Watanabe et al.
Progress in Earth and Planetary Science (2023) 10:40
https://doi.org/10.1186/s40645-023-00567-x

Progress in Earth and Planetary Science

REVIEW

Open Access

Geological history of the land area between Okinawa Jima and Miyako Jima of the Ryukyu Islands, Japan, and its phylogeographical significance for the terrestrial organisms of these and adjacent islands

Nana Watanabe[1], Kohsaku Arai[2], Makoto Otsubo[3], Mamoru Toda[4], Atsushi Tominaga[5], Shun Chiyonobu[6], Tokiyuki Sato[6], Tadahiro Ikeda[7], Akio Takahashi[8], Hidetoshi Ota[7] and Yasufumi Iryu[1*]

Abstract

The modern and Late Pleistocene terrestrial fauna of Miyako Jima and adjacent islands (the Miyako Islands) in the southern Ryukyu Islands, southwestern Japan, includes some endemic taxa or genetically unique populations that exclusively have closest allies in the more isolated Okinawa Jima and adjacent islands (the Okinawa Islands) than in the Yaeyama Islands, which are located southwest of the Miyako Islands with much narrower intervening straits. Those taxa or populations include representatives of lineages that have physiologically highly limited ability for over-sea dispersal and the Miyako Islands are currently separated from the Okinawa Islands by at least 300 km of open water; therefore, the formation of this phylogeographical pattern is perplexing. In this study, we review the late Cenozoic geology of the Miyako Islands, southern Okinawa Jima, the Okinawa–Miyako submarine plateau (OMSP; a plateau located between Okinawa Jima and Miyako Jima), and the Kerama gap, which is a depression between the OMSP and Okinawa Jima. We then consider the origin of the modern and Late Pleistocene terrestrial animals, including a number of non-volant vertebrates on the Miyako Islands. Finally, we propose a new hypothesis (the OMSP hypothesis) to explain the enigmatic composition of modern and Late Pleistocene terrestrial vertebrate fauna of the islands. Southern Okinawa Jima was uplifted and emerged after ca. 2 Ma and was temporarily connected to the OMSP, which is likely to have emerged earlier than southern Okinawa Jima, to form a large island extending from Okinawa Jima to the Miyako Islands with a NE–SW direction of ~400 km. Subsequently, Okinawa Jima became separated from the OMSP when the Ryukyu Group—which is composed of Quaternary reef and associated fore-reef and shelf deposits—began to accumulate around the island at 1.7–1.4 Ma. During the interval from 2.0 to 1.7–1.4 Ma, numerous terrestrial animals, including flightless vertebrates, extended their distribution to the OMSP. Although the Miyako Islands repeatedly underwent complete submergence during deposition of the main part of the Ryukyu Group (1.25–0.4 Ma), they were uplifted and emerged to become a land area after ca. 0.4 Ma. In contrast, the OMSP

*Correspondence:
Yasufumi Iryu
yasufumi.iryu.d8@tohoku.ac.jp
Full list of author information is available at the end of the article

subsided after ca. 0.4 Ma and was almost completely submerged after 0.27 Ma. During ca. 0.4–0.27 Ma, terrestrial animals migrated from the OMSP to the Miyako Islands.

Keywords Ryukyu Islands, Kerama gap, Okinawa–Miyako submarine plateau, Pleistocene, Shimajiri Group, Ryukyu Group, Vertebrate, Phylogeography, OMSP hypothesis

1 Introduction

The Ryukyu Islands are a chain of islands extending 1200 km from Tanegashima in the northeast (30° 44′ N, 131° 0′ E) to Yonaguni Jima in the southwest (24° 27′ N, 123° 0′ E), and they represent a typical island-arc–trench system, which has been generated by subduction of the Philippine Sea Plate along the Ryukyu Trench beneath the Eurasian Plate (Fig. 1). The Ryukyu Islands are geographically divided into the North, Central, and South Ryukyus by two major faults underlying the Tokara gap and the Kerama gap. The Okinawa Trough is a backarc basin that separates the island arc from the East China

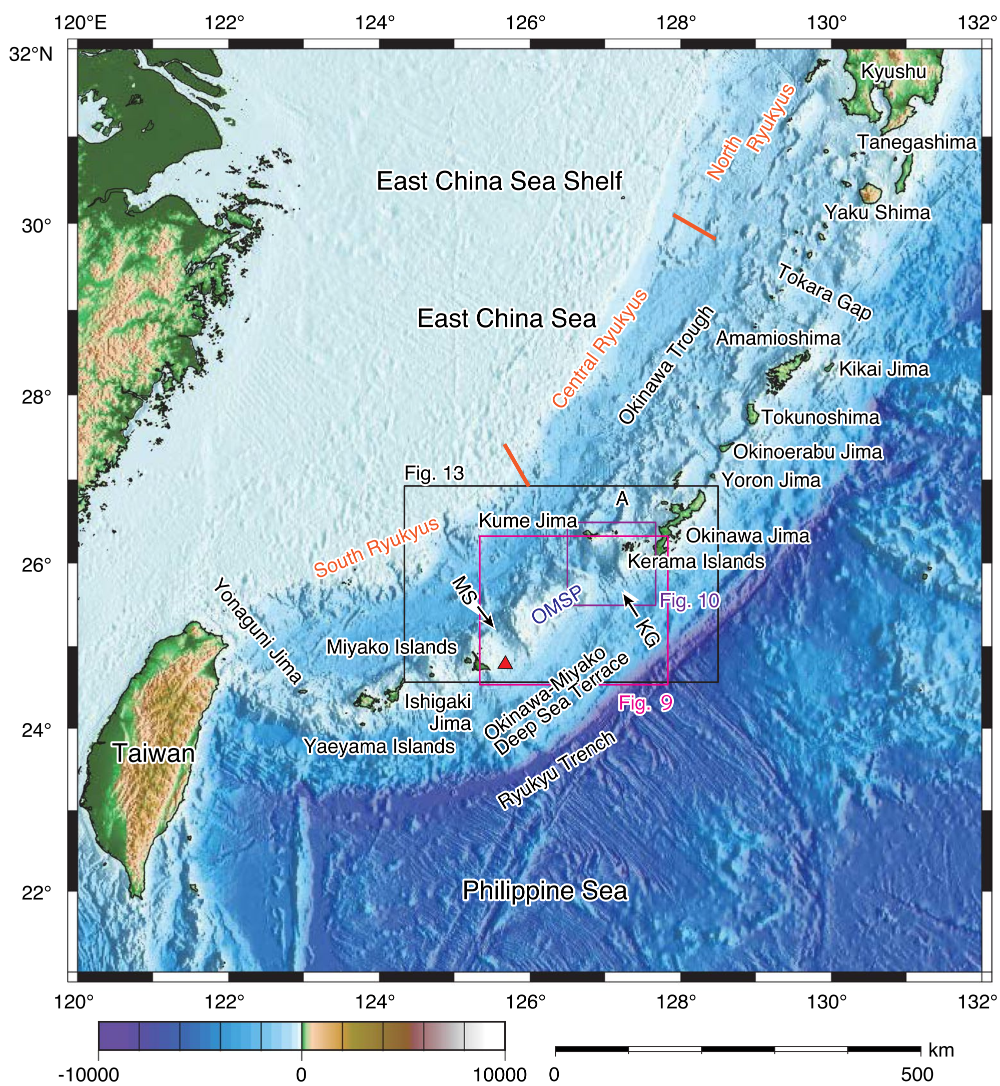

Fig. 1 Topography and bathymetry of the Ryukyu Island Arc. Map of the topography and bathymetry of the Ryukyu Island Arc and its surroundings. *A* Aguni Jima, *KG* Kerama gap, *MS* Mikako saddle, *OMSP* Okinawa–Miyako submarine plateau. The red triangle indicates the location of MITI Miyakojima-Oki well. The map was prepared using Generic Mapping Tools (Wessel et al. 2019; available at https://www.generic-mapping-tools.org; accessed 1 Nov 2021). Elevation and depth data are from SRTM15+V2.4 (https://doi.org/10.1029/2019EA000658; accessed 1 Dec 2021)

Sea Shelf. The Kuroshio Current, a major warm current emerging to the east of Luzon Island, enters the East China Sea through the strait between Taiwan and Yonaguni Jima, flows northeastward along the island chain, and then bifurcates to the southwest of Yakushima (Fig. 1). The main current changes its direction and exits to the Pacific through the Tokara Strait (the strait between Amamioshima and Yaku Shima), and a subsidiary current flows northward along Kyushu. Although the Ryukyu Islands are located at relatively high latitudes in the coral reef province, most of the islands and islets are fringed by coral reefs owing to the predominant flow of this warm current along them.

The Ryukyu Islands are often called “the Galapagos of the Orient” because their modern terrestrial fauna and flora are characterized by a high proportion of endemic taxa, such as *Pentalagus furnessi* (Amami-rabbit), *Gallirallus okinawae* (a flightless rail named Yambaru-kuina), *Protobothrops flavoviridis* (a venomous snake named Habu), and *Cheirotonus jambar* (a long-armed scarab beetle named Yanbaru-tenagakogane) (Government of Japan 2019). Several hypothetical scenarios have been proposed to explain this current biogeographic pattern by assuming their ancestors’ migration to and isolation within the past Ryukyu Islands in response to radical temporal changes in the configuration of land there. Kizaki and Oshiro (1977), for example, attempted to reconstruct the geological evolution of the Ryukyu Islands and invoked temporal changes in the extent and shape of each component island to explain the origin and migration pathway of terrestrial fauna of the Ryukyu Islands. Those authors assumed that the Ryukyu Islands were uplifted after deposition of the Upper Miocene–Lower Pleistocene Shimajiri Group, which is composed mostly of siliciclastic rocks, forming a land bridge from the Eurasian continent to the current Tokara Strait during the Early Pleistocene, and that the terrestrial animals migrated from the continent via this land bridge. The hypothesis of the Pleistocene land bridge was subsequently repeatedly proposed by various studies but with some modifications (e.g., Ujiié 1986; Koba 1992; Kimura 1996, 2002; Oshiro and Nohara 2000; Ujiié and Kaneko 2006). These paleogeographic reconstructions were based primarily on the classical theory of orogeny, lacking the perspective of plate tectonics and the expansion of the Okinawa Trough, which would have had a significant influence on the paleoenvironment of the Ryukyu Islands were not considered (for comparison of the paleogeographic maps of those previous studies, see Furukawa and Fujitani 2014).

Recent molecular phylogenetic and evolutionary studies of various lineages of terrestrial organisms on the Ryukyu Islands have yielded results that are clearly inconsistent with these hypotheses (e.g., Dedeine et al. 2016; Xu et al. 2016). For example, a number of amphibian and reptile lineages occurring in the present-day Central Ryukyus have been isolated from the Eurasian continent and the South and North Ryukyus since the Pliocene or earlier (Ota 1998; Okamoto 2017). To resolve these contradictions, we integrate the latest geological, paleontological, and phylogeographical data and propose a new hypothesis (the OMSP hypothesis) to explain temporal changes in the configuration of islands (OMSP = Okinawa–Miyako submarine plateau; Fig. 1). The present study introduces this more plausible hypothesis and presents a model to explain the enigmatic modern and Late Pleistocene terrestrial vertebrate fauna of the Miyako Islands, Miyako Jima and its adjacent islands (Ogami Jima, Ikema Jima, Kurima Jima, Irabu Jima, and Shimoii Shima).

Although the Miyako Islands belong to the South Ryukyus, modern and Late Pleistocene terrestrial vertebrates, the latter of which have been found in fissure, cavity, and cave deposits (Fig. 2a), include not only taxa common to other islands of the South Ryukyus but also those that are endemic to the Miyako Islands and are otherwise common to the Central Ryukyus (e.g., Ota 1998, 2003; Tominaga et al. 2019) (see Sects. 3.6 and 3.7). The occurrence of taxa exclusive to the Central Ryukyus or of populations genetically closest to those

(See figure on next page.)

Fig. 2 Outcrop photographs of upper Cenozoic deposits on Miyako Jima and Okinawa Jima. **a** Cavity-filling deposits (arrowed) with terrestrial vertebrate fossils at an outcrop near Nishihara, Miyako Jima. *S* Shimajiri Group, *R* Ryukyu Group. Scale bar = 1 m. **b** Stratigraphic relationship between the Shimajiri Group and the Chinen Formation at the Urizun outcrop in Chinen, southern Okinawa Jima. Dark-gray siltstone (S) of the Shinzato Formation (Shimajiri Group) overlain by light-gray fine-grained siltstone of the lower Chinen Formation (LC), which in turn is overlain by beige bioclastic grainstone of the upper Chinen Formation (UC). Limestone of the Naha Formation (Ryukyu Group) occurs at the top of this outcrop. However, its contact with the Chinen Formation is not observed. Scale bar = 5 m. **c** Limestone of the Ryukyu Group (R) unconformably overlying siltstone (S) of the Yonahama Formation (Shimajiri Group) at an outcrop near Nishihara, Miyako Jima. Scale bar = 2 m. **d** Limestones of the Ryukyu Group (the Itoman and Naha formations) unconformably overlying siltstone of the Shimajiri Group at an outcrop ~ 500 m southeast of Yamagusuku, Itoman City, Okinawa Jima. N, Naha Formation; I, Itoman Formation; S, Shinzato Formation. Scale bar = 1 m. **e** Diagenetically altered limestone of the Itoman Formation (I) overlain by limestones of the Naha Formation (N) at Maehira Quarry near Maehira. The altered limestone is abundant in siltstone blocks derived from the Shimajiri Group. Scale bar = 2 m. **f** Well-sorted detrital limestone (= bioclastic grainstone) of the Minatogawa Formation (M) unconformably overlying detrital limestone (= bioclastic packstone) of subunit 1R of the Naha Formation (N) at an outcrop located to the southeast of Aragusuku, Yaese Town, Okinawa Jima. Scale bar = 1 m

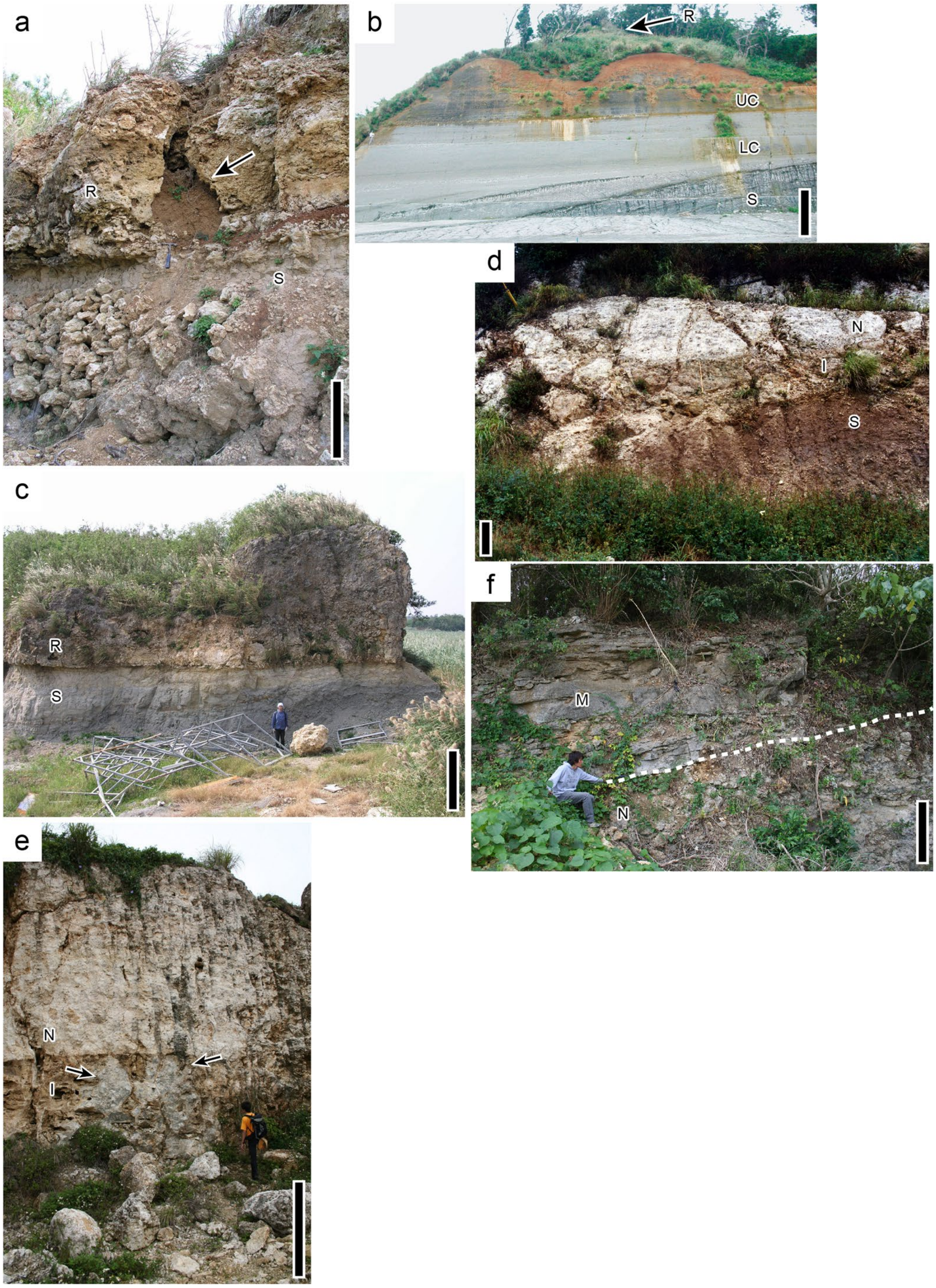

Fig. 2 (See legend on previous page.)

in the Central Ryukyus is enigmatic because the Miyako Islands are separated from Okinawa Jima, the nearest major island of the Central Ryukyus, by ~300 km of sea, which is a large barrier for taxa with limited or non-existent over-sea dispersal ability. Indeed, a distinct discontinuity in nonvolant terrestrial fauna has generally been recognized between the Miyako Islands and the Okinawa Islands (e.g., Ota 2000; Komaki 2021). On the basis of geological, paleontological, and molecular phylogeographical data, this study shows that the OMSP emerged sometime between 5.53 and 0.27 Ma and acted as a land bridge for these animals to migrate from the Miyako Islands to the Okinawa Islands.

Results of deep-sea tow and submersible surveys have led some authors to suspect that Okinawa Jima and Miyako Jima were connected by a land bridge sometime during the period from 0.24 Ma to 20 ka, followed by rapid subsidence (Monma et al. 1991; Kimura et al. 1991, 1992). However, this hypothesis has not been widely supported because it assumes the occurrence of large-scale subsidence (up to 2000 m) during a geologically short period (ca. 20 kyr) and because the sedimentary environments and chronology of the upper Cenozoic deposits on these islands were not well constrained at that time. In this paper, we show that a land bridge between Okinawa Jima and Miyako Jima did not exist and that the presumed rapid subsidence did not occur during such periods (0.24 Ma–20 ka and < 20 ka, respectively) by analyzing and interpreting sedimentological and chronological–biochronological data collected by Kimura et al. (1991, 1992).

Geographical names used here follow the Gazetteer of Japan 2007 (Geographical Survey Institute of Japan and Japan Coast Guard 2007). However, in this paper, the word "Island" is removed from the official name of each island for the sake of brevity. For example, Miyako Jima Island is described as "Miyako Jima".

2 Island biogeography–phylogeography and geology

Islands are where the theory of evolution emerged. It is well known that Darwin and Wallace's attempts to understand island biota led to the formulation of the new concept of biological evolution (Darwin 1859; Wallace 1863) Island biogeography is a branch of biogeography that focuses on islands (e.g., Whittaker and Fernandez-Palacios 2007). Depending on perspective, biogeography can be broadly divided into historical biogeography and ecological biogeography. Historical biogeography attempts to reconstruct the origin, dispersal, and extinction of taxa and biota. In contrast, ecological biogeography aims to explain geographic variations in the diversity and spatiotemporal distribution of taxa in terms of their interactions with the physical and biological environment. The study of island biogeography follows this division.

A controversial topic in historical biogeography is whether island organisms have migrated over a land bridge that was connected to a relatively large land mass (vicariance) or across oceans (dispersal) (de Queiroz 2005; Cowie and Holland 2006; Yoder and Nowak 2006; Grandcolas et al. 2008). One reason for the prolonged controversy is that even organisms on continental islands once connected by a land bridge may have migrated to islands across the sea after they were separated and isolated. Molecular phylogenetic techniques have been used to address whether vicariance or dispersal has been the main mechanism of establishing island populations. The approach using these techniques attempts to determine the phylogenetic relationships and divergence times between extant island taxa and their ancestors and compare them with the geological ages of the islands to infer whether the island taxa arrived via a land bridge or by over-sea dispersal.

Island biogeography–phylogeography and geology are complementary. For example, the land bridge and dispersal (over-sea) theories have both been proposed to explain the island taxa on the Galapagos Islands. However, the formation of a land bridge around the islands has been ruled out by increased knowledge of ocean-floor geology. As another example, the biogeography of the Malay Archipelago is highly complex, and faunal boundaries such as the Wallace Line and the Weber Line have been drawn. This complex biogeography is known to have resulted from the location of the archipelago at the junction of four major plates in combination with past sea-level changes (Ali and Heaney 2021). These are examples where the distribution of organisms can be reasonably explained by the geology of the islands and their surroundings. Conversely, the distribution of organisms may provide constraints on reconstructing Earth's history. It is well known that Alfred Wegener (1929) cited the geographic distribution of *Mesosaurus* (a Permian aquatic reptile), *Cynognathus* and *Lystrosaurus* (Triassic terrestrial reptiles), and *Glossopteris* (a Permian seed fern) as essential pieces of evidence supporting the Theory of Continental Drift.

