RELATIONSHIPS AND NOMENCLATURAL STATUS OF THE NOOTKA CYPRESS (CALLITROPSIS NOOTKATENSIS, CUPRESSACEAE)

Zsolt Debreczy

International Dendrological Research Institute P.O. Box 812910, Wellesley, MA 02482 dendro@t-online.hu, dzsgy-2@rcn.com

Kathy Musial

Huntington Botanical Gardens 1151 Oxford Rd., San Marino, CA 91108

Robert A. Price

Biological Consulting P.O. Box 448, Alameda, CA 94501

István Rácz

Hungarian Natural History Museum H-1087 Budapest, Könyves K. Krt.40

ABSTRACT

While working on the manuscript of Conifers Around the World (in press), the authors encountered classification nomenclature questions surrounding the Nootka Cypress, originally described as Cupressus nootkatensis D. Don, 1824. The combination Callitropsis nootkatensis was later implicitly suggested for this taxon by Oersted as the sole species in his new genus Callitropsis, but was not published in accordance with the current International Code of Botanical Nomenclature. The combination first appears in the literature in Florin (1944), with the name attributed to Oersted, and was validated by Little (2006), who treated the species as the type of a broader genus including the New World lineage of Cupressus. The taxon has long been treated as a species of Chamaecyparis, but this placement is supported by only a limited number of non-unique morphological characters and is not supported by more recent molecular comparisons. Based on recent DNA sequence comparisons, the distinctive Nootka Cypress can appropriately be treated in a monotypic Callitropsis, in a

ditypic genus with the Vietnamese Yellow Cypress (originally published as *Xanthocyparis vietnamensis*), or in a larger generic clade with the New World *Cupressus*. In the following paper we discuss its complex nomenclatural and taxonomic history and morphological distinctness. *Phytologia* 91(1):140-159 (April, 2009).

KEY WORDS: Callitropsis, Callitropsis nootkatensis, Cupressus, Xanthocyparis, Nootka Cypress, Vietnamese Yellow Cypress.

BACKGROUND

In 2005, while working on the manuscript of *Conifers Around the World* (Debreczy and Rácz, in press), the authors came across classification and nomenclature questions surrounding the North American taxon well-known by its common names Nootka Cypress, Alaska Cedar, Yellow Cedar, and Alaska Yellow Cedar (Little, 1980; Rehder, 1940). In this paper we refer to it as Nootka Cypress, following its original scientific name. It was first published as *Cupressus nootkatensis* D. Don in Lambert, Descr. Pinus 2: 18, 1824, and has subsequently been placed in three other genera: *Chamaecyparis* (1841), *Callitropsis* (1864), and most recently, *Xanthocyparis* (2002). Due to its combination of vegetative and reproductive characters sharing some features with both *Cupressus* and *Chamaecyparis*, its taxonomic position has long been debated, and its nomenclature has also been subject to confusion.

NOMENCLATURE OF NOOTKA CYPRESS

Danish botanist Anders Sandoe Örsted (≡Oersted; Fig. 1), in a detailed, richly illustrated 1864 publication, considered the cone structure of Nootka Cypress distinct enough from *Chamaecyparis* for the taxon to be placed in its own genus, which he named *Callitropsis*. Though Oersted gave a Latin diagnosis for the genus *Callitropsis*, and assigned only *Chamaecyparis nootkatensis* ("nutkaensis") to it, he did not directly write out the new combination *Callitropsis nootkatensis* in accordance with the International Code of Botanical Nomenclature (ICBN) rules for pre-1953 publication of botanical names (McNeill et

al., 2006). Therefore the combination was not validly published and has been dealt with in a variety of ways by subsequent authors.

The genus name *Callitropsis* Oersted and the combination *Callitropsis nootkatensis* were noted by (Carl) Rudolf Florin (1944) when he published the genus name *Neocallitropsis* as an avowed substitute for the later homonym *Callitropsis* Compton (Compton, 1922, p. 432). Though the name *Callitropsis nootkatensis* was attributed to Oersted, it was apparently first written out by Florin (1944), though not as a "comb. nov." in accordance with the ICBN. Little (2006) cited Florin as the author of the combination (see below), apparently validating the name (Gandhi, pers. comm.). The name *Callitropsis nootkatensis* Oersted was also cited by Erdtman and Norin (1966) in a footnote in relation to its chemical distinctness from *Chamaecyparis*, but not in a nomenclatural context.

