

Leaf Compressions of *Buxus* from the Upper Miocene of Japan

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The genus *Buxus* is characterized by small and coriaceous leaves with peculiar venation. Its fossils have frequently been recorded from the Upper Tertiary rocks of Europe, southeastern Russia and East Asia. Cuticular details of *Buxus* leaves from the European Tertiary were described by MÄDLER (1939), STRAUS (1969) and others. Recently, GIVULESCO (1971) enumerated the fossil localities and their geological horizons hitherto known in Europe and European Russia.

In general, most of leaf remains from the Tertiary of Japan are found as impression fossils, which are not subject to anatomical studies. Only sediments younger than Late Miocene often yield leaves with carbonized materials. MIKI (1937) noted the cuticular characters of *Buxus*, *Ilex* and *Viscum* leaves in his paper on the Pliocene and Pleistocene floras from Akashi, Japan. However, no detailed study has been made on the cuticular features of angiosperms from the Miocene of Japan.

As part of his investigation of the Late Miocene floras from northeastern Honshu, the author has found many *Buxus* leaf compressions which are suitable for the cuticular analysis. In this paper the author describes the detailed features of venation and cuticles of *Buxus* together with gross morphology on the basis of leaves from the Upper Miocene of Japan. In addition, summarizing previously known records of the fossil *Buxus* from Japan and its adjacent regions, the author briefly discusses the past distribution and ecological implication.

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Description of the Species

Class Magnoliopsida (Dicotyledones)

Subclass Dilleniidae

Order Euphorbiales

Family Buxaceae

Genus *Buxus* L.

Buxus protojaponica TANAI et ONOE, *emend. nov.*

Pl. 1, figs. 1–7; Pl. 2, figs. 1–6.

Buxus protojaponica TANAI et ONOE, 1961, p. 46, pl. 14, fig. 5. — TANAI, 1961, p. 354, pl. 25, fig. 6. — TANAI & N. SUZUKI, 1963, p. 135, pl. 26, fig. 6. — HUZIOKA, 1963, p. 206, pl. 36, figs. 1, 1a. — ISHIDA, 1970, p. 93, pl. 15, figs. 13, 14. — HUZIOKA & UEMURA, 1973, p. 716, pl. 12, figs. 6–8. — OZAKI, 1974, p. 16, pl. 3, fig. 5. — ONOE, 1974, p. 50, pl. 11, figs. 1, 2. — MURAI, 1976, pl. 2, fig. 5.

Buxus japonica MUELL. ARG., MIKI, 1937, p. 320, fig. 7 A–B. — MIKI, 1941, p. 281, text-fig. 16 D. — TAKAHASHI, 1954, p. 60, pl. 7, fig. 13 a–g. — SUZUKI, K., 1961, p. 77, pl. 16, figs. 11–13. — MURAI, 1963, p. 96, pl. 14, figs. 14–16.

Type: TANAI and ONOE, 1961, pl. 14, fig. 5, Onbara, Maniwa-gun, Okayama Prefecture; Ningyo-toge Formation (Late Miocene).

Materials: There are about 40 leaf compressions and impressions in the Paleobotanical Collections of the Department of Paleontology, National Science Museum in Tokyo and in the Institute of Mining Geology of the Mining College, Akita University in Akita (abbreviated as NSM PP and AKMG, respectively). Many specimens are well preserved leaf compressions which frequently curl up from matrix when they are dried.

Leaf compressions were easily picked up from mudstone matrix, submerged in dilute H₂O₂ solution about for overnight, washed thoroughly, and then mounted in glyceric jelly or Bioleit (a xylene soluble synthetic resin manufactured by Oken-shoji Co., Tokyo). For cuticle preparations the usual maceration technique (nitric acid followed by alkali) was used and plant fragments were mounted in glyceric jelly.

