

Arata Momohara¹: Survival and extinction of the Taxodiaceae in the Quaternary of Japan

Abstract The research history and stratigraphic occurrence of Taxodiaceae macrofossils from the Plio-Pleistocene sediments in central Japan were reviewed and the process of survival and extinction of the Taxodiaceae are discussed. *Taiwania* and *Sequoia* became extinct in the late Pliocene and the earliest Early Pleistocene. *Metasequoia* and *Glyptostrobus* became extinct in the latest Early Pleistocene. *Cunninghamia* survived up to the Middle Pleistocene and then became extinct. The extinction of these genera occurred in and around the well-defined stages of global climatic deterioration as shown in the marine oxygen isotope curves. During the same period the uplift of mountains around sedimentary basins increased and should have caused the other conifers including *Cryptomeria*, Cupressaceae, and Pinaceae to increase in abundance. The flood plain habitat of *Metasequoia* and *Glyptostrobus* was susceptible to orogenic and eustatic events that became more prevalent during the late early Pleistocene. Active uplift of mountains fragmented the alluvial lowlands and restricted the movement of *Metasequoia* and *Glyptostrobus* as climate and sea level changed.

Introduction

Cryptomeria represents the sole genus of the Taxodiaceae that is presently distributed in Japan, whereas the Plio-Pleistocene sediments include *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, and *Taiwania* (Miki, 1950). Their fossil records since the Pliocene in Japan have been described in detail (Miki, 1950) along with those of related allies including *Sciadopitys* and Cupressaceae (s.s.) (Miki, 1958). Because Plio-Pleistocene sediments including plant fossils are well developed and have been studied based on tephrostratigraphy, magnetostratigraphy, and micropalaeontology, the vegetation history of such conifers in Japan can be very well correlated with global environment change represented by the development of glacial-interglacial climatic changes.

Fossil Taxodiaceae including *Metasequoia* are common and abundant in the Plio-Pleistocene fossil assemblages in central Japan. Thus, the reason for their extinction in Japan is one of the most interesting subjects in the history of the Japanese flora. In addition, their former common occurrence and abrupt extinction has enabled geologists to use them as index fossils for correlation of Quaternary strata (Itihara, 1960). Plant macrofossil data examined stratigraphically and sedimentologically can elucidate the history of survival and extinction of the Taxodiaceae in East Asia. This paper reviews the research history of the plant fossil biostratigraphy of the Plio-Pleistocene based on fossil

Taxodiaceae and describes the process of extinction of the Taxodiaceae with reference to the development of the Japanese modern flora and Quaternary climatic changes.

Research history of Plio-Pleistocene biostratigraphy of the Taxodiaceae in Japan

Plant macrofossils including fruits and seeds from the late Miocene and Plio-Pleistocene sediments in central Japan were studied intensively by Miki (1933, 1937, 1938, 1941) to elucidate the origin of the modern Japanese flora. Miki (1941) described *Metasequoia disticha* and *M. japonica* with *Cunninghamia konishii*, *Glyptostrobus pensilis*, and *Sequoia sempervirens* from the “*Pinus trifolia* bed” of the porcelain clay formations that are distributed in and around the areas of Seto and Tajimi in the northeast of Nagoya, central Japan. Miki (1941) correlated the *Pinus trifolia* bed with the lower Pliocene based on a comparison with the other Neogene and Quaternary floras. As the result of intensive research of fossil floras in central Japan, Miki (1948) classified the fossil assemblages into seven “floral beds” based on the floral components and their stratigraphic positions. Among them, he distinguished the “*Pinus trifolia* bed” and the “*Metasequoia* bed” from the other Pleistocene floral beds based on the occurrence of Taxodiaceae now extinct in Japan and correlated them with the Pliocene.

Since 1950s, the stratigraphic positions of fossil as-

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semblages described by Miki have been re-examined in detail accompanied by investigations on the Quaternary stratigraphy of the Osaka Group by Huzita (1954) and Itihara (1960). Itihara (1960) correlated the uppermost occurrence of *Metasequoia* with the Ma 2 Marine bed of the Osaka Group. This horizon is now correlated with Marine Isotope Stage (MIS) 24, at about 0.9 Ma in the late early Pleistocene (Yoshikawa & Mitamura, 1999). Itihara (1960) named exotic elements including *Metasequoia* as “*Metasequoia* flora” that became extinct in cold stages in and before the late early Pleistocene and used them as index fossils for stratigraphic correlation of the Osaka Group.

