A REVISION OF *PAXISTIMA* (CELASTRACEAE)

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ABSTRACT

Paxistima Raf. (Celastraceae), a North American genus of shrubs and subshrubs, has a confusing nomenclatural history. The genus name has four spellings in the literature. Although the name of the eastern species, *P. canbyi* Gray, is unequivocal, two specific epithets have been in use for the western species. In 1943, Wheeler concluded that *Paxistima* was the correct spelling of the genus, and that *myrtifolia* was the correct epithet for the western species. Wheeler combined several taxa into *Paxistima myrtifolia* (Nutt.) Wheeler, and indicated the possible existence of an uninvestigated (Mexican) taxon. After our review of the literature, the name of the western species is determined to be *P. myrsinites* (Pursh) Raf. Based on our numerical phenetic analyses, two species of *Paxistima*, *P. canbyi* and *P. myrsinites*, are recognized. We have clarified the holotypification of *P. canbyi*, and have selected a lectotype for *P. myrsinites*. A new subspecies, *Paxistima myrsinites* subsp. *mexicana* Navaro and Blackwell, is described herein.

INTRODUCTION

Paxistima Raf. is a small genus of Celastraceae interpreted as having from two to six species. A taxonomic synopsis of the genus was published in 1943 (Wheeler). The present study revises and augments Wheeler's nomenclatural and taxonomic treatment.

Paxistima is a North American genus of small evergreen shrubs or subshrubs with opposite leaves and small, perfect, 4-merous flowers on axillary pedicels. Within the Celastraceae *Paxistima* is the only capsule-fruited, 4-merous, 2-loculed genus in which the ovary is joined with the disk rather than sitting upon it.

The nomenclature of *Paxistima* has a confused past. This is especially so in regard to the type, *P. myrsinites*, which was first published by Pursh (1814) as "*Ilex? myrsinites*" based on specimens from the Lewis and Clark expedition of 1805-1806. Nuttall made the transfer of *Ilex myrsinites* to *Myginda* in 1818, as *Myginda myrtifolia*. As suggested by Wheeler (1943), Nuttall may have felt that "*myrtifolia*" was less similar to an existing epithet ("*myrsinoides*" HBK) within *Myginda* than was "*myrsinites*," and hence the superfluous alteration of the epithet. Regardless, Rafinesque (1818) in his "Review of Pursh's Flora of North America" wrote that he called *Ilex myrsinites*, "*Pachistima*," though he did not reference where he used the name. In 1819(a), in a review of Nuttall's work, Rafinesque stated

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"The *Ilex myrsinites* of Pursh, is now called *Myginda myrtifolia* by N., but it belongs to neither genus; we deem it quite a peculiar genus, and call it *Pachistima*." Again in 1819(b) Rafinesque wrote that he placed *Ilex myrsinites* Pursh and *Myginda myrtifolia* Nuttall into a new genus which he called *Pachistima*. In none of his three early publications dealing with "*Pachistima*" (1818; 1819a,b) did Rafinesque include a description of his new genus, and so it has been considered (Wheeler 1943; Uttal 1986) to be a *nomen nudum*. It was approximately 20 years later when Rafinesque (1838) actually published the genus with a description; then he spelled it *Paxistima* (not *Pachistima*), and only then did he formally make the nomenclatural combination with *myrsinites*.

Also in 1838, Torrey and Gray (*A Flora of North America*) described the genus *Oreophila*, ascribing credit to Nuttall and transferring *Myginda myrtifolia* Nutt. (based on *Ilex myrsinites* Pursh) to *Oreophila*, as *O. myrtifolia*. However, the name *Oreophila* Nutt. ex T. & G. (Celastraceae) was preoccupied by *Oreophila* D. Don (1833), a genus in the Compositae. In 1840 Endlicher (in *Genera Plantarum*) recognized the genus *Oreophila* in the sense of Torrey and Gray (giving, inexplicably, sole credit to Nuttall); however, in his 1841 supplement, Endlicher reduced *Oreophila myrtifolia* to the synonymy of "Pachystima" (as spelled by Endlicher, not by Rafinesque). Meisner (1843) published an additional permutation of the spelling of the name *Pachistima*, as "*Pachystigma*." Since then, no new genera, generic synonyms, or additional spellings of the generic name have been published, although disagreement as to the generic spelling, as well as to which specific epithet to employ for the type species, has continued.

In 1878 Watson noted Rafinesque's 1818 publication in which Rafinesque used the spelling *Pachistima*. Watson also listed the 1838 publication, *Sylva Telluriana*, in which it was considered that Rafinesque validated the generic name but spelled it *Paxistima*. Watson, however, used the spelling *Pachystima*. In 1906 Piper employed the spelling *Pachistima* but referenced the wrong publication, *Flora Telluriana* instead of *Sylva Telluriana*. It was Wheeler's (1943) finding of the reference to *Sylva Telluriana* (Rafinesque, 1838) in Watson's (1878) work which led him to consider the correct spelling for the genus to be *Paxistima*.

As indicated, in his 1838 publication Rafinesque finally made the combination "*Paxistima myrsinites*." Rafinesque stated that he originally made the connection of the epithet *myrsinites* with *Paxistima* (or *Pachistima*) in 1817, but there is no evidence of this, and no reference cited. Regardless, Wheeler (1943) asserted, because Pursh provisionally published his name *Ilex? myrsinites*, i.e. with a question mark, that the original specific epithet, *myrsinites*, should not be accepted but rather that the epithet

should be *myrtifolia* based on Nuttall's *Myginda myrtifolia*. Consequently, Wheeler employed the new combination *Paxistima myrtifolia* (Nutt.) Wheeler.

In addition to the original species, which we are calling *Paxistima myrsinites* (Pursh) Raf., four other species have been described. In 1873 Asa Gray published a new species endemic to limited areas of the eastern United States, "*Pachystima*" *canbyi*. This was based on plants collected from Giles County, Virginia in 1869 by William Canby, although originally discovered by him in 1868 (1858?, cf. Canby in Gray, 1873). *Paxistima canbyi* Gray continues to be recognized as a species, as does *P. myrsinites*.

