. Today, the fauna of the Ryukyus consists of many endemic small animals but lacks large and middle-sized animals except for the wild boar. The late Pleistocene fauna throughout the islands has not been studied thoroughly; it has only been cursorily reviewed by several authors [31–33]. The consensus is that the Pleistocene fauna was similar to the existing fauna of each island. There were several middle-sized animals that are now extinct: one or two species of middle-sized deer and a species of middle-sized tortoise. They became extinct almost simultaneously at the end of the Pleistocene, but the precise timing of extinction is not known yet.

The flora of the Pleistocene Ryukyus was shrouded in mystery. Kuroda and Ozawa (1998) studied pollen samples obtained from a boring core specimen extracted from Izena Island, which is northwest of Okinawa Island [34]. They suggested that the evergreen broad-leaved forest reduced in size and the pine tree became dominant during the LGM. However, the composition of the terminal-Pleistocene fossil-amphibian species of the southern area was similar to the modern fauna of the northern broad-leaved evergreen forest area of Okinawa Island [35]. A dominance of forest species is also reported among avifauna [36, 37], reptiles, and mice [38–40] at the Minatogawa site, a terminal-Pleistocene site of Okinawa Island (**Figures 1** and **2**, **Table 1**). Based on the composition of these fossil species, we can assume that a large area of Okinawa Island was covered with a broad-leaved evergreen forest during the late Pleistocene and even the LGM period.

# 3. A possible migration route estimated from the Phylogenetic studies of Paleolithic Ryukyu Islanders

Limestone is widely dispersed throughout the Ryukyu Islands, especially in the southwestern half of them. Karstic caves are well suited for preserving

bone remains, and there are many Pleistocene fossil sites. Paleolithic research in the Ryukyu Islands began with the discovery of human bone fragments that were mixed with extinct animal fossils in several karstic caves [13]. After the discovery of these partial human fossils, researchers began an exhaustive survey for Paleolithic human remains. In 1970, four well-preserved adult human fossils were discovered at the Minatogawa site, Okinawa Island. The Minatogawa human fossils were about 20,000 years old based on the Carbon-14 dating of the charcoal obtained in their vicinity (Figure 2) [14, 41, 42]. Their morphological features and phylogenetic positions were investigated primarily through morphological studies. The Minatogawa human had many morphological traits such as relatively short stature, short clavicles, and a slender upper body with relatively robust lower limb bones. They differ from those of Jomon people, the Holocene hunting-gathering-fishing people who lived in the Japanese Archipelago including the Ryukyu Islands, from 3000 to 15,000 years ago [43–45]. Despite these differences, the Minatogawa people were previously considered ancestors of Jomon and modern Japanese people, based mainly on the morphological characteristics of the skull [14, 44, 45].

In the 2000s, researchers conducted a more detailed comparison of the Minatogawa human fossils and a relatively larger sample of Jomon and modern Japanese people using newly developed methods such as three-dimensional scanning and computed tomography. These studies indicated that there are many differences between the Minatogawa humans and the Jomon/Modern Japanese people even in the skull morphology, including the length and thickness of tooth roots [46], the three-dimensional morphology of the glabellar region [47], the shape of the braincase [48], and the mandible shapes [49]. If there are so many differences, we may need to reconsider the traditional hypothesis that the Minatogawa people were a direct ancestor of Jomon and modern Japanese people.

Genetic analysis of modern Okinawan people also suggests the weakness of the relationship between the Pleistocene and Holocene populations of the Ryukyu Islands. Sato et al. indicated that modern Okinawan people diverged from the continental group (Han Chinese) more recently than 15,000 years ago, based on a comparison of the modern Okinawan genome [50]. If so, the Paleolithic people who had lived in the Ryukyus before this divergence would have little or no genetic contribution to the present population of Okinawa.

