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Paleovegetation reconstruction of fossil forests dominated by *Metasequoia* and *Glyptostrobus* from the late Pliocene Kobiwako Group, central Japan

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Abstract. A late Pliocene (1.8–1.9 Ma) wetland fossil forest community that was dominated by *Metasequoia* and *Glyptostrobus* was reconstructed based on the species composition of the stumps and other plant macrofossil assemblages. The plant fossils were recovered from a fossil forest preserved in deposits of the Kobiwako Group that are exposed in the Echi River, Shiga Prefecture, central Japan. Fossil wood of *Metasequoia* and *Glyptostrobus* was distinguished based on anatomical characteristics. Apportionment of the wood from different horizons in the fossil forest indicates *Metasequoia* grew over a long period of time in a stable environment, while *Glyptostrobus* and *Alnus* grew in unstable environments characterized by short-interval floods. The fossil forest as a whole represents a fluvial back-marsh environment.

The upland forest was composed of mixed evergreen conifers and deciduous broad-leaved trees including *Chamaecyparis pisifera*, *Tsuga*, *Magnolia*, and *Acer*. Aquatic and wetland herbs such as *Cyperus*, *Carex*, *Scirpus*, *Polygonum*, and *Menyanthes* grew in and around the wetland forest. The assemblage of fossil plants recovered from the fossil forest consists of plants that are currently distributed in the cool temperate climate zone, such as *Picea*, *Thuja*, *Betula maximowicziana*, *Pterocarya rhoifolia*, and *Menyanthes trifoliata*. *Glyptostrobus* is distributed only in subtropical areas at present, but it also grew under a cool temperate climate zone in Japan during the latest Pliocene.

Key words: fossil forest, *Glyptostrobus*, Kobiwako Group, late Pliocene, *Metasequoia*, paleovegetation

Introduction

Metasequoia and *Glyptostrobus* are monotypic genera of the Taxodiaceae (Cupressaceae *sensu lato*) and fossils of these genera are common in Tertiary-age floras of the Northern Hemisphere (Florin, 1963; Yu, 1995). Their fossil records show they were distributed widely in both the Eurasian and North American continents during the Paleogene, but went extinct in North America and Europe during the Miocene and Pliocene and are now restricted to small populations in eastern Asia (Matsumoto *et al.*, 1997; LePage *et al.*, 2005; LePage, 2007).

Metasequoia glyptostroboides Hu *et* Cheng is naturally distributed in humid and slightly waterlogged places in mountain valleys in the middle reaches of the Yangze River (Fu and Jin, 1992; LePage *et al.*, 2005). On the other hand, *Glyptostrobus pensilis* (D. Don) K. Koch is distributed in wetlands and waterlogged places in the lowlands of northern Vietnam and southern China (Li and Xia, 2004; Farjon, 2005). Although the two taxa are now distributed in different habitats and in separate geographical regions, remains of both taxa have been found together in fossil assemblages from the Tertiary of the Canadian Arctic (e.g., McIver and Basinger, 1993), northeastern Russia (e.g., Budantsev, 1994), and Japan (e.g., Miki, 1948). Such fossil assemblages sometimes accompany fossil stumps that have been described as taxodiaceous wood (e.g., Christie and McMillan, 1991; Williams *et al.*, 2003a, 2003b).

From the late Pliocene sediments (ca. 1.8 Ma) of the Kobiwako Group, a fossil forest dominated by taxodiaceous wood was discovered with cones and shoots of *Metasequoia* and *Glyptostrobus* in the bed of the Echi River, Shiga Prefecture, central Japan (Echigawa Petri-

Figure 1. The occurrence of carbonized *in situ* fossil stumps located at the Echigawa fossil forest.

fied Forest Research Group, 1993; Figure 1). This fossil forest is the youngest in the world in which macrofossils of both genera occur together with taxodiaceous wood.

Itoh (1993) identified the fossil wood as that of "Taxodiaceae", but did not recognize characters that would allow the wood to be identified further as either that of *Metasequoia* or *Glyptostrobus*.

Differences in anatomical features between *Metasequoia* and *Glyptostrobus* were clarified by Visscher and Jagels (2003) based on their observation of wood from extant trees. Kumagai *et al.* (1995) had already separated fossil wood from the Eocene fossil forests of the Canadian Arctic into *Metasequoia* and "cf. *Glyptostrobus*" based on wood anatomy. Given that these studies indicated that *Metasequoia* and *Glyptostrobus* should also be distinguishable on the basis of wood anatomy, this approach was used to provide a detailed reconstruction of the spatial and temporal distribution of *Metasequoia* and *Glyptostrobus* in the late Pliocene Echigawa fossil forest. Although these previous studies did not identify taphonomic differences between the layers containing *Glyptostrobus* and those containing *Metasequoia*, there should have been recognizable or at least subtle differences in the depositional environments given the different ecological requirements the extant species need to grow and reproduce (Fu and Jin, 1992; Vann, 2005).

In this study, we reexamined the fossil wood described by Itoh (1993) from the Echigawa fossil forest to distinguish *Metasequoia* and *Glyptostrobus* wood based on the criteria of Visscher and Jagels (2003) so that we could assess the temporal and spatial distribution of these species within this fossil forest. In addition, based on the species composition of the plant macrofossil and pollen assemblages preserved within the fossil forest deposits, we reconstructed the paleovegetation in and around this late Pliocene *Metasequoia*- and *Glyptostrobus*-dominated fossil forest.

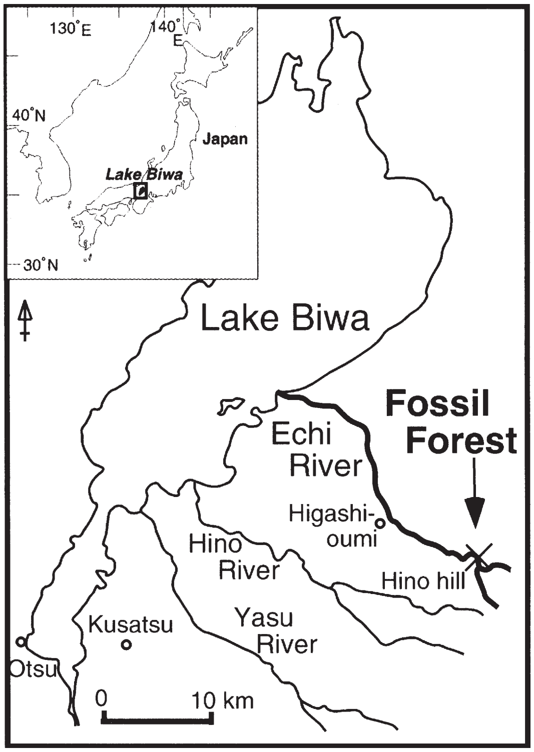

Figure 2. Location of the Echigawa fossil forest.

Geology and occurrence of the fossil forest

A late Pliocene fossil forest was found in the riverbed of the Echi River in Higashiomi City, Shiga Prefecture (35°5'N, 136°17'E, altitude 178 m), central Japan (Figures 1, 2). The sediment sequence containing the fossil wood is about 13.4 m thick and consists of sand, mud, and organic silt that is assigned to the Kobiwako Group. The uppermost part of the unit is 2.5 m thick (from HA to HC in Figure 3), and crops out widely in the riverbed. Because the dip of these sediments is almost horizontal, abundant *in situ* fossil stumps and roots are also exposed on the bedding plane (Figure 1). The part of the unit containing the stumps and roots is composed of silt, organic silt, mud, and alternating layers of silt and sand (Figure 3). Sand and gravel beds attest to fluvial channel-fills and intercalate with the silt and mud (Amemori *et al.*, 1993).