In 1904 Edith Farr published a new species, "*Pachystima*" *macrophylla*, discovered in the Selkirk Mountains of British Columbia. In 1906 she published two additional species, *P. krautteri*, found in Siskiyou County, California and *P. schaefferi*, also found in the Selkirk Mountains. As for other taxa, two varieties of *Myginda myrtifolia* Nutt. were described by Hooker in 1840: Variety "alpha" *minor* corresponds with the putative type of *Ilex? myrsinites* (cf. Wheeler 1943); Wheeler believed that variety "beta" *major* corresponds with a second specimen from the Lewis and Clark expedition. Wheeler combined all of Farr's species and both of Hooker's varieties into "*Paxistima myrtifolia*," which he referred to as "a widespread and polymorphic species of the western United States and Canada." We agree with Wheeler's disposition of taxa considered synonyms; however, our interpretation of the nomenclature of the original species is different. We present in the Systematic Treatment, under *Orthography and Nomenclature*, the reasons that we consider *Paxistima myrsinites* to be the correct name.

In 1923 Standley made reference to a possible additional species of *Paxistima* growing in Mexico. He had seen only a single specimen but considered that it was indeed different from previously described species. Apparently, insufficient material was available to allow Wheeler (1943) to make an adequate determination of the putative Mexican taxon, although he alluded to its possible existence. A number of Mexican specimens have now accumulated in various herbaria in the United States and Mexico upon which a decision may be made as to the recognition of another taxon within *Paxistima*; this has been one focus of the present investigation.

MATERIALS AND METHODS

Approximately 1640 dried specimens of *Paxistima* were examined during this study. Specimens, including any types, were studied from the following herbaria (abbreviations after Holmgren, Keuken and Schofield 1981): A, ANSM, ARIZ, ASU, BHO, CAS, CM, DS, GH, IND, JEPS, KE, KNK, KY, LL, MSC, MU, MUHW, NCSC, NCU, ODU, OS, PH,

POM, RSA, TENN, TEX, UC, UNL, UNM, US, UT, WTU, WVA. Additionally, photographs of type specimens were made available during this study by the Academy of Natural Sciences of Philadelphia and by the Royal Botanical Gardens, Kew, England. From specimens studied, 140 were selected to represent the range of morphological variation within the genus, and a list of character state variation for 15 characters (those demonstrably variable among potential taxa) was established (Table 1) by careful comparison of these specimens. Each specimen was subsequently scored for each character, and numerical analyses were then performed using Statistical Analysis System (SAS) programs. Within SAS (version 5, 1985), both PRINCOMP, i.e. Principal Components Analysis (PCA) procedure, and FASTCLUS (which uses cluster seeding methodology, cf. Anderberg 1973) were employed, sequentially, in phenetic analysis to aid in the determination of the number and rank of the taxa which should be recognized. The linear composite variables (eigenvectors) which were outputted from PRINCOMP were inputted directly into FASTCLUS since, in contrast to at least some variables in the raw data, these eigenvectors (principal components) are uncorrelated with each other (SAS Institute 1985). The cubic clustering criterion (score indicative of optimal number of groupings, outputted from FASTCLUS) is most valid on large data sets (more than 100 OTU'S) in which uncorrelated variables are entered into the program. Keys, descriptions, distributional information, and complete synonomies are provided for taxa recognized. All specimens examined in the study are annotated. A card file containing the herbarium label information for each specimen is maintained in the Miami University Herbarium (MU).

NUMERICAL ANALYSIS AND DISCUSSION OF TAXA

As indicated, 15 characters (Table 1) were found to vary among the putative taxa of *Paxistima*. A substantial portion of this phenetic variation between taxa was extracted from the data set (based on the 15 characters) by principal components analysis (PRINCOMP procedure of SAS). The values (eigenvalues) of the first three principal components (first three eigenvectors) account for 57.8% of the total variance in the specimens (Table 2). Table 3 shows the first three components by character and the amount of variance. A scatter plot of OTUs (specimens) projected upon principal component one versus principal component two provides the greatest separation between taxa (Fig. 1); plots of other pairings of the first three components do not as clearly delineate the taxa. The character loadings of component one indicate that the characters primarily responsible for the variation (separation) observed in the taxa are blade length, blade

TABLE 1. Fifteen vegetative and floral characters used in Principal Components Analysis of *Paxistima*.

1. Adventitious roots: present/absent
2. Blade length
3. Blade width
4. Blade length from apex to widest point
5. Length of blade toothed
6. Petiole length
7. Blade teeth: pointed/rounded
8. Blade secondary veins below: evident/indistinct
9. Number of leaf pairs per unit length
10. Blade margin: revolute/not or subrevolute
11. Blade apical angle
12. Flowers: average number per nodal inflorescence
13. Length of central inflorescence axis
14. Calyx lobe length
15. Calyx lobe width

TABLE 2. Cumulative variance accounted for by the first eight principal components.

Principal component 1	0.371551
Principal component 2	0.486881
Principal component 3	0.577820
Principal component 4	0.651571
Principal component 5	0.718813
Principal component 6	0.772390
Principal component 7	0.822138
Principal component 8	0.862849

TABLE 3. The first three principal components (eigenvectors) and the amount of variance in each character.

	Eigenvectors		
Characters	1	2	3
1	0.198363	0.503841	0.048926
2	0.347826	0.301759	0.148375
3	0.384297	0.025179	0.014257
4	0.336087	0.212749	0.134065
5	0.360205	0.220944	0.079408
6	0.216563	0.001895	0.188342
7	0.261845	0.074394	0.043714
8	0.227593	0.170500	0.178999
9	0.317034	0.118163	0.140525
10	0.188620	0.249411	0.038666
11	0.196223	0.044555	0.176109
12	0.110797	0.173056	0.621414
13	0.005623	0.426972	0.506604
14	0.215398	0.284063	0.348118
15	0.220742	0.393276	0.255808

width, length of blade to its widest point, length of blade toothed and the number of leaf-pairs per cm per branch (see Table 1 and Table 3). In the second principal component, the presence/absence of adventitious roots and the length of the central inflorescence axis are most important.

Three more or less distinct groups can be recognized in the ordination produced by principal components analysis (Fig 1): one corresponds to *Paxistima canbyi*, the taxon endemic to areas of the central Appalachian Mountains and its foothills; another corresponds to *P. myrsinites*, a species widespread throughout the Rocky Mountains; a third is circumscribed by specimens, not previously studied together, collected in mountainous areas of northeastern Mexico. The range of these Mexican specimens is not contiguous with the range of the Rocky Mountain taxon. Although geographically disjunct, there is, however, some intergradation in morphology, and consequently overlap in the ordination, between specimens of *P. myrsinites* collected in the United States and the Mexican specimens. Therefore, we are designating the Mexican populations as a subspecies of *P. myrsinites* (following the concept of Du Rietz 1930), rather than recognizing them as distinct species. The Mexican populations constitute a significant geographic facies of *P. myrsinites*, and consequently subspecies rather than varietal rank seems appropriate (see Du Rietz). It is interesting that a (lesser) tendency toward intergradation also occurs between the Mexican populations and *P. canbyi*; possible interpretations of this observation will be discussed under Distribution and Geofloristic History.

