

Evolution of dioecious/ monecious taxa in *Juniperus*, contrasted with *Cupressus*, *Hesperocyparis*, *Callitropsis* and *Xanthocyparis* (Cupressaceae)

Robert P. Adams

Baylor-Utah Lab, Baylor University, 201 N 5500 W, Hurricane, UT, 84737, USA
robert_Adams@baylor.edu

ABSTRACT

Dioecy and monoecy were mapped onto phylogenies of *Juniperus* and related genera. Related genera were uniformly monecious. In contrast, the direct ancestor of *Juniperus* appears to have been dioecious, because dioecy exhibits universal occurrence in sect. *Caryocedrus* (*J. drupacea*) and for all species of sect. *Juniperus*. Monoecy appears to have re-emerged in section *Sabina*. The re-emergence of monoecy appears to have occurred in 5 evolutionary events: in the *californica-grandis-occidentalis-osteosperma* species of the serrate leaf junipers of North America; almost universally in the smooth leaf, turbinate, 1-seeded cone, clade centered in eastern Mediterranean and central Asia; in the *excelsa* complex; in the *chinensis* complex of central Asia and China; and in the *phoeniceal turbinata* clade of the Mediterranean region. The genus *Juniperus*, seems to run counter-current to other closely related genera (*Cupressus*, *Hesperocyparis*, *Callitropsis*, *Xanthocyparis*) which are uniformly monoecious. In contrast, *Juniperus*, perhaps the most recently evolved conifer, initially evolved the atypical dioecious sexual system, then later in its evolution has (re-)evolved monoecy among many phylogenetically advanced species. Published on-line www.phytologia.org *Phytologia* 100(4): 248-255 (Dec 21, 2018). ISSN 030319430.

KEY WORDS: Monecious, Monoecy, Dioecious, Dioecy, *Juniperus*, *Cupressus*, *Hesperocyparis*, *Callitropsis*, *Xanthocyparis*, Cupressaceae, sexual systems, evolution.

Recently, Walas et al. (2018) reviewed the literature on sexual systems in gymnosperms. They reported about 65% of the gymnosperm taxa were dioecious. This is in stark contrast to angiosperms where dioecy is reported at about 6% (Renner, 2014; Renner and Ricklefs, 1995; Weiblen et al., 2000).

Dioecy has, potentially, some advantages over monoecy: complete exclusion of risk of self-pollination and optimization of resources for both male and female functions (Walas, et al., 2018). However, Walas et al. (2018) note that dioecy is not so well suited as an optimal system for fixed or sedentary taxa. Monoecy can be an advantage when no other breeding partner is nearby (Charnov, 1982; Munoz-Reinoso, 2018). In addition, because only female plants produce seeds in dioecious taxa, only half of the plants in a population are producing seed compared to monecious taxa. It does seem that monecious plants may offer an advantage in colonization of new habitats, especially by long distance dispersal, as in the cases of *Juniperus* colonization on distant, isolated islands such as Bermuda, the Caribbean Islands, the Azores, Canary Islands, etc. Among gymnosperm families (Table 1), some are almost exclusively monecious (Araucariaceae, 94.6%; Pinaceae, 100%; Sciadopityaceae, 100%) or two-thirds monecious (Cupressaceae, 64.4%). However, most families (8) are almost exclusively dioecious (Table 1). The Cupressaceae has the largest number of mixed sexual systems (taxa with both monecious and dioecious plants within a species).

Two robust phylogenies of the *Callitropsis*, *Cupressus*, *Hesperocyparis*, *Juniperus*, *Xanthocyparis* complex have recently been published. One was based on 73 nuclear genes (Mao, et al. 2018) and the other utilized the complete chloroplast genome sequences (Zhu et al, 2018). This, along with the phylogeny of *Juniperus* (Adams and Schwarzbach 2013), make it now possible to place the sexual system onto phylogenetic trees to examine if the occurrences of dioecy and monoecy is correlated with phylogeny. The purpose of the present paper is to report on phylogenetic distribution of sexual

systems within *Juniperus* and in a closely related group of Cupressaceae genera (*Callitropsis*, *Cupressus*, *Hesperocyparis*, *Juniperus* and *Xanthocyparis*).

