

Research paper

Recent advances on phylogenomics of gymnosperms and a new classification

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ABSTRACT

Living gymnosperms comprise four major groups: cycads, *Ginkgo*, conifers, and gnetophytes. Relationships among/within these lineages have not been fully resolved. Next generation sequencing has made available a large number of sequences, including both plastomes and single-copy nuclear genes, for reconstruction of solid phylogenetic trees. Recent advances in gymnosperm phylogenomic studies have updated our knowledge of gymnosperm systematics. Here, we review major advances of gymnosperm phylogeny over the past 10 years and propose an updated classification of extant gymnosperms. This new classification includes three classes (Cycadopsida, Ginkgoopsida, and Pinopsida), five subclasses (Cycadidae, Ginkgoideae, Cupressidae, Pinidae, and Gnetidae), eight orders (Cycadales, Ginkgoales, Araucariales, Cupressales, Pinales, Ephedrales, Gnetales, and Welwitschiales), 13 families, and 86 genera. We also described six new tribes including Acropyleae Y. Yang, Austrocedreae Y. Yang, Chamaecyparidae Y. Yang, Microcachrydeae Y. Yang, Papuacedreae Y. Yang, and Prumnopityeae Y. Yang, and made 27 new combinations in the genus *Sabina*.

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1. Introduction

Gymnosperms are a group of early-diverging seed plants defined by having ovules or seeds completely or partly exposed (vs. ovules enclosed in carpels in angiosperms) (Yang et al., 2017). Gymnosperms constitute one of the four major groups of land plants (the other three being bryophytes, ferns and fern allies, and

angiosperms) and possess some characters similar to ferns (e.g., circinnate young leaves in *Cycas* L., and presence of archegonia in female gametophytes and spermatozoids in cycads and *Ginkgo* L.), as well as similarities to angiosperms (e.g., possessing ovules/seeds and pollen tubes) (Christenhusz et al., 2011; Stevenson, 2013; Yang et al., 2017).

The origin of gymnosperms can be dated back to the mid-Devonian; *Runcaria heinzelinii* Stockmans is one of the oldest seed-like structures from Belgium with an age of ca. 385 myr (million years) (Gerrienne et al., 2004). This non-flowering seed plant group radiated and dominated land vegetation at the end of the Paleozoic (Rothwell and Scheckler, 1988). Almost all the living

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conifer families have a fossil record by the middle Jurassic (Taylor et al., 2009; Rothwell et al., 2012; Spencer et al., 2015; Farjon, 2018). The dominance of gymnosperms in the terrestrial vegetation has gradually declined since the origin and diversification of flowering plants in the Early Cretaceous. Today, gymnosperms retain their dominance in ca. 39% forests on Earth, being represented by four groups including 86 genera and over 1000 species (Christenhusz et al., 2011; Yang et al., 2017). The low species diversity of modern gymnosperms is largely explained by Cenozoic extinction of ancient lineages (Crisp and Cook, 2011); however many extant species originated from recent (Miocene) re-diversification (Davis and Schaefer, 2011; Nagalingum et al., 2011).

Relationships at the family level or above have been subject to debate. Is the family Ginkgoaceae related to cycads or to conifers? Are gnetophytes sister to Pinaceae or to conifers? Is the family Cephalotaxaceae nested within Taxaceae or not? (Wang and Ran, 2014; Yang et al., 2017; Ji et al., 2021). Recent phylogenomic data address these problems (Wu et al., 2013; Ran et al., 2018a; Stull et al., 2021). In addition, new progress has been made in a few families including Cycadaceae (Nagalingum et al., 2011; Salas-Leiva et al., 2013; Condamine et al., 2015), Ginkgoaceae (Zhao et al., 2019; Liu et al., 2021), Pinaceae (Ran et al., 2018b), Cupressaceae (Mao et al., 2012, 2019; Yang et al., 2012; Qu et al., 2017), Podocarpaceae (Knopf et al., 2012; Klaus and Matzke, 2020), and Taxaceae (Majeed et al., 2019; Ji et al., 2021; Xiong et al., 2021).

Taxonomy should be based on phylogeny. The most recent linear systematic arrangement of the gymnosperms is that of Christenhusz et al. (2011). This classification is widely adopted, although it contains a number of flaws. First, the classification is based on phylogenetic results using only a few molecular markers, so relationships among certain groups are not well-resolved (Chaw et al., 1997, 2000; Ran et al., 2010). Second, these authors ranked the four morphological groups into four subclasses, which do not reflect the latest phylogenomic advances concerning relationships of the four groups. For instance, whether *Ginkgo* is close to cycads or to conifers is unclear in their classification. Third, the subclass Pinidae is paraphyletic according to recent studies, with Gnetidae nested within Pinidae and they together form a monophyletic group sister to a clade including the remaining conifers (conifer II, Ran et al., 2018a; Stull et al., 2021). Recent phylogenomic results have reinforced this gnepine hypothesis (Ran et al., 2018a; Stull et al., 2021; Liu et al., 2022). Fourth, the sequence of the three families within the Gnetidae is not in accordance with their relationships. Christenhusz et al. (2011) treated the Welwitschiaceae at the beginning of the Gnetidae, followed by Gnetaceae and Ephedraceae successively. However, the Ephedraceae as the basal family within the Gnetidae is well-established (Lu et al., 2014; Ran et al., 2018a; Stull et al., 2021), so the sequence should be Ephedraceae, Gnetaceae, and Welwitschiaceae. Fifth, recent phylogenetic advances require that some generic changes are made, e.g., the *Xanthocyparis* complex and the *Callitris* complex (Terry et al., 2012; Zhu et al., 2018; Mao et al., 2019). Here we have summarized new advances in gymnosperm phylogeny and propose a new classification of extant gymnosperms.

2. Recent advances

2.1. Relationships of *Ginkgo*

Ginkgo represents an ancient lineage of seed plants containing a single relict species native to China (Lyu, 2019; Zhao et al., 2019). Recent phylogenomic studies have shown that a few natural populations of this relict species are sporadically scattered in eastern, southern and southwestern China (Gong et al., 2008; Zhao et al.,

2019). Its phylogenetic relationships with other lineages have been controversial. Some authors have argued that *Ginkgo* is close to cycads (Wu et al., 2013; Li et al., 2017; Ran et al., 2018a; Stull et al., 2021), which is supported by a number of reproductive characters, e.g., motile spermatozooids, branched pollen tubes functioning as haustoria, boat-shaped pollen, fleshy seeds with the integument differentiating into three layers (outer fleshy sarcotesta, middle sclerotesta, and inner membranous endotesta), and slow growth of pollen tubes in the female gametophyte (Gifford and Foster, 1989). Other researchers have suggested that *Ginkgo* is close to conifers plus gnetophytes (Gugerli et al., 2001; Ran et al., 2010), because they all possess simple leaves, monopodial branching, pycnoxylic wood, female organs organized into a compound female cone (the spur shoot) with the long ovulate peduncle axillary to scale leaves that are helically arranged on the spur shoot (vs. large compound leaves, bifurcate branching or unbranched stems, manoxylic wood, female cones simple with megasporophylls directly and helically arranged) (Gifford and Foster, 1989; Douglas et al., 2007). Christenhusz et al. (2011) treated *Ginkgo* as a separate subclass (Ginkgoideae) parallel to the other three subclasses including Cycadidae, Pinidae, and Gnetidae. Recent phylogenomics based on thousands of single-copy nuclear genes have consistently suggested that ginkgophyte is sister to cycadophyte (Ran et al., 2018a; Stull et al., 2021; Liu et al., 2022). Considering its unusual morphology and phylogeny, we treat *Ginkgo* as a class here in this updated classification of gymnosperms.