The FASTCLUS program of SAS provided further insight into group structure within the genus *Paxistima*. FASTCLUS is a disjoint clustering (but non-tree producing) procedure which employs nearest centroid sorting, i.e. cluster seeding, techniques (Anderberg 1973); preassignment of number of groups is requisite to the procedure. We ran this procedure for one, two, three and six groups respectively — constituting all putative divisions previously recognized within *Paxistima*. The principal components analysis demonstrated that no more than two taxa, i.e. *P. canbyi* and *P. myrsinites*, are clearly distinct at the species level, although three groupings may be discerned from the analysis. When the principal components were entered into FASTCLUS, the most favorable clustering score (cubic clustering criterion value), indicative of the optimum number of clusters, suggested the existence of three groups as well. Hence, results of the FASTCLUS procedure support the recognition of two subspecies (*myrsinites* and *mexicana*) within *P. myrsinites*, as well as the existence of *P. canbyi*. Our delimitation of three taxa of *Paxistima* — *P. canbyi*, *P. myrsinites* subspecies *myrsinites* and *P. myrsinites* subspecies *mexicana* — is thus

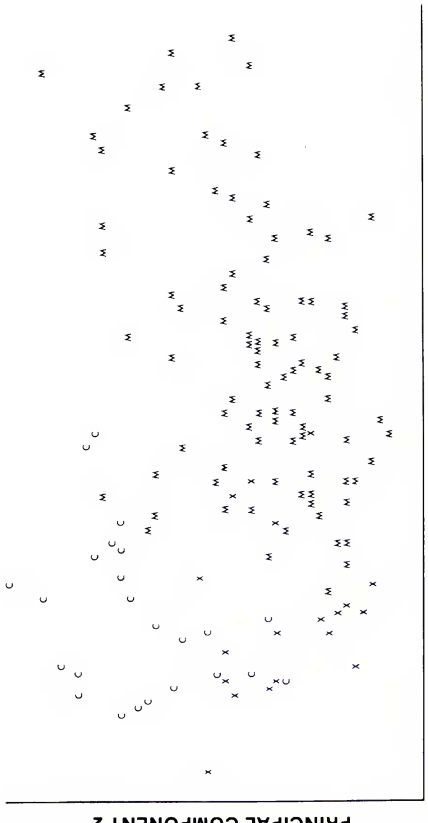

FIG. 1. Bivariate plot of first two principal components in morphological analysis of *Paxistima*. M = *P. Myrsinites* subsp. *myrsinites*, X = *P. myrtinites* subsp. *mexicana*, C = *P. canbyi*.

substantiated by the numerical phenetic analyses performed, i.e., when the results of both PRINCOMP and FASTCLUS are considered in consort.

If one examines the numerical data, the numerical analysis, the keys to taxa, and the descriptions, it will be apparent that all three taxa of *Paxistima* differ only by a number of seemingly minor characters, with overlapping character states. Although obviously debatable, if taken collectively, and considered in context of the disjunct nature of major super-groups of populations of *Paxistima*, we believe that the data (as analysed by computer) support the recognition (or continued recognition) of three taxa, as opposed to the submergence of all taxa into a single, fragmented, polymorphic species. Although the taxa of *Paxistima* are what we would term "statistical taxa," not distinguished by any one or a few infallible, totally clear-cut characters, the taxa are nonetheless rather readily recognized by their overall patterns when viewed on herbarium sheets, or in the field as we have seen them. As alluded to in the concluding section on Distribution and Geofloristic History, the taxa of *Paxistima* may well represent the now disjunct and somewhat divergent descendants of a single, wide-ranging, polymorphic ancestral species of the North American Arcto-Tertiary flora. Should all taxa survive, we would predict only a greater divergence of taxa through time, given their present geographic isolation and scant opportunity for gene exchange.

SYSTEMATIC TREATMENT

The Genus *Paxistima*

PAXISTIMA Raf., Sylva Telluriana 42. 1838. (spelled *Pachistima* by Rafinesque, 1818, 1819a and b, a *nomen nudum*; *Pachystima* by Endlicher, 1841; and *Pachystigma* by Meisner, 1843). — Type: *Paxistima myrsinites* (Pursh) Rafinesque.

Oreophila Nutt. ex Torrey & Gray, A Flora of North America 1:258. 1838 (Celastraceae); non *Oreophila* D. Don, Trans. Linn. soc. of London 16:178. 1833 (Compositae). *Oreophila* T.& G. is thus a later homonym.

Low, evergreen, glabrous, much branched shrub or subshrub with subterranean rhizomes; adventitious roots often present on lower portions of stems; branches terete, with rough bark. Leaves simple, smooth, serrulate to crenulate (rarely subentire), coriaceous, opposite (decussate), short-petioled, with small caducous stipules. Flowers small, perfect, axillary, solitary or in simple dichasia (rarely fascicled or in compound dichasia); calyx lobes 4, imbricate, green, widely ovate, small; petals 4, maroon (occasionally green), trullate, longer than calyx lobes; stamens 4, inserted in the edge of a broad nectar disc, the anthers introrse, the filaments short, awl-shaped (occasionally longer and thread-like); ovary 2-loculed, superior

but sunken in the disc; style short to obsolete; stigma capitate to linear-clavate (rarely obscurely 2-lobed). Fruit an oblong, 2-loculed capsule. Seeds 1 or 2, oblong, erect, enclosed in a membranaceous, white, cleft aril; endosperm fleshy. Flowers and fruits developing from early spring to early summer; flower buds formed the preceding summer, although some undergo anthesis prematurely (later in the season in which they are formed).

ORTHOGRAPHY AND NOMENCLATURE: As noted by Wheeler (1943) and Uttal (1986), the spelling of the genus name should be *Paxistima*. Rafinesque provided no description in his early publications (1818; 1819a,b) when he spelled the name "*Pachistima*." His references variously to Pursh's and Nuttall's descriptions in these publications might appear to achieve validation by direct reference, but do not because neither Pursh nor Nuttall were attempting to describe new genera or sections of genera in this particular case (cf. Article 41.2, *International Code of Botanical Nomenclature*, Greuter et al. 1988). The first generic description or diagnosis legally attachable to the genus occurred in 1838 (*in situ* in *Silva Telluriana*) when Rafinesque employed the spelling *Paxistima*.