Table 1. Distributions of monoecious, dioecious and mixed (monoecious and dioecious plants within a taxon) species in various gymnosperm families (adapted from Walas, et al. 2018).

Family	Total species reported on	Monecious	mixed (M&D)	Dioecious	% Dioecious
Araucariaceae	37	35	0	2	5.4%
Cupressaceae	135	87	8	40	29.6
Cycadaceae	107	0	0	107	100.0
Ephedraceae	54	0	0	54	100.0
Ginkgoaceae		0	0	1	100.0
Gnetaceae	39	0	0	39	100.0
Pinaceae	224	222	2	0	0.0
Podocarpaceae	178	6	3	169	94.9
Sciadopityaceae	1	1	0	0	0.0
Taxaceae	32	1	1	30	93.7
Welwitschiaceae	1	0	0	1	100.0
Zamiaceae	224	0	0	224	100.0
Total	1033	352 (34.1%)	14 (1.36%)	667 (64.56%)	

MATERIALS AND METHODS

Information on dioecy or monoecy was obtained from Adams' monograph of *Juniperus* (Adams 2014; Farjon 2005). For *Callitropsis*, *Cupressus*, *Hesperocyparis* and *Xanthocyparis*, information was from Walas et al. 2018 and Farjon 2005.

RESULTS AND DISCUSSION

Table 2 shows the classification of 119 *Juniperus* taxa as to their sexual system with 88 taxa dioecious (73.9%) and 31 taxa (26.1%) having some degree of monoecy as: 12 taxa monoecious (10.2%); 13 taxa dioecious & monoecious (10.9%); 6 taxa mostly dioecious but rarely monoecious (5.0%). Vasek (1966) made a very detailed study of thousands of specimens and natural plants to determine the frequency of dioecious vs. monecious plants within a population and taxon. So, we do have quantitative data of monoecy in *J. californica* (1.9% monecious), *J. grandis* (Vasey treated as *J. occidentalis* subsp. *australis*) (5.1%), *J. occidentalis* (47.6%) and *J. osteosperma* (89.2%).

In addition, Jordano (1991) conducted a detailed study of monoecy and sex expression in *J. phoenicea* in Spain and Morocco. He found although *J. phoenicea* is considered monoecious, in reality, most trees in a population are 'mostly with pollen cones and few seed cones' ('male plants') or 'mostly with seed cones and a few pollen cones' ('female plants') with a few plants that produced numerous pollen cones and seed cones ('true monecious' plants). This situation he called a 'functionally subdioecious breeding system'. Just in this issue of Phytologia, Munoz-Reinoso (2018) reported finding 1 monecious tree in a population of dioecious *J. oxycedrus* var. *badia* trees. For a more detailed review of sex expression in *Juniperus*, the reader is referred to Adams (2014, chapter 9). It should be noted that I have examined thousands of juniper trees in the field over the past 50 years and have encountered a few 'monecious' trees (with a few male cones, and many female cones, or many male cones and a few female seed cones) in 'dioecious' taxa of most species.

Table 2. Classification of all *Juniperus* species and varieties (119) by sexual system (dioecious, monocious or both, within a taxon). Data from Adams (2014) and Vasek (1966) for percentage monocious data for *J. californica*, *J. grandis* (*J. occidentalis* subsp. *australis*), *J. occidentalis* and *J. osteosperma*.