Then, is there an affinity between the Minatogawa people and the surrounding populations? Kaifu et al. suggested that their slender mandible morphology may be similar to that of the modern Australo-Melanesian who are found throughout parts of Southeast Asia and Oceania today [49]. A morphological study of the recently unearthed 27,000-year-old human skull from Shiraho-Saonetabaru Cave in Ishigaki Island suggests a possible relationship between Paleolithic Ryukyu Islanders and prehistoric Southeast Asians. Kono et al. pointed out that the Paleolithic skull of the Shiraho-Saonetabaru showed a morphological similarity to that of the Mesolithic Vietnamese [51]. This result coincides with the results of ancient mtDNA analyses of two other Paleolithic human bone fragments obtained from the same site. The haplotypes B4 and R were obtained in the mtDNA analyses [52]. The current center of the distribution of haplotype B4 is in Southeast Asia, and that of haplotype R is an ancestral haplotype of the haplogroup that includes European, Southeast Asian, and Australian Aboriginal people [52].

In summary, these results indicate that Paleolithic people traveled to the Ryukyu Islands through Southeast Asia after leaving Africa. They appear to have little or no similarity with the Holocene populations of the Japanese Archipelago in terms of morphological and genetic traits. However, morphological and genetic research of Paleolithic people from this area is still underway. The recent excavation at Sakitari



#### Figure 3.

Section of trench I and pit 1 of Sakitari cave. Partial human remains and animal remains consumed by humans were obtained from layers I to III. Artifacts were unearthed from layers I and II (see also **Figure 4**).

Cave indicates that Paleolithic people occupied Okinawa Island almost continuously from 30,000 to 13,000 years ago (**Figure 3**). Studies of the other Paleolithic individuals excavated from Shiraho-Saonetabaru Cave and the human bones recently discovered in Sakitari Cave near the Minatogawa site will provide insight into this problem in the near future.

#### 4. Material culture of Paleolithic Ryukyu Islands

In contrast to the relatively good preservation of human bone, few artifacts have been found from the Paleolithic sites of the Ryukyu Islands. Small amorphous flakes made of chert, quartz, and shales and sandstone cobble tools were found at several sites. Notably, several types of flake tools, which are often discovered at Paleolithic sites in mainland Japan, are restricted to islands north of Tokunoshima (**Table 1**). No chipped stone tools of Paleolithic age have been found from Okinawa or other southern islands.

All the stone materials were available at surrounding area of each site, and no obvious oversea transportation of stone material is known in the Paleolithic Ryukyu Islands. It seems a strange phenomenon since Paleolithic people came across the sea to the Ryukyu Islands and probably were familiar with maritime technologies, including oversea voyage [1, 11]. In mainland Japan, Paleolithic people translocated obsidians beyond the sea [53]. Although the possible oversea transportation of wild pigs more than 20,000 years ago is suggested in the southern and the central Ryukyus [31, 54], it is controversial as discussed later.

The small amorphous flakes and cobble tools are not suitable for typological study or analysis of usage. The Paleolithic and Neolithic cultures of the northern Ryukyus were closely related to those of Kyusyu Island, Japan, as mentioned above. However, the cultures of the central and southern Ryukyus have little in common with them. In the Holocene, the Jomon and subsequent mainland Japanese cultures influenced the prehistoric cultures of the central Ryukyus. In the southern Ryukyus, endemic prehistoric culture continued until 1000 years ago. After the tenth century, the inhabitants eventually constructed a cultural network

throughout the Ryukyus. Cultural exchange across islands was difficult in prehistoric times. In summary, the Paleolithic people and culture of the central and the southern Ryukyus seem different from those of mainland Japan, probably because of the difficulty in oversea voyage between the islands.