It is plausible that Rafinesque (1838) may have written the Greek "chi" or "χ" for the "ch" in *Pachistima* leading to an accidental change to the "x" (*Paxistima*) spelling; but this is only speculation and not justification for a change back to the "ch" spelling, although Merrill (1949) indicated "*Pachistima*" to be "universally accepted." Regarding meaning and gender, *Paxistima* may be a corruption of *pachys* (thick) and *stigma* (Genaust 1976). Since *stigma* is neuter, *Paxistima* could as well be interpreted as neuter. However, this again is difficult to prove, and consequently we are following Wheeler's (1943) apparent recognition of *Paxistima* as feminine.

Concerning the name of the original species, Pursh's (1814) inclusion of a question mark in *Ilex(?) myrsinites* does not invalidate the publication of the epithet *myrsinites*. Although Wheeler's (1943) interpretation of *I. myrsinites* as a provisional name may have been reasonable at the time, according to the present edition of the code the use of a question mark does not obviate publication when the author (Pursh) accepted the species, but merely expressed taxonomic doubt as to which genus it belonged (cf. Article 34.2, *International Code*). The valid combination *Paxistima myrsinites* was made by Rafinesque in 1838. The correct name and citation of the original species is thus *Paxistima myrsinites* (Pursh) Rafinesque (1838), not *Paxistima myrtifolia* (Nutt.) Wheeler (1943).

SPECIES AND SUBSPECIES OF *PAXISTIMA*

A. Shrub or subshrub 20 to 100 cm high (typically not prostrate); leaves usually 1 – 2 pairs per cm of branch length; inflorescences averaging 6 – 10 per branch; western U.S., southwestern Canada, northeastern Mexico . . . 1) *P. myrsinites*

B. Shrub or subshrub 30 – 100 cm high; leaves 1 – 2 pairs per cm of branch length; blades lanceolate to obovate or oblanceolate, typically 11 – 27 mm long; inflorescences averaging 10 per branch; western United States, southwestern Canada ..... 1A. *P. myrsinites* subsp. *myrsinites*

B. Shrub or subshrub 20 – 45 cm high; leaves 2(3 – 4) pairs per cm of branch length; blades lanceolate, typically 8 – 12 mm long; inflorescences averaging 6 per branch; northeastern Mexico ..... 1B. *P. myrsinites* subsp. *mexicana*

A. Subshrub (tending to be prostrate) 10 – 40 cm high; leaves 2 – 4 pairs per cm of branch length; inflorescences averaging 4 per branch; eastern United States ..... 2) *P. canbyi*

1. Paxistima myrsinites (Pursh) Raf., Sylva Telluriana 42. 1838.

Shrub or subshrub, usually densely branched, 20 to 100 cm high; the lower portion of the stems sometimes prostrate; adventitious roots may be present. Leaves approximate, 1 – 2 (occasionally 3 – 4) pairs per cm; blades ovate (elliptic) to lanceolate (oblanceolate), (6-)8 – 27(-40) mm long, (3-)4 – 10(-15) mm wide; blade margins serrulate to crenulate (occasionally entire), revolute to subrevolute or not revolute (sometimes thickened when not revolute); teeth pointed or rounded, extending from apex to 1/3 to 4/5 of blade length; blade secondary veins indistinct below (occasionally evident); blade apex obtuse, apical angle 90° – 165°; petioles (0.8-)1 – 2(-2.5) mm long. Inflorescence axillary or terminal, averaging 9.3(3 – 21) per branch, generally composed of 1 – 2(-3) flowers each; length of central or only inflorescence axis 2 – 4 mm. Calyx lobes widely depressed-ovate to very widely ovate, slightly imbricate. Petals exceeding the calyx lobes, commonly maroon (those from buds from preceding season), occasionally green (those from buds from current season). Fruits 4 – 7 mm long.

Two subspecies, *Paxistima myrsinites* subsp. *myrsinites* and *P. myrsinites* subsp. *mexicana*, are recognized within this species. The typification of *P. myrsinites* is discussed under the subspecies *P. myrsinites* subsp. *myrsinites*. *Paxistima myrsinites* subsp. *mexicana* is described as new.

1A. Paxistima myrsinites (Pursh) Raf. subsp. myrsinites.

Ilex? myrsinites Pursh, Fl. Amer. Sept., 1. 119. 1814. — Lectotype: *Lewis s.n.*, 1806 (PH, photograph!; see typification, below).

Myginda myrtifolia Nutt., Gen. N. Amer. Pl. 109. 1818. — Type: same as *Ilex? myrsinites* Pursh. The spelling changed to *myrtifolia* by Nuttall, and hence the epithet *myrtifolia* is a superfluous name.

Myginda myrtifolia var. "alpha" *minor* Hooker, Fl. Bor.-Amer. 120 – 121. 1840. — Type: Apparently considered by Hooker to correspond to original material of *Ilex? myrsinites* Pursh.

Myginda myrtifolia var. "beta" *major* Hooker, Fl. Bor.-Amer. 120 – 121. 1840. — Type: *Douglas s.n.* as annotated by J. Ewan (K *s.n.*, photograph!).

Oreophila myrtifolia (Nutt.) Nutt. ex Torrey & Gray, Fl. N. Amer. 1. 258 – 259. 1838 – 1843.

Pachystima macrophylla Farr, Trans. & Proc. Bot. Soc. Pennsylvania 1:421 – 422. 1904. — Type: *Farr s.n.* (PH 37408!, GH *s.n.*!).

Pachystima krautteri Farr, Ottawa Naturalist 20:108. 1906. — Type: *Krautter s.n.* (holotype: PH 42752!).

Pachystima schaefferi Farr, Ottawa Naturalist 20:108. 1906. — Type: *Schaffer 512* (holotype: PH s.n.!).

Paxistima myrtifolia (Nutt.) Wheeler, Amer. Midl. Naturalist 29:793 – 794. 1943.

Shrub (20-)30 – 100 cm high, the stems sometimes nearly prostrate; adventitious roots may be present. Leaves approximate, 1 – 2 pairs (rarely more) per cm of branch length; blades obovate to oblanceolate, occasionally ovate (or elliptic) to lanceolate (or narrowly elliptic), (9-)11 – 27(-40) mm long, 4 – 10(-15) mm wide; blade margins serrulate to crenulate (occasionally entire), revolute to subrevolute or not (sometimes thickened when not revolute); teeth pointed or rounded, extending from apex to 2/5 to 7/10 (occasionally 4/5) of blade length; blade secondary veins indistinct below (occasionally evident); blade apex obtuse, the apical angle (90°-) 105° – 165°; petioles generally (0.8-)1 – 2(-2.5) mm long. Inflorescences axillary or terminal, averaging 10(3 – 21) per branch, generally composed of (1-)2(-3) flowers each; length of central or only inflorescence axis (1.5-) 2 – 4(-8) mm. Calyx lobes depressed-ovate to very widely depressed ovate, slightly imbricate. Fruits 4 – 7 mm long.