2.2. Relationships of gnetophytes and conifers

Gnetophytes have a number of unusual characters, e.g., bisexual cones, vessels in secondary wood, ovules partially enclosed in one or two outer envelopes, dicot-like pinnately veined broad leaves in *Gnetum* L., modified to a membranous sheath in *Ephedra* L. and giant strap-shaped leaves in *Welwitschia* Hook. f., archegonia absent in *Gnetum* and *Welwitschia* but present in *Ephedra* (Gifford and Foster, 1989). This unique set of characters has led many people to believe that the gnetophytes are direct ancestors (pseudanthial hypothesis) or relatives of ancestors of the angiosperms (anthophyte and euanthial hypotheses) (Yang et al., 2004; Friis et al., 2011). However, molecular phylogenetic studies have indicated that gnetophytes constitute a monophyletic group that is either sister to the Pinaceae (gnepine hypothesis, Gugerli et al., 2001; Ran et al., 2018a; Stull et al., 2021; Liu et al., 2022), or to the Cupressophytes, including Sciadopityaceae, Cupressaceae and Taxaceae (gnecup hypothesis, Wu et al., 2013), or to the conifers (gnetifer hypothesis, Ran et al., 2010), or to other living gymnosperms (Wang and Ran, 2014), or to other living seed plants (Wang and Ran, 2014; Song et al., 2021; Niu et al., 2022). Nuclear genomes of Gnetaceae and Welwitschiaceae were published recently (Wan et al., 2018, 2021). Phylogenomic results based on thousands of single-copy nuclear genes reinforce the gnepine hypothesis and negate the monophyly of conifers (Ran et al., 2018a; Stull et al., 2021; Liu et al., 2022). Accordingly, the traditional concept of conifers should be revised in a new classification. Here we classify conifers and gnetophytes in the class Pinopsida, and further divide the class into three subclasses representing the three major lineages.

2.3. Araucariaceae and Podocarpaceae

The sister relationship of the conifer families Podocarpaceae and Araucariaceae has been firmly established. However, traditional classification based on morphology classified them into different orders (Pilger and Melchior, 1954; *Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita*, 1978) as the two families

possess quite different morphology of female cones: Podocarpaceae possess reduced and usually fleshy cones, while Araucariaceae have typical woody cones. However, recent phylogenetic studies have consistently suggested that Podocarpaceae and Araucariaceae form a clade sister to another clade including Sciadopityaceae, Cupressaceae, and Taxaceae (Li et al., 2017; Ran et al., 2018a; Stull et al., 2021; Liu et al., 2022). Hence, we classify the two families in the order Araucariales. In addition, we classified the family Podocarpaceae according to a recent phylogenomic study that resulted in robust intergeneric relationships within the family (Chen et al., 2022).

2.4. Cupressaceae, Sciadopityaceae, and Taxaceae

Traditionally, *Sciadopitys* Siebold & Zucc. was included in Taxodiaceae, which was kept separate from Cupressaceae s.s. (*Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita*, 1978). Most phylogenetic studies have given rise to the clade including Sciadopityaceae, Cupressaceae s.l., and Taxaceae s.l. (Sciadopityaceae are sister to a clade including Cupressaceae s.l. and Taxaceae s.l.) (Ran et al., 2018a; Stull et al., 2021), though occasionally Sciadopityaceae are considered as the sister of the Podocarpaceae–Araucariaceae clade (Lu et al., 2014). Taxodiaceae, excluding *Sciadopitys*, are paraphyletic, and members of Taxodiaceae plus Cupressaceae s.s. constitute a monophyletic group (Gadek et al., 2000; Li and Yang, 2002; Lu et al., 2014; Ran et al., 2018a). These molecular phylogenetic results support a separation of Sciadopityaceae from Cupressaceae s.l. and incorporation of Taxodiaceae into Cupressaceae s.l. This phylogenetic result is tenable because it shows a tendency to reduction of female cones, i.e., *Sciadopitys* and the basal lineages of Cupressaceae usually having typical female cones, while late-diverged groups possess reduced female cones. In Taxaceae s.s., the female cones are so reduced and specialized that they have lost the seed scale complex typically present in other conifer families.

Phylogenetic relationships of *Cephalotaxus* Siebold & Zucc., the sole genus in Cephalotaxaceae, have been controversial. Lu et al. (2014) and Majeed et al. (2019) indicated that *Cephalotaxus* is nested within Taxaceae s.s., thus supporting an incorporation of Cephalotaxaceae into Taxaceae, i.e., Taxaceae s.l. However, a few recent studies determined that *Cephalotaxus* alone constitutes a clade sister to Taxaceae s.s. including *Austrotaxus* Compton, *Taxus* L., *Pseudotaxus* W.C. Cheng, *Amentotaxus* Pilg., and *Torreya* Arn. (Ran et al., 2018a; Ji et al., 2021; Stull et al., 2021; Liu et al., 2022), thus supporting a separation of Cephalotaxaceae from Taxaceae s.s. In an extreme case, the family Cephalotaxaceae was found to be sister to a clade including Taxaceae and Cupressaceae (Ran et al., 2010), which shows the necessity to separate Cephalotaxaceae from Taxaceae.

Morphologically, the two families are very different from one another in their female reproductive organs. In Cephalotaxaceae, the female organs are organized into a cone which consists of a number of morphological units, each of which consists of a vegetative bract subtending two axillary ovules. The ovule possesses a fleshy aril developed from the receptacle, the funiculus is more or less elongated into a short pedicel in the process of ripening. The family Taxaceae is a conifer without typical female cones—the female cone is highly reduced and specialized and consists of only a single seed having a fleshy aril; no seed scale complex is found in the family, whereas other conifer families possess female cones comprising bract scale and seed scale complexes. Some researchers have proposed that the aril of Taxaceae s.s. is a modified seed scale complex (see Taylor et al., 2009). However, a recent teratological and ontogenetic study suggests that the aril of *Pseudotaxus* is actually derived from a pair of leaves, not from a modified branch or integument (Dörken et al., 2018). This new observation is interesting and falsifies a long-standing hypothesis regarding the origin of the aril in

Taxaceae s.s. Based on that study, it is clear that there is no seed scale complex in the family Taxaceae s.s. Despite the structural difference of reproductive organs, however, for taxonomic purposes, a separation of Cephalotaxaceae from Taxaceae seems reasonable, because most recent phylogenetic results support a sister relationship between Cephalotaxaceae and Taxaceae s.s., and the female cones are quite different in the two families.

2.5. Relationships of the *Callitropsis*–*Cupressus*–*Hesperocyparis*–*Xanthocyparis* complex

Farjon and his collaborators described a new genus collected from Vietnam, i.e., *Xanthocyparis* Farjon & T.H. Nguyen (Farjon et al., 2002). The nomenclature of this genus and subsequent molecular systematic studies resulted in debates and taxonomic chaos within *Cupressus* L. and related genera (Farjon et al., 2002; Little, 2006; de Laubenfels, 2009; Zhu et al., 2018). Farjon et al. (2002) included *Callitropsis* Oerst. in the genus *Xanthocyparis*, i.e., *Xanthocyparis nootkatensis* (D. Don) Farjon & Harder. This inclusion made the name *Xanthocyparis* superfluous and illegitimate in nomenclature. For further use of *Xanthocyparis*, Mill and Farjon (2006) proposed to conserve *Xanthocyparis* against *Callitropsis*, and the nomenclature committee accepted their proposal (Brummitt, 2007). Little (2006) constructed a phylogeny of *Xanthocyparis*, *Callitropsis*, and *Cupressus* s.s., and found that *Cupressus* is diphyletic; he thus treated *Xanthocyparis*, *Callitropsis* and the New World *Cupressus* as a single genus. He adopted *Callitropsis* s.l. as the correct generic name and made a number of new combinations. But phylogenetic relationships among these generic clades were not resolved in that study. Christenhusz et al. (2011) took a conservative option and incorporated *Xanthocyparis*, *Callitropsis*, and *Hesperocyparis* Bartel & R.A. Price into *Cupressus*, which is paraphyletic with respect to *Juniperus* (Mao et al., 2019). Terry et al. (2012), Zhu et al. (2018), and Mao et al. (2019) resolved the phylogenetic relationships of these genera and recognized *Xanthocyparis* s.s., *Callitropsis* s.s., *Hesperocyparis* (New World *Cupressus*) and *Cupressus* s.s. (Old World *Cupressus*). *Callitropsis* s.s. and *Xanthocyparis* s.s. do not form a clade in these recent phylogenies; thus, Farjon's incorporation of *Callitropsis* s.s. into *Xanthocyparis* s.l. is untenable.