The material culture of the Paleolithic Ryukyu Islands was a mystery until the authors and colleagues found a variety of shell artifacts and stone tools in the Paleolithic sediments of Sakitari Cave, Okinawa Island (**Figure 4**) [16, 55, 56]. The shell artifacts uncovered from the 20,000 to 23,000-year-old sediments (layer II) of Sakitari Cave consist of fishhooks, two types of scrapers, and two types of beads. The fishhooks were made of *Trochus* shells, similarly to the hooks found in the Paleolithic site of Timor [19]. Therefore, the fishhook technology distributed around the western Pacific might be related to each other, though the locations of the sites differ; Sakitari Cave is a riverside cave and a seasonal campsite for seeking freshwater animal resources such as crabs and snails [16], while the Asitau kuru (Jerimalai Shelter), Timor, is a coastal site for marine resources such as fish and shellfish [5, 19, 57].

The Sakitari assemblage is unique in its lack of stone tools. There were three 13,000-year-old amorphous quartz flakes [55] and a 23,000-year-old tiny fragment of sandstone, which probably was used to grind fishhooks [16]. The Paleolithic stone artifacts of Sakitari Cave consist of only these four items, while many more shell artifacts were unearthed from the same sediments (**Figure 4**). Paleolithic shell flakes were reported in *Homo sapiens* sites of Philippines [58] and Indonesia [59] dating back to 30,000 years ago. It is known that pre-sapiens hominin also uses shellfish tools [60], so it may be difficult to talk about the relevance of culture with shellfish tools alone. But the Paleolithic culture of ISEA and Okinawa seems similar in terms of shell flakes and fishhooks.

However, Sakitari assemblage is quite unique in the dominance of shell artifacts. It probably is linked to the distribution of stone and shell materials on the island. There is no good stone material for making tools except the low-quality chert and small-sized quartz, which are available only in the northern half of Okinawa Island. In contrast to this stone distribution, shells are abundantly available on the island, especially in the coastal area. Sakitari Cave is located at the southern end of



#### Figure 4.

Isolated human teeth and artifacts obtained from layer II (20,000–23,000 years ago; a-p) and layer I (13,000–16,000 years ago; q-v) of Sakitari cave. (a) Human tooth (right lower third molar), (b) shell fishhook, (c-i) bivalve shell scraper (Callista chinensis), (j, k) bivalve shell scraper (Septifer bilocularis), (l, m) bivalve shell bead (Sunetta kirai), (n-p) Scaphopoda bead, (q) human tooth (right upper deciduous canine), (r-t) quartz flake, (u, v) snail shell bead (Pyrene testudinaria).

Okinawa Island, a stone-poor region. At present, it is about 2 km inland from the nearest coast, and it was 5–6 km away from the coast around 20,000–23,000 years ago. Therefore, the Paleolithic people of Sakitari Cave were able to access the coast easily and collect shells and other marine products such as fish. The unique material culture of Sakitari Cave was suitable for the island environment, and it represents the behavioral plasticity of the Paleolithic people and their capacity to adapt to the stone-poor, shell-rich island environment of Okinawa.

## 5. Plastic behavior in the utilization of animal resources

The behavioral plasticity of Paleolithic people is observable in their material culture and hunting-gathering actions. The Paleolithic people in Sakitari Cave mostly consumed freshwater crabs (Japanese mitten crab) and freshwater snails. They also ate small vertebrates such as mice, birds, lizards, snakes, frogs, and fish (freshwater and marine). The food waste in Sakitari indicates that small, nocturnal animals living in or near the river were dominant. As in the general example of island fauna, the fauna of Okinawa Island lacks large terrestrial mammals (Figure 5). At the first stage of human arrival, there were two species of middle- or small-sized deer and one species of a middle-sized tortoise [33], but they went extinct probably earlier than 30,000 years ago [42, 54]. Based on the limitedness of the terrestrial fauna, some researchers theorize that Paleolithic people were unable to maintain their population on the small island [61, 62]. However, research of the Sakitari remains revealed that the Paleolithic people maintained their population for nearly 20,000 years by consuming small, aquatic animals, which generally are highly reproductive and densely inhabited the area compared to large and middle-sized mammals. This unique, effective use of animal resources enabled the Paleolithic hunter-gatherers to live on relatively small islands for a long time.

