

Hybrids of *Thuja occidentalis* and *T. plicata* (Cupressaceae) – Is this a fact or misunderstanding?

Mieszańce *Thuja occidentalis* i *T. plicata* (Cupressaceae)
– fakt czy nieporozumienie?

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ABSTRACT: *Thuja occidentalis* and *T. plicata* belong to alien trees most frequently cultivated in Europe. Morphologically they differ significantly from each other and their natural ranges are geographically isolated, hence the taxonomic status of both taxa has never been questioned. In cultivation, however, these species are often very difficult to distinguish so speculations appeared that they can hybridize with each other. Reports about their hybrids growing in the Kórnik Arboretum, Poland, have been delivered several times; for the first time in 1933, then in 1957 and in 1981. In the latter publication, based on those hybrids, a new nothospecies *Thuja ×plicatoides* was described. That name, however, was not validly published, because its Latin diagnosis was limited only to a few words and no mention was made of how the hybrid differed from its parental species. The analysis of numerous arborvitae specimens growing in the Kórnik Arboretum, and in many other places in Poland, has shown that the earlier reports about the occurrence of *Thuja* hybrids in cultivation were fully justified. The results of this study were documented by numerous photographs showing the main diagnostic features of *T. occidentalis*, *T. plicata* and their hybrids. Special attention was paid to the characteristics of cones, which are rarely used in the *Thuja* taxonomy. The shape of cone scales, the length of the scale mucro and the structure of small ‘lips’ on the scale apices turned out to be significant cone features; the latter was used for the first time when distinguishing between both *Thuja* species. The cone and leaf features made it possible to recognize not only ‘pure’ species, but also their hybrids. The name *Thuja ×plicatoides* Seneta, for formal reasons has been rejected, so for the hybrids a new name *Thuja ×senetiana* has been proposed, which commemorates Włodzimierz Seneta, an outstanding Polish dendrologist.

Key words: Kórnik Arboretum, *Thuja occidentalis*, *T. plicata*, hybrids, *T. ×senetiana*

Introduction

The genus *Thuja* includes five geographically isolated species; two of them, western arborvitae (*T. occidentalis* L.) and giant arborvitae (*T. plicata* Donn ex D.Don), have quite an extensive geographical range in North America, whereas the remaining ones, *T. koraiensis* Nakai, *T. standishii* (Gordon) Carrière and *T. sutchuenensis* Franch., occur in a few, probably relict, localities in East Asia (fig. 1). The genetic separateness of *Thuja* species has been fully confirmed by molecular research (Li & Xiang, 2005; Peng & Wang, 2008).

Asian arborvitae thrive in Europe almost only in the richest dendrological collections, whereas American taxa belong to the most frequently grown foreign species of trees and quite often dominate among the conifers in parks, cemeteries and in home gardens. Western arborvitae was brought to Europe already about 1566 (Chambers, 1993), and giant arborvitae much later, i.e. not until the 19th century. According to Rehder (1927), it was introduced in 1853; however, in Wodzicki's dendrological collection in Niedzwiedz (S Poland) that species had already grown 20 years earlier (Wodzicki, 1833).

Thuja occidentalis and *T. plicata* are geographically isolated and do not hybridize in nature so in their native range they can be easily determined even without careful analysis of their distinctive features. However, while identifying the

cultivated plants, especially those of unknown origin, it becomes indispensable to compare the features recognized for both taxa as diagnostic. In most dendrology textbooks, and also in floras, similar sets of features differentiating those species are mentioned, which mainly refer to their leaves:

- *Thuja occidentalis*: its scale leaves on the adaxial side of branchlets are light green and matt, those on the abaxial side brighter, yellowish or light green, and without distinct waxy markings; the lateral leaf apices short, blunt and ± curved towards the inside, at most slightly overlapping the leaves developed above; the resin glands in the leaves of its main (primary growth) shoots bubble-like bulging, well visible to the naked eye, in the remaining ones translucent; cones 8–12 mm in length, with three pairs of scales, those with a short, 0.2 mm long, mucro at their apex.
- *Thuja plicata*: its scale leaves on the adaxial side of shoots dark green and ± shiny, and on the abaxial side develop whitish markings of waxy bloom; the lateral leaves narrowly acute, their apices erect or delicately curved towards the shoot axis, always slightly overlapping the leaves developed above; the resin glands in the leaves of the main shoots are poorly noticeable, not or at most weakly translucent. Cones 10–16(–18) mm in length, with 4–5 pairs of scales and with a longer, approximately 1 mm long, mucro at their apex.

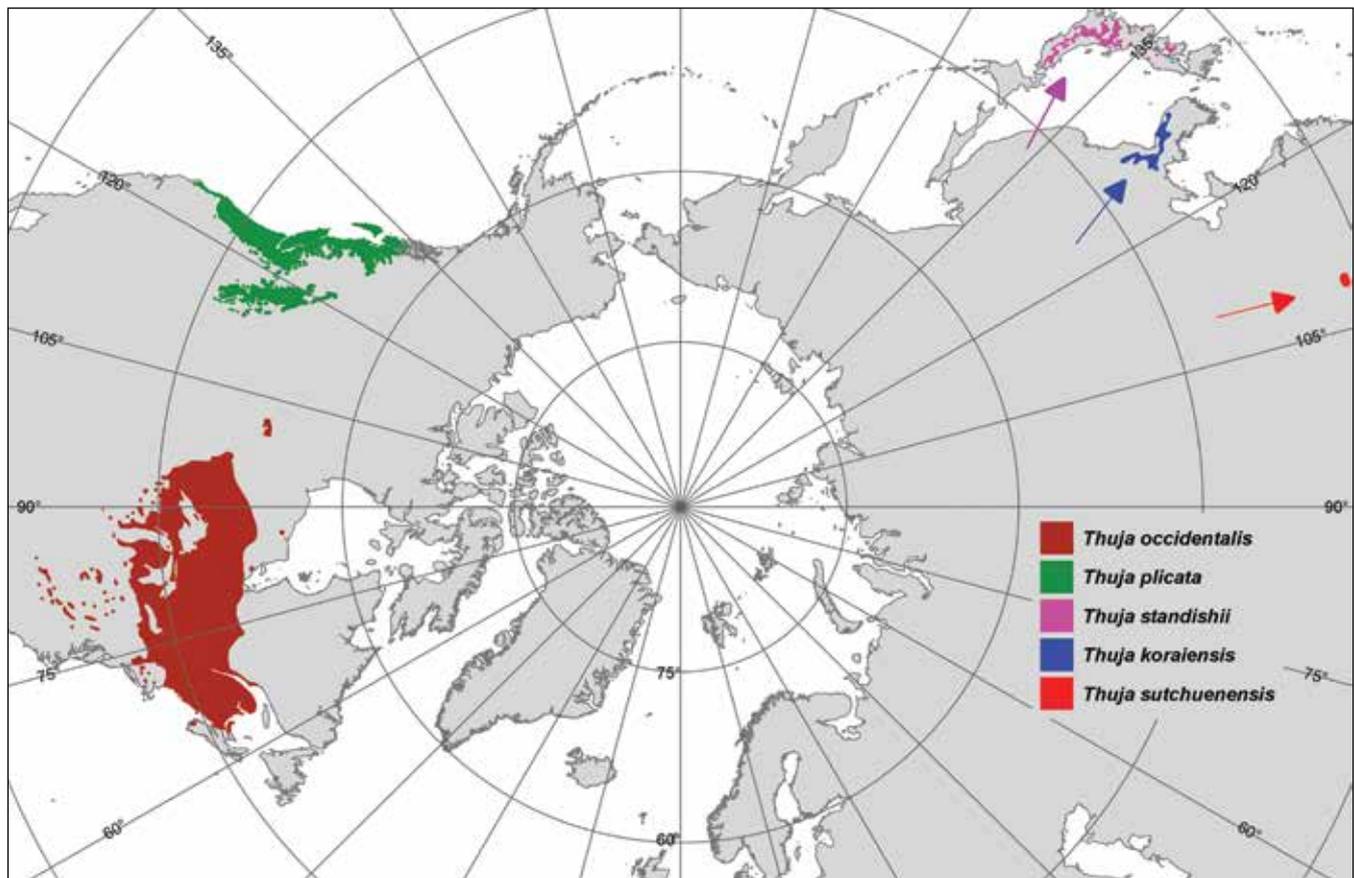


Fig. 1. Geographical distribution of *Thuja* species. The map compilation was based on Little (1971), Qin et al. (2017) and Worth (2019)

Ryc. 1. Rozmieszczenie geograficzne gatunków rodzaju *Thuja*. Mapa opracowana na podstawie Little'a (1971), Qina et al. (2017) i Wortha (2019)

As regards individuals within their native range or with documented origin, the above-mentioned sets of features are rather sufficient to easily distinguish *T. occidentalis* from *T. plicata*. However, identification of arborvitae in cultivation is often ambiguous or not possible since at least some of the above-mentioned species' distinctive features do not correlate with one another.

