

TAXONOMY AND NOMENCLATURE OF *TAXUS* (TAXACEAE)

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ABSTRACT

A taxonomic treatment of *Taxus* (Taxaceae) is presented, based on morphological characters. The genus is proposed to have 24 species and 55 varieties; 24 species and 26 varieties are presented in a key and classified into three main groups, two subgroups, and two alliances. Previously existing names were applied to 15 species and six varieties—*T. baccata* L. and its varieties—var. *dovastoniana* Leighton, var. *elegantissima* Hort. ex C. Lawson, var. *glauca* Jacques ex Carrière, var. *pyramidalis* Hort. ex C. Lawson, and var. *variegata* Watson; *T. brevifolia* Nutt., *T. caespitosa* Nakai, *T. canadensis* Marshall, *T. celebica* (Warb.) H.L. Li, *T. chinensis* (Pilg.) Rehder, *T. contorta* Griff., *T. cuspidata* Siebold & Zucc., *T. fastigiata* Lindl., *T. globosa* Schldtl., *T. mairei* (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu, *T. recurvata* Hort. ex C. Lawson, *T. sumatrana* (Miq.) de Laub., *T. umbraculifera* (Siebold ex Endl.) C. Lawson, *T. wallichiana* Zucc. and var. *yunnanensis* (W.C. Cheng & L.K. Fu) C. T. Kuan. Six new species—***T. biternata*** Spjut, ***T. florinii*** Spjut, ***T. kingstonii*** Spjut, ***T. obscura*** Spjut, ***T. phytonii*** Spjut, and ***T. suffnessii*** Spjut, and four new varieties—***T. brevifolia*** Nutt. var. ***polychaeta*** Spjut, ***T. brevifolia*** Nutt. var. ***reptaneta*** Spjut, ***T. caespitosa*** Nakai var. ***angustifolia*** Spjut and ***T. contorta*** Griff. var. ***mucronata*** Spjut are described. Eight new combinations are made: ***T. caespitosa*** var. ***latifolia*** (Pilg.) Spjut, ***T. canadensis*** var. ***adpressa*** (Carrière) Spjut, ***T. canadensis*** var. ***minor*** (Michx.) Spjut, ***T. globosa*** var. ***floridana*** (Nutt. ex Chapm.) Spjut, ***T. mairei*** (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu var. ***speciosa*** (Florin) Spjut, ***T. umbraculifera*** var. ***hicksii*** (Hort. ex Rehder) Spjut, ***T. umbraculifera*** var. ***microcarpa*** (Trautv.) Spjut, and ***T. umbraculifera*** (Siebold ex Endl.) C. Lawson var. ***nana*** (Rehder) Spjut. Taxonomy and nomenclature are discussed for each species and variety.

RESUMEN

Se presenta un tratamiento taxonómico de *Taxus* (Taxaceae) basado en caracteres morfológicos. Se propone que el género tenga 24 especies y 55 variedades; 24 especies y 26 variedades se presentan en una clave y se clasifican en tres grupos principales, dos subgrupos, y dos alianzas. Los nombres existentes previamente se aplicaron a 15 especies y seis variedades—*T. baccata* L. y sus variedades—var. *dovastoniana* Leighton, var. *elegantissima* Hort. ex C. Lawson, var. *glauca* Jacques ex Carrière, var. *pyramidalis* Hort. ex C. Lawson, y var. *variegata* Watson; *T. brevifolia* Nutt., *T. caespitosa* Nakai, *T. canadensis* Marshall, *T. celebica* (Warb.) H.L. Li, *T. chinensis* (Pilg.) Rehder, *T. contorta* Griff., *T. cuspidata* Siebold & Zucc., *T. fastigiata* Lindl., *T. globosa* Schldtl., *T. mairei* (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu, *T. recurvata* Hort. ex C. Lawson, *T. sumatrana* (Miq.) de Laub., *T. umbraculifera* (Siebold ex Endl.) C. Lawson, *T. wallichiana* Zucc. y var. *yunnanensis* (W.C. Cheng & L.K. Fu) C. T. Kuan. Se describen seis especies nuevas—***T. biternata*** Spjut, ***T. florinii*** Spjut, ***T. kingstonii*** Spjut, ***T. obscura*** Spjut, ***T. phytonii*** Spjut, and ***T. suffnessii*** Spjut, and four new varieties—***T. brevifolia*** Nutt. var. ***polychaeta*** Spjut, ***T. brevifolia*** Nutt. var. ***reptaneta*** Spjut, ***T. caespitosa*** Nakai var. ***angustifolia*** Spjut y ***T. contorta*** Griff. var. ***mucronata*** Spjut. Se hacen ocho nuevas combinaciones: ***T. caespitosa*** var. ***latifolia*** (Pilg.) Spjut, ***T. canadensis*** var. ***adpressa*** (Carrière) Spjut, ***T. canadensis*** var. ***minor*** (Michx.) Spjut, ***T. globosa*** var. ***floridana*** (Nutt. ex Chapm.) Spjut, ***T. mairei*** (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu var. ***speciosa*** (Florin) Spjut, ***T. umbraculifera*** var. ***hicksii*** (Hort. ex Rehder) Spjut, ***T. umbraculifera*** var. ***microcarpa*** (Trautv.) Spjut, y ***T. umbraculifera*** (Siebold ex Endl.) C. Lawson var. ***nana*** (Rehder) Spjut. Se discute la taxonomía y la nomenclatura de todas las especies y variedades.

INTRODUCTION

The genus *Taxus* (Taxaceae) has long been indicated to have 7–12 species or subspecies (Cope 1998; Farjon 1998, 2001; Pilger 1903, 1916; Silba 1984, 1986; Spjut 1992); however, Spjut (2000c; www.worldbotanical.com) has proposed recognition of 24 species and 55 varieties. The taxonomy of *Taxus* has been controversial because the species do not appear reproductively isolated except by geography (Farjon 1998; Pilger 1903; Silba 1984), although Collins et al. (2003) reported that *Taxus* hybrids may have impaired meiosis or less functional pollen. The genus ranges from temperate North America into subtropical Central America, and from temperate Eurasia to subtropical Southeast Asia (Cope 1998).

Molecular and morphological studies of *Taxus* have distinguished genotypes that differentiate (1) individuals within populations (Collins et al. 2003; El-Kassaby & Yanchuk 1995; Saikia et al. 2000; Spjut 2007), (2) distinct populations within geographic regions (Doede et al. 1993; El-Kassaby & Yanchuk 1994; von Hertel and Kohlstock 1996; Hilfiker et al. 2004; Spjut 2007), and (3) alleged geographically distinct species

(Collins et al. 2003; Doede et al. 1993; Florin 1948a, 1948b, 1948c; Hils 1993; J. Li et al. 2001; N. Li & Fu 1997; Krupkin unpublished, 1994; Orr 1937; Spjut 2007; Vance & Krupkin 1993). Molecular studies for the most part have been geographically based, in which plants have been randomly selected; little attempt has been made to correlate genetic differences or haplotypes with morphological characters (Corradini et al. 2002), while new species have been recently described based on morphology and geographical data (N. Li & Fu 1997).

The geographic species of *Taxus* that have received support from molecular and/or morphological studies include those in North America (*T. brevifolia* Nutt., *T. canadensis* Marshall, *T. globosa* Schltldl. var. *globosa*, and var. *floridana* [Nutt. ex Chapm.] Spjut; Hils 1993; J. Li et al. 2001; Spjut 1992, 1993, 2007; Vance & Krupkin 1993), the Euro-Mediterranean *T. baccata* L., the Sino-Japanese *T. cuspidata* Siebold & Zucc. (Collins et al. 2003; J. Li et al. 2001), and the tropical Southeast Asian *T. sumatrana* (Miq.) de Laubenfels (received as *T. chinensis* (Pilg.) Rehder (Phyton Inc., Krupkin pers. comm. 1994). Jianhua Li et al. (2001) have further shown that the North American species, *T. brevifolia* and *T. globosa* (from both Mexico and Florida), which belong to Spjut's (1998b, 2000b) *Wallichiana* Subgroup, form a well-supported clade separated from a large weakly supported clade represented by *T. baccata*, *T. canadensis*, *T. chinensis*, *T. cuspidata* and cultivars, and that "low sequence divergence between *T. floridana* from Florida, and *T. globosa* from Mexico suggest very recent separation between the lineages in these regions and is consistent with treating these populations as belonging to the same species."

There is also molecular data to support distinction of less geographically separated species. Wang et al. (2000) showed a sharp contrast between RAPD bands of *T. chinensis* and *T. mairei* (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu among other species of taxads included in their study. An unpublished report on Himalayan yews found the northwestern Himalayan yew (*T. contorta* Griff.) distinct from the East Himalayan *T. wallichiana* Zucc. and the Euro-Mediterranean *Baccata* Alliance (Amin pers. comm.). A specimen received from Phyton Inc., reportedly from southwestern China, was thought to be distinct from *T. chinensis* (Kadkade pers. comm. 1997); indeed, it had been proposed as a new species from morphological study of herbarium specimens (*T. florinii* Spjut in adnot., June 1996, A).

Despite the wealth of papers on the chemistry of *Taxus* in regard to developing anticancer diterpenoid compounds (taxoids) for use in cancer chemotherapy (Appendino 1995; Kingston et al. 1990; Kingston 2005), not a single comprehensive study has emerged on the phylogeny of the genus. One might expect that a genus with supposedly only eight species (Silba 1986) would be relatively simple to resolve taxonomically by molecular data. Undoubtedly the traditional geographic species of *Taxus* have been investigated by molecular data, but lack of a definitive phylogenetic treatment would seem to reflect the need for morphological studies to define the species as a guide for the molecular investigations.

Spjut (1998a, 2006, 2007) suggested that much of the variation in leaf anatomical features of *Taxus*—in the eastern Himalayas to southwestern China—could be explained by post-Pliocene hybridization between formerly distinct Tertiary species. *Taxus engelhardtii* Kvaček, for example, a Tertiary species discovered from leaves in Oligocene deposits in Europe, is much like the extant *T. mairei* (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu in subtropical laurophyll forests of southern China; the fossil species differs in having papillae on the abaxial leaf midrib (Spjut 2007). Similarly, a *Taxus* sp. from a Middle Miocene deposit in western North America (Kvaček & Rember 2000) has the leaf anatomical features of *T. brevifolia* (papillose abaxial margins and midrib, large marginal cells, stomata in 4–7 rows), but differs slightly in the the leaves appearing flattened and less mucronate; recently, it has been described as a new species (Kvaček & Rember submitted). Two other Tertiary leaf fossils of *Taxus* from European deposits of late Miocene to Pliocene age are closely similar to *T. canadensis* (Kvaček 1984, Spjut 2007), a species native to east-central North America but also recognized to occur in the Euro-Mediterranean region (Spjut 2000b, 2007). Intermediates between extant *T. baccata* and *T. canadensis* in the Euro-Mediterranean region, which have a partially papillose marginal zone, seem best explained by hybridization (Spjut 2006).

Collins et al. (2003), in a molecular study of *Taxus canadensis*, *T. cuspidata*, and *T. baccata*, identified

three different DNA chloroplast types, which support three stomata band types described by Spjut (2003, www.worldbotanical.com) for the *Baccata* Group, and suggested that these differences indicate “a long period of isolation.” Their study also included numerous cultivars or “hybrids” (*T. × media*) between *T. cuspidata* and *T. baccata* and between *T. canadensis* and *T. cuspidata*, none of which were found to have identical genotypes. To explain the higher level of diversity in cultivars, they suggested that multiple hybrid events have occurred over time, but it is also likely that other genotypes, which may belong to other species, have contributed to the hybrid complex not present in their putatively wild samples. This reflects a conservative view that only one species of *Taxus* exists within a geographic region; further, in the view here, distinct morphological ecotypes of *Taxus* with parapatric distributions are considered worthy of taxonomic rank as species or varieties.

The IUCN (2004, 2006), in reference to a Conifer Specialist Group 1998 (Farjon & Page 1999), which adopted the nomenclature in Farjon (1998), recently listed *Taxus brevifolia* as a threatened species, one that is not rare but reportedly threatened due to the need for taxol derivatives from plant sources for the commercial production of anticancer drugs. Other species of *Taxus* listed by the IUCN are *T. globosa* (including var. *floridana*) and *T. wallichiana*. The latter name is meant to also include *T. contorta*, but Farjon’s (2001) treatment of *T. contorta* as a synonym of *T. wallichiana* is without taxonomic support (no types or specimens were cited, no keys are provided, nor are there any references to such data; see also CITES (2001, 2004). Awaiting a standard taxonomic foundation upon which species and varieties can be identified according to the International Code of Botanical Nomenclature (ICBN, Greuter et al. 2000), all species and varieties in the genus *Taxus*, whether described or undescribed, perhaps should be considered rare, threatened, or endangered.

This paper presents a key to 24 species and 26 varieties of *Taxus* based on chemical (byproducts) and morphological differences. Six new species and four new varieties are described, and eight new combinations are made. Lectotypes or neotypes are designated or proposed for 23 of the species and the additional varieties mentioned. Descriptions and specimen citations are provided primarily for new taxa in connection with a paper on biogeographical data of *Taxus* (Spjut 2007). Also included in the present study are varieties of *T. brevifolia*, *T. caespitosa* Nakai, *T. canadensis*, and *T. umbraculifera* (Siebold ex Endl.) C. Lawson, which are not mentioned in Spjut (2007); therefore, specimen citations are also provided for these. The taxonomy and nomenclature of each taxon are discussed.

MATERIALS AND METHODS

More than 1,000 specimens of *Taxus* have been studied, 845 of which are documented with details on leaf anatomical data (Spjut 2007).

Early in the study, ca.100 representative specimens of *Taxus* throughout its range identified 11 species and one variety by morphological features that best fit the traditional geographical concept (Spjut 1992, 1993; Spjut in Hils 1993). The characters were based on leaf anatomical features that included the number of stomata rows, distribution of papillae on abaxial midrib, shape of epidermal cells, curvature of the abaxial midrib, and the color of the stomata bands as compared to the non-stomata regions (Spjut 1992).

As the study progressed, many specimens from Eurasia could not be accommodated in the morphological key according to the traditional geographic species concept; consequently, this concept was abandoned. Herbarium specimens were then strictly classified according to pattern recognition as evident from characters of branching, bud-scale texture and size, change in color of branchlets from 1st to 2nd year, leaf arrangement, leaf shape, leaf thickness, leaf color, leaf curvature lengthwise and across both surfaces, changes in leaf curvature near margins and along midrib, shape of cones in bud and at maturity, distribution of papillae along the abaxial leaf margin, and other characters of lesser importance (described in DELTA format, Spjut USDA Memorandum 1995). Data on numbers of stomata rows and number of marginal cells are presented elsewhere (Spjut 2007). Only color and phyllotaxy are further discussed (below). References for eco-geographical data on species are cited when relevant to data on herbarium specimens.

Results of the author's revised taxonomic concepts were presented at annual scientific meetings in Baltimore (Spjut (1998a,b) and Portland (Spjut 2000a,b,c), which included papers on the evolution in the *Taxus* leaf, phytogeography of the genus *Taxus*, a key to all species and varieties of *Taxus* (Spjut 2000a), and the occurrence of *Taxus canadensis* in both North America and the Euro-Mediterranean region (Spjut 2000b). Manuscripts were also submitted for peer review in 1999 and 2000; one of these was later placed on the internet (Spjut 2003) from which data were extracted and incorporated into the present paper.

Taxonomic species concept

The species concept in *Taxus* in the sections that follow is based on pattern recognition employing the traditional method of defining species in keys; a taxonomic method in which my primary objective has been to classify specimens in the fewest number of species and varieties that can be reasonably distinguished from one another. Their character features, as presented in the following keys, can be seen in specimen photos with data from labels at www.worldbotanical.com. My view of *Taxus* species is that they were most distinct by the end of the Tertiary as a result of former geographical and ecological isolation, and that hybridization and introgression since the Pliocene has blurred their distinction (Spjut 2007). Examples of species and varieties that were allegedly more widespread and appear to be losing their identity through introgression are *Taxus* OCR (*T. ocreata* Spjut ined.) (China), *Taxus* SCU (*T. scutata* Spjut ined.) (China), *T. suffnessii* Spjut (Myanmar), *T. wallichiana* var. *yunnanensis* (W.C. Cheng & L.K. Fu) C. T. Kuan (NE India to SW China), and *T. contorta* Griff. var. *mucronata* Spjut (Bhutan, Nepal).

The taxonomic value of characters was evaluated subjectively by their apparent correlation with other characters. Species identification usually depended upon specimens having a combination of two or more character attributes. As experience was acquired in identifying *Taxus*, many species could be recognized by gross morphological features of branching, phyllotaxy, and color; however, detailed examination of a leaf under a microscope for other character features was also necessary to confirm identification (e.g., see discussion under *T. kingstonii* Spjut). Ideally, one might further employ chromatographic or molecular characters, but it remains to be demonstrated whether such information can be efficiently extracted from herbarium specimens. Needles from a number of herbarium specimens were subjected to DNA extraction, but there was little extractable DNA (Da Cheng, pers. comm. 2007; Krupkin, pers. comm. 1994).

Variation in color as it may relate to chemotaxonomic characters

A key character for recognizing differences between species groups is the occurrence and distribution of reddish colored cells in leaf tissues as seen in dried herbarium specimens. Differences in color are also employed as taxonomic characters at the species level; for example, *T. baccata* has nearly concolorous leaf surfaces in contrast to strongly discolorous leaf surfaces in *T. recurvata* Hort. ex C. Lawson, and *T. kingstonii* is identified by its rusty orange color compared to a blood red color in *T. mairei*.

The reddish to orange cells are obviously the result of chemical byproducts. These have yet to be identified, but they apparently are phenolics that oxidize slowly in collected and dried specimens to form the reddish resinous substances observed in cell walls of leaf epidermal and mesophyll layers. The color changes may occur over a period of many months or years except for species in the *Sumatrana* Group in which the color change occurs usually within a week after a specimen is collected and dried. *Taxus* contains cyanogenic glucosides (Khan & Parveen 1987) that break down and release benzaldehyde related compounds when plants are damaged (Seigler 1991; van Genderen et al. 1996). These include taxiphyllin, dhurrine, triglocholine, and isotriglocholine (Khan & Parveen 1987).

Other potentially useful compounds in *Taxus* are biflavones, which are known to have chemotaxonomic value in gymnosperms in addition to biological value as antifungal, anti-bacterial, and antiviral agents (Krauze-Baranowska & Wiwart 2003). For example, in the Podocarpaceae, the presence or absence of various flavonoid glycosides (Markham et al. 1985) has been found to correlate with recent morphological taxonomic concepts of its genera and species (de Laubenfels 1969), and biflavones have been shown to be localized in leaf epidermal cells of conifers with the aid of aluminum chloride-induced fluorescence (Gadek et al. 1984). *Taxus* biflavones include sciadopitysin, ginkgetin, kayaflavone, amentoflavone 7-O-methylamentoflavone

in European and Himalayan species, and bilobetin and 4-O-methylamentoflavone in samples from Poland (Krauze-Baranowska & Wiwart 2003). Appendino (1995) has noted uncharacterized pro-anthocyanidins, “based on 3-flavanols of the *cis* and *trans* type,” are “probably responsible for the red color of a paste made from bark of a Himalayan species.” Also, apocarotenoids have been found in a Himalayan yew but not in European yew (Appendino 1995).

Leaf parenchyma of *Taxus* also contains essential oils, but *Taxus* is deficient in monoterpenes that are usually present in conifers (Appendino 1995; Jean et al. 1993). *Taxus* is best known for anticancer diterpenoid compounds (taxoids), particularly taxol (Wani et al. 1971), from which semi-synthetic derivatives are used for treating cancer (Kingston et al. 1990; Kingston 1996, 2005). Numerous novel taxoids have been discovered in the genus (Appendino 1995); however, most reports are of little taxonomic value because studies have focused on novel discoveries (Appendino 1995) and because the genus has been in critical need of taxonomic study. Most taxoids of pharmacological interest are widely distributed and vary in yield according to plant parts, location, season, drying conditions, and species (Croom 1995; Dempsey & Hook 2000; Griffith & Hook 1996; Hook et al. 1999; van Rozendaal et al. 2000). Nevertheless, Spjut et al. (1993) reported chemotaxonomic relationships based on taxoid content between similar morphs of *T. brevifolia* var. *reptaneta* when compared to var. *brevifolia*, and Chang (unpublished, pers. comm.) found chemotaxonomic differences for taxoid hplc profiles between cultivars and between *Taxus kingstonii* and other *Taxus* species in Taiwan. Although chemotaxonomic studies are lacking, Appendino (1995) has suggested that yews in Europe are characterized by the presence of taxine B, those in the Pacific Northwest by the presence of abeotaxane type alkaloids, and the Himalayan yews have 13,14-dihydroxylated taxoids not found in other regions.

Leaf phyllotaxy (frequency), arrangement (distribution), and orientation

These terms have similar but slightly different meanings in this paper.

Phyllotaxy.—refers to the frequency at which leaves develop along a twig as determined between two leaves that occur in direct alignment. The frequency is generally expressed as a ratio of the number of leaf cycles over the number of leaves in a cycle over the total number of leaves, the latter being a sum of the preceding two numbers and representing what are known as Fibonacci numbers. Camefort (1956) recognized four different patterns in *Taxus baccata*, a 2-3-5 that may spiral to the left or to the right, a 3-5-8, and a 5-8-13. Because differences in phyllotaxy can relate to branch thickness (Camefort 1956), phyllotaxy is generally described as dense, lax, or remote and by whether adjacent leaves along one side of the branch overlap along their margins.

Leaf arrangement.—The phyllotaxy in *Taxus* may also be described as spiral, as opposed to opposite, whorled, or alternate in other plant genera; however, a distinction is also made in regard to the directional and distribution pattern in which leaves spread from branchlets. In the Dovaston yew (*T. baccata* var. *dovastoniana* Leighton), for example, leaves on the uppermost side of the branchlet point upwards and towards the branch apex, while those along the sides and underneath spread outwards (horizontally). In the Maire's yew (*T. mairei*), leaves spread horizontally along two sides of branchlet nearly in one plane and thus appear distichous or “two-ranked” (but not truly two-ranked), in contrast to a radial arrangement of the Irish yew (*T. fastigiata* Lindley, not a true whorl), in which the leaves are mostly erect except for curving downwards along the blade. A further distinction is whether leaves along one side of a branchlet are mostly parallel to one another (e.g., *T. baccata*) or crisscross (e.g., *T. recurvata*) as seen in pressed specimens, and whether they appear more imbricate (e.g., *T. caespitosa*) or decussate (e.g., *T. umbraculifera*).

Leaf orientation.—This is in regard to the direction that leaves spread as a result of phototropic response. Leaves generally twist and/or bend towards light so that the adaxial surface faces upward (Hill & Scriven 1998). Leaves in most species of *Taxus* tend to spread horizontally in shade and upwards in sunlight. Habit and branching may also be correlated with leaf orientation. For example, the columnar growth form of the Irish yew (*T. fastigiata*) with ascending to erect branches appears to be an adaptation to growth in open habitats. Because the branchlets ascend upwards, the leaves would not be expected to spread much out-

wards; thus, their erect radial orientation is seen as a correlated feature. *Taxus caespitosa*, sometimes found with prostrate branches in open habitats, exhibits a phyllotaxy that may be described as dense with a leaf arrangement referred to as radial-imbricate, and because all the leaves on horizontal (caespitose) branchlets point upwards in the same direction, the orientation is also referred to as erect-secund.

Species Groups, Subgroups, Alliances, and Complexes

No formal classification of sections or subsections within the genus is proposed at this time, but species of *Taxus* are classified into three groups. Within the groups, two subgroups and two alliances are recognized, based on leaf epidermal cell shape, development of epidermal papillae, and on color of stomata bands in contrast to adjacent epidermal regions (Spjut 1998b). The **Wallichiana Group** includes the *Wallichiana* and *Chinensis* Subgroups; the **Baccata Group** includes the *Baccata* and *Cuspidata* Alliances; the **Sumatrana Group** is not subdivided. Alliances refer to taxa that share morphological features within geographical regions, whereas taxonomic groups and subgroups are not geographically isolated. Within species alliances or groups, species complexes are recognized to distinguish, for example, plants with radial distribution of leaves (*T. umbraculifera* complex) vs. leaves appearing in a two-ranked arrangement (*T. cuspidata* complex).

Nomenclature, references, authorities

Species and varietal names are typified to validate the data in this study and in Spjut (2007). Descriptions of species and full details on specimens cited are omitted for species already established; detailed descriptions and specimen citations for all taxa can be found online at www.worldbotanical.com. Six new species are described, *Taxus biternata*, *T. florinii*, *T. kingstonii*, *T. obscura*, *T. phytonii*, and *T. suffnessii*, because their leaf anatomical data are relevant to taxonomic data in another study (Spjut 2007) that supports the taxonomy in this paper. Authors for scientific names are indicated in full when the taxon name is first mentioned and are subsequently abbreviated (fide Brummitt & Powell 1992) when there is no reference to a publication.

KEYS TO GROUPS, SUBGROUPS AND ALLIANCES OF TAXUS

1. Leaf epidermal cells tall rectangular or \pm angular-isodiametric in T-sect. and usually reddish in herbarium specimens, papillose on the abaxial midrib; North America (SE Alaska and W Florida) to Central America (Honduras, El Salvador), Himalayas, SW China _____ **I. Wallichiana Group (IA Wallichiana Subgroup)**
1. Leaf epidermal cells \pm elliptical or wide rectangular in T-sect., 1.5–3.5 times as wide as tall, or if isodiametric not reddish in dried herbarium specimens, variable in development of midrib papillae.
 2. Stomata bands in dried leaves not sharply differentiated from adjacent marginal and midrib regions, the abaxial surface green to yellowish green, slightly darker green on midrib and along margins, or uniformly reddish green.
 3. Leaves with reddish cells primarily epidermal; papillae \pm equally developed across stomata bands and midrib, often more prominent along cell walls; stomata sometimes on midrib, (11–)13–19(–21) rows per band; E Himalayas to China _____ **IB. Wallichiana Group (Chinensis Subgroup)**
 3. Leaves with reddish cells primarily in mesophyll; papillae often less developed on midrib than on stomata bands, or more medial than marginal (*T. baccata* Alliance, Euro-Mediterranean, W Himalayas), or papillae reduced along cell walls—appearing conrescent (*T. cuspidata* Alliance, NE temp. Asia); stomata less than 13 rows per band in NE temp. Amer.; Euro-Mediterranean, up to 17 rows per band in temp. E Asia _____ **III. Baccata Group**
 2. Stomata bands in dried leaves distinct from glossy marginal and midrib epidermal cells, the midrib entirely smooth to papillose on outer half, or smooth from mid region to base, often discolored—blood red—in contrast to the yellowish green to yellowish orange stomata bands.
 4. Leaf epidermis with cell walls meeting at sharp angles, mostly smooth on midrib and marginal region (8–36 cells wide); stomata rarely in transverse rows; leaf papillae more medial than marginal; E Himalayas to Indonesia _____ **II. Sumatrana Group**
 4. Leaf epidermis with cells meeting at rounded angles, mostly papillose to 2–6(–12) cells from margin, sometimes less on midrib; stomata often in transverse rows; leaf papillae marginal; E Himalayas to Indonesia _____ **IB. Chinensis Subgroup**

KEYS TO THE SPECIES AND VARIETIES OF *TAXUS*

I. WALLICHIANA GROUP: SUBGROUP IA WALLICHIANA

1. Stomata 12 or more rows per band; E Himalayas, SW China.
 2. Persistent bud-scales relatively large, 2–3 mm long, nearly plane with distinct midnerve (Fig. 1); Myanmar _____ **4. *T. suffnessii***
 2. Persistent bud-scales nerveless, or nearly so, concave, less than 2 mm long and 1 mm wide (Fig. 2), if scales not evident or leaves obtuse see *Chinensis* Subgroup; E Himalayas, Nepal to SW China (var. *yunnanensis* distinguished by abaxial leaf marginal zone having long narrow cells bordered by shorter and much wider papillose cells with medial papillae, or by a lanceolate leaf shape in SW China) _____ **5. *T. wallichiana***
1. Stomata less than 12 rows per band.
 3. Abaxial leaf epidermal cells gradually narrower and shorter from stomata band to margin, mostly isodiametric in T-sect., generally 3–10× l/w, fusiform and sinuous (wavy along cell walls) on abaxial surface, or rarely rectangular; *Taxus globosa*.
 4. Papillae prominent on most of the abaxial leaf surface, the marginal cells mostly sinuous (Fig. 3, type); El Salvador to NE Mexico _____ **3a. *T. globosa* var. *globosa***
 4. Papillae less prominent on midrib and marginal zone than on stomata band, the marginal cells ± rectangular (Fig. 4, type); Mexico (Nuevo Leon/Tamaulipas, Veracruz), U.S. (Florida) _____ **3b. *T. globosa* var. *floridana***
 3. Abaxial leaf epidermal cells abruptly shorter and wider in marginal region, often taller than wide in T-sect.
 5. Stomata 7–10(–12 rows); China (Yunnan, Sichuan) _____ **2. *T. florinii***
 5. Stomata 4–7(–9) rows; NW North America _____ **1. *T. brevifolia***
 6. Cones elongate, often with a narrow stipelike base _____ **1b. *T. brevifolia* var. *polychaeta***
 6. Cones appearing sessile.
 7. Trees, reproducing by adventitious shoots _____ **1a. *T. brevifolia* var. *brevifolia***
 7. Layering shrubs, often forming thickets _____ **1c. *T. brevifolia* var. *reptaneta***

I. SUBGROUP IB CHINENSIS

1. Dried leaf surfaces ±concolorous, or yellowish green on abaxial surface.
 2. Bud-scales conspicuous at base of branchlets; Yunnan, Sichuan _____ **11. *Taxus* sp. SCU**
 2. Bud-scales minute, vestigial or absent at base of 1st yr branchlets.
 3. Leaves obtuse, usually oblong (less than 10× l/w); Vietnam, China _____ **6. *T. chinensis***
 3. Leaves acuminate (10–15× l/w); Vietnam, Philippines, China (Taiwan), Indonesia. _____ **9. *Taxus* sp. REH**
1. Dried leaf surfaces discolorous, or yellowish orange on abaxial surface.
 4. Leaves obtuse, dull rugose on adaxial surface; Yunnan, Sichuan _____ **10. *Taxus* sp. OCR**
 4. Leaves acute to acuminate, smooth or glossy on adaxial surface when dried.
 5. Leaves spreading parallel at nearly right angles; Nepal, NE India, Malaya, China (Taiwan, Yunnan), Philippines _____ **8. *T. phytonii***
 5. Leaves spreading at oblique angles, crisscrossing in pressed specimens; Myanmar, China (Fujian, Taiwan), Philippines, Indonesia (Sulawesi, Sumatera) _____ **7. *T. obscura***

II. SUMATRANA GROUP

1. Dried leaves rusty orange, at least near apex, often rust colored on abaxial surface in contrast to a darker green or bronze green colored adaxial surface, generally twisted obliquely to the stem axis, often recurved along blade to sharply pointed apex, with midrib rounded on both surfaces; generally thick and rigid; mostly 1700–3000 m, NE India to China (including Taiwan) _____ **13. *T. kingstonii***
1. Dried leaves green to reddish, or with a blood reddish discoloration along abaxial margins and on midrib, generally twisted nearly perpendicular to stem axis, the adjacent leaf edges often closely parallel, obtuse to acuminate, the abaxial midrib usually elevated and truncate, or flush, usually with a channel; generally thin and flaccid; mostly below 1200 m in China.
 2. Leaves oblong to linear, obtuse to acute, or elliptical and acuminate; leaf epidermal cells larger (mamillillose) on abaxial than adaxial midrib in T-sect., appearing short trapezoidal from surface view; S China _____ **14. *T. mairei***
 3. Branchlets limp, often much isodichotomous; leaves closely parallel along one side of branchlet; seed purplish _____ **14a. *T. mairei* var. *mairei***
 3. Branchlets rigid, occasionally isodichotomous; leaves unevenly spaced along branchlets; seed tan _____ **14b. *T. mairei* var. *speciosa***
2. Leaves long linear to lanceolate, acuminate; leaf epidermal cells in T-sect. not larger on abaxial than adaxial midrib, nearly rectangular in surface view; E Himalayas to Indonesia, Philippines.



FIG. 1. *Taxus suffensii*. Close-up of persistent scales showing prominent midnerve; Kingdon Ward 20902, Myanmar (isotype, BM).

4. Dried leaves plane to convex on adaxial surface _____ **12. *T. celebica***
 4. Dried leaves puckered, especially upper third of leaf _____ **15. *T. sumatrana***

III. BACCATA GROUP

1. Abaxial surface of leaves mostly papillose between margin and stomata band—to within 8 rows of cells from margin (e.g., Fig. 5), papillae nearly medial, the cell walls thin or smooth; leaves often curved downwards along the blade (except *T. contorta* var. *mucronata*); Euro- Mediterranean, W & C Himalayas _____ **16. *T. baccata* Alliance**
2. Leaf mesophyll with idioblasts (parenchyma cells with reddish walls), loosely connected; NW to central Himalayas (var. *mucronata* distinguished by shorter more reflexed leaves with a wider bare marginal zone of cells) _____ **17. *T. contorta***
2. Leaf parenchyma cells often dark in color, not reddish, adhesive.
- 2a. Plants columnar; leaves radial, recurved _____ **18. *T. fastigiata***
- 2a. Plants variable in habit; leaves overlapping, not distinctly radial.
- 2b. Leaf surfaces discoloured, blades recurved, convex, revolute _____ **19. *T. recurvata***
- 2b. Leaves ±concolorous, straight or falcate, plane or revolute _____ **16. *T. baccata***
- 2c. Leaves spreading outwards along two sides of branchlets in one plane, appearing distichous.
- 2d. Leaves not overlapping, branching isodichotomous _____ **16a. *T. baccata* var. *baccata***
- 2d. Leaves overlapping, branching irregular _____ **16c. *T. baccata* var. *elegantissima***
- 2c. Leaves spreading outwards along two sides of branchlets in one plane, appearing distichous.
- 2c. Leaves erect or radial on lower parts of branchlets.
- 2e. Branchlets and leaves yellowish orange in part; branchlets often recurved; leaves erect near ends of branchlets _____ **16d. *T. baccata* var. *glauca***
- 2e. Branchlets uniformly green, yellowish green to dark green; branchlets not recurved, spreading or drooping; leaves variable.
- 2f. Branching mostly pinnate _____ **16f. *T. baccata* var. *variegata***
- 2f. Branchlets crowded terminally, appearing to arise digitately or isodichotomously.
- 2g. Leaves yellowish green, falling off by the third year; branching isodichotomous _____ **16e. *T. baccata* var. *pyramidalis***



FIG. 2. *Taxus wallichiana* var. *wallichiana*. Close-up of persistent scales lacking distinct midnerve; Khasia, India, *Hooker & Thomson 77 ex Herb. Bunge (P)*.

- 2g. Leaves dark green, persistent; branching subdigitate, pinnate, or subfastigate _____ **16b. *T. baccata* var. *dovastoniana***
1. Leaves mostly smooth between stomata band and margin, usually lacking papillae across 8–24 rows of cells, the papillae often concentric on upper surface of cells near cell walls; leaf blades often curved upwards, or sharply bent or curved downwards along petiole; temperate E Asia and NE North America, Euro-Mediterranean _____ **23. *T. cuspidata* Alliance**
3. Leaves spreading more by narrow petioles, the petioles more curved than sharply bent, or petiole curving nearer junction with branchlet than with blade; stomata (4–)5–9(–11) rows per band; leaf papillae often obscure; plants usually low, creeping shrubs _____ **22. *T. canadensis* complex**
4. Leaves acute to acuminate, gradually tapering to an acute margin as seen in T-sect., usually revolute along margins, the abaxial surface with keeled midrib and mostly rectangular epidermal cells; common in NEN America, occasional in Euro-Mediterranean: Morocco, Portugal (Madeira), Spain, Sweden, Estonia _____ **22a. *T. canadensis* var. *canadensis***
4. Leaves obtuse to acute, rounded along margins in T-sect., not revolute, with flush midrib and with trapezoidal or rectangular epidermal cells.
5. Leaves crowded, erect, recurved; NE Amer., Madeira _____ **22c. *T. canadensis* var. *minor***
5. Leaves lax, mostly straight, spreading nearly at right angles; occasional, England, Madeira, France, Sweden, Norway, Estonia, Slovenia, U.S. (Iowa). _____ **22b. *T. canadensis* var. *adpressa***
3. Petioles more bent than curved, bending nearer junction with blade and also clasping the branchlet, the blades often (ad)pressed to branchlet; stomata (7–)9–14(–17) rows per band; papillae always prominent in stomata bands; plants variable in habit.
6. Leaves mostly two ranked to apex of branchlets; seed angled _____ ***T. cuspidata* complex**
7. Branchlets short and much divided; leaves in a flat (horizontal) spray (Fig. 6), more strongly revolute in upper third when dried; common understory tree, NE temp. Asia _____ **20. *T. biternata***
7. Branchlets mostly long pinnate; leaves erect (Fig. 7), uniformly revolute along margins when dried; shrub or tree—appearing adapted to exposed habitats, Japan, Korea _____ **23. *T. cuspidata***
6. Leaves in \pm two or more decussate ranks or radial; seed rounded _____ **24. *T. umbraculifera* complex**
8. Leaves \pm erect and imbricate _____ **21. *T. caespitosa***

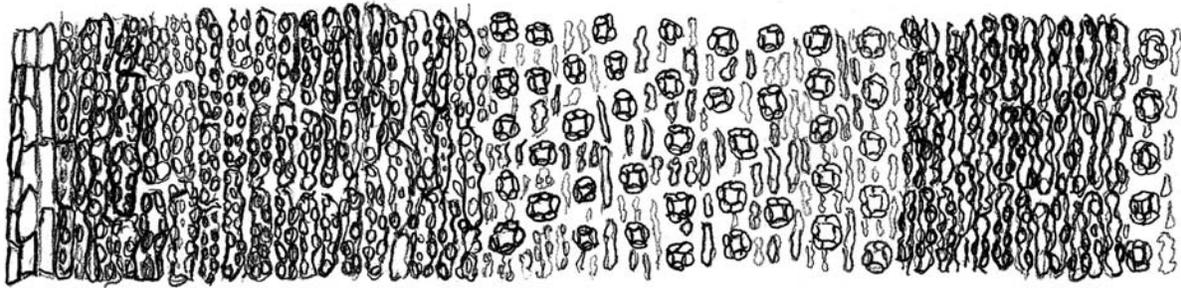


FIG. 3. *Taxus globosa* var. *globosa*. Illustration of abaxial surface of leaf as seen in the medial region from margin to midrib; showing stomata band with 9 rows of stomata and sinuous epidermal cells, a character feature related to the marginal position of papillae on epidermal cells, drawn from lectotype (K).