Itihara and Kamei (1970) divided the Osaka Group into three parts: the upper part without *Metasequoia* fossils, the lower part including *Metasequoia*, and the lowermost part bearing *Sequoia*, *Pseudolarix*, *Keteleeria*, and *Liquidambar* that he considered to be remnants of the “*Pinus trifolia* flora”. Itihara and Kamei (1970) situated the boundary between the lower and lowermost part of the Osaka Group to the horizon above the Olduvai Paleomagnetic Subchron, at about 1.7 Ma. This horizon had been the Plio-Pleistocene boundary before Global Stratotype Section and Points (GSSP) ratified it to the Gauss-Matuyama boundary at 2.58 Ma in 2009 (Gibbard et al., 2009). However, the plant macrofossil data between 3.0 Ma and 1.3 Ma used for their stratigraphic division are limited. Momohara (1992) studied stratigraphic occurrence of plant macrofossils deposited between ca. 3.5 Ma and 1.3 Ma and identified a major change of flora that occurred between 3.3 and 2.6 Ma in the late Pliocene (Momohara, 1994, 2010). The age of the porcelain clay formation that contains the “*Pinus trifolia* bed” is now correlated with the early Late Miocene based on the fission track ages (ca. 12–9 Ma) of tephras in the porcelain clay formation (Todo Collaborative Research Group, 1999; Nakajima et al., 2004).

Stratigraphic occurrence of the Taxodiaceae in central Japan

Floral change from the middle Pliocene to the Pleistocene in Japan is characterized by the extinction of plants that flourished during the Neogene and an increase and/or emergence of elements that are dominant in the recent cool temperate and sub-alpine forests of Japan. The middle Pliocene flora between 3.5 and 3.3 Ma is rich in taxa that are endemic to the extant floras of the Yangtze River Valley in China (Fig. 1; Momohara, 2010) and the composition is similar to the late Miocene “*Pinus trifolia* flora”. The paleoclimate reconstructed from composition of fossil assemblages

indicates the warmest climate in the Plio-Pleistocene based on the occurrence of *Reevesia* sp. (Sterculiaceae). *Reevesia* is distributed in the areas that the warmth index (WI) is larger than 160 °C month (Momohara, 1999). The WI is defined as the annual sum of monthly mean temperature with +5 degrees centigrade as the threshold, where the summation is made for the month in which the mean temperature is above +5 degrees Celsius (Kira, 1991). The fossil flora includes taxodiaceous elements such as *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, and *Taiwania* and does not include *Cryptomeria*. The early and middle Pliocene flora and fauna indicate biotic interconnection between Japan and the Asian continent since the late Miocene.

The Japanese Islands were assumed to have been isolated from the Asian continent between about 3.6–3.1 Ma based on occurrence of warm-current marine biota from sediments along the Japan Sea (Kitamura & Kimoto, 2004). The land bridges between China and Japan were considered to have existed at three times since the late Pliocene, (1.2 Ma, 0.63 Ma, and 0.43 Ma) based on the comparative research of Proboscidian faunas within both areas (Taruno, 2010). Deposition of loess in north China since 2.6 Ma indicates the development of a cold and dry winter monsoon that influenced the distribution of plants in eastern Asia. The winter monsoon should have been increased snowfall in the areas along the Japan Sea during the interglacial stages because it absorbed water vapor that was supplied by the Tsushima Warm Current that prevailed after the opening of the straits between China and Japan. These events appear to have accelerated the development and differentiation of the modern and compositionally distinct Japanese floras from the ancient Neogene floras that show an affinity with the modern floras of the Yangtze River Valley in China.