Taking into account that both arborvitae taxa have been grown in parks and gardens for over 150 years, often one next to the other, and that they have the same number of chromosomes ($2n = 22$) (Chambers, 1993), bloom profusely and develop viable seeds, one should simply expect that their hybrids should appear in such conditions. Hybridization of species in cultivation, which are geographically isolated in nature, is not anything exceptional, also in gymnosperms. Hybrids of *Taxus baccata* L. and *T. cuspidata* Siebold & Zucc. (*T. ×media* Rehder), *Pinus wallichiana* A.B.Jacks. and *P. strobus* L. (*P. ×schwerinii* Fitschen), and most of all *Thuja plicata* and *T. standishii*, a hybrid described as *T. occidentalis* L. var. *giganteoides* Poulsen, can serve as examples. They show that the reproductive isolation between those species, apart from the geographical barrier, does not exist or at least is not tight enough.

The first information about *T. occidentalis* and *T. plicata* hybrids growing in the Kórnik Gardens was given by Antoni Wróblewski, the first director of that institution. In the collection inventory, one of such specimens was described by him (under registry number 265) as *Thuja gigantea* × *occidentalis* Hort. Kórnik, with a note: 'nursery, a big tree'. Most likely, a photograph of that specimen was placed by Wróblewski (1933) in a publication presenting coniferous trees and shrubs of the Kórnik Arboretum with the following caption: 'An arborvitae tree (*Thuja gigantea* Nutt. × *occidentalis* L.)' (fig. 2). It was a two- or three-stem tree, and judging by the child standing nearby, it reached the height of about 15 m. Therefore, one can assume that the specimen was bred by Jan Działyński, the Arboretum proprietor, long before taking care of the park collection by Wróblewski in 1926. The seeds, most probably harvested from that specimen, were offered three times under the name *Thuja plicata* × *occidentalis* Hort. in the Kórnik *Index Seminum* in the years 1934, 1936–1937 (Dolatowski, 1992). Unfortunately, that specimen has not survived until today.

Suszka (1956), in a detailed study on the Kórnik Park arborvitae, mentioned several times specimens of 'transition type' between *T. plicata* and *T. occidentalis*, and assumed that some specimens grown there under the names of '*T. occidentalis* var. *alba* Gord.', '*T. occidentalis* var. *aureo-spicata* Beissn.', '*T. occidentalis* var. *plicata* Mast.', and '*T. gigantea* var. *aureo-variegata* Hort.' could in fact also be such hybrids. However, he definitely did not decide to explicitly distinguish them as hybrids. Almost a quarter of a century later, the problem of the arborvitae hybrids was mentioned again, this time by Seneta (1981) in a textbook entitled: *Coniferous trees and shrubs*. According to him, *T. occidentalis* and *T. plicata* hybrids undoubtedly existed and were grown in such great numbers that it would be reasonable to describe a new nothospecies, which could encompass such plants. In his textbook, Seneta suggested the

name *Thuja ×plicatoides* for those hybrids. His remarks quite explicitly showed that the description of that taxon was made based on the plant grown in Kórnik and identified by him as *T. occidentalis* 'Aureospicata', but unfortunately he did not indicate an exact 'type specimen' of a newly described species. Moreover, Seneta erroneously included to a new hybrid species the 'Giganteoides' cultivar, which had been formerly associated with *T. occidentalis* (den Ouden & Boom, 1965), but later turned out to be a hybrid of *T. plicata* × *T. standishii* (Martin & Tripp, 1997).

Our preliminary investigation of the arborvitae in the Kórnik Arboretum confirmed opinions of Wróblewski (l.c.), Suszka (l.c.) and Seneta (l.c.) on the occurrence of the hybrids of *T. occidentalis* and *T. plicata* in cultivation. In the Polish dendrology literature, the name *Thuja ×plicatoides*, after its first mention in print, appeared again in the new edition of *Dendrologia* (Seneta & Dolatowski, 1997), but this time also a popular variety 'Smaragd', ranked till then among *T. occidentalis*, was assigned to that hybrid taxon. Since then, in most Polish nurseries, that cultivar has been on offer as *Thuja ×plicatoides* 'Smaragd'. The West European dendrology textbooks, even the latest ones, such as *Flora der Gehölze* (Roloff & Bärtels, 2008) and *Fitschen Gehölzflora*

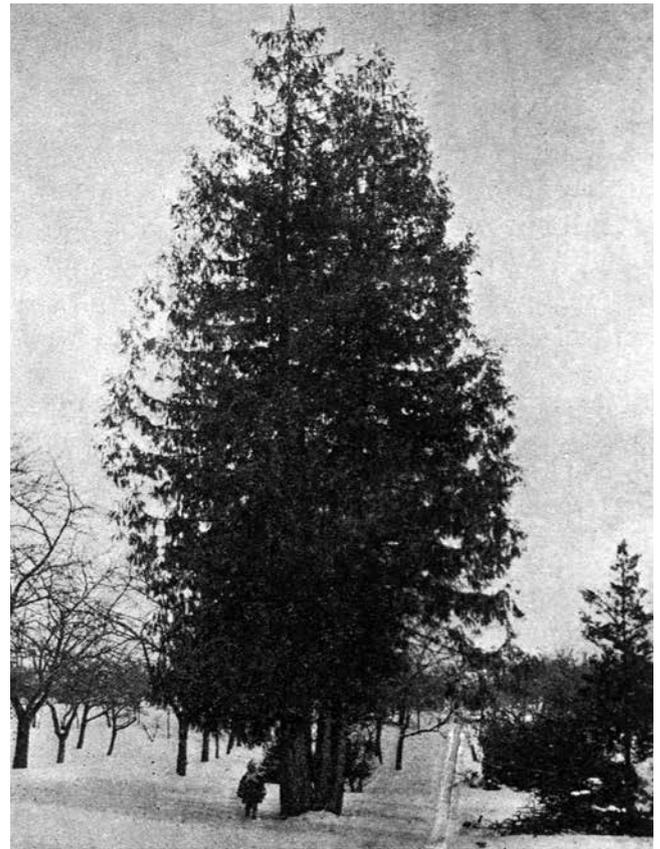


Fig. 2. A *Thuja* specimen bred in Kórnik and identified by Antoni Wróblewski as *Thuja gigantea* Nutt. × *occidentalis* L. The picture was published in 1933. The tree, which at that time was about 15 m high, is no longer alive

Ryc. 2. Okaz żywotnika wyhodowany w kolekcji kórnickiej, zidentyfikowany przez Antoniego Wróblewskiego jako *Thuja gigantea* Nutt. × *occidentalis* L. Zdjęcie opublikowane w 1933 roku. Drzewo to, mające wówczas wysokość około 15 m, nie dotrwało do naszych czasów

(Schmidt, 2017), did not refer to the existence of hybrids of both arborvitae at all. The name *Thuja ×plicatoides* was mentioned in the *Encyclopedia of Conifers* (Auders & Spicer, 2012), published by the Royal Horticulture Society, but with a note: 'Further information is needed'.

Aim, material and methods

Our study focused on verifying current information from the literature and our first conclusions concerning the existence of hybrids of *Thuja occidentalis* and *T. plicata*. The analyses included almost all specimens of both species encountered by us in several biggest dendrological collections in Poland, as well as those grown in parks, green areas, cemeteries and in private gardens. However, the collection of the Kórnik Arboretum, abounding in arborvitae, was the main source of trees for comparisons. On the whole, it was an extremely diverse collection of plants including specimens of different origin, obtained from the seed germination or sprout rooting and quite often originated spontaneously from self-seeding or by rooting the lowest, creeping branches. Primarily, it was necessary to identify the specimens which without reservations represented 'pure' parent species. Observations of the specimens of *T. plicata* bred from the seeds harvested in natural sites and cultivated in the Arboretum in Rogów, and on old, more than 120-year-old plantations in the forest districts of Łopuchówko (fig. 3) and Piaski in the region of Wielkopolska (Greater Poland), turned out to be especially useful.

