

## Distribution of island endemic animals and the late Middle Pleistocene land bridges as evidence of sea level rise of 1,000 m since 430 ka

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**Abstract.** Many endemic animals from the Pleistocene to the present are found on some islands around the world. In this paper, the distribution of endemic faunas and their transition in the islands of the world are examined. As a result, it became clear that many endemic faunas of the islands were converted after the late Middle Pleistocene and became unique. All islands with endemic fauna since the late Middle Pleistocene are connected to the nearest continent only at isobaths of 1,000 m or more. Because terrestrial animal migration occurs in their habitat environment, it is thought that these animals migrated through the land bridge that was formed in the late Middle Pleistocene, then an endemic fauna was formed after that was isolated to the island by the sea level rise of 1,000 m. In other words, the sea level in the late Middle Pleistocene was 1,000 m lower than the present, and the subsequent rise in sea level is thought to have led to the formation of endemic faunas on islands separated from the continent by the sea since the late Middle Pleistocene.

**Keywords:** land bridge, Pleistocene, insular mammals, sea level rise, Wallacea, Mediterranean

### Introduction

It is known that many insular endemic mammals including proboscideans, artiodactyls, carnivores, rodents, insectivores, bats and lagomorphs inhabited the world's islands from the Pleistocene to the present (Van der Geer et al., 2010). However, it is still unclear how these animals migrated to the islands and how these endemic species were formed.

Van der Geer et al. (2010), who summarized the distribution of fossil mammals and their faunal evolution on islands around the world, showed that there were faunal transformations during the Pleistocene on each island, that the timing of faunal transformations coincided in some cases, and that many of these last transformations occurred in the late Middle Pleistocene or the Late Pleistocene.

The author postulated that island arcs and the continental slopes were formed by crustal uplift and sea level rise of up to 1,000 m since the late Middle Pleistocene, about 430 ka (Shiba, 2017a, 2017b, 2021). In other words, during the late Middle Pleistocene, the sea level was about 1,000 m lower than at the present level, and the subsequent large-scale uplift of island arcs and continents, and together with the simultaneous uplift of the seafloor, is thought to have raised the sea level by 1,000 m by the present time, forming the present land and seafloor topography (Shiba, 2017a, 2017b).

If we assume that the coastline in the late Middle Pleistocene was 1,000 m lower than the present sea level, many of the islands would be connected to the continent. In this paper, the author summarizes the evolution of the Pleistocene mammalian faunas of islands and the timing of their conversion, based mainly on the data on the world's islands mammals compiled by Van der Geer et al. (2010). Then, assuming that the shallower than 1,000 m depth areas around these islands were terrestrial at some time in the past, the author examines the causes of the endemic fauna of the islands. This paper is a remake of Shiba (2020) and has been translated into English.

In Van der Geer et al. (2010), the base of the Pleistocene is the Calabrian base based on the pre-2009 chronology as 1.806 Ma, which is cited directly in this paper. The terms "pygmy" and "dwarf" are also used according to Van der Geer et al. (2010), with "pygmy" used for particularly small forms, half or less than the size of the ancestor, "dwarf" for 60-80% of the size, and "small" for 90% of the size.

### Faunal Changes in the Honshu region of the Japanese Archipelago

The Japanese Archipelago, excluding the Ryukyu Islands, consists mainly of the Honshu region and Hokkaido. The Honshu region includes Honshu, Kyushu and Shikoku islands. The Tsugaru Strait, the Korean Strait, and the Tsushima Strait, which are the peripheral boundaries of the Honshu region, did not become land during the Last Glacial period, suggesting that the Honshu region was isolated from the continent for hundreds of thousands of years before that. For this reason, these straits are considered as biogeographic boundaries (Fig. 1).

According to the paleontological study of small mammals in Japanese Archipelago by Kawamura et al. (1989), about half of



**Fig. 1** Bathymetric chart around the Japanese Archipelago showing the biogeographic boundaries (white thick dotted lines). St.: Strait. Thin dotted line is shown depth of 100 m. The seafloor shallower than depth of 1,000 m shows the land area in the late Middle Pleistocene. The seafloor topography is based on NOAA bathymetric data.

the extant mammals, such as Shinto shrew (*Sorex shinto*), Japanese shrew-mole (*Urotrichus talpoides*), Japanese mountain mole (*Euroscaptor mizura*), large Japanese field mouse (*Apodemus speciosus*), raccoon dog (*Nyctereutes procyonoides*), and ermine (*Mustela erminea*), appeared as fossils during the Middle Pleistocene, and they had already become endemic during this period. In particular, the genera *Dymecodon*, *Urotrichus*, and *Glirulus* are endemic even at the genus level, and they are considered to be the basis of the mammalian fauna of the Honshu region as survivors of the Neogene period (Kamei et al., 1988).

In the Early Miocene, about 20 Ma, the Japanese Archipelago was located at the eastern margin of the Chinese continent, and most of the southern part of the Sea of Japan was still land. However, in the Middle Miocene, about 16 Ma, the region of the Sea of Japan submerged due to sea level rise, and the Japanese Archipelago appeared as an island arc. In the Late Miocene, about 10 Ma, the spine of the present-day Japanese Archipelago was uplifted to form the prototype, and the present-day Japanese Archipelago was formed by the uplift of island arc and sea level rise, especially during the Pleistocene (Shiba, 2017a, 2017b). In the Pleistocene, the Japanese Archipelago was temporarily connected to the continent for several times, and the phylogeny of organisms distributed around the continent is thought to have migrated to the Japanese Archipelago.

Based on the study of fossil proboscideans by Kawamura (1998, 2014) and Konishi and Yoshikawa (1999) concluded that *Mammuthus trogontheri* arrived in the Honshu region from China about 1.2 Ma (Marine oxygen isotope stage: MIS 36), *Stegodon orientalis* from the south via the East China Sea about 630 ka (MIS 16), and *Paleoloxodon naumanni* from the northern China via the Korean Peninsula about 430 ka (MIS 12). Kawamura (2014) argued that the arrival of each of these faunas from the continent was not a mass transfer, but rather a limited arrival due to the short span of time and unstable existence of the land bridge.

These proboscideans are thought to have been introduced to the Japanese Archipelago at different times, and to have become endemic soon afterwards as they inhabited the Japanese Archipelago in isolation, separated from the continent by the sea. According to Saegusa (2005), *Paleoloxodon naumanni* is closely related to the Stuttgart type of *Elephas antiquus*, whose skull type is older than that of *Elephas namadicus* found in China, and that the Stuttgart type, which was migrated to Japan at MIS 10 (about 350 ka) or shortly before, evolved as an isolated continental survivor.

In other words, most of the mammals currently inhabiting the Honshu region of the Japanese Archipelago are composed of



**Fig. 2** Bathymetric chart around the Ryukyu Islands showing the biogeographic boundaries (white thick dotted lines). St.: Strait. Thin dotted line is shown depth of 100 m. The seafloor shallower than depth of 1,000 m shows the land area in the late Middle Pleistocene. The seafloor topography is based on NOAA bathymetric data.

species that were migrated to the Honshu region when it was connected to the continent several times since the Late Miocene, and were isolated and endemic. The last of these migrations is thought to be the time when the ancestors of the *Paleoloxodon naumanni* arrived from the continent in the late Middle Pleistocene, 430 ka.

### **The terrestrial herpetofauna and land bridge in the Ryukyu Islands**

The boundary between the Palearctic and the Oriental Districts of zoogeography in Japan is the Watase's Line between the Japanese Archipelago and Ryukyu Islands, which corresponds to a deep fissure (the Tokara Gap) of more than 1,000 m depth between Akuseki and Kotakara Islands in the southern Tokara Islands between Amami-Oshima and Kyushu. (Fig. 2). On the western side of the Tokara Gap, a 1,000 m depth line connects the Ryukyu Islands with Kyushu to the north, but this area is shallow because it is buried by Pliocene and Pleistocene volcanic sediments (Aiba and Sekiya, 1979), and was separated by the sea during the Pliocene and Pleistocene (Hoshino, 1983).

In terms of herpetofauna, most of the reptiles in the Amami/Okinawa Islands consist of the Habu (genus *Protobothrops*), the Ryukyu green snake (*Cycophiops semicarinatus*) and the blue viper (*Takydromus smaragdinus*), with the northern limit south of Kodakara Island, while the northern reptiles in the Tokara Gap consist of the Japanese common species of the genus *Elaphe*, such as the Japanese striped snake and rat snake, which are not distributed in the Amami/Okinawa Islands even at the genus level (Hikita, 2002).