Taxon, nomenclature of Adams, 2014	Plants: dioecious, monocious or both
<i>J. angosturana</i> R. P. Adams	dioecious
<i>J. arizonica</i> (R. P. Adams) R. P. Adams	dioecious
<i>J. ashei</i> Buchholz	dioecious
<i>J. barbadensis</i> L.	dioecious
<i>J. barbadensis</i> var. <i>lucayana</i> (Britton) R. P. Adams	dioecious
<i>J. bermudiana</i> L.	dioecious
<i>J. blancoi</i> var. <i>huehuentensis</i> R. P. Adams, S. Gonzalez, and M. G. Elizondo	dioecious
<i>J. blancoi</i> var. <i>mucronata</i> (R. P. Adams) Farjon	dioecious
<i>J. blancoi</i> Martinez var. <i>blancoi</i>	dioecious
<i>J. brevifolia</i> (Seub.) Ant.	dioecious
<i>J. californica</i> Carriere	dioecious, rarely monocious (1.9%)
<i>J. californica</i> f. <i>lutheyana</i> J. T. Howell & Twisselm.	dioecious
<i>J. carinata</i> (Y. K. Yu & L. K. Fu) R. P. Adams	dioecious
<i>J. cedrus</i> Webb & Berthol.	dioecious
<i>J. chinensis</i> var. <i>procumbens</i> Sieb.ex Endl.	monocious
<i>J. chinensis</i> var. <i>sargentii</i> Henry	dioecious, rarely monocious
<i>J. chinensis</i> L. var. <i>chinensis</i>	dioecious
<i>J. coahuilensis</i> (Martinez) Gaussen ex R. P. Adams	dioecious
<i>J. comitana</i> Martinez	dioecious
<i>J. communis</i> L. var. <i>communis</i>	dioecious
<i>J. communis</i> var. <i>charlottensis</i> R. P. Adams	dioecious
<i>J. communis</i> var. <i>depressa</i> Pursh	dioecious
<i>J. communis</i> var. <i>hemisphaerica</i> (J. & C. Presl) Parl.	dioecious
<i>J. communis</i> var. <i>kamchatkensis</i> R. P. Adams	dioecious
<i>J. communis</i> var. <i>kellei</i> R. P. Adams	dioecious
<i>J. communis</i> var. <i>megistocarpa</i> Fernald & H. St. John	dioecious
<i>J. communis</i> var. <i>nipponica</i> (Maxim.) E. H. Wilson	dioecious
<i>J. communis</i> var. <i>saxatilis</i> Pall. (only in eastern hemisphere)	dioecious
<i>J. convallium</i> f. <i>pendula</i> (Cheng & L. K. Fu) R. P. Adams	dioecious & monocious
<i>J. convallium</i> Rehder & Wilson	dioecious & monocious
<i>J. coxii</i> A.B. Jacks	dioecious
<i>J. davurica</i> var. <i>arenaria</i> (E. H. Wilson) R. P. Adams	dioecious
<i>J. davurica</i> var. <i>mongolensis</i> (R. P. Adams) R. P. Adams	dioecious
<i>J. davurica</i> Pall.	dioecious
<i>J. deltooides</i> R. P. Adams	dioecious
<i>J. deltooides</i> var. <i>spilinanus</i> (Yalt., Elicin & Terzioglu) Terzioglu	dioecious
<i>J. deppeana</i> var. <i>patoniana</i> (Martinez) Zanoni	dioecious
<i>J. deppeana</i> var. <i>robusta</i> Martinez	dioecious
<i>J. deppeana</i> forma <i>elongata</i> R. P. Adams	dioecious
<i>J. deppeana</i> forma <i>sperryi</i> (Correll) R. P. Adams	dioecious
<i>J. deppeana</i> forma <i>zacatacensis</i> (Mart.) R. P. Adams	dioecious
<i>J. deppeana</i> Steudel var. <i>deppeana</i>	dioecious
<i>J. deppeana</i> var. <i>gamboana</i> (Mart.) R. P. Adams	dioecious, rarely monocious
<i>J. drupacea</i> Labill.	dioecious
<i>J. durangensis</i> var. <i>topiensis</i> R. P. Adams & S. Gonzalez	dioecious

