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BOTANICAL HISTORY

"The Distribution, Morphology and Classification of *Taiwania*" (Cupressaceae): An Unpublished Manuscript (1941) by John Theodore Buchholz (1888–1951)

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ABSTRACT: A recently discovered unpublished manuscript on *Taiwania cryptomerioides* (Cupressaceae) written by John Theodore Buchholz (1888–1951), probably in 1941, is published with 25 added notes, plus a recently discovered unpublished diagram entitled "Phylogeny of conifers. J. T. Buchholz — 1941." The manuscript and diagram are important in expanding our understanding of the research and interpretations of this renowned worker on the anatomy, morphology (especially embryology), and systematics of gymnosperms.

KEY WORDS: Buchholz, conifer phylogeny, conifers, Cupressaceae, embryology, gymnosperms, Taiwan, *Taiwania cryptomerioides.*

INTRODUCTION

In the spring and summer of 1936, John Theodore Buchholz (14 July 1888–1 July 1951; Fig. 1–2) visited California and made detailed studies of the vegetative morphology, reproductive morphology, and embryology of *Sequoiadendron giganteum* (giant sequoia, big tree, or Sierra redwood) and *Sequoia sempervirens* (redwood or coast redwood). These two monotypic genera are endemic to western North America: *Sequoiadendron giganteum* to the western slope of the Sierra Nevada of California, *Sequoia sempervirens* to coastal central and northern California and adjacent southwestern Oregon. Buchholz's work (1937, 1938, 1939a–c) culminated in his 1939 (1939c) segregation of *Sequoiadendron* from *Sequoia,* a proposal that was initially highly controversial and unpopular (Dayton, 1943; Jones, 1943; Schmid, 2012b).

Buchholz (Ph.D. 1917, University of Chicago) held professorships in botany at the universities of Arkansas (1919–26), Texas (1926–29), and Illinois (1929–51). Schmid (2012b) provides biographical information on Buchholz (see also Jones and Tippo, 1952, and various notes below, especially note 25), discusses his collection techniques in 1936 for morphological and embryological studies, and lists herbarium vouchers of *Sequoiadendron giganteum* that Buchholz made in 1936 and 1940; he did not make herbarium vouchers of *Sequoia sempervirens.*

I have an extensive reprint collection of 42 of Buchholz's papers (1918–51), most of which deal with gymnosperms (see Jones and Tippo, 1952). I acquired the collection from the effects of Adriance S. Foster (1901–73; see Gifford, 1974) of the University of California, Berkeley, after Foster's death. Possibly as a source for writing his classic morphology book (Foster and Gifford, 1959), Foster had acquired the collection from Clarence Sterling (1919–96; see Feeney et al., 1997), whose signature appears on 18 of the reprints. Sterling was a plant anatomist-morphologist in the Department of Food Science and Technology, University of California, Davis. His Ph.D. dissertation was based on a study of the shoot apex of *Sequoia* (Sterling, 1944) under Foster's direction. After publishing on *Sequoia* and other conifers Sterling exchanged reprints with Buchholz.

The reprint collection includes a 13-page, double-spaced, good-quality carbon copy on onionskin paper of an unpublished manuscript by Buchholz entitled "The distribution, morphology and classification of *Taiwania."* About a third of this unillustrated, unannotated manuscript is a literature review; the rest is original embryological observations on a seed cone and seeds of fragmentary herbarium material. Buchholz (MS p. 6) initiated the study to determine if the Asian monotypic genus *Taiwania* (see note 1) is related to his *"Sequoia* group" (Sequoioideae) consisting of *Sequoiadendron, Athrotaxis,* and *Sequoia*. However, in the manuscript (p. 11) he placed *Taiwania cryptomerioides* (Fig. 3–4), along with *Cunninghamia*, in the Cunninghamioideae (Buchholz, 1946, 1948, would later place these two genera in Taxodioideae).

The manuscript is undated but appears to have been written between 1941 and 1944, most likely in 1941, on

Fig. 1. John Theodore Buchholz (14 July 1888–1 July 1951), Ph.D. 1917, University of Chicago), with professorships in botany at the universities of Arkansas (1919–26), Texas (1926–29), and Illinois (1929–51). A: Circa 1920, Arkansas. B: Undated, probably at Texas. [Smithsonian Institution Archives (2012), reproduced by permission.]

the basis of the following internal and external evidence:

(1) In his manuscript Buchholz cites two papers that had appeared in issues dated December 1940: Buchholz (1940) on embryogeny of the related genus *Cunninghamia,* and Butts and Buchholz (1940) on cotyledon numbers in conifers. [Buchholz's unpublished manuscript has an incomplete citation for the doctoral dissertation of his student: "9 Kaeiser, Margaret. 1940" (see note 18). Curiously, Kaeiser (1940) is cited in full in Buchholz (1940) and in abbreviated form in Butts and Buchholz (1940).]

(2) Buchholz (1940: p. 881) wrote in his *Cunninghamia* paper that "unfortunately nothing is known concerning its [*Taiwania*'s] internal morphology or life history." Because the unpublished manuscript on *Taiwania* presents some new information, one can conclude that it post-dates the 1940 paper.

(3) Because *Cunninghamia* and *Taiwania* were considered related by Buchholz (1933; Fig. 5) and earlier workers (Hayata, 1912; Pilger, 1926; Sorger, 1925; Wilson, 1926), Buchholz logically would have wanted to study this taxon soon after completing his study on *Cunninghamia*, which was published in December 1940.

(4) I had hoped to obtain a more precise date for Buchholz's unpublished manuscript by examining collections in herbaria as well as Buchholz's correspondence in archives (Alice Eastwood Papers, Special Collections, California Academy of Sciences Library, San Francisco, 2012; University of Illinois Archives, 2012).

Buchholz states in his manuscript that Alice Eastwood (1859–1953; see Daniel, 2008; Schwartz, 1997) of the California Academy of Sciences (CAS) had sent him "a cone and some seeds" from a specimen of *Taiwania* collected in 1918 in Taiwan. On 21 December 2011 I visited the herbarium and library archives of CAS. Unfortunately, the herbarium sheets of *Taiwania* lack annotations by Eastwood, and the six archived letters (10 pages total) that Buchholz wrote to Eastwood from 1933 to 1944 do not mention *Taiwania.* Moreover, Dina Allen of the University of Illinois Archives informed me (pers. comm., 22 Dec. 2011): "I went through approximately 1,500 pages of correspondence. Unfortunately, I did not find any correspondence between Alice Eastwood and John T. Buchholz." Nevertheless, it is clear from Buchholz's botanical correspondence with Eastwood and other persons archived at CAS and the University of Illinois that by 1944 (he wrote at least 21 letters from January through December 1944) he was heavily involved with research on *Podocarpus.* This emphasis, which would occupy Buchholz until his death in July 1951 (see Schmid, 2012b), favors an earlier date for his manuscript on *Taiwania,* namely, 1941.

(5) Moreover, the California archives contain a diagram titled "Phylogeny of conifers. J. T. Buchholz

Fig. 2. Buchholz (undated, but in 1940s) holding a persistent, unopened, green seed cone of *Sequoiadendron giganteum* (giant sequoia, big tree, or Sierra redwood); portrait painted by his daughter and noted artist, Olive Miriam Buchholz Parmelee (1913–70). [Photo enhanced by Steve Ruzin from original photo by Thomas Jacobs, from Department of Plant Biology, University of Illinois (2012), reproduced by permission.]

— 1941" (Fig. 5) that was inserted after a letter dated 16 June 1941 that Buchholz had written to Eastwood. The letter does not comment on the diagram. The date of the letter and the 1941 date on the previously unpublished diagram provide the strongest evidence for a 1941 date for Buchholz's manuscript.

(6) I had hoped that a second copy of the manuscript might contain annotations to elucidate when it was written, but the University of Illinois Archives also does not have any manuscripts written by Buchholz (Dina Allen, pers. comm., 22 Dec. 2011). Incidentally, my copy of the manuscript will be donated to these archives when this paper is published.

Buchholz apparently intended to publish his manuscript on *Taiwania* in the *Transactions of the Illinois State Academy of Science* because it uses a style of reference citation then adopted by that journal. However, the manuscript was never published: Jones and Tippo (1952) do not cite it; an Internet search provided no information. I have no explanation why Buchholz never published the manuscript on *Taiwania* or his diagram on the "phylogeny of conifers" (Fig. 5) that apparently was to accompany the manuscript.

MATERIALS AND METHODS

Buchholz's manuscript is presented with only minor editorial modifications of the text, including the 13-reference bibliography, that is: punctuation, capitalization, use of boldface and italics, corrections of misspellings, corrections of references, and consistent use of numbers written as such or spelled out. Other word substitutions take two forms: *(1)* In cases such as "forms [taxa]" the unbracketed word or phrase is

Buchholz's whereas the bracketed word or phrase is my substitution. *(2)* In cases such as "wide ["long"]" the unbracketed word is my substitution whereas the bracketed word is Buchholz's (hence the quotation marks used). I otherwise retained Buchholz's writing style and resisted indulging in cherished word changes (Schmid, 1983). I also use bracketed information in Buchholz's text for mostly brief editorial comments, for instance, "Burma [now Myanmar]" or "160 feet [49 m]" or "[see note 5]." For clarity in Buchholz's 1941 manuscript I bolded the reference numbers and italicized genera and species as well as titles of books and journals, or their abbreviations.