Typification: No prior type was chosen for *Paxistima myrsinites* (i.e., subsp. *myrsinites*), as confirmed by Wheeler (1943). Two specimens (collected by Meriwether Lewis) were mentioned by Pursh (1814) in his description of *Ilex? myrsinites*, one from "near the Pacific Ocean," collected November 16, 1805, the other from "on the Rocky-mountain," collected June 16, 1806. The Lewis and Clark Herbarium at the Academy of Natural Sciences, Philadelphia, contains specimens so designated. An 1805 specimen is also in the herbarium of the Royal Botanic Garden, Kew, England. The Kew specimen is, however, part of a mixed collection (with a *Berberis* specimen) and is problematic as type material. The 1806 (Rocky Mountain) specimen (PH) seems preferable as the lectotype, and we so designate it.

Distribution: Variously known as mountain-lover, Oregon boxwood, myrtle pachistima, myrtle box-leaf and box-leaf, *Paxistima myrsinites* subsp. *myrsinites* is common in the mountain ranges of western North America at altitudes of 600 to 3350 meters. Its range extends from southern British Columbia and Alberta south into Arizona and New

Mexico. The flowers bloom from mid-March to mid-July. This subspecies is quite variable in vegetative morphology. Further investigation may reveal genetic or clinal bases for this polymorphism.

Representative specimens: CANADA: **Alberta**: Watertown Lakes Park, trail to Bertha Lake, 12 Jun 1925, *Malte and Watson 289* (WTU). **British Columbia**: Bear Creek Station, Selkirk Mountains, 25 May 1905, *Schaffer s.n.* (GH, PH, Type of *P. schaefferi*); Bear Creek Station, eastern slope Selkirk Mountains, 20 Aug 1904, *Farr s.n.(GH, PH, Isotype of P. macrophylla)*; Deer Park, Lower Arrow Lake, 4 Jun 1889, *Macoun 40584a* (MSC); Vancouver Island, Thetis Lake, four mi NW of Victoria, 15 May 1956, *Calder, Parmelee and Taylor 16363* (UC).

UNITED STATES: **Arizona**: **Apache Co.**: Lukachukai Mountains, wooded N slope, 1 Jun 1950, *Clark 15329* (UNM). **Cochise Co.**: Chiricauhua National Monument, Echo Park Trail, 15 Aug 1975, *Mason and McManus 3166* (ARIZ). Coconino Co.: Oak Creek Canyon, West Fork, 10 mi N of Sedona, West Fork trail #108, 23 Mar 1988, *Navaro s.n.* (MU). **California**: **Del Norte Co.**: Shelly Creek Canyon, 3 mi S of Old Monumental, 21 May 1937, *Parks and Parks 5646* (DS). **Humboldt Co.**: Trinity Summit, 2 mi E of Box Camp, 23 Jun 1942, *Tracy 17246* (UC). **Marin Co.**: Mt. Tamalpais, midway between Laurel Dell and Barth's Retreat, 16 Mar 1941, *Howell 16155* (CAS). **Shasta Co.**: northern Sierra Nevada, Hatchet Creek, E of Round Mountain, 18 Jul 1930, *Benson 2217* (POM). **Siskiyou Co.**: Black Butte, 15 Jul 1905, *Krautter s.n.* (PH, Holotype of *P. krautteri*); Black Butte, 15 Jul 1905, *Krautter s.n.* (PH, Isotype of *P. krautteri*). **Yuba Co.**: Willow Creek, near Camptonville, 6 Mar 1966, *Mott s.n.* (CAS). **Colorado**: **Garfield Co.**: Trappers' Lake, 30 Jul 1933, *Hermann 5503* (GH). **Grand Co.**: Routt National Forest, Gore Pass on Highway 84, 1 Aug 1962, *Porter and Porter 9187* (MSC). **Gunnison Co.**: old town of Gothic, E side of East River, 23 Jun 1952, *Barrell 43-52* (US). **Las Animas Co.**: above Whiskey Pass Rd., 6 mi W of Monument Lake campground, 18 Jun 1941, *Robbins s.n.* (ARIZ). **Montezuma Co.**: Mesa Verde National Park, rocky canyon below main lodge, 10 Jul 1941, *McVaugh s.n.* (UC). **Summit Co.**: 8 mi N of Silverthorne, Blue R. Valley, 22 Jun 1982, *Weber and Wittman 16214* (CM). **Idaho**: **Adams Co.**: SW slope of Smith Mountain, 10 Jul 1930, *Borell s.n.* (CAS). **Bear Lake Co.**: Bear Lake, Aug 1921, *Chamberlain s.n.* (DS). **Bonner Co.**: 5 mi W of Sand Point, slope above Clark's Fork River, 14 May 1936, *Hitchcock 2891* (WTU). **Clearwater Co.**: in brush at summit between Bovill and Elk River, 21 May 1949, *Cronquist 5781* (NCSC). **Idaho Co.**: Lolo Pass, 27 May 1938, *Barkley 2417* (POM). **Teton Co.**: 6 mi W of Driggs, Packsaddle Creek Canyon, 1 Jul 1968, *Muir s.n.* (POM). **Montana**: **Flathead Co.**: Rescue Creek and US 2, 28 Jun 1950, *Marshall 1176* (MSC). **Glacier Co.**: Glacier National Park, trail to Mount Brown lookout, 7 Jul 1939, *Bailey and Bailey 113* (TENN). **Powell Co.**: 2 mi NW of Woodworth School, Cottonwood Creek, 21 May 1933, *Hitchcock 1584* (POM). **New Mexico**: **Catron Co.**: Gila Primitive Area, 21 May 1937, *Sharp and Orr 332* (PH). **Grant Co.**: 5 mi N of Pinos Altos, mountain side above Cherry Creek, 24 Apr 1947, *McVaugh and Grant 8051* (GH). **Otero Co.**: Sacramento Mountains, Karr Canyon, about 1 mi W of N.M. highway 64, 10 Jul 1980, *Worthington 6192* (ARIZ). **Rio Arriba Co.**: Jemez Mountains, San Pedro Parks, 12 Jun 1964, *Martin, Smith and Schmitt 64-18* (UNM). **San Miguel Co.**: headwaters of the Rio Las Trampas, west of Spring Mountain, 21 Sept 1972, *Fosberg 54499* (POM). **Taos Co.**: 3 mi SE of Taos, Devisadero Peak, 7 Jun 1979, *Baker 1033* (NCU). **Oregon**: **Baker Co.**: near Cornucopia, Wallowa Mountains, Pine Creek, 30 Jun 1935, *Jones 7204* (UC). **Deschutes Co.**: 4 mi N of North Sister Mountains, near McKenzie Pass, 22 Jun 1939, *Hitchcock and Martin 4862* (POM). **Hood River Co.**: Mount Hood National Forest, near Sherwood