2.6. *Arceuthos*, *Juniperus* and *Sabina*

In *Flora Reipublicae Popularis Sinicae*, *Sabina* Mill. was treated as a separate genus from *Juniperus* L. (Wang et al., 1978), but in *Flora of China*, *Sabina* was incorporated into the latter. *Sabina* is easily distinguished from *Juniperus* s.s. based on morphology, i.e., presence of acicular leaves in *Juniperus* s.s. (vs. existence of both acicular and scale leaves in *Sabina*), acicular leaves having joints at the base in *Juniperus* s.s. (vs. no joints at the base in *Sabina*), terminal buds prominent in *Juniperus* s.s. (vs. inconspicuous in *Sabina*), seed scales ternately arranged in *Juniperus* s.s. (vs. decussately or ternately arranged in *Sabina*), and ovules between seed scales in *Juniperus* s.s. (vs. ovules inserted on the ventral side of seed scales in *Sabina*). Adams (2008) reconstructed a phylogeny using nrITS and plastome *trnC-trnD* sequences which supported a subdivision of the genus into three sections: sect. *Caryocedrus* Endl., sect. *Juniperus*, and sect. *Sabina* (Mill.) Spach. Mao et al. (2010) obtained a well-resolved phylogeny of *Juniperus* s.l. and confirmed these three sections. Adams (2008) tabulated the morphological differences between the three sections including the leaf shape, female cone size, female cone texture, and female cone color. Reproductive differences between the three sections were corroborated in Jagel and Dörken (2015). Considering the agreement between the phylogenetic results and the morphological differences, it seems reasonable to divide the genus *Juniperus* into three genera, *Juniperus* s.s. (sect.

Juniperus), *Sabina* (sect. *Sabina*), and *Arceuthos* Antoine & Kotschy (sect. *Caryocedrus*). *Arceuthos* possesses winter terminal buds, leaves with a basal abscission zone, large female cones (18–25 mm) with 3 whorls of ternately arranged seed scales and seeds fused together in a hard bony-textured nut. *Juniperus* s.s. is similar to *Arceuthos* in the presence of winter terminal buds and basal abscission zone of leaves, having valvate seed scales and bearing one seed on each fertile scale, but differs from the latter in the female cone being smaller (6–15 mm vs. 18–25 mm in *Arceuthos*) and having three free seeds (vs. fused seeds in *Arceuthos*). *Sabina* is markedly distinguished from *Arceuthos* and *Juniperus* s.s. by having leaves decurrent down stem, female cones with peltate seed scales and free, unfused seeds, but lacking winter terminal buds and basal abscission zone (Adams, 2008, 2014).

2.7. Callitris, Actinostrobus and Neocallitropsis

Recent phylogenetic studies have suggested that *Actinostrobus* Miq. and *Neocallitropsis* Florin are nested within *Callitris* Vent. (Piggin and Bruhl, 2010; Larter et al., 2017). This result inevitably leads to an inclusion of the oligo-specific *Actinostrobus* and the monotypic *Neocallitropsis* into *Callitris*. Here we have treated *Actinostrobus* and *Neocallitropsis* as synonyms of *Callitris*.

3. An updated classification

This new classification of extant gymnosperms (Acrogymnospermae/Pinophytina) contains three classes, five subclasses, eight orders, 13 families, and 86 genera (Table 1; Fig. 1). Our classification differs from Christenhusz et al. (2011) in a number of aspects. First, we divide the extant gymnosperms into three classes, i.e., Cycadopsida including cycads, Ginkgoopsida encompassing *Ginkgo*, and Pinopsida containing conifers and gnetophytes. There is no class category in the classification of Christenhusz et al. (2011). Second, we divide the living gymnosperms into five subclasses, Cycadidae, Ginkgoideae, and Gnetidae are the same as those in Christenhusz et al. (2011), but we classify conifers into two subclasses: Pinidae including Pinaceae, and Cupressidae containing the remaining conifer families (Araucariaceae, Podocarpaceae, Sciadopityaceae, Cupressaceae, Cephalotaxaceae, and Taxaceae). The linear sequence of the five subclasses is basically according to their phylogenetic relationships and morphological specialization, i.e., Cycadidae, Ginkgoideae, Cupressidae, Pinidae, and Gnetidae. Third, we treat Cephalotaxaceae as a separate family from Taxaceae; thus, there are 13 families in our new classification. Fourth, we recognize *Arceuthos*, *Callitropsis*, *Hesperocyparis*, *Pectinopitys* C.N. Page, *Sabina*, and *Xanthocyparis*, and accept *Actinostrobus* and *Neocallitropsis* as synonyms of *Callitris*, and *Fokienia* as synonymous with *Chamaecyparis*

Table 1
Diversity of gymnosperm families.

Family	Genus	Species
Araucariaceae	3	40
Cephalotaxaceae	1	10
Cupressaceae	31	169
Cycadaceae	1	126
Ephedraceae	1	70
Ginkgoaceae	1	1
Gnetaceae	1	46
Pinaceae	11	272
Podocarpaceae	20	181
Sciadopityaceae	1	1
Taxaceae	5	29
Welwitschiaceae	1	1
Zamiaceae	9	255
Total	86	1201

(Rushforth, 2007; Page, 2019; Wang et al., 2022). Fifth, we describe six new tribes (Acropyleae, Austrocedreae, Chamaecyparideae, Microcachrydeae, Papuacedreae, and Prumnopityeae).

3.1. Taxonomic treatment

A synoptic classification is provided here; and the new classification with synonyms is in Appendix 1. In addition, we also provide a key and diagnoses of families in Appendix 2, and a global species list of extant gymnosperms in Appendix 3.