The references in Buchholz's manuscript to the 25 numbered notes are for the extensive comments that follow. I quote from Buchholz's correspondence held in the University of Illinois Archives (2012). Nomenclature for genera and species mentioned in Buchholz's and my text is updated fide Farjon (2005, 2010; see also Earle, 2011, and Eckenwalder, 2009) and is summarized in Table 1.

THE DISTRIBUTION, MORPHOLOGY AND CLASSIFICATION OF *TAIWANIA,*

by J. T. Buchholz [1941]

Taiwania cryptomerioides [the genus is monotypic; see note 1 and Table 1] is one of the rarest of conifers in cultivation. A tree now [1941] about 12 feet [3.7 m] high was planted in lower Hillside Park [now Orpet Park] in Santa Barbara, California, in 1923 by Mr. E. O. Orpet [see note 2], who obtained the specimen as a potted plant from the Arnold Arboretum. This is probably the best specimen to be found in cultivation in America. Another good sized example may be seen in the Huntington Botanical Garden in San Marino, California. A small specimen less than 2 feet [.6 m] tall is growing in the Botanical Garden of Golden Gate Park, San Francisco [see notes 3 and 4]. It is believed that all of these plants were introduced originally by the Arnold Arboretum from seeds collected by E. H. Wilson [see note 5] in Formosa [now Taiwan; see note 6] in 1918. It is possible that the species may be found elsewhere [cultivated] in the United States, but it is not hardy and may be expected only as a conservatory plant [for "the myth of ... tenderness" see Grimshaw (2011: pp. 45–46; also note 7)].

[See note 7 for modern references discussing the distribution, morphology, and relationships of *Taiwania cryptomerioides.*]

Taiwania is one of a number of conifers having the branches and leaves more or less dimorphic. Both stems and leaves differ on various parts of the plant. The stems that form leaders are much more stout and vigorous than the lateral branches. The leaves that clothe the leader are smaller and more nearly scale-like while the larger leaves borne on lateral branches are scythe-shaped and flattened vertically [Fig. 3D–F]. Both kinds of leaves are decurrent on the stem, and leaf bases [*end of MS page 1*] persist to clothe the stem for many years. The leaves become most extremely scale-like on the reproductive branches of old trees [Fig.3 B–C, G, 4C, D]. The species roots easily from cuttings, but when these are selected from the twigs of lateral branches, they remain very slender and tend to droop. They are slow to develop a leader and may fail entirely in this respect.

Taiwania seems to be a rare conifer even in its native range—Formosa, China, Burma [now Myanmar] and Tibet [now Xizang Zizhiqu, China; also found in Vietnam; see notes 1 and 7]. It grows in the tropical rain forest at high altitudes, was originally discovered in Formosa (1904) [by Nariaki Konishi, was] described as a new species by Hayata [see note 8] in 1906 (**6**), and was long regarded as an endemic of this island. However, records have been found indicating that a specimen was collected as early as 1912 in the Myitkyina District of Upper Burma, where the vernacular name was recorded as "Shoak" (**10**). It was collected by Dr. Handel-Mazzetti [see notes 5 and 9] in 1916 at Tschamutong in the northwestern part of Yunnan, China, at an altitude between 7300 and 7900 feet [2225–2408 m] (**13**), and by Joseph Rock [see note 5] in 1932 in the mountains of Tibet. Its distribution is therefore discontinuous over an east-west area more than 1000 miles [1609 km] wide ["long"], where it occurs as a rare form [tree] in association with other species. [See note 1 summarizing currently known distribution.]

Mr. E. H. Wilson [see note 5] did not find it in the parts of China explored by him, but [he] collected it in Formosa in 1918 [see notes 10 and 14]; the seeds which he collected at that time were the source of plants cultivated in America. In Formosa, *Taiwania* grows in a jungle with other conifers such as [*end of MS page 2*] *Abies, Picea* and *Chamaecyparis* (**7, 8**). At altitudes of 6000 to 8000 feet [1829–2438 m] the climate is

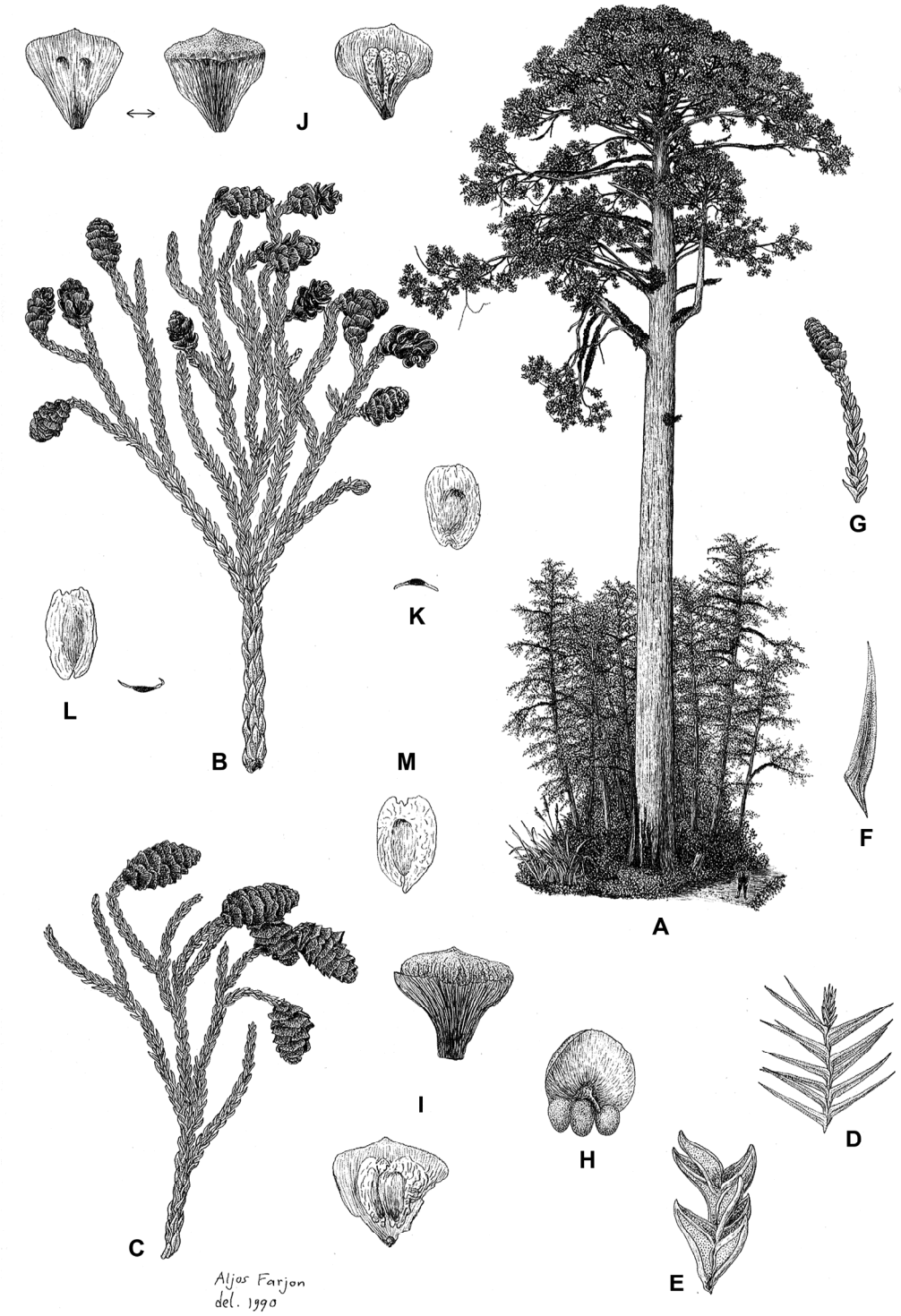

Fig. 3. ***Taiwania cryptomerioides.*** **A: Habit of old tree. B–C: Branches with leaves and seed cones, x 0.8. D: Branchlet with juvenile leaves, x 0.8. E: Branchlet with mature leaves, x 3.2. F: Juvenile leaf, x 1.6. G: Branchlet with leaves and seed cone, x 0.8. H: Microsporophyll with three pollen sacs, adaxial view, x 16. I–J: Seed cone scales, abaxial views, adaxial views with attached seeds and/or seed scars, x 2.4. K–M: Seeds, x 3.2. [Drawings by Aljos Farjon: A from photos of E. H. Wilson, 1918; B, J–L from** ***N. Konishi s.n.*** **(lectotype, holotype, TI); C, E, I, M from** ***H. Handel-Mazzetti 9664*** **(WU); D, F, G from** ***C. G. G. J. van Steenis 20,757*** **(L); H from** ***E. H. Wilson 8644*** **(B). Plate and caption from Farjon (2005: pp. 92–93), reproduced by permission.]**

described as cool throughout the year. In a deep valley the trees are said to be scattered about as solitary specimens attaining a height of 160 feet [49 m; see end of note 3] and a trunk diameter of about 7 feet [2 m]. The mature trees are quite branchless for a height of about 70 feet [21 m], with the branches giving the trees a conical or rather cylindrical form [Fig. 3A, 4A], a habit which resembles *Cryptomeria* [the genus is monotypic, *C. japonica;* see Table 1], but with branchlets and foliage more clustered toward the ends of the branches [Fig. 3A–C].