Forest Camp, 13 Aug 1933, *Jones 4198* (POM). **Lake Co.**: Gearhart Mountain region, 3 mi E of Finley Corral, 21 Jul 1932, *Applegate 7918* (CAS). **Josephine Co.**: Siskiyou Mountains, Steamboat Ranger Camp on Sturgis Creek, 5 Aug 1930, *Applegate 6597* (CAS). **Polk Co.**: 4 mi SW of Buell, bank along Mill Creek, 1 Jul 1930, *Peck 16204* (UC). **Utah: Box Elder Co.**: Raft River mountains, Clear Creek Canyon, 24 Jun 1947, *Preece 644* (UT). **Cache Co.**: W of Tony Grove Lake, rocky cliffs, 25 Aug 1950, *Thieret and Thieret 204* (GH). **Kane Co.**: Bryce Canyon National Park, one half mi E of Rainbow Point, 17 Jun 1957, *Buchanan 132* (UT). **Salt Lake Co.**: top of Clayton Peak, Big Cottonwood Canyon, 18 Jul 1960, *Cottam, Allan and Rowland 16491* (UT, CAS). **San Juan Co.**: canyon wall opposite Augusta Natural Bridge, 14 Sep 1939, *Cutler s.n.* (GH). **Washington Co.**: Zion National Park, Hidden Canyon, *Weights 9772* (UT). **Washington**: **Chelan Co.** open woods near Merritt, 12 May 1934, *Jones 4754* (ARIZ). **Columbia Co.**: Blue Mountains, stream banks, 23 Jun 1897, *Horner s.n.* (GH). **Island Co.**: Whidby Island, Goose Rock, 21 May 1933, *Thompson 8940* (GH). **Lewis Co.**: Mount Ranier National Park, trail to Trump Park from Christine Falls, 3 Jul 1970, *Duffield 372* (MU). **Okanogan Co.**: near summit on Twisp cut-off, 27 May 1932, *Fiker 717* (DS). **Snohomish Co.**: 14 mi N of Seattle, Jun 1892, *Piper s.n.* (MSC). **Spokane Co.**: Mount Carleton, 21 Jul 1902, *Kreiger 2861* (WTU). **Wyoming: Fremont Co.**: along a small creek half way between Lander and South Pass City, 23 Jun 1939, *Craig and Craig 3575* (POM). **Teton Co.**: Teton Pass, 10 Jul 1959, *Porter and Porter 7902* (DS).

1B. Paxistima myrsinites (Pursh) Raf. subsp. mexicana Navaro & Blackwell, subsp. nov.

Differt a subsp. *myrsinites* statura parva, foliis coarctatioribus et parvis, et inflorescentiis pauctioribus (6) per ramos.

Shrub or subshrub 20—45 cm high, the stems sometimes prostrate; adventitious roots may be present. Leaves approximate, 2 (occasionally 3—4) pairs per cm of branch length; blades lanceolate (6-)8—12(-15) mm long, (3-)4(-5) mm wide; blade margins crenulate (occasionally serrulate, rarely entire), revolute; teeth generally rounded (occasionally pointed), extending from apex to 1/3 to 3/5 (occasionally 3/4) of blade length; blade secondary veins indistinct below; blade apex obtuse, the apical angle generally 90°(-135°); petioles (0.8-)1(-2.5) mm long. Inflorescences axillary or terminal, averaging 6(3—9) per branch, generally composed of 1(-2) flowers each; length of central or only inflorescence axis (1.5-)2—4(-5) mm. Calyx lobes widely depressed-ovate to very widely ovate, slightly imbricate. Fruits 4—5 mm long.

Type: **MEXICO. Coahuila**. Municipality of Arteaga, La Siberia, Sierra de la Marta, 27 May 1982, *Villarreal 1678* (holotype: MU 134452; isotype: TEX *s.n.*).

Distribution: *Paxistima myrsinites* subsp. *mexicana* is apparently restricted to mountainous regions of three Mexican states: southeastern Coahuila, southern Nuevo Leon and southwestern Tamaulipas. It grows at altitudes of 2440 to 3500 meters on open hillsides or in forests of pine, fir and oak. The flowers may be found in bloom from late March to mid-July.

Representative specimens: MEXICO: **Coahuila**: municipality of Arteaga, La Siberia, 6 km SE of San Antonio de las Alazanas, 27 May 1982, *Villarreal 1678* (MU, TEX, Type of *P. myrsinites* subsp. *mexicana*); municipality of Arteaga, Puerto de la Siberia, 10 Oct 1970, *Marroquin 1994* (UNL); municipality of Arteaga, Sierra Madre Oriental, 26 Jul 1975, *Robert and Passini s.n.* (ANSM); 40 mi S of Saltillo, Sierra Madre, Jul 1880, *Palmer s.n.* (PH); 26 km NW of Fraile, 16 Jul 1941, *Stanford, Retherford and Northcraft 454* (CAS); Sierra de la Marta, 17 May 1981, *Poole 2324, Hinton and Nixon* (TEX). **Nuevo Leon**: municipality of Galeana, road to summit of Certo Potosi, 12.5 mi from 18 de Marzo, 18 May 1982, *Dorr 2270 and Atkins* (TEX, ARIZ); municipality of Galeana, canyon below Las Canoas on Cerro Potosi, 20 Jul 1935 Mueller s.n. (GH); municipality of Galeana, *Sierra La Marta, 19 Apr 1981, Hinton 18158* (TEX); municipality of Zaragoza, El Salto, 29 May 1980, *Flores O. s.n.* (UNL). **Tamaulipas**: 20 km NE of Miquihuana, Cerro El Borrado, 2 Apr 1969, *Gonzales-Quintero 3855* (MSC); on E and S slopes of summit of Pena Nevada, 19 Jul 1949, *Stanford, Lauber and Taylor s.n.* (RSA).

2. PAXISTIMA CANBYI Gray, Proc. Amer. Acad. Arts 8:620. 1873. (spelled *Pachystima canbyi* by Gray — TYPE: 1869, *Canby s.n.* (HOLOTYPE: GH!; see typification, below).