- Pinophytina** Cronquist, Takht. & Zimmerm. ex Reveal (松亚门)
- Cl. 1. **Cycadopsida** Brongn. (苏铁纲)
- Subcl. 1. **Cycadidae** Pax (苏铁亚纲)
- Ord. 1. **Cycadales** Pers. ex Bercht. & J. Presl (苏铁目)
- Fam. 1. **Cycadaceae** Pers. (苏铁科)
- Cycas* L.
- Fam. 2. **Zamiaceae** Horan. (泽米铁科)
- Subfam. 1. **Diooideae** Pilg. (双子铁亚科)
- Trib. 1. **Dioeae** J. Schust. (双子铁族)
- Dioon** Lindl., nom. cons. (双子铁属)
- Subfam. 2. **Zamioideae** Potonié (泽米铁亚科)
- Trib. 2. **Boweniaeae** J. Schust. (多羽铁族)
- Bowenia** Hook. f. (多羽铁属)
- Trib. 3. **Zamieae** Miq. (泽米铁族)
- Ceratozamia** Brongn. (角状铁属)
- Microcycas** (Miq.) A. DC. (小苏铁属)
- Stangeria** T. Moore (蕨铁属)
- Zamia** L., nom. cons. (泽米铁属)
- Trib. 4. **Encephalarteae** Miq. (非洲铁族)
- Encephalartos** Lehm. (非洲铁属)
- Lepidozamia** Regel (鳞木铁属)
- Macrozamia** Miq. (澳洲铁属)
- Cl. 2. **Ginkgoopsida** Engl. (银杏纲)
- Subcl. 2. **Ginkgoideae** Engl. (银杏亚纲)
- Ord. 2. **Ginkgoales** Gorozh. (银杏目)
- Fam. 3. **Ginkgoaceae** Engl., nom. cons. (银杏科)
- Ginkgo** L. (银杏属)
- Cl. 3. **Pinopsida** Burnett (松纲)
- Subcl. 3. **Cupressidae** Doweld (柏亚纲)
- Ord. 3. **Araucariales** Gorozh. (南洋杉目)
- Fam. 4. **Araucariaceae** Henkel et W. Hochst., nom. cons. (南洋杉科)
- Agathis** Salisb., nom. cons. (贝壳杉属)
- Araucaria** Juss. (南洋杉属)
- Wollemia** W.G. Jones et al. (凤尾杉属)
- Fam. 5. **Podocarpaceae** Endl., nom. cons. (罗汉松科)
- Subfam. 1. **Phyllocladoideae** W. Hochst. (叶枝杉亚科)
- Trib. 1. **Phyllocladeae** Dumort. (叶枝杉族)
- Halocarpus** Quinn (白袍杉属)
- Lagarostrobos** Quinn (泣松属)
- Lepidothamnus** Phil. (沼银松属)
- Manoao** Molloy (白银松属)
- Parasitaxus** de Laub. (寄生松属)
- Phyllocladus** Rich. ex Mirb., nom. cons. (叶枝杉属)
- Trib. 2. **Prumnopityeae** Y. Yang, trib. nov. (核果杉族)
- Pectinopitys** C.N. Page (梳叶杉属)
- Prumnopitys** Phil. (核果杉属)
- Sundacarpus** (J. Buchholz et N.E. Gray) C.N. Page (巽他杉属)
- Subfam. 2. **Podocarpoideae** Beilschm. (罗汉松亚科)
- Trib. 3. **Saxegothaeae** Gordon (卓杉族)
- Saxegothaea** Lindl., nom. cons. (卓杉属)
- Trib. 4. **Microcachrydeae** Y. Yang, trib. nov. (寒寿松族)
- Microcachrys** Hook. f. (寒寿松属)
- Trib. 5. **Pherosphaereae** Pilg. (小泣松族)
- Pherosphaera** W. Archer bis (小泣松属)

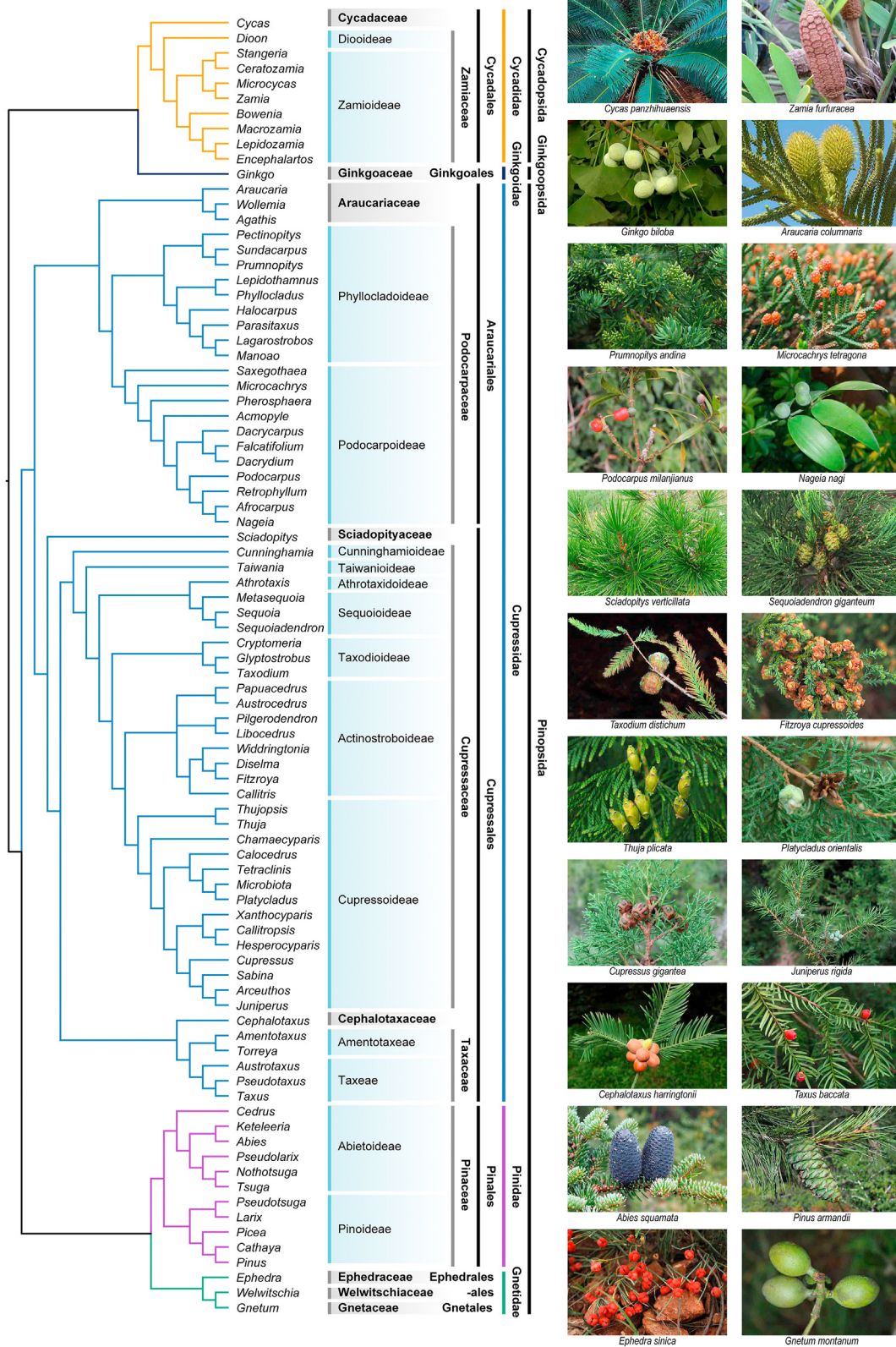


Fig. 1. Cladogram displaying phylogenetic relationships among extant gymnosperms. Clade color indicates subclasses. Relationships are basically according to recent gymnosperm phylogenies (Lu et al., 2014; Ran et al., 2018a; Stull et al., 2021), Cupressaceae (Mao et al., 2010, 2012, 2019), Cycadales (Condamine et al., 2015), Pinaceae (Ran et al., 2018b), Podocarpaceae (Chen et al., 2022).