The comparative material included also specimens of *Thuja occidentalis* and *T. plicata*, collected in their natural habitats and kept in the herbarium of the Institute of Dendrology of the Polish Academy of Sciences in Kórnik. Access to the biggest American herbaria with detailed photographs of arborvitae collected within their native ranges was of the utmost importance. In the field, on live plants, additional morphological features were assessed: habit of a tree, its trunk base and the bark of older specimens (rhytidome).

The documentation material, which was collected for further observations, encompassed shoots, the last year's open cones and this year's juvenile cones, fully developed but still closed. Such closed cones allowed us to assess their shape and determine to what degree the cone scales overlap each other. As far as it was possible, we also analysed cones in their early developmental stage. Already in the field, we assigned tentatively each of examined specimens to one of the parental species or their putative hybrid.

Results

A substantial majority of cultivated arborvitae has uncertain origin being generative or vegetative progeny of the earlier introduced trees, however, some of them did not differ at all from the pure parental species, i.e. the plants with documented native origin. They also fully corresponded to the specimens from American herbaria and also to the descriptions of both species presented in American floras and dendrology textbooks (Rehder, 1927; Elias, 1980; Chambers, 1993). On the other hand, there are many specimens for which unambiguous determination is impossible. Some of them show ± intermediate range or combination of features characteristic to both parental species, while the others are more similar to one of them, including such plants which practically seemed to be almost 'pure' species, but have a small admixture of characters pointing out to the introgression. We had an impression that the arborvitae under analysis created a morphological continuum whose border morphotypes corresponded to *T. occidentalis* or *T. plicata*. So numerous intermediate morphotypes, which occur only in cultivation, may indicate a long lasting hybridization of both species.

The comparative analyses of many plants of the *Thuja occidentalis* – *T. plicata* circle encountered in cultivation revealed that undoubtedly hybrids of both those taxa constituted a considerable part of them. As such, they are not recognizable mainly due to a poor, usually quite superficial knowledge of features of their parental species and in practice they are



Fig. 3. The *Thuja plicata* forest plantation in the Łopuchówko Forest District. Plants grown from the seeds harvested in natural localities of this species were planted there in the 1870s. One of the plantations was founded as part of Schwappach's provenance studies. The stems of trees have buttresses characteristic of this species (photo W. Danielewicz)

Ryc. 3. Plantacja leśna *Thuja plicata* w Nadleśnictwie Łopuchówko. Rośliny pochodzące z nasion zebranych na naturalnych stanowiskach tego gatunku posadzone tu w latach 70. XIX w. w ramach doświadczeń proweniencyjnych Schwappacha. Pnie drzew z charakterystycznymi dla tego gatunku przyporami (fot. W. Danielewicz)

mostly included into one of the both species. In the case of the taxa under analysis, the greatest diagnostic significance is attributed to the features of leaves. In literature, descriptions of cones are rather laconic and, generally, only differences in the number of scale pairs and in the size of the mucro on their tips are emphasized. In Seneta (1981), the following description refers to *T. occidentalis*: ‘develops cones 8–12 mm long with 4–5 pairs of scales’, and another to *T. plicata*: ‘cones similar to *T. occidentalis*, with slightly greater mucro at the scale apices’. Cones are described in a similar way by most authors with the exception of Sękowski (1980), who in the key for identification of arborvitae cultivated in Poland said about the cones of *T. occidentalis*: ‘cones with leathery scales, all of them (except for the two lower ones) of equal length (in some varieties – hybrids? – of almost equal length)’. And about the cones of *T. plicata* (and *T. standishii*) he mentioned: ‘cones with leathery scales always distinctly different in length and that is why the apices of internal scales of closed cones always protruding’ (all quotations were translated from Polish). To conclude, such rather insufficiently precise descriptions of cones help to a small degree to distinguish *Thuja* species and are totally of no use at identifying hybrids.

A thorough analysis of many specimens of western and giant arborvitae showed that contrary to popular opinion, their cones differed so considerably that it was possible to

correctly distinguish both species, and with some experience also their hybrids. Clear differences in the structure of cones in both species can be seen in many photographs presented on the Internet and taken in natural habitats of *Thuja occidentalis* and *T. plicata*, as well as in those accessible in virtual herbaria (fig. 4). One can generally come to similar conclusions looking at the photographs and drawings of cones in most dendrology textbooks (e.g. in: Browicz & Bugała, 1966; Gaussen, 1968; Mitchell, 1972; Seneta, 1981 and Farjon, 2005). Our observations clearly revealed that cones, as compared to leaves, are only slightly affected by the environment. Only their size seems to be more susceptible to changes; even on the same tree larger cones can develop on more prominently exposed and stronger branches. They retain, however, their characteristic appearance even in those cultivars which display vegetative features strongly altered due to diverse mutations.

Although the structure of cones is more complex than the structure of leaves, it has not been precisely described to date. Cones of all *Thuja* species possess the same general structure (figs. 4–7). They consist of 5–6 pairs of decussate, imbricate, concave scales. Their size and shape depend on their position on the cone axis. Above a pair of changeable, usually small basal scales, 2–3 pairs of the largest, ± broad fertile scales appear, and above them, 1–2 pairs of considerably

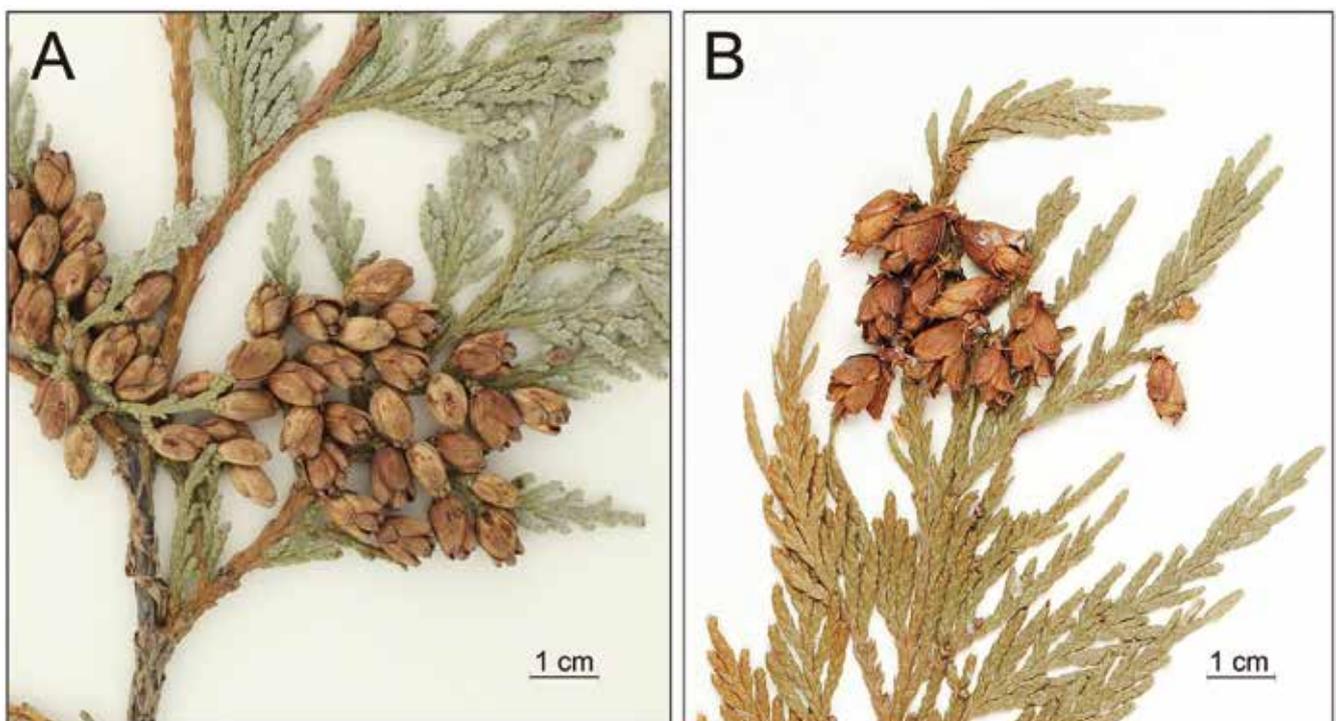


Fig. 4. The identification of arborvitae growing in the wild does not cause any problems, even based on photographs. Fragments of the *Thuja* herbarium specimens collected in natural habitats. (A) *T. occidentalis*. This image (v0204975 WIS) is property of the Wisconsin State Herbarium, University of Wisconsin. (B) *T. plicata*. This image (00017241 NYBG) is property of the C.V. Starr Virtual Herbarium of the New York Botanical Garden (<http://sweetgum.nybg.org/science/vh/>). The images were published with permission of their proprietors

Ryc. 4. Rozróżnianie dziko rosnących żywotników nawet na podstawie fotografii nie sprawia najmniejszych problemów. Fragmenty okazów zielnikowych żywotników zebranych na naturalnych stanowiskach. (A) *Thuja occidentalis* (v0204975 WIS). To zdjęcie jest własnością Wisconsin State Herbarium, University of Wisconsin. (B) *T. plicata* (00017241 NYBG). To zdjęcie jest własnością C.V. Starr Virtual Herbarium New York Botanical Garden.