<i>J. durangensis</i> Martinez	dioecious
<i>J. erectopatens</i> (Cheng & L. K. Fu) R. P. Adams	dioecious
<i>J. excelsa</i> M.-Bieb. var. <i>excelsa</i>	dioecious & monecious
<i>J. fargesii</i> (Rehder & Wils.) Kom.	dioecious
<i>J. flaccida</i> Schlecht.	dioecious
<i>J. foetidissima</i> Willd.	dioecious & monecious
<i>J. formosana</i> Hayata	dioecious
<i>J. gracilior</i> Pilger	dioecious
<i>J. gracilior</i> var. <i>ekmanii</i> (Florin) R. P. Adams	dioecious
<i>J. gracilior</i> var. <i>saxicola</i> (Britton & P. Wilson) R. P. Adams	dioecious
<i>J. gracilior</i> var. <i>urbaniana</i> (Pilger & Ekman) R. P. Adams	dioecious
<i>J. grandis</i> R. P. Adams	dioecious, 5.1% monecious
<i>J. horizontalis</i> Moench	dioecious
<i>J. indica</i> var. <i>caespitosa</i> Farjon	dioecious & monecious
<i>J. indica</i> Bertol.	dioecious & monecious
<i>J. jackii</i> (Rehder) R. P. Adams	dioecious
<i>J. jaliscana</i> Martinez	dioecious
<i>J. komarovii</i> Florin	dioecious & monecious
<i>J. macrocarpa</i> Sibth. & Sm.	dioecious
<i>J. maderensis</i> (Menezes) R. P. Adams	dioecious
<i>J. mairei</i> Lemee & Lev.	dioecious
<i>J. maritima</i> R. P. Adams	dioecious
<i>J. martinezii</i> Perez de la Rosa	dioecious
<i>J. microsperma</i> (Cheng & L. K. Fu) R. P. Adams	dioecious & monecious
<i>J. monosperma</i> (Engelm.) Sarg.	dioecious
<i>J. monticola</i> forma <i>compacta</i> Martinez	dioecious
<i>J. monticola</i> forma <i>orizabensis</i> Martinez	dioecious
<i>J. monticola</i> Martinez forma <i>monticola</i>	dioecious
<i>J. morrisonicola</i> Hayata	dioecious & monecious
<i>J. navicularis</i> Gand.	dioecious
<i>J. occidentalis</i> f. <i>corbetii</i> R. P. Adams	dioecious & monecious
<i>J. occidentalis</i> Hook.	dioecious, 52.4% & monecious, 47.6%
<i>J. osteosperma</i> (Torr.) Little	monecious, 89.2%, seldom dioecious, 10.8%
<i>J. ovata</i> (R. P. Adams) R. P. Adams	dioecious
<i>J. oxycedrus</i> L.	dioecious
<i>J. phoenicea</i> L.	monecious, rarely dioecious
<i>J. pinchotii</i> Sudworth	dioecious
<i>J. pingii</i> Cheng & Ferre.	monecious
<i>J. pingii</i> var. <i>miehei</i> Farjon	monecious
<i>J. poblana</i> (Martinez) R. P. Adams	dioecious
<i>J. poblana</i> var. <i>decurrens</i> R. P. Adams	dioecious
<i>J. polycarpos</i> K. Koch	dioecious
<i>J. polycarpos</i> var. <i>turcomanica</i> (B. Fedtsch.) R. P. Adams	dioecious
<i>J. procera</i> Hochst. ex. Endl.	dioecious & monecious
<i>J. przewalskii</i> Kom.	monecious
<i>J. pseudosabina</i> Fisch., Mey. & Ave-Lall.	dioecious, rarely monecious
<i>J. recurva</i> Buch.-Ham. ex D. Don.	monecious, rarely dioecious
<i>J. rigida</i> var. <i>conferta</i> (Parl.) Patschka	dioecious
<i>J. rigida</i> Mig. in Sieb. var. <i>rigida</i>	dioecious
<i>J. rushforthiana</i> (R. P. Adams) R. P. Adams	monecious
<i>J. sabina</i> L.	dioecious, rarely monecious
<i>J. sabina</i> var. <i>balkanensis</i> R. P. Adams & A. N. Tashev	dioecious, rarely monecious