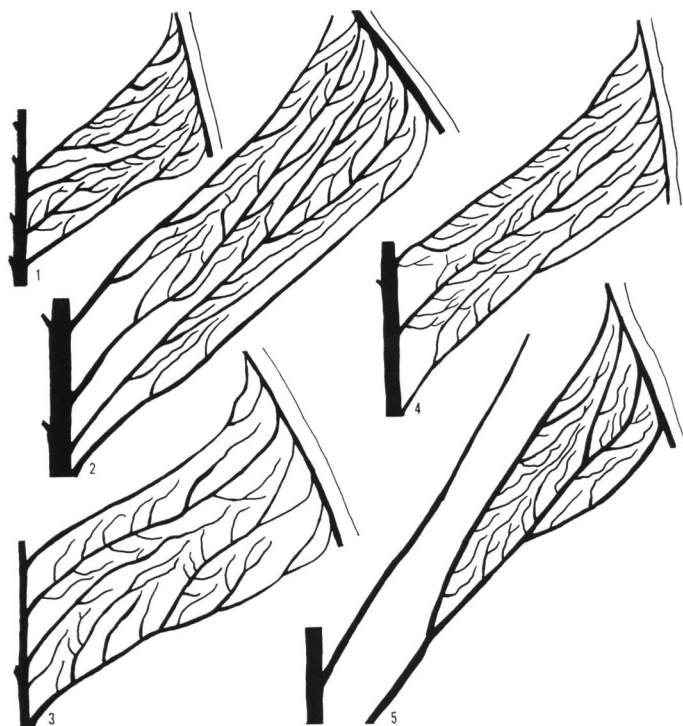
The registered specimens examined are as follows; Tayama flora: Ohara, Arayacho, Ninohe-gun, Iwate Pref., Tayama Formation (Late Miocene), AKMG 7716, 7717, 7918, 7920, 7921, 7936, NSM PP 15329, 16797, 16798. Miyata flora: Miyata Formation (Late Miocene), Kamihinokinai, Nishiki-mura, Senpoku-gun, Akita Pref.: loc. Miyata, AKMG 7124 (HUZIOKA & UEMURA, 1973, pl. 12, fig. 7), 7125, 7126, 7127 (op. cit., fig. 8), 7129, 7153b, NSM PP 6350 (op. cit., fig. 6), 6351–6353, 15323–15328; loc. Tozawa, AKMG 7176b; loc. Tozawa-2, NSM PP 6385; loc. Kami-tozawa, AKMG 7325; loc. Hinokinaimatazawa, AKMG 7382, 7399, NSM PP 6399b; loc. Hinokinaimatazawa-2, AKMG 7460; loc. Horinaizawa, AKMG 7162. Tatsumi-toge flora: Tatsumi-toge, Saji-mura, Yazu-gun, Tottori Pref., Tatsumi-toge Formation (Late Miocene), NSM PP 16796.

Supplementary description: Leaves small, 15–26 mm long and 6.5–10.5 mm wide, ranging in shape from elliptic, obovate to oblanceolate; base acute to rounded, apex

emarginate or rarely rounded; nearly glabrous except for both on the petiole and leaf margin near the base; margin entire. Mid-primary vein stout, straight in course, tapering to the apex; lateral primary vein thinner than the mid-primary vein, apparently originating from the petiole, and forming a marked marginal vein 0.25 mm within the margin; numerous (more than 20) secondary veins diverging from the mid-primary vein at angles of 30–60°, dichotomously ramified 2–4 times, straight or slightly curving up, then joining the lateral primary vein; tertiary vein (highest order of vein) rather stout in their emerging point, diverging at an acute angle from the secondaries, exmedially ramified, dendriform, irregularly tapering and ending freely in intercostal area; areolation lacking. Petiole thick and stout, up to 2 mm long, slightly twisted. Texture thick coriaceous.