Two volcanic beds crop out in and around the study site. The Naka volcanic ash layer indicating the Olduvai normal subchron (C2n) (Nakayama, 1993), lies about 10

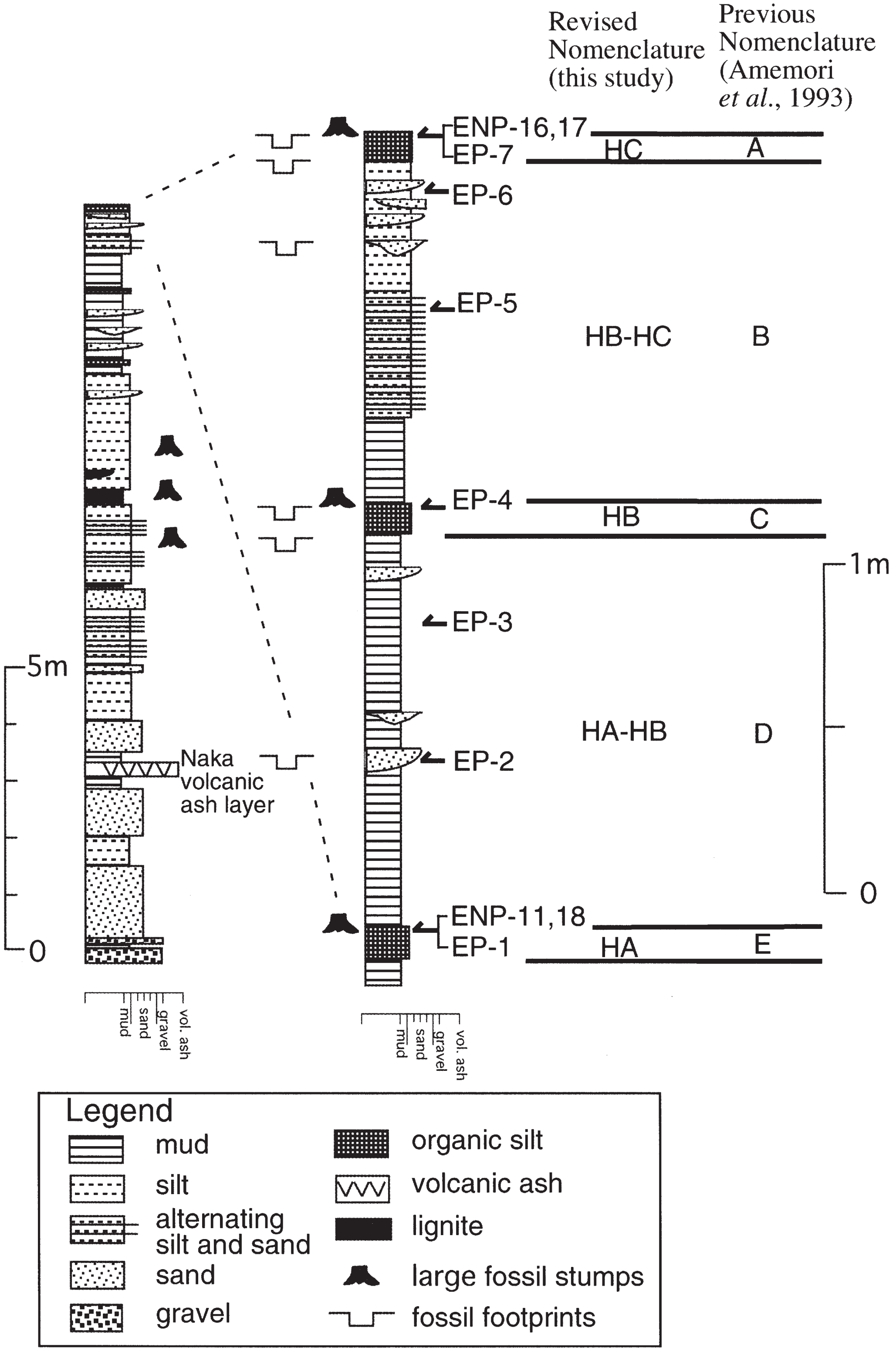

Figure 3. Columnar sections showing the horizons of fossil stumps and samples locations at the Echigawa site based on Amemori *et al.* (1993). EP1-7: horizons of plant macrofossil samples. HA, HA-HB, HB, HB-HC, HC: horizons of fossil stumps. ENP-11, 16, 17, 18: horizons of pollen analysis by Mizutani (1993).

m below the uppermost horizon (HC) of fossil stumps (Amemori *et al.*, 1993), while the Kitawaki volcanic ash layer occurs in an outcrop near the study site, and is stratigraphically located about 20 m above the HC horizon (Yoshikawa, 1993). The Kitawaki volcanic ash layer is correlated with the Fukuda volcanic ash layer of the Osaka Group that indicates normal magnetic polarity above the Olduvai normal subchron (C2n) and has been fission-track-dated to 1.75 Ma (Yoshikawa, 1984; Yoshikawa *et al.*, 1996). Therefore, the age of this fossil forest is estimated to be 1.8–1.9 Ma and is late Pliocene in age.

This fossil forest was composed of 129 *in situ* stumps distributed over an area of about 6,510 m^2 (155 m long, 42 m wide) (Echigawa Petrified Forest Research Group, 1993). All of the stumps are mummified and show compression to some extent, as shown by the deformed annual rings. From this assemblage of fossils, three groups of fossils are recognized; stumps with roots, roots with stems that are eroded, and stems (trunks). The Echigawa Petrified Forest Research Group (1993) collected and described in detail 53 well preserved stumps from the 129 exposed specimens. These specimens comprised 19 stumps with trunks and roots, 22 with trunks only, and 12 with root only (Table 1).

In this study, the stratigraphy of the fossil forest beds by Amemori *et al.* (1993) was revised and the five fossil forest beds labeled A to E in descending order from the top of the section were renamed as follows: beds A, C, and E are renamed as HC, HB, and HA, and beds B and D are now called HA-HB and HB-HC, respectively (Figure 3). In beds HC, HB, and HA, the trunk bases and flattened root systems were distributed in the uppermost part of discrete organic-rich silt beds that were about 10 cm thick each. In contrast, the fossil stumps in HB-HC and HA-HB were scattered in sediments composed of poorly sorted silt, mud, and alternating silt and sand layers.

Materials and methods

To identify the fossil wood, we reexamined the specimens that were studied by Itoh (1993) that are now curated at the Research Institute for Sustainable Humanosphere, Kyoto University, Japan (registration numbers: KYO_ID_1_EW–KYO_ID_53_EW). Specimens of the 53 fossil samples collected in 1991 were mounted as cross, radial, and tangential sections on glass slides (Table, 1). Identification of the *Metasequoia* and *Glyptostrobus* woods was based on the methodology provided in Visscher and Jagels (2003), and that of the other taxa was based on the IAWA handbook (IAWA, 1989, 2004).

In 1991 plant macrofossils were collected from seven horizons (EP-1 to EP-7; Figure 3) and an inventory of the taxa present was compiled by Yamakawa (1993). However, counts of the number of specimens of each taxon were not compiled. In this part of the study, we reexamined the plant macrofossils previously identified and counted the number of macrofossils in each of the samples. Of the seven horizons, EP-1, 4, and 7 were located in the organic silt situated below the horizons in which the fossil stumps were rooted (HA, HB, and HC, respectively). Sediment blocks of about 2000 cm^3 were taken from each horizon and soaked in a 2% aqueous solution of NaOH for two or three days. The solution was then neutralized with 2% acetic acid, and the residues were washed on a series of 1.0 mm, 0.5 mm, and 0.25 mm mesh sieves. The plant macrofossils remaining in the sieves were identified under a stereomicroscope, then placed in vials containing 70% ethanol. All of the plant macrofossil specimens collected for this study were deposited in the Lake Biwa Museum, Shiga Prefecture, Japan (LBM0112000273–0112000545, LBM 0112001671–0112001870).

Results

Identification of fossil wood

Itoh (1993) identified 53 fossil wood samples and grouped them as follows: 26 were Taxodiaceae, six were conifers, 15 were *Alnus*, two were Rosaceae, one was *Fraxinus*, two were diffuse-porous wood, and one was ring-porous wood. Registration numbers were not assigned to six samples and the results of their identification were not indicated in that paper. We reexamined the six samples and recognized KYO_ID_1_EW (stump no. 1) as diffuse-porous wood, KYO_ID_45, 48, and 53_EW (stump nos. 45, 48, and 53) as Taxodiaceae, and KYO_ID_49 and 51_EW (stump nos. 49 and 51) as *Alnus*. Taxodiaceous wood was characterized by possessing an abrupt transition from early wood to late wood and scattered parenchyma cells parallel to annual ring boundaries in cross section, and taxodioid-type cross-field pits.

KYO_ID_5_EW (stump no. 5) reported as a "conifer" by Itoh (1993), was reidentified as *Alnus* based on the aggregated rays visible in cross and tangential sections. KYO_ID_41_EW (stump no. 41) identified as "Rosaceae" by Itoh (1993), had characteristics of *Sorbus*. In cross section the ray parenchyma is arranged in two rows with medium-sized vessels scattered in the secondary xylem (Figure 4a), and in radial section many small pits are arranged as reticulate perforations (Figure 4b).

Among the 26 samples identified as Taxodiaceae by Itoh (1993), we recognized four samples as *Metase-*

Table 1. List of fossil standing stumps in the bed of the Echi River, based on Echigawa Petrified Forest Research Group (1993).