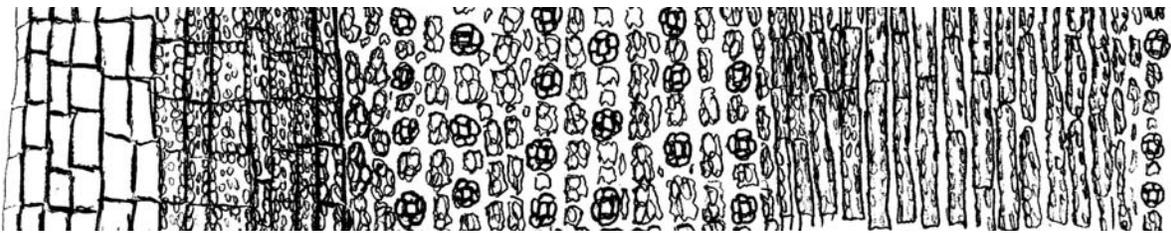
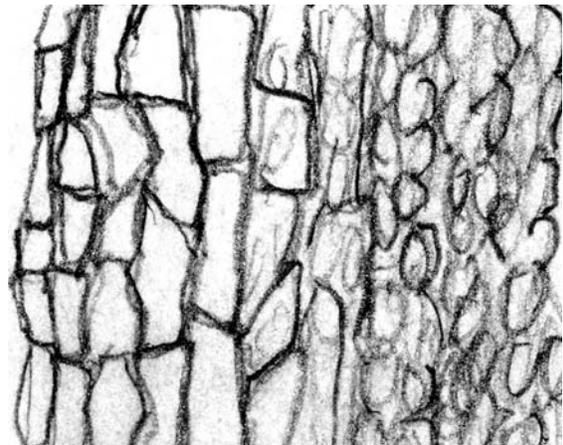


FIG. 4. *Taxus globosa* var. *floridana*. Illustration of abaxial surface of leaf as seen in the medial region from margin to midrib; showing stomata band with 7 rows of stomata and rectangular epidermal cells with less prominent papillae in comparison to var. *globosa*, drawn from original material (K).

FIG. 5. Abaxial leaf margin with 5 rows of smooth cells, followed by 2 rows of obscurely papillose cells and 3 rows of prominently papillose cells. Image scanned from author's sketch of leaf fragment on specimen packet of *Taxus recurvata*, Lewis 721 (BM).



- 9a. Branches ascending to erect with many short, crowded branchlets; leaves mostly radial (Fig. 8); Japan _____ **21a. *T. caespitosa* var. *caespitosa***
- 9a. Plants with distinct trailing or wide spreading branches; branchlets with mixed two-ranked and erect second leaves.
- 9b. Branches ascending to wide spreading; leaves oblong or linear, 2-4 mm wide; Korea, Japan, SE Russia, NE China _____ **21c. *T. caespitosa* var. *latifolia***
- 9b. Branches prostrate with erect branchlets; leaves linear, relatively narrow, ca. 2 mm wide; Korea, Japan _____ **21b. *T. caespitosa* var. *angustifolia***
8. Leaves \pm reflexed and decussate (Fig. 9) _____ **24. *T. umbraculifera***
- 10a. Flat-topped shrub, layering _____ **24c. *T. umbraculifera* var. *microcarpa***
- 10a. Hemispherical to columnar shrub or tree.



Figs. 6–7. Comparison of branching in *Taxus* species of the Cuspidata Alliance. 6 (top). *Taxus biternata*, cultivated, Forestry Research Institute, South Korea, photo and specimen by Kang Hyeon Ka s.n. 7 (bottom). *Taxus cuspidata*, cultivated, Secrest Arboretum, Wooster, Ohio, photo by Richard Spjut.

- 10b. Low rounded shrub _____ **24d. *T. umbraculifera* var. *nana***
 10b. Tall shrubs or trees.
 10c. Columnar with ascending to erect branchlets _____ **24b. *T. umbraculifera* var. *hicksii***
 10c. Pyramidal, diffusely branched _____ **24a. *T. umbraculifera* var. *umbraculifera***

TAXONOMY AND NOMENCLATURE

I. WALLICHIANA GROUP

The *Wallichiana* (Species) Group is recognized by the leaves having reddish epidermal cells and scarcely differentiated stomata bands as seen in herbarium specimens, in contrast to idioblasts in the spongy mesophyll in the *Baccata* Alliance, which includes the northwestern Himalayan *T. contorta*.

IA. *Wallichiana* Subgroup.—This subgroup is differentiated from the *Chinensis* Subgroup by leaves having taller than wide or isodiametric angular epidermal cells in transverse section, and by the obscurely differentiated stomata bands; the papillose epidermal cells often extend to four cells or less from the margin. Included are three species distributed from the eastern Himalayas to Yunnan, Sichuan, and western Hubei (2000–3700 m elevation) and two species in North America (from near sea level to 2670 m).

1. *Taxus brevifolia* Nutt., N. Amer. Sylva 3:86. 1849, t. 108 captioned “*Taxus occidentalis*,” without reference to specimens. (**Fig. 10**). *Taxus baccata* L. var. *brevifolia* (Nutt.) Koehne, Deutsche Dendrol. 6. 1893. *Taxus baccata* L. subsp. *brevifolia* (Nutt.) Pilger in Engler, Pflanzenreich 4(5):113. 1903. TYPE: U.S.A. [OREGON]: “Columbia woods,” “Nuttall Herb.” without collector, date of collection and collector’s number (lectotype designated here: from uncited specimens—original material: Nuttall Herbarium—BM! # 38752, annotated “*T. occidentalis*,”—top left specimen of three on one sheet, with mature male cones; ISOLECTOTYPES: K!, PH!).

Taxus boursieri Carrière, Rev. Hort. sér 4, 3:228. 1854. TYPE: U.S.A. CALIFORNIA: Siskiyou Co.: Shasta Springs, Aug. 1894, *Jepson s.n.* (NEOTYPE designated here: US!). Carrière cited no specimens and original material is unknown, but he noted that the species was from California: “Forests near stream with *Pseudotsuga*, *Abies grandis*, *Pinus lambertiana*; arborescent shrub with slender branches, leaves 1.5–1.8 cm long, glaucous below.”

Taxus lindleyana M.A. Murray, Edinburgh New Philos. J. 1:294. 1855. Also, Rev. Hort. sér 4, 4:379. 1855 (by J. Decainse). TYPE: U.S.A. CALIFORNIA: N and E of San Francisco between 40° and 41° latitude [Klamath Region], “along sides of a glen, under the shade of larger trees” (LECTOTYPE designated here: selected from original material of two uncited specimens at E, the one with the following handwritten notations (1) “*Taxus lindleyana*” (in bold black ink, handwriting probably Murray) (2) “Murray,” “Ed. N. Philos. Journ. 1854,” “Legn. California” (in red faded ink, handwriting undetermined, perhaps R. Jameson) and (3) “probably only a form of *T. baccata*, perhaps the *T. cuspidatus* [spelling?] of Sieb. & Zucc.” (in thin black ink, handwriting unknown—appearing different from the other two), and with the accession number E 00030316!). Described by Murray in his publications as a large tree, 30–40 ft high, with a circumference 50–70 inches in diam, and with very long pendant branches. The other specimen is indicated to have come from Vancouver, possibly collected by Murray before 1855. Judging from other plants described by Murray from his California trip in 1854, the lectotype may have been collected near Dunsmuir in Oct. 1854.

Common name.—Pacific yew.

Distribution and ecology.—SE coastal Alaska to central California—the Klamath Mts., Coast Ranges and W Sierra Nevada to Sequoia Natl. Park—and from the S Canadian Rockies in British Columbia and W Alberta south to W Montana. Often in shade of old-growth forests on N slopes, but also valley forests and seral communities along streams and forest margins; from sea level to 2650 m, in mixed evergreen and montane coniferous forests, generally Douglas fir (Eliot 1938) and lowland fir (Bolsinger & Jaramillo 1990), western hemlock along W Cascades (Franklin & Dyrness 1969), or sitka spruce and western red cedar in the northern range (Taylor 1932; Taylor & Taylor 1980).

This species was first discovered by David Douglas in 1825 (Sargent 1896), who after arriving in Astoria OR that year on April 11 (Oldham 2005) had spent much of that year collecting in the Pacific Northwest. His base of operations was the Hudson Bay Company located at Fort Vancouver just north of Portland on the Washington state side of the Columbia River, arriving there on April 20 (Oldham 2005). However, there apparently are no specimens of *T. brevifolia* by Douglas. Nuttall had also collected along the Columbia River during 1834–1835 (Graustein 1950/51); one of the labels on the type sheet refers to *T. floridana*, a species that was not discovered until 1833, a name that Nuttall had proposed sometime before 1860, the year it was legitimately described. Hitchcock et al. (1969) indicated reference to a type “Nuttall, ‘In the dense maritime



FIGS. 8–9. Comparison of leaf arrangements in *Taxus* species of the Cuspidata Alliance. 8 (top). *Taxus caespitosa* with imbricate ascending leaves, cultivated, Secrest Arboretum, Wooster, Ohio. 9 (bottom) *Taxus umbraculifera*, with spreading to reflexed somewhat decussate leaves, cultivated, Secrest Arboretum.



FIGS. 10A–C. Type specimens of *Taxus brevifolia*. A (left). Herbarium sheet at BM, Nuttall Herbarium. B (top right), close-up of lectotype (BM), upper left specimen, showing adaxial surface of leaves and mature male cones on 1st yr branchlets. C (lower right). Close-up of the abaxial surface of leaves and persistent bud-scales at the base of branchlets in the lower specimen on the herbarium sheet in Fig. 10A.

forest of the Oregon” while Pilger (1903) noted that yew had been observed by Douglas in the Oregon forests along the Columbia River. A review of the geographical distribution of *T. brevifolia* by Spjut (1977) reported the occurrence of Pacific yew near Portland and other areas in the nearby Mt. Hood National Forest where trees were known to reach a height of 20–25 m. The presence of mature male cones on the type indicates it would likely have been collected during the spring. Thus, Oregon is likely the state locality for the type where possibly collected by Nuttall himself during the spring of 1835; the handwriting on the type label compares favorably with that on other Nuttall types (NY, virtual herbarium of types, particularly for specimens from the “Columbia woods”).

Taxus brevifolia is distinguished from the closely related *T. globosa* by the leaves having enlarged epidermal cells along the abaxial surface between the stomata bands and margins, narrower stomata bands with fewer stomata rows, and leaf blades tapering to an obtuse but mucronate apex. Leaf stomata range from 4–7(–9) rows per band with the higher counts (7–9 rows) more frequent in specimens from the Sierra Nevada and lower counts (4–6 rows) more often found in the Klamath Region, Coast Ranges, Cascades, and Rocky Mountains (Spjut 2007). The relatively wide abaxial leaf margins lack papillae on 2–11 cells across.

The leaf epidermal cells in transverse leaf sections often appear tall rectangular as in the East Himalayan *T. wallichiana*, *T. suffnessii*, and the Southwest China *T. florinii*. The similar number of stomata rows per band between *T. florinii* and *T. brevifolia* may be the result of convergent evolution (homoplasy) within the *Wallichiana* Subgroup.

The type has leaves spreading nearly at right angles and appearing dark metallic green on the adaxial surface. Other specimens differ by a reddish orange color (e.g., lectotype for *T. lindleyana*), or by a glaucous abaxial surface (e.g., neotype for *T. boursieri*). These differences may justify reevaluations of taxonomic status in further studies.

Taxus brevifolia has been a major source of taxol (paclitaxel) employed in cancer chemotherapy, first isolated from stem-bark (Wani et al. 1971). Historical accounts on the procurement of *Taxus* species for the NCI antitumor screening are given by Croom (1995) and by Goodman and Walsh (2001); the latter draws extensively on information from memoranda, letters, and interviews concerning availability of *T. brevifolia* for supply of taxol in the short and long term.

Currently, three varieties are recognized by differences in cones, habit, and vegetative reproduction. The typical variety, a tree usually scattered in the understory of old growth forests, produces cones similar to most other yew species. Variety *polychaeta* is distinguished by longer cones with persistent scales, whereas var. *reptaneta* differs by the layering habit in which the plants often form thickets, in contrast to the typical variety reproducing vegetatively by adventitious shoots from trunks or roots.

1a. *Taxus brevifolia* var. **brevifolia**

Common name.—Pacific yew.

Tree, *reproducing by adventitious shoots* from trunks or roots, 6–13(–25) m tall, bole to 60(–130) cm diam.; branches horizontal to upwardly ascending, sometimes drooping near ends, dividing more unequally than equally, yellowish orange to reddish orange, or maroon; bud scales persistent on 2nd–3rd yr branchlets, conspicuous, 2–3 seriate, paleaceous, chartaceous, closely to loosely adnate, plane to slightly concave, indurate, brownish, 1–1.5(–2) mm long. *Cone scales forming a basal hemispherical cup*; male cones ellipsoidal in bud, 4 mm long, 2 mm wide; *sporangia exerted*. Seed on 1st or 2nd yr or older branchlets, *longer than the pedunculate axis*, rounded, slightly 2–4 angular, ellipsoid to ovoid, tapering to apex from mid region, or rather abruptly near apex, 5–8 mm long, to 4 mm diam.; aril red, reddish orange, yellowish orange, or rarely yellow, Aug–Sep.

1b. *Taxus brevifolia* Nutt. var. *polychaeta* Spjut, var. nov. (Fig. 11). TYPE: U.S.A. WASHINGTON. Thurston Co.: Mud Bay, near Tacoma, 3 Sep 1938, E.G. Meyer 1589 (HOLOTYPE: K!).

Ab var. *brevifolia*, strobili elongati, lumbriciformis, squamae persistentibus.

Similar to *T. brevifolia* var. *brevifolia* in habit, differing by the longer seed cones; the seed appearing stipitate, seed shorter than the long crooked cone axis (stalk) in the type, cone scales persistent; male cones elongate with scales persistent to near apex.

Common name.—Worm-cone yew.

Distribution and ecology.—California (Mendocino Co., Sonoma Co.), Washington (Thurston Co. near Mud Bay and Tacoma), Idaho (near Coeur d'Alene); observed to be rare in a redwood-grand fir-nutmeg forest in Sonoma Co., California.

Additional specimens. **CALIFORNIA. (Marin, Sonoma, or Mendocino Co.):** 1854, *Bigelow s.n.* (US); Salmon Creek (Sonoma or Mendocino Co.?), *McMurphy 315* (US). **Sonoma Co.:** near Mendocino Co. line, 7 km E of Stewarts Point, *Rich Spjut & Rick Spjut 16021* (BM, BRIT, E. GH, K, US, wba). **IDAHO.** Without collection data, US Forest Service, received from Marion Blatch, Coeur d'Alene Nursery, 26 June 1992 (wba).

Variety *polychaeta* is distinct for its elongate, worm-like cones. The California specimens have shorter cones than those specimens from further north—coastal Washington (type) and from near the Idaho/Washington state line. In var. *reptaneta*, female cones may appear similarly elongate on older branchlets, while both male and female cones on younger branchlets appear typical of the species. This is in further contrast to the male specimen of var. *polychaeta* collected by John Milton Bigelow from California.

A specimen of var. *polychaeta* that was collected by James Ira McMurphy (1871–1943), who had lived in Mendocino County, mentions only Salmon Creek; it may have been from the town of Salmon Creek just



FIG. 11. Close-up of branchlet of *Taxus brevifolia* var. *polychaeta* showing three wormlike cones, one with seed; near Tacoma WA, Fred Meyer 1589 (holotype, K).

north of Bodega Bay in Sonoma Co., or from west of the town along Salmon Creek itself, or possibly from Big Salmon Creek just south of Albion along the Mendocino coast, or another more inland site in Mendocino County where there is a Salmon Creek ca. 12 km E of Willits in the Mendocino National Forest. A recent plant inventory of Big Salmon Creek does not include yew (Chanslor Wetlands Wildlife Project, website accessed 2006), although this area had been logged.

In any case, the coastal occurrence of yew in California is rare. One record for Sonoma County was by Milo Baker from near Annapolis where populations have since been reported from nearby Fuller Creek and its north-facing drainages; however, in a brief survey of this area we were able to find only the one tree; which belonged to var. *polychaeta*; it was growing next to *Torreya californica* Torr. in a redwood forest (Rich Spjut & Rick Spjut 16021). John Bigelow was also known to have collected in Marin, Sonoma, and Mendocino counties (CNPS, Marin Chapter, website); thus, the McMurphy specimen of var. *polychaeta* was probably collected just north of Bodega Bay in view of our find (Spjut & Spjut 16021), which also seems significant in regard to 18 endemic taxa that are recognized for Sonoma County (Best et al. 1996). Another report for southern Mendocino County indicated that yew is rare in a ravine on Sea Ranch; however, this area was reportedly logged in early 1900s and early 1990s; thus, yew may once have been more common there. It is of interest to note the plant associations of two rare disjunct taxa of closely related yew in the United States that include both US species of *Torreya*, one in California (*Torreya californica*) that is first reported here with *Taxus* in a redwood forest region, and the other in Florida (*Torreya taxifolia*) in a white cedar forest as described in more detail under *T. globosa* var. *floridana*.

A duplicate specimen of F.G. Meyer 1589 at the Smithsonian Institution (US) is not considered an isotype because the seed cone in this specimen is typical for *T. brevifolia*. This may lead one to question whether cone development in var. *polychaeta* is some sort of aberration within the 'normal' population; however, both male and female cones of *T. brevifolia* var. *polychaeta* show the morphological feature of elongated cones.

Also, most collections of var. *polychaeta* appear coastal. Molecular differences have been reported between coastal and inland plants of *T. brevifolia* (El-Kassaby et al. 1994, 1995), which included a distinct genotype on Vancouver Island in contrast to other yew populations studied in British Columbia.

1c. *Taxus brevifolia* Nutt. var. *reptaneta* Spjut, var. nov. (Figs. 12–13). TYPE: U.S.A. CALIFORNIA. Siskiyou Co.: near corner of Humboldt and Trinity Cos., Salmon Mts., 1 mi E to SE of Salmon Mt., near the NW corner of the Trinity Alps Wilderness boundary, Klamath Natl. For., 19 mi S of the town of the Forks of the Salmon on McNeal Creek Rd, West Fork of Knownothing Creek, ca. 1250 m, along N-facing slopes of ravine in mixed evergreen forest of Douglas fir, white fir, ponderosa pine, tan oak, snowbush, dogwood, hazelnut and big-leaf maple, shrub with long scandent stems ascending to 5 m or more, stems layering, forming thickets, both male and female plants present, occasional male cones with pollen, female cones with seed but mostly without fleshy aril, one with pale yellowish aril, 11 Sep 1990, R. Spjut & T. Spjut 11835, with seed (HOLOTYPE: US!; ISOTYPES: BM!, BRIT!, EI!, GH!, KI!, WBA!).

Differt a var. *brevifolia* frutex caulibus ascendentibus, ramis reptantibus, 0.3–5 m altis, propaginis, faciens dumetia.

Rhizomatous (layering) shrub with decumbent to ascending or contorted trunks, to 5 m high, typically forming dense impenetrable thickets on open steep, narrow ravines, or more distantly spaced, either as low creeping shrubs or arborescent in understory on slopes or in valleys with coniferous forests. Leaves similar to var. *brevifolia*, often darker and duller on upper surface, slightly revolute along margins, more densely papillose on abaxial midrib with papillae in 3–4 rows on each cell; midrib appearing more elevated, often ca. 18 cells wide; stomata often in 4–6 regular rows per band. Male cones abundantly produced, ovoid in bud, 3 mm long and 2 mm wide, scales ca. 5 in series; sporophylls ca. 8, united into a column ca. 2 mm long, umbrelliform above, each with 5 microsporangia (0.9 mm diam.). Female bud cones ca. 1 mm long, scales overlapping, ca. 5 seriate; seed maturing on 1st or 2-yr growth; rounded, ellipsoid to ovoid, 6–8 mm long, 4 mm diam., often without fully developed aril. Aril red, reddish orange, yellowish orange, or rarely yellow, maturing Aug–Sep.

Common name.—Thicket yew.

Distribution and ecology.—Rocky Mountains in British Columbia, Idaho and Montana; E Cascades in Oregon and Washington; Klamath Mountains in Oregon and California; scattered or forming dense thickets on steep sunny slopes of avalanche shoots, along streams, or in dense shade of valley forests, 1000–2000 m; in the Siskiyou Mountains occurring regularly between 3500 and 4000 ft on N to E slopes; probably in the Coast Ranges, Oregon to British Columbia (Arno & Hammerly 1977), reported also from the Cascade Ranges in California, near Mt. Shasta (Bolsinger, pers. comm. 2007).

Additional Specimens: **CALIFORNIA. Siskiyou Co.:** Klamath Natl. For., Marble Mountain Wilderness, Lake-of-the-Island, 1722–1820 m, forming thickets, mostly male plants on open talus and steep rocky slopes, or one female thicket observed on level soil in forest understory along lake shore, in association with red fir, mountain hemlock, western white pine, incense cedar and other conifers, Spjut 16013–16015 (BRIT, GH, US, wba). **MONTANA. Lincoln Co.:** near northern panhandle of Idaho, Kootenai National Forest, Libby Mt., Snowshoe Mine Rd, T28N R31W Sec. 5, 48°12' N, 115°38.34' W, 3287 ft, Spjut & Deevy 12303 (wba); **Flathead Co.:** Flathead Natl. For., 4 mi N of Columbia Falls, Spur For. Rd 316G (Canyon Creek Rd), ½ mi W of jct. 316 and 316 G, T31N R20W Sec. 9, 3800 ft, 48°28' N, 114° 10' W, 3491 ft, with subalpine fir, grand fir, white pine, red cedar, hemlock, aspen, larch, plants predominantly male, Spjut & Donner 12306 (US, wba). **OREGON. Clackamas Co.:** Mt. Hood Natl. For., ca. 4 mi. N of Timothy Lake, FS Road 58 to Little Crater Lake, ca. 0.5 mi from jct. with RS Road 42 (Skyline Drive), ravine or basin forest, 121°43' W, 54°08.59' N, 3400 ft, Spjut 12301 (US, wba). **WASHINGTON. Chelan Co.:** N Cascades: Wenatchee Natl. For., Icicle Creek drainage, 18 mi W of Leavenworth, Black Pine Horse Camp, scattered, somewhat scandent, at base of conifer trees in old growth forest of Douglas fir, grand fir, western white pine, and Englemann spruce, and also forming thickets locally on flats or gentle slopes, 47°36' N, 120°56' W, 3050 ft, Spjut 12302, 12101 (US, wba).

Taxus brevifolia var. *reptaneta* is recognized by its layering habit; however, as with *T. canadensis*, the layering branch may die and rot away, leaving the individuals solitary (Bannan 1942). Plants vary in size, density and branching, but trunks are similar in their ascending form (Fig. 13). In the typical habitat—along steep open ravines—distinct trunks develop to 50 cm or more in diameter and grow within 1 m of each other, each bearing many divaricate branches that are often longer than the main trunk. The collective growth forms impenetrable thickets, hence the epithet *reptaneta*. In more shaded environments—as in the eastern Cascades of Washington—plants are less crowded and sometimes exhibit a peculiar growth in that individuals sprawl around the base of trees such as Douglas fir, occasionally twisting and wrapping around its trunk. In the Rocky Mountains other shrub forms grow less than 50 cm high, creeping along the ground



FIG. 12A–B. *Taxus brevifolia* var. *reptaneta*, seed and mature male cones, Klamath Mts., CA. A (top). Herbarium specimen in part, showing persistent scales at base of branchlets, abaxial surface of leaves with recurved margins, and seed without fleshy aril; near Salmon Mt., *R. Spjut* & *T. Spjut* 11835 (isotype, wba). B (bottom). Close-up of branchlet with mature male cones; N-facing slope above Lake-of-the-Island, Marble Mt. Wilderness, *Spjut* 16013 (wba).



FIG. 13A–C. Habit of *Taxus brevifolia* var. *reptaneta*. A (top). Eastern slopes of the Cascades, E of Portland, OR, growing on fairly level ground in forested valley, trunks sharply ascending near base. B–C (bottom). Rocky Mts., NW Montana, Libby Mt. B (bottom left). Massive prostrate trunk pointed to by the USDA Forester David Deevy. C (bottom right). Shows the numerous old trunks of yew as they grew, defoliated and debarked for extraction of the anticancer chemical taxol (paclitaxel).

much like some *T. canadensis* of northeastern North America. Yew thickets may be male or female, but male thickets were observed to be more common.

In the Klamath Mountains of California, I have observed thicket yew to occur predictably in steep ravines and on steep banks with a north to northeast exposure at elevations from 1000–1200 m; however, I have also found it at higher elevations in the Marble Mountain Wilderness such as near English Peak (1720–1820 m, Lake-of-the-Island, *Spjut 16013*). It is interesting that the typical variety generally occurs at higher and lower elevations in the California Klamath Region (e.g., 450 m, E fork of Willow Creek, *Terrell et al. 4170*; 700 m, Tannery Gulch, Trinity Lake, *Spjut 10179*; 1500–2000 m, Marble Mt. Wilderness near Lovers Camp, *Spjut 10721*). Many of the more northern locations of var. *reptaneta*—in Oregon and Washington—are at slightly

lower elevations, corresponding to the more northern latitude occurrences. These observations suggest that var. *reptaneta* is a distinct ecotype within the range of var. *brevifolia*.

Other shrub forms in the Rocky Mountains of Canada are also evident. A specimen from the Selkirk Range (British Columbia) differs by broader (oblong) clasping leaves with a pale glaucous green color on the adaxial surface, while other leaves on the same plant are narrower and linear on what appears to be a layering branch. Another growing on steep exposed rocky cliffs near Golden (British Columbia) has ascending stems from a burl-like base. In further study these plants, which are considered here as belonging to var. *reptaneta*, may prove to be new varieties.

Eight samples of var. *reptaneta* were collected from California, eastern Cascades in Oregon and Washington and from the Rocky Mountains in northwestern Montana to determine whether differences in taxoid content were correlated with tree and shrub varieties of *T. brevifolia* (Spjut et al. 1993). The taxoid content was most similar in samples that were also most similar morphologically, which were from northwestern Montana and northern California (type locality for var. *reptaneta*), in comparison to samples of var. *brevifolia*. These plants differed from those at other locations by the darker green thick leaves and by an abundance of male cones on branchlets of the current season.

2. *Taxus florinii* Spjut, sp. nov. (Fig. 14). TYPE: CHINA. YUNNAN: Litiping between Likiang and Weihai, tree 17 ft, in mixed forests by stream, 11 Oct 1939, R.C. Ching 21980 (HOLOTYPE: A!, stomata 10 rows per band, abaxial marginal zone 5–6 cells across, the cells thick-walled).

Similis a *T. wallichiana*, praecipue differt foliis decrescentes stomata et latis marginali, 7–12 seriata/zona.

Shrub or tree to 13 m high; young branchlets yellowish green, abruptly changing to reddish purple in 2nd yr; bud-scales persistent on 1–2 yr branchlets in most specimens, 2–3 seriate, deltoid, concave, ca. 0.3–0.5 mm long, obscurely to prominently carinate, closely attached. Leaves arranged ±distichous, homomallous, linear-lanceolate, acuminate, straight to falcate, 1.5–3.5(–4.7) cm long, 2.0–4.0 mm wide, 200–350 µm in thick, dark glossy green above (dried leaves, similarly noted by collectors on fresh specimens), glaucous to yellowish green below (in dried specimens, also noted as yellow green in field), slightly convex above (adaxial) to a rounded midrib, channeled along each side below mid region to base, less concave below (abaxial) to a flush to slightly rounded midrib, margins plane to slightly revolute; adaxial epidermal cells nearly quadrate in transverse section, occasionally taller than wide, 20–50 µm tall, 20–40 µm wide; abaxial epidermal cells narrower and not as tall as upper along midrib and marginal regions, rounded to partly angular in transverse section, 5–12 µm tall, 15–25 µm wide, numbering 16–20 across marginal region, trapezoidal to short rectangular, 1–3× l/w near margins, longer nearer stomata bands, 3–5× l/w, and on midrib, 5–10× l/w; papillae lacking near margins on 2–10 cells across, positioned more marginally than medially on midrib in 1–2 alternating rows, medially to marginally on accessory cells, and along cell walls in marginal zone; stomata bands narrower than marginal zones; stomata in 7–12 rows per band. Male cones maturing on 1st and 2nd yr twigs, subcylindrical in bud, 3 mm wide, 4 mm long, yellowish green, the scales 4–5 seriate; microsporangia 5–6 on each sporophyll, pinkish, spongy. Female cones initiating on current season growth, subcylindric in bud, 2–4 mm long, maturing 1st and 2nd yr, or on much older branchlets in one specimen, the scales 5–6 seriate; seed ovoid to globose, to 5 mm long, 5 mm diam., pale (yellowish) in color, sharply pointed at apex, covered in part by red aril, Aug.

Common name.—Florin yew.

Distribution and ecology.—Endemic to China (Xinjiang Uygur, Sichuan, Yunnan); forest or pasture or along streams, 2500–3700 m.

Additional specimens. **CHINA. Sichuan.** Handwriting illegible, 3500 m, *Schneider 1429* (K); Ngaitaschekou trans flumen Yalung ad septentr oppodi. Yenyüen, 28°15'N, 2800–3500 m, *Handel-Mazzetti 2602* (K); Shalie Valley on Muzhiyan Shan above Old Muli, Muli country, ca. 2980 m, frequent in narrow, steep SW facing gully, tree to 5 m, leaves dark green above, yellowish green below, *Fliegner et al. 1129* (K). **Xinjiang Uygur (“SoC.W. Sikiang”):** “NW Yunnan,” Tamichung, tree 20–30 ft, in fr., open pasture, R.C. Ching 21505 (A). **Yunnan.** NW, Mt. Fo Ludu, NW of Li-Kiang, W of the Yangtze, J.F. Rock 18502 (A, US); mostly illegible, 3000–3200 m, C. *Schneider 2918* (A, K); no locality data, T.T. Yu 11076 (A); Dokerla, 3100 m, Yu 7848 (BM); Litiping Range, Mekong-Yangtze divide, E of Weihsi,

J.F. Rock 11573 (A, US); Sikang, Me-kong, Tsa-wa-rung, 2500 m, C.W. Wang 65475 (A); Mekong-Salween Divide, Forrest 19967 (S: C-2084); S Chungtien, Kung-shiang-shu, Snow Mt on the way to Kai-Lou-wei, on Yangtze bank, 2700 m, by stream in wooded side of valley, tree 20 ft, K.M. Feng 3235 (A); same locality, 3200 m, in mixed forest, shrub 15 ft, in fruit, K.M. Feng 1809 (A); Wei-si Hsien, 2500 m, forest, C.W. Wang 67735 (A); Zhongdian, Haba Shan, 27°22'28 N, 100°05'50 E., 3347 m, *Alpine Garden Soc. Exped.* 309 (K).

Taxus florinii is recognized by the leaves having tall angular epidermal cells and narrow stomata bands relative to a broad region of marginal cells, the stomata usually in 7–12 rows per band. As in *T. brevifolia*, the Florin yew is variable in the number of leaf marginal cells that lack papillae on the abaxial surface, ranging from 2–16 cells across.

Specimens of Florin yew with fewer than 10 stomata rows per band are easily distinguished from related species in Asia, but not necessarily from those in North America; *Schneider 2918* from Sichuan, for example, is similar to *T. brevifolia* in the leaves having 7(–9) stomata rows per band bordered by short broad irregularly shaped epidermal cells in the marginal zone, whereas *Handel Manzzetti 2602*—that is also from Sichuan—has 11 stomata rows per band—and is not easily distinguished from *T. globosa*. Thus, *T. florinii* and *T. brevifolia* could be included under *T. globosa*. However, the American species generally differ by their pale yellowish green branchlets and by the more strongly convex adaxial leaf surface—especially towards leaf apex, in contrast to the dark purplish (rarely orange) branchlets in the 2nd yr and more plane leaves of *T. florinii*. Other apparent differences are the midrib epidermal cells in T-section that in *T. florinii* appear smaller, thicker-walled and less angular on the abaxial surface than the adaxial surface, whereas in the American species there seems to be less difference in the size of the epidermal cells between the two leaf surfaces as seen in the midrib region.

Etymology.—The epithet is in honor of Rudolf Florin who published extensively on taxads based on leaf anatomical characteristics. Despite his controversial ideas on taxad evolution—such as proposing that they be treated in a new class—I have found his reviews and data to be of great value.

3. *Taxus globosa* Schltld., *Linnaea* 12:496. 1838. (Figs. 3, 15). *Taxus baccata* L. subsp. *globosa* (Schltld.) Pilger, *Planzenreich* 18 (iv, 5):114. 1903. TYPE: MEXICO. HILDAGO: Real del Monte, Cerro de las Nabajas, [Sep] 1837, *Ehrenberg s.n.* (LECTOTYPE designated here: ex Museum botanica Berolinense (K!); ISOLECOTYPES: L, S, US!). No specimens cited, original material at B destroyed. Parlotore (1868) cited an Ehrenberg collection with number from the type locality, *Ehrenberg 817*, which may be at FI.

Taxus globosa is characterized by leaves having quadrangular epidermal cells as seen in transverse section, stomata in (5–)7–11 rows per band, and alternately arranged papillae along cell walls. Higher counts of stomata, 9–11 rows per band, were found in specimens from Central America and southern Mexico, compared to lower counts, 5–7 rows per band seen more in specimens from the northern range in Mexico and in the Florida panhandle (Spjut 2007). The abaxial leaf margins vary from 2–5 cells across (without papillae) except for one specimen from Veracruz, while all five specimens from Florida have a slightly broader marginal (epapillose) region, 5–9 cells across.

The species is traditionally known to occur from Mexico to Honduras; however, at the northern-most range in Mexico, specimens are difficult to distinguish from those in Florida; therefore, the Florida yew is



FIG. 14. *Taxus florinii*, Herbarium specimen in part, showing seed on 1st yr branchlet; Yunnan, China, Rock 18502 (US).



FIG. 15. Herbarium specimen in part, *Taxus globosa*, Ehrenberg s.n. (lectotype, K).

reduced to variety of *T. globosa*.

3a. *Taxus globosa* var. *globosa*

Common name.—Mesoamerican yew.

Distribution and ecology.—S Mexico (Veracruz, Hidalgo, Mexico, Oaxaca), Guatemala (Baja Verapaz, El Progreso [Sierra de las Minas, Volcán de Santa Luisa], Zacapa [Volcán Gemelos, Monte Virgen] Huehuetenango [Sierra de los Cuchumatanes, Cerro Cananán]) to British Honduras (Merrendón, San Idalfonso, Omoa, Montecillos, Opalaca, Congolón) and El Salvador; montane cloud forests above 2,000 m.

3b. *Taxus globosa* Schldl. var. *floridana* (Nutt. ex Chapm.) Spjut, comb. nov. (Figs. 4, 16). *BASEONYM*: *Taxus floridana* Nutt. ex Chapman, Fl. South. U.S. 436. 1860. *Taxus baccata* L. subsp. *floridana* (Nutt. ex Chapm.) Pilger, Pflanzenreich 4(5):113. 1903. *Taxus canadensis* Marshall var. *floridana* (Nutt. ex Chapm.) Silba, Phytologia Mem. 7:72. 1984. *TYPE*: U.S.A. FLORIDA: near Aspalaga, 1833, Croom s.n. (LECTOTYPE designated here: PH!). No specimens cited in original description. According to Sargent (1896), the Florida yew was first discovered by Hardy Croom in 1833 near Aspalaga. He further stated that “[t]he first notice of this, without description or specific name, was published in 1834 in the American Journal of Science (xxvi. 314)...It was next mentioned by Nuttall in 1849 (Sylva iii: 92) who doubtfully attached to it the name of *Taxus montana* [synonym for *Torreya taxifolia*], although Croom’s specimen in the herbarium of the Philadelphia Academy was, he says, marked *Taxus floridana*, the name adopted by Chapman when the species was finally described in 1860.” A specimen at PH was found with label in what appears to be Nuttall’s handwriting bearing the name *Taxus floridana*, indicating it was collected by Croom. However, another name, *T. croomii*, had been proposed, evidently by Chapman with reference to a Chapman list (1845 fide annotation by K. Wurdach, 1987, specimen at PH) as seen on other specimens from C.W. Short (PH), Bentham Herbarium (K), Herbarium Careyanum (K), all of which may represent original material. Chapman indicated that Nuttall was the source for the epithet; the specimen at PH bearing the name *T. floridana*, therefore, was selected as lectotype. The type material for the 1860 edition of the flora by Chapman reportedly went to Columbia University, which is now at NY (Stafleu & Cowan 1976), but no possible type specimens for *Taxus* from Chapman are currently listed among the types at NY (virtual herbarium).



FIG. 16. *Taxus globosa* var. *floridana*, close-up of branchlets and leaves of a herbarium specimen; handwritten notations on a label "*Taxus croomii*" Chapman List, Florida (original material, K).

Common name.—Florida yew.

Distribution and ecology.—N Mexico (Nuevo Leon, Tamaulipas, Veracruz), W Florida (rare, Apalachicola River; *Chamaecyparis* swamp ca. 8 mi SE of Bristol).

The Florida yew, which differs by the abaxial leaf surface having a broader marginal area of nearly rectangular epidermal cells with less prominent papillae, occurs in northern Mexico and in the panhandle of Florida. In Florida it is found not much above sea level on bluffs and in ravines along 15 miles of the Apalachicola River in a mixed evergreen forest of *Fagus grandiflora* Ehrh. and *Magnolia grandiflora* L. with *Torreya taxifolia* Arn., *Kalmia latifolia* L., *Quercus laurifolia* Michx., *Pinus glabra* Walter, *Ilex opaca* Aiton, *Symplocos tinctoria* (L.) L'Hér., and *Vaccinium elliotii* Chapm., and locally in a white-cedar (*Chamaecyparis thuyoides* [L.] Britton, Sterns & Poggenb.) swamp eight miles southeast of Bristol (Kurz 1937). In northern Mexico, it occurs between 2000 and 2500 m, which is at lower elevations than generally reported for the typical variety.

The Florida yew has allegedly retained the ancestral features of leaf epidermal papillae on the midrib, and the angular isodiametric epidermal cells (as seen in T-section), contrary to what might be expected for yew growing in a seasonally hot and humid climate at relatively low elevations. An example is *Taxus mairei* in mixed mesophytic forests of southern China; it lacks papillae on the abaxial midrib and has elliptical epidermal cells (T-section). Variety *globosa*, occurring in a subtropical montane forest with less seasonal variation in temperature and precipitation, shows only minor differences in numbers of leaf stomata rows and marginal cells compared to var. *floridana*. Perhaps there was not enough time for the Florida yew to have evolved significant morphological differences between the oscillating periods of climate change during the Pleistocene, or perhaps introgression has occurred between formerly distinct ecospecies, one found along the Gulf coastal plain and another in the upland areas. The overlap of key morphological features at the northernmost range of the species in Mexico would seem to indicate former contact in that region between two ecotypes, whereas the plants of limited occurrence in Florida are viewed here as relicts barely surviving instead of adapting to the present climate.

4. *Taxus suffnessii* Spjut, sp. nov. (**Figs. 1, 17**). TYPE: MYANMAR. North Triangle (Wring Burma above Ahkail), 9000–10,000 ft, in forest and thickets, young leaves bronze, shrub or small tree, 24 May 1953, *Kingdon Ward 20902* (HOLOTYPE: A!, with seed; leaf with 12–13 stomata rows/band; ISOTYPE: BM!, leaf with 16 stomata rows/band, lacking papillae across 2 marginal cells).

Arbor vel frutex similis a *T. wallichiana*, praecipue differt perulae persistens ampliatis, ovatis, 2–3 mm longis, folia oblongas ad leviter ellipticas, 1.5 cm longis, 3.0 mm latis, supra cellula epidermibus ca. 50–60 µm altis, ca. 50 µm latis.