The extensive consumption of marine resources was reported in ISEA [19, 23–26]. Paleolithic immigrants who came to this area developed diverse fishing and shellfishing



**Figure 5.** *Terrestrial and freshwater animals of Okinawa Island.* 

activity. The exploitation of variety of marine resources may be one of the factors that enabled Paleolithic migration to the variety of islands. As indicated by the studies on human remains and shell artifacts, relation between Okinawa and ISEA is suggested again in the viewpoint of aquatic resource usage. However, dominance of the freshwater animals is the unique point of Paleolithic Okinawa. One reason may be the limited terrestrial animals, and another reason may be seasonality. The oxygen isotope study on freshwater snails indicated that these freshwater animals were consumed mainly in autumn [16]. Paleolithic people of Okinawa may have used more marine resources in other seasons, though we do not have any evidence at present.

Another notable behavior of Paleolithic Ryukyu Islanders is the possible translocation of wild pigs earlier than 20,000 years ago. Researchers have reported that the Pleistocene translocation of animals occurred in Cyprus around 11,000 years ago [63] and Manus Island around 13,000 years ago [64]. In the case of the Ryukyu Islands, after the extinction of the endemic deer between 30,000 and 35,000 years ago, wild pigs appeared and increased in number around 20,000 to 27,000 years ago [31, 39, 54, 65]. Because Okinawa Island was isolated from the Eurasia continent, mainland Japan, and the remaining Ryukyu Islands during the Pleistocene [27], the increase in the wild pig population might have resulted from people translocating pigs onto the islands from elsewhere [31, 54, 66]. However, one difficulty in this scenario is the recent analysis of the mtDNA of extant wild pigs which showed that the current Ryukyu wild pig population (Sus scrofa ryukyuanus) is a unique, endemic species of the Ryukyu Islands. It was separated from the Eurasian wild pig populations much earlier than the human arrival, probably during the middle Pleistocene [67]. Another difficulty is an ancient DNA study of wild pigs from Holocene archeological sites which suggests the possible translocation of pigs by Holocene prehistoric people [68]. We do not know the genetic relation between the Paleolithic and modern wild pig population of the Ryukyus, and how the Holocene prehistoric translocation of pigs affected the genetic traits of the Ryukyu wild pigs. Therefore, the details of when and how the endemic Ryukyu wild pigs were distributed throughout the Ryukyu Islands remain controversial.

### 6. Conclusion

Paleolithic people immigrated to the Ryukyu Islands more than 36,000 years ago. Morphological and genetic studies of Paleolithic human fossils from this area have indicated that they probably came through Southeast Asia in the course of the worldwide dispersal of early modern humans. The common use of shell tools including fishhooks and the remarkable consumption of aquatic resources as foods by Paleolithic Ryukyu Islanders suggest the relation to the ISEA.

However, Paleolithic Okinawan culture was unique in dominance of marine shell artifacts and biased consumption of freshwater animals. This unique lifestyle adapted to the stone-poor and shell-rich environment of the island, where there were limited terrestrial animals. The adaptive lifestyle on Okinawa, which is a relatively small oceanic island, suggests the plasticity of Paleolithic people's behavior. Their behavioral plasticity may be one of the driving forces that enabled *Homo sapiens* to migrate to various environments all over the world.

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## References

[1] Kaifu Y, Lin C, Goto A, Ikeya N, Yamada M, Chiang W-C, et al. Paleolithic seafaring in East Asia: Testing the bamboo raft hypothesis. Antiquity. 2019;**93**(372):1424-1441

[2] Sutikna T, Tocheri MW, Morwood MJ, Saptomo EW, Awe RD, Wasisto S, et al. Revised stratigraphy and chronology for Homo floresiensis at Liang Bua in Indonesia. Nature. 2016;**532**(7599):366-369

[3] Ingicco T, van den Bergh GD,
Jago-On C, Bahain JJ, Chacón MG,
Amano N, et al. Earliest known hominin activity in the Philippines by
709 thousand years ago. Nature.
2018;557(7704):233