The name *Callitropsis nootkatensis* then faded into obscurity, and the species was widely treated as *Chamaecyparis nootkatensis* (D. Don) Spach until evidence was obtained from tropolone and biflavonoid chemistry (Erdtman and Norin, 1966; Gadek and Quinn, 1985) and from phylogenetic analyses of morphology and DNA sequence data (Gadek et al., 2000; Farjon et al., 2002; Little et al., 2004; Xiang and Li, 2005; Little, 2006) that the species was misplaced in *Chamaecyparis*. Even though Florin's substitution of *Neocallitropsis* for *Callitropsis* Compton was widely accepted, the basis of that change, Oersted's name *Callitropsis*, was infrequently used in the literature until Little et al. (2004).

When a new cupressoid conifer was discovered in karst areas of northern Vietnam in 1999, it was soon described as the new genus *Xanthocyparis* Farjon & H. T. Nguyễn and species *Xanthocyparis* vietnamensis Farjon & H. T. Nguyễn (Farjon et al., 2002). These authors found *X. vietnamensis* (Vietnamese Yellow Cypress) to be so similar in cone morphology to Nootka Cypress that they included the latter in the new genus and renamed it *Xanthocyparis nootkatensis* (D. Don) Farjon & Harder. However, Little et al. (2004) pointed out that if treating the two species as members of the same genus, the name *Xanthocyparis* was invalid since *Callitropsis* Oersted had priority.

In February 2006 a proposal to conserve the name Xanthocyparis against Callitropsis Oersted was published (Mill and Farjon, 2006). Mill and Farjon, while also pointing out that Oersted did not make the new combination in the current manner, acknowledged that Callitropsis Oersted was validly published and that it should have been adopted for the new Vietnamese conifer and Nootka Cypress, making their publication of the name Xanthocyparis illegitimate according to ICBN Art. 52.1 (McNeill et al., 2006). Thus the present authors believe that the generic name Callitropsis Oersted should be given continued priority over Xanthocyparis when the two species are placed in the same genus, that Callitropsis Oersted is the correct generic name for the Nootka Cypress when the genus is treated as monotypic, and a monotypic Xanthocyparis is valid as its type is X. vietnamensis, not Nootka Cypress. Although in 2007 the Nomenclature Committee for Vascular Plants of the International Association for Plant Taxonomy (IAPT) voted to recommend conservation of Xanthocyparis over Callitropsis when the two species are placed in the same genus (Brummitt, 2007), the present authors believe that use of the much earlier generic name Callitropsis will cause no undue problems and that the customary rule of priority should be applied. Thus, this issue should be revisited before being voted on by the broader membership of the IAPT at the Eighteenth International Botanical Congress in 2011.

In October 2006, in a paper emphasizing phylogenetic analyses of nuclear and chloroplast DNA as well as morphological data, Little (2006) retained the generic name Callitropsis, but applied it to a broader lineage including C. nootkatensis, Xanthocyparis vietnamensis, and the New World lineage of Cupressus, a taxonomic judgment that we discuss under "Generic Classification" below. In 2004 Little et al. cited the combination as "C[allitropsis]. nootkatensis (D. Don) Oerst. Apparently recognizing the problems with the publication of the combination, Little subsequently (2006) attributed Callitropsis nootkatensis to Florin. At the top of his Taxonomic Treatment, Little appears to cite the type species of Callitropsis Oersted as "Callitropsis nootkatensis" (D. Don in Lambert) Florin, Regnum Veg. 100: 266. 1979." Regnum Vegetabile 100 is the Index Nominum Genericorum (Plantarum), in which the type of the genus name is listed as Cupressus nootkatensis D. Don. The name Callitropsis nootkatensis does not

appear there (Farr et al, 1979). Later in his list of combinations recognized in the expanded genus *Callitropsis*, Little more appropriately cites the species as "*Callitropsis nootkatensis* (D. Don in Lambert) Florin, Palaeontographica, Abt. B, Paläophytol. 85:590. 1944". Florin (1944), as previously noted, did write out the combination *Callitropsis nootkatensis* as a name from Oersted, but did not formally propose it as a new combination, instead later referring to the taxon as *Chamaecyparis nootkatensis* (p. 606, l.c.).