Morphological investigations have been confined to the study of herbarium specimens. Hayata (**6**–**8**) gave the essential taxonomic details in his descriptions. However, he misinterpreted the structure of the scale of the seed cone and regarded it as having a minute outer bract at the base where it joins the cone axis. This error was pointed out by Sorger (**13**) [see note 11], who studied the [seed] cones that were collected by Handel-Mazzetti in Yunnan [in 1916; see note 9], and he [Sorger] also had before him some of the [male] material collected by Wilson in Formosa [in 1918; see notes 10 and 11].

Hayata (**7, 8**) had concluded that *Taiwania* is most nearly related to *Cunninghamia* and *Athrotaxis*—that its taxonomic position is between these two genera. Sorger (**13**) made a study of the cones, the wood anatomy and the histology of the leaves, comparing them with corresponding structures in *Cunninghamia, Athrotaxis* and other related genera. As already mentioned, his interpretation of the morphology of the scale of the [*end of MS page 3*] seed cone differed from that of Hayata; he [Sorger] concluded that the scale and bract are completely fused into a single member [technically, a bract-cone-scale complex] as they appear to be in some species of *Athrotaxis* and that the minute bract which Hayata observed and illustrated, was only a snag resulting from the manner in which the scales were torn away from the cone axis. The cone scale has the same morphology as that of *Athrotaxis* and *Cunninghamia,* although in the latter genus, the tip of the ovuliferous scale is still evident as a small ligular structure on the surface of the bract with which it is fused.

The result of Sorger's investigation of the wood when compared with the related genera and also with certain Cupressaceae indicated that nothing could be found in the anatomy which would distinguish *Taiwania* from other genera or associate it more closely with any one or another of the related forms [taxa].

The pollen cones of *Taiwania* are grouped in clusters of 3–5 at the ends of branches [Fig. 4C]. This is in agreement with *Cunninghamia* and *Cryptomeria* and differs from *Athrotaxis* where the pollen cones are borne singly. Sorger found, however, that when there are only 3–4 cones per cluster, the pollen sacs (sporangia) on the microsporophylls [male sporophylls] of these cones are most numerous, up to 4 [per microsporophyll]; when there are 5 cones per cluster, the number of pollen sacs in these cones is less numerous, usually only 2 [per microsporophyll] at the tip of the cone [see Fig. 3H for a microsporophyll with three pollen sacs]. In all cases the [*end of MS page 4*] larger number of pollen sacs is found in the sporophylls near the base[s] of the cones, the minimum number near the apices ["apex"] (**8**). [*Buchholz's paragraph divided*]

At this point Sorger examined the number of sporangia per sporophyll in the pollen cone[s] of several species of *Athrotaxis* and found that in *A. cupressoides* the number of pollen sacs per sporophyll is 3–4 in the lower portion of the cone and is 2 only near the tip of the pollen cone. However, in *A. selaginoides* all sporophylls have only 2 pollen sacs. Both *Cryptomeria* and *Cunninghamia* have 3–4 sporangia per sporophyll in the pollen cones, which are similarly clustered at the ends of the branches. Hooker (see note 12) had given 2 as the number of pollen sacs per sporophyll for all species of *Athrotaxis.* Thus, in spite of the difference in the clustered condition of the pollen cones in *Taiwania* and the solitary cones in all species of *Athrotaxis,* a point of closer approach toward agreement between the genera was found in the number of sporangia per sporophyll. Of course, the discovery of 3–4 sporangia per sporophyll in one of the species of *Athrotaxis* would not serve to separate *Taiwania* from *Cryptomeria* and *Cunninghamia.* This fact would only tend to strengthen the basis of separating *Athrotaxis* from the Pinaceae and Podocarpaceae, in which 2 sporangia per sporophyll are so characteristically constant, and [would] justify its [i.e., *Athrotaxis*] inclusion in Taxodiaceae generally, nearly all of which have more than 2 sporangia per sporophyll. [*end of MS page 5*]

In the internal anatomy of the leaves Sorger found that the small scale leaves of *Taiwania* resemble the leaves of *Athrotaxis* more closely than [those of] any of the [other] genera in question. The larger scythe-shaped leaves of *Taiwania,* which are borne on vegetative branches, have little in common with the leaves of *Cunninghamia* or any of the forms [taxa] except *Cryptomeria.* However, *Cryptomeria* is ruled out as a close relative because of its erect seed. Since the reproductive structures yielded no features which would associate *Taiwania* more closely with *Athrotaxis* or *Cunninghamia,* Sorger was forced to base his conclusions on vegetative characters, and here leaf anatomy provided a feature of resemblance. On this basis he concluded that *Taiwania* stands somewhat closer to *Athrotaxis* than to *Cunninghamia.*

More recently, the morphology of *Athrotaxis selaginoides* [not *"cupressoides"*] has been investigated by Saxton and Doyle (**12**), who showed that this species

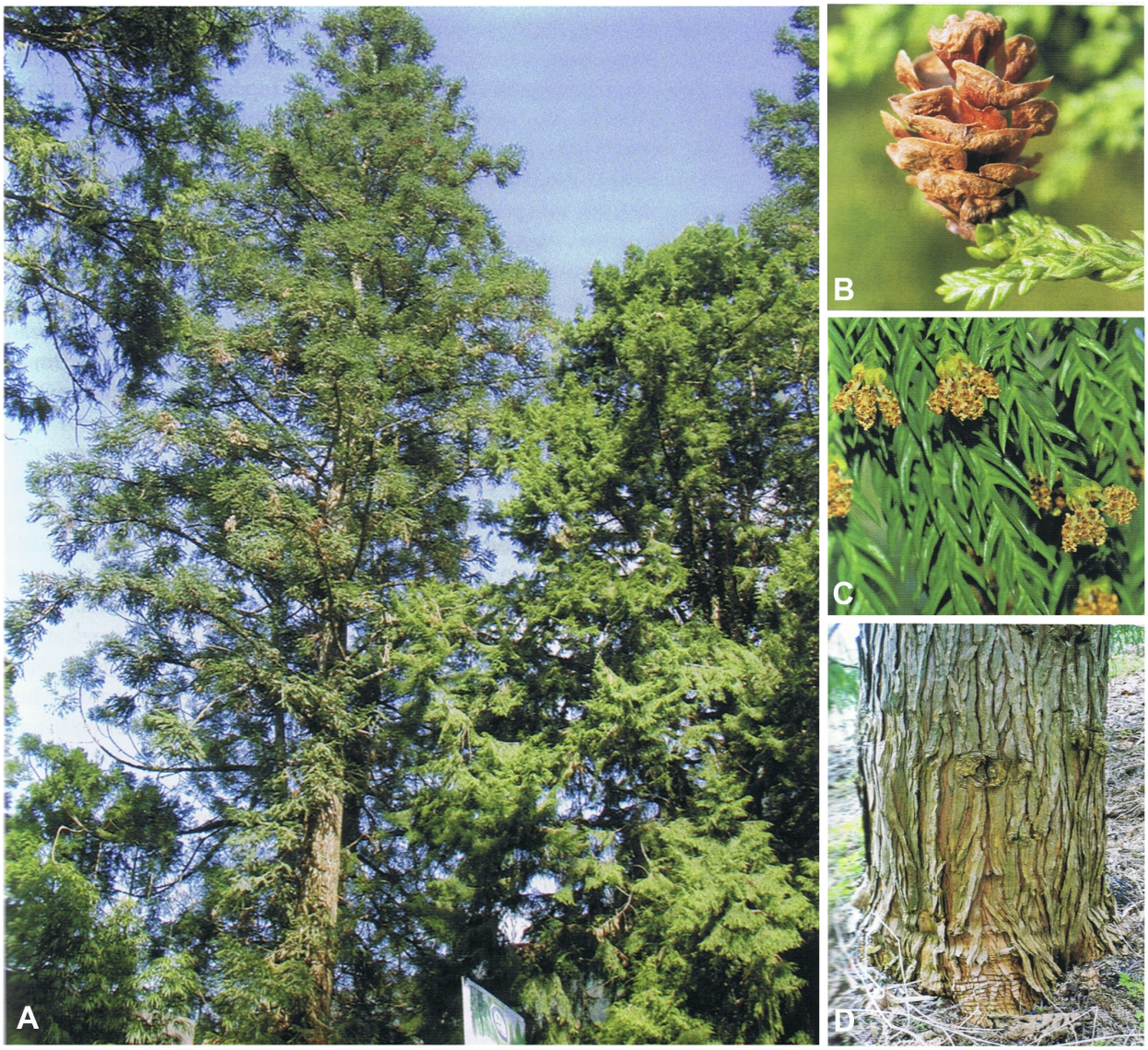

Fig. 4. *Taiwania cryptomerioides*. A: Habit of tree that Bunzō Hayata planted in 1907 in Chitou, Taiwan. B: Lower trunk and bark. C: Male cones. D: Erect seed cone. [Grimshaw (2011: pp. 35, 43), International Dendrology Society (www.dendrology.org), reproduced by permission.]