The floral change succeeded in a stepwise manner since the late Pliocene (Momohara, 1994). During the first stage of climatic deterioration in the latest Pliocene (ca. 3.3–2.6 Ma), *Taiwania* became extinct and *Cryptomeria* and several members of the Cupressaceae including *Chamaecyparis pisifera*, *Thuja*, and *Thujopsis dolabrata*, appeared and increased in abundance in the fossil assemblages in central Japan. *Picea*, *Abies*, and *Pinus* subgen. *Haploxylon* show a similar pattern of appearance and increased abundance at the same time. Among 70 woody and liana taxa that became extinct since the late Miocene, 20 taxa (29%) became extinct in central Japan between 3.3 and 2.6 Ma, indicating the largest event of floral modernization since the late Miocene (Momohara, 2010). Only four taxa including *Sequoia* (2.5 Ma), *Pseudolarix* (2.2 Ma), *Liquidambar*

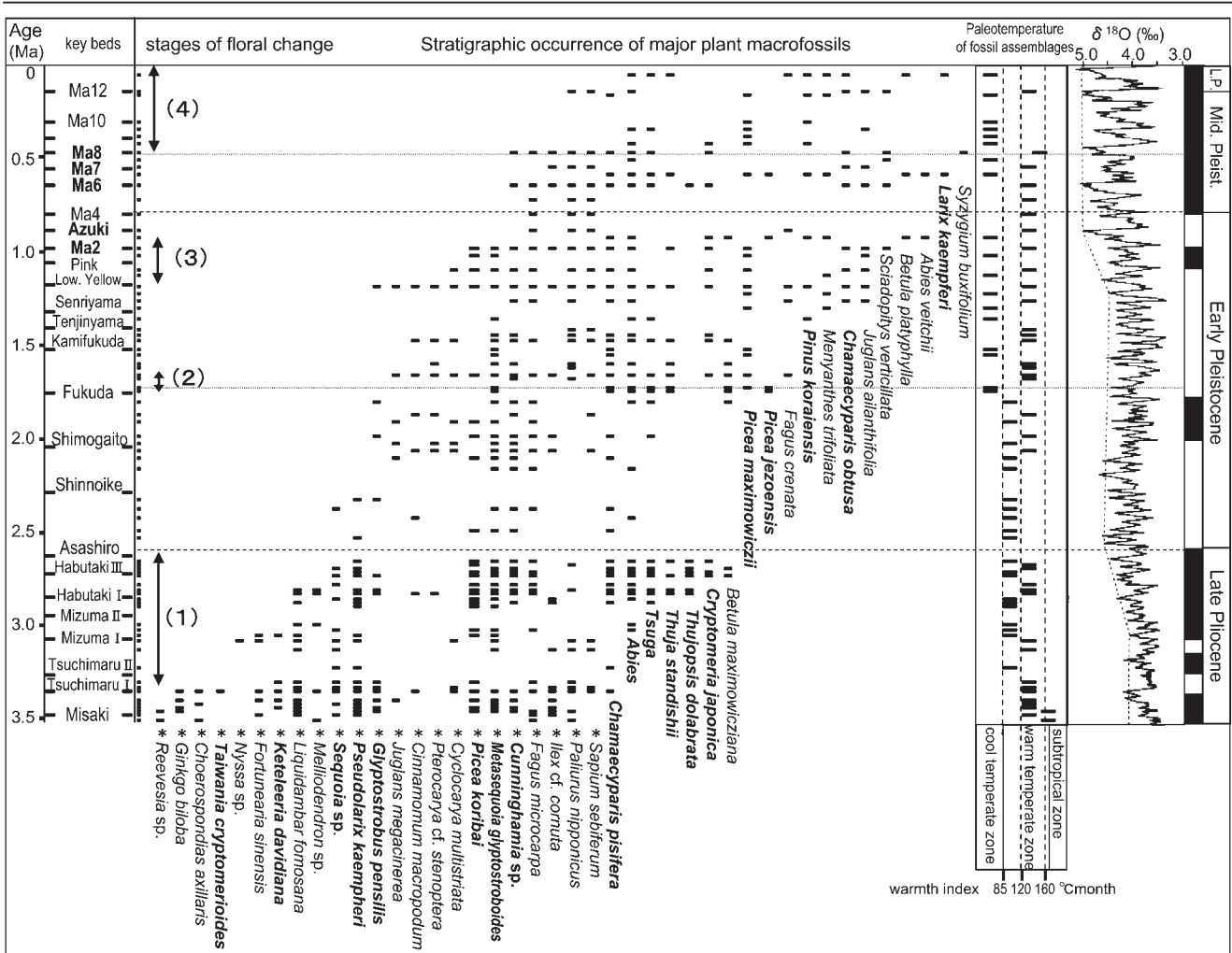


Fig. 1 Stratigraphic distribution of selected plant macrofossils in the Osaka Group and the Shobudani Formation in central Japan (modified from Momohara, 1994, 2010, ©JAQUA). Ages of major floral change stages suggested by Momohara (1994) were modified based on recent stratigraphic data (Momohara, 2010). Marine isotope curve was modified from Shackleton (1995).