Tree or shrub; branchlets unequally divided, gray to purplish on older growth; *bud scales* 3–4 seriate, persistent to the 3rd yr or longer, paleaceous, indurate, grayish, deltoid, closely to loosely adnate, lower scales concave with a distinct midnerve, uppermost scales slightly cuspidate and aristate, ca. 3 mm long and 2 mm wide. *Leaves* lacking on older twigs, nearly two-ranked, overlapping slightly, *oblong to slightly elliptical or widest above the mid region*, straight, mostly ca. 1.5 cm long, 3.0 mm wide, 250–350 µm thick, bronze to blackish green and concave above to a rounded or acutely keeled midrib, yellowish green and convex below to a rounded keeled midrib, abruptly revolute near margins. Adaxial epidermal cells quadrangular in T-sect., or taller than wide, to 60 µm tall and 50 µm wide; abaxial non-stomata epidermal cells not as large, 12–25 µm high and wide, quadrangular, papillose to near leaf margins; papillae prominent, globose, in 3–4 rows, notably medial on marginal cells and marginal on midrib cells or equally developed on accessory cells in a stellar arrangement; stomata 12–20 rows per band. Male cones not seen. Female cones maturing on current season growth, scales overlapping in 5–6 ranks; seed appearing succulent or deformed, conical, dark colored with notable yellowish neck, ca. 3 mm long, 1.5 mm wide.

Common name.—Suffness yew.

Distribution and ecology.—E Himalayas: Endemic to Myanmar; 1950–3048 m.

Additional specimens. **MYANMAR. Upper Burma:** Hkyet, 27°45' N, 97°50' E, 9000–10,000 ft, *Kingdon Ward 13003* (BM); Myintkyina, Sumprabum, 8600 ft, *Hla & Koko 4028* (K); W Central Esakan, 6400 ft, in thick forest, *Kingdon Ward 21901* (A).

Taxus suffnessii stands apart from other species of *Taxus* in many features. These include the relatively large

tall-rectangular epidermal cells, the large persistent bud-scales with a distinct mid nerve, prominent papillae on the abaxial surface of leaves extending nearly to the margin, a relatively broad leaf shape—appearing widest above the mid region, and leaves not spreading in one plane along two sides of a branchlet. Although the number of stomata rows varies from 12–20, the highest number of stomata rows seems related to the papillose cells extending to the leaf margin, or within 2 cells from the margin; essentially, the stomata band covers the entire abaxial leaf surface. The poorly differentiated stomatal bands would, therefore, seem to be an ancestral trait.

The Suffness yew is similar to *T. wallichiana* that differs by the smaller, more polished, nearly nerveless bud-scales and sometimes by the older reddish orange branchlets as seen in the typical variety from northeastern India, in contrast to a purplish color in the Suffness yew; however, intermediates are apparent. Examples are *Kingdon Ward 21901* from West Central Myanmar (at “6400 ft”) and *Beer 25316* from Nepal (above Sedua, 9400 ft). They have fewer and slightly smaller bud-scales at base of branchlets but still show the characteristic midnerve, while they also differ by having longer (linear) leaves. *Kingdon Ward 21901* (BM) is referred to *T. suffnessii* by the entirely papillose abaxial leaf surface (Spjut 2007). The specimen from Nepal, however, is identified *T. aff. wallichiana* (Spjut 2007), while similarity to *T. suffnessii* is further evident by the tall-rectangular epidermal cells in leaf transverse sections in contrast to what is generally seen in *T. wallichiana*. The relatively large epidermal cells are a striking character feature of *T. suffnessii* and also other species such as *T. florinii* and *T. brevifolia*. The extent to which this character can be further employed to differentiate species of *Taxus* needs further study.

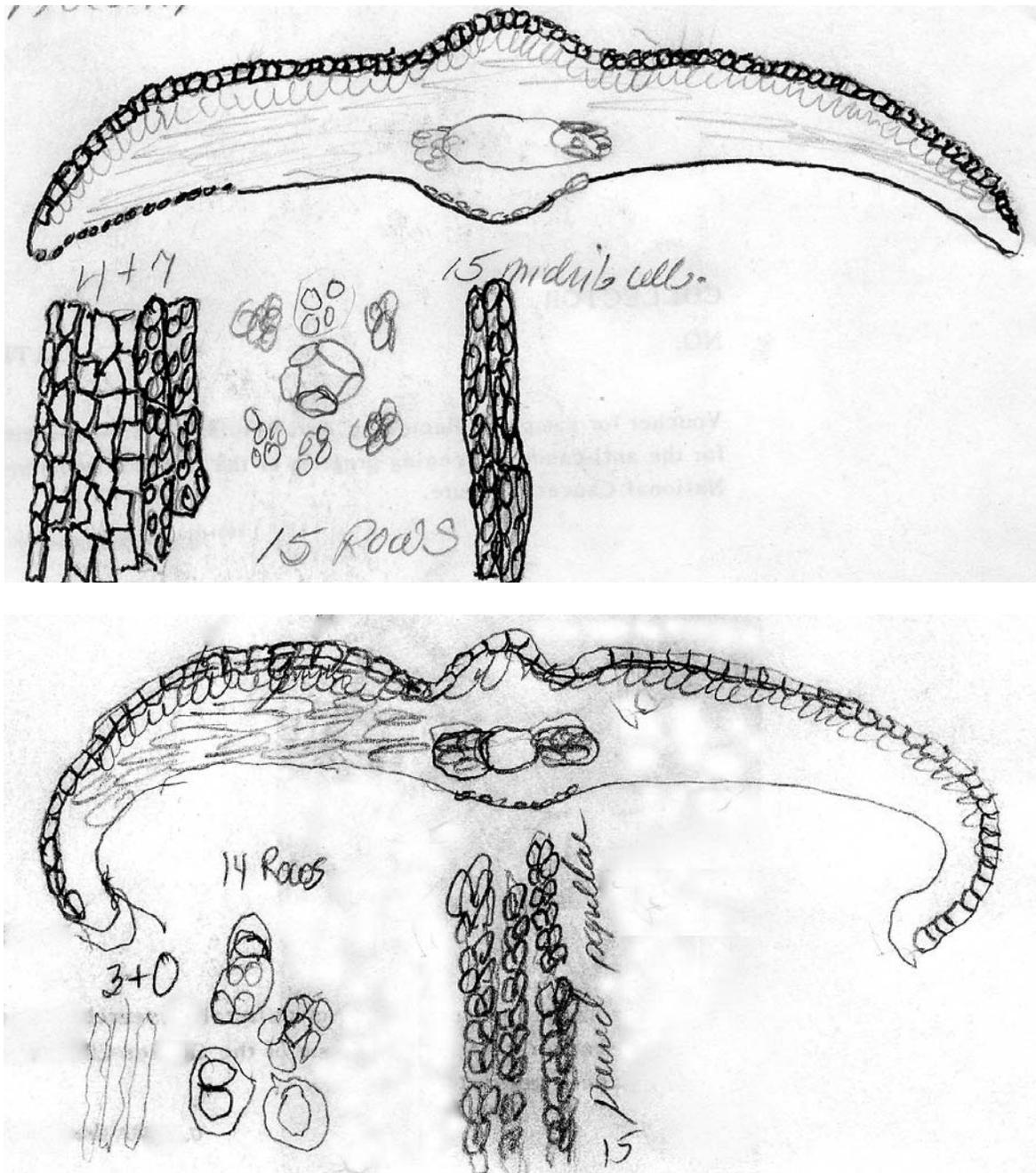
Taxus suffnessii is named in honor of the late Matthew Suffness in recognition of his dedication to screening natural products in the search of new drugs to treat cancer and of the strong encouragement I received from him in this endeavor. He became Chief of the Natural Products Branch in the National Cancer Institute after Jonathan Hartwell retired in 1976, following a brief leadership by John Douros. In 1986, Dr. Suffness became more involved in extramural contracts, often serving as consultant to various drug discovery groups. He focused on identifying novel leads that showed promise for development as new anticancer drugs, one of which was taxol. It is ironic that a major compilation on taxol research to which he served as sole editor (Suffness 1995) would not appear until just after his death from cancer in the spring of 1995.

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5. *Taxus wallichiana* Zucc. in Siebold & Zucc., Abh. math.-phys. CL.K. Bayer. Akad. Wiss. (München) 1 (3):803, Tab. 5. 1843. (Figs. 18–21). *Taxus baccata* L. subsp. *wallichiana* (Zucc.) Pilger in Engler, Pflanzenreich IV (5):112. 1903. *Taxus baccata* var. *wallichiana* (Zucc.) C.K. Schneider ex Silva Tarouca, Freiland-Nadelgehölz. 276. 1913. No specimens cited by Zuccarini, but he provided an illustration with reference to another earlier illustration in Wallich (1826, *Tentamen florae Nepalensis* 57, Tab. 44), Wallich’s name “*Taxus nucifera*?” (excluding synonyms) and Wallich’s observations that the species occurred in mountains around Sheopore [Shivapuri], Kathamadu, Nepal). Original material at M includes four specimens from Wallich and/or his collectors:



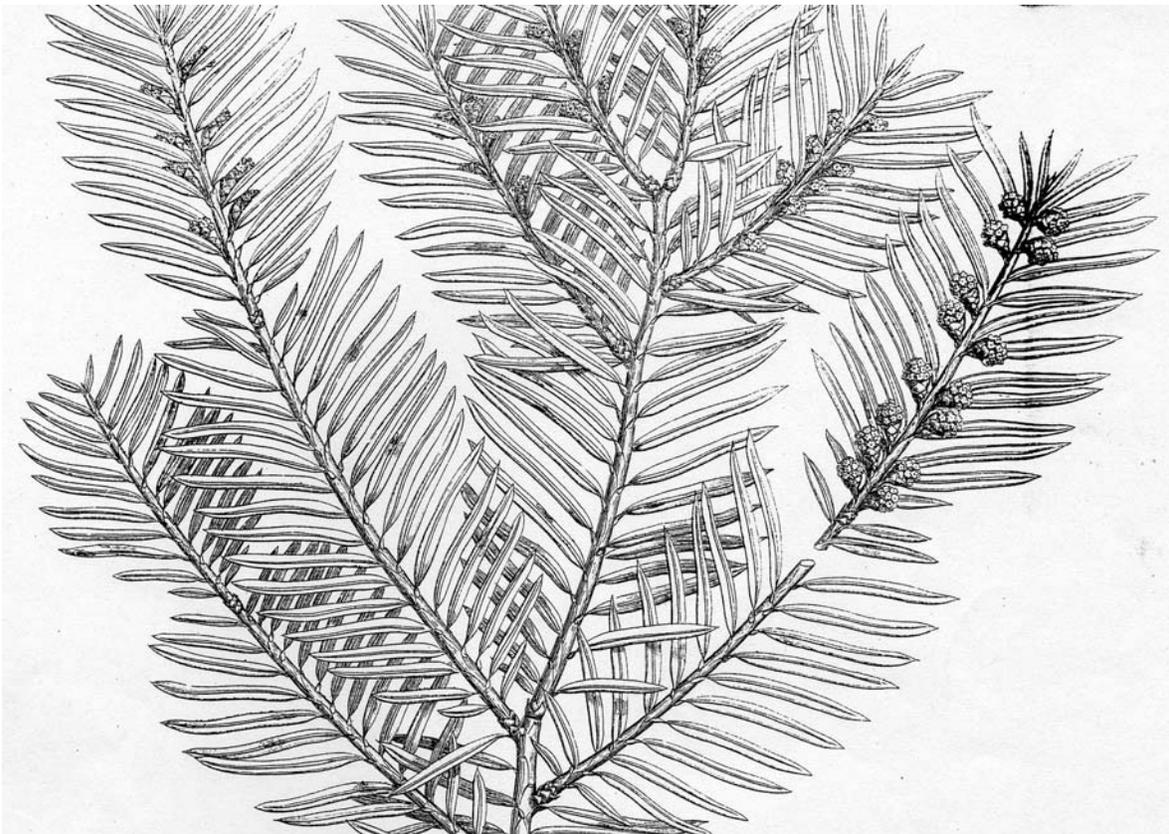
FIG. 17. *Taxus suffnessii*, branchlets showing slightly elliptical leaves and characteristic persistent scales at base; Myanmar, *Kingdon Ward 20902* (holotype, A).



FIGS. 18–19. Scanned images from sketches on 9×12 cm specimen packets showing leaf cross sections and abaxial epidermal sections in the mid region of a leaf for two varieties of *Taxus wallichiana*. 18 (top). Var. *wallichiana*, Bhutan, Ludlow & Sherriff 1234 (BM), shows abaxial leaf surface to have 4 rows of irregularly quadrate to rectangular cells without papillae followed by 7 rows of epidermal cells that are slightly larger, somewhat rectangular with alternate papillae, and indicated to have 15 rows of stomata and a midrib of 15 cells across with alternate papillae. 19 (bottom). Variety *yunnanensis*, Sikkim, J. D. Hooker (K), indicating abaxial marginal zone has three rows of long cells without papillae, followed by 14 rows of stomata, without a region of papillose cells. Midrib cells shown to have erect opposite papillae. The revolute leaf margin as seen from the leaf cross section shown for var. *yunnanensis* is also a feature that is more common to that variety.



FIGS. 20–21. Original material of *Taxus wallichiana*. 20 (left). Lectotype, *Wallich s.n.*, E India (M) showing branchlets, abaxial surface of leaves and mature male cones. 21 (below). Illustration in Siebold & Zuccarini (1843, Tab. 5).



(1) Wallich s.n., year 1835, eastern India; with Herb. Zuccarini label, (2) [Wallich] 6054A on label from Schultes, indicated to be from Kumaon but most likely from Nepal (see East India Co., *Numerical list of dried specimens collected under the superintendence of Dr. Wallich* [1828–1849]; determined by Spjut as *T. wallichiana*), (3) [Wallich] 6054/a from Nepal, ex Herb. Hort. Bot. Calcuttensis (determined by Spjut as *T. contorta*) and (4) [Blinkworth] 6054B from Kumaon (determined by Spjut as *T. contorta*). LECTOTYPE designated by Spjut in adnot., 23 March 1995 and here: INDIA: eastern, *communicavit Wallich, year 1835—Wallich s.n.* (M!) with mature male cones, and label “Herb. Zuccarini” Among the specimens at M, the lectotype is also the best match for the illustration in Siebold & Zuccarini (1843)—a photocopy reproduced here (Fig. 21). Additionally, two of the four specimens at M that bear Wallich numbers 6054/a and 6054b appear to have the wrong labels attached (or reversed) based on study of Wallich duplicates at other herbaria (GH, K, NY, P, PH, S); however, only one specimen is clearly associated with Zuccarini’s study of *T. wallichiana* (Siebold & Zuccarini 1843), the lectotype. Duplicates of Wallich 6054A, which might be equivalent to isosyntypes (indicated as type below), are detailed as follows
by institution: **GH:** label with handwriting similar to Wallich, “*Taxus nucifera* Wall.” “Napalia.” s.n. **K:** Four sheets. (1) with two specimens, the larger specimen has a pasted label below it with handwriting “6054a” and no indication of locality data, the smaller one is a single branch with mature seed, correctly annotated *T. wallichiana* by S. G. Harrison, but it is not 6054A, or not a type since it is not from a male plant; (2) two specimens, one large specimen with an imprinted stamp nearby—Herb. Hookerianum, with handwriting similar to Wallich, 6054/A, Nepal, accompanied by a smaller specimen in left corner, with a large label below, Watt 6493 from Manipur, det. *T. wallichiana* by Spjut; (3) has four specimens, but only the lower left specimen is a type (*T. wallichiana*), below it are several labels, one printed—ex Herb. *George Gordon*, presented by J. D. Hooker, 1878, the other bears handwritten annotation—“*Taxus wallichiana*,” two largest specimens with letters *a* and *b* written nearby on left and right, respectively, and with Herb. Benthamum imprinted in center, belong to *T. contorta*; uppermost annotated *T. virgata*, det. by Spjut to be a young shoot of *T. baccata*. **NY:** 2 sheets, 6054A, NY accession numbers 30328 and 30329 (det. via photocopy). **P:** “Napalia,” 6054 with “A” inserted, annotated *Taxus nucifera* Kaempf.? on label ex. Herb. Richard, and additional label ex. Herb. E. Drake. **PH:** “6054A Wallich.”

Zuccarini was one of many recipients of specimens distributed by Wallich who generally assigned collection numbers to species rather than to specimens in which a particular specimen number may come from different localities and from different collectors. For example, Wallich 6054A has been reported from Central Midlands near Kathmandu Valley in Nepal (Anonymous 1913; Hara et al. 1978), and also from “Cachemiro” (Parlatore 1868), but most likely 6054A was collected from around Kathmandu (Dan Nicolson, pers. comm. 1995) during 1822 (“Wallich’s Catalogue” 1831–1832, Stafleu & Cowan 1988; Wallich 1826). Wallich was not allowed to leave the Valley of Kathmandu, while his collectors were able to collect, for example, northwest of Kathmandu Valley on the Holy mountain of Gossain (Nicolson, pers. comm., 1995). Wallich specimens of *T. wallichiana* with notations of “Kumaon” appear to be an error in numbering or labeling since collections from “Kumaon,” which generally belong to *T. contorta*, were collected by Robert Blinkworth as indicated in Wallich’s numerical list (“Wallich’s Catalogue” 1831–1832, Stafleu & Cowan 1988). Wallich’s collections for numbers 6054a, 6054b, which were collected prior to 1826, were distributed sometime between 1831 and 1832 (Anonymous 1913).

However, the lectotype, a specimen collected by Wallich from eastern India—received by Zuccarini in 1835 without number—would appear to be a later collection unrelated to the distribution of Wallich’s Catalogue and herbarium. Indeed, Wallich was in Assam in 1835 (Burkhill 1965). It should be further noted that an illustration in Siebold and Zuccarini (1843, Tab. 5, reproduced here as Fig. 21) most closely resembles the lectotype among the specimens at M as seen by the branching and distribution of male cones. The lectotype is also characterized by reddish orange branchlets, non-inflated epidermal cells on abaxial surface of leaves, 12–15 stomata rows per band, and marginally positioned papillae on epidermal cells.

Two varieties are recognized by differences along the abaxial leaf margin as seen by the size and shape of epidermal cells and by the position of papillae.

5a. *Taxus wallichiana* var. *wallichiana*

Common name.—Wallich yew.

Distribution and ecology.—C Himalayas to SW China; Nepal, Bhutan, NE India (Assam, Manipur, Khasia Hills, West Bengal), Myanmar, China (SE Tibet, Sichuan, Yunnan); montane coniferous forests with *Picea*, *Abies*, *Tsuga*, or broadleaved evergreen forests of *Lithocarpus*, or *Quercus*, (1500–) 2300–3200 m. In Nepal evidently occurring abundantly with *Abies spectabilis* (D. Don) Spach on limestone (Stainton 1972), and in Bhutan apparently scattered from Ha to Mongar districts (Grierson & Long 1983).

Typical *T. wallichiana* is identified by the pale reddish orange branchlets, persistent cuspidate bud-

scales (Pilger 1916), linear leaves arcuate near base (Orr 1937; Pilger 1903), conically shaped seeds (Orr 1937) that often mature on 2nd year or older branches (in the Himalayas), and angularly shaped epidermal leaf cells in T-section. Its leaves are further distinguished from those of *T. contorta* by the adhesive, bone-like parenchyma cells, and by (11–)13–18(–21) rows of stomata per band. Plants from Nepal, West Bengal, Khasia, and Bhutan are similar to the type.

Taxus wallichiana has been the name applied to all yews in southeastern Asia (Hu 1964; Pilger 1903 as subsp. *wallichiana*); however, de Laubenfels (1988) adopted *T. sumatrana* for his treatment of gymnosperm taxa in Flora Malesiana. He indicated that several species may overlap in the eastern Himalayas, suggesting that *T. wallichiana* was outside the Flora Malesiana region. *Taxus wallichiana* has largely been ignored by Rehder (e.g., Rehder 1940, 1949) and Hortus Third (Liberty Hyde Bailey Hortorium Staff 1976), while others have mentioned it as a species confined to the Himalayas (Krüssmann 1985), or more limited to the northwestern Himalayas (Wilson 1926), or as one of two partially sympatric species predominantly Himalayan in distribution (Silba 1984). Since Pilger (1903, 1916) did not cite any specimens for *Taxus* in the western Himalayas but indicated *T. wallichiana* to occur in eastern Himalayas, this omission may reflect uncertainty on his part, as he noted there were intermediates to *T. baccata*.

While I do not accept all morphological variants of *Taxus* in southeastern Asia to belong to a single species, Handel-Manzetti (1929), Florin (1948a), and Hu (1964) also recognized more than one sympatric species in Asia by the lack of papillae on the abaxial leaf midrib, which I consider applicable to the *Sumatrana* Group as a whole.

The taxonomic and ecological significance of midrib papillae on the abaxial epidermal surface of leaves in *Taxus* has been noted by Bertrand (1874), Deryugina & Nesterovich (1981), Florin (1931, 1948b), von Frimmel (1911), Orr (1937), and Spjut (1992, 1993, 1998a, 2000a; Spjut in Hils 1993); however, Kwei & Hu (1974) and Cheng & Fu (1978) recognized intermediates with partially papillose midribs between *T. wallichiana* (papillose midrib) and *T. sumatrana* (smooth midrib). The latter was treated as a variety under two illegitimate combinations (*T. chinensis* var. *mairei*, *T. wallichiana* var. *mairei*). Spjut (1992, 1993, 1998b, 2000a), however, found other features that support their distinction not only as species but as species groups, such as epidermal cells in transverse sections appearing angular in the *Wallichiana* Subgroup of species (C & E Himalayas to SW China; North America) and elliptical in the *Sumatrana* Group of species (E Himalayas to Indonesia, Philippines).

Taxus wallichiana is interpreted to occur on Mt. Emei in Sichuan (China), where it intergrades with *T. chinensis*. Subtle differences in size of bud-scales and color of branchlets make it difficult to consistently separate the two species. Problematical plants may be hybrids between *T. wallichiana* var. *yunnanensis* and *T. chinensis* and/or possibly another species distinguishable by slightly larger and more persistent scales at the base of branchlets.

5b. *Taxus wallichiana* Zucc. var. *yunnanensis* (W.C. Cheng & L.K. Fu) C.T. Kuan, Fl. Sichuan. 2:215. 1983. (Fig. 19). *Taxus yunnanensis* W.C. Cheng & L.K. Fu, Acta Phytotax. Sin. 13(4):86, fig. 52, 4–7. 1975. *Taxus chinensis* (Pilg.) Rehder var. *yunnanensis* (W.C. Cheng & L.K. Fu) L.K. Fu, Vasc. Pl. Hengduan Mount. 1:214. 1993. TYPE: CHINA. TIBET: ZAYUL, 2100 m, 2 Aug 1973, Zhang 916 (HOLOTYPE: CAF; ISOTYPE: PEI, leaf fragment! photocopy!). TOPOTYPES: detached leaves, without collector or date, “type locality” (PEI); Kingdon Ward 10398 (Zayul, Rong Tō Valley, 8000 ft, spreading tree with brilliant green foliage, amongst deciduous trees on slopes and in gullies, BM!).

Common name.—Yunnan yew.

Distribution and ecology.—India (Sikkim, Nagaland), Myanmar, China (Tibet, Yunnan, Sichuan); mixed forests types, generally higher in elevation than var. *wallichiana*, 2100–3500 m, occurring with *Larix griffithiana* Carrière and *Picea spinulosa* (Griff.) A. Henry in the Sikkim region (Rau 1974).

Taxus yunnanensis has been confused with *T. wallichiana* in the *Flora of China* (Cheng & Fu 1978). The authors had evidently considered the type for *T. wallichiana* to represent the species mainly in northwestern Himalayas; consequently, they described *T. yunnanensis*—indicating it was found in the eastern Himalayas (Bhutan, Tibet, Myanmar) to Yunnan and Sichuan (Cheng et al. 1975; Cheng & Fu 1978). Later, it was reduced

to a variety of *T. wallichiana*, as cited above, and more recently placed in synonymy (Li & Fu 1997), although it had been included in synonymy by de Laubenfels (1988) under his broadly circumscribed *T. sumatrana*. Li and Fu (1997), in placing *T. yunnanensis* in synonymy with *T. wallichiana*, created a new name for the yew distributed in the northwest Himalayas, *T. fuana*, but this is antedated by *T. contorta*. The English edition of the *Flora of China* (Fu et al. 1999) follows Li and Fu (1997), while Farjon (1998, 2001) maintained the illegitimate name with a narrower geographic distribution that seemed to reflect only the type locality.

Most specimens I annotated *T. yunnanensis* (A, GH, July 1996; BM, Oct. 1997; Spjut 1998b) are from Yunnan and Sichuan. They are distinguished from typical *T. wallichiana* by the leaves appearing slightly wider (nearly lanceolate), more evenly distributed, less markedly curved across the adaxial surface and paler green below than above, and having medial papillae on the abaxial epidermal cells. At the time I had seen only leaf fragments of a type—from Tibet near the border with Myanmar and India; it differed from the type of *T. wallichiana* by the abaxial surface having a broad region of large epidermal cells with medial papillae between the margin and stomata band. These features were seen more often in yew specimens from Yunnan and Sichuan than from northeastern India. Later, I received a B&W photocopy of a PE isotype from Dr. Z-y. Cao, who had earlier sent me leaf fragments of topotypes, and I found that the leaf arrangement and shape compare more closely to the type of *T. wallichiana* than to specimens from Yunnan and Sichuan. Thus, plants most typical of this variety, as seen in northeastern India and nearby Tibet, are intermediate forms distinguishable only by leaf anatomical characters. For this reason, *T. yunnanensis* is reduced to a variety. Nevertheless, it is important to differentiate these and one other related species (*T. florinii*), in order to distinguish the North American species (*T. brevifolia*, *T. globosa*) from their Asian relatives; otherwise, they may have to be included under *T. wallichiana*.

Variety *yunnanensis* is distinguished by the abaxial leaf marginal zone having relatively long narrow epipillose cells (2–4 cells wide) in contrast to the irregularly quadrangle shape in var. *wallichiana*. This region of narrow elongate cells, 2–4 cells wide, is usually followed by much wider zone of papillose cells (5–15 cells across), but a transitional zone of papillose cells may be absent (Fig. 19B). In transverse sections the leaves also appear thinner and more revolute along margins, and specimens from Tibet (type locality), Myanmar and Naja Hill in northeastern India have taller epidermal cells along the abaxial leaf marginal zone. Another characteristic feature of var. *yunnanensis* is that papillae are mostly opposite and erect, best observed on the abaxial midrib (and also marginal cells). Photomicrographs of leaf stomata bands for species of *Taxus* in Jinxing and Yuxi (2000) show excellent resolution at 1000× for the medial (opposite) papillae that characterizes *T. wallichiana* var. *yunnanensis* (referred to as *T. yunnanensis*), in contrast to the marginal (alternate) arrangement seen in their *T. chinensis*, a species in which the papillae arrangement is similar to that of *T. wallichiana* var. *wallichiana*. Their photos presented for *T. wallichiana*, however, are of *T. contorta* as seen by the narrow linear cells with only a single row of papillae.

IB. Wallichiana Group, Subgroup *Chinensis*.—The *Chinensis* Subgroup is characterized by leaves having elliptical to rarely wide rectangular epidermal cells in transverse sections, notably larger on the adaxial surface than abaxial surface, and stomata that align both anticlinally and periclinally. Plants with angular epidermal leaf cells, as viewed in T-section, are included if they have yellowish (ochre) tinted branches, vestigial bud-scales at base of branchlets, and oblong leaves. The *Chinensis* Subgroup comprises *T. chinensis* and two proposed (undescribed) species in central China, occurring between 150 m and 2500 m in elevation, and three other species that extend into the Himalayas to Nepal and from the Pacific to the Philippines and to Indonesia, where mostly found above 2000 m (*T. obscura*, *T. phytonii*, *Taxus* sp. undescribed—*Taxus* REH).

Introgression with species of the *Sumatrana* Group, *Wallichiana* Subgroup and *Cuspidata* Alliance is evident in the northern-most and southern-most ranges of the *Chinensis* Subgroup. The northern range of the *Chinensis* Subgroup is in central China, represented by *T. chinensis*. In this region, *T. chinensis* has sharply divergent leaves devoid of papillae across 8–12 abaxial marginal cells (e.g., *Henry 7097* from western Sichuan). This is also seen in *T. umbraculifera* (*Cuspidata* Alliance) of northeastern China, Korea and Japan. At the southernmost range—in Indonesia and the Philippines—are two other species of the *Chinensis* Subgroup;

one *Taxus obscura* is similar to *T. chinensis* in the leaf shape, texture and lack of epidermal papillae across 8–9 marginal cells, and another, *Taxus phytonii*, that resembles *T. sumatrana* in the leaves having a reddish color along marginal and midrib epidermal cells. The latter is also similar to *T. wallichiana* in the linear leaf shape, two-ranked leaf arrangement, and in the persistence of bud-scales at base of branchlets.

Although leaf stomata in *Taxus* develop in periclinal rows, stomata in the *Chinensis* Subgroup often align transversely with the stoma anticlinally oriented. The *Sumatrana* Group, in contrast, has stomata arranged \pm alternately to each other along adjacent rows. The anticlinal stomata in the *Chinensis* Subgroup, in which the stomata bands are further differentiated from adjacent epidermal cells by color, have been observed mostly in Taiwan and Luzon specimens. Other specimens from mainland China have less distinct stomata bands as evident by a more uniformly yellowish orange to reddish color on the abaxial leaf surface.

6. *Taxus chinensis* (Pilg.) Rehder, J. Arnold Arbor. 1:51. 1919. (Fig. 22). *Taxus baccata* L. [subsp. *cuspidata* (Siebold & Zucc.) Pilg.] var. *chinensis* Pilger, Pflanzenreich IV, 5:112. 1903. *Taxus cuspidata* Siebold & Zucc. var. *chinensis* (Pilg.) C.K. Schneider ex Silva Tarouca, Freiland-Nadelgehölz. 276. 1913. *Taxus wallichiana* Zucc. var. *chinensis* (Pilg.) Florin, Acta Hort. Berg. 14, 8:378. 1948. TYPE: CHINA. E SICHUAN: Wushanhsien, 2000–3000 m, year 1885–1888, Henry 7155, with seed (LECTOTYPE by Rehder & Wilson in Sargent, Pl. Wilson. 2:8. 1914: A-18682; ISOLECTOTYPES: BM!, E, GH!, K!, S fragment, US!). The A and GH sheets were annotated by Hu as “type” and “isotype,” respectively. SYNTYPES: Henry 6913, Farges 128. Pilger cited several collections but did not designate a type.

Taxus baccata L. var. *sinensis* A. Henry, Elwes & Henry, Trees Gr. Brit. and Irel. 1:100. 1906. Nomen illegit. (ICBN Art. 53.3, Ex. 9). TYPE: CHINA. E SICHUAN: Wushanhsien, 2000–3000 m, 1885–1888, Henry 7097 (LECTOTYPE designated here: E; ISOLECTOTYPES: A!, BM!, P!, US!). No specimens cited; original material at E, Henry nos. 6913 from Hubei, 7097 and 7155 from Sichuan.

Common name.—China yew.

Distribution and ecology.—Mostly China (Guangxi, Gansu, Yunnan, Sichuan, Guizhou, Hubei, Anhui, Zhejiang), one collection from Vietnam (Hiep & Chan 405, P); forest, or forest margins, or open scrub, “under rocky cliffs,” “often among bamboos,” generally 1000–2800 m. Reported also at elevations as low as 150 m (Hu 1964). In Sichuan found more in the drier “mixed mesophytic forest” or “transitional zone” to an evergreen oak forest, in contrast with *T. wallichiana* occurring more in hemlock-spruce-fir forests (Wang 1961). In Vietnam “a shade tolerant” species of limestone in understory of evergreen forest of *Pinus kwangtungensis* Chun & Tsiang, *Podocarpus neriifolius* D. Don, *P. nilgeri* Foxw. and other broad-leaved trees, 1000–1600 m (Hiep 1998).

Taxus chinensis is distinguished by the pale yellowish green or “yellowish ochre” to “bronze” (“Prisma-color” chart) color on older branchlets (“dun colored”; Orr 1937) and by the relatively short (oblong), thick leaves, usually with conspicuous midrib papillae along epidermal cell walls. In making this distinction, I have independently reached the same conclusion as that by Pilger (1903, 1916), Orr (1937), Florin (1948a), and Hu (1964) for recognizing this taxon by its leaf and bud-scale characteristics, and also that by Orr (1937) for its branch color. Although branchlets of *T. wallichiana* vary in color from reddish orange to purplish, they lack this yellowish pigmentation, or are not yellowish green.

The leaf stomata bands are bordered by 4–12 marginal cells. The stomata develop in 11–19 (–21) rows per band and are sometimes evident on the midrib.

The name *T. chinensis* was once used for any yew occurring naturally in China (Rehder 1940), and also Taiwan, the Philippines, and Indonesia (Wilson 1926)—until the earlier legitimate names, which had been classified in *Cephalotaxus* and *Tsuga*, were applied; the ICBN (Art. 11.4, 11.5) requires that the earliest epithet be adopted regardless of the genus it was erroneously assigned to—unless conserved. Rehder (1936), for example, discovered one—*Tsuga mairei* Lemée & Lév., but continued to use his name, *T. chinensis*, whereas Parlatore (1868) and Pilger (1903, 1916) had reported several earlier names (*Cephalotaxus sumatrana*, *Cephalotaxus celebica*), whose epithets were eventually adopted, *T. celebica* (H.L. Li 1963), *T. sumatrana* (de Laubenfels 1978); however, the correct name for a single subtropical species as applied by these authors would have to be *T. wallichiana*.

Not all taxonomists accept just one species of *Taxus* in southern China; Florin (1948a), for example, felt there were at least two: *T. chinensis*, which he treated as a variety of *T. wallichiana* with distribution primarily

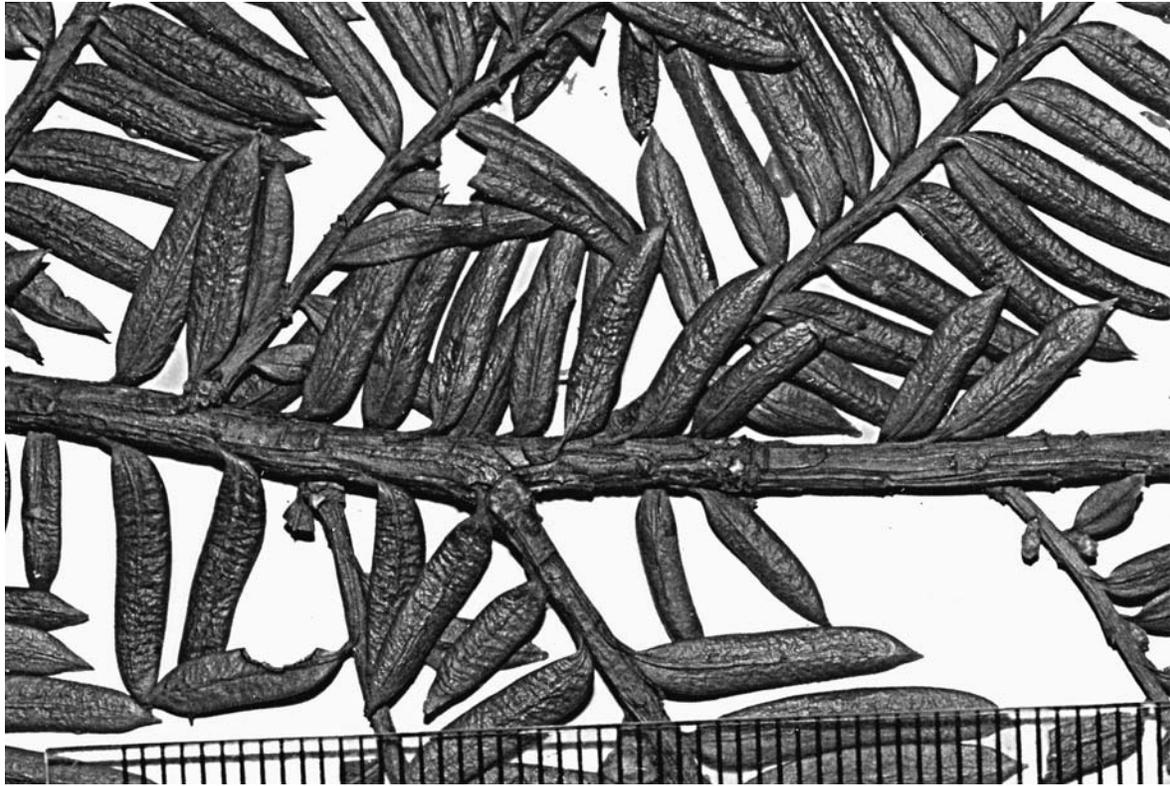


FIG. 22. *Taxus chinensis*, distinguished by absence of scales at base of branchlets and by the oblong leaves strongly convex across the adaxial surface, E Sichuan, China (isolectotype, K).

in Sichuan, and another that he considered a new species, *T. speciosa* Florin, which was not entirely new since it had been earlier described, as already indicated, and Florin himself mentioned the names in synonymy (Cheng & Fu 1978). Florin's two species were distinguished by the presence or absence of papillae on the abaxial leaf midrib, and var. *chinensis* was further distinguished from var. *wallichiana* (in the Himalayas) by the relatively shorter (oblong v. linear) leaves. He also indicated that *T. baccata* var. *sinensis* was synonymous with var. *chinensis* according to communications he had with Orr at Edinburgh, who had sent him leaves of Henry's collections (Henry 7155), which Henry himself had named var. *sinensis*. Although I have not studied the Edinburgh specimens of Henry's collections, the type for var. *sinensis* (Henry 7097) was selected based on material at E sent to Florin, who cited Henry 7097, 7155; the latter (7155) is the type for *T. chinensis*.

Botanists in China have since recognized up to four species and one variety of *Taxus* in China (Cheng & Fu 1978); however, they have misapplied and illegitimately combined previously known names. These included *T. chinensis* var. *mairei* (Lemée & Lév.) W.C. Cheng & L.K. Fu (illegit.), *T. wallichiana* (misapplied to *T. contorta*), and *T. yunnanensis* (superfluous for *T. wallichiana*). Hu (1964) followed Florin's treatment (1948a) except that she maintained *T. chinensis* as a species. Cheng & Fu (1978), however, reduced it again to a variety, but not according to ICBN, as just indicated. *Taxus chinensis* and *T. mairei* were considered to differ only as varieties because the distinguishing feature—presence or absence of papillae on the leaf midrib (undersurface)—could not always be clearly decided due to the occurrence of intermediates (Kwei & Hu 1974; Cheng & Fu 1978), and also because the type for *Cephalotaxus celebica* Warb. had not been studied (Hu 1964; Cheng & Fu 1978). Hu (1964) concluded that the type for *T. speciosa* did not significantly differ from that of *Taxus (Tsuga) mairei* (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu, whereas the type for *Cephalotaxus celebica* might differ because the only specimen she saw from the Celebes Islands (*Neth. Ind. For. Serv. bb:19577, A*)



FIG. 23. *Taxus obscura*, distinguished in part by the branchlets and leaves overlapping in pressed specimens, the leaves often crisscrossing, in contrast to less crowded branchlets and a more parallel leaf arrangement in *T. phytonii*; Philippines, de Laubenfels P668 (holotype, A).