[4] Détroit F, Mijares AS, Corny J, Daver G, Zanolli C, Dizon E, et al. A new species of homo from the Late Pleistocene of the Philippines. Nature. 2019;**568**(7751):181

[5] O'Connor S. Crossing the Wallace line: The maritime skills of the earliest colonists in the Wallacean archipelago. In: Kaifu Y, Izuho M, Goebel T, Sato H, Ono A, editors. Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. College Station: Texas A&M University Press; 2015. pp. 214-224

[6] Habgood PJ, Franklin NR. The revolution that didn't arrive: A review of Pleistocene Sahul. Journal of Human Evolution. 2008;**55**:187-222

[7] Erlandson JM, Fitzpatrick SM. Oceans, islands, and coasts: Current perspectives on the role of the sea in human prehistory. The Journal of Island and Coastal Archaeology. 2006;**1**(1):5-32

[8] Erlandson JM. A deep history for the Pacific: Where past, present, and future meet. Journal of Pacific Archaeology.2010;1(2):111-114 [9] Braje TJ, Leppard TP, Fitzpatrick SM, Erlandson JM. Archaeology, historical ecology and anthropogenic island ecosystems. Environmental Conservation. 2017;44(3):286-297

[10] O'Connor S, Louys J, Kealy S, Samper Carro SC. Hominin dispersal and settlement east of Huxley's line. Current Anthropology. 2017;**58** (Suppl 17):S567-S582

[11] Kaifu Y, Fujita M, Yoneda M, Yamasaki S. Pleistocene seafaring and colonization of the Ryukyu Islands, southwestern Japan. In: Kaifu Y, Izuho M, Goebel T, Sato H, Ono A, editors. Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. College Station: Texas A&M University Press; 2015. pp. 345-361

[12] Kaifu Y, Fujita M. Fossil record of early modern humans in East Asia. Quaternary International. 2012;**248**:2-11

[13] Suzuki H. Pleistocene man in Japan. Journal of the Anthropological Society of Nippon. 1982;**90**:11-26

[14] Suzuki H, Hanihara K. The Minatogawa Man: The Upper Pleistocene Man from the Island of Okinawa. Bulletin No. 19, University Museum of the University of Tokyo, University of Tokyo Press; 1982. p. 208

[15] Sakura H. Pleistocene human fossil remains from Pinza-Abu (Goat Cave), Miyako Island, Okinawa, Japan. Report on Excavation of the Pinza-Abu Cave, Education Board of Miyakojima City; 1985. pp. 161-176

[16] Fujita M, Yamasaki S, Katagiri C, Oshiro I, Sano K, Kurozumi T, et al. Advanced maritime adaptation in the western Pacific coastal region extends back to 35,000-30,000 years before present. Proceedings of the National Academy of Sciences. 2016;**113**:11184-11189 [17] Clarkson C, Jacobs Z, Marwick B,
Fullagar R, Wallis L, Smith M, et al.
Human occupation of northern
Australia by 65,000 years ago. Nature.
2017;547(7663):306

[18] O'Connell JF, Allen J, MAJ W, Williams AN, CSM T, Spooner NA, et al. When did Homo sapiens first reach Southeast Asia and Sahul? Proceedings of the National Academy of Sciences. 2018;**115**(34):8482-8490

[19] O'Connor S, Ono R, Clarkson C.
Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. Science.
2011;334:1117-1121

[20] Yellen JE, Brooks AS, Cornelissen E, Mehlman MJ, Stewart K. A middle stone age worked bone industry from Katanda, upper Semliki Valley, Zaire. Science. 1995;**268**(5210):553-556

[21] Henshilwood CS, Sealy JC, Yates R, Cruz-Uribe K, Goldberg P, Grine FE, et al. Blombos cave, southern cape, South Africa: Preliminary report on the 1992-1999 excavations of the middle stone age levels. Journal of Archaeological Science. 2001;**28**(4):421-448