(2.2 Ma), and *Ginkgo biloba* (1.5 Ma) became extinct from central Japan between 2.6 and 1.2 Ma.

The composition of fossil assemblages about 1.7 Ma in age shows that the lowland climate in central Japan became colder at this time. In the assemblages, *Metasequoia* occurred with cool temperate and subarctic taxa including *Picea maximowiczii*, *Picea jezoensis*, and *Betula maximowicziana*. The lack of taxa with a northern limit of distribution in the warm-temperate zone (WI > 85 °C month) indicated a paleoclimate representative of a cool temperate zone. However plant extinctions did not occur in and around this stage.

Extinction of 11 taxa from central Japan in the latest Early Pleistocene (ca. 1.2–0.9 Ma) represents the second major period of floral change. The sedimentary

facies of the stage show the beginning of alternation of marine and non-marine sediments above the Ma-1 Marine Beds (MIS 37) to the Ma2 Marine Beds (MIS 25) accompanied by more pronounced sea-level fluctuations (Yoshikawa & Mitamura, 1999). *Glyptostrobus*, *Cyclocarya multistriata*, *Juglans megacineria*, *Pterocarya stenoptera*, and *Davidia involucreta* became extinct in the horizons below the Lower Yellow tephra deposited at about 1.2 Ma. *Metasequoia* went extinct along with *Picea koribai* above the uppermost horizons in the Ma2 marine clay bed in the Osaka Group (Fig. 1). Elements of the modern Japanese cool temperate and subarctic vegetation dominated. Taxa such as *Pinus koraiensis*, *Menyanthes trifoliata*, *Chamaecyparis obtusa*, *Juglans ailanthifolia*, *Sciadopitys verticillata*,

Betula platyphylla, and *Abies veitchii* appeared and increased in abundance in and around this stage. The last occurrence of *Metasequoia* pollen and macrofossils occurs in several different, but approximately coeval stratigraphic horizons in and around Osaka. These include in the non-marine beds below the Ma2 (MIS 25) in the Nara Basin, west of Osaka and in the Ma2 Marine Bed in the Osaka and Kyoto Basins (Kitaba et al., 2011). The apparent widespread onset of the last occurrence of *Metasequoia* in differing units indicates that its distribution in the ancient sedimentary basin decreased gradually during a transition from a colder stage (MIS 30–26) to a warmer stage (MIS 25).

Exotic elements including *Cunninghamia* survived up to the middle Pleistocene (MIS 13, ca. 0.5 Ma) in spite of a severe cold stage in the horizon between the Ma6 and Ma7 Marine Beds that is suggested by the occurrence of subarctic elements including *Larix kaempheri* and *Vaccinium oxycocum*. All of the exotic elements, including 14 taxa that survived strong climatic fluctuations since the latest Early Pleistocene, occur in fossil assemblages from the Ma8 Marine Bed (MIS 11 and/or MIS 13) (Momohara, 2010). Those elements then went extinct between MIS 11 and the last glacial maximum (MIS 2) (Momohara, 1994).