Zdjęcia opublikowane za zgodą obu instytucji

narrower sterile apical scales. Each of the scales (except the apical ones) has two layers (figs. 6–8): external, which is thin, lignifying early with a pointed, short, brown or black mucro (identical to the top of the ovular scale in flower cones) and a thicker, growing longer and lignifying later, internal layer (adaxial) which in young closed cones tightly adheres to the scale situated above. On top of the scale (except the apical ones), those two layers are shallowly but quite distinctly divided creating a sort of lips. They are of \pm equal length or the inner one is clearly longer than the external one and makes something like a collar above it. The presence of

this collar or a lack of it in the largest fertile scales is very important for the identification of both species. The shape of the largest scales (usually the second scale pair from the bottom) turned out to be an important, hardly changeable diagnostic feature of arborvitae (fig. 8).

Closed *T. occidentalis* cones are \pm ellipsoidal to broadly ellipsoidal or barrel-like in shape (figs. 4A, 5A–B, 6C, 7F). The scales of the second pair from the bottom are oblong-elliptical to broadly elliptical, usually the broadest in the middle or slightly below (fig. 8A). The lips on the scale tips (except for the bottom ones) are \pm of the same length, hence

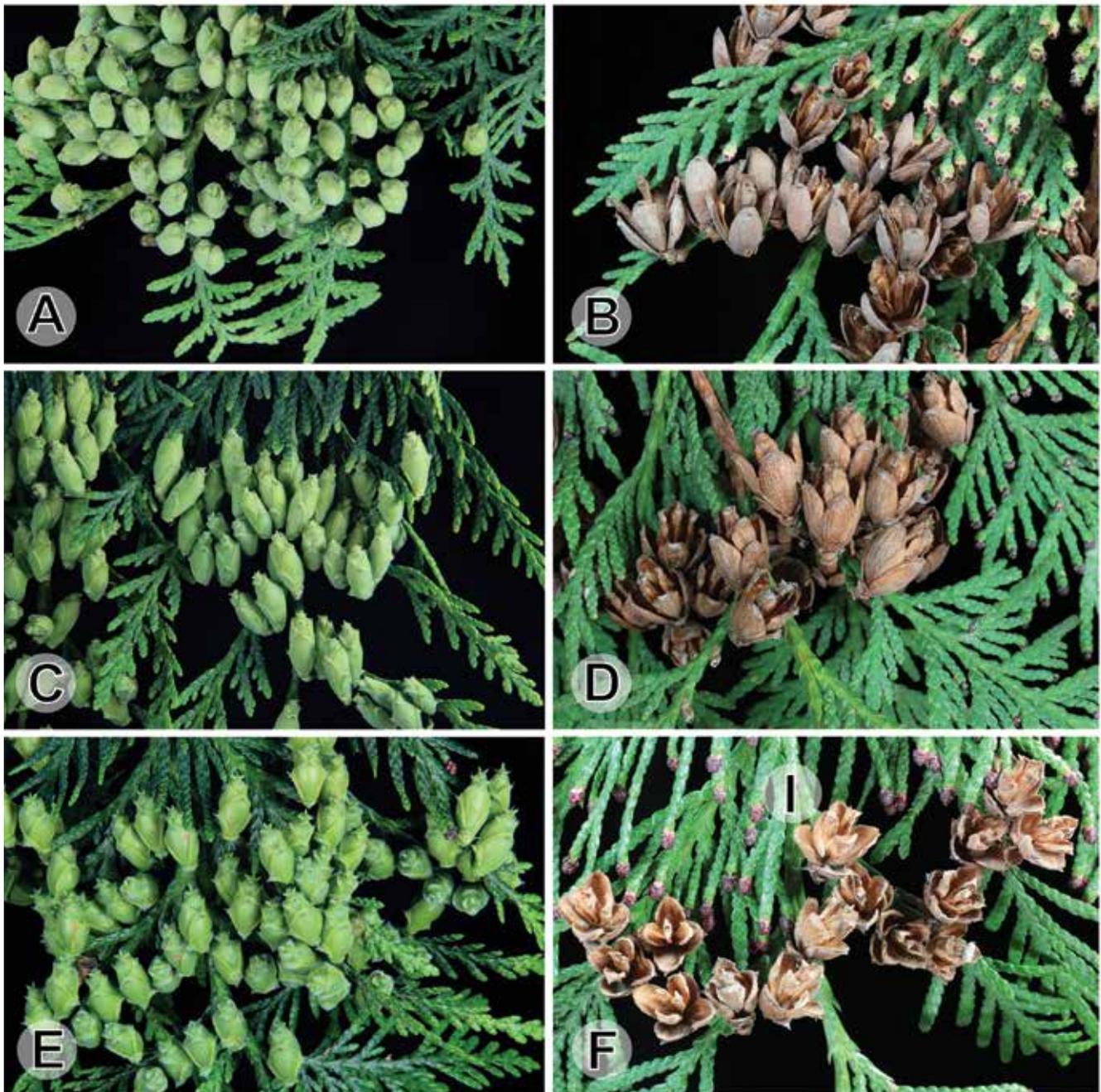


Fig. 5. *Thuja occidentalis* (A–B), *T. plicata* (E–F) and a hybrid of these species (C–D). Branchlets with juvenile, fully developed closed cones, June 2019 (left), and branchlets with open last year's cones, April 2019 (right) (photo W. Danielewicz)

Ryc. 5. *Thuja occidentalis* (A–B), *T. plicata* (E–F) i mieszańiec tych gatunków (C–D). Po lewej – pędy z młodymi, w pełni wykształconymi zamkniętymi szyszkami (czerwiec 2019); po prawej – pędy z otwartymi ubiegłorocznymi szyszkami (kwiecień 2019) (fot. W. Danielewicz)