Shrub or subshrub 10 – 40 cm high, tending to spread in vegetative clones; older portion of stems prostrate, the upper portion ascending; adventitious roots common on lower stem. Leaves closely approximate, 2 – 4 pairs (rarely more) per cm of branch length; blades narrowly elliptic to lanceolate, 11 – 22 mm long, 2.3 – 6.2 mm wide; blade margins serrulate to crenulate, strongly revolute; teeth pointed or rounded, extending from apex to 1/3 to 4/5 of blade length; blade secondary veins indistinct below; blade apex obtuse, the apical angle 105° – 120°; petioles (0.5-)1(-1.1) mm long. Inflorescences axillary or terminal, averaging 4(1 – 6) per branch, generally composed of 1 – 2(3) flowers each; length of central or only inflorescence axis (1-)2 – 6(-14) mm. Calyx lobes widely depressed-ovate to widely ovate, slightly imbricate. Petals exceeding the calyx lobes, commonly maroon (those from buds from preceding season), occasionally green (those from buds from current season). Fruits 4 mm long, rarely seen.

Typification: A specimen at the Gray Herbarium (collected by Canby in 1869) was annotated as the holotype by Vernon Bates in 1984. Asa Gray's 1873 description of *Paxistima canbyi* states, "Mr. Canby discovered the Alleghenian species in 1868, and obtained flowering specimens upon a second visit to the station in the spring of 1869." In actuality a small sterile specimen was collected by Canby in 1868 (1858?; cf. Canby in Gray, 1873). However, in regard to collection of specimens by Canby, Gray alluded only to those gathered in 1869 (these being flowering specimens, presumably from a single collection), and it was apparently these upon which Gray based his new species. Consequently, the May, 1869 collection

by Canby (William Canby s.n.) from Giles County, Virginia is the type collection; the specimen at GH, annotated by Bates, is accepted as the holotype; an isotype is at US.

Distribution: *Paxistima canbyi*, variously called Canby's mountain-lover, cliff-green or rat-stripper, occurs very locally in the Appalachian Mountain region of the eastern United States; it is found on dry to moist, sunny to shaded, northwest to southwest facing, limestone bluffs and ravines in South-central Ohio and Pennsylvania through the Virginias into Kentucky, North Carolina and northern Tennessee. The North Carolina population is at an old nursery site and is considered to have been introduced (Hardin 1963). The presence of *P. canbyi* in North Carolina was, however, noticed as long ago as 1883 by Chapman, and *P. canbyi* is likely native to North Carolina. Endemic to a small number of areas in these states mentioned above, *P. canbyi* is listed in Category Two of plants of federal concern, i.e., more data needed to support listing as threatened or endangered (Ohio Division of Natural Areas and Preserves 1988). *Paxistima canbyi* typically flowers from late March into May, the flowers developing from buds formed during the preceding season. However,a small number of flowers may arise from buds of the current season; these may bloom during the summer.

Representative specimens: UNITED STATES: KENTUCKY: **Carter Co.**: Carrer Caves, Devil's Backbone Ridge, 29 May 1986, *Navaro s.n.* (MU); Carter Caves, limestone cliff opposite entrance, 29 May 1986, *Navaro s.n.* (MU). **Pulaski Co.**: Tatesville, 1 mi S, Lake Cumberland, 10 May 1976, *Stephens s.n.* (TENN). OHIO: **Adams Co.**: Brush Creek Twp., Edge of Appalachia Preserve, 9 Apr 1987, *Navaro s.n.* (MU). **Highland Co.**: Brush Creek Twp., Ft. Hill St. Memorial Park, 1 Apr 1973, *Bourdo and Roberts 3294* (OS). NORTH CAROLINA: 1874, *Canby s.n.* (PH). PENNSYLVANIA: **Bedford CO.**: Cliff at Lutzville, 6 May 1950, *Henry and Baker s.n.* (CM); Juniata R. near Lutzville, 6 May 1950, *Krouse 97* (CM). TENNESSEE: **Hawkins Co.**: bluff above South Fork Holston River, Bays Mt. near Laurel Run Gorge, 21 Apr 1984, *Somers and Smith s.n.* (TENN). VIRGINIA: **Frederick Co.**: west of Middletown, above Cedar Creek, 20 Sep 1931, *Griscom and Hunnewell s.n.* (GH). **Giles Co.**: May 1869, *Canby s.n.* (GH, holotype). **Rockbridge Co.**: VMI post, above Maury R., 22 Apr 1963, *Gupton s.n.* (NCU). **Scott Co.**: Natural Tunnel, around the rim of tunnel, 17 May 1968, *James 9686* (NCU). **Wythe Co.**: near Wytheville, Jun 1875, *Shriver 483* (GH). WEST VIRGINIA: **Greenbriar Co.**: Chocolate Drop, limestone cliff facing Greenbriar R., 1 Aug 1931, *McNeill s.n.* (WVA). **Mercer Co.**: mouth of Brush Creek, 4 May 1976, *Grafton s.n.* (WVA). **Mineral Co.**: near Keyser, May 1936, *Chapman s.n.* (WVA).

DISTRIBUTION AND GEOFLORISTRIC HISTORY

The present distribution of *Paxistima* in North America (Fig. 2) is probably attributable to its presence in the temperate Arcto-Tertiary forests, and to subsequent geoclimatic restrictions upon these forests, i.e., orogenic activity, cooling/drying, glaciations. According to Chaney

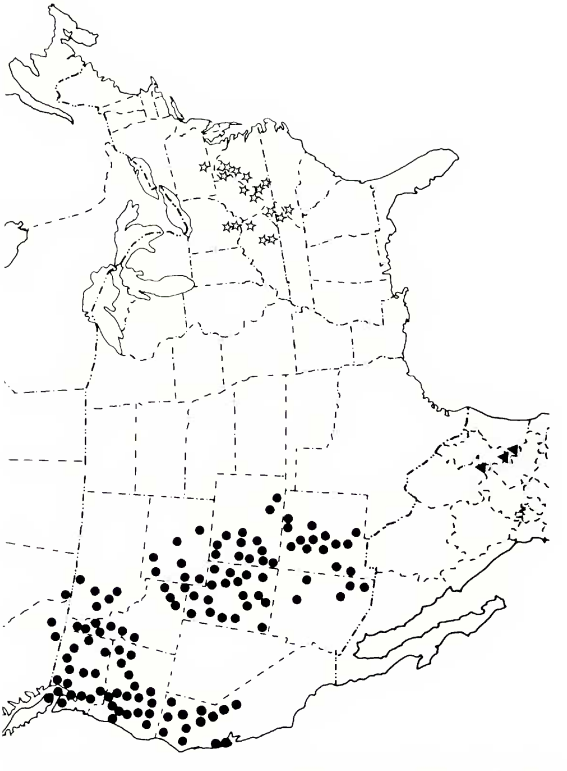

FIG. 2. Geographic distribution of *Paxistima* in North America. Star = *P. canbyi*, solid circle = *P. myrsinites* subsp. *myrsinites*, triangle = *P. myrsinites* subsp. *mexicana*.