Cuticular anatomy: Both the upper and the lower epidermis thick; lower epidermis much cutinized than the upper. Ordinary cells of the upper and lower epidermis pentagonal, hexagonal (predominant) to polygonal in outline, averaging 30–35 μ in diameter; anticlinal cell walls 3–5 μ thick, smooth; marked surface ornamentation absent, but with many fine crystal cavities. Cells over veins more or less rectangular, nearly parallel to the major venation. Leaf margin cells somewhat irregular in outline, hexagonal to polygonal, with 8–10 layers parallel to the leaf margin, 20–40 μ long and about 20 μ broad; anticlinal cell walls thick and much cutinized than the ordinary cells. Stomata confined to the lower surface, randomly distributed over the leaf except for the area of outer rim, long axis of guard cells more or less parallel to the direction of secondary veins; guard cells 20–25 $\mu \times$ 6–10 μ , length of stomatal apparatus 15–20 μ ; each pair of guard cells slightly sunken below the surface of the surrounding subsidiary cells; outer margin contacting subsidiary cells of the guard cells thickly cutinized; subsidiary cells paracytic, 35–40 μ in length. Unicellular hairs on the petiole and basal margin of leaves long conical, about 110 μ in length.

Comparison and remarks: These leaves on hand are identical with *Buxus protojaponica* TANAI et ONOE, which was originally described from the Late Miocene Hoki flora, in their characteristic shape, texture and venation. The leaves of the genus *Buxus* are unique in their shape with emarginate apex, venation and cuticular features. Among these features, the venation pattern is particularly noticeable (figs. 1–5): (1) the lateral primaries originating from the petiole to form the marginal vein, (2) secondary veins dichotomously branching and sending off numerous tertiary veins, (3) exmedially ramifying tertiary veins, (4) higher ordered veins not developed, and (5) lacking areolation. These characteristics of venation are highly unusual for dicotyledon leaves. Some leaves such as *Alyxia* (Apocynaceae), *Diospyros* (Ebenaceae), *Drypetes* (Euphorbiaceae), *Severinia* (Rutaceae), *Eugenia*, *Decaspermum* and *Syzygium* (Myrtaceae), and *Manilkara* and *Sideroxylon* (Sapotaceae) have, at a glance, similar leaf forms and venation. However, they differ considerably in having admedial tertiaries and higher ordered veins. So far as the author could examine, the tertiary venation pattern found in the leaflets of *Rhus* (Anacardiaceae) is somewhat similar to that of *Buxus*. In *Rhus* leaflets, however, higher ordered veins (4th) are well developed



Figs. 1–5. Details of venation of some related living *Buxus*. all $\times 10$. 1. *B. microphylla* SIEB. et ZUCC. 2, 3. *B. microphylla* var. *japonica* (MUELL. ARG.) REHD. et WILS. 4. *B. sempervirens* L. 5. *B. wallichiana* AL. BR.

and form areoles intruded by freely ending ultimate veins of the same order.

Five species of *Buxus*, *B. corchica* POJARK., *B. microphylla* SIEB. et ZUCC. (syn. *B. japonica* MUELL. ARG.), *B. pliocenica* SAPORTA et MARION, *B. protojaponica* TANAI et ONOE, *B. sempervirens* L. (including *B. sempervirens fossilis* ENGELHARDT) have been described from the Tertiary of Eurasia. These species are closely similar to each other. Epidermal features of fossil *Buxus* from East Asia were first noted by MIKI (1937) based on leaf compressions from the Akashi Pliocene (the *Stegodon* beds). MÄDLER (1939) described epidermal features of *B. sempervirens fossilis* from the Pliocene of Frankfurt am Main. He mentioned that the leaves described by MIKI were indistinguishable from the Frankfurt leaves in their epidermal structure. Recently, the detailed study on the leaf epidermis of *Buxus* from the Pliocene of Europe has been published by STRAUS (1969) and GIVULESCO (1971). These two authors referred their leaves to the living species *B. sempervirens* L.

The leaves of *B. protojaponica* closely resemble those of European fossils, *B. pliocenica* and *B. sempervirens*, in both the external and epidermal structures. The former species differs from the European species in the presence of hairs on the

petiole and basal margin of leaves, and the hypostomatic condition. The leaves referred to *B. japonica* MUELL. ARG. by MIKI (1937, 1941) and other authors from the Upper Miocene and Pliocene of Japan are probably conspecific with the present species in their shape and venation. Besides them, the leaf and fruit of *Buxus* were reported from the Miocene of China and Korea; namely, *B. sempervirens* by DEPAPE (1932, p. 18, fig. 5 c) and *B. miosempervirens* ENDO [*nom. nud.*] by ENDO (1955, pl. 27, fig. 3). However, comparisons with *B. protojaponica* are difficult because of their poor illustrations.

