Recent advances on phylogenomics of gymnosperms and a new classification

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A B S T R A C T
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 (Cycadaidae, Ginkgoidae, 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 Acropleyeeae Y. Yang, Austrocedreae Y. Yang, Chamaecyparidae Y. Yang, Microcachrydeae Y. Yang, Papuaecreae Y. Yang, and Prumuniptieae Y. Yang, and made 27 new combinations in the genus Sabina.

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., circinate young leaves in Cycos 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 heinzeltii 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
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 Schaeffer, 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 Cycadaeae (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, 2015; 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 subgroups, 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, pynoxylwood, 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, manoxylwood, 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 (Ginkgoidea) 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, dictot-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 mono-phyletic 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 Cupressophytae, 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 Plgl., 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 pedicle 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. Nguyén (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 (2008) proposed to conserve Xanthocyparis against Callitropsis, and the nomenclature committee accepted their proposal (Brunnutt, 2007). Little (2006) constructed a phylogeny of Xanthocyparis, Callitropsis, and Cupressus s.s., and found that Cupressus is diphylectic; 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. Arceuthous, 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 Neocalitropsis

Recent phylogenetic studies have suggested that Actinostrobus Miq. and Neocalitropsis 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 Neocalitropsis into Callitris. Here we have treated Actinostrobus and Neocalitropsis as synonyms of Callitris.

3. An updated classification

This new classification of extant gymnosperms (Acrogymnospermae/Pinophyta) 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., Cycadidae, Cephalotaxaceae, and Taxaceae. The linear sequence of the five subclasses is basically according to their phylogenetic relationships and morphological specialization, i.e., Cycadidae, Ginkgoidae, 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 Xanthoxyphaceae, and accept Actinostrobus and Neocalitropsis as synonyms of Callitris, and Fokienia as synonymous with Chamaecyparis (Rushforth, 2007; Page, 2019; Wang et al., 2022). Fifth, we describe six new tribes (Acropyleae, Aucstrocedraceae, Chamaecyparidaceae, Microcachryaeae, Pappacreadeae, and Prunopytidae).

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.

**Table 1**

| 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    |
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.* (械孢杉族)

*Acmopyle* Pilg. (械孢杉属)

Trib. 7. *Dacrydaceae* Gordon (陆均松族)

*Dacrycarpus* (Endl.) de Laub. (鸡鸣松属)

*Dacrydium* Sol. ex G. Forst. (陆均松属)

*Falcifolium* de Laub. (镰叶杉属)

Trib. 8. *Podocarpaceae* Dumort. (罗汉松族)

*Afrocarpus* (B. 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)

*Rhombus* 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* Siliba (杉木亚科)

*Cunninghamia* R. Br., *nom. cons.* (杉木属)

Subfam. 2. *Taiwaniioideae* L.Chu Li (台湾杉亚科)

*Taiwania* Hayata (台湾杉属)

Subfam. 3. *Athrotaxioideae* 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 ex W.C. Cheng, *nom. cons.* (水杉属)

*Sequoia* Endl., *nom. cons.* (红杉属)

*Sequoiadendron* J. Buchholz (红杉属)

Trib. 3. *Libocedraceae* Endl. (甜柏族)

*Libocedrus* Endl. (甜柏属)

*Pinus* L. (松属)

Subcl. 5. *Gnetidae* Pax (买麻藤亚纲)

Ord. 6. *Ephedrales* Dumort. (麻黄目)

Subfam. 7. *Gnetaceae* Skottsb. ex Reveal (买麻藤科)

Trib. 1. *Gnetum* Mill. (买麻藤属)

3.2. Description of new taxa

3.2.1. *Acmopyleae* Y. Yang, *trib. nov.* (械孢杉族 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 epimatum.

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. *Austrocedraceae* Y. Yang, *trib. nov.* (智利杉柏族 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.
including S Argentina (Chubut, Neuquen, Rio Negro) and S Chile (Valparaiso, OHiggins, 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

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

**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.

**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
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 cylinrical, consisting of 8–30 peltate microsporophylls. Female cone 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. (槟果杉族 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, Halmahera, 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. (安古斯图拉柏)

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

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

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

### 3.3.2. Sabina arizonica (R.P. Adams) Y. Yang et K.S. Mao, comb. nov. (亚利桑那柏柏)

**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. (阿什柏柏)

**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. (布朗科柏柏)

**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. (科阿瓦拉柏柏)

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

**Synonym:** Juniperus coahuilensis (Martínez) Gaussen 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. (恰帕斯柏柏)

**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. (墨西哥柏柏)

**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. (小果里枝柏柏)

**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* (Stud.) Y. Yang et K.S. Mao, *comb. nov.*

*Basionym*: Juniperus deppeana Stud., Nomencl. Bot. [Stuedel] 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.*

*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.*

*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.*

*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.*

*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, Intermont. Fl. [Croonquist et al.] 239 (1972).

**Distribution**: United States (California, Nevada).

3.3.14. *Sabina jaliscana* (Martínez) Y. Yang et K.S. Mao, *comb. nov.*

*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.*

*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.*

*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.*

*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.*

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

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

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

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

**Synonyms**: 
- 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.*

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

**Synonyms**: 
- 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.*

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

**Synonyms**: 
- 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, Tamaulipas, Zacatecas).

3.3.22. *Sabina poblana* (Martínez) Y. Yang et K.S. Mao, *comb. nov.*

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

**Synonyms**: 
- 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.*

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

**Synonyms**: 
- Juniperus ashei var. saltillensis (H. M. Hall) Silba, Phytologia Mem. VII: 32 (1984).
3.3.24. Sabina saxicola (Britton et P. Wilson) Y. Yang et K.S. Mao, comb. nov. (岩生松)

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

Synonyms: Juniperus barbadiensis subsp. saxicola (Britton et P. Wilson) Borhidi, Acta Bot. Hung. 37: 90 (1992); Juniperus barbadiensis 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. (斯坦利松)

Basionym: Juniperus standleyi Steyerm., Pblld. 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. (清津松)

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. tsukushiensis (Masam.) Silba, J. Int. Conifer Preserv. Soc. 13(1): 6 (2006).

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

3.3.27. Sabina zanoni (R.P. Adams) Y. Yang et K.S. Mao, comb. nov. (扎罗尼松)

Basionym: Juniperus zanoni 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; DFK and KR polished the English; YY, D.K. Ferguson, B. Liu et al. conceived the idea and prepared the manuscript; BL pre-prepared the cladograms; DFK and KR polished the English; YY, D.K. Ferguson, B. Liu et al. pre-conceived the idea and prepared the manuscript.

Declaration of competing interest
We declare that we have no conflict of interest.

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Appendix A. Supplementary data
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