Trib. 6. **Acmopyleae** Y. Yang, *trib. nov.* (绒袍杉族)
Acmopyle Pilg. (绒袍杉属)
 Trib. 7. **Dacrydiaceae** Gordon (陆均松族)
Dacrycarpus (Endl.) de Laub. (鸡毛松属)
Dacrydium Sol. ex G. Forst. (陆均松属)
Falcatifolium de Laub. (镰叶杉属)
 Trib. 8. **Podocarpeae** Dumort. (罗汉松族)
Afrocarpus (J. Buchholz & N.E. Gray) C.N. Page (非洲杉属)
Nageia Gaertn. (竹柏属)
Podocarpus L'Hér. ex Pers., *nom. cons.* (罗汉松属)
Retrophyllum C.N. Page (扭叶杉属)
 Ord. 4. **Cupressales** Link (柏目)
 Fam. 6. **Sciadopityaceae** Luerss. (金松科)
Sciadopitys Siebold & Zucc. (金松属)
 Fam. 7. **Cupressaceae** Gray, *nom. cons.* (柏科)
 Subfam. 1. **Cunninghamioideae** Silba (杉木亚科)
Cunninghamia R. Br., *nom. cons.* (杉木属)
 Subfam. 2. **Taiwanioideae** L.Chu Li (台湾杉亚科)
Taiwania Hayata (台湾杉属)
 Subfam. 3. **Athrotaxidoideae** L.Chu Li (密叶杉亚科)
Athrotaxis D. Don (密叶杉属)
 Subfam. 4. **Sequoioideae** Quinn (红杉亚科)
Metasequoia Hu & W.C. Cheng, *nom. cons.* (水杉属)
Sequoia Endl., *nom. cons.* (红杉属)
Sequoiadendron J. Buchholz (巨杉属)
 Subfam. 5. **Taxodioideae** Endl. ex K. Koch (落羽杉亚科)
Cryptomeria D. Don (柳杉属)
Glyptostrobus Endl. (水松属)
Taxodium Rich. (落羽杉属)
 Subfam. 6. **Actinostroboideae** Koehne (星鳞柏亚科)
 Trib. 1. **Papuacedreae** Y. Yang, *trib. nov.* (巴布亚柏族)
Papuacedrus H.L. Li (巴布亚柏属)
 Trib. 2. **Austrocedreae** Y. Yang, *trib. nov.* (智利翠柏族)
Austrocedrus Florin & Boutelje (智利翠柏属)
 Trib. 3. **Libocedreae** H.L. Li (甜柏族)
Libocedrus Endl. (甜柏属)
Pilgerodendron Florin (火地柏属)
 Trib. 4. **Diselmeae** Henkel & W. Hochst. (寒寿柏族)
Diselma Hook. f. (寒寿柏属)
Fitzroya Hook. f. ex Lindl., *nom. cons.* (智利乔柏属)
Widdringtonia Endl. (南非柏属)
 Trib. 5. **Actinostroboeae** Henkel et W. Hochst. (星鳞柏族)
Callitris Vent. (澳柏属)
 Subfam. 7. **Cupressoideae** Sweet (柏木亚科)
 Trib. 6. **Thujopsidaeae** Henkel et W. Hochst. (罗汉柏族)
Thuja L. (崖柏属)
Thujopsis Siebold et Zucc. ex Endl., *nom. cons.* (罗汉柏属)
 Trib. 7. **Chamaecyparideae** Y. Yang, *trib. nov.* (扁柏族)
Chamaecyparis Spach (扁柏属)
 Trib. 8. **Tetraclineae** H.L. Li (香漆柏族)
Calocedrus Kurz (翠柏属)
Microbiota Kom. (胡柏属)
Platyclusus Spach (侧柏属)
Tetraclinis Mast. (香漆柏属)
 Trib. 9. **Cupresseae** Dumort. (柏木族)
Arceuthos Antoine et Kotschy (合子刺柏属)
Callitropsis Oerst. (北美金柏属)
Cupressus L. (柏木属)
Hesperocyparis Bartel & R.A. Price (美洲柏木属)
Juniperus L. (刺柏属)
Sabina Mill. (圆柏属)
Xanthocyparis Farjon et T.H. Nguyen, *nom. cons.* (金柏属)
 Fam. 8. **Cephalotaxaceae** Neger (三尖杉科)
Cephalotaxus Siebold et Zucc. ex Endl. (三尖杉属)
 Fam. 9. **Taxaceae** Gray, *nom. cons.* (红豆杉科)

Trib. 1. **Amentotaxae** W.C. Cheng et C.D. Chu (穗花杉族)
Amentotaxus Pilg. (穗花杉属)
Torreya Arn., *nom. cons.* (榧属)
 Trib. 2. **Taxaeae** Rich. ex Duby (红豆杉族)
Austrotaxus Compton (南紫杉属)
Pseudotaxus W.C. Cheng (白豆杉属)
Taxus L. (红豆杉属)
 Subcl. 4. **Pinidae** Cronquist, Takht. et W. Zimm. (松亚纲)
 Ord. 5. **Pinales** Gorozh. (松目)
 Fam. 10. **Pinaceae** Spreng. ex F. Rudolphi, *nom. cons.* (松科)
 Subfam. 1. **Abietoideae** Sweet (冷杉亚科)
 Trib. 1. **Cedreae** Tiegh. (雪松族)
Cedrus Trew, *nom. cons.* (雪松属)
 Trib. 2. **Abieteeae** Dumort. (冷杉族)
Abies Mill. (冷杉属)
Keteleeria Carrière (油杉属)
 Trib. 3. **Pseudolariceae** L. Chu Li (金钱松族)
Nothotsuga Hu ex C.N. Page (长苞铁杉属)
Pseudolarix Gordon, *nom. cons.* (金钱松属)
Tsuga (Endl.) Carrière (铁杉属)
 Subfam. 2. **Pinoideae** W. Hochst. (松亚科)
 Trib. 4. **Lariceae** Rouy (落叶松族)
Larix Mill. (落叶松属)
Pseudotsuga Carrière (黄杉属)
 Trib. 5. **Pineae** Bluff et Fingerh. (松族)
Cathaya Chun et Kuang, *nom. cons.* (银杉属)
Picea A. Dietr. (云杉属)
Pinus L. (松属)
 Subcl. 5. **Gnetidae** Pax (买麻藤亚纲)
 Ord. 6. **Ephedrales** Dumort. (麻黄目)
 Fam. 11. **Ephedraceae** Dumort., *nom. cons.* (麻黄科)
Ephedra Tourn. ex L. (麻黄属)
 Ord. 7. **Welwitschiales** Skotts. ex Reveal (百岁兰目)
 Fam. 12. **Welwitschiaceae** Caruel, *nom. cons.* (百岁兰科)
Welwitschia Hook. f., *nom. cons.* (百岁兰属)
 Ord. 8. **Gnetales** Mart. (买麻藤目)
 Fam. 13. **Gnetaceae** Blume, *nom. cons.* (买麻藤科)
Gnetum L. (买麻藤属)

3.2. Description of new taxa

3.2.1. **Acmopyleae** Y. Yang, *trib. nov.* (绒袍杉族 新拟)

Type: *Acmopyle* Pilg.

Diagnosis. Dioecious small trees, evergreen. Leaves spirally arranged; dimorphic: small and scale-like on leading and reproductive shoots, bigger and foliar on lateral vegetative shoots. Male cones consisting of spirally arranged, triangular microsporophylls; pollen bisaccate. Female cones solitary, forming an irregular fleshy and verrucose receptacle. Seeds solitary, nearly erect at maturity, partially covered with a bluish, fleshy epimatium.

Diversity and distribution. The monotypic tribe belongs to Podocarpaceae and has two species that are disjunctly distributed in New Caledonia and Fiji (Fig. 2).

3.2.2. **Austrocedreae** Y. Yang, *trib. nov.* (智利翠柏族 新拟)

Type. *Austrocedrus* Florin & Boutelje

Diagnosis. Dioecious trees, evergreen. Leaves scale-like; lateral leaves thick, curving inwards at the apex; facial leaves blunt, having an indistinct gland on the adaxial surface and white stomatal bands on the abaxial surface; facial leaves slightly smaller than lateral ones. Female cones solitary, consisting of two pairs of seed scales, the lower pair smaller and reflexed; seed scales having a subapical bract apex. Seeds unequally 2-winged.

