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The Late Pleistocene Terrestrial Turtle Fauna of the Ryukyu Archipelago and Its Paleogeographic Implications

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The Ryukyu Archipelago is a chain of continental islands located between the mainland Japan and Taiwan. First emerging as an eastern margin of the Eurasian continent, this archipelago has supposedly been formed through an extension of the Okinawa Trough along the eastern side of the continent since the Late Miocene. Based on the current faunal characteristics and tectonic structure, the archipelago is usually divided into three regions: 1) northern Ryukyus, consisting of the Osumi Group and the northern Tokara islands, characterized by numerical dominance of species common to the mainland Japan; 2) central Ryukyus, consisting of the southern Tokara islands, the Amami Group, and the Okinawa Group, characterized by a high ratio of endemic taxa, and 3) southern Ryukyus, consisting of the Miyako Group and the Yaeyama Group, characterized by a high frequency of species common to Taiwan but with occasional subspeciation. Boundaries between these three regions correspond to the two deep straits (>1,000 m in depth) crossing the island chain - the Tokara Strait separating 1) and 2), and the Kerama Gap separating 2) and 3). Isolation of the central Ryukyus from the surrounding landmasses is generally considered to have initiated as early as the Late Miocene. In contrast, most recent authors suspect that the islands of the northern and southern Ryukyus remained connected, respectively, to the mainland Japan and Taiwan until the Middle Pleistocene.

Recent biochemical and molecular phylogeographical studies of some extant vertebrate lineages yielded results that did not largely contradict with such paleogeographical hypothesis of the Ryukyus. Even so, however, each of these studies is not necessarily free from noises from various sources, such as localized extinction of representatives of a given lineage and genetic drifts in relevant populations. Therefore, the above scenario regarding the Ryukyu paleogeography still needs verification, idealistically from different lines of evidence.

It is known that fossils, when exist, can offer a fascinating opportunity to test historical scenarios hypothesized from data from extant organisms. Fortunately, most islands of the Ryukyus are more or less covered by the Pleistocene coral reef complex deposits that are collectively referred to as the Ryukyu Group (so-called "Ryukyu Limestone"), because these deposits often provide favorable environment to successfully preserve the latest Pleistocene animal fossils in fissures and cave deposits. Nevertheless, the taxonomic status and phylogenetic affinities remain uncertain for most fossils excavated in the Ryukyu Archipelago chiefly due to the paucity of approaches using appropriate comparative materials. This has been reducing values of these fossils as the source of information for the Ryukyu paleogeography.

Of the organisms commonly fossilized, the turtles (Reptilia, Testudines) is one of the

most informative groups in the above context, because their skeletons including the shell elements have a number of characters useful to infer historical relationships among representatives of various localities and of various dates. Keeping this advantage in mind, I have investigated taxonomic status and phylogenetic affinities of terrestrial turtle fossils discovered from the Ryukyu Archipelago.

Present terrestrial turtle fauna of the Ryukyu Archipelago consists only of three geoemydid species, *Geoemyda japonica*, *Cuora flavomarginata evelynae*, and *Mauremys mutica kami*. They seemingly follow the generally accepted geohistorical scenario as above, because the central Ryukyu species, *G. japonica*, is obviously at a highly relict state, whereas the two southern Ryukyu subspecies, *C. f. evelynae* and *M. m. kami*, have conspecific populations in Taiwan and southeastern continent. However, such concordance with the currently prevailing paleogeographical hypothesis of the Ryukyus is not necessarily true with the extinct chelonians found from the Late Pleistocene fissures and cave deposits. For example, the geoemydid fossils from the Miyako Group, initially referred to as *Mauremys mutica*, has recently proved to represent an undescribed extinct species, whose close relatives, while obviously including *M. japonica* from the mainland Japan, remain undiscovered from Taiwan or southeastern continent. Moreover, some turtle fossils from both the central Ryukyus (Amami and Okinawa Groups) and the southern Ryukyus (Miyako Group) have proved to represent a single testudinid species, *Manouria oyamai*. Fossils of the genus *Geoemyda* discovered from Tokunoshima of the Amami Group offered a case of substantial divergence within the central Ryukyus, because they, while obviously sister to *G. japonica* of the Okinawa Group, are distinct from the latter in a few osteological characters. Each of these requires an additional *ad hoc* hypothesis or otherwise, necessitates drastic modification of the currently prevailing paleogeographical hypothesis of the Ryukyus.

Those and other turtle fossils (i.e., those representing undescribed *Cuora* species on Okinawajima Island, apparently unique geoemydid species on Kumejima Island, etc.) indicate that the Pleistocene turtle fauna of the Ryukyus was at least a few times as rich in species number as the present turtle fauna, and that such rich state continued by the very end of the Pleistocene. This means that the majority of the Late Pleistocene turtles in this archipelago went extinct during the last 10,000-25,000 years, leaving a few species that might “happen” to support the currently prevailing paleogeographical hypothesis (see above). It is suggested that such abrupt extinction of the majority of terrestrial turtles was a part of the massive extinction of terrestrial vertebrates in the Late Pleistocene Ryukyus, which was caused presumably by human colonization, or rapid and prominent climate change, or both.

The number of turtle taxa excavated from the Ryukyus has been consistently increasing these days. Therefore, more comprehensive studies on the basis of additional fossils are much desired in near future for our better understandings of diversification and extinction of the turtles in the Ryukyu Archipelago. Then, concordance of these events with the hypothesized Ryukyu paleogeography should be carefully re-examined.