<i>J. saltillensis</i> M. T. Hall	dioecious
<i>J. saltuaria</i> Rehder & Wils.	monecious
<i>J. scopulorum</i> Sarg.	dioecious
<i>J. semiglobosa</i> Regel var. <i>semiglobosa</i>	dioecious
<i>J. semiglobosa</i> var. <i>jarkendensis</i> (Kom.) R. P. Adams	dioecious
<i>J. semiglobosa</i> var. <i>talassica</i> (Lipsky) Silba	dioecious
<i>J. seravschanica</i> Kom.	dioecious
<i>J. squamata</i> var. <i>wilsonii</i> (Rehder) R. P. Adams	dioecious
<i>J. squamata</i> Buch.-Ham. ex D. Don in Lambert	monecious, rarely dioecious
<i>J. standleyi</i> Steyermark	dioecious
<i>J. taxifolia</i> Hook. & Arn.	dioecious
<i>J. taxifolia</i> var. <i>lutchuensis</i> (Koidz.) Satake	dioecious
<i>J. thurifera</i> L. var. <i>thurifera</i>	dioecious
<i>J. thurifera</i> var. <i>africana</i> Maire	dioecious
<i>J. tibetica</i> Kom.	monecious
<i>J. tsukusiensis</i> var. <i>taiwanensis</i> (R. P. Adams & C-F. Hsieh) R. P. Adams	dioecious
<i>J. tsukusiensis</i> var. <i>tsukusiensis</i> Masam.	dioecious
<i>J. turbinata</i> Guss.	dioecious & monecious
<i>J. uncinata</i> (R. P. Adams) R. P. Adams	monecious, rarely dioecious
<i>J. virginiana</i> L. var. <i>virginiana</i>	dioecious
<i>J. virginiana</i> var. <i>silicicola</i> (Small) E. Murray	dioecious
<i>J. zanonii</i> R. P. Adams	dioecious
Summary: completely dioecious (74.8%); Not completely dioecious 31 (25.2%); 12 monoecious (10.2%); 13 dioecious & monoecious (10.9%); 6 mostly dioecious, rarely monoecious (5.0%)	

To examine the phylogenetic distribution of dioecious and monoecious taxa, these traits were mapped onto a phylogenetic tree (Adams, 2014; Adams and Schwarzbach, 2013) shown in figure 1. The incidence of dioecy groups by clades (Fig. 1): all of sect. *Caryocedrus* and sect. *Juniperus* are dioecious; monoecy is only found in sect. *Sabina*, and even there, monoecy is grouped by clades. The serrate leaf margined junipers of the western hemisphere (percent data from Vasek, 1966) have 4 taxa with monoecy: *J. californica* (rarely monecious, 1.9%), *J. grandis* (5.1% monecious), *J. occidentalis*, 47.6% monecious) and *J. osteosperma* (89.2% monecious). This appears to be an isolated case of monoecy among the dioecious taxa of the serrate *Juniperus* of the western hemisphere (Fig. 1). The clade of smooth leaf, turbinate, 1-seeded cones, junipers of the eastern hemisphere (India to western China to Taiwan), contain only 3 taxa that appear to be dioecious: *J. fargesii*, *J. carinata*, and *J. coxii* and these are uncertain, because of limited observations of plants in the field by the author. They may be partially monecious. Fifteen (15) of the 18 taxa in this clade are monecious or partially monecious (Fig. 1). The third case of monoecy is in the excelsa group, smooth leaves, ovoid, multi-seeded cones, eastern hemisphere (eastern Mediterranean to western China, and Japan). This clade is composed a sub-clade of the *virginiana* group in the western hemisphere, that are all dioecious and a loose assemblage of junipers, of which approximately half are monoecious taxa (Fig. 1).

Finally, the fourth clade with monoecy is the *phoenicea/ turbinata* clade in the Mediterranean (Fig. 1). Both taxa in this clade have considerable monoecy. It might be noted *Hesperocyparis arizonica* and *H. bakeri* (outgroup) are both monecious.