A land bridge connecting two-thirds of the Ryukyu Islands to the Eurasian continent was assumed to have formed during the Quaternary (Kizaki and Oshiro 1977). However, phylogenetic studies of amphibians and reptiles have refuted this interpretation (Ota 1998), and this view is supported by geological evidence (Iryu et al. 2006). It is thus concluded that the integration of phylogeography and geoscientific knowledge is the best way to elucidate the geological development of islands and the establishment and maintenance mechanisms of island biota.

3 Review

3.1 Geology of the Miyako Islands

3.1.1 Shimajiri Group

The Cenozoic succession on the Miyako Islands consists of the Pliocene to Lower Pleistocene Shimajiri Group consisting of siliciclastic rocks and the Pleistocene Ryukyu Group composed chiefly of carbonates formed in coral reefs and associated fore-reefs to shelves. Deep drilling of the MITI Miyakojima-Oki well (Figs. 1 and 3) has revealed that the Shimajiri Group is underlain by

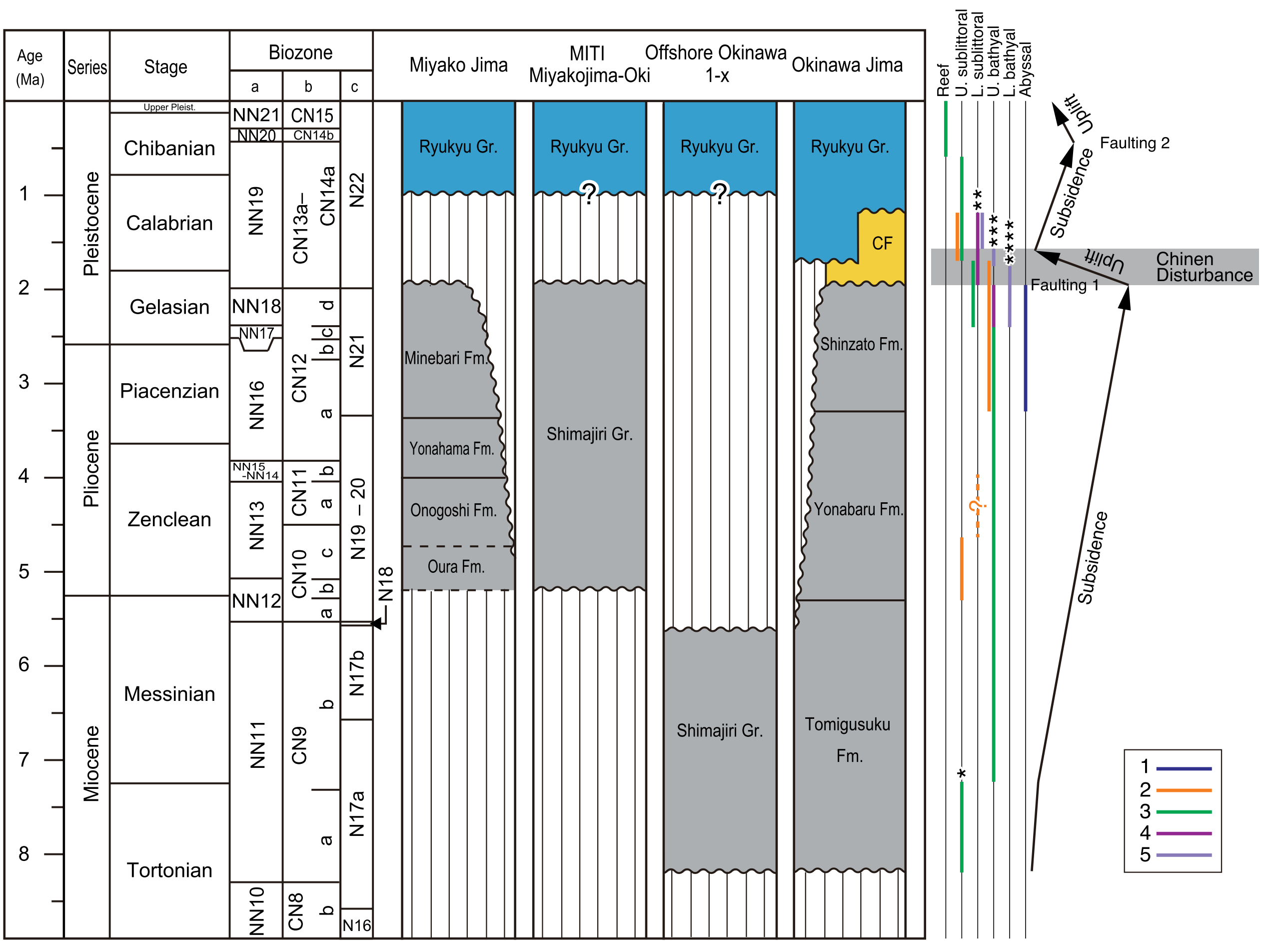

Fig. 3 Correlation of upper Cenozoic successions. Upper Cenozoic successions on and around the Miyako Islands, on the OMSP, and on Okinawa Jima, together with their correlations and ages. Paleobathymetric changes and tectonic movements of southern Okinawa Jima are also shown. Upper Pleistocene and Holocene deposits are not illustrated. Data: Miyako Jima, Sato et al. (2002), Hanagata and Nobuhara (2015); MITI Miyakojima-Oki well, Tsuburaya and Sato (1985); Offshore Okinawa 1 – X well, Aiba and Sekiya (1979), Sato et al. (2022); Okinawa Jima, Tanaka and Ujiié (1984), Hanagata (2004), Sato et al. (2004), Odawara et al. (2005b), Chiyonobu et al. (2009), Fujita et al. (2011), Imai et al. (2017). Biozones: a CN zones, calcareous nannofossil zones of Okada and Bukry (1980); b PL zones, planktic foraminiferal zones of Berggren et al. (1995); c N zones: standard tropical–subtropical planktic foraminiferal zones of Blow (1969). Paleobathymetry: 1, Mollusks, Ogasawara and Masuda (1983); 2, Mollusks, Noda 1980, 1988; 3, Ostracods (Nohara 1987); 4, Benthic foraminifers (Nakagawa et al. 2001); 5, Benthic foraminifers (Matsumoto et al. in press). Note that the vertical lengths of the bars for biozones do not denote actual chronological ranges. *sublittoral; **upper shelf slope (100–300 m water depth); ***upper continental slope (< 500 water depth); ****lower continental slope (500–1500 water depth). Tectonic movement: Faulting 1, formation of normal faults cutting the Shimajiri Group; Faulting 2, formation of faults cutting the Shimajiri Group and the main body of the Ryukyu Group

the Lower Miocene Yaeyama Group (Tsuburaya and Sato 1985). The lower interval of the Yaeyama Group is composed of quartz-rich sandstone and black mudstone with a shallow-marine limestone bed at the top. The lower interval correlates to the Lower Miocene via planktic foraminiferal zones N6–N8 (Blow 1969) and calcareous nannofossil zones CN2–CN3? (Okada and Bukry 1980). The upper interval consists mainly of partly calcareous, fine-grained sandstone alternating with mudstone, intercalated with coal beds. No age-diagnostic fossils have been found in the upper interval. The Yaeyama Group has been discovered in the Miyako R-1 Exploratory Well drilled on Miyako Jima (Kato 2016). The Yaeyama Group is interpreted to have been deposited in non-marine and shallow-marine environments on the basis of lithological characteristics (e.g., the occurrence of coal beds and shallow-marine carbonate rocks).

Several lithostratigraphic frameworks have been proposed for the Shimajiri Group on the Miyako Islands. These frameworks are essentially similar but vary in terms of stratigraphic nomenclature (Doan et al. 1960; Ujiié and Oki 1974; Yazaki 1978; Yazaki and Oyama 1979; Nakamori 1985). The lithostratigraphy of the Shimajiri Group is outlined here following Nakamori (1985). The

Shimajiri Group includes the Oura, Onogoshi, Yonahama, and Minebari formations (Fig. 3). The Oura Formation (> 600 m thick) is composed mainly of sandstone, siltstone, and their alternations, together with granule to cobble conglomerates. Oyster (*Crassostrea gigas*) and lignite beds are intercalated in the lower interval of this formation, whereas the upper interval yields mollusks and solitary corals. Lithological characteristics and fossil assemblages imply that the depositional environments of the lower and upper intervals were brackish (intertidal zone of an inner bay) and open-marine shallower than 50–60 m water depth, respectively (Ogasawara and Masuda 1983). The occurrence of a fossil elephant, *Trilophodon* (which is currently considered a junior synonym of *Gomphotherium*), possibly from the Oura Formation (Hasegawa et al. 1973), suggests that there was a land area around the Miyako Islands during the deposition of this formation. The Onogoshi Formation (600 m thick) comprises massive or weakly bedded siltstone and mudstone yielding mollusks and solitary corals. The lower interval of the formation is considered to have been deposited in an open-marine environment shallower than 50–60 m water depth, like that of the upper interval of the Oura Formation. In contrast, the upper interval of the Onogoshi Formation is thought to have accumulated on a deeper (lower sublittoral to upper bathyal) muddy bottom (Ogasawara and Masuda 1983). The main lithology of the Yonahama Formation (700 m thick) is tuffaceous siltstone with interlayers of tuff. The individual interlayers measure several centimeters to 1 m thick and contain abundant pumice. This formation yields mollusks and solitary corals and is more abundant in planktic foraminifers and calcareous nannofossils than the other three formations, suggesting a more pelagic and deeper setting than that of the Onogoshi Formation. The molluskan assemblages consist of upper bathyal taxa together with those reworked from shallow (upper sublittoral) deposits (Ogasawara and Masuda 1983). The Minebari Formation (500 m thick) consists predominantly of rhythmic alternations of sandstone and siltstone with tuff interlayers. A single set of sandstone and siltstone is 6–40 cm thick. Although mollusks and solitary corals have been found in this formation, they are less common than in the other formations of the Shimajiri Group. The lithology and fossil assemblages are thought to indicate a return to a lower sublittoral environment (Nakamori 1985). In contrast, Nobuhara (2001) reported bathyal molluskan assemblages with high species diversity (more than 80 species) from this formation.

The geological age of the Shimajiri Group on Miyako Jima is uncertain, with two different views having been presented. Planktic foraminiferal biostratigraphy has been used to determine an age range from the Late Miocene to the Calabrian for the Shimajiri Group (Ujiié and Oki 1974; Yazaki 1978). Kato (2016) measured strontium (Sr) isotopes of foraminifers, supporting the Late Miocene initiation of sedimentation of the group (as early as 7 Ma). Hanagata and Nobuhara (2015) demonstrated that the stratigraphic interval comprising the upper part of the Onogoshi Formation to the Minebari Formation correlates to zones PL 1 (Messinian to Zanclean) to PL 5 (Piacenzian to Gelasian) defined by Berggren et al. (1995). It has not been possible to place chronological constraints on the Oura Formation because *Globorotalia tumida*, an age-diagnostic planktic foraminifer for PL 1, is a deep thermocline species and is extremely rare or does not occur in the Oura Formation, which consists of shallow-marine sedimentary rocks. However, planktic foraminiferal and calcareous nannofossil biostratigraphy and magnetostratigraphy have been used to constrain the age of the Shimajiri Group to the Zanclean–Gelasian (Nakagawa et al. 1976; Nakamori 1985; Sato et al. 2002). Nannofossils indicating a Late Miocene age have not been found at the site from which Ujiié and Oki (1974) reported age-diagnostic planktic foraminifers for the Late Miocene (Sato et al. 2022). Sato et al. (2002) showed that horizons stratigraphically higher than those investigated by Hanagata and Nobuhara (2015) in the Minebari Formation are as young as ca. 2 Ma. Consequently, all or most of the Shimajiri Group is Zanclean to Gelasian in age.

3.1.2 Ryukyu Group

The Ryukyu Group (MacNeil 1960), formerly termed the Riukiu Limestone (Yabe and Hanzawa 1930), is composed of Pleistocene carbonate deposits that were formed in coral reefs and associated fore-reefs to shelves and coeval non-marine siliciclastic sedimentary rocks. The group is distributed over most of the islands of the Central and South Ryukyus, where the deposits are found up to ~ 200 m in elevation. The Ryukyu Group on the Miyako Islands has been divided into the Miyakojima Limestone and the Shimojijima Limestone (Nakamori 1985). The former constitutes the main body of the Ryukyu Group, occurs throughout the Miyako Islands, and is cut by numerous normal faults that strike NNW–SSE and are downthrown to the east, exhibiting cuesta-like landforms (Fig. 5). In contrast, the latter comprises younger reef deposits with limited horizontal and vertical distribution and is found only on Shimoji Shima and Irabu Jima, where it unconformably overlies the Miyakojima Limestone. The Miyakojima Limestone is interpreted as being represented by three cycles of reef deposits, each of which begins with detrital or larger foraminiferal limestones and is terminated by coral limestone. Because the abovementioned studies were conducted before the full-scale introduction of a new sedimentological framework into the stratigraphic scheme of the Ryukyu Group, the stratigraphic division (cycle) is the opposite of that used presently (unit). The Shimojijima Limestone was not confirmed by Sagawa et al. (2001), and thus its existence is uncertain.

Since the 1980s, extensive investigations of biota and sediments have been conducted in coral reefs and associated shallow lagoons and fore-reefs to island shelves around the Ryukyu Islands (e.g., hermatypic corals, Nakamori 1986; nongeniculate coralline algae, Iryu 1992; rhodoliths, Matsuda and Iryu 2011), and these have shown the ecological and sedimentological specificity of many benthic organisms and sediments and have identified characteristic assemblages and sediments in each of the topographic zones and sub-areas there (e.g., Iryu et al. 1995). On the basis of the findings of those studies, a classification for carbonate rocks of the Ryukyu Group was proposed initially by Nakamori (1986) and subsequently refined by Nakamori et al. (1995) and Iryu et al. (1998). Application of this classification has enabled the lithostratigraphy of numerous islands and areas to be established (e.g., Yoron Jima, Odawara and Iryu 1999; Irabu Jima and Shimoji Shima, Sagawa et al. 2001; Tokunoshima, Yamada et al. 2003; Yomitan (Okinawa Jima), Odawara et al. 2005b; Itoman (Okinawa Jima), Kaneko and Ujiié 2006; Sagae et al. 2012; Motobu Peninsula (Okinawa Jima), Yamamoto et al. 2006). In those studies, the stratigraphic succession of the Ryukyu Group was divided into several units. A single unit is defined as a sequence that was initiated during a sea-level lowstand, developed through a subsequent transgression and highstand, and terminated in a regression (Yamamoto et al. 2006; Fig. 4). Vertically, a single unit consists of shallow-water reef deposits (mostly coral limestone) in proximal (inland and higher-elevation) areas and of relatively deep-water off-reef deposits (rhodolith, *Cycloclypeus-Operculina*, and detrital limestones) in distal (coastal and lower elevation) areas. Between the proximal and distal areas, a single unit is composed of coral limestone grading upward into deeper limestones overlain by coral limestone. The uppermost limestone is observed in only a few cases. Laterally, the proximally situated coral limestone is surrounded by the distally located rhodolith, *Cycloclypeus-Operculina*, and detrital limestones.

Iryu et al. (2006) established the correlation of the Ryukyu Group on islands from Kikai Jima in the north to Yonaguni Jima in the south. We updated the correlation of Iryu et al. (2006), demonstrating the unit-level correlation of the Ryukyu Group on Okinawa Jima and the Miyako Islands and correlated the units of the main body of the Ryukyu Group with Marine Isotope Stages (MISs; Emiliani 1955; Lisiecki and Raymo 2005; Ahn et al. 2017).

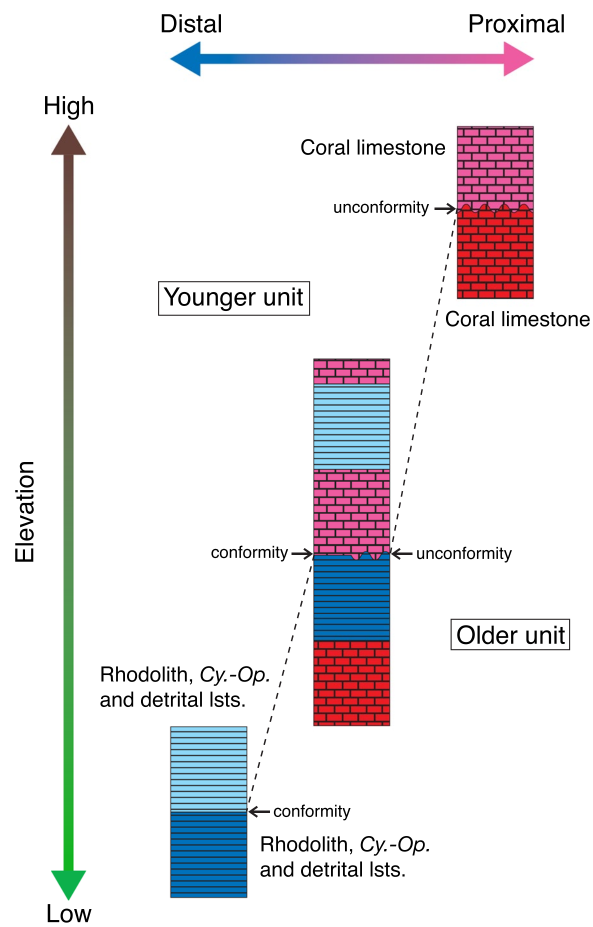

Fig. 4 Stratigraphic succession of limestones within the Ryukyu Group. Schematic figure showing stratigraphic succession and the spatial arrangement of limestones within the Ryukyu Group (modified from Yamamoto et al. 2006). *Cy.-Op., Cycloclypeus-Operculina*

We correlated units of the Ryukyu Group and MISs, assuming that a single unit was formed during a period from one even-numbered MIS (during a lowstand of sea level and a following transgression) to a subsequent odd-numbered MIS (during a highstand and a following regression).

The Miyako Islands are covered entirely by the Ryukyu Group (Figs. 2c and 5). No formal description based on the new sedimentological framework has been published to date on the lithostratigraphy of the main body (up to 60 m thick) of the Ryukyu Group on Miyako Jima. Yamada (2002) reported that the main body consists of five units (Fig. 5). According to Anai et al. (2017), these units were deposited during the period from 0.99 Ma (first occurrence (FO) of *Gephyrocapsa parallela*; hereafter, numerical ages of Upper Pliocene to Quaternary calcareous nannofossil datums follow Sato et al. 2009) to 0.45 Ma (last occurrence (LO) of *Pseudoemiliania lacunose*), and

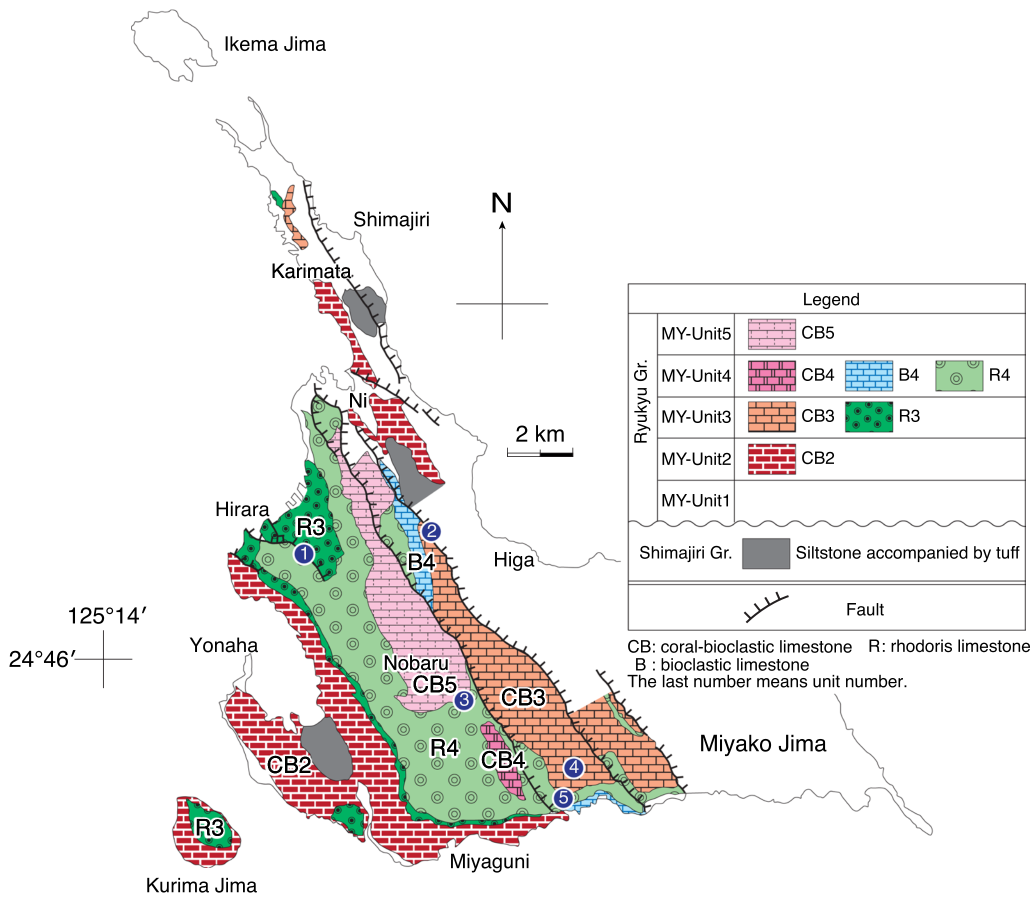

Fig. 5 Geological map of the Ryukyu Group on Miyako Jima. The Ryukyu Group on this island consists of five units (modified from Yamada 2002). *Ni* Nishihara; 1, Tsuzupisuki-Abu cave; 2, Tanahara cave; 3, Pinza-Abu cave; 4, Mumyo-no-ana cave; 5, Amaga cave

the Brunhes–Matuyama boundary is located in MY-Unit 4 (Fig. 6). Considering these chronological constraints and a conformable stratigraphic succession of the five units, MY-Units 1, 2, 3, 4, and 5 are thought to have been deposited during MIS 26–25, 24–23, 22–21, 20–19, and 18–17 (0.96–0.65 Ma), respectively.