One can understandably regard Callitropsis nootkatensis (D. Don) Oersted or Callitropsis nootkatensis (D. Don) Florin as implicit combinations that were validly published under pre-1953 rules of the ICBN (vide Articles 33.2 and 33.3, McNeill, 2006). However, the combination did not appear in the International Plant Names Index (IPNI) as of 31 December 2008. While preparing this manuscript, a query from author Musial to a colleague to clarify a discrepancy in the D. Don citation eventually led to Dr. Kanchi Gandhi of the Gray Herbarium, Harvard University (also an editor for IPNI). An unexpected outcome of the correspondence on 16 January 2009 was that on 17 January 2009 "Callitropsis nootkatensis Oerst. nom. inval." and "Callitropsis nootkatensis Oerst. ex Florin" were posted to IPNI. Further queries by Musial led Gandhi to maintain that the validity of the Florin (1944) publication was questionable and that Little (2006) might have inadvertently validated the name (Gandhi, pers. comm.). The complexity of the issue led Gandhi to consult with other IPNI editors and experts (see acknowledgements), and as of 26 January 2009, Callitropsis nootkatensis Oerst, ex Florin was also declared nom. inval. and the name validated as Callitropsis nootkatensis (D. Don) Florin ex D. P. Little, Syst. Bot. 31(3): 474, 2006; basionym Cupressus nootkatensis D. Don in Lambert, Descr. Pinus 2: 18, 1824 (IPNI, 2009). Little had formally recognized the taxon and cited its basionym in accordance with ICBN Art. 33.4, 34.1, and 46.4 (McNeill, 2006). Gandhi (pers. comm.) mentioned two alternative citations: Callitropsis nootkatensis (D. Don) Oersted ex D. P. Little or Callitropsis nootkatensis (D. Don) D. P. Little. Present authors preference is for Oersted to be credited, and on 27 January 2009 Gandhi agreed and amended the IPNI record to Callitropsis nootkatensis (D. Don) Oersted ex D. P. Little (IPNI, 2009).

GENERIC CLASSIFICATION OF THE NOOTKA CYPRESS

Generic delimitation in the Cupressaceae sensu stricto has been more subjective than in most families of conifers due to the limited number of reproductive and vegetative characters distinguishing the approximately twenty currently recognized genera (Farjon, 2005). DNA sequence comparisons have provided independent appraisals of the relationships among these genera, and support a natural grouping including the cypresses (Cupressus sensu lato), junipers, Nootka Cypress, and Vietnamese Yellow Cypress (Gadek et al., 2000; Little et al., 2004; Xiang and Li, 2005; Little, 2006). Within this lineage, ITS sequence comparisons suggest that Nootka Cypress is the closest relative of Vietnamese Yellow Cypress (Little et al., 2004; Xiang and Li, 2005). This is consistent with the similarities in seed cone and pollen cone morphology noted by Farjon et al. (2002), but the support for a ditypic lineage comprising these two species is not strong in the other phylogenetic analyses presented by Little (2006). Thus using a total-evidence approach one can either recognize both as monotypic genera, likely with a long separate evolutionary history but with limited morphological differentiation, or treat them together as a ditypic genus.

There is strong support from several lines of DNA sequence data for the inclusion of these two species in a broader phylogenetic group also including an additional well-supported lineage, the New World species of Cupressus (Little et al., 2004; Xiang and Li, 2005; Little, 2006). This has been a surprise to morphological systematists, since the New World Cupressus species are characterized by large, many-seeded, serotinous (with few exceptions) seed-cones that are retained for long periods on the shoots, and thus appear more similar to the Old World species of Cupressus than to the Nootka Cypress and Vietnamese Yellow Cypress. The molecular groupings are consistent, however, with the fact that the Nootka Cypress is crossable with several species of New World Cupressus (Jackson and Dallimore, 1926; Mitchell, 1970). The widely grown Leyland Cypress (Chamaecyparis nootkatensis × Cupressus macrocarpa) is apparently at least sometimes fertile (Jackson and Dallimore, 1926), which is highly unusual for conifers if these groups are regarded as separate genera, and also suggests that they are closely related. Thus, Little (2006) has treated the Nootka Cypress, Vietnamese Yellow Cypress, and New World

Cupressus in a single genus as species of Callitropsis, a rather unorthodox approach given the differences in morphology between these taxa, but fully consistent with the molecular phylogenetic groupings of the taxa without requiring a new generic name for the New World cypresses.