There are three more distributional boundaries between the Ryukyu Islands, Taiwan and the mainland. The Hachisuka's Line is located between the Okinawa and Miyako Islands, the Southern Sakishima Line is located between the Yaeyama Islands and Taiwan, and the Taiwan Strait Line is located between Taiwan and the mainland. Among these distribution boundaries, the Hachisuka's Line corresponds to the Kerama Gap, which is the deepest with a depth of over 1,000 m. In addition, the Yonaguni Strait, which separates Taiwan from the Yaeyama Islands and is deeper than 500 m, corresponds to the Southern Sakishima Islands Line. In contrast, the continental shelf connects the continent with Taiwan.

Hikita (2002) made a comparison of the terrestrial herpetofauna among these regions in the Ryukyu Islands, and found that most of the closely related species between the Okinawa/Amami Islands and the Yaeyama/Miyako Islands were differentiated at the species level, while most of the species between the Yaeyama/Miyako Islands and Taiwan were differentiated only at the subspecies level. Hikita (2002) stated that the land bridge of the Ryukyu Islands first extended from the continent through Taiwan to the Tokara Gap, then was divided by the Kerama Gap, and finally by the Yonaguni Strait. In other words, the Pleistocene land bridge extended only from Taiwan to the Miyako Islands, and the Okinawa/Amami Islands were isolated from the rest of the world by the Tokara and Kerama Gaps.

### **The terrestrial mammals on the islands of the Wallacea District**

Wallace (1863) distinguished between the fauna of the regions east and west of the boundary of biological distribution (Wallace's Line), which runs from the Lombok Strait between the Indonesian islands of Bali and Lombok through the western side of Sulawesi, the Makassar Strait, to the south of Mindanao in the Philippine Archipelago. Huxley (1968) extended the boundary through the Sulu Sea and then west of the Philippines between Borneo and Sulu (Fig. 3). The Huxley's Line, which is the eastern margin of the Oriental District, is roughly at the eastern edge of the outer continental shelf and corresponds to the eastern coastline of Southeast Asia during the Last Glacial Maximum.

The area between the Wallace's or Huxley's Lines and the Weber's or Lydecker's Lines, which marks the western edge of the Australian District, is called Wallacea District, the boundary area between the Oriental and Australian Districts. The islands of the Wallacea District include the Philippine Archipelago, Sulawesi, and Flores, which are still rich in endemic animal species, and fossil endemics such as stegodons and other proboscideans, rhinoceros, water buffalos, wild boars, and deer have been discovered in the Pleistocene series.

#### **Java**

Java, an island west of the Wallace's Line, is important in considering the distribution of animals on the islands of the Wallacea District, so here is summary of its biostratigraphy according to Van der Geer et al. (2010).

The island arc of Java started to rise due to volcanic activity in the Late Pliocene, and the western and central parts of Java became land due to gradual uplift since 1.8 Ma. During the Early Pleistocene, the mammals inhabiting Java are characterized by small hippopotamuses and deer, and small mastodons, but during the Middle Pleistocene, elements of mainland Southeast Asia continued to arrive on Java, and this fauna is characterized by *Homo erectus* and endemic small stegodons. At the end of the Middle Pleistocene, animals from the rainforest elements of mainland Southeast Asia migrated to the Indonesian Archipelago.

From Java, seven consecutive faunas have been recognized (De Vos et al., 1982; Sondaar, 1984), and Van der Geer et al.



**Fig. 3** Bathymetric chart around the Wallacea District showing biogeographic boundaries (white thick dotted lines) and the distribution of insular proboscideans. Thin dotted line is shown depth of 100 m. The seafloor shallower than depth of 1,000 m shows the land area in the late Middle Pleistocene. The seafloor topography is based on NOAA bathymetric data.

(2010) divided them into four major periods: (1) the Late Pliocene to Early Pleistocene (the Satir fauna), (2) the Middle Pleistocene (the Ci Saat fauna, the Trinil H. K. fauna, the Kedung Brubus fauna, and the Ngandong fauna), (3) Late Pleistocene (the Punung fauna), and (4) Holocene (the Wajak fauna). A summary of these faunas is given below, following Van der Geer et al. (2010).

(1) The Late Pliocene to Early Pleistocene fauna is represented by a mastodon (*Sinomastodon bumiajuensis*), a small hippopotamus (*Hexaprotodon sivajavanicus*), unidentified cervids, a giant tortoise *Geochelone* and perhaps pygmy stegodons.

(2) The fauna of the Middle Pleistocene is closely related to that of the Siwalik fauna of India, and is represented by *Homo electus*, the short-faced hyena (*Pachyrocota brevirostris*), the Javanese stegodon (*Stegodon trigonocephalus*), the Javanese elephant (*Elephas husdrindicus*), the Kendeng rhinoceros (*Rhinoceros unicornis kendengindicus*), the antelope (*Duboisia santeng*), and the Lydekker's deer (*Cervus (Axis) lydekkeri*).

(3) The fauna of the Late Pleistocene was formed by the arrival in the Indonesian Archipelago of new elements of the tropical rainforest fauna of the mainland at the end of the Middle Pleistocene. These are represented by the India elephant (*Elephas maximus*), orang-utan (*Pongo pygmaeus*), gibbon (*Hylobates syndactylus*), the pig-tailed macaque (*Macaca nemestrina*), the Sunda

tiger (*Panthera tigris sondaica*), the Sumatran rhino (*Dicerorhinus sumatrensis*), the Malayan bear (*Ursus malayanus*), serow (*Nemorhaedus sumatraensis*), water buffalo (*Bubalus bubalis*), and wild boar (*Sus scrofa vittatus*).

(4) The fauna of the Holocene is thought to have been recently replaced by present-day species or to have evolved from earlier Pleistocene inhabitants.

### Flores

Flores is one of the Lesser Sunda Islands east of Java (Bali, Lombok, Sumba, Sumbawa, Flores, and Timor), and is not connected to Java and Bali on the Sunda continental shelf by the Lombok Strait west of Lombok. The Lombok Strait is 18 km wide at its narrowest point, contiguous at the isobath at a depth of 250 m or more, it was not contiguous at the low sea level during the Last Glacial Maximum.

Flores emerged above the sea surface between about 15 and 21 Ma during the Early to Middle Miocene (Nishimura et al., 1981) and has been rising since the end of the Pliocene (Van den Bergh, 1999). The southern half is composed of Pliocene to Pleistocene volcanoes, while the southeastern and southwestern margins are composed of younger active volcanoes.

Flores was inhabited in the Middle and Late Pleistocene by pygmy and dwarf stegodons, giant rats, komodo dragons, and enigmatic species of dwarf human. According to Van der Geer et al. (2010), three faunas can be distinguished on Flores: (1) the Early Pleistocene (Fauna A), (2) the Middle Pleistocene (Fauna B), and (3) the Late Pleistocene.

(1) Fauna A of the Early Pleistocene is characterized by a pygmy stegodon (*Stegodon sondaari*), which is about half the size of Java stegodon (*Stegodon trigonocephalus*) and shows a mixture of primitive and advanced traits. The fission track age of the stratum in which the fauna was found is 0.9 Ma (Van der Geer et al., 2010).

(2) Fauna B of the Middle Pleistocene shows that mammals migrated to Flores approximately during the transition between the Early Pleistocene and Middle Pleistocene. The new mammalian elements are a middle-sized stegodon (*Stegodon florensis*), a middle-sized cave rat (*Hoijeromys nusatenggara*), and an early hominin (Van der Geer et al. 2010). Morwood et al. (1998) dated volcanic layers at about 0.88 and 0.68 Ma from this biozone. Fossils of early humans have not been found, and proof of their presence stems only from lithic artefacts. The primitive tools are found in association with fossils of the stegodon and in the same area where tektites belonging to the Australian strewnfield, dated to 0.8 Ma, are found (Van der Geer et al., 2010).

(3) The fauna of the Late Pleistocene is a variation of the fauna of the Middle Pleistocene, without major changes in the fauna of the Middle Pleistocene, characterized by a dwarf stegodon (*Stegodon florensis insularis*) (Van der Geer et al., 2010). The dwarf stegodon is smaller than its ancestor from the previous biozone (Van den Bergh et al, 2008). This fauna is also characterized by a dwarf human (*Homo floresiensis*) (Brown et al., 2004).

### Sulawesi

Sulawesi, formerly known as Celebes, is the largest of the Sunda Archipelago to the east of Borneo. Sulawesi is separated from Borneo by the Makassar Strait, which is over 2,000 m deep, but is contiguous with the Java Sea to its south by a 1,000 m deep isobath.

Sulawesi is currently home to a number of endemic species and subspecies, including the babirusa (*Babyrousa babyrussa*), the anoa (*Bubalus depressicornis*), the marsupial (*Ailurops ursinus*), the Sulawesi black macaque (*Macaca nigra*), the Muna-Buton macaque (*M. brunnescens*), the Heck's macaque (*M. hecki*), the Gorontalo macaque (*M. nigrescens*), the Dian's tarsier (*Tarsius dentatus*), and the pygmy tarsier (*T. pumilus*).