Horizon	Sample Number	Taxon (this study)	State	Trunk Diameter (cm)		Height (cm)	Root length (cm)
				Major Axis	Minor Axis		
HC	40	_Metasequoia_**	stump	100	85	90	300
HC	39	Taxodiaceae	trunk	140	90	36	–
HC	45*	Taxodiaceae	root	–	–	40	310
HC	46	Taxodiaceae	root	–	–	40	180
HB-HC	26	_Glyptostrobus_**	stump	85	65	95	220
HB-HC	29	_Glyptostrobus_**	trunk	17	13	–	–
HB-HC	35	_Glyptostrobus_**	trunk	29	20	–	–
HB-HC	44	_Glyptostrobus_**	trunk	12	9	20	–
HB-HC	24	Taxodiaceae	stump	30	20	–	110
HB-HC	23	Taxodiaceae	trunk	10	7	–	–
HB-HC	25	Taxodiaceae	stump	–	–	35	25
HB-HC	43	Taxodiaceae	root	–	–	–	40
HB-HC	37	Conifer	trunk	10	8	20	–
HB-HC	30	Conifer	root	–	–	–	6
HB-HC	7	_Alnus_	stump	30	30	–	90
HB-HC	9	_Alnus_	stump	20	15	–	80
HB-HC	19	_Alnus_	stump	16	13	25	55
HB-HC	32	_Alnus_	stump	20	20	–	60
HB-HC	38	_Alnus_	stump	30	30	25	75
HB-HC	51*	_Alnus_	stump	20	20	–	70
HB-HC	8	_Alnus_	stump	30	25	–	–
HB-HC	10	_Alnus_	trunk	20	10	–	–
HB-HC	12	_Alnus_	trunk	17	17	–	–
HB-HC	42	_Alnus_	trunk	45	35	–	–
HB-HC	41	_Sorbus_**	trunk	8	8	–	–
HB-HC	36	Rosaceae	stump	11	6	14	40
HB-HC	22	Ring-porous wood	trunk	8	4	–	–
HB	28	_Metasequoia_**	stump	155	150	125	540
HB	14	Taxodiaceae	stump	75	70	45	220
HB	48*	Taxodiaceae	stump	170	150	–	360
HB	15	Taxodiaceae	root	–	–	–	380
HB	20	Taxodiaceae	root	–	–	–	60
HB	27	Taxodiaceae	stump	–	–	110	210
HB	47	Conifer	stump	125	115	–	220
HB	21	_Alnus_	root	–	–	–	43
HB	17	_Fraxinus_	root	–	–	–	9
HB	31	Diffuse-porous wood	root	–	–	–	45
HA-HB	16	_Glyptostrobus_**	trunk	17	12	–	–
HA-HB	53*	Taxodiaceae	stump	20	10	–	50
HA-HB	13	Taxodiaceae	trunk	95	65	25	–
HA-HB	52	Taxodiaceae	trunk	48	25	–	–
HA-HB	50	Conifer	trunk	150	120	–	–
HA-HB	19	Conifer	root	–	–	–	25
HA-HB	6	_Alnus_	stump	14	7	–	18
HA-HB	5	_Alnus_**	trunk	18	17	–	–
HA-HB	49*	_Alnus_	stump	14	10	–	–
HA	2	_Metasequoia_**	stump	190	145	70	320
HA	3	_Metasequoia_**	stump	110	100	–	375
HA	4	Taxodiaceae	stump	130	110	–	370
–	33	_Glyptostrobus_**	trunk	5	5	–	–
–	34	_Glyptostrobus_**	trunk	10	8	15	–
–	11	_Alnus_	trunk	25	15	–	–
–	1*	Diffuse-porous wood	trunk	13	8	–	–

Based on Echigawa Petrified Forest Research Group (1993)
– unknown
* unidentified specimens of Itoh (1993)
** specimens reidentified in this study

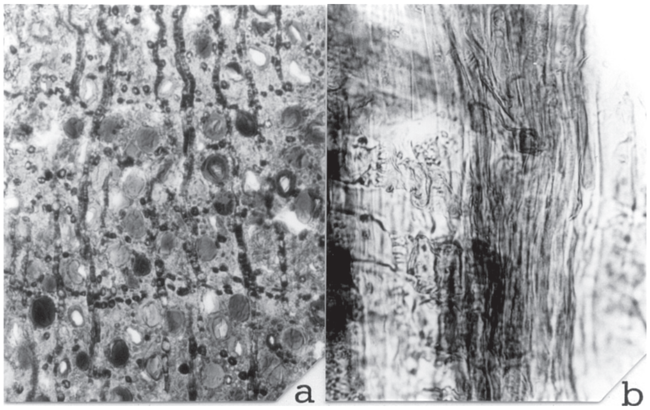

Figure 4. Fossil wood of *Sorbus* (KYO_ID_41_EW, stump no. 41, horizon HB-HC): **a**, cross section, ×100, showing ray parenchyma arranged in two rows, with medium-sized vessels scattered in the secondary xylem; **b**, radial section, ×400, showing reticulate perforations.

quoia (KYO_ID_2, 3, 28, and 40_EW) and seven as *Glyptostrobus* (KYO_ID_16, 26, 29, 33, 34, 35, and 44_EW). The most distinctive differences between the *Metasequoia* and *Glyptostrobus* woods were the presence of gaps between the ray cells and the arrangement and maximum height of the ray cell stacks (Table 2). *Metasequoia* lacked gaps between the ray cells in radial and tangential section (Figure 5-2b). The cross-field pits of the taxodioid type were arranged in one or two rows oppositely (Figure 5-2a). The ray cells formed stacks of less than 10 cells for the most part, but maxima of 33–47 cells were observed (Figure 5-2b). In contrast, *Glyptostrobus* had visible gaps between the ray cells in tangential as well as radial section (Figures 6-2a, 6-2c). The cross-field pits of the taxodioid type were randomly arranged in two or three rows (Figure 6-2a). Most of the stacks of the ray cells were less than 10 cells, as in *Metasequoia*, but the maximum cell stacks did not exceed 28 cells in height, which contrasts slightly with

Table 2. Anatomical features of fossil and extant *Metasequoia* and *Glyptostrobus* wood samples

Sample Number	Longitudinal Parenchyma		Ray					Taxon
	Horizontal End Walls	Gaps	Cross-field pits		Width	Maximum Number of Stacks		
			Number	Arrangement				
2	smooth, occasionally nodular	absent	1–2	opposite, horizontal single row	uniseriate, rarely partly biseriate	40		M
3	smooth, sparsely nodular	absent	2–3	arranged in 2 rows	uniseriate, or occasionally partly biseriate	65		M
16	nodular, occasionally smooth curve	present	2, rarely 3	randam, arranged in 2 rows	uniseriate	16		G
26	smooth curve, or nodular	present	2–3	randam, arranged in 2–3 rows	uniseriate, occasionally partly biseriate	28		G
28	smooth	absent	2–3	arranged in horizonal 2 rows, occasionally in 3 rows	uniseriate, rarely partly biseriate	33		M
29	nodular	present	1–3	randam, or arranged in 1–3 rows	uniseriate, rarely partly biseriate	16		G
33	smooth curve	present	2–4	randam, arranged in 2–4 rows	uniseriate, occasionally partly biseriate	23		G
34	smooth curve	present	2–3	randam, arranged in 2–3 rows	uniseriate, occasionally partly biseriate	21		G
35	smooth curve, sparsely nodular	present	2–3	randam, arranged in 2–3 rows	uniseriate, or rarely partly biseriate	21		G
40	smooth curve	absent	1–2	opposite, horizontal single row	uniseriate, rarely partly biseriate	47		M
44	smooth, or nodular	present	1–3	randam, arranged in 2–3 rows				G
EM	usually smooth; occasionally slightly nodular	absent or very rare	1–5 (frequently 2–4)	single horizontal rows; random in marginal cells	uniseriate, or partly biseriate	38		M
EG	usually nodular; occasionally smooth	visible	1–6	random, not aligned; arranged in 2 rows	uniseriate	29		G

M: *Metasequoia*, G: *Glyptostrobus*, EM: extant *Metasequoia glyptostroboides*, EG: extant *Glyptostorobus pensilis*,
–: unknown, Max.: Maximum. Based on Visscher and Jagels (2003)