[22] Marean CW. Pinnacle point cave 13B (Western Cape Province, South Africa) in context: The cape floral kingdom, shellfish, and modern human origins. Journal of Human Evolution. 2010;**59**(3-4):425-443

[23] Ono R, Soegondho S, Yoneda M. Changing marine exploitation during late Pleistocene in northern Wallacea: Shell remains from Leang Sarru Rockshelter in Talaud Islands. Asian Perspectives. 2009;**48**:318-341

[24] Pawlik AF, Piper PJ, Faylona MGPG, Padilla SG, Carlos J, Mijares ASB, et al. Adaptation and foraging from the terminal Pleistocene to the early Holocene: Excavation at Bubog on Ilin Island, Philippines. Journal of Field Archaeology. 2014;**39**(3):230-247

[25] Samper Carro SC, O'Connor S, Louys J, Hawkins S, Mahirta M. Human maritime subsistence strategies in the lesser Sunda Islands during the terminal Pleistocene-early Holocene: New evidence from Alor, Indonesia. Quaternary International. 2016;**416**:64-79

[26] Boulanger C, Ingicco T, Piper PJ, Amano N, Grouard S, Ono R, et al. Coastal subsistence strategies and mangrove swamp evolution at Budog I Rockshelter (Ilin Island, Mindoro, Philippines) from the late Pleistocene to the mid-Holocene. The Journal of Island and Coastal Archaeology. 2019;**14**:584-604

[27] Furukawa M, Fujitani T.Comparative study on PleistocenePaleogeographic maps of Ryukyu arc.Bulletin of the Faculty of Science,University of the Ryukyus. 2014;98:1-8

[28] Holt BG, Lessard JP, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, et al. An update of Wallace's zoogeographic regions of the world. Science. 2013;**339**(6115):74-78

[29] Ota H. Toward a synthesis of paleontological and neontological information on the terrestrial vertebrates of the Ryukyu archipelago.
I. Systematic and biogeographic review. Journal of Fossil Research.
2003;36:43-59

[30] Takahashi A, Otsuka H, Ota H. Systematic review of late Pleistocene turtles (Reptilia: Chelonii) from the Ryukyu Archipelago, Japan, with special reference to Paleogeographical implications. Pacific Science. 2008;**62**:395-402

[31] Kawamura A, Chang CH, Kawamura Y. Middle Pleistocene to Holocene mammal faunas of the

Ryukyu Islands and Taiwan: An updated review incorporating results of recent research. Quaternary International. 2016;**397**:117-135

[32] Oshiro I, Nohara T. Distribution of Pleistocene terrestrial vertebrates and their migration to the Ryukyus. Tropics. 2000;**10**:41-50

[33] Otsuka H, Takahashi A. Pleistocene vertebrate faunas in the Ryukyu Islands: Their migration and extinction. Tropics. 2000;**10**:25-40

[34] Kuroda T, Ozawa T. Paleoclimatic and vegetational changes during the Pleistocene and Holocene in the Ryukyu Islands inferred from pollen assemblages. Journal of Geography. 1996;**105**:328-342

[35] Nakamura Y, Ota H. Late Pleistocene-Holocene amphibians from Okinawajima Island in the Ryukyu archipelago, Japan: Reconfirmed faunal endemicity and the Holocene range collapse of forest-dwelling species. Palaeontologia Electronica. 2015;**18**:1-26

[36] Matsuoka H. The late Pleistocene fossil birds of the central and southern Ryukyu Islands, and their zoogeographical implications for the recent avifauna of the archipelago. Tropics. 2000;**10**:165-188

[37] Matsuoka H, Hasegawa Y. Birds around the Minatogawa man: The late Pleistocene avian fossil assemblage of the Minatogawa fissure, southern part of Okinawa Island, Central Ryukyu Islands, Japan. Bulletin of Gunma Museum of Natural History. 2018;**22**:1-21

