TSUGA

Tsuga, especially Tsuga growing in the Southeastern United States

Part four
including the pages 291-298 (of 247-305)
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p. 291

3. **Tsuga** (Endlicher) Carrière, Traité Conif. ed. 1. 185. 1855.

Evergreen trees with pendulous leading shoots and branches. Bark usually furrowed and scaly. Wood pale, without normal resin canals; ray tracheids and axial parenchyma regularly present. Leaves spirally arranged (often appearing 2-ranked due to twisting of leaf bases), linear, flattened and bearing 2 whitened

abaxial stomatiferous bands [or quadrangular and bearing stomata above and beneath], narrowing abruptly to a short petiole, abscising at maturity from the ultimately ligneous leaf bases; apex obtuse and often notched, or acute; margin entire or minutely serrulate; fibrovascular bundle double; resin canal single, abaxial to the vascular cylinder. Pollen cones (microsporangiate strobili) small (ca. 1 cm long), subglobose, stalked, borne singly in leaf axils of previous year; microsporophylls prolonged at tip into a short crest or knob; microsporangia subglobose, transversely dehiscent; pollen grains with saccae reduced to a circular "frill" [or bisaccate in sect. HESPEROPEUCE]. Ovulate cones terminal on short branches, maturing the first year; mature ovulate cones relatively small (1–4[–7] cm long), usually pendulous [rarely erect], with cone scales persistent; bracts shorter than scales [to somewhat protrusive in *T. longibracteata*]; ovuliferous scales suborbicular to oblong, entire or minutely lacerate. Seeds with delicate, obliquely oblong terminal wings; seed coat thin, bearing resin vesicles; cotyledons 2–7. Chromosome number $2n = 24$. LECTOTYPE SPECIES: *Tsuga Sieboldii* Carr.;[5] see Britton & Brown, Illus. Fl. No. U.S. & Canada, ed. 2. **1:** 62. 1913. (Name in Japanese for one of the species.)—HEMLOCK.

A genus of ten or more species of forest trees in the Temperate Zone of eastern and western North America and eastern Asia west to the Himalayas, both at low elevations and in mountain areas up to near timberline. Four well-marked species occur in the United States, including two in our region, and at least six grow in Asia. Over ten species have been described from China (Downie; Flous, 1936b, 1937), of which several are doubtfully distinct and have been placed in synonymy by Cheng & Fu. Thorough study of their patterns of variability is badly needed. Fossils indicate that the genus was more widespread and diverse in the past, having occurred in Europe well into the Tertiary (Florin, 1963; Kirchheimer; Sivak, 1973).

The species of *Tsuga* have generally been divided into two sections: TSUGA (sect. *Eutsuga* Engelm., sect. *Micropeuce* (Spach) Schneider), with pollen saccae reduced to a frill and stomata only on the lower (abaxial) leaf surface, and HESPEROPEUCE Engelm., with bisaccate pollen and less-flattened, amphistomatic leaves. Section HESPEROPEUCE consists of only two extant species, *T. Mertensiana* (Bong.) Carr. in western North America and *T. longibracteata* Cheng in southern China. The latter species, which is unusual in the genus in having the ovulate cones strongly ascending at maturity and the cone-scale bracts exserted, has otherwise been treated in sect. *Heopeuce* Keng & Keng, and in subg. *Paleotsuga* Miki, which was based on fossil material. French workers of the Toulouse school, beginning with Campo-Duplan & Gaussen, have proposed that the two species of sect. HESPEROPEUCE are actually stabilized intergeneric hybrids, as discussed below.

Section TSUGA is represented in our area by two species. *Tsuga canadensis* (L.) Carr. (*T. americana* (Miller) Farw.), Canada hemlock, eastern hemlock,

[5] *Abies Araragi* Sieb., Verh. Batav. Genootsch. **12:** 12. 1830 (*Tsuga Araragi* (Sieb.) Koehne), is an earlier name for *T. Sieboldii*. It was published without a usable description, illustration, or type and was only secondarily validated by Siebold & Zuccarini, Fl. Jap. **2:** 15. 1842, under *Abies Tsuga* Sieb. & Zucc. I thus accept the widely used name *T. Sieboldii* Carr. as correct.