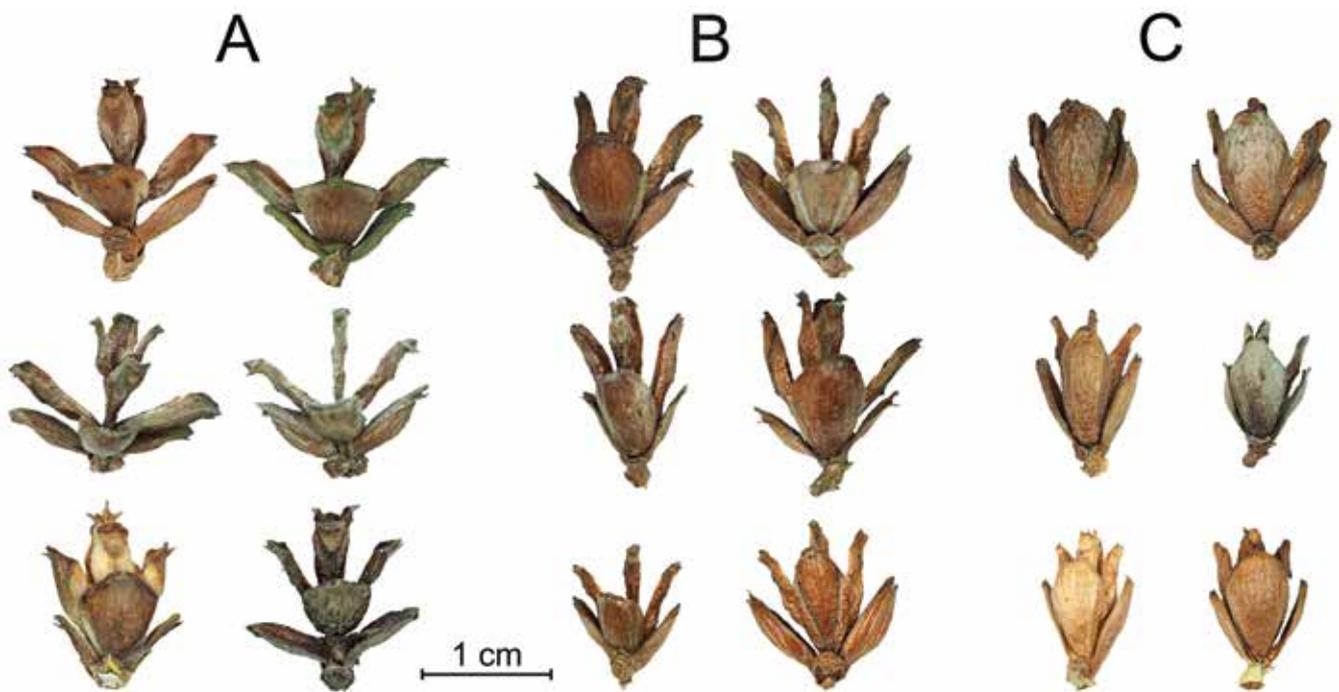


Fig. 6. Dry open cones of the arborvitae under examination. Contrary to the cones of *Thuja occidentalis* (C), the cones of *T. plicata* (A) are widely open, while those of hybrids (B) resemble parent species to varying degrees (photo P. Kosiński)

Ryc. 6. Suche, otwarte szyszki badanych żywotników. W przeciwieństwie do *Thuja occidentalis* (C) szyszki *T. plicata* (A) są szeroko rozchylone, natomiast szyszki mieszańców (B) przypominają w różnym stopniu gatunki rodzicielskie (fot. P. Kosiński)



Fig. 7. Fully developed, closed cones of: *Thuja plicata* (A), *T. occidentalis* × *plicata* (B–E) and *T. occidentalis* (F). At that stage of development, differences in the shape of cones of parental species and their intermediate character in hybrids are easily visible. Compared to *T. occidentalis*, the cones of *T. plicata* are distinctly narrowed in the upper part (photo P. Kosiński)

Ryc. 7. W pełni wykształcone, zamknięte szyszki *Thuja plicata* (A), *T. occidentalis* × *plicata* (B–E) and *T. occidentalis* (F). W tym stadium szczególnie dobrze widoczne są różnice w kształcie szyszek obu gatunków, a także ich pośredni charakter u mieszańców. W porównaniu z żywotnikiem zachodnim szyszki żywotnika olbrzymiego są w górnej części wyraźnie zwężone (fot. P. Kosiński)

there is no distinct collar formed by the internal layer of the scale; the outer lips with a triangular mucro, 0.1–0.2 mm long, are straight and directed upwards. The scales of dry cones are not broadly open, at most at an angle 15–20°. The cones of such a structure fully correlate with matt, yellowish-green leaves and a strongly bulging, bubble-like glands in the leaves of primary branches and with a shallowly and narrowly furrowed rhytidome of mature trees (fig. 9G–I).

Closed cones of *Thuja plicata* are usually distinctly narrowed over the upper edge of largest scales hence they

are ± jug-shaped (figs. 5E, 7A). Their fertile scales of the second pair from the bottom are (broadly) obovate, sometimes almost rhomboid, the broadest above the middle of their length (fig. 8C). The lips at scale apices are clearly of different length: the inner ones are considerably longer and make characteristic collars above the external lips, which, together with an apical broadly-triangular, piercing mucro, 0.8–1 mm long, are ± bent outwards (figs. 4B, 6A, 7A). The scales of dry cones are broadly open at an angle of approximately 45° (fig. 6A).



Fig. 8. The differences among the scale cones of *Thuja occidentalis* (A), *T. plicata* (C) and their hybrid (B). Usually, 2–3 middle pairs of scales are fertile. Clear differences between parental species are visible in the scale shape of the second pair from the bottom. In the former species, they are elliptical and the widest in the middle of their length, whereas in the latter one they are (broadly) obovate, the widest above the middle of their length. The scales of cones from hybrids are usually only slightly wider above the middle of their length (photo P. Kosiński)

Ryc. 8. Zróżnicowanie łusek w obrębie szyszek *Thuja occidentalis* (A), *T. plicata* (C) i u ich mieszańca (B). Płodne są zwykle 2–3 środkowe pary łusek. Wyraźne różnice między rodzicielskimi gatunkami widoczne są w kształcie łusek drugiej pary od dołu. U pierwszego gatunku są one eliptyczne, najszersze w połowie długości, u drugiego (szeroko) odwrotnie jajowate, najszersze powyżej połowy długości, natomiast w szyszkach mieszańca tych gatunków są one tylko nieznacznie szersze powyżej połowy długości (fot. P. Kosiński)

The cone structure of giant arborvitae also strongly correlates with the features of leaves, which are always dark green and clearly shiny on their surfaces. Their resin glands on the leaf surface are deeply sunken into the parenchyma tissue and their presence can only be recognized by a small,

lighter, narrowly-elliptic mark. Triangular white waxy markings on leaves of the abaxial side of branchlets are thought to be very characteristic for that species and their presence is frequently highlighted in descriptions and identification keys, but, in fact, they do not always occur in such a form:

they are often narrow, sometimes well visible only close to leaf margins, sometimes they are merely greyish, hardly ever they fail to develop at all. However, the surface of the leaves on adaxial side of branchlets (not covered with a white wax) is always dark green and shiny. The trunks of mature specimens with such cones and leaves are covered with deeply furrowed rhytidome that comes off with broad stripes (figs. 9A–C, 10).

A diagnostic value of some cone features was appreciated just as important as leaf characteristics only in a few latest studies (Cui et al., 2015; Sun et al., 2019). Our conclusions concerning the structure of the arborvitae cones are congruent with the opinion of Sun et al. (l.c.) that significant differences between the cones of *Thuja occidentalis* and *T. plicata* can be detected in the shape of the pair of the largest fertile scales, i.e. usually the second pair from the