The Ryukyu Group on Irabu Jima and Shimoji Shima reaches 100 m in thickness and is composed of 13 units (Figs. 6 and 7; Sagawa et al. 2001). Of these, the four lowest units (1–4) consist of reddish, diagenetically altered limestones. The main body of the Ryukyu Group (units 1–12) forms a stratigraphic architecture of aggradation and retrogradation. Accordingly, the islands and their environs are inferred to have subsided during the deposition of the main body. In contrast, unit 13 is up to 12 m thick and consists chiefly of coral limestone that extends seaward (offlapping) over the main body and is limited in its distribution to submarine cores drilled to the south of Irabu Jima (i.e., to the west of Miyako Jima). The spatial configuration of unit 13 and its stratigraphic relationship with the main body indicates a rapid tectonic transition in this area, whereby subsidence ceased after the deposition of unit 12 and uplift of the area began (Sagawa et al. 2001). Four calcareous nannofossil datums are present in the main body (Fig. 6): LO of large *Gephyrocapsa* spp. (1.18 Ma) in unit 2, FO of *G. parallela* (0.99 Ma) in unit 4, LO of *Reticulofenestra asanoi* (0.85 Ma) in unit 7, and LO of *Pseudoemiliania lacunosa* (0.45 Ma) in unit 12. Bio- and magnetostratigraphic data (Sagawa et al. 2001; Anai et al. 2017) allow the units of the Ryukyu Group on the Miyako Islands to be correlated with each other and with MISs (Fig. 6). This correlation indicates that coral reef formation started earlier on Irabu Jima and Shimoji Shima (at 1.25 Ma) than on Miyako Jima (at 0.96 Ma) and that the uppermost unit (unit 13) was formed after the rapid transition in tectonic movement from subsidence to uplift (at ca. 0.4 Ma). However, units 3–4, 6 and 8–11 are not well correlated with MISs. Because the negative $\delta^{18}O$ excursion of MIS 32 was relatively small, the reef and off-reef deposits that formed during MISs 34–31, which should have been separated into two units, were likely described as a single unit (unit 3) by Sagawa et al. (2001). It is also the case for unit 6. Conversely, because MIS 15 is characterized by double peaks, two units of

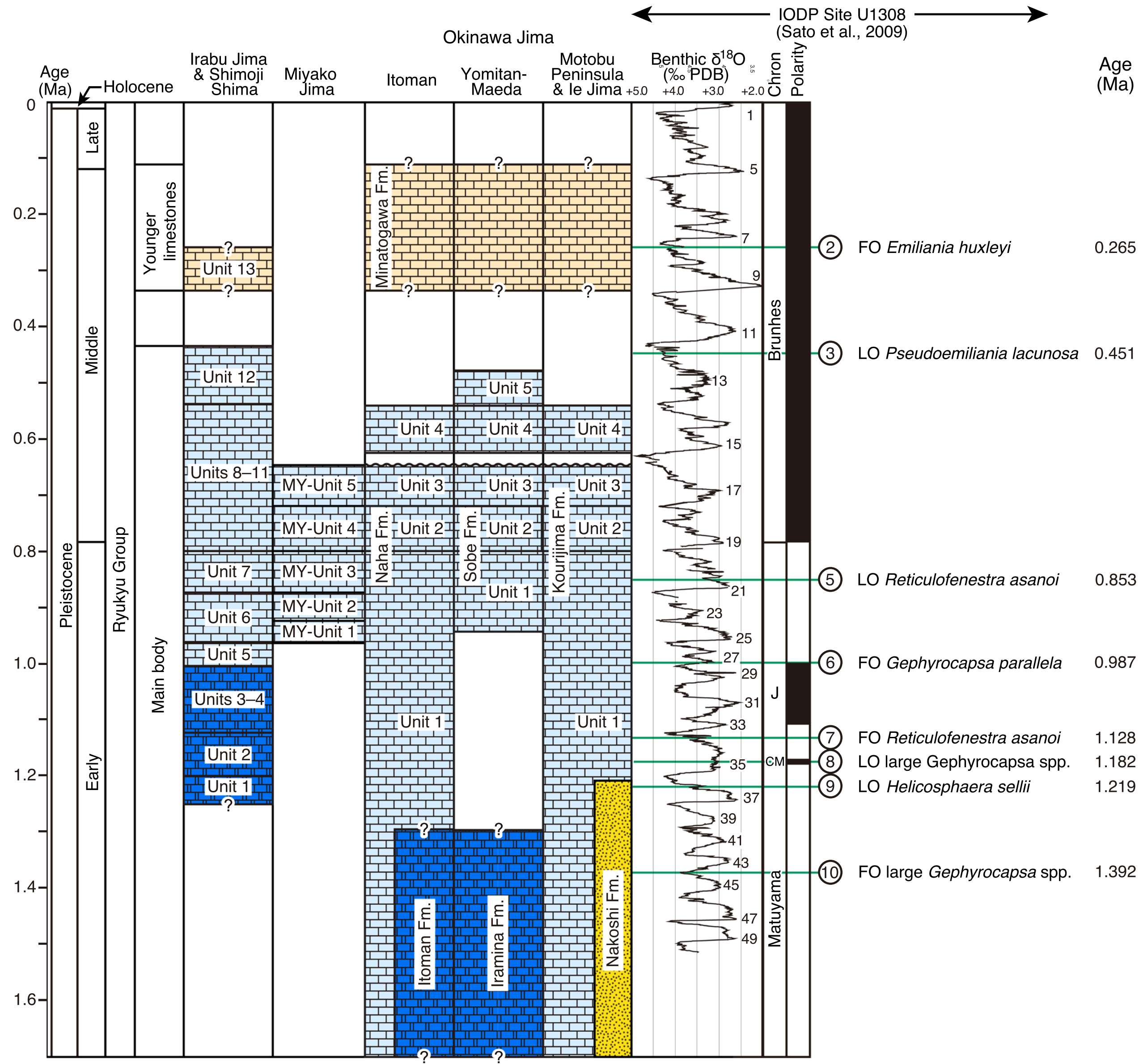

Fig. 6 Correlation of the Ryukyu Group. Correlation of the Ryukyu Group on the Miyako Islands and three areas of Okinawa Jima with oxygen isotope stratigraphy and calcareous nannofossil biostratigraphy established at Integrated Ocean Drilling Program Site U1308 in the North Atlantic Ocean (Sato et al. 2009). Numbers on the oxygen isotope stratigraphy denote Marine Isotope Stages. We correlated units of the Ryukyu Group and Marine Isotope Stages, assuming that a single unit was formed in response to a single cycle of glacioeustatic sea-level change and corresponding to deep-sea benthic foraminiferal $\delta^{18}O$ values. Dark-blue successions represent shallow-water reef deposits (mostly coral limestone) that have been altered by meteoric diagenesis to show reddish staining. They include the lower part of the Ryukyu Group on Irabu Jima and the Itoman Formation and its equivalents on Okinawa Jima

reef and off-reef deposits (units 10 and 11) might have formed during this stage.

3.2 Geology of Okinawa Jima

3.2.1 Shimajiri Group

The Shimajiri Group is distributed on southern Okinawa Jima, where it is divided into three formations; i.e., the Tomigusuku, Yonabaru, and Shinzato formations, in ascending stratigraphic order (Fig. 3; Natori 1976). The Tomigusuku Formation is composed of alternating beds of sandstone and mudstone, identified as turbidites (Ujiié and Kaneko 2006). The formation is divided into 13 units (T1 to T13, from youngest to oldest; Fukuta et al. 1970; Okinawa Natural Gas Research Group 1971), with odd

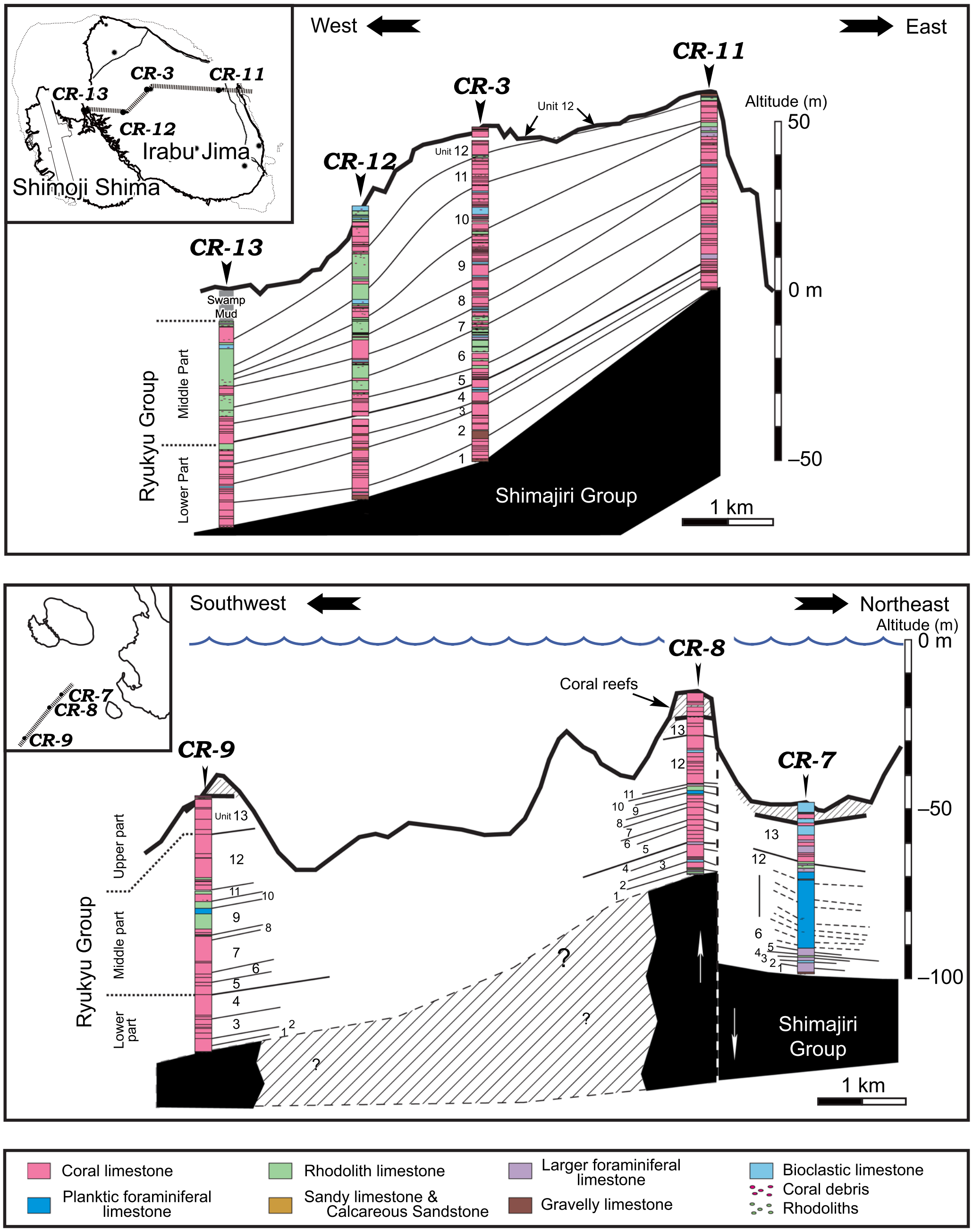

Fig. 7 Geological cross-sections through the Ryukyu Group on Irabu Jima and Shimoji Shima. The Ryukyu Group on the two islands is up to 100 m in thickness and is divided into 13 units (modified from Sagawa et al. 2001)

numbers corresponding to sandstone-dominated intervals. The basal unit (T13) is dominated by sandstone with basal conglomerates (30 m thick) and correlates to the Oroku Sandstone Member (Makino and Higuchi 1967). The Yonabaru and Shinzato formations consist mainly of mudstones with thin tuff and sandstone interlayers. The latter formation is distinguished from the former by its more numerous interlayers of tuff. The three formations appear to constitute a conformable sequence.

On the basis of their paleontological analysis of molluskan assemblages and a review of previous studies on assemblages of mollusks and brachiopods (MacNeil 1960; Fukuta et al. 1970), Ogasawara and Masuda (1983) suggested deepening of the depositional environment starting from a sublittoral zone (~ 50 m water depth) during deposition of the lower interval of the Yonabaru Formation to a bathyal zone (~ 1000 m water depth) during deposition of the Shinzato Formation (Fig. 3). The environment during deposition of the Tomigusuku Formation has not been specified. Noda (1980, 1988) reported abyssal mollusk species from the Shinzato Formation, suggesting a deeper setting for the deposition of this formation than had previously been considered. Ostracod assemblages show that the deepening occurred earlier than mollusks suggest (Nohara 1987): sublittoral during deposition of the lower Tomigusuku Formation; upper bathyal during deposition of the middle Tomigusku to lower Shinzato formations; and outer sublittoral during deposition of the upper Shinzato to lower Chinen formations. Nakagawa et al. (2001) reported two benthic foraminiferal assemblages from the Shinzato Formation, both of which were interpreted to indicate a shelf-slope environment with a water depth of > 250 m on the basis of a comparison with benthic foraminiferal assemblages from around the Miyako Islands (Kodato and Nakagawa 1993). Benthic foraminiferal assemblages at the Urizun outcrop (Sato et al. 2004) indicate a deeper setting (lower continental slope, 500–1500 m water depth) for the upper Shinzato Formation (Matsumoto et al. in press). In contrast, Ujiié and Kaneko (2006) proposed a bathyal depositional environment for the Shimajiri Group on the basis of the abundant occurrence of "*Globocassidulina subglobosa* and var." throughout the group and the overlying Chinen Formation. Overall, we infer the following reconstruction of the depositional environment of the Shimajiri Group: sublittoral during deposition of the lower Tomigusuku Formation; bathyal during deposition of the middle Tomigusku to lower Shinzato formations; and lower sublittoral to upper bathyal (200–300 m water depth) or deeper during deposition of the upper Shinzato Formation.

Planktic foraminiferal and calcareous nannofossil biostratigraphy indicates that the Shimajiri Group on Okinawa Jima correlates to the Upper Miocene (Tortonian) to Lower Pleistocene (Gelasian); i.e., the N17–N21 and CN9a–CN12d zones (Fig. 3; Tanaka and Ujiié 1984; Hanagata 2004; Sato et al. 2004; Imai et al. 2017). Ujiié and Kaneko (2006) correlated the lower Tomigusuku Formation on Okinawa Island with the CN9a Zone and suggested that the N16/N17 boundary is located within this zone. However, according to recent microfossil biostratigraphy, the N16/N17 zone boundary is lower than the CN9 Zone (Raffi et al. 2020). Therefore, the biostratigraphy of Ujiié and Kaneko (2006) is in marked contrast to the currently proposed biostratigraphy. Although Tanaka and Ujiié (1984) reported that the stratigraphic position of the shift from dextral to sinistral coiling preference in *Pulleniatina* and the CN12d/CN13a boundary both lie in the upper Shinzato Formation, the interval including these two events corresponds to the lower Chinen Formation of Nakagawa et al. (2001) (Sato et al. 2004). On the basis of the above data, the depositional age of the Shimajiri Formation is estimated to be ca. 8 to ca. 2 Ma.

3.2.2 Chinen Formation

The Chinen Formation is a transitional lithofacies between the Shimajiri and Ryukyu groups. Its distribution is limited to southern Okinawa Jima, where it is exposed along the eastern coast from Uezato via Chinen to Katsuren Peninsula and sporadically on the western coast at Naha Port (Fig. 8; Nakagawa et al. 2001; Chiyonobu et al. 2009; Fujita et al. 2011). Differing definitions of the Chinen Formation (for a review, see Chiyonobu et al. 2009) had complicated study of the stratigraphy and chronology of the upper Cenozoic succession on Okinawa Jima until Nakagawa et al. (2001) established that this formation consists of lower and upper intervals. The lower Chinen Formation is composed of calcareous siltstone that is similar in lithology to mudstone of the Shinzato Formation but slightly coarser and more poorly bedded (Fig. 2b). The upper Chinen Formation comprises well-bedded detrital limestone (bioclastic packstone) consisting mainly of benthic foraminifers (including large benthic foraminifers), mollusks, brachiopods, bryozoans, and echinoids. Corals and coralline algae are absent or occur only very rarely.

Ogasawara and Masuda (1983) inferred rapid shallowing during the deposition of the Chinen Formation, as the molluskan assemblage in the lower interval of this formation includes many bathyal taxa that are also common in the Shinzato Formation and because those in the middle and upper intervals comprise upper sublittoral species (Fig. 3). Ostracod assemblages indicate that the shallowing started during deposition of the upper Shinzato Formation and that the lower and upper intervals of the Chinen Formation were deposited in the outer sublittoral zone and reefs (Nohara 1987). This reconstruction agrees roughly with that deduced from benthic foraminifers by Nakagawa et al. (2001), who identified four assemblages, all of which indicate that the shelf-slope environment ranging in water depth from 100 to 300 m. On the basis of paleontological analysis of benthic foraminiferal assemblages of the Shinzato and Chinen formations and geochemical analysis of dolomite concretions at the boundary between the two formations, Matsumoto et al. (in press) concluded that the Shimajiri Basin was rapidly uplifted by 250 ± 100 m at ca. 2 Ma and termed this tectonic event the "Chinen Disturbance" event. Those authors suggested that the relative sea-level fall caused by

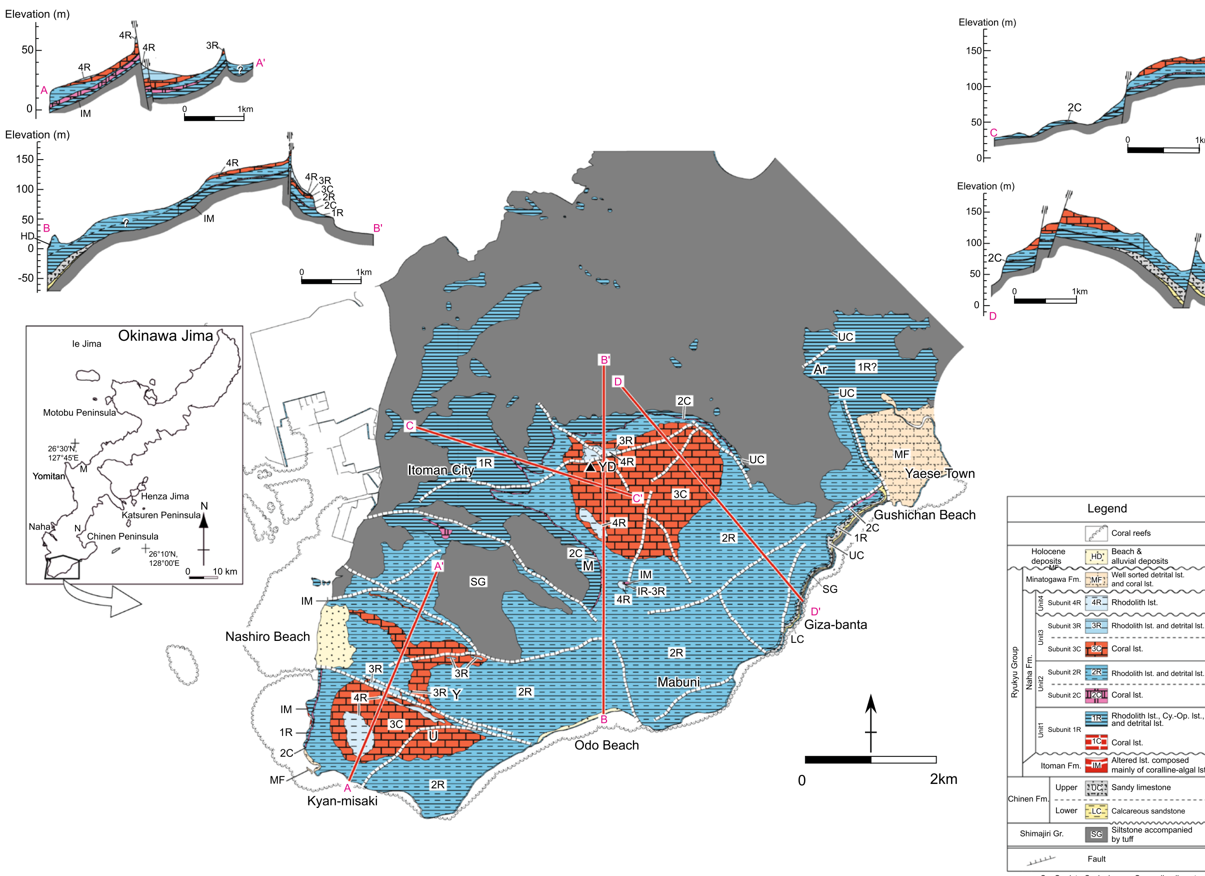

Fig. 8 Geological map of the Ryukyu Group on southern Okinawa Jima. Geological map and cross-sections of the Ryukyu Group on southern Okinawa Jima (after Sagae et al. 2012). Geological map: *Ar* Aragusuku, *M* Maehira, *U* Uezato, *Y* Yamagusuku, *YD* Yoza-dake. Index map in the left panel: *M* Maeda, *N* Nishihara

this uplift destabilized methane hydrate in sediments of the Shimajiri Group, drastically increasing the methane supply and flux, which led to the formation of methane-derived dolomite concretions at the boundary. The uplift was generated by the vertical component of the right-lateral strike-slip faulting that formed the Kerama gap (Arai and Inoue 2022).