hemlock-spruce, $2n = 24$, is a widely distributed species in the northeastern United States and adjacent Canada (Little, 1971, *maps 91N, E*) that occurs west to Wisconsin, eastern Minnesota, eastern Ohio, and southern Indiana. It is widely distributed in the Appalachian region of our area, ranging south to northern Georgia and northwestern Alabama and west to central Tennessee. It occurs in moist valleys and ravines and sometimes on steep, usually north-facing slopes at lower elevations in the northern part of its range, and on moist slopes and streamsides up to 1500 m altitude in our region. Ecogeographic variation in physiological and morphological features is pronounced between northern and southern provenances of the overall range and between north and south of the Tension Zone in Wisconsin (Eickmeier *et al.*; Ruth), although discrete infraspecific taxa have not been proposed on this basis. *Tsuga canadensis* is characterized by distichous, minutely serrulate leaves with rounded apices, pubescent young branchlets, and short-stalked, brownish to grayish ovulate cones with suborbicular scales. It differs from the rather similar western North American *T. heterophylla* (Raf.) Sarg. in having a broader tree crown and narrower, more sharply defined white stomatal bands on the abaxial leaf surface.

Tsuga caroliniana Engelm., Carolina hemlock, crag hemlock, southern hemlock, $2n = 24$, is a much more narrowly distributed species, occurring locally on dry slopes and ridges and along streamsides in the Appalachian Mountains from western Virginia and northeastern Tennessee south to extreme northeastern Georgia and northwestern South Carolina (Little, 1971, *map 94E*), generally at higher elevations than *T. canadensis*. It differs from the latter in having clearly spirally arranged, entire leaves (see FIGURE 3b) and larger (2–3.5 cm long), yellowish, early-deciduous cones with oblong (vs. broadly rounded) scales (see FIGURE 3k, l, r). Although the two species are reported occasionally to occur sympatrically (e.g., in Stokes County, North Carolina, and Roanoke County, Virginia; Coker & Totten; C. E. Wood, pers. comm.), despite differences in habitat preference, they are very distinct morphologically, and hybridization between them has not been reported.

Tsuga is distinguished from all other genera of the Pinaceae by its abruptly petiolate leaves with only a single resin canal abaxial to the vascular tissue. The genus has often been treated as similar to *Picea* because the twigs of both are roughened by the persistent leaf bases, the cones are usually pendulous at maturity, and prominent short-shoots are lacking. The two genera differ, however, in embryogeny and in their pollination mechanisms (Owens & Blake; Owens & Molder), as well as in the characters of root, stem, and seed anatomy that separate *Tsuga* and the other abietoid genera from *Picea* and the other pinoid genera.

Campo-Duplan & Gaussen and subsequent workers of the Toulouse school in France have proposed that *Tsuga Mertensiana* is an intergeneric hybrid of the western North American *T. heterophylla* and *Picea sitchensis* (Bong.) Carr., and that *T. longibracteata* is a hybrid of *Tsuga* and *Keteleeria*. These hypotheses were based primarily on purported intermediacy for a series of morphological characters and irregularities in the bisaccate pollen of the two hemlock species. No case of natural or artificial hybridization has been confirmed for either of