From a macro-morphological aspect Nootka Cypress stands out from both Cupressus and Chamaecyparis and it has distinct differences from Xanthocyparis (see "Morphological Distinctness" below). Nootka Cypress can be considered as a "chamaecyparoid" cypress that, like Chamaecyparis, currently occurs in cold-temperate climates; in the case of Nootka Cypress, specifically in cool-wet boreal forests reaching as far north as 60°N. In submediterranean climates (home to regionally adjacent "true cypresses") it is restricted to cool north slopes and high elevations where it even occurs as a groundcover shrub (Griffin & Critchfield, 1976). Occurring from northwestern California to Alaska, Nootka Cypress is one of the most northern-ranging members of the Cupressaceae. The traditionally placed in Cupressus (Old World as well as New World lineages) often occur in zonal to extrazonal mediterranean or submediterranean climates well reflected in their mostly small to medium size and upright raceme-type branchlet system. The subtropical or summer-rain tropical taxa of the genus that are adapted to humid climates and face strong competition from broad-leaved angiosperm trees are large trees with often pendulous fern-like sprays or filiferous foliage, resulting in a relatively large assimilation surface and a rain (or snow) shedding foliage system (e.g. Cupressus cashmeriana, C. funebris, C. lusitanica).

MORPHOLOGICAL DISTINCTNESS OF NOOTKA CYPRESS VERSUS CHAMAECYPARIS, CUPRESSUS, AND XANTHOCYPARIS

Compared with Chamaecyparis (Fig. 2). Nootka Cypress is similar to species of Chamaecyparis in having flattened branchlets, conduplicate lateral scale-leaves, and small globose cones with few basally developing seeds (2–4 per cone-scale). Nootka Cypress differs significantly from all Chamaecyparis species in its wood and leaf chemistry (Erdtman and Norin, 1966; Gadek and Quinn, 1985) and is

placed outside of Chamaecyparis in a separate lineage with the chemically more similar Cupressus and Juniperus in DNA sequence comparisons (Xiang and Li, 2005; Little, 2006). Morphologically, Nootka Cypress differs from Chamaecyparis in its uniform amphistomatic adult scale-leaves without obvious white stomatal patches on the down-facing sides of the branchlets, the whorl-like arrangement of its 2(-3) pairs of cone-scales, without rudimentary sterile terminal scale pairs but with a free cone-axis tip (columella), and cones maturing in (1-)2 years. Chamaecyparis has strongly dimorphic facial and lateral scale-leaves, stomata arranged in (pruinose) patches on the down-facing side of the branchlets, cones with clearly decussately developing (5)6-12 scales (3-6 pairs), with the 2-4 terminal scales sterile and connate to form a column (Jagel and Stützel, 2001). In its overall morphology, Nootka Cypress appears to be more of "chamaecyparoid" (mesomorphic) Cupressus-relative than cupressoid Chamaecyparis. The cones of Callitropsis nootkatensis (a, fig. 2, top) have a conspicuous resin-filled conical extension (columella) beyond the base of the terminal cone-scales, a feature otherwise only typical of the Australasian genus Callitris and relatives from Cupressaceae subfamily Callitroideae (inset: h, fig. 2, Callitris rhomboide, i: vasculature of Callitris preissii). In X. vietnamensis (b, fig. 2, top) the columella is rudimentary (only a slightly raised area that can barely be considered column-like). The other genera have a longer cone-axis (relative to their cone sizes) associated with a usually larger number of cone-scales with terminal cone-scales fertile (Cupressus), or a few pairs form a sterile apical column.

Compared with *Cupressus* (Fig. 2). Nootka Cypress is similar to the New World *Cupressus* species in having more or less globose seed-cones often maturing in 2 years and adult foliage that is uniform with amphistomatic scale-leaves. It differs in having relatively small seed-cones (ca. 1 cm vs. 1–4 cm) that open in 1–2 years rather than often being retained for long periods on the tree and opening in response to fire. The cone-scales in Nootka Cypress are basifixed and not heavily thickened, while they are medifixed (peltate) and often much thickened and woody in *Cupressus*. Seeds are relatively few per cone-scale (2–4), flattened, and broadly winged, versus many per cone-scale (5–20), typically lenticular or faceted, and narrowly winged in *Cupressus*. Pollen cones have only 2(–3) large pollen sacs per

sporophyll, vs. 3–6 (up to 10 in *C. macrocarpa*) smaller pollen sacs in *Cupressus*. DNA sequence studies (Xiang and Li, 2005; Little, 2006) strongly indicate that the Nootka Cypress is a close relative of the New World cypress lineage but there is no evidence that it or the related Vietnamese Yellow Cypress is derived from within the New World cypress lineage. Instead they are positioned as the closest outside relatives, as suggested by the morphological differences.