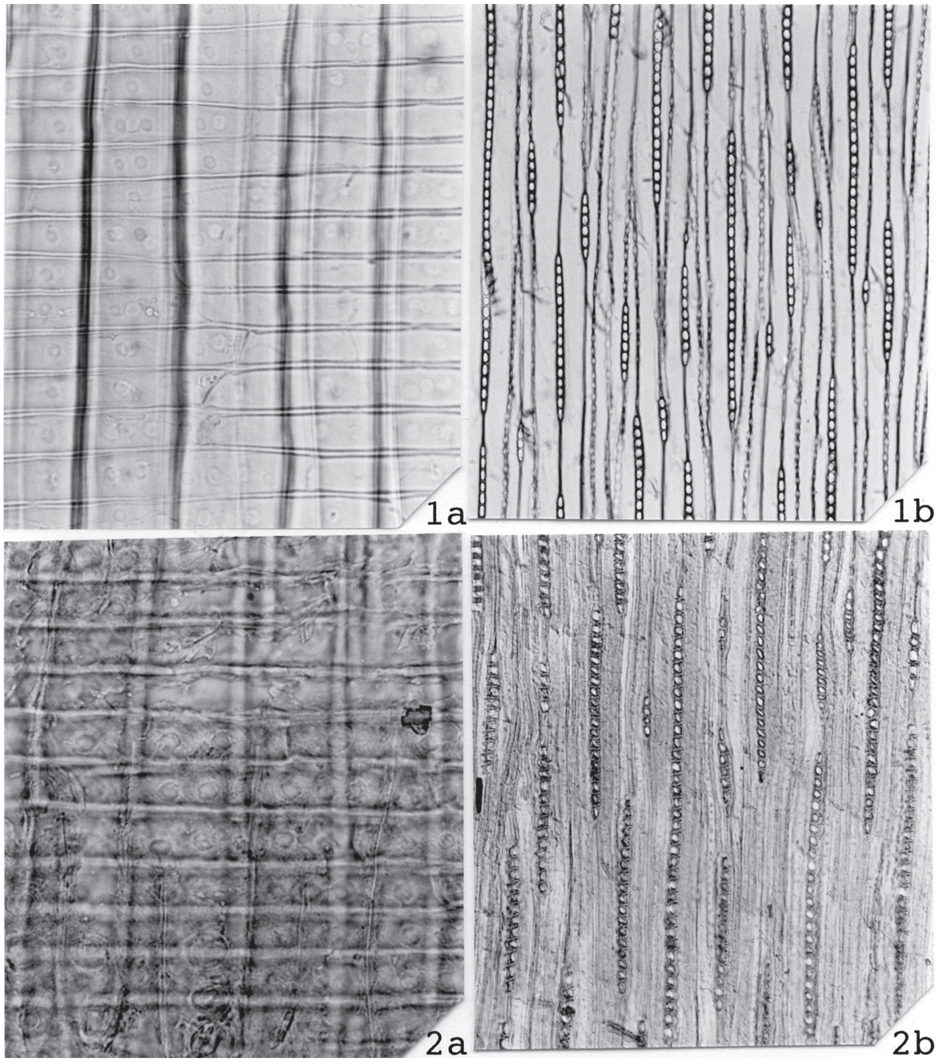

Figure 5. Extant and fossil wood of *Metasequoia*. **1.** Extant *Metasequoia glyptostroboides* wood obtained from Nagai Park in Osaka City: a, radial section, ×400; b, tangential section, ×100. **2.** Fossil *Metasequoia* wood (KYO_ID_3_EW, stump no. 3 in horizon HA): a, radial section, ×400, showing no gaps between ray cells, two or three cross-field pits in the radial walls, and uniseriate or opposite biseriate rows of rays in the early wood; b, tangential section, ×100, showing ray parenchyma cells stacked from three to more than 30 cells high.

what is seen in *Metasequoia* (Figure 6-2b).

The remaining taxodiaceous wood samples were compared to extant samples of *Sequoia*, *Cunninghamia*, *Cryptomeria*, *Taiwania*, and *Taxodium*. The fossil samples possessed narrower biseriate rays compared to that of *Sequoia* and *Cunninghamia*, lacked the admixed cupressoid-type cross-field pits observed in *Taxodium* and *Taiwania*, and the maximum number of cell stacks was more than 11 and differed from *Cryptomeria*. Although it was not possible to identify the remaining taxodiaceous wood samples to the generic level, we are assuming that these specimens are probably either *Metasequoia* or *Glyptostrobus*.

Composition and distribution of fossil stumps

Of the 53 wood samples that we reexamined, 16 were identified as Taxodiaceae, seven were identified as *Glyptostrobus*, four were *Metasequoia*, five were conifers, 15 were *Alnus*, there was one each of *Fraxinus*, *Sorbus*, and Rosaceae, and two were of diffuse-porous wood (Table 1). Assuming that the Taxodiaceae samples are *Metasequoia* and *Glyptostrobus*, *Metasequoia* and *Glyptostrobus* comprised 51% of the samples that were reexamined, and *Alnus* accounted for 28% of the 53 fossil wood specimens (Table 3).

Twelve of the stumps that were more than 75 cm in trunk diameter were identified as conifers: four *Metasequoia*, one *Glyptostrobus*, five Taxodiaceae, and two

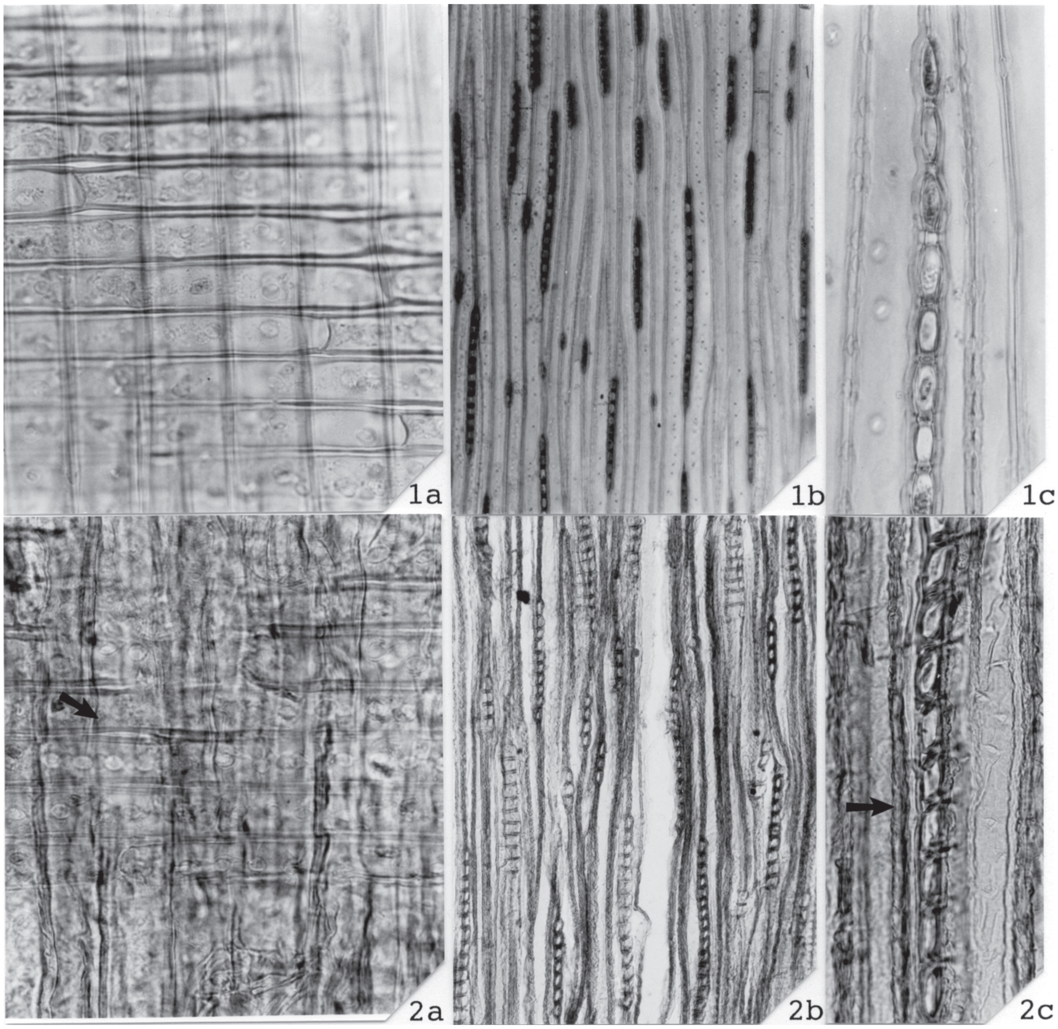

Figure 6. Extant and fossil wood of *Glyptostrobus*. **1.** Extant *Glyptostrobus pensilis* wood from a tree of ca. 20 cm diameter at breast height (DBH) at the Lake Biwa Museum: a, radial section, ×400; b, tangential section, ×100; c, stack of ray parenchyma cells, ×400. **2.** Fossil *Glyptostrobus* wood (KYO_ID_35_EW, stump no. 35 in horizon HB-HC): a, radial section, ×400, with arrow showing a gap between ray cells (also discernable in the tangential section), two cross-field pits in the radial walls, and random or biseriate rows of ray cells in the early wood; b, tangential section, ×100, showing straight uniseriate and rare partly biseriate ray cells, with maximal ray parenchyma cell stacking of usually less than 28 cells; c, ray parenchyma in tangential section, ×400, with arrow showing a gap between ray cells.

conifers. All four *Metasequoia* samples were from the largest size class, with a trunk diameter of greater than 100 cm, with the largest having a major axis diameter of 190 cm. On the other hand, the *Glyptostrobus* samples were from smaller stumps with major axis diameters of between 5 and 29 cm (Table 1). The major axis diameter of the *Alnus* trunks varied between 14 and 45 cm (22.8 cm in mean) and the two *Sorbus* and Rosaceae stumps were both less than 11 cm in diameter (Table 1).