In Sulawesi, Van den Bergh et al. (2001) and Van der Geer et al. (2010) distinguished three faunas: (1) the Late Pliocene to Early Pleistocene Walanae faunal unit, (2) the Middle or Late Pleistocene Tanrung faunal unit, and (3) the Late Pleistocene to present fauna (Fig. 4).

(1) The Walanae faunal unit consists mainly of the Sulawesi dwarf elephant (*Stegoloxodon celebensis*), the giant Sulawesi pig (*Celebochoerus heekereni*) and the dwarf stegodon (*Stegodon sompoensis*). The oldest occurrence of this fauna is at about 2.5 Ma (Van der Geer et al., 2010).

(2) The Tanrung faunal unit is poorly represented and therefore also poorly known. Recorded elements are a large elephant (*Elephas* sp.), a medium-sized stegodon (*Stegodon* sp. B), and a short-legged form of the Sulawesi pig (*Celebochoerus* sp.) (Van der Geer et al., 2010).

(3) The Late Pleistocene to present fauna is clearly distinguished from the earlier fauna by the absence of proboscideans and giant pigs, and is thought to have been established in South Sulawesi during the Late Pleistocene by the gradual replacement of endemic species with new ones introduced to Sulawesi towards the end of the Tanrung faunal unit in the Middle Pleistocene (Van den Bergh et al., 2001). This fauna seems to have undergone the effects of long-term isolation and evolved into endemic forms, as noted by Wallace (1863).

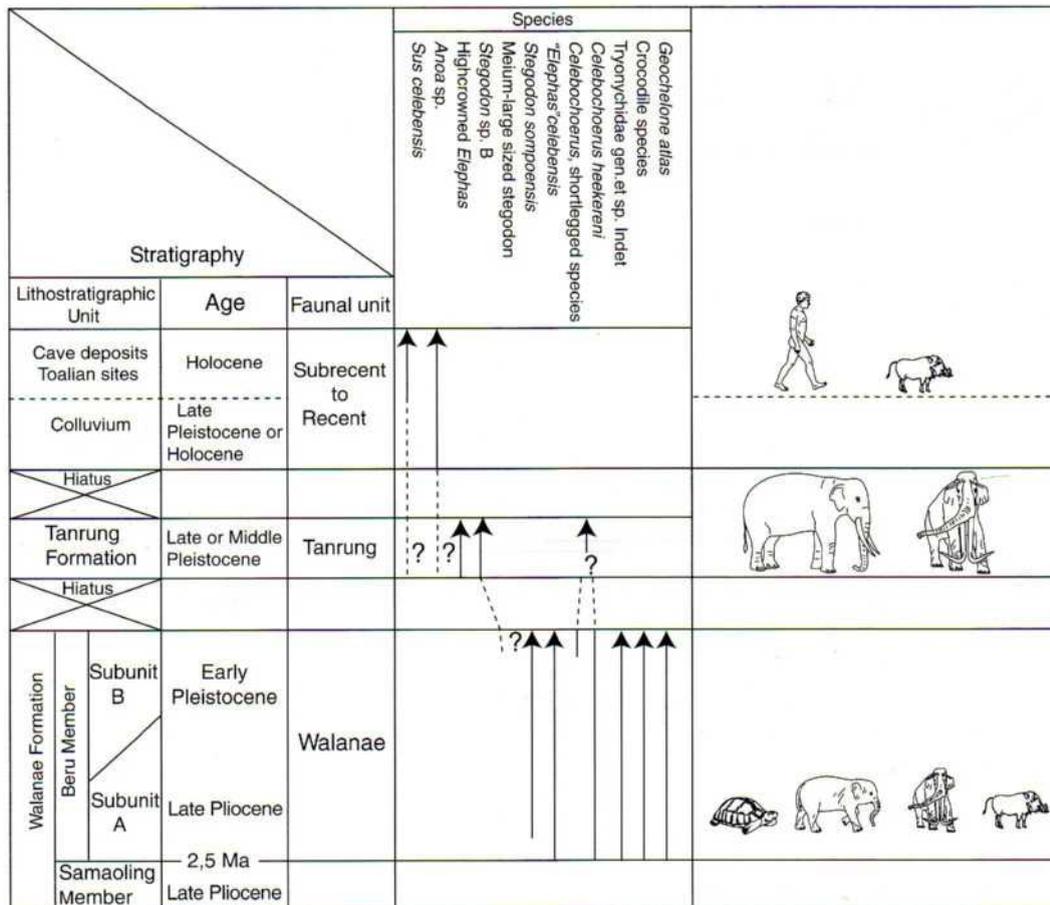


Fig. 4 Stratigraphic scheme, showing the land vertebrate faunal succession of Sulawesi (From Van der Geer et al., 2010). The subrecent to recent fauna is omitted.

### The Philippine Archipelago

The Philippine Archipelago consists of more than 7,000 islands located between Borneo and Taiwan. Croft et al. (2006) reconstructed the paleogeography of the Philippine Archipelago during the Last Glacial Maximum by dividing it into isobaths of 120 m depth and showed that they consisted of six major paleo-islands: Greater Luzon, Mindoro, Greater Palawan, Greater Negros-Panay, Greater Mindanao, and Greater Sulu.

The northern end of the Philippine Archipelago is separated from Taiwan by a seafloor of more than 2,000 m in depth. On the southwest side, Palawan is contiguous with Borneo at a depth of 200 m. However, Greater Palawan and Mindoro are contiguous only at a depth of 500 m. Borneo and Mindanao are contiguous at the 500 m depth isobath, and the southern tip of Mindanao is contiguous with Sulawesi only at the 1,500 m depth isobath.

The Philippine Archipelago is currently home to a large number of endemic species, even surpassing Madagascar in their degree of endemism. The main endemic species are the Philippine sambar (*Cervus mariannus*), the Prince Alfred's deer (*Cervus alfredi*), the Philippine tarsier (*Tarsius syrichta*), the Philippine flying lemur (*Cynocephalus volans*), the Philippine long-tailed macaque (*Macaca fascicularis philippinensis*), and several bat species and many endemic rodents (Muridae) (Van der Geer et al., 2010).

A reliable biostratigraphy for the Philippine Archipelago has not yet been established due to the scarcity of fossil records and the unknown stratigraphic contrast between the different islands. However, Van der Geer et al. (2010) distinguished three faunas: (1) the Middle to Late Pleistocene, (2) the Late Pleistocene, and (3) the Late Pleistocene to Holocene.

(1) The Middle to Late Pleistocene fauna is distributed in Greater Luzon, Greater Negros-Panay, and Greater Mindanao. This fauna includes a large stegodon (*Stegodon luzonensis*), a large elephant (*Elephas* sp.), a rhinoceros (*Rhinoceros philippinensis*), a Luzon buffalo (*Bubalus* sp.), a Mindoro buffalo (*Bubalus mindorensis*), and a Cebu buffalo (*Bubalus cebus*), a Luzon wild boar (*Sus* sp.), and a deer (*Cervus* sp.) from Luzon and Palawan. Stegodon fossils are found together with tektites and stone tools that have been dated to 0.8 Ma (Van der Geer et al., 2010).

(2) The Late Pleistocene fauna includes a dwarf deer (*Cervus* spp.) and a giant rat (*Rattus* cf. *everetti*) from Masbate Island (Greater Negros-Panay) (Van der Geer et al., 2010).

(3) The fauna of the Late Pleistocene to Holocene is the ancestor of the present fauna, which arrived at the end of the Pleistocene or the beginning of the Holocene. These species underwent speciation under isolation, and as result developed one of the most unique faunas in the world with regard to the level of endemic species (Van der Geer et al., 2010).

#### **Fauna of the Wallacea District since the Middle Pleistocene and its formation period**

The fauna of Java, excluding the Holocene, consists of the Early, the Middle and the Late Pleistocene faunas (Van der Geer et al., 2010). The Late Pleistocene fauna (the Punung fauna) replaced the Middle Pleistocene fauna, which was closely related to the earlier Siwalik fauna, and was formed at the end of the Middle Pleistocene when a new component of the rainforest fauna typical of mainland Southeast Asia migrated to the Indonesian Archipelago (Van der Geer et al., 2010).

In Flores, there were faunal transformations during the Early and Middle Pleistocene, and the fauna of the Late Pleistocene is a variation of the fauna of the Middle Pleistocene (Van der Geer et al., 2010). The time of conversion between fauna A of the Early Pleistocene and fauna B of the Middle Pleistocene may be around 0.9 Ma, because the stratigraphic level of fauna A is 0.9 ka, and fauna B includes volcanic ash layer of 0.88 Ma and tektites of 0.8 Ma (Morwood et al., 1998; Van der Geer et al., 2010).