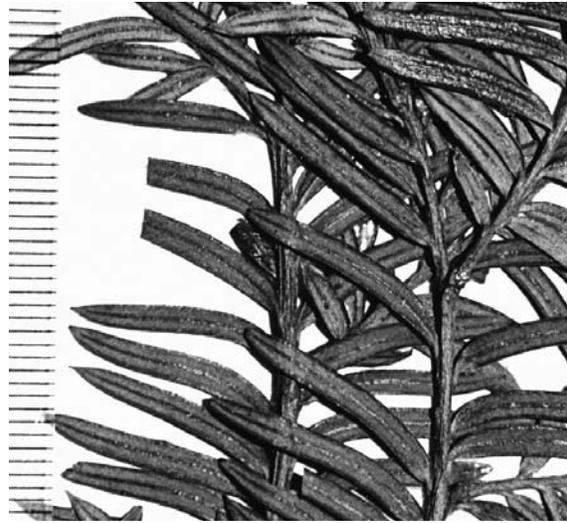


FIG. 24. *Taxus phytonii*, showing parallel leaf arrangement and persistent bud-scales at base of branchlets; Taiwan, Wilson 11154 (holotype, A).

had leaves with a papillose abaxial midrib, and in her opinion this was distinct from the types of *T. mairei* and *T. speciosa*.

I have studied the same specimens that Hu studied at the Harvard University herbaria (A GH, annotated by Hu, July 1955) and largely concur with her identifications of *T. chinensis* (Hu 1964). Additionally, I have studied other specimens from Sulawesi, namely the type for *Podocarpus* (*Taxus*) *celebicus* Hemsl. (K), *Teysmann 14190* (U), and a photocopy of a holotype fragment for *Cephalotaxus celebica* Warb. (S); these have similarly shaped leaves with a smooth midrib and broad marginal area of partially papillose cells on the abaxial surface; the “Neth. Ind For.” specimen (A), in contrast, differs in having a papillose midrib as noted by Hu (1964). Based on Florin’s (1948a) account and the similarity in leaf shape of the two type specimens, in which I have recognized *T. celebica* by its long acuminate leaves (tapering from mid region; e.g., *H. Smith 10401* [BM], Plate 6 in Florin 1948a), I see no reason to disagree with Florin—that the Warburg type for *Cephalotaxus celebica* lacks papillae along the abaxial midrib; thus, while Cheng and Fu (1978) could have adopted this name in their revised treatment of Taxaceae in the *Flora of China*, the correct name under their species concept is *T. sumatrana*; the basionym (*Cephalotaxus sumatrana*) was mentioned by Parlotore (1868) and Pilger (1903), the latter of which was cited by Cheng and Fu (1978).

7. *Taxus obscura* Spjut, sp. nov. (Fig. 23). TYPE: THE PHILIPPINES. LUZON: Mt. Banahao, 2100 m, tree 8 m, common on ridge in mossy forest, aril bright red, 26 Aug 1978, de Laubenfels P668 (HOLOTYPE, A! [Spjut in adnot., *T. phytonii* var. *obscura* in ed.]; with seed; leaf with 11 stomata rows/band, abaxial marginal border of 4 smooth cells across in 2 quadrate rows and 2 inflated rows, trapezoidal in shape, followed by 5–6 rows of papillose cells; abaxial leaf midrib 15 cells wide, papillose on most cells, papillae covering the entire cell surface). De Laubenfels prepared a separate specimen from a male plant from the same gathering, P-669. Type also illustrated in de Laubenfels (1988).

Species haec ab *Taxus chinensis*, differt foliis linearibus, valdes discoloribus, 1–2 (–3) cm longis, 1.5–2.5 mm latis, acutibus, 0.200–0.300 mm crassis, supra convexa, subtus concava ad plana, stomata vitta ferruginea, (10–)11–13(–15) seriata/zonas.

Tree 5–15 m high; ultimate branchlets crowded, long, weeping or flexuous, yellowish green, dull rusty brown to orange with age; bud-scales scarcely persistent at base of branchlets, the scale scars similar to those of *T. chinensis*, longest persistent scales ca. 1 mm long (to 2 mm long in *Loher 7129*). Leaves often lost by the 3rd yr, spreading obliquely and closely overlapping in ± two ranks, frequently crisscrossing in herbarium

specimens, especially near ends of branchlets, oblong, or slightly elliptical, recurved, evenly tapered to an acuminate sharply pointed apex, abruptly bent downwards to apex, 1–2(–3) cm long, 1.5–2.5 mm wide, 200–300 μm thick, dark olive green, resinous glossy and convex across adaxial surface to a recessed acute darker midrib with channels along each basal side, rugose in dried specimens; abaxial surface slightly concave across to a slightly elevated midrib, the midrib rounded to truncate, flush or slightly elevated, plane to abruptly revolute near margins; upper adaxial epidermal cells in transverse section broad elliptical to nearly short rectangular, thin-walled, (12–)20–25(–30) μm tall, 25–30 (–40) μm wide, abaxial margin 2–4(–11) cells across without papillae, papillose across 1–7 cells; marginal and midrib cells not as tall as those on adaxial surface, 12–15 μm tall, 15 μm wide, the epapillose marginal cells short trapezoidal to nearly quadrate, usually inflated in 2–4 rows, \pm rectangular nearer stomata band, narrower and longer on midrib (3–7 l/w), usually entirely papillose across the midrib, rarely only partly papillose on midrib, or rarely lacking midrib papillae in lower half of leaf, papillae opposite or more often alternate in 1–3 irregular rows across each cell, covering most of the cell; stomata bands abruptly differentiated by color from surrounding epidermal cells, yellowish orange or yellowish green, broader than the marginal region; stomata diamphicyclic, anticlinal in orientation, in (10–)11–13(–15) continuous rows per band. Male cones subglobose in bud, 4 mm long, scales imbricate, overlapping in 4 ranks, microsporophylls lobulate; microsporangia ± 8 , pale pink with a broad dark reddish center. Female cones subcylindric, 2 mm long in bud; scales overlapping in 5 ranks, greenish, longest scale at base conduplicate; seed rounded, conical, 5–6 mm long, 4–5 mm diam., tapering to apex from the middle.

Common name.—Obscure yew.

Distribution.—Forest margins, 2000–2450 m. Myanmar, China (Fujian, Taiwan), The Philippines (Luzon), Indonesia (Sumatera, Sulawesi).

Additional specimens: **MYANMAR (BURMA).** Ruby Mines, 6500 ft, *Oliver* (K); Ruby Mines, no elevation data, 14 Sep 1894, *Oliver* (K). **CHINA. Fujian:** Puchen, *Chung* 3866 (A). **THE PHILIPPINES. Luzon:** Mt. Pulog, 18°26' N, 120°54' E, tree 12 m, leaves dark glossy green above, dull green beneath, *Jacobs* 7171 (K); Benquet Prov., Laguna, Mt. Santo Tomas, *Leaño* 25128 (A, US); Mt. Tonglon, Aug 1906, *Curran* s.n. (US), *Curran* 5015 (P, PH); Benquet Prov., *Merrill* 839 (U, US); Mt. Pauai, 2450 m; *Sulit* 7582 (A); Central Luzon, *Loher* s.n. (US); Mangitquiran, *Loher* 4850 (K, US); Laguna Prov., Mt. Banahao, 2100 m, *Loher* 7129 (US), 7139 (US); Luconia, summit of Mt. Majayjay, 7500 ft, *ex Hook. Herb.* (K); Mt. Majayjay, *Wilkes Exped.* 1838–1842 (GH); Lepanto Dist., Mt. Data, *Ramos & Edaño* 40234 (K, P). Locality data uncertain: *Y. Sugilara*, *Ex TUS* (GH). **INDONESIA. Sulawesi:** Celebes an Ond., Gowa Lambaja, 2000 m, *Neth. Ind. For. Serv.* bb:20887 (K). **Sumatera:** Tharolanden, 1400 ft, *Boschprophakion* 7709 (U).

Taxus obscura is recognized by the pendulous branchlets and by the oblong leaves that in herbarium specimens show a sharp contrast in color between the adaxial and abaxial surfaces—dark glossy green above and yellowish orange (rusty) below (dried specimens). The weeping aspect of the branchlets is evident in herbarium specimens by their flexuous appearance.

Occasional specimens, e.g., *Loher* 7129 (US) from the Philippines and *Lobb* 461 (BM) from Malaya, have rigid branchlets. They resemble *T. kingstonii* but are referred to the *Chinensis* Subgroup by the narrow leaves with fusiform shaped epidermal cells on the abaxial midrib and irregularly shaped quadrate and inflated epidermal cells along the abaxial marginal zone. *Loher* 7129 is assigned to *T. obscura* by the overlapping leaf arrangement with leaves frequently crisscrossing, but still differs from the majority of specimens assigned to this species by its rather long linear leaves, whereas *Lobb* 461 with its more parallel two-ranked leaf arrangement is placed under *T. phytonii*, a determination that is further supported by the reddish colored epidermal cells on the abaxial midrib. Both specimens may be hybrids between *T. sumatrana* and *T. phytonii*, or may prove to be distinct varieties in further study.

In my 1996 annotations, a number of other specimens from Fujian, the Philippines and Indonesia were identified *T. kingstonii* by the rusty orange colored leaves with relatively thick lip-like margins (e.g., *Sulit* 7582 [A], *Curran* 7911 [US] and *Loher* 4850 [US]). *Taxus obscura* was then distinguished as a variety of *T. phytonii* by the lack of marginal papillae on the abaxial midrib. In further study, more taxonomic emphasis was placed on branching and phyllotaxy, less on position of epidermal papillae, in distinguishing *T. obscura* from *T. phytonii*; consequently, other differences became apparent between these species. As a result the

taxonomy of *T. obscura* broadened to include more specimens from the Philippines and Indonesia, while that of *T. kingstonii* was narrowed to exclude all specimens from these areas. The specimen from Fujian also differs by the leaves having a wider marginal zone of epiderma cells, 11 cells across, accompanied by lack of papillae on outer midrib cells; otherwise, it agrees with *T. obscura*.

Taxus obscura differs from *T. phytonii* not only in branching and phyllotaxy but also by leaf length and color and by the scales. The branchlets in *Taxus phytonii* spread more widely and scarcely overlap in pressed specimens, and the leaves are more distinctly linear and lie closely parallel along one side of a branchlet in pressed specimens, in contrast to a more crisscrossed crowded arrangement in *T. obscura*. The stomata bands of *T. phytonii* show a sharper contrast in color from the marginal cells, appearing yellowish green compared to the reddish margins and midrib, whereas stomata bands of *Taxus obscura* show less of a contrast in color from the adjacent midrib and marginal zones, usually the stomata bands appear yellowish orange, occasionally entirely green. The bud-scales of *T. obscura* are smaller and less persistent at base of branchlets, and cone scales are mostly imbricate, in contrast to scales of *T. phytonii* appearing more conspicuous at base of branchlets and decussate on cones.

8. *Taxus phytonii* Spjut, sp. nov. (Fig. 24). TYPE: CHINA. TAIWAN: mts. W of Karenko, 23 Nov 1918, *Wilson 11154* (HOLOTYPE: A!; ISOTYPE: US! Leaves with 12–13 stomata rows/band, abaxial marginal border of 6 smooth cells across with ± 2 rows of quadrate cells across and 4 rows of inflated trapezoidal cells, followed by a region of 10 papillose cells wide, the papillae mostly along cell walls).

Similar to *T. obscura*, praecipue differt folia longiora, linearis, 2–3 cm longis, complanatus, stomata zonatas flavovirescens, margines et costa rufus, perulae persistens.

Similar to *T. obscura*, tree 5–20 m; ultimate branchlets crowded, weeping or horizontal, yellowish green, dull rusty brown with age; bud-scales mostly persistent in 3–4 ranks, spreading, thick, ovate to lanceolate or cuspidate, concave, some smooth, others carinate, often pale yellowish or brownish, longest scales ca. 1 mm long. Leaves flaccid, two-ranked, not overlapping to slightly overlapping, linear falcate, slightly recurved, evenly tapered to an acuminate sharply pointed apex, 2–3 cm long, 1.5–2.5 mm wide, 200–300 μm thick; dark olive green and strongly convex across the adaxial surface to a depressed acute midrib that is channeled along base, mostly yellowish green to yellowish orange and slightly concave across the abaxial surface with a slightly elevated and rounded midrib, curved more near margins, or margins plane; adaxial epidermal cells in transverse section elliptical to nearly wide rectangular, thin-walled, 12–20 μm tall, 25–30 (–40) μm wide; abaxial marginal and midrib cells similar, or smaller, 12–15 μm tall, 15 μm wide, the marginal zone usually 9–13 cells across, usually papillose to about 4 cells from margins, papillose entirely in one specimen from India, or lacking in papillae across 8 cells in *Alvarey 18369* from Luzon, the epapillose cells short trapezoidal to nearly quadrate, usually inflated in 2–4 rows, rectangular nearer stomata band, narrower and longer on midrib, 3–7 times longer than wide on midrib, midrib papillose entirely or lacking in papillae from near the mid region to base of leaf, papillae strongly marginal in 1–3 irregular rows across each cell, often not covering the entire cell; stomata bands abruptly differentiated from surrounding epidermal cells by color, yellowish orange or yellowish green, broader than the marginal region; stomata diamphicyclic, anticlinal in orientation, 10–12 (–14) rows/band, the abaxial margins and midrib usually reddish in herbarium specimens. Male cones subglobose in bud, 4 mm long, scales overlapping in 4 ranks, sporophylls lobulate, microsporangia ± 8 , pale pink with a broad dark reddish resinous center. Female cones subcylindric, and 2 mm long in bud; scales overlapping in 5 ranks, \pm decussate, greenish, longest scale at base conduplicate; seed rounded, conical, 5–6 mm long, 4–5 mm diam., tapering to apex from the middle.

Common name.—Phyton yew.

Distribution.—2000–2800 m, Nepal, NE India, Thailand, China (Yunnan, Taiwan), Philippines (Luzon).

Additional specimens: **NEPAL.** *Williams 1014* (BM). **INDIA. Assam:** Pachaksihri, Laluma, 94°15'E, 27°45'N, 7000 ft, *Ludlow & Sherriff 3719* (BM). **THAILAND. Malaya:** *Lobb 461* (BM). **CHINA. Yunnan:** Wei-se Hsien 2800 m, tree 30 ft in forest *Tsai 59874* (A). **Taiwan.** *Tongshi, C-j. Chang: Tongshi 1*, 5 (p.p., Rt. 210/6k), 7 (p.p., Rt. 210/16k), *TD-1* (wba). **THE PHILIPPINES. Luzon:** Mt. Banahao, *Ocampo 27920* (A, P); *Curran 7911* (US); Mt. Santo Tomas, *Elmer 6244* (P, US); Benguet Prov., *Alvarey 18369* (BM). Locality not clear—handwriting not legible, possibly Mt. Harui, *Harain Letty*, 17 Oct 1802, in adnot. *Taxus tosua topue*, p.p. (BM, GH).

Taxus phytonii differs from *T. obscura* by the relatively longer leaves, 2–3 cm long, that spread mostly parallel as seen along one side of a branchlet, and by other features as discussed under *T. obscura*. The leaf characteristics of *T. phytonii* are remarkably consistent at disjunct locations. For example, *Tsai 59874* from Yunnan and *Wilson 11154* from Taiwan appear almost identical not only in their leaf shape but also in their leaf color and in their leaf anatomy in which papillae are positioned marginally on midrib cells and in which stomata occur in 11–12 rows per band. *Ludlow & Sherriff 3719* from northeastern India also has these features, while differing slightly in papillae extending entirely across the abaxial leaf surface, instead of just 2–4 cells from the margin.

Taxus phytonii shows affinity to *T. wallichiana* by the relatively long narrow leaves that spread nearly parallel to each other, and also to *T. chinensis* by the yellowish tinted branchlets and by leaves that have broad elliptical epidermal cells as seen in transverse section. Additionally, the branchlet color and phyllotaxy of *T. phytonii* are similar to that of the North American *T. globosa*, which differs by longer leaf epidermal cells near the abaxial margins, also appearing quadrangular in transverse sections.

Etymology.—The epithet *phytonii* is in tribute to an achievement by a company named Phyton (formerly at Ithaca, NY, now in New Jersey) for the commercial production of the anticancer drug taxol by tissue culture; their production facility is located in Germany. Their commercial methodology hopefully will eliminate the harvest of wild plants to obtain the taxoids.

9–11. *Taxus* spp. undescribed, aff. *T. chinensis*. The following proposed species need further study.

9—Taxus REH (*T. rehderiana* ined.); Vietnam, China (Taiwan), Indonesia (Sulawesi).

Taxus “REH” (*Taxus* aff. *chinensis*, Spjut in adnot. GH, P), recognized from five specimens, differs from the preceding two species (*T. obscura*, *T. phytonii*) by the longer leaves showing less of a contrast in color between the two surfaces, particularly in the paler green color on the adaxial surface, and also by the abaxial leaf surface having a wider marginal zone (smooth cells) except for two specimens from Vietnam that have a relatively narrow leaf margin (4 cells wide). Generally, the specimens resemble *T. wallichiana* in the long linear leaves but have more features in common with *T. chinensis* as seen in the pale yellowish green color of the branchlets, the minute scales at the base of branchlets, the elliptical shape of the leaf epidermal cells in transverse section, and in the tapered seeds. In my 1996–1997 annotations, the specimens from Vietnam were identified as *Taxus* aff. *chinensis*, while those from Sulawesi and Taiwan were referred to *T. phytonii*. Additionally, a specimen by *Purdum s.n.* (GH) from northern China: (Shaanxi: Tai-pei-shan *fide* Rehder & Wilson in Sargent 1914) is similar in the gross features of branching and color, and also in the leaf anatomical feature of marginal papillae on the abaxial midrib epidermis; however, it is referred to *T. biternata* by the relatively fewer stomata rows (7 rows per band), and by the persistent dark spreading scales at the base of branchlets. A specimen from the Philippines, *Loher 7129*, as discussed earlier under *T. obscura*, may also belong here.

10–11. Taxus spp. aff. **chinensis**. **10—Taxus “OCR”** (*T. ocreata* ined. Spjut in adnot., A, BM); China (Yunnan, Sichuan), rocks, 1500 m. **11—Taxus “SCU”** (*T. scutata* ined. Spjut in adnot., A, BM) China (Yunnan, Sichuan, W Hubei), 1200–1400 m.

These proposed species are similar to *T. chinensis* except for conspicuous persistent bud-scales at base of branchlets, in which they differ from one another by the bud-scale characteristics. *Taxus* SCU has persistent scales, numbering 10–20 or more, loosely attached with a shape like overgrown toenails that are ready to fall off. The scales in *Taxus* OCR, in contrast, tightly adhere to branchlets and look more like teeth.

Taxus OCR shows remarkable similarity at two disjunct locations, *Cheng 2890* from Sichuan and *Feng 11937* from Yunnan, but there are also intermediates in duplicates of *Cheng 2890*. It is not clear, however, whether these came from the same plant. Additionally, *Feng* also collected at the same site in Yunnan on two occasions where his first collection (*Feng 11937*) was from a tree and his second (*Feng 12105*), just nine days later, was from a shrub that was also indicated to be common. Collectors do not always pick from the

same plant when assigning collections to the same number. It is also apparent from genetic studies in other species of *Taxus* that unique genotypes exist within populations (El-Kassaby & Yanchuk 1995).

Taxus SCU is also similar to *T. wallichiana* that differs by the fewer scales and longer leaves; however, occasional specimens from the Himalayas and China also appear intermediate by the presence of fewer scales and shorter leaves, or by longer leaves and more scales.

The combination of characters for *Taxus* OCR and SCU appear, on one hand, worthy of taxonomic distinction, and especially necessary for taxonomic clarification of related species—*T. wallichiana* and *T. chinensis*, while on the other hand, it would seem prudent that field studies be conducted to evaluate variation in the bud-scale character features at a particular location.

II. SUMATRANA GROUP

The *Sumatrana* Group is characterized by leaves having a relatively broad region of marginal cells adjacent to the stomata bands, usually from 8–36 cells across. This is often evident in dried specimens by a glossy reddish discoloration. The epidermal (accessory) cells in stomata bands are further differentiated from marginal and midrib regions by their shorter length and broader width. Leaves in the other species groups usually have stomata bands bordered by fewer cells, or they are less differentiated by color and development of papillae. The *Sumatrana* Group (Spjut 1998b, 2000c) is generally found at lower elevations on mainland Asia, below 1700 m (Hu 1964), or below 1200 m (Li & Fu 1997), than *T. wallichiana*, which usually occurs above 2300 m.

The taxonomy of this *Sumatrana* Group is difficult due to overlapping character traits among the species and varieties that follow. Previous taxonomists have recognized only one taxon in this group, either as a variety (Cheng & Fu 1975, 1978; Li & Fu 1997) or as a species (Florin 1948a; Handel Manzetti 1929; Hu 1964), but they have not applied the correct name. *Taxus sumatrana* has been the name applied to all yews in southwest Asia (de Laubenfels 1978), but this is antedated by *T. wallichiana*. This very broad concept of *T. wallichiana* leads to difficulty in distinguishing between *T. cuspidata* and its allies in the *Baccata* Group. Farjon (1998, 2001) indicated that *T. sumatrana* occurs only in Indonesia and the Philippines, but his interpretation, as also stated elsewhere, is without taxonomic support.

Thus, I have found it necessary to recognize more than one species in the *Sumatrana* Group—based on differences in the leaves. Within the *Sumatrana* Group, I distinguish *T. mairei* by the narrow elliptic to oblong leaves tapering to an acute to obtuse apex and by the raised midrib on the abaxial surface, appearing truncated to channeled with relatively short trapezoidal, somewhat inflated (mammillose) epidermal cells (Spjut 1998b; and as indicated in crude illustrations that accompanied my annotations: A, GH in June 1996; BM in April 2005). Leaves of *T. sumatrana* differ by the linear to lanceolate shape tapering to an acuminate apex and by the nearly rectangular shape of abaxial epidermal cells. *Taxus mairei* var. *speciosa* differs from typical *T. mairei* in features of rigidity of branches and leaves, branching pattern, phyllotaxy, and color (in dried specimens), but differences overlap in many of the character attributes. One new species, *T. kingstonii*, is recognized by its slightly larger persistent bud-scales at base of branchlets, and by leaves that are rigid, evenly tapered to base and apex, and by the rusty orange color in the herbarium, especially along the stomata bands. Differences in seed shape and color are also evident among these taxa, but field studies are needed to better evaluate the taxonomy of seed characteristics.

Although the width of the abaxial leaf marginal zone varies in *Taxus*, this, nevertheless, appears to have partial correlation to species within the *Sumatrana* Group. For example, among 15 specimens cited for *T. celebica* (Spjut 2007, Fig. 6), which has the widest leaf margin (that borders the stomata band) of any species of *Taxus*, 11 specimens were found to have 27 or more marginal cells. Two specimens with 22 and 24 bare cells across the abaxial leaf margin are within the range commonly found for *T. mairei*, while two others with a narrower marginal border fall within the range of *T. kingstonii*. Whether more taxonomic emphasis should be placed on the number of cells across the abaxial marginal region needs further study.

A wide range in variation for shape and length of epidermal cells has been observed in juvenile foliage

of *T. mairei*, whereas the mature leaves are distinguished by the inflated, short wedge-shaped epidermal cells (1–3× l/w) on the abaxial midrib. Juvenile and adult foliage may differ in conifers such as *Podocarpus*, in which species cannot be differentiated by their juvenile foliage (de Laubenfels 1969). Leaf shape and development of papillae in *Taxus* may also vary with exposure on the same plant as noted for plants in Taiwan and Indonesia (de Laubenfels 1978, 1988). Differences in mature and juvenile leaves of *T. mairei* are noted in this study in which mature leaves are oblong and taper to an acute apex, while immature leaves may appear elliptical and acuminate to apex.

12. *Taxus celebica* (Warb.) H.L. Li, Woody Fl. Taiwan 34. 1963. (**Fig. 25**). *Cephalotaxus celebica* Warburg, Monsun. 1:194. 1900. TYPE: INDONESIA. SULAWESI (CELEBES): southern, Gipfel des Wawo-Kraeng [one of the summits of G. Bonthain], on the forest-clad summit, 2800 m [Nov 1888], WARBURG 16889 (HOLOTYPE: S photocopy!; ISOTYPE: B-destroyed). Only one specimen was cited by Warburg, although he did not specifically indicate that it was the type. The S specimen is a fragment of the original collection at B. Warburg distinguished his *C. celebica* from *C. sumatrana* Miq. and excluded *Podocarpus celebicus* Hemsl.

Podocarpus celebicus Hemsley, Kew Bull. 39. 1896. TYPE: INDONESIA. SULAWESI (SOUTH CELEBES): Bonthain Peak, 7000–10,000 ft, Sep 1895 A.H. Everett 35 (HOLOTYPE: K!).

Common name.—Celebes Yew.

Distribution and ecology.—Nepal, Bhutan, NE India, South Vietnam, China (Tibet, Yunnan, Sichuan), Indonesia (Sulawesi); forest margins below 1530–3100.

Taxus celebica is recognized by the relatively large, glossy, often pale green, lanceolate plane leaves that taper to an acuminate apex and by the narrow stomata bands relative to a broad marginal zone of long (>10× l/w) rectangular cells, (18–)24–36 cells across. The stomata rows generally number (8–)12–14 per band, compared to (11–)14–19(–21) rows in *T. mairei*. Variation in number of marginal cells (Spjut 2007) appears partially correlated to the region of the leaf where sections are obtained as the leaf blade is strongly tapered from base to apex.

Leaf stomata bands of *T. celebica* often appear distinct from other species in the genus by the short wedged-shape (<3× l/w) accessory cells that have relatively small (minute) medial papillae, appearing more distantly spaced from one another, in contrast to papillae covering the entire surface of the epidermal cells in other species. Examples are specimens from Yunnan (*Forrest 7798*), Sichuan (*H. Smith 10401*, Plate 6 in Florin 1948a), South Vietnam (*Schmind s.n.*), Bhutan (*Cooper & Bulley 2833*), Khasia (*Clarke 38308*), and Tibet (*Kingdon Ward 19324*).

Intermediates between *T. celebica* and *T. mairei* var. *speciosa*, however, are apparent. My 1996–1997 annotations of *T. celebica* were based on leaves having most of the following taxonomic features: long linear to lanceolate shape, acuminate apex, long epidermal cells, obscure palisade layer of parenchyma cells, and appearing flattened in T-section. Recently, it was decided that taxonomic weight should be given to the lanceolate shape of the leaf tapering to an acuminate apex (Spjut 2007). Examples that were formerly annotated *T. celebica*—but subsequently referred to *T. mairei* var. *speciosa*—are from Fujian (*Price 1258b*), Guizhou (*Steward et al. 328*), Sichuan (*Wang 20541*), Guangdong (*Nanling Expedition 1838*), and Ningxia Huizu (*Chao 1223*). Other plants of var. *speciosa* with similar but more distant phyllotaxy are cultivated at the Royal Botanic Gardens at Kew and at Edinburgh (photos in Krüssmann 1985, plate 133; van Gelderen and van Hoey Smith 1996), and juvenile leaves received from Phytion Inc. (as *T. chinensis*). The cultivated plants were reportedly grown from seed of *Wilson 1265*. It is interesting to note that herbarium specimens of the wild plants collected in China and of a plant cultivated at the Kew Gardens appear very similar (www.worldbotanical.com).

13. *Taxus kingstonii* Spjut, sp. nov. (**Figs. 26–27**). TYPE: CHINA. TAIWAN: Arisan Prov., Kagi, 2833 m [Mt. Alishan], tree 25 ft × 2 ft, only one seen, 2 Feb 1918, *Wilson 9738* (HOLOTYPE: A! [with male cones; leaves with 10–11 stomata rows per band, abaxial margins of 8 smooth, thick-walled, trapezoidal, anticlinal to periclinal arranged cells across, followed by 5 rows of papillose cells, midribs 12 cells wide, mostly smooth, papillose on outer 2 rows]; ISOTYPES: BM! [leaves with 13 stomata rows and 9 marginal smooth cells, midribs mostly smooth except upper third of leaf, papillose on outer 2 rows of cells], K!, US p.p.!).

Similis a *T. sumatrana* et affnibus, praecipue differt foliis coloris ferruginibus vel calendulibus; folia obliquata disposita, rigida, oblonga



FIG. 25. *Taxus celebica*, distinguished by the relatively flat leaf with a broad abaxial marginal zone and narrow stomata bands; Indonesia, Sulawesi, Everett 35 (holotype, *Podocarpus celebicus*, K).

ad elliptica vel sublancoolata; ventralibus epidermae cellulae quasi rectangularis, inflatus proximus marginalis, costa interdum papillosa, proparte papillosa versas de marginali, sine papillae (7–)8–12(–20) cellulae marginales latis; stomata 11–15 seriata/zona.

Shrub or tree to 12 m high, bole to 65 cm diam; branchlets unequally (type) to equally divided, yellowish green and gradually becoming yellowish with tint of either red, orange or brown; bud scales mostly persistent, 3–4 seriate, turgid, ovate, concave, carinate near apex on upper scales, tan to chestnut brown, lower bud-scales ca. 1.5 mm long. *Leaves rigid, spreading usually at less than right angles to branchlets, not parallel to one another, more evenly tapered to base and apex than in T. mairei*, lanceolate, narrowly elliptical to oblong (type), or linear in other morphs, evenly tapered to an acute, sharply pointed apex, recurved and/or twisted downwards, 1.5–2.5 cm long, 3.0–3.5 mm wide, 0.35–0.50 mm thick, dark green and convex above to rounded midrib, the adaxial midrib somewhat acute in lower half, often not evident near apex, paler green to yellowish green and convex below, or plane to concave below to rounded or flush midrib, often with orange tint in the herbarium, or dull rusty brown in the herbarium, thickened and liplike near margins, or plane and slightly revolute near margins; adaxial epidermal cells in T-sect. wider than tall, nearly wide rectangular, or elliptical in T-sect., usually 20–25 μm tall and 25–30 μm wide, thin-walled, slightly inflated; abaxial epidermal cells similar in T-sect. but not as large, 15–25 μm tall, 20–30 μm wide, slightly inflated near margin in 2–5 rows, more nearly rectangular in 7–11 cell rows near stomata bands, usually relatively short on midrib, 1–4(–10) \times l/w, sharply 4–6 angled, often wider and more slanted at one end (trapezoidal), not inflated (in T-sect) as in *T. mairei*, papillose to ca. (7–)8–12(–20) rows of cells from margins, typically without papillae on midrib (except young leaves), or partially papillose on outer midrib; papillae submarginal to medial in 2–3 irregular rows across each cell. Stomata bands broader than the non-stomatal region, olive green in fresh material; yellowish orange in dried leaves; stomata continuous in 11–15 rows, separated by 1–2 rows of accessory cells, stoma often with a blackish halo. Male cones globose, ca. 4 mm diam, yellowish green, scales generally 4-seriate; pollen sacs mostly 6, pale pink with reddish mid region and patchy resinous areas.



FIGS. 26-27. *Taxus kingstonii*, distinguished in part by leaf blades twisted and tapered to base; herbarium specimen and illustration, China, Taiwan. 26 (top). *Wilson 9738* (holotype, A). 27 (bottom left). H.-I. Li., *Woody flora of Taiwan* (1963, Fig. 2).

Female cone in bud subcylindric, ca. 2 mm long, greenish, scales mostly 5-seriate, conduplicate at base, maturing on 1st yr branchlets; seeds ovoid, dull, tan or purplish, stained by aril, angular where tapering to apex, or not angled, to 7 mm long, 4 mm wide.

Common name.—Kingston yew.

Distribution and ecology.—India (Khasi Hills), Myanmar, China (Tibet, Gansu, Shaanxi, Sichuan, Yunnan, Taiwan); forest margins or summits, 2450–2833 m in Taiwan, to 800 m on mainland Asia.

Additional specimens: **INDIA. Khasia:** *Hooker L77* (PH), 1337 (K); *Simmons 484* (P), Nungluai, 5000 ft, *Mann* (K, P). **MYANMAR (Burma):** Bernsrdmyo, Ruby Mines, 5600 ft (K). **CHINA. Tibet:** Oriental, Haut Mekong, Tsekou to Nekou, *Soulie 1411* (P: 2 sheets). **Gansu:** *F. N. Meyer 1790 ex USDA* (P). **Shaanxi (Shensi):** Tsin-lin au Lao-lin, 3000 m, year 1872 *Davis s.n.* (P). **Sichuan:** Tachienlu *Cheng 1001* (BM), *Cheng 1475* (P). **Yunnan:** Shweli-Salween Divide, 10,000 ft, 25°20' N, shrub 10–20 ft, open shady thickets, *Forrest 11789* (BM, K), Salween, *Forrest 12087* (K, S: C-2093), *Forrest s.n.* (A); Ma-Chang-Kai, valley, 25°30' N, 6000 ft., shrub, 20–30 ft., in thickets, Dec 1918, *Forrest 9462* (A, K), *Forrest 15945* (BM, K); Salween E of Tengyueh, to summit of Shwell, Shwelli River, *Rock 7587* (US). **Taiwan:** Paseian San [Pahsienshan], *Hsi 165* (PH); *Liu et al. 437*, (M, T, US; Fig. 3 in Li, Woody Fl. Taiwan,); Mt. Ammachan, *Liu 0389* (A, K), Arizan, Nitak (PH); Mt. Ammasshan, Taichung Hsien, *C.C. Tseng s.n.* (BH); *C-j. Chang* without locality data, *Tongshi #6*, 4 Mar 1993 (wba).

Taxus kingstonii is recognized by its relatively turgid recurved leaves (twist and curve downwards along their blades) that taper rather evenly to apex, and by their rusty orange color on the abaxial leaf surface (dried specimens). In herbarium specimens, the leaves often crisscross, especially near apex of branchlets. In other species of the *Sumatrana* Group, leaves are more reddish or greenish in color and evenly two-ranked and tightly adpressed to branchlets. The Kingston yew often has tightly adhering, strongly nerved bud-scales at the base of young branchlets, whereas scales in related species are similar to those of *T. chinensis*—generally smaller, less imbricate, or often not evident. The Kingston yew generally occurs at elevations between that of *T. mairei* (below 1200 m) and *T. wallichiana* (above 2300 m).

The Kingston yew tends to have the narrowest abaxial leaf margin among species of the *Sumatrana* Group, while this does not appear to be offset by wider stomata bands as most specimens were found to have 12–13 stomata rows per band (Spjut 2007). The width of the marginal region shows two patterns, one occurring around (6–)8–9 cells wide as seen by plants from Myanmar and Taiwan, and another ranging from (10–)12–16(–20) cells wide as seen in plants from Yunnan, Gansu, and Sichuan. This is in contrast to leaves of *Taxus mairei* that show a wider range in variation in which most specimens have 14 stomata rows per band and 14–24 marginal cells without papillae. This indicates a higher density of stomata in leaves of *T. mairei*. Variation in leaf anatomical data for *T. kingstonii* may be due to hybridization with *T. wallichiana* in northeastern India, with *T. chinensis* and *T. mairei* in Shaanxi, Gansu and Sichuan, and with *T. celebica* in Yunnan.

Taxus kingstonii includes specimens from Yunnan, India, and Taiwan that have been considered a distinct species by their long narrow, wide spreading leaves tapering to an acuminate apex as recognized by the epithet in regard to the acuminate leaf (Spjut unpublished, key to species of *Taxus*, USDA Memorandum 1995). They have the characteristic pale to rusty orange color on the abaxial leaf surface, but differ in the broader marginal zone of trapezoidal to short rectangular epidermal cells, a feature that is seen more in *T. mairei*. However, the abaxial midrib and marginal epidermal cells have thicker walls in contrast to bulging (mammillose) cells of *T. mairei*; the epidermal cell walls of *T. mairei* are often so thin that they appear transparent to the chloroplast of the spongy parenchyma cells. The character attribute of the acuminate leaf is similar to that of *T. celebica* and *T. sumatrana*; the latter distinguished by dried leaves appearing blood red along the midrib and marginal zones in sharp contrast to the yellowish green stomatal bands, the former by larger and more flattened leaves with a pale green color on the adaxial surface. Some specimens from India were annotated during 1996–1997 as *T. celebica*; however, in further study of a large number of specimens obtained by Professor C-j Chang (Purdue University) from Taiwan, the concept of *T. kingstonii* was broadened to include the specimens from northeastern India and Yunnan.

Despite the similarity of *T. kingstonii* to other species in the *Sumatrana* Group, it will probably be confused most often with *T. chinensis*. A number of specimens at BM, K and P, which I annotated *T. chinensis* (Oct 1997) at the time of my visit to these institutions—based on examination of leaves under a dissecting

scope—were later discovered to belong to *T. kingstonii* as a result of examining leaf sections under a compound microscope and discovering that papillae were lacking along the abaxial midrib and marginal zones. These specimens, including the type from Taiwan, appear closely related to *T. chinensis* by the leaf epidermal cells appearing larger on the adaxial surface than the abaxial surface as seen in transverse sections, and by the abaxial leaf surface having a rounded keeled midrib.

Taxus kingstonii is named in honor of David G. I. Kingston, a chemist who has done extensive work on elucidating and summarizing the taxane chemistry of the genus (e.g., Kingston 1996, 2005; Kingston et al. 1990). Taxol, from which the drug paclitaxel is marketed and used to treat ovarian and other cancers, was originally isolated from dried bark of *T. brevifolia*; however, fresh leaves of many species of *Taxus* have proved suitable for obtaining taxoids. Taxol was first characterized by Monroe Wall's group (Research Triangle Institute, Wani et al. 1971). They also discovered other significant antitumor agents such as camptothecin and holacanthone (Wall et al. 1972).

14. *Taxus mairei* (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu, Illustr. Native & Introd. Lign. Pl. Taiwan 1:16. 1960. (Figs. 28–29). *Tsuga mairei* Lemée & H. Lévillé, Monde des-Pl. sér. 2, 16:20. 1914. *Taxus chinensis* Rehder var. *mairei* (Lemée & H. Lév.) W.C. Cheng & L.K. Fu, Fl. Hupehensis 1:28. 1976 (also indicated as comb. nov. in Fl. Reipub. Pop. Sin. 7:443. 1978). *Taxus wallichiana* Zucc. var. *mairei* (Lemée & H. Lév.) L.K. Fu & Nan Li, Novon 7:264. 1997. TYPE: CHINA. YUNNAN: Dongchuan, 700–800 m, May 1912, *Maire s.n.* (HOLOTYPE [fide Rehder 1936]: E; ISOTYPES: A [fragment from E]!, BM!, P!).

Rehder (1936) reportedly found a holotype for *Tsuga mairei* at the Royal Botanic Garden at Edinburgh (E); however, it is not clear whether the Maire type at E was the only specimen “used” by the authors (ICBN Art. 9.1) since Lemée and Lévillé (in Lévillé 1914) did not cite specimens, and I have seen duplicates of Maire specimens at the Museum of Natural History in London (BM) and at the Museum of Natural History in Paris (P). The duplicate material at BM, although not from the Lévillé Herbarium, was also from E, presumably distributed after they purchased the Lévillé Herbarium in 1919 (Stafleu & Cowan 1979). Additionally, a fragment of the holotype of *T. mairei* is preserved in the Arnold Arboretum (A). The ICBN (Greuter et al. 2000) regards a fragment of a holotype as an isotype if the holotype was designated (Art. 8.3, Ex. 5), but in my opinion a distinction such as merotype should be made because other duplicate specimens at other institutions (isotypes) may have come from different plants.

Taxus mairei is distinguished from other species of the *Sumatrana* Group by the two ranked leaves spreading at nearly right angles, by the abaxial surface of leaves having a truncated but elevated midrib with epidermal cells larger in diameter than those on the adaxial surface (as seen in T-section), appearing mammillose. The midrib is usually channeled, especially in the mid region of the leaf.