has characteristics which may associate it with the *Sequoia* group. These are: lateral archegonia and pollen tube and some other features which concern the embryo. These characteristics may place *Athrotaxis* in a position between *Sequoiadendron* and *Sequoia* (**1**–**3**). When this was realized the writer became interested in *Taiwania* as a subject of special study, to determine whether or not it might possibly be a fourth member of the *Sequoia* group. [*end of MS page 6*]

It has been found impossible to obtain properly preserved collections of *Taiwania* suitable for a more detailed morphological study. The trees growing in California have not produced cones and are not likely to be reproductive for many years. The only available source of material for study is from dried herbarium specimens. Through the kindness of Miss Alice Eastwood [see note 13] of the California Academy of Sciences I have received a [seed] cone and some seeds from the 1918 collection of E. H. Wilson [see notes 5, 7, 10, 11, and especially 14], also some seeds from a collection in the herbarium of the University of Pennsylvania, marked "Tozan, Nitak, Oct. 1906—Plantes Saghaliensis" [see note 15]. When these materials were carefully examined it was found that there are a number of morphological details not previously noted and [that] these new facts provide a more complete answer to the question of the current taxonomic position of *Taiwania.*

The seeds examined were mostly abortive ovules. Five seeds contained fairly matured embryos, three of

which had embryos with 2 cotyledons; the embryo of another had 3 cotyledons, and a third seed had "twins"—2 equally developed dicotyledonous embryos within the same seed. The embryos all have hypocotyls which are longer than the cotyledons, and the calyptroperiblem [see note 16] remains very small. The stem-tip primordium, distinctly observable between the cotyledons in cleared preparations, remains low and undeveloped in the matured embryo of the seed. [*end of MS page 7*]

The abortive ovules fall into two classes, those that had become aborted so early that no trace of gametophytic contents could be found, and others in which the dried mummies of the female gametophytes could be identified and examined. The latter could be softened sufficiently in water to permit dissection.

It appears that at the time of collection of the Formosa[n] material (Nov. [not "Oct."] 1918) [of *Taiwania*] [see note 14] the good seeds had been fully matured. The shriveled female gametophytes observed in abortive ovules resulted from ovules that had developed up to the time of fertilization before withering. A few of the ovules had become aborted after an embryo had developed, but these embryo systems had been too poorly preserved to yield much information with respect to the embryogeny. All that could be observed indicated a close agreement with the embryogeny of *Cunninghamia* (**4**). The pollen tube is not lateral but terminal in position, a prosuspensor is formed, and the separate remains of a large number of embryos indicated cleavage polyembryony.

The female gametophyte is flattened and more or less oblong, with its archegonial end slightly truncated. It agrees with *Cunninghamia* and *Cryptomeria,* and not with *Sequoiadendron* or *Sequoia.* This appears to exclude *Taiwania* from the *Sequoia* group.

Most of the gametophytes had archegonia, and these were always situated at the micropylar end. They [*end of MS page 8*] were found to be grouped into an archegonial complex of from 4 to 7 archegonia. One gametophyte had 4, six gametophytes had 5, three had 6, and one had 7 archegonia. One of the largest of these mummified gametophytes was embedded [in wax] and sectioned serially. This operation was very disappointing compared with the structures observable in dissected preparations that had been stained and mounted in glycerine jelly. However, the thickness of the megaspore membrane could be measured, and this was found to be two layered and less than 1 micron in thickness. The core of sterile tissue found in the center of the archegonial complex of *Cunninghamia* was entirely absent in this ovule [of *Taiwania*] and could not be found in any of the archegonial groups dissected from the gametophytes. In every other detail the gametophytes correspond very closely to ["with"] those of *Cunninghamia,* except that they are much smaller. The reproductive morphology [of *Taiwania*] also agrees with that of *Cryptomeria,* but the thin-walled inverted seed of *Taiwania* excludes it from the closest association with the latter, or with *Taxodium* and *Glyptostrobus* [the genus is monotypic, *G. pensilis;* see Table 1], whose seeds are erect.

Another feature [of *Taiwania*] that was noticed is the very thin seed coat. No stony layer was found in the integumentary tissue. A bract at the base of the cone scale, reported by Hayata [1906, 1907, 1912], could not be found. The writer was also interested in searching for the thin "ligule" found behind and above the seed in *Cunninghamia.* [*end of MS page 9*] This was also absent in all specimens [of *Taiwania*] that were examined.

In re-examining the morphological facts it is possible to fix the phylogenetic affinity of *Taiwania* and to place it close[r] to *Cunninghamia* rather than [to] *Athrotaxis* [Fig. 5; see note 17], for the latter has a lateral pollen tube and a lateral archegonial group which is actually situated close to the chalazal end of the female gametophyte. As already stated, the inverted ovule excludes it [*Taiwania*] from close association with *Cryptomeria* and *Taxodium,* which have thick seed coats, [and] erect ovules which are less fattened and without distinct wings. Also, the cotyledon number [of *Taiwania*], given by Hayata as 2, is essentially confirmed in finding 5 out of 6 embryos with 2 cotyledons. Miss Kaeiser (**9**) [see note 18] has shown that *Taxodium* usually has 6 cotyledons, and Butts and Buchholz (**5**) [see note 19] have found 3 the usual number in *Cryptomeria. Cunninghamia* (**4**) usually has 2 cotyledons, though occasionally 3 have been observed. *Glyptostrobus pensilis* [as *"G. heterophylla"*] has 4–5 cotyledons.

Taiwania bears 2 or only 1 seed per cone scale [Fig. 3I–M]. *Cunninghamia* has 3 or 2. In this respect *Taiwania* seems to represent the end member of a reduction series that may have been derived from the condition found in *Cunninghamia* [Fig. 5; see note 17]. As Sorger pointed out, the clustered condition found in the pollen cones [Fig. 4C] relates *Taiwania* closely to *Cunninghamia,* in which the seed cones are also clustered. Seed cones are not [*end of MS page 10*] clustered in *Taiwania.* However, this difference in the single solitary terminal seed cone of *Taiwania* [Fig. 3B–C, G, 4D] may also be due to a similar reduction.

The position of *Taiwania* seems to be higher or more specialized than that of *Cunninghamia* [Fig. 5; see note 17]. This is indicated by the more compact grouping and smaller number of archegonia, with absence of the central core of sterile tissue in the complex, by the reduced number of seeds, which is 2 or 1 rather than 3 or 2, by the solitary seed cones having a