Sulawesi also underwent faunal transformations during the Early, the Middle and the Late Pleistocene, of which the Late Pleistocene to present fauna is thought to have been formed by the gradual replacement of newly introduced species with endemic species in the Tanrung fauna of the Middle Pleistocene (Van der Geer et al. 2010).

In the Philippine Archipelago, the conversion from the Middle to Late Pleistocene fauna to the Late Pleistocene fauna probably occurred in the late Middle Pleistocene. However, because the biostratigraphy of the Philippine Archipelago has not been established and the characteristics of the fauna in each region of the Philippines are not clear, the details of this process are unknown. It is estimated that new fauna arrived at the end of the Pleistocene or the beginning of the Holocene (Van der Geer et al., 2010).

The Early, the Middle, and the Late Pleistocene faunas are unique to Java, Flores, Sulawesi, and the Philippines in the Wallacea District. Of these, the period of conversion from the Middle Pleistocene fauna to the Late Pleistocene fauna is thought to fall in the latter part of the Middle Pleistocene, although the specific age value of the conversion period for each island is unknown.

#### **The terrestrial mammals on the islands of the Mediterranean Sea**

The Mediterranean Sea is surrounded by the Eurasian continent to the north and east, the African continent to the south, the Atlantic Ocean to the west through the Gibraltar Strait, and the Marmara Sea and the Black Sea to the east through the Dardanelles and Bosphorus Straits. There are many islands in the Mediterranean Sea. In the western and central Mediterranean Sea, the Balearic Islands of Spain in the western part, Sardinia and Corsica in the Tyrrhenian Sea of the west of the Italian Peninsula, and Sicily and Malta in the south of the Italian Peninsula. In the eastern Mediterranean Sea, there are many islands such as the Cyclades in the Aegean Sea between Greece and Turkey, and Crete and Rhodes bound the southern border of the Aegean Sea, Cyprus is further south of Turkey.

Most of these Mediterranean islands were not connected to the continent by land when the sea level dropped by about 100 m during the Last Glacial Maximum (Fig. 5). However, fossils of many species of endemic mammals such as proboscideans, hippopotamuses, deer, otters and shrews have been found in the Pleistocene series of many of these islands.

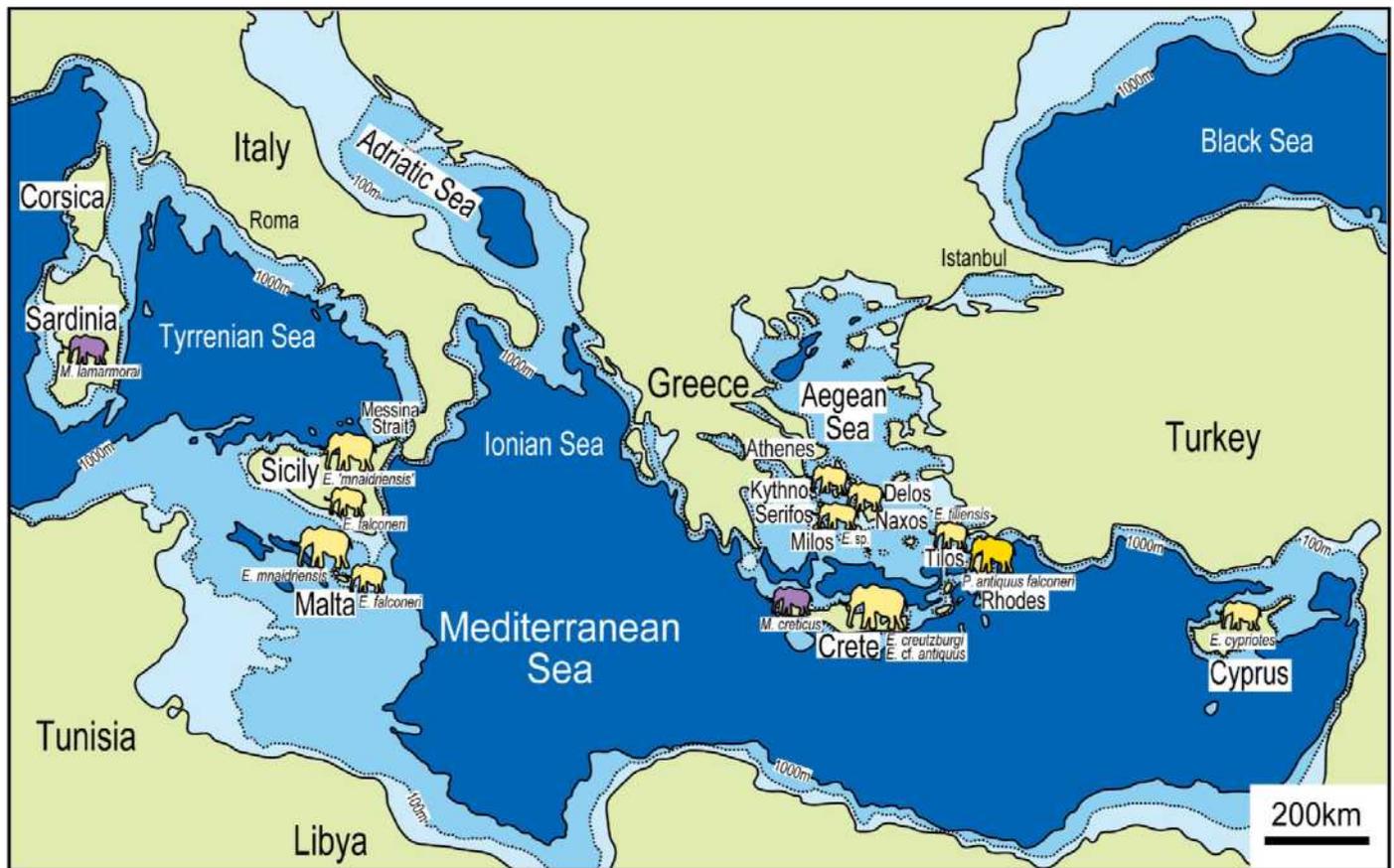
#### **Cyprus**

Cyprus, the third largest island in the Mediterranean Sea, emerged from the sea during the Miocene. Cyprus is separated from the Turkish mainland by a distance of about 80 km at the shortest point, where the seafloor extends to a depth of 500 m or more, and is connected by a 1,000 m deep isobath.

On Cyprus, two faunas are recognized: (1) the Late? Pleistocene and (2) the Holocene faunas (Van der Geer et al., 2010).

(1) The strata of the Late? Pleistocene yield fossils of a pygmy hippopotamus (*Phanourios minor*) and a dwarf elephant (*Elephas cypriotes*). The pygmy hippopotamus is the smallest hippopotamus of all known insular hippopotamuses and account for more than 90% of the mammal fossils found on Cyprus. This may be due to its lack of terrestrial predators or competitors, which allowed it to adapt well to all environments on the island (Van der Geer et al., 2010). *Elephas cypriotes* is thought to have been derived from *E. antiquus*. Elephants and pygmy hippopotamuses were introduced to this island in the late Middle Pleistocene and adapted to the island's area through subsequent isolation, becoming insular, or dwarfed, and endemic (Van der Geer et al., 2010).

(2) The Holocene fauna is in principle a mainland fauna, although rather impoverished, unbalanced and endemic on at most the subspecies level (Van der Geer et al. 2010). The Holocene fauna of Cyprus includes red fox (*Vulpes vulpes indutus*), Cypriot mouflon (*Ovis orientalis ohion*), small rats and bats. It is probable that these mammals, except for the bats, were introduced



**Fig. 5** Bathymetric chart around the Mediterranean Sea showing the distribution of insular proboscideans. Thin dotted line is shown depth of 100 m. The seafloor shallower than depth of 1,000 m shows the land area in the late Middle Pleistocene. The seafloor topography is based on NOAA bathymetric data.

through human agency.

### Crete

Crete is the largest island in Greece, located in the Cretan Sea between Greece and Turkey, and is connected to the Peloponnese of Greece by a 1,000 m deep isobath.