[38] Nohara T, Irei S. Animal remains of the Minatogawa fissure site. In: Minatogawa Fissure Site. Gushikami Village, Okinawa: Board of Education; 2002. pp. 29-87

[39] Hasegawa Y, Anezaki T, Oyama S, Matsuoka H, Chinen S. Late Pleistocene mammals from Minatogawa man site, southern Okinawa Island and on the morphological changes of the largest wild boar specimens. Bulletin of Gunma Museum of Natural History. 2018;**22**:23-49

[40] Takahashi A, Ikeda T, Manabe M, Hasegawa Y. Freshwater and terrestrial turtle fossils discovered from the Minatogawa man site, southern part of Okinawajima Island, Ryukyu archipelago, southwestern Japan. Bulletin of the Gunma Museum of Natural History. 2018;**22**:51-58

[41] Suwa G, Fujita M, Yamasaki S, Oshiro I, Baba H, Shinzato N, et al. New insights on the excavation and chronological status of the Late Pleistocene Minatogawa human fossils from Okinawa prefecture. Anthropological Science. 2011;**119**:125-136

[42] Hasegawa Y, Chinzei K, Nohara T, Ikeya N, Wada H, Oyama S. Topography and deposits of Late Pleistocene Minatogawa man site, Okinawa, Ryukyu Islands. Bulletin of Gunma Museum of Natural History. 2017;**21**:7-18

[43] Baba H, Endo B. Chapter 4:
Postcranial skeleton of the Minatogawa man. In: Suzuki H, Hanihara K, editors.
The Minatogawa Man. Tokyo: Bulletin
19, The University Museum of the
University of Tokyo; 1982. pp. 61-159

[44] Baba H, Narasaki S. Minatogawa man, the oldest type of modern Homo sapiens in East Asia. Quaternary Research. 1991;**30**:221-230

[45] Baba H, Narasaki S, Ohyama S. Minatogawa hominid fossils and evolution of late Pleistocene humans in East Asia. Anthropological Science. 1998;**106**:27-45

[46] Suwa G, Fukase H, Kono RT, Kubo D, Fujita M. Mandibular tooth root size in modern Japanese, prehistoric Jomon, and Late Pleistocene Minatogawa human fossils. Anthropological Science. 2011;**119**:159-171

[47] Saso A, Matsukawa S, Suwa G. Comparative analysis of the glabellar region morphology of the late Pleistocene Minatogawa crania: A threedimensional approach. Anthropological Science. 2011;**119**:113-121

[48] Kubo D, Kono RT, Suwa G. A micro-CT based study of the endocranial morphology of the Minatogawa I cranium. Anthropological Science. 2011;**119**:123-135

[49] Kaifu Y, Fujita M, Kono RT, Baba H. Late Pleistocene modern human mandibles from the Minatogawa fissure site, Okinawa, Japan: Morphological affinities and implications for modern human dispersals in East Asia. Anthropological Science. 2011;**119**:137-157

[50] Sato T, Nakagome S, Watanabe C, Yamaguchi K, Kawaguchi A, Koganebuchi K, et al. Genome-wide SNP analysis reveals population structure and demographic history of the Ryukyu islanders in the southern part of the Japanese archipelago. Molecular Biology and Evolution. 2014;**31**:2929-2940

[51] Kono RT, Okazaki K, Nakaza H, Tokumine R, Katagiri C, Doi N. 3D digital reconstruction, preliminary morphometric analysis, and facial approximation of Shiraho 4 skull. Anthropological Science. 2018;**126**(1):15-36

[52] Shinoda K, Adachi N.
Ancient mtDNA analysis of human remains found from ShirahoSaonetabaru Cave Site. The ShirahoSaonetabaru Cave Site, Okinawa
Prefectural Archaeological Center
Excavation Report, 2013; No. 65.
pp. 219-234 [53] Ikeya N. Maritime transport of obsidian in Japan during the upper Paleolithic. In: Kaifu Y, Izuho M, Goebel T, Sato H, Ono A, editors.
Emergence and Diversity of Modern Human Behavior in Paleolithic Asia.
College Station: Texas A&M University Press; 2015. pp. 362-375