(1947), "The Arcto-Tertiary Flora has survived in North America at middle latitudes in two main provinces, an eastern characterized by broad-leafed, deciduous trees, and a western characterized by conifers, broad-leafed evergreens, and broad-leafed deciduous trees and shrubs." The two species of *Paxistima*, *P. canbyi* and *P. myrsinites*, are indeed presently restricted, respectively, to parts of these two regions.

Additionally, the pattern and the restricted (localized) nature of the present distribution of *P. canbyi* have led some (e.g. Transeau 1941) to consider this distribution explainable by association with the former northwest-flowing, preglacial Teays River. However, populations generally lie outside the supposed Teays drainage *per se* (see Steeg 1946, for an account of the Teays drainage). On the other hand, several populations may be circumstantially related to the boundaries of the glacial lake (Lake Tight) formed by ice blockage of the Teays (Wolfe 1942; Braun 1950). The details of the explanation of the distribution of *P. canbyi* require further elucidation.

The origin and relationships of *Paxistima myrsinites* subspecies *mexicana* are worthy of conjecture. Although most similar to subspecies *myrsinites*, the variation of subspecies *mexicana* in the "morphological direction" of *P. canbyi* (Fig. 1) suggests that the Arcto-Tertiary antecedents of present day *Paxistima* perhaps constituted one transcontinental species complex which later became disjunct (developing more or less morphologically distinct entities) as a consequence of geoclimatic events, such as those mentioned previously. Subspecies *mexicana* may represent relic populations of the former *myrsinites-canbyi* complex, remaining in a refugium in the mountains of Northeast Mexico; it could also represent a third line of development from an ancestral species.

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REFERENCES

ANDERBERG, M.R. 1973. Cluster analysis for Applications. Academic Press, New York.

BRAUN, E.L. 1950. Deciduous forests of eastern North America. Hafner Press, New York.

CHANEY, R.W. 1947. Tertiary centers and migration routes. Ecol. Monogr. 17:139 – 148.
CHAPMAN, A.W. 1883. Flora of the southern United States. Ivison, Blakeman, Taylor and Co., New York.
DON, D. 1833. Descriptions of the new genera and species of the class Compositae belonging to the floras of Peru, Mexico and Chile. Trans. Linn. Soc. London 16:178.
DU RIETZ, G. E. 1930. The fundamental units of biological taxonomy. Botanisk Tidsskrift 24:333 – 428.
ENDLICHER, S. 1836 – 1840. Genera plantarum secundum ordines naturales. Beck, Vienna.
ENDLICHER, S. 1841. Genera plantarum secundum ordines naturales, Supplement. Beck, Vienna.
FARR, E.M. 1904. Notes on some interesting British Columbian plants. Trans.& Proc. Bot. Soc. Pennsylvania 1:417 – 425.
FARR, E.M. 1906. Some new plants from the Canadian Rockies and Selkirks. Ottawa Naturalist 20:105 – 111.
GENAUST, H. 1976. Etymologisches Worterbuch der botanischen Pflanzennamen. Birkhauser Verlag, Basel.
GRAY, A. 1873. Characters of new genera and species of plants. Proc. Amer. Acad. Arts 8:620 – 631.
GREUTER, W. et al.(eds.). 1988. International code of botanical nomenclature. Koeltz Scientific Books, Konigstein, Federal Republic of Germany.
HARDIN, J.W. 1963. *Pachystima canbyi* in North Carolina. Castanea 28:177 – 178.
HOLMGREN, P.K., W. KEUKEN and E.K. SCHOFIELD. 1981. Index herbariorum I. Bohn, Scheltema and Holkema, Utrecht.
HOOKER, W.J. 1840. Flora Boreali-Americana. Henry G. Bohn, London.
MEISNER, C.F. 1843. Plantarum vascularium genera. Libraria Weidmannia, Leipzig.
MERRILL, E.D. 1949. Index Rafinesquianus. Arnold Arboretum, Jamaica Plain, Massachusetts.
NUTTALL, T. 1818. The genera of North American plants, and a catalogue of the species, to the Year 1817. Philadelphia.
OHIO DIVISION OF NATURAL AREAS AND PRESERVES. 1988. Rare native Ohio vascular plants: 1988 – 1989 Status List. Ohio Department of Natural Resources, Columbus. 13.
PIPER, C.V. 1906. Contr. U. S. Natl. Herb. 11. Flora of the State of Washington. Government Printing Office, Washington.
PURSH, F. 1814. Flora americae septentrionalis,I. White, Cochrane, and Company, London.
RAFINESQUE, C.S. 1818. Review of Pursh's flora of North America. Amer. Monthly Mag.& Crit. Rev. II(3):175.
RAFINESQUE, C.S. 1819a. Review of the genera of North American plants and a catalogue of the species in the year 1817 by Thomas Nuttall. Amer. Monthly Mag. & Crit. Rev. IV:184 – 191.
RAFINESQUE, C.S. 1819b. Remarques, critiques et synonymiques. J. Phys. Chim. Hist. Nat. Arts 89:256 – 262.
RAFINESQUE, C.S. 1838. Sylva Telluriana. Philadelphia.
SAS Institute, Inc. 1985. SAS user's guide: Statistics, Version 5 Edition. Cary, North Carolina.

STANDLEY, P.C. 1920 – 1926. Contr. U. S. Natl. Herb. 23. Trees and shrubs of Mexico. Government Printing Office, Washington.
STEEG, K. V. 1946. The Teays river. Ohio J. Sci. 46:297 – 307.
TORREY, J. and GRAY, A. 1838. A Flora of North America I. Wiley and Putnam, New York.
TRANSEAU, E. N. 1941. Prehistoric factors in the development of the vegetation of Ohio. Ohio J. Sci. 41:207 – 211.
UTTAL, L.J. 1986. Once and for all it is *Paxistima*. Castanea 51:67 – 68.
WATSON, S. 1878. Bibliographical index to North American Botany. Smithsonian Misc. Collect., XV. Smithsonian Institution, Washington.
WHEELER, L.C. 1943. History and orthography of the celastraceous genus "*Pachystima*" Rafinesque. Amer. Midl. Naturalist 29:792 – 795.
WOLFE, J.N. 1942. Species isolation and a proglacial lake in southern Ohio. Ohio J. Sci. 42:2 – 11.