The living *Buxus* includes about 70 species in Eurasia, Africa and Central America (AIRY SHAW, 1973). HATUSIMA (1942) distinguished 26 species in temperate, subtropical and tropical regions of Asia, and divided these Asiatic *Buxus* into two sections, Eugeniobuxus and Eubuxus. Unfortunately, the examination of living species of *Buxus*, especially those in Africa (sect. *Buxella* and *Notobuxus*) and in Central America (sect. *Tricera*) has been made insufficiently. However, nearly all the fossil leaves which were described up to the present belong to the sect. *Eubuxus* in their small leaves with emarginate apex and densely spaced secondary venation.

Among the living species of the sect. *Eubuxus*, *B. protojaponica* has a resemblance to leaves of the following species: *B. microphylla* STEB. et ZUCC. and its subspecies or varieties in Japan, Korea, Taiwan and China; *B. wallichiana* AL. BR. in Himalaya and India; *B. sempervirens* L. in Europe, North Africa and Asia Minor; and *B. corchica* POJARK. in Caucasus. Among all, the fossil leaves show the closest resemblance to those of *B. microphylla*, though specific separation of each on the basis of leaves is rather difficult. It seems better to retain the name of *B. protojaponica* in the Tertiary of East Asia, because the definite reproductive organs corresponding to this fossil species are unknown at present.

Some Distributional and Ecological Remarks

The fossils of *Buxus* are confined to Eurasia and all the species probably belong to the sect. *Eubuxus* as discussed earlier. In Europe *Buxus* species increased their individual number toward the younger Tertiary in relation to lowering temperature and increasing continentality (STRAUS, 1969).

Fossil occurrence of the genus *Buxus* in Japan and its adjacent regions is shown in fig. 6. MATSUO (1971, p. 701, pl. 4, fig. 11) described *Buxus* sp. from the Oligocene in Kechi, Tsushima Island, though it is not well illustrated. An Early Miocene occurrence was only reported by TANAI and N. SUZUKI (1963) from Kaminokuni in southwestern Hokkaido. Common occurrence of the genus *Buxus* in Japan is known from Middle Miocene floras under the warm and humid climate, though only one or two specimens are recorded in each fossil flora. From Upper Miocene sediments of Japan *B. protojaponica* is commonly found at many localities. In the Miyata flora it comprises 46 specimens (1.23%) of the total specimens of the flora (HUZIOKA & UEMURA, 1973) and in the Tayama flora 14 specimens (3.3%). Late Miocene