Compared with Xanthocyparis vietnamensis (Figs. 3-4). The Nootka Cypress is most similar to the Vietnamese Yellow Cypress in having small more or less globose seed-cones (ca. 1 cm) with 2(-3) pairs of cone-scales on a short axis (thus appearing in whorls) with relatively few seeds per cone-scale (generally 2-4). The seeds of both are flattened and have two thin lateral wings. The pollen cones have 2(-3) relatively large pollen sacs per sporophyll. None of these shared characters are unique in the Cupressaceae and thus they provide only limited support for a distinct phylogenetic lineage consisting of these two species (Little, 2006). The two species differ in several morphological characters with uncertain phylogenetic importance such as scale-leaf, cone, and seed properties but differ most prominently in that leaves of both the needle-like juvenile form and scale-like adult form are commonly found on adult trees of the Vietnamese Yellow Cypress, and this is not the case in the Nootka Cypress or New World cypresses. In Nootka Cypress the columella terminating the cone-axis is usually evident, while it is very reduced or rudimentary in Vietnamese Yellow Cypress (Figs. 3-4). The seeds are smooth in Nootka Cypress but are conspicuously "warty" from tiny resin-blisters in Vietnamese Yellow Cypress

DNA studies of the ITS region tend to support a close sister-group relationship between these two species (Little et al., 2004; Xiang and Li, 2005), but other DNA sequence comparisons place them near one another in an unresolved trichotomy with the New World cypress lineage. The lineage including *Callitropsis nootkatensis* has an extensive fossil record in western North America dating back to ca. 50 MYA in the Eocene Epoch (Edwards, 1983, 1984). The chemistry of the Vietnamese Yellow Cypress is apparently not yet studied, but based on our current knowledge this would be unlikely to resolve generic relationships in the group.

At this time we choose to maintain *Callitropsis nootkatensis* and *Xanthocyparis vietnamensis* as members of closely related monotypic genera, which given their substantial geographic separation have probably had long evolutionary histories. Further study may provide new morphological or molecular characters that are uniquely shared by these two species or these two plus the New World cypresses, which would more strongly support a broader genus *Callitropsis*.

SUMMARY

The tortuous nomenclatural history of *Callitropsis nootkatensis* has apparently been resolved and the combination *Callitropsis nootkatensis* is now considered validly published and should be attributed to (D. Don) Oersted ex D. P. Little. *Xanthocyparis* is a valid name without need of conservation as long as the genus is kept monotypic with *X. vietnamensis* as its sole species. The morphological similarities between these two species, primarily in seed- and pollen-cone structure, are not unique within the family and thus may constitute only equivocal evidence in support of a separate generic lineage. Thus from a classification standpoint, the Nootka Cypress and Vietnamese Yellow Cypress are probably best considered members of closely related monotypic genera (*Callitropsis nootkatensis* and *Xanthocyparis vietnamensis* respectively) until stronger support of their phylogenetic relationship is available.

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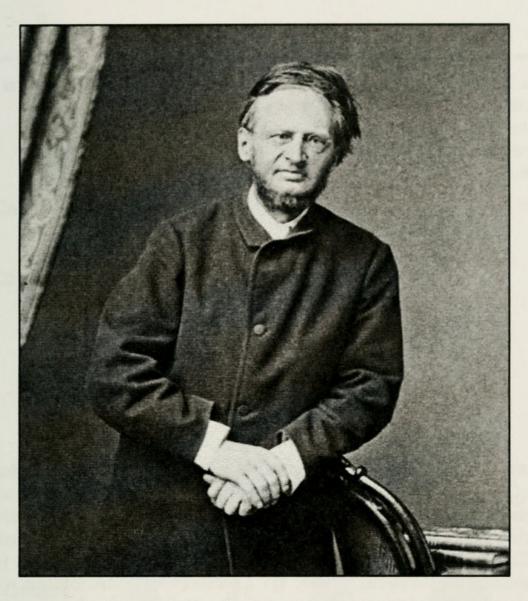


Figure 1: Anders Sandoe Örsted (1816–1872), Danish botanist, mycologist, zoologist, and marine biologist. In his long-overlooked study of the differences in cone morphology of *Chamaecyparis nootkatensis* and other cypresses he describes a new genus for Nootka Cypress, *Callitropsis*. Photograph by Johannes Peterson, Courtesy of the Botanical Library, University of Copenhagen, Denmark.