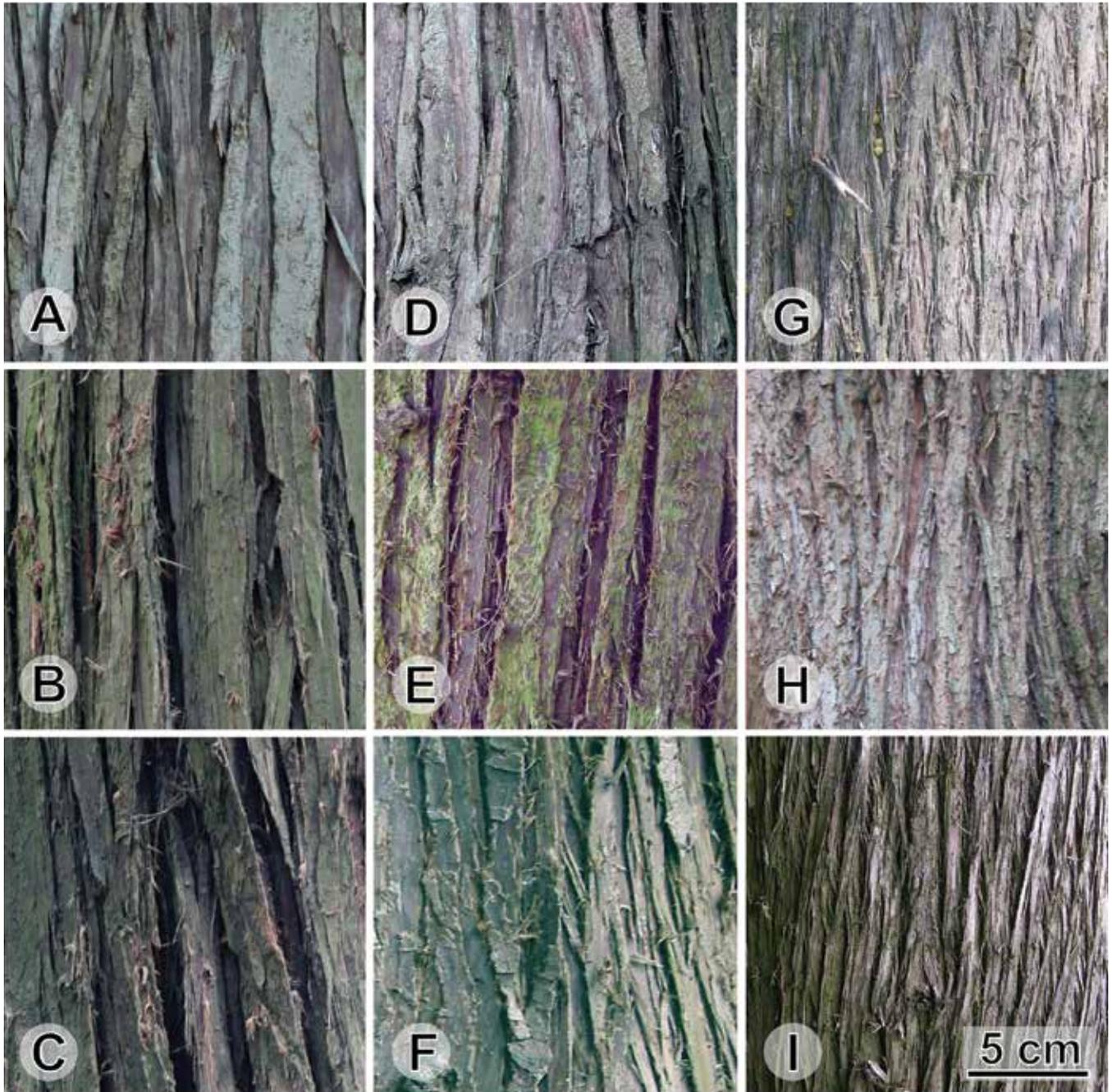


Fig. 9. The bark on the trunks of arborvitae under study. Clear differences in their bark structure are mainly visible in the depth of bark furrows and distances between them. Compared to *T. occidentalis* (G–I), the bark of which is shallowly furrowed and peels off with narrow strips, the bark of *T. plicata* (A–C) is deeply furrowed, and the furrows are more distant from each other, hence the bark peels off with much broader strips. The bark of hybrids (D–F) usually seems to be more similar to the bark of *T. plicata*; however, it is never so deeply furrowed (photos A–D W. Danielewicz; E–I J. Zieliński)

Ryc. 9. Kora na pniach omawianych żywotników. Wyraźne różnice w budowie ich kory zaznaczają się przede wszystkim w głębokości bruzd i odległości między nimi. W porównaniu z płytko bruzdowaną i łuszczącą się wąskimi pasmami korą *Thuja occidentalis* (G–I) kora na pniach *T. plicata* (A–C) kora jest głęboko bruzdowana, a same bruzdy względem siebie bardziej odległe, przez co łuszczy się ona znacznie szerszymi pasmami. Kora mieszańców (D–F) wydaje się na ogół bardziej podobna do kory tego drugiego gatunku, jednak nie jest nigdy tak głęboko bruzdowana (fot. A–D: W. Danielewicz; E–I: J. Zieliński)

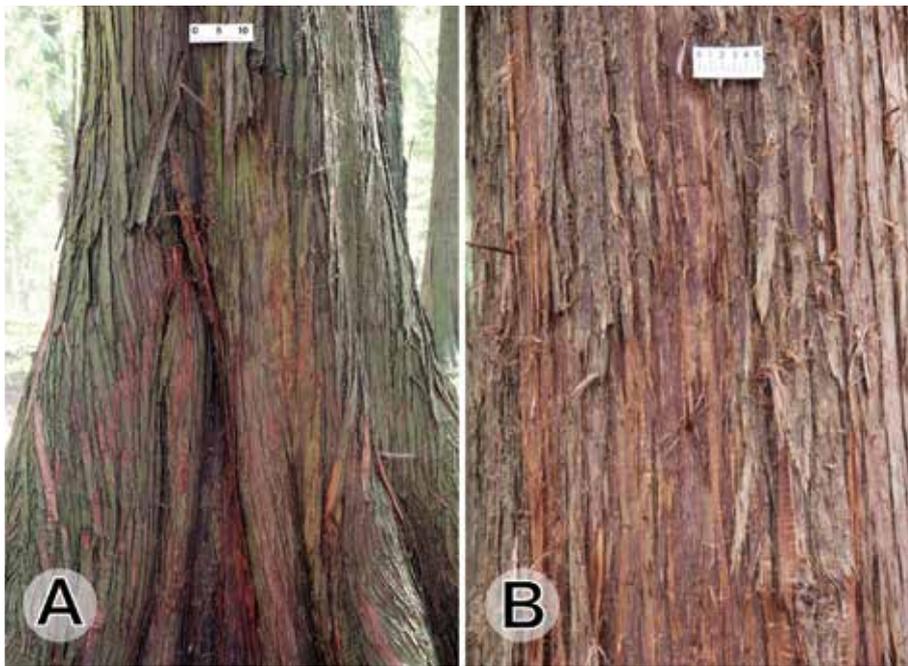


Fig. 10. The bark on the trunks of old *Thuja plicata* trees tends to be varied, from \pm regularly furrowed with smooth periderm remnants to a typical rhytidome that comes off the trunk in the form of long thick slats or/and peels off with soft reddish fibers. Just after dropping the bark slats, the inner red rhytidome layers become visible. Both images from the same plantation in Łopuchówko (photo W. Danielewicz)

Ryc. 10. Kora na pniach starych drzew *Thuja plicata* bywa różna, od \pm regularnie bruzdowanej z resztkami gładkiej perydermy po typową martwicę odpadającą od pnia długimi, grubymi listwami lub/i złączającą się miękkimi pasemkami rudawych włókien. Tuż po odpadnięciu grubych listew stają się widoczne czerwone wewnętrzne warstwy martwicy. Obydwa zdjęcia z tej samej plantacji w Łopuchówku (fot. W. Danielewicz)

bottom of a cone (fig. 7). However, the analysis of the scale shape should be conducted on at least several cones since basal scales may be sometimes exceptionally large and at the same time fertile, which can be the cause of errors, especially in the case of the alleged hybrids.

The comparisons of young conelets, at the beginning of the postfloral stage, revealed that they differed considerably enough to draw conclusions about taxonomic

classification of the specimens analysed. Especially, differences concerning orientation of a sharp mucro at the apex of scales (except for the basal ones) are visible (fig. 11). More distinct deviations from the described above combination of characteristics of foliage, cones and the bark in a specimen, sometimes even greatly similar to one of the species, indicate usually its hybrid origin (figs. 5–9).

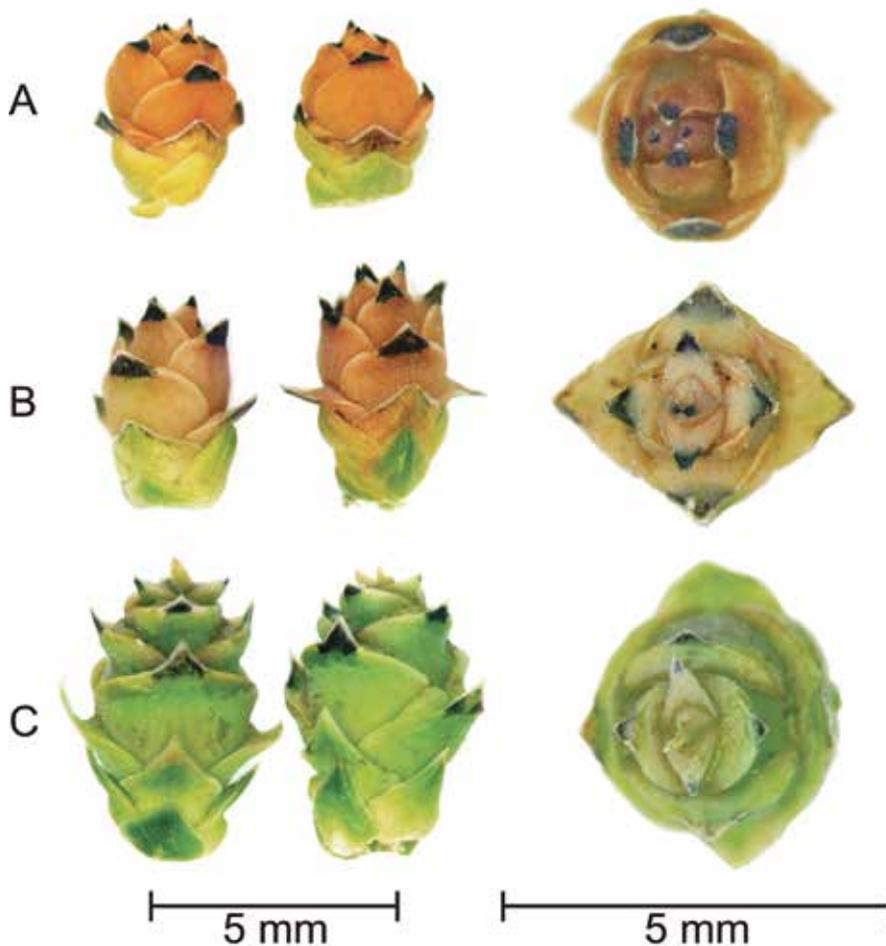


Fig. 11. The identification of *Thuja occidentalis* (A), *T. plicata* (C) and their hybrids (B) is possible based on female cones at very early stages of their development. Differences in the position of the terminal acute scale mucros are visible; in the former species, the mucro is \pm bent inside, while in the latter, because of the quicker growth of the inner scale layer, on all scales the mucros are \pm bent outwards. In hybrids (at that stage of development), the black mucro assumes a vertical position (photo P. Kosiński)