In horizons HA, HB, and HC, large *Metasequoia* and Taxodiaceae stumps were common and *Glyptostrobus* and *Alnus* were rare. In contrast, horizons HA-HB and HB-HC contained medium-size stumps of mainly *Alnus*

Table 3. Composition of fossil wood samples identified from the Echi River

Taxon	Total	%
Taxodiaceae	16	30.2
Alnus	15	28.3
Glyptostrobus	7	13.2
Conifer	5	9.4
Metasequoia	4	7.5
Diffuse-porous tree	2	3.8
Fraxinus	1	1.9
Sorbus	1	1.9
Rosaceae	1	1.9
Ring-porous tree	1	1.9
	53	100.0

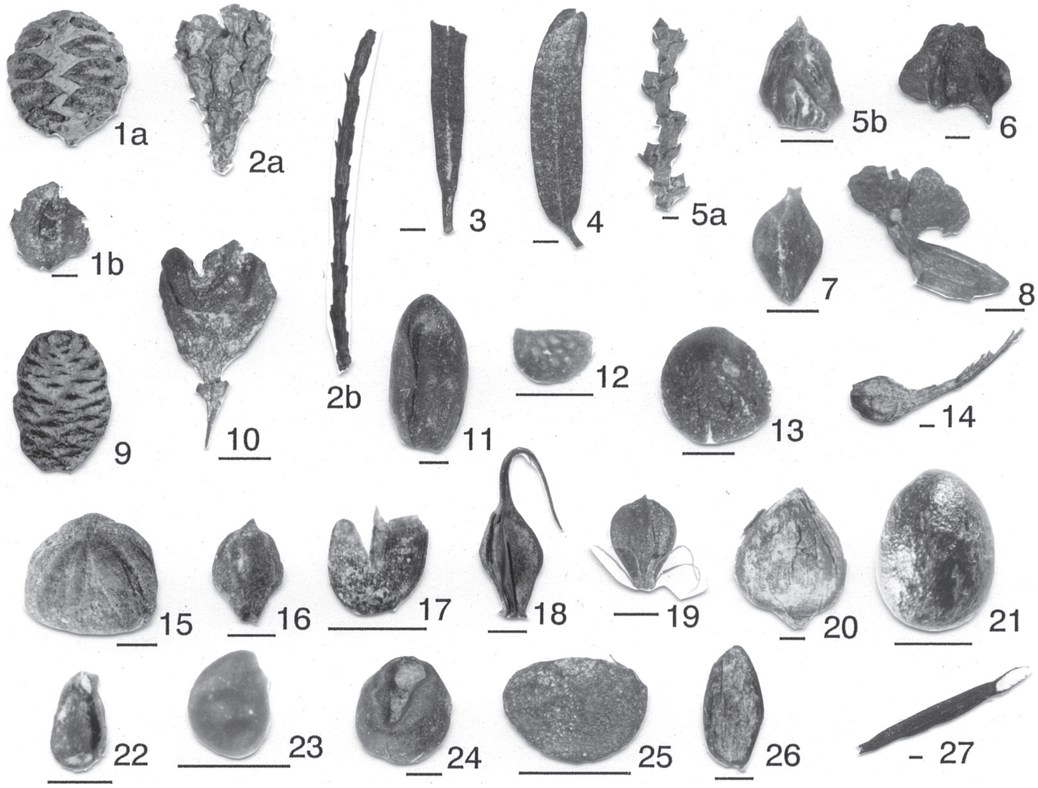

Figure 7. Plant macrofossils from the bed of the Echi River. (Scale bars 1 mm, but absent for specimens shown at actual size). **1.** *Metasequoia glyptostroboides*: a, ovulate cone, (LBM0112000581, EP-1); b, seed (LBM0112000466-04, EP-1). **2.** *Glyptostrobus pensilis*: a, cone (LBM0112000467-01, EP-1); b, shoot (LBM0112000467-03, EP-1). **3.** *Abies* sp., leaf (LBM0112000495, EP-3). **4.** *Tsuga* sp., leaf (LBM0112000468, EP-1). **5.** *Chamaecyparis pisifera*: a, leaf (LBM0112000470, EP-1); b, seed (LBM0112001693, EP-1). **6.** *Pterocarya rhoifolia*, fruit (LBM0112000515, EP-5). **7.** *Betula grossa*, bract (LBM0112001764, EP-5). **8.** *Betula maximowicziana*, fruit (LBM0112001843, EP-5). **9.** *Alnus japonica*, infructescence (LBM0112000582, EP-1). **10.** *Hemiptelea mikii*, fruit (LBM0112000498, EP-3). **11.** *Hamamelis* sp., seed (LBM0112000517, EP-5). **12.** *Rubus* sp., endocarp (LBM0112001794, EP-7). **13.** *Stephanandra incisa*, seed (LBM0112001691, EP-1). **14.** *Acer* sp., fruit (LBM0112000475, EP-1). **15.** *Cornus controversa*, endocarp (LBM0112000516, EP-5). **16.** *Sparganium* sp., fruit (LBM0112000520, EP-5). **17.** *Sagittaria* sp., fruit (LBM0112000542, EP-6). **18.** *Carex* sp. A, fruit (LBM011200 0478, EP-1). **19.** *Scirpus* sp. A, fruit (LBM0112000535-1, EP-7). **20.** *Polygonum* sp., fruit (LBM0112000505, EP-4). **21.** *Menyanthes trifollata*, seed (LBM0112000531, EP-7). **22.** *Lycopus* sp., fruit (LBM0112001745, EP-4). **23.** *Potentilla* sp. B, fruit (LBM0112001820, EP-7). **24.** *Euphorbia* sp., seed (LBM0112000530, EP-1). **25.** *Physalis* sp., seed (LBM0112001809, EP-7). **26.** Asteraceae trib. Cardueae gen. *et* sp. indet., fruit (LBM0112001716, EP-2). **27.** *Bidens* sp., fruit (LBM0112000543, EP-6).

and *Glyptostrobus*, with some Taxodiaceae and broadleaf trees such as *Sorbus* and Rosacae. The largest *Glyptostrobus* stump was 85 cm in diameter and one large conifer stump of 150 cm in trunk diameter was present in horizons HB-HC and HA-HB, respectively.

Composition of plant macrofossil assemblage

The seven plant macrofossil assemblages (EP-1 to EP-7 in Figure 2) included seed cones, fruits, seeds, leaves, and shoots of representatives from 32 families, 46 genera, and 60 species (Table 4; Figure 7). Tree taxa comprised 16 families, 23 genera, and 27 species. Three of the tree genera are extinct from Japan: *Metasequoia*, *Glyptostrobus*, and *Hemiptelea*. The fossil seeds of *Sapium sebiferum* described by Yamakawa (1993) was reidentified as *Euphorbia* sp., and a branch of "*Sequoia* sp.?" was reidentified as a shoot of *Glyptostrobus pensilis*. In addition, fruits of *Pterocarya stenoptera* were reidentified as *P. rhoifolia*, and endocarps of *Cornus microcarpa* as *C. controversa*.

The composition of the assemblages from EP-1 to EP-7 was similar from one to the other. Among the tree taxa, *Metasequoia*, *Glyptostrobus*, and *Alnus* were included in all of the assemblages. *Metasequoia* was represented by abundant leaves, short shoots, seed cones, and seeds in assemblages except for EP-6 and EP-7 (Table 4). Fruits and infructescences of *Alnus* were common in most of the assemblages. Leaves, shoots and seed cones of *Glyptostrobus* occurred rarely, except in EP-1. Seeds and leaves of *Chamaecyparis pisifera* occurred

Table 4. List of plant macrofossils obtained from the Echigawa fossil forest.

