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***Limnobiophyllum expansum* (Araceae) from the early Miocene Hiramaki Formation in the Kani Basin, Gifu Prefecture, Central Japan**

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Abstract. *Limnobiophyllum expansum* (Lemnoideae, Araceae) was newly found in the lower Miocene (18.4–17.0 Ma) Hiramaki Formation of the Mizunami Group in the Kani Basin, Gifu Prefecture, central Japan. This genus was distributed widely in the Northern Hemisphere from the Late Cretaceous to the Paleocene, but a Miocene descendant (*L. expansum*) was reported only from Europe; the Bohemian Basin, the Czech Republic (early Miocene), Paldau, Austria (late Miocene), Schrotzburg, Switzerland (late Miocene) and Sośnica, Poland (late Miocene). Our finding is the first record of a Miocene *Limnobiophyllum* from an area other than Europe. The aquatic flora of Japan during the early Miocene is poorly documented, but this finding suggests a link between the aquatic floras of Europe and Asia.

Key words: aquatic flora, Hiramaki Formation, *Limnobiophyllum*, Miocene, Mizunami Group

Introduction

The early Miocene floras of Japan can be divided into Aniai- and Daijima-type floras (Tanai, 1961, 1967, 1991, 1992). The Aniai-type flora thrived from the latest Oligocene to the early Miocene (24–20 Ma) and consists of deciduous broad-leaved angiosperms and conifers (Tanai, 1961, 1967, 1991, 1992). The Daijima-type flora flourished mainly in the late early Miocene (18–16 Ma) and consists of evergreen and deciduous broad-leaved angiosperms and conifers (Tanai, 1961, 1967, 1991, 1992). It has been suggested that the global temperature was high from the late Oligocene to the middle Miocene (26–15 Ma) and declined slightly from the latest Oligocene to the early Miocene (24–17 Ma) (Zachos *et al.*, 2008). The age of the Aniai-type flora roughly corresponds to the period of the temperature decline, while the Daijima-type flora developed during the subsequent warming (Tanai, 1991, 1992).

However, this floristic scheme is inferred based on arborescent species. It is widely accepted that extant aquatic vascular plants have wider distributions than terrestrial vascular plants, as many aquatic species occur in several climatic zones or geographically separated areas (Sculthorpe, 1967; Cook, 1990). Santamaría (2002) pointed out that physiological and propagational traits (e.g., stress-tolerance, clonal growth, etc.) that are polyphyletic in aquatic vascular plants best explain their wide distributions, rather than climate or geographic barriers. These facts imply that fossil aquatic plants also had wide distributions, unlike arborescent species whose distributions are more sensitive to climate or geographic barriers. Nevertheless, there is limited information on the aquatic vegetation of Japan, especially for the early Miocene and the few paleobotanical studies of early Miocene aquatic species of Japan (*e.g.*, Huzioka, 1964; Ozaki, 1978) did not focus on their distributions.

Genus *Limnobiophyllum* is an extinct floating aquatic monocot. It has stoloniferous rosettes bearing one to four (two in many cases) round to reniform leaves

and dimorphic root systems: roots that arise adventitiously from the nodes and those that arise from root-bearing axes (Kvaček, 1995; Stockey *et al.*, 1997). The architecture of *Limnobiophyllum* is similar to that of the extant aquatic genus *Spirodela* (Lemnoideae, Araceae), except for stolons that connect the rosettes and dimorphic root-bearing habit (Dawson, 1875; Kvaček, 1995; Stockey *et al.*, 1997; Stockey, 2006). Phylogenetic analyses using morphological characters placed *Limnobiophyllum* as a sister to extant Lemnoideae within the Araceae based on synapomorphies, such as vegetative propagation by fragmentation and globose pollen with a monoporate aperture (Stockey *et al.*, 1997). Two *Limnobiophyllum* species have been described: *Limnobiophyllum scutatum* (Dawson) Krassilov and *Limnobiophyllum expansum* (Heer) Kvaček. *Limnobiophyllum scutatum* is known from the Upper Cretaceous to Oligocene of North America (Stockey *et al.*, 1997, 2007), the Upper Cretaceous to the Paleocene of Eurasia (Krassilov, 1976; Akhmetiev and Shevireva, 1989; Kvaček, 1995) and the Paleocene of Spitsbergen (Budantsev and Golovneva, 2009); it had a wide distribution in the Paleocene, as expected from its aquatic habitat. By contrast, *L. expansum* is reported only from the Miocene of Europe; the lower Miocene of the Bohemian Basin, the Czech Republic (Kvaček, 1995, 1998, 2003; Kvaček and Hurník, 2000), and the upper Miocene of Schrotzburg, Switzerland (Heer, 1859; Hantke, 1954), Paldau, Austria (Krenn, 1998) and Sośnica, Poland (Collinson *et al.*, 2001).

Here, we report *Limnobiophyllum expansum* from the lower Miocene Hiramaki Formation of the Mizunami Group in the Kani Basin, Gifu Prefecture, central Japan. This is the first report of *L. expansum* outside Europe, which suggests that the species had a wide distribution during the early Miocene. This finding also provides a new perspective for reconsidering the early Miocene flora of Japan in light of the distributional uniqueness of aquatic vascular plants.