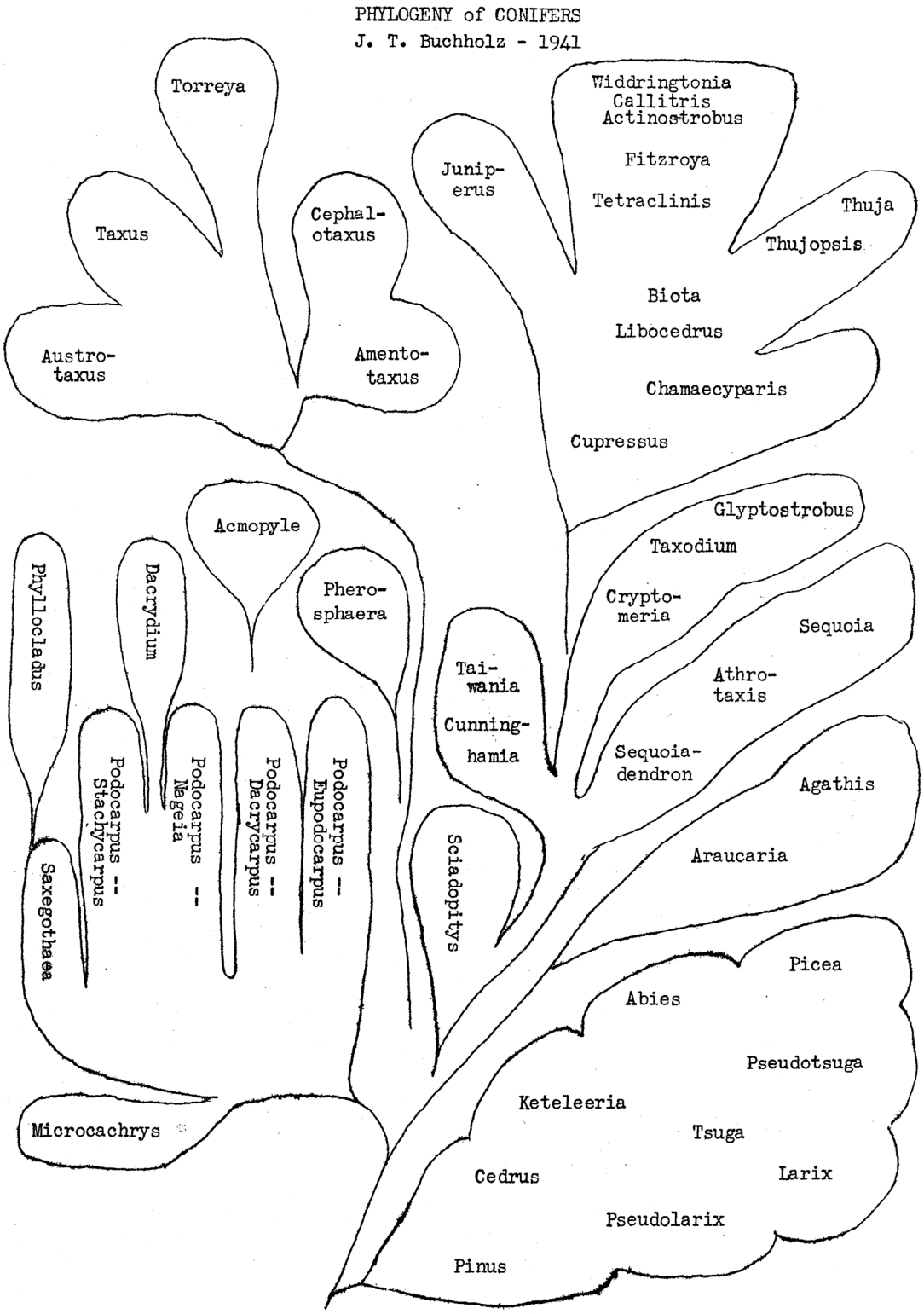

Fig. 5. "Phylogeny of conifers. J. T. Buchholz — 1941": an unpublished diagram in the library archives of the California Academy of Sciences (see note 22). [Alice Eastwood Papers, California Academy of Sciences Archive (2012), reproduced by permission

smaller number of scales, and by the general reduction in size of ["or"] all vegetative and reproductive parts.

The relationship between the members of the Taxodiaceae (**4, 11**) may now be clarified considerably. The writer [Buchholz, 1931, 1933] pointed out previously that *Sciadopitys* [the genus is monotypic, *S. verticallata;* see Table 1] stands apart from all of the others [other conifer genera], possibly by itself in a separate sub-family or family [see note 20]. Branching off from this are three sub-families [see note 21]:

Sequoioideae [not "Sequoiadeae"], including *Sequoiadendron, Athrotaxis* and *Sequoia;*
Cunninghamioideae [not "Cunninghameae"], including *Cunninghamia* and *Taiwania;*
Taxodioideae, including *Cryptomeria, Taxodium* and *Glyptostrobus*

[Fig. 5; see notes 22 and 23]. The last named genus has 4–5 cotyledons, so that all three of the genera of Taxodioideae have 3 or more cotyledons, erect seeds and several other important characters that separate them from the Cunninghamioideae ["Cunninghameae"].

Dept. of Botany
University of Illinois
Urbana, Ill. [*end of MS page 11*]

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5 Butts, Dorothy [Agnes] and Buchholz, J. T. 1940. Cotyledon numbers in conifers. *Trans. Ill.* [*Illinois State*] *Acad. Sci.* 33:58–62. [See note 19.]

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7 ——. 1907. On *Taiwania* and its affinity to other genera. *Bot. Mag. Tokyo* 21:21–28. [+1 pl.]

8 ——. 1912. *Taiwania cryptomerioides* Hay. *Icon. Pl. Formosa* II (1912):148–149. [See complete citation below.]

9 Kaeiser, Margaret. 1940. [Incomplete citation by Buchholz; see discussion in introduction and note 18 as well as complete citation below.]

10 Orr, M. Y. 1933. *Taiwania* in Burma—a new record. *Notes Roy. Bot. Gard. Edinburgh* 18:6. [*end of MS page 12*]

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12 Saxton, W. T. and J. Doyle. 1929. The ovule and gametophytes of *Athrotaxis selaginoides,* Don. *Annals of Bot.* 43:833–840.

13 Sorger, O. 1925. Die systematische Stellung von *Taiwania cryptomerioides* Hayata. *Österreichische Bot. Zeit.* 74:81–102. [*end of MS page 13*]

Notes for Buchholz's Unpublished Manuscript (1941) on *Taiwania*

(1) *Taiwania* Hayata (1906), monotypic: *T. cryptomerioides* Hayata (1906).

Synonymy (extant taxa): *T. flousiana* Gaussen (1939), *T. cryptomerioides* var. *flousiana* (Gaussen) Silba (1984), *Taiwania yunnanensis* Koidzumi (1942).

Common names: Taiwania, coffin tree, coffin-tree, Formosan redwood, Taiwan cedar, tai wan shan, Taiwanya sugi.

Fossil species: See references following, especially LePage (2009).

Distribution of genus: "China: NW Yunnan, SE Xizang (Tibet); NE Myanmar (Burma); Taiwan: Nantou District; [N] Vietnam: Lao Cai, Van Ban District. (Other reported localities in China are here considered to be based on introduced trees.)" (Farjon, 2010: pp. 954–955). For details see Farjon (2005), Chou et al. (2011), and Grimshaw (2011). For collections and localities of *Taiwania* see notes 5, 7, 9–11, 14, and 15. For cultivated specimens see notes 3, 4, and 7.

Taiwania was widely distributed in the Northern Hemisphere (Europe, Alaska, Japan, China, Siberia, etc.) from the Early Cretaceous to the Late Pliocene and "has remained almost unchanged in its morphology for over 100 Myr" (Chou et al., 2011: p. 1992 for the quote; LePage, 2009; see also Farjon, 2005, Farjon and Ortiz Garcia, 2003, Grimshaw, 2011, and Liu and Su, 1983). The present insular population (Taiwan) and mainland Asian populations (Yunnan-Myanmar and northern Vietnam) of *T. cryptomerioides* are genetically distinct and "potential refugia" (Chou et al., 2011).

Taxonomy: Chou et al. (2011), Conifers of the world (2012), Eckenwalder (2009), Farjon (2005, 2010), Fu et al. (1999b), Grey-Wilson and Cribb (2011), Grimshaw (2011), LePage (2009), and Liu and Su (1983) accept one extant species, *T. cryptomerioides.* In contrast, Earle (2011) and Li and Keng (1994) also accept *T. flousiana.* Finally, Ohashi (2009: p. 8) is equivocal "whether *Taiwania* consists of one or two species or one species with two varieties."

According to Earle (2011), *Taiwania flousiana* is "usually treated as a variety of *T. cryptomerioides,* [but] is here segregated as a species largely because the Burma-mainland China populations are ecologically distinct, have presumably been separate from the Taiwan populations for a long time, and have a sensitive conservation status." However, Liu and Su (1983: p. 77) concluded convincingly: "The morphological variations found in Taiwan plants cover those cited in the other two species [*T. flousiana* and *T. yunnanensis*]. Readily distinguished characters between these [three] species are ambiguous. Due to the isolated geographical distributions, the differentiation of local populations may be expected. This remains to be studied in the future. As far as the species rank is concerned, it is reasonable to relegate the two later proposed species to the synonyms of *Taiwania cryptomerioides*."

(2) English-born Edward Owen Orpet (1863–1956) was Superintendent of Parks, Santa Barbara, California, from 1921 to 1930. In 1921 he established Hillside Park, a small parcel (1.6 ha/4 acre) designed by stepbrothers John Charles Olmsted (1852–1920) and Frederick Law Olmsted, Jr. (1870–1957). Their father was Frederick Law Olmsted (1822–1903), the noted designer of Central Park, New York. Hillside Park was renamed Orpet Park in 1963. In 1930 Orpet retired to devote full time to his nursery business. His placard read "EO Orpet—Rare Plants, Bulbs, Cacti." A prominent horticulturist and orchidologist, Orpet introduced *Pyracantha angustifolia* (Rosaceae) and dozens of other taxa to cultivation in California and the American Southwest (Cartas, 2012; Muller and Haller, 2005: p. 6).

(3) In a 13 October 1936 letter to A. E. Rehder, Arnold Arboretum, Jamaica Plain, Massachusetts, Buchholz wrote: "In Hillside Park [now Orpet Park; see note 2], Santa Barbara, is a fine specimen of *Taiwania cryptomerioides* which has developed a fine leader and is now about 5 to 6 feet [1.5–1.8 m] high. I have a photograph of this but [it is] not so very good since the camera moved slightly ...." In his unpublished manuscript Buchholz noted that this specimen was "now [1941] about 12 feet [3.7 m] high."

On 19 October 1936 Buchholz wrote Orpet, the famed nurseryman in Santa Barbara, California (see note 2), a follow-up letter about his findings: "When I visited your nursery last April inquiring about rare conifers in cultivation [in California], you expressed the wish to be informed if I found anything especially interesting, and especially if I found *Taiwania cryptomerioides* growing anywhere aside from Hillside Park in Santa Barbara. I found the latter species *only* [emphasis added] in Golden Gate Park, San Francisco, and a much smaller specimen than the one in Santa Barbara." In his 1941 manuscript Buchholz noted that the Golden Gate specimen is "less than 2 feet [.6 m] tall" and that the Hillside Park tree "is probably the best specimen to be found in cultivation in America."

Furthermore, "another good sized example may be seen in the Huntington Botanical Garden in San Marino, California." Buchholz probably "discovered" or learned about this third specimen during his 1940 trip to California (see Schmid, 2012b). Grimshaw (2011: pp. 48–58) discusses modern plantings of *Taiwania* cultivated in North America and elsewhere.