Taxon	Fossil	Occurrence						
		EP-1	EP-2	EP-3	EP-4	EP-5	EP-6	EP-7
Trees								
Pinaceae								
Abies sp.	L	3	4	5		3		
Picea sp.	L	1	2			1		
Tsuga sp.	L	7	2	2				
Taxodiaceae								
Metasequoia glyptostroboides	L	83	74	14	15	9	2	
	Sh	41	29	3	9	10		1
	C	2						
	Cs	4				2		
	Ca	4				3		
	S	34	21	9	5	10	6	
Glyptostrobus pensilis	Sh	+	+	+	+	+		+
	C	1						
	Cs	11					6	
Cupressaceae								
Chamaecyparis pisifera	Sh	+	+	+	+	+	+	
	S	7	8	20		6		
Chamaecyparis sp.	Sh	+	+					
Thuja sp.	Sh		+					
Juglandaceae								
Pterocarya rhoifolia	Nl					1		1
Fagaceae								
Fagus sp.	N						1	
	Cu						6	
Betulaceae								
Alnus japonica	If	3			1	1	1	
	Nl	14	8	3	6		34	2
Alnus sp.	L			1				
	If	3		2	1	2		2
	Nl							26
Betula grossa	Fb					1		
Betula maximowicziana	F					1		3
Ulmaceae								
Hemiptelea mikii	F		1	1				
Magnoliaceae								
Magnolia sp.	S	1				1		2
Hamamelidaceae								
Hamamelis sp.	S					2		
Rosaceae								
Stephanandra incisa	S	1				1		
Rubus sp.	E	1	1			1		2
Malus sp.	S					1		
Leguminosae								
Wisteria sp.	L	1						
Aquifoliaceae								
Ilex sp.	E					1		
Aceraceae								
Acer sp.	F	2	2			1		
Cornaceae								
Cornus controversa	E					2		
Cornus sp.	E		2	1				
Vervenaceae								
Clerodendrum sp.	E					1		
Styracaceae								
Styrax japonica	S	5						
Herbs								
Sparganiaceae								
Sparganium sp.	F	1				1		2
Alismataceae								
Alisma sp.	F				3			
Sagittaria sp.	F						3	15
Poaceae gen. *et* sp. A	F				1			3
Poaceae gen. *et* sp. B	F							5
Poaceae gen. *et* sp. C	G							5
Cyperaceae								
Scirpus sp. A	F	7		3	42	6	2	5
Scirpus sp. B	F							12
Cyperus sp. A	F	13	9	11	1	5	2	3
Cyperus sp. B	F				1	5	2	
Cyperus sp. C	F				7	1		
Cyperus sp. D	F							46
Cyperus sp. E	F							83
Carex sect. *Carex* sp.	F	13	7	1	14	9	36	246
Carex sp. A	F	4			1	2		9
Carex sp. B	F	6	3	1		6	1	21
Carex sp. C	F						3	33
Carex sp. D	F	4			22	2		100
Carex sp. E	F							29
Urticaceae								
Pilea sp. A	F				1			3
Pilea sp. B	F						3	
Boehmeria sp.	Pa							1
Urticaceae gen. *et* sp.	F						1	
Polygonaceae								
Polygonum sp. A	F	1	5		5	1	7	6
	Pa			2	4			
Polygonum sp. B	Pa					6		
Ranunculaceae								
Dichocarpum trachyspermum	S			1				
Ranunculus sp.	F		3		2		5	2
Rosaceae								
Potentilla sp. A	F							12
Potentilla sp. B	F							180
Euphorbiaceae								
Euphorbia sp. A	S	1				2		
Euphorbia sp. B	S							1
Euphorbiaceae gen. *et* sp.	S				1			
Balsaminaceae								
Impatiens sp.	S					1		
Hypericaceae								
Hypericum sp.	S							1
Violaceae								
Viola sp.	S	1				1		6
Menyanthaceae								
Menyanthes trifoliata	S				+			1
Labiatae								
Perilla sp.	F					2		
Mosla dianthera	F				9			1
Mosla sp.	F	1						
Lycopus sp.	F				3			9
Clinopodium sp.	F	3						
Lamiaceae gen. *et* sp. A	F					1		1
Lamiaceae gen. *et* sp. B	F							1
Solanaceae								
Physalis sp.	S							24
Solanaceae gen. *et* sp.	S						1	
Asteraceae								
Bidens sp.	F						1	
Asteraceae trib. Cardueae gen. *et* sp.	F		1					

C: cone, Ca: cone axis, Cs: cone scale, Cu: cupule, E: endocarp, F: fruit, Fb: fruiting bract, G: glume, If: infructescence, L: leaf, N: nut, Nl: nutlet, Pa: fruit with perianth, S: seed, Sh: Shoot, +: Present.

commonly except in EP-7, whereas *Tsuga*, *Abies*, and *Picea* were represented only by leaves in EP-1, EP-2, EP-3, and EP-5. These evergreen conifers were rare or absent in assemblages EP-4, EP-6, and EP-7. Leaves of broadleaf trees were preserved, but it was only possible to identify those of the Leguminosae. Among broadleaf trees, seeds of *Magnolia*, fruits of *Acer*, and endocarps of *Rubus* and *Cornus* were relatively common compared to all other fruits in the assemblages. The extinct species *Hemiptelea mikii* occurred in EP-2 and EP-3. Broadleaf trees that are mainly distributed in the cool-temperate zone such as *Pterocarya rhoifolia* and *Betula maximowicziana* were found in EP-5 and EP-7.

The herbaceous taxa comprised 16 families, 23 genera, and 37 species, and consisted mainly of aquatic and wetland plants including *Sparganium*, Alismataceae, Cyperaceae, *Polygonum*, *Lycopus*, and *Menyanthes*. Among the seven assemblages, EP-7 was rich in herbaceous taxa and included 31 species. Fruits of *Scirpus*, *Cyperus*, *Carex*, and *Polygonum* were abundant in all of the assemblages; each genus was represented by two or more taxa based on external features of the fruits. Fruits of *Ranunculus* were relatively common in some of the assemblages. The representative cool-temperate taxon, *Menyanthes trifoliata*, occurred in EP-4, but some were also identified in EP-7 (Table 4).

The fruit fossil of *Pterocarya rhoifolia* is the oldest record in Japan. Momohara *et al.* (1997) reviewed the stratigraphic occurrence of *P. rhoifolia* and reported that it was found only in Pleistocene sediments. Although fossil seeds of *Menyanthes trifoliata* occur in the late Pliocene sediments of the Yamato Group in the Aizu Basin, northern Japan (Manabe and Suzuki, 1988), the occurrence of *M. trifoliata* in our deposits provide the oldest report of this taxon from central and southern Japan.

Discussion

Composition and ecological characteristics of the fossil forest

The fluvial sedimentary facies indicates that the Echigawa fossil forest was part of a wetland forest mosaic. The sediments containing the fossil stumps and plant macrofossil assemblages are composed of alternating silt and sand units that were deposited in a fluvial back marsh with occasional overflow of silt and sand from the channel (Amemori *et al.*, 1993). The plant macrofossil assemblages, mainly composed of aquatic and wetland plants such as Cyperaceae, *Sparganium*, and *Polygonum*, also indicate the dominance of wetland vegetation in and around the fossil forest (Table 4). Amemori *et al.* (1993) examined the sedimentary facies of the fossil stumps and showed the large stumps stood in organic silt beds. The distribution of the fossil stumps among the five horizons (HA, HA-HB, HB, HB-HC, and HC: Figure 3) indicates successive stages of forest regeneration and growth following periods of major disturbance and burial of the forest by sediment.

The organic silt beds, in which are the fossil forests of horizons HA, HB, and HC, are the paleosols in which the forest trees were rooted (Figure 3). In horizons HA, HB, and HC, Taxodiaceae and *Metasequoia* stumps of more than 90 cm in diameter were present. *Metasequoia* was represented by various and abundant plant parts (e.g., leaves, cones, and seeds) from the organic silts of EP-1 located in horizon HA and EP-4 from horizon HB (Table 4). Shoots and seed cones of *Glyptostrobus* are rare compared to those of *Metasequoia* in those horizons. Based on the relative abundance of the various isolated fossil remains of *Metasequoia*, the stumps of Taxodiaceae and conifers in horizons HC and HB are most probably those of *Metasequoia*. If this assumption is true, then *Metasequoia* was clearly a dominant constituent in the wetland forest in horizons HA, HB, and HC.

The proboscidean footprints found in horizons HA and HB (Okamura, 1993) show that the upper boundary of such organic silt deposits was the actual ground surface prior to burial of the fossil stumps. The large-diameter trunks in those horizons indicate that the influx of sediment into these depressional areas was minimal and had little effect on tree growth given the size of the preserved stumps and stems. The largest number of annual rings counted was 329, in stump no. 28 (Kobayakawa, 1993), which further supports the idea that these forests were stable and not subject to major disturbance for long periods of time.

In contrast, the fossil stumps in the sediments of horizon HB-HC comprise many specimens of *Alnus* and *Glyptostrobus*. The trunk diameters are smaller (< 22 cm) compared to those of trees found in horizons HA, HB, and HC, except for one stump of *Glyptostrobus*, which was 85 cm in diameter. Woody remains of *Metasequoia* were not found in this horizon. The horizons of the bases of the stumps and the roots are scattered throughout the sediment in contrast to horizons HA and HB. The occurrence of alternating silt and sand sediments in HB-HC indicates that the trees were growing in a dynamic environment and often buried by sediments in recurring floods. The small diameter of the trunks indicates that the wetland forest composed of *Alnus* and *Glyptostrobus* was probably disturbed by flooding occurring over short time intervals.