Diversity and distribution. The monotypic tribe belongs to Cupressaceae and is distributed in southern South America

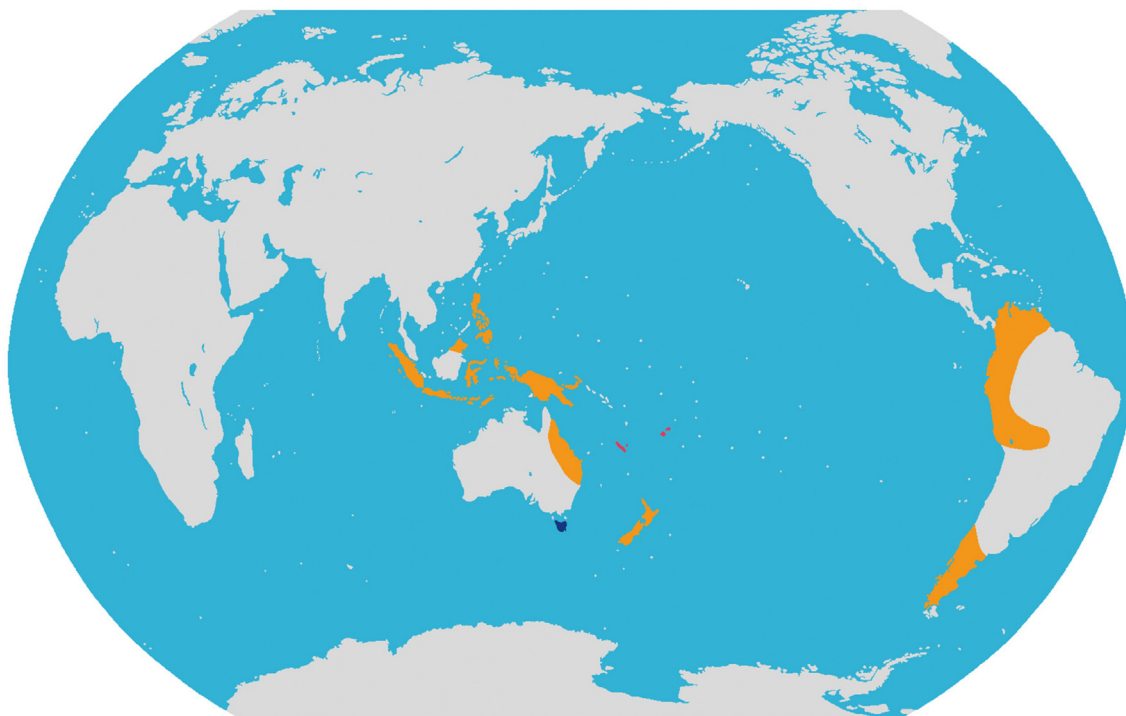


Fig. 2. Distribution of the three new tribes of Podocarpaceae. Pink: *Acropyleae* Y. Yang, *trib. nov.*; Blue: *Microcachrydeae* Y. Yang, *trib. nov.*; Orange: *Prumnopityeae* Y. Yang, *trib. nov.*

including S Argentina (Chubut, Neuquen, Rio Negro) and S Chile (Valparaiso, O'Higgins, Maule, Bio Bio, Araucania, Los Lagos, Reg. Metropolitana) (Fig. 3).

3.2.3. *Chamaecyparideae* Y. Yang, *trib. nov.* (扁柏族 新拟)
Type. *Chamaecyparis* Spach

Diagnosis. Monoecious trees or rarely shrubs. Branchlets usually dorsiventrally flattened in fan-shaped or pinnately flattened sprays. Leaves opposite in four series, juvenile leaves subulate, mature leaves scale-like, green above, possessing white or greenish white stomatal bands below. Male cones ovoid or oblong, consisting of 2–3 pairs of microsporophylls. Female cones woody, globose

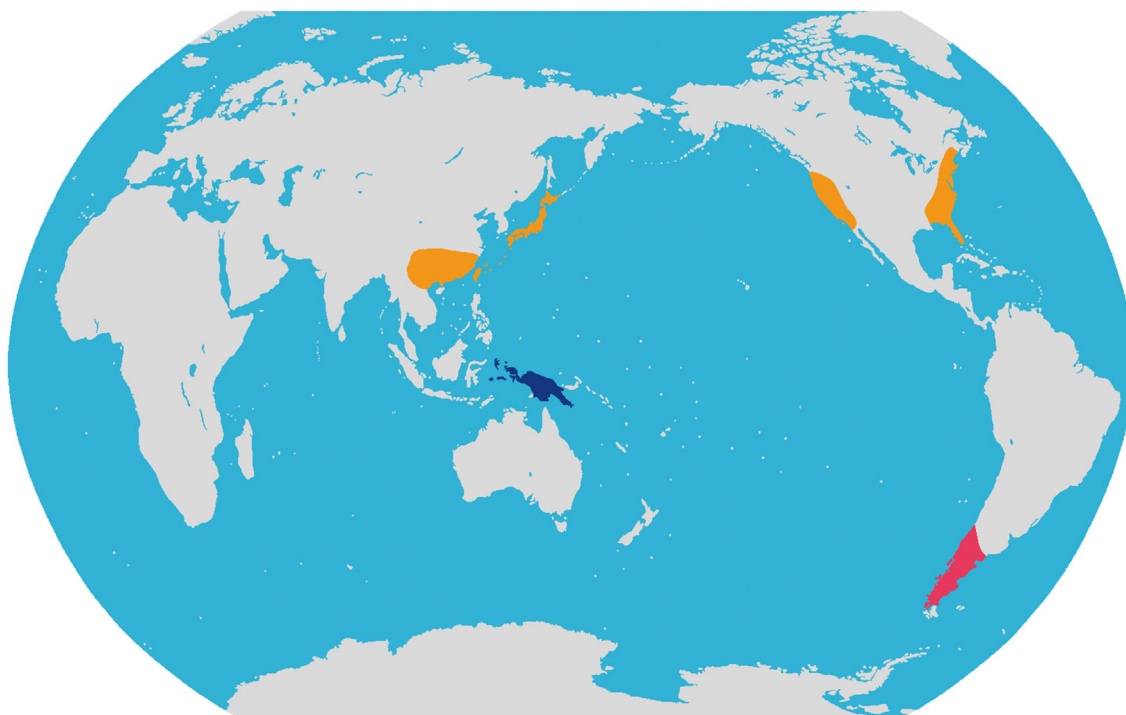


Fig. 3. Distribution map of the three new tribes of Cupressaceae. Pink: *Austrocedreae* Y. Yang, *trib. nov.*; Orange *Chamaecyparideae* Y. Yang, *trib. nov.*; Blue: *Papuacedreae* Y. Yang, *trib. nov.*

to ovoid-globose, consisting of 4–8 pairs of decussate, peltate, woody seed scales, terminal pair fused. Seeds normally 2–4 per seed scale, possessing two lateral membranous wings.

Diversity and distribution. The monotypic tribe belongs to Cupressaceae and contains only one genus and is disjunctly distributed in E Asia (Japan and southern China) and N America (Fig. 3).

3.2.4. *Microcachrydeae* Y. Yang, **trib. nov.** (寒寿松族 新拟)

Type. *Microcachrys* Hook.f.

Diagnosis. Monoecious prostrate shrubs, evergreen. Branches spreading. Twigs 4-angled in cross section. Leaves triangular, small, usually lanceolate and decurrent on whip shoots, triangular and keeled on lateral twigs. Male cones terminal. Seed cones terminal, ovoid to globose, fleshy and bright red when ripe. Only one inverted seed per fertile seed scale, partially covered by an asymmetrical cup-like epimatium at the base.

Diversity and distribution. This monotypic tribe belongs to Podocarpaceae and includes only *Microcachrys* (one species), which is distributed in W Tasmania, Australia (Fig. 2).

3.2.5. *Papuacedreae* Y. Yang, **trib. nov.** (巴布亚柏族 新拟)

Type. *Papuacedrus* H.L. Li.

Diagnosis. Tall trees, rarely shrubs. Branches and twigs usually flattened, glabrous, with flattened leaves. Leaves on lateral twigs scale-like, decussate or in whorls of four; facial leaves smaller than lateral leaves; rhombic, lanceolate to oblong; two broad stomatal bands on abaxial surface. Male cones cylindrical, consisting of 8–30 peltate microsporophylls. Female cones terminal, consisting of two decussate pairs of seed scales, upper pair larger; seed scales having a small and recurved bract apex in the middle part. Seeds 2–4, angular ovoid or oblique; wings 2 on opposite sides, membranous.

Diversity and distribution. This monotypic tribe belongs to Cupressaceae and contains only *Papuacedrus* (one species), which is restricted to New Guinea and Maluku (the Moluccas) (Fig. 3).

3.2.6. *Prumnopityeae* Y. Yang, **trib. nov.** (核果杉族 新拟)

Type. *Prumnopitys* Phil.