Ryc. 11. Rozpoznawanie *Thuja occidentalis* (A), *T. plicata* (C) oraz mieszańców tych gatunków (B) możliwe jest również na podstawie ich żeńskich szyszek już w bardzo wczesnych stadiach ich rozwoju. Widoczne są zwłaszcza różnice w pozycji ostrego wyrostka w szczytowej partii łusek (z wyjątkiem nasadowych). U pierwszego z tych gatunków jest on \pm zagięty do środka, natomiast u drugiego, w efekcie szybszego rozrastania się wewnętrznej warstwy łusek, na wszystkich łuskach zostaje on \pm odchylony na zewnątrz. U mieszańców (na tym etapie rozwoju szyszek) ciemny wyrostek na wierzchołkowych łuskach ma pozycję pionową (fot. P. Kosiński)

Our findings, documented by numerous illustrations, definitely confirm former reports about the existence of hybrids between *Thuja occidentalis* and *T. plicata*. Those hybrids turned out to be more numerous than we had thought before. However, a considerable part of this hybrid swarm might have originated from rooted stems of already existing hybrids (figs. 12–16). Our observations confirm an earlier opinion (Seneta, 1981; Seneta & Dolatowski, 1997) about

hybrid origin of the ‘Aureospicata’ and ‘Smaragd’ cultivars. The former, with a distinguishing yellowish foliage on young branchlets, is generally very similar to the western arborvitae, but it differs from it with poorly bulging, almost invisible resin glands in the middle leaves of primary stems, and with cones, which to a greater extent are more similar to *T. plicata* than to *T. occidentalis* (fig. 17). The ‘Smaragd’ resembles largely columnar cultivars of *T. occidentalis*, such



Fig. 12. *Thuja occidentalis* × *plicata* hybrids grow in many places of the Kórnik Arboretum. The hedge fragment of old specimens in a new part of the Arboretum in the grounds of the former nursery. Possibly, it may be the vegetative progeny of the specimen presented in fig. 2, bred at the turn of the 1930's and 1940's. In respect to the crown shape and bark structure they are closer to *T. plicata* than to *T. occidentalis* (Kórnik Arboretum, Inv. No XXXIV/194–198, 204–207) (photo J. Zieliński)

Ryc. 12. Mieszzańce *Thuja occidentalis* × *plicata* rosną w wielu miejscach Arboretum Kórnickiego. Fragment szpalery starych osobników w nowej części Arboretum, na terenie dawnej szkółki. Niewykluczone, że jest to wegetatywne potomstwo rośliny przedstawionej na ryc. 2, wyhodowane na przełomie lat 30. i 40. ubiegłego wieku. Pod względem kształtu korony i budowy kory są one bliższe *T. plicata* niż *T. occidentalis* (Arboretum Kórnickie, nr inw. XXXIV/194–198, 204–207) (fot. J. Zieliński)



Fig. 13. The trunk of one of the oldest specimens of *Thuja occidentalis* × *plicata* in the Kórnik Arboretum; the tree is over 80 years old and has a circumference of nearly 2.5 m at its base (Inv. No III/482). It is very possible that its origin is also related to the plant presented in fig. 2 (photo P. Kosiński)

Ryc. 13. Pień jednego z najstarszych okazów *Thuja occidentalis* × *plicata* w Arboretum Kórnickim; drzewo liczy ponad 80 lat i u podstawy ma obwód blisko 2,5 m (nr inw. III/482). Bardzo możliwe, że jego pochodzenie ma również bezpośredni związek z rośliną przedstawioną na ryc. 2 (fot. P. Kosiński)



Fig. 14. An old specimen of *Thuja occidentalis* × *plicata* surrounded by younger specimens originated from its rooted lowest branches. Kórnik Arboretum (Inv. No XXXIV/214) (photo J. Zieliński)

Ryc. 14. Stary okaz *Thuja occidentalis* × *plicata* w otoczeniu znacznie młodszych, powstałych przez ukorzenie jego najniższych konarów. Arboretum Kórnickie, nr inw. XXXIV/214 (fot. J. Zieliński)



Fig. 15. One of the younger Kórnik hybrids of *Thuja occidentalis* × *plicata*. A robust, two-stemmed tree previously identified as *T. plicata* grows outside the Kórnik Arboretum, just at the entrance to the Institute of Dendrology by the Parkowa Street side (photo J. Zieliński)

Ryc. 15. Jeden z młodszych kórnickich mieszańców *Thuja occidentalis* × *plicata*. Bujne, dwupniowe drzewo, identyfikowane dotychczas jako *T. plicata*, rośnie tuż poza terenem Arboretum Kórnickiego, nieopodal wjazdu do Instytutu Dendrologii od strony ul. Parkowej (fot. J. Zieliński)



Fig. 16. Freely growing *Thuja occidentalis* × *plicata* specimens are often more attractive than the parental species of this hybrid: they develop a slender regular habit after *T. plicata*, and are densely branched after *T. occidentalis*. Kórnik, the square at Średzka Street (photo J. Zieliński)

Ryc. 16. Swobodnie rosnące osobniki *Thuja occidentalis* × *plicata* są często bardziej efektowne od gatunków rodzicielskich tego mieszańca – po *T. plicata* dziedziczą regularny smukły pokrój, a po *T. occidentalis* gęste ugałęzienie. Kórnik, plac przy ulicy Średzkiej (fot. J. Zieliński)

as the ‘Columna’ and ‘Malonyana’, but as compared to them it has weakly bulging glands in the leaves and the cone scales with a longer and distinct ‘collar-like’ internal layer, and a considerably longer mucro at the scale apices. The cones of that variety usually remain underdeveloped and dry out early (figs. 18–19). Our observations also unveiled that the cultivar ‘Stolwijk’ with its cones indeed similar to those of *T. plicata*, but with indistinct resin glands in leaves and

foliage, also belongs to the circle of *Thuja* × *senetiana* (fig. 20). It is very probable that some other cultivars associated so far with *T. occidentalis* will turn out to be hybrids.

In the light of the above observations, Seneta’s decision (1981) about encompassing hybrids under a common species name seems to be fully justified. However, the taxon distinguished by Seneta was accompanied by a laconic Latin diagnosis: ‘*Thuja occidentalis* × *T. plicata*; hybrida inter



Fig. 17. The cultivar ‘Aureospicata’, included mostly in *Thuja occidentalis*, is actually a hybrid of this species with *T. plicata*, which is mainly seen in the structure of its cones (photo W. Danielewicz)

Ryc. 17. Kultuwar ‘Aureospicata’, kojarzony najczęściej z *Thuja occidentalis*, jest mieszańcem tego gatunku z *T. plicata*, na co głównie wskazuje budowa jego szyszek (fot. W. Danielewicz)



Fig. 18. The *Thuja* ‘Smaragd’, usually treated as a cultivar of *T. occidentalis*, is a hybrid of this species with *T. plicata*. Its cones are very similar to the cones of the latter parental species, but they are much smaller and mostly not fully developed (photo W. Danielewicz)

Ryc. 18. *Thuja* ‘Smaragd’ traktowana najczęściej jako kultuwar *T. occidentalis* jest mieszańcem tego gatunku z *T. plicata*. Jej szyszki są bardzo podobne do szyszek tego drugiego gatunku rodzicielskiego, choć znacznie mniejsze i zwykle niezupełnie wykształcone (fot. W. Danielewicz)



Fig. 19. The *Thuja* ‘Smaragd’; a branchlet with mature cones. The same specimen as in fig. 18 (photo W. Danielewicz)