Because large stumps of *Metasequoia* and smaller stumps of *Alnus* and *Glyptostrobus* do not occur in the

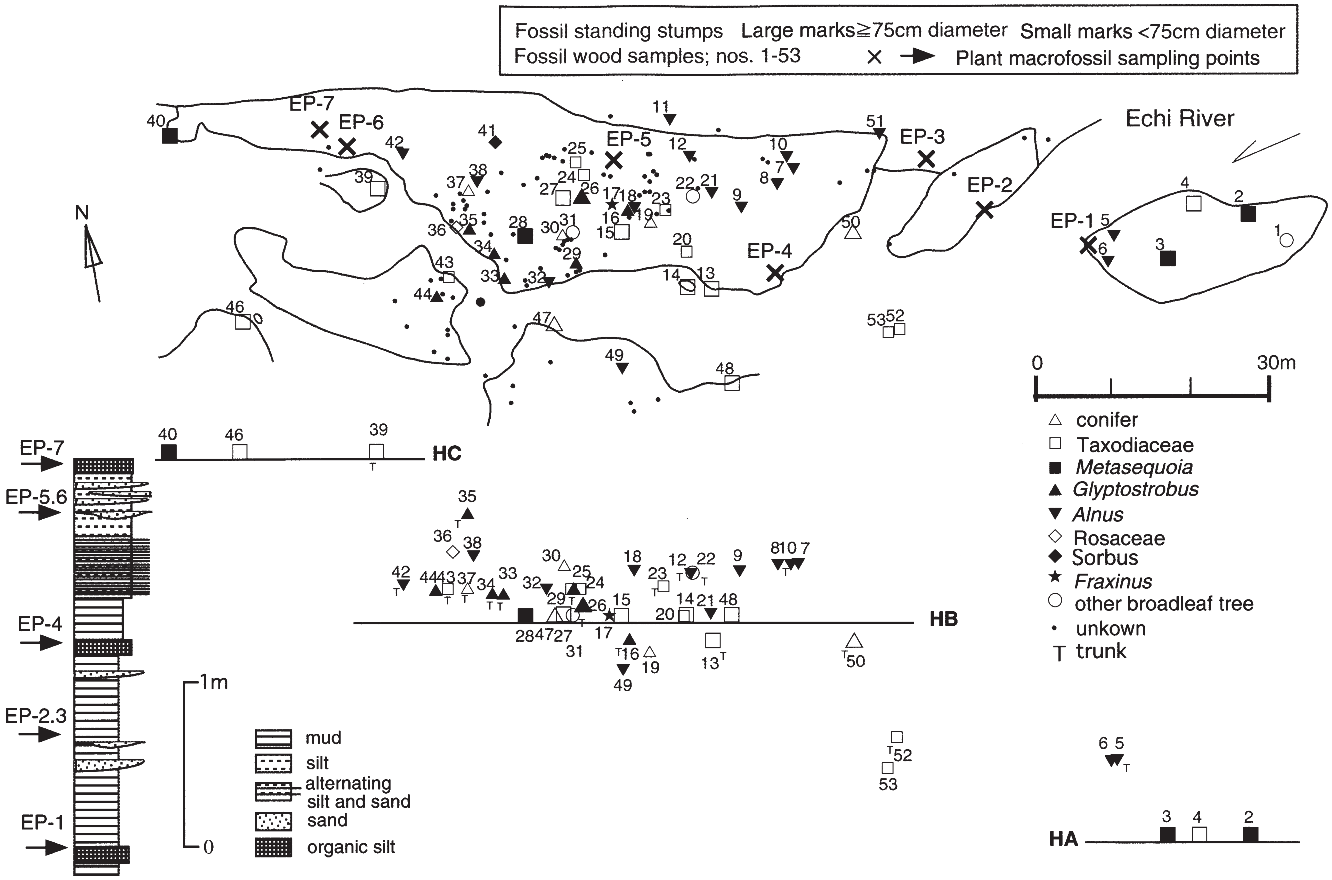

Figure 8. Temporal and spatial distribution of the *in situ* fossil in the Echi River, based on Amemori *et al.* data (1993). Contour interval lines show the topography of the riverbed.

same horizons (Figure 8), two types of wetland forest are recognized. They may represent different growth or successional stages of the forest and/or different habitats within a larger forested floodplain mosaic. The forest composed of *Alnus* and *Glyptostrobus* may represent a pioneer stage following disturbance by flooding. These taxa occupy unstable, flood-prone environments, while *Metasequoia* could only have grown to a great size and age under more stable environments.

The habitats requirements of extant *Metasequoia*, *Glyptostrobus*, and *Alnus* are currently different from one another (Lang, 1999). *Glyptostrobus* is distributed in waterlogged places in the flood plains of the lower reaches of large rivers in southern China and northern Vietnam (Li and Xia, 2004; Farjon, 2005). *Alnus* also occupies back marshes of fluvial plains in the temperate zone of the Northern Hemisphere. Both taxa tolerate anaerobic stagnant water and *Glyptostrobus* develops pneumatophores similar to those of *Taxodium* (Fu and Jin, 1992). Natural stands of *Metasequoia* are distributed at present in wet places in small valleys along the upper reaches of the Yangtze River (LePage *et al.*, 2005). Some of the roots of the trees along the river are waterlogged, but the water is not stagnant (Momohara *et al.*, 1993). The habitat of extant *Alnus* and *Glyptostrobus* in the flood plain is susceptible to floods, but that of *Metasequoia* does not suffer minor flood disturbances. Considering the ecological characteristics of extant species, the composition and occurrence of the fossil forest indicate that the wetland forests dominated by *Glyptostrobus* and *Alnus* and those dominated by *Metasequoia* existed separately during the late Pliocene. This suggests that the differences in forest composition and habitats observed in these late Pliocene ecosystems were being controlled by the prevailing hydrologic and flood disturbance regimes. The results of this study indicate that the ecological preferences of *Metasequoia* and *Glyptostrobus* were distinct during the late Pliocene. While it is difficult to determine with certainty whether such differences in habitat partitioning were prevalent in Late Mesozoic and Cenozoic fossil forests where *Metasequoia* and *Glyptostrobus* coexisted, our study demonstrates the importance of performing high-resolution stratigraphic studies where these taxa cooccur.

Paleovegetation in and around the fossil forest and its paleoclimatic implications

Based on the composition of the fossil stumps that we examined, the wetland forest was dominated by *Metasequoia*, *Glyptostrobus*, and *Alnus*, and included *Fraxinus*, *Sorbus*, and Rosaceae as minor elements (Table 3). The other arboreal taxa included in the plant macrofossil assemblages EP-1, EP-4, and EP-7 (i.e., the same horizons as the fossil forest beds), seem to have been more adapted to riparian habitats than to the wetland forest itself. This suggests that there may have been limited transport of the plant remains from nearby extrabasinal sources into the wetlands. Examples that support this interpretation are the evergreen conifer *Chamaecyparis pisifera*, *Abies*, *Picea*, and *Tsuga* along with deciduous broadleaf trees like *Pterocarya rhoifolia*, *Betula maximowicziana*, *Magnolia*, and *Acer*.

Palynological analysis of the sediments in and below horizons HA (ENP11 and 18) and HC (ENP16 and 17) by Mizutani (1993) indicated that *Alnus* is the most dominant taxon (ca. 30–40%), while *Tsuga*, *Cryptomeria-Sequoia* and *Metasequoia-Glyptostrobus* occupy about 10–15% of the total arboreal pollen. Pollen of broadleaf trees other than Alnus, such as *Juglans-Pterocarya*, *Carpinus*, *Fagus*, *Quercus* subgen. *Lepidobalanus*, and *Ulmus-Zelkova*, occurs at less than 5% each. Most of the pollen of *Alnus*, *Metasequoia*, and *Glyptostrobus* would have been derived from the wetland forest, and thus the hinterland of the fluvial back marsh evidently featured a mixed evergreen conifer and deciduous broadleaf forest.

The palynological study of Mizutani (1993) also indicated that the aquatic and wetland herbs including Cyperaceae and *Polygonum* dominated the vegetation in and around the fossil forest. Pollen of *Persicaria* and *Echinocauron* was abundant (ca. 3–15% of the total arboreal pollen), with Gramineae (ca. 2–5%) dominant in the herbaceous pollen assemblages. Fossil fern spores amounted to 15–20% of the total pollen and spore count. The relatively high amount of fern spores suggests the occurrence of wetland fern vegetation in and around the fossil forest, but no fossil fern fronds were found in the plant macrofossil assemblages (Table 4).

The composition of the plant macrofossil assemblages accompanying the fossil forest shows characteristics of the Pleistocene cold stages (Momohara, 1994) except for the occurrence of *Glyptostrobus*. Plants distributed mainly in the cool-temperate zone, such as *Picea*, *Thuja*, *Chamaecyparis pisifera*, *Betula maximowicziana*, *Pterocarya rhoifolia*, and *Menyanthes trifoliata*, were included in all of the plant macrofossil assemblages associated with the fossil forest. The plants that are currently distributed in the warm-temperate zone are not included in the fossil forest assemblage except for *Glyptostrobus*. This suggests that the climate during deposition of the fossil forest was under a cool-temperate regime and the change of composition of wetland forest from one dominated by *Glyptostrobus* and *Alnus* to a *Metasequoia* -dominated forest was not caused by climatic changes. *Glyptostrobus* is now distributed in the subtropics at present, but in the latest Pliocene, it grew in a cool-temperate zone climate.