Calcareous nannofossil biostratigraphy indicates that sedimentation of the Chinen Formation started and ended earlier in Uezato and Chinen than on Katsuren Peninsula and at Naha Port. In Chinen, the sedimentation started slightly before 1.99 Ma (LO *Discoaster brouweri*) and ended at 1.71–1.39 Ma (1.71 Ma, FO *Gephyrocapsa oceanica*; 1.39 Ma, FO of large *Gephyrocapsa* spp.) (Sato et al. 2004; Odawara et al. 2005a). The Chinen Formation on Katsuren Peninsula ranges in age from 1.99 to 1.76 Ma (1.76 Ma, FO of *Gephyrocapsa caribbeanica*) to 1.39–1.18 Ma (1.18 Ma, LO of large *Gephyrocapsa* spp.) (Chiyonobu et al. 2009). The age of the Chinen Formation at Naha Port ranges from 1.71 to 1.39 Ma (Fujita et al. 2011). These findings suggest that the upper interval of the Chinen Formation corresponds to the lower interval of the Naha Formation.

3.2.3 Ryukyu Group

The Ryukyu Group is distributed on southern and central Okinawa Jima and is exposed up to 170 m above sea level (Fig. 8). The group, which unconformably overlies the Shimajiri Group (Fig. 2d) and unconformably/conformably overlies the Chinen Formation, consists of the Naha Formation and its correlatives, which exhibit a common stratigraphic succession but vary in terms of the stratigraphic nomenclature, as well as younger limestones (Fig. 6). The Naha Formation and its correlatives constitute the main body of the Ryukyu Group and the younger limestones expand seaward, offlapping over the main body, with relatively limited distribution. The Naha Formation and its correlatives are composed of up to five units. Unit 1 is composed of proximal coral limestone and distal detrital limestone. The reddish, diagenetically altered coral limestone is assigned to another lithostratigraphic unit, the Itoman Formation (Fig. 2e;

Kaneko and Ito 2006). Locally, conglomerates and calcareous sandstones were deposited in an embayment on northern Motobu Peninsula (i.e., the Guga and Nakoshi formations, respectively; Yamamoto et al. 2006). In contrast, the distal detrital limestone shows no indications of episodic subaerial exposure. Units 2–4 consist of coral limestone that grades upward into deeper-water facies consisting of rhodoliths, *Cycloclypeus*-*Operculina*, and detrital limestones. Unit 5 is known only from the Yomitan (Odawara et al. 2005b) and consists exclusively of coral limestone. The drastic change in sedimentation between unit 1 and units 2–4 is considered to have been caused by an increased amplitude of sea-level change at ca. 0.8 Ma, possibly related to the Middle Pleistocene Transition (Yamamoto et al. 2006). Unit 4 unconformably overlies unit 3 on southern and central Okinawa Jima (Itoman, Yomitan-Maeda, and Motobu Peninsula) and Ie Jima (Fig. 8; Muraoka et al. 2005; Odawara et al. 2005b; Takeuchi et al. 2006; Yamamoto et al. 2006; Sagae et al. 2012). This unconformity is found on Okinoerabu Jima and Tokunoshima (Iryu et al. 1998; Yamada et al. 2003) and is considered to have been caused by a sea-level fall during the MIS 16 glacial period. The sea level fall during this period was greater than that during other preceding and subsequent glacial periods if it is assumed that δ^{18}O time series of deep-sea benthic foraminifers (Fig. 6) indicate eustatic sea-level changes (Miller et al. 2005). Although this interpretation is based on the foraminiferal δ^{18}O time series from IODP Site U13081 in the North Atlantic Ocean (Fig. 6; Sato et al. 2009), it holds even when using the LR04 stack (Lisiecki and Raymo 2005) and the Prob-stack (Ahn et al. 2017) as the time series. Units 1–5 form a stratigraphic architecture of aggradation and retrogradation, indicating that subsidence continued during the deposition of these units (Fig. 3) to produce accommodation space for reef deposits that formed during subsequent sea-level fluctuations.

The Ryukyu Group on Okinawa Jima is chronologically constrained by calcareous nannofossil biostratigraphy like that on the Miyako Islands. The FO of large *Gephyrocapsa* spp. (1.39 Ma) and LO of *R. asanoi* (0.85 Ma) are located in a lower horizon of unit 1 and immediately below unit 2, respectively (Fig. 6). The FO of *G. oceanica* (1.71 Ma) and LO of *P. lacunosa* (0.45 Ma) have not been detected. The lithostratigraphy and calcareous nannofossil biostratigraphy of the Ryukyu Group allow these units to be correlated with MISs (Fig. 6), whereby unit 1 and units 2–4 were deposited during 1.7–0.8 and 0.8–0.5 Ma, respectively. This interpretation agrees well with Sr isotope ages (1.6–1.3 Ma) obtained from the Itoman Formation, which were reported by Kaneko and Ito (2006) and recalculated in this study based on "The Geologic Time Scale 2020" (Gradstein et al. 2020).

The younger limestones have not been chronologically constrained because of the lack of age-diagnostic fossils. However, Nakamori et al. (1999) argued that the Minatogawa Formation (Fig. 2f), which comprises younger limestone on southern Okinawa Jima, must have been deposited during the last or penultimate interglacial stage, as deduced from the Holocene uplift rate (0.4 mm/years) and the resulting terrace altitude.

The main body of the Ryukyu Group on southern Okinawa Jima is cut by numerous normal faults striking ENE–WSW and ESE–WNW and downthrown predominantly to the north (Fig. 8). Several minor faults cut the Minatogawa Formation.

3.3 Geology of the Okinawa–Miyako submarine plateau

A submarine plateau lies between Okinawa Jima and Miyako Jima (Hamamoto et al. 1979), which was referred to as the "500 m Deep Island Shelf" by Ujiié (1980) and is described in the present study as the OMSP. The OMSP is approximately rectangular in plan view, extending NE–SW with a long side of ~ 135 km and a short side of ~ 35–75 km (Fig. 9). The northeastern end of the OMSP is separated from Okinawa Jima by the Kerama gap, and the southwestern end is separated from Miyako Jima by the Miyako saddle. The OMSP consists of three flat plains that shallow successively from east to west. The shallowest water depths of the eastern and middle plains are 137 m (Higashi-Daikyu-Sone) and 100 m (Nishi-Daikyu-Sone), respectively. The western plain is known as the Miyako-Sone submarine platform (Arai et al. 2014), and its shallowest depth is 21 m at the Zyuho-Sone. This shallowing trend is due to displacement on NW–SE-trending normal faults that are downthrown to the northeast. The southeastern and northwestern margins of the OMSP are truncated by the shelf slopes down to the Ryukyu Trench and the Okinawa Trough, respectively.

Litho- and biostratigraphic analyses have revealed that drillcore deposits from the offshore Okinawa 1 − x well drilled at 215.5 m water depth on the northeastern OMSP (Fig. 9) consist mostly of thick (~ 2700 m) siltstone with fine- and very fine-grained sandstone of the Shimajiri Group underlain by phyllite and overlain by ~ 50 m-thick limestone that may be assigned to the Shimanto Belt and the Ryukyu Group, respectively (Aiba and Sekiya 1979; Sato et al. 2022). *Discoaster quinqueramus* and *D. berggrenii*, which define the top and bottom of the calcareous nannofossil zone NN11 (Martini 1971; = CN9), occur continuously in the Shimajiri Group succession, indicating that the group in this well correlates to the Tortonian–Messinian (Late Miocene) between 8.10 and 5.53 Ma. Although calcareous nannofossils are rare and poorly preserved in the Ryukyu Group, a drillcore

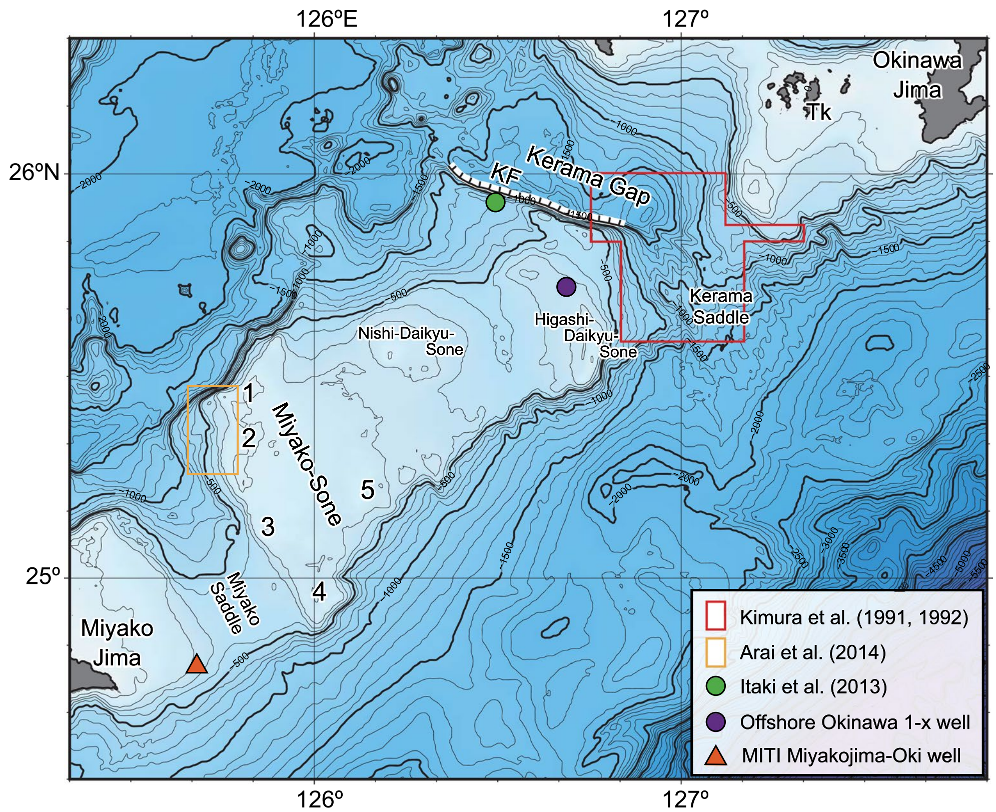

Fig. 9 Bathymetric map of the Okinawa–Miyako submarine plateau. Numbers on the index map indicate banks developed on the platform: 1, Kita Zyuho-Tai; 2, Zyuho-Sone; 3, Hozan-Sone; 4, Minami Hozan-Tai; and 5, Higashi Zyuho-Tai. This map was prepared using Generic Mapping Tools (Wessel et al. 2019). Elevation and depth data are from SRTM15+V2.4 (https://doi.org/10.1029/2019EA000658; accessed 1 Dec 2021). *KF* Kerama fault, *Tk* Tokashiki Jima in the Kerama Islands

sample from the base of the Ryukyu Group contains *Gephyrocapsa parrallela*, which first emerged at 0.99 Ma.

The age of the lower boundary of the Shimajiri Group in the offshore Okinawa 1 – x well (ca. 8 Ma) is similar to that on southern Okinawa Jima (Imai et al. 2017). In contrast, the sedimentation of this group started ca. 2.7 Myr later on Miyako Jima and off its eastern coast (MITI Miyakojima-Oki well; Fig. 9) compared with the northeastern OMSP and Okinawa Jima (Fig. 3). The upper boundary of the Shimajiri Group in the offshore Okinawa 1 – x well (> 5.53 Ma) is at least 3.5 Myr older than that on Miyako Jima and off its eastern coast and Okinawa Jima (ca. 2 Ma). Considering the transition from a siltstone-dominant lithology to a lithology dominated by calcareous fine- and very fine-grained sandstone occupying the uppermost ~ 220 m of the Shimajiri Group in the offshore Okinawa 1 – x well and the large sedimentary gap between the Shimajiri and Ryukyu groups, it is likely that the OMSP was uplifted to form a land area during the Late Miocene at the earliest or the Plio-Pleistocene (but not later than 2 Ma), either when deposition of the Shimajiri Group ceased here earlier than in other regions or when the upper part of the Shimajiri Group (ca. 5.5–2 Ma) was emerged and eroded. The reported age of the Ryukyu Group (< 0.99 Ma) does not necessarily mean that this group dates back to 0.99 Ma on the OMSP but instead reflects a lack of tight chronological constraints owing to the low abundance and poor preservation of calcareous nannofossils. Considering that < 0.27 Ma (age corresponding to the FO of *Emiliania huxleyi*; Sato et al. 2009) carbonate rocks extend over the western margin of the OMSP (Arai et al. 2014) and the Kerama saddle (Fig. 9), a topographic high in the Kemama gap that is interjacent between Okinawa Jima and the OMSP (see Sect. 3.4; Kimura et al. 1991, 1992), they might also cover the eastern margin of the OMSP.

Itaki et al. (2013) collected marine sediments containing fossilized barnacles and molluskan shells along with rounded gravels perforated by boring shells from the northern margin of Higashi-Daikyu-Sone (25° 56′ N, 126° 29′ E; 762 m water depth). The mollusks include two species (*Arca boucardi* and *Cardita leana*) that commonly inhabit the intertidal to upper subtidal zone (0–20 m water depth; Okutani 2017). Calcareous nannofossils retrieved from mollusk-bearing mudstone indicate an age of 1.71–1.39 Ma (denoted here as 1.7–1.4 Ma). This age corresponds to that of the lowest horizon of the Ryukyu Group on Okinawa Jima. Although it is uncertain from which part of Higashi-Daikyu-Sone the mudstone containing these fossils was derived, the occurrence of these fossils suggests that the OMSP may have emerged and expanded in land area until 1.7–1.4 Ma, after deposition of the Shimajiri Group.

Bathymetric mapping and observations of the seafloor using a remotely operated vehicle (Hyper-Dolphin 3 K) on the slopes of the Miyako saddle in the southwestern margin of the OMSP indicate the presence of terraces at water depths of 140, 330, 400, and 680 m and a number of NW–SE-trending faults that extend perpendicular to the axis of the Ryukyu Island Arc (Arai et al. 2014). The surveys revealed that well-indurated carbonate rocks are exposed in terrace margins and on upper slopes and that the lower slopes are covered with modern carbonate sediments. The well-indurated rocks are composed exclusively of off-reef to shelf–shelf-slope carbonates consisting chiefly of bioclastic packstone and rhodolith floatstone. Calcareous nannofossils from the well-indurated carbonate rocks indicate a latest Early–Late Pleistocene age (< 0.85 Ma), which suggests that the rocks correlate to the Ryukyu Group. With increasing distance westward from the western plain of the OMSP, coeval well-indurated carbonate rocks are found at progressively lower levels owing to displacement on normal faults with downthrow to the west. These fault blocks correspond to the abovementioned terraces. As the younger carbonates (0.27–0 Ma) are displaced (Arai et al. 2014, Fig. 8), the faulting must have continued after 0.27 Ma. Calcareous nannofossil biostratigraphic ages and rock sample lithologies (mostly bioclastic packstone and rhodolith floatstone) show that 0.45–0.27 and < 0.27 Ma limestones offlap/overlie 0.85–0.45 Ma limestones on the slope and < 0.27 Ma limestones extend over the western plain of the OMSP (Arai et al. 2014). This evidence indicates that the OMSP, or at least its southeastern margin, began to subside after 0.45 Ma and mostly became sufficiently deep for deposition of the abovementioned offshore facies after 0.27 Ma.

3.4 Geology of the Kerama gap and Kerama saddle

The Kerama gap is a NW–SE-trending structural rift between Okinawa Jima and the OMSP (Figs. 9 and 10). This gap has a steep slope on the southwestern side and a gentler slope on the northeastern side, reaches a maximum water depth of 2100 m (Kato et al. 1982), and is connected to the Okinawa–Miyako Deep Sea Terrace (Fig. 1; Matsumoto et al. 1996; Okamura et al. 2017). Numerous submarine canyons (the Kerama Canyons; Kato et al. 1982) occur on the trench slope of the Ryukyu Trench. The Kerama gap is believed to be underlain by a left-lateral strike-slip fault that displaces pre-Neogene basement of the Ryukyu Islands (Kizaki 1985). Submarine topographic and geological investigations have revealed that the Kerama gap was formed by the activity of a group of NW–SE-trending normal faults during the Pleistocene (Kimura et al. 1991, 1992; Matsumoto and Kimura 1991; Kimura 1996; Matsumoto et al. 1996).

The Kerama saddle (Kimura et al. 1991) is a NE–SW-trending ridge in the southeastern Kerama gap, truncated on the top by a flat, eroded plane extending ~ 40 km from northeast to southwest (Figs. 9 and 10a). Kimura et al. (1991, 1992) made observations of submarine topography and geology and performed sedimentological and chronological analyses of rock samples collected from the Kerama saddle using a multibeam echo sounder (Sea Beam), a towed deep-sea camera, and a submersible (SHINKAI 2000). The stratigraphic succession in this saddle was interpreted to comprise the Shimajiri Group and overlying Ryukyu Group. Calcareous nannofossils and planktic foraminifers were retrieved from Shimajiri Group rock samples collected from the Kerama saddle, 16–50 km east of the offshore Okinawa 1 − x well (Fig. 9). However, because Kimura et al. (1992) observed calcareous nannofossils under a light microscope at magnifications of 400× and 600×, which is not high enough to identify them at the species level (Sato 2013), their chronological interpretation is questionable. Kimura et al. (1991) reported calcareous nannofossil species *Discoaster berggrenii* and *D. quinqueramus* from the Shimajiri Group at Site DT-26. The occurrence of these two species indicates an age of 8.10–5.53 Ma (CN 9). *Ceratolithus acutus* was reported from sites DT-27, DT-28, DT-29, and DT-30(b). The occurrence of this species is limited to the period between 5.36 and 5.04 Ma (Raffi et al. 2020). Although these calcareous nannofossil biostratigraphic ages (8.01–5.04 Ma) are inconsistent with planktic foraminiferal biostratigraphic ages (N22; < 1.93 Ma), as discussed by Kimura et al. (1991), the former accord well with the chronology of the Shimajiri Group established from the offshore Okinawa 1 − x well (8.10–5.53 Ma; Sato et al. 2022) and indicate a large sedimentary gap between the Shimajiri and Ryukyu groups, which is consistent with the interpretation that the OMSP was uplifted to form a land area during the Late Miocene or later period.

The Ryukyu Group in the Kerama saddle has been divided into the Ryukyu Limestone and the overlying Kerama Formation (Kimura et al. 1991, 1992). The Ryukyu Limestone is subdivided into the Naha Limestone equivalent and the Minatogawa Limestone equivalent. The samples assigned to the Naha Limestone

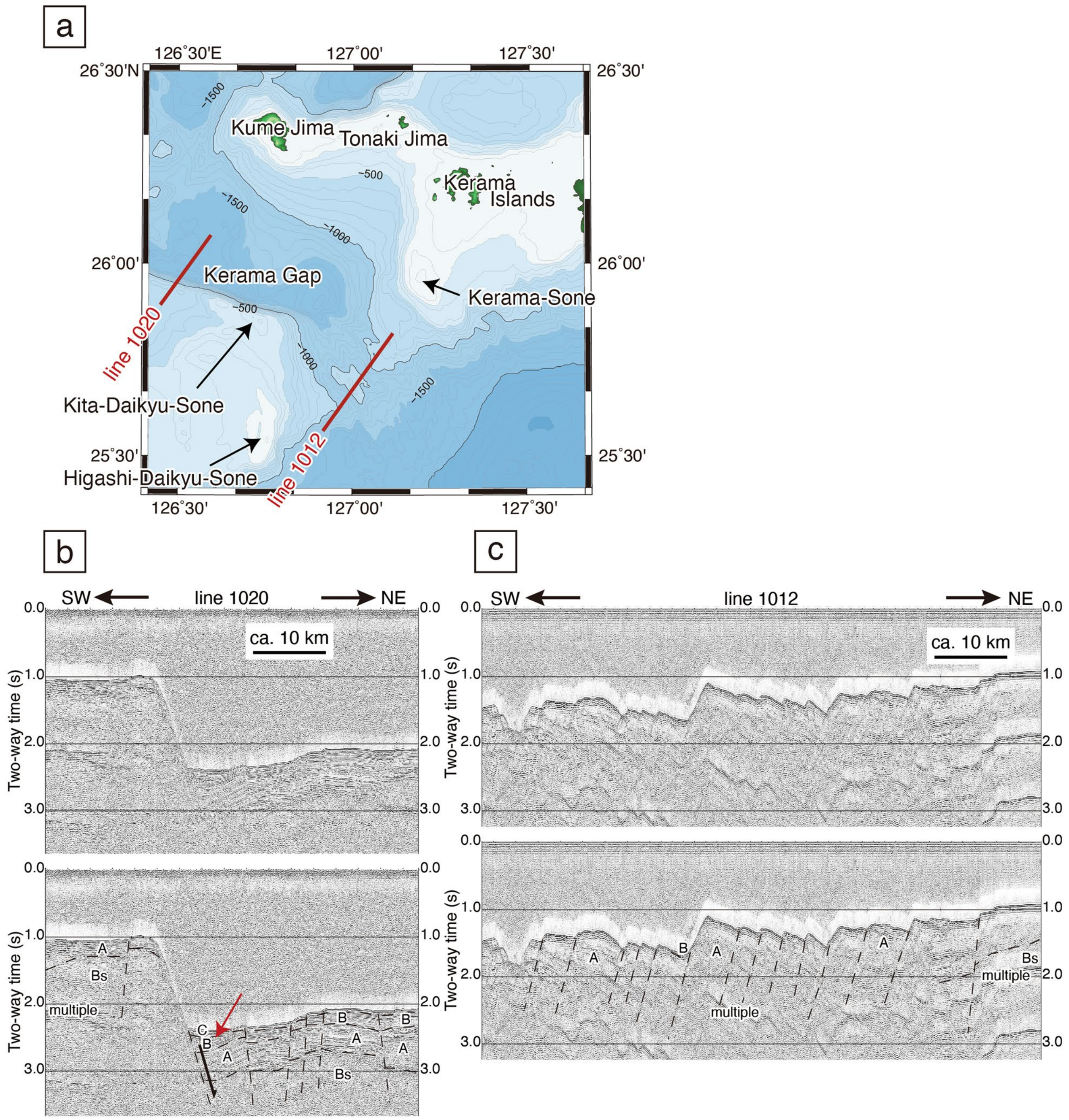

Fig. 10 Seismic sections of the Kerama gap. **a** Submarine topography of the Kerama gap. This map was prepared using Generic Mapping Tools (Wessel et al. 2019). Elevation and depth data are from SRTM15+V2.4 (https://doi.org/10.1029/2019EA000658; accessed 1 Dec 2021). **b** and **c** Seismic sections along lines 1020 and 1012, respectively. Note that the Ryukyu Group equivalent increases its thickness from the basin side toward the fault scarp along the northeastern margin of the OMSP (arrowed). A, Shimajiri Group equivalent; B, Ryukyu Group equivalent; C, Sediment younger than the Ryukyu Group; Bs, Acoustic basement

equivalent have yielded calcareous nannofossils characteristic of the CN15 Zone (< 0.27 Ma). This chronological constraint was considered by those authors to be supported by an electron spin resonance (ESR) age of 0.24 Ma measured for a bivalve (*Amusium pleuronectes*). In contrast, relatively porous and weakly consolidated limestones were assigned by those authors to the Minatogawa Limestone equivalent and considered to be formed during the last interglacial period (MIS 5e), following Kawana (1988).