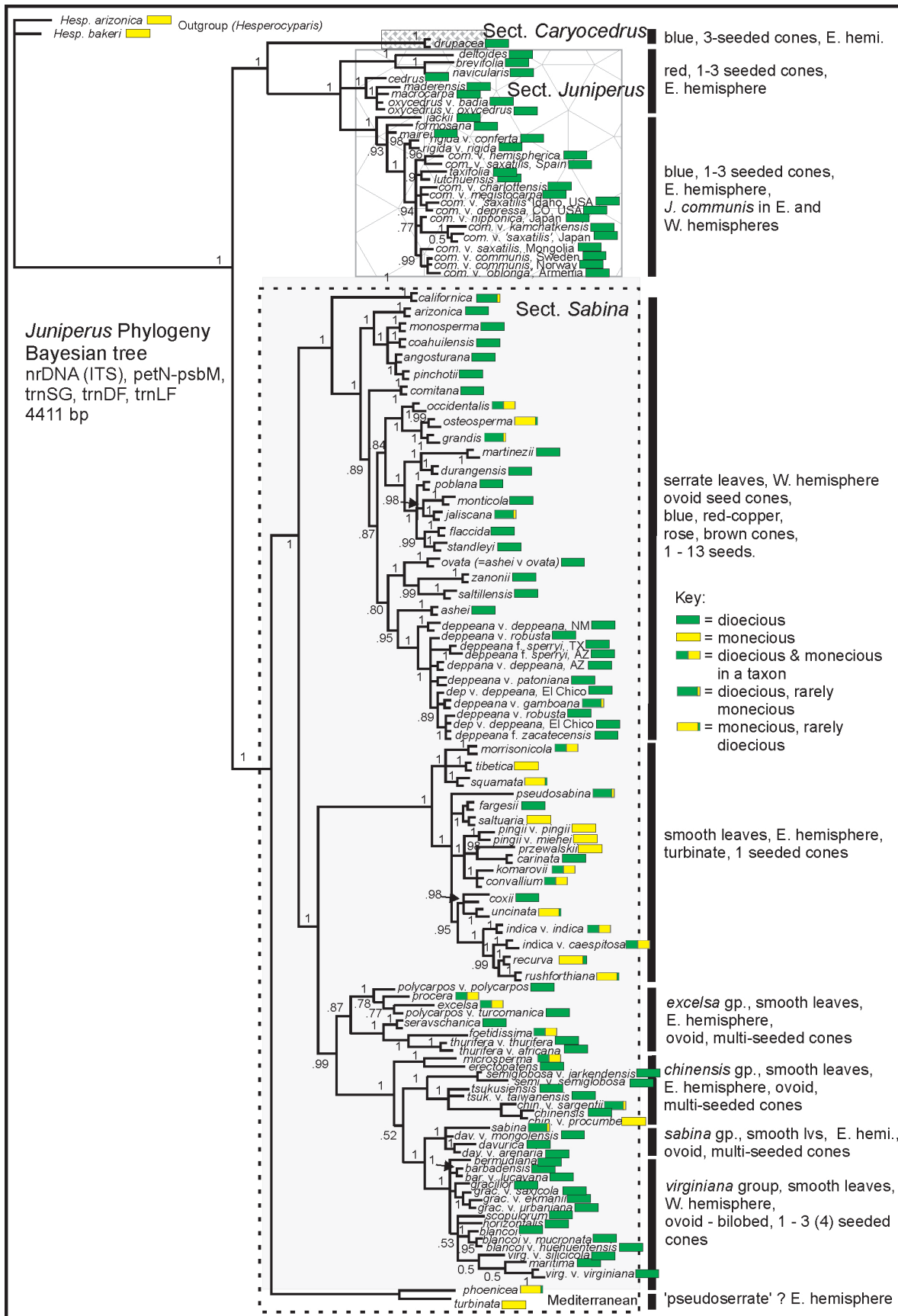


Figure 1. Bayesian phylogenetic tree of *Juniperus* with sexual system imposed.

All of the closely related relatives of *Juniperus* (Mao, et al. 2018; Zhu et al, 2018) are monecious (Table 2). This is also true (Fig. 2) for distant relatives (*Calocedrus*, *Microbiota*, *Platycladus*, *Thuja*).

Table 2. Sexual systems in cypresses (data ex Farjon, 2005; Rushforth, pers. comm.; Walas et al. 2018).