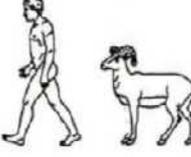
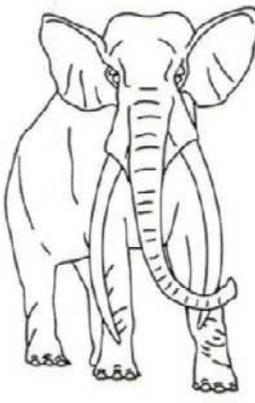
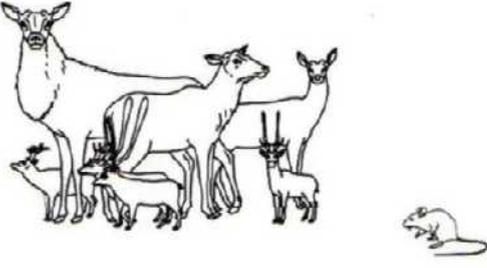
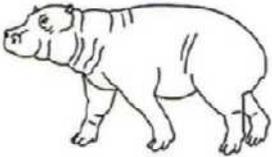
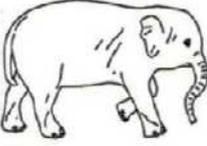
An endemic Pleistocene mammalian fauna is known from Crete, including dwarf deer, dwarf proboscideans, dwarf hippopotamus, and large mice. The pre-Pleistocene mammal fossils are of the Late Miocene age and belong to a continental type, but two distinct major biotic zones were recognized in the Pleistocene, with major faunal transformations at the boundaries of these zones (Sondaar et al., 1986; Dermitzakis and De Vos, 1987).

Crete was connected to the mainland until the Late Miocene. Gradually, Crete became fragmented into small pieces during the Late Miocene and Early Pliocene. The region became largely submerged towards the end of Pliocene Period, during what is known as the Pliocene transgression (Dermitzakis and Sondaar, 1978) and forming the present landscape at the end of the Pliocene or Early Pleistocene (Van der Geer et al., 2010). According to Van der Geer et al. (2010), excluding the Late Miocene biozones, Crete is divided into two biozones: (1) the *Kritimys* zone (the Early Pleistocene to early Middle Pleistocene) and (2) the *Mus* zone (the late Middle Pleistocene to late Late Pleistocene) (Fig. 6).

(1) The *Kritimys* zone is represented by the Cretan rat (*Kritimys*), the Cretan pygmy mammoth (*Mammuthus creticus*) and the Creutzburg's dwarf hippopotamus (*Hippopotamus creutzburgi*). According to Van der Geer et al. (2010), the absolute ages obtained by AAR and ESR of hippopotamus molar fragments range between 850 ka and 375 ka. Mol et al. (1996) estimated that the mainland ancestor of the pygmy mammoth was probably the southern mammoth (*Mammuthus meridionalis*).

(2) The *Mus* zone is represented by two species of common mice (*Mus bateae*, *M. minotaurus*), the Creutzburg's elephant (*Elephas creutzburgi*, *E. antiquus creutzburgi* or *E. cf. antiquus*), the Cretan deer (seven species of the genus *Candiacervus*), the Cretan otter (*Lutrogale cretensis*), and the Cretan shrew (*Crociodura zimmermanni*), which were introduced and endemic before the late Middle Pleistocene (Van der Geer et al., 2010).

### The Aegean Islands

Zones	Subzones	Range-zones			
				Holocene	
Mus	Mus minotaurus	Elephas creutzburgi		Pleistocene	
		Elephas antiquus			
	Mus bateae				
Kritimys	Kritimys catraus	Hippopotamus creutzburgi parvus			
		Hippopotamus creutzburgi creutzburgi			
	Kritimys kiridus	Elephas creticus			
	K. aff. kiridus				

**Fig. 6** Stratigraphic scheme, showing the land vertebrate faunal succession of Crete (Simplified version of figure from Van der Geer et al., 2010).

Fossils of dwarf elephants during the Late Pleistocene have also been found on the Aegean islands of Tilos, Rhodes, Naxos, and Delos. These islands are not contiguous with the continent at the 100 m depth isobath, but are distributed on a plateau above the seafloor at depths of 500 m to 1,000 m.

On Tilos, 11,000 fossil proboscideans were found, with a large variation in their size, and they were identified to two different subspecies (*Palaeoloxodon antiquus falconeri* and *P. a. mnaidriensis*) (Symeonidis et al., 1973). Theodorou et al. (2007) described a new species (*Elephas tiliensis*) from among them, and the absolute age of this new elephant ranges from about 45 ka to 3.5 ka.

The fossils from Naxos and Delos belong to a dwarf elephant that has not yet been described, with an elephant's maxilla from Naxos, an elephant's molar from Delos, and elephant remains from Rhodes, Ross and Serifos, and Kythnos. In addition, there are reports of proboscidean fossils from Rhodes, Ross and Serifos, and Kinos, but few species have been described and the material is untraceable (Van der Geer et al., 2010).

### Sicily

Sicily is a large island in the central Mediterranean, close to the southwestern tip of the Italian Peninsula by the Messina Strait, which is 3 km wide at its narrowest point. The Messina Strait is contiguous with the peninsula by isobaths at depth of 250 m.

Van der Geer et al. (2010) described the geological history and faunal evolution of Sicily since the Pliocene as follows. Sicily consisted of two islands in the Early Pliocene and Early Pleistocene, and the southern part of Calabria in the southern tip of the Italian Peninsula was also a series of islands with northern Sicily. The distance between Sicily and Calabria, the Messina Strait, varied in accordance with changing sea levels during the Pleistocene. Apart from this strait, the isthmus of Catanzaro between the north and south part of Calabria also played an important filter role in the colonization events of Sicily and Malta.

Sicily is characterized by a continuous mammalian endemic fauna that includes dwarf elephants and dwarf hippopotamuses

and giant dormice during the Pleistocene. Since then, Sicily has gradually lost its isolation and the number of mainland species inhabiting the island has increased. During the early Middle Pleistocene, Sicily was connected to Malta, sharing the same endemic fauna. This connection was lost before the end of the Pleistocene and both islands harboured their own endemic faunas.

The Pleistocene vertebrate assemblages of Sicily are generally known as Faunal Complexes. According to Van der Geer et al. (2010), it consists of excluding the Holocene fauna, (1) the Early Pleistocene fauna (the Monte Pellegrino Faunal Complex), (2) the early and middle Middle Pleistocene fauna (the *Elephas falconeri* Faunal Complex), (3) the late Middle Pleistocene to early Late Pleistocene fauna (the *Elephas 'mnaidriensis'* Faunal Complex), and (4) the Latest Pleistocene fauna (the Gotta San Teodoro-Contrada Pianetti Faunal Complex).

(1) The Early Pleistocene fauna is represented by a marten (*Mustelercta arzilla*), a large red-toothed shrew (*Asoriculus burgioi*), a large field mouse (*Apodemus maximus*), two large dormice (*Leithia* sp. *Maltamys* cf. *gollcheri*), a ctenodactylid (*Pellegrinia panormensis*), and a hare (*Hypolagus peregrinus*) (Van der Geer et al., 2010). The shrew evolved in parallel with the other Mediterranean insular red-toothed shrews, all of which are thought to have originated from a clade of common ancestors, and the dormouse genera *Leithia* and *Maltamys* are regarded as relics of an older fauna of the Messinian age (Late Miocene) by Daams and De Bruijn (1995).

(2) The early and middle Middle Pleistocene fauna is highly endemic and impoverished. Its only known elements are the pygmy elephant (*Elephas falconeri*), a shrew (*Crocidura esuae*), a giant dormice (*Leithia melitensis*), two large dormice (*Leithia cartei* and *Maltamys gollcheri*), the Sicilian otter (*Lutra trinacriae*), and bats (Van der Geer et al. 2010). Fossil pygmy elephants were dated to  $455 \pm 90$  ka using amino-acid racemization by Bada et al. (1991). This fauna is almost identical to the fauna of Malta at this time, and provides evidence that Sicily and Malta were connected and became one island. The habitat of the pygmy elephants is thought to consist of an open environment with sparse tree cover, dominated by grasses, and was much like the habitat of the extant African elephant as indicated by pollen analysed by Bertoldi et al. (1989) and Suc et al. (1995). The Sicilian and Maltese extant shrew might in turn have descended from the Saharan shrew (*Crocidura tarfayaensis*), as ascertained by Dubey et al. (2007), based on DNA.

(3) The late Middle Pleistocene and early Late Pleistocene fauna is represented by an endemic small elephant (*Elephas 'mnaidriensis'*) and a small hippopotamus (*Hippopotamus pentlandi*). In this period, a new invasion of mainland species took place. Other new insular elements of this fauna are fallow deer (*Dama carburangelensis*), aurochs (*Bos primigenius*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), brown bear (*Ursus arctos*), European bison (*Bison priscus*), grey wolf (*Canis lupus*), lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), and European hedgehogs (*Erinaceus europaeus*), all typical for a warm period (Van der Geer et al. 2010). Dating by ESR on teeth enamel of *Elephas 'mnaidriensis'* and *Hippopotamus pentlandi* by Rhodes (1996), provided an age ranging between  $146 \pm 28.7$  ka and  $88.2 \pm 19.5$  ka.