The Kerama Formation unconformably overlies the Ryukyu Limestone and is composed of the Kerama Limestone and the overlying Kerama Conglomerate. The Kerama Limestone is distinguished from the Minatogawa Limestone equivalent mainly on the basis of its younger ages of approximately 100–30 ka, as determined using accelerator mass spectrometry (AMS) ^{14}C dating of pteropod shells and uranium-series dating by non-destructive γ-ray spectrometry of bulk carbonate samples. The Kerama Conglomerate consists of clasts derived from the Shimajiri Group and the Ryukyu Limestone with a matrix of unconsolidated medium- to coarse-grained sand that yields foraminifers, calcareous nannofossils, and mollusks, from which biogenic carbonate has yielded AMS ^{14}C ages of 20–19 ka.

Kimura et al. (1992) argued that the Kerama gap intermittently emerged and formed part of a land bridge that extended to the Eurasian continent sometime during the period 0.24 Ma to 20 ka. This argument was based on two essential assumptions, although no supporting data exist for them. First, the Kerama Formation unconformably overlies the Ryukyu Limestone, and there is a sedimentary gap between these two stratigraphic units, which was caused by tectonic uplift and the subsequent emergence and erosion of the Kerama saddle. Second, the Minatogawa Limestone equivalent and the Kerama Formation are composed of shallow-water deposits. However, no evidence was presented by Kimura et al. (1992) for the unconformable relationship between the Ryukyu Limestone and the Kerama Limestone. According to hand-specimen and thin-section observations by S. Matsuda (pers. comm., 2021), the limestones collected by Kimura et al. (1991, 1992) from the Kerama saddle were exclusively pelagic limestone (bioclastic packstone with planktic foraminifers), and no shallow-water carbonate rocks were collected. This view is supported by the occurrence of pteropods, a common component in shelf to shelf-slope sediments around the modern Ryukyus (e.g., Tsuji 1993), in the Kerama Limestone (Kimura et al. 1992). These observations suggest that the Kerama saddle area was not located in a shallow-water environment but in a sufficiently and consistently deep-water environment for the formation of pelagic limestone during deposition of the Ryukyu Limestone and the Kerama Formation in the sense of Kimura et al. (1991, 1992). In other words, the Kerama saddle area has been flooded for the last <0.27 Myr; therefore, the hypothesis that the Kerama gap emerged intermittently during the period 0.24 Ma to 20 ka and then rapidly subsided is unlikely.

The marine geological map by Arai and Inoue (2022) shows that the Shimajiri Group equivalent (SGE) is exposed in the Kerama saddle and that its overlying unit (Ryukyu Group equivalent; RGE) extends into the Kerama Canyons located on the trench side of the Kerama gap. The occurrence of the RGE has been confirmed by grab-sampled rocks that correlate to the CN14a Zone [Calabrian to Chibanian (Early to Middle Pleistocene), between 0.99 and 0.45 Ma]. In Sect. 3.5, we discuss the formation of the Kerama gap, referring to the abovementioned data.

3.5 Marine geology of the Kerama gap and surrounds

Arai and Inoue (2022) discussed the formation and evolution of the Kerama gap with respect to marine geological data. To the west of Okinawa Jima, acoustic basement is continuously exposed from east to west on the seafloor from Okinawa Jima to the Kerama Islands (Fig. 10a). In addition, exposed acoustic basement connecting Tonaki Jima and Kume Jima from east to west extends northward to around Aguni Jima. These patterns suggest that the acoustic basement is essentially continuous from east (Okinawa Jima) to west (Kume Jima). During the transgression from the Miocene to the Pliocene, muddy deposits of the SGE onlapped unconformably over the acoustic basement. The Shimajiri Group, which consists of muddy forearc deposits, accumulated on southern Okinawa Jima. The tectonic deformation that formed the Kerama gap caused the demise of sedimentary basins of the Shimajiri Group and its equivalent. Kimura et al. (1991) divided the tectonic movement into two stages, the first resulting in the Kerama fault (Fig. 9; Kato et al. 1982) and the second generating a group of normal faults in the Kerama saddle. Alternatively, Arai and Inoue (2022) argued that a series of tectonic movements formed these faults.

The SGE is well stratified in seismic sections, suggesting that it was deposited in a basin-floor setting. Normal faults cutting the SGE strike WNW to ESE, parallel to the steep northern slope of the northeastern OMSP (Figs. 9 and 10a, b), and are downthrown to the north. The occurrence of a positive flower structures on the basin side of the faults suggests that they are predominantly right-lateral strike-slip faults rather than simple normal faults (Fig. 11). The vertical component of these faults has resulted in more than 1000 m of displacement of the SGE, suggesting that large-scale tectonic movements occurred after deposition of the SGE (Fig. 10b). The overlying RGE increases in thickness from the basin side toward the fault scarp along the northeastern margin of the OMSP (arrowed in Fig. 10b), indicating that the vertical displacement continued during deposition of the RGE. In contrast, on the basin side, the flower structures deform the seafloor topography and cut the RGE, again suggesting that post-SGE tectonic movements continued

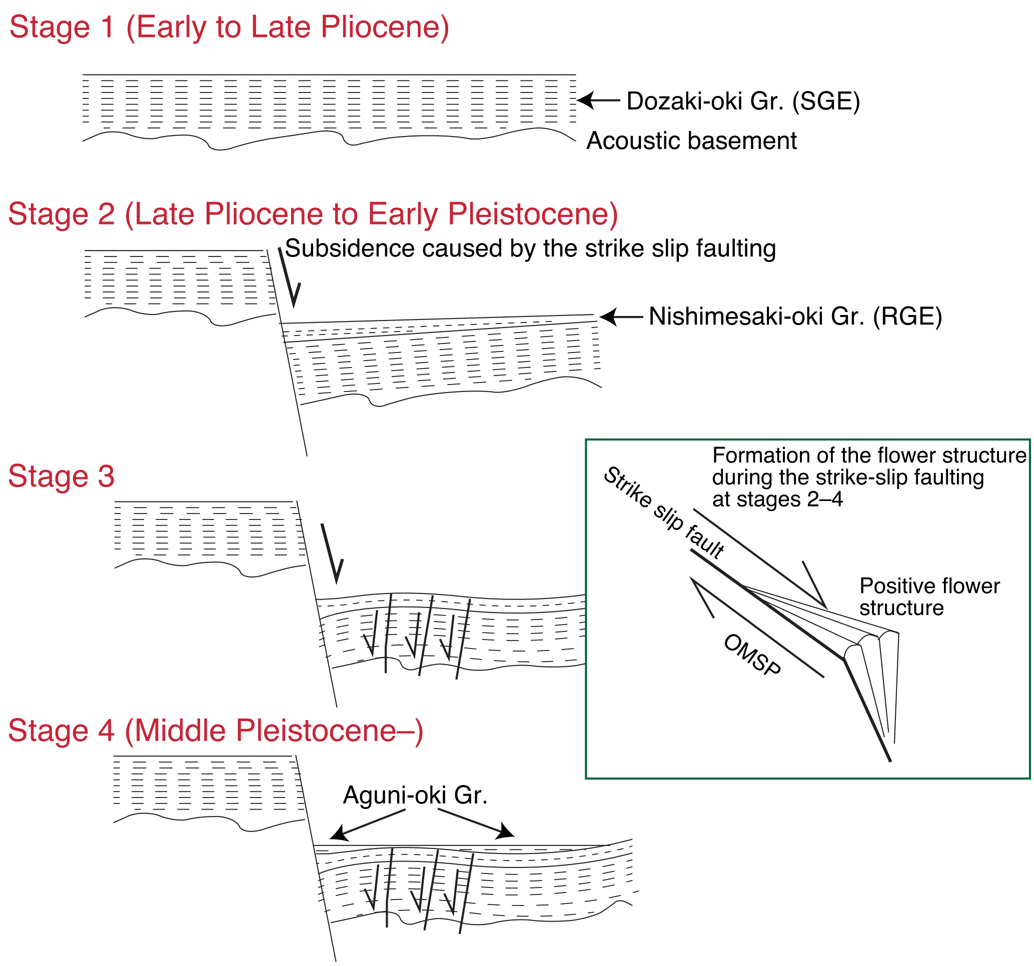

Fig. 11 Schematic diagram showing the formation of the Kerama gap (modified from Arai and Inoue 2022). Stage 1: Deposition of the Douzaki-oki Group on basement rock. Stage 2: Strike-slip faulting, resulting in subsidence of the Kerama gap; Stage 3: Deposition of the Nishimesaki-Oki Group and formation of a positive the flower structure in the Kerama gap; Stage 4: Local deposition of the Aguni-oki Group

with a more significant right-lateral slip component during and after deposition of the RGE. These geological observations suggest that the right-lateral strike-slip faulting that formed the Kerama gap also caused the associated subsidence of this gap and uplift of southern Okinawa Jima and the OMSP, which had been a sedimentary basin for the Shimajiri Group and its equivalent, to form a land area extending from Okinawa Jima via the OMSP to Miyako Jima. The occurrence of the topographic high (the Kerama saddle) in the Kerama gap and a group of normal faults located on the trench side of the saddle are considered to be products of these tectonic movements.

The Tokara and Kerama gaps were initially regarded as having been formed by left-lateral strike-slip faults characterized by the en echelon arrangement of zonal tectonic belts (e.g., Konishi 1965; Ujiié 1980). However, the distribution and geological structure of the Shimajiri and Ryukyu groups and their equivalents indicate that the Kerama gap represents a right-lateral strike-slip fault that was generated by the opening of the Okinawa Trough, causing a trenchward displacement of the Okinawa Jima side relative to the OMSP side. Owing to the trenchward displacement, the right-lateral faulting was associated with large vertical displacement only in the western part of the Kerama gap. In contrast, a group of normal faults extending across the island arc was formed to the southwest of the Kerama Islands, corresponding to the trench-side exit of the Kerama gap and the eastern side of the strike-slip fault, on account of the effect of stretching of the arc (Arai et al. 2018). These normal faults extend mostly NW–SE and are downthrown to the southwest (Fig. 10c). The vertical displacement of each fault is ~ 150 m (0.2 s two-way travel time), which clearly reflects subsidence of the Kerama saddle.

3.6 Vertebrate fossils from Miyako Jima

Abundant vertebrate fossils have been found in fissure, cavity, and cave deposits on the Ryukyu Islands (e.g., Hasegawa 1980; Oshiro and Nohara 2000; Ota 2003). These fossils provide important data about the original fauna on the islands before alteration from human impacts drove native taxa to extinction or favored the establishment of exotic taxa. This is particularly evident on Miyako Jima, where many vertebrate fossils have been found in cave deposits. The first record of mammalian fossils on the island was provided by Tokunaga (1936), who mentioned the occurrence of deer antlers but without any additional information. Subsequently, Otuka (1941) reported fossils of elephants (identified in a recent study as *Mammuthus trogontherii*, a species of mammoth known from the Eurasian continent and Taiwan; Taruno and Kawamura 2007) and deer (*Capreolus* as *C. tokunagai*).

Since World War II, numerous vertebrate fossils of Late Pleistocene and Holocene age have been recovered from cave deposits in Tanahara, Amaga, and Pinza-Abu caves, and most recently from those in Mumyo-no-ana and Tsuzupisuki-Abu caves (e.g., Department of Education, Okinawa Prefectural Government 1985; Miyakojima City Board of Education 2015). These fossils range in age from 25.8 or 26.8 to 8.7 ka (uncalibrated ^{14}C dates; Kawamura et al. 2016). The most scientifically successful excavations were conducted at Pinza-Abu cave in 1982, 1983, and 1984 (Department of Education, Okinawa Prefectural Government 1985), from which 34 species of vertebrates (including *Homo sapiens*) were reported, according to the compilation by Hasegawa (2012).

The Late Pleistocene–Holocene vertebrate assemblages found in the caves of Miyako Jima are quite different in composition from comparable assemblages from other Ryukyu Islands, including Okinawa Jima and Ishigaki

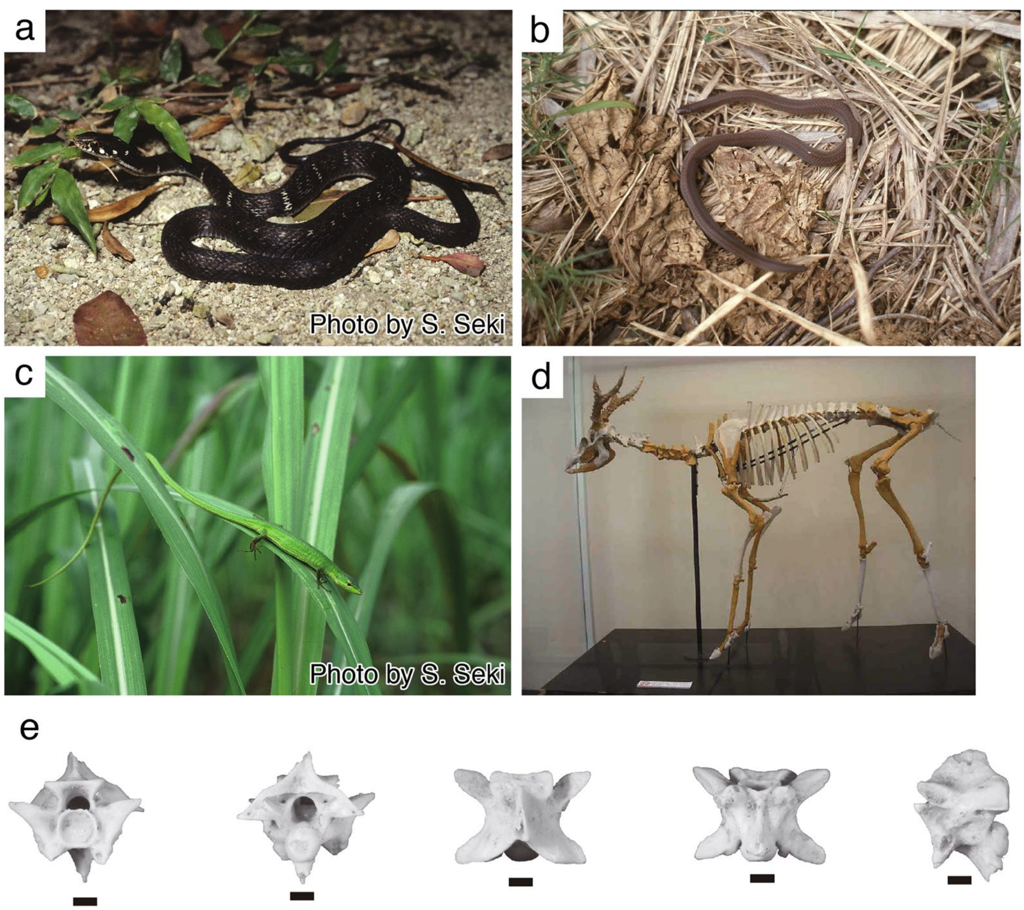

Fig. 12 Modern and fossil vertebrates from Miyako Jima, supporting the OMSP hypothesis. **a** *Hebius concelarus*; **b** *Calamaria pfefferi*; **c** *Takydromus toyamai*; **d** *Capreolus miyakoensis* (reconstructed skeleton housed in Okinawa Prefectural Museum and Art Museum); **e** Vertebra of fossil *Protobothrops* sp. (Ikeda 2007) from Amaga cave (Late Pleistocene, 38,180 ± 180 cal yr BP; Otsuka et al. 2008). Scale bar = 2 mm

Jima (Ota 2003; Hasegawa 2012; Kawamura et al. 2016), as the former include species unique to Miyako Jima [e.g., *Capreolus miyakoensis* (roe deer; Fig. 12d), *Diplothrix* (or *Rattus*) *miyakoensis* (rat), *Mauremys oshiroi* (freshwater turtle), vivarids (including an undescribed large-bodied *Protobothrops* snake; Fig. 12e; Ikeda 2007), and two undescribed flightless birds (a crane and a *Gallirallus* rail); Matsuoka 2000; Hasegawa 2012; Kawaguchi et al. 2009; Takahashi et al. 2015], or those shared exclusively with eastern Eurasia and Taiwan [e.g., *Microtus fortis* (vole); Kaneko and Hasegawa 1995], besides the species found from a broad range of the Late Pleistocene in the South and Central Ryukyus [e.g., *Manouria oyamai* (tortoise): Takahashi et al. 2018]. Of the Late Pleistocene Miyako Jima endemics, *C. miyakoensis* and *M. oshiroi* have their possible closest extant relatives in eastern Eurasia and mainland Japan, respectively (Hasegawa 2012; Takahashi et al. 2015), whereas *D. miyakoensis*, *Protobothrops* sp., and *Gallirallus* sp. are supposedly closest to *D. legata, P. flavoviridis*, and *G. okinawae*, all of which are extant species endemic to the Central Ryukyus, respectively.

Because the Miyako Islands were submerged repeatedly during 1.25–0.4 Ma, these animals are inferred to have migrated into the islands after ca. 0.4 Ma, when the tectonic movement of the islands changed from subsidence to uplift, making them emergent even during sea-level highstands (Sagawa et al. 2001). Most importantly, these terrestrial Miyako Jima animals include those that clearly had limited or no over-sea dispersal ability. It is thus highly likely that the occurrences of these animals reflect the temporary existence of an exposed land area between Okinawa Jima and Miyako Jima, which acted as a land bridge or at least closely spaced islets for their migrations onto Miyako Jima from the Central Ryukyus. However, as the OMSP has a flat top, it is more likely to have formed a single flat island rather than a series of islets. Some topographic highs, such as Higashi-Daikyu-Sone, Nishi-Daikyu-Sone, and Kita Zyuho-Tai, may have existed as hills above the flat top.

3.7 Extant endemic species of the Miyako Islands

The current endemic species/lineages of terrestrial animals on the Miyako Islands include *Hebius concelarus* (Miyako keelback snake ; Fig. 12a), *Calamaria pfefferi* (Pfeffer's reed snake; Fig. 12b), *Takydromus toyamai* (Miyako grass lizard; Fig. 12c), *Bufo gargarizans miyakonis* (Miyako toad), the Miyako lineage of *Microhyla okinavensis* (Okinawa rice frog), and *Geothelphusa miyakoensis* (Miyako freshwater crab). All of these animals have difficulty in extending their distribution across oceans. The divergence times of *H. concelarus* and the Miyako lineage of *M. okinavensis* from their respective most closely related species and lineages have been estimated by modern, objective methods in recent molecular studies (Kaito and Toda 2016; Tominaga et al. 2019). The most closely related species and lineage for each are the Okinawa lineages of *H. pryeri* and *M. okinavensis*, respectively, both of which inhabit Okinawa Jima and its neighboring islands. The divergence time between the Okinawa lineages of *H. pryeri* and *H. concelarus* has been estimated as 2.82 (1.98–3.68) or 2.74 (1.82–3.71) Ma (Kaito and Toda 2016). The divergence time between the Okinawa and Miyako lineages of *M. okinavensis* has been estimated as 4.67 (2.8–6.48) Ma (Tominaga et al. 2019). Thus, both *H. concelarus* and the Miyako lineage of *M. okinavensis* seem to have been maintained as independent lineages for at least the last 2–3 Myr. It is known that the estimates of divergence times for the animals vary markedly. However, because the estimations of times in both Kaito and Toda (2016) and Tominaga et al. (2019) appear to have been made objectively, it is clear that both *H. concelarus* and the Miyako lineage of *M. okinavensis* have long evolutions extending back much farther than ca. 0.4 Ma, when uplift of the Miyako Islands began. Assuming that the two species, as well as other terrestrial endemics, evolved independently on the island that once existed adjacent to Miyako Jima, their evolutionary histories are explainable.