Figs. 2–4 Comparison of *Callitropsis*, *Xanthocyparis*, *Chamaecyparis* and the New and Old World Cypresses. abbreviations: *ad*=adaxial; *ab*=abaxial; *sd*=seed; *col*=columella; *trp*=terminal resin pit; *axrp*=axillary resin pit; *stcs*=sterile terminal cone-scale.

Figure 2. Longitudinal sections of cones and dissected cone vasculature in *Callitris*, *Callitropsis*, *Xanthocyparis*, *Chamaecyparis*, and representative New World (NW) and Old World (OW) *Cupressus* species. (a) *Callitropsis nootkatensis*, (b) *Xanthocyparis vietnamensis*, (c) *Cupressus macnabiana* (NW), (d) *Cupressus macrocarpa* (NW), (e) *Cupressus sempervirens* (OW), (f) *Chamaecyparis lawsoniana*, (g) *Chamaecyparis obtusa* var. *formosana*, (h) *Callitris rhomboidea*, note that the columella is multi-parted for this species, (i) *Callitris preissii*.

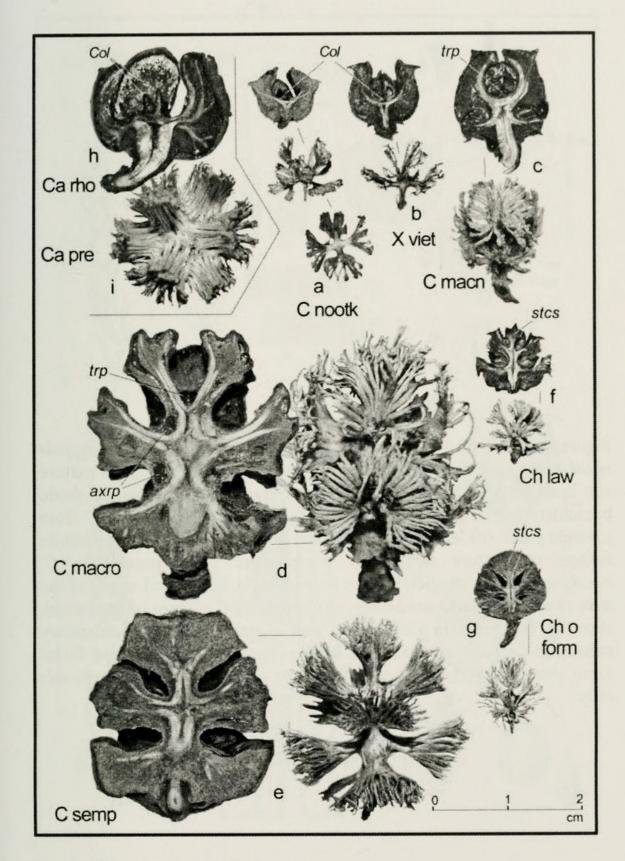


Figure 2. See caption on facing page.

Figure 3: Selected morphological structures of A: Callitropsis nootkatensis and B: Xanthocyparis vietnamensis. (a) Spray of mature sun branchlets with detail of individual branchlet; (b) detail of shade branchlet; (c) detail of leafy shoot, a leaf, and leaf surfaces from juvenile plant; (d) leafy shoot and detail of leaf from persistent juvenile foliage on mature tree of X. vietnamensis (not present in C. nootkatensis); (e) conelet; (f) two perpendicularly oriented views of the mature and unopened seed-cone; (g) longitudinal section of seed-cone, showing columella in Callitropsis and elevated area as rudimentary columella in Xanthocyparis and seeds; (h) seeds in lateral and facial view showing warty resin-glands on the surface of X. vietnamensis only.