In the wild *Taiwania cryptomerioides* is a very large tree, in fact, "the tallest [native] tree in China" (Cox and Hutchison, 2008: p. 375). The species commonly reaches heights of 60 to 70 m and rarely 75 to 80 m (Chou et al., 2011; Earle, 2011; Eckenwalder, 2009; Farjon, 2005, 2010; Fu et al., 1999b; Grimshaw, 2011; Handel-Mazzetti, 1996; Li and Keng, 1994; Liu and Su, 1983; Wilson, 1926).

(4) The San Francisco Botanical Garden (formerly Strybing Arboretum) in Golden Gate Park currently has four plantings of *Taiwania cryptomerioides.* These appreciably post-date the plant Buchholz mentions (see note 3), which "most likely ... died prior to 1958, when the garden was first inventoried" (David Kruse-Pickler, pers. comm., 21 Dec. 2011).

(5) China's seed-plant flora consists of some 30,000 species (56% or about 16,800 endemic), 3184 genera (6.9% or about 220 endemic), and about 353 families (statistics from Grey-Wilson and Cribb, 2011: p. 1). Floristic diversity is greatest in western China, which has the richest temperate flora in the world.

These are the great names involving the heyday of European-American exploration of China and the collection of its appreciable botanical riches, and also, in Rock's case, its ethnological bounties: American David Grandison Fairchild (1869–1954), Scot George Forrest (1873–1932), Austrian Heinrich Freiherr von Handel-Mazzetti (1882–1940), Irish (but Scot-born) Augustine Henry (1857–1930), English Frank Kingdon-Ward (born Francis Kingdon Ward; 1885–1958), Dutch-American Frank Nicholas Meyer (1875–1918), Austrian-American Joseph Francis Charles Rock (1884–1962), and English-American Ernest Henry Wilson (1876–1930).

Handel-Mazzetti was stranded in China by World War I and spent five years traveling and making over 13,000 collections of plants in southern China (Yunnan, Sichuan, etc.), Burma (now Myanmar), and Tibet (now Xizang Zizhiqu) (Handel-Mazzetti, 1996, an English translation of the 1927 German edition). His work is significant because his contemporaries or predecessors focused on other regions or other subjects (Schmid,

1997): Wilson barely touched Yunnan in his emphasis on areas north of the Yangtse; Rock published mainly on ethnology and little on botany, although he made extensive collections; the books of Kingdon-Ward on plant-hunting lack a taxonomic focus; Forrest never completed his intended book on his travels.

Five of the aforenoted eight classic plant explorers-collectors would collect *Taiwania cryptomerioides:* Kingdon-Ward in Burma (1938, 1939), Forrest in Yunnan (1918) and Tibet (1921, 1922), Rock in Yunnan (1932), and, most importantly, Handel-Mazzetti in Yunnan (1916), and Wilson in Taiwan (1918) (Conifers of the world, 2012; Farjon, 2005; Grimshaw, 2011; Handel-Mazzetti, 1996; Howard, 1980; Wilson, 1926).

(6) After the First Sino-Japanese War (1894–95) the Qing Dynasty of China ceded Taiwan (then known as Formosa) and associated islands (Penghu) to Japan. The Japanese occupation ended in 1945 along with World War II. The Chinese civil war (1927–50) ended with the establishment of The Peoples Republic of China on mainland Asia and the Republic of China on Taiwan.

(7) For modern references discussing the distribution, morphology, and relationships of *Taiwania cryptomerioides* see Chou et al. (2011), Conifers of the world (2012), Earle (2011), Eckenwalder (2009), Farjon (2005, 2010), Farjon and Ortiz Garcia (2003), Fu et al. (1999b), Grimshaw (2011), LePage (2009), Li and Keng (1994), Liu and Su (1983), and Ohashi (2009). Figures 3 and 4 are from, respectively, Farjon (2005) and Grimshaw (2011).

Buchholz (quote from MS p. 7) "found [it] impossible to obtain properly preserved [pickled] collections of *Taiwania* suitable for a more detailed morphological [embryological] study" and therefore had to rely on "dried herbarium specimens" supplied "through the kindness of Miss Alice Eastwood" (see notes 13 and 14).

Liu and Su (1983: p. 7) stated that there had been less morphological, palynological, and embryological study of *Taiwania* compared to "studies [of] most other genera of Taxodiaceae, [which] are far more comprehensive." Liu and Su (1983) published 42 pages on the "microsporangiate strobilus and microsporegenesis," "palynological characters and male gametophyte," "megasporangiate strobilus and megasporogenesis," "female gametophyte and fertilization," and "embryogeny and seed morphology" (these are the titles of the five sections on pp. 34–75). Liu and Su (1983) analyzed 190 characters (155 qualitative, 35 quantitative) by numerical taxonomy to evaluate the overall phenetic affinities between *Taiwania* and other taxodiaceous genera. (See also Farjon and Ortiz Garcia (2003) for cone and ovule development in *Taiwania.*)

Grimshaw's (2011) detailed paper on *Taiwania* has a dendrological and taxonomic focus and thus lacks information on palynology and embryology. Schmid (2012a) praised Grimshaw (2011) as follows: "A Google [search] for *Taiwania cryptomerioides* serendipitously led to [*International Dendrology Society yearbook 2010*] ... [and] John Grimshaw's lengthy, scholarly, and fascinating ... article entitled 'Tree of the year: *Taiwania cryptomerioides'* (pp. 24–57), also known as Formosan redwood, Taiwan cedar, coffin tree, and other monikers. Grimshaw's captivating 34-page account of this monotypic genus, which occurs in Vietnam, Myanmar (Burma), China, Tibet, and Taiwan (Formosa), is easily the best and most comprehensive description of the species I have seen. It is divided into the following sections: preface ('foreword'); introduction; phylogeny and systematics; taxonomic description; distribution and genetic diversity; ecology; forestry and utilization; conservation; conservation in cultivation; introduction to cultivation; propagation; growing *Taiwania; Taiwania* around the world (Europe; North America; Australasia); references (3 pages). Embellishing the text are 18 photos, 15 in color, and 3 historical ones in B&W [black-and-white]. On initially perusing the article I thought the first B&W photo of Taiwanese workers in 1912 hewing a log was one of a coffin being lowered into eternity. A color photo shows Bunzō Hayata's (1874–1934; see [Ohashi, 2009]) type specimen of *T. cryptomerioides* Hayata (1906) that had been collected on Mount Morrison … [the name non-natives often use for Yu-Shan] by Nariaki Konishi in 1904. The two other B&W figures are 1918 photos by E. O. Wilson (1876–1930): a habitat photo in Taiwan and a tree of this species that Hayata had planted in 1907 in Chitou, Taiwan" (Fig. 4A is a recent color photo of Hayata's Chitou planting).

(8) The Japanese botanist Bunzō Hayata (1874–1934) made important contributions to the flora of Taiwan. He "was the founding father of the study of the flora of Taiwan. From 1900 to 1921 ... he named about 1600 new taxa of vascular plants from Taiwan" fide Ohashi (2009: p. 1). His seminal biography has 11 photos of Hayata, 29 of conifers. See also Grimshaw (2011).

(9) On 15 September 2012 the Brahms database Conifers of the world (2012), which is diligently maintained by Aljos Farjon, listed for *Taiwania* two collections (6 specimen sheets) that Handel-Mazzetti had made in northwestern Yunnan in June and August 1916 (respectively, *Handel-Mazzetti 8915, 9664*). (My "collections" and "specimen sheets" are, respectively, "records" and "specimens" in the parlance of the database.) The database noted the following: *8915:* "branch with juvenile leaves"; *9664:* "branch with

mature leaves and seed cones." Wilson (1926: p. 58) regarded "Handel-Mazzetti's finding of *Taiwania* in northwestern Yunnan [as] one of the most interesting discoveries in recent work on the Chinese flora." Sorger (see note 11) studied *9664*.

(10) Conifers of the world (2012) on 15 September 2012 listed for *Taiwania* seven collections (24 specimen sheets) that Wilson had made in Taiwan in 1918. Four collections are from 29 January (*9690*) or 4 or 9 February (*9836, 9837, 9909*), whereas two collections are from 2 November (*10,853, 10,854*). *Wilson 8644* dated "1900-00-00" is an error; Wilson was in Taiwan only in 1918 (Howard 1980). The database noted the following: *9690:* "small tree with juvenile foliage"; *10,853:* "2 sheets at K, one with branchlet with very small cones up to 11 mm long"; *10,854:* "some seed cones large, 17–18 mm long." Buchholz studied *10,853* (for elaboration see note 14).