A recent phylogenetic study of the operculate land snail *Cyclophorus turgidus* has also suggested a close relationship between the Okinawa and Miyako lineages (Hirano et al. 2022). According to that study, the most closely related taxon to the Miyako lineage (*C. turgidus miyakonis*) is *C. turgidus turgidus* from northern Okinawa Jima, with a divergence time of 0.92 (1.46–0.41) Ma. Considering the range (95% confidence interval) for the time, the distinction between the Okinawa and Miyako lineages of *C. turgidus* also seems to be consistent with our new hypothesis (the OMSP hypothesis, see Sect. 4) of the uplift and emergence of the OMSP during the Late Miocene or later period and its connection with Okinawa Jima and subsequent separation between the OMSP and Okinawa Jima during the Early Pleistocene (1.71–1.39 Ma).

Segawa (2011) conducted a molecular phylogenetic study of the freshwater crab genus *Geothelphusa* and estimated the divergence time between *G. miyakoensis* on Miyako Jima and its sister species *G. levicervix* of Tokashiki Jima (Fig. 9), an islet ~25 km west of Okinawa Jima, to be no older than 0.16 Ma. This estimate is much smaller than those for other terrestrial taxa/lineages between Miyako Jima and the Okinawa Islands (see above), and even if the OMSP had been uplifted and emerged during the the Late Miocene or later period, this would be inconsistent with the above estimation. As in many other studies that have estimated divergence times in organisms using the molecular clock method, the adequacy of Segawa's (2011) estimate is strongly influenced by the adequacy of assuming a particular divergence time for calibration, which is that the divergence time for another pair of *Geothelphusa* species, one occurring on the southwestern side and the other on the northeastern side of the broad gap between land, including the Tokara Strait, corresponds to the inferred time of strait formation (1.6 Ma). However, neither of the two *Geothelphusa* representatives occur on lands immediately adjacent to the Tokara Strait; therefore, the value of divergence used for calibration may be underestimated substantially. To estimate the divergence time between *G. levicerevix* and *G. miyakoensis* with certainty, more reliable calibration points for the genus are required.

Takydromus toyamai, *Calamaria pfefferi*, and *Bufo gargarizans miyakonis* are also notable extant endemic species of the Miyako Islands. The closest relatives or subspecies of all three species are distributed in the eastern part of the Eurasian continent (mainland China) and Taiwan. However, the same or closely related species are not distributed on Okinawa Jima and its neighboring islands or on the Yaeyama Islands (Ota 1998). The processes of the migration to and colonization of the Miyako Islands by these endemic species remain unknown. Three migration routes are assumed for the endemic species/subspecies on the Miyako Islands with limited or no over-sea dispersal ability:

(1) Ancestors of the endemic taxa were isolated from mainland China on the Ryukyu Islands by the opening of the Okinawa Trough (<6 Ma; Kamata and Kodama 1999), survived in some islands of the Central and North Ryukyu Islands, and migrated to the Miyako Islands via the OMSP at <0.4 Ma. They could survive only on the Miyako Islands as endemic taxa. However, they were unable to migrate to the Yaeyama Islands, located 130 km west of the Miyako Islands and separated by sea.

(2) Because the distance between mainland China and the Ryukyu Islands was much shorter than at present during the early stage of the opening of the Okinawa Trough (ca. 6 Ma), the ancestors of the endemic taxa might have migrated from mainland China to some islands of the Ryukyu Islands, from where they migrated to the Miyako Islands at <0.4 Ma.

(3) The current endemic taxa or their ancestors reached the Miyako Islands from southern China or Taiwan by using intervening islands/islets as stepping stones (e.g., Yang et al. 2018).

4 OMSP hypothesis

The Miyako Islands repeatedly underwent complete submergence during deposition of the main body of the Ryukyu Group (1.25–0.4 Ma). Therefore, it is certain that the vertebrate fossils from fissure, cavity, and cave deposits on these islands are those of taxa that migrated to the islands after ca. 0.4 Ma when the islands were uplifted to become a stable land area. Some of these fossil vertebrates or their close relatives are found in the Central Ryukyu Islands (e.g., *Diplothrix miyakoensis*, *Protobothrops* sp., and *Gallirallus* sp.; see Sect. 3.6). Moreover, some of the species/lineages that are currently confined to the Miyako Islands, such as *Hebius concelarus*, the Miyako lineage of *Microhyla okinavensis,* and *Geothelfusa miyakoensis*, also have their closest relatives but with slight morphological and genetic differences on Okinawa Jima and/or adjacent Central Ryukyu Islands. These groups of fossils and extant animals on the Miyako Islands are likely to have migrated from the Central Ryukyu Islands. However, Miyako Jima and Okinawa Jima (or islets in the vicinity of the latter) are currently separated by a distance of ~300 km over open sea, and these taxa have limited or no ability for over-sea dispersal. To resolve this apparent discrepancy, we propose the "OMSP hypothesis", which is that the OMSP once emerged to form a land area that temporarily acted as a land bridge or at least a series of islets for some terrestrial animals to reach Miyako Jima from Okinawa Jima or its vicinity. Details of this hypothesis are presented below in chronological order.

4.1 Chronological snapshots

4.1.1 After deposition of the Shimajiri Group to before deposition of the Ryukyu Group

The uppermost Shimajiri Group in the offshore Okinawa 1−x well drilled on the northeastern OMSP is correlated to the NN11 (=CN9) Zone [Tortonian to Messinian (Late Miocene), 8.10 to 5.53 Ma], which is older than that on the Miyako Islands and Okinawa Jima (ca. 2 Ma). The OMSP appears to have been uplifted earlier than the Miyako Islands and Okinawa Jima and existed as a terrestrial area from the Late Miocene or later period.

Uplift of the Miyako Islands and Okinawa Jima began when deposition of the Shimajiri Group (Minebari and Shinzato formations, respectively) had ceased at ca. 2 Ma (Fig. 3). On Okinawa Jima, the central axis of the southern part of this island, which is defined as a NE–SW-trending area with higher elevations extending from present-day Nishihara to Itoman (Fig. 8), emerged at this time (Fig. 13a). In contrast, on the northwestern and southeastern sides of the central axis (present-day Naha Port and Katsuren and Chinen peninsulas, respectively; Fig. 8), uplift started later than (and/or was not as pronounced as) that along the central axis. The Chinen Formation was deposited in a shelf environment on both sides of the central axis. The Miyako Islands emerged at essentially the same time (ca. 2 Ma) as the central axis

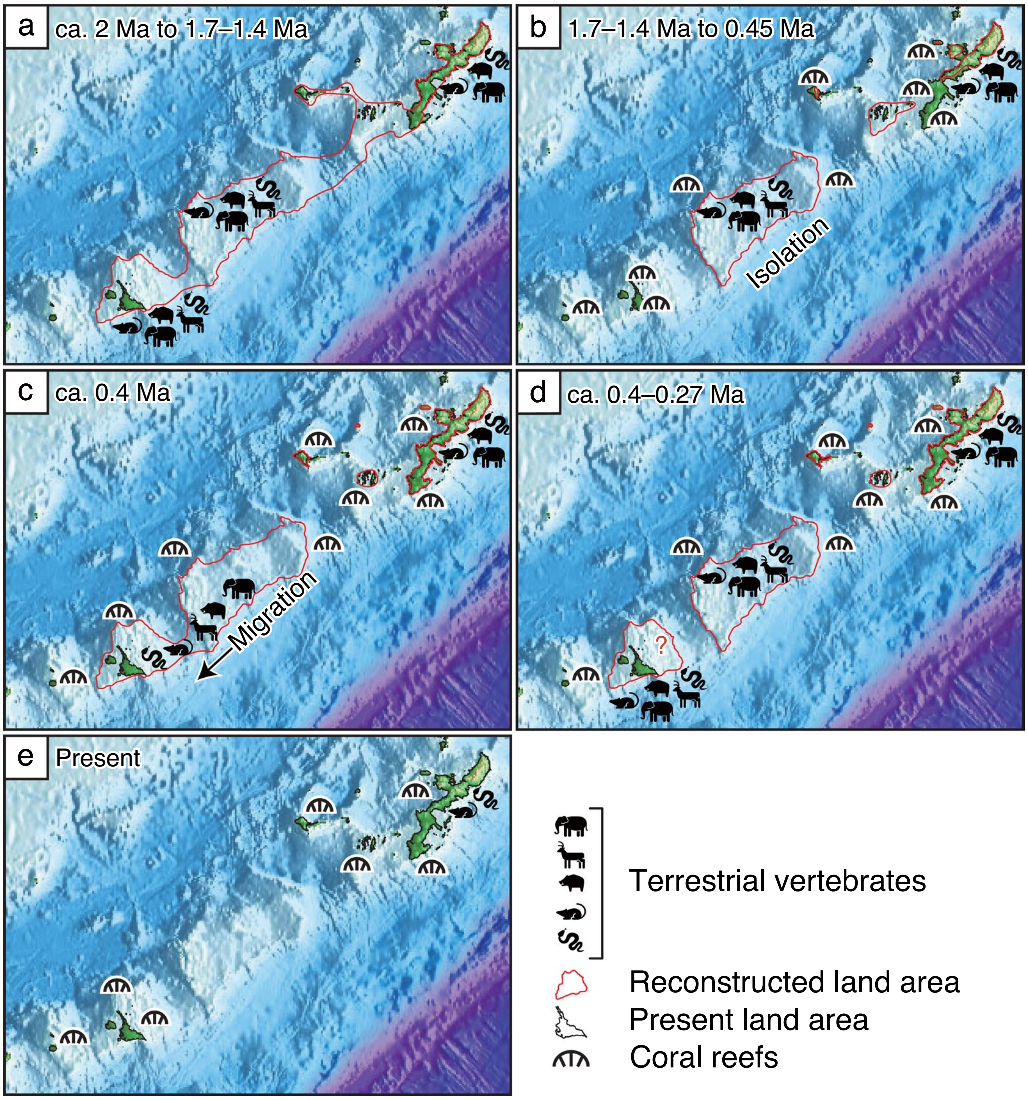

Fig. 13 Changes in the paleogeography of the Okinawa–Miyako area and migration of terrestrial vertebrates. Chronological snapshots of the Okinawa–Miyako area and the migration of terrestrial vertebrates to the Miyako Islands. The background map (topography and bathymetry) is derived from Fig. 1. **a** Period from after deposition of the Shimajiri Group to before deposition of the Ryukyu Group (ca. 2 to 1.7–1.4 Ma). We assume that the areas where the Ryukyu Group unconformably overlies the Shimajiri Group and where the Chichibu and Shimanto accretionary complexes occur were land areas during this period. **b** Period of interglacial highstands of sea level during deposition of the main body of the Ryukyu Group (1.7–1.4 to 0.45 Ma). We assume that the area currently covered by the main body was submerged, where coral reefs and associated fore-reefs and shelves were distributed. Note that reef formation started significantly later on the Miyako Islands (1.25 Ma on Irabu Jima and 0.96 Ma on Miyako Jima) than on Okinawa Jima (1.7–1.4 Ma). **c** Period immediately after deposition of the main body of the Ryukyu Group (ca. 0.4 Ma). **d** Period after deposition of the main body of the Ryukyu Group (ca. 0.4–0.27 Ma). The OMSP was almost completely submerged after 0.27 Ma. **e** Present. The vertebrate symbols denote, from upper to lower, elephant, deer, wild boar, mouse, and snake. See the Sects. 3.6 and 3.7 for the relevant taxa

of the southern part of Okinawa Jima. As far as southern Okinawa Jima, the Kerama saddle, and the OMSP, this uplift was driven by the vertical component (up to 1000 m displacement) of the right-lateral strike-slip faulting that formed the Kerama gap, corresponding to the Chinen Disturbance event (Matsumoto et al. in press).

During the interval between ca. 2 and 1.7–1.4 Ma (after deposition of the Shimajiri Formation and before deposition of the Ryukyu Group), Okinawa Jima and the OMSP (and even the Miyako Islands) were connected to form a single land area extending ~ 400 km NE–SW (Fig. 13a). The animals and plants that inhabited Okinawa Jima expanded their distribution throughout this large island, which corresponds to the Early Pleistocene land bridge that was assumed to have existed during the period 2.0–1.1 Ma to explain, for example, the presence of *Hebius concelarus*, an endemic snake from Miyako Jima (Kaito and Toda 2016).

4.1.2 During deposition of the main body of the Ryukyu Group

The main body of the Ryukyu Group began to be deposited between 1.7 and 1.4 Ma in southern and central Okinawa Jima (Fig. 13b). Coral reefs were formed in the shallow waters surrounding the island, and bioclastic sediments dominated locally by rhodoliths accumulated in off-reef to shelf areas. These reef to shelf carbonates were deposited corresponding to Quaternary glacioeustatic changes in sea level, during which central to southern Okinawa Jima continuously subsided to produce accommodation space for reef deposits that formed during subsequent changes in sea level. As a result, the central to southern of Okinawa Jima were submerged repeatedly, meaning that this island was separated from the OMSP by sea.

Deposition of the Ryukyu Group started at 1.25 Ma on Irabu Jima and 0.96 Ma on Miyako Jima, later than on Okinawa Jima. No reef to shelf carbonates are known to have been deposited after 0.65 Ma on Miyako Jima. However, the stratigraphy of the Ryukyu Group on Miyako Jima has not been studied over the entire island, and it is likely that deposition continued until ca. 0.4 Ma on Miyako Jima, as on Irabu Jima. On the Miyako Islands, reef to shelf carbonates were deposited corresponding to Quaternary glacioeustatic sea-level changes, during which the islands subsided. Because the Miyako Islands are completely covered by the Ryukyu Group, the islands are inferred to have been submerged repeatedly during its deposition. So far as we know, on the OMSP, the limestones that formed during 0.85–0.27 Ma are distributed on the slope, and those that were deposited during 0.27–0 Ma extend over the plateau and the upper slope. The abovementioned findings suggest that the plateau emerged an island (or closely spaced islets) sometime between 5.53 and 0.27 Ma (i.e., after deposition of the Shimajiri Group and before deposition of < 0.27 Ma limestone). We are convinced that many of the animals which have been found in fissure, cavity, and cave deposits on Miyako Jima (such as those at Pinza-Abu cave) and had limited or no over-sea dispersal ability are common to or related to those on Okinawa Jima or more northerly islands and could have survived only on areas of the OMSP exposed above sea level during this period. Otherwise, we would be forced to assume an utterly improbable migration scenario from Okinawa Jima to the Miyako Islands that involved crossing 300 km of sea after deposition of main body of the Ryukyu Group (< 0.4 Ma on the Miyako Islands), despite the non-existent or limited over-sea dispersal ability of these animals. Some Late Pleistocene and extant endemic species on the Miyako Islands are thought to have diverged on the OMSP during this period. For example, the divergence time of *H. concelarus* has been estimated at 3.7–1.8 Ma (Kaito and Toda 2016). This estimate of divergence time is likely slightly too old due to factors such as ancestral polymorphisms and geographic genetic variation in the ancestral taxon. Thus, it is roughly compatible with the timing of the isolation of the OMSP from Okinawa Jima (1.7–1.4 Ma) inferred from geological data. This compatibility supports the OMSP hypothesis proposed in this paper.

4.1.3 After deposition of the main body of the Ryukyu Group

The Miyako Islands and Okinawa Jima began to be uplifted after deposition of the main body of the Ryukyu Group (ca. 0.4 Ma on the Miyako Islands and < 0.45 Ma on Okinawa Jima). The OMSP was temporarily connected to the Miyako Islands (Fig. 13c). The animals that inhabited the OMSP migrated to the Miyako Islands after ca. 0.4 Ma. NNW–SSE-trending normal faults downthrown to the east formed on the Miyako Islands, and Miyako Jima was separated from the OMSP by this faulting (Fig. 13d). In contrast, ENE–WSW- and ESE–WNW-trending normal faults formed on Okinawa Jima. At the same time, the OMSP subsided with the formation of NW–SE-trending normal faults downthrown to the northeast, resulting in a submarine plateau topography that is higher in the southwest and lower in the northeast. This faulting-induced subsidence began after 0.45 Ma, and the OMSP became mostly deep enough for the deposition of off-reef to shelf and/or shelf-slope carbonates after 0.27 Ma (Fig. 13d and e), except for the southwestern part, which emerged during sea-level lowstands (Arai et al. 2016). In conclusion, the animals that inhabited the OMSP migrated to the Miyako Islands after the emergence of the Miyako Islands and before the submergence of the OMSP (0.4–0.27 Ma).

Several faults cut the Minatogawa Formation, although the displacements along these faults are small (mostly less than several centimeters, with an exception as large as 1.5 m), suggesting that the faulting was almost finished before deposition of the Minatogawa Formation and its equivalent younger limestones (Fig. 6). However, the age of the Minatogawa Formation is not well constrained, and determination of its age is required in future research.

4.2 Tectonic implications

We discuss the subsidence of the area extending from Okinawa Jima to Miyako Jima with reference to the formation of normal faults in the island areas of the Ryukyu Island Arc (RIA) during the Quaternary. In most of the island areas of the RIA, such as Okinawa Jima and Miyako Jima, the tension axis inferred from earthquake mechanism solutions is parallel to the orientation of the island arc (Kubo and Fukuyama 2003; Otsubo et al. 2008). Anderson's theory (Anderson 1951) predicts that the stress field with a tension axis parallel to the island arc is expected to form normal faults that strike across the island arc. The orientation of tension axis in the RIA is consistent with the development of NW–SE-striking normal faults (Kizaki 1985; Matsumoto et al. 2009; Arai et al. 2014), some of which have been reported as active faults (Active Fault Research Group 1991). The development of the normal faults was associated with the opening of the Okinawa Trough (an active backarc basin) as "arc-parallel stretching", an elongational deformation that develops parallel to the island arc owing to the overhang of the island arc to the trench side caused by the opening of the Okinawa Trough (Fabbri and Fournier 1999; Fournier et al. 2001; Kubo and Fukuyama 2003). Given that these normal faults cut the Ryukyu Group on Okinawa Jima and Miyako Jima, the onset of the island-arc parallel stretching is inferred as having occurred between post-Ryukyu Group deposition (after ca. 0.4 Ma) and the present. As the opening of the Okinawa Trough became active at ca. 0.2 Ma (Sibuet et al. 1998), subsidence of the OMSP below sea level was most likely driven by the opening of the Okinawa Trough. This interpretation is in accordance with the marine geological data described in Sect. 3.5.

Insights into the Quaternary subsidence of the Kerama gap and the OMSP can be gained from the pattern of free-air gravity anomalies. A free-air gravity anomaly with a long wavelength represents deviation from the isostatic state and indicates that tectonic forces are dynamically supporting the topography (Melosh and Raefsky 1980). The free-air gravity anomaly pattern for the area of the RIA is shown in Fig. 14 (Sawada et al. 2009). The anomalies are positive around islands of the RIA (Matsumoto et al. 1996). In contrast, the anomalies are negative in the Kerama gap, breaking the positive anomaly pattern around the RIA (Matsumoto et al. 1996). These negative anomalies indicate that the Kerama gap is deeper than the state in which isostasy can be established. Free-air gravity anomalies over the Kerama gap are more negative than those over the Okinawa Trough, which is currently undergoing rifting, and they are slightly positive over the OMSP, although the seafloor of the OMSP (50–500 m water depth; Fig. 9) is shallower than that over the

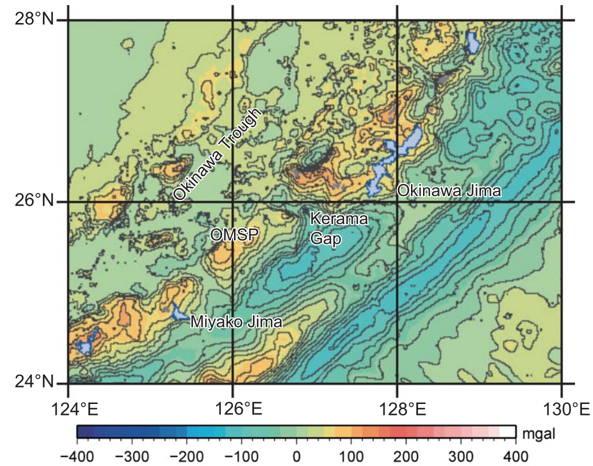

Fig. 14 Free-air gravity anomaly pattern derived from observed gravity and bathymetry data for the Ryukyu Island Arc (Sawada et al. 2009)

Kerama gap (2100 m water depth at the deepest point) (Sawada et al. 2009). The positive anomalies over the OMSP are similar to those over the island areas around Okinawa Jima and Miyako Jima and imply that the OMSP has maintained isostasy under active normal faulting. Considering the difference in seafloor depth between the Kerama gap and the OMSP, we suggest that the difference in the free-air gravity anomalies represents the difference in subsidence rate of the Kerama gap and the OMSP after deposition of the Ryukyu Group.

Furthermore, although Okinawa Jima, Miyako Jima, and the OMSP have positive free-air gravity anomalies, the OMSP is slightly smaller than both Okinawa Jima and Miyako Jima (Fig. 14). The area between the Kerama gap and the Miyako saddle, including the OMSP, is located at the hinge of flexure of the Ryukyu Arc (Fig. 1). The locations of Okinawa Jima, Miyako Jima, and the OMSP may have caused spatial differences in the amount of subsidence caused by NW–SE-trending normal faults owing to parallel stretching of the island arc. The differences may be expressed as uplift of Okinawa Jima and Miyako Jima and subsidence of the OMSP over the past 400 kyr.