Taxus mairei, like *T. chinensis*, has a long history of nomenclatural confusion. As indicated previously, the original authors thought they had a species of hemlock (*Tsuga*). Rehder (1936), upon discovering that *Tsuga mairei* Lemée & H. Lévillé (Lévillé 1914) belonged to *Taxus*, treated it as a synonym of *T. chinensis*; however, the ICBN (Art. 11.4) requires the earlier epithet, *mairei*, be adopted (S.Y. Hu, in Liu, Illustr. Nat. Ind. Lign. Pl. Taiwan 16. 1960). Cheng and Fu (1978) also made the illegitimate combination—*T. chinensis* var. *mairei*—which has since been transferred—*T. wallichiana* var. *mairei* (Lemée & H. Lév.) Fu & Li (in Li & Fu 1997). It must be emphasized that “in no case does a name have priority outside the rank in which it is published” (Art. 11.2); the epithet *chinensis* was employed at the varietal rank by Pilger (1903), and also by Florin (1948a). Rehder recognized *T. chinensis* as a species in 1919; whereas the epithet *mairei* was not used for a variety, but as a species epithet by Lemée and Lévillé in 1914, five years earlier; therefore, *mairei* has priority over *chinensis* in choice of epithet for a species, but has no priority whatsoever as a variety.

Regardless of the nomenclatural misapplications of the name, the taxonomic application in recent years has been to treat yews in subtropical China under the epithet “*mairei*” if their leaves lack papillae on the abaxial midrib (Fu et al. 1999). The species epithet *sumatrana*, an earlier available name, was not applied because botanists in China had not seen its type (Cheng & Fu 1978; Hu 1964; Li & Fu 1997); instead, they selected *mairei* for the varietal epithet—placing it under *T. wallichiana*.

Two varieties are recognized by differences in rigidity, branching, and phyllotaxy.

14a. *Taxus mairei* var. *mairei*

Common name.—Maire yew.

Distribution and ecology.—China (Sichuan, Yunnan, Anhui, Guizhou, Guangxi, Jiangxi, Fujian, Hunan, Guangdong, Zhejiang, Taiwan); forest margins, 300–1300 m.

Taxus mairei var. *mairei* is identified by zigzag branching, by the complanate leaves—arranged neatly in two-ranks in which the margins of adjacent leaves along one side of the branchlet are closely parallel—and by the mammillose (enlarged) cells on the abaxial midrib. Leaves also appear sessile; i.e., they are addressed to the branchlet at the base of the blade, and spread at right angles as they bend and twist. Leaves of var. *speciosa* are similar in shape but often larger in size, more unequally spaced along one side of a branchlet, differ only slightly in anatomy, but often differ in color—by remaining green when dried. Specimens of var. *speciosa* tend to have less dichotomous branching, or a more distinct monopodial branch.

The zigzag branching of *T. mairei* is perhaps an ancestral trait. This branching is seen mostly in southeastern China along coastal provinces as far north and inland as Hunan. Yews further north near Vladvostok, Russian Federation (*Palczewski* 3601), South Korea (*Wilson* 9332), and Japan (*K. Muijabe* 17 Sep 1910, A) show other dichotomous branching treated under *T. umbraculifera* var. *microcarpa*, which is also recognized by crowded (overlapping) leaves oriented in \pm decussate ranks. It may be noted that leaves of *T. umbraculifera*, *T. chinensis*, and *T. kingstonii* are relatively thick with a rounded (keeled) midrib, in contrast to thinner leaves in *T. mairei* that have a truncated to channeled midrib. *Taxus biternata*, a common species in temperate E Asia, easily recognized for its much-divided branchlets, has a phyllotaxy that is more similar to *T. sumatrana* than to other species of the *T. cuspidata* Alliance.

Occasional specimens of *T. mairei* are recognized to have an abaxial leaf epidermis of the *T. chinensis* type—as seen by the development of papillae on the midrib and along the marginal zone to ca. 8 cells from margin. Examples are *Ching* 1676 (A, P) from Zhejiang at “2600 ft,” and



Figs. 28–29. *Taxus mairei* var. *mairei*, distinguished by the isodichotomous branching and the closely parallel leaf arrangement. 28 (top). N Yunnan, *Maire s.n.*, photo of specimen at E (holotype) with fragment at A (isolectotype). 29 (bottom). *Maire* 131 (BM).

Chiao & Fan 464 (A, P, US) from Sichuan at “200 m.” These specimens also lack the enlarged mammillose midrib cells that characterize *T. mairei*, and the specimen from Zhejiang further differs in having rectangular shaped epidermal cells in transverse section. These specimens may be hybrids, or perhaps they are relicts of a *T. florinii*-*T. chinensis* complex from which *T. mairei* may have evolved. Leaves of *T. engelhardtii* from an Oligocene deposit in Europe are remarkably similar to these specimens of *T. mairei* in leaf arrangement, shape and anatomical details (Spjut 2007).

14b. *Taxus mairei* (Lemée & H. Lév.) S.Y. Hu ex T.S. Liu var. ***speciosa*** (Florin) Spjut, comb. et stat. nov. (**Fig. 30**). BASIONYM: *Taxus speciosa* Florin, Act. Hort. Berg. 14(8):382. 1948. TYPE: CHINA. GUIZHOU: [Fanjing Mts.] Kiangkow, 450 m, in light woods, tree 8 m high, fruit red, 8 Dec 1930, Y. Tsiang 7525 (HOLOTYPE: S; ISOTYPES: A!, BM!, K!, NY photocopy!, US!).

Common name.—Special yew.

Distribution and ecology.—China (S Shaanxi, Sichuan, NE Yunnan, Guizhou, N Guangxi, Hunan, Guangdong, W Hubei, Jiangxi, Zhejiang, Fujian, Taiwan); forest margins, near streams or open areas on hillsides, 100–750(–1600) m.

Taxus mairei var. *speciosa* is recognized by having alternate branchlets along a common branch, and by leaves appearing greenish and unequally spaced along branchlets in dried specimens. It appears to occur more frequently in the interior provinces of China, in contrast to var. *mairei* being found more along coastal provinces; however, exceptions include the type for *T. mairei* from N Yunnan and other specimens from Sichuan.

Taxus speciosa was described by Florin to distinguish a yew in China by the leaves having a smooth midrib from one other in China that he recognized to have a papillose midrib, which he had determined to represent *T. wallichiana* var. *chinensis* based on study of its type. The taxonomic feature of a smooth midrib was also erroneously described for *T. chinensis* by Handel-Mazzetti (1929). Florin (1948a) correctly realized that *T. chinensis* was closely related to *T. wallichiana* even though he only mentioned the type for *T. chinensis* and not *T. wallichiana*, although he had studied a duplicate specimen of the original material (*Wallich 6054A*). However, Florin incorrectly provided another name for the species that he distinguished by the absence of leaf papillae on the abaxial midrib; he cited not only an earlier name—*Cephalotaxus celebica*, but also its type (*Warburg 16889*). Other authorities soon realized this error (Cheng & Fu 1978), and Florin’s name was replaced by *T. mairei* S.Y. Hu (Liu 1960), who had also distinguished it from *T. chinensis* according to Florin taxonomy as evident by her 1955 annotations of Harvard specimens (Hu 1964).

Notwithstanding, *T. mairei* was soon replaced by an earlier name *T. celebica* (Warb.) Li (1963), who recognized only one species in China even though Hu (1964) indicated she adopted *T. mairei* because the type for *Cephalotaxus celebica* Warb. might differ based on one specimen she saw from Sulawesi that had a papillose midrib. She might have further assumed that the Berlin type of *C. celebica* was destroyed; however, as noted previously, Florin took a fragment of the Berlin type to Stockholm. It is surprising that an earlier name mentioned by Pilger (1903), *C. sumatrana*, had been neglected, until finally applied by de Laubenfels (1978). Although *T. speciosa* was founded upon nomenclatural error, it can still be recognized if its type can be shown to belong to a distinct species; however, in this study, the epithet is retained for a distinct variety.

15. *Taxus sumatrana* (Miq.) de Laubenfels, *Kalikasan*, Philipp. J. Biol. 7:151. 1978. (**Fig. 31**). *Cephalotaxus sumatrana* Miquel, Fl. Ind. Bat. 2:1076. 1859. TYPE: INDONESIA. SUMATERA: western, Fort de Kock, 3000 m, without date, *Teysmann s.n.* (HOLOTYPE: U!).

Common name.—Sumatera yew.

Distribution and ecology.—E Nepal, India (Khasia) Thailand, China (Zhejiang, Taiwan), The Philippines, and Indonesia (Sulawesi, Sumatera); mossy forests, 650–3000 m.

Taxus sumatrana is distinguished by the relatively thin (flaccid) leaves that taper to an acuminate apex and pucker on drying, curling inward along margins, often drying dark shiny green above (adaxial surface) and reddish green along margins and midrib below (abaxial surface). The abaxial surface has long rectangular epidermal cells, but are shorter in about 4 rows nearest the margin, and often half of the marginal cells are papillose towards the stomata band. The papillae develop in ±several opposite rows on each cell in contrast to alternately arranged papillae in the *Chinensis* Subgroup.



FIG. 30. *Taxus mairei* var. *speciosa*, distinguished by the predominant monopodial branching, Guizhou, China, *Tsiang* 7525, isotype (A).



FIG. 31. *Taxus sumatrana*, distinguished by the puckered leaf tapering to an acuminate apex, and by the abaxial leaf surface having an elevated and truncated midrib that is darker in color (and also the marginal zones) than the stomata bands; Sumatra, *Teysmann s.n.* (holotype, U).

the abaxial midrib and marginal zones ($\pm 3\text{--}12\times l/w$). Another with larger paler green leaves, either with shorter epidermal cells ($\pm 1\text{--}5\times l/w$), or with both longer and shorter cells, occurs in Nepal and Khasi, and a third in Taiwan, Luzon, and Sumatera has dull olive colored leaves.

III. BACCATA GROUP

The *Baccata* Group is divided into two species alliances based on leaf anatomical features of the stomata band as defined by its width and stomata density: (1) the Euro-Mediterranean *Baccata* Alliance and (2) the E Asian *Cuspidata* Alliance.

Differences in stomata density are evident by the number of stomata rows in a band relative to the absence of papillae on marginal cells. The *Baccata* Alliance has fewer stomata in slightly wider bands—at least by 4 cells—in which the stomata bands and their adjacent papillose cells usually extend to 4 cells from the margins, whereas the *Cuspidata* Alliance has a higher density of stomata in narrower bands, most often bordered by a marginal zone of 8–18 smooth cells across.

Other differences in the leaves between these species alliances include the arrangement of accessory cells, the prominence of papillae, and the number of the marginal papillose cells. In the *Baccata* Alliance, the accessory cells are often fusiform with papillae usually covering most of the cell. Their arrangement is diamphicyclic (Florin 1931) except for a narrow straight line of cells between stomata rows. A transitional region of fusiform papillose cells extends to a marginal zone of shorter rectangular or trapezoidal cells that lack papillae. Stomata bands in the *Cuspidata* Alliance, in contrast, usually have \pm pentangular to quadrangular or triangular accessory cells with concrescent papillae. Their stomata rows are not separated by a line of cells; rather, stomata often share the same stomata pit.

A third type of stomata band is found in *T. canadensis*, which is included in the *Cuspidata* Alliance even though it occurs in northeastern North America and the Euro-Mediterranean. Stomata bands of *T. canadensis* are much narrower (Nicolosi 1982)—bordered by at least 11 epapillose marginal cells across. Its stomata aperture and the irregular alignment of stomata rows are similar to *T. baccata* (Kvaček 1984), while the absence of papillae across a broad margin indicates a close relationship to *T. cuspidata*.

The distinction of these stomata band types may be correlated with molecular data. Collins et al. (2003) recognized three distinct DNA chloroplast types based on specimens identified as *T. baccata*, *T. cuspidata* and *T. canadensis*. They further suggested that these species probably evolved over a long period of time.

Leaves from two specimens, one from Taiwan (de Laubenfels P670 & P671), and another from the Philippines (de Laubenfels P650), have relatively narrow marginal zones without papillae. These specimens may key to species in the *Chinensis* Subgroup, but they are clearly related to *T. sumatrana* by the reddish discoloration along the abaxial midrib and marginal zones (as seen under low magnification, 10 \times), and by the rectangular shape of the abaxial epidermal cells and puckered leaf blades, which are more strongly curled inwards in upper third.

Three varieties of *T. sumatrana* are apparent. They differ in leaf size and color. The typical one—occurring in Indonesia, the Philippines, Thailand, and Jiangsu—has relatively smaller leaves with a dark green adaxial surface, and relatively long epidermal cells on

These basic types of stomata bands (*baccata*, *canadensis*, *cuspidata*)—as measured by the width of the band relative to the marginal region, 4, 8, and 12 cells in from the margin—are each postulated as an ancestral type. Hybrids, however, are apparent not only between species of these band types, but also with the *Sumatrana* Group as evidenced by the wider leaf margins—generally 16, 24 and 32 cells across. Various combination of other leaf anatomical feature—position and size of papillae on cells, shape of chloroplast, color of chloroplast and cell walls when dried, and shape and arrangement of parenchyma cells—also seem best explained by hybridization. The anatomical features appear independently inherited of gross morphological features such as habit, branching, and phyllotaxy.

III A. *Baccata* Alliance.—*Distribution and ecology*—Europe, N Africa, SW Asia (Euro-Mediterranean) and NW Himalayas; the Euro-Mediterranean plants in various hardwood and mixed mesophytic forest types, sea level to 500 m in the northern range, to 2000 m in S Europe, or to 2500 m in the Atlas Mountains of N Africa. In hardwood forests with beech (*Fagus orientalis* Lipsky), basswood (*Tilia* spp.), elm (*Ulmus* spp.), oak (*Quercus* spp.) and ash (*Fraxinus* spp.), or mixed hardwood-conifer with beech and spruce [*Picea abies* (L.) Karsten] (Browicz & Zieliński 1982; Duffey 1980) and occasional black pine (*Pinus heldreichii* Christ; Voliotis 1986). Around the Black Sea in beech-fir-spruce forests [*Abies nordmanniana* (Stev.) Spach, *A. cilicica* (Ant. & Kotschy) Carr., *Picea orientalis* (L.) Link], or spruce absent (Browicz & Zieliński 1982), or in the British Isles, forming single dominant woodlands with a closed canopy lacking understory shrubs and herbs (Thomas & Polwart 2003).

Yew plants of the *Baccata* Alliance are characterized by falcate or recurved leaves that overlap or criss-cross when branchlets are pressed, and by the abaxial surface of leaves having a transitional zone of papillose epidermal cells between stomata bands and a narrow bare marginal border, usually 4–7 cells wide.

One species of *Taxus* has been generally recognized in the Euro-Mediterranean region, *T. baccata*; however, leaf anatomical data clearly indicate two, *T. canadensis* and *T. baccata*, and additional species, *T. fastigiata* and *T. recurvata*, and varieties are evident by other morphological differences. The species allied to *T. baccata* and *T. cuspidata* are most distinct in Europe and eastern Asia, respectively, and least distinct in the Caucasus Mountains. *Taxus canadensis*, which has been traditionally known from eastern North America, is also recognized to occur in the Caucasus Mountains, Scandinavia, Estonia, and southwestern Mediterranean.

Taxus baccata has included numerous varieties or forms (Beissner 1891; Carrière 1855a, 1867; Elwes & Henry 1906; Gordon & Glendenning 1858; Gordon 1875; Knight 1850; Krüssmann 1985; Lawson et al. 1851; Loudon 1844; den Ouden & Boom 1965; Pilger 1903, 1916), recognized mostly from horticulture. The more distinct taxa have been treated in Bailey (1923, 1933), Carrière (1855a, 1867), Elwes and Henry (1906), Gordon and Glendenning (1858), Gordon (1875), and Pilger (1903, 1916). Prior to Beissner (1891) and Pilger (1903), these were often considered varieties; Rehder (in Bailey 1902, 1923, 1933), for example, initially treated them as varieties but later as “garden forms” (Rehder 1940, 1949). As evident in these publications, names for many yews in the horticultural trade were not clearly differentiated (taxonomically) prior to 1855.

Those in Carrière (1855a); therefore, are given priority in the present treatment except where earlier legitimate names can be applied. Nothing is known about his types or the existence of his herbarium material (Stafleu & Cowan 1976), and I would assume that his knowledge of yew taxonomy was based on descriptive information in literature and study of living material at gardens in France. Authors who have later described more taxa (e.g., Carrière 1867; Gordon & Glendenning 1858) have not always followed priority. And it should be noted that although horticultural material may exist in gardens, valid names cannot be based on living material; preserved specimens are required. Moreover, plants brought into cultivation from the wild must retain the names that were applied to the wild specimens.

Many specimens collected in the wild compare favorably with varieties described during the 19th century, while other varieties described later, as summarized in Chadwick and Keen (1976), Krüssmann (1985), and den Ouden and Boom (1965), appear to be only minor variations in color and habit that probably originated

from hybridization and selection of existing garden plants. Molecular data by Collins et al. (2003) indicate that many cultivars are genetically distinct.

It is also conceivable that many introductions could have originated before the yew horticultural trade developed—in the late 16th century (Mitchell 1974); the presence of *Homo sapiens* in the British Isles dates back to 5500 yr. For instance, “the oldest wooden artifact” used by man in the British Isles is a yew spear, which has been found in elephant remains 4600+ yr old (Godwin 1975), while in later times yews have been planted and harvested for the construction of long bows (Hageneder 2007; Mitchell 1974; Thomas & Polwart 2003). The existence of old yew trees in many churchyards (Loudon 1844; Lowe 1897) is also evidence of a long history of yew associated with religious beliefs, and Tittensor (1980) has suggested that yew woodlands in southern England originated from trees that marked “parish boundaries.”

In selecting neotypes, the available varietal names were considered based on priority of publication, current usage, and information in the original description, but not all varietal and cultivar names are accounted for in this treatment. This paper mentions those that appear more common and widely distributed. Unfortunately, it has not been possible to evaluate their character features in the field, and to determine to what extent yew populations may show polymorphisms and introgression, while it may be further noted that much of the yew habitat has already been destroyed by human activities (Heinze 2004). Nevertheless, molecular investigations are being undertaken to assess the genetic variability in various countries such as the United Kingdom, Spain, Portugal, Austria, Germany, Slovakia, and Switzerland as evident from various abstracts and reports on web sites.

16. *Taxus baccata* Linnaeus, Sp. Pl. 1040. 1753. (**Figs. 32**). LECTOTYPE, designated by Jonsell & Jarvis in Jarvis et al. 1993: Clifford Herb., 464, *Taxus* No. 1 (BM!).

Of eleven varieties of *Taxus baccata* proposed by (Spjut unpublished, www.worldbotanical.com), five, in addition to the typical variety, are mentioned below. All are widely distributed in the Euro-Mediterranean region.

16a. *Taxus baccata* var. *baccata*

Common name.—European yew.

Distribution.—Euro-Mediterranean.

Taxus baccata var. *baccata* is characterized by having equally divided horizontal to pendulous branchlets with leaves \pm spreading in the same plane along opposite sides of a branchlet (two-ranked), the adjacent leaves parallel to slightly overlapping or crisscrossing in dried specimens. In most other varieties leaves curve upwards on horizontal branchlets. *Taxus baccata* var. *washingtonii* (Hort. ex Richard Smith) Beissner, which is thought to have originated in horticulture, is possibly of hybrid origin with *Taxus canadensis* as one of its parental types (Gordon 1875); however, a number of specimens from eastern Europe also appear to be natural hybrids between *T. canadensis* in Europe and *T. baccata*.

16b. *Taxus baccata* L. var. *dovastoniana* Leighton, Fl. Shropshire 497. 1841. (**Figs. 33–35**). TYPE: ENGLAND.

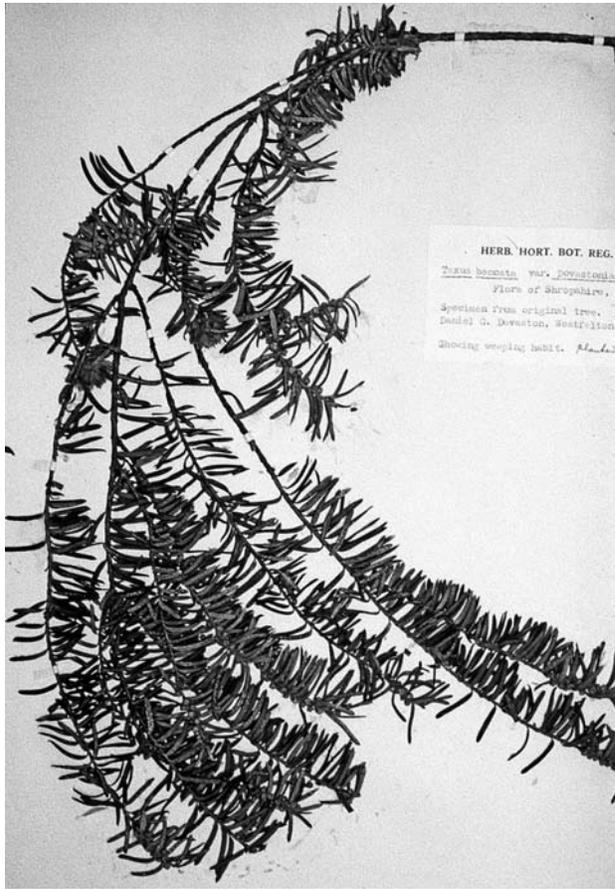
SALIK CO.: “Raised by John Dovaston in Westfelton near Shrewbury in 1777” (Loudon 1844), 1863, *Westfelton ex Herb. Bidwell*, annotated “*T. dovostonianum* Leighton,” with seed (NEOTYPE designated here: BM! [leaves with stomata in 10 rows per band, abaxial marginal border of 4 smooth cells]). Related material, BM: “original tree at Westfelton” *communic. Jackson s.n.*, without seed, with galls [10 stomata rows per band, 4–5 abaxial smooth marginal cells]; other material at K. Original herbarium material unknown; however, the neotype is from the original tree that was recognized and illustrated by Loudon in 1838 by common name, and noted to have been “56 ft” tall in 1836. Leighton (1841) made specific reference to Loudon’s illustration (“p. 2083, fig. 1990”), which was of the whole tree; this “cannot be critically identified for purposes of the precise application of the name of a taxon” (ICBN Art. 9.7).

The Dovaston yew is distinguished by relatively long undivided pendulous branchlets from ascending to horizontal branches and by the oblong leaves that spread vertically and horizontally. The type has dark green leaves with lateral and lower leaves spreading along two sides of branchlets and uppermost leaves spreading upwards. The female cones of the Dovaston yew often develop near ends of branchlets that apparently have terminated growth, and arillocarpia develop in pairs as noted by Leighton (1841). *Taxus baccata* var. *glauca* can be difficult to distinguish; it is recognized by the recurved branchlets that are more evenly distributed along the main branch.



Figs. 32A–B. *Taxus baccata*, distinguished by the isodichotomous branching and leaves spreading mostly parallel to each other. A (top). Lectotype (BM). B (bottom). Close-up of branchlet with leaves and mature male cones (lectotype).

- 16c. *Taxus baccata* L. var. *elegantissima*.** [Hort. ex] [Ravenscroft] [C.]Lawson et al., Abietineae—List Pl. Fir Tribe No. 10, 82. 1851. (**Fig. 36**). *Taxus baccata* L. f. *elegantissima* Beissner, Syst. Eintheil. Conif. 23. 1887. *Taxus baccata* L. (var.) *argentea* Loudon ex Gordon & Glendenning, Pinetum 312. 1858. TYPE: SPAIN. BALEARES: 1600 m, 15 Mar 1917, *Bianor-Maire* s.n. (NEOTYPE designated here: BM! with male cones [abaxial surface of leaves with 9 stomata rows per band, lacking papillae across 5–9 rectangular cells near margin]). Original herbarium material and origin unknown; horticultural form developed in the Handworth Nursery (den Ouden & Boom 1965).



FIGS. 33–35. *Taxus baccata* var. *dovostoniana*, distinguished by the terminally digitate long pendant branchlets (in the type). 33 (top left). Specimen from original tree (K). 34 (top right). Specimen at BM (neotype), branch with arillocarpia, from the original tree, with annotation—*Taxus dovostonianum* Leighton. 35 (lower left). Illustration reproduced from Carrière (1861).

The elegant yew is recognized by long linear leaves tapering gradually to an acute or acuminate apex, and by the leaves often appearing in hair-like tufts near apex of branchlets. The dried leaves are dark—almost blackish green above (adaxial surface)—and rusty orange below (abaxial surface), but on live plants—in cultivation—leaves have been described as “striped pale yellow, later whitish” (Lawson et al. 1851; Rehder 1940), or under more shady conditions, leaves may appear green to golden in sunlight (den Ouden & Boom 1965). Occasional herbarium specimens have these features (preserved).



FIG. 36. *Taxus baccata* var. *elegantissima*, distinguished by the linear leaves appearing two ranked and in hair-like tufts near apex of branchlets; Spain, Bianor-Maire (neotype, BM).

The cv. ‘Repandens’—that is common in cultivation in the eastern United States—appears related to this variety. Its low shrubby habit with a flat-topped crown may have been derived from a plant similar to what has been described for *T. baccata* var. *washingtonii*.

16d. *Taxus baccata* L. var. *glauca* Jacques ex Carrière, *Traité gén. Conif.* 519. 1855. (**Fig. 37**). *Taxus baccata* L. (f.) *glauca* (Carrière) Beissner, *Handb. Nadelholzk.* 175. 1891. TYPE: ARMENIA: Tschunakuchi, horticulture—ex *Herb. Petropolitani*, [year 1899] *Szovich 610* (NEOTYPE designated here: S: C-2072!), [with seed (leaf with 10 stomata rows per band, abaxial margin 4 cells across without papillae, midrib papillose)]; ISONEOTYPE: P! [with seed (leaf with 9 stomata rows per band, abaxial margin—4 smooth cells, papillose midrib)]. Related material: Hort. Ex Hillier Arboretum, England, 22 Mar 1976, “BM (NH) 1247,” in adnot. *T. baccata* ‘Glauc’ (‘Nigra’), “Blue John” (BM!). Original herbarium material and origin unknown.

Taxus baccata var. *glauca* is distinguished by the leaves that overlap parallel to each other while pointing upwards (erect secund), especially near apex of recurved or horizontal branchlets, and by appearing yellow in dried herbarium specimens, and by abruptly tapering to an obtuse apex. The branchlets are yellowish orange and recurved in many specimens. The Dovaston yew, which overlaps with the *glauca* yew in character attributes of color and pendulous branchlets, differs by the darker leaf color as seen in dried specimens, and by the uppermost leaves often directed towards apex of branchlets.

Variety *glauca* includes at least three horticultural forms. (1) The cv. ‘Glauc’ or ‘Nigra’ or ‘Blue John’, based on a specimen from the Hillier’s Arboretum (BM), has long recurved branchlets with oblong glaucous (caesious) leaves, lacking in the yellowish color. (2) A second one, f. *horizontalis* (Carrière), allegedly a cultivar that originated in France, is known for its long horizontal branches (Knight 1850; Callen 1977), while it may be distinguished by its golden color (f. *semperaurea* Dallimore; Rehder 1940, 1949). (3) A third—that is typical—has pendulous branchlets, and includes a specimen from horticulture under the name f. *pendula* as recognized by C. Baenitz indicated on annotation label of a herbarium specimen (US: 1395580).

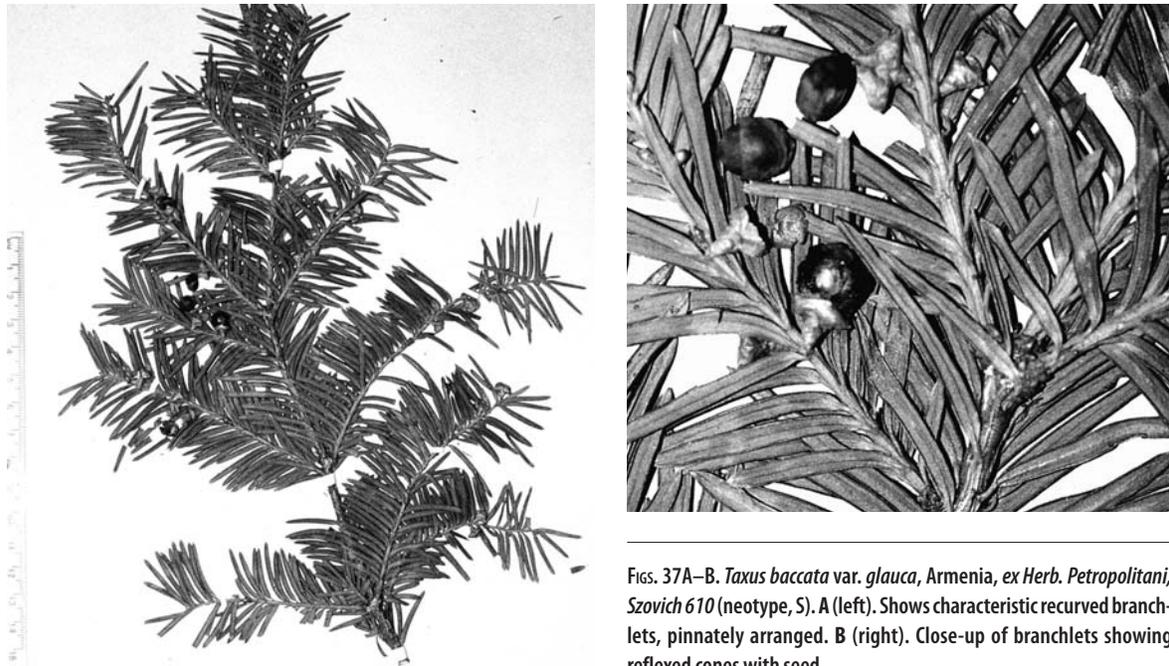
16e. *Taxus baccata* L. var. *pyramidalis* [Hort. ex] [Ravenscroft] [C.] Lawson, *Abietineae—List Pl. Fir Tribe No. 10, 83.* 1851. (**Fig. 38**). *Taxus baccata* L. [f.] *pyramidalis* Beissner, *Handb. Nadelholzk.* 175. 1891. *Taxus communis pyramidalis* Nelson, *Pinaceae* 172. 1866. *Taxus pyramidalis* Severin in Möller’s *Deutsch. Gärt.-Zeit.* 41:227. 1926. TYPE: FRANCE: Lanau Mutohir (Girandi), along marsh, 1 Sep 1930, *Tidestrom 12814*, with seed (NEOTYPE designated here: US!). Origin of material in horticulture unknown; original herbarium material unknown.

This variety is recognized by the equally divided flexuous branchlets that have a yellowish orange color and are often without leaves by the 3rd year and by leaves diverging widely from younger branchlets. It appears related to var. *elegantissima* by the paucity of cones. A specimen from Norway (*Gamble*) has darker metallic leaves instead of the more common yellowish green color. Leaves generally lack papillae across 4–6 cells near margins and are partly to entirely papillose across the midrib. Plants with more distinct radial orientation of leaves, which appear intermediate to var. *glauca*, may be distinguished as var. *ericoides* and var. *erecta* (Spjut unpubl., worldbotanical.com).

16f. *Taxus baccata* L. var. *variegata* Weston, *Bot. Univ.* 1:292, 347. 1770. (**Fig. 39**). *Taxus baccata* var. *foli-variegata*, Loudon, *Arbor. Brit.* 4:2068. 1838, “*T. b. 6 foliis variegates.*” (nom. illeg. superfl.). *Taxus baccata* (var.) *variegata aurea* Carrière, *Traité gén. conif.* 518. 1855 (nom. illeg. superfl.); *Taxus baccata* (var.) *aurea* Carrière, *Traité gén. conif.* 734. 1867 (nom. illeg. superfl.). *Taxus baccata* subf. *aureo-variegata* Pilger, *Pflanzenreich* 18 (iv, 5):114. 1903 (nom. illeg. superfl.). *Taxus baccata* f. *aurea* (Carrière) Pilger, *Mitt. Deutsch. Dendrol. Ges.* 25:11. 1916 (nom. illeg. superfl.). *Taxus communis aurea* [Nelson] *Pinaceae* 172. 1866 (nom. illeg. superfl.). TYPE: FINLAND: Ålandia, Lemland, *Florström s.n.* (NEOTYPE designated here: BM! [leaf with 11/12 stomata rows per band and an abaxial marginal area of 4 rows of rectangular, smooth cells]). Original material and origin unknown.

Taxus baccata var. *variegata* is recognized by stiffly spreading branchlets with erect leaves that are mostly dull olive green. The plants appear to be mostly shrubs. Tree forms that appear evident with more wide spreading branches may be referred to as var. *jacksonii* (Spjut unpublished, worldbotanical.com). These varieties, as well as a specimen from Iran referred to as var. *subpyramidalis* (Spjut unpubl., worldbotanical.com), are similar to *T. cuspidata*.

17. *Taxus contorta* Griffith, *Not. Pl. asiat.* 4: 28. 1854. “*Taxus contortus?* Vide Itinerary Notes, p. 351, No. 116.” See also Itin. pl. Khasyah mts., II:351. (1847–) 1848 (Book III, Chapter II, “Affghanistan Flora,



FIGS. 37A–B. *Taxus baccata* var. *glauca*, Armenia, ex Herb. Petropolitani, Szovich 610 (neotype, S). A (left). Shows characteristic recurved branchlets, pinnately arranged. B (right). Close-up of branchlets showing reflexed cones with seed.

Second year Kafiristhan. 116. *Taxus?*”] (**Fig. 40**). TYPE: AFGHANISTAN: W of Kabul, “Bharowul, in woods, 7000–7500 ft” (locality data from Griffith nos. 112–114 in Itin. pl. Khasyah mts, collected during 1839–1841), Griffith 5002 (LECTOTYPE designated here: K [lower right specimen of three on a single sheet, with label indicating it was collected from Afghanistan, distributed by Royal Gardens, Kew, 1862–3, accompanied by another label in handwriting with two words, Kafiristan, Griffith; the other two specimens evidently belong to another single collection by another collector from another location with a handwritten note on a label indicating that the bark was used in a tea in Ladakh, det. by Spjut as *T. contorta*]. Original material at K, a single specimen, Griffith 5002; however, the same number was used by Griffith for specimens he collected at other locations; e.g., *Taxus wallichiana* from Assam. No specimens cited, but locations from where specimens were reportedly collected are sequentially numbered in Griffith’s Notes 1847–48.

Griffith, in his earlier publication, noted “Arbor, foliis alternis linearibus compressis, sulcato univeniis basi $\frac{1}{2}$ tortis. Brought from Kafiristhan with the preceding [*Pinus*], the undersurface of the leaves subsequently becomes uppermost from torsion of the base. The change takes place gradually judging from the slight obliquity of young leaves. Stomata blocked up, with a brown curious cuticular substance.” Griffin later published the name *Taxus contorta* in Not. Pl. Asiat. 4:28. 1854 (“*Taxus contortus?* Vide Itinerary Notes, p. 351, No. 116”).

Taxus fuana Nan Li & R. R. Mill in Li & Fu, Novon 7:263. 1997.—TYPE: CHINA. TIBET (XIZANG): Jilong, 3000 m, Qingzhang Expedition 7032 (HOLOTYPE: PE!).

Taxus orientalis Bertoloni, Mem. Acad. Sci. Bologna ser. 2, 1, 229, pl. 2. 1862. No specimens cited, illustration provided, other original material consists only of a single specimen at BOLO. TYPE: INDIA. Northeastern India, western Sikkim [“Stim”], 8000 ft, without collector’s name, without collection number, filed separately in the herbarium of A. Bertoloni, with two labels, handwriting with locality data the same as that published by A. Bertoloni (HOLOTYPE: BOLO [BOLO0007756!], leaf fragments!). Bertoloni also described this taxon in Misc. Bot. 23:17, Tab. 2. 1862.

Two varieties are distinguished by leaf spread and length.

17a. *Taxus contorta* var. *contorta*

Common name.—West Himalayan yew.

Distribution and ecology.—Mixed coniferous-hardwood forests of W Himalayas, 2300–3500 m; Afghanistan, Pakistan, India, W Nepal, and China (SW Tibet). Noted to be common in the Garhwal and Kumaon regions at elevations near 8500 ft (Gamble 1922; Gordon 1875), where clouds often hang in oak-conifer forests of *Quercus semecarpifolia* Sm., *Abies pindrow* (D. Don) Royle, and *Rhododendron arboreum* Sm. (Freitag 1971; Rau 1974). In the Uri Range closely associated with *Abies pindrow*-*Picea smithiana* (Wall.) Boiss. forest (Sapru 1975), a vegetation type common to the higher ranges in the W and C Himalayas of India and Nepal

(Champion & Seth 1968; Rau 1974). In the Kumaon and Nepal regions mostly on N side of the Himalayas in hemlock (*Tsuga dumosa* [D. Don] Eichler) forests with spruce (*Picea smithiana*) as a common associate (Rau 1974), especially near Rara Lake in W Nepal (Stainton 1972).

Taxus contorta is easily identified in the herbarium by the relatively long and straight narrow leaves that are generally crowded along stems in nearly two ranks, which in the typical form generally do not spread more than 60° from branchlets. The leaf mesophyll contains distinctive parenchyma cells (idioblasts) that in the herbarium slowly develop a yellowish to reddish color, as determined in part from 1-year old specimens (Amin 25025, 25045, 25149 from Pakistan, KIB) that show only minor discoloration of cell walls. The idioblasts occur predominantly across the mid region of the leaf mesophyll and around the diffusion area of the vascular bundle. The cell walls have striations that may suggest a type of sclerenchyma cell, but this appears to be a secretory product—a terpenoid compound—in the cell that when dried becomes deposited on the cell walls. Rao and Malaviya (1965) described what they called “osteo-sclereids” in leaves of one of four varieties of *T. baccata* they reportedly studied from cultivated specimens in Sri Lanka and India; however, their illustrations of leaf sections show thicker-walled cells that are sclereids. I have not seen these “osteo-sclereids” in yew leaves, while I have observed similar cells in Asian species of *Torreya*.

The spongy parenchyma cells of many *T. baccata* specimens have similar idioblasts as seen by their spherical shape and dark color, but lack striated cell walls, and do not fall out when sectioned. Species in the *Cuspidata* Alliance (E Asia) generally have a leaf mesophyll largely of loose spherical to ellipsoidal cells connected together by short cylindrical cells without idioblasts.

Taxus contorta is more related to *T. baccata* than to *T. wallichiana* by the relatively low number of leaf stomata rows per band—usually 7–8, by features of the leaf parenchyma cells as just described, and by the green to olivaceous color in leaves of dried specimens. The leaf mesophyll of *T. wallichiana* has periclinally oriented cells connected in a skeletal-like net; in longitudinal sections these cells appear like bones. It is interesting that *T. baccata* shows more variation (in Europe) than *T. contorta* (in the Himalayas) in branching, leaf arrangement and leaf anatomy. Of particular relevance is the occurrence of papillae on the abaxial midrib of leaves—that in *T. baccata* can be densely papillose (e.g., lectotype), or entirely smooth (e.g., *Curic s.n.*, from Bosnia, K), whereas *T. contorta* always has a densely papillose midrib.

The close relationship between the European *T. baccata* and Himalayan *T. contorta* was recognized by Handel-Mazzetti (1929) and by Florin—who, in his annotations of specimens at Stockholm (S), treated it as a subspecies of *T. baccata*, adopting the epithet of *T. orientalis* Bertol., a later name.