[54] Fujita M, Yamasaki S, Sugawara H, Eda M. Body size reduction in wild boar (*Sus scrofa*) from the late Pleistocene Maehira fissure site in Okinawa-Jima Island, Japan, with relevance to human arrival. Quaternary International. 2014;**339**:289-299

[55] Yamasaki S, Fujita M, Katagiri C, Kunikita D, Matsu'ura S, Suwa G, et al. Excavations (2009-2011) at Sakitari-do cave site, Nanjo city, Okinawa prefecture — A new Late Pleistocene paleoanthropological site. Anthropological Science. 2012;**120**:121-134

[56] Yamasaki S, Fujita M, Katagiri C, Kurozumi T, Kaifu Y. Human use of marine shells from Late Pleistocene layers of Sakitari-do cave site, Nanjo city, Okinawa prefecture. Anthropological Science. 2014;**122**:9-27

[57] Langley MC, O'Connor S, Piotto E. 42,000-year-old worked and pigmentstained *Nautilus* shell from Jerimalai (Timor-Leste): Evidence for an early coastal adaptation in ISEA. Journal of Human Evolution. 2016;**97**:1-16

[58] Pawlik AF, Piper PJ. The Philippines from c. 14,000 to 4,000 cal. BP in regional context. Cambridge Archaeological Journal. 2019;**29**(1):1-22

[59] Szabó K, Brumm A, Bellwood P.Shell artefact production at 32,000-28,000 BP in island SoutheastAsia. Current Anthropology.2007;48(5):701-723

[60] Villa P, Soriano S, Pollarolo L, Smriglio C, Gaeta M, D'Orazio M,

et al. Neandertals on the beach: Use of marine resources at Grotta Dei Moscerini (Latium, Italy). PLoS One. 2020;**15**:e00226690

[61] Takamiya H. Initial colonization, and subsistence adaptation processes in the late prehistory of the island of Okinawa. The Bulletin of the Indo-Pacific Prehistory Association. 1996;**15**:143-150

[62] Bellwood P. Migration and the origins of Homo sapiens. In: Kaifu Y, Izuho M, Goebel T, Sato H, Ono A, editors. Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. College Station: Texas A&M University Press; 2015. pp. 51-58

[63] Vigne J-D, Zazzo A, Saliege J-F, Poplin F, Guilaine J, Simmons A. Pre-Neolithic wild boar management and introduction to Cyprus more than 11,400 years ago. Proceedings of the National Academy of Sciences. 2009;**22**:16135-16138

[64] Williams C. Faunal composition of Pamwak site, Manus Island, PNG. In: Galipaud J-C, Lilley I, editors. Le Pacifique de 5000 à 2000 Avant le Présent: Suppléments à l'Histoire d'une Colonisation. Paris: Institut de Recherche pour le Developpement; 1999. p. 241e249

[65] Hasegawa Y. Notes on vertebrate fossils from late Pleistocene to Holocene of Ryukyu islands, Japan. Quaternary Research. 1980;**18**:263-267

[66] Harunari H. Relationship between the extinction of the big mammals and the human activities at the late Pleistocene in Japan. Bulletin of the National Museum of Japanese History. 2001;**90**:1-52

[67] Yoshikawa S, Miura M, Watanabe S, Lin L-K, Ota H, Mizoguchi Y. Historical relationships among wild boar populations of the Ryukyu archipelago and other Eurasian regions, as inferred from mitochondrial cytochrome b gene sequences. Zoological Science. 2016;**33**:520-526

[68] Takahashi R, Kurosawa Y, Adachi N, Hongo H. DNA analysis of modern Ryukyu wild boar: as a basic data for interpretation of results of ancient DNA analyses of archaeological samples. Zooarchaeology. 2017;**33**:63-77