(4) The Latest Pleistocene fauna includes the large mammals of the earlier *Elephas 'mnaidriensis'* fauna, but more mainland taxa, including the European ass (*Equus hydruntinus*) arrived on the island at the end of this stage. The new micromammals of this period are the common field mouse (*Apodemus silvaticus*), the pine vole (*Microtus savii*) and Sicilian shrew (*Crocidura sicula*), (Van der Geer et al., 2010).

## Malta

Malta is a small island south of Sicily, which is not connected to Sicily by the 100 m depth isobath, but is connected by the 200 m depth isobath. Malta was connected to Sicily in the early Middle Pleistocene, but sea level rise by the end of the Pleistocene separated Malta from Sicily. Since that period, Malta has harboured its own endemic fauna, consisting mainly of dwarf proboscideans, dwarf deer and giant dormice. The fauna of Malta was divided by Van der Geer et al. (2010) into (1) the middle Middle Pleistocene, (2) the late Middle Pleistocene, and (3) the Late Pleistocene, excluding the Holocene fauna, as follows.

(1) The middle Middle Pleistocene fauna is characterized by the Sicilian dwarf elephant (*Elephas falconeri*) and a giant dormouse (*Leithia melitensis*), two large dormice (*Maltamys gollcheri* and *M. wiedincitensis*), the Maltese otter (*Lutra euxena*) and a white-toothed shrew (*Crocidura esuae*). Malta was connected by land with Sicily, based on the occurrence of the same species of dwarf elephant, dormice and shrew.

(2) The late Middle Pleistocene fauna is thought to have been formed by new arrivals, represented by the Maltese dwarf hippopotamus (*Hippopotamus melitensis*) and a small elephant (*Elephas mnaidriensis*). The main difference between the Sicilian fauna and the Maltese fauna of this period is the smaller size of the Maltese hippopotamus and elephant in combination with a larger degree of endemism of the Maltese fauna.

(3) The Late Pleistocene fauna consists mainly of the endemic short-limbed deer (*Cervus* sp.), a burrowing vole (*Microtus (Pitimus) melitensis*) and a white-toothed shrew (*Crocidura* sp.), all new immigrants. The Late Pleistocene fauna of Malta is more endemic than that of Sicily, and the fauna as a whole is much poorer than that from Sicily.

## Sardinia and Corsica

Sardinia and Corsica are two large islands in the Tyrrhenian Sea on the western side of the Italian Peninsula. The two islands are contiguous at the 100 m depth isobath, so they were one island until the beginning of the Holocene. Therefore, the fauna of Sardinia and Corsica are practically the same. The Corsica Channel between Corsica and Elba Island on the west coast of the Italian Peninsula is about 50 km wide and deeper than 200 m. Corsica and Elba island are contiguous at an isobath of 500 m depth.

Sardinia and Corsica were a part of the adjacent continent during the Eocene, isolated from the continent at the beginning of the Miocene. At the onset of the Late Miocene Messinian salinity crisis (Hsü et al., 1977), Sardinia and Corsica became a part of the Italian region of Tuscany, forming the Tusco-Sardinian paleobioprovince. During the Middle Pliocene and Early Pleistocene, Sardinia and Corsica again were isolated from the mainland, but they were connected to the continent several times and new animal elements were introduced. It is thought to have been completely isolated from mainland Italy after the late Middle Pleistocene (Van der Geer et al., 2010).

The fauna of Sardinia and Corsica is divided into five groups by Van der Geer et al. (2010): (1) the Early to Middle Eocene, (2) the Early Miocene, (3) the Late Miocene, (4) the Middle Pliocene to Early Pleistocene, and (5) the late Early Pleistocene to Early Holocene. Here, the fauna groups of (1) to (3) omitted and start with (4), because this paper focuses mainly on the fauna of the Pleistocene.

(4) The fauna of the Middle Pliocene and the Early Pleistocene is balanced through impoverished, characterized by goral-like caprids (*Nesogoral melonii* and *Nesogoral cenisae*), a small pig (*Sus sondaari*), a macaque (*Macaca majori*), a hunting hyena (*Chasmaporthetes melei*), a small bovid (*Asoletragus gentryi*), an undetermined caprid, a mustelid (*Pannonictis* sp.), and several micromammals, including a large field mouse (*Apodemus mannu*), a small field mouse (*Rhagapodemus azzarolii*, *R. minor*), a dormouse (*Tyrrhenoglis*), a shrew (*Asoriculus* aff. *gibberodon*), a mole (*Talpa* sp.), a pika (*Prolagus* aff. *P. sorbinii*), and a rabbit (*Oryctolagus*). This fauna is generally characterized by small mammals. This fauna, generally referred to as the *Nesogoral* fauna after the goral-like caprid, was probably introduced by a land bridge that existed during the Late Miocene Messinian salinity crisis and formed as the result of a long period of subsequent isolation during the Pliocene (Van der Geer et al., 2010).

(5) The fauna of the late Early Pleistocene to early Holocene is dominated by a canid (*Cynotherium* sp.), a small vole (*Microtus* (*Tyrrhenicola*) *sondaari*), a large deer (*Megaloceros* sp.), red-toothed shrews (*Asoriculus similis* and *Asoriculus corsicanus*) and possibly human (*Homo sapiens*). Fossils of Sardinian large deer have been obtained from strata dated to 450 ka and 367 ka. And the ancestors of the dwarf mammoth (*Mammuthus lamarmorae*) arrived on the island during the late Middle Pleistocene. The fauna of this period was unbalanced, strongly endemic, and probably evolved here after a long period of isolation, but from the Middle Pleistocene onwards it developed a fauna that was slightly different from the earlier ones (Van der Geer et al., 2010).

#### **Fauna of the late Middle Pleistocene of the Mediterranean Islands and its formation period**

The Pleistocene mammalian faunas of the Mediterranean islands show that most of them underwent major transformations in the early and late Middle Pleistocene. In Crete, that is a typical example, two biological zones are recognized: the Early to Middle Pleistocene (*Kritimys* Zone), represented by Cretan pygmy mammoth and Creutzburg's dwarf hippopotamus, and the Middle to Late Pleistocene (*Mus* Zone), represented by Creutzburg's elephant and Cretan deer. The mammals of the *Mus* Zone were introduced and endemic in the late Middle Pleistocene (Van der Geer et al. 2010).

In Cyprus, there is a Late? Pleistocene pygmy or dwarf fauna, which are thought to have migrated to the island in the late Middle Pleistocene (Van der Geer et al. 2010). The Late Pleistocene elephant fossils have also been found on the Aegean islands, and Van der Geer et al. (2010) state that the Cyclades Islands probably formed one large island during the Late Pleistocene.

In Sicily and Malta, the early and middle Middle Pleistocene and the late Middle to early Late Pleistocene mammalian faunas are highly endemic, represented by a pygmy elephant. The latter is thought to have been formed in Sicily by new introductions of species from mainland Italy between  $455 \pm 90$  ka (Bada et al. 1991) and  $146.8 \pm 28.7$  ka (Rhodes 1996) in the late Middle Pleistocene. The Maltese fauna is more isolated than that of Sicily due to the small size of Malta compared to Sicily and the extremely restricted number of species that came to the island. The composition of the Maltese fauna is thought to have been unique and different from that of the Sicilian fauna, even in the same period. Sicily may have been connected to the Italian Peninsula during the Late Pleistocene.

The Pleistocene fauna of Sardinia and Corsica consists of the Middle Pliocene to Early Pleistocene and the late Early Pleistocene to early Holocene faunas. Since the Middle Pleistocene, the fauna has been slightly different from the earlier ones, and the ancestor of the dwarf mammoth (*Mammuthus lamarmorae*) arrived on the island during the late Middle Pleistocene (Van der Geer et al. 2010).

This suggests that there was a major shift in the mammalian fauna of many of the Mediterranean islands at some time in the late Middle Pleistocene, with the arrival of new animals to the islands, although precise age values are not available.

### Foxes and mammoths of the Channel Islands of California

The Channel Islands form a group of eight isles along the coast of southern California in the Pacific Ocean, from Los Angeles to San Diego, across the Santa Barbara Channel. The six isles of the Islands are home to a small gray fox called the Island fox (*Urocyon littoralis*), which is found only in this Islands.

The Channel Islands consist of the northern and southern groups. The northern group is separated from the mainland by the Santa Barbara Channel, which is approximately 20 km wide and 300 m deep. The group consists of four isles aligned in an east-west direction: Anagapa, Santa Cruz, Santa Rosa, and San Miguel. The south group consists of four isles, from east to west: Santa Catalina, San Clemente, Santa Barbara and San Nicolas (Fig. 7).