(11) Austrian Otto Sorger was born on 11 June 1900 (death date unknown, but probably post-1977) in Grafenschlag, Lower Austria (Archiv der Universität Wien, 2012). His doctoral dissertation, "Die systematische Stellung von *Taiwania cryptomerioides* Hayata" (1924, typescript 29 pp., 3 pls.) at the University of Vienna (Universität Wien, Bibliothek, 2012), was published under the same title in 1925 in a detailed, 22-page paper in *Österreichische botanische Zeitschrift.* Sorger (1925: p. 100) acknowledged his great indebtedness to his "dear teacher" ("verehrten Lehrer"), the Austrian macro-systematist Richard Wettstein (1863–1931). Sorger studied the wood and leaf anatomy and seed-cone morphology of *Taiwania* (Fig. 3I–J, 4D) from a specimen collected in 1916 in Yunnan, China, by Austrian explorer Handel-Mazzetti (undoubtedly his *9664* collection; see notes 5 and 9), and also the pollen-cone morphology from a specimens collected in 1918 in Taiwan by English-American Wilson (see notes 5, 7, and 10).

Sorger became a high-school teacher and coauthored two multi-edition textbooks for high-school students: *Lehre vom menschlichen Körper* (7 editions 1967–77) by Gertrud Soos and Sorger, and *Pflanzenkunde für die unteren Klassen der allgemeinbildenden höheren Schulen* (e.g., 4th edition 1970) by Johanna Enslein, Ingrid Brecher, Soos, and Sorger. Otto Sorger was married to Friederike Sorger, née Schmied (28 Oct. 1914–2001), "an Austrian botanist [who] collected ca. 18,000 specimens during 29 visits to Turkey between 1962 and 1988" (Baytop, 2010: p. 190).

(12) Buchholz does not give a reference for Kew systematist William Jackson Hooker (1785–1865). However, it must be his *Icones plantarum* (1843, vol. 2, n.s.) in which he figures (but does not describe) 2 pollen sacs per sporophyll in three of the four species of *Athrotaxis* (as *"Arthrotaxis"*) that he recognized: *A. cupressoides, A. tetragona* (= *Microcachrys tetragona* in Podocarpaceae fide Earle, 2011, Eckenwalder, 2009, and Farjon, 2005, 2010), and *A. selaginoides,* respectively, on plates 559, 560, and 574; plate 573 is of an incomplete specimen of *A.* ×*laxifolia*. Farjon (2005, 2010) notes for the genus "2–4" pollen sacs, with "2" in both *A.* ×*laxifolia* and *A. selaginoides* and "(2–)3–4" in *A. cupressoides*. Eckenwalder (2009) notes for the genus just 2 pollen sacs.

(13) California taxonomist Alice Eastwood (1859–1953), Curator of Botany and Director of the Herbarium at the California Academy of Sciences (1893–1948), was a specialist in the plants of western North America. After the 1906 San Francisco earthquake she heroically saved 1497 type specimens from the fire destroying the herbarium. Eastwood retired on 19 January 1949 on her 90th birthday. See Daniel (2008) and Schwartz (1997).

(14) The herbarium of the California Academy of Sciences (CAS) has three sheets of *Taiwania* collected by Wilson in Taiwan in 1918, none of which bear annotations by Eastwood: *9690* from 29 January, *9836* from 4 February, and a packet of material labeled "Taiwania seeds collected by Wilson in Formosa 1918, No. 10853." The last is mounted on a sheet of *Taiwania* with a 1914 collection made by "Drs. Fred & Charlotte Baker" [s.n.] and labeled "Mt. Ari [Ali Shan], Formosa. 7600 ft. [2315 m]. Nov. 26/14" (Rebecca Peters, pers. comm., 12 Dec. 2011, with supplemental observations by R. Schmid, 21 Dec. 2011). I surmise that there was a paper shortage at the end of World War I and that it was expedient to glue the packet onto an old sheet of *Taiwania.* Incidentally, Conifers of the world (2012) on 15 September 2012 did not list this 1914 collection. A Google search for "'fred baker' 'charlotte baker'" etc. revealed considerable information on these doctors (respectively, 1854–1937, 1855–1936), who collected extensively in Formosa, the Philippines, and elsewhere in Asia, and who settled in San Diego after Charlotte developed malaria.

Eastwood thus supplied Buchholz with material from *Wilson 10,853* collected in Taiwan on 2 November 1918 (see note 10). The "Oct. 1918" date in Buchholz's manuscript is an error.

(15) Conifers of the world (2012) on 15 September 2012 did not list this 1906 collection.

(16) Buchholz and Old (1933: p. 42) proposed the

term "calyptroperiblem" for the distinctive embryonic root tip of gymnosperms consisting of combined meristems for root cap (calyptrogen) and appreciable cortex (periblem).

(17) Buchholz's conclusions made in 1941 correspond to those of Farjon and Ortiz Garcia (2003: pp. 8, 10, and 14 for the following quotes). They concluded that *"Cunninghamia* shares many characters with *Taiwania* and to a lesser extent with *Athrotaxis"* and that the first "two genera represent basal, and possibly related, clades in the phylogeny of Cupressaceae" s.l. *Taiwania* is the endpoint in the "final reduction of the ovuliferous scale." Liu and Su (1983: p. 5) likewise concluded: *Taiwania* "represents the ultimate reduction of sporophylls and the total fusion of bract with the sterile component of seed scale complex (ovuliferous scale)." Finally, Chou et al. (2011: p. 1997) used molecular clock modeling with fossil calibrations to set "the earliest common ancestor of both *Taiwania* and *Cunninghamia* ... at the Early Cretaceous: 122.5 ± 7.65 Ma."

(18) Margaret Kaeiser (1912–73), B.S. 1934, M.S. 1936, University of Oklahoma, Ph.D. 1940, University of Illinois, did her doctoral dissertation under Buchholz (Kaeiser, 1940) and from 1947 to 1973 was a professor of botany and forestry in the Department of Botany, Southern Illinois University, Carbondale (Southern Illinois University Carbondale, 2006). Buchholz's famous female students were Kaeiser and Netta Elizabeth Gray (1913–70), M.A. 1941, University of Illinois (never a Ph.D.). Gray studied *Podocarpus* (see Schmid, 2012b).

(19) Dorothy Agnes Butts (1905–76, or later), B.A. summa cum laude 1928, M.A. 1940, University of Illinois, did her master's dissertation under Buchholz (Butts, 1940) and taught botany at various institutions in Illinois, especially in Rockford (Reflections ..., 2010).

(20) Buchholz's "separate sub-family or family" for the monotypic genus *Sciadopitys* would be, respectively, *(1)* Sciadopityoideae in the traditional Taxodiaceae (now Cupressaceae) or *(2)* the segregate Sciadopityaceae. The segregate family is now generally recognized (Earle, 2011; Eckenwalder, 2009; Farjon, 2005, 2010, Table 1; Farjon and Ortiz Garcia, 2003; Fu et al., 1999a; but not Conifers of the world, 2012). In contrast, Buchholz (1946, 1948), Liu and Su (1983), and Pilger (1926) favored Sciadopityoideae in Taxodiaceae. *"Sciadopitys* [is] in a close phylogenetic relationship with Cupressaceae s.l." according to Farjon and Ortiz Garcia (2003: p. 14).

(21) Buchholz's "Sequoiadeae" and "Cunninghameae" are tribes, not subfamilies.

(22) Buchholz's unpublished manuscript is not illustrated. On 21 December 2011 when I checked the library archives of the California Academy of Sciences for Eastwood-Buchholz correspondence (see note 13), I found a diagram titled "Phylogeny of conifers. J. T. Buchholz — 1941" that was inserted after a letter dated 16 June 1941. None of the six archived letters from Buchholz to Eastwood mention the phylogenetic diagram. However, it nicely ties in with the last paragraph of Buchholz's manuscript. The diagram was never published (see note 24 for a likely unpublished precursor) and thus is reproduced here as Fig. 5, courtesy of the archives.

(23) A modern, worldwide classification of conifers (Farjon, 2005, 2010) recognizes 8 families, 9 subfamilies, and 70 genera [see Table 1, including for Earle (2011) and Eckenwalder (2009)].

Buchholz's (1946, 1948) last classification of conifers recognized 7 families, 10 subfamilies, and 50 genera and is outlined below, with placement of the 12 genera mentioned in his unpublished manuscript on *Taiwania* (see also Table 1):

- Pinaceae: 9 genera, including *Picea, Abies*
- Araucariaceae: 2 genera
- Taxodiaceae: 9 genera
  - Sciadopityoideae: *Sciadopitys*
  - Sequoioideae (as "Sequoideae"): *Sequoiadendron, Athrotaxis, Sequoia*
  - Taxodioideae
    - Sec. I, *Cunninghamia, Taiwania*
    - Sec. II, *Cryptomeria, Glyptostrobus, Taxodium*
- Cupressaceae: 18 genera
  - Cupressoideae: 2 genera, including *Chamaecyparis*
  - Callitroideae: 5 genera
  - Thujoideae: 9 genera
  - Juniperoideae: 2 genera
- Podocarpaceae: 7 genera
  - Pherosphaeroideae: 1 genus
  - Podocarpoideae: 5 genera
  - Phyllocladoideae: 1 genus
- Cephalotaxaceae: 2 genera
- Taxaceae: 3 genera

Earlier, Buchholz (1933: p. 112 for the quotations; see also note 24) had recognized in the Coniferales two suborders with 10 families (the *-marked were not accepted by Buchholz, 1946, 1948) and 46 genera:

(A) "Phanerostrobilares," with mostly monoecious species having "well developed and usually conspicuous seed cones" that are "nearly all woody"