Other botanists have independently recognized *T. contorta* as distinct from *T. baccata* and *T. wallichiana*, but by names that are not always in accordance with the ICBN. For instance, Handel-Mazzetti (1929) correctly realized that *T. wallichiana* could be based on *Wallich 6054A*, but referred the Northwest Himalayan yew to *T. orientalis*. He was also aware of *T. contorta*, which he considered a nomen nudum; however, Griffith (1854) referred back to his earlier 1848 publication (see nomenclature citations above); thus, *T. contorta* is not a nomen nudum (Art. 32.3, 32.4, 34.1), and predates *T. orientalis* Bertoloni (1862). Franco (1964), who reviewed Taxaceae for *Flora Europaea*, also recognized the west Himalayan yew (*T. contorta*) as a distinct species, but he annotated specimens (BM) by another name (*T. angustifolia* Franco, ined., dated 1956) that if published would have been illegitimate; more recently, Nan Li and R. R. Mill (Li & Fu 1997) reached a similar conclusion, but did publish their superfluous name, *T. fuana*. Occasional collections by Polunin et al. (e.g., No. 432, BM) had been correctly determined, while most herbarium collections of this species have been misidentified as *T. wallichiana*.

It is not clear to what extent Wallich and Griffith had distinguished yews in the Himalayas. Wallich's (1826) *Tentamen Florae Nepalensis* recognized only one species, determined as *T. wallichiana* by Zuccarrini (Siebold & Zuccarini 1843); however, Wallich specimens of *Taxus* numbered 6054, differentiated by letters A-E, suggest they were distinguished—at least by collectors and location, and may include an annotation *T. virgata* Wall. (nomen nudum), which I have identified as *T. wallichiana* (*Blinkworth s.n.* BM, reportedly from Kumaon, but probably from Nepal), or *T. baccata* (young shoot on sheet with 3 other specimens of *T. contorta*, *Wallich 6054*, ex Herb. Gordon, with “b” indicated lightly in pencil, K; probably added for comparison). Most



FIGS. 38A–B. *Taxus baccata* var. *pyramidalis*, distinguished in part by wide spreading, often isodichotomous, branchlets, France, Tidestrom 12814 (neotype, US). A (top). Herbarium specimen. B (lower left insert). Close-up of branchlet showing seed and persistent bud-scales.



FIGS. 39A–B. *Taxus baccata* var. *variegata*, distinguished by the rigid pinnate branching and lack of glaucous color, the abaxial surface of the leaves appearing rusty orange; Finland, *Florström s.n.* (neotype, BM). A (left). Herbarium specimen. B (top right). Close-up of branchlet with terminal male cones.

Wallich 6054A (from Nepal) belong to *T. wallichiana*, whereas most *Wallich 6054B* (from Kumaon) are *T. contorta*. Griffith, who worked with Wallich on occasion (Burkhill 1965), also assigned mixed collections of *Taxus* to the same number with different data; the type, for example, is from Afghanistan, but other labels with this number (*Griffith 5002*) indicate the specimens were collected in the eastern Himalayas. Griffith (1854) recognized possibly two species from Bhutan, distinguished by “axillary” and “terminal” “inflorescences” and



FIG. 40. Herbarium sheet at K with three specimens, all are *Taxus contorta*, the one on right from Afghanistan, Griffith 5002, lectotype, the species distinguished in part by the relatively straight leaf blades in contrast to the falcate leaf in *T. wallichiana*.

a third “3. *Taxus contortus?*” by reference to his collection from Afghanistan. I have noted that three species of *Taxus* are represented in Griffith collections, and also from J. D. Hooker in the Gray Herbarium (J. D. Hooker 77, 87, GH) with three different species (*T. contorta*, *T. kingstonii*, *T. wallichiana*) all on one herbarium sheet reportedly from Khasia, 5000–6000 ft, and from other locations in India.

Although *T. contorta* appears quite distinct from *T. wallichiana*, hybrids seem evident by the respective higher and lower counts of stomata rows where geographical ranges of these species overlap in central and east Himalayas. This includes the type for *T. orientalis* (BOLO!) from Sikkim. In several leaves studied of the *T. orientalis* type, the parenchyma cells were found to be those of the *T. contorta* type, whereas the slightly larger epidermal cells (20–25 µm tall, 25–35 µm wide) along with the higher stomata counts (10–11 rows per band) indicate affinity to *T. wallichiana*. Additionally, the absence of bud-scales at the base of branchlets, and the strongly revolute linear leaves (illustrated by Bertoloni 1862) are other features I associate with *T. contorta*. Specimens of *T. wallichiana* var. *yunnanensis* from Sikkim were found to have fewer stomata rows (e.g., 13 rows, Kurz s.n. A; 14 rows, J. D. Hooker & Thomson A, GH, K) compared to specimens from other regions.

17b. *Taxus contorta* Griff. var. ***mucronata*** Spjut, var. nov. (**Fig. 41**). *Taxus mucronata* Spjut ined. in adnot. (BM [Oct 1997], A [Jun 1996]). TYPE: BHUTAN (Eastern). HA: 27°22' 89°18', 9,000 ft, tree 15 ft, 11 Apr 1949, Ludlow et al. 16035, with male cones (HOLOTYPE: A!; ISOTYPE: BM!).

Differt a var. *contorta* folia breviora valdes divaricatis, 5–10 longiora quam latiora.

Tree to 3 m or more; leaves sharply bent at base of blade, 1.5–2.5 cm long, ca. 2 mm wide; abaxial margin up to 23 cells across, the epidermal cells irregularly quadrate in up to 6 rows nearest the margin, becoming long fusiform to rectangular towards the stomata band and on midrib, mostly 3–7× l/w, papillose on more than half of the marginal cells—to within 8 (–5) cells across from margins and entirely on midrib; stomata bands greenish, or yellowish green, narrower than the marginal region, with 9–11 rows of stomata; spongy mesophyll with idioblasts. Male cone scales 4–5 seriate; sporangiophores 8, united into a ribbed column ca. 2 mm long, thickened at apex of column, separating into 8 umbrellalike segments, each with 5–8-cuculately lobed microsporangia ca. 1 mm diam. Seed in one specimen globose, reddish.

Common name.—Mucronate-leaved yew.

Distribution and ecology.—Nepal, Bhutan; upper forest region, 2300–3100 m.

Additional specimens: **NEPAL**. *Dobremez 2106* (BM); Marayandi Valley, 3100 m, *Wraber 514* (BM); ridge S of Bhahwe Sekh, 9000 ft, *Polunin et al. 1873* (BM); Dhawalagiri Zone, Mustang Dist., Ghasa, 2300 m, *Mikage et al. 9550282* (BM).

I annotated one specimen from the Arnold Arboretum Herbarium (A) as “*Taxus mucronata* Spjut (ined.)” in June 1996, designating it as type. Other specimens at the Museum of Natural History in London (BM) and the Kew Herbarium (K) were later discovered and similarly annotated (Oct. 1997), including an isotype at BM. An illustration in Cheng and Fu (1978) for *T. wallichiana*, redrawn for the English edition of the *Flora of China* (Fu et al. 1999) as representative of *T. fuana*, was thought to have originally been drawn from the type specimen for *T. fuana* as reported on the WBA website (2003–2006); however, upon study of the images of the PE *Taxus* collections that were made available online during 2006, the holotype for *T. fuana* was found to belong to the typical variety. Although *Taxus fuana* was not described until Nov 1997, all specimens I saw at K (Oct. 1997) bearing the annotated name *T. fuana* by Nan Li and R.R. Mill belonged to var. *contorta*, whereas specimens I recognized as “*T. mucronata* Spjut ined.” were not annotated by Nan Li and R. R. Mill. Additionally, Farjon (1998) indicated *T. fuana* to occur only in Tibet, but the basis for his decision on this and other species he recognized in *Taxus* is without taxonomic merit. In a review of specimen images of *Taxus* on the PE virtual herbarium, other specimens of *T. contorta* var. *contorta* were found listed under *T. wallichiana*, and also erroneously identified as *T. wallichiana*, while I might add that none of the specimens I studied in herbaria outside China had specimens of *T. contorta* from China.

Variety *mucronata* is distinguished from the typical variety by the relatively shorter and more sharply reflexed leaves—more at base of blade than near junction with branchlet. Leaves also differ from most



FIG. 41A-B. *Taxus contorta* var. *mucronata*, distinguished in part by the relatively short reflexed leaves. A (left). Herbarium specimen (holotype, A). B (right). Close-up of branchlets with male cones.

specimens of the typical variety by their abaxial surface having a smooth marginal border of 5–8 irregularly quadrate epidermal cells, and 9–11 stomata rows per band. Despite these differences, occasional specimens from Nepal are difficult to assign to either variety. An analysis of the leaf arrangement in *T. contorta* specimens shows that leaves increasingly diverge at wider angles going from west to east in the Himalayas. This also appears correlated also with an increase in number of stomata rows per band (Spjut 2006). The higher stomata counts and wider angle of divergence in leaves of *T. contorta*, however, are characteristics of *T. wallichiana*, whereas the wider leaf margin and reflexed leaves are also characteristics of *T. umbraculifera*. Nevertheless, the apparent hybrids between the two varieties of *T. contorta* would seem to justify varietal status for var. *mucronata*.

18. *Taxus fastigiata* Lindley, Syn. Brit. Flora 241. 1829. (**Fig. 42**). *Taxus baccata* L. (var.) *fastigiata* (Lindl.) Loudon, Arbor. frutic. britt. 4:2066. 1838. *Taxus baccata* L. f. *fastigiata* (Lindl.) Pilger, Pflanzenreich 18 (iv, 5):115. 1903. *Taxus baccata* L. var. *hibernica* Hooker ex Henkel & Hochstetter, Syn. Nadelhölzer 356. 1865 (nom. illeg. superfl.). TYPE: IRELAND: from Florence Court, ex Herb. Jackson, Sep 1890, Stewart s.n. (NEOTYPE designated here: K!). No specimens cited, none reported in the Lindley Herbarium. Original material unknown. Ireland, “mountains of Fermanagh” Parish of Killesher near Aghenteroark, George Willis, without herbarium specimens; fide Veitch et al. (1881)—quoting from manuscript by Lord Kinnarid with further reference to Rossie Priory, 8 Sep 1867—transplanted to Florence Court ca. one hundred years ago; thus originally collected in 1767, or as early as 1740 fide internet sources.

Common name.—Irish yew.

Distribution.—British Isles—United Kingdom (Ireland, Scotland, England), Sardinia?

The Irish yew (*T. fastigiata*) has long been considered distinct from other yews; yet, most authorities have treated it as a synonym of *T. baccata*. Its radial orientation of leaves is similar to east Asian *T. umbraculifera* in bending downwards (recurved) and to *T. caespitosa* in the imbricate arrangement, and it is also similar



FIG. 42. *Taxus fastigiata*, distinguished by the erect to ascending branches and by the imbricate arrangement of dark green leaves with blades that curve downwards from base to apex; Florence Court, ex Herb. Jackson, Stewart s.n. (neotype, K).

to a Euro-Mediterranean variety of *T. baccata* from Morocco. The Euro-Mediterranean plants with radial spreading leaves, which occur near the western continental distribution limits of the genus, are relatively rare. The columnar habit, associated with radial orientation of leaves, would seem to be an adaptation to open habitats such as bogs, fens, lake shores, or areas along sea coasts.

Taxus fastigiata is known primarily from two plants that once grew in the Cuilcagh Mountains in Fermanagh County, Ireland. A farmer named George Willis dug up two female plants; one was planted in his garden, the other was given to his landlord, Lord Enniskillen, who planted it at Florence Court (Veitch et al. 1881). Willis's yew died in 1865, but the Florence yew prospered, and subsequently has become the source for many horticultural varieties (Veitch et al. 1881). Additionally, male plants appear evident at North Mundham in Sussex, England (Bean 1953), and specimens from Tweeddale in Scotland may also be native. Irish yew is common in cultivation in the United States, especially in the west where it can be maintained in hot and dry climates, temperatures often exceeding 100°F as evident at Redding, CA.

The common "English yew," which I recognize as *T. recurvata*, is distinguished from typical *T. baccata* by the arcuate leaves that curve downwards. Specimens from the British Isles show a more radial orientation of leaves compared to specimens from central and Eastern Europe. The leaves of *T. recurvata* from the British Isles also appear to develop closer together on branchlets and are darker green in color as seen in *T. fastigiata*. This includes a specimen from Neopath Castle Scotland (K) that in my opinion is a hybrid between male *T. recurvata* and female *T. fastigiata*; the collectors Bean and Hill indicated it was a "distinct variety" by its "plumose growth."

Several varieties of Irish yew are proposed (www.worldbotanical.com). One appears to be a low shrub in the British Isles and possibly on Sardinia; the other, a tree, is known only from Scotland and England. The Scotland plants, which are from Lock Lomond, differ from the typical Irish yew in the branches ascending more widely. The relationships of the proposed varieties require more study.

As mentioned elsewhere in this paper, and in Spjut (2007), the *Cuspidata* Alliance includes plants with a similar phyllotaxy to that of the Irish yew, particularly in specimens from the islands of Sakhalin, Hokkaido, and Honshu. I annotated one specimen from Sakhalin Island (*Dvorakovskaia & Bokina*, A) as *T. fastigiata* in June 1996 because the recurved leaves with a purplish green color seemed characteristic of the Irish yew; however, I now regard it as *T. caespitosa* var. *latifolia*. Another specimen of this variety from Sakhalin Island, *Flanakan & Kirkham* 203 (K), resembles *T. baccata* var. *glauca* in the upturned leaves with a yellowish green color. The Asian *T. caespitosa* is usually distinguishable by the spreading leaves that bend or curve more along their petioles instead of along their blades.

19. *Taxus recurvata* Hort. ex [Ravenscroft] [C.] Lawson, Abietineae—List Pl. Fir Tribe No. 10, 83 ("A handsome and distinct species with recurved branchlets and leaves mostly directed upwards"). 1851. (**Fig. 43**). *Taxus baccata* L. [var.] *recurvata* (Hort. ex C. Lawson) Carrière, Traité gén. Conif. 520 ("Branches étalées, divariquées, alongées, peu ramifées, le plus souvent réfléchies"; "feuilles longues et étroites, falquées-countour-nées, involutes." "Cette variété ne peut être confondue avec aucune autre"). 1855. TYPE: ENGLAND: SUSSEX: Bury Hill, near summit on chalk, 24 Aug 1933, *Hubbard s.n.* (NEOTYPE designated here: K! [with mature seed; leaf with 8 stomata rows per band and abaxial marginal border of 4 smooth cells]. Original material unknown.

Common name.—English yew.

Distribution.—Europe, SW Asia (Caucasus Mts.).

This species is recognized by plants having most of the following characteristics in common: arcuate leaves, i.e. the leaves are recurved (turned downwards), the leaves crisscross more than parallel each other along one side of a branchlet, the adaxial leaf surface appearing strongly convex, leaves discolorous, and prismatic seeds developing on branchlets of the current season. *Taxus baccata* differs by paler green leaves with the blades facing in the same plane as that of branchlets, and with leaves along one side of the branchlet overlapping more than crisscrossing each other, and also curving upwards instead of downwards.

Taxus recurvata has intermediate phyllotaxy between the radial type of *T. fastigiata* and the distichous-like arrangement of *T. baccata*. In the British Isles, *T. recurvata* is common to chalk downs where "yew woods" form a climax community as evident from specimens that correspond to literature (Watt 1926; Rodwell



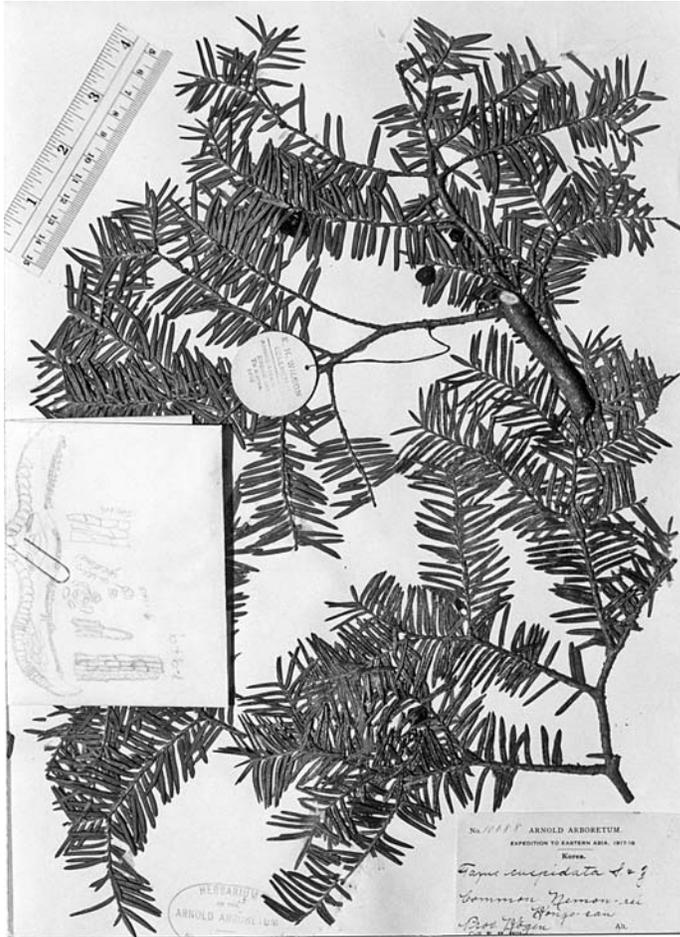
FIGS. 43A–B. *Taxus recurvata*, distinguished by the recurved branchlets, crisscrossing leaves with sharp contrast in color between the abaxial and adaxial surfaces; England, Hubbard s.n. (neotype, K). A (left). Herbarium specimen. B (above). Close-up of leaves and seeds.

et al. 1991—as *T. baccata*). Drawings and photos in Loudon (1844), Watt (1926), and Rodwell et al. (1991) show the twisted branches that characterize this species. Specimens from Ireland identified as *T. baccata* var. *glauca* may be an introduction as yew is generally rare in Ireland; however, one record is known to occur with *Arbutus unedo*, a species more commonly found in the Mediterranean flora. The natural occurrence of yew in Scotland has also been considered rare (Godwin 1975; Mitchell 1974)—where two different varieties of *T. fastigiata* are proposed, one from Inchcailloch Island (Loch Lomond) and another from near Tweeddale. A large tree—with a circumference of 16 m, from near Fortingall—is thought to be the oldest living yew in Europe, estimated at 3000 yr (Voliotis 1986) to 5000 (–9000) yr on internet sources. I have not studied specimens of this plant but photos on the web show the isodichotomously divided branches from the trunk that suggests *T. baccata*, and one fuzzy photo showing leaves on pendant branches that further suggest *T. baccata* var. *dovastoniana*.

Plants with less distinct radial orientation and more distant leaves are proposed as distinct varieties (Spjut, unpubl., www.worldbotanical.com). They differ by leaf length. One with long narrow linear leaves, which includes specimens from Madeira, British Isles and Romania, is difficult to distinguish from *T. contorta*.

IIIB. BACCATA GROUP, CUSPIDATA ALLIANCE

Yews of this alliance are recognized by leaves spreading from branchlets more by bending of their petioles than by curving of their blades, and by having a relatively broad abaxial margin zone of epidermal cells without papillae, usually from 8–24 cells across. Another less obvious distinction is that the epidermal cells are slightly wider and shorter than those of the *Baccata* Alliance, except for *T. canadensis*. Five species and 15 varieties are recognized.



FIGS. 44A–B. *Taxus biternata*, distinguished by the much-divided thin branchlets, leaves pinched inwards ca. two-thirds up from the base, and by cones maturing on branchlets of the current season; South Korea, Wilson 10688 (holotype, A). A (top). Herbarium specimen. B (bottom). Branchlets and leaves with two arillocarpia.



The taxa are very difficult to distinguish as they intergrade; *Taxus biternata* and *T. caespitosa* var. *caespitosa* are most distinct.

20. *Taxus biternata* Spjut, sp. nov. (Figs. 6, 44). TYPE: SOUTH KOREA. KYOG[SANG] PROV.: Kyongsan, Nemon-rei, common or abundant, 15 Sep 1917, Wilson 10688 (HOLOTYPE: A! with arillocarpia (abaxial leaf with marginal zone of 8–9 smooth cells, 9 papillose cells, stomata 9 rows per band, midrib lacking papillae); ISOTYPES: K! (leaf with marginal zone of 6 cells across without papillae followed by 8 rows of papillose cells, 7 stomata rows, and midrib with marginal papillae), US!).

Taxus microcarpa (Trautv.) Spjut ined. (in adnot.: A, BH, BM, GH, K, NA, P).

Taxus canadensis affinis, a qua imprimis differt arbor, ad 30 m alta, arillocarpia maturibus ramulus primus et stomata (7–)9–13(–16) seriata/zona; ramis anisodichotomis horizontalibus, ramulis diffusibus biternatifidibus; folia pectinatum disposita, patentia, linearia, 1.5–2.5 cm longa, 1.5–2.5 mm lata, acuta ad acuminata, 0.150–0.300 mm crassa, supra ramis petiolibus contorta, supra convexa, subtus concava ad plana, cellulas epidermis supra 0.8–25 μ m alta, 20–30 μ m lata, quasi elliptica in sectione transversala; ventralibus epidermae cellulae quasi rectangulara, non inflata proximus marginalia, costa interdum papillosa vel laevis, proparte papillosa versas de maginalia, sine papillae (6–)8–12(–19) cellulae marginales latis.

Trees or shrubs with erect trunks and horizontal branches, to 30 m high; *branchlets often short and much-divided*, subpinnately arranged but unequally divided, appearing ternately divided or with short delicate tertiary branchlets, horizontal or weeping, yellowish green when young, yellowish orange with age; bud-scales closely overlapping in 3–4 ranks, mostly persistent to the 3rd yr, thick, deltoid, concave, medially recurved and incurved towards apex to form a cusp, with an obscurely thickened midnerve, ca. 1 mm long, spreading from base of branchlets. Leaves persistent on older twigs, or lacking, green upon drying, in two-ranked like arrangement to apex, linear, straight to slightly falcate, 1–2 cm long, 1–2 mm wide, 150–250 μ m thick, pale green and convex above to a rounded midrib that forms a channel along the base of the midrib, pale yellowish green and concave below to a rounded midrib, revolute near margins 30–90° in dried leaves, more notably revolute at upper one-third of leaf; adaxial epidermal cells in T-sect. elliptical, 10–15 μ m tall, 25–40 μ m wide; abaxial epidermal cells similar or larger, 10–15 μ m tall, 15–25 μ m wide, numbering 11–18 between margin and stomata band, mostly rectangular, or sinuous near the stomata band, 3–7 \times l/w except quadrate in 1–3 rows near margins, epapillose entirely across the marginal region, or marginal region often partially papillose, often epapillose on (6–) 8–18 cells in from the margins, occasionally with obscure papillae on midrib, papillae usually more prominent on marginal cells bordering stomata band, in 2 opposite rows; stomata bands broader than the marginal region, with 7–13(–16) stomata rows per band. Male bud cones globose, ca. 1 mm diam.; scales 4-seriate; sporophylls ca. 14, united into a terete, smooth or obscurely ribbed column, thickened at apex, spreading shortly above, each branch bearing 8–10 lobed, cucullate sporangia. Female cone scales 4–5 seriate; aril red or pink with tinge of white, with a deep cup, drying dark purple; seed subglobose, obscurely angled where tapering to apex in upper half, 4 mm long, 2–4 mm diam.

Common name.—Delicate branch yew.

Distribution and ecology.—China (NE, Manchuria), Russian Federation (SE Region), North Korea, South Korea, Japan; forests, 800–1400 m. In NE China dominant in “mixed broad-leaved deciduous and needle-leaved evergreen forests” (Hou 1983). On N Hokkaido (Japan), “fairly common” within a mixed conifer hardwood forest of *Picea jezoensis* (Siebold & Zucc.) Carrière, *P. glehnii* (F. Schmidt) Mast., *Abies sachalinensis* (F. Schmidt) Mast., *Populus maximowiczii* A. Henry, *Kalopanax septemlobus* (Thunb.) Koidz., *Ulmus japonica* Siebold, and *Acer pictum* Thunb. ex Murray (Wilson 1916, as *T. cuspidata*). Common in cultivation, including Cv. ‘Capitata’ and shrub forms misapplied to *T. media* Rehder. At the Seirest Arboretum, apparently spreading by seed among native deciduous hardwoods.

Additional specimens. **RUSSIAN FEDERATION. Far East Region:** Pryanyk For. Div., Zalesse Village, silver fir-cedar-broad-leaved forest, B. *Cerereu* (in Russian, A). **Manchuria:** Northern, Sochintzest, forest, small trees 20 Sep 1931, *Skvortzov s.n.* (A). **CHINA. Jilin** (Kirin), 5 Sep 1931, C. H. Chen 539 (A); Mandshuria SE, *ex herb. hort. bot. Petropolitani*, 1860, Maximowicz, iter secundum (A, US); Northern China {**Shaanxi:** Tai-pei-shan *fide* Rehder & Wilson in Sargent 1914], *Purdum s.n.* (GH). **[South] Korea.** Kyoglsang] Prov.: Kyongsan, Nemon-rei, common or abundant, Wilson 10519 (A, BM, US), Wilson 10688 (A, BM); N. Heian Prov., O.G.M. Co. Mines, Pukchin & Takkari, 833–1000 m, not uncommon in moist forests, Wilson 8685 (A, K, US); Shinkabachin Heizanchien to Ehoshin, Kankyo-N Heian divide, rare, 5 Sep 1917, Wilson 9097 (A); Seoul, East Palace Park 24 Sep 1905, *Jack s.n.* (A). **JAPAN. Hokkaido:** Cosl Mines, Utishini, tree,

20 Sep 1892, *Sargent s.n.* (A); Aza-akaigawa in Morin-machi, 42°0'N 140°39'E, near stream in open woodland, 200 m, tree 20 ft, seeds embedded in reddish aril, *Meyer et al.* 19261 (NA); Teshikaga-Machi, 3.2 km SE of Lake Kusharo, road 243, Kawakami-gun, Kushiro, 43.35 N, 144.23 E, *Meyer et al.* 19112 (NA); Hokkaido, Kitami prov., common in moist woods, tree 15 m × 1.5 m, 17 Aug 1914, *Wilson* 7399 (A). **HONSHU:** Sernja prov., Yamanaka on Fuji-san, abundant, tree 6–3 m × 1.5–2.6 m, *Wilson* 7778 (A, K); Kai prov., around village of Nakaihinsen, common hedge, *Wilson* 7544 (A); Nagano-ken, Okmachi, *Uno* 2611 (A, BH); Yokohama, *ex Herb. Hort Petro., Maximowicz* (P); Kamikawa, *Nitzelius* (S: C-2111); Tokyo Pref.: Oizuni, Nepymawku *Makino* 43775 (S: C-2111); Mt. Kiyosumi, *Makino* 43779 (S: C-2122); Sapporo, Yezo, 21 Jun 1903, *Arimoto s.n.* (A).

Taxus biternata is easily identified by its tree habit with an erect bole and horizontal diffuse branching, and by the much divided slender branchlets with a two ranked leaf arrangement. The tree habit not only distinguishes it from *T. cuspidata*, which differs by long ascending or recurved branches, but also from a shrub yew originally described as *T. baccata* var. *microcarpa*. A detailed study by Kolesnikov (1935) showed that the tree variety (*T. biternata*)—which he referred to *T. cuspidata*—and shrub yew were parapatric with distinct morphological and ecological characteristics. The shrub yew, *T. umbraculifera* var. *microcarpa*, is also similar to *T. canadensis* in layering, but differs in its flat-topped radial growth—as illustrated by Kolesnikov (1935), and by the much smaller paler seed, shaped like a “Hershey Kiss.”

Occasional specimens of *T. canadensis* from North America (e.g., *Travis* 119, Maine, PH), Estonia (e.g., *Lundström* 742, S), and others from Europe (e.g., *Handel Mazzetti*, Mt. Olympus, Greece, K) and SW Asia (e.g., *Davis* 13667, Turkey, K) are similar to *T. biternata* in the linear leaves spreading in two ranks with more strongly revolute margins in the upper third as seen in dried specimens. While most specimens can be distinguished by branching, the 3rd yr branchlets of *T. canadensis* have a purplish tint, in contrast to yellowish orange in *T. biternata*. A Maack specimen without number from Manchuria, mounted with the type with *T. baccata* var. *microcarpa* (GH), however, has a leaf spread and color that is hard to distinguish from *T. canadensis*. The female cone scales appearing on the current season growth compare more favorably with *T. biternata*. *Taxus canadensis* seed often mature on 2nd yr or older growth as seen in herbarium specimens; while I also recognize that field studies are needed throughout the range of the species to further substantiate the taxonomic value of this character.

In southeastern Manchuria, *T. biternata* appears to hybridize with *T. umbraculifera* var. *microcarpa* and var. *umbraculifera*. Plants with linear leaves (10× l/w or more) that are strongly recurved in upper third are referred to *T. biternata*. Those with relatively short leaves (oblong, 5–8× l/w) are considered var. *microcarpa*.

21. *Taxus caespitosa* Nakai, Ch[Ty]ōsen Sanrin Kaihō (J. Kor. For. Soc.) 158:40. 1938. (**Figs. 8, 45**). *Taxus cuspidata* Siebold & Zucc. var. *caespitosa* (Nakai) Q.L. Wang, *Clavis Pl. Chinae Bor.-Or.*, ed. 2:73. 1995. TYPE: JAPAN: 15 Jul 1922, *Sawada s.n.* (LECTOTYPE designated here: TI!). The reference to the type specimen in the typographical format quoted from Nakai (1938) is interpreted here as belonging to either of the two specimens cited; the other, *Kimura s.n.*, Aug 1924 (TI), is here identified as *Taxus umbraculifera* var. *nana*. TOPOTYPES: *Wilson* (A!), *Makino* 43792 (S!).

Taxus umbraculifera subsp. *latifolia* (Pilger) Spjut ined. (in adnot. A).

Three varieties are recognized.

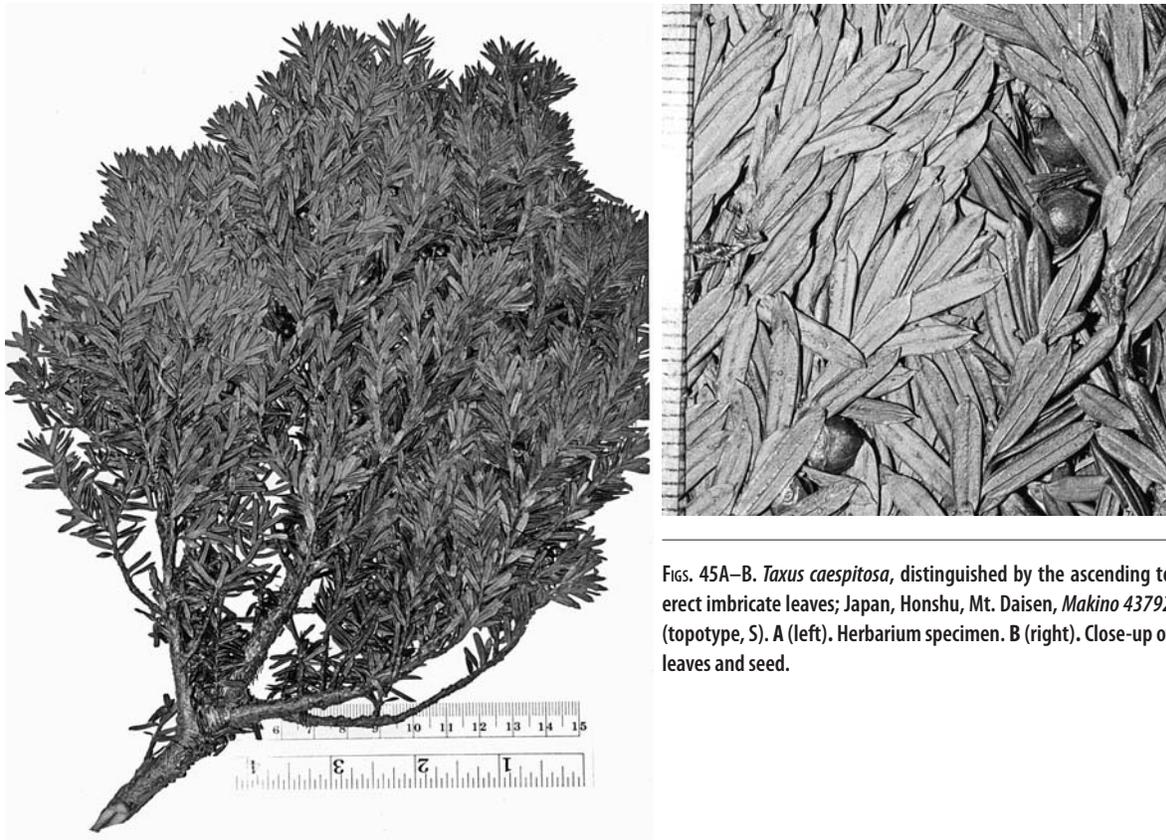
21a. *Taxus caespitosa* var. *caespitosa*

Common name.—Caespitose yew.

Distribution and ecology.—Russian Federation (Sakhalin Is.), Korea, Japan.

Additional specimens: **RUSSIAN FEDERATION. Sakhalin Is.:** *Schmidt s.n.* (GH). **KOREA.** In forest, Aug 1907, *Faurie* 1512 (A, BM, E). **JAPAN. Honshu:** Niigata, Yuzawa-machi, Minamiuonuma-gun, in *Pinus pumila* scrub, 1650 m, evergreen shrub 0.8 m high, fr red, 3 Oct 1979, *Taoda* 3887 (A); Hakkada, windswept slopes, 1000–2000 m, bush 1–1.5 m, rare, 4 Jul 1914, *Wilson* 7133 (A); Mutsu Prov., Mt. Hakkoda, *Mizushima* 1985 (A); Ohobu near Kobe Calt, 19 Mar 1955, *Muroi* 1058, annotated *T. cuspidata* var. *umbraculifera* (A). **CULTIVATION. OHIO. Secrest Arboretum:** ‘Colean’, A30-131; ‘Dwarf Japanese Yew’ A30-163; ‘Hill Anglo-Japanese Yew’ A30-264.

Taxus caespitosa var. *caespitosa* is identified by the crowded branches and radial distribution of leaves that have an erect orientation. The leaves appear more imbricate than decussate, and curve upwards along the petioles and the blades in the same direction they spiral. *Wilson* (1916) described plants he saw in Japan as having prostrate branches (from which erect branchlets apparently arise). This is evident in herbarium specimens by the one-sided development of branchlets, which includes specimens from the type locality, Mt. Daisen,



Figs. 45A–B. *Taxus caespitosa*, distinguished by the ascending to erect imbricate leaves; Japan, Honshu, Mt. Daisen, Makino 43792 (topotype, S). A (left). Herbarium specimen. B (right). Close-up of leaves and seed.

obtained by Wilson and by Makino. However, cultivars that I have seen as belonging to this variety are not prostrate shrubs, and do not show the small seeds seen in herbarium specimens of wild plants.

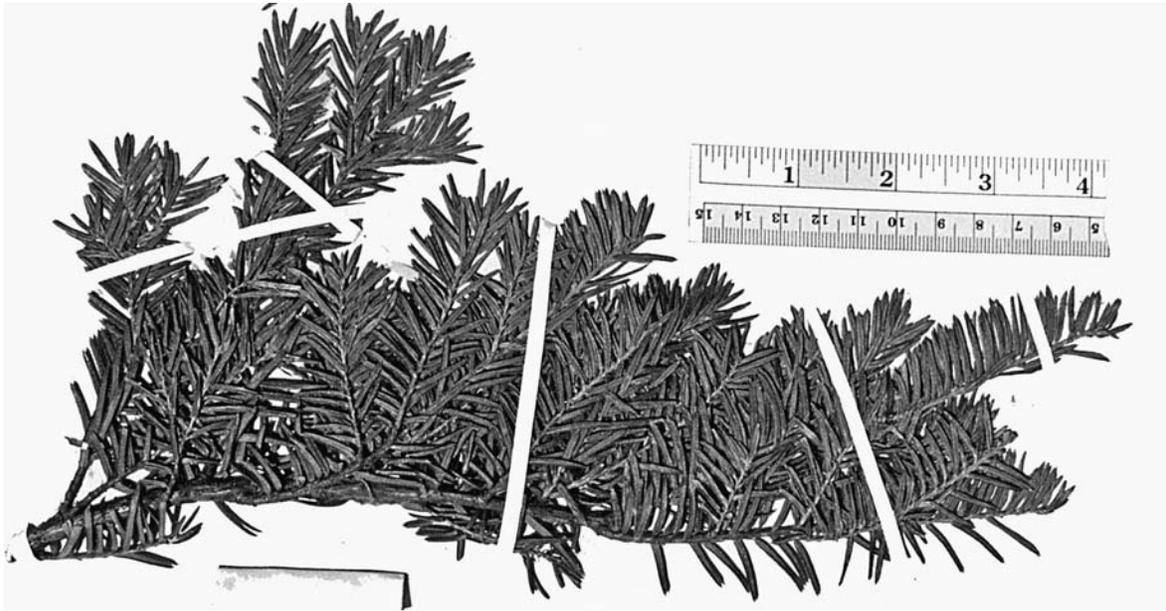
In E Asia where shrub yews show evidence of considerable diversity in habit and in phyllotaxy, the one sided branching and secund leaves of var. *caespitosa* are postulated as ancestral traits allegedly retained in plants with ascending to erect basal branches; these plants are referred to var. *latifolia*. Kolesnikov (1935) regarded the presence of yew in the Manchurian flora as an archaic element having little historical relationship to the rest of the vascular flora, while shrub yews in other regions have been noted to occur in environments that are distinct from their tree relatives such as reported by Elias and Korzhenevsky (1992) for shrub yews in Ukraine and Georgia. Two other distinct shrub types are also recognized in North America, *T. brevifolia* var. *reptaneta* in the Pacific NW has a characteristic habit with a distinct ecology, and *T. canadensis* in NE America has long been known for its shrubby monoecious habit.

21b. *Taxus caespitosa* Nakai var. *angustifolia* Spjut, var. nov. (Figs. 46–47). TYPE: JAPAN. PROV. KOZUKE: Oze-ga-hara, “shrubby habit, “leaves dark green,” “yellowish green beneath,” 26 Aug 1950, Mizushima 401 (HOLOTYPE: A! [leaves with a double row of palisade parenchyma cells, a marginal zone of 14 cells across lacking papillae, 9–10 stomata rows per band; seed]).

Varietas nova frutex, var. *caespitosa* proxima, cujus ramis primus prostratus, ramulosus numerosus, erectus; folia pectinatum disposita, patentia, linearis, 1.5–2.0 cm longa, 1.5 mm lata, acuta, ± 0.200 mm crassa, \pm disticha; semen ovata, purpurascens, 5 mm longa.

Apparently prostrate, bearing numerous erect reddish orange branchlets, persistent bud-scales few, cuspidate, ca. 1 mm. long; leaves mostly distichous, spreading from erect branchlets, erect on horizontal branchlets, reportedly dark green above, yellowish below, becoming reddish green in the herbarium, revolute along margins when dried, 1.5–2.0 mm long, ca. 1.5 mm wide, lacking papillae entirely across 14 marginal cells and on and midrib; with 9–10 stomata rows per band. Seed near base of branchlets, ovoid, purplish, tapering to sharp apex.

Common name.—Ground cover yew.