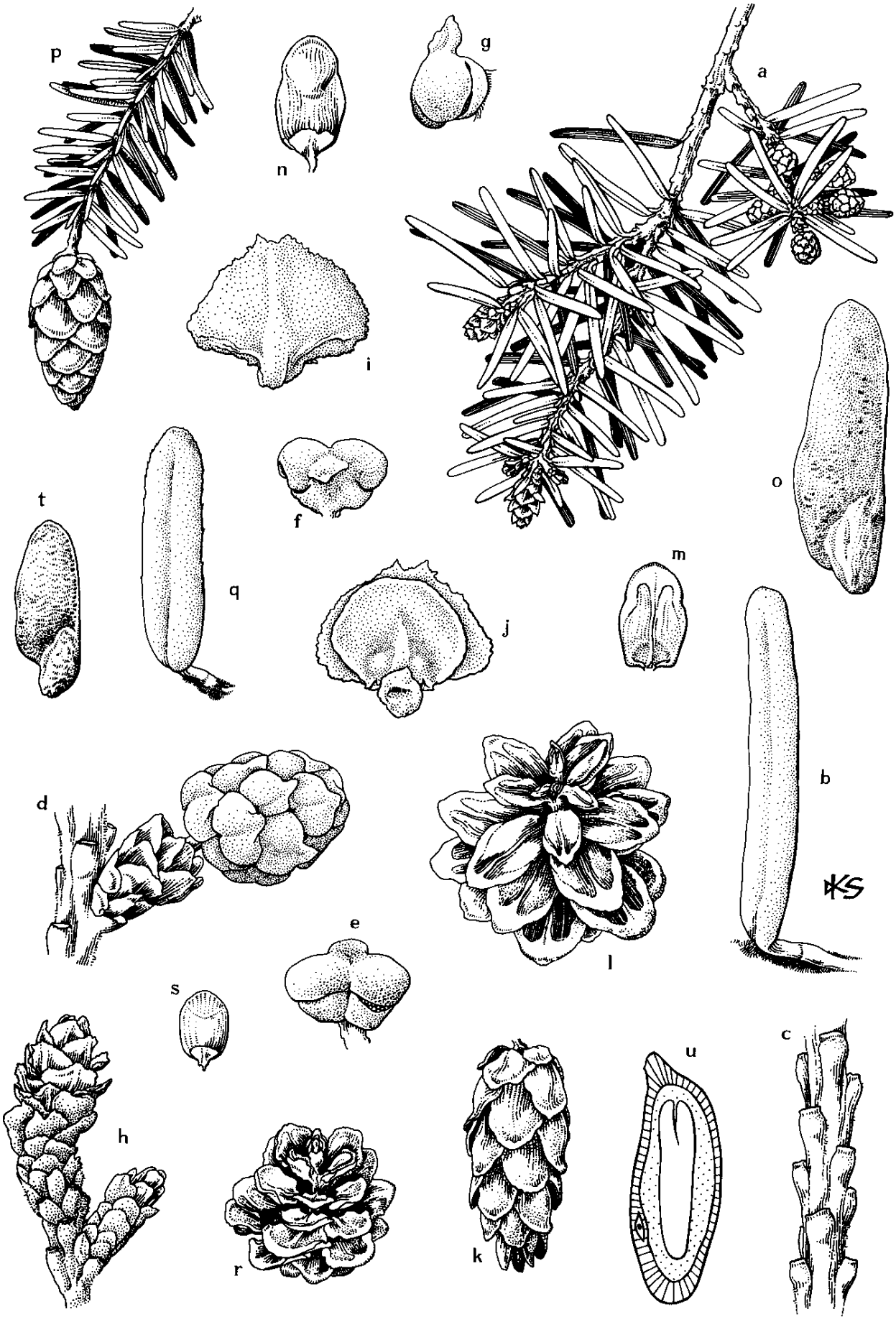

FIGURE 3

the pairs of genera, however, and it is far more likely that the two taxa involved are merely surviving species that have retained primitive states (e.g., bisaccate pollen) instead of the derived ones seen in sect. TSUGA. Comparison of leaf-terpenoid profiles (Von Rudloff, 1975a, b), immunological distances from seed proteins (Prager *et al.*; Price *et al.*), and patterns of embryological development (Owens & Molder) all show *T. Mertensiana* to be quite similar to other species of *Tsuga* but not to *Picea.*

Chromosome numbers, all $2n = 24$, are known for six species, including all four North American ones (Kuo *et al.*; Sax & Sax; Vabré-Durrieu, 1954b). The karyotype of nine approximately isobrachial and three heterobrachial chromosomes is similar to that of *Picea* (see Khoshoo, 1962; Sax & Sax).

Interspecific hybridization is extremely infrequent among the North American species. *Tsuga* ×*Jeffreyi* (Henry) Henry is a cultivated plant of unknown origin that is morphologically intermediate between *T. Mertensiana* and *T. heterophylla.* Attempts at artificial hybridization between these taxa have been unsuccessful (Meagher; Taylor), but a portion of the infrequent morphological intermediates from areas of near sympatry have proved to be intermediate in leaf-phenolic profile (Taylor).