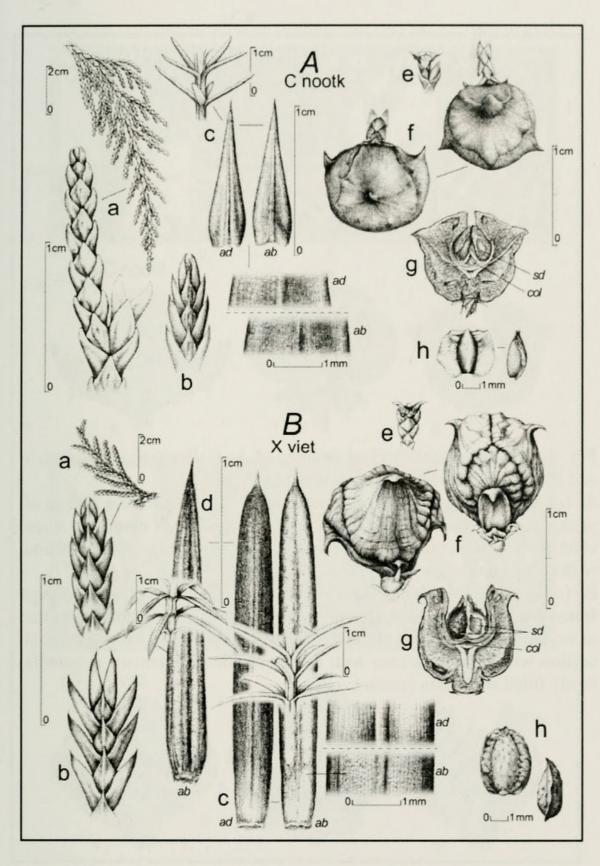


Figure 3. See caption on facing page.

Fig. 4: Selected morphological features of A: *Callitropsis nootkatensis* and B: *Xanthocyparis vietnamensis* in photographs.

A: (a) juvenile branchlets from young plant; (b) semijuvenile foliage of young plant; (c) shade and (d) sun branchlets of adult plant; the same cone from (e) lateral and (f) axial views and (g) longitudinal section with columella (arrow).

B: (a) juvenile branchlets from young plant; (b) juvenile-type foliage from an adult plant; (c) shade and (d) sun branchlets of adult plant; the same cone from (e) lateral and (f) axial views and (g) longitudinal section with columella area with barely visible rudimentary columella thinly filled with resin (arrow).

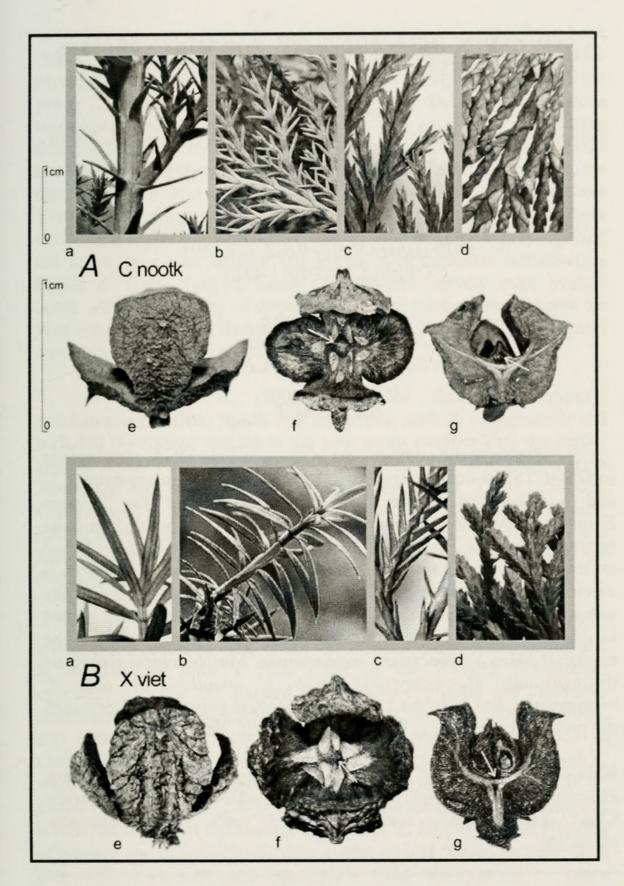


Figure 4. See caption on facing page.



Debreczy, Zsolt et al. 2009. "Relationships and nomenclatural status of the Nootka Cypress (Calliptropsis nootkatensis, Cupressaceae)." *Phytologia* 91(1), 140–159.

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