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References

Amemori, K., Arakawa, T., Kitagawa, A., Kobayakawa, T., Taga, M., Tajima, T., Tamura, M., Nishikawa, K., and Mitsuya, N., 1993: Geology and sedimentary environment of Echigawa Petrified Forest, Shiga Prefecture, Japan. *In*, Echigawa Petrified Forest Research Group *eds.*, Echigawa Petrified Forest, *Research Report of the Lake Biwa Museum Project Office*, no. 1, p. 15–31. (*in Japanese*)

Budantsev, L. Y., 1994: The fossil flora of the Paleogene climatic optimum in north eastern Asia. *In*, Boulter, M. C. and Fisher, H. C. *ed.*, *Cenozoic plants and climates of the Arctic*, NATO ASI series, Global Environmental Change, vol. 27, p. 127–149. Springer-Verlag, New York.

Christie, R. L. and McMillan, N. J., 1991: Tertiary fossil forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. *Geological Survey of Canada Bulletin*, 403, 227 p.

Echigawa Petrified Forest Research Group, 1993: Echigawa Petrified Forest. *Research Report of the Lake Biwa Museum Project Office*, no. 1, 129 p. (*in Japanese*)

Farjon, A., 2005: *A Monograph of Cupressaceae and Sciadopitys*, 648 p. Royal Botanic Gardens, Kew.

Florin, R., 1963: The distribution of conifer and taxad genera in time and space. Acta Horti Bergiani, Bd. 20, no. 4, p. 121–312.

Fu, L. G. and Jin, J. M., 1992: *China Plant Red Data Book-Rare and Endangered Plants*, Volume 1, 741 p. Science Press, Beijing.

International Association of Wood Anatomists Committee, 1989: IAWA list of microscopic features for hardwood identification. *In* Wheeler, E. A., Bass, P. and Gasson, P. E. *eds.*, *IAWA Bulletin*, new series vol. 10, no. 3, p. 219–332. International Association of

Wood Anatomists, Leiden.

International Association of Wood Anatomists Committee, 2004: IAWA list of microscopic features for softwood identification. *In* Richter, H. G., Grosser, D., Heinz, I., and Gasson, P. E. *eds.*, *IAWA Journal* vol. 25, no. 1, p. 1–70. International Association of Wood Anatomists, Leiden.

Itoh, T., 1993: Fossil wood of the petrified forest around the Echi River, Shiga Prefecture. *In*, Echigawa Petrified Forest Research Group *eds.*, Echigawa Petrified Forest, *Research Report of the Lake Biwa Museum Project Office*, no. 1, p. 33–45. (*in Japanese*)

Kobayakawa, T., 1993: Tree rings of fossil wood from the petrified forest in the Echi River, Shiga Prefecture. *In*, Echigawa Petrified Forest Research Group *eds.*, Echigawa Petrified Forest, *Research Report of the Lake Biwa Museum Project Office*, no. 1, p. 47–55. (*in Japanese*)

Kumagai, H., Sweda, T., Hayashi, K., Kojima, S., Basinger, J. F., Shibuya, M., and Fukao, Y., 1995: Growth-ring analysis of Early Tertiary conifer woods from the Canadian High Arctic and its paleoclimatic interpretation. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 116, p. 247–262.

Lang, H., 1999: *Wetland vegetation in China*, 553 p. Science Press, Beijing. (*in Chinese*)

LePage, B. A., 2007: The taxonomy and biogeographic history of *Glyptostrobus* Endlicher (Cupressaceae). *Bulletin of the Peabody Museum of Natural History of Yale University*, vol. 48, p. 359–426.

LePage, B. A., Williams, C. J., and Yang, H., 2005: *The Geobiology and Ecology of Metasequoia*, 434 p. Springer, Dordrecht.

Li, F.-G. and Xia, N.-H., 2004: The geographical distribution and cause of threat to *Glyptostrobus pensilis* (Taxodiaceae). *Journal of Tropical and Subtropical Botany*, vol. 12, p. 13–20. (*in Chinese with English abstract*)

Manabe, K. and Suzuki, K., 1988: Stratigraphy and correlation of the non-marine Pliocene-Pleistocene in northeast Honshu, Japan. *The Memoirs of the Geological Society of Japan*, no. 30, p. 39–50. (*in Japanese with English abstract*)

Matsumoto, M., Ohsawa, A. T., Nishida, M., and Nishida, H., 1997: *Glyptostrobus rubenosawaensis* sp. nov., a new permineralized conifer species from the Middle Miocene, central Hokkaido, Japan. *Paleontological Research*, vol. 1, p. 81–99.

McIver, E. E. and Basinger, J. F., 1993: Flora of the Ravenscrag Formation (Paleocene), southwestern Saskatchewan, Canada. *Palaeontography of Canada*, vol. 10, p. 1–167.

Miki, S., 1948: Floral remains in Kinki and adjacent districts since the Pliocene with description of 8 new species. *Mineralogy and Geology (Kobutsu to Chishitsu)*, vol. 2, p. 105–144. (*in Japanese with English abstract*)

Mizutani, A., 1993: Fossil pollen from the petrified forest in the Echi River, Shiga Prefecture. *In*, Echigawa Petrified Forest Research Group *eds.*, Echigawa Petrified Forest, *Research Report of the Lake Biwa Museum Project Office*, no. 1, p. 67–73. (*in Japanese*)

Momohara,A., Yin, K. Yamakawa, C., and Gu, M., 1993: Natural habitats of *Metasequoia glyptostroboides* in Lichuan, Hubei Province, China. *Japanese Journal of Historical Botany*, vol. 1, p. 73–80. (*in Japanese*)

Momohara, A.,1994: Floral and paleoenvironmental history from the late Pliocene to middle Pleistocene in and around central Japan. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 108, p. 281–293.

Momohara, A., Mizuno, K., and Okitsu, S., 1997: Plant macrofossil assemblages in the latest early Pleistocene cold stage from the upper member of the Shobudani Formation, southwestern Japan. *Japanese Journal of Historical Botany*, vol. 5, p. 29–37. (*in Japanese with English abstract*)

Nakayama, K., 1993: Paleomagnetism of the volcanic ash layers of the Kobiwako Group around the Echi River, Shiga Prefecture. *In*, Echigawa Petrified Forest Research Group *eds.*, Echigawa Petrified Forest, *Research Report of the Lake Biwa Museum Project Office*, no. 1, p. 115–120. (*in Japanese*)

Okamura, Y., 1993: Fossil footprints from the Echi River, Shiga Prefecture. *In*, Echigawa Petrified Forest Research Group *eds.*, Echigawa Petrified Forest, *Research Report of the Lake Biwa Museum Project Office*, no. 1, p. 81–95. (*in Japanese*)

Vann, D. R., 2005: Physiological ecology of *Metasequoia glyptostroboides* Hu *et* Cheng. *In*, LePage, B.A., Williams, C.J., and Yang, H., *eds.*, *The Geobiology and Ecology of Metasequoia*, p. 305–333. Springer, Dordrecht.

Visscher, G. E. and Jagels, R., 2003: Separation of *Metasequoia* and *Glyptostrobus* (Cupressaceae) based on wood anatomy. *IAWA Journal*, vol. 24, no. 4, p. 439–450.

Williams, C. J., Johnson, A. H., LePage, B. A., Vann, D. R., and Taylor, K. D., 2003a: Reconstruction of Tertiary *Metasequoia* forests I. Test of a method for biomass determination based on stem dimensions. *Paleobiology*, vol. 29, p. 256–270.

Williams, C. J., Johnson, A. H., LePage, B. A., Vann, D. R., and Sweda, T., 2003b: Reconstruction of Tertiary *Metasequoia* forests II. Structure, biomass and productivity of Eocene floodplain forests in the Canadian Arctic. *Paleobiology*, vol. 29, p. 271–292.

Yamakawa, C., 1993: Fossil plants obtained from the petrified Forest in the Echi River, Shiga Prefecture. *In*, Echigawa Petrified Forest Research Group *eds.*, Echigawa Petrified Forest, *Research Report of the Lake Biwa Museum Project Office*, no. 1, p. 57–65. (*in Japanese*)

Yoshikawa, S., 1984: Volcamic ash layers in the Osaka and Kobiwako Group, Kinki District, Japan. *Journal of Geosciences, Osaka City University*, vol. 27, p. 1–40.

Yoshikawa, S., 1993: Volcanic ash layers of the Kobiwako Group around the Echi River, Shiga Prefecture. *In*, Echigawa Petrified Forest Research Group *eds.*, Echigawa Petrified Forest. *Research Report of the Lake Biwa Museum Project Office*, no. 1, p. 97–103. (*in Japanese*)

Yoshikawa, S., Satoguchi, Y., and Nagahashi, Y., 1996: A widespread volcanic ash bed in the horizon close to the Pliocene-Pleistocene boundary: Fukuda-Tsujimatagawa-Kd38 volcanic ash bed occurring in central Japan. *Journal of Geological Society of Japan*, vol. 102, p. 258–270. (*in Japanese with English abstract*)

Yu, Y.-F., 1995: Origin, evolution and distribution of the Taxodiaceae. *Acta Phytotaxonomica Sinica*, vol. 33, p. 362–389.