5 Conclusions

In this paper, we have proposed a new hypothesis (the OMSP hypothesis) to at least partially explain the origin of modern and Late Pleistocene terrestrial vertebrates of the Miyako Islands and the timing and pathway of their migration to the islands. The terrestrial vertebrates include extant and fossil taxa that are common with those on Okinawa Jima currently separated by ~300 km of sea, despite their limited or non-existent ability for over-sea dispersal. Such fossil vertebrates are commonly found in fissure, cavity, and cave deposits. Southern Okinawa Jima was rapidly uplifted and became a land area after deposition of the Shimajiri Gruop had ceased at ca. 2 Ma. This land area was connected to the OMSP, which had been uplifted and emerged during the Late Miocene or later period, forming a large island extending ~400 km NE–SW. The terrestrial animals and plants inhabiting Okinawa Jima expanded their distribution throughout the large island. Subsequently, Okinawa Jima subsided, to be flooded and fringed by coral reefs at 1.7–1.4 Ma, when the island was separated from the OMSP. Therefore, the migration of terrestrial organisms occurred during a rather narrow interval at ca. 2 to 1.7–1.4 Ma. The subsidence lasted until <0.45 Ma, during deposition of the main body of the Ryukyu Group. The Miyako Islands were also uplifted after deposition of the group had ceased at ca. 2 Ma. The islands repeatedly underwent complete submergence during deposition of the main body of the Ryukyu Group (1.25–0.4 Ma). The islands were then uplifted and emerged to become a land area after ca. 0.4 Ma. In contrast, the OMSP began to subside after 0.45 Ma and mostly became sufficiently deep for deposition of the abovementioned offshore facies after 0.27 Ma. During the interval from ca. 0.4 to 0.27 Ma, terrestrial vertebrates moved from the OMSP to the Miyako Islands.

The OMSP hypothesis is a new hypothesis based on an integration of geology and phylogeography. To verify and refine this hypothesis, it is essential to obtain basic geological data for the OMSP, as reliable data are currently limited for this plateau (e.g., Arai et al. 2014, 2016) and only a single well has been drilled there (offshore Okinawa I−x well; Aiba and Sekiya 1979; Sato et al. 2022). There is also a need for ocean drilling at multiple locations on the OMSP.

Abbreviations

AMS	Accelerator mass spectrometry
CN zones	Neogene coccolith zone of Okada and Bukry (1980)
EPL	Early Pleistocene land bridge
FO	First occurrence
LO	Last occurrence
MITI	Ministry of International Trade and Industry of Japan
N zones	Neogene planktic foraminiferal zones of Blow (1969)
NN zones	Neogene nannofossil zones of Martini (1971)
OMSP	Okinawa–Miyako submarine plateau
PL zones	Pliocene planktic foraminiferal zones of Berggren et al. (1995)
RGE	Ryukyu Group equivalent
SGE	Shimajiri Group equivalent

Acknowledgements
YI thanks all students affiliated to the Laboratory for Carbonate Sedimentology and Geochemistry Laboratory, Tohoku University, and who worked on the stratigraphy of the Ryukyu Group. All authors express special thanks to N. Kaneko of GSJ/AIST, S. Seki, and Okinawa Prefectural Museum and Art Museum for providing photographs (Figs. 2d and 12a, c and d, respectively). The geological map of Miyako Jima (Fig. 5) is courtesy of S. Yamada. We thank H. Takayanagi and M. Arakane for preparing the figures. This manuscript was improved by comments and suggestions of the Editor (H. Kawahata) and three anonymous reviewers.

Author contributions
NW, KA, HO, and YI conceptualized and designed this study. KA and MO examined the OMSP hypothesis from the perspectives of marine geology and structural geology, respectively. SC, TS, and YI performed sedimentological and biochronological analyses of the Ryukyu Group. HO, MT, AT, TI, and ATk contributed to this study from the perspective of phylogeography. All authors collaborated in the interpretation of data and the preparation of the manuscript. The final manuscript was read and approved by all authors.

Funding
This study was partly financially supported by Frontier Research in Duo (FRiD) of Tohoku University to YI.

Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai 980-8578, Japan. [2]Research Institute of Geology and Geoinformation, Geological Survey of Japan/AIST, Tsukuba 305-8567, Japan. [3]Research Institute of Earthquake and Volcano Geology, Geological Survey of Japan/AIST, Tsukuba 305-8567, Japan. [4]Tropical Biosphere Research Center, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan. [5]Faculty of Education, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan. [6]Department of Earth Resource Science, Akita University, Akita 010-8502, Japan. [7]Institute of Natural and Environmental Sciences, University of Hyogo, and the Museum of Nature and Human Activities, Sanda, Hyogo 669-1546, Japan. [8]Faculty of Biosphere-Geosphere Science, Okayama University of Science, Ridaicho 1-1, Kitaku, Okayama 700-0005, Japan.

Received: 3 October 2022 Accepted: 29 June 2023
Published online: 20 July 2023

References

Active Fault Research Group (1991) Active faults in Japan sheet: maps and inventories. University of Tokyo Press, Tokyo

Ahn S, Khider D, Lisiecki LE, Lawrence CE (2017) A probabilistic Pliocene–Pleistocene stack of benthic $\delta^{18}O$ using a profile hidden Markov model. Dyn Stat Clim Syst 2:dzx002. https://doi.org/10.1093/climsys/dzx002

Aiba J, Sekiya E (1979) Distribution and characteristics of the Neogene sedimentary basins around the Nansei-Shoto (Ryukyu Islands). J Jpn Assoc Petrol Technol 44:329–340. https://doi.org/10.3720/japt.44.329. (**in Japanese with English abstract**)

Ali JR, Heaney LR (2021) Wallace's line, Wallacea, and associated divides and areas: history of a tortuous tangle of ideas and labels. Biol Rev 96:922–942. https://doi.org/10.1111/brv.12683

Anai C, Shibuya H, Mochizuki S (2017) Magnetostratigraphy of the Ryukyu Group in Miyakojima Island, Okinawa, Japan. J Geol Soc Jpn 123:1035–1048. https://doi.org/10.5575/geosoc.2017.0052. (**in Japanese with English abstract**)

Anderson EM (1951) The dynamics of faulting and dyke formation with application to Britain, 2nd edn. Oliver & Boyd, Edinburgh

Arai K, Inoue T (2022) Geological map of the vicinity of Kumejima Island. Marine geology map series, no. 92, Geological Survey of Japan, AIST, Tsukuba. Retrieved from https://www.gsj.jp/Map/EN/marine-geology.html#092. Accessed 10 Sept 2022 **(in Japanese with English abstract)**

Arai K, Machiyama H, Chiyonobu S, Matsuda H, Sasaki K, Humblet M, Iryu Y (2014) Subsidence of the Miyako-Sone submarine carbonate platform, east of Miyako-jima Island, northwestern Pacific Ocean. Isl Arc 23:1–15. https://doi.org/10.1111/iar.12051
Arai K, Matsuda H, Sasaki K, Machiyama H, Yamaguchi T, Inoue T, Sato T, Takayanagi H, Iryu Y (2016) A newly discovered submerged reef on the Miyako-Sone platform, Ryukyu Island Arc, Northwestern Pacific. Mar Geol 373:49–54. https://doi.org/10.1016/j.margeo.2016.01.007
Arai K, Inoue T, Sato T (2018) High-density surveys conducted to reveal active deformations of the upper forearc slope along the Ryukyu Trench, western Pacific, Japan. Prog Earth Planet Sci 5:45. https://doi.org/10.1186/s40645-018-0199-0
Berggren WA, Kent DV, Swisher CC III, Aubry M-P (1995) A revised cenozoicgeochronology and chronostratigraphy. In: Berggren WA, Kent DV, Aubry M-P, Hardenbol J (eds) Geochronology, time scales and global stratigraphic correlation: a unified temporal framework for an historical geology, vol 54. SEPM Special Publication, Society for Sedimentary Geology (SEPM), Tulsa, pp 129–212
Blow WH (1969) Late middle eocene to recent planktonic foraminiferal biostratigraphy. In: Brönniman P, Renz HH (eds) Proceedings of the first international conference on planktonic microfossils, Geneva, 1967, vol 1. E. J. Brill, Leiden
Chiyonobu S, Saruwatari H, Sato T, Kabamoto J, Iryu Y (2009) Geologic ages of the Chinen Formation on the Katsuren Peninsula, Okinawa-jima based on calcareous nannofossil biostratigraphy. J Geol Soc Jpn 115:528–539. https://doi.org/10.5575/geosoc.115.528. (**in Japanese with English abstract**)
Cowie RH, Holland BS (2006) Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. J Biogeogr 33:193–198. https://doi.org/10.1111/j.1365-2699.2005.01383.x
Darwin C (1859) On the origin of species by means of natural selection. John Murray, London
de Queiroz A (2005) The resurrection of oceanic dispersal in historical biogeography. Trends Ecol Evol 20:68–73. https://doi.org/10.1016/j.tree.2004.11.006
Dedeine F, Dupont S, Guyot S, Matsuura K, Wang C, Habibpour B, Bagneres A-G, Mantovani B, Luchetti A (2016) Historical biogeography of *Reticulitermes* termites (Isoptera: Rhinotermitidae) inferred from analyses of mitochondrial and nuclear loci. Mol Phyl Evol 94:778–790. https://doi.org/10.1016/j.ympev.2015.10.020
Department of Education, Okinawa Prefectural Government (ed) (1985) Pinza-Abu: reports on excavation of the Pinza-Abu cave. Department of Education, Okinawa Prefectural Government, Naha **(in Japanese)**
Doan DB, Pasdur JE, Fosberg FR (1960) Military geology of the Miyako archipelago, Ryukyu-retto. Geological Surveys Branch, Intelligence Division, Office of the Engineer, HQ, US Army Forces, Far East, Personnel of US Geological Survey
Emiliani C (1955) Pleistocene temperatures. J Geol 63:538–578. https://doi.org/10.1086/626295
Fabbri O, Fournier M (1999) Extension in the southern Ryukyu arc (Japan): link with oblique subduction and back arc rifting. Tectonics 18:486–497. https://doi.org/10.1029/1999TC900001
Fournier M, Fabbri O, Angelier J, Cadet JP (2001) Regional seismicity and onland deformation in the Ryukyu arc: implication for the kinematics of opening of the Okinawa Trough. J Geophys Res Solid Earth 106:13751–13768. https://doi.org/10.1029/2001JB900010
Fujita K, Chiyonobu S, Mizobuchi T, Iryu Y (2011) Discovery and significance of the Chinen Formation from a submarine core drilled off Naha Port, Okinawa-jima, southwestern Japan. J Geol Soc Jpn 117:625–631. https://doi.org/10.5575/geosoc.2011.0016. (**in Japanese with English abstract**)
Fukuta O, Motojima K, Ijima S, Oyama K, Fujii N, Ueda Y, Sato Y, Suzuki T, Kageyama K, Natori H, Takai S, Tanaka S, Ogawa K, Suda Y, Oka S, Ishigaki K, Katoh K, Fujinuki T, Kawano M, Nagata S, Hirukawa T, Itoh S, Murakami T, Ishida M, Murase T (1970) Natural gas resources of the Ryukyu Islands—preliminary report by the 5th phase survey team of GSJ. Bull Geol Surv Jpn 21:627–672 (**in Japanese with English abstract**)
Furukawa M, Fujitani T (2014) Comparative study of Pleistocene paleogeographic maps of Ryukyu Arc. Bull Fac Sci Univ Ryukyus 98:1–8 (**in Japanese with English abstract**)
Geographical Survey Institute of Japan and Japan Coast Guard (2007) Gazetteer of Japan. Retrieved from https://www.gsi.go.jp/kihonjohochousa/gazetteer.html. Accessed 4 Sept 2022
Government of Japan (2019) Nomination of Amami-Oshima island, Tokunoshima island, Northern part of Okinawa island, and Iriomote island for inscription on the world heritage list. Government of Japan. Retrieved from https://kyushu.env.go.jp/okinawa/amami-okinawa/world-natural-heritage/plan/pdf/a-1-e.pdf. Accessed 19Apr 2023
Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (eds) (2020) Geologic time scale 2020. Elsevier, Amsterdam
Grandcolas P, Murienne J, Robillard T, Desutter-Grandcolas L, Jourdan H, Guilbert E, Deharveng L (2008) New Caledonia: A very old Darwinian island? Philos Trans R Soc Lond B Biol Sci 363:3309–3317. https://doi.org/10.1098/rstb.2008.0122
Hamamoto F, Sakurai M, Nagano M (1979) Submarine geology off the Miyako and Yaeyama Islands. Rep Hydrogr Res 14:1–34 (**in Japanese with English abstract**)
Hanagata S (2004) Pliocene–Pleistocene planktonic foraminiferal biostratigraphy in the Miyagijima and adjacent islands, off Katsuren Peninsula, east of Okinawa-jima, Japan. Bull Mizunami Fos Mus 31:37–48 (**in Japanese with English abstract**)
Hanagata S, Nobuhara T (2015) Illustrated guide to Pliocene foraminifera from Miyakojima, Ryukyu Island Arc, with comments on biostratigraphy. Palaeontol Electron 1(18):1–140. https://doi.org/10.26879/444
Hasegawa Y (1980) Notes on vertebrate fossils from late Pleistocene to Holocene of Ryukyu Islands, Japan. Quat Res 18:263–267. https://doi.org/10.4116/jaqua.18.263. (**in Japanese with English abstract**)
Hasegawa Y (2012) Origin of modern manmals in Japan. Mamm Sci 52:233–247. https://doi.org/10.11238/mammalianscience.52.233. (**in Japanese with English abstract**)
Hasegawa Y, Otsuka H, Nohara A (1973) Fossil vertebrates from the Miyako Island (Studies of the palaeovertebrates fauna of Ryukyu Islands, Japan. Part I). Mem Natl Mus Natr Sci 6:39–52
Hirano T, Saito T, von Oheimb PW, von Oheimb KCM, Do TV, Yamazaki D, Kameda Y, Chiba S (2022) Patterns of diversification of the operculate land snail genus *Cyclophorus* (Caenogastropoda: Cyclophoridae) on the Ryukyu Islands, Japan. Mol Phylogenet Evol 169:107407. https://doi.org/10.1016/j.ympev.2022.107407
Ikeda T (2007) Comparative morphological study of Vertebrae of snakes occurring in Japan and adjacent regions, and fossil snake Vertebrae (Reptilia:Squamata) from the Early and latest Pleistocene on the Ryukyu Islands, southwestern Japan. Ph.D. dissertation, Kagoshima University, Kagoshima, Japan
Imai R, Sato T, Iryu Y (2017) Calcareous nannofossil assemblages of the upper Miocene to Pliocene Shimajiri Group on Okinawa-jima, Ryukyu Islands, southwestern Japan. J Asian Ear Sci 135:16–24. https://doi.org/10.1016/j.jseaes.2016.12.011
Iryu Y (1992) Fossil nonarticulated coralline algae as depth indicators for the Ryukyu Group. Trans Proc Paleontol Soc Jpn New Ser 167:1165–1179. https://doi.org/10.14825/prpsj1951.1992.167_1165
Iryu Y, Nakamori T, Matsuda S, Abe O (1995) Distribution of marine organisms and its geological significance in the modern reef complex of the Ryukyu Islands. Sedim Geol 99:243–258. https://doi.org/10.1016/0037-0738(95)00047-C
Iryu Y, Nakamori T, Yamada T (1998) Pleistocene reef complex deposits in the Central Ryukyus, south-western Japan. In: Camoin G, Davies PJ (eds) Reefs and carbonate platforms in the Pacific and Indian Oceans. Special Publications of the International Association of Sedimentologists, vol 25. Blackwell Sci. Ltd., Oxford, pp 197–213
Iryu Y, Matsuda H, Machiyama H, Piller WE, Quinn TM, Mutti M (2006) Introductory perspective on the COREF Project. Isl Arc 15:393–406. https://doi.org/10.1111/j.1440-1738.2006.00537.x
Itaki T, Arai K, Oda H, Kaneko N, Nakashima R, Tanaka Y (2013) Mid-Pleistocene fossil assemblage collected from lower part of "the 500 m island shelf" in the Okinawa area. In: Abstracts and programs, the 2013 annual meeting of the Palaeontological Society of Japan, Kumamoto, Kumamoto Pref, 28–30 Jun 2013 **(in Japanese)**
Kaito T, Toda M (2016) The biogeographical history of Asian keelback snakes of the genus *Hebius* (Squamata: Colubridae: Natricinae) in the Ryukyu