(fleshy only in *Juniperus*): 34 genera
Pinaceae: 9 genera
Araucariaceae: 2 genera
*Sciadopityaceae (as "Sciadopitaceae"): 1 genus
Taxodiaceae: 7 genera, including *Taiwania* and *Sequoia* s.l. with *Sequoiadendron*
Cupressaceae: 15 genera in 4 subfamilies as above

(B) "Aphanostrobilares," with mostly dioecious species having chiefly "small or poorly developed cones, or the cones ... reduced to only a few scales and usually the cone or the ovule ... fleshy": 12 genera
*Saxegothaeaceae: 2 genera
Podocarpaceae: 4 genera
*Pherosphaeraceae: 1 genus
Cephalotaceae: 2 genera
Taxaceae: 3 genera

Even earlier, Pilger (1926), who is also cited in Buchholz's *Taiwania* manuscript, had recognized 7 conifer families, with 47 genera: Taxaceae (3 genera), Podocarpaceae (7 genera, including Pherosphaeraceae, Saxegothaeaceae), Araucariaceae (2 genera), Cephalotaxaceae (2 genera), Pinaceae (9 genera), Taxodiaceae (8 genera, including Sciadopityoideae with *Sciadopitys* and Taxodioideae with *Sequoia* s.l. (including *Sequoiadendron*), *Taxodium, Glyptostrobus, Cryptomeria, Athrotaxis, Taiwania,* and *Cunninghamia*), and Cupressaceae (16 genera). Buchholz (1933) accepted the segregates Pherosphaeraceae, Saxegothaeaceae, and Sciadopityaceae on the basis of embryological and taxonomic grounds.

(24) Buchholz's publication entitled "The classification of Coniferales" was published in June 1933 in the *Transactions of the Illinois State Academy of Science.* This was a one-and-a-half page abstract of a talk presented at the 25th annual meeting of the Academy held in May 1932. Two of Buchholz's letters, now available in the University of Illinois Archives (2012), clarify the 1933 abstract, which curiously Buchholz alludes to but does not cite in his 1941 unpublished manuscript:

(1) Buchholz commented in a 26 September 1936 letter to A. F. Blakeslee, Cold Spring Harbor, New York: "Lastly, I have wondered whether I might not plan to offer a paper summarizing the work on the taxonomy, morphology, and embryology of conifers as it affects the classification, the relationship of families, etc. This is a thing I worked on for many yeas, and have presented in part before [an] Illinois Academy meeting several years ago, but the diagram of the family tree was omitted from the brief abstract which was recorded then. Now I have firm convictions and a better background of first hand information."

(2) On 15 March 1938 D. A. Johansen, Stanford, California, requested a reprint of Buchholz's 1933 paper on conifer classification: "I am now in the middle of the Coniferales portion of a new text on *Plant Microtechnique* [Johansen, 1940], and wish to follow your scheme of classifying the families [see note 23)." Buchholz responded on 23 March 1938:

> I have your letter ... regarding a reprint which I am sending. This particular one catches Chamberlain (see note 25) and myself in a kind of jam. I had it in manuscript when I first showed the scheme [the classification outline for conifers] to Dr. Chamberlain as he was writing his book [*Gymnosperms: Structure and evolution,* 1935]. He was enthusiastic about my scheme so I sent it in for publication; later he asked to see it and then refused to accept the rather ambiguous long names Phanerostrobilares and Aphanostrobilares [see note 23], so I suggested to him that I would just as soon call these groups Pinares and Taxares (these endings 'ares' being those proposed by British botanists at [the 1930] Cambridge Congress for sub-orders, but not formally accepted). He was so enthusiastic about these substitute names that he went ahead and used them [see Chamberlain (1935: pp. 229–230)], but I found it too late to revise the manuscript which was then in print but not issued [as noted above, this was in June 1933]. However, now I've committed myself to these group names and cannot change, even if I want to do so. I suppose I can use the names Pinares and Taxares as of Chamberlain, however, and that is what I would prefer to have you do on his authority [see Johansen (1940: p. 425), who cites Buchholz (1933) and Chamberlain (1935) for Pinares and Taxares]. Otherwise I am more convinced than ever that the subdivisions of this classifications [*sic*] into families, etc. is about right.
>
> Unfortunately, I had to cut down a paper of 4–5 pages to less than two pages and left out the more important discussional portion [and, as mentioned above, the phylogenetic diagram]. At that time, during the depression economy, the Illinois Academy could print only abstracts.

Consequently, it is clear that Buchholz's 1941 diagram of the "Phylogeny of conifers" (Fig. 5; see note 22) is a direct descendent of a version prepared in 1932 for a talk presented in May 1932 at the Illinois State Academy of Science but not published in its transactions in 1933 (Buchholz, 1933).

(25) Buchholz was a product of the famous labs of John Merle Coulter (1851–1928) and Charles Joseph

Table 1. Classification of conifers by Farjon (2005, 2010), with nomenclature and taxonomic authorities for genera mentioned in text[a]

Araucariaceae: 3 genera (1 monotypic), 37 species
Cephalotaxaceae: 1 genus, 8 species
Cupressaceae: 30 genera (17 monotypic), 135 species
  Cunninghamioideae: 1 genus, 2 species
    Cunninghamia R. Br.: 2 species
  Taiwanioideae: 1 genus (monotypic), 1 species
    Taiwania Hayata: 1 species: *T. cryptomerioides* Hayata (including *T. flousiana*—see note 1)
  Athrotaxoideae: 1 genus, 3 species
    Athrotaxis D. Don: 3 species: *A. cupressoides* D. Don, *A.* ×*laxifolia* Hook., *A. selaginoides* D. Don
  Sequoioideae: 3 genera (3 monotypic), 3 species
    Sequoia Endl.: 1 species: *S. sempervirens* (D. Don) Endl.
    Sequoiadendron J. Buchholz: 1 species: *S. giganteum* (Lindl.) J. Buchholz
  Taxodioideae: 3 genera (2 monotypic), 4 species
    Cryptomeria D. Don: 1 species: *C. japonica* (Thunb. *ex* L. f.) D. Don
    Glyptostrobus Endl.: 1 species: *G. pensilis* (Staunton *ex* D. Don) K. Koch [as *"G. heterophylla"* (Brong.) Endl.]
    Taxodium Rich.: 2 species
  Cupressoideae: 21 genera (11 monotypic), 122 species
    Chamaecyparis Spach: 5 species
    Juniperus L.: 53 species
Phyllocladaceae: 1 genus, 4 species
Pinaceae: 11 genera (3 monotypic), 230 (not "231") species
  Pinoideae: 3 genera (1 monotypic), 152 species
    Picea A. Dietr.: 38 species
  Laricoideae: 2 genera, 15 species
  Abietoideae: 6 genera (2 monotypic), 63 (not "64") species
    Abies Mill.: 46 (not "47") species
Podocarpaceae: 18 genera (6 monotypic), 174 species
  Microcachrys Hook. f.: 1 species: *M. tetragona* (Hook.) Hook. f. (= *Athrotaxis tetragona* Hook.)
  Podocarpus L'Hér. *ex* Pers.: 97 species
Sciadopityaceae: 1 genus (monotypic), 1 species
  Sciadopitys Siebold & Zucc.: 1 species: *S. verticillata* (Thunb.) Siebold & Zucc.
Taxaceae: 5 genera (2 monotypic), 24 species
Total: 8 families, 9 subfamilies, 70 genera (30 monotypic), 614 (not "615") species

[a]Modern, worldwide classification of conifers after Farjon (2010: pp. 33-53; see also Farjon, 2005 and notes 17, 20, and 23). Eckenwalder (2009) accepts 6 families (with Cephalotaxaceae included in Taxaceae, and Phyllocladaceae included in Podocarpaceae), 67 genera (28 monotypic), and 546 species. See tabular comparison in Schmid (2010), who gives corrected numbers for species. Earle (2011) accepts 7 families (with Phyllocladaceae included in Podocarpaceae), 68 genera (29 monotypic), and 616 species. For Buchholz's (1933, 1946, 1948) classifications and phylogeny of conifers see, respectively, notes 23 and 24 and Fig. 5.

Chamberlain (1863–1943) at the University of Chicago (Buchholz, 1943; Cowles, 1929). Morphological research of these labs focused on the embryology of angiosperms and especially gymnosperms; Buchholz's doctoral research on pine embryology (Ph.D. 1917), published as Buchholz (1918), was done under Chamberlain's direction.

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"台灣杉屬的分布、型態與分類"—一份來自John Theodore Buchholz（1888–1951）寫於1941年的未發表手稿

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摘要：本文章發表了一篇出自於John Theodore Buchholz (1888–1951) 的未發表手稿，這篇未發表的手稿最近才被發現，很可能寫於1941年。除了發表原有手稿外，本文也提供了25個關於此手稿的額外註記，以及一張繪於1941年未曾發表的"松柏類植物譜系圖 J. T. Buchholz — 1941"。這篇未發表的手稿及譜系圖，對後世研究這位聞名的植物學家將有極大的助益。

關鍵詞：Buchholz、松柏類植物譜系、松柏類植物、柏科、植物胚胎學、裸子植物、台灣、台灣杉。