In the northern group of the Islands, 145 of the plant and animal species observed today are endemic. Santa Rosa is home to more than 100 species of land birds, three species of mammals (fox, skunk, and rat), two species of amphibians, three species of reptiles, seabirds and sea lions, and six species of plants found only on the isle (Web site of National Park Service Channel Islands). And fossils of dwarf mammoth (*Mammuthus exilis*) and Columbian mammoth (*M. columbi*) have been excavated on the isles of Santa Cruz, Santa Rosa, and San Miguel in the northern group (Agenbroad 1998).

The Island fox (*U. littoralis*) is similar to, but distinct from, the Gray fox (*U. cinereoargenteus*), which is distributed from USA to Colombia, and is divided into different subspecies on each of the six isles where it occurs (Animal Diversity Web Univ.



**Fig. 7** Bathymetric chart around the Channel Islands of California showing the distribution of insular fox and mammoth. Thin dotted line is shown depth of 100 m. The seafloor shallower than depth of 1,000 m shows the land area in the late Middle Pleistocene. The seafloor topography is based on NOAA bathymetric data.

Michigan Mus. Zoology). In other words, *U. littoralis santacruzae* inhabits on Santa Cruz, *U. l. santarosae* on Santa Rosa, and *U. l. littoralis* on San Miguel in the northern group, and *U. l. catalinae* on Santa Catalina, *U. l. clementae* on San Clemente, and *U. l. dickeyi* on San Nicolas in the southern group. No Island fox inhabits in the two remaining isles of the Islands: Anagapa and Santa Barbara. The reason for this is that these isles are so small compared to the isles where the foxes live that they could not live there due to lack of food.

The Late Pleistocene to Holocene fossil fauna of the northern group consists of dwarf mammoth (*Mammuthus exilis*), the Is-

land fox (*U. littoalis*), a sea otter (*Enhydra lutris*), a large deer mouse (*Peromyscus nesodytes*) and a small deer mouse (*P. an-yapahensis*). Apart from the dwarf mammoth, a mainland American mammoth (*M. columbi*) also occurs, and a single proboscidean tooth have been recovered from San Nicolas in the southern group (Van der Geer et al., 2010).

As to how the Island fox and the dwarf mammoth came to inhabit the Channel Islands, there are theories that the Island fox was transported as a pet by native Americans (Collins, 1991) and that the mammoth swam across (Johnson, 1978).

### Wolves of the Falkland Islands

The Falkland Islands are located in the South Atlantic Ocean, 500 km from Patagonia, Argentina, and consists of two large islands, the East Falkland and the West Falkland, and 776 isles (Fig. 8). The Falkland Islands are cold and mostly barren, but the flat land of the East Falkland Island has been turned into sheep pastures by the British colonists. On these cold, isolated islands, there were wolves.

The Falkland wolf (*Dusicyon australis*) of the Falkland Islands was alive when Charles Darwin visited there in 1834 on the Beagle, and is mentioned in Darwin's *The Voyage of the Beagle* (Darwin, 1956). The Falkland wolf fed on birds such as geese and penguins and on marine animals such as seals that inhabited the islands. Phylogenetically, the Falkland wolf is closely relat-



**Fig. 8** Bathymetric chart around the Falkland Islands showing the distribution of insular wolf. Thin dotted line is shown depth of 100 m. The seafloor shallower than depth of 1,000 m shows the land area in the late Middle Pleistocene. The seafloor topography is based on NOAA bathymetric data.

ed to the South American fossil species *D. avus* (Van der Geer et al., 2010).

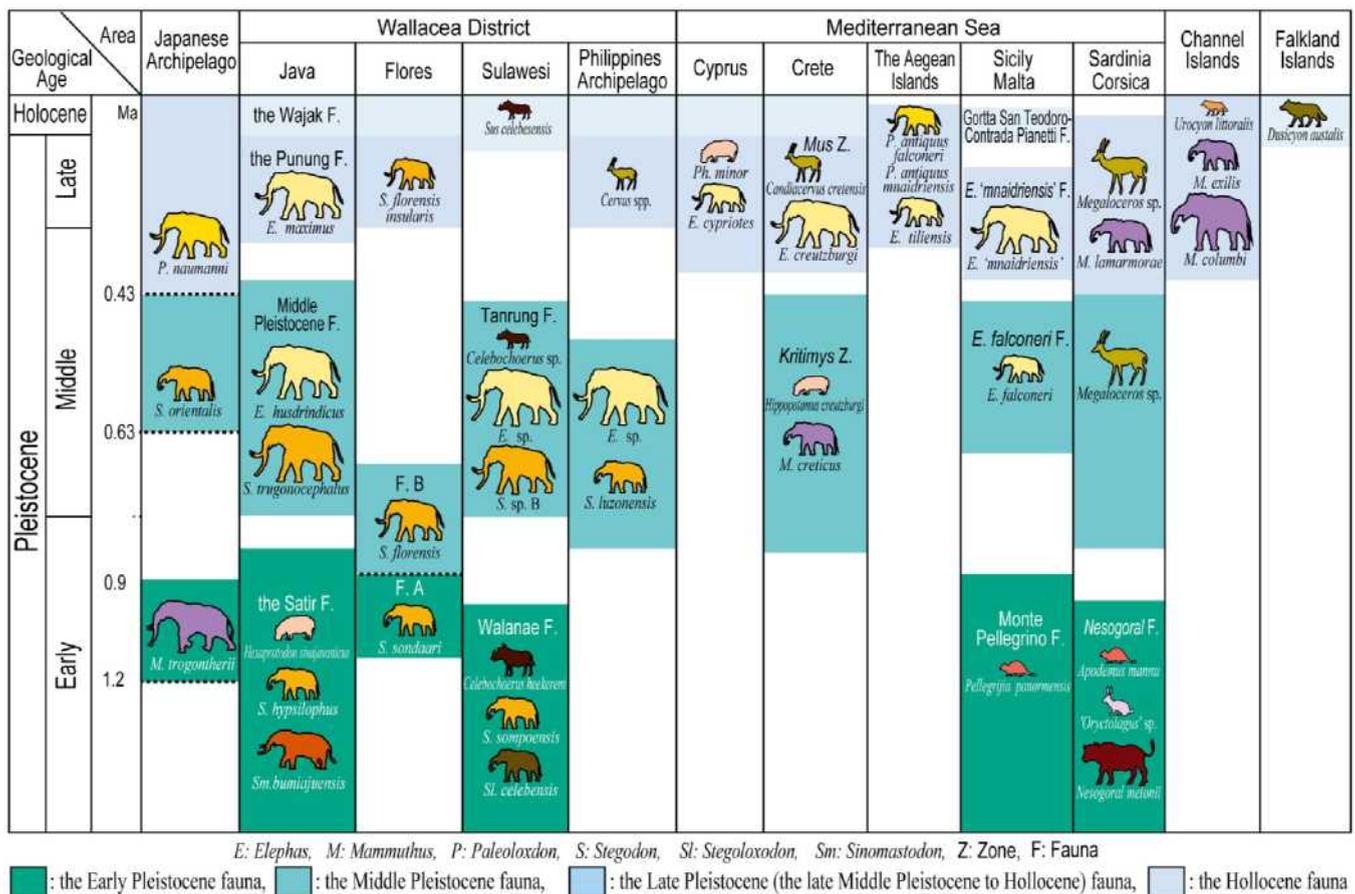


Fig. 9 Stratigraphic distribution of the insular mammalian faunas in each island of the world.

**Distribution of endemic faunas on the islands and land bridges in the late Middle Pleistocene**

In this paper, we have reviewed mainly the distribution and evolution of the endemic mammalian faunas of the world's islands, especially since the Pleistocene. The mammals that inhabited the world's islands since the Late Pleistocene, have been endemic to each island. Fig. 9 shows the stratigraphic distribution of the insular mammalian faunas in each island of the world.

**Honshu region of the Japanese Archipelago**

In the Honshu region of the Japanese Archipelago, Konishi and Yoshikawa (1999) and Kawamura (2014) have shown from proboscidean fossils that the *Paleoloxodon naumanni* was introduced from northern China via the Korean Peninsula 430 ka. This suggests that the most recent arrival of the fauna leading to the present occurred 430 ka, when the ancestors of the *P. naumanni* arrived in the late Middle Pleistocene. If the sea level 430 ka was 1,000 m lower than the present level, as described by Shiba (2017a, 2017b), the land bridge connecting the continent and the Japanese Archipelago would be as shown by the 1,000 m depth contour in Fig. 1. The land bridge in the late Middle Pleistocene was submerged due to the gradual rise of sea level, and the Honshu region was separated from the continent by the sea, and trapped animals evolved into endemic species.