FIGS. 46A–B. *Taxus caespitosa* var. *angustifolia*, distinguished in part by the one sided branching—apparently from a prostrate stem (branch) with erect branchlets—and by the relatively thin, linear leaves that are revolute along margins when dried; Japan, Mizushima 401 (holotype A). A (above). Herbarium specimen, showing an apparent prostrate branch and erect branchlets. B (left). Close-up of leaves and seed.

Distribution.—Korea, Japan.

This variety is recognized by the relatively thin, narrow leaves as in *T. biternata*, but apparently has the habit of *T. caespitosa* var. *caespitosa* as shown in Fig. 50, reproduced from the Illustrated Encyclopedia of Fauna & Flora of Korea (Chung 1965). In this reference, the species is reported to be a shrub that is distinguished by layering.

Additional specimens: None. Known only from the type and illustration.

21c. *Taxus caespitosa* Nakai var. *latifolia* (Pilger) Spjut, comb. nov. (Fig. 48). BASIONYM: *Taxus baccata* L. [subsp. *cuspidata* (Siebold & Zuccarini) Pilger] var. *latifolia* Pilger, Pflanzenreich 4(5):112. 1903. *Taxus cuspidata* var. *latifolia* (Pilger) Nakai, J. Kor. For. Soc. 158:39. 1938. TYPE: JAPAN: HOKKAIDO: Hakodate, [with two labels, one dated 30 Dec 1890 and another dated 1888], *Faurie* 6345 (LECTOTYPE designated here: P! [with male cones (abaxial leaf with 18 smooth marginal cells followed by a stomata band with 11 rows of stomata, and a smooth midrib)]; ISOLECTOTYPE: K fragment!). Syntypes: from E Russian Federation and Japan.

Additional specimens. **RUSSIA FEDERATION. Sakhalin Is.:** 46°37'N, 142°53'E, Prigarodne, mixed conifer (*Abies, Picea*)/broadleaved (*Betula, Sorbus*) woodland, 150 m, to 1.8 m high, *Flanakan & Kirkham* 203 (K). **Korea:** in forest, 800 m, 19 Jul 1910, *Taquet* 4455 (A); without locality data, *Faurie* 117 (P), 3406 (P), 5975 (P). **JAPAN. Hokkaido:** Shiribeshi Prov., Shiribeshi-san, branches wide spreading,

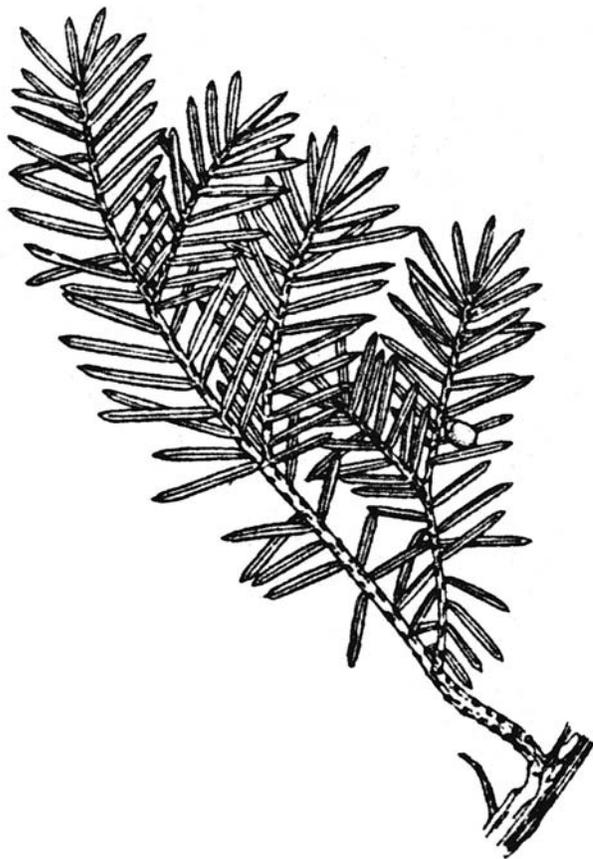


FIG. 47. *Taxus caespitosa* var. *angustifolia*, reproduced from Illustrated Encyclopedia of Fauna & Flora of Korea (Chung 1965, as *T. caespitosa*). Description of plant in that reference indicated that it reproduces by layering.

an earlier name *T. baccata* var. *microcarpa*; however, two lectotypes—as applied to two different varietal names—were selected from four syntypes (*Faurie* 5975, 6345, *Maack* s.n., *Schmidt* s.n.) as cited by Pilger (1903). *Faurie* 6345 at P was selected as lectotype for var. *latifolia* because it is a whole specimen mounted alone, and because it has cones (male), compared to other *Faurie* specimens that were usually sterile and mounted with other specimens on a single sheet as seen in other herbaria. *Maack* from Heilongjiang at GH is the lectotype for *T. baccata* var. *microcarpa* (bottom specimen of two mounted on one sheet). A specimen by *Schmidt* from Sakhalin Island at GH, referred to in the present study as var. *caespitosa*, is a reddish specimen mounted among several other greenish specimens on the same sheet—regarded as *T. umbraculifera* var. *nana*—possibly collected by Augustowoz. Nakai (1938) also distinguished var. *latifolia* by leaves 3–4.5 mm wide and indicated that var. *nana*, an earlier name, was known only in horticulture; however, var. *nana* has been recognized to occur naturally in Japan (Ohwi 1965).

22. *Taxus canadensis* Marshall, Arbust. Amer. 151. 1785. (Fig. 49). *Taxus baccata* L. var. *canadensis* (Marshall) Gray, Man. Bot. N. United States, ed. 2, 425. 1856. *Taxus baccata* L. subsp. *canadensis* (Marshall) Pilger, Pflanzenreich 18 (iv, 5):113. 1903. TYPE: U.S.A. VERMONT: 1877, *C.G. Pringle* s.n. (NEOTYPE designated here: US! [leaf with abaxial marginal region of 16–18 smooth cells, stomata bands papillose throughout with stomata in 6 irregular rows per band]). Original material unknown. A specimen at the Museum of Natural History in London (BM) collected by Joseph Banks in 1766 refers to “Marsh. Hb.,” which suggests a possible type. However, the existence of material used by Marshall is unknown. His publication (Marshall 1785) was related to his sales catalogue (Silber & deWolf 1970). A neotype was selected based on a cone-bearing specimen that showed the most common morphology.

1–2 m, common, 1300–2000 m, 27 Jul 1914, *Wilson* 7265 (A). **Honshu:** Mutsu Prov., Mt. Hakkoda, erect tree, 8 Jul 1952, *Mizushima* 1989 (A). without locality data, *Faurie* 5114 (P: 2 sheets). Locality unknown: *Folley* s.n., identified *T. cuspidata* ‘*nana*’ (K).

Variety *latifolia* is best distinguished by the flexuous branchlets with overlapping erect leaves; however, it varies widely in habit. It may produce a single main branch that creeps along the ground and layers as evident in *Faurie* 5114 from Japan, *Faurie* 3406 & 5975 from Korea, *Flanagan & Kirkham* from Sakhalin Is., and *Folley* from cultivation. Erect forms are recognized by branches and leaves that develop primarily on one side of the plant. *Wilson* (1916) described plants from Shiribishi-san in Japan as either “prostrate on the ground” or as a “broad shrub, 1–2 m high.” The prostrate form could be treated as another distinct variety. *Chang* (pers. comm.) found significant differences in taxane ratios in specimens that I identified as two forms of *T. caespitosa* that were reportedly grown under similar conditions in a greenhouse.

Pilger (1903) distinguished var. *latifolia* from var. *cuspidata* by the densely branched habit, relatively wide leaves (to 2 mm wide), and small, depressed globose seeds. His description partly agrees with that given by *Trautvetter* (in *Maximowicz* 1859) for



FIGS. 48A–B. *Taxus caespitosa* var. *latifolia*, distinguished by the spreading branchlets with ascending to erect, imbricate leaves; Japan: *Faurie* 6345 (lectotype, P). A (left). Herbarium specimen. B (below). Close-up of branchlets with leaves and male cones.





FIGS. 49A–B. *Taxus canadensis*, neotype. U.S.A., Vermont, Pringle, yr 1877 (US). A (left). Herbarium specimen. B (below). Close-up of branchlet showing mature male cones. Var. *canadensis* distinguished by the linear acute leaves spreading horizontally along two sides of a branchlet.



Taxus canadensis is distinguished by leaves having relatively narrow stomata bands bordered by 8 or more marginal cells. Stomata usually number 5–7(–9) rows per band in American plants, or from 4–11 rows per band in Euro-Mediterranean plants. The marginal zone along the abaxial surface of the leaf varies from 12–18 cells wide in specimens from North America, and from 8–24 cells wide in specimens from the Euro-Mediterranean. American plants have papillae confined to stomata bands, sometimes only along a stomata row. Except for one specimen from Ithaca NY, the Euro-Mediterranean plants also differ by more conspicuous papillae in stomata bands with papillose cells sometimes extending into the adjacent marginal zone. The European plants could be referred to fossil species *T. inopinata* Givulescu or *T. grandis* Krausel. The consistent absence of papillae along the abaxial leaf margin in American plants clearly indicates that development of epidermal papillae is genetically fixed.

Taxus canadensis has also been distinguished from related species by its monoecious habit in which plants often creep along the ground and spread by layering (Allison 1991; Bannan 1942), but these characters are rarely reported on labels of herbarium specimens. Nevertheless, *T. canadensis* is not always monoecious (Allison 1991), and perhaps tree forms exist; a specimen I cited from Sainte Baume (France) is where the oldest yew trees are known in France, “attaining a girth of 11½ feet” (Elwes & Henry 1906), and where yew was once abundant (Elwes & Henry 1906). Layering in European yew is thought to be rare, but nevertheless known from Scandinavia (Elwes & Henry 1906) where I have also identified *T. canadensis* from herbarium specimens. The occurrence of *T. canadensis* in Scandinavia is further evident in a photograph of a plant on Saaremaa Island in Estonia that clearly shows a low sprawling plant in a forest understory (of spruce, *Picea abies* [L.] H. Karst; Korpela’s Index, website), which I have further identified as *T. canadensis* var. *adpressa*.

Two other character features that reinforce identification of *T. canadensis* outside North America are bud-scales at base of branchlets and color of leaves. In the Canada yew, bud-scales remain rather loosely attached at base of branchlets, and are usually keeled or folded along the mid-nerve, often appearing incurved or cuspidate above the mid region as in *T. biternata* (see Cope 1998 for illustrations of bud-scale features). This is in contrast to scales of the *T. baccata* and its allies that show various other combinations of character attributes. In *T. baccata* var. *baccata*, bud-scales at base of branchlets are loosely attached, but still thick and obtuse, not at all incurved or cuspidate, or other varieties of *T. baccata* have similar thickened obtuse scales more tightly adpressed to branchlets, or in the related *T. recurvata*, bud-scales are thickened cuspidate but not tightly adpressed to branchlets. The other character feature of *T. canadensis* is the dark green color of leaves as determined from general observation and from under the microscope. Most specimen leaves of *T. baccata* differ by a yellowish green, olive green, or glaucous green color. Exceptions occur in specimens from eastern Europe and southwestern Asia where color and anatomical differences overlap between *T. canadensis* and *T. baccata*.

Three varieties of *T. canadensis* are recognized. The typical variety is frequently isodichotomously branched with leaves in pressed specimens appearing crisscrossed in pairs along one side of a branchlet. The leaves are broad linear and spread from branchlets at their petioles in which the blades are relatively straight. Variety *adpressa* differs by irregular alternate branching and by having oblong and truncated leaves near apex, which is acute or obtuse, while var. *minor* is recognized by the crowded erect (secund) leaves. In further studies additional varieties may be distinguished; an example is *Hayek & Hayek s.n.* (BM) from Styria Superior in Austria that is similar to var. *minor* except for the branchlets that appear more recurved with narrower erect leaves, features that are seen more in *T. cuspidata*.

22a. *Taxus canadensis* var. *canadensis*

Common name.—Canada yew.

Distribution and ecology.—E North America (Manitoba near Lake Winnipeg south to Indiana, Newfoundland south along the Appalachian Mts. to NW North Carolina and Tygart Creek, Kentucky), NW Africa, Europe, W Asia; shady wet places, benches above rivers, or among rocks or soil in bottomland forests of mixed hardwoods and conifers, especially hemlock and beech, 300–1500 m.



Fig. 50. *T. canadensis* var. *adpressa*. Reproduced from Carrière (1855b), neotype. Var. *adpressa* distinguished by the oblong, obtuse leaves generally spreading along two sides of a branchlet, overlapping slightly.

Spjut, comb. nov. (Fig. 51). BASIONYM: *Taxus baccata* β *minor* Michx., Fl. Bot. Amer. 2:245. 1803. *Taxus minor* (Michx.) Britton, Bull. Torrey Bot. Club 4:167. 1893, no specimens cited. Original Material at P, a single specimen. TYPE: CANADA. ex Herb. A. Michaux (HOLOTYPE: P!).

Common name.—Minor yew.

Distribution.—NE U.S., E Canada, Portugal (Madeira), Austria.

This differs from var. *canadensis* by the more densely leafy branches with the leaves tending to be obtuse and falcate-secund.

23. *Taxus cuspidata* Siebold & Zucc., Abh. Königl. Bayer. Akad. Wiss., Math.-Phys. München, III, 801. 1843 (in footnote: ref. to Siebold and Zuccarini, Fl. Jap. II. tab. 128 and to [a description] *T. baccata* in Thunberg (1784, Fl. Jap. 275, “foliis solitariis, linearibus, cuspidatis, approximatis”). (Figs. 7, 52). No specimens cited. *Taxus baccata* L. (var.) *cuspidata* Carrière, Coniferae 733. 1867; *T. baccata* subsp. *cuspidata* (Siebold & Zucc.) Pilger,

22b. *Taxus canadensis* Marshall var. ***adpressa*** (Hort. ex Carrière) Spjut, comb. nov. (Fig. 50). BASIONYM: *Taxus* [*baccata* var.] *adpressa* Hort. ex Carrière, Rev. Hort., sér 4, 4:93, fig. 8. 1855 (and *Traité gén. conif.* 520. 1855). *Taxus baccata* L. [var.] *adpressa* (Carrière) Carrière, *Traité gén. conif.* 731. 1867. TYPE: Described from horticulture, original material unknown (NEOTYPE designated here: Illust. Fig. 8 in Carrière, Rev. Hort., sér 4, 4:93. 1855).

Cephalotaxus tardiva Siebold ex Endlicher, Syn. conif., 239. 1847. *Taxus tardiva* (Siebold ex Endl.) Hort. ex Knight, Syn. conif. pl. 52 (1850); *T. tardiva* (Siebold ex. Endl.) Hort. ex Lindl. & Gordon, J. Hort. Soc. 5:227. 1850. *Taxus baccata* f. *tardiva* Pilger, Pflanzenreich 18 (iv, 5):114. 1903.

Common name.—Rigid-leaf yew.

Distribution.—E North America, Europe, W Asia.

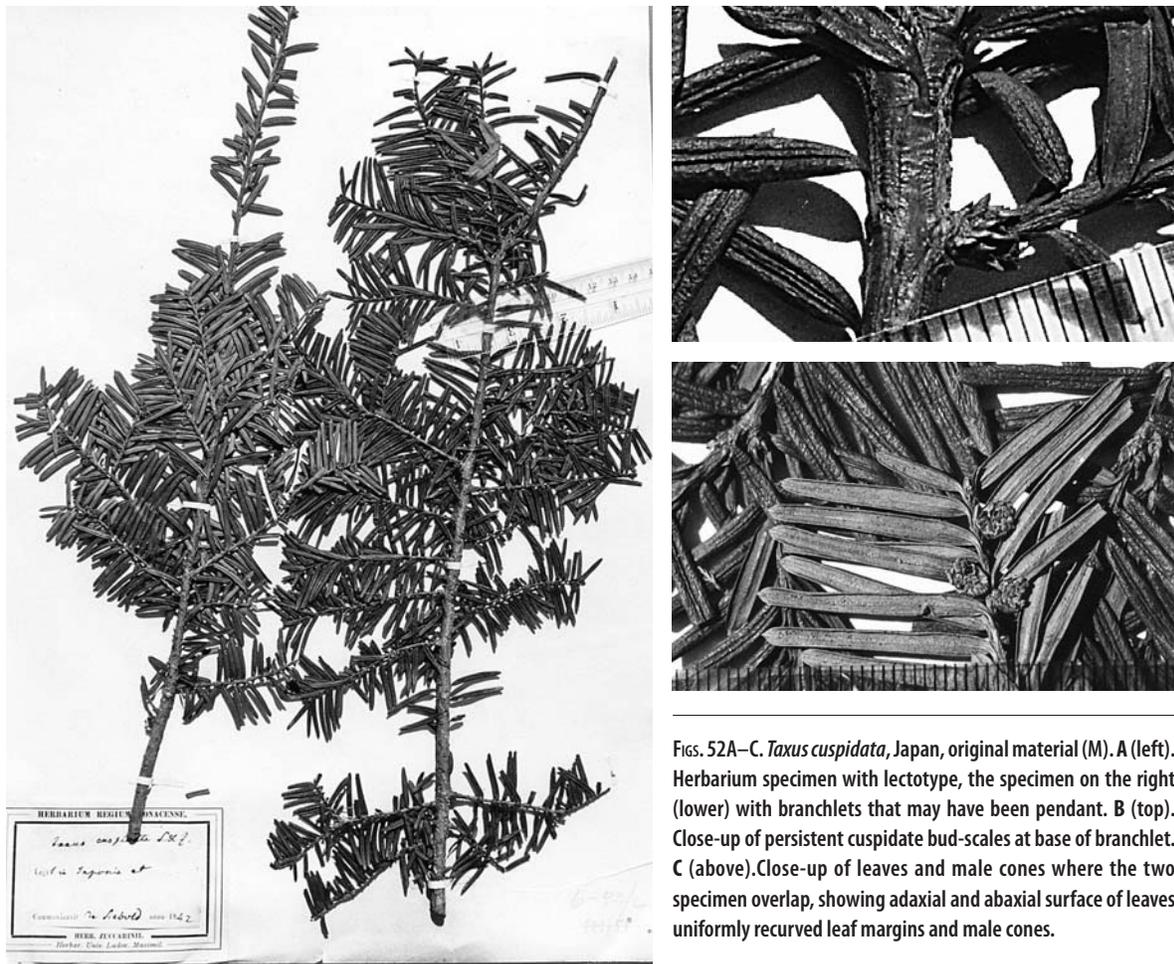
The name for this taxon has been confused in the literature. If recognized as a species, the correct name would be *Taxus tardiva*, but as a variety, the epithet *adpressa* has priority. Carrière referred to it both ways in 1855, as a species in *Revue Horticole*, and as a horticultural variety in *Traité Général des Conifères* under the binomial name, *Taxus adpressa*, with many synonyms listed, including *T. baccata adpressa* with reference to his earlier journal publication (Carrière 1855b). The ICBN (Art. 11.2, 11.4) indicates that priority is determined by the “final epithet,” which “*Taxus adpressa*” was indicated to be a variety, and although in a binomial format, the epithet has priority as variety over *Cephalotaxus tardiva* that was first recognized as a species.

This variety is generally known in horticulture where it was thought to originate as a natural seedling in a nursery at Chester, England in 1826 (Bean 1953; Elwes & Henry 1906; Pilger 1916; Wilson 1916), but also recognized to occur occasionally in the wild (Krüssmann 1985). Others have reported it native to China and Japan (Endlicher 1847; Koch 1873), and still other reports mentioned it as occurring in California, in association with sugar pine, ponderosa pine, Douglas fir and other species (*Revue Horticole* 1848, 1849).

22c. *Taxus canadensis* Marshall var. ***minor*** (Michx.)



Fig. 51. *Taxus canadensis* var. *minor*. Canada, ex Herb. A. Michaux (holotype, P). Var. *minor* distinguished by spreading to recurved branchlets with ascending (secund), closely overlapping, leaves.



FIGS. 52A–C. *Taxus cuspidata*, Japan, original material (M). A (left). Herbarium specimen with lectotype, the specimen on the right (lower) with branchlets that may have been pendant. B (top). Close-up of persistent cuspidate bud-scales at base of branchlet. C (bottom). Close-up of leaves and male cones where the two specimens overlap, showing adaxial and abaxial surface of leaves uniformly recurved leaf margins and male cones.

Planzenreich 4(5):112. 1903. Original material at M. TYPE: JAPAN: (LECTOTYPE designated here: M!, sheet with the following data on labels “*Legit in Japonia et Communicavit de Siebold, anno 1842,*” Herbarium Regium Monacense,” “Herb. Zuccarini,” and “Herbar. Univ. Ludov. Maximil.,” the specimen on the right of two mounted on the same sheet, with mature male cones; the left specimen also identified as *T. cuspidata*; ISOLECTOTYPES: M!, K!, apparently from the same plant as lectotype but with other data on labels).

Taxus cuspidata is possibly native to Hokkaido, Japan, but apparently rare except perhaps in arboreta. Two specimens that were collected by Jack from Hokkaido (A) are clearly related to the type as seen in phyllo-taxy, color, and leaf anatomy. The leaf anatomical data in Spjut (2007) show the specimens to have a wider abaxial margin, 16–24 cells wide, compared to a margin of 8–15 (-18) cells across in all other specimens from the Sino-Japanese Region. These three specimens appeared to have the most conspicuous persistent bud-scales of all yews in that region, a character trait that reinforces the choice of the lectotype.

The authorship and publication date for *T. cuspidata* have been confused in the literature. The official date of the volume for Siebold and Zuccarini’s *Flora Japonica*, in which *T. cuspidata* was intended to be described as a new species, did not appear until 1870; yet, reference to this publication, including a figure (Tab. 129 instead of Tab. 128), was first made by Siebold and Zuccarini (1843) 27 years earlier at which time they cited the name in footnote with further reference to a description in Thunberg (1784, *Flora Japonica*). Siebold and Zuccarini’s (1846) synopsis of plant taxa in Japan, which many authorities cite as the valid publication date (e.g., Farjon 1998; Fu et al. 1999), does not provide a plant description of *T. cuspidata*; only an indirect reference to *T. baccata* in Thunberg, *Flora Japonica* (1784). Aside from Siebold and Zuccarini (1843), the first direct description of *T. cuspidata* appeared in Endlicher (1847). Others have since also provided a description for the species (e.g., Carrière 1855a; Lawson et al. 1851; Parlato 1868) before Miquel published

Siebold and Zuccarini (1870), in which these earlier references were noted. However, Siebold and Zuccarini's (1843) earlier reference to a description in Thunberg (1784) satisfies the requirement for valid publication of "*Taxus cuspidata* Sieb. & Zuccar." (Art. 32.1), indicating also the origin of the epithet ("cuspidatis").

The leaves of *T. cuspidata* overlap along branchlets with an orientation that varies according to the direction of the branchlet, appearing partially erect and slightly radial as in *T. umbraculifera*, or two-ranked as in *T. biternata*. Indeed, the phyllotaxy of the type appears intermediate between that of *T. umbraculifera* and *T. biternata*. Other specimens assigned to *T. caespitosa* var. *latifolia* are similar to *T. cuspidata* in their long flexuous branchlets (e.g., Makino 43769 from Honshu, Maximowicz from Manchuria, Dvorakovskia & Bokina from Sakhalin Is.).

Cultivars that I have studied at the Secret Arboretum in Ohio (Chadwick & Keen 1976) are identified as belonging to this species by the dome-like to pyramidal crown with a definite leader, and by the branches also with a definite leader that ascend upwards from which hang many long simple branchlets. In other cultivars the branchlets are stiff and recurved. The habit is reminiscent of the European Dovaston yew (*T. baccata* var. *dovastoniana* Leighton)—recognized for its weeping branches—and to other European plants known in horticulture as *T. baccata* var. *glauca* Carrière (US: 1396503 "f. *glauca* = f. *subglaucescens* Jacq.;" ex Hillier's Arboretum BM; ex Herb. Petropolitani, Szovich 610, S; C. Baenitz US, "f. *pendula*"). Thus, I wonder if *T. cuspidata* is of horticultural origin. Wilson (1916) commented that he was not sure whether the yew plants he saw in Japan were natural or cultivated, and since Siebold and Zuccarini (1870) noted that yew there occurred in horticulture, in cultivation around temples, and spontaneously in the mountains, it is possible that the original material came from horticulture. Also, it is interesting to note that Carrière (1861) thought that the Dovaston yew was native to Japan.

This problem is complicated by naturally occurring intermediates between the *Baccata* and *Cuspidata* Alliances as evident from anatomical data and other key characters. Examples of intermediates that are included in the *Baccata* Alliance are from Sweden (*Bjornstrorn*, ex Mus. Stockholm), Finland (*Finlandee Exsic.* 419 K, p.p., bottom specimen), and the Caucasus Mountains (*Busch s.n.*). These are not easily distinguished from occasional ones in the *Cuspidata* Alliance such as from Hokkaido (*Makino 43769*), Korea (*Faurie s.n.* A, *Wilson 9484*), and Sakhalin Island (*Dvorakovskia & Bokina*). Being able to discern the key differences among these problematic Eurasian specimens requires considerable familiarity with *Taxus*.

Another example is *Hayek & Hayek s.n.* (BM), discussed earlier under *T. canadensis*, from Styria Superior in Austria (Spjut 2007, appendix), that seems to differ from *T. cuspidata* only by its dull olive green color, in contrast to a yellowish orange color on branchlets in the E Asian specimens. From a taxonomic point of view, the majority of the specimens fall within the *Baccata* and *Cuspidata* Alliances. However, in further consideration to the distribution of *T. canadensis* in the Euro-Mediterranean Region and eastern North America, the *Baccata* and *Cuspidata* Alliances were possibly derived from an ancestral boreal complex that was perhaps distributed from northeastern North America to northeastern Asia. Thus, these intermediates could be relicts of that former complex.

24. *Taxus umbraculifera* (Siebold ex Endl.) [Ravenscroft] [C.] Lawson, Abietineae—List Pl. Fir Tribe 10:80. 1851. (Figs. 9, 53–54). *Cephalotaxus umbraculifera* Siebold ex Endlicher, Syn. Conif. 239. 1847. *Taxus cuspidata* Siebold & Zucc. var. *umbraculifera*, Makino in Makino & Nemoto, Cat. Jap. pl. 407. 1914 (Also, Illus. Fl. Nippon. 1925 typographical error, spelling "ambraculifera," see ICBN Art. 61 and corrected spelling by Makino, Illus. Fl. Nippon 910, fig. 2730. 1931). TYPE: JAPAN: (NEOTYPE designated here: illust. in Makino, Illus. Fl. Nippon, fig. 2730. 1931.). EPITYPE designated here: JAPAN. HONSHU: Hyogo Pref., Mt. Hyonoson, 30 Aug 1948, Muroi 30, ex Herb. Hiroshi Muroi, Kobe, identified by Muroi as *T. cuspidata* var. *ambraculifera* Makino (A!). Original material unknown.

The origin of the name *T. umbraculifera* may be horticultural (Gordon & Glendenning 1858, Gordon 1875); however, *Cephalotaxus umbraculifera* was attributed to Siebold by Endlicher (1847) who provided a detailed description but expressed doubt as to whether the species was distinct from *Taxus cuspidata*. Ravenscroft is recognized in Stafleu and Cowan (1983) as the contributor for Lawson et al. (1851), who attributed *C. umbraculifera* to Siebold and Zuccarini, and indicated it was a synonym of *T. cuspidata*; however, the authority for the name is indicated to be Lawson because lack of internal evidence in Lawson et al. (1851) for



Figs. 53–54. *Taxus umbraculifera* var. *umbraculifera*. 53 (top). Neotype, Makino, Illus. Fl. Nippon (1931, Fig. 2730). 54 (above). Epitype, Japan, Honshu, Muroi 30 (A). Var. *umbraculifera* distinguished by spreading to ascending branchlets with leaves sharply bent downwards at petiole, the leaves also appearing in a decussate arrangement when looking down from apex of branchlet.

24a. *Taxus umbraculifera* var. *umbraculifera*

Common name.—Umbrelliform yew.

Distribution.—Japan, Russian Federation—Manchuria.

Ravenscroft as the authority, ICBN Art. 35.5. The epithet suggests an umbrella-like leaf arrangement (Fig. 59), not the two-ranked leaves as described by Endlicher (1847). Ravenscroft (Lawson et al. 1851), who treated the species in section *Cephalotaxus* of *Taxus*, indicated that branches are verticillate with “distichous” branchlets. I have not seen any original material, and herbaria that I have contacted in this regard for Siebold specimens reportedly have none. Nevertheless, an illustration in Makino (1931) clearly depicts the umbrelliform leaf arrangement that is distinctive for this species. In later manuals on the flora of Japan (e.g., Ohwi 1965), var. *nana* Rehder (1902) became the name for this taxon, but this is antedated by var. *microcarpa* Trautvetter (in Maximowicz 1859); however, these names are applied to different (and distinct) taxa in the present study.

The leaves of *T. umbraculifera* appear in star-like (almost decussate) manner when looking down the branch from apex, and unlike *T. caespitosa*, the blades of *T. umbraculifera* will face different directions. Leaves appear perpendicular to the plane along one side of a branchlet and in the same plane along another side of branchlet. This is not easily determined in pressed specimens; however, the crisscrossed blades partly reflect this, which is in contrast to the radial orientation of leaves in *T. caespitosa* that all twist in the same manner, appearing imbricate when observed from above the apex of the branchlet. The leaves of *T. umbraculifera* are also sharply reflexed at their petioles, in contrast to bending upwards (erect) in *T. caespitosa*; this difference accounts for the two-ranked appearance in *T. umbraculifera*, in contrast to the second appearance in *T. caespitosa* often seen on older branchlets.

Four varieties of *T. umbraculifera* are recognized by differences in habit and leaf arrangement.

Additional specimens: **JAPAN. Honshu:** Kanagawa Pref., Mt. Ooyama, shrub 2 m high, cult., 25 Oct 1952, *Suzuki 499003* (A); Shunane Pref., Mt. Sentsu-zan, *Naito s.n.* (A). **RUSSIAN FEDERATION.** Mandshuria SE: Ex herb. hort. bot. Petro. yr 1860, *Maximowicz* (S).

Variety *umbraculifera* appears mostly arborescent with wide spreading branches. It is recognized by the radial distribution of leaves on erect branchlets, especially near apex, and the appearance of a decussate to nearly two-ranked arrangement on horizontal branchlets.

24b. Taxus umbraculifera (Siebold ex Endl.) Ravenscroft var. **hicksii** (Hort. ex Rehder) Spjut, comb. nov.

BASIONYM: *Taxus media* Rehder f. *hicksii* (Hort.) Rehder [*T. cuspidata hicksii* Hort. in synonym.], J. Arnold Arbor. 4:108. 1923. *Taxus cuspidata* var. *hicksii* (Hort. ex Rehder) Bailey, Cult. Evergreens 189. 1923. TYPE: U.S.A. NEW YORK: horticultural specimen from Hicks Nursery, Westbury, Long Island, 28 Sep 1922, *Arnold Arboretum 8036* (HOLOTYPE: A!). Bailey (1923) attributed the combination to Rehder even though it has not been determined whether Bailey's publication predates that of Rehder (8 May 1923). All conditions for valid publication are met in Rehder (1923) but not in Bailey (1923); therefore, the name in Rehder (1923) is considered the basionym (see ICBN Art. 45.1) even though Rehder cited a synonym used in horticulture without reference to an authority or publication and implied that it was a basionym.

Common name.—Hicks yew.

Distribution.—Endemic to Japan.

Additional specimens: **JAPAN. Iwate-Pref.:** Asagishi, Muroi 3593 (A). Nagano Pref.: Kamikochi, Muroi 3715 (A). **Gifu-Pref.:** Takayama, Muroi 3698 (A). **Hyogo Pref.:** Kumatugi, Mikata-gun, Muroi 5603 (A); Mt. Hatibuse Muroi 5424 (A); Wakasugi, Muroi 5648 (A). **CULTIVATION: Maryland:** Laurel, residential area, 8495 Imperial Drive, *Spjut s.n.* (wba); Arnold, residential area, 757 Dunberry, 1 Aug 1999, *Spjut s.n.* (wba).

Variety *hicksii* is distinguished by its columnar habit with erect branchlets and erect linear leaves that spread in a radial arrangement. The leaves may appear two-ranked on lower branchlets, but if the branchlets are turned over, the underside will be seen to have some of the leaves reflexed.

Although described from horticulture, this variety appears to occur naturally in Japan, based on four specimens from there that are remarkably similar to the type. It also raises the question as to whether the variety independently evolved there as a hybrid, or whether it may have been introduced into Japan from North America, since the specimens cited above were collected during the mid 1950s—after the Hicks yew was described by Rehder (1923). The Hick's yew supposedly originated from seed of "*T. cuspidata* 'Nana'" sometime around 1900 (den Ouden & Boom 1965). Molecular data in Collins et al. (2003) placed the Hick's yew with *T. × media* Rehder; however, their study did not include morphological characters.

24c. Taxus umbraculifera var. **microcarpa** (Trautv.) Spjut, comb. nov. (**Figs. 55–58**).

BASIONYM: *Taxus baccata* L. var. *microcarpa* Trautvetter in Maxim., Mem. Acad. Sci. St. Petersburg. Sav. Etrang. 9:259 (Prim. Fl. Amur.). 1859. *Taxus cuspidata* Siebold & Zucc. var. *microcarpa* (Trautv.) Kolesnikov, Bull. Far E. Branch Acad. Sci., USSR 13:43, fig. 2. 1935. *Taxus cuspidata* Siebold & Zucc. var. *microcarpa* (Trautv.) S-Y. Hu, Taiwania 10:21. 1964 (nomen comb. superfl., illegit.). TYPE: CHINA. MANCHURIA: Heilongjiang, Exped. Soc Geogr., 1 May 1855, *Maack s.n.* (LECTOTYPE designated here: GH!, lower of two specimens; isotype: P!, upper of two specimens on one sheet). Original type not specified; original material (syntypes) from several locations, one from Manchuria (1 May 1855, reportedly sterile, GH! P!), and another from Sakhalin Is. (Weyrich, Sep. 1853, with fruit, KFTA?).

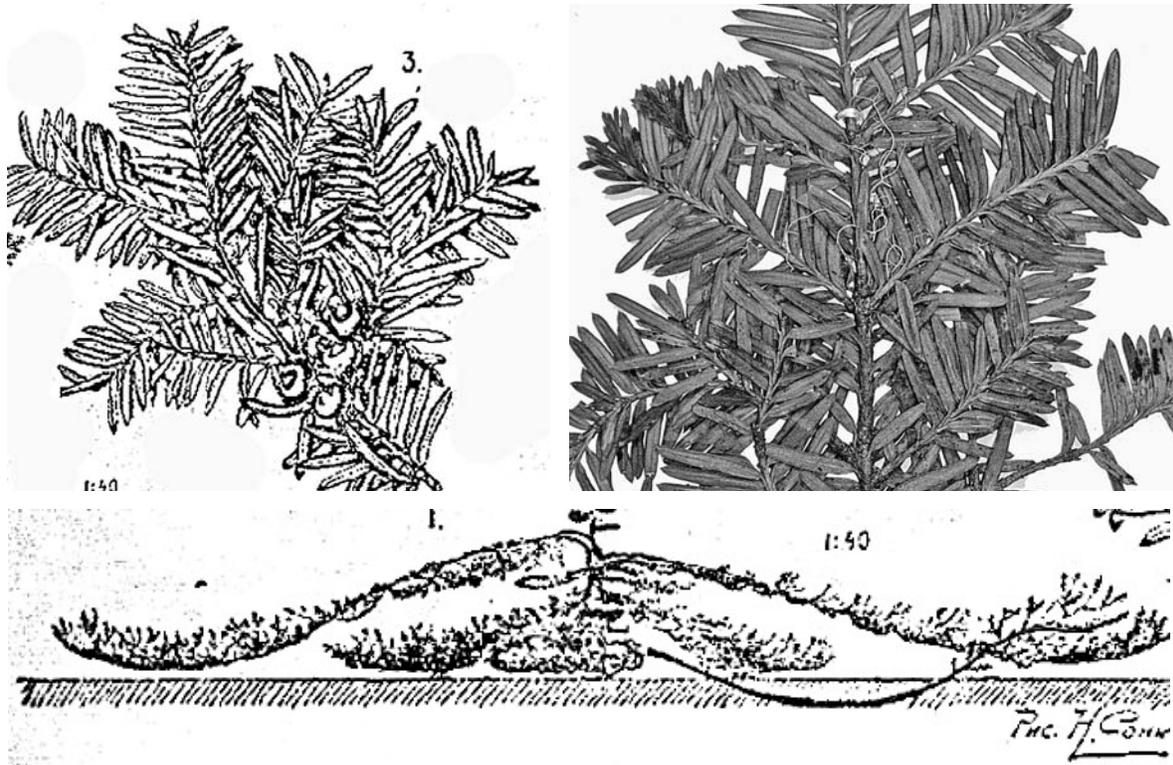
Taxus umbraculifera subsp. *laxa* Spjut ined. TYPE: KOREA. Ooryong-too (Oagelet Island), 0–900 m, bush or small tree, common, *Wilson 8538* (HOLOTYPE: A!; ISOTYPE: US!).

Common name.—Small seed yew.

Distribution.—NE temperate Asia.

Additional specimens: **RUSSIAN FEDERATION. Primorie [Primorskiy] Prov.:** vicinity of Vladivostok, *Palczewsky 3601* (A, K, US); Bay of Peter, the First Sea Reserve, Island of Stenin, 26 Apr 1979, *Kyepinova s.n.* (in Russian, A). **Manchuria Region:** Korea septentrionalis provincia Pen-nian Muorum Jahn... Frajectus Lpatan-ien, 27 Jun 1897, *Komarov 88* (A); Rossica, Aultzo Prov., Ussuri [Ussuzieusis] insula Afnold, Komarov 88 (P); Manchuria: Rossica *Palczewsky [Komarov] 88* (BM, K, US [ex Herb. Baenitz]). **SOUTH KOREA:** Nemon-rei, Kyongsan, tree up to 50 ft, common, 12 Oct 1917, *Wilson 9332* (A); Herb. Lugd. Batv. (P); *Zuccarini 593*, in adnot. *T. baccata* (M). **JAPAN. Hokkaido:** Ishikasi Prov., Apr 1884, *K. Muijabe s.n.* (A). Nanokwa, Tosa, 18 Apr 1888, *Watanabe s.n.* (A); Sapporo, Agric. College, 15 Jun 1885 (A), Jun 1878 (A); Sapporo, *Siebold, ex Herb. Zuccarini* (GH); Mt. Nantai, Lake Chuzenji, 20 Aug 1904, *Mochizuki s.n.* (A). **Honshu:** Yokohama, yr 1862, *ex Herb. USDA 1888* (US: top specimen); Japan, no locality or collector data (US 1311889); Hida, Takayama, 17 Sep 1910 (A); Yokohama, yr 1862, *ex Herb. USDA 1888* (P, p.p.; US, lower of 2 specimens); no locality data, *Kiaraboku s.n.* (US 1311889).