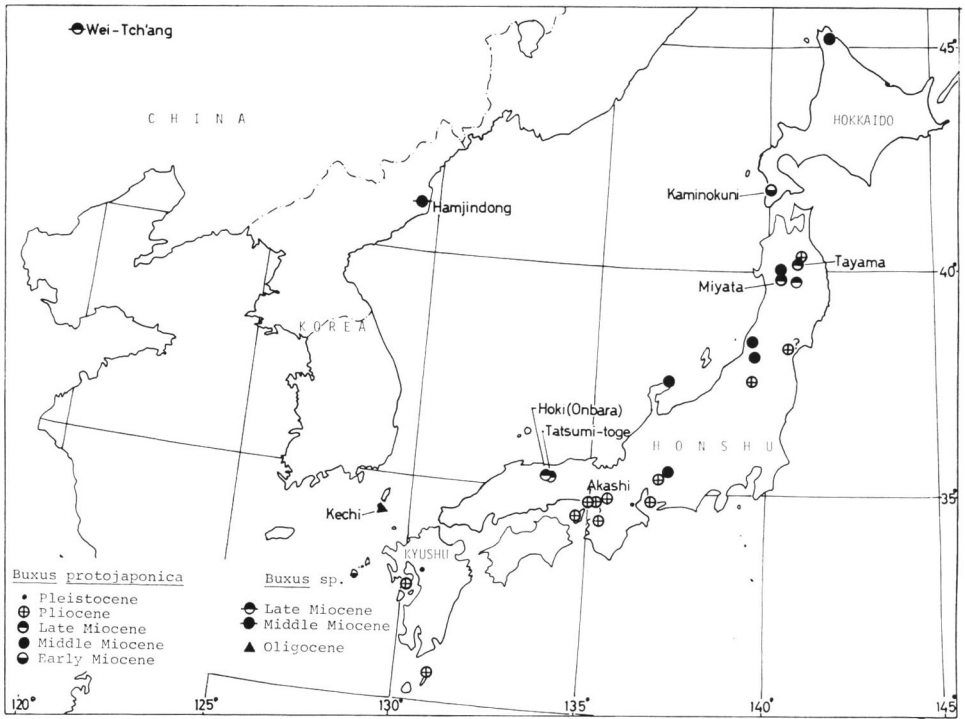


Fig. 6. Distribution of fossil *Buxus* in Japan and its adjacent regions.

floras, in contrast with Middle Miocene floras, consist mainly of temperate deciduous trees such as *Populus*, *Salix*, *Pterocarya*, *Alnus*, *Betula*, *Carpinus*, *Fagus*, *Quercus*, *Ulmus*, *Prunus*, *Sorbus*, *Wistaria*, *Acer* and *Kalopanax*; of these trees *Fagus* is particularly predominant. A number of *Buxus* leaves have been known from the Pliocene and Plio-Pleistocene sediments in Honshu and Kyushu (MIKI, 1937, 1941 & 1948; MIKI & KOKAWA, 1962; K. SUZUKI, 1961; TAKAHASHI, 1954). The floras from these sediments are composed of temperate trees and belong to the Shinjo and Akashi type floras called by TANAI (1961). These *Buxus*-bearing floras are considered to be a lowland flora with a few exceptions. Compared with the records of *Buxus* from the Upper Miocene and Pliocene, the Pleistocene occurrence is rather poor.

Modern *Buxus* species are evergreen shrubs and are distributed in more or less dry stands such as rocky places and limestone hills in warm-temperate and subtropical regions. Regarding the habitat, *B. protojaponica* seems to have inhabited under humid climatic condition as that of the present-day Japanese Islands at least since the Late Miocene time. It probably grew in temperate forests mingled with other undergrowth trees, though a more precise habitat condition can not be presumed.

To conclude, the genus *Buxus* first appeared in the Oligocene to Early Miocene time in East Asia. During the Middle Miocene *B. protojaponica* extended its dis-

tributional area. It was commonly distributed in temperate forests in the Late Miocene and Pliocene time, adapting itself to the cooling climate and changing physiography of the Japanese Islands.

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Explanation of Plates

Plate 1

Specimens of leaves of *Buxus protojaponica* TANAI et ONOE

- Fig. 1. NSM PP 15325, loc. Miyata, $\times 3.3$.
- Fig. 2. NSM PP 15327, loc. Miyata, $\times 3.3$.
- Fig. 3. NSM PP 15329, loc. Ohara, $\times 3.3$.
- Fig. 4. NSM PP 15326, loc. Miyata, $\times 3.3$.
- Fig. 5. NSM PP 15324, loc. Miyata, $\times 3.5$.
- Fig. 6. NSM PP 15328, loc. Miyata, $\times 4$.
- Fig. 7. Enlarged fig. 3, to show the fine venation, $\times 11$.

Plate 2

Cuticles of *Buxus protojaponica* TANAI et ONOE

- Fig. 1. Lower epidermis, NSM PP 15325, loc. Miyata, $\times 120$.
- Fig. 2. Unicellular hairs on the petiole, NSM PP 16797, loc. Ohara, $\times 120$.
- Figs. 3, 4. Upper epidermis, AKMG 7918, loc. Ohara; fig. 3, $\times 120$; fig. 4, $\times 240$.
- Figs. 5, 6. Lower epidermis, AKMG 7918, loc. Ohara; fig. 5, $\times 240$; fig. 6, $\times 480$.