**The Ryukyu Islands**

In the Ryukyu Islands, Hikita's interregional comparison (Hikita, 2002) of terrestrial herpetofauna showed that the land bridge initially extended from the continent through Taiwan to the Tokara Gap, but later in the Pleistocene it was divided by the Kerama Gap, and the Okinawa/Amami Islands were not connected to the continent and the Yaeyama/Miyako Islands. In the Ryukyu Islands, following the contour line at a depth of 1,000 m, the Okinawa/Amami Islands and the Taiwan/Yaeyama Islands are separated by the Kerama Gap, which well explains the Pleistocene Taiwan/Yaeyama Islands land bridge and the existence of the Okinawa/Amami Islands paleo-land shown by Hikita (2002) (See Fig. 2).

**The Wallacea District**

The Early Pleistocene, the Middle Pleistocene and the Late Pleistocene faunas are unique to Java, Flores, Sulawesi and the Philippine Archipelago in the Wallacea District. The last of these faunal transformations is thought to have occurred in the late Middle Pleistocene.

Audley-Charles (1981) proposed that the Banggai and Sula Islands, Seram, and Buru around Sulawesi were exposed as a vast land area (Stegoland) in the Late Pleistocene or earlier, and that the western part of Sulawesi was intermittently connected to Borneo through the partially exposed the Makassar Strait. In contrast, Van der Geer et al. (2010) argued that the sea around Sulawesi is a 1,000 m deep strait, making such a sea level drop unlikely. However, if the seafloor at depths of 1,000 m or less was once land, then Sulawesi would be connected to Borneo from the Sula Islands. Furthermore, Flores and the Philippines are also land-locked from the continent, which explains the distribution of endemic terrestrial animals on these islands (See Fig. 3).

### **Islands of the Mediterranean Sea**

Islands of the Mediterranean Sea, i.e., Cyprus, Crete, the Aegean islands, Sicily and Malta, Sardinia and Corsica, have endemic faunas from the late Middle Pleistocene to Late Pleistocene Period, and their formation and conversion from earlier faunas are considered to be the late Middle Pleistocene. Fig. 5 shows the Mediterranean Sea at depths of 1,000 m or more in the sea and shallower depths on the land. If we assume that in the late Middle Pleistocene, the area shallower than the present depth of 1,000 m was a continental land area, new fauna migrated from the continent to these islands, which then became isolated from the continent and formed their own unique fauna.

The seafloor between the Italian Peninsula and Tunisia in Africa is shallower than 1,000 m deep and stretches from north to south, dividing the Mediterranean Sea into east and west. If this seafloor was once land, it would explain the analogous relationship with the African fauna in the Pleistocene fauna of Sicily shown by Dubey et al. (2007).

### **The Channel Islands and the Falkland Islands**

In the Channel Islands, if we follow the 1,000 m depth isobath from California to the Channel Islands on the west coast of the Americas, all eight islands of the Channel Islands are a land area extending from California. If the seafloor shallower than today's depth of 1,000 m were once land, there would have been a vast land area along the present California coast (See Fig. 7). Probably in the late Middle Pleistocene, the common ancestor of the Gray fox and Island fox of present-day California may have lived in the natural environment of the west coast of the Americas, which is vastly larger than it is today.

The Falkland Islands are a contiguous land area from South America when divided by the 1,000 m depth contour line (See Fig. 8). In other words, if we assume that the sea level was 1,000 m lower than the present at some point in the past, the islands were part of the South American continent and was isolated by the subsequent rise in sea level, so that the Falkland wolf survived as an endemic species on the islands, feeding on marine animals.

### **Land bridges and terrestrial animal migration in the late Middle Pleistocene**

The late Middle Pleistocene to Late Pleistocene faunas in the Honshu region of the Japanese Archipelago, the islands of the Wallacea District, the Mediterranean Sea, and the Channel Islands described in this paper can be considered to have been formed and converted from earlier faunas during the late Middle Pleistocene. This suggests that mainland animals migrated due to the connection between the islands and the continent caused by the expansion of the land area in the late Middle Pleistocene. It is also possible that this was the same time that the fauna of the late Middle Pleistocene was formed in the Honshu region of the Japanese Archipelago.

All islands with endemic fauna since the late Middle Pleistocene shown in this paper are connected to the nearest continent only at isobaths of 1,000 m or more. Assuming that the coastline existed at the present-day depth of 1,000 m the late Middle Pleistocene, the islands described in this paper would all be a part of the adjacent continent. In other words, the sea level in the late Middle Pleistocene was 1,000 m lower than the present, and the subsequent sea level rise is thought to have led to the formation of endemic faunas on islands separated from the continent by the sea since the late Middle Pleistocene.

The migration of terrestrial animals to ocean islands has been explained by Van der Geer et al. (2010) and many other researchers, especially biologists, by the swimming ability of elephants and deer and the dispersal of sweepstakes (Simpson, 1965) by natural rafts (Matthew, 1918). Sweepstake means horse races, lotteries, etc., with little chance of success due to the danger of crossing oceans, but great success if done well (Simpson, 1984).

However, in addition to elephants and deer, many other species are endemic to the islands, including grassland rodents and arboreal monkeys. In addition, the migration of terrestrial animals is limited to one-way traffic from continents to islands. The stratigraphic distribution of the faunas of the world's islands suggests that new faunas were formed in many islands almost since the late Middle Pleistocene (See Fig. 9). These results suggest that the migration of terrestrial animals to islands is mainly due to the expansion of their habitats, and that the formation or transformation of island fauna is not due to the accidental migration of animals across the sea.

Even if a few elephants or deer were to cross an island by chance, as in the case of the Sweepstake dispersal, it is unlikely that they would be able to reproduce and continue to live there. I also believe that if such coincidental events occur frequently

enough to allow animal exchange between islands and continents, then island endemism will not form.

Van der Geer et al. (2010) found that the fauna of the islands was characterized by imbalance and poverty, which had a strong filtering effect on migration to the islands. However, this may be due in part to the short time that land bridges have been able to cross to the island and the limited natural environment of these bridges. Furthermore, as the area of the island shrank due to isolation, the number of species that could adapt to changes in the natural environment was limited, and the composition of new niches may have caused the formation of endemic species within the island. In other words, the ancestors of the endemic species on the islands did not migrate by chance with their swimming ability or ability to ride on rafts with a rare chance of winning the lottery, but migrated within the same habitat of the continents and islands that were once connected by land.

It may be difficult to believe that the sea level has risen by almost 1,000 m since the late Middle Pleistocene. However, as mentioned by Shiba (2017a, 2017b), the formation of the Pleistocene around Suruga Bay involved uplift of the seafloor and sea level rise as well as land, and the formation of Suruga Bay and the continental slope (Inouchi et al. 1978) also occurred during this period. As for the sea level rise of 1,000 m during the Pleistocene, Hoshino (1975a, 1983) has already made a pioneering study that the sea level was 1,000 m lower during the Villafranchian period, and then rose by 1,000 m due to the Sicilian sea level rise based on the flat surface of the continental slope and the deltaic deposits distributed there. Hoshino (1962, 1975b, 1998) argued that the sea level at the latest Miocene was 2,000 m lower than the present level, and has since risen to the present level, because the terminal depth of the world's submarine valleys is at a depth of 2,000 m everywhere, and the youngest strata that make up the valley floor are the latest Miocene. Hoshino (1978) also attributes the distribution of Messinian evaporites on the seafloor at a depth of 2,000 m in the Mediterranean Sea (Hsü et al., 1977) to the 2,000 m lower sea level at the latest Miocene, and suggested that the sea level rose in stages with the uplift of the earth's crust.

If the sea level rises by 1,000 m in 430,000 years, the average rise in sea level will be 2.33 mm/year. If the sea level were to rise at such a rate, it would rise by 2.33 m in 1,000 years, and we would expect the land area to rise by the same amount or more. The rise of sea level is caused by the uplift of the ocean floor, ocean ridges, ocean rise, etc., or by volcanic activity on the sea floor, which raises the sea floor and pushes up the seawater above it (Hoshino, 1983, 1991, 1992). The cause is thought to be the large-scale uplift movement of the crust caused by the uplift of tholeiitic basaltic magmas from the upper mantle and their intrusive into the crust, as described by Hoshino (1998, 2014). Such crustal uplift was not confined to the sea floor, but was more pronounced on land, and land remained land because the uplift on land was greater than that on the sea floor.

The sea level in a region is the amount of crustal uplift in that region minus the amount of sea level rise. A positive value indicates uplift in relation to sea level, while a negative value indicates subsidence (submergence). In other words, the islands with endemic species since the late Middle Pleistocene are the areas of relative subsidence because they did not rise as much as land areas during the 1,000 m rise in sea level. The animals that inhabited these islands are not only valuable relics that evolved and survived while adapting to their isolated environment, but also are thought to be important in conveying the evolution of life and the history of the Earth.

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