Diagnosis. Dioecious trees, evergreen. Leaves flattened, linear, 1-veined, spirally arranged, appearing distichous, decurrent. Pollen cones aggregated into spikes. Seed cones consisting of one to a few spirally arranged bracts; only one single erect ovule axillary to the small distal bracts; lacking any fleshy receptacle at maturity. Seeds ovoid, with a drupe-like, thick, fleshy, colored, and globose or ovoid-elliptic epimatium.

Diversity and distribution. This tribe belongs to Podocarpaceae and includes eight species in three genera, i.e., *Pectinopitys*, *Prumnopitys*, *Sundacarpus*. These genera are distributed in SE Asia, East Australia, New Caledonia and New Zealand, and from Chile to Venezuela and Costa Rica (Fig. 2). *Pectinopitys* has six species that are distributed in South America (2), Costa Rica (1), New Zealand (1), New Caledonia (1), and Australia (1). *Prumnopitys* has three species that are distributed in South America (2), Fiji (1), and New Zealand (1). *Sundacarpus* is monotypic and distributed in Australia (NE-Queensland); New Guinea (Irian Jaya, Papua New Guinea); Bismarck Arch. (New Britain, New Ireland); Moluccas (Buru, Halmaheira, Morotai); Lesser Sunda Isl. (Timor, Flores, West Sumbawa, Lombok); Java; C-Sulawesi; SW-Sulawesi; Borneo; Sumatra; Philippines.

3.3. New combinations

We treat *Sabina* as a separate genus, and transfer 27 names from *Juniperus* to *Sabina*.

3.3.1. *Sabina angosturana* (R.P. Adams) Y. Yang et K.S. Mao, **comb. nov.** (安吉斯图拉圆柏)

Basionym: *Juniperus angosturana* R.P. Adams, Biochem. Syst. Ecol. 22(7): 704 (1994).

Synonym: *Juniperus monosperma* var. *gracilis* Martínez, Anales Inst. Biol. Univ. Nac. Autón. México, Bot. 17: 111 (1946).

Distribution: Mexico (Coahuila, Hidalgo, Nuevo Leon, San Luis Potosí, Tamaulipas).

3.3.2. *Sabina arizonica* (R.P. Adams) Y. Yang et K.S. Mao, **comb. nov.** (亚利桑那圆柏)

Basionym: *Juniperus coahuilensis* var. *arizonica* R. P. Adams, Biochem. Syst. Ecol. 22(7): 708 (1994).

Synonym: *Juniperus arizonica* (R.P. Adams) R.P. Adams, Phytologia 88(3): 306 (2006).

Distribution: Mexico (Sonora); United States (Arizona, New Mexico).

3.3.3. *Sabina ashei* (J. Buchholz) Y. Yang et K.S. Mao, **comb. nov.** (阿什圆柏)

Basionym: *Juniperus ashei* J. Buchholz, Bot. Gaz. 9: 329, Figs. 1 and 2 (1930).

Distribution: Mexico (Coahuila); United States (Arkansas, Missouri, Oklahoma, Texas).

3.3.4. *Sabina blancoi* (Martínez) Y. Yang et K.S. Mao, **comb. nov.** (布兰科圆柏)

Basionym: *Juniperus blancoi* Martínez, Anales Inst. Biol. Univ. Nac. México 17: 73, Figs. 59–63 (1946).

Distribution: Mexico (Chihuahua, Durango, Mexico, Sonora).

3.3.5. *Sabina coahuilensis* (Martínez) Y. Yang et K.S. Mao, **comb. nov.** (科阿韦拉圆柏)

Basionym: *Juniperus erythrocarpa* var. *coahuilensis* Martínez, Anales Inst. Biol. Univ. Nac. México 17: 114, Figs. 95–97 (1946).

Synonym: *Juniperus coahuilensis* (Martínez) Gausson ex R. P. Adams, Phytologia 74: 413 (1993).

Distribution: Mexico (Chihuahua, Coahuila, Durango, Nayarit, Tamaulipas, Zacatecas); United States (Texas).

3.3.6. *Sabina comitana* (Martínez) Y. Yang et K.S. Mao, **comb. nov.** (恰帕斯圆柏)

Basionym: *Juniperus comitana* Martínez, Anales Inst. Biol. Univ. Nac. México 15: 12, Figs. 5–8 (1944).

Distribution: Guatemala; Mexico (Chiapas).

3.3.7. *Sabina compacta* (Martínez) Y. Yang et K.S. Mao, **comb. et stat. nov.** (墨西哥圆柏)

Basionym: *Juniperus monticola* f. *compacta* Martínez, Anales Inst. Biol. Univ. Nac. México 17: 85, Figs. 71–73 (1946).

Synonyms: *Juniperus monticola* subsp. *compacta* (Martínez) Silba, J. Int. Conifer Preserv. Soc. 13(1): 12 (2006); *Juniperus compacta* (Martínez) R. P. Adams, Phytologia 89(3): 368 (2007), *nom. inval.*

Distribution: Guatemala; Mexico (Guerrero, Hidalgo, Jalisco, Mexico City, Mexico, Michoacán, Nuevo Leon, Puebla, Veracruz).

3.3.8. *Sabina coxii* (A.B. Jacks.) Y. Yang et K.S. Mao, **comb. nov.** (小果垂枝圆柏)

Basionym: *Juniperus coxii* A.B. Jacks., New Fl. & Silva v. 33 (1932).

Synonym: *Juniperus recurva* var. *coxii* (A.B. Jacks.) Melville, Kew Bull. 13: 533 (1959).

Distribution: Bhutan; China (Xizang, Yunnan); India (Sikkim); Myanmar.

3.3.9. **Sabina deppeana** (Steud.) Y. Yang et K.S. Mao, **comb. nov.** (鳄柏)

Basionym: *Juniperus deppeana* Steud., Nomencl. Bot. [Steudel] ed. 2, 835 (1841).

Distribution: Mexico (Chihuahua, Coahuila, Durango, Hidalgo, Oaxaca, Puebla, Sonora, Veracruz, Zacatecas); United States (Arizona, New Mexico, Texas).

3.3.10. **Sabina durangensis** (Martínez) Y. Yang et K.S. Mao, **comb. nov.** (杜兰戈圆柏)

Basionym: *Juniperus durangensis* Martínez, Anales Inst. Biol. Univ. Nac. México 17: 94, Figs. 80–84 (1946).

Distribution: Mexico (Aguascalientes, Chihuahua, Durango, Jalisco, Sonora, Zacatecas).

3.3.11. **Sabina erectopatens** (W.C. Cheng et L.K. Fu) Y. Yang et K.S. Mao, **comb. nov.** (松潘圆柏)

Basionym: *Sabina vulgaris* var. *erectopatens* W.C. Cheng et L.K. Fu, Acta Phytotax. Sin. 13(4): 86 (1975).

Synonyms: *Juniperus sabina* var. *erectopatens* (W.C. Cheng et L.K. Fu) Y.F. Yu et L.K. Fu, Novon 7(4): 444 (1998); *Juniperus erectopatens* (W.C. Cheng et L.K. Fu) R.P. Adams, Biochem. Syst. Ecol. 27(7): 723 (1999).

Distribution: China (Sichuan).

3.3.12. **Sabina gracilior** (Pilg.) Y. Yang et K.S. Mao, **comb. nov.** (海地圆柏)

Basionym: *Juniperus gracilior* Pilg., Symb. Antill. (Urban). 7(4): 481 (1913).

Distribution: Dominican Republic; Haiti.

3.3.13. **Sabina grandis** (R.P. Adams) Y. Yang et K.S. Mao, **comb. nov.** (加州大圆柏)

Basionym: *Juniperus grandis* R.P. Adams, Phytologia 88(3): 306 (2006).