Ryc. 19. *Thuja* ‘Smaragd’; pęd z dojrzałymi szyszkami. Ten sam okaz co na ryc. 18 (fot. W. Danielewicz)



Fig. 20. The cultivar ‘Stolwijk’, assigned to *Thuja occidentalis*, represents, in fact, a hybrid of this species with *T. plicata*. This is evidenced by its cone structure, clearly referring to the cones of *T. plicata*, and by indistinct resin bubbles in its leaves (June 2019). From the latter species, it differs mainly by displaying the yellowish-green colour of foliage on the abaxial side of branchlets (photo W. Danielewicz)

Ryc. 20. Kultuwar ‘Stolwijk’, łączony z *Thuja occidentalis*, reprezentuje w rzeczywistości mieszańca tego gatunku z *T. plicata*. Świadczą o tym jego szyszki wyraźnie nawiązujące budową do *T. plicata* oraz niewyraźne pęcherzyki żywiczne na liściach (czerwiec 2019). Od tego gatunku różni się głównie żółtawozielonym zabarwieniem liści po dolnej stronie pędów (fot. W. Danielewicz)

parent[es]', which does not explain how it differs from its parental species. Moreover, a type of a new taxon has not been designated. For these reasons, pursuant to Article 38.2 of the *International Code of Nomenclature for algae, fungi, and plants* (Turland et al., 2018), the name *Thuja ×plicatoides* suggested by the author cannot be treated as validly published. In the *International Plant Name Index* (www.ipni.org), it has existed for a long time as a 'nomen invalidum'. This taxon has been described here once again in accordance with the requirements of the above mentioned *Code*, but this time under a new species name of *Thuja ×senetiana*, commemorating the name of the late outstanding Polish dendrologist.

Thuja ×senetiana Ziel., nothospecies nova
(*T. ×plicatoides* Seneta, nomen invalidum)

Plants intermediate between *Thuja occidentalis* and *T. plicata*. They differ from the former species by the following features: more vigorous growth, smaller resin glands in the middle leaves, cones ovoid (not ellipsoid); the inner layer of cone scales somewhat longer than the outer scale layer, the mucro at the apex of the cone scales longer than 0.2 mm and usually slightly bent out; from the latter species they can be distinguished by dull green leaves on the adaxial side of stems, yellowish-green on the abaxial side, by ovoid or ellipsoid cones (not jug-like) and by a shorter mucro (0.3–0.5 mm) on the apex of the cone scales.

Holotype: Poland, Kórnik Arboretum, Section VII; Inv. No VII/36; 9.04.2019, 6.06.2019; coll. J. Zieliński; KOR 53770 (fig. 22).

The *Thuja ×senetiana* is an extremely diversified group of intermediate forms between *T. occidentalis* and *T. plicata*, to a different degree similar to their parental species. As the species type, it has been selected the specimen (fig. 21) having an erect habit with rather narrow, broadly columnar dense crown, with slightly sagging branchlets, with leaves green on the adaxial side of branchlets and yellowish green on their abaxial side. In other its features, it is ± intermediate between giant and western arborvitae.



Fig. 21. *Thuja ×senetiana*. A specimen selected as the type of this nothospecies. Kórnik Arboretum. Section VI, Inv. No VII/36 (photo P. Kosiński)

Ryc. 21. *Thuja ×senetiana*. Okaz wybrany jako typ tego mieszańcowego gatunku. Arboretum Kórnickie. Sekcja VII, nr inw. VII/36 (fot. P. Kosiński)



Fig. 22. A holotype: a herbarium specimen collected from the tree (see fig. 21) representing the type of *Thuja x senetiana*, KOR 53770 (digitized in the Institute of Dendrology PAS)

Ryc. 22. Holotyp – okaz zielnikowy zebrany z drzewa (patrz ryc. 21) reprezentującego typ *Thuja x senetiana*, KOR 53770 (digitalizacja w Instytucie Dendrologii PAN)

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References

- Auders AG, Spicer DP. 2012. Encyclopedia of Conifers. Part 2. London: Royal Horticultural Society.
- Browicz K, Bugała W. 1966. Opisy morfologiczne drzew i krzewów. In: Białobok S, Hellwig Z eds. Drzewoznawstwo. Warszawa: Państwowe Wydawnictwo Rolnicze i Leśne, 47–591 + maps.
- Chambers KL. 1993. Thuja L. In: Morin NR ed. Flora of North America. Part 2. New York–Oxford: Oxford University Press, 410–430.
- Cui YM, Sun B, Wang HF, Ferguson DK, Wang YF, Li CS, Yang J, Ma QW. 2015. Exploring the formation of a disjunctive pattern between Eastern Asia and North America based on fossil evidence from Thuja (Cupressaceae). PLoS ONE 10(9):e0138544 DOI: 10.1371/journal.pone.0138544.
- Dolatowski J. 1992. Materiały do historii Arboretum Kórnickiego – Index Seminum. Rocznik Dendrologiczny 40:13–22.
- Elias TS. 1980. Trees of North America. New York: Book Division, Times Mirror Magazines.
- Farjon A. 2005. A monograph of Cupressaceae and Sciadopitys. Kew: Royal Botanic Gardens.
- Gaussen H. 1968. Les Gymnospermes actuelles et fossiles. Fascicule 10. Toulouse: Faculté de Sciences.
- Li JH, Xiang QP. 2005. Phylogeny and biogeography of Thuja L. (Cupressaceae), an Eastern Asian and North American disjunct genus. Journal of Integrative Plant Biology 47(6):651–659.
- Little EL Jr. 1971. Atlas of United States trees 1. Miscellaneous Publication 1146. Washington: U.S. Department of Agriculture, Forest Service.
- International Plant Names Index. Available at: <https://www.ipni.org> (accessed January 10, 2019).
- Martin S, Tripp K. 1997. The tale of Thuja ‘Green Giant’. American Conifer Society Bulletin 14(4):153–155.
- Mitchell AF. 1972. Conifers of the British Isles. London: Her Majesty's Stationery Office.
- Ouden P den, Boom DK. 1965. Manual of cultivated conifers. The Hague: Martinus Nijhoff.
- Peng D, Wang XQ. 2008. Reticulate evolution in Thuja inferred from multiple gene sequences: Implications for the study of biogeographical disjunction between eastern Asia and North America. Molecular Phylogenetics and Evolution 47:1190–1202.
- Qin A, Liu B, Guo Q, Bussmann RW, Ma F, Jian Z, Xu G, Pei S. 2017. Maxent modeling for predicting impacts of climate change on the potential distribution of Thuja sutchuenensis Franch., an extremely endangered conifer from southwestern China. Global Ecology and Conservation 10:139–146.
- Rehder A. 1927. Manual of trees and shrubs. New York: The Macmillan Company.
- Rolloff A, Bärtels A. 2008. Flora der Gehölze. Stuttgart: Eugen Ulmer KG.
- Schmidt PA. 2017. Thuja. In: Schmidt PA, Schulz B, Hecker U eds. Fichten Gehölzflora. Wiebelsheim: Quelle & Meyer Verlag, 907–909.
- Seneta W. 1981. Drzewa i krzewy iglaste. Warszawa: Państwowe Wydawnictwo Naukowe.
- Seneta W, Dolatowski J. 1997. Dendrologia. Warszawa: Państwowe Wydawnictwo Naukowe.
- Sękowski B. 1980. Klucze do oznaczania gatunków i odmian roślin nagozalążkowych spotykanych w Polsce. Skrypty Akademii Rolniczej w Poznaniu. Poznań: Wydawnictwo Akademii Rolniczej w Poznaniu.
- Sun B, Cui YM, Wang HF, Ferguson DK, Xiang QP, Ma QW, Wang YF. 2019. Recognizing the species of Thuja (Cupressaceae) based on their cone and foliage morphology. Phytotaxa 219(2):101–117.
- Suszka B. 1956. Gatunki i odmiany żywotników w Arboretum Kórnickim. Arboretum Kórnickie 2:15–43.
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF eds. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books.
- Wodzicki S. 1833. Dziennik Ogrodniczy na rok 1833. Kraków: St. Gieszkowski
- Worth JRP. 2019. Current distribution and climatic range of the Japanese endemic conifer Thuja standishii (Cupressaceae). Bulletin of FFPRI 18(3): 275–288.
- Wróblewski A. 1933. Drzewa i krzewy szpilkowe ogrodów Kórnickich. Rocznik Polskiego Towarzystwa Dendrologicznego 5:1–30.