Taxon	Plants: dioecious, monecious or both; ex Farjon, 2005; Walas et al. 2018.
<i>Callitropsis nootkatensis</i>	monecious
<i>Cupressus cashmeriana</i>	monecious
<i>Cupressus chengiana</i>	monecious
<i>Cupressus duclouxiana</i>	monecious
<i>Cupressus dupreziana</i>	monecious
<i>Cupressus funebris</i>	monecious
<i>Cupressus gigantea</i>	monecious
<i>Cupressus sempervirens</i>	monecious
<i>Cupressus tonkinensis</i>	monecious
<i>Cupressus torulosa</i>	monecious
<i>Hesperocyparis arizonica</i>	monecious
<i>Hesperocyparis bakeri</i>	monecious
<i>Hesperocyparis benthamii</i>	monecious
<i>Hesperocyparis glabra</i>	monecious
<i>Hesperocyparis goveniana</i>	monecious
<i>Hesperocyparis guadalupensis</i>	monecious
<i>Hesperocyparis lusitanica</i>	monecious
<i>Hesperocyparis macnabiana</i>	monecious
<i>Hesperocyparis macrocarpa</i>	monecious
<i>Hesperocyparis sargentii</i>	monecious
<i>Xanthocyparis vietnamensis</i>	monecious

Plotting the sexual systems onto phylogenies of Mao, et al. 2018 and Zhu et al, 2018, clearly suggests that ancestors of *Juniperus* were monecious (yellow boxes, Figs.1,2). However, the direct ancestor of *Juniperus* appears to have been dioecious (green boxes, Figs. 1,2), because dioecy exhibits

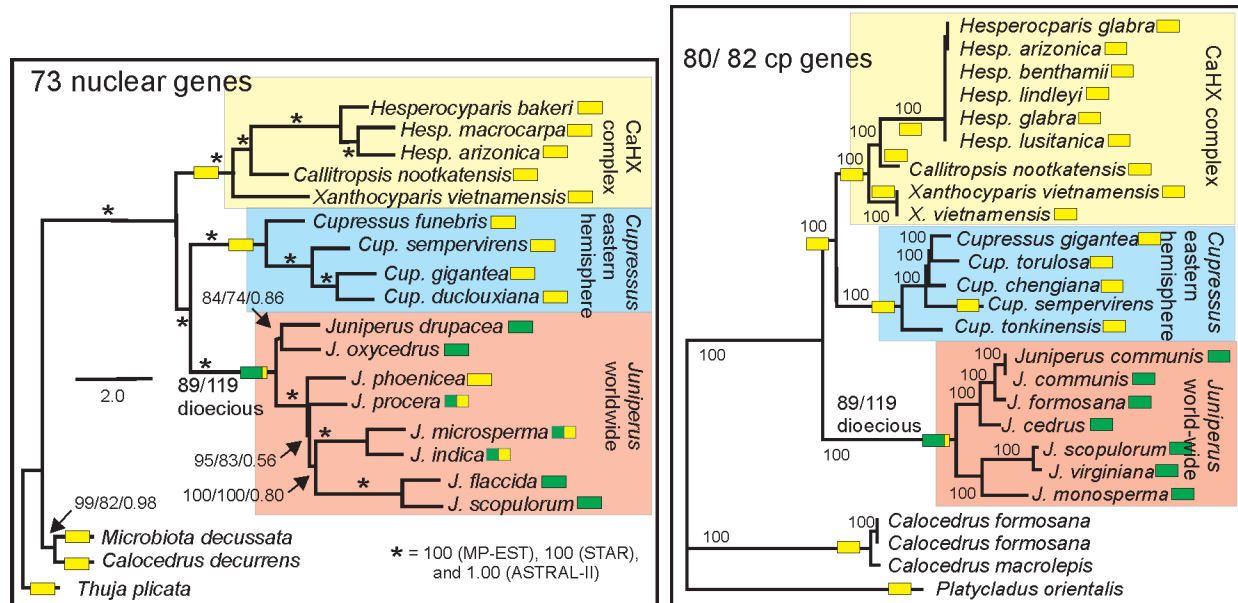


Figure 2. (left) Phylogeny of cypress-juniper clade based on 73 nuclear genes (Mao et al. 2018) with dioecy (green) and monoecy (yellow) included. (right) Phylogeny based on complete chloroplast genome sequencing (Zhu, et al. 2018) with dioecy and monoecy included. See text for discussion.

universal occurrence in sect. *Caryocedrus* (*J. drupacea*) and for all species of sect. *Juniperus* (*J. communis* and related species, Figs. 1, 2). Section *Sabina* is considered the most advanced section of *Juniperus*, and it is there, that one finds the re-emergence of monoecy.