Comparative pollen morphology of *Tsuga* has been treated in detail by Campo, G. Erdtman (1957, 1965), Sivak, and Ueno (1957). The species of sect. TSUGA are unique in the Pinaceae in having the pollen saccae reduced to a circular frill and in often having spinules atop the verrucate surface ornamentation (G. Erdtman, 1957, 1965; Sivak, 1973). The spinules are apparently absent in *T. canadensis* and are relatively small in *T. caroliniana* and *T. heterophylla* (Sivak, 1973). The size of the two saccae is quite variable within the species of sect. HESPEROPEUCE (Campo; Ho & Sziklai), and fossil *Tsuga* pollen

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FIGURE 3. **Tsuga.** a–o, *T. caroliniana*: a, branchlet at time of shedding of pollen, microsporangiate strobili at upper right, 2 ovulate strobili terminating branches below, × 1; b, leaf, showing characteristic entire margin, × 5; c, part of twig after leaf abscission, showing persistent leaf bases, × 6; d, microsporangiate strobilus with bud scales at base, × 6; e–g, microsporophyll with dehisced sporangia, viewed from below, from above, and from side, × 10; h, twig (leaves removed) with terminal ovulate cone (subtended by bud scales), very young leaves beginning to show at tip of short twiglet at right, × 3; i, cone-sale bract (abaxial view) at time of pollination, the smaller ovuliferous scale above completely hidden, × 10; j, adaxial view of ovuliferous scale and bract at time of pollination, micropyles of the 2 ovules below, × 10; k, mature cone in moist condition, cone scales appressed, × 1; l, mature dry cone, seeds already shed, impressions of seed wings conspicuous on ovuliferous scales, × 1; m, n, mature cone scale, adaxial and abaxial views, bract showing at base in n, × 1; o, seed with wing, adaxial view, × 3. p–u, *T. canadensis*: p, branchlet with mature unopened cone (compare leaf arrangement with "a," noting especially the smaller appressed leaves on upper side), × 1; q, leaf, showing serrulate margin and abrupt narrowing to petiole, × 5; r, mature dry cone with seeds shed (compare to "l"), × 1; s, mature cone scale, abaxial view, with bract at base, × 1; t, seed with wing, adaxial view, × 3; u, diagrammatic longitudinal section of seed, with seed coat hatched, megagametophyte stippled, and embryo (with 2 cotyledons) unshaded, × 10.

has been reported to show a wide range of variation between saccate and frilled forms (Kirchheimer; Wodehouse).

In accord with the differences in pollen form, the pollination mechanisms of *Tsuga Mertensiana* and members of sect. TSUGA are quite dissimilar, although both lack the pollination-drop mechanism of *Picea* and *Pinus*. The relatively smooth pollen of *T. Mertensiana* is caught on microdroplets on the integumentary flaps (Owens & Blake). In contrast, the spinulose pollen surface of species such as *T. heterophylla* apparently aids in its adherence to the waxy surface of the bracts, which are much more prominent than the cone scales at this stage of development (Colangelli & Owens; Owens & Blake). Although this unusual pollen-capture mechanism has also been reported in *T. dumosa* (D. Don) Eichler, it needs to be documented in other species of sect. TSUGA (Doyle & O'Leary).

Leaf anatomy of *Tsuga canadensis* has been studied in detail by Gambles & Dengler. Crystals, presumably of calcium oxalate, on the outer surfaces of the leaf-parenchyma cells are an unusual feature to be sought in other species of the genus.

Relatively few comparative chemical studies of *Tsuga* have been made (see Hegnauer, 1962, 1986). Von Rudloff (1975a, b), comparing leaf-terpene profiles of each of the North American species except *T. caroliniana,* found *T. Mertensiana* to be more or less intermediate between *T. heterophylla* and *T. canadensis* and not at all similar to *Picea sitchensis*. Leaf-phenolic pigments of seven species of *Tsuga* were compared by Taylor, yielding a cluster diagram agreeing rather poorly with morphological data. Immunological comparisons of seed-protein extracts (Prager *et al.*; Price *et al.*) indicate that *T. heterophylla* and *T. Mertensiana* are more similar to one another than to representatives of any other pinaceous genus.

Both of our species of *Tsuga* are utilized as ornamentals in the eastern United States, and numerous cultivars of *T. canadensis* have been selected (Den Ouden & Boom; Krüssmann). Bark of *Tsuga* is rich in tannins, and that of *T. canadensis* has been heavily exploited for use in the tanning industry. Wood of most *Tsuga* species is relatively soft and is used most often for crates and paper pulp, while that of *T. heterophylla* is often employed for construction purposes.

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END OF TSUGA