Material and Geological Settings

In the Kani Basin, the Miocene Mizunami Group is divided into the Hachiya, Nakamura, and Hiramaki formations in ascending order (Shikano, 1995). These consist of lacustrine and fluvial deposits (Itoigawa, 1980; Shikano, 1995). Aniai-type floras with some warm elements was reported from the Hachiya and Nakamura formations (Ina *et al.*, 1983, 1985, 2007), while a Daijima-type flora was found in the Hiramaki Formation (Ina, 1977). The estimated age of the Hiramaki Formation is 18.4–17.0 Ma by fission-track dating (Shikano, 2003).

Plant fossils were collected from locality HK019 (35°26'08"N, 137°05'27"E) in Hiragaito, Kani City (Figure 1), where the upper part of the Hiramaki Formation forms an outcrop along the Kani River (T. Yamada, unpublished data). *Limnobiophyllum* plants were contained in mudstone, along with emergent *Nelumbo* sp. and floating *Salvinia* sp. Several stumps of Taxodioideae (Cupressaceae) and *Glyptostrobus* shoots are found in the mudstone. Details of this aquatic plant community will be discussed in separate papers.

All specimens are stored in the Paleobotanical Collections of the National Museum of Nature and Science, Tsukuba (NSM PP).

Systematic Palaeobotany

Class Magnoliopsida

Order Alismatales R. Br. ex Bercht. and J. Presl, 1820

Family Araceae Juss., 1789

Genus *Limnobiophyllum* Krassilov, 1973 emend. Kvaček, 1995

Type species.—*Limnobiophyllum scutatatum* (Dawson, 1875) Krassilov, 1973.

Limnobiophyllum expansum (Heer, 1859) Kvaček, 1995

Figure 2A–F

Cotyledo, Goeppert, 1855, p. 40, pl. 26, fig. 46.

Hiraea expansa Heer, 1859, p. 65, pl. 121, figs. 16–16b.

Hydromystria expansa (Heer) Hantke, 1954, p. 81, pl. 14, figs 9–12.

Limnobiophyllum expansum (Heer) Kvaček, 1995, p. 51, text, figs. 2–6; Krenn, 1998, p. 210, pl. 1, fig. 7; Kvaček, 1998, pl. 2, fig. 2; Kvaček and Hurník, 2000, p. 22, pl. 10, fig. 7; Collinson *et al.*, 2001, p. 273–274, figs. 10.1–3.

Specimens examined.—NSM PP-12251a (Figure 2A, E), NSM PP-12252 (Figure 2B), NSM PP-12253 (Figure 2C, D), NSM PP-12251b (Figure 2F), NSM PP-12254–12272.

Description.—Two leaves of different sizes are usually found in a rosette (Figure 2A, B), although four leaves are arranged spirally in some rosettes (Figure 2C, D). The rosettes are interconnected by stolons (Figure 2A, B, E). Numerous adventitious roots arise from the rosette base, as well as from the rooting axes, which are presumably the primary roots (Figure 2A, C, E).

The leaves are slightly asymmetrical, with a suborbicular to reniform outline, and are sessile (Figure 2A–D, F). The largest leaf in a rosette is 1.4–3.7 cm long (Figure 2A–D, F). The leaf base is cordate and the apex is slightly depressed (Figure 2B, F, arrowheads). The leaf margin is entire (Figure 2A–D, F). Venation is campylodromous and 10–12 primaries radiate from the leaf base (Figure 2 A–D, F). Secondaries arise at an acute angle (ca. 30°) and tertiaries run almost perpendicular to adjacent primaries, secondaries, or marginal veins (Figure 2C, D).

Adventitious roots radiating from a node are 0.2–0.25 mm wide, 7.5–10 mm long, and unbranched (Figure 2C, E). Rooting axes are 0.8–1.0 mm wide, 1.2–2.2 cm

long and bear roots spirally (Figure 2C, E). Roots from the rooting axes are 0.15–0.2 mm wide and 0.25–0.5 mm long (Figure 2C, E).

Stolons are ca. 1.5 mm wide and the intervals between adjacent nodes are 0.8–2.5 cm long (Figure 2A, E). A vein-like structure is visible in stolons, presumably representing a vascular bundle (Figure 2A, E).

Remarks.—Our specimens are clearly identified as a species in the genus *Limnobiophyllum* based on the following characters: rosettes bearing two to four leaves (mainly two) that are interconnected by stolons; suborbicular to reniform leaves with campylodromous venation consisting of ca. 10 primaries; adventitious roots radiating from each node; and rooting axes born at the node (Krassilov, 1973; Kvaček, 1995; Stockey *et al.*, 1997). An apical notch is usually present in the leaves of *L. expansum* (Kvaček, 1995), while it is rarely developed in *L. scutatum* (Stockey *et al.*, 1997). The apical notch was clearly present in our specimens when the leaf apex was preserved. Consequently, these were identified as *L. expansum*.