Synonyms: *Juniperus occidentalis* subsp. *australis* Vasek, Brittonia 18: 352 (1966); *Juniperus occidentalis* var. *australis* (Vasek) A.H. Holmgren et N.H. Holmgren, Intermount. Fl. [Cronquist et al.] 239 (1972).

Distribution: United States (California, Nevada).

3.3.14. **Sabina jaliscana** (Martínez) Y. Yang et K.S. Mao, **comb. nov.** (哈利斯科圆柏)

Basionym: *Juniperus jaliscana* Martínez, Anales Inst. Biol. Univ. Nac. México 17: 69, Figs. 55–58 (1946).

Distribution: Mexico (Durango, Jalisco).

3.3.15. **Sabina jarkendensis** (Kom.) Y. Yang et K.S. Mao, **comb. nov.** (昆仑圆柏)

Basionym: *Juniperus jarkendensis* Kom., Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 4: 181 (1923).

Synonyms: *Sabina vulgaris* var. *jarkendensis* (Kom.) C.Y. Yang, Fl. Reipubl. Popularis Sin. 7: 360 (1978); *Juniperus sabina* var. *jarkendensis* (Kom.) Silba, Phytologia 68(1): 33 (1990); *Juniperus semiglobosa* var. *jarkendensis* (Kom.) R.P. Adams, Phytologia 94(3): 354 (2012).

Distribution: China (Xinjiang, Xizang).

3.3.16. **Sabina maritima** (R.P. Adams) Y. Yang et K.S. Mao, **comb. nov.** (温哥华圆柏)

Basionym: *Juniperus maritima* R.P. Adams, Phytologia 89(3): 278 (2007).

Distribution: Canada (Alberta, British Columbia); Mexico (Chihuahua, Coahuila); United States (Arizona, Nebraska, Nevada, New Mexico, North Dakota, South Dakota, Utah).

3.3.17. **Sabina martinezii** (Pérez de la Rosa) Y. Yang et K.S. Mao, **comb. nov.** (马丁内斯圆柏)

Basionym: *Juniperus martinezii* Pérez de la Rosa, Phytologia 57: 81 (1985).

Synonyms: *Juniperus flaccida* var. *martinezii* (Pérez de la Rosa) Silba, Phytologia 58: 367 (1985); *Juniperus flaccida* subsp. *martinezii* (Pérez de la Rosa) Silba, J. Int. Conifer Preserv. Soc. 13(1): 9 (2006).

Distribution: Mexico (Jalisco: Cuatralba Mountains).

3.3.18. **Sabina monticola** (Martínez) Y. Yang et K.S. Mao, **comb. nov.** (中美山圆柏)

Basionym: *Juniperus monticola* Martínez, Anales Inst. Biol. Univ. Nac. México 17: 79 (1946).

Distribution: Guatemala; Mexico (Guerrero, Hidalgo, Jalisco, Mexico City, Mexico, Michoacán, Nuevo Leon, Puebla, Veracruz, Peña Sierra Nevada, Tamaulipas, San Luis Potosí).

3.3.19. **Sabina morrisonicola** (Hayata) Y. Yang et K.S. Mao, **comb. nov.** (玉山圆柏)

Basionym: *Juniperus morrisonicola* Hayata, J. Linn. Soc., Bot. 38: 298 (1908).

Synonym: *Juniperus squamata* var. *morrisonicola* (Hayata) H.L. Li et H. Keng, Taiwania 5: 81 (1954).

Distribution: China (Taiwan).

3.3.20. **Sabina mucronata** (R.P. Adams) Y. Yang et K.S. Mao, **comb. nov.** (短尖圆柏)

Basionym: *Juniperus mucronata* R.P. Adams, Biochem. Syst. Ecol. 28(2): 158 (2000).

Synonym: *Juniperus blancoi* var. *mucronata* (R.P. Adams) Farjon, World Checkl. & Bibliogr. Conifers ed. 2, 60 (2001).

Distribution: Mexico (Sonora, Chihuahua).

3.3.21. **Sabina pinchotii** (Sudw.) Y. Yang et K.S. Mao, **comb. nov.** (平肖圆柏)

Basionym: *Juniperus pinchotii* Sudw., Forest. Irrig. 11: 204, Figs. 1–4 (1905).

Synonym: *Juniperus monosperma* var. *pinchotii* (Sudw.) Melle, Phytologia 4: 29 (1952).

Distribution: United States (Oklahoma, Arizona, New Mexico, Texas); Mexico (Chihuahua, Coahuila, Durango, Nuevo Leon, Sonora, Tamaulipa, Zacatecas, Zacatecas).

3.3.22. **Sabina poblana** (Martínez) Y. Yang et K.S. Mao, **comb. nov.** (普埃布罗圆柏)

Basionym: *Juniperus flaccida* var. *poblana* Martínez, Anales Inst. Biol. Univ. Nac. México 17: 31 (1946).

Synonym: *Juniperus poblana* (Martínez) R.P. Adams, Phytologia 88(3): 239 (2006); *Juniperus flaccida* subsp. *poblana* (Martínez) Silba, J. Int. Conifer Preserv. Soc. 13(1): 10 (2006).

Distribution: Mexico (Coahuila, Guerrero, Jalisco, Michoacán, Nuevo Leon, Oaxaca, Puebla, Zacatecas).

3.3.23. **Sabina saltillensis** (M.T. Hall) Y. Yang et K.S. Mao, **comb. nov.** (萨尔迪罗圆柏)

Basionym: *Juniperus saltillensis* M. T. Hall, Fieldiana, Bot. 34: 45, Figs. 1–7 (1971).

Synonym: *Juniperus ashei* var. *saltillensis* (H. M. Hall) Silba, Phytologia Mem. VII: 32 (1984).

Distribution: Mexico (Chihuahua, Coahuila, Nuevo Leon, Zacatecas).

3.3.24. **Sabina saxicola** (Britton et P. Wilson) Y. Yang et K.S. Mao, **comb. nov.** (岩生圆柏)

Basionym: *Juniperus saxicola* Britton et P. Wilson, Bull. Torrey Bot. Club 50: 35 (1923).

Synonyms: *Juniperus barbadensis* subsp. *saxicola* (Britton et P. Wilson) Borhidi, Acta Bot. Hung. 37: 90 (1992); *Juniperus barbadensis* var. *saxicola* (Britton et P. Wilson) Silba, J. Int. Conifer Preserv. Soc. 7(1): 25 (2000).

Distribution: Cuba.

3.3.25. **Sabina standleyi** (Steyerm.) Y. Yang et K.S. Mao, **comb. nov.** (斯坦利圆柏)

Basionym: *Juniperus standleyi* Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 3 (1943).

Distribution: Guatemala; Mexico (Chiapas).

3.3.26. **Sabina tsukusiensis** (Masam.) Y. Yang et K.S. Mao, **comb. nov.** (清水圆柏)

Basionym: *Juniperus tsukusiensis* Masam., Bot. Mag. (Tokyo) 44: 50 (1930).

Synonyms: *Juniperus chinensis* var. *tsukushiensis* (Masam.) Masam., J. Soc. Trop. Agric. 2: 152 (1930); *Juniperus chinensis* subsp. *tsukusiensis* (Masam.) Silba, J. Int. Conifer Preserv. Soc. 13(1): 6 (2006).

Distribution: Japan (Kyushu); China (Taiwan).

3.3.27. **Sabina zanonii** (R.P. Adams) Y. Yang et K.S. Mao, **comb. nov.** (扎罗尼圆柏)

Basionym: *Juniperus zanonii* R.P. Adams, Phytologia 92(1): 112, Figs. 1–5 (2010).

Distribution: Mexico (Nuevo Leon).

Author contributions

YY conceived the idea and prepared the manuscript; BL prepared the cladograms; DKF and KR polished the English; YY, DKF, BL, KSM, LMG, SZZ, TW, KR, and ZXZ discussed, revised, and finalized the manuscript.

Declaration of competing interest

We declare that we have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pld.2022.05.003>.

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