The re-emergence of monoecy appears to have occurred in 5 events: in the *californica-grandis-occidentalis-osteosperma* species of the serrate leaf junipers of North America; almost universally in the smooth leaf, turbinate, 1-seeded cone, clade centered in eastern Mediterranean and central Asia; in the *excelsa* and *chinensis* complexes of central Asia and China; and in the *phoenicea/ turbinata* clade of the Mediterranean region.

Walas et al. (Table 3, 2018) reported that dioecy was more common in tropical gymnosperms whereas monoecy was more common colder climate gymnosperms. This does not appear to be the case in *Juniperus* in which cold-tolerant species are mostly dioecious.

In summary, the genus *Juniperus*, seems to run counter-current to other closely related genera (*Cupressus*, *Hesperocyparis*, *Callitropsis*, *Xanthocyparis*) which are uniformly monoecious. In contrast, *Juniperus*, perhaps the most recently evolved conifer, with the evolution of nutritious, small cones that are easily dispersed by birds over long distances, initially evolved the atypical dioecious sexual system, then later in its evolution has (re-) evolved monoecy among many phylogenetically advanced species.

ACKNOWLEDGEMENTS

This work supported by funds from Baylor University.

LITERATURE CITED

- Adams, R. P. 2014. *Junipers of the World: The genus Juniperus*, 4th Edition. Trafford Publ., Bloomington, IN.
- Adams, R. P. and A. E. Schwarzbach. 2013. Phylogeny of *Juniperus* using nrDNA and four cpDNA regions. *Phytologia* 95: 179-187.
- Charnov, E. L. 1982. The theory of sex allocation. Princeton monograph in population biology. (Vol. 18). Princeton University Press, New Jersey.
- Farjon, A. 2005. A monograph of Cupressaceae and *Sciadopitys*. Royal Botanic Gardens, Kew. Richmond, Surrey, UK.
- Mao, K-S., M. Ruhsam, Y-Z. Ma, S. W. Graham, J-Q. Liu, P. Thomas, R. I Milne and P. W. Hollingsworth. 2018. A transcriptome-based resolution for a key taxonomic controversy in Cupressaceae. *Ann. Bot.* XX: 1-15.
- Munoz-Reinoso, J. C. 2018. Advantages of being a monecious Juniper. *Phytologia* 100: 205-207.
- Renner, S. S. 2014. The relative and absolute frequencies of angiosperm sexual systems: Dioecy, monoecy, gynodioecy, and an updated online database. *Am. J. Bot.* 101: 1588-1596.
- Renner, S. S. and R. E. Ricklefs. 1995. Dioecy and its correlates in the flowering plants. *Amer. J. Bot.* 82: 596-606.
- Jordano, P. 1991. Gender variation and expression of monoecy in *Juniperus phoenicea* (L.) (Cupressaceae). *Bot. Gaz.* 152: 476-485.
- Vasek, F. C. 1966. The distribution and taxonomy of three western junipers. *Brittonia* 18: 350-372.
- Wallas, L., W. Mandryk, P. A. Thomas, Z. Tyrala-Wierucka and G. Iszkulo. 2018. Sexual systems in gymnosperms: A review. *Basic and Applied Ecology* 31: 1-9.
- Wiehlen, G. D., R. K. Oyama and M. Donoghue. 2000. Phylogenetic analysis of dioecy in monocotyledons. *Amer. Naturalist* 155: 46-58.
- Zhu, A., Weishu Fan, R. P. Adams and J. P. Mower. 2018. Phylogenomic evidence for ancient recombination between plastid genomes of the *Cupressus-Juniperus-Xanthocyparis* complex (Cupressaceae). *BMC Evolutionary Biology* 18:137, doi.org/10.1186/s12862-018-1258-2.