Process of plant survival and extinction of the Taxodiaceae in central Japan

The extinction documented in the fossil record occurred during transition periods of climatic fluctuation and a downward shift of the glacial climate shown in the marine oxygen isotope curves (e.g., Shackleton, 1995). The development of the northern hemisphere ice sheet marked the first stage of climatic deterioration between the latest Pliocene (ca. 3 Ma) and the Plio-Pleistocene boundary. A second event occurred between the Mid-Pleistocene climatic transition and the onset of the 100,000 year interval glacial-interglacial cycles that marked a shift to a colder glacial regime (e.g., Pisias & Moore, 1981). The last event is establishment of full glacial-interglacial cycles that represent the rapid transition from maximal glacial to full interglacial conditions (e.g., Shackleton, 1997). The fossil assemblages from a fossil forest dominated by *Metasequoia* and *Glyptostrobus* in the early Pleistocene Kobiwako Group (ca. 1.8 Ma) include cool temperate plants such as *Menyanthes*, *Betula*, and *Pterocarya rhoifolia* (Yamakawa et al., 2008). *Metasequoia* occurs in fossil assemblages from the late Early Pleistocene cold stages under a cool temperate climate (Momohara et al., 1990). Such occurrence indicates a cold tolerance of *Metasequoia* and *Glyptostrobus*, and thus their extinc-

tion cannot be explained only by the climatic cooling that occurred during this period.

Topographical change in and around the sedimentary basin is considered to be another important factor that may explain extinction (Momohara, 1994). The stages of plant extinction coincide with active or transitional phases of orogenic movement documented in central Japan on the basis of lithostratigraphy and geotectonics by Mizuno (2010). *Metasequoia* and *Glyptostrobus* fossils are commonly distributed on Plio-Pleistocene alluvial plains of inland basins in central Japan. The occurrence of *in situ* fossil forests in fluvial back marsh sediments indicates the floodplain habitat of *Metasequoia* and *Glyptostrobus* (Yamakawa et al., 2008). This kind of habitat was susceptible to orogenic and eustatic events that were more prevalent during the late early Pleistocene.

Active uplift of mountains fragmented alluvial lowlands and restricted the habitats of *Metasequoia* and *Glyptostrobus*. These changes in topography were accompanied by more pronounced eustatic sea level fluctuations after 1.2 Ma. Evidence of limited alluvial lowlands comes from an analysis of the distribution of marine clay beds up to the base of mountains surrounding former alluvial plains (Itihara et al., 1991). Orogenic movements may have favored an increase in the abundance of *Cryptomeria*, *Sciadopitys*, Cupressaceae (*s.s.*), and Pinaceae that grow well on steep slopes and ridges. Such conifers should have migrated more easily than wetland plants like *Metasequoia* and *Glyptostrobus* as climate and sea level changed.

The inland basins in central and western Japan and the coastal plains along the Japan Sea that were habitats of *Metasequoia* and *Glyptostrobus* were subjected to a cold and dry continental climate in the late Quaternary glacial stages. This is indicated by pollen assemblages from the last glacial maximum that indicated the prevalence of mixed coniferous and deciduous broad-leaved forests that are similar to modern forests in Northeast China and the Amur Region (Tsukada, 1988). The last glacial refugia of *Cryptomeria* were limited to coastal regions in central and western Japan (Tsukada, 1982). Refugia of floodplain plants like *Metasequoia* and *Glyptostrobus* were possibly limited in to alluvial plains along the Pacific coast of Japan in the late Quaternary. However, active uplift of mountains along the Pacific coast would have limited the distribution of these alluvial plains. In addition, many of these plains would have been rapidly submersed during the sea level-rise associated with the termination of glacial stages. Thus, eustatic changes prevailing in the late Quaternary probably accelerated the ex-

tion of *Metasequoia* and *Glyptostrobus* in alluvial plain environments whereas *Cryptomeria* migrated to the abundant upland areas to survive.

Extinction of the Taxodiaceae including *Cunninghamia*, *Glyptostrobus*, *Sequoia*, and *Taxodium* were recorded in NW Europe during the last 3.5 Ma (van der Hammen et al., 1971). The cause of plant extinction from Europe has been attributed to climatic deterioration (van der Hammen et al., 1971; Svenning, 2003) that was represented by a dominance of non-arboreal pollen in diagrams of glacial stages (e.g., Zagwijn, 1960; Tzedakis et al., 2006). During these glacial stages, Japan was also influenced by a strong winter monsoon that caused thick accumulation of loess sequences in north China. However, arboreal taxa are almost dominant and Tertiary relicts such as *Cryptomeria*, *Sciadopitys*, and *Fagus* maintain their occurrence in pollen diagrams of glacial stages in central and western Japan (e.g., Miyoshi et al., 1999). This explains that active uplift of mountains and changing sea level should have played an important role in the Pleistocene extinction of some tree taxa.

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