This variety is best recognized by isodichotomous branching, the oblong leaf shape (ca. 8× l/w) and crisscross



FIGS. 55–58. Comparison of illustrations with herbarium specimens of *Taxus umbraculifera* var. *microcarpa*. 55 (upper left). Illustration from Kolesnikov (1935, as *T. cuspidata* var. *microcarpa*). 56 (upper right). Herbarium specimen, Manchuria, *Palczewski ex Herb. Baenitz* (US). 57 (center). Illustration showing habit of plant from side view (Kolesnikov 1935), appearing radial in outline from top view (not shown). 58 (right). Type herbarium sheet in the Gray Herbarium, *Maack Exped. 1855* (GH). The upper specimen annotated by S-y. Hu—*T. cuspidata* var. *microcarpa*—the type for her illegitimate combination (Hu 1964); however, the specimen that best compares with Trautvetter's description of *T. baccata* var. *microcarpa* (basionym), a low shrub with a small seed, illustrated by Kolesnikov (1935), is the lower specimen (lectotype). The upper specimen is identified in this publication as *T. biternata*, described as a new species, a tree with diffuse branching, and a relatively large seed.



leaf arrangement. Trautvetter (in Maximowicz 1859) distinguished var. *microcarpa* from *T. baccata* by the smaller—wider than tall—seed (Pilger 1903), and Kolesnikov (1935) further indicated it was a low rounded shrub—0.5–1.5 m high and 5–7 m in diam.—that reproduced by layering (Fig. 68). Kolesnikov (1935) had recognized two morphological different varieties (tree and shrub yews) occurring in different habitat types in southeastern Russian Federation.

In my 1996–1997 annotations (*Taxus microcarpa* [Trautv.] Spjut ined.; *Taxus umbraculifera* subsp. *laxa* Spjut ined.), I had concluded that a specimen annotated by S-y. Hu in GH was the type for *T. baccata* var. *microcarpa* (see Fig. 66 and Hu 1964), but upon later reviewing the illustrations in Kolesnikov (1935), reproduced here in Figs. 63–64, it was quite clear this was not its type but rather a specimen below it on the same herbarium sheet. The interpretation of the taxon by Kolesnikov (1935), based on Trautvetter (in Maximowicz 1859), must be preserved; therefore, *T. biternata* is described as a new species, and “*T. umbraculifera* subsp. *laxa* Spjut” will remain an unpublished name.

24d. *Taxus umbraculifera* var. *nana* (Rehder) Spjut, comb. nov. (**Figs. 59**). BASIONYM: *Taxus cuspidata* var. *nana* [Hort. ex] Rehder in L.H. Bailey, Cyclopedia Amer. Hort. 1773. 1902. *Taxus cuspidata* f. *nana* (Rehder) Wilson, Conif. Taxads Japan 13. 1916. TYPE: JAPAN. HONSHU: Pref. Hyogo, Mt. Hyonosen, 1100–1400 m, in *Fagus* forest with sasa thicket, on ridge, shrub 2 m, fr red, 11 Aug 1983, Murata 44671, det. as *T. cuspidata* var. *nana* Rehder (NEOTYPE designated here: A!). Described from horticulture, no specimens cited and original material unclear.

Common name.—Dwarf yew.

Distribution.—E Russia (islands), China (Shanxi), Japan.

Additional specimens: **RUSSIAN FEDERATION. Far East:** Primorskiy Region, Sea Reserve, Island Bolshoy Pelis, *Borzova* s.n. (in Russian, A); Sakhalin, ex herbario horti Petropolitani, Augustinowicz, *T. baccata* var. *microcarpa*, Schmidt, p.p., with *T. caespitosa* var. *caespitosa* (A). **CHINA. Shanxi:** (“Schenhsi merid”): Taipei-schan, 1936, G. Fenzel 972 (A). **JAPAN.** Mt. Fujiwara Mie pref., Muroi 1969 (A); Mt. Himekami, Iwate pref, 14 Sep 1955, Muroi 5933 (A); Japan, no additional data, *Faurie* s.n. (P). **CULTIVATION. U.S.A. Ohio:** Secrest Arboretum, cultivars ‘Newport,’ ‘Hatfield.’

The epithet “*nana*” implies a dwarf plant, and Rehder (1902) described *T. cuspidata* var. *nana* as a “dwarf compact form with shorter leaves” in regard to a horticultural plant. Rehder (1949) later considered it only a form. Nevertheless, others applied the varietal name to native plants in Japan. The plants were characterized as low shrubs with a radial orientation of leaves, found mostly along the seaside of Japan (Ohwi 1965).

Variety *nana* is a low, densely branched shrub with oblong leaves that are mostly radial and crisscrossing in herbarium specimens, appearing dark glossy green above (adaxial surface) and paler below (abaxial surface).

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Thanks also to Dan Nicolson for helpful discussions on nomenclatural matters; John Thieret for his twice



FIGS. 59A–B. *Taxus umbraculifera* var. *nana*, Mt. Hyonosen, Japan (neotype, A). A (left). Herbarium specimen, all specimens appear to be from the same plant. B (right). Close-up of top specimen showing leaves and arillocarpium.

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REFERENCES

ALLISON, T.D. 1991. Variation in sex expression in Canada yew (*Taxus canadensis*). *Amer. J. Bot.* 78:569–578.

- ANONYMOUS. 1913. XLIII—The Wallichian Herbarium. *Kew Bull.* 1913:255–263.
- APPENDINO, G. 1995. The phytochemistry of the yew tree. *Nat. Prod. Rep.* 12:349–360.
- ARNO, S.F. and R.P. HAMMERLY. 1977. Northwest trees. The Mountaineers, Seattle.
- BAILEY, L.H. 1902. *Cyclopedia of American horticulture, R–Z.* MacMillan Co., New York.
- BAILEY, L.H. 1923. *The cultivated evergreens.* MacMillan Co., New York.
- BAILEY, L.H. 1933. *The cultivated conifers of North America.* MacMillan Co., New York.
- BANNAN, M. W. 1942. Notes on the origin of adventitious roots in the native Ontario conifers. *Amer. J. Bot.* 29:593–598.
- BEAN, J.W. 1953. *Trees and shrubs hardy in the British Isles—Vol. III (7th ed.).* John Murray, London.
- BEISSNER, L. 1891. *Handbuch der Nadelholzkunde.* Verlag von Paul Parey, Berlin.
- BERTOLONI, A. 1862. *Miscellanea botanica XXIII.* Mem. Acad. Sci. sér 2:228–229, tab.
- BERTRAND, C.E. 1874. Anatomie comparée des tiges et des feuilles chez les Gnétacées et les Conifères. *Ann. Sci. Nat. Bot. sér. 5,* 20:6–153.
- BEST, C., J.T. HOWELL, W. KNIGHT, I. KNIGHT, and M. WELLS. 1996. *Flora of Sonoma County.* CNPS Press.
- BOLSINGER, C.L. 2007. Personal communication. Occurrence of thicket yew (*Taxus brevifolia* var. *reptaneta*) in the Cascade Ranges of California, near Mt. Shasta.
- BOLSINGER, C.L. and A.E. JARAMILLO. 1990. *Taxus brevifolia* Nutt. Pacific Yew. In: R.M. Burns and B.H. Honkala, eds. *Silvics of North America, conifers, 1:*573–579. USDA For. Serv. Hdbk. 564.
- BROWICZ, K. and J. ZIELIŃSKI 1982. Chorology of trees and shrubs in South-West Asia and adjacent regions. *Polish Scientific Publishers, Vol. 1:*17, Warszawa.
- BRUMMITT, R.K. and C.E. POWELL (eds.) 1992. *Authors of plant names.* Royal Botanic Gardens, Kew.
- BURKHILL, I.H. 1965. *Chapters on the history of botany in India.* Botanical Survey of India, Calcutta.
- CALIFORNIA NATIVE PLANT SOCIETY (CNPS). Website, accessed March 2006. <http://www.marin.cc.ca.us/cnps/>.
- CALLEN, G. 1977. *Les Confères cultivés en Europe. Vol. II,* ed. J. B. Baillièrè, Coll. Tech. Hort. Spéc.
- CAMEFORT, H. 1956. Étude de la structure du point végétatif et des variations phyllotaxiques chez quelques gymnospermes. *Ann. Des Sci. Nat. Bot. sér. 17(1):*103–120.
- CARRIÈRE, E-A. 1855a. *Traité general des Conifères.* Chez l'auteur, Rue de Buffon, Paris.
- CARRIÈRE, E-A. 1855b. *Biota orientalis, Biota pyramidalis, et Taxus adpressa.* *Rev. Hort.* (1855):93–96.
- CARRIÈRE, E-A. 1861. *If de Dowaston.* *Rev. Hort.* (1861):175–176.
- CARRIÈRE, E-A. 1867. *Traité general des Conifères. Nouvelle Éd.* Chez l'auteur, Rue de Buffon, Paris.
- CHADWICK, L.C. and R.A. KEEN. 1976. A study of the genus *Taxus.* *Ohio Agric. Res. Bull.* 1086.
- CHAMPION, H.G. and S.K. SETH. 1968. *A revised survey of the forest types of India.* Manager of Publications Delhi, India Press, Nasik.
- CHANSLOR WETLANDS WILDLIFE PROJECT, Website. Accessed March 2006. *Plants of the Salmon Creek Watershed.* <http://www.sonomawetlands.org/Plants-Trees-Fix3.htm>.
- CHENG (ZHENG), W-C., L-K. FU, and C-Y. CHENG. 1975. *Gymnospermae Sinicae.* *Acta Phytotax. Sin.* 13(4):56–90& 66 illus., 17 plates.
- CHENG (ZHENG) W-C., and L-K. FU. 1978. *Taxaceae.* In: *Fl. Reipub. Pop. Sin.* 7, *Gymnospermae. Agendae Academiae Sinicae.* [English Translation].
- CHUNG, T.H. 1965. *Illustrated encyclopedia of fauna and flora of Korea. Vol. 5. Tracheophyta.* Ministry of Education, Plant Series, Samhwa Publ. Co. [In: Korean except for Latin names and English Forward].
- CITES [CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA]. 2001. Review of the genus *Taxus.* Eleventh meeting of the plants committee Langkawi (Malaysia), 3–7 Sep. "Document prepared by the United States of America." PC 11 Doc 22. 5 pp. <http://www.cites.org/eng/com/pc/11/E-PC11-22.pdf>.
- CITES [Convention on International Trade in Endangered Species of Wild Fauna and Flora]. 2004. Amendments to Appendices I and II of CITES. Thirteenth Meeting of the Conference of the Parties, Bangkok, Thailand, October 2–14, 2004. <http://www.cites.org/eng/cop/13/prop/E13-P48.pdf>; <http://www.iucnredlist.org/search/details.php/34041/all>

- COLLINS, D., R.R. MILL, and M. MÖLLER. 2003. Species separation of *Taxus baccata*, *T. canadensis*, and *T. cuspidata* (Taxaceae) and origins of their reputed hybrids inferred from RAPD and cpDNA data. *Amer. J. Bot.* 90:175–182.
- COPE, E.A. 1998. Taxaceae: The genera and cultivated species. *Bot. Rev.* 64:291–322.
- CORRADINI, P., C. EDELIN, A. BRUNEAU, and A. BOUCHARD. 2002. Architectural and genotypic variation in the clonal shrub *Taxus canadensis* as determined from random amplified polymorphic DNA and amplified fragment length polymorphism. *Canad. J. Bot.* 80:205–219.
- CROOM, E.M., JR. 1995. *Taxus* for taxol and taxoids. In: M.S. Suffness, ed. *Taxol. Science and applications*. CRC Press. Pp. 37–70.
- DA CHENG, H. 2007. Personal communication. Unable to extract DNA from 1–15 yr old herbarium specimens of *Taxus globosa* var. *floridana*, *T. brevifolia* var. *brevifolia*, var. *polychaeta*, and var. *reptaneta*. Chinese Academy of Sciences, Dalian Institute of Chemical Physics, Biotechnology, Dalian, China.
- DEMPSEY, D. and I. HOOK. 2000. Yew (*Taxus*) species—chemical and morphological variations. *Pharm. Biol.* 38:274–280.
- DERYUGINA, T.F. and N.D. NESTEROVICH. 1981. Peculiarities of the morphological and anatomical structure of conifer needles of some *Taxus* L. species. *Dokl. Akad. Nauk Bel. S.S.R.* 25(7):652–655 [Russian with English summary].
- DOEDE, D.L., E. CARROLL, R. WESTFALL, R. MILLER, J.H. KITZMILLER, and K.M.B. SNADER. 1993. Geographic variation in allozymes and taxol, and propagation by root cuttings in Pacific yew. In: *International yew resource conference. Yew (Taxus) conservation biology and interactions*, Berkeley, CA (abstract). Pp. 10.
- DUFFEY, E. 1980. Ecological history of yew *Taxus baccata* in southern England. *Biol. Conserv.* 17:243–265.
- ELIAS, T.S. and V. KORZHENEVSKY. 1992. The presence of taxol and related compounds in *Taxus baccata* native to the Ukraine (Crimea), Georgia, and southern Russia. *Aliso* 13:463–470.
- ELIOT, W.A. 1938. *Forest trees of the Pacific Coast*. Putnam, NY.
- EL-KASSABY, Y.A. and A.D. YANCHUK. 1994. Genetic diversity, differentiation, and inbreeding in Pacific yew from British Columbia. *J. Hered.* 85:112–117.
- EL-KASSABY, Y.A. and A.D. YANCHUK. 1995. Genetic variation of Pacific Yew in British Columbia and its conservation. In: Ph. Baradat, W.T. Adams and G. Müller-Starck, eds. *Population genetics and genetic conservation of forest trees*. Academic Publishing, Amsterdam, The Netherlands. Pp. 227–235.
- ELWES, J.W. and A. HENRY 1906. *The trees of Great Britain and Ireland*. Priv. Printer, Edinburgh.
- ENDLICHER, S. 1847. *Synopsis coniferarum*. Scheitlin & Zollikofer, Sangalli.
- FARJON, A. 1998. *World checklist and bibliography of conifers*. The Royal Botanic Gardens, Kew.
- FARJON, A. 2001. *World Checklist and Bibliography of Conifers*. 2nd edition. The Bath Press, Bath, United Kingdom.
- FARJON, A. and C.N. PAGE (Compilers). 1999. *Conifers. Status survey and conservation action plan*. Species Survival Commission Conifer Specialist Group, International Union for Conservation of Nature and Natural Resources, Gland, Switzerland. Frequently cited as Conifer Specialist Group 1998 with further reference to data collection forms for conifer species completed by the SSC [Species Survival Commission] Conifer Specialist Group between 1996 and 1998. IUCN, Gland, Switzerland and Cambridge, UK. 121p.
- FLORIN, R. 1931. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. *Kongl. Svenska Vetenskapsakad. Handl.* 10:45–588.
- FLORIN, R. 1948a. Enumeration of gymnosperms collected on Swedish expeditions to western and northwestern China. *Acta Horti Berg.* 14:343–384.
- FLORIN, R. 1948b. On the morphology and relationships of the Taxaceae. *Bot. Gaz.* 110:31–39.
- FLORIN, R. 1948c. On *Nothotaxus*, a new genus of the Taxaceae, from eastern China. *Acta Horti Berg.* 14:385–395, plates 1–3.
- FRANCO, J.A. 1964. *Taxus*. *Fl. Europaea* 1:39.
- FRANKLIN, J.F., and C.T. DYRNESS. 1969. *Vegetation of Oregon and Washington*. USDA For. Res. Pap. PNW-80.
- FREITAG, H. 1971. Studies in the natural vegetation of Afghanistan. In: P.H. Davis, P.C. Harper, and I.C. Hedge, eds. *Plant life of south-west Asia*, Bot. Soc. Edinburgh. Pp. 89–106.
- FRIMMEL, F. VON. 1911. Die untere Kutikula des *Taxus*-Blattesein Lichtreflektor. *Oesterr. Bot. Z.* 61:216–223.

- FU, L-k, N. LI, and R.R. MILL. 1999. Taxaceae. Fl. China 4:89–96, Missouri Botanical Garden Press, St. Louis.
- GADEK, P.A., C.J. QUINN, and A.E. ASHFORD. 1984. Localization of the biflavonoid fraction in plant leaves, with special reference to *Agathis robusta* (C. Moore ex F. Muell.) F.m. Bail. Austral. J. Bot. 32:15–31.
- GAMBLE, J.S. 1922. A manual of Indian timbers. Sampson Low, Marston & Co, London.
- GENDEREN, H. van, L. M. SCHOONHOVEN, and A. FUCHS. 1996. Chemisch-ecologische flora van Nederland en België en inleiding over aard en ecologische betekenis van secundaire plantestoffen, KNNV Uitgeverij, Utrecht.
- GODWIN, H. 1975. History of the British flora (2nd ed.). Cambridge University Press.
- GOODMAN, J. and V. WALSH. 2001. The story of taxol. Nature and politics in the pursuit of an anti-cancer drug. Cambridge University Press.
- GORDON, G. 1875. The pinetum: being a synopsis of all the coniferous plants at present known, with descriptions, history and synonyms (2nd ed.). Henry C. Bohn, London.
- GORDON, G. and R. GLENDENNING. 1858. The pinetum: being a synopsis of all the coniferous plants at present known, with descriptions, history and synonyms. Henry C. Bohn, London.
- GRAUSTEIN, J.E. 1950/51. Nuttall's travels into the old Northwest. Chronica Bot. 14 (1–2). i–vii, 1–86, 9 plates and 9 pp of captions, index.
- GREUTER, W., J. MCNEILL, F.R. BARRIE, H.M. BURDET, V. DEMOULIN, T.S. FILGUEIRAS, D. NICOLSON, P.C. SILVA, J.E. SKOG, P. TREHANE, N.J. TURLAND, and D.L. HAWKSWORTH. 2000. International code of botanical nomenclature (Saint Louis Code) adopted by the 16th International Botanical Congress. St. Louis, MO, July–August 1999. Koeltz Scientific Books, Königstein, Germany.
- Grierson, A.J.C. and D.G. LONG. 1983. Flora of Bhutan. Vol 1. Pt. 1. Royal Botanic Garden, Edinburgh.
- GRIFFIN, J. and I. HOOK. 1996. Taxol content of Irish yews. Planta Med. 386: 370–372.
- GRIFFITH, W. 1854. Notulae ad plantas asiaticas. Posthumous papers bequeathed to the Honorable The East India Company, arranged by John M'Clelland, Bishops' College Press, Calcutta. Vol. 4.
- HAGENEDER, F. 2007. Yew. A history. Sutton Publishing Ltd., Thrupp-Stroud-Goucestershire.
- HANDEL-MAZZETTI, H. 1929. Symbolae Sinicae. Julius Springer, Wien.
- HARA, H., W.T. STEARN, and L.H.J. WILLIAMS. 1978. An enumeration of the flowering plants of Nepal. Vol. 1. British Museum, London.
- HEINZE, B. 2004. Zur Populationsbiologie der gemeinen Eibe (*Taxus baccata*). Centralblatt für das gesamte Forstwesen 121:47–59.
- HERTEL, H. VON and N. KOHLSTOCK. 1996. Genetische Variation und geographische Struktur von Eibenvorkommen (*Taxus baccata* L.) in Mecklenburg-Vorpommern. Silvae Genet. 45:290–294.
- HIEP, N.T. 1998. The gymnosperms of Vietnam. In: Z. Aoluo and W. Sugong, eds. Proceedings of the First International Symposium on Floristic characteristics and diversity of East Asian plants, July 25–27, 1996, Kunming, Yunnan. China Higher Education Press Beijing and Springer-Verlag Berlin Heidelberg. Pp. 91–103.
- HILFIKER, K., R. HOLDEREGGER, P. ROTACH, and F. GUGERLI. 2004. Dynamics of genetic variation in *Taxus baccata*: local versus regional perspectives. Canad. J. Bot. 82:219–227.
- HILL, K.D. and L.J. SCRIVEN. 1998. The fossil record of conifers in Australia. Fl. Australia 48:527–537.
- HILS, M. 1993. Taxaceae Gray. Yew family. Fl. North America 2:423–427.
- HISTORYLINK.ORG. 2007. The Online Encyclopedia of Washington State History, Essay 7298. http://historylink.org/essays/output.cfm?file_id=7298.
- HITCHCOCK, C.L., A. CRONQUIST, M. OWNBEY and J.W. THOMPSON. 1969. Vascular plants of the Pacific Northwest I. University of Washington Press, Seattle.
- HOOKE I., C. POUPAT, A. AHOND, D. GUENARD, F. GUERITTE, M-T. ADELIN, X-P. WANG, D. DEMPSEY, S. BREUILLE and P. POTIER. 1999. Seasonal variation of neutral and basic taxoid contents in shoots of European Yew (*Taxus baccata*). Phytochemistry 53:1041–1045.
- HOU, H-Y. 1983. Vegetation of China with reference to its geographical distribution. Ann. Missouri Bot. Gard. 70:509–548.
- HU, S-y. 1964. [Notes on] the Flora of China. Taiwania:13–62.

- IUCN. 2004. Red List of Threatened Species. With reference to Conifer Specialist Group 1998. www.iucnredlist.org [updated 2006].
- JARVIS, C.E., F.R. BARRIE, D.M. ALLAN, and J.L. REVEAL. 1993. A list of Linnaean generic names and their types. *Regnum Veg.* 127.
- JEAN, F.-I., F.-X. GARNEAU, G.J. COLLIN, and M. BOUHAJIB. 1993. The essential oil and glycosidically bound volatile compounds of *Taxus canadensis* Marsh. *J. Essential Oil Res.* 5:7–11.
- JINXING, L. and H. YUXI (eds.). 2000. Atlas of structure of gymnosperms. Science Press, Beijing.
- KHAN, N. U.-D. and N. PARVEEN, 1987. The constituents of the genus *Taxus*. *J. Sci. Industr. Res.* 46:512–516.
- KINGSTON, D.G.I. 1996. Improving on nature. *Taxane J.* 2:20–27.
- KINGSTON, D.G.I. 2005. Taxol and its analogs. In: G.M. Cragg, D.G.I. Kingston and D.J. Newman, eds. *Anticancer agents from natural products*. CRC Taylor & Francis, Boca Raton, FL. Pp. 89–122.
- KINGSTON, D.G.I., G. SAMARANAYAKE, and C.A. IVEY. 1990. The chemistry of taxol, a clinically useful anticancer agent. *J. Nat. Prod.* 55:1–12.
- KNIGHT, J. 1850. A synopsis of the coniferous plants grown in Great Britain and sold by Knight and Perry at the exotic nursery, Kings Road, Chelsea. Longman, Brown, Green, and Longmans, London.
- KOCH, K. 1873. *Dendrologie*. Verlag von Ferdinand Enke (Erlangen).
- KOLESNIKOV, B. P. 1935. On the shrubby kind of the spiky yew (*Taxus cuspidata* S. et Z.). *Bull. Far E. Branch Acad. Sci., USSR* 31–47 (In Russian with English summary).
- KORPELA, I. ILKKA KORPELA'S INDEX, WEBSITE. 2006 (March). Photo of *Taxus canadensis* var. *adpressa*, referred to as *T. baccata*, indicated to have been photographed in Estonia. Cited by WBA (www.worldbotanical.com) web site since 2003. http://honeybee.helsinki.fi/users/korpela/taxus_baccata.html.
- KRAUZE-BARANOWSKA, M. and M. WIWART. 2003. Antifungal activity of biflavones from *Taxus baccata* and *Ginkgo biloba*. *Z. Naturf.* 58c:65–69.
- KRÜSSMANN, G. 1985. *Manual of cultivated conifers*, translated by M.E. Epp. H-D. Warda and G. S. Daniels, eds. Timber Press, Portland.
- KRUPKIN, A.B. 1994 (unpublished & pers. comm.). Report on PCR results for selected samples of *Taxus* received by Phyton Inc. from Sweden, Korea, China and The Philippines.
- KURZ, H. 1937. A new and remarkable habitat for the endemic Florida yew. *Torreya* 27:90–92.
- KVAČEK, Z. [1984 fide author notation on reprint.]. Tertiary taxads of NW Bohemia. 1982 *Acta Univ. Carol., Geol., Pokorný* 4:471–491.
- KVAČEK, Z., and W.C. REMBER. 2000. Shared Miocene conifers of the Clarkia flora and Europe. *Acta Univ. Carol. Geol.* 44:75–85.
- KVAČEK, Z., and W.C. REMBER. Under Review. *Calocedrus robustior* (Cupressaceae) and *Taxus howardii* (Taxaceae): Two new conifers from the Middle Miocene of the western North America (Clarkia area, Latah Formation, northern Idaho). *Paleobios*.
- KWEI, Y.-L., and S.-Y. HU. 1974. [Epidermal feature of leaves of *Taxus* in relation to taxonomy]. *Acta Phytotax. Sin.* 12(3):329–334, plate 67 [Chinese with English summary].
- LAUBENFELS, D.J., DE. 1969. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. *J. Arnold Arbor.* 50:315–369.
- LAUBENFELS, D.J., DE. 1978. The taxonomy of Philippine Coniferae and Taxaceae. *Kalikasan* 7:117–152.
- LAUBENFELS, D.J., DE. 1988. Coniferales. *Fl. Malesiana* 10(3):337–453.
- LAWSON, P. and SON [C. LAWSON]. 1851. The fir tribe. No. X. Abietineae. List of seeds, plants, etc. Private press, Peter Lawson, Edinburgh [Note: Stafleu & Cowan (1979) indicate that for a later major publication, *The pinetum britannicum*, Ravenscroft compiled the text and Lindley and other botanists the descriptions. Peter Lawson was mainly an editor and Charles Lawson, the son of Peter, was the botanist; copy of relevant pages reviewed for this paper was obtained at BM].
- LEIGHTON, W.A. 1841. A flora of Shropshire. John van Voorst, London & John Davies, Shrewsbury.
- LÉVEILLÉ, H. 1914. *Le Monde des Plantes*. Sér. 2, 16:88, 20.

- LI, H.-L. 1963. Woody flora of Taiwan. Livingston Publ. Co., Narberth, PA.
- LI, J., C.C. DAVIS, P. DEL TREDICI, and M.J. DONOGHUE. 2001. Phylogeny and biogeography of *Taxus* (Taxaceae) inferred from sequences of the internal transcribed spacer region of nuclear ribosomal DNA. *Harv. Pap. Bot.* 6: 267–274.
- LI, N. and L.-K. FU. 1997. Notes on gymnosperms I. Taxonomic treatments of some Chinese conifers. *Novon* 7:261–264.
- LIBERTY HYDE BAILEY HORTORIUM, STAFF. 1976. *Hortus* third. Macmillan Publishing Co., New York.
- LIU, T.-S. 1960. Illustrations of native and introduced ligneous plants of Taiwan. Vol. 1. National Taiwan University.
- LOUDON, J.C. 1844. *Arboretum et fruticetum Britannicum*. Longman, Brown, Green and Longmans, London.
- LOWE, J. 1897. *The yew trees of Great Britain and Ireland*. MacMillan and Co., Ltd., London.
- MAKINO, T. 1931. *Illustrated flora of Nippon, with the cultivated and naturalized plants*. Honkuryukwan Co., Ltd., Japan. {Note: date from print on external binding, cited by others as 1940.}
- MARKHAM, K.R., R.F. WEBBY, L.A. WHITEHOUSE, B.J. MOLLOY, C. VILAIN, and R. MUES. 1985. Support from flavonoid glycoside distribution for the division of *Podocarpus* in New Zealand. *New Zealand J. Bot.* 24:1–13.
- MARSHALL, H. 1785. *Arbustum Americanum*. Joseph Crukshank, Philadelphia, PA.
- MAXIMOWICZ, C.J. 1859. *Primitiae florum amurensis*. Buchdruckerei der kaiserlichen Akademie der Wissenschaften, St. Petersburg.
- MITCHELL, J. 1974. The yew trees of lynchionag, Dunbartonshire. *Trans. Bot. Soc. Edinburgh* 42:163–166.
- NAKAI, T. 1938. Indigenous species of conifers and taxads of Korea and Manchuria, and their distribution. *Chôsen Sanrin Kaihō (J. Kor. For. Soc.)* 158:21.
- NICOLOSI, R.T. 1982. Morphological features of leaves and pollen as in aid in separating selected species and cultivars within the genus *Taxus*. Thesis, Ph.D., Ohio State University.
- OHWI, J. 1965. *Flora of Japan*. English translation, eds. F. G. Meyer & E. H. Walker, Smithsonian Institution, Washington, DC.
- OLDHAM, K. 2005. David Douglas arrives at Fort Vancouver to begin two years of botanical exploration on April 20, 1825. *HistoryLink.org*. The Online Encyclopedia of Washington State History, Essay 7298 (Accessed Feb. 2007, http://www.historylink.org/essays/output.cfm?file_id=7298).
- ORR, M.Y. 1937. On the value for diagnostic purposes of certain of the anatomical features of conifer leaves. *Notes Roy. Bot. Gard. Edinburgh* 94:256–265 & Plates.
- OUDEN, P. DEN and B.K. BOOM. 1965. *Manual of cultivated conifers*. M. Nijhoff, Hague.
- PARLATORE, P. 1868. Coniferae. In: A. de Candolle, *Prodromus systematis naturalis regni vegetabilis* 16 (2):361–524.
- PILGER, R. 1903. Taxaceae-Taxoideae—Taxeae. *Taxus*. In: Engler, *Das Pflanzenreich* IV:110–116.
- PILGER, R. 1916. Die Taxales. *Mitt. Deutsch. Dendrol. Ges.* 25:1–28.
- RAO, A.R. and M. MALAVIYA. 1965. On the distribution, structure, and ontogeny of sclereids in *Taxus baccata*. *Linn. Proc. Natl. Inst. Sci. India* 31:114–122.
- RAU, M.A. 1974. Vegetation and phytogeography of the Himalaya. In: M.S. Mani, ed. *Ecology and biogeography of India*, W. Junk, Hague. Pp. 247–280.
- REHDER, A. 1902. *Taxus*. In: L.H. Bailey and W. Miller, *Cyclopedia of American horticulture*. Vol. 4 (R–Z). The MacMillan Co., NY.
- REHDER, A. 1919. New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum. *J. Arnold Arb.* 1:44–60.
- REHDER, A. 1923. New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum. *Taxus media* hybr. nov., *Taxus media* f. *hatfieldii* forma nov., *Taxus media* f. *hicksii*, comb. nov. *J. Arnold Arbor.* 4:107–109.
- REHDER, A. 1936. Notes on the ligneous plants described by H. Léveillé from eastern Asia. *Taxaceae*. *J. Arnold Arb.* 17:54.
- REHDER, A. 1940. *Manual of cultivated trees and shrubs* (2nd ed.). MacMillan Co., NY.

- REHDER, A. 1949. Bibliography of cultivated trees and shrubs. Arnold Arboretum, Jamaica Plain, MA.
- RODWELL, J.S. (ed.), C.D. PIGOTT, D.A. RATCLIFFE, A.J.C. MALLOCH, H.J.B. BIRKS, M.C.F. PROCTOR, E.W. SHIMWELL, J.P. HUNTLEY, E. RADFORD, M.J. WIGGINTON, and P. WILKINS. 1991. British plant communities. Vol. 1. Woodland and scrub. Cambridge University Press.
- ROZENDAAL, E.L.M., G.P. LELYVELD, and T.A. VAN BECK. 2000. Screening of the needles of different yew species and cultivars for paclitaxel and related taxoids. *Phytochemistry* 53:383–389.
- SAIKIA, D, S. P.S. KHANUJA, A.K. SHASANY, M.P. DAROKAR, A.K. KUKREJA, and S. KUMAR. 2000. Assessment of diversity among *Taxus wallichiana* accessions from northeast India using RAPD analysis. *IPGRI Newsletter* 121:27–31.
- SAPRU, B.L. 1975. Vegetational studies in Jhelum Valley. *Botanique* 6:151–164.
- SARGENT, C.E. 1896. The silva of North America. X. Houghton, Mifflin & Co., Boston and New York.
- SEIGLER, D.S. 1991. Cyanide and cyanogenic glycosides. In: G.A. Rosenthal and M.R. Berenbaum, eds. *Herbivores: their interactions with secondary plant metabolites*. Academic Press, San Diego, CA. Pp. 35–78.
- SIEBOLD, P.F., VON and J.G. ZUCCARINI. 1843. Plantarum, quas in Japonia collegit Dr. Ph. Fr. de Siebold. *Genera Nova. Notis characteristicis delineationibusque illustrata proponunt*, I. *Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.* 3.
- SIEBOLD, P.F., VON and J.G. ZUCCARINI. 1846. *Florae japonicae familiae naturales*. *Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.* 4:123–240.
- SIEBOLD, P.F., VON and J.G. ZUCCARINI [1870]. *Flora japonica*, pts 6–10 [Descriptions by F.A.W. Miquel and published by Miquel]. *Lugduni batavorum*.
- SILBA, J. 1984. An international census of the coniferae, I. *Phytologia Mem.* 7:1–79.
- SILBA, J. 1986. *Encyclopaedia coniferae*. *Phytologia Mem.* 8:1–217.
- SILBER, M. and G.P. DEWOLF, JR. 1970. Yews in fiction and fact. *Arnoldia* 30:139–147.
- SPJUT, R.W. 1977 (July 14). *Taxus brevifolia* Nutt. (Taxaceae), nomenclature, description, distribution, ecology, comments, uses, other, references, and attachments—table 8 from Franklin and Dyrness 1969, distribution maps. USDA ARS Medicinal Plant Resources Laboratory, Beltsville, MD. 12 pp (circulated to USDA lab scientists, NCI; content also incorporated into NCI solicitations for large collections of stem-bark sent to prospective bidders in the Pacific Northwest, 1978–1990; copy available at <http://www.worldbotanical.com/TAXNA.HTM>).
- SPJUT, R.W. 1992. A taxonomic key to the species of *Taxus*. NCI Workshop on *Taxus*, Taxol, and Taxotere, Rockville, MD (Abstract only).
- SPJUT, R.W. 1993. Reliable morphological characters for distinguishing species of *Taxus* (Abstract). In: International yew resource conference. Yew (*Taxus*) conservation biology and interactions. Berkeley, CA. Pp. 39–40.
- SPJUT, R.W. 1995 (May 25). Research proposal on taxonomic revision of *Taxus*. USDA ARS Memorandum to Thomas S. Elias, Director, National Arboretum, with references, key to species of *Taxus* dated 24 Apr 1995, character list in DELTA format. Photocopy at <http://www.worldbotanical.com/TAXNA.HTM>.
- SPJUT, R.W. 1998. (a) Morphological evolution in the *Taxus* leaf and its significance to recognizing ecological species within the genus. (b) Species of *Taxus*. Presented at the AIBS Annual Meeting, American Systematic Plant Taxonomists, Baltimore Convention Center, MD, 5 Aug. 1998. Abstracts published on the Internet, Botanical Society of America (URL: <http://www.botany.org/>).
- SPJUT, R.W. 2000. Three papers presented at the joint meetings of the Botanical Society of America and American Systematic Plant Taxonomists, Portland, OR, August, abstracts published online and *Amer. J. Bot.*
- (a) A phytogeographical analysis and classification of leaf morphological features in *Taxus* (Taxaceae). <http://www.ou.edu/cas/botany-micro/botany2000/section13/abstracts/27.shtml>.
- (b) The morphological relationships of *Taxus canadensis* (Taxaceae) in North America and Eurasia. <http://www.ou.edu/cas/botany-micro/botany2000/section13/abstracts/28.shtml>
- (c) A revised taxonomic key to species and varieties of *Taxus* (Poster). <http://www.ou.edu/cas/botany-micro/botany2000/section13/abstracts/166.shtml>. (Note key also presented on the WBA website in 2003, extracted from an poster document of 24 pages that included 270 figures).
- SPJUT, R.W. 2003. Unpublished. Nomenclatural and taxonomic review of three species and two varieties of *Taxus* (Taxaceae) in Asia. Prepared 1998, submitted to Sida in 2000, placed on the web, www.worldbotanical.com,

2003. Additional reviews: *Taxus* (Overview of *Taxus*, 1999). Keys and descriptions for species of *Taxus*, Introduction to taxonomy of *Taxus*, (2003). North America (1999) and Species groups and subgroups (2003). All revised in 2006, 2007. www.worldbotanical.com.
- SPJUT, R.W. 2006. Biogeographical data on putative hybrids for species of *Taxus* (Taxaceae) in the Himalayas and North America. Abstract, Botanical Society of America, Chico, CA, July 29–Aug 2. <http://www.botanyconference.org/engine/search/index.php?func=detail&aid=37>
- SPJUT, R.W. 2007. A phylogeographical analysis of *Taxus* (Taxaceae) based on leaf anatomical characters. *J. Bot. Res. Inst. Texas*: 1(1):291–332.
- SPJUT, R.W., J-Y. ZHOU, and C-J CHANG. 1993. Comparison of taxane content between two different native yews from the Pacific northwest. Poster/Abstract, 34th Annual Meeting, Amer. Soc. Pharmacog., San Diego, CA.
- STAFLEU, F.A., and R. S. COWAN. 1976–1988. TL-2. Taxonomic literature. 7 Vols. W. Junk, Hague.
- STAINTON, J.D.A. 1972. *Forests of Nepal*. Camelot Press, London.
- SUFFNESS, M (ed.). 1995. TAXOL. Science and applications. CRC Press, Inc.
- TAYLOR, R.L. 1932. The successional trend and its relation to second growth forests in southeastern Alaska. *Ecology* 13:381–390.
- TAYLOR, R.L. and S. TAYLOR. 1980. *Taxus brevifolia* in British Columbia. *Davidsonia* 12:89–94.
- THOMAS, P.A. and A. POLWART. 2003. Biological flora of the British Isles. *Taxus baccata* L. *J. Ecol.* 91:489–524.
- THUNBERG, C.P. 1784. *Flora Japonica*. Mülleriano, Lipsiae.
- TITTENSOR, R.M. 1980. Ecological history of yew *Taxus baccata* in southern England. *Biological Conservation* 17:243–265.
- VANCE, N.C. and A.B. KRUPKIN. 1993. Using restriction fragment length polymorphisms to assess genetic variability among yew taxa. *Yew (Taxus) conservation biology and interactions*: 34, Berkeley, CA (abstract).
- VEITCH, J. and SONS. 1881. *A manual of the Coniferae*. Published by the authors, Kings Road, Chelsea.
- VOLIOTIS, D. 1986. Historic and environmental significance of the yew (*Taxus baccata* L.). *Israel J. Bot.* 35:47–52.
- WALL, M.E., M.C. WANI, and H. TAYLOR. 1972. Isolation and chemical characterization of antitumor agents from plants. *Cancer Treat. Rep.* 60:1011–1030.
- WALLICH, N. 1826. *Tentamen florum nepalensis illustratae*. Fasc. 2. Calcutta and Serampore.
- WANG, C-W. 1961. *The forests of China*. Maria Moors Cabot Foundation No. 5, Harvard University, Cambridge, i-ix & 1–313.
- WANG, T., Y-J. SU, J-M. ZHU, G-K. FAN, and C. HUANG. 2000. RAPD analyses of Taxaceae and its related taxa. *Acta Sci. Nat. Univ. Sunyatseni* 39:120–130.
- WANI, M.C., H.L. TAYLOR, M.E. WALL, P. COGGON, and A.T. McPHAIL. 1971. Plant antitumor agents. VI. The isolation and structure of taxol, a novel antileukemic and antitumor agent from *Taxus brevifolia*. *J. Amer. Chem. Soc.* 93:2325–2327.
- WATT, A.S. 1926. Yew communities of the South Downs. *J. Ecol.* 14:282–310.
- WILSON, E.H. 1916. *The conifers and taxads of Japan*. Publ. Arnold Arbor. 8:1–91, Cambridge Univ. Press, Cambridge, MA.
- WILSON, E.H. 1926. Taxaceae. In: *The taxads and conifers of Yunnan*. *J. Arnold Arbor.* 7:39–42.