A possible vascular strand is visible in the stolons of our specimens, as in Kvaček's (1995) specimens, while it is not clearly seen in *Limnobiophyllum scutatum* (Stockey *et al.*, 1997). Rosettes with more than two leaves are not known for *L. expansum* (Kvaček, 1995), but this could be due to a small sample size, as Stockey *et al.* (1997) pointed out.

Discussion

Aquatic vascular plants tend to have wide distributions compared with their terrestrial relatives and often occur in several climatic zones or geographically separated areas (Sculthorpe, 1967; Cook, 1990). This tendency is found polyphyletically in vascular plants (Sculthorpe, 1967; Cook, 1990). Santamaría (2002) attributes this distribution of aquatic vascular plants to their modes of propagation. Aquatic vascular

plants can form sexual and asexual propagules. Sexual propagules (seeds and spores) are long-lived, enabling the long-distance dispersal of an aquatic species by animals. When long-dispersal succeeds, the aquatic species can proliferate clonally and occupy the new habitat rapidly. Clonal propagation is also effective for invading similar nearby habitats (Santamaría, 2002). Therefore, a few successes in long-distance immigration are sufficient for settling a new area, and recent population genetic studies increasingly support this scenario (e.g., Katayama *et al.*, 2016).

Climate and geographic barriers are less crucial than biological traits as explanatory factors for the distributions of aquatic vascular plants, but they have limited effects on the distribution (Santamaría, 2002). However, the land constituting the present Japanese Archipelago was close to the eastern margin of Eurasia from the late Oligocene to the mid Miocene (Jolivet *et al.*, 1994; Maruyama *et al.*, 1997; Yanai *et al.*, 2010). In addition, it has been suggested that swamps with taxodiaceous conifers distributed in the mid-latitudes from Asia to Europe (Krassilov, 1994; Kovar-Eder *et al.*, 2001; Vickulin *et al.*, 2003; Lepage, 2007; Ivanov *et al.*, 2011), where subtropical to temperate climatic conditions were prevailed (Wolfe, 1985; Tiffney and Manchester, 2001; Herold *et al.*, 2010). This geological background, and the biological traits of aquatic plants predict that aquatic fossil species, could have been shared between Europe and Asia, including Japan, in the early half of the Miocene.

This study provides an example supporting this hypothesis, by reporting *Limnobiophyllum expansum* from the lower Miocene of Japan, which had previously been found only in the Miocene of Europe (Heer, 1859; Hantke, 1954; Kvaček, 1995, 1998, 2003; Krenn, 1998; Kvaček and Hurník, 2000; Collinson *et al.*, 2001). Our *Limnobiophyllum* fossils were found in a *Glyptostrobus* swamp along with *Salvinia* sp. (T. Yamada, unpublished data), as in the aquatic flora reported from the lower Miocene of Bohemia, the Czech Republic (Kvaček, 1998, 2003). Although detailed taxonomic

studies of the Hiramaki fossils are ongoing, these should reveal a closer link between the aquatic floras of Europe and Japan during the early Miocene.

The congeneric *Limnobiophyllum scutatum* was distributed in North America, Spitsbergen, and Asia during the Paleocene (Krassilov, 1973, 1976; Akhmetiev and Shevireva, 1989; Kvaček, 1995; Stockey *et al.*, 1997, 2007; Budantsev and Golovneva, 2009), while *L. expansum* was distributed in Europe (Kvaček, 1995, 1998, 2003; Kvaček and Hurník, 2000) and Japan in the early Miocene. These records suggest that the two *Limnobiophyllum* species had distributions as wide as those of extant species of Lemnoideae (Cook, 1990). They also imply that there was a turnover of species between the Paleocene and Miocene. There is only one *Limnobiophyllum* record from North America during this period (Stockey *et al.*, 2007), but future studies of Eocene to Oligocene *Limnobiophyllum* should reveal how this species turnover and subsequent spread were achieved. Since Lemnoideae constitutes the basal group within Araceae, along with Gymnostachydoideae and Orontioideae (Cabrera *et al.*, 2008; Nauheimer *et al.*, 2012), the distributional history of *Limnobiophyllum* in relation to its ecology is worth exploring to better understand the early evolution of this family.

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Figure legends

Figure 1. Distribution of the Mizunami Group (dotted shading) based on Yamada *et al.* (1990) and the fossil locality (HK019) in the Kani Basin, Gifu Prefecture.

Figure 2. *Limnobiophyllum expansum* from the Hiramaki Formation. **A**, rosettes connected by stolons, NSM PP-12251a. **B**, two rosettes connected by a stolon, NSM PP-12252. Note the notch in the leaf (arrowhead). **C**, rosettes compressed with the apical side (right) and basal (left) sides upward, NSM PP-12253. The left rosette bears roots from a node along with the rooting axis. **D**, line drawing of the right rosette in C. Four leaves are visible in the rosette. **E**, close-up of A showing two rosettes connected by stolons. **F**, counterpart of the rightmost rosette in A, PP-12251b. Note the notch in the leaf (arrowhead). Abbreviations: l, leaf; n, node; r, root; ra, rooting axis; s, stolon. Scale bars indicate 1 cm.