Archipelago, Japan. Biol J Linn Soc 118:187–199. https://doi.org/10.1111/bij.12726
Kamata H, Kodama K (1999) Volcanic history and tectonics of the Southwest Japan Arc. Isl Arc 8:393–403. https://doi.org/10.1046/j.1440-1738.1999.00241
Kaneko Y, Hasegawa Y (1995) Some fossil arvicolid rodents from the Pinza-Abu cave, Miyako Island, the Ryukyu Islands, Japan. Bull Biogeogr Soc Jpn 50:23–37
Kaneko N, Ito T (2006) Age of the Itoman Formation (new to science) at base of the Ryukyu Group in southern part of the Okinawa-jima, Ryukyu Islands, Japan. Bull Geol Surv Jpn 57:159–168 (**in Japanese with English abstract**)
Kaneko N, Ujiié H (2006) Geology of the Itoman and Kudaka Jima district. Quad Ser, 1:50,000, Geol Surv Jpn, Agency Indust Sci Tech, Tsukuba (in Japanese with English abstract). Retrieved from https://www.gsj.jp/Map/JP/geology4-16.html#18015. Accessed 19 Apr 2023
Kato S (2016) Strontium isotope ages of the Shimajiri Group in Miyako-jima, Okinawa Prefecture, Japan. Bull Mizunami Fossil Mus 42:75–83 (**in Japanese with English abstract**)
Kato S, Katsura T, Hirano K (1982) Submarine geology off Okinawa Island. Rep Hydrog Res 17:31–70
Kawaguchi S, Kaneko Y, Hasegawa Y (2009) A new species of the fossil murine rodent from the Pinza-Abu cave, the Miyako Island of the Ryukyu Archipelago, Japan. Bull Gunma Mus Nat Hist 13:15–28 (**in Japanese with English abstract**)
Kawamura A, Chang CH, Kawamura Y (2016) 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. https://doi.org/10.1016/j.quaint.2015.06.044
Kawana T (1988) The geomorphology of the Ryukyu Islands. Shinseitosho Shuppan, Okinawa (**in Japanese**)
Kimura M (1996) Quaternary paleogeography of the Ryukyu Arc. J Geogr (chigaku Zasshi) 105:259–285. https://doi.org/10.5026/jgeography.105.3_259. (**in Japanese with English abstract**)
Kimura M (2002) Geologic evolution and paleogeography of the Ryukyu Island Arc. In: Kimura M (ed) The geologic evolution of the Ryukyu Island Arc and the immigration of organisms. Okinawa Times, Naha (**in Japanese; original title translated**)
Kimura M, Monma H, Matsumoto T, Aoki M, Otsuka K, Mitsuzawa K, Tanaka Y, Ono T (1991) Tectonic movement at the Kerama Saddle in the Eastern Margin of the Okinawa Trough. In: The 7th symposium on deep-sea research using the submersible "SHINKAI 2000" system, pp 131–145. Retrieved from https://dl.ndl.go.jp/en/pid/9592892. Accessed 19 Apr 2013 **(in Japanese with English abstract)**
Kimura M, Matsumoto T, Nakamura T, Otsuka K, Nishida S, Aoki M, Ono T, Danno K (1992) Diving survey of the Krama Saddle in the eastern margin of the Okinawa Tough: Probable sunken land-bridge during the last glacial age. In: Proceedings of the JAMSTEC symposium deep sea research, vol 8, pp 107–133. Retrieved from https://dl.ndl.go.jp/pid/9592926. Accessed 19 Apr 2013 **(in Japanese with English abstract)**
Kizaki K (1985) Geology of the Ryukyu Island Arc. Okinawa Times, Naha (**in Japanese; original title translated**)
Kizaki K, Oshiro I (1977) Paleogeography of the Ryukyu Islands. Mar Sci Mon (kaiyo Kagaku) 9:542–549 (**in Japanese; original title translated**)
Koba M (1992) Influx of Kuroshio Current into the Okinawa Trough and inauguration of Quaternary coral reef building in the Ryukyu Island Arc, Japan. Quat Res (daiyonki Kenkyu) 31:359–373. https://doi.org/10.4116/jaqua.31.359. (**in Japanese; original title translated**)
Kodato T, Nakagawa H (1993) Recent benthic foraminiferal assemblages of Miyako Island, the Ryukyu Islands, southwest of Japan. Rep Tech Res Ctr Jpn Natl Oil Corp 24:93–110 (**in Japanese with English abstract**)
Komaki S (2021) Widespread misperception about a major East Asian biogeographic boundary exposed through bibliographic survey and biogeographic meta-analysis. J Biogeogr 48:2375–2386. https://doi.org/10.1111/jbi.14210
Konishi K (1965) Geotectonic framework of the Ryukyu Islands. J Geol Soc Jpn 71:437–457. https://doi.org/10.5575/geosoc.71.437. (**in Japanese with English abstract**)
Kubo A, Fukuyama E (2003) Stress field along the Ryukyu Arc and Okinawa Trough inferred from moment tensors of shallow earthquakes. Earth Planet Sci Lett 210:305–316. https://doi.org/10.1016/S0012-821X(03)00132-8
Lisiecki LE, Raymo ME (2005) A Pliocene–Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. Paleoceanography 20:PA1003. https://doi.org/10.1029/2004PA001071
MacNeil FS (1960) The tertiary and quaternary gastropoda of Okinawa. US Geol Surv Prof Pap 339:1–148. https://doi.org/10.3133/pp339
Makino T, Higuchi Y (1967) Geological study of the natural gas resources in the southern Okinawa Islands. J Jpn Assoc Petrol Technol 32:49–59. https://doi.org/10.3720/japt.32.49. (**in Japanese with English abstract**)
Martini E (1971) Standard tertiary and quaternary calcareous nannoplankton zonation. In: Farinacci A (ed) Proceedings of the II planktonic conference, Roma 1970, vol 2, Tecnoscienza, Rome, pp 739–785
Matsuda S, Iryu Y (2011) Rhodoliths from deep fore-reef to shelf areas around Okinawa-jima, Ryukyu Islands, Japan. Mar Geol 282:215–230. https://doi.org/10.1016/j.margeo.2011.02.013
Matsumoto T, Kimura M (1991) Detailed bathymetric survey of recent crustal deformation in the Ryukyu arc—result of Leg 1 of DK90–8-NSS Cruise by the R/V "Kaiyo". Technical report Japan Marine Science and Technology Center, vol 26, pp 1–10. Retrieved from https://dl.ndl.go.jp/en/pid/8791982. Accessed 19 Apr 2023 **(in Japanese with English abstract)**
Matsumoto T, Kimura M, Nakamura A, Aoki M (1996) Detailed Bathymetric features of Tokara and Kerama gaps in the Ryukyu Arc. J Geogr (chigaku Zasshi) 105:286–296. https://doi.org/10.5026/jgeography.105.3_286. (**in Japanese with English abstract**)
Matsumoto T, Shinjo R, Nakamura M, Kimura M, Ono T (2009) Submarine active normal faults completely crossing the southwest Ryukyu Arc. Tectonophysics 466:289–299. https://doi.org/10.1016/j.tecto.2007.11.032
Matsumoto R, Takeuchi R, Nakagawa H, Sato, T, Iryu Y, Matsuda H, Komatsubara J, Sato M (in press) Formation of methane-derived dolomite concretions in Okinawa-Jima, Southwest Japan during the Early Pleistocene "Chinen Disturbance". J Geol Soc Jpn **(in Japanese with English abstract)**
Matsuoka H (2000) The Late Pleistocene fossil birds of the Central and Southern Ryukyu Islands, and their zoogeographical implications for recent avifauna of the archipelago. Tropics 10:165–188. https://doi.org/10.3759/tropics.10.165
Melosh HJ, Raefsky A (1980) The dynamical origin of subduction zone topography. Geophys J Internat 60:333–354. https://doi.org/10.1111/j.1365-246X.1980.tb04812.x
Miller KG, Kominz MA, Browning JV, Wright JD, Mountain GS, Katz ME, Sugarman PJ, Cramer BS, Christie-Blick N, Pekar SF (2005) The Phanerozoic record of global sea-level change. Science 310:1293–1298. https://doi.org/10.1126/science.1116412
Miyakojima City Board of Education (ed) (2015) Arafu Site, Tsudupisuki-abu Cave, and Tomori-motojima Site: Report on the Excavation Research of the Archaeological Sites in Miyakojima City, Miyakojima City Board of Education, Miyakojima City **(in Japanese; original title traslated)**
Monma H, Kimura M, Aoki M, Deep Sea Research Group, Hotta H (1991) Preliminary report of deep tow surveys in the Okinawa Trough (DK89–1-OKN-Leg 2). Technical report Japan Marine Science and Technology Center, vol 25, pp 131–146. Retrieved from https://dl.ndl.go.jp/ja/pid/8791971. Accessed 19 Apr 2013 **(in Japanese with English abstract)**
Muraoka A, Iryu Y, Odawara K, Yamada T, Sato T (2005) Stratigraphy of the Ryukyu Group in Maeda-misaki area, Okinawa jima, Ryukyu Islands, Japan. J Jpn Coral Reef Soc 7:23–36. https://doi.org/10.3755/jcrs.2005.23. (**in Japanese with English abstract**)
Nakagawa H, Niitsuma N, Murakami M, Watanabe T (1976) Outline of the magnetostratigraphy of the Shimajiri Group in Miyako Jima and Kume Jima, Okinawa Prefecture. In: Kizaki K (ed) Geological Studies of the Ryukyu Islands, vol 1. Matsumoto Type, Naha, pp 55–63 (**in Japanese; original title translated**)
Nakagawa H, Matsuda H, Sato T, Hiratsuka M, Oda M (2001) Preliminary study on sedimentary facies and depositional age of the Chinen Formation in the southern part of Okinawa Island. J Sedim Soc Jpn 53:99–101. https://doi.org/10.4096/jssj1995.53.61. (**in Japanese**)
Nakamori T (1985) Geology of Miyako Gunto, Ryukyu Islands, Japan. Contrib Inst Geol Paleontol Tohoku Univ 84:23–39 (**in Japanese with English abstract**)

Nakamori T (1986) Community structures of Recent and Pleistocene hermatypic corals in the Ryukyu Islands, Japan. The science reports of the Tohoku University. Second series (Geology), vol 56, pp 71–133. Retrieved from https://tohoku.repo.nii.ac.jp/?action=pages_view_main&active_action=repository_view_main_item_detail&item_id=12053&item_no=1&page_id=33&block_id=46. Accessed 19 Apr 2023

Nakamori T, Iryu Y, Yamada T (1995) Development of coral reefs of the Ryukyu Islands (southwest Japan, East China Sea) during Pleistocene sea-level change. Sediment Geol 99:215–231. https://doi.org/10.1016/0037-0738(95)00045-A

Nakamori T, Iryu Y, Matsuda S (1999) 8th International symposium on fossil Cnidaria and Porifera, field trip A1, recent and pleistocene coral reefs in the Ryukyu Islands. Japan. Sasaki Printing & Publishing Co., Ltd., Sendai

Natori H (1976) Planktonic foraminiferal biostratigraphy and datum planes in the Late Cenozoic sedimentary sequence in Okinawa-jima, Japan. In: Takayanagi Y, Saito T (eds) Progress in micropaleontology: selected papers in honor of Prof. Kiyoshi Asano. Micropaleontology Press, New York, pp 214–243

Nobuhara T (2001) Bathyal molluscan assemblages with high species diversity from the Upper Pliocene Minebari Formation, the southern Ryukyu Island Arc. Venus 60:113

Noda H (1980) Molluscan fossils from the Ryukyu Islands, southwestern Japan. Part 1. Gastropoda and Pelecypoda from the Shinzato Formation in southeastern part of Okinawa-jima. Sci Rep Inst Geosci Univ Tsukuba Sec B 1:1–95

Noda H (1988) Molluscan fossils from the Ryukyu Islands, Southwest Japan. Part 2. Gastropoda and Pelecypoda from the Shinzato Formation in middle part of Okinawa-jima. Sci Rep Inst Geosci Univ Tsukuba Sec B 1:1–95

Nohara T (1987) Cenozoic ostracodes of Okinawa-jima. Bull Coll Educ Univ Ryukyus 30:1–105

Odawara K, Iryu Y (1999) Pleistocene coral reef deposits (the Ryukyu Group) on Yoron-jima, Kagoshima Prefecture, Japan. J Geol Soc Jpn 105:273–288. https://doi.org/10.5575/geosoc.105.273. (**in Japanese with English abstract**)

Odawara K, Iryu Y, Matsuda H, Sato T, Chiyonobu S, Sakuma D (2005a) Geologic ages of the Chinen Formation and "Reddish Limestone" in Komesu and Giza areas in southern Okinawa-jima based on calcareous nannofossil biostratigraphy. J Geol Soc Jpn 111:224–233. https://doi.org/10.5575/geosoc.2011.0016. (**in Japanese with English abstract**)

Odawara K, Kudo S, Iryu Y, Sato T (2005b) Stratigraphy of the Zakimi Formation and the Ryukyu Group in Yomitan area, Okinawa-jima, Ryukyu Islands, Japan. J Geol Soc Jpn 111:313–331. https://doi.org/10.5575/geosoc.111.313. (**in Japanese with English abstract**)

Ogasawara K, Masuda K (1983) Notes on the paleoenvironments based upon the Cenozoic molluscs in the Ryukyu Islands. Mem Geol Soc Jpn 22:95–105 (**in Japanese with English abstract**)

Okada H, Bukry D (1980) Supplementary modification and introduction of code numbers to the low-latitude coccolith biostratigraphic zonation (Bukry, 1973, 1975). Mar Micropaleontol 5:321–325. https://doi.org/10.1016/0377-8398(80)90016-X

Okamoto T (2017) Historical biogeography of the terrestrial reptiles of Japan: a comparative analysis of geographic ranges and molecular phylogenies. In: Motokawa M, Kajihara H (eds) Species diversity of animals in Japan. Springer, Tokyo, pp 135–163. https://doi.org/10.1007/978-4-431-56432-4_5

Okamura Y, Nishizawa A, Oikawa M, Horiuchi D (2017) Differential subsidence of the forearc wedge of the Ryukyu (Nansei-Shoto) Arc caused by subduction of ridges on the Philippine Sea Plate. Tectonophysics 717:399–412. https://doi.org/10.1016/j.tecto.2017.08.025

Okinawa Natural Gas Research Group (1971) History and results of natural gas survey in Okinawa Jima. J Jpn Assoc Petrol Technol 36:153–169. https://doi.org/10.3720/japt.36.153. (**in Japanese, original title translated**)

Okutani T (ed) (2017) Marine mollusks in Japan, 2nd edn. Tokai University Press, Hiratsuka

Oshiro T, Nohara A (2000) Distribution of Pleistocene terrestrial vertebrates and their migration to the Ryukyus. Trop 10:41–50. https://doi.org/10.3759/tropics.10.41

Ota H (1998) Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Res Popul Ecol 40:189–204. https://doi.org/10.1007/BF02763404

Ota H (2000) The current geographic faunal pattern of reptiles and amphibians of the Ryukyu Archipelago and adjacent regions. Tropics 10:51–62. https://doi.org/10.3759/tropics.10.51

Ota H (2003) Toward a synthesis of paleontological and neontological information on the terrestrial vertebrates of the Ryukyu Archipelago. (1) Systematic biogeographic review. J Fossil Res 36:43–59

Otsubo M, Yamaji A, Kubo A (2008) Determination of stresses from heterogeneous focal mechanism data: an adaptation of the multiple inverse method. Tectonophysics 457:150–160. https://doi.org/10.1016/j.tecto.2008.06.012

Otsuka H, Nakamura T, Ota T (2008) ^{14}C ages of vertebrate fossil beds in the Ryukyu Islands, South Japan. In: Summaries of researches using AMS at Nagoya University, vol 19, pp 135–153. Retrieved from https://www.nendai.nagoya-u.ac.jp/tande_report/2007/otsuka2007.pdf. Accessed 23 Apr 2023

Otuka Y (1941) On the stratigraphic horizon of Elephas from Miyako Is., Ryukyu Islands, Japan. Proc Imp Acad Jpn 17:43–47. https://doi.org/10.2183/pjab1912.17.43

Raffi I, Wade BS, Pälike H (2020) Chapter 29, The Neogene period. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (eds) Geologic time scale 2020, vol 2. Elsevier, Amsterdam, pp 1141–1215

Sagae K, Humblet M, Odawara K, Chiyonobu S, Sato T, Kabamoto J, Takayanagi H, Iryu Y (2012) Stratigraphy of the Ryukyu Group in southern Okinawa-jima, Ryukyu Islands, Japan. J Geol Soc Jpn 118:117–136. https://doi.org/10.5575/geosoc.2011.0009. (**in Japanese with English abstract**)

Sagawa N, Nakamori T, Iryu Y (2001) Pleistocene reef development in the southwest Ryukyu Islands, Japan. Palaeogeogr Palaeoclimatol Palaeoecol 175:303–323. https://doi.org/10.1016/S0031-0182(01)00377-7

Sato T (2013) Basic structure of light microscope. In: Oda M, Sato T (eds) Research manual for micropaleontology. Asakura Publishing Co. Ltd., Tokyo, pp 44–49 (**in Japanese**)

Sato T, Saito T, Yuguchi S, Nakagawa H, Kameo K, Takayama T (2002) Late Pliocene calcareous nannofossil paleobiogeography of the Pacific Ocean: evidence for glaciation at 2.75 Ma. Rev Mex Cienc Geol 19:175–189

Sato T, Nakagawa H, Komatsubara J, Matsumoto R, Iryu Y, Matsuda H, Omura A, Odawara K, Takeuchi R (2004) Geologic age of the Chinen Formation in southern Okinawa-jima based on calcareous microfossils. J Geol Soc Jpn 110:35–50. https://doi.org/10.5575/geosoc.110.38. (**in Japanese with English abstract**)

Sato T, Chiyonobu S, Hodell DA (2009) Data report: quaternary calcareous nannofossil datums and biochronology in the North Atlantic Ocean, IODP Site U1308. In: Channell JET, Kanamatsu T, Sato T, Stein R, Alvarez Zarikian CA, Malone MJ (eds) Proceeding of the Integrated Ocean Drilling Program, College Station, vol 303/306. Integrated Ocean Drilling Program Management International, Inc., Washington

Sato T, Watanabe N, Yamamoto K, Iryu Y (2022) Calcareous nannofossil biostratigraphy of the upper Cenozoic in the Okinawa-Miyako submarine plateau in the Ryukyu Islands. J Geol Sco Jpn 128:215–220. https://doi.org/10.5575/geosoc.2022.0018. (**in Japanese with English abstract**)

Sawada A, Sasahara N, Honda R, Kono Y (2009) Marine gravity datasets around the Japanese Islands without noticeable inconsistency. Tech Bull Hydrogr Oceanogr 27:78–86 (**in Japanese**)

Segawa R (2011) Molecular phylogenetic study of Potamidae. In: Kawai T, Nakata K (eds) Shrimp, crabs, and crayfish—conservation and biology of freshwater crustaceans. Seibutsu Kenkyusha, Tokyo, pp 103–125 (**in Japanese**)

Sibuet JC, Deffontaines B, Hsu SK, Thareau N, Le Formal JP, Liu CS, Party ACT (1998) Okinawa Trough backarc basin: early tectonic and magmatic evolution. J Geophys Res 103:30245–30267. https://doi.org/10.1029/98JB01823

Takahashi A, Otsuka H, Ota H (2015) A new species of the genus *Mauremys* (Testudines: Geoemydidae) from the upper Pleistocene of Miyakojima Island, Ryukyus Archipelago, Japan. Curr Herpetol 34:149–163. https://doi.org/10.5358/hsj.34.149

Takahashi A, Hirayama R, Otsuka H (2018) Systematic revision of *Manouria oyamai* (Testudines, Testudinidae), based on new material from the Upper Pleistocene of Okinawajima Island, the Ryukyu Archipelago,

Japan, and its paleogeographic implications. J Vertebr Paleontol 38:e1427594. https://doi.org/10.1080/02724634.2017.1427594
Takeuchi T, Iryu Y, Sato T, Chiyonobu S, Yamada S, Odawara K, Abe E (2006) Pleistocene reef development and stratigraphy on Ie-jima, the Ryukyu Islands, southwestern Japan. In: Proceedings of the 10th international coral reef symposium, Okinawa, Japan, June 28–July 2, 2004, pp 536–546
Tanaka Y, Ujiié H (1984) A standard late Cenozoic microbiostratigraphy in southern Okinawa-jima, Japan. Part 1. Calcareous nannoplankton zones and their correlation to the planktonic foraminferal zones. Bull Nat Sci Mus Tokyo Ser C 10:141–168
Taruno H, Kawamura Y (2007) A revision of Japanese primitive mammoths—their taxonomy, chronospatial distribution, evolution and irrunigration. Jubilee Publication in Commemoration of Prof. Kamei Tadao's 80th Birthday, Tokyo **(in Japanese with English abstract)**
Tokunaga S (1936) A fossil elephant tooth discovered in Miyakozima, an island of the Ryukyu Archipelago, Japan. Proc Imp Acad Jpn 16:122–124. https://doi.org/10.2183/pjab1912.16.122
Tominaga A, Matsui M, Shimoji N, Khonsue W, Wu CS, Toda M, Eto K, Nishikawa K, Ota H (2019) Relict distribution of Microhyla (Amphibia: Microhylidae) in the Ryukyu Archipelago: high diversity in East Asia maintained by insularization. Zool Scr 48:440–453. https://doi.org/10.1111/zsc.12361
Tsuburaya H, Sato T (1985) MITI—Miyakojima Oki. J Jpn Assoc Petrol Technol 50:25–33. https://doi.org/10.3720/japt.50.25. (**in Japanese, original title translated**)
Tsuji Y (1993) Tide influenced high energy environments and rhodolith-associated carbonate deposition on the outer shelf and slope off the Miyako Islands, southern Ryukyu Island Arc, Japan. Mar Geol 113:255–271. https://doi.org/10.1016/0025-3227(93)90021-M
Ujiié H (1980) Significance of "500m Deep Island Shelf" surrounding the southern Ryukyu Island Arc for its Quaternary geological history. Quat Res (daiyonki Kenkyu) 18:209–219. https://doi.org/10.4116/jaqua.18.209. (**in Japanese with English abstract**)
Ujiié H (1986) Beneath the Ryukyu Island Arc: sedimentology and geology. Shinsei-tosho, Naha (**in Japanese; Original title translated**)
Ujiié H, Kaneko N (2006) Geology of the Naha and Okinawashi-Nambu district. Quad Ser, 1:50,000, Geol Surv Jpn, Agency Indust Sci Tech, Tsukuba (in Japanese with English abstract). Retrieved from https://www.gsj.jp/Map/JP/geology4-16.html#18015. Accessed 19Apr 2023
Ujiié H, Oki K (1974) Uppermost Miocene-lower Pleistocene planktonic foraminifera from the Shimajiri Group of Miyako-jima, Ryukyu Islands. Mem Nat Sci Mus Tokyo 7:31–52 (**in Japanese with English abstract**)
Wallace AR (1863) On the physical geography of the Malay Archipelago. J R Geogr Soc Lond 33:217–234. https://doi.org/10.2307/1798448
Wegener A (1929) Die Entstehung der Kontinente und Ozeane. Friedrich Vieweg & Sohn Akt. Ges., Braunschweig; Japanese (trans: Miyashiro A, Shido F, 1981). Maruzen Co., Ltd., Tokyo
Wessel P, Luis JF, Uieda L, Scharroo R, Wobbe F, Smith WHF, Tian D (2019) The generic mapping tools version 6. Geochem Geophys Geosys 20:5556–5564. https://doi.org/10.1029/2019GC008515
Whittaker RJ, Fernandez-Palacios JM (2007) Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, Oxford
Xu X, Liu F, Chen J, Ono H, Agnarsson I, Li D, Kuntner M (2016) Pre-Pleistocene geological events shaping diversification and distribution of primitively segmented spiders on East Asian margins. J Biogeogr 43:1004–1019. https://doi.org/10.1111/jbi.12687
Yabe H, Hanzawa S (1930) A stratigraphic study of Tertiary foraminiferous rocks in Taiwan. In: Committee on the Jubilee Events in Commemoration of Professor Takuji Ogawa's 60th Birthday (Ed) Jubilee Publication in the Commemoration of Professor Takuji Ogawa's 60th Birthday, Kobundo-shobo, Kyoto, pp 83–126 **(in Japanese, original title translated)**
Yamada S (2002) Initiation and development of coral reefs and tectonic movements in the South Ryukyu during the Pleistocene. Dissertation, Kumamoto University. https://core.ac.uk/download/pdf/57725546.pdf. Accessed 21 Apr 2021 **(in Japanese, original title translated)**
Yamada T, Fujita K, Iryu Y (2003) The Ryukyu Group (Pleistocene coral reef complex deposits) on Toku-no-shima, Kagoshima Prefecture, Japan. J Geol Soc Jpn 109:495–517. https://doi.org/10.5575/geosoc.109.495. (**in Japanese with English abstract**)
Yamamoto K, Iryu Y, Sato T, Chiyonobu S, Sagae K, Abe E (2006) Responses of coral reefs to increased amplitude of sea-level changes at the Mid-Pleistocene Climate Transition. Palaeogeogr Palaeoclimatol Palaeoecol 241:160–175. https://doi.org/10.1016/j.palaeo.2006.06.014
Yang SF, Komaki S, Brown RM, Lin SM (2018) Riding the Kuroshio Current: Stepping stone dispersal of the Okinawa tree lizard across the East Asian Island Arc. J Biogeogr 45:37–50. https://doi.org/10.1111/jbi.13111
Yazaki K (1978) About the Shimajiri Group of Miyako-jima, Ryukyu Islands. In: Kizaki K (ed) Geological study of the Ryukyu Islands, vol 3. Shashoku Center Co., Ltd., Naha, pp 81–88 (**in Japanese with English abstract**)
Yazaki K, Oyama K (1979) Geology of the Miyakojima-hokubu district. Quad Ser, scale 1: 50,000, Geol Surv Jpn, Kawasaki. Retrieved from https://www.gsj.jp/Map/JP/geology4-16.html#18015. Accessed 19Apr 2023 **(in Japanese with English Abstract)**
Yoder AD, Nowak MD (2006) Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. Annu Rev Ecol Evol Syst 37:405–431. https://doi.org/10.1146/annurev.ecolsys.37.